

1991

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Recommended Citation

Clifford, H. T. (1991) "Germination Patterns in Dicotyledons," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 13: Iss. 1, Article 9.

Available at: <https://scholarship.claremont.edu/aliso/vol13/iss1/9>

GERMINATION PATTERNS IN DICOTYLEDONS¹

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ABSTRACT

Seedlings of about 3500 species of dicotyledons were classified as exhibiting either phanerocotylar or cryptocotylar germination. The percentages of cryptocotylar species in the orders as circumscribed by Dahlgren (J. Linn. Soc., Bot. 80:91-124, 1980) were calculated and grouped into five classes whose distributions were plotted onto a bubble-diagram. The resulting pattern revealed a concentration of cryptocotily in primitive families thereby supporting the view that within the dicotyledons, cryptocotily is the primitive germination pattern.

Key words: cryptocotily, germination.

INTRODUCTION

Although dycotyledon seedlings may be classified into several groups on the basis of the relationships between the cotyledons and testa (de Vogel 1980), most species have seedlings that may be described as phanerocotylar or cryptocotylar (Duke 1965). In the former, the cotyledons ultimately escape from the testa whereas in the latter they remain enclosed indefinitely.

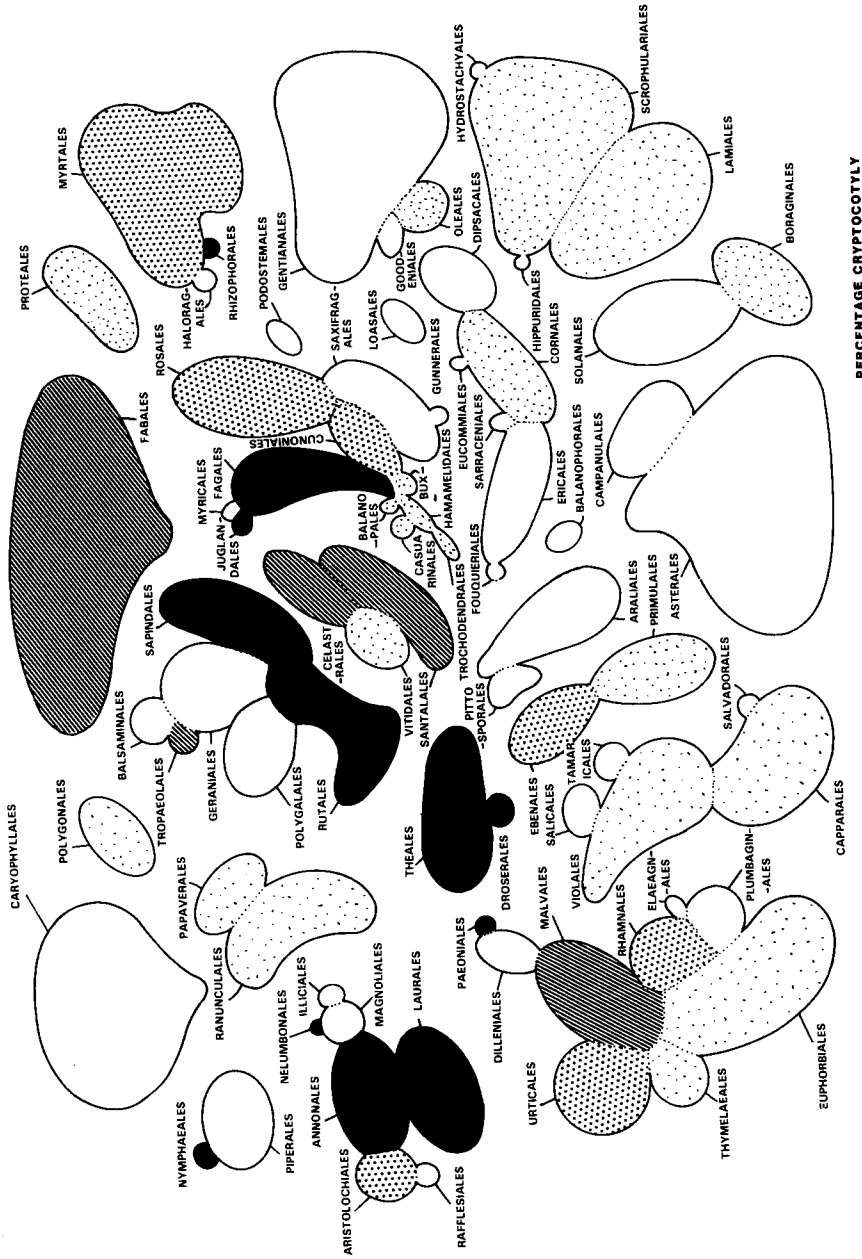
Whereas phanerocotylar species generally exhibit epigeal germination and cryptocotylar species hypogeal germination, there are exceptions. For example, the seedlings of *Lobelia* are phanerocotylar with cotyledons which expand under the soil (Fraser 1931) and the seedlings of *Myristica* have cotyledons that are included permanently within the testa, which is carried up above the soil (Müller 1887).

