A conspectus of and key to Greek Isoetes (Isoetaceae), based on a reassessment of Haussknecht's gatherings of 1885

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Abstract

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The three *Isoetes* species recorded from Thessalia (Thessaly) in N Greece by Haussknecht, in 1899, under the names *I. setacea*, *I. heldreichii*, and *I. phrygia*, were reassessed using megaspore and microspore ornamentation in addition to macromorphological features. "*Isoetes setacea*" is not the SW European *I. delilei* to which the name *I. setacea* was generally misapplied, nor "*I. echinospora*" as it has been called due to a misunderstanding, but a so far undescribed species here named *I. haussknechtii*; it has not been found again in Haussknecht's locality but has recently turned up in Peloponnisos and the E Aegean Islands. *I. heldreichii*, described from Haussknecht's gathering, is apparently extinct. The record of *I. phrygia* was based on misidentified *I. gymnocarpa.* Even so, contrary to prevailing opinion, Haussknecht was justified in raising Boissier's *I. histrix* var. *phrygia* to specific rank; genuine *I. phrygia* has recently been discovered in Kriti (Crete). The inventory of Greek *Isoetes* now comprises seven species, of which *I. phrygia* and *I. todaroana* are newly recorded here. Greek specimens studied are cited for all of them, and a key for their identification is presented. The names *I. heldreichii* and *I. phrygia* are typified.

Additional key words: Greece, Haussknecht, *Isoetes haussknechtii*, *Isoetes setacea*, *Isoetes delilei*, *Isoetes heldreichii*, *Isoetes phrygia*, *Isoetes todaroana*, key, lectotypification, new species

Introduction

When Carl Haussknecht in June–July 1885, jointly with Theodor von Heldreich, undertook his botanical expedition to Thessalia (Thessaly), no *Isoetes* species had yet been reported from the Balkan Peninsula. At least, this is what Haussknecht (1899) himself claimed; in fact, Boissier (1884) had published reports of *I. histrix* var. *subinermis* from Peloponnisos and the Ionian Island of Zakynthos, which arguably are part of the Balkans. Be this as it may, the three species then collected by Haussknecht, which he referred to as (in this order) *I. setacea*, *I. heldreichii* and *I. phrygia*, were indeed new for Greece and the Balkan countries. What is more, even though the second species was described as new to science based on Haussknecht's material, none of the three has so far been properly understood, and none has been found again in Thessalia since 1885.

Isoetes, an unobtrusive plant easily mistaken for a sterile grass tuft, was and still is one of the most poorly collected genera of the Greek flora. This is not surprising. Clearly, you need a special knack to spot and collect these plants. Haussknecht is one of the few who had that knack; his companion Heldreich, who for all we know may never in a lifetime (80 years) of busy collecting have sampled a quillwort specimen himself, had no such knack. (The gathering of *I. histrix* near Kissamos in Kriti [Crete], credited to Heldreich by Halácsy 1904, is in fact due to Elysée Reverchon.)

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At the end of the trip to Thessalia, when it came to dividing the harvest, the arrangement was apparently made that the fellow travellers would share all their gatherings, each to label the material independently as his own. Whereas Haussknecht undertook to study the plants critically and eventually published the results, under the title "Symbolae ad floram Graecam", in seven parts between 1892 and 1899, the practical-minded Heldreich was quick in distributing his duplicates. We have seen a photocopy of a letter in Richard von Wettstein's hand (location of original unknown), dated 6 Feb 1886 and presumably addressed to Alexander Braun in Berlin, which shows that Wettstein had received two of "Heldreich's" *Isoetes* specimens. He writes [in German; translation ours]: "The one from Karditza is an excellent new species of the group of the *Aquaticae* A. Br., which hitherto had no representative in the whole Orient. I name it *I. Heldreichii*. The second *Isoetes* from Korona in Pindos is certainly *I. setacea* Bosc of the group of the *Amphibiae* R. Br. [sic!]. Also a very interesting find, because the plant is so far known with certainty only from France."

In June 1995, when preparing the pteridophyte treatment for volume 1 of "Flora hellenica" (eventually to be removed from that volume), the prospective author Brigitte Zimmer, in the company of one of us (W.G.), visited Haussknecht's *Isoetes* collecting places in the hope of finding the plants again. Alas in vain, partly because those places had not been accurately located and at least partly because the plants' natural habitats of 1885 are now gone. The present paper aims in its first part to clarify the identity of Haussknecht's *Isoetes* collections of 1885. In the wake of that reassessment, an inventory of the *Isoetes* species currently known from Greece is presented, as well as a key for their identification.

Material and methods

Our study is based on relevant literature and on the material in the herbaria B, FI and PAL (including PAL-Gr), plus selected specimens from other herbaria. We obtained on loan specimens from B, JE and P, and have seen high-resolution digital images available online or provided on request from several herbaria, including G, NAP and WU (acronyms according to Thiers 2015+). Additional specimens, collected by I. Bazos on Lesvos and E. Bergmeier in Kriti, where kindly provided by the collectors.

In specimen citation, the standard ELOT 743 (ELOT 2001) has been used for the transcription from Greek to Latin script of the names of provinces ("Nom.", nomos), former districts ("Ep.", eparchia) and other places, not necessarily the spelling used on the labels. Geographical coordinates, when not mentioned on the labels, were added by us resorting to Google Earth (version 8 July 2008; http://www.google.com/earth/).

In addition to Greek material, we examined type specimens, or original material, or specimens from the locus classicus, for the names *Isoetes delilei* Rothm. (*I. setacea* auct.; Greuter & Troia 2015), *I. phrygia* (Boiss.) Hausskn., *I. olympica* A. Braun, and *I. libanotica* Musselman & al. (Bolin & al. 2011).

Spores as well as cuttings from the middle part of the blade of dried leaves were mounted untreated onto SEM stubs using double-stick tape, coated with gold/palladium and examined under an Oxford Leo 440 SEM. Terms used for describing megaspore and microspore ornamentation are those defined by Hickey (1986) and Musselman (2003), respectively.

In the case of Greek "*Isoetes setacea*" a preliminary anatomical study was made by optical microscopy. For that purpose, small leaf cuttings were taken from herbarium specimens and soaked in sodium hydroxide (6 %) for c. 10 minutes to soften the tissue (Rolleri & Prada 2007).

Results

Haussknecht's gatherings

A general question may be asked first: can the plants collected jointly by Haussknecht and Heldreich, even though distributed independently by those two botanists and with their respective own labels, be regarded as being duplicates of a single gathering? The question is of nomenclatural relevance when it comes to designating types of the names of newly described taxa. The ICN (McNeill & al. 2012) stipulates that duplicates are "parts of a single gathering of a single species or infraspecific taxon made by the same collector(s) at one time". Factually, in the present case, these conditions are met, even though this is not obvious from the labels alone; but then, the ICN does not stipulate that the label texts of duplicates must be identical. Our preference is to rate substance higher than form and to consider the duplicate criterion fulfilled – even when Haussknecht, probably confused by the duality of dates between the Julian calendar (then still official in Greece) and the more generally known Gregorian calendar, is often ambivalent in placing a given collecting event in June or July.

The three *Isoetes* taxa mentioned by Haussknecht (1899) do indeed correspond to as many different species, but two were misnamed; the exception being *I. heldreichii.*

Isoetes heldreichii – Fig. 1C, 1F, 1I, 1L, 2C, 2F, 3C.

