

Essays on the Morphology of Palms

P. B. TOMLINSON

Department of Botany, The University, Leeds, England

I. GERMINATION AND THE SEEDLING

Because palm seeds have been most easily available to botanists of temperate countries the development of their seedlings is much more fully understood than is the construction of mature palms. Gatin (1, 2) is the chief authority on the subject.

Palms have a single seed leaf or cotyledon. When the palm seed germinates and its minute embryo grows, the cotyledon never expands a green, assimilating blade but remains partly or wholly underground. This type of germination is called hypogeal. Even though much modified, parts of the cotyledon corresponding to the blade, petiole and cylindrical sheath of a normal leaf can often be recognized.

The apex of the cotyledon, corresponding to the leaf blade, remains embedded in the endosperm or food reserve of the seed. It functions as a suctional organ or haustorium and since it continues to grow, often to a great size, as the seedling develops it is an object of great interest. In the cocoid and some borassoid palms, where the endosperm is hollow, the sucker eventually fills the central cavity. In the coconut itself the haustorium may become as big as a man's fist. In those palm seeds in which the endosperm is ruminant or otherwise folded, the sucker eventually replaces the endosperm and so adopts its irregular shape. The surface layers of the haustorium secrete enzymes which convert the inert materials of the endosperm into soluble substances which pass through the coty-

ledon and so nourish the seedling until it is capable of independent growth.

According to the amount of extension of the different parts of the cotyledon, several types of germination can be recognised in palms. *Phoenix* is the best known example of the first type (fig. 33Aa-c). The sucker (h.) enlarges until it occupies the space within the seed formerly filled by endosperm. When dissected from the seed it resembles a narrowly peltate leaf. The cotyledonary petiole (p.), but more particularly the sheath (sh.), elongates until the cotyledon is several centimetres long. As a result the undeveloped plantlet is carried well below the soil surface. Eventually the first leaves of the seedling grow out through a long, narrow oblique cleft representing the mouth of the sheath. This cleft is present in the embryo. It enlarges as the sheath elongates but only becomes obvious when the plumule (pl.) is exerted. The appearance of the plumule is preceded by that of the radicle (r.), or first root. The rudiments of this first root are present in the embryo, ensheathed by cotyledonary tissues. As it grows, it bursts through the base of the cotyledon and so resembles a prolongation of the cotyledonary organ. The radicle persists for only a limited period, then, as in all monocotyledons, since it is incapable of growth in thickness, it is replaced by adventitious roots originating at the base of the developing stem. The first plumular leaf (I.) consists of a protective sheath alone, without a green

blade. Its apex is pointed and rigid and is very effective in penetrating to the soil surface. Subsequent leaves, at first enveloped by this sheath, eventually expand their green blades above the soil surface (II.).

Apart from *Phoenix*, this type of germination is characteristic of the fan palms of the coryphoid and borassoid groups, together with feather-palms of the caryotoid alliance and certain members of the cocoid group.

A second type of germination closely resembles that described above, except that an additional organ, the ligule (l.), is developed (fig. B). This is a tubular structure produced by proliferation of cells around the mouth of the cotyledonary sheath. It is present in certain coryphoid palms, such as *Livistona*, *Sabal* and *Washingtonia*, together with some cocoid palms, as *Jubaea*. A tubular ligule, on the other hand, is not characteristic of adult palm leaves except in many scandent genera in which the leaf sheath itself is long, narrow and cylindrical. In some small palms, e.g. *Bactris*, a ligule is only seen in undeveloped leaves and becomes disorganized as the leaf matures. Most palms with a ligulate cotyledon do not have a ligule on subsequent leaves.

