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A TAXONOMIC REVISION OF ISOETES L. (ISOETACEAE) IN PAPUASIA

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SUMMARY

In this revision 4 endemic species, one with two varieties, are recognized from the alpine and subalpine regions of New Guinea. *Isoetes stevensii* Croft, *I. hopei* Croft, and *I. neoguineensis* Baker var. *rheophila* Croft are described as new. Scanning electron micrographs of the megaspores and microspores, which furnish important diagnostic characters, are presented for all the taxa in Papuasia as well as for the possibly related species, *I. philippinensis* Alston.

INTRODUCTION

Isoetes was first recorded from the Island of New Guinea in 1898 by Baron Ferdinand von Mueller (von Mueller, 1898). Although he referred to it in passing as *Isoetes neoguineensis* the name was not validly published until 1899 (Baker, 1899). The family has been monographed twice since then (Sadebeck, 1901; Pfeiffer, 1922), but it was not until 1945 that it was realised that New Guinea had more than one species of *Isoetes* (Alston, 1945).

Since the last account of *Isoetes* in Papuasia (Alston, 1959) the number of specimens available for study has increased almost ten-fold. This additional material has shown Alston's account to be inadequate, both in terms of the number of taxa recognized and the degree of variation within these taxa. The present revision is based on the collections of the Papua New Guinea National Herbarium (LAE), C.S.I.R.O. Herbarium Australiense (CANB), and type material from the herbaria of the Royal Botanic Gardens, Kew (K) and the Arnold Arboretum (A), and has been supplemented by field work on four of the five taxa.

CHARACTERS USED IN SPECIES DELIMITATION

Habit. The most common habit in Papuasia is that of a submerged aquatic rosette of still alpine or subalpine tarns, exhibited by 3 of the 5 taxa. The leaves are turgid and spreading, holding their positions even when removed from the water (Plate 19). The flowing habit differs from the aquatic rosette in that the leaves are much longer and narrower and are unable to support themselves when removed from the water; they are not as turgid and will not easily break when bent. It is known from a single collection and further collections are required to see if there is any intergradation with the aquatic rosette. The compact terrestrial cushion contrasts with both these habit types. The rootstock is imbedded some 7 cm below the surface of the ground, the leaves arising as a compact cylindrical column, spreading

abruptly at the surface (Plate 21). Again this habit type is represented by a single collection. No intermediates between the terrestrial cushion and the other two habit types are know.

Plate 19 & 20. Rootstock of *Isoetes habbemensis* Alston. — 19. lateral view, ×½; 20. seen from below, tip cut off, ×⅔. (both from *Croft 56*).

Plate 21. *Isoetes hopei* Croft, habit (*ANU 16114*, holotype in situ).

Lobes of rootstock. Alston (1959) considered the lobing of the rootstock to be a useful character for separating the Malesian species. However, subsequent collections and field studies of populations of *I. habbemensis*, *I. stevensii*, and *I. neoguineensis* have shown the lobes to vary between 2 and 5 in populations, with the 3-lobed state the most usual (Plate 19, 20).

Leaves. The leaves are rather poor in good macroscopic characters. The length of the leaf in mature individuals is very variable within populations and ranges overlap far too much to be of use in separating taxa, with the exception of that with the flowing habit. The texture of the leaf, a very difficult aspect to describe, and to a limited extent the schape, show a good degree of correlation with the structure of the megaspore. The terrestrial species *I. hopei* has coarse leathery leaves. The remaining species fall into two groups: *I. habbemensis* and *I. stevensii* with coarser broader leaves and *I. neoguineensis* with finer narrower leaves. Of the former group *I. habbemensis* appears to have coarser leaves than *I. stevensii*. The shape of the leaf base shows no correlation with other characters and varies too much within individuals to be of any use taxonomically.

Ligule. While useful taxonomically in other regions, the shape and size of the ligule varies too insignificantly to be of any use in Papuasia, being in all cases small and ± deltoid.

Velum. The presence and shape, or absence of a velum is a very useful diagnostic character in *Isoetes*. All species in Papuasia lack a velum, emphasising their close relationship.

Megaspores. In one instance, *I. hopei*, the size difference of the megaspore is a significant character and correlates with differences in habit and megaspore sculpturing. The ornamentation of the megaspore is by far the most significant character for separating taxa in Papuasia, the 4 species recognized being readily determined solely by this character. The four character states are:

i) psilate, absence of any relief other than trilete and equatorial ridges (Plate 1, 2);

ii) rugulose, finely and irregularly wrinkled of relief lower than the trilete ridges (Plate 4, 6);

iii) evenly reticulate, an open, regular honeycomb-like reticulum of even relief less than the trilete ridges (Plate 17);

iv) unevenly reticulate, an open regular reticulum of uneven or jagged relief often exceeding that of the trilete ridges and often appearing warty (Plate 10, 11, 13, 14).

The megaspores are about $\frac{3}{4}$ mm diameter and the ornamentation can be readily discerned with a hand-lens of 10 × magnification.

Microspores. The microspores of the Papuasia species are all ± spinulose. The ranges of size in all species overlap, but that in one species, *I. stevensii*, could be considered significantly smaller than the others.

Gametophyte. The gametophyte and its development may provide diagnostic characters, but has yet to be investigated in the Papuasian taxa.

