A SURVEY OF PHLYCTIDOCARPA (UMBELLIFERAE) USING THE LIGHT AND SCANNING ELECTRON MICROSCOPE

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ABSTRACT. A detailed description of the morphology and anatomy of *Phlyctidocarpa* is provided as a supplement to the original description, and as a source of further data for the discussion of the relationships of this little-known and remarkable monotypic genus.

One of the more interesting taxa to be recognized within the Umbelliferae recently has been the new genus, *Phlyctidocarpa*, from South West Africa. This monotypic taxon was brought to the attention of one of us (J.F.M.C.) by Mr W. Marais, then of the South African National Herbarium, Pretoria, and was described by both of us (Cannon & Theobald, 1967) upon securing sufficient material from this region through Professor H. Merxmüller, München. The material was recognized as unique and worthy of generic recognition on the basis of the very unusual fruits which are covered with distinct rows of large, clavate vesicles. From what little ecological data we have it appears that this species is adapted to seasonally xeric habitats in the northwestern part of South West Africa with the fruit vesicles probably representing an adaptive feature for either water or wind dispersal. Within the Flora of South West Africa (Schreiber, 1967), however, there are no apparent close relatives and any relationship that may have existed to taxa in adjacent regions was not apparent at the time of the initiation of this study. We noted in our earlier paper a possible relationship with *Rhyticarpus* from southern Africa, but this was rather tenuous. At that time an apparent disposition within the subfamily Apioideae—tribe Ammineae—subtribe Carineae was postulated. However, much of this was based on a rather superficial survey of gross anatomy and morphology of the fruit. In order to clearly determine its relationships a detailed investigation using light and scanning electron microscopes was undertaken. We now have a much clearer understanding of *Phlyctidocarpa* and its possible relationships, but there is evidently a need for further studies of this nature within the Umbelliferae.

MATERIAL AND METHODS

Samples of different parts of the plant were examined and obtained from the collections of *Giess*, *Volk*, & *Bleissner* 6075 (Holotype, M; Farm Eldorado, Outjo District, South West Africa, 28 iii 1963) and *Winter* & *Leistner* 5739 (Paratype, PRE; Orupembe waterhole, Kaokoveld, South West Africa, 5 v 1957). Selection was made carefully and kept to an absolute minimum because of the scarcity and importance of this material. For light microscope study the material was "revived" by boiling it in water

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for 15–30 minutes, cooling, and then transferring to FAA until needed. Subsequent treatment included clearing in a 2.5 per cent NaOH solution for 24 hours, washing in several changes of water, and then immersion for 15–30 minutes in a dilute solution of a commercial hypochlorite solution "Chlorox". After this series of steps the material was again washed in water and then passed through an ethyl alcohol series of 30 and 50 per cent alcohol with the material remaining in each for several hours. It was then transferred to a tertiary butyl alcohol series prior to infiltration with paraffin and sectioning on a rotary microtome as outlined by Jensen (1962). In several instances the material was found to be exceptionally good and equivalent to fresh material. This we attribute to good fortune.

Material for the scanning electron microscope portion of this study was removed from the specimen sheets and taken to a commercial concern (Applied Space Products, 1786 West Lincoln Avenue, Anaheim, California, U.S.A.), where the material was properly gold-coated prior to examination on a Jelco Scanning Electron Microscope. Photos and negatives were prepared simultaneously through the use of 4X5 Polaroid Type 55 P/N film. Contact prints of some of these pictures will be described in the following detailed notes on *Phlyctidocarpa*.

Leaf, stem, and inflorescence

Morphology

Leaves ternately-pinnatisect (Fig. 1a), up to 8 cm long, blade of lower leaves up to 4 cm long, petioles ca. as long, blade of upper leaves usually longer relative to the petiole, ultimate divisions linear-lanceolate, few-toothed, glabrous.

Stems erect, 50-60 cm long, unbranched below.

Umbels compound, 2-4.5 cm in diameter, rays 4–5, 1–3 cm long; bracts 3–4, linear-lanceolate, unequal, 9–12 mm long; umbellets 5-flowered, pedicels capillary, 5–10 mm long; bractlets 2, linear-lanceolate, 2–4 mm long; flowers of terminal compound umbels hermaphrodite, those of lateral compound umbels male.

