

PACIFIC CAPSULAR MYRTACEAE I.  
REPRODUCTIVE MORPHOLOGY OF ARILLASTRUM  
GUMMIFERUM PANCH. EX BAILLON (NEW CALEDONIA)<sup>1</sup>

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INTRODUCTION

Niendenzu (in E. & P., Nat. Pfl. Fam. 3, 7, 1893, 87—89) included the following genera in his subtribe *Metrosiderinae*: *Metrosideros*, *Spermolepis*<sup>2</sup> (= *Arillastrum*), *Lysicarpus*, *Cloëzia*, *Tepualia*, *Syncarpia*, *Xanthostemon*, *Pleurocalyptus*, and *Tristania*. The *Metrosiderinae* was distinguished from the *Leptosperminae* by usually having flowers in axillary groups, not solitary, and from the *Eucalyptinae* by having narrow, not broad based petals.

A preliminary survey of the above genera indicates that Niendenzu's subtribe *Metrosiderinae* is not a natural group and in this paper, the first of a series, a critical examination of reproductive features of *Arillastrum* Panch. ex Baillon leads to the conclusion that this genus, notwithstanding its narrow petal bases, is most nearly related to the genera comprising Niendenzu's subtribe *Eucalyptinae*.

*Arillastrum* is a monotypic genus endemic to New Caledonia. It is a tree up to 30 metres high and it was formerly common at lower elevations on serpentine terrain in the southern part of the island, where it often formed almost pure stands. The vernacular name for the species is 'Chêne gomme' (gum oak), which reflects both its value as timber and the abundance of a resinous secretion.

The leaves (fig. 1) are opposite, with petioles several centimetres long and broadly ovate, dorsiventral laminae up to 15 × 10 cm.

MORPHOLOGY

**Inflorescences**

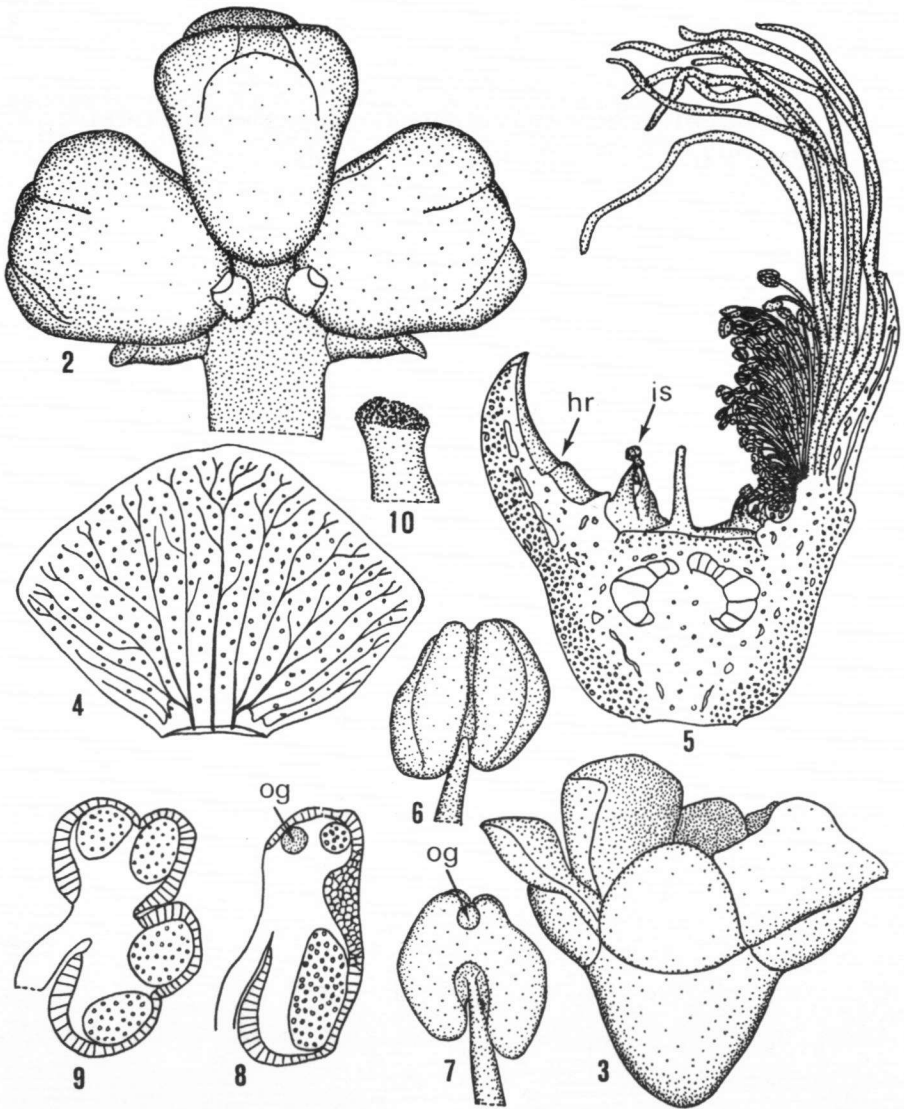
The inflorescences develop in the axils of the last 3—6 pairs of leaves on a branch which terminates in a dormant vegetative bud. The subtending leaves become progressively reduced in size towards the branch tips (fig. 1).