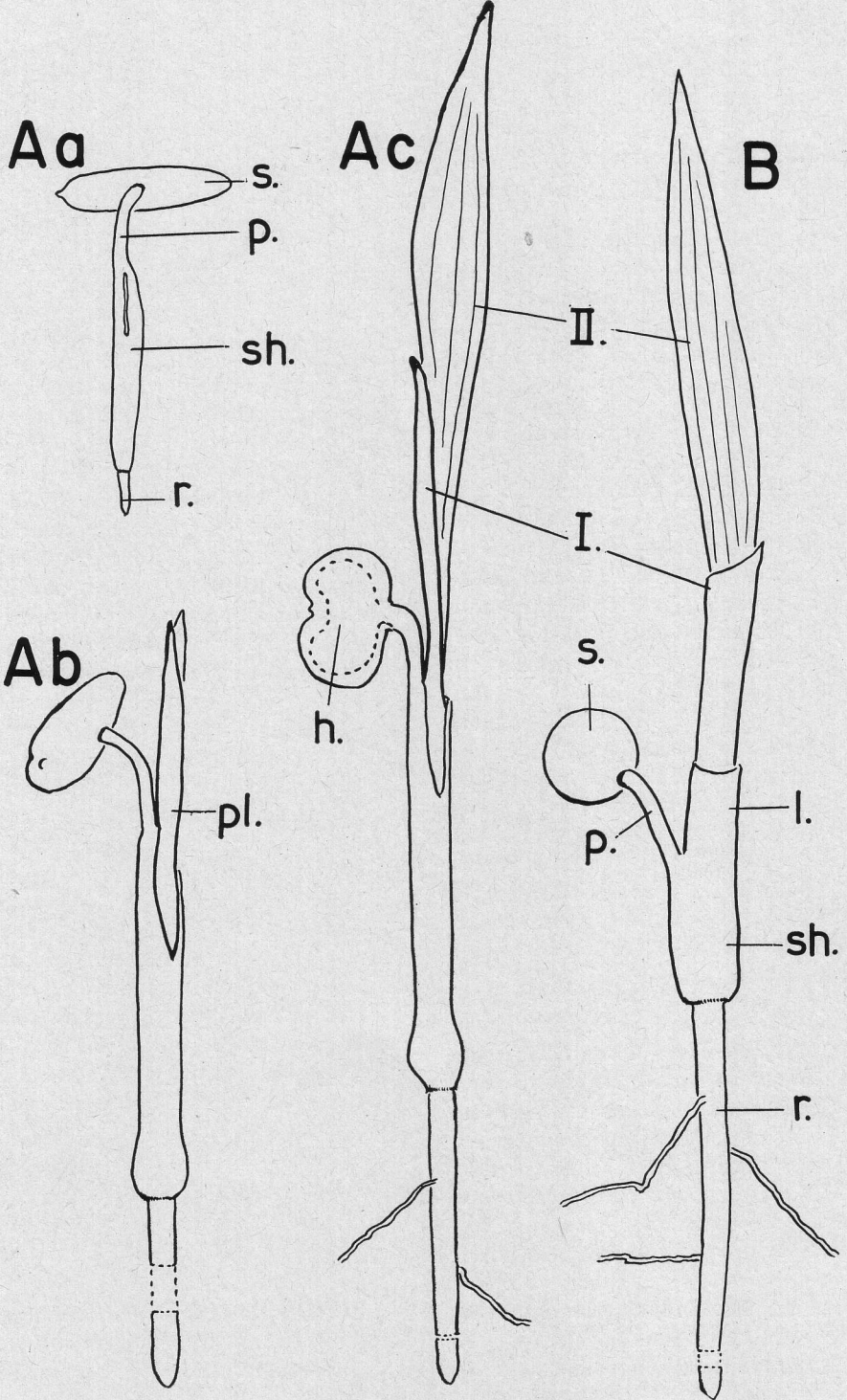
The above methods of germination, in which the tender plantlet is buried well below the soil surface, may be of adaptive significance in palms of dry situations. Many palms of arid regions undoubtedly derive benefits from long cotyledonary organs. In *Borassus* and *Hyphaene*, for example, the fleshy cotyledon may be up to two feet long and it is often eaten as a succulent vegetable by the natives of India and parts of Africa. On the other hand, the way in which the radicle first develops does not