Isoetes heldreichii was described as a new species by Wettstein (1886), based on one of the specimens distributed by Heldreich under his own labels. The name supposedly honours the discoverer (Wettstein: "ich benenne diese Pflanze zu Ehren ihres hochverdienten Entdeckers"). The real finder, Haussknecht, did not raise a fuss over that mistaken dedication but made it clear on several of his labels that he was the true discoverer "detexit Haussknecht" and in one case (in B) he explicitly stated "detex. Hskn. nec Heldr." (found by Haussknecht,

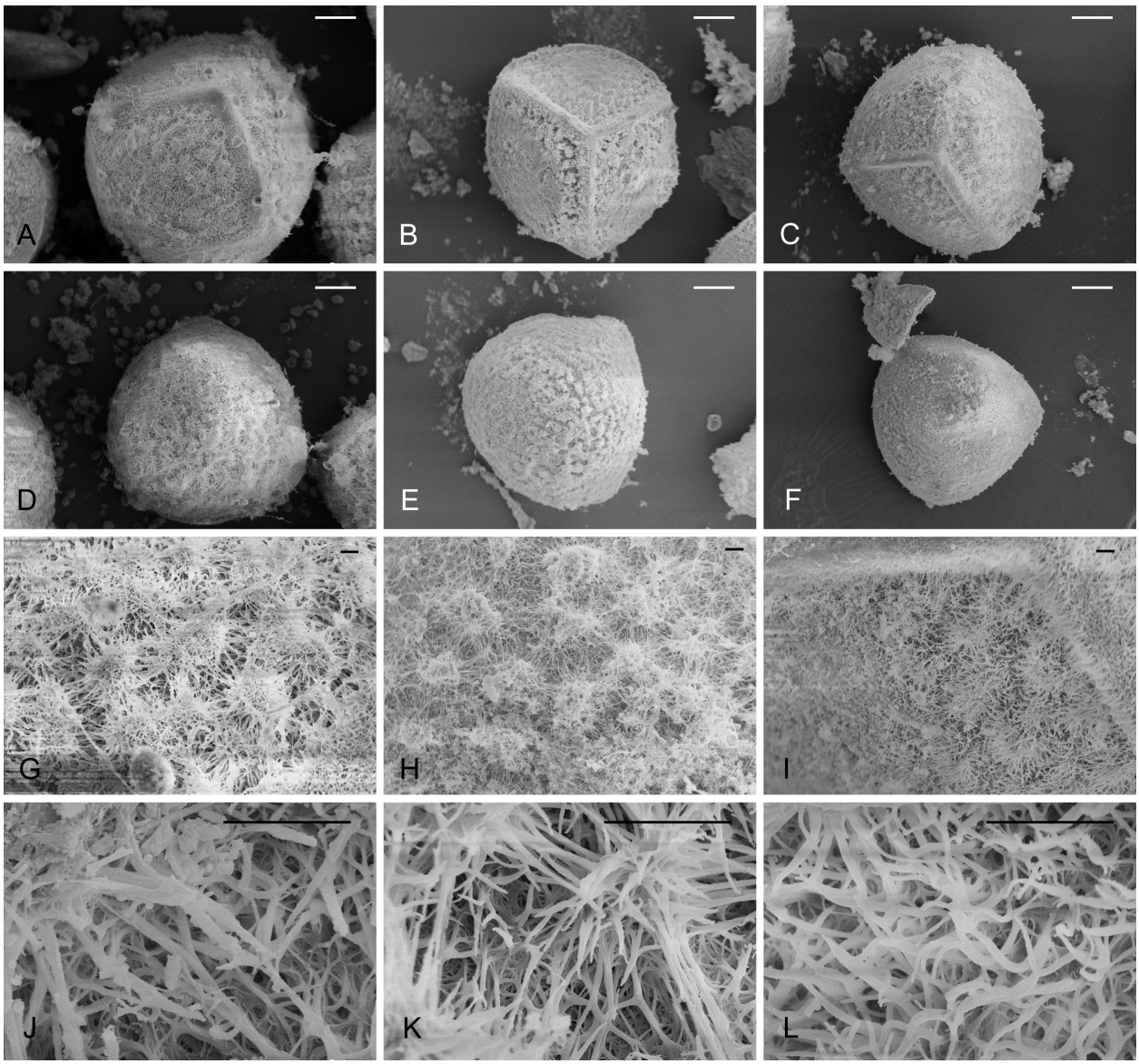

Fig. 1. SEM images of megaspores. – A, D, G, J: *Isoetes delilei* (B 20-108305); B, E, H, K: *I. haussknechtii* (B 20-97168); C, F, I, L: *I. heldreichii* (B 20-97363). – Scale bars: A–F = 100 µm; G–L = 10 µm.

not Heldreich). As declared on the original labels and in Wettstein's description, *I. heldreichii* was an aquatic species, growing under water throughout the year. Considering that it was collected submerged in July, one may confidently exclude that it belongs to the "amphibious" species.

The plant's original habitat, at Palaiokastro near Karditsa, was completely destroyed when the springs that fed it were intercepted to provide water for the nearby city of Karditsa. By consequence, and in view of the lack of gatherings of the species from other places, *Isoetes heldreichii* must be considered as extinct. Of course one can always hope that the species will one day be rediscovered, perhaps but not necessarily in some suitable place nearby. Such rediscovery has indeed been reported recently (Troia in Greuter 2012), but the notice was premature and is here disclaimed. The (preliminary) identification of a gathering from C Peloponnisos as *I. heldreichii* proved to be an error, as discussed under the following item.

"*Isoetes setacea*"

For this species as well, abundant material was collected and widely distributed. Some of the labels show Haussknecht's original, subsequently deleted identification as "*Isoetes velata*"; all bear Wettstein's determination (mentioned in his letter cited above), "*Isoetes setacea* Del.", which refers to the misapplication, by Delile, of the name *I. setacea* Lam. to the species correctly known as *I. delilei* Rothm. (see Greuter & Troia 2015 for detailed explanations). As *I. delilei* and Haussknecht's plant are different species (see below), Wettstein's use of misapplied "*I. setacea*" for the latter was in fact a second-

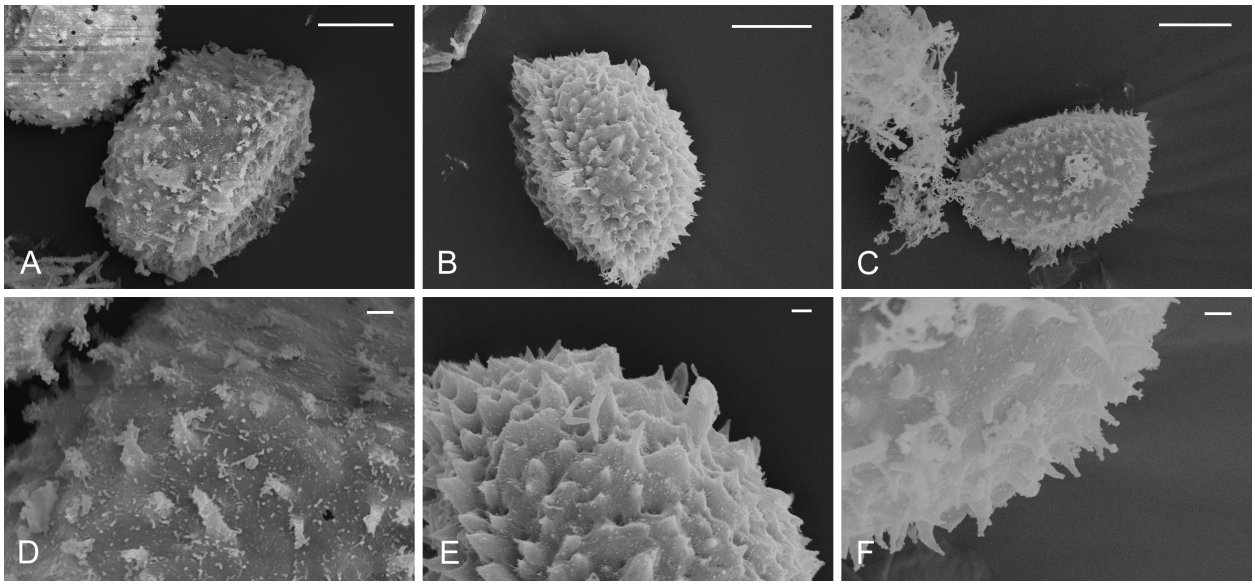

Fig. 2. SEM images of microspores. – A, D: *Isoetes delilei* (B 20-108305); B, E: *I. haussknechtii* (B 20-97168); C, F: *I. heldreichii* (B 20-97363). – Scale bars: A–C = 10 µm; D–F = 1 µm.

degree misapplication. But worse was to come. Jermy (1964) misapplied the name "*I. setacea*" to yet another, completely different species, *I. echinospora* Durieu; when that error was undone (Jalas & Suominen 1972), the Haussknecht record through some misunderstanding remained linked, not to *I. delilei* as had been the intent but to *I. echinospora.* Ever since, the immortal ghost of a Greek "*I. echinospora*" – a third-degree misapplication – pervades the relevant literature (Greuter & al. 1984; Derrick & al. 1987; Jermy & Akeroyd 1993; Dimopoulos & al. 2013). To close the circle, Christenhusz & Raab-Straube (2013) are now citing what is ultimately a single gathering twice under different, misapplied species names: "*I. echinospora*" and "*I. setacea*".

