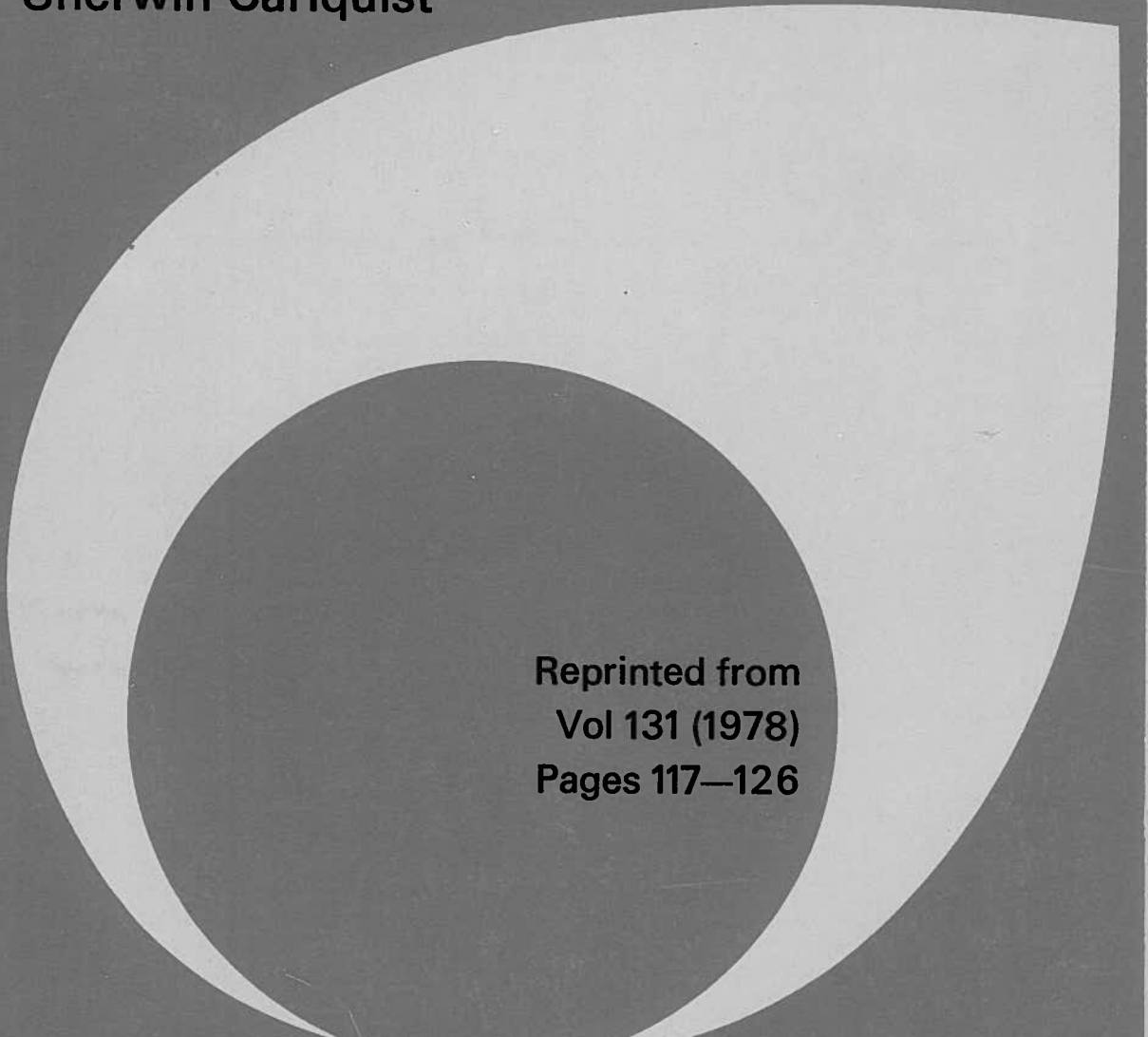


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**Vegetative anatomy and systematics  
of Grubbiaceae**  
Sherwin Carlquist



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# Vegetative anatomy and systematics of Grubbiaceae

Sherwin Carlquist

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*Grubbia* nodes are trilacunar. Leaves have recurved margins, upper epidermis with thick cuticle or a cutinized thick wall, a single layer of palisade (including strands of crystal-bearing cells), 3–5 layers of spongy tissue, and a lower epidermis bearing anomocytic stomata and numerous non-glandular unicellular trichomes. Expression of these cell types varies among the three species and their subspecific entities, and shows close correspondence to the taxonomic system. Only a single genus should be recognized. No species or species-group has unique anatomical features. Foliar and nodal anatomy offer only a small amount of information on systematic position of Grubbiaceae, but could be construed as supporting a "rosoid" affinity.

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The three species of the South African family Grubbiaceae have what could be termed *Erica*-like leaves. This leaf form is widespread in the various groups of dicotyledons in the fynbos vegetation of Cape Province. Because *Erica*-like leaves have evolved numerous times independently, their anatomy presents a conformation of considerable ecological significance. Although *Erica*-like leaves have received attention on various occasions, each example studied offers potential information on this phenomenon. The parallelisms involved in this leaf form must also be understood in order that true phylogenetic relationships can be discerned.

Wood anatomy of Grubbiaceae has been summarized earlier (Carlquist 1977 a). Do aspects of vegetative anatomy other than wood offer data useful in deciding the phylogenetic position of Grubbiaceae? Van Tieghem's (1897) data are suggestive, but incomplete. Fagerlind (1947) has devoted a paper to the probable affinities of Grubbiaceae, but his conclusion that the family is ericalean does not seem strongly supported. Although data from vegetative anatomy may not be decisive by themselves, they may favor some interpretations more than others.

