THE GENUS ISOETES IN INDIA

by DIVYA DARSHAN PANT and GOPAL KRISHNA SRIVASTAVA,
Department of Botany, Allahabad University, Allahabad

(Communicated by P. Maheshwari, F.N.I.)

(Received January 27, 1962)

ABSTRACT

Two new species of Isoetes (I. panchanani and I. indica) are described from Ram Nai, Rewa, Madhya Pradesh, and a comparative account of the diagnostic characters of these and other Indian species of the genus and their geographical distribution is given. Importance of spore characters, occurrence of polymorphic megaspores and the nature of trabeculae are also briefly discussed.

INTRODUCTION

Despite the fact that the earliest recorded Indian species of the genus Isoetes, I. coromandelina L., was recorded by Linnaeus in 1781, no other species was described from this so-called subcontinent till 1938 when Mahabalé erected a second species I. sahyadrii1 for some much smaller plants from the Sahyadri hills. Two more species were subsequently added to the list, viz. I. sampathkumarani Rao (1944) from South India and I. dixitei Shende (1945) from Maharashtra, and up to date these are the only four species described from the various regions of our vast country with their diverse climatic and other environmental conditions. On the contrary, about twenty species have been recorded from the United States alone and six species are described from a small country like France (as enumerated by Reed 1953). It is therefore not at all surprising that in our preliminary attempts at Isoetes collecting in various regions, we have come across two new species of the genus, viz. I. panchanani n. sp. and I. indica n. sp., which are being recorded here for the first time.

Ekambaram and Venkatanathan (1933) studied the sporogenesis in I. coromandelina while Bhambie (1957) has described its shoot apex. Sharma (1958, 1959, 1961) described the vegetative structure, some stages of the formation and germination of megaspores, and the shoot apex in I. sampathkumarani. Abraham and Ninan (1958) and Ninan (1958) have studied the chromosomes of I. coromandelina and I. sampathkumarani. However, no one

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1 The species is referred to as I. sahyadriensis by Sharma (1958) perhaps because the ending 'ensis' would be more appropriate since the species is named after the locality Sahyadri hills.
has, so far, made a systematic study of spores of Indian species of *Isoetes*, and accordingly the morphology of the megasporas of three out of four previously described Indian species of the genus and the two new ones are described here. We could have no access to the Types, but our observations are based on abundant duplicates collected and obtained from Type localities. In spite of our best efforts, we were unable to get specimens of the fourth species, *I. sahyadrii* Mahabalé. The Type of this species is reportedly deposited in the Department of Biology, Gujarat College, Ahmedabad (India), but we are informed by Mr. H. D. Noronha, the present Head of the Botany Department, that these are not traceable. We made repeated efforts to secure some material from the author of the species, Prof. T. S. Mahabalé, but he too was unable to give us even a few sporophylls for comparison. We have also not seen a reportedly new but hitherto unnamed species of *Isoetes* mentioned by Sharma, Patil and Moghé (1958) from Omkareshwar in Madhya Pradesh.

Drawings and photographs of all dry spores have been taken under incident light illumination, and all mounted specimens are sketched and photographed under transmitted light. Drawings and photographs of wet specimens have been usually made from glycerine jelly mounts, but where specimens are mounted in Canada balsam it is mentioned in the legend. Unless otherwise stated, text-figures are magnified 100 times and photographs 80 times.

**Description**

*Isoetes panchanani* n. sp.

(Pl. XIII, figs. 1-4; Pl. XVI, fig. 41; Text-figs. 1; 2, A-I)

*Diagnosis.*—Rhizomorpha vulgo alte biloba. Folia 4–38 numero, singula 7–24 cm longa, viridia, tenua; limbus fere cylindricus, sed paulum complanatus, ad latus adaxiale, basi dilatata et complanata, marginibus membranaceis, apice fastigato. Stomata adsunt in parte apicali, ad basim vero desunt. Loculi aeris 4, fibrillis peripheralibus nullis. Ligula triangularis, longior quam lata. Velum; Ut plurimum operiens ca. dimidium sporangii, raro totum sporangium. Megasporangia ovalia, 3–5 mm longa, 2–3 mm lata; megasporophylla exteriora supportant sporangia nigrescentia, interiora vero albida; facies megasporangiorum saepe maculis fusce brunneis ornata. Microsporangia non visa.

Megasporae dimorphicae, duplici megasporarum forma praesente in eodem sporangio, magnitudine atque interna externaque structura variabilium. Megasporae largiores: 330–407 μ diam. (mediocris. ex 100 sporis 376 μ); sporarum partietes 4-seriati, faciebus distantibus perisporii et exosporii vulgaris distincte reticulatis, faciebus vero proximis jugo multiplici irregulariter confluentae alto laminae similis ornatis, jugis triradiatis rectis, jugis commissuralibus vero
tenuiter sinuosis, mesosporio tenui, pulchre granuloso, firmiter ad exosporium fixo, endosporio rotundo, tenui, translucenti, laevi. Megasporae minores: 240–330 μ (278 μ mediocr. ex 100 sporis); parietes 3—seriati, faciebus distantibus perisporii et exosporii monstrantibus tuberculos plurimos, tubercularum basi saepc unita; faciebus vero sporarum proximis monstrantibus unum tantum tuberculum in singulis arolis pyramicis; mesosporii saccus faciliter separabilis, rotundo triangularis; mesosporium tenue, granulosum; endosporium nullum. Omnes maturae megasporae nigrae cum madidae, albae vero cum siccae.

Locus.—Ad vicum Ram Nai proper Rewa in Madhya Pradesh. in India. Plantae gregario crescunt ad margines lacucae huc profundae intermixtae cum I. indica et I. coromandelina.

Holotypus.—(Pant Pl. IA) Positus in Herbario Kewensi in Anglia; isotypi (Pant Pl. IB–H) positi in herbario Indico Nationali, ad Calcuttam; in herbario Forest Research Institute ad Dehra Dun; in herbario Missouri Botanical Garden, Missouri (U.S.A.), in herbario sectionis systematics et geographica plantae apud Academy Scientiae U.S.S.R. Leningradensis (U.S.S.R.); in herbario sectionis Botanices universitatis Allahabadensis ad Allahabad; in herbario Kewensi in Anglia et in herbario sectionis Botanices universitatis Delhi (Delhi).

Type characters.—Rhizomorph : typically deeply two-lobed. Leaves: 4 to 38, 7 to 24 cm long, green, slender, limb almost cylindrical but upper side slightly flattened; base expanded, flattened, showing membranous margins, apex tapering. Stomata: present in apical portion, lacking towards base. Air chambers four, peripheral strands none. Ligule: triangular longer than broad. Velum: usually covering about half of sporangium (rarely complete). Megasporangia: oval, 3 to 5 mm long, 2 to 3 mm broad. Outer megasporophylls with blackish sporangia, inner megasporangia whitish; surface of various megasporangia often showing dark brown spots. Microsporangia: not observed.

Megasporae dimorphic, two forms of megasporae occurring inside same sporangium and differing in relative size, external and internal structure. Larger megasporae: 330 to 407 μ in diameter (376 μ average of 100),1 spore wall four-layered, distal surfaces of ‘perispore’ and ‘exospore’ generally distinctly reticulate, their proximal surfaces with irregular confluent high blade-like ridges, triradiate ridges straight, commissural ridges slightly sinuous, ‘mesospore’ finely granular, firmly attached to ‘exospore’, ‘endospore’ round, thin,

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1 In order to find a suitable number for the determination of the average size of megasporae in various species, we measured the diameters of 500 megasporae in each case and then calculated their average diameters on the basis of the first 10, 25, 50, 75, 100, 200, 300, 400 and 500. Graphs of these (Text-fig. 3, A) show clearly that, as a rule, averages calculated from 100 or 200 spores do not significantly differ from those based on higher numbers.
translucent, smooth. Smaller megaspores: 240 to 330 \( \mu \) (278 \( \mu \) average of 100), spore wall three-layered, distal surface of ‘perispore’ and ‘exospore’ showing numerous tubercles, tubercle bases often joined; proximal surfaces of spores generally showing only one tubercle in each pyramidal area; ‘mesospore’ thin, granulose, ‘endospore’ none. All mature megaspores black when wet, white when dry.

**Occurrence.**—Village Ram Nai, Rewa, Madhya Pradesh (India). Plants growing gregariously along the margin of a shallow pond intermixed with *I. indica* and *I. coromandelina* and also at Panchgani intermixed with *I. dixitei*.