Isoetes delilei is a lowland species confined to the W Mediterranean area, and even though it is related to Haussknecht's Greek plant, both are different; the latter, in fact, has not yet been described. We shall name it *I. haussknechtii* after its discoverer Haussknecht, in partial compensation for the moral tort he suffered when *I. heldreichii* was named.

The single gathering on which Haussknecht's record is based was made at an altitude of about 1050 m on the high plateau (oropedio) of Nevropolis. It is hard to locate the collecting site with the aid of modern maps. When searching for the plant at its place of origin, in 1995 together with B. Zimmer, I (W. G.) was under the misapprehension that the Nevropolis plateau had been flooded after the construction of the Tavropos dam in 1960 and now lies at the bottom of the large artificial lake of Plastira; so we searched the border of that lake for possible suitable places. As the record of altitudes shows, this was an error: the Plastira lake level is less than 800 m. In reality, the Nevropolis plateau is situated to the west of the Plastira Lake, around the village of Neochori. That area does not appear to have been heavily affected by recent changes, except perhaps by the abandonment of traditional agro-pastural exploitation, so that there is a real chance that *Isoetes haussknechtii* may be rediscovered one day; and even if it should never again turn up in Thessalia, it is not an extinct species: it turned out that the plant gathered in C Peloponnisos and too hastily identified as *I. heldreichii* (see above) is in fact indistinguishable from *I. haussknechtii.* Moreover, we received from I. Bazos specimens from much lower altitudes on the NE Aegean island of Lesvos that also belong here; they were mentioned as "*Isoetes* sp." in Bazos & Yannitsaros (1999).

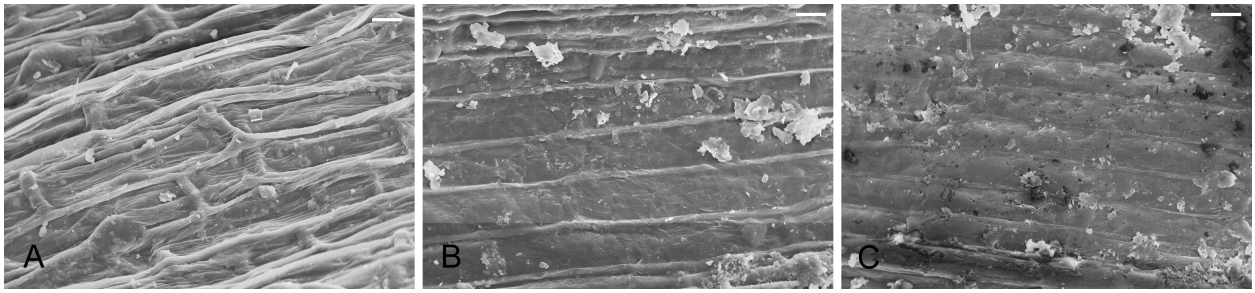

Fig. 3. SEM images of outer surfaces of leaf epidermal cells. – A: *Isoetes delilei* (B 20-108305); B: *I. haussknechtii* (B 20-97168); C: *I. heldreichii* (B 20-97363). – Scale bars: A–C = 10 µm.

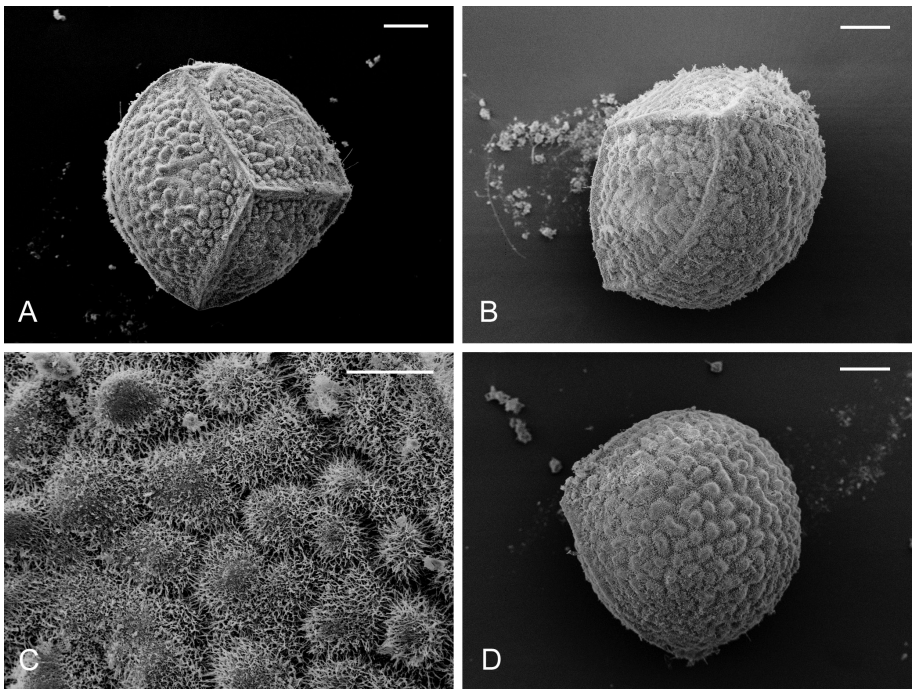

Fig. 4. SEM images of megaspores from Haussknecht's Greek gathering of "*Isoetes phrygia*", i.e., *Isoetes gymnocarpa* (JE). – A: proximal view; B: equatorial view; C: detail of the surface; D: distal view. – Scale bars: A, B, D = 100 µm; C = 30 µm.

Isoetes haussknechtii Troia & Greuter, **sp. nov.** – Fig. 1B, 1E, 1H, 1K, 2B, 2E, 3B.
Holotype (see p. 398 for details): PAL-Gr 49913; isotypes: B, BEO, BRNM, MA, SALA, UPA, W.

Descriptio — Herba perennis amphibia. *Cormus* trilobus, radicibus dichotomis. *Folia* 12–20(–40), (12–)25–40 cm longa, inferne membranaceo-alata, basi ad 3–4 mm, in media parte c. 1–2 mm lata; cuticula cellularum epidermalium laevis; lacunae in sectione transversali 4, magnae, fasciculi collenchymatosi fibrarum numerosi, peripherici; stomata elliptica. *Phyllopodia* desunt. *Velum* nullum. *Macrosporae* candidae, sphaeroideae, 450–570 µm diametro, annulo horizontali cinctae, hemisphaerio proximali tricostatae, undique tuberculatae. *Microsporae* ellipsoideae, 25–32 µm longae, echinato-cristatae.

Diagnosis — *Isoetes delilei* Rothm. cui proxima, tuberculis macrosporarum majoribus et minus numerosis nec non cuticula epidermidis foliorum longitudinaliter striulata differt; *I. heldreichii* Wettst. foliis brevioribus minus numerosis et habitu aquatico discedit; ambae vero microsporas aculeatas nec echinato-cristatas exhibent (tabula 1).

Description — Herbs perennial, amphibious. *Stem* (corm) trilobate, with dichotomous roots. *Leaves* 12–20(–40), (12–)25–40 cm long, 3–4 mm wide at base, 1–2 mm wide at mid-length, with wide membranous margin at base, margin gradually narrowed to disappear above sporangium level (at c. $^1/_5$ of total leaf length); epidermal cells smooth, without cuticular ornamentation, but anticlinal longitudinal cell walls bulging outward to form continuous, prominent ridges ("cuticular pegs" of Prada & Rolleri 2005); stomata elliptic; hypodermal collenchymatous bands mostly small but numerous; air chambers 4, with translacunar diaphragms. *Phyllopodia* absent, but 3–4 mm wide and 2–4 mm long triangular scales occasionally present. *Velum* none. *Megaspores* 450–570 µm (521 µm on average) in diam., white, densely covered on all faces with small warts or tubercles (composed of rodlets agglutinated into small tufts). *Microspores* 25–32 µm (30 µm on average) long, densely echinato-cristate.

