Preliminary Observations on Floral Biology in Mangrove Rhizophoraceae

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ABSTRACT

The tribe Rhizophoreae (Rhizophoraceae) includes the largest taxonomic assemblage exclusively of mangroves, with 4 genera and about 18 species. *Rhizophora* is pan-tropical; *Bruguiera*, *Ceriops*, and *Kandelia* have an Indo-Malayan distribution. All species have the same basic floral structure, but field observations demonstrate a wide variety of pollination mechanisms. Variation in such features as size and orientation of flowers, number of flowers per inflorescence, number of stamens, time of stamen dehiscence, and method of pollen discharge can be shown to have direct relevance to pollination biology. Pollen vectors may be predominantly wind (*Rhizophora*, as deduced from circumstantial evidence) or animals (remaining genera, as observed directly). An explosive method of pollen release occurs in *Bruguiera* and *Ceriops tagal*, but is modified to suit a range of flower visitors such as birds in the large-flowered *Bruguiera* species (e.g., *B. gymnorrhiza*) or butterflies and other insects in the small-flowered *Bruguiera* species (e.g., *B. parviflora*) and moths in *Ceriops tagal*. *Ceriops decandra* lacks the explosive mechanism of pollen release, as does *Kandelia*. Since these taxa often form mixed communities a high degree of partitioning of pollinator resource is achieved.

INTEREST IN THE REPRODUCTIVE BIOLOGY of mangroves has largely centered on seedling development and dispersal since embryo development on the parent plant to a seedling stage (vivipary) is more frequently shown in this group of plants than in any other. Studies on floral ecology are very few, as van Steenis (1958) points out, but knowledge of reproductive capacity and interspecific sterility barriers must begin with a consideration of flower function. The most extensive studies are those of Guppy (1906) on *Rhizophora*. The present account is a summary of information obtained during field work in mangrove communities, mainly in Papua New Guinea and Queensland, and surveys floral biology of Rhizophoraceae in a provisional way. Field work provided the opportunity to observe flower visitors and floral mechanisms in *Bruguiera*, *Ceriops*, and *Rhizophora*. Additional information has come from other parts of the South Pacific (mainly Fiji and New Caledonia) and in South Florida. No field observations on *Kandelia* have been made. Although information is incomplete it is sufficient to demonstrate a wide range of pollination mechanisms which occur in plants with a fundamentally similar floral construction, suggesting a fairly complete division of pollinator resources.

The field observations have been supplemented by detailed morphological, anatomical, and developmental studies of fluid-preserved material, which will form the basis for a separate comparative account. All taxa in the section Rhizophoreae of Rhizophoraceae have been studied, and the comparative data accumulated permit some speculation about floral evolution, although this must remain tentative until comparable information for non-mangrove Rhizophoraceae has been assembled.

That the Rhizophoreae include distinctive floral mechanisms is evident from the early summary and reports of Gehrmann (1911) and Porsch (1924, p. 611) who recorded the explosive method of pollen release in *Bruguiera sexangula*, associated with bird visitors, an observation more recently confirmed by Davey (1975) in southeast Africa. We can now report that all *Bruguiera* species have explosive pollen release, but that two main agents trigger the process, insects in the small-flowered species, birds in the large-flowered species. *Ceriops tagal* is similarly explosive, but triggered mainly by moths. *Ceriops decandra* lacks explosive dehiscence, and pollen vectors are as yet unknown.

Despite the abundance and wide distribution of *Rhizophora* there is no extended treatment of its floral biology. Guppy (1906) provided information about floral mechanism in Fijian *Rhizophora* species, but did not comment on vectors. Gill and Tomlinson (1969) have suggested, but without much supporting evidence, that *R. mangle* is wind-pollinated; Kress (1975) observed insect visitors to *Rhi*-

zophora in South Florida; and there is one record of bees visiting the flowers of *R. stylosa* in Java (Docters van Leeuwen, 1927). Our comparative observations lead us to the conclusion that the flowers of most *Rhizophora* species are basically wind-pollinated, although they may be a pollen source for insects and may even retain vestiges of insect attraction in odor and nectar. *Rhizophora stylosa* appears to be pollinated by small bees and wind.

Since the taxa involved are wide-ranging (pantropical in *Rhizophora*) and our field work is necessarily geographically restricted, it is clear that our descriptions must serve only as an introduction and our conclusions may not be universally applicable. Further field studies in different geographic areas are needed. At the same time our observations are sufficiently complete to indicate an example of adaptive biological radiation in a widespread and economically important tropical group which is probably monophyletic.

MATERIALS AND METHODS

Most detailed observations were made at field sites in Queensland (3 Mile Creek and Cape Ferguson, Townsville and Missionary Bay, Hinchinbrook Island), but these have been supplemented by more general observations in Australasia. Unless otherwise stated, observations refer to the Queensland localities.

TABLE 1. *The number of pollen grains per flower (P), ovules per flower (O), and pollen grains produced per ovule (P/O) in species of the Rhizophoraceae. The number of pollen grains per flower and per ovule are given in thousands; ovule numbers are the most commonly observed values.*

Genus and species	P x 10³	O	P/O x 10³	Pollen vector
Rhizophora apiculata	5256	4	1314	
R. mucronata	2096	4	524	Wind
R. X lamarckii[a]	4000	4	1000	
Bruguiera (Type 1)				
B. *gymnorrhiza*	1800	6	300	
B. *exaristata*	1080	6	180	Birds
Bruguiera (Type 2)				
B. *cylindrica*	176	6	29	
B. *parviflora*	4.8	6	0.8	Insects
Ceriops decandra	84	4	21	(Insects?)
Ceriops tagal	9.2	6	1.5	Moths
Kandelia candel	659	6	170	(Insects?)

[a]Pollen frequently aborted.

DETERMINATION OF POLLEN-OVULE RATIOS.—To determine the number of pollen grains produced per flower and the number of pollen grains produced per ovule (P/O ratio), two anthers were dissected from

unopened flowers. The anthers were macerated completely in several drops of filtered sea water. Additional filtered sea water was added to bring the suspension of particulates up to a volume of approximately 10 ml. The suspension was violently agitated for 30 seconds to free any pollen grains still enclosed by the anther tissue, and then filtered through a 50 micron screen mesh to remove tissue debris. Virtually no pollen grains were trapped in this screen, nor did they clump or settle, at least within the few minutes that the suspension was utilized. A Coulter Counter (model TAII, Coulter Electronics, Hialeah, Florida), normally used for counting cell numbers as in blood samples, was then used to count the number of pollen grains in a subsample of this suspension, or if the pollen density was still too high to count, in a more dilute suspension. Successive subsamples from the same pollen suspension gave virtually identical counts. The number of pollen grains in each of two anthers of *Bruguiera parviflora*, *Ceriops tagal*, and *Kandelia candel* were counted completely after the anthers were macerated in a drop of iodine solution.

In order to confirm the results of the Coulter Counter, two anthers each of *Bruguiera gymnorrhiza*, *Rhizophora mucronata*, *R. X lamarckii*, and *R. apiculata* were macerated, agitated and suspended in 4 ml of a solution of 1 part aqueous iodine to 2 parts glycerine. The pollen grains suspended in one drop (0.025 ml) of this solution were counted. This manual counting method gave similar results to the Coulter Counter figures, supporting the validity of both approaches. The results are presented in table 1.

STIGMA RECEPTIVITY.—The onset of stigma receptivity in *Bruguiera exaristata* and *Rhizophora stylosa* was determined by floating stigmas in α naphthylacetate. This produced a color reaction, i.e., metabolically active surface cells indicative of esterase activity, by coupling with hexazotised pararosanilin, which in turn is indicative of stigma receptivity (Heslop-Harrison *et al.* 1975).

TAXONOMY

The section Rhizophoreae of Rhizophoraceae includes four genera distinguished by their exclusively mangrove habitat and marked vivipary such that the hypocotyl of the embryo protrudes from the fruit while still on the parent tree, the seedling being the unit of dispersal (e.g., figs. 4C F; 6B; 7C). They are further recognized by a combination of wood anatomical characters as distinctive as in many entire families (van Vliet 1976). Of the four genera *Rhizophora* (figs. 8 and 9) is pantropical with three or
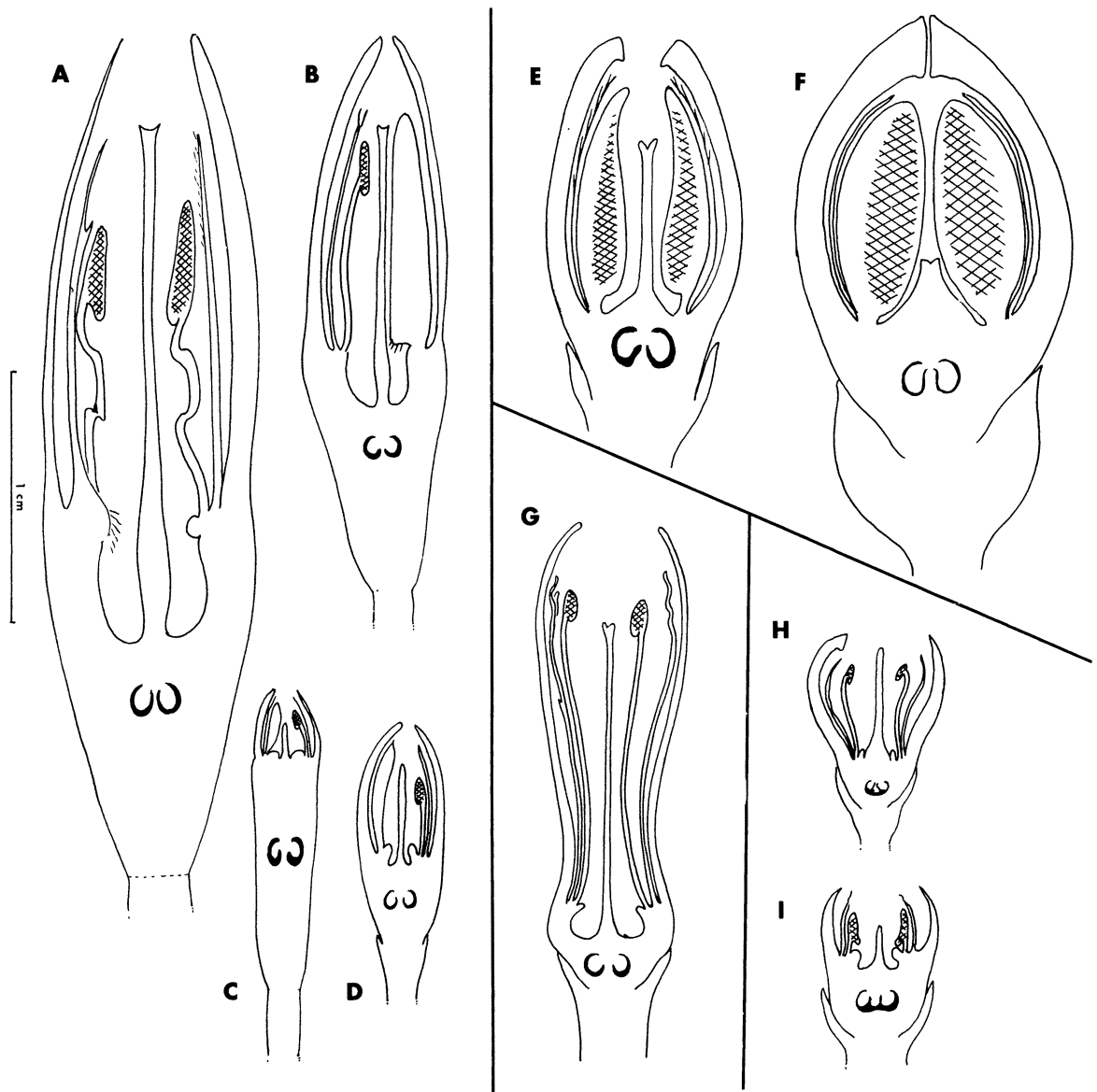
FIGURE 1. Longitudinal sections of flowers in Rhizophoraceae, drawn with a camera lucida, all with the same orientation which is not necessarily as in nature (see text). Flowers drawn were at a comparable stage of development, i.e., at or shortly before anthesis. Hatching in anthers indicates approximate extent of sporogenous tissue. Bracteoles occur below the flowers in D-I. *Bruguiera*: large-flowered species represented by *Bruguiera gymnorrhiza* (A), and *B. exaristata* (B); small-flowered species represented by *B. parviflora* (C), and *B. cylindrica* (D); *Rhizophora*, represented by *Rhizophora stylosa* (E), and *R. apiculata* (F); *Kandelia candel* (Chai s.n., Sarawak) (G), and *Ceriops*, represented by *C. tagal* (H), and *C. decandra* (I). All material collected by P. B. Tomlinson except for *Kandelia candel.*

