

The genus *Pilularia* L. remains relatively poorly known, although recent work on its phylogenetic position (Nagalingum *et al.* 2008) as well as the function and structure of spores in this heterosporous genus (Schneider & Pryer 2002) have improved our understanding of its diversity and relationships. The exact number of species is not certain; currently five or less are recognized (Large & Braggins 1989; Nagalingum *et al.* 2008).

The first record of the genus in southern Africa—identified tentatively as *P. americana* A. Braun on the basis of both vegetative and sexual characters—was collected from Nieuwoudtville on the Bokkeveld Escarpment in 2001, at an altitude of \pm 800 m. There, *P. americana* grows immersed and emergent on the periphery of seasonal pans, in a region receiving winter/spring rainfall of 500–650 mm per annum (Roux 2002). During April 2010, a second collection of this cryptic genus, representing a novel species, was gathered from tarns in the southern Drakensberg of KwaZulu-Natal, at more than twice the Bokkeveld altitude, and over 1 000 km distant. This latest collection is of a diminutive species, significantly smaller than *P. americana* in many vegetative and sexual respects, and with an ecological requirement of perennial submersion in deep, sandstone tarns. Circinate vernation is not obvious in either taxon known from South Africa. This is in contrast to North American material of *P. americana* in which circinate vernation is reported to be a prominent character (Johnson 2010). Roux (2002) neither described nor illustrated this inward coiling feature of the frond for the Nieuwoudtville plants, unlike Cook (2004), whose illustration and text was presumably based on extra-South African material.

Fresh samples were viewed in water, using a Nikon AZ100 microscope. Longitudinal views through megaspores were obtained on a Nikon 80i microscope, using 1 μ m toluidene blue-stained sections of material embedded in epoxy resin, using standard procedures. Light microscope images and measurement data were acquired using NIS Elements D software (Nikon, Japan). For scanning electron microscopy (SEM), samples were fixed chemically, dehydrated in a graded ethanol series and dried using hexamethyldisilazane (SPI Supplies, US), mounted on stubs using double-sided carbon tape and rendered conductive by sputter coating with

gold. Samples were viewed using a LEO 1450 SEM (Carl Zeiss, Germany).

Pilularia dracomontana N.R. Crouch & J. Wesley-Smith, sp. nov., *P. americanae* A. Braun similis sed sporocarpis minoribus solum 3–5 megasporas in quoque soro continentibus, acrolamella proportione valde longiori, foliis etiam brevioribus (usque ad 14 mm, non 15–100 mm longis), sine vernatione manifeste circinata, internodiis brevioribus (usque ad 4.2 mm, non 30 mm), differt. *Pilularia dracomontana* a speciebus omnibus aliis generis sporocarpia in plantis immersis, non emerisis nec emergentibus pariendo, differt.

TYPE.—KwaZulu-Natal: 2929 (Underberg): Cobham, growing submerged in a sandstone tarn above Lakes Cave, 2 160 m, (–CB), 1 April 2010, N. Crouch 1268 (PRE, holo., NH, iso.).

Plants aquatic, mat-forming. *Rhizome* filiform, creeping, irregularly branched, up to 0.24 mm diam., set with 1–5 roots at nodes, internodes (1.47–)2.70(–4.2) mm long, initially sparsely hairy, glabrous with age, mostly with a few hairs at frond base, hairs up to 5 cells long. *Fronde* borne singly at nodes, erect, simple, setiform, (8.9–)11.98(–13.66) mm long, basally with few laterally attached, 3-celled hairs, glabrous apically. *Sporocarp* subterranean, globose, (1.49–)1.58(–1.7) mm diam., laterally attached, cream-coloured and densely hairy when young, atrocastaneous and sparsely hairy when mature, hairs up to 5 cells long, appressed; sporocarps 4-locular, dehiscing into 4 valves, each locule with a single sorus containing micro- and megasporangia; sporocarp pedicel arising from node on rhizome, up to 1.43 \times 0.21 mm, produced laterally. *Microsporangia* clavate, several per sorus, wall one cell layer thick, hyaline, each bearing 28–32 microspores. *Microspores* trilete, circular in polar view, elliptic in equatorial view, laesurae short, perispore hyaline, much larger than spore, episporium densely rugulate, (44.23–)49.88(–53.41) μ m diam. at equator and (36.03–)42.25(–51.95) μ m diam. at poles, pseudo-endospore (intine) evident below exine layer. *Megasporangia* ellipsoid, wall one cell layer thick, hyaline, 3–5 per sorus (12–19 per sporangium), each bearing a single megaspore. *Megasporae* spherical in polar, and broadly elliptic in lateral view, with prominently ridged acro-