Leaf Anatomy

Surface of the lamina. *Epidermis* (Fig. 1c): adaxial and abaxial interveinal cells irregular in outline, anticlinal walls sinuous; stomata scattered over both surfaces, much more abundant abaxially, anomocyctic, rarely one of the surrounding cells slightly smaller. *Trichomes*: absent.

Transverse section of lamina (Fig. 1b). *Epidermis*: adaxial and abaxial similar, more or less rectangular, square or periclinally extended, outer wall slightly thicker than inner; stomata more abundant abaxially, at surface. *Mesophyll*: dorsiventral palisade 1-layered; spongy 5–6-layered, cells very small, round to irregular, somewhat loosely arranged; substomatal spaces large. *Vascular bundles*: equidistant from adaxial and abaxial surfaces, bundle sheath parenchymatous, without extensions to adaxial and abaxial epidermis. *Collenchyma and sclerenchyma*: absent. *Secretory canals*: solitary large canal on abaxial side of midrib and larger vascular bundles. *Crystals:* absent.

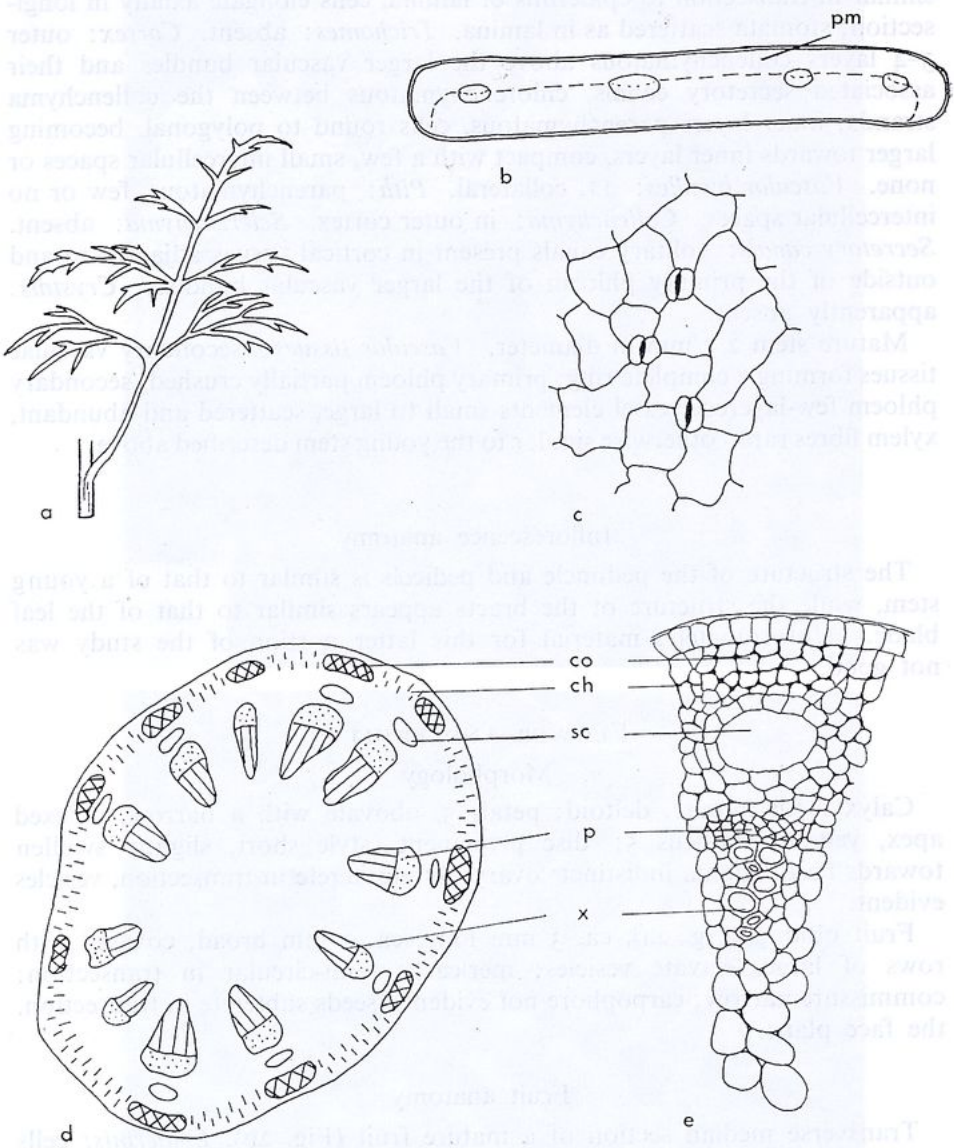

FIG. 1. Vegetative morphology and anatomy of *Phlyctidocarpa flava* Cannon & Theobald: a, leaf (redrawn from Cannon & Theobald, 1967), × 0.6; b, transection (diagrammatic) of lamina, × 50; c, surface view of abaxial stomata, × 350; d, transection (diagrammatic) of stem, × 50; e, transection of portion of stem, × 150. Details: *ch*, chlorenchyma; *co*, collenchyma; *p*, phloem; *pm*, palisade mesophyll; *sc*, secretory canal (vitta); *x*, xylem.

Stem anatomy

Young herbaceous stem 0·8 mm in diameter (Fig. 1d, e). *Epidermis:* similar in transection to epidermis of lamina, cells elongate axially in longi-section; stomata scattered as in lamina. *Trichomes*: absent. *Cortex*: outer 3–4 layers collenchymatous above the larger vascular bundles and their associated secretory canals, chlorenchymatous between the collenchyma strands; inner layers parenchymatous, cells round to polygonal, becoming larger towards inner layers, compact with a few, small intercellular spaces or none. *Vascular bundles*: 11, collateral. *Pith*: parenchymatous, few or no intercellular spaces. *Collenchyma*: in outer cortex. *Sclerenchyma*: absent. *Secretory canals*: solitary canals present in cortical tissues adjacent to and outside of the primary phloem of the larger vascular bundles. *Crystals*: apparently absent.