FIGURES 2 and 3 *Bruguiera* (large-flowered species). Figure 2. *Bruguiera gymnorrhiza* (from a specimen cultivated at "The Kampong" Douglas Road, Miami, Florida). A, branched shoot with apposition growth (x ¼); B. terminal bud enclosed by stipules (x ½), open leaves removed, the detailed figure with the stipules removed (x 3); C, detail of inside of detached stipule (x 3) showing numerous colleters; D, petal from inside partly unfolded (x 3), to show main diagnostic feature distinguishing this species from *B. sexangula*. Figure 3. *Bruguiera sexangula* (from fluid-preserved material, P. B. Tomlinson, 30 October 1974, Bootless Bay, East of Port Moresby, Papua New Guinea). A floral diagram; B, flower in l. s. (x 3/2) with the petals enveloping the stamens; inset detail of stigma (x 3); C, flower from the side (x 1); D, flower from above (x 3/2), all petals and stamens "sprung"; E, diagram of stamen pair with dotted outline of enclosing petal; F, open petal, abaxial (outside) view (x 3); G, open petal, adaxial (inside) view (x 3).

Bruguiera gymnorrhiza

Bruguiera sexangula
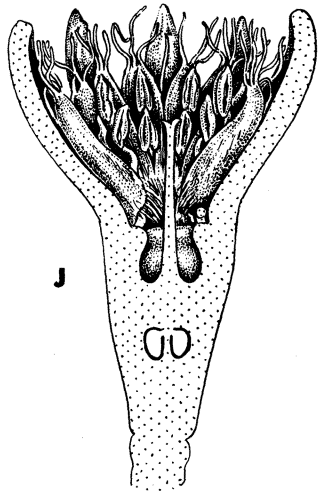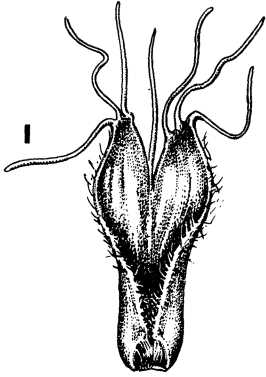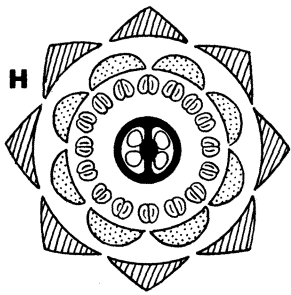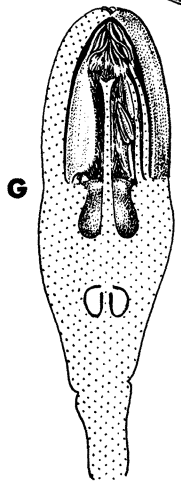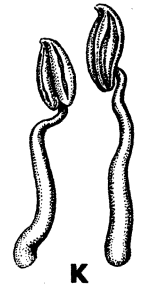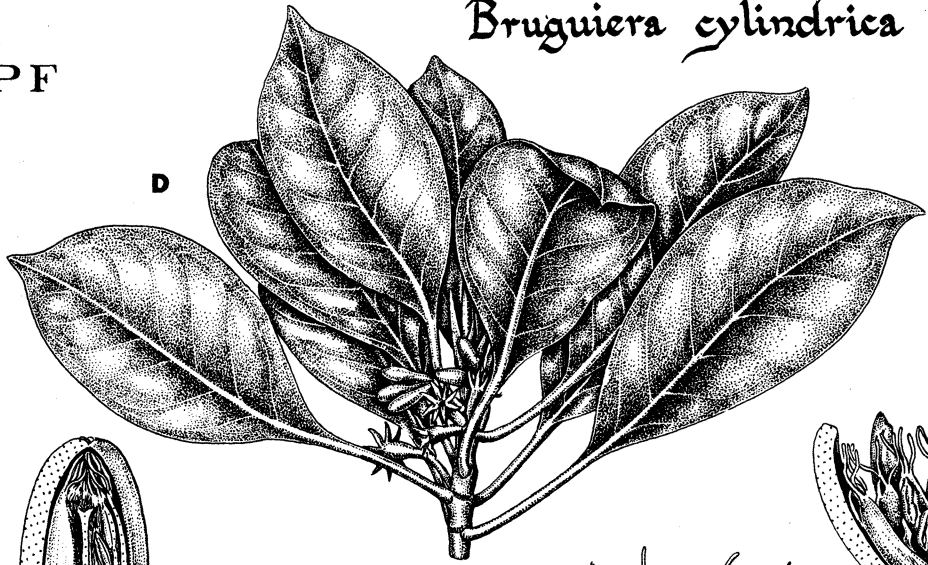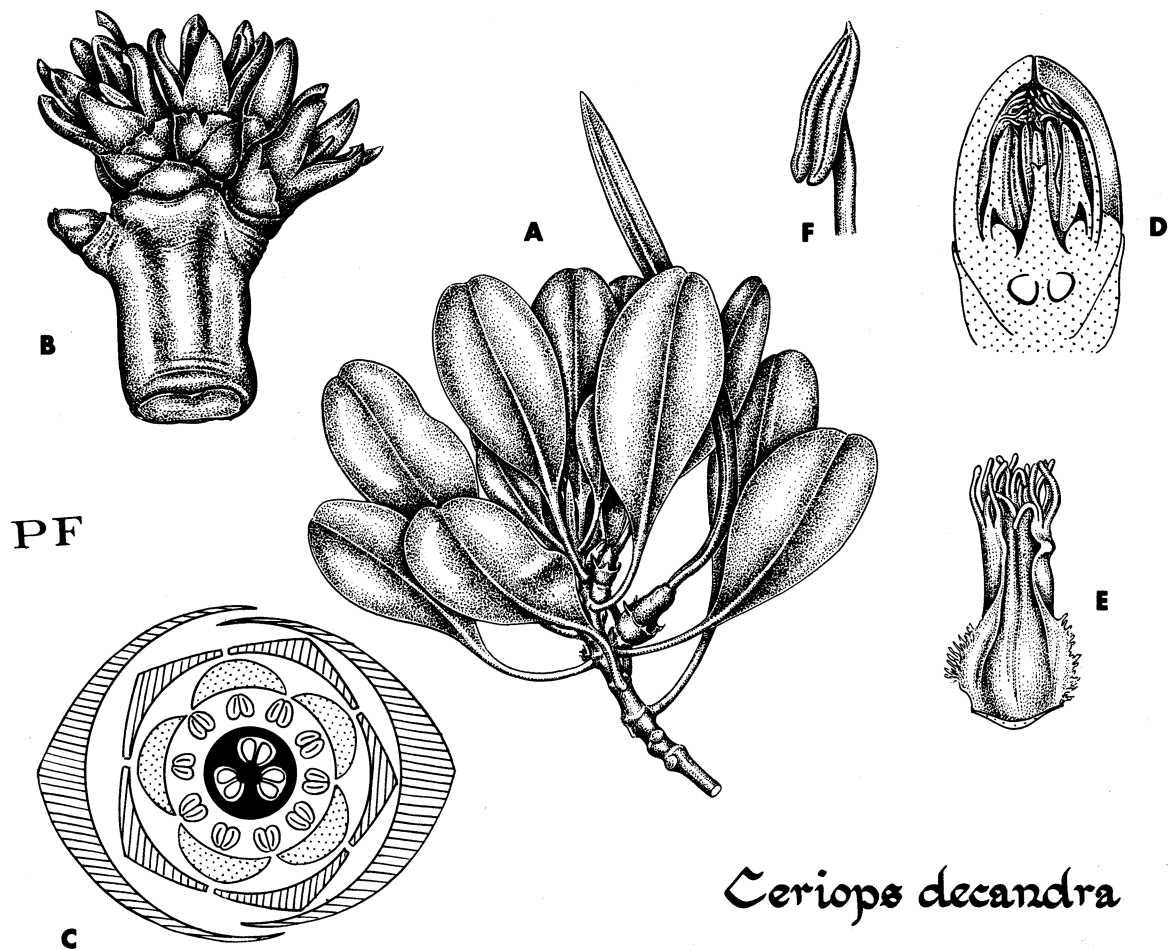
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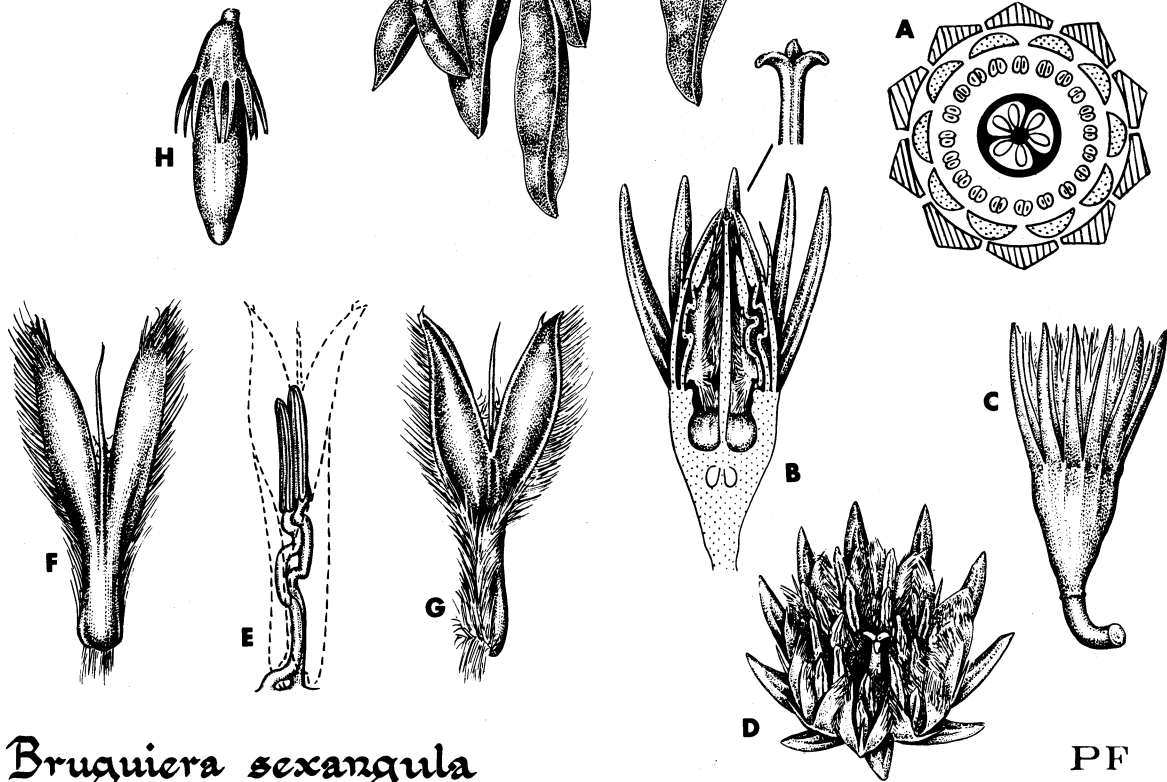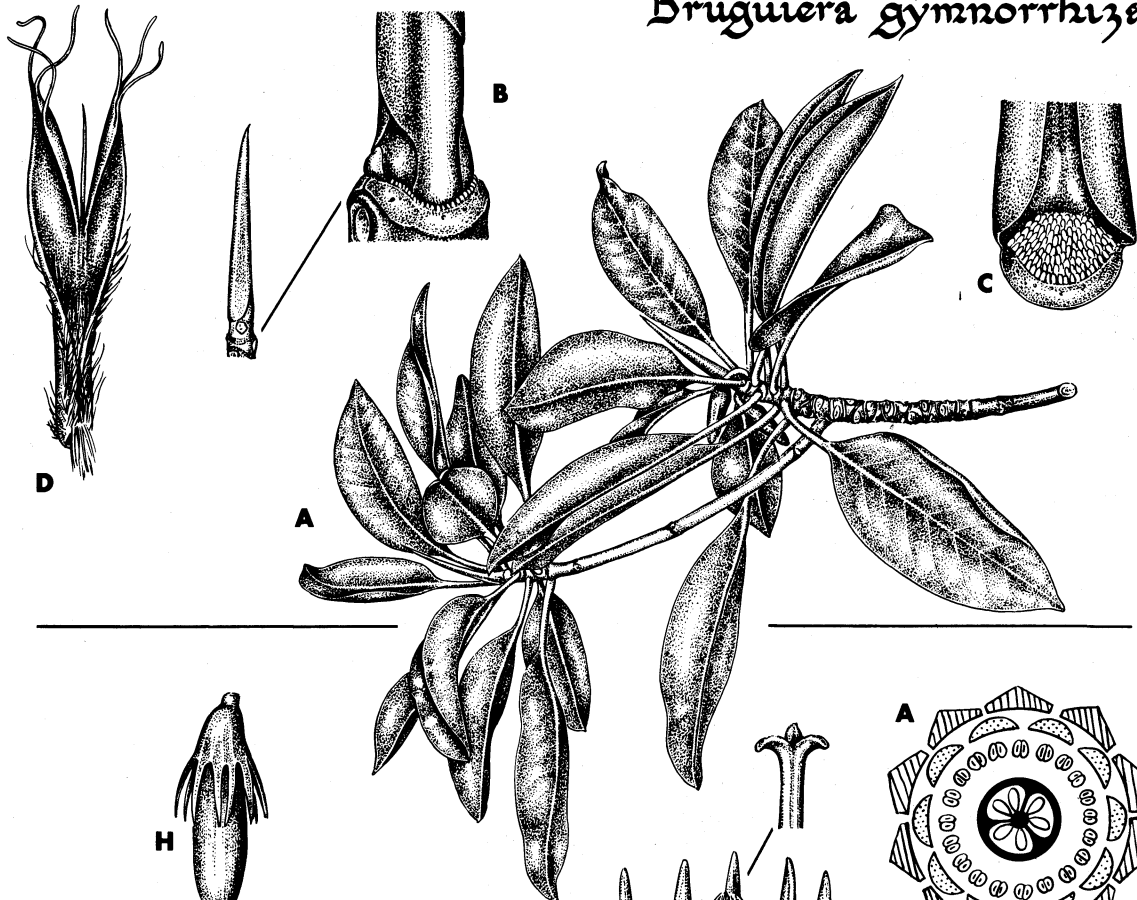
Bruguiera parviflora
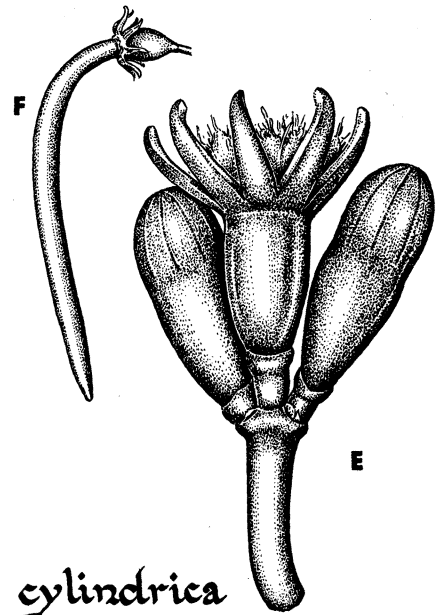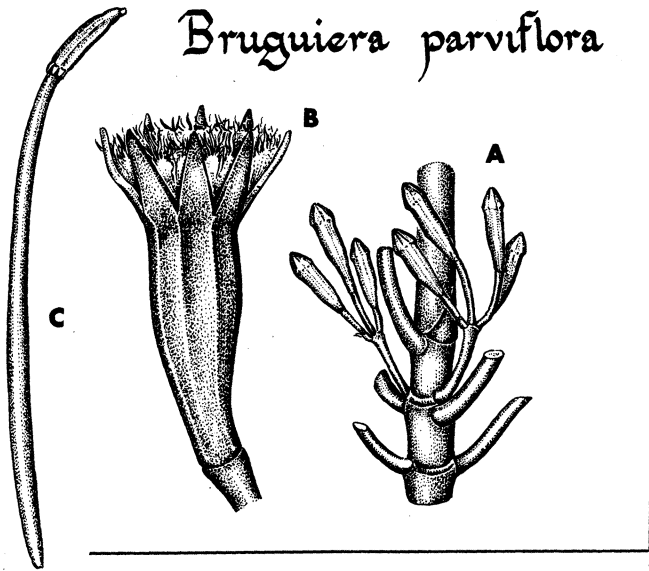
Bruguiera cylindrica

PF

PF

Ceriops decandra

FIGURE 5. *Ceriops decandra* (from fluid-preserved material, P. B. Tomlinson, 20 June 1977, Deluge Inlet, Hinchinbrook Island, Queensland). A, shoot with erect seedling (x ½); B, congested inflorescence, apparently dichotomizing (x 3); C, floral diagram with bracteoles; D, flower bud in l. s. (x 8); E, single petal (x 10); F, single stamen (x 10).

