

Studies in Cyperaceae in southern Africa 26: Glume epidermal silica deposits as a character in generic delimitation of *Costularia* and *Cyathocoma* as distinct from *Tetraria* and other allies

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Differences of opinion encountered in the generic placement of species that fall within *Costularia* C.B. Clarke, *Cyathocoma* Nees (= *Macrochaetium* Steud.) and *Tetraria* P. Beauv., are outlined and attention is drawn to the inadequate documentation of Cape species and genera of the tribe *Schoeneae* Dum., particularly in relation to possible extra territorial relatives.

Using results obtained from electron scanning of surface topography of the epidermal cells of the flanks of mature glumes, a case is made for the resuscitation of an already well-known technique, namely, the microphotography of nail varnish imprints, as a cheap and rapid means of contributing to the reliable generic identification collectively, of *Costularia* and *Cyathocoma*, as distinct from *Tetraria*, *Epischoenus* and *Carpha*.

Meningverskille wat teëgekomp is in die generiese plasing van spesies wat binne *Costularia* C.B. Clarke, *Cyathocoma* Nees (= *Macrochaetium* Steud.) en *Tetraria* P. Beauv. val, word omskryf en aandag word gevestig op die onvoldoende dokumentasie van Kaapse spesies en genera van die tribus *Schoeneae* Dum., veral in verband met moontlike bykomende territoriale naverwante.

Resultate verkry deur elektronafasting van die oppervlak-topografie van epidermale selle van die sye van volwasse kelkkaffies, word gebruik om gronde aan te voer vir die heringebruikname van 'n reeds goed bekende tegniek, naamlik die mikrografiese van afdrukke in naelpolitoer, as 'n goedkoop en vinnige middel wat kan bydra tot die betroubare generiese identifikasie, gesamentlik, van *Costularia* en *Cyathocoma*, in teenstelling met *Tetraria*, *Epischoenus* en *Carpha*.

Keywords: Silica bodies, glume epidermal cells, *Costularia*, *Cyathocoma*, *Tetraria*.

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Introduction

In southern Africa, genera that fall within the tribe Schoeneae Dum. (Goetghebeur 1986: 697 et seq.) are in need of study in relation to possible relatives on other land masses. Some of these genera are regarded as southern African endemics, for example *Epischoenus* C.B. Clarke, *Trianoptiles* Fenzl [= *Ecklonea* Steud.], *Neesenbeckia* Levyns and *Macrochaetium**. Others, such as *Carpha* R. Br., *Costularia* C.B. Clarke and *Tetraria* P. Beauv., while being represented in southern Africa, have outliers especially in the east, that may or may not require transfer or generic recognition in their own right. *Schoenus* L., presently regarded as predominantly south-eastern Asian and Australian, has two subcosmopolitan species, one of which is sparsely represented in southern Africa. *Epischoenus* is very closely affiliated.

Goetghebeur (1986: 702) holds the opinion that in Schoeneae there are genera that may be regarded each as a 'nucleus', surrounded by others closely related morphologically that may be termed 'satellite' genera. This is well supported by the taxo-

nomic history of members of the tribe that have been subjected to generic transfer by different workers according to data available to them and their own perceptions of generic limits. The positioning of some species is straightforward; however, others are still uncertainly generically attributed. *Tetraria brevicaulis* C.B. Clarke [= *Costularia brevicaulis* (C.B. Clarke) C.B. Clarke] is one such equivocal example. *Macrochaetium ecklonii* (Nees) Levyns and *M. hexandrum* were maintained as distinct from *Tetraria* by Levyns (1947: 80) only because of imperfect knowledge of the group as a whole. However, her contention that transfer to *Tetraria* might be necessary was not supported by the later work of Metcalfe (1971: 369), who described a type of silica body in the leaf epidermis of *Macrochaetium* that had not been reported for *Tetraria*. Koyama (1961: 74) also took a wide view by including *Costularia*, *Macrochaetium* and *Epischoenus* within *Tetraria*, but study of the epidermal tissue of leaves and associated silica deposits did not support such amalgamation. Metcalfe (1971: 516) found 'No close similarity between *Costularia* and *Tetraria*...' and (l.c.: 179) '*Costularia* shows no marked resemblance to *Tetraria* in which it is placed by Koyama'.