**Type.**—Holotype (*Pant Pt. IA*) deposited in Herbarium, Kew, Great Britain. Isotypes (*Pant Pt. IB–H*) deposited in the National Herbarium, Calcutta; Herbarium, Forest Research Institute, Dehra Dun; Herbarium, Missouri Botanical Garden, Missouri (U.S.A.); Herbarium of the Department of Systematics and Plant Geography of the Academy of Sciences of U.S.S.R., Leningrad (U.S.S.R.); Herbarium, Botany Department, Allahabad University; Herbarium, Kew, Great Britain; and Herbarium, Botany Department, Delhi University (Delhi).

**Description and comparison.**—The main collection of the species comes from Ram Nai, Rewa, but in our collection of material of *I. dixitei* Shende from Panchgani we found a single plant which resembles *I. panchanani*, amongst other things, in having reticulate megaspores. However, this odd plant differs from *I. panchanani*, firstly, in having a complete velum which covers the entire surface of its sporangia, leaving only a small slit-like aperture at the base and, secondly, in possessing slightly larger, bigger megaspores (350 to 458 \( \mu \) in diameter) and slightly smaller, small megaspores (152 to 305 \( \mu \)). Moreover, the brown spots of thick-walled cells generally seen in the sporangial wall of *I. panchanani* are not present in any sporangia of this plant. As we have come across only a single plant of this type and as it resembles *I. panchanani* in many respects, we have provisionally included it in that species.

According to the classification given by Pfoffer (1922), *I. panchanani* falls under the section Reticulatae. Strictly speaking no other Indian species could be referred to this section of the genus although megaspores of *I. sampathkumarani* are also described as showing ‘upper segments marked with reticulate branched ridges’ and would thus seemingly appear to resemble those of *I. panchanani*. However, we find that all megaspores of *I. sampathkumarani* merely show a jumble of crowded branched ridges on the distal side and are never clearly reticulate. These ridges of *I. sampathkumarani* are uneven in height and show rounded tubercles, the ridges are apparently formed by confluent tubercle bases as described for *I. flaccida* var. *alata* (Pfoffer 1922). In contrast, the distal surface of the larger megaspores of *I. panchanani* shows distinct polygonal meshes (lumina) bounded by more or less even ridges (muri). Smaller megaspores of *I. panchanani* show only one tubercle
in each pyramic area on the proximal side and numerous coalesced tubercles (like those of *I. sampathkumarani* on the distal side, while the smaller mega-
spores of *I. sampathkumarani* often show numerous tubercles on both sides. The plants of *I. panchanani* are distinctly larger than those of *I. sampath-
kumarani* (plants of *I. panchanani* are 7 to 24 cm long, those of *I. sampath-
kumarani* are 1.5 to 11 cm long). Moreover, preliminary chromosome counts in smears of root tips of *I. panchanani* show that their chromo-
some number is between 43 and 45. This is considerably lower than the number in *I. sampathkumarani*, where Abraham and Ninan (1958) and Ninan (1958) have reported 66 chromosomes. Clearly, *I. panchanani* is quite different from all other hitherto described Indian species.

Among species belonging to the section Reticulatae reported from various other parts of the world, we may compare it with *I. martii* A. Br. and *I. engelmanii* A. Br. which resemble it in size and absence or poor development of peripheral strands. It would, however, appear that, besides other details, *I. panchanani* differs from all of them in having dimorphic megaspores. In addition the megaspores of *I. panchanani* are smaller than those of any of these species (megaspore diameters of *I. foelolata*, *I. martii* and *I. engelmanii* are 360 to 560 μ (600 μ); 580 to 600 μ; and 400 to 570 μ (615 μ) respectively, while megaspores of *I. panchanani* measure 225 to 407 μ). We are unable to make a detailed comparison between *I. panchanani* and these species as we have no access to their material.

We have great pleasure in naming the species after Professor Panchanan Maheshwari of Delhi who has greatly inspired and helped us in our work.

*Isoetes indica* n. sp.  

(Pl. XIV, figs. 16–25; Pl. XV, figs. 30–35; Pl. XVI, figs. 39, 40; Text-figs. 4, A–D; 5, A–H; 6, A–H; 7, A–M)

*Diagnosis.*—Rhizomorpha vulgo 3-loba, nonnumquam 4-loba. Folia 
numero 9–35, singula 8–55 cm longa, viridia, tenuia; limbus fere cylindricus, 
sed ad latus adaxiale paulum complanatus; basi dilatata, complanata, mon-
strante margines membranaceos; apice fastigato. Stomata: adsunt in parte 
apicali, desunt vero ad basin. Aeris loculi 4, fibrillis peripheralibus 4–6, 
fibrillis accessoris plurimis. Ligula cordata, longior quam lata. Velum 
nullum. Megasporangia griseola, elongata, 6–19 mm longa, 4–9 mm lata. 
Megasporangia in sporophyllis externis continent cellulas innumerables parvas 
et steriles praeter megasporas, megasporangia interiora vero absque cellulis 
sterilibus. Microsporangia: adsunt tantum in quibusdam sporophillis interior-
ibus, albida, ovalia, 4–6 mm longa, 3–4 mm lata.

Singula sporangia continent megasporas magnitudinis variae; praeterea, 
sporangia exteriora monstrant cellulas parvas steriles. Megasporae vulgo
THE GENUS *ISORITES* IN INDIA

dividuntur in tres formas, hic vocatas megasporas largiores, megasporas mediocres et megasporas minores. Largiores megasporae: 458–636 μ diam. (523 μ, mediocr. ex 100 sporis), parietibus 4-seriatis, faciebus distantibus et proximis perisporii et exosporii tuberculatis, tuberculis fastigatis, ut plurimum apicibus aubacutis. Juga triradiata recta, saepe furcata; juga commissuralia sinuosa; mesosporium tenue, pulchre granulosum, firmiter exosporio fixum; endosporium rotundatum, tenue, translucens, laeve. Megasporae mediocres: 407–509 μ diam. (453 μ, mediocr. ex 100 sporis), parietibus 3-seriatis, faciebus distantibus et proximis perisporii et exosporii monstrantibus plurimos tuberculos ut plurimum subacutus; juga triradiata et commissuralia sinuosa, priora vero saepe furcata; mesosporii saccus faciliter separabilis, rotunde triangulares; mesosporium tenue, granulosum, endosporio nullo vel inseparabili. Megasporae minores: 89–380 μ diam. (210 μ mediocr. ex 100 sporis), parietibus 3-seriatis, faciebus distantibus perisporii et exosporii monstrantibus unum vel plures tuberculos, faciebus vero proximis monstrantibus tuberculos singulos in singulis areis pyramidis; mesosporium tenue, granulosum, endosporio nullo. Cellulae sterile: 13–18 μ diam. (16 μ, mediocr. ex 100 cellulis), rotundae vel rotunde quadrangulares, transparentes, granulosae, ornatae annulo vel margine incrassato. Megasporae omnes griseae colore cum madidae, albae cum sicca.

Cellulae sterile: 13–18 μ diam. (16 μ, mediocr. 34 μ, ex 100) albae, dimorphae, bilaterales vel tetrahedrales, sporae utriusque formae saepe praesentes in uno eodemque sporangio, triletae quidem rotundatae, monoletae vero ovales, parietibus bi-seriatis, superficie exterioris seriei cutinata, pulchre tuberculata, interioris vero seriei levis, saepe una pluresve sporae (Vulgo oppositae sporae) in massa tetrasporica abortivae.

*Locus.*—Ad vicum Ram Nai, prope Rewa, in Madhya Pradesh in India. Plantae crescent gregarie ad marginem lacunae haud profundae intermixtae cum *I. panchananii* et *I. coromandelina*.

*Holotypus.*—(*Pant Pt. 2A*) Positus in Herbario Kewensi in Anglia; isotypi (*Pant Pt. 2B–H*) positi in herbario Indico Nationali ad Calcuttam; in herbario Forest Research Institute ad Dehra Dun; in herbario Missouri Botanical Garden, Missouri (U.S.A.); in herbario sectionis sytematics et geographic plantaep apud Academy Scientiae U.S.S.R. Leningradensis (U.S.S.R.); in herbario sectionis Botanices universitatis Allahabadensis ad Allahabad; in herbario Kewensi in Anglia et in herbario sectionis Botanices universitatis Delhi (Delhi).