four species forming an "Atlantic" group, four or five species forming an "Indo-Pacific" group with an overlap between the two groups in the Fiji-Tonga area. There is good evidence that *R. X lamarckii* in the South Pacific (Tomlinson and Womersley 1976) and *R. X harrisonii* in West Africa and South America (Breteler 1969) are sterile hybrids rarely producing seedlings. A sterile hybrid *R. X selala* (Tomlinson 1978), which occurs in Fiji (Guppy 1906, Richmond and Ackerman 1975), has recently been shown to occur in New Caledonia. This breakdown of sterility barriers between species which are closely related still requires an adequate genetic explanation.

The other genera are restricted to the Indo-Pacific region and their taxonomy and nomenclature seem highly stable, although one quite widely distrib-

FIGURE 4. *Bruguiera* (small-flowered species). A-C, *Bruguiera parviflora* (from fluid-preserved material, P. B. Tomlinson, 23 October 1974, Labu Lagoon, Lae, Papua New Guinea); A, insertion of two inflorescences on shoot with leaves removed, terminal bud not shown completely (x ½); B, single flower, side view (x 3); petals and stamens "sprung"; C, mature detached seedling (x ½). D-K, *Bruguiera cylindrica* (from fluid-preserved material, P. B. Tomlinson, 5 November 1974, Taurama, Link Road ca. 2 km northeast of Barracks, Port Moresby, Papua New Guinea); D, distal end of flowering shoot (x ½); E, three-flowered inflorescence to show cymose construction (x 3); F, mature detached seedling (x ½); G, l. s. unopened flower (x 4); H, floral diagram; I, single petal after pollen release (x 9); J, l. s. opened flower (x 4) with petals and stamens "sprung"; K, antesepalous (left) and antepetalous (right) stamen (x 9).

