Studies in Annonaceae. III

The leaf indument in *Anaxagorea*

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SUMMARY

An unusual type of trichome is described for *Anaxagorea (Annonaceae)*. On top of the stalk cell, extremely thinwalled cells form single, branched or stellate trichomes. The terminal cell(s) always end bluntly. When the thinwalled cells have been shed, the thick cuticle of the stalk cell remains as a cylindrical scar. Until now, this trichome type has not yet been found in other annonaceous genera. Our data contradict reports of other authors (Jovet-Ast 1942, Kramer 1969, Roth 1981) with regard to occurrence and structure of hairs in *Anaxagorea*.

INTRODUCTION

During the preparation of the generic revision of *Anaxagorea* (Maas & Westra 1984, 1985) our attention was drawn to the fact that subsequent reports in the literature (a.o. Jovet-Ast 1942, Kramer 1969, Roth 1981) on presence and type of trichomes in *Anaxagorea* are often conflicting. For instance, for *A. acuminata,* Kramer (1969) reports hairs to be absent. Jovet-Ast (1942) mentioned single hairs consisting of 1–4 basal cells and an enlarged obtuse terminal cell. Timmerman, in a preliminary survey of the genus (pers. comm.), suggested the presence of coffee brown stellate hairs on the abaxial leaf side. Deviating results may be due to several reasons. Although in all species a leaf indument was found (this paper), the leaves are nearly always becoming glabrous with age. The trichomes are very tiny, so that often a hand lensd is not sufficient to establish the exact shape of the hairs.

The use of a light microscope in the study of hairs of *Anaxagorea* appeared not very effective, as most hairs fall off during the preparation of the slides.

As already indicated by, for instance, Theobald c.s. (1979), the use of a Scanning Electron Microscope (S.E.M.) reduces the preparation of the samples to a minimum. Therefore we decided to use the S.E.M. technique for a survey of *Anaxagorea* with respect to the trichome types on the leaves.

In the genus revision (Maas & Westra 1984, 1985) 25 species were recognized. In this study, the two still unnamed species are left out. Of *Anaxagorea macrantha* and *A. manausensis* only the type collections were available. We judged it unwarranted to take samples from these specimens. With the exception of *A. allenii,* the remaining species are represented in this study.

MATERIAL AND METHODS

All samples of *Anaxagorea* were taken from herbarium vouchers, mainly from the Utrecht Herbarium. All studied samples were recently (re-)identified. They are listed at the end of this paper. For this S.E.M. study three abaxial leaf samples of about 0.2 sq.cm were cut off: one section near the leaf base including the primary vein, one section near the leaf base halfway between primary vein and margin, and one section of the lamina from the middle of the leaf. The samples were fixed on a specimen holder with a conductive glue, sputtered with gold in a sputter coater (Edwards), and studied in a Cambridge Stereoscan 600 M. In case no trichomes were found on mature leaves, the samples were taken from young leaves. For comparison, fresh samples of *A. acuminata* (J.J. de Granville 5473) were fixed in a 2.5% glutaraldehyde solution, buffered with a Na-K-phosphate buffer. The samples were post-fixed in 1% OsO_4 in the same buffer, dehydrated in a graded series of aceton, critical point dried, and sputtered with gold.

At present, an elaborate study of the leaf anatomy in Annonaceae is carried out in Utrecht (J. van Setten). She kindly put her slide collection at our disposal. Thus we could compare the S.E.M. results with light-optical observations.

As pointed out by Theobald c.s. (1979), the terms used to describe the trichome morphology and anatomy are mostly rather imprecise and may be a source of confusion. In this study, we will follow the terminology of these authors and use the terms: simple, to indicate unbranched hairs; branched, to indicate 2–5-armed hairs; and stellate, to indicate hairs with more than 5 arms.

RESULTS AND DISCUSSION

Presence of trichomes

In all species of *Anaxagorea* studied, an indument was found on the abaxial leaf side, independent of the place of sampling. Rarely scanty trichomes occur on the adaxial leaf surface.

Fries (1959) used the absence of hairs to distinguish between asiatic and neotropical species. Kramer (1969) reported that the 12 neotropical and asiatic species studied by him are glabrous.

On juvenile leaves we always found trichomes on lamina and primary vein. On mature leaves they become scanty, but remain at least on the leaf base and along the primary vein.

Colour of the indument

The colour of the trichomes is often light- to dark brown, tending to red in *A. brachycarpa, A. brevipedicellata, A. petiolata,* and *A. phaeocarpa. A rufa* is remarkable because of its abundant purple hairs. In *A. pachypetala* the hairs are whitish.