*Type characters.*—*Rhizomorph:* Usually three-lobed, sometimes four-lobed. *Leaves:* 9 to 35, 8 to 55 cm long, green, slender; limb almost cylindrical but upper side slightly flattened, base expanded, flattened, showing membranous margins; apex tapering. *Stomata:* present in apical portion, lacking towards base. Air chambers four, peripheral strands 4 to 6, accessory strands many. *Ligule:* cordate, longer than broad. *Velum:* absent. *Megasporangia:*
greyish, elongated 6 to 19 mm long, 4 to 9 mm broad. Megasporangia in outermost sporophylls containing innumerable small sterile cells besides megasporas, inner megasporangia without sterile cells. Microsporangia present only in a few inner sporophylls, whitish, oval 4 to 6 mm long, 3 to 4 mm broad.

Individual sporangia containing megasporas of various sizes; outer sporangia, in addition, showing small sterile cells. Megasporas usually distinguishable into three forms—termed larger megasporas, megasporas of medium size and smaller megasporas. Larger megasporas: 458 to 636 μ in diameter (523 μ average of 100), spore wall four-layered, distal and proximal surfaces of 'perispore' and 'exospore' tuberculate, tubercles tapering, mostly with pointed ends. Triradiate ridges straight, often bifurcated; commissural ridges sinusous; mesospore thin finely granulose, firmly attached to 'exospore'; 'endospore' round, thin, translucent, smooth. Megasporas of medium size: 407 to 509 μ in diameter (453 μ average of 100), spore wall three-layered, distal and proximal surfaces of 'perispore' and 'exospore' showing numerous mostly pointed tubercles; triradiate and commissural ridges sinusous, triradiate rays often bifurcated; mesospore sac easily separable, roundly triangular; mesospore thin, granulose, 'endospore' none or inseparable. Smaller megasporas: 89 to 380 μ in diameter (210 μ average of 100), spore wall three-layered, distal surfaces of 'perispore' and 'exospore' showing one or more tubercles, their proximal surfaces showing only one tubercle in each pyramidal area; 'mesospore', thin granulose; 'endospore' none. Sterile cells: 13 to 18 μ in diameter (16 μ average of 100), round or roundly quadrangular, transparent, granulose with a thickened rim or margin. All megasporas grey in colour when wet, white when dry. Microspores: 16 to 48 μ in diameter (34 μ average of 100), white, dimorphic, bilateral or tetrahedral, two types of microspores often occurring inside one and same sporangium. Trilete spores rounded, monolete spores oval, spore wall two-layered, surface of outer layer cutinized, finely tuberculate, inner layer smooth. Often one or more spores (commonly two opposite ones) in a tetrad abortive.

Occurrence.— Village Ram Nai, Rewa, Madhya Pradesh (India). Plants growing gregariously along the margin of a shallow pond intermixed with I. panchanani and I. coromandelina.

Type.— Holotype (Pant Pt. 2A) deposited in Herbarium, Kew, Great Britain. Isotypes (Pant Pt. 2B-H) deposited in the National Herbarium, Calcutta; Herbarium, Forest Research Institute, Dehra Dun; Herbarium, Missouri Botanical Garden, Missouri (U.S.A.); Herbarium of the Department of Systematics and Plant Geography of the Academy of Sciences of U.S.S.R., Leningrad (U.S.S.R.); Herbarium, Botany Department, Allahabad University; Herbarium, Kew, Great Britain, and Herbarium, Botany Department, Delhi University (Delhi).
Description and comparison.—While collecting plants of *I. indica* growing under water, we happened to come across four remarkable megasporophylls each having twin sporangia placed side by side (see Pl. XV, fig. 35; Text-fig. 4, D). Our attempts to trace out the parent plant proved unsuccessful, but as all of them came from a single spot we believe that all of the four sporophylls belong to the same individual. The nature of the sporophylls and the spores inside the megasporangia are otherwise in all respects identical to those of *I. indica*, and it would be, for the present, simplest to regard them as abnormal.

A unique feature of all sporangia in *I. indica* is the presence of occasional multicellular hair-like outgrowths in the trabeculae (see Pl. XV, fig. 30; Text-fig. 7, A). These protrude between the spores and can easily break off (broken parts of these may come off with spores when they are taken out of a sporangium—see Pl. XV, fig. 34; Text-fig. 7, C–F). Some of these growths show a glandular-looking, granular, multicellular head or a body made up of a chain of small bead-like cells (see Text-fig. 7, B). These filaments normally stain deeper red with safranin than the cells of the trabeculae and in this character resemble the spores—possibly they represent chains of abortive fertile cells (see p. 259).

Though *I. indica* is closely associated with *I. panchanandii* in the field and the two species are found growing side by side, they differ from each other in a number of features. The plants of *I. indica* are the first to come up after the onset of rains in July and being larger they soon become conspicuous. The plants of *I. panchanandii* come up later and attain their full size only by the end of October or in November when plants of *I. indica* have already started yellowing. The plants of *I. indica* are distinctly larger than those of *I. panchanandii* (plants of *I. indica* are up to 55 cm long, while those of *I. panchanandii* are only 7 to 24 cm long). The rhizomorphs of *I. indica* are three- to four-lobed while those of *I. panchanandii* are normally two-lobed. A velum is absent in *I. indica*, but that of *I. panchanandii* is more or less well developed covering about half of the surface of the sporangium. Above all, the megaspores of *I. indica* are tubercululate while those of *I. panchanandii* are reticulate.

*I. indica* may also be compared with the remaining Indian species of the genus, e.g. *I. sahyadrii*, *I. dixitei* and *I. coromandelina*, which too belong to section Tuberculatae of Pfeiffer. The distal surface of the megaspores of *I. sahyadrii* and *I. dixitei* shows large and small tubercles intermixed with each other; the tubercles of *I. indica* are more or less uniform in size. The pants of *I. sahyadrii* and *I. dixitei* are smaller than those of *I. indica*. *I. indica* resembles *I. dixitei* in showing sterile cells in outermost sporangia. However, HF treated megaspores of *I. dixitei* show characteristic frill-like equatorial expansions at the angles; these are typically absent in the megaspores of *I. indica* (although some of its megaspores may show distinct but very narrow
angular expansions, yet in *I. dixitei* their breadth is 95 to 200 μ, while in *I. indica* it is only 70 to 95 μ).

*I. indica* comes closest to *I. coromandelina*. The plants of the two species resemble each other in their average size, similarly lobed rhizomorphs, size and form of leaves, absence of velum, and tuberculate megaspores. However, the megaspores of the two species are clearly distinct. The tubercles in the megaspores of *I. indica* are larger and gradually tapering towards their relatively more pointed ends, while those in the megaspores of *I. coromandelina* are mostly short and rounded. We have examined the megaspores of specimens referable to *I. coromandelina* from various localities, viz. Madras, Kakinada (only young sporangia seen), Varanasi, Gyanpur, Meerut, Lucknow, Baroda, Rewa and Lohgara. We are definite that the short blunt-ended tubercles are a common feature in all of them (including even the exceptionally large form from Baroda). The Type of *I. coromandelina* is not available to us, but Mr. F. Ballard of Royal Botanic Gardens, Kew, has confirmed that the tuberculate surface of the megaspores of *I. indica* is different from that seen in *I. coromandelina*. Moreover, the commissional ridges in megaspores of *I. indica* are sinuous, while they are straight in *I. coromandelina*. Again, the triradiate and commissional ridges of megaspores of intermediate size in *I. indica* are sinuous, while they are straight in *I. coromandelina*. The triradiate rays of megaspores in *I. indica* are mostly bifurcated, but in *I. coromandelina* they are always simple. The occurrence of sterile cells in the outermost sporangia of *I. indica* (these are not found in *I. coromandelina*) strengthens the separation of *I. indica* from *I. coromandelina*. Moreover, the microspores of *I. indica* are 16–48 μ in diam., distinctly tuberculate and clearly different from those of *I. coromandelina* which are reported to be 26–33 μ in diam. and smooth (see Pfeiffer 1922), although according to Knox (1950) they may be rugose to papillate.

Amongst species described from other countries, *I. indica* comes closest to *I. setacea* Bosc described from France and *I. malinverniana* Cesat and De Not from Italy. Among other characters, these species resemble *I. indica* in the absence of a velum and the presence of peripheral strands. However, from the available descriptions of *I. setacea* and *I. malinverniana*, *I. indica* appears clearly different in showing more than one type of megaspores (no such variations are described for the megaspores of the French and Italian species). Nevertheless, the tubercles of *I. malinverniana*, whose megaspore surface is described as covered with coarse, rounded processes, would appear to be very

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1 Plants of *I. coromandelina* found in Baroda are exceptional in being much larger than those of the same species found in other localities. The size of these according to the figures given by Gaekwad and Deshmukh (1954) would be about 60 cm, but a specimen given to us by Prof. Gonzalves is 80 cm long (only about 20 cm shorter than the plants of the largest species, *I. japonica*).
close to those of *I. indica* (the tubercles of *I. indica* are mostly with pointed ends).

