THE GENUS *SONNERATIA* AND ITS FOSSIL ALLIES

T. S. MAHABALÉ & J. V. DESHPANDE
Botany Department, University of Poona, Poona

ABSTRACT

The development, morphology and structure of the flower, embryo, fruit and seeds in two species of *Sonneratia*, *S. acida* L. and *S. apetala* Ham. are given; and they are compared with the structure of the flower of *Sahnianthus* Shukla and with that of the fruit and seed of *Enigmocarpon parijai* Sahni, considered to be the fruit of *Sahnianthus*. The flowers of *Sonneratia* closely resemble in many gross features those of *Sahnianthus* and possess in addition bracts and a loose tissue of floral nectary around the base of the ovary. The fruit wall in *S. acida* and *Enigmocarpon parijai* also possesses arenchyma and nests of sclereids.

The fruit of *S. acida* dehisces irregularly as in *Enigmocarpon* and has no persistent calyx as in the fruit of *S. apetala*. The general structure of the fruit, placentation and vascular supply in the two are also more or less similar. The seeds of *Enigmocarpon parijai*, however, are said to possess both hypostase and epistase. There is a clear hypostase in *Sonneratia*, but no real epistase in it, like that in the Malpighiaceae. The inner wall of the inner integument in *Sonneratia* is very thin. When detached, it looks like a compressed hood in the micropyle in matured seeds. There is a conical nucellar beak on top of embryo sac in both the species of *Sonneratia* and is pushed up a little in the micropyle. The net result of compression during the further development of seeds is that the inner integument with its thin inner wall comes to lie over the nucellar beak, like the frayed end of a whip and gives an appearance of an epistase lying in the micropyle. There is, however, no organic continuity between the two, and, therefore, it is not a true epistase as in Malpighiaceae. In the seed of *Enigmocarpon parijai* also, there is no continuity between the basal conical part of the so-called epistase and the frayed whip-like end lying in the micropyle. It is, therefore, suggested that it may also have been formed of two distinct components, the nucellar beak on the top of the embryo sac and the thin integumental part lying above it in the micropyle. It was further observed that there is hypostase in several members of the Lythraceae such as *Ammania*, *Woodfordia* and *Cuphea*. They do not have a real epistase but only a nucellar beak.

INTRODUCTION

THE genera *Sonneratia*, *Duabanga* and *Xenodendron*, formerly included in the family Lythraceae, are now put in a separate family Sonneratiaceae, as they differ from it in having a partial union of the ovary with receptacle, sub-basal or parietal placentation, smooth pollen grains with equatorial germ pores and the presence of bast bundles in the pith. The genus *Sonneratia* comprises five species, some of which are not much known even taxonomically. They are spread from tropical East Africa to India, Philippine Islands and North Australia. *Duabanga* has two species spread from Eastern Himalayas to New Guinea, in addition to Andaman, Nicobar and Rutland Islands. *Xenodendron*, the least known of these three genera, is monotypic and is restricted to New Guinea. *Sonneratia*, on the other hand, is far more widely distributed. Its species inhabit coral terraces, shallow waters of calm seas as mangroves, banks of tidal rivers and creeks, in tropical East Africa, North Madagascar, Seychelles, west coast of India, Sunderbans, mouths of Godavari, Krishna, Coleroon and other rivers in India, Ceylon, Andamans, Mergui coast of Burma, Malaya, Java, Sumatra, Borneo, Celebes, Philippine Islands, Moluccas, New Guinea and North Australia. *S. acida* L. inhabits estuaries, but can also grow in localities where there is fresh water, occasionally inundated by sea-water. Thus, for example, it is said to be growing along the stream bed of the river Lepo-Lepo in Celebes. *S. apetala* Buch-Ham. grows in mangrove swamps, very rarely in estuaries (PL. 1, FIG. 1). Five species of this genus recognized by taxonomists, their distinctive characters, habitat and distribution are given in the accompanying table, and the map shows their geographical distribution (*see* also BACKER & VAN STEENIS, 1951).

Two species of *Sonneratia*, *S. acida* L. and *S. apetala* Buch-Ham., occur in the Bombay Island. As the family is not much known, it was thought worthwhile making a detailed study of it with a view to throwing some light on such points in it as needed confirmation or elucidation of certain structures seen in it. Another reason for undertaking the present investigation has been the enigmatic fruit and the flower from the Tertiaries of the Deccan Intertrappean series described under the names *Enigmocarpon* and *Sahnianthus* respectively by Sahni (1943) and Shukla (1944), supposed to be related to the members of Lythraceae.

TABLE 1 — SHOWING THE HABITAT, DISTRIBUTION AND DIAGNOSTIC FEATURES OF THE SPECIES OF *SONNERATIA*

NAME OF THE SPECIES	HABITAT	DISTINCTIVE FEATURES	DISTRIBUTION
1. *S. acida* L. (=*S. caseolaria*)	Mangrove swamps, especially near estuaries	1) Calyx 5-8 — lobed 2) Inner side of sepals greenish or yellowish white 3) Calyx lobes under fruit — flat, expanded; tube — obscurely ribbed 4) Petals dark red 5) Filaments of stamens — lower part red, upper white 6) Stigma capitate	West coast of India, deltaic forests of Bengal, Ceylon, Mergui coast of Burma, from tropical S.E. Asia to N. Australia, Solomon Islands. New Hebrides in Malaysia, Malay Peninsula, Java (also Madwa), Sumatra (also Simatur and Bankia), Borneo, Celebes, Philippines, Moluccas, Timor and New Guinea
2 *S. apetala* Buch-Ham.	Mangrove swamps	1) Flowers 4-6 — merous 2) Petals absent 3) Stigma large, fungiform	Creeks of Konkan, Bombay Island, mouths of the rivers Godavari, Krishna, Coleroon; Sunderbans, Trans-gangetic Peninsula from Orissa to Chittagong; Pegu, Moulmein; Ceylon; tropical shores of Africa and Australia
3. *S. alba* J. Sm.	Shallow parts of calm seas, mouths of tidal creeks; prefers salt water; grows well on sandy soil	1) Inner side of calyx red 2) Calyx tube ribbed, segments under ripe fruit entirely reflexed 3) Petals white or lower half tinged with red 4) Filaments white	N. Madagascar, Seychelles, tropical Africa, S.E. Continental Asia, Andamans to N. Australia, Micronesia, Solomon Islands, the New Hebrides and N. Caledonia in Malaysia, Malay Peninsula, Java, Sumatra, Lesser Sunda Islands, Borneo, Celebes, Philippines, Moluccas, New Guinea and New Ireland
4. *S. griffithi* Kurz.	Mangrove swamps	1) Calyx 5-8 — lobed, smooth 2) Calyx lobes under the ripe fruit—flat, expanded; tube—obscurely ribbed	Bengal, Chittagong, Burma, Mergui, Andamans, W. Malay Peninsula
5. *S. ovata* Backer	Sand-side of tidal forests in less salty parts of sandy soil	1) Calyx verruculose, distinctly ribbed 2) Calyx segments ascending, adpressed against the ripe fruit 3) Petals absent	Siam, Malay Peninsula, Java, S. Celebes, Moluccas, S.E. New Guinea

A detailed study of the organogeny, anthesis, embryology, the structure of flower, fruit and seeds was made. Some members of Lythraceae such as *Cuphea*, *Woodfordia*, *Lagerstroemia* and *Ammania* were also examined for comparison with *Enigmocarpon* and *Sahnianthus* collected by one of us (T.S.M.) at Mohagaon Kalan (Dist. Chhindwara, M.P.). Material of *S. acida* and *S. apetala* was collected locally at Bombay and fixed in F.A.A. Mature seeds of both the species possess very hard testa and needed softening by 10 per cent KOH solution. Distribution of tannin in the cells of seed coats was studied by fixing the material in 2 per cent ferrous sulphate solution recommended by Johansen (1940, p. 107). The sections were cut in the usual manner by paraffin method and stained either with Heidenhain's iron-haematoxylin or with safranin and light-green or with gentian violet and erythrosin, all of which gave good results.

PREVIOUS LITERATURE

A brief account of the embryology of *S. apetala* has been given by Karsten (1891) and a detailed account of it in *S. apetala* and *Duabanga sonneratioides* by Venkateswarlu (1937). Mauritzon (1939) has also described the megasporogenesis and female gametophyte in *S. acida* and in *D. sonneratioides*. The development of embryo in *D. sonneratioides* has been given by Venkateswarlu (1937) and that in *S. acida* is given here. A detailed account of the fossil fruit *Enigmocarpon parijai* has been given by Sahni (1943) and of the chertified flower *Sahnianthus* by Shukla (1944). Shukla (1944) has also discussed its affinities. Recently Mrs. Chitaley (1950, 1951, 1955) and Verma (1956) have made some additional observations on the flower of *Sahnianthus*, and Ramanujam (1954) has found the wood of *Sonneratia* in Cuddalore series in South Arcot district.