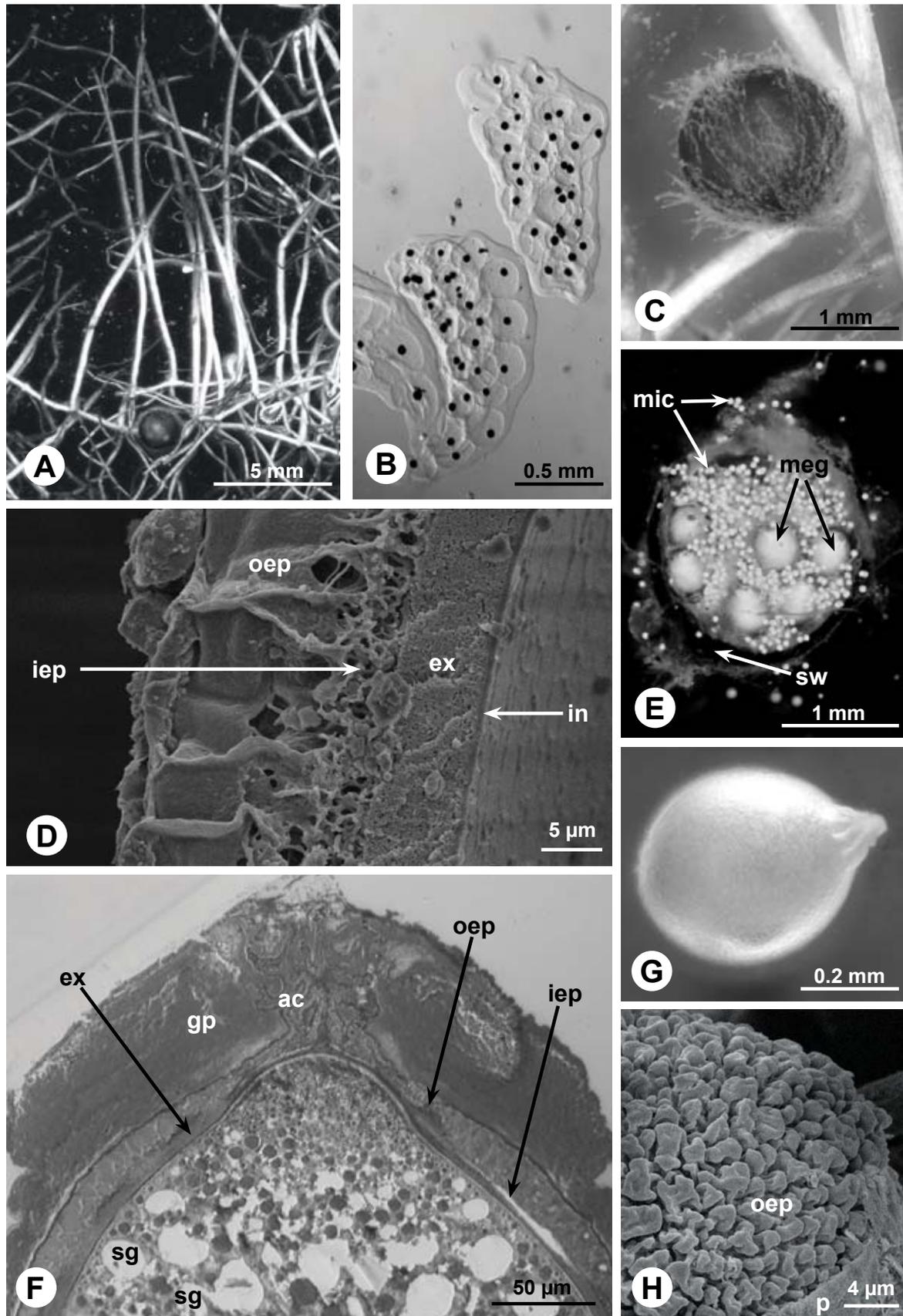


FIGURE 19.—*Pilularia dracomontana*. A, fertile mat portion, fronds borne singly at nodes; B, clavate microsporangia, intact with microspores surrounded by hyaline perispore; C, intact sporocarp unevenly covered with multicellular appressed hairs; D, t/s microspore wall; E, apical view of mechanically ruptured mature sporocarp; F, l/s distal end of mature megaspore; G, megaspore with apical papilla-like laesura (acrolamella); H, partially dissected microspore. ac, acrolamella; ex, exine layer; gp, gelatinous perine layer; iep, inner episporic sublayer; in, intine layer; meg, hyaline megasporangia; mic, microspores; oep, rugulate outer episporic sublayer; p, dehydrated perine layer; sg, starch grain; sw, sporocarp wall.

lamella (apical papilla-like laesura) (76.86–)99.54(–120.07) μm long, perispore hyaline, much larger than megaspore, both perispore and epispore thicker around distal pole than at equator, outer sublayer of epispore deeply plicate giving it a finely rugose appearance, inner sublayer of epispore much thinner than outer sublayer, pseudoendospore (intine) evident below exine layer, epispore up to 346 μm in length (excluding acrolamella) and up to 329 μm at equator. Figure 19.