**Isoetes coromandelina** L.

(Pl. XIV, figs. 26–29; Pl. XVI, fig. 38; Text-fig. 8, A–J)

Although a photograph of the spores of *I. coromandelina* given by Pfeiffer (1922, Pl. 12, fig. 2) clearly shows two forms of megaspores yet no one, amongst the numerous authors who have described this species, has ever mentioned the dimorphism of its spores. Even Ekambaram and Venkatanathan (1933) who have made a detailed study of its sporogenesis failed to notice this character. Analysis of plentiful material which we obtained from widely distant localities, like Madras, Kakinada, Bengal, Baroda, Varanasi, Lucknow, Meerut, Rewa and Lohgara (Allahabad) and have assigned to this species, shows that its megaspores are always distinctly dimorphic. The two types of spores, some large and others smaller, differ also in other details and occur inside one and the same sporangium.

**Table I**

*I. coromandelina* variations in size of adult plants and megaspores in material from different localities

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<td>Lucknow</td>
<td>..</td>
<td>407–483</td>
</tr>
<tr>
<td>Meerut (only two plants examined)</td>
<td>Up to 41</td>
<td>458–572</td>
</tr>
<tr>
<td>Ram Nai (Rewa)</td>
<td>..</td>
<td>356–547</td>
</tr>
<tr>
<td>Varanasi</td>
<td>..</td>
<td>483–667</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Name of species and localities</th>
<th>Number of sporangia</th>
<th>Number of megasporas in a single sporangium</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Large</td>
<td>Medium</td>
</tr>
</tbody>
</table>

**1. coromandelina**

Madras  | 1 | 338 | 300 | 9 | 647 |
Baroda  | 1 | 315 | 334 | 6 | 655 |
Chirhula (Rewa)  | 1 | 203 | 220 | 5 | 428 |
Gyanpur  | 1 | 336 | 427 | 6 | 829 |
Lohgara  | 1 | 494 | 513 | 194 | 1,201 |
Lucknow  | 1 | 341 | 359 | 12 | 712 |
Meerut  | 1 | 402 | 460 | 59 | 921 |
Ram Nai (Rewa)  | 1 | 738 | 757 | 94 | 1,589 |
Varanasi  | 1 | 563 | 513 | 43 | 1,119 |

**1. indica**

Ram Nai (Rewa)  | 1 | 881 | 983 | 201 | 62 | 2,127 |
|                | 2 | 939 | 961 | 417 | 28 | 2,345 |
|                | 3 | 590 | 683 | 166 | 10 | 1,449 |
|                | 4 | 939 | 876 | 167 | 25 | 2,107 |
|                | 5 | 265 | 334 | 76 | 8 | 703 |

**1. dizitei**

Panchgani  | 1 | 52 | 52 | 2 | 106 |
|           | 2 | 93 | 93 | . | 186 |
|           | 3 | 92 | 99 | 1 | 192 |
|           | 4 | 132 | 135 | . | 267 |
|           | 5 | 137 | 147 | 1 | 285 |

**1. sampalkavarami**

Bangalore  | 1 | 39 | 42 | 4 | 85 |
|           | 2 | 45 | 45 | 1 | 91 |
|           | 3 | 45 | 45 | 1 | 91 |
|           | 4 | 47 | 48 | 1 | 96 |
|           | 5 | 47 | 49 | 1 | 97 |

**1. panchrami**

Ram Nai (Rewa)  | 1 | 44 | 40 | 1 | 85 |
|                | 2 | 53 | 56 | 3 | 112 |
|                | 3 | 62 | 60 | . | 122 |
|                | 4 | 70 | 67 | 2 | 139 |
|                | 5 | 88 | 88 | . | 176 |

Larger megasporas of Madras plants are 465 to 660 μ in diameter (average diameter of 100 megasporas is 525 μ). Megasporas of plants from other localities are more or less of the same size except that the megasporas of
plants from Lohgara, Ram Nai (Rewa) and Lucknow are somewhat smaller (see Table I). The spore wall is four-layered. The 'perispore' and the 'exospore' are both tuberculate; the tubercles have rounded ends. The only variation noticed in surface characters of megaspores is the frequent occurrence of some tubercles with confluent bases and a greater frequency of joined spores (see Table II) in plants collected from Lohgara. We do not regard these as specific characters because confluent tubercles are also present in megaspores of plants collected from Lucknow and Ram Nai, but in these they are relatively less common. The 'mesospore' is thin, granular, and firmly attached to the 'exospore'. The 'endospore' is rounded, thin, translucent and smooth. The triradiate and commissural ridges are straight.

**Smaller megaspores** are 356 to 458 μ in diameter (average diameter of 100 spores is 432 μ). The spore wall is three-layered. The 'perispore' and the 'exospore' are both tuberculate, there being numerous tubercles on the distal side, but on the proximal side each pyramic area generally shows a single tubercle. The 'mesospore sac' is ca. 2 μ thick and granular. The 'endospore' is absent or inseparable. The triradiate and commissural ridges are straight.

The only variations seen in the size of plants and megaspores in material from different localities which we have attributed to *I. coromandelina* are given in Table I.

**Table III**

*Frequency of stomata and stomatal indices of various species of Isoetes*

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Average stomatal index</th>
<th>Average stomatal frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>I. coromandelina</em></td>
<td>10.1</td>
<td>65</td>
</tr>
<tr>
<td><em>I. dixitei</em></td>
<td>8.05</td>
<td>69</td>
</tr>
<tr>
<td><em>I. indica</em></td>
<td>9.8</td>
<td>73.9</td>
</tr>
<tr>
<td><em>I. sampathkumarani</em></td>
<td>5.9</td>
<td>28.7</td>
</tr>
<tr>
<td><em>I. panchananii</em></td>
<td>4.5</td>
<td>26.7</td>
</tr>
</tbody>
</table>

**Isoetes sampathkumarani** Rao

(Pl. XIII, figs. 5–8; Text-fig. 9, A–F)

The occurrence of megaspores of two sizes in this species has already been noticed by Sharma (1959), but she has neither given their size ranges nor has she described their structural differences. These details are accordingly mentioned below:

**Larger megaspores** are 356 to 458 μ in diameter (average diameter of 100 spores is 395 μ). The spore wall is four-layered. The 'perispore' and the
'exospore' are both tuberculate; the tubercle bases are sometimes confluent more clearly on the distal side. The 'mesospore' is finely granular and firmly attached to the 'exospore'. The 'endospore' is round, thin, translucent and smooth, the triradiate ridges are straight and commissural ridges are slightly sinuous.

Smaller megaspores are 280 to 381 μ in diameter (average diameter of 100 spores is 345 μ). The spore wall is three-layered. The 'perispore' and the 'exospore' are tuberculate. The tubercle bases are often joined. The 'mesospore sac' is 2 μ thick and granular. The 'endospore' is absent. The triradiate ridges are straight and the commissural ridges are slightly sinuous.

*Isoetes dixitei* Shende

(Pl. XIII, figs. 9-15; Pl. XVI, figs. 36, 37; Text-fig. 10, A-J)

The megaspores of this species are fully described by Shende (1945) but in a single plant from Panchgani, which is otherwise referable to *I. dixitei*, the tubercles on the distal side of the megaspores are distinctly larger and far apart (see Pl. XIII, figs. 13, 14).

Among various Indian species, dimorphic megaspores were first noticed in *I. dixitei* by Shende (1945), but as he has not made any statistical analysis of their size and structural details these are given below:

Larger megaspores are 483 to 660 μ in diameter (average diameter of 100 spores is 554 μ). The spore wall is four-layered, the 'perispore' and 'exospore' show uneven tubercles on both sides. The angles of the 'exospore' show frill-like expansions 167–200 μ wide. The 'mesospore' is thin, reticulately pitted and adherent to the 'exospore'. The 'endospore' is round, thin, translucent and smooth. The triradiate and commissural ridges are straight.

Smaller megaspores are 320 to 458 μ in diameter (average diameter of 100 spores is 410 μ). The spore wall is three-layered. The 'perispore' and the 'exospore' are tuberculate, the tubercles are of uneven size. The angles of the 'exospore' show frill-like equatorial expansions 95–172 μ wide. The 'mesospore sac' is 2 μ thick and granular. An 'endospore' is absent. The triradiate rays are sinuous and the commissural ridges are straight.