Instability pertains and will continue while knowledge is inadequate.

This article is concerned with silica bodies and associated features of the abaxial epidermal cells of the flanks of glumes of some of the controversial taxa already named. Glumes are generally interpreted as reduced and specialized leaves that subtend florets and therefore our results should correlate with results from Metcalfe's investigations on foliage leaves. The technique employed is not new; perhaps it is somewhat neglected as a simple and rapid procedure helpful in preliminary identification. It needs wide application to explore its reliability and usefulness as

*Note: Goetghebeur (1986: 779) pointed out that *Cyathocoma* Nees (type species *C. ecklonii* Nees), which dates from 1834, has priority over *Macrochaetium* Steud. [type species *M. hexandrum* (Nees) Pfeif.] published in 1855. The relationship between these two species is very close indeed. We believe they are not distinct at generic level; therefore, we follow Goetghebeur (1986: 799) in recognizing both as species of *Cyathocoma*. However, the combination *C. hexandra* (Nees) Goetgh. was provisional (Goetghebeur 1986: 799) and has not yet been published. As this species is considered in the text that follows, the later generic name *Macrochaetium* will be used in place of *Cyathocoma* in this article. According to Simpson (1993: 8-12), neither *Cyathocoma* nor *Macrochaetium* are recognized at K, BM or E. Both are placed under *Tetraria*.

another criterion of generic delimitation. It does not serve in species distinction.

Materials and Methods

Procedure for preparation of slides for study with light microscope

Clear nail varnish was thinly applied to a small area of the flank of a glume. After 2–3 h, this varnish was peeled off using fine-pointed forceps and placed on a glass slide in a drop of Gurr's Aquamount Mountant. The side of the impression that had been in contact with the glume tissue was always kept uppermost. A cover slip was applied. Representative preparations were photographed using an Olympus BH2 photomicroscope.

Procedure for electron scanning preparations

A glume was mounted on a stub by means of double-sided aluminium foil on double-sided cello tape, then sputter-coated with gold-palladium by means of a Polaron E 5100 sputter coater. Stubs were viewed under an Hitachi S 570 scanning electron microscope.

Selection of plant material

Herbarium specimens of the various taxa to be studied that carried a satisfactory number of well-developed spikelets were selected. Spikelets at approximately the same stage of development (early maturity) were used throughout for uniformity. A glume positioned midway up the length of a spikelet was treated with varnish; another glume from a comparable position on the same, or another spikelet, was removed for electron scanning.

Results

The procedure followed for the preparation of slides for study with the light microscope produces an impression of the glume surface. Projections from the glume surface are therefore represented by depressions which show in the photographs as darker spots (Figures 1B,D,F,H,J,L). Electron scanning microscopy shows the glume surface topography with projections from the surface visible as raised 'warts' or very much smaller 'pimple'-like outgrowths (Figures 1A,C,E,G,I,K). Each genus investigated was considered individually and by means of one representative species. Only if species within a genus differ significantly were more than one species considered.

Costularia

Representative species: *C. natalensis*

Metcalfe (1971: 178) wrote of this genus as follows:

'The species of *Costularia* from Africa and Madagascar that have been examined are unusual amongst the Cyperaceae owing to the presence of small cones or sand-like bodies associated with sinuations in the anticlinal walls of the epidermal cells of the leaf. Although the exact nature of these bodies has not been determined, it seems that they may, so to speak, be a substitute for the conical silica-bodies that occur in most Cyperaceae. In this respect these species differ from *C. paludosa* [(R. Br.) C.B. Clarke = *Tricostularia paludosa* (R. Br.) Benth.] from Queensland, Australia, and *C. pilisepala* [(Steud.) Kern] (*urvilleana*) [= *Lophoschoenus urvilleanus* Stapf] from North Borneo with their coarsely nodular silica-bodies.'

