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POLLINATION DROP IN RELATION TO CONE MORPHOLOGY IN PODOCARPACEAE: A NOVEL REPRODUCTIVE MECHANISM[1]

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Observation of ovulate cones at the time of pollination in the southern coniferous family Podocarpaceae demonstrates a distinctive method of pollen capture, involving an extended pollination drop. Ovules in all genera of the family are orthotropous and single within the axil of each fertile bract. In *Microstrobus* and *Phyllocladus* ovules are erect (i.e., the micropyle directed away from the cone axis) and are not associated with an ovule-supporting structure (epimatium). Pollen in these two genera must land directly on the pollination drop in the way usual for gymnosperms, as observed in *Phyllocladus.* In all other genera, the ovule is inverted (i.e., the micropyle is directed toward the cone axis) and supported by a specialized ovule-supporting structure (epimatium). In *Saxegothaea* there is no pollination drop and gametes are delivered to the ovule by pollen tube growth. Pollination drops were observed in seven of the remaining genera. In these genera the drop extends over the adjacent bract surface or cone axis and can retain pollen that has arrived prior to drop secretion ("pollen scavenging"). The pollen floats upward into the micropylar cavity. The configuration of the cone in other genera in which a pollination drop has not yet been observed directly suggests that pollen scavenging is general within the family and may increase pollination efficiency by extending pollination in space and time. Increased pollination efficiency may relate to the reduction of ovule number in each cone, often to one in many genera, a derived condition. A biological perspective suggests that animal dispersal of large seeds may be the ultimate adaptive driving force that has generated the need for greater pollination efficiency.

We here document that the pollination drop mechanism of many members of the southern hemisphere coniferous family Podocarpaceae (podocarps) differs from that in most gymnosperms. The drop can "scavenge" pollen that has previously fallen near the ovule, prior to drop secretion. Presumably this increases the efficiency of pollination and is correlated with the reduced number of ovules per cone in most podocarps. The Podocarpaceae, unlike most other conifers, are largely characterized by fleshy seeds dispersed by animals (mainly birds).

A pollination drop is known to be produced in all species of Cephalotaxaceae, Cupressaceae, Taxaceae, and Taxodiaceae that have been studied (Takaso, 1990). In Araucariaceae no pollination drop occurs, the gametes being delivered to the micropyle by pollen tube growth (Eames, 1913; Haines, Prakash, and Nikles, 1984). The greatest diversity in pollination mechanisms is known for Pinaceae, in which a pollination drop is reported for *Picea* and *Pinus,* while other genera have mechanisms without drop secretion, such as pollen engulfment or pollen tube growth (Doyle, 1945). Absence of a drop is considered derived since the presence of a pollination drop may be a very ancient feature of gymnosperms (cf. Rothwell, 1977). In Podocarpaceae there has been no observation of pollination mechanisms in naturally growing trees. Doyle (1945) suggested that the Podocarpaceae formed a parallel series to the Pinaceae, also involving loss of a pollination drop, but he described a pollination drop only in one species each of *Podocarpus* and *Prumnopitys* cultivated in Irish gardens. *Saxegothaea,* which lacks a pollination drop (Norèn, 1908; Doyle and O'Leary, 1935), was

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TABLE 1. *Podocarpaceae. Taxa with an observed pollination drop*

Taxon	Locality[a]	No. fertile bracts	Ovule orientation[b]
Dacrycarpus dacrydioides	Huia (NZ)	1(–2)	Inverted
Halocarpus kirkii	Kelly's Road, Waitemata (NZ)	2–3	Inverted
Lagarostrobos colensoi	Cult. Auckland Univ. Campus (NZ)	2–3	Inverted
Lepidothamnus intermedius	Kauaeranga For. Res. (NZ)	1(–2)	Obliquely erect
Lepidothamnus laxifolius	Tongariro Nat. Park (NZ)	1(–2)	Obliquely erect
Microcachrys tetragona	Mt. Field Nat. Park (T)	8–16	Inverted
Phyllocladus aspleniifolius var. *alpinus*	Tongariro Nat. Park (NZ)	1–5	Erect
Phyllocladus trichomanoides	Cornwall Park, Auckland (NZ)	2–7	Erect
Podocarpus macrophyllus	Cult. Fairchild Tropical Garden (US)	1–2	Inverted
Podocarpus nivalis	Tongariro Nat. Park (NZ)	1–2	Inverted
Podocarpus totara	Manurewa Bot. Gard. (NZ)	1–2	Inverted
Prumnopitys andina	Cult. Hobart Bot. Gard. (T)	5–10	Inverted
Prumnopitys ferruginea	Waitakere Hills (NZ)	1(–2)	Inverted
Prumnopitys taxifolia	Manurewa Bot. Gard. (NZ)	5–10	Inverted

[a] NZ = North Island, New Zealand, T = Tasmania, US = United States.

[b] Morphological orientation with respect to cone axis.

considered by Doyle to be highly derived and analogous to *Tsuga.* Our observations greatly amplify the picture for Podocarpaceae and show many unique features of their pollination; perhaps only in *Picea* and *Pinus,* which have an ability to retain pollen prior to drop secretion, may parallels be drawn (Owens, Simpson, and Molder, 1981; Owens, Simpson, and Caron, 1987).

The Podocarpaceae includes 18 genera (17 if *Phyllocladus* is excluded as Phyllocladaceae; Page, 1990) and about 200 species of shrubs and trees, with a wide distribution in the Gondwana region, i.e., present day Africa, southeast Asia, Australasia, and South America (De Laubenfels, 1988). New Caledonia (18 spp.) and New Zealand (17 spp). both represent local centers of diversity and endemism. Plants typically occupy montane habitats in the tropics, but in New Zealand are a major component of the mixed podocarp forest at all altitudes and are frequently dominant. Recent generic realignment has greatly clarified the status of certain groups, chiefly by dismemberment of the large and previously unnatural genera, *Dacrydium* and *Podocarpus* (e.g., Tegner, 1967; Quinn, 1970, 1982, 1987; De Laubenfels, 1972, 1988; Page, 1989, 1990).

MATERIALS AND METHODS

Observations were made on field-grown trees from wild and cultivated populations in the period September to December 1989, in New Zealand, Tasmania, and New Caledonia. Recognition of the pollination process was facilitated by continual monitoring of shoot development in a diversity of podocarps undertaken for phenological and developmental purposes. Most observations were made on populations in the Auckland region of New Zealand (Table 1) since these provided convenient access to photomicrographic facilities. Pollination drops can be observed directly in the field with a hand lens. Detached shoots with ovulate cones at the stage of pollination were brought into a sheltered room, kept in water, and enclosed in a plastic bag. This usually results in drop secretion in a normal way. Pollination drop secretion is mostly in the late evening, and the drops are normally resorbed by late morning, but enclosed cut shoots can retain drops for several days. In *Microcachrys tetragona,* fresh cones flown from Tasmania to Auckland permitted the photography of pollination drops in this way. Microphotography of cones at the stage of pollination was done with a Wild stereomicroscope using Ektachrome color transparency film (ASA 100); Figs. 1–9, 12–20 are black-and-white reproductions from these transparencies.

Some manipulation of ovules with and without captured pollen grains was done under the microscope to understand the mechanics of pollen movement. Reorientation of ovules with enclosed pollen demonstrated the buoyancy of pollen within natural drops, or within drops simulated by adding water.