DESCRIPTION

The sequence of organogeny of floral parts in *S. acida* and *S. apetala* is, sepals, petals when present, stamens and carpels (TEXT-FIGS. 1-5 & 6-9). The same sequence was observed in *Lawsonia inermis* by Joshi & Venkateswarlu (1935-36). The flower of *S. acida* is bracteolate, its calyx tube somewhat cup-like, sepals 5-8, petals 5-8, stamens numerous, inserted on the calyx tube, and

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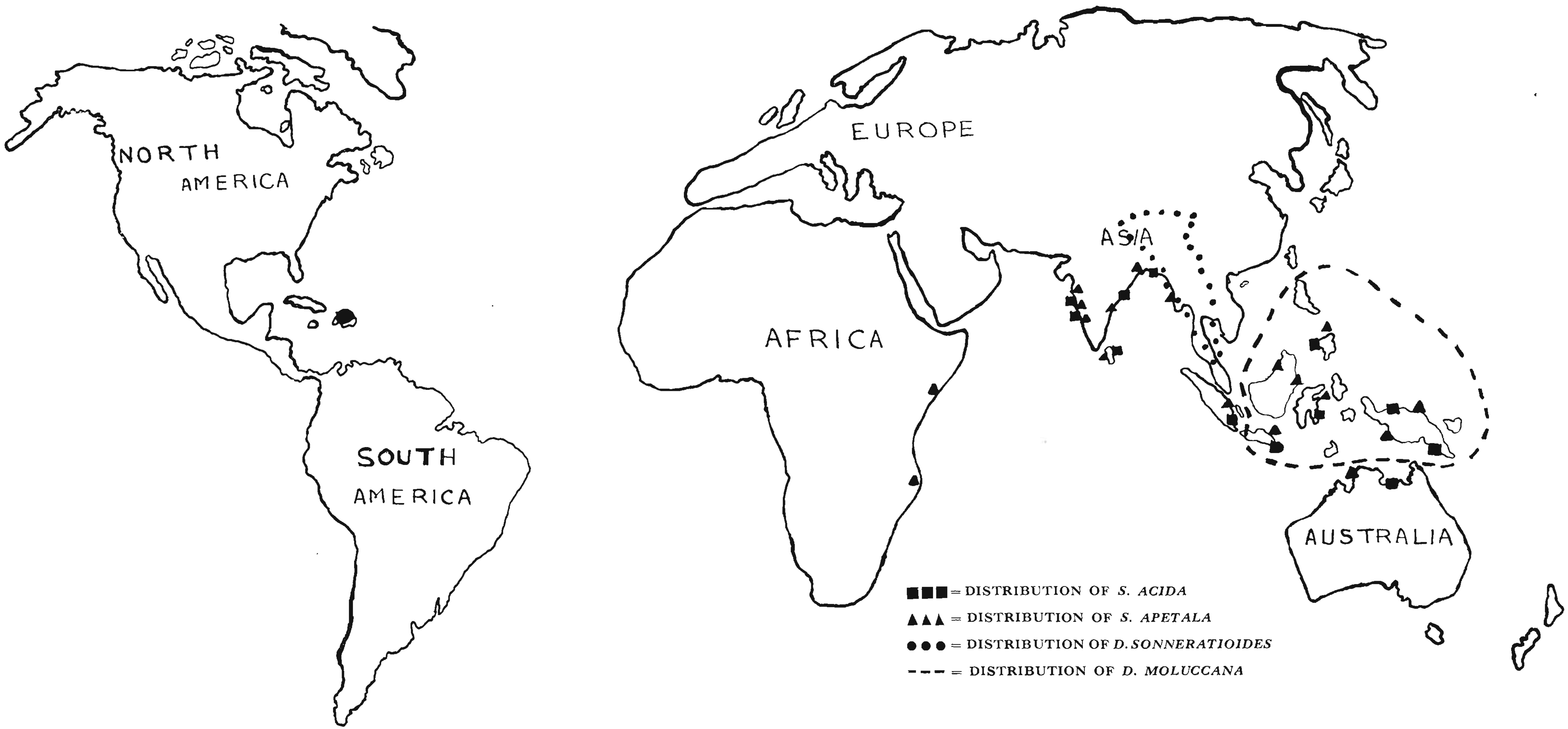
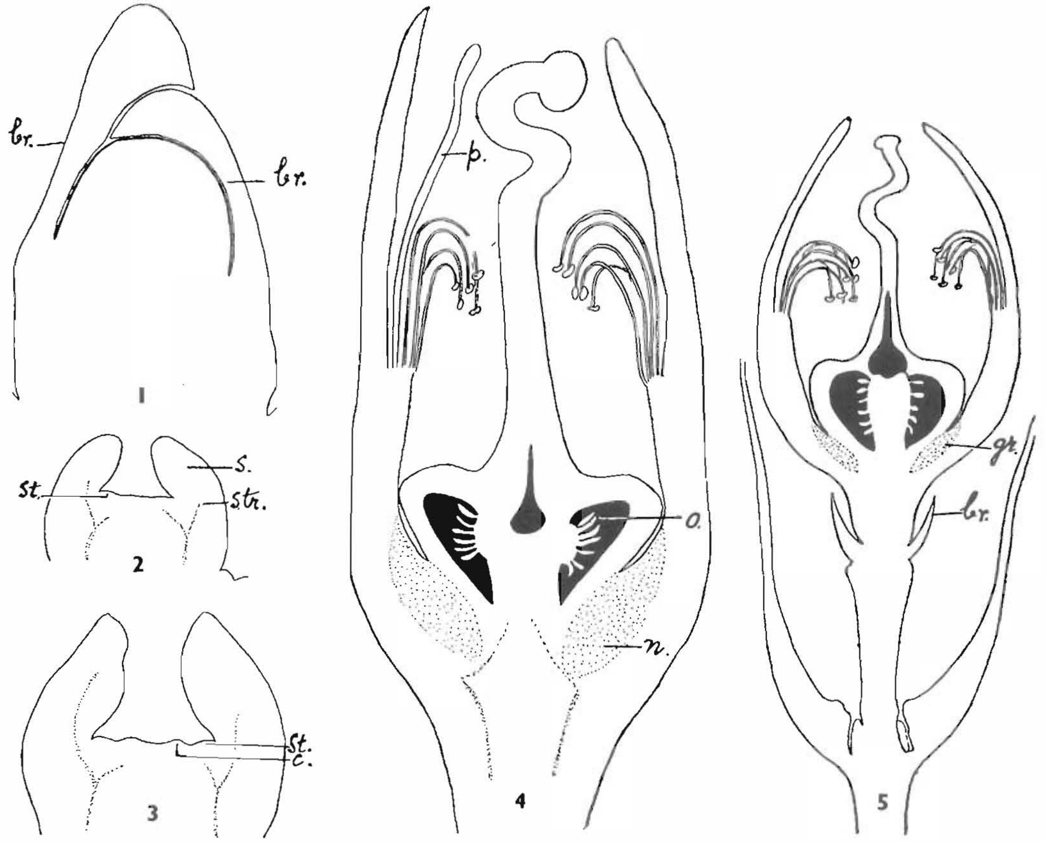