Our study of *C. natalensis* showed conclusively that the 'small cones or sand-like bodies' described by Metcalfe were present as projections from sinuations in the anticlinal walls of epidermal cells of the glume flanks (Figure 1A). In all specimens examined, larger projections were also present. These were located at one end only of a cell, and did not exceed one per cell. Some variability in the degree of their development was evident; either they

projected as 'warts', or they caused raising of the height of the cell above the general surface without being as well defined as a 'wart'. Metcalfe (1971: 172) termed these 'papillae' or 'silicified papillae' or 'silica bodies', dependent, it would seem, upon the degree of prominence and visibility of the silica body within the papilla, and the extent of protuberance of the papilla above the leaf surface. The papillae and the sand-like bodies impart a feeling of roughness to the glume surface that may be detected by touch (glumes asperulous or scabrous).

C. melleri C.B. Clarke

We found the glume flank topography to differ somewhat from that of *C. natalensis*. The small cones or sand-like bodies were closer together and did not project as clearly as in *C. natalensis* (Figure 1A). Papillae were lacking. We examined glumes from the same specimen, the leaves of which were examined by Metcalfe [*Baron 2846* (K)]. Metcalfe (1971: Figure 25D) illustrated the sand-like silica bodies of a single epidermal cell, but showed no papilla or larger silica body. This author did not differentiate *C. melleri* from *C. natalensis*, nor did he comment upon differences observed (Metcalfe 1971: 172, under silica bodies).

C. pilisepala [= *Lophoschoenus urvilleanus*]

Metcalfe (1971: 174 & Figure 26E) found epidermal cells of the adaxial leaf surface lacking the sinuations of the anticlinal walls that are a feature of species from Africa and Madagascar. These cells also differed in shape and in their contents, 'some [were] filled with finely granular material of undetermined nature, but others [were] apparently filled with silica'. We found glume structure to agree with leaf structure as described by Metcalfe (above). Examination for texture proved the glumes to be smooth, not asperulous or scabrous to the touch as for *C. natalensis* and other African and Madagascan species of the genus.

Macrochaetium

Representative species: *M. hexandrum*

Our findings for this species agree with those of Metcalfe (1971: 367 & Figures 6A–C, p. 17). The small spicular luminal projections are difficult to observe in Figure 1C, but they are present. They are more readily seen in Figure 1E, lower right (*M. ecklonii*). The texture of the glumes was asperulous, as in *Costularia*.

Tetraria

Representative species: *T. cuspidata*

Figure 2H shows the appearance of abaxial epidermal cells of the flank of a glume. The silica bodies are luminal. There is no evidence of the 'small cones or sand-like bodies associated with sinuations in the anticlinal walls' that characterize cells in the epidermal cells of *Macrochaetium* and *Costularia*.

Variability in cell size and in the number of luminal conical bodies per cell and in the presence or absence of satellites in association with these bodies was found in the range of species studied, but there was no trace at all of the small cones characteristic of *Macrochaetium* and *Costularia*.

Epischoenus

Representative species: *E. complanatus*

According to Metcalfe (1971: 251), silica bodies in this genus consist of very small bodies of variable shape set in what appear to be flanges developed from the anticlinal walls of the epidermal cells. Figure 2K should be compared with Metcalfe's (1971) Figure 33C. These differ from the arrangement of silica bodies in the anticlinal walls of *Macrochaetium* and *Costularia*. No confusion of genera on the basis of epidermal silica deposits is likely.

