

CLEISTOGAMY: A TOOL FOR THE STUDY OF FLORAL MORPHOGENESIS, FUNCTION AND EVOLUTION¹

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I. ABSTRACT

Cleistogamy—the production of open (chasmogamous—CH) and closed (cleistogamous—CL) floral forms by a species—is widespread among the angiosperms. While the CL flower is autogamous, the CH flower may provide a means for outcrossing. The term “cleistogamy” has also been used to describe other phenomena. A classification of types of cleistogamy is proposed. In this review, a restricted definition of cleistogamy is used to refer to species which show real floral dimorphisms, with divergent developmental pathways leading to CL and CH as well as intermediate floral forms. Reductions in the androecium and corolla are the most common feature of the CL flowers. The structural, develop-

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mental, and functional aspects of cleistogamy are reviewed. Evidence is presented to show that the CL flowers have modifications in their development which ensure self pollination. A proposal is made for using this phenomenon of dimorphic flower production as a system for the study of floral morphogenesis, function and evolution.

ZUSAMMENFASSUNG

Kleistogamie, die Produktion offener (chasmogamer—CH) und geschlossener (kleistogamer—CL) floraler Formen durch eine Spezies, ist weitverbreitet unter den Angiospermen. Während die CL Blüte autogam ist, kann die CH Blüte ein Medium bieten für Fremdbestäubung. Die Bezeichnung "Kleistogamie" ist auch benutzt worden zur Beschreibung anderer Phänomene. Eine Klassifikation von Arten der Kleistogamie wird vorgeschlagen. In diesem Überblick wird eine bergrenzte Definition von Kleistogamie benutzt bei der Bezugnahme auf Spezies, welche wirkliche florale Dimorphismen zeigen, wobei divergente Entwicklungswege zu CL, CH und auch dazwischenliegenden floralen Formen führen. Reduzierungen im Staubblatt und in der Blumenkrone sind die gewöhnlichste Charakteristik der CL Blüten. Die Struktur-, Wachstums- und Funktionsaspekte der Kleistogamie werden besprochen. Belege werden geboten, welche zeigen, daß die CL Blüten Modifikationen in ihrer Entwicklung aufweisen, welche die Selbstbestäubung garantieren. Ein Vorschlag wird unterbreitet, dieses Phänomen dimorpher Blütenproduktion als ein System für die Untersuchung floraler Morphogenese, Funktion und evolution zu benutzen.

II. INTRODUCTION

Cleistogamy, as first defined by Kuhn (1867) refers to the production of flowers that self in the bud. The term is most often used to describe species which produce open (chasmogamous—CH) and closed (cleistogamous—CL) flowers which never achieve anthesis but set good seed. This condition is widespread in the angiosperms (see Camp and Gilly, 1943; Connor, 1981; Darwin, 1877; Maheshwari, 1962; Ritzerow, 1908; Uphof, 1938, for lists of cleistogamous species). My latest count from the literature is 56 families, 287 species. Among these species there is a considerable range of dimorphic expressions; sometimes there is a mere lack of floral expansion at anthesis [referred to as "pseudocleistogamy" (Hansgrig, 1891)]; in other cases a CL floral form with a highly modified morphology is produced habitually along with fully developed CH, as well as pseudocleistogamous (PCL) forms. In the latter case, at least two floral developmental pathways exist in one individual organism.

III. SIGNIFICANCE OF CLEISTOGAMY

In a brief review of cleistogamy featuring a developmental study of *Commelina forskalaei* and *C. benghalensis*, Maheshwari (1962) supported Darwin's (1877) hypothesis that CL flowers were modified forms of CH flowers adapted for self pollination and representing an inherited, alternative mode of reproduction. His proposal countered the prevalent idea in the literature that CL flowers were arrested forms of CH flowers induced solely by environmental conditions and with no modifications to ensure self pollination (Goebel, 1904, 1905; Ritzerow, 1908; Uphof, 1938). Since Uphof's review in 1938, studies of cleistogamy in general have taken an approach similar to Maheshwari's (1962). A genetic basis to cleistogamy has been suggested for a number of species (Bates and Henson, 1955; Bernstrom, 1950; Donnelly, 1979; Khoshoo et al., 1969; Lee et al., 1976; Long, 1966, 1977). Bates and Henson (1955) found that the inheritance of CH flowers in *Lespedeza cuneata* involves 58 to 102 genes. They found only 36% of the variation in this character to be due to heritable factors. Clay (in press) found that, while both environmental and genetic factors affected the expression of cleistogamy in *Danthonia spicata*, the genetic factors were more important. Further study of the genetics of cleistogamy is necessary; especially an understanding of the extent to which hereditary factors are responsible for the variation in floral form both within and between plants in a population.

In every case studied, environmental factors influence the production of CL and CH floral forms; but, when the organism is grown under natural conditions, both floral forms occur at some point in the life cycle of most plants (Brown, 1952; Chouard, 1948; Evans, 1956; Evans and Hughs, 1961; Harlan, 1945; Heslop-Harrison, 1961; Hodgkinson and Quinn, 1978; Langer and Wilson, 1965; Lord, 1980a; Schemske, 1978; Waller, 1980). This indicates that the CL floral form is an integral part of the plant's life history and not just an arrested form induced by poor growth conditions.

Frequent reports of cleistogamy are appearing in the systematic, plant breeding and ecological literature. Presumably, as the reproductive biology of more species is studied, the significance of this floral polymorphism will be better understood. It would be useful at this time to distinguish true dimorphic floral production from other examples of self pollination in the bud.

IV. CLASSIFICATION OF TYPES OF CLEISTOGAMY

The controversy over whether or not cleistogamy was induced solely by the environment probably arose from the fact that "cleistogamy" referred to a range of phenomena. The range is from species with flowers which self-pollinate in the bud prior to anthesis, to cases where CL flow-

ers are highly modified floral forms produced by a plant along with CH flowers. In all of these species, floral form is influenced by environmental factors to some degree, with poor growth conditions usually inducing a predominance of CL flowers.

To clarify the issue, it now becomes necessary to treat cases of pseudocleistogamy separately from those of "true" cleistogamy where dimorphic floral forms are produced habitually by an individual species. Hackel (1906) proposed a system to classify types of cleistogamy in the grasses where the phenomenon is widespread (Connor, 1979). I have modified that classification to include all cleistogamous species dividing them into four categories:

Preanthesis cleistogamy.—This refers to cases where bud pollination occurs followed by anthesis. This is common in cultivated legumes, grasses and other crop plants (Frankel and Galun, 1977).