ACKNOWLEDGEMENTS

The author wishes to thank the Assistant Director, Papua New Guinea Office of Forests Division of Botany, for granting permission to undertake this study. Sincerest thanks are due to Dr. Bill Barker who not only translated the descriptions into latin, but who provided continual polemic and encouragement throughout the study and invaluable criticism in bringing the first drafts to a publishable form. Mr. Graig Marsden and Mr. Robert Chinnock both read the manuscript and provided valuable criticism. Dr. Geoff Hope kindly provided the photograph of *Isoetes hopei* in situ and much discussion. The curators/directors of the C.S.I.R.O. Herbarium Australiense and the herbaria of the Royal Botanic Gardens Kew and the Arnold Arboretum were very kind in making type material available on loan. The scanning electron micrographs were prepared by Mr. Craig Marsden of the Botany Department, University of Adelaide on an ETEC Autoscan scanning electron microscope (see Marsden, 1976).

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ISOETES

Isoetes L., Sp. Pl. (1753) 1100; Gen. Pl. ed. 5 (1754) 846; Sadebeck, in Engler & Prantl, Pfl. Fam. 1, 4 (1901) 756–779; Pfeiffer, Ann. Miss. Bot. Gard. 8 (1922) 76–232; Alston, Fl. Males. II, 1 (1959) 62–64.

Sporophyte heterosporous, herbaceous, terrestrial or submerged aquatic. *Roots* dichotomous, arising from between lobes of a 2–5-lobed, flattened, corm-like rootstock, which may accumulate large quantities of dead overlapping tissue. *Leaves* numerous (to 100 or more), arising in a tuft from flattened apex of rootstock, imbricate basally, glabrous, linear or linear-triangular, terete or ± flattened adaxially to ± triquetrous, entire, proximally winged with base broadly expanded, with a single unbranched vascular strand; mesophyll divided by 4 longitudinal septate cavities; stomata present on one or both surfaces, or lacking; ligule arising from an adaxial basal cavity above the sporangial cavity, deltoid to subulate, 1–2 mm long (–15 mm outside Papuasia), mucilage-secreting at least when young, lacking cuticle and chlorophyll. All leaves sporophylls or potentially so. *Sporangia* solitary, in an adaxial basal cavity, elliptic to oblong, 4–11 mm long, broadly adnate to sporophyll, irregularly and incompletely septate, thin-walled, annulus lacking, dehiscing by decay of sporangial walls; a membranous velum absent or (outside Papuasia) partially or entirely covering the sporangium, extending downwards from the apex of the sporangium and attached to the sides of the sporangial cavity. *Megasporangia* containing 50–300 megaspores; megaspores trilete, 250–2900 μm diameter, smooth or variously sculptured with warts, ridges, spines, etc., drying white to grey (to black outside Papuasia). *Microsporangia* containing 150,000–1,000,000 microspores; microspores monolete, 20–45 μm long, spinulose or (outside Papuasia) smooth, scabrous or papillose. *Gametophyte* dioecious, microscopic; development of prothallus within cell wall of spore; megagametophyte with 1–12 archegonia; microgametophyte with a single antheridium, antherozoids with 15 flagella.

Distribution: About 125 species, in most parts of the world, except the smaller Pacific islands, mainly in temperate regions. In Papuasia there are 4 species, scattered along the central cordillera of the New Guinea mainland from Mt. Carstensz (Mt. Jaya) to Mt. Victoria. Fig. 1.

Ecology: Fully or partially aquatic in still or slow-flowing waters, or terrestrial in moist places. The Papuasian taxa are restricted to high altitude grassland. *Isoetes neoguineensis*, *I. habbemensis*, and *I. stevensii* are found in alpine tarns from 2800 to 3900 m altitude, mostly above 3300 m. *I. hopei* is a terrestrial plant of hummock bogs around 3600 m altitude. The aquatic species can withstand a certain degree of exposure and have been collected several times from almost dry pools.

In Papuasia dispersal of spores is primarily by means of water; one mode in the aquatic Papuasian species is by detached sporophylls, which can often be seen floating on the surface of the tarns.

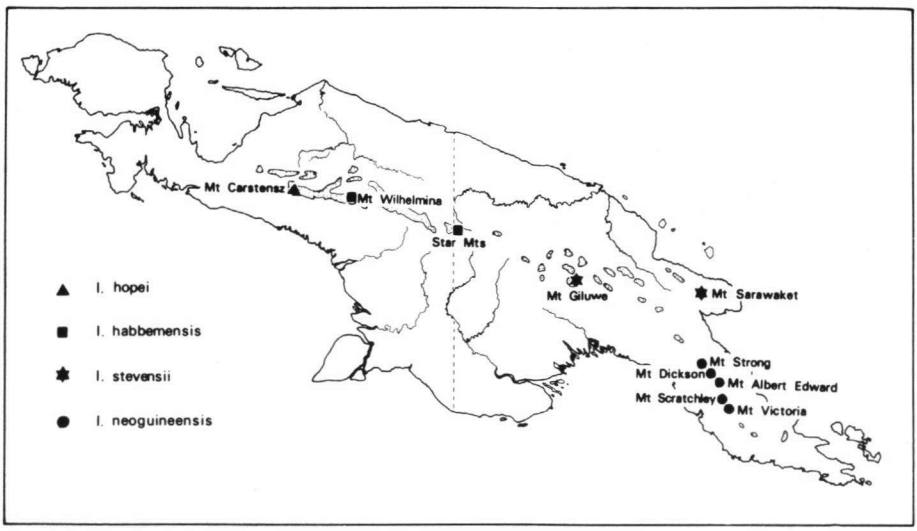


Fig. 1. The distribution of *Isoetes* in Papuasia. Shaded areas above 3000 m altitude.

There is no evidence from the collections available to suggest any degree of seasonality in the growth or spore production of *Isoetes* in Papuasia.

