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Seed coat structure in *Didissandra*, *Ridleyandra* and *Raphiocarpus* (Gesneriaceae)

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(With 6 figures)

Key words: Gesneriaceae, *Didissandra*, *Ridleyandra*, *Raphiocarpus*.
– Seed coat structure.

Abstract

The seed coat structure of *Didissandra*, *Ridleyandra*, *Raphiocarpus* (previously all placed in *Didissandra*) is investigated and discussed with regard to its taxonomic significance. While the species of *Didissandra* sect. *Didissandra* display a distinct and fairly uniform testa structure, the two species of sect. *Cyrtandroides* differ markedly, not only from sect. *Didissandra*, but also from each other. *Ridleyandra* has (with one or two exceptions) a very uniform and characteristic testa pattern. This is found both in the Malayan species (with long-tubed flowers; sect. *Ridleyandra*) and the Bornean ones (with short-tubed or flat-faced flowers; sect. *Stilpnothrix*) and thus confirms their congenerity. Seed coat structure in *Raphiocarpus* is heterogeneous, reflecting the obviously artificial nature of the genus.

Zusammenfassung

Die Samenoberflächen von *Didissandra*-, *Ridleyandra*- und *Raphiocarpus*-Arten werden untersucht und im Hinblick auf ihre taxonomische Bedeutung diskutiert. Während die Arten von *Didissandra* sect. *Didissandra* ein einheitliches Muster aufweisen, ist das bei den beiden Arten der Sektion *Cyrtandroides* nicht der Fall. *Ridleyandra* zeichnet sich ebenfalls durch einen sehr charakteristischen Testatyp aus. Dieser ist (mit wenigen Ausnahmen) in beiden Sektionen vertreten und verbindet damit die malaiischen Arten (mit langröhrigen Blüten; sect. *Ridleyandra*) mit den borneensischen (mit kurzhöhrigen bis flachkronigen Blüten; sect. *Stilpnothrix*). Die Testamorphologie der *Raphiocarpus*-Arten ist uneinheitlich, was als ein weiterer Hinweis auf die Künstlichkeit der Gattung gewertet werden kann.

Introduction

When trying to split the artificial genus *Didissandra* C. B. Clarke into more natural units (WEBER & BURTT 1998a), seed morphology was also

included in the character evaluation. The results are presented here in a separate paper, because the comparisons and number of illustrations would have gone beyond the limits of the general paper. Some results proved very significant for the circumscription of supraspecific taxa, others raise new problems.

Material & Methods

Seeds were removed from fruits of herbarium specimens, glued onto aluminium stubs, coated with gold, and photographed in a SEM JEOL T-300 at various magnifications.

The plants were for some part collected by the first author during field trips to Malaysia (1984, 1986, 1987), the others were obtained from the herbaria E, K, L, P, PE, W and WU.

List of taxa examined and source of material (the figures in parenthesis indicate the total number of species):

Didissandra sect. *Cyrtandroides* (2)

D. anisanthera B. L. Burtt: BURTT B. 12917, E.

D. frutescens Jack: WEBER 840805-1/2, WU.

Didissandra sect. *Didissandra* (8)

D. brachycarpa A. Weber & B. L. Burtt: DE WILDE & DE WILDE-DUYFJES 19467, L.

D. elongata Jack ssp. *elongata*: HORSFIELD s.n., s.d., Sumatra, BM (type); BORSSUM 1444, 1738, L; HOTTA & OKADA 184/9, L.

D. elongata ssp. *burleyi* A. Weber & B. L. Burtt: BURLEY, TUKIRIN & al. 1139, E.

D. elongata ssp. *montana* (Blume) A. WEBER & B. L. BURTT: KUHL & VAN HASSELT s.n., L (type of *D. montana* Blume).

D. elongata ssp. *minor* (Ridl.) A. Weber & B. L. Burtt: BURLEY, TUKIRIN & al. 1147, L.

D. sprengelii C. B. Clarke: BECCARI 679, K.

D. triflora C. B. Clarke: BROOKE 9588, L.

D. wildeana A. Weber & B. L. Burtt: DE WILDE & DE WILDE-DUYFJES 18797, 18866, L.

Ridleyandra sect. *Ridleyandra* (18)

R. atrocyanea (Ridl.) A. Weber: WEBER 870520-1/12, WU.

R. kerrii A. Weber: KERR 7608, K (type).

R. longisepala (Ridl.) A. Weber: WEBER 870623-2/4, WU.

R. morganii (Franch.) A. Weber: WEBER 870624-1/3, WU.

R. porphyrantha (Kiew & A. Weber) A. Weber: WEBER & ANTHONYSAMY 840711-1/3, WU (type).

R. quercifolia (Ridl.) A. Weber: VOGEL & WEBER 790822-1/2, WU.

R. stellata A. Weber: WEBER 870520-1/3, WU.

Ridleyandra sect. *Stilpnothrix* (5)

