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Studies in the liverwort family Aneuraceae (Metzgeriales) from southern Africa. 1. The genus *Aneura* and its local representative

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ABSTRACT

This is the first of several projected articles dealing with the southern African Aneuraceae H.Klinggr. The family is cosmopolitan and comprises two subfamilies, only one of which, the Aneuroideae, with two genera, *Aneura* Dumort. and *Riccardia* Gray, occurs locally. Because of the taxonomic problems associated with this family and the scarcity of fruiting material, only one taxon in the genus *Aneura*, *A. pinguis* (L.) Dumort., has so far been accepted in this treatment. This is not meant to imply, however, that *A. pseudopinguis* Herzog does not occur in southern Africa; only, that the specimens I have examined, all belong to *A. pinguis*. A description and illustrations of *A. pinguis*, together with a distribution map are provided.

INTRODUCTION

One of the relatively smaller families within the order Metzgeriales, is the cosmopolitan Aneuraceae H.Klinggr. It is divided into two subfamilies, which together comprise only four genera, but more than 200 species worldwide. Only one subfamily, the Aneuroideae (Schuster 1992), with two genera, occurs in southern Africa: *Aneura* Dumort. with one locally, infrequently collected species, and the more common *Riccardia* Gray, with several species. These two hygrophilous genera are related. Initially, and up to the middle of the 20th century, they were treated as synonyms, 'sometimes using the former name and sometimes the latter, for the same taxon' (Grolle 1993).

The genera *Aneura* and *Riccardia* may be separated as follows:

Aneura

Thalli prostrate, closely adherent to substrate, fleshy, bright green and with somewhat greasy lustre, robust, 2–4(–7) mm wide, ligulate; apices rounded or scarcely emarginate; branching subsimple, developing few lateral pinnae; oil bodies in cells numerous, clear and small, 2.5–7.5 µm diam.; in cross section thallus (9)10–15 (or more) cells thick medianly, thallus gradually becoming thinner toward undulate or plicate margins. Rhizoids restricted to median ventral surface. Gemmae absent in local species.

Dioicous; male branches with 2–4 irregular rows of antheridia; female branches rudimentary with inflorescences sessile and ventrally hidden in deep lateral notch, archegonia in 2 or more rows; shoot-calyptra large, clavate, rounded at summit, corona inconspicuous; seta thick, 9–16 cells diam.; capsule valves with thickenings along longitudinal walls of epidermal cells on both adaxial and abaxial surfaces; spores 18.0–27.5 µm diam.

Riccardia

Thalli prostrate, rarely erect, pale to deep green, relatively delicate and narrow, 0.5–2.0 mm wide, linear to lingulate; apices emarginate, rounded or truncate; branching freely, mostly uni- to rarely multipinnate; oil bodies sometimes absent in epidermal cells, otherwise 1–3(4) per cell, brown or black, large, 7.5–20.0 × 5–9 µm, ovoid, spherical or ellipsoid; in cross section axis up to 9 cells thick, margins plane. Rhizoids scattered on ventral surface. Gemmae endogenously produced on dorsal surface of thallus and 2-celled.

Dioicous, autoicous or heteroicous; male branches lateral, linear, with 2 regular rows of antheridia in 2–8 pairs; female branches lateral, well developed, with 2 rows of archegonia; shoot-calyptra medium-sized, clavate or cylindrical, corona conspicuous; seta slender, 4 cells diam.; capsule valves with thickenings confined to adaxial faces of longitudinal radial walls of epidermal cells.

In both genera there is little anatomical differentiation, usually without any distinction between the wings and midrib or nerve (the epithet *Aneura*, signifies the absence of a nerve). Because of their simplicity in organization, there are few distinctive characters. Moreover, frequent variability, apparently environmentally induced, in those few features that are available, make them difficult to study. Taxonomically it is widely accepted that the Aneuraceae is one of the most troublesome families among the Hepaticae.

The long, narrow thalli of *Riccardia* species in particular, often grow in intricately intertwined, densely overlying mats, with more than one species sometimes being present. The branches are rather brittle, and unravelling and cleaning them for study needs to be done with care and is time-consuming. Sterile plants are of little value, as gametangial and sporophytic characters are necessary for the correct placing of specimens; unfortunately, they are frequently without sporophytes, although they may produce gametangia. Furthermore, as they soon disappear, the oil bodies in samples from fresh plants, that are preferably kept in a refrigerator at 5°–6°C, need to be

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photographed and studied as soon as possible after collection. Data from disintegrating oil bodies can be misleading.