N o t e s : To date there has been no detailed anatomical study of the Papuasian taxa. There are no cytological records and no studies of the gametophyte.

Alston (1959) described the roots as being dark brown to black, presumably entirely from herbarium material. In live material of *I. habbemensis*, *I. stevensii*, and *I. neoguineensis* the roots are white, the older ones becoming mid-brown. The roots of *I. hopei* are reported to be white (Hope, pers, comm.).

The leaves of the three Papuasian species of *Isoetes* collected by the author, *I. habbemensis*, *I. stevensii*, and *I. neoguineensis*, had a distinctive, acrid, slightly fishy smell when fresh. This was taken to be a character of the plant itself rather than that of any algal slime, etc., since nothing else in the pond shared this unique odour.

KEY TO THE TAXA OF ISOETES IN PAPUASIA

1. Plants terrestrial; leaves thick and leathery, ± triquetrous distally, ± 3–5 mm wide at the middle; megaspores psilate, 800 μm or more in diameter (Plate 1, 2). *Mt. Carstensz*. . . . . **1. I. hopei**
1. Plants aquatic; leaves thin and ± fleshy, terete distally, 1–3 mm wide at the middle; megaspores finely rugulose, or reticulate, or irregularly and deeply reticulate and/or warty; 500–700(?–800) μm diameter.
   2. Megaspore ornamentation finely and irregularly rugulose (Plate 4, 6); leaves generally 2–3 mm wide at the middle. *Mt. Wilhelmina (Mt. Mandala) and Star Mts*. . . . . **2. I. habbemensis**
   2. Megaspore ornamentation regularly reticulate, of even or irregular relief, often resembling prominent warts on the proximal surfaces; leaves generally 1–3 mm wide at the middle.

3. Megaspore ornamentation shallowly reticulate, of even relief and lower than that of the trilete ridge (Plate 7); leaves 2–3 mm wide at the middle. *Mt. Giluwe and Mt. Sarawaket* . . . . . **3. I. stevensii**
3. Megaspore ornamentation deeply reticulate or of uneven relief, as high as the trilete ridge, often appearing ± warty (Plate 10, 11, 13, 14); leaves 1–2 mm wide at the middle. *Owen Stanley Ranges* . . **4. I. neoguineensis**
   4. Leaves less than 20 cm long, ± stiff and spreading; plants of stagnant alpine tarns or lakes. . . . . **4a.** var. **neoguineensis**
   4. Leaves 35–40 cm long, ± flexible, flowing in current; plants of streams **4b.** var. **rheophila**

1. Isoetes hopei Croft, *sp. nov.* — plate 1–3, 21.

Herba rosula terrestris; caudex cormoideus ca. 7 cm infra turbarii paginam. *Folia* ca. 100, usque ad 12 cm longa, in medio 3–5 mm lata, infra turbarii paginam pallida, supra perviridia, basaliter late dilatata, usque ad ca. 8 mm lata, et caudici late affixa, in partibus distalibus crassa coriaceaque, plus minusve triquetra praesertim in distalibus 2–4 cm, alis exiguis in sicco manifestis; stomata deficientia; ligula late deltoidea, 1–1.5 mm lata. *Sporangia* elliptico-oblonga, usque ad 6 × 3 mm; velum deficiens. *Megasporangia:* megasporae 800–875 μm diametro, in sicco pallide cineraceae usque albidae porca trileta usque ca. 25 μm alta, cetero sculptura nulla. *Microsporangia* plane brunneo-punctata; microsporae 39–46 μm longae, dense spinulosae, in sicco pallide brunneae.

Typus: *G. S. Hope ANU 16114* (CANB), Kemabu Plateau, Carstensz Mt., Irian Jaya, 6-3-1972.

Rosette herb, terrestrial, with a corm-like rootstock ± 7 cm below surface of bog. *Leaves* ± 100, to 12 cm long, 3–5 mm wide at middle, pale beneath ground, dark green above the ground, basally broadly dilated to ± 8 mm wide and broadly attached to rootstock, distally thick and leathery, ± triquetrous, especially in distal 2–4 cm, with evidence of slight wings in dried material; stomata absent; ligule broadly deltoid, 1–1.5 mm wide. *Sporangia* elliptic-oblong, to 6 × 3 mm; velum absent. *Megasporangia:* megaspores 800–875 μm diameter, pale grey to almost white when dry, with trilete ridge to ± 25 μm high, ornamentation otherwise lacking on all surfaces. *Microsporangia* evenly dark brown punctate; microspores 39–46 μm long, densely spinulose, pale brown when dry.

Distribution: Only known from type collection from Mt. Carstensz (Mt. Jaya). Fig. 1.

Ecology: 'hard hummock bog in wet areas. Alt. 3630 m. Rare rosette plant, hard tops, succulent leaves and thick rootstock...'. A photograph of *I. hopei* in situ (Plate 21) indicates an association with *Ranunculus, Potentilla foersteriana, Plantago stenophylla, Poa cf. callosa, Styphelia suaveolens, Centrolepis philippinensis, Deyeuxia brassii, Vaccinium amblyandrum*, etc., (Hope, pers. comm.). It is unique among Malesian *Isoetes* in occupying a terrestrial habitat.

Notes: The megaspores are superficially similar to those of *Isoetes habbemensis* Alston, but they bear no trace of the fine wrinkles present on the megaspores of that species. Moreover, they are consistently at least 30% larger.

I am indebted to Dr. G. S. Hope, after whom this species is named, for drawing to my attention the possibility of a new *Isoetes* among his Mt. Carstensz collections (Hope, 1976a).