Mature stem 2·7 mm in diameter. *Vascular tissues*: secondary vascular tissues forming a complete ring; primary phloem partially crushed; secondary phloem few-layered, vessel elements small to large, scattered and abundant, xylem fibres rare; otherwise similar to the young stem described above.

Inflorescence anatomy

The structure of the peduncle and pedicels is similar to that of a young stem, while the structure of the bracts appears similar to that of the leaf blade. Unfortunately, material for this latter portion of the study was not good.

Flower and fruit

Morphology

Calyx teeth minute, deltoid; petals 5, obovate with a narrow, inflexed apex, yellow; stamens 5; disc prominent; style short, slightly swollen towards base; stigma indistinct; ovary oblong, terete in transection, vesicles evident.

Fruit oblong (Fig. 2a), ca. 3 mm long, ca. 2 mm broad, covered with rows of large, clavate vesicles; mericarps semi-circular in transection; commissure narrow; carpophore not evident; seeds subterete in transection, the face plane.

Fruit anatomy

Transverse median section of a mature fruit (Fig. 2b). *Epidermis:* cells rectangular, square to periclinally extended, thin walled; cells on outer, exposed surfaces of vesicles non-papillose, cuticle very thick; cells along sides of vesicles and at base of grooves between the stalks of the vesicles papillose, cuticle thin; papillae narrow, pointed; cells along commissure non-papillose, cuticle thin. *Mesocarp*: cells within vesicles large, very thin-walled, collapsing at maturity; cells within stalk of vesicle parenchymatous, thin-walled, with abundant crystals; cells of body of fruit surrounding seed parenchymatous, 7–8-layered, becoming smaller towards endocarp. *Endocarp*: 1–2-layered, parenchymatous, transversely elongate, darkly staining. *Vascular bundles*: 5 rib bundles in each mericarp, collateral, each associated with two rows of vesicles, carpophore bundles one per mericarp. *Collenchyma and sclerenchyma*:

