A Comparative Anatomical Study of the Grapevine Shoot: I Epidermis[1]

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Material gathered from three positions on the shoot and cane during véraison and two weeks after harvest were investigated for taxonomic features concerning the epidermis. Stomata and lenticels were present in all the cultivars studied, but trichomes were frequently present only on 99 Richter. Based on epidermal characteristics a dendogram giving the percentage similarity between cultivars, was constructed, and from this was concluded that concerning taxonomic features on *Vitis vinifera* L. cultivars tend to have a more than 90% similarity irrespective of the position on the shoot.

The identification of *Vitis* spp and cultivars based on leaf ampelography (Orffer, 1966; Galet, 1979), polen morphology (Ahmedulla, Hayrynen & Wolfe, 1980) and anatomy (Manzoni, 1952; Pongracz, 1969) is widely practised throughout the world. Comparative and descriptive anatomy of grapevine shoots and canes is a neglected field of study.

The cuticle of *Vitis* consists of layers of soft wax containing alcohols, aldehydes, fatty acids, esters and hydrocarbons (Chambers & Possingham, 1963; Possingham *et al.*, 1967; Gentlini, 1969; Radler, 1970). According to Radler (1970) the cuticle differs from that of other plant species in that it contains no oleïnolic acid. Studies by Bonnet (according to Viala & Péchoutré, 1910) and Beukman (1962) on cuticle thickness of grape epicarp (skin), as well as those by Hegedüs (1969a) and Racz (1973) on the cuticle thickness of *Vitis* leaves, indicate that this feature, which varies from 0,7 to 3,0 μm for these organs, is strongly dependent on the cultivar.

Similar results on cultivar dependence of stomatal density and type are found for *Vitis* leaves (Hegedüs, 1969b; 1974a; Sievers, 1971; Düring, 1980). According to Cutler (1978) stomata on the cane are of a type similar to those of the leaves, although present in smaller quantities. Stomatal density in the shoot of *Vitis vinifera* L. cv. Pinot noir varies from 5-10 cells. mm^{-2} whilst on the cane the variation is from 2 to 3 cells. mm^{-2} (Bessis, 1978). According to Bessis (1978) typical lenticels do not occur in the subgenus *Euvitis* although Esau (1965) reported the presence of lenticells.

Trichome density of canes is of taxonomic value and can be described as glabrous (*V. vinifera*), long hair present (growing tip of *V. champini* P. cv. Ramsey), trichomes on the nodes and/or internodes of 99R (*V. berlandieri* P. x *V. rupestris* S.) and trichomes exclusively on the nodes of 101-14 Mgt (*V. riparia* M. x *V rupestris*) (Orffer, 1966). Galet (1967) has constructed a key partly based on the presence of different trichome types on the shoot of 33 *Vitis* spp. Criteria used varied from the presence of multicellular thorns (*V. daviddi* F.) to a glabrous cane (*V. vinifera*).

Studies in which epidermal cell features are of taxonomic value in the plant kingdom are quoted by Linsbauer (1930) and Carlquist (1961). Guillon (1905) showed that anatomical differences between *Vitis* spp are clearly perceptible in the epidermal cells. A study was undertaken to evaluate a number of anatomical features of the grapevine shoot as an aid to the identification of species and cultivars (Swanepoel, 1983). According to Sokal & Sneath (1963) at least 40 and preferably 60 features should be incorporated in any numerical analysis. Classifying taxa using leaf morphology and structure, Hill (1980) found classifications based on 31 features and a subset of 17 similar. Watson, Williamson & Lance (1966) and Johnson (1982) indicate that the number of features necessary for a satisfactory classification could be much smaller than that suggested by Sokal & Sneath (1963). The aim of this paper is to describe and evaluate some features of the epidermis of the shoot and to discuss some of its taxonomic implications.

MATERIALS AND METHODS

Material: The cultivars used in this study are shown in Table 1.