On account of the dimorphism of its spores, Shende has compared his amphibious species *I. dixitei* with terrestrial forms like *I. welwitschii* A. Br. and *I. aequinoctialis* Welw. described from Africa, but he has not at all compared this species with any other Indian species, not even with *I. sahyadrii* which is reported to occur, besides Mysore State, in the Panchgani area (Maharashtra) itself, wherefrom *I. dixitei* is also reported. We, too, are unable to make any first-hand comparison between these two species as the material of *I. sahyadrii* is inaccessible to us, but a critical study of their descriptions clearly points out that except for a few points both the species resemble each
other rather closely. Plants of both species possess a three-lobed rhizomorph; about the same number and size of leaves; a cordate ligule and uneven tubercles on their megaspores. Nevertheless, *I. dixitei* differs from *I. sahyadrii* in the presence of peripheral strands (peripheral strands are reported to be absent in *I. sahyadrii*) and in having a rudimentary velum (the velum in *I. sahyadrii* is reported to be more or less complete). In addition, dimorphic megaspores and sterile cells like those of *I. dixitei* have not been reported in *I. sahyadrii*, but as in the case of dimorphic megaspores of *I. coromandelina*, it is possible that this character has remained unnoticed in *I. sahyadrii*. We may also mention that as the sterile cells are present only in the outer sporophylls, it is quite likely that this character, too, has remained unobserved. As far as the presence or absence of peripheral strands is concerned, this may or may not be important as there are some species, e.g. *I. ovata* Pfeiffer and *I. howellii* Engelm., where the peripheral strands are sometimes present but at other times absent (see Pfeiffer 1922). We have also observed that the reportedly rudimentary velum of *I. dixitei* may sometimes cover about half of the sporangium. The real differences between these two rather similar species therefore need to be checked.

**Discussion**

*Total number of spores per sporangium*

The total number of microspores was not determined as microsporangia of all species were not available, but counts were made of the total number of megaspores produced by individual sporangia of each of the five available species (see Table II). According to Foster and Gifford (1959) the number of megaspores produced by each megasporangium of *Isoetes* ranges between 100 to 300. Our observations show that the number is far greater in *I. indica* (703 to 2,345) and *I. coromandelina* (428 to 1,589).

*Polymorphism of spores and abnormal united spores*

The dimorphism of microspores (occurrence of monocete and trilette spores) in *Isoetes* is already well known (see Pfeiffer 1922), but the present study reveals that five out of the six named Indian species of *Isoetes* have dimorphic or polymorphic megaspores. In forms with dimorphic spores about half the total number of spores in a sporangium are large and the other half relatively small (the counts of the two types of spores in the various Indian species are given in Table I). The various forms of megaspores obtained from a single sporangium not only differ in size but also in surface sculpturing, nature of triradiate rays and other details. The surface of a large megaspore in *I. coromandelina* and *I. dixitei* shows a number of tubercles both on the proximal and the distal sides, but in the smaller megaspores a few
or a single tubercle is seen in each pyramidal area on the proximal side (the distal side shows numerous tubercles). The triradiate rays of larger megaspores of *I. dixitei*, *I. panchananii* and *I. indica* are straight, while those of smaller megaspores are sinuous; the two types of rays are vividly seen when a smaller and a larger megaspore are found united (see Pl. XVI, fig. 37; Text-fig. 11, G). The larger megaspores are more or less spherical, while the smaller ones are somewhat triangular and flattened. The dissection of a larger megaspore yields four distinct layers, viz. ‘perispore’, ‘exospore’, ‘mesospore’ and ‘endospore’, but only the first three layers are seen in a smaller megaspore, the fourth layer ‘endospore’ being either absent or inseparable.

Besides the usual occurrence of various forms of trilete megaspores, the spores of *I. indica* are unique in having rays one or more of which are often bifurcated in a variety of ways. The total number of spores without any bifurcated ray is greater than that of spores with bifurcated rays. Among spores with forked rays, a majority show only one ray bifurcated but in others two or all the three rays may be forked. Sometimes these divided rays form a sort of polygonal pattern.

The occurrence of polymorphic spores in the same species and their being found in the same sporangium raises serious problems for the characterization of genera or species of fossil megaspores. The size of spores, the nature of their triradiate rays, and the number of their spore coats if taken in individual spores, all appear to be more or less unreliable for the species of *Isoetes*. Even the sculpturing of the ‘perispore’ and ‘exospore’ is variable but as a rule more trustworthy. Our observations thus emphasize a suggestion put forth by Pant and Nautiyal (1960) that genera and species of fossil sporomorphs based on spores from intact sporangia would in any case be more reliable than those based on isolated spores. Moreover, a critical analysis of these characteristics is essential before one can use them for specific diagnoses as we have already suggested (Pant and Srivastava 1961).

As far as we know in earlier accounts, dimorphic spores are reported to occur only in three species of *Isoetes*, i.e. *I. welwitschii* A. Br., *I. aequinocitialis* Welw. and *I. dixitei*, but photographs of megaspores of *I. schweinfurthii* A. Br. and *I. coromandelina* given by Pfeiffer (1922, Pl. 12, figs. 1, 2) also possibly show apparently two distinct types of megaspores, although there is no mention of dimorphic megaspores anywhere in the description of these species. Numerous sectional views of sporangia figured by various authors, e.g. those of *I. lacustris* by McLean and Ivimey-Cook (1951, fig. 611) and *I. howelli* by Foster and Gifford (1959, figs. 8–21, D) also show smaller outlines of some contained megaspores, but this could even be due to a tangential plane of sectioning.

Besides the genus *Isoetes*, wide intraspecific variations in spore size are well known in some Pteridophyta like *Selaginella* (Duerden 1929),
Calamostachys binneyana (Williamson and Scott 1894), Cyathea dealbata, Notolaena sinuata, N. affinis, Ceratopteris and Platyzoma (Bower 1935), but distinct dimorphism of megaspores of the type found in Isoetes is not reported anywhere else. However, a case of two sizes of spores occurring in two regions of the same sporangium is presented by Calamostachys americana (Arnold 1958) where the two types of spores are regarded by Arnold as microand megaspores. Such mixed occurrence of heterospores is unknown in any other living or fossil plant, although Chaloner (1958) cautiously discusses and rejects such a possibility for the two smaller and two larger spores in tetrads of Didymosporites scotti or the single tetrads found inside the megasporangia of Stauropteris burntislandica (Bensonites fusiformis).

The normal occurrence of dimorphic pollen grains is also reported in some angiosperms, e.g. in certain members of the Plumbaginaceae and Primulaceae. In Primula farinosa and P. veris the two types of pollen grains not only differ in their size but also in their shape and the number of apertures (see Erdtman 1952). According to Erdtman (1952) pollen grains of ‘spiralaperturate’ and ‘zonaperturate’ types are reported in the same flower of Thunbergia grandiflora; whereas in Dicliptera javanica eight pollen types were found in one and the same anther. They were different in polarity, symmetry, aperture number (2 to 6) and shape, but apparently not in exine stratification.

Besides the two usual forms of megaspores, we often found abnormal joined megaspores and microspores. Such abnormal megaspores are found in all investigated Indian species of Isoetes. They are fused in a variety of ways. In most cases only two megaspores are joined on their proximal sides but sometimes there is a similar union of three (see Pl. XVI, fig. 39). We never found all the four megaspores of a tetrad united, although a joined tetrad of four unequal microspores, two large and two small, was seen in I. indica (see Pl. XV, fig. 32). The spores may be joined either bodily or by one or more short tubular connections formed by the joined spore wall through which the cytoplasm of the two spores is connected. The fused spores may sometimes show up to four tubes joining their proximal faces. Spores which are fused bodily (a spore of this type is also figured by Sharma 1959) may show a single longitudinal ridge with forked ends; obviously it is formed by a straight line union of two rays in their triradiate marks and by a reduction of the remaining two rays in each trilet.

United spores are normally reported in no other pteridophyte although otherwise inseparable spores are found in some bryophytes and angiosperms. In some species of Riccia, e.g. R. synspora and R. curtisii (Schiffner 1908; McAllister 1928), the spores of a tetrad adhere tenaciously in spore balls even after they have fully matured. They are dispersed in fours and the subsequent germination gives rise to compact groups of four plants. Adherent tetrads of spores occur also in Sphaerocarpos (Schiffner 1893). In the
angiosperms united tetrads or polyads of pollen grains are found in some genera of Mimosoideae, Apocynaceae, Asclepiadaceae (Erdtman 1952). In some other Asclepiadaceae and Orchidaceae the entire contents of the pollen sac may be united into a pollinium. However, no tubular connections like those found in the megaspores of Isoetes are reported in any bryophytes or angiosperms.

