

# CONIFERALES (D.J. de Laubenfels, Syracuse, N.Y.)

## General Introduction

In spite of generalized impressions sometimes advanced about the decline and decrease of the Gymnosperms through the enormous development of the Angiosperms in the Cretaceous and their rapidly accelerated development in the Tertiary, it must be realized that this impression is confusing as far as *Coniferales* are concerned.

It is of course a truism that the Gymnosperms are completely outnumbered in genera and species by the Angiosperms, the latter occupying terrain earlier beset by Gymnosperms. It must be realized, however, that possibly the almost entirely woody Gymnosperms did never have the potential for producing such immense numbers of genera and species as now found among the Angiosperms. This statement is also valid for the *Coniferales*.

The *Coniferales* were only part of the Cretaceous richness in Gymnosperms and whereas many Gymnosperm groups became extinct or lived on with meagre remains, *Coniferales* — though proportionally with few genera and few species — still represent a most essential part of the world's standing timber and involve a huge biomass through their sociability and their morphology: usually a large size and the little tapering of their cylindrical boles.

The 'decline idea' is thus not valid for the *Coniferales* and this is further validated by their extremely wide ecological capacity, as they thrive from the Arctic to the Antarctic, in all major parts of the globe, in the lowland, the hills and the mountains, and in the tropics from the seashore almost to the alpine zone, a colossal range, among the Angiosperms shared or approached by only very few families, e.g. *Ericaceae* and *Fagaceae*.

This universal presence is also due to their most diverse ecological capacities. *Coniferales* are represented on the permafrost of the taiga as well as in hot semi-deserts, on all sorts of soils, from mineral-rich to mineral-poor, even in peat-swamps, enabling them to stand all sorts of environmental conditions.

In the forest vegetation they show not seldom a high power of competition, often leading to dominance or codominance, often coupled with longevity.

Some are aggressive and tend to fill gaps in the vegetation by possessing nomad ecology.

Seed is mostly produced in ample quantity; seedlings may be shade-tolerant or -intolerant. A number of species are distinctly fire-resistant.

From these facts can be concluded that *Coniferales* are not just 'on the decline', but that they form still a most successful super-order of the Gymnosperms.

**Distribution.** With 12 genera the *Coniferales* are well represented in the Malesian tropics, while elsewhere in the world only in the rich Sino-Japanese flora is there a substantially larger concentration of conifer genera; nearby Taiwan for example has 15 genera (only four of which are shared with Malesia, viz. *Nageia*, *Podocarpus*, *Taxus*, and *Pinus*). Eight wide ranging conifer genera of Antarctic affinities are today well established throughout Malesia up to the westernmost margins and four of these extend well beyond onto the continental part of Asia (*Dacrycarpus*, *Dacrydium*, *Nageia*, and *Podocarpus*). All are strictly confined to rain-forest habitats.

Seven of these have seeds dispersed by birds, the eighth (*Agathis*) has small seeds with large membranous wings. Except for the genus *Phyllocladus*, these genera are well represented at low and medium elevations and it is not necessary to imagine long-range dispersal between isolated mountain peaks as far as altitude is concerned. We have, however, to keep in mind that through the insular physiography of Malesia there may have been the necessity of crossing sea barriers. Unfortunately too little is known in detail about the precise distribution of land and sea in the course of the Tertiary.

Two Holarctic conifer genera (*Taxus*, *Pinus*) penetrate into western Malesia and two more Antarctic genera are at present confined to the eastern half of Malesia (*Libocedrus*, *Araucaria*). The fossil record, although incomplete, suggests that the situation was quite different as late as the Miocene.

Fossil record. Palaeozoic floras of Permo-carboniferous age are known from Sumatra and New Guinea. The Sumatra material shows affinities to Euramerican floras and, by the presence of *Gigantopteris* especially to the Cathaysian flora of Southeast Asia (JONGMANS & GOTHAN, 1935). In New Guinea fossil floras of Gondwana type as well as with a Cathaysian character are found (JONGMANS, 1940; LACEY, 1975), leading HAMILTON (1979) to suspect that at that time New Guinea was situated at mid-latitudes with land connections both to Sumatra and the Australian continent.

A Mesozoic flora dated as Neocomian (Lower Cretaceous) has been described by SMILEY (1970) from the Malay Peninsula. Although considerably poorer in species than the Palaeozoic ones, it is of interest because of the presence of two conifer genera, *Frenelopsis* of Cupressaceous affinity preserved as macrofossils and the fossil pollen genus *Classopollis*, derived from the extinct family of *Cheirolepidaceae*. *Frenelopsis* ranges from Lower to Upper Cretaceous and was widely distributed in North America, Europe and Asia. *Classopollis* is cosmopolitan and ranges from the Jurassic to the Upper Cretaceous. The general composition of this Lower Cretaceous flora clearly suggests links to Eurasian and North American floras.

MULLER (1968) has described a rich and well preserved Upper Cretaceous microflora from Sarawak, NW. Borneo, in which *Caytoniales* (*Caytonipollenites*), *Podocarpaceae* (*Zonalapollenites*), *Araucariaceae* (*Araucariacites*), *Cheirolepidaceae* (*Classopollis*), *Cupressaceae* or *Taxodiaceae* (*Inaperturopollenites*) and a rich assemblage of bisaccate pollen grains of Pinaceous or Podocarpaceous affinity represent the Coniferalean element. Although most of these genera are cosmopolitan, the presence of the bisaccate genus *Rugubivesiculites* is of considerable interest, since this has been recorded only from the northern hemisphere.

Tertiary floras from Malesia, which include both macro- and micro-floras, are mainly restricted to the post-Eocene and, for the Angiosperm component, show a composition not unlike the present one (KRÄUSEL, 1929; POSTHUMUS, 1929, 1931; ANDERSON & MULLER, 1975). However, the reliability of identification of many of these records, especially the older leaf remains, is questionable. An exception may be made for wood of *Dipterocarpaceae*, for which family also fossil pollen records are available, showing that, at least in the post-Eocene, this family was well established in West Malasia.

