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A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view

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ABSTRACT

Descriptive "keys", including definitions and explanatory diagrams, are given for the standardization and simplification of anatomical descriptions of the epidermides of grass leaf blades as seen in surface view. About 340 characters of the epidermis are included with ample room for expansion. Notes on variation and taxonomic importance of the characters are also included.

RÉSUMÉ

PROCÉDURE DE STANDARDISATION DE L'ANATOMIE COMPARÉE DE LA FEUILLE CHEZ LES POACÉES. II. L'ÉPIDERME VU DU DESSUS

On donne des "clés" descriptives, incluant des définitions et des diagrammes explicatifs, pour la standardisation et la simplification des descriptions anatomiques de l'épiderme du limbe foliaire des graminées, vu du dessus. Environ 340 *caractéristiques de l'épiderme y sont incluses et il reste possible d'élargir considérablement ce nombre. On y joint également des notes sur la variation et l'importance taxonomique des caractères.*

INTRODUCTION

The importance of anatomy in agrostological studies has resulted in the rapid accumulation of an extensive body of literature with attendant problems of lack of uniformity with definitions and descriptions. Valuable data are, therefore, commonly not applicable to the family as a whole and comparisons cannot be drawn with any degree of assurance. This problem was greatly ameliorated by the publication in 1960 of Anatomy of the Monocotyledons. 1. Gramineae by C. R. Metcalfe and the present paper is a further attempt to stabilize this terminology and, at the same time to present a system whereby description and comparison of grass leaf anatomy will be simplified and standardized. See Ellis (1976) for a more comprehensive introduction.

DESCRIPTIVE KEYS

In an attempt to achieve the necessary uniformity, descriptive "keys" have been compiled for use as a framework for anatomical descriptions of the epidermis of the grass leaf-blade as viewed in surface view. The "keys", which incorporate both definitions and diagrams, have been designed to enable the user to standardize descriptions and the hierarchical layout has been chosen to facilitate the speed and ease at which complete, comparative descriptions can be compiled. Anatomical characters, and all other information considered to be of diagnostic or taxonomic importance, and gathered from an extensive survey of the relevant literature, have been included. The keys should, therefore, prove adequate for all tribes of the Poaceae.

The hierarchical tabulation of the characters has been used to expedite their use but they do not in any other way conform to any acknowledged key format or design. However, if a statement, at any level of the hierarchy, does not apply to the specimen being examined, no subsequent statements or characters of a lower rank are relevant. The user, therefore, merely proceeds to the next character of equal rank or indentation, and, if applicable, works inwards noting all the relevant numbered end points before working back outwards until the same level or rank as that of the originally chosen statement is reached. Thus, the "keys" are not dichotomous or true indented keys, but by using this type of format all the possible characters are recorded in a constant descriptive sequence. Each character is assigned a constant number and the recording of these numbers effects a saving in time and space. Furthermore, this system enables easy conversion to edge punched and feature cards as well as for electronic data processing by computer. In addition, it is ensured that all possible structures are rapidly and routinely noted in a rational sequence which simplifies compilation of descriptions of the various taxa. By employing a standard sequence significant differences become more readily evident.

In order for the standardization of terminology and descriptions to be effective, it is essential that comparative material be examined. Therefore, in this study, all descriptions refer to material taken at a point about halfway between the blade apex and the ligule of mature basal leaves. Flag leaves on flowering culms were avoided where possible. By standardizing on the material studied in this way infraspecific differences may be assessed.

In describing epidermal structure, Metcalfe (1960) has been followed. Thus, for descriptive purposes, it is assumed that the long axis of the leaf is horizontal. Visualized like this, it is possible to refer to zones and files of cells that lie parallel to the long axis as being "horizontal". The direction at right angles to the long axis is vertical for descriptive purposes.

It is important to note that other workers have not necessarily adopted this descriptive viewpoint. In fact, most authors have neglected to explain how they have visualized the epidermis when compiling descriptions. This lack of a standard convention undoubtedly leaves room for misunderstanding and misinterpretation of descriptions. For example, Bobrov (1955) uses "elongated in the direction of the blade" for horizontal *cf.* Metcalfe (1960), whereas Martin (1955) visualizes the veins as being vertical.

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1. INTERCOSTAL LONG CELLS

Includes cells that are usually elongated horizontally and are relatively narrow vertically and are situated in the intercostal zones of the epidermis. Excludes the interstomatal long cells, stomata, intercostal short cells and costal long cells. Bulliform cells as seen in surface view fall under intercostal long cells but are difficult to identify with any degree of certainty and thus only cells which vary in appearance with focus are termed bulliform cells.

DESCRIPTION OF CELL SHAPE: All applicable differences present on specimen to be included.

Ratio of horizontal (length) and vertical (width) dimensions:
- *Elongated* cells; length 3x, or more than 3x longer than width . . . 101*
- *Shortened* cells; less than 3x longer than wide:
  - Length slightly greater than width . . . 102*
  - Length and width approximately equal . . . 103*
  - Length less than width; tall and narrow . . . 104*

Side walls; anticlinal horizontal long walls:
- *Parallel* to one another; cells rectangular, square or trapezoidal . . . 105*
- *Angled outwards;* cells hexagonal . . . 106*
- *Bowed outwards;* cells inflated . . . 107*

End walls; anticlinal vertical cross-members:
- *Vertical;* at right angles to the horizontal walls . . . 108*
- *Angled* or *Sloping* in relation to the horizontal walls . . . 109*
- *Rounded;* cells of the inflated type . . . 110*
- *Overlapping* one another; interlocking . . . 111*

Thickness of horizontal and vertical anticlinal walls of long cells; appearance probably dependant upon the extent of development of the cuticular flanges; in general this indicates cuticle thickness:
- *Unthickened;* thin-walled; no cuticular flanges present . . . 112*
- *Slightly* thickened; slight cuticular flanges probably developed . . . 113*
- *Moderately* thickened; cuticular flanges developed . . . 114*
- *Heavily* thickened; deep, well-developed cuticular flanges probably present . . . 115*
- *Pitted* or beaded; visible pits developed in thickened walls . . . 116*

Undulations of horizontal anticlinal walls of long cells; sinuosity; measured and described in terms of waves i.e. the variables frequency, amplitude and wave-lengh:
- *Straight* walls; not undulate . . . 117*
- *Irregular;* slightly undulating or wavy; wave-length long, amplitude shallow and frequency low . . . 118*
- *Slightly* undulating; faintly corrugated; wave-length short, amplitude shallow and frequency high . . . 119*
- *Moderately* undulating; often irregular; wave-length short, amplitude variable and frequency high . . . 120*
- *Deeply* undulating; strongly corrugated; wave-length short, amplitude relatively deep and frequency high:
  - Ω-shaped . . . 121*
  - U-shaped . . . 122*

VARIATION IN CELL SHAPE

Cell shape as determined by the relative lengths and shapes of the horizontal and vertical anticlinal walls:
- *Variable shape:*
  - Shape varies in single *files* of intercostal long cells . . . 123*
  - Shape varies in diffirent *areas* of the preparation e.g. near margin or midrib . . . 124*
  - Shape varies across a single intercostal *zone* e.g. hexagonal cells centrally and rectangular cells laterally . . . 125*
- *Constant* or relatively constant shape in intercostal zones throughout the preparation . . . 126

Cell size; usually cell length determines differences; ratio of length to width may vary but shape (rectangular cuboid or hexagonal) remains constant:
- *Variable* size:
  - Size varies in single *files* of intercostal long cells . . . 127*
  - Size varies in different *areas* of the preparation e.g. near margin or midrib . . . 128*
  - Size varies across a single intercostal *zone:*
    - Narrower cells in centre of intercostal zones . . . 129*
    - Wider cells in centre of intercostal zones . . . 130*
- *Constant* or relatively constant size in intercostal zones throughout the preparation . . . 131

DISTRIBUTION OF ASSOCIATED CELLS: All types of intercostal short cells and appendages present between the intercostal long cells of the files included.

No short cells between the adjacent long cells; long cells adjoin one another . . . 132*

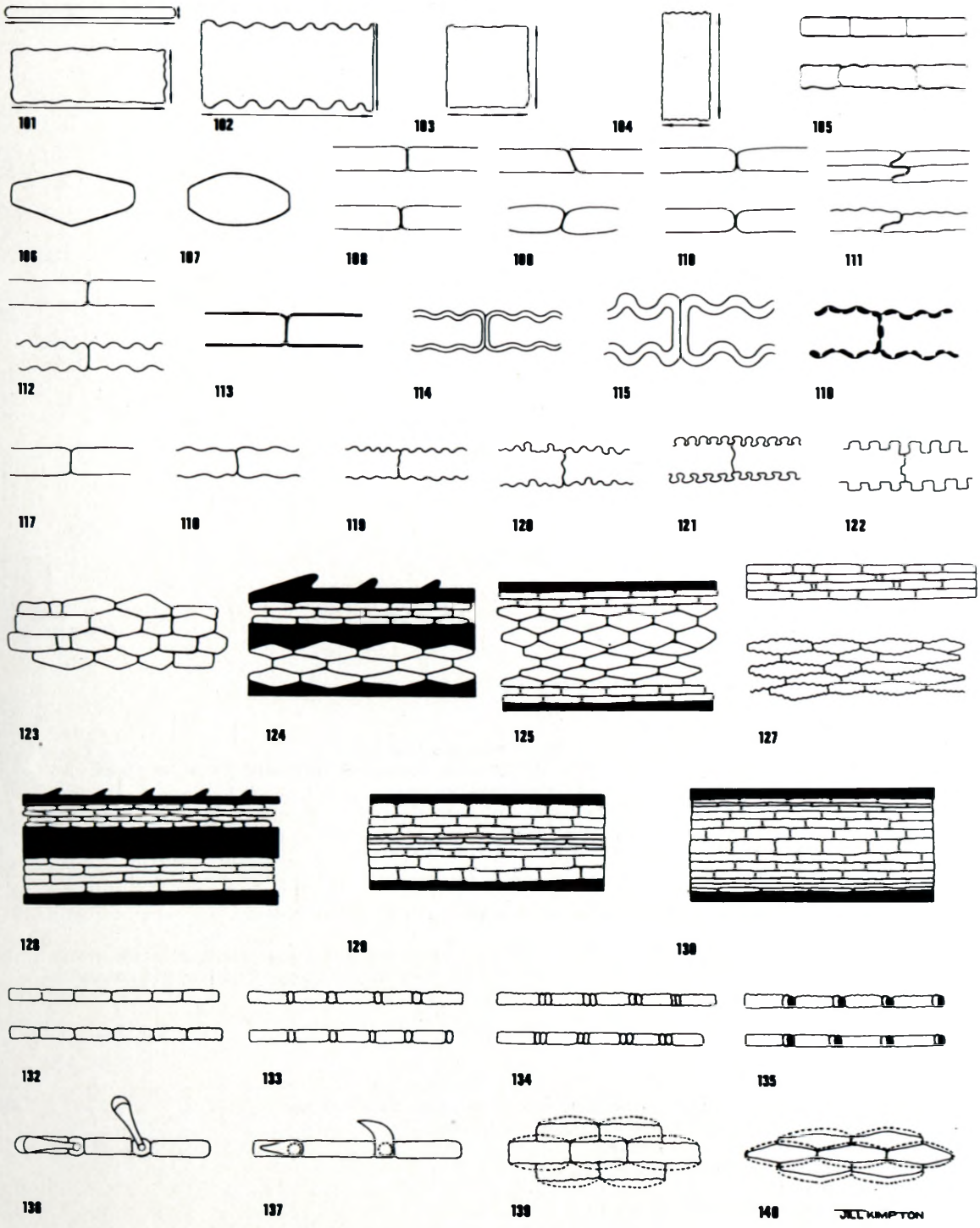
Intercostal short cells separating adjacent long cells of the files; mentioned only if frequent i.e. between 50% or more of the long cells:
- *Single* short cells present between successive long cells . . . 133*
- *Pairs* of short cells present between successive long cells . . . 134*
- *Silico-suberose* couples or cork-silica cell pairs between successive long cells . . . 135*
- *Micro-hairs* present between successive long cells . . . 136*
- *Hooks* and/or prickles present between successive long cells . . . 137*

DESCRIPTION OF BULLIFORM CELLS: Usually grouped with intercostal long cells but it is often very difficult to distinguish them from inflated intercostal long cells; in surface view a bulliform cell typically has an outline or shape that varies with different focal levels; they are usually thin-walled and are often inflated.

No bulliform cells present on surface of the preparation examined . . . 138*

Present; varying in appearance with focus; inflated, thin-walled:
- *Rectangular* in shape . . . 139*
- *Hexagonal* in shape . . . 140*

INTERCOSTAL LONG CELLS



2. STOMATA

The stomatal complexes as well as the interstomatal long cells are included in this section. They are both confined to the intercostal zones and are usually in well-defined bands.

STOMATAL COMPLEXES: The stomatal complex or stomatal apparatus consists of a pair of guard cells with their lumina enlarged at either end and more constricted in the middle as seen in surface view. These together with the pore between them form the stoma. Both the guard cells are accompanied on their outer, horizontal faces by a pair of subsidiary or accessory cells differing in shape and size from the other epidermal cells. The shape of the stomatal complex is determined by the outline of these subsidiary cells. This shape is often variable and then all different shapes that occur fairly frequently (about 25% of the stomata visible) must be mentioned.

DESCRIPTION: Determined by subsidiary cell shape in surface view. Intermediate types often present and all common types must be mentioned.

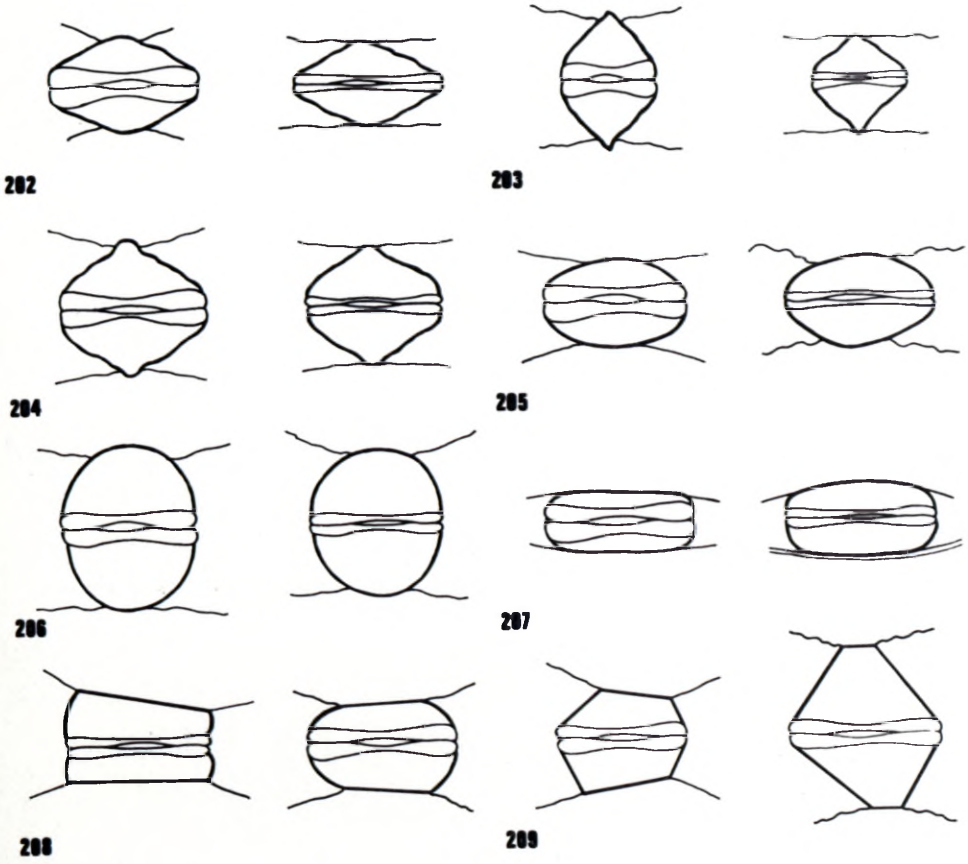
- **Absent**; no stomata visible on surface of preparation examined 201
- **Types** of stomata present; determined by shape of subsidiary cells:
  - *Triangular;* panicoid types:
    - Low triangular; long and broadly angular subsidiary cells 202*
    - High triangular; wide and markedly angular subsidiary cells:
      - Apex not evaginated; diamond-shaped stomatal complex 203*
      - Apex drawn out into a point; evagination often containing the nucleus 204*
  - *Dome-shaped;* subsidiary cells rounded:
    - Low dome-shaped; ovoid; vertical width of the subsidiary cells smaller in relation to the horizontal length 205*
    - Tall dome-shaped; vertical width of the subsidiary cells greater in relation to the horizontal length 206*
  - *Parallel-sided* subsidiary cells; rectangular in outline; stomatal complex long and narrow 207*
  - *Flat-topped;* outer, horizontal walls of the subsidiary cells straight; often short and may be parallel:
    - Rounded with flattened top 208*
    - Side walls and outer horizontal wall straight 209*
- **Distribution** of the stomata in the intercostal zones:
  - *One* row of stomata in each intercostal zone most common:
    - Always one row of stomata in all intercostal zones 210
    - Usually one row but sometimes two rows of stomata present 211
    - Usually one row but sometimes two or three rows of stomata present 212
  - *Two* rows of stomata in each intercostal zone most common:
    - Always two rows of stomata in all intercostal zones 213
    - Usually two rows but sometimes one row of stomata present 214
    - Usually two rows but sometimes three or more rows of stomata present 215
  - *Three* rows of stomata in each intercostal zone most common:
    - Always three rows or stomata in all intercostal zones 216
    - Usually three rows of stomata but sometimes more or less present 217
  - *Four* rows of stomata in each intercostal zone most common 218
  - *Five* rows of stomata in each intercostal zone most common 219
  - *More* than five rows of stomata in each intercostal zone 220
- **Arrangement** of the rows of stomata in the intercostal zones:
  - *Definite* rows of stomata present:
    - Rows separated by files consisting of intercostal long cells:
      - Separated by more than one file of intercostal long cells 221*
      - Separated by only one file of long cells 222*
    - Rows adjacent to one another; not separated by files of intercostal long cells 223*
  - *Not* in definite rows but stomata present throughout the intercostal zone in any horizontal file of long cells; may be as many rows of stomata as there are intercostal files of long cells 224
- **Position** of the rows of stomata in the intercostal zones:
  - *Centrally* situated rows in the centre of the intercostal zones 225
  - *Restricted* stomatal rows; restricted to narrow zones adjoining the costal zones:
    - Double row adjoining the costal zones 226
    - Single row adjoining the costal zones 227
  - *Throughout* intercostal zones; stomatal rows not restricted to areas in the intercostal zones 228

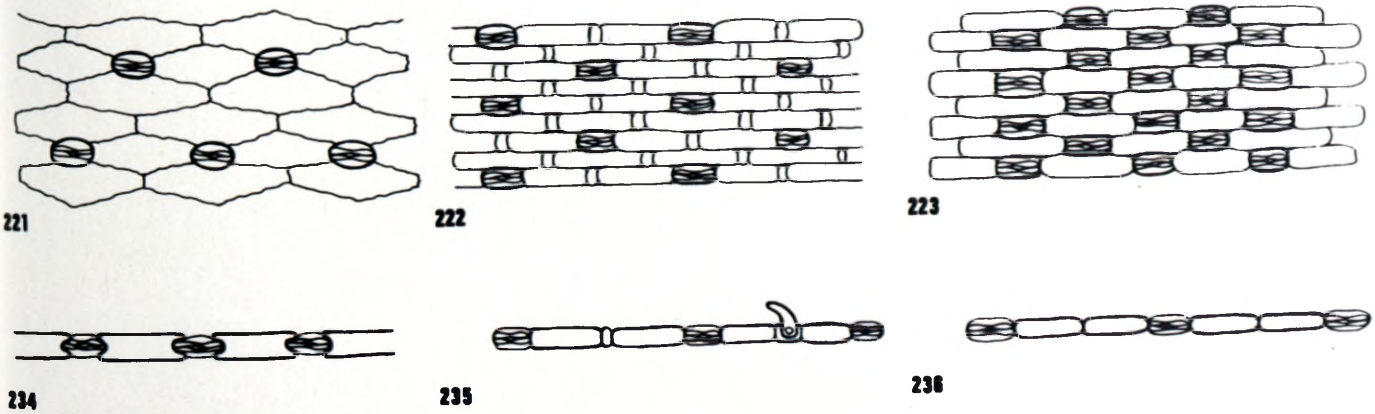
INTERSTOMATAL LONG CELLS: The interstomatal long cells lie in the same horizontal, longitudinal files as the stomata i.e. in the stomatal rows. They are only recognisable if the stomata are fairly frequent, regularly spaced and arranged in definite stomatal rows.

DESCRIPTION:

- **Absent**; no interstomatal long cells present:
  - *No* stomata present on surface examined 229
  - *Infrequent* stomata; successive stomata of a row separated by more than three long cells 230
- **Size** of intercostal long cells; greatest horizontal and vertical dimensions:
  - *Relatively long;* cells 3x or more longer than wide 231
  - *Relatively short;* cells less than 3x longer than wide:
    - Length more than width 232
    - Length and width approximately equal; square 233
- **Arrangement** of files of interstomatal long cells in relation to successive stomata of a row:
  - *One* interstomatal cell between successive stomata; with concave ends 234*
  - *Two* interstomatal cells between successive stomata:
    - Separated by short cells or hairs 235*
    - Adjoin one another 236*
  - *More* than two interstomatal cells between successive stomata of a row:
    - Separated by short cells or hairs 237
    - Adjoin one another 238

STOMATA





3. INTERCOSTAL SHORT CELLS

Includes cells that are usually nearly equidimensional in shape but may be somewhat longer horizontally than they are vertically or their vertical width may exceed their horizontal length. They are, however, always smaller than the intercostal long cells with which they often alternate in horizontal rows. Intercostal short cells occur in pairs such as cork and silica cells or are solitary such as short intercostal cells and the cells from which micro-hairs, hooks and prickles arise. The silica bodies contained within typical silica cells of the cork-silica cell pairs are not included in this section but are described under Silica Bodies. Similarly, stomatal complexes and the cells of the cushion base of macro-hairs are excluded and described under the relevant sections.

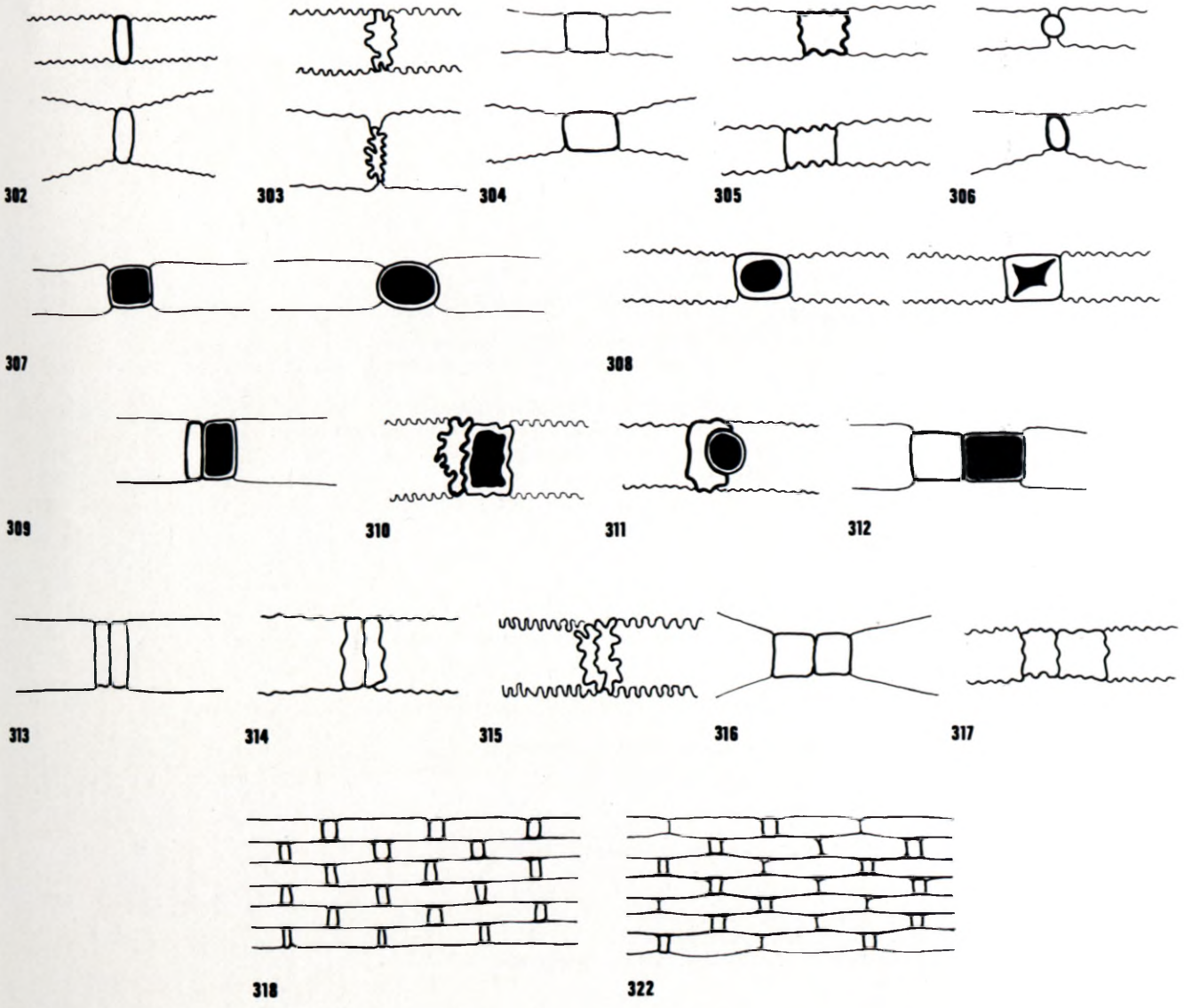
DESCRIPTION OF SHORT CELLS: For variable types include all different types that occur on the preparation.

- **Absent;** no short cells in intercostal zones of surface examined 301
- **Solitary** short cells; includes cells from which hooks and micro-hairs arise:
  - *Unsilicified;* excludes only cells containing a distinct silica body; if cell walls only are silicified they are included here:
    - Tall and narrow in shape; vertical dimension greater than horizontal dimension:
      - Smooth outline 302*
      - Crenate outline 303*
    - Square or rectangular in shape:
      - Smooth walls 304*
      - Sinuous or undulating walls 305*
    - Round or elliptical in shape 306*
  - *Silicified* silica cells containing distinct silica body or phytolith; solitary; excludes silicified cork cells, hooks or prickles; silica body described under Silica Bodies:
    - Silica body and silica cell of same or similar shape 307*
    - Silica body and silica cell different in shape 308*
- **Paired short cells** situated between long cells:
  - *Silico-suberose couples;* intercostal cork-silica cell pairs:
    - Shape of cork cell; silica body described under Silica Bodies:
      - Tall and narrow:
        - With smooth outlines 309*
        - With crenate or irregular outlines 310*
      - Crescentic, enfolding the silica cell 311*
      - Square to rectangular in shape 312*
  - *Short cell pairs;* excludes cork and silica cells; included are cells from which hooks and micro-hairs arise:
    - Tall and narrow; both cells of the pair vertically elongated:
      - Smooth outline 313*
      - Irregular outline 314*
      - Crenate outline 315*
    - Square to rectangular; either one or both cells:
      - Straight walls 316*
      - Sinuous or undulating walls 317*

DESTRIBUTION OF SHORT CELLS:

- **Location** of short cells or cell pairs in relation to long cells:
  - *Between* each successive long cell in a file; present at both ends of each long cell:
    - Between all or most long cells i.e. 75% or more of the long cells with a short cell or cell pair between them 318*
    - Common between long cells only in the region flanking the costal zone 319
    - Irregular; presence varies for different areas of the preparation 320
    - Rare throughout the preparation 321
  - *Between* pairs of successive long cells in a file; present at only one end of each long cell:
    - Present between most or all alternative long cells i.e. 75% or more of the long cells 322*
    - Irregular; presence differs for different areas of the preparation 323
    - Rare throughout the preparation 324

INTERCOSTAL SHORT CELLS



4. PAPILLAE

Papillae are variously shaped protrusions from the outer walls of epidermal long and short cells particularly of the intercostal zones. When viewed in surface view they may appear as small conical, cutinised structures or may appear larger, inflated and usually thin-walled. A single papillus per cell is most commonly found but there may be numerous papillae, arranged in several rows or even of two different types, present on each individual long cell.

DESCRIPTION OF PAPILLAE: Include all diferent types present but continue with distribution and arrangement of each separate type before commencing with descriptions of other types of papillae that may be present on the specimen.

- **Absent**; no papillae present on the epidermal cells of the preparation 401
- **Circular** or **Rounded** papillae as seen in surface view; conical:
  - *Large;* diameter of the papillae more than $\frac{1}{2}$ the vertical width of the long cells; only a single horizontal row of large papillae can be accommodated on individual long cells:
    - Unthickened, dome-shaped, inflated 402*
    - Slightly thickened, inflated; apex often appears concave (interference contrast microscopy) 403*
    - Thick-walled, inflated; often fairly elongated; apex often appears concave (interference contrast microscopy) . . 404*
  - *Small;* diameter of the papillae usually less than $\frac{1}{2}$ the vertical width of the long cells; more than one horizontal row of small papillae can be accomodated side by side on individual long cells:
    - Thin-walled, inflated 405*
    - Thickened, cuticular, variously shaped 406*
- **Oblique** papillae; many papillae seen in side view; during specimen preparation the elongated and often hair-like papillae become folded over in many cases:
  - *Unthickened* papillae; walls not thickened:
    - Large; entire outer wall of long cell convex and inflated; often overarch neighbouring cells 407*
    - Distinct, not incorporating the entire outer wall; restricted to distinct part of the outer wall; may overarch neighbouring cells 408*
  - *Distally thickened;* only extremity of papillus thickened 409*
  - *Thickened* papillae; walls thickened 410*
  - *Globose,* inflated; often in chains in costal zones 411*

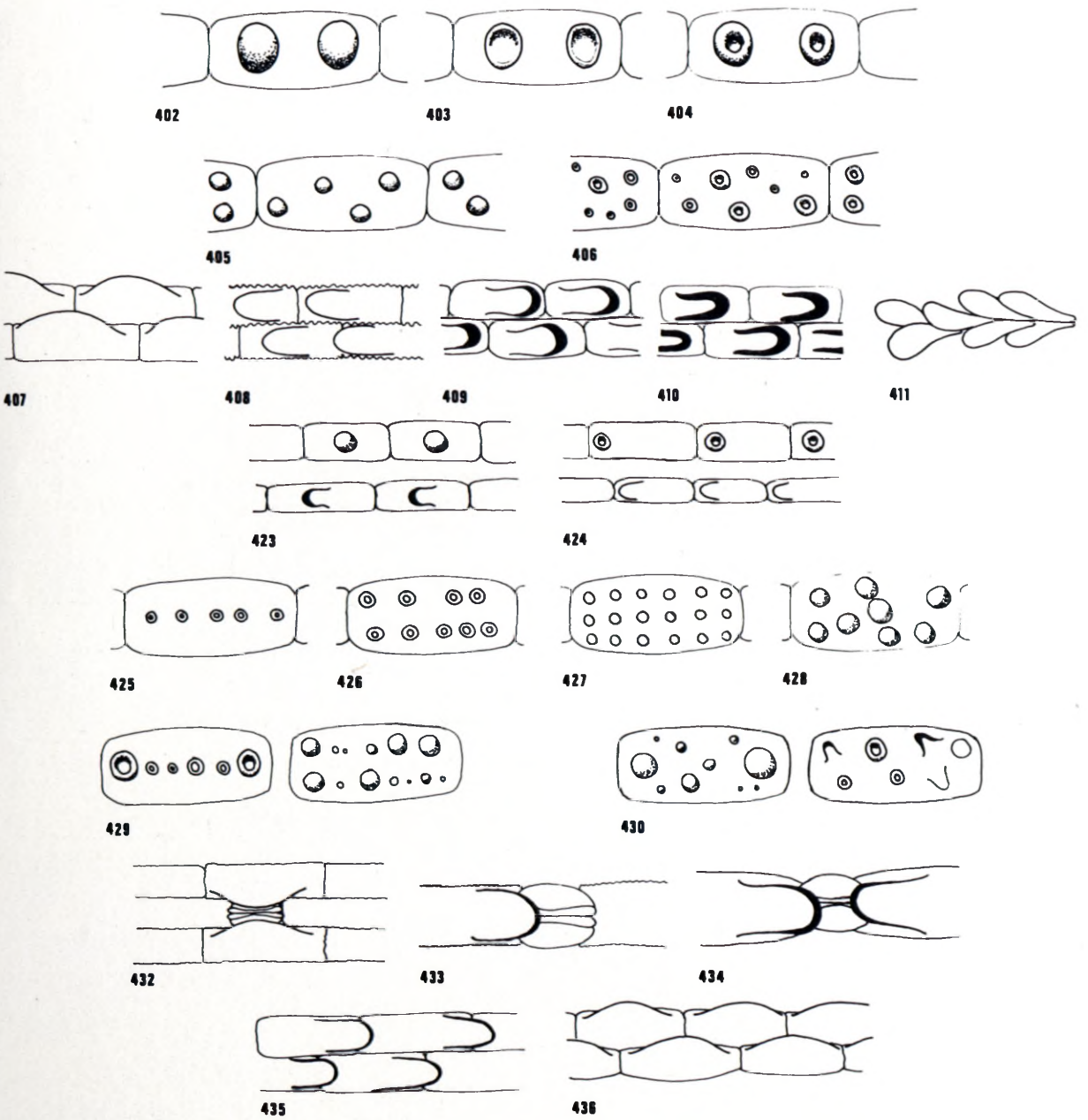
DISTRIBUTION OF PAPILLAE: Include all locations represented.

- **Intercostal** zone epidermal cells papillate.
  - *Bulliform cells* of intercostal zone with papillae:
    - Present on many or all bulliform cells; more than 50% of cells papillate 412
    - Present on relatively few bulliform cells; less than 50% of cells papillate 413
  - *Interstomatal* long cells with papillae:
    - Present on many or all interstomatal long cells; more than 50% of cells papillate 414
    - Present on relatively few interstomatal long cells; less than 50% of cells papillate 415
  - *Intercostal long cells* with papillae:
    - Present on many or all intercostal long cells; more than 50% of cells papillate 416
    - Present only on long cells at the edges of the intercostal zones; not in the central areas 417
    - Present on relatively few intercostal long cells; less than 50% of cells papillate 418
  - *Intercostal short cells* papillate; includes cork cells 419
- **Costal** zone epidermal cells papillate:
  - *Costal long cells* papillate:
    - Present on many or all costal long cells 420
    - Present on few costal long cells; infrequent 421
  - *Costal short cells* papillate 422

ARRANGEMENT OF PAPILLAE: Arrangement on individual cells and association with neighbouring cells.

- **One** papillus per cell:
  - *Centrally* positioned 423*
  - *Distally* situated on epidermal cells 424*
- **More** than one papillus per cell:
  - *Same type;* all papillae on individual cells of the same size and shape:
    - Arranged in a single horizontal row 425*
    - Arranged in two or more horizontal rows 426*
    - Arranged in vertical as well as horizontal rows 427*
    - Irregularly arranged 428*
  - *Different type;* papillae of different sizes or shapes present on individual cells:
    - Arranged in one or more horizontal rows 429*
    - Irregularly arranged 430*
- **Association** of papillae with neighbouring cells:
  - *No* overarching of neighbouring cells; papillae not oblique 431
  - *Overarch* adjacent cells in same or adjacent horizontal file of long cells:
    - Overarch the stomata:
      - From intercostal long cells 432*
      - From interstomatal long cells:
        - Overarch from only one adjacent interstomatal long cell in the same file 433*
        - Overarch from both adjacent interstomatal long cells of the same file 434*
    - Overarch neighbouring intercostal long cells:
      - From the same file of long cells 435*
      - From the adjacent file of long cells 436*

PAPILLAE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5. PRICKLE HAIRS

Robust, pointed structures with swollen bases arising directly from, and forming an integral part of the epidermis. Generally with thick, lignified walls. May conveniently be divided into two main types, prickles and hooks, on the basis of size. Intermediate types do occur, and also included are angular prickles and asperites. Descriptions refer to shape as seen in surface view but prickle hairs are often seen laterally and their lateral appearance is also included. Dimensions are gauged by the distance between parallel lines projected through the tip of the barb and the ends of the base furthest and nearest the barb tip.

PRICKLES:

Usually larger than hooks and with elongated, oval or elliptical bases. Excludes any prickles present on the leaf margin. Also known as aiguillons, asperites or teeth.

DESCRIPTION OF PRICKLES:

Absent; presumed missing i.e. no prickles observed on surface examined 501

Base size; estimated by comparison with the size (length) of the stomata of the same leaf:

Small prickles; base shorter than the stomata 502*

Medium prickles; base as long or slightly longer than the stomata 503*

Large prickles; base at least twice as long as the stomata 504*

Barb size; estimated by comparison with the size (length) of the base of the same prickle as seen in surface view:

Long barb; barb as long or longer than the base 505*

Short barb; barb shorter than the base 506*

Unbarbed or unpointed; incipient asperity 507*

Barb shape in relation to base; as seen in lateral view:

No prickles visible in side view 508

Barb developed basally from the apex of the base 509*

Barb developed from the apex of the base but slightly raised 510*

Barb not developed from the apex of the conical base; raised 511*

Barb with recurved point not developed from the apex of the base 512*

Barb orientation in relation to leaf blade:

Point to leaf apex; all in same direction 513

Point in both directions; apically and basally 514

DISTRIBUTION OF PRICKLES:

Intercostal; present in intercostal zone; usually small and transitional prickles:

Interstomatal long cell files with prickles 515

Intercostal long cell files with micro hairs and prickles 516

Other intercostal files with prickles 517

Costal; present in costal zones overlying any vascular bundle order:

One-three files of cells comprise all or some of the costal zones:

Frequent; not more than 5 silica bodies between successive prickles of a file 518

Infrequent; more than 5 silica bodies between successive prickles of a file 519

Rare; present in only some 1–3 file costal zones; irregular distribution 520

More than three files of cells comprise all or some of the costal zones:

Single file of prickles per costal zone:

Frequent; not more than 5 silica bodies between successive prickles of a file 521

Infrequent; more than 5 silica bodies between successive prickles of a file 522

As many files of prickles present as there are files of silica bodies per costal zone:

Frequent; not more than 5 silica bodies between successive prickles of a file 523

Infrequent; more than 5 silica bodies between successive prickles of a file 524

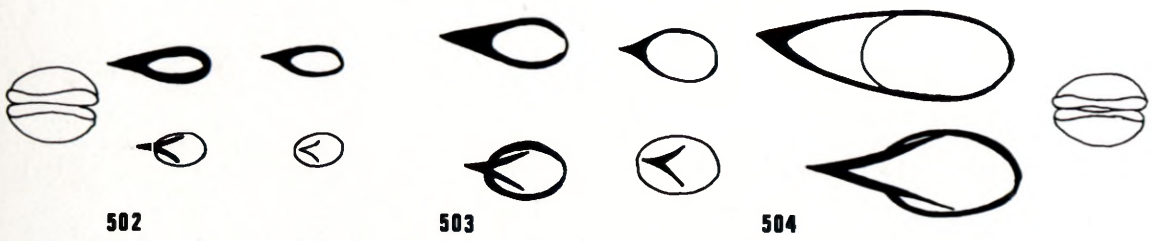
Single row of prickles at margins of costal zone; often seen in side view:

Interlocking with prickles of adjacent costal zone; overlying stomatal groove 525*

Do not interlock 526

Irregular, scarce; often more common in costal zones nearer margin 527

PRICKLES



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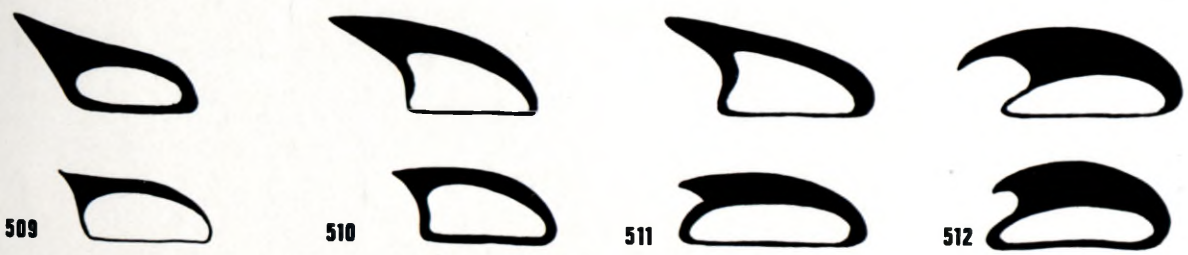

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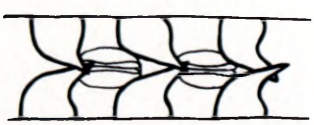

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5. PRICKLE HAIRS CONTINUED

HOOKS:
Smaller than prickles usually with rounded bases. Generally present in intercostal zones. Also termed crochets or crown cells.

DISTRIBUTION OF HOOKS:

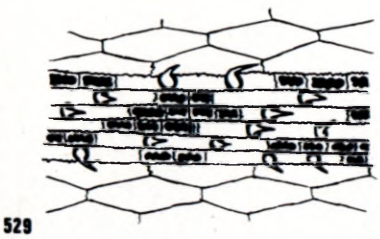
- **Absent;** presumed missing; not observed on surface of preparation examined 528
- **Costal;** present in costal zones of the leaf:
  - *Throughout* costal zones; not limited to any area of costal zones 529*
  - *On margins* of costal zones only 530*
- **Intercostal;** present in intercostal zones of the leaf:
  - *Adjacent* to costal zone; between intercostal long cells adjacent to costal zones 531*
  - *Centrally* located in intercostal zones; this type often in bulliform cell files 532*
  - *Interstomatal;* in same files as stomata 533*

ANGULAR PRICKLES OF MARGIN:
Includes only prickle hairs present on the leaf margin.

DESCRIPTION OF ANGULAR PRICKLES:

- **No leaf margin present on preparation** 534
- **Absent;** leaf margin present but no prickles present 535
- **Base size;** estimated by comparison with the length of the stomata of the same leaf:
  - *Small;* base shorter than the stomata 536*
  - *Medium;* base as long or slightly longer than the stomata 537*
  - *Large;* base much longer than the stomata; more than 2x 538*
- **Barb length** in relation to length of base:
  - *Short;* less than length of base 539*
  - *Medium;* as long as or slightly longer than base 540*
  - *Long;* much longer than the base, more than 2x as long 541*

HOOKS AND ANGULAR PRICKLES



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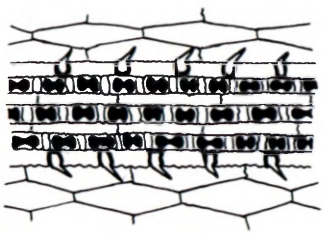

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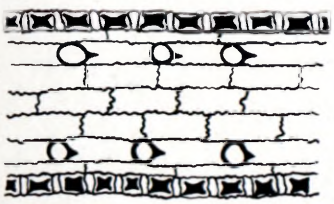

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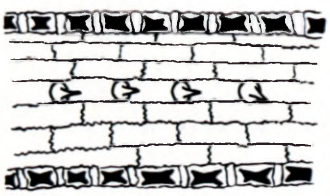

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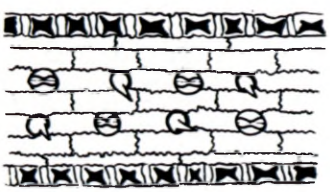

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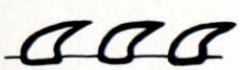

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6. MICRO-HAIRS

Micro-hairs are commonly termed bicellar trichomes although one-celled hairs do occur that are clearly homologous with the two-celled hairs. The distal cell is invariably very thin-walled and often is absent. Micro-hairs are valuable diagnostic characters and their presence alone is important. Thus preparations must be carefully examined as the hairs often occur infrequently and the mere presence of a solitary hair on a preparation may be taxonomically important.

DESCRIPTION: Continue further under Distribution for all types that occur.

- **Absent**; presumed missing i.e. none observed on surface of preparation examined . . . 601
- **Unicellular**, rounded to dome-shaped; Sporobolus type; associated with a cork cell . . . 602*
- **Bicellular**, two-celled; bicellar micro-hairs:
  - *Only basal cell* remains or is visible . . . 603
  - *Relative lengths* of basal and distal cells:
    - Approximately equal in length . . . 604*
    - Basal cell shorter than distal cell:
      - Basal cell less than $\frac{1}{2}$ the length of the distal cell . . . 605*
      - Basal cell only slightly shorter than the distal cell . . . 606*
    - Basal cell longer than distal cell:
      - Basal cell 2x, or more than 2x, longer than the distal cell . . . 607*
      - Basal cell slightly longer than the distal cell . . . 608*
  - *Relative shapes* of basal and distal cells:
    - Both cells approximately the same shape:
      - Cells of micro-hair narrow or thin:
        - Markedly elongated; micro-hair longer than the stomatal complex . . . 609*
        - Slender but short; micro-hair shorter than the stomatal complex . . . 610*
      - Cells of micro-hairs inflated and rounded . . . 611*
    - Basal cell less inflated than the distal cell; clavate hair . . . 612*
    - Basal cell more inflated than the distal cell . . . 613*
  - *Relative thickness* of basal and distal cell walls:
    - Walls of both cells approximately equal in thickness . . . 614*
    - Wall of distal cell thinner than wall of basal cell; often deciduous . . . 615*
  - *Shape* of distal cell:
    - Length equal to or less than width . . . 616*
    - Length slightly more than the width; length not more than 2x the width . . . 617*
    - Length much more than the width; length more than 2x the width . . . 618*
  - *Apex* of distal cell:
    - Broadly rounded to dome-shaped . . . 619*
    - Slightly tapered; tapering to a rounded apex . . . 620*
    - Tapered to a definite point . . . 621*
    - Sharply pointed . . . 622*
  - *Length* of basal cell:
    - Lenth approximately equal to width; not more than 2x the width . . . 623*
    - Length much greater than the width; more than 2x . . . 624*
  - *Shape* of base or attachment of basal cell:
    - Constricted base:
      - Inverted cone-shaped . . . 625*
      - Cupule-shaped . . . 626*
      - Parallel-sided; point of attachment small . . . 627*
    - Expanded base; not constricted:
      - Constriction above bulbous base . . . 628*
      - Parallel-sided . . . 629*
      - Bulbous i.e. broadly inflated . . . 630*
  - *Emergence* of base from short cell:
    - Turned at right angles to the short cell as seen in surface view . . . 631*
    - Emerges straight out of short cell; no angle at base . . . 632*

DISTRIBUTION: To be considered separately for each type of hair present.

- **Intercostal**; occur in intercostal zone between long cells:
  - Between both intercostal long cells and interstomatal cells . . . 633
  - Between intercostal long cells only; not between interstomatal cells:
    - Near costal zone; between stomatal bands and costal zone . . . 634
    - In the centre of the intercostal zone . . . 635
  - Between interstomatal long cells only . . . 636

MICRO-HAIRS


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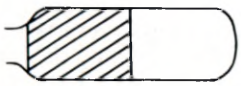
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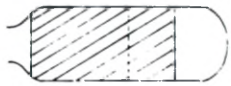
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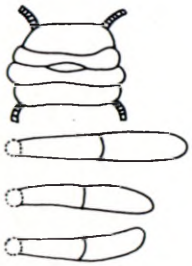
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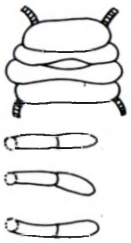
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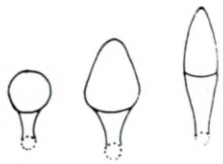
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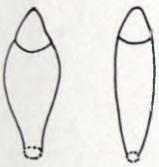
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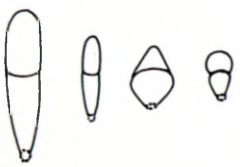
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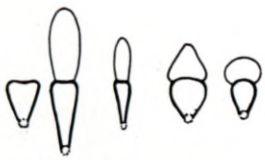
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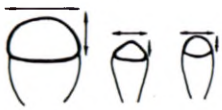
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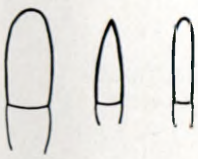
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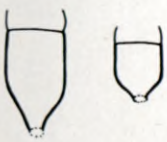
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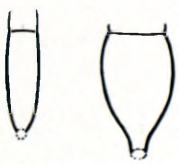
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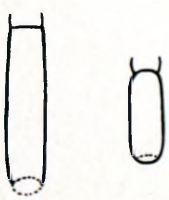
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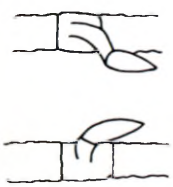
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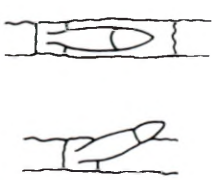
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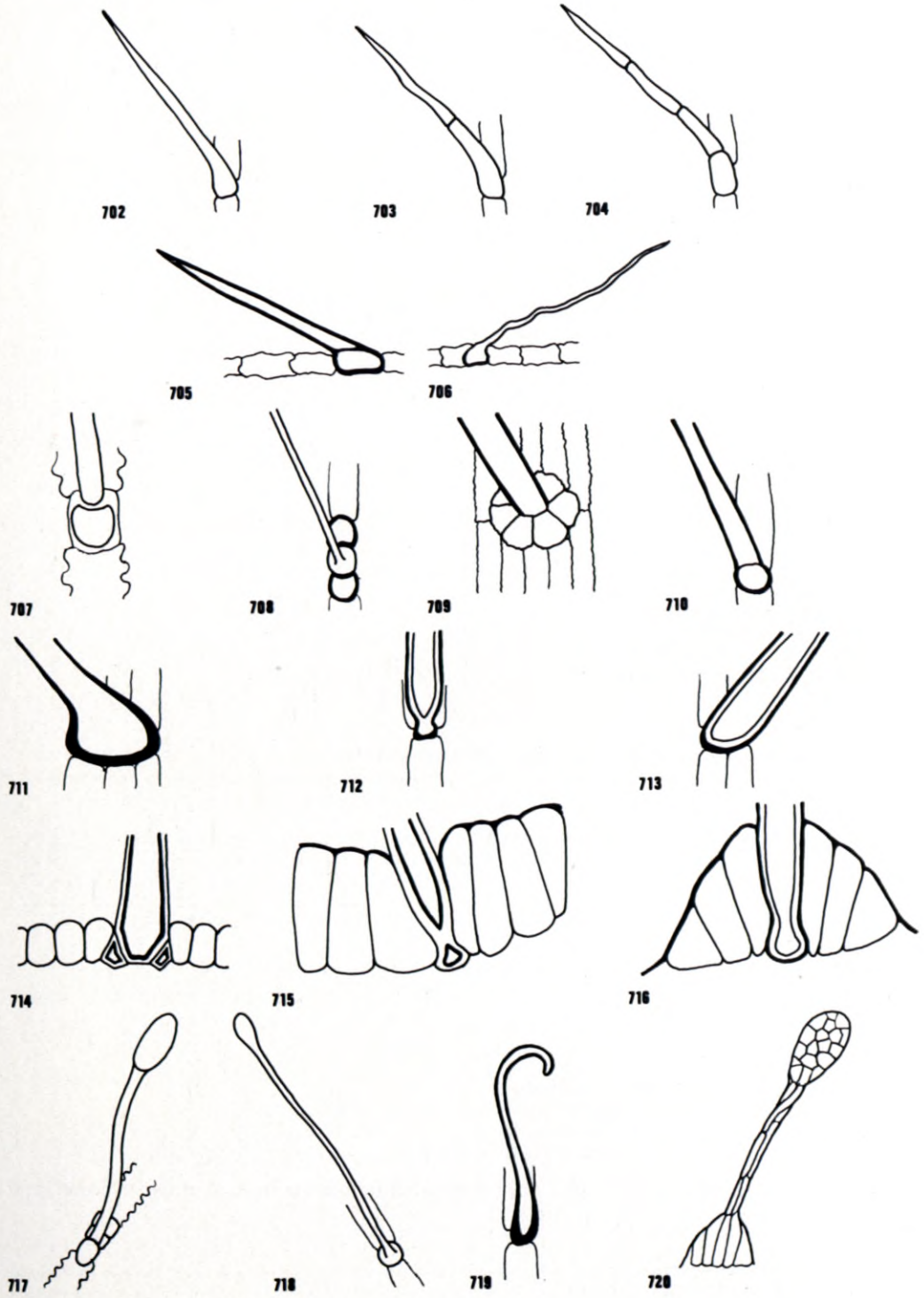
7. MACRO-HAIRS

Includes all trichomes not included under micro-hairs or prickles. Invariably the macro-hairs are much longer than the micro-hairs and are generally unicellular although fine transverse partitions are sometimes present. The hairs vary in length, in flexibility, in the degree of cell-wall thickening and may possess superficial or sunken bases. Hairs with sunken bases may, or may not, be accompanied by specialized epidermal cells. Most uni-cellular macro-hairs are probably homologous with prickles and are often difficult to distinguish apart, especially in cases where prickles have long barbs or where macro-hairs are short and rigid. In such instances it is advisable to describe the hairs under both prickles and macro-hairs and to make a special note of this fact.

DESCRIPTION:

- **Absent:** no macro-hairs seen and therefore presumed absent . . . 701
- **Number of cells comprising the macro-hairs:**
  - *Unicellular* macro-hairs present . . . 702*
  - *Bicellular* macro-hairs present . . . 703*
  - *Multicellular* macro-hairs present . . . 704*
- **Flexibility** of macro-hairs; correlated to wall thickness of hair cell/s:
  - *Hard,* stiff hairs usually with thickened walls . . . 705*
  - *Soft,* thin-walled hairs often damaged during preparation; slender . . . 706*
- **Epidermal cells** associated with base of macro-hair:
  - *One* specialized hemispherical epidermal cell accompanying base of hair . . . 707*
  - *Two* (sometimes one) specialized cells accompanying base of hair . . . 708*
  - *Many,* usually smaller, specialized epidermal cells accompanying base of hair . . . 709*
  - *No* specialized cells associated with base of macro-hair . . . 710*
- **Nature** of base of hair:
  - *Swollen* in relation to hair thickness . . . 711*
  - *Constricted* in relation to hair thickness . . . 712*
  - *Undifferentiated* in relation to hair thickness . . . 713*
- **Association** of the base of the macro-hairs with the epidermis; often difficult to ascertain from epidermal preparations:
  - *Superficial;* base constitutes part of the epidermis . . . 714*
  - *Sunken* base embedded between and often below surrounding epidermal cells:
    - Sunken below general level of the epidermis . . . 715*
    - Raised epidermal cells with sunken hair base surrounding hair; cushion hair . . . 716*
- **Specialized types** of macro-hairs; not included above:
  - *Stalked,* glandular bicellar hair; *Enneapogon* type . . . 717*
  - *Unicellular* macro-hairs with swollen tips . . . 718*
  - *Crozier* hairs . . . 719*
  - *Multicellular* clavate hairs . . . 720*
- **Length** of macro-hairs; measurements taken by comparison with the known field of view of the microscope. These categories are standardized for the Zeiss Standard RA microscope fitted with x10 Kpl W eyepieces. If hairs of variable length are present include all relevant categories:
  - *X16 Objective:*
    - More than twice the field of view at x160 i.e. longer than 2,25 mm . . . 721
    - Equal to or slightly more than the field of view at x160 i.e. between 1,125 mm – 2,25 m long . . . 722
    - Less than the field of view at x160 i.e. less than 1,125 mm long . . . 723
- **Frequency** of occurrence of macro-hairs on surface of leaf examined:
  - *Abundant;* more than 10 hairs visible in field of view at x160 . . . 724
  - *Frequent;* between 3 and 10 hairs visible in field of view at x160 . . . 725
  - *Scarce:* 1 or 2 hairs visible in field of view at x160 . . . 726
  - *Irregular;* parts of leaf without hairs; present on other areas . . . 727
- **Distribution** of macro-hairs in the various zones of the leaf surface:
  - *Intercostal* exclusively . . . 728
  - *Costal* exclusively . . . 729
  - *Both* costal and intercostal in distribution . . . 730
  - *Leaf margins* only or mainly . . . 731

MACRO-HAIRS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8. SILICA BODIES

Silica cells are idioblasts present in both the costal and intercostal zones and containing silica bodies or opal phytoliths of characteristic shapes. The shapes of the silica cells are not necessarily the same as those of the silica bodies contained in them and it must be carefully noted that for descriptive purposes only the shape of the silica body is described. All applicable variations in shape present on the specimen must be included. Immediately after each different type of silica body has been described, continue with distribution and further descriptive details before commencing with any other types of silica bodies which may be present on the specimens.

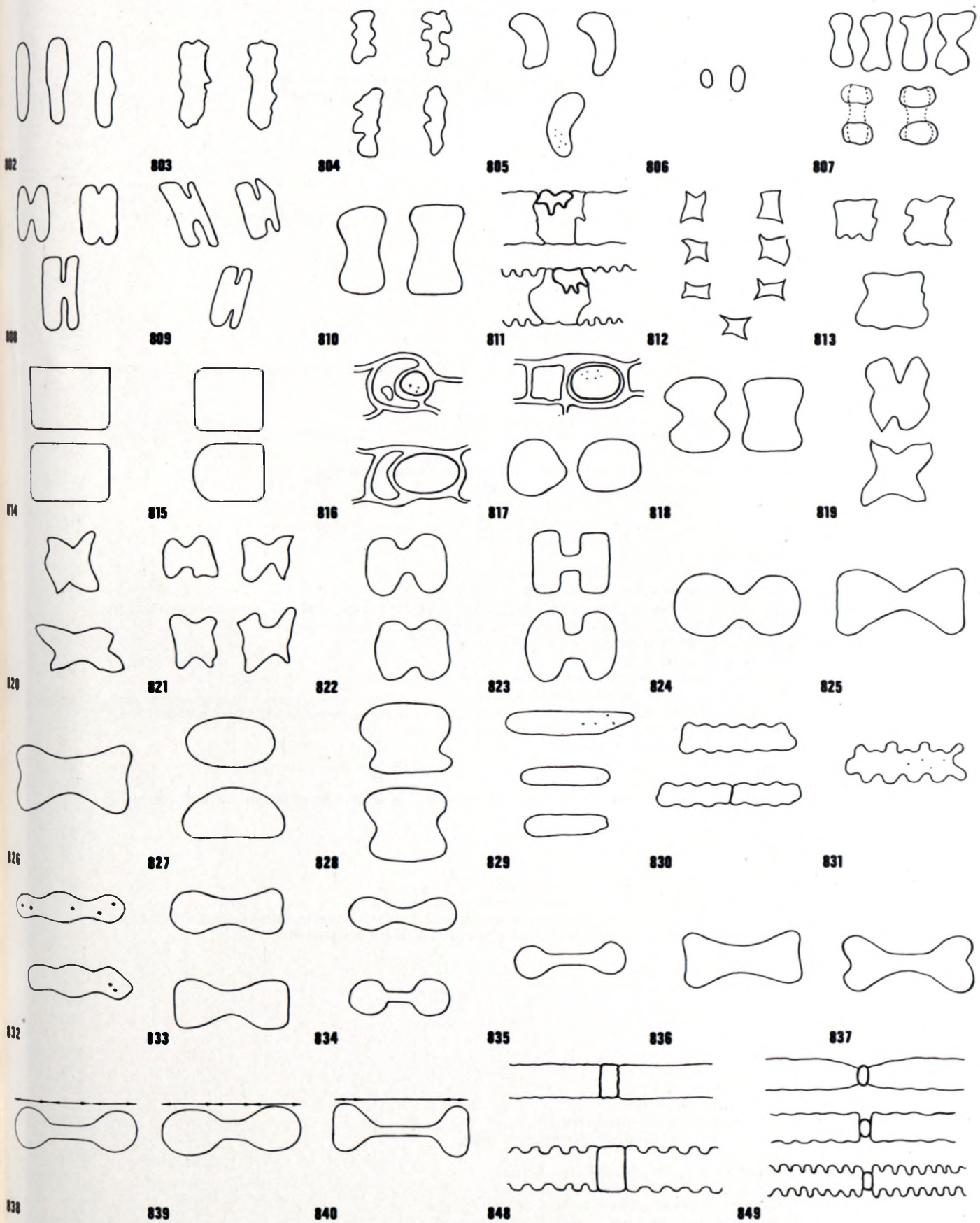
DESCRIPTION: Based on outline of the silica bodies when viewed from above and when granules in focus.

- **Absent** i.e. no silica bodies observed on surface examined . . . 801
- **Vertically elongated,** tall; vertical dimensions greater than horizontal dimensions:
  - *Tall and narrow* (sometimes more square-shaped):
    - Smooth, regular outline . . . 802*
    - Irregular outline . . . 803*
    - Crenate or scalloped outline . . . 804*
  - *Crescent- or kidney*-shaped . . . 805*
  - *Elliptical* in shape . . . 806*
  - *Dumb-bell/cross*-shaped:
    - *Oryza*-type; vertically arranged dumb-bell shaped; vary with focus . . . 807*
    - Short, tall and perpendicular . . . 808*
    - Short, tall and tilted or angular . . . 809*
  - *Saddle*-shaped, tall . . . 810*
- **Equidimensional;** vertical and horizontal dimensions approximately equal:
  - *Small and crenate;* closely enveloped by accompanying short/cork cell . . . 811*
  - *Acutely angled,* sometimes resemble crystals; often intercostal . . . 812*
  - *Squarish,* angular, with irregular outlines . . . 813*
  - *Square,* cubical or slightly rectangular . . . 814*
  - *Cuboid,* more or less squarish with rounded corners; sub-circular . . . 815*
  - *Round,* circular in shape:
    - Fitting into a concavity of a cork cell . . . 816*
    - Not intimately associated with a cork cell . . . 817*
  - *Saddle*--shaped, rounded, shortened, double-axe shaped . . . 818*
  - *Cross*-shaped, with four apices not rounded cf. dumb-bell shaped:
    - Regular, perpendicular . . . 819*
    - Irregular, tilted . . . 820*
  - *Irregular dumb-bell* shaped; intermediate between cross- and dumb-bell shaped . . . 821*
  - *Dumb-bell* shaped, relatively short, not elongate:
    - Nature of central region of dumb-bell:
      - Wide middle/central portion . . . 822*
      - Constricted, narrow central portion . . . 823*
    - Nature of ends of dumb-bell shaped bodies:
      - Rounded . . . 824*
      - Flattened . . . 825*
      - Indented . . . 826*
- **Horizontally elongated;** horizontal dimensions greater than vertical dimensions:
  - *Oblong* in outline . . . 827*
  - *Saddle*-shaped; elongate . . . 828*
  - *Elongate* with rounded ends:
    - Smooth outline . . . 829*
    - Sinuous outline . . . 830*
    - Crenate outline . . . 831*
    - Nodular outline or shape . . . 832*
  - *Dumb-bell* shaped; elongated:
    - Nature of central region of dumb-bell:
      - Wide middle/central portion . . . 833*
      - Constricted, narrow central portion . . . 834*
    - Nature of ends of dumb-bell shaped bodies:
      - Rounded . . . 835*
      - Flattened . . . 836*
      - Indented . . . 837*
    - Length of central portion of dumb-bell shaped bodies:
      - Equal to one third of the total length of the body . . . 838*
      - Less than one third of the total length of the body . . . 839*
      - Greater than one third of the total length of the body . . . 840*

DISTRIBUTION AND DESCRIPTION CONTINUED: To be completed independently for each of the different types of silica body present on the specimen.

- **Distribution:**
  - *Costal zones:*
    - Present throughout the costal zones . . . 841
    - Present on outer edges of the costal zones only . . . 842
  - *Intercostal zones:*
    - Present throughout the intercostal zones . . . 843
    - Present only on outer edges of the intercostal zones . . . 844
- **Description** continued:
  - *Granules:*
    - Not seen in silica bodies . . . 845
    - Present in silica bodies . . . 846
    - Cracks in silica bodies visible . . . 847
  - *Width;* vertical dimensions:
    - Approximately the same as that of adjacent short or long cells . . . 848*
    - Much less than that of adjacent short or long cells . . . 849*

SILICA BODIES



9. COSTAL SHORT CELLS

All costal epidermal cells are incorporated in this section. Includes cork cells (suberised cells), silica cells (silicified short elements), prickles, ordinary equidimensional to rectangular costal short cells and costal long cells. Excludes only the bodies contained within the costal silica cells.

DESCRIPTION AND ARRANGEMENT: Include all applicable different types.

Horizontal arrangement; composition of all individual horizontal files, with or without silica bodies:

Costal short cells only; perhaps a few silica cells or costal long cells interspersed along files:

Short, square to slightly rectangular:

With sinuous walls 901*

With straight walls 902*

Rectangular cells but not more than 3x longer than wide:

Same width as intercostal long cells 903*

Narrower than intercostal long cells 904*

Costal long cells predominate; perhaps a few silica cells or costal short cells interspersed along files; includes only cells more than 3x longer than wide:

Width of long cells:

Same width as intercostal long cells 905*

Narrower than intercostal long cells; often extremely long 906*

Nature of other cells in files:

Files consist entirely of costal long cells 907*

Paired short cells between successive long cells 908*

Solitary short cells between successive long cells 909*

Silico-suberose couples; cork-silica cell pairs; closely associated cork and silica cells separated by normal costal short or long cells:

Frequency of occurrence in costal files of cells:

Common in files; separated by few (1–3) costal short cells:

Separated by short, or slightly rectangular cells 910*

Separated by rectangular cells 911*

Infrequent in files; separated by numerous short cells (or a few very long cells):

Separated by many short or slightly rectangular cells 912*

Separated by numerous rectangular costal short cells 913*

Separated by few very long costal long cells 914*

Relative shape of cork and silica cells comprising the pairs:

Cork cell same shape as silica body 915*

Cork cell tall and narrow; silica body not tall and narrow 916*

Cork cell crescentic and enfolding the silica body 917*

Intermediate between silico-suberose couples and alternating condition; a single cork cell may thus sometimes be associated with two adjoining silica cells and sometimes silica cells may be without cork cells:

Relative shape of cork and silica cells:

Cork cell same shape as silica body 918*

Cork cell tall and narrow; silica body not tall and narrow 919*

Cork cell crescentic and often enfolding the silica body 920*

Alternating silica cells and costal short cells; pairs not distinguishable as the sequence in a file is silica, short (cork), silica, short (cork), etc. and not silica, cork, short, silica, cork, short, silica etc.:

Regular arrangement along individual files:

Short to square short or cork cells 921*

Rectangular to long cork or short cells 922*

Irregular arrangement along individual files; short sections with 2–5 cork or short cells in place of alternating silica and short cells:

Short to square short or cork cells 923

Rectangular to long cork or short cells 924

Silica cells most common along individual files:

Silica cells in short rows (2–6) between 1–2 short cells 925*

Silica cells only; perhaps a few non-silicified short cells or prickles present 926*

Vertical arrangement of horizontal costal files adjacent to third and first order vascular bundles i.e. band with the least number of files and bands with the largest number of files per costal zone (if distinguishable):

Number of files per costal zone:

1 file of cells comprises costal zone 927

2 files of cells comprise costal zone 928

3 files of cells comprise costal zone 929

4 files of cells comprise costal zone 930

5 files of cells comprise costal zone 931

6 files of cells comprise costal zone 932

7 files of cells comprise costal zone 933

8 files of cells comprise costal zone 934

9 files of cells comprise costal zone 935

10 or more files of cells comprise costal zone 936

Composition of alternating files of cells comprising costal zone.

All files similar in composition 937

Composition of alternating files of costal zones differ:

For zones comprised of 3 files of cells:

1 file with silica cells and 2 files of costal short or long cells 938

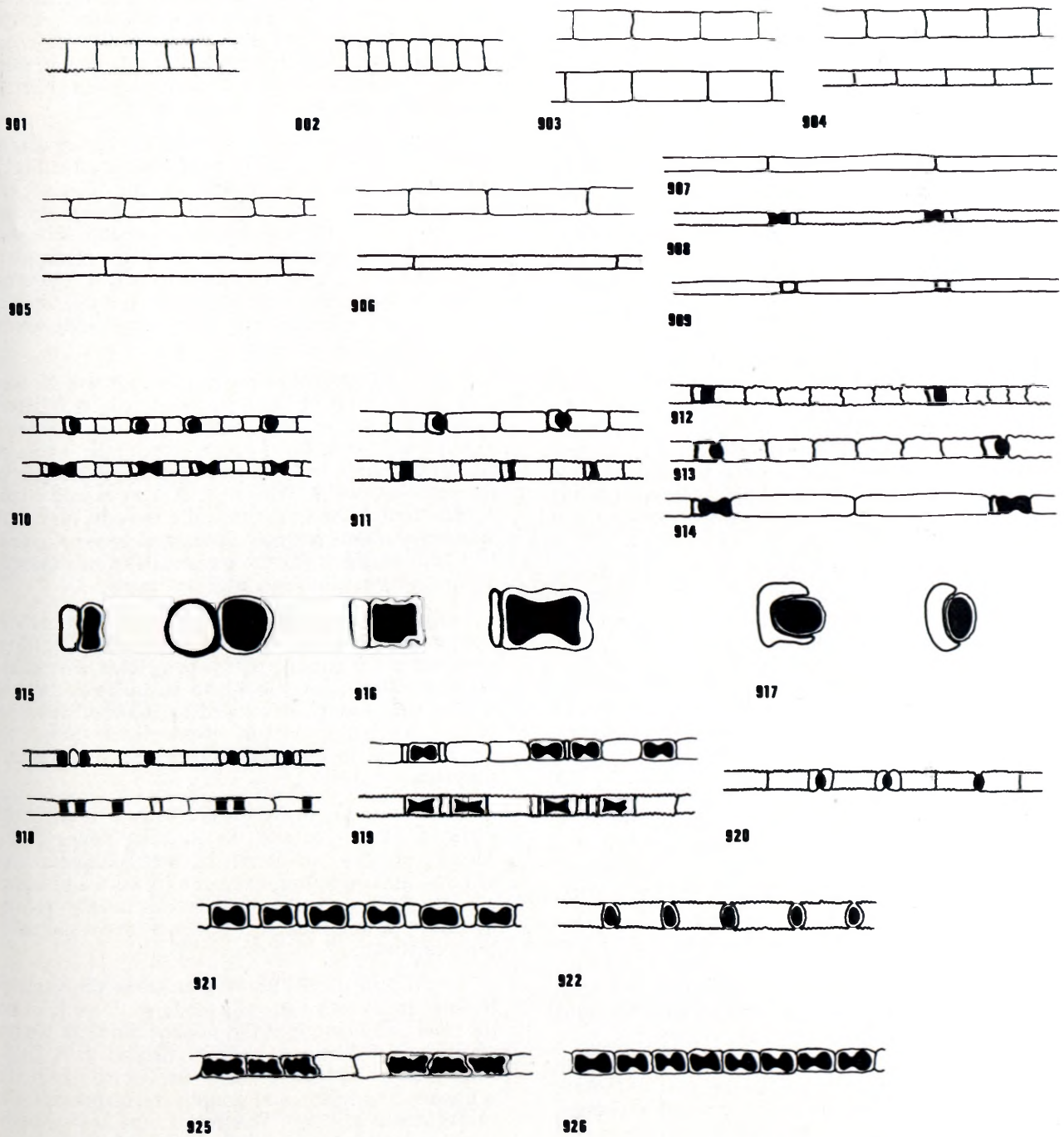
2 files with silica cells and 1 file of costal short or long cells 939

For all zones comprised of more than 3 files of cells:

Files with silica cells alternate with a single file of costal short or long cells 940

Files with silica cells separated by 2 or more files of costal short or long cells 941

COSTAL SHORT CELLS



ANATOMICAL CHARACTERS

The following presents a brief conspectus of the nature of the various structures used in describing grass leaf anatomy, as well as their range of structural variation. Where relevant, an account is given of the function or development of these structures and the factors which contribute to their variability. Their importance as either taxonomic or diagnostic characters is stressed.

Before commencing with a detailed description of the individual cell types, it is necessary to give a brief description of the plant cuticle as well as the arangement of the individual cell types in the different zones of the leaf lamina. This background should result in a better appreciation of the relationship of the epidermal cells to one another and to the hypodermis and other internal tissues.

Epidermal preparations of grass leaf blades are either produced by macerating techniques, resulting in acellular preparations, or by scraping techniques by which the epidermal cell layer and attached cuticle is studied in surface view. It is important to have some understanding of the relationship between the epidermal cells and the cuticle to satisfactorily interpret the patterns and structure visible in these preparations.

Stace (1965) gives a lucid description of the cuticle of vascular plants. Separating any two cellulose cell walls of adjacent cells throughout the plant is a cellulose-free layer known as the middle lamella, consisting basically of calcium and magnesium pectates. The outer surface of the epidermal cells are adjacent to the environment, rather than a neighbouring cell, and it is on this surface that the cuticle is formed. Roelofsen (1952, 1959) ascertained the precise structure of this cuticle using polarising and electron microscopy.

External to the normal cellulose cell wall of the outer face of each epidermal cell, a thin layer of pectic material, which is presumably continuous with the middle lamellae of the underlying anticlinal walls of the epidermal cells, may be present. Exterior to this is usually a two-layered wall termed the cuticular membrane (Roelofsen, 1952, 1959). The inner portion of this, the cuticular layer, is composed primarily of a cellulosic framework between the micro-fibrils of which is encrusted large amounts of cutin by the process of cutinization (Esau, 1960). The outermost part of the cuticular membrane is usually the cuticle proper. This is a thin layer, lacking cellulose and composed mainly of cutin adcrusted to the cuticular layer by the process of cuticularization (Esau, 1960).

Rarely are all four layers as clearly defined as above, but generally there is an increase in cutin outwards and a corresponding increase in cellulose inwards. Very often the pectic layer is absent, the inner cutin-free cell wall gradually merging into the outer cellulose-free cutin layer.

Where the outer walls of adjacent epidermal cells meet, the cuticular layer usually projects downward between the cellulose cell walls, forming the three-dimensional network of cuticular flanges so evident on acellular epidermal preparations. The length of the flanges varies from their virtual absence to their reaching to the inner wall of the epidermis. The flanges are formed by the cuticular layer alone, the cuticle remaining a thin extra-cellular uninterrupted membrane continuous over the leaf surface, being interrupted only by the stomata.

From this description of cuticular membrane structure, it will be evident that in acellular preparations, whether the membrane is isolated by enzymatic maceration, usually a pectinase (Orgell, 1955), or acid maceration, the flanges will be present on the inner surface of the preparations. These represent the position of the epidermal cell walls and are clearly visible when viewed from above or below because the cuticular membrane is much thicker at the position of these flanges. The outer surface of such preparations will still retain any hairs, papillae or striations.