MAP SHOWING THE GEOGRAPHICAL DISTRIBUTION OF THE SPECIES OF *Sonneratia*

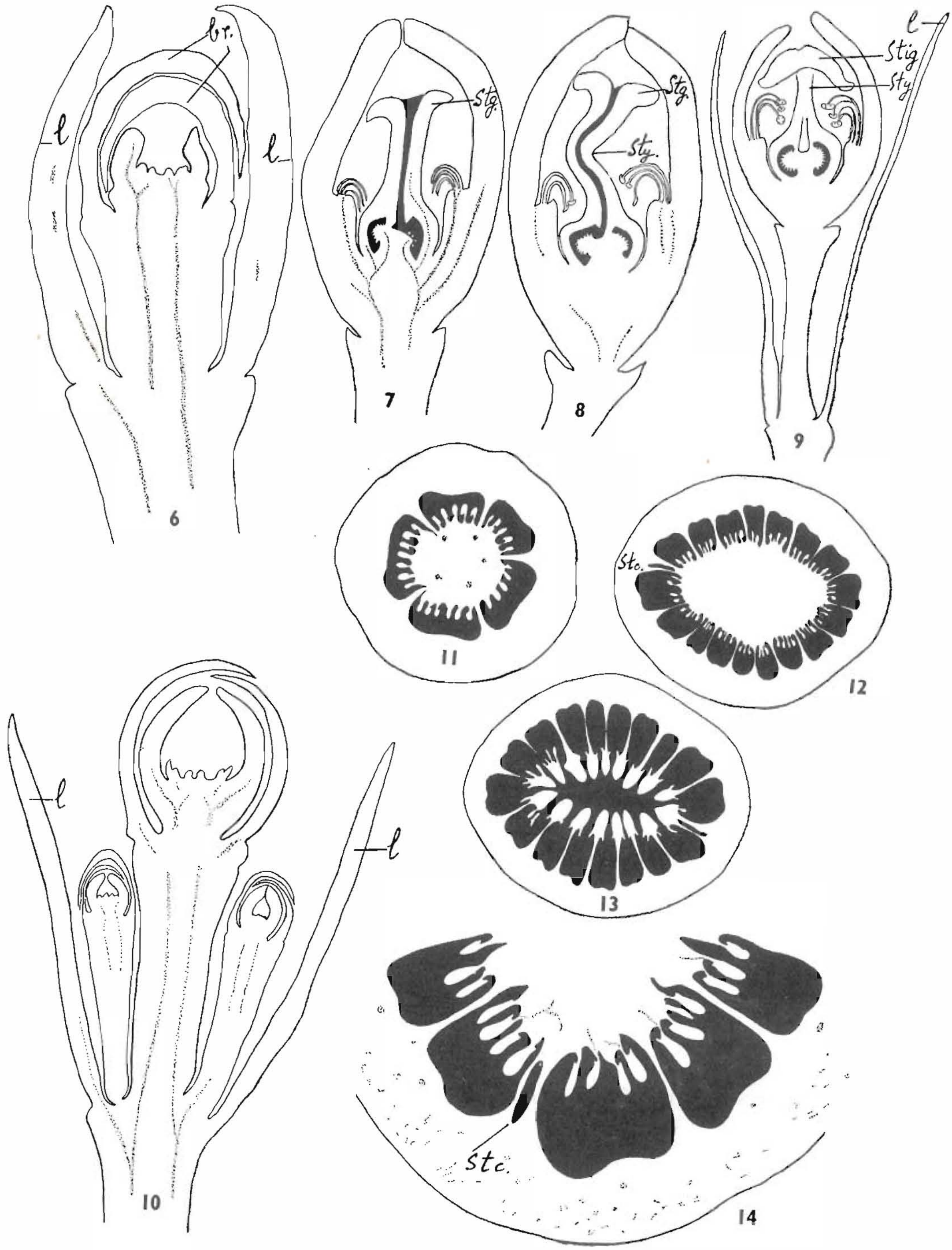


TEXT-FIGS. 1-5 — *S. acida* L. Development of flower. 1, L.S. of flower primordium (*br*, bract). × 130. 2, 3, L.S. of a flower bud: *S.*, sepals; *Str.*, sepal trace; *St.*, stamen primordium. × 42. 4, L.S. of a developing flower showing contorted style. × 4. 5, L.S. of flower bud showing bracteoles and nectary × 2.

ovary with axile placentation having 16-20 loculi (TEXT-FIGS. 4, 5, 12, 13, 14 & PL. 1, FIGS. 5-6). In *Punica granatum* this sequence is sepals, petals, gynaecium and stamens (TUNG, 1935).

A remarkable feature of the flower of *S. acida* is the presence of a soft flabby tissue below ovary in which it lies partly embedded (TEXT-FIG. 4 & PL. 1, FIGS. 5, 6). This tissue consists of thin-walled parenchyma and is possibly a nectary. It is more prominent in this species than in *S. apetala*. On account of this tissue the fruit in *S. acida* gets easily detached at maturity from the surrounding calyx (PL. 1, FIG. 8). Flowers of this species open at night. The anthers are kidney-shaped. The filaments are attached to the centre or to one side. The pollen grains in *S. acida* and *S. apetala* are binucleate at the time of shedding (TEXT-FIGS. 17-19 & PL. 2, FIG. 14 & PL. 3, FIG. 20), their exine has three germ pores in equatorial position. The pollen grains in *S. acida* are $67 \times 27\,\mu$, slightly larger than those of *S. apetala* in which they are spheroidal. (PL. 3, FIG. 20).

Structure of the Mature Ovary — Gynaecium of *S. apetala* is composed of 4-6 carpels, and that of *S. acida*, 16-20 (TEXT-FIGS. 12-14). Occasionally, however, one does come across a carpel which does not bear ovules in *S. acida* (TEXT-FIGS. 12-14, *Stc.*), The loculus of such a carpel is reduced to a small narrow cavity and it starts at a higher level than the loculi of the fertile carpels. In the basal 4/5 part of the ovary, the carpellary margins meet in the centre and form the axile placentation. The ovules lie mostly in 4 rows



TEXT-FIGS. 6-14 — 6-11: *S. apetala* Ham. Development of a flower bud (L.S.). 6, flower bud (L.S.): *l*, leaf; *br.*, bract. × 19. 7, 8, the same showing zigzag style (*Sty.*), and stigma (*Stg.*). × 8. 9, the same enclosed in leaves (*l*); *Sty*, style; *Stig*, stigma. × 3·5. 10, L.S. of inflorescence showing two lateral buds in the axils of leaves and the terminal bud. Note bracts in all buds. × 7·5. 11, T.S. of ovary showing 5 carpels, 5 vascular bundles in the central receptacle and 5 loculi. × 3·5. 12-14: *S. acida* L. T.S. of ovary showing 17 fertile loculi and one aborted (*Stc.*). 12, T.S. of the basal part of an ovary showing solid central axis. × 3·5. 13, T.S. of apical part of ovary showing central cavity. × 3·5. 14, T.S. of ovary magnified to show sterile carpel (*Stc.*). × 11.

on each carpel in *S. acida* (TEXT-FIG. 14 & PL. 2, FIG. 11). A longitudinal section of the ovary in *S. acida*, however, shows that the ovules in the upper part of the ovary are ascending, those in the middle part more or less horizontal and those in the basal part distinctly pendulous (TEXT-FIG. 4). In the upper $\frac{1}{3}$ part, the carpellary margins fail to meet in the centre and consequently the ovules are borne on the enlarged margins of the septa (TEXT-FIG. 13). Opposite the dorsal bundle of the carpels, there is a longitudinal ridge on the inner surface towards the loculi. The dorsal and lateral bundles of the carpels branch in the wall (PL. 2, FIG. 11).

Structure of the Mature Ovule — A mature ovule is stalked, anatropous and bitegumentary (TEXT-FIG. 15). The micropyle is zigzag and is formed by the inner integument. There is a small space at the chalazal end between the two integuments (TEXT-FIG. 15 & PL. 2, FIG. 15).

The nucellus is nearly straight, except for a small curvature towards the chalaza. Just above the embryo sac the cells are arranged in more or less radial rows. The nucellar cells below the embryo sac are also regularly arranged to form a strand of elongated cells (*see* PL. 2, FIG. 15). Such a strand of elongated cells has been recorded in many members of Lythraceae by Joshi & Venkateswarlu (1935-36) and also in *Duabanga sonneratioides* by Venkateswarlu (1937). He, however, states that such a strand is absent in *S. apetala*.

The outer and inner integuments are distinctly two-layered for the greater part, except near the micropylar zone (TEXT-FIGS. 15, 16 & PL. 3, FIGS. 16-18). The vascular bundle of the raphe ends in a few short branches at the chalaza (PL. 2, FIG. 15).

The embryo sac is about 310 μ long and 60 μ in diameter. In egg-apparatus, synergids as usual have a large vacuole at the chalazal end. The nucleus is located in the upper part (TEXT-FIGS. 15 & 20). The egg-cell shows the presence of a vacuole towards the micropylar end and nucleus towards the chalazal end. The antipodals are ephemeral and usually disappear before the fusion of micropylar part of the embryo sac. Fat bodies are present in the embryo sac (TEXT-FIGS. 15, 20, *f.b.* & PL. 3, FIG. 22).

