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MISSOURI BOTANICAL GARDEN

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25 YEARS OF BOTANY
1947–1972

INTRODUCTION

This volume contains a review of the progress in various fields of botany during the period following the Second World War. Taken together, the articles which make it up create a broad vista of the plant sciences, and they were written for this purpose by leaders in their fields so that researchers, teachers, and students could have readily available a summation of the high spots of our development during the highly productive quarter-century beginning in 1947.

The articles grew out of a symposium which was held at the University of Minnesota in connection with a joint meeting of all sections of the Botanical Society of America and the American Institute of Biological Sciences. The symposium, which was held on 28 August 1972, was convened not only to commemorate the close interactions of the Botanical Society of America and the American Institute of Biological Sciences, but also to present an historical summary of the major progress in botanical science.

The years 1947–1972 saw an explosion of scientific activity in the world like nothing which had preceded. Research productivity far exceeded anything known in the past. After the return to "peace," many nations greatly expanded public support for scientific research, including numerous, non-applied, "pure" disciplines. Stimulated, for example in physics, by the discoveries in nature of nuclear energy, and in biology, by the elucidation of the nature of the genetic code, governments—as well as foundations and private granting agencies—were willing to contribute vast sums of money. In some fields, indeed, science became practically an international race. Tied with this, we saw a trend of vast expansion of educational institutions to accommodate the rapidly burgeoning populations of students. Schools, colleges, and universities were enlarged, and many new ones came into existence. There was intense demand (often even competition) for new teachers and professors, and the number of doctoral theses in botany, as well as in other sciences, mushroomed, as did the number of new books and articles in journals. More and more interdisciplinary pursuits arose, and we watched the growth of new or modified fields, such as chemical systematics, numerical taxonomy, paleoecology, and molecular biology, to name a few.

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Over the past several years we have entered a new phase. Now that the distribution of research funds, the birth of new institutions, and the demand for teachers and professors have begun to plateau, and now that we are settling down to a more steady rate of activity, it seems desirable to record what happened in botany during the period of the "boom days," not only for its reference value to students of plant biology, but for its position in the history of science.

Our contributors were chosen by colleagues in their own disciplines as representing not only outstanding leaders themselves, but also as individuals who were well acquainted with and close to the growth in their respective subjects during the twenty-five year period. The articles fall into two categories—those concerned with the biology of the different plant groups per se, and those dealing with general biological disciplines as they pertain to plants. Thus we have articles on the fungi, the algae, the lichens, the bryophytes, and the pteridophytes. We did not have special articles on the seed plants, but many of the new developments in their study are embodied in the treatments of plant physiology, ecology, systematics, paleobotany, and palynology. In addition, for perspective, there is an article on the historical aspects of the study of plants for the period under survey.

To all those who contributed to the successful completion of this book we express our heartiest thanks, including those who helped in the selection of the subjects and the contributors, and in designing the format. I wish to thank the various persons in the Botanical Society of America who gave their time and energy to this project, in particular Barbara F. Palser, secretary, and Samuel N. Postlethwait, program chairman, for their help in getting the original symposium together, and Norman H. Boke, Harold C. Bold, and Charles Heimsch, of the committee appointed to oversee the publication. In particular we are indebted to the officers of the Missouri Botanical Garden, Peter H. Raven, director, and Marshall R. Crosby, editor, for their interest and help in bringing this volume together in its final form.—*W. H. Wagner, Jr., Ann Arbor, Michigan.*

25 **years of botany**

MYCOLOGY
1947–1972[1]

F. K. Sparrow[2]

Each of us will, I am sure, approach his staggering assignment in a different manner.

I propose to discuss what to me have been the outstanding contributions in the last 25 years to the following selected areas:

1. Cultivation of Rusts in axenic culture
2. Ultrastructure investigations
3. Sexuality
4. Hymenomycete Taxonomy
5. Marine Mycology
6. Helpful Books and Papers

At a year-a-minute I hardly knew what else to do. If you feel other choices should have been made, I can only say: I could not agree more with you.

1. Rusts in Axenic Culture

To most of us "rusts" conjure up visions of a truly elite group of well-ordered, tidy, absolutely obligate parasites. These are arrayed with a dazzling variety of spore forms, and from the investigations of the great de Bary, are known to be capable of leaping from one vascular plant host to another in regular sequence, much as a trapeze artist high up in the circus tent "floats through the air with the greatest of ease." To the old-line rust man these organisms have always seemed safe enough from the depredations and indignities of the physiologists and biochemists. But no more!

It might be said that starting with the successful work of the late Victor Cutter and his associates, a concerted attack was initiated by way of infected tissue culture of host material, to bring these obligate parasites into culture. They reported success in Apple Rust, Holyhock Rust and Jack-in-Pulpit Rust and secured saprophytic outgrowths into culture media. There followed in a few years in other laboratories a series of investigations on Flax Rust. Tissue

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[1] This paper was written when the topic was to be "20" rather than "25 years of botany." I am indebted to various colleagues for their opinions as to what should be included here. Particularly am I grateful to G. C. Ainsworth for suggestions. The anthropoid depicted in Fig. 1 is the creation of Prof. Frank Johnson, Princeton.

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culture of infected host material was used and mycelium and spores from cotyledonary calluses employed to inoculate agar dishes of special media on which saprophytic outgrowths of the rust were obtained. Dark leathery stromatic areas formed in these culture dishes and yielded on the binucleate mycelium spores resembling uredospores and teliospores. Even after 1½ years of subculture on artificial media the binucleate mycelium maintained its pathogenicity to explanted flax cotyledons when the inoculum was placed on their cut ends in culture.

Of general biological interest here was the fact that in cultures contaminated with other fungi, the slow-growing rust was quickly overrun and suppressed. This suggested that as a saprophyte it probably could not meet the competition it would encounter under natural conditions.

Stem Rust of Wheat has also been brought into axenic culture without recourse to infected host tissue culture. Here batches of uncontaminated uredospores from laboratory-infected plants were sown directly onto the solidified culture medium.

A good mycelial growth was obtained, and in a few cultures in the brown stroma which formed, uredospore-like and teliospore-like structures developed.

Cambial explants of pine infected with White Pine Blister Rust have been secured in tissue culture, and pycnia- and aecia-like sori produced.

Thus, representatives of five different rust genera (*Gymnosporangium, Uromyces, Puccinia, Cronartium,* and *Melampsora*) have been grown in culture. We can hope for a fruitful period ahead in rust physiology and biochemistry and significant contributions towards solving some of the riddles of obligate parasitism.

2. ULTRASTRUCTURE INVESTIGATIONS

It has been said that the electron microscope is having an effect on biology comparable with that of the optical microscope in the 17th century.

A study of the ultrastructure of both vegetative and reproductive parts of fungi has yielded much new information and has helped explain many puzzling "half-facts" obtained in the past by pushing the light microscope to its limits. For example, by light microscope, the cross walls of the basidiomycete hyphae were seen to be perforated and with barrel-shaped thickenings. With EM, however, the intricacy of what has been called the "dolipore" septum stands revealed. The necessity for such a complicated structure is not known. Dolipore septa have been said to be as characteristic of Basidiomycetes—certainly of Hymenomycetes—as basidia and clamp connections. They are indeed remarkable objects.

As elsewhere, the electron microscope has revealed in searching detail a wide variety of extranuclear bodies in the cell, and these findings have been exploited by the cell biologist, physiologist and even phylogenist. Let me give an example of the latter. The motile cells of fungi, primarily zoospores, have always seemed to me to provide one of the best clues to the interrelationships of zoosporic fungi, as well as to suggest the features of the ancestral stock from which they arose. Thus, the posteriorly uniflagellate Chytridiomycetes must have been derived from posteriorly uniflagellate ancestral stock.

Now, almost at its inception, EM work was directed towards the internal structure of motile cells of both algae and fungi and of their flagella. Incidently, a wondrous uniformity in flagellar structure was immediately apparent, *i.e.* that these whips were composed of two central fibrils surrounded by nine others. Much was also soon learned about the internal structure of the posteriorly uniflagellate Chytridiomycete zoospore. EM revealed for the first time a situation that would make even the most lethargic phylogenist squirm with joy in his padded armchair. There was clear evidence that near the basal apparatus of the single flagellum, which has its origin in the centriole, there was a second centriole, at an angle to it, and lacking a flagellum. This situation was quickly pointed to as evidence for the biflagellate origin of the Chytridiomycete line—the second centriole being considered a vestigial flagellum base. Recent further EM studies on the zoospore of another Chytridiomycete have shown that the functional centriole or kinetosome has a series of props which attaches it to the plasmalemma of the spore body. Such props have also been found on the non-functional centriole, strong evidence for the presence at one time of a functioning second flagellum. The chytrid ancestor would therefore be a biflagellate organism. Other features of this zoospore have been discovered. Thus incidental to a splendid series of papers over the years on the biochemical morphogenesis of the Chytridiomycete *Blastocladiella*, EM work revealed the presence of a remarkable, large, single mitochondrion, the "*seitenkörper*" of light microscopy. Furthermore, it was found in the related genus *Allomyces* that the prominent "nuclear cap" present in a more or less organized state in nearly all Chytridiomycetes, and first seen by light microscopy, was composed primarily of ribosomes. Examples such as these could be cited infinitum. I think all of us will agree that by means of this remarkable instrument, EM, a new dimension has been added to the study of fungi, and indeed to the study of all organisms.

3. SEXUALITY

Certainly one of the most interesting aspects of life even among fungi is sex. In this group, as elsewhere, sex assumes a variety of forms transcending even the most ingenious machinations of mere mammals.

The Fungi Imperfecti is an assemblage of well over 15,000 species thrown together because of the lack of a "perfect stage." Perfection here means possession of a sexual cycle. Over the years puzzlement has arisen as to how they have managed to meet so successfully during eons of time the evolutionary stresses to which they have been subjected, with no visible means of producing recombinants.

The crafty creatures have in fact been found to have invented a sub rosa sexual process, termed "parasexuality," which insures them the fruits of genetic recombination.

This was first worked out in the laboratory in the "Imperfect" *Aspergillus nidulans*, which also has a perfect (sexual) stage *Emericella nidulans*, a fact which made it possible to define clearly the features of the parasexual cycle. Parasexuality has as its first step "heterokaryosis." This has been defined as "the coexistence of genetically different nuclei in cytoplasmic continuity with one another" in hyphae. Hyphal anastomosis followed by nuclear migration through the lateral walls is probably the commonest, but not the only way, of producing a heterokaryon in a cell. Conjuate divisions in such heterokaryotic cells and subsequent migrations through pores in the cross walls spread the heterokaryotic condition throughout the mycelial mass. The sequence of stages in parasexuality in simplified form taken from Dr. Alexopoulos' well-known textbook is as follows:

1. Formation of heterokaryotic mycelium.
2. Fusion between two nuclei.
   a. Fusion between like nuclei.
   b. Fusion between unlike nuclei.
3. Multiplication of diploid nuclei side by side with the haploid nuclei.
4. Occasional mitotic crossing-over during the multiplication of the diploid-nuclei.
5. Sorting out of diploid nuclei.
6. Occasional haploidization of the diploid nuclei.
7. Sorting out of new haploid strains.

The "sorting out" is accomplished by single nuclei migrating out into conidia or non-sexual propagules, which are borne in chains on the swollen head of the conidiophore.

By such an "alternative to sex," a single thallus at Step 2 may have in varying numbers in its cells: haploid nuclei like those of contributing and receptive thalli; haploids with new genetic recombinations; and homozygous and heterozygous diploids. Since *Aspergillus nidulans* also has a sexual stage, recombinants obtained by old-fashioned sexual methods are available for comparison. It has been calculated that recombinations produced by parasexual methods are 500 fold less than those achieved by the sexual cycle. Nonetheless, when one considers the countless populations in nature with their millions of nuclei built up over many thousands of years, even such meager numbers "add up." Other Imperfecti, Ascomycetes, and even the Corn Smut fungus show capacities for parasexual reproduction. With great objectivity, the discoverers and workers with parasexuality very sensibly ask two questions: Does it operate in nature? Does it operate with adequate efficiency?

While on the general topic of sexual mechanisms, three other developments of recent years should be mentioned. The first of these is the location of meiosis in the sexual cycle. In certain Oomycetes such as *Pythium, Phytophthora, Achlya,* and *Dictyuchus* this is no longer thought to take place at the germination of the encysted zygote—the oospore—but in the sex organs themselves just prior to fertilization. The thallus is therefore diploid as are the zoospores. Both cytological and genetical evidence confirm this. On the other hand, in species of *Allomyces* with anisogamous sexual reproduction by swimming gametes and alternation of isomorphic gametophyte and sporophyte generations, meiosis takes place upon germination of thick-walled resting spores borne on the diploid sporophyte. Incidentally, in *Allomyces* interspecific hybrids have been produced from parental types belonging to polyploid series.

The second has to do with the sporadic occurrence of oospores in the Potato Blight fungus, *Phytophthora infestans.* Ever since de Bary's demonstration 99 years ago that this fungus was the cause of the devastating Irish Potato Blight—a disease not without political overtones on the national level in this country—interest centered on how it reproduced sexually. *Phytophthora* was eventually found to be bisexual with oogonia and peculiar amphigynous antheridia. Thick-walled oospores were produced, but only very rarely, even in culture. This was puzzling since sexual reproduction had been suspected of being an important source of observed variation in the pathogenesis of new isolates to resistant varieties of potatoes.

In recent years, with the mating type-idea in mind, numerous single-spore isolations from all over the world have been assembled and paired. In one investigation 109 isolates were obtained from the United States, Mexico, Western Europe, South Africa, and the West Indies. Abundant oospore production took place whenever any one of three particular Mexican isolates (four had been isolated) was paired with any one of the 106 others. That is, there evidently exists in this bisexual fungus two mating types, one represented by the three Mexican isolates and the second by the 106 others, from widely separated geographic localities. A further investigation of the strains existing in the vicinity of Mexico City revealed that of 95 isolates, the two mating types occurred in a ratio of approximately 1:1.

Mating type systems have also been found to occur in the Myxomycetes among the myxamoebae which fuse to form the diploid plasmodium. Incidentally, on the controversial question of the place of occurrence of meiosis, both new cytological observations and measurements at different stages of DNA content of plasmodium and spores, support the contention that this process takes place just prior to spore delimitation in the fruiting body.

A third area is that of sex hormones. There is a steadily accumulating body of evidence to support de Bary's postulate of the last century that what we now call hormones are active in the sexual systems of certain fungi. Such a single hormone has been clearly demonstrated to be active in the sexual reproduction of the Chytridiomycete *Allomyces*, a fungus on which so much other interesting and productive work has been done. This hormone has been isolated, chemically defined, and its empirical formula and molecular weight determined. Its name "SIRENIN" clearly conveys, I believe, just who does what here.

The equally classic demonstration, this time of a two-hormonal system, in the oogamous *Achlya bisexualis* is now a fixture in all mycology textbooks. In recent years Hormone A, produced of course, by the female plant, is active in inducing antheridial formation on the male plant. Furthermore, it has recently been isolated, chemically characterized and named "antheridiole." "Comehitherole" might be a better name.

Those of you over 30 years of age will remember I am sure, the Bread Mold-zygospore story from Elementary Botany. Among the Mucors ("Bread molds"), simple but elegant experiments have supported Burgeff's early work on the activity of hormones in zygophore attraction. Recent experiments have substantiated the theory that these hormones are volatile and are transmitted through the atmosphere.

The existence in ascomycetous yeasts of a hormone system active in the copulatory interactions between plus and minus strains involving conjugation tube-formation has been clearly demonstrated. In the heterothallic Ascomycete *Ascobolus* considerable evidence has been presented for the existence of a multi-hormonal system in the sexual process. Here, a spore-like oidium (male) and the trichogyne of an ascogonial (female) complex are involved.

These, and many other examples that might be cited, make it clear that the field of sexuality in fungi continues to offer a challenge to our investigative talents.

4. HYMENOMYCETE TAXONOMY

It has been estimated that about 1000 publications a year appear in the field of fungus taxonomy, of which the greatest number deals with the mushroom, toadstool, puff-ball complex. Papers on Imperfecti run a close second. Hymenial Basidiomycetes are beyond doubt the most popular objects among fungi, and legions of death-defying mycophagists roam the woods.

The past 25 years have seen a great change in the specialist's approach to Hymenomycete taxonomy. There has evidently been a final release from the shackles of the artificial Friesian classification of the early 19th century and the recognition that the "gross morphological features, on which it is based, were many times the result of parallel evolution." In both the fleshy Agaricales and the woody Aphyllophorales (bracket fungi, etc.) what has been termed the "hyphal approach" has been increasingly employed. Painstaking dissection-out of the hyphae, not mere sectioning, has resulted in the recognition of three basic hyphal types:

1. *Generative hyphae* with thin walls, more or less septate, and branched; with or without clamp connections. These hyphae give rise to the other types and to the hymenium bearing the basidia.
2. *Skeletal hyphae* with thick walls, septate or non-septate, branched or unbranched, straight or flexuous, with thin-walled apices.
3. *Binding hyphae* which are narrow, thick-walled, much-branched, non-septate, interwoven, and often coralloid. These bind the other types together, when they are in the same fruiting body.

These provide anatomical characters of considerable significance in detecting relationships. Using hyphal analysis, three main types of fruiting body anatomy, of increasing complexity, are recognized:

1. "Monomitic," with generative hyphae only.
2. "Dimitic," with generative and skeletal hyphae.
3. "Trimitic," with all three kinds.

This "mitic system" is now a well-established tool in the field, and its application along with traditional approaches to a study of interrelationships is resulting in a realignment in classification of familiar forms and providing a fresh stimulus to hymenomycete taxonomy.

5. MARINE FUNGI

It can certainly be said that the last two and one-half decades have seen a steady increase in investigations on marine fungi. This has been particularly true of saprobic species as compared with those found parasitic on marine algae and animals, which occupied the attention of the few early observers. Numbers of papers have appeared on the many Ascomycetes and Fungi Imperfecti which decay pilings and other wooden marine installations. Indeed, in the last 20 years, 60% of the nearly 200 species of lignicolous marine fungi now known have been discovered.

A second notable area of modern investigation has been certain zoosporic marine fungi. These are pelagic, non-filamentous forms which occupy the same ecological niche as marine bacteria. By means of simple baiting techniques they have been found everywhere they have been looked for, including Arctic and Antarctic waters. Quantitative and biochemical studies are presently being carried out on these oftentimes new and puzzling organisms, and we are learning something of their significance as detritus decomposers in marine ecosystems.

A third area of marine mycology has been the investigations on true marine yeasts. Near continental land masses yeasts are plentiful but with rare exceptions are usually terrestrial species of transitory status in marine waters, or adaptive forms which can survive both environments. In remote reaches of the ocean, dense yeast populations have "been associated with plankton zones rich in organic matter." Also, boundaries of water masses with opposing densities tend to accumulate organic matter, and these too have high yeast populations. Very recently, a variety of these fungi has been isolated from Antarctic waters, including representatives of new genera. Of great interest mycologically is the discovery that certain supposed species of *Candida* and *Torulopsis*, common "imperfect" yeasts, are, in fact, Heterobasidiomycetes with conjugating basidiospores, clamp connections and spherical, smut-like, binucleate teliospores (or chlamydospores). These upon germination give rise to four-celled heterobasidia and basidiospores. A self-sporulating phase has also been found.

It is evident that the open oceans have barely been touched by mycologists and that there exists here a rich field for investigation. Furthermore, microbiological research programs must take fungi into account in any ecosystem studies.

6. HELPFUL BOOKS AND PAPERS

Many helpful books and papers have been published in mycology in recent years, as well as new editions, brought up to date, of older standard treatises. The bibliography lists many of these, but to those interested, the 1971 edition of the *Dictionary of Fungi* put out by the Commonwealth Mycological Institute at Kew is the best source for tracking down major monographs in various areas. This dictionary is a notable contribution in itself, as attested by the fact that it is now in its sixth edition.

As to the future: It has been estimated that there are 250,000 species of fungi, about the same as flowering plants, of which about 100,000 have been named, leaving 150,000 yet to be found. About 1500–2000 species a year are

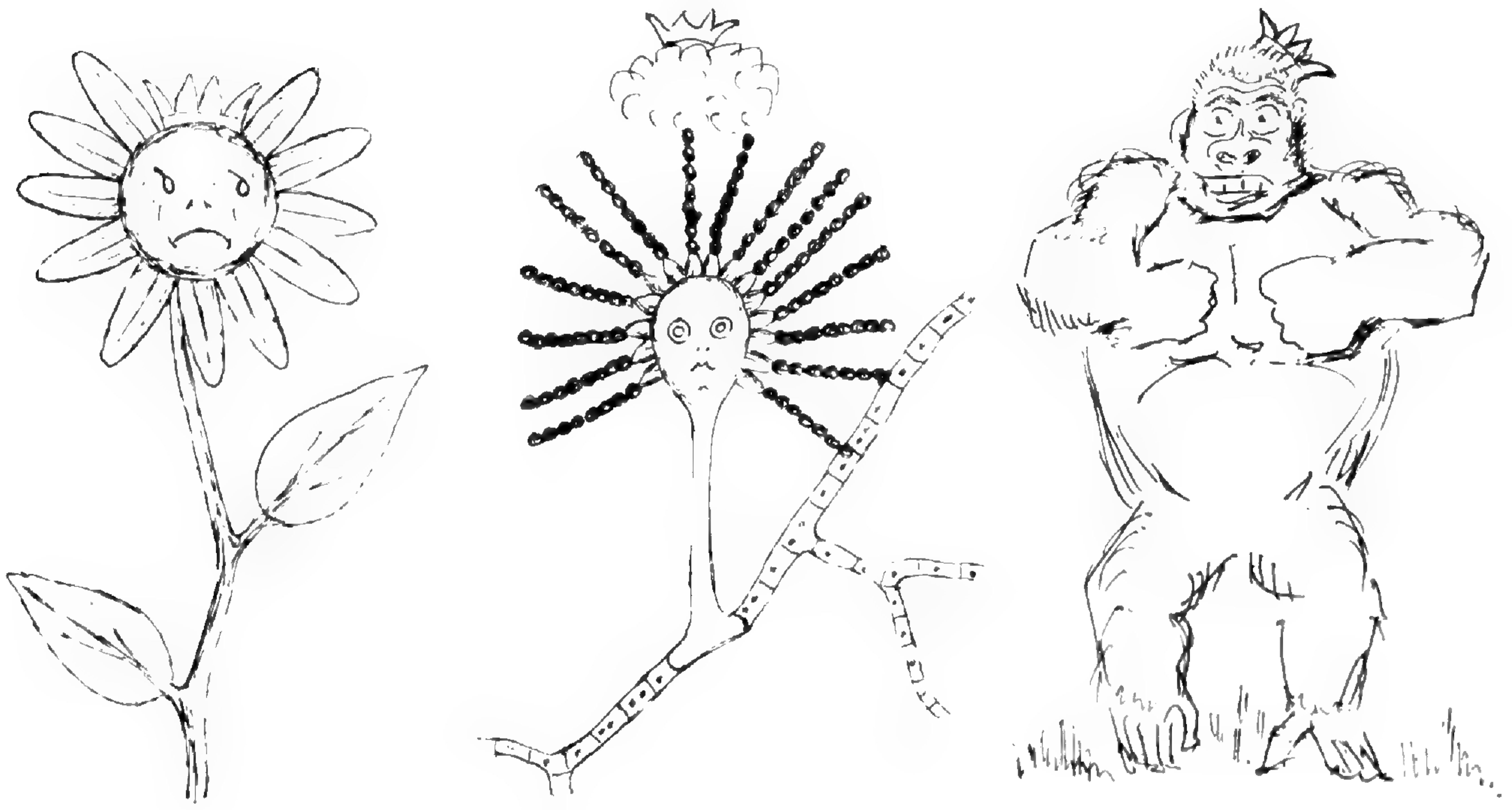

FIGURE 1. There are three kingdoms.

being described. With such rich picking I foresee nearly a century of continued exploration, especially in the tropics and oceans, which thus far have been relatively neglected. Among the forms yet to be found will be some which will prove admirable tools for various fundamental biological processes. Surely there must be at least two more Nobel Prizes to accompany the one awarded *Neurospora*! Let us hope, too, that considerable attention will be paid to the precise activities of fungi in the various ecosystems.

There has been no time to dwell on the newer approaches to phylogeny and relationships. Some papers on these are listed in bibliography.

One last development should perhaps be appended here and it is illustrated by the figure (Fig. 1). There has been a resurgence of the three-kingdom idea. I am all for it!

BIBLIOGRAPHY

RUST CULTURE

BUSHNELL, W. R. 1968. In vitro development of an Australian isolate of *Puccinia graminis* f. sp. *tritici*. Phytopathology 58: 526.

COFFEY, M. D., A. BOSE & M. SHAW. 1969. In vitro growth of gelatin suspensions of uredospores of *Puccinia graminis* f. sp. *tritici*. Canad. Jour. Bot. 47: 129.

———. 1970. In vitro culture of the flax rust, *Melampsora lini*. Canad. Jour. Bot. 48: 773.

CUTTER, V. M., JR. 1959 [1961]. Studies on the isolation and growth of plant rusts in host tissue cultures and upon synthetic media. I. *Gymnosporangium*. Mycologia 51: 248.

———. 1960. An axenic culture of *Puccinia malvacearum*. Amer. Soc. Bacteriol. Bull. 7: 26.

———. 1960 [1961]. Studies on the isolation and growth of plant rusts in host tissue cultures and upon synthetic media. II. *Uromyces aritryphyllii*. Mycologia 52: 726.

HARVEY, A. E. & J. L. GRASHAM. 1969. Growth of the rust fungus *Cronartium ribicola* in tissue cultures of *Pinus monticola*. Canad. Jour. Bot. 47: 663.

HOTSON, H. H. & V. M. CUTTER, JR. 1951. The isolation and culture of *Gymnosporangium juniperi-virginianae* Schw. upon artificial media. Proc. Natl. Acad. U.S.A. 37: 400.

TUREL, F. L. M. 1969. Saprophytic development of the flax rust *Melampsora lini*, race No. 3. Canad. Jour. Bot. 47: 821.

———. 1969. Low temperature requirement for saprophytic flax rust cultures. Canad. Jour. Bot. 47: 1637.

———. 1971. Pathogenicity and developmental differences of three saprophytically growing isolates of the flax rust fungus *Melampsora lini,* race 3. Canad. Jour. Bot. 49: 1993.

WILLIAMS, P. G., K. J. SCOTT & J. L. KUHL. 1966. Vegetative growth of *Puccinia graminis* f. sp. *tritici* in vitro. Phytopathology 56: 1418.

———, ——— & D. J. MACLEAN. 1967. Sporulation and pathogenicity of *Puccinia graminis* f. sp. *tritici* grown on an artificial medium. Phytopathology 57: 326.

ELECTRON MICROSCOPY

FULLER, M. S. 1966. Structure of the uniflagellate zoospores of aquatic Phycomycetes. Pp. 67–84, *in* "Colston Papers." No. 18. Butterworths, London.

KOCH, W. J. 1956. Studies of the motile cells of chytrids. I. Electron microscope observations of the flagellum, blepharoplast and rhizoplast. Amer. Jour. Bot. 43: 811. [There is a series of papers on this subject by Koch.]

MOORE, R. T. 1965. The ultrastructure of fungal cells. P. 95, *in* G. C. Ainsworth & A. H. Sussman (editors), "The Fungi." 1.

OLSEN, L. W. & M. S. FULLER. 1968. Ultrastructure evidence for the biflagellate origin of the uniflagellate fungal zoospore. Arch. Mikrobiol. 62: 237.

REICHLE, R. E. & M. S. FULLER. 1967. The fine structure of *Blastocladiella emersonii* zoospores. Amer. Jour. Bot. 54: 81.

SEXUALITY, MEIOSIS, AND HORMONES

ALEXOPOULOS, C. J. 1966. Morphogenesis in the Myxomycetes. P. 211, *in* G. C. Ainsworth & A. H. Sussman (editors), "The Fungi." 2.

——— & G. G. ZABKA. 1962. Production of hybrids between physiological races of the true slime mould *Didymium iridis.* Nature 193: 598.

BANBURY, G. H. 1954. Processes controlling zygophore formation in *Mucor mucedo.* Nature 173: 499.

———. 1955. Physiological studies in the Mucorales. III. The zygotropism of zygophores of *Mucor mucedo.* Jour. Exp. Bot. 6: 235.

BISTIS, G. N. 1956. Sexuality in *Ascobolus stercorarius.* I. Morphology of the ascogonium; plasmogamy; evidence for a sexual hormonal mechanism. Amer. Jour. Bot. 43: 389.

———. 1957. Sexuality of *Ascobolus stercorarius.* II. Preliminary experiments on various aspects of the sexual process. Amer. Jour. Bot. 44: 436.

BONNER, J. T. 1963. How slime molds communicate. Sci. Amer. 209(2): 84–93.

DEE, J. 1960. A mating type system in an acellular slime-mould. Nature 185: 780.

EMERSON, R. & C. M. WILSON. 1954. Interspecific hybrids and the cytogenetics and cytotaxonomy of *Eu-Allomyces.* Mycologia 46: 393.

GREGG, J. H. 1966. Organization and synthesis in the cellular slime moulds. P. 235, *in* G. C. Ainsworth & A. H. Sussman (editors), "The Fungi." 2.

GALLEGLY, M. E. & J. GALINDO. 1958. Mating types and oospores of *Phytophthora infestans* in nature in Mexico. Phytopathology 48: 274.

LEVI, I. D. 1956. Mating reaction in yeasts. Nature 177: 753.

MACHLIS, L. 1966. Sex hormones in fungi. P. 415, *in* G. C. Ainsworth & A. H. Sussman (editors), "The Fungi." 2.

PLEMPEL, M. 1957. Die Sexualstoffe der Mucoraceae. Arch. Mikrobiol. 26: 151.

———. 1960. Die zygotropische Reaktion bei Mucorineen. I. Mitteilung. Planta 55: 254.

ROMERO, S. & D. C. ERWIN. 1967. Genetic recombination in germinated oospores of *Phytophthora infestans.* Nature 215: 1393.

SANSOME, E. 1961. Meiosis in the oogonium and antheridium of *Pythium debaryanum.* Nature 191: 827.

———. 1963. Meiosis in *Pythium debaryanum* Hesse and its significance in the life-history of the Biflagellatae. Trans. Brit. Mycol. Soc. 46: 63.

SMOOT, J. J., F. J. GOUGH, H. A. LAMEY, J. J. EICHENMULLER & M. E. GALLEGLY. 1958. Production and germination of oospores of *Phytophthora infestans.* Phytopathology 48: 165.

THERRIEN, C. D. 1965. Microspectrophotometric analysis of nuclear deoxyribonucleic acid in some Myxomycetes. Ph.D. dissertation, Univ. Texas. [cited in Alexopoulos, 1966 above.]

WILSON, C. M. 1952. Meiosis in *Allomyces*. Bull. Torrey Bot. Club 79: 139.

——— & I. K. ROSS. 1955. Meiosis in the Myxomycetes. Amer. Jour. Bot. 42: 743.

HYMENOMYCETE TAXONOMY

CORNER, E. J. H. 1966. A Monograph of Cantherelloid Fungi. Oxford Univ. Press. 255 pp.

DONK, M. A. 1964. A conspectus of the families of Aphyllophorales. Persoonia 3: 199.

KORF, R. P. 1958. Japanese Discomycetes, 1–8. Sci. Rep. Yokohama Natl. Univ. Sect. 2. 7: 1–35.

SINGER, R. 1962. The Agaricales in Modern Taxonomy. J. Cramer, Weinheim. 915 pp.

——— & A. H. SMITH. 1960. Studies on secotiaceous fungi. X. The astrogastracous series. Mem. Torrey Bot. Club 21: 122. [There is a series of papers by these two authors on these fungi.]

MARINE FUNGI

BAHNWEG, G. & F. K. SPARROW. 1972. *Aplanochytrium kerguelensis* gen. nov., a new Phycomycete from subantarctic marine waters. Arch. Mikrobiol. 81: 45.

BELSKY, M. M. & S. GOLDSTEIN. 1964. Glucose metabolism of *Thraustochytrium roseum*, a nonfilamentous marine Phycomycete. Arch. Mikrobiol. 49: 375.

FELL, J. W., A. C. STATZELL, I. L. HUNTER & H. J. PHAFF. 1969. *Leucosporidium* gen. nov., the heterobasidiomycetous stage of several yeasts of the genus *Candida*. Antonie van Leeuwenhoek Ned. Tijdschr. Hyg. 35: 433.

GAERTNER, A. 1968. Die Fluktuationen mariner niederer Pilze in der Deutschen Bucht 1965 und 1966. Veröff. Inst. Meeresforsch. Bremerhaven. Sond. 3: 105. [There are many papers on marine fungi in this journal.]

———. 1969. Marine niedere Pilze in Nordsee und Nordatlantik. Ber. Deutsch. Bot. Ges. 82: 287.

GOLDSTEIN, S. 1963. Development and nutrition of a new species of *Thraustochytrium*. Amer. Jour. Bot. 50: 271.

——— & M. M. BELSKY. 1964. Axenic culture studies of a new marine Phycomycete possessing an unusual type of asexual reproduction. Amer. Jour. Bot. 51: 72.

JOHNSON, T. W., JR. & F. K. SPARROW. 1961. Fungi in Oceans and Estuaries. Cramer, Weinheim. xxii + 668 pp.

KOHLMEYER, J. 1960. Wood-inhabiting marine fungi from the Pacific Northwest and California. Nova Hedwigia 2: 293–343.

——— & E. KOHLMEYER. 1964. Synoptic Plates of Higher Marine Fungi. Ed. 2. Hafner, N.Y. 64 pp. [There is a long series of papers by the Kohlmeyers on these fungi.]

PHYLOGENY

BARKLEY, F. A. 1967. Outline Classification of Organisms. Hopkins Press, Providence, R.I. 25 pp. [Privately printed.]

BARTNICKI-GARCIA, S. 1970. Cell wall composition and other biochemical markers in fungal phylogeny. Pp. 81–103, *in* J. B. Harborne, "Phytochemical Phylogeny." Academic Press, New York.

CANTINO, E. C. & G. F. TURIAN. 1959. Physiology and development of lower fungi (Phycomycetes). Annual Rev. Microbiol. 13: 97.

COPELAND, H. F. 1956. The Classification of Lower Organisms. Pacific Books. Palo Alto, California.

HALL, R. 1969. Molecular approaches to taxonomy of fungi. Bot. Rev. 35: 285.

KLEIN, R. M. & A. CRONQUIST. 1967. A consideration of the evolutionary and taxonomic significance of some biochemical, micromorphological and physiological characters in Thallophytes. Quart. Rev. Biol. 42: 105.

KREISEL, H. 1964. Grundzuge eines natürlichen Systems der Pilze. G. Fischer, Jena. 245 pp.

LEJOHN, H. P. 1971. Relationships between uridine nucleotide sugar activation of glutamic dehydrogenases in fungi and existence of chitin and cellulose in their walls. Biochem. Biophys. Res. Commun. 42: 538.

———. 1971. Enzyme regulation, lysine pathways and cell wall structures as possible indicators of the major lines of evolution in fungi. Nature 231: 164.

LOVETT, J. S. & J. A. HASLBY. 1971. Molecular weights of the ribosomal ribonucleic acid of fungi. Arch. Mikrobiol. 80: 191.

MARTIN, G. W. 1955. Are fungi plants? Mycologia 47: 779.

STORCK, R. & C. J. ALEXOPOULOS. 1970. Deoxyribonucleic acid of fungi. Bacteriolog. Rev. 34: 126.

TYRRELL, D. 1969. Biochemical systematics and fungi. Bot. Rev. 35: 305.

WHITTAKER, R. H. 1969. New concepts of kingdoms of organisms. Science 163: 156.

HELPFUL BOOKS AND PAPERS

AINSWORTH, G. C. 1971. Dictionary of the Fungi. Ed. 6. Commonwealth Mycological Institute, Kew, Surrey. x + 663 pp.

——— & A. H. SUSSMAN (editors). The Fungi, an Advanced Treatise. Vol. 1. The Fungal Cell. 1965.—Vol. 2. The Fungal Organism. 1966.—Vol. 3. The Fungal Population. 1968.—Vol. 4. (and F. K. Sparrow) A Taxonomic Review with Keys. 1974.—Vol. 4a. Ascomycetes and Fungi Imperfecti.—Vol. 4b. Basidiomycetes and Lower Fungi.

ALEXOPOULOS, C. J. 1962. Introductory Mycology. Ed. 2. Wiley. xviii + 613 pp.

BURNETT, J. Y. 1968. Fundamentals of Mycology. Arnold. London. xiii + 546 pp.

EMERSON, R. 1958. Mycological organization. Mycologia 50: 589. [Aids to the presentation of fungi in teaching laboratory.]

GRAY, W. D. & C. J. ALEXOPOULOS. 1968. Biology of Myxomycetes.

HUGHES, S. J. 1953. Conidiophores, conidia and classification. Canad. Jour. Bot. 31: 577. [A fundamental paper on a new scheme for classification of conidiophore and conidium development in hyphomycetes. It is being followed in all new work on Hyphomycetes (Fungi Imperfecti).]

25 **years of botany**

PHYCOLOGY
1947–1972[1]

Harold C. Bold[2]

To condense the significant developments of 25 years of such a dynamic field as phycology into a 30-minute review is obviously impossible, so that in preparing this paper I have of necessity been selective and have omitted certain topics and publications which another reviewer might consider relevant. Furthermore, it is, of course, not feasible to cite all the authors and their research reports which have contributed to the phenomenal development of phycology during the last 25 years. One indication of this development is some statistics from *Biological Abstracts*. The 1948 volume contained 146 abstracts relating to algae, most of the papers abstracted having been published in 1947. In the 1971 volume 656 papers on algae were abstracted. To conserve space, in many instances, I have cited only the most current reference to a given topic, since the earlier literature would be referred to therein.

As I reflected on the development of phycology, not only during the past 25 years, but also that which I have been privileged to witness since my undergraduate student days (which began at the college level 46 years ago), two conclusions emerged clearly: (1) Phycology has broadened in scope, and its horizons have expanded to embrace aspects of the algae other than taxonomy and morphology. I do not mean here to deprecate these important aspects of the subject, which are as indispensable today as they always have been, but, as I plan to emphasize later, their achievements have been *enriched* by this increasingly broad scope. (2) Most of the major contributions to phycology became possible when phycologists began to grow algae in the laboratory instead of confining their efforts exclusively to the field and herbarium. Here again, I do not intend to minimize the contributions of these branches of phycology. Figure 1 presents my own views regarding the relationships of various areas of phycology. With few exceptions, advances in phycology have been achieved because investigators were using algae in unialgal or axenic cultures.

I would like now to comment briefly on improvements in algal culture

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Ann. Missouri Bot. Gard. 61: 14–44. 1974.

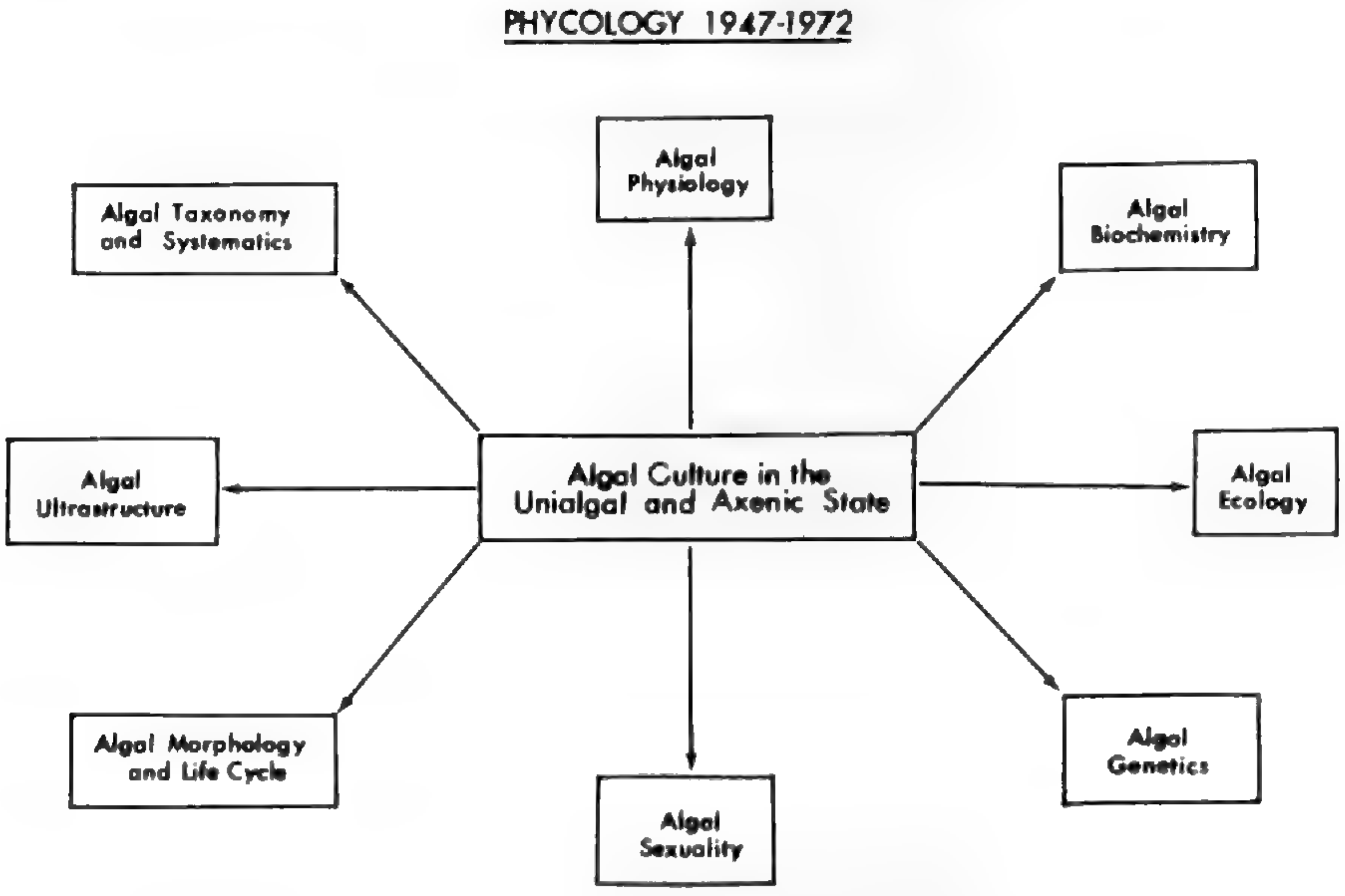

FIGURE 1. The relationships of the various fields of phycology.

methods and then to call to your attention significant developments in our knowledge of algal ultrastructure, morphology and life cycles, physiology, biochemistry, genetics and sexuality, and ecology. Some of these areas are inextricably related, so that there are alternatives of categorization regarding the data I am reviewing.

THE CULTIVATION OF ALGAE IN THE LABORATORY

The cultivation of algae in the laboratory, which probably had its inception in the laboratory of Famintzin (1871), became more widespread after Beijerinck (1890) in Holland isolated *Chlorella* from ditch water. The technique of algal cultivation was exploited by Klebs (1896) in Germany, by Chodat (1909, 1913) in Switzerland, and later by many others, so that already by 1942, in reviewing the subject (Bold, 1942), I was obliged to cite 503 significant references.

Progress in algal culture was greatly influenced by the broad microbiological outlook of E. G. Pringsheim which culminated in the publication of his small, but classical, book on the subject in 1946. Significant contributions in methods of algal culture have been the papers of Lewin (1959) and Provasoli and Pintner (1960). This microbiological approach has been responsible for the foundation and maintenance of the great culture collections of living algae such as those at Prague and later at Cambridge (England), Bloomington (Indiana), Göttingen, Paris, and Tokyo. The importance of such culture collections for the advancement of algal taxonomy, for which they serve as reference herbaria of living specimens, and for algal physiology and genetics, for which they supply pedigreed strains, cannot be sufficiently emphasized.

Although at first mostly species of freshwater green microalgae were cultivated, thanks to the investigations of Hämmerling (1931), who concocted "Erdschreiber" Medium; to Provasoli, McLachlan, and Droop (1957), Provasoli (1964, 1968), Stosch (1964), and Kornmann (1970), an ever-increasing diversity of marine algae has been taken into cultivation in the laboratory. Concomitantly, there has been an increase in the culture of algae from the soil and from specialized habitats, such as lithophilic algae and symbionts of various types. The long list and supplementary lists of algal cultures (Starr, 1964, 1971) available at the Indiana collection and in other collections testify eloquently regarding the great advances in algal cultivation.

While, in the not-too-distant past, it was necessary to ship living marine algae from the coasts to inland colleges and universities (and then only during the winter) to provide them for laboratory instruction, thanks to the culture media devised by those cited above, it is now possible and relatively simple to maintain living marine green, brown, and red algae and to demonstrate their life cycles in inland laboratories, without reference to season. One of the greatest advances for experimental work was the technique of synchronous culture (Hoogenhort, 1963). A great boon to those who culture marine algae was J. Lewin's (1966) report that germanium dioxide inhibits the growth of diatoms.

In application of improved culture methods, there have been great advances in the cultivation of algae as supplements for animal feeds, as food for increasing the growth rate and reproduction of economically important marine animals, and in the cultivation of species prized as human food. The recent report (McLachlan, Chen & Edelstein, 1971) of the cultivation of four species of *Fucus* in the laboratory, starting from zygotes, one of the species having been grown to sexual maturity, is certainly compelling evidence that the art of algal cultivation has advanced since the time of Famintzin (1871) and especially during the last 25 years. The fruits of these improvements in the cultivation of algae have made possible the striking advances in many other areas of phycology, a theme which I will continue to emphasize. Thankfully, the formerly often-repeated remonstrance that algae cultivated in the laboratory are "abnormal" or "atypical," with the naive implication that conditions in nature are always *uniformly* "normal" and "typical," is less prevalent than it used to be. Their significance has been considerably vitiated by comparative culture in field and laboratory such as in the investigations of Trainor (1965), Cox and Bold (1966), Druehl (1967) and Edwards (1969*a*, *b*, 1970), a practice which should be more widespread, as emphasized by Pringsheim (1967).

ALGAL TAXONOMY AND SYSTEMATICS

Although in 1972, algal taxonomy (and taxonomy in general) is viewed as too "traditional," "classical," or "static" by many of our more parochial colleagues, I nevertheless believe that it is here to stay, and that it will continue to play an indispensable role in other branches of phycology and biology. If any further evidence of the necessity for competent phycological taxonomists were lacking, such instances as the frequent confusion in the identity of strains of *Anacystis*, *Chlorella*, *Scenedesmus*, and *Phaeodactylum* (J. Lewin, 1958), all used extensively in physiological and biochemical investigations, should plead this need eloquently.

The past 25 years have witnessed the publication of a number of major summaries of regional floras and taxonomic treatments. Among others may be cited Dawson's (1963) *Marine Red Algae of Pacific Mexico*; Taylor's (1960) *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*; the revised edition of Prescott's (1962) *Algae of the Western Great Lakes Area*; Volume 1 of Patrick and Reimer's (1966) *Diatoms of the United States*; Hollenberg and Abbott's (1966) *Supplement to Smith's Marine Algae of the Monterey Peninsula*; and the three monumental volumes of Bourrelly (1966, 1968, 1970).

Round (1963, 1971), Christensen (1964), Hoek (1964), Prescott (1964), Papenfuss (1966), and Dixon (1970) have discussed some of the advances and problems of algal taxonomy, and Papenfuss (1955) has reviewed its history. It is clear that for many groups of algae and for many parts of the world, considerably more "basic taxonomy" is urgently required. For example, we have only recently begun to make progress in the taxonomy of soil algae (Bold, 1970), and there are many marine, freshwater, and edaphic sites on earth yet to be explored. Beyond this alpha level, however, the identification and classification of algae are coming to be based on an increasingly broad spectrum of criteria. Furthermore, it has become evident that for many algal species, field observations, and even study of herbarium specimens, are, of themselves, insufficient for the elucidation of identity and relationships. For example, the identity of *Derbesia* with *Halicystis*, of *Porphyra* with *Conchocelis*, and of *Trailliella* with *Bonnemaisonia* could never have been ascertained, had their complicated life cycles not been elucidated in laboratory cultures.

More and more during the last 25 years, phycologists have turned to studies of populations in the field and in laboratory cultures in seeking solutions to taxonomic problems. Stanier *et al.* (1971) have vigorously emphasized the absolute indispensability of *clonal* cultures in elucidation of the classification of coccoid blue-green algae, which incidentally, they decree are bacteria, in view of their prokaryotic organization (in spite of their possession of chlorophyll *a* and their photosynthesis with free oxygen evolution). The reports of Kantz and Bold (1969) and of Baker and Bold (1970) demonstrate the value of cultures in the classification of filamentous blue-green algae as well. The series of investigations of green microalgae in my own laboratory and those of Trainor and Hilton (1966), Cox and Deason (1968), Fott and Nováková (1969), and Shihira and Krauss (1965) demonstrate clearly that the taxonomy of these organisms must be based on populations grown in culture, if possible in defined media, and under reproducible environmental conditions. Furthermore, a number of supplementary physiological characteristics have proven valuable in screening and classifying isolates of microalgae of certain large genera (*e.g. Chlorococcum*, Archibald & Bold, 1970), and this approach has been emphasized in the taxonomy of *Chlorella* (Shihira & Krauss, 1965; Kessler & Czygan, 1970; Kessler & Zweier, 1971). The taxonomy of even the more complex filamentous green algae like the Ulotrichaceae (Mattox & Bold, 1962), *Stigeoclonium* (Cox & Bold, 1966), and other Chaetophorales (Tupa, 1972) can best be elucidated with the aid of cultures. Such a methodology would certainly greatly improve our understanding of the range of variation in such large groups as the desmids, Zygnemataceae, Oedogoniales, diatoms, and many others.

The monographic studies of Pringsheim (1956) on *Euglena*, of Pocock (1960) on *Hydrodictyon*, Hoek (1963) on *Cladophora*, of Fott and Nováková (1969) on *Chlorella*, of Komárková-Legnerová (1969) on *Ankistrodesmus* and *Monora-*

phidium, of Řeháková (1969) on *Oocystis*, and of Sulek (1969) on *Pediastrum* exemplify taxonomic contributions which rest on especially sound foundations. Such studies are laborious and time-consuming, but they will stand the test of time. Furthermore, the algae which they describe are available to posterity as living cultures for comparative study. More monographic studies of this caliber are hopefully to be anticipated.

Several other techniques have been applied relatively recently, with some success, to algal taxonomy and systematics. McGuire (1969) applied the methods of numerical taxonomy to 17 taxa of the genus *Chlorococcum*, while Brown and Bold (1964), with the aid of Lester, explored the efficacy of the serological approach to elucidating relationships among the members of that genus and of *Tetracystis*. McLean (1968) explored differences in pigmentation in *Chlorococcum* as an aid in elucidating their taxonomy. Nichols *et al.* (1968) have studied affinities of certain chlorococcacean algae and isolates of the red alga, *Porphyridium*, using pyrolysis-gas-liquid chromatography with interesting results. Sprung and Wujek (1971) used the same technique in clarifying the taxonomy of *Pleurastrum*. Thomas and Brown (1970*a*, *b*) and Thomas and Delcarpio (1971) have explored isozyme analysis in establishing relationships in *Chlorococcum*, *Protosiphon*, and *Chlamydomonas*.

Electron microscopy has provided additional helpful criteria for algal taxonomy. Thus, Brown and Bold (1964) reported differences in the organization of the chloroplast, pyrenoid, mitochondria, Golgi apparatus, and cell walls of 11 species of *Tetracystis*, while Brown and McLean (1969) found differences in the organization of the pyrenoid valuable taxonomically at the specific level. Recently, Mix (1972) has proposed that differences in the ultrastructural organization of the cell walls of certain desmids should be considered a basic criterion in their classification, and Komárek and Ludvík (1972) used the same criteria in classifying species of *Scenedesmus*. Finally, I would draw attention to the important discussion of Klein and Cronquist (1967) regarding the taxonomic significance of biochemical, ultrastructural, and physiological characteristics of algae (and of bacteria, slime molds, and fungi).

This incomplete summary indicates that, as in other groups of organisms, algal taxonomy is being established and revised in the light of a number of criteria in addition to the morphological; it is thus far from static.

ALGAL ULTRASTRUCTURE

The phenomenal expansion in our knowledge of algal ultrastructure obviously is correlated with the increasing availability of electron microscopes beginning about 1950 and with continuing improvements in technique. Ultrastructural studies of algae by such investigators as Manton and associates, Bisalputra, Weier, Dodge, Leedale, Gantt, Brown, Lang, Pickett-Heaps, Gibbs, Hoffman, Pankratz, and Bowen, to cite but a few, have contributed fundamental biological data, for example:

1) The concepts of Prokaryota, Mesokaryota (Dodge, 1971), and Eukaryota developed through ultrastructural studies of blue-green (Lang, 1968; Walsby,

1972) and other algae as the results of these could be correlated with studies of other organisms.

2) The hypotheses that eukaryotic cellular organization in plants and animals arose by the establishment of various symbioses, as discussed by Raven (1970), Margulis (1970), Schnepf and Brown (1971), and Lee (1972), are clearly related to our knowledge of algal ultrastructure. The demonstration by Green (1970) and Taylor (1970) that the chloroplasts of *Codium* and *Caulerpa* can live as symbiotic organelles within marine opisthobranchs and photosynthesize there is highly significant in this connection.

3) The demonstration of the presence of DNA in the chloroplast by Ris and Plaut (1962).

4) The generalization regarding the organization (9 + 2) of flagella and cilia throughout the plant and animal world rests on an extensive foundation in algal ultrastructure (Manton, 1956).

5) The establishment of the precise site of the photosynthetic pigments, primary and accessory, and their development is based largely on ultrastructural studies of algae (*e.g.* Gantt & Conti, 1966, 1969).

6) Major changes in the phylogenetic classification of algae are founded on data from algal ultrastructure, *e.g.* the Prasinophyceae (Manton, Oates & Parke, 1963), Haptophyceae (Christensen, 1962; Manton, 1966), and Eustigmatophyceae (Hibberd & Leedale, 1972).

7) Studies of cytokinesis in *Ulothrix, Stigeoclonium, Oedogonium* and desmids and related forms by McBride (1970); Floyd, Stewart, and Mattox (1971, 1972); Pickett-Heaps (1972*a, c*), Pickett-Heaps and Fowke (1969); and Pickett-Heaps and Marchant (1972) have provided evidence of strikingly different modes of partitioning of cells. The cell plate, characteristic of the *so-called* higher plants, occurs only in certain green algae, but its relation to the dividing nuclei and spindle is not strictly comparable, according to Pickett-Heaps (1972*a*).

8) Of the greatest significance, in my opinion, are the reports of Manton (1966, 1967); Manton and Parke (1965); Manton and Peterfi (1969); Manton and Leedale (1969); Manton, Oates, and Parke (1963); Brown (1969); Brown *et al.* (1969, 1970); Gooday (1972); Pienaar (1969*a, b*); Franke and Brown (1971); Outka and Williams (1971); and Herth *et al.* (1972) which have provided unequivocal evidence of the production of structured units (scales and coccoliths) within cisternae of the Golgi apparatus and their translocation to the surface of the flagellar membrane and plasmalemma. The chemical evidence of Brown and the Freiburg group that these scales in *Pleurochrysis* contain cellulose is the first clear evidence of the site of its production and pathway of translocation to the cellular surface.

9) The demonstration of the existence and replication of viruses in algae by Safferman (1968); Goldstein *et al.* (1967); Smith, Brown, and Walne (1967); Brown (1972); Pickett-Heaps (1972*b*); and Toth and Wilce (1972).

10) Finally, the summaries of Dodge (1969) on the algal eyespot and the recent study of Bartlett *et al.* (1972) thereon; of Gibbs (1970) on the algal chloroplast; and of Griffiths (1970) on the pyrenoid; and of Dodge and Crawford (1970) on the dinoflagellate cell wall; and of Godward (1966) and Leedale

(1970) on nuclear cytology of the algae, provide impressive evidence of our advancing knowledge of algal ultrastructure.

ALGAL MORPHOLOGY AND LIFE CYCLES

Well before the beginning (1947) of the period of this review, it was known that three different basic types of life cycle, with various modifications, occurred among the algae. These include: (1) the haplobiontic types with a single free-living organism, either haploid (*Chlamydomonas, Spirogyra*) or diploid (*Acetabularia*), and the diplobiontic type with (2) isomorphic (*Ulva, Cladophora, Ectocarpus*) or (3) heteromorphic (*Laminaria*) alternates. During the period under review our knowledge has been considerably extended and refined, thanks to advances in the cultivation of algae in the laboratory, in some cases with correlated field studies. For example, although earlier inferred to be so on genetic grounds, *Chlamydomonas* was proven cytologically to be haplobiontic and haploid with zygotic meiosis by Buffaloe (1958), while Godward (1961) presented unequivocal cytological evidence of a similar cycle in *Spirogyra crassa.*

Kornmann (1970) has emphasized the advances in our knowledge of marine algal life cycles based on laboratory cultivation. In the green siphonous algae, interesting examples of alternation of generations have been established by this method. Thus, for example, *Halicystis ovalis* and *Derbesia marina* were shown by Kornmann (1938) and *D. tenuissima* and *H. parvula* by Feldmann (1950) to be alternate manifestations of the same organism; *Bryopsis plumosa* has been shown by Rietma (1971) to have several different types of life cycle, while Hustede (1964) has reported that *Bryopsis halymeniae* and *Derbesia neglecta* belong to the same cycle. The heteromorphic alternation of *Spongomorpha coalita* and *S. aeruginosa* and *Codiolum petrocelidis* has been elucidated by both Fan (1959) and Kornmann (1964).

Among the brown algae, Wynne (1969) investigated the life cycles of eleven species in culture, demonstrating heteromorphic alternation in *Haplogloia andersonii* and *Soranthera ulvoidea,* both undergoing sexual reproduction, while the other nine species displayed entirely asexual reproduction. Müller (1967) has amplified our knowledge of the life cycle of the widespread *Ectocarpus siliculosus,* which cycle varies in different localities. He has very recently (1972) shown by means of laboratory cultures that *E. fasciculatus* var. *refractus* is the sporophytic phase of *E. draparnaldioides.*

The investigations of Stosch and Drebes (1964) and of Drebes (1966) are classical in their elucidation of the reproductive cycle in controlled laboratory culture of the marine centric diatom *Stephanopyxis turris* and of *S. palmeriana,* both diploid organisms with gametic meiosis. One yearns for research reports of similar incisiveness regarding the reproductive process of pennate diatoms, especially freshwater species. Stosch (1964, 1965) has also demonstrated sexual reproduction in the dinoflagellate *Ceratium.*

The most extensive and significant additions to our knowledge of algal life cycles concern the red algae, and the reviews of Feldmann (1952), Drew (1955), Knaggs (1969), and Martin (1969) have summarized these. Here the role of the culture method is especially impressive. As an example of new information developed during the period under review may be cited Drew's (1954) demonstration that *Porphyra* is an alternate in the life cycle involving the genus *Conchocelis,* known long before her discovery of this relationship as a distinct, shell-inhabiting genus. Numerous investigations of life cycles in species of *Bangia* and *Porphyra* have been made in the interim (*e.g.* Bird, Chen & McLachlan, 1972).

The long-accepted dictum that the "lower" Florideae (essentially the Nemaliales) were haplobiontic and haploid was shattered by Mullahy (1952) and then by Magne (1961*a, b*); the former failed to find the anticipated zygotic meiosis in *Lemanea australis,* and the latter demonstrated that the post-zygotic fertile filaments (gonimoblasts) of *Nemalion, Scinaia,* and *Lemanea* are diploid.

In the interim, it has been demonstrated for a number of the Nemaliales that an alternation of heteromorphic generations is the pattern, although cytological evidence of the site of meiosis, presumably in the tetrasporangia, is largely absent (Knaggs, 1969). Here may be cited such heteromorphic cycles as those of *Falkenbergia* (tetrasporic) and *Asparagopsis* (Feldmann, 1965); and *Nemalion* with its microscopic filamentous, tetrasporic alternate (Fries, 1967; Umezaki, 1967). Magne (1967) has reported that in *Lemanea mamillosa* the diploid carpospores produce prostrate filaments upon which, in turn, the characteristic macroscopic plants develop. Meiosis occurs in the cells of the latter in their juvenile stage.

By contrast, Edwards (1969*a*, 1970) has confirmed through laboratory culture and field observations, the occurrence of a diplobiontic isomorphic life cycle in *Callithamnion byssoides* and *Polysiphonia boldii,* as have Chen and McLachlan (1972) for *Chondrus crispus* and Ogata, Matsui, and Nakamura (1972) for *Gracillaria verrucosa.*

In an important contribution, West (1968) has reported on the life cycle of *Acrochaetium pectinatum* in which the tetrasporophytes are larger than the gametophytes. Of special interest to this reviewer was the occurrence of protogynous gametophytes which later produced spermatangia, a condition similar to that in *Equisetum* (Duckett, 1970). In *Rhodochorton purpureum* West (1969) found again that the tetrasporophytes are larger than the gametophytes. Even more remarkable was the apparent absence of carpospores and the direct development of the tetrasporophyte from the diploid post-fertilization (gonimoblast) filaments. *Rhodochorton concrescens,* by contrast, seemingly lacks sexual reproduction, the tetraspores developing directly into new tetrasporophytes (West, 1970). In both *Acrochaetium* and *Rhodochorton,* tetraspore production is favored by short daylengths (8–10 hours).

Finally, in blue-green algae, Lazaroff (1966) and Kantz and Bold (1969) have described the occurrence of cyclic development in *Nostoc* and *Anabaena.*

Algal Physiology

Although many researches on algae involve them as "systems" for the investigation of certain physiological and biochemical phenomena, a number have focused on the algae as organisms; the latter will be emphasized in the following discussion, so that the vast literature on algal photosynthesis is not cited at all in this summary.

Of prime importance in the literature is the comprehensive *Physiology and Biochemistry of Algae* edited by Ralph Lewin (1962) which is currently under revision. Summaries of algal physiology with emphasis on nutrition have been prepared by Myers (1951), Fogg (1953), and Krauss (1958). Syrett (1962), Hutner and Provasoli (1964), and Naylor (1970) have discussed nitrogen metabolism in algae. Holm-Hansen (1968) and Wolk (1973)[3] have published an important summary of the ecology, physiology, and biochemistry of blue-green algae.

Comparative physiological investigations of microalgal genera with many species, *e.g. Chlamydomonas* (Cain, 1965); chlorosarcinaceaen algae (Groover & Bold, 1969); and *Chlorococcum* (Archibald & Bold, 1970) have revealed that the organisms differ in their "preferences" for various types of nitrogen and that some are extremely versatile in this respect. Of considerable interest is the ability of some microalgae to use nitrogen in gelatine, apparently by producing extracellular enzymes (*e.g.* Archibald & Bold, 1970). Pringsheim and Pringsheim (1959) have surveyed comparatively the nutrition of a number of colonial Volvocales.

Although many blue-green and green algae have been grown axenically in defined inorganic culture media, a number, both freshwater and marine, have not been grown successfully in the absence of soil extract. Of these *Oedogonium* had been especially recalcitrant until Hill and Machlis (1970) succeeded in compounding a defined medium which supported good growth.[4] They discovered differences between the male and female strains of *Ocardiacum* in growth rate in relation to nitrogen concentration, in dry weight, and in time of production of the sex organs. It is of interest that substances in soil may exhibit striking morphogenetic effects. Thus, although Stewart (1971) was able to obtain excellent growth of *Characiosiphon rivularis* in defined media, no supplement except soil or soil extract would support formation of the elongate sacs.

Fewer brown and red algae have been grown axenically, so that less is known of their nutrition. However, the work of Druehl and Hsiao (1969) and of Luning and Dring (1972) on *Laminaria* gametophytes and that of Lewin and Robertson (1971) on *Asterocytis* and of Fries (1963) and Fries and Petterson (1968) have provided valuable data for brown and red algae.

Kylin and Das (1967) have reported a number of morphogenetic effects of various chemical elements on *Scenedesmus* as similar to those cited by Trainor (1970) for a number of other algae. According to Lewin (1961), more than 2000 strains of algae have been shown to have growth-factor requirements.

The capacity of algae for heterotrophic growth, based on the early experiments of Robert Chodat, has been confirmed, and the responses of algae to supplementary carbon under various conditions have been explored by a number of investigators. For example, J. Lewin (1953) reported that 13 of 42 strains of

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[3] Although not in the original manuscript, this 1973 reference has been added because of its importance.

[4] However, see J. L. Machlis, Jour. Phycol. 9: 343. 1973.

pennate diatoms could grow heterotrophically in darkness with glucose as the sole carbon source. It is well known that the responses of algae to such supplemental carbon compounds are variable (Wiedeman & Bold, 1965) and range from inhibition to stimulation. The effects differ in different algae in light and in darkness and under aerobic *vs.* anaerobic conditions.