2. Isoetes habbemensis Alston. — Plate 4–6, 19, 20.

I. habbemensis Alston, J. Arn. 26 (1945) 180; Fl. Males. II, 1 (1959) 64, fig. 1. — T y p e : *L. J. Brass 9440* (A, *n. v.*; iso in LAE).

Submerged rosette herb. *Rootstock* (2–)3(–4)-lobed. *Leaves* several in smaller plants to numerous in larger plants, linear-triangular, to ± 15(–30) cm long, 2–3 mm wide at the middle, pale yellow basally grading to dark green distally, with base broadly dilated, to ± 1 cm wide and broadly attached over ± 15 mm to rootstock, basal part winged, flat to slightly concave or convex adaxially, rounded abaxially, distal half ± terete, apex acute; stomata absent; ligule broadly deltoid, 1–1.5 mm wide. *Sporangia* elliptic, oblong, or ovate, to 10 × 4 mm, cream to pale brown; velum absent. *Megasporangia:* megaspores 507–594 μm diameter, with trilete ridge ±30 μm high, irregularly low rugulose-scaberulous on distal surface, less so on proximal surface, pale grey-white when dry. *Microsporangia* sparsely dark punctate; microspores ±43 μm long, densely spinulose, brown when dry.

D i s t r i b u t i o n : The central cordillera of western New Guinea from Lake Habbema and Mt. Wilhelmina (Mt. Mandala) (*Brass and Meyer-Drees 9974, n.v.*), to the Snow Mts. and Mts. Scorpion and Auriga of the Star Mountains. Western limits presently not known but not found on Mt. Carstensz (Mt. Jaya) (Hope, 1976a). Fig. 1.

E c o l o g y : Locally abundant in shallow alpine tarns (50 cm or less deep) and along the margins of larger lakes from 3200–3300 m altitude. Mostly entirely aquatic, rooted in peaty sediment, but may be exposed during drier periods.

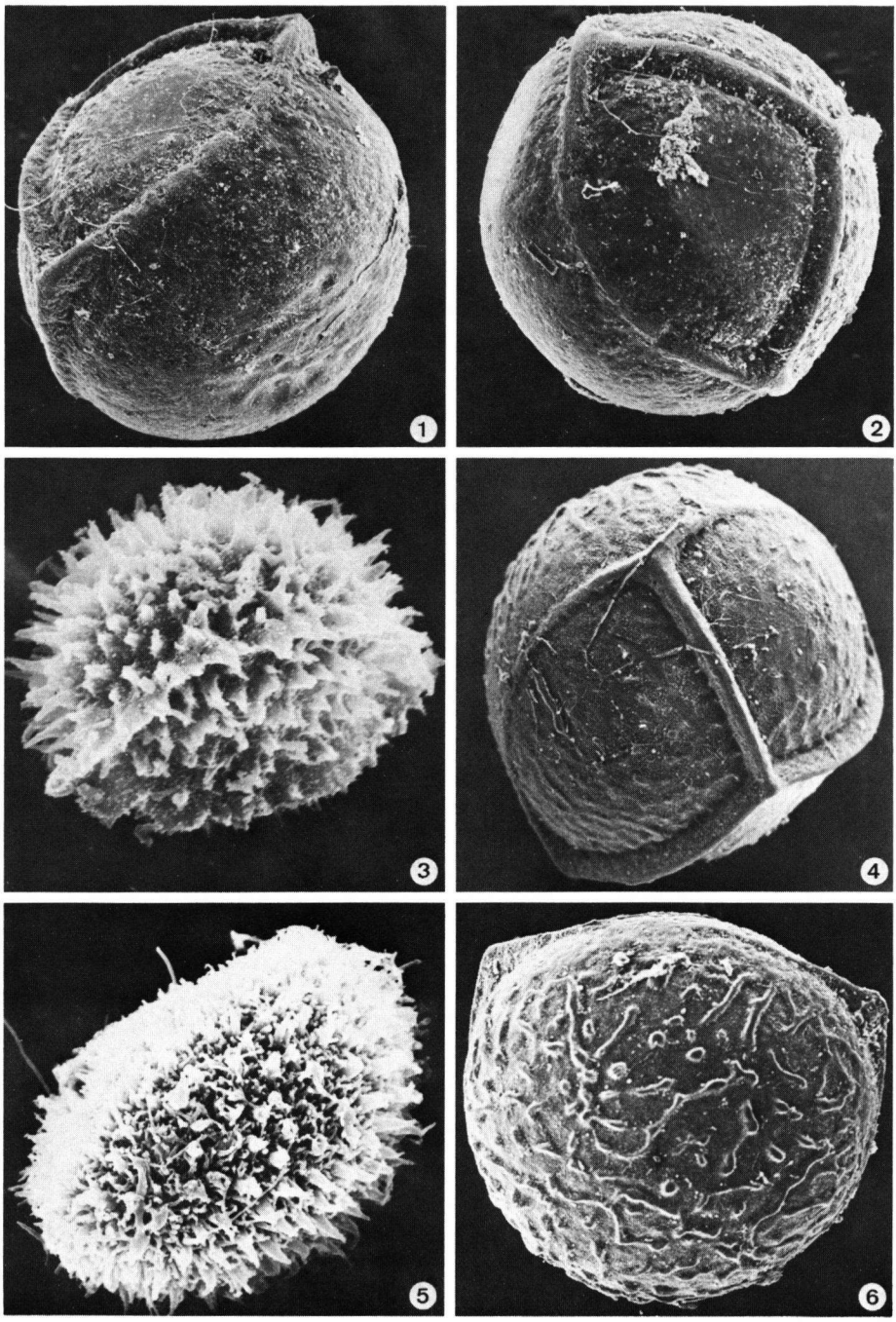
New Guinea. Lake Habbema, 3225 m, 8-1938, *Brass 9440* (LAE), *9441* (LAE; a small plant with strongly recurved leaves). Star Mts., NW. slopes Mt. Auriga, 3300 m, 5-1975, *Veldkamp 6543* (L, LAE; spirit material and population seen). S. slopes Mt. Scorpion, 3300 m, 24-5-1975, *Croft 56* (K, L, LAE, NSW), *Croft and Lelean LAE 65873* (A, BISH, BRI, CANB, E, K, L, LAE, M, NSW, US).