RESULTS

General mechanisms*—Cone orientation—*An intrinsic feature of the pollination mechanism of most podocarps is the erect orientation of the cone at the time of pollination, commonly brought about by growth curvature at the time the cone expands. *Phyllocladus* is an example of an exceptional genus because cones are borne at the margins of phylloclades and have no preferred orientation (Fig. 1). Otherwise, cone reorientation can be pronounced, the mechanism depending on whether the cone is terminal or lateral on a vegetative shoot. In *Microcachrys* (Fig. 2), terminal cones are erected by growth at the base of the cone axis. In *Dacrydium cupressinum* (Fig. 3), the cones occur at the ends of usually short vegetative axes, and the upturning of the shoot tip is the first evidence that allows reproductive axes to be distinguished from vegetative axes. In other *Dacrydium* species with robust axes this curvature is not possible and cone orientation depends on the orthotropy of the whole shoot (e.g., Fig. 35). In most other taxa cone erection occurs just as the cone expands, as in *Dacrycarpus* (Fig. 4) and *Lagarostrobos colensoi* (Fig. 5). In some *Prumnopitys* species (e.g., *P. taxifolia,* Fig. 6) the candlelike erection of young elongated cones is pronounced because they are lateral and contrast with the dark foliage. Curvature is here possible within the whole cone axis, as demonstrated experimentally by Doyle (1945), who produced S-shaped cones by reorientating branches.

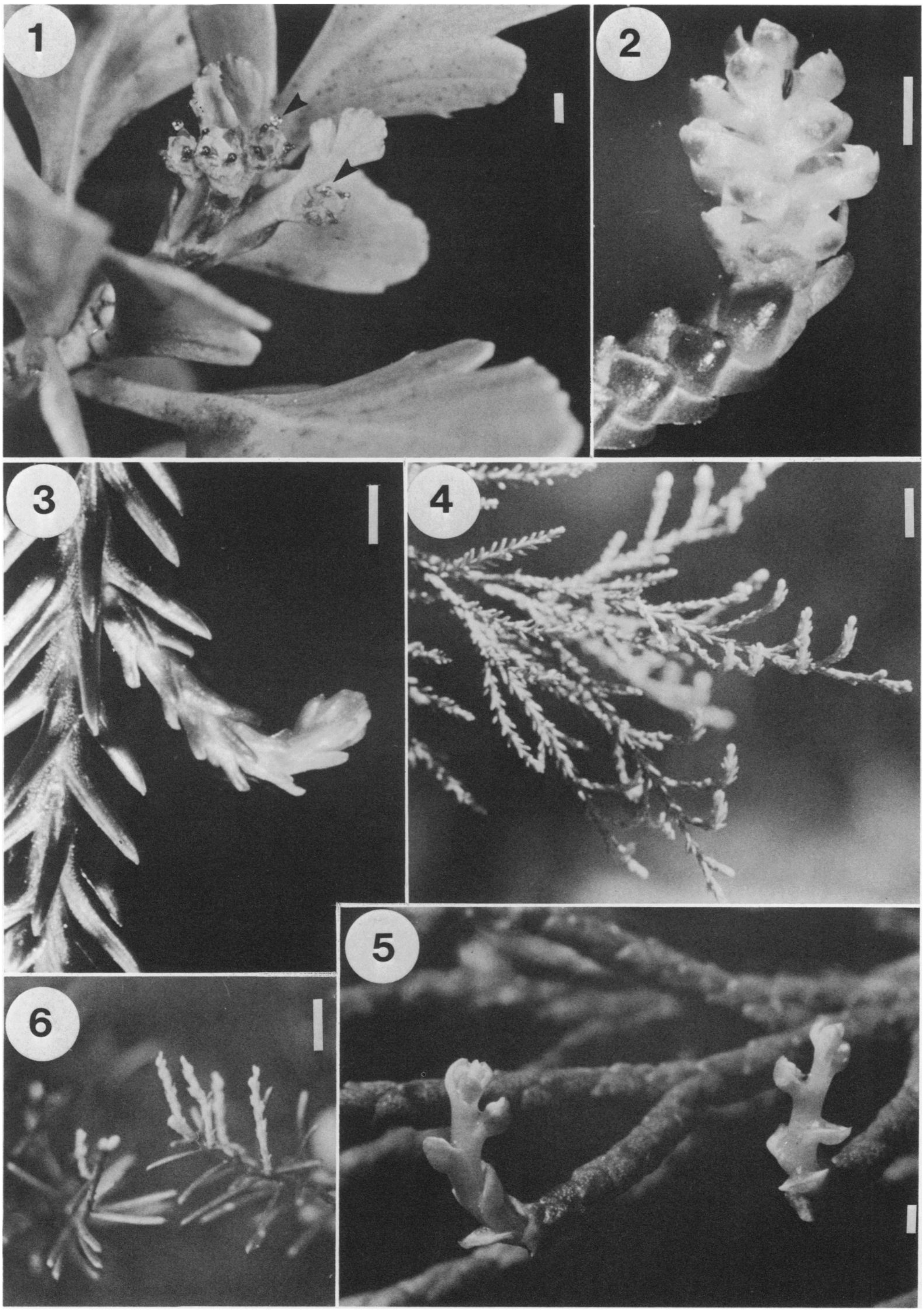
In *Podocarpus,* the cones are lateral at the base of the new shoots and subtended by either bud-scales or proximal foliage leaves. Orientation is the result of the curvature of the longer (e.g., *P. totara*) or shorter (e.g., *P. nivalis*) naked portion of the cone axis ("peduncle"). The extent of curvature depends on the orientation of the parent branch (cf. Figs. 7, 8).

The overall negative geotropism, whatever its mechanism, results in erect cones and ovules with the micropyle directed downward (Fig. 9). This orientation is necessary for the pollination mechanism to work, and in Figs. 12–37 cones and ovules are illustrated in their natural position.

Pollination mechanism—In the 13 taxa listed positively in Table 1, a pollination drop has been observed in species of the genera *Dacrycarpus, Halocarpus, Lagarostrobos, Lepidothamnus, Microcachrys, Phyllocladus, Podocarpus,* and *Prumnopitys.* Cones at the time of drop secretion are illustrated in Figs. 12–20. In all taxa except *Phyllocladus* a common mechanism is shown and may be described generally before details are presented for individual taxa. The mechanism in principle is shown in Fig. 11. The mechanism in *Phyllocladus* (and probably *Microstrobus*) is the same as generalized for gymnosperms with a pollination drop as in most other families (Fig. 10).

The beginning of drop secretion usually occurs in the late evening (9–10 p.m.), and the drop is resorbed during the following morning. It can be sustained longer if the shoots are enclosed in a plastic bag, as described under Materials and Methods. Figure 17 shows the beginning of drop secretion at 9 p.m.; other illustrations are of drops photographed in the morning following drop secretion. The pollination drop in all taxa except *Phyllocladus* involves secretion of the drop onto some adjacent wettable surface in such a way that while retaining contact with the micropylar orifice, the drop picks up wind-borne pollen either directly or, more importantly, indirectly from wettable areas where pollen may already have been deposited (e.g., Zone X in Fig. 11). Nonwettable and wettable areas are distinguished chiefly by the presence or absence of white, waxy surface deposits. Wax may cover inner and outer surfaces of the epimatium and even the outer surface of the micropyle, where this protrudes. In some *Prumnopitys* species the wettable region is structurally specialized as a "gutter," with raised margins as described later. In all taxa with inverted ovules and erect cones, once the secreted drop has made contact with the adjacent wettable surface and adheres to it by capillarity, it spreads downward by gravity, but retains contact with the micropylar orifice (e.g., Fig. 9). The extent of the drop's spread is determined by its volume and the topography of the cone; it is most extended in species of *Prumnopitys* with the grooved, gutterlike axis. Pollen can either arrive after the drop is secreted, or arrive before and adhere to the wettable surface. Captured grains float upward in the drop and become concentrated at the micropylar orifice. With drying or resorption of the drop the pollen is drawn into the micropyle and comes to rest in the pollen chamber on the nucellus. Pollinated cones can be identified by dissection, because accumulated pollen can be observed microscopically. Pollinated cones also can be identified by reversing the process, i.e., if a drop of water is added to the micropylar region and the ovule erected by turning the cone upside down, existing pollen floats out of the pollen chamber provided no air bubble has been trapped. Reinverting the ovule causes the normal process of pollen flotation to be repeated. This simple manipulation demonstrates the dependence of the mechanism on pollen buoyancy.