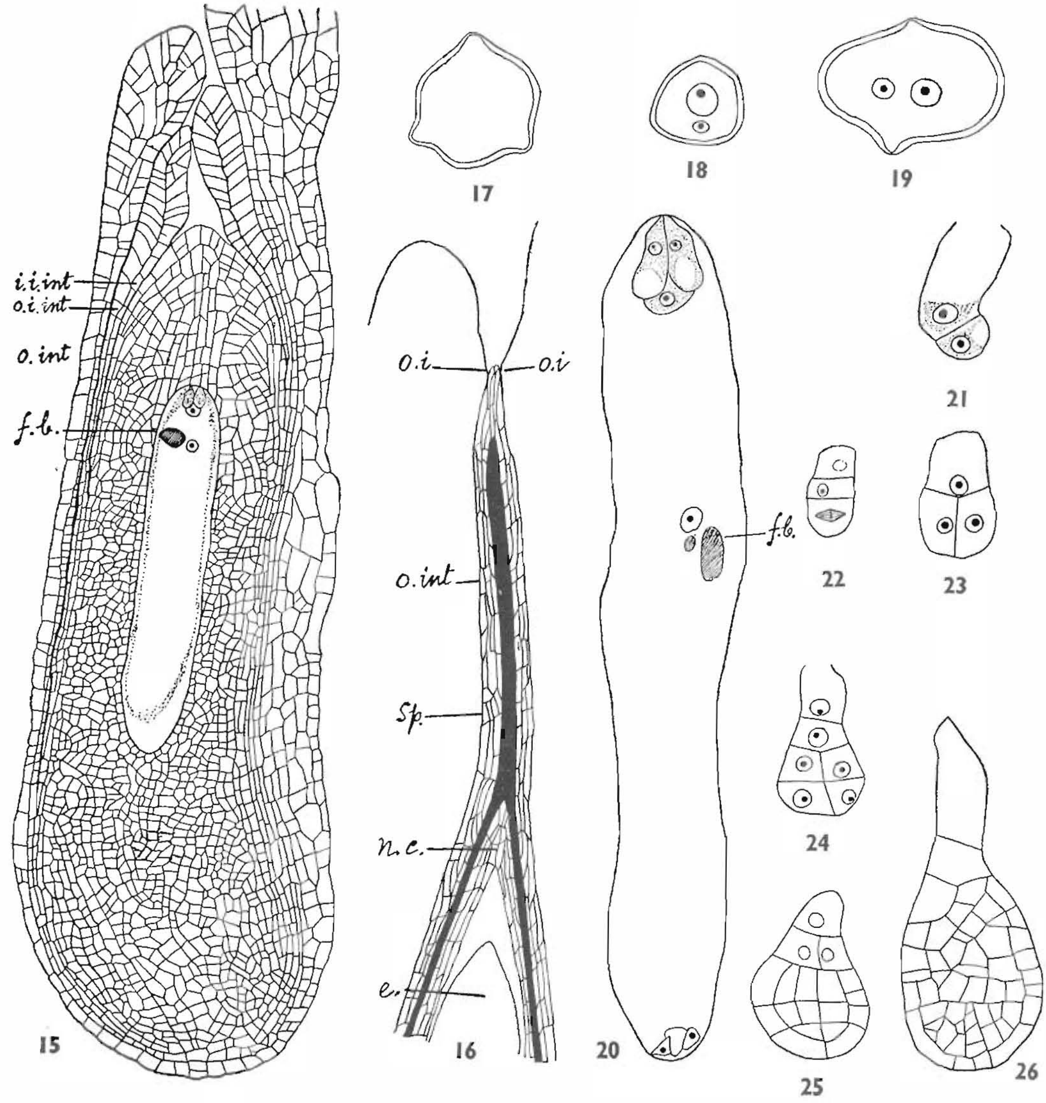
Embryo — After fertilization, the zygote in *S. apetala* divides and forms a pro-embryo of two or three cells (TEXT-FIG. 22). The terminal cells form the embryo proper. By two longitudinal divisions, a quadrant is formed (TEXT-FIG. 23). A transverse division in each one of the cells of the quadrant gives rise to an octant (TEXT-FIG. 24). The four terminal cells of the octant divide further (TEXT-FIGS. 25, 26) and develop into cotyledons and stem, while the four basal cells form hypocotyl and primary root. In *S. acida* the basal cell of the pro-embryo is much enlarged (TEXT-FIG. 21).

Endosperm development starts with free nuclear divisions, but ultimately walls are formed from periphery towards the centre. As the embryo develops, the endosperm gets disorganized, so that in a mature seed only a single layer of endosperm is seen at the micropylar region a little below the nucellar cap (PL. 3, FIGS. 17, 18).

Hypostase — The cells at the chalaza, at the point of the origin of the two integuments gradually change in appearance. They stain densely (PL. 3, FIG. 21) and form the hypostase which appears crescent-shaped in longitudinal sections of the seed (PL. 3, FIG. 19, *hy.*).

The Nucellar Cap — As the seed matures, the nucellus gets gradually reduced, being eaten up by the developing endosperm. A few cells of the nucellus just below the micropyle remain persistent and form a sort of nucellar cap (PL. 3, FIG. 18). On the sides, the nucellus is completely absorbed except the outer wall of the outermost layer lying in contact with the inner integument. This wall is suberized and stains brilliant red with Sudan IV. The cells of the nucellar cap are also suberized and show the same staining reactions.

This persistent nucellar cap formed from the nucellus represents a well-marked tissue in the micropylar region (TEXT-FIG. 16 & PL. 3, FIGS. 16-18) and perhaps corresponds morphologically with the so-called epistase. A distinct epistase developed from the nucellus, projecting through the micropyle, is known in the Malpighiaceae (STENOR, 1937; SUBHA RAO, 1940), but is not of common occurrence in other plants. The presence of nucellar cap, on the other hand, is not so uncommon and is reported in many plants belonging to diverse families such as in *Lemna minor* (Family — Lemnaceae), *Costus speciosum* (Family — Zingiberaceae), *Typhonium trilobetum, Peltandra virginica, Arum maculatum, Acorus calamus* (Family — Araceae), *Strelitzia Reginae, Heliconia aurantica* (Family —



TEXT-FIGS. 15-26 — 15, *S. acida* L. A mature ovule with embryo sac (L.S.): *i.i.int.*, inner lining of the inner integument; *o.i.int.*, outer lining of the inner integument; *o.int.*, outer integument; *f.b.*, food-body. × 130. 16, *S. acida* L. L.S. of a young seed showing a part of micropyle in which the nucellar cap is seen lying above the endosperm of the embryo: *o.int.*, outer integument; *Sp.*, spongy tissue; *n.c.*, nucellar cap; *e.*, endosperm. × 70. 17-20, *S. acida* L. Pollen grains, embryo sac and embryo. 17-19, pollen grains. × 425. 20, mature embryo sac. Note the food-body (*f.b.*) lying near the endosperm nucleus. × 425. 21-25, *S. apetala* Ham. Stages in the development of embryo. × 425. 21, two-celled embryo. 22, three-celled embryo. 23, two-celled pro-embryo. 24, embryo in octant stage. 25, an advanced embryo in globular stage. 26, *S. acida* L. An advanced embryo. × 425.

Musaceae), *Stromanthe lutea*, *Calanthea picturata* (Family — Marantaceae), etc.

The cells of the inner layer of the inner integument gradually get more and more compressed as the seed matures.

The Seed Coats — The inner seed coat: During the development of seed, the two-layered inner integument of the ovule gets differentiated into two layers, the outer and inner. The inner one remains single-layered except at the micropylar end where it becomes 2-3-layered (TEXT-FIG. 16 & PL. 3, FIG. 22). Tannin is deposited in this layer on account of which it looks dark in sections fixed in ferrous sulphate solution recommended by Johansen (1940, p. 107). In older seeds this inner layer in the micropylar region gets compressed due to the pressure of the outer layer and appears like a long narrow strip above the centre of the nucellar cap and looks as if it is a continuation of the nucellus, giving an impression of a well-developed epistase. But from Text-fig. 16 and Pl. 3, Figs. 16-18 and 22, it will be clear that this structure looking like epistase is not of nucellar origin only and hence is not a true epistase (TEXT-FIG. 16), as it is partly formed by the nucellar cap and partly by the inner integument.

