

EPIDERMAL LEAF CHARACTERS OF THE WINTERACEAE

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SUMMARY

Leaf epidermal features (mostly studied in cuticular macerations) of 146 specimens, belonging to c. 33 species of all the 6 genera of the *Winteraceae* are described in detail. Typical for most representatives is the occurrence of alveolar material of cutinaceous nature overlying the cuticle proper, and usually occluding the stomata. Special attention is paid to the appearance, distribution and significance of this alveolar material. The taxonomic value of the characters described is discussed.

All genera show an overlap with one or more genera in a varying number of leaf epidermal characters, so absolute diagnostic characters at the genus level are absent. It is also impossible to recognize distinct groups of genera. *Exospermum* and *Belliolum* are entirely within the leaf epidermal range of *Bubbia*. *Drimys* section *Tasmannia* and *Bubbia perrieri* take the most isolated positions within the family.

Drimys piperita shows an enormous range of variation, which is further analysed using 85 specimens belonging to 38 of the 39 entities recognized by Vink. Of 12 entities more than one specimen was studied, affording the conclusion that in most entities the cuticular features are fairly constant, though some entities are very variable and certain characters are almost always variable at the level of the entity. For *Drimys piperita* as a whole a number of characters (shape and relative size of the stomata, shape of epidermal cells over midrib, undulations of anticlinal flanges, subdivisions of subsidiary cells) are mutually correlated and show, moreover, positive trends of correlation with the usual habitat of the entities. The glandular structures, typical for *D. piperita*, are described for the first time.

INTRODUCTION

The cuticles of some representatives of the *Winteraceae* have received the attention of several authors in the past. The most striking feature usually reported for the family is the presence of plugs occluding the stomatal apertures (Wulff, 1898; Ziegenspeck, 1941; Bailey & Nast, 1944b, Bondeson; 1952; Vink, 1970). Occhioni & Occhioni (1947) and Rao (1939) apparently overlooked these structures in their studies of *Drimys brasiliensis* and *Drimys winteri* respectively. Wulff and Ziegenspeck considered the plugs to be of a waxy composition. Bailey & Nast more elaborately discussed the nature of these plugs, and suggested a cutinaceous composition, though admitting to present no full-proof evidence. Vink clearly distinguished between waxy and cutinaceous alveolar occlusions, both present in *Winteraceae*.

The family of the *Winteraceae*, usually considered to be primitive amongst the Dicotyledons, comprises 6 genera. The revisions of Smith (1943 a+b) and Vink (1970) have been used as the basis for this anatomical study. The genus *Drimys* accordingly comprises 2 sections: *Drimys* with 4 species in America, ranging from Cape Horn to South Mexico (Smith, 1943a) and section *Tasmannia* with 5 species (according to Vink's recent revision, in which he subdivided *D. piperita* in 37 'entities'; Smith recognized 36 species), ranging from Malasia to Australia. *Pseudowintera* occurs with 3 species in New Zealand (Vink). The genus *Exospermum* from New Caledonia comprises two species according to Smith (1943b). Vink considers these to be one species (unpublished private communication). *Bubbia* is composed of 30 species in Smith's treatment (1943b), occurring in New Guinea, New Caledonia, Australia, and Lord Howe I. More recently Capuron (1963) described one more species: *Bubbia perrieri* from Madagascar. *Belliolum* has 4 species in New Caledonia and 4 in the Solomon Is. (Smith, 1943b). *Zygogynum* is on record with 6 species, all confined to New Caledonia (Smith, 1943b).

This study was carried out in the first place to elucidate the peculiar structures reported on by a number of authors, and in the second place to make a more or less comprehensive survey of the range of variation of the epidermal characters in the different taxa of the *Winteraceae* in general, and in *Drimys piperita* in particular. Moreover, it was hoped that such a study would be of some use for the discussion of affinities within the family. Besides it was thought to be of some help for paleobotanists in the identification of fossil plant remains (cf. Jähnichen, 1959).

MATERIALS AND METHODS

One mature leaf was selected from each of the 146 herbarium specimens used for this study. All material is from the Rijksherbarium at Leiden, except for the type specimens of *Zygogynum baillonii* (Pancher s.n.) and *Bubbia perrieri* (Perrier de la Bathie 10150), which were obtained from the Paris Herbarium. Of *Drimys winteri* fresh leaves were pickled from a specimen cultivated at Royal Botanic Gardens at Kew.

All material used for cuticular macerations was boiled in water. Parts from the middle of the lamina, including midrib and leaf margin, were macerated overnight in a mixture of equal volumes of 20% hydrogen peroxide and glacial acetic acid at 60°C; the cuticles obtained were stained in a solution of Sudan IV in alcohol 70%, and finally mounted in glycerin-jelly.

From 17 leaves also transverse sections were made through the middle of the lamina and the distal part of the petiole, with a Reichert sliding microtome. Part of the sections was stained with a mixture of safranin and haematoxylin for permanent euparal mounts, the remainder was stained with Sudan IV and mounted in glycerin-jelly.

For Scanning Electron Microscope studies fragments of 62 leaves were extracted with ether for one hour at room temperature and subsequently rinsed in fresh ether in order to remove any wax. The leaf fragments were coated with carbon and gold.

The distribution of the specimens over the different genera is as follows. The number of species studied is indicated between brackets behind the generic name.

	Macerations	S.E.M.	Transverse sections
1. <i>Drimys</i>			
sect. <i>Tasmannia</i> (5)	89	33	8
(<i>D. piperita</i>)	(85)	(29)	(8)
sect. <i>Drimys</i> (4)	8	10	1
2. <i>Pseudowintera</i> (3)	4	4	1
3. <i>Exospermum</i> (1)	1	1	1
4. <i>Belliolum</i> (2)	2	2	1
5. <i>Bubbia</i> (18)	36	10	4
6. <i>Zygogynum</i> (6)	6	3	1

Collection numbers of the herbarium specimens studied are listed at the end of the generic descriptions, and in table I for *Drimys piperita*.

Stomatal sizes were measured at 1000 × magnification, using an eye-piece micrometer; 25 measurements were made per leaf.

A SURVEY OF THE CUTICULAR CHARACTERS IN WINTERACEAE

Introduction

Most of the terms used in this descriptive part are taken from Stace (1965), who also gave more general information about cuticles. Usually the leaf cuticle is two-layered. The inner layer: the *cuticular layer*, consists of a cellulose framework, incrustated with cutin; the outer layer: the *cuticle proper*, is mainly composed of cutin. The cuticular layer may appear granular in the light microscope or smooth. Bailey and Nast (1944b) reported that in *Winteraceae* a third, *alveolar layer* may be present overlying the cuticle proper. The alveolar layer is not homogeneous and usually has a white colour as a result of the presence of air in the interstices. This layer is insoluble in boiling water or ether and stains positively with Sudan IV. Therefore, the composition is apparently cutinaceous. The birefringence reported by Bailey & Nast is, however, no decisive proof for the cutinaceous nature (see Martin and Juniper, 1970).

In cuticular preparations the features of the underlying cuticle proper and the cuticular layer are often obscured by this alveolar material.

Wax may also be present as the outermost layer, either on top of the cuticle proper, or overlying the alveolar layer if the latter is present. Because of the ephemeral nature of wax on herbarium specimens (depending on the drying procedures etc.) wax deposits have not been considered in this study, except for *Drimys* section *Tasmannia* (phot. 27 & 28).

Thickness of the cuticle

Although macerated cuticular preparations yield no detailed information about the thickness of the cuticle, one gains an impression of its relative thickness during the micro-technical procedures. Some cuticles are rather stiff and stain deeply with Sudan IV, others are very delicate and hardly take up any stain. Between these extremes of very thick and very thin cuticles all intermediates are encountered. Transverse sections were made of 17 specimens representing all the six genera, so that some absolute figures on thickness are available. The range from 2 to 25 μm for the abaxial side has been subdivided

as follows: (very) thin, 2—5 μm ; medium thickness, 6—10 μm ; thick, 11—20 μm ; very thick, over 20 μm . These terms are used in the descriptions. The cuticle on the adaxial side is always somewhat thicker and ranges from 3 to 30 μm .

Alveolar material (phot. 25, 26, 29—42)

Alveolar material occurs in some or all species of the six genera of the *Winteraceae*. In some species of *Drimys* and in *Bubbia perrieri* it is absent. The alveolar material may be present in different forms. In the light microscope it may be very finely to coarsely granular. On S.E.M. photographs this material turns out to be a dense three-dimensional reticulum. In some *Winteraceae* the alveolar material may be restricted to the rims of the stomata or to the whole front cavity of the stomata (alveolar stomatal plugs), in others it extends from the front cavity to over the subsidiary cells and the neighbouring cells, or the whole epidermis may be covered. In some cases solid pieces of cutin of irregular form and size stand out in the alveolar layer giving it a heterogeneous and warty appearance. In others a solid layer of cutin may form a tectum-like structure locally over the more finely reticulate alveolar material.

The distribution and qualitative features of the alveolar material in *Winteraceae* can thus be classified as given below. This classification is used in the descriptions of the genera.

A. Distribution:

1. Alveolar material absent (phot. 1—3, 6—8).
2. Alveolar material on rims of stomata (phot. 25).
3. Stomatal plugs present (phot. 26).
4. Alveolar material also extending over neighbouring cells (phot. 29, 31).
5. Alveolar material covering the whole epidermis (phot. 32—39).

B. Qualitative features:

1. Alveolar material without protruding solid pieces of cutin; indicated as 'homogeneous' (phot. 31, 32, 42).
2. Alveolar material with protruding solid pieces of cutin; indicated as 'heterogeneous' (phot. 33—37, 39).
3. Alveolar material with tectum-like structures (phot. 41).

In cuticular macerations it is usually impossible to distinguish whether a cuticle is granular due to alveolar material or due to internal granular structure of the cuticular layer. Therefore alveolar material is only recorded if the presence of this material has been established otherwise (e.g. transverse sections, S. E. Micrographs). This means that a cuticle indicated as granular may be alveolar, unless the absence of alveolar material is stated.

Unspecialized cells

A. Outline (fig. 1; phot. 9, 10, 18—21).

The unspecialized cells are usually isodiametric (hexagonal) to elongated. The latter are randomly orientated and more frequent in the lower than in the upper epidermis.

Where the epidermis overlies the subepidermal oil cells, the arrangement of the cells may be modified to a various extent. Often a radiate arrangement of cells, not unlike a hairbase in some other Dicotyledonous families, is present here. The cuticle on these

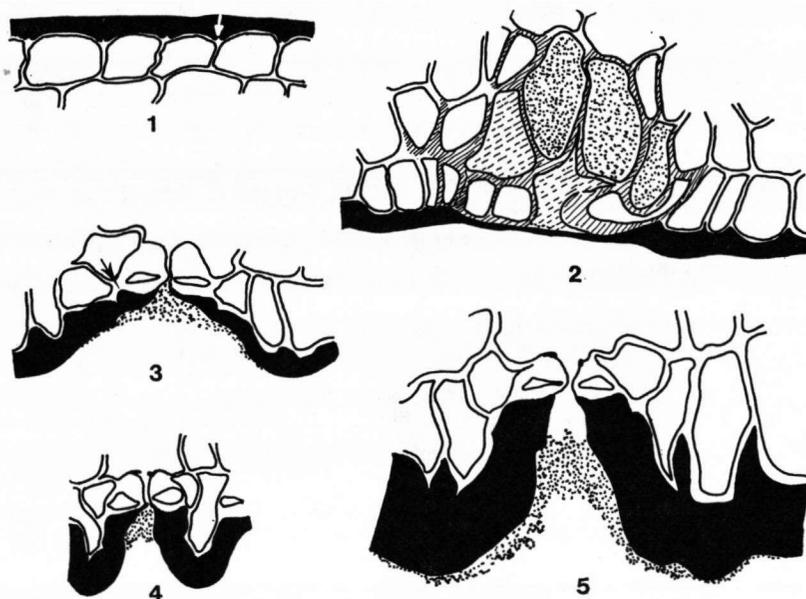


Fig. 1—5. Camera lucida drawings of transverse sections, all $\times 700$. — 1. *Pseudowintera axillaris* (Travers s.n.), adaxial epidermis with grooved anticlinal flanges (arrow). — 2. *Drimys piperita* 'montis-wilhelmi' (Vink 17392), 'gland'. — 3. *Bubbia howeana* (Van Balgooy 1111), stoma with locally thick cuticle over outer wall of guard cells (arrow). — 4. *Bubbia pachyantha* (Brass 4371), guard cells and subsidiary cells sunken. — 5. *Bubbia vieillardii* (Viellard 16), guard cells and subsidiary cells sunken. black: cuticle. — lines: suberized cell wall material (broken lines: ibid. in surface view). — dots: granular 'secretory' material in fig. 2; alveolar material in fig. 3—5.

places may either be thicker or thinner than over the remainder of the unspecialized cells, and the anticlinal flanges may be less or much more strongly developed (phot. 10).