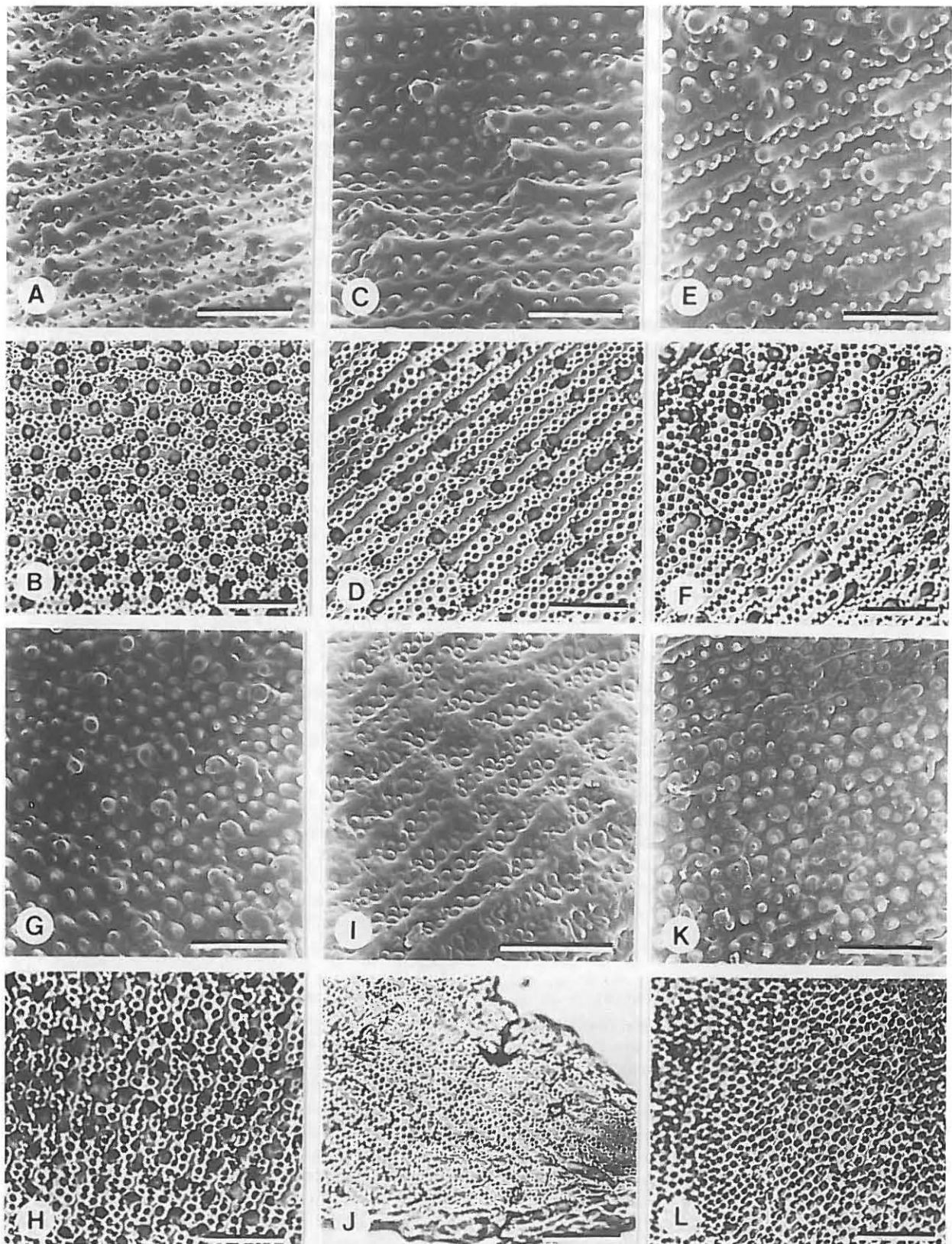


Figure 1 Glume surfaces of species of *Costularia* (African and Madagascan) and *Macrochaetium*; SEM and photomicroscopy of nail varnish impressions. A, B, C. *natalensis*, Browning 579 (NU). C, D, *M. hexandrum*, Levyns s.n. (BOL 57552). E, F, *M. ecklonii*, Esterhuysen 20067 (BOL). G, H, *C. baroni*, Baron 3316 (K). I, J, *C. melleri*, Meller s.n. (K). K, L, *C. pantopoda* var. *grandispicus* Perrier de la Bathie 2729 (K). Scale bars: A, C, E, G, I, K (SEM): 50 μ m; B, D, F, H, J, L (photomicroscopy of nail varnish impressions): 100 μ m.