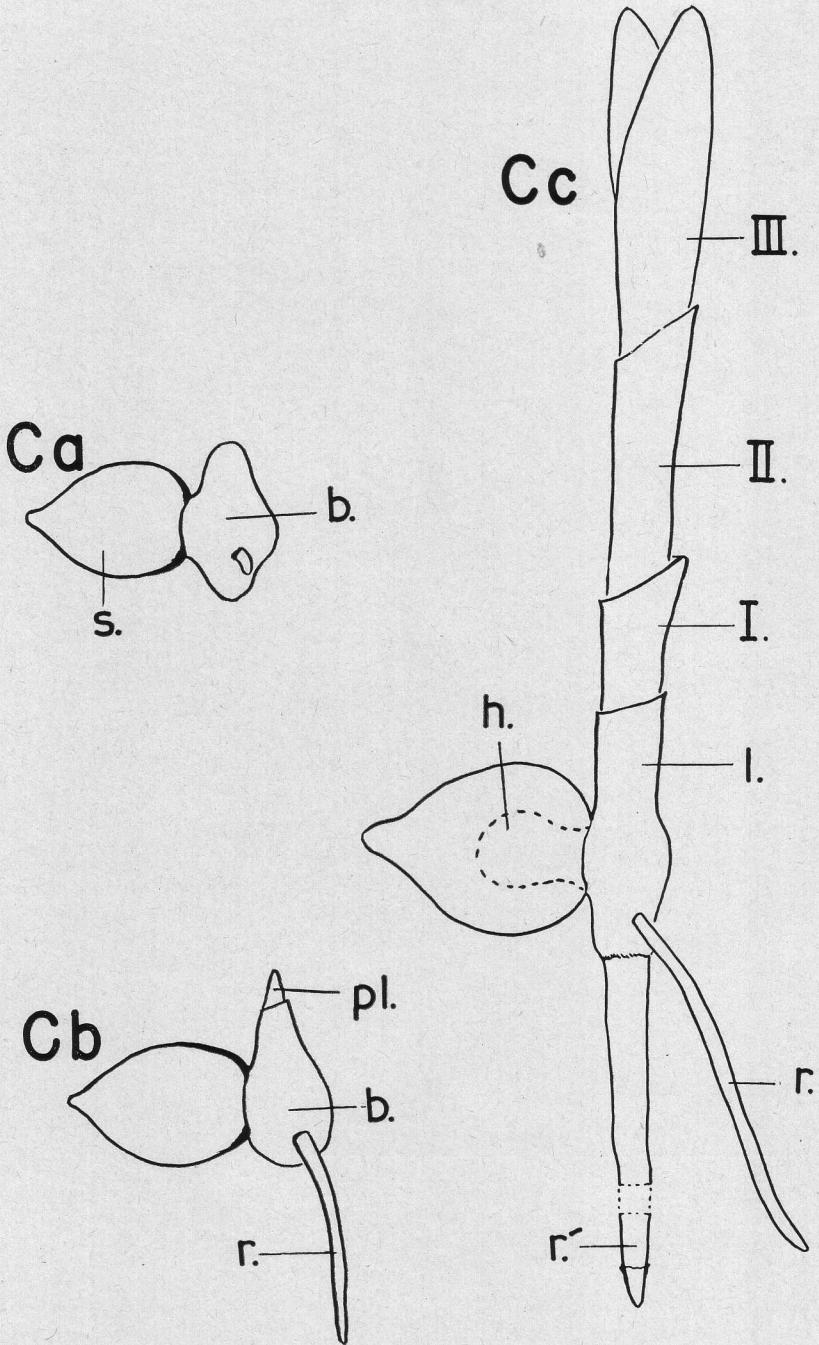
suggest a moisture-seeking function. Except in *Trachycarpus*, it never develops absorptive root hairs and branch roots are few.

The cotyledonary organ of the double coconut, *Lodoicea maldivica*, is most peculiar. Instead of growing vertically it grows horizontally for a distance of many feet and forms a thick cord connecting the seedling to the remote seed (3).