Although formerly thought to be obligately autotrophic, Hoare *et al.* (1971) and Khoja and Whitton (1971) have reported the heterotrophic growth of eighteen strains of blue-green algae in darkness.

Investigations of nitrogen fixation by blue-green algae *in situ* and in the laboratory have been numerous and incisive during the last few years of the period under review. Although the capacity for nitrogen fixation was for some period thought to be limited to heterocystous species and ascribed to the heterocyst (Stewart *et al.*, 1969; Kulasooriya, Lang & Fay, 1972), there is also evidence that species lacking heterocysts, *e.g.* species of *Plecotonema* and *Gloeocapsa* (Rippka *et al.*, 1971), also can fix nitrogen. Ohmori and Hattori (1971) are not convinced that the heterocyst is the sole site of nitrogen fixation.

Algae also have been the objects of a number of photobiological investigations during the last 25 years. Some of these relate to the site and mechanism of phototaxis in the motile cells of algae with red eyespots (Wolken, 1960; Diehn, 1969; Cobb, 1963; Batra & Tolin, 1964; Arnott & Brown, 1967) while others (Wagner, Haupt & Laux, 1972) have dealt with the light-related movements of the chloroplast in *Mougeotia,* which orients with its broad surface to red light and with its edge to white light of low intensity, phytochrome being mediative in the latter movement. Nultsch *et al.* (1971), in a recent study of phototaxis in *Chlamydomonas reinhardtii,*[5] have reported its positive phototactic response in light intensities ranging between 10 and 100,000 lux. The action spectrum was the UV region and in wavelengths up to 550 nm with peaks at 503 and 443. Huth (1970, 1971) has analyzed the mechanism of patterns of phototaxis in *Volvox aureus.*

In the blue-green alga *Nostoc,* Lazaroff (1966) has shown that the developmental stages may be controlled by changing the wavelength of incident light. Red light (650 nm) evokes the organization of the filamentous stage from the aseriate one; this can be reversed by green light.

ALGAL BIOCHEMISTRY

Several biochemical aspects of algae have already been cited in earlier sections of this review, and many are covered in Lewin's (1962) *Physiology and Biochemistry of Algae.* Percival and McDowell (1967) have summarized the chemistry of algal food reserves and structural polysaccharides. Klein and Cronquist (1967) have discussed algal carotenoids and other pigments and carbohydrates, lipids, and sterols as they are relevant to algal phylogeny. They also have evaluated metabolic processes in algae comparatively and the classification of algae in light of biochemical and morphological criteria. In the present

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[5] Dangeard (1888; Recherches sur les Algues inférieures. Ann. Sci. Nat., 7^e Sér. Bot. 7: 105–175.) in his original description named the organism *E. reinhardtii* in dedication to "P. M. Reinhardt" as Trainor (1959) pointed out.

section, investigations of the cell walls of algae will be emphasized, with lesser attention to other topics.

Parker (1970*b*) defined the comprehensive and time-consuming procedures necessary for precise determination of the chemical composition of algal cell walls. Unfortunately, few such studies have been made on any wide range of organisms, so that too much has often been inferred about the chemistry of algal cell walls on the basis of too little data from the study of too few organisms. Kreger (1962) has summarized a good deal of information regarding this topic, but this has been modified to some extent by subsequent investigations.

Holm-Hansen, Prasad, and Lewin (1965) and Punnett and Derrenbacker (1966) reported that diaminopimelic acid is a component of the cell-wall mucopeptides of certain blue-green algae and some bacteria, in confirmation of an earlier report of Work and Dewey (1953). In the interim, other amino acids, including muramic acid and glucose amine have been reported in blue-green algal cell walls (Allsopp, 1969). Vance and Ward (1969) were able to induce degradation of the inner, rigid wall layer in blue-green algae with lysozyme (muramidase) which also digests the mucopolymers of bacterial walls. These and other considerations led Stanier *et al.* (1971) to interpret the blue-green algae as bacteria.

Cellulose is present in brown algae (Black, 1950). Parker (1970*b*) has discussed wall chemistry in relation to the phylogeny of siphonous green algae (*sensu lato*). It is clear in this group that cellulose seems to be lacking from the Acrosiphonales and Dasycladales (*e.g. Acetabularia*). Dawes (1966) found five types of wall organization in the 11 orders of green algae representatives of which he examined electron microscopically. Preston's (1968) account of algal cell walls, both cellulosic and otherwise, is extremely lucid and helpful to the general reader.

The outer, firm, "cuticular" layer, which occurs on the cell walls of a number of algae, was investigated by Hanic and Craigie (1969). They were able to isolate this "cuticle" from certain green, brown, and red marine algae and, upon chemical analysis, found it to be rich in protein (70–80%). It should be noted, as an example of rapid change in our knowledge of algal cell walls, that Kreger (1962) had stated ". . . in the few instances where pure, native walls were investigated in detail, *small quantities*[6] of lipid and protein were also present."

Of considerable interest is the recent report of Miller, Lamport, and Miller (1972) that hydroxyproline heterooligosaccharides occur in the cell walls of two species of *Chlamydomonas* and *Volvox carteri.* This is in marked contrast to the presence of homooligosaccharides (arabinosides) which characterize the walls of other plants "from the Spermatophytes to the green alga *Chlorella.*" These authors suggest that the change from the relatively weak hydroxyproline heterooligosaccharides to homooligopolysaccharides may be correlated with the evolution of a more rigid plant cell wall.

The investigation of the cell walls of desmids by Mix (1972) has been referred to earlier (p. 18). Lorch and Weber (1972) have recently reported on the chemistry of the cell wall in the desmid *Pleurotaenium*, while Roberts,

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[6] Italicized by H. C. Bold.

Gurney-Smith, and Hills (1972) have studied the cell wall of *Chlamydomonas reinhardtii.*

Preston (1968), in his review of algal cell walls, writes: "As a group seaweeds have considerably broadened our understanding of the structure of plant cell walls. The earlier generalization that cellulose occurs in the cell walls of all green plants is no longer tenable." In some algae, according to Preston, polymers of xylose and mannose plus proteins compose the cell walls. Herth *et al.* (1972) have shown this to be the case, for example, in *Pleurochrysis scherfellii.*

Dawes, Scott, and Bowler (1961) and Dawes (1966) have made comparative studies of algal cell walls using fresh material and light and electron microscopy, while Reimann, J. Lewin, and Volcani (1966) have investigated the development of the cell walls of certain diatoms. They found that the siliceous frustule is enveloped by an organic matrix on all sides, the silica being deposited within a special silicalemma, the latter a three-layered membrane.

Pigments in algae have been discussed by several authors in Lewin's (1962) synthesis. Czygan (1968, 1969) has studied the nature and synthesis of secondary carotenoids in 164 strains of green algae. Kleinig (1969) has investigated the carotenoid pigment of 50 species of 9 siphonous groups of green algae and has attempted to correlate their distribution with the taxonomy of the organisms, as Parker (1970*b*) did on the basis of wall composition.

In a series of excellent papers correlating microscopy and cellular chemistry, McCully (1966, 1968*a, b*) has reported on the vegetative and reproductive tissues of *Fucus.*

Finally, biochemical properties of algae are related to their use as food and in other ways of importance to mankind. Krauss (1962) has reviewed the mass culture of algae for food, while Boney (1965), Levring, Hoppe, and Schmid (1969), and Zajic's (1970) volume present data regarding the uses of marine algae and their products.

ALGAL ECOLOGY

Algae, as primary producers in the ecosystem, have received considerable attention (Odum & Odum, 1955; Fogg, 1965). They have also become increasingly recognized for their importance in water pollution. Thus, Ryther (1969) states that in photosynthesis carried out by algae, there are fixed annually in oceans $1.5–1.8 \times 10^{10}$ tons of carbon. The importance of algae in providing oxygen for the degradative bacteria in waste disposal has been recognized (Bartsch, 1960) and exploited, and the deleterious effects of over-population by blue-green algae in such systems are well known.

A number of aspects of the ecology of freshwater algae have been discussed in a publication edited by Tryon and Hartman (1960). The volume includes papers on algal distribution (by Whitford), algae of flowing waters (by Blum), algae of blooms and poisonous algae (by Prescott), extracellular toxins, stimulators and inhibitors produced by algae (Hartman), and algae in relation to oxidation processes (by Bartsch). Schindler (1971) has reviewed much of the literature on nutrients in the eutrophication of freshwater lakes and has presented data from the experimental eutrophication of an oligotrophic lake. Brown and

Richardson (1968) have been able to correlate algal classification with light intensity and its effects on growth, pigmentation, photosynthesis, and cellular morphology by studying experimentally representatives of ten algal divisions.

Investigations of marine algal ecology have flourished since 1947 with improvement in methods of analyzing the environment and of sampling, including scuba diving and submarine algal growth chambers (Chapman, 1964). The excellent books of Lewis (1964), Boney (1966), and Dawson (1966) are basic to the field. Investigations of marine algal ecology are exemplified by the contributions of Lee (1966), Neushul (1967), Wood and Hargraves (1969), and Forstner and Rützler (1970). Zaneveld (1969) has recently discussed the factors involved in marine algal zonation. Druehl (1967), using field and transplant studies and cultures, was able to correlate the differing distribution of two species of *Laminaria* with differences in temperature, salinity, and motion of the water. Pollock (1969) also performed transplantation experiments with two distinct forms of *Fucus distichus*. Edwards (1969*b*) has made an incisive field and experimental study of some algae of the Texas Gulf Coast.

There have been significant investigations of algae and of the environment in special habitats such as the cryoflora (Stein & Brooke, 1964; Stein & Amundsen, 1967; Thomas, 1972), thermophilic algae (Brock, 1967; Castenholz, 1969), and algae of the soil (Parker, 1961; Parker & Turner, 1961), and in the air (Brown *et al.*, 1964; Schlichting, 1970; Brown, 1971). The last-cited investigations are related to the vast field of the interrelations of the organisms in microcommunities. Thus, Parker and Turner have demonstrated the existence of various relationships in a soil community, including protocooperation, commensalism, neutralism, amensalism, competition, and parasitism.

Fitzgerald (1969) has recorded in field and laboratory investigations the basis for competition among bacteria, algae, and aquatic angiosperms. For example, *Myriophyllum* and *Ceratophyllum* inhibit the development of plankton algae under field, but not under laboratory, conditions. However, in nitrogen-limited cultures, the antagonistic effect of angiosperms on algae was evident. A number of other interrelationships were described by Fitzgerald. In another contribution (1970) he has shown that in lakes, algae and weeds with adequate nitrogen and/or phosphorus do not share these with nitrogen- or phosphorus-limited algae, but the nitrogen and phosphorus from killed weeds and algae are available to nutrient-limited algae.

Especially fruitful have been the investigations of the nature of the more intimate associations between algae and animals. Here may be cited first the apparent morphogenetic role of the green flagellate *Platymonas roscoffensis* in the development of the worm *Convoluta roscoffensis* (Oschman, 1966) and the details of this relationship (Provasoli, Yamasu & Manton, 1968). Muscatine (1967, 1971) and associates (1967) and Trench and associates (1971, 1972) have studied the physiology of green algae (zoochlorellae) in a ciliate protozoan, in a sponge, and in *Hydra*, and of certain golden-brown algae (zooxanthellae) living within the gastrodermal cells of corals and sea anemones. These investigations have shown radioautographically the liberation of soluble products of photosynthesis and their incorporation in the host tissue. Furthermore, it has been observed that the latter stimulates the algal cells to greater productivity, as compared with that of free-living algae of the same strain; the host tissue also affects the permeability of the algal cells.

Of special ecological significance has been the increasingly frequent demonstration of "leakage" of various synthesized products from living algal cells into their surrounding liquid environment. Here may be cited the papers of Lewin (1956*a*), Droop (1961), Whitton (1965), Fogg (1966), Guillard and Hellebust (1971), Aaronson *et al.* (1971), Huntsman (1972), and Ramus (1972). These authors, and others, have demonstrated the liberation by algae into the environment of vitamin B_{12}, biotin, amino acids, and various organic carbon compounds; these thus become available to other organisms. Guillard and Hellebust have estimated that as much as 7 μg/liter of acrylic acid and 0.3 mg/liter of polysaccharides can be liberated into the sea by a bloom of the haptophycean *Phaeocystis poucheti.* The papers of Carlucci and Bowes (1970*a, b*) are especially important in this connection. Kuenzler (1970) reported that large amounts of organic phosphorus compounds are secreted into the medium by eight species of planktonic marine algae.

The secretion of such benign substances into the water reminds one of the toxic compounds which are produced by algae. The many investigations of these have been summarized by Gorham (1964) and Shilo (1967).

With reference to the secretion into the environment of vitamins, Parker and Wachtel (1971), using *Euglena gracilis,* strain Z, as the assay organism, in accordance with the method of Robbins, Hervey, and Stebbins (1950), were able to demonstrate the presence of vitamin B_{12} in rainwater. Similarly, using *Lactobacillus plantarum,* they showed that niacin and biotin were also present. Parker (1968) correlated the appearance and disappearance of blooms of *Chlamydomonas* with the rise and decline of vitamin B_{12} following rains. Finally, in this connection, Parker (1970*a*) proposed the presence, in clouds, of aeroplankton in which microorganisms may exist in an active, rather than dormant, state. A recent paper by Davis (1972) has discussed the remarkable powers of survival of desiccated algae and the possible mechanisms of such survival.

Evidence that airborne algae are causative agents in inhalant allergy has been educed by McElhenney *et al.* (1962) and Bernstein and Safferman (1970), while Moiekeha *et al.* (1971) have reported that human dermatitis is cause by *Lyngbya majuscula,* and they have investigated the properties of the toxic factor. The medical aspects of phycology have been ably summarized by Schwimmer and Schwimmer (1964).

The algae of lichens (Ahmadjian, 1967) and the interrelationships of the component phycobionts and mycobionts of lichens have received considerable attention during the period under review. A number of electron-microscopic studies of lichens (*e.g.* Brown & Wilson, 1968; Jacobs & Ahmadjian, 1969; Gallum *et al.,* 1970; Webber & Webber, 1970) have sought to elucidate the relationships of the lichen partners. There is a parallel in these relationships and that of algae and animals, alluded to above, in that substances (nitrogenous and carbohydrate) synthesized in the algal cells are transferred to the fungi (Richardson *et al.,* 1968; Milbank & Kershaw, 1969; Kershaw & Milbank, 1970; Jacobs &

Ahmadjian, 1971). The fungus controls the rate of secretion from the algal cells, and the association has been interpreted as "controlled parasitism" by Milbank and Kershaw.

There have been a number of interesting studies regarding the dispersal of algae. Maguire (1963) has reported the colonization of wide-mouth bottles filled with sterile, artificial lake water, by a number of algae (and animals). This is not surprising in view of the reports of Brown, Larson, and Bold (1964) and Schlichting (1964, 1969) of the abundance of airborne algae. Proctor (1966); Parsons, Schlichting, and Stewart (1966); and Milliger and Schlichting (1968) have demonstrated the importance of animal vectors in the dispersal of algae. Brown (1971) has recently analyzed the dispersal of soil algae by wind across the island of Oahu, Hawaii.

ALGAL SEXUALITY

Although much of the published work of the late Dr. Franz Moewus could not be substantiated, it seemingly had a strong impact on the field of algal sexuality and genetics in stimulating other investigators to study these phenomena in algae. Thus, at the beginning of the period under review, the late G. M. Smith, Luigi Provasoli, and I, among others, were engaged in isolating what we hoped would be heterothallic strains of *Chlamydomonas* (because we had been unable to obtain Moewus' cultures) to be used in experimental work and teaching. Up to that time, availability of algae undergoing sexual reproduction was largely dependent on chance field collections. As a result, there were taken into culture *C. moewusii* (by Provasoli, in 1948), *C. reinhardtii* (by G. M. Smith, *ca.* 1944) and *C. chlamydogama* (Bold, *ca.* 1947), all isogamous, heterothallic species. Later Moewus' *C. eugametos*, interfertile, if not identical, with *C. moewusii* became available. This had an important impact, where it was taken advantage of, because it became possible for the first time to demonstrate sexually reproducing populations of these organisms at will (Starr, 1964; Hoshaw, 1961) and thus perhaps encouraged attempts to induce sexual reproduction of other algae in the laboratory. As a consequence, thanks to the efforts of many investigators, the Culture Collection at Indiana University, and others, now maintain a considerable stock of algae which can be readily manipulated so as to undergo sexual reproduction. In addition to the species of *Chlamydomonas* already cited, there are available strains of *Gonium, Volvulina, Pandorina, Eudorina, Ploeodorina, Platydorina,* and *Volvox*, of the Volvocaceae, which series displays isogamous, heterogamous, and oogamous sexuality. Furthermore, sexual strains of *Oedogonium, Sirogonium, Zygnema, Spirogyra, Cosmarium, Closterium,* and other desmids are also available for demonstration of sexual reproduction.

Several significant lines of investigation developed with respect to the sexual process in algae. These include first of all increased understanding of the process itself through electron-microscopic and chemical study; the relation of environmental parameters to the control of the sexual process and an analysis of its components; genetical studies based on the availability of mutants. Important summaries of algal sexuality and/or genetics have been published in the *Encyclopedia of Plant Physiology* by Ettl *et al.* (1967), Köhler (1967*a, b*), Förster

(1967), and elsewhere by Lewin (1954), Rawitscher-Kunkel and Machlis (1972), and Wiese (1969).

Algal sexuality was early studied at the ultrastructural level by Manton and Friedmann (1960) in *Prasiola*. They demonstrated that gametic contact was through one flagellum of the male gamete which activated the flagellaless female gamete as it entered the cytoplasm of the latter. Lewin and Meinhart had demonstrated earlier (1953) that the isogamous gametes of *Chlamydomonas moewusii*, after agglutination of their flagella, became connected by a strand, as in *C. chlamydogama* (Bold, 1949; Van Dover, 1972) and in *C. eugametos* (Brown, Johnson & Bold, 1968). Friedmann, Colwin, and Colwin (1968) and Brown *et al.* (1968) have investigated the sexual process in *C. reinhardtii* and *C. eugametos*, respectively, and have demonstrated significant differences, *e.g.* the presence of fertilization tubules in the former and their absence in the latter. The plasma papilla of walled gametes has a dynamic role in initiating plasmogamy which was also observed by Van Dover (1972) in *C. chlamydogama*; the latter differs somewhat from both *C. reinhardtii* and *C. eugametos* in its sexual process.

Bråten (1971), using electron microscopy, has investigated gametic union in *Ulva mutabilis*. Here again, gametic contact is by the flagella. Plasmogamy is completed within 5 minutes and karyogamy within 30 minutes. One of the gametic chloroplasts degenerates, unlike its behavior in *Chlamydomonas* (Brown *et al.*, 1968; Van Dover, 1972).

Sager and Granick (1954), Lewin (1956*b*), Trainor (1959), Wiese and Jones (1963), and Jones (1970) have been able to synchronize and to control the sexual process in several species of *Chlamydomonas*. It has been shown clearly that the onset of sexual reproduction is associated with decrease in available nitrogen (Sager & Granick, 1954; Trainor, 1959; Wiese & Jones, 1963; Jones, 1970) and by conditions which favor photosynthesis. Flagellar agglutination of compatible individuals, when mixed, is occasioned by glycoproteins (Förster, Wiese & Braunitzer, 1956) which are identified as surface components by Wiese (1965). Wiese and Metz (1969) have shown that trypsin interferes with the formation of the gametic connecting strands and earlier inhibits gametic agglutination.

Sexual reproduction has been investigated in depth in a number of other algae. Hoffman (1961) has determined the environmental conditions which evoke maximum sexual reproduction in *Oedogonium cardiacum* and demonstrated (1960) the existence of a sperm attractant in the culture medium in which female filaments had matured. Rawitscher-Kunkel and Machlis (1962) have described the steps in the hormonal control of sexual reproduction in *O. borisianum*, which has dwarf males. Our knowledge of sexuality and genetics of the desmids has been augmented through the investigations of Starr (1959), Cook (1963), Biebel (1964), Brandham and Godward (1965), and Hoshaw and Hilton (1966), among others.

Of great significance and future promise are the investigations of Starr and his associates of the sexual process in volvocacean algae. These have involved studies of populations of various genera (*Gonium*, Stein, 1966; *Pandorina*, Coleman, 1959; *Eudorina*, Goldstein, 1964; *Volvulina*, Carefoot, 1966) in which clones from various sources were tested for sexual compatibility. Still more exciting is the work of Darden (1966, 1970), Starr (1968, 1969), Kochert (1968), McCracken and Starr (1970), and Vande Berg and Starr (1971) who have demonstrated the existence of a system of inducing substances secreted into the medium which evoke sexual maturation of vegetative individuals as males and/or females. These inducers are to some degree specific and variable in their effects in different species.

In this connection, the work of Müller on sexual reproduction in the brown alga *Ectocarpus* is especially significant. The physiologically female gametes secrete a volatile attractant, ectocarpin, which attracts the male gametes. The chemical structure of the ectocarpin has been elucidated by Müller *et al.* (1971) as allo-*cis*-1-(cycloheptadien-2′,5′ yl)-butene-1.

A number of other investigations of sexual reproduction in algae merit citation. At the ultrastructural level, these include the work of Hoshaw (1965) on *Sirogonium*; Pickett-Heaps and Fowke (1969) on *Closterium*; of Fowke and Pickett-Heaps (1971) on *Spirogyra*; and of Pollock (1970) on *Fucus*.

Among algae other than green algae, sexual reproduction of two species of the marine centric diatom *Stephanopyxis* has been controlled in culture and elegantly analyzed by Stosch and Drebes (1964) and Drebes (1966), as has the sexual process in the dinoflagellate *Ceratium cornutum* by Stosch (1965). Discussion of sexual reproduction in red algae, of course, has been included in the numerous papers on algal life cycles cited in an earlier section. Of the major algal groups, sexual reproduction is seemingly absent only from the blue-green algae and euglenoids (see, however, Leedale, 1967, regarding *Phacus*.)

Algal Genetics

The simplicity of organization and the haploidy of *Chlamydomonas* suggested more than 50 years ago to Pascher (1916, 1918) the advantages of that organism for genetic investigations. With the availability of heterothallic sexual strains in culture beginning in the late 1940's, genetic studies of *Chlamydomonas* were undertaken by a number of investigators, and these continue to the present. The occurrence of meiosis during zygote germination was inferred on genetic grounds and demonstrated cytologically for four species by Buffaloe (1958) who determined their chromosome number as $n = 8$; this was confirmed for *C. reinhardtii* by Levine and Folsome (1959) and recently by Dr. M. Maguire (personal communication), who also has demonstrated zygotic meiosis in that organism. Loppes, Matagne & Strukert (1972), however, report the chromosome complement of *C. reinhardtii* to be $n = 16$.

Other than those reported by Moewus (*e.g.*, 1940), Lewin (1950*a*, *b*, 1952, 1953) was the first to induce mutagenesis in *Chlamydomonas*. Obtained by ultraviolet irradiation, these mutants included morphological (*e.g.* lacking flagella), physiological (*e.g.* paralyzed flagella), and biochemical (*e.g.* vitamin-requiring) deviants. In studies of these, Lewin was able to demonstrate Mendelian segregation of nine characters and linkage (two groups) and to elucidate further the action of certain genes. Gowans (1960) and McBride and Gowans (1967) have made genetic investigations of *Chlamydomonas eugametos*. The genetics of *C. reinhardtii* has been investigated in depth chiefly by Sager (*e.g.* Sager & Ramanis, 1970), Levine (*e.g.* Levine & Goodenough, 1970), and Gillham (*e.g.* 1969). It has been shown that there are in this organism two distinct genetic systems consisting of genes which are inherited according to Mendelian ratios and those showing uniparental (UP) inheritance. The latter were discovered by Sager (1954) in her study of streptomycin-resistant mutants. Gillham (1969) has recently summarized much information and the relevant literature on UP inheritance and other aspects of the genetics of *Chlamydomonas.* The traditional-type genes fall into 16 linkage groups in *C. reinhardtii* (Hastings *et al.*, 1965). Levine and Ebersold (1960) and Mattoni (1968) have reviewed the earlier literature on the genetics and cytology of *Chlamydomonas*, while more recently Levine and Goodenough (1970) have summarized the genetics of chloroplasts and photosynthesis in *C. reinhardtii.* In the numerous genetical studies of *Chlamydomonas*, as pointed out by Levine and Goodenough (1970), there have been involved chromosomal and molecular genetics in combination with biophysics, biochemistry, and ultrastructure.

Finally, Føyn in a series of investigations (1958–1962) has concerned himself with mutagenesis and genetics in *Ulva mutabilis*; such investigations are being extended by Fjeld (1970, 1971, 1972).

Conclusion

From this somewhat eclectic review of the past 25 years of phycology, it should be clear that the study of algae is no longer limited in its perspectives and achievements: phycology has become sophisticated in its methods and biological in its viewpoint and scientific impact. In eloquent testimony of this, in addition to the literature cited by this reviewer, one may cite the following:

1) The organization of thriving national phycological societies with their dates of founding as indicated (which, except in one case, coincide with the period under review), in the United States (1946), Great Britain (1951), Japan (1952), France (1955), Czechoslovakia (1955), Philippines (1956), India (1959), and Venezuela (1966). The International Phycological Society was founded in 1961 and currently numbers 675 members; the Phycological Society of America has a current membership of approximately 1350.

2) The establishment of culture collections of living algae, many of them type species, at Bloomington, Indiana; Cambridge (England); Prague; Tokyo; and Paris.

3) The increase in number of courses in phycology and of phycologists added to the curricula and faculties, respectively, in colleges and universities.

4) The increase in availability of courses in phycology and inland and marine field stations in the United States.

5) The existence and expansion of such phycological journals as *Revue Algologique, Journal of Phycology, Phykos, Phycologia, Botanica Marina,* and the *British Phycological Journal.*

6) The organization of seven international seaweed conferences and publication of their proceedings and of a number of other phycological conferences and

symposia ("Algae and Man" at the NATO Advanced Study Institute in Louisville in 1962; the U.S.—Japan Conference on Cultures and Collections of Algae at Tokyo and Hakone, 1966; "Algae, Man and the Environment" in 1967 at Syracuse University.)

Finally, if any reassurance were required that phycology would continue to flourish in the future, one would need only to examine, in even cursory fashion, the magnificent volume entitled *Selected Papers in Phycology* published under the editorship of Drs. James R. Rosowski and Bruce C. Parker, with the cooperation of approximately forty other *younger* phycologists. This book contains 79 key papers together with incisive criticisms, comments, and comprehensive bibliographies—all eminent and tangible manifestations that the future of phycology rests in competent hands!

BIBLIOGRAPHY

Certain composite and general publications are marked with an asterisk (*).

AARONSON, S., B. DE ANGELIS, O. FRANK & H. BAKER. 1971. Secretion of vitamins and amino acids into the environment by *Ochromonas danica*. Jour. Phycol. 7: 215–218.

AHMADJIAN, V. 1967. A guide to the algae occurring as lichen symbionts: isolation, culture, cultural physiology, and identification. Phycologia 6: 127–160.

ALLSOPP, A. 1969. Phylogenetic relationships of the Procaryota and the origin of the eucaryotic cell. New Phytol. 68: 591–612.

ARCHIBALD, P. A. & H. C. BOLD. 1970. Phycological Studies XI. The genus *Chlorococcum* Meneghini. Univ. Texas Publ. 7015.

ARNOTT, H. J. & R. M. BROWN, JR. 1967. Ultrastructure of the eyespot and its possible significance in phototaxis of *Tetracystis excentrica*. Jour. Protozool. 14: 529–539.

BAKER, A. F. & H. C. BOLD. 1970. Phycological Studies X. Taxonomic studies in the Oscillatoriaceae. Univ. Texas Publ. 7004.

BARTLETT, C., P. L. WALNE, O. J. SCHWARTZ & D. H. BROWN. 1972. Large scale isolation and purification of eyespot granules from *Euglena gracilis* var. *bacillaris*. Pl. Physiol. 49: 881–885.

BARTSCH, A. F. 1960. Algae in relation to oxidation processes in natural waters. Pymatuning Laboratory, Special Publ. 2: 56–71. Univ. Pittsburgh.

BATRA, P. P. & G. TOLIN. 1964. Phototaxis in *Euglena*. I. Isolation of the eye-spot granules and identification of the eye-spot pigments. Biochim. Biophys. Acta 79: 371–378.

BEIJERINCK, M. W. 1890. Kulturversuche mit Zoochlorellen, Lichengonidien und anderen niederen Algen. Bot. Zeit. 48: 725–739; 741–754; 757–768; 781–785.

BERNSTEIN, I. L. & R. S. SAFFERMAN. 1970. Viable algae in house dust. Nature 227: 851–852.

BIEBEL, P. 1964. The sexual cycle of *Netrium digitus*. Amer. Jour. Bot. 51: 697–704.

BIRD, C. J., M. CHEN & J. MCLACHLAN. 1972. The culture of *Porphyra linearis* (Bangiales, Rhodophyceae). Canad. Jour. Bot. 50: 1859–1863.

BLACK, W. A. P. 1950. The seasonal variation in the cellulose content of the common Scottish Laminariaceae and Fucaceae. Jour. Mar. Biol. Assoc. U.K. 29: 379–387.

BOLD, H. C. 1942. The cultivation of algae. Bot. Rev. 8: 69–138.

———. 1949. The morphology of *Chlamydomonas chlamydogama*. Bull. Torrey Bot. Club 76: 101–108.

*———. 1968. Some reflections on four decades of phycology. *In* D. F. Jackson (editor), "Algae, Man and the Environment." Syracuse Univ. Press.

———. 1970. Some aspects of the taxonomy of soil algae. Ann. New York Acad. Sci. 175: 601–616.

*BONEY, A. D. 1966. A Biology of the Marine Algae. Hutchinson Educational Ltd., London. 216 pp.

*BOURRELLY, P. 1966. Les Algues d'eau douce I. Algues vertes. 511 pp. 1968. II. Les algues jaunes et brunes. 438 pp. 1970. III. Algues bleues et rouges. N. Boubee et ie., Paris. 512 pp.

BRANDHAM, P. E. & M. B. E. GODWARD. 1965. The inheritance of mating types in desmids. New Phytol. 64: 428–435.

BRÅTEN, T. 1971. The ultrastructure of fertilization and zygote formation in the green alga *Ulva mutabilis* Føyn. Jour. Cell Sci. 9: 621–635.

BROCK, T. D. 1967. Life at high temperatures. Science. 158: 1012–1019.

BROWN, R. M., JR. 1969. Observations on the relationship of the Golgi apparatus to wall formation in the marine chrysophycean alga, *Pleurochrysis scherffelii* Pringsheim. Jour. Cell Biol. 41: 109–123.

———. 1971. Studies of Hawaiian freshwater and soil algae. I. The atmospheric dispersal of algae and fern spores across the island of Oahu, Hawaii. *In* B. C. Parker & R. M. Brown, Jr. (editors), "Contributions in Phycology," Allen Press, Lawrence, Kansas.

———. 1972. Algal viruses. *In* K. Smith & M. Lauffer (editors), "Advances in Virus Research." 17: 243–277. Academic Press, New York.

——— & H. C. BOLD. 1964. Phycological Studies V. Comparative studies of the algae genera *Tetracystis* and *Chlorococcum*. Univ. Texas Publ. 6417.

——— & R. J. MCLEAN. 1969. New taxonomic criteria in classification of *Chlorococcum* species. II. Pyrenoid fine structure. Jour. Phycol. 4: 114–118.

——— & R. WILSON. 1968. Electron microscopy of the lichen *Physcia aipolia* (Ehrh.) Nyl. Jour. Phycol. 4: 230–240.

———, C. JOHNSON & H. C. BOLD. 1968. Electron and phase-contrast microscopy of sexual reproduction in *Chlamydomonas moewusii*. Jour. Phycol. 4: 100–120.

———, D. A. LARSON & H. C. BOLD. 1964. Airborne algae; their abundance and heterogeneity. Science 143: 583–585.

———, W. W. FRANKE, H. KLEINIG, H. FALK & P. SITTE. 1969. Cellulosic wall component produced by the Golgi apparatus of *Pleurochrysis scherffelii*. Science 166: 894–896.

———, ———, ———, ——— & ———. 1970. Scale formation in chrysophycean algae. I. Cellulosic and noncellulosic wall components made by the Golgi apparatus. Jour. Cell Biol. 45: 246–271.

BROWN, T. E. & F. L. RICHARDSON. 1968. The effect of growth environment on the physiology of algae: light intensity. Jour. Phycol. 4: 38–54.

BUFFALOE, N. D. 1958. A comparative cytological study of four species of *Chlamydomonas*. Bull. Torrey Bot. Club 85: 157–178.

CAIN, J. 1965. Nitrogen utilization in 38 freshwater chlamydomonad algae. Canad. Jour. Bot. 43: 1367–1378.

CARLUCCI, A. F. & P. M. BOWES. 1970*a*. Production of vitamin B_{12}, thiamine, and biotin by phytoplankton. Jour. Phycol. 6: 351–357.

——— & ———. 1970*b*. Vitamin production and utilization by phytoplankton in mixed culture. Jour. Phycol. 6: 393–400.

CAREFOOT, J. R. 1966. Sexual reproduction and intercrossing in *Volvulina steinii*. Jour. Phycol. 2: 150–159.

CASTENHOLZ, R. W. 1969. Thermophilic blue-green algae and the thermal environment. Bacteriol. Rev. 33: 476–504.

CHAPMAN, V. J. 1964. A submarine algae growth chamber for studies in benthic productivity. Ecology 45: 889–892.

CHEN, L. C-M. & J. MCLACHLAN. 1972. The life history of *Chondrus crispus* in culture. Canad. Jour. Bot. 50: 1055–1060.

CHODAT, R. 1909. Étude critique et expérimentale sur le polymorphisme des algues. Genève.

———. 1913. Monographie d'algues en culture pure. Matér. Fl. Crypt. Suisse. 4: 1–266.

*CHRISTENSEN, T. 1962. Alger. *In* T. W. Böcher, M. Lange & T. Sørensen, "Botanik." Vol. 2, No. 2. Copenhagen.

———. 1964. The gross classification of algae. Pp. 59–64, *in* D. F. Jackson (editor), "Algae and Man." Plenum Press. New York.

COBB, H. D. 1963. An *in vivo* absorption spectrum of the eyespot of *Euglena mesnili*. Texas Jour. Sci. 15: 231–235.

COLEMAN, A. W. 1959. Sexual isolation in *Pandorina morum*. Jour. Protozool. 6: 249–264.

COOK, P. W. 1963. Variation in vegetative and sexual morphology among the small curved species of *Closterium*. Phycologia 3: 1–18.

COX, E. R. & H. C. BOLD. 1966. Phycological Studies. VII. Taxonomic investigations of *Stigeoclonium*. Univ. Texas Publ. 6618.

——— & T. R. DEASON. 1968. *Axilosphaera* and *Heterotetracystis*, new chlorosphaeracean genera from Tennessee soil. Jour. Phycol. 4: 240–249.

Czygan, F. 1968. Sekundär-Carotinoide in Grünalgen. I. Chemie, Vorkommen und Kaktoren, welche die Bildung dieser Polyene beeinflussen. Arch. Mikrobiol. 61: 81–102.

———. 1969. Sekundär-Carotinoide in Grünalgen. II. Untersuchungen zur Biogenese. Arch. Mikrobiol. 62: 209–236.

Darden, W. H. 1966. Sexual differentiation in *Volvox aureus*. Jour. Protozool. 13: 234–255.

———. 1970. Hormonal control of sexuality in the genus *Volvox*. Ann. New York Acad. Sci. 175: 757–763.

Davis, J. S. 1972. Survival records in algae, and the survival role of certain algal pigments, fats and mucilaginous substances. Biologist 54: 52–93.

Dawes, C. J. 1966. A light and electron-microscope survey of algal cell walls. II. Chlorophyceae. Ohio Jour. Sci. 66: 317–326.

———, F. W. Scott & E. Bowler. 1961. A light and electron-microscopic survey of algal cell walls. I. Phaeophyta and Rhodophyta. Amer. Jour. Bot. 48: 925–934.

*Dawson, E. Y. 1963. Marine Red algae of Pacific Mexico. Part 8. Ceramiales: Dasyaceae, Rhodomelaceae. Nova Hedwigia 6: 401–481 [See Bibliography for Parts 1–7.]

*———. 1966. Marine Botany. Holt, Rinehart, and Urnston, New York. 371 pp.

*DeVirville, A. D. 1964. Proceedings of the Fourth International Seaweed Symposium (Biarritz). Macmillan Co. 467 pp.

Diehn, B. 1969. Action spectra of the phototactic responses in *Euglena*. Biochim. Biophys. Acta 177: 136–143.

Dixon, P. 1970. A critique of the taxonomy of marine algae. Ann. New York Acad. Sci. 175: 617–622.

Dodge, J. D. 1969. The fine structure of algal eyespots. Brit. Phycol. Jour. 4: 199–210.

———. 1971. A dinoflagellate with both a mesokaryotic and a eucaryotic nucleus. I. Fine structure of the nuclei. Protoplasma 70: 145–157.

——— & R. M. Crawford. 1970. A survey of thecal fine structure in the Dinophyceae. Bot. Jour. Linn. Soc. 63: 53–67.

Drebes, G. 1966. On the life history of the marine plankton diatom *Stephanopyxis palmeriana*. Helgoländer Wiss. Meeresuntersuch. 13: 101–114.

Drew, K. M. 1954. Studies in the Bangioideae. III. The life-history of *Porphyra umbilicalis* (L.) Kütz. var. *laciniata* (Light) J. Ag. Ann. Bot., n.s. 18: 183–211.

———. 1955. Life histories in the algae. Biol. Rev. 30: 343–390.

Droop, M. R. 1961. Vitamin B_{12} and marine ecology: the response of *Monochrysis lutheri*. Jour. Mar. Biol. Assoc. U.K. 41: 69–76.

Druehl, L. D. 1967. Distribution of two species of *Laminaria* as related to some environmental factors. Jour. Phycol. 3: 103–108.

——— & S. I. C. Hsiao. 1969. Axenic culture of Laminariales in defined media. Phycologia 8: 47–49.

Duckett, J. G. 1970. Sexual behavior in the genus *Equisetum*, subgenus *Equisetum*. Bot. Jour. Linn. Soc. 63: 327–352.

Earle, S. A. 1969. Phaeophyta of the eastern Gulf of Mexico. Phycologia 7: 71–254.

Edwards, P. 1969*a*. The life history of *Callithamnion byssoides* in culture. Jour. Phycol. 5: 266–268.

———. 1969*b*. Field and cultural studies of the seasonal periodicity of growth and reproduction of selected Texas benthic marine algae. Contr. Mar. Sci. 14: 59–114.

———. 1970. Field and cultural observations on the growth and reproduction of *Polysiphonia denudata* from Texas. Brit. Phycol. Jour. 5: 145–153.

*Ettl, H., D. G. Müller, K. Neumann, H. A. von Stosch & W. Weber. 1967. Vegetative Fortpflanzung, Parthenogenese und Apogamie bei Algen. Encycl. Pl. Physiol. 18: 597–776.

Famintzin, A. 1871. Die anorganische Salze als ausgezeichnetes Hülfsmittel zum Studium der Entwickelung niederer chlorophyllhaltiger Organismen. Bull. Acad. Imp. Sci. Saint-Pétersbourg 17: 31–70.

Fan, K. 1959. Studies on the life histories of marine algae. I. *Codiolum petrocelidis* and *Spongomorpha coalita*. Bull. Torrey Bot. Club 86: 1–12.

Feldmann, J. 1950. Sur l'existence d'une alternance de générations entre l'*Halicystis parvula* Schmitz et le *Derbesia tenuissima* (de Not.) Crn. Compt. Rend. Hebd. Séances Acad. Sci. 230: 322–323.

———. 1952. Les cycles de reproduction des algues et leurs rapports avec la phylogénie. Rév. Cytol. Biol. Vég. 13: 1–49.

———. 1965. Le développement des tetraspores de *Falkenbergia rufolanosa* et le cycle des Bonnemaisoniales. Rev. Gén. Bot. 72: 621–626.

Fitzgerald, G. P. 1969. Some factors in the competition or antagonism among bacteria, algae, and aquatic weeds. Jour. Phycol. 5: 351–359.

———. 1970. Evaluation of the availability of sources of nitrogen and phosphorus for algae. Jour. Phycol. 6: 239–247.

Fjeld, A. 1970. A chromosomal factor exerting a predetermining effect on morphogenesis in the multicellular green alga *Ulva mutabilis*. Genet. Res. 15: 309–316.

———. 1971. Genetic control of cellular differentiation in *Ulva mutabilis*. Induced chimeras. Hereditas 69: 59–66.

———. 1972. Genetic control of cellular differentiation in *Ulva mutabilis*. Gene effects in early development. Develop. Biol. 28: 326–343.

Floyd, G. L., K. D. Stewart & K. R. Mattox. 1971. Cytokinesis and plasmodesmata in *Ulothrix*. Jour. Phycol. 7: 306–320.

———, ——— & ———. 1972. Comparative cytology of *Ulothrix* and *Stigeoclonium*. Jour. Phycol. 8: 68–81.

*Fogg, G. E. 1953. The Metabolism of Algae. Methuen and Co. Ltd., London. 149 pp.

*———. 1965. Algal Cultures and Phytoplankton Ecology. Univ. Wisconsin Press. 126 pp.

———. 1966. The extracellular products of algae. Oceanog. Mar. Biol. Annual Rev. 4: 195–212.

*Förster, H. 1967. Geschlechtsfactoren bei haplogenotypischer Bestimmung. Encycl. Pl. Physiol. 18: 31–50.

———, L. Wiese & G. Braunitzer. 1956. Über das agglutinierend wirkende Gynogmon von *Chlamydomonas eugametos*. Zeitschr. Naturforsch. 11*b*: 315–317.

Forstner, H. & K. Rützler. 1970. Measurements of the micro-climate in littoral marine habitats. Oceanogr. Mar. Biol. Annual Rev. 8: 225–249.

Fott, B. & M. Nováková. 1969. A monograph of the genus *Chlorella*; the fresh water species. Pp. 10–74, *in* "Studies in Phycology." Academia (Czechoskovakia).

Fowke, L. C. & J. D. Pickett-Heaps. 1971. Conjugation in *Spirogyra*. Jour. Phycol. 7: 285–294.

Føyn, B. 1958. Über die Sexualität und den Generationswechsel von *Ulva mutabilis* (N.S.). Arch. Protistenk. 102: 473–480.

———. 1959. Geschlechtskontrollierte Vererbung bei der marinen Grünalge *Ulva mutabilis*. Arch. Protistenk. 104: 236–253.

———. 1960. Sex-linked inheritance in *Ulva*. Biol. Bull. 118: 407–411.

———. 1961. Globose, a recessive mutant in *Ulva mutabilis*. Bot. Mar. 3: 60–63.

———. 1962*a*. Diploid gametes in *Ulva*. Nature 193: 300–301.

———. 1962*b*. Two linked autosomal genes in *Ulva mutabilis*. Bot. Mar. 4: 156–162.

Franke, W. W. & R. M. Brown, Jr. 1971. Scale formation in chrysophycean algae. III. Negatively stained scales of the coccolithophorid *Hymenomonas*. Arch. Mikrobiol. 77: 12–19.

*Frederick, J. F. and R. F. Klein (editors). 1970. Phylogenesis and morphogenesis in the algae. Ann. New York Acad. Sci. 175: 413–781.

Friedmann, I. L., A. L. Colwin & L. H. Colwin. 1968. Fine structural aspects of fertilization in *Chlamydomonas reinhardi* [*sic*]. Jour. Cell Sci. 3: 115–128.

Fries, L. 1963. On the cultivation of axenic red algae. Physiol. Pl. 16: 695–708.

———. 1967. The sporophyte of *Nemalion multifidum* (Weber et Mohr) J. Ag. Svensk Bot. Tidskr. 61: 452–462.

——— & H. Petterson. 1968. On the physiology of the red alga *Asterocytis ramosa* in axenic culture. Brit. Phycol. Bull. 3: 417–422.

Gallum, M., N. Paran & Y. Ben-Shaul. 1970. The fungus-alga association in the Lecanoraceae: an ultrastructural study. New Phytol. 69: 599–603.

Gantt, E. & S. F. Conti. 1966. Granules associated with the chloroplast lamellae of *Porphyridium cruentum*. Jour. Cell Biol. 29: 423–434.

——— & ———. 1969. Ultrastructure of blue-green algae. Jour. Bacteriol. 97: 1486–1493.

Gibbs, S. P. 1970. The comparative ultrastructure of the algal chloroplast. Ann. New York Acad. Sci. 175: 454–473.

Gillham, N. W. 1969. Uniparental inheritance in *Chlamydomonas reinhardi* [*sic*]. Amer. Naturalist 103: 355–388.

GODWARD, M. B. E. 1961. Meiosis in *Spirogyra crassa.* Heredity 16: 53–62.

*———. 1966. The chromosomes of the algae. Edw. Arnold, Ltd., London.

GOLDSTEIN, M. 1964. Speciation and mating behavior in *Eudorina.* Jour. Protozool. 11: 317–344.

GOLDSTEIN, D. A., I. J. BENDET, M. A. LAUFFER & K. M. SMITH. 1967. Some biological and physiochemical properties of blue-green algal virus LPP-1. Virology 32: 601–613.

GOODAY, G. W. 1972. A biochemical and autoradiographic study of the role of the Golgi bodies in thecal formation in *Platymonas tetrathele.* Jour. Exp. Bot. 23: 959–971.

GORHAM, P. R. 1964. Toxic algae. *In* D. F. Jackson (editor), "Algae and Man." Plenum Press.

GOWANS, C. S. 1960. Some genetic investigations on *Chlamydomonas eugametos.* Zeitschr. Vererbungl. 91: 63–73.

GREEN, R. W. 1970. Symbiosis in sacoglossan opisthobranches; functional capacity of symbiotic chloroplasts. Mar. Biol. 7: 138–143.

GRIFFITHS, D. J. 1970. The pyrenoid. Bot. Rev. 36: 29–58.

GROOVER, R. D. & H. C. BOLD. 1969. Phycological studies VIII. The taxonomy and comparative physiology of the Chlorosarcinales and certain other edaphic algae. Univ. Texas Publ. 6907.

GUILLARD, R. R. L. & J. A. HELLEBUST. 1971. Growth and the production of extracellular substances by two strains of *Phaeocystis poucheti.* Jour. Phycol. 7: 330–338.

HÄMMERLING, J. 1931. Entwicklung und Formbildungsvermögen von *Acetabularia mediterranea.* Biol. Zentralbl. 51: 633–647.

HANIC, L. A. & J. S. CRAIGIE. 1969. Studies on the algal cuticle. Jour. Phycol. 5: 89–102.

HASTINGS, P. J., E. E. LEVINE, E. COSBEY, M. O. HUDOCK, N. W. GILLHAM, S. J. SUSZYCKI, R. LOPPES & R. P. LEVINE. 1965. The linkage groups of *Chlamydomonas reinhardi* [*sic*]. Micro. Genet. Bull. 23: 17–19.

HERTH, W., W. W. FRANKE, J. STADLER, H. BITTINGER, G. KEILICH & R. M. BROWN, JR. 1972. Further characterization of the alkali-stable material from the scales of *Pleurochrysis scherffelii*: a cellulosic glycoprotein. Planta 105: 79–92.

HIBBERD, D. J. & G. F. LEEDALE. 1972. Observations on the cytology and ultrastructure of the new algal class, Eustigmatophyceae. Ann. Bot. 36: 49–71.

HILL, G. J. C. & L. MACHLIS. 1970. Defined media for growth and gamete production by the green alga, *Oedogonium cardiacum.* Pl. Physiol. 46: 224–226.

HOARE, D. S., L. O. INGRAM, E. L. THURSTON & R. WALKUP. 1971. Dark heterotrophic growth of an endophytic blue-green alga. Arch. Mikrobiol. 78: 310–321.

HOEK, C. VAN DEN. 1963. Revision of the European Species of *Cladophora.* E. J. Brill, Leiden.

———. 1964. Criteria and procedures in present day algal taxonomy. Pp. 31–58, *in* D. F. Jackson (editor), "Algae and Man." Plenum Press.

HOFFMAN, L. R. 1960. Chemotaxis of *Oedogonium* sperms. Southw. Naturalist 5: 111–116.

———. 1961. Studies of the morphology, cytology and reproduction of *Oedogonium* and *Oedocladium.* Ph.D. Dissertation. Univ. of Texas at Austin.

HOLLENBERG, G. J. & I. A. ABBOTT. 1966. Supplement to Smith's Marine Algae of the Monterey Peninsula. Stanford Univ. Press.

HOLM-HANSEN, O. 1968. Ecology, physiology and biochemistry of blue-green algae. Annual Rev. Microbiol. 22: 47–70.

———, R. PRASAD & R. A. LEWIN. 1965. Occurrence of α, ϵ-diaminopimelic acid in algae and flexibacteria. Phycologia 5: 1–14.

HOOGENHORT, H. 1963. Synchronous cultures of algae. Phycologia 2: 135–147.

HOSHAW, R. W. 1961. Sexual cycles of three green algae for laboratory study. Amer. Biol. Teacher 23: 489–499.

———. 1965. A cultural study of *Sirogonium melanosporium.* Jour. Phycol. 1: 134–138.

——— & R. L. HILTON, JR. 1966. Observations on the sexual cycle of the saccoderm desmid *Spirotaenia condensata.* Jour. Arizona Acad. Sci. 4: 88–92.

HUNTSMAN, S. A. 1972. Organic excretion by *Dunaliella tertiolecta.* Jour. Phycol. 8: 59–63.

HUSTEDE, H. 1964. Entwicklungsphysiologische Untersuchungeu über den Generationswechsel zwischen *Derbesia neglecta* Berth. und *Bryopsis halymeniae* Berth. Biol. Mar. 6: 134–142.

Huth, K. 1970. Bewegung und Orientierung bei *Volvox aureus* Ehrb. I. Mechanismus der phototaktischen Reaktion. Zeitschr. Pflanzenphysiol. 62: 436–450.

———. 1971. Bewegung und Orientierung bei *Volvox aureus* Ehrb. II. Richtungsabweichung bei taktischen Reaktionen. Zeitschr. Pflanzenphysiol. 63: 344–351.

Hutner, S. H. & L. Provasoli. 1964. Nutrition of algae. Annual Rev. Pl. Physiol. 15: 37–56.

*Jackson, D. F. (editor). 1964. Algae and Man. Plenum Press, New York. 434 pp.

*———. 1967. Algae, Man and the Environment. Syracuse Univ. Press. 554 pp.

Jacobs, J. B. & V. Ahmadjian. 1969. The ultrastructure of lichens. I. A general survey. Jour. Phycol. 5: 227–240.

——— & ———. 1971. The ultrastructure of lichens. IV. Movement of carbon products from alga to fungus as demonstrated by high-resolution radio-autography. New Phytol. 70: 47–50.

Jones, R. F. 1970. Physiological and biochemical aspects of growth and gametogenesis in *Chlamydomonas reinhardtii*. Ann. New York Acad. Sci. 175: 648–659.

Kantz, P. T. & H. C. Bold. 1969. Phycological Studies XI. Morphological and taxonomic investigations of *Nostoc* and *Anabaena* in culture. Univ. Texas Publ. 6904.

Kershaw, K. A. & J. W. Milbank. 1970. Nitrogen metabolism in lichens. II. The partition of cephalodial-fixed nitrogen between the mycobiont and phycobiont of *Peltigera apthosa*. New Phytol. 69: 75–79.

Kessler, E. & F. Czygan. 1970. Physiologische und biochemische Beiträge zur Taxonomie der Gattung *Chlorella*. IV. Verwertung organischer Stickstoffverbindungen. Arch. Mikrobiol. 70: 211–216.

——— & I. Zweier. 1971. Physiologische und biochemische Beiträge zur Taxonomie der Gattung *Chlorella*. V. Die auxotrophen und mesotrophen Arten. Arch. Mikrobiol. 79: 44–48.

Khoja, T. & B. A. Whitton. 1971. Heterotrophic growth of blue-green algae. Arch. Mikrobiol. 79: 280–282.

*Klebs, G. 1896. Die Bedingungen der Fortflanzung bei einiger Algen und Pilzen. Gustav Fischer, Jena.

*Klein, R. M. & A. Cronquist. 1967. A consideration of the evolutionary and taxonomic significance of some biochemical, micromorphological, and physiological characters in thallophytes. Quart. Rev. Biol. 42: 105–296.

Kleinig, H. 1969. Carotenoids of siphonous green algae: a chemotaxonomical study. Jour. Phycol. 4: 281–284.

Knaggs, F. W. 1969. A review of florideophycidean life histories and of the culture techniques employed in their investigation. Nova Hedwigia 18: 293–330.

Kochert, G. 1968. Differentiation of reproductive cells in *Volvox carteri*. Jour. Protozool. 15: 438–452.

*Köhler, K. 1967*a*. Die chemischen Grundlagen der Befruchtung (Gamone). Encycl. Pl. Physiol. 18: 282–320.

———. 1967*b*. Phänotypische Geshlechtsbestimmung bei Algen. Encycl. Pl. Physiol. 18: 110–120.

Komárek, J. & L. Ludvík. 1972. Die Zellwandeultrastruktur als taxonomische Merkmal in der Gattung *Scenedesmus* 2. Taxonomische Auswertung der untersuchten Arten. Arch. Hydrobiol. Suppl. 41: 11–47.

Komárková, J. 1969. The systematics and ontogenesis of the genera *Anikistrodesmus* Corda. and *Monoraphidium* gen. nov. Pp. 75–144, *in* "Studies in Phycology."

Kornmann, P. 1938. Zur Entwicklungsgeschichte von *Derbesia* und *Halicystis*. Planta 28: 464–470.

———. 1964. Zur Biölogie von *Spongomorpha aeruginosa* (L.) van den Hoek. Helgoländer Wiss. Meeresuntersuch. 11: 200–208.

———. 1970. Advances in marine phycology on the basis of cultivation. Helgoländer Wiss. Meeresuntersuch. 20: 39–61.

Krauss, R. W. 1958. Physiology of freshwater algae. Annual Rev. Pl. Physiol. 9: 207–244.

———. 1962. Mass culture of algae for food and other organic compounds. Amer. Jour. Bot. 49: 425–435.

Kreger, D. R. 1962. Cell walls. Chapter 19, *in* R. A. Lewin (editor), "Physiology and Biochemistry of Algae." Academic Press, New York. 929 pp.

Kuenzler, E. J. 1970. Dissolved organic phosphorus excretion in marine phytoplankton. Jour. Phycol. 6: 7–13.

KULASOORIYA, S. A., N. LANG & P. FAY. 1972. The heterocysts of blue-green algae. III. Differentiation and nitrogenase activity. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 181: 199–209.

KYLIN, A. & G. DAS. 1967. Calcium and strontium as micronutrients and morphogenetic factors for *Scenedesmus*. Phycologia 6: 201–210.

LANG, N. 1968. The fine structure of blue-green algae. Annual Rev. Microbiol. 22: 15–46.

LAZAROFF, N. 1966. Photoreduction and photoreversal of the nostocacean developmental cycle. Jour. Phycol. 2: 7–17.

LEE, R. E. 1972. Origin of plastids and the phylogeny of algae. Nature 237: 44–46.

LEE, R. K. S. 1966. Development of marine benthic algal communities on Vancouver Island, British Columbia. Pp. 101–120, *in* R. L. Taylor & R. A. Ludwig (editors), "The Evolution of Canada's Flora." Univ. Toronto Press.

*LEEDALE, G. 1967. The Euglenoid Flagellates. Prentice Hall, Inc., Englewood Cliffs. 241 pp.

———. 1970. Phylogenetic aspects of nuclear cytology in the algae. Ann. New York Acad. Sci. 175: 429–453.

LEVINE, R. P. & W. T. EBERSOLD. 1960. The genetics and cytology of *Chlamydomonas*. Annual Rev. Microbiol. 14: 197–216.

——— & C. E. FOLSOME. 1959. The nuclear cycle in *Chlamydomonas reinhardi* [*sic*]. Zeitschr. Vererbungsl. 98: 193–202.

——— & U. W. GOODENOUGH. 1970. The genetics of photosynthesis and of the chloroplasts in *Chlamydomonas reinhardi* [*sic*]. Annual Rev. Genet. 4: 397–408.

*LEVRING, T., H. A. HOPPE & O. J. SCHMID. 1969. Marine Algae. A survey of research and utilization. W. de Gruyter, Berlin and New York. 421 pp.

LEWIN, J. C. 1953. Heterotrophy in diatoms. Jour. Gen. Microbiol. 9: 305–313.

———. 1958. The taxonomic position of *Phaeodactylum tricornutum*. Jour. Gen. Microbiol. 18: 427–432.

———. 1966. Silicon metabolism in diatoms. V. Germanium dioxide, a specific inhibitor of diatom growth. Phycologia 6: 1–12.

LEWIN, R. A. 1950*a*. Gamete behavior in *Chlamydomonas*. Nature 166: 76.

———. 1950*b*. Genetics of *Chlamydomonas moewusii* Gerloff. Proc. Seventh Int. Bot. Congress, Stockholm.

———. 1952. Ultraviolet-induced mutation in *Chlamydomonas moewusii* Gerloff. Jour. Gen. Microbiol. 6: 233–248.

———. 1953. The genetics of *Chlamydomonas moewusii* Gerloff. Jour. Genet. 51: 543–560.

———. 1954. Sex in unicellular algae. Pp. 100–133, *in* D. H. Wenrich (editor), "Sex in Microorganisms." A.A.A.S., Washington, D.C.

———. 1956*a*. Extracellular polysaccharides of green algae. Canad. Jour. Microbiol. 2: 655–672.

———. 1956*b*. Control of sexual activity in *Chlamydomonas* by light. Jour. Gen. Microbiol. 15: 170–185.

———. 1959. The isolation of algae. Rev. Algol. 3: 181–197.

———. 1961. Growth factors: Metabolic factors limiting growth. Phytoflagellates and algae. Encycl. Pl. Physiol. 14: 401–417.

*——— (editor). 1962. Physiology and Biochemistry of Algae. Academic Press, New York. 929 pp.

——— & J. O. MEINHART. 1953. Studies on the flagella of algae. III. Electron micrographs of *Chlamydomonas moewusii*. Canad. Jour. Bot. 31: 711–717.

——— & J. A. ROBERTSON. 1971. Influence of salinity on the form of *Asterocytis* in pure culture. Jour. Phycol. 7: 236–238.

*LEWIS, J. R. 1964. The Ecology of Rocky Shores. The English Universities Press Ltd., London. 323 pp.

LOPPES, R., R. MATAGNE & P. L. STRUKERT. 1972. Complementation at the *Arg*.-7 locus in *Chlamydomonas reinhardi* [*sic*]. Heredity 28: 239–251.

LORCH, D. W. & A. WEBER. 1972. Über die Chemie der Zellwand von *Pleurotaenium trabecula* var. *rectum* (Chlorophyta). Arch. Mikrobiol. 83: 129–140.

LUNING, K. & M. J. DRING. 1972. Reproduction induced by blue light in female gametophytes of *Laminaria saccharina*. Planta 104: 252–256.

MAGNE, F. 1961*a*. Sur le cycle cytologique de *Nemalion helminthoides* (Velley) Batters. Comp. Rend. Hebd. Séances Acad. Sci. Paris 252: 157–159.

———. 1961*b*. Sur la caryologie de deux Rhodophycées considérées jusqu'ici comme à cycle entièrement haplophasique. Comp. Rend. Hebd. Séances Acad. Sci. Paris 252: 4023–4024.

———. 1967. Sur l'existence, chez le *Lemanea,* d'une type de cycle de développement encore inconnu chez les algus rouges. Comp. Rend. Hebd. Séances Acad. Sci. Paris 264D: 2632–2633.

Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161–185.

Manton, I. 1956. Plant cilia and associated organelles. Pp. 61–71, *in* D. Rudnick (editor), "Cellular Mechanisms in Differentiation and Growth."

———. 1966. Observations on scale production in *Prymnesium parvum.* Jour. Cell Sci. 1: 375–380.

———. 1967. Further observations on scale formation in *Chrysochromulina chiton.* Jour. Cell Sci. 2: 411–418.

——— & I. Friedmann. 1960. Gametes, fertilization and zygote development in *Prasiola stipitata* Suhr. II. Electron microscopy. Nova Hedwigia 1: 443–462.

——— & G. F. Leedale. 1969. Observation of the microanatomy of *Coccolithus pelgicus* and *Cricosphaera carterae* with special reference to the origin and nature of coccoliths and scales. Jour. Mar. Biol. Assoc. U.K. 49: 1–16.

——— & M. Parke. 1965. Observation on the fine structure of two species of *Platymonas* with special reference to flagellar scales and the mode of origin of the theca. Jour. Mar. Biol. Assoc. U.K. 45: 743–754.

——— & L. S. Peterfi. 1969. Observations on the fine structure of coccoliths, scales and the protoplast of a freshwater coccolithophorid, *Hymenomonas roseola* Stein, with supplementary observations on the protoplast of *Cricosphaera carterae.* Proc. Roy. Soc. London, Ser. B., Biol. Sci. 172: 1–15.

———, K. Oates & M. Parke. 1963. Observations on the fine structure of the *Pyramimonas* stage of *Halosphaera* and preliminary observations on three species of *Pyramimonas.* Jour. Mar. Biol. Assoc. U.K. 43: 225–238.

*Margalef, R. (editor). 1969. Proceedings of the Sixth International Seaweed Symposium. (Santiago de Compostela, Sept. 9–13, 1968). Madrid. 782 pp.

*Margulis, L. 1970. Origin of Eukaryotic Cells. Yale Univ. Press, New Haven. 349 pp.

Martin, M. T. 1969. A review of life cycles in the Nemalionales and some allied genera. Brit. Phycol. Jour. 4: 145–158.

Mattoni, R. H. T. 1968. Trends in algal genetics. Ch. 11, pp. 201–211, *in* D. F. Jackson (editor), "Algae, Man and the Environment."

Mattox, K. R. & H. C. Bold. 1962. Phycological Studies. III. The taxonomy of certain ulotrichacean algae. Univ. Texas Publ. 6222.

McBride, G. E. 1970. Cytokinesis and ultrastructure in *Fritschiella tuberosa* Iyengar. Arch. Protistenkd. 112: 365–375.

McBride, J. C. & C. S. Gowans. 1967. Pyrithiamine resistance in *Chlamydomonas eugametos.* Genetics 56: 405–412.

McCracken, M. D. & R. C. Starr. 1970. Induction and development of reproductive cells in the K-32 strains of *Volvox rousseletii.* Arch. Protistenkd. 112: 262–282.

McCully, M. E. 1966. Histological studies on the genus *Fucus.* I. Light microscopy of the mature vegetative plant. Protoplasma 62: 287–305.

———. 1968*a*. Histological studies on the genus *Fucus.* II. Histology of the reproductive tissues. Protoplasma 66: 205–230.

———. 1968*b*. Histological studies on the genus *Fucus.* III. Fine structure and possible functions of the epidermal cells of the vegetative thallus. Jour. Cell Sci. 3: 1–16.

McElhenney, T. R., H. C. Bold, R. M. Brown, Jr. & J. P. McGovern. 1962. Algae: a cause of inhalant allergy in children. Ann. Allergy 20: 739–743.

McGuire, R. F. 1969. Attributes of *Chlorococcum* species: a numerical analysis. Jour. Phycol. 5: 220–226.

McLachlan, J., L. C. M. Chen & T. Edelstein. 1971. The culture of four species of *Fucus* under laboratory conditions. Canad. Jour. Bot. 49: 1463–1469.

McLean, R. J. 1968. New taxonomic criteria in classification of *Chlorococcum* species. I. Pigmentation. Jour. Phycol. 4: 328–332.

Milbank, J. W. & K. A. Kershaw. 1969. Nitrogen metabolism in lichens. I. Nitrogen fixation in the cephalodia of *Peltigera apthosa.* New Phytol. 68: 721–729.

Miller, D. H., D. T. A. Lamport & M. Miller. 1972. Hydroxyproline heterooligosaccharides in *Chlamydomonas.* Science 176: 918–920.

Milliger, L. E. & H. E. Schlichting, Jr. 1968. The passive dispersal of viable algae and protozoa by an aquatic beetle. Trans. Amer. Microscop. Soc. 87: 443–448.

Mix, M. 1972. Die Feinstruktur der Zellwande bei Mesotaeniaceae und Gonatozygaceae mit einer vergleichenden Betrachtung der verschiedenen Wandtypen der Conjugatophyceae und über deren systematischen Wert. Arch. Mikrobiol. 81: 197–220.

Moewus, F. 1940. Die Analyse von 42 erblichen Eigenschaften der *Chlamydomonas eugametos* Gruppe. I–III. Zeit. Indukt. Abstammungs-Vererbungsl. 78: 418–462; 463–500; 501–522.