Carpha

Representative species: *C. filifolia*

Glume flank cells in this species are long and narrow, often lack-

ing silica bodies. When present, the small 'cone-shaped' bodies are regularly placed in a single, central line in the cell lumen. In our experience, relatively few files of cells contained bodies, but

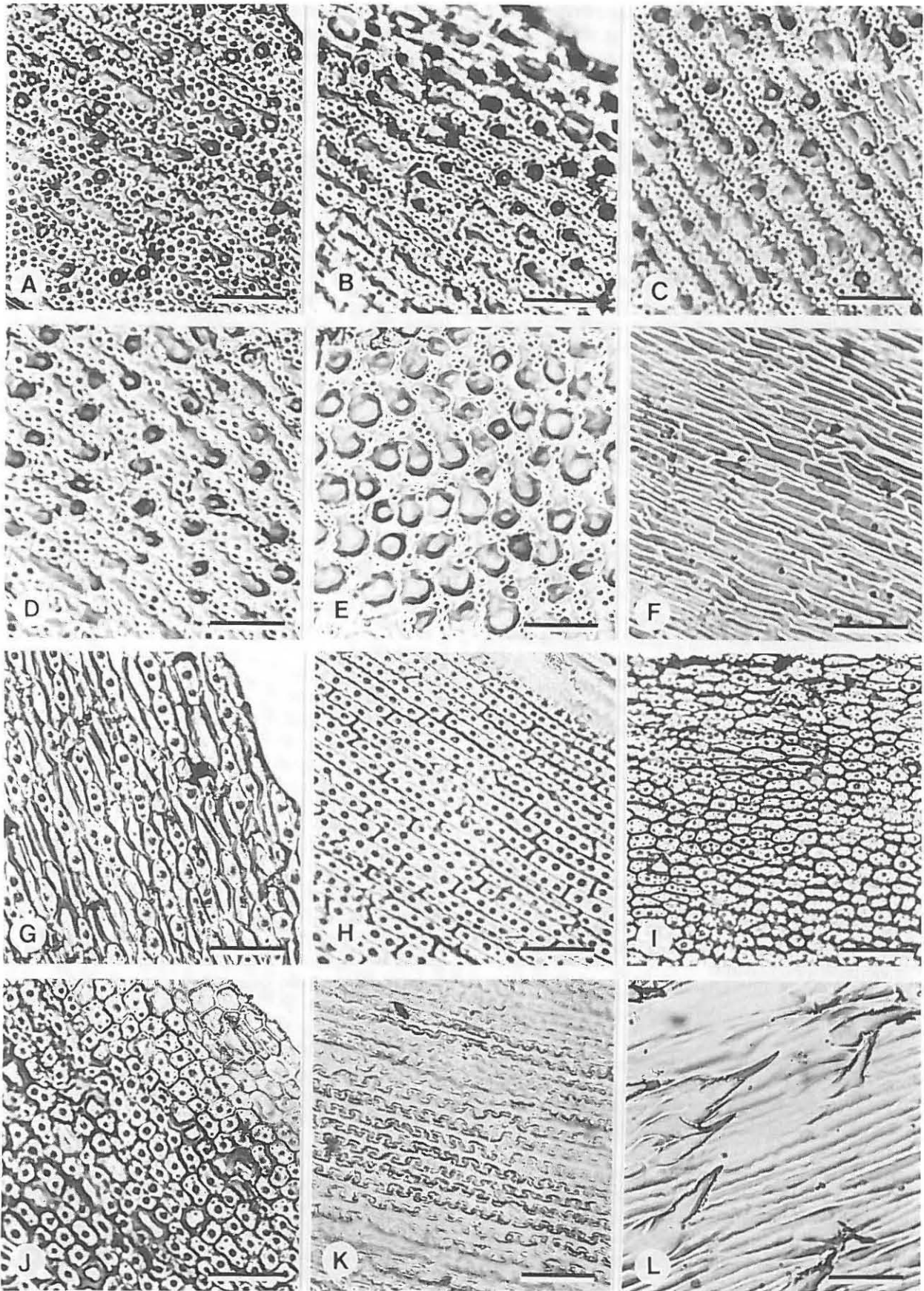


Figure 2 Glume surfaces (photomicroscopy of nail varnish impressions). *Tetraria bachmannii*, note relationship to *Macrochaetium*, **A**, Moll 4789 (NU); **B**, Venter & Vorster 107 (NU); **C**, Balkwill & Manning 423 (NU). *Costularia brevicaulis*, **D**, Henderson 1286 (NU), mature glume; **E**, Williams 3084 (NU), very young glume; *C. pilisepala*, **F**, Clemens J. & M.S. 51062 (MICH). *Tetraria*, **G**, *T. robusta*, Browning 384 (NU); *T. cuspidata*, **H**, Browning 561 (NU); *T. usambarensis*, **I**, Tait s.n. [Tanganyika 1949], (NU); **J**, *T. fimbriolata*, Getliffe 1123 (NU). *Epischoenus*, **K**, *E. complanatus*, Esterhuysen 8181 (BOL). *Carpha*, **L**, *C. glomerata*, Browning 228 (NU), note impressions of epidermal hairs. Scale bars: A-L, 100 μ m.

this may differ with the provenance of the plants examined. No trace was found of small, sand-like bodies in the anticlinal walls that characterize *Macrochaetium* and *Costularia*.

Discussion

Results we derived from the study of silica bodies contained within the epidermal cells of the flanks of glumes, correlated with the findings of Metcalfe (1971) for foliage leaves. This confirmation supported our belief that the use of nail varnish as a coating to give an impression of surface topography provides a simple, effective, cheap and reliable method by which members of the genera *Macrochaetium* and *Costularia* can be distinguished from members of allied genera (*Tetraria*, *Epischoenus* and *Carpha*).