Table 1. Comparison of some morphological, anatomical and ecological characteristics of *Isoetes delilei*, *I. haussknechtii*, and *I. heldreichii*. Diagnostic features are in bold.

	Isoetes delilei	***Isoetes haussknechtii***	***Isoetes heldreichii***
number of leaves	20–21(–60)	12–20(–40)	**7–10(–14)**
leaf length [cm]	33–38	(12–)25–40	**16–18**
leaf width [mm]	1–2	1–2	**1**
cuticula of leaf epidermis cells	**striate**	smooth	smooth
peripheral strands	yes	yes	yes
velum	no	no	no
megaspore diameter [µm]	505–641	450–570	340–570
megaspore ornamentation	**tuberculate**	densely tuberculate	densely tuberculate
microspore length [µm]	28–32	25–32	27–32
microspore ornamentation	aculeate	**echinato-cristate**	aculeate
habitat	amphibious	amphibious	**aquatic**

Note — The main differential features between the similar and presumably closely related species, *Isoetes setacea*, *I. haussknechtii*, and *I. heldreichii*, are set out in Table 1.

"*Isoetes phrygia*"

Haussknecht (1899) in his "Symbolae" upgraded Boissier's (1884) *Isoetes histrix* var. *phrygia* to species rank and applied the resulting binomial to the third of his Thessalian *Isoetes* gatherings. Regrettably, by an obvious oversight, he omitted the locality data for it and only mentioned the habitat: "in terra subhumida alveorum saxorum, *Junco bufonio*, *Radiolae linoidi* consociata". Furthermore, we did not find Greek specimens by Haussknecht or Heldreich labelled "*Isoetes phrygia*". There are however a few 1885 specimens labelled either "*Isoetes Hystrix DR.*" by Heldreich (WU 40155) or just "*Isoetes*" by Haussknecht (B 20-97381, JE), which do correspond with Haussknecht's "*Isoetes phrygia*" of the "Symbolae". There is threefold proof for that assessment: (1) this is the only 1885 *Isoetes* material not otherwise accounted for in the "Symbolae"; (2) the habitat mentioned on the JE label, "in humid. arenos. *Junc. bufon.* consociat.", is an abbreviated version of the "Symbolae" text; and (3) the single locality in which *Radiola linoides* Roth had been collected on that excursion (Haussknecht 1893: 60) coincides with the *Isoetes* locality: "Agrafa (Dolopia veterum): reg. inf. Pindi in oropedio Nevropolis, 3500'" – which, one will note, is the very locality of "*Isoetes setacea*", too.

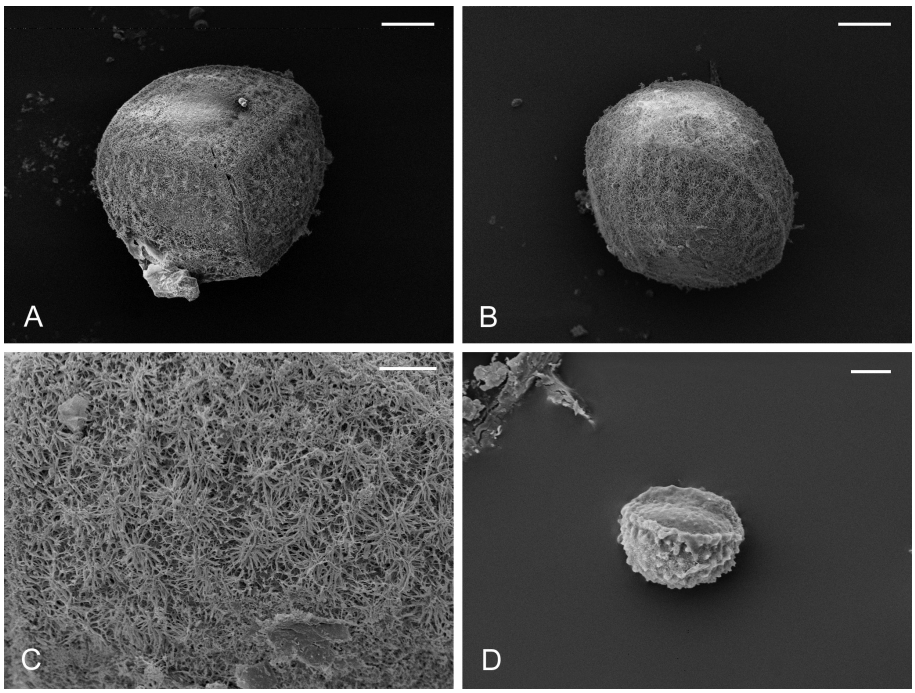

Fig. 5. SEM images of *Isoetes phrygia* spores (isotype, P 214771). – A: megaspore, proximal view; B: megaspore, equatorial view; C: megaspore, detail of the surface; D: microspore. – Scale bars: A, B = 100 µm; C = 30 µm; D = 10 µm.

The plants of that gathering belong to *Isoetes gymnocarpa*, a taxon that has been considered a mere variety, if not a plain synonym, of *I. histrix.* Boissier (1884), as noted above, referred the first Greek *Isoetes* records ever to the same taxon, using the name *I. histrix* var. *subinermis* for it; and we ourselves (in Greuter 2012) again reported it under the junior synonym *I. sicula.* As with *I. histrix* it is a terrestrial species provided with phyllopodia: black, indurate remains of dead leaves encircling the leaf rosette at its base; it also has megaspores similar to those of *I. histrix*, with pronounced verrucose ornamentation and a prominent equatorial girdle (Fig. 4). Contrary to *I. histrix* proper, however, the phyllopodia in *I. gymnocarpa* do not end in two lateral, subulate horns but in three irregularly triangular teeth of about the same length.

May we, then, conclude that Haussknecht's identification was basically correct and that *Isoetes phrygia* is another junior synonym of *I. gymnocarpa*? Indeed, with few exceptions, authors have generally considered Boissier's *I. histrix* var. *phrygia* as a synonym of either *I. histrix* (sensu lato) or *I. histrix* var. *subinermis*, and they could feel justified in so doing by the statement, in Boissier's protologue, that his new variety was characterized by phyllopodia ending in triangular teeth rather than subulate horns. Surprisingly, when looking at the original specimen in the Boissier herbarium and at its duplicates elsewhere, we found that Boissier's cited statement is plainly wrong: none of the plants collected by Balansa in Phrygia (in present-day WC Turkey) has phyllopodia at all! On the basis of this fact, and of the differences in megaspore ornamentation also mentioned in the protologue (megaspore with few inconspicuous tubercles, almost smooth, the transversal line all but obsolete – Fig. 5), we conclude that Boissier's gut feeling, "forsan species propria", was correct, that Haussknecht had been justified in raising the taxon to species rank, but that in so doing he had applied it to the wrong species.

Conspectus of Greek *Isoetes*

We list those synonyms and misapplied names under which Greek taxa appear in relevant basic literature: Boissier (1884), Haussknecht (1899), Halácsy (1904), Hayek (1924), Jermy (1964), Davis (1965), Jalas & Suominen (1972), Greuter & al. (1984), Derrick & al. (1987), Jermy & Akeroyd (1993), Dimopoulos & al.

(2013), and Christenhusz & Raab-Straube (2013), adding basionyms when appropriate. Misapplication statements refer only to records concerning Greece; p.p. (pro parte) is used when various Greek taxa are included under the same name. Recent floristic records are, non-exhaustively, mentioned under Notes when they can be interpreted with confidence.

Isoetes durieui Bory in Compt. Rend. Hebd. Séances Acad. Sci. 18: 1166. 1844. – Type: see Troia & Greuter (2014). – Jalas & Suominen (1972: 31); Greuter & al. (1984: 4); Derrick & al. (1987: 40); Jermy & Akeroyd (1993: 7); Bazos & Yannitsaros (1999: 425); Dimopoulos & al. (2013: 38); Christenhusz & Raab-Straube (2013).