The occurrence of polymorphic and abnormal joined spores may be due to meiotic irregularities and structural hybridity reported by Abraham and Ninan (1958) and Ninan (1958) in the case of *I. coromandeliana*, but no such irregularities are so far reported in the other species.

*Abnormal sporophylls*

The possession of a single medianly placed adaxial sporangium by each sporophyll of lycopsids is regarded by Bower (1935) and others as the most characteristic feature of the lycopsids, and it is indeed remarkable that there are normally no known exceptions to this rule. The occurrence of abnormal bisporangiate sporophylls in *I. indica* is therefore of unusual significance. The only other abnormal sporophyll known to us is that of *Lycostachys protostelicus* where Pant and Walton (1961, Pl. I, fig. 5, and Text-fig. 2, F) have reported the occurrence of a sporophyll with two subarchesporial pads (one proximal and the other distal), but otherwise the sporangial wall is continuous and the sporangium has a single continuous cavity. Such abnormalities mean nothing if they are mere monstrosities, but if they represent reversions they might indicate relationships of lycopsids, even though remote, with plants having polysporangiate sporophylls, e.g. Noeggerathiales, Sphenophyllales or Psilotales.

*Dissemination of spores*

According to Duthie (1929) megaspores of some South African species of *Isoetes* are disseminated by earthworms. Sharma (1959) found no earthworms in the mud where *I. sampathkumaranii* grows. We have, however, repeatedly observed that at Ram Nai (Rewa) earthworms are especially common in the mud around the rhizomorphs of *Isoetes* plants. We have cultivated some of these plants in the Botany Garden at Allahabad and earthworms in this mud became so plentiful that the animal collector of our Zoology Department got tempted and uprooted the plants (without our permission) and took away a large haul of the worms. We have analysed the castings of these worms and found large numbers of *Isoetes* megaspores. The silicious coat of these megaspores undoubtedly protects them from the action of cellulases and other enzymes found in the alimentary canal of the earthworm and they pass out unscathed as reported already by Duthie. The majority of earthworms in the mud, as indicated by the faecal pellets, belonged to the genus *Phere clergy*. 

58
Presence of a columella in lycopsids

The presence of a sterile columella and elaters is well known in the large capsules of many bryophytes and except for the occurrence of a columella in the sporangium of Horneophyton lignieri these features are regarded to be totally absent in the sporangia of all Pteridophyta. However, the large sporangia of many lycopsids show a central columella-like sterile subarchesporial pad (see Zeiller 1911; Pant and Walton 1961; Text-fig. 2, A, E and H) with unbranched or branched trabeculae. The elater-like multicelled filamentous growths of sterile cells, reported here in the sporangia of I. indica, also appear like the pseudoelaters of the Anthocerotales. After breaking off from the trabeculae they too can occur intermixed with spores, but in being initially attached to the sterile trabeculae they remind us of the elaterophores of bryophytes like Pellia or Riccardia. In a recent paper on the columellar structure of Dendroceros and Megaceros, Proskauer (1960) points out that the columella in these genera may not only show elongated cells with thin walls, but some of them may have spiral thickenings like those present in typical elaters. We could even compare the two types of cells in these columellae with the tracheidial and phloem cells of the vascular plants. Likewise, considering the columella-like subarchesporial sterile pads and trabeculae in the sporangia of some lycopsids, e.g. Lycostachys (Pant and Walton 1961), we find that these too are made up of xylem-like transfusion tissue and tracheidial cells and the columella of Horneophyton is reported to be a direct continuation of the phloem in its stem. Obviously, lycopod subarchesporial pads, their trabeculae and sterile filamentous growths (as found in I. indica) not only appear to be similar in position, form and function to the columellae, elaterophores or pseudoelaters of some bryophytes and Horneophyton, but we believe that the two types of structures are truly comparable and that a columella should no longer be regarded as a monopoly of the bryophytes. Indeed, the facts presented above seem to lend some support to a suggestion put forth by Crow (1946) that 'the elaters of the liverwort sporogonium are homologous with the tracheids of vascular plants. When arranged in a central elaterophore they occupy the same relative position as the protostele of the vascular plant shoot and probably serve the same function'.

Geographical distribution of Indian species

The two new species of Isoetes (I. panchananii and I. indica) described in the present paper raise the total number of Indian species of the genus to six. Among these, I. coromandelina appears to be the most widely distributed. From time to time it has been recorded by various workers from Bengal (Griffith 1849; Prain 1908), the Coromandel Coast (Ekambaram and Venkatanathan 1933; Abraham and Ninan 1958), Maharashtra (McCann 1931, 1934; Mirashi
and Paradkar 1961), Varanasi (Bharadwaja 1935), Baroda (Gaekwad and Deshmukh 1954), Gyanpur (Saksena and Ambusht 1957), Kerala (Abraham and Ninan 1958), Lucknow (see footnote by Pant in Saksena and Ambusht 1957), Meerut (Bhambie 1957). Panigrahi and Chowdhury (1962) have recorded the occurrence of *I. coromandelina* at Padmnapur, Eastern India. We have recently found plants of the species growing by the side of streams and pools in Lohgara (27 miles south-west of Allahabad), Ram Nai and Chirhula (9 and 2 miles, respectively, from Rewa), Madhya Pradesh. An unusually large form of *Isoetes* attributable to *I. coromandelina* is reported by Gaekwad and Deshmukh (1954) from Baroda. We have examined some plants of this form (one of which is about 80 cm long) and its megaspores, and we confirm that, except for the larger size of plants, the megaspores and other features of the Baroda form are in no way different from those of a typical plant of *I. coromandelina*. The species has thus been reported from widely scattered localities, e.g. from Baroda in the west to parts of Bengal and other places in the east and as far as Meerut in the north to localities situated in the southernmost State of Kerala. Doubtless, the species should have a very wide distribution all over India.

Other Indian species of *Isoetes* appear to have a more restricted distribution. *I. sahyadrii* is reported from the mountain lake on the tableland at Panchgani (Maharashtra), 4,500 ft above sea-level, and in ponds on the grassy tops of the Kalahattigiri, Baba Budhangiri and other peaks of the Sahyadris in Mysore State (Mahabalé 1938). *I. dixitii*, too, is reported from some shallow rock pools in the tableland at Panchgani (Shende 1946). *I. sampathkumaranii* grows along water margins in shallow depressions of granite rocks in the Lalbagh Government Botanic Gardens at Bangalore in Mysore State (Rao 1944) and also in Waltair in Andhra State (see Abraham and Ninan 1958; Sharma 1959). The distribution of the various species is shown in Text-fig. 12.

**Taxonomy of Indian species**

As will be clear from the foregoing account, the various Indian species of *Isoetes* could be distinguished by their spore characters alone, although features like size of plants, number of lobes in the rhizomorph, nature of velum and the presence or absence of peripheral strands supply valuable distinctions. The number and character of chromosomes could be yet another additional character (Abraham and Ninan 1958), but this requires properly fixed material of the various species. We hope to complete this at a later date, but in the meantime we have tried to look for other supplementary characters for distinguishing species, viz. nature of epidermis and distribution of stomata in leaves and the character of sporangial epidermis. The epidermal cells in all examined species are in regular longitudinal rows and stomata occur in four longitudinal
bands opposite the air chambers. The form and arrangement of stomata suggests that their two longitudinally placed guard cells are formed as a result of the formation of a longitudinal wall in individual cells of these rows (stoma mother cells), and when the stomatal opening is formed and the guard cells enlarge to assume their adult form they push the adjacent cells of the two lateral rows sideways and press or partially crush them (see Pl. XVI, fig. 40; Text-figs. 2, I; 4, C). Occasionally a lateral cell adjacent to a guard cell may also divide longitudinally into two but normally they do not form a stoma; possibly, as Bunning (1956) suggests, due to their lying in the inhibitory field of the adjacent meristemoids. On the basis of stomatal frequency and index, the Indian species of the genus come under two groups. One of the groups consists of *I. coromandelina*, *I. indica* and *I. dixitei* which show a relatively higher frequency of stomata, and the other group consisting of *I. sampathkumarani* and *I. panchanani* shows a relatively low frequency of stomata (the figures for the various species are given in Table III). The sporangial epidermis of *I. panchanani* shows two types of cells, there is a ground work of thin-walled colourless cells with interspersed patches of thick-walled brown cells (see Pl. XVI, fig. 41; Text-fig. 2, H) which appear as the characteristic brown spots on the sporangium (see Text-fig. 2, G). Similar brown cells occur less frequently in the epidermis of *I. sampathkumarani*. The chief characteristics of the various Indian species of the genus are summarized in Table IV and an artificial key for their identification is given below:—

**Key**

A. Adult plants generally more robust (as a rule more than 25 cm long).
   Rhizomorph: three-lobed; peripheral strands present; velum absent; megaspores tuberculate.