3. Isoetes stevensii Croft, *sp. nov.* — Plate 7–9.

Herba rosula, aquatica, submersa; caudes (2–)3(–4)-lobatus. *Folia* aliquot usque numerosa, linearitriangularia, usque ad 19 cm sed plerumque ca. 10 cm longa, ad medium 2–3 mm lata, basaliter pallide flava gradatim in partibus distalibus perviridia, basi late dilata, usque ad 1 cm lata et caudici per 10 mm late affixa, dimidio proximali alato, adaxialiter plus minusve plano, abaxialiter rotundato, dimidio distali tereti, apice acuto; stomata deficientia; ligula late deltoidea, 1–1.5 mm lata. *Sporangia* elliptico-oblonga, usque ad 6 × 4 mm, cremea usqua pallide brunnea; velum deficiens. *Megasporangia:* megasporae 492–598 μm diametro, in sicco pallide cineraceae usque albidae, porca trileta ca. 30 μm alta, sculptura in paginis omnibus reticulata, altitudinis uniformis et porca trileta inferioris. *Microsporangia* sparsim punctata; microsporae 35–39 μm longae, dense spinulosae, in sicco brunneae.

T y p u s : *Stevens et Foreman LAE 52251* (LAE), East Mt. Giluwe, 3600 m, 15-8-1972. Isotypi (*non visi*): A, BRI, CANB, K, L, NSW.

Plate 1–6. Spores of *Isoetes*. — 1 & 2. *I. hopei* Croft, megaspores (*ANU 16114*, holotype CANB), × 65 and × 70 resp.; 3. ditto, microspore (*ANU 16114*, holotype CANB), × 1400; 4 & 6. *I. habbemensis* Alston, megaspore (*Brass 9440*, isotype LAE), both × 80; 5. ditto, microspore (*Brass 9440*, isotype LAE), × 1650.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Submerged rosette herb. *Rootstock* (2–)3(–4)-lobed. *Leaves* several in smaller plants to numerous in larger plants, linear-triangular, to 19 cm long but mostly ± 10 cm long, 2–3 mm wide at the middle, pale yellow basally grading to dark green distally, base broadly dilated to ± 1 cm wide and broadly attached over 10 mm to the rootstock, proximal half winged, ± flat adaxially, rounded abaxially, distal half terete, apex acute; stomata absent; ligule broadly deltoid, 1–1.5 mm wide. *Sporangia* elliptic-oblong, to 6 × 4 mm, cream to pale brown; velum absent. *Megasporangia:* megaspores 492–598 μm diameter, pale grey to white when dry, trilete ridge ± 30 μm high, ornamentation on all surfaces reticulate, of even relief, lower than the trilete ridge. *Microsporangia* sparsely dark punctate: microspores 35–39 μm long, densely spinulose, brown when dry.

Distribution: Known only from Mt. Giluwe and Mt. Sarawaket. Fig. 1.

Ecology: Shallow alpine tarns (less than 50 cm deep) at 3400 to 3600 m altitude. The plants can apparently withstand periodic exposure in dry periods.

Notes: The reticulate megaspores of this species are suggestive of *I. philippinensis* (Merr. & Perry, 1940). However, examination of the type (*Zwickey 776*, Plate 16–18) revealed that *I. philippinensis* has a more uneven reticulum that is not at all confluent with the trilete ridge, resembling an irregular series of wrinkles rather than the honey-comb-like ornamentation of *I. stevensii*, which is confluent with the trilete ridge. Furthermore, *I. philippinensis* has a long flowing habit not known in *I. stevensii*, and has finely scabrous rather than spinulose microspores.

The ornamentation of the megaspore is like that of *I. habbemensis*, being lower than that of the trilete ridge. In design, however, it more closely approaches *I. neoguineensis*, being reticulate rather than honey-comb-like in appearance.

The single specimen from Mt. Sarawaket is tentatively placed in this species. It differs from the Mt. Giluwe collections in having megaspores that are more strongly embossed with a reticulum of even height approximating that of the trilete ridge. Further collections of this population are required to resolve whether the Sarawaket specimen deserves separate taxonomic status.

