



## Flora of Panama

Robert E. Woodson, Jr.; Robert W. Schery

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# FLORA OF PANAMA

BY

ROBERT E. WOODSON, JR.

AND

ROBERT W. SCHERY

*Missouri Botanical Garden*

AND COLLABORATORS

*Flora of Panama* is a compilation of the indigenous and naturalized vascular plants of the Republic of Panama, following generally the system of Engler and Prantl. The treatments of the various families follow consecutively as nearly as is practicable and are of a critical nature, including synonymy, descriptions, and citation of representative Panamanian exsiccatae for each species. The compilers of the *Flora* have been aided in their work very materially by the extensive contributions of American and European specialists of wide repute in the case of numerous critical families. As is customary, such contributions are credited directly to the authors concerned.

*Flora of Panama* will appear in the ANNALS OF THE MISSOURI BOTANICAL GARDEN as contributions accumulate. Since the completed work will be extensive, it will consist of a number of parts designated numerically, each with separate pagination and pertinent illustrations. The first portion of the work to be published will begin the taxonomic treatment of the Gymnospermae and Monocotyledoneae, and will be designated as Part II. General discussions of historical, geographical, physiographic and floristic relations, to be published later, will constitute Part I. Full indices, together with *addendae* and *corrigendae*, will occupy the final part.

The unusual nature of *Flora of Panama* will necessitate a change in the policy of the Missouri Botanical Garden regarding reprints, which will not be generally distributed except to collaborators. Reprints of the various parts of the *Flora*, suitable for permanent binding, will be offered for sale by the Missouri Botanical Garden. Prices upon application.

MISSOURI BOTANICAL GARDEN

St. Louis, Mo.

## PREFACE

Formally begun in 1943, the *Flora of Panama* is complete with this issue. The broadside distributed by Woodson as an insert in the first fascicle of the *Flora* and reproduced opposite this page is a prospectus of what was planned. The completed flora follows Woodson's guidelines remarkably closely, though significant changes and (we hope) improvements were made along the way by a succession of contributors and editors, many of whom were not even born when the project began. Over 100 scientists have contributed to its preparation, and publication has extended over 38 years, from 1943 to the present. A short description of the *Flora* is provided below, and a history of collecting activities by Dwyer updates his earlier (1964) paper on the subject. A symposium celebrating completion of the *Flora* was held in Panama in April 1980, and the keynote address given at that event by Peter H. Raven outlines the problems facing future activities in Panama and other developing countries. The *Flora of Panama* is a beginning in the assessment of plant diversity in Panama; many additions to this body of knowledge have already appeared in the literature, and many more additions and changes will be generated by further field work and study.—W. G. D'ARCY



## THE *FLORA OF PANAMA*: HISTORICAL OUTLINE AND SELECTED BIBLIOGRAPHY

W. G. D'ARCY<sup>1</sup>

Formally begun in 1943, and prepared with the assistance of 103 contributors, the *Flora of Panama* includes coverage of over 6,200 species. Publication of the *Flora* in parts in the ANNALS OF THE MISSOURI BOTANICAL GARDEN ensured its wide distribution to botanical institutions around the world. It is the first attempt to survey all plants growing in Panama, and as such, it is the basis on which botanical studies in the future must rest. Although uneven in content and inadequate in some parts, it is nevertheless a good starting point for assessing plant diversity in the isthmus: the great increase in known diversity since the appearance of early parts of the *Flora* makes clear the need for further effort. It is likely that a final inventory of vascular plant species occurring in Panama will include 9,000–10,000 species.

Before commencement of the *Flora*, the Missouri Botanical Garden had for a number of years been interested in Panamanian plants beginning with the visit in 1922 by Jesse M. Greenman, then Curator of the Herbarium at the Garden. A tropical station was established in 1926 at Ancon which was at first concerned with providing living plants for show and study in the greenhouses in St. Louis, but which soon generated interest in the collection and study of herbarium specimens. Several scientific expeditions were sent to Panama in the 1930's and by the end of this decade several "Contributions toward a *Flora* of Panama" were published in the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The history of this early period is related by Dwyer (1964), and the contents of the "Contributions" and the early parts of the *Flora* are reviewed by Robyns (1965). Croat's (1978) section on History of Botanical Studies also gives a good resumé of plant collecting activities in much of the country.

The *Flora* was initiated by Robert E. Woodson, Jr. (1904–1963) who edited the first parts with the assistance, until 1952, of Robert W. Schery (1917– ). From about the time Schery's departure until the late 1950's there was a hiatus in activity on the *Flora*. In 1958 the *Flora* resumed publication with several contributors besides Woodson, most notably Loran C. Nevling, who was on the staff of the the Missouri Botanical Garden for much of 1949, and slightly later (from 1960) James A. Duke, who was a staff botanist at the Garden. The *Flora* received its first funding from the National Science Foundation in 1957, and support has been continuous since then. In the early 1960's activity on the *Flora* grew, as André Robyns was hired to direct the project, and momentum was sufficient that with the death of Woodson in 1963, publication continued almost uninterrupted. Walter H. Lewis became Director of the Herbarium in 1964, and he improved the activity and professional level of standards of the *Flora* project. In 1968, Duncan M. Porter replaced Robyns as editor, and by the time of his departure in 1972, Porter was able to boast that all remaining parts of

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the *Flora* had specialists committed to preparing the treatments. During Porter's time as editor of the *Flora*, contributions were made by Joan W. Nowicke who was hired to prepare treatments. Following Porter's departure the *Flora of Panama* project, which by now included an active field program, was directed by Thomas B. Croat, and the editorial aspects of the project were assigned to W. G. D'Arcy. In 1977, as he became engaged in a major study of the Araceae, Croat relinquished management of the project to D'Arcy who saw the *Flora* to completion.

In April 1980, with all treatments ready in at least manuscript form, a symposium was held in Panama City to celebrate completion of the *Flora*. This was supported by the Missouri Botanical Garden, the National Science Foundation, the University of Panama, the Smithsonian Tropical Research Institute, the Panamanian conservation commission (RENARE), the Joyce Foundation, and other organizations. About 350 participants gathered to hear a four day program of papers on Panama's natural history.

The concept of the *Flora* expanded somewhat over the years. Initially the number of species was thought to be small, and the published *Flora* was arranged so it could be extracted from the ANNALS for use as a separate manual. Thus early parts had "*Flora*" pagination as well as pagination of the ANNALS. In all cases citations should be made using the ANNALS pagination in the upper corners of the pages and not to the "*Flora*" pagination in lower center. The "*Flora*" pagination was discontinued after publication of the first parts of the Leguminosae in 1950. Other features of the *Flora* also expanded over time. From a policy of studying only material available in the Missouri Botanical Garden, it became normal procedure to borrow all Panamanian specimens from all institutions with significant holdings of Panamanian plants, the most noteworthy being: A, DUKE, F, GH, FSU, MO, OS, PMA, SCZ, and US, and especially important specimens were studied from many other institutions. In early parts of the *Flora*, cultivated and introduced plants were ignored, but later it became the rule to attempt to account for all species. Illustrations at first represented only a few of the families, but it later became the policy to include one illustration of each genus, and in large genera, one illustration for each 10 species. Original illustrations were preferred; only in a few cases were older illustrations republished. When it became evident that much of the flora must, because of the poor state of knowledge about neotropical plants, be revisionary in scope, and that a second edition of the *Flora* would be unlikely for many years, the *Flora* began to include information on nomenclatural typification, and many of the treatments became semi-monographic in scope.