Moiekeha, S. N., G. W. Chu & L. R. Berger. 1971. Dermatitis-producing alga *Lyngya majuscula* Gomont in Hawaii. I. Isolation and chemical characterization of the toxic factor. Jour. Phycol. 7: 4–8.

———, ——— & ———. 1971. Dermatitis-producing alga *Lyngya majuscula* Gomont in Hawaii. II. Biological properties of the toxic factor. Jour. Phycol. 7: 8–13.

Mullahy, J. H. 1952. The morphology and cytology of *Lemanea australis* Atk. Bull. Torrey Bot. Club 79: 393–403; 471–484.

Müller, D. G. 1967. Generationswechsel, Kernphasenwechsel und Sexualität der Braunalge *Ectocarpus siliculosus* in Kulturversuch. Planta 75: 39–54.

———. 1972. Life cycle of the brown alga *Ectocarpus fasciculatus* var. *refractus* (Kütz.) Ardis (Phaeophyceae, Ectocarpales) in culture. Phycologia 11: 11–13.

———, L. Jaenicke, M. Donike & T. Akintobi. 1971. Sex attractant in a brown alga: chemical structure. Science 171: 815–817.

Muscatine, L. 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. Science 156: 516–519.

———. 1971. Experiments on green algae coexistent with zooxanthellae in sea anemones. Pacific Sci. 25: 13–21.

———, S. Karakashian & M. W. Karakashian. 1967. Soluble extra-cellular products of algae symbiotic with a ciliate, a sponge and a mutant *Hydra.* Comp. Biochem. Physiol. 20: 1–12.

Myers, J. 1951. Physiology of algae. Annual Rev. Microbiol. 5: 157–180.

Naylor, A. W. 1970. Phylogenetic aspects of nitrogen metabolism in algae. Ann. New York Acad. Sci. 175: 511–523.

Neushul, M. 1967. Studies on subtidal marine vegetation in western Washington. Ecology 48: 83–94.

Nichols, H. W., D. J. Anderson, J. I. Shaw & M. R. Sommerfeld. 1968. Pyrolysis-gas-liquid chromatographic analysis of chlorophycean and rhodophycean algae. Jour. Phycol. 4: 362–368.

Nultsch, W., G. Throm & I. von Runscha. 1971. Phototaktische Untersuchungen an *Chlamydomonas reinhardii* [*sic*] Dangeard in homokontinuierlicher Kultur. Arch. Mikrobiol. 80: 351–369.

Odum, H. T. & E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25: 291–320.

Ogata, E., T. Matsui & H. Nakamura. 1972. The life cycle of *Gracilaria verrucosa* (Rhodophyceae, Gigartinales) *in vitro.* Phycologia 11: 75–80.

Ohmori, M. & A. Hattori. 1971. Nitrogen fixation and heterocysts in the blue-green alga *Anabaena cylindrica.* Pl. Cell Physiol. 12: 961–967.

Oschman, J. L. 1966. Development of the symbiosis of *Convoluta roscoffensis* Graff and *Platymonas* sp. Jour. Phycol. 2: 105–111.

Outka, D. E. & D. C. Williams. 1971. Sequential coccolith morphogenesis in *Hymenomonas carterae.* Jour. Protozool. 18: 285–297.

Papenfuss, G. F. 1955. Classification of algae. Pp. 115–224, *in* "A Century of Progress in the Natural Sciences, 1853–1953." California Acad. Nat. Sci., San Francisco.

———. 1966. A review of the present system of classification of the Florideophycideae. Phycologia 5: 247–255.

Parker, B. C. 1961. Facultative heterotrophy in certain soil algae from the ecological viewpoint. Ecology 42: 381–386.

———. 1968. Rain as a source of vitamin B_{12}. Nature 219: 617–618.

———. 1970*a*. Life in the sky. Nat. Hist. 76: 54–59.

———. 1970*b*. Significance of cell wall chemistry to phylogeny in the algae. Ann. New York Acad. Sci. 175: 417–428.

——— & B. L. Turner. 1961. "Operational niches" and "Community-interaction values" as determined from *in vitro* studies of some soil algae. Evolution 15: 228–238.

——— & M. A. Wachtel. 1971. Seasonal distribution of cobalanins, biotin, and niacin in rainwater. *In* J. Cairns, Jr. (editor), "The structure and function of fresh-water microbial communities." Virginia Polytech. Inst. State Univ. Res. Monogr. 3.

Parsons, W. M., H. E. Schlichting & K. W. Stewart. 1966. Inflight transport of algae and protozoa by selected *Odonata*. Trans. Amer. Microscop. Soc. 85: 520–527.

Pascher, A. 1916. Über die Kreuzung einzelliger, haploider Organismen: *Chlamydomonas*. Ber. Deutsch. Bot. Ges. 34: 228–242.

———. 1918. Über die Beziehung der Reduktionsteilung zur Mendelschen Spaltung. Ber. Deutsch. Bot. Ges. 36: 163–168.

Patrick, R. & C. W. Reimer. 1966. The Diatoms of the United States. Vol. 1. Acad. Nat. Sci., Philadelphia.

*Percival, E. & R. H. McDowell. 1967. Chemistry and Enzymology of Marine Algal Polysaccharides. Academic Press, London and New York. 219 pp.

Pickett-Heaps, J. D. 1972*a*. Variation in mitosis and cytokinesis in plant cells: its significance in the phylogeny and evolution of ultrastructural systems. Cytobios 17: 59–77.

———. 1972*b*. A possible virus infection in the green alga *Oedogonium*. Jour. Phycol. 8: 44–47.

———. 1972*c*. Cell division in *Klebshormidium subtilissimum* (formerly *Ulothrix subtilissima*), and its possible phylogenetic significance. Cytobios 6: 167–183.

——— & L. C. Fowke. 1969. Cell division in *Oedogonium*. I. Mitosis, cytokinesis and cell elongation. Austral. Jour. Biol. Sci. 22: 857–894.

——— & H. J. Marchant. 1972. The phylogeny of green algae: a new proposal. Cytobios 24: 255–264.

Pienaar, R. N. 1969*a*. The fine structure of *Hymenomonas* (*Cricosphaera*) *carterae*. I. External morphology. Jour. Cell Sci. 4: 561–567.

———. 1969*b*. The fine structure of *Hymenomonas* (*Cricosphaera*) *carterae*. II. Observations of scale and coccolith production. Jour. Phycol. 5: 321–331.

Pocock, M. A. 1960. *Hydrodictyon*: a comparative biological study. Jour. S. Afr. Bot. 26: 167–327.

Pollock, E. G. 1969. Interzonal transplantation of embryos and mature plants of *Fucus*. Pp. 345–356, *in* "Proceedings of the Sixth International Seaweed Symposium."

———. 1970. Fertilization in *Fucus*. Planta 92: 85–99.

*Prescott, G. W. 1962. Algae of the Western Great Lakes Area. W. C. Brown, Dubuque, Iowa.

———. 1964. Contributions of current research to algal systematics. Pp. 1–30, *in* D. F. Jackson (editor), "Algae and Man." Plenum Press, New York.

Preston, R. D. 1968. Plants without cellulose. Sci. Amer. 218(6): 102–108.

Pringsheim, E. G. 1946. Pure Cultures of Algae, their Preparation and Maintenance. Cambridge Univ. Press.

———. 1956. Contributions toward a monograph of the genus *Euglena*. Nova Acta Leop. 18: 1–168.

———. 1967. Phycology in the field and in the laboratory. Jour. Phycol. 3: 93–95.

——— & O. Pringsheim. 1959. Die Ernährung koloniebildender Volvocales. Biol. Zentralbl. 78: 937–971.

Proctor, V. W. 1966. Dispersal of desmids by water birds. Phycologia 5: 227–232.

Provasoli, L. 1964. Growing marine seaweeds. *In* A. D. DeVirville & J. Feldmann (editors), "Proceedings of the Fourth International Seaweed Symposium at Biarritz." Macmillan Co.

———. 1968. Media and prospects for the cultivation of marine algae. Pp. 63–75, *in* A. Watanabe & A. Hattori (editors), "Cultures and Collections of Algae." Proc. U.S.—Japan Conf. Hakone, Sept. 1966. Jap. Soc. Plant. Physiol.

——— & I. J. Pintner. 1960. Artificial media for freshwater algae: problems and suggestions. Pp. 84–96, *in* C. A. Tryon, Jr. & R. T. Hartman (editors), "The Ecology of Algae." Spec. Pub. 2, Pymatung Lab. Field Biol. Univ. Pittsburgh.

———, J. A. McLachlan & M. R. Droop. 1957. The development of artificial media for marine algae. Arch. Mikrobiol. 25: 392–428.

———, T. Yamasu & I. Manton. 1968. Experiments on the resynthesis of symbiosis in

Convoluta roscoffensis with different flagellate cultures. Jour. Mar. Biol. Assoc. U.K. 48: 465–479.

PUNNETT, T. & E. C. DERRENBACKER. 1966. The amino acid composition of algal cell walls. Jour. Gen. Microbiol. 44: 105–114.

RAMUS, J. 1972. The production of extracellular polysaccharide by the unicellular red alga *Porphyridium aerugineum*. Jour. Phycol. 8: 97–111.

RAVEN, P. H. 1970. A multiple origin of plastids and mitochondria. Science 159: 641–646.

RAWITSCHER-KUNKEL, E. & L. MACHLIS. 1962. The hormonal integration of sexual reproduction in *Oedogonium*. Amer. Jour. Bot. 49: 177–183.

REIMANN, B. E. F., J. LEWIN & B. E. VOLCANI. 1966. Studies on the biochemistry and fine structure of silica shell formation in diatoms. II. The structure of the cell wall of *Navicula pelliculosa* (Breb.) Hilse. Jour. Phycol. 12: 74–84.

ŘEHÁKOVÁ, H. 1969. Die Variabiltät der Arten der Gattung *Oocystis* A. Braun. Pp. 145–196, *in* "Studies in Phycology." Academia.

RICHARDSON, D. N. S., D. J. HILL & D. C. SMITH. 1968. Lichen physiology. XI. The role of the alga in determining the patterns of carbohydrate movement between lichen symbionts. New Phytol. 67: 469–486.

RIETMA, H. 1971. Life-history studies in the genus *Bryopsis* (Chlorophyceae). V. Life-histories in *Bryopsis hypnoides* Lamx. from different points along the European coasts. Acta Bot. Neerl. 20: 291–298.

RIPPKA, R., A. NEILSON, R. KUNISAWA & G. COHEN-BAZIRE. 1971. Nitrogen fixation by unicellular blue-green algae. Arch. Mikrobiol. 76: 341–348.

RIS, H. & W. PLAUT. 1962. Ultrastructure of DNA-containing areas in the chloroplast of *Chlamydomonas*. Jour. Cell Biol. 13: 383–391.

ROBBINS, W. J., A. HERVEY & M. E. STEBBINS. 1950. Studies of *Euglena* and vitamin B_{12}. Bull. Torrey Bot. Club 77: 423–441.

ROBERTS, K., M. GURNEY-SMITH & G. J. HILLS. 1972. Composition and morphogenesis of the cell wall of *Chlamydomonas reinhardi* [*sic*]. Jour. Ultrastruct. Res. 40: 599–613.

*ROSOWSKI, J. R. & B. C. PARKER (editors). 1971. Selected Papers in Phycology. Dept. Botany, Univ. of Nebraska, Lincoln. 876 pp.

ROUND, F. E. 1963. The taxonomy of the Chlorophyta. Brit. Phycol. Bull. 2: 224–225.

———. 1971. The taxonomy of the Chlorophyta. II. Brit. Phycol. Bull. 6: 235–264.

RYTHER, J. H. 1969. Photosynthesis and fish production in the sea. Science 166: 72–74.

SAFFERMAN, R. S. 1968. Virus diseases in blue-green algae. Ch. 21, pp. 429–439, *in* D. F. Jackson (editor), "Algae, Man and the Environment."

SAGER, R. 1954. Mendelian and non-Mendelian inheritance of streptomycin resistance in *Chlamydomonas*. Proc. Natl. Acad. U.S.A. 40: 356–363.

——— & S. GRANICK. 1954. Nutritional control of sexuality in *Chlamydomonas reinhardi* [*sic*]. Jour. Gen. Physiol. 37: 729–742.

——— & Z. RAMANIS. 1970. A genetic map of non-Mendelian genes in *Chlamydomonas*. Proc. Natl. Acad. U.S.A. 65: 593–600.

SCHINDLER, D. W. 1971. Carbon, nitrogen, and phosphorus and the eutrophication of freshwater lakes. Jour. Phycol. 7: 321–329.

SCHLICHTING, H. E., JR. 1964. Meteorological conditions affecting the dispersal of airborne algae and protozoa. Lloydia 27: 64–78.

———. 1969. The importance of airborne algae and protozoa. Jour. Air Pollution Control Assoc. 19: 946–951.

———. 1970. Airborne algae and protozoa. Carolina Tips 33: 33–34.

SCHNEPF, E. & R. M. BROWN, JR. 1971. On relationships between endosymbiosis and the origin of plastids and mitochondria. Results and Problems in Cell Differentiation 2: 299–322.

SCHWIMMER, D. & M. SCHWIMMER. 1964. Algae and medicine. *In* D. F. Jackson (editor), "Algae and Man." Plenum Press.

SHIHIRA, I. & R. W. KRAUSS. 1965. *Chlorella.* Univ. Maryland, College Park.

SHILO, M. 1967. Formation and mode of action of algal toxins. Bacteriol. Rev. 31: 180–193.

*SMITH, G. M. (editor). 1951. The Manual of Phycology. Chronica Botanica Co., Waltham, Mass. 375 pp.

SMITH, K. M., R. M. BROWN, JR. & P. L. WALNE. 1967. Ultrastructural and time-lapse studies on the replication cycle of the blue-green algal virus LPP-1. Virology 31: 329–337.

SPRUNG, D. C. & D. E. WUJEK. 1971. Chemotaxonomic studies of *Pleurastrum* Chodat by means of pyrolysis gas-liquid chromatography. Phycologia 10: 251–254.

STANIER, R. Y., R. KUNISAIVA, M. MANDEL & G. COHEN-BAZIRE. 1971. Purification and properties of unicellular blue-green algae (Order Chroococcales). Bacteriol. Rev. 35: 171–205.

STARR, R. C. 1959. Sexual reproduction in certain species of *Cosmarium*. Arch. Protistenk. 104: 155–164.

———. 1964. The culture collection of algae at Indiana University. Amer. Jour. Bot. 51: 1013–1044.

———. 1968. Cellular differentiation in *Volvox*. Proc. Natl. Acad. U.S.A. 59: 1082–1088.

———. 1969. Structure, reproduction and differentiation in *Volvox carterae* f. *nagariensis* Strains H K 9 and 10. Arch. Protistenk. 111: 204–222.

———. 1971. The culture collection of algae at Indiana University: additions to the collection July 1966–July 1971. Jour. Phycol. 7: 350–362.

STEIN, J. 1966. Growth and mating of *Gonium pectorale* (Volvocales) on defined media. Jour. Phycol. 2: 23–28.

——— & C. C. AMUNDSEN. 1967. Studies on snow algae and fungi from the Front Range of Colorado. Canad. Jour. Bot. 45: 2033–2045.

——— & R. C. BROOKE. 1964. Red snow from Mt. Seymour, British Columbia. Canad. Jour. Bot. 42: 1183–1188.

STEWART, J. K. 1971. The biology of the green alga *Characiosiphon rivularis* Iyengar. Ph.D. Dissertation, The University of Texas at Austin.

STEWART, W. D. P., A. HAYSTEAD & H. W. PEARSON. 1969. Nitrogenase activity in the heterocysts of filamentous blue-green algae. Nature 224: 226–228.

STOSCH, H. A. VON. 1964. Wirkungen von Jod und Arsenit auf Meeresalgen in Kultur. *In* A. D. De Virville & J. Feldmann (editors), "Proceedings of the Fourth International Seaweed Symposium at Biarritz." The Macmillan Co.

———. 1965. Sexualität bei *Ceratium cornutum* (Dinophyta). Die Naturwiss. 5: 111–113.

——— & G. DREBES. 1964. Entwicklungsgeschichtliche Untersuchungen an zentrischen Diatomeen. 4. Die Plankton Diatomee, *Stephanopyxis turris*, ihre Behandlung und Entwicklungsgeschichte. Helgoländer Wiss. Meeresuntersuch. 11: 209–257.

SULEK, J., JR. 1969. Taxonomische Übersicht der Gattung *Pediastrum* Meyen. Pp. 197–261, *in* "Studies in Phycology." Academia.

SYRETT, P. J. 1962. Nitrogen assimilation. Pp. 171–188, *in* R. A. Lewin (editor), "Physiology and Biochemistry of Algae." Academic Press.

TAYLOR, D. L. 1970. Chloroplasts as symbiotic organelles. Int. Rev. Cytol. 27: 29–64.

*TAYLOR, W. R. 1960. Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas. Univ. Michigan Press, Ann Arbor.

THOMAS, D. L. & R. M. BROWN, JR. 1970*a*. Isoenzyme analysis and morphological variation of thirty-two isolates of *Protosiphon*. Phycologia 9: 285–292.

——— & ———. 1970*b*. New taxonomic criteria in the classification of *Chlorococcum* species. III. Isoenzyme analysis. Jour. Phycol. 6: 293–299.

——— & J. B. DELCARPIO. 1971. Electrophoretic analysis of enzymes from three species of *Chlamydomonas*. Amer. Jour. Bot. 58: 716–720.

THOMAS, W. H. 1972. Observations on snow algae in California. Jour. Phycol. 8: 1–9.

TOTH, R. & R. T. WILCE. 1972. Viruslike particles in the marine alga *Chorda tomentosa* Lyngbye (Phaeophyceae). Jour. Phycol. 8: 126–130.

TRAINOR, F. R. 1959. A comparative study of sexual reproduction in four species of *Chlamydomonas*. Amer. Jour. Bot. 46: 65–70.

———. 1965. A study of *Scenedesmus* incubated in nature and in the laboratory. Canad. Jour. Bot. 43: 701–706.

———. 1970. Algal morphogenesis: nutritional factors. Ann. New York Acad. Sci. 175: 749–756.

——— & R. L. HILTON. 1966. *Chlorosarcinopsis variabilis* sp. nova from a Connecticut cornfield soil. Jour. Phycol. 2: 156–159.

TRENCH, R. K. 1971*a*. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. I. The assimilation of photosynthetic products of zooxanthellae by two marine coelenterates. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 177: 225–235.

———. 1971*b*. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. II. Liberation of fixed ^{14}C by zooxanthellae *in vitro*. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 177: 237–250.

———. 1971*c*. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. III. The effect of homogenates of host tissue on the excretion of photosynthetic products *in vitro* by zooxanthellae from two marine coelenterates. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 177: 251–264.

———, M. E. TRENCH & L. MUSCATINE. 1972. Symbiotic chloroplasts; their photosynthetic products and contribution to mucus synthesis in two marine slugs. Biol. Bull. 142: 335–349.

*TRYON, C. A., JR. & R. T. HARTMAN. 1960. The Ecology of Algae. Special Publ. 2, Pymatuning Laboratory, Univ. Pittsburgh.

TUPA, D. 1972. An investigation of certain chaetophoralean algae. Ph.D. Dissertation, The University of Texas at Austin.

UMEZAKI, L. 1967. The tetrasporophyte of *Nemalion vermiculare* Suringar. Rev. Algol. 9: 19–24.

VANCE, B. D. & H. B. WARD. 1969. Preparation of metabolically active protoplasts of blue-green algae. Jour. Phycol. 1: 1–5.

VANDE BERG, W. J. & R. C. STARR. 1971. Structure, reproduction and differentiation in *Volvox gigas* and *Volvox powersii*. Arch. Protistenk. 113: 195–210.

VAN DOVER, B. 1972. Studies of the ultrastructure and reproduction of several species of *Chlamydomonas* and *Carteria*. Ph.D. Dissertation. The University of Texas at Austin.

WAGNER, G., W. HAUPT & A. LAUX. 1972. Reversible inhibition of chloroplast movement by cytochalasin B in the green alga *Mougeotia*. Science 176: 808–809.

WALSBY, A. E. 1972. Structure and function of gas vacuoles. Bacteriol. Rev. 36: 1–32.

WEBBER, M. M. & P. J. WEBBER. 1970. Ultrastructure of lichen haustoria: symbiosis in *Parmelia sulcata*. Canad. Jour. Bot. 48: 1521–1524.

WEST, J. A. 1968. Morphology and reproduction of the red alga *Acrochaetium pectinata* in culture. Jour. Phycol. 4: 89–99.

———. 1969. The life histories of *Rhodochorton purpureum* and *R. tenue* in culture. Jour. Phycol. 5: 12–21.

———. 1970. The life history of *Rhodochorton concrescens* in culture. Brit. Phycol. Jour. 5: 179–186.

WHITTON, B. A. 1965. Extracellular products of blue-green algae. Jour. Gen. Microbiol. 40: 1–11.

WIEDEMAN, V. E. & H. C. BOLD. 1965. Heterotrophic growth of selected waste-stabilization pond algae. Jour. Phycol. 1: 66–69.

WIESE, L. 1965. On sexual agglutination and mating-type substances (gamones) in isogamous heterothallic chlamydomonads. I. Evidence of the identity of the gamones with the surface components responsible for sexual flagellar contact. Jour. Phycol. 1: 46–54.

———. 1969. Algae. Ch. 4, pp. 135–188, *in* "Fertilization." Vol. 2. Academic Press, New York.

——— & R. F. JONES. 1963. Studies on gamete copulation in heterothallic chlamydomonads. Jour. Cell. Comp. Phys. 61: 265–274.

——— & C. B. METZ. 1969. On the trypsin sensitivity of fertilization as studied with living gametes in *Chlamydomonas*. Biol. Bull. 136: 483–493.

WOLK, C. P. 1973. Physiology and cytological chemistry of blue-green algae. Bacteriol. Rev. 37: 32–101.

WOLKEN, J. J. 1960. Photoreceptors: comparative studies. *In* "Comparative Biochemistry of Photoreactive Systems." Symposia on Comparative Biology 1. Academic Press. New York.

WOOD, R. D. & P. E. HARGRAVES. 1969. Comparative benthic plant ecology by Scuba-monitored quadrats. Hydrobiologia 33: 561–586.

WORK, E. & D. C. DEWEY. 1953. The distribution of α, ε–diaminopimelic acid among various micro-organisms. Jour. Gen. Microbiol. 9: 394–409.

WYNNE, M. J. 1969. Life history and systematic studies of some Pacific North American Phaeophyceae (Brown algae). Univ. California Pub. Bot. 50: 1–88.

*YOUNG, E. G. & J. L. MCLACHLAN (editors). 1966. Proceedings of the Fifth International Seaweed Symposium (Halifax). Pergamon Press. 424 pp.

*ZAJIC, J. E. (editor). 1970. Properties and Products of Algae. Plenum Press. 154 pp.

ZANEVELD, J. S. 1969. Factors controlling the delimitation of littoral benthic marine algal zonation. Amer. Zoologist 9: 367–391.

25 years of botany

LICHENOLOGY IN NORTH AMERICA
1947–1972

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In assessing the advances of lichenology in North America during the past quarter century it is essential to have an understanding of the situation as it existed at the start. The literature was not very abundant, nor was it readily available to many people in understanding or in fact. The then recently published manual by Bruce Fink (1935) was highly technical and difficult to use. His excellent *Lichens of Minnesota* (1910) with more comprehensive descriptions was occasionally on the secondhand market. Some of us were able to purchase Tuckerman's *North American Lichens* (1881, 1888) and used these with some difficulty in understanding how terms should be applied to the lichens at hand. The very fine literature of Europe was unavailable to most would-be lichenologists because of its rarity in libraries as well as language barriers. The monographs on North American lichens were rare indeed—Willey (1890) on *Arthonia*, and Berry (1941) on *Parmelia*. The brightest spot was with respect to the genus *Cladonia*. The very great and penetrating works on this genus by Alexander Evans and his prompt and willing help to beginners plus the aid he enlisted of Raymond H. Torrey fostered an interest in these lichens, especially along the East Coast.

Other workers active in lichenology in this period included A. W. C. T. Herre, who had just returned from his long stay in the Philippines working on fishes and resumed work and publishing on lichens. His 1913 thesis on the lichens of the Santa Cruz Peninsula is still very valuable. Herre worked for a time at Stanford University before he was required to retire but continued to be helpful to many by correspondence. Carroll W. Dodge had published on the Antarctic lichens (Dodge & Baker, 1938) but also had several students, including E. C. Berry, George A. Llano, and E. D. Rudolph. Grace Howard at Wellesley College was working on the lichens of the state of Washington which she published (1950) after her retirement and in association with the University of Washington. At the University of Michigan Joyce Hedrick Jones continued as curator of the Bruce Fink collections which had been acquired by that university. Several students, including Henry A. Imshaug, were being guided by the University of Michigan mycologist, Alexander H. Smith. The New Jersey rhododendron grower Guy G. Nearing, who had been interested by Raymond Torrey in lichens, was

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in this period publishing his *Lichen Book* (1947), hand setting the pages with his own fonts and printing the parts on his own small hand press. We must include Margaret Fulford of the University of Cincinnati who stirred the interest of several students, including W. L. Culberson, in continuing work with lichens. W. L. Dix, another of Torrey's disciples and a Latin teacher in Staten Island schools, was also active as a student of *Cladonias*. Babette Brown Coleman was working on the ecology of lichens in upstate New York, and Josiah Lowe was producing an excellent paper on *Lecidea* in the Adirondacks. Roy Latham of Long Island, yet another of Torrey's coterie, was interested in *Cladonia alpestris* and *Cetraria islandica*. I. Mackenzie Lamb, later to become Director of the Farlow Herbarium, was still abroad and had not migrated to this continent. When all is considered, the active number of lichen students a quarter century ago was really rather small. The progress and interest in this group of organisms as objects of study has accelerated and deepened immensely. The breadth of approaches has also widened.

Lichen Chemistry

Probably the most significant advance in the study of lichens on this continent has been the application of chemistry to lichen taxonomy. Although founded upon earlier researches in Germany by Hess and Zopf, it was not possible to advance much until the work of Asahina in Japan, commencing in the 1930's and 1940's and continuing to the present, made it possible to identify lichen substances by the microscopic crystals formed by the reactions of organic reagents with extracts requiring but a tiny portion of a lichen thallus. This fascinating new development was enthusiastically embraced by Alexander Evans at Yale and led to a long series of studies on the genus *Cladonia*, which appeared in papers from 1943–1955 (list in Thomson, 1967*c*). At about the time the Culbersons were at Wisconsin as graduate students, they became interested in the field of lichen chemistry and taxonomy and have collaborated since with remarkable results. A long series of papers by either William or Chicita or both has culminated in the production of the 1969 book *Chemical and Botanical Guide to Lichen Products* by Chicita F. Culberson and its 1970 supplement in *The Bryologist*. These are landmark contributions to the field of lichenology. Chicita Culberson has also been developing to a fine art the use of thin-layer chromatography in the solution of problems involving lichen chemistry, and she and students working with her will be contributing much in that field which still has many, many opportunities to exploit. The 1970 paper on a standardized method for the identification of lichen products is an important contribution which is already influencing procedures in lichen research (C. F. Culberson & Kristinsson, 1970). Much lichen chemistry as applied to taxonomic problems has also been contributed by Mason E. Hale, Jr., starting with papers published from 1952 on. His discussion of the relationship between chemistry and the evolution of lichens (1966) has been influential in the development of thought in that field and will be recognized as such. Another earlier (1956) paper on the fluorescence of lichen products brought to this country the use of a new and helpful tool, the use of ultraviolet light, in lichen systematics. It provided one more set of characteristics by which decisions in identification could be made. Of course, the fluorescence is dependent upon the products contained in the lichens, but this tool has been used to great advantage in the systematics of *Thamnolia, Pyxine, Cladonia,* and *Cetraria,* among others.

LICHEN TAXONOMY

The status of revisions of the genera of lichens of North America is very uneven. Few papers have been published on the crustose lichens: *Placynthium, Arctomia, Vestergrenopsis, Massalongia,* and *Koerberia* by Henssen (1963*a–d*, 1969), *Ochrolechia* by Howard (1970) and Verseghy (1962), *Rhizocarpon* (Thomson, 1967*a*), *Cyphelium* (Weber, 1967), the Trypetheliaceae (Johnson, 1959), *Haematomma* (W. L. Culberson, 1963), and the Heppiaceae by Wetmore (1970). Rudolph is working upon *Caloplaca,* Sheard upon *Rinodina,* Imshaug upon *Buellia,* Hale upon Thelotremaceae, R. A. Anderson upon *Lecidea,* Dibben upon *Pertusaria,* and Thomson upon *Staurothele,* but many more genera need to be studied in the decades ahead. The larger foliose and fruticose lichens have been much better studied, and the past two decades especially have vastly improved our knowledge of these. There are larger papers now available on *Alectoria* (Motyka, 1964), *Anaptychia* (Kurokawa, 1962; W. L. Culberson, 1966), *Baeomyces* (Thomson, 1967*b*), *Cetraria* and related genera (W. L. Culberson & Culberson, 1965, 1967, 1968), *Cladonia* (Thomson, 1967*c*), *Parmelia* (Ahti, 1966, 1969; Hale, 1965; Hale & Kurokawa, 1964), *Peltigera* (Thomson, 1950), *Physcia* (Thomson, 1963), *Pseudevernia* (Hale, 1968), *Nephroma* (Wetmore, 1960), *Tholurna* (Otto, 1972), and Umbilicariaceae (Llano, 1950, 1956). I. M. Lamb continues with the preparation of his immense monograph on *Stereocaulon.* In addition to these are many shorter papers which can be found in the "Recent Literature on Lichens," listings regularly published by W. L. Culberson in *The Bryologist.* Of indispensible help to the lichenologist is I. M. Lamb's *Index Nominum Lichenum* (1963) which continued the Zahlbruckner *Catalogus Lichenum Universalis.*

FLORISTICS

The greatest activity apparent in North American lichenology has been a spate of papers inventorying the lichens of local areas or states. Many of these papers have been stimulated by the policy of the American Bryological and Lichenological Society holding its meetings with the A.I.B.S., and as the meetings were held in various parts of the continent from New England to Florida, California, Washington, or Alberta, the associated forays have been reported upon with concomitant increase in knowledge of the lichens of those areas. There are over a hundred papers produced during this period, too numerous to list here, but of interest may be the diversity of the states represented: Alabama, 3 papers; Alaska, 15 papers; Arizona, 4 papers; Arkansas, 1 paper; California, 5 papers; Connecticut, 3 papers plus a long series by Evans; Delaware, 1 paper; District of Columbia, 1 paper; Florida, 2 papers; Georgia, 1 paper; Idaho, 4 papers; Louisiana, 2 papers; Maryland, 1 paper; Michigan, 4 papers; Minnesota, 3 papers; Mississippi, 1 paper; Missouri, 1 paper; Montana, 2 papers; New Jersey, 1 paper; New Mexico, 3 papers; New York, 4 papers; Oklahoma, 2 papers; Ohio, 2 papers; Oregon, 1 paper; South Dakota, 1 paper; Tennessee, 3 papers; Utah, 1 paper; Virginia, 5 papers; Washington, 8 papers; Wisconsin, 6 papers; and Wyoming, 1 paper. In addition to records in these geographically oriented papers, other states have been represented by records in papers upon particular taxonomic groups. It is sufficient to call attention to the fact that many states are not represented on the above lists and are as yet to be worked upon. Even the 30 mentioned above are incompletely known and still will be needing much more work in the future. Our Canadian colleagues, I. M. Brodo, George Otto, C. D. Bird, J. W. Sheard, D. F. S. Richardson, Jan Looman, George Scotter, J. D. H. Lambert, Vladimir Krajina, and R. E. Longton are all busy adding to the regional information on their side of the border.

This period seems to have been a period of stock-taking, of the compilation of catalogs or area lists with intent of producing further area studies. Such listings include Colorado (Shushan & Anderson, 1969), Mexico (Imshaug, 1956), New Mexico (Egan, 1972), Long Island, New York (Brodo, 1968), Wyoming and South Dakota (Wetmore, 1967), and Washington (Thomson, 1969). Our Canadian colleagues have produced similar inventories on Quebec (Lepage, 1947–1949, 1958); Alberta, Saskatchewan, and Manitoba (Bird, 1966); British Columbia (Ahti & Otto, 1967); and Yukon (Bird, 1967). Wetmore has compiled one on Tasmania (1963) and Imshaug one on the West Indies (1957). Nor should we forget the extremely helpful checklists of North American lichens compiled by Hale and Culberson (1956, 1960, 1966, and 1970).

Extraterritorial papers have been produced on South America, the Galapagos Islands, Antarctica, and the Antarctic Islands by G. A. Llano, W. A. Weber, I. M. Lamb, C. W. Dodge, and E. D. Rudolph. These very numerous and intensive papers are not listed here but can easily be found in the Culberson literature listings. They represent a very large step forward, especially in the most important vegetation of Antarctica, an area which has but two angiosperms, 50 mosses, and over 400 species of lichens.

Manuals and Aids

Perhaps most important in the recruitment of new talent and interest in lichenology is the production of manuals and illustrated books for the beginner. The *Lichen Handbook* (1961) and *How to Know the Lichens* (1969) by Mason E. Hale, Jr. are among the most important advances in our field, as they open the field to beginners. Hitherto it was very difficult to get a start in lichenology without the assistance of someone to guide the first steps in identification. These new manuals, containing illustrations and keys, of the common larger species of foliose and fruticose lichens make it possible for a beginner to get a reasonable start in lichenology. The crustose lichens are still a difficult task, and although outdated the Fink *Lichen Flora* (1935) is still the only reference for a starter to use. Very fine manuals for the beginner to use are the Taylor *Lichens of Ohio*, parts 1 and 2 (1967, 1968), covering the larger lichens of that state. For the beginner in lichen chemistry the appropriate parts of Hale (1961), Taylor (1967, 1968), or Thomson (1967*c*) will serve well in securing a foundation knowledge as they are well illustrated with the crystalline reaction products. For continued study, *The Bryologist*, published by the American Bryological and Lichenological Society, is essential as it has many articles on lichens in its issues. As an entrance into the literature it is also essential to consult the series of listings "Recent Literature on Lichens" which William Culberson founded in 1955 while at the University of Wisconsin and which he still produces for practically every issue of *The Bryologist*. It is a very essential service because the literature of lichenology is so far scattered amid so many and sometimes obscure publications. In this connection it is necessary to note the founding of the British Lichen Society in 1958 and its publication *The Lichenologist* with a first number in 1958 and a continual enlargement and improved quality since then. The British Lichen Society boasts of over 400 members, attesting to the swelling interest in these organisms (?). Even more recent is the founding of the *Lichenological Newsletter* in April 1967 by Vernon Ahmadjian, Irwin Brodo, and Mason E. Hale, Jr., as a "house organ" by which lichenists can keep informed of each other's activities and opinions. The typesetting and printing of this is done by Hale and son as a labor of love. An International Association for Lichenology was also formed during the XI Botanical Congress at Seattle. Vernon Ahmadjian (United States) and Irwin Brodo (Canada) serve as the American representatives on the council.

Lichen Ecology

Turning now to ecological studies of lichens, we find several new and important aspects of lichenology have developed in this continent over the past quarter century. Earlier works of ecological nature had been produced by Bruce Fink and his students. In the main, these consisted of lists of lichens growing in particular habitats. A break with this tradition occurred in a paper by Wolfe, Wareham, and Scofield (1949) emphasizing the influence of microclimates on plant distributions. A major new approach to the ecology of cryptogams is exemplified by the papers of Hale (1952*a*, 1955) and W. L. Culberson (1955*a*, 1955*b*), who utilized the ordination of communities and their components, mosses and lichens, to obtain an unbiased reflection of the situation in the field in the forests of Wisconsin. Studies using similar approaches but enlarging the scope of the communities have been published by Looman (1964) on grasslands and by Foote (1966) on rock outcrops. Deeper incursion into the mathematics of such ecologies may be found in the works of Beals (1965) and Yarranton (1969).

For some reason, perhaps the slowness of growth rates in lichens, there seems to have been a strong interest in measurement of this, and a number of papers have appeared on this subject, notable ones being by Hale (1954, 1959), Brodo (1965), Pegau (1968), and Scotter (1963). An important application of studies on growth rate became known as lichenometry through the perspicuous and internationally famous work of the late Roland Beschel of Canada. Beschel made numerous studies of the retreats of glaciers and icecaps, using the age of lichens as a dating device (Beschel, 1961). The oldest lichens known to him, according to his publications, were 4,500 years of age, among the world's oldest living things. The productivity of lichens has barely been touched with one paper on alpine lichen productivity by Bliss (1966) and one by Scotter (1962).

With the advent of the nuclear bombs and the worldwide dissemination of the products of the tests, there came an interest in the fallout of the tests and their influence on the lichens, which obtain a large part of their mineral nutrition from the dusts of the atmosphere. The classic paper in this field is that by Palmer *et al.* (1963) on cesium-137 in Alaskan Eskimos, pointing out the short food chain involving only lichens, caribou, and Eskimos of the Anaktuvuk Pass, Alaska, region. This short chain brings unusually high radioactivities to man. A further paper by Salo and Miettinen (1964) showed the accumulation of strontium-90 and cesium-137 in arctic vegetation, and still further papers by Hanson (1967) and Plummer and Helseth (1965) have also dealt with this problem. A paper by Woodwell and Gannutz (1967) is important in demonstrating the effects of gamma radiation on a forest lichen community in an experimental setting. Undoubtedly, further researchers will have very much more to say upon this extremely serious problem.

Another environmental problem, although not perhaps a new one, since Nylander in the 1850's complained of the influence of the air pollution in Paris on lichen distributions, is that of air pollution. Studies of the relationships of lichens to polluted air have been common for some time in Europe. In fact, certain lichens, according to Barkman, have become extinct in parts of Europe as a consequence of air pollution. LeBlanc and Rao, in Quebec, have made such problems a major study and a classic paper is theirs on the effects of the pollution by an iron-scintering plant in Ontario on the cryptogamic vegetation (Rao & LeBlanc, 1967). In other studies they have published on the effects of urban environments on lichen distributions (LeBlanc, 1961). Another important paper is that by Brodo (1966) on lichen ecology in central Long Island, New York, pointing out the effects of air pollution in that region.

A paper in lichen ecology important in introducing a new technique for transplanting corticolous lichens (or mosses) by the use of bark plugs is that by Brodo (1961*b*).

Comparatively few studies of water and temperature relations of lichens have been carried out in this country. These have been the subject of investigations in Germany and Japan especially. But a few investigators on this continent should be mentioned, including L. C. Pearson (1969), who studied the influence of temperature and humidity on the distribution of lichens in a Minnesota bog, and Klepper (1968), who compared the water relations of a moss and a lichen.

The first of papers involving the physiological ecology of lichens has just appeared from the laboratory of Michael Adams (1971), but the future will see a number of studies in this genre as his students come to the publishing stage. Currently he is working on the rates of photosynthesis and respiration as influenced by external factors.

William Weber (1962, 1967) has written on environmental modification in crustose lichens in the arid Southwest, showing that some of the modifications which have been called species are merely the same plant under different environmental conditions. These are important papers, expressing a point of view shared by many lichenologists.

The relationships between caribou, forest fires, and lichens have been reported upon in depth by G. W. Scotter in a series of papers (1962, 1963, 1964, 1967).

Much work remains to be done in lichen ecology. Only a few of the communities have been adequately described and little is known of the autecology of any of the species. Looking ahead shows this a field with much promise for studies.

Lichen Physiology

The physiology of the lichen combination and of its components is under very active investigation in Europe, particularly in Britain and Holland, as well as Germany and Finland. In North America this field is mainly developed by Vernon Ahmadjian and his students. After a long series of experiments with the isolation of lichen components and their resynthesis into lichens, he has achieved the greatest success with *Endocarpon pusillum* and *Staurothele clopima* (Ahmadjian & Heikkila, 1970). A very fine summary of this area of investigation, one which seems to challenge lichen physiologists most, is contained in the book *The Lichen Symbiosis* by Ahmadjian (1967). This book is important also in suggesting intriguing problems for further investigation. L. C. Bliss has been contributing studies on photosynthesis and respiration in alpine lichens (Bliss & Hadley, 1964). As already mentioned, Michael Adams is pursuing a similar field of endeavor, and we can look forward to contributions from such investigations. It would seem to me that the area of lichen physiology is currently under exploited in this country and that there is a good possibility for further contributions.

Morphology

The current status of studies of lichen morphology is that it is surprisingly quiescent on this continent. Excellent contributions are coming from Britain, Germany, France, and Scandinavia, but little from North America. Two papers influential in directing thought on a problem of importance in taxonomy as well as morphology are Weber's (1962, 1967) papers on the influence of the environment on the structure of crustose lichens. By influencing the characteristics of the lichens, the environment has brought about modifications which some taxonomists have translated into superfluous species. A major interest in morphology in North America seems to be the use of the new tool, the electron microscope, in studying the ultrastructure of lichens. As yet, only a few contributions have appeared: a general survey by Jacobs and Ahmadjian (1969), one on *Xanthoria* by Bednar and Juniper (1964), one on *Physcia aipolia* by Rudolph and Giesy (1966), and another on the same lichen by Brown and Wilson (1968), and one on *Endocarpon pusillum* by Ahmadjian and Jacobs (1970) are samples of the state and development of the art. I have seen only one paper on lichens using the still more recent instrument, the scanning electron microscope, by Hawksworth (1969) of England on the surface of various *Alectoria* species, demonstrating that this tool indeed may be of help in lichen studies.

Economic Uses

Little investigation on economic uses of lichens has been made. Two review articles by G. A. Llano (1948, 1951) constitute the major contribution in this area and are mainly concerned with historical uses, although also giving an excellent description of current practices using lichens in home-dyeing in Sweden. A book by Eileen Bolton (1960) makes available to the layman the results of her experiments in the use of lichens as dyestuffs. An earlier period of investigation of lichens as sources of antibiotics seems to have run its course, and no further papers have appeared upon this topic in recent years.

In summary, it may be stated that the currently strong fields in the investigation of lichens include chemistry, and also its relationship to taxonomy; taxonomy, with immense amounts yet to be done; distributions over the continent which need to be studied, with that of many states comparatively unknown, and the lichens of Mexico which are especially in need of study. Ecological studies are in progress at a number of institutions, and many opportunities still exist in this field for investigation. Lichen physiology is under investigation but with much yet to be learned. Morphology and economic uses are currently of scant interest and yet could be revived in the future. The interest in lichens as subjects of investigation should continue the strong and steady increase which has been shown in the last quarter century.

Bibliography

Adams, M. S. 1971. Effects of drying at three temperatures on carbon dioxide exchange of *Cladonia rangiferina* (L.) Wigg. Phytosynthetica 5: 124–127.

Ahmadjian, V. 1967. The Lichen Symbiosis. Blaisdell. 152 pp.

——— & H. Heikkila. 1970. The culture and synthesis of *Endocarpon pusillum* and *Staurothele clopima*. Lichenologist 4: 259–267.

——— & J. B. Jacobs. 1970. The ultrastructure of lichens III. *Endocarpon pusillum*. Lichenologist 4: 268–270.

Ahti, T. 1966. *Parmelia olivacea* and the allied non-isidiate and non-sorediate corticolous lichens in the Northern Hemisphere. Acta Bot. Fenn. 70: 3–68.

———. 1969. Notes on brown species of *Parmelia* in North America. Bryologist 72: 233–239.

——— & G. F. Otto. 1967. Lichens of British Columbia. Preliminary Checklist. [Processed publication.] 40 pp.

Beals, E. W. 1965 [1966]. Ordination of some corticolous cryptogamic communities in south-central Wisconsin. Oikos 16: 1–8.

Bednar, T. W. & B. E. Juniper. 1964. Microfibrillar structure in the fungal portions of the lichen *Xanthoria parietina* (L.) Th. Fr. Exp. Cell. Res. 36: 680–683.

Berry, E. C. 1941. A monograph of the genus *Parmelia* in North America. Ann. Missouri Bot. Gard. 28: 31–146.

Beschel, R. E. 1961. Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). Pp. 1044–1062, "Geology of the Arctic."

Bird, C. D. 1966. A catalogue of the lichens reported from Alberta, Saskatchewan and Manitoba. [Processed publication.] 46 pp.

———. 1967. A catalogue of the lichens reported from the Yukon. [Processed publication.] 16 pp.

Bliss, L. C. 1966. Plant productivity in alpine environments on Mt. Washington, New Hampshire. Ecol. Monogr. 36: 125–155.

——— & E. B. Hadley. 1964. Photosynthesis and respiration of alpine lichens. Amer. Jour. Bot. 51: 870–874.

Bolton, E. M. 1960. Lichens for Vegetable Dyeing. Studio Books. 63 pp.

Brodo, I. M. 1961*a*. A study of lichen ecology in central Long Island, New York. Amer. Midl. Naturalist 65: 290–310.

———. 1961*b*. Transplant experiments with corticolous lichens using a new technique. Ecology 42: 838–841.

———. 1965. Studies of growth rates of corticolous lichens on Long Island, New York. Bryologist 68: 451–456.

———. 1966. Lichen growth and cities: A study on Long Island, New York. Bryologist 69: 427–449.

———. 1968. The lichens of Long Island, New York: A vegetational and floristic analysis. Bull. New York State Mus. 410: 1–330.

BROWN, R. M. & R. WILSON. 1968. Electron microscopy of the lichen *Physcia aipolia* (Ehrh.) Nyl. Jour. Phycol. 4: 230–240.

CULBERSON, C. F. 1969. Chemical and Botanical Guide to Lichen Products. Univ. North Carolina Press. 628 pp.

———. 1970. Supplement to "Chemical and Botanical Guide to Lichen Products." Bryologist 73: 177–377.

——— & H. KRISTINSSON. 1970. A standardized method for the identification of lichen products. Jour. Chromatogr. 46: 85–93.

CULBERSON, W. L. 1955*a*. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Ecol. Monogr. 25: 215–231.

———. 1955*b*. Qualitative and quantitative studies on the distribution of corticolous lichens and bryophytes in Wisconsin. Lloydia 18: 25–36.

———. 1963. A summary of the lichen genus *Haematomma* in North America. Bryologist 66: 224–236.

———. 1965. *Cetraria chicitae*, a new and widely distributed lichen species. Bryologist 68: 95–99.

———. 1966. Chemistry and taxonomy of the lichen genera *Heterodermia* and *Anaptychia* in the Carolinas. Bryologist 69: 472–487.

——— & C. F. CULBERSON. 1965. *Asahinea*. A new genus in the Parmeliaceae. Brittonia 17: 182–190.

——— & ———. 1967. A new taxonomy for the *Cetraria ciliaris* group. Bryologist 70: 158–166.

——— & ———. 1968. The lichen genera *Cetrelia* and *Platismatia* (Parmeliaceae). Contr. U.S. Natl. Herb. 37: 449–558.

DODGE, C. W. & G. BAKER. 1938. The second Byrd Antarctic expedition—Botany. II. Lichens and lichen parasites. Ann. Missouri Bot. Gard. 25: 515–718.

EGAN, R. S. 1972. Catalog of the lichens of New Mexico. Bryologist 75: 7–35.

FINK, B. 1910. Lichens of Minnesota. Contr. U.S. Natl. Herb. 14: 1–269.

———. 1935. The Lichen Flora of the United States. Univ. Michigan Press.

FOOTE, K. G. 1966. The vegetation of lichens and bryophytes on the limestone outcrops in the Driftless Area of Wisconsin. Bryologist 69: 265–292.

HALE, M. E., JR. 1952*a*. Vertical distribution of cryptogams in a virgin forest in Wisconsin. Ecology 33: 398–406.

———. 1952*b*. Studies on the lichen *Rinodina oreina* in North America. Bull. Torrey Bot. Club 79: 251–259.

———. 1954. First report on lichen growth rate and succession at Aton Forest, Connecticut. Bryologist 57: 244–247.

———. 1955. Phytosociology of corticolous cryptogams in the upland forests of southern Wisconsin. Ecology 36: 45–63.

———. 1956. Fluorescence of lichen depsides and depsidones as a taxonomic criterion. Castanea 21: 30–32.

———. 1959. Studies on lichen growth rate and succession. Bull. Torrey Bot. Club 86: 126–129.

———. 1961. Lichen Handbook. Smithsonian Institution Press. 178 pp.

———. 1965. A monograph of *Parmelia* subgenus *Amphigymnia*. Contr. U.S. Natl. Herb. 36: 193–358.

———. 1966. Chemistry and evolution in lichens. Israel Jour. Bot. 15: 150–157.

———. 1968. A synopsis of the lichen genus *Pseudevernia*. Bryologist 71: 1–11.

———. 1969. How to Know the Lichens. W. C. Brown Co. 226 pp.

——— & W. L. CULBERSON. 1956. A checklist of the lichens of the United States, Canada and Alaska. Castanea 21: 73–105.

——— & ———. 1960. A second checklist of the lichens of the continental United States and Canada. Bryologist 63: 137–172.

——— & ———. 1966. A third checklist of the lichens of the continental United States and Canada. Bryologist 69: 141–182.

——— & ———. 1970. A fourth checklist of the lichens of the continental United States and Canada. Bryologist 73: 499–543.

——— & S. KUROKAWA. 1964. Studies on *Parmelia* subgenus *Parmelia*. Contr. U.S. Natl. Herb. 36: 121–191.

HANSON, W. C. 1967. Cesium-137 in Alaskan lichens, caribou and Eskimos. Health Physiol. 13: 383–389.

HAWKSWORTH, D. L. 1969. The scanning electron microscope. An aid to the study of cortical hyphal orientation in the lichen genera *Alectoria* and *Cornicularia*. Jour. Microscop. 8: 753–760.

HENSSEN, A. 1963*a*. Eine Revision der Flechtenfamilien Lichenaceae und Ephebaceae. Symb. Bot. Upsal. 18: 1–123.

———. 1963*b*. Study of the genus *Koerberia*. Canad. Jour. Bot. 41: 1347–1356.

——— 1963*c*. The North American species of *Massalongia* and generic relationships. Canad. Jour. Bot. 41: 1331–1346.

———. 1963*d*. The North American species of *Placynthium*. Canad. Jour. Bot. 41: 1687–1724.

———. 1969. Eine Studie über die Gattung *Arctomia*. Svensk. Bot. Tidskr. 63: 126–138.

HOWARD, G. E. 1950. Lichens of the state of Washington. Univ. Washington Press. 187 pp.

———. 1970. The Lichen genus *Ochrolechia* in North America north of Mexico. Bryologist 73: 93–130.

IMSHAUG, H. A. 1956. Catalogue of Mexican Lichens. Rev. Bryol. Lichénol. 25: 321–385.

———. 1957. Catalogue of West Indian Lichens. Bull. Sci. Jamaica, Sci. Ser. 6: 1–153.

JACOBS, B. J. & V. AHMADJIAN. 1969. The ultrastructure of lichens. I. A general survey. Jour. Phycol. 5: 227–240.

JOHNSON, G. T. 1959. The Trypetheliaceae of Mississippi. Mycologia 51: 741–750.

KLEPPER, B. 1968. A comparison of the water relations of a moss and a lichen. Nova Hedwigia 15: 13–20.

KUROKAWA, S. 1962. A monograph of the genus *Anaptychia*. Beih. Nova Hedwigia 6: 1–115.

LAMB, I. M. 1963. Index nominum Lichenum inter Annos 1932 et 1960 divulgatorum. Ronald Press, New York. 809 pp.

LEBLANC, F. 1961. Influence de l'atmosphère poluée des grandes agglomérations urbaines sur les épiphytes corticoles. Rev. Canad. Biol. 20: 823–827.

——— & D. N. RAO. 1966. Réaction de quelques lichens et mousses épiphytiques à l'anhydride sulfreux dans la région de Sudbury, Ontario. Bryologist 69: 338–346.

LEPAGE, E. 1947–1949. Les lichens, les mousses et les hépatiques de Québec. Naturaliste Canad. 74: 93–101, 225–240, 280–292; 75: 31–48, 90–96, 174–184, 228–256; 76: 45–88.

———. 1958. Premier supplement au catalogue des lichens du Québec. Naturaliste Canad. 85: 169–198.

LLANO, G. A. 1948. Economic uses of lichens. Econ. Bot. 2: 15–45.

———. 1950. A monograph of the lichen family Umbilicariaceae in the Western Hemisphere. Off. Naval Res. (Navexos P-831), Washington, D.C. 281 pp.

———. 1951. Economic uses of lichens. Smithsonian Rep. 1950: 385–422.

———. 1956. New Umbilicariaceae from the Western Hemisphere, with a key to genera. Jour. Washington Acad. Sci. 46: 183–185.

LOOMAN, J. 1964. The distribution of some lichen communities in the prairie provinces and adjacent parts of the Great Plains. Bryologist 67: 209–224.

MOTYKA, J. 1936–1938. Lichenum generis *Usnea* studium monographicum. Vols. 1 and 2. Leopoli.

———. 1964. The North American species of *Alectoria*. Bryologist 67: 1–44.

NEARING, G. G. 1947. The Lichen Book. Author, Ridgewood, N.J. 648 pp.

OTTO, G. F. 1972. New localities for *Tholurna dissimilis* in western North America. Bryologist 75: 88–90.

PALMER, H. E., W. C. HANSON, B. I. GRIFFIN & W. C. ROESCH. 1963. Cesium-137 in Alaskan Eskimos. Science 142: 64–66.

PEARSON, L. C. 1969. Influence of temperature and humidity on distribution of lichens in a Minnesota bog. Ecology 50: 740–746.

PEGAU, R. E. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. Arctic 21: 255–259.

PLUMMER, G. L. & F. HELSETH. 1965. Movement and distribution of radionuclides on granitic outcrops within the Georgia Piedmont. Health Physiol. 11: 1423–1428.

RAO, D. N. & F. LEBLANC. 1967. Influence of an iron scintering plant on corticolous epiphytes in Wawa, Ontario. Bryologist 70: 141–157.

RUDOLPH, E. D. & R. M. GIESY. 1966. Electron microscope studies of lichen reproductive structures in *Physcia aipolia*. Mycologia 58: 786–796.

SALO, A. & J. K. MIETTINEN. 1964. Strontium-90 and Caesium-137 in Arctic vegetation during 1961. Nature 201: 1177–1179.

SCOTTER, G. W. 1962. Productivity of arboreal lichens and their possible importance to barren-ground caribou (*Rangifer arcticus*). Arch. Soc. Zool. Bot. Fenn. "Vanamo" 16: 155–161.

———. 1963. Growth rates of *Cladonia alpestris*, *C. mitis*, and *C. rangiferina* in the Taltson River region, N.W.T. Canad. Jour. Bot. 41: 1199–1202.

———. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. Canad. Wildlife Serv. Bull. 18: 1–111.

———. 1967. The winter diet of barren-ground caribou in northern Canada. Canad. Field-Naturalist 81: 33–39.

SHUSHAN, S. & R. A. ANDERSON. 1969. Catalog of the lichens of Colorado. Bryologist 72: 451–483.

TAYLOR, C. 1967. Lichens of Ohio. Part 1. Foliose Lichens. Ohio Biol. Surv. Biol. Notes 3: 1–147.

———. 1968. Lichens of Ohio. Part 2. Foliose and Cladoniform Lichens. Ohio Biol. Surv. Biol. Notes 4: 153–227; appendix 1–22.

THOMSON, J. W. 1950. The species of *Peltigera* of North America north of Mexico. Amer. Midl. Naturalist 44: 1–68.

———. 1963. The lichen genus *Physcia* in North America. Beih. Nova Hedwigia 7: 1–172.

———. 1967*a*. Notes on *Rhizocarpon* in the Arctic. Nova Hedwigia 14: 421–481.

———. 1967*b*. The lichen genus *Baeomyces* in North America north of Mexico. Bryologist 70: 285–298.

———. 1967*c* [1968]. The lichen genus *Cladonia* in North America. Univ. Toronto Press. 172 pp.

———. 1969. A catalogue of lichens of the State of Washington. [Processed publication.] 59 pp.

TUCKERMAN, E. 1881. A Synopsis of the North American Lichens. Part I, comprising the Parmeliacei, Cladoniei, and Coenogoniei. Boston. 261 pp.

———. 1888. A Synopsis of the North American Lichens. Part II, comprising the Lecideacei, and in part the Graphidacei. New Bedford, Massachusetts. 176 pp.

VERSEGHY, K. 1962. Die Gattung *Ochrolechia*. Beih. Nova Hedwigia 1: 1–146.

WEBER, W. A. 1962. Environmental modification and the taxonomy of the crustose lichens. Svensk Bot. Tidskr. 56: 293–333.

———. 1967. Environmental modification in crustose lichens II. Fruticose growth forms in *Aspicilia*. Aquilo, Ser. Bot. 6: 43–51.

———. 1967. A synopsis of the North American species of *Cyphelium*. Bryologist 70: 197–203.

WETMORE, C. M. 1960. The lichen genus *Nephroma* in North and Middle America. Michigan State Univ. Biol. Ser. 1: 371–452.

———. 1963. Catalogue of the lichens of Tasmania. Rev. Bryol. Lichénol. 32: 223–264.

———. 1967 [1968]. Lichens of the Black Hills of South Dakota and Wyoming. Publ. Mus. Michigan State Univ. Biol. Ser. 3: 209–464.

———. 1970. The lichen family Heppiaceae in North America. Ann. Missouri Bot. Gard. 57: 158–209.

WILLEY, H. 1890. A synopsis of the genus *Arthonia*. New Bedford, Massachusetts. 62 pp.

WOLFE, J. N., R. T. WAREHAM & H. T. SCOFIELD. 1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biol. Surv. Bull. 8: 1–267.

WOODWELL, G. M. & T. P. GANNUTZ. 1967. Effects of chronic gamma irradiation on lichen communities of a forest. Amer. Jour. Bot. 54: 1210–1215.

YARRANTON, G. A. 1969. Pattern analysis by regression. Ecology 50: 390–395.

25 years of botany

BRYOLOGY[1]

1947–1972

LEWIS E. ANDERSON[2]

Mosses and liverworts are regarded by most phylogenists as evolutionary misfits or failures, a status they assumed when investigators during the early decades forced them out of the main phylogenetic stream of land evolution. Some evolutionists think of them as a degenerate group of misdirected tracheophytes. Whatever their origins and however little their contributions to the main stream of evolution may have been, bryophytes occupy a firm, if modest and unassuming, position in nature. Their productivity contributions are not great, but, as Forman (1969*a*) has pointed out, the standing crop of bryophytes in an ecosystem is sufficient to be taken into account. They harbor more insects and invertebrates than is generally appreciated, and they are a regular food source for some animals. Nevertheless, bryophytes are almost totally free from economic involvements. Excepting the modest peat moss industry, the small favor they find in a few Japanese gardens and their limited usefulness as packing materials for shipping live plants, mosses and liverworts have no economic worth. A recent report from British Columbia, however, states that an outbreak of contact dermatitis and some lesser allergic reactions among forest workers was traced to skin contacts with the leafy liverwort, *Frullania nisquallensis* Sull. (Mitchell *et al.*, 1969).

Still, bryophytes are well adapted to their limited role in nature. Together with lichens, they have a remarkable and perhaps unique protoplasmic organization which enables them to endure a wide range of ecological tolerances and to occupy niches and crannies befitting their small size. Unlike higher plants, which require hours and sometimes days to recover from severe drought, bryophytes and lichens recover instantly and can resume photosynthesis immediately after rains, dews, fogs, and high humidities. They are well integrated into the ecosystem into which they make a modest and essential input.

Progress in bryology during the past 25 years has been substantial. The number of investigators increased dramatically. Long regarded as a field for amateurs, bryology during this period made the final transition into a discipline that is now almost wholly populated by professionally trained individuals. With this shift has come more sophisticated techniques, a greater infusion of sub-

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stantive information from other areas of botany and science, and a general increase in the scientific stature of the field. In 1954, for the first time the International Botanical Congress acknowledged bryology as a botanical discipline by recognizing it as a separate Section at the Paris Congress. There are now greatly enlarged opportunities both in this country and abroad for graduate training in bryology. Many, if not most, of the larger herbaria and museums have trained and salaried bryologists on their staffs, a refreshing change from the handful of mainly volunteers in the 1920's and 1930's. A greatly heightened general interest in bryology is evident at college and university levels, and the uniqueness of mosses and liverworts as research materials is being appreciated more and more by experimentalists and others seeking new materials for approaches to basic problems.

Review articles summarizing progress in bryology were published by Steere (1955), covering the period 1853–1953, as part of a symposium commemorating a century of progress in the natural sciences, and by Richards (1959), who published a more selective summary in the *Vistas of Botany* series. An excellent survey of the general biology of bryophytes is contained in the small but exceedingly useful volume by Watson (1964). Doyle (1970), in briefer fashion, covers selected areas of recent progress in bryological research, especially developmental aspects, in his small book on mosses and ferns. Schuster (1966), in the first volume of his *The Hepaticae and Anthoceratae of North America*, includes a voluminous account of the state of knowledge of liverworts up to that time. I have drawn heavily from these sources. Available are a number of splendid reviews of specialized areas, which I shall refer to under appropriate headings.

Finding no better way to organize the information, I have followed Steere's general scheme of presentation by dividing the subject matter of bryology into specialized categories, and summarizing progress category by category.

COMMUNICATIONS

Only two journals devoted entirely to bryological (and lichenological) research were extant at the beginning of the present 25-year period, *The Bryologist*, published by the American Bryological and Lichenological Society, and *Revue Bryologique et Lichénologique*, published by Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris.

In 1947, three new journals devoted primarily to bryological research were established. The British Bryological Society replaced their *Annual Report* with the *Transactions of the British Bryological Society*. In 1972, the *Transactions* were replaced by the *Journal of Bryology*, which will be published semiannually. The *Journal of the Hattori Botanical Laboratory* was established in Japan, by S. Hattori, just a year after the founding of the Laboratory itself, in 1946. *Buxbaumia*, a small mimeographed journal, was started in 1947, by W. Meijer, principally for communications of the Dutch Bryological Society.

Herzogia was established in 1969 by the newly founded society, Bryologisch-Lichenologische Arbeitsgemeinschaft für Mitteleuropa, and *Lindbergia*, established in 1971, is jointly published by the Nordic Bryological Society and the Dutch Bryological Society.

During the Eleventh International Botanical Congress, at Seattle, in 1969, the assembled bryologists established the International Association of Bryologists. Under the umbrella of the International Association for Plant Taxonomy, an international *Bulletin of Bryology* began publication in the May, 1972, issue of *Taxon* (21: 375–376).

Special Works

A notable accomplishment in bryology is the completion of *Index Muscorum* (Wijk, Margadant & Florschütz, 1959–1969), a world index to the published names of mosses. For each name the place of publication, an indication of its validity, and world distribution is given. A similar undertaking for hepatics, *Index Hepaticarum*, is under way (Bonner, 1962–1966). Six parts have been issued to date. Two noteworthy bibliographic contributions by Sayre are her *Dates of Publication* (1959) and her bibliography of published exsiccatae of algae, lichens, hepaticae, and mosses (1969, 1971). These are invaluable taxonomic aids.

Floristics

Despite increased interest in experimentation, biosystematics, and other modern approaches, the bulk of bryological research continues to be exploratory. A very large amount of effort has been directed toward local and regional work, but increased opportunities for travel combined with improved accessibility to many remote and heretofore poorly known areas, have resulted in an unprecedented number of bryological collections during the past quarter century. Because of space limitations, it is not possible to review the vast assemblage of literature resulting from these explorations. This is not to indicate that the catalogues of species resulting from collecting expeditions or the vast amount of data, ecological and otherwise, that often accompany such reports are unimportant. The herbarium and literature records which accumulate from the enormous numbers of these undertakings form the backbone of floristic, revisional, phytogeographic, phylogenetic, and other basic studies.

For a while it was thought that perhaps the discovery of the remarkable liverwort, *Cryptothallus mirabilis* (Malmborg, 1933, 1934), in Europe, might be the last truly exciting bryophyte to be discovered. Richards (1959) calls it the most remarkable bryophyte discovery of the 20th century! It is a colorless saprophyte that lives on decaying organic matter, usually on thick layers of humus under forests, and is often associated with large mosses such as *Hylocomium splendens*, *Mnium undulatum*, *Rhytidiadelphus loreus*, etc. As far as known, *Cryptothallus* is the only bryophyte which is wholly saprophytic, although there are other liverworts and apparently a few mosses that are partially saprophytic. The thallus is filled with a "mycorhizal" fungus, which is endophytic and subject to digestion by the liverwort cell (Williams, 1950). *Cryptothallus* is a monotypic genus and is closely related to *Riccardia*.