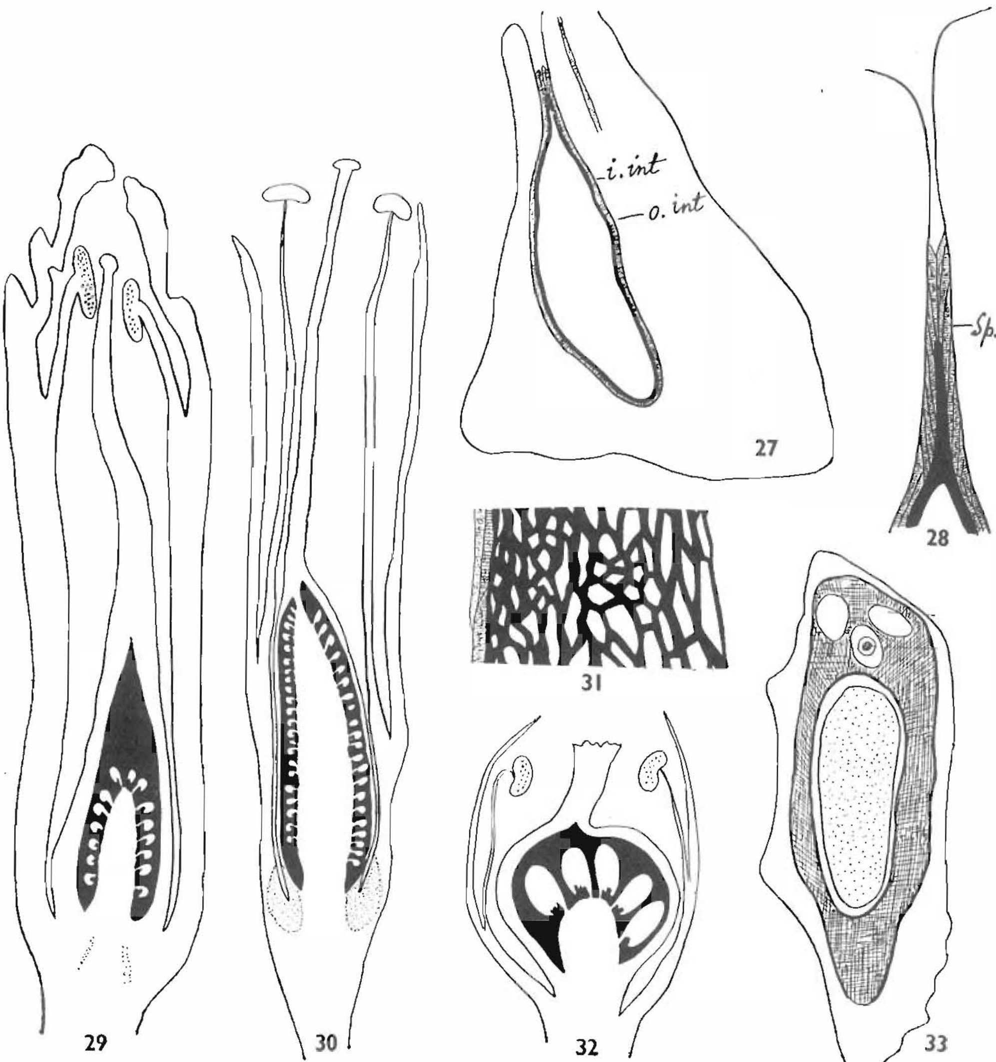
The outer layer of the inner integument divides periclinally in the micropylar region and also on the sides and becomes 2-4 layers thick (TEXT-FIG. 15, *o.i.int.* & PL. 3, FIG. 22). These layers are characterized by spiral and reticulate thickenings on their walls as was noted by Venkateswarlu (1937) in *Duabanga sonneratioides*. Their walls are slightly lignified. They do not get stained with safranin, but do show staining reaction of lignin when treated with aniline sulphate and phloroglucin. They form a complete covering around the embryo which can be removed intact from the seed. These spiral thickenings are generally considered to be a special feature of the Sonneratiaceae; but it may be stated here that they were noticed by us also in a species of *Lagerstroemia*, *L. flos-reginae* belonging to Lythraceae (TEXT-FIGS. 27, 28). The previous workers (JOSHI & VENKATESWARLU, 1935-36) on this plant and other members of this family had not reported them in the genus *Sonneratia* or in the members of Lythraceae.

The outer seed coat: The outer integument becomes many-layered and gets differentiated into many types of cells. Its inner layers are composed of highly thickened cells of different shape (TEXT-FIG. 31). Their walls are thick and lumen very narrow. They have numerous pits. They form sclerotic part of the seed coat. The middle part of the outer seed coat is made up of large, thin-walled cells and some small, slightly thick-walled cells. The former contribute to the formation of the spongy tissue of the seed coat. The small slightly thick-walled cells go to form the outer layers of the seed coat. At the micropylar end the spongy tissue lies between the raphe and the inner thick-walled zone of the outer integument. As the raphe turns towards chalaza, it cuts it through the spongy tissue. A transverse section of the seed at this level shows two spongy areas on either side of the raphe (TEXT-FIG. 33).

The Structure of Mature Fruit — The fruit of *S. acida* (PL. 1, FIG. 8), as stated earlier, is dry and not fleshy like that of *S. apetala* (PL. 1, FIG. 9). It dehisces irregularly by vertical slits in *S. acida* (PL. 1, FIG. 8), whereas in *S. apetala* it breaks open by the deterioration of the fleshy fruit wall. The fruits fall on the mud flats on the seacoast, where these plants grow as mangroves. There are 16-20 loculi to it in *S. acida* (PL. 2, FIGS. 10 & 12) and 5-6 in *S. apetala*. A T.S. of mature fruit in *S. acida* shows a thick central axis to which seeds are attached (PL. 2, FIG. 12). There is a central cavity in the axis in the upper part of the fruit. The wall of the fruit is spongy and composed of thin parenchymatous cells (PL. 2, FIGS. 11 & 13).

Having described the living members, we may now turn our attention to the related fossils. Two well-known Tertiary genera from the Deccan Intertrappean series of Madhya Pradesh are believed to belong to Lythraceae. One is a petrified flower and the other a fruit, called *Enigmocarpon* and *Sahnianthus* respectively and are described in detail by Sahni (1943) and Shukla (1944) respectively. Recently Verma (1956) has described another flower, called *Sahnipushpum shuklai* which he refers also to Sonneratiaceae without giving sufficient reasons. Sahni (1943) and Shukla (1944) have also discussed the affinities of these two fossils and have referred them to Lythraceous affinity. Mrs. Chitaley (1950, 1951, 1955) also has made some additional observations on the presence of bracts and pollen grains in *Sahnianthus*. A re-investigation of these two fossils, therefore, was made for comparing their structures with those in the members of the living Sonneratiaceae and Lythraceae, in order to throw some further light on the problem of their affinities with *Sonneratia* or with some genera of the Lythraceae.

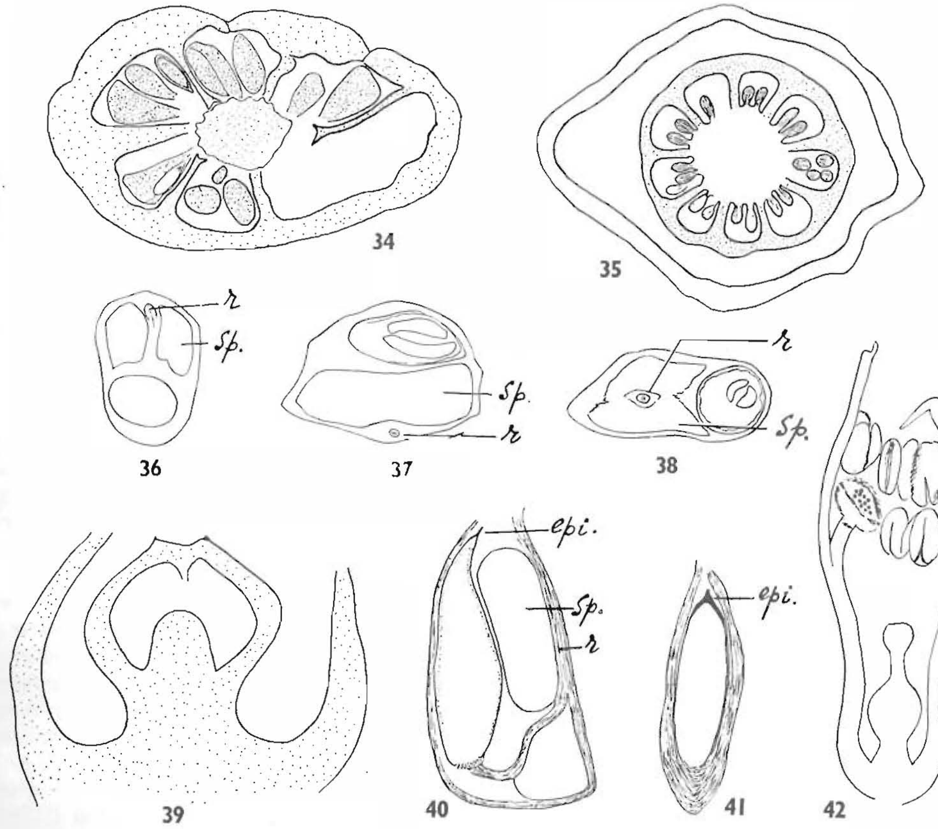
The flower *Sahnianthus* Shukla is actinomorphic and hermaphrodite. Its calyx is valvate and 8-lobed and stores some sort of secretory fluid (PL. 4, FIG. 28). Corolla is absent and stamens are more than 8. Filaments are inflexed in bud. The pollen



TEXT-FIGS. 27-33 — 27, *Lagerstroemia flos-reginae* Retz. L.S. of seed showing scalariform thickenings on the inner lining of the inner integument. × 11. 28, the same with apical part magnified. Note cells with scalariform thickenings. × 42. 29, *Cuphea ignea*. L.S. of flower showing the structure of ovary. × 7·5. 30, *Woodfordia fructicosa* S. Kurz. L.S. of flower showing the structure of the ovary. × 7·5. 31, *S. acida* L. Sclerotic cells in the outer seed coat. × 155. 32, *Ammania baccifera* L. L.S. of flower showing the structure of ovary. × 42. 33, *S. acida* L. T.S. of seed. Note raphe, embryo, and the air-cavities around the raphe. × 18.

grains are tricolpate. The 6-9 locular ovary is said to be stalked (TEXT-FIGS. 35, 39, 42 & PL. 4, FIG. 28). The stalk possibly is the result of the loss of spongy tissue at the base of the ovary while getting fossilized (PL. 4, FIG. 28). The placentation is axile (TEXT-FIGS. 35), but at the top the ovary is incompletely septate. The flowers are described as heterostylous. The stalk of the ovary is partially embedded in the midst of a flabby tissue, possibly nectary as that in *S. acida* (PL. 1, FIGS. 5, 6) (compare PL. 4, FIG. 28 with PL. 4, FIG. 25).