Phyllocladus is exceptional because the drop mechanism conforms to that general for conifers, i.e., the pollination drop is secreted and retained by the micropyle, without contacting any adjacent surface (Figs. 1, 10). This condition is correlated with the absence of any



Figs. 1–6. Cone orientation in Podocarpaceae; cones terminal on vegetative shoots in 2–5, lateral in 6. **1.** *Phyllocladus aspleniifolius* var. *alpinus,* shoot with young ovulate cones on phylloclade margins, arrowheads = pollination drops. **2.** *Microcachrys tetragona,* ovulate cone at time of pollination, terminal on vegetative shoot and erected by unequal growth of base of cone axis. **3.** *Dacrydium cupressinum,* very young ovulate cone, erected by curvature of distal portion of supporting axis. **4.** *Dacrycarpus dacrydioides,* ovulate cones at time of pollination, each erected by curvature of supporting axis. **5.** *Lagarostrobos colensoi,* ovulate cones at time of pollination, erected by curvature of sterile portion of cone axis. **6.** *Prumnopitys taxifolia,* ovulate cones, lateral on previous year's vegetative shoot, each showing a strong negatively geotropic response. Bars = 1 mm in Figs. 1, 2, 3, 5, and 1 cm in Figs. 4, 6.

preferred cone orientation with respect to gravity and the absence of an epimatium.

Cone structure—Figures 12–20 document details of ovulate cone morphology at the time of pollination in some of the taxa in which a pollination drop has been observed. Figures 21–30 show structural details for a similar range, incorporating both surface and sectional views of whole cones and single ovulate complexes. Figures 31–37 show similar details in taxa in which a pollination drop has not yet been observed, but in which the cone configuration suggests that it is likely to occur. The cones of podocarps are minute at the time of pollination, usually of the order of 3–5 mm long. They include a series of spirally arranged bracts, one or more of which is fertile, i.e., subtends an ovulate structure. *Microcachrys* has cone bracts arranged in whorls. In taxa like *Microcachrys* (Figs. 2, 12), *Microstrobus* (Fig. 31), *Phyllocladus* (Figs. 1, 23), and especially *Saxegothaea*, the reproductive structure is indeed conelike because the axis is short and several ovules (one per fertile bract) are developed. Otherwise, in many taxa there are only one to two ovules, and the unit little resembles a cone.

A diagnostic feature for the family is the presence of a single ovule associated with each fertile bract. In most podocarps the ovule is further supported in its pollinating position by a partly or wholly enveloping structure, the epimatium, an appendage of uncertain homology (densely stippled in Figs. 21–37). Furthermore, in almost all of these specialized examples, the ovule is inverted in its orientation so that the micropyle is directed toward the cone axis (cf. Fig. 11). In most genera with inverted ovules the cone axis always grows erect so that the ovule is topographically as well as morphologically inverted. One exception is *Lagarostrobos franklinii* (Tasmania), which has erect ovules but inverted cones, so that the same topographic orientation as other genera is achieved (Fig. 32). In *Lepidothamnus* the

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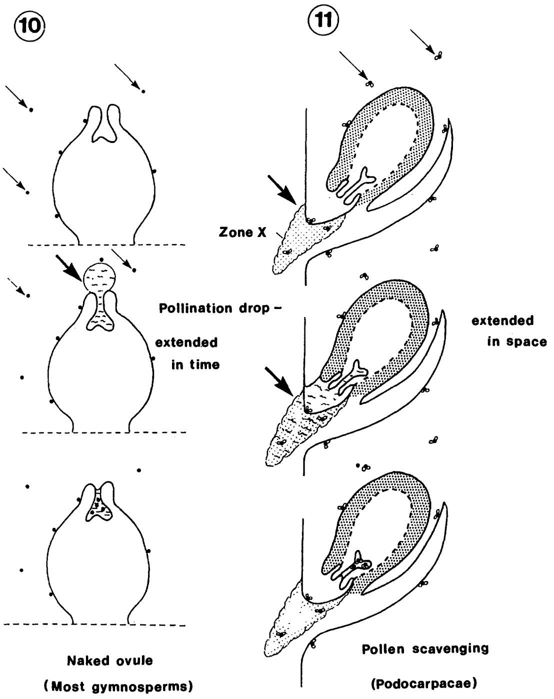
Figs. 7–9. Pollination drops in *Podocarpus nivalis*; ovulate cones are lateral at the base of the new season's growth and erected by curvature of base of cone axis, whether the supporting shoot is horizontal (Fig. 7) or vertical (Fig. 8). **7.** Cone with two ovules, the two pollination drops fused (arrowhead). **8.** Each cone with a single ovule; arrowheads = pollination drop. **9.** Detail of cone with single ovule, the pollination drop extended down the subtending cone axis; b = bract, e = epimatium, m = micropyle, pd = pollination drop, r = receptacle, consisting of fused bases of two bracts (cf. Figs. 24, 25). Bars = 1 mm.



Figs. 10, 11. Methods of pollen capture in gymnosperms in chronological sequence from above. **10.** Naked ovule of most gymnosperms with a pollination drop. Prior to secretion of a pollination drop, ovule may receive undirected and ineffective pollen (small arrows); subsequently, pollination drop is secreted and becomes trap for pollen. The period of effective pollen capture (large arrow) can only be extended for the duration of drop presentation; finally, the drop is resorbed and pollen is drawn into the pollen chamber. Pollen may or may not be winged. **11.** Pollen scavenging in Podocarpaceae. Ovule partly or wholly enclosed by epimatium (dotted). At first, cone receives pollen (small arrows = ineffective pollen), some falling in region designated Zone X, adjacent to the micropyle of the ovule, which is always inverted (morphologically or topographically); subsequently, the pollination drop is secreted through the micropyle onto Zone X where existing pollen is picked up, pollen floats into the pollen chamber; finally, the drop is resorbed and most of the pollen remains in the pollen chamber. The pollination period (large arrow) is extended both in time (pollen may be functional that falls on the cone before the drop is secreted) and space (Zone X increases the size of the target), i.e., there is pollen scavenging.

ovule is obliquely erect as is evident when the seed matures (Fig. 27). In *Dacrydium,* the ovule is inverted at pollination but may become partly erected during seed development (Fig. 34). As already stated, precise ovule orientation with respect to gravity is essential to the pollination mechanism in most taxa. Exceptional genera that lack an epimatium are *Microstrobus* (two species) and *Phyllocladus* (four species); both these genera have erect ovules, and all species are alike.

Information about cone morphology and ovule orientation is summarized in Table 1. In the most reduced and presumably most derived condition, the cone includes a series of sterile bracts and a single fertile bract, the solitary ovule being subterminal (e.g., *Dacrycarpus dacrydioides,* Fig. 30; *Decussocarpus comptonii,* Fig. 36; *Falcatifolium taxoides,* Fig. 37; *Parasitaxus ustus,* Fig. 33; and *Prumnopitys ferruginea,* Fig. 29).