Specimens seen — W Aegean Islands: Nom. Evvoia, Ep. Chalkis: between Prokopio and Pili, Strongylolakkas, valley near the chapel Ag. Triti, 38°44'50"N, 23°32'00"E, 80 m, 4 Apr 1995, *Greuter & Zimmer 24290* (B, PAL-Gr 46568, MEL). — C Aegean Islands: Nom. Kyklades: Andros, Ag. Simeon, in the village area, 37°56'N, 24°48'E, 400–500 m, 9 May 1991, *Snogerup & Snogerup 8020* (B 20-148468). — E Aegean Islands: Nom. Lesvos, Ep. Limnos: Ag. Efstratios, 3 km E of the harbour, 39°32'N, 25°01'E, 180 m, 19 May 1988, *Snogerup & Snogerup 5820* (B 20-92131). — S Aegean Islands: Nom. Dodekanisos: Karpathos, Lastos, 35°34'30"N, 27°08'30"E, 720 m, 1 Apr 1998, *Böhling & Raus 7416* (B 20-131564 p.p.).

Note — Terrestrial. First collected in Greece (W Aegean islands, Evvoia) by W. Ludwig in 1957 or 1958 (Rechinger 1961: 302; Krause & al. 1963: 375), where it may form mixed stands with *Isoetes gymnocarpa* on ophiolithic schists. It appears to be scattered throughout the Aegean archipelago, having been furthermore reported from Kriti (Böhling & Raus in Greuter & Raus 2000: 229; Bergmeier & Abrahamczyk 2008: 443; Bergmeier 2011: 171), Samothraki in the N Aegean (Akeroyd & Preston 1987: 352) and Lesvos in the E Aegean (Bazos & Yannitsaros 1999: 425, with map); but to our knowledge it has not as yet been collected on the Greek mainland. Not mapped; see map in Akeroyd & Preston (1987).

Isoetes gymnocarpa (Gennari) A. Braun in Monatsber. Koenigl. Preuss. Akad. Wiss. Berlin 1863: 555. 1864 ≡ *Cephaloceraton gymnocarpum* Gennari in Comment. Soc. Crittog. Ital. 1: 113. 1862. – Type: see Troia & Greuter (2014). – Christenhusz & Raab-Straube (2013).

= *I. histrix* var. *subinermis* (Gennari) Motelay & Vendryès in Actes Soc. Linn. Bordeaux 36: 400. 1883 ≡ *Cephaloceraton histrix* var. *subinerme* Gennari in Comment. Soc. Crittog. Ital. 1: 112. 1862 ≡ *I. histrix* f. *subinermis* (Gennari) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 12. 1924. – Type: see Troia & Greuter (2014). – Boissier (1884: 748); Halácsy (1904: 481); Hayek (1924: 12); Davis (1965: 38).

= *I. sicula* Tod. in Giorn. Sci. Nat. Econ. Palermo 1: 251. 1866. – Neotype: see Troia & Greuter (2014). – Troia in Greuter (2012: 24); Dimopoulos & al. (2013: 38).

– "*I. phrygia*" sensu Haussknecht (1899: 72); Hayek (1924: 13).

– "*I. histrix* var. *phrygia*" sensu Halácsy (1904: 481).

– "*I. histrix*" sensu Jermy (1964: 6 p.p.); Jalas & Suominen (1972: 31 p.p.); Greuter & al. (1984: 4 p.p.); Derrick & al. (1987: 40 p.p.); Jermy & Akeroyd (1993: 7 p.p.); Bazos & Yannitsaros (1999: 425–427 p.p.); Dimopoulos & al. (2013: 38 p.p.).

Specimens seen — Peloponnisos: Nom. Achaia, Ep. Patra: sea shore S of Kalogria, 38°09'05"N, 21°22'10"E, 2–5 m, 15 Jun 1995, *Kamari & al. 2626* (B, PAL-Gr 53626, SALA, UPA); ibid., Loutra Kounoupeli (SW of Patra), 38°05'40"N, 21°20'20"E, 29 Apr 1996, *Raabe* (B 20-122868). — C Greece: Nom. Aitoloakarnania, Ep. Nafpaktos: by the coast 1 km W of Andirrio, 38°20'N, 21°45'E, 0–1 m, 1 May 1996, *Nielsen 11065* p.p. (B 20-121323 p.p.). — Thessalia: Nom. and Ep. Karditsa: Agrafa (Dolopia veterum): in oropedio Nevropolis regionis inferioris Pindi, c. 39°17'N, 21°43'E, 3500', 23 Jun 1885, *Heldreich* (WU 40155); ibid., 24 Jun 1885, *Haussknecht* (JE); ibid., 3000', Jun 1885, *Haussknecht* (B 20-97381 [lower half]). — Thraki: Nom. Evros, Ep. Soufli: 1 km S of Dadia, 41°07'20"N, 26°13'E, 100 m, 13 Jun 1992, *Greuter & al. 23295* (B 20-97377, PAL-Gr 45661). — W Aegean Islands: Nom. Evvoia, Ep. Chalkis: between Prokopio and Pili, Strongylolakkas, valley near the chapel Ag. Triti, 38°44'50"N, 23°32'00"E, 80 m, 4 Apr 1995, *Greuter & Zimmer 24292* (B, PAL-Gr 46570, MEL). — C Aegean Islands: Nom. Kyklades: island of Paros, Kolympithres, 2 km W of Naousa, 37°07'30"N, 25°12'40"E, 10 m, 22 Apr 1991, *Raus & Schiers 15996* (B 20-148469 p.p., FI). — E Aegean Islands: Nom. Lesvos, Ep. Mithymna: Lesvos, c. 3.5 km N of Kalloni, 39°15'15"N, 26°12'45"E, 110 m, 25 Feb 1995, *Bazos 2062* (herb. Bazos); ibid., near Moni Limonos NW of Kalloni, 39°14'50"N, 26°10'26"E, 140 m, 25 Feb 1995, *Bazos 2069* (PAL-Gr); ibid., NNE of the Petrified Forest Park, 39°13'22"N, 25°54'58"E, 310 m, 6 May 1999, *Bazos 3755* (herb. Bazos); Ep. Mytilini: Lesvos, between Agiasos and Vasilika, Mikri Limni, 39°06'36"N, 26°15'56"E, 210 m, 16 May 1995, *Bazos 2421* (herb. Bazos); ibid., c. 10 km SE of Mantamados, near the road to Mytilini, 39°15'13"N, 26°24'41"E, 20 m, 6 Apr 1998, *Bazos 3129* p.p. (herb. Bazos). — S Aegean Islands: Nom. Dodekanisos: Karpathos, Lastos, 35°34'30"N, 27°08'30"E, 720 m, 1 Apr 1998, *Böhling & Raus 7416* (B 20-131564 p.p.).

Note — Terrestrial. The most widespread *Isoetes* species in Greece (Fig. 6). Apparently, most Greek records of the (much rarer) *Isoetes histrix* refer to *I. gymnocarpa*. However, the exact distribution of both species in Greece remains unknown until a much wider range of material