The fruit called *Enigmocarpon parijai* Sahni is 7-9 locular (TEXT-FIG. 34 & PL. 4, FIGS. 23 & 24). It shows loculicidal



TEXT-FIGS. 34-42 — 34, *Enigmocarpon parijai* Sahni. T.S. of fruit. × 3·5. 35, *Sahnianthus* Shukla. T.S. of flower showing ovary with 9 loculi. × 8. 36-38, *Enigmocarpon parijai* Sahni. Seeds T.S.: *r*, raphe; *Sp.*, spongy tissue. × 14. 39, *Sahnianthus* Shukla. L.S. of flower. × 22. 40-41, L.S. of seed of *Enigmocarpon parijai* Sahni, showing the so-called epistase (*epi.*); *sp.*, spongy tissue; *r*, raphe. × 13. 42, *Sahnianthus* Shukla. L.S. of flower. × 13.

[Figs. 36-38 after Sahni (1943) and Fig. 42 after Shukla (1944)]

dehiscence (TEXT-FIG. 34 & PL. 4, FIG. 23), the wall of the fruit being spongy (PL. 4, FIG. 27). The seeds are many; chalaza is obliquely placed; raphe is thick; and seed coat has distinct air-cavities (PL. 4, FIG. 26). Hypostase is present and an epistase-like organ is frayed in between the inner integument (PL. 4, FIG. 26). The structure of the seeds in fossil as given by Sahni (1943) is shown in Text-figs. 36-38 and as seen in our fossil material in L.S. in Text-figs. 40-41 and in Pl. 4, Fig. 26.

DISCUSSION

The Lythraceous affinity of *Sahnianthus* suggested by Shukla rests largely, among other characters, on the presence of the following features made out by him (*see* SHUKLA, 1944): (i) heterostyly, (ii) episepalous stamens, at least 8, (iii) tubular gibbous calyx, (iv) axile placentation, and (v) superior ovary with a stalk. To these may be added the observations made by Mrs. Chitaley (1951, 1955), namely the presence of bracts and nature of the pollen grains. The students of angiosperm embryology very well know that the characters listed above are of such a generalized nature that they are distributed over more than one family. One can, therefore, find them both in Lythraceae as well as in Sonneratiaceae.

The flowers of *Sonneratia* and *Sahnianthus* do have features in common such as the presence of pedicellate flowers, gibbous calyx, valvate sepals, episepalous stamens inflexed in bud, 2-lobed anthers, dorsifixed and curved connective situated at one-third the distance from the tip of the anther, pollen grains with three germ pores, axile placentation, anatropous ovules, micropyle bent towards the funicle, etc. But the flowers of *Sonneratia* (PL. 1, FIG. 7) are very large compared to those of *Sahnianthus*. There is no real heterostyly in *Sahnianthus* as in *Sonneratia*, the length of the style depending only on the developmental stage of the flower (PL. 1, FIGS. 3-8). The ovary is said to be distinctly stalked in *Sahnianthus*, while it is not so in *Sonneratia*. However, from a study of the structures met with in mature flowers of *Sonneratia* and those in *Sahnianthus*, it appears that the stalk of the ovary in the latter is the result of the loss of a spongy tissue of the nectary in fossilization similar to that found surrounding the ovary of *Sonneratia* today (cf. PL. 4, FIGS. 25 & 28 and also with PL. 1, FIGS. 4-6). As a matter of fact even in Lythraceae, excepting the genus *Loffensia*, other members do not have stalked ovary. The bracts and bractioles seen in *Sonneratia* are certainly comparable with those in *Sahnianthus* (PL. 1, FIG. 2 & TEXT-FIGS. 4, 5, 6, 9 & 10).

The pollen grains of *Sahnianthus* as described by Shukla (1944) and Mrs. Chitaley (1951) do not show an important Lythraceous feature given by Engler (1898, p. 18), namely the presence of vertical ridges. The absence of this feature definitely goes against the Lythraceous alliance of *Sahnianthus*, as do the bracts and bracteoles found by Mrs. Chitaley in *Sahnianthus*. As a matter of fact these characters resemble more those in *Sonneratia* than those in any other Lythraceous genera like *Decodon*, *Heimia* and *Grislea* each, because of certain features. In other respects the fossil flower retains its own individuality and very small size, and hence Shukla (1944) considers it to be an extinct member of the fossil Lythraceae. But, as will be seen from above, the resemblances between *Sahnianthus* and *Sonneratia* are far more outstanding than those between any members of Lythraceae; and hence there is a strong probability that the nearest allies of *Sahnianthus* and *Enigmocarpon* were perhaps some members of Sonneratiaceae, living or fossil, rather than members of Lythraceae.

Enigmocarpon — The fruit of *Enigmocarpon parijai* has been fully described by Sahni (1943). It is a capsule showing loculicidal dehiscence. In *S. acida*, the fruit wall gets dried up and shows a few vertical cracks. There is, however, no regular loculicidal dehiscence in it, or in any other species of *Sonneratia* as in *Enigmocarpon*.

The seed structure of *Enigmocarpon* has also been very fully described by Sahni (1943). These seeds show a considerable similarity to the seeds of *Sonneratia* in point of shape, raphe and its course, the presence and distribution of the spongy tissue, presence of epistase-like structure, not found in the Lythraceae. There is spongy tissue between the vascular bundle and thick cells of the seed coat in *Enigmocarpon*, just as in *S. acida* and *S. apetala*. In both of them, as the raphe turns towards the vascular bundle, it forms hypostase and divides the spongy tissue into two parts, on account of which the spongy tissue comes to lie on the outer side of the raphe later. However, the development of spongy tissue in *Sonneratia* is poor as compared with that in *Enigmocarpon* in which it is very conspicuous. The long thick-walled fibres seen on the outer side of the spongy tissue in *Enigmocarpon* are absent in *Sonneratia*, but their place is taken by small and thick-walled cells found in the latter.

A characteristic feature of the seed of *Enigmocarpon* described by Sahni (1943) is epistase. He considers it to be a very important organ of this seed. But, as already remarked, real epistase developed from the nucellus is on the whole a rarity in plants, and, therefore, a careful search of it was made by studying young and matured seeds in the two species of *Sonneratia* under investigation and in members of the Lythraceae like *Lagerstroemia*, *Ammania*, *Woodfordia* and *Cuphea* (TEXT-FIGS. 27-30 & 32). It was found that the whip-like process of the epistase-like organ in *Enigmocarpon* really represents the compressed end of the inner integument which is slightly longer than the outer one. The persistent nucellar cap is pushed in it and it forms the basal triangular part of the so-called epistase in *Enigmocarpon* and gets adpressed. Its upper end is frayed into micropyle and looks like a continuation of the nucellar cap lying under it. But in this connection, it may be stated here that a similar structure was also noticed by us in *Ammania* and *Cuphea*. A re-examination of the fossil fruit *Enigmocarpon* showed that there is no true epistase in this plant, morphologically identical with the epistase of the

Malpighiaceae and the other families. It is really the nucellar cap adpressed against the thin, tailed, whip-like portion of the inner integument similar to what is found in species of *Sonneratia* like *S. acida* or *S. apetala*. The so-called epistase in *Enigmocarpon*, therefore, is a composite structure formed by the compressed inner wall of the inner integument, as was suggested by Maheshwari (*see* SAHNI, 1943, footnote on p. 75), plus the nucellar cap found in this investigation. The fruit and seed structure of *Enigmocarpon* thus shows closer resemblance to *Sonneratia* than to members of the Lythraceae and hence its affinities are more intimate with the Sonneratiaceae. It should, however, be realized that while discussing the affinities of a flower or fruit, now perhaps more than 60 million years ago, one has to be very cautious, and must be ready to revise his opinion if and when the new facts come to light. But, for the present, they strongly suggest Sonneratiaceous affinities for *Sahnianthus* and *Enigmocarpon* rather than Lythraceous, unless one visualizes that in such a distant past the two families might have been together and got separated later in the post-Eocene period, which may not be unlikely.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATE 1

1. *S. apetala* Ham. A tree growing near a fresh-water creek at Mumbra, Bombay.
2. *S. acida* L. L.S. of young flower showing bracts and leaf. × 3·3.
3. The same showing a little more advanced stage. × 3·3
4. *S. apetala* Ham. L.S. of a young flower. Note contorted style and large funnel-shaped stigma. × 4.
5, 6. *S. acida* L. L.S. of flower showing the structure of ovary, style, stigma and nectary at the base of the ovary. (FIG. 5 — × 2 and FIG. 6 — × 41).
7. *S. acida* L. A flower fully opened at night. × ½ N.S.
8. *S. acida* L. A fruit: Note the long persistent style. × ⅔ N.S.
9. *S. apetala* Ham. Fruit: Note the persistent calyx in this species. × ¼ N.S.

PLATE 2

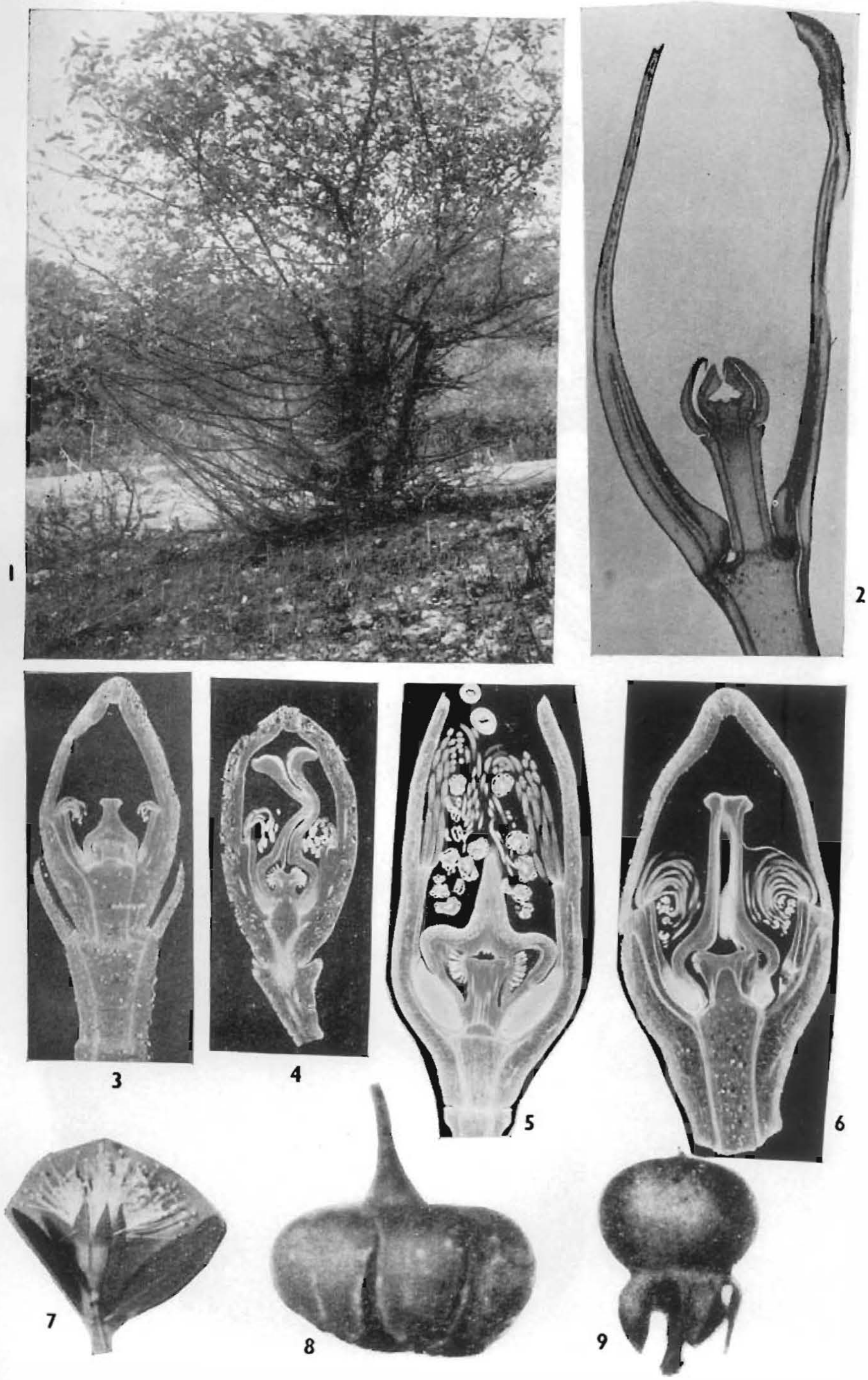
10-15. *S. acida* L. showing the structure of ovary, its wall, carpels, fruit and seed.
10. T.S. of fruit showing seeds cut in different planes. × 4.
11. T.S. of a part of ovary showing two carpellary chambers. × 19.
12. T.S. of a fully matured fruit. × 2.
13. T.S. of wall showing loose cells full of air-cavities and nests of sclereids. × 38.
14. Pollen grains. × 400.
15. L.S. of a mature ovule showing hypostase (*hy*), embryo sac, and raphe × 115.

PLATE 3

16. *S. acida* L. L.S. of seed showing two integuments and nucellar cap projecting in the micropyle. Note the frayed end of nucellar cap (*epi*) lying in between the inner integument. × 20.
17. *S. acida* L. L.S. of a young seed showing embryo and the so-called epistase (*epi*) formed by the long frayed end of the nucellar cap. × 20.
18. The same in slightly older ovule. Note the nucellar cap (*n.c.*). × 20.
19. *S. apetala* Ham. L.S. of a ovule showing hypostase (*hy.*) and the embryo cavity. × 20.
20. Pollen grains. × 500.
21. *S. apetala* Ham. Cells of hypostase full of dark cell-contents. × 200.
22. *S. acida* L. L.S. of mature seed showing nucellar cap, scalariform thickenings on the outer lining of the inner integument and thin cells of the inner linings of the inner integument. × 38.

PLATE 4

23. *Emigmocarpon parijai* Sahni. L.S. of fruit (obliquely fractured). × 7.
24. The same in T.S. showing 8 loculi in the upper part of the fruit and the hollow cavity in the central receptacle. × 2½ N.S. (After SAHNI, 1943).
25. *S. acida* L. L.S. of a flower bud showing nectary (N) around the base of the ovary. × 10.
26. *Enigmocarpon parijai* Sahni. L.S. of two seeds. Note the nucellar cap and the so-called epistase in the two seeds. × 29.
27. *Enigmocarpon parijai* Sahni. Wall of the fossil fruit showing loose air-cavities and nests of sclereids like those seen in the fruit wall of *S. acida* L. shown in Fig. 55. × 20.
28. *Sahnianthus* Shukla. L.S. of flower showing the structure of the ovary and the cavity formed around it by the loose tissue of nectary. × 34. This is taken as hypanthum by some authors.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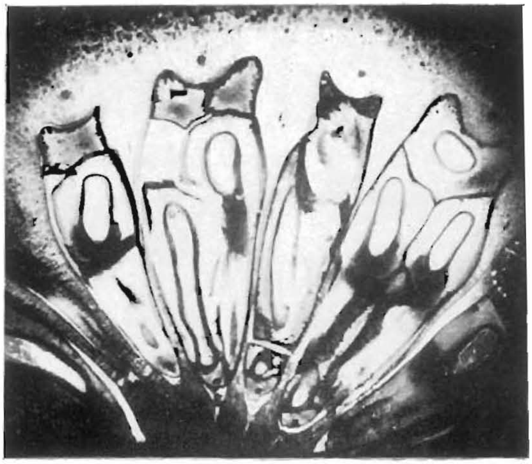
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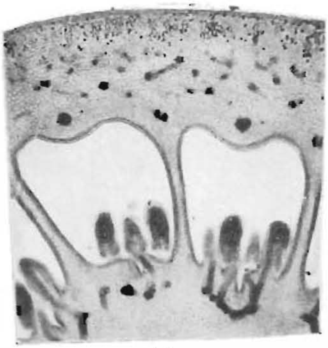
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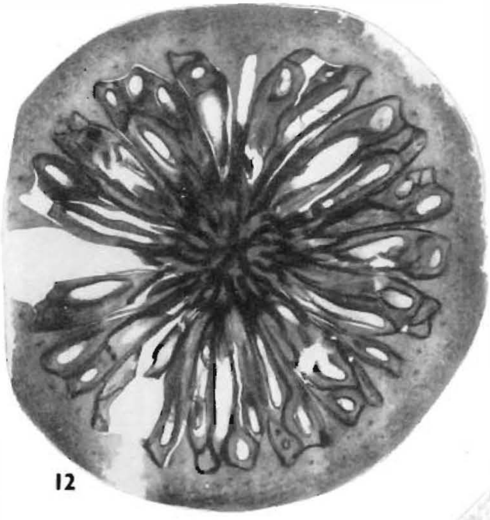
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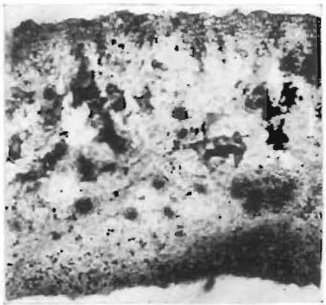
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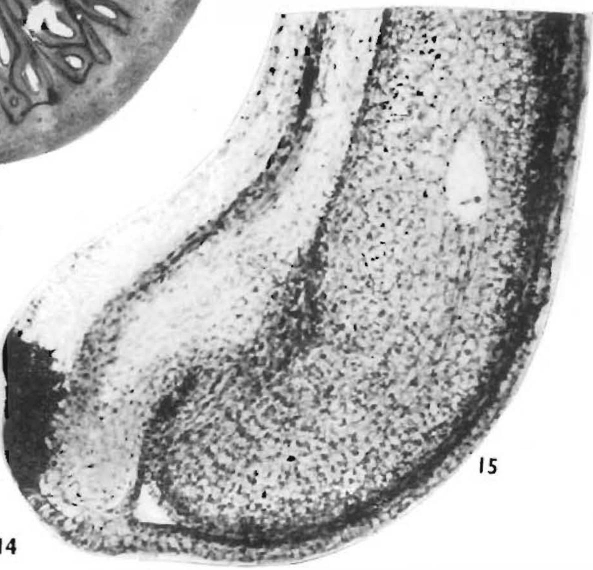
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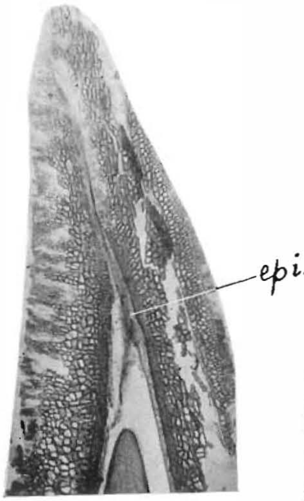

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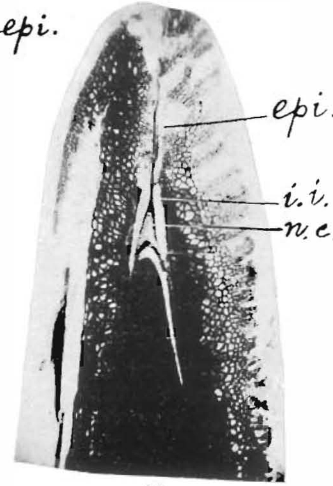

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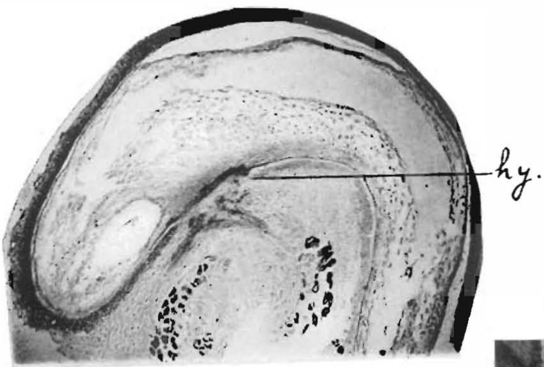

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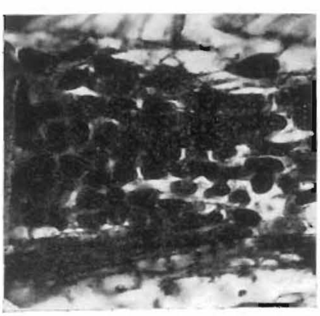
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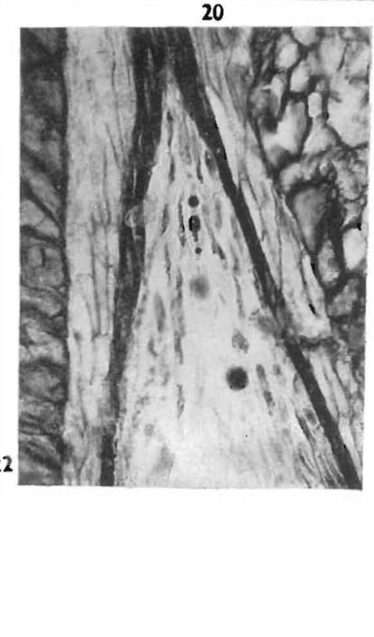

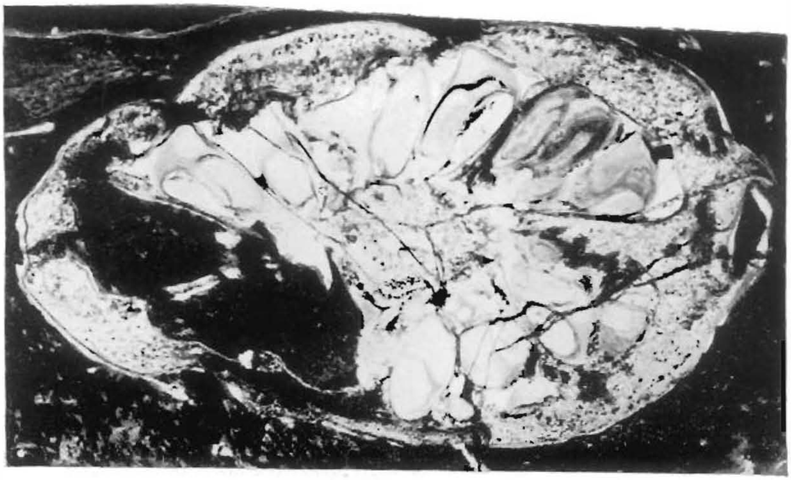

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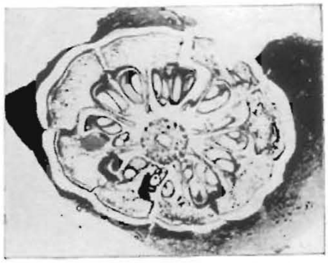

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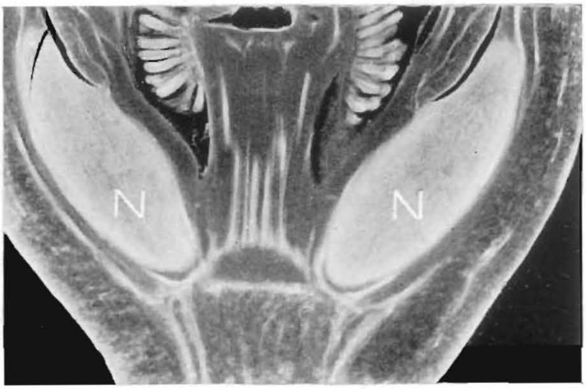

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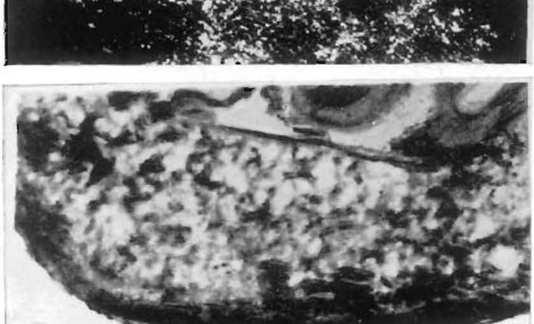

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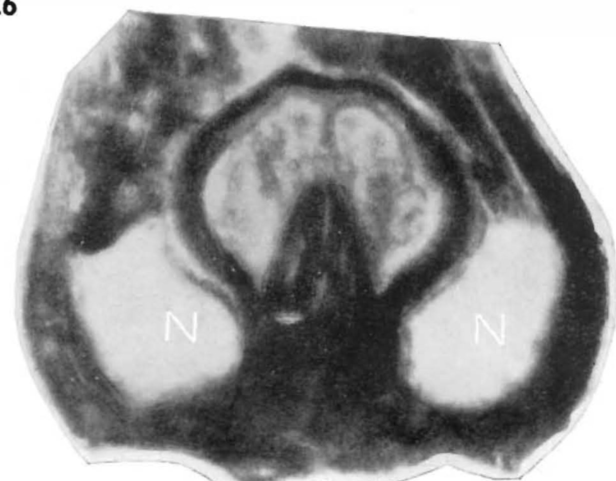

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