The phylogenetic significance of germination patterns is uncertain and both phanerocotily and cryptocotily have been proposed as primitive (Clifford 1984). In an attempt to resolve between these two viewpoints the taxonomic distribution of germination pattern throughout the dicotyledons was investigated using the classification system of Dahlgren (1980). That scheme is avowedly phylogenetic, and recognizes a large number of orders and superorders whose relationships are expressed in a figure that lends itself readily to displaying the distributions of characters. Only in a few respects does the scheme differ from that subsequently published but without a diagram (Dahlgren 1983).

DATA

From personal observation and reference to the literature, seedlings of about 3500 species were classified as to being either phanerocotylar or cryptocotylar. Where the record was unillustrated, epigeal germination was taken to mean phanerocotylar and hypogeal to mean cryptocotylar. Whilst this procedure will have introduced some error into the results, it is regarded as minor and as not influencing the overall pattern.

The numbers of species with phanerocotylar and cryptocotylar germination at order level are given in Table 1. On the basis of these results the orders were



grouped into five grades of cryptocotyly whose distribution is shown in Figure 1.

Of the seven small orders for which no frequencies are given, the Balanophorales have no cotyledons (Cronquist 1981).

DISCUSSION

From both Table 1 and Figure 1 it is evident that cryptocotylar species are not randomly distributed throughout the taxonomic system. Whereas cryptocotylar species do not occur amongst the Asterflorae or Caryophylliflorae they are abundant throughout the Theiflorae, most orders of the Rutiflorae, and the two large orders of Magnoliiflorae. The general pattern is one of increasing frequency of cryptocotyly towards the center of the bubble diagram with only small specialized orders showing high frequencies elsewhere in the system.

The reasons for this are not clear, for although most orders exhibiting cryptocotyly are rich in woody species with large seeds there are notable exceptions. In particular the Paeoniales and Droserales are both largely herbaceous, and the latter have minute seeds. In Figure 1 the Paeoniales are placed in the Malviflorae, but in his later classification Dahlgren (1983) transferred them to an emended Theiflorae from which the Droserales had been removed to Rosiflorae. Two orders of the Rosiflorae, the Fagales and Juglandales, are rich in cryptocotylar species. Knowledge of the germination patterns did not promote these transfers, which none-the-less do not alter the general pattern of cryptocotyly within the dicotyledons.

Given there are two basic germination patterns in the dicotyledons it is of interest to speculate on which is the more primitive. Unfortunately, the fossil record is inadequate and so evidence must be sought elsewhere.

One approach is to consider the behavior of seedlings in presumed primitive angiosperm groups such as the Magnoliiflorae, but this is of little help for both phanerocotylar and cryptocotylar species occur in the superorder. Alternatively, the seedling type in the sister-group to the Magnoliophyta could be taken as the primitive condition if the group could be identified.