Ceriops tagal
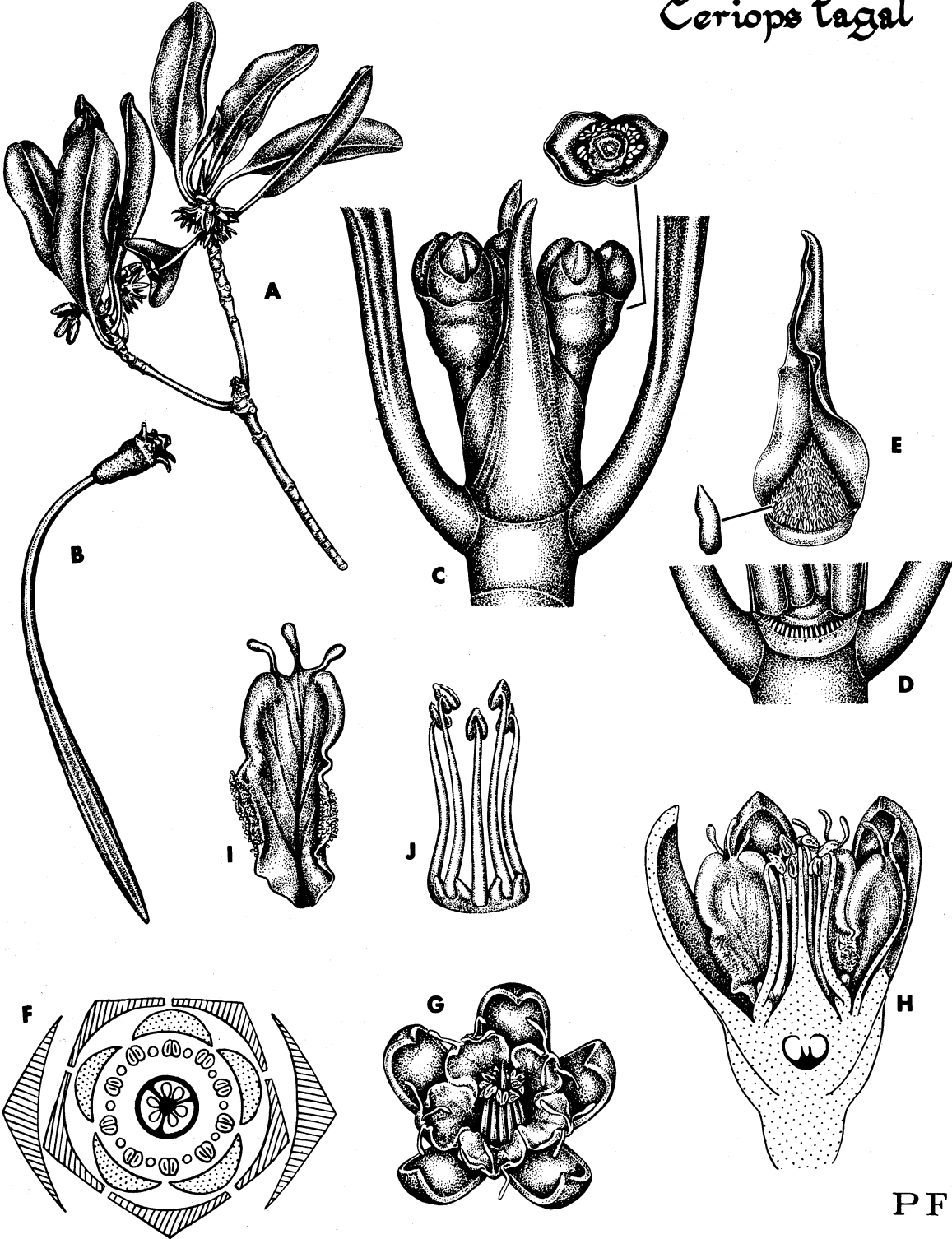
uted species of *Bruguiera* was described only recently (Ding Hou 1957). *Bruguiera* (figs. 2-4) includes six species some more widespread than others. *Ceriops* (figs. 5 and 6) includes at least two species, one widespread. *Kandelia* (fig. 7) is monotypic and has the most restricted range. No evidence of hybridization occurs in these taxa. The ecology, morphology, and nomenclature of the family in Malesia is summarized by Ding Hou (1958). Tables 2 and 3 summarize relevant information on floral morphology, discussed in detail below.

MORPHOLOGY

ARCHITECTURE.—In their vegetative habit most species correspond to the definition of Attims's model (Hallé and Oldeman 1970, Hallé *et al.* 1978) because they have continuous growth with usually intermittent (i.e., non-episodic) branching, lateral flowers, and branches which essentially repeat the pattern of growth of the parent axis. *Bruguiera gymnorrhiza* and *B. sexangula* conform strictly to Aubréville's model since "Terminalia-branching" is ex-

pressed in lateral branches from the moment of inception (Hallé *et al.* 1978:189). In *Rhizophora* distal branches more or less gradually adopt this form, as illustrated in Hallé *et al.* (1978:53), where the condition is referred to by the more general term "plagiotropy by apposition growth." The net result is a series of sympodia with each unit terminating in a leafy rosette (fig. 2A). In *Ceriops* (fig. 5A, 6A) and the small-flowered species of *Bruguiera* (fig. 4D) branches remain more erect, so that the overall crown shape tends to be more narrowly conical. Total height in all species depends very much on edaphic conditions; *Rhizophora*, for example, varies from scrubby plants 2 or 3 m tall, to majestic single-trunked trees 30 m tall, and supported by massive aerial root buttresses.

All sequentially reproduced appendages in these taxa, including flowers, are lateral, i.e., sexual reproduction has no influence on architecture, and all develop within terminal buds. Prolepsis occurs rarely and only after damage to a terminal bud (Hallé *et al.* 1978:42).

TABLE 2. *Floral features in Rhizophoraceae.*[a]

	Kandelia (fig. 7)	Ceriops decandra (fig. 5)	tagal (figs. 6, 11B)	Bruguiera large fl. spp. (figs. 2, 3, 10)	small fl. spp. (figs. 4, 11A)	Rhizophora (figs. 8, 9, 11, C, D)
No. of species	1	1	1	3	3	5-9
Inflorescence type	3	3	3	1	2	3
Flower orientation	pendulous	± erect	± erect	recurved	erect	± pendulous
Flower visitors (most frequent)	?	?	moths	birds	butterflies	bees ?
Pollen vector (main)	insects (?)	insects (?)	moths	birds	insects	wind
No. sepal lobes and petals	5(-6)	5(-6)	5(-6)	8-14	8-10	4
No. stamens (basic)	numerous	10-12	10-12	16-28	16-20	8-16
Precocious anther dehiscence	—	—	+	+	+	+
Explosive pollen release	—	—	+	+	+	—
Filament length	long	short	long	long	long	± sessile
Anther locules	4	4	4	4	4	multi-locellate
Petal color at anthesis	white	white	white	brown	brown	creamy-white
Petal appendages	filamentous (fig. 7I)	club-shaped (fig. 5E)	club-shaped (fig. 6I)	bristles (figs. 2D; 3F, G)	bristles (fig. 4I)	hairs or absent (figs. 8H, 9I)
Ovule number	6	6	6	(4-)6(-8)	4(-6)	4
Flowers per inflorescence	2-10	2-10 (sometimes numerous)	2-10	1	2-10	2-numerous

[a]Detailed information for *Rhizophora* is provided in table 3.

FIGURE 6. *Ceriops tagal* (from fluid-preserved material, P. B. Tomlinson, 21 March 1976, Barune, Papua New Guinea). A, branched shoot with flowers (x ½); B, mature detached seedling (x ½); C, details of terminal bud with expanding inflorescences (x 3): inset, cupular bracteoles (x 4) with flower removed to show colleters; D, terminal bud (x 3) shown in figure C with stipules removed to show nodal series of colleters; E, detailed stipule from within (x 3) to show extensive development of colleters (inset: single colleter (x 20); F, floral diagram; G, flower from above (x 6), petals and stamens "sprung"; H, flower including bracteole pair in l.s. (x 6); I, single petal (x 10); J, Detail of stamens and presumed nectaries (x 10).

Kandelia candel
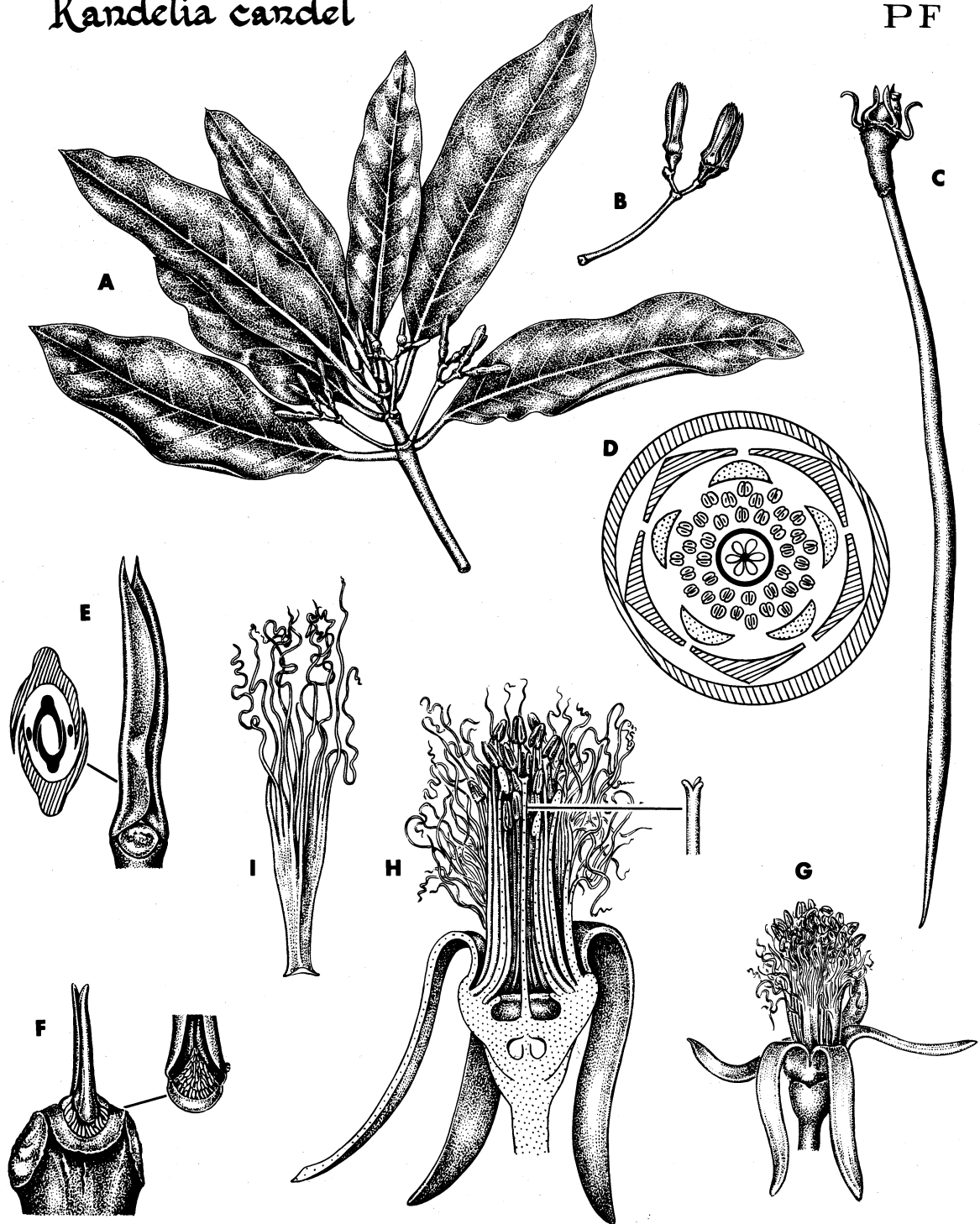
BUD MORPHOLOGY.—A characteristic feature of bud morphology in Rhizophoraceae is the pair of caducous stipules associated with the youngest pair of expanded leaves (figs. 2B, 6D). Until they fall they enclose all younger organs and form a cavity which is filled with either fluid (as in *Rhizophora*) or semi-solid mucilaginous material (as in *Ceriops*). This exudate is apparently produced by the series of colleters on the inner surface of the stipule base and at its attachment (figs. 2C, 6D, E; 7E, F). Similar colleters occur in the axils of bracts (fig. 6C, inset). There is evidence that the fluid exudate of *Rhizophora* contains sugar and is attractive to birds (Primack and Tomlinson 1978), a device which possibly reduces those insect predators which are likely to be eaten by birds.