Pseudocleistogamy.—This refers to cases where no morphological differences occur between CL and CH flowers other than a lack of expansion and anthesis in CL flowers. This phenomenon is induced by an environmental factor such as drought (Loew, 1906; Uphof, 1938). These pseudocleistogamous (PCL) flowers usually have the ability to self in the bud so there may be some subtle physiological modification in the closed flowers of these species. Uphof (1938) documented many examples of pseudocleistogamy.

Complete cleistogamy.—This refers to species which produce only CL flowers, such as some orchids (Uphof, 1938) and grasses (Connor, 1979). These species should be studied in their native habitat to be sure that CH flowers are never produced. Darwin (1877) was suspicious of reports such as these because they were often made about plants grown under unnatural conditions. Genetic varieties of some species do exist that produce only CL floral forms (Dille and Knowles, 1975; Frankel and Galun, 1977; Khoshoo et al., 1969).

"True" cleistogamy.—This refers to cases where floral dimorphisms result from divergent developmental pathways in a single species or an individual. The CL flowers are modified forms of the CH flowers characterized mainly by reductions in stamen size and/or number and corolla size. Such reductions are due to more than a mere lack of expansion at anthesis in the CL flower. Intermediate forms are reported frequently with PCL flowers also a feature of these species (Goebel, 1904; Ritzerow, 1908). Darwin (1877) suggested that habitually dimorphic species evolved from those that had the capability to respond to poor growth conditions by producing autogamous PCL flowers.

Table I contains a conservative list of such dimorphic species. These can be broken into two categories: (1) dimorphism among individuals

where entire plants or even populations produce only CL or CH flowers and, more commonly, (2) dimorphism within an individual, where CL and CH flowers are produced by a single plant. The latter examples are indicated as such in the Table only when information was available from the literature.

V. COMPARATIVE STUDY OF CLEISTOGAMOUS AND CHASMOGAMOUS FLOWERS

Structural Differences

Much of the structural work on cleistogamy has been done on dimorphic species. This work compares the two extreme floral forms, CL and CH, with frequent mention of the occurrence of a range of intermediates. The works of von Mohl (1863) and Darwin (1877) represent two early attempts to describe the morphology of CL flowers. Both men noted the reduction in the size of the CL flower, with the androecium and corolla most affected. Darwin was struck by the lack of floral attractants in the autogamous CL flowers such as nectar and odor and he noted that the CL flowers were produced before, simultaneously with, or after CH flowers, often on a single plant with many gradations between the two extremes. These were first hand descriptions of CL flowers from plants that, in Darwin's case, had been grown by the author. Darwin concluded that the CL flowers functioned to provide large numbers of seed at low cost and to ensure fertilization under poor climatic conditions.

The early morphologists, Goebel (1904, 1905) and Ritzerow (1908) provided detailed descriptions of CL flowers. They both made the distinction between pseudocleistogamy, or inhibition of anthesis, and real cleistogamy. Ritzerow (1908) described the two floral forms of 30 species noting the existence of transitional forms as well. In all cases there existed reductions in the corolla and androecium of the CL flowers with fewer and/or smaller anthers. When pollen germinated inside the anthers of the CL flowers, pollen tubes could exit from an open stomium or through the anther wall in a closed anther (i.e., *Oxalis acetosella*, most *Viola* spp., *Polygala polygama*, *Houstonia minor*, *Halimium glomeratum*). In a few cases, the endothecium was found to be rudimentary in the CL anthers (*Oxalis acetosella*, *Houstonia minor*, *Amphicarpa monoica*). Ritzerow (1908) further reported that the calyx and gynoecium were least affected in CL flowers; however there were exceptions to this, with reductions in size of the ovary and stigma occurring in *Viola* spp., *Oxalis acetosella*, *Halimium glomeratum*, *Aspicarpa hirtella*, *A. longipes*, *Amphicarpa monoica*, *Houstonia minor*, *Polygala polygama* and *Specularia perfoliata*.

A reduction in the number of carpels occurred in *Aspicarpa longipes*,

Table I
Cleistogamous species that bear dimorphic flowers.

| Species | (+) Dimorphic flowers produced on an individual | Reference |
|--------------------------------|--|-----------------------------------|
| Monocots | | |
| Commelinaceae | | |
| <i>Commelina benghalensis</i> | + | Maheshwari & Maheshwari, 1955 |
| <i>C. forskalaei</i> | + | Maheshwari & Maheshwari, 1955 |
| <i>C. indehiscens</i> | + | Maheshwari & Baldev, 1958 |
| <i>C. nudiflora</i> | + | Maheshwari & Baldev, 1958 |
| <i>C. virginica</i> | + | Maheshwari, 1962 |
| Gramineae (=Poaceae) | | |
| | | Connor, 1979 |
| | | (list of 70 cleistogamous genera) |
| <i>Amphicarpum floridanum</i> | + | Weatherwax, 1934 |
| <i>A. purshii</i> | + | McNamara & Quinn, 1977 |
| <i>Aristida basirimea</i> | | Ritzerow, 1908 |
| <i>A. gracilis</i> | | Ritzerow, 1908 |
| <i>Avena scalarivalvis</i> | + | Uphof, 1938 |
| <i>Bothriochloa decipiens</i> | + | Heslop-Harrison, 1961 |
| <i>Bromus carinatus</i> | + | Harlan, 1945 |
| <i>B. unioloides</i> | + | Langer & Wilson, 1965 |
| <i>Cleistogenes</i> sp. | + | Stopp, 1958 |
| <i>Danthonia caespitosa</i> | + | Hodgkinson & Quinn, 1978 |
| <i>D. californica</i> | | Dobrenz & Beetle, 1966 |
| <i>D. sericea</i> | + | Weatherwax, 1928 |
| <i>D. spicata</i> | + | Weatherwax, 1928 |
| | | Dobrenz & Beetle, 1966 |
| <i>D. unispicata</i> | + | Dobrenz & Beetle, 1966 |
| <i>Enneapogon</i> sp. | + | Stopp, 1958 |
| <i>Festuca microstachys</i> | + | Kannenbergh & Allard, 1967 |
| <i>F. myurus</i> | | Ritzerow, 1908 |
| <i>Leersia oryzoides</i> | + | Darwin, 1877 |
| <i>Microlaena stipoides</i> | + | Connor & Matthews, 1977 |
| <i>M. polynoda</i> | + | Connor & Matthews, 1977 |
| <i>Panicum clandestinum</i> | + | Uphof, 1938 |
| <i>Sorghum</i> sp. | + | Doggett, 1970 |
| <i>Sporobolus vaginiflorus</i> | + | Ritzerow, 1908 |
| <i>S. minor</i> | | Ritzerow, 1908 |