The anticlinal flanges may be straight (phot. 20), curved (phot. 18, 19) or undulated (sinuous) (phot. 21). Undulations of the anticlinal flanges may be restricted to the peripheral parts of the cuticular flanges, the inner part being straight. Thin areas of the cuticle may be present in the loops of the undulations, but if present they are rather inconspicuous. The anticlinal flanges may be grooved along their edge (fig. 1). This results in a double appearance as seen in surface view (see phot. 9).

B. Pitting (phot. 14—19).

In about 50% of the specimens of *Drimys piperita* studied and in the majority of the other specimens the cuticular flanges are variously pitted.

In surface view the pitting may give a beaded appearance to the anticlinal flanges, or pits may be present as fine lines perpendicular to the cell wall. Sometimes the cuticular flanges are perforated by such large pits that a broken line results. Because of the presence of intermediate structures and of the fact that the form of the pitting may vary even in the same leaf, the form of pitting is not recorded in the descriptions.

The presence or absence of pits may also be variable, even within an entity, but this character has been listed because the distinction between the two conditions is more easy,

and the demonstration of the variability within genera, species, and entities was regarded of sufficient relevance.

Pitting is not mentioned in the paper by Stace, but this character is elaborated by Wilkinson in her extensive thesis on the leaf anatomy of *Anacardiaceae* (London 1971, unpublished). Van Staveren & Baas (1973) used this character as an additional means for the separation of the Icacinaceous genera on leaf cuticles.

The term pitting is used because of the similarity in appearance of ordinary cell wall pits and the interruptions in the anticlinal cuticular flanges as seen in surface view. Whether cuticular pitting is continuous with pits in the cellulose walls or functionally comparable to ordinary pits, I do not know.

C. Sculpturing of the cuticle (phot. 2—5).

1. Striations.

In a small number of species the adaxial cuticle may show conspicuous cuticular striations. This feature was occasionally found in *Drimys* section *Tasmannia* and in *Pseudowintera*. In *Bubbia*, 8 out of the 36 specimens studied possessed striations (phot. 5).

2. Irregular sculpturing.

In three entities of *Drimys piperita* the abaxial cuticles are irregularly sculptured; viz. 5 'pittosporoides', 8 'crassipes' (phot. 2), and 32 'cordata' (phot. 3).

3. Ridges.

In *Drimys* sometimes ridges are found on the outer side of the cuticle, corresponding with the anticlinal flanges (abaxial side in *Drimys purpurascens* phot. 4) or more or less corresponding with a group of epidermal cells (adaxial side of some specimens in section *Drimys*).

D. Size

Epidermal cell size is very variable and ranges between about 250 and 1000 square μm for e.g. *Drimys piperita* (*sensu* Vink) in the abaxial epidermis. Even in the same leaf a wide range may be encountered (e.g. 400—1000 square μm in the only specimen studied of *Drimys lanceolata*).

E. Papillae (phot. 6, 7, 37).

Papillae are of rare occurrence within the *Winteraceae*. Blunt papillae, one on each unspecialized cell of the abaxial epidermis, are a constant feature of the entities 'papillata' and 'apetala' of *Drimys piperita*. Very low papillae are found in one of the specimens studied in entity 'xerophila' of *Drimys piperita*. Bailey & Nast (1944b) also reported papillae as a variable feature in some varieties of *Drimys brasiliensis*. In the two specimens studied intensively for this paper, papillae were absent, but a quick survey of the 19 herbarium specimens available revealed 5 collections to have distinct warty papillae (phot. 37). The inconstancy of this feature is not uncommon (cf. Baas, 1970; Jansen & Baas, 1973).

Venation as apparent in cuticular preparations

In this paper prominence of veins means the modification of the epidermal pattern over the veins as compared with the epidermal pattern over the rest of the lamina.

In the abaxial epidermis the venation pattern usually does not leave any mark on the cell arrangement. Only the midrib usually stands out by the arrangement of cells in rows. Sometimes the midrib is also hardly traceable in cuticular preparations.

In the abaxial epidermis the midrib always shows up because of the modifications in arrangement and shape of the epidermal cells. If strongly modified (which is the rule), the cells are rectangular and arranged in rows parallel to the midrib. Usually cell families can be recognized, evidencing that in the ontogeny cells became subdivided perpendicular to the midrib. The cells over the midrib may be longer than wide, squarish, or wider than long, depending on the degree of subdivision (phot. 22—24).

If the midrib does not influence the epidermal pattern to a great extent, the cells are less modified as compared with the unspecialized cells over the remainder of the lamina, and are square to elongated, sometimes even with curved to undulated anticlinal flanges if this condition prevails in the unspecialized cells.

Primary, secondary, and minor veins are often prominent. In that case, the higher the order of the veins the less prominent they are.

Stomatal complex

Stomata are confined to the abaxial epidermis and are usually randomly distributed and orientated; rarely they are arranged in irregular arches or clusters. Stomata are generally absent from the midrib, and in the rare instances that they do occur on the midrib, the stomatal complex always shows abnormalities.

The distribution and frequency of the stomata is very variable between and within the different species and entities. The stomatal index is also not constant. This will be further elaborated on p. 395 for *Drimys piperita*.

The stomatal type is paracytic, except in *Bubbia perrieri* where only few paracytic stomata occur and the majority of the stomata is of the anomocytic type.

The guard cell pairs may be almost circular, oval, or slender and elongated, the whole range sometimes being present in the same leaf. The dimensions of the guard cells show an enormous range. The extreme average values of the dimensions of the guard cell pairs are $28 \times 17 \mu\text{m}$ in entity '*oligandra*' of *Drimys piperita* and $56 \times 41 \mu\text{m}$ in *Zygogynum vieillardii*. However, differences in size between the guard cell pairs in a single leaf may amount to $8 \mu\text{m}$ for the length and $6 \mu\text{m}$ or more for the width. These measurements do not include the so-called giant or water stomata, which are of infrequent occurrence throughout *Winteraceae*, except for *Drimys* section *Drimys*, where they are more frequent.

Outer stomatal ledges are usually not well developed, as seen in cuticular macerations, except in a few entities of *Drimys piperita* (phot. 1) and in *Bubbia perrieri* (phot. 8). A peristomal rim is present in some representatives of *Drimys* section *Tasmannia* (phot. 13). Often the guard cells and sometimes the subsidiary cells are slightly (rarely deeply and abruptly) sunken below the level of the remainder of the epidermal cells.

In *Drimys* the subsidiary cells may be variously subdivided. Frequently extra division walls are present parallel or perpendicular to the pore. Sometimes only the subsidiary cells show cuticular striations (in *Drimys*). The cuticle is sometimes thicker or thinner over the guard cells and/or subsidiary cells than over the unspecialized cells.

Cork warts and 'glands'

Cork warts are very rare in the leaves of *Winteraceae* and probably always of traumatic origin. In *Drimys piperita* structures occur not unlike cork warts as seen in surface view (phot. 11). They consist of a variable number of large subepidermal cells with suberized walls and granular contents, surrounded and covered by radiately arranged more heavily suberized epidermal and subepidermal cells (fig. 2). Presumably these structures are glandu-

lar and will therefore be referred to as 'glands' in the descriptions. In surface view they can sometimes not be distinguished from cork warts. In median transverse section they are quite different, because of the presence of large secretory cells. In some other species of the family more or less similar structures have been rarely observed, but in the absence of transverse sections it could not be established whether these should be interpreted as cork warts or as 'glands'.

ANATOMICAL DESCRIPTIONS

1. *BELLIOLUM* VAN TIEGHEM

The two species of *Belliolum* studied differ very much in cuticular characters, so that it is justified to give a separate description of each of them.

Belliolum crassifolium (Baill.) v. Tiegh. (phot. 42)

Cuticle thick to very thick; anticlinal flanges well developed.

A b a x i a l s u r f a c e. Stomata randomly distributed, outlines not distinct, almost circular to broadly oval, with alveolar plugs. Stomata and subsidiary cells deeply sunken below the level of the unspecialized cells. Subsidiary cells not subdivided. *Unspecialized cells* usually with finely homogeneous alveolar material (phot. 42); cells somewhat bigger than guard cell pairs. Anticlinal flanges curved and pitted. Cells over the *midrib* squarish to longer than wide; other veins not prominent.

A d a x i a l s u r f a c e. Cuticle granular; anticlinal flanges straight, obscured by very thick cuticle which shows grooves corresponding with the anticlinal flanges partly surrounding groups of cells. Cells over the *midrib* hardly modified; other veins not prominent.

Material studied. New Caledonia: *Balansa 582*.

Belliolum haplopus (Burt) A. C. Smith

Cuticle thin; anticlinal flanges poorly developed.

A b a x i a l s u r f a c e. Stomata randomly distributed, outlines marked by broad granular bands as in *Bubbia*, almost circular to oval, with alveolar plugs and therefore more deeply staining than the remainder of the cuticle, very slightly sunken. Subsidiary cells not subdivided. *Unspecialized cells*: cells surrounding stomatal complex covered with homogeneous alveolar material; remainder of cuticle smooth; anticlinal flanges curved and irregularly coarsely granular. Cells of about the same size as guard cell pairs. Cells over the *midrib* longer than wide, other veins not prominent.

A d a x i a l s u r f a c e. Cuticle finely granular, anticlinal flanges straight to curved, only indicated by more densely and coarsely granular appearance of the cuticle. Cells over the *midrib* hardly modified; other veins not prominent.

Material studied. Solomon Is.: *Foreman NGF 45689*.

2. *BUBBIA* VAN TIEGHEM

(fig. 3—5, phot. 5, 8, 10, 16—18, 39 & 40)

Generic description based on 33 specimens (15 recognized species and 18 unrevised and unnamed specimens), excluding *B. perrieri*, *B. pachyantha*, and *B. vieillardii*.

N o t e. In the absence of a recent satisfactory taxonomic revision much of the material was incompletely or unreliably named. Therefore I refrained from specifying the distri-

bution of the epidermal features over the different species. This will be done as an addition to Vink's forthcoming revision of the genus.

Cuticle very thin to very thick, sometimes striated; anticlinal flanges faint to well developed, sometimes obscured by alveolar material on the abaxial surface.

A b a x i a l s u r f a c e. Stomata usually randomly distributed, rarely clustered, with alveolar plugs, not or slightly sunken. Outlines of guard cell pairs rarely distinct, but usually indicated by broad granular bands of locally thick cuticle, which are whether or not fused at the polar ends of the guard cells, resulting in variable and irregular outlines, even within a single leaf (phot. 10, fig. 3). Remainder of cuticle overlying the guard cells thinner or thicker than over unspecialized cells, due to a greater or smaller amount of alveolar material. Subsidiary cells rarely subdivided. *Unspecialized cells* with a granular to almost smooth cuticle (whether granular nature is due to alveolar material or to a granular cuticular layer cannot always be established in cuticular macerations); anticlinal flanges usually straight to curved, rarely slightly sinuous, thin to very thick, usually heavily pitted, occasionally appearing as double bands due to grooved anticlinal flanges, rarely with irregular thickenings, sometimes appearing entirely granular. Alveolar material heterogeneous and continuous over the whole surface in 10 specimens, homogeneous and continuous or only present around the stomata in the remainder. Size of unspecialized cells about $\frac{1}{2}$ —2 \times that of the guard cell pairs, fairly constant within a specimen. Cells over the *midrib* squarish to longer than wide, wider than long in 4 specimens. Other veins usually not prominent, first and second order veins fairly prominent in 3 specimens, a complete network fairly prominent in epidermis of 5 specimens.

A d a x i a l s u r f a c e. Cuticle smooth, granular or with broad striae; anticlinal flanges straight to curved, sometimes sinuous, whether or not pitted. *Midrib* usually prominent, other veins usually not.