It is also recommended that plants should be studied in cultivation.

Meenks (1987) is of the opinion that herbarium collections are often useless, particularly if they are more than 20 years old. Type specimens are, however, far older generally, yet one needs to study them to compare them with fresh, living collections, however difficult that may be.

HISTORICAL NOTES

The Aneuraceae have been relatively poorly studied in southern Africa. Lehmann (1829) described our first new local taxon, *Aneura* (sub *Jungermannia*) *fastigiata*, collected by Ecklon on Devil's Peak and Table Mountain and compared it to *A.* (sub *J.*) *multifida*, which he also reported from Table Mountain, as well as two varieties of it. Gottsche *et al.* (1844–1847) accepted the presence of *A. fastigiata*, but compared it to *A. palmata*. They also briefly mentioned Ecklon's collections of *A. pinnatifida* and *A. multifida* from Promontorium Bonae Spei (Gottsche *et al.* 1844–1847: 788).

No further species were recorded from tropical or southern Africa (Jones 1956), until Stephani (1886) reported *R. pinguis* L. from S. Tomé. During 1890–1893 and 1917 Stephani described more than 20 new species from the African continent and the Mascareignes. Gola (1914) and Pearson (1922) each described one new species from Africa. Sim (1926) described no new species in his treatment, and only briefly mentioned *A. fastigiata* and *A. compacta*. Then, in 1952, S.W. Arnell described five new species from southern Africa. In 1963, he placed one of them, *R. submarginata*, in synonymy under the Brazilian species *R. pseudopinguis* Herzog (1942), although he had previously agreed with Jones (1956) that it was identical with *R. pinguis*. Jones (1956) was very conservative in his treatment of *Riccardia* species in tropical Africa. He placed some of Stephani's species in synonymy and made several new combinations, transferring four of Stephani's *Aneura* species to *Riccardia*, as the distinctions between the two genera had become generally accepted by then. Vanden Berghen (1972) reported the presence of *A. pseudopinguis* from Shaba, Kafubu and Lufira in Zaïre (Democratic Republic of Congo).

In 1981, Jones drew attention to an inversion of specific epithets that had occurred on the herbarium labels of the type specimens of *A. congoana* Steph. and *A. congoensis* Steph. Later, Jones & Harrington (1983) reported *R. angusticosta* and *R. limbata* from Sierra Leone and Ghana, as well as an unidentified *Riccardia* species from Ghana. Gradstein *et al.* (1983) announced the presence of *A. pseudopinguis* in West and East Africa, and in the same article Pócs transferred it from *Riccardia* to *Aneura*.

The last treatment of East African Aneuraceae was by Meenks & Pócs (1985), as a large number of unidentified specimens and new information had accumulated in the meantime. Although they present a key to the African species of the family, and give extensive lists of specimens examined, literature records and distribution maps, only one species, *R. compacta*, is illustrated. Illustrations by Arnell (1952, 1963) are generally poor and Stephani's *Icones* (1985) are not freely available. Schuster (1992) remarked, with some justification, that African taxa of the Aneuraceae remain poorly known, as Arnell's treatment is far from satisfactory.

It is accordingly considered necessary to revise at least the southern African members of the Aneuraceae, which often represent southern extensions of range, and to give good illustrations wherever possible. This publication is the first in a series of projected papers on the local Aneuraceae.

METHODS AND MATERIAL STUDIED

With some exceptions, the same methodology as was employed in my treatment of southern African *Fossombronia* species (Perold 1997), is followed here: 1, samples of field-collected specimens were fixed in FAA on the day of collection; 2, more samples were selected for oil body study and cultivation and initially kept at 5°–6°C in transparent screw boxes, lined with damp filter paper; and 3, the rest of the specimens, destined to be held in the herbarium, were allowed to air-dry rapidly. Only traditional morphological-anatomical and histological methods were employed. Far less extensive use of the SEM was made in this study, however, as the spores of our local *Riccardia* species do not display marked differences in their ornamentation. The drawings were based on photographs taken with a camera mounted on a Nikon light microscope. The Degree Reference System (Edwards & Leistner 1971) was again used for recording distribution data.

