CUTICULAR CHARACTERS AS AN AID TO THE TAXONOMY OF THE SOUTH-WEST AFRICAN SPECIES OF COMBRETUM

by

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In connexion with A. W. Exell's treatment of the genus Combretum for "Prodromus of a Flora of South-West Africa" (in press)+) I have carried out an investigation of the cuticular patterns of the fifteen species and two subspecies therein recognised.

Cuticular studies afford a very convenient method of examining the characters of the leaf epidermis and its outgrowths (trichomes), since, whilst the epidermis itself is not able to be removed without some difficuty and often then only fragmentarily, the cuticle can be removed in toto with considerable speed and ease, even in extremely old herbarium specimens. It is not proposed to give details of the methods of the isolation and mounting of cuticles used in this study, as these will be described at a later date in a more comprehensive account, but in essential the technique involves the dissolution of the cellular tissue by means of a macerating solution and the staining and mounting of the isolated cuticles. These cuticular preparations show all the normal epidermal characters (such as the form of the epidermal cells, of the stomata and of the trichomes) since these are imprinted on to the cuticle during development, and in addition the cuticles themselves often provide some further diagnostic characters.

The genus Combretum, in common with some other genera, shows two characters of particular diagnostic importance which may be briefly outlined here.

+) This work should be consulted for the citation, synonymy, etc. of the species.

The first is the possession of typical 'Combretaceous hairs', originally described by Heiden (1893). These hairs (Fig. 2, 9-10) are very peculiar in that they possess a double wall. According to Heiden the protoplast of the originally long, pointed, simple, unicellular hair shrinks during development, and when it has become confined to a relatively small region at the base of the hair it secretes a second, internal cell-wall. The original, external wall often becomes very thick due to continued deposition of cellulose by the shrinking protoplast, but even so it rarely becomes cutinised so that it is not or is only fragmentarily represented in cuticular preparations. The second, internal wall, however, is usually cutinised and presents a fairly typical feature of the cuticular preparations of the genus. Combretaceous hairs are found in every species of the Combretaceae examined, and are rarely accompanied by other types of hair. Apparently these typical hairs are found elsewhere only in the Cistaceae (Solereder, 1908). It has been found that the shape of the second internal cell-wall is frequently a diagnostic character, both generically and specifically.

The second feature of interest is the presence in many species of C o m b r e t u m (as well as in one or two other genera of the Combretaceae and in many other families) of 'scales', which are usually glandular in nature. These scales, which were surveyed and classified by Bachmann (1886), provide useful means of identifying the species of C o m b r e t u m in which they occur. It has been found, however, that the system of classification used by Bachmann, although useful in classifying the individual scales themselves, is unsatisfactory from the species point of view. In the present investigation the scales were studied by leaf-scrapings as a supplement to the study of cuticular preparations. They are present in ten of the fifteen species under consideration, of which only C. e r y t h r o p h y l l u m (Burch.)Sond. has been previously investigated (Bachmann, 1886; Heiden, 1893). Although reference to scales is often made in normal taxonomic keys, an exact definition and thus a precise idea of them is not possible without a detailed microscopic examination. Indeed even their presence in two of the species examined, C. e n g l e r i Schinz and C. z e y h e r i Sond., is not usually detectable without the aid of a microscope, due to their small size; and in other species they are often obscured by glutinous secretions

(e.g. C. apiculatum Sond.) or by dense indumentum (e.g. C. apiculatum ssp. leutweinii (Schinz) Exell). In fact in many works on the Combretaceae the statement 'scales absent' may often mean that the scales are not apparent or are very inconspicuous when viewed with the ordinary lens.

In Combretum the scales are very short-stalked or in some cases sessile, peltate, and either disc- or bowl-shaped. In families other than the Combretaceae scales, when present, are usually very conspicuously different in form (Bachmann, 1886; Solereder, 1908). It was found that the scales alone afforded a very good method for differentiating between the ten lepidote species. The other five species, and one of the ten lepidote species (C. albopunctatum Suesseng.), possess distinctive stalked glands. The scales and glands of the fifteen South-West African species of Combretum are represented in Figs. 1 - 2. By means of these trichomes, coupled with other cuticular characters, it is possible to distinguish with ease all the seventeen taxa. A key to the latter is given here and it is of real importance to note that a single leaf (or a small part thereof) enables correct determination to be effected. It must be pointed out, however, that this is only a small sample of the genus and much work remains to be done before it can be determined whether the above statement is applicable to the whole range of species.

Key to South-West African Species of Combretum using only Cuticular Characters

1 Peltate or bowl-shaped scales present on at least one leaf surface, scales 40-350 μ across, frequently obscured by indumentum or glutinous secretions:....2.

1a Scales absent from leaves; glands with ovoid or spherical heads up to 75 μ across present, though sometimes very sparsely: . . . . . 12.

2 Scales very conspicuous, contiguous and/or overlapping over whole of both epidermi, 120-300 μ across; marginal cells of scales 40-100 in number; only the midrib and major lateral veins distinguished on the cuticle; leaf more or less devoid of hair bases (Fig. 1,2): . . . . . 2. C. imberbe

2a Scales never contiguous on upper epidermis (and often sparse there), if over 120 μ then completely absent

from midrib and veins of both epidermi; marginal cells 7-50 in number: . . . . . 3.

3 Scales large, 150-350μ across, more or less circular; marginal cells c. 25-50 in number, outer edges not or only slightly scalloped; most scales with most or all marginal cells squarish or tangentionally elongated; scales conspicuous but sparse on lower epidermis, very sparse or absent on upper; leaves very sparsely pubescent; conspicuous pouches (acarodomatia) present in the axils of the major lateral veins and midrib on the lower epidermis (Fig. 1,1): . . . . . 1. C. celastroides

3a Scales 40-175μ across: if over 130μ across then most marginal cells radially elongated with scalloped outer edges and either scales or hairs abundant on lower epidermis: . . . . . 4.

4 Scales 75-175μ across, never simply circular but wavy-edged and/or marginal cells greatly and irregularly scalloped; scales either simply divided by radial walls into radial cells which are subdivided by tangentional and/or extra radial walls, or complexly divided by rather irregular walls so that no radial cells are discrete: . . . . . 5.

4a Scales 40-100μ across, circular or outer edge of each marginal cell simply and regularly convex (scalloped); radial cells discrete, either not subdivided or each simply subdivided by tangentional and/or extra radial walls: . . . . . 7.

5 Scales 100-175μ across; radial walls rarely or never reaching from the margin to centre of scale so that radial cells are not discrete; most marginal cells radially elongated (Fig. 1,3): . . . . . 7. C. mechowianum

5a Scales 75-125μ across; most radial walls reaching from margin to centre of scale; most radial cells discrete, either not subdivided or more usually simply divided by tangentional and extra radial walls and marginal cells tangentionally elongated: . . . . . 6.

6 Scale margins slightly to very wavy; all walls of scales thin and many often undulate; scales transparent, cuticle not striated; outlines of upper epidermal cells conspicuous; cuticle of upper epidermis clear, not striated (Fig. 1,4):....8. C. hereroense

6a Scale margins slightly and regularly wavy; radial walls of scales thick, straight and spoke-like; tangentional walls also thick and straight; scales opaque, cuticle often striated; outlines of upper epidermal cells not visible; cuticle of upper epidermis very conspicuously striated (Fig. 1,5): . . . . . 10. C. molle

7 Scales 60-100 μ across, divided into 7-10 radial cells with convex outer edges by very thin walls, rarely subdivided; scales conspicuously bowl-shaped, usually filled with dense secretory products, only on lower epidermis; simple unicellular sac-like trichomes present on upper epidermis (Fig. 1,6): .. . . . . 3. C. albopunctatum

7a Scales 40-100 μ across; radial cells subdivided or not; scales flat and peltate, never bowl-shaped, on both epidermi; scales and Combretaceous hairs the only trichomes present: . . . . . 8.

8 Scales 50-100 μ across, always some over 60 μ , present on upper epidermis to an equal or greater extent than on lower; all or most cells of upper and lower epidermi with straight walls: . . . . . 9.

8a Scales 40-75 μ across, always some under 50 μ , sparser on upper epidermis than on lower; intervenar cells of both epidermi with conspicuously undulate walls: . . . . . 11.

9 Scales composed of 10-16 radial cells, never subdivided; inner compartments of hairs long, parallel sided for part of the length; stomata absent from the upper epidermis (Fig. 1,7):4. C. erythrophyllum

9a Scales composed of 7-10 radial cells, often subdivided; inner compartments of hair shortly and regularly conical; stomata very frequent on the upper epidermis (C. apiculatum): . . . . . 10.

10 Hair bases very frequent on midrib and veins of both epidermi; hair bases conspicuously differing from scale bases in that adjacent epidermal cells are not radially elongated; scales 60-100 μ across: 5b. C. apiculatum ssp. leutweinii

10a Hair bases extremely sparse on all parts of the leaf; scales 50-75 μ across (Fig. 2,1): . . . . . 5a. C. apiculatum ssp. apiculatum

11 Radial cells of scales c. 10-14 in number, often sub-divided; midrib, veins and some secondary veins

distinguishable, but no venule reticulum present; cuticle not or scarcely striated around stomata (Fig. 2,2): . . . . . 9. C. engleri

11a Radial cells of scales c. 7-10 in number, often subdivided; midrib, veins and venule reticulum very conspicuous; cuticle conspicuously radially striated around each stoma (Fig. 2,3): ..... 11. C. zeyheri

12 Glands frequent in inter-venule islands of lower epidermis, absent elsewhere; head circular in top view, elliptic in side view, c. 50 µ across, usually filled with dense contents; stalks very short, not over 10 µ long; venule reticulum very marked and raised on the lower epidermis (C. psidioides):..13.

12a Glands not confined to lower epidermal inter-venule islands, or if apparently so then extremely sparse, usually on the upper epidermis and/or veins of the lower epidermis; head various; stalks of all or most glands long and conspicuous, over 10 µ long and up to 200 µ long; lower epidermis rarely markedly reticulate, reticulum never raised: . . . . . 14.

13 Lower epidermis scarcely more pubescent than upper; hair bases mostly confined to the veins and venules of lower epidermis, and there frequent (Fig.2,4): . . . . . 6a. C. psidioides ssp. psidioides

13a Lower epidermis densely tomentose, upper much less pubescent; hair bases abundant in inter-venule islands as well as on the veins and venules of lower epidermis: . . . . 6b. C. psidioides ssp. dinteri

14 Cells of both epidermi strongly undulate-walled, though cell outlines often faint; stomata frequent on upper epidermis as well as on lower; glands rather sparse in lower epidermal inter-venule islands, very sparse elsewhere, head obovoid, stalk-cells uniseriate and stalks up to c. 35 µ long (Fig. 2,5): . . . . . 12. C. platypetalum

14a Cells of both epidermi or at least of upper epidermis straight-walled; stomata confined to lower epidermis or not; glands various: . . . . . 15.

15 Cell outlines of both epidermi conspicuous; cuticle not striated; stomata frequent in islands of upper epidermis; glands very sparse (Fig. 2,5): . . . . 15. C. wattii

15a Cell outlines of both epidermi extremely faint; cuticle conspicuously striated radially to each stoma

and hair base; stomata more or less absent from upper epidermis; glands frequent either on lower epidermis or on midrib of upper epidermis:.....16.

16 Glands confined to midrib of upper epidermis, frequent there; stalk-cells uniseriate, stalks up to 50 μ long; hair bases very frequent on both epidermi, small, rarely over 25 μ across (Fig.2,6): . . . . . 14. C. mossambicense

16a Glands frequent on lower epidermis, some at least with stalks over 100 μ long and cells partially multiseriate; upper epidermis sparsely hairy; hair bases often very large, frequently 40 μ or more across (Fig. 2,8): . . . . . 13. C. oxystachyum

Although it is unnecessary to describe the cuticular characters of all the seventeen taxa in full, it is perhaps desirable to indicate the major points of importance that resulted from the present study. These may be enumerated:

1. The taxonomic conclusions arrived at by means of cuticular investigations agreed very closely with those reached by Exell using more orthodox methods. This may be illustrated by three specific examples:
a) The contention that C. dinteri Schinz would be better reduced to subspecific rank under C. psidioides Welw. was supported, since both possess in common the peculiar glands (Fig. 2,4) and differ only in the distribution of hair bases. The same is true of C. kwinkiti De Wild., a plant not reaching as far south as South-West Africa, which has hair bases very sparse on the veins and venules of the lower epidermis, but abundant in the inter-venule islands.
b) Similarly no difference in the cuticles of C. apiculatum and C. leutweinii Schinz was discovered other than in the degree of pubescence. Exell has accordingly relegated the latter to subspecific rank.
c) Various 'species' which Exell has included under C. mechowianum O.Hoffm. were investigated. These included C. schinzii Engl., C. suluense Engl. & Diels, C. coriaceum Schinz and C. pachycarpum Engl.& Diels. No constant differences could be found, the forms apparently grading into one another with respect to the only characters observed to be variable - the degree of pubescence and the size and abundance of the scales. The more glabrous forms usually possessed larger, more abundant scales. These observations thus tended to support the treatment of the

whole group as a single variable species.

2. Of the specimens examined by Exell during his revision of the group, the identity of but one (which lacked flowers), originally labelled C. leutweinii, remained in doubt. I examined this and found that it possessed cuticular characters unlike those of any of the other taxa known from South-West Africa, and a search amongst likely specimens from neighbouring territories enabled the specimen in question to be referred to C. molle R.Br.agg. Cuticular characters may thus actually be of use in cases where orthodox methods fail or provide inconclusive results. Cuticular characters were also of special use in the case of C. albopunctatum, which possesses scales of a very characteristic pattern. A study of the scales of certain Rhodesian specimens of Combretum enabled some to be placed conclusively in C. albopunctatum, and the rest to be conclusively excluded from that species. In this case cuticular studies extended the known geographical range of the species, and also showed a hitherto unknown extreme of range in leaf-shape. C. albopunctatum is unfortunately not known in flower, so cuticular studies are here of particular importance.

3. It will be evident from the foregoing notes that cuticular characters fall into two main types: those which are more exact manifestations of normal macroscopic characters, such as pubescence and venule reticulation; and those which are not evident from macroscopic studies, such as cell-shape and stomatal anatomy.

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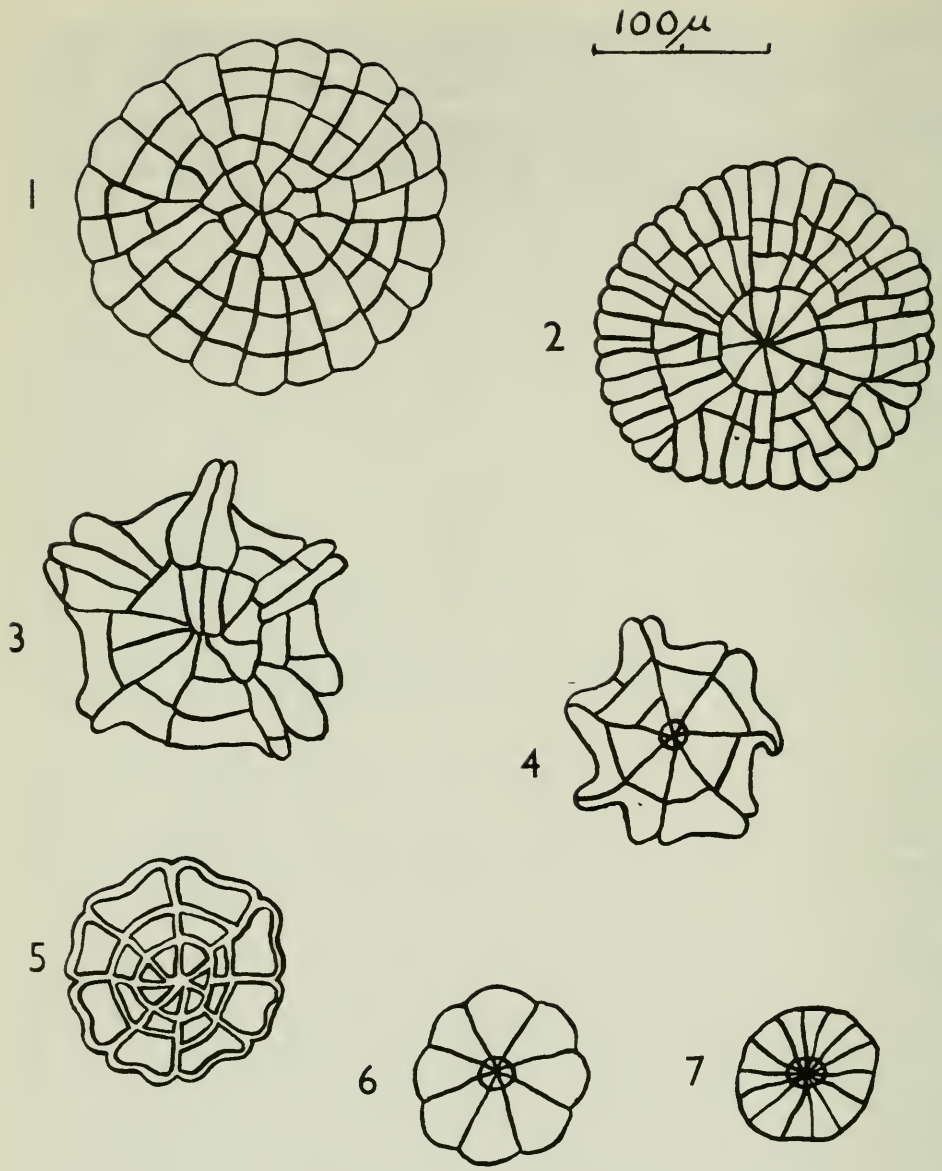

Fig. I - Scales of Combretum ssp.: I, C. celastroides; 2, C. imberbe; 3, C. mechowianum; 4, C. hereroense; 5, C. molle; 6, C. albopunctatum; 7, C. erythrophyllum.

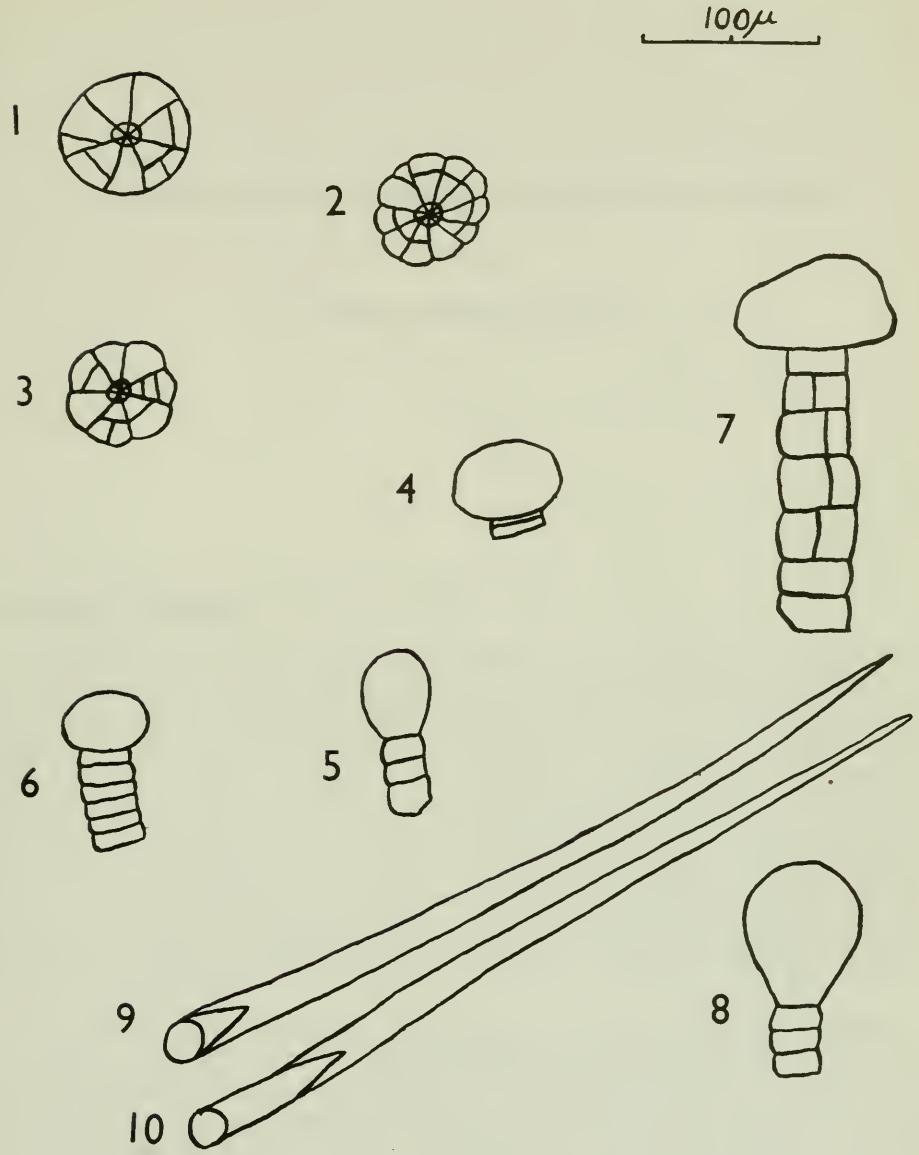

Fig. II - 1-3, Scales; 4-8, Glands; 9-10, Combretaceous Hairs of Combretum ssp.: 1, C. apiculatum; 2, C. engleri; 3, C. zeyheri; 4, C. psidioides; 5, C. platypetalum & C. wattii; 6, C. mossambicense; 7 & 8, C. oxystachyum; 9, C. apiculatum; 10, C. erythrophyllum.