Table I
Continued.

| Species | (+) Dimorphic flowers produced on an individual | Reference |
|---------------------------------------|--|----------------------------------|
| <i>Stipa leucotricha</i> | + | Brown, 1952 Dyksterhuis, 1945 |
| <i>Triodia decumbens</i> | + | Ritzerow, 1908 |
| <i>Triplasis purpurea</i> | + | Chase, 1918 |
| Hydrocharitaceae | | |
| <i>Ottelia ovalifolia</i> | | Ernst-Schwarzenbach, 1956 |
| Juncaceae | | |
| <i>Juncus bufonius</i> | | Ritzerow, 1908 |
| Plantaginaceae | | |
| <i>Plantago virginica</i> | + | Mesler, 1977 |
| <i>Plantago</i> sect. <i>Novorbis</i> | | Schurhoff, 1924 |
| Pontederiaceae | | |
| <i>Heteranthera Kotschuyana</i> | + | Ritzerow, 1908 |
| <i>Monochoria vaginalis</i> | + | Juliano, 1931 |
| Dicots | | |
| Acanthaceae | | |
| <i>Dipterocanthus</i> sp. | | Uphof, 1938 |
| <i>Ruellia brittoniana</i> | + | Long, 1977 Long & Uttal, 1962 |
| <i>R. caroliniensis</i> | + | Long, 1971 Long & Uttal, 1962 |
| <i>R. humilis</i> | + | Long & Uttal, 1962 |
| <i>R. lorentziana</i> | | Sell, 1977 |
| <i>R. nudiflora</i> | + | Long, 1977 |
| <i>R. pedunculata</i> | + | Long & Uttal, 1962 |
| <i>R. strepens</i> | + | Long & Uttal, 1962 |
| <i>R. tuberosa</i> | + | Long, 1977 |
| <i>Schauerianus</i> spp. | | Uphof, 1938 |
| Balsaminaceae | | |
| <i>Impatiens biflora</i> | + | Schemske, 1978 |
| <i>I. capensis</i> | + | Rust, 1977 Waller, 1979 |

Table I
Continued.

| Species | (+) Dmorphic flowers produced on an individual | Reference |
|--|---|--|
| <i>I. fulva</i> | + | Bennett, 1873 Carroll, 1919 |
| <i>I. noli me tangere</i> | + | Uphof, 1938 |
| <i>I. pallida</i> | + | Rust, 1977 Schemske, 1978 |
| <i>I. parviflora</i> | + | Evans & Hughs, 1961 |
| Boraginaceae | | |
| <i>Lithospermum calycosum</i> | + | Johnston, 1952 |
| <i>L. confine</i> | + | Johnston, 1952 |
| <i>L. incisuro</i> | + | Johnston, 1952 |
| <i>L. mirabile</i> | + | Johnston, 1952 |
| <i>L. parksii</i> | + | Johnston, 1952 |
| Campanulaceae | | |
| <i>Triodanis perfoliata</i> | + | Ritzerow, 1908 Trent, 1940 |
| <i>T. perfoliata</i> var. <i>biflora</i> | + | Bradley, 1975 |
| Cistaceae | | |
| <i>Halimium glomeratum</i> | + | Ritzerow, 1908 |
| <i>Helianthemum cahiricum</i> | + | Ritzerow, 1908 |
| Compositae (=Asteraceae) | | |
| <i>Gymnarrhena micrantha</i> | + | Koller & Roth, 1964 |
| Cruciferae (=Brassicaceae) | | |
| <i>Cardamine chenopodifolia</i> | + | Gorzynski, 1930, 1935 Uphof, 1938 |
| Gentianaceae | | |
| <i>Sebaea oligantha</i> ^a | + | Raynal, 1967 |
| Gesneriaceae | | |
| <i>Streptocarpus nobilis</i> | | Pargney & Dexheimer, 1976 |
| Labiatae (=Lamiaceae) | | |
| <i>Lamium amplexicaule</i> | + | Lord, 1979 Lindman, 1908 Gorzynski, 1929 |

Table I
Continued.

| Species | (+) Dimorphic flowers produced on an individual | Reference |
|-------------------------------|--|--|
| Leguminosae | | |
| <i>Amphicarpa monoica</i> | + | Allard, 1932 Ritzerow, 1908 |
| <i>A. edgeworthii</i> | + | Fukui & Takahashi, 1975 |
| <i>Glycine tabacina</i> | | Newell & Hymowitz, 1980 |
| <i>Lathyrus ciliolatus</i> | + | Mattatia, 1976 |
| <i>Lespedeza cuneata</i> | + | Donnelly, 1979 McKee & Hyland, 1941 |
| <i>L. cystoides</i> | + | McKee & Hyland, 1941 |
| <i>L. daurica</i> | + | Hanson & Cope, 1955 |
| <i>L. floribunda</i> | + | Hanson & Cope, 1955 |
| <i>L. inschanica</i> | + | Hanson & Cope, 1955 |
| <i>L. latissima</i> | + | Hanson & Cope, 1955 |
| <i>L. repens</i> | + | Hanson & Cope, 1955 |
| <i>L. stipulacea</i> | + | Hanson, 1943, 1953 |
| <i>L. striata</i> | + | Hanson & Cope, 1955 |
| <i>L. stuevei</i> | + | Hanson & Cope, 1955 |
| <i>L. virgata</i> | + | Hanson & Cope, 1955 |
| <i>L. virginica</i> | + | Hanson & Cope, 1955 |
| <i>Ononis alopecuroides</i> | + | Ritzerow, 1908 |
| <i>O. columnae</i> | | Ritzerow, 1908 |
| <i>O. minutissima</i> | | Darwin, 1877 |
| <i>Tephrosia heteranthera</i> | | Uphof, 1938 |
| <i>Vicia amphicarpaea</i> | + | Negrean & Dihoru, 1972 |
| <i>Voandzeia</i> sp. | + | Darwin, 1877 |
| Lentibulariaceae | | |
| <i>Utricularia juncea</i> | + | Kondo, 1972 |
| Malpighiaceae | | |
| <i>Aspicarpa</i> sp. | + | Anderson, 1980 |
| <i>A. hirtella</i> | | Ritzerow, 1908 |
| <i>A. lanata</i> | | Ritzerow, 1908 |
| <i>A. longipes</i> | | Ritzerow, 1908 |
| <i>Camarea</i> sp. | + | Anderson, 1980 |
| <i>Gaudichaudia</i> sp. | + | Anderson, 1980 |
| <i>Janusia guaranitica</i> | + | Anderson, 1980 |