Whilst there is no unanimity as to the sister-group of the angiosperms, the cycads are strongly implicated in three recent cladistic analyses of the relationships of the major groups of seed plants by Bremer (1985) and Doyle and Donoghue (1986a, b). In the most recent of these analyses (Doyle and Donoghue 1986b) the cycads plus *Peltaspermum* form a sister-group to a clade comprising Glossopteridales, *Caytonia*, angiosperms, Bennetiales, Pentoxylales, *Ephedra*, *Gnetum*, and *Welwitschia*. Of those taxa in the later clade whose seedlings are known, all except the angiosperms are exclusively phanerocotylar. Inasmuch as the angiosperms in this analysis are the sister-group to a subclade containing *Ephedra*, *Gnetum*, and *Welwitschia* phanerocotyly may be regarded as derived in the angiosperms. Further support for this view is afforded by the universal occurrence of cryptocotyly amongst the cycads and the sister-group to the major clade that includes the angiosperms. That phanerocotyly is derived in the angiosperms has also been proposed by Grushvitskyi (1963), de Vogel (1980), and Clifford (1984).

←

Fig. 1. The relative frequencies of cryptocotyly amongst orders and superorders of Dahlgren (1980).

Table 1. The frequencies of species with phanerocotylar and cryptocotylar germination grouped in the orders and superorders of Dahlgren (1983) (n.a. = not applicable; — = no records available).

| Taxa | Number of species | |
|-------------------|-------------------|---------------|
| | Phanerocotylar | Cryptocotylar |
| ARALIIFLORAE | 107 | 0 |
| Araliales | 95 | 0 |
| Pittosporales | 12 | 0 |
| ASTERIFLORAE | 178 | 0 |
| Asterales | 156 | 0 |
| Campanulales | 22 | 0 |
| BALANOPHORIFLORAE | n.a. | n.a. |
| Balanophorales | n.a. | n.a. |
| CARYOPHYLLIFLORAE | 168 | 0 |
| Caryophyllales | 168 | 0 |
| CORNIFLORAE | 233 | 2 |
| Cornales | 45 | 2 |
| Dipsacales | 1 | 0 |
| Ericales | 181 | 0 |
| Eucommiales | 1 | 0 |
| Fouquieriales | 4 | 0 |
| Sarraceniales | 1 | 0 |
| FABIFLORAE | 427 | 109 |
| Fabales | 427 | 109 |
| GENTIANIFLORAE | 117 | 7 |
| Gentianales | 102 | 6 |
| Goodeniales | 3 | 0 |
| Oleales | 12 | 1 |
| LAMIIFLORAE | 262 | 10 |
| Hippuridales | 1 | 0 |
| Hydrostachyales | 1 | 0 |
| Lamiales | 107 | 6 |
| Scrophulariales | 153 | 4 |
| LOASIFLORAE | 5 | 0 |
| Loasales | 5 | 0 |
| MAGNOLIIFLORAE | 36 | 39 |
| Annonales | 22 | 16 |
| Aristolochiales | 4 | 1 |
| Chloranthales | — | — |
| Illiciales | 1 | 0 |
| Lactoridales | — | — |
| Laurales | 3 | 21 |
| Magnoliales | 6 | 0 |
| Nelumbonales | 0 | 1 |
| Rafflesiales | — | — |
| MALVIFLORAE | 276 | 61 |
| Elaeagnales | 3 | 0 |
| Euphorbiales | 103 | 5 |
| Malvales | 108 | 40 |
| Rhamnales | 13 | 2 |
| Thymeleales | 5 | 3 |
| Urticales | 44 | 11 |

Table 1. Continued.