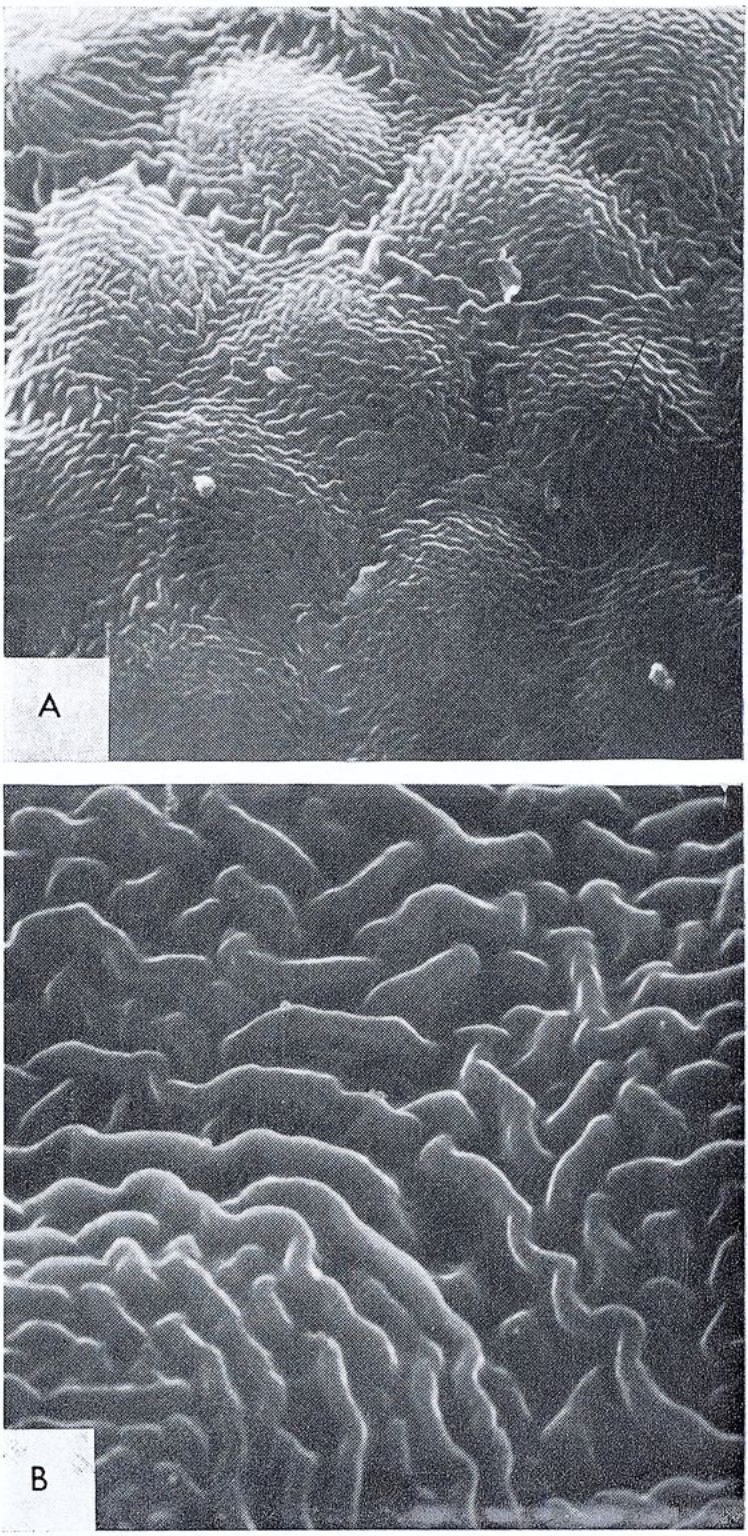

PLATE 2. Scanning electron photomicrographs of the fruit of *Phlyctidocarpa flava* Cannon & Theobald: A, outer exposed surface of fruit vesicle, × 100; B, lateral view of fruit vesicle, × 300.