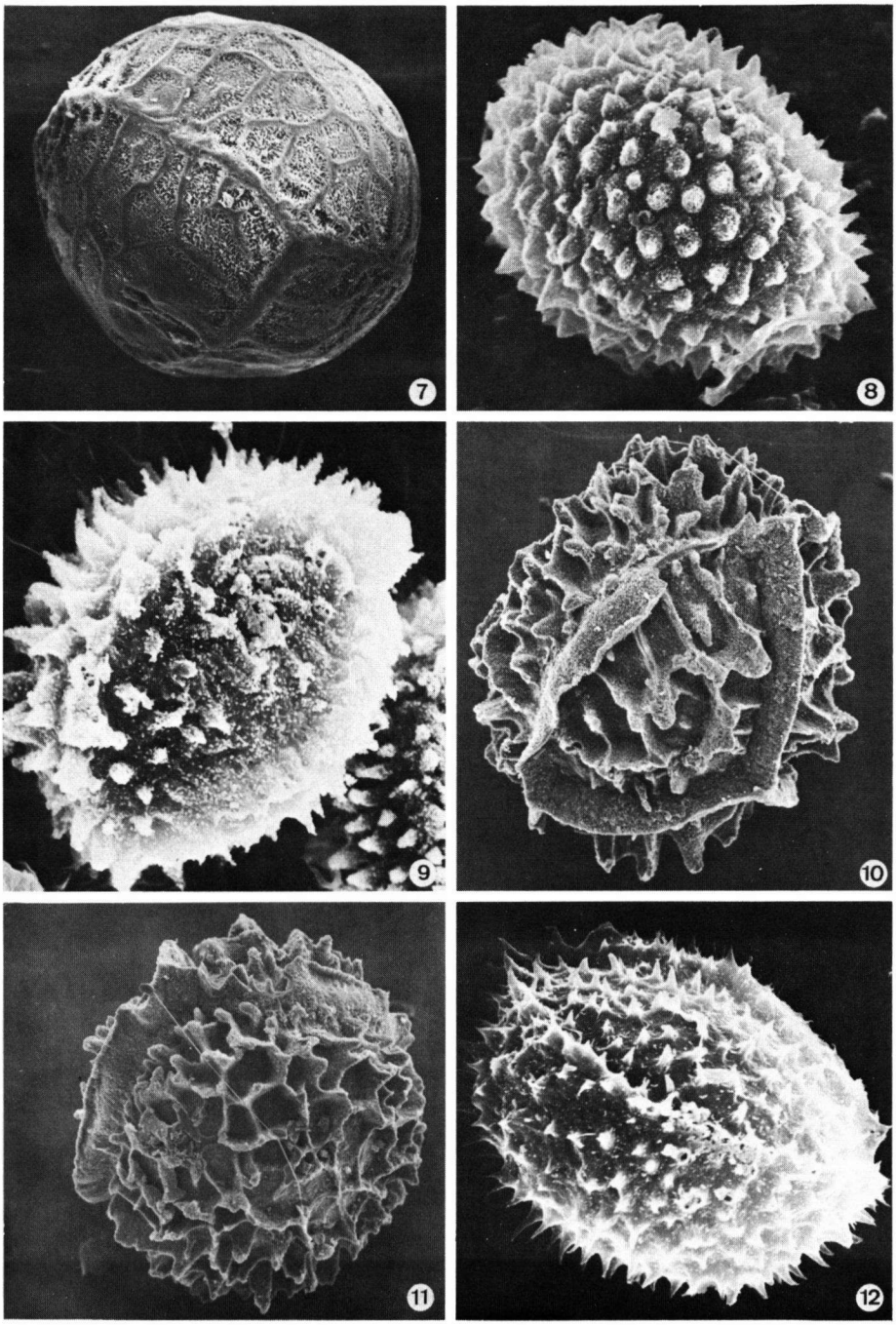
New Guinea. E. Mt. Giluwe. 3660 m, 19-9-1969, *Coode, Wardle, and Katik NGF 40229* (LAE); 3600 m, 15-8-1972, *Stevens and Foreman LAE 52251* (LAE). W. Mt. Giluwe. 3700 m, 21-1-1979, *Croft 708* (K, L, LAE, NSW); 3450 m, 22-9-1961, *Pullen 2833* (LAE); 3800 m, 26-6-1976, *van Royen 11261 & 11264* (BISH, LAE); 3450 m, 4-8-1961, *Schodde 1843 & 1843A* (LAE); 3600 m, 16-7-1971, *Wade & McVean ANU 7756* (LAE). Mt. Sarawaket, Kenzohroh, 3450 m, 14-9-1964, *Hoogland 9846* (LAE).

4. Isoetes neoguineensis Baker. — Plate 10–15.

I. neoguineensis Baker, Kew Bull. (1899) 122; Sadebeck in Engler & Prantl, Nat. Pfl. Fam. 1,4 (1901) 776; Pfeiffer, Ann. Mo. Bot. Gard. 9 (1922) 211; Posthumus in van Steenis, Bull. Jard. Bot. Buit. III, 13 (1934) 169; Alston, Fl. Mal. II, 1 (1959) 64. — *I. neoguineensis* F. v. M., Ann. Rep. Brit. N. Guinea 1897-8 (1898) 149, *nomen nudum*. — Type: *A. Giulianetti s.n.* (K).

Isoetes sp.: Coode and Stevens, Papua New Guinea Sci, Soc. Proc. 23 (1972) 25.

Plate 7–12. Spores of *Isoetes*. — 7. *I. stevensii* Croft, megaspore (*LAE 52251*, holotype LAE), × 100; 8. ditto, microspore (*LAE 52251*, holotype LAE), × 1470; 9. ditto, microspore (*Schodde 1843*, LAE), × 1790; 10 & 11. *I. neoguineensis* Baker var. *neoguineensis*, megaspores (*LAE 51360*, LAE), both × 66; 12. ditto, microspore (*LAE 51360*, LAE), × 1650.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Distribution: A species with two varieties restricted to the Owen Stanley Range, from Mt. Strong to Mt. Victoria. Fig. 1.