Specimens examined
(held at PRE, unless otherwise indicated)

S.W. Arnell 1552, 1766 (types of *R. submarginata* BOL); *1782* (BOL); *1803, 1844* (S).

Burgoyne 2462.

Cholnoky s.n. (S) KwaZulu-Natal; grid unknown and not indicated on Figure 2.

Koekemoer 2063.

Perold 3774, 3823. Perold & Koekemoer 4304, 4483, 4504, 4514.

Aneuraceae *H.Klinggr.*, Die höheren Cryptogamen Preussens: 11 (1858); Müll.Frib.: 492 (1951–1958); S.W.Arnell: 84 (1963); Furuki: 306 (1991); R.M.Schust.: 545 (1992); Paton: 537 (1999); Bednarek-Ochyra et al.: 178 (2000). Type: *Aneura* Dumort.

Plants thalloid, prostrate or sometimes ascending, bright green with greasy lustre or light to dark green, robust and fleshy, lingulate to sublinear, 2–4(–6) mm wide or narrow and thin, relatively delicate, mostly linear, 0.5–2.0 mm wide, apices rounded or emarginate, margins undulate, sometimes flat or plane and entire. *Branching* virtually simple to sparse, branches laterally and irregularly lobed or freely pinnate to quadripinnate,

occasionally crowded. *Dorsal epidermal cells* generally somewhat smaller than internal cells, not otherwise differentiated, usually thin-walled, occasionally with minute trigones, 5–7-angled. *Oil bodies* in each cell, either numerous and then small and hyaline, or only 1–3(4), and then large, finely granular and brown or black, rarely absent. *Cross section* of main axis plano-convex to concavo-convex with weakly recurved margins, or flattened to biconvex; pluristratose medianly, usually 9–15 cells thick, gradually thinning out laterally to margins, acute, winged, or obtuse, without discrete midrib, internally homogeneous, lower cells sometimes with basidiomycete fungal hyphae. *Mucilage papillae* often in 2 alternate ventral rows, one on each side of midline and/or clustered at apex of thallus. *Rhizoids* restricted to ventral median area or scattered over ventral surface of thallus. *Asexual reproduction* absent or by 2-celled, endogenously produced gemmae.

Dioicous, monoicous or synoicous. *Sexual branches* lateral from main thallus, short and determinate in length; male branches single or in sympodial pairs or in threes, antheridia in up to 4 irregular rows or in 2 regular rows of antheridial chambers, each containing a single antheridium, dorsally exposed; female branches within deep lateral notch of thallus or almost sessile laterally, archegonia in 2 or more rows, protected by papilliform or finger-like paraphyses. *Shoot-calyptra* large, clavate or cylindrical, with wall several cell layers thick, surface almost smooth or bearing papillose outgrowths. *Seta* thick, 10–12 cells diam., or slender and only 4 cells diam. *Capsule* ellipsoidal, 4-valved, wall bistratose, outer cell layer with bands of thickening on adaxial and abaxial radial walls; inner cell layer with bands of thickening on adaxial and abaxial radial and inner tangential walls, or else, outer cell layer with bands of thickening on adaxial radial and inner tangential walls, without bands of thickening on inner cell layer. *Spores* relatively small, up to 27.5 µm diam., finely papillose, or only up to ± 20 µm diam., minutely scabrate. *Elaters* up to ± 350 µm long, uni-spiral, band reddish brown, 7.5–10.0 µm wide, tapering at both ends. *Elaterophores* in fascicles at apices of valves.

Aneura *Dumort.*, Commentationes Botanicae: 115 (1822); Hewson: 184 (1970); Furuki: 308 (1991); R.M.Schust.: 551 (1992); Paton: 537 (1999). Type species: *Aneura pinguis* (L.) Dumort.

Jungermannia pinguis L.: 1136 (1753).

Trichostylium Corda: 116 (1835); Nees: 475 (1838); R.M.Schust.: 53 (1958).

Riccardia subgenus *Trichostylium* Mizut. & S.Hatt.: 35 (1957).