These flanges, however, are not synonomous with the cell walls which were present for some distance on either side of the flanges. Thus, in cuticular preparations cell wall thickness and, subsequently, epidermal cell size, cannot be determined. For this reason, some workers prefer the term 'cell outline' when referring to cuticular preparations (Stace, 1965).

In certain plants one or more of the sub-epidermal layers in addition may also be covered by a cuticular membrane. This inner cuticle on hypodermal and mesophyll cells, especially the cells lining the air chambers below the stomata, may sometimes be seen on cuticular preparations prepared by maceration. This inner cutin layer is continuous with the external cuticle through the stomata (Esau, 1960). Sitholey (1971) terms the entire structure, internal and external cuticle, the cuticular skeleton.

In scraped epidermal preparations, it will be seen that the outlines of the epidermal cells may either remain constant, or vary, with change in focus level. The former condition occurs when the cuticular flanges penetrate only between the upper portion of the anticlinal walls. Where the flanges extend to the whole depth of the epidermal cells, the cells may show differing patterns at their upper and lower surfaces. It is thus common for the outer wall to be distinctly sinuous whereas the inner wall is straight.

The mature thickness of the cuticular membrane is not attained until a fairly late stage in leaf development when cell enlargement is completed. The membrane is often thick enough to be isolated, and the flanges well enough developed to show cell outlines before the leaf is mature. Nevertheless absolutely mature leaves are essential for comparative taxonomic purposes.

Environmental conditions are known to affect the cuticular membrane and the cuticular flange depth. Thicker cuticles are correlated with sunshine, drier soil and air conditions, exposure to wind and higher altitude. This cuticular thickness is usually accompanied by a thickening of the outer epidermal cellulose cell wall.

The epidermal cells above and below the vascular bundles are usually variously modified. Depending on the extent and nature of this modification, the lamina of grass leaf blades is usually divided into longitudinal zones with the costal zones lying opposite the veins and the intercostal zones present between the veins (Metcalfe, 1960). This costal zone has variously been termed vascular bundle or nerve epidermis and the intercostal zone is also known as inter-vascular bundle or inter-nerve epidermis (Davies, 1959) and even longitudinal stomatal zone (Bobrov, 1955).

These two zones differ from one another most conspicuously in species where sclerenchyma is well developed in association with the vascular bundles

only and where these sclerenchyma strands or girders are actually in direct contact with the epidermis (Jozwik, 1969). In these cases the costal epidermal cell walls are usually lignified and the cells are long and narrow. The intercostal cells are then much wider, unlignified and stomata are only present in this zone.

In many species the epidermis is more uniform and these two zones are then not so distinct. An example is where the hypodermal sclerenchyma occurs in the intercostal zones as well as the costal zones. In general, the more xeromorphic a leaf the less conspicuous are the veins on the cuticle (Stace, 1965) or the epidermis. The epidermis overlying vascular bundles with no sclerenchyma strands or girders need not necessarily be altered however and, in these instances, the costal zones are indistinguishable. This situation occurs frequently where bulliform cells overly the third order bundles. There is also variation in epidermal structure over vascular bundles of different orders and the lamina over the midrib, or from near the margins, can differ from the remainder (Metcalfe, 1960). Thus, in studying epidermal structure, comparison of epidermal preparations with transverse sections of the leaf are essential for accurate descriptions.

The presence or absence and frequency of commissural veins from one vascular bundle to another may also be taxonomically important (Slade, 1970). These cross veins are also known as transverse connections (Bobrov, 1955) or transverse anastomoses (Esau, 1960). These transverse vascular bundles may only contain a single file of tracheary elements and a single file of sieve-tube elements.

Intercostal long cells

The intercostal zone epidermis is generally made up of cells of two distinct sizes. The larger cells are elongated horizontally and are relatively narrow vertically. These are commonly referred to as long cells (Metcalfe, 1960; Gould, 1968) but are also termed undifferentiated (Davies, 1959) or fundamental (Prat, 1948) elements. These cells usually constitute the greater part of the epidermal surface area. Cells of the smaller category are normally much more nearly equidimensional in shape and are known as short cells (Metcalfe, 1960) or differentiated elements (Prat, 1948; Davies, 1959).

Both types of cell generally occur together in the same leaf. The shapes of long cells are fairly uniform and they exhibit inconspicuous differences such as variation in width and length, wall thickness and the extent to which walls are sinuate, papillate, or pitted. This contrasts markedly with the short cells which are often differentiated into such diverse structures as silica cells, cork cells, hooks, prickles or micro-hairs.

Gould (1968) is, nevertheless, of the opinion that significant differences in long cell structure exist among genera and even among species of the same genus. The basic types of long cells have proved very useful for broad surveys of the grasses (Metcalfe, 1960), but they are not adequate for all purposes since there are many intermediates and variants. For detailed studies of limited numbers of species, it may be necessary to introduce some additional types for descriptive purposes.

Although the shape, size and other characters of the long cells exhibit a wide range of genotypic variation, which has definite taxonomic applications, it must be remembered that these cells show an extreme degree of phenotypic variation which is elsewhere only paralleled by characters such as hairiness (Stace, 1965). Thus caution is needed in the taxonomic use of long cell characters.

Variation in epidermal cell size is great, especially that of the intercostal long cells. Thus, epidermal cells are larger on leaves from more humid or shady situations and smaller with drier air and soil and with greater altitude (Stace, 1965). Slade (1970) has shown that the mean length of long cells in shade leaves of *Poa alpina* was 51 per cent greater than in sun leaves. In general, these changes are proportional to a change in leaf area and cell length increase causes leaf length increases but the same number of cells are present in horizontal files in both sun and shade leaves.

Prat (1948) states that it is only the long cells that are sensitive to auxins. The length of a long cell in the meristematic base of the leaf can be suddenly increased by up to 200 times by hormone application. Short cells, on the other hand, are affected very little by hormones, probably on account of their precocious senescence and silicification (Blackman, 1969). Hence, their shape and size is more constant and reliable for taxonomic purposes.

Variability of epidermal cell size is not only dependent on environmental factors and genetic variation but is also due to leaf age, position of the leaf on the plant and the position of the epidermal cells in the leaf. Thus, in order for long cell size to be useful as a taxonomic character, care must be taken to use strictly comparable material and to ascertain the degree of variation present.

Long cell shape can be assessed quantitatively in two ways by finding the ratios of length: end width as well as the end width: median width (Borrill, 1961). These give a quantitative assessment of shape variation from square or rectangular to hexagonal.

The epidermal cells gain their characteristic adult shape gradually from the time that cell division ceases onwards, and in general this is not completed until the process of cell expansion has ended. It is for this reason that absolutely mature leaves must be examined to reliably determine cell shape.

The anticlinal walls of the epidermal cells are either straight or variously undulate or sinuous (Stace, 1965). These undulations are also known as folds (Wylie, 1943), corrugations (Martin, 1955) or waves (Watson, 1942).

The sinuosity of the cell wall can be expressed quantitatively by considering the undulations as waves and by measuring the variables frequency, amplitude and wave-length (Stace, 1956). These three variables amply express all the characters of the cell wall undulations except the shape of the waves. These may either be V-, U- or Ω-shaped.

The exact causes of the epidermal cell wall undulations are uncertain, but the two main theories suggest that it is either due to the tensions set up between the mesophyll and the epidermis or that it is caused by the method of hardening of the differentiating cuticular membrane (Watson, 1942). It has been observed that, whereas many cells have the anticlinal walls undulate throughout their height, some only have the outer part undulate, and thus the second hypothesis appears more likely.

Watson (1942) is of the opinion that the hardening of the cuticle extends gradually over the surface from the central area of the outer, free tangential wall.

Further cell expansion will be limited at those points where this hardening first reaches the anticlinal walls, i.e. where the undulations extend most deeply into the cell lumen. In other places the cell wall is still expandable. Thus, the outward projecting undulations can further stretch until plasticity is limited by hardening of the cuticle. The final amplitude of the undulations is only reached when the cells attain full size and will depend to some extent on the rate of hardening of the cuticular membrane.

The relative advantages and disadvantages of undulate walls are unknown, but Wylie (1942) put forward the theory that the undulations of the anticlinal walls increase the area of lateral contact between adjacent epidermal cells. This fact, together with the pitting in the anticlinal epidermal cell walls is thought to favour lateral conduction of water through the epidermis which thus functions in water storage and transfer and not only as a protective covering for the leaf. However, the fact that straight walled long cells are commoner in xerophytes appears to cast some doubt on this proposed function (Stace, 1965). In shade conditions, where the cuticle hardens much less rapidly than in strong light, the undulations are much more pronounced and the lower ends of the anticlinal walls show an amplitude identical with that of the outer surface (Watson, 1942). In sunlight, on the other hand, the inner side usually remains straight although the outer side may be undulate because the plastic stage of the cell walls is much shorter. This explains this phenomenon, but does not satisfactorily ascribe a function to the undulations of the long cell anticlinal walls. However, the lateral interlocking and infolding of the epidermal cells probably adds rigidity to the leaf and prevents collapse when water is withdrawn (Fisher, 1939).

It is thus clear that, once again, mature leaves must be studied in order to ascertain the degree of undulation of the walls. Few other characters of the epidermis show as much variation as the cell wall undulations and, although this has been used taxonomically, its use requires the most extreme caution.

The size, shape and undulations of the intercostal long cells can vary vertically across a single intercostal zone. Thus the intercostal long cells adjoining the adjacent costal zone are often comparatively short and wide with markedly undulate walls whereas the centrally located long cells are longer and narrower with straighter walls (Kaufman *et al.*, 1969).

Silicification of long cells occurs erratically in many species (Parry & Smithson, 1964). In older leaves, either isolated long cells or large numbers of adjacent ones may become silicified. The opal of these cells is rather cloudy, contrasting strongly with the smooth, clear silica bodies which occupy silica cells. The shape of the long cell silica bodies conforms closely with the outline of the long cells themselves.

Stomata

Stomatal complexes have been the subject of extensive study throughout the plant kingdom by morphologists and anatomists as well as physiologists. Regrettably their terminology has become confusing with descriptive terms being used in differing senses by these different disciplines. The following terms (Van Cotthem, 1970) are necessary to describe the stomatal complexes of the Poaceae:

(a) stoma—the pair of guard cells and the pore or stomatal aperture (Stace, 1965) enclosed by them;

(b) stomatal complex—the stoma and surrounding cells participating in the mechanism of closing and opening of the pore. This is termed the stomatal apparatus by Stace (1965);

(c) subsidiary cells—epidermal cells surrounding the stoma which differ in shape or size from other epidermal cells. These are also known as accessory cells (Stace, 1965);

(d) neighbouring cells—epidermal cells surrounding the stoma which are indistinguishable from those of the remainder of the epidermis such as the interstomatal long cells.

Paliwal (1969) classifies the stomata of the Poaceae under the dwisahkoshik (biperigenous) category which is recognized by the presence of two subsidiary cells placed laterally on the guard cells. These two guard cells are characteristically shaped as seen in surface view. They are elongated and bone- or dumbbell shaped with expanded, thin-walled ends linked by narrow, thick-walled middle portions. The lumina and protoplast is consequently modified in shape, being an elliptical mass at either end connected by a thin protoplasmic strand through the thick-walled central canal (Brown & Johnson, 1962). The nuclei of the guard cells appear as two ellipses connected by a narrow thread (Fahn, 1967). The thickening of the walls of the central canal can ultimately isolate the opposite terminals of the guard cells resulting in the formation of two nuclei per guard cell (Flint & Moreland, 1946).

As a result of turgor increase in this type of guard cell, the thin-walled expanded tips swell so pushing apart the inflexible middle portions of the cells and thus opening the stomatal pore (Fahn, 1967). In young leaves, before the differentiation of the guard cell walls is complete, the stomata remain closed.

Each guard cell is physically and functionally (Fahn, 1967; Gould, 1968) closely associated with a subsidiary cell located laterally on the outer side, away from the stomatal pore. These are conspicuous, distinctively shaped cells and stand out in marked contrast with the remainder of the epidermal cells. These cells owe their origin to the adjacent protodermal cells (Paliwal, 1969). This is known as perigenous development of the stomatal complex in contrast to the mesogenous type where the subsidiary cells and the guard cells are formed from the same mother cell (Roth & Chausnitzer, 1969). Thus, formation of the stomatal complex involves three mitotic divisions. Two asymmetric divisions in the two lateral epidermal long cell rows give rise to the subsidiary cells and another asymmetrical division in the central row forms two unequal cells—the guard mother cell and the future interstomatal cell. This guard mother cell divides transversely to form the two guard cells (Zeiger, 1971). Further differentiation of the stomatal complex involves differential cell expansion and wall thickening (Kaufman *et al.*, 1971).

Grass stomatal complexes can be classified according to the shapes of the subsidiary cells as seen in surface view. Various types are recognized for descriptive purposes. The dome-shaped (Metcalfe, 1960) type is also known as ovoid (Prat, 1948) and the parallel sided type (Metcalfe, 1960) as rectangular (Reeder & Ellington, 1960) or lozengic (Prat, 1948). The triangular type has also been called diamond shaped or rhombic (De Lisle, 1963) and sometimes this type has a small lateral evagination in which the nucleus may be located at the triangle apex (Lersten & Pohl, 1969).

These types are often sufficiently distinctive to be used for diagnostic and taxonomic purposes (Metcalfe, 1960). However, stomata of more than one type may occur together in a single leaf and the shape can be somewhat intermediate in certain species.

The stomata of the Poaceae are confined to the intercostal zones and each intercostal zone may include one or more stomatal bands depending on the species. Furthermore, each band may include one or more rows of stomata. The number of bands and rows of stomata in each intercostal zone varies not only from one species to another but also in different parts of a single leaf blade or in leaves taken from different levels of the same plant. De Winter (1951) has shown that the number of stomatal rows adjacent to vascular bundles of different orders differs in *Pseudobromus*.

The distribution and frequency of stomata are conspicuous characters and are often of considerable systematic and diagnostic value (Stace, 1965). However, they are often directly related to the ecology of the plant and are thus not likely to be of great phylogenetic value.

It has been shown that stomata become longer in shade, in moist air and in moist soil and Wilson (1971) has demonstrated considerable phenotypic variation both between and within populations in stomatal length. Other workers have found no difference in stomatal size between sun and shade leaves of a given species.

Stomatal frequency is a quantitative character that has been extensively used in the literature. However, the number of stomata formed on a given leaf is determined at the end of the period of cell division and long before the leaf reaches its full size. Thus, the stomatal frequency expressed as the number of stomata per unit area clearly decreases as the leaf expands and the degree of expansion is dependent on a number of environmental factors as well. Thus only mature leaves are acceptable for comparative measurements of stomatal frequency. Moreover the stomatal frequency often varies considerably on different leaves of the same plant or on different parts of the same leaf. Environmental factors can also regulate stomatal frequency. This is lowered by humidity, wet ground, shade, protection from wind and lower altitude but temperature variations affect frequency only minimally (Miskin & Rasmusson, 1970).