Special mechanisms—Taxa vary in the details of the process according to ovule number and cone topography as described in detail for individual taxa.

Phyllocladus spp.—Ovules are erect and inserted in the axil of the bract (Fig. 23), but have no preferred orientation with respect to gravity. At the time of pollination an aril is present but little developed (cf. Tomlinson, Takaso, and Rattenbury, 1989). The pollination drop remains on the micropyle (o in Fig. 23) and does not contact adjacent surfaces (Fig. 1).

Podocarpus species—*Podocarpus* (sensu stricto) is very uniform in its cone morphology (Figs. 24, 25) and seemingly also in its pollination mechanism, which is constant in the few species that have been observed. The pollination drop (Fig. 9) is secreted onto the receptacle formed by the two inflated bracts of the cone, one or both of which may be fertile (Figs. 7, 8, 24, 25). The amount of secreted fluid is sufficiently copious that it can run down the groove between the two bracts. Where there are two ovules the separate drops usually combine (Figs. 7, 8).

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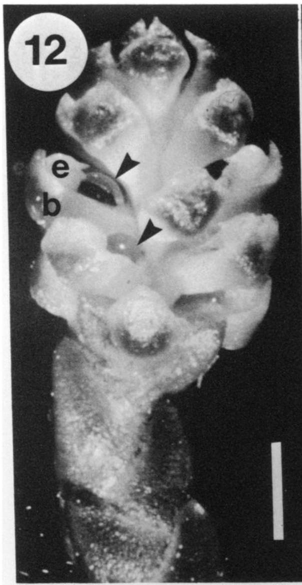
Figs. 12–20. Ovulate cones in Podocarpaceae at time of pollination. **12.** *Microcachrys tetragona.* **13.** *Halocarpus kirkii.* **14.** *Dacrycarpus dacrydioides.* **15.** *Lepidothamnus intermedius.* **16.** *Lepidothamnus laxifolius.* **17.** *Lagarostrobos colensoi,* single fertile cone scale with commencement of drop secretion (cf. Fig. 5). **18.** *Prumnopitys ferruginea.* **19.** *Prumnopitys taxifolia,* portion of single cone with one complete unit (cf. Fig. 6). **20.