Material studied. New Guinea: *B. argentea* A.C.Sm.: Brass 4740. — *B. archboldiana* A.C.Sm.: Brass 12712. — *B. glauca* A.C.Sm.: Brass 7191. — *B. idenburgensis* A.C.Sm.: Brass 13028. — *B. megacarpa* A.C.Sm.: Brass 10249. — *B. spec.*: v. Balgooy 697, 708 & 968; Vink 17239 & 17544; Kalkman 5163; Brass 29487; Sayers NGF 21535; Schodde & Craven 5082 & 4750; Versteegh BW 12618; Sleumer & Vink BW 14293; Westerhuis BW 5429; v. Royen NGF 20218; Hoogland & Craven 10535.

New Caledonia: *B. amplexicaulis* Parm.: Forster 167; Bernier 1167. — *B. balansae* (Baill.) v. Tiegh.: Balansa 1844. — *B. heteroneura* v. Tiegh.: Deplanche 293. — *B. isoneura* v. Tiegh.: Vieillard 17; Mackee 18699. — *B. pancheri* Burtt: Aubréville-Heine 282. — *B. pauciflora* Dandy: Thorne 28302. — *B. rivularis* Burtt: Mackee 13750. — *B. schlechteri* Guill.: Hürlimann 984.

Australia: *B. semecarpoides* (F. v. M.) Burtt: W. T. Jones 1486. — *B. whiteana* A. C. Sm.: Kajewski 1495. Lord Howe Island: *B. howeana* (F. v. M.) v. Tiegh.: v. Balgooy 1111.

Aberrant species of *Bubbia*:

***Bubbia pachyantha* A. C. Smith**

Cuticle thick; anticlinal flanges well developed.

A b a x i a l s u r f a c e. Stomata arranged in irregular arches or circles, with alveolar plugs, outline not distinct, seemingly not paracytic but almost cyclocytic, due to the fact that the guard cells are deeply sunken and the larger part of the subsidiary cells is overlain by the surrounding unspecialized cells, which take the appearance of a circle of subsidiary cells. The stomatal pore is accordingly situated at the bottom of a funnel-shaped crypt lined with alveolar material (phot. 40). Subsidiary cells rarely subdivided. *Unspecialized cells* with a granular cuticle, without alveolar material, much smaller than guard cell pairs. Anticlinal flanges straight, pitted, very narrow except for the cell corners where conspicuous tapering pegs are present. Cells over the *midrib* longer than wide, other veins not prominent.

Adaxial surface. Cuticle smooth; anticlinal flanges straight, not pitted. Midrib and veins not prominent.

Material studied. New Guinea: *Brass 4371* (type).

***Bubbia vieillardii* Guillaum.**

This species resembles *B. pachyantha* very closely. It differs in the random distribution of the stomata, the even more strongly sunken guard cells and subsidiary cells, the thicker anticlinal flanges of the abaxial unspecialized cells with blunter pegs at the cell corners, and the occurrence of some pits in the anticlinal flanges of the adaxial epidermis. Moreover the outer surface of the abaxial epidermis shows grooves corresponding with the anticlinal cell walls. These grooves are absent in *B. pachyantha*, but also present in *Bellium crassifolium*, as seen with S.E.M. Midrib not seen.

Material studied. New Caledonia: *Vieillard 16*.

Note. Features as reported for *B. pachyantha* and *B. vieillardii* are usually considered as xeromorphic. Data on the ecology of these species were unfortunately not available.

***Bubbia perrieri* Capuron**

Cuticle very thin, anticlinal flanges poorly developed.

Abaxial surface. Stomata randomly distributed, outlines distinct, usually not paracytic but anomocytic, guard cells slightly raised above the level of the epidermis, without alveolar plugs, with distinct outer cuticular ledges. *Unspecialized cells* finely granular, not alveolar; anticlinal flanges straight to curved, pitted. Cells bigger than the guard cell pairs. *Midrib* extremely wide with epidermal cells that are longer than wide, other veins not prominent.

Adaxial surface. Cuticle finely granular, anticlinal flanges straight and pitted. Cells over the midrib longer than wide, other veins not prominent.

Material studied. Madagascar: *Perrier de la Bathie 10150* (type).

3. DRIMYS J. R. & G. FORSTER

Within the genus *Drimys* the sections *Tasmannia* and *Drimys* are quite distinct from each other in cuticular characters. Therefore a separate description is given for each section.

Section *Tasmannia* (R. Br.) F.v.M.

(fig. 2, 6 & 7, phot. 1—4, 6, 7, 11—14, 20—28, table I)

Cuticle very thin to fairly thick, rarely with irregular sculpturing or ridges (phot. 2—4); anticlinal flanges faint to well developed.

Abaxial surface. Stomata randomly distributed, rarely clustered, outlines distinct, almost circular (length to width ratio *c.* 1.1) to slender and elongated (length to width ratio up to *c.* 1.9), size range 28—44 × 17—32 μm, usually with wax plugs, rarely with rather small alveolar plugs (*D. piperita*, entities 'chartacea', 'montis-wilhelmi', and 'robusta' (phot. 25 & 26), and *D. stipitata*), occasionally not plugged at all. Stomata in the same level as unspecialized cells to slightly sunken in most species and entities, conspicuously sunken in *D. piperita*, entities 'pittosporoides', 'papillata' (phot. 6), 'crassipes' (phot. 2), 'myrtoides' (phot. 13), 'robusta' (phot. 26), 'densifolia', 'cordata', 'apetala' (phot. 7), and

'*xerophila*' (phot. 27 & 28). Peristomal rim distinct in macerations of most entities with conspicuously sunken stomata (phot. 13) and in some species and entities with slightly sunken stomata. Cuticle over guard cells and subsidiary cells of same thickness or thinner than cuticle over unspecialized cells. Cuticle over subsidiary cells sometimes striated. Subsidiary cells not subdivided, except for many entities of *D. piperita*. *Unspecialized cells* never with alveolar material, usually granular; anticlinal flanges straight to undulated, with or without pits. Cells much smaller to much larger than the guard cell pairs. Cells over the *midrib* wider than long, squarish, or longer than wide; prominence of veins variable. 'Glands' usually present (fig. 2, phot. 1).

A d a x i a l s u r f a c e. Cuticle usually granular; anticlinal flanges straight to undulated, with or without pits. Cells over the *midrib* wider than long, squarish or longer than wide, sometimes not modified; prominence of other veins variable.

Material studied. *D. insipida* (R. Br. ex DC.) Druce: *NSW 57944*. — *D. lanceolata* (Poirot) Baill.: *NSW 120577*. — *D. piperita* Hook. f. see table I. — *D. purpurascens* Vickery: *Schodde 3212*. — *D. stipitata* Vickery: *NSW 68493*. (All from Australia except for the entities 1—36 of *D. piperita*, which are from New Guinea).

Section *Drimys* (phot. 33—38)

Cuticle thin to fairly thick, rarely striated (*D. winteri* var. *winteri*); anticlinal flanges well developed (sometimes obscured by overlying alveolar material).

A b a x i a l s u r f a c e. Stomata randomly distributed, outlines distinct, almost circular to broadly oval, with alveolar plugs (except for *D. winteri*, *Thorne s.n.*, phot. 38), not or very slightly sunken. Subsidiary cells usually subdivided parallel to the pore. *Unspecialized cells* mostly covered with alveolar material; alveolar material restricted to the cells surrounding the stomatal complex in *D. granadensis* var. *granadensis*, homogeneous (*D. granadensis* var. *granadensis*, *D. winteri* var. *chilensis*), heterogeneous (*D. brasiliensis*, *D. granadensis* var. *mexicana* and *D. winteri* var. *winteri*), or with tectum-like structures (*D. confertifolia* and to a lesser extent *D. winteri* var. *winteri*). Anticlinal flanges straight with infrequent pits. Cell size $\frac{1}{2}$ — $3 \times$ that of guard cell pairs. Cells over *midrib* wider than long to squarish; other veins not prominent.

A d a x i a l s u r f a c e. Cuticle smooth or finely granular; anticlinal flanges straight without pits. Groups of cells surrounded by cuticular rims in *D. confertifolia* and *D. winteri*. *Midrib* prominent, but shape of epidermal cells hardly modified; other veins not prominent.

Material studied. South America: *D. confertifolia* Phil.: *Bertero 1453*. — *D. brasiliensis* Miers var. *angustifolia*: Herb. Lugd. Bat. sheet 908. 126—1467; var. *brasiliensis*: Reitz & Klein 10395 a. — *D. granadensis* L. var. *granadensis*: *Lehmann 5130*; var. *mexicana*: *Hartweg 444*. — *D. winteri* J. R. & G. Forst. var. *chilensis*: *Zöllner 4837*; var. *winteri*: Herb. Lugd. Bat. sheet 908. 128—1468; *Thorne s.n.* (8-3-1963, *culta* in Los Angeles, U.S.A.).

N o t e. Although water stomata occur throughout the *Winteraceae*, they are more abundant and outstanding in this section than anywhere else in the family.

4. EXOSPERMUM VAN TIEGHEM

(phot. 15)

Generic description based on one specimen of the only species *Exospermum stipitatum* recognized by Vink (private comm.). Cuticle thin; anticlinal flanges poorly developed. *A b a x i a l s u r f a c e*. Stomata randomly distributed, outlines hardly distinct to vaguely demarcated by broad granular bands of locally thick cuticle, which are fused at the polar

ends of the guard cells, with alveolar plugs, not sunken. Subsidiary cells not subdivided. *Unspecialized cells* not covered with alveolar material, granular; anticlinal flanges straight, heavily pitted. Cells of about equal size or slightly smaller than guard cell pairs. Cells over the *midrib* longer than wide; other veins hardly prominent.

A d a x i a l s u r f a c e. Cuticle granular; anticlinal flanges straight, only indicated by a more densely granular appearance of the cuticle. Cells over the *midrib* hardly modified, but more or less arranged in rows; other veins not prominent.

Material studied. New Caledonia: *Mackee 18714*.

5. PSEUDOWINTERA DANDY

(phot. 9, 29—32)

Generic description based on one specimen of each of the three species recognized by Vink (1970).

Cuticle of medium thickness; anticlinal flanges poorly developed and only vaguely demarcated in cuticular macerations.

A b a x i a l s u r f a c e. Stomata randomly distributed, almost circular to elongated, outlines of guard cell pairs and subsidiary cells hardly demarcated, with alveolar plugs, extending at least over the subsidiary cells. Plugs sunken below level of outer periclinal walls of unspecialized cells in *P. traversii* (phot. 31), \pm in the same plane in the other two species. Subsidiary cells not subdivided. *Unspecialized cells* covered with more or less homogeneous (phot. 32) or distinctly heterogeneous alveolar material in *P. colorata*, partly (near stomata) or not covered with homogeneous alveolar material in *P. axillaris* and *P. traversii*. Cells of about the same size as or slightly larger than the guard cell pairs in *P. axillaris* and *P. traversii*; smaller in *P. colorata*. Anticlinal flanges hardly or not pitted; straight to curved in *P. colorata*, curved in *P. axillaris*, and undulated and grooved in *P. traversii* (phot. 9). Cells over the *midrib* squarish to longer than wide; other veins not prominent.

A d a x i a l s u r f a c e. Cuticle very finely granular, partly striated in *P. colorata*. Anticlinal flanges pitted, curved, and grooved in *P. axillaris* (fig. 1); not pitted, and straight in *P. colorata*; not pitted and straight with irregular thickenings in *P. traversii*. *Midrib* and other veins not prominent.

Material studied. New Zealand: *P. axillaris* (J. R. & G. Forst.) Dandy: *H. H. Travers s.n.* — *P. colorata* (Raoul) Dandy: *H. H. Travers s.n.*; *NSW 68548* — *P. traversii* (Buchanan) Dandy: *Given 503*.

6. ZYGOGYNUM BAILLON

(phot. 19 & 41)

Generic description based on one specimen of each of the six species recognized by Smith (1943b). One can clearly distinguish two groups of three species each, with different cuticular characters. The groups are described separately.

Group I: *Z. bailloni*, *Z. bicolor*, *Z. vieillardii*.

Cuticle fairly to very thick; anticlinal flanges well developed.