Over the years there was a large increase in the quantity and quality of collections available to the collaborators on the *Flora*. In the 1930's most collections studied were those of Woodson and collectors directly concerned with production of the *Flora*, such as Paul C. Allen (1911–1963) Russell J. Seibert, and Julian A. Steyermark (1909– ) although in some cases the collections of Paul C. Standley and others were reexamined. In the 1960's a series of expeditions was sent to Panama from St. Louis, and a number of other collectors became important contributors to the available stock of herbarium material; John D. Dwyer and James A. Duke were perhaps most noteworthy at this time. Neither of these was

directly concerned with preparation of the *Flora* at the time when they did their most important collecting. Walter H. Lewis led several expeditions to Panama in the late 1960's and early 1970's, and his encouragement was of great importance in guiding the flora at that time. In about 1970, the assignment of Thomas Croat to prepare the Flora of Barro Colorado Island wrought great changes in the way that the Panamanian flora was to be perceived and studied. Croat became a resident in the isthmus for several years during which time he established a field station facility with housing, drying facilities and field vehicle capability. Croat and his successors at the station were able to make the first intensive collections of tropical wet forest regions. This ecological zone, which largely follows the Caribbean coast, is much richer in species than any other part of Panama, and it had been the least populated and least accessible. Families with important numbers of forest species were soon found to have twice as many or more species in Panama than had been supposed under even the most expansive earlier estimates. Families prepared before the early 1970's are found to have only a token representation of the flora actually present, and recently prepared families seriously understate the size of the actual flora. The intensive collecting program maintained since 1970, and especially the investigation of tropical wet areas, has revealed a flora much richer than previously suspected, and it has added excitement to the study of Panama's plant life. A result is that the *Flora* greatly understates the actual situation: continuing study will supplement what has already been published, and the *Flora* together with new publications of present and future workers will give a reasonable picture of the plant diversity in the Isthmus of Panama.

The *Flora of Panama* deals only with seed plants and includes just over 6,200 species. The pteridophytes are being treated separately by David B. Lellinger, Smithsonian Institution, together with the pteridophytes of Costa Rica and the Department of Chocó, Colombia. Lellinger (pers. comm.) estimates that he will record about 700 species from Panama. The bryophytes have not as yet been treated in floristic fashion, although active studies are under way by Prof. Noris Salazar and associates at the University of Panama. Marshall R. Crosby, Missouri Botanical Garden, estimates (pers. comm.) that there are about 400 species of mosses in Panama. The total derived from the above estimates—7,300 species including seed plants, pteridophytes, and mosses—greatly underestimates the total flora, for the figure for seed plants omits many species. The total flora is more likely in excess of 9,000 species.

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# THE HISTORY OF PLANT COLLECTING IN PANAMA (1700–1981)<sup>1</sup>

JOHN D. DWYER<sup>2</sup>

This talk is dedicated to the memory of Dr. Robert Woodson, Jr., late Curator of the Herbarium of the Missouri Botanical Garden and Professor of Botany at Washington University, who died in 1963. His name, together with that of Dr. Robert W. Schery, has been on the title page of every issue of the *Flora of Panama* in the ANNALS OF THE MISSOURI BOTANICAL GARDEN.

While this paper is historical in character, a point dealing with the present and the future will be made: that Panama is and will be in need of more intensive collection.

I estimate that about 750 botanists or naturalists have collected plants in Panama for permanent deposit in herbaria. This may seem to be an exaggeration, considering that my current unpublished list (see also Dwyer, 1964, 1968) includes the names of only 450 collectors. In defense of this estimate of 750 let me point out that new collectors can be found without much difficulty by examining herbarium specimens and through searching the literature. The list includes the names of all who have collected without regard to the quantity of collection numbers. The term "number" does not include duplicate material included under a specific number.

Throughout the world there are about one half million numbers of Panamanian plants. Of these about a quarter of a million are deposited in the Missouri Botanical Garden. In the last decade and a half five botanists from the Missouri Botanical Garden have collected approximately 50,000 numbers, these, for the most part, being gathered in non-team fashion (Table 1).

As this is a historical treatment of plant collecting in the Republic of Panama, we start at the beginning when in 1700 James Wallace collected several herbarium specimens in the ill-fated Scotch Colony on the Atlantic Coast of the old Province of Darién.

It is appropriate to divide the 280 years of plant collecting into 3 phases:

1. 1700–1914.
2. 1915–1957.
3. 1958–1981.

The first phase runs from the period of the Scotch Colony in Darién to the opening of the Panama Canal. The second period is marked initially by a lull period during and immediately after World War I, followed by some field work and considerable herbarium study, this to be again interrupted by a war, World War II. The third period, the golden period, extends from 1958, the year when William L. Stern and Kenton L. Chambers made an exciting collecting trip into Panama, up to the present time when herbarium material is being collected on a year-round basis.

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TABLE 1. Collectors with largest numbers of collections from Panama. \* Indicates individual was a staff member of, student at or professional collector for the Missouri Botanical Garden.

*Croat, T.	23,000	*D'Arcy, W.	5,000
Standley, P.	7,500	Dressler, R.	4,000
*Gentry, A.	7,000	*Dwyer, J.	4,500
Duke, J.	6,000	*Hammel, B.	4,500
*Mori, S.	6,000	*Lewis et al.	3,700
*Folsom, J.	5,000	*Allen, P.	3,600
*Nee, M.	5,000	Pittier, H.	3,600
Tyson, E.	5,000	*von Wedel, H.	3,000

A glance at Table 2 shows that in the first period (1700–1914) a shift from domination of plant collecting by Europeans to an eventual takeover by North Americans is obvious. Some collections made in this period may never have been cited as *exsiccatae*, e.g. those of Joseph Jussieu, Robert Millar, and B. Roezl. Particularly noteworthy are the collections of Berthold Seemann, who wrote the first flora of Panama (Seemann, 1854) as well as those of Henri Pittier, numbering over 1,850, drawn from one end of Panama to the other (Dwyer, 1973). Several Christian Brothers living in Panama City collected several hundred numbers beginning in 1912. Interestingly, almost all the Americans who collected in the first period were from the eastern United States.

The second period (1915–1957) obviously overlaps somewhat with the first, making it the most difficult of the three to bring into proper perspective. Paul Standley's collection of 7,500 numbers in 5 months (end of 1923 and beginning of 1924, and one month in 1925) served as a basis for his *Flora of the Canal Zone* (Standley, 1928) and the *Flora of Barro Colorado Island* (Standley, 1927). He demonstrated his extraordinary ability in the field. His collections, mostly unicates, were confined to the Canal Zone and the vicinity of Panama City.

As early as 1922 Jesse M. Greenman, Curator of the Herbarium at the Garden, made a few collections of phanerogams in Panama, and in 1923 the Missouri Botanical Garden was attracted to Panama by the living orchid collection of a retired postman, C. W. Powell, living in Balboa. To house this collection, received as a gift, the Garden maintained a tropical station at Ancon Hill, Canal Zone, this surviving until 1939.

Beginning in 1934, up to the beginning of World War II, several botanists, functioning mostly in team fashion, collected throughout the isthmus, especially Paul Allen, Carrol Dodge, A. A. Hunter, Russell Seibert, Robert Schery, Julian Steyermark, and Robert Woodson, Jr. I estimate that their collections in Panama amount to fewer than 10,000 numbers. The figure would be considerably higher if the vast majority of the 5,000 specimens collected by Woodson, Allen, and Seibert in 1947 were not destroyed by fire. In this second period the greatest exhibition of collecting was by C. V. Piper of the U. S. National Herbarium who, in 1923, collected 1,000 numbers in 10 days!

From 1948 until his death in 1963 Woodson believed that Panama had been adequately collected, and that the *Flora of Panama* could be written successfully by relying almost exclusively on the collections in the herbarium cases of the Garden. In light of the experience of the last two decades, this was a great mistake

TABLE 2. Early collectors of Panamanian plants.