Further, to test this hypothesis, we used the method for the re-identification of certain species and exsiccata that previously were in doubt. Our findings follow.

Costularia brevicaulis [= *Tetraria brevicaulis*]

Representative specimens clearly showed the silica bodies of the glume flanks to relate to those of species of *Costularia*, not *Tetraria*.

Tetraria bachmannii Kük.

Moll 4789, because of the presence of six stamens, was placed under *Macrochaetium hexandrum* by Gordon-Gray (1972: 111). Continuing investigation revealed unacceptable differences from that species. Lacking further material following unsuccessful attempts at re-location, this specimen, and *Balkwill & Manning 423* in which spikelets are very young, were tentatively transferred, pending availability of further material of both numbers, to *Tetraria* (Gordon-Gray, in press). We are indebted to C. Archer (PRE) for an additional specimen (*Venter & Vorster 107*) and for information that the three exsiccata referred to are representatives of a taxon originally placed by Clarke (1894: 663) as a variety of *Tetraria thurii* P. Beauv. (syntypes: Pondoland, *Bachmann 66, 67*). *Tetraria thurii* sensu Clarke (1898: 289–290) and Kükenthal (1940: 244–245) was shown to be *Macrochaetium ecklonii* (Levyns 1947: 77).

The silica bodies of epidermal cells of the glume flanks of *Moll 4789* (Figure 2A), *Venter & Vorster 107* (Figure 2B) and *Balkwill & Manning 423* (Figure 2C) are those of *Macrochaetium*, not *Tetraria*. Transfer will depend upon the assessment of a totality of morphological features.