A b a x i a l s u r f a c e. Stomata randomly distributed, outlines distinct, widely oval, with alveolar plugs, not or very slightly sunken. Cuticle over guard cells and subsidiary cells thinner than over unspecialized cells. Subsidiary cells not subdivided. *Unspecialized*

cells entirely covered by homogeneous alveolar material; anticlinal flanges curved, with irregular thickenings (phot. 19) and closely spaced minute pits. Cells of about equal size or slightly bigger than guard cell pairs. Cells over *midrib* longer than wide; other veins not prominent.

A d a x i a l s u r f a c e. Cuticle very finely granular; anticlinal flanges straight to curved at high focus, straight at low focus, not pitted. Cells over *midrib* hardly modified, but more or less arranged in rows; other veins not prominent.

Material studied. New Caledonia: *Z. bailloni* v. Tiegh.: *Pancher s.n.* (type). — *Z. bicolor* v. Tiegh.: *Thorne 28642*. — *Z. vieillardii* Baill.: *Thorne 28676*.

Group II: *Z. pomiferum*, *Z. spathulatum*, *Z. balansae*.

Cuticle very thin; anticlinal flanges very poorly developed and vaguely or hardly at all demarcated in cuticular macerations.

A b a x i a l s u r f a c e. Stomata randomly distributed, outlines of guard cells vaguely demarcated by broad granular bands of locally thick cuticle, which are not fused at the polar ends of the guard cells, with alveolar plugs (phot. 41), not or very slightly sunken. Subsidiary cells not subdivided. *Unspecialized cells* not covered by alveolar material, granular; anticlinal flanges straight to curved, only indicated by a more densely granular appearance of the cuticle. Cells larger than guard cell pairs. Cells over *midrib* (only present in one specimen) longer than wide; other veins not prominent.

A d a x i a l s u r f a c e. Cuticle coarsely granular, cell outlines not visible in cuticle due to no or too weak development of anticlinal flanges. Anticlinal walls straight to curved as based on outlines of cellulose walls.

Material studied. New Caledonia: *Z. pomiferum* Baill.: *Foster 218*. — *Z. spathulatum* v. Tiegh.: *McKee 4791*. — *Z. balansae* v. Tiegh.: *McKee 5093*.

Notes. 1. The subdivision of *Zygogynum* into two groups as based on cuticular characters coincides with a grouping of species using exomorphic characters (Vink, personal communication).

2. Stomatal size was determined for one species only. The values: $56 \times 42 \mu\text{m}$ are typical for the whole genus and much higher than in the other genera.

VARIATION OF THE CUTICULAR CHARACTERS WITHIN *DRIMYS PIPERITA*

Introduction

It is obvious from the generic description that the variation in *Drimys* section *Tasmannia* is enormous. The whole range described for this section can be found within the complex species *Drimys piperita* with its 39 entities as delimited by Vink (1970) using exomorphic characters.

Usually it is impossible to discuss correlations of anatomical features with prevailing climatic conditions on the leaf epidermal variation using herbarium material. For *Drimys piperita*, however, the situation was different because much rather well documented material was available, and some gaps in the information about the habitat could be filled by personal information from Dr. Vink. Therefore an attempt could be made to establish such relationships between ecological conditions and cuticular characters.

Of *Drimys piperita* 85 specimens were studied. In order to study the variation within the entities, more than one specimen was studied of each of 12 entities.

Epidermal variability within entities of *Drimys piperita*

In this section the variation encountered in those entities, of which more than one herbarium specimen was studied, will be discussed. One has to bear in mind that interpreting the variation found in a limited number of herbarium specimens can only be tentative. The variation discussed below is also summarized in table I.

Entity 4 'versteegii'

Four collections were studied, all from the edges of the shrubbery or open grassland, but from different localities. The stomata in *Hartley 12800* are more circular and the 'glands' are less abundant than in the other collections, but — on the whole — all four collections are rather uniform.

Entity 8 'crassipes'

The two collections studied are from the shrubbery on Mt. Wilhelm. The two specimens are strikingly similar and are characterized by irregular cuticular sculpturing and unusual shaped guard cells with incurved anticlinal walls (phot. 2, 12). The only differences between the two specimens are the more prominent veins and more abundant 'glands' in *v. Balgooy 776*.

Entity 9 'montis-wilhelmi'

Ten collections were studied: 4 from Mt. Ambua (summit at 3555 m), 4 from Mt. Ne (3340 m), 1 from Mt. Giluwe, and 1 from Mt. Amungwiwa. The former 8 collections are from localities which are very close together, the collection from Mt. Giluwe at 80 km distance from these. Mt. Amungwiwa is situated about 400 km further to the East. The collections were from different altitudinal vegetation zones, viz. mossy forest, alpine shrubbery and open vegetation of the summit regions. Collections from the mossy forest are *Vink 17415* (shade form) from the South slope of Mt. Ambua, and *Vink 17160* and *17108* (shade form) from Mt. Ne. subalpine shrubbery specimens are *Vink 17420* (Mt. Ambua), *Schodde 1839* (Mt. Giluwe), and *Womersley NGF 18000* (Mt. Amungwiwa). Open summit vegetation specimens are *Vink 17392* (Mt. Ambua) and *Vink 17121* (Mt. Ne).

The leaves of the shade forms are somewhat larger (41—58 × 18—19 mm) than the exposed ones from the alpine shrubbery (15—38 × 7—18 mm). Stomatal size seems to follow the same trend: in shade forms 34—38 × 26—28 μm, in shrubbery specimens 33—34 × 25—26 μm on Mt. Ne as well as on Mt. Ambua. However, the differences are very small and in *NGF 18000* from the shrubbery of Mt. Amungwiwa the stomata are just as large as in the shade forms on the other mountains.

Irrespective of the altitude and vegetation type, the epidermal cells in collections from Mt. Ne, Mt. Giluwe and Mt. Amungwiwa tend to be comparatively smaller ($\frac{3}{4}$ — $\frac{1}{2}$ × size of guard cell pairs) than in the specimens from Mt. Ambua ($\frac{3}{4}$ — $\frac{1}{2}$ × size of guard cell pairs).

In *Vink 17121* from the summit of Mt. Ne, leaves of 4 different parts of the same shrub were available. Besides a water shoot, exposed leaves and leaves inserted at lower levels on the plant were studied. Leaf size increases from the top to the bottom of the shrub: 32 × 13, 35 × 18, and 41 × 18 mm resp. (size of leaves used for macerations and representative for the trend in the specimen). The size of the lower leaves is thus within the range of that of the shade forms. However, stomatal size and epidermal cell size are very constant.

Water shoot leaves were available in *Vink 17934* and *17121*. These leaves are somewhat larger than the ordinary leaves of the same plant, but in other respects they do not differ considerably. *Vink 17121* has larger epidermal cells and curved instead of straight anticlinal flanges, compared with normal leaves of the same collection. Stomatal size was the same as in the ordinary leaves.

This entity thus appears to be quite uniform for stomatal size and qualitative cuticular characters. The stomatal index, however, is very variable. Extreme values are 8 and 13 within this entity for leaves of comparable habitat. The stomatal index is therefore of little diagnostic value here.

Entity 10 'giluwe'

Of this entity 6 collections were studied. *Vink 17450*, *17315*, and *Frodin NGF 28243* are specimens from the forests of Mt. Ambua. Those three collections are rather similar, in *Vink 17315* the stomata are somewhat more slender and elongated and in the *Frodin* collection the unspecialized cells are somewhat smaller than in the other two collections. *Vink 17411* is a more xeromorphic form from the shrubbery of the same mountain. A comparison with the former three collections reveals that the unspecialized cells are somewhat smaller and the anticlinal flanges are straight. This is in agreement with *Zalinski's Law* (*Maximov, 1929*) concerning characters associated with xeromorphism. Moreover the cells over the midrib are squarish instead of longer than wide.

A comparison of *Vink 17163* (a seedling from the forest of Mt. Ambua) with the first three collections shows that here the stomata are larger and elongated (as in *Vink 17315*) the unspecialized cells are larger and the anticlinal flanges are more undulated at the adaxial surface. The anticlinal flanges at the abaxial surface are so faint that it could not be established whether they are undulated and/or pitted or not.

This entity is fairly constant and the variation reported may be due to differences in habitat.

Entity 12 'nettoti'

The three collections studied are from a narrow altitudinal range. Two are from open vegetation, one is from the mossy forest. The three specimens are very similar in most cuticular characters. The only differences are to be found on the adaxial surface. In the specimen from the mossy forest the anticlinal flanges are undulated; in the specimens from the shrubbery they are less undulated, or curved to almost straight. In the latter case the venation is also less prominent. This type of variation may be of phenotypic nature, possibly induced by different light intensities and/or humidity.

Entity 13 'fistulosa'

The two specimens, both from Mt. Doorman, are very similar. The differences concern mainly the stomatal size and the prominence of veins. The doubtfully identified specimen (*Lam 1630*) deviates in a few more characters (see table I).

Entity 22 'coriacea'

This very-large-leaved entity has its habitat in the forests. The 7 specimens studied are from a wide geographical range in New Guinea. The entity is very variable, particularly in its qualitative cuticular characters: the anticlinal flanges may vary from straight to

undulated, they may be pitted or not; the subsidiary cells may be subdivided or not, and the cells over the midrib range from squarish to longer than wide. The variation in the different characters is, however, not mutually correlated.

Entity 25 'heteromera'

This entity was split up into several regional complexes by Vink (1970: 299). The cuticles of 6 specimens were used for this study. From complex *a* the specimen was from Mt. Elandora, complex *b* was represented by 2 specimens from Mt. Ambua and a specimen from the Ibiwara plain between Mt. Ambua and Mt. Kerewa, complex *c* by a specimen from Mt. Wilhelm, and complex *d* by a specimen from Mt. Shungol.

Entity 'heteromera' is very variable in its ecology as well as in its cuticular characters. Not only are the differences between the complexes very great, but also within complex *b*, of which 3 specimens were studied, a considerable variation was encountered. In the latter case this variation can be related to the different types of habitat (mossy forest, shrubbery, and open vegetation) in a similar way as could be done for *D. piperita* as a whole (see p. 397). The very large stomata in *Brass 30291* (complex *c*) are exceptional for this entity.

Entity 26 'polymera'

The habitat of only one of the 3 specimens studied is known (mossy forest). The anticlinal flanges of the stomata in one of the specimens (*Saunders 738*) were so faint that no reliable measurements could be made. In most cuticular features the three specimens resemble each other very much.

Entity 35 'oligandra'

One of the two collections studied was from an epiphytic plant (*Brass 12975*). The appearance of both collections is rather similar, but there are considerable differences in the stomatal complex. In *Brass 12975* the stomata are much bigger, but the length to width ratio is the same as in the other specimen (*v. Royen & Sleumer 7084*). The subsidiary cells show cuticular striations in the former, not in the latter specimen. *Van Royen & Sleumer 7084* stands out by distinct outer cuticular ledges. The plants belonging to this entity are also very variable in exomorphic features (Vink 1970: 344).

Entity 39 'xerophila'

Ecological data were not available for the three specimens studied. Except for the large variation in leaf size, the three collections were found to be very similar.

Conclusions

The cuticular variation within the entities may differ widely. In the material analysed here, there is a striking tendency for the xeromorphic entities (e.g. 'montis-wilhelmi', 'versteegii', and 'xerophila') to be less variable than the more mesomorphic entities (e.g. 'coriacea' and 'heteromera'). This tendency may give a false impression, however, because the geographical range over which the collections were made should be taken into account, and this range happens to be greater for the mesomorphic entities than for the xeromorphic entities studied in more detail here.

There is no way of telling which part of the variation is genotypic and which part is phenotypic. Most of the entities treated here are, however, in spite of the diverse habitats they may grow in, sufficiently constant to suggest that most of the cuticular features of these entities are genetically fixed. This would also provide arguments in the discussion whether the entities as considered by Vink are natural groups. For entities 25 '*heteromera*', 35 '*oligandra*', and 38 '*membranea*' the leaf epidermal evidence suggests that this is not the case. Entity 22 '*coriacea*' is also very heterogeneous. However, much more material would have to be studied to use leaf epidermal characters taxonomically at the vague level of the entity.

Variation of the characters in *Drimys piperita* as a whole

While making macerations, I was struck by the enormous range in leaf sizes. This is by no means an anatomical character, but it was nevertheless surprising that, within a leaf size range from 3×2 to 160×62 mm, no relation could be found with any anatomical character. The variation of an additional character found in making macerations was that of the cuticle thickness, ranging from very thin to thick.