| Taxa | Number of species | |
|-------------------|-------------------|---------------|
| | Phanerocotylar | Cryptocotylar |
| MYRTIFLORAE | 241 | 37 |
| Chrysobalanales | — | — |
| Haloragales | 2 | 0 |
| Myrtales | 236 | 27 |
| Rhizophorales | 3 | 10 |
| NYMPHAEIFLORAE | 5 | 4 |
| Nymphaeales | 1 | 4 |
| Piperales | 4 | 0 |
| PLUMBAGINIFLORAE | 5 | 0 |
| Plumbaginales | 5 | 0 |
| PODOSTEMIFLORAE | 2 | 0 |
| Podostemales | 2 | 0 |
| POLYGONIFLORAE | 36 | 1 |
| Polygonales | 36 | 1 |
| PRIMULIFLORAE | 74 | 8 |
| Ebenales | 49 | 5 |
| Primulales | 30 | 1 |
| PROTEIFLORAE | 95 | 5 |
| Proteales | 95 | 5 |
| RANUNCULIFLORAE | 80 | 6 |
| Papaverales | 24 | 2 |
| Ranunculales | 56 | 4 |
| ROSIFLORAE | 177 | 50 |
| Balanophales | — | — |
| Buxales | 1 | 0 |
| Casuarinales | 8 | 0 |
| Cercidiphyllales | 2 | 0 |
| Cunoniales | 7 | 1 |
| Droserales | 9 | 11 |
| Fagales | 18 | 10 |
| Geissolomomatales | — | — |
| Gunnerales | 2 | 0 |
| Hamamelidales | 5 | 0 |
| Juglandales | 4 | 8 |
| Myricales | 2 | 0 |
| Rosales | 90 | 20 |
| Saxifragales | 26 | 0 |
| Trochondendrales | 1 | 0 |
| RUTIFLORAE | 190 | 114 |
| Balsaminales | 3 | 0 |
| Geraniales | 44 | 0 |
| Polygalales | 8 | 4 |
| Rutales | 79 | 46 |
| Sapindales | 55 | 61 |
| Tropaeolales | 1 | 3 |

Table 1. Continued.

| Taxa | Number of species | |
|---------------|-------------------|---------------|
| | Phanerocotylar | Cryptocotylar |
| SANTALIFLORAE | 46 | 13 |
| Celastrales | 10 | 4 |
| Santalales | 31 | 9 |
| Vitales | 5 | 0 |
| SOLANIFLORAE | 174 | 1 |
| Boraginales | 49 | 1 |
| Solanales | 125 | 0 |
| THEIFLORAE | 37 | 32 |
| Dilleniales | 7 | 0 |
| Paeoniales | 1 | 2 |
| Theales | 29 | 30 |
| VIOLIFLORAE | 185 | 8 |
| Capparales | 114 | 4 |
| Cucurbitales | 26 | 2 |
| Salicales | 10 | 0 |
| Salvadorales | — | — |
| Tamaricales | 2 | 0 |
| Violales | 33 | 2 |
| Total | 3156 | 505 |

On the basis of comparative morphology, Grushvitskyi (1963) proposed that seedlings with fleshy enclosed cotyledons be regarded as primitive. Amongst the examples he cited were seedlings that resembled those of *Horsfieldia* from which de Vogel (1980) was able to derive all others within the dicotyledons, thereby making the cryptocotylar condition primitive. In addition, he noted that seedlings of *Horsfieldia* resembled those of cycads. Furthermore, *Horsfieldia* belongs to the Magnoliiflorae, which is rich in primitive species and which Clifford (1984) showed to be rich in cryptocotyly.

Accordingly, the widely held opinion that cryptocotyly is advanced in the dicotyledons (Eames 1961) should be treated with caution.

ACKNOWLEDGMENTS

The assistance of Albert Steginga in compiling the basic data reported upon and the comments of Dr. E. de Vogel on an early draft of the manuscript are gratefully acknowledged.

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FOOTNOTE

- ¹ This note is presented in memory of Rolf Dahlgren, a distinguished colleague and fine friend.