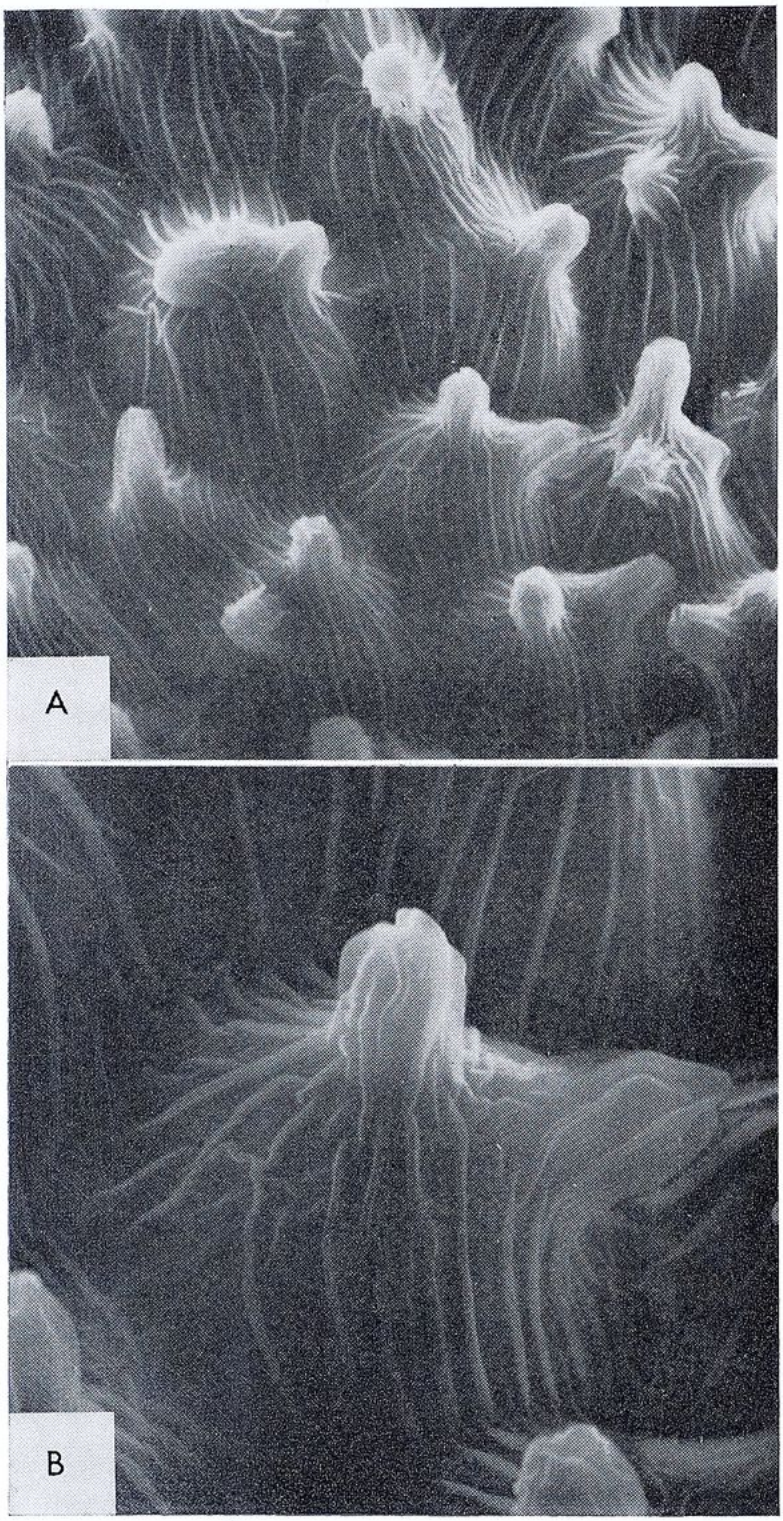

PLATE 3. Scanning electron photomicrographs of outer surface of fruit vesicle of *Phlyctidocarpa flava* Cannon & Theobald: A, × 1,000. B, × 5,000.