Table I
Continued.

| Species | (+) Dimorphic flowers produced on an individual | Reference |
|---------------------------------|--|----------------------------------|
| Malvaceae | | |
| <i>Gossypium australe</i> | + | Fryxell, 1978 |
| <i>G. bickii</i> | + | Fryxell, 1978 |
| <i>G. nelsonii</i> | + | Fryxell, 1978 |
| <i>G. somalense</i> | + | Fryxell, 1978 |
| Nyctaginaceae | | |
| <i>Acleisanthes longiflora</i> | + | Spellenberg & Delson, 1977 |
| <i>Ammocodon chenopodioides</i> | + | Spellenberg & Delson, 1977 |
| <i>Mirabilis nyctaginea</i> | | Cruden, 1973 |
| <i>Selinocarpus lanceolatus</i> | | Spellenberg & Delson, 1977 |
| Oxalidaceae | | |
| <i>Oxalis acetosella</i> | | Darwin, 1877 Gorczynski, 1929 |
| <i>O. corniculata</i> | | Uphof, 1938 |
| <i>O. micrantha</i> | | Uphof, 1938 |
| <i>O. stricta</i> | | Uphof, 1938 |
| Polemoniaceae | | |
| <i>Collomia grandiflora</i> | + | Ritzerow, 1908 Wilken, 1977 |
| Polygalaceae | | |
| <i>Polygala pauciflora</i> | + | Ritzerow, 1908 |
| <i>P. polygama</i> | + | Ritzerow, 1908 |
| Polygonaceae | | |
| <i>Polygonum thunbergii</i> | + | Sawamura, 1969 |
| Rubiaceae | | |
| <i>Houstonia caerulea</i> | | Ritzerow, 1908 |
| <i>H. minor</i> | | Ritzerow, 1908 |
| Scrophulariaceae | | |
| <i>Antirrhinum cooperi</i> | + | Brandege, 1900 |
| <i>A. filipes</i> | + | Brandege, 1900 |
| <i>A. subsessile</i> | + | Brandege, 1900 |
| <i>A. watsoni</i> | + | Brandege, 1900 |
| <i>Linaria canadensis</i> | + | Brandege, 1900 |

Table I
Continued.

| Species | (+) Dimorphic flowers produced on an individual | Reference |
|--|--|---|
| <i>Vandellia nummularifolia</i> | | Ritzerow, 1908 |
| <i>V. sessiflora</i> | | Darwin, 1877 |
| Solanaceae | | |
| <i>Salpiglossis sinuata</i> | + | Lee et al., 1976, 1979 |
| <i>Solanum cleistogamum</i> | + | Symon, 1971 |
| Violaceae | | |
| <i>Cubelium concolor</i> | + | Nieuwland, 1916 |
| <i>Viola</i> spp. sect. <i>Nominium</i> , <i>Dischidium</i> | + | Rickett, 1932 (referenced in Camp & Gilly, 1943) |
| <i>V. arenaria</i> | + | Chouard, 1948 |
| <i>V. blanda</i> | + | Culver & Beattie, 1978 |
| <i>V. canina</i> | + | Darwin, 1877 |
| <i>V. collina</i> | + | Uphof, 1938 |
| <i>V. cunninghamii</i> | + | Holdsworth, 1966 |
| <i>V. hirta</i> | + | Chouard, 1948 Darwin, 1877 |
| <i>V. lancifolia</i> | + | Chouard, 1948 |
| <i>V. mirabilis</i> | + | Goebel, 1905 |
| <i>V. nana</i> | + | Darwin, 1877 |
| <i>V. odorata</i> | + | Goebel, 1905 Gorczynski, 1929 Madge, 1929 Théron, 1939 |
| <i>V. palustris</i> | + | Evans, 1956 |
| <i>V. papilionacea</i> | + | Culver & Beattie, 1978 |
| <i>V. pensylvanica</i> | + | Culver & Beattie, 1978 |
| <i>V. rafinesquii</i> | + | Clausen, 1963 |
| <i>V. riviniana</i> | + | Valentine, 1941 West, 1930 |
| <i>V. rostrata</i> | + | Culver & Beattie, 1978 |
| <i>V. roxburghiana</i> | + | Darwin, 1877 |
| <i>V. sororia</i> | + | Solbrig et al., 1980 |
| <i>V. stricta</i> | + | Rickett, 1932 (referenced in Camp & Gilly, 1943) |
| <i>V. sylvestris</i> | + | Chouard, 1948 |
| <i>V. triloba</i> | + | Culver & Beattie, 1978 |

^a This species has heterostylous CH flowers and subterranean CL flowers.

A. hirtella and *Specularia perfoliata*. Trent (1940) confirmed this for *Specularia*, demonstrating reduction in all CL floral organs. Gorczynski (1930) reported that the subterranean fruit of *Cardamine chenopodifolia* had a different morphology from that of the aerial CH fruit. In these amphicarpic species three floral forms may occur, subterranean and aerial CL flowers, as well as the aerial CH flowers (van der Pijl, 1972). *Vicia amphicarpala* has only CH aerial flowers with subterranean CL flowers (Negrean and Dihoru, 1972). *Ottelia* (Ernst-Schwarzenbach, 1956), *Lespedeza* spp. (Cope, 1966; McKee and Hyland, 1941), *Salpiglossis sinuata* (Lee et al., 1979), *Microlaena polynoda* (Connor and Matthews, 1977), and *Danthonia spicata* (Dobrenz and Beetle, 1966) also have modified CL fruits. Culver and Beattie (1978) found that elaiosomes of CL seeds were larger than those of CH seeds in several species of *Viola*.

