PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Ficus

E. J. H. Corner

Phil. Trans. R. Soc. Lond. B 1969 **255**, 567-570
doi: 10.1098/rstb.1969.0026

Ficus

By E. J. H. Corner, F.R.S.
Botany School, University of Cambridge

My account of *Ficus* in the Solomon Islands has opportunely been published (Corner 1967). I shall repeat only the main points of biogeographical interest. The genus appealed to me over 30 years ago as an instance from which one could learn the course of evolution in the flowering plant. Yet it was not until I had the chance of exploring the Solomons that my understanding of its phylogeny and dispersal began to clear. These islands have a rich fig-flora with numerous endemic species illustrating in three groups (*Auriculisperma*, *Sycidium* and *Sycocarpus*) the manner of evolution that has occurred in all groups of the genus. This course can be read from the construction of the fig and the leaf. Then, this fig-flora has very particular connexions with surrounding islands that is in no way random. The evolution of *Ficus* in Melanesia reflects its geological history. Other flowering plants, from the more primitive and vessel-less Magnolialean genera to the advanced, such as the Aroid and Scitamineous, reveal the same connexions, but their phylogeny has not, or cannot, be worked out with the same precision. *Ficus*, of course, is a highly advanced genus of an advanced family Moraceae, the place and time of origin of which is not known, but it has found special opportunities in the Solomons and supplied thence a notable contribution to the Malaysian, as well as the Melanesian, flora. There is no question here of the origin of flowering plants; we are dealing with the Tertiary distribution of ancient and modern angiosperm genera which, as Croizat (1958) has emphasized, still toe the lines of Cretaceous geography.

The fig-flora of the Solomons, including Bougainville Island, is uniformly characteristic, not only through its endemics but through the absence of many common species of New Guinea. The fig-flora of the Bismarck Archipelago belongs with that of New Guinea. Though Bougainville is nearer to New Ireland than to San Cristobal, they share almost equally the Solomons' fig-flora which has not been found on New Ireland. I emphasize this because I have heard no reason other than the botanical why Bougainville should be classed with the island arc of the Solomons. The evidence confirms my faith in plants as the biogeographical pioneers into whose established domains the animals found their ways.

The fig-flora of the Solomons is lowland. It has not evolved montane species such as occur on the Asian mainland, in Borneo, and in New Guinea where species can be found up to 3300 m alt.; in the Solomons no fig was found above 1800 m and most did not reach 1600 m. The fig-flora accentuates the distinction in the Solomons between the lowland Malaysian forest and the montane forest which, except for the absence of *Nothofagus*, is Australasian.

Such a rich flora (63 species of which 23 are endemic) implies a long-standing archipelago of islands at least the size of Kolombangara with close proximity of the islands (? not exceeding 10 to 50 miles apart), if not a much greater extent of land, and this land discrete from the Bismarck's, New Hebrides, and New Caledonia. The sectional evolution of *Ficus* has been in large lands, such as Borneo, New Guinea, Australia and the continents of Asia, Africa and America. Along the Lesser Sunda arc, as in the Molucca Islands and Micronesia, *Ficus* has not evolved but survived or deteriorated.

The main alliance of the fig-flora is with New Guinea and western Malaysia, corresponding with the general relationship of the Solomons' flora whether fern or flowering plant; but there are indisputable and strong connexions with New Caledonia, independent of New Guinea or Queensland, with New Hebrides and with Fiji, which also seems to have been independent of New Hebrides. Thus *Ficus* holds a central position in the Solomons' arc where it has evidence of being near the origin of the subgroups *Pharmacosycea*, *Sycidium* and *Auriculisperma*, if not of *Sycocarpus*. It contrasts with New Guinea where the subgroups *Adenosperma* and *Malvanthera* are centred; both have entered the Solomons and reached New Hebrides (not Fiji or New Caledonia), but have undergone little or no evolution in these islands. The geographical facts can be given a time sequence through the phylogeny of the subgroups for the very reason that *Ficus* is a genus of high evolutionary capacity in which primitive forms are retained side by side with the advanced; thus *F. salomonensis* grows with *F. indigofera*, *F. septica* and, *F. macrothyrsa* and *F. cristobalensis* grows with *F. illiberalis*. The zoological comparison would be the co-existence today of the species of the ancestral line of elephants along with the latest, but plant-evolution and migration is different from animal.

The first attempt at explaining the wide distribution of *Ficus* is to assume that its small seeds are easily transported by casual means such as sea-currents, wind, and the flight of birds and bats. There is no proof, but it is clear from the facts that this may happen over small distances. Thus Jaagi Island, about 2 miles off the east end of Santa Isabel, was a *Casuarina–Barringtonia* sand bank and is being colonized by plants, including seven species of *Ficus*, by such means from the mainland (see pp. 571–573). Then, secondly, miraculous feats by cyclones may in time account for the wide distribution. There is no evidence, however, of such random effect in the distribution in *Ficus*, which section by section maps out migration routes and static fronts of phytogeography. There is, however, plenty of evidence that oceans are effective barriers. Thus, of seven widespread coastal banyans of Malaysia, which reach their eastern limit in the Santa Cruz Islands only, *F microcarpa* has reached New Caledonia and that, evidently, via Queensland; and none of the 19 endemic species of *Ficus* in New Caledonia has escaped. The common sea-shore *F. austrina* of New Guinea, the Solomons and New Hebrides has not reached New Caledonia or Fiji; nor has the very common, bat-distributed inland *F. adenosperma* (Celebes to New Hebrides). The common *F. septica* spread from Sumatra, Formosa and Ryu Kyu islands to Queensland and New Hebrides has not reached Fiji, New Caledonia, or even the Asian mainland. The common *F. ampelas* and *F. melinocarpa* of almost as wide distribution and stemming certainly from the complex of *Sycidium* in the Solomons, have not even reached Queensland. The common *F. chartacea* of the south-east Asian mainland is in Singapore and north Borneo but has not reached Java or Sarawak. *F. gul*, *F. wassa*, and *F. crassinervia*, common in New Guinea and the Solomons, have not reached Queensland. Then, of course, where time has been so much longer and opportunity for chance dispersal so much greater, no Sumatran fig has crossed the Indian Ocean to Africa, no African fig to