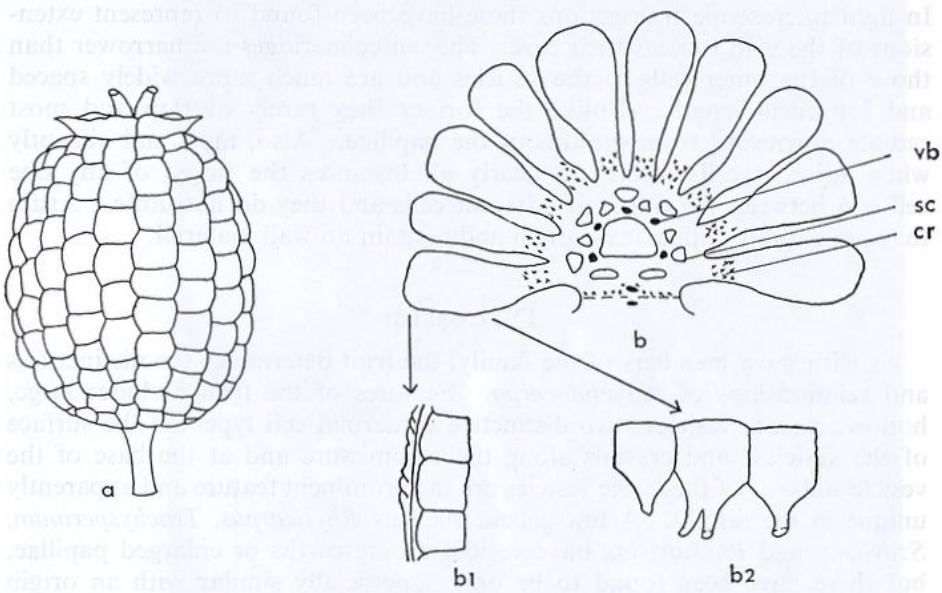

FIG. 2. Fruit morphology and anatomy of *Phlyctidocarpa flava* Cannon & Theobald: a, mature fruit, lateral view (redrawn from Cannon & Theobald, 1967), × 10; b, transection of mature mericarp and epidermal cells (redrawn in part from Cannon & Theobald, 1967), × 22; b1, outer epidermal cells, × 100, b2, lateral epidermal cells, × 100. Details: *cr*, crystal; *sc*, secretory canal (vitta); *vb*, vascular bundle.

absent. *Secretory canals*: 11 per mericarp; 5 large and each associated with, and above, a rib vascular bundle; 4 slightly smaller and intercostal; two along the commissure. *Crystals*: large druses along commissure and in the base of each vesicle stalk. *Commissure*: flat, parenchyma cells collapsing at maturity, carpophore not evident.

SCANNING ELECTRON MICROGRAPHS

As can be seen in Plate 2, A, B, there are distinct differences in the vesicles as seen in surface and lateral views. These differences extend beyond that of the mere presence or absence of papillae as seen under the light microscope. Cells on the exposed outer portions of the vesicles are slightly bulging and polygonal in outline. At the magnification of Plate 2, A only faint evidence is seen of the distinctive cuticular ropy ridges that are clearly evident in Plate 3, A, B. These ridges are generally short in length and appear to intertwine with each other. The ridges between adjacent cells are usually larger, longer and more loosely spaced than those that cover the surface of the cells themselves. From light microscope study it is evident that these ridges are solely cuticular in make-up and include little or no cell wall material.

Epidermal cells on the sides of the vesicle (Plate 4, A, B) are distinctly different in both shape and cuticular pattern. The cells are much more inflated and have one to three distinct papillae projecting from their tops. These papillae are most often paired (Plate 4, B) and in close proximity.

In light microscope transections these have been found to represent extensions of the wall to near their tips. The cuticular ridges are narrower than those of the outer cells of the vesicles and are much more widely spaced and longer in length. Unlike the former they rarely overlap and most radiate downward from the tips of the papillae. Also, most end abruptly when adjacent cells meet. In nearly all instances the ridges of any one cell end between the ridges of adjacent cells and they do not unite. Again they are entirely cuticular in origin and contain no wall material.