** *Lagarostrobos colensoi,* whole cone, pollination drops from two separate ovules have fused (arrowhead). b = fertile bract; sb = sterile bract; e = epimatium; m = micropyle; r = receptacle; g = groove; arrowheads = pollination drop or its recent remains. Bars = 1 mm.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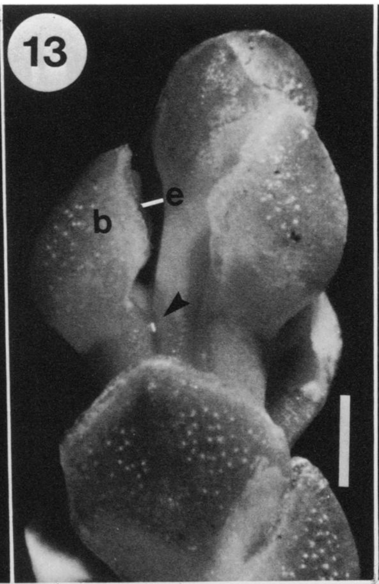
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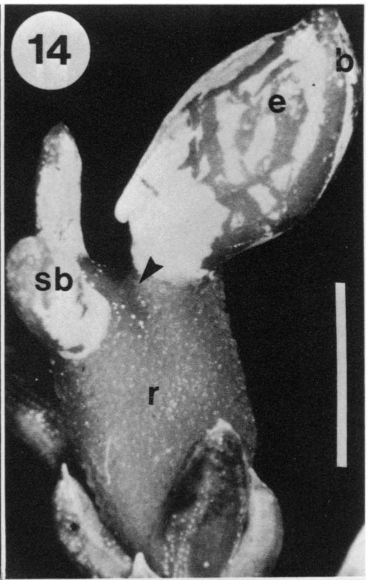
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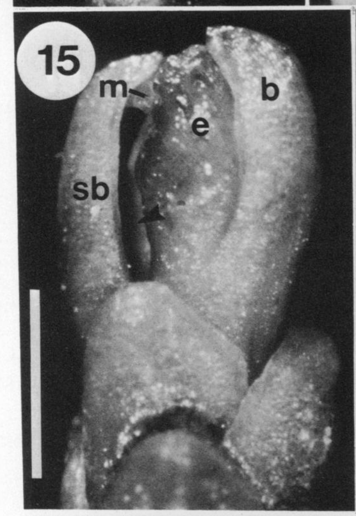
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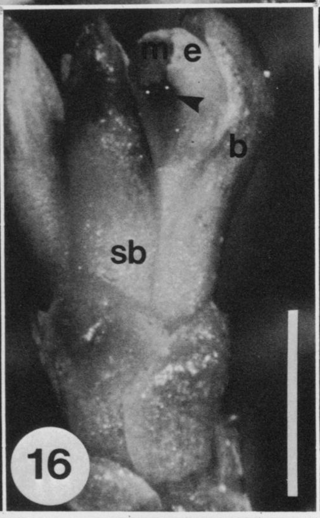
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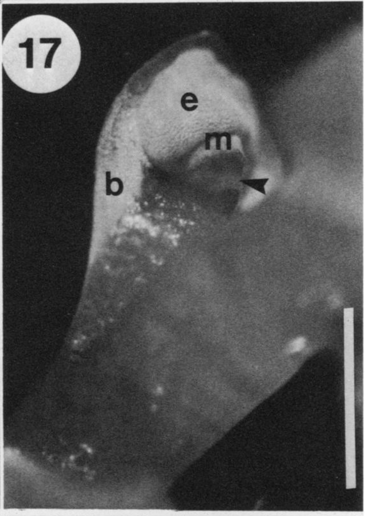
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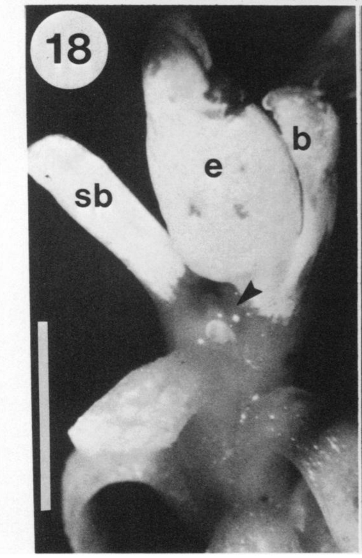
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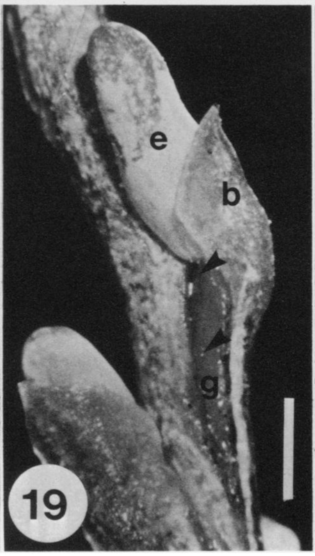
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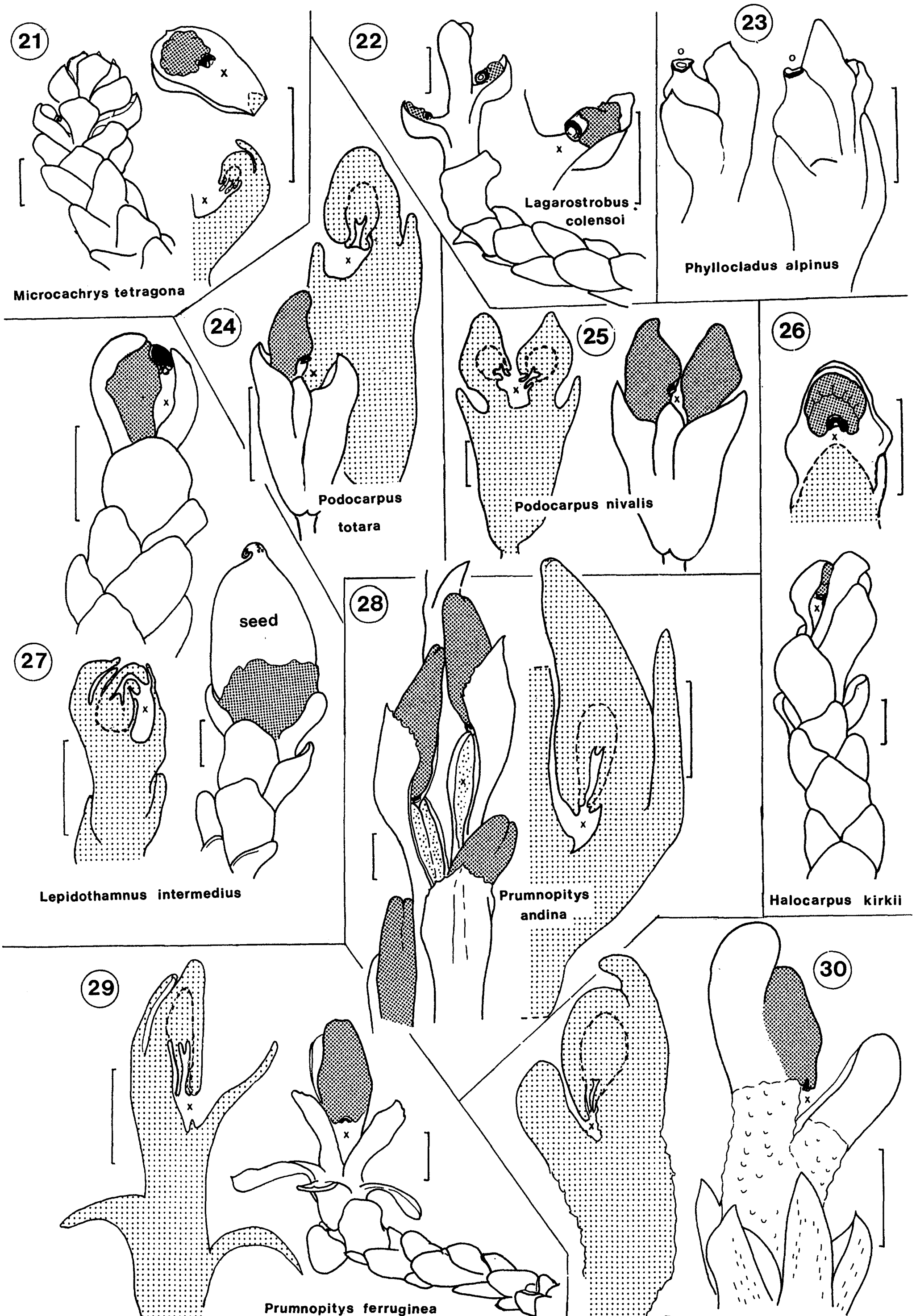
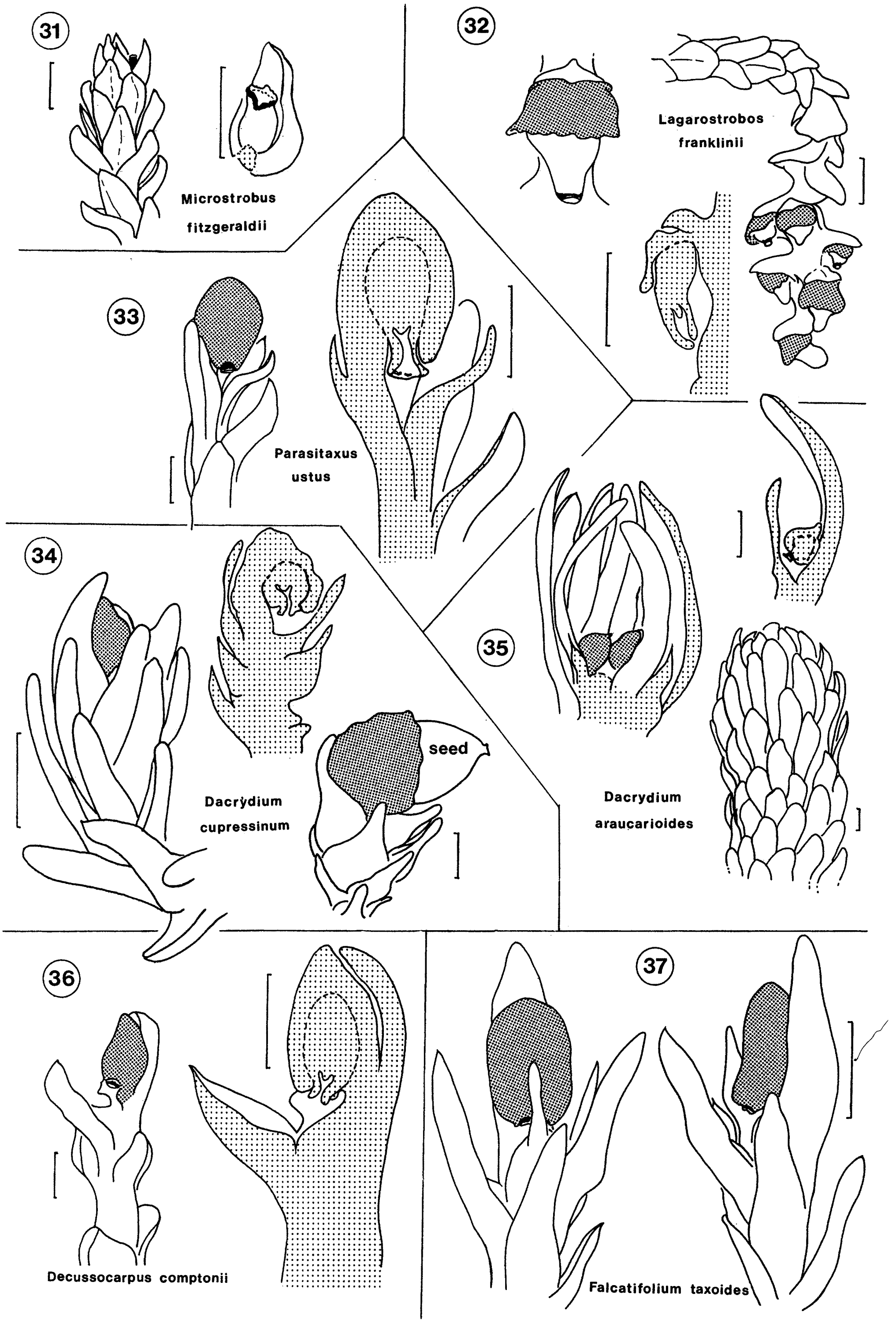


Figs. 21–30. Cone and ovulate structures in certain Podocarpaceae whose pollination drops have been observed, in surface view and section; from camera lucida drawings. **21.** *Microcachrys tetragona.* **22.** *Lagarostrobos colensoi.* **23.** *Phyllocladus aspleniifolius* var. *alpinus*; o = micropylar orifice. **24.** *Podocarpus totara.* **25.** *Podocarpus nivalis.* **26.** *Halocarpus kirkii.* **27.** *Lepidothamnus intermedius.* **28.** *Prumnopitys andina.* **29.** *Prumnopitys ferruginea.* **30.** *Dacrycarpus dacrydioides.* Cut surfaces = stippled; epimatium = shaded; micropyle where visible = solid black. In all figures (except Fig. 23) region that receives extended pollination drop indicated by X; X developed as an elongated "gutter" (stippled) in Fig. 28. Bars = 1 mm.