An equally or, perhaps, even more remarkable find, however, was made in the high mountains of Japan, in 1951, when the liverwort, *Takakia lepidozioides,* was discovered by N. Takaki. Hattori and Mizutani (1958) have described its peculiarities in considerable detail. It lacks rhizoids; it has an erect stem with a median strand; the leaves are of one kind (isophyllous), linear-cylindrical, usually two or three together; and the branching is exogenous. Besides, it has the lowest chromosome number of any hepatic, $n = 4$ (Tatuno, 1958). R. M. Schuster was so impressed with its distinctiveness that he was quoted by Hattori and Mizutani (1958) as having said (*in litt.*) "I am still not sure, but I suspect that a Class parallel with Musci, Hepaticae and Anthocerotae is at hand." Watson (1964) adds, "If this were so, the discovery of *Takakia* would be a landmark in the history of bryology," which it may be, anyway. Schuster (1966), after mildly repenting for his excessive taxonomic exuberance in having suggested a somewhat over-classification of *Takakia,* calls attention to Grolle's (1959) exuberance in stating that *Takakia* is not even an hepatic! There seems to be general agreement among hepaticologists (including Schuster and Grolle) now, however, that *Takakia* belongs in a separate order, the Takakiales. This unique liverwort thus provides stiff competition with *Cryptothallus* for "the bryophyte discovery of the century." *Takakia* has since been found in the Queen Charlotte Islands and on the mainland of British Columbia and on Mt. Kinabalu, Borneo. A second species, *T. ceratophylla,* has been described, and it has been recorded from Lochen, Nepal, and Aleut Point, Amchitka, Alaska (Sharp & Hattori, 1967).

The greatest floristic progress in bryology during this quarter century has unquestionably been made in northern countries and, broadly speaking, the Arctic. Steere (1971), in a review of Arctic bryology, has summarized progress in this fascinating area. Major floras have appeared dealing with the Hepaticae (Arnell, 1956) and the mosses of Fennoscandia (Norway, Sweden, Denmark and Finland) (Nyholm, 1954–1969); the mosses of both European and Asiatic Russia, including comprehensive floras by Lazarenko (1951), Savicz-Lyubitzkaya (1952), Abramova, Ladyzhenskaya and Savicz-Lyubitskaya (1954), Abramova, Savicz-Lyubitskaya and Smirnova (1961), and Savicz-Lyubitzkaya and Smirnova (Sphagnaceae of the U.S.S.R.) (1968), and regional floras and handbooks of Russia, by Shlyakov (Khibin Mts.) (1961), Dombrovskaya and Shlyakov (northern European part) (1967), Bardunov (Central Siberia) (1969), and Mel'nichuk (Central Russia and South European part) (1970). One of the most ambitious floristic tasks ever attempted is that by Savicz-Lyubitzkaya and Smirnova (1970), who are preparing a handbook of the mosses of the entire U.S.S.R. The first of two projected volumes has appeared, comprising the acrocarpous mosses, and treats 706 species. This volume contains 824 pages of text and 416 illustrations, each consisting of many figures.

W. C. Steere has had in preparation for a number of years a moss flora of Arctic North America. With the help of many collaborators he has gathered an astonishing number of collections and a great amount of data from the northern part of the continent from Alaska to and including Greenland. A flora of Arctic America is thus imminent.

In the Antarctic, S. Greene and his students and colleagues from the British Antarctic Survey have in progress a very broad spectrum of bryological studies, including, in addition to floristics, cenological studies, productivity measurements and comparisons with other areas, growth form studies, phenological observations, etc. (*e.g.* see Greene & Longton, 1970). Greene (1968) has summarized the moss flora of Antarctica, and the first part of a projected moss flora of the Antarctic has already appeared (Greene *et al.*, 1970).

During the period under consideration, comprehensive floras have been published for Czechoslovakia (Pilous, 1948; Šmarda, 1948); Hungary (Boros, 1968); Poland (Hepatics) (Szweykowski, 1958); Yugoslavia (Pavletić, 1955); Japan (Sakurai, 1954); New Zealand (Sainsbury, 1955); Latin America (leafy Hepaticae) (Fulford, 1963*a*, 1966, 1968); Guatemala (Bartram, 1949); Jamaica (Crum & Bartram, 1958); South Africa (Arnell, 1963); Surinam (part I) (Florschütz, 1964); and eastern India (part I) (Gangulee, 1969).

In North America, Schuster (1966, 1969*a*) has completed two huge volumes of his projected hepatic flora of eastern North America, an endeavor that obviously will extend into many volumes. H. A. Crum and L. E. Anderson have in preparation a moss flora of eastern North America, which is nearing completion. An excellent regional moss flora was recently published by E. Lawton (1971), covering the Pacific Northwest. State moss floras completed during this period include Indiana (Welch, 1957); Florida (Breen, 1963); Michigan (Darlington, 1964); and Redfearn (1972) has completed a flora (with abbreviated descriptions) of the Interior Highlands of Missouri, Arkansas, and Oklahoma. A completed manuscript left by the late S. Flowers on the mosses of Utah will hopefully be published in the future. Regional and state hepatic treatments include central and western New York (Schuster, 1949); Minnesota and adjacent areas (Schuster, 1953, 1957, 1958); Utah (Flowers, 1954, 1961); and the mid-Gulf Coastal Plain (Breil, 1970).

FOSSIL BRYOPHYTES

We are fortunate in having useful summaries on fossil bryophytes which have appeared in recent years. Lundblad (1954) reviewed the records of fossil liverworts up to that time, and since then the whole field of bryophyte palaeobotany has been reviewed by Savicz-Lyubitskaya and Abramov (1959), Jovet-Ast (1967) and Lacey (1969). It is not quite true that there are so few fossil bryophytes known that it is pointless to discuss them. Since Walton's (1925, 1928) eventful work on Carboniferous bryophytes, there has been a steady increase in the number of real or presumed bryophytes from many different geological formations in many countries. For example, Jovet-Ast (1967) lists a total of 68 pre-Tertiary bryophytes (17 mosses and 9 liverworts from the Palaeozoic; 8 mosses and 34 liverworts in the Mesozoic). This is slightly more than twice as many as were listed eight years earlier by Savicz-Lyubitskaya & Abramov (1959).

The earliest geological record of a bryophyte is the fossil hepatic, *Hepaticites devonicus*, described by Hueber (1961) from the lowermost Upper Devonian (Frasnian), on South Mountain, Schoharie County, New York. The plant consists of a ribbon-like thallose part, dichotomously branched, bearing rhizoids (or long teeth) along the margin. Hueber compared it with *Pallavicinia* and

Metzgeria, which it resembles strongly. Schuster (1966) agrees and thinks it is definitely a member of the Metzgeriales.

It seems clear now that thalloid hepatics were widespread in Carboniferous times. According to Schuster (1966) they form the earliest hepatic "flora." Jovet-Ast (1967) lists many other species from Jurassic and Cretaceous deposits that clearly belong to Jungermanniales Anacrogynae and Marchantiales.

Krasilov (1970) described fossils from some Far Eastern Jurassic beds, which have been referred to the Jungermanniales Acrogynae, the true leafy liverworts. Two new genera were described, each with a single species. Jovet-Ast, in her review, mentions a single Jurassic fossil from Graham Land, which has divided leaves and resembles a leafy liverwort, but Krasilov's record apparently is the earliest fossil liverwort that is clearly referable to the Jungermanniales Acrogynae. Jovet-Ast lists about 50 species distributed in 20 genera from Tertiary and Quaternary deposits.

There is still doubt about the identity of the *Riccia*-like fossils reported from the Upper Carboniferous (Pennsylvanian), which Walton, with some reservations, named *Hepaticites*. Schuster (1966) thinks they are better placed in the Metzgeriales. If correct, the earliest representative of the Marchantiales comes from the Middle Triassic. Unfortunately, there are no known records of fossils of the Anthoceratales. The earliest tentative records are based on spores found in the Tertiary.

The oldest moss fossils are still the long-known fragments from the Upper Carboniferous of France, whose relationships are obscure, although they are vaguely polytrichaceous. By far the most remarkable bryofossil discoveries of our period were made by Neuberg (Lacy, 1969). She described 14 species of mosses distributed among 10 genera (12 species and 9 genera were new to science) from the Lower and Upper Permian deposits from some basins in Angarida, U.S.S.R. The plants were embedded in fine shales and were excellently preserved. Her illustrations are exceptionally clear and reveal a wealth of details about the mosses. Several specimens somewhat resemble the modern genus *Sphagnum*. The fossil leaves are composed of two kinds of cells, but they are not differentiated into the dead hyaline cells and the narrow green cells, as are our modern *Sphagna*. Watson (1964) notes that these fossils have a close resemblance to the condition seen in very young *Sphagnum* leaves today.

From this material, Neuberg described a genus, *Intia*, which is strikingly similar to our present day *Mnium* or possibly *Bryum*. Unfortunately, there are no sporophytes. Gams (1962) has taken Neuberg severely to task for assigning these Permian fossil genera (*Jungajia*, *Vorcutanullaria*, and *Protosphagnum*) to the new order Protosphagnales and thinks she was premature in assigning *Intia* to the Eu-Bryales. Gams stresses the large size and strong nerve seen in the leaves of Neuberg's Protosphagnales and believes these early mosses could well have had a greater affinity with Polytrichales and Dicranales than with modern *Sphagnum*. He maintains the latter's origin is still obscure.

Little progress has been made toward elucidating the uncertain affinities of a number of Palaeozoic plants which have been described as resembling liverworts or mosses. Still other problematic fossils have been added recently (Lacy, 1969). The startling Ordovician reports (Kozlowski & Greguss, 1959; Greguss, 1959) of fossil Bryophyta, however, proved to be contaminating fragments of recent plants; the alleged sporogonia of *Musciphyton* are apparently root-tubercles of *Carex.*

In summary, early fossil history shows rather clearly that the principal groups of hepatics and mosses were already present before the end of the Palaeozoic. Even the earliest fossils resemble rather closely present day groups of mosses and liverworts. On present evidence, the Jungermanniales Anacrogyne pre-date the Marchantiales, and these in turn predate the Sphaerocarpales. Jungermanniales Acrogynae and Anthocerotales judging from fossils are relatively recent. This is the reverse of most current thought on the evolutionary sequences. There is no hint, thus far, in the fossil record to indicate the relative ages of the groups of Musci.

Phytogeography

Herzog (1926) in his monumental work, *Geographie der Moose,* outlined the principal patterns of geographical distribution of bryophytes. Subsequent researches have added refinements, filled in gaps, and focused attention on historical, ecological, and biological factors influencing distribution. Herzog convincingly argued against the long-held notion that bryophytes, because of their light wind-blown spores, could be expected to be distributed widely, and that individual species (or other taxa) could be expected to be found any place which provided the proper environment for growth. Evidence accumulated during the past two decades strongly support Herzog's opposition to this view.

The distributional patterns of bryophytes strongly parallel those of higher plants. A statement from a recent review by Crum (1972) expresses the logic of this parallel very forcefully:

> "The mosses so intimately associated with [higher plants] have been subjected to the same geologic, climatic, and ecologic conditions of the past, as well as present-day controls which permit continued survival. It is necessary to stress the fact that the species of mosses are natural biologically significant units of taxonomy fully comparable to plants higher in the evolutionary scale, as proven by considerations of ecology and phytogeography. As in the higher plants, their ranges of distribution are a result of slow, step-by-step progression from a center of origin paced to slow and gradual geographic, climatic, and biotic alterations of the past. Their ranges may, over geologic ages, have become dissected by topographic and climatic changes. Historical, ecological, and biological factors determine their distribution patterns. Long-range accidental dispersal is highly unlikely. Mosses have moved in the past as members of whole floras in migration, not as individuals and not aimlessly, but along natural migratory routes."

A number of investigators have called attention to the resemblance between the fossil distribution of higher plants and the modern distributional patterns of mosses and liverworts, which more nearly resemble those of ferns and some of the primitive gymnosperms. The fossil ranges of particular sections of the gymnosperm genera, *Podocarpus* and *Araucaria*, closely parallel the modern distributions of many of the "primitive" taxa of Jungermanniales and Metzgeriales (Fulford, 1951, 1963*b*; Schuster, 1969*b*). Since the fossil ranges of the conifers are late Mesozoic and early Cenozoic, Schuster was tempted to extrapolate cautiously from fossil Coniferales to living Jungermanniae. Schuster notes that in the general circumsubantarctic region, the "*Nothofagus* Zone," there are a larger number of the "primitive" taxa of Jungermanniales (28 genera) and Metzgeriales (5 genera) than in any other comparable region. Only 14 of these "primitive" genera occur in the Australasian-Malaysian region, suggesting that "perhaps the Jungermanniae originated in the panantarctic region and have undergone a 'northward shift' as did some Coniferales." The quotation, "northward shift," is from Florin (1940), who mapped the fossil ranges of *Araucaria* and *Podocarpus* and suggested that there may have been a general migration of floras northward, presumably during Tertiary times. Thus, Schuster thinks the evidence points to an origin of the Jungermanniae in cool or temperate, moist regions rather than in the Australasian-Malaysian tropical areas, as has sometimes been assumed.

The role of the Southern Appalachian Mountains as refugia for survivors of the Arctotertiary flora has been much discussed (Sharp, 1937, 1939, 1941; Iwatsuki, 1958; Billings & Anderson, 1966; Iwatsuki & Sharp, 1967; Anderson, 1971). The clearest exposition of this whole subject, however, is contained in Crum's (1951) unpublished doctoral dissertation, available only in microfilm or facsimile. A small part of the substance of this excellent treatise has recently appeared in a review by Crum (1972) on the geographic origins of the mosses of the Eastern Deciduous Forest of North America. As outlined by Crum, the causes of these disjunctive patterns are related to the moderate climates of the late Mesozoic and early Tertiary which allowed a relatively uniform flora, circumboreally and southward in Europe, Asia and North America. The not inconsiderable fossil record of Tertiary bryophytes substantiates this (Steere, 1946; Jovet-Ast, 1967). Then cooler and drier climates toward Late Tertiary forced the flora to shift southward, creating dissections and eliminating many taxa from large regions such as central and western North America (coupled also with orogenic changes). Pleistocene glaciations and invasions of marine waters left the Southern Appalachians as the only major refugium in eastern North America where plants could have survived uninterruptedly, but since Carboniferous the driftless area in north-central United States, possible Nunataks, and the Orange Island area of Florida may have provided intermittent Tertiary refuges. Further depletion of the Arctotertiary remnants in eastern North America occurred during the post-Pleistocene hypsithermal period, which must have decimated the Arctotertiary bryophytes of the Interior Highlands to a greater extent than those of the Southern Appalachians. Billings and Anderson (1966) have studied the microclimatic characteristics of some of the endemic and disjunct bryophytes in the southern Blue Ridge Mountains and demonstrated that temperatures in some of the recessed habitats of bryophytes in certain of the deep gorges are much milder than on adjoining ridges and that the substrates in the gorges can remain moist through extreme dry periods. Furthermore, the annual rainfall in these gorges apparently averages in excess of 100 inches and in wet years may reach 125 inches. Except for the high rainfall, comparable habitats occur throughout the Southern Appalachians and doubtless have harbored a large number of taxa of the Arctotertiary flora, which in less suitable habitats might not have survived.

Two exhaustive phytogeographic studies of European bryophytes have appeared recently. Størmer (1969) summarizes 30 years of painstaking research and has produced an account of environmental conditions in southern and western Norway which he thinks have influenced oceanic distributional patterns of mosses. This is surely a model study of its kind. A similar but somewhat less exhaustive treatment of oceanic or Atlantic bryophytes was carried out by Ratcliffe (1968) in the British Isles. Other significant contributions to bryogeography include the demonstration of eastern Asiatic affinities in the Caucasian bryoflora (Abramova & Abramov, 1966); an exhaustive analysis of components of different regions of southwest Germany (Düll, 1969); a thorough analysis of the bryophyte flora of western Europe (Gaume, 1954), demonstrating its heavy circumboreal element (38%); the first phytogeographic analysis of the mosses of India (Srinivasan, 1968); an important volume on the phytogeography of the mosses of Formosa (Wang, 1970); the distributional relationships of the bryophytes of the Pacific Northwest of the United States (Schofield, 1969); affinities of the mosses of the Gulf Coastal Plain of the United States and Mexico (Pursell & Reese, 1970); and an analysis of West Indian distributional patterns of mosses (Crosby, 1969*b*).

DISPERSAL

There is an old dictum for microorganisms: "Everything is everywhere, but the milieu selects." Any bryologist, however, who is familiar with distributional patterns of mosses and liverworts will find it difficult to subscribe to this dictum. Much is known about spore and propagule discharge in bryophytes (*e.g.* Ingold, 1959, 1965; Pais, 1966), but except that they are small, produced in huge numbers, and presumably wind borne little is known about their dissemination. There is a paradox. Bryophyte spores are presumed to be light and bouyant (although I know of no data), they are undoubtedly capable of being carried long distances by wind, especially if one thinks of hurricanes and typhoons, yet, as Crum (1972) notes, "they are neither ubiquitous nor haphazard in distribution . . . . their ranges so often conform to the obviously meaningful patterns of distribution occupied by higher plants [that they supply] indirect evidence of historical significance. By force of numbers such examples provide virtual proof."

Very few reliable data exist concerning the numbers and kinds of moss and liverwort spores and propagules in the atmosphere. The vast amount of data concerning atmospheric pollen does not provide information on bryophyte spores. Rudolph (1970) trapped diaspores over the Antarctic, but found the incidence of diaspores of algae, mosses and lichens to be very low. Significantly, he identified only spores representing local plants. Pettersson (1940) germinated 2000 moss spores obtained in a single day from rainwater in Finland, but, except for 278 plants of *Aloina brevirostris*, which does not occur in Finland, the 14 species he could identify were all local. He postulated that the spores of *Aloina* came from Siberia, some 2900 km to the east, but it was later determined they more likely came from Sweden, some 600 km away. Of much greater interest is the fantastic number of spores of *Aloina* that came down with the rain. Pettersson estimated that no less than 60,000,000,000/km^2 fell with the single day's rain in the vicinity of Tvärminne. Such studies urgently need repeating.

Birds are often mentioned as possible carriers of bryophyte propagules. Unusual disjunctive occurrences have occasionally been attributed to migratory birds, but there is rarely convincing evidence. Proctor (1961) found that ducks eat the liverwort, *Riella*, and that the spores pass through and germinate well afterwards. This should provide a good dispersal mechanism, but, in fact, the distribution of *Riella* in Europe is extremely limited. Thus, some other explanation for its rarity must be sought.

Long range dispersal obviously occurred in populating remote islands, such as Hawaii. Carlquist (1966) has considered at length the problems of island geography, but almost entirely from the point of view of higher plants and animals. Unfortunately, bryologists cannot consider these problems very seriously at the present time, because the global taxonomy of only a handful of genera is known. Johannsson (1968) observed that *Bryum argenteum* and *Funaria hygrometrica* were the first inhabitants of the newly formed (1963) volcanic island, Surtsey, 20 miles off the coast of Iceland, but only 3 miles from the southernmost part of the Vestmann Islands. That the pioneer occupants should be two cosmopolitan weeds instead of, perhaps, a species of *Rhacomitrium*, which forms thick mats over thousands of square kilometers of bare volcanic rock on Iceland, is a fact that should be pondered.

Monographic Studies

One of the most serious weaknesses of bryophyte knowledge has been the rarity of critical monographic and revisional studies of genera and families, especially on a world-wide, or even continental basis. Bryogeographical studies especially have suffered because the nature and composition of distributional patterns depend directly upon the soundness of the taxonomic interpretations. Whether a taxon is an endemic, a disjunct, widely distributed or even cosmopolitan often hinges upon taxonomic judgments. Species are best evaluated and interpreted when the entire genus or section can be compared throughout its range. Bischler and Joly (1969) demonstrated in *Calypogeia* that species groupings based on a limited geographical area cannot be extrapolated to the remainder of the genus without important modifications. World-wide monographs are still few, but interest in revisional studies has increased. At the risk of slighting some significant revisions, I will list some recent treatments that readily come to mind: European and North American *Lescuraea* (Lawton, 1959); Japanese Bryaceae (Ochi, 1959); Nearctic Plagiochilaceae (Schuster, 1959–1960); Fontinalaceae, world-wide (Welch, 1960); New World *Calymperes* (Reese, 1961); Latin American *Calypogeia* (Bischler, 1962–1963); generic conspectus of North American Brachytheciaceae (Robinson, 1962); *Leptoscyphus*, world-wide (Grolle, 1962);

Asiatic and Pacific *Neckeropsis* (Touw, 1962); generic synopsis of Lejeuneaceae (Schuster, 1963); *Syzygiella*, world-wide (Inoue, 1966); generic conspectus of Mniaceae, world-wide (Koponen, 1968); *Radula*, world-wide (Castle, 1968, summary of 12 publications over 32 years); *Balantiopsis*, world-wide (Engel, 1968); Latin American *Frullania* (Stotler, 1969); North American *Plagiothecium* (Ireland, 1969*a*); Treubiaceae, world-wide (Schuster & Scott, 1969); *Pilotrichum*, world-wide (Crosby, 1969*a*); Latin American *Porella* (Swails, 1970); *Andreaea* (costate species), world-wide (Schultze-Motel, 1970); European Sphagnaceae (Isoviita, 1966, 1970); Japanese *Plagiothecium* (Iwatsuki, 1970); generic conspectus of Polytrichaceae, world-wide (G. L. Smith, 1971); Hypnodendraceae, world-wide (Touw, 1971); Hookeriaceae, Greater Antilles (Welch, 1971, conclusion); *Atrichum*, world-wide (Nyholm, 1971), North American (Ireland, 1969*b*).

Ecology

Early ecological research in bryophytes soon established clear-cut correlations between species or groups of species and their habitats. Community studies became numerous during the 1930's and the 1940's, especially in Europe, where the methods of the Zürich-Montpellier school were promptly applied to bryophytes. Bryocenological studies have continued during the past decades, especially in England and Japan. Gimingham and his co-workers (Gimingham & Robertson, 1950; Gimingham & Birse, 1957; Birse, 1958) reintroduced the concept of growth-forms in ecological analyses of bryophyte vegetation. They modified the growth-form classifications established earlier by Amann and by Herzog and showed that particular growth-forms were fitted to particular habitats. Since the same growth-forms recur in similar habitats regardless of the species present, Gimingham and associates were able to express the community structure in terms of growth-form. Iwatsuki (1960) adopted Gimingham's system with slight modifications in an intensive study of the epiphytic bryophyte communities of Japan.

Another major work which involves both bryophytes and lichens is Barkman's (1958) definitive treatise on phytosociology and ecology of cryptogamic epiphytes. There is renewed interest in this work because of the enormous research effort now being expended on the effects of atmospheric pollution on epiphytic bryophytes and lichens. Barkman's paper, astonishingly detailed, considers the characteristics of the habitat, microclimate, physical properties of tree bark, its nutrient content, acidity, water regime, etc. He groups the epiphytes according to Braun-Blanquet's system, but he also classifies them according to growth-form. Included are successional studies, dispersal observations, geographical ranges, and a critical analysis of methods of studying cryptogamic epiphytes.

Another model work which combines taxonomy, floristics and ecology in an almost unique way is that of Mårtensson (1955*a*, 1956, 1955*b*) on the bryophytes of the Torneträsk area, which is in northern Swedish Lapland. The nomenclature, taxonomy, distribution, and habitat of each species is exhaustively discussed, and the final part of the work provides climatic, geographical, and environmental data which are related to the bryophytes as a whole. Anyone contemplating a regional vegetational study would be well-advised to study this excellent work in advance.

A less exhaustive but more sophisticated approach to the study of epiphytes is that of Hoffman and Kazmierski (1969) and Hoffman (1971). They selected a single substrate species, *Pseudotsuga menziesii*, in the Olympic Peninsula, Washington, analyzed habitat and substrate conditions, catalogued the bryophytes and lichens, and obtained data on frequency and abundance. Using Pielou's formulae, they obtained "indexes of diversity," which take into account numbers of species present and their importance. Thus they have a quantitative expression of the total information content of the entire biological aggregation. Yarrington's (1967, 1970) detailed analyses of saxicolous bryophytes and lichens employ a novel mathematical model to arrive at estimates of the determinants of species frequencies.

Controlled environmental studies were probably first carried out by Buch (Schuster, 1966: 134), in the 1920's, although, as Schuster notes, his pioneer efforts have been little applied. Forman (1964) designed a micro-phytotron with which he determined rather precisely the range of environmental factors for growth and reproduction of the moss, *Tetraphis pellucida*. Armed with these data, he was then able to construct a map which indicated where, in North America, this moss might be expected to be found. The "predictability map" coincided remarkably well with the actual range of *Tetraphis pellucida*. But there has been almost no follow-up of this type of study. In Europe, however, Szweykowski and his students (Szweykowski & Vogel, 1966; Szweykowski & Kozlicka, 1969; Szweykowski & Krzakowaa, 1969) have grown a wide variety of hepatics under identical conditions to determine whether the variations are ecotypic. Significantly, they found that most of the variations in the species they studied were not ecotypic, that is, the variations appeared to be non-genetic. For example, he cultured North American and European populations of the exceedingly variable *Geocalyx graveolens* under similar conditions, and found that populations from the two continents were identical.

Only recently have bryophytes been considered important enough to be included in standing crop measurements in ecosystems. Forman (1969*a*) measured the biomass of the total bryophyte standing crop in each of 9 ecosystems on Mt. Washington, New Hampshire, and found variations from 2 gm/m^2 to 238 gm/m^2, with the mean calories per unit area varying from 8 Kcal/m^2 to 921 Kcal/m^2. The standing crop increased from oak woods at lower elevations to northern hardwoods to coniferous woods to high alpine to alpine just above timberline. Curiously, there is little variation in caloric values among the different species of mosses. The highest measured by Forman was *Thuidium delicatulum*, 4305 cal/g, and the lowest was *Dicranella heteromalla*, 3747 cal/g (Forman, 1969*b*). Longton (1970) found the biomass of pure stands of *Polytrichum alpestre*, in the Antarctic, to range from 342 gm/m^2 on Signy Island to 507 gm/m^2 on South Georgia. Other productivity figures for bryophytes in polar regions are given by Clark *et al.* (1971).

PHYSIOLOGICAL ECOLOGY

Excepting species that grow in continuously wet or moist places, bryophytes lead at least semi-xerophytic lives. They lack root systems, their conducting systems are primitive or lacking entirely, and, most important, they have no mechanism for water storage or for water retention beyond that which will barely sustain life. The water regime to which nearly all non-aquatic bryophytes are adapted is as follows: saturation of plants by rain, dew or fog; immediate increase in metabolic activities, including resumption of photosynthesis within minutes, if or as soon as there is sufficient light; when rain stops and humidity drops, plants begin to lose water by evaporation; as plants dry out, metabolism, including photosynthesis, decreases, and at a certain level of desiccation photosynthesis stops, other metabolic activities decline to a low level commensurate with temperature, and growth slows and eventually ceases; plants remain inactive until rewetted, when the routine begins anew.

There are specific differences in the rate at which leaves and shoots gain or lose water (Mel'nichuk, 1959; Clausen, 1964), although certain species may gain water fast and lose water slowly; other species may gain water slowly and lose water fast. Also, rate of water loss and/or gain are not necessarily correlated with whether the particular species are xerophytes, hydrophytes, or mesophytes. Although there are differences among different species of bryophytes in the amounts of water they can retain at various humidities, especially low humidities, no correlations have been found between water holding capacity and the habitats they occupy. Similarly, species differ in their abilities to absorb water vapor from the atmosphere, and this ability also does not correlate with xerophytism (Patterson, 1964).

Atmospheric humidities, however, do have a pronounced effect on survival of bryophytes, and Clausen (1952, 1964) and many others have shown there is great variation among species in their tolerances to drought and consequently desiccation. Clausen has shown for liverworts a close connection between conditions of humidity in their natural habitats and the tolerance of the species to drought (see, especially Clausen, 1964). It is not the water-holding capacity of the moss or liverwort that adapts it to a xeric habitat, but its ability to resist drying out (Clausen, 1952). The specific structural or protoplasmic features which enable one species to lose water slower than another are not really known. Devices such as appressed leaves, crisping or shriveling of leaves, curling of leaf margins, thickened leaf cells, etc. probably have much to do with, as Watson (1964) states, "holding tenaciously that minimum quantity of water which is necessary for survival." Stocker (1956) reports that dead moss plants and living moss plants, surprisingly, lose water at about the same rate. This should be reinvestigated.

The water content of corticolous bryophytes (and lichens) is assumed to be in equilibrium with the relative humidity of the surrounding atmosphere. Corticoles apparently absorb little or no water from the bark substrate. Hosokawa and his collaborators (for a review, see Hosokawa *et al.*, 1964) demonstrated a correlation between water content (not the ability to retain water, however) and growth form of epiphytes. The moss cushion holds more water, but it is a physical capacity and not a mechanism of the individual plant. The cushion also loses water faster. Osmotic values of individual epiphytic species increase from the base of the tree to the crown; apparently, the higher the osmotic value of a species, the greater its resistance to desiccation and the higher its vertical range on trees (Hosokawa *et al.*, 1964).

Resistance by species of bryophytes to heat does seem to be correlated with habitat (Lange, 1955; Clausen, 1964). Species that normally grow in moist, shaded habitats were killed or severely damaged by temperatures of 70°C, while species inhabiting dry, exposed rocky sites survived temperatures up to 110°C. Tolerance to cold often accompanies the capacity to withstand desiccation, at least in the hepatics tested by Clausen. Many hepatics withstood freezing in ice at –10°C, but not many could tolerate –40°C for 24–26 hours. Winter temperatures in Antarctica may fall below –40°C (Greene & Longton, 1970), but the vegetation is covered by an insulating blanket of snow for up to nine months each year. Longton (cited in Greene & Longton, 1970) found that young sporophytes of *Polytrichum alpestre*, collected on South Georgia, in the overwintering stage with sporophytes still immersed within the perichaetium, developed normally at 10°C after they had been kept at –10°C for 14 months and then slowly thawed. Anderson and Crum (1958) found that many mosses with capsules in premeiotic stages stored at 0–5°C will undergo meiosis and produce normal spores at these temperatures.

Rates of photosynthesis that mosses and liverworts can attain at various light intensities and at various levels of water stress are of prime importance in habitat selection. The ability of bryophytes (and lichens) to undergo severe desiccation, recover immediately upon wetting, and resume photosynthesis within minutes is an adaptation which permits them to take advantage of slight showers, dews, and high humidities. Furthermore, it is an adaptation that compensates for their inability to store and retain water. At the same time bryophytes must possess a type of protoplasm which can bind or hold sufficient water to remain alive under extreme conditions of water stress. Malta (1921) obtained protonemata from 19-year-old herbarium specimens of *Anoectangium compactum*, while Keever (1957) regenerated *Grimmia laevigata* which had been in the herbarium for 3–10 years. Keever, incidentally, found that the protonema of *Grimmia pilifera*, which grows on bare exposed rocks, is also extremely drought resistant. Once established, which required wetting propagules at 4–5-day intervals, protonema could withstand long periods without water. Even some aquatic species are surprisingly resistant to desiccation. Glime (1971) found two species of *Fontinalis*, a genus whose species are confined to water, capable of withstanding drying for one year.

Lange's (1969) data on reactivation of photosynthesis are useful in assessing ecological capabilities. Some species of mosses which have been dried well below the compensation point for photosynthesis can take in enough water vapor when placed under high relative humidities (94–98%) to resume rather high rates of photosynthesis. Other species lack this ability and must be physically wetted before they will resume a full rate of photosynthesis. The latter species resume high photosynthetic rates within a few minutes after wetting. Lange found that some species could reactivate photosynthesis in 98% relative humidity but not in 94%, while other species could absorb sufficient water in 94% relative humidity to resume photosynthesis. Desiccation has a subsequent retarding effect on assimilation and respiration in both liverworts and mosses (Hinshiri & Proctor, 1971). Lee and Stewart (1971) found intraspecific differences in the effect of moisture stress on photosynthesis in mosses. Obviously, plants whose photosynthetic rates are higher when water contents are low have an advantage in drier sites. But, other factors are involved. There is a complicated interaction among photosynthetic rates, light intensity, and water content of the moss. Hosakowa *et al.* (1964) found significant species differences among epiphytic mosses in photosynthetic rates at high and low light intensities in combination with different levels of water stress. These are important researches which hold promise for explaining more explicitly the habitat restrictions of bryophytes.

PHYSIOLOGY

Considerable progress has been made during the past two decades in the physiology of development of bryophytes. There is now a voluminous literature on the subject, which can be treated here only briefly. A recent review (Bopp, 1968) is available. The transition from protonemal growth to the formation of leafy moss plants has intrigued developmentalists, who learned from the early morphologists that the transition begins with a change in the cell division patterns of single cells. The change is gene controlled, for Oehlkers (1965) has shown that by x-raying spores, the normal three-sided apical cell can be altered to one and two sides. Resulting leafy plants are greatly modified. X-ray mutants, however, can be made to revert back to three-sided apical cells by lowering the light intensity, adding glucose, or by IAA treatment. A series of metabolic processes obviously are involved in the development of three-sided apical cells (Bopp, 1968).

The effect of kinetin (6-furfuryl-aminopurine) on protonemal bud formation has been investigated intensively. Kinetin increases the number of buds in protonemal cultures and can induce bud formation under conditions which are normally unfavorable, namely under low light intensities, even total darkness, and when grown in blue light, all of which in the absence of kinetin prevent bud formation. Kinetin also nullifies the inhibitory effects of IAA and coconut milk. On the other hand, spontaneous and kinetin-induced bud formation can be specifically inhibited by actinomycin D. Since the latter is known to inhibit the DNA-dependent RNA synthesis, production of mRNA is probably necessary for bud formation (Bopp, 1968).

Bauer (1966) isolated a substance from callus cultures of sporophytes, which he called bryokinin, that induced buds in large numbers in bud-less mutants of *Funaria*. A substance which has been called "factor H" inhibits caulonema growth at high concentrations but promotes bud formation at low concentrations. Factor H diffuses from intact protonemata into the substrate in rather large amounts. Comparable substances exist in the protonema of other mosses (Bopp, 1968) and could be responsible for the normal differentiation pattern in protonemata.

A large body of literature on the physiology of reproduction in bryophytes (for a summary, see Benson-Evans, 1964) indicates the existence of both long and short day plants and that some species are day length neutral and will produce sex organs without regard to day length. Most day length studies have been carried out with liverworts, probably because they are easier to culture. Among mosses, only *Sphagnum plumulosum* Roell. has been found to be photoperiodic. Benson-Evans (1964) established it as a short-day plant. Most mosses investigated so far produce sex organs in response to temperature regimes (Benson-Evans, 1964), or they have endogenous rhythms that usually amount to an annual cycle (Clark *et al.*, 1971; Newton, 1972). The Anthocerotales are normally short-day plants, but Proskauer (1967) found that Himalayan members produced sex organs under a long-day regime, which he thought might have phylogenetic overtones.

Mineral economy in bryophytes is poorly understood. The source of minerals and how they are absorbed is not clear. Whether the rhizoid system acts as an absorbing mechanism for minerals or water is debatable. Some time ago, it was pointed out by Romell (1939) that mosses often contain kinds and quantities of minerals that could not be supplied by the substrate. Tamm (1964) presents evidence in the case of *Hylocomium splendens*, a moss that forms carpets in forests, especially under spruce-fir, that tree crowns release minerals by rain washings, which the moss carpet then absorbs. Since it is known that *H. splendens* can not absorb sufficient water from below to maintain itself, it must be assumed that absorption occurs through leaves and stems. An additional function of the dense paraphyllia clothing the stems of *Hylocomium* and many other mosses (other than increasing water capacity) might be an increase in absorbing surface in mineral uptake. Except for nitrogen, Tamm found the mineral content of the moss carpets in good accord with that of the trapped rain water from beneath the tree crowns. Tamm acknowledges that nitrate in rain water is insufficient to account for the amounts found in the moss and that its source is enigmatic. Possibly, he suggests, it comes from organic matter washed down from the tree crowns, perhaps partly from leached amino acids, and from insects or bird excreta, or from dust particles. He does not rule out direct absorption of gaseous ammonia from the air, but evidence is lacking.

Mosses can accumulate and concentrate minerals beyond that found in the substrate. Tallis (1959) found that the moss, *Racomitrium lanuginosum*, contains a higher concentration of iron than would be expected judging from the iron content of the substrate. Richards (1959) cites an interesting example of farmers in North Wales who say that phosphate dressings should not be applied to pastures where there is a lot of moss mixed with the grass because the moss takes up most of the phosphate. This might be evidence that bryophytes concentrate large amounts of phosphate. Shacklette (1965) considers that bryophytes may be useful in regional geochemical evaluations because of their ability to concentrate the rare earth elements that may not be detected in other sampling media.

Experimental Morphology

The outstanding feature of all bryophytes is their unifying life cycle, which consists of two alternating phases or generations, grossly dissimilar in morphology, but equally important. Although the sporophyte is always attached to the gametophyte and is thus never independent, as in pteridophytes, its degree of nutritional dependence is not always obvious. Except for the leafy liverworts, the sporophytes of most mosses and hepatics contain abundant chlorophyll and probably manufacture most, if not all of their food. Transfer of water, minerals, and carbohydrates from gametophyte to sporophyte have been adequately demonstrated. Bopp and Weninger (1971) found that water from the central strand of the gametophyte passes to the vaginula, a sheath at the base of the sporophyte whose function has been vague, then into the sporophyte. Yet, Krupa (1969) has shown that at certain stages of its development the sporophyte of *Funaria hygrometrica* is fully autotrophic. Watson (1964) states that the *Funaria* capsule has a photosynthetic capacity equal to that of 14 leaves from the *Funaria* gametophyte, which exceeds the usual number of leaves on a single gametophyte. On the other hand, Paolillo and Bazzaz (1969) found that sporophytes of *Polytrichum juniperinum* which they measured never reached compensation point, but they confirmed Krupa's and Watson's statements that in *Funaria* sporophytes there is net photosynthetic activity.

Apogamy and apospory have been known in bryophytes for a long time, and the ease with which diploid gametophytes and haploid sporophytes can be produced early caused morphologists to dismiss the notion that the number of sets of chromosomes influenced gametophytic or sporophytic differentiation. If any further evidence was needed, Lal (1961) has produced it. He grew callus masses from the stem and venter wall of *Physcomitrium coorgense* and obtained both leafy gametophytes and apogamous sporophytes from the same callus. He did not determine the chromosome number of the apogamous sporophytes, but there is no reason to believe they were not haploid. The sporophytes were sterile; there were no meiotic divisions. Bauer (1956) discovered an even more remarkable case of apogamy in *Georgia* (= *Tetraphis*) *pellucida*. In a diploid protonemal culture which had been derived aposporously from young sporophytes, and had been cultivated on a drier than usual medium, Bauer noticed that numerous protonemal buds developed directly into sporophytes, thus completely bypassing the leafy gametophytic stage. Occasional apogamous sporophytes produced viable spores which germinated and grew into filamentous protonema. Lowry (1954) observed that retention of the calyptra on young detached setae tends to inhibit capsule formation and to stimulate regeneration of protonema direct from these setae. Bauer's (1963) additional observation that following regeneration in culture, the balance of sex determination is disturbed, is important. He found that the tendency to femaleness is progressively weakened, finally resulting in a stable male population. These studies suggest profitable areas for experimentation.

It is worth noting that gametophytes of bryophytes can be induced to regenerate protonemata which develop into other gametophytes. They are also capable of apogamous development directly into sporophytes. Sporophytes, however, can be induced to produce only gametophytes. Bryophyte sporophytes, unlike pteridophytes, do not regenerate directly into other sporophytes.

ANATOMY

Progress in bryophyte anatomy in the decades under consideration has come mainly from a reexamination of the so-called conduction systems of mosses and liverworts. In addition to basic life cycle distinctions, bryophytes differ from vascular plants in lacking xylem and phloem. The presence of internal water- and metabolite-conducting systems in mosses and liverworts is therefore of considerable importance, especially from a phylogenetic point of view. Are the conducting systems of bryophytes analogous to xylem and phloem, or are they truly homologous, representing reduction from a better developed vascular system of some ancestral type? Two reviews are available, J. L. Smith's (1966) studies of conducting systems in hepatics, and Hébant's (1970) summary of research in mosses. It should be noted that the latter is strongly biased in favor of a regressive evolutionary explanation.

Conducting systems in liverworts involve only water movement, which is restricted to a few genera, mainly in the family Pallaviciniaceae of the anacrogynous Jungermanniales. Gametophytes of all of the genera concerned are prostrate, with a ribbon-like thallus, which is composed of a thickened midrib and unistratose wings. The conducting systems of three genera were studied by Smith (1966), utilizing both light and electron microscopical methods. The conducting systems consist of from one to eight strands located in the center of the midrib. The strand is composed of elongate, thick-walled, pitted conducting cells, with somewhat slanted end walls. When mature, the cells are devoid of protoplasm, and many of the pits have coalesced into elongate compound pits, richly ornamenting the walls. Experiments by Smith with eosin solution demonstrate beyond question that the conducting cells transport water more rapidly than do the surrounding cortical cells. The conducting cells have a superficial resemblance to the "hydroids" of mosses, which have also been shown to conduct water, but Smith thinks "the moss hydroid cells are presumably no more phylogenetically related to the hepatic conducting cells than the latter are to the tracheids of vascular plants." The hepatic conducting cells are a functional puzzle, in that they occur in horizontally-growing thallose species which grow in moist or wet situations. They are absent in erect-growing liverworts, in which a conducting system might offer some advantages.

The conducting system in mosses is more complex than the hepatic system and more variable from group to group. The most specialized system is found in the Polytrichales. The following account is based mainly on the papers of Eschrich and Steiner (1967, 1968*a*, 1968*b*), Kawai (1969), Kawai and Ikeda (1970), and Hébant (1970).

The water-conducting cells in mosses are called hydroids and are comparable to the conducting cells of liverworts. The hydroids occupy the center of the stem and consist of numerous strands of elongated, thick- or thin-walled cells with oblique end walls. When mature, the hydroids are dead cells, devoid of protoplasm. Surrounding the central strand of hydroids is a cylinder of cells called leptoids, which have been shown to conduct metabolites. The development of leptoids is fascinating and has been worked out in detail with the aid of the electron microscope by Eschrich and Steiner (1968*b*). Early in development they undergo a change in protoplasmic structure, during which the endoplasmic reticulum is rearranged or dissolved into a lysosome-like structure. The plasmodesmata of the lateral walls become plugged with callose, and the endoplasmic reticulum reemerges in the rearranged form of hollow cylinders extending from one end wall to the other. These cylindrical cisterns are connected from one leptoid to the next by plasmodesmata, which, in mature cells, are limited to the end walls. The leptoids have oblique walls with 9–12 plasmodesmata/μm^2. A comparable development has been described in the phloem of certain ferns, and the ultrastructure of the moss leptoid has certain features in common with tracheids of vascular plants. Eschrich and Steiner (1967) reported that ^{14}C-labeled assimilates moved in the leptom cylinder of *Polytrichum commune* at the rate of 32 cm/hour. The hydroids and ground tissue remained unlabeled.

Only a loose connection exists between the axial conducting system and the leaves. "Leaf traces" are produced by branching of the conducting strands, but the "traces" do not connect with the elements of the midrib of the leaves. Only the Polytrichales have hydroids and leptoids in both gametophytes and sporophytes; certain mosses (*e.g. Funaria, Splachnum*) have both hydroids and leptoids in the setae of the sporophyte, but only hydroids in the gametophyte; others possess only hydroids in both gametophyte and sporophyte (*Dicranum, Brachythecium*); *Neckera* and *Buxbaumia* have no conducting system in the gametophyte, but it is present in the sporophyte; and many mosses have no conducting tissues in either phase. A complete summary of the variations in mosses can be found in Kawai's papers.

It is not possible at this time to assess the significance of conducting systems in bryophytes. In strict terms of function, it might be well to recall that the conduction of water in both mosses and liverworts is largely external by capillary means (Patterson, 1964). Anatomically, in spite of superficial resemblances of hydroids to tracheids they differ fundamentally in ontogeny, wall structure, composition, and ornamentation. The connection between leptoids and sieve tubes is perhaps even more tenuous; the resemblances are mainly that they share the vertical, cylindrical orientation of the endoplasmic reticulum and to a lesser extent perforated end walls which permit continuous cisternal connections from cell to cell. Hébant (1970) thinks the leptoids of mosses suggest the more differentiated "phloem" elements of *Rhynia* or *Psilotum* or even the protophloem cells of most other vascular plants. He thinks the conducting systems in mosses are homologous with those of vascular plants and that they have been derived through regressive evolution. Hébant cites *Trichomanes* as a comparable example of regression of the conductive system in the pteridophytes and calls attention to the fact that vascular tissues can be experimentally produced in the gametophytes of ferns and lycopods. Hébant's enthusiasm has carried him to the point that he would be willing to use the term *phloem* to designate the leptom of mosses. Apparently he is not quite ready to apply the term *xylem* for the hydroid system.

An alternative interpretation is that the similarities between the conducting systems of bryophytes and vascular plants represent a remarkable case of convergent evolution and that the hydroids are analogous to xylem and the leptoids are analogous to phloem, or more specifically to sieve tubes. There is no real evidence for either interpretation.

Scanning EM studies have barely begun in bryophytes. McClymont and Larson (1964) and Miyoshi (1969*a*, 1969*b*) have examined spores with the SEM, and, as expected, small sculptured details appear that are not visible with the light microscope. Not enough genera have been examined to determine the systematic significance of the differences, however. Robinson (1971) has looked at leaf surfaces and peristomes with the SEM. He found that the leaf surface of *Philonotis* is covered with very tiny micropapillae which are not visible under the light microscope. The so-called C-shaped papillae of *Tortula* as seen with the ordinary microscope are not real, according to Robinson. The appearance is due to an optical effect produced by three sides of the papillae being steeper. Peristome SEM photographs reveal micropapillae on the larger normally visible papillae in some species. Taxonomic promise for the SEM is indicated by Robinson's observation that the peristome fine markings of *Rhamphidium* are unlike other pottiaceous genera and thus may not belong to the Pottiaceae.

Cytology

Chromosome information, especially chromosome numbers, of bryophytes has accumulated almost unbelievably during the past two decades. Berrie (1963) thinks the chromosomes of liverworts are probably better known than those of any other group of plants. While this is surely not the case in mosses, an enormous amount of data is now available. Steere (1972) has recently summarized the published reports of chromosome numbers in bryophytes. A complete tabular listing of numbers was published by Anderson (1962) for mosses and by Berrie (1960), but since then scores of species have been investigated. A later paper by Anderson (1964) reviews chromosome knowledge in mosses in relation to systematics.

By far the greatest majority of hepatics, probably 75%, have the number, $n = 9$; the Aneuraceae have doubtfully the number, $n = 10$; the number, $n = 8$, occurs in certain of the Marchantiales, the Sphaerocarpales, and some of the Jungermanniales Anacrogynae; the Anthocerotae have the number, $n = 5$, except in Japan, where the number seems to be 6; and *Takakia* has the lowest number, $n = 4$. Apparently there is little infraspecific variability in the chromosomes of hepatics. Aneuploidy is rare, and polyploidy is relatively uncommon, compared with mosses and higher plants. Schuster (1966) estimates 15% of the species of hepatics are polyploid, but this is probably an excessive figure.

In strong contrast, chromosome numbers of mosses are more diverse and more variable within and among species. All species of *Sphagnum* have the number, $n = 19$ (+ a variable number of m-chromosomes) or a multiple of 19; Andreaeales all have the number, $n = 11$; but few of the remaining families have consistent numbers. An exception is the entire order of Polytrichales, including the largest living bryophyte, *Dawsonia*. All have the base number, $n = 7$, and its multiple. The Dicranales have rather consistent numbers, $n = 12$, $n = 13$, $n = 14$, with 13 the most common number, and there is considerable ploidy. The majority of the pleurocarpous mosses seem to have either the number, $n = 10$ or

11, depending upon the presence or absence of the m-chromosome. There are notable exceptions, however. In the Hypnaceae, the numbers, $n = 6, 7, 8, 9, 10, 11, 12, 14, 16$, are known, in addition to the ploids. An even more diverse aneuploid series occurs in the Brachytheciaceae.

Chromosome numbers have been of little value in establishing relationships in bryophytes, especially hepatics. In mosses, polyploidy has at least limited value in the systematics of certain groups. In *Mnium*, for example, many species have the number, $n = 7$, and some have correspondingly paired species with the number, $n = 14$. The numbers, $n = 6$ and $n = 8$, are also known in the genus (*sensu lato*). The numbers have systematic significance as was pointed out by Lowry (1948) and others. Anderson and Bryan (1956) demonstrated a diploid-tetraploid-relationship between two taxonomically overlapping species of *Fissidens, F. cristatus* and *F. adiantoides*. A number of other moss genera have similar diploid-tetraploid species pairs, *e.g. Philonotis, Atrichum, Ptychromitrium,* and *Pleuridium*. In a large number of species of mosses there is infraspecific polyploidy, *Ditrichum pallidum, Dicranum fuscescens, Distichium capillaceum, Grimmia confertum, Pohlia longicollis, Hedwigia ciliata, Drepanocladus involvens*, and many others. But, in just about all cases, the diploids and tetraploids are indistinguishable. Lazarenko (1967) has stated that polyploids deserve specific rank, referring to the genus *Atrichum*, but few, if any, bryologists agree. Some species have a polyploid series, *e.g. Funaria hygrometrica*, $n = 14$, 28 and 56.

Perhaps the most significant chromosome feature of bryophytes is the fairly close resemblances of chromosome types and behavior between mosses and liverworts. The chromosomes of both groups have large heterochromatic regions, and nearly all species in both groups have certain chromosomes that are almost entirely heterochromatic. Both mosses and liverworts have a high incidence of m- micro-) chromosomes, which are small, usually achiasmic chromosomes with a characteristic meiotic behavior. They may pair loosely at meiosis, or they may be variously distantly paired. Often at meiosis, each m-half-bivalent (or univalent, as the case may be) divides prior to metaphase-I, resulting in four loosely associated quarter-chromatids. Each quarter-chromatid congresses independently and, apparently, undergoes segregation. At least they are distributed, one to each of the four spore nuclei with a high degree of regularity (see Anderson, 1964, for a résumé of m-chromosome behavior).

In some species, and perhaps genera, m-chromosomes appear to be a regular member of the karyotype and are never absent. Nearly all of the hepatics are in this category and some mosses, of which *Orthotrichum* is an example. In many species of mosses, however, the m-chromosome is supernumerary, and shares some characteristics with the B-chromosomes of higher plants. They differ in meiotic behavior and very likely in origin, which are sufficient reasons to maintain the distinctions between them. To my knowledge, only one species, *Weissia controversa*, has been sampled sufficiently to determine the frequency of m-chromosome populations. Anderson and Lemmon (1972) sampled over 400 populations of *W. controversa* and found that 84% had the number, $n = 13$, with 16% having the number, $n = 13 + \mathrm{m}$. The m-chromosome-populations were not randomly distributed. In the Atlantic Coastal Plain, m-chromosome frequency was 23%, in the Piedmont Plateau, 12%, and in the Southern Appalachian Mountains, it was only 3%. No explanation was offered for these geographical differences.

A second chromosomal feature of bryophytes, shared by both mosses and liverworts, is the presence of one chromosome in the complement which is conspicuously larger than the other members. Japanese cytologists call it an "H-chromosome," referring to the fact that it is usually largely heterochromatic, and in interphase nuclei shows up as a large heteropycnotic body (or two such bodies in sporophytic tissues). During interphase, the heteropycnotic H-chromosome can easily be confused with the nucleolus. This large chromosome has a primary and secondary kinetochore, which are, respectively, median and subterminal. During mitosis it utilizes the median or primary, but at meiosis it may use either, which results in a bewildering variety of configurations at metaphase-I, including situations in which one half-bivalent of a pair uses the submedian kinetochore, while its opposing mate utilizes the median. The appearance is not unlike that of a heteromorphic chromosome pair (Anderson, 1964; Anderson & Lemmon, 1972).

GENETICS

In contrast to the burst of cytological research in bryology during the past 25 years, there has been almost no progress in the genetics of bryophytes. Informational level is about where it was in 1945, when Allen last reviewed it, and the lack of progress can be noted by comparing Allen's review with that of Lewis in 1961.

Additional examples of familiar sex chromosome systems have been found in hepatics, but no new systems have been uncovered. Heterochromosomal pairs, long suspected in mosses, but shrouded in disagreement (Lewis, 1961), were demonstrated unequivocally in the genus *Macromitrium* by Ramsay (1966). Her photographs and drawings of *M. daemelii* and *M. archeri* clearly reveal a dimorphic pair of chromosomes at M-I of meiosis. Although contrasting measurements were not given, the "X-chromosome" is several times longer than the "Y," thus a chromosome complement of $8 + X/Y$ is proposed. Female leafy plants are large and normal for the genus, while the male plants are tiny and epiphytic on the leaves of the female plants. She was unable to observe chromosomes in the male gametophyte, but the complement of the female included a large chromosome which she easily concluded was the X, although absolute proof is lacking.

Sex chromosomes in *Macromitrium* had long been suspected because the dioicous species appeared to have two sizes of spores. Ramsay (1966) also noted two sizes in the spores of the species she studied, but a statistical treatment was necessary to demonstrate this. When graphed, a sort of bimodal curve of size classes of spores was produced, but it is not very convincing. Of more interest is the fact that Ramsay claims she could distinguish the two types of spores by color, one class being dark green, the other yellow to brown. Apparently Ramsay did not carry out germination experiments.

Putative natural hybrids among mosses continue to be described. The first claim for amphidiploidy was made by Khanna (1960), who found the tetraploid chromosome number, $n = 26$, in *Weissia* [*Astomum*] *exserta*, in India. He claims that *W. exserta* capsules are intermediate between *W.* [*Astomum*] *crispum* and *W. controversa*, and therefore *W. exserta* must have arisen through hybridization of these two species, followed by chromosome doubling. Meiosis in *W. exserta* is normal in all respects, and the spores appeared normal, but he did not test their viability.

Reese and Lemmon (1965) described natural hybrid capsules between *Astomum ludovicianum* and *Weissia controversa*, as being intermediate between the two parents, and containing spores which ranged from 0–2% viability in various hybrid capsules. Later, Anderson and Lemmon (1972) were able to study meiosis in apparent similar hybrids and their assumed parents. Each parent and the hybrid were found to have the number, $n = 13 + \mathrm{m}$. Meiosis was completely regular in the hybrid, and four normal-appearing tetrad cells were described. The tetrad cells, however, fail to enlarge and soon shrivel and abort. Anderson and Lemmon concluded that sterility results from either genic imbalances in the segregated haploid chromosome sets or from imbalances brought about by very small structural differences that do not impair synapses.

EVOLUTION AND CLASSIFICATION

Nearly all bryologists and vascular plant systematists agree that bryophytes are not ancestral to the vascular plants or their presumed fossil progenitors. It is also generally agreed that none of the three bryophyte classes recognized today are ancestral to any of the others. But popular and current as these views may be, they are based on speculative logic and not facts. There is no fossil evidence to relate bryophytes to either the green algae or the tracheophytes. Similarities in photosynthetic pigments and systems, life history homologies, and certain cellular details of modern day forms are the principal features which tie the three groups together. The antithetic theory has been largely abandoned, but there are still defenders who rise vigorously to its support (*e.g.* Meeuse, 1966). Schuster (1966) presents a strong defense of the currently accepted notion that bryophytes represent a derived group through reductions. This theory derives the entire archegoniate evolutionary line from a green alga with alternation of similar phases, and postulates a more or less direct line of evolution to the tracheophytes. At some point or points along this line a branch or branches (depending upon how polyphyletic one wishes to be about deriving the bryophytes) developed in which the sporophyte became essentially parasitic upon the gametophyte or at least remained physically attached to it. Most of the arguments center around how far up the line the bryophytes branched off. Opinions range from deriving them from either already evolved, full-fledged tracheophytes or at least a close ancestor of the tracheophytes, to the point of view that branching of the bryophyte line or lines occurred much earlier and closer to the algal progenitor. Also at issue is, how much resemblance to the present-day bryophytes did the main tracheophyte line have when the branching off occurred? Unless additional fossil material comes to light or some other fresh evidence is forthcoming, the subject is likely to remain, as Richards (1959) puts it, "a fascinating subject for speculation."

BIBLIOGRAPHY

ABRAMOV, A. L. & I. I. ABRAMOV. 1966. [Species muscorum rarae e Sibiria et Oriente extremo.] Novit. Syst. Pl. non Vasc. [Acad. Sci. USSR, Inst. Komarov] 1966: 302–315. [In Russian.]

———, K. I. LADYZHENSKAYA & L. I. SAVICZ-LYUBITSKAYA. 1954. [Flora Plantarum Cryptogamarum URSS. Vol. 3. Musci frondosi (2). Andreaeales, nec non Bryales (Tetraphidales, Polytrichales, Buxbaumiales, Schistostegales.)] Izdatel'stvo Akad. Nauk SSSR, Inst. Bot. V. L. Komarov. Moscow & Leningrad. [In Russian; English subtitle.]

———, L. I. SAVICZ-LYUBITSKAYA & Z. N. SMIRNOVA. 1961. [Manual of Leafy Mosses of Arctic USSR.] Akad. Nauk SSSR, Bot. Inst. V. L. Komarov. Moscow & Leningrad. [In Russian.]

ALLEN, C. E. 1945. Genetics of Bryophytes. II. Bot. Rev. 11: 260–287.

ANDERSON, L. E. 1962. Chromosome numbers: Bryophytes. Pp. 45–57 *in* P. L. Altman & D. S. Dittmer (editors), "Growth, Including Reproduction and Morphological Development." FASEB Biological Handbook Series. Washington, D.C. xii + 608 pp.

———. 1964. Biosystematic evaluations in the Musci. Phytomorphology 14: 27–51.

———. 1971. Geographical relationships of the mosses of the southern Appalachian Mountains. Pp. 101–115 *in* "The distributional history of the biota of the southern Appalachians. Part II. Flora." Virginia Polytechn. Inst. & St. Univ. Res. Div. Monogr. 2.

——— & V. S. BRYAN. 1956. A cytotaxonomic investigation of *Fissidens cristatus* Wils. and *F. adiantoides* Hedw. in North America. Rev. Bryol. Lichénol. 25: 254–267.

——— & H. A. CRUM. 1958. Cytotaxonomic studies of the mosses of the Canadian Rocky Mountains. Bull. Natl. Mus. Canada, Contr. Bot. 160: 1–89.

——— & B. E. LEMMON. 1972. Cytological studies of natural hybrids between species of the moss genera, *Astomum* and *Weissia*. Ann. Missouri Bot. Gard. 59: 382–416.

ARNELL, S. 1956. Illustrated Moss Flora of Fennoscandia. I. Hepaticae. Lund. 308 pp., figs. 1–97.

———. 1963. Hepaticae of South Africa. Stockholm. 411 pp., illustrated.

BARDUNOV, L. V. 1969. [The Handbook of the Mosses of Central Siberia]. Illustrated. Acad. Sci. USSR, Siberian Branch. Izdatel'stvo "Nauka," Leningrad. [In Russian.]

BARKMAN, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Netherlands. xii + 628 pp., figs. 1–21, 50 maps. [Reprinted in 1970.]

BARTRAM, E. B. 1949. Mosses of Guatemala. Fieldiana, Bot. 25: 1–442.

BAUER, L. 1956. Über vegetative Sporogonbildung bei einer diploiden Sippe von *Georgia pellucida*. Planta 46: 604–618.

———. 1963. On the stabilization of the male sexual tendency in Musci. Jour. Linn. Soc., Bot. 58: 337–342.

———. 1966. Über ein Kinin aus Kalluszellen von Laubmoosen und seine Rolle bei der Morphogenese. Ber. Deutsch. Bot. Ges. 79: 207.

BENSON-EVANS, K. 1964. Physiology of the reproduction of bryophytes. Bryologist 67: 431–445.

BERRIE, G. K. 1960. The chromosome numbers of liverworts (Hepaticae and Anthocerotae). Trans. Brit. Bryol. Soc. 3: 688–705.

———. 1963. Cytology and phylogeny of liverworts. Evolution 17: 347–357.

BILLINGS, W. D. & L. E. ANDERSON. 1966. Some microclimatic characteristics of habitats of endemic and disjunct bryophytes in the southern Blue Ridge. Bryologist 69: 76–95.

BIRSE, E. M. 1958. Ecological studies on growth-form in bryophytes. III. The relationship between the growth-form of mosses and ground water supply. Jour. Ecol. 46: 9–27; IV. Growth-form distribution in a deciduous wood. 46: 29–42.

BISCHLER, H. 1962–63. The genus *Calypogeia* Raddi in Central and South America. I. Introduction and subgenera *Mnioloma* and *Caracoma*. Candollea 18: 19–51; II. Subgenus *Calypogeia*, subgroups 1, 2, & 3; 18: 54–93; III. Subgenus *Calypogeia*, subgroups 4, 5. 18: 95–128.

——— & P. JOLY. 1969. Essais d'application de méthodes de traitement numerique des informations systématiques. II. Études des espèces européennes, africaines et sud-américaines de *Calypogeia*. Rev. Bryol. Lichénol. 36: 691–714.

BONNER, C. E. B. 1962–1966. Index Hepaticarum. Pts. I–VI. Weinheim.

BOPP, M. 1968. Control of differentiation in fern-allies and bryophytes. Annual. Rev. Pl. Physiol. 19: 361–380.

——— & H.-P. WENINGER. 1971. Wassertransport vom Gametophyten zum Sporophyten bei Laubmoosen. Zeitschr. Pflanzenphysiol. 64: 190–198.

BOROS, Á. 1968. Bryogeographie und Ungarns. Budapest. 466 pp., figs. 1–88.

BREEN, R. S. 1963. Mosses of Florida. Gainesville. xliv + 273 pp., 133 pl.

BREIL, D. A. 1970. Liverworts of the Mid-Gulf Coastal Plain. Bryologist 73: 409–491.

CARLQUIST, S. 1966. The biota of long-distance dispersal. I. Principles of dispersal and evolution. Quart. Rev. Biol. 41: 247–270.

CASTLE, H. 1968. *Radula* (L.) Dumortier. A synopsis of the taxonomic revision of the genus. Rev. Bryol. Lichénol. 36: 5–44.

CLARK, G. C. S., S. W. GREENE & D. M. GREENE. 1971. Productivity of bryophytes in polar regions. Ann. Bot. 35: 99–108.

CLAUSEN, E. 1952. Hepatics and humidity, a study on the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. Dansk Bot. Ark. 15: 5–80.

———. 1964. The tolerance of hepatics to desiccation and temperature. Bryologist 67: 411–417.

CROSBY, M. R. 1969*a*. A revision of the tropical American moss genus *Pilotrichum*. Bryologist 72: 275–343.

———. 1969*b*. Distribution patterns of West Indian mosses. Ann. Missouri Bot. Gard. 56: 409–416.

CRUM, H. A. 1951. The Appalachian-Ozarkian Element in the Moss Flora of Mexico with a Checklist of all Known Mexican Mosses. Ph.D. Dissertation, Univ. of Michigan, Ann Arbor.

———. 1972. The geographic origins of the mosses of North America's Eastern Deciduous Forest. Jour. Hattori Bot. Lab. 35: 269–298.

——— & E. B. BARTRAM. 1958. A survey of the moss flora of Jamaica. Bull. Inst. Jamaica, Sci. Ser. 8: 1–90.

DARLINGTON, H. T. 1964. The Mosses of Michigan. Ed. Howard Crum. Cranbrook Inst. Sci. Bull. 47. x + 212 pp., figs. 1–147. Bloomfield Hills.

DOMBROVSKAYA, A. V. & R. N. SHLYAKOV. 1967. [A Brief Treatment of the Lichens and Mosses of the Northern European Part of USSR.] Illustrated. Akad. Nauk SSSR; Izdatel'stvo "Nauka," Leningrad. [In Russian.]

DOYLE, W. T. 1970. The Biology of Higher Cryptogams. New York. vii + 163 pp.

DÜLL, R. 1969. Übersicht zur Bryogeographie Südwestdeutschlands unter besonderer Berücksightingung der Arealtypen. Herzogia 1: 215–320.

ENGEL, J. J. 1968. A taxonomic monograph of the genus *Balantiopsis* (Hepaticae). Nova Hedwigia 16: 83–130.

ESCHRICH, W. & M. STEINER. 1967. Autoradiographische Untersuchungen zum Stoffransport bei *Polytrichum commune*. Planta 74: 330–349.

——— & ———. 1968*a*. Die Struktur des Leitgewebesystems von *Polytrichum commune*. Planta 82: 33–49.

——— & ———. 1968*b*. Die submikroskopische Struktur der Assimilatleitbahnen von *Polytrichum commune*. Planta 82: 321–336.

FLORIN, R. 1940. The Tertiary fossil conifers of south Chile and their phytogeographical significance. Kongl. Svenska Vetenskapsakad. Handl., ser. 3. 19: 1–107.

FLORSCHÜTZ, P. A. 1964. The Mosses of Suriname. Part 1. Leiden. xxvii + 271 pp., figs. 1–107.

FLOWERS, S. 1954. Liverworts of Utah. Proc. Utah Acad. Sci. 31(1953–1954): 93–100.

———. 1961. The Hepaticae of Utah. Univ. Utah Biol. Ser. 12(2): 1–89.