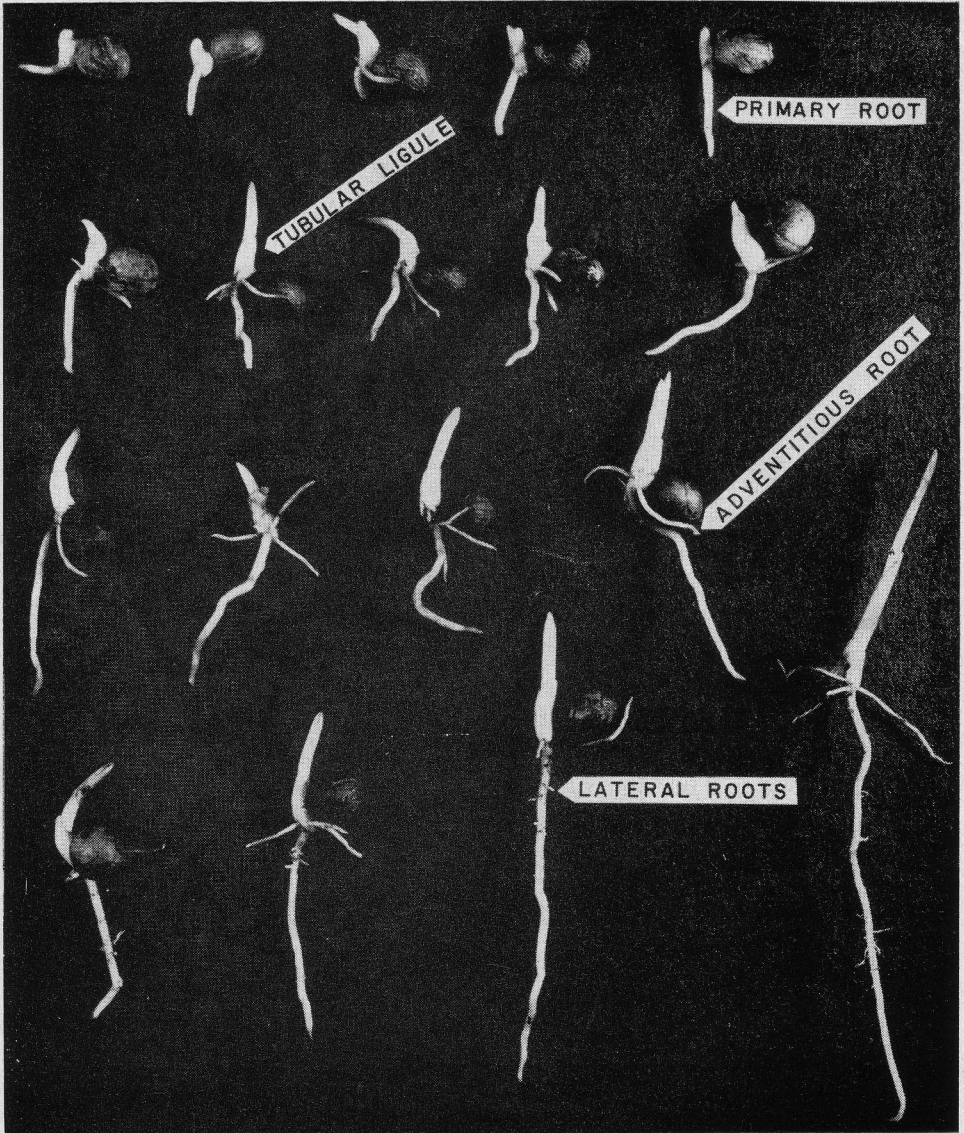
A third type of germination occurs in the remaining palms. This has been described in detail in *Archontophoenix* (fig. Ca-c) by Gatin. In this type the cotyledon scarcely elongates and the seedling develops adjacent to the seed. The embryo is curved and as the cotyledon grows the plantlet is extruded from the seed in a button (b.) of tissue. Parts of the cotyledon corresponding to a petiole and sheath are not obvious, but a sucker (h.), representing the cotyledonary blade, remains embedded in the seed. However, a prominent ligule (l.) is always developed at right angles to the cotyledonary axis. It is a cylindrical outgrowth from the margins of the cleft which represents the open end of a sheath. The plumule (pl.) eventually protrudes through this ligule. Because the embryo is curved, the radicle grows out at an oblique angle to the plumule. This first root (r.) is narrow and of restricted growth and is soon replaced by a wide lateral root (r.') which extends in the long axis of the plumule and so plays the role of principal root. Eventually, however, this also is replaced by lateral roots from the young stem. The plumule develops two bladeless sheaths (I., II.) before a leaf with a green blade appears (III.).