Thalli prostrate, clear green and greasy, robust, fleshy, dorsally flat or slightly concave, gradually thinning out from thick median region to margins, smooth, up to 35 mm long, 2–4(–6) mm wide, lingulate to sublinear, apices rounded or slightly emarginate, margins undulate, sometimes flat. *Branching* sparse and irregular. *Oil bodies* (2–)5–24(–67) in all dorsal epidermal and inner cells, subglobose or ovoid, 2.5–5.0 µm diam., hyaline. *Cross section* of thallus (9)10–15 cells thick medianly, acute at margins. *Mucilage papillae* only on ventral surface of thallus, in 2 rows, one on each side of midline and clustered at branch apices. *Rhizoids* restricted to median area of ventral surface of thallus. *Asexual reproduction* absent, gemmae unknown in local species.

Dioicous. Heterothallic. *Male thalli* somewhat smaller, antheridial branches single or sympodially paired and antheridia in up to 4 irregular rows, separating walls usually bistratose, dorso-lateral wing up to 6 cells wide. *Female branches* shielded and hidden in deep, lateral notches of thallus, paraphyses around and between archegonia. *Shoot-calyptrae* large, ± 10 mm long, fleshy, wall ± 500 µm thick, corona inconspicuous. *Setae* massive, 10–12 cells diam., spirally twisted. *Capsules* ellipsoidal, 4-valved, bistratose, epidermal cells with nodular thickenings of both adaxial and abaxial radial longitudinal walls; inner cell walls with numerous annular or semiannular (tangential) bands. *Spores* finely papillose, 20.0–27.5 µm diam. *Elaters* up to 350 µm long, 10 µm wide, unispiral.

Aneura pinguis (*L.*) *Dumort.*, Commentationes Botanicae: 115 (1822); Dumort.: 86 (1831); Gottsche et al.: 493 (1844–1847); Steph.: 762/272 (1899); Müll.Frib.: 331 (1908); Brown & Braggins (with question mark): 117 (1989); Furuki: 311 (1991); R.M.Schust.: 555 (1992); Paton: 539 (1999). *Jungermannia pinguis* L.: 1136 (1753). *Riccardia pinguis* (L.) Gray: 683 (1821); Müll.Frib.: 494 (1951–1958); S.W.Arnell: 30 (1956); E.W.Jones: 84 (1956). *Trichostylium pinguis* R.M.Schust.: 53 (1958). Type: 'Habitat in Europae paludibus', sin. coll., *Dill.* in 'Historia Muscorum: 509. Lichenastrum no. 42, t. 74, fig. 42 (1741)' [OXF, syn.; H–SOL, isosyn.].

R. viridissima Schiffn.: 176 (1898). *A. viridissima* (Schiffn.) Steph.: 763/273 (1899). Type: Java, Prov. Batavia, in monte Megamendon, *Schiffner 235*, syntype (JE, L, PR, PRC, W), fide Furuki 1991.

A. laurentiana Steph.: 32 (1917). *R. laurentiana* (Steph.) Demaret: 306 (1942). Type: Congo, env. d'Eala, *Laurent 64* (G).

R. submarginata S.W.Arnell: 139 (1952). Types: Deepwall Forest Reserve, ½ mile south of Forest Station, *S.W. Arnell 1552, 1766* (BOL!; S).

A complete list of synonyms is provided in R.M. Schuster (1992: 555, 556).

Thalli prostrate, in patches, bright green, with greasy lustre, smooth, yellow when dried, opaque, becoming translucent toward margins, otherwise fleshy, robust, axis plane to slightly concave, subsimple, lingulate to sublinear, 15–35 mm long, 2–6(–7) mm wide, apices rounded, margins entire, undulate to somewhat crisped or lobed. *Branching* sparse, not pinnate, often short, sometimes long, irregularly furcate. *Dorsal epidermal cells* (Figure 1H) from above, 4–6(7)-sided, thin-walled, 50.0–87.5 × 37.5–62.5 µm; subdorsal cells (Figure 1I) 112.5–175.0 × 87.5–132.5 µm; subventral cells 100–160 × 50–75 µm; ventral epidermal cells 62.5–100.0 × 37.5–50.0 µm. *Oil bodies* in all cells, several to numerous, (2–)5–24(–67), small, 2.5–5.0 µm diam., spherical to subspherical or ovoid, faintly granular, inconspicuous,