Four leaf-epidermal characters of the abaxial surface in *Drimys piperita* appeared to show trends of mutual correlation. These characters are:

1. The estimated size of the unspecialized cells as compared with the size of the guard cell pairs.
2. The length to width ratio of the stomatal cell pair (phot. 20 & 21).
3. The outline of the anticlinal flanges, i.e. whether they are straight, curved or undulated (phot. 20 & 21).
4. The outline of the epidermal cells over the midrib. These cells may be longer than wide, squarish, wider than long, or not modified as compared with the unspecialized cells (phot. 22—24).

The four characters listed above, are compiled in a diagram (fig. 6) for the New Guinean entities of *Drimys piperita*. The entities 3 '*buxifolia*', 7 '*papillata*', and 25 '*heteromera*' are not taken into account. From '*buxifolia*' no material was available; in '*papillata*' no measurements could be made due to the papillae, and '*heteromera*' is so variable in itself that the inclusion in a graph would be meaningless.

The length to width ratio of the stomatal cell pair is plotted on the horizontal axis and the estimated ratio of the stomatal size to epidermal cell size is indicated on the vertical axis. The latter character varies continuously within *Drimys piperita*, but for practical reasons I subdivided the range in 5 arbitrarily chosen ratios. Straight anticlinal flanges are given in white, curved ones in hatched, and undulated ones in solid black figures. Wider than long cells over the midrib are symbolized by procumbent rectangulars, squarish cells by squares, and longer than wide cells by upright rectangulars. When the cells over the midrib have the same outline as the unspecialized cells, this is indicated by a circle.

The trends of positive correlations found in fig. 6 are the following: On the one extreme, small unspecialized cells are found in combination with almost circular stomatal cell pairs, wider than long cells over the midrib, and straight anticlinal flanges; on the other extreme large unspecialized cells are found in combination with slender and elongated stomatal cell pairs, longer than wide cells over the midrib and undulated anticlinal flanges. Between those two extremes a complete range of intermediates is found. Yet another character, viz. 'subdivisions of the subsidiary cells', appears to be correlated with this trend: leaves with small unspecialized cells usually have subsidiary cells which are sub-

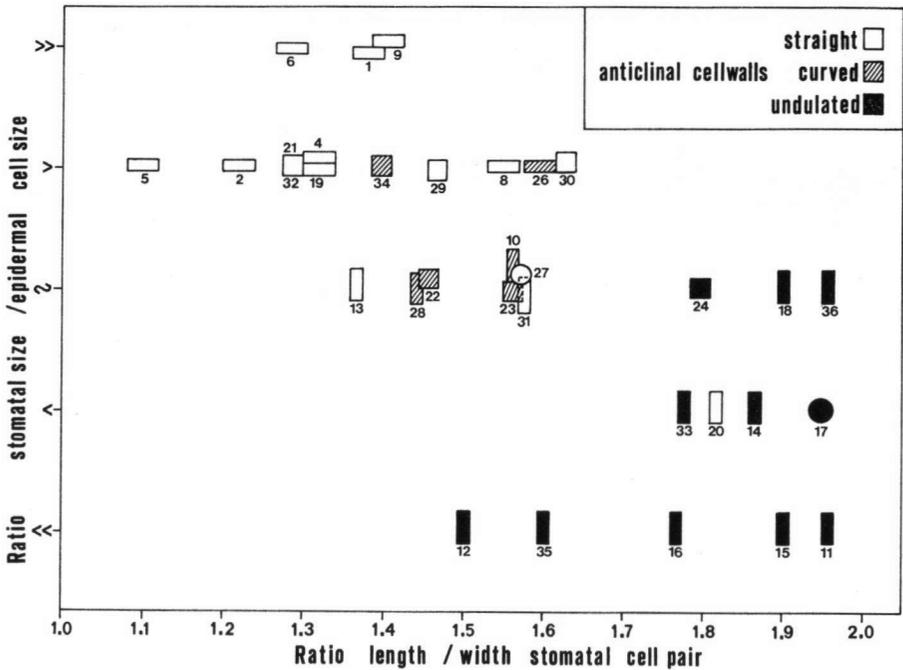


Fig. 6. Correlation of epidermal characters in the New Guinean entities of *Drimys piperita* (see also text on p 397). — Outlines of abaxial cells over midrib indicated as follows: circles: cells not modified. — squares: cells squarish. — procumbent rectangulars: cells wider than long. — erect rectangulars: cells longer than wide.

divided and in leaves with large epidermal cells the subsidiary cells are usually not subdivided.

In fig. 7 the trends of variation of the four characters mentioned above are compared with the usual habitat of the entities (data from Vink, 1970). The scales on the horizontal and vertical axis are the same as in fig. 6; straight, curved, and undulated anticlinal flanges are also indicated in the same way as in fig. 6. The squares mean that the entity concerned usually is found in open vegetation; circles: in shrubbery; and triangles: in forests. The general trend here is that entities with small unspecialized cells, with more circular stomata, with cells over the midrib wider than long, and with straight anticlinal flanges are found in open vegetation, and that entities with large unspecialized cells, with slender and elongated stomata, with cells over the midrib longer than wide, and with undulated anticlinal flanges are found in the forest.

The characters found in the entities on the upper left side of fig. 6 are usually considered as xeromorphic (Zalenski's Law, Maximov, 1929). The degree of xeromorphy is decreasing to the lower right side of the figure. This coincides with the data on the vegetation type as described above, but it is impossible to conclude from my data whether this variation in *Drimys piperita* is phenotypic or genotypic. The fact that in most entities in which more material was studied the characters used in the diagrams are fairly constant, plead for the suggestion that these characters are genetically fixed within an entity. But there are also indications for variations that are perhaps phenotypic, as e.g. the xeromorphic form

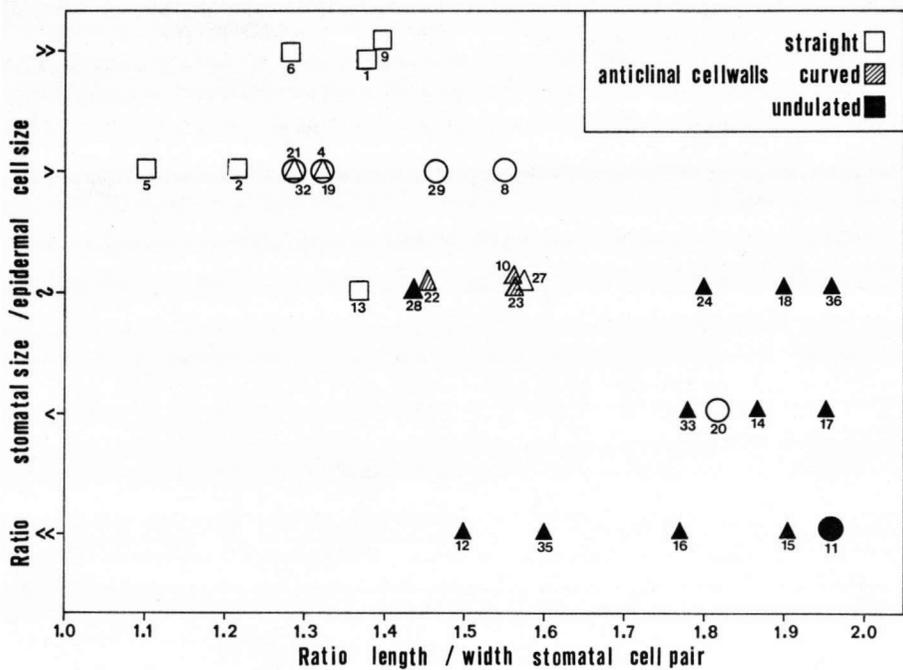


Fig. 7. Epidermal characters of the New Guinean entities of *Drimys piperita* and their usual habitats (data from Vink, 1970). Entities plotted as in fig. 6. Some entities of which data were insufficient are omitted. squares: entities from open vegetation. — circles: entities from shrubby. — triangles: entities from forests.

studied in 'giluwe' (Vink 17411) and the variation encountered in the three collections in 'heteromera b', which show trends to more xeromorphic entities according to Zalenksi's Law.

DISCUSSIONS

The value of the characters used

Most of the characters described are very variable. The diagnostic value of these characters may be different in the different genera, sections, or species, depending on the variational range within each taxon. Obviously the diagnostic value also depends on the level of the taxon involved. Particularly because of the different variational ranges in the different taxa of the same rank, it is impossible to assess the diagnostic value of each individual character within the family as a whole.

The value at the genus and section level.

Most characters are so variable and overlapping at the genus or section level that their diagnostic value is very low. The few remaining characters are almost never absolute. The presence of alveolar material is a constant character except for the (larger) part of section *Tasmannia* and *Bubbia perrieri*. In section *Tasmannia*, the absence of alveolar material is characteristic, except for small alveolar plugs in *Drimys stipitata* and the entities 'chartacea',

'*montis-wilhelmi*', and '*robusta*' of *Drimys piperita*. But in this section the alveolar material never extends to over at least the subsidiary cells, which is typical for the section *Drimys* and the other genera.

Very large stomata are characteristic for *Zygogynum*, but are also found on one specimen of *Bubbia*. Subdivisions of the subsidiary cells are found in all the specimens studied in section *Drimys*, but also in a part of section *Tasmannia*.

The distinctness of the outlines of the stomata is rather constant for the different genera, except for *Bubbia*.

Water stomata occur incidentally in all the genera of the *Winteraceae*, but are more numerous and outstanding in section *Drimys*.

The value at the species level.

Except for *Drimys piperita* only incidentally more than one specimen of the same species has been studied. Both specimens of *Bubbia amplexicaulis* are very similar and this is also the case with the two specimens studied of *Bubbia isoneura*. In *Drimys winteri* the stomata are provided with alveolar plugs, but in one specimen (*Thorne s.n.*, 8-3-1963, cult. hort. Los Angeles) these plugs are absent, despite the fact that the whole abaxial side of the leaf is covered with a layer of homogeneous alveolar material (phot. 38).

Therefore it is impossible to estimate the taxonomic value of the characters at the species level and it is dangerous to extrapolate the results obtained from *Drimys piperita*.

The characters in *Drimys piperita*, which are mutually related as shown on p. 398 are usually constant and thus diagnostically important at the entity level. The pitting of the anticlinal flanges, a granular cuticle, and the prominence of the veins are even variable within the entities and therefore of minor importance. The occurrence of 'glands' at the abaxial surface is a constant feature and characteristic in *Drimys piperita*.

Taxonomic implications

As stated before, alveolar material is usually lacking in section *Tasmannia*, and where it is present in this section it is always confined to the stomata. In the remainder of the family this alveolar material is always present except for *Bubbia perrieri*. Vink used the absence of alveolar plugs in section *Tasmannia* in his thesis (1970: 248) as one of the characters to delimitate this section from section *Drimys*. From this paper it is obvious that this character is not so absolute, but if also the type of alveolar material is taken into account it is, in my opinion, a character strong enough to set section *Tasmannia* apart from the remainder of the family.

By the presence of heterogeneous alveolar material the section *Drimys* is separable from the remainder of the family, except for *Bubbia pro parte* and one specimen of *Pseudowintera colorata*, where it also occurs. Moreover this section stands out by the more numerous and obvious water stomata and the subdivisions of the subsidiary cells.

Exospermum and *Belliolum* fall in the range of variation of *Bubbia*. *Exospermum stipitatum* (Mackee 13750) and *Belliolum haplopus* (Foreman NGF 45689) are rather similar in cuticular characters and resemble e.g. *Schodde & Craven 5082* and *Sayers NGF 21535* in *Bubbia* rather closely. The more xeromorphic *Belliolum crassifolium* (Balansa 582) resembles *Bubbia vieillardii* (Vieillard 16) in its leaf epidermis.

The three species of *Pseudowintera* are also within the variation range of *Bubbia* (cf. *Schodde & Craven 4750*) for most of their characters, but they lack the granular bands over the anticlinal flanges of the guard cells typical for *Bubbia*. The few specimens in *Bubbia* also lacking those bands are not very similar to the specimens of *Pseudowintera*.

Group I of *Zygogynum* (see description p. 392) is distinct from most *Bubbia* material studied by its very large stomata, with distinct outer anticlinal flanges and unspecialized cells with peculiar anticlinal flanges (phot. 19), but this group is linked to *Bubbia* by *Bubbia balansae* (*Balansa 1844*) (phot. 18) which has the same features. Group II of *Zygogynum* is very similar to *Bubbia* except for its much larger stomata.

The genus *Bubbia* shows a very wide range in cuticular characters, mainly by the varied appearance of the alveolar material, and the absence of the granular bands over the anticlinal flanges of the guard cells in some specimens. The range is considerably extended by aberrant species such as *Bubbia balansae*, *Bubbia pachyantha*, *Bubbia perrieri*, and *Bubbia vieillardii*. For that matter, the genus shows a considerable overlap with most of the genera (*Belliolum*, *Exospermum*, *Pseudowintera*, and *Zygogynum* I & II). The significance of the variation encountered within *Bubbia* cannot be estimated yet, in the lack of a recent taxonomic revision.

Special attention has to be paid to *Bubbia perrieri*. The majority of the stomata in this species is anomocytic and only a few are paracytic. *Bubbia perrieri* is for that matter exceptional in the *Winteraceae* (as is *Liriodendron* in the *Magnoliaceae*; Baranova, 1972: 454). Moreover *Bubbia perrieri* has distinct outer stomatal ledges and this feature is only found in this family in a few entities of *Drimys piperita*, but *Bubbia perrieri* is not similar in appearance to any entity of *Drimys piperita*. The placing of *Bubbia perrieri* in *Bubbia* is very doubtful using cuticular characters only. Capuron (1963), who described this species on exomorphic features placed it in *Bubbia* in the absence of a better alternative. On the grounds of cuticular features it is also impossible to place it in any other genus and possibly it deserves generic status. Baranova (1972) arrived at the same conclusion.

Within not less than 4 of the 6 genera (*Belliolum*, *Bubbia*, *Drimys*, and *Zygogynum*) a discontinuous variation in cuticular characters is encountered by which the genera can be either split into two groups (*Drimys*, *Belliolum*, and *Zygogynum*), or by which aberrant species take isolated positions (*Bubbia*). The differences within the genera are sometimes greater than between the genera (cf. *Zygogynum*).

As a conclusion one may state that all genera show an overlap in a varying number of cuticular characters, and that no distinct groups of genera can be recognized. *Drimys* section *Tasmannia* and especially *Bubbia perrieri* take the most isolated positions within the family. The occurrence of alveolar material in all genera may be regarded as a confirmation of mutual affinity.

In her study of leaf epidermal features of the *Magnoliaceae* and related families, Baranova (1972) also included 19 species of *Winteraceae*, representing all the genera except *Exospermum*. She divided the family into two groups: group I comprising *Drimys* and *Tasmannia*; group II the other genera. According to her, group I is characterized by rather thin-walled guard cells, subsidiary cells, and unspecialized cells, whilst group II usually has thick-walled epidermal cells. My results show that such a characterization is not valid, since both forms occur in both groups. The characterization by Baranova of her groups I and II by qualitative cuticular characters ('patterned and alveolar in group I, and merely grainy in group II') is erroneous, and also contradictory to her own illustrations. It may well be that the inconsistencies in her paper were due to the transformation of her Russian thesis into an abbreviated English version. Anyway, my study of more specimens has indicated that a clear grouping of the genera on the grounds of a combination of epidermal characters is not possible within the *Winteraceae*.

Baranova's results on 5 species of *Belliolum*, where she found anatomical support for Smith's (1943b) subdivision in a New Caledonian group and a group from the Solomon Islands, are in full agreement with my results on only two species.

Although Bailey & Nast (1944b) were the first to give a survey of the epidermal range in the *Winteraceae*, they did not draw conclusions on the taxonomic value within the family. Their data on petiole anatomy (1944a) are in full agreement with mine, and I therefore refrain from repeating their observations here.

The interrelations of the entities in *Drimys piperita*

From the revision of Vink (1970) it is clear that the pattern of relationships between the entities in *Drimys piperita* is a very complex and reticulate one. It is by no means the intention to unravel this pattern with the help of the cuticular characters of only 85 specimens. A disadvantage is that a number of characters, viz. those characters which are more or less constant for the entities, show trends of correlation with the usual habitat of the entities concerned as described on p. 397. If it is assumed that those characters have become genetically fixed, parallelism in the phylogeny of less related (groups of) entities might obscure the real relationships. On the contrary, related entities might differ considerably as a result of divergence. This means that fig. 6 can not be considered as a 'picture' for the relationships between the entities. A second difficulty is that the characters involved show a continuous range in *Drimys piperita*. For all these reasons it is obvious that, based on cuticular characters only, the mutual relationships cannot be discussed. Some entities are very similar in epidermal appearance as: 'versteegii' and 'montis-wilhelmi'; the series 'microphylla', 'vaccinoides', 'myrtoides', and 'elongata'; 'beccariana' and 'robusta'; and 'coriacea' and 'obovata', but this is thus no guarantee for close natural affinity. However, the similarity with the results of Vink are striking.

Physiological significance of stomatal occlusions

Plugs of alveolar material or sometimes of only wax are found in nearly all *Winteraceae*. Moreover, the alveolar plugs are covered with an almost solid layer of cutin in some representatives. It seems reasonable to assume that such plugs inhibit gas exchange to a great extent.

Jeffree *et al.* (1971) calculated the restriction of the gas exchange by wax plugs in the stomata of *Picea sitchensis*. They concluded that the rate of transpiration was reduced by about two thirds, but that the rate of photosynthesis was only reduced by one third. The vesselless water transporting tissue of the *Winteraceae* and the plugging of the stomata have led to the suggestion that those plugs may be of adaptive significance in this family (Bailey & Nast, 1944b; Bailey, 1953). The presence of waxy plugs in the stomata of *Coniferae* has been cited in favour of this hypothesis (Bailey & Nast, 1944b), but their absence in vesselless *Trochodendron* and *Tetracentron* was used as an argument to refute this suggestion. Bailey (1953), however, pointed out that *Trochodendron* and *Tetracentron* have a higher proportion of scalariform bordered pits than *Winteraceae* and that presumably these woods have a better water conductivity. Moreover, a great number of the stomata in *Trochodendron* were said to be nonfunctional, and in *Tetracentron* aggregations of large tracheids were considered to facilitate water transport to such an extent that no leaf anatomical adaptations seem to be necessary.

There are some additional arguments which go to show that the utmost caution should be observed in conclusions about the adaptive significance of stomatal plugs as a compensation for the low water transporting capacity of vesselless secondary xylem.

1. Several representatives of the *Winteraceae* do not have alveolar plugs (most entities and species of *Drimys* section *Tasmania*, and *Bubbia perrieri*), nor has an indication been found in herbarium material of some of these representatives that waxy plugs are present. This implies that occluded stomata are not of absolute necessity for *Winteraceae* to survive.
2. Occluded stomata also occur in number of Dicotyledons with simply perforated vessels (Wulff, 1898).
3. The water conducting capacity of the wood of the *Winteraceae* is not known. The vesselless nature does not always imply a low capacity for water transport, as can be concluded from experiments with a number of conifers where conductivity and peak velocities of water were higher than in some diffuse porous hardwoods (cf. Zimmermann & Brown, 1971).

Thus no well founded conclusion can as yet been drawn about the functional and adaptive significance of occluded stomata within *Winteraceae*. The same applies to any functional value one might like to attach to deeply sunken stomata or high papillae occurring in a few scattered species. For instance, the entities of *D. piperita* with sunken stomata represent all ecological types: epiphytes, shrublets from open vegetation, and shrubs and trees from dense forests.

This family certainly invites a thorough physiological study on the water balance of its representatives. Ultrastructural research on the nature of the pit membranes in the tracheid-walls would, moreover, be necessary to bring our understanding of the water transport in this group on the same level as that of conifers. Another question of functional significance which remains to be answered is at which stage of development the occlusions of the stomata by alveolar material or wax becomes effective, and whether young leaves without occluded stomata play any role at all in the water balance of the plant. Of *Zygogynum baillonii* (Pancher s.n., type) I compared a young leaf with a mature leaf, and found the alveolar material to be equally developed in both, which would suggest that this role can be of very minor importance at most.

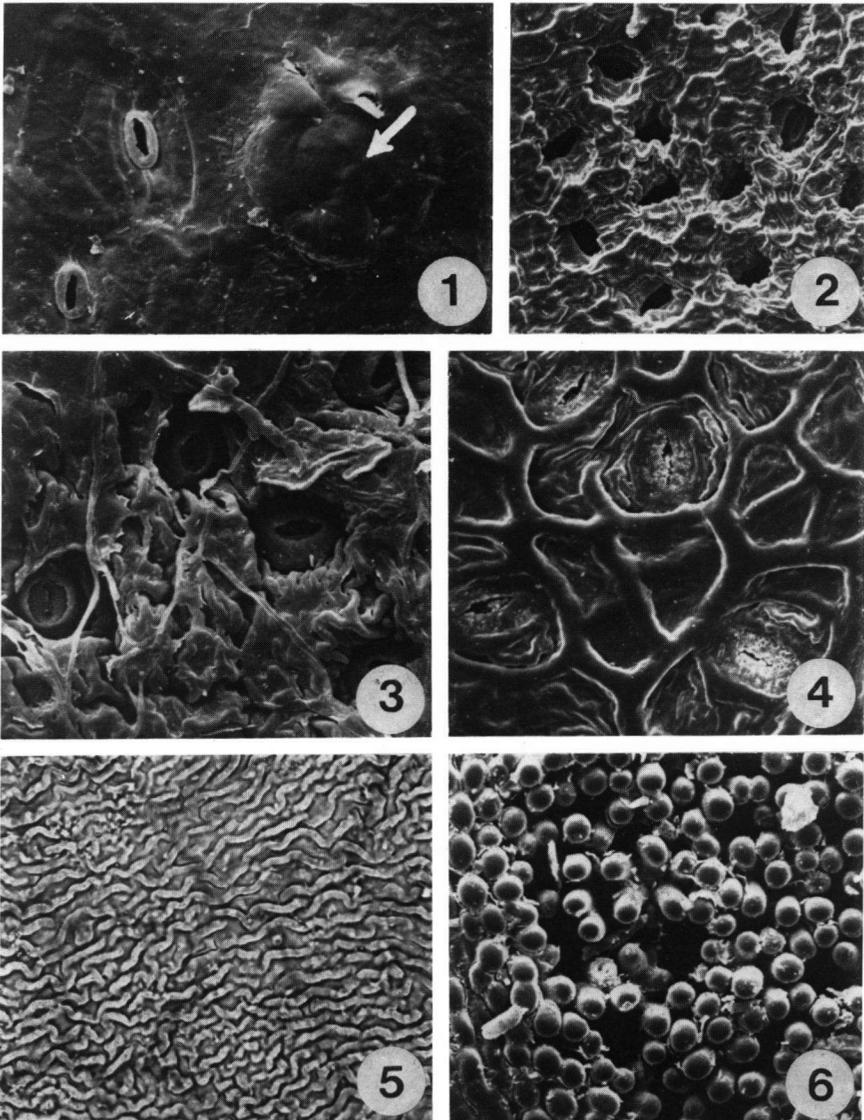
However, further ontogenetic studies in more genera and with still younger material remain necessary. Such a study, if carried out at the ultrastructural level, would possibly also throw some light on the mystery of how living cells succeed in overlying their cuticles with alveolar material of a cutinaceous nature.

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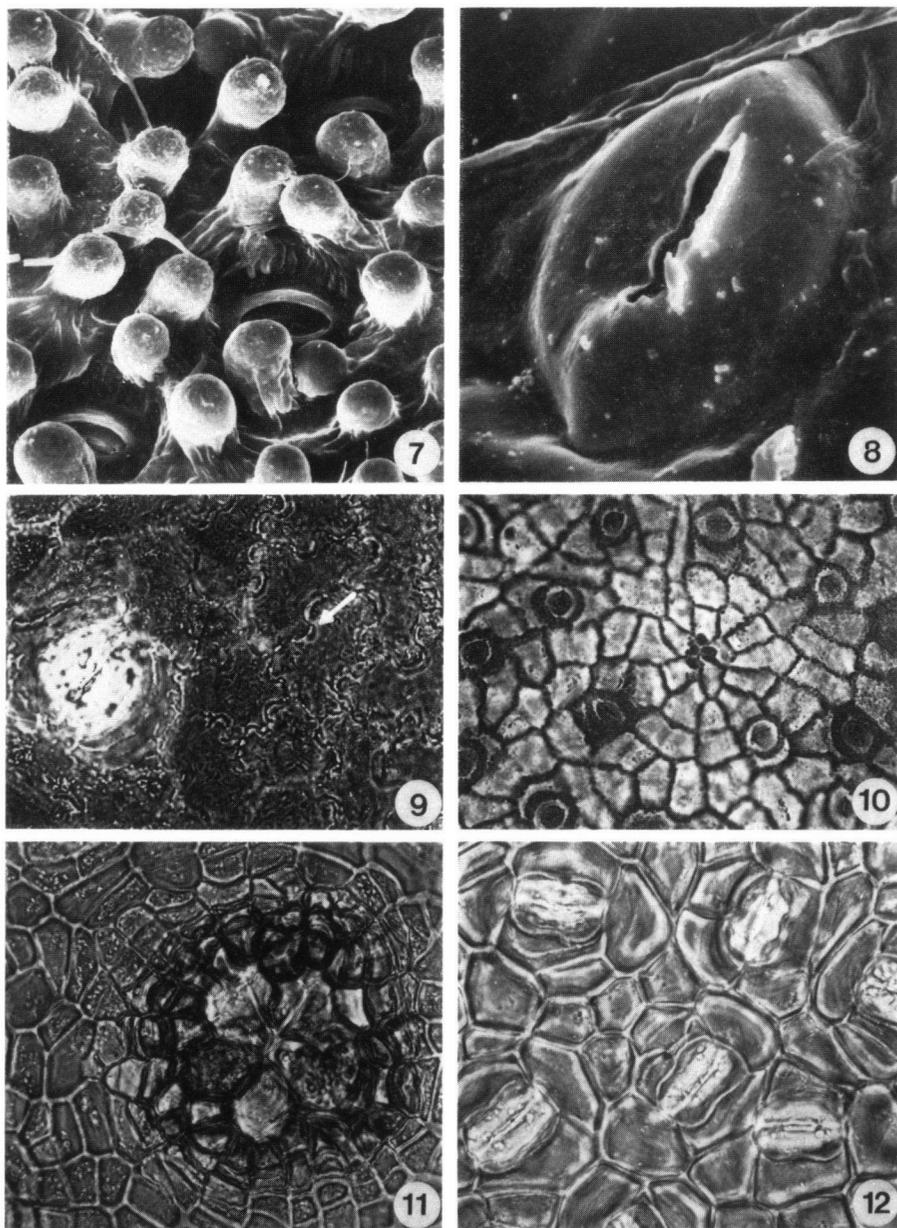
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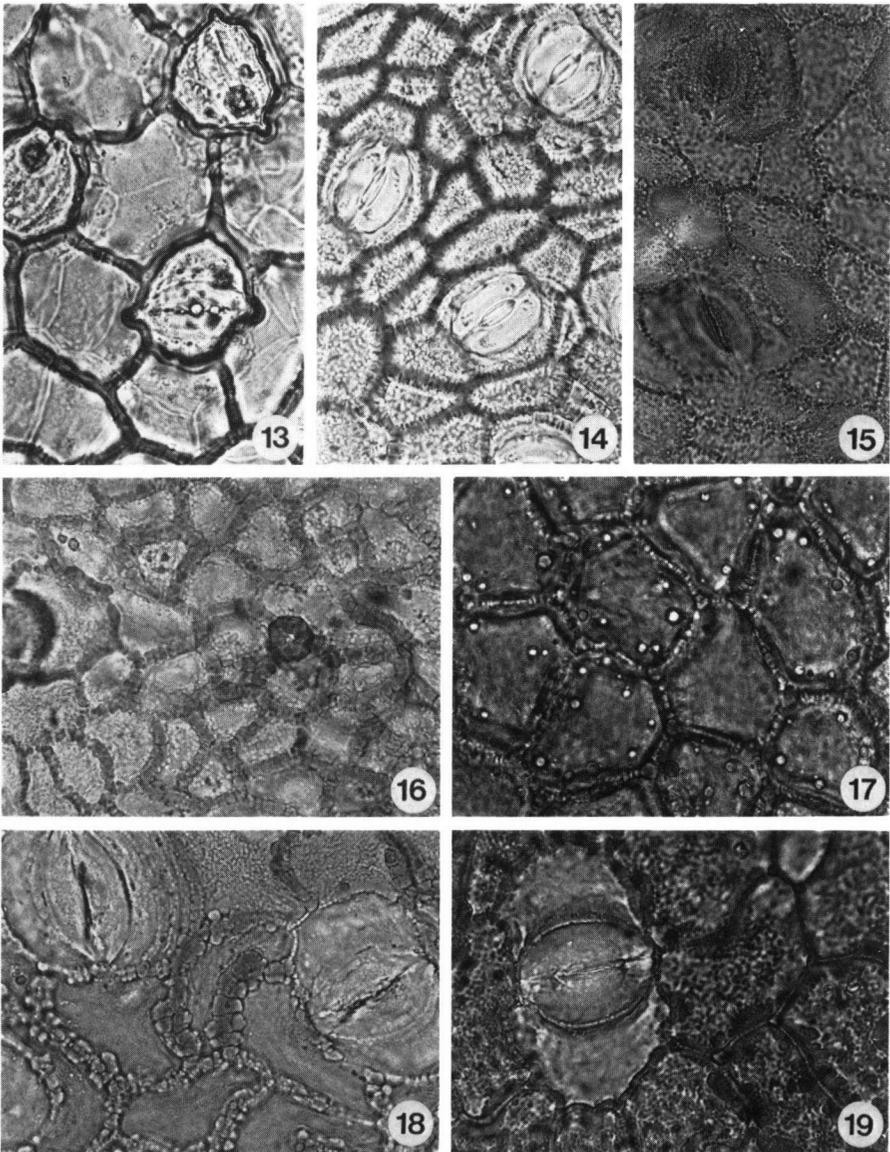


1. *Drimys piperita* 'nettoti' (Van Royen & Sleumer 7936), outer stomatal ledges and 'gland' (arrow), SEM, ab., $\times 500$. — 2. *Drimys piperita* 'crassipes' (Van Balgooy 776), irregularly sculptured cuticle and sunken stomata, SEM, ab., $\times 200$. — 3. *Drimys piperita* 'cordata' (Borgmann 78), irregularly sculptured cuticle and sunken stomata, SEM, ab., $\times 500$. — 4. *Drimys purpurascens* (Schodde 3212), ridges on the cuticle corresponding with anticlinal flanges underneath, SEM, ab., $\times 500$. — 5. *Bubbia* spec. (Schodde & Craven 5082), cuticular striations, LM, ad., $\times 530$. — 6. *Drimys piperita* 'papillata' (Kalkman 4504), epidermal papillae, SEM, ab., $\times 200$.

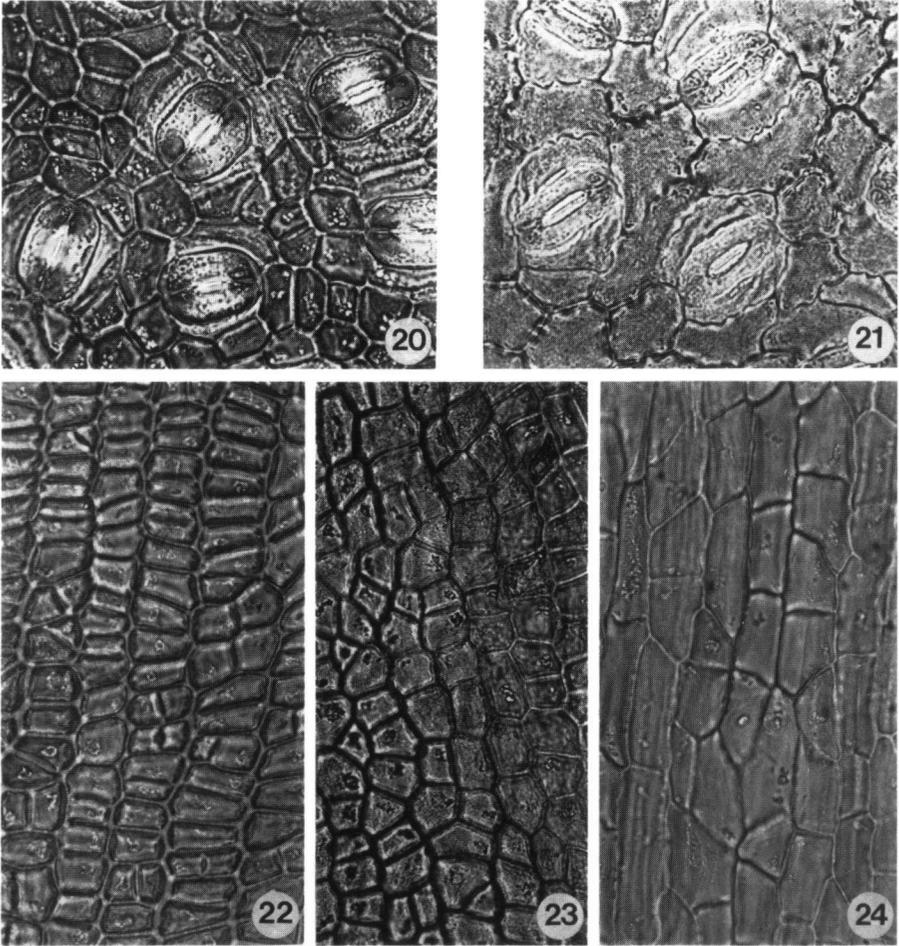
ab.=abaxial surface; ad.=adaxial surface; LM=photomicrograph taken through the light microscope; SEM=Scanning electron micrograph; T.S.=transverse section.



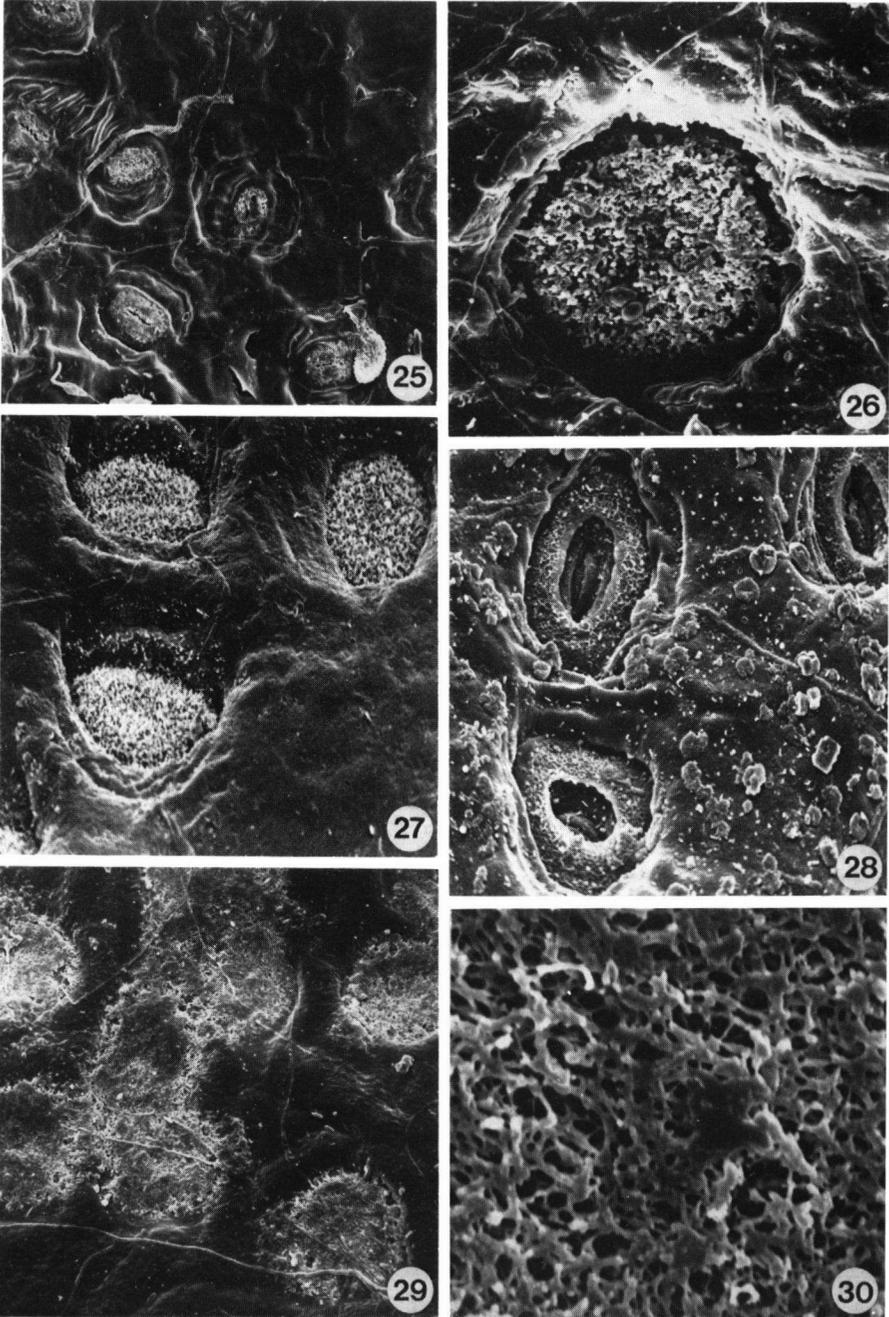
7. *Drimys piperita* 'apetala' (Schodde 3227), epidermal papillae, SEM, ab., $\times 600$. — 8. *Bubbia perrieri* (Perrier de la Bathie 10150), stoma with well developed outer stomatal ledges, SEM, ab., $\times 3300$. — 9. *Pseudowintera traversii* (Given 503), grooved (arrow) and undulated anticlinal flanges, LM, ab., $\times 350$. — 10. *Bubbia spec.* (Van Balgooy 697), radiate epidermal pattern over oil cell, and irregular outlines of guard cells, LM, ab., $\times 350$. — 11. *Drimys piperita* 'montis-wilhelmi' (Vink 17160), 'gland', LM, ab., $\times 350$. — 12. *Drimys piperita* 'crassipes' (Van Balgooy 776), guard cells with incurved outer anticlinal walls, LM, ab., $\times 350$.