Ritzerow (1908) observed normal pollen in the CL anthers of all the species investigated and never suspected that apomixis was occurring except in some genera of the Malpighiaceae. Anderson's (1980) work on the highly modified CL flowers of four genera in this family has recently demonstrated a unique cryptic self pollination that could have been mistaken for apomixis. Trent (1942) suspected apomixis in the CL flowers of *Specularia perfoliata*, but further study is necessary to establish this. Illg (1977) reported asexual adventive embryony as well as normal sexual fertilization in *Maxillaria cleistogama* (Orchidaceae).

By far the most common type of structural study of cleistogamy has been a comparison of mega- and microsporogenesis, gametogenesis and embryology of the CL and CH flowers (Gorczynski, 1929, 1930, 1935; Hanson, 1943, 1953; Madge, 1929; Maheshwari and Baldev, 1958; Pargney and Dexheimer, 1976; Pargney, 1977; Sell, 1977; Théron, 1939; Trent, 1942; West, 1930). In all cases studied these processes appear similar in both floral forms at the light microscope level.

Ritzerow (1908) concluded her survey by agreeing with Goebel's (1904) hypothesis that CL flowers were arrested forms of CH flowers due to suppression of growth with no special modifications in the CL flowers to ensure self pollination. Uphof (1938) also accepted this conclusion and went so far as to say that all the morphological and developmental differences between CL and CH flowers "have no connection with the concept of cleistogamy." The implication in all of these studies is that the CL flowers set seed autogamously merely as a consequence of a lack of corolla expansion due to poor growth conditions.

Lindman (1908) first suggested that the closed corolla of the CL flowers in the cleistogamous species *Lamium amplexicaule* was a consequence of cleistogamy rather than a cause of it. He suggested that precocious maturation of the anthers in the CL flowers was followed by precocious pollination and that lack of corolla expansion was a result of this. Recent

work (Lord, 1980a) on the development of and hormonal controls on CL floral production in *Lamium* supports Lindman's hypothesis. This suggests that special modifications in the CL floral organs do occur; in fact, a number of studies have demonstrated such modifications especially in the pollination process of the CL flowers. In all cases, fewer pollen grains are produced in CL compared to CH flowers, and pollen germination always occurs inside the anther sac (Staedtler, 1923). Bennett (1873), Gorczynski (1929), Madge (1929), Théron (1939), and West (1930) noted that pollen tubes germinated through the upper walls of the unopened CL anthers of some *Viola* spp. This phenomenon has been reported in a number of other CL species including *Salpiglossis sinuata* (Lee et al., 1979), *Lespedeza* spp. (Hanson, 1943), and *Plantago virginica* (Mesler, 1977). In *Ottelia* (Ernst-Schwarzenbach, 1956) and *Cardamine chenopodifolia* (Gorczynski, 1930), the anther wall next to the stigma is reported to degenerate before pollen germinates in the CL anther, thus providing an exit for the pollen tubes.

The CL pollen itself is often reduced in size and has a thinner wall (Darwin, 1877; Hanson, 1943; Lee et al., 1979; Spellenberg and Delson, 1977). Pargney studied male gametogenesis at the ultrastructural level in the CL and CH flowers of *Streptocarpus nobilis* (Pargney and Dexheimer, 1976), *Viola* spp. (Pargney, 1977) and *Oxalis corniculata* (Pargney, 1978). In these species, divergences appear at the microspore stage. Cleistogamous pollen grains show retarded starch formation though at maturity they have more starch than the CH pollen grains. Further study at the ultrastructural level may reveal differences in the development of pollen and ovules of CL and CH flowers not detectable at the light microscope level. Since the pollination process is often quite different in the two floral forms, it is possible that subtle structural and physiological differences occur between CL and CH pollen.

Anderson's (1980) study of CL pollination and fertilization in four genera of the Malpighiaceae has revealed the most bizarre of the modifications in CL flower pollination described so far. The anthers in these highly reduced CL flowers never open, nor do their pollen tubes grow through the anther walls. Rather, the tubes penetrate the staminal filament and grow down to the receptacle and up to the carpels and nucellar beaks of the ovules. Most of these CL flowers have no petals, only one stamen, two carpels, and no styles. They were once thought to be apomicts (Ritzrow, 1908). If intermediate forms do exist between the CL and CH flowers, they would facilitate a comparative study to determine how such modifications evolved.

As Darwin (1877) predicted, modifications in the development of CL flowers do exist, which ensure self pollination in these obligately autogamous flowers. These modifications occur primarily in the corolla, sta-

mens, stigma and style, and further structural study is necessary to determine the extent to which the pollination process in the CL flower has been modified from that in the CH flower.

Developmental Relationships

Leaves are assumed to be more plastic than flowers, meaning that they are subject to changes in form more easily as a result of varying environment during development than are flowers. Cleistogamous species demonstrate a supposedly rare example of hermaphroditic floral plasticity. These dimorphic floral forms can be used to address floral morphogenetic questions in comparative studies analogous to those already done on leaf development. When the different floral forms occur on separate plants or in specific positions in the inflorescence of an individual, or if they can be induced separately with particular growth conditions, a population of genetically related though slightly variant forms is provided for morphogenetic study. When intermediates exist between the extreme CL and CH floral forms, D. G. Lloyd (pers. comm.) has suggested using the phrase "bimodal distribution of functional phenotypes" to describe floral variation. This would serve to call our attention to the intermediates.

An hypothesis posed by early morphologists is that the process of developmental arrest explains the form of the reduced organs in the CL flower (Carroll, 1919; Goebel, 1904, 1905; Ritzerow, 1908). "Arrest" implies a truncation or cessation of development along the pathway prescribed by the fully developed structure (Troll, 1939). Goebel's (1904) suggestion that a lack of cell expansion alone explained the reduced mature CL flower in *Lamium amplexicaule* is not accurate (Lord, 1980c). Rather, modification in both cell division and expansion occurs in the corolla and anthers of the CL flower. In this case, the calyx and gynoecium of the two floral forms appear unmodified; apparently a mechanism operates to dissociate development in the gynoecium/calyx and the androecium/corolla in the CL flower. A number of studies have reported precocious development of the CL flower (Harlan, 1945; Langer and Wilson, 1965; Lindman, 1908; Lord, 1979; Théron, 1939), which suggests that "precocity" is a better term than arrest to describe the process leading to CL floral production. These two ideas are not mutually exclusive; a CL anther may show arrested cell division early in its growth, and then as a result mature precociously as a smaller organ. One alternative hypothesis is that the CL anther matures at the same time, but instead of being truncated in its development, grows more slowly than the CH anther so that it has fewer cells at maturity. Of course, there are other alternative hypotheses to explain organ reduction in the CL flower. Lee et al. (1979) claimed that cell expansion arrest alone can explain the

reduced form of the CL corolla in *Salpiglossis sinuata*. Comparative ontogenetic study of CH and CL flowers would establish whether divergence in development of floral forms occurs at inception or later during organ growth, and the extent of the divergence.