Figs. 31–37. Cones and ovulate structures in Podocarpaceae whose pollination drops have not yet been observed. **31.** *Microstrobus fitzgeraldii.* **32.** *Lagarostrobos franklinii,* ovule is morphologically erect, but cone is pendulous. **33.** *Parasitaxus ustus.* **34.** *Dacrydium cupressinum.* **35.** *Dacrydium araucarioides.* **36.** *Decussocarpus comptonii.* **37.** *Falcatifolium taxoides,* shading conventions as in Figs. 21–30. Bars = 1 mm.

Microcachrys—Ovules are inserted distally on the bract (Fig. 21); the pollination drop, therefore, adheres to the adaxial surface of the bract base (Fig. 12). Under artificial conditions, drops may persist for several days.

Lagarostrobos colensoi—Cones are terminal on the vegetative shoots (Fig. 5) with the ovule distal on the short bract (Fig. 22). The drop originates from the micropyle (Fig. 17) and extends over the adaxial surface of the bract onto the cone axis, accumulating in the bract axil; drops from adjacent ovules may fuse (Fig. 20). Further spread is prevented primarily by nonwettable waxy deposits.

Halocarpus kirkii—This resembles *Lagarostrobos colensoi* but with the cone condensed and more robust (Fig. 26). The fertile bracts are less divergent so that the drop has a narrower meniscus and extends farther down the cone axis (Fig. 13).

Lepidothamnus spp.—In *Lepidothamnus laxifolius* the cones are terminal on leafy shoots, the cone axis is condensed, and limited reorientation is primarily the result of generalized growth curvature of the fertile shoot. A series of two or three penultimate sterile bracts forms a palisade that creates a shallow open receptacle into which the drop extends and is retained by capillarity (Fig. 16). A diagnostic feature of the genus is the hooked micropyle (persistent in the seed) and the obliquely erect orientation of the ovule (cf. *L. intermedius*, Fig. 27). Under these circumstances captured pollen travels initially upward into the downwardly directed micropylar orifice. It is then drawn into the pollen chamber in the reverse direction by capillarity as the drop either dries or is resorbed. The U-shaped passage can be reversed and repeated by reorientating the cone. Here, then, there is an outer pollen receptacle, as well as a pollen chamber. *Lepidothamnus intermedius* is distinct in that the pollination receptacle is more completely sealed because the hooked micropyle seems consistently to be lodged under the tip of the opposing sterile bract (Figs. 15, 27).

Dacrycarpus dacrydioides—There are two or three bracts, fused basally to form a fleshy papillate receptacle (Fig. 14). The receptacle enlarges and colors abruptly at the time of seed dispersal. The distal part of the bract is represented by a small waxy protuberance, developed very early in cone differentiation, the receptacle itself appearing later in association with ovule initiation. One (less commonly two) bracts are fertile, the fertile bract being adnate to the epimatium (Fig. 30). The pollination drop is secreted onto the surface of the receptacle, its spread possibly being facilitated by the papillae (Fig. 14). Contrast between white, waxy, nonwettable and green, nonwaxy, wettable surfaces is pronounced.

Prumnopitys andina and P. taxifolia—The cones have an elongated axis (up to 3 cm long), with numerous (up to 12) widely separated ovules, each subtended by one of the spirally arranged bracts (Fig. 6). The mouth of the micropyle is applied directly to a shallow, wettable groove, which represents the decurrent base of the bract insertion and contrasts with the waxy, nonwettable remaining surfaces (Fig. 19). The margin of the groove is slightly raised so that a veritable "gutter" is formed (Fig. 28). Pollen is readily observed within the gutter, both prior and subsequent to the secretion of the drop. The accumulation of excess pollen in the micropylar region of the groove after drop absorption suggests that pollen scavenging is effective.

Prumnopitys ferruginea—Cones are borne laterally toward the base of previous year shoots. They continue growth throughout winter so that a long axis with a series of sterile overlapping fleshy bracts is produced. At the time of pollination the distal part of the axis, which bears a series of more delicate spreading sterile bracts, elongates and becomes oriented vertically. The ultimate two or four bracts are narrow, cylindrical, white, waxy, and nonwettable (Fig. 18). Usually only the ultimate or penultimate bract, in a pseudoterminal position, is fertile (Fig. 29). The bract remains free of the epimatium. The pollination drop is secreted onto the somewhat inflated cone axis and can spread extensively over the whole wettable surface (Fig. 18).

Other Podocarpaceae—Other taxa with a construction that conforms to the generalized arrangement suitable for pollen scavenging include *Acmopyle, Decussocarpus, Falcatifolium,* and *Parasitaxus.* We have observed the last three close to, but not at, the time of pollination and have not yet recorded pollination drops on them. However, the close similarity in ovule orientation suggests the same mechanism. These and other taxa may be discussed individually (Figs. 32–37).

Lagarostrobos franklinii—Cones are terminal on vegetative shoots, but pendulous at the time of pollination (A. Shapcott, personal communication). Unlike *L. colensoi,* the ovule is morphologically erect and with a less well-developed epimatium that encircles only the base of the ovule (Fig. 32). Under these circumstances the ovule is topographically inverted and the pollen-scavenging mechanism seems possible.

Parasitaxus ustus—Cones are terminal on erect vegetative branches and include a single pseudoterminal ovule in the axil of the ultimate or penultimate bract (Fig. 33). The micropylar orifice is applied to the cone axis, suitable for pollen scavenging.

Dacrydium spp.—This genus remains problematic. In *D. cupressinum* the cones are terminal on upturned vegetative shoots (Fig. 3). The usually solitary ovule is inverted (Fig. 34), but we have not observed a pollination drop. In *D. araucarioides,* cones are indistinctly differentiated from vegetative buds since the numerous overlapping outer bracts are not divergent and the cone axis does not elongate (Fig. 35). One or two ovules occupy the central cavity surrounded by the palisade of sterile bracts. Ovules are inverted and subtended by a large bract. It is difficult to understand how pollen reaches these structures, which are completely enclosed. More field work on this widely distributed genus is required.

Decussocarpus comptonii—Cones are lateral on previous season's vegetative shoots, with a single subterminal ovule (Fig. 36). Bract and epimatium are free.

Falcatifolium taxoides—There is a single subterminal ovule surrounding the epimatium, usually with the tip of a sterile bract opposed (Fig. 37). Again the micropyle faces the upper part of the cone axis.

DISCUSSION

Robert Brown (1827) distinguished gymnosperms from angiosperms most precisely on the basis of the mechanism of pollen reception. He pointed out that in gymnosperms the ovule receives the pollen directly; that is, the pollen must be captured by the micropylar orifice of the ovule (cf. Fig. 10), but in angiosperms the pollen is received by the stigma of the ovary and gametes are delivered to the ovule by a pollen tube. The distinction is functional, but is usually translated into structural terms since gymnosperms or "naked seeded plants" are defined by their "naked" ovules. However, although they lack any consistently specialized enclosing structure, the developing seeds are indeed protected in various ways. Brown's point emphasized that in gymnosperms only at the time of pollination does pollen have direct access to the ovules. Angiosperms or "enclosed seeded plants," in contrast, have their ovules consistently enclosed in a carpel, a structure preventing direct access of pollen to the ovules, but with a stigmatic surface for pollen reception. Relative efficiency of pollination in gymnosperms and angiosperms must be understood in these terms.