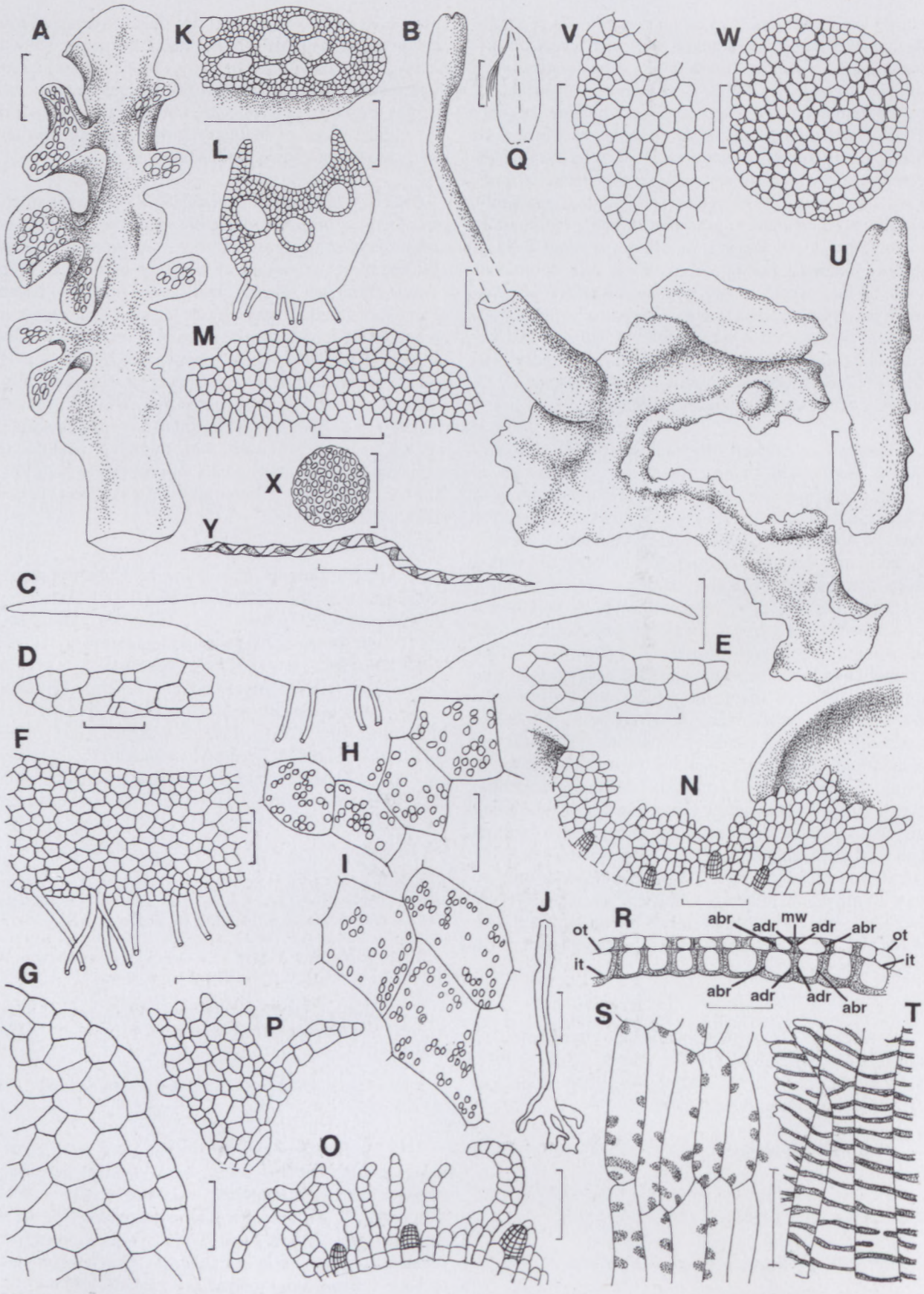


FIGURE 1.—*Aneura pinguis*. A, male thallus with antheridial branches; B, female thallus with calyptra, shortened seta and capsule, old, collapsed calyptra on upper right, very young calyptra opposite it. C–I, thallus: C, c/s; D, E, c/s marginal part; F, c/s median part; G, margin from above; H, dorsal epidermal cells with oil bodies; I, subdorsal cells with oil bodies. J, rhizoid with ramified tip and internal mycorrhizal hypha. K–M, male branches: K, partly from side, only one wing shown; L, c/s; M, wing. N, O, young female branches: N, ventral view, located at notch in thallus margin; O, lateral view. P, paraphysis. Q–T, capsule: Q, valve with elaterophore at tip. R, c/s part of bistratose wall, with thickenings: abr, abaxial radial; adr, adaxial radial; mw, median; it, inner tangential; ot, outer tangential. S, thickenings of outer cell layer; T, thickenings of inner cell layer. U, calyptra; V, c/s calyptra; W, c/s seta; X, spore; Y, elater. A, B, N, S, T, W–Y, *Perold & Koekemoer 4504*; C, D, F, H, I, K–M, O–R, U, V, *Perold & Koekemoer 4514*; E, G, *Perold & Koekemoer 4483*; J, *Perold 3823*. Scale bars: A, B, U, 2 mm; C, K, L, 500 µm; D, E, G, J, S, T, 100 µm; H, I, R, Y, 50 µm; Q, 1 mm; F, M–P, V, W, 250 µm; X, 25 µm.

colourless, scattered or occasionally aggregated in clusters. *Marginal cells* (Figure 1G): outermost row unistratose, rectangular, 47.5–75.0 × 25–45 µm, inner cells angular, bistratose, 42.5–55.0 × 37.5–62.5 µm. *Cross section* of thallus (Figure 1C) plano-convex to concavo-convex, with wings weakly recurved, medianly pluristratose (Figure 1F), 9–15 cells (or 460–650 µm) thick, gradually becoming thinner laterally, epidermal cells chlorophyllose, 37.5–50.0 µm high, shallower than internal, hyaline cells, but not forming a distinctive layer; margins acute, bordered by bistratose wing, 3 cells wide plus a single conical cell (Figure 1D, E), ± 50 µm high. *Mucilage papillae* clustered at ventral apices of branches and spaced along 2 rows, one on each side of midline, clavate, 105–114 × 42.5–51.0 µm, not persistent. *Rhizoids* restricted to ventral median area, 17.5–25.0 µm wide, sometimes ramified at tips and occasionally with mycorrhizal hyphae (Figure 1J). *Asexual reproduction* by gemmae absent.