FORMAN, R. T. T. 1964. Growth under controlled conditions to explain the hierarchical distribution of a moss, *Tetraphis pellucida*. Ecol. Monogr. 34: 1–25.

———. 1969*a*. Comparison of coverage, biomass and energy as measures of standing crop of bryophytes in various ecosystems. Bull. Torrey Bot. Club 96: 582–591.

———. 1969*b*. Caloric values of bryophytes. Bryologist 71: 344–347.

FULFORD, M. 1951. Distribution patterns of the genera of the leafy Hepaticae of South America. Evolution 5: 243–264.

———. 1963*a*, 1968. Manual of the leafy Hepaticae of Latin America. I. Mem. New York Bot. Gard. 11(1): 1–172. 1963; II. 11(2): 173–276. 1966; III. 11(3): 277–392. 1968.

———. 1963*b*. Continental drift and distribution patterns in the leafy Hepaticae. *In* A. C. Munyan (editor), "Polar Wandering and Continental Drift." Soc. Econ. Palaeontol. Mineral. Tulsa.

GAMS, H. 1962. Remarques ultérieures sur la phylogénie des Sphaignes. Rev. Bryol. Lichénol. 31: 1–4.

GANGULEE, H. C. 1969. Mosses of Eastern India and Adjacent Regions. Fasc. 1. Calcutta. xiii + 170 pp., figs. 1–78; 41 maps.

GAUME, R. 1954. Les éléments de la flora bryologique de Bretagne (suite et fin). Rev. Bryol. Lichénol. 23: 291–294.

GIMINGHAM, C. H. & E. M. BIRSE. 1957. Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habit. Jour. Ecol. 45: 533–545; II. Experimental studies on growth-form in mosses. 45: 721–733.

——— & E. T. ROBERTSON. 1950. Preliminary investigations on the structure of bryophytic communities. Trans. Brit. Bryol. Soc. 1: 330–344.

GLIME, J. M. 1971. Response of two species of *Fontinalis* to field isolation from stream water. Bryologist 74: 383–386.

GREENE, S. W. 1968. Studies in Antarctic Bryology. I. A basic check list for mosses. Rev. Bryol. Lichénol. 36: 132–138.

——— & R. E. LONGTON. 1970. The effects of climate on Antarctic plants. *In* M. W. Holdgate (editor), "Antarctic Ecology." Vol. 2. London.

———, D. M. GREENE, P. D. BROWN, B. S. & J. M. PACEY. 1970. Antarctic Moss Flora. I. The genera *Andreaea, Pohlia, Polytrichum, Psilopilum* and *Sarconeurum*. Brit. Antarctic Surv., Sci. Rep. 64. 118 pp., figs. 1–29. London.

GREGUSS, P. 1959. Die Entdeckung von Urkormorphyten aus dem Ordivicium. Proc. IXth Int. Bot. Congr., Montreal 1: 1–9.

GROLLE, R. 1959. Über *Herpocladium fissum* Mitt. Ein Nachtrag zu "Was ist *Pachyglossa*?" Rev. Bryol. Lichénol. 28: 346–350.

———. 1962. Monographie der Lebermoosgattung *Leptoscyphus* Mitt. Nova Acta Leop. 25: 1–143.

HATTORI, S. & M. MIZUTANI. 1958. What is *Takakia lepidozioides*? Jour. Hattori Bot. Lab. 20: 295–303.

HÉBANT, C. 1970. A new look at the conducting tissues of mosses (Bryopsida): their structure, distribution and significance. Phytomorphology 20: 390–410.

HERZOG, T. 1926. Geographie der Moose. Jena. xi + 439 pp., figs. 1–151, pls. 1–8.

HINSHIRI, H. M. & M. C. F. PROCTOR. 1971. The effect of desiccation on subsequent assimilation and respiration of the bryophytes *Anomodon viticulosus* and *Porella platyphylla*. New Phytol. 70: 527–538.

HOFFMAN, G. R. 1971. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. II. Diversity of the vegetation. Bryologist 74: 413–427.

——— & R. G. KAZMIERSKI. 1969. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. I. A description of the vegetation. Bryologist 72: 1–19.

HOSOKAWA, T., N. ODANA & H. TAGAWA. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. Bryologist 67: 396–411.

HUEBER, F. M. 1961. *Hepaticites devonicus,* a new fossil liverwort from the Devonian of New York. Ann. Missouri Bot. Gard. 48: 125–132.

INGOLD, C. T. 1959. Peristome teeth and spore discharge in mosses. Trans. Bot. Soc. Edinburgh 38: 76–88.

———. 1965. Spore Liberation. Oxford. ix + 210 pp., illustrated.

INOUE, H. 1966. A monograph of the hepatic genus *Syzygiella*. Jour. Hattori Bot. Lab. 29: 171–213.

IRELAND, R. R. 1969*a*. A taxonomic revision of the genus *Plagiothecium* for North America, north of Mexico. Natl. Mus. Canada, Publ. Bot. 1. vii + 118 pp., 23 pls., 8 maps.

———. 1969*b*. Taxonomic studies on the genus *Atrichum* in North America. Canad. Jour. Bot. 47: 353–368.

ISOVIITA, P. 1966. Studies on *Sphagnum*. I. Nomenclatural revision of the European taxa. Ann. Bot. Fenn. 3: 199–264.

———. 1970. Studies on *Sphagnum*. II. Synopsis of the distribution in Finland and adjacent parts of Norway and the U.S.S.R. Ann. Bot. Fenn. 7: 157–162.

IWATSUKI, Z. 1958. Correlations between the moss floras of Japan and of the Southern Appalachians. Jour. Hattori Bot. Lab. 20: 304–352.

———. 1960. The epiphytic bryophyte communities in Japan. Jour. Hattori Bot. Lab. 22: 160–350.

———. 1970. A revision of *Plagiothecium* and its related genera from Japan and her adjacent areas. I. Jour. Hattori Bot. Lab. 33: 331–380.

——— & A. J. SHARP. 1967. The bryogeographical relationships between Eastern Asia and North America. 1. Jour. Hattori Bot. Lab. 30: 152–170.

JOHANNSSON, B. 1968. Bryological observations on Surtsey. Surtsey Res. Progr. Rep. (Surtsey Res. Soc., Reykjavik) 4: 61.

JOVET-AST, S. 1967. Bryophyta. Pp. 19–186, *in* E. Boureau, "Traité de Paléobotanique." Vol. 2. Paris.

KAWAI, I. 1969. Studies on the affinity regarding the conducting tissue of the sporophyte in the Musci. (2) On the seta in some species of the family Polytrichaceae. Sci. Rep. Kanazawa Univ. 14(1): 39–57.

——— & K. IKEDA. 1970. Systematic studies on the conducting tissue of the gametophyte in Musci. (1) On the affinity regarding the conducting tissue of the stem in some species of Polytrichaceae. Sci. Rep. Kanazawa Univ. 15(2): 71–98.

KEEVER, C. 1957. Establishment of *Grimmia laevigata* on granite and its method of establishment. Ecology 38: 422–429.

KHANNA, K. R. 1960. Studies in natural hybridization in the genus *Weisia*. Bryologist 63: 1–16.

KOPONEN, T. 1968. Generic revision of Mniaceae Mitt. (Bryophyta). Ann. Bot. Fenn. 5: 117–151.

KOZLOWSKI, R. & P. GREGUSS. 1959. Discovery of Ordovician land plants (preliminary communication). Acta Palaeontol. Polon. 4: 1–9.

KRASILOV, V. A. 1970. [Leafy Hepaticae from the Jurassic Period in the Bureya river basin.] Akad. Nauk SSSR (Moscow) 3: 131–142. [In Russian.]

KRUPA, J. 1969. Photosynthetic activity and productivity of the sporophyte of *Funaria hygrometrica*. Acta Soc. Bot. Poloniae 38: 207–215.

LACEY, W. S. 1969. Fossil bryophytes. Biol. Rev. 44: 189–205.

LAL, M. 1961. *In vitro* production of apogamous sporogonia in *Physcomitrium coorgense* Broth. Phytomorphology 11: 263–269.

LANGE, O. L. 1955. Untersuchungen über die Hitzresistenz der Moose in Beziehung zu ihrer Verbreitung. I. Die resistenz stark ausgetrockneter Moose. Flora 142: 381–399.

———. 1969. CO_2-Gaswechsel von Moosen nach Wasserdampfaufnahme aus dem Luftraum. Planta 89: 90–94.

LAWTON, E. 1959. Revision of the genus *Lescuraea* in Europe and North America. Bull. Torrey Bot. Club 84: 281–307.

———. 1971. Moss Flora of the Pacific Northwest. Nichinan. xiii + 362 pp., pls. 1–195.

LAZARENKO, A. S. 1951. [Manual of the Leafy Mosses of White Russia]. Minsk: Akad. Nauk Belorusskoi SSR. 397 pp. [Title and text in Russian.]

———. 1967. Polyploidy in the evolution of Musci. Tsitologiia i Genetika 1(2): 15–26. [English summary.]

LEE, J. A. & G. R. STEWART. 1971. Desiccation injury in mosses. I. Intraspecific differences in the effect of moisture stress on photosynthesis. New Phytol. 70: 1061–1068.

LEWIS, K. R. 1961. The genetics of bryophytes. Trans. Brit. Bryol. Soc. 4: 111–130.

LONGTON, R. E. 1970. Growth and productivity of the moss *Polytrichum alpestre* Hoppe in Antarctic regions. Pp. 818–837, *in* M. W. Holdgate (editor), "Antarctic Ecology." Vol. 2. London.

LOWRY, R. J. 1948. A cytotaxonomic study of the genus *Mnium*. Mem. Torrey Bot. Club 20: 1–42.

———. 1954. Observations upon the regeneration of *Mnium cuspidatum* setae. Bryologist 57: 147–149.

LUNDBLAD, B. 1954. Contributions to the geological history of the Hepaticae. Fossil Marchantiales from the Rhaetic-Liassic coalmines of Skromberga (Province of Scania), Sweden. Svensk Bot. Tidskr. 48: 381–417.

MALMBORG, S. VON. 1933. *Cryptothallus* nov. gen. Ein saprophytischen Lebermoos. Ann. Bryol. 6: 122–123.

———. 1934. Weiteres über die Gattung *Cryptothallus*. Ann. Bryol. 7: 108–110.

MALTA, N. 1921. Versuche über die Widerstandsfähigkeit der Moose gegen Austrocknung. Acta Univ. Latv. 1: 125–129.

MÅRTENSSON, O. 1955*a*–1956. Bryophytes of the Torneträsk area, northern Swedish Lappland. I. Hepaticae; II. Musci; III. General part, Review of the Torneträsk area and comments on the lists of Hepaticae and Musci. Kongl. Svenska Vetenskapsakad. Handl. 23(5): 1–69; 23(10): 1–163.

———. 1955*b*. Bryophytes of the Torneträsk area, northern Swedish Lappland. Summary. Uppsala.

McClymont, J. W. & D. A. Larson. 1964. An electron microscope study of spore wall structure in the Musci. Amer. Jour. Bot. 51: 195–200.

Meeuse, A. D. J. 1966. The early evolution of the Archegoniatae: a reappraisal. Acta Bot. Neerl. 15: 162–177.

Mel'nichuk, W. M. 1959. Zum Wasseraushalt der Moose. Rev. Bryol. Lichénol. 28: 223–234.

———. 1970. [Manual of the Leafy Mosses of the Central Region and the South European Part of the USSR.] Akad. Nauk Ukrain. SSR. Inst. Bot. Illustrated. Isdatel'stvo "Naukova Dumka." Kiev. [In Russian.]

Mitchell, J. C., W. B. Schofield, B. Singh & G. H. N. Towers. 1969. Allergy to *Frullania*. Arch. Derm. 100: 46–49.

Miyoshi, N. 1969*a*. On the fine structure of the spore surface in the Musci. I. Misc. Bryol. Lichenol. 5: 57–58.

———. 1969*b*. On the fine structure of the spore surface in the Musci. II. Jour. Jap. Bot. 44: 295–298.

Newton, M. E. 1972. An investigation of photoperiod and temperature in relation to the life cycles of *Mnium hornum* Hedw. and *M. undulatum* Sw. (Musci) with reference to their histology. Bot. Jour. Linn. Soc. 65: 189–209.

Nyholm, Elsa. 1954–1969. Illustrated Moss Flora of Fennoscandia. II. Musci. Fasc. 1, 87 pp., figs. 1–37. 1954; fasc. 2, pp. 85–189, figs. 38–93. 1956; fasc. 3, pp. 189–288, figs. 94–163. 1958; fasc. 4, pp. 287–408, figs. 163–259. 1960; fasc. 5, pp. 407–647, figs. 259–423. 1965; fasc. 6, pp. 647–799, figs. 423–498. 1969.

———. 1971. Studies in the genus *Atrichum* P. Beauv. A short survey of the genus and species. Lindbergia 1: 1–33.

Ochi, H. 1959. A revision of the Bryaceae of Japan and adjacent regions. Biol. Inst., Tottori. 1959. 124 pp.

Oehlkers, F. 1965. Entwicklungsgeschichte Rönteninduzierter Mutanten von *Funaria hygrometrica* L. Zeit. Vererbungsl. 96: 234–249.

Pais, M. S. 1966. Les types de mouvement du péristome des mousses et les conditions climatiques. Revista Biol. Lisbon 5: 239–250.

Paolillo, D. J. & F. A. Bazzaz. 1969. Photosynthesis in sporophytes of *Polytrichum* and *Funaria*. Bryologist 71: 335–343.

Patterson, P. M. 1964. Problems presented by bryophytic xerophytism. Bryologist 67: 390–396.

Pavletić, Z. 1955. Prodromus flore briofita Jugoslavije. Zagreb. xxi + 578 pp. [In Croatian, with German summary.]

Pettersson, B. 1940. Experimentelle Untersuchungen über die euanemochore Verbreitung der Sporenpflanzen. Acta Bot. Fenn. 25: 1–102.

Pilous, Z. 1948. Naše Mechy. Illustrovany Kliě Kurčovani mechu československych. Praha. 326 pp.

Proctor, V. W. 1961. Dispersal of *Riella* spores by waterfowl. Bryologist 64: 58–61.

Proskauer, J. 1967. Studies on Anthocerotales. VII. On day length and the western Himalayan hornwort flora, and on some problems in cytology. Phytomorphology 17: 61–70.

Pursell, R. A. & W. D. Reese. 1970. Phytogeographic affinities of the mosses of the Gulf Coastal Plain of the United States and Mexico. Jour. Hattori Bot. Lab. 33: 115–152.

Ramsay, H. P. 1966. Sex chromosomes in *Macromitrium*. Bryologist 69: 295–311.

Ratcliffe, D. A. 1968. An ecological account of Atlantic bryophytes in the British Isles. New Phytol. 67: 365–439.

Redfearn, P. L., Jr. 1972. Mosses of the Interior Highlands of North America. Ann. Missouri Bot. Gard. 59: 1–104.

Reese, W. D. 1961. The genus *Calymperes* in the Americas. Bryologist 64: 89–140.

——— & Betty E. Lemmon. 1965. A natural hybrid between *Weissia* and *Astomum* and notes on the nomenclature of the North American species of *Astomum*. Bryologist 68: 277–283.

Richards, P. W. 1959. Bryophyta. Pp. 387–420, *in* W. D. Turrill (editor), "Vistas of Botany."

ROBINSON, H. 1962. Generic revisions of North American Brachytheciaceae. Bryologist 65: 73–146.

———. 1971. Scanning electron microscope studies on moss leaves and peristomes. Bryologist 74: 473–483.

ROMELL, L. G. 1939. Production de litière et croissance annuelle de la myrtille et des mousses dans les forêts de Pin sylvestre nordiques. Svensk Bot. Tidskr. 33: 366–382.

RUDOLPH, E. D. 1970. Local dissemination of plant propagules in Antarctica. *In* M. W. Holdgate (editor), "Antarctic Ecology." Vol. 2. London.

SAINSBURY, G. O. K. 1955. A Handbook of the New Zealand Mosses. Roy. Soc. New Zealand Bull. 5: 1–490.

SAKURAI, K. 1954. Muscologia Japonica. Tokyo. 247 pp.

SAVICZ-LYUBITZKAYA, L. I. 1952. [Flora Spore-bearing Plants, USSR. Vol. 1. *Sphagnum.*] Acad. Sci. USSR. Moscow & Leningrad. [Russian title and text.]

——— & I. I. ABRAMOV. 1959. The geological annals of Bryophyta. Rev. Bryol. Lichénol. 28: 330–342.

——— & Z. N. SMIRNOVA. 1968. [The Handbook of Sphagnaceae of the USSR.] Akad. Nauk SSSR, Komarov Bot. Inst. Izdatel'stvo "Nauka," Leningrad. [In Russian.]

——— & ———. 1970. [The Handbook of Mosses of the USSR. Vol. I. The Mosses Acrocarpous.] Akad. Nauk SSSR, Komarov Bot. Inst. Izdatel'stvo "Nauka." Leningrad. [In Russian.]

SAYRE, G. 1959. Dates of Publications Describing Musci, 1801–1821. Troy, New York. 102 pp.

———. 1969, 1971. Cryptogamae Exsiccatae—an annotated bibliography of published exsiccatae of Algae, Lichens, Hepaticae and Musci. Mem. New York Bot. Gard. 19(1): 1–174. 1969; 19(2): 175–276. 1971.

SCHOFIELD, W. B. 1969. Phytogeography of northwestern North America. Bryophytes and vascular plants. Madroño 20: 155–207.

SCHULTZE-MOTEL, W. 1970. Monographie der Laubmoosgattung *Andreaea.* 1. Die costaten Arten. Willdenowia 6: 25–110.

SCHUSTER, R. M. 1949. The ecology and distribution of Hepaticae in central and western New York. Amer. Midl. Naturalist 42: 513–712.

———. 1953–1958. Boreal Hepaticae, a manual of the liverworts of Minnesota and adjacent regions. I. Amer. Midl. Naturalist 49: 257–684. 1953; II. Ecology, 57: 203–299. 1957; III. Phytogeography, 59: 257–332. 1958.

———. 1959–1960. A monograph of the nearctic Plagiochilaceae. I. Introduction and Sect. *Asplenioides.* Amer. Midl. Naturalist 62: 1–166; II. Sect. *Zonatae* to Sect. *Parallelae,* 62: 257–395. 1959; III. Sect. *Contiguae* to Conclusion, 63: 1–130. 1960.

———. 1963. Annotated synopsis of the genera and subgenera of Lejeuneaceae. Nova Hedwigia 9: 1–203.

———. 1966, 1969*a*. The Hepaticae and Anthocerotae of North America. 1. xvii + 802 pp., figs. 1–84. 1966; 2. xii + 1062 pp., figs. 85–301. 1969. New York.

———. 1969*b*. Problems of antipodal distribution in lower land plants. Taxon 18: 46–91.

——— & G. A. M. SCOTT. 1969. A study of the family Treubiaceae (Hepaticae: Metzgeriales). Jour. Hattori Bot. Lab. 32: 219–268.

SHACKLETTE, H. T. 1965. Element content of bryophytes. Geol. Surv. Bull. 1198 D. U.S. Govt. Printing Office, Washington.

SHARP, A. J. 1937. Tropical bryophytes in the southern Appalachians. Ann. Bryol. 11: 141–144.

———. 1939. Taxonomic and ecological studies of eastern Tennessee bryophytes. Amer. Midl. Naturalist 21: 267–354.

———. 1941. Some historical factors and the distribution of southern Appalachian bryophytes. Bryologist 44: 16–18.

——— & S. HATTORI. 1967. *Takakia ceratophylla* found in the Aleutians. Misc. Bryol. Lichen. 4: 120.

SHLYAKOV, R. N. 1961. [Flora of the Leafy Mosses of the Khibin Mountains.] Murmansk. [In Russian.]

ŠMARDA, J. 1948. Mechy Slovenska ČSR. Čas. Zemsnského Mus. Brně 32: 1–75.

SMITH, G. L. 1971. Conspectus of the genera of Polytrichaceae. Mem. New York Bot. Gard. 21(3): 1–83.

SMITH, J. L. 1966. The liverworts *Pallavicinia* and *Symphyogyna* and their conducting system. Univ. California Publ. Bot. 39: 1–46.

Srinivasan, K. S. 1968. An ecological and distributional resumé of the liverworts and mosses of India. Bull. Bot. Surv. India 10: 377–380.

Steere, W. C. 1946. Cenozoic and Mesozoic bryophytes of North America. Amer. Midl. Naturalist 36: 298–324.

———. 1955. Bryology. Pp. 267–299, *in* "A Century of Progress in the Natural Sciences, 1853–1953." California Acad. Sci., San Francisco.

———. 1971. A review of Arctic bryology. Bryologist 74: 428–441.

———. 1972. Chromosome numbers in bryophytes. Jour. Hattori Bot. Lab. 35: 99–125.

Stocker, O. 1956. Die Transpiration der Thallophyten. *In* "Ruhland's Handbuch der Pflanzenphysiologie." Vol. 3. Berlin.

Størmer, P. 1969. Mosses with a Western and Southern Distribution in Norway. Oslo. 288 pp., figs. 1–206.

Stotler, R. E. 1969. The genus *Frullania* in Latin America. Nova Hedwigia 18: 397–555.

Swails, L. F. 1970. The genus *Porella* in Latin America. Nova Hedwigia 19: 201–291.

Szweykowski, J. 1958. Prodromus florae hepaticarum Poloniae. Spraw. Poznańsk. Towarz. Przyjac. Nauk 19: 1–600.

——— & M. Kozlicka. 1969. The variability of Polish *Ptilidium* species as grown in parallel cultures under identical conditions. Bull. Soc. Amis Sci. Lett. Poznań, sér. D, Sci. Biol. 9: 71–84.

——— & M. Krzakowaa. 1969. The variability of *Plagiochila asplenioides* (L.) Dum. *s. l.* as grown in parallel cultures under identical conditions. 1. The status of *Plagiochila major* (Nees) S. Arnell. Bull. Soc. Amis Sci. Lett. Poznań, sér. D, Sci. Biol. 9: 85–103.

——— & S. Vogel. 1966. Experimental comparison of variability in American and European populations of *Geocalyx graveolens* (Hepaticae, Harpanthaceae). Fragm. Florist. Geobot. 7: 51–57.

Tallis, J. H. 1959. Studies in the biology and ecology of *Rhacomitrium lanuginosum* Brid. II. Growth, reproduction and physiology. Jour. Ecol. 47: 325–350.

Tamm, C. O. 1964. Growth of *Hylocomium splendens* in relation to tree canopy. Bryologist 67: 423–426.

Tatuno, S. 1958. Chromosomen bei *Takakia lepidozioides* Hattori & Inoue. Jour. Hattori Bot. Lab. 20: 119–123.

Touw, A. 1962. Revision of the moss-genus *Neckeropsis* (Neckeraceae). I. Asiatic and Pacific species. Blumea 11: 373–425.

———. 1971. A taxonomic revision of the Hypnodendraceae (Musci). Blumea 19: 211–354.

Walton, J. 1925. Carboniferous Bryophyta. I. Hepaticae. Ann. Bot. 39: 563–572.

———. 1928. Carboniferous Bryophyta. II. Hepaticae and Musci. Ann. Bot. 42: 707–716.

Wang, C. K. 1970. Phytogeography of the Mosses of Formosa. Taiwan. xvi + 576 pp., 45 figs.

Watson, E. V. 1964. The Structure and Life of Bryophytes. Hutchinson University Library, London. 192 pp., figs. 1–20.

Welch, Winona H. 1957. Mosses of Indiana. Indianapolis. 478 pp., figs. 1–254.

———. 1960. A Monograph of the Fontinalaceae. The Hague. iv + 357 pp., figs. 1–87.

———. 1971. The Hookeriaceae of Jamaica, Hispaniola, and Puerto Rico. Bryologist 74: 77–130.

Wijk, R. van der, W. D. Margadant & P. A. Florschütz. 1959–1969. Index Muscorum. 1. Regnum Veg. 17: 1–548. 1959; 2. 26: 1–535. 1962; 3. 33: 1–529. 1964; 4. 48: 1–604. 1967; 5. 65: 1–604. 1969. Utrecht.

Williams, S. 1950. The occurrence of *Cryptothallus mirabilis* Malmb. in Scotland. Trans. Brit. Bryol. Soc. 1: 357–366.

Yarrington, G. A. 1967. A quantitative study of the bryophyte and macrolichen vegetation of the Dartmoor granite. Lichenologist 3: 392–408.

———. 1970. Towards a mathematical model of limestone pavement vegetation. III. Estimation of the determinants of species frequencies. Canad. Jour. Bot. 48: 1387–1404.

25 years of botany

PTERIDOLOGY
1947–1972[1]

W. H. Wagner, Jr.[2]

Few botanical fields have experienced such expansion in the past 25 years as pteridology. When I began my doctoral dissertation in 1947, it was hardly considered a separate field, but things have changed. Evidence of its increasing recognition comes from many sources. For example, various institutions have appointed individuals specifically for their competence in pteridology. In the United States active programs in research on pteridophytes are being fostered at such centers as University of California (Berkeley), University of Southern California, Duke University, Harvard University, University of Massachusetts, University of Michigan (Ann Arbor), New York Botanical Garden, University of Tennessee, Vanderbilt University, and the U.S. National Museum. The two major publications devoted exclusively to pteridology have steadily improved in their format and quality—The *British Fern Gazette* under the editorship of Clive Jermy of the British Museum, and *The American Fern Journal* under David B. Lellinger and the late Conrad V. Morton of the Smithsonian Institution. A new Section of Pteridology was set up in 1970 by the Botanical Society of America. During the past five years, the American Institute of Biological Sciences has published in its journal *BioScience* two symposia based upon pteridophytes.

Someone has said, "Pteridology is the study of plants with a particular way of life." Pteridophytes have kept the ancient life cycle of early land plants, involving two distinct free-living generations. Students of these plants deal with their special features, the distinctive alternation of generations in particular. What contributions can the unique features of pteridophytes make to the understanding of basic biological phenomena? What can we conclude about their evolution, natural history, and systematics—past and present? With this scope, it is rather hard to say, in all cases, who is and who is not a pteridologist. A physiologist or morphologist might use lower vascular plants in his research, but only incidentally to other similar studies involving other kinds of plants. On the contrary, a physiologist or morphologist might focus entirely upon pteridophytes and their distinctive attributes. With such a broad spectrum, I have had

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to be somewhat arbitrary in choosing what researchers and what research to embody in this review.

Why has pteridology grown so much these last 25 years? In one respect this field is no different from others—pteridology profited from the financial support for basic research in all fields, which increased tremendously during this period. The idea of governmental support for basic science led to such agencies as the National Science Foundation, which has been a major factor in our progress. Hand-in-hand with granting agencies has been a general burgeoning of academic activity everywhere—a "Golden Age" for academia, for research, and for the training of doctoral candidates. Only now, with the levelling off of population increase, is the critical demand subsiding for new Ph.D.'s.

Another stimulus for pteridology resulted from various interactions of pteridologists with other disciplines. Formerly the field consisted mainly of comparative morphology and taxonomy, as represented in the work of such authors as J. G. Baker, R. H. Beddome, F. O. Bower, D. H. Campbell, H. Christ, C. Christensen, E. B. Copeland, G. E. Davenport, L. Diels, G. Hieronymus, W. R. Maxon, C. V. Morton, L. Underwood, and C. A. Weatherby. But now many cross-connections exist with other fields, as was so beautifully evidenced a short while ago in the joint symposium of the American Institute of Biological Sciences and the Botanical Society of America entitled "Ferns as Tools in Solving Biological Problems." Held at Indiana University, Bloomington, in 1970, this symposium called attention to the value of ferns for understanding alternation of generations (Whittier, 1971), development of gametophytes (Voeller, 1971), development of sporophytes (White, 1971), polyploidy and gene dosage (DeMaggio, 1971), and genetics (Klekowski, 1971).

In respect particularly to physiology and development, research on pteridophytes has been greatly influenced by Ralph H. Wetmore and his graduate students and co-workers at Harvard University, and by C. W. Wardlaw and his group at University of Manchester. Much of their work was recently reviewed by Richard A. White (1971). In genetics and cytology, the initial impetus came largely from Irene Manton and her students at the University of Leeds. Only recently have chemical systematists developed studies involving pteridophytes, and it is too soon to tell how important this interface will prove to be. The ecology of pteridophytes, as illustrated, for example, in the classic *p*H and edaphic investigations of Edgar T. Wherry of the University of Pennsylvania, has remained at low ebb since his retirement, except for the explorations of A. R. Kruckeberg (1964) at the University of Washington involving the association of western North American ferns with serpentine rock outcroppings. In a recent AIBS symposium held at Columbus, Ohio, in connection with the Flora North America Project, various aspects of the geography of pteridophytes were discussed. The individual papers were published in *BioScience* (Volume 19, Number 9, September, 1969). Rolla Tryon's contributions to our knowledge of fern distribution (1969, 1970*a, b*) are noteworthy in demonstrating how closely geographical understanding depends upon taxonomic interpretation.

Another strong factor in the recent expansion of pteridology is the stimulation from controversies about systematics and taxonomy. Here I refer particularly to the differing hypotheses of such investigators as the Chinese pteridologist R. C. Ching (1940); the Dane, Carl Christensen (1938); the American, Edwin B. Copeland (1947); the Britisher, R. E. Holttum (1946, 1949); the Indian, B. K. Nayar (1970); and the Italian, Rodolfo E. G. Pichi-Sermolli (1958). Issues that have been raised by their conflicting phylogenies and classifications involve not simplistic questions of whether to lump or to split but instead fundamental questions of evolutionary relationships.

Below are reviewed some of the high spots of pteridology, as I see them, which have appeared during the past quarter century. I have confined myself mainly to American pteridology, and much of what is reported here was published in the *American Journal of Botany* and *American Fern Journal.* Irene Manton (1955) has already summarized the overall history of pteridology during the period 1853–1953 in the California Academy of Sciences' book *A Century of Progress in the Natural Sciences.* Pteridology in the United States up to approximately the beginnings of the period of the present review has been described by Rolla Tryon (1969) in connection with the XI International Botanical Congress in the book entitled *A Short History of Botany in the United States*, edited by Joseph Ewan.

I shall emphasize here some of the changing concepts and viewpoints in pteridology. One can examine these from several standpoints, but I shall divide the report into two major parts—the biology of the phases of the life cycle; and the diversity of pteridophytes, their origin, evolution, and classification. The paleobotany of pteridophytes is reviewed elsewhere in this symposium.

Biology of the Gametophyte

The classic alternation—haploid spore, gametophyte, gametangia, gametes; diploid zygote, embryo, sporophyte, sporangium—is revealed to be considerably more diverse than we had traditionally thought. Although we had recognized the variables of spores, for example, they had not been applied to systematics of ferns to any great extent. Such variables as the *spore wall*, especially the presence or absence of the so-called "perispore," the more or less "loose" outer jacket surrounding the exospore; the *pigmentation*, in particular the presence or absence of chlorophyll; *geometry*, tetrahedral *vs.* bilateral; and *sexual differentiation*, especially heterospory and the attendant endosporic and parasitic condition of the gametophyte all have considerable potential in establishing phylogenetic relationships. It was A. H. G. Alston (1956) of the British Museum who first applied spore structure in a major revision of the higher ferns. In a paper remarkable for its impact in view of its brevity, Alston recognized the naturalness of the group of ferns in which bilateral and perisporial spores prevail, a concept now becoming widely accepted by pteridologists. I predict that in identification keys of the future, the spore characters will more and more be exploited. The recent use of scanning electron microscopy for spore surfaces (*e.g.* Britton, 1972) has produced much of value, especially in the interpretation of closely related species and hybrids.

Lloyd and Klekowski (1970) demonstrated that spores containing chlorophyll have appeared in a wide variety of phylogenetic lines—Horsetails, Equisetaceae;

Royal ferns, Osmundaceae; Rainforest polypodies, Grammitidaceae; Filmy-ferns, Hymenophyllaceae; and scattered genera in several other families. Thus we may conclude that adaptive forces are operative. All of the green spores are distinguished further by having thin walls, and Lloyd and Klekowski suggest that these spores are adapted for very quick germination and development. The seemingly fundamental difference betwen bilateral and tetrahedral spores has broken down to some extent, due to researches of the past couple of decades. We now know that both architectural types may exist within the same genus or even species. The so-called "scar"—triradiate in tetrahedral spores, and straight in bilateral—may actually vary from spore to spore in certain apogamous ferns, especially the mitospores of the apogamous *Polypodium dispersum* reported by Evans (1964).

Our comprehension of sexual differentiation of gametophytes has been augmented by the work of Jeffrey G. Duckett, Ulrich Näf, Bruce Voeller, and Richard L. Hauke. John H. Miller (1968) and Voeller (1971) have summarized much of this work, as well as the role of fern gametophytes as experimental material. Commonly, in spite of the absence of obvious spore-size differences, we find that laboratory cultures comprise clearly differentiated male and female gametophytes. In many cases, this differentiation proves to be controlled by antheridogens—hormones which stimulate formation of male organs. Holttum (1956) discussed the nature and possible relationships of the odd Australian fern, *Platyzoma,* in which the spore cases contain either 16 large spores or 32 small spores. Later, Alice Tryon (1964) grew the spores, and she found that the larger ones formed archegonial prothallia, the smaller ones, antheridial. These prothallia have the ability, apparently, to become bisexual in later development—at least the archegonial prothallia—and this suggests that the initial differentiation may be nutritional in origin and dependent upon the number of divisions of the archesporium in forming spore mother cells.

Alma G. Stokey and Lenette Rogers Atkinson (1964) have made valuable comparative studies of "higher fern" gametophytes, those belonging to genera formerly placed in Polypodiaceae *sens. lat.* These authors show that gametophytes, in spite of their basic simplicity, possess numerous characters that had been ignored in systematics by earlier workers. This research provides a good example, by the way, of the kind of stimulation provided by differing hypotheses. Miss Stokey, who taught at Mount Holyoke and died several years ago, told me herself in the early fifties that she had been disinterested in comparative morphology of "polypodiaceous" gametophytes until she learned of the extensive differences of opinion regarding their systematic relationships.

Nayar and Kaur (1971) reviewed the comparative morphology of homosporous fern gametophytes in detail, including summaries of spore germination, prothallial development, the structure of the mature prothallus, vegetative propagation, and apogamy. A most useful summary of the characteristics of gametophytes of each of the taxonomic groups is given (p. 323–371). (The literature titles on gametophytes cited by Nayar and Kaur for the period 1561–1946 total 159; those for the period 1947–1970 total 240—an excellent illustration of expansion of pteridology after World War II.) Vegetative specializations of gametophytes reach extremes in such plants as *Trichomanes holopterum* (Farrar & Wagner, 1968), in which root-like and rhizome-like functions of anchorage and absorption are accomplished by rhizoid-bearing filament systems, and leaf-like functions by upright blade-like thallus lobes which are determinate. The rhizoids of this gametophyte are dimorphic, some peg-like and some glandular. Gemmae, spindle-shaped and four-celled, are produced upon the thallus tips. Such gametophytes have evolved specializations comparable to those of certain bryophytes. Indeed—like bryophytes—these gametophytes make up the dominant generation.

Subterranean, mycorrhizal gametophytes have been found to exist in ferns where they had never been suspected before. Also there has been considerable success in culturing these heterotrophic plants under experimental conditions for the first time. David W. Bierhorst (as summarized in his recent book *Morphology of Vascular Plants*, 1971) describes a number of new discoveries he has made regarding these peculiar prothallia. They are without chlorophyll ordinarily, and are found more or less buried in soil. We earlier knew that they occurred in members of Psilotaceae, Lycopodiaceae, and Ophioglossaceae, but Bierhorst found them also in the fern genus *Stromatopteris* (placed traditionally in Gleicheniaceae, but recently in a family of its own) and in *Schizaea sens. lat.* (Schizaeaceae).

Freeberg and Wetmore (1957), in connection with experimental studies of *Lycopodium*, made an extraordinary discovery: Not only could they grow the usually massive mycorrhizal gametophytes of *L. complanatum* and *L. selago* from spores in culture, but the cultured prothallia—devoid of fungi—proved to be small, green, branching structures remarkably like the photosynthetic gametophytes of *L. cernuum*. Freeberg and Wetmore have thus shown that the mycorrhizal condition in the species they studied is facultative and that the plants can be grown without fungi and actually "converted" into gametophytes like those of other sections of the genus. Taxonomists in recent years have tended to separate some lycopods into distinct genera: *Diphasium* (to which *L. complanatum* would belong), *Huperzia* (including *L. selago*), and *Lycopodiella* (including *L. cernuum*). This classification rested in large measure upon characters of gametophytes found under natural conditions. If the distinctive gametophytes of two lycopod "genera" can be grown artificially under conditions that make them develop into the gametophyte-type of a third "genus," then one may well question the value of the gametophyte in the taxonomy of clubmosses.

Dean P. Whittier of Vanderbilt University reported the first successful experimental culture of gametophytes of Ophioglossaceae in 1972. He cultured spores of the common wintergreen grapefern, *Botrychium dissectum*, on a medium containing inorganic nutrients and sucrose and was able to produce gametophytes remarkably like those in the wild, except for the total absence of the symbiotic fungus. Whittier's techniques will now make it possible to initiate biosystematic experimentation upon these taxonomically difficult and confusing plants.

The studies of bracken fern gametophytes by David Wilkie (1956) showed apparent incompatibility systems in operation. In spite of the simultaneous presence of both male and female sexual organs on the gametophytes, cross-fertilization took place in approximately 80–90% of the zygotes. However, subsequent work by Klekowski and Baker (1966) and Klekowski (1971, 1972) confirmed that the prevailing state in a variety of different fern taxa was self-compatibility. Intragametophytic fertilization is readily possible on hermaphroditic gametophytes bearing both functional antheridia and archegonia. Any zygote which arises from the fusion of gametes originating in a single gametophyte is completely homozygous. Accordingly, Klekowski and his co-workers at University of Massachusetts are capitalizing on this ability for self-fertilization to make inquiries into such genetic phenomena as the expression of genes in both the gametophyte and the sporophyte, as well as problems of genetic load.

The consequences of Klekowski's discoveries for the understanding of long-distance dispersal in ferns are obvious: If a single spore has the ability to produce a self-compatible and bisexual gametophyte, the probabilities of single-spore species dispersal and establishment are greatly heightened. Highly isolated disjuncts may not necessarily constitute relicts, therefore; on the contrary, they may be merely casual and sporadic "wanderers."

To many plant biologists one of the strangest findings of pteridology in the past 25 years has been the existence of "independent fern gametophytes"—gametophytes which form the dominant generation. Now known in at least four genera of ferns in three families, they are widespread in temperate North America. The best known of them is the gametophyte of the shoestring fern, *Vittaria* (Wagner & Sharp, 1963), which has an extensive distribution in the Appalachians. Locally abundant in grottoes of rock cliffs, the plants appear as delicate mats of pale-green thalli resembling small liverworts. The gametophytes of filmy-ferns, *Trichomanes*, resemble clusters of filamentous green algae such as *Cladophora* (Wagner & Evers, 1963; Farrar, 1967). The gametophytes of shoestring fern never produce sporophytes in the Appalachian region, and those of filmy-ferns very rarely produce sporophytes. In the state of Virginia, for example, where *Trichomanes* gametophytes are well known, the sporophyte has never been discovered. The ribbon-like clonal prothallia of the filmy-fern genus *Hymenophyllum* (or its segregates) is now known from numerous populations in the southern Appalachians (Farrar, 1967) as well as western North America as far north as Alaska, as reported by T. M. C. Taylor of the University of British Columbia (1967). In his intensive studies of the biology of these plants, Donald R. Farrar of Iowa State University ran into a family of plants new to North America, the Grammitidaceae. Over 900 miles north of its normal range, the species *Grammitis nimbata* grows on damp rocks under a waterfall in the mountains of North Carolina. Although the gametophyte is locally abundant in this locality, the only sporophytes are tiny and obviously imperfectly developed, apparently dying long before they reach full size. All of these "independent gametophytes"—*Vittaria, Trichomanes, Hymenophyllum,* and *Grammitis*—belong to tropical rain forest families and are growing in North America far to the north of their major distribution centers. They survive because of their ability to produce large clonal mats and to disperse themselves by tiny, wind-borne prothallial gemmae.

BIOLOGY OF THE SPOROPHYTE

Turning now to advances in our understanding of the sporophyte, there have been a number of changes as a result of new data. A question has existed, for example, regarding the homology of the dictyostele of the ferns and the eustele of most seed plants. Beck (1970) and his students at University of Michigan (Ann Arbor) have determined that, in addition to already recognized differences between these stelar types, the forms of the gaps in the two groups are not comparable. These workers suggest therefore that the steles in seed plants and in ferns had different pathways of origin. More and more the possibility seems plausible that fern steles may have resulted from evolutionary reduction, including the loss of the cauline stele and its replacement by strands of leaf traces (*cf.* Wagner, 1964*b*).

Richard A. White (1963*a, b*) investigated the tracheary elements of the stems of ferns and showed trends comparable to those established for flowering plants. Such changes as (1) shortening of tracheary elements, (2) increase in occurrence of modified (alternate and opposite) pits on the lateral walls, (3) increase in occurrence of end plates, and (4) appearance of cells having the characteristics of vessel members all seem to be related to increase in evolutionary divergence. Cells having all or most of the characteristics of true vessel elements were reported by White in such diverse fern genera as bracken, *Pteridium*; cloak fern, *Notholaena*; cliff-fern, *Woodsia*; and water-clover, *Marsilea*. Bierhorst (1958) reported the discovery of vessels in Equisetaceae. He also reviewed the comparative structure of tracheary elements in vascular plants in general (1960). Charles Hébant (1969) reports numerous observations on the phloem of tropical ferns. The doctoral dissertation of Charles H. Lamoureux of the University of Hawaii on the comparative structure of the phloem of vascular cryptogams has been summarized and integrated with our knowledge of phloem in other plant groups by Katherine Esau (1969) in her comprehensive book entitled *The Phloem*. The unique anatomical relationships of the plant parts in the quillwort genus *Isoëtes* have finally been analyzed in a very thorough study, including sporeling to adult stages, by Dominick Paolillo (1963).

When we entered the period of this review, the so-called "Telome Theory" of Zimmerman (as summarized by him in 1959) prevailed, and the ancestral leaf type of the living ferns was conceived of as a dichotomous stem system, finely divided into multiple branches. However, comparisons of leaf structure in living ferns show two basic organization plans—pinnate and dichotomous. The dichotomous types involve at least four unrelated patterns of organization (Wagner, 1952*b*) and were probably separately derived from the pinnate type of architecture. The consensus now tends toward the view that today's dichotomously constructed fern leaves are advanced, and that the immediate ancestor of extant ferns had pinnate fronds. In his discussion of evolution of leaves of living ferns, Rolla Tryon (1964*a*) agrees that "There is convincing evidence . . . that the pinnate-determinate leaf form has evolved into all of the other principal forms, and on this basis [is] the primitive type."

As to the ultimate origin of the fern leaf in the evolution of land plants, the problem has become more complicated over the past few years. Previously, the conflicting theories were the Telome Theory and the Enation Theory. The latter finds its support largely in evidence from ontogeny—the ontogeny of the leaf primordium, the development of the midrib, and so on. The Telome Theory depends in large part on extrapolations from Devonian psilophytes, and most pteridologists are not sure how to evaluate it. An intriguing new theory enunciated by David Bierhorst has complicated the picture by arguing that the leaflets of ferns may actually have originated from modified enations like those found in *Psilotum* and *Tmesipteris*. This hypothesis is outlined in two detailed papers (Bierhorst, 1968, 1969) but is still too new for evaluation.

In view of the fundamental importance of leaf venation patterns in determination of generic relationships and in view of our need to understand the functional roles of free *vs.* anastomosing veins, we are glad to note that there has been a series of detailed ontogenetic studies in recent years. Thomas Pray's (1960, 1962) comparison of the development of open and closed venations was followed by similar studies by Noboru Hara (1962, 1964) and by W. Hagemann (1964, 1965, 1967), the last papers notable for the Nomarski interference-contrast microscopy. Among current descriptions of foliar ontogeny in ferns, those of the genera *Adiantum, Matteuccia, Nephrolepis, Onoclea,* and *Regnellidium* are outstanding.

Attention has been focussed on leaves of unusual form. Barbara Joe Hoshizaki of the University of California (Los Angeles) studied the remarkable fronds of the epiphytic genus *Platycerium*. These ferns, popular in horticulture, are known as "staghorns" because of their flat basal fronds which collect humus and their antler-like, repeatedly divided, projecting leaves. Hoshizaki (1972) found trends involving changes from foliaceous to broad, scale-like basal fronds and from unmodified to strongly differentiated sporophylls.

Taxa of interspecific hybrid origin commonly display strikingly irregular foliar structure. Leaf parts so far shown to have asymmetrical development in interspecific crosses include venation patterns, form of foliar propagules, soriation patterns, dimorphic leaf parts, abscission joints, and blade and leaflet outlines (Wagner, 1962; Meyer, 1965*a*). The fern genera in which the phenomenon of foliar irregularity of hybrids has been discovered include *Asplenium, Cheilanthes, Colysis, Cystopteris, Dryopteris, Grammitis, Osmunda, Pityrogramma, Pleuroderris, Polypodium, Polystichum, Pteris,* and *Woodsia* in a total of six families or subfamilies. Some of the "irregular" hybrids are fertile and widespread amphidiploids.

Among characters of the leaf epidermis, the stomates have attracted intensive interest. Van Cotthem's (1970) major comparative research on stomates in fern leaves involved some 250 genera. He showed that stomatal type has strong diagnostic value in the systematics of ferns and that it can be used as a signpost of affinities. Five distinctive new stomatal types were encountered by him. Within a single genus, Mickel and Votava (1971) uncovered unexpected diversity of stomatal form in water-clover, *Marsilea*, some of which has taxonomic value.

The sorus and sporangia still have fundamental importance in assessing the relationships and recognizing families and genera of ferns. However, an increasing number of instances are turning up in which the sorus by itself can be misleading. A fine example is the Hawaiian fern genus *Diellia*, which has sori remarkably like those of *Lindsaea*. Comprehensive investigations demonstrate that *Diellia* is actually a very close relative of the spleenworts, *Asplenium*. *Diellia* evolved from the parent genus *Asplenium* by outward migration of the dorsal sori to the marginal or submarginal position, changing its orientation in the process (Wagner, 1952*a*, 1953). Similarly, Copeland (1947) on the basis of a number of characters came to the conclusion that the remarkably *Pteris*-like sorus of the Central American genus *Dictyoxiphium* arose from the dorsal, round, and indusiate sorus of the halberd fern, *Tectaria*. In these examples use of the sorus alone had been very misleading in placing the genera taxonomically. We may conclude from situations such as these that the sorus is capable of drastic alteration, including profound changes in overall form and position. The sorus may move from the margin to the dorsal surface in evolution, or the reverse. F. O. Bower's classical idea of the "Phyletic Slide" of the sorus has been shown in recent years to be subject to so many exceptions that it is not at all certain whether the marginal or the dorsal condition is primitive, or, indeed, whether both conditions may not have existed in even the most primitive ferns (*cf.* Wagner, 1964*b*).

Since publication of Arthur J. Eames' (1936) text on morphology of lower vascular plants, and the more recent one by Adriance Foster and Ernest Gifford (1959) covering the same subject, our interpretations of leptosporangial ontogeny have changed. Traditionally, it was believed that the sporangium of the higher ferns originated by segmentation of a single apical cell (*e.g.* Foster & Gifford, 1959: 271). However, Kenneth Wilson (1958*a, b*) revealed that the typical leptosporangia he examined come about through a process of cellular intercalation. In genera with 1-rowed and 2-rowed stalks, namely *Xiphopteris* (Grammitidaceae), and *Pyrrosia* and *Phlebodium* (Polypodiaceae), Wilson could find no apical cell. On the basis of his findings, he proposes that the "tapetal initials be interpreted as inner wall cells of the capsule, while the term 'archesporium' be limited to designate the cell which produces the sporocytes," and he cites Bower's conclusion of the 1920's (commonly overlooked by morphologists) that there is little fundamental difference between eu- and leptosporangia, there being a general sequence of forms from one extreme to the other.

Perhaps as many as one-third of all living fern species display sterile trichomes or paraphyses mixed with the sporangia, but the classification of these structures—indeed even their definition—has been the subject of controversy (A. Tryon, 1965, and R. Tryon, 1965, *vs.* Wagner, 1964*a*, 1965). Nelly Pirard (1947) wrote a detailed account of these organs, and numerous authors of systematic revisions and monographs have shown growing awareness of their usefulness in taxonomy. On the basis of topographical origin, fern paraphyses may be categorized as (a) receptacular, (b) sporangium-borne, and (c) indusial, but the variations of these trichomes are very considerable, involving features of shape and construction as well as presence or absence of secretions. In spite of our recent accumulation of more descriptive knowledge of these trichomes, the functions of paraphyses are still in doubt.

It might be well to mention at this point that one of the most disappointing aspects of the past 25 years of pteridology is the near absence of studies correlating structure and function. We still do not know the significance of soriation, of the various sporangial types, or of the different leaf forms and stem forms in ecological terms. Our knowledge of the biology of the sporophyte is still at the level of descriptive morphology, with little or no comprehension of how organs perform their activities in the life of the plant. We hope that the next quarter-century will see expansion of research in structure-function relationships.

Cytogenetics

Of all approaches to the study of pteridophytes in the past quarter-century, this has been unquestionably the most active area of research in terms of number of workers and publications. Under "cytogenetics" I include chromosomes, hybridization, breeding systems, and apomixis. The study of pteridophyte cytogenetics was delayed until recent years because the numerous chromosomes had baffled cytologists technically. The numbers were so high that many workers felt that accurate interpretations were impossible. Not until Irene Manton's landmark book *Problems of Cytology and Evolution in the Pteridophyta* (1950) did this type of investigation begin in earnest. Manton established very high standards for accuracy in her work. Using mainly the squash technique (in some cases supplemented by sections), she set up the rigorous requirement that only photographable chromosomes could be used as evidence.

Workers in many countries, including Canada (*e.g.* Donald M. Britton), England (John Lovis, Trevor Walker, Stanley Walker), Finland (Veikko Sorsa), Germany (Dieter E. Meyer), Hungary (G. Vida), India (P. N. Mehra and his students and co-workers, including S. S. Bir, D. S. Loyal, and A. S. Verma), Japan (M. Nishida, S. Kurita), New Zealand (G. Brownlie), and the United States (A. Murray Evans, J. T. Mickel, A. and D. Löve, Irving W. Knobloch, F. A. Lang, and W. H. and F. S. Wagner), have built a corpus of karyological knowledge of pteridophytes in only a score of years that has, in many cases, drastically revised our thinking and understanding of systematic relationships of species, genera, and even families.

Among the numerous conclusions that have emerged are the following: Homosporous pteridophytes, with rare exceptions, tend to have high basic chromosome numbers, these ranging from ca. 20 to 50. Heterosporous pteridophytes, on the contrary, show base numbers which are much lower and more like those of seed plants. Polyploidy is very common, reaching its highest level in the adder's-tongues, *Ophioglossum* spp., some of which are reported to have $2n$ numbers greater than 1,200. Aneuploid series tend to be correlated with the generic and subgeneric level—for example, the fragile-ferns, *Cystopteris*, have $x = 42$; wood-ferns, *Dryopteris*, and hollyferns, *Polystichum*, have $x = 41$; and halberd ferns, *Tectaria*, and oak-ferns, *Gymnocarpium*, have $x = 40$. The numbers 29, 30, 36, and 37 seem to be especially common and widespread among ferns. Hybridization is rampant in many genera and families, usually producing sterile crosses, but sometimes resulting in fertile amphidiploids. Apomixis is also widespread among the ferns, and apogamous life cycles are now known in such diverse genera as *Pteris, Thelypteris, Dryopteris, Pellaea,* and *Asplenium.* Chiarugi (1960) and Fabbri (1963, 1965) have brought together the literature reports of chromosome numbers of pteridophytes. Indexed by families and genera, and arranged in tabular form, these compilations are extremely useful.

Obviously all of this new cytogenetic information has had a profound impact on taxonomy. Indeed, some workers have gone so far as to apply the so-called "Biological Species Concept" to otherwise similar populations, if the populations happened to differ in chromosome number. A good example is the widespread hart's-tongue fern, *Phyllitis scolopendrium*, known to have in different parts of its range diploid and tetraploid varieties. More recently, however, most workers have come to regard such cytological variants as varieties or forms.

Biosystematic studies of North American ferns have emphasized three genera in particular: spleenworts, *Asplenium* (Wagner, 1954; Smith & Levin, 1963); woodferns, *Dryopteris* (S. Walker, 1960, 1961, 1969; R. Tryon & Britton, 1966; Wagner & Hagenah, 1962; Wagner, 1971); and cliffbrakes, *Pellaea* (A. Tryon & Britton, 1958; A. Tryon, 1968). In *Asplenium* and *Dryopteris*, hybridization and chromosome doubling produced many distinctive taxa. Reticulation has been the dominant source of changes. In *Pellaea* transformations from sexual to apomictic life cycles have been prominent, having occurred in some cases within the same taxon (see below).

Of the numerous cytotaxonomic surveys that have been carried out in the New World during the past score of years, that by Trevor G. Walker (1966) of Newcastle-upon-Tyne on the pteridophytes of Jamaica has been a model. Approximately 270 cytotypes were investigated by him, including first observations of several genera as well as analyses of a number of species complexes and interspecific hybrids. Trevor Walker's work remains the most extensive survey of any area of the American tropics and clearly indicates that similar studies are needed elsewhere.

Much exciting cytogenetic work has dealt with a type of apomixis in ferns known as apogamy. Apogamous ferns show alternation of generations, but both generations have the same chromosome number, and the sporophytes spring directly from the vegetative tissues of the gametophyte. Manton (1950) confirmed what had earlier been reported by W. Döpp, namely that at meiosis the chromosomes of apogamous ferns pair irregularly, resulting in abortion of spores and sterility. Cytogenetically, apogamous ferns behave therefore like hybrids. Nevertheless, by a more or less regularized doubling of chromosomes in the spore mother cells, a high percentage of normal meiosis is made possible, and normal spores are produced, these larger than sexual spores. This is made possible by doubling in the archesporial tissue; the formula of A^1B^2 is doubled to $A^1A^1B^2B^2$, and the spore mother cells become amphidiploid. Only those spore mother cells with the doubled condition can produce reproductive spores. These germinate, when they fall on an appropriate substratum, into normal-looking prothallia, but only antheridia are produced as a rule. The sporophyte arises directly from the gametophyte tissue behind the apical notch. It first appears as a more or less vascularized bud which then enlarges and forms leaves, rhizome, and roots. The type of apogamous reproduction described here has been found in surprisingly many ferns during the past couple of decades. In some floras, in fact, as many as 5–10% of all ferns reproduce in this manner. Meiotic apogamy is especially frequent in rock-inhabiting adiantoid ferns (*e.g. Cheilanthes, Pellaea*) and their woodland relatives (*e.g. Adiantum, Pteris*). In rock ferns, apogamy may be a xerophytic adaptation.

Among the variations of apomixis recently discovered, the life cycle of *Polypodium dispersum* discovered by A. Murray Evans (1964) is very remarkable, for there is no change whatsoever in chromosome number at any point. This common Florida polypody has a completely somatic alternation of generations. During sporogenesis the triploid sporophyte ($x = 37$) exhibits 111 unpaired chromosomes, 16 spore mother cells, and 32 viable diplospores. The gametophyte lacks sex organs entirely and simply transforms into a sporophyte. Although we might regard such a fern as this as an evolutionary dead end and limited in adaptability, Evans (1969) has pointed out that it is dispersed over an enormous geographical range (Greater Antilles, and on the mainland from Florida and Mexico to as far south as Bolivia and Brazil). Thus, in spite of its seemingly highly limited genetic potentialities, *P. dispersum* has managed to become very successfully adapted to its environment.

In spite of loss of syngamy in their own life cycles, the apogamous ferns apparently can cross with other species. The hybrid derivatives involve apogamous parent times sexual parent and are apogamous themselves. Trevor Walker (1962) found examples of this phenomenon in the brakes, *Pteris*. In the United States, the limestone spleenwort of the Southeast known as *Asplenium* × *heteroresiliens* (Wagner, 1966; Morzenti, 1966) is the intermediate of the sexual tetraploid *A. heterochroum* and the apogamous triploid *A. resiliens*. In Canada, Mulligan, Cinque-Mars, and Cody (1972) report a hybrid between two very common ferns—the sexual broad beech fern, *Phegopteris hexagonoptera*, and the apogamous narrow beech fern, *P. polypodioides*. There is much evidence, therefore, that the sperms of apogamous ferns can fertilize the archegonia of sexual ferns.

Morzenti (1967) discovered that most "sterile" hybrid ferns can produce at least a few good spores from which gametophytes will grow. Indeed, in one case she postulates that a gametophyte of a "sterile" hybrid may have backcrossed with a sexually normal species to produce a distinctive taxon. According to her, the morphological and cytological facts strongly suggest that the Florida fern known as *Asplenium plenum* arose as a cross (AAB_1B_2) between a sexual $2x$ species, *A. abscissum* (AA), and a "sterile" $3x$ hybrid, *A. curtissii* (AB_1B_2). She has found that the "sterile" hybrid gametophytes usually have viable sperms. "Sterile" hybrid gametophytes also have the ability to produce apogamous sporophytes.

At first, in the study of apogamy, we assumed that the ferns showing it were interspecific hybrids. Evidence for this came from two facts: (a) that meiosis in nondoubled spore mother cells showed strong cytogenetic irregularities and (b) that many of the apogamous ferns, including such familiar North American ferns as stiff spleenwort, *Asplenium resiliens*; narrow beech fern, *Phegopteris polypodioides*; and purple cliffbrake, *Pellaea atropurpurea*, are triploid or have other odd numbers of genomes. Now we realize, however, that apogamous ferns are not necessarily interspecific hybrids. It was discovered that the familiar eastern American smooth cliffbrake, *Pellaea glabella* var. *glabella*, may exist in two different forms—one a sexual diploid, the other an apogamous tetraploid (Wagner, Farrar & Chen, 1965). On limestone cliffs near Van Buren, Missouri, both cytological forms occur. Alice Tryon (1968) has now reported comparable conditions in several other species of cliffbrakes (these involving diploids and triploids), thus suggesting that the presence of apogamous and sexual forms within species and even varieties of this genus may not be unusual.

Many indications have been revealed over the past two decades that in ferns multivalent formation during meiosis is exceptional. Although we are not sure of the situation during the earlier stages of prophase, by the time of metaphase I there is a marked tendency for chromosome pairs to form, even when presumably homologous chromosomes are present in triplicate or quadruplicate. In one unusual experiment described by Verma and Loyal (1960) the chromosome complement of Venus-hair fern, *Adiantum capillus-veneris*, was doubled by the application of colchicine to form an autotetraploid. Remarkably, at meiotic metaphase the spore mother cells formed a majority of normal-appearing pairs. Tetravalents were few, and normal spores ensued. Verma's expriment strongly suggests that we should entertain two entirely different explanations for the *n* pairs—*n* singles pairing behavior we so commonly observe in triploid ferns. In one case, the tetraploid parent may be an autotetraploid taxon, AAAA, the other a normal diploid, BB, and the hybrid AAB; the homologous chromosomes now pair with one another but the nonhomologous chromosomes remain unpaired. In the other case, the tetraploid parent may be an allotetraploid, AABB, the other a normal diploid BB, and the hybrid ABB, the homologous chromosomes also pairing with one another but now coming both from the tetraploid and the diploid taxa, rather than from the tetraploid alone. The work of G. Vida of Magyar Tudományos Akademia, Budapest, Hungary, has been especially pertinent: in his studies of European ferns (Vida, 1970, 1972), he found pairing patterns that would not have been predicted by conventional ideas of chromosome homology. Genetic controls of pairing *per se*, such as those now well known in various grain crops, probably occur also in the ferns.

One of the most striking features of the diploid hybrids in pteridophytes is the absence or near-absence of pairs. Nevertheless, a striking exception has been found. Trevor Walker (1958) discovered in Ceylon that two very distinct species of brakes, *Pteris quadriaurita* and *P. multiaurita*, cross with each other where the natural habitat has been disturbed by man. The hybrids that are formed are nearly 100% fertile diploids. The meiotic process of the hybrids is normal, typical pairs are formed, and the spores are viable. What is more, the hybrids interbreed among themselves to form hybrid swarms with various combinations of the parental characteristics. Trevor Walker's discovery remains the only case of this nature in the literature of pteridology.

Systematics and Taxonomy

Our period began with the publication in 1947 of the influential *Genera Filicum* by Edwin Bingham Copeland of the University of California (Berkeley).

In his career, spanning two-thirds of a century, Copeland was one of the most productive pteridologists the United States has ever produced (biography and bibliography are given in Wagner, 1964*a*, *b*). Josef Poelt (1956, 1959, 1961) of the Institut für systematischen Botanik und Pflanzengeographie, Berlin, and Dieter E. Meyer (1963, 1964, 1965*b*, 1966, 1968, 1970) of the Botanischer Garten und Museum, Berlin, have provided us with an extremely valuable series of summaries of the systematics of pteridophytes in the journal *Fortschritte der Botanik.* Admirably succinct, these digests cover the period since 1947 and deal with various subjects, including cytology, hybridization, and morphology, as they bear upon systematics. They also treat floristics and ferns in cultivation.

In recent years the publication of nomenclatural indices has had inestimable value in assisting taxonomists with their library and herbarium procedures. Rodolfo E. G. Pichi-Sermolli of the Istituto Botanico "Hanbury," The University, Genova, working with a committee of the International Association for Plant Taxonomy, published a new, very much needed, supplement to Carl Christensen's indices covering pteridology up through 1933. The new volume, entitled *Index filicum. Supplementum Quartum pro annis 1934–1960* (Pichi-Sermolli, 1965) differs from the earlier ones of Christensen in that new names only are cited, thus avoiding taxonomic interpretations. One used to hear the complaint that of pteridophytes only the ferns had been provided with nomenclatural indices, but now this situation has been alleviated. Herter (1949) compiled an index to *Lycopodium*, and Clyde F. Reed has published several other important nomenclators for nonfilicinean pteridophytes: *Isoëtes* (1953), *Selaginella* (1965–66), Psilotales (1966), and Equisetaceae (1971, 1972). Of the studies of types of New World pteridophytes in European herbaria, those of the late Conrad V. Morton of the United States National Museum (*e.g.* Morton, 1967*b*, *c*, 1969, 1970) have been very useful and resulted in distribution of type photographs to a number of American herbaria.

In addition to much routine taxonomy, over three dozen major revisions and/or monographs have been published in the past 25 years. In general, recent monographic research has been notable for its more thorough, analytical approach; there has been an attempt to deal with more than mere key-making, nomenclature, and identification—the staples of traditional alpha taxonomy. Today's monographer of pteridophytes displays more and more the broadly gauged biological approach, using data from many fields of botany and biology. All of the recent monographic work cannot be reviewed here.[3]

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[3] However, some of the prominent examples dealing with U.S. and New World pteridophytes may be listed as follows: LYCOPODIACEAE: *Lycopodium* sect. *Complanata* (Wilce, 1965). SELAGINELLACEAE: *Selaginella rupestris* complex (R. Tryon, 1955); *Selaginella*, Heterophyllae (Alston, 1955); spores, North American *Selaginella* (A. Tryon, 1949); spores, Mexico and Central America (Hellwig, 1969). ISOËTACEAE: *Isoëtes*, Southeastern U.S. (Reed, 1965). EQUISETACEAE: *Equisetum* subg. *Hippochaete* (Hauke, 1963). OSMUNDACEAE: *Osmunda*, especially fossil species (C. N. Miller, 1967). PLAGIOGYRIACEAE: *Plagiogyria* sect. *Carinatae* (Lellinger, 1971). POLYPODIACEAE (including grammitid ferns): Polypodiaceae and Grammitidaceae of Argentina (de la Sota, 1960); *Ctenopteris* (Copeland, 1956); *Grammitis* (Copeland, 1952*a*); *Grammitis*, Ecuador (Morton, 1967*b*); *Platycerium* (Hoshizaki, 1972); *Polypodium*, Chile (Looser, 1951); *Polypodium pectina-*

After the death of William R. Maxon, Conrad V. Morton took full charge of the Division of Ferns, Department of Botany, U.S. National Museum. Morton fostered New World pteridology probably more than any other single individual through his encouragement of students and ready aid to all researchers. His own studies were heavily oriented toward the herbarium and literature. He was interested not only in professional research and teaching, but he gave time and energy to amateurs as well. Among his contributions are papers on cultivated ferns (*e.g.* Morton, 1957*a*, *b*, *c*, *d*, 1958, 1960*a*, 1963*a*, 1965) which are especially timely in the midst of the currently burgeoning enthusiasm for using ferns in horticulture (as illustrated by the Los Angeles International Fern Society, a recently formed group with presently over 1,000 members, and by the spectacular sales of the book *Ferns to Know and Grow* by Gordon Foster, 1971) Morton's demise in the summer of 1972 marked the end of a most productive pteridological career.