Pollen transfer in conifers is by wind but is evidently inefficient because it requires large amounts of pollen to be dispersed randomly to a very small target. Increasing the efficiency of pollen capture may be considered selectively advantageous, but has been little examined in gymnosperms as a biological mechanism. Pollen capture in conifers may be facilitated by the aerodynamics of cone construction (Niklas, 1984), but this simply concentrates pollen within the vicinity of the target. In many gymnosperms, as in most conifers, the size of the ultimate site for pollen reception is increased by the secretion of a drop of fluid, which exudes from the micropyle and remains for some period of time (Fig. 10). Other mechanisms occur and are clearly derived within the gymnosperms (Doyle, 1945). However, if we accept the claim of Rothwell (1977) for the existence of pollination drops in fossil ovules of Carboniferous gymnosperms, then the pollination drop is an ancestral feature in modern groups. Interest, therefore, centers on a mechanism that may increase the efficiency of pollination and be a major feature of the reproductive biology of Podocarpaceae. The relatively few podocarps with a cone morphology not suited to the mechanism (*Microstrobos, Phyllocladus, Saxegothaea*) may be interpreted as either ancestral or derived. *Saxegothaea* is clearly derived, because of its many structural peculiarities; it lacks a pollination drop, and the pollen germinates away from the ovule (Norèn, 1908; Doyle and O'Leary, 1935; Looby and Doyle, 1939). It parallels, in this respect, the situation in a number of Pinaceae that lack a pollination drop (Doyle, 1945; Owens and Molder, 1975), most strikingly in the genus *Hesperopeuce* (= *Tsuga mertensiana*; Page, 1989). This similarity among the two families is assumed to be a convergence between distinct phyletic lines. On the other hand, the mechanism known for *Phyllocladus,* and presumed for *Microstrobus,* seems ancestral within the family since it corresponds to the type generalized within the gymnosperms (and apparently characterizing the families Cephalotaxaceae, Cupressaceae, Taxaceae, and Taxodiaceae in their entirety). An extension in time of the pollen capture process is known for *Picea* and *Pinus.* Here the ovule is provided with a pair of micropylar arms that secrete minute "droplets," rendering the arms viscous. Pollen can adhere to these arms and be picked up subsequently when the normal pollen drop, secreted by the nucellus, is produced. Effectively this extends the period of pollen reception by the ovule, as discussed by Owens, Simpson, and Molder (1987) and constitutes a minimal kind of pollen scavenging.

If one accepts this comparative interpretation, then the cone morphology of the majority of podocarps possessing inverted ovules represents a derived condition specialized in relation to a process that renders pollination more efficient. This immediately raises the question of the morphological nature of the epimatium, which is absent from *Microstrobus* and *Phyllocladus,* since there is such a close correlation between the presence of an epimatium and the secretion of a pollination drop. In the conventional view generated by Sinnott (1913) and accepted by subsequent authors (e.g., Wilde, 1944; Florin, 1954), part for part comparison of the axillary fertile complex of the ovulate cones of Pinaceae and Podocarpaceae is possible (Fig. 38). In Pinaceae, there is a pair of ovules inserted basally and with inverse orientation on a scale (the ovuliferous scale) in the axil of each fertile bract. The ovuliferous scale itself is homologized with the reduced branch axis found in some presumed ancestors (the Cordaitales and extinct transitional groups of conifers).

This paleobotanical evidence was assembled by the extensive comparative studies of Florin (e.g., 1951, 1954). The single ovule of podocarps has, for the most part, the same inverted orientation as in Pinaceae, and the presumed ovuliferous scale is conventionally homologized with the epimatium, which often encloses the ovule to greater or lesser extent. Support for the homology of epimatium with the ovuliferous scale comes from comparative anatomy. Both structures have a vascular supply in which xylem and phloem have an inverted orientation (Fig. 38), i.e., with xylem abaxial rather than adaxial (Sinnott, 1913). The simplest (but not necessarily ancestral) condition is then represented by taxa like *Microcachrys* and *Saxegothaea,* with a more obvious cone-like organization, since each cone has several fertile bracts. *Saxegothaea* is, however, specialized in its pollination mechanism. In most other podocarps, the seed cones are highly specialized, commonly with only one or two fertile bracts and with the morphology at the time of pollination related to the "pollen scavenging" process. Commonly there is a relatively specialized area (Fig. 11, Zone X) adapted for reception of pollen and the pollination drop. The aberrant genera *Phyllocladus* and *Microstrobus* are placed in this traditional scheme as derived entities, the epimatium in *Phyllocladus* being homologized with the arillate structure that develops late in cone ontogeny (Tomlinson, Takaso, and Rattenbury, 1989), unlike the epimatium, which is a necessary precursor to ovule initiation (Tomlinson, unpublished data). The simplest condition, that of *Microstrobus* (Fig. 31), is then considered to be totally derived by reduction. The overall picture invokes the evolutionary loss of the epimatium, the aril in *Phyllocladus* being its vestige. Clearly, this picture depends on an interpretation of the epimatium solely in conventional terms and is supported by vascular analysis and comparative morphology of mature cones (Stiles, 1912; Sinnott, 1913; Wilde, 1944). Florin (1951, 1954) incorporated this view into his generalized picture of cone reduction in conifers but made no new observations.

In biological terms, the function of the epimatium has been little discussed. The structure has no consistent role in the development of the fleshiness that characterizes the disseminules and is essential to their dispersal. A fleshy structure can be produced in a diversity of ways (Fig. 38, lower left). For example, in *Dacrycarpus* a fleshy receptacle is formed by the base of the bracts beneath the seed, the distal part of the fertile bract being adnate to the epimatium, which is not fleshy. *Podocarpus* is somewhat similar, but the bract is not adnate. In *Dacrydium* the epimatium envelopes only the base of the seed, which is otherwise exposed (Fig. 34). In *Prumnopitys* the epimatium becomes the attractive fleshy structure, the bract remaining unelaborated (Fig. 38). In taxa like *Lepidothamnus,* the epimatium, which is relatively conspicuous at the time of pollination, shows little further enlargement in the maturation of the seed (Fig. 27), the basal portion of the cone axis becomes red and fleshy, the seed coat becoming a contrasted black. These few examples illustrate the divergent developmental possibilities during seed maturation, involving various parts of these highly specialized cones and without consistent participation of the epimatium.