Dioicous. *Male plants* (Figure 1A) somewhat smaller than female plants, axis up to 17 × 3.5–4.2 mm and medianly 9–11 cell layers thick, in close proximity to female plants, virtually touching; antheridial branches (Figure 1K) lateral, solitary, sublinear, 2.8 mm long or more, ± 1.15 mm wide and ± 850 µm thick (Figure 1L), scalloped, bistratose wings (Figure 1M), 300–500 µm or 6–8 cells wide, a continuation of thallus margin; otherwise divided into 2 or 3 branches, from near base or further along, up to 2.4 mm wide, antheridial chambers very irregularly arranged, not in rows, 2–4 across width of branch; antheridia subglobular, 200–250 µm wide, cavity walls between them bistratose; after antheridial production, branch may continue vegetative growth. *Female plants* (Figure 1B) with archegonial branches very short, ventral to lateral notch in thallus margin, at base of deep sinus and obscured by reflexed thallus folds on each side (Figure 1N), archegonia in rows, hidden by densely crowded paraphyses, up to ± 500 µm long, composed of single strands of cells joined end to end (Figure 1O) or partly of 3 or more rows of laterally joined cells (Figure 1P). *Calyptra* clavate, large (Figure 1U), 10–12 mm long, ± 2 mm diam., wall 8 or 9 cell layers (± 500 µm) thick, cells in cross section (Figure 1V) 5–7-sided, 65–100 × 62.5–75.0 µm, outermost cells of wall in surface view long-rectangular, 150–170 × 60–75 µm, in lower part of calyptra often developing rhizoids, but becoming nearly smooth with age, corona inconspicuous, base partly sheathed by adjacent, suberect thallus margins. *Seta* up to 21 mm long, somewhat spirally twisted, 750 µm or 15 cells diam. in cross section (Figure 1W), marginal cells small, 32.5–47.5 × 25–40 µm, inner cells round, 55–75 µm diam. *Capsules* oblong-ovoid, reddish brown, 2500–3250 µm long, with 4 valves, each one ± 1050 µm (or ± 42 cells) wide, bistratose, to either side of midline of every valve, thickenings laid down as a mirror image; epidermal (outer) cells in external longitudinal view (Figure 1S) with nodular thickenings, cells usually narrowly rectangular, 162.5–232.5 × 15.0–37.5 µm, in cross section (Figure 1R), thickenings only rarely extending slightly across outer tangential walls, mostly on adaxial radial and abaxial radial walls; inner cells in internal longitudinal view (Figure 1T) less regular, tapering or with oblique end walls, 142.5–220.0 × 32.5–67.5 µm, in cross section (Figure 1R) adaxial radial longitudinal walls all develop bands which extend across inner tangential walls and connect with abaxial radial bands on opposite side of cell, thickenings therefore ± U-shaped (Figure 1R). *Spores* 20.0–27.5 µm diam., dark brown, papillose (Figure 1X). *Elaters* (Figure 1Y) 212.5–350.0 × 10 µm, with single spiral band, ± 10 µm broad, pinkish red, tapering to ends, these without spiral. *Elaterophores* 1000–1445 × 220 µm, one at tip of each valve (Figure 1Q). *Chromosome no.*: n = 10 (Fritsch 1982).

Aneura pinguis is subcosmopolitan in its distribution and has been reported from many localities worldwide; South America and Australia are, however, excluded. It is also present in southern Africa, but is infrequently collected (Figure 2). It grows on soil or rotting wood, in permanently damp areas, often fed by seepages.

DISCUSSION

Aneura specimens have recently been collected at a few localities in Mpumalanga, Eastern Free State, KwaZulu-Natal, Western and Eastern Cape, but *Perold & Koekemoer 4405 & 4415* from Garcia's Pass, near Ladismith in Western Cape, are the only specimens that are fertile, with both mature male plants bearing ripe antheridia on lateral branches, as well as female plants with calyptrae and ripe capsules. Samples of these have been preserved in FAA for future reference. These specimens have been referred to *Aneura pinguis* because of the following characters: 1, the large, bright green, rather greasy-looking, fleshy and opaque thalli; 2, thalli in cross section medianly up to 15 cell rows thick; 3, each cell with several to many minute, colourless oil bodies; 4, 2–4 rows of antheridial chambers; 5, spores that are 20.0–27.5 µm diam. On one side of the same male thallus of *Perold & Koekemoer 4514*, there are a few short, ligulate male branches, bearing the antheridia in 2 or 3 rows, whereas on its opposite side, there are several furcate male branches, some of which are wider and rounder at the apices, with up to 4 irregular rows of numerous antheridia.

Meenks & Pócs (1985) have drawn up a short table differentiating between *A. pinguis* and *A. pseudopinguis*,

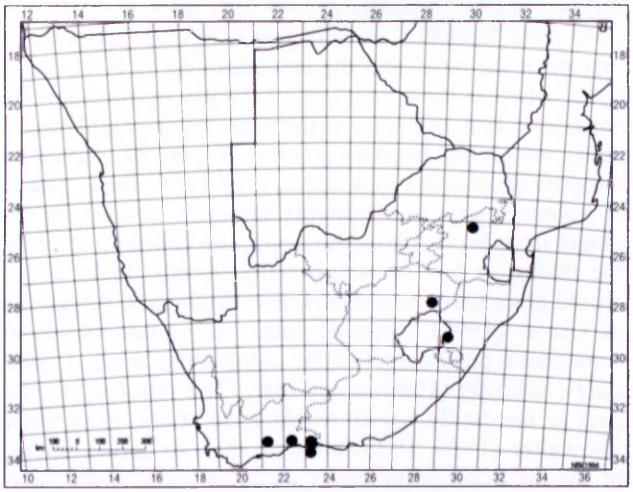


FIGURE 2.—Distribution of *Aneura pinguis* in southern Africa.

but there appears to be some overlap in the characters assigned to these two species in our local specimens. Meenks & Pócs regard *A. pinguis* as having opaque thalli, medianly (9)10–20 cells thick, with relatively short male lobes, which seldom branch and contain 2–5(6) pairs of antheridia; the spores are 20–25 µm diam. On the other hand, *A. pseudopinguis* thalli are, according to them, translucent, medianly only 5–8(9) cells thick, the male branches are longer, often with 3 (seldom 4) rows or 7–10(–20) pairs of antheridia, and the spores are 13–16 µm diam.