Pteridophyte floristicians have been highly active since 1947, but no attempt will be made here to enumerate all of the publications for the New World. Suffice it to say, Morton's (1960*b*) enumeration of fern books for different regions of the United States takes us up to 1960. It includes all of the major references except for three that have appeared since, namely Edgar T. Wherry's two *Guides*—one for northeastern United States and Canada (1961), the other for the Southeast (1964)—and T. M. C. Taylor's *Pacific Northwest Ferns and their Allies* (1970), which is as useful in northwestern United States as it is in western Canada. The bulk of recent floristic research is as yet unpublished, because the field studies are currently still under way, as, for example, those on Mexico by John T. Mickel of the New York Botanical Garden. The work on Peru by Rolla Tryon (1964*c*) has yielded several publications, of which the major one, treating the dennstaedtioid to oleandroid ferns, is more than 250 pages long. This work is notable for the fact that the author examined the holotypes or isotypes of approximately 80% of all the taxa included. Jamaican pteridophytes are presently being investigated by George R. Proctor, who published a preliminary checklist of the known taxa in 1953. Knobloch and Correll's book

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tum-plumula complex (Evans, 1969); *Polypodium vulgare* complex, northwestern North America (Lang, 1971); *Solanopteris* (Wagner, 1972); *Xiphopteris* Copeland, 1952*b*). SCHIZAEACEAE: Schizaeaceae, Guayana (Lellinger, 1969*a*); *Anemia* subg. *Coptophyllum* (Mickel, 1962). ADIANTACEAE (including vittarioid ferns): *Gymnopteris* (Lellinger, 1969*b*); *Doryopteris* (R. Tryon, 1942); *Eriosorus* (A. Tryon, 1970); *Jamesonia* (A. Tryon, 1962); *Mildella* (Hall & Lellinger, 1967); *Notholaena* (R. Tryon, 1956); *Pityrogramma* (R. Tryon, 1962); *Pellaea* (A. Tryon, 1957); *Pterozonium* (Lellinger, 1967); Vittariaceae (R. Tryon, 1964*b*). CYATHEACEAE (including hymenophylloid ferns): *Dennstaedtia* (R. Tryon, 1960); *Lindsaea* (Kramer, 1957); Hymenophyllaceae, classification (Morton, 1968); *Hymenophyllum* sect. *Sphaerocionium* (Morton, 1947); *Pteridium* (R. Tryon, 1941); *Sphaeropteris* (R. Tryon, 1971); "Tree ferns" (Holttum & Sen, 1961; R. Tryon, 1970*b*). ASPLENIACEAE (including "aspidioid" ferns): *Asplenium* (Morton & Lellinger, 1966); *Cystopteris* (Blasdell, 1963); *Diellia*, Hawaii (Wagner, 1952*a*); *Doodia*, Hawaii (Blasdell, 1956); *Dryopteris*, eastern U.S. cytotaxonomy (S. Walker, 1955, 1960, 1961, 1969; Tryon & Britton, 1966; Wagner, 1971); *Elaphoglossum*, Hawaii (Anderson & Crosby, 1966); Brazil (Alston, 1958), French West Indies (Morton, 1948); *Lastreopsis* (Tindale, 1965); Onocleoid ferns (Lloyd, 1971); *Tectaria*, Mexico (Morton, 1966*b*); *Thelypteris*, broad classification (Morton, 1963*b*), sect. *Cyclosorus* (A. Smith, 1971); *Woodsia* (Brown, 1964). SALVINIACEAE: *Salvinia* (Sota, 1962, 1964).

(1962) *Ferns and Fern Allies of Chihuahua, Mexico* is an attractive example of modern pteridophyte floristics.

Chemical systematics lags far behind cytogenetics of pteridophytes, but such beginnings as there are promise much for the future. One of the most famous papers on pteridophytes of the past score of years is that by Dale M. Smith and Donald A. Levin on the chromatography of Appalachian aspleniums. Working at the time at the University of Illinois, Urbana, Smith and Levin (1963) made an elegant demonstration of additive effects of different combinations of parental flavinoid compounds in interspecific hybrids. Scattered among the other investigations of pteridophyte chemistry, those of Carl-Johan Widén of the University of Helsinki, and his co-workers (Widén, 1969; Widén, Sorsa & Sarvela, 1970; Widén, Vida, von Euw & Reichstein, 1971) have been particularly numerous. Dealing with the phloroglucinol compounds of the woodferns, *Dryopteris*, they are serving to supplement information from geography, morphology, and cytology on the intricate relationships of these plants. Ecdysones in ferns are now known in both sporophyte and gametophyte generations (Kaplanis, *et al.*, 1967; McMorris & Voeller, 1971). The stage is now set to see whether such substances have allelopathic roles, for example in the oft-observed lack of insect grazers on ferns and other pteridophytes. The "Jimmy fern," *Notholaena cochisensis*, so-called because it produces a nervous affliction of sheep known as "jimmies," is well known for being fatally poisonous. However, close relatives, such as *N. sinuata*, with which it grows, are apparently innocuous. In spite of Weatherby's and others' treatments of the toxic *N. cochisensis* as only a "variety" of the nontoxic and sympatric *N. sinuata*, Richard Hevly (1965) reports that these ferns differ from one another in over 15 characters of anatomy, morphology, and physiology.

In general, species concepts have been refined in the 1950's and 1960's so that they coincide with modern thinking of population biologists. Normally, populations differing in numerous characters and coexisting in the same habitats, are now treated as distinct species, as is the custom in zoology. With only a few exceptions, most pteridologists have arrived at a general agreement on practical species definition, as illustrated by their taxonomic interpretations. The disagreement is provided by several authors who, for various reasons, have emphasized the use of the category "variety," and thus have led to the major discrepancy in treatment in New World ferns. One argument is that if two taxa are commonly found confused in herbarium collections, they should be placed in one species. Or, if two taxa require special effort to tell apart (*e.g.* need the use of a hand lens), they should be merged. Part of the argument also stems from the notion that floras and revisions are written mainly for botanically inclined amateurs who wish to recognize species quickly and easily. Thus we find the limestone oak fern, *Gymnocarpium robertianum*, being given varietal status under common oak fern, *G. dryopteris*. Fancy fern, *Dryopteris intermedia*, is made a variety of the spinulose woodfern, *D. spinulosa*. Mountain cliff fern, *Woodsia scopulina*, is reduced to a variety under Oregon woodsia, *W. oregana*. One of the curious by-products of this effort has been to treat interspecific hybrids as varieties of one or the other parent, the choice of which is usually arbitrary, *i.e.* whether the writer thinks it "looks more like one than the other." For example, Trudell's hybrid spleenwort, *Asplenium* × *trudellii* (= *A. montanum* × *pinnatifidum*) is made a variety of *A. pinnatifidum.* Leaders in this manner of using the varietal category over the past 25 years have been Bernard Boivin of the Department of Agriculture, Ottawa; Rolla and Alice Tryon of the Gray Herbarium, Harvard; and Clyde F. Reed of Howard University and Reed Herbarium, Baltimore. The progenitor of the "Variety Movement" was evidently Charles A. Weatherby of Harvard, who did much to counteract what he regarded as a "preoccupation with the species level" in ferns.

Seemingly the best illustration of potentially "good" varieties in ferns (*i.e.* in the sense of zoological subspecies) in North America would be those of the goldback fern, *Pityrogramma triangularis*, in western United States, as described by Karen Alt and Verne Grant (1960). Nevertheless, recent investigations by Dale M. Smith and his co-workers (1971) at University of California, Santa Barbara, indicate that even in goldback ferns, there is a possibility that the use of the category variety should be questioned.

Among the numerous species and hybrids described during the past 25 years, a few might be called "outstanding." Every kind of plant teaches us something, but some teach us more than others. We are all familiar with pteridophyte genera with dozens or hundreds of species—all of them more or less alike, merely low-level variations on a theme, differing in minor ways. Outstanding new taxa are ones which (a) strongly extend the known dimensions of a particular evolutionary line in terms of scope of biological diversity, or (b) which tie together previously discrete lines, either by (1) "missing links" in the patristic sense, or by (2) hybrids. Explorations, both in the wild and in the herbarium, have uncovered a number of such taxa, highly significant in terms of our understanding of evolution and systematics.

The taxonomically vexing quillworts, *Isoëtes*, have recently been exposed to what we hope may be the start of a long line of careful, analytical field investigations. Matthews and Murdy (1969) encountered morphologically intermediate populations (which they did not name) between the traditional species, *I. melanospora* and *I. piedmontana.* The intermediates were growing in sites ecologically intermediate between the habitats of the two "species." The Matthews and Murdy work casts considerable doubt on quillwort classifications based exclusively on observations of herbarium specimens and suggests that experiments (*e.g.* transplants and uniform garden) may be necessary to resolve our problems. Several workers have investigated the remarkable plant *Stylites* (E. Amstutz, 1957; Rauh & Falk, 1959*a*, *b*; Meyer, 1958) from the Andes which widely extends the morphological scope of known Isoëtaceae in characters of leaves, stems, and roots. Whether or not *Stylites* should be regarded as a distinct quillwort genus, there is no question that it broadens our concepts of quillworts.

In the whiskfern family, Psilotaceae, Rouffa (1971) discussed a bizarre *Psilotum* cultivar 'Green Giraffe's Antlers' which lacks any appendages on the stems. Suggesting in a number of ways the Devonian rhynioids, the plant was brought from Japan to America by John L. Creech of the Plant Exploration Division of the New Crops Research Branch, U.S. Department of Agriculture.

Having terminal sporangia on its long stems and lacking either leaves or roots, 'Giraffe's antlers' will become a popular teaching object in biology and botany courses. We are indebted to the staff of Longwood Gardens, Kennett Square, Pennsylvania, for having grown this plant for introduction into the United States.

In the adder's-tongue family, Ophioglossaceae, Tagawa (1939) described *Ophioglossum kawamurae*, in which the leaves are evidently fertile spikes only; sterile blades are nonexistent. The petiole-like organs upon which the spikes are borne possess parallel veins with occasional areoles. Together with *O. simplex* Ridley from Sumatra and *O. lineare* Schlechter and Brause from "New Mecklenburg" (= New Ireland), *O. kawamurae*, known only as a rarity in Japan, makes the third member of the genus in which the normal sterile segment is absent. In Schizaeaceae, Mickel (1967) reports an instructive species of *Anemia*, which has the most primitive foliar condition known in this genus, the basal fertile pinnae being but little modified in size, lamination, and posture, contrary to the usual concept of blade structure in this genus. *Anemia colimensis* Mickel, known only from the state of Colima, Mexico, also displays a number of other primitive characters as well, making it an unusually important plant from an evolutionary standpoint. Until recently, the extraordinary polypodioid fern, *Solanopteris brunei* (Wercklé) Wagner, of Central America was practically unknown. Possessing highly modified ant-filled tubers, it is the only known immediate relative of S. *bifrons*, and in certain ways connects that species with more typical simple-bladed polypods (Wagner, 1972).

Among the adiantoid ferns, Pichi-Sermolli (1946) reported a plant superficially resembling *Aleuritopteris farinosa* but differing from that well-known fern in a peculiar combination of characters: gradate sorus consisting of only one or two spore cases, these very large and almost sessile; and stomium absent. These and other characters seem so distinctive that the author set up a new family based on it, the Nigripteridaceae. *Nigripteris scioana* remains unique, because its annulus consists of cells all of the walls of which, including the outer ones, are equally and strongly indurated. This mode of dehiscence is unknown elsewhere. Researchers have recognized several unusual hybrids, these "intergeneric" according to past classifications. Alice Tryon (1970) described *Eriosorus* × *Jamesonia* crosses, the presence of which tends to confirm the hypothesis that the two "genera" are actually very close in affinities. Rolla Tryon enumerated a series of hybrids of *Trismeria* and *Pityrogramma*, all of which supported his conclusion that *Trismeria* should be subsumed under *Pityrogramma* (R. Tryon, 1962). Partly on the basis of the hybrid fern originally described as *Cheilanthes carlotta-halliae*, which morphologically connects the entities traditionally known as *Pellaea densa* and *Aspidotis californica*, Lellinger (1968) placed all three in the genus *Aspidotis*. More and more in the past few years, the presence of "intergeneric" hybrids such as these is being used as a decisive factor in combining genera. Using this criterion, we may be forced to combine *Tectaria* and *Dictyoxiphium*, *Pleopeltis* and *Polypodium*, and practically all the genera of asplenioid ferns, including *Camptosorus*, *Ceterach*, *Phyllitis*, and *Asplenium*.

Among aspidioid ferns, the paddle-fern genus, *Elaphoglossum*, comprises several hundred species in the tropics and has been considered to be unusually uniform because of its simple, unlobed blade form. Now two remarkable species have turned up, their leaves deviating drastically from the standard pattern. One of them, *Elaphoglossum cardenasii*, from the Andes, has pedately lobed blades, the lobes narrow and dagger-like (Wagner, 1954). Gómez (1971) reports another new species, *Peltapteris peruviana*, which is a morphological link between *Elaphoglossum* and typical *Peltapteris* in that the blades are more or less deeply lobed. Another such "missing link" was described from Hawaii—*Asplenium leucostegioides*, a fern which ties together the endemic Hawaiian genus *Diellia* with typical spleenworts, *Asplenium* (Wagner, 1953). The last two species, the *Peltapteris* and the *Asplenium*, are prime examples of *patristic* (as opposed to *hybrid*) intermediates, the finding of which confirms previously postulated hypotheses of intergeneric relationships. Indeed, their presence makes us wonder whether we should not reduce the entire genus *Peltapteris* to *Elaphoglossum* and the genus *Diellia* to *Asplenium*.

The broad phylogenetic relationships of pteridophytes have received intense interest and, on occasion, hot controversy. Of the two major symposia in recent years, that in 1963 on the "Origin and Evolution of Ferns" was presented at the American Institute of Biological Sciences meeting at Oregon State University (Corvallis). Theodore Delevoryas (1964) assembled the contributions in the *Memoirs of the Torrey Botanical Club*. An international meeting on "The Phylogeny and Classification of the Filicopsida" was held by the Linnean Society of London in collaboration with the British Pteridological Society, London, 1972. The most obvious trend in recent classifications has been toward splitting families into smaller and smaller units. Such activity has done little or nothing to enhance our understanding of relationships. Emphasizing finer and finer differences as these are discovered, such fragmentation tends to satisfy those whose interests are more inclined toward identification and key-making than toward patterns of relationship. As to the latter, we are observing increasing acceptance of Bower's idea that the classical "catch-all," Polypodiaceae, constitutes a mixture of different evolutionary lines, and this is reflected in many of the newer classifications.

Much progress has been made toward a more objective and scientifically useful conception of fern phylogeny and classification, and a great deal of it has grown out of our deeper understandings of the many aspects of pteridology which have made advances over the past 25 years.

BIBLIOGRAPHY

ALSTON, A. H. G. 1955. The heterophyllous *Selaginellae* of continental North America. Bull. Brit. Mus. Nat. Hist. Bot. 1: 222–274, pl. 5–6.

———. 1956. The subdivision of the Polypodiaceae. Taxon 5: 23–25.

———. 1958. The Brazilian species of *Elaphoglossum*. Bol. Soc. Brot. 32: 1–32.

ALT, K. S. & V. GRANT. 1960. Cytotaxonomic observations on the Goldback fern. Brittonia 12: 153–170.

AMSTUTZ, E. 1957. *Stylites*, a new genus of Isoëtaceae. Ann. Missouri Bot. Gard. 44: 121–123.

ANDERSON, W. R. & M. R. CROSBY. 1966. A revision of the Hawaiian species of *Elaphoglossum*. Brittonia 18: 380–397.

ATKINSON, L. R. 1965. The gametophyte of *Cystodium*. Amer. Fern. Jour. 55: 32–35.

——— & A. G. STOKEY. 1964. Comparative morphology of the gametophyte of homosporous ferns. Phytomorphology 14: 51–70.

BECK, C. B. 1970. The appearance of gymnospermous structure. Biol. Rev. 45: 379–400.

Bierhorst, D. W. 1958. Vessels in *Equisetum.* Amer. Jour. Bot. 46: 534–537.

———. 1960. Observations on tracheary elements. Phytomorphology 10: 249–305.

———. 1968. On the Stromatopteridaceae (fam. nov.) and on the Psilotaceae. Phytomorphology 18: 232–268.

———. 1969. On *Stromatopteris* and its ill-defined organs. Amer. Jour. Bot. 56: 160–174.

———. 1971. Morphology of Vascular Plants. Macmillan Co., New York and London. vi + 560 pp.

Blasdell, R. F. 1956. A comparative study of Hawaiian species of *Doodia.* Bull. Torrey Bot. Club 83: 62–71.

———. 1963. A monographic study of the fern genus *Cystopteris.* Mem. Torrey Bot. Club 21: 1–102.

Britton, D. M. 1968. The spores of four species of spinulose woodferns (*Dryopteris*) in eastern North America. Rhodora 70: 340–347.

———. 1972. Spore ornamentation in the *Dryopteris spinulosa* complex. Canad. Jour. Bot. 50: 1617–1621.

Brown, D. F. M. 1964. A monographic study of the fern genus *Woodsia.* Beih. Nova Hedwigia 16: i–x, 1–154, pl. 1–40.

Chiarugi, A. 1960. Tavole cromosomiche delle Pteridophyta. Caryologia 13: 27–150.

Ching, R. C. 1940. On natural classification of the family "Polypodiaceae." Sunyatsenia 5: 201–268.

Christensen, C. 1906. Index Filicum. Copenhagen.

———. 1913. Index Filicum, supplementum pro annis 1906–1912. Copenhagen.

———. 1934. Index Filicum, supplementum tertium pro annis 1917–1933. Copenhagen.

———. 1938. Filicineae. Pp. 512–550, *in* F. Verdoorn (editor), "Manual of Pteridology." Chronica Botanica, Waltham, Massachusetts.

Copeland, E. B. 1947. Genera Filicum. Chronica Botanica, Waltham, Massachusetts. xvi + 247 pp., X pl.

———. 1952*a*. *Grammitis.* Philippine Jour. Sci. 80: 93–271, pl. 1–6.

———. 1952*b*. The American species of *Xiphopteris.* Amer. Fern. Jour. 42: 93–110.

———. 1956. *Ctenopteris* in America. Philippine Jour. Sci. 84: 381–473.

Cotthem, W. Van. 1970. Comparative morphological study of the stomata in the Filicopsida. Bull. Jard. Bot. Natl. Belg. 40: 81–239.

Delevoryas, T. (editor). 1964. Origin and Evolution of Ferns. A Symposium. Mem. Torrey Bot. Club 21: 1–95.

DeMaggio, A. E. 1971. Ferns as a model system for studying polyploidy and gene dosage effects. BioScience 21: 313–316.

Duckett, J. G. 1970. Sexual behavior of the genus *Equisetum,* subgenus *Equisetum.* Bot. Jour. Linn. Soc. 63: 327–352.

———. 1972. Sexual behavior of the genus *Equisetum,* subgenus *Hippochaete.* Bot. Jour. Linn. Soc. 65: 87–108.

Eames, A. J. 1936. Morphology of Vascular Plants. Lower groups (Psilophytales to Filicales). McGraw-Hill Co., New York and London. xviii + 433 pp.

Esau, K. 1969. The Phloem. Pp. 1–105, *in* "Encyclopedia of Plant Anatomy. Histology." Vol. 5 (Part 2). Gebrüder Borntraeger, Berlin, Stuttgart.

Evans, A. M. 1964. Ameiotic alternation of generations: A new life cycle in the ferns. Science 143: 261–263.

———. 1969. Interspecific relationships in the *Polypodium pectinatum-plumula* complex. Ann. Missouri Bot. Gard. 55: 193–293.

Fabbri, F. 1963. Primo supplemento alle *Tavole Cromosomiche delle Pteridophyta* di Alberto Chiarugi. Caryologia 16: 237–335.

———. 1965. Secondo supplemento alle *Tavole Cromosomiche delle Pteridophyta* di Alberto Chiarugi. Caryologia 18: 675–731.

Farrar, D. R. 1967. Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the southern Appalachians. Science 155: 1266–1267.

——— & W. H. Wagner, Jr. 1968. The gametophyte of *Trichomanes holopterum* Kunze. Bot. Gaz. (Crawfordsville) 129: 210–219.

Foster, A. S. & E. M. Gifford, Jr. 1959. Comparative Morphology of Vascular Plants. W. H. Freeman and Co., San Francisco. xii + 555 pp.

Foster, F. G. 1971. Ferns to Know and Grow. Hawthorn Books, Inc., New York. xiv + 258 pp.

Freeberg, J. A. & R. H. Wetmore. 1957. Gametophytes of *Lycopodium* as grown *in vitro.* Phytomorphology 7: 204–217.

Gómez, L. D. 1971. Una nueva especie del género *Peltapteris* Link de los Andes peruanos. Revista Biol. Trop. 18: 217–219.

Hagemann, W. 1964. Vergleichende Untersuchungen zur Entwicklungsgeschichte des Farnsprosses. I. Morphogenese und Histogenese am Sprossscheitel leptosporangiater Farnes. Beitr. Biol. Pflanzen. 40: 27–64.

———. 1965. II. Die Blattentwicklung in der Gattung *Adiantum* L. Beitr. Biol. Pflanzen. 41: 405–468.

———. 1967. Bemerkungen zur Entwicklung und Differenzierung des Farnblattes und das Fiederwachstum von *Regnellidium diphyllum* Lind. Zeitschr. Pflanzenphysiol. 57: 26–45.

Hall, C. C. & D. B. Lellinger. 1967. A revision of the fern genus *Mildella.* Amer. Fern Jour. 57: 113–134.

Hara, N. 1962. Histogenesis of the venation in the pinnule of *Matteuccia struthiopteris* Todaro. Sci. Pap. Coll. Gen. Educ. Univ. Tokyo, 12: 57–63.

———. 1964. Ontogeny of the reticulate venation in the pinna of *Onoclea sensibilis.* Bot. Mag. (Tokyo) 77: 381–387.

Hauke, R. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete.* Beih. Nova Hedwigia 8: 1–123, pl. 1–22.

———. 1966. A systematic study of *Equisetum arvense.* Nova Hedwigia 13: 81–109, pl. 1–9.

———. 1967. Sexuality in a wild population of *Equisetum arvense* gametophytes. Amer. Fern Jour. 57: 59–66.

———. 1969. Gametophyte development in Latin American horsetails. Bull. Torrey Bot. Club 96: 568–577.

———. 1971. The effect of light quality and intensity on sexual expression in *Equisetum* gametophytes. Amer. Jour. Bot. 58: 373–377.

Hébant, C. 1969. Observations sur le phloème de quelques Filicinées tropicales. Naturalia Monspel. Sér. Bot. 20: 135–196, pl. 48–58.

Hellwig, R. L. 1969. Spores of the heterophyllous *Selaginellae* of Mexico and Central America. Ann. Missouri Bot. Gard. 56: 444–464.

Herter, G. 1949. Index Lycopodiorum. Herbarium Herter, Montevideo, Uruguay. iv + 120 pp.

Hevly, R. H. 1965. Studies of the sinuous cloak-fern (*Notholaena sinuata*) complex. Jour. Arizona Acad. Sci. 3: 205–208.

Holttum, R. E. 1946. A revised classification of leptosporangiate ferns. Jour. Linn. Soc. Bot. 53: 123–186.

———. 1949. The classification of ferns. Biol. Rev. 24: 267–296.

———. 1956. On the nature and possible relationships of the fern genus *Platyzoma* R. Br. Kew Bull. 3: 251–253.

——— & U. Senn. 1961. Morphology and classification of the tree ferns. Phytomorphology 11: 406–420.

Hoshizaki, B. J. 1972. Morphology and phylogeny of *Platycerium* species. Biotropica 42: 93–117.

Kaplanis, J. N., M. J. Thompson, W. E. Robbins & B. M. Bryce. 1967. Insect hormones: Alpha ecdysone and 20-hydroxyecdysone in bracken fern. Science 157: 1436–1438.

Klekowski, E. J., Jr. 1971. Ferns and genetics. BioScience 21: 317–322.

———. 1972. Evidence against genetic self-incompatibility in the homosporous fern *Pteridium aquilinum.* Evolution 26: 66–73.

——— & H. G. Baker. 1966. Evolutionary significance of polyploidy in the Pteridophyta. Science 153: 305–307.

Knobloch, I. W. & D. S. Correll. 1962. Ferns and Fern Allies of Chihuahua, Mexico. Texas Research Foundation, Renner, Texas. xiii + 198 pp.

Kramer, K. U. 1957. A revision of the genus *Lindsaea* in the New World with notes on allied genera. Acta Bot. Neerl. 6: 97–290.

Kruckeberg, A. R. 1964. Ferns associated with ultramafic rocks in the Pacific Northwest. Amer. Fern Jour. 54: 113–126.

Lang, F. A. 1971. The *Polypodium vulgare* complex in the Pacific Northwest. Madroño 21: 235–254.

Lellinger, D. B. 1966. *Nephopteris*, a new genus of ferns from Colombia. Amer. Fern Jour. 56: 180–182.

———. 1967. *Pterozonium* (Filicales: Polypodiaceae). Pp. 2–23, *in* B. Maguire, "The Botany of the Guayana Highland—Part VII." Mem. New York Bot. Gard., 17(1).

———. 1968. A note on *Aspidotis.* Amer. Fern Jour. 58: 140.

———. 1969*a.* The botany of the Guayana Highland—Part VIII. Schizaeaceae. Mem. New York Bot. Gard. 18: 2–11.

———. 1969*b.* The taxonomic position of *Coniogramme americana.* Amer. Fern Jour. 59: 61–65.

———. 1971. The American species of *Plagiogyria* sect. *Carinatae.* Amer. Fern Jour. 61: 110–118.

LOOSER, G. 1951. El género *Polypodium* y sus representantes chilenos. Revista Univ. Catolica Chile 36: 13–82.

LLOYD, R. M. 1971. Systematics of the onocleoid ferns. Univ. California Publ. Bot. 61: 1–93.

——— & E. J. KLEKOWSKI, JR. 1970. Spore germination and viability in Pteridophyta: Evolutionary significance of chlorophyllous spores. Biotropica 2: 120–137.

MANTON, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge Univ. Press. xi + 316 pp.

———. 1955. Pteridology. Pp. 301–321, *in* "A Century of Progress in the Natural Sciences." California Acad. Sci., San Francisco.

MATTHEWS, J. F. & W. H. MURDY. 1969. A study of *Isoëtes* common to the granite outcrops of the southeastern piedmont, United States. Bot. Gaz. (Crawfordsville) 130: 53–61.

MCMORRIS, T. C. & B. VOELLER. 1971. Ecdysones from gametophytic tissues of a fern. Phytochemistry 10: 3253–3254.

MEYER, D. E. 1958. Über ein interessantes Brachsenkraut aus Peru. Willdenowia 2: 32–40.

———. 1963. Systematik der Farnpflanzen. Bericht über das Jahr 1962. Fortschr. Bot. 25: 71–80.

———. 1964. Systematik der Farnpflanzen. Bericht über das Jahr 1963. Fortschr. Bot. 26: 84–93.

———. 1965*a.* Zum morphogenetischen Prinzip der Irregularität von Artbastarden und Bastarden, von Blickpunkt der Systematik. Willdenowia 4: 63–73.

———. 1965*b.* Systematik der Farnpflanzen. Bericht über das Jahr 1964. Willdenowia 27: 341–347.

———. 1966. Systematik der Farnpflanzen. Willdenowia 28: 251–257.

———. 1968. Systematik der Farnpflanzen. Willdenowia 30: 302–313.

———. 1970. Systematik der Farnpflanzen. Willdenowia 32: 280–289.

MICKEL, J. T. 1962. A monographic study of the fern genus *Anemia,* subgenus *Coptophyllum.* Iowa State Jour. Sci. 36: 349–482.

———. 1967. The phylogenetic position of *Anemia colimensis.* Amer. Jour. Bot. 54: 432–437.

——— & F. V. VOTAVA. 1971. Leaf epidermal studies in *Marsilea.* Amer. Fern Jour. 61: 101–109.

MILLER, C. N., JR. 1967. Evolution of the fern genus *Osmunda.* Contrib. Mus. Paleontol. Univ. Michigan 21: 139–203.

MILLER, J. H. 1968. Fern gametophytes as experimental material. Bot. Rev. 34: 361–440.

MORTON, C. V. 1947. The American species of *Hymenophyllum* sect. *Sphaerocionium.* Contr. U.S. Natl. Herb. 29: 139–201.

———. 1948. Notes on *Elaphoglossum*—II. The species of the French West Indies. Amer. Fern Jour. 38: 202–214.

———. 1957*a.* Observations on cultivated ferns. I. Amer. Fern Jour. 47: 7–14.

———. 1957*b.* Observations on cultivated ferns, II. The proper generic name of the Holly Fern. Amer. Fern Jour. 47: 52–55.

———. 1957*c.* Observations on cultivated ferns, III. The species of *Microlepia.* Amer. Fern Jour. 47: 102–108.

———. 1957*d.* Observations on cultivated ferns, IV. The species of *Davallia.* Amer. Fern Jour. 47: 143–148.

———. 1958. Observations on cultivated ferns, V. The species and forms of *Nephrolepis.* Amer. Fern Jour. 48: 18–27.

———. 1960*a.* Observations on cultivated ferns, VI. The ferns currently known as *Rumohra.* Amer. Fern Jour. 50: 145–155.

———. 1960*b*. Some fern books for different regions of the United States. Amer. Fern Jour. 50: 169–178.

———. 1963*a*. Observations on cultivated ferns, VII. The mother ferns. Amer. Fern Jour. 53: 81–94.

———. 1963*b*. The classification of *Thelypteris*. Amer. Fern Jour. 53: 149–154.

———. 1965. Observations on cultivated ferns, VIII. *Stenochlaena*. Amer. Fern Jour. 55: 164–166.

———. 1966*a*. The Polypodiaceae subfamily Asplenioideae in Venezuela. Mem. New York Bot. Gard. 15: 1–49.

———. 1966*b*. The Mexican species of *Tectaria*. Amer. Fern Jour. 56: 120–137.

———. 1967*a*. Studies of fern types, I. Contr. U.S. Natl. Herb. 38: 29–83.

———. 1967*b*. The genus *Grammitis* in Ecuador. Contr. U.S. Natl. Herb. 38: 85–123.

———. 1967*c*. The fern herbarium of André Michaux. Amer. Fern Jour. 57: 166–182.

———. 1968. The genera, subgenera, and sections of the Hymenophyllaceae. Contr. U.S. Natl. Herb. 38: 153–214.

———. 1969. The fern collections in some European herbaria, III. Amer. Fern Jour. 59: 48–55.

———. 1970. The fern collections in some European herbaria, VI. Amer. Fern Jour. 60: 49–61.

——— & DAVID B. LELLINGER. 1966. The Polypodiaceae subfamily Asplenioideae in Venezuela. Mem. New York Bot. Gard. 15: 1–49.

MORZENTI, V. M. 1966. Morphological and cytological data on southeastern United States species of the *Asplenium heterochroum-resiliens* complex. Amer. Fern Jour. 56: 167–177.

———. 1967. *Asplenium plenum*: a fern which suggests an unusual method of species formation. Amer. Jour. Bot. 54: 1061–1068.

MULLIGAN, G. A., L. CINQUE-MARS & W. J. CODY. 1972. Natural interspecific hybridization between sexual and apogamous species of the beech fern genus *Phegopteris* Fée. Canad. Jour. Bot. 50: 1295–1300.

NÄF, U. 1958. On the physiology of antheridium formation in the bracken fern *Pteridium aquilinum* (L.) Kuhn. Physiol. Pl. 11: 728–746.

———. 1962. Developmental physiology of lower archegoniates. Annual Rev. Pl. Physiol. 13: 507–532.

———. 1967. On the induction of a phase inhibitory to antheridium formation in the juvenile prothallus of the fern species *Anemia phyllitidis*. Zeitschr. Bot. 56: 353–365.

NAYAR, B. K. 1970. A phylogenetic classification of the homosporous ferns. Taxon 19: 229–236.

——— & S. KAUR. 1971. Gametophytes of homosporous ferns. Bot. Rev. 37: 295–396.

PAOLILLO, D. J., JR. 1963. The Developmental Anatomy of *Isoëtes*. Illinois Biol. Monogr. 31. Univ. Illinois Press, Urbana. 130 pp.

PICHI-SERMOLLI, R. E. G. 1946. Nigripteridaceae e *Nigripteris*, nuova famiglia e nuovo genere delle Filicales. Nuovo Giorn. Bot. Ital., n.s. 53: 129–169.

———. 1958. The higher taxa of the Pteridophyta and their classification. Pp. 70–90, *in* O. Hedberg (editor), "Systematics of Today." Almquist and Wiksells, Uppsala.

———. 1965. Index filicum. Suppl. quartum pro annis 1934–1960. Regnum Veg. 37: i–xiv, 1–370.

PIRARD, N. 1947. Sporanges, paraphyses et organes connexes chez les Fougères. Cellule 51: 155–184, pls. 2–3.

POELT, J. 1956. Systematik der Pteridophyten. Fortschr. Bot. 18: 83–93.

———. 1959. Systematik der Farnpflanzen. Bericht über die Jahre 1957 und 1958. Fortschr. Bot. 21: 86–97.

———. 1961. Systematik der Farnpflanzen. Bericht über die Jahre 1959 und 1960. Fortschr. Bot. 23: 57–74.

PRAY, T. R. 1960. Ontogeny of the open dichotomous venation in the pinna of the fern *Nephrolepis*. Amer. Jour. Bot. 47: 319–328.

———. 1962. Ontogeny of the closed dichotomous venation of *Regnellidium*. Amer. Jour. Bot. 49: 464–472.

PROCTOR, G. R. 1953. A preliminary checklist of Jamaican pteridophytes. Bull. Inst. Jamaica. Sci. Ser. 5. 89 pp., 3 pl.

RAUH, W. & H. FALK. 1959*a*. *Stylites* E. Amstutz, eine neue Isoëtacee aus den Hochandern Perus. 1. Teil: Morphologie, Anatomie, und Entwicklungsgeschichte der Vegetationsorgane. Sitzungsber. Heidelberg, Akad. Wiss. 1959: 1–83.

——— & ———. 1959*b*. *Stylites* E. Amstutz, eine neue Isoëtacee aus den Hochandern Perus. 2. Teil: Zur Anatomie des Stammes mit besonderer Berücksichtigung der Verdikungsprozesse. Sitzungsber. Heidelberg. Akad. Wiss. 1959: 87–160.

Reed, C. F. 1953. Index Isoëtales. Bol. Soc. Brot. 27: 1–72.

———. 1965. *Isoëtes* in southeastern United States. Phytologia 12: 369–400.

———. 1965–66. Index Selaginellarum. Mem. Soc. Brot. 18: 1–287.

———. 1966. Index Psilotales. Bol. Soc. Brot. 40: 71–96.

———. 1971. Index to Equisetophyta. Part 2: Recentes. Reed Herbarium, Baltimore, Maryland. 128 pp.

———. 1972. Index to Equisetophyta. Part 1: Fossiles. Reed Herbarium, Baltimore, Maryland. 402 pp.

Rouffa, A. S. 1971. An appendageless *Psilotum*. Introduction to aerial shoot morphology. Amer. Fern Jour. 61: 75–86.

Smith, A. R. 1971. Systematics of the neotropical species of *Thelypteris* section *Cyclosorus*. Univ. California Publ. Bot. 59: i–vi, 1–143.

Smith, D. M., S. P. Craig & J. Santarosa. 1971. Cytological and chemical variation in *Pityrogramma triangularis*. Amer. Jour. Bot. 58: 292–299.

——— & D. A. Levin. 1963. A chromatographic study of reticulate evolution in the Appalachian *Asplenium* complex. Amer. Jour. Bot. 50: 952–958.

Sota, E. R. de la. 1960. Polypodiaceae y Grammitidaceae argentinas. Opera Lilloana 5: 1–229.

———. 1962. Contribución al conocimiento de las Salviniaceae neotropicales. Darwiniana 12: 465–520.

———. 1964. Contribución al conocimiento de las Salviniaceae neotropicales. V. *Salvinia sprucei* Kuhn. Darwiniana 13: 529–536.

Tagawa, M. 1939. *Ophioglossum kawamurae* Tagawa, a new species from Japan. Acta Phytotax. Geobot. 8: 134–136.

Taylor, T. M. C. 1967. *Mecodium wrightii* in British Columbia and Alaska. Amer. Fern Jour. 57: 1–6.

———. 1970. Pacific Northwest Ferns and their Allies. Univ. Toronto Press, Toronto. ix + 247 pp.

Tindale, M. D. 1965. A monograph of the genus *Lastreopsis* Ching. Contr. New South Wales Natl. Herb. 3: 249–339, pl. ix–xiii.

Tryon, A. F. 1949. Spores of the genus *Selaginella* in North America, north of Mexico. Ann. Missouri Bot. Gard. 36: 413–431.

———. 1957. A revision of the fern genus *Pellaea* section *Pellaea*. Ann. Missouri Bot. Gard. 44: 125–193.

———. 1962. A monograph of the fern genus *Jamesonia*. Contr. Gray Herb. 191: 109–197.

———. 1964. *Platyzoma*—A Queensland fern with incipient heterospory. Amer. Jour. Bot. 51: 939–942.

———. 1965. Trichomes and paraphyses in ferns. Taxon 14: 214–217.

———. 1968. Comparisons of sexual and apogamous races in the fern genus *Pellaea*. Rhodora 70: 1–24.

———. 1970. A monograph of the fern genus *Eriosorus*. Contr. Gray Herb. 200: 54–174.

——— & D. M. Britton. 1958. Cytotaxonomic studies on the fern genus *Pellaea*. Evolution 12: 137–145.

Tryon, R. M., Jr. 1941. Revision of the genus *Pteridium*. Rhodora 43: 1–70.

———. 1942. A revision of the genus *Doryopteris*. Contr. Gray Herb. 143: 3–80.

———. 1955. *Selaginella rupestris* and its allies. Ann. Missouri Bot. Gard. 42: 1–99.

———. 1956. A revision of the American species of *Notholaena*. Contr. Gray Herb. 179: 1–106.

———. 1960. A review of the genus *Dennstaedtia* in America. Contr. Gray Herb. 187: 23–52.

———. 1962. Taxonomic fern notes. II. *Pityrogramma* (including *Trismeria*) and *Anogramma*. Contr. Gray Herb. 189: 52–76.

———. 1964*a*. Evolution in the leaf of living ferns. Mem. Torrey Bot. Club 21(5): 73–85.

———. 1964*b*. Taxonomic fern notes. IV. Some American vittarioid ferns. Rhodora 66: 110–117.

———. 1964*c*. The ferns of Peru. Polypodiaceae (Dennstaedtieae to Oleandreae). Contr. Gray Herb. 194: 1–253.

———. 1965. Paraphyses in the ferns. Taxon 14: 213–214.

———. 1969. Pteridology. *In* J. Ewan (editor), "A Short History of Botany in the United States." Hafner Publ. Co., New York and London.

———. 1970*a*. Development and evolution of fern floras of oceanic islands. Biotropica 2: 76–84.

———. 1970*b*. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 3–53.

———. 1971. The American tree ferns allied to *Sphaeropteris horrida*. Rhodora 73: 1–19.

——— & D. M. Britton. 1966. A study of variation in the cytotypes of *Dryopteris spinulosa*. Rhodora 68: 59–92.

Verma, S. C. & D. S. Loyal. 1960. Colchi-autotetraploidy in *Adiantum capillus-veneris*. Nature 188: 1210–1211.

Vida, G. 1970. The nature of polyploidy in *Asplenium ruta-muraria* L. and *A. lepidum* Presl. Caryologia 23: 525–547.

———. 1972. Cytotaxonomy and genome analysis of European ferns. Symp. Biol. Hung. 12: 51–60.

Voeller, B. 1971. Developmental physiology of fern gametophytes: Relevance for Biology. BioScience 21: 266–270.

Wagner, W. H., Jr. 1952*a*. The fern genus *Diellia*. Its structure, affinities, and taxonomy. Univ. California Publ. Bot. 26: 1–212, pl. 1–21.

———. 1952*b*. Types of foliar dichotomy in living ferns. Amer. Jour. Bot. 39: 578–592.

———. 1953. An *Asplenium* prototype of the genus *Diellia*. Bull. Torrey Bot. Club 80: 76–94.

———. 1954. A Bolivian *Elaphoglossum* of unique leaf structure. Bull. Torrey Bot. Club 81: 61–67.

———. 1962. Irregular morphological development in hybrid ferns. Phytomorphology 12: 87–100.

———. 1964*a*. Paraphyses: Filicineae. Taxon 13: 56–64.

———. 1964*b*. The evolutionary patterns of living ferns. Bull. Torrey Bot. Club 21: 86–95.

———. 1964*c*. Edwin Bingham Copeland (1873–1964) and his contributions to pteridology. Amer. Fern Jour. 54: 177–188.

———. 1964*d*. Edwin Bingham Copeland, 1873–1964. Taxon 14: 33–41.

———. 1965. Fern paraphyses: Comments on recent papers. Taxon 14: 299–302.

———. 1966. Two new species of ferns from the United States. Amer. Fern Jour. 56: 3–7.

———. 1971. Evolution of *Dryopteris* in relation to the Appalachians. *In* P. C. Holt (editor), "The Distributional History of the Biota of the Southern Appalachians. Part II: Flora." Virginia Polytech. Inst. Res. Div. Monogr. 2: 147–192.

———. 1972. *Solanopteris brunei*, a little-known fern epiphyte with dimorphic stems. Amer. Fern Jour. 62: 33–43.

——— & R. A. Evers. 1963. Sterile prothallial clones (*Trichomanes*?) locally abundant on Illinois sandstones. Amer. Jour. Bot. 50: 623.

——— & Dale J. Hagenah. 1962. *Dryopteris* in the Huron Mountain Club area of Michigan. Brittonia 14: 90–100.

——— & A. J. Sharp. 1963. A remarkably reduced vascular plant in the United States. Science 142: 1483–1484.

——— & F. S. Wagner. 1965. Rochester area Log ferns (*Dryopteris celsa*) and their hybrids. Proc. Rochester Acad. Sci. 11: 57–71.

———, D. R. Farrar & K. L. Chen. 1965. A new sexual form of *Pellaea glabella* var. *glabella* from Missouri. Amer. Fern Jour. 55: 171–178.

Walker, S. 1955. Cytogenetic studies in the *Dryopteris spinulosa* complex. I. Watsonia 3: 193–209.

———. 1960. Evolution within the genus *Dryopteris*. Proc. Linn. Soc. London 171: 130–132.

———. 1961. Cytogenetic studies in the *Dryopteris spinulosa* complex. II. Amer. Jour. Bot. 48: 104–112.

———. 1969. Identification of a diploid ancestral genome in the *Dryopteris spinulosa* complex. Brit. Fern Gaz. 10: 97–99.

Walker, T. G. 1958. Hybridization in some species of *Pteris* L. Evolution 12: 82–92.

———. 1962. Cytology and evolution in the fern genus *Pteris* L. Evolution 16: 27–43.

———. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh 66: 179–237, pl. 1–5.

WHERRY, E. T. 1961. The Fern Guide. Northeastern and Midland United States and Canada. Doubleday and Co., Garden City, New Jersey. 318 pp.

———. 1964. The Southern Fern Guide. Southeastern and South-Midland United States. Doubleday and Co., Garden City, New Jersey. 349 pp.

WHITE, R. A. 1963*a*. Tracheary elements of the ferns. I. Factors which influence tracheid length; correlation of length with evolutionary divergence. Amer. Jour. Bot. 50: 447–455.

———. 1963*b*. Tracheary elements of the ferns. II. Morphology of tracheary elements; conclusions. Amer. Jour. Bot. 50: 514–522.

———. 1971. Experimental studies of the sporophytes of ferns. BioScience 21: 271–275.

WHITTIER, D. P. 1971. The value of ferns in an understanding of the alternation of generations. BioScience 21: 225–227.

———. 1972. Gametophytes of *Botrychium dissectum* in axenic culture. Amer. Jour. Bot. 59: 677. [Abstract.]

WIDÉN, C.-J. 1969. Chemotaxonomic investigations on Finnish *Dryopteris* species and related North American taxa. Acad. Sci. Fenn., Ser. A. IV. Biol. 143: 1–19.

———, V. SORSA & J. SARVELA. 1970. *Dryopteris dilatata* s. lat. in Europe and the island of Madeira. Acta Bot. Fenn. 91: 1–30.

———, G. VIDA, J. VON EUW & T. REICHSTEIN. 1971. Die Phloroglucide von *Dryopteris villarii* (Bell.) Woynar und anderer Farne der Gattung *Dryopteris* sowie die mögliche Abstammung von *D. filix-mas* (L.) Schott. Helv. Chim. Acta 54: 2824–2850.

WILCE, J. H. 1965. Section *Complanata* of the genus *Lycopodium*. Beih. Nova Hedwigia 19: i–ix, 1–233, pl. I–XL.

WILKIE, D. 1956. Incompatibility in bracken. Heredity 10: 247–256.

WILSON, K. A. 1958*a*. Ontogeny of the sporangium of *Phlebodium* (*Polypodium*) *aureum*. Amer. Jour. Bot. 45: 483–491.

———. 1958*b*. Ontogeny of the sporangia in *Xiphopteris serrulata* and *Pyrrosia nuda*. Jour. Arnold Arbor. 39: 478–493.

ZIMMERMAN, W. 1959. Die Phylogenie der Pflanzen. Gustav Fischer, Stuttgart. xxiv + 777 pp.

25 years of botany

PLANT PHYSIOLOGY
1947–1972

CLEON ROSS[1] AND FRANK B. SALISBURY[2]

The task of surveying developments in plant physiology occurring in the last 25 years has been both challenging and interesting. Some have stated that the science of plant physiology came of age in 1950 with publication of the first *Annual Review*, edited by Daniel Arnon and Leonard Machlis. It was just 25 years ago that the decision to publish these reviews was made. We shall trace some of the significant developments occurring since, with occasional speculation as to where progress might lead in the next 25 years. Space limitations necessitate that much good work of many excellent scientists cannot be mentioned.

WATER RELATIONS

The idea that the thermodynamic status of water in plant cells (presently referred to as water potential, ψ) is controlled by two major factors, the osmotic (ψ_π) and pressure potentials (ψ_p) was firmly established 25 years ago, even though the terminology and symbols were different. To be consistent with soil physicists, soil chemists, and most plant physiologists working in the area, our textbook (Salisbury & Ross, 1969) describes the relations among these factors as

$$\psi = \psi_\pi + \psi_p$$

where ψ and ψ_π are always negative (O'Leary, 1970), but ψ_p may be positive or negative, depending on whether pressure or tension exists in the cells. This equation proves easier for most beginning students to understand than earlier ones, perhaps since the concept that water flows "downhill" toward a more negative water potential is easier to grasp.

Terminology, however, is only a convenience, not a tool, and we must ask what has been accomplished in this area. Development of the ingenious thermocouple psychrometers and the pressure bomb apparatus has allowed far more accurate measurements of osmotic, water, and pressure potentials during the last decade. The resulting more quantitative data, many of which were obtained by Paul Kramer and his students, allow us to better predict when plants will or will not absorb water from soil of a particular water status and which parts of the

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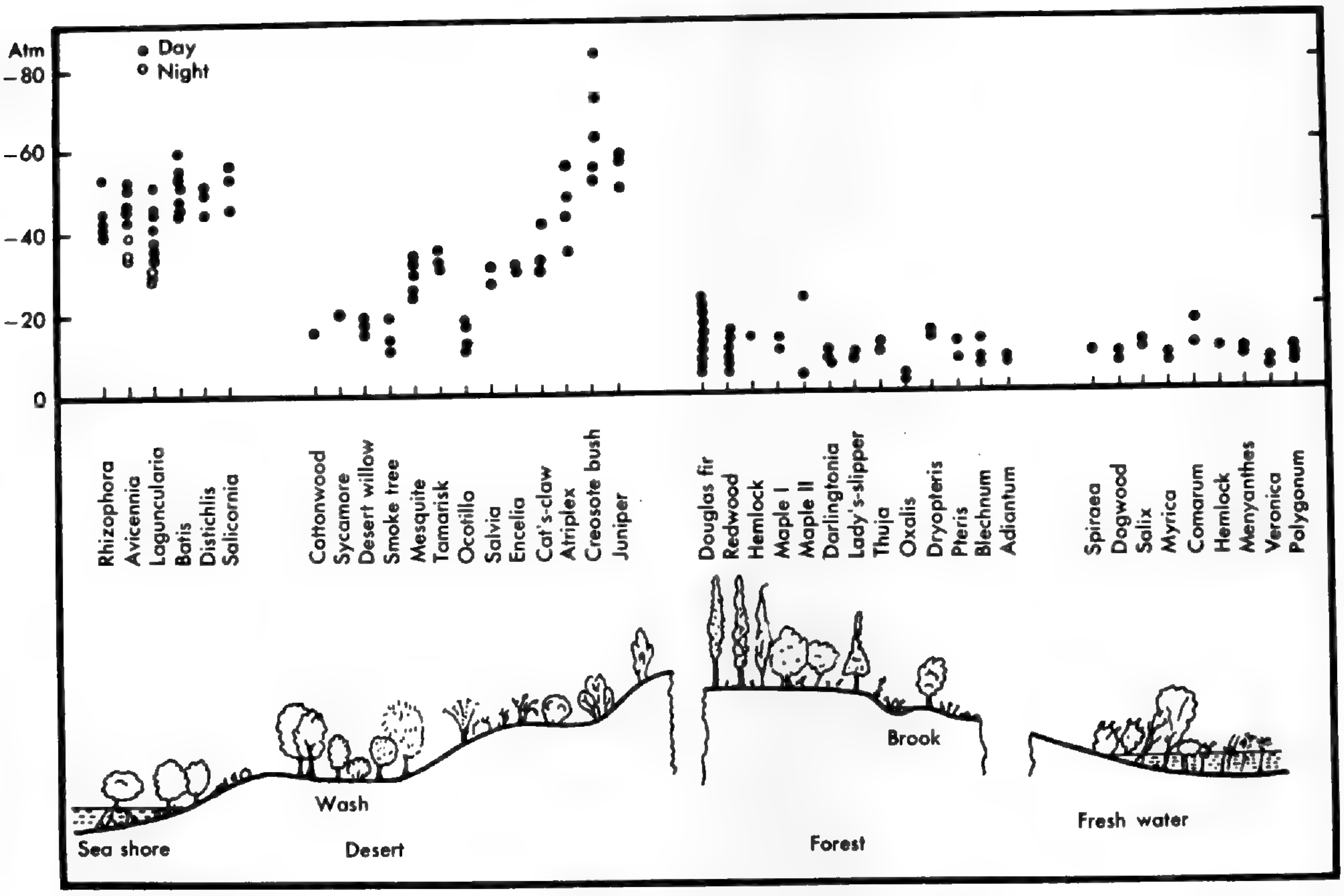

FIGURE 1. Xylem tensions in various species of different habitats. Most measurements were taken during daylight in strong sunlight. Night values are commonly several atmospheres less negative. (From P. F. Scholander, H. T. Hammel, E. D. Bradstreet & E. A. Hemmingsen. 1965. Science 148: 339–346. Copyright 1965 by the American Association for the Advancement of Science. Used by permission.)

shoot will absorb water from the others under numerous conditions. Furthermore, a few recent studies have quantified the relation of pressure potential to cellular growth (Cleland, 1971*a*). Among the greatest contributions were those of P. F. Scholander and co-workers in the early 1960's (Scholander *et al.*, 1965). Their use of the pressure bomb apparatus showed convincingly that the xylem transport stream of numerous plants contains water under tension, just as Dixon, Joly, and Askenasy had predicted in the 1890's. Scholander's data also show greater tensions in species growing in dry than in moist habitats and during daylight than at night (Fig. 1); also as predicted, the tensions increase with height in a given tree. These observations rank among the most important of those supporting the cohesion theory explanation as to how trees can lift water ten times higher than a vacuum pump.

Another significant advance in water relations physiology is the recent implication of inorganic ions, particularly potassium, in stomatal opening and closing. After many years of conjecture about the role of starch, sugars, *p*H, temperature, CO_2, and rhythms, the road to understanding this and other (Satter *et al.*, 1970) turgor movements seems much straighter. Fujino (1967) and Fischer (1968) discovered that stomatal opening is correlated with guard cell potassium contents. Dramatic differences in potassium contents of guard cells from open and closed stomates can be shown using either the electron probe microanalyzer or by a sodium cobaltinitrite stain (Fig. 2).

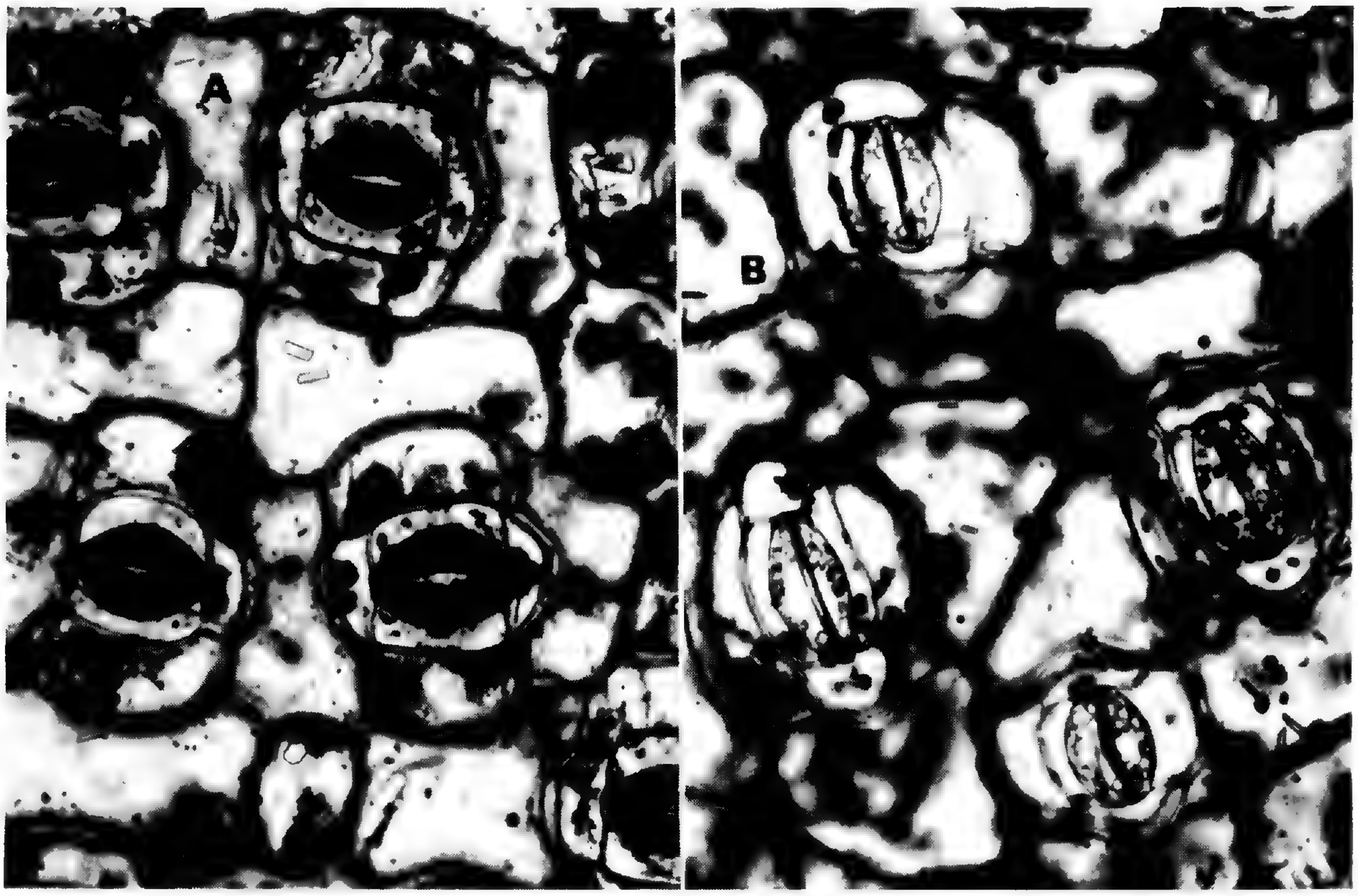

FIGURE 2. Accumulation of potassium ions in guard cells of open stomates in *Commelina communis* L. Epidermal strips were stained with sodium cobaltinitrite followed by ammonium sulfide to produce darkly stained regions where potassium ions were most concentrated. Background staining which appears out of focus is due to mesophyll attached to the underside of epidermis.—A. Epidermis from leaves kept in bright light and CO_2-starved for 3 hours (stomata were open prior to staining).—B. Epidermis from leaves with stomata closed in darkness. (From T. A. Mansfield. 1970. School Sci. Rev. 52: 316–325. Used by permission.)

Additional observations indicate the specificity of potassium in this response, quantitative relations between stomatal opening and guard cell K^+ contents, and the source of absorbed K^+, at least in maize leaves (Raschke & Fellows, 1971). Lending further support to the potassium pump theory is the fact that the fungal toxin fusicoccin, which increases stomatal opening and transpiration rates, also increases absorption of K^+ by guard cells (Turner, 1972). Alternatively, abscisic acid (ABA), a plant hormone discovered in the 1960's causes stomatal closing and loss of guard cell potassium (Mansfield & Jones, 1971). The closing effect is detectable within 5 minutes (Cummins *et al.*, 1971), indicating that as in certain other hormonal responses mentioned later, membrane properties are altered. In spite of these and other results relating K^+ changes to stomatal opening, some experts in this area remain unconvinced of the primary role attributed to them. As with so many other debatable issues in our field, more data will eventually decide it.

An important practical problem probably dependent upon understanding stomatal physiology is the control of transpiration to increase yields in areas where water is scarce. The last 20 years have included many unsuccessful or unfeasible attempts with various antitranspirants. Abscisic acid derivatives are among the latest to offer some hope in this respect (Jones & Mansfield, 1971).

SOLUTE TRANSPORT

The pioneering efforts of R. Collander, F. C. Steward, D. R. Hoagland, T. C. Broyer and others had, well before 1950, established that plant cells can accumulate several ions against a concentration gradient and that this is an oxygen-dependent process (Steward & Sutcliffe, 1959). The problem remained to explain the connection between aerobic respiration and the transport process. H. Lundegårdh (1955) proposed that salt accumulation depended upon increased respiration resulting from the presence of the salt anion. An electron transport system was thought to move anions inwardly in exchange for outwardly transported electrons; cations were presumably absorbed passively in exchange for H^+ released from respiratory substrates. Demonstrations during the 1950's that mitochondria contain the respiratory electron transport system gradually forced the conclusion that the connection between their oxidative activity and solute absorption must be mediated by some transportable energy carrier, presumably ATP. Numerous results from the use of inhibitors of oxidative phosphorylation strongly suggest that it is indeed ATP that provides this connection.

Those accepting this hypothesis have asked how the energy in ATP is harnessed to solute transport. T. K. Hodges and his colleagues have provided considerable support for the role of a Na-K specific, plasmalemma ATPase in restricting sodium absorption but facilitating potassium uptake, just as in animal cells. A correlation between rubidium uptake (indicative of K^+ absorption) and ATPase activity in corn, wheat, oats, and barley measured by them is shown in Fig. 3. Inhibitors of ATP synthesis interfere with absorption of several other inorganic ions and charged and uncharged organic molecules. There is no compelling reason to believe that ATPase-like enzymes of the membranes are necessary to transport these substances into plant cells. Nevertheless, much evidence now supports the existence of fairly specific carriers capable of transporting numerous solutes.

Emanuel Epstein appears to have been the first strong proponent of the role of carriers in ion uptake by plants, and he and his colleagues obtained much of the initial evidence for them (Epstein, 1956). They discovered that absorption of several ions is mediated by separate plasma membrane transport systems, one group (type 2) operating at relatively high ion concentrations (greater than about 1 mM) and another (type 1) of higher affinity operating also at considerably lower concentrations (Epstein, 1972). The type 1 systems (carriers ?) seem of greater significance in ion absorption by roots because of the usual low nutrient concentrations in soils. Both may be involved in intercellular transport in cases where the internal solute concentrations are much higher. We still must learn how such transport systems function and how they respond to ATP, if, as seems probable, they indeed do.

The last decade shows an amazing and deserved increase of interest in membranes, in part due to the much more widespread availability of electron microscopes and scientists trained to use them. A recent review by Cook (1971) summarizes progress in this area. We still do not know how membranes are assembled, but this seems essential to understand such things as solute transport, secretion, cell growth, action of certain hormones, fusion of protoplasts, cellular

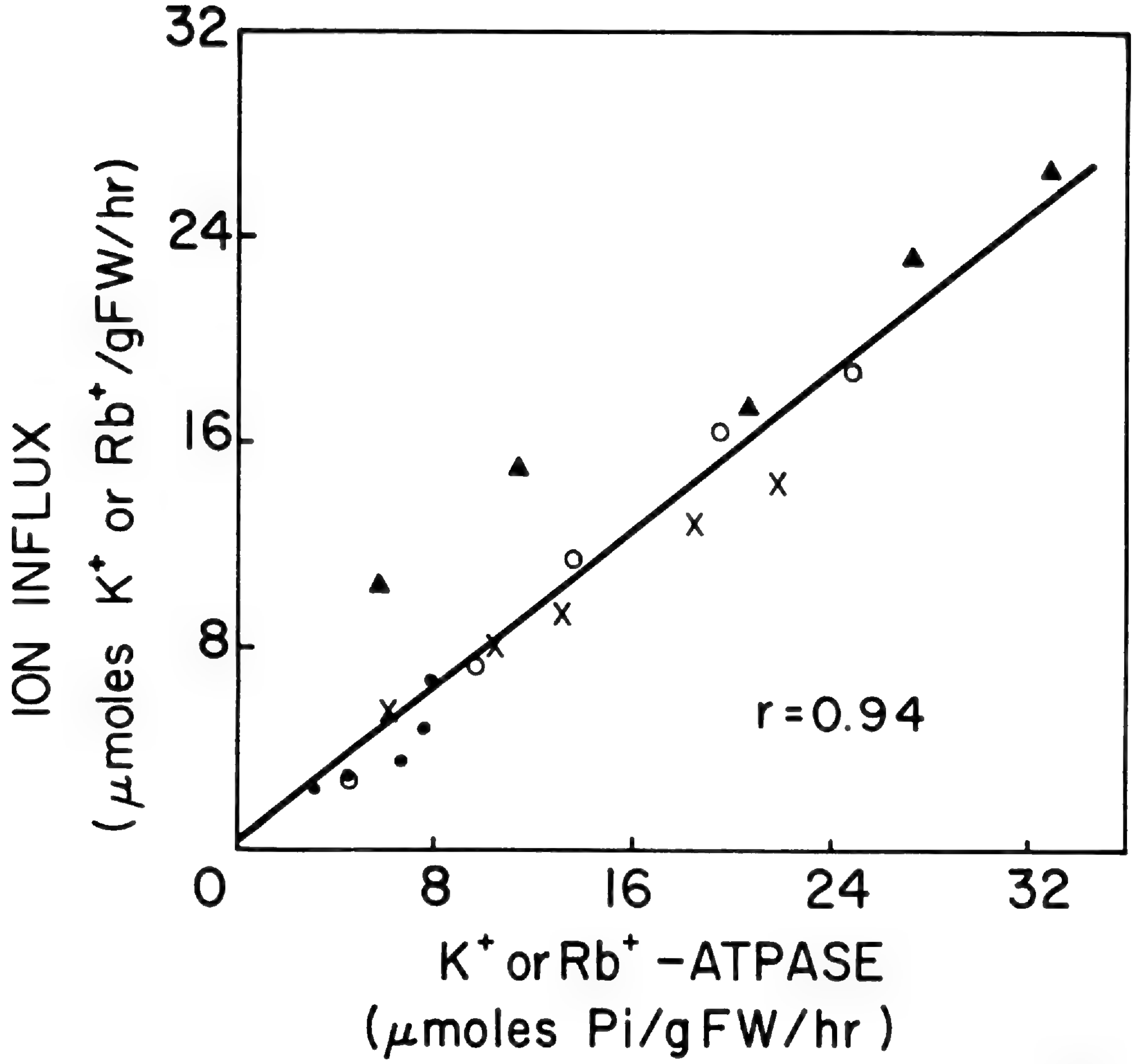

FIGURE 3. Correlation between Rb^+ or K^+ absorption and the Rb^+ or K^+-stimulated ATPase activity for corn (●), wheat (×), oats (○) and barley (▲). Data were obtained with five external Rb^+ concentrations between 0.0 and 50 mM. (From J. D. Fisher, D. Hansen & T. K. Hodges. 1970. Pl. Physiol. 46: 812–814. Used by permission.)

self-recognition, and perhaps certain problems in plant disease resistance. A limiting factor has been and will continue to be the availability of pure membranes, especially plasma membranes, but progress is also being made here (Hodges *et al.*, 1972).