INFLORESCENCE MORPHOLOGY.—Reproductive axes in all species occur singly in each axil of a leaf pair (figs. 2-11) and are initiated within the terminal bud. They become visible when the enclosing stipule of the subtending leaf abscises (e.g., figs. 4A; 6C). Development is essentially continuous and seemingly synchronous with vegetative shoot extension, although there is a longer or shorter period of inflorescence maturation before flowers open. This period is longest in most *Rhizophora* species because inflorescence branching before final flower initiation is extensive (e.g., fig. 8A). In the extreme example of *R. apiculata* the flowers are not fully mature until the inflorescence occupies a position below the terminal leafy rosette (figs. 9A, B), a feature shown later to have important biological consequences. Most taxa have some periodicity of flower production, determined endogenously or exogenously, but in many cases by a combination of both mechanisms. Gill and Tomlinson (1971) showed that *Rhizophora* in South Florida is essentially ever-flowering but with

TABLE 3. *Floral features in* Rhizophora.

Species	Distribution[a]	Inflorescence[b] No. of branch orders	1st node	flower number	Stamen[c] No.	Petals	Style length[d]	Reference[e]
A. "Fertile" group								
apiculata	Indo-Malayan	1(-2)	2	2(-4)	12	glabrous	short	3, 6
mangle	Atlantic	1-2(-3)	2, 3	2-5	8	hairy	long	4
mucronata	Indo-Malayan	2-4	2	4-16	8	hairy	short	3
racemosa	Atlantic	2-5	2	4-numerous	8	hairy	long	1, 2
samoensis	Pacific	1-2(-3)	2, 3	2-5	8	hairy	long	5, 7
stylosa	Indo-Malayan —Pacific	2-4	2	4-16(+)	8	hairy	long	3, 6
B. "Sterile" group (+ putative parents)								
X *harrisonii* (*mangle* X *racemosa*)	Atlantic	2-5	2	4-numerous	c.8	hairy	long	1, 2
X *lamarckii* (*apiculata* X *stylosa*)	Australasia	2	2	4	c.16	sl. hairy	long	6
X *selala* (*samoensis* X *stylosa*)	Fiji, New Caledonia	1-2(-3)	2, 3	2-7	8	hairy	long	5, 7

[a]Distribution is very generalized and distinguishes essentially between "Indo-Malayan" (i.e., East Africa to the western Pacific) from "Atlantic" (west Africa-Caribbean, but including in part the Pacific coast of South America). More restricted distributions are specified.
[b]Inflorescence branches refers to number of bifurcations (2) or trifurcations (3) below flowers and usual range of actual flower numbers. "Numerous" refers to numbers greater than 32.
[c]Stamen number refers to usual number, where it is not 8, the range may be considerable e.g., 7-21 in *R. X lamarckii*.
[d]Style length merely distinguishes short (sessile stigmas or style < 1 mm) from long (style > 1 mm).
[e]References to details of floral morphology as follows: 1. Breteler (1969), 2. Breteler (1977), 3. Ding Hou (1958), 4. Gill and Tomlinson (1969), 5. Guppy (1906), 6. Tomlinson and Womersley (1976), and 7. Tomlinson (1978).

FIGURE 7. *Kandelia candel* (from fluid-preserved material, Paul Chai, s.n., Sarawak). A, terminal leafy shoot with flower buds (x 1/3); B, entire few-flowered inflorescence (x ½); C, detached mature seedling (x 1/3); D, floral diagram; E, Vegetative bud represented by enveloping stipules (x 3/2) (inset: diagram of bud in t.s.; stipules cross-hatched, leaves and branch axes solid black); F, details of vegetative bud in E with stipules removed to show colleters (x 3) (inset: detail of detached stipule to show colleters); G, flower from the side (x 3/2); H, flower in l.s. (x 3) (inset: detail of stigma); I, a single petal (x 4).

seasonal fluctuation in the rate of flower production. In Queensland there is evident seasonality in flowering, fruiting, and seeding, even in *Rhizophora* species. Here *Bruguiera* is in flower from May to August and must constitute a major nectar source at a time when other terrestrial plants are generally not flowering. Three basic flower arrangements exist:

1. FLOWERS SOLITARY. These occur in *Bruguiera exaristata*, *B. gymnorrhiza*, and *B. sexangula*, which may be referred to collectively as "large-flowered *Bruguieras*" (fig. 10). The flowers are large (2 cm long or more), pedicellate, without bracteoles, typically recurved so they point away from the terminal vegetative bud, and are pendulous. Protection of the mature floral parts is here provided only by the massive floral cup and sepal lobes. The distinction between this and the next type is not absolute, since

cymes occasionally are initiated.

2. FLOWERS IN REGULAR CYMES. These occur in *Bruguiera cylindrica*, *B. hainesii*, and *B. parviflora* which may be referred to collectively as "small-flowered *Bruguieras*" (figs. 4, 11A). The flowers are relatively small (1 cm long or less) and typically erect, have peduncles and pedicels extended and bracteoles vestigial. The basic unit is a regular dichasium. Protection of the mature floral parts is again provided solely by the individual flower cups and sepal lobes.

3. FLOWERS IN DICHOTOMIZING PANICLES. In *Ceriops* (figs. 5B; 6C), *Kandelia* (figs. 7A, B), and *Rhizophora* (figs. 8A, 9B), the flowers are moderately large to quite small, peduncles and pedicels are variously extended, the flowers often sessile, and the bracts and bracteoles well-developed, enclosing in-
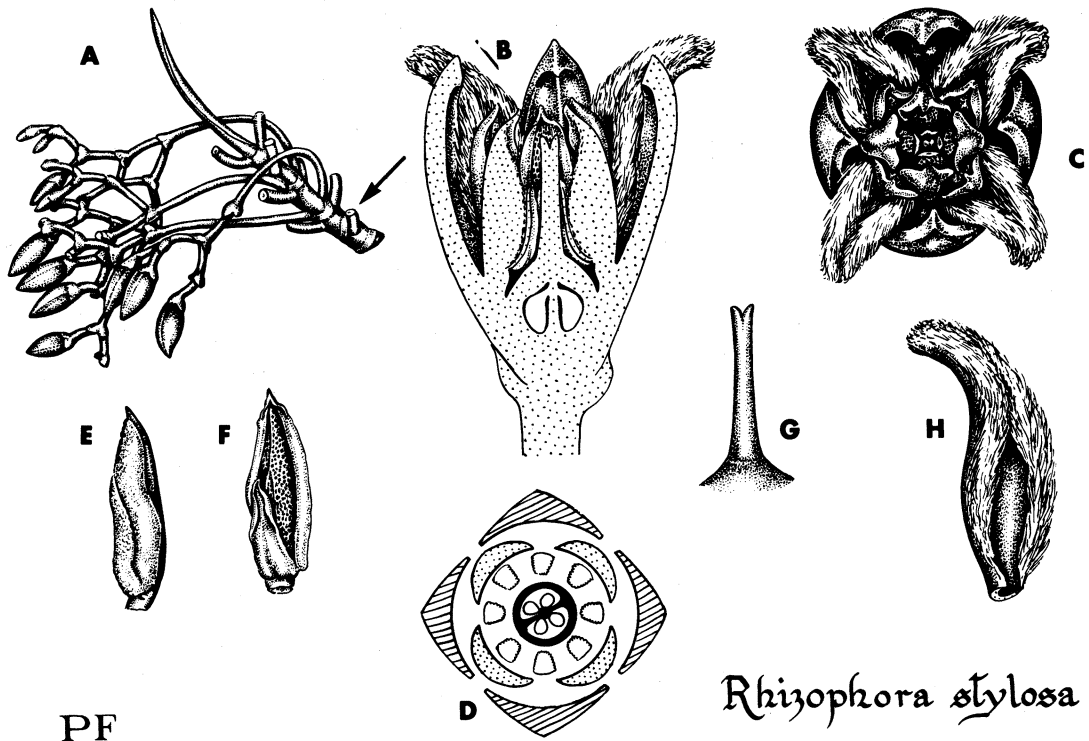
FIGURE 8. *Rhizophora stylosa* (from fluid-preserved material, P. B. Tomlinson, 30 X 74C, Bootless Bay, Port Moresby, Papua New Guinea), inflorescence and floral morphology. A, leafy shoot with leaves cut off to show much-branched inflorescence within the leafy rosette (x ½), position of oldest leaf pair shown by arrow; B, open flower in l.s. (x 3); C, open flower from above (x 3); D, floral diagram; E, undehisced stamen (x 3); F, dehisced stamen (x 3); G, style (x 3); H, petal (x 3).

FIGURE 9. *Rhizophora apiculata* (from fluid-preserved material, P. B. Tomlinson, 18 X 74C, Singaua, Lae, Papua New Guinea), inflorescence and floral morphology. A, leafy shoot with young flower buds (x ¼); B, flowering shoot with foliage leaves cut off to show mature flowers below leafy rosette (x ½), position of oldest leaf pair shown by arrows; C, open flower with bracteolar cup in side view (x 3); D, open flower in l.s. (x 3); E, open flower from above (x 3); F, details of ± sessile stigma (x 3); G, floral diagram; H, dehisced stamen, adaxial view (x 3); I, Petal (x 3).

C D F E G H I PF A B
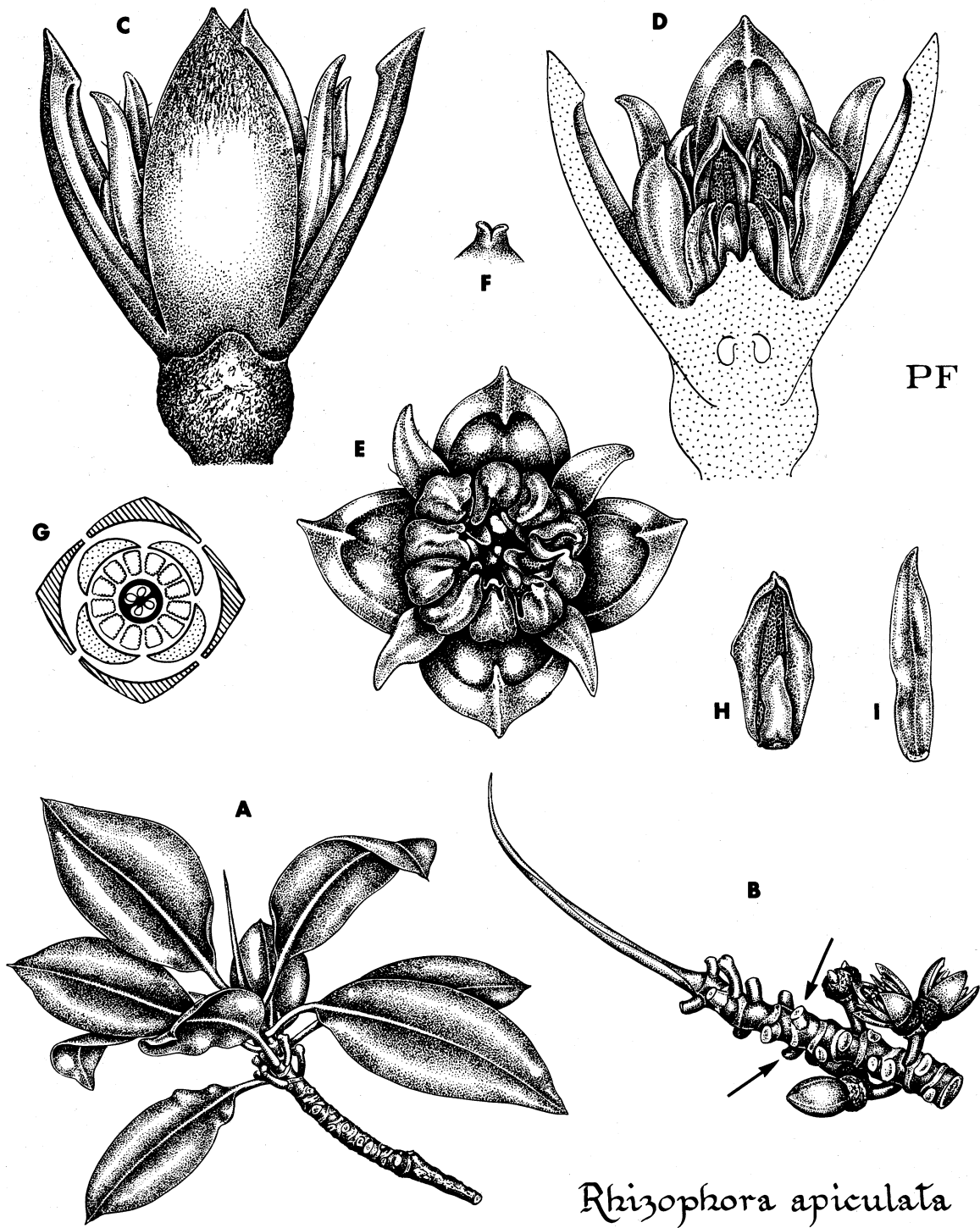
Rhizophora apiculata

FIGURE 11. Floral aspects in small-flowered *Bruguiera*, *Ceriops*, and *Rhizophora*. A, *Bruguiera parviflora*, Missionary Bay, Hinchinbrook Island, North Queensland; leafy rosette from above to show erect flowers. B. *Ceriops tagal*, same locality; opening and open flowers. C and D, *Rhizophora X lamarckii*, same locality. C, recently opened flower from below, some stamens already lost; D, leafy shoot to show pendulous flowers.

FIGURE 10. *Bruguiera*, floral aspects in large-flowered species. A-D. *B. gymnorrhiza*, Missionary Bay, Hinchinbrook Island, North Queensland. A, leafy rosette with 2 axillary flowers at the time of flower opening; B, flower from below with petals in closed position, before pollen dispersal; C, old flower with petals and stamens lost; D, flower from below immediately after explosive discharge of pollen by opening of petals. E-F. *B. exaristata*, Three Mile Creek, Townsville, North Queensland. E, flower buds and open flowers in characteristic pendulous position; F, two flowers from below, the right one with unopened petals (cf. fig. B), the left with petals and stamens lost.

florescence branches and flowers to a late stage of development. Protection of developing parts, including flowers, to quite a late stage of development is provided by the thick fleshy bracts. The bracts of *Rhizophora apiculata* are quite corky (fig. 9B).

This third type of inflorescence is unusual among angiosperms because the axis bifurcates by equal dichotomy in planes mutually at right angles, each fork being associated with a pair of thick bracts which subtend the next higher branch order and enclose younger, developing parts. The same type of inflorescence is known for other Rhizophoraceae, e.g., *Carallia*. The flowers themselves are subtended by a pair of empty bracteoles. When equal dichotomy is regular, a simple power law (base 2) determines flower number according to sequence 2, 4, 8, 16 . . . etc., but for higher orders irregularities appear by abortion of certain axes so that the actual number of flowers is less than the potential number as determined by number of forks. Rarely is reduction (or abortion) so complete that a single flower is developed, as we have observed in *R. mucronata*. An underlying cymose construction is also suggested by a very occasional dichasium in this species. *Rhizophora mangle* and *R. X selala* are exceptional in that axes frequently trifurcate at the first (rarely subsequent) node so that numbers occur which are initiated by this trifurcation and subsequent dichotomy (e.g., 3, 5, 7). For *Ceriops* there is some indication of a division into four axes at the first node (e.g., fig. 5B).

Flower number varies in this inflorescence type but within narrow limits for most species, two (rarely four) in *R. apiculata,* four in *R. X lamarckii,* up to over 100 in vigorous speciments of *R. X harrisonii* and *R. racemosa*; where branching, up to seven orders, has occurred. For *Ceriops*, flower numbers are usually low (2-11), but in Queensland populations of *C. decandra* exceptionally high numbers (30-40) have been observed.

The essential mechanical and biological features of this type of inflorescence provide the continuous protection of the youngest units by a successive series of organs (bracts, bracteoles, and finally sepals). Flowers are normally inverted, this being conspicuous in long-pedunculate species like *R. racemosa* and *R. stylosa* where the whole inflorescence becomes inverted by curvature of its axis. This feature seems biologically adaptive in terms of pollen dispersal, as suggested later. Chai (pers. comm.) records the flowers of *Kandelia* to be inverted at maturity.

FLOWER SIZE.—This feature is correlated with the elaboration of the inflorescence in a very general sense, so that larger flowers are either solitary, or borne on little-branched inflorescences. However, in the most elaborate inflorescence of *R. X. harrisonii*, the flowers are still larger than those in *Ceriops*. The extensive range of flower sizes is illustrated in figure 1 at a standard magnification. Flower size is correlated more closely with the size of the pollinator.

FLORAL PLAN.—All rhizophoraceous flowers have a well-developed, thick, fleshy floral cup (or hypanthium) with free valvate sepals which enclose the inner parts until anthesis and always persist in the fruit (e.g., fig. 3H). The calyx cup is either flat (often with a distinct disc), or ranges from shallow to very deep. Petals are free, equal in number to and alternating with the sepals, and usually provided with diagnostically useful appendages (hairs or club-shaped structures). Stamens are usually twice the number of petals, with one series antesepalous, the other antepetalous, and all inserted on the rim of the calyx cup. These common features are illustrated in the floral diagrams in figures 3-9. *Kandelia* is exceptional in the numerous (30-40) stamens (fig. 7D). Anthers dehisce within the flower bud, except in *Ceriops decandra* and *Kandelia*, although this action does not lead to automatic self-pollination. The ovary is inferior, with two or more locules. Ovules are few, large and relatively fixed in number for each taxon (the numbers cited in table 1 refer to the most common values). There is a simple persistent style with two or more obscure stigmas. The number of parts is relatively fixed and therefore diagnostic for each taxon. Information is summarized in tables 2 and 3 and details are shown in figures 2-9.

Figure 1 also shows that the shape of the floral cup is very variable and to a large extent correlated with flower size. Thus the large-flowered *Bruguiera* species (figs. 1A, B) have a deep calyx cup which becomes nectar-filled at anthesis. Small-flowered *Bruguiera* species (figs. 1C, D) and *Ceriops* (figs. 1H, I) have a well-developed, flat-topped, or lobed disc which encloses the base of the stamens. The disc of *Rhizophora* is scarcely developed, and the top of the ovary is more or less conical (figs. 1E, F). *Ceriops tagal* has a very shallow, half-inferior ovary but apparent nectar glands alternate with the stamens (fig. 6J). The calyx cup of *Kandelia* is shallow (fig. 1G).

Functionally all flowers are comparable in that the valvate calyx lobes separate at anthesis, diverging to greater or lesser degree, to expose the petals which adopt various configurations. Petals and stamens fall or are blown from the open flower after they abscise within one (*Rhizophora*), or a few (other genera),

days. This leaves the central stigma alone in the "empty" flower. At no time is there obvious stigmatic secretion or divergence of stigmas; stigma receptivity has been established by chemical tests, as described earlier. Older stigmas become black, but the style usually persists in the fruit. Unfertilized flowers abscise early.

Despite this uniform floral plan at least six, quite elaborate, pollination mechanisms are involved, to some extent the categories cutting across taxonomic boundaries. Three of the categories involve explosive release of pollen by the same mechanism and may be described collectively, but the basic subdivision is still established by the pollen vector.