WALLACE, J.	Scottish	1700
JUSSIEU, JOS. DE	French	17??
MILLAR, R.	English	1734
MEE, L.	French	1789
HAENKE, T.	Bohemian	1780–1791
BILLBERG, J.	Swedish	1826
DAHLIN, E.	Finnish	1826–1831
CUMING, H.	English	1830–1831
HINDS, B.	English	1837 etc.
BARCLAY, G.	English	1837 etc.
SINCLAIR, A.	English	1837 etc.
LOBB, W.	English	1843
SEEMANN, B.	German	1846; 1847; 1848; 1849
WARSEWIEZ, J.	Polish	1848; 1850
BEHR, H.	German	1848
FENDLER, A.	American	1848–1849
BALL, J.	Irish	1852
HALSTED, M.	American	1850–1854
KUNTZE, O.	German	1874
DUCHASSAING, E.	French	1849–1851
HAYES, S.	American	before 1863
ROEHL, B.	Czech	1869
HART, J.	English	1885
COWELL, J.	American	1905
HOWE, M.	American	1909–1910
WILLIAMS, R. S.	American	1908
PITTIER, H.	Swiss	1910–1911; 1914–1915
POWELL, C.	American	1907–1927
OSTENFELD, C.	Dane	1921–1922
BRO. GERVAIS	Panamanian	1912
BRO. CELESTINE	Panamanian	1912
STEVEN, F. L.	American	1924
MACBRIDE, J.	American	1918
ROSE, J.	American	1918
MAXON, W.	American	1911; 1923
HITCHCOCK, A. A.	American	1911
KILLIP, E. P.	American	1917–1918; 1922
PIPER, C. V.	American	1923
GOLDMAN, F. A.	American	189?–19??
CHRISTOPHERSEN, E.	Norwegian	19??

in judgement, although the lack of money for field work and the pressure of his academic responsibilities have to be considered. As we shall see in the third and last phase, the numbers of novelties being described from Panama, especially in the last decade, e.g., in the Ericaceae, Araceae, Rubiaceae, strongly support such criticism (Table 3).

In 1949 Ivan Johnston's *The Botany of San Jose Island* was an outstanding contribution, based essentially on a study of his own collections and those of C. O. Erlanson and J. Harlow. In this period the collections of George P. Cooper and George Slater amounted to about 450 numbers from the little explored province of Bocas del Toro, the higher reaches of which remain little explored today.

In 1958, in my opinion, the field trip of William Stern and Kenton Chambers, both then faculty members at the Yale School of Forestry, initiated the third stage of plant collecting in the isthmus, reöpening the door of Panama as a land

TABLE 3. Families published in *Flora of Panama* (1970–1980) and the numbers of new or recently described species.

Year	Number of Families	Total Species	Percentage New or Recently Described Species
1970	5	91	1
1975	11	413	12.5
1976	9	207	10
1978	8	217	32
1980	1	415	23

of promise for the systematics of flowering plants and ferns (Standley & Stern, 1960). The following year, Stern, Chambers, John Ebinger, and I collected more than 1,200 numbers, principally in Darien. In 1960, Duke University, under the auspices of the U.S. Army Research Office, initiated a decade of collecting in Panama. In 1963 Dr. Edwin Tyson, then of Florida State University, shifted much of his research in zoology to the systematics of the angiosperms. His collections, amounting to 5,000 numbers, were housed in the U.S. Army Tropic Test Center, Canal Zone (Dwyer, 1967), which later became Summit Herbarium (Croat, 1971).

Soon after Woodson died in 1963, Walter H. Lewis became Director of the Herbarium of the Missouri Botanical Garden. He immediately set to work getting grant support for botanical exploration in Panama. Table 4 shows that in 1966 and 1967 13 Garden staff members and students made collecting trips in Panama. At about this time Robert L. Dressler became resident botanist with the Smithsonian Tropical Research Institute, at first living on Barro Colorado Island. His own collections and personal studies, particularly on orchids, coupled with his willingness to assist all of those botanizing in Panama, has been of inestimable value over the past 17 years.

One of those profiting from the grant support generated by Walter Lewis was Thomas B. Croat. His accomplishments in collecting during the past 14 years in Panama defy description. Statistics indicate (Table 1) that he tripled the number of plants collected by Paul Standley. Croat's total from the isthmus is more than 23,000 numbers. (See Croat, 1978.)

A glance at Table 1, which shows those who collected more than 3,000 numbers in Panama, is revealing. With the exception of Walter Lewis, this list scores

TABLE 4. Collectors who accompanied Walter Lewis on field trips to Panama (1966–1969).  
\* Indicates individual was staff member of or student at Missouri Botanical Garden.

*Baker, K.	Escobar, N.
*Blackwell, W.	*Hawker, J.
*Burch, D.	Little, C. O.
Correa A., M.	*Macbryde, B.
*Croat, T.	*Oliver, R.
*Crosby, M.	*Robertson, K.
Dressler, R.	*Robyns, A.
Duke, J.	*Verhoek
*Dwyer, J.	Zaborowski, A.
*Elias, T.	

TABLE 5. Resident collectors at Summit Herbarium, Panama.

Antonio, Thomas M.	May 1979–July 1980
Croat, Thomas B.	March 1970–August 1971
	February 1976–September 1976
Folsom, James P.	January 1977–January 1978
Gentry, Alwyn H.	August 1971–October 1972
Hammel, Barry E.	January 1978–May 1979
Kennedy, Helen	September 1972–May 1973
Mori, Scott A.	September 1974–August 1975
Nee, Michael	August 1973–June 1974
Sytsma, Kenneth J.	August 1980–
Witherspoon, John T.	September 1975–November 1975

only those who collected alone. Thus some collectors on the list may also have assisted in team efforts. I have no statistics for the numbers collected by Sydney McDaniel, now in Panama, although they are several thousand.

In 1969, in the Canal Zone, the Missouri Botanical Garden established a field station with a house trailer and a modest herbarium (Croat, 1972). This allows pre-doctoral or post-doctoral students to pursue their research in systematics, as well as to collect. The Garden's resident collectors in Panama, who were also curators of Summit Herbarium, are shown in Table 5.

In 1973 the Missouri Botanical Garden in Panama and the Smithsonian Tropical Research Institute combined their herbarium resources in a restored portion of the former Tivoli Hotel in Balboa, Canal Zone (Croat & Crosby, 1974).

That the Missouri Botanical Garden dominated plant collecting in Panama from the 1940's onward is obvious. However when one considers the extensive collecting done by Edwin Tyson in the 1960's, as well as by Sydney McDaniel and Kurt Blum, sent into Panama originally by Robert Godfrey of Florida State University, as well as the extensive collecting of James Duke over the 1960–1970 decade, under the aegis of the U.S. Army and Battelle Memorial Institute, as well as the eight botanical expeditions of Robert L. Wilbur of Duke University and his students: Frank Almeda, James Luteyn, Richard Weaver, Robin Foster and others, a more fair perspective of collecting in Panama emerges. Wilbur himself has collected some 1,500 numbers in Panama.

Special tribute is due Novencido Escobar and Mireya D. Correa A. of Panama University for building up, over the past decade, the herbarium at Panama University, now numbering over 16,000 sheets.

TABLE 6. Collectors who made largest collections from provinces of Panama.

Bocas Del Toro	von Wedel, H.	3,000
Chiriquí	Croat, T.	3,640
Coclé	Folsom, J.	1,415
Colón	Croat, T.	1,052
Darién	Duke, J.	2,300
Herrera	Folsom, J.	120
Los Santos	Lewis et al.	458
Veraguas	Croat, T.	1,510
San Blas	Duke, J.	500
Canal Zone	Croat, T.	10,737

Today, in Central America, the most exciting country for plant collecting is Panama. Evidence of this is the 15 new species of Rubiaceae which are awaiting description at the Missouri Botanical Garden, these having been encountered since sending off my manuscript of the Rubiaceae of Panama with a total of 415 species at the end of 1979 (Dwyer, 1980). Table 3 shows the numbers of recently described species in parts of the *Flora of Panama*. There are certain areas of Panama, e.g. the Fortuna Dam area, where a single day of intensive collecting will usually yield one or more species of flowering plants new to science. Obviously collectors are penetrating such areas because they and others before them have searched them out, often under great hardship. Also, new roads have been opened in the republic in recent years and local landing strips and helicopter pads have been established in remote areas, often related to industrial or national projects. The collector is aware that pristine collecting grounds of today may fall prey to tomorrow's ax of destruction. Deference is due the Government of Panama for granting collecting permits to qualified collectors. Many institutions reciprocate by forwarding identified duplicate specimens to the Herbarium of the Universidad de Panamá, the national repository.