At this point, it is necessary to propose testable hypotheses that incorporate a means of measuring developmental rates in terms of cell division and elongation in the homologous organs of CL and CH flowers. Langer and Wilson (1965) showed that CL anthers of *Bromus unioloides* developed more slowly than CH anthers, achieving a smaller size at maturity; however anther dehiscence and pollination were precocious. Slight differences in organ growth rates (detected using allometric analyses) distinguish the various floral forms in *L. amplexicaule* (Lord, 1979). The duration of development up to meiosis in the anthers appeared to be the same in both flowers of this species though the CL anthers were smaller at maturity. Presumably, the mitotic rate or the duration of mitosis in cells of the developing CL anther is decreased. Pollination occurs precociously in the CL flowers of *Lamium*. Harlan (1945) suggested that a shorter meiotic duration in the CL anthers of *Bromus carinatus* explained precocious pollination in this species. Since all cleistogamous species show a reduction in the androecium and corolla there may be a common denominator in CL flower development with an initial reduction in anther tissue causing a subsequent reduction in the corolla and precocious pollination.

Uphof (1938) discussed the variety of external environmental factors that increase the percentage of CL flowers produced by a plant, but few studies have attempted to characterize the "internal" or physiological factors that directly control the switch from one floral type to the other. Lee et al. (1978) suggested that a burst of ethylene production in the CL flower of *Salpiglossis sinuata* at pollination was responsible for arrested corolla expansion. Exogenous application of a compound that releases ethylene retarded corolla development in both CL and CH flowers. This might explain the lack of anthesis in the CL flower; but the divergence in stamen development, resulting in smaller anthers in the CL flower, must occur at a much earlier stage before ethylene levels appear different in the two floral forms. In *L. amplexicaule*, exogenously applied gibberellin (GA_3 or GA_7) induces open flower production, but the anther morphology in these induced CH flowers is typical of CL flowers (Lord, 1980a). Gibberellin induces floral expansion and anthesis in *Collomia grandiflora* as well (Lord, unpubl.), but as with *L. amplexicaule*, the hormone has not acted as a trigger to produce a true CH floral form. In vitro study of the induction of CL and CH floral forms, coordinated with in vivo study may shed some light on the mechanism that controls the switch from CL to CH floral production and vice versa. An increase

(Uphof, 1938) in the percentage of CL floral forms often occurs when cleistogamous species are water stressed. Dieter Wilken (pers. comm.) postulated that an increase in the plants' abscissic acid (ABA) level, which is often correlated with water stress (Quarrie and Jones, 1977), may be the trigger that induces CL floral production. Since ABA and gibberellins are known to interact in various growth phenomena (Chrispeels and Varner, 1966) they may play a role together in regulating CL and CH floral production in *L. amplexicaule* and *C. grandiflora*.

Varying proportions of the different floral types may occur within an individual and between individuals. Prior to a developmental study, it would be wise to determine the extent of environmental vs. genetic controls on this variation in the sample population, using plants grown under uniform, controlled growth conditions (Falconer, 1961).

There are parallels between the variation in floral form in many cleistogamous species and the phenomena of foliar heterophylly and heteroblasty (Lord, 1979, 1980c; Ritzerow, 1908; Uphof, 1938). In seasonally cleistogamous species like *Viola* spp., photoperiod and temperature determine the floral form produced (Chouard, 1948; Evans, 1956). These cases are analogous to those of heterophyllous, land/water, leaf forms that occur in amphibious plants. Dimorphic leaf forms, separated usually by some intermediates, are inducible by environmental cues (Allsopp, 1955; Bostrack and Millington, 1962; Cook, 1969; McCully and Dale, 1961; Schmidt and Millington, 1968).

Heteroblasty implies a "fixed phenotypic variation" (Bradshaw, 1965) expressed as an ontogenetic shift in leaf form in a progressively developing shoot system (Allsopp, 1967; Ashby and Wangermann, 1950; Crotty, 1955; Feldman and Cutter, 1970; Goebel, 1898; Kaplan, 1973, 1980; Owens, 1968). Since some cleistogamous species exhibit what appear to be ontogenetic shifts in floral form in the inflorescence (inflorescence heteroblasty), it is appropriate to study the phenomenon in the same manner in which foliar heteroblasty has been studied. This means studying floral form in the context of inflorescence development; describing floral variation as a function of floral position in the developing inflorescence. Many examples of within-plant floral variations exist in the angiosperms where positional effects occur (Heslop-Harrison, 1957). Harper (1977) refers to within-plant differences in seed and fruit morphology and behavior as cases of somatic polymorphism which he believes to be widespread. He claims this situation allows for a "degree of sensitivity for adjustment of the proportion of morphs which is lacking in genetic polymorphisms." He continues, observing that "morphs can be altered directly by environmental influences on the seed parent and allocation of resources to the 2 seed types can be subtle and directly responsive to environmental change." To some extent, the same may be said of the

variety of floral forms in cleistogamous species. Uphof (1938) presented the phenomenon of cleistogamy as an example of floral plasticity; but if fixed ontogenetic shifts in floral form occur in the inflorescence, then developmental constraints in the system exist that should also be recognized.

Functional Differences in the Breeding System

Uphof (1938) questioned the value of CL flower production. Darwin (1877) and others (Beattie, 1976; Camp and Gilly, 1943; Kannenberg and Allard, 1967; Long, 1971; Rust, 1977; Schemske, 1978; Waller, 1979) considered cleistogamy to be an adaptation to ensure seed set by selfing in the relatively inexpensive CL flowers, outcrossing being effected by the CH flowers when vectors were available. That CL flowers offer a means for self-seed production is no longer questioned but the role of the CH flower in gene exchange now has to be tested.