R. ornata (C. B. Clarke) B. L. Burtt: Native coll. 245, E; CHING S. 42153, L; PAIE 42552, L; RIDLEY 12311, BM.

R. rufa (C. B. Clarke) B. L. Burtt: ELSENER 240, E.

R. tenella (B. L. Burtt) B. L. Burtt: BURTT & MARTIN B. 5059, E.

R. sp. (aff. *tenella*?): CLEMENS & CLEMENS 34032, L.

Raphiocarpus (11)*R. clemensiae* (Pellegr.) B. L. Burtt: POILANE 31090, P.*R. sinicus* Chun: PAN K. Y. 9.8.1986, PE.*R. annamensis* (Pellegr.) B. L. Burtt: POILANE 12502, P.*R. begoniifolia* (Lévl.) B. L. Burtt: HENRY 9413B, E.*R. petelotii* (Pellegr.) B. L. Burtt: PETELOT 5039, P.*R. sesquifolia* : WILSON 5052, K.**Results***Didissandra*

The genus, formerly a waste-basket to which around 80 species (with a geographical distribution from S. China to Java) have been ascribed since its establishment by CLARKE (1883), emerged from the redefinition and revision as a genus of 8 species restricted to the Malay Peninsula, Sumatra, Borneo and Java (WEBER & BURTT 1998b). Two sections can be distinguished: sect. *Cyrtandroides* (with 2 species) and sect. *Didissandra* (6 species).

On grounds of the tall stature and the large flowers sect. *Cyrtandroides* appears as the more primitive part of the genus. In *D. frutescens*, occurring in the northeast of the Malay Peninsula, the seeds are broadly elliptical, sometimes with somewhat pointed ends. The length is c. 300 - 350 µm, width c. 200 - 230 µm, the l/w-ratio is 1,6:1 (for more precise figures see Table 1). The endothelial cells underlying the testa are large, polygonal and not very obvious in the intact seed. The testa cells are also polygonal, but as usual much smaller. The contiguous cell walls (side walls) are inconspicuous and scarcely visible, the outer cell surface appears striate by slightly raised, broad bars (Fig. 1 a, b). The orientation of the bars is oblique to the longitudinal axis of the seed and varies from cell to cell.

The seeds of the Bornean *D. anisanthera* are somewhat larger (Table 1), but similar in shape (l/w ratio c. 1,7:1). The testa structure is, however, very different. The contiguous cell walls are slightly thickened and fused to a single line, but in general very inconspicuous and difficult to see. From the middle of the cells, but also from peripheral parts (? side walls) there arise tongue-like structures with a smooth and plain surface. Sometimes they are somewhat bipartite and anvil-like. These structures are located on a distinct rise (pad) on the cell surface (Fig. 1 c, d).

Sect. *Didissandra*, from which – with the exception of *D. ternata* – all species could be investigated¹, proved uniform and distinctive. Size and

¹ Two species, *D. elongata* and *D. sprengelii*, were already investigated by BEAUFORT MURPHY (1983), but the reproduced seed photographs are not very informative. The third species of *Didissandra* s.lat. included in her work, *D. johorica*, is not relevant here; it must be referred to *Henckelia* (see WEBER & BURTT 1998b).

Table 1

Measurements and length/width-ratios of seeds of *Didissandra*, *Ridleyandra* and *Raphiocarpus*.

Species	Length (μm)	width (μm)	l/w-ratio (approx.)	number of seeds measured
<i>Didissandra</i> sect. <i>Cyrtandroides</i>				
<i>D. anisanthera</i>	479,00 \pm 20,00	276,67 \pm 33,29	1,7:1	3
<i>D. frutescens</i>	339,17 \pm 42,95	210,83 \pm 17,03	1,6:1	12
<i>Didissandra</i> sect. <i>Didissandra</i>				
<i>D. brachycarpa</i>	335,00 \pm 21,21	215,00 \pm 21,21	1,6:1	2
<i>D. elongata</i> ssp. <i>elongata</i> Hotta & Okada 184/9 (L)	426,67 \pm 27,14	295,83 \pm 42,94	1,4:1	6
<i>D. elongata</i> ssp. <i>burleyi</i>	315,83 \pm 25,18	161,67 \pm 23,17	2,0:1	6
<i>D. elongata</i> ssp. <i>montana</i>	430,00 \pm 42,43	310,00 \pm 14,14	1,4:1	2
<i>D. elongata</i> ssp. <i>minor</i>	415,00 \pm 42,43	242,50 \pm 31,82	1,7:1	2
<i>D. sprengelii</i>	405	260	1,6:1	1
<i>D. triflora</i>	392,50 \pm 10,61	212,50 \pm 10,61	1,9:1	2
<i>D. wildeana</i>	415,00 \pm 22,91	283,33 \pm 17,56	1,5:1	3
<i>Ridleyandra</i> sect. <i>Ridleyandra</i>				
<i>R. atrocyanea</i>	488,33 \pm 25,17	266,67 \pm 20,21	1,8:1	3
<i>R. kerrii</i>	521,25 \pm 25,32	201,88 \pm 18,70	2,6:1	8
<i>R. longisepala</i>	508,75 \pm 63,56	255,00 \pm 41,23	2,0:1	4
<i>R. morganii</i>	522,00 \pm 20,62	215,00 \pm 23,08	2,4:1	4
<i>R. porphyrantha</i>	474,62 \pm 44,32	203,85 \pm 17,34	2,3:1	13
<i>R. quercifolia</i>	630	185	3,4:1	1
<i>R. stellata</i>	440	226,50 \pm 2,12	1,9:1	2
<i>Ridleyandra</i> sect. <i>Stilpnothrix</i>				
<i>R. ornata</i>	452,13 \pm 33,62	184,33 \pm 17,51	2,5:1	15
<i>R. rufa</i>	435	190	2,3:1	1
<i>R. tenella</i>	460	270	1,7:1	1
<i>R. sp.</i> (aff. <i>tenella</i> ?)	380	200	1,9:1	1
<i>Raphiocarpus</i>				
<i>R. clemensiae</i>	421,00 \pm 15,17	244,00 \pm 2,24	1,7:1	5
<i>R. sinicus</i>	600,00 \pm 66,83	251,00 \pm 10,31	2,4:1	4
<i>R. annamensis</i>	432,50 \pm 31,82	250,00 \pm 14,14	1,7:1	2
<i>R. begoniifolia</i>	510	235	2,2:1	1
<i>R. petelotii</i>	730	220	3,3:1	1
<i>R. sesquifolia</i>	517,50 \pm 38,89	190,00 \pm 14,14	2,7:1	2