In conclusion, it is appropriate to pinpoint certain geographical areas of Panama which are "rich and recent" from the viewpoint of botanical collecting, at the same time acknowledging the pioneer efforts of the botanists. Such a listing is never complete. Only those localities botanized in realistic fashion for the first time between 1967 and the present are considered. Certain relatively new collecting areas, e.g. Cerro Jefe (Prov. Panamá from 1965) and Cerro Pirré (Prov. Darién from 1960) have not been included as their "discovery" predated 1967. Table 6 indicates how the various provinces of Panama have benefited from the attentions of different collectors.

- 1967—James Duke and Joseph Kirkbride, Jr. botanized from Chiriquí Grande (Prov. Bocas del Toro) to Caldera (Prov. Chiriquí).
- 1967—Walter Lewis, Thomas Croat, and Jon Hawker made important collections at Río Concepción (Prov. Veraguas). In the same year Will Blackwell and Mireya Correa A. made important collections at Santa Catalina.
- 1971—Thomas Croat collected from Guasimo (Prov. Colón) to Miguel de la Borda (Prov. Colón), using a canoe.
- 1973—Thomas Croat, Ronald Liesner and Philip Busey botanized in the tropical wet forest on the Burica Peninsula at Bartolo Limite–Rabo de Puerco area (Prov. Chiriquí), utilizing a vehicle. Today the road is overgrown.
- 1978—Robert Dressler pioneered in collecting from La Pintada (Prov. Coclé) to Coclecito (Prov. Coclé).
- 1975—Scott Mori was the first to collect at Cerro Colorado (Prov. Chiriquí), close to the Continental Divide, at an elevation of 1,200–1,500 m. Cerro Colorado is the site of a copper mine, easily accessible by road. Mori, together with Alwyn Gentry, explored botanically the summit of Cerro Tacacaruna, elev. 1,975 m, on the Panama-Colombia border.

- 1976—Thomas Croat collected in the Azuero Peninsula walking for 6 hours to the headwaters of the Río Pedregal (Prov. Los Santos) from Jobero in the same province, southwest of Tonosi.
- 1977—James Folsom began an era of rewarding collecting on the divide above El Cope (Prov. Coclé).
- 1978—Barry Hammel collected at two important sites: at Cerro Bruja (Prov. Colón) and the headwaters of the Río Indio and Río Boqueron (Prov. Panamá); from Gualaca (Prov. Chiriquí) to the Fortuna Dam site, proceeding to Cerro Hornito (Prov. Chiriquí).
- 1979—Barry Hammel collected at Cerro Pate Macho (Prov. Chiriquí, the Río Culebra (Prov. Chiriquí), as well as along the Río Concepción (Prov. Veraguas, especially at a one-man operated gold mine).

There is, of course, a limit to the number of species in Panama, as well as choice collecting sites. It is strange, however, that despite almost 300 years of collecting, the yield of novelties in our day is so great. Since the opening of the Panama Canal in 1914, more endemics have been described from the isthmus than between 1700 and 1913. The richness of the flora is a reflection of the soil and climate of this great tropical country. It is no less a tribute to the efforts of the botanists who have been so richly rewarded.

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## RESEARCH, TROPICAL ECOLOGY AND THE FUTURE OF PANAMA<sup>1</sup>

PETER H. RAVEN<sup>2</sup>

Me es muy grato estar presente esta noche para celebrar la feliz conclusión de la *Flora de Panamá*, una obra que ha ocupado la atención de científicos de varias instituciones por casi cuatro décadas. Iniciada por el Jardín Botánico de Missouri, la *Flora de Panamá* surgió de una larga y fructífera colaboración entre los científicos de la República de Panamá, de los Estados Unidos de Norteamérica, así como de otros países, y esperamos sinceramente que esta obra servirá para estimular un creciente interés y comprensión de las plantas de este hermoso país. La privilegiada posición geográfica de Panamá, uniendo América del Sur con América del Norte, y bañada tanto por el Atlántico como por el Pacífico, ha producido tal profusión y variedad de plantas, que Panamá reúne por sí sola tantas especies de plantas que todo el continente de Europa, un área doscientos veces más grande.

Las ponencias que hemos escuchado en este interesante simposio, tan hábilmente organizado por la Doctora Mireya Correa de la Universidad de Panamá y por el Doctor William D'Arcy del Jardín Botánico de Missouri, dan fé de la gran riqueza biológica de Panamá. Estas ponencias servirán de base para un nuevo libro sobre la historia natural del país, que se editará para celebrar la finalización de la *Flora*, y con miras a contribuir al aprecio y al uso racional de los recursos naturales del país.

Panamá está en condiciones especiales para hacer grandes aportes a la biología y agricultura tropical. Tiene una ubicación geográfica única e instituciones bien conocidas tanto nacional como internacionalmente. Por un lado, el futuro bienestar de sus ciudadanos dependerá en gran parte del uso inteligente de las informaciones disponibles acerca de los recursos naturales del país. Por otra parte, estas mismas instituciones, distinguidas tanto en ciencias básicas como aplicadas, pueden jugar un papel clave en el desarrollo de conocimientos para el beneficio de los seres humanos de toda la faja tropical del mundo.

Unas cuantas estadísticas ayudarán a demostrar cuán importantes serán estos conocimientos. Hace un siglo, los bosques tropicales húmedos ocupaban una superficie mucho mayor que Estados Unidos, México, y América Central juntos. Desde entonces, más de la mitad de estos bosques han sido talados o alterados, y con el actual ritmo de conversión, los bosques estarán totalmente destruidos dentro de treinta años. Por supuesto que el ritmo de destrucción es irregular, pero se calcula que en la mayor parte de la zona tropical, no quedarán áreas significativas de bosques húmedos tropicales dentro de veinte años. Para entonces, las dos terceras partes de la población mundial estará viviendo en zonas tropicales. Esta destrucción de bosques conducirá a una extinción masiva de animales y plantas, muchos de los cuales no pueden reproducirse fuera de los bosques primarios.

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Estas transformaciones de bosques, equivalentes a la desaparición, cada *dos* años, de un área de bosque natural del tamaño de toda la América Central, son la consecuencia del desarrollo de los recursos naturales para el aprovechamiento humano. Si fuese verdad que de estas transformaciones resultase un beneficio humano continuo, éstas serían bienvenidas; sin embargo, para una gran parte del trópico, sobre todo para las zonas actualmente ocupadas por los bosques húmedos tropicales, éste *no* es el caso. Nuestros conocimientos actuales simplemente no alcanzan sino para utilizar una porción mínima de estos suelos para la producción agrícola a largo plazo, y de esta manera, hay que considerar a los bosques y suelos como recursos naturales *NO* renovables. Así, nuestro gran desafío como científicos e investigadores en el trópico será el de *aplicar* nuestros conocimientos en el campo práctico para diseñar sistemas agrícolas y agroforestales a largo plazo, mientras luchamos por *concentrar* los sistemas más productivos en las tierras más idóneas. Si logramos acelerar el inventario de la flora y fauna tropical a la vez que adelantamos estudios intensivos de ecosistemas críticos, podremos unir la información necesaria para obtener soluciones prácticas, y ofrecer alternativas a las presiones y necesidades urgentes e inaplazables de una población creciente.