I. Triradiate ridges of megaspores normally simple, ends of megaspore tubercles generally rounded. Sterile cells absent, microspores smooth or rugose to papillate. *I. coromandelina*

II. Triradiate ridges in megaspores often branched, ends of megaspore tubercles generally tapering, sterile cells present in outer megasporangia, microspores tuberculate. *I. indica*

B. Adult plants generally small, typically less than 25 cm long.

I. Megaspores tuberculate.

a. Rhizomorph three-lobed, megaspore tubercles of unequal size, tubercle bases not confluent.
1. Peripheral strands present, velum rudimentary. *I. dixitei*

2. Peripheral strands absent, velum almost complete.
   
   *I. sahyadriii*

   b. Rhizomorph two-lobed, megaspore, tubercle bases confluent, giving rise to irregular branched ridges. Velum incomplete covering about half to 2/3 of sporangial surface, peripheral strands none.
   
   *I. sampathkumaranii*

II. Megaspores clearly reticulate.

Rhizomorph two-lobed, velum usually covering about half of sporangial surface (rarely complete). *I. panchananii*

**SUMMARY**

Two new species of *Isoetes*, viz. *I. panchananii* and *I. indica*, are reported from village Ram Nai near the township of Rewa in the State of Madhya Pradesh. Based on the work of previous workers, the paper also gives a comparative account of the diagnostic characters of the various previously described Indian species of the genus. A few hitherto undescribed details of megaspores in *I. coromandelina*, *I. dixitei* and *I. sampathkumaranii* are also mentioned and dimorphic or polymorphic and peculiar-joined megaspores are reported in five out of six Indian species. Some unique abnormal megasporophylls with a pair of adaxial sporangia are described in *I. indica*. A brief account of the geographical distribution and a key for the identification of the various Indian species is given. The columella-like nature of the trabeculae and subarchesporial pads of lycopods is discussed in the light of the occurrence of peculiar elater or pseudocelator-like growths on the trabeculae of *I. indica*.

**ACKNOWLEDGEMENTS**

We are deeply indebted to Father H. Santapau, F.N.I., Chief Botanist, Botanical Survey of India, for taking the trouble of rendering the diagnoses of our two new species into Latin and for his suggestions. Our thanks are also due to Sir George Taylor, Director, Royal Botanic Gardens, Kew, for getting our specimens compared with their authentically identified specimens and we are grateful to Mr. F. Ballard for the trouble he has taken in doing so.

We thank the Council of Scientific and Industrial Research for financial help and the award of a Junior Research Fellowship to one of us (G. K. S.). Our special thanks are due to Prof. P. Maheshwari, F.N.I., Chairman of the Biological Committee of the C.S.I.R., for his kind help and valuable suggestions.
THE GENUS ISOetes IN INDIA

We are thankful to the following scientists who have helped us generously in giving or obtaining material of Isoetes from different localities:—Dr. S. C. Agarwal, Lucknow; Mr. A. K. Dutt, Burdwan; Prof. Ella Gonzalves, Bombay; Dr. M. H. M. Gowda, Bangalore; Dr. A. P. Mehrotra, Gyanpur; Dr. (Mrs.) Radha Pant, Allahabad; Prof. V. Puri, F.N.I., Meerut; Prof. T. S. Sadasivan, F.N.I., Madras; Mr. Arvind Sakshena, Rewa; Dr. J. Sen, Calcutta; Dr. Sreeramamurthy, Kakinada; and Prof. J. Venkateswarlu, F.N.I., Waltair. We are also thankful to our colleagues Dr. D. D. Nautiyal, Km. Bharati Mehra, Mr. B. K. Varma and Mr. M. K. Agarwal for help in the collection of plants and in many other ways.

REFERENCES

EXPLANATION OF PLATES

PLATE XIII

I. panchanani n. sp.

Fig. 1, 2. Proximal views of dry large and small megaspores.
Fig. 3, 4. Distal views of dry small and large megaspores.

I. sampathkumarani

Fig. 5, 6. Proximal views of dry large and small megaspores.
Fig. 7, 8. Distal views of dry small and large megaspores.

I. dixiti

Fig. 9, 10. Proximal views of dry large and small megaspores.
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Fig. 15. Distal view of a dry large typical megaspore showing numerous uneven tubercles.

PLATE XIV

I. indica n. sp.

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I. coromandelina

Fig. 26, 27. Proximal views of dry small and large megaspores.
Fig. 28. Distal view of a dry small megaspore.
Fig. 29. Side view of a dry large megaspore showing a straight commissural ridge (r).
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PLATE XV

I. indica n. sp.

Fig. 30. A portion of a mounted trabecula showing a number of hair-like growths. × 347.
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of trabeculae. × 264.
Fig. 35. Abnormal sporophyll showing a pair of sporangia. × 9.

PLATE XVI

I. dizitei

Fig. 36. Mounted pair of small megaspores showing a continuous spore wall with a tubular
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I. coromandelina

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I. indica n. sp.

Fig. 39. Three joined megaspores of a tetrad showing tubular connections.
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I. panchananii n. sp.

Fig. 41. Mounted sporangial epidermis showing patches of thick-walled cells with brown (dark)
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Text-fig. 2. I. panchanamii n. sp. A, B, proximal views of dry small and large megaspores (see also Pl. XIII, figs. 1, 2). C, distal view of a dry large megaspore showing surface reticulations (see also Pl. XIII, fig. 4). D, E, mounted HF treated large and small megaspores (the outer layer 'perispore' has dissolved). F, squash preparation of mitosis in root tip cell. × 800. G, base of leaf showing brown patches on the sporangial surface. × 9. H, sporangial epidermis magnified to show thin, translucent and thick-walled dark brown cells. × 200 (see also Pl. XVI, fig. 41). I, leaf cuticle showing rows of elongated epidermal cells and longitudinally placed stomata. Note the longitudinally divided cells in a row of epidermal cells between two stomata. × 200.
TEXT-FIG. 3. A, variations in the calculated average diameters of 10, 25, 50, 75, 100, 200, 300, 400 and 500 megaspores of I. coromandelina, I. indica, I. dixitei, I. sampathkumarani and I. panchananii. B, frequency of various types of megaspores found in a single sporangium of I. indica. Columns represent numbers of spores; a, with simple rays, b, with one forked ray, c, with two forked rays, d, with three rays forked and e, with a somewhat reticulate pattern of rays.
**TEXT-FIG. 4. I. indica n. sp.**