Leaf anatomy in dicotyledons often shows variations corresponding to the taxonomy of particular groups. That this is true within Grubbiaceae is therefore not surprising. Van Tieghem (1897) demonstrated anatomical differences between the two species of *Grubbia* he studied. There is now a total of three species incorporating six subspecific taxa within the genus (Carlquist 1977 a). All of the data accumulated on leaf anatomy of Grubbiaceae thus far are the work of Solereder (1908) and Van Tieghem (1897). Metcalfe & Chalk (1950) summarize this data.

## Material and methods

Liquid-preserved material was available for typical *Grubbia rosmarinifolia* Berg. (Carlquist 4707, 4962), *G. rourkei* Carlquist (Carlquist 5115), and *G. tomentosa* (Thunb.) Harms (Carlquist 5010, 5068). Fixed material was prepared using formalin-acetic-alcohol. Voucher specimens are located in RSA, NBG, and other herbaria. Portions of herbarium specimens of other taxa proved suitable for anatomical study: *G. rosmarinifolia* subsp. *gracilis* (Salter) Carlquist (Lewis 1321, SAM); *G. rosmarinifolia* subsp. *hirsuta* E. Mey. ex A. DC.) Carlquist (Compton 20986, NBG); and *G. rosmarinifolia* subsp. *rosmarinifolia* var. *pinifolia* (Sonder) Carlquist (Stokoe 60060, SAM). I am grateful to Dr John Rourke, Curator of the Compton Herbarium, Kirstenbosch, for this material. Herbarium

material portions were expanded in warm 2.5 per cent NaOH, partly clearing the stems, petioles, and leaves. When fully expanded, leaves and stems were subjected to changes of water and stored in 50 per cent ethyl alcohol.

Both fixed material and treated herbarium material were infiltrated with paraffin, sectioned, and stained according to frequently-used techniques in a safranin-fast green series. Transsections, longitudinal (parasagittal) and paradermal sections of leaves were prepared. Transsections of petioles and serial transsections of nodal regions of stems were obtained. Microtechnical tasks were performed by Dr Larry DeBuhr.

The taxonomic concepts developed earlier (Carlquist 1977 a) guided selection of material. The use of liquid-preserved specimens permitted me to judge whether sections of the treated herbarium specimens were both qualitatively and quantitatively comparable to those of liquid-preserved material. In fact, the two kinds of material proved identical except for protoplasts, so that all comparisons are, in fact, quite reliable.

### Leaf

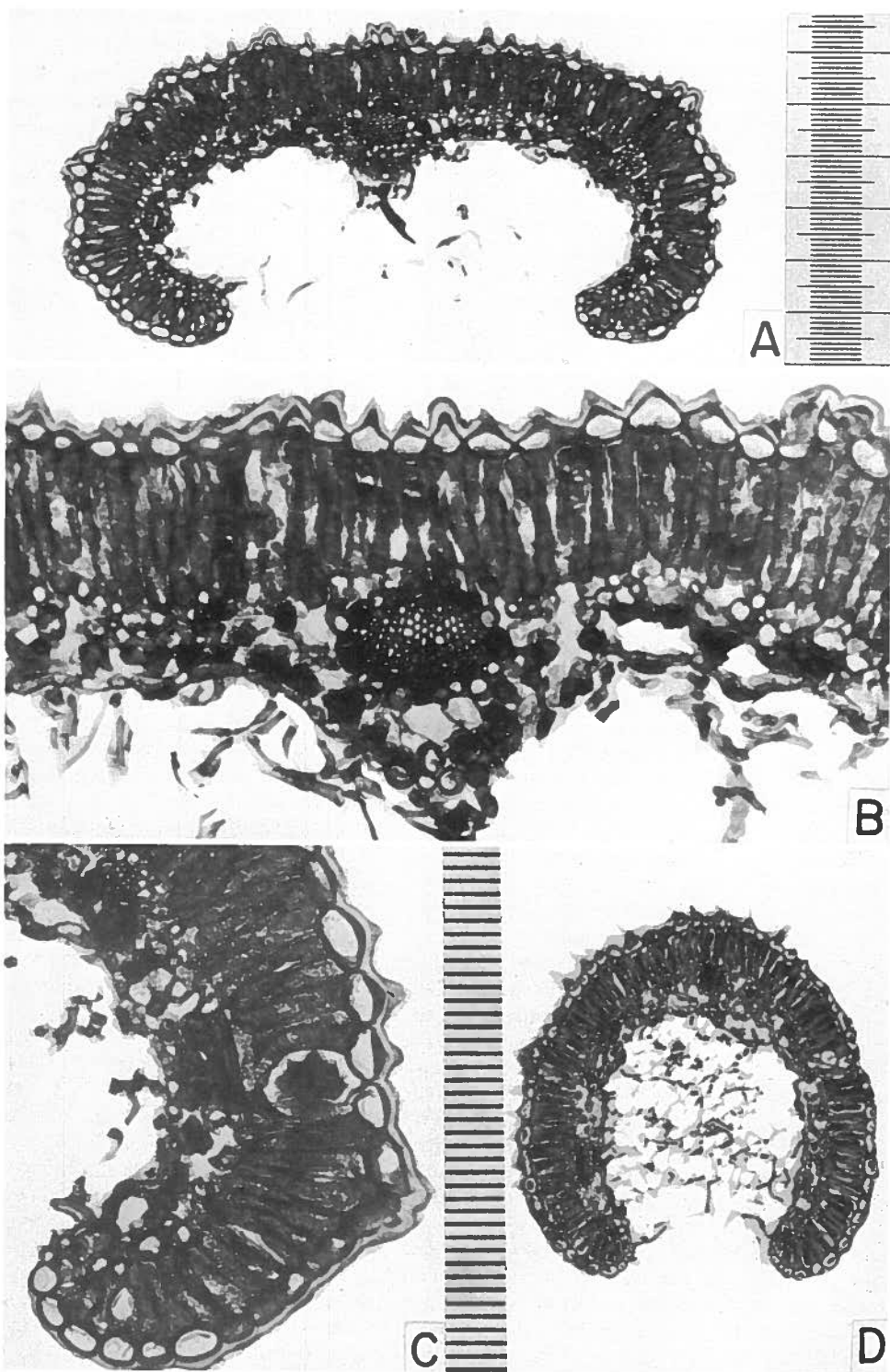
In transsection, all *Grubbia* leaves can be said to have recurved margins (Figs. 1 A, C, D, 2 A, 4 A, B). Cells of the upper epidermis are much larger than those of the lower epidermis. All trichomes are non-glandular and unicellular. They are borne most abundantly on lower leaf surfaces (Figs. 1 B, C, 2 C, 4 A, B). All stomata occur on abaxial leaf surfaces, intermingled with trichomes. Guard cells have very thick cutinized walls, with the lumen constricted, slit-like as seen in sectional view, parallel to the leaf surface. Subsidiary cells are not present (Fig. 2 B). Subsidiary cells may appear to be present in paradermal sections. However, such cells prove to be outwardly-bent epidermal cells supporting the guard-cell pair (Fig. 3 C, upper left), and these epidermal cells do not differ from other epidermal cells in any way that would distinguish them as subsidiary cells. Cells of both the upper and the lower epidermis are polygonal as seen in face view. A single layer of palisade chlorenchyma cells, often exceptionally long and slender, is present beneath the adaxial epidermis (Figs. 1 B, C, 2 C, 3 A, 4 A, B).