La tecnología de las zonas templadas, basada en milenios de experiencia de agricultura continua, *no se puede* aplicar a la mayoría del trópico; *poco* se hace actualmente para proveer la información tan indispensable para las zonas tropicales. Mientras tanto, la transformación de tierras para usos a corto plazo las hace inútiles para el futuro. De esto comentaré más adelante. Sin embargo, es precisamente en este área que Panamá puede aportar una contribución insustituible al bienestar humano y a su propia prosperidad.

Resumiendo, tenemos por delante una tarea difícil: la de armonizar el desarrollo económico y social de una población en aumento, con la preservación, aunque sea parcial, de un mundo biológico que todavía nos oculta sus mayores riquezas.

Panama, where the former island continent of South America was joined to North America about 3.1 million years ago (Keigwin, 1978; Marshall et al., 1979), is biologically one of the most critical and fascinating areas of the world's tropics. The plants and animals of South America, isolated for more than 100 million years, had an ultimate common origin with those of Africa. As South America converged on North America through the 65 million years of the Tertiary Period, its tropical biota, dispersed across the ever-narrower sea, invaded North America in greater and greater numbers. Panama, which has been occupied primarily by open savanna-type vegetation for much of the past three million years, provided the keystone linkage. For this reason, and because of its geographical situation, its 50,000 square kilometers are occupied by the richest and most diverse assemblage of plants and animals of any area of comparable size.

I have already mentioned that Panama has nearly as many kinds of flowering plants as all of Europe; it may also be pointed out that it has, in just over 52,000 km<sup>2</sup>, about a third as many species of flowering plants as all of tropical Africa (30,000 species), an area of 20 million square kilometers (Brenan, 1978)! Comparable figures could be provided for most groups of animals that are well enough

known to allow such calculations. They illustrate clearly that even by tropical standards Panama is exceptionally rich biologically. It is in fact this rich diversity of the plants and animals of Panama that is so properly a source of national pride, and the reason we have all gathered here for this most enjoyable symposium.

Adding to its special interest, Panama was the area where the last direct connection between the marine biota of the Atlantic and Pacific existed, and the area where this connection was finally severed three million years ago. As a result, Atlantic and Pacific marine plants and animals not only exist in close proximity, but they exist in such a way that three million years of divergence between the derivatives of some formerly continuous populations can be timed accurately—a natural evolutionary experiment without parallel.

For these and many other reasons, biologists historically have found Panama an exciting and interesting place in which to carry out their studies. Institutions such as the Universidad de Panamá, the Gorgas Memorial Laboratory, and the Smithsonian Tropical Research Institute (STRI) have made significant contributions to our knowledge of the biota of the Republic and their significance for man. A continued dedication to the importance of broadening this knowledge and utilizing it wisely in development has been signaled in recent years by the establishment of RENARE,<sup>3</sup> by the biological and ecological studies carried out under the auspices of IRHE,<sup>4</sup> and by the special position accorded to STRI under the terms of the Canal Treaty.

The Government of Panama has explicitly recognized the principles of conservation and wise management of land as the basis for sustainable development by the formation of RENARE, in which conservation and development are linked for the benefit of all the people of the Republic. Among the more notable recent accomplishments have been the active efforts to protect the watershed of the Canal, including both the projected reforestation schemes and the establishment by President Royo of the adjacent 24,000-hectare Parque Nacional la Libertad; the establishment of Barro Colorado Island as a nature monument and its scheduled enlargement in 1999 at the conclusion of the treaty period; the plans for national parks in Darién along the Colombian border, along the Costa Rican border, and surrounding Volcán Barú, the highest mountain in the Republic, in the western highlands; the consistent efforts by IRHE and other agencies to conduct meaningful biological and ecological inventories before carrying out large-scale public works; and the educational components included in many of these efforts.

Notwithstanding the great biological interest in the natural resources of Panama, the government's clear realization that the prosperity of the people rests upon the wise utilization of these resources, and the current implementation of many outstanding efforts to realize the consequences of this relationship, very serious problems face the Republic. These problems are, for the most part, shared with the other countries of the tropics, where, as already pointed out, some two-thirds of the world's population will be living by the end of the 20th century.

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<sup>3</sup> RENARE: Dirección Nacional de Recursos Naturales Renovables.

<sup>4</sup> IRHE: Instituto de Recursos Hidro-Eléctricos.

Although the populations of most tropical countries are growing very rapidly—many at a rate at which they will have doubled by early in the next century—population is by no means the only factor involved in the worldwide ecological crisis facing not only Panama but every other tropical country in the world. Panama itself provides a graphic illustration of this relationship. With just under two million people in some 50,000 square kilometers, Panama may be compared not only with the Netherlands, with some 14 million people inhabiting 41,000 square kilometers, but also with Java, which has some 90 million people living in an area only about two-and-a-half times the size of Panama (129,500 km<sup>2</sup>). The annual increase in the population of Java is nearly as great as the entire population of Panama! Granted that there are more extensive areas of relatively fertile soil in Java than in Panama, a comparison between the two regions, both located near the equator, illustrates graphically the way in which different patterns of land-use can affect population density. It also must be recognized that the relatively small population of Panama has already destroyed more than half of the original forest resources, and may, unless alternatives fostered by the Government prove effective, make short work of the rest.

In Java, the heavy utilization of naturally moist or irrigated rice-lands located on relatively fertile soils is an important element in the nutrition of the people. In addition, the homestead gardens of the rural people in Java provide a rich source of diverse foods, many of them derived from the native forests. Protein is largely provided by fish, some cultured, chickens, goats, and, in non-Moslem areas, by swine. In contrast, land use in Panama, particularly in the long-occupied and once relatively fertile deciduous-forest lands of the Azuero Peninsula, as Stanley Heckadon has emphasized earlier in this symposium, is based on “roza” grain agriculture followed by cattle pasture. These uses are highly destructive of the fertility of the soil when the density of people practicing them becomes too great, and large numbers of *santeños* (from Los Santos Province, on the Azuero Peninsula) are now emigrating to other areas, with potentially serious consequences to which we shall turn our attention later.

Panama is in the fortunate situation of being able to derive much of its income from world trade, but, despite this, the wise use of natural resources is still of basic importance for the country. There is much to be said for regional and local self-sufficiency in a world in which the current energy crisis is just the first symptom of worldwide shortage of raw materials of all kinds that fuels inflation everywhere. No one can guarantee the continued operation of the world economic system under growing pressures of this magnitude, and if Panama is to feed, clothe, and shelter twice as many people early in the next century at least as well as is possible now, or actually to better their lot, the country will need to make extremely wise and forward-looking decisions about the proper utilization of its resources now.

These decisions ideally should be made against a background of continued attention to slowing the rate of population growth as much as possible. This will be extremely difficult at first, with about 43 percent of the population under 15 years of age, but the individual prosperity of fewer people utilizing an identical set of resources in the future will obviously be greater than otherwise. For this reason, the continuing efforts of the Government to decelerate the rate of growth

of Panama's population appear to be well justified, despite the apparent paradox of the *relatively* low population level as compared with those of other areas.

The principal elements necessary for improving the lot of the Panamanian people are the same as those necessary throughout the tropics of the world. They are all related to the search for finding ways to implement agricultural, forestry, or other kinds of systems that will sustain human life on areas now occupied with different kinds of natural vegetation, on a diverse array of tropical soils. The most direct reason that the population density (40 people per km<sup>2</sup>) of Panama cannot, with the application of present technology, equal that of the Netherlands (340 per km<sup>2</sup>), where the per capita gross national product is nearly six times as high as it is in Panama, is that we simply do not know how to utilize most soils of Panama, or most other tropical soils, in as productive a way as is possible in many temperate regions.

