

## Studies in the liverwort family Aneuraceae (Metzgeriales) from southern Africa. 5. *Riccardia amazonica*

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### ABSTRACT

*Riccardia amazonica* (Spruce) Schiffn. ex Gradst. is described and illustrated, as fresh material from southern Africa has recently come to hand. Several tropical African species of the genus had previously been placed in synonymy with this South American species; their type specimens have now also been studied.

### INTRODUCTION

*Aneura amazonica* was first described by Spruce (1885) from specimens collected in the Amazon at San Carlos and San Gabriel, on the banks of the Negro River, where it grew on fallen, half-rotten tree trunks. Jones (1956) remarked on the similarity 'between *Riccardia stephanii* and some of the South American plants which Stephani determined as *A. amazonica* Spruce, though the resemblance to Spruce's type gathering is less close'. Jones made some new combinations but mostly treated the generic names, *Aneura* and *Riccardia* as synonyms. He proceeded to place *Aneura stephanii* Besch. ex Steph., \*\**A. congoensis* Steph., '*A. angusticostata*' Steph., *A. grosselimbata* Steph. and *A. travisiana* Pearson in synonymy under *R. stephanii* Besch. ex Steph. Previously, Arnell (1952) had described *R. campanuliflora* as a new species from South Africa and had illustrated it. Subsequently, Arnell (1963) accepted Jones's synonyms of *R. stephanii* and added *R. campanuliflora* to this list, using his earlier drawing of *R. campanuliflora* to illustrate his description of *R. stephanii*. Vanden Berghen (1972), however, observed that the description of *R. stephanii* by Arnell (1963) and the drawings which accompany it, correspond manifestly with a different taxon from that circumscribed by Jones (1956), who had examined the type of *Aneura stephanii*, collected in 'Congo-Brazzaville'. I agree with Vanden Berghen and, after re-examining the type collection, have not here included *R. campanuliflora* as a synonym of *R. amazonica*, although I have done so elsewhere (Perold in prep.). Compared to *R. amazonica*, it is a rather more robust plant.

According to Jones (1956) there are puzzling intermediate forms and mixtures 'which make it very difficult to decide whether *R. limbata*, *R. erosa* and *R. stephanii* represent distinct genotypes.' Furthermore, he regarded *R. erosa* as closely resembling *R. stephanii* and added that 'there is no doubt, however, that plants corresponding to these three species do occur in pure patches,' and he formed the impression that in the field they were specifically distinct.

In 1983 Jones & Harrington placed *R. stephanii* in synonymy under *R. angusticosta* [or '*angusticostata*' (Steph.) Grolle (1973)], when they reported its presence from Sierra Leone and Ghana. They concluded that *R. angusticosta*, *R. erosa* and *R. limbata* were at most, varieties of a single species, with much ill-defined intraspecific variation.

After examining a large number of specimens, mainly from Kenya and Tanzania, Meenks & Pócs (1985) concluded that *R. stephanii* was synonymous with *R. amazonica* Spruce. They also quoted 13 literature records, showing it to be a widely distributed species.

Gradstein & Hekking (1979) reported *R. amazonica* from Magdalena, San Sebastian, Colombia, at an altitude of 2 600 m, whereas Gradstein *et al.* (2001) reported it from lowland rainforest, so it has a wide altitudinal amplitude, as was also noted by Meenks & Pócs (1985).

A fresh, fruiting specimen of *R. amazonica* was recently collected in the neighbourhood of Buffelskloof Nature Reserve, near Lydenburg. Some of it has been cultivated to observe the oil bodies, the branching and other characters, while the rest had been allowed to dry, to serve as a herbarium specimen.

***Riccardia amazonica* (Spruce) Schiffn. ex Gradst.** in Gradst. & Hekking, *Journal of the Hattori Botanical Laboratory* 45: 129 (1979); Meenks & Pócs: 83 (1985). Type: Brazil, San Carlos del Rio Negro, 'in trunco putrido', Spruce s.n. ('H16') (MANCH cc [= computer catalogue no.] 1680, lecto.!).

*Aneura amazonica* Spruce: 545 (1885); Steph.: 734 (1901–1905).

*A. stephanii* Besch. ex Steph.: 735 (1901–1905). Type: Congo, Brazzaville, Thollon (G!).

*A. angusticosta* Steph.: 724 (1913). *R. angusticostata* (Steph.) Grolle: 550 (1973). *R. angusticosta* (Steph.) Grolle as corrected in Geissler & Bischler (eds): 47 (1990). Type: Usambara, *Bruennthaler* (G!).

*A. congoana* Steph.: 23 (1917–1924). Type: Congo Belge, Bolombo, Laurent (G!).

*A. grosselimbata* Steph.: 29 (1917–1924). Type: Ost Usambara, Amani, Engler (G!).

*A. travisiana* Pearson: 1 (1921). Type: French Cameroons, Duala, Travis (MANCH).

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\*\* Should be *R. congoana* (Jones 1980).



*R. stephanii* (Besch. ex Steph.) E.W.Jones: 81 (1956), hom. illeg. Wigginton & Grolle: 205 (1996).

Thalli rather small, prostrate, creeping, in 2 or 3 loosely to quite densely overlying layers forming intricate mats, bottom layer in patches or strips firmly adherent to substrate, bright green when fresh, margins turning translucent as chloroplasts disappear; when dry, duller green. *Main axis* (Figure 1A) up to 13 or 14 mm long, generally retaining its dominance, width, particularly in male plants (Figure 1B), not uniform, 500–800  $\mu\text{m}$  wide, alternately widening before branching and narrowing again afterwards, segments wedge-shaped, dorsally plane, branching pinnate or occasionally bipinnate, not always equally well developed on both sides, sometimes distally trifurcate or subpalmate, occasionally with lateral incipient branches, apically shallowly notched medianly, adjacent cells meristematic, margins winged; ultimate segment often linear, 575–875  $\times$  285–500  $\mu\text{m}$ . *Primary branches* lateral, opposite or subopposite, 350–650  $\mu\text{m}$  between pinnae, spreading obliquely at angles of less than 45° with axis, up to 1800  $\mu\text{m}$  long, 375–525  $\mu\text{m}$  wide (Figure 1C), secondary branches/pinnules quite rare, rather weak and occasionally just lateral swellings on primary branches, 375–500  $\times$  275–375  $\mu\text{m}$ . *Stolons* sometimes developing laterally from main axis or from base of primary branches, up to 1375  $\times$  100–140  $\mu\text{m}$ . *Dorsal epidermal cells* in median part of apical segment of main axis 5–7-sided (Figure 1D), thin-walled, 40.0–67.5  $\times$  25.0–37.5  $\mu\text{m}$ , subdorsal cells larger, 4–6-sided, 92.5–135.0  $\times$  30.0–37.5  $\mu\text{m}$ , ventral epidermal cells 42.5–65.0  $\times$  25–35  $\mu\text{m}$ . *Oil bodies* present in most dorsal and ventral epidermal cells, 10–14  $\times$  7.5–10.0  $\mu\text{m}$ , and in internal cells, where larger, 12.5–22.5  $\times$  12–15  $\mu\text{m}$ , also in  $\pm$  20% of marginal cells, but more common in intramarginal cells, 1 or 2 per cell, and if 2, one smaller than the other, lying close together, subspherical, ellipsoid or ovoid, ends rounded or acute, light brown, finely granular. *Margins* of ultimate pinnules (Figure 1E) entire to slightly crenulate, outer cells smaller than intramarginal ones, subquadrate to rectangular, 22.5–40.0  $\times$  17.5–35.0  $\mu\text{m}$ , intramarginal cells 4–6-sided, 37.5–55.0  $\times$  27.5–32.5  $\mu\text{m}$ , mostly parallel to margin, not in diverging rows. *Cross sections* of main axis: at  $\pm$  middle of ultimate segment (Figure 1F, G) plano-convex,  $\pm$  300  $\mu\text{m}$  wide, 60–90  $\mu\text{m}$  or 3 cell rows thick medianly, tapering laterally to unistratose margins,  $\pm$  90  $\mu\text{m}$  or 3 cells wide, dorsal epidermal cells  $\pm$  rectangular, 15–20  $\mu\text{m}$  thick, internal cells few,  $\pm$  25  $\mu\text{m}$  thick, ventral cells 10–20  $\mu\text{m}$  thick; at upper portion (Figure 1H) plano-convex,  $\pm$  500  $\mu\text{m}$  wide,  $\pm$  90  $\mu\text{m}$  or 4 cell rows thick medianly, tapering to unistratose margins,  $\pm$  45  $\mu\text{m}$  or 2 cells wide; at lower portion (Figure 1I) slightly concavo-convex,  $\pm$  520  $\mu\text{m}$  wide,  $\pm$  60  $\mu\text{m}$  or 3 cell rows thick medianly, tapering to unistratose margins, 2 or 3 cells or up to 105  $\mu\text{m}$  wide; primary branch (Figure 1J)  $\pm$  60  $\mu\text{m}$  or 3 cell rows thick medianly, unistratose margins 2 or 3 cells wide. *Mucilage papillae* ventral, clustered at shallow apical notch of branches, 27.5–45.0  $\times$  10–15  $\mu\text{m}$  above, lower down  $\pm$  7.5  $\mu\text{m}$  wide, thicker-walled above, club-shaped, soon becoming spaced in 2 acropetal rows, one on either side of midline, not persistent. *Rhizoids* ventral on axes, sometimes in submarginal strips, elsewhere in patches, 7.5–12.5  $\mu\text{m}$  wide, occasionally the tips several times branched. *Asexual reproduction* by gemmae (Figure 1K) observed in cultured plants, on dorsal surface of upper branches, each of the 2 cells 22.5–25.0  $\times$  30  $\mu\text{m}$ , joined

together at their flat basal wall, the outer walls semi-circular.

Dioicous. Male plants up to 8.5 mm long. *Antheridial branches* (Figure 1A) along main axes obliquely lateral, opposite or subopposite one another, or opposite a primary branch, otherwise without an opposite pinna, rarely 2 male branches close together, nearly adjoining basally, occasionally male branch near base of primary pinna, oblong-linear, 300–750  $\mu\text{m}$  long, mostly stipitate, up to 275  $\mu\text{m}$  wide, bearing 4 or 5(6) pairs of antheridia, cavities  $\pm$  60  $\times$  85  $\mu\text{m}$ , separated by single row of cells, 45–50  $\times$  40–50  $\mu\text{m}$  (Figure 1L), sometimes basally winged on one or both sides, wing up to 3 cell rows wide, below merging with axis wing, branch in cross section (Figure 1M)  $\pm$  190  $\mu\text{m}$  high, marginal cells erect, enlarged, from side (50–)60–70  $\times$  30–40  $\mu\text{m}$ . *Gynoeceal branches* (Figure 1N) solitary, arising laterally along axis, subopposite primary branch or without opposite branching close by, otherwise below primary branch, near base of axis, youngest branches rounded, 190–250  $\times$  250–260  $\mu\text{m}$ , including paraphyses (Figure 1O), unfertilized branches elongating up to 400  $\mu\text{m}$  and with up to 6 pairs of archegonia, paraphyses along both margins, some with single strands of cells, 37.5–50.0  $\times$  25–30  $\mu\text{m}$ , joined together end to end, others with 2–5 rows of laterally fused cells, 52–125  $\mu\text{m}$  wide,  $\pm$  arching over archegonia. *Calyptra* (Figure 1P) clavate, at maturity 1875–2250  $\times$  425–500  $\mu\text{m}$  above, slightly narrowing below, cross section of wall (Figure 1Q) up to 130  $\mu\text{m}$  or 4 cell layers thick, outermost row with scattered, single-celled papillae, extending upwards to apex, where grouped together to form a corona (Figure 1P<sub>1</sub>), cells 82.5–125.0  $\times$  32.5–40.0  $\mu\text{m}$ . *Seta* (Figure 1P<sub>3</sub>) up to 11.5  $\times$  130–150  $\mu\text{m}$ , with 4 inner and 12 outer cell rows, i.e. 4 cells diam. *Capsule* (Figure 1P<sub>2</sub>)  $\pm$  ellipsoidal, valves 640–730  $\times$  200–350  $\mu\text{m}$  or 16–19 cells wide, bistratose; cells of epidermal layer in external longitudinal view (Figure 2A) 55.0–112.5  $\times$  10–20  $\mu\text{m}$ , end walls straight or oblique, with vertical (radial) thickenings, evident as nodular brown bulges along radial walls; inner cells (Figure 2B) 85.0–162.5  $\times$  10–15  $\mu\text{m}$ , without nodular thickenings, but those on epidermal wall still visible through thin wall; in cross section (Figure 1R) cells in epidermal layer  $\pm$  10  $\mu\text{m}$  thick, thickenings on adaxial radial and abaxial radial walls extending slightly onto outer and inner tangential walls, bands on 2 sides of median wall alternating with each other in a mirror image; inner cells  $\pm$  5  $\mu\text{m}$  thick, with faint, ill-defined bands. *Spores* (Figure 1S) 12.5–16.0  $\mu\text{m}$  diam., globose, exine layer  $\pm$  smooth. *Elaters* (Figure 1T) 200–275  $\times$  10  $\mu\text{m}$ , with spiral band  $\pm$  10  $\mu\text{m}$  wide, tapering to unspiralled apices.

## DISCUSSION

The above description and illustration are based on a recent collection in Mpumalanga by M. Koekemoer. The plants grew on a fallen tree trunk lying across a stream at an altitude of 1 479 m. *R. amazonica* was also recorded from Lesotho by Hodgetts *et al.* (1999) at Bokong headwaters, Leribe Dist., altitude 3 000 m and was once collected at Hogsback, Eastern Cape (as *R. stephanii*) by Shaun Russell (Figure 3). It is surely more widespread in southern Africa, but I think one ought to disregard Arnell's (1963) reports of it from Western Cape (under *R. stephanii* and *R. campanuliflora*). It is not, however, intended to rule out entirely its possible presence in Western Cape.

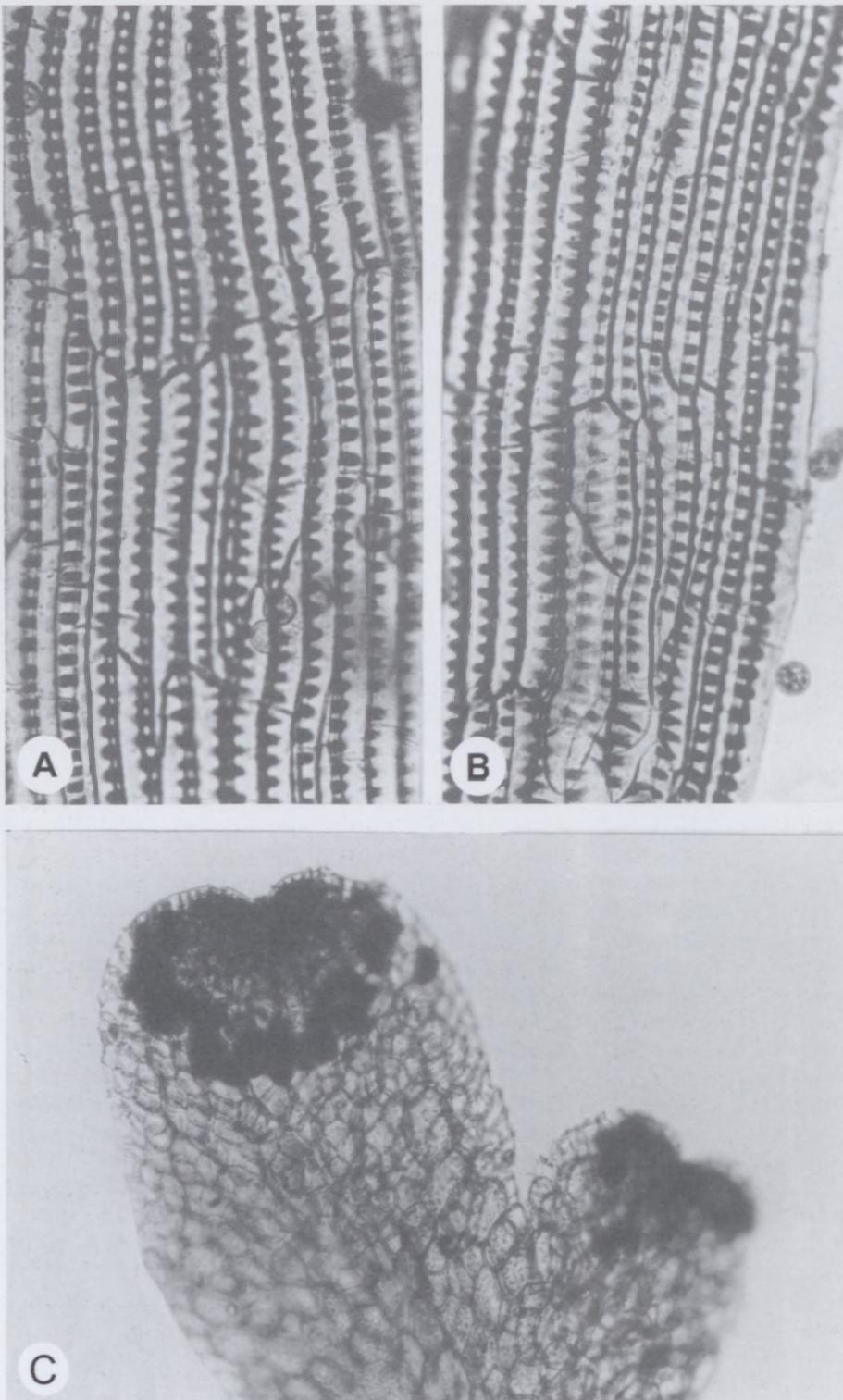


FIGURE 2.—*Riccardia amazonica*, Koekemoer 2217. A, cells of epidermal layer of wall of valve in external longitudinal view,  $\times 389$ ; B, cells of inner layer of wall of valve in internal longitudinal view,  $\times 389$ ; C, dark stained infestation at apices of primary and secondary branches,  $\times 194$ .

According to Meenks & Pócs (1985), *R. amazonica* is widespread in tropical Africa also in tropical South America (Meenks 1987).

Except for Spruce's (1885) original description of *R. amazonica*, there also are Stephani's (1901–1905), as well as one (not seen) in a manuscript by Meenks (Van Zanten & Gradstein 1988). Otherwise, all I could find are the short descriptions of its later synonyms by Stephani (1913, 1917–1924), as well as Jones's (1956) and Vanden Berghen's (1972) of *R. stephanii*. Meenks & Pócs (1985) give some notes on *R. amazonica*. Illustrations are also few, namely, Jones's (1956) drawings of *R. stephanii*, as well as Vanden Berghen's (1972), Stephani's *Icones*

(1985) and recently, Figure 67G–I of *R. amazonica* in Gradstein *et al.* (2001).

In a comparison of the type specimens of *R. amazonica*, *R. angusticosta*, *R. congoana*, *R. grosselimbata* and *R. stephanii* with the Koekemoer collection, the latter appears to be closest to *R. stephanii*, even sharing some kind of dark stained infestation (Figure 2C) in several of the apices of the ultimate segments of the main axes and quite a few of the primary branches in field-grown material. The male branches of *R. stephanii* are, however, considerably longer with up to 14 pairs of antheridia and conspicuous marginal cells. For the most part, the type specimens of the above synonyms are tiny plants, all

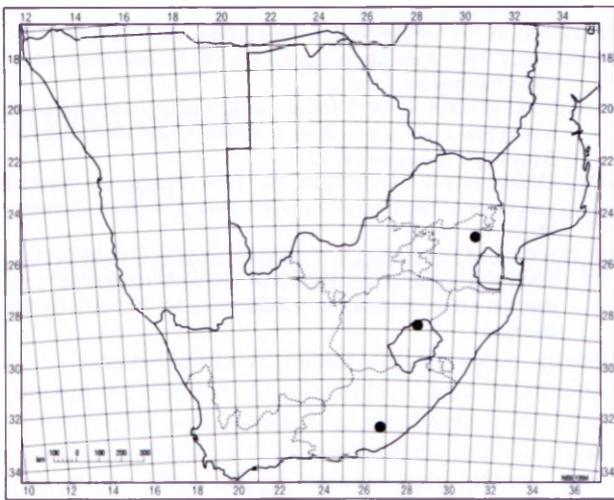


FIGURE 3.—Distribution of *Riccardia amazonica* in southern Africa.

growing on decaying wood. However, I have to agree with Jones (1956) that the resemblance between *R. stephanii* and Spruce's type gathering (of *R. amazonica*) 'is less close'.

In his study on polyploidy in some West African species of *Riccardia*, Berrie (1966) remarked that there were at least two races within a population of *R. stephanii*: one dioicous race with a chromosome number of 10 (diploid), the other monoicous with  $n = 20$  (tetraploid). There was also some indirect evidence of a third race with  $n = 40$ . With such diversity in the chromosome numbers of *R. stephanii* one could expect to find morphological diversity as well.

The Koekemoer collection is clearly dioicous. On the other hand, Meenks & Pócs (1985) found that the collections they studied from East Africa 'all proved to be monoicous', whereas the South American specimens were apparently dioicous. Jones (1956) described *R. stephanii* as 'monoicous, but often apparently dioicous', concluding on p. 81, 'it is not easy to demonstrate the monoicousness', though referring here to other species. Spruce (1885) described the calyptra of *R. amazonica* as encircled below by broadly cuneate-crenate external bracts, which alternate with shorter inner bracts. Only one row of paraphyses around the base of the calyptra was observed in the present study. Meenks & Pócs (1985) state that *R. amazonica* can be distinguished from related taxa 'by the absence of a wing along the main axis (occasionally a 1 or 2 cells wide wing is present near the branching points)'. According to Spruce (1885) the 'stem' is winged between the pinnae and cuneately widened. Serial cross sections of the main axis of *R. amazonica* that I cut, show a 2-cell wide wing on either side, particularly in male plants.

Jones (1956) described the oil bodies of *R. stephanii* as '1 or 2 per cell, spherical or oval,  $10\text{--}12 \times 10\text{--}15 \mu\text{m}$ , compound, of well-defined droplets c.  $2 \mu\text{m}$  diam.' Kis & Pócs (1997) report the oil bodies in *R. amazonica* as '1(–2) per cell,  $3\text{--}9 \times 18\text{--}40 \mu\text{m}$ ', and illustrate 2 together in one cell and another one in part of an adjoining cell; 2 are ovoid and 1 is vermiform, the latter quite unlike those in Jones's description of *R. stephanii*'s oil bodies as

well as my own findings. Stephani (1901–1905) placed *Aneura amazonica*, *A. stephanii*, *A. tenuicostata* Schiffn. and *A. vitiensis* Steph. together in the group 'Plantae parvae vel exiguae'.

*R. amazonica* specimens are distinguished by the following characters: 1, small, rather delicate, prostrate thalli, in 2 or 3 overlying layers; 2, branching on one side of main axis often poorly developed; 3, dioicous, with male thalli often somewhat smaller; 4, main axis with a 2-cell wide wing on either side, particularly noticeable in male thalli; 5, pinnae with unistratose wings, 2 or 3 cells wide, marginal cells entire to slightly crenulate; and 6, calyptra wall with papillae forming a corona at the top.

#### SPECIMENS EXAMINED

Koekemoer 2217. Mpumalanga. Lisabon Plantation bordering Buffelskloof Nature Reserve. Lisabon/Uitkyk concrete weir, on fallen tree trunk lying over stream, alt. 1 479 m (PRE).

Shaun Russell CH12618, N'tosana Forest. Hogsback (PRE).

Spruce MANCH cc1679, cc1687.

Also type specimens of the synonyms held at G, as listed under *Riccardia amazonica* (Spruce) Schiffn. ex Gradst.

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