TABLE 1

Genetic and geographical origin of experimental material

Species Combination	Cultivar	Geographical locality
Vitis champini Planch	Ramsey	Nietvoorbij, Stellenbosch
V. riparia Michx	Riparia Gloire de Montpellier	Welgevallen, Stellenbosch
V. rupestris Scheele	Rupestris du Lot	Welgevallen, Stellenbosch
V. vinifera L.	Cape Riesling	Nietvoorbij, Stellenbosch
V. vinifera	Chenin blanc	Nietvoorbij, Stellenbosch
V. vinifera	Cinsaut	Nietvoorbij, Stellenbosch
V. vinifera	Colombar	Nietvoorbij, Stellenbosch
V. vinifera	Pinotage	Nietvoorbij, Stellenbosch
V. vinifera	Pinot noir	Nietvoorbij, Stellenbosch
V. berlandieri P. x *V. rupestris*	99 Richter	Nietvoorbij, Stellenbosch
V. aestivalis Michx x *V. cinerea* Engelm. x *V. vinifera*	Jacquez	Nietvoorbij, Stellenbosch

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Six replications consisting of 20 three to five year old vines per replication grown under the same climatic conditions and on similar trellised systems for scion – (Slanting) and for the rootstocks (Greiner-Decker), were used.

METHODS

Preparation methods: Material was fixed in 6% gluteraldehyde in pH 7,2 sodium cacodylate buffer (0,05 M) and washed in the same buffer. For studies with scanning electron microscopy, the material was prepared according to a method described by De la Harpe & Archer (1982), after which it was studied with an ISI-100A. For light microscopy the material was dehydrated in a graded acetone series, embedded in Spurr's medium (Spurr, 1969) and 1 μm sections were cut with a Sorvall MT 5000 ultramicrotome using glass knives. The sections were stained with either toluidine blue (pH 9,6) or paragon (O'Brien, Feder & McCully, 1964) and studied with a Zeiss photomicroscope.

Characteristics: Seven quantitative and three qualitative characteristics were determined (Table 2).

TABLE 2

Epidermal characteristics of *Vitis* spp.

Number	Feature	Unit
1	Median of cuticle diameter	μm
*2	Presence of stomata : Absent = 0 Present = 1	
3	Stomatal frequency	(mm^{-2})
*4	Presence of lenticels : Absent = 0 Present = 1	
5	Lenticel frequency	(mm^{-2})
*6	Presence of trichomes : Absent = 0 Present = 1	
7	Median of anticlinal diameter of epidermis cells	μm
8	Median fo periclinal diameter of epidermis cells	μm
9	Median of cuticle diameter : Median of anticlinal diameter of epidermis cells	
10	Median of anticlinal diameter of epidermis cells : Median of periclinal diameter of epidermis cells	

*Qualitative characteristics

Characters 1, 7 and 8 were measured with an apparatus developed and described by Swart (1983) which consisted of a digitizer connected to a mini-computer (HP 1000). Standard statistical calculations e.g. mean, median and standard deviation (σ) were calculated immediately. After the first 15 measurements the number of observations needed to detect significant differences at a 95% confidence level was calculated. Depending on the variation in the data set, an additional number of measurements (if necessary) was made to satisfy this demand. Since the mean of these measurements are often affected by the occurrence of a few very low or high values the median was used in this study as it is regarded as being a more representative value (Sokal & Rohlf, 1969).

Cuticle thickness represents the distance between the epidermal cell wall and the outer layer of cuticle substrate, while anticlinal and periclinal diameters represent the maximum distance between the periclinal and anticlinal cell walls respectively. The other features were determined with the aid of scanning electron micrographs.

Numerical analysis: A cluster analysis was executed on the Univac 1100 computer of the University of Stellenbosch using a programme by Van Wyk (1978). The programme calculates the percentage similarity between individuals and for the purpose of this investigation, the equation of Canberra (cited by Snedecor & Cochran, 1974) was employed. The formulas used in these calculations for both quantitative and qualitative features are given by Du Plessis & Van Wyk (1982). The percentage similarity is used to cluster the individuals by means of centroid linkage and a table from which a dendogram can be constructed is given.

RESULTS AND DISCUSSION

Cuticle thickness: The thickness of the cuticle of the shoot varied from 3,1 μm in the apical zone of 99R to 5,8 μm in the basal zone of Jacquez (*V. aestivalis* M. x *V. cinerea* E. x *V. vinifera*) (Table 3). With the exceptions of *V. vinifera* cvs. Pinotage (σ = 1,4), Pinot noir (σ = 0,8) and Jacquez (σ = 1,1) this feature had little intracultivar variation over different positions of the shoot. The biggest intercultivar variation, however, occurred at the basal zone where the median varied from 3,3 μm (99R) to 5,8 μm (Jacquez).