DIRECT OBSERVATIONS ON POLLINATION MECHANISMS

EXPLOSIVE POLLEN RELEASE.—In all *Bruguiera* species and in *Ceriops tagal* the stamens become enclosed in pairs by the petals, i.e., each petal functions as a pouch enclosing both an antepetalous and an antesepalous stamen. The latter is initiated opposite a sepal, but early in development it twists (either to the right or left, but always in the same direction in a single flower) so that as the petal base enlarges it grows around the stamen. This antesepalous stamen is slightly lower in the flower than the antepetalous stamen because of the basal twist in the filament (e.g., figs. 3E, 4K). Tension is developed because the stamens press against the interlocked margins of the petal, whose dorsal attachment is thickened. When the flower expands the petal tends to bend back, but is retained in an erect position by the adherent ventral margins. Marginal hairs seem to be important in holding the petals in the folded position. Shortly before the flower opens the stamens dehisce. At anthesis, the sepals diverge presenting the closed, erect petals in the "cocked" position. Suitably triggered, the petal margins unzip instantaneously and fly apart, releasing the stamens which catapult the loose pollen toward the center of the, flower, often as a visible cloud. Presumably much of the pollen would be projected onto the head of an animal vector, but none were trapped to obtain more precise information. Flowers in *Bruguiera gymnorrhiza* before and after pollen release are shown in figures 10B and 10D, respectively.

The mechanism for triggering a flower varies in different sized flowers and according to the flower visitor, as described below. Each petal behaves independently so that multiple visits are possible, and individual flowers with combinations of closed and open petals can be found.

After the petal-stamen catapult has "fired," the petals lie back against the calyx lobes with the empty stamens twisted and disorganized (figs. 3D, 10D). All abscise and usually fall within a day or two (fig. 10C). Untriggered petals may retain their tension for up to 10 days, and they may be lost without ever opening. Accidental triggering of petals, at least in the large-flowered *Bruguiera* species, seems rare so that a flower visitor appears essential for pollen dispersal.

BIRD-POLLINATION IN LARGE-FLOWERED BRUGUIERAS (Type 1).—In Queensland the flowers of *B. exaristata* (figs. 10E, F) are visited by the yellow-breasted sunbird (*Nectarinia jugularis*) and honey eaters (Meliphagidae). Birds often forage in pairs, a male and a female, calling frequently, with the male actively chasing other birds out of the territory. The birds perch on the stout branches and turn their heads upward to take nectar via their curved bills; they were observed to trip the explosive mechanism, releasing clouds of pollen but without being disturbed by the explosion. Birds also move frequently between plants, and could act as effective pollen dispersers; they feed on a few flowers on each plant and also eat insects.

Flowers are pendulous and open slowly over a period of about 24 hours, the petals at first exposed as brown pouches alternating with the spreading sepals which are conspicuous against the foliage. Stigmas are not receptive on the first day the flower is open, but become receptive on the second or third day and remain so after the stamens and petals have fallen.

Individual flowers are visited for as much as eight days after opening, and in one set of measurements stamens continued to be triggered separately over a period of 7 days. Copious nectar accumulates in the deep calyx cup and is retained by the petal base and its associated hairs. In unvisited flowers it overflows onto the petals where it becomes viscous by evaporation and so inhibits the explosive mechanism.

Stamens persist in either the triggered or tripped state for up to 10 days in measured examples, but they eventually fall with the petals as a single unit or in smaller groups of stamens and petals whether or not they have been fired.

After the petals and stamens have fallen nectar continues to be secreted, the stigma remains receptive, and birds continue to visit the "empty" flowers. This action and the initially delayed stigma receptivity constitute a partial, but weak, outbreeding mechanism via partial protandry.

Triggering of petal explosion is effected by touching sensitive basal hairs, especially those which project into the center of the flower over the entrance to the calyx cup. Neither the tip of the petal nor its apical hairs are sensitive. Appropriately, therefore, triggering can only be stimulated by fairly vigorous probing into the calyx cup.

The flowers of *B. gymnorrhiza* (figs. 10A-C) are larger than those of *B. exaristata*, and the calyx is red. We have observed flowers visited by the graceful honey eater (*Meliphaga gracilis*) and less frequently by the dusky honey eater (*Myzomela obscura*). Birds again feed in pairs; they fly between the trees with the males calling frequently in a way which suggests territorial warning. Pollinator activity is high, and in one measured sample five out of seven flowers possessed exploded petals only one day after the flowers had opened. *Bruguiera sexangula*, illustrated in detail in figure 3, is distinguished mainly by the petal appendages (figs. 2D; 3F; G), and has the same explosive mechanism as other species. We have not had the opportunity to watch pollination ourselves, but bird visitors are well known (Davey 1975).

In summary we note the following adaptations for bird pollination: 1. Recurved pedicels of solitary flowers to facilitate access by birds perched below and perhaps also to prevent rain from diluting the nectar; twigs are stout. 2. Flowers are all attractive by virtue of the spreading stellate calyx lobes and in two species (*B. gymnorrhiza, B. sexangula*) by the reddish outer surface of the hypanthium. 3. Copious nectar production, secreted into a deep calyx cup, suitable for an active pollinator. 4. Large flowers with a heavy construction suitable for a powerful pollinator like a bird.

We also note that at Missionary Bay, Hinchinbrook Island, *B. gymnorrhiza* was the only nectar-producing plant to flower in winter (July) and at Townsville (3 Mile Creek), where *B. exaristata* was observed, few other plants were in flower at the same time. Consequently, in winter, when these observations were made, *Bruguiera* becomes a very important nectar source for birds. Clearly also the mangrove environment is edaphically suited to winter flowering, since trees are not limited by soil moisture. Birds are the major pollinators of many other Australian tree species (Ford and Paton 1976, Paton and Ford 1976) so there may be a high dependence in birds on nectar supply.

BUTTERFLY-POLLINATION IN SMALL-FLOWERED BRUGUIERAS (Type 2).—Large butterflies feeding on open flowers and so triggering pollen release have been observed by us in *B. parviflora*. Here because of the smaller flowers, the explosion is not violent and no visible cloud of pollen is observed; petals can be triggered by a delicate touch to the distal parts. These flowers are not likely to be robbed by birds because they secrete very little nectar. They have no evident odor. It is likely that other insects, e.g., bees, visit the flowers and may also function as vectors.

Adaptations to butterfly pollination in this species may be summarized as follows, although it might be said equally that these are reasons why the flowers are *not* bird-pollinated: Flowers are not recurved, and are displayed to the outside of the tree crown (figs. 4A, 11A); flowers are small (compared with bird-pollinated flowers); branchlets are thin and insufficient for bird perching; petals are greenish-yellow; calyx cup is flat, nectar is produced in small quantities; and pollen is released by delicate, distal stimulation of petals.

Bruguiera cylindrica is very similar to *B. parviflora* and is here illustrated in detail (figs. 4D-J). The floral cup is shorter than in *B. parviflora*, with a distinct calyx cup. We have not observed flower visitors, but expect that these will be insects. The remaining species, *B. hainesii*, also has explosive pollen release, but further details are lacking.

MOTH-POLLINATION IN *Ceriops tagal* (Type 3).— The flower of this species, although with the same mechanism as the previous two groups, is specialized to a different pollen vector in its function (fig. 6). In North Queensland we have observed flowers to open mainly in the later afternoon (fig. 11B) and emit a faint but characteristic fragrance during the night. The white petals are not conspicuous when folded but become so after they have unfolded. We have seen moths visiting the flowers in the early evening, and they are the presumed agents of pollen transfer, but other insects could easily perform the function since the nectariferous disc is exposed.

Adaptations for moth pollination are as follows: small flower and flower parts suited to a weak pollinator; delicate explosive mechanism, triggered by a delicate stimulation of distal parts which will not injure the pollinator; petals white, and visible at night; flowers fragrant at night, characteristic of moth flowers; and a tiny amount of nectar, suggesting a small insect vector.

The illustration of petals in *C. tagal* in Ding Hou (1958) which shows them fused to form a ring and their description as "coherent at the base with uncinate hairs" refers to them after explosion but in dried specimens. The same artefact can be observed in fluid-preserved material. It is not a primary fea-

ture of the pollination process, since it refers to juxtaposition of the petals (fig. 6I) after they have been triggred (fig. 6G).

NON-EXPLOSIVE POLLEN RELEASE BY *Ceriops decandra* (Type 4).—Flowers (figs. 5C-F) in this species lack the petal-stamen configuration on which the explosive mechanism of *C. tagal* depends. Stamens have relatively short thick filaments (fig. 5F) and remain in their original antesepalous or antepetalous position. The petals (fig. 5E) become interlocked marginally by basal hairs, i.e., as illustrated by Ding Hou (1958) for *C. tagal*, and this circumstance produces a short corolla tube, crowned by the series of clavate appendages.

We have no details of flower visitors in this species, but it is evident that the mechanism is less elaborate than for *C. tagal* with which it is much contrasted. Chai (pers. comm.) refers to the flowers of this species as non-scented and being visited by Trigonid bees, especially during early morning.

WIND-POLLINATION IN *Rhizophora* (Type 5).— Despite the variation in stamen number and petal hairiness, the floral mechanism is essentially the same in all *Rhizophora* species, and we interpret it as facilitating wind-pollination, providing evidence (below) from pollen-ovule ratios and other sources. Flowers open at any time of day, and the calyx lobes may separate quite widely, as in *R. mangle*, or only slightly as in *R. apiculata* and *R. racemosa*. The multilocellate anthers (figs. 8E, F; 9H) dehisce before the flower opens via the adaxial flap which falls against the base of the style. When the style is short, as in *R. apiculata* (figs. 9D, F), the stigma may be occluded by the adaxial flap, although this does not seem to be part of the floral mechanics. For all species of *Rhizophora* except *R. apiculata* (fig. 9I) and *R. X lamarckii,* the petal margins are provided with a dense weft of filamentous hairs (fig. 8H) which grow into the space between the anthers in the closely packed flower bud. Because of precocious anther dehiscence the hairs become coated with the powdery pollen mass, whose release is facilitated by the multilocellate condition and the method of dehiscence by a flap. As the flower opens much of the pollen is drawn out by the petals, which become more or less recurved in all the species with hairy petals (fig. 8C). Dispersal of the pollen is easily facilitated when the flower is shaken by the wind and is further promoted by hygroscopic movement of the intertwined petal hairs, which are released in a flicking motion. The marked tendency for flowers to be inverted or pendulous (figs. 11C, D) seems important in this mechanism.

The stage of pollen release is short, petals and stamens usually falling within 24 hours of flower opening, as noted by Guppy (1906). This condition should be contrasted with that of *Bruguiera* where flowers remain functional at the unopened petal stage for up to 10 days.

The stigma of *Rhizophora stylosa* becomes receptive on the second day after the flower has opened and hence normally after the stamens and petals have fallen. Pollen grains accumulate on a specific region of the stigma only when the stigma is receptive. As a result, an individual flower is generally incapable of self-pollination. In the population under study, most flowers fall with their petals still attached, before they become receptive to pollen. Some other presumed endogenous mechanism controls fruit set since pollination does not seem limiting.