In this type of germination, in which a ligule is always developed, there is much less variation between different





33. A. *Phoenix dactylifera* ($\times 1$); a-c, seedling at three successive stages of growth. B, *Washingtonia filifera* ($\times 1$), seedling. C, *Archontophoenix Cunninghamiana* ($\times 1\frac{1}{2}$); a-c, seedling at three successive stages of growth. b. "button"; h. haustorium; l. ligule; p. petiole; pl. plumule; r. radicle; r'. first adventitious root; s. seed; sh. cotyledonary sheath; I-III. plumular leaves of successive stages.



34. Early stages in the germination of royal palm seeds (*Roystonea*). A primary root develops first (top row) followed by two to five whorled adventitious roots (2nd and 3rd rows). Lateral roots then appear on the latter (4th row). Photograph and notes by Jean L. Smith, Department of Botany, University of Florida, Gainesville, Florida.

species than in the first two types. Seedlings of this *Archontophoenix*-type probably are natural occupants of shaded and moist situations where burial of the seedling by an elongated

cotyledon is of no ecological advantage.

In distinguishing these three types of germination Gatin showed that each was correlated with a particular type of embryo. In the *Phoenix*-type the embryo

is straight and the plumule and radicle lie in its axis. In the *Archontophoenix*-type the whole embryo is curved, whilst in the *Washingtonia*-type, although the embryo is straight, the plumule and radicle are situated obliquely to its long axis.

A fourth type of germination in palms has been suggested for *Nypa* and *Phytelephas* in which it is said that it is the radicle which forms the suctorial organ. Reports are conflicting and observations need confirming. Gatin (1) indicates that *Phytelephas* is not different from *Phoenix*.

Literature Cited

1. Gatin, C. L. 1906. Recherches Anatomiques et Chimiques sur la Germination des Palmiers. *Annales des Sciences Naturelles (Botanique)* ser. 9, 3: 191-314.
2. ———— 1912. *Les Palmiers*. Paris.
3. Thiselton-Dyer, W. T. 1910. Germination of the Double Coco-nut. *Annals of Botany, London* 24: 223-230.

Gregório Gregorievich Bondar, 1881 - 1959

Some people are privileged to know palms intimately. Such a person was Dr. Gregório Bondar of Brazil who died in February 1959 leaving us a legacy of his published papers on palms of Brazil written from first-hand knowledge of them. The following account of his life is abbreviated from a fuller autobiographical sketch in Portuguese to be found in *Revista de Entomologia* 14: 313-319, 1943, augmented by information provided by Dr. Bondar's daughter, Dona Jacy Bondar Nogueira and Dr. Klare S. Markley. Dona Jacy is a botanist in her own right, translator of the above account, and author of *Glossário*

de Palmeiras Oleaginosas e Ceríferas and *Glossário de Plantas Oleaginosas e Ceríferas. II. Euforbiaceas*. Dr. Markley is a horticulture specialist with the United States Operations Mission to Brazil and was associated with Dr. Bondar in his work.

Gregório Gregorievich Bondar was born on November 18, 1881, in the village of Malaia, Burumca, district of Zolotonocha, Department of Poltava, Russia. There he attended primary school until 1892. His family emigrated in 1894 to the Department of Jenisseisk in the center of Siberia where Dr. Bondar farmed and served as a notary in several places before entering the Seminary of Kransnojarsk from which he graduated in June, 1902. For three years thereafter he taught in primary schools in Siberia until events of the Russo-Japanese war and the following political upheaval forced him to leave Russia for Manchuria where he remained until 1908 under another name.

In June, 1908, Dr. Bondar moved to France where he attended the Agricultural Institute of Nancy University under his own name, graduating as an agronomist in 1910. A fugitive still from political charges in Russia, he went to Brazil in that same year and was naturalized in 1913. During the years from 1910 to the end of 1915, he worked at the Instituto Agronomico de Campinas and taught at the Escola Superior de Agricultura de Piracicaba as a professor of farm zoology and entomology.

Early in 1916, Dr. Bondar returned to Russia and joined the armed forces. Near the end of the year he was arrested for his political crime of 1905, sent to Siberia in January, 1917, and then freed after the revolution of February 17, 1917. Thereafter he held political and