The ratio cuticle thickness to anticlinal diameter (Table 3) was significantly (P = 0,05) higher in Riparia Gloire de Montpellier than in all the other cultivars studied which indicated that this cultivar has a well developed cuticle. The ratio anticlinal to periclinal diameter is indicative of the convexness of the cells since the higher the ratio, the more convex the cell. Due to the higher values found at the shoot apices, particularly with *V. vinifera*, it could be said that the degree of convexity was dependent on shoot age since in a basipetal direction (increasing age) the outside periclinal cell wall flattens.

Stomata and lenticels: Stomata were present on the shoot while lenticels occurred on the canes of all the cultivars investigated. The presence of stomata on the cane was not noted due to the indistinct and poor perceptibility of these structures, but lenticels were distinguished on parts of the shoots and canes of Ramsey, *V riparia* cv. Riparia Gloire de Montpellier, *V. vinifera* cvs. Cinsaut, Chenin blanc and Pinot noir as well as 99R and Jacquez. Although previous workers did not report typical lenticels on the cane, the observations through the scanning (Fig. 1) and light microscope (Fig. 2) indicated that lenticels were present on the canes studied.

Stomata density varied from 3 mm^{-2} (*V. rupestris* cv. du Lot; Riparia Gloire de Montpellier) to 12 mm^{-2} (*V. vinifera*) while intermediate quantities were found in Ramsey, 99R and Jacquez. In contrast to the stomatal frequency, where three distinct groups were obtained, the lenticel frequency appeared to be constant for *Vitis* and varied from 2 to 5 cells. mm^{-2} (Table 3).

On the apical zones of the shoots of Ramsey, Chenin blanc and Pinot noir the stomata were carried out on excrescences (Fig. 3) or short caulicules (Fig. 4a). On basal pieces of shoots the stomata were collapsed and (Fig. 4b, c) can be substituted by lenticels. This substitution of stomata into lenticels during the ontogenetic process was also described by Perold (1927).

TABLE 3

Values for epidermal features of the shoot and the cane of *Vitis* spp. used in this study.

Cultivar \ Characteristics		1**	2	3	4		5		6		7	8	9	10
		S***	S	S	S	C	S	C	S	C	S	S	S	S
Ramsey	*A	4.9	1	7	0	1	0	3	1	0	13.1	18.5	0.37	0.71
	M	4.4	1	7	0	1	0	3	1	0	13.5	26.6	0.33	0.51
	B	4.4	1	7	1	1	3	3	1	0	13.6	36.2	0.32	0.38
Riparia Gloire	A	4.1	1	3	0	1	0	3	0	0	8.6	22.1	0.48	0.39
de Montpellier	M	5.0	1	3	1	1	3	3	0	0	8.8	36.4	0.57	0.24
	B	5.0	1	3	1	1	3	3	0	0	9.9	32.1	0.51	0.31
Rupestris	A	4.0	1	3	0	1	0	3	0	0	15.1	31.3	0.26	0.48
du Lot	M	4.1	1	3	0	1	0	3	0	0	15.6	34.2	0.26	0.46
	B	4.2	1	3	0	1	0	3	0	0	16.6	40.5	0.25	0.41
Cape Riesling	A	4.4	1	12	0	1	0	3	0	0	13.5	17.7	0.33	0.76
	M	4.3	1	12	0	1	0	3	0	0	13.5	32.2	0.32	0.42
	B	4.8	1	12	0	1	0	3	0	0	15.4	27.6	0.31	0.56
Chenin blanc	A	4.2	1	12	0	1	0	3	0	0	10.1	13.8	0.42	0.73
	M	4.3	1	12	0	1	0	3	0	0	10.2	17.8	0.42	0.57
	B	4.5	1	12	1	1	3	3	0	0	11.3	21.8	0.40	0.52
Cinsaut	A	3.1	1	12	0	1	0	3	1	0	14.5	15.3	0.22	0.95
	M	3.8	1	12	1	1	2	3	1	0	14.1	31.9	0.27	0.44
	B	3.7	1	12	1	1	2	3	1	0	13.6	33.4	0.27	0.41
Colombar	A	4.4	1	12	0	1	0	3	0	0	15.8	16.8	0.28	0.94
	M	3.6	1	12	0	1	0	3	0	0	12.7	35.4	0.28	0.36
	B	4.0	1	12	0	1	0	3	0	0	12.2	31.1	0.33	0.39
Pinotage	A	3.2	1	12	0	1	0	3	0	0	10.9	15.2	0.29	0.72
	M	5.7	1	12	0	1	0	3	0	0	13.7	26.2	0.41	0.52
	B	5.7	1	12	0	1	0	3	0	0	14.1	27.9	0.40	0.51
Pinot noir	A	5.2	1	12	1	1	3	3	0	0	14.4	17.4	0.36	0.83
	M	4.3	1	12	1	1	3	3	0	0	12.7	17.0	0.34	0.75
	B	5.8	1	12	1	1	3	3	0	0	11.5	20.7	0.50	0.56
99R	A	3.1	1	8	0	1	0	3	1	1	11.9	22.2	0.26	0.54
	M	3.3	1	8	1	1	3	3	1	1	9.8	21.8	0.34	0.45
	B	3.3	1	8	1	1	3	3	1	1	11.0	36.2	0.30	0.30
Jacquez	A	3.7	1	8	0	1	0	3	0	0	12.7	19.9	0.29	0.64
	M	4.9	1	8	1	1	2	3	0	0	10.2	33.7	0.48	0.30
	B	5.8	1	8	1	1	2	3	0	0	11.9	37.3	0.49	0.32

* A : Apical; M : Middle; B : Basal
** See Table 2
*** S : Shoot
C : Cane

Trichomes: Short trichomes (bristles) occurred on the surface of 99R shoots (Fig. 5). If this was compared with the results of Galet (1967) this feature appeared to be typical of *V. berlandieri* (one of the species parents of 99R) since *V. rupestris* (the other parent) is glabrous. Long trichomes (hair) were observed on the apical parts of the shoots of Ramsey, Cinsaut and Jacquez (Fig. 6).

Epidermal cells: An uniseriate epidermis was present in all the cultivars studied. The anticlinal diameter varied from 8,6 μm (apical zones of Riparia Gloire de Montpellier) to 16,6 μm (basal zones of Rupestris du Lot) (Table 3). Considering the three positions on the shoot, Rupestris du Lot has a significantly higher and Riparia Gloire de Montpellier a significantly lower ($P = 0,05$) value in every position than all the other cultivars studied.

The periclinal diameter showed a bigger intercultivar variation than the anticlinal diameter with Rupestris du Lot having significantly higher and Chenin blanc and Pinot noir significantly lower ($P = 0,05$) values. Variance width and standard deviation were bigger than those of the anticlinal diameter (Fig. 7) with the biggest variance width and standard deviation occurring in Riparia Gloire de Montpellier, Rupestris du Lot, Cape Riesling, Cinsaut and Jacquez.

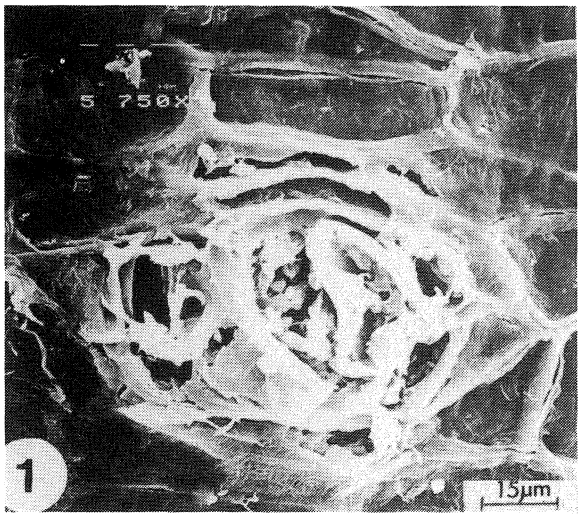


FIGURE 1
Scanning electron micrograph of a lenticel on the shoot of *Vitis vinifera* L. cv. Pinot noir.

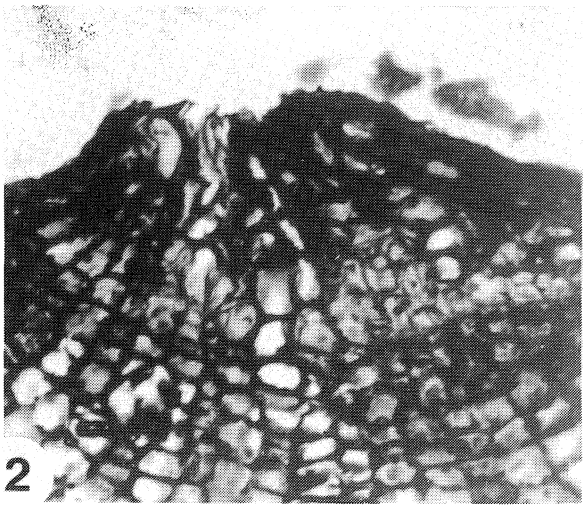


FIGURE 2
Light-micrograph of a lenticel on the shoot of *V. vinifera* cv. Pinot noir.

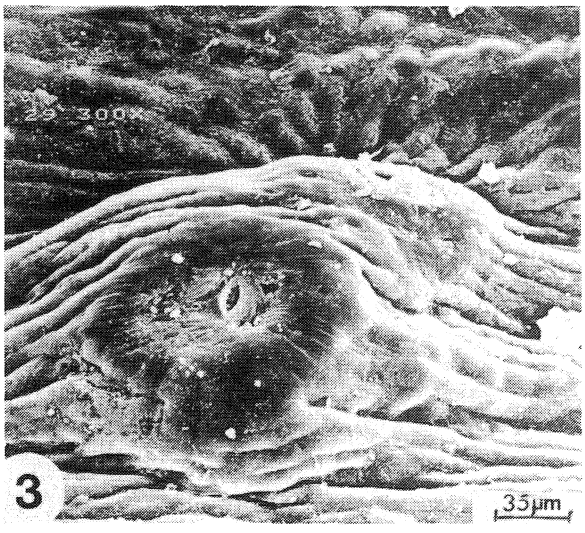
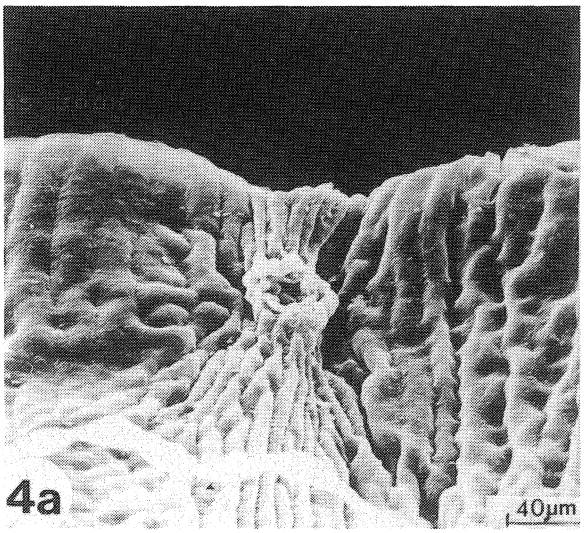
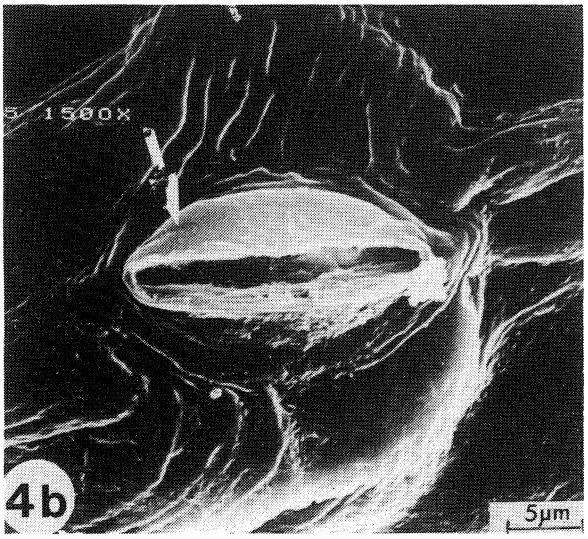


FIGURE 3
Stomata on excrescences on the apical zone of the shoot of *V. vinifera* cv. Chenin blanc.