4a. var. **neoguineensis. — Plate 10 – 12.**

Submerged rosette herb. *Rootstock* 3 – 4(– 5)-lobed. *Leaves* several in smaller plants to numerous in larger plants, linear-triangular, 10 – 17 cm long, 1 – 2 mm wide at the middle, pale yellow basally grading to dark green distally, base broadly dilated to ± 1 cm wide and broadly attached over ± 10 mm to rootstock. Proximal half winged, ± flat adaxially, rounded abaxially, distal half terete, apex acute; stomata absent (?or few); ligule broadly deltoid, 1 – 5 mm wide. *Sporangia* elliptic-oblong, to 6 × 3 mm, cream to pale brown; velum absent. *Megasporangia:* megaspores 510 – 710(– 800) μm diameter, pale grey-white when dry, with trilete ridge 30 – 50 μm high, ornamentation on distal surface a reticulum of irregular relief, about the same height as the trilete ridge, on proximal surface irregularly reticulate and/or deeply scabrous. *Microsporangia* sparsely dark punctate; microspores 35 – 42 μm long, minutely spinulose, brown when dry.

Distribution: The Owen Stanley Range of eastern New Guinea (Mt. Strong, Mt. Dickson, Mt. Albert Edward, Mt. Scratchley, and Mt. Victoria). Fig. 1.

Ecology: Growing in peaty sediments of shallow alpine tarns (50 cm or less deep) from 2800 – 4000 m. Mostly entirely aquatic, but may be exposed during drier periods.

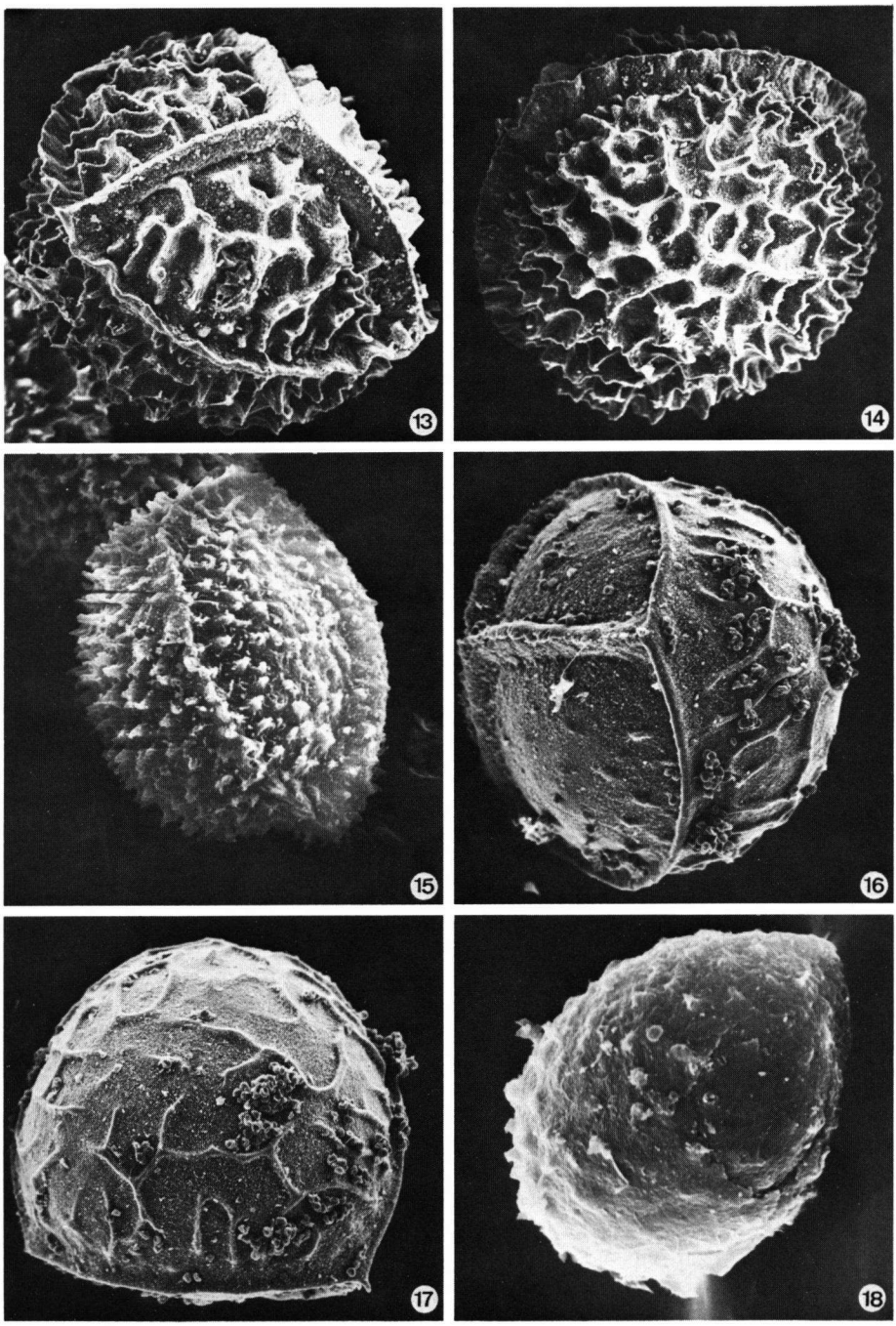
New Guinea. Owen Stanley Range. Mt. Victoria: 3500 m, 13-7-1974, *Craven 3070* (LAE); 3600 m, 13-7-1974, *Croft LAE 61775* (A, BM, CANB, K, L, LAE, NSW). Mt. Scratchley: 3000 – 3900 m, 1896, *Giulianetti s.n.* (K); 3300 m, 7-5-1971, *Coode and Stevens NGF 46337* (LAE; spirit material). Mt. Albert Edward: 3680 m, 6-1933, *Brass 4366* (A); 3800 m, 22-6-1974, *Craven 2717* (LAE; population seen); 3600 m, 27-6-1976, *Croft and Lelean LAE 61483* (A, BM, CANB, K, L, LAE, NSW); 3700 m, 27-10-1975, *Kanai 753570* (LAE); 3600 m, 3-4-1976, *Kores WEI 1569* (LAE); 3700 m, 10-11-1970, *Passer s.n.* (UPNG; FAA material only); Neon Basin, 2800 m, 28-6-1974, *Croft LAE 61531* (A, BM, CANB, K, L, LAE, NSW). Mt. Dickson: 3450 m, 11-12-1964, *Hartley 13011* (LAE). Mt. Strong: 3450 m, 30-4-1971, *Coode and Stevens NGF 54201* (LAE; spirit material); 3450 m, 3-5-1971, *Coode and Stevens NGF 46254* (LAE; spirit material, a 5-lobed specimen); 3420 m, 25-4-1971, *Stevens and Coode LAE 51360* (LAE; spirit material; CANB).