An alternative to the idea that evolution in cone morphology of podocarps has proceeded by specialization and ultimately loss of the ovuliferous cone can be based on the pollination mechanism. In this interpretation, the

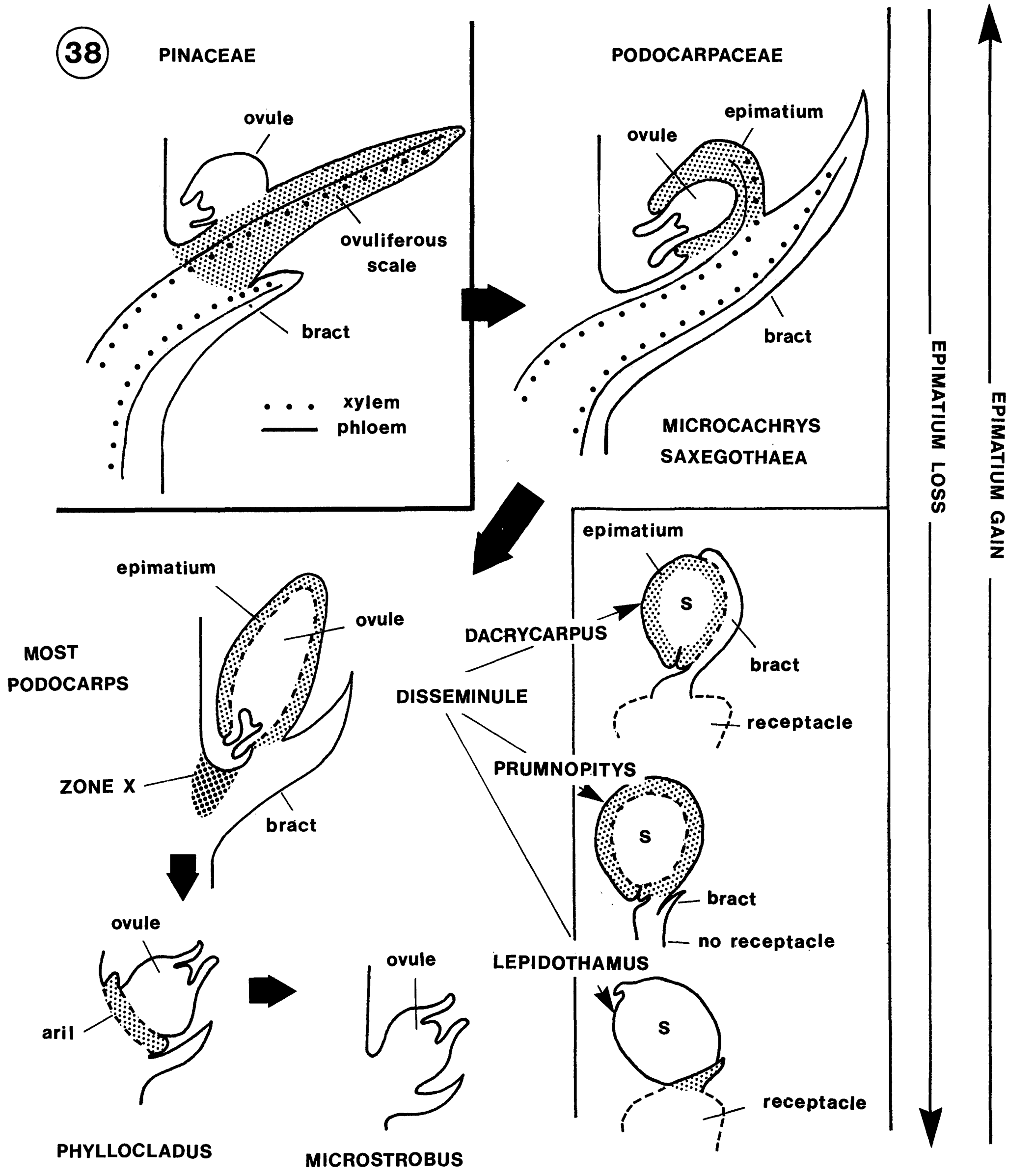


Fig. 38. Evolutionary morphology of the podocarpaceous cone. Pinaceae: the conventional interpretation of the ovuliferous scale as a branch homologue with inverted vascular bundles. Podocarpaceae: the same configuration with the ovuliferous scale an epimatium, as in *Microcachrys* and *Saxegothaea*. The arrangement in most podocarps with one to two ovules per cone and the pollination mechanism described here may be derived from the condition in these two genera. *Phyllocladus* and *Microstrobos* then represent the ultimate reduction, with the epimatium reduced to a late-developing aril (*Phyllocladus*); or wholly absent (*Microstrobus*). This implies loss of the epimatium as an evolutionary trend (arrow, right). In the development of the seed (S) into a fleshy dispersal unit in other genera, the epimatium may variously or may not contribute to the disseminule (fruit analogue) as illustrated by *Dacrycarpus*, *Prumnopitys*, and *Lepidothamnus*. However, the situation can be reversed and the epimatium derived de novo (arrow far right), if the progressive specialization of the pollination mechanism is considered, as we hypothesize.

epimatium has arisen de novo and it represents a structure intimately associated with the pollen scavenging process. An ancestry for the Podocarpaceae within a group that may have lacked an ovuliferous scale may not be difficult to postulate, since the condition occurs in the transition conifers, e.g., *Ullmannia* (Stewart, 1983). Preliminary developmental evidence shows that the epimatium always precedes ovule initiation in such a way that it produces the inverted ovule orientation, an essential ingredient of the pollen scavenging mechanism.

One must emphasize that ovules in gymnosperms are always orthotropous and have no inherent mechanism for reorientation (unlike angiosperms with their frequent double integuments and inherent capability for curvature). Epimatium and outer integument may have equivalent biological properties, but this is not to imply that they are homologues. The conventional evolutionary scenario presented in Fig. 38 thus can be reversed, with *Microstrobus* and *Phyllocladus* being the antecedent types, reflected in their erect ovules and simple pollination mechanism. The aril of *Phyllocladus* could then be the precursor for the epimatium that has become the characteristic feature of most podocarps, but as a derived and not an ancestral structure. *Lagarostrobos franklinii* could fit into this picture since ovule inversion is determined by cone inversion (Fig. 32).

Other aspects of the structure and biology of podocarps complicate both evolutionary scenarios. Pollen in most podocarps is saccate, or winged (Tegner, 1965; Pocknall, 1981), i.e., with two or three bladderlike extensions of the exine (as in the familiar textbook illustrations of *Pinus*). Doyle (1945) suggested that these structures were essential for maintaining pollen buoyancy in the pollen drop, but not in air. He noted a close correlation between the presence of winged pollen and a pollination drop in Pinaceae. A similar situation may exist in Podocarpaceae; *Saxegothaea* lacks winged pollen. In *Phyllocladus* the wings can be described only as vestigial. *Dacrydium* lacks wings for the most part, according to Tegner (1965), but not *D. cupressinum,* according to Pocknall (1981). Clearly the situation deserves reexamination in the family as a whole. A further biological mechanism proposed by Doyle (1945) was that pollen wings guaranteed a preferred orientation of the pollen on the nucellus in order to facilitate pollen germination. Observations by Lill and Sweet (1977) on *Pinus radiata* do not support this idea.

Dacrydium may be a key genus in these biological interpretations. It apparently lacks pollen wings, has a cone morphology, seemingly with totally enclosed ovules, and no pollination drop has yet been reported. The preliminary nature of our observations should be clear from this discussion, but points the way to further necessary field work and direct observation of the mechanism.

The Podocarpaceae, with an intriguing "Gondwana" distribution, have been relatively neglected by botanists, and the role they play in interpreting evolutionary processes in conifers has been minimized, largely because of ignorance. The current demonstration of specialized mechanisms in their pollination biology shows that their further detailed examination can be pursued with scientific benefit, especially as increasing emphasis has been put on pollination as the adaptive driving force for the origin and specialization of the seed habit (Haig and Westoby, 1989). However, one cannot disassociate one aspect of the reproductive process from another. A characteristic feature of most podocarps is a disseminule composed of a large seed and associated fleshy, brightly colored structures and correlated with animal dispersal. Selection for this dispersal unit seems directed toward reduction of ovule number per cone. A typological reduction series exists within the family; this may mirror the interdependence between pollination efficiency, seed biology, and cone morphology. Podocarps clearly have distinctive demographic properties (Ogden, 1985) as well as unusual seed and seedling strategies (Philipson and Molloy, 1990), all ultimately dependent on highly derived cone morphologies. Continued field work on the family should be pursued, because it will clarify the systematics and relationships of this distinctive and important southern group of plants.

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