Strands of two to four cells, each containing a druse or a rhomboidal crystal, are formed idiosyncratically in the palisade layer. These crystaliferous cells are much wider than chlorenchymatic palisade cells. Depending on the species, a minimum of two to five layers of spongy tissue occur abaxial to the palisade; more numerous layers occur where veins are present. Seven or more veins (including veinlets) are present in a lamina. Of these, the largest may have fibers near the xylem pole, or both xylem and phloem poles of several veins may be associated with fibers. Tannin deposits are present in large quantities in palisade cells, but to a lesser extent also in other cells, especially those near veins (Fig. 1 B, 2 C, 3 A). Modal variations characterizing particular taxa are given below.

*Grubbia rosmarinifolia* subsp. *gracilis* (Fig. 1 D). About seven small veins are present in the lamina as seen in transsection. The midvein is not associated with an externally prominent midrib. A few fibers were observed near the xylem of the midvein; no fibers were seen in other veins. The leaf margin is not notably recurved; instead, the entire leaf responds to desiccation by curvature of the whole lamina (Fig. 1 D), thereby resembling a single-pocketed type rather than a double-pocketed leaf (e.g., *G. rourkei*, Fig. 2 A). Strands of druse-bearing cells in the palisade consist of two, mostly three cells. Three spongy layers typically present. The leaves studied had laminae about 1.25 mm wide. The outer wall of adaxial epidermal cells was about 10  $\mu\text{m}$  thick, of which about 5  $\mu\text{m}$  was epidermal wall proper and 5  $\mu\text{m}$  was the superposed cuticle. The papillate shape of cells of the adaxial epidermis is related to the presence of very short, sparsely distributed trichomes. Trichomes on the abaxial epidermis slender and thick-walled as in subsp. *rosmarinifolia*.

*Grubbia rosmarinifolia* subsp. *hirsuta* (Fig. 4 C). Numerous veins present in lamina as seen in transsection. Midvein not associated with a pro-

Fig. 1. *Grubbia rosmarinifolia*, leaf sections. – A–C: subsp. *rosmarinifolia*, Carlquist 4707. – A: TS of lamina, showing recurved margins. – B: Portion of lamina including midrib; papillate nature of adaxial epidermis cells is evident. – C: Margin of lamina, adaxial surface to the right; a druse is visible in an enlarged cell in the palisade layer. – D: subsp. *gracilis*, Lewis 1321. TS of lamina. – The photomicrographs have been enlarged at the same scales as applicable photomicrographs of stage micrometer scale. A, D, scale to the right of A (finest division 10  $\mu\text{m}$ ). B, C, scale to the right of C (divisions 10  $\mu\text{m}$ ).



minent midrib. Fibers are associated with xylem of all veins, especially abundant on the adaxial side of the midvein. Leaf margins are recurved as in typical *G. rosmarinifolia*. Strands of druse-bearing cells in the palisade consist of two to four, but mostly three cells. Four layers of spongy chlorenchyma are typically present. The leaves studied had a lamina width of approximately 1.85 mm. Thickness of the outer wall of the adaxial epidermis is about 23  $\mu\text{m}$ , of which 5  $\mu\text{m}$  was the wall proper and 18  $\mu\text{m}$  the superposed cuticle. Trichomes on the adaxial surface related to papillate epidermal cell shape. These trichomes are very thick-walled (Fig. 4 C); the wall does not seem cutinized or lignified in its staining reactions. Trichomes on the adaxial surface much more slender, gradually tapered from the widened base (as in subsp. *rosmarinifolia*); trichome base narrowed appreciably where it is inserted into the epidermis.