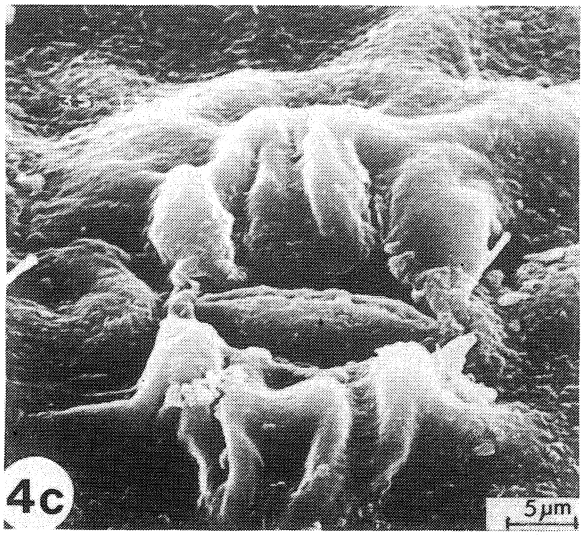


FIGURE 4
Scanning electron micrographs of stomata of *V. champini* Planch. cv. Ramsey to indicate different intermediate forms from raised (a) to sunken (c).

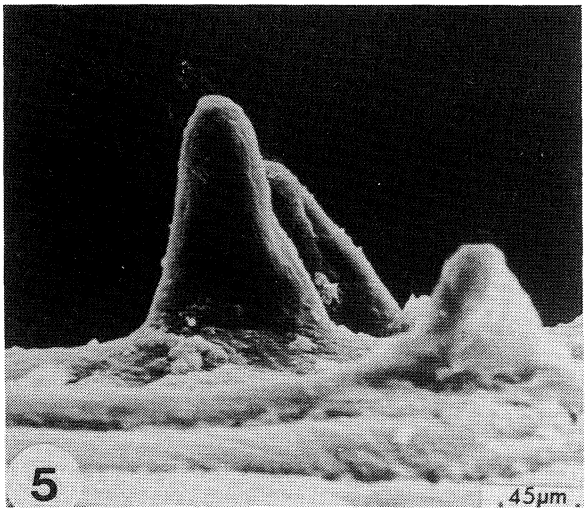


FIGURE 5
Trichomes on the shoot of 99 R (*V. berlandieri* Planch. x *V. rupestris* Scheele).

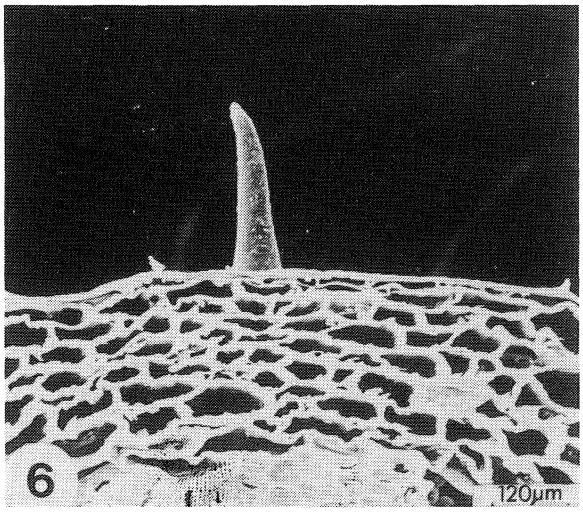


FIGURE 6
Short, isolated trichome on the apical zone of Jacquez (*V. aestivalis* Michx x *V. cinerea* Engelm. x *V. vinifera*).

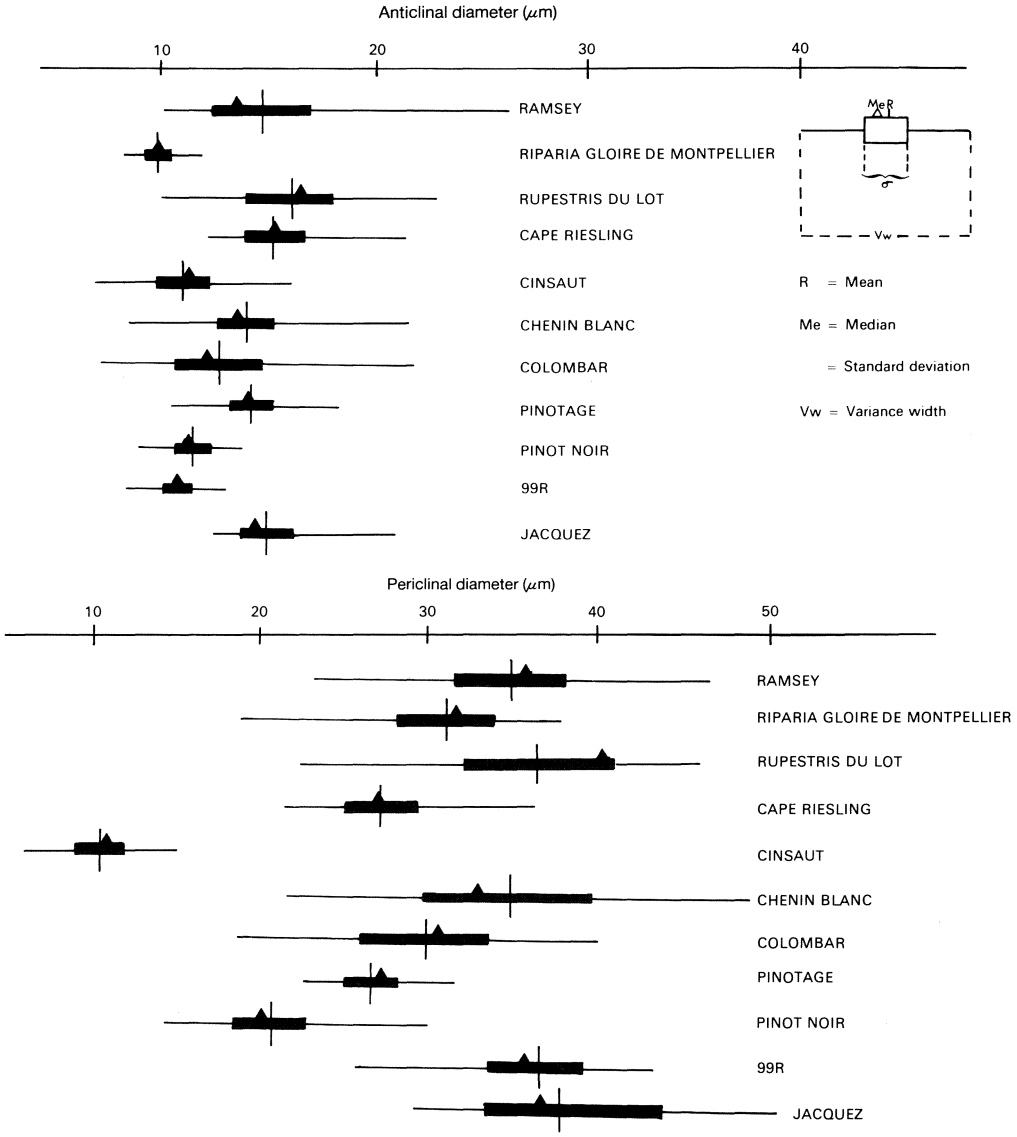


FIGURE 7
Dice-diagrams to illustrate variance width and standard deviation in (A) anticlinal and (B) periclinal diameter of epidermal cells of the basal zone of *Vitis* spp. used in this study.