National schemes have not governed the patterns of land use in Latin America in the past, any more than they have governed the patterns of land use in other regions of the world. What is a problem, however, is that when forest is cleared in most temperate regions, or prairies are plowed, the resulting fields are productive and, with proper management, remain so indefinitely. The kinds of agriculture that function well in temperate regions, however, cannot be transferred wholesale to the tropics, and it is our collective tragedy that we are just starting to act upon the consequences of this fact. The current estimate of Brazilian officials is that no more than 0.3 percent of the Amazon forest can be put into sustainable agriculture, and although the soils of Panama are generally better, the sad truth is that no one really knows how to manage most of those now occupied by moist forest for sustained yield once they are cleared. There is virtually no tropical deciduous forest left in Panama today, and the agricultural practices which have ruined the fertility of this potentially more productive region are now being transferred to the humid lowland forests of the Darién and of Bocas del Toro on the western part of the Caribbean slope, where they will produce food for only a year or two, instead of a decade or two. There is urgency in attempting to restore the fertility and productivity of the ravaged Azuero Peninsula, but technology known at present will not allow the sustained cultivation of the Darién or the Caribbean forests. Where, then, are the hungry santeños to turn?

The moist forests that still persist in the northwestern and eastern portions of the Republic are inhabited by the richest and most diverse array of plants and animals of the entire Central American region. Some of them might be useful directly as sources of human food, shelter, energy, medicine, or for other purposes, but the only hope of discovering the extent to which this may be true will be to survey these forests biologically as rapidly as possible and to concentrate in the course of these studies on groups of organisms of known or suspected economic importance. In addition, as much as possible should be learned about the functioning of the undisturbed forest that exists in these regions, because only such knowledge offers hope of utilizing them on a sustainable basis or modifying them into some other form from which useful products could be derived. Meanwhile, because these forests cannot, by and large, be put into sustainable agricultural use with currently available technology, the forests should be conserved to the greatest extent possible while we are gaining knowledge, and the modifi-

cations that are allowed meanwhile should be as limited as possible in order to help secure the future prosperity of the country. These deceptively rich and productive-looking forests are simply not a suitable locale for most kinds of development, and such development can, in most cases, lead only to their total depletion, often with severe economic loss to those responsible.

For reasons just outlined, both the citizens of Panama and those who live elsewhere have genuine reason to applaud the establishment of the Darién Frontier National Park and the strategic plans that are being developed for the proper management of this area under the guidance and supervision of RENARE. The coöperation between Panama and Colombia that has made possible the progress to date has also been evident in the development of the 200,000 hectare Parque de la Amistad on the Cordillera de Talamanca between Panama and Costa Rica. Of equal importance are the efforts to reforest large denuded sections of the Panama Canal, and for the management of the Volcán Barú park, including the integral management of the Rio Caldera watershed.

Commendable as these schemes for preservation and restoration of natural resources are, however, the real problem facing Panama is how to guarantee people an adequate diet without wrecking the natural resources of the country completely—in other words, how to utilize the land on a sustainable basis, and to make the connotation of the word “renovable” in RENARE meaningful. These are global themes, and they have been stated with exceptional clarity and force in the World Conservation Strategy, promulgated by the International Union for the Conservation of Nature and Natural Resources (IUCN) in early March of this year. Throughout the tropics of the world, both multinational corporations, which presumably have a choice, and the peasant poor, who for the most part do not, are rapidly destroying the productive ecological systems on which human livelihood depends, without the creation of viable alternatives. The solution, both for Panama and throughout the tropics, depends upon a reversal of the forces that are destroying these ecological systems. Some of the elements that might be involved include the following:

Afforestation schemes for the protection of watersheds, such as those that are currently being conducted by RENARE in the watershed of the Canal and elsewhere, and by IRHE around the Bayano Dam, are of special importance. The establishment of forest plantations and of areas devoted to agro-forestry, coupled with soil conservation measures and the improvement of pastures on areas that can sustain cattle grazing, all have immediate desirable consequences, among them the provision of employment for rural populations. National policy can help to prevent the institutional squandering of the national patrimony of forest resources for short-term gain, but only the provision of employment and the ability to feed their children properly can divert the santeños from the moist forests of the northwest and east, where they can cut off the trees and grow a crop or two before the soils are depleted.

Panama will be well served by learning as much as possible about its existing natural resources and by applying the information gained as directly as possible to their sustainable utilization. In this process, the traditional national institutions such as the universities have a vital role to play, and they should be funded in such a way that they can make the contribution of which they are capable, at the

same time that new institutions are established. Meanwhile, the land should be developed as wisely as possible, with highly productive modes of agriculture concentrated in areas, such as perhaps portions of Chiriquí Province, where they can be carried out on a sustainable basis. Large-scale irrigation schemes should be developed elsewhere in appropriate areas to further the concentration of productive agriculture. Much more attention needs to be paid in Panama and everywhere else in the tropics to the improvement of the lot of rural agriculturists, and information needs to be brought as efficiently from other areas of the world with similar climates to be used locally. For example, *Brosimum alicastrum* is a tree crop well known in southern Mexico as a highly productive source of flour that can be grown in many forest soils. Might it not be just as suitable for cultivation in portions of Panama?

There is a worldwide crisis that threatens all portions of the tropics. During the course of the next generation, a majority of all undisturbed tropical forest will be modified for human use, and hundreds of thousands of species of plants and animals will become extinct. Only the prompt accumulation of knowledge and its direct application to human welfare will help to ameliorate the situation; the traditional *laissez-faire* outlook on the operation of multinational concerns and neglect of the welfare of rural farmers that characterize all too many tropical countries will only serve to make the situation worse.

In this situation, it seems possible that Panama, a country blessed with abundant and diverse kinds of plants and animals, relatively fertile soils, a varied topography, the presence of several significant international institutions, the worldwide interest of ecologists and other biologists, a well conceived governmental program that links conservation and the wise use of natural resources with development according to ecologically sound principles, and an impressive array of resident scientists and of national institutions, will be able to make a significant contribution. If Panama can continue to expand and to accelerate its efforts at intelligent self-development, this small country, located at the crossroads of North and South America, of the tropical Atlantic and Pacific, and forming one of the most intense zones of contact between Hispanic and Anglo-American culture, has the potentiality of contributing in a significant way to the destiny of other countries throughout the tropics of the world. We who have come here to celebrate the completion of the *Flora of Panama* pledge ourselves to help as much as we can in striving to attain that transcendently important goal.

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## CONTRIBUTORS TO THE *FLORA OF PANAMA*

The over one-hundred contributors to families or parts of families to the *Flora of Panama* are listed below, together with their institutional affiliation when the contribution was published. When multiple authors are listed, the institution is always that of the first: the institution of the other will be found in a listing at the second author's name. Some authors published from two institutions, and an asterisk (\*) is used to indicate those families published while at the second address.—W. G. D'ARCY

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ALLEN, C. K. Missouri Botanical Garden.	Lauraceae.
ALLEN, P. H. Missouri Botanical Garden.	Orchidaceae (part).
AMSHOFF, G. J. H. State University of Utrecht.	Myrtaceae.
AUSTIN, DANIEL F. Missouri Botanical Garden. Florida Atlantic University.*	Convolvulaceae*; Polemoniaceae; Trigoniaceae.
BAILEY, L. H. Cornell University.	Palmae [Palmaceae]; Rosaceae: <i>Rubus</i> .
BARKLEY, T. M. Kansas State University.	Compositae: Senecioneae.
BLACKWELL, WILL H., JR. —— & DODSON. Missouri Botanical Garden.	Loganiaceae; Sapotaceae. Anacardiaceae.
BURCH, DEREK & WEBSTER. Missouri Botanical Garden.	Euphorbiaceae.
BURGER, W. C. Missouri Botanical Garden.	Moraceae: <i>Sorocea</i> .
BUSEY, PHILIP. University of Florida Agricultural Research Center, Ft. Lauderdale.	Compositae: Elephantopidinae.
CANNE, JUDITH M. University of Guelph, Guelph, Ontario, Canada.	Compositae: Galinsoginae.
CONSTANCE, L. & MATHIAS. University of California, Berkeley.	Umbelliferae.
CORREA, A., M.D. & TAYLOR, B. Universidad de Panamá.	Droseraceae.
CROAT, THOMAS B. Missouri Botanical Garden. —— & CUATRECASAS.	Gnetaceae; Hydrophyllaceae; Sapindaceae; Staphyleaceae. Malpighiaceae.
CUATRECASAS, JOSÉ. Smithsonian Institution. —— & CROAT.	Brunelliaceae; Sterculiaceae: <i>Theobroma</i> . Malpighiaceae.
DANDY, J. E. British Museum (N.H.).	Magnoliaceae; Winteraceae.

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TABLE I. CONTINUED

D'ARCY, W. G. Missouri Botanical Garden.	Basellaceae; Bataceae; Callitrichaceae; Capparaceae—Tovarioideae; Caprifoliaceae; Ceratophyllaceae; Cistaceae; Compositae: Introduction, Anthemideae, Astereae, Coreopsidinae, Heliantheae—introduction, Helianthinae, Inuleae; Guttiferae; Hippocastanaceae; Leguminosae: <i>Abrus</i> , <i>Calopogonium</i> , <i>Canavalia</i> , <i>Centrosema</i> , <i>Cologania</i> , <i>Cymbosema</i> , <i>Galactia</i> , <i>Mucuna</i> , <i>Pachyrhizus</i> , <i>Pueraria</i> , <i>Stizolobium</i> , <i>Teramnus</i> , <i>Trifolium</i> , <i>Ilex</i> ; Oleaceae; Pedaliaceae; Plantaginaceae; Quiinaceae; Salicaceae; Scrophulariaceae; Solanaceae; Styracaceae; Symplocaceae; Theophrastaceae.
—— & DWYER.	Leguminosae: <i>Erythrina</i> .
—— & LACKEY.	Leguminosae: <i>Macroptilium</i> , <i>Phaseolus</i> , <i>Vigna</i> .
—— & POSTON.	Leguminosae: <i>Lablab</i> .
—— & TOMB.	Compositae: Lactuaceae.
—— & SCHANEN.	Erythroxyllaceae.
DEN HARTOG, C. Rijksherbarium, Leiden.	Hydrocharitaceae.
DEROON, A. C. State University of Utrecht.	Marcgraviaceae.
DEWOLF, G. D., JR. University of Cambridge, Cambridge.	Moraceae: <i>Ficus</i> .
DILLON, MICHAEL O. Field Museum of Natural History.	Leguminosae: <i>Acosmium</i> , <i>Aeschynomene</i> , <i>Alysicarpus</i> , <i>Ateleia</i> , <i>Chaetocalyx</i> , <i>Dussia</i> , <i>Myroxylon</i> , <i>Ormosia</i> , <i>Zornia</i> .
DODSON, CALAWAY H. Missouri Botanical Garden.	Anacardiaceae; Coriariaceae.
—— & ROBYNS.	Hippocrateaceae.
DUKE, J. A. Missouri Botanical Garden.	Amaranthaceae; Berbaridaceae; Caryophyllaceae; Ceratophyllaceae; Chenopodiaceae; Monimiaceae; Myristicaceae; Nymphaeaceae; Polygonaceae; Ranunculaceae.
DUNN, DAVID, B. University of Missouri, Columbia.	Leguminosae: <i>Lupinus</i> .
DURKEE, L. H. Grinnell College, Grinnell, Iowa.	Acanthaceae.
DWYER, JOHN D. Missouri Botanical Garden.	Leguminosae: Papilionoideae; Ochnaceae; Rubiaceae.
—— & D'ARCY.	Leguminosae: <i>Erythrina</i> .
EDWIN, GABRIEL. Field Museum of Natural History.	Aquifoliaceae.
—— & HOU. Roosevelt University, Chicago.	Celastraceae.
ELIAS, THOMAS S. Missouri Botanical Garden. The Carey Arboretum, Millbrook, New York.*	Compositae: Vernoniinae*; Menyanthaceae; Cyrillaceae; Balsaminaceae; Vitaceae.
——* & PORTER*.	Rutaceae*.



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——* & ROBYNS*.	Gentianaceae*.
EPLING, CARL C. & NOWICKE. University of California, Los Angeles.	Labiatae.
EXELL, A. W. British Museum (N.H.).	Combretaceae.
FANTZ, PAUL R. North Carolina State University.	Leguminosae: <i>Clitoria</i> .
FRIES, R. E. University of Uppsala.	Annonaceae.
GARDNER, ROBERT C. Ohio State University.	Compositae: Cardueae.
GENTRY, ALWYN H. Missouri Botanical Garden.	Bignoniaceae; Buxaceae; Humiriaceae; Rafflesiaceae; Sabiaceae.
GLEASON, H. A. New York Botanical Garden.	Melastomataceae.
GREGORY, D. P. Missouri Botanical Garden.	Rhizophoraceae.
HAYNES, ROBERT R. Ohio State University.	Orobanchaceae.
—— & WENTZ.	Najadaceae; Potamogetonaceae.
HERMANN, F. J. United States Department of Agriculture, Beltsville, Maryland.	Leguminosae: <i>Lonchocarpus</i> .
HERRERA-MACBRYDE, OLGA & LEWIS. Missouri Botanical Garden.	Polygalaceae.
HOU, DING & EDWIN. Rijksherbarium, Leiden.	Celastraceae.
HOWARD, R. A. The Arnold Arboretum of Harvard University	Icacinaceae; Polygonaceae: <i>Coccoloba</i> .
HUNTER, GORDON E. Murray State College, Murray, Kentucky.	Dilleniaceae.
JONKER, F. P. State University of Utrecht.	Burmanniaceae.
KEIL, DAVID J. Ohio State University.	Compositae: Tageteae.
KILLIP, E. P. Smithsonian Institution.	Amaryllidaceae: <i>Bomarea</i> ; Urticaceae.
LACKEY, JAMES A. & D'ARCY. Smithsonian Institution.	Leguminosae: <i>Macroptilium</i> , <i>Phaseolus</i> , <i>Vigna</i> .
LEWIS, WALTER H. Missouri Botanical Garden.	Dichapetalaceae.
—— & HERRERA-MACBRYDE.	Polygalaceae.
LOURTEIG, ALICIA. Laboratoire de Phanérogamie, Paris.	Oxalidaceae.
LUNDELL, CYRUS LONGWORTH. Texas Research Institute, Renner.	Myrsinaceae.
LUTEYN, JAMES L. & WILBUR. New York Botanical Garden.	Ericaceae.