*Grubbia rosmarinifolia* subsp. *rosmarinifolia* var. *rosmarinifolia* (Fig. 1 A-C). Numerous veins present in lamina as seen in transection although only three of these are major veins (Fig. 1 A, C). Fibers adjacent to xylem and phloem poles of the midvein and some other veins. A distinct midrib, with papillate epidermal cells like those of the adaxial epidermis, present abaxial to the midvein. Leaf margins are recurved, forming a pocket subdivided into two channels by the midrib (Fig. 1 A). Strands of druse-bearing cells in the palisade layer composed of one to three, but mostly a pair of cells. Both druses and simple rhomboidal crystals may be observed in these cells; druses are not highly complex, but appear to be formed from the union of a few rhomboidal crystals. An appreciable number of druse-containing cells, not subdivided in any way, occur idioblastically in the spongy tissue as well. Three spongy layers typically occur on the abaxial side of the leaf. Leaves studied were 2.0-2.5 mm wide. The thickness of the outer wall of the adaxial epidermis was about 23  $\mu\text{m}$ , of which about 5  $\mu\text{m}$  was comprised by the wall proper, and about 18  $\mu\text{m}$  by the superposed cuticle. Trichomes on the adaxial epidermis are short and sparse, and are related to the papillate shape of epidermal cells. Trichomes on the abaxial surface are narrow, moderately thin to notably thick-walled; these trichomes are tapered from a widened

base. The base abruptly narrows into the peg-like constricted end inserted into the epidermis.

*Grubbia rosmarinifolia* subsp. *rosmarinifolia* var. *pinifolia*. Leaves of this variety are like those of var. *rosmarinifolia* except in the following respects. Cells of the adaxial epidermis not notably papillate, a fact probably related to the lack of hairs on this epidermis. Thickness of the outer wall of the adaxial epidermis was about 14  $\mu\text{m}$ , of which about 4  $\mu\text{m}$  was comprised by the wall proper, and about 10  $\mu\text{m}$  by the superposed cuticle. The leaf studied was about 2.0 mm wide.

*Grubbia rourkei* (Fig. 2). Numerous veins, mostly minor, present in the lamina as seen in transection. A few fibers observed adjacent to the xylem and phloem poles of the midvein (Fig. 2 C), but not near other veins. A midrib clearly differentiated on the abaxial side of the leaf (Fig. 2 C), with large epidermal cells like those of the adaxial epidermis. Leaf margins more markedly recurved than in other species, forming two pockets each of which is densely filled with trichomes (Fig. 2 A, C). Strands of crystal-bearing cells in the palisade are composed of one to three, but mostly two cells. Crystals in these cells mostly rhomboidal; a few druses can be said to be present by aggregation of two or three crystals per cell. Four spongy layers typically occur abaxial to this palisade. The leaf studied had a width of 2.2 mm. Thickness of the outer wall of the adaxial epidermal cells was about 14  $\mu\text{m}$ , of which 7  $\mu\text{m}$  was composed of the wall proper and 7  $\mu\text{m}$  of the superposed cuticle. The upper epidermis of this species is highly distinctive (Fig. 2 C). Cells, often in pairs, are elongate as seen in sectional view, forming emergences three-dimensionally. The cuticle is separated from epidermal walls in the valleys formed between pairs of epidermal cells. This separation is undoubtedly related to a subcuticular accumulation of a varnish-like substance which gives leaves a white or sordid-white color when fresh (yellowish in dried specimens). Subcuticular accumulation of such a substance is rather like the subcuticular accumulation of oils and oleoresins in glandular trichomes of various dicotyledons. The epidermis of *G. rourkei* is connected to the palisade by peg-like or arm-like extensions (Fig. 2 C). No epidermal cells are appressed directly to palisade cells. Trichomes

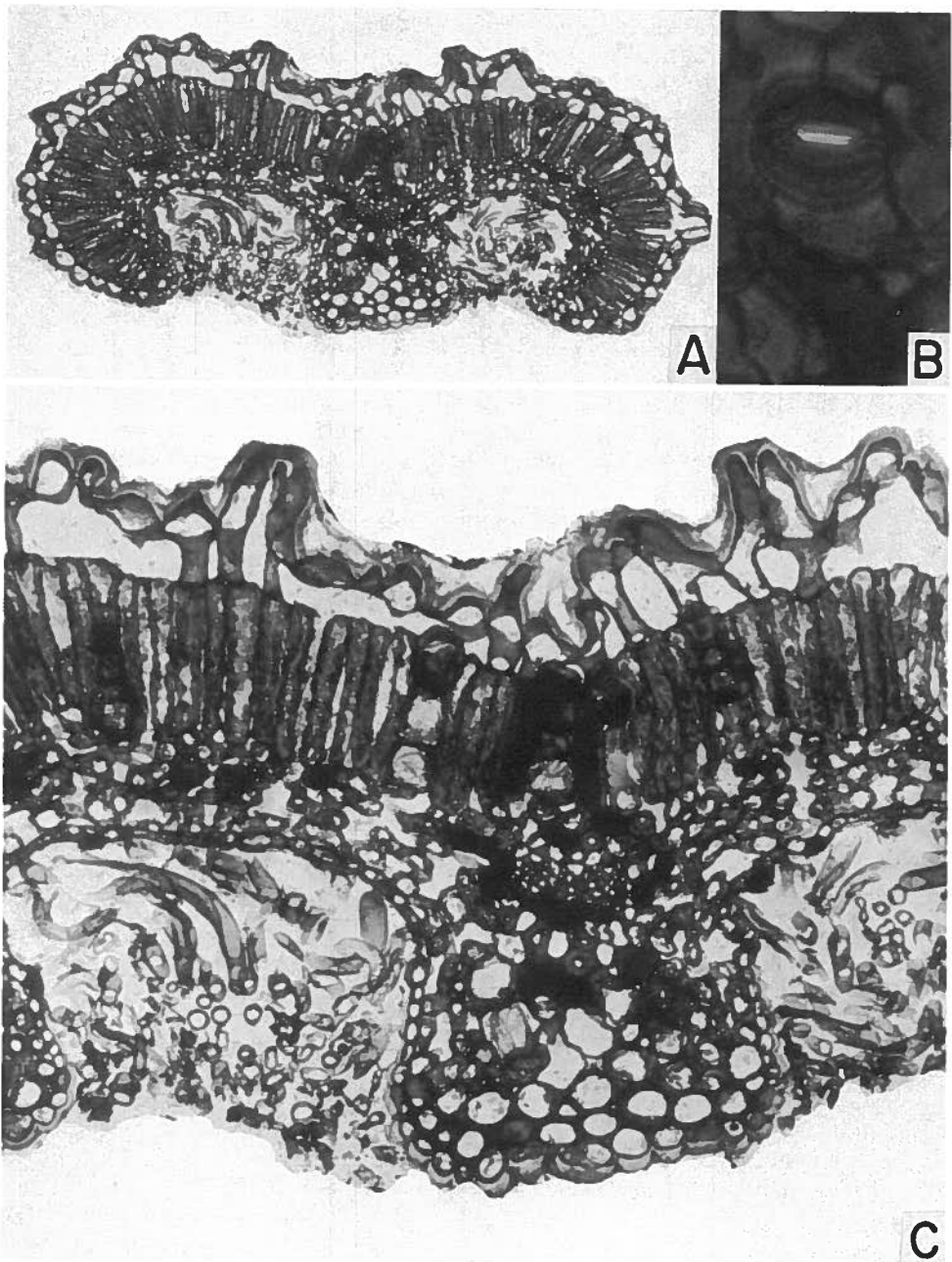


Fig. 2. *Grubbia rourkei*, Carlquist 5115, leaf sections. - A: TS of entire lamina, showing markedly recurved margins. - B: Stoma and adjacent epidermal cells, from paradermal section. - C: TS, central portion of lamina, showing midrib. - A, magnification as in Fig. 1 A. B, magnification as in Fig. 3 C. C, magnification as in Fig. 1 C.



on the abaxial surface are wide, but narrower than those in *G. tomentosa*. They are markedly widened or vesicular from a peg-like base inserted in the epidermis, then gradually tapered to the tip.

*Grubbia tomentosa* (Figs. 3, 4 A, B). Numerous veins present in the lamina, which is wider than that in other species (Fig. 4 A, B). Midvein much larger than other veins (Fig. 3 A). Midvein, if large, may have two portions (Fig. 3 A). The abaxial collateral bundle of the midvein is normal in orientation. The smaller adaxial bundle, perhaps derived from an adaxial meristem, is inverted in orientation. Fibers are present near xylem and phloem of major veins, and are moderately abundant. The midrib (Fig. 3 A) is well differentiated, and epidermal cells of the abaxial epidermis of the midrib bear thick walls like those of the adaxial epidermis. Leaf margins are recurved (Fig. 4 A, B), but the lamina is too broad for the formation of a distinct pocket or channel. Crystal-bearing cells occur in strands of two to four cells in the palisade (Fig. 4 B). Crystals in these cells are mostly rhomboidal, but a few simple druses, composed of two or several rhomboidal crystals, are present. Four or five spongy layers occur. Leaves studied had widths of 6.5 mm and 3.8 mm, respectively. The outer wall of the adaxial epidermal cells is cutinized, and no discrete cuticle overlying the wall proper is present. This wall is 32  $\mu\text{m}$  and 21  $\mu\text{m}$  thick in the two leaves mentioned, respectively. Trichomes are virtually absent on the adaxial surface. Cells of the adaxial epidermis are, in places, connected with the palisade by limited wall portions, but not by marked arm-like extensions as in *G. rourkei*. The trichomes on the abaxial epidermis are wide, moderately thick-walled, and moderately dense. The trichomes have a narrow peg-like base (Fig. 3 B), inserted into the epidermis, above which the trichome flares, then tapers gradually toward its apex.

### Petiole

Petioles of the three species of *Grubbia* conform to the same basic vascular plan. Three traces (a midvein and two laterals) occur almost the length of the petiole. In the upper portion of the petiole, the three fuse just prior to departure of the first secondaries. Ground tissue of petioles contains idioblastic crystal-bearing cells: druses in *G. rosmarinifolia*; less complex druses and solitary rhomboidal crystals in *G. rourkei*; solitary rhomboidal crystals in *G. tomentosa*. The midvein in petioles of *G. rourkei* and *G. tomentosa* is hemiamphicribal. This conformation extends in the midvein where lamina is present, as in *G. tomentosa*, Fig. 3 A. The epidermal cells in all species of *Grubbia* are firmly adherent to the cells of the petiolar ground tissue, which are circular in transection. This contrasts with the adaxial leaf epidermis in *G. tomentosa* and especially *G. rourkei*. Epidermal cells in petioles are, for each species, very like those illustrated for the lamina in these respective species. There are no separations between the cuticle and epidermal cells in petioles, nor is there any chlorenchyma.

### Node

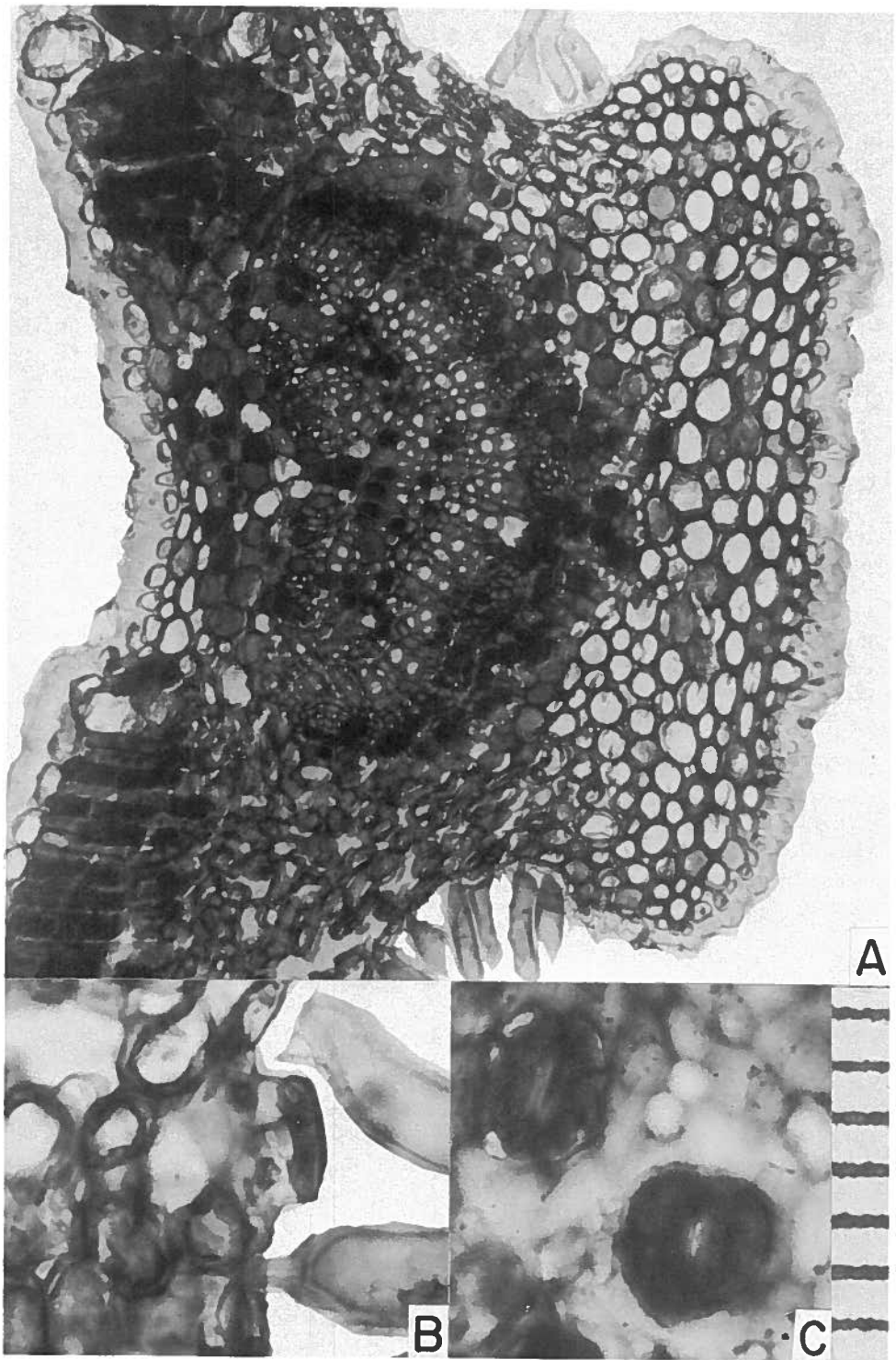
All three species of *Grubbia* have trilacunar nodes. The laterals traverse the sheath formed by the petiolar bases (see Carlquist 1977 a). Leaves are opposite in all species of *Grubbia*. The adjacent laterals join below the node, a familiar pattern in trilacunar nodes with opposite leaves. Thus four vein departures occur at each node: two supplying midveins; two supplying, by branching as one follows them upward, the four lateral veins in the two petioles.

### Stem

Solereder (1908) claimed a difference between hypodermis and cortical cells in *G. rosmarinifolia*, but no such cortical differentiation in stems of *G. tomentosa*. My material showed a tannin-filled hypodermis, consisting of relatively

Fig. 3. *Grubbia tomentosa*, Carlquist 5010, leaf sections. - A: TS of midrib region, adaxial face to the left. - B: TS of lamina portion, showing raised guard cells and amphora-shaped bases of trichomes. - C: Stomata and adjacent epidermal cells, from a paradermal section. - A, magnification as in Fig. 1 C. B, C, scale to the right of C (divisions 10  $\mu\text{m}$ ).





small, thin-walled cells, in *G. rosmarinifolia* and in *G. rourkei*. Epidermal cells of stems in these species also were filled with tannins. The stems of *G. tomentosa* showed no hypodermal differentiation. Solereder (1908) also claimed presence of separate strands of "pericyclic" fibers in stems of *G. rosmarinifolia*, but presence of a continuous sheath of fibers in stems of *G. tomentosa*. My material showed a discontinuous sheath of fibers in stems of all three species. The alleged contrast could probably be obtained by selection of stems from these three species, however, for some sections show large gaps, some show small gaps in the fiber sheath in any of the species. As noted by Solereder, pith cells have moderately thick lignified walls. The cells are circular in outline, with relatively angular intercellular spaces. Tannins are abundant in some pith cells. Scattered cortical cells contain druses in *G. rosmarinifolia*, solitary rhomboidal crystals in *G. rourkei* and *G. tomentosa*. The cuticle thickness and trichome characteristics described for leaves of the three species apply to the epidermis of stems also (epidermal cells like those of adaxial leaf epidermis, trichomes like those of abaxial leaf epidermis).

#### Systematic correlations within Grubbiaceae

Foliar anatomy corresponds closely to the system I proposed earlier for Grubbiaceae (Carlquist 1977 a). The division between the two sections is validated. One cannot say that there are any anatomical structures present in *G. rosmarinifolia*, type species of the genus, which are not also present in the two species of section *Strobilocarpus*, *G. rourkei* and *G. tomentosa*. Rather, there are differences in expression of characters (e.g., thick-walled trichomes vs. thin-walled trichomes). This situation does not suggest that two genera should be recognized.

Leaf anatomy of *G. rourkei* places it close to *G. tomentosa*, but with some notable differences. The narrower leaves of *G. rourkei* form pockets on the abaxial surface, corresponding to the *Erica*-like leaf form, much more clearly than do the broader leaves of *G. tomentosa*. These pockets can function in forming zones for attenuating the gradient of humidity from transpiring leaf surfaces to the open air. Attenuation of this gradient is indeed suggested by the dense

felt of trichomes, a denser accumulation than in other species of *Grubbia*. The trichomes are thinner walled than those of *G. tomentosa* and not lignified. The adaxial epidermis of *G. rourkei* is connected to the subtending palisade by arm-like connections of the epidermal cells. These connections are much more differentiated than in *G. tomentosa*, where the epidermal cells may have limited interfaces with palisade cells, but no attenuations into arms. The outer wall of epidermal cells in *G. rourkei* is differentiated into a cuticle, loose from the epidermal wall it overlies. Spaces between the cuticle and wall accumulate varnish-like materials. In *G. tomentosa*, the epidermal wall is cutinized, but no differentiation into a wall proper and overlying cuticle occurs.

Leaves of *G. rosmarinifolia* differ from those of *G. tomentosa* by possessing the following features: midrib not differentiated; crystals in palisade are druses rather than solitary rhomboidal crystals; cells of the adaxial epidermis with moderately thin cell wall and cuticle, cells papillate; trichomes on abaxial leaf surface slender, thick-walled, not widening out markedly from the narrow base, curved rather than straight; usually three, rather than four or five, spongy layers present.

The three subspecies of *G. rosmarinifolia* may be differentiated by virtue of foliar anatomy. Leaves of *G. rosmarinifolia* subsp. *gracilis* lack marked recurvature of margins and have only about seven veins, as seen in transection. Leaves of *G. rosmarinifolia* subsp. *hirsuta* have numerous straight hairs, which have thick non-lignified walls, on the adaxial surface. Leaves of *G. rosmarinifolia* subsp. *rosmarinifolia* have recurved margins, numerous veins as seen in transection, and, on the adaxial surface of the leaf, very sparse, short, straight, non-glandular trichomes. Papillate shape of adaxial epidermal cells is related to the fact that these cells may bear hairs in *G. rosmarinifolia* subsp. *rosmarinifolia*. Within this subspecies, var. *pinifolia* tends to have fewer trichomes on the adaxial surface and accordingly few papillate epidermal cells.

#### Systematic position of Grubbiaceae

Solereder (1908) has refuted, on anatomical bases, the classical idea that Grubbiaceae should be allied to Santalaceae. Nevertheless, that idea