For Gymnosperms the situation is different and the presence of pollen of *Ephedra*, *Pinus*, *Picea* and *Tsuga* in the Oligocene and Miocene of NW. Borneo, accompanied by pollen of *Alnus*, its disappearance from the record at the end of the Miocene, followed by immigration of *Phyllocladus* and *Dacrycarpus* in the Plio-Pleistocene suggests considerable change in the coniferous elements in West Malesia (MULLER, 1966; STEIN, 1978). *Dacrydium* pollen, which was absent in the Upper Cretaceous-Paleocene assemblages studied by MULLER (1968) from Sarawak is first recorded for the Oligocene.

MULLER (*l.c.*) has attributed the disappearance of the Asian-montane element to peneplanation, but STEIN (*l.c.*) believes that they also may have suffered from competition with other forest elements in submontane habitats. Significantly, *Pinus* has survived longest in NW. Borneo and is still present today in N. Sumatra and the Philippines.

KHAN (1976) has established the presence of pollen of the following typical southern conifers in the Upper Miocene and Pliocene of New Guinea: *Dacrydium*, *Dacrycarpus* and *Microcachrys*, the latter disappearing from the record at the end of the Pliocene. Here the southern conifers are accompanied by *Nothofagus*.

This evidence indicates that, in Borneo, boreal conifers have been replaced by Antarctic ones, immigrating from the direction of New Guinea. *Dacrydium* may have reached western Malesia already in the Oligocene, while *Phyllocladus* and *Dacrycarpus* only reached Borneo in the Pliocene. In New Guinea the latter two were present earlier. This reflects the collision of the northwest moving Australian plate with the Celebes-Borneo area in the mid-Tertiary (HAMILTON, 1979; STEIN, 1978). Before this period Antarctic conifers may have been absent in West Malesia which has remained, at least since the Cretaceous, within reach of the Southeast Asian continent, as indi-

cated by the presence of boreal conifers, both in the Cretaceous and Tertiary of the Malay Peninsula and Borneo. New Guinea presumably had been in close contact with Australia since the Palaeozoic.

From FLORIN's masterwork (1963) one could deduce that *Cryptomeria*-like conifers should have occurred in Malesia, since they are found fossil in the Triassic of both Asia and Australia, fading away in the early Cretaceous. Similarly, relatives of *Austrotaxus* of New Caledonia, *Athrotaxis* of Tasmania and various *Cupressaceae*, especially *Libocedrus*, all genera with Holarctic affinities, must have occurred in the Cretaceous of Malesia, inasmuch as these genera flourish beyond to the east and south. There are also reports of fossils belonging to *Podocarpaceae* and *Araucariaceae* from Holarctic regions and they could have migrated through Malesia at the same time, but only fossil *Araucaria* pollen is known from the Upper Cretaceous of Borneo.

The main conclusion from the fossil record is that, at least from the Lower Cretaceous onwards till the Oligocene, virtually no southern conifers reached West Malesia where in the Upper Cretaceous and, more strikingly, in the Oligocene and Miocene a distinct Asian conifer element was present. Only at the mid-Tertiary collision of Australia + New Guinea with West Malesia did an invasion of southern conifers take place, in stages leading to the present-day distribution pattern. However, it is clear that large gaps in our knowledge still exist and it seems most desirable to have reliable records from the Upper Cretaceous and Lower Tertiary of Java, Celebes, the Lesser Sunda Islands and New Guinea to allow a further confirmation of what is at present still a very tentative picture.

I appreciated very much the collaboration of the late Dr. J. MULLER (Leiden) in framing this paragraph on the fossil record.

*References:* ANDERSON & MULLER, Rev. Palaeobot. Palynol. 19 (1975) 291–351; FLORIN, Acta Horti Berg. 20(4) (1963) 121–312; HAMILTON, U.S. Geol. Surv. Prof. Pap. 1078 (1979) 1–345; JONGMANS, Meded. Geol. Bur. Mijngedebied Heerlen 1938-1939 (1940) 263–274; JONGMANS & GOTHAN, Jaarb. Mijnwezen in Ned. Indië 1930, Verh. V.59, pt. 2 (1935) 71–201; KHAN, Austr. J. Bot. 24 (1976) 783–791; KRÄUSEL, Verh. Geol. Mijnbouwkw. Gen. Ned. Kol., Geol. Serie II (1929) 1–44; LACEY in Campbell (ed.), Gondwana Geology, Austr. Nat. Univ. Press (1975) 125–134; MULLER, Blumea 14 (1966) 231–235; Micropaleontology 14 (1968) 1–37; POSTHUMUS, Bull. Jard. Bot. Btzg III, 10 (1929) 374–384; Leiden Geol. Meded. 5 (1931) 485–508; SMILEY, Geol. Soc. of Malaysia, Bull. n. 3 (1970) 77–113; STEIN, Biogeographica 11 (1978) 1–168.

*Ecology.* As mentioned above, the ecology of conifers shows a considerable variation and a summary may facilitate and stimulate the reader to delve in the text for further details.

No main vegetation type, except aquatics and very dry seasonal lowland, is in Malesia devoid of conifers. Though varying in density, they form an essential part of the forest and other vegetation. In the collecting numberlists of the Indonesian Forestry Service they form from one half to two percent of the total, depending on the area. Biomass of standing timber will attain probably a much higher percentage.

Conifers are among the tallest tree species in Malesia. Many possess massive straight boles, mostly cylindric, rising to or over the canopy with a height of 40–50 m. Some reach still larger dimension and tower as emergents over the canopy, equalling the tallest size of the largest *Dipterocarpaceae*; notably species of the genera *Agathis*, *Araucaria* and *Pinus* may reach 70–75 m in height, the occasional record being a tree of *Araucaria hunsteinii* of 89 m (B. GRAY, J. Ecol. 63, 1975, 273).

Small conifers are also well represented in Malesia. Mature specimens of no more than 1 m in height are found of *Nageia maximus* in Bornean swamp forests and of *Podocarpus micropedunculatus* on the edges of clearings in and near Brunei. Small conifers are also found in scrub in the mountains, e.g. *Dacrydium medium* on G. Tahan (Malaya). Colonies of prostrate *Podocarpus brassii* var. *humilis* occur on the mountains of New Guinea. Stunted specimens of many other species are found in poor, rocky habitats in the mountains.

*Altitude.* Lowland species are for example *Podocarpus polystachyus* which may be locally com-

mon (e.g. in Malaya) on sandy bluffs on the seashore and on low limestone outcrops. *Dacrydium pectinatum* and *D. micropedunculatum* can be locally common on low lying sand shoals (e.g. in S. Borneo), while the former along with *Agathis borneensis* may form nearly solid stands on lowland podsols (kerangas) or lowland peat-forest in Borneo almost at sea-level. The latter occurs sometimes in such quantity as to be worthy of exploitation for timber.

A genus 'descending' to low altitude is *Pinus*: in West Luzon and in Mindoro. *Pinus merkusii* reaches sometimes as low as 50 m altitude as a pioneer in pyrogenous grasslands and up to 150 m on volcanic ash streams (lahars) and lavastreams in N. Sumatra. Descent has also been reported for *Araucaria cunninghamii* on steep rocky ridges and spurs, occasionally as low down as 75–100 m, the 'normal' low parameter being c. 500 m.

With increasing elevation conifer populations become more frequent. At high altitudes species become fewer but it is not uncommon to find subalpine forest, whether or not turned into mossy forest, dominated by one or a few species of conifers. For example, the summit forest on Mt Leuser (N. Sumatra) is often dominated by a drooping conifer, *Dacrycarpus imbricatus* var. *curvulus*; on Mt Suckling (Papua New Guinea) *Araucaria cunninghamii* is the dominant conifer.

*Climate.* As mentioned above, in Malesia conifers shun the seasonally very dry lowlands of eastern Java and the Lesser Sunda Islands. They are also rather rare in the mountain rain-forest in this climatically seasonal belt, but *Dacrycarpus imbricatus* is found as far as Timor as a distinct constituent of the mountain forest; after devastation single trees may even survive as relicts in pyrogenous grassland, adorned with beards of *Usnea*.

*Soils.* Many conifers prefer nutrient-poor soils, and are often even confined to them, but there are also species which are mostly found on richer latosols, e.g. *Dacrycarpus imbricatus* which grows excellently on young volcanic soils.

As mentioned above, quite a number of conifers grow, sometimes in great quantity, on alluvial sandflats or on podsolized sands and sandstone (kerangas) and in peat-swamps, but they are not always limited to such habitat, as both *Dacrydium pectinatum* and *Agathis borneensis* are also commonly met as scattered individuals in middle elevation rain-forest.

Some conifers, particularly of the genus *Podocarpus*, thrive on ultrabasic bedrock in Malesia (as well as in New Caledonia), dense stunted forest with plenty of *Podocarpus confertus* in Borneo and *Podocarpus ridleyi* in Malaya are examples.

On Mt Soroako (Celebes) scattered specimens of *Agathis*, *Dacrydium*, *Podocarpus* and *Nageia* are found on ultrabasic bedrock. This may also be true for localized populations of *Podocarpus deflexus* of Malaya and N. Sumatra.

More precise data about possibly specialized soil types are unknown for a number of species with restricted ranges, e.g. *Podocarpus levis* in Central Malesia, *Dacrydium medium* in Malaya and Sumatra, *Dacrydium ericoides* in Borneo, *Dacrydium spathoides* in New Guinea, and *Agathis flavescens* in Malaya.

A curious conifer taxon is *Dacrydium cornwalliana* which is found in the mountains of West New Guinea (BW 697) restricted to deep black peat, reminding of the habitat of some *Dacrydium* and *Dacrycarpus* species occurring in peat under temperate conditions in New Zealand; both the former species and *Dacrycarpus steupii* are the only peat-swamp forest trees of Malesia so far known. Fig. 14.

As to limestone, it can in general be said that conifers are rare on this bedrock. In western Malesia *Podocarpus polystachyus* occurs on low limestone outcrops; in Borneo and Celebes *Agathis* is also found on soils derived from limestone, and *Dacrycarpus imbricatus* is found on similar soils on Mt Perdido in Timor.

*Autecology.* In general Malesian conifers are constituents of the rain-forest and as such are dark-germinators, their seedlings growing up under very low light intensity. Germination and up-growth of seedlings in shade is also the rule for high altitudes, but pioneering of conifers on disturbed, pyrogenous open land, at 2500–3000 m altitude was observed for *Libocedrus* and *Phyllocladus* by HOOGLAND.

A clear exception are the species of *Pinus*, *P. merkusii* and *P. kesiya*, which are light-demanding germinators. They may form permanent, dominant climax stands on very steep, rocky mountain slopes where no litter remains to prohibit germination. One can observe this on the Leuser massif in N. Sumatra at some 2500 m altitude. This occurrence is rare, the main occurrence is of a temporary nature, pioneers starting a succession, viz. bare soil of talus, volcanic mudstreams (lahars), lavastreams, earth- and rockslides, places torn open by earthquakes, and further man-made pyrogenous grassland. In the latter they occupy in W. Luzon and N. Sumatra large surfaces which are consequently converted into large, mostly savannah-like stands of *Pinus*. Under undisturbed conditions secondary forest and finally new primary forest will grow up among the pines, the litter and shade of which prohibits their own regeneration. But as *Pinus* is a long-lived pioneer, under such conditions the pines — which may possibly reach an age of 200–300 years — will remain towering over the later primary forest.

Seed of many tropical Malesian conifers rather soon loses its germination power, in line with other rain-forest trees. That of *Araucaria hunsteinii* is down to zero in ten weeks. According to WHITMORE the viability of seed of *Agathis* drops rapidly and also that of *Araucaria cunninghamii*. This is also valid for *Pinus merkusii*. On the other hand seed in *Podocarpaceae* may require as much as a year to germinate.

To the autecology also belongs the matter of the *mycorrhiza*, but unfortunately little is known of this relation. It is certain that one of the exomycorrhiza of *Pinus merkusii* is a *Boletus*, but it seems that for *Pinus* and probably other conifers more genera of fungi are involved. BEVEGE (1968) and HONG (Mal. Flor. 41, 1978, 225) have established that in the species of *Araucaria* an unidentified species of *Endogone* forms an endotrophic mycorrhiza.

*Sociology*. Mostly conifers occur scattered through the forest, but a number of species have a tendency to occur socially in places. By their large mature size they are then often observed as emergents. It must be remarked, however, that occurrences are often local: *Agathis* is for instance in Celebes above some 1600–2000 m (where it rather suddenly becomes abundant) and in the Moluccas present in most mountain forests and also in the north of West New Guinea, where it is tapped on a commercial scale, but in Papua New Guinea it is very scarce and local.

The same can be said of *Araucaria* in New Guinea, especially *A. hunsteinii*, which is found as an upper-canopy dominant in the Bulolo area and a few other places, but is elsewhere absent and not found in West New Guinea. In most instances we are ignorant about the underlying cause.

As mentioned above, *Podocarpus polystachyus* is locally common to subdominant in sandy lowland in Malaya and Borneo, and so are *Dacrydium pectinatum* and *Podocarpus micropedunculatus* in Borneo, where the former, sometimes together with *Agathis borneensis*, may form local stands on lowland podsols (kerangas) or in lowland peat-forest, with very acid soil conditions. *Agathis borneensis* may also form locally dense stands in the upper canopy. In passing we remark that hardly ever conifers are found in forest dominated by dipterocarps, with the possible exception of the heath-forest in Borneo. In the West Javanese mixed mountain forest (e.g. on Mt Gedeh) there are three large emergents very common: *Altingia excelsa* (*Hamam*.), together with two conifers, *Dacrycarpus imbricatus* and *Podocarpus bracteatus*. But on Mt Tjeremai, a volcano in W. Central Java, there is between c. 1800–2500 m a very large gregarious dominant stand of *Dacrycarpus imbricatus* only. It remains unclear to what factor in the past this has to be ascribed.

In other islands other species of conifers may be very common or gain subdominance in the higher mountains. In Sumatra for example *Dacrydium elatum* — used for Christmas trees — and on Mt Leuser *Dacrycarpus imbricatus* var. *curvulus*, the drooping pine. A similar role in mountain forest is found with the dense stunted forests of *Podocarpus confertus* in Borneo and of *Podocarpus ridleyi* in Malaya on ultrabasic bedrock. Localized subdominance is found: *Podocarpus deflexus* and *Agathis flavescens* in Malaya, *Dacrydium medium* in Malaya and Sumatra, and *Dacrydium ericoides* in Borneo.

Mostly conifers occur scattered in the mixed broad-leaved rain-forest, not infrequently represented by several species; e.g. KALKMAN & VINK found on the Doma Peaks in Central New Guinea

*Libocedrus papuana* as an emergent, accompanied by *Dacrycarpus expansus*, *Phyllocladus hypophyllus*, and *Podocarpus pseudobracteatus* (Blumea 18, 1970, 119).

**Anatomy.** The most important wood anatomical surveys of *Coniferales* are by E.W.J. PHILIPS, Identification of softwoods, For. Prod. Res. Bull. London 22 (1948, repr. 1966), and by P. GREGUSS, Identification of living Gymnosperms on the basis of xyotomy, Budapest (1955), Xyotomy of the living conifers, Budapest (1972). Additional data for Malesia and adjacent regions can be found in R. KANEHIRA, Identification of Philippine woods by anatomical characters, Taihoku (1924) 231–244; H.H. JANSSONIUS, Mikrographie des Holzes der auf Java vorkommenden Baumarten 6 (1936) 469–494; H. DESCH, Mal. For. Rec. 15 (1954) 630–632; M. KAEISER, Phytomorphology 4 (1954) 39–47; J. VAN DER BURGH, Rev. Palaeobot. Palyn. 15 (1973) 73–275; S. HAYASHI c.s., Micrographic atlas of Southeast Asian timber, Kyoto (1973); T. FURUNO, Res. Rep. Foreign Wood 6, Shimane Univ., Matsue (1977); J.H. FUNDTER & J.H. WISSE, Meded. Landbouwhogeschool Wageningen 77-9 (1977); K. OGATA, Identification of Southeast Asian timbers (in Japanese), Jap. Ass. Wood Technology (1985).

Despite the seemingly homogeneous microscopic structure of the vesselless wood of conifers, there are a number of highly diagnostic wood anatomical differences at various levels of the taxonomic hierarchy which can be profitably used for identification and which can help in the reconstruction of a natural classification. In the Malesian representatives of the *Coniferales* a number of genera can be immediately recognized on unique, single or combined characters:

*Pinus* — Vertical and horizontal resin ducts present, cross field pits (*i.e.*, pits from tracheids to ray parenchyma cells) fenestriform or pinoid, ray tracheids present. (N.B.: resin ducts and ray tracheids are absent from all other Malesian *Coniferales*.)

*Agathis* and *Araucaria* — Pits on tracheids alternate and in a closely spaced honeycomb-like pattern ('araucaroid').

*Taxus* — Tracheids with distinct spiral thickenings.

*Libocedrus* — Cross field pits strictly cupressoid (*i.e.*, with narrow, included apertures).

*Podocarpaceae* — The distinction of *Podocarpaceae* from *Libocedrus* is fairly subtle: cross field pits in *Podocarpaceae* often include cupressoid types but almost invariably also other types such as taxodioid, pinoid, or piceoid pits. Most Malesian *Podocarpaceae* and *Libocedrus* have fairly common to abundant axial parenchyma in their wood, a feature absent from the other conifers. However, *Phyllocladus* and at least some temperate species of *Dacrydium* lack axial parenchyma. Presence or absence of parenchyma has been used as an important character for sectional delimitation in *Podocarpus sensu lato* by KAEISER, *l.c.*, but some of her observations have been contradicted in a more detailed study by R.N. PATEL, New Zeal. J. Bot. 5 (1967) 307–321. The evidence available from the literature at present suggests that the wood anatomical variation pattern within the *Podocarpaceae* does not coincide with generic delimitation; further studies of well-authenticated samples are needed to assess the taxonomic significance of the wood anatomical variation in this family.

**Leaf anatomy** can also play a useful role in identification and classification of the *Coniferales*, as exemplified in the study by J.T. BUCHHOLZ & N.E. GRAY, J. Arn. Arb. 29 (1948) 49–76 on the systematics of *Podocarpus sensu lato* and by J.W. LANYON, A card key to *Pinus* based on needle anatomy, Min. Conservation, N.S.W., Australia (1966), also including the two anatomically distinct Malesian species *Pinus merkusii* and *P. kesiya*. The extensive leaf anatomical literature on conifers is summarized in K. NAPP-ZINN, Encyclopedia of Plant Anatomy 8 (1), Berlin (1966). — P. BAAS.

**Palynology.** In general gymnospermous pollen is distinguished from angiospermous pollen by the alveolate-granular structure of the sexine, the lamellate structure of the nexine, and the presence of one distal aperture. With the exception of some primitive ranalean groups Angiosperms have pollen with a columellate sexine, a non-lamellate nexine, and 3 or more equatorial apertures, or have pollen with attributes that can be derived from this basic pattern. The structure of the sexine seems at present the most reliable character.

The only aperture in pollen of *Coniferales* is always distal. Mostly it is a thin area (leptoma) in the exine, which is often further distinguishable by a different ornamentation. In *Araucariaceae* this area is large and circular, in *Cupressaceae* and *Taxaceae* small and circular; in *Pinaceae* and *Podocarpaceae* it is mostly large and oblong. When large, the thin area may also have a harmomegathic function beside participating in the germination process. Sometimes an aperture is difficult to trace.

A remarkable feature of some *Coniferales* pollen types is the presence of air bladders (wings, sacci) at the distal pole beside the aperture. *Araucariaceae*, *Cupressaceae* and *Taxaceae* have none, but most *Pinaceae* (except *Larix*, *Pseudotsuga*) and *Podocarpaceae* (except *Saxegothaea*) have 2 or 3 of them. Grains without bladders are more or less spherical; those with bladders have a spherical, lens-shaped, or oblong corpus.

Most *Coniferales* pollen is medium-sized (25–50  $\mu\text{m}$ ). Pinaceous grains measure (40–)50–70 (–80)  $\mu\text{m}$ ; the corpus of the likewise saccate podocarpaceous grains are mostly smaller (up to 50  $\mu\text{m}$ ). Both cupressaceous and taxaceous grains range from 18 to c. 36  $\mu\text{m}$ . Araucariaceous grain size varies from 40–60  $\mu\text{m}$  (*Agathis*) to 60–90  $\mu\text{m}$  (*Araucaria*). In addition *Araucaria* pollen differs from that of *Agathis* by the presence of a proximal annular thickening.

There is a great deal of variation with regard to wall stratification and structure. *Araucariaceae*, *Cupressaceae*, and *Taxaceae* have a thick intine compared with the exine. In *Cupressaceae* the intine is even very thick, often comprising much more than half of the grain volume. A thick intine has the capacity of swelling after moistening and probably plays an important role in the germination process. In *Pinaceae* and *Podocarpaceae* the intine is proportionally less thick. The nexine is lamellate in all *Coniferales*. The sexine is alveolate-granular in *Araucariaceae*, *Cupressaceae*, and *Taxaceae*, in *Larix* and *Pseudotsuga* of the *Pinaceae*, and in *Saxegothaea* of the *Podocarpaceae*; in all the rest of the *Pinaceae* and the *Podocarpaceae* the sexine offers a columellate-tectate appearance superficially like the situation in Angiosperms, essentially being a variation of the alveolate structure. In *Pinaceae*, *Podocarpaceae*, and in most *Araucariaceae* pollen the sexine is thicker than the nexine, at least at the proximal side (cappa). In *Cupressaceae*, *Taxaceae*, and part of *Araucariaceae* pollen the nexine is the thickest layer. In the latter three families the surface of the sexine has a perine-like covering, consisting of small (< 1  $\mu\text{m}$ ) granules (orbicules), which is absent in *Pinaceae* and *Podocarpaceae*.

Air bladders or sacci form a remarkable aspect of the pollen wall of most *Pinaceae* and *Podocarpaceae*. Sacci develop by proliferation of the alveolate layer of the wall. Probably they function in both flight and harmomegathy of a grain. All *Pinaceae* have 2 sacci, except *Larix* and *Pseudotsuga* which are devoid of them and are fundamentally different from other *Pinaceae*. *Tsuga* mostly has pollen with one distal saccus encircling the aperture. In *Podocarpaceae* the genus *Saxegothaea* has no sacci and is therefore, and also on account of other features, considered as related to the *Araucariaceae*. In *Podocarpaceae* there is more variation in respect to the number, shape, and size of the sacci than in *Pinaceae*. Pollen grains of *Dacrycarpus* are provided with 3 sacci, those of *Nageia*, *Podocarpus*, and *Prumnopitys* with 2. *Phyllocladus* and *Falcatifolium* pollen also have 2 sacci, but in the first they are very small and in the latter they are narrowly connected around the aperture. In *Dacrydium* a type occurs which has one fully radiosymmetric saccus around the aperture. *Dacrydium* has also the *Podocarpus*-like bisaccate type. Saccate pollen of the extra-Malesian podocarpaceous genera has 2 sacci (*Acropyle*, *Parasitaxus*) or 3 sacci (*Microcachrys*, *Pherosphaera*). In the latter two genera and in *Dacrycarpus* sometimes grains occur which have 4, 5 or 6 sacci due to aberrant tetrad configuration.

Pollen of the extra-Malesian *Cephalotaxaceae* and *Taxodiaceae* is largely similar to that of *Cupressaceae* and *Taxaceae*.

*Coniferales* are probably strictly wind-pollinated, the pollen being not sticky, smooth-surfaced, and sometimes provided with sacci. In the former two characters *Coniferales* pollen resembles some wind-pollinated Angiosperms (e.g. *Gramineae*, *Betulaceae*).

References: ERDTMAN, Pollen and spore morphology/plant taxonomy, Gymnospermae (1957)

5–44, illus., (1965) 9–82, text; POCKNALL, *New Zeal. J. Bot.* 19 (1981) 67–95, 259–266, 267–272; SIVAK, *Pollen et Spores* 17 (1975) 349–421; STAPLIN c.s., *Rev. Palaeobot. Palyn.* 3 (1976) 297–310; TENGNÉR, *Bot. Notis.* 118 (1965) 450–452; VAN CAMPO, *C. R. Acad. Sc. Paris* 272 (1971) 2071–2074; WALKER, *The evolutionary significance of the exine*, *Linn. Soc. Symp. Ser. 1* (1976) 251–308; WEND, *J. Inst. Polyt. Osaka City Univ.* 11 (1960) 109–136; WODEHOUSE, *Pollen grains* (1935). — R.W.J.M. VAN DER HAM.

**Phytochemistry & Chemotaxonomy.** Chemical characters of *Coniferales* were summarized twice in 'Chemotaxonomie der Pflanzen' (HEGNAUER, 1962, vol. 1: 293–440, 478–482; 1986, vol. 7: 462–554, 801–802). Here rather extensive bibliographies can be found for all families of *Gymnospermae*, *Cycadopsida*, *Coniferopsida*, *Taxopsida* and *Chlamydospermae*.

General characters of *Coniferales* are: cuticular waxes of the so-called estolide-type; lignin which usually lacks the syringyl component; seeds which store predominantly starch or oils with unusual fatty acids, i.e. bi-tetra-unsaturated C<sub>18</sub>- and C<sub>20</sub>-acids with an isolated double bond in 5-position; accumulation of cyclitols such as pinitol, sequoyitol and (or) 0-methylmucoinositol in leaves, bark and wood; storage of shikimic and (or) quinic acid in leaves; accumulation of lignans (phenylpropanoid dimers) and (or) agatharesinol-type norlignans in wood, bark, traumatic resins and leaves (here sometimes as glycosides); production and exudation after injury of oleo-resins or gum-resins.

Oleo-resins and gum-resins are deposited in schizogenic canals and cavities which seem to be lacking only in some representatives of *Taxaceae*. Oleo-resins are mixtures of essential oils and resins; turpentine is the essential oil produced by distillation of oleo-resins obtained from several species of *Pinus*. Gum-resins are mixtures of essential oil, resin and mucilage; *Araucaria* is the main producer of gum-resins among *Coniferales*. The predominant constituents of the essential oils of most *Coniferales* are mono- and sesquiterpenoids; some members of *Podocarpaceae* and other families produce appreciable amounts of steam-volatile diterpene hydrocarbons and hence yield diterpene-rich essential oils. The resins of *Coniferales* are mainly composed of diterpenoids; often diterpene acids predominate. Colophony or rosin is the resin part of pine oleo-resins and Manila copal is the hard oleo-resin from *Agathis dammara*. Amber or succinite is the fossil resin of pines and Kauri copal is fossilized *Agathis* resin.

Tannins are ubiquitous in *Coniferales*. They are represented in the taxon exclusively by the so-called condensed tannins and their building stones, the catechins and proanthocyanidins. Gall- and ellagitannins are totally lacking.

Other classes of compounds which seem to be totally absent from *Coniferales* are iridoid compounds, cardenolides and steroidal saponins. The same seems to be true of triterpenoids of the ursane, oleanane and lupane classes, and hence of corresponding saponins.

Triterpenoids are represented in *Coniferales* by lanostane-type tetracyclic, onocerane-type tetra- and pentacyclic, and hopane-type pentacyclic compounds. Steroids are represented by the ubiquitous phytosterols; moreover, the frequent occurrence of phytoecdysones in rather high concentrations is somewhat typical of the taxon. In the products of steroid and triterpenoid metabolism *Coniferales* strongly resemble Pteridophytes.

Polyphenolic compounds other than lignans and tannins are accumulated by all conifers but, besides the general occurrence of flavonoids as a group, most classes of compounds and many individual compounds are restricted to taxa of lower levels such as infrageneric, generic and suprageneric entities. The same is true of alkaloids and several other classes of chemical constituents. Some examples to illustrate the situation follow.

Agathisflavone-, amentoflavone-, cupressuflavone-, robustaflavone- and hinokiflavone-type biflavones seem to be nearly ubiquitous in leaves of Gymnosperms, but are lacking in *Pinaceae* which yielded hitherto only one biflavonoid, the flavone-flavonol dimer abiesin.