Costularia pilisepala (Steud.) Kern and *Tetraria borneensis* Kern

These species, both Malesian, have not been incontrovertibly placed. Kern (1974: 664) listed seven features by which *Tetraria borneensis* was assigned to *Tetraria*, but stated that there were strong affinities with *Costularia pilisepala*, the only member of *Costularia* in Malesia.

Goetghebeur (1986: 790) critically considered differences between *Tetraria* and *Costularia*, but stated that without further special investigation of the auricles of stamens in *Costularia* and the embryography of *T. borneensis*, he was not prepared to pass opinion on the critical generic placing of the two Malesian species under discussion.

Our findings from glume epidermal silica bodies are that *C. pilisepala* (Figure 2F) does not conform with the African and Madagascan species of *Costularia* as the cell walls are straight, not convolute, and lack sand-like silica deposits, while cone-shaped silica is absent from the lumina. We believe the species fits more precisely with species from New Caledonia.

The epidermal silica conformation of *T. borneensis* does not fit

with that of either *Costularia* or *Macrochaetium* as described and illustrated in this study. In our opinion the two florets with six stamens each in this species indicates a possible relationship with *Macrochaetium* of southern Africa, but the number and size of the spikelets, and the position of the bisexual floret, relate more closely to *Costularia*.

Costularia and *Macrochaetium*

The conformation and placement of the silica bodies in epidermal cells of leaves and glumes of these genera suggest a close relationship between them – far closer affinity than exists between either genus and *Tetraria*, or *Epischoenus*, or *Carpha*.

On this same criterion, differences distinguishing *Costularia* and *Macrochaetium* are of degree only. The main distinction we found was that cells were shorter and narrower in *Costularia natalensis* than in the two species of *Macrochaetium* studied (compare Figures 1A, B with Figures 1C–F). However, cell dimensions are difficult to record accurately with statistical reliability, and no attempt was made to achieve this, except that young glumes, in which cell size may not be fully expanded, were avoided. Also, in young tissue it is likely that silica deposition will not be complete, resulting perhaps in less reliable conformation (compare Figures 2D and E).

Metcalfe (1971: 179, 516) twice expressed his finding of a lack of resemblance between the genera *Costularia* and *Tetraria*. We have been unable to find any mention by him of the relationship of *Costularia* to *Macrochaetium* that has become apparent in our study of these associated genera.

Conclusions

The southern African species of *Costularia* require re-evaluation in a world context of the genus. Taxa from Madagascar form a group in which specific limits are not clearly defined. There appear to be very close affinities with the African representatives. Affinity is also close between the Afro/Mascarene complex and some species from New Caledonia, but the majority of these, placed by Raynal (1974: 376) in subgenus *Lophoschoenus*, are far less intimately affiliated.

The southern African *Macrochaetium* species, with which must be included *Tetraria bachmannii*, should likewise be revised, then re-evaluated in relation to *Costularia* worldwide. In the whole context, the puzzling and geographically isolated *Costularia pilisepala* and *Tetraria borneensis* undoubtedly require special consideration. From such a study, 'nuclei' from which 'satellites' have been derived, may become more clearly delineated.

Taxa and vouchers studied

These are arranged alphabetically by genera and species. Herbaria in which the specimens are deposited and the country of collection of each voucher are given.

Carpha

- C. capitellata* (Nees) Boeck., Transvaal, *Getliffe et al. 56* (NU).
- C. bracteosa* C.B. Clarke, Cape Province, *Taylor 5988* (NU).
- C. filifolia* Reid & Arnold, Lesotho, *Schwabe 0171* (NU).
- C. glomerata* (Thunb.) Nees, Natal, *Browning 228* (NU).
- Carpha* sp., Cape Province, *Esterhuysen 28040* (NU).