Sumatra, Malaya, or America, and no American fig to Africa. Yet, *Pharmacosycea*, stemming from the particular complex of New Caledonia and the Solomons has reached Ceylon and Brazil. There are no wild figs in New Zealand, though many can be grown in the North Island. Clearly, *Ficus* is not distributable except over land or through archipelagoes (Van Steenis (1964) gives 100 km as the maximum separation of large islands for the land-effect of an archipelago). The weak part of fig-distribution seems to be in the very short life of the fig-insect: recent observations indicate that this is only 24 to 48 h in the flying stage (Hill 1967).

Accordingly, from the affinity of the fig floras of the different parts of Melanesia and from the necessity for effective land-bridges, I have postulated four sources or routes of *Ficus* migration: the Melanesian Foreland (relating the Philippines via the north side of New Guinea with the Solomons and Fiji), the Australian Foreland (relating Madagascar, the Timor Arc, the south side of New Guinea, Australia and New Caledonia), the Solomons–New Hebrides–New Caledonia bridge, and the tropical Pacific fig-route to explain the occurrence of subgen. *Pharmacosycea* and many other plants such as *Trophis*, *Spathiphyllum*, *Dianella* and *Heliconia* on both sides of the tropical Pacific. The Melanesian Foreland corresponds with the oldest part of the Solomons, as the Pacific province of Coleman (1966), and represents the most effective migration route of *Ficus* between the Solomons and western Malaysia. The Australian Foreland explains many of the peculiarities of the New Caledonian flora, particularly its differences from that of the Solomons. The Solomons –New Hebrides–New Caledonia island arc is necessary to link the most peculiar fig-flora of New Caledonia with that of the Solomons: it explain also the case of *Belliolum*. Then, if one looks for the genera that might have been related to pre-*Ficus* there is *Antiaropsis* in New Guinea and *Sparattosyce* in New Caledonia, though neither with 'fig-insects'. Into this ancient complex pivoting about the Solomons, there comes the problem of the relatively primitive subgen. *Pharmacosycea*.

If, therefore, through this phyletic and geographical analysis of *Ficus*, such land-connexions seem essential, they would have supplied the opportunities for other plants and animals, and there is no need to invoke the risky means of long-distance dispersal by chance, except to explain the most casual, least effective, and freak occurrences. The most widespread palm, *Nipa* admirably adapted for sea dispersal, has not reached New Caledonia or Fiji, yet some fruits of the palm *Pelagodoxa* were washed up in a storm on the south coast of San Cristobal about 20 years ago, where they have given rise to a small colony. The origin of this rare palm, identified as *P. henryi*, is not known; it may be a native of San Cristobal; it may have come from New Hebrides; or it may have been introduced by man.

I realize that these conclusions are contrary to those advocated by Dr Lee and Mr Peake, and by Dr Thorne in his discussion of the origin of the flora of New Caledonia, but I must repeat that there is no evidence of random drift in the distribution of *Ficus*. The oldest species, for which the opportunities for random dispersal must have been greatest, are the least widely distributed. Mr Peake has shown that the ratio of specific number to regional area for *Ficus* in Malaysia and Melanesia can be computed by a geometric rule relating number directly with area. I am not sure if it would hold if Australia, Africa, and tropical America were included. It does not hold within the Solomons for the small island of Kolombangara has as many species as Bougainville Island, and Singapore has more species than Fiji. Moreover, the rule does not explain in any way why sections are developed regionally or why *Sycidium*, *Pharmacosycea*, and *Sycocarpus* converge on the Solomons. There should be more species of *Pharmacosycea* ser. *Nervosae* in Borneo (2) and the Asian mainland (1) than in the Solomons (8). The rule seems to be a statistical effect of oversimplification.

References (Corner)

Coleman, P. J. 1966 The Solomon Islands as an island arc. *Nature, Lond.* **211**, 1249 1250.

Corner, E. J. H. 1967 Ficus in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc.* B **253**, 23–159.

Croizat, L. 1958 *Panbiogeography.* Caracas: L. Croizat.

Hill, D. S. 1967 *Figs of Hong Kong.* Hong Kong University Press.

Steenis, C. G. G. J. van 1964 On the origin of island floras. *Advanc. Sci.* pp. 79–92.

Thorne, R. F. 1965 Floristic relations of New Caledonia. *Univ. Iowa Stud. nat. Hist.* **20**, 1–65.