Cephalotaxin-type alkaloids occur in all species of *Cephalotaxus*.

All members of the genus *Taxus* (but not the other representatives of *Taxaceae*) produce taxane-type diterpenoids which are often esterified with the so-called Wintersteiner acid, which is a dime-



thylamino derivative of a hydroxydihydrocinnamic acid; the resulting nitrogen-containing constituents, such as the taxines and related compounds, are the 'Taxus alkaloids'; they are accompanied in *Taxus* by the cyanogenic glucoside taxiphyllin. The latter too seems not to occur in other genera of *Taxaceae*, but is present in *Metasequoia* and in some species of *Juniperus*.

In *Podocarpaceae* several tendencies concerning secondary metabolism are recognizable: essential oils with appreciable amounts of diterpene hydrocarbons, ferruginol- and totarol-type phenolic diterpenes, bitter and biologically highly active mono- and bisnorditerpenoid lactones such as nagilactone, and accumulation of large amounts of phytoecdysones such as the makistrones and the podecdysones are examples of such family-characteristic tendencies. At the same time the family is the only representative of conifers which makes use of anthocyanins to advert its diaspores: red to pink fleshy parts of *Dacrydium*, *Phyllocladus*, and *Podocarpus* diaspores contain an array of anthocyanins; anthocyanins may also be present in young leaves and strobili; the latter feature is not restricted to *Podocarpaceae*, however.

Antibiotically active carvacrol and thymol derivatives and tropolone-type mono- and sesquiterpene compounds are present in the wood of many *Cupressaceae*, including *Libocedrus s.l.*

Exudates of many species of *Araucaria* contain larger amounts of mucilage than most other conifers; they are true gum-resins; ANDERSON and MUNRO observed 20–80% of mucilage in *Araucaria*-exudates with 10–20% of uronic acids, 50–70% galactose and up to 7% of the rather unusual sugar acofriose (3-O-methylrhamnose) as building stones. Acofriose is also present in mucilages of *Cycadaceae*.

An array of low-molecular phenolic compounds, such as hydroxyacetophenones, stilbenes, dihydrostilbenes and phenylpropanoids (monolignols) is known from *Pinaceae*; they occur free and as glycosides and often have a taxon-characteristic distribution, and hence can be useful as taxonomic characters. Pinosylvin and its monomethyl ether have been interpreted as phytoalexins of *Pinus* because their synthesis is induced in the softwood after infection; normally these antifungal compounds are present in *Pinus* only in hardwoods and in barks.

Flavonoid patterns were taxonomically exploited by many phytochemists; flavonoids yielded characters applicable at all levels of the taxonomic hierarchy. Just one example: C-glycoflavones have not yet been traced in *Araucariaceae*, *Cephalotaxaceae*, *Cupressaceae* and *Taxaceae*, and seem to be restricted in *Pinaceae* to *Abies*, *Keteleeria*, *Tsuga* and *Larix*; moreover, they were detected in *Podocarpaceae* in some species of *Podocarpus*.

In recent times detailed analyses of essential oils were performed during biosystematic studies of a number of American conifers; the results proved to be rather promising; in many instances a better understanding of complex population structures was made possible by such investigations.

As a whole *Coniferales* are chemically well characterized by the general presence of several classes of chemical constituents and by the total absence of others. Moreover, secondary metabolites yielded a large number of characters applicable at different levels of the taxonomic hierarchy. — R. HEGNAUER.

**Systematics. Generic delimitation.** Four genera replace earlier broad treatments of the genus *Podocarpus*, all of which I recognized in 1969 (J. Arn. Arb. 50: 274–369); in part they had formerly been distinguished as sections of this genus. Certainly there exist substantial relationships between them, but it must be well recognized that this is no sufficient reason for adopting a one-genus concept for the whole. As a matter of fact the morphological differences between these sharply distinct genera are at least of equal taxonomic 'weight' as compared to the differences between many other groups of northern hemisphere coniferous genera unequivocally distinguished. On the other hand I cannot adhere to the recent splitting of the genus *Libocedrus*. For further argumentation I refer to the text under the genera in the taxonomic part.

**Cultivation.** A fairly large number of exotic conifers are cultivated in Malesia, in part for testing them for forestry purposes, reafforestation, in part as ornamentals in gardens and parks.

It falls outside the scope of this Flora to treat the cultivated exotics like the native species, none

of them is naturalized. Quite some have been incorporated in BACKER & BAKHUIZEN VAN DEN BRINK's Flora of Java (Vol. 1, 1963, 87–95) which may be useful for their identification. A more general work that I can advise for identifying cultivated conifers is W. DALLIMORE & A.B. JACKSON, A handbook for Coniferae and Ginkgoaceae, 4th ed., revised by S.G. HARRISON (1966).

Of native conifers several are in cultivation for various purposes. *Agathis philippinensis* is frequently cultivated as a wayside tree in W. Java and probably elsewhere, and occasionally found in parks. *Araucaria cunninghamii* is frequently planted in parks and gardens as an ornamental tree. *Araucaria hunsteinii*, of which very large dominating complexes are found in some places in the Bulolo area in Papua New Guinea, is exploited from native growths, but the cleared territory is replanted with it on a large scale, because of the valued timber used for plywood. *Dacrydium elatum* is, according to CORNER, widely planted in the hills in Malaya for ornamental purpose. Finally *Pinus merkusii* is widely used for reforestation and in addition for timber and the tapping of resin for the turpentine industry; notable huge complexes are found at Aek na Uli on the eastern hills around Lake Toba in N. Sumatra; large complexes are also found in S. Celebes; it is also used as an ornamental in parks and gardens.