CARBOHYDRATE TRANSPORT

It was recognized before the 1940's that sieve tube elements of the phloem are responsible for most of the long distance movement of sugars from one part of the plant to another, that sucrose is a common and important transportable sugar, that flow is retarded by low temperatures or metabolic inhibitors, and, from studies with dyes such as fluorescein, flow rates were estimated to be at least 0.5 cm/minute. Subsequent results have verified and extended the important role of sucrose as a transport sugar (Zimmerman, 1957) and indicate that reducing sugars such as glucose and fructose are not significant translocatable carbohydrates (Swanson & El-Shishiney, 1958). Stachyose, raffinose, verbascose, and certain sugar alcohols were found to be transported in some species.

A major controversy in the late 1940's (see Curtis & Clark, 1950) that still persists is the mechanism causing this flow. The widespread use of radioactive tracers and numerous electron micrographs of conducting cells have failed to solve the problem. The pressure-flow hypothesis advanced by E. Münch in 1930 has been favored over the years as the most reasonable mechanism, but not by all investigators. No alternative explanation has yet been supported by convincing evidence, even though there are problems with pressure-flow (Spanner, 1971). Some of the criticisms made against it have recently been explained (Cataldo *et al.*, 1972). An understanding of the mechanism of phloem transport should help explain how several environmental, nutritional, and hormonal factors affect this process.

Mineral Nutrition

With the exception of chlorine, the present list of 16 elements believed essential for most higher plants was well recognized by 1947. Even before 1930 chlorine (chloride) had been demonstrated to stimulate growth of some species, but it was the work of Broyer *et al.* (1954) that convinced us of its general essentiality. Sodium, too, was repeatedly shown to stimulate growth of certain species, and very recently (Brownell & Crossland, 1972) it was concluded to be an essential micronutrient for species having the C_4 photosynthetic pathway.

Other advances in mineral nutrition have concerned functions of the elements. Epstein's recent book (Epstein, 1972) lists more details. We consider that elucidation of the role of molybdenum in nitrate reduction and nitrogen fixation, of chloride and manganase in the Hill reaction, of copper in plastocyanin (a photosynthetic electron transport pigment), of potassium in synthesis of starch and proteins, of magnesium in numerous reactions involving ATP, of iron in cytochromes and ferredoxin, and of calcium in maintaining normal membrane functions to be especially significant. Of course, several other functions for these and other elements have been demonstrated by biochemically-trained investigators. Unfortunately, we still must learn the biochemical function of boron.

Important advances in understanding the mechanism of nitrogen fixation were made, especially during the 1960's. A research team at DuPont was the first to obtain active cell-free extracts from free-living bacteria (Carnahan *et al.*, 1960), while Harold Evans' group at Oregon State prepared the first such extract from root nodules (Koch *et al.*, 1967). Prior to 1960, due to pioneering work of R. H. Burris and others, it was known that molybdenum was required for fixation, that H_2, CO, NO, and N_2O were inhibitors, that a hydrogenase was present in several N-fixers that could release H_2 when N_2 was limiting, and that NH_4^+ was the principal fixation product. Subsequent fractionation work showed the active nitrogenase system to consist of two essential proteins, one containing iron and molybdenum and the other iron. We should soon learn how these proteins interact, the established but poorly understood role of ATP in the fixation process, and the source of electrons used to reduce N_2 (Bergersen, 1971).

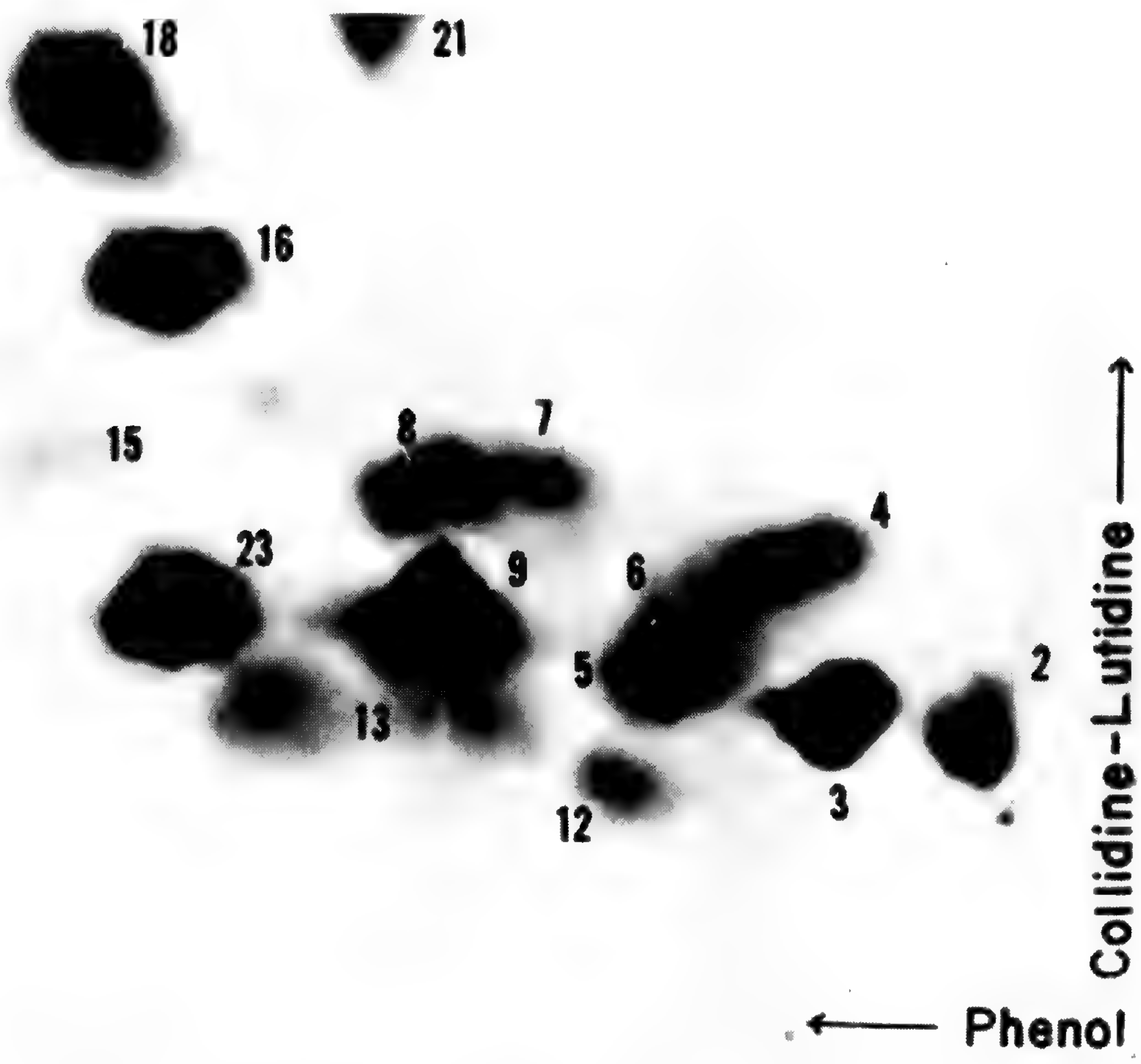

Figure 4. The ninhydrin-reactive, alcohol soluble nitrogen compounds of the potato tuber separated by two-dimensional paper chromatography. (From C. E. Dent, W. Stepka & F. C. Steward. 1947. Nature 160:682. Used by permission.)

A related discovery by various groups having both biochemical and ecological significance was that nitrogenase from several organisms can also reduce acetylene to ethylene. This now allows far more rapid, sensitive, and convenient field or laboratory analyses of nitrogen fixation (Hardy *et al.*, 1968), because a gas chromatograph to separate and quantitate the ethylene product is the only expensive equipment required.

The 1960's were also years of considerable efforts toward understanding mechanisms of and factors controlling reduction of nitrate and sulfate and their conversions into amino acids, processes for which we often forget to thank plants. There seems little doubt that we now know much more about reduction of nitrate than of sulfate. Nitrate reduction was recently reviewed by L. Beevers and R. H. Hageman (1969), two who have contributed much in this area. Evidence strongly indicates that conversion of nitrate to nitrite by nitrate reductase occurs in either roots or shoots with the aid of electrons derived from NADH. NADH arises from oxidation of 3-phosphoglyceraldehyde. This probably explains the long-recognized fact that nitrate disappears rapidly from leaves transferred from darkness to light, although the action of light (phytochrome-mediated) in inducing synthesis of nitrate reductase and other proteins (Travis & Key, 1971; Pine & Klein, 1972) may also be involved.

Subsequent reduction of nitrite in leaves is presently thought to occur using electrons derived from the photosynthetic electron transport system, after nitrite moves from the cytoplasm into the plastids. The source of electrons for conversion of nitrite to ammonia in roots (where ferredoxin is apparently absent) is still unknown. Further steps converting nitrogen of ammonia to glutamate and glutamine, and then to other amino acids, pyrimidine nucleotides, and proteins have been largely solved, but the origin of asparagine and the biosynthesis of purine nucleotides in plants require much more work.

One of the most important contributions to studies of nitrogen metabolism, in fact to metabolic studies in general, was the discovery of paper chromatography by Martin and Synge about 1941. F. C. Steward and his colleagues, who have contributed much information about nitrogen metabolism in plants, were the first to report results from the use of this technique with plant extracts. One of their early separations of potato tuber amino acids is illustrated in Fig. 4.

Photosynthesis and Photorespiration

To list even the highlight discoveries made in the last 25 years of photosynthesis research would require more space than we are permitted. Fortunately, the number of published reviews and books dealing with the subject is large, and even the *Annual Review of Biochemistry* frequently covers this aspect of plant metabolism. We shall therefore be much briefer than the subject deserves.

The utilization of radioactive ^{14}C in clever experiments led by Melvin Calvin and A. A. Benson solved the pathway of CO_2 fixation in most plant species. This work began about 25 years ago and, like so many other biochemical investigations, was aided by the then recent discovery of paper chromatography. The Calvin-Benson cycle requires input of ATP and reducing power to reduce 3-phosphoglycerate and to maintain the cycle. Three groups of investigators almost simultaneously demonstrated that light-driven water splitting causes NADP reduction, and the important experiments of Daniel Arnon and his colleagues showed that the necessary ATP arises in the chloroplasts from energy provided by light.

The following years seem to have been devoted largely to establishing the widespread nature and quantitative aspects of the above observations and to elucidating the photosynthetic electron transport pathway. The discovery by Robert Emerson *et al.* (1957) that the photosynthetic inefficiency of red light (680–720 nm) could be overcome by simultaneous addition of shorter wavelength (*i.e.* 640–670 nm) energy suggested that two photoreactions sensitized by different pigments cooperated in photosynthesis. Improved optical systems allowing differential spectroscopic measurements showed light-driven absorbance changes in a number of chloroplast electron transport pathway pigments. These absorbance changes and other data led to various formulations of the Hill-Bendall two-pigment series scheme for electron flow so familiar to present students of photosynthesis. Nevertheless, further results from Arnon's laboratory suggest that a third photoact may be required (Arnon, 1971). Further work is obviously needed.

We recall, in the early 1960's discussing a certain graduate student research project with which we were unimpressed and stating that it appeared about as worthwhile as investigating how another plant species fixes CO_2. Such dogmatic

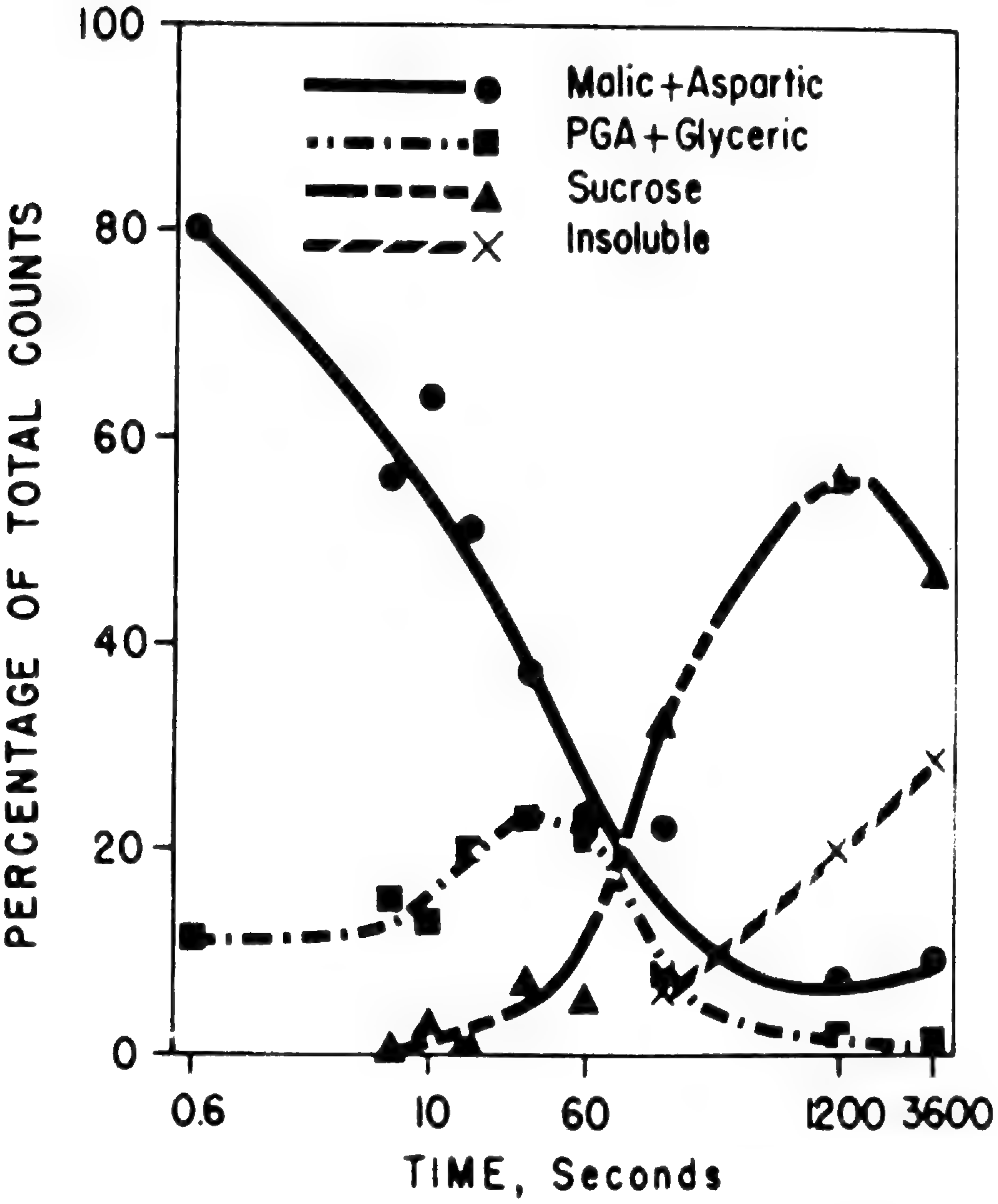

FIGURE 5. Distribution of photosynthetic products in sugarcane leaves emphasizing predominance of 4-carbon acids at short time intervals. Results averaged from 16 experiments. (From H. P. Kortschak, C. E. Hartt & G. O. Burr. 1965. Pl. Physiol. 40: 209–213. Used by permission.)

ideas were soon changed, however, by the modestly written report of Hugo Kortschak *et al.* (1965) showing that the initial photosynthetic products of sugar cane leaves are malic and aspartic acids, not phosphoglycerate (Fig. 5). These results were confirmed and extended to other species by M. D. Hatch, C. R. Slack, and others. The so-called C_4 photosynthetic pathway, still incompletely understood but beginning with formation of oxaloacetate via condensation of CO_2 and phosphoenolpyruvate, became apparent from these studies (Hatch & Slack, 1970).

One of the most interesting facts about C_4 plants is that they commonly have high rates of net photosynthesis. These high rates are apparently at least in part due to low rates of respiratory CO_2 loss in the light (low rates of photorespiration). Sugar cane, corn, sorghum, and several other grasses of tropical origin possess the C_4 pathway, but so do certain dicots and sedges. The light-stimulated loss of fixed CO_2 in C_3 (Calvin-Benson cycle) plants is believed to result from oxidation of phosphoglycolic acid, which itself is apparently produced from ribulose-diP or a sugar phosphate in the Calvin-Benson cycle. Phosphoglycolate is apparently not produced by the C_4 pathway, so C_4 plants lose less CO_2 via photorespiratory oxidation of glycolate.

G. Bowes and W. L. Ogren (1972; Bowes *et al.*, 1971) showed that ribulose diphosphate carboxylase, the principal photosynthetic enzyme of C_3 plants, can catalyze a still different reaction between ribulose-diP and molecular oxygen to produce phosphoglycolate (3-phosphoglycerate is assumed to be the other product). Oxygen seems to bind to the same site of the enzyme as CO_2; in any case it inhibits CO_2 fixation. These data may explain the long-known inhibition of photosynthesis by oxygen (Warburg effect) and perhaps the principal source of photorespiratory substrate.

Other Aspects of Plant Metabolism

The availability of radioisotopes, especially ^{14}C, ^{32}P, ^{3}H, and ^{35}S, combined with ultracentrifuges and numerous chromatographic techniques, created an information explosion that will serve as a solid foundation for future plant physiologists. Elucidation of reactions in glycolysis, the Krebs cycle, the pentose phosphate pathway of respiration, synthesis and breakdown of fats, synthesis of sucrose, starch, cellulose, nucleic acids, proteins, and numerous phenolic compounds was either largely solved or put on a firm basis in the 1950's and 1960's. Establishment of the reaction sequence whereby electrons flow from respiratory substrates to oxygen in the mitochondria and how this is coupled to ATP synthesis has not been totally solved, although vigorous work is continuing (Ikuma, 1972; Schwartz, 1971).

We were told, facetiously we think, that the way certain biochemists distinguished plants from animals 20 years ago was to simply learn whether or not they contained cholesterol. However, chemotaxonomists have more faith in data involving several compounds, and so it proved with cholesterol, for this sterol was found in red algae in 1958 and in potato plants in 1963 (Heftmann, 1965). Still other sterols, carotenoids, miscellaneous terpenes, gibberellins, the isopentenyl group of several cytokinins, and probably abscisic acid were shown in the last 10 years or so to be synthesized from acetyl coenzyme A through the mevalonic acid pathway. In most cases we find that more is known about their formations than their functions. The same can generally be said about numerous phenolic compounds, including anthocyanins, flavonols, flavones, and coumarins.

In spite of the vast amount of information about the kinds of reactions occurring in intermediary metabolism, we are still quite ignorant about why some pathways occur more readily in some cells than in others, in short, how metabolism is controlled. Rapid advances in protein chemistry (for example the discovery of allosteric properties of enzymes) give us guidelines for attacking the problem, but there is still an incredible amount of work left for the next 20 years and more.

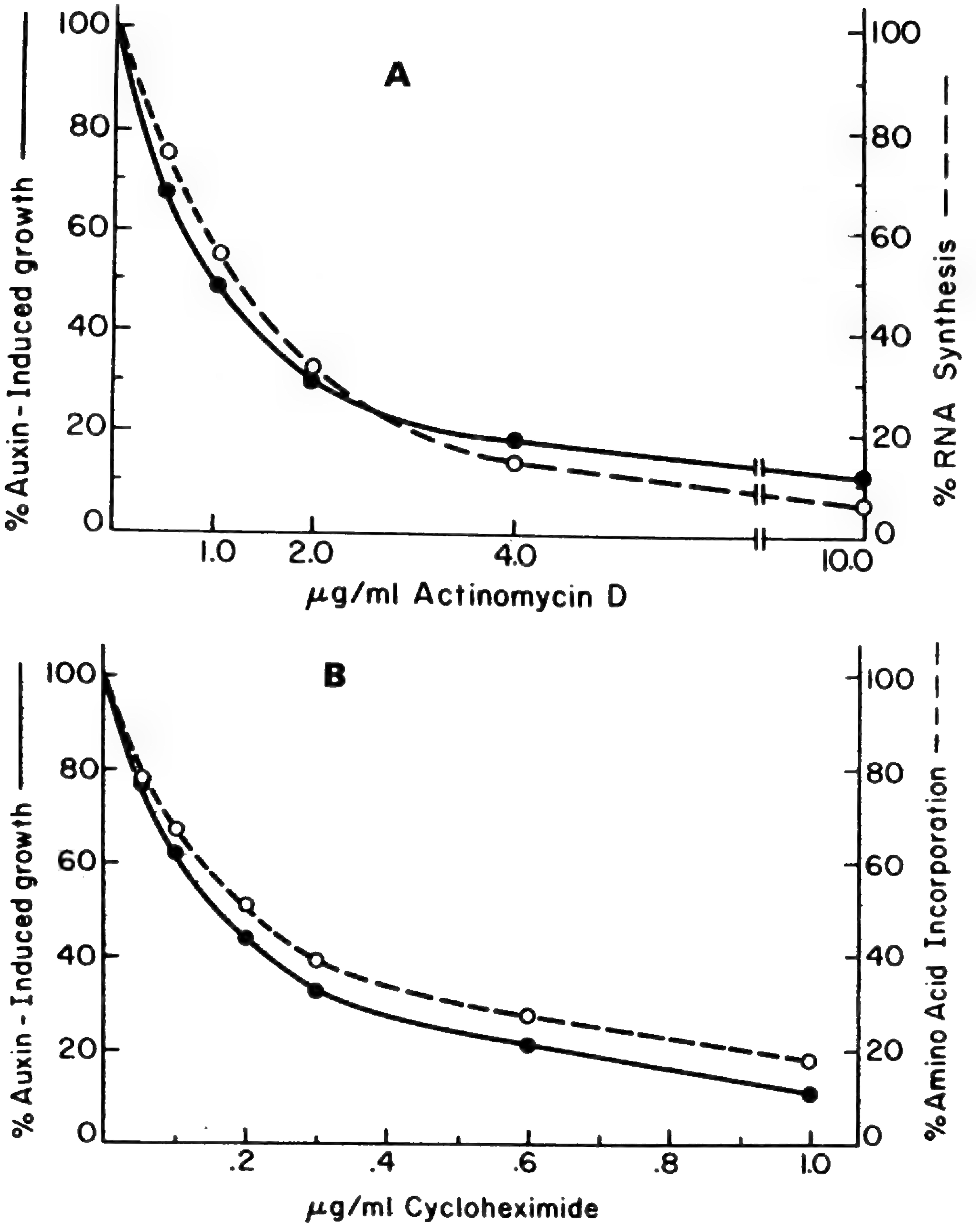

FIGURE 6. Parallel inhibition of auxin-induced growth of soybean hypocotyl sections and RNA or protein synthesis by actinomycin D or cycloheximide.—A. Growth and ADP-^{14}C incorporation into RNA were measured during a 4 hour interval after pretreatment with various concentrations of actinomycin D.—B. Growth and leucine-^{14}C incorporation into protein were measured during a 4 hour interval after pretreatment with various concentrations of cycloheximide. The auxin used in both A and B was 2,4-D, 10 μg/ml. (From J. L. Key, N. M. Barnett & C. Y. Lin. 1967. Ann. New York Acad. Sci. 144: 49–62. Used by permission.)

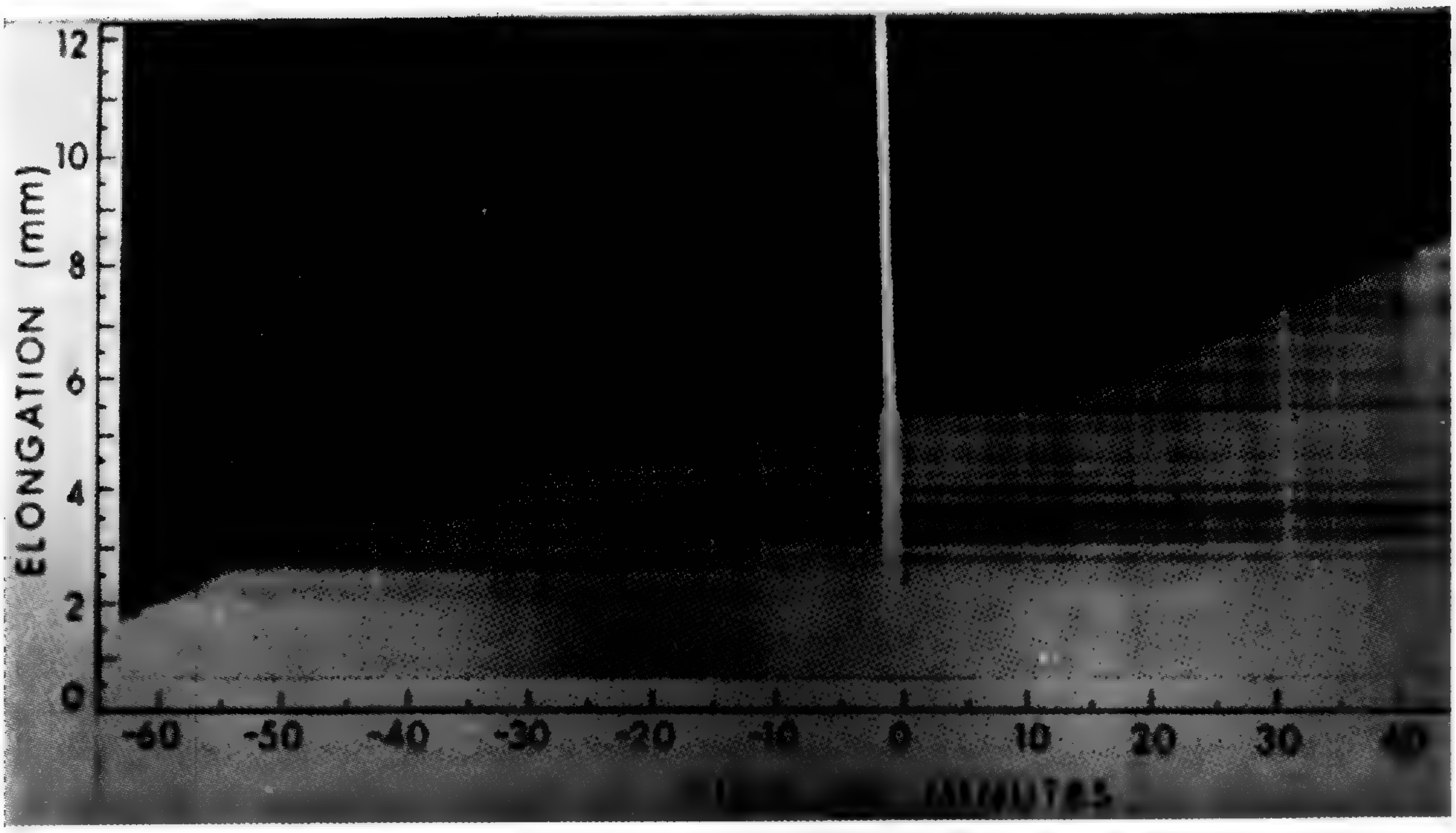

Figure 7. Shadowgraph apparatus record of growth of excised oat (*Avena sativa* var. Victory) coleoptile sections. The incubation medium was changed from water to 3 μg/ml IAA at the time corresponding to the vertical white line. The rapid elongation at the beginning of the record is the result of tactile stimulation of the coleoptiles during experimental manipulations. (From M. L. Evans & P. M. Ray. 1969. Jour. Gen. Physiol. 53: 1–20. Used by permission.)

Hormones in Growth and Development

After elucidation of the structure of DNA by Watson and Crick in 1953 and the subsequent discovery of various kinds of RNA molecules and their roles in protein synthesis, it seemed that attempts to solve nearly all developmental problems implicated DNA, messenger RNA, and enzymes. These macromolecules undoubtedly do participate in most developmental phenomena, but there are cases where "information" in the first two is not again called upon. F. C. Steward, in the prefatory chapter to the 1971 *Annual Review of Plant Physiology*, expressed the rapidly growing skepticism of many others concerning the "all-inclusive" embracement of the DNA → mRNA → enzyme hypothesis, when he asked ". . . is it credible that throughout ontogeny cells must always ask the permission of their nuclei for each and every act they perform?" But the discoveries concerning molecular biology, combined with the growing appreciation of biochemistry, certainly brought new outlooks and new approaches in the 1950's to the problem of solving how plants grow and differentiate. Questions could then be directed more at the cellular and molecular level, and indeed they were.

The rate of growth is a subject that has received a vast amount of study, catalyzed by Frits Went's discovery of auxin in 1926. Much of the subsequent auxin research has concerned how IAA and commercially synthesized auxins function. The classic 1930 work of A. N. Heyn showed that they increase cell wall plasticity (irreversible deformability), yet we still do not know how this is accomplished. A promising discovery was made in the early 1960's indicating

FIGURE 8. Growth stimulation of *Phaseolus vulgaris* L. by a gibberellin-containing extract prepared from seeds of the same variety (Black Valentine). An ether extract of seeds was evaporated and 125 μg of the residue was mixed with lanolin and applied as a band around the first internode of the plant on the right. Plants were photographed 3 weeks after treatment. Plant on the left was untreated. (Photograph courtesy of Dr. John W. Mitchell.)

that growth stimulation by auxins required synthesis of new messenger RNA and proteins (Noodén & Thimann, 1966; Key, 1964). The approach by these and other workers was to add selected inhibitors of RNA and protein synthesis to excised, auxin-responsive tissues, then determine effects of the inhibitors upon growth. Some interesting results of this technique are in Fig. 6. There are striking parallels between the extent of inhibition of both protein synthesis and growth and RNA synthesis and growth.

Careful kinetic studies of growth rates after auxin addition to various tissues eventually modified the apparent conclusions concerning the need for new RNA and protein synthesis in auxin action. Michael Evans and Peter Ray (1969) published the first extensive results. The crucial observations were that a lag period of only about 10 minutes preceded detectable growth increases by IAA (Fig. 7) and that inhibitors of RNA and protein synthesis did not increase the lag time. Still other experiments in which IAA was caused to reach its active site more rapidly showed no detectable lag in growth stimulation (Nissl & Zenk, 1969). A present interpretation of the inhibitor and kinetic studies is that auxins can initially stimulate growth by an unknown mechanism independent of RNA and protein synthesis, but that this mechanism does require a pre-existing protein(s) of a fairly short half-life (Cleland, 1971*b*). Continued growth requires its replenishment by reactions requiring RNA synthesis.

Twenty-five years ago physiologists were aware that hormones other than auxin probably participated in plant growth, but almost nothing was known about them. However, another powerful kind of growth regulator (now known as one of the gibberellins) had already been discovered by Kurosawa in Formosa in 1926, corresponding closely to Went's discovery of auxin. Not until the 1950's did scientists in western countries begin to investigate the gibberellins; activity of these compounds was soon found in higher plants (Fig. 8) (Mitchell *et al.*, 1951). Subsequent use of thin layer and gas chromatographic techniques combined with mass spectrometry has so far allowed the identification of more than thirty different naturally occurring gibberellins. The number of physiological responses known to be affected by them is at least as large (Bailiss & Hill, 1971; Lang, 1970).

The 1950's also brought about the discovery of cytokinins, initially in the laboratories of F. Skoog and F. C. Steward. These compounds, most of which are adenine derivatives, are best known for their ability to stimulate cell division and to retard senescence (Fig. 9) (Kende, 1971). Abscisic acid was discovered independently and concurrently in the early 1960's by F. T. Addicott and P. F. Wareing and their colleagues. As contrasted to cytokinins, abscisic acid accelerates senescence and generally retards growth. It is probably at least in part responsible for dormancy of buds and seeds of many species (Wareing & Phillips, 1970). The last decade also showed that ethylene has several properties of a plant hormone. In particular, it seems to be causally involved in both fruit ripening and in abscission processes (Burg & Burg, 1965; Jackson & Osborne, 1970).

Following the discovery that several hormone-induced physiological responses in animals are due to enhanced production of cyclic AMP, some evi-

FIGURE 9. Senescence of a trifoliate bean leaf caused by treating the primary leaves of cuttings with the synthetic cytokinin benzyladenine (30 μg/ml) at 4 day intervals. (From A. C. Leopold & M. Kawase. 1964. Amer. Jour. Bot. 51: 294–298. Used by permission.)

dence that this nucleotide may mediate auxin and gibberellin responses has recently been obtained. In addition, there is evidence for the presence of still other unidentified plant hormones, for example those formed under the proper environmental conditions that cause flowering and tuber formation (Evans, 1971).

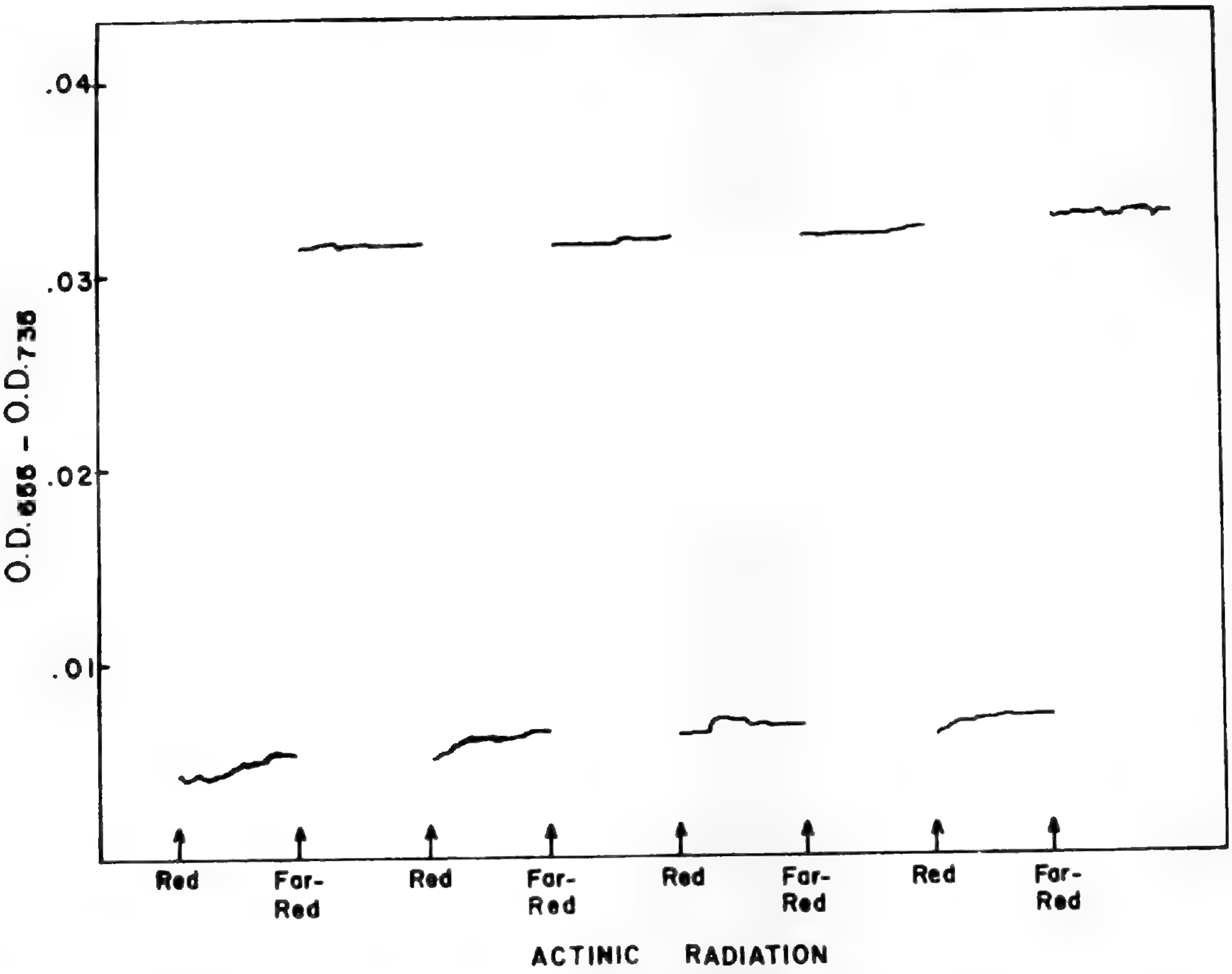

FIGURE 10. Influence of red and far-red light treatments upon subsequent absorption of these wavelengths by a phytochrome-containing extract of etiolated maize shoots. (From W. L. Butler, K. H. Norris, H. W. Siegelman & S. B. Hendricks. 1959. Proc. Natl. Acad. U.S.A. 45: 1703–1708. Used by permission.)

PHOTOMORPHOGENESIS

Although numerous effects of light upon plant development have been recognized for many years, the discovery of phytochrome by a cooperative effort of several USDA researchers, led by Harry Borthwick and Sterling Hendricks, did most to increase our understanding of this important area. Biological evidence for a photoreversible pigment capable of maximally absorbing either red or far-red radiation arose from their discovery of the opposite and freely reversible effects of these wavelengths upon lettuce seed germination (Borthwick *et al.*, 1952). Physical evidence for the pigment was first published in 1959 (Butler *et al.*, 1959) (Fig. 10). Since then, an impressive number of other responses to phytochrome in both lower and higher photosynthetic plants has been demonstrated.

Initial ideas were that P_{fr} (the principal far-red absorbing form of phytochrome) catalytically controls a central reaction of metabolism, yet no enzymatic function of phytochrome has yet been discovered. Some work of H. Mohr and his collaborators suggests that P_{fr} controls the activity of certain genes (Mohr, 1969). Certainly the numerous and profound effects upon development suggest that changing patterns of enzyme activities result from phytochrome activation.

However, the initial effect of P_{fr} is probably upon a membrane, and "permission" of the nucleus may be asked only later. Just as with auxins and cell elongation and abscisic acid and stomatal closing, some responses to red and far-red light are exhibited too soon to allow formation of new messenger RNA and enzyme molecules (Briggs & Rice, 1972).

A rapid phytochrome effect was first demonstrated by Fondeville *et al.* (1966), involving turgor changes causing leaflet movements of *Mimosa pudica* L. Satter *et al.* (1970) showed that such turgor changes involve phytochrome control over movement of potassium ions between cells on opposite sides of the pulvinus. Perhaps even more dramatic was the discovery by Takuma Tanada (1968) that phytochrome controls, within seconds, whether or not excised root tips stick to a negatively charged glass surface. It has been demonstrated that phytochrome exists very near or in the plasma membrane, even though it may also reside elsewhere in the cell (Briggs & Rice, 1972). These results raise the interesting questions of how phytochrome transformation causes changes in membrane permeability and how these changes, in turn, are translated into altered patterns of growth and development. One can speculate that release of ions, known hormones, or perhaps even cyclic AMP is involved, but we do not understand what actually occurs.

Flowering and Biological Clocks

The heart of photoperiodism (of which control of flowering in many species is an excellent example) is the presence of a biological time measuring device, or clock. Erwin Bünning suggested in 1932 that the clock measuring the relative lengths of day and night in photoperiodism was equivalent to the clock controlling circadian rhythms, but this idea was largely ignored in the United States until the 1950's. Plant physiologists eventually became interested in biological clocks and performed experiments to determine whether time measurement in photoperiodism is similar to that in circadian rhythms. The two proved to have several important characteristics in common, including temperature independence (or compensation), changing sensitivities to light, and the ability to be phase-shifted. Yet time measurement as displayed by leaf movements is not closely coupled to time measurement in photoperiodisms, indicating either the presence of separate but similar clocks or a highly complex and labile coupling system.

The postulated flowering hormone (Chailakhyan, 1968; Evans, 1971) remains to be identified, although the occasional preparation of extracts containing a promoting substance continues to raise our hopes that this will eventually be accomplished. Several studies indicate that inhibitors are involved in the flowering process, at least in some species. In addition, some experts believe that a complex of hormones must interact in the initiation of flowering.

Certainly one of the greatest lessons we have learned about the flowering process is that virtually every species has its own peculiar response characteristics. In spite of these differences, the potential practical advantages of identifying florigen or florigens should stimulate more research in this area. We hope that during the next 25 years chemicals will be developed to control flowering, thus aiding geneticists and increasing food production.

Important problems in growth and differentiation remain for the future. It will be necessary but not sufficient to learn how hormones, phytochrome, and a still unidentified photoreceptor of blue light initially act. The overwhelming process of establishing how these substances interact and integrate metabolic processes to cause the normal development of a plant must still be performed, probably with help from computers.

From the 1940's when so many physiological problems seemed to be explained away by "changes in membrane permeability," the trend in the 1950's and 1960's was to attempt to seek biochemical answers, *i.e.* a responsible enzyme, nucleic acid, or hormone. But the pendulum seems to have returned to membranes, and many of the answers apparently still lie in these mysterious but variable assemblages of proteins and lipids. Our future students must be educated and trained accordingly.

Looking back over the past 25 years, we are impressed that it is a long time in terms of the discoveries made. The next 25 years will no doubt be even longer on this basis, and we can predict that most of the important remaining problems of a *chemical* nature concerning water relations, phloem translocation, membrane transport, nutrition, and general metabolism will be solved during this time. But to really understand growth and development of any eukaryotic organism will require much longer. Nevertheless, present "genetic engineering" ideas of transforming nitrogen fixing genes via protoplast fusion (Cocking, 1972; Power & Cocking, 1971) into cereal grains to increase food production in countries unable to pay for nitrogen fertilizers seems to be a worthwhile and perhaps feasible goal. So also does the manipulation of certain species to eliminate photorespiration and increase net photosynthetic rates. However, research money is essential, and uncertainty as to its availability could make our "crystal ball" as useless as all the others. It is apparent that dramatic increases in financial aid from federal agencies (especially the National Science Foundation and National Institutes of Health) for plant physiology research can no longer be expected. Hopefully, the needed work will still be carried on at an undiminished pace.

BIBLIOGRAPHY

ARNON, D. I. 1971. The light reactions of photosynthesis. Proc. Natl. Acad. U.S.A. 68: 2883–2892.

BAILISS, K. W. & T. A. HILL. 1971. Biological assays for gibberellins. Bot. Rev. (Lancaster) 37: 437–479.

BEEVERS, L. & R. H. HAGEMAN. 1969. Nitrate reduction in higher plants. Annual Rev. Pl. Physiol. 20: 495–522.

BERGERSEN, F. J. 1971. Biochemistry of symbiotic nitrogen fixation in legumes. Annual Rev. Pl. Physiol. 22: 121–140.

BORTHWICK, H. A., S. B. HENDRICKS, M. W. PARKER, E. H. TOOLE & V. K. TOOLE. 1952. A reversible photoreaction controlling seed germination. Proc. Natl. Acad. U.S.A. 38: 662–666.

BOWES, G. & W. L. OGREN. 1972. Oxygen inhibition and other properties of soybean ribulose 1,5-diphosphate carboxylase. Jour. Biol. Chem. 247: 2171–2176.

———, ——— & R. H. HAGEMAN. 1971. Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. Biochem. Biophys. Res. Commun. 45: 716–722.

Briggs, W. R. & H. V. Rice. 1972. Phytochrome: chemical and physical properties and mechanism of action. Annual Rev. Pl. Physiol. 23: 293–334.

Brownell, P. F. & C. J. Crossland. 1972. The requirement for sodium as a micronutrient by species having the C_4 dicarboxylic photosynthetic pathway. Pl. Physiol. 49: 794–797.

Broyer, T. C., A. B. Carlton, C. M. Johnson & P. R. Stout. 1954. Chlorine—a micronutrient element for higher plants. Pl. Physiol. 29: 526–532.

Burg, S. P. & E. A. Burg. 1965. Ethylene action and the ripening of fruits. Science 148: 1190–1196.

Butler, W. L., K. H. Norris, H. W. Siegelman & S. B. Hendricks. 1959. Detection, assay, and preliminary purification of the pigment controlling photoresponsive development of plants. Proc. Natl. Acad. U.S.A. 45: 1703–1708.

Carnahan, J. E., L. E. Mortenson, H. F. Mower & J. E. Castle. 1960. Nitrogen fixation in cell-free extracts of *Clostridium pasteurianum.* Biochim. Biophys. Acta 44: 520–535.

Cataldo, D. A., A. L. Christy & C. L. Coulsen. 1972. Solution-flow in the phloem. II. Phloem transport of THO in *Beta vulgaris.* Pl. Physiol. 49: 690–695.

Chailakhyan, M. K. 1968. Internal factors of plant flowering. Annual Rev. Pl. Physiol. 19: 1–36.

Cleland, R. 1971*a.* Cell wall extension. Annual Rev. Pl. Physiol. 22: 197–222.

———. 1971*b.* Instability of the growth-limiting proteins of the *Avena* coleoptile and their pool size in relation to auxin. Planta 99: 1–11.

Cocking, E. C. 1972. Plant cell protoplasts-isolation and development. Annual Rev. Pl. Physiol. 23: 29–50.

Cook, G. M. W. 1971. Membrane structure and function. Annual Rev. Pl. Physiol. 22: 97–120.

Cummins, W. R., H. Kende & K. Raschke. 1971. Specificity and reversibility of the rapid stomatal response of abcisic acid. Planta 99: 347–351.

Curtis, O. F. & D. G. Clark. 1950. Introduction to Plant Physiology. McGraw-Hill Book Co., Inc. New York.

Emerson, R., R. Chalmers & C. Cederstrand. 1957. Some factors influencing the long-wave limit of photosynthesis. Proc. Natl. Acad. U.S.A. 43: 133–143.

Epstein, E. 1956. Mineral nutrition of plants: mechanisms of uptake and transport. Annual Rev. Pl. Physiol. 7: 1–24.

———. 1972. Mineral Nutrition of Plants: Principles and Perspectives. John Wiley and Sons, Inc. New York.

Evans, L. T. 1971. Flower induction and the florigen concept. Annual Rev. Pl. Physiol. 22: 365–394.

Evans, M. L. & P. M. Ray. 1969. Timing of the auxin response in coleoptiles and its implications regarding auxin action. Jour. Gen. Physiol. 53: 1–20.

Fischer, R. A. 1968. Stomatal opening: role of potassium uptake by guard cells. Science 160: 784–785.

Fondeville, J. C., H. A. Borthwick & S. B. Hendricks. 1966. Leaflet movement of *Mimosa pudica* L. indicative of phytochrome action. Planta 69: 357–364.

Fujino, M. 1967. Adenosine triphosphate and adenosine triphosphatase in stomatal movement. Sci. Bull. Fac. Educ. Nagasaki Univ. 18: 1–47.

Hardy, R. W. F., R. D. Holsten, E. K. Jackson & R. C. Burns. 1968. The acetylene-ethylene assay for N_2 fixation: laboratory and field evaluation. Pl. Physiol. 43: 1185–1207.

Hatch, M. D. & C. R. Slack. 1970. Photosynthetic CO_2-fixation pathways. Annual Rev. Pl. Physiol. 21: 141–162.

Heftmann, E. 1965. Steroids. Pp. 693–716, *in* J. Bonner & J. E. Varner (editors), "Plant Biochemistry." Academic Press. New York.

Hodges, T. K., R. T. Leonard, C. E. Bracker & T. W. Keenan. 1972. Purification of an ion-stimulated adenosine triphosphatase from plant roots: association with plasma membranes. Proc. Natl. Acad. U.S.A. 69: 3307–3311.

Ikuma, H. 1972. Electron transport in plant respiration. Annual Rev. Pl. Physiol. 23: 419–436.

Jackson, M. B. & D. J. Osborne. 1970. Ethylene, the natural regulator of leaf abscission. Nature 225: 1019–1022.

Jones, R. J. & T. A. Mansfield. 1971. Antitranspirant activity of the methyl and phenyl esters of abscisic acid. Nature 231: 331–332.

Kende, H. 1971. The Cytokinins. Int. Rev. Cytol. 31: 301–338.

Key, J. L. 1964. Ribonucleic acid and protein synthesis as essential processes for cell elongation. Pl. Physiol. 39: 365–370.

Koch, B., H. J. Evans & S. Russell. 1967. Reduction of acetylene and nitrogen gas by breis and cell-free extracts of soybean root nodules. Pl. Physiol. 42: 466–468.

Kortschak, H. P., C. E. Hartt & G. O. Burr. 1965. Carbon dioxide fixation in sugarcane leaves. Pl. Physiol. 40: 209–213.

Lang, A. 1970. Gibberellins: structure and metabolism. Annual Rev. Pl. Physiol. 21: 537–570.

Lundegårdh, H. 1955. Mechanisms of absorption, transport, accumulation, and secretion of ions. Annual Rev. Pl. Physiol. 6: 1–24.

Mansfield, T. A. & R. L. Jones. 1971. Effects of abscisic acid on potassium uptake and starch content of stomatal guard cells. Planta 101: 147–158.

Mitchell, J. W., D. P. Skaggs & W. P. Anderson. 1951. Plant growth-stimulating hormones in immature bean seeds. Science 114: 159–161.

Mohr, H. 1969. Photomorphogenesis. Pp. 509–556, *in* M. B. Wilkins (editor), "Physiology of Plant Growth and Development." McGraw-Hill Publ. Co. Ltd. London.

Nissl, D. & M. H. Zenk. 1969. Evidence against induction of protein synthesis during auxin-induced initial elongation of oat coleoptiles. Planta 89: 323–341.

Noodén, L. D. & K. V. Thimann. 1966. Action of inhibitors of RNA and protein synthesis on cell enlargement. Pl. Physiol. 41: 157–164.

O'Leary, J. W. 1970. Can there be a positive water potential in plants? BioScience 20: 858–859.

Pine, K. & A. O. Klein. 1972. Regulation of polysome formation in etiolated bean leaves by light. Develop. Biol. 28: 280–289.

Power, J. B. & E. C. Cocking. 1971. Fusion of plant protoplasts. Sci. Prog. (Oxford) 59: 181–198.

Raschke, K. & M. P. Fellows. 1971. Stomatal movement in *Zea mays*: shuttle of potassium between guard cells and subsidiary cells. Planta 101: 296–316.

Salisbury, F. B. & C. Ross. 1969. Plant Physiology. Wadsworth Publ. Co. Belmont, California.

Satter, R. L., P. Marinoff & A. W. Galston. 1970. Phytochrome controlled nyctinasty in *Albizzia julibrissin*. II. Potassium flux as a basis for leaflet movement. Amer. Jour. Bot. 57: 916–926.

Scholander, P. F., H. T. Hammel, E. D. Bradstreet & E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148: 339–346.

Schwartz, M. 1971. The relation of ion transport to phosphorylation. Annual Rev. Pl. Physiol. 22: 469–484.

Spanner, D. C. 1971. Transport in the phloem. Nature 232: 157–161.

Steward, F. C. & J. F. Sutcliffe. 1959. Plants in relation to inorganic salts. Pp. 253–478, *in* F. C. Steward (editor), "Plant Physiology." Vol. 2. Academic Press. New York.

Swanson, C. A. & E. D. H. El-Shishiney. 1958. Translocation of sugars in grapes. Pl. Physiol. 33: 33–37.

Tanada, T. 1968. A rapid photoreversible response of barley root tips in the presence of 3-indoleacetic acid. Proc. Natl. Acad. U.S.A. 59: 376–380.

Travis, R. L. & J. L. Key. 1971. Correlation between polyribosome level and the ability to induce nitrate reductase in dark-grown corn seedlings. Pl. Physiol. 48: 617–620.

Turner, N. C. 1972. K^+ uptake of guard cells stimulated by fusicoccin. Nature 235: 341–342.

Wareing, P. F. & I. D. J. Phillips. 1970. The control of growth and differentiation in plants. Pergamon Press. Oxford, England.

Zimmerman, M. H. 1957. Translocation of organic substances in trees. I. The nature of the sugars in the sieve tube exudate of trees. Pl. Physiol. 32: 288–291.

25 years of botany

PLANT ECOLOGY
1947–1972[1]

ROBERT P. MCINTOSH[2]

Twenty-five years encompass roughly a human generation, the larger part of a professional life, and one-third of the span of ecology as a recognized biological science. Perhaps this is too short a time to develop a self-conscious historical viewpoint in a science, and it is striking how little has been published, in any systematic way, on the history of ecology or on the lives of its leading figures. It seems appropriate to begin this paper with a plea for more adequate recognition and documentation of the antecedents of ecology (*e.g.* Egerton, 1969; Stauffer, 1960), the history of ecology (*e.g.* Pearsall, 1964; Sears, 1969), accounts of the development of particular aspects of ecology (*e.g.* E. P. Odum, 1968; Major, 1969; Whittaker, 1962, 1967; McIntosh, 1967), personal reminiscences, biography, or autobiography (*e.g.* Gleason, 1953; Livingston, 1948), or a consideration of ecology during some time span (*e.g.* Gleason, 1936; Steere, 1958).

History is measured not only by span of time but by pace of events, a rate process in current usage, and the past 25 years have been marked by a rapidly increasing rate of change. Division of time for the purpose of reviewing historical development is necessarily arbitrary, but beginning this review of 25 years of ecology ca. 1947 has a certain logic. It coincides with the end of a world-wide trauma which had occupied the attention of ecologists, interrupted the training of new ecologists, and created a lull in the progress of ecology. It marks the

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[1] In my preoccupation with this topic over the past two months I have asked many persons, "What do you think were the significant developments in plant ecology during the past 25 years?" I am indebted to a number of ecologists who made helpful suggestions concerning particular aspects of the past 25 years in ecology: Dwight Billings, Helmut Lieth, Murray F. Buell, Forest Stearns, Edward O. Beals, Stanley Auerbach, Robert Platt, Calvin McMillan, Paul Sears, John Brooks, Josephine K. Doherty, Arthur R. Kruckeberg, C. H. Muller, A. D. Bradshaw, Peter Greig-Smith, Robert Wetzel, William S. Benninghoff, J. Roger Bray, E. J. Dyksterhuis, Theodore Kozlowski, Orrie Loucks, Robert Whittaker, Jerry Franklin, Daniel Janzen, J. K. Marshall, Jerry Kline, William Niering, Alton A. Lindsey, David Goodall, George Sprugel, Edward J. Cushing, Edward S. Deevey, George Lauff, Donald Hall, Pat Werner. If I have omitted anyone whom I plagued with my questions, I apologize. Grant Cottam made numerous suggestions on organization and graciously allowed me to quote one of his less ribald limericks, which was co-authored by David Parkhurst. My colleagues at Notre Dame, Theodore Crovello, Quentin Ross, Thomas Poulson, and Carl von Ende, read and commented on the manuscript at various stages of preparation.

Like the maker of dictionaries, the best I can hope for is to escape censure for errors of omission or misinterpretation for which I remain responsible.

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beginning of the professional careers of a large number of ecologists who have lived through and initiated many changes and are still active in the field, although now calling themselves, euphemistically, middle-aged. It also marks the beginning of a genuine turning point in science brought about, in part, by development of radically new techniques in several other discplines which gradually filtered into ecology and by a markedly different view of science and its relation to society, illustrated in Vannevar Bush's, *Science The Endless Frontier* (1945). Ecology is only recently receiving the full impact of these two developments.

Fortuitously for a historical look at plant ecology, the epoch was initiated by Frank Egler's (1951) acid "Commentary on American plant ecology, based on the textbooks of 1947–49," which serves as a brief history of plant ecology, in the United States at least, and as a perceptive ecologist's view of plant ecology as represented in the leading textbooks of the day. Dr. Egler noted, correctly I believe, the general emphasis on phytosociology, the largely single-factor studies of autecology, the enormous accumulation of facts with limited theoretical or philosophical framework to hang them on, the uncritical acceptance of simple causality, and the provincial tone of plant ecology in America.

In the United States, at least, one of the dramatic developments in ecology in the last 25 years is that it has become "big science" and international science, at least relative to its early experience. The tradition of ecology as the product of individual ecologists, or at best small groups, with very sketchy funding has changed. Most ecologists, prior to World War II, were university staff members with a few in government agencies and even fewer, such as F. E. Clements, supported for a time by the Carnegie Foundation. In the post-war period, the advent of large-scale, particularly federal, funding has greatly changed the ecologist's standard of living; and the increased interest in ecology has helped spread ecology to all parts of the United States, moved it out of a largely academic scene, and precipitated ecologists into the international set, as many work in areas outside the United States or junket widely to international meetings. It is only recently that you could go to your Chevrolet garage and have your car ECOLOGIZED.

The National Science Foundation (NSF) was a major force in the transformation of expectations of ecologists. Established in 1950, it awarded its first grants for plant ecological work in 1952 to G. W. Prescott for work on arctic algae and to E. Abbe for studies of the biogeography of arctic and subarctic areas. The sums involved, under $10,000, were modest by recent standards. In 1956 there was a substantial increase in the number of awards, the size of the awards, and the nature of the research. Several studies of trophic structure, productivity, and nutrient cycling evidence the beginnings of a major development in plant ecology.

In 1966 and 1967 the NSF seemed most excited about molecular biology, but 1967 also brought the International Biological Program (IBP), which had been organized in 1965, from the planning into the early operational stage. The IBP has had enormous, perhaps cataclysmic, impact on the nature of ecological research. It was essentially the ecological response to the problems of the human environment, and its major concern was the biological basis of productivity and human welfare. It is, basically, a large-scale, programmed, research effort and, in a sense, creates a managerial class of ecologists. A comment such as "Unfortunately, the administrative and funding obligations of 'big ecosystems' science have precluded any significant advances in our research program since last November," would have been unthinkable to ecologists two decades ago and is hard to grasp even now. Integrated research groups, involving hundreds of people, with funding in the millions of dollars and predicated on international cooperation, are a dramatic departure from tradition in ecology and presage important changes in plant ecology in the future. The establishment of the IBP Program in the NSF as a funding unit suggests something on the order of the first ecological Manhattan Project, the consequences of which are only dimly seen.

A second major source of funds as well as new techniques and research approaches in plant ecology was the Atomic Energy Commission (AEC). After World War II, John Wolfe left plant ecology at Ohio State University for the Washington scene, one of the first ecologists to occupy a strategic position there. As Chief of the Environmental Sciences Branch of the Division of Biology and Medicine of the AEC, he was influential in the developing research efforts of the AEC as it slowly became aware of the health and environmental hazards of radiation. Ecological work was begun as early as 1955 by E. P. Odum at the Savannah River Plant; and ecological work at the Hanford Plant, the Nevada Test Site, and Oak Ridge National Laboratory was also under way. The small ecological program at Oak Ridge, under Stanley Auerbach, a section of the Health Physics Division, started expanding about 1958 becoming, perhaps, the largest group in a single, organized, ecological-research enterprise. It recently was established as a separate Division of the Laboratory and the headquarters of the Eastern Deciduous Forest Biome of the IBP. The AEC also funded work at various universities and was a factor in the development of extensive ecological research programs in the southeastern United States.

Corollary to the availability of large scale funding, and of research made possible by it, was the impact of new and expensive equipment now available to the ecologist. In the late forties a well-equipped ecologist was described as one with a *p*H kit in hand and an atmometer or two in his back pocket. The new breed of ecologist would probably have to look up atmometer in his dictionary. Essential tools for some kinds of ecology now include gas analyzers, chromatographs, respirometers, spectrophotometers, neutron probes, calorimeters, biotelemetry, the ubiquitous computer, growth chambers, and the biotron. Some of these are now available for routine classroom use and make possible work by students which would have been impossible for the most distinguished plant ecologist of 25 years ago.

It is striking to note that H. A. Gleason (1936), writing on "Twenty-five years of ecology, 1910–1935" said, ". . . attention has been largely directed toward the discovery of the fundamental underlying principles which govern and control all phenomena of the living plant in its natural environment and toward the application of these principles to several economic problems and to other broader problems of pure botany." This statement, generalized to include animals, would be equally apt to describe the self image ecologists have of themselves in the period 1947–1972, but sometimes those in the latter period suggest that this attitude is peculiar to themselves.

QUANTITATIVE PLANT ECOLOGY

The period was marked by a rapid rise of interest in and application of quantitative techniques which have transformed plant ecology and discommoded some of its older practitioners. Some years ago, when quantitative ecology involved no more than simple arithmetic and elementary algebra and geometry, one ecologist dismissed it as "numerology." Even Stanley Cain (1944), one of the pioneers of quantitative methods of sampling and analysis in plant ecology, had reservations about the ultimate utility of mathematics and commented, "Ecological factors may not only be difficult of solution because of interaction of factors and responses but may really be insoluble in a mathematical sense." Others questioned the utility of quantitative approaches to phytosociology, and some ecologists simply ignored them. Traditionally, in plant ecology quantitative ecology meant the use of quantitative methods of sampling and data analysis of vegetation studies—in a word, phytosociology.

Sampling and statistics—The 1950's saw much attention given to sampling problems and quantitative analysis of vegetation. Plant ecologists, as revealed in the excellent reviews by Goodall (1952), were concerned with problems of quantitative sampling of plant species, effects of quadrat size, shape, and spacing on the results, the vexing problem of dispersion of individuals, the relation of frequency and density measurements, species-area curves and minimal area of a community, associations and correlations between species, and the omnipresent problem of homogeneity.

An important addition to the sampling repertoire was the introduction of point or distance measures (Cottam & Curtis, 1949), which increased the efficiency of sampling and the quantity of data collected, posing problems of data analysis for subsequent ecological studies. The appearance, in 1957, of Greig-Smith's *Quantitative Plant Ecology* was another important landmark, being the first book codifying quantitative methods for the ecologist and stimulating plant ecologists to use them more knowledgeably. The use of statistical methods in this period was largely empirical and often somewhat naive, but Goodall (1970*a*), Greig-Smith (1957), and, more recently, Pielou (1969) have contributed to the increasing rigor and sophistication of statistical work by plant ecologists. Increasingly, in recent years, ecologists with better statistical training, and statisticians, with or without biological interests, have introduced new methods and more effective applications of statistics in ecology, although mutual incomprehension, if not antagonism, is sometimes still with us.

The multivolume review, *Statistical Ecology* (Patil, Pielou & Waters, 1971), is ample evidence of the increasing interest in statistical ecology. The basic problem of distribution of individuals is still with us. Greig-Smith's (1957) studies of pattern analysis emphasized the nature and scale of pattern and the heterogeneity exhibited in plant distribution. The importance of pattern or heterogeneity in the interactions of organisms and the functioning of the ecosystem is still inadequately investigated, and random or homogenous models are widely used for the sake of simplicity and generality, the biological realities notwithstanding.

Sampling and statistics are increasingly applied to studies of plant population dynamics, and the newer thrusts of population ecology, largely developed by animal ecologists, are being increasingly felt in plant ecology (Harper, 1964; Hett & Loucks, 1971). It has seemed that animal ecologists have concentrated most of their quantitative study on populations, particularly on population dynamics, and plant ecologists on communities, with only passing attention to population dynamics. This is changing now as plant ecologists, largely stimulated by the work of John Harper and his students, find population dynamics studies intriguing. Animal ecologists, conversely, are increasingly studying communities (taxocenes) and, in some instances, they recognize that plant ecologists have done so too.

Ordination and classification—The preoccupation of plant ecologists with description and analysis of vegetation and the plant community throughout the history of the science has frequently been noted or even deplored. The plethora of schools and methodologies of phytosociology has created much confusion. The comprehensive review of the classification of plant communities by Whittaker (1962) was certainly one of the major contributions to an understanding of traditional schools of phytosociology, particularly the several Continental schools.

Stemming from the traditional interest in vegetation studies, the long-term dispute concerning the nature of the plant community was a prominent part of plant ecology during the 1950's and 1960's. The individualistic concept of H. A. Gleason, Ramensky, and other plant ecologists, was resurrected at the beginning of the period considered here (McIntosh, 1967). In 1951 additional evidence for the individualistic concept was seen in the continuum concept (Curtis & McIntosh, 1951) and in Whittaker's (1951) criticism of the plant association and climatic climax concepts. The continuum or gradient approach to vegetation analysis was developed in detail by J. T. Curtis and his students at Wisconsin (Curtis, 1959) and by R. H. Whittaker, first in his Smoky Mountain studies and subsequently in diverse places (Whittaker, 1967). Other plant ecologists, particularly in Poland, had developed similar techniques and concepts. The continuum or gradient view of vegetation has been widely adopted by plant ecologists and the significance and development of these concepts have recently been reviewed by McIntosh (1967), Dansereau (1968), and Whittaker (1967). Not all ecologists are convinced of the merits of either concept or methods, and Daubenmire (1966) and Langford and Buell (1969), among others, have criticized both. It may be that the association-continuum dichotomy will go on, ad infinitum, like the particle-wavelength concepts of light. At least there are now two views, and what one does not explain the other might. It is probably fair to say that plant ecologists take the individualistic concept of species tolerances (niche) as all but axiomatic, and the individualistic concept of the community is accepted as a widely useful concept in accord with the recognized heterogeneity of environment and genetic make-up of species.