Cleistogamous species may be useful tools for measuring levels of self pollination in a population (Kannenberg and Allard, 1967; Levin, 1968; Rust, 1977; Schemske, 1978; Stitt, 1946; Waller, 1979, 1980). However, the percentage of CH flowers produced by a plant may not be an accurate indicator of the level of outcrossing (Clay, pers. comm.; Lord, 1980b). For example, in *L. amplexicaule* L., only 10% of the CH flowers fail to set seed in the absence of vectors (Bernstrom, 1952). Bagged CH flowers of *C. grandiflora* show low seed set compared to field controls (Wilken, 1977). This phenomenon is true for a number of *Impatiens* species as well (Schemske, 1978; Waller, 1979). When *C. grandiflora* was grown in the greenhouse, the main inflorescence head showed a decrease in fertility with the shift in floral form from CL to CH (Lord, unpubl.). Floral form in many cleistogamous species may be a close approximation to function in the field but some level of both geitonogamy and autogamy is usually possible in the CH flowers.

Gene markers would be very useful to test for levels of outcrossing between CH flowers in a population. Stitt (1946) used procumbent habit as a marker in *Lespedeza cuneata* and estimated that 70.4% of the seed from CH flowers resulted from cross pollination. Allozymic analysis of the breeding system in populations with different percentages of CL and CH flowers would also provide some direct evidence of a relationship between floral form and function in cleistogamous species.

Developmental study is essential for understanding the dynamics of floral function. In species with self-compatible, hermaphroditic flowers, slight changes in the relative positioning and timing of maturation of the sexual parts may result in modifications of the breeding system (Breese, 1959; Frankel and Galun, 1977; Hinton, 1976; Moore and Lewis, 1965;

Rick et al., 1978; Schoen, In press; Tomlinson et al., 1979; Vasek, 1968). The physiological aspects of pollination in CL flowers have not been studied sufficiently to determine whether fundamental differences exist between these and the CH flowers. Lee et al. (1978) found that the stigmatic extract from CH flowers stimulated CH pollen germination in vitro in *Salpiglossis sinuata*. They suggested that at the time of stigmatic exudate production, the stigma's proximity to the anthers in the CL floral bud induced pollen germination in the closed anthers. They attempted, unsuccessfully, to pollinate CL flowers with CH pollen, and they postulated the cause of this apparent cross incompatibility to be due to morphological dissimilarities between the styles of the two floral forms. However, this is not a sufficient explanation for such a phenomenon. The plants used were inbred lines. First, there was a CH line producing only CH flowers; then there was a CL line which produced CH flowers first, then later CL flowers. The shift in production was inducible by long daylength and 25°C temperature. There is a genetic basis to the production of dimorphic floral forms in *S. sinuata*: CC genotypes are predominantly cleistogamous, Cc are intermediate and cc are usually completely chasmogamous (Lee et al., 1976). The CL pollen parent in the cross compatibility experiment had solid yellow flowers while the CH pollen parent had dilute red flowers. Adding CH pollen to CL stigmas at pollination resulted in only yellow offspring, indicating that they were all derived from self pollination. Similarly, placing CL pollen on a CH stigma failed to result in seed set.

Since both CL and CH flowers may be borne on a single plant, it would be interesting to see if this incompatibility occurs between flowers on an individual. Since crosses were successful between the infrequent CH flowers on the CC plant and CH flowers on the cc plant, the incompatibility is not between the two genomes, but only between the two floral forms. The CL pollen may have different germination requirements than CH pollen. CL pollen, for example, may be viable for only a short time and CL stigmas receptive only briefly, in which case, the timing of such a cross would be crucial. It is possible that the CL pollen and stigmatic exudate are physiologically different from those in the CH flower. If there is a difference in pollen-stigma compatibility of the two floral forms, then it is conceivable that a shift in compatibility could occur within a single inflorescence bearing both CL and CH floral forms. In *L. amplexicaule*, Bernstrom (1950) often found that hand pollinating the self-compatible CH flowers did not overcome their apparent decreased ability to set selfed seed as compared to CL flowers on the same plant. There is evidence (Lord, unpubl.) that cryptic self-incompatibility exists in the CH flowers of this species expressed as outcrossed pollen tubes growing faster in the style than selfed pollen tubes.

This area of pollination biology in cleistogamous species is very intriguing and needs further structural, physiological and genetic study. Some questions to be addressed are: (1) What induces pollen germination in the CL anthers and what prevents anther dehiscence in a number of CL species, and (2) Are there physiological differences between CL and CH flowers in their pollination processes? Since cleistogamy as a desirable character is often selected in crop breeding programs, knowledge of the processes that lead to it should be extremely useful to plant breeders (Frankel and Galun, 1977). Sanders and Hamrick (1980) have demonstrated that hermaphroditic, self-compatible species show variation in their breeding system. The basis for this variation may be strictly genetic or environmental, or a combination of both effects. There may also be within-plant variation in the breeding system expressed as ontogenetic shifts in form and function of flowers in the inflorescence. No doubt, slight modifications in the timing of anther dehiscence and stigma receptivity, as well as the relative positioning of these structures in self-compatible species can strongly affect breeding systems. Cleistogamy represents a good comparative system to study the developmental and physiological mechanisms that allow for such variation.

VI. CLEISTOGAMY AS A MODEL SYSTEM TO STUDY FLORAL FUNCTION AND EVOLUTION

The renewed interest in breeding systems at the population level has led to a fresh awareness of the variation and complexity of floral form and function in the angiosperms (Richards, 1979). Biosystematists and populations biologists (Ganders, 1979; Ornduff, 1978; Schoen, In press; Whalen, 1978) are currently elucidating the functional aspects of floral structure. There is enough preliminary field and experimental data on breeding systems in a number of species to warrant morphological study of these same species in conjunction with simple studies of their breeding systems. The best response to Carlquist's (1969) call for a more functional approach to the study of floral morphology would be to combine knowledge gained from the study of variation in floral form and function in an individual with that of breeding systems on a population level. Population study of cleistogamous species' reproductive biology is difficult, not only because the variation in floral form depends, to some degree, on environmental conditions, but also because it occurs both within and between individuals. A few studies have demonstrated that the predominant floral form is CL (Schemske, 1978; Solbrig et al., 1980; Waller, 1979). In his review, entitled 'The plant as a metapopulation,' White (1979) suggested using the term "metapopulation" for describing homologous structures on a genetic individual. He also discussed the demography of subunitary

parts, but restricted himself to vegetative structures. A similar approach which considers reproductive units like flowers is necessary to adequately describe a phenomenon as variable as cleistogamy.

Study of the floral form and breeding system of an organism is intimately related to the general study of contemporary evolution in plant species (Baker, 1959; Grant and Grant, 1965). Cleistogamy can provide a comparative system to determine developmental processes that lead to changes in floral form. Mechanisms which control such changes can then be investigated more easily. With such knowledge, researchers could better address questions about the evolution of diverse floral morphologies and breeding systems in particular taxonomic groups (Stebbins, 1974).

Knowledge of ontogenetic events resulting in morphological change will allow us to test predictions of how new forms arose phylogenetically (Alberch et al., 1979). Morphologists have long recognized the need for developmental data to elucidate phylogenetic trends in the angiosperms (Kaplan, 1971; Sattler, 1966; Tucker, 1974, 1979; Uhl and Moore, 1980). Kaplan (1971) summarized the modern approach to relating ontogeny and phylogeny: "If we agree that phylogeny proceeds through a succession of modified ontogenies (De Beer, 1951), then the comparative study of developmental events responsible for small morphological differences between related species can help to specify the nature of the ontogenetic modifications that result in these evolutionary changes." Stebbins (1974) repeatedly claimed that such an approach to the study of evolution is now imperative: "The modern approach to understanding evolutionary change in terms of altered developmental sequences must be basically synthetic. It must begin with careful quantitative analyses of developmental patterns in related species and genera." Heterochrony, or changes in developmental timing, may be responsible for much of the variation in floral form seen in extant groups. This line of thinking has currently been popularized for animal evolution in Gould's book 'Ontogeny and phylogeny' (Gould, 1977). In an attempt to determine the likely developmental processes responsible for the evolution of floral form in the genus *Delphinium*, Guerrant (1980) compared size and shape growth of the flowers of two species, *D. nudicaule* and *D. decorum*. Guerrant invoked the process of evolutionary juvenilization or neoteny (Alberch et al., 1979) to explain the derivation of the hummingbird pollinated *D. nudicaule* from a bee pollinated ancestor like *D. decorum*.

A limitation to such comparative studies between two different contemporary species is that we can never be sure that the observed mechanisms of morphological change are similar to those responsible for past evolutionary change in the group (Kaplan, 1971). A partial remedy to this situation is the use of a comparative system where a series of different

but homologous forms occur within a single individual. There are many examples among cleistogamous angiosperms where at least two floral forms are borne by one genotype. These divergent floral types of one species can be as disjunct in their morphologies as are the floral forms borne by different species (Uphof, 1938). Comparisons of floral development between related species will be aided by knowledge of the processes that lead to modifications within species. It may be that the open system of growth in plants will make them better subjects than animals for testing hypotheses about the relationship between ontogenetic processes and phylogenetic change.

A common denominator that characterizes CL flowers in all cleistogamous species is a reduction in the corolla and the androecium, usually of anther size and/or number in the latter. A developmental coordination appears to exist between the epipetalous stamens and corolla in the mint, *Lamium amplexicaule* L. (Lord, 1979). The reduced CL corolla appears to be a result of the reduced anther tissue in these flowers. Exogenously applied GA₃ causes corolla expansion in CL flowers of *L. amplexicaule* L. (Lord, 1980a) and *Collomia grandiflora* (Lord, unpubl.). Since gibberellins, supposedly produced in anthers, have been implicated in the expansion of floral parts in a number of species (Greyson and Tepfer, 1967; Murakami, 1975; Zieslin et al., 1974), it is possible that the smaller anther size of the CL flowers results in gibberellin levels too low to permit anthesis. Plack (1957, 1958) used the same reasoning to explain reduction in the female flowers of the gynodioecious mint *Glechoma hederacea*. Emasculation of hermaphroditic flowers resulted in a reduced corolla characteristic of the male-sterile female flowers. Application of GA₃ to the female flower induced corolla expansion.

Reduction of corolla size is a common occurrence in the female flowers of gynodioecious (Baker, 1948), gynomonoecious and dioecious species (Darwin, 1877), though the correlation between male sterility and corolla reduction does not always hold (Lloyd and Webb, 1977). Reduction in corolla size often accompanies male sterility when it occurs naturally in a population of a hermaphroditic species, e.g., *Gilia achilleifolia* (Schoen, pers. comm.), *Epilobium* spp. (Michaelis, 1954) or when it is specifically selected for (Frankel and Galun, 1977; Izhar, 1972; Lewis, 1941). In flax, male-sterile lines often have reduced corollas that fail to open, looking like CL flowers (Thompson and Miller, 1978). The reductions in androecium and corolla seen in the development of the CL flower may be analogous to those which occurred in the evolution of autogamous species where similar reductions are common (Arroyo, 1973; Frankel and Galun, 1977; Lloyd, 1965; Moore and Lewis, 1965; Ornduff, 1969; Rollins, 1963; Stebbins, 1957a). Cruden (1977) found a correlation between decrease in pollen/ovule (P/O) ratios, reduction in corolla size and the evolution from

xenogamy to autogamy in related species. The decrease in P/O ratio most often meant a reduction in pollen number due to production of smaller anthers. An explanation often given for such a reduction in corolla size in the evolution of autogamy, is that of relaxed selection for a conspicuous flower to attract pollinators (Moore and Lewis, 1965; Ornduff, 1969). Darwin (1877) doubted whether natural selection was involved in this form change. Results from the study of floral development in *L. amplexicaule* (Lord, 1979, 1980a) suggest that a reduction in corolla size in CL flowers may be an immediate developmental consequence of a reduced androecium.

It is generally accepted that selfers arose, for the most part, from related outcrossers (Arroyo, 1973; Breese, 1959; Brown and Jain, 1979; Ellstrand and Levin, 1980; Gottlieb, 1973; Jain, 1976; Stebbins, 1957b); that the condition is generally derived. Comparing floral development in a cleistogamous species, with CL and CH flowers, to an autogamous relative, with reduced CH flowers, may provide the morphogenetic information to account for the changes in floral form associated with the evolution of self pollination in a genus.

To identify the agents of evolutionary change in floral form in the angiosperms, we must use a multifaceted approach, including knowledge gained from the study of developmental correlations and constraints on form (Nelson, 1954) and studies of floral function in an organism's breeding system (Stebbins, 1957a).

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