A. a young plant. × 1.  
B. a sporophyll from a mature plant. × 1.  
C. mounted cuticle of upper part of leaf showing rows of elongated epidermal cells and longitudinally placed stomata. × 133 (see also Pl. XVI, fig. 40).  
D. abnormal sporophyll showing a pair of sporangia. × 6 (see also Pl. XV, fig. 35).
TEXT-FIG. 5. *I. indica* n. sp.  A, proximal view of a dry large megaspore (see also Pl. XIV, fig. 16).  B, mounted large megaspore.  C, mounted HF treated large megaspore (the outer layer 'perispore' has dissolved).  D, side view of a dry large megaspore to show tubercles and sinuous commissural ridges (see also Pl. XIV, fig. 20).  E, proximal view of a dry medium-sized megaspore (see also Pl. XIV, fig. 17).  F, G, mounted sterile cells showing minute surface tubercles.  X 1,250 (see also Pl. XIV, figs. 23, 24).  H, distal side of a dry medium-sized megaspore.
TEXT-FIG. 6. *I. indica* n. sp.  
A, mounted medium-sized megaspore.  
B, proximal view of a dry medium-sized megaspore with one forked ray.  
C, F, proximal views of dry medium-sized megaspores showing forked rays forming somewhat reticulate patterns.  
D, E, proximal views of dry medium-sized and large megaspores showing all trilete rays forked (see also Pl. XIV, figs. 18, 19).  
G, proximal view of a dry medium-sized megaspore with two forked rays.  
H, mounted HF treated medium-sized megaspore with one forked ray.
TEXT-FIG. 7. *I. indica* n. sp. A, a portion of mounted trabecula from a microsporangium showing a number of hair-like outgrowths. The rounded outline on the right side is of an underlying microspore (see also Pl. XV, fig. 30). B, a portion of mounted trabecula showing simple and glandular hair-like outgrowths. C–F, mounted broken portions of sterile hair-like outgrowths of trabeculae. G, mounted monolete microspore. H, mounted joined pair of microspores. I, mounted trilete microspore. J, mounted small (abortive) microspore. K, mounted large microspore. L, mounted tetrad of two large and two small united microspores. M, mounted microspore highly magnified to show surface tubercles (see also Pl. XV, fig. 32). Figs. A–L × 500; M × 1,250.
Text-fig. 8. *I. coromandelina*. A, B, proximal views of dry large and small megaspores (see also Pl. XIV, figs. 26, 27). C, D, distal views of dry large and small megaspores (see also Pl. XIV, figs. 28, 29). E, F, mounted large and small megaspores. G, H, mounted HF treated small and large megaspores (the outer layer ‘periapore’ has dissolved). I, mounted inner sac ‘endospore’ of a large megaspore. J, mounted inner sac ‘mesospore’ of a small megaspore (all after Pant and Srivastava 1961).
TEXT-FIG. 9. *I. sampathkumaranii*. A, B, proximal views of dry large and small megaspores (see also Pl. XIII, figs. 5, 6). C, distal side of a dry large megaspore. D, E, mounted HF treated small and large megaspores (the outer layer 'perispore' has dissolved). F, sporangial epidermis magnified to show thin-walled translucent cells with a few thick-walled dark brown cells in between. × 200.
Text-fig. 10. *I. dicilei*. A, proximal view of a dry large megaspore (see also Pl. XIII, fig. 9). B, mounted large megaspore. C, distal view of a dry large megaspore showing large and small tubercles intermixed (see also Pl. XIII, fig. 15). D, a mounted fragment of reticulately pitted 'mesospore' of a large megaspore (see also Pl. XIII, fig. 11). E, mounted HF treated large megaspore. The frills are clearly seen at the three angles, the outer layer 'perispore' has dissolved. F, proximal view of a dry small megaspore with sinuous trilete rays (see also Pl. XIII, fig. 10). G, mounted HF treated small megaspore. The frills are clearly seen at the angles, the outer layer 'perispore' has dissolved (see also Pl. XIII, fig. 12). H, distal side of a dry small megaspore, showing numerous small tubercles intermixed with a few large ones. I, J, mounted sterile cells. × 500.
Text Fig. 11. A-D, I. coromandelica; E-G, I. dixitei. A, proximal view of a pair of dry bodily joined megaspores. B, mounted immature megaspore showing a short and two long trilette rays. C, mounted pair of a large and a small megaspores joined by four tubes (see also Pl. XVI, fig. 38). D, mounted HF treated megaspore in Fig. A, the outer layer 'perispore' has dissolved. E, a mounted four-angled small megaspore (possibly due to a forked ray) showing frills at all four angles. F, mounted pair of small megaspores showing a continuous spore wall with a tubular connection-like constriction in the middle (see also Pl. XVI, fig. 36). G, Canada balsam mounted pair of megaspores showing one large megaspore united with a small one. Note the tubular constriction in the continuous wall and the protoplasmic connection between the two spores through it (see also Pl. XVI, fig. 37).
Text-fig. 12. Map of India showing geographical distribution of *Isoetes*.
<table>
<thead>
<tr>
<th>Table IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chief characters of Indian species of Isoetes</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Isoetes coromandeliana Linnaeus (1781)</th>
<th>I. indica n. sp.</th>
<th>I. sahyadrii Mahabale (1938)</th>
<th>I. dixitei Shendo (1943)</th>
<th>I. saptakumarantii Rao (1944)</th>
<th>I. panchananantii n. sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Length of plant</strong></td>
<td>Up to 60 cm (A form from Baroda up to 80 cm)</td>
<td>Up to 56 cm</td>
<td>Up to 20 cm</td>
<td>Up to 20 cm</td>
<td>Up to 11 cm</td>
<td>Up to 24 cm</td>
</tr>
<tr>
<td><strong>Number of lobes in rhizomorph</strong></td>
<td>Typically 3—often 4-5</td>
<td>Usually 3, sometimes 4</td>
<td>Typically 3</td>
<td>Typically 3</td>
<td>Typically 2</td>
<td>Typically 2</td>
</tr>
<tr>
<td><strong>Number of leaves in a typical plant</strong></td>
<td>20–60</td>
<td>9–35</td>
<td>7–15</td>
<td>8–20</td>
<td>3–16</td>
<td>4–38</td>
</tr>
<tr>
<td><strong>Peripheral strands</strong></td>
<td>Main 4, with several accessory strands</td>
<td>Main 4–6, with many accessory strands</td>
<td>Absent</td>
<td>Main 4, with 20–30 subsidiary strands</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td><strong>Veils</strong></td>
<td>Absent</td>
<td>Absent</td>
<td>Almost complete</td>
<td>Rudimentary</td>
<td>Half or two-thirds</td>
<td>About half (rarely complete)</td>
</tr>
<tr>
<td><strong>Megasporangia</strong></td>
<td>Circular to oval</td>
<td>Elongated</td>
<td>Almost round</td>
<td>Oval</td>
<td>Oval</td>
<td>Oval</td>
</tr>
<tr>
<td>Length: 12 mm</td>
<td>Length: 6–19 mm</td>
<td>Diam.: 2 mm</td>
<td>Length: 2–6 mm</td>
<td>Length: 2–6 mm</td>
<td>Length: 2–6 mm</td>
<td></td>
</tr>
<tr>
<td>Breadth: 9 mm</td>
<td>Breadth: 4–9 mm</td>
<td></td>
<td>Breadth: 2–4·5 mm</td>
<td>Breadth: 2–4·5 mm</td>
<td>Breadth: 2–3 mm</td>
<td></td>
</tr>
<tr>
<td><strong>Microsporangia</strong></td>
<td>No description available</td>
<td>Oval</td>
<td>No description available</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td><strong>Megasporangia</strong></td>
<td>Dimorphic</td>
<td>Polymorphic</td>
<td>Megasporangia: 325–430 μ in diam. Surface tuberculate, tubercles blunt and rounded</td>
<td>Dimorphic</td>
<td>Dimorphic</td>
<td>Dimorphic</td>
</tr>
<tr>
<td>Colour of mature megaspores</td>
<td>White when dry, grey when wet</td>
<td>White when dry, grey when wet</td>
<td>Creamy when dry, dark brown when wet</td>
<td>White when dry, ash-coloured when wet (from normal megasporangia); pale brown when dry, slightly chocolate when wet (from sporangia containing sterile cells)</td>
<td>White when dry, fuscous black when wet</td>
<td>White when dry, black when wet</td>
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<tr>
<td><strong>Microspores</strong></td>
<td>26–33 µ in diam., chiefly 30 µ. Surface: smooth (Pfeiffer 1922) or rugose to papillate (Knox 1950)</td>
<td>30 µ in diameter. Surface marked with spines</td>
<td>27–30 µ in diam. Surface muricate</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td><strong>Colour of microspores</strong></td>
<td>Red brown or paler</td>
<td>White</td>
<td>Not described</td>
<td>Reddish brown</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>Sterile cells</strong></td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td><strong>Chromosomes</strong></td>
<td>According to Ekambaram and Venkataraman 1933, the haploid number is 16. In diploid plants 2n = 22 and a fragment (or B chromosome?). In some triploid plants 2n = 33 and a fragment (Abraham and Ninan 1958; Ninan 1958)</td>
<td>Between 43 and 45, possibly 44.</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Between 43 and 45, possibly 44.</td>
</tr>
</tbody>
</table>

THE GENUS HOSTES IN INDIA
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<tbody>
<tr>
<td><strong>Distribution</strong></td>
<td>Localities in Kerala, Tamilnad, Andhra and generally on the Coromandel Coast up to Puducherry and Bengal in Eastern India; Gyanpur, Lohagara, Lucknow, Meerut and Varanasi in U.P.; Chirhu and Ram Nai near Rewa in Madhya Pradesh and Maharashtra and up to Gujarat in Western India</td>
<td>Ram Nai near Rewa (Madhya Pradesh)</td>
<td>Panchgani (Maharashtra); Ka'ahattigiri, Baba Budhangiri and other peaks of the Sahyadri Hills (Mysore)</td>
<td>Panchgani (Maharashtra)</td>
<td>Bangalore (Mysore) and Waltair (Andhra)</td>
<td>Ram Nai near Rewa (Madhya Pradesh); Panchgani (Maharashtra)</td>
</tr>
</tbody>
</table>