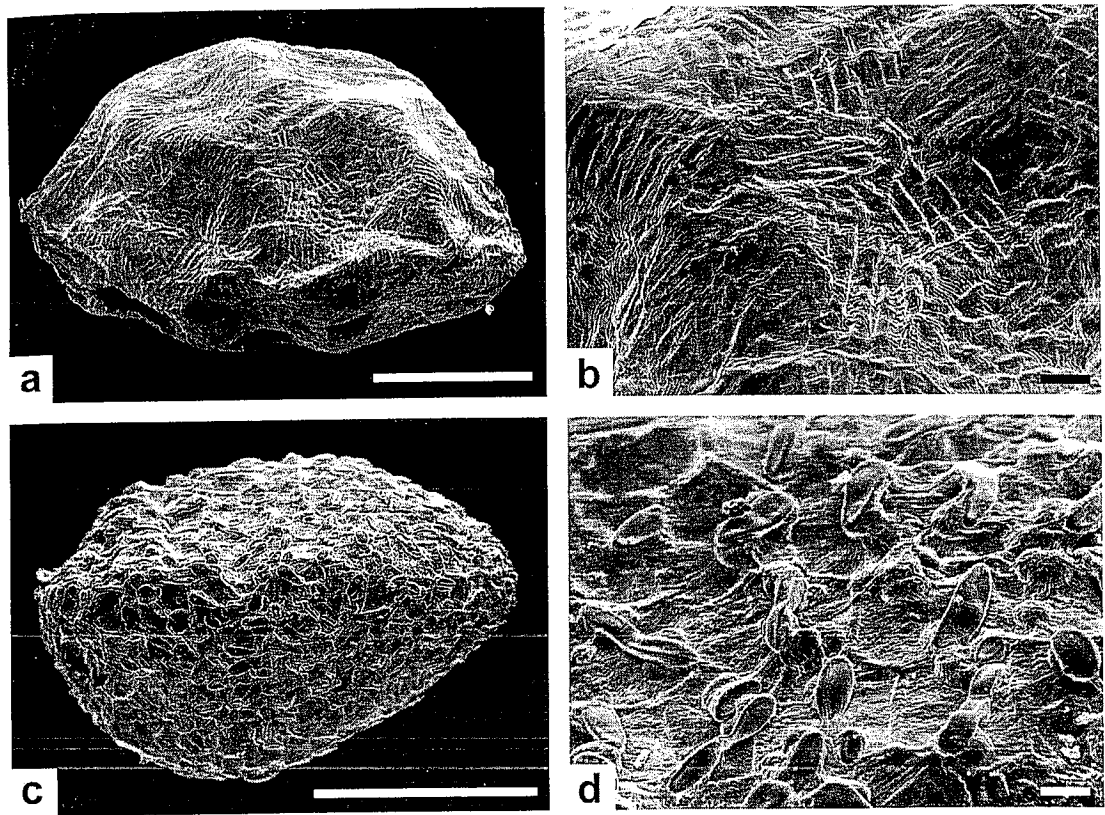


Fig. 1. a, b *Didissandra frutescens* (WEBER 840805-1/2, WU); c, d *D. anisanthera* (BURTT 12917, E). Bar: a, c 100 µm; b, d 10 µm.

shape is fairly similar as in sect. *Cyrtandroides* (l/w-ratio 1,5 - 2:1). The surface of the testa cells is plain, but the contiguous walls bear large, globose or apically flattened knobs. The knobs of the contiguous walls roughly alternate, so that pig-tail-like borders may be formed around the cells (Fig. 2 a-c). In *D. elongata*, the knobs sometimes become confluent, especially towards the seed apices (Fig. 2 d).