Fortunately the above variation can apparently be almost entirely cancelled by recording stomatal frequency in terms of the proportion of stomata to epidermal cells. Since the variation in stomatal frequency caused by environmental factors is apparently primarily due to the increase or decrease in epidermal cell size and not to cell number, this stomatal index is not affected. Unfortunately stomatal indices have not been used in the Poaceae, probably because the stomata exhibit such a regular pattern of zonation and are not randomly distributed as in dicotyledons for example.

There are numerous examples of variation in stomatal frequency and distribution on individual grass leaf blades. Although Miskin & Rasmusson (1970) found stomatal frequencies on the adaxial and abaxial surface of *Hordeum* to be the same, Bobrov (1955) found the stomata to be more abundant on the upper than on the lower surface of *Poa*. Stomata may even be absent on the abaxial surface altogether as on many permanently infolded leaves. However, in *Themeda triandra* the reverse occurs and there are fewer stomata on the upper surface (Mes & Aymer-Ainslee, 1935). At the base of the leaf there appear to be more stomata per unit area than elsewhere (Bobrov, 1955) and conversely stomata are more numerous nearer the leaf apex and nearer the margin (Mes & Aymer-Ainslee, 1935).

Variation in stomatal frequency is affected by the position of the leaf on the plant. Stomatal frequencies, therefore, appear to decrease progressively from the flag leaf to the basal leaves with the flag leaves having approximately twice as many stomata per unit area as the basal leaves (Miskin & Rasmusson, 1970).

This phenotypic variation can be taxonomically significant. Flint and Moreland (1946) found that the range in variation between varieties of sugar cane was less than that within a given variety. Factors such as position, rate of growth, turgidity of tissue and exposure to light resulted in greater variation in stomatal characteristics than that between varieties.

Certain structural adaptations of the stomata and associated structures are developed in response to environmental conditions. Grasses from dry localities often have stomata restricted to the sides and bases of furrows on the leaf surface. These leaves tend to become inrolled in dry conditions, the stomata thus being protected. In other xeromorphic species the stomata are protected by overlapping papillae, by interlocking prickles, the stomata may be sunken below the level of the epidermal cells (Merida, 1970) or the leaf may be permanently infolded with the abaxial surface being devoid of stomata.

Interstomatal long cells are cells that lie in the same horizontal files as the stomata and serve to separate the individual stomata in a file from one another. When the stomata in any given file are numerous, each successive stomatal complex is separated from its neighbour in the file by a single interstomatal long cell. Both end walls of these particular interstomatal cells will therefore be concave where they fit around the stomata.

Intercostal short cells

These cells are usually nearly equidimensional inl shape and are always shorter than the intercostal long cells with which they generally alternate in horizontar rows. The intercostal short cells are either solitary oe occur in pairs and are then known as silico-suberos. couples or cork-silica cell pairs (Kaufman *et al.*, 1970)

These intercostal short cells may be infrequent or absent in some species (Metcalfe, 1960). The frequency of occurrence of short cells and the contrasting of their presence in the costal and intercostal zones are worth considering for diagnostic purposes.

It is important to note that usually the costal short cells are not the same shape or arranged in the same manner as those of the intercostal zones. Thus, in comparative work, it is important to ensure that no confusion arises through comparing intercostal short cells with costal short cells (Metcalfe, 1960). Generally the morphology of the costal short cells appears to be taxonomically more important than the intercostal short cells but, nevertheless, both should be examined.

In short cell pairs, whether they be silico-suberose couples or not, the basal member of the couple is always the cork cell or suberous cell (Prat, 1948). It is thus possible to use these cell pairs for orientation purposes (Prat, 1948; Parry & Smithson, 1964; Sangster, 1970; Kaufman *et al.*, 1970). The silica cell or exodermic cell (micro-hair base) is always nearest

the leaf-blade apex and the sequence from apex to ligule (or downwards on the culm and sheath) is long cell, silica cell, cork cell, long cell, etc.

The intercostal short cells, alternating with the long epidermal cells, are the products of assymmetric divisions of intercalary meristem cells (Kaufman *et al.*, 1970). Short cells produced by these divisions can give rise to silico-suberose couples, stomata or trichomes.

A brief description of the microscopic changes that characterize the primary stages of differentiation of cork-silica cell pairs is useful in that it gives a fuller appreciation of the development of the taxonomically very important silica bodies. A short epidermal cell, which is going to form a silico-suberose couple, undergoes a symmetrical, transverse division, giving rise to two daughter cells of equal size and similar morphology. The basal member of the pair then forms a cup-like depression along its upper side and the upper cell forms a basal protrusion conforming to the shape of the depression in the future cork cell. The potential silica cell also enlarges outwards resulting in this cell protruding from the epidermis somewhat. These changes involve only differential wall thickening and cell expansion.

The nucleus of the silica cell disintegrates, whereas the cork cell retains its nucleus. Later, after the complete breakdown of the nucleus, the upper cell begins to accumulate silica which is deposited as long chains in the lumen of the cell. The lower cell of each pair retains its nucleus at maturity and accumulates no silica. This is the cork cell and usually contains a solid deposit of some organic substance (Artschwager, 1930) and has suberized cell walls (Prat, 1948).

Papillae

The outer surface of epidermal cells may be flat or convex to various degrees or the cells may bear small conical processes. These are known as papillae and the epidermides or cells which bear papillae are termed papillate (Stace, 1965). These protrusions of the outer wall are variously shaped and all gradations from simple conical papillae to longer structures, better described as hairs, exist. These belong to the exodermic elements of Prat (1932) and in the context as used in the Poaceae cells with the entire surface of the outer wall inflated are also termed papillate. Thus, papillae are either distinct, highly cutinised (Metcalfe, 1960) protrusions or thin-walled, dome-shaped and inflated. Inflated papillae often serve to protect the stomata by overarching them, either from the interstomatal long cells or from the adjacent files of intercostal long cells.

Papillae occur mostly on the intercostal long cells but dome-shaped costal structures are characteristic of a few species (Metcalfe, 1960). There may be one to many papillae per cell, either in one or several rows. More than one type of papillus may be present on a given epidermis or cell. The papillus is generally centrally placed but may be distally located on the side of the cell nearest the apex of the leaf.

These structures occur sporadically throughout the Poaceae and they are particularly common in, and characteristic of, certain taxonomic groups such as the bamboos. Heavily cutinized papillae are particularly prevalent on grasses from dry localities (Metcalfe, 1960) or saline habitats.

Prickle hairs

These are tough, shortly pointed structures with swollen bases and short, sharp spines or barbs which arise directly from, and form an integral part of the epidermis. These structures generally have thick lignified walls (Metcalfe, 1960) and are the cause of the rough or scabrous feel of the leaf. As the prickle hairs are generally all reflexed in the same direction, the leaves only feel scabrous when rubbed in the opposite direction. Prickle hairs are often silicified (Parry and Smithson, 1964) resulting in the formation of hook-shaped opal phytoliths (Baker, 1960). Silicified prickle hairs appear to be composed of material of two different refractive indices probably opal of differing water contents as observed in *Avena sativa* by Baker (1960). These silicified prickle hairs are characterized by an inner core of translucent opal surmounted by an outer layered sheath of crystal clear opal, which is initially precipitated (Baker, 1960).

Prickle hairs may conveniently be divided into two main types distinguished mainly on the basis of differing size:

(a) Prickles which have elongated oval or elliptical bases and are usually larger than hooks. These structures are also known variously as aiguillons (Bowden, 1964), asperites (Davies, 1969), teeth (Leigh, 1961), or retrorse barbs (De Winter, 1951). The angular prickles of the leaf margin comprise a distinct group within this category and generally differ from the typical prickles occurring elsewhere on the same leaf. Structures that resemble, in size and shape, typical prickle bases but lack barbs are sometimes observed on grass leaf epidermides. This condition is known as incipient asperity (Davies, 1959) and these structures may be mature but unbarbed structures although Metcalfe (1960) points out that all prickles may pass through an unbarbed stage during their ontogenetic development. This possibility needs further investigation. In this context it is interesting to note that Vickery (1935) considers all prickle hairs to be reduced hairs.

(b) Hooks have rounded bases and are smaller than prickles. Hooks are generally located in the intercostal zones. These structures have also been termed crochets or crown cells (Prat, 1932).

Prickles and hooks may occur together or alone in the same grass leaf or they may both be absent. They are encountered in both zones of the leaf, but usually prickles are costal and hooks intercostal. The short barbs of these prickle hairs are usually directed towards the leaf apex (Metcalfe, 1960), as do the spines of the marginal angular prickles (Lersten & Pohl, 1969), and can thus be helpful in orientating epidermal preparations. There are exceptions where the prickle hairs point both apically and basally, however.

Prickle hairs are usually paired with short cells adjacent to them in the same files. It seems reasonable to assume that prickles and short cells are homologous (Metcalfe, 1960).

In some xerophytic grass species the prickles from adjacent costal zones overly the intervening intercostal zone. These interlocking prickles serve to protect the underlying stomatal groove. This type of situation is only found in leaves with narrow, relatively deep furrows as well as ribs especially on the abaxial surface.

Relative proportions of barb length to base size can be gauged by projecting parallel lines through the apex of the barb and the opposite ends of the prickle hair base. In this study base size is assessed by comparison with the length of the stomata on the same leaf.

Micro-hairs

In the Poaceae the occurrence and form of micro-hairs are characters of considerable taxonomic significance. Many agrostologists (Reeder *et al.*, 1965) consider micro-hairs to be characters of fundamental systematic importance in this family where superficial morphological similarity does not necessarily represent close phylogenetic relationship.

Micro-hairs are typically less than 0,12 mm long (Johnston & Watson, 1977) and can be recognised by generally being much smaller than macro-hairs. They are usually two-celled and are often called bicellar hairs or trichomes (Lersten & Pohl, 1969) and consist of a basal cell connected to an intercostal short cell and a distal, apical cell. The bicellular nature of these hairs is not always immediately apparent because the distal cell, which is invariably very thin-walled, is easily damaged, and often missing, especially on herbarium material. Even when the distal cell remains intact it is often obscure because the very thin wall does not stain readily. The basal cell walls are sclerified and the distal cell wall is cellulosic (Prat, 1948). This difference in wall thickness is also taxonomically significant as it is in the panicoid grasses that the distal wall is exceptionally thin whereas in the chloridoid type of micro-hair the walls of both cells are practically the same thickness (Tateoka *et al.*, 1959).

It is suspected that micro-hairs function in the secretion of some undetermined substance, or substances (Metcalfe, 1960). It is possible that the distal cell is destroyed when the secreted material is discharged. This deciduous nature of the apical cell further restricts the use of the form of this cell for diagnostic purposes.

The term micro-hair is preferred to bicellar hair by Metcalfe (1960) because single-celled micro-hairs do occur in certain groups e.g. *Sporobolus*. These one-celled hairs are clearly homologous with bicellar micro-hairs and cannot be regarded as macro-hairs. Metcalfe (1960) is, therefore, of the opinion that distinctions in the size and functions of hairs are more fundamental than whether they are one- or two-celled.

Micro-hairs invariably occur in the intercostal zones of the leaf epidermis—either in the stomatal bands or between these bands and the costal zones. They arise from an intercostal short cell, or cell pair, situated between successive long cells in a file. Micro-hairs are present on either or both the adaxial and abaxial epidermides. Many species, especially those with permanently infolded leaves and lacking abaxial stomata, have no micro-hairs on the commonly examined abaxial surface, but they are present on the adaxial epidermis from which preparations are less easily made. This reason, and the fact that micro-hairs are easily rubbed off, leads Metcalfe and Clifford (1968) to advise caution in stating whether micro-hairs are absent and they suggest the use of the expression "none seen" as an alternative.

The absence or presence of micro-hairs is also possibly not as meaningful taxonomically as is generally accepted in the light of variation observed in *Cortaderia selloana* (Metcalfe & Clifford, 1968). Nevertheless, the presence or absence of micro-hairs appears to be constant for species, with only the above known exception, and both the presence and form of micro-hairs are very consistent at generic and major group levels (Johnston & Watson, 1977). They appear to be lacking in all festucoids, whereas all other groups universally possess them (Metcalfe, 1960; Watson & Clifford, 1976).

Two distinct types of micro-hair are easily recognized. The panicoid type has a relatively long and narrow or tapered distal cell whereas, in the chloridoid type, in contrast, the distal cell is markedly inflated or hemispherical. Numerous terms have been used to describe micro-hair shape but it is more satisfactory to express this as a ratio of total hair length to maximum hair width (Tateoka *et al.*, 1959). This ratio is, therefore, numerically larger in chloridoid than panicoid micro-hairs. Thus total length of the hairs, their dimensions and the relative lengths of the basal and distal cells appear to be the most satisfactory characteristics for taxonomic purposes. As the shape of the fragile distal cell can easily be distorted, caution must be exercised when relying on the shape of micro-hairs as a taxonomic character (Metcalfe, 1960).

Panicoid hairs have been described as rod-like (Tateoka *et al.*, 1959) but chloridoid hairs are variously known as club- or globe-shaped (Tateoka *et al.*, 1959), clavate (Decker, 1964) or "ice cream cone"-like (Reeder *et al.*, 1965).

Certain micro-hairs resemble neither of the above two types. *Neostapfia* and *Orcuttia* possess "mushroom-button" micro-hairs (Metcalfe, 1960; Stebbins & Crampton, 1961) and *Neostapfia* also has unique "crozier" hairs. Sunken micro-hairs occur in *Neeragrostis* (Nicora, 1962) and *Triodia* (Burbidge, 1946) where the hairs located in the adaxial groove consist of a bulbous-based basal cell embedded between the epidermal cells with a small apical cell. This description resembles papillae in section and may, in fact, represent mistaken papillae.

The hairs of the Pappophoreae have been discussed by numerous authors (Prat, 1936; Caceras, 1958; Jacques-Felix, 1962; Reeder, 1965). These are elongated bicellar hairs with a glandular, usually bulbous, apical cell and a slender, much elongated, basal cell. Stebbins and Crampton (1961) were of the opinion that the stalk was composed of two cells so that the hair is actually tricellar and De Wet (1958) states that the micro-hairs of *Schmidtia* and *Enneapogon* are typically eragrostoid. In the present context these hairs, together with crozier hairs, are considered with macro-hairs because of their larger size (greater than 0,12 mm long) and because they are associated with modified epidermal cells which characterize macro-hairs.

Silicification of the macro-hairs has been observed in some species (Parry & Smithson, 1964). Usually only the basal cell is observed in a silicified condition. However, the possibility of the distal cell becoming silicified but subsequently lost cannot be excluded.

Macro-hairs

Macro-hairs are much longer than micro-hairs. They are characteristically unicellular although sometimes fine, transverse partitions are seen (De Winter, 1951a; Metcalfe, 1960). Macro-hairs are often associated with one or more epidermal cells differing variously from the typical epidermal long cells. Intercostal macro-hairs generally conform to this definition but hairs frequently encountered on the costal zones and on the leaf margin are also referred to this type.

The distinction between macro-hairs and prickles is often not clear and Metcalfe (1960) considers these

two hair types to be homologous. This is especially true when prickles possess exceptionally long barps as is common on leaf margins. In these cases, when it is difficult to decide where the distinction between a macro-hair and a prickle hair should be drawn, it is suggested that they be described under both hair types. However, if the hairs are relatively short and robust (as is characteristic of prickles) but are associated with specialized epidermal long cells then they can be regarded as macro-hairs. Prickles, therefore, arise from modified short cells whereas macro-hairs usually have modified long cells associated with their bases.

Macro-hairs vary considerably in length even on a single leaf, in flexibility, in wall thickness, and in the extent to which their bases are sunken between the surrounding epidermal cells. These hairs with sunken bases are often associated with epidermal cells that are larger, more inflated and raised above the general level of the leaf surface than are the typical long cells. A hemispherical protuberance is thus formed. This type of macro-hair is referred to as a cushion hair and is intercostal in occurrence. Bowden (1971) considers these thin-walled cushion cells to have high sugar concentrations and concludes that they are the sites of the leaf nectaries in *Andropogon gayanus*. Cushion hairs form the visible leaf pubescence which is visible with the naked eye or hand lens.

Macro-hairs are generally of no more than specific diagnostic value and variation in respect of length, frequency, cell wall thickness and the extent to which they are rigid and straight or flexible and bent have restricted taxonomic use. Metcalfe (1960) considers these differences to be useful only as confirmatory characters for the identification of species.

Hair frequency, in particular, is often unreliable for taxonomic purposes as the number of trichomes is determined when the leaf is very young and the density therefore drops as the leaf expands (Stace, 1965). Thus leaf age needs to be standardized but, in addition, macro-hair frequency is also affected by a variety of environmental conditions. Hairs are more abundant with more sunlight, greater wind exposure, drier air, drier soil and greater altitude. Glabrescence is another factor complicating macro-hair frequency (Stace, 1965). This involves the gradual loss of macro-hairs with age but fortunately in the case of cushion hairs the bases remain visible even when the hair is lost. Furthermore, the number of macro-hairs varies from leaf to leaf and on a single leaf the basal parts of the leaf blade are more pubescent than the distal parts (Liversidge, 1970).

The nature of the trichome base, particularly in the cushion type of macro-hair, frequently provides characters of importance (Stace, 1965). The hair base itself may be constricted or swollen in relation to the hair thickness. The nature of this base can often be more reliably determined from transverse sections of the leaf (Ellis, 1976). The extent that the base of the macro-hair is sunken below the level of the epidermal cells appears to be significant. Deeply sunken bases are generally characteristic of grasses from warmer climates and the more superficial bases are more common in temperate grasses (Metcalfe, 1960). The extent to which the hair bases are sunken or not is generally not easy to determine from epidermal preparations and, in addition, the sunken hairs easily become dislodged during preparation by the scraping method. It must be noted, however, that similar hair types occur in various genera between which there is not thought to be close affinity and thus macro-hair form is of only limited use above the species level.

Atypical macro-hairs such as crozier hairs and the stalked glandular hairs of the Pappophoreae (Stewart, 1964), on the other hand, are significant taxonomically at the generic level and above. These taxonomically important hairs are included under macro-hairs in the present context, although they are discussed more fully under micro-hairs, when they are often included by other authors.

A unique and distinctive type of multi-cellular clavate macro-hair has been described from several *Panicum* species (Kabuye & Wood, 1969). These hairs arise from conical bases in the intercostal zones. Above the base the hair consists of a multiseriate stem of elongated cells and widens to a head consisting of iso-diametric cells. In the mature condition these cells of the head contain a yellowish, sticky substance. Large cells on the distal side of the hair base hold the hair erect when they are turgid.

Silica bodies

Silica bodies are discrete deposits of hydrated silica present in the epidermal cells. These distinct solid opaline bodies are deposited in the lumens of specific and specialized silica cells or idioblasts. This deposition results in distinct structures, generally of constant shape and predictable location. Even although silica is virtually transparent and has a glassy appearance they are, nevertheless, easily visible microscopically because they have a distinct dark outline.

Silica bodies or Kieselkörper are also known as opal phytoliths (Parry & Smithson, 1964; Sangster, 1970). This term is distinct from the term silica body or spodogram (Edwards, 1935) which often includes both the typical bodies formed in the silica cells as well as atypical bodies sometimes present in other epidermal cells. This second type of intra-cellular silica deposit always conforms closely to the shape of the original cell whereas the shape of a phytolith may be independent of that of the idioblast in which it is laid down. This distinction is definitely justified but, as the term silica body has found such general acceptance in taxonomic and comparative anatomical literature, the term silica body has been retained.

Typical silica body deposition commonly occurs in costal idioblasts, which alternate with non-silica cells in parallel files throughout the costal zones. In addition, intercostal idioblasts occur at regular intervals between the intercostal long cells. Generally each apically orientated silica cell is contiguous with a basal cork cell and both together form a silico-suberose couple (Sangster, 1970) or cork-silica cell pair (Kaufman *et al.*, 1970).

Typical silica bodies, therefore, rarely occur in adjacent cells but are invariably located in alternate or more widely separated cells. This is a distinctive feature of these bodies and contrasts markedly with the characteristic silicification of adjacent cells in atypical silica deposition (Parry & Smithson, 1964).

The shapes of typical silica bodies or phytoliths are very important for taxonomic purposes (Metcalfe, 1960; Blackman & Parry, 1968). However, caution must be exercised as the shapes of these silica bodies are not necessarily the same as the outlines of the silica cells in which they are located. It is, therefore, essential to state unambiguously whether a silica cell or silica body is being referred to. In the past the lack of a clear distinction in this respect has been somewhat

confusing and once again emphasises the need for standardizing terminology.

Silica cells become precociously filled with a gel of colloidal silica which becomes a solid transparent body as the protoplasm dies (Prat, 1948). In the centre of the mass of solid silica small spherical cavities, granules, vesicles or droplets are usually present (Fahn, 1967). These minute granules, which occur singly or in groups, have been regarded as the occluded nucleus (Prat, 1932), or remnants of the disintegrated cytoplasm (Blackman, 1969), which have been trapped during penetration of the silica. The presence of these granules suggests that the solidification of the silica gel occurs suddenly (Blackman & Parry, 1968), a fact which was demonstrated by Kaufman *et al.* (1969a). Sometimes the silica bodies are cracked or fragmented, but Blackman (1969) is of the opinion that this is an artefact resulting from stress during the preparation of leaf scrapes or strips.

For taxonomic purposes silica bodies are normally described as seen in surface view. Nevertheless an understanding of their three-dimensional appearance is useful. In transverse section silica bodies characteristically have a concave outer surface which may become exaggerated as a result of dehydration—either during the preparation of the material or naturally (Blackman, 1969). The degree of concavity is also dependent on where a particular section is taken as the bodies are generally more concave in their central parts. These trough-shaped silica bodies are typical of the costal zones and in the past these thin-walled concave costal epidermal cells have been mistaken for passage cells (Goossens & Theron, 1934) and Jeffries (1916) considered these "peculiar" cells to be plate cells.

Intercostal silica bodies, on the other hand, are often cone-shaped in three-dimensional view. The cone tapers toward the leaf interior as viewed in section (Parry & Smithson, 1964).

The preparation and interpretation of epidermal preparations showing silica bodies demands an appreciation of the properties of opal or solid hydrated silica (Parry & Smithson, 1958). This substance is chemically stable, is not destroyed by heat and is soluble in hydrofluoric acid. The refractive index of silica is low and consequently silica bodies have distinctly higher relief than the surrounding tissue when preparations are mounted in mounting media with higher refractive indices such as Canada balsam. It is interesting to note that this only applies to silica deposited in the silica cells and that the appearance of atypical silica is normally indistinct even in Canada balsam mounts (Blackman & Parry, 1968).

Various shapes of silica bodies have been recognized and these types are very important as they are characteristic of tribes or even sub-families of the Poaceae (Blackman & Parry, 1968). To avoid causing considerable confusion, however, it is essential that these shapes be described relative to their orientation on the leaf surface. This is because similar shaped silica bodies can be positioned at right angles in different species. Thus, the typical oryzoid silica body is characteristically dumb-bell shaped but in contrast to the panicoid type is orientated with the long axis vertically and not horizontally (Tateoka, 1963).

Shapes of silica bodies are normally described as seen in surface view. Round and oval silica bodies have also been termed hat-shaped (Parry & Smithson, 1964). Oblong, linear, rod-shaped or rectangular (Chih-Ying Wu, 1958) bodies belong to the category costal rods (Parry & Smithson, 1964). Crescent-shaped or half-moon (Prat, 1948) silica bodies have been described, as have saddle-shaped bodies. This type is also known as double-axe-shaped (Reeder & Ellington, 1960; Gould, 1968) or the battle-axe type (Prat, 1948). Dumb-bell silica bodies are bilobed structures with a trough-shaped outer surface and a narrow isthmus and the nodular or sinuous type has three or more expanded areas. The cross-shaped silica body is similar to the dumb-bell except that it has only a short narrow central part.

Silica body form and arrangement exhibit a limited degree of variation. Thus, costal silica bodies of a somewhat larger size are present on the abaxial surface of the leaf blade than on the same surface of the leaf sheath, but the sheath has many more intercostal bodies (Parry & Smithson, 1964), with the greatest number being concentrated at the base of the sheath (Blackman, 1968). The adaxial surface of the blade possesses fewer silica bodies with the intercostal bodies being absent and the costal bodies being less common but larger than those of the abaxial epidermis. Abaxial intercostal bodies are often more abundant towards the ligule with either a gradual, or an abrupt, change along the blade (Parry & Smithson, 1964). Alternatively in some species these intercostal bodies may be evenly distributed throughout the abaxial leaf epidermis.

Various environmental and ontogenetic factors may also affect the silica body pattern. pH of the soil and availability of silica can result in larger or smaller silica bodies (Sangster, 1970). On any given plant there may be variation depending on the position of the particular leaf on the plant (Parry & Smithson, 1964) with the number of silica bodies increasing from juvenile to adult leaves (Blackman, 1968), although the characteristic pattern and form of the bodies themselves is maintained. Intercostal silica bodies increase, and costal bodies decrease, from the juvenile to the adult leaves. Age of the leaf is also very important, as silica deposition follows the basipetal maturation gradient within the leaf (Sangster, 1970).

The mechanism by which silica accumulates in potential silica cells is unknown (Blackman & Parry, 1968). However, the consistent formation of regular bodies is indirect evidence for an active mechanism of silica deposition although no enzymes active in silica deposition are presently known.

A passive non-metabolic mechanism, whereby silica accumulates at the leaf surface due to transpiration, is also possible (Sangster & Parry, 1971). Prat (1948) suggests that developing silica cells undergo premature senescence, which is accompanied by a change in pH. Such a change could initiate silica precipitation. Alternatively, if the structure of the outer wall or cuticle allowed more rapid transpiration to occur, silica solutions would accumulate in these cells resulting in gel and opal formation (Blackman & Parry, 1968). The difficulty in explaining the regular pattern of typical silica body deposition casts some doubt on these passive theories of silica deposition as does the fact that silica is accumulated by silica cells whether still ensheathed or not (Kaufman *et al.*, 1969). This conflicts with Blackman (1968), who found that silica deposition only occurs when leaves are fully expanded. Nevertheless, exposure to sunlight and the atmosphere, and the corresponding increase in transpiration, is possibly not essential for the silicification process.

In addition, different kinds of cells in the epidermal system may have different mechanisms whereby they accumulate silica (Kaufman *et al.*, 1969). Atypical silica is probably laid down not at the same time, nor by the same mechanism, as typical silica but rather as a result of environmental factors such as damage (Parry & Smithson, 1963) or high silica concentrations in the soil.

The uptake of silica by plants can be explained simply in terms of the concentration of silica in the soil solution and the amount of water transpired (Jones & Handreck, 1965). Silica is thus passively taken up in the transpiration stream but different plants take up different amounts of silica from a given soil. For example, in grasses the proportion of silica is ten to twenty times greater than in leguminous plants (Jones & Handreck, 1965). In addition, plants of the same species absorb different amounts of silica when grown on different soils.

The function of silica deposition is also not certain. It has been suggested that silicification represents the disposal of an unwanted substance. However, if this were the case then the atypical silicification of bulliform and long cells, which account for a much greater storage volume of silica than do the phytoliths (Parry & Smithson, 1963), would be a much more efficient system. On the other hand, deposition of silica bodies regularly and evenly over the leaf surface appears to distribute a given volume of silica over a greater area. If silica, therefore, functions as mechanical protection against insect attack (Ponnaiya, 1951; Yoshida *et al.*, 1959), this type of silicification could represent efficient use of this material and the greater deposition of silica on the abaxial surfaces of the leaf is in keeping with this proposed function (Parry & Smithson, 1964). Raeside (1970) is of the opinion that silica probably also helps to support plants when they are near their wilting points and this controlled petrification may be an economical means for grasses to attain rigidity with minimum expenditure of photosynthate (Drum, 1968).

A brief discussion of silica deposits other than the phytoliths proper, that are commonly present in the Poaceae, will probably help to make the distinction between these and the other types of silica deposits clear. Both intra- and extracellular deposits of silica occur in the grasses in addition to the typical silica bodies, sometimes in proportions which assume considerable physiological and anatomical significance (Sangster, 1970).

Two types of extracellular silicification occur. Membrane silicification results in thin films of silica bearing faint impressions of epidermal structures (Parry & Smithson, 1964). In addition, the intercellular air spaces between the sub-epidermal cells may become filled with silica.

Numerous types of atypical intracellular silicification are also found. These include long cell phytoliths (Sangster, 1968), which correspond to the original shape of the intercostal or costal long cells in which they are deposited and consequently have protuberances corresponding to the undulations of the cell wall. In other silicified long cells the silica may only be impregnated in the cell walls (Kaufman *et al.*, 1969). Pit phytoliths are minute opaline deposits in the simple pits of the outer periclinal walls of the epidermal long cells (Sangster, 1970a). Each aperture appears to be blocked and filled with silica. Intracellular silicification may also occur in the following epidermal cell types: bulliform cells, stomatal guard and subsidiary cells, cork cells, micro-hairs, macrohairs and very commonly, prickles (Parry & Smithson, 1964; Blackman & Parry, 1968; Kaufman *et al.* 1969). In addition, rectangular bodies may be formed in the cells of the sub-epidermal layers (Lanning *et al.*, 1958) and, especially in older leaves, silicification of sclerenchyma fibres and collenchyma occurs (Sangster, 1970a). Some of these atypical extra- and intracellular types of silica deposition can be expected to interfere with the mesophyll functions and could contribute to senescence. It is of interest to note that this type of silicification normally occurs much later than in the normal idioblasts (Sangster, 1970a).

CONCLUSION

It is hoped that this attempt to introduce uniform standards to the description of grass leaf blade epidermides will stress the need for standardization of terminology in these studies. If this can be achieved, anatomical descriptions will have a much wider application in the fields of comparative leaf anatomy and grass systematics in general.

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UITTREKSEL

Omskrywende sleutels, definisies en diagramme, vir die standaardisering, vereenvoudiging, en beskrywing van die epidermisstruktuur van grasblare, word aangegee. Ongeveer 340 *eienskappe is ingesluit met die moontlikheid vir uitbreiding tot* 999. *Aantekeninge van die variasie en die taksonomiese waarde van die eienskappe word ook verstrek.*

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