Rhizophora apiculata (fig. 9E) shows the wind-pollination mechanism in its most complete form. The calyx lobes diverge least, the petals neither recurve nor retain pollen since they are glabrous, and a simple pepper-pot mechanism is sufficient to disperse the pollen dust. Slow development of the flowers such that they are mature only below the leafy rosette on each branch (e.g., fig. 9B) can be interpreted as a simple device which facilitates pollen dispersal by minimizing interference of the tree's own foliage. Equally this may facilitate capture of pollen by receptive flowers.

Insect visitors to the flowers of most *Rhizophora* species are not common. We have recorded occasional pollen-collecting bees visiting flowers of *R. mangle* in South Florida and of *R. X lamarckii* in Queensland. Bees visit certain populations of *R. stylosa* in abundance to collect pollen. These bees, as well as occasional butterflies and birds, visit the flowers after the petals and stamens have abscised, seemingly because their scars will exude fluid. In other large populations of *R. stylosa* at the same time of year, no flower visitors were observed.

Evidence for the wind-pollination mechanism in *Rhizophora* may be summarized as follows: light powdery pollen is produced in great abundance (see pollen-ovule ratios below); anthesis in bud, pollen sifted out with no animal agent necessary for dispersal; pollinator attractants more or less absent, i.e., little nectar or fragrance produced, and the abundant pollen is diffusely presented; stamens are short-lived, falling the same day as the flower opens; flowers are typically pendulous at maturity and, for *R. apiculata,* opening below the leafy rosettes; extensive pure stands of trees occur in a windy environment; and greased slides suspended in stands of *Rhizophora*

both in Queensland and South Florida retain abundant wind-borne pollen.

Against this evidence, however, it must be noted that the stigma is not elaborated in the manner usual for wind-pollinated species.

INDIRECT OBSERVATIONS

POLLINATOR PREDATORS.—Supporting evidence that pollinators in pollination Types 2 and 3 above are insects comes from the observation that crab spiders (family Thomisidae) position themselves below flowers. We have observed an unidentified dark-colored spider catching moths on *Ceriops tagal.* Green crab-spiders, which are much the same color as the inflorescence of *Bruguiera parviflora,* position themselves below flowers, but we did not observe any insect captures.

In contrast, no crab spiders were observed on *Rhizophora* flowers or the flowers of the bird-pollinated *Bruguiera* species (Type 1). We have evidence that *Rhizophora* promotes bird visitors via sugar secretions from its terminal buds (Primack and Tomlinson 1978). In both examples attracted birds would eat spiders.

POLLEN-OVULE RATIOS.—Comparative evidence that contrasts the different types of pollination mechanism is provided in the measurements of pollen-ovule ratios in table 1. *Rhizophora* has appreciably higher values than the bird-pollinated *Bruguiera* species (which have usually more stamens). This large production of pollen is typical of wind-pollinated species. The bird-pollinated *Bruguiera* species produce over 100 times as much pollen per ovule as the insect-pollinated species of *Bruguiera* and *Ceriops.* These values and differences are comparable to those obtained by Cruden (1976, 1977).

DISCUSSION

BIOLOGICAL CONSIDERATIONS.—The information presented above, although it is incomplete at many points, is sufficient to show that although the Rhizophoreae have a similar floral construction, they exhibit a wide range of pollination mechanisms. The situation may be summarized in the following diagnostic key:

1 Pollination predominantly by wind (anthers dehiscent in the flower bud).
  2 Mature flowers within the leafy cluster
    .... *Rhizophora* (most species)
  2 Mature flowers below the leafy cluster
    .... *R. apiculata*

1 Pollination by animals[1]
  3 Pollination mechanism explosive (anthers dehiscent in the flower bud).
    4 Pollination by day-time visitors.
      5 Pollination by birds ....
        large-flowered *Bruguiera* species (e.g., *B. exaristata, B. gymnorrhiza, B. sexangula*)
      5 Pollination by butterflies ....
        small-flowered *Bruguiera* species (e.g., *B. cylindrica, B. hainesii, B. parviflora*)
    4 Pollination by night-time visitors.
      6 Pollination by moths
        .... *Ceriops tagal*
  3 Pollination mechanism not explosive (anthers not dehiscent in the flower bud).
    7 Pollination by small, short-tongued animals .... *Ceriops decandra*[2]
    7 Pollination by fairly large, longer-tongued animals......*Kandelia candel*[2]

These biological features can be related directly to morphological features which include differences in size of flowers, differences in details of inflorescence and floral construction, and differences in floral mechanisms (summarized in table 2 and illustrated in the several figures). The most elaborate type involves an explosive projection of pollen triggered by flower visitors. Early authors who investigated the bird mechanism of triggering in *Bruguiera gymnorrhiza* (Gehrmann 1911, Porsch 1924) suggested that the bird visits were secondary and that the explosive mechanism of dispersal was for anemophily. However, it seems unlikely that so elaborate a mechanism involving copious nectar production, a massive calyx, and precise flower orientation, could be developed in relation to anemophily, especially as we now know that firing of the mechanism depends on a flower visitor. Furthermore, the differentiation of flowers according to size, scent, number per inflorescence, and orientation such that birds on the one hand and different kinds of insects on the other become specialized flower visitors makes it unlikely that the mechanism is directed toward anemophily. Undoubtedly where a cloud of light pollen is released wind dispersal is possible, especially in the large-flowered *Bruguiera* species, but this seems incidental to the real vector.

Floral energetics clearly vary in the different pol-

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[1] Only the usual and presumed most effective pollinator is included, flowers may receive a diversity of visitors.
[2] No direct observations made.

lination types. A high nectar and pollen production by *Bruguiera exaristata* and by *B. gymnorrhiza* all suggest that bird pollination is energetically costly and also relatively inefficient at moving pollen grains from the anthers to receptive stigmas. One presumed advantage to the plants of bird pollination is that the birds forage actively in weather conditions unsuitable for insects. Furthermore, though birds may be inefficient in their dispersal of pollen, their tendency to fly actively from plant to plant may compensate in providing a high degree of cross-pollination. In contrast, the low pollen/ovule ratios of the insect-pollinated species suggests a more efficient system less costly to the plant. Here flowers adapted for insect pollination may place the pollen more precisely on the pollinator, in contrast to the bird-pollinated flowers in which the flower apparently projects a cloud of pollen onto the head of the bird. These *Bruguiera* species may be compared with *Metrosideros* (Myrtaceae) studied by Carpenter (1976) in Hawaii. Here bird-pollination seems particularly efficient in relation to a presumed partial self-compatability, and large-flowered *Bruguiera* species may be comparable. However, a detailed investigation using the careful quantification adopted by Carpenter still remains to be carried out.

We have also provided evidence on the basis of floral mechanisms, orientation, and high pollen-ovule ratio that *Rhizophora* is predominantly wind-pollinated; the greatest specialization for wind-pollination shown by *R. apiculata* with its pepper-pot mechanism and essentially ramiflorous condition; and the least specialization shown by *R. stylosa* which is actively visited by bees. The abundance and wide dispersability of *Rhizophora* pollen is shown in the work of Muller (1959) on sediments in the Orinoco delta, where there is no other existing genus of Rhizophoraceae to confuse the picture. *Rhizophora* pollen predominates in most of his samples. His conclusion that *Rhizophora* is wind-pollinated is fully supported here and the abundance of wind-borne pollen in existing *Rhizophora* communities is easily verified. More recently it has been shown that pollen in different *Rhizophora* species is scarcely distinguishable (Muller and Caratina 1977). This finding would suggest a uniform pollination mechanism.

Undoubtedly *Rhizophora* is the most successful mangrove in terms of wide distribution and abundance of individuals. Wind-pollination may partially account for both the success of *Rhizophora* and the frequency of putative hybrids. In contrast the range restriction associated with specialized flower visitors is suggested by *Bruguiera exaristata*, whose limited geographical distribution coincides quite closely with its major flower visitor (*Nectarinia jugularis*). However, it is not usual for a high degree of interdependence to develop between plant and bird in bird-pollinated species (Carpenter, 1976).

Further extensive work on the rhizophoraceous mangroves, especially in different geographical areas, is an obvious requirement to substantiate many of the claims in this paper. It is hoped that this outline will prove useful in orienting future research workers.

A serious deficiency in our approach is that we remain uncertain of floral physiology and genetic mechanisms for isolation. That there is some mechanism of self-sterility is suggested by the relative infrequency of fruit set in *Rhizophora*, 0-11 percent of all flowers according to measurements at different times of year (Gill and Tomlinson 1971, and Kress 1974) in Florida.

We have commented upon the likely mechanism for out-crossing provided by the partial protandry of large-flowered *Bruguiera* species, and if stigma receptivity is universally delayed, dichogamy may be an effective device. In contrast, self-compatibility is suggested for *Rhizophora* by Kress (1974) on the basis of the ability of isolated greenhouse-grown plants to set fruit and the ratio of albino to normal seedlings in individual trees which show this marker. It is clear that future research must concentrate on stigma receptivity and the genetic mechanisms for preventing selfing.

EVOLUTIONARY CONSIDERATIONS.—The wide range of mechanisms developed by the Rhizophoreae allows some speculation about their evolutionary divergence since it seems reasonable to assume a monophyletic origin for them in view of vivipary and the other common features they share (van Vliet 1976). *Kandelia* represents the least specialized type of floral mechanism which may approximate the ancestral state. However, we still lack details about its floral biology. *Ceriops decandra* is comparatively unspecialized and may also reflect an ancestral state, but again we lack details of flower functioning. The explosive mechanism represents a considerable specialization and a monophyletic origin seems likely. *Ceriops* may be the key genus in this process since it includes both specialized and unspecialized taxa. Adaptive radiation leads to the *Bruguiera* condition. *Rhizophora* represents a different line of evolution, directed toward anemophily, but probably having had an ancestral entomophilous condition; vestiges of this may be seen in taxa like *R. mangle* and *R. stylosa* on the basis of reports of flower odor, sometimes

nectar, and flower visitors (mainly for pollen) (Kress 1974). *Rhizophora apiculata* in contrast seems most specialized for wind pollination, the pollen being shaken out of a half-open flower, borne below the leafy crown of the twig. *Rhizophora* may still be in an active state of evolution, since interspecific sterility barriers seem to break down readily, leading to hybrid swarms of which *R. X lamarckii* in the New Papuasian area (Tomlinson and Womersley 1976), *R. X harrisonii* in the Caribbean-West African area (Breteler 1969, 1977), and *R. X selala* in Fiji and New Caledonia (Tomlinson 1978) represent examples. The problem here is of understanding the genetic basis for the breeding mechanism of *Rhizophora*.

Our present understanding is therefore preliminary and incomplete. There is much scope for further extended work on the floral biology of mangroves.

ACKNOWLEDGEMENTS

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