Ridleyandra

According to our revision (WEBER & BURTT 1998c) this segregate of *Didissandra* comprises some 23 species, 18 (forming the type section) occurring in the Malay Peninsula, the rest (sect. *Stilpnothrix*) in Borneo (including Natuna Islands). Seeds of 11 species (7/4 as to sections) were available for examination.

The seeds are larger than in *Didissandra*, at average c. 500 µm long and 200 - 250 µm broad. Shape is usually ellipsoidal, the l/w-ratio is often c. 2:1. The endothelial cells are scarcely recognizable from outside, a slight

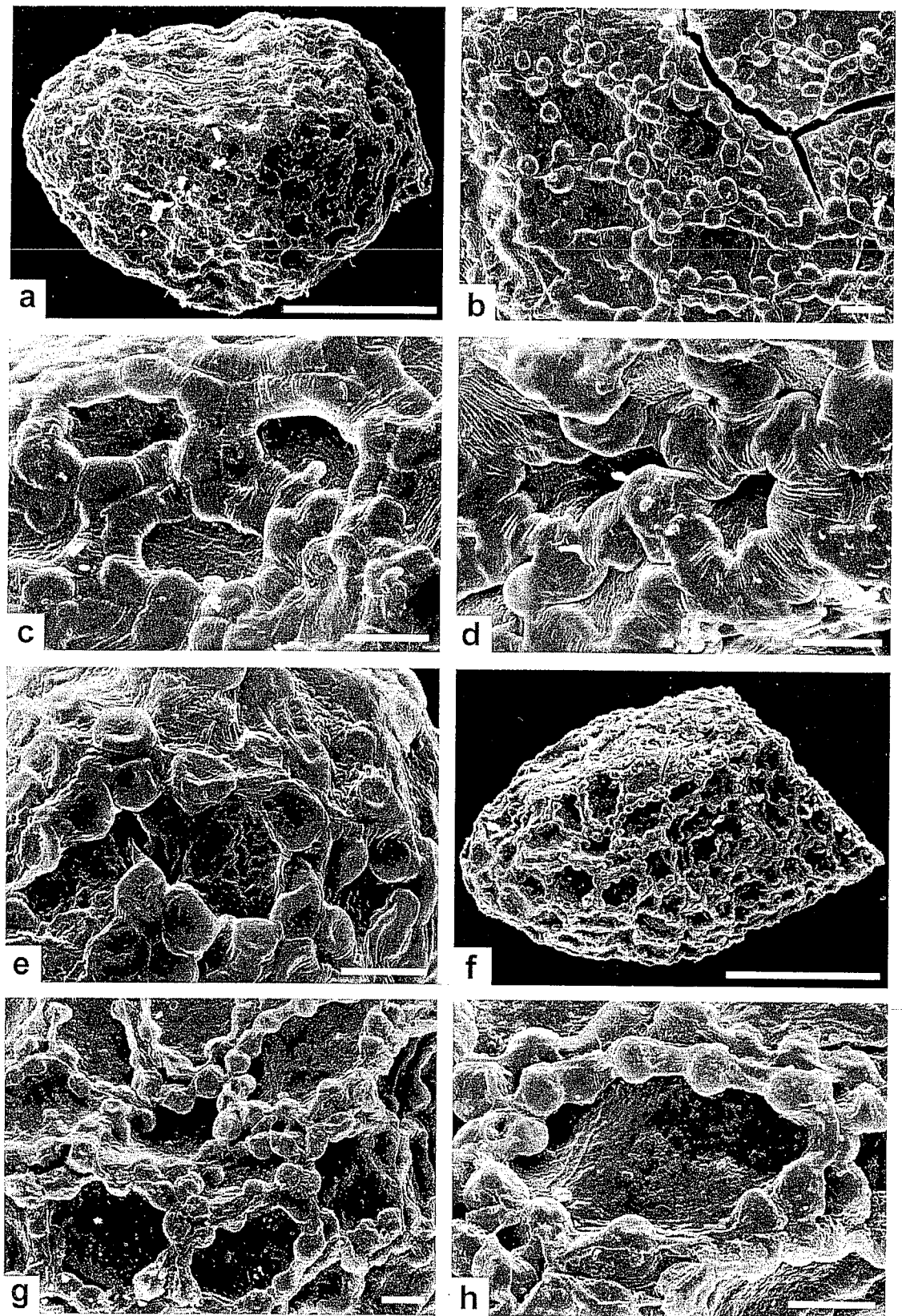


Fig. 2.a-c *Didissandra elongata* (BORSSUM 1444, L); d *D. elongata* (HOTTA & OKADA 184/9, L); e *D. triflora* (BROOKE 9588, L); f-h *D. wildeana* (DE WILDE & DE WILDE-DUYFIES 18797, L). Bar: a, f 100 µm; b-d, g-h 10 µm.

indication is found in *R. atrocyanea*. The testa cells are elongated in longitudinal direction, the contiguous cell walls are not prominently developed, sometimes scarcely visible. In the cell centre there is a distinct, narrow rectangular ridge (Fig. 3). The ridges are orientated in longitudinal direction and run fairly parallel. The ends of ridges show sometimes transversal side projections (Fig. 3 d). When the rows of testa-cells are in strict line, the ridges of these cells fuse at the narrow ends and run over some longer distance (especially to be seen in *R. rufa*, Fig. 3 f).

There is, however, a remarkable exception: *R. tenella*. This curious tiny plant has seeds of a quite different appearance. Here the central ridges are lacking and the contiguous cell walls exhibit conspicuous half-moon- or sickle-shaped thickenings (Fig. 4 a, b).

There is another plant [listed as *R. sp.* (aff. *tenella*?)], possibly a new species and related to *R. tenella* (4 c, d), which has similar thickenings along the contiguous walls.

Raphiocarpus

This segregate of *Didissandra* includes two shrubby species; seeds of both have been examined (for measurements see Table 1). The one is *R. sinicus*, the type species of the genus (Fig. 5 a, b), the other *R. clemensiae* (Fig. 5 c, d). The seeds of both species are similar in the form of the endothelial cells and the surface structure. The endothelial cells are transversally narrowed, with the borders forming conspicuous transversal ridges. In contrast, the testa cells covering the endothelial cells are elongated in longitudinal direction. Along the contiguous walls there are disc-like thickenings with flat or slightly depressed upper surface. In form and sometimes alternate arrangement they are reminiscent of those in *Didissandra*, but the cells and the thickenings are distinctly smaller.

The seeds of four herbaceous species were available for investigation (in the remaining ones, ripe fruits are unknown). In *R. sesquifolius*, *R. begoniifolius* and *R. petelotii* the seeds are similar to some extent. Particularly in the latter two species the large, polygonal endothelial cells can be well seen, forming longitudinal rows. Seed shape is ellipsoidal, in *R. petelotii* tending to be spindle-shaped (l/w-ratio over 3:1). The surface of the testa cells is without distinct ornamentation. The contiguous walls are completely fused to a unitary crest (semicircular in transverse section). The seeds of *C. annamensis*, however, have a quite different appearance: the polygonal endothelial cells are rather irregularly arranged; the testa cells have very indistinct side walls and are evenly and densely studded with small hemispherical, elliptical or reniform protuberances (Fig. 6 g, h).

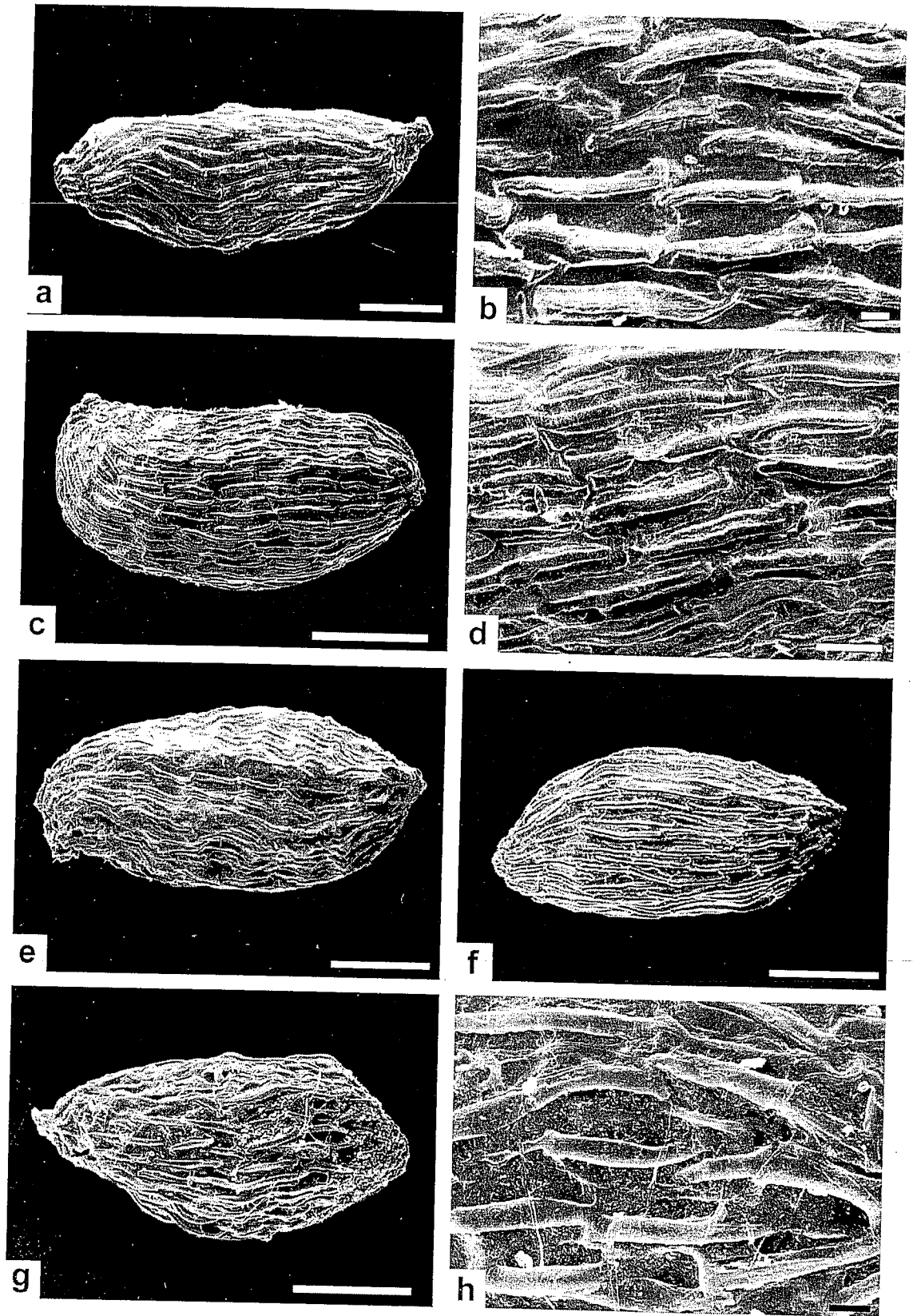


Fig. 3. a, b *Ridleyandra porphyrantha* (WEBER 840711-1/3); c, d *R. longisepala* (WEBER 870623.2/2, WU); e *R. atrocyanea* (WEBER 870520-1/12, WU); f *R. rufa* (ELSENER 240, E); g, h *R. ornata* (CHING S. 42153, L). Bar: a, c, e-g 100 μ m; b, d, h 10 μ m.

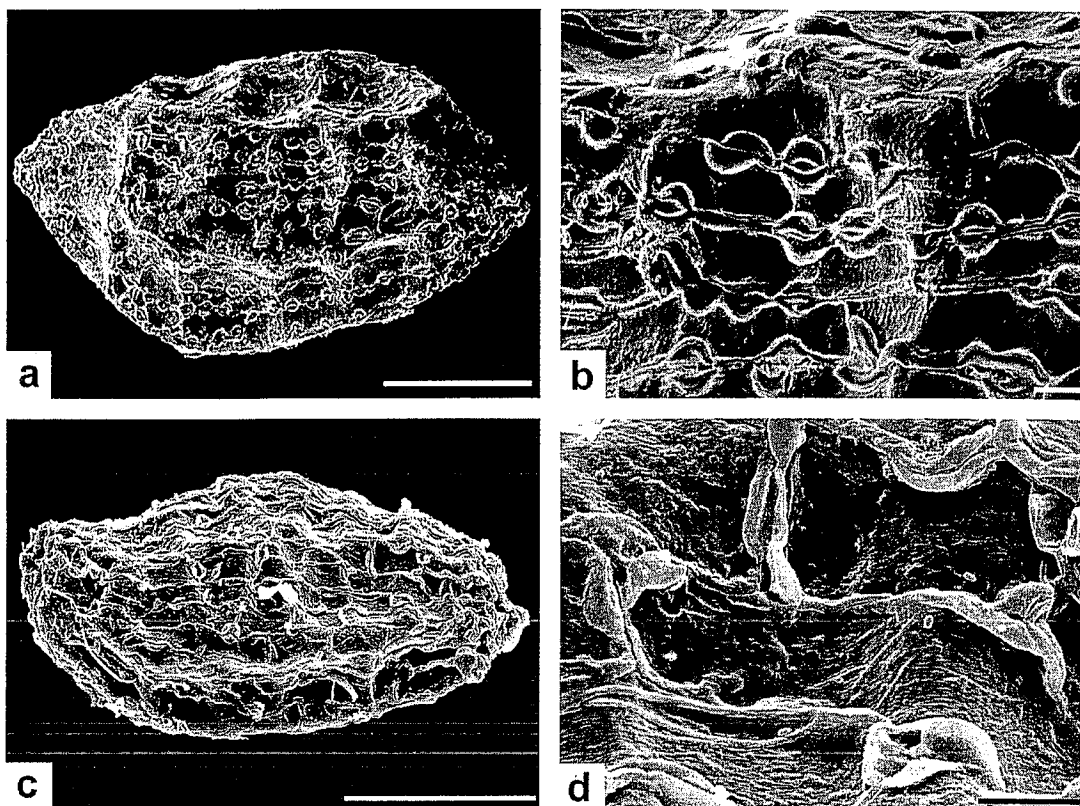


Fig. 4. a,b *Ridleyandra tenella* (BURTT & MARTIN B. 5059, E); c, d *R. sp.* (aff. *tenella*?) (J. & M. S. CLEMENS 34032, L). Bar: a, c 100 μ m; b, d 10 μ m.

Discussion

Seed morphology indeed seems to provide significant characters for the separation and delimitation of the species and species groups formerly ascribed to *Didissandra*.

(1) *Didissandra*. Within *Didissandra* s. str. the type section is remarkably distinctive and uniform. The seeds can be recognized at once by the moniliform borders of the testa cells. The similarity exhibited by all species² demonstrates that the relationship is very close. It is particularly important to note that *D. triflora*, which has only two fertile stamens and which has formerly been sometimes regarded as a *Didymocarpus*, fits well into *Didissandra* by its seed characters.

The two species of sect. *Cyrtandroides* differ remarkably, not only from sect. *Didissandra* but also from each other. Though on the one hand,

² Only *D. ternata* could not be examined; but this is certainly closely related to *D. elongata*, differing only by the ternate leaves that are glabrous on the upper side.

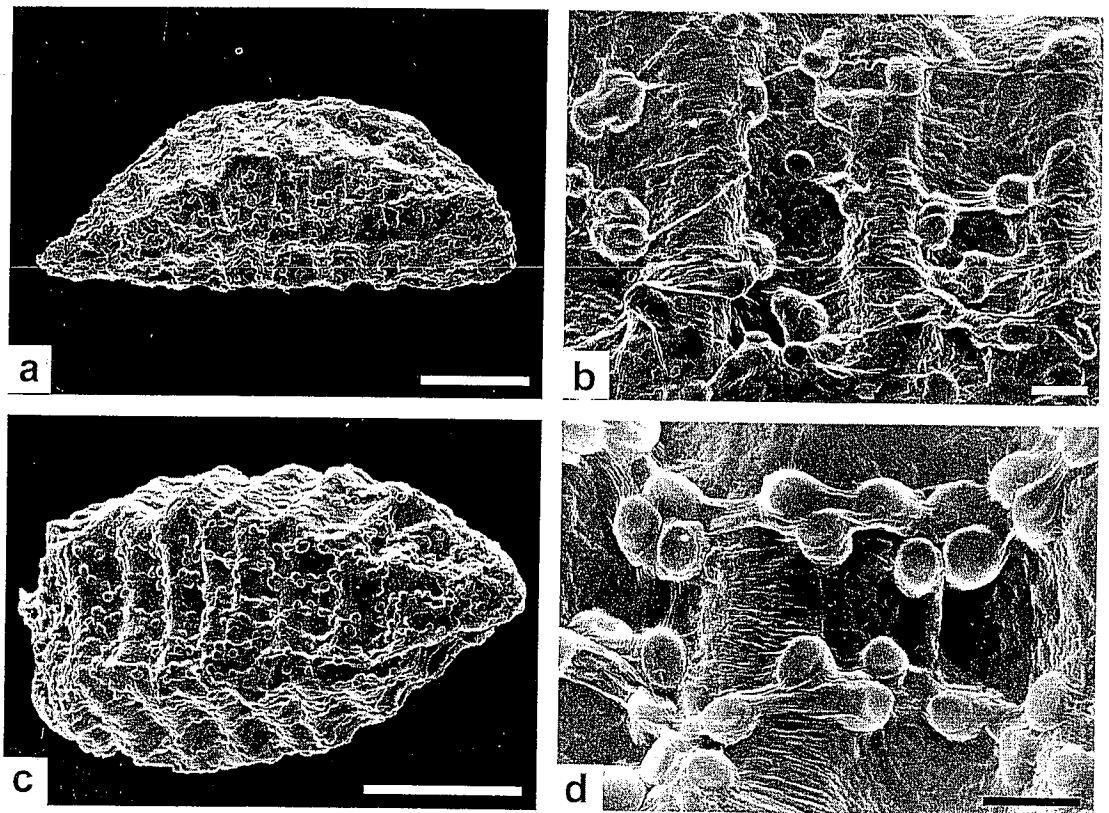


Fig. 5. a, b *Raphiocarpus sinicus* (PAN KAY-YU s.n. 1987, PE); c, d *R. clemensiae* (POILANE 31090, P). Bar: a, c 100 μ m; b, d 10 μ m.

there is little doubt that the two species are related (the habit, flower and fruit characters are in good accordance), the different seed structure may be seen in relation to the remote geographical distribution (NE Malay Peninsula vs. Borneo) which points to an ancient event of speciation.

(2) *Ridleyandra*. In this new genus seed morphology is most characteristic and remarkably uniform. In particular, the surface characters demonstrate that the Malayan species with their long-tubed flowers (sect. *Ridleyandra*) and the Bornean species with short-tubed to flat-faced flowers (sect. *Stilpnothrix*) are closely related, so that they can be placed in a single genus.

The anomalous seed structure of *R. tenella*, however, raises the question if that species (and another similar, undescribed plant) has its correct position in *Ridleyandra* or eventually belongs to a separate genus. More information on other characters is needed before a decision can be made. The transfer to *Ridleyandra*, therefore, must be regarded as a provisional measure.

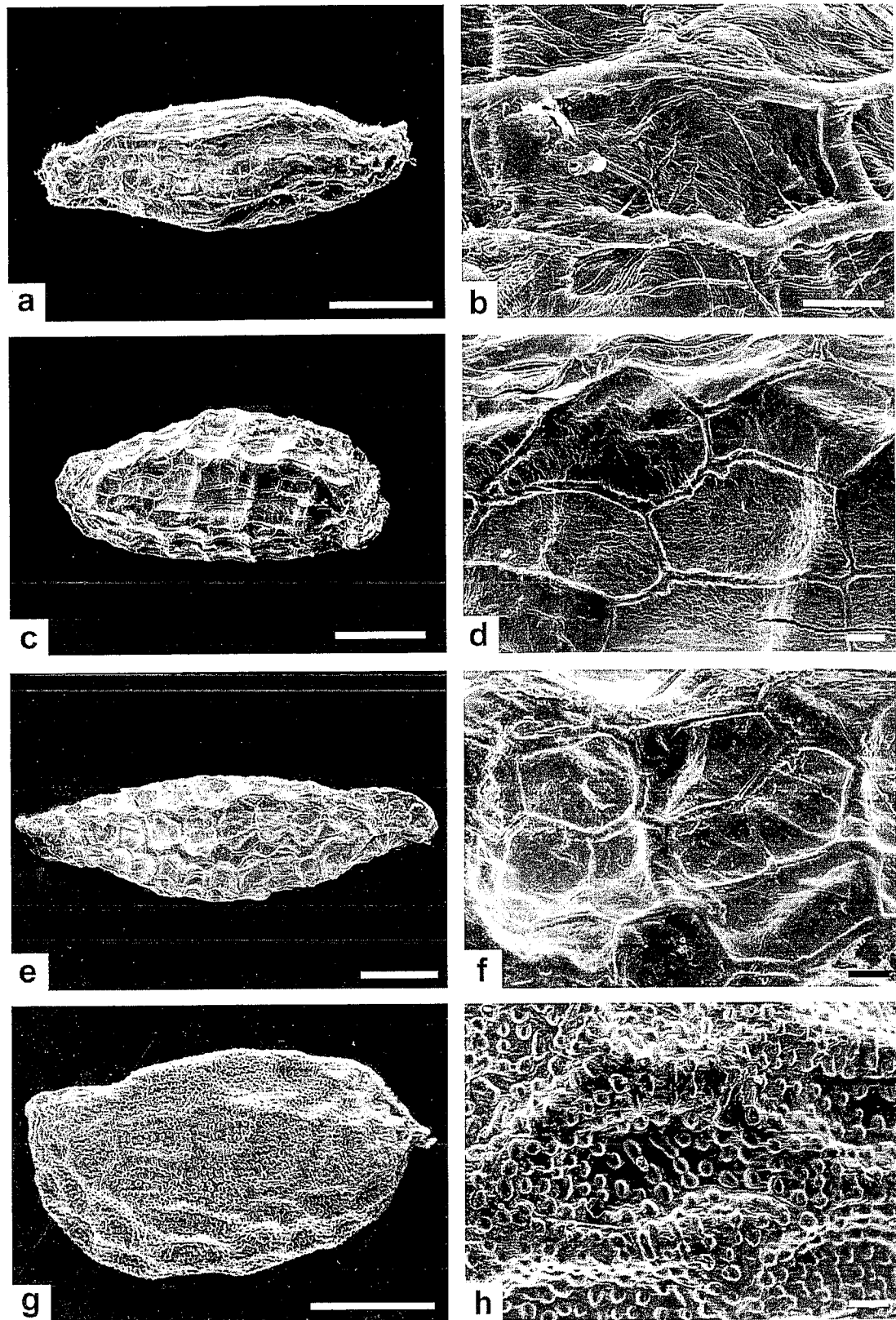


Fig. 6. a, b *Raphiocarpus sesquifolius* (WILSON 5052, K); c, d *R. begoniifolius* (HENRY 9413B, E); e, f *R. petelotii* (PETELOT s.n., VIII 1931; P); g, h *R. annamensis* (POILANE 12502, P). Bar: a, c, e, g 100 µm; b, d, f, h 10 µm.

(3) *Raphiocarpus*. The two shrubby species of *Raphiocarpus* fit quite well into a single pattern. The herbaceous *R. sesquifolius*, *R. begoniifolius* and *R. petelotii* also hang together. *R. annamensis*, however, has a quite different seed. The remaining species, and several undescribed plants from Vietnam, lack fruiting material, make it impossible to reach final decisions on the limits of *Raphiocarpus*.

In habit *R. sesquifolius* is morphologically quite distinct by its single, apical, strongly anisophyllous leaf pair. The support from seed morphology, that other species show a very similar (though simple and wide-spread) testa-pattern, is welcome. On the other hand, the quite distinctive type found in *R. annamensis* strengthens the view that *Raphiocarpus* may be a very heterogeneous assemblage of tetrandrous species (see WEBER & BURTT 1998c). Unfortunately, the individual species are very ill-known and little can be done to clarify the situation until new and better collections become available.

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