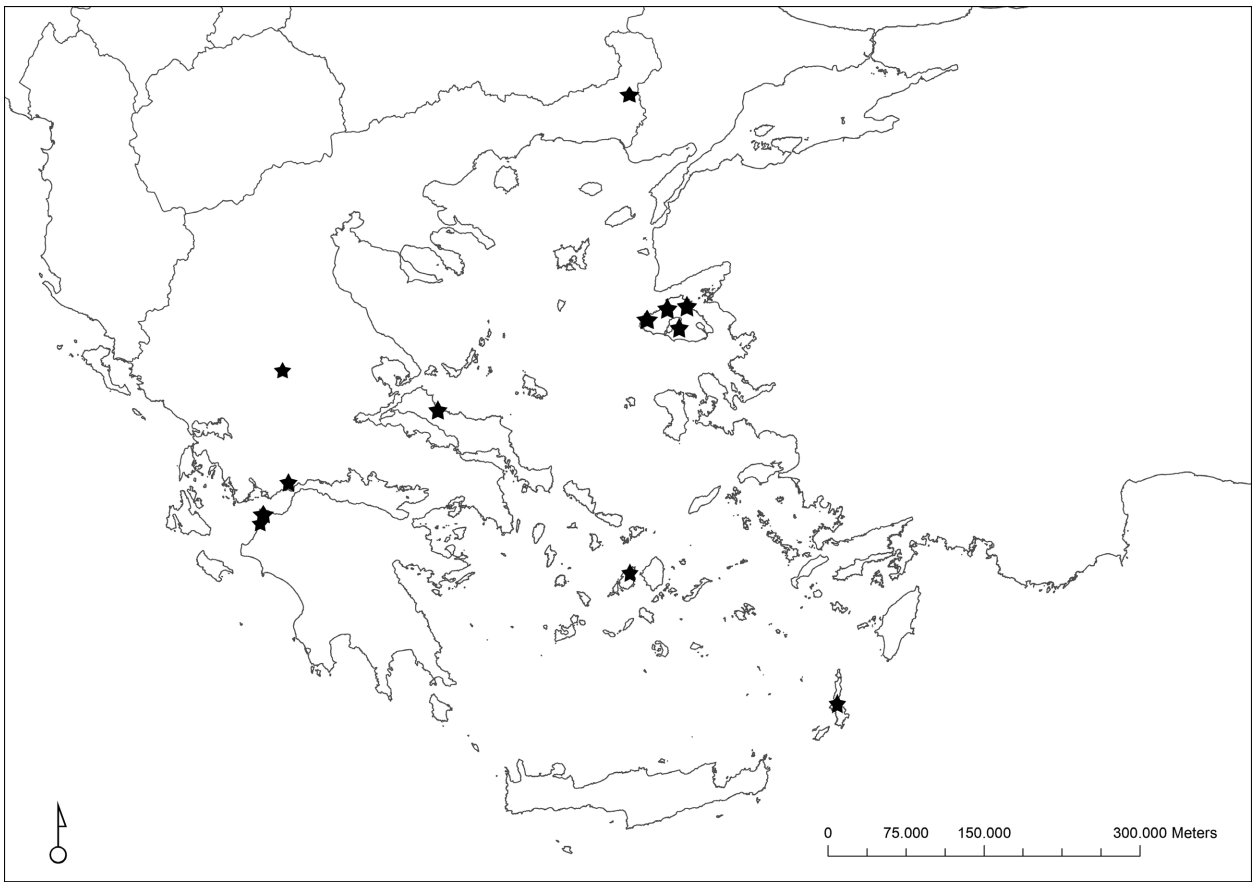

Fig. 6. Map of the Greek distribution of *Isoetes gymnocarpa,* based on verified specimens.

is revised. In particular, no material from the Ionian Islands has yet been seen, from where both *I. histrix* var. *subinermis* (Boissier 1884: Zakynthos; Festi & Prosser 2008: Kerkyra) and genuine *I. histrix* (Halácsy 1904 and several subsequent authors: Kerkyra) have been reported; *I. gymnocarpa* is the more likely taxon to occur there, but *I. todaroana* is also a possibility – or perhaps both may occur. It is very likely that the report of "*I. phrygia*" from the FYR Makedonija (Micevski 1985), being based on the treatment of Hayek (1924) and thus referring to a plant with shortly toothed phyllopodia, also belongs here.

Isoetes haussknechtii Troia & Greuter – see p. 395.

– "*I. setacea*" sensu Haussknecht (1899: 72); Halácsy (1904: 481); Hayek (1924: 12); Christenhusz & Raab-Straube (2013).
– "*I. echinospora*" sensu Jalas & Suominen (1972: 28); Greuter & al. (1984: 4); Derrick & al. (1987: 40); Jermy & Akeroyd (1993: 6); Dimopoulos & al. (2013: 38); Christenhusz & Raab-Straube (2013).
– "*I. heldreichii*" sensu Troia in Greuter (2012: 23); Dimopoulos (2013: 38 p.p.).
– "*Isoetes* sp.", Bazos & Yannitsaros (1999: 427).

Specimens seen — Peloponnisos: Nom. Arkadia, Ep. Mantineia: 6 km NNE of Tripoli, Tripoli-Pyrgos road, by the branching of the road to Nestani, 37°33'30"N, 22°24'10"E, 650 m, 31 May 1995, *Kamari & al. 322* (PAL-Gr 49913 [holotype], B, BEO, BRNM, MA, SALA, UPA, W [isotypes]). — Thessalia: Nom. and Ep. Karditsa: Agrafa (Dolopia veterum): in uliginosis oropedii Nevropolis regionis inferioris Pindi, c. 39°17'N, 21°43'E, 3500', 5 Jul 1885, *Heldreich* Herb. Graec. Norm. 899 (B 97168, P 6141706, PAL 20468, WU 40156); ibid., "Jun" 1885, *Haussknecht* (JE, P 1255148). — E Aegean Islands: Nom. Lesvos, Ep. Mytilini: Lesvos, between Agiasos and Vasilika, Mikri Limni, 39°06'36"N, 26°15'56"E, 210 m, 25 May 1994, *Bazos 1747* (PAL-Gr); ibid, c. 5 km WNW of Lampou Myloi, 39°09'50"N, 26°22'04"E, 215 m, 11 Apr 1995, *Bazos 2125* (PAL-Gr); ibid., 13 May 1995, *Bazos 2336* (herb. Bazos); ibid., 11 May 2014, *Bazos & Zervou 4642* (PAL-Gr).

Note — Amphibious. See above for details. Map: Fig. 7.

Isoetes heldreichii Wettst. in Verh. K.K. Zool.-Bot. Ges. Wien 36: 269. 1886. – **Lectotype (designated here):** WU 31761 [details below]. – Haussknecht (1899: 72); Halácsy (1904: 481); Hayek (1924: 12); Jermy (1964: 6); Jalas & Suominen (1972: 30); Greuter & al. (1984: 4); Derrick & al. (1987: 40); Jermy & Akeroyd (1993: 6); Dimopoulos & al. (2013: 38); Christenhusz & Raab-Straube (2013).

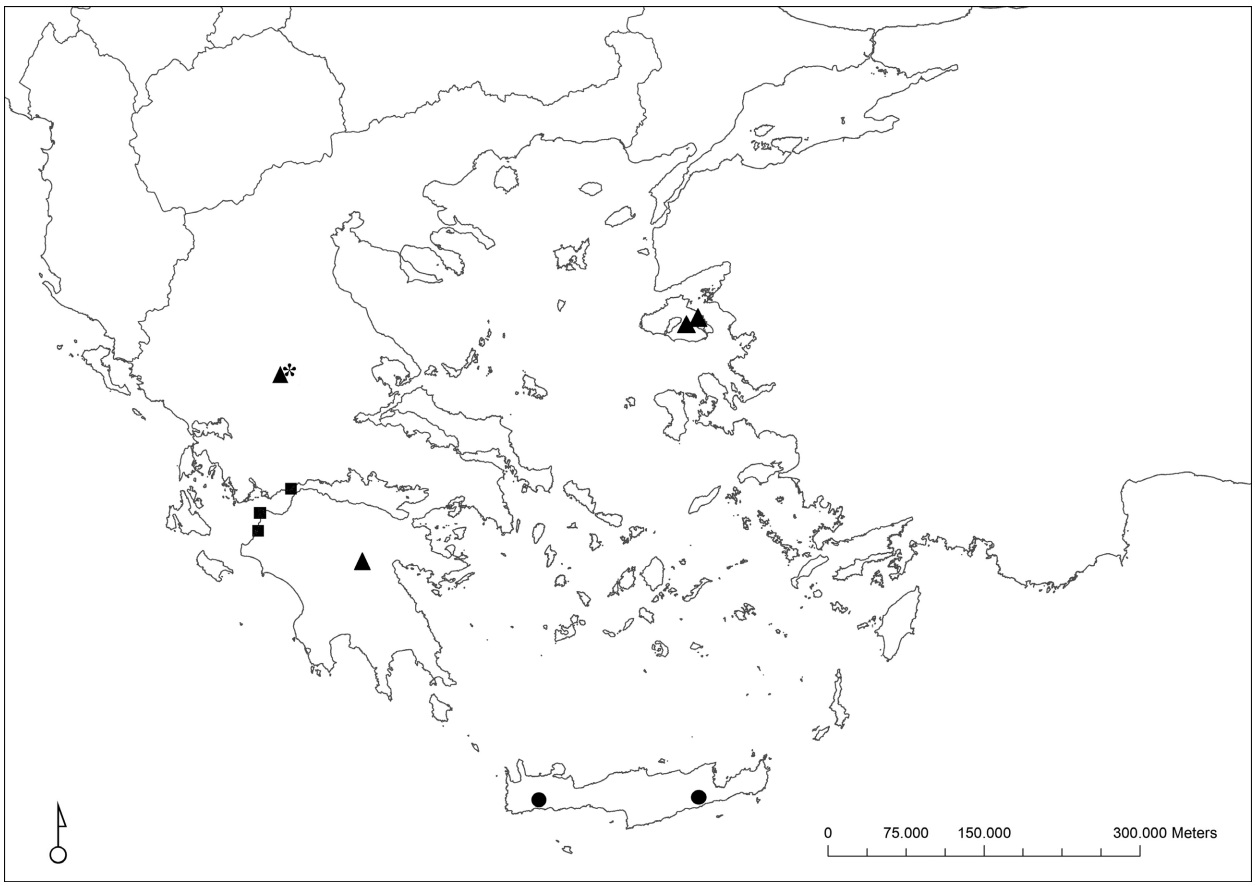

Fig. 7. Map of the Greek distribution of *Isoetes* species, based on verified specimens – ✻: *I. heldreichii* (presumed extinct); ▲: *I. haussknechtii*; ●: *I. phrygia*; ■: *I. todaroana.*

Specimens seen — Thessalia: Nom. and Ep. Karditsa: in uliginosis prope Palaiokastro [planitiei Karditsa / ad Pindi radices], "Jun"/Jul 1885, 39°20'N, 21°49'E, *Haussknecht* (B 20-97128, -97361 to -97364, -136491, JE 7330 to 7332, WU 40157); ibid., prope Karditsa in palude prope Palaiokastro, 10 Jul 1885, *Heldreich* (B 20-97359, -97360, -136490, WU 31761 [lectotype], 31762).

Note — Aquatic. A local endemic. Presumed extinct. Map: Fig. 7.

Isoetes histrix Bory in in Compt. Rend. Hebd. Séances Acad. Sci. 18: 1167. 1844. – Type: see Troia & Greuter (2014). – Halácsy (1904: 480); Jermy (1964: 6 p.p.); Jalas & Suominen (1972: 31 p.p.); Greuter & al. (1984: 4 p.p.); Derrick & al. (1987: 40 p.p.); Jermy & Akeroyd (1993: 7 p.p.); Bazos & Yannitsaros (1999: 425–427 p.p.); Dimopoulos & al. (2013: 38 p.p.); Christenhusz & Raab-Straube (2013 p.p.).

Specimens seen — C Aegean Islands: Nom. Kyklades: island of Paros, Kolympithres, 2 km W of Naousa, 37°07'30"N, 25°12'40"E, 10 m, 22 Apr 1991, *Raus & Schiers 15996* (B 20-148469 p.p.); ibid., Naxos, Ilias, 37°02'43"N, 25°27'10"E, 210–230 m, 25 Apr 1995, *Böhling* (B 20-124740). — E Aegean Islands: Nom. Lesvos, Ep. Mytilini: Lesvos, c. 10 km SE of Mantamados, near the road to Mytilini, 39°15'13"N, 26°24'41"E, 20 m, 6 Apr 1998, *Bazos 3129* p.p. (herb. Bazos). — S Aegean Islands: Kriti, Nom. Chania, Ep. Kissamos: [without locality], 12 Mar 1884, *Reverchon* in Baenitz, Herb. Eur. (FI); ibid., [*Reverchon*, lacking data, ex herb.] Fritze (B 20-24327).

Note — Terrestrial. Apparently rare in Greece, known with certainty only from the C, E and S Aegean Islands; to be looked for elsewhere. Most Greek records of "*Isoetes histrix*" verified by us so far belong to *I. gymnocarpa.* Bazos & Yannitsaros (1999) gave a detailed account of the distribution of *I. histrix* in Greece, mapping its Aegean portion, but these data likely, for the most part, belong to *I. gymnocarpa*. Not mapped.

Isoetes phrygia (Boiss.) Hausskn. in Mitth. Thüring. Bot. Vereins, ser. 2, 13–14: 72. 1899 ≡ *I. histrix* var. *phrygia* Boiss., Fl. Orient. 5: 748. 1884. – **Lectotype (designated here):** collines rocheuses dominant le village de Kaïageul, à 2 lieues au SO d'Ouchak (Phrygie), 30 May 1857, *Balansa*, Pl. d'Orient 1327 (G-BOIS 330495; isolectotypes: G 430491, 430492, NAP, P 214770, 214771).

– "*Isoetes velata*" sensu Dimopoulos (2013: 38); Christenhusz & Raab-Straube (2013).

Specimens seen — S Aegean Islands: Kriti, Nom. Chania, Ep. Selinos: plateau d'Omalos, 35°20'45"N, 23°54'20"E, c. 1100 m, 18 May 1993, *Deschatres* (PAL-Gr 38924); Nom. Iraklio, Ep. Viannos: Limni Omalou, SO-Teil der Omalos-Ebene, 35°04'13"N, 25°27'22"E, 1330 m, 24 Jun 2010, *Bergmeier 10-202* (herb. Bergmeier).

Notes — Amphibious. Apparently first collected on the [western] Omalos plain by Dutartre in April (fide Deschatres in schedis) then by Deschatres in May 1983, provisionally identified as "*Isoetes velata*" and sent for verification to C. Prada, with unknown result. Some plants, lacking spores, grew submerged at a depth of 20–30 cm; other, fertile ones, on the shore of the pond (label information). The same species was found on the [eastern] Omalos plain, in 1997, by Böhling, and later by others (Böhling & al 2002: 70, without locality; Bergmeier 2011: 171–172; both as "*I. velata*"). In Greece (and perhaps also in Phrygia) it is apparently confined to a characteristic habitat: temporary ponds at the bottom of mountain poljes, at elevations between 1000 and 1300 m. Map: Fig. 7.

Isoetes velata A. Braun is an illegitimate name; the correct name for the species thus known is *I. longissima* Bory (Troia & Greuter 2014). That species is apparently absent from the E Mediterranean countries. Dimopoulos & al. (2013) also reported the presence of "*I. velata*" in the C Aegean Islands (Kyklades), but as long as we have not checked the basis for that record we have to dismiss it.

Isoetes phrygia is easily distinguishable from similar *Isoetes* species by combining absence of phyllopodia and velum with minutely tuberculate (almost smooth) megaspores with an indistinct equatorial girdle (Fig. 5). Having examined the respective types we can confirm the distinctness of *I. phrygia*, not only from the velum-bearing *I. longissima* but also from the more similar *I. olympica* A. Braun from the Bithynian Olympus (Uludağ in NW Turkey) and *I. libanotica* Musselman & al. from Mt Lebanon.

Isoetes todaroana Troia & Raimondo in Amer. Fern J. 99: 238. 2010. – Type: see Troia & Raimondo (2010). – No previous Greek records are known.

Specimens seen — Peloponnisos: Nom. Achaia, Ep. Patra: an der Küste zwischen Brinia und Manolada, b[ei]. Brinia, 38°02'30"N, 21°20'20"E, 15 May 1995, *Raabe* (B 20-122031); ibid., Kalogria beach bei Araxos, Viehweiden an der Straße nach Metochi, 38°07'30"N, 21°23'10"E, 28 Apr 1994, *Raabe* (B 20-122032). — C Greece: Nom. Aitoloakarnania, Ep. Nafpaktos: by the coast, 1 km W of Andirrio, 38°20'N, 21°45'E, 0–1 m, 1 May 1996, *Nielsen 11065* p.p. (B 20-121323 p.p.).

Note — Terrestrial. The distinction from *Isoetes gymnocarpa*, which sometimes grows in closely contiguous populations, is not always easy, because the phyllopodia that characterize the latter species are not always evident. *Isoetes todaroana* was described from Sicily (Troia & Raimondo 2010), but *I. iapygia* Ernandes & al. (2010) from S Italy, which we once provisionally treated as distinct (Troia & Greuter 2014), we now (Troia & Greuter 2015) consider as its synonym, thus bridging the apparent chorological gap. Map: Fig. 7.

A key to Greek *Isoetes* species

1. Plants with numerous hardened, persistent black phyllopodia on top of the corm and around the leaf bases **2**
– Plants without phyllopodia (but sometimes with seasonal, non-hardened scales) **4**
2. Phyllopodia with 3–10 mm long lateral spine-like teeth, without (or with reduced) central tooth . . . . . ***I. histrix***
– Phyllopodia with 3 irregular small teeth of similar length **3**
3. Megaspore >600 µm in diam., with alveolate ornamentation . . . . . ***I. durieui***
– Megaspore <500 µm in diam., with tuberculate ornamentation . . . . . ***I. gymnocarpa***
4. Plants aquatic (permanently submerged); leaves 7–10 (–14), >10 cm long on average . . . . . ***I. heldreichii***
– Plants terrestrial or amphibious (temporarily submerged during the wet season); leaves either shorter or more numerous (12–20 or more) **5**
5. Plants tall; leaves >10 cm long on average and 1–2 mm wide at mid-length; microspores echinate-cristate . . . . . ***I. haussknechtii***
– Plants dwarf; leaves <10 cm long on average and <1 mm wide at mid-length; microspores echinate . **6**
6. Mature sporangium not covered by a velum; leaf with 4 air chambers; megaspores with small tubercles and an indistinct equatorial girdle . . . . . ***I. phrygia***
– Mature sporangium covered by a velum; leaf with 2 air chambers; megaspore prominently tuberculate and with well-marked equatorial girdle . . . . ***I. todaroana***

Discussion

Isoetes species have the well-deserved reputation of presenting few and not always reliable features with diagnostic potential. This situation has improved to some degree thanks to studies of the fine, often ultrastructural details of leaves and spores (Hickey 1986; Musselman 2003; Rolleri & Prada 2007). As a result, several new *Isoetes* species have been described in recent years that could not be diagnosed previously. For the purpose of studying Greek *Isoetes* taxa we resorted to SEM analysis, but only to a limited extent. We found that other, classically used features, more easily observed for practical purposes, retain their value. The following considerations apply more particularly to the three similar species, *I. delilei*, *I. haussknechtii* and *I. heldreichii*, but are also valid by analogy for other cases.

Macromorphology — Leaf size and number proved useful to discriminate between *Isoetes heldreichii*, a small plant with relatively few, short and thin leaves, and larger species like *I. haussknechtii* and *I. delilei* (see Table 1). These differences were used by Wettstein (1886) to distinguish his new *I. heldreichii* from the Nevropolis plants that he referred to "*I. setacea*", in spite of their obvious similarities.

Leaf epidermis — Rolleri & Prada (2007) made a comparative study of outer surfaces of leaf epidermis for a considerable number of species, including *Isoetes delilei* (their "*I. setacea*"). They found epidermal surface features to provide good diagnostic characters at species level and commended their inclusion in taxonomic descriptions. Our study confirmed their findings for *I. delilei* (l.c. 2007: fig. 3E), which presents fine, parallel longitudinal striae on the outer cell surfaces, between the continuous prominent ridges that crown the longitudinal anticlinal cell walls. In contrast, in *I. haussknechtii* and *I. heldreichii* the longitudinal ridges are less prominent and the cuticular surface between them is virtually smooth (Fig. 3).

Leaf cross section — We found that the leaves of *Isoetes haussknechtii* have smaller air chambers, with thicker walls, than those of *I. delilei,* in which the air chambers are large and thin-walled. The variability of this feature within and between populations and around the seasonal cycle remains to be tested. According to Budke & al. (2005: 177), lacunar wall thickness is potentially correlated with habitat. The presence, number and arrangement of peripheral fibres have been considered diagnostic by, e.g. Pfeiffer (1922) and Prada & Rolleri (2003), but not by all authors. The presence of fibres seems to be correlated with habitat preferences (Pfeiffer 1922, Takamiya & al. 1997): aquatic species usually lack mechanical support tissue, which is well developed in terrestrial and amphibious species.

Spore size and texture — Even today, identification of *Isoetes* species largely rests on megaspore and microspore ornamentation and size (Pfeiffer 1922; Hickey 1986; Macluf & al. 2006). Megaspore and microspore dimensions of *I. haussknechtii*, *I. heldreichii* and *I. delilei* are similar; our measurements for the latter agree with those of Berthet & Lecocq (1977) for the same species. All three species are also similar as to megaspore ornamentation, even though there are small differences in the size and density of the tubercles (Fig. 1, Table 1). However, microspore ornamentation provides a clear difference between *I. haussknechtii*, with a cristate or echinato-cristate pattern, and *I. delilei* or *I. heldreichii* with aculeate microspores (Fig. 2).

Taxonomy — We do not venture to suggest affinities of Greek *Isoetes* taxa among themselves and with other species. Owing to frequent parallel or convergent evolution in the genus (Hickey 1986; Taylor & Hickey 1992), it is risky to form an opinion on species relationship based on anatomy and morphology alone. In this genus perhaps more than in any other, DNA sequence analysis alone may, in the future, permit us to speculate soundly on phylogenetic pathways and patterns.

Conclusions

Knowledge of Greek *Isoetes* started late. First came Boissier's (1884) record of *I. gymnocarpa* (as *I. histrix* var. *subinermis*), not based on material verified by himself. Haussknecht (1899) raised the species total to three: *I. gymnocarpa* (as "*I. phrygia*"), *I. heldreichii* (described previously by Wettstein 1886), and *I. haussknechtii* (as "*I. setacea*", later to become "*I. echinospora*"). Halácsy (1904) added *I. histrix*, Rechinger (1961) *I. durieui*, Böhling & al. (2002) *I. phrygia* (as "*I. velata*"). The recent Greek checklist of Dimopoulos & al. (2013), by consequence, lists six *Isoetes* species, but only half of them under their correct name. Christenhusz & Raab-Straube (2013) even reach a total of seven, by listing the same species (*I. haussknechtii*) under two different misapplied names ("*I. echinospora*" and "*I. setaca*").

The present revision brings the Greek species total to seven, by adding *Isoetes todaroana*, and establishes the correct names for three formerly misnamed species: *I. gymnocarpa* ("*I. phrygia*", "*I. histrix*" auct. p.p., *I. histrix* var. *subinermis*, *I. sicula*), *I. phrygia* ("*I. velata*"), and the newly described *I. haussknechtii* ("*I. setacea*", "*I. echinospora*", "*I. heldreichii*"). The narrow-endemic *I. heldreichii*, the single truly aquatic Greek representative of the genus, must unfortunately be considered extinct. *I. delilei* ("*I. setacea*"), *I. echinospora* and *I. longissima* (*I. velata*) are to be definitely excluded from the flora of Greece: nor do they occur elsewhere in the E Mediterranean area and the Balkan Peninsula – noting that the former Bulgarian record of *I. echinospora* has been shown to be an error for *I. lacustris* L. (Stefanova & Ivanova 2000).

Isoetes species are still among the most severely undercollected members of the Greek flora. Even though several recent collections have come to our attention, we are convinced that the currently known distributional patterns are far from complete and that many new area records, perhaps even further additional species can and will be added in the future. Also, new observations on habitat preferences are to be encouraged, as the traditional distinction between aquatic, amphibious and terrestrial habit is not always clear, being mostly inferred on the base of label data. The definitions we have been using should be tested for their validity in practice. We have considered aquatic those species that live and set spores consistently in the submerged state; amphibious those that depend on a periodically flooded habitat, although they become fertile more often (or exclusively?) when that habitat falls dry; and terrestrial those that, while tol-

erating temporary flooding, do not depend on it and usually keep their leaves aerial throughout their period of vegetation.

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