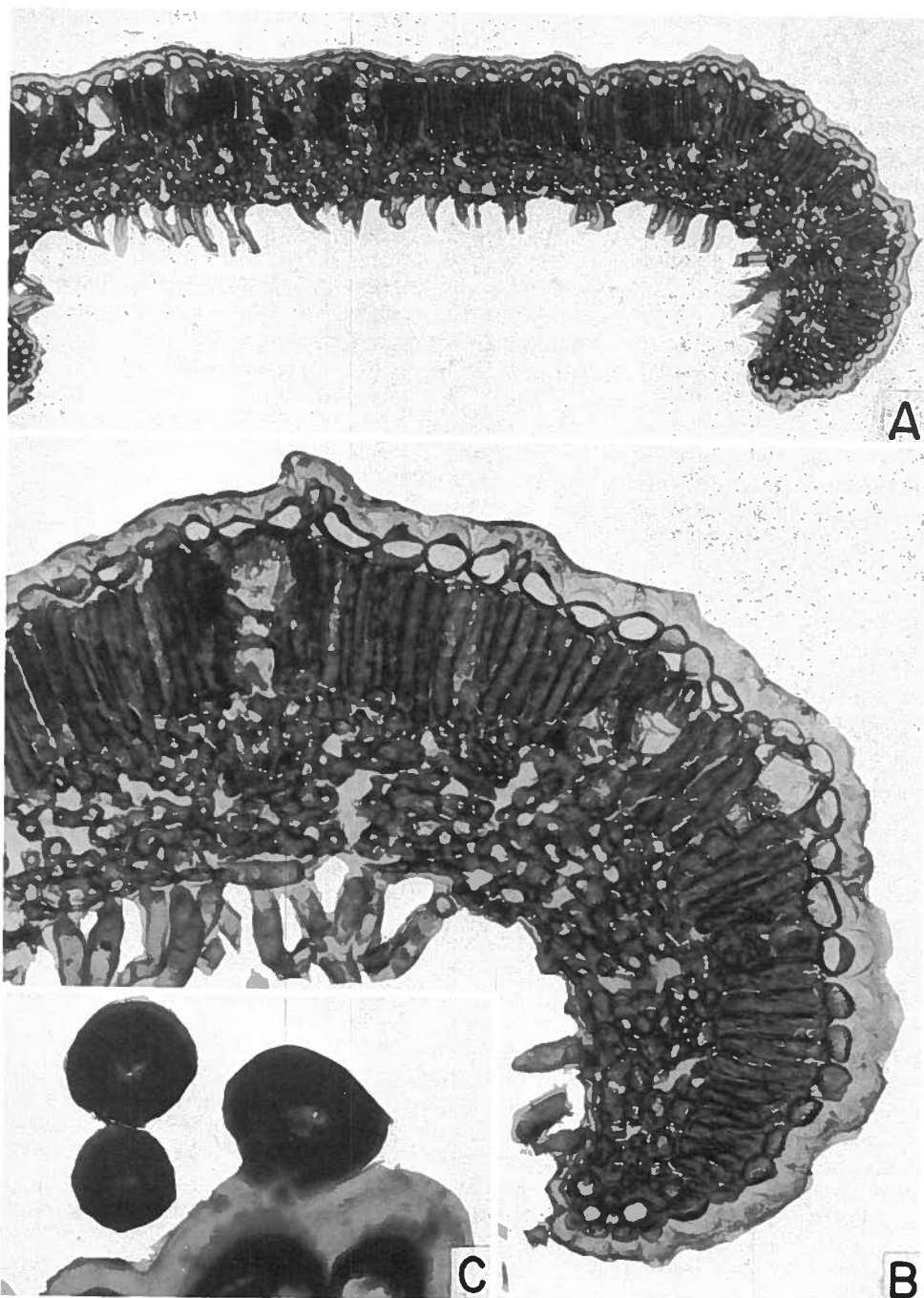


Fig. 4. *Grubbia*, leaf sections. - A, B: *G. tomentosa*, Carlquist 5010. - A: Lamina, margin at right, midrib portion at extreme left. - B: Margin region enlarged; rhomboidal crystals visible in large cells of palisade region. - C: *G. rosmarinifolia* subsp. *hirsuta*, Compton 20986. Portion of adaxial epidermis from TS of leaf. Hispid trichomes show as dark circles. - A, magnification as in Fig. 1 A. B, magnification as in Fig. 1 C. C, magnification as in Fig. 3 C.

still persists (see Carlquist 1977 b for a resumé). The idea that Grubbiaceae have affinities with Ericaceae, offered by Fagerlind (1948), does not seem strongly supported at present. For example, Ericaceae have unilacunar nodes, whereas those of Grubbiaceae are trilacunar. One characteristic does not decide the relationship of a family of dicotyledons, however. The most viable proposition appears to be the rosoid position suggested in a general way by Van Tieghem (1897), and in more specific ways by such recent authors as Thorne (1968, 1976). Such "rosoid" families as Pittosporaceae, Escalloniaceae, and Grossulariaceae agree with Grubbiaceae in such vegetative features as trilacunar nodes, the occurrence of crystals in leaves, and the presence of non-glandular trichomes on leaves. The literature on phylogenetic placement of Grubbiaceae has been reviewed earlier (Carlquist 1977 b). Before more secure concepts can be presented, data from floral anatomy, ovule morphology, embryology, seed anatomy, and pollen structure must be studied.

#### Ecological implications of leaf anatomy

The *Erica*-like leaf in *Grubbia* is an adaptation to xeromorphy according to Marloth (1913). Marloth mentions that relative humidity can fall as low as 25% in *Grubbia* localities, thereby providing a reason for foliar xeromorphy in plants which grow in wet soils, as does *Grubbia rosmarinifolia* typically. A drop in relative humidity is probably less important per se than the winds which occur so markedly in montane Cape Province. In the above account, the term "ericoid" is deliberately avoided. A mystique has developed concerning the definition of "ericoid" leaves. These definitions may be regarded as a mystique because particular morphological criteria are used as a source of definition, not the function of the ericoid leaves. Thus, leaves with somewhat different morphology but essentially the same general shape and function may be regarded as "ericoid" or "non-ericoid" under that scheme. The term "*Erica*-like" is used above to denote a foliar structure which has the effect of (1) condensa-

tion in size and shape to achieve lowered transpiration; (2) comparatively dense chlorenchyma appropriate to sunny localities with low soil moisture, low humidity, or both, for periods of various duration; (3) attenuation of a moisture gradient from the stomatal-bearing surface of leaf to the exterior, through pockets, hairs, or other devices. *Erica*-like may be used to connote one morphological feature, a tendency toward a linear shape. Wider leaves might be expected, if they grow in the same type of environment, to have some compensatory features. Within the genus *Grubbia*, there is a very rough correlation, subject to exceptions. The leaves of *G. tomentosa* are wider than those of other species, but their epidermal walls are very thick; there is no cuticle, but the entire thickness of the wall is cutinized.

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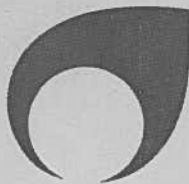
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## Key to the species of *Bobartia*

1. Inflorescence lax, paniculate. Stem subterete, leaves flat ..... 2
- Inflorescence dense, more or less capitate. Stem and leaves externally very similar ..... 3
2. Flowers mauve ..... 15. *B. lilacina*
- Flowers yellow ..... 14. *B. paniculata*



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