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MACBRYDE, BRUCE. Missouri Botanical Garden.	Geraniaceae.
MANNING, W. E. Bucknell University.	Juglandaceae.
MATHIAS, M. E. & CONSTANCE. University of California, Los Angeles.	Umbelliferae.
MAXWELL, RICHARD H. Indiana University Southeast, Albany.	Leguminosae: <i>Dioclea</i> .
MCCCLINTOCK, ELIZABETH. California Academy of Sciences.	Saxifragaceae.
MCLAUGHLIN, LEO & WINDLER. Towson State College, Towson, Maryland.	Leguminosae: <i>Croatalaria</i> .
MCVAUGH, R. University of Michigan.	Rosaceae.
MEYER, FREDRICK G. National Arboretum, Washington, D.C.	Valerianaceae.
MOLDENKE, H. N. New York Botanical Garden. 303 Parkside Road, Plainfield, N.J.*	Avicenniaceae*; Eriocaulaceae; Verbenaceae*.
MORTON, C. V. Smithsonian Institution.	Dioscoreaceae; Smilacaceae.
MULLER, C. H. University of California.	Fagaceae.
MUNZ, P. A. Rancho Santa Ana Botanic Garden.	Onagraceae.
NEVLING, L. I., JR. Missouri Botanical Garden.	Aizoaceae; Araliaceae; Balanophoraceae; Chloranthaceae; Corylaceae; Lacistemaceae; Lythraceae; Myricaceae; Olacaceae; Opiliaceae; Portulacaceae; Proteaceae; Ulmaceae.
NOWICKE, JOAN W. Missouri Botanical Garden.	Apocynaceae; Boraginaceae; Rhamnaceae.
—— & EPLING.	Labiatae.
PFEIFER, H. W. Missouri Botanical Garden.	Aristolochiaceae.
PORTER, DUNCAN M. Missouri Botanical Garden.	Bursaraceae; Simarubaceae; Zygophyllaceae.
—— & CUATRECASAS. National Science Foundation.	Brunelliaceae.
—— & ELIAS. Virginia Polytechnic Institute, Blacksburg.	Rutaceae.
POSTON, MURIEL E. Howard University, Washington, D.C.	Leguminosae: <i>Cajanus</i> , <i>Flemingia</i> , <i>Rhynchosia</i> .
—— & D'ARCY.	Leguminosae: <i>Lablab</i> .
PRANCE, GHILLEAN T. New York Botanical Garden.	Caryocaraceae.
RAEDER, KATHERINE. Missouri Botanical Garden.	Phytolaccaceae.

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RHODES, D. G. Missouri Botanical Garden.	Menispermaceae.
RIZZINI, C. T. Jardim Botânico, Rio de Janeiro.	Loranthaceae.
ROBERTSON, KENNETH R. Missouri Botanical Garden.	Clethraceae.
ROBSON, NORMAN K. B. British Museum (N.H.).	Hypericaceae.
ROBYNS, ANDRÉ. Missouri Botanical Garden.	Bixaceae; Bombacaceae; Cochlospermaceae; Flacourtiaceae; Malvaceae; Sterculiaceae; Theaceae; Tiliaceae; Turneraceae; Violaceae; Vochysiaceae.
—— & ELIAS. Jardin Botanique National de Belgique, Miese.	Gentianaceae.
ROLLINS, R. C. Gray Herbarium.	Cruciferae.
SCHANEN, NOEL & D'ARCY. Missouri Botanical Garden.	Erythroxylaceae.
SCHERY, ROBERT W. Missouri Botanical Garden.	Leguminosae: Caesalpinoideae; Mimosoideae; Pontederiaceae.
—— & SCHUBERT.	Begoniaceae.
SCHUBERT, B. G. The Arnold Arboretum.	Leguminosae: <i>Desmodium</i> .
—— & SCHERY.	Begoniaceae.
SIMPSON, BERYL BRINTNALL. Smithsonian Institution.	Compositae: Mutiseae.
SMITH, C. EARLE, JR. Crops Research Division, Agricultural Research Service, U.S.D.A., Beltsville, Maryland.	Elaeocarpaceae; Meliaceae.
SMITH, LYMAN B. Smithsonian Institution.	Bromeliaceae.
SPARRE, BENKT. Swedish Museum of Natural History, Stockholm, Sweden.	Tropaeolaceae.
SPELLMAN, DAVID L. Missouri Botanical Garden.	Asclepiadaceae.
STANDLEY, P. C. Field Museum of Natural History.	Araceae.
STUESSY, TOD F. Ohio State University.	Compositae: Ambrosiinae, Melampodiinae, Ziniinae.
SVENSON, H. K. Brooklyn Botanic Garden.	Cyperaceae.
SWALLEN, J. R. Smithsonian Institution.	Gramineae.
TAYLOR, PETER. Royal Botanic Gardens, Kew.	Lentibulariaceae.
TAYLOR B., A.S. & CORREA. Universidad de Panamá.	Droseraceae.

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TOMB, A. SPENCER & D'ARCY. Kansas State University.	Compositae: Lactuaceae.
VAN ROYEN, P. Rijksherbarium, Leiden.	Podostemonaceae.
VERHOEK-WILLIAMS, SUSAN. Missouri Botanical Garden.	Plumbaginaceae; Primulaceae.
VIVALDI, JOSÉ L. Universidad de Puerto Rico.	Malpighiaceae: <i>Malpighia</i> .
WEBSTER, GRADY L. & BURCH. University of California, Davis.	Euphorbiaceae.
WENTZ, W. ALAN & HAYNES. Ohio State University.	Najadaceae; Potamogetonaceae.
WHITE, F. University of Oxford, Oxford, England.	Ebenaceae.
WHITE, PETER S. Uplands Field Laboratory, Great Smoky Mts. National Park, Gatlinberg, Tennessee.	Leguminosae: <i>Barbiera</i> , <i>Cracca</i> , <i>Dalea</i> , <i>Diphysa</i> , <i>Gliricidia</i> , <i>Indigofera</i> , <i>Lennaea</i> , <i>Sesbania</i> , <i>Sophora</i> , <i>Stylosanthes</i> , <i>Tephrosia</i> , <i>Willardia</i> .
WILBUR, ROBERT L. Duke University, Durham, N.C.	Campanulaceae.
—— & LUTEYN.	Ericaceae.
WILLIAMS, L. O. Harvard University.	Orchidaceae (part).
WINDLER, DONALD R. & McLAUGHLIN. Towson State College, Towson, Maryland.	Leguminosae: <i>Crotalaria</i> .
WOODSON, R. E., JR. Missouri Botanical Garden.	Alismataceae [Alismaceae]; Amaryllidaceae; Bataceae [Batidaceae]; Butomaceae; Cactaceae; Cannaceae; Capparaceae [Capparidaceae]; Caricaceae; Commelinaceae; Connaraceae; Cornaceae; Crassulaceae; Cunoniaceae; Cycadaceae; Cyclanthaceae; Haemodoraceae; Haloragaceae [Haloragidaceae]; Hernandiaceae; Iridaceae; Juncaceae; Lecythydaceae; Lemnaceae; Liliaceae; Loasaceae; Maranthaceae; Mayacaceae; Moraceae; Moringaceae; Musaceae; Nyctaginaceae; Papaveraceae; Passifloraceae; Potamogetonaceae; Rapateaceae; Resedaceae; Salicaceae; Taxaceae; Thymelaeaceae; Tovariaceae; Triuridaceae; Typhaceae; Velloziaceae; Xyridaceae; Zingiberaceae.
YUNKER, T. G. De Pauw University.	Piperaceae.
WUNDERLIN, RICHARD P. University of South Florida.	Cucurbitaceae.

INDEXES TO THE FAMILIES  
IN THE  
*FLORA OF PANAMA*

The *Flora* was divided into numbered parts using Roman numerals. The systematic treatment of the families is complete as Parts II–IX and indexes follow. Part I is not missing: it will be used to publish “general discussions of historical, geographical, physiographic, and floristic relations” and other information pertaining to the *Flora of Panama*, as outlined in Woodson’s broadside (see pg. ii).

Early in the *Flora* program, families known or thought to occur in Panama were assigned a sequential series of numbers, “following generally the system of Engler and Prantl.” These are the Arabic numbers preceding each family name in the Systematic Index. A few families were found to occur in Panama as the project progressed, and they were assigned numbers and letters within the original sequence. Other families thought to occur in Panama have not been found there, but notes to this effect were published in the *Flora* series for completeness. Family names in the Systematic Index are followed by the volume(s), pages, and year(s) of the ANNALS in which they appeared.

Family names in the Alphabetical Index are followed by the volume number(s), pages, and year of the volume(s) of the ANNALS in which they appeared. Numbers in parentheses are the *Flora of Panama* part numbers (Roman numerals) and systematic family numbers (Arabic numerals) assigned to each family.  
—*M. R. Crosby*

SYSTEMATIC INDEX TO THE FAMILIES  
IN THE  
*FLORA OF PANAMA*

Family names are followed by the volume number(s), pages, and year of the volume(s) in which they appeared.

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