In the specimens they studied, Gradstein *et al.* (1983) regarded the identity as confirmed in 'only the records of plants possessing either male branches or spores'. They also report that in African samples of *A. pseudopinguis* 'usually only one sex is found in a particular locality'. This is contrary to the findings in our two fertile collections referred to above, and may provide further evidence that we are dealing with *A. pinguis*.

In 1952 Arnell reported his new *Riccardia submarginata* from Deepwall Forest Reserve. There were no mature capsules with spores, but the median cross sections of the thalli were given as 15 cell rows thick. In my examination of Arnell's specimens the median cross sections of the thalli ranged from 8–13 cell rows thick.

As already remarked in the paragraphs on 'Historical notes', Arnell had admitted to Jones (1956) that, the Deepwall specimens were identical to *R. pinguis*, although later, Arnell (1963) placed *R. submarginata* in synonymy under *R. pseudopinguis*. Arnell was familiar with European representatives of *R. pinguis*, as he had described it in 1956 in his *Flora Fennoscandia*. Arnell (1963) also gave vegetative characters, based on the size of the thallus cells in *R. pinguis*, but these characters appear to be in contradiction with his own account of Scandinavian *A. pinguis*, as noted by Gradstein *et al.* (1983).

Vanden Berghen (1972) reported the Congoan presence of *A. pseudopinguis* from Shaba, Kafubu in Lufira. Hodgetts *et al.* (1999) also reported *A. pseudopinguis* from Lesotho, northeast and west of New Oxbow Lodge, but gave no details of their plants. Herzog (1942) described his new species, *R. pseudopinguis*, from Brazil as follows: thallus is medianly 6–8 cells thick in cross section, male branches are elongated, ligulate, sometimes furcate at the base, and the antheridia are in 8–10 serial pairs, whereas the spores are 13–16 µm in diameter. He suggested that previous collections from neighbouring areas, which had been assigned to *R. pinguis*, should be checked against his new species. In 1956, Jones placed *R. submarginata* in synonymy under *R. pinguis*. In his plants from West Africa, however, the central portion of the thallus is 5–7 or occasionally 9 cells thick, which would place them nearer to *A. pseudopinguis*. Wigginton & Grolle (1996) observed that, '*A. pseudopinguis* is sometimes considered to be conspecific with *A. pinguis*'. Schuster (1989) noted that, 'The status of *A. pinguis s. lat.* badly needs world-wide study. Ever since Showalter (1926, 1928) showed that, so-called 'races' of the holarctic populations were, in some cases intersterile, the matter of how to define this species has been highly uncertain'. Furthermore, it seemed most unlikely to Schuster that a species could occur in the Arctic polar desert of Ellesmere Island and also in tropical and subtropical areas. He concluded this paragraph with the following observation, 'Recent study has also shown that the tropical American-African plants formerly referred to *A. pinguis* represent *A. pseudopinguis* Herz'.

According to Meenks & Pócs (1985), however, both taxa occur in East Africa, as well as in West Africa (Gradstein *et al.* 1983), but *A. pinguis* appears to be rarer in tropical Africa than *A. pseudopinguis*. In southern Africa, *A. pinguis* is very infrequently collected and fertile plants are the exception by far, rather than the rule; this scarcity of fruiting material further complicates the study of these plants. To quote Proskauer (1971), '*Riccardia pinguis*, a species which we have long known to present a nightmarish problem ..., probably requiring more than a single lifetime of research for a minimum understanding'.

Stephani (1899) placed *R. latissima* (Spruce) Schiffn. in synonymy under *R. pinguis*. However, Meenks & De Jong (1985) note that, the oil bodies in *A. latissima* are bright brown, not clear and colourless, as they are in *A. pinguis*. Furthermore, a chromosome no. n = 8, has been reported by Nakata & Inoue (1989) for *A. latissima*, whereas the chromosome no. n = 10 is given for *A. pinguis*. Stephani's synonymy of *A. latissima* under *A. pinguis*, is, accordingly not accepted here.

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