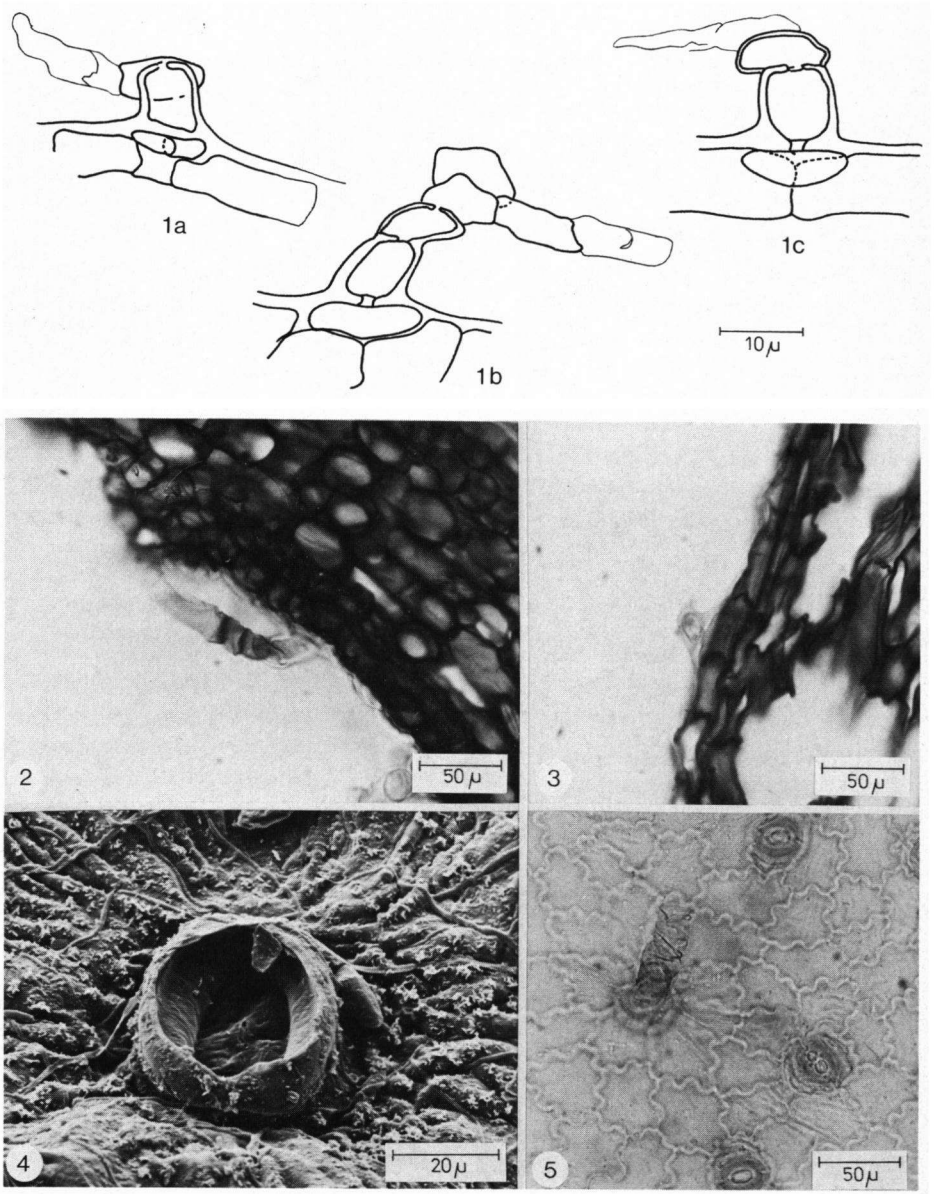

Plate I.

Trichomes of *Anaxagorea.* 1. Drawings of simple trichomes indicating the cutinized wall surrounding the stalk cell. -a.b. *A. phaeocarpa.* -c. *A. prinoides.* 2. *A. phaeocarpa,* simple trichome (LO). 3. *A. luzonensis,* cuticular rim (LO). 4. *A. dolichocarpa* (Wessels Boer 2098), cuticular rim (SEM). 5. *A. phaeocarpa,* simple trichome with collapsed top cells (LO).

This variation may at least partly be due to the contents of the top cell, which is often filled with dark brown amorphous substances, as was already reported by Jovet-Ast (1942).

Types of trichomes

In the specimens studied, simple (Fig. 6), branched (Fig. 10), or stellate (Figs.

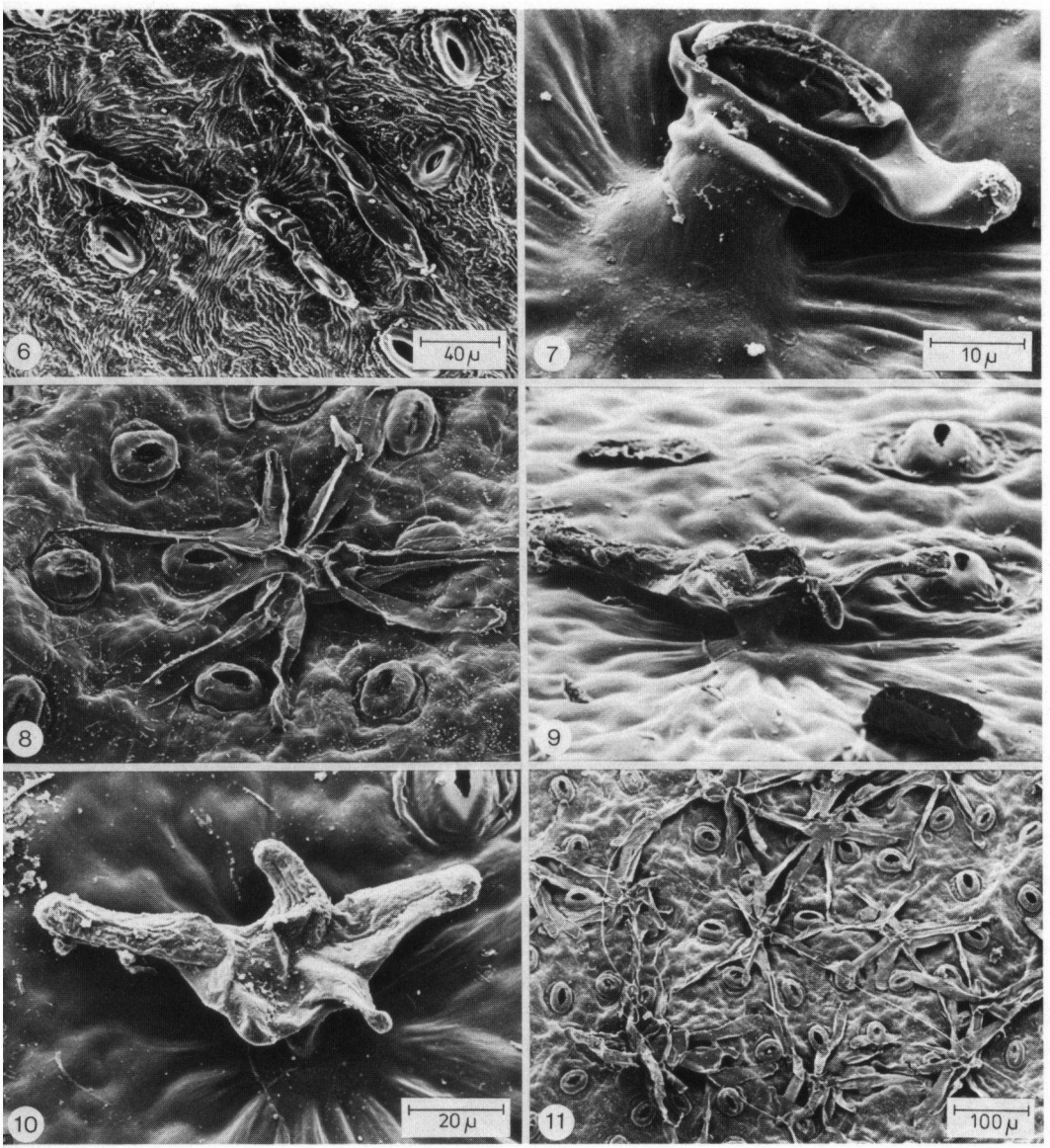

Plate II.

Trichomes of *Anaxagorea* (SEM). 6. *A. borneensis* (Laijanai S 34147), simple trichomes. 7–10. *A. acuminata* (de Granville 5473), branched and stellate trichomes. 11. *A. gigantophylla*, stellate trichomes.

8, 11) hairs were found, or a mixture of two or three types. (See paragraph on taxonomic and diagnostic value.)

As far as we could establish, all trichomes have one or two stalk cells surrounded by a cuticular rim (Figs. 1, 2). This structure remains as a cylindrical scar, also when the top cells have been fallen off (Figs. 3, 4).

This contradicts Roth's report of tufted hairs in part of the species of *Anaxagorea* (1982). In his description (p. 20) and schematic drawings he suggests that the stellate hairs are clusters of single trichomes.

On top of the stalk cells, 1 to 4 cells can form a uniseriate, simple trichome (Fig. 2). These cells are thin-walled, and collapse easily (Fig. 5, 6). The maximum length of the trichomes varies from 70 to 125 μm, but the overlap between the species blurs the differences.

In other cases, on top of the stalk cell, a poorly to frequently branched structure can be found. Differences in number and length of the branches are found. Transitions, however, occur. These hinder a distinction in categories. The branches are extremely thin-walled (Fig. 7) and are always collapsed in a fanciful way, both in the material taken from a living specimen of *A. acuminata* and samples taken from herbarium vouchers (Fig. 8). In most specimens, these branched structures fall off quite easily, especially during boiling or staining procedures, leaving the cuticular rim around the basal cell on the leaf surface. The scanty light optical observations confirm the extremely thin cell walls. It was impossible to establish the number of cells involved in the construction of the branched top-structure, due to the collapsing and folding of the walls. In many cases we got the impression, that the whole distal part consists of one enlarged arachnoid cell (Fig. 9).