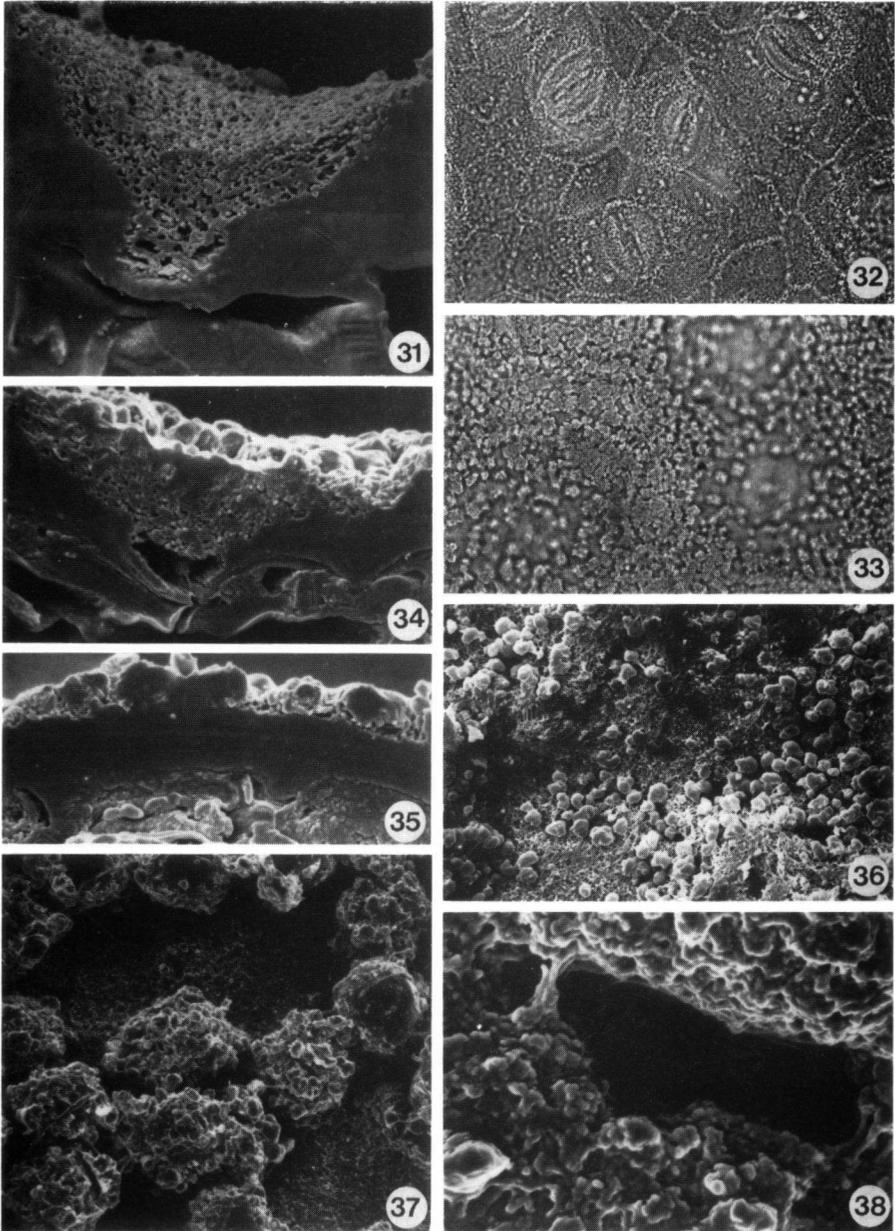
13. *Drimys piperita* 'myrtooides' (Hoogland & Craven 10840), sunken stomata with peristomal rim, LM, ab., $\times 350$. — 14—19. Different forms of pitting in anticlinal flanges, all LM, $\times 350$. — 14. *Drimys piperita* 'coriacea' (Vink 16927), ab. — 15. *Exospermum stipitatum* (Mackee 18714), ab. — 16. *Bubbia archboldiana* (Brass 12712), ab. — 17. *Bubbia balansae* (Balansa 1844), ad. — 18. *Bubbia balansae* (Balansa 1844), anticlinal flanges with irregular outlines, ab. — 19. *Zygogynum vieillardii* (Thorne 28676), anticlinal flanges as in *Bubbia balansae*, cf. phot. 18, ab.



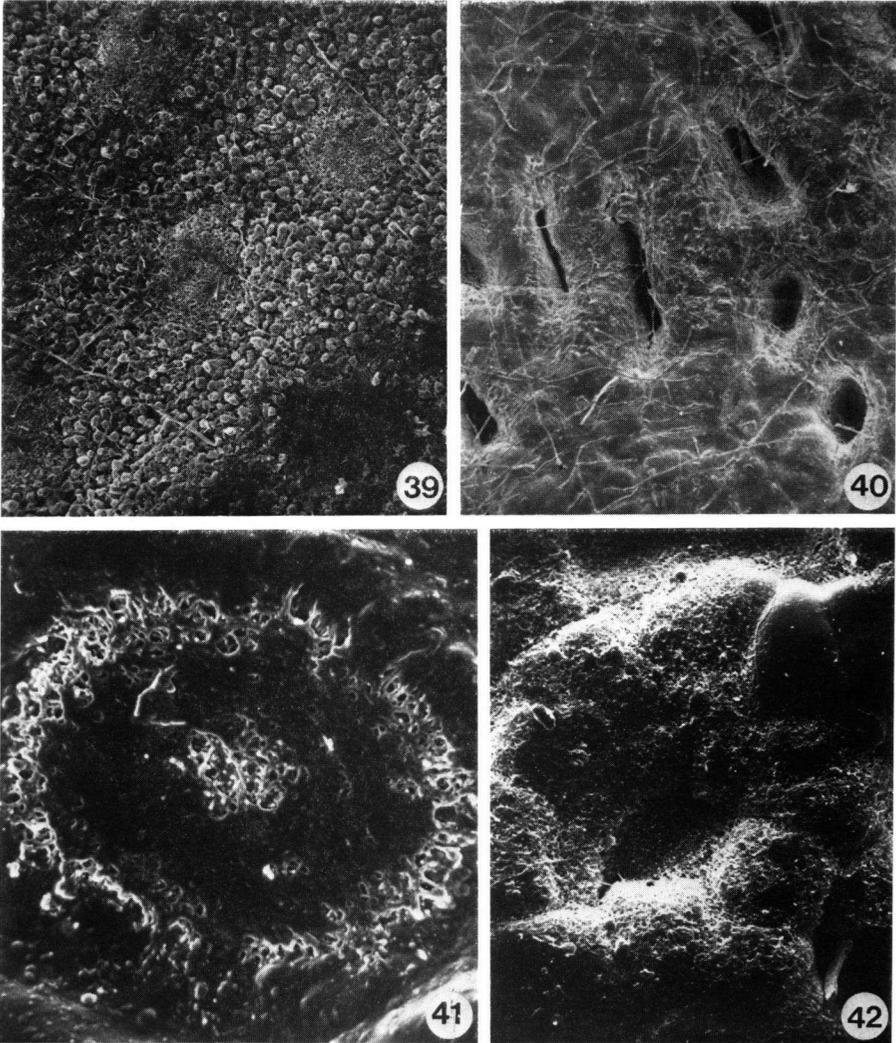
20—24. all LM, ab., $\times 350$. — 20. *Drimys piperita* 'montis-wilhelmi' (Vink 17160), showing straight anticlinal flanges, relatively wide stomata, and relatively small unspecialized cells. — 21. *Drimys piperita* 'acutifolia' (Eyma 4424), showing undulated anticlinal flanges, relatively narrow stomata, and relatively large unspecialized cells. — 22—24. Cell shape and arrangement over abaxial side of midrib. — 22. *Drimys piperita* 'montis-wilhelmi' (Vink 17160), cells over midrib wider than long. — 23. *Drimys piperita* 'coriacea' (Vink 16927), cells over midrib squarish. — 24. *Drimys piperita* 'hatamensis' (BW 14243), cells over midrib longer than wide.



25—30. all SEM, ab. — 25. *Drimys piperita* 'chartacea' (Vink 16820), alveolar material over rims of guard cells, $\times 350$. — 26. *Drimys piperita* 'robusta' (Sleumer & Vink BW 14132), small alveolar plug, $\times 1330$. — 27. *Drimys piperita* 'xerophila' (Burbidge & Gray 6344), wax plugs over stomata of untreated leaf, $\times 550$. — 28. *Ibid.*, wax plugs removed in boiling water, $\times 600$. — 29. *Pseudowintera axillaris* (Travers s.n.), alveolar plugs extending over subsidiary cells, $\times 350$. — 30. *Ibid.*, detail of alveolar material, $\times 3500$.



31. *Pseudowintera traversii* (Given 503), T.S. through stoma with alveolar material extending over subsidiary cells, SEM, $\times 1200$. — 32. *Pseudowintera colorata* (Travers s.n.), alveolar material homogeneous, covering the whole epidermis, LM, ab., $\times 320$. — 33. *Drimys winteri* var. *winteri* (Herb. Lugd. Bat. sheet 908. 1261—468), alveolar material heterogeneous, covering the whole epidermis. LM, ab., $\times 320$. — 34. Ibid., T. S. through stoma, SEM, $\times 1200$. — 35. Ibid., T. S. through unspecialized abaxial cells, SEM, $\times 1200$. — 36. *Drimys granadensis* var. *mexicana* (Hartweg 444), alveolar material heterogeneous, covering the whole epidermis, SEM, ab., $\times 600$. — 37. *Drimys brasiliensis* var. *brasiliensis* (Burchell A173), showing warty papillae and alveolar material over stomatal complex, SEM, ab., $\times 600$. — 38. *Drimys winteri* (Thorne s.n.), alveolar material present except over stomatal pore, SEM, ab., $\times 3000$.



39—42. all SEM, ab. — 39. *Bubbia pauciflora* (Thorne 28302), alveolar material heterogeneous, covering the whole epidermis, cf. phot. 36, $\times 350$. — 40. *Bubbia pachyantha* (Brass 4371), funnel-shaped crypts lined with alveolar material, leading towards stomata, $\times 350$. — 41. *Zygogynum pomiferum* (Foster 218), alveolar plug with tectum-like structure overlying most of alveolar material, $\times 1330$. — 42. *Belliolum crassifolium* (Balansa 582), alveolar material homogeneous, $\times 350$.