A significant aspect of quantitative plant ecology in this era was the introduction of new methods of analyzing vegetation data, described as ordination and classification or clustering methods, which radically changed the way plant ecologists looked at their data. Simple linear ordinations represented in the early continuum and gradient efforts were replaced by multidimensional ordinations such as that of Bray and Curtis (1957). Subsequently other methods were adopted, particularly principal components (Greig-Smith, 2nd ed., 1964). Goodall was, perhaps, the first to use factor analysis in plant ecology, but it was not widely used until 1960. Development of these methods of vegetational analysis required consideration of numerous problems, especially selection of data, numerical methods of comparing samples or stands (*i.e.* similarity or distance indices, Orloci, 1972), and the evaluation of diverse techniques of ordination used in combination with these to process vegetational data.

Most recently, studies of ordination methods have explored the problem of how well ordinations reflect the actual relations in the vegetation, because the available techniques presume linearity, but species and environment are not linearly related (Austin & Noy-Meir, 1971). Austin and Noy-Meir express concern about the future utility of ordination methods and even state that only the primitive continuum analysis avoids the problem of distortion due to nonlinearity of species response to environment. It is probable, however, that with appropriate adaptation and better understanding by ecologists of the properties and limitations of similarity measures and ordination methods they will continue to be used and to be useful.

In the early development of ordinations these were contrasted both philosophically and methodologically with the traditional vegetational classifications of Clements or Braun-Blanquet. Ordinations do not differ in this way from the methods of numerical classification which have also been recently introduced into vegetation studies, particularly in the distinguished work of W. T. Williams and Joyce Lambert (Lambert and Williams, 1966). Data sets can profitably be analyzed by either ordination or classification methods, and in neither case has the last word been said. Lambert and Dale (1964) consider the relative merits of ordination and classification, and Williams (1971) reviews the principles of clustering methods. Classification methods have been effectively applied by Williams and his associates to Australian tropical rain forest, and numerous articles, particularly in the British *Journal of Ecology*, have illustrated a variety of methods. A less well known paper comparing ordination and classification, and giving an excellent account of the basis of these, is that of Groenewoud (1965). Lieth and Moore (1971) apply numerical clustering methods to the phytosociological concepts of the Braun-Blanquet school.

In Europe there were parallel developments in quantitative plant ecology. The presumably monolithic Sigmatist school of plant ecology, which for most ecologists is personified by J. Braun-Blanquet, was still very much in being as represented by a new edition of Professor Braun-Blanquet's *Pflanzensoziologie* (1964). The basic philosophy of the Sigmatist school has not changed as the recent developments of quantitative plant ecology are not represented or are even deplored as not suitable. Nevertheless, this edition is, like the earlier one, a major landmark in plant ecology. Other European workers were actively developing and using ordination and classification methods during the period (Gounot, 1969; Maarel, 1969).

Numerous Japanese plant ecologists were also using quantitative methods. The development of extensive plant ecological studies by Japanese workers (or, at least, an awareness of them in the United States) was a departure from the traditional focus of western plant ecology.

Mathematical modeling and population studies, more recently used in plant ecology, have introduced different, more varied, and increasingly more sophisticated mathematical methods into ecology. Diverse methods of analysis have been widely used in both ecology and systematics (Crovello, 1970). While the uses of statistical and mathematical procedures in current ecology are pervasive, they are not without their dangers, and even mathematically minded ecologists have issued certain caveats. R. H. Whittaker (1967), discussing the application of mathematical techniques to vegetation, said, "It is the case, however, and no fault of mathematically inclined ecologists, that the character of species distributions and compositional gradients imply diminishing returns from complex mathematical treatment of vegetation."

Nevertheless, the pressures are strong for biology and ecology to become more mathematically oriented disciplines. Waterman (1965) called for more theoretical and mathematical approaches saying, "Only in this way can biology outgrow the stigma of being a mere descriptive science and rise to the level of a rigorous intellectual discipline"—a statement which may set some teeth on edge. Pielou (1969) commented, "ecology is essentially a mathematical subject." Watt (1966), Van Dyne 1969*b*), Patten (1971), Gates (1968), and other ecologists have stressed the need for more mathematics in ecology and more training in mathematics for a new breed of ecologists.

The interest of ecologists in statistical and mathematical ecology and, more particularly, the reciprocal interest of statisticians and mathematicians in ecology are dramatic developments of the last decade. However, there is much still to be done to put together fruitful combinations of mathematics and ecology in the same individual or, alternatively, to bring together productive combinations of statisticians, or mathematicians and ecologists, an effort which is now actively underway, particularly in the IBP. Goodall (1970*a*) observed, ". . . fruitful models and hypotheses for statistical ecology are likely to be based on biological rather than purely mathematical premises. In statistical ecology, in the past, mathematical and statistical considerations have too often played the role of master rather than servant; the subject is likely to mark time until its biological aspects resume their rightful place."

The thrust of the last 25 years has clearly been towards more mathematical analysis in plant ecology. It may sometimes be thought that it has raised more questions than it has produced answers, and the most fruitful balance has yet to be struck between mathematical abstraction and "real" world biology. The best, or worst, is yet to come.

THE NEW ECOLOGY—SYSTEMS ECOLOGY

Perhaps the most far reaching of all of the developments of the last twenty-five years in ecology is the meteoric rise of the ecosystem concept (*i.e.* the complex of organisms and environment) in the consciousness and rhetoric of ecologists. The term ecosystem is not new. It was coined in 1935 by the classical British plant ecologist, Sir Arthur Tansley, and the concept is much older as Major (1969) notes. What is new is an intensified and determined effort to actually encompass the whole of community and environment and to treat it in a quantitative way as a functional biological entity. In the view of the trophic-dynamic or functional ecologist, the ecosystem is a functional entity with internal homeostasis, identifiable boundaries, and recognizable relations between its subcomponents. The basic ecological hypothesis to be tested is whether the landscape is organized into logical patterns of self-sustaining, dynamic, and internally-regulated components (Reichle & Auerbach, 1972).

Much of the recent focus on the functional ecosystem, stemming from the pioneer work of R. Lindeman (1942), is due to the research, writing, lecturing, and personalities of the brothers Odum (E. P. and H. T.) and to the influential textbook, *Fundamentals of Ecology* (E. P. Odum, 1953). Although ecologists traditionally urged a holistic view of nature and agreed on the importance of the ecosystem concept, their usual practice was to study some limited facet of the whole, *e.g.* plant or animal population or community and limited factor(s) of the environment. The emphasis on the ecosystem as the study unit for ecologists is significant in diminishing the familiar distinction between plant and animal ecology. This is, in fact, one of the striking developments of recent years. Ecosystem ecology, except in very simple systems, will most likely be the province of group efforts such as those being developed in the IBP. Blair *et al.* (1968) stated, ". . . ecologists will have to learn to curb some of their individuality, learn to work in large teams harmoniously and effectively and develop ways of sharing data. What is needed is nothing less than a new psychology or a new sociology for ecologists." As is usual in such cases, the individual focus will be on the manager. One can only hope, to return to my earlier Manhattan Project analogy, that large-scale ecosystem ecology will have its Oppenheimer. A number of ecologists have emphasized the importance given the ecosystem as the "new ecology" (E. P. Odum, 1964) or even previewed the ecology of the future (Watt, 1966).

The confrontation with the full complexity of ecological systems, forced upon ecology by the urgent demand for solutions to pressing problems, is a landmark of recent ecology. Ecologists have often talked about the complexity of the ecosystem but have seldom, until recently, done anything about it. The major difference between the old and the "new ecology" is not the ecosystem concept or the recognition of its complexity and wholeness but the accumulation of techniques, instruments and wherewithal for analysis of ecosystems, and the pressure of environmental concerns forcing ecology to do something—*now*. A major thrust of current ecology is to develop techniques for dealing with the inherent complexity of the ecosystem with sufficient precision to allow prediction of the consequences of specific actions. A number of ecosystem attributes are extensions of traditional concerns of plant ecology.

Productivity—Production of plant material, or yield, is a traditional concern of the forester, range manager, and agriculturist and has been extensively studied by them, but it was not until recently that it became a primary interest of the plant ecologist. The terms production or productivity were not indexed in *Ecology* prior to 1949, and the first citation is for plankton, in 1952. *Ecological Monographs* had one citation of grassland production as early as 1936, but it stood alone. The standard plant-ecology textbooks of the 1950's, did not index the words. Productivity studies, particularly in phytoplankton, had, however, been going on for some time before and following the work of Lindeman (1942) who, in one inspired paper, outlined the essentials of trophic ecology. The threshold of production citations in the literature is about 1963. The "in-word" was *dynamic*, which was transformed from its older use in Clementsian-dominated plant ecology, where it meant successional changes, to mean the function of the ecosystem or the processes operating in it.

Early plant ecologists recorded crude estimates of the resident living matter (biomass or standing crop) on an area. Plant ecologists concerned with the functional or trophic approach now attempt to measure the rate of energy inflow into the vegetation (gross primary productivity) as the first and most important step of the operation of the living world. The plant uses energy in maintaining itself (respiration), the remainder is stored in its tissues (biomass) as growth (net primary productivity), and an enormous literature has developed in the last two decades concerning plant biomass and productivity. Much of this has been concerned with the development of techniques for measuring gross and net primary productivity (Reichle, 1970; Young, 1968). One of the older and standard techniques is the harvest method, which involves collecting the standing crop on small, replicated plots at different times during a season and inferring rates of production from the changes. Corrections must be made for losses to herbivores, mortality, disappearance, and biomass carried over from previous years. An elaboration of this technique for more complex forests has been developed, which depends on logarithmic regressions calculated from measured dimensions such as diameter-breast-height and twig size from plants of all ages and sizes (Whittaker & Woodwell, 1968).

Other techniques for measuring primary productivity depend on direct measures of CO_2 exchange in chambers enclosing portions of the community or on indirect estimates of CO_2 or O_2 exchange. This is readily done for small plants in enclosures, and one effort applied it to a section of tropical forest (H. T. Odum & Pigeon, 1970). Gas-exchange techniques have been applied to whole open ecosystems and community productivity estimates made (Woodwell & Botkin, 1970), although these techniques are not yet effective replacements for the harvest methods.

Harvest or standing crop measurements have been used in aquatic systems as in terrestrial ecology, but oxygen and carbon dioxide measurements are more widely used in aquatic habitats (Goldman, 1966). Much current work is directed at developing better measures of primary productivity, and Goldman commented that a disproportionate amount of effort is spent on finding out just what is being measured. Productivity in aquatic systems has been extensively studied (Goldman, 1966; Kozlovsky, 1968; Likens, 1972; Riley, 1972; Wetzel, 1965). The traditional emphasis in aquatic studies has been on phytoplankton productivity, but recently the role of macrophytes has been considered (Wetzel, 1965). In Wetzel's view, macrophytes dominate the productivity of most lakes and, in many ways, regulate the production of the open water. Productivity is one of the classical criteria for classifying lakes as oligotrophic or eutrophic (Hutchinson, 1969; Likens, 1972).

Given effective measurement of productivity, or even before, ecologists became interested in relating primary productivity to other aspects of ecosystem function. The relation of gross primary productivity to incident solar energy is generally low, less than 2%, and the efficiency of net primary productivity is generally less than 1%. The efficiency of primary production and its comparison to efficiencies of other trophic elements of an ecosystem is reviewed, for aquatic systems, by Kozlovsky (1968).

It is commonly held that gross primary productivity (P) exceeds the rate of total community respiration (R) in an early successional or pioneer community so that the P/R ratio exceeds one. As long as this is true, biomass accumulates in the system (E. P. Odum, 1968, 1969). The P/R ratio presumably decreases to one in a mature or climax system so that the standing crop (biomass) will increase to a maximum and stabilize. The ratio of gross primary productivity to total community respiration is thus said to be an expression of successional status and should be related to numerous developmental trends in succession; *i.e.* as the P/R ratio approaches one, total biomass should increase, species diversity should increase, species should be more specialized (narrower niches), mineral cycling should slow and more of the nutrients be incorporated in the biomass, and a larger fraction of the available energy should be directed toward maintenance of the system.

Although the precision of the measurements may still leave something to be desired, primary productivity measures have been made in many habitats around the world and generalizations based on these now appear in the ecological literature and in ecological theory. Recent compilations (Rodin & Bazilevich, 1965) have presented comparable data for many different areas of the world, and comparisons of productivity are now widely available. Gross primary productivity varies greatly, as expected, ranging from 120 $g/m^2/yr$ in desert to 6700 $g/m^2/yr$ in tropical forest. Grassland productivity (500 $g/m^2/yr$), in general, is lower than forest productivity (4300 $g/m^2/yr$), and marine habitats range in productivity from 200 $g/m^2/yr$ in open ocean to 3300 $g/m^2/yr$ in estuaries (Whittaker, 1970). Lieth (1972) estimated the total, annual, net primary production of the world as 155.2×10^9 t dry matter, approximately two-thirds produced on land and one-third in the oceans.

Recent developments concerning differences in photosynthetic capacity of plants may substantially modify present estimates of primary productivity (Black, 1971). Two major groups of plants have been identified differing in morphological, physiological, biochemical and ecological ways which manifest a two- to three-fold difference in their capacity to fix CO_2. Plants with high-photosynthetic capacity are distinguished morphologically by a layer of photosynthetic, chloroplast-containing cells in the vascular bundle sheath and different structural features of chloroplasts and mitochondria. Physiologically they have a high-photosynthetic temperature optimum (30–40°C *vs.* 10–25°C), high light optimum (10,000–12,000 ft-c *vs.* 1000–4000 ft-c), low CO_2 compensation point (0–10 ppm *vs.* 30–70 ppm), are not inhibited by increases in O_2 concentration alone and do not exhibit photorespiration. This group is linked with earlier ecological studies of efficiency of water use in that high photosynthetic capacity plants have low water requirements.

The ecological implications of these findings are not clearly developed, but it is suggested that high photosynthetic capacity plants are effective competitors (Black, 1971) and that they are particularly adapted to grow in the severe environments of arid or mountain regions. A number of species of particular interest to ecologists have been identified as high photosynthetic capacity plants, *e.g. Andropogon scoparius, Spartina* spp.; numerous crop plants such as maize, sugar cane, sorghum; and members of several weedy genera *Setaria, Digitaria,* and *Amaranthus.* However, other notorious weeds such as *Agropyron repens, Ambrosia artemisiifolia, A. trifida,* and *Daucus carota* are low photosynthetic capacity plants. A second aspect of plant physiology having a significant impact on ecology is the increased recognition of photorespiration (Jackson & Volk, 1970). The fact that respiratory rates in some species are increased substantially by light must be taken into account in productivity studies where respiration is often assumed to be constant or is equated with dark respiration, particularly in aquatic plant work. Many of the earlier measurements of respiration inferred from dark respiration will have to be reassessed.

Nutrient cycling—Studies of plant nutrients and nutrient cycling have increased concomitantly with studies of primary productivity. The importance of nutrients as a factor in plant growth was asserted in the classical work of Justus Liebig, is explicit in traditional plant ecology, and implicit in many considerations of plant competition and adaptation (Rorison, 1969). A dramatic development of the past decade is the quantitative study of the distribution of nutrients in the living and nonliving portions of ecosystems (Rodin & Bazilevich, 1967) and their movement or cycling in both terrestrial and aquatic systems and, to some degree, between them—the "Odyssey of the atom" in Aldo Leopold's apt phrase. Recognition of the vital importance of the process of biogeochemical cycles to human welfare and concern about losses of critical nutrients, such as phosphorus, has stimulated interest in the study of nutrient cycles in ecosystems and losses from them.

Detailed studies of nutrient cycling in small forested watersheds, as in the extended series of studies on the Hubbard Brook (Bormann & Likens, 1969) provided new insight into the functioning of the ecosystem and the basis for more effective management. They demonstrated the effectiveness of the forest in holding and cycling nutrients and provided detailed budgets for several nutrient ions. Clear cutting and prevention of regrowth, for example, increased waterflow, produced marked changes in the nitrogen cycle, and greatly increased net loss of nutrient ions from the ecosystem (Ca ×9, Mg ×8, K ×20). Hutchinson (1969) commented that a lake must be considered as a part of its drainage basin, and Likens and Bormann also noted the potential effect of deforestation on a lake.

The importance of nutrient cycling in an arctic ecosystem was demonstrated by A. M. Schultz (1969), who showed that cyclic population abundance of lemmings is related to the nutritional quality of the forage as nutrients, particularly P and Ca, become bound in undecomposed organic matter. Nutrients in tropical forest are largely bound up in the vegetation, and Went and Stark (1968) have asserted the importance of mycorrhizal fungi in capturing nutrients as they are released by decomposers in the soil and retaining them in the living biomass. An intriguing phenomenon commonly noted is the leaching of nutrients from the vegetation, a seemingly profligate waste of energy even though the nutrients are retained within the ecosystem (Tukey, 1970). The role of nutrient cycling in ecosystem function has recently been reviewed by Pomeroy (1970) and the importance of soils in the process by Witkamp (1971). Witkamp and others have emphasized the importance of detritus in the nutrient flow of both terrestrial and aquatic systems.

Energetics—Some years ago Paul Sears casually pointed out the relevance of the laws of thermodynamics to ecology. Since that time the subject of ecosystem energetics has burgeoned. Gates (1968) commented, "Ecology . . . must be understood from the standpoint of energy flow, organism temperature, diffusion theory, chemical rate processes and modern molecular biology." According to E. P. Odum (1968), ecoenergetics is the core of ecosystem analysis. The energy limits of primary productivity and its eventual disposition to other elements of the ecosystem are the concerns of ecological energetics the principal rule being that energy is not recycled. In some systems, energy is fixed in place by the existing vegetation (autochthonous); in streams, caves, and deep waters a large fraction of the available energy derives from external (allochthonous) sources of organic material.

David Gates, a second generation ecologist (his father was F. C. Gates), but himself trained as a physicist, urges the application of physical, micrometeorological, and mathematical tools to plant ecology to produce detailed energy budgets (Gates, 1968). This includes the incident radiant energy absorbed plus energy changes due to conduction, convection, evaporation, and that stored or respired by the organism or stand. Gates asserted that, given adequate data, the analytic quantitative methodology is at hand so that, ". . . one can synthesize the entire vegetation structure leaf by leaf, foliage unit by foliage unit, plant by plant and finally for an entire stand." Gates' approaches to plant ecology have not been widely adopted, and the prospect of their being implemented in the near future seems unlikely, at least until the revolution in mathematical ecology foreseen by a number of ecologists has occurred.

The more familiar "center" of energetic ecology is concerned largely with the assimilated energy at any trophic level and that lost by respiration (the metabolic component of Gates) or the transfer of energy between trophic levels. A notable proponent is H. T. Odum (1971), whose early studies of trophic organization of aquatic systems and more recent studies of tropical rain forest systems rely heavily on models of electrical circuitry and the use of the analogue computer. H. T. Odum is, perhaps, the major representative of the engineering approach to ecology and, like a number of "systems ecologists" with a strongly mathematical bent (K. E. F. Watt, C. S. Holling), he has gone on to trans-ecology becoming involved in sociological, economic, and even religious systems (H. T. Odum, 1971). Many other plant and animal ecologists have concerned themselves with energy, its measurement in ecological systems, and its implications for ecological theory (Watt, 1968; Jordan, 1971).

The common denominator of energetics studies is the calorie. Caloric values are now available for many different biological materials, most of which are not of interest to the ordinary weight watcher. One problem is the applicability of the calorie to the description of the interactions among organisms. Are all calories equal? It is familiar in human nutrition, and among alcoholics, that high calorie intake may be accompanied by deficiencies of protein, mineral nutrients or vitamins. Plant materials certainly vary in palatability and digestibility with some high calorie items not among the most palatable or digestible. Paine (1971) has reviewed the techniques of ecological calorimetry and questions the faith in the usefulness of the calorie implicit in most energetic studies, especially of herbivores, *i.e.* the calorie is a physically precise measurement but not so ecologically. Goldman (1966), in a consideration of aquatic primary productivity and the utility of energy conversion measures, said, "Not only do the primary producers themselves have rather different abilities to utilize the available light energy, but the consumers of this trophic level are not bomb calorimeters and have very different abilities to utilize the calories that they consume."

Modeling and simulation—The rise to the level of consciousness of ecologists of models and modeling and the importance and utility of models is certainly one of the most fascinating phenomena of the last decade. A model, in its broadest terms, is a simplified representation of something, commonly in some form of abstract symbolism. Its aim is to facilitate understanding, and when the model becomes too complex and the interpretive process too unwieldy the model loses much of its utility. To paraphrase what someone once said of language, a model is a symbolic representation of our thoughts or a cloak for their absence. A model does not necessarily aim to represent the whole of "reality." It is always, for ecosystems, an imperfect representation of it (Goodall, 1972). Models come in all shapes, sizes, and degrees of sophistication. A new category of specialist, the modeler, has been introduced onto the ecological scene in the IBP. To them a model is a representation of ideas about the ecosystem, or some part of it in mathematical form, usually in systems of differential equations. Model making in ecology has been transformed from an individual, rather offhand activity to a group activity, weighted by mathematically trained persons, as model complexity increased.

Forest and Greenstein (1966) and Nooney (1965) give general discussions of models for the biologist. Recent, detailed bibliographies of models in ecology are those of Kadlec (1971) and O'Neill, Hett and Sollins (1970). Mathematical models in ecology are considered in Jeffers (1972) and Goodall (1972). I found Goodall's discussion particularly helpful.

A mathematical model has been described as a calculating engine which produces a result for a given input. Simulation is essentially a trial of a model, usually on a computer, to ascertain the consequences of the model under a given set of conditions (inputs). It enables the ecologist to run numerous trials of the model with different hypothetical inputs and with different variables to locate the sensitivities of the system. Simulation models are considered by Goodall (1970*b*) and Patten (1971).

Models are not new to ecology, and they demonstrate a remarkable persistence once established. Raunkaier proposed one of the first quantitative models in plant ecology (of frequency distribution of plant life-form) about 1918. If this model produced a "J"-shaped frequency curve, it presumably defined a homogeneous community. From 1920 to 1960, the inadequacies of the Raunkaier model were discussed in the literature, but it continued as a feature of the standard textbooks and appeared in research papers (McIntosh, 1962). Although Goodall (1970*a*) sheds new light on the Raunkaier model, it is not generally useful for determining homogeneity.

The premier model of ecology is the familiar Volterra, Lotka, Gause equation which has been used for forty years as a basis for theoretical population ecology and more recently as a basis for community ecology. MacArthur (1972) commented that the simple results of Gause's experiments misled ecologists for forty years and that much effort has been spent trying to disprove the obsolete competitive exclusion principle. MacArthur called for a new perspective on the degree of heterogeneity required to sustain two or more species rather than showing that only one can exist in a homogeneous environment.

Another instructive instance is MacArthur's own "broken-stick" model which was based upon the assumption of random distribution of resources among species. It was widely tested on animal, and some plant, communities, the inference being that a fit to MacArthur's model suggested a homogeneous community. After extensive evaluation, the model was found wanting and even its author described it "as an obsolete approach to community ecology which should be allowed to die a natural death." This was not so easy, and the model continued to be used until Hairston (1969) felt obliged to drive a holly stake through its "heart" in an effort to keep it in its grave. Hairston noted ". . . that no biological significance can be attributed to the fact that a collection does or does not show a fit to the broken-stick model, and its usefulness in any ecological context is challenged." References to it are still encountered; and, though broken even when new, it displays remarkable resilience. In the era of the "new ecology" in which models are created freely, often at considerable cost, there ought to be a new willingness on the part of ecologists to both accept models, look at them in terms of their empirical or heuristic utility, and then resolutely discard those lacking either virtue.

Systems analysis—The extreme complexity of ecological systems has often daunted ecologists. It is the thesis of the "new ecology" that the time has come for a significant advance in the understanding of ecosystems by means of systems analysis. According to Patten (1971), ecology is ". . . in transition from a 'soft' science, synecology, to a 'hard' science, systems ecology . . ."; he noted that his book is a creation of young people at a time when ". . . youth in America is experimenting with, if not revising and reorganizing, the ethical and moral basis of contemporary civilized life." E. P. Odum (1971) in the third edition of his textbook *Fundamentals of Ecology* described systems ecology as ". . . the wave of the future . . ." and noted several pioneers (G. Van Dyne, J. Olson, B. Patten, K. Watt, C. Holling, and H. T. Odum) who are ". . . revolutionizing the field of ecology and providing a vital link with engineering where systems analyses procedures have been in use for some time." The methods of systems analysis were developed by engineers to apply to man-designed and -operated systems, and their application to biological ecosystems which have a "mind" of their own may, as Reichle and Auerbach (1972) noted, call for new developments in systems analysis—feedback in systems parlance. It is no help to ecologists living through the "revolutionizing" of the field of ecology to find that systems theory, the stimulus for the revolution, ". . . amounts to a profound revolution in science—a revolution which will transform human thought as deeply as did the earlier ones of Galileo and Newton" (Rosen, 1972).

Perhaps the first linking of ecology with systems theory was Margalef's paper in *The Yearbook of General Systems* for 1958. It was not, however, until sometime in the mid-1960's that systems analysis, as a more-or-less explicit discipline, became a force in ecological studies. The first citation of systems analysis in standard ecological journals is, apparently, Patten and Witkamp (1967); and, in 1970, Dale described what systems analysis is, or should be, for ecology. It is part of the revolutionary nature of systems analysis in ecology that it first appeared largely outside of the conventional ecological literature in unusual, if not underground, publications. An assiduous reader of the familiar ecological journals or even a staunch pursuer of *Biological Abstracts* might, through 1970, be quite unaware of the impact of systems analysis on recent ecology. Systems analysis, as applied to ecology, was found primarily in *Memo Reports of the IBP Biomes* and in four recent books (Watt, 1966, 1968; Van Dyne, 1969*a*; Patten, 1971) which developed and advocated the ecosystem concept and systems analysis in ecology. Three of these books are collections of articles. Watt's (1966) contains no botanical material, and, as Watt (1970) notes, Van Dyne (1969*a*) has only one of ten articles which deals with animals. Although the essence of systems analysis is mathematics, Watt (1970) described Van Dyne's book as "one of the most totally nonmathematical books on modern science" he had ever seen. Watt asserted that the difference in approach between his and Van Dyne's book is between those who ". . . insist that to understand the natural world we must have a great deal of detailed information about many different parts of that world . . ." and those who ". . . believe that a system can be understood in terms of a small number of general principles."

Rosen (1972) stated that "systems theory is in an exceedingly exciting dynamical phase of growth," which could as well be said of ecology. If ecologists can withstand all the dual excitement, the combination may be beneficial, although that remains to be seen. Two clear gains of systems analysis are that it forces a clear statement of the parts and relations of the ecosystem and it requires an ordered approach to the complexities of ecosystems. It is not clear, however, that systems analysis will bring the ecological millennium that has been suggested, and some ecologists have reservations. Loucks (1972) provided an effective demonstration of the utility of a limited systems model, of movement of DDT in ecosystems, in an adversary proceeding.

The ecosystem concept and systems ecology obviously incorporate more than traditional plant ecology, but it is impossible to consider recent developments in plant ecology without reference to the whole of ecology—the "new ecology." In fact, one of the obvious implications of emphasis on ecosystem ecology is a breakdown in the discreteness of plant and animal ecology. This has been evidenced for some time in the trend toward general textbooks and courses in ecology in the last twenty years. That ecosystem ecology may have substantial effect on the education of ecologists is evidenced in the frequent proposals for restructuring the training of ecologists (Van Dyne, 1969*b*; Watt, 1966).

Plant-animal interactions—A long standing tradition of the Ecological Society of America was that its presidency alternated between plant and animal ecologists. At the 1972 meeting of the AIBS, at which this paper was presented, it was announced that this tradition will lapse.

A significant development of recent years was the rise in interest of ecologists in the plant-animal interface which further blurs the traditional distinction between plant and animal ecologist. Harper (1967, 1969) commented on the difficulty of finding biologists able or willing to deal with the plant-animal interface but noted the importance to ecology of the questions which must be examined there. The flurry of controversy inspired by the Hairston, Smith and Slobodkin (1960) exercise in deductive ecology focused attention on population control in communities; and their "the world is green" thesis argued, that vegetation was rarely severely depleted by herbivores and, therefore, was subject to control by limited resources. Most of the subsequent controversy revolved around the inferences concerning animals, but Harper (1969) commented that the presence of abundant vegetation does not demonstrate that vegetation is not controlled by herbivores or that herbivores are not controlled by predators. Much more experimentation is needed to provide definitive evidence of the reciprocal roles of plant and herbivore in population control, community structure and function, and the comparative importance of predation and competition. Janzen (1970) placed major importance on the role of seed and seedling predators in controlling plant populations in tropical rain forest. He argued that distance and density related predation by species-specific insects on seeds and seedlings of trees is the reason for the high diversity of tree species in tropical rain forest and for a tendency of rain forest trees to be regularly distributed. Harper (1969) stated that herbivory may enhance plant diversity if moderate but, like other stresses, decrease it if extreme. The role of an insect in controlling the population of *Hypericum perforatum* and restricting it to shaded habitats, when its ecological optimum is in sunlit areas, is a dramatic example of the plant/animal interface and its implications for plant ecologists (Harper, 1969).

Chemical interactions between plant and animal have also excited much interest (Whittaker & Feeney, 1971). Studies of food preference, palatability, and nutritional value are increasing and are increasingly needed, in the context of ecosystem analysis. The evolution, and functioning in an ecosystem, of generalist or specialist feeders or plant users are aspects of interest to plant and animal ecologists and hybrids between them. Chemical attributes of plants from catnip to marijuana and their impact on organisms from cat to man is a subject of great current interest (Dethier, 1970).

The entire subject of plant-animal interactions has important connections with theories of population control, hence community organization (*e.g.* competition or predation), and several previously discrete sections of ecology are coming together on this ground.

AUTECOLOGY AND PHYSIOLOGICAL ECOLOGY

One of the notable developments of this period is the increased recognition of the complexity of environmental interaction with plants (Billings, 1957) and the increased sophistication of techniques for measurement and analysis of environmental variables (Bainbridge *et al.*, 1965; Kozlowski, 1968; Wadsworth, 1968). John Wolfe (1949) published a landmark in environmental analysis of a small area demonstrating the great variation in microenvironment. Platt and Griffiths (1964) commented on the postwar revolution in methods for measuring environment. The most recent development is remote sensing, particularly from high altitudes (Johnson, 1969), but its utility to ecological studies is not clearly demonstrated. The revolution in instrumentation and automatic recording of data is not an unmixed blessing for it threatens to flood the ecologist with data in quantities with which he is not always able to cope. Even with modern methods of data analysis and computing facilities, judicious judgment may be needed as Gates (1968) noted.

The possibility of growing plants in closely controlled environments was hailed as a major development in achieving an understanding of the way physical environmental factors influence plant growth, and a great deal of work has been done on assessing the effects of individual variables or combinations of these on individual plants or plant populations (Evans, 1963). The recognition of the importance of changing conditions and of the effects of different cycles of environmental factors on plant responses was particularly significant. Most studies in controlled environments have been done with single plants or populations of single species or strains, and much of the work in this area has been done by agricultural physiologists (Rorison, 1969). A major problem faced by plant ecologists is the extrapolation of results from controlled experiment under controlled conditions using single plants, single species populations, or even simple mixtures of species to field conditions with variable and heterogeneous environment and multi-species mixtures (Evans, 1963). Ellenberg's (1956) experiment on the effect of water table on growth of pasture grasses is an excellent example of this. He showed that several grass species growing alone had the same "physiological optimum," but when grown in multispecies mixtures their response to the environmental variable changed radically, and they had separate and distinct optima. This type of observation raises many questions about detailed physiological experimentation in controlled conditions and its utility to ecology. Major (1958) commented, ". . . as a matter of fact, no physiological data known to the writer have been able to explain why a particular plant grows naturally where it does . . ."

Extensive studies of the arctic and alpine greatly expanded our understanding of the adaptation of plants to rigorous environments. After World War II, there was a burst of effort to describe the vegetation of the arctic and its relation to permafrost. The Naval Arctic Research Laboratory was a center of this work, and the Project Chariot studies also contributed to understanding of arctic ecosystems (Wilimovsky & Wolfe, 1966). During the 1950's and 1960's, studies of arctic and alpine plants by Billings and his students examined the problems of physiological adaptation to low temperature environments (Billings & Mooney, 1968). The subject of cold resistance and acclimation in other than arctic plants has also developed new viewpoints. Weiser (1970) considered the adaptations of woody plants to cold resistance and cold injury and suggested that there are multiple pathways to acclimation to low temperatures. Phenology, requiring long and detailed recording of biological events, was represented at the beginning of the period by Leopold and Jones (1947). Limited progress was made in phenology of native species until about 1965 when the IBP initiated a phenology program which aims at establishment of a large network to record phenological data on key species of plants and animals (Lieth, 1970). Lieth emphasized the importance of phenology to ecosystem analysis and productivity studies. New techniques of mapping and modeling are being developed along with highly organized data collection.

EVOLUTION, GENECOLOGY, AND POPULATION ECOLOGY

Harper (1967) said, "The theory of evolution by natural selection is an ecological theory . . . adopted and brought up by the science of genetics." Plants evolved in natural situations in a context of other organisms, and the mutual interests of geneticists, physiologists, ecologists, systematists, and evolutionists, and the reciprocal importance of ecological concepts to evolution, genetics, and systematics have been increasingly recognized since World War II. *The American Naturalist* has, in the view of its editors, ". . . been in the forefront of the attempt to make ecology genetical and evolutionary" (Lewontin & Baker, 1970). It is difficult to identify the contributions of ecologists in an area of overlapping disciplines. However, a large body of work has developed in recent years demonstrating genetic heterogeneity within taxonomic entities and its significance for ecology. The history of genecology was reviewed by Heslop-Harrison (1964), and the many areas of interaction of plant systematics and plant ecology by Kruckeberg (1969).

The problems of ecotypic variation in plants have been somewhat swept under the rug in community and ecosystem ecology probably because they complicated the analysis of an already complex situation. McMillan (1960) was a major contributor to understanding the role of ecotypes in community organization and contended that the genetic gradients within a species are the key to continuity of a vegetation type over a gradient of habitat variation. Bradshaw (1972) asserted that, "The range of distribution of a species is therefore very dependent on its capacity to evolve local distinct populations." He suggested that the ecological amplitude of a species (niche is the current in-word) has a strong genetical component. The unexpectedly rapid adaptation of plant populations is of particular interest in the joint context of genetics and ecology (Antonovics *et al.*, 1971). Does it follow that species with narrow ecological amplitude (niche breadth) are those with limited capacity for genetic variation? The concept of niche and its measurement is currently a hyperactive area of ecology, although relatively little has been done with plants (McNaughton & Wolfe, 1970).

The problems of coexistence—The work of John Harper and his students was a major contribution to plant ecology in the past twenty years (Harper, 1964, 1967, 1969). Harper and his associates have addressed themselves to questions of plant population dynamics, adopting quantitative and experimental approaches previously largely used by animal ecologists. They particularly studied reproductive strategy and population regulation of plants, especially as controlled by competition. Harper's view is that the analytic, experimental approach of attacking smaller components of a large problem will lead to an understanding of the synecological properties of plants. He asserted that "their combining properties" may be determined experimentally by growing the species in all combinations. This is similar to the concept of the matrix of competition coefficients currently in vogue among some animal ecologists.

The consequence of coexistence of species is the community or, in a broader sense, the ecosystem. A major thrust of recent ecology is the attempt to develop an adequate understanding of the processes which operate in and control an integrated community. Ordination studies have emphasized the plant community as a group of species in which the ecological amplitude, or niche breadth, of a species is largely influenced by the proximity and effect of competing species. Whittaker (1967) stated it succinctly, "Species evolve toward niche diversification by which direct competition within the community is avoided. They evolve also toward habitat diversification, toward occupation of scattered positions in environmental hyperspace so that plant species are in general not competing with one another in their population center." Competition was regarded as a major force in population control and community organization by traditional plant ecologists, but they did little experimental work on competition. Harper's studies of competition and coexistence have clarified the process of plant competition and its role in the plant community (Harper, 1964, 1967). His observations on alien- and self-thinning are particularly interesting in that they demonstrate a mechanism by which competing populations may coexist contrary to the tradition of the competitive exclusion principle. Harper (1967) and Hett and Loucks (1971) calculated survivorship of plants and found the relationship between time and the log number of survivors was linear.

Competition has also been assumed to have a major function in the evolution and succession of communities. The traditional view has been that communities evolved as organized entities (McIntosh, 1967, 1970; Ross, 1962), but the understanding of community evolution is even less clear than of their distribution, structure or function. Whittaker and Woodwell (1972) considered the evolution of natural communities. Loucks (1970) linked population processes and community production to succession and community evolution, and urged the pressing relevance of these seemingly abstruse ideas to modern man. Baker and Stebbins (1965) related evolution and adaptation of plants to succession.

Allelopathy—The study of chemical interactions between organisms is an extremely rapidly expanding field of ecology (Whittaker & Feeney, 1971). Allelopathy, the suppression of growth of higher plants by a chemical released from another higher plant, is closely linked with competition for common resources, and Harper prefers to use the term interference to include all cases of hardship created by one plant for another, including allelopathy.

That certain plants have toxic or inhibiting effects on other plants has been known since 1881. These substances may be leached from the tissues, volatilized from leaves, exuded from roots, or released or produced in the decomposition of any part of the plant. They may be autotoxic or inhibit other species. The main difficulty in studies of allelopathy is demonstrating that a species does, in fact, inhibit the growth of plants in nature and have a substantial influence on plant populations, their distribution, plant communities, and phenomena such as succession. Among the best demonstrations to date of the effects of allelopathy in plant communities are those of C. H. Muller and his students in chaparral (Moral & Muller, 1970; Muller, 1970). Muller and his group have shown the inhibition of germination of seeds and of seedling growth in hard chaparral and the effect of fire in releasing herb seeds from inhibition by the above ground parts of shrubs. Rice and his associates have demonstrated the inhibition of nitrogen-fixing and nitrifying bacteria by seed plants and allelopathy in grassland (Rice, 1971; Wilson & Rice, 1968).

The study of population responses, particularly in the field, and of the role of allelopathy in connection with other factors regulating populations (*e.g.* competition or predation) or its role in the ecosystem is barely begun.

THEORETICAL ECOLOGY

One of the most salient developments in ecology, essentially of the last decade, has been an increase of interest in, and calls for, a theoretical basis for ecology. Gates (1968) commented, "Ecology must have a strong theoretical basis before it can advance significantly . . . ." Lewontin (1970) commented on the major transformation of ecology from a qualitative, descriptive science to a quantitative and theoretical one. He attributed the change to a union of mathematics and evolution, and said that the theoretical framework for ecology (as for population genetics) was "*the concept of the vector field in n-dimensional space.*" He also cited the analogy of particle physics as a model for theoretical ecology.

By the nature of a theoretical approach it is impossible to segregate plant and animal ecology, and although some of the more prominent theoretical ecologists have concerned themselves largely with animal populations or communities, their ideas are usually generalized to plants. In any event, if ecology is going to become a theoretical science, it will have to encompass all organisms.

One of the recent approaches to an ecological theory borrowed from information theory. Margalef was, perhaps, the first to suggest the interpretation of ecological communities and processes, such as competition and succession, in terms of information theory. The information-theoretic (Shannon-Weaver) equation lent itself to ready quantitation of almost anything that came to hand and a rash of papers on diversity resulted. Plant ecologists had long been intrigued by species-area curves or species-individual curves, and it is these relationships which are the crux of the diversity problem. Preston (1962) explored numerical relations of species and individuals in a more mathematical way. Diversity has developed, since 1960, as one of the most intriguing attributes of communities, particularly of theoretical ecology. Margalef (1968) commented, ". . . the ecologist sees in any measure of diversity an expression of constructing feedback systems or any sort of links in a given assemblage of species." Diversity has been said to be related to niche number, breadth, packing and overlap, to rigorous or stable environments, to productivity, biomass, body size, and climax. In short it is regarded as a fundamental attribute of the community (Pielou, 1969; Whittaker, 1972). Perhaps the best overview of the vexing problem of diversity measurement is given by Auclair and Goff (1971) and of diversity generally by Whittaker (1972). Hill (1973) provides a clarification of the information theory index, showing it to be simply one of a continuum of index values relating number of species to abundance and asserting that it has no particular merit deriving from its links to information theory and statistical thermodynamics. The most widespread concept about diversity is that increased diversity leads to increased stability (E. P. Odum, 1972). This idea, which is taken as almost axiomatic by some ecologists, was strongly criticized by Hairston *et al.* (1968). It was also thoroughly, but not conclusively, aired in a recent symposium (Brookhaven National Laboratory, 1970). Not the least of the difficulties is agreeing on the meaning of stability. Loucks (1970) noted that long term stability reduces diversity.

Another significant front, or at least a popular front, is the theory of the niche. It stems substantially from the formalized statement of the ecological niche by G. E. Hutchinson (1957). The concept of the niche as an N-dimensional hyperspace (said by Lewontin to be the basis of ecological theory) has been seized upon, particularly by animal ecologists; but a few ecologists working with plants have ventured into this field (McNaughton & Wolfe 1970). It appears that there is much left to be said about niche, and plant and animal ecologists are commonly writing about the same concept without paying much attention to each other. Perhaps the best thing yet written about niche is the following previously unpublished limerick which I quote by the gracious permission of authors Grant Cottam and David Parkhurst.

"Consider the concept of niche.
If I knew what it meant I'd be rich.
Its dimensions are N
And a knowledge of Zen
Is essential to fathom the bitch."

The major concept introduced and formalized by traditional ecology is that of succession. If traditional ecology had a theory it was succession, and Frederick Clements was, in effect, its Lamarck or its Darwin, depending on one's view. Perhaps the most difficult problems of theoretical ecology were the attempt to incorporate succession into the ecosystem concept (E. P. Odum, 1969) and the prediction of trends to be expected in the successional development of ecosystems. The most examined prediction, diversity and stability as mentioned above, is not always substantiated (Reiners *et al.*, 1970). It is clear that much remains to be done in establishing a bridge between traditional succession and climax concepts and recent views of ecosystem development and ecological process. In fact, the literature on succession is so diffuse and often contradictory that it is hard to make effective comparisons (Horn, 1971; Langford & Buell, 1969; Loucks, 1970; Margalef, 1968; Olson, 1958; E. P. Odum, 1969; Whittaker, 1953), and much rethinking and clarification of successional concepts is in order.

RADIATION ECOLOGY

The period we are considering is essentially the "atomic age," beginning with the first atomic explosions in 1945. Studies using radioactive tracers in natural environments began in the late 1940's, perhaps the earliest being those of Hutchinson and Bowen (1947). The International Atomic Energy Commission was established in the early 1950's, and the First International Conference on the Peaceful Uses of Atomic Energy, in 1955, included a paper on the consideration of the total environment in power reactor waste disposal, a consideration still very much with us. From relatively modest beginnings, circa 1955, radioecology grew rapidly. The several symposia (Hungate, 1966; Nelson & Evans, 1969; V. Schultz & Klement, 1963) and other AEC publications (H. T. Odum & Pigeon, 1970; Wilimovsky & Wolfe, 1966) are impressive (and literally weighty) summaries of the progress of radioecology. Auerbach (1965) gave an excellent history and summary of the state of radionuclide studies and future prospects at that time.

Studies on the impact of radiation on particular ecological processes (*i.e.* growth, competition) forced studies of the basic processes and advanced the science of ecology. The desire to trace the spread of radioactive nuclides required an improved understanding of nutrient cycling in general, and the observed complexities and need for projections of consequences forced the examination of the whole ecosystem and the development of techniques for analyzing it. Thus, the use of radioactive tracers to demonstrate the links within a food web, studies of rates of turnover of radionuclides within trophic levels, and the use of radioactive tracers to clarify and to quantify cycles in ecosystems are important contributions of radioecology.

In the last decade radiation impact studies on whole communities or ecosystems have been particularly interesting (Smith, 1970; Woodwell & Whittaker, 1968*b*). A temperate forest community subjected to chronic high levels of radiation showed several kinds of changes: (1) Reduction in structure and growth form. (2) Replacement of dominants along the radiation gradient. (3) Changes, usually decreases, in production. (4) Decrease in diversity. Among vascular plants the sedges were most resistant, old field herbs intermediate, and woody forest plants least resistant to radiation stress. Woodwell suggested that radiation studies of whole communities offer general insights into the mechanisms of community structure and their evolution. Sensitivity to radiation increased, according to Woodwell, in the more complex system due to changes in community plasticity and structure and intrinsic characteristics of the species. Smith (1970), in a similar study of gamma-irradiation of a tropical rain forest, said his result does not support Woodwell's view, although he noted that primary forest species were more sensitive to radiation than secondary (pioneer) forest species. According to Smith, the more complex tropical forest was not, as expected, more vulnerable to disturbance than simpler systems. Radiation has been an important new tool for ecologists, but the crux of the problems appears to be in the interpretation of ecological processes and organization which have been certainly elucidated by effective use of radiation techniques.

PALEOECOLOGY

Plant ecology is, to a large degree, a historical science. It is difficult to envision an effective consideration of the distribution and characteristics of plants and vegetation which does not take into account the historical record as reconstructed in a variety of ways. Perhaps, the major development in paleoecology of the post-World War II era was radiocarbon dating. This technique, based on the known rate of decay of C_{14}, made possible much more precise (*e.g.* error estimates of a few tens or hundreds of years in spans of 1,000–20,000 years) dating of vegetational and climatic events and revealed how rapidly gross migrations of vegetation have occurred. The time scale in which it was thought vegetational and climatic changes occur was sharply contracted by findings based on radiocarbon dates, and the whole pace of vegetational and climatic change was seen in a new light. The traditional concept of a regional climax under a stable climate is much less plausible when viewed against the rapidly changing scene revealed by recent work in paleoecology.

The trends and pace of vegetational and climatic change have been discovered largely by palynology, the study of fossil pollen. The vegetation of an area was typically inferred from the relative frequency of the pollen grains of different species found in peat and lake sediments, but treating the pollen rain as percentages had severe limitations. A major achievement was the modification of the technique by M. B. Davis (1969) to estimate the annual pollen influx into the sediment (grains/cm^2/yr). Techniques to extract pollens from soils, modern and fossil, have been increasingly used in studies of prehistoric vegetation and associated animal and human populations (Iversen, 1969). The extension of palynology by this technique into quite recent times and development of more precise time scales have led to extensive cooperation between archeologists and palynologists (Berglund, 1968). Archeological studies using macroscopic plant materials are also current and adding to our understanding of early man and his impact on the landscape.

Much of the pioneer work on palynology was done in North Europe, particularly Scandinavia, and the glaciated North Temperate and subarctic zones are most studied by this technique, probably because of the extensive peat bogs in which pollens were readily preserved and greater familiarity with the pollens of these areas. Recently, palynology has been extended to non-glaciated (Martin,

1963) and tropical regions (Ogle, 1970), and the vegetation of these areas has been shown to have changed strikingly in the last 10,000 years, which raised questions about widespread theories of stability in non-glaciated regions (Vuilleumier, 1971). The traditional ecological assumptions concerning the grasslands of the Great Plains and their relation to climate has been questioned by Wells (1970) on palynological and macrofossil evidence of forest cover in the plains region.

Another approach to vegetational history is tree-ring chronology, which has become more precise in recent years (Fritts, 1966). Perhaps, the most dramatic development was the discovery of the unprecedented age of bristlecone pine (*Pinus aristata*), a tree associated with severe timberline environments. Trees 3,000–4,000 years old were discovered by E. Shulman in 1953 and 1954, and Ferguson (1968) reported one of 7,100 years.

TROPICAL ECOLOGY

The pioneer book on the tropical rain forest by P. W. Richards (1952) was certainly a landmark in postwar ecology. Richards noted that many botanists, and certainly ecologists, regarded the rain forest as unusual and exotic, when it is in fact a protoype and should be more productive of ecological principles than temperate forest (Richards, 1963). An outstanding characteristic of tropical rain forest is its richness in species, and it is this which has provided grounds for so much intriguing speculation. One of the early concerns was the appropriateness of the time-honored, if not hoary, association problem in the rain forest (Richards, 1963; Poore, 1967). This question is as unsettled as it is in the temperate zone, and Richards, at least, believes that the bewildering complexity of the rain forest is effectively considered as a continuum much as the temperate forests in which the concept was developed. J. P. Schultz (1960) used quantitative methods in Suriname forests and concluded, "The hylaean forests probably form the best illustration of the principles of species individuality and community continuity," which ideas are familiar as Gleason's "individualistic concept of the plant association." Greig-Smith (1971) and Webb *et al.* (1970) considered more recent application of methods of numerical analysis to tropical rain forest.

The impetus for tropical ecology was furthered by the founding in 1960 of the journal *Tropical Ecology* and the establishment in the early 1960's of a tropical group in the British Ecological Society and the Organization for Tropical Studies in the United States, which has supported research and, particularly, an educational program in Costa Rica. A major effort, concentrated on one area of tropical forest in Puerto Rico (H. T. Odum & Pigeon, 1970). H. T. Odum, for example, studied the nutrient cycling of the rain forest, and Tukey (1970) studied the leaching of inorganic nutrients and metabolites from the leaves of forest trees, noting that both may be important facets of the nutrient cycle of tropical forest. Went and Stark (1968) have recently emphasized the role of mycorrhizae in the nutrient cycle of rain forest; and the function of nutrient leaching from the leaves, the role of evapotranspiration in nutrient flow, and the role of mycorrhizae are all part of an intriguing and as yet unresolved problem.

Many ecologists equate tropical ecology with rain forest. Much of recent theory on diversity or evolution in the tropics uses the term in this restricted sense. There is much more to be learned from the tropics; and studies of other vegetation types, while less in the theoretical ecologist's eye, also increased rapidly in the last two decades. General vegetation studies (Walter, 1971), studies of the American tropics by Beard (1955), of forest environments in tropical areas by Holdridge *et al.* (1971), seasonal vegetation of forest and adjacent savanna by Hopkins (1970), and of savanna by Bourliere and Hadley (1970) all suggest the rapid expansion of interest in tropical vegetation.

The rise of interest in tropical ecology is linked to the political emergence of many tropical nations and to their need for developing their resources. A major concern is expanding food production and developing agricultural techniques appropriate to tropical regions. The problems of laterite soils with low nutrient status and the tradition of shifting agriculture, which is widespread in the tropics, need to be reviewed in conjunction with the enormous problems of insect and other herbivores which are multiplied in the tropics. Janzen (1972) offered a rather pessimistic and critical assessment of the current state of tropical ecology, emphasizing the importance of applied ecology for the tropics. Janzen's (1970) own studies of the plant-animal interface in the tropics stressed the importance of the seed predator as a controlling factor in tropical forest, suggesting that this is different from temperate forest. This is a facet of the general difference of opinion among ecologists about the relative importance of competition and predation in the control of populations and community organization which needs careful assessment. A concern frequently voiced (Gómez-Pompa *et al.*, 1972) is that the tropical forest will be gone before ecological studies can be made, due to the rapid increase in population and despoilation of the forest for a rather dubious future in agriculture.

Plant Ecology and the Environmental Movement

Although ecology and genetics are essentially twins, genetics by the late forties was much more established in the academic world, its contributions to evolutionary and systematic biology were central, the value of genetics to crop and animal breeding was well established, and its potential for human well-being were becoming familiar to the general public as popular books and articles on genetics were widely available. Ecology, on the other hand, was little known outside academic circles, and its potential for human well-being was not understood, even by many of its students. In spite of a half-century of pioneer work, ecology was peripheral, if not disreputable, in most biology departments and was entirely absent in some. Only a few books by plant ecologists, such as Paul Sears' *Deserts on the March* (1935), called the attention of the general public to the real problems of the environment and gave an ecological perspective to these. The recent flood of semipopular, popular, and polemic books about the environment and ecology is a dramatic turn of events, although not an entirely unmixed blessing for ecology. In any event, ecology has come of age, although its turbulence suggests more a stage of adolescence.

The environmental movement threatens to change ecology from a science to an ideology, and some ecologists, at least, from scientists to gurus (Barash, 1973). A major difficulty in reviewing developments of the past decade is to decide who is an ecologist, as an already diffuse and eclectic discipline becomes infused with new ideas from other disciplines and is pulled in many directions by evangelists of all sorts. The sweet smell of success heard in the land is a great mixed metaphor to describe the current state of ecology. Ecology has always been closely aligned with the conservation movement, and the scientific basis of conservation was linked closely to ecology (Darling, 1964). Ecology has been frequently described as a "point-of-view." It is this aspect of ecology which has been transmuted into a populist movement, has dragged even some reluctant politicians into the environmental arena, and has, reciprocally, pushed some ecologists into the domain of public affairs, if not political office at this writing. Events of the past decade are so far reaching in their impact on ecology generally, and on plant ecology and what it may become (or what may become of it), that it would be improper to omit some consideration of these events. The essence of the environmental movement is that it has become clear to almost anyone with any perception of the world that man's fate is, intimately and ultimately, tied up with the natural and managed biological systems of the earth and that these are now in varying states of disrepair. The degree of pessimism varies, but optimists are very few and generally guarded. Only a very few see, with C. L. Sulzberger (1972), ". . . dreams of fertilizing the Sahara or warming up Antarctica with nuclear power, thus rendering habitable millions of new acres," or "a breakout from planet Earth . . . in fleets of immense spacecraft" and the seeding of ". . . distant planets and still more distant stars so that they become habitable for human beings. . . ." Ecologists in general concur with L. B. Slobodkin (1968) who stated, ". . . while ecology may, in fact must, continue to develop as an intellectual discipline, there must also be an increasing interaction between ecologists and public affairs in the broadest sense."

The rise of public interest in the environment has thrust ecology onto center stage and has had some striking consequences. It has raised the question of whether there is such a thing as a certifiable professional ecologist and whether ecologists have need of a specific set of ethics other than Aldo Leopold's "environment ethic." Southern (1970) noted that some have asserted that ecology is far too important to be left to ecologists, and he asked the question—Who else? Certainly ecology is not a closed system and never has been. It feeds on the insights and techniques of other natural and social sciences. In the present environmental crisis, it needs all the help it can get. Nevertheless in spite of the old canards that ecology is simply applied physiology, advanced natural history, or the newer definition of ecology as a mathematical subject or simply a flow of energy (ergo physics writ large), ecology has a unique tradition and contribution to make to human well-being. Its central concepts are the crux of the environmental revolution.

Plant ecologists have enlarged their horizons and entered into public affairs and environmental concerns transcending their botanical interests. Most plant ecologists are involved in matters which are logical extensions and even obligations of their ecological training. Ecologists certainly have no claim to knowing it all; in fact one of their problems is that they know so little as compared to the magnitude of the problems they are being called upon to face in conjunction with experts from many other scientific and nonscientific fields (Goodman *et al.*, 1965; Handler, 1970; National Science Board Report, 1971). The National Environmental Policy Act of 1969 (NEPA) requires filing and evaluation of environmental impact statements for proposed construction (*e.g.* power plants) and activities (*e.g.* spraying programs, stream diversions). The enforcement of this law by administrative action and by the courts requires that ecological expertise be used in preparing, evaluating, and, where necessary, litigating these statements. Plant ecologists, limnologists, physicists, engineers, and mathematicians are now working together in teams preparing these statements, and many more ecologists will be involved in the future. This is a completely new role for ecologists who, in the past, had little opportunity to weight actions affecting the environment before the fact and were confined to after-the-fact criticism. Real expertise and precise knowledge will be demanded not only by the trial of one's publication by his peers but in adversary proceedings where feelings will not be spared or ignorance (even if excusable) passed over (Loucks, 1972).

Ecological research has traditionally had a reciprocal relationship with applied facets of resource management. Plant ecology, particularly, drew on and contributed to agriculture, game management, forestry, and range management. The distinction between applied and basic research has become less discrete of late. Books of recent decades, such as S. M. Spurr's *Forest Ecology* (1964) and R. R. Humphrey's *Range Ecology* (1962), indicate these mutual interests. E. J. Dyksterhuis (1958) was a notable intermediary between range management and plant ecology. Dyksterhuis related ecological methods of gradient analysis to the quantification of range degeneration and showed that potential plant cover for various physical environments could be predicted. J. E. Weaver's professional career, spanning almost the whole of the existence of plant ecology, was capped by his *North American Prairie* (1954), which added to his enormously productive studies of grassland as a basis for management. No discussion of the past 25 years would be complete without mention of E. Lucy Braun's (1950) *Deciduous Forests of Eastern North America*, summarizing the work, including her own extensive studies, on that biome as a basis for both plant ecology and forestry. Even the much despised weed, largely a product of human affairs, has been demonstrated to be a remarkably useful and worthwhile subject of ecological research, as Harper's (1960) *The Biology of Weeds* shows.

Two recent additions to the ecological periodical literature, *Journal of Applied Ecology* and *Human Ecology*, suggest the applied and utilitarian emphasis of current ecology. Research Applied to National Needs (RANN) is granting some 4.5 million dollars in fiscal year 1973 to extend ecosystem analysis of large biomes to include socio-economic and political factors critical to planning and management of resources. This research is closely tied to the IBP program also supported by NSF and is directed toward translating that basic ecological program into management practice.

The Institute of Ecology (TIE) was founded in 1971 by ecologists and developed the ecologist's view of important problems of environmental quality in *Man in the Living Environment* (The Institute of Ecology, 1972). TIE is an international organization devoted to ecological research to meet human needs, to incorporation of ecological analyses in policy formation, and to education of the public on environmental issues. In effect, TIE is a group with the function of bringing together the necessary ecological and other skills and the urgent research problems associated with the now recognized crisis of environment and life-support systems.

Plant ecologists are called upon to provide professional expertise in areas of resource management including problems of urban waste disposal on agricultural or forest lands; impact of human recreational use on vegetation and soils; revegetation of strip-mined lands; erosion control of coastal areas and river bottoms; the role of fire and herbicides in vegetation management; the impact on, and movements of, pollutants through ecosystems; factors affecting primary productivity of diverse ecosystems; and innumerable other environmental concerns (Goodman *et al.*, 1965). Much can be done using the ecological knowledge already available, but applied ecology needs an expanded science of ecology which is dependent on bringing to fruition aspects of quantitative, theoretical, and ecosystem ecology which were initiated in the past two and one half decades.

BIBLIOGRAPHY

ANTONOVICS, J., A. D. BRADSHAW & R. G. TURNER. 1971. Heavy metal tolerance in plants. Advances Ecol. Res. 7: 1–85.

AUCLAIR, A. N. & F. G. GOFF. 1971. Diversity relations of upland forests in the western Great Lakes area. Amer. Naturalist 105: 499–528.

AUERBACH, S. I. 1965. Radionuclide cycling: Current uses and future needs. Health Phys. 11: 1355–1361.

AUSTIN, M. P. & I. NOY-MEIR. 1971. The problem of nonlinearity in ordination: experiments with two gradient models. Jour. Ecol. 59: 763–773.

BAINBRIDGE, R., G. C. EVANS & O. RACKHAM (editors). 1965. Light as an Ecological Factor. Blackwell Sci. Publ., Oxford. 452 pp.

BAKER, H. G. & G. L. STEBBINS. 1965. The Genetics of Colonizing Species. Academic Press, New York. 588 pp.

BEARD, J. S. 1955. The classification of tropical American vegetation types. Ecology 36: 89–101.

BARASH, D. P. 1973. The ecologist as Zen master. Amer. Midl. Naturalist 89: 214–217.

BERGLUND, B. 1968. Impact of man on the Scandinavian landscape during the late postglacial. Oikos: Suppl. 12. 103 pp.

BILLINGS, W. D. 1957. Physiological ecology. Annual Rev. Pl. Physiol. 9: 375–392.

——— & H. A. MOONEY. 1968. The ecology of arctic and alpine plants. Biol. Rev. 43: 481–529.

BLACK, C. C. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. Advances Ecol. Res. 7: 87–114.

BLAIR, W. F., S. I. AUERBACH, D. M. GATES, R. F. INGER & B. H. KETCHUM. 1968. The importance of ecology and the study of ecosystems. Hearing before the Committee on Interior and Insular Affairs, U.S. Senate, and the Committee on Science and Astronautics, U.S. House of Representatives, 19th Congress, 2nd Session. No. 8, pp. 154–158.

BORMANN, F. H. & G. E. LIKENS. 1969. The watershed ecosystem concept and studies of nutrient cycles. Pp. 49–93, *in* G. Van Dyne, "The Ecosystem Concept in Natural Resource Management." Academic Press, New York.

BOURLIERE, F. & M. HADLEY. 1970. The ecology of tropical savanna. Annual Rev. Ecol. Syst. 1: 125–152.

BRADSHAW, A. D. 1972. Some of the evolutionary consequences of being a plant. Pp. 25–47, *in* T. Dobzhansky, M. K. Hecht & W. C. Steere (editors), "Evolutionary Biology." Vol. 5. Appleton-Century-Crofts, New York.

BRAUN, E. L. 1950. Deciduous Forests of Eastern North America. Blakiston, Philadelphia. 596 pp.

BRAUN-BLANQUET, J. 1964. Pflanzensoziologie. Springer-Verlag, Wein. 865 pp.

BRAY, J. R. & J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.

BROOKHAVEN NATIONAL LABORATORY. 1970. Diversity and stability in ecological systems. Brookhaven Natl. Lab. Symposium No. 22.

BUSH, V. 1945. Science, the Endless Frontier. U.S. Govt. Printing Office. Washington, D.C. 184 pp.

CAIN, S. A. 1944. Foundations of Plant Geography. Harper and Brothers, New York. 556 pp.

COTTAM, G. & J. T. CURTIS. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology 30: 101–104.

CROVELLO, T. J. 1970. Analysis of character variation in ecology and systematics. Annual Rev. Ecol. Syst. 1: 55–98.

CURTIS, J. T. 1959. The vegetation of Wisconsin. An ordination of plant communities. Univ. of Wisconsin Press, Madison. 657 pp.

——— & R. P. MCINTOSH. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 479–496.

DALE, M. P. 1970. Systems analysis and ecology. Ecology 51: 2–16.

DANSEREAU, P. 1968. The continuum concept of vegetation: responses. Bot. Rev. 34: 253–332.

DARLING, F. F. 1964. Conservation and ecological theory. Jour. Ecol. 53 (Suppl.): 39–45.

DAUBENMIRE, R. 1966. Vegetation: identification of typal communities. Science 151: 291–298.

DAVIS, M. B. 1969. Palynology and environmental history during the Quaternary period. Amer. Sci. 57: 317–332.

DETHIER, V. C. 1970. Chemical interactions between plants and insects. Pp. 82–102, *in* E. Sondheimer & J. B. Simeone (editors), "Chemical Ecology." Academic Press, New York.

DYKSTERHUIS, E. J. 1958. Ecological principles in range evaluation. Bot. Rev. 24: 253–272.

EGERTON, F. N. 1969. Richard Bradley's understanding of biological productivity: A study of eighteenth century ecological ideas. Jour. Hist. Biol. 2: 391–409.

EGLER, F. E. 1951. A commentary on American plant ecology based on the textbooks of 1947–1949. Ecology 32: 673–695.

ELLENBERG, H. 1956. Einfuhring in die Phytologie. Bd. 4 Grundlagen der Vegetationgliederung, 1 Teil. Aufgaben und Methoden der Vegetationskunde. H. Walter, editor. Stuttgart. 136 pp.

EVANS, L. T. 1963. Environmental Control of Plant Growth. Academic Press, New York. 449 pp.

FERGUSON, C. W. 1968. Bristlecone pine: Science and aesthetics. Science 159: 839–846.

FOREST, H. S. & H. GREENSTEIN. 1966. Biologists as philosophers. BioScience 16: 783–788.

FRITTS, H. C. 1966. Growth rings of trees: Their correlation with climate. Science 154: 973–979.

GATES, D. 1968. Toward understanding ecosystems. Advances Ecol. Res. 5: 1–36.

GLEASON, H. A. 1936. Twenty-five years of ecology, 1910–1935. Mem. Brooklyn Bot. Gard. 4: 41–49.

———. 1953. Autobiographical letter. Bull. Ecol. Soc. Amer. 34: 40–42.

GOLDMAN, C. R. (editor). 1966. Primary Productivity in Aquatic Environments. Univ. of California Press, Berkeley. 464 pp.

GÓMEZ-POMPA, A., C. VÁZQUEZ-YANES & S. GUEVARA. 1972. The tropical rain forest: A nonrenewable resource. Science 177: 762–765.

GOODALL, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. 27: 194–245.

———. 1970*a*. Statistical plant ecology. Annual Rev. Ecol. Syst. 1: 55–98.

———. 1970*b*. Simulation of grazing systems. Pp. 51–74, *in* D. A. Jameson (editor), "Modeling and Systems Analysis in Range Science." Sci. Ser. No. 5. Colorado State Univ., Fort Collins.

———. 1972. Building and testing ecosystem models. Pp. 173–194, *in* J. N. R. Jeffers (editor), "Mathematical Models in Ecology." Blackwell Sci. Publ., Oxford.

GOODMAN, G. T., R. W. EDWARDS & J. M. LAMBERT (editors). 1965. Ecology and the Industrial Society. John Wiley & Sons Inc., New York. 395 pp.

GOUNOT, M. 1969. Méthodes d'Étude Quantitative de la Végétation. Masson et Cie, Paris. 314 pp.

GREIG-SMITH, P. 1957. Quantitative Plant Ecology. (1st ