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MORPHOLOGY OF THE "SQUAMELLAE" IN THE LIGHT OF THEIR ONTOGENY

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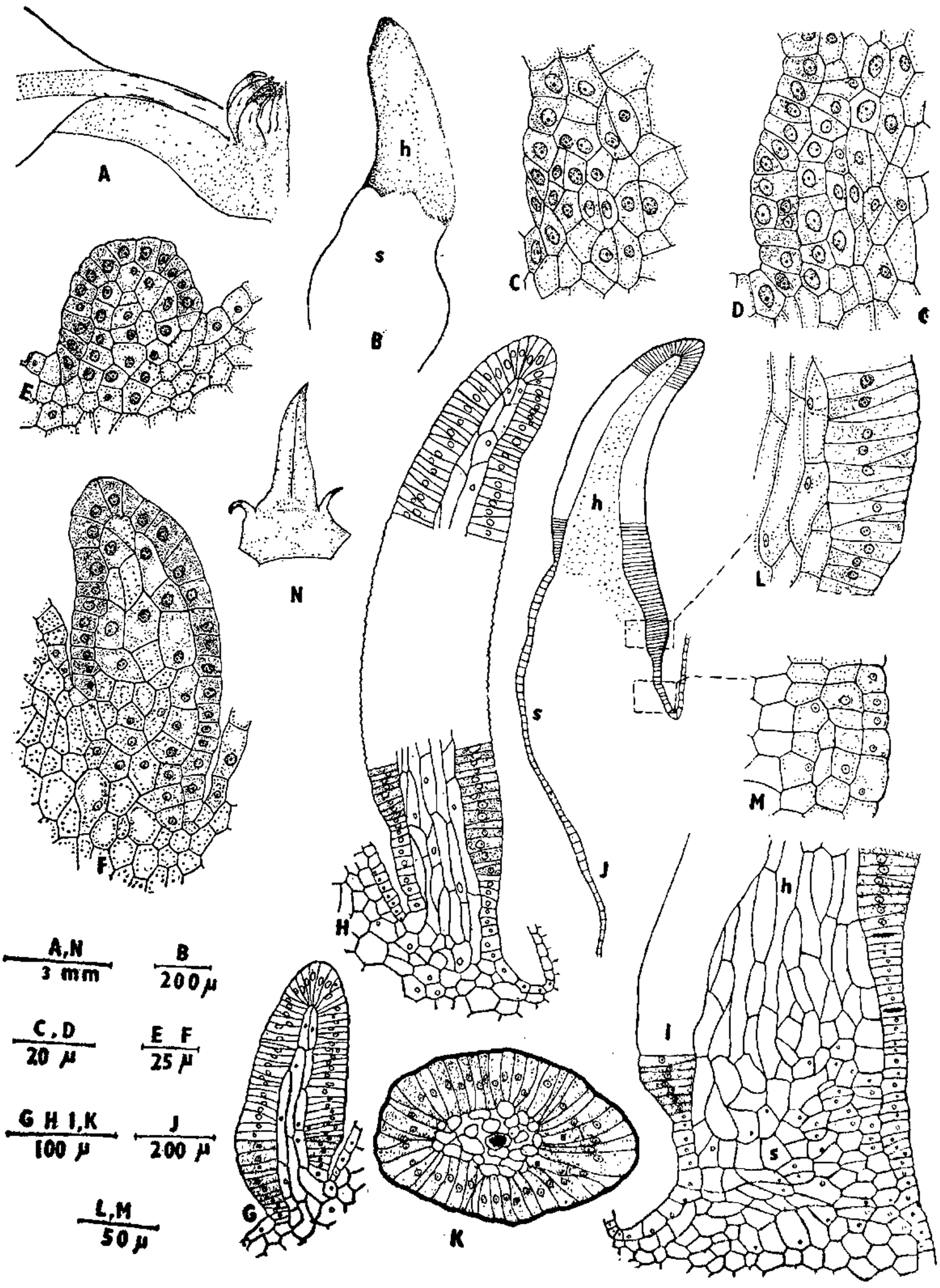
SQUAMELLAE (or colleters), which are a characteristic feature of the Apocynaceæ, Asclepiadaceæ and others,[8-12] have been variously interpreted in the literature, *viz.*, as hairs,[12] stipules,[2,6,8-11] ligules[9] and receptacular outgrowths.[8,9] But all these workers have drawn conclusions from the mature structure of the squamellæ and their organographic position rather than on their ontogeny. The authors present here their findings on the ontogeny of the squamellæ in *Allamanda cathartica* L., and *Tabernæmontana divaricata* (L.) R. Br. (Apocynaceæ), because of the conclusive nature of the evidence they provide relating to their morphology.

Allamanda cathartica: The squamellæ occur only at the leaf-base towards its adaxial side (Fig. A). Each leaf bears 10 to 13 squamellæ arranged in a transverse row which in young buds cover the shoot apex; none occur on the sepals unlike in some other species of the family,[1,8,9] though one or two are borne on the distal margin of the bracts and bracteoles (Fig. N). While young, the squamellæ secrete a sticky substance which coats the shoot apex all over, probably providing it protection. The substance is brown-yellow and transparent, insoluble in water, alcohol, acetone, benzene and petroleum ether, but liquefies at high temperature; hence it is considered to be a high polymer resin. The squamellæ are 1·5 mm. long and 0·3 mm. broad, differentiated into a stalk and a head (Fig. B). The stalk is nearly cylindrical, but abaxially more curved (Fig. J), while the head, obliquely placed on the stalk, is somewhat flattened parallel to the leaf surface as shown by its transection (Fig. K). In longisections the epidermal cells of the stalk appear isodiametrical to elongated and those of the ground tissue mostly isodiametrical (Fig. M), whereas the head consists of palisade-like epidermis of densely stained cells and ground tissue of mostly elongated elements (Fig. L). The stalk is green and photosynthetic, whereas the head is brown-coloured, and glandular in nature. The details of the ontogeny are as follows:—