The peduncles are up to 5 or 6 cm long and broaden distally to about 5—6 mm wide. They are strongly flattened dorsiventrally.

The inflorescences are cymose and where the number in a group is large the lowermost may have 7 flowers each, with a reduction usually to 3 for those nearer the branch tip (fig. 2). The flowers are completely sessile. Each terminal flower is ebracteate and each

<sup>1</sup> I am very grateful to Dr H. S. McKee and M. J. M. Veillon for collecting the material on which this account is based.

<sup>2</sup> *Spermolepis* Brongniart and Gris (Bull. Soc. Bot. Fr. 10, 1863, 577) was invalid as Rafinesque (Neogenyt. 1825, 2) had already used the name for a genus of the *Umbelliferae*. Baillon (Hist. Pl. 6, 1877, 363) adopted the name *Arillastrum*, which was originally suggested by Pancher, the collector of the type material.



Figs 2—10. *Arillastrum gummiferum* Panch. ex Baill. — 2. Inflorescence with 3 flower buds,  $\times 2\frac{1}{2}$ . — 3. Habit of flower with stamens removed,  $\times 2\frac{1}{2}$ . — 4. Petal; open circles: oil glands; solid spots: stone cells;  $\times 5$ . — 5. L. S. flower through sepal to left and petal and inner and outer stamen groups to right; oil glands and oil tubes outlined; solid spots: stone cells; hr: hypanthial rim; is: inner stamens;  $\times 4$ . — 6. Front view anther,  $\times 32$ . — 7. Rear view anther; og: oil gland;  $\times 32$ . — 8. Near median L. S. anther; og: oil gland;  $\times 64$ . — 9. T. S. anther,  $\times 64$ . — 10. Stigma,  $\times 32$ .

lateral flower is subtended by a bract and has a pair of bracteoles at its base. The bracts and bracteoles are narrow, thick, and obliquely truncated at the tip (fig. 2).

### Perianth

Each flower has 4 free sepals and 4 free petals (fig. 3), imbricate in the bud. The sepals are thick and semi-orbicular with usually 3 vascular strands entering at the base. The petals (fig. 4) are moderately thick, white to cream in colour, broadly rhomboidal to almost orbicular and narrowed to the base, where usually 3 vascular strands enter. Both sepals and petals have numerous scattered stone cells and spherical oil glands and in addition continuous oil tubes accompanying the veins on their adaxial sides. The sepals and petals are inserted to the outside of a continuous ledge which may be regarded as the upper rim of the largely nectar-secreting tissue lining the inner surface of the hypanthium.

### Stamens

The stamens arise in 4 main, tangentially elongated groups from the hypanthial rim, the centre of each group being situated inward from the insertion of a petal (fig. 5, 18). Adjacent groups almost meet in front of the sepals. They are up to 20 filaments long at their outer edges and up to 10 filaments wide adjacent to the petal insertions. The outermost 2 or 3 rows of filaments have no anthers and are thus staminodes. They are coarse, long, and often irregularly twisted (fig. 5). The outermost stamens are usually only about half as long as the staminodes and the filaments of the other stamens become progressively shorter and more slender in an inward direction (fig. 5). There is no fusion among the stamens or staminodes.

Between each main stamen group and the position where the hypanthial lining overlaps the top of the ovary there is a smaller group of 10—20 stamens, irregularly fused in 1 or 2 row(s) (fig. 5). Most of these inner stamens have an abnormal appearance with short filaments, narrowing abruptly from broad bases, and relatively large anthers of an irregular shape. Occasional appendages appear to be intermediate in form between stamens and styles.