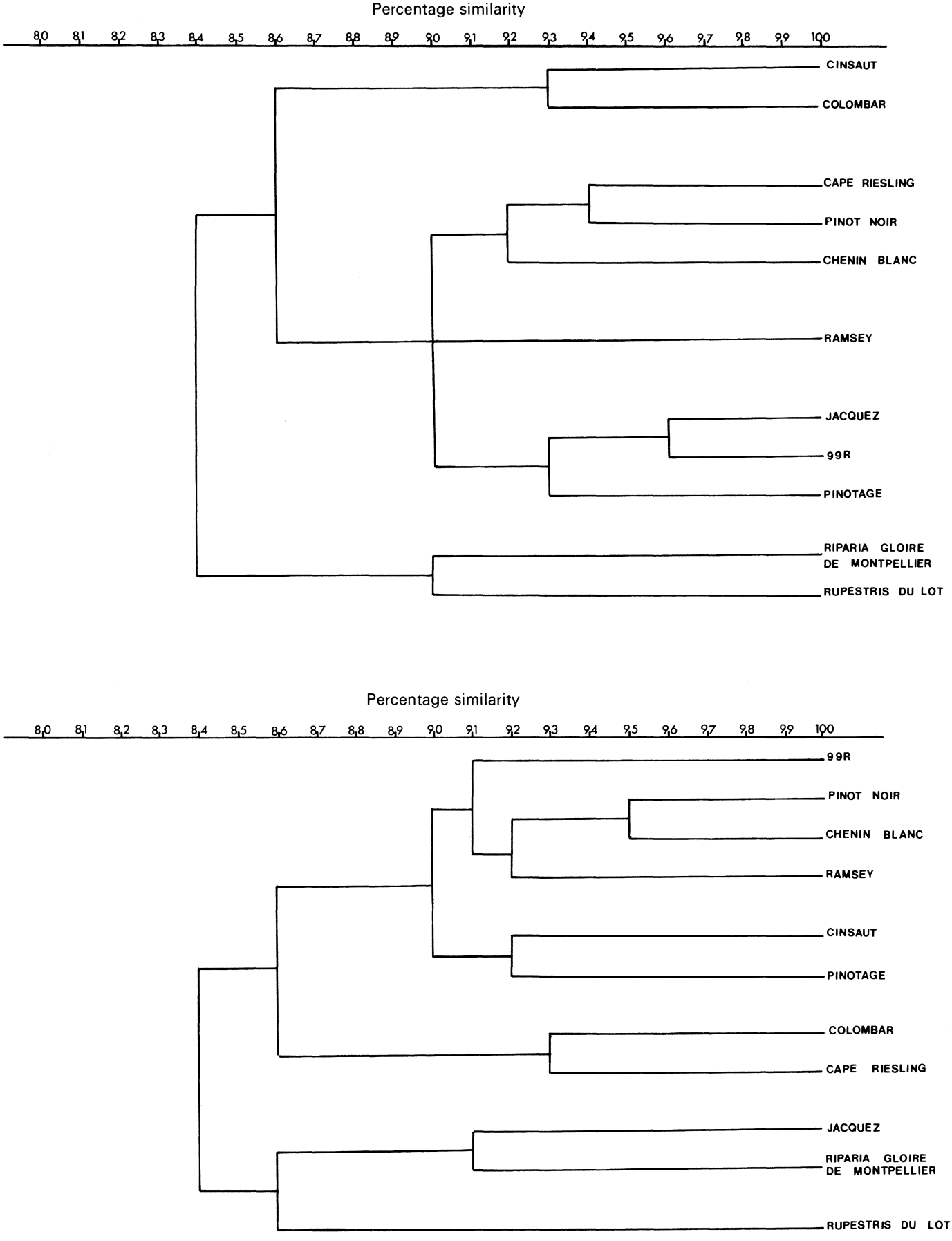


FIGURE 8
Taxonomic value of characteristics of epidermal cells of shoots of *Vitis* species and cultivars.

The walls of these cultivars were more convex than those of Riparia Gloire de Montpellier, in which case the values were significantly (P = 0,05) lower.

Numerical Analysis: Dendograms based on the epidermal features of the three positions on the shoot indicate that the *V. vinifera* – cultivars had a good resemblance (90%), while Riparia Gloire de Montpellier and Rupestris du Lot had a 90% resemblance at the apical zones (Fig. 8a) and Riparia Gloire de Montpellier, Rupestris du Lot and Jacquez a 86% resemblance at the middle zone (Fig. 8b). Similar trends were observed at the basal zones of the shoot. From Fig. 8a it was evident that the *V. vinifera* – cultivars from 2 distinct phenons with Pinotage the only cultivar to cluster with 99R and Jacquez. Although not exactly the same, the clustering of cultivars in the middle zone was quite similar to those in the apical zones concerning the percentage resemblance between cultivars.

CONCLUSIONS

Although the results are only applicable in the Stellenbosch area, certain epidermal features appear to be of taxonomic value in identifying shoots of the species studied. Although lenticel frequency is relatively constant within a specie, other morphological features such as the presence of stomata and lenticels, stomatal density and the presence of trichomes on the shoot do show intercultivar variation, although not of very large taxonomic value.

Epidermis cell features and cuticle diameter however, could be of taxonomic value on a cultivar level. A numerical analysis indicated that certain cultivars have a large resemblance with each other e.g. the *V. vinifera* – cultivars forming two distinct phenons. Results from the dendograms constructed showed results similar to those of the botanical classification of *Vitis*.

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