Costularia

- C. baroni* C.B. Clarke [= *C. pantopoda* C.B. Clarke var. *baroni* (C.B. Clarke) Kük.], Madagascar, *Baron 3316* (K) Type of *C. baroni*.
- C. brevicaulis* (C.B. Clarke) C.B. Clarke, South Africa, Cape Province, *Henderson, M.R. 1286* (NU); *I. Williams 3084*

(NU ex MO).

- C. laxa* Cherm., Madagascar, *Humbert 5883* (K) Type.
C. melleri C.B. Clarke, Madagascar, *Meller s.n.* (Aug. 1862) (K) Type.
C. natalensis C.B. Clarke, Zimbabwe, *Browning 579, 670* (NU); Malawi, *Brunmit 9668* (K); *Blackmore et al. 393* (K); *Chapman 8367* (K); Mozambique, *Tinley 2287* (K); South Africa, *Hilliard & Burt 14279, 14342* (NU); *Alexander 207* (NU).
C. pantopoda C.B. Clarke var. *grandispicus* Kük., Madagascar, *Perrier de la Bathie 2729* (K) Type.
C. pilisepala (Steud.) Kern (= *Lophoschoenus urvilleanus* Stapf), Borneo, *J. & M.S. Clemens 51062* (MICH).
C. recurva (Ridl.) C.B. Clarke, Madagascar, *Baron 4193* (K) Type.

Epischoenus

All Cape Province.

- E. adnatus* Levyns, *Esterhuysen 15222* (BOL).
E. cernuus Levyns, *Levyns 9387* (BOL).
E. complanatus Levyns, *Esterhuysen 8181* (BOL).
E. dregeanus (Boeck.) Levyns, *Esterhuysen 12668* (BOL).
E. gracilis Levyns, *Esterhuysen 11812* (BOL).
E. lucidus (C.B. Clarke) Levyns, *Esterhuysen 11592* (BOL).
E. quadrangularis (Boeck.) C.B. Clarke, *Esterhuysen 27308* (BOL).
E. villosus Levyns, *Levyns 8884* (BOL).

Macrochaetium

- M. ecklonii* (Nees) Levyns, Cape Province, *Levyns 9244* (BOL); *Esterhuysen 20067* (BOL).
M. hexandrum (Nees) Pfeiffer, Cape Province, *Esterhuysen 6812, 13596*, (BOL); *Fourcade 1007a* (BOL); *Levyns s.n.* (BOL 57552); *Getliffe 1181* (NU).

Tetraria

- All South Africa except *T. borneensis* and *T. usambarensis*
Tetraria bachmannii Kük. [= *T. thuarii* P. Beauv. var. *gracilior* C.B. Clarke], Transkei, *Venter & Vorster 107* (NU); Natal, *Balkwill & Manning 423* (NU); *Moll 4789* (NU).
T. borneensis Kern, Borneo, *Purseglove P559* (L); *Anderson 9876* (L).
T. cuspidata (Rottb.) C.B. Clarke, *Browning 651, 371* (NU); *Esterhuysen 8847* (NU); *Gordon-Gray 6516* (NU); *Huntley*

785 (NU); *Trauseld 799* (NU); *Ward 2761, 7180* (NU); *Ward & Begg 11352* (NU).

- T. fimbriolata* (Nees) C.B. Clarke, *Getliffe 1123* (NU); *Getliffe 1136* (NU).
T. macowaniana B.L. Burt, *Hilliard & Burt 7792, 18350* (NU).
T. microstachys (Vahl) Pfeiffer, *Taylor 6061* (NU).
T. pygmaea Levyns, *Getliffe 1103* (NU).
T. robusta (Kunth) C.B. Clarke, *Browning 384* (NU).
T. thermalis (L.) C.B. Clarke, *Compton, R.H. 17098* (NU).
T. usambarensis K. Schum., Tanzania, *Tait s.n.* (Tanganyika 1949).
T. ustulata (L.) C.B. Clarke, *Getliffe 1062* (NU).
Tetraria sp., *Getliffe 1069* (NU); *K. & F. Ellery 92/177* (NU).

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