Uphof (1062), citing Keller (1890), describes hairs with one or two cutinized stalk cells, shedding the apical cells (which may be simple or branched) for representatives of families like *Myrtaceae, Papilionaceae, Proteaceae, Pittosporaceae, Compositae;* none of these families are related to the *Annonaceae.* Koster & Baas (1981) in their study on the leaf anatomy of *Myristicaceae,* report peculiar trichomes, described as 'sympodially branched, uniseriate trichomes'. They consist of cutinized stalk cells comparable with those found in *Anaxagorea,* with one to many cells on top of each other, each cell with one or two sharp branches, thus often suggesting a stellate structure. In all species of *Anaxagorea,* the trichomes end bluntly. In branched or stellate trichomes this applies to the individual branches. Jovet-Ast (1942) already reported blunt top cells and considered them characteristic for the genus *Anaxagorea.*

Taxonomic and diagnostic value of trichome types in Anaxagorea.

As is mentioned before, the structure of the trichomes found in specimens of *Anaxagorea* is rather constant in the structure of the stalk cells and the appearance of the distal part. The only variation is found in the number and length of branches. This structure is not yet found in other annonaceous genera and therefore confirms the taxonomic concept of the genus *Anaxagorea* (Fries 1959; Maas & Westra 1984, 1985).

Our study is based on one or two specimens per species (see list of material). This fact makes it impossible to ascribe here taxonomic value below the genus level to the variation in shape, size and frequency of the trichomes.

Keeping in mind the overlapping variation found in, e.g. the number and length of the branches, and the fact that most leaves are glabrescent, we are convinced that the diagnostic value will remain restricted, even if, after careful examination of many specimens, the following cautious remarks should prove to remain true.

In samples of five species, only simple trichomes were found. For the three asiatic species, *A. borneensis, A. javanica*, and *A. luzonensis*, this was also reported by other authors (Jovet-Ast 1942, Roth 1981). This is in contradiction with Fries (1959) who described glabrous leaves. The trichomes in *A. angustifolia* and *A. brachycarpa* are similar, and so are the simple trichomes forming part of the indument of the other species.

In the specimens of the central American species *A. crassipetala, A. guatemalensis,* and *A. panamensis,* and in the South American species *A. pachypetala, P. prinoides*, and *A. silvatica*, we found a mixture of simple and 2–4-branched trichomes.

In the specimens of the other species (all South American) the trichomes are at least partly stellate, with branches of different length. In most specimens they have a thick-set appearance, but in some specimens, e.g. of *A. gigantophylla* and *A. dolichocarpa* p.p., the abundant trichomes show slender branches. This confirms preliminary reports of Timmerman (pers.comm.), but contradicts Jovet-Ast's statement, that in *A. acuminata* exclusively simple hairs are found.

LIST OF MATERIAL

Anaxagorea acuminata (Dunal) A.DC.: de Granville 5473; Steyermark et al. 105877.
Anaxagorea angustifolia Timmerman: Fróes 22217.
Anaxagorea borneensis (Becc.) James Sincl.: Laijanai S 34147; Sibat ak luang S 23040.
Anaxagorea brachycarpa R.E. Fries: Steyermark et al. 103039; Vásquez et al. 218.
Anaxagorea brevipedicellata Timmerman: Campbell et al. P 22403.
Anaxagorea brevipes Benth.: Killip et al. 28599.
Anaxagorea crassipetala Hemsley: Schunke Vigo 10006; Stevens et al. 5078.
Anaxagorea dolichocarpa Sprague & Sandw.: Steyermark et al. 120859; Wessels Boer 2098.
Anaxagorea floribunda Timmerman: Gentry et al. 27626.
Anaxagorea gigantophylla R.E. Fries: Maguire et al. 60311.
Anaxagorea guatemalensis Standley: Contreras 9338.
Anaxagorea javanica Blume var. *tripetala* Corner: Sinclair et al. 7655.
Anaxagorea luzonensis A. Gray: Loher 30.
Anaxagorea pachypetala (Diels) R.E. Fries: Schunke Vigo 6281.
Anaxagorea panamensis Standley: Folsom et al. 1699.
Anaxagorea petiolata R.E. Fries: Steyermark et al. 106015.
Anaxagorea phaeocarpa Martius: Prance et al. 24259.
Anaxagorea prinoides St. Hil.: Prance et al. 1925.
Anaxagorea rufa Timmerman: Liesner 8476.
Anaxagorea silvatica R.E. Fries: Mexia 4696.

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