4b. var. **rheophila** Croft, *var. nov.* — **Plate 13 – 15.**

Herba rosula, aquatica, submersa, rivulara, foliis in aqua trahentibus. *Caudex* trilobatus. *Folia* numerosa, angusto-linearia, 35 – 45 cm longa, ad medium ca. 1.5 mm lata, basi late dilatata usque ad 1.5 cm lata, caudici per ca. 1.5 cm late affixa, in partibus proximalibus alata, adaxialiter plana, abaxialiter rotundata, distalibus teretia, apice acuta; ad basem albida, in partibus distalibus abrupte viridia. *Sporangia* oblonga, usque ad 6 × 11 mm; structure sporarum, amplitudo formaque *I. neoguineensi* var. *neoguineensi* similaris.

Typus: *J. R. Croft LAE 61486* (LAE), Neon Basin, Mt. Albert Edward, 2800 m, 28-6-1974. Isotypi: L, CANB, K, BM.

Plate 13 – 18. Spores of *Isoetes*. — 13 & 14. *I. neoguineensis* Baker var. *rheophila* Croft, megaspores (*LAE 61486*, holotype LAE), × 90 and × 80 resp.; 15. ditto, microspore (*LAE 61486*, holotype LAE), × 1200; 16 & 17. *I. philippinensis* Merr. & Perry, megaspores (*Zwickey 776*, holotype A), × 110 and × 100 resp.; 18. ditto, microspore (*Zwickey 776*, holotype A), × 2270.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Submerged rosette herb with leaves trailing in stream. *Rootstock* 3-lobed. *Leaves* very numerous, narrow-linear, 35–45 cm long, ± 1.5 mm wide at the middle, base broadly dilated to 1.5 cm wide, broadly attached over ± 1.5 cm to rootstock, proximally winged, flat adaxially, rounded abaxially, distally terete, apex acute; white basally, abruptly grading to medium green distally. *Sporangia* oblong, to 6 × 11 mm; spore size, shape, and ornamentation as for *I. neoguineensis* var. *neoguineensis*.

Distribution: Only known from the type collection from a restricted population in the Neon Basin, an extensive intermontane grassland basin in the Owen Stanley Range. Fig. 1.

Ecology: Trailing in stream, ± 70 cm below surface of water.

Notes: The habit of this variety resembles *I. philippinensis* Merrill and Perry rather than *I. neoguineensis* var. *neoguineensis*. However, the ornamentation of the megaspores is clearly that of *I. neoguineensis*, the ridges being even more dense than those of the type variety. *I. philippinensis* has an irregular reticulate ornamentation not at all confluent with the trilete ridge (Plate 16, 17). Very little is known about the phenotypic plasticity of *Isoetes*, and further research could show that tarn plants transplanted into suitable streams develop the long flowing habit. However, the fact that *Isoetes* has not otherwise been found in other such available habitats in Papuasia suggests that this population was genetically different from those populations in the still tarns.

DISCUSSION

The four New Guinea species are represented by a geographically disjunct series of populations along the central cordillera (fig. 1). The ornamentation of the megaspore, while quite different between the populations of each mountain complex, represents a geographic series of increasing complexity and relief from west to east, thus: *I. hopei* (smooth) – *I. habbemensis* (rugulose) – *I. stevensii*, Mt. Giluwe population (low even reticulate) – *I. stevensii*, Mt Sarawaket population (pronounced even reticulate) – *I. neoguineensis* (very pronounced reticulate with uneven relief). This cline in spore ornamentation is correlated with a decrease in the thickness of the leaves with the very leathery *I. hopei* at one extreme and the fine leaved *I. neoguineensis* at the other, and with *I. stevensii* and *I. habbemensis* intermediate.

This evidence strongly suggests that the closely related New Guinea species represent the remnants of a more or less continuous east-west cline that may have existed during the glacial period of about 34,000 years ago when the tree-line is estimated to have been depressed about 1500 m (Hope, 1976b). This depression is considered to be sufficient to present an almost continuous range of potential habitats for *Isoetes*. The existence of this cline suggests that the previous subdivision of the genus on the basis of megaspore sculpturing (Pfeiffer, 1922), while being useful for species identification, does not represent phylogenetic relationships, at least in the Papuasian species. A core recently collected by Dr. G. S. Hope from a tarn in the Star Mountains contains layers of *I. habbemensis* megaspores extending to the lowermost peaty sediments. These have been dated to 13,250 ± 395 years B. P. (Hope, pers. comm.). A study of the spores along the sediment profile may shed some light on the recent evolution of the spore ornamentation in this species.