Distribution: *Pilularia dracomontana* is thus far known only from three tarns in the Cobham District of the KwaZulu-Natal Drakensberg (Figure 20). The site is at the upper limit of the Southern Drakensberg Highland Grassland (Gd 4), almost on the boundary of uKhahlamba Basalt Grassland (Gd 7) (Mucina *et al.* 2006). *P. dracomontana* grows with an undescribed species of *Isoetes* (aff. *I. transvaalensis* Jermy & Schelpe) in deep sandstone tarns on a southern aspect. Plants grow in silt at the bottom of the tarns, at a depth of ± 40 cm, with fronds buried $\frac{1}{4}$ to $\frac{1}{2}$ of their length. In habitat, plants annually receive precipitation of $\pm 1\ 120$ mm from summer rainfall, but also winter snow; the tarns ice over frequently between June and August. No plants have been observed to grow as emergents in soil on the perimeter of the tarns, indicating that *P. dracomontana* may be an obligate submerged hydrophyte, at least in its vegetative state. Given its diminutive size and arcane form, this species may well be more widespread in suitable habitat in the Drakensberg, but has been overlooked to date. Plants are locally abundant in the Cobham tarns, which range in diameter from 10–15 m.

Etymology: the specific epithet *dracomontana* is a geographic indicator of the distribution of this species, which is known only from the KwaZulu-Natal Drakensberg.

Diagnostic characters: *Pilularia dracomontana* differs from *P. americana* in both vegetative and sexual characters, and is smaller in several respects. Mature sporocarps of *P. americana* have a mean diameter of 2.67 mm and contain 12–20 megaspores per sorus (Large & Braggins 1989), whereas the corresponding values for *P. dracomontana* are 1.58 mm, and 3–5 megaspores respectively. The apical papilla-like laesura (acrolamella) of the megaspores of *P. dracomontana* is proportionately much longer (at $\pm 23\%$) than its equivalent in *P. americana*, which has been documented as $\pm 12.5\%$ of the total spore length (Tryon & Lugardon 1991). Leaf lengths of *P. americana* range from 15–50(–100) mm (Correll 1956; Large & Braggins 1989; Mickel & Smith 2004), whereas leaves of the new species are no longer than 14 mm, on average attaining < 12 mm. The leaves of *P. americana* from North America exhibit obvious circinate vernation (Johnson 2010), but this feature is yet to be observed in *P. dracomontana*; additionally, more than one leaf per node has been observed in *P. americana* (Correll 1956), whereas *P. dracomontana* invariably produces only one per node. Internode lengths recorded by Roux (2002) for *P. americana* are up to 11 mm and by Grounds (1974) up to 30 mm; the maximum observed in *P. dracomontana* is only 4.2 mm. Comparison of the Drakensberg species with the two other 4-locular pillworts, *P. novae-zelandiae* Kirk and *P. novae-hollandiae* A.Braun, reveals real differences

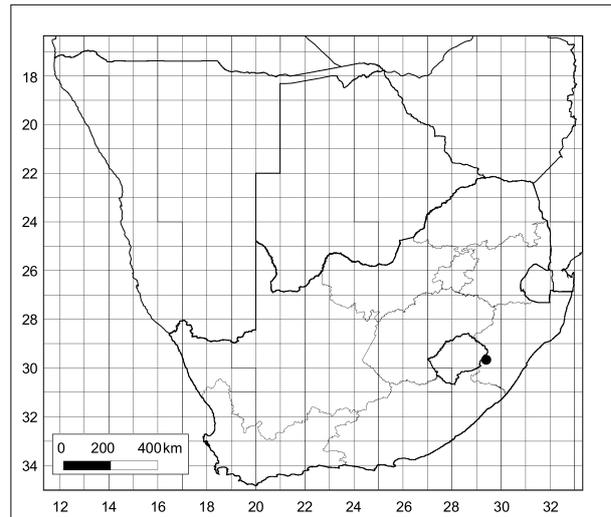


FIGURE 20.—Known distribution of *Pilularia dracomontana*, ●.

in the size of fronds, pedicels, sporocarp diameters, megaspores per sporocarp, and spore dimensions (Large & Braggins 1989). Some authors (e.g. Nagalingum *et al.* 2008) consider these two last-mentioned *Pilularia* species to be conspecific, and New World specimens previously referred to *P. americana* to likely belong to at least two taxa. The European species, *P. minuta* Durieu (known also from North Africa) and *P. globulifera* L., each possess only two locules. The non-emergent yet prolific fertile character (at a submerged depth of 40 cm) of *P. dracomontana* appears unique in the genus: *Pilularia* is otherwise consistently reported (Tryon & Tryon 1982; Mickel & Smith 2004) to produce sporocarps only on emergent plants.

Specimen examined

Pilularia americana

NORTHERN CAPE—3119 (Calvinia): Nieuwoudtville, in mud on edge of seasonal pan, (–AC), 10-10-2001, *J.P.Roux 3156* (NBG).

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