Squamellæ develop from primordia consisting of protoderm and the subtending subprotoderm elements appearing at the base of the leaf on its adaxial face when it is about 500 μ long (Fig. C). At this stage the leaf consists of mere protoderm, ground meristem and procambium indicating the phase of its cell multiplication rather than differentiation of any tissues. The primordial cells appear distinctive from the adjacent ones due to their relatively dense cytoplasm (Fig. C). The protoderm cells divide anticlinally, with occasional oblique and periclinal divisions, while the subprotoderm cells in various planes, particularly in transverse ones (Figs. C and D). Consequently, the primordium becomes elongated and grows upward, parallel to the leaf on which it is borne (Fig. E). The epidermal as well as ground elements of the squamellæ at this stage remain nearly isodiametrical (Figs. E and F). Later, while the ground cells elongate axially, the epidermal cells divide through rapid anticlines (occasionally in

oblique and periclinal planes) to cope with the increasing length of the ground tissue (Fig. G). With this, the differentiation phase of the head comes to an end, for it now possesses a core of elongated cells and a palisade-like densely stained epidermis as seen in mature condition (compare Fig. G with Fig. L). Meanwhile, the stalk also begins differentiation. The first change noticed consists in the occurrence of rapid anticlines in the basal cell



FIGS. A–N. *Allamanda cathartica.* Fig. A. Leaf-base with the squamellæ. Fig. B. A single squamella. Figs. C–H. Developmental stages from l.s. leaf. Fig. I. Stalk of a developing squamella showing subdivisions in the hitherto axially elongated ground cells. Fig. J L.S. mature squamella from l.s. leaf (Diagrammatically represented). Fig. K. T.S. head of mature squamella. Fig. L. A sector of the head of mature squamella shown in Fig. J., enlarged. Fig. M. A sector of the stalk of mature squamella J, enlarged. Fig. N. A bract with two squamellæ on its margin. (*s* = stalk ; *h* = head.)

tiers of the protoderm (Fig. G), but since the cells thus produced soon start elongation and vacuolation, they appear narrower and longer than the overlying palisade form epidermis of the head (Fig. H). The ground cells of the corresponding basal region which were so far longer than broad (Fig. H), now divide through anticlines and other planes and become nearly isodiametrical (Fig. I) as seen in the mature stalk (Fig. M). The squamella later enters the phase of its maturation when all its cells become enlarged. Neither vascular tissue nor laticifers, a characteristic of the other parts of the plant, appear in the squamellæ. Occasional ground cells, however, show sphærocrystals (Fig. K).

Tabernæmontana divaricata: Leaves as well as sepals bear the squamellæ adaxially at their base. On the leaf they are numerous and occupy almost the entire basal area, while on the sepal 4 or 5 are situated at its middle about 2 mm. above the base and parallel to each other. No squamellæ occur on the bracts and bracteoles as in *Allamanda cathartica*. The squamellæ of both the leaf and sepals are nearly of the same size being about one-third to half a millimeter in length and half as much or lesser in breadth; unlike in *Allamanda cathartica*, their stalk is quite short or almost absent. As in the above species, they are non-laticiferous and non-vasculated. The squamellæ of the leaf follow the same pattern of development as in *Allamanda cathartica*, except that the stalk is shortly developed, while in the sepals only the head is differentiated.

From the ontogeny as well as other characters it is obvious that the squamellæ, in the two species investigated, cannot be regarded as hairy structures as has been described in the past,[12] since they are derived from a primordium made up of both protoderm and ground elements. That they are stipular in nature[2,9,11] is also not tenable on more than one ground. Unlike the stipules which are derived from the leaf-base as its lateral extensions,[4] the squamellæ are produced from the leaf adaxial surface. The squamellæ also do not develop a marginal meristem as in the stipules.[4] Besides they are borne at the distal margin of the bracts and bracteoles as in *Allamanda cathartica*, a position never occupied by the stipules. Finally, the squamellæ are numerous and adaxially situated at the leaf-base unlike the stipules.

Rao and Ganguli[9] regarded the non-vasculated squamellæ comparable to the ligule. This is equally not suggestive in as much as their origin is from a primordium made up of both protoderm and ground elements unlike that of the ligule which is initiated through periclines in the foliar protoderm.[3] Further the ligule represents an appendage of a specific location, the junction of the leaf-sheath and blade in the Gramineæ, whereas the squamellae may be borne near the base of the leaf and sepals and also at the margin of the bracts and braceteoles. Agarwal's view (*See* Refs. 8 and 9) that the squamellæ represent receptacular outgrowths is not acceptable for neither do they originate from nor borne by the receptacle.

In view of the peculiar features shown by the squamellæ in their development, structure and organographic distribution, we therefore conclude that they represent emergences of a glandular nature. Regarding the emergences, Ramayya[7] has recently shown that they bear the following essential characters: (1) originate from a primordium consisting of protoderm and subprotoderm elements, (2) as in the case of major plant organs consist of the three fundamental tissue systems, epidermis, ground tissue and vascular tissue (the last may be absent) and (3) are borne both by the stem and foliar appendages. It is obvious that squamellæ whether vasculated or non-vasculated conform to the above definition.

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