Discussion

As with most members of the family, the fruit determines the distinctness and relationships of *Phlyctidocarpa*. Features of the fruit include: large, hollow, clavate vesicles; two distinctive epidermal cell types on the surface of the vesicles; and crystals along the commissure and at the base of the vesicle stalks. Of these, the vesicles are the prominent feature and apparently unique in the family. A few genera such as *Rhyticarpus*, *Trachyspermum*, *Szovitsia*, and *Physotrichia* have vesicular outgrowths or enlarged papillae, but these have been found to be only superficially similar with an origin apparently independent of that of *Phlyctidocarpa* (personal observation, W.L.T.). *Physotrichia* shares a geographic proximity in the Angolan flora in the form of *P. welwitschii*, but differs in habit, gross vegetative morphology, calyx structure, and papillae size and appearance. It also apparently lacks the crystal layers found in *Phlyctidocarpa* as these have not been reported in the literature. These crystal layers and the arrangement of the vittae (oil canals) places *Phlyctidocarpa* in Drude's (1897-98) Ammineae heteroclitae of his subtribe Carinae of the tribe Ammineae (Apieae). It is interesting that the majority of taxa within this group are also South African in origin. The relationship of the crystal arrangement in this group to that found in the Saniculoideae was noted by Drude (1897-98) but its significance is still unclear, although there may be some relationship to possible similar pro-umbelliferous ancestors in the southern hemisphere flora.

Unfortunately little electron microscopy has been done with members of the family aside from the valuable work of Heywood and his associates (1971) dealing with the Caucalideae. As described above, *Phlyctidocarpa* has been found to have an interesting and unusual epidermal pattern as yet unfound in any other member of the family. A broad survey of the Apioideae (Theobald, unpublished) has not revealed any taxa similar to *Phlyctidocarpa*.

Vegetatively *Phlyctidocarpa* does not exhibit any very unusual morphological or anatomical features which set it apart from most apioid umbellifers. For example, the presence of anomocytic stomata agrees with that reported by Metcalfe & Chalk (1950) for a large number of members of the family, including such apioid genera as *Ammi*, *Conium*, *Coriandrum*, *Peucedanum*, *Seseli*, *Laserpitium*, etc. However, Guyot (1971) described the stomata of these, as well as most apioid taxa, as being anisocytic or a more highly evolved derivative thereof. In the case of *Phlyctidocarpa*, however, there is no doubt that it is anomocytic. If Guyot's observations are correct the only similar genera would be *Cicuta*, *Conopodium*, *Heracleum*, and *Thaspia*, which represent a wide range of tribes according to any of the

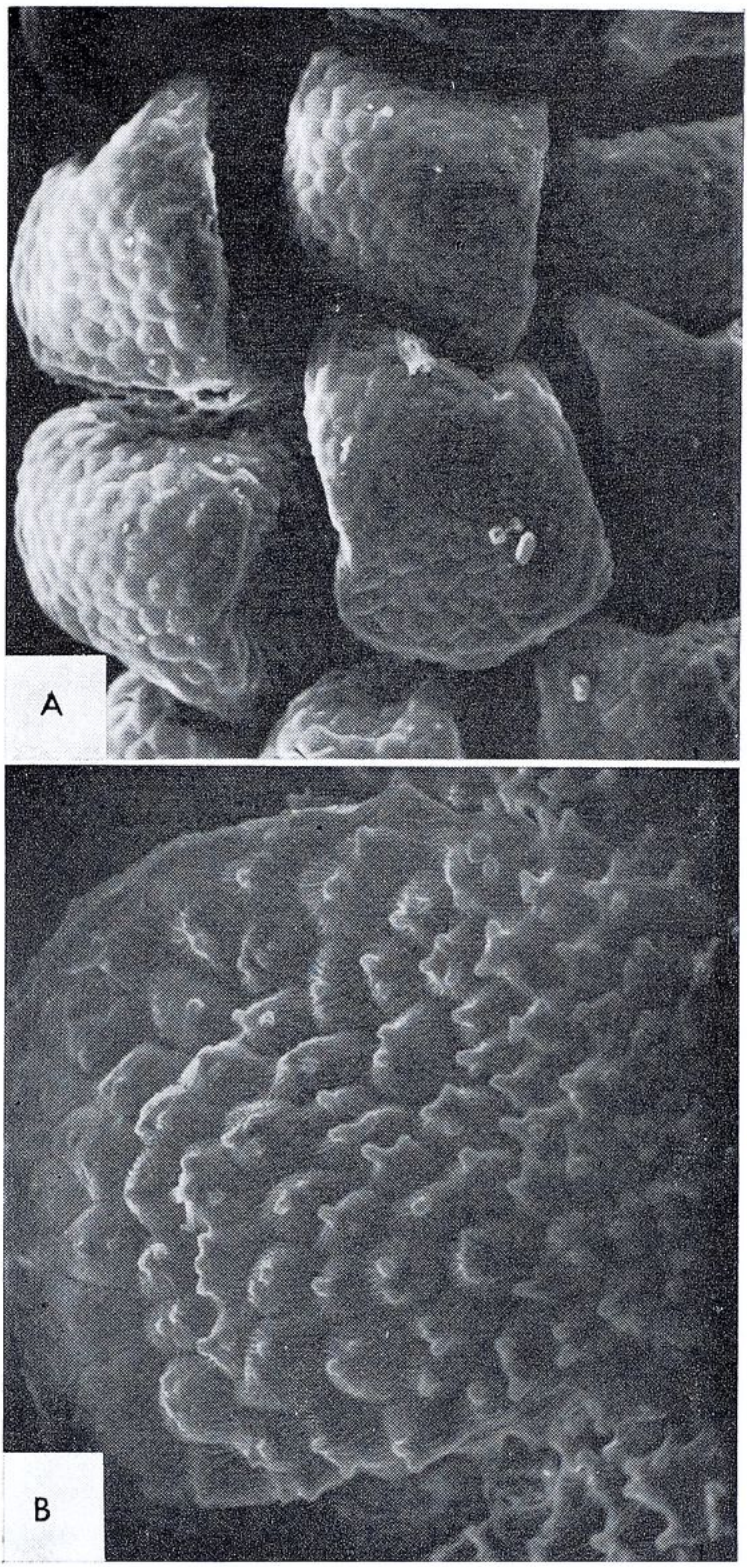

PLATE 4. Scanning electron photomicrographs of lateral surface of fruit vesicle of *Phlyctidocarpa flava* Cannon & Theobald: A, × 1,000; B, × 3,000.

systems of classification yet devised for the family (Bentham, 1867; Drude, 1897-98; Koso-Poljansky, 1916; Cerceau-Larrival, 1962). The absence of any parenchymatous or collenchymatous bundle sheath extensions to either epidermis is rare for the family (Metcalfe & Chalk, 1950) and may prove significant.

Anatomically the stem is similar to such diverse genera as *Foeniculum*, *Apium*, *Daucus*, *Smyrnium*, and *Peucedanum*. None of the features noted by Lemesle (1926) for other xerophytic members of the family nor medullary bundles reported for members of the family by Metcalfe & Chalk (1950) was evident. This supports the note by Metcalfe & Chalk (1950) that, "In spite of these ecological specializations the basic structure is remarkably uniform throughout the family."

Present knowledge of *Phlyctidocarpa*, especially concerning fruit structure, suggests that it belongs in Drude's (1897-98) tribe Ammineae (Apieae). This tribe is the largest in the family and has been noted as one of critical importance in the evolution of the subfamily Apioideae (Theobald, 1971). In this review it is postulated that those taxa with a relatively indistinctive bicarpellate fruit (i.e., some Ammineae) may represent a more primitive condition from which other groups, such as the winged and flattened fruited Peucedaneae evolved. Unfortunately, Drude's classification is based primarily on mature fruit structure and has not taken into account developmental changes from flower to fruit and the ecological specializations of the taxa involved. The many forms found in the subfamily including hooked, winged, or vesicular fruits appear to represent separate lines in the evolution of various dispersal mechanisms. Current investigations by one of us (W.L.T.) on members of the Ammineae indicate that, like the Peucedaneae (Theobald, 1971), Ammineae represents a diverse assemblage of many unrelated forms held together only by the similarity of gross features of the mature fruit. *Phlyctidocarpa* like others in the Ammineae may represent a highly evolved taxon filling a particular ecological niche. In this regard it is like those taxa recognized by Drude as representing distinctive members of other tribes such as the Peucedaneae, Caucalideae, and Laserpiteae.

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