In nurseries, especially of *Agathis*, a single specimen of an older seedling already provided with mycorrhiza is planted in the centre of the beds in order to speed upgrowth of seedlings.

An important point for silviculturists is the fact that, as mentioned above, the seed of many tropical conifers soon loses germination power. For *Pinus merkusii*, which is distributed on a large scale, very special care must be taken to keep the sundried seed in sealed metal containers with charcoal; even with these precautions a rather rapid loss of germination power takes place. This has been subject to extensive study. Keeping seed storage cooled is also applied.

The timber of the large-sized species of all genera is most valuable, but only few are planted for this purpose on a large scale. This is in part due to the fact that of most species growth is slow, with the exception of *Pinus* species. It depends also for what purpose the timber is used, for pulp, sawn timber or high quality veneer. WHITMORE mentioned for *Agathis* in Java a rotation period of 30 years for pulp, and 50 years for veneer. For *Araucaria* in New Guinea a rotation period of 60 years is reckoned for plywood.

**Economic uses.** As mentioned above all larger species of all genera provide excellent timber. In addition, species of *Agathis* are tapped large-scale, especially in the Moluccas and New Guinea, and to a less extent in Borneo and Celebes, for the resin ('copal' or 'manila copal', wrongly 'damar'). In addition to the resin obtained from living trees, large bodies of subterranean resin of vanished trees are collected. The market for manila copal declined after the introduction of oil-based synthetics but there is still a use for special purposes.

The resin of *Pinus merkusii*, and to a less extent that of *P. kesiya*, is collected for the turpentine industry. In N. Sumatra, in the vicinity of Takengon, there was a large factory for this purpose. See C. BRANDTS BUYS c.s. (Meded. Proefstation Boschwezen 19, 1928).

**References in synonymy.** A remark must be made about the references in the synonymy of the species. I have omitted in many cases the mention of names without description or notes which occur in so many local plant lists and casual enumerations. This was made especially urgent by the fact that the names used in these lists, e.g. of *Agathis* and *Podocarpus*, are often wrong according to my classification. To account for all these 'non' or 'sensu' names would have caused an unnecessarily complicated synonymy. If collectors' numbers were cited in these local lists, proper identity of these records can easily be checked by means of the 'Identification Lists of Malesian Specimens' n. 61 (1982), which was issued separately by the Rijksherbarium, Leiden.

KEY TO THE FAMILIES  
based on sexual characters

1. Ovules strictly terminal on short fertile shoots, erect, wingless. Pollen sacs usually several on each microsporophyll. Two single trace cotyledons ..... **Taxaceae**
1. Ovules produced on axillary structures of a fertile shoot.

- 2. Seed usually cupped by a fringing epimatium or the inverted seed even completely enclosed by a leathery or fleshy structure, rarely naked and rarely erect, solitary, wingless. Reduced cone bracts often fleshy. Two pollen sacs on each microsporophyll. Cotyledons usually two fused pairs, occasionally more **Podocarpaceae**
- 2. Seed produced on an erect, woody, rarely fleshy scale which is often fused with the fertile bract, erect or inverted, occasionally solitary, more often two or more per fertile scale, usually with one or more wing(s).
- 3. Fertile bract and scale fused, sometimes indistinguishable. Seeds solitary or in variable numbers. More than two pollen sacs on each microsporophyll. Cotyledons usually 2-4.
- 4. Seed inverted, solitary; large mature seed cones disarticulate. Leaves spirally placed or opposite-decussate and distant. Cotyledons four or two fused pairs ..... **Araucariaceae**
- 4. Seed erect, solitary or in variable numbers; small mature seed cone does not disarticulate. Leaves crowded, opposite-decussate or whorled. Cotyledons two or occasionally more, not fused.. **Cupressaceae**
- 3. Fertile bract separate from scale and not woody. Seeds two per scale, inverted, each with a single wing. Two pollen sacs per microsporophyll. Leaves spirally placed. Cotyledons more than two .. **Pinaceae**

**ARTIFICIAL KEY TO THE FAMILIES**  
*based on vegetative characters*

- 1. Leaves spirally attached, sometimes distichous.
- 2. Leaves (needles) in bundles of 2-3 with a basal sheath (*Pinus*) ..... **Pinaceae**
- 2. Leaves not in bundles with a basal sheath.
- 3. Leaves needle-like or scale-like.
- 4. Leaves scale-like (*Dacrycarpus, Dacrydium*) ..... **Podocarpaceae**
- 4. Leaves needle-like, triangular or quadrangular in cross-section.
- 5. Tree with a very dominant primary trunk with regularly placed whorls of lateral branches. Seeds dry, in large bracteate cones (*Araucaria cunninghamii*) ..... **Araucariaceae**
- 5. Tree quite irregularly branched. Seeds few, in reduced cones (*Dacrycarpus, Dacrydium, Falcatifolium*) ..... **Podocarpaceae**
- 3. Leaves distinctly flattened and often broad.
- 6. Leaves bifacially flattened, linear, less than 2.5 mm wide, with a basal constriction (*Taxus*) **Taxaceae**
- 6. Leaves if linear either bilaterally flattened, or more than 2.5 mm wide, or without a basal constriction (*Dacrycarpus, Falcatifolium, Phyllocladus, Podocarpus, Prumnopitys*) ..... **Podocarpaceae**
- 1. Leaves decussate, often distichous.
- 7. Leaves scale-like (*Libocedrus*) ..... **Cupressaceae**
- 7. Leaves broad and many-veined.
- 8. Leaves sessile, clasping, lanceate from a broad base (*Araucaria hunsteinii*) ..... **Araucariaceae**
- 8. Leaves broad, not with a stem-clasping base.
- 9. Terminal bud hemispherical (*Agathis*) ..... **Araucariaceae**
- 9. Terminal bud acute (*Nageia*) ..... **Podocarpaceae**