The inner stamens curve outward while those of the outer groups curve inward.

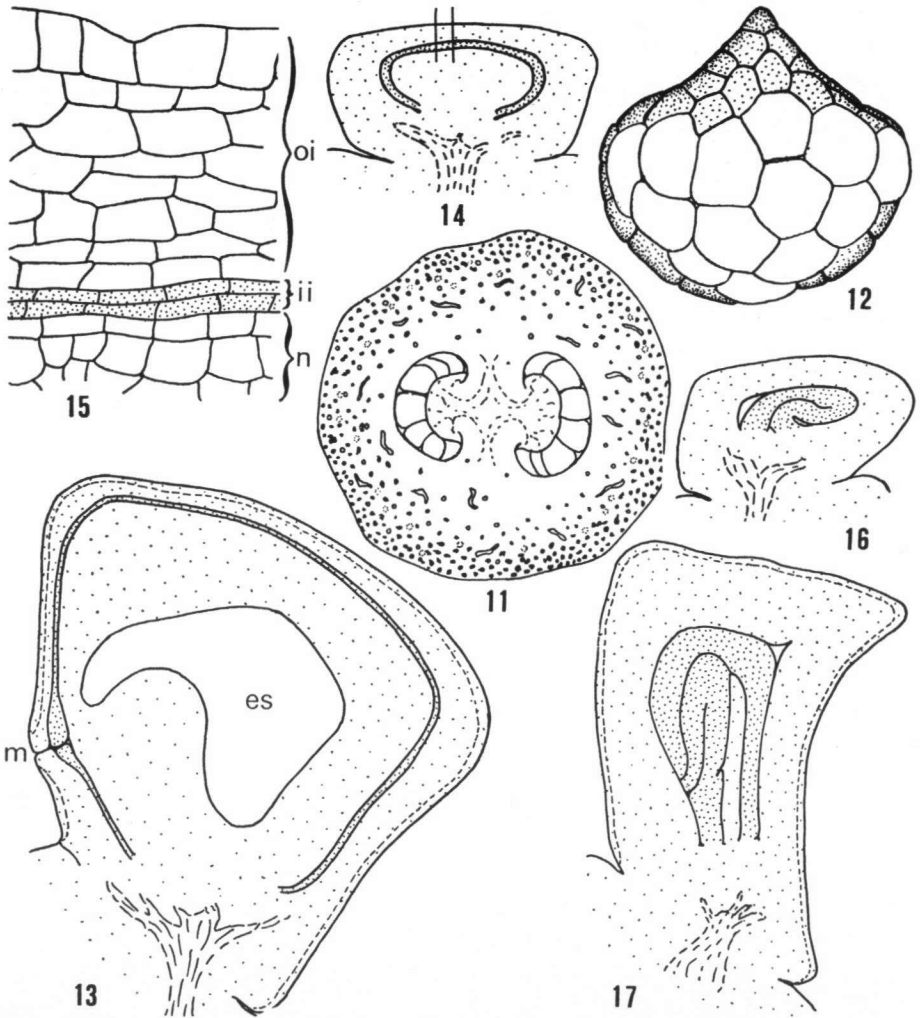
The anthers of the normal stamens (fig. 6, 7) are dorsifixed and versatile with 4 pollen sacs and longitudinal dehiscence. There is a single prominent oil gland at the tip of the anther above the insertion of the filament (fig. 7, 8). At maturity the epidermis of the anther has disappeared (fig. 8, 9).

### Style

The free surface of the ovary is nearly flat to moderately convex. The style, which is not sunken into the apex of the ovary, is short and solid with a small convex stigma (fig. 5, 10).

### Placentation

There are 2 locules in the ovary (fig. 11) which is completely inferior (fig. 5). The placentas are axile, almost circular in outline but narrowing to a point at the top. They bear ovules and ovulodes in a distinctive pattern (fig. 12). The small ovulodes occupy the narrow upper part and the periphery of the placenta and so surround the more or less centrally located ovules. There are about twice as many ovulodes as ovules, on an average 24 of the former to 12 of the latter.



Figs 11—17. *Arillastrum gummiferum* Panch. ex Baill. — 11. T. S. ovary; oil glands and oil tubes outlined; solid spots: stone cells; dotted circles: vascular bundles;  $\times 5$ . — 12. Group of ovules and ovulodes; ovulodes stippled;  $\times 12$ . — 13. L. S. ovule from open flower; light stipple: nucellus and outer integument; dark stipple: inner integument; m: micropyle; es: embryo sac; the pigmented outer epidermis of the outer integument is indicated by the broken line;  $\times 70$ . — 14. Ovule from advanced flower bud; L. S. at right angles to plane of section of fig. 13; light stipple: nucellus and outer integument; dark stipple: inner integument;  $\times 70$ . — 15. Cell detail of integuments and nucellus of lined part in fig. 14; oi: outer integument; ii: inner integument; n: nucellus;  $\times 500$ . — 16. L. S. ovulode from advanced flower bud; dark stipple: inner integument; light stipple: outer integument;  $\times 70$ . — 17. L. S. ovulode from open flower; dark stipple: inner integument; light stipple: outer integument and nucellus;  $\times 70$ .

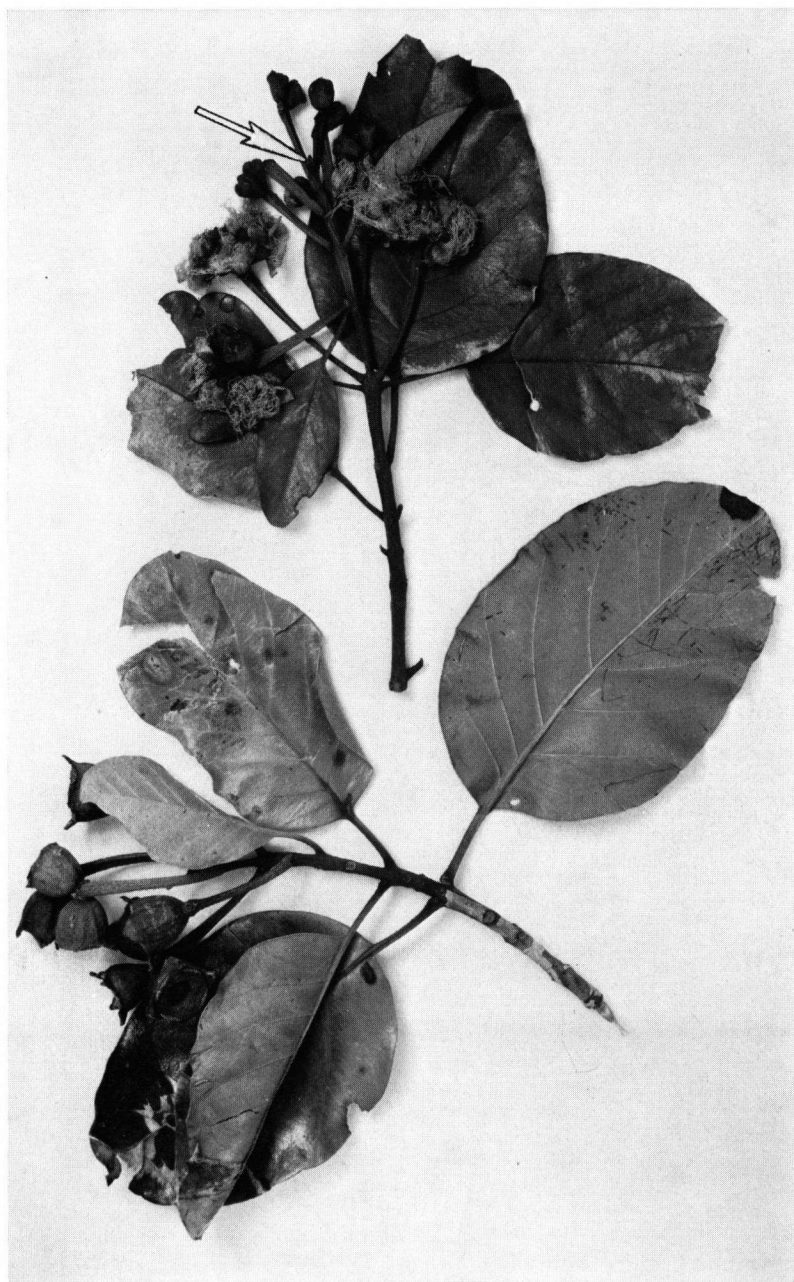


Fig. 1. *Arillastrum gummiferum* Panch. ex Baill. — Habit of leaves and flowering and fruiting branch tips. The arrow indicates the dormant vegetative apex of the flowering branch;  $\times \frac{1}{2}$ . (Photo M. D. King, Vict. Univ., Wellington).

### Ovules and ovulodes

The ovules are campylotropous and crassinucellar with 2 integuments (fig. 13). On the side of the ovule furthest from the chalaza (fig. 14, 15) the outer integument is 6—8 cells thick and the inner integument 2 cells thick. At this stage the cells of the outer epidermis of the outer integument have brown contents, presumably tannin. Both integuments increase in thickness towards the chalaza.

The ovulodes are also campylotropous with thick inner and outer integuments and a rudimentary nucellus (fig. 16, 17).

### Fruit

The fruit becomes very hard and woody (fig. 1). The sepals are persistent and the scars of the petals and outer, but not inner, groups of stamens are usually discernable (fig. 18). The capsule splits open loculicidally and the style is often split into 2 parts. (fig. 18).

### Seeds

Usually only one of the ovules in each locule matures into a fertile seed. It becomes more or less kidney-shaped and as it takes up most of the space in the locule, it becomes closely invested by the flattened, scale-like structures derived from the enlarged abortive ovules (fig. 18). The ovulodes mature into smaller structures which do not become so strongly flattened (fig. 20).

When the fertile seed is removed 6 or 7 of the scales derived from the abortive ovules remain attached to it at the base by cobweb-like material (fig. 21). These scales were mistakenly interpreted by Pancher as an aril. The 'cobweb' is an open network of a transparent substance (fig. 22) with a pattern very similar to that of the epidermal cells of the scales. Perhaps it is derived from some substance secreted by the testa of the fertile seed which solidifies in the depressions external to the radial walls of the epidermal cells of the scales.

The hilum of the fertile seed is quite large with the vascular bundle scar usually centrally located (fig. 23). The micropyle and its associated testa ridge is situated near to the hilum (fig. 23).

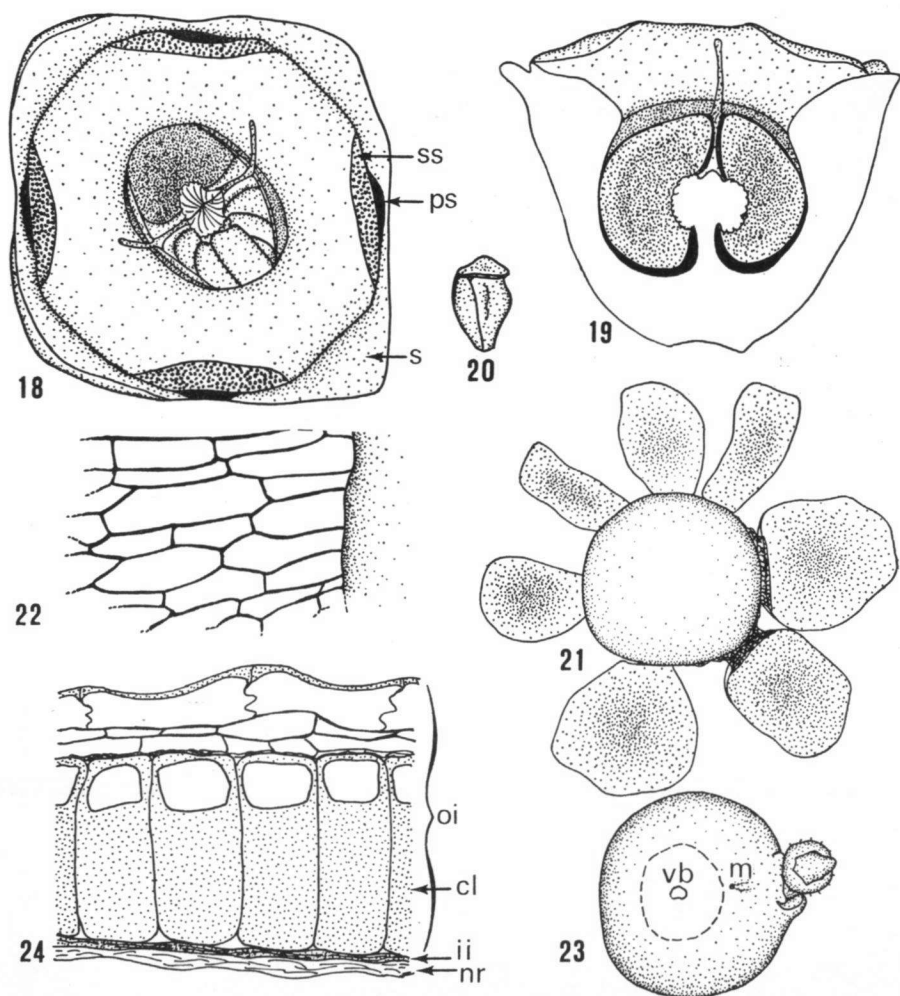
The testa is derived from both integuments (fig. 24). The cells of the inner epidermis of the outer integument enlarge greatly in a radial direction and their walls, particularly the outer walls, become very heavily thickened. The small lumen of each cell becomes filled with a single prismatic crystal. The outer layers of the outer integument have brown contents. The cells of the outer epidermis are elongated tangentially and have moderately thickened outer walls. The middle cell layers have little wall thickening and are often completely collapsed. The cells of the inner integument also have brown contents and moderately thickened walls and are greatly flattened tangentially. Inside the inner integument flattened remnants of nucellus tissue are discernable.

In the position of the hilum (fig. 25) the 'crystal layer' of the outer integument is interrupted, but the outer layers are continuous. Here also the inner integument expands into a brown coloured tissue many layers thick.

The nucellar remnant also increases in thickness beneath the hilum.

The scales derived from the abortive ovules consist of little more than the outer epidermis of the outer integument in which the outer and radial cell walls have become greatly thickened (fig. 26). In places a few inner cells of the outer integument are also present.

In the derivatives of the ovulodes both integuments are represented in the testa (fig. 27, 28). As in the abortive ovules the outer epidermis of the outer integument has cells with



Figs 18—24. *Arillastrum gummiferum* Panch. ex Baill. — 18. View of upper surface of dehiscent fruit with one locule empty and the other containing a fertile seed enclosed by abortive ovule scales; s: sepal; ss: stamen scars; ps: petal scar; x  $2\frac{1}{2}$ . — 19. L. S. mature fruit with ovules and ovulodes removed, x  $2\frac{1}{2}$ . — 20. Habit of ovulode, x 5. — 21. Habit of fertile seed with attached abortive ovule scales, x 5. — 22. Detail of 'cobweb' material with part of fertile seed to right, x 70. — 23. Ventral view of germinating fertile seed; hilum outlined by broken line; vb: vascular bundle scar; m: micropyle; x 5. — 24. Cell detail of section through testa of fertile seed; oi: outer integument; cl: crystal layer; ii: inner integument; nr: nucellus remnant; x 500.

thickened outer and radial walls. The inner layers of the outer integument are enlarged and irregularly thickened and the cells of the inner integument have moderately thickened walls and are greatly flattened.

### Embryo

The embryo completely fills the seed coat (fig. 29). The hypocotyl lies more or less parallel to the hilum surface, so that the radicle is situated, and later emerges, at some distance from the micropyle. The small radicle is almost completely enclosed by an integument or sheath-like outgrowth from the hypocotyl (fig. 29, 30) which is in contact with the testa.

The epicotyl is rudimentary and covered with short, stout, multicellular hairs (fig. 29, 31).

The cotyledons (fig. 32) are large, more or less kidney-shaped, and about  $1\frac{1}{2}$  times broader than long with one lateral half somewhat narrower than the other. They are strongly deflexed in the seed, almost to the base of the hypocotyl, and are then folded upwards, so that the tip of each cotyledon comes to lie close to its base. (fig. 29). The narrower half of each cotyledon is enclosed by the broader half of the other (fig. 29, 31).

At germination the hypocotyl breaks through the testa at some distance from the micropyle (fig. 23) and the radicle begins to grow out rapidly from the hypocotyl sheath (fig. 33).

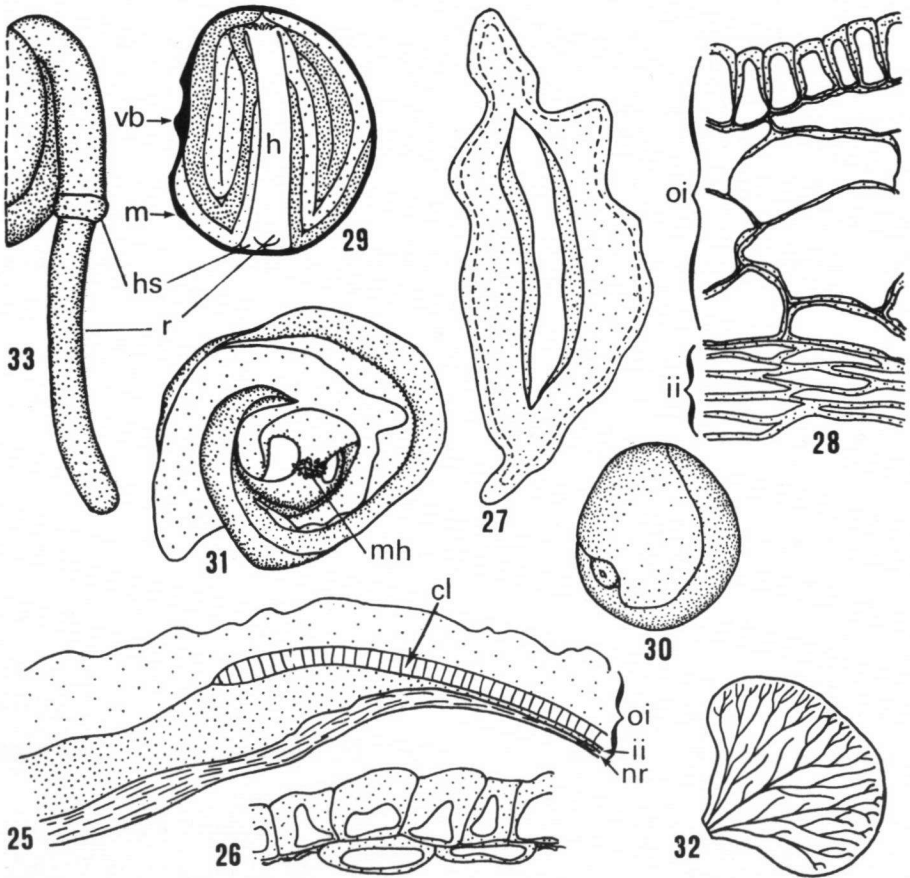
### DISCUSSION

The foregoing account shows that *Arillastrum* differs from the type genus (see part 2 of this series) of Niedenzu's subtribe *Metrosiderinae* in many features. The most outstanding of these distinguishing features of *Arillastrum* are as follows:

(a) Stone cells; (b) oil tubes; (c) stamens in groups; (d) stamens in many whorls; (e) staminodes; (f) ovulodes; (g) constant pattern in arrangement of ovules and ovulodes on the placenta; (h) campylotropous ovules; (i) multilayered outer integument; (j) single fertile seed per locule; (k) 'cobweb' material attaching sterile seed to fertile seed; (l) crystal layer in testa; (m) radicle not emerging through micropyle; (n) hypocotyl sheath; (o) broad cotyledons; (p) deflexed cotyledons; (q) cotyledons partly enclosing each other; (r) distal half of cotyledons reflexed.

Features, c, d, e, f, g, h, i, j, l, m, n, o, p, q are also reported for at least some species of *Eucalyptus* and related genera. Features a, b, k, r may be peculiar to *Arillastrum*.





Figs 25—33. *Arillastrum gummiferum* Panch. ex Baill. — 25. L. S. testa of fertile seed at boundary of hilum; oi: outer integument; cl: crystal layer; ii: inner integument; nr: nucellus remnant; x 70. — 26. T. S. testa of abortive ovule scale, x 500. — 27. T. S. structure derived from an ovulode; dark stipple: inner integument; light stipple: outer integument; x 50. — 28. Cell detail; T. S. testa of ovulode; oi: outer integument; ii: inner integument; x 500. — 29. L. S. fertile seed in plane of hilum and micropyle; one cotyledon with dark, the other with light stipple; vb: vascular bundle scar; m: micropyle; h: hypocotyl; hs: hypocotyl sheath; r: radicle; x 8. — 30. Dormant embryo with hypocotyl sheath and radicle visible at lower left, x 5. — 31. View of young seedling from above to show how cotyledons are folded into each other; one cotyledon with dark, the other with light stipple; mh: multicellular hairs covering epicotyl; x 5. — 32. Cotyledon, x 2½. — 33. Hypocotyl and radicle of germinating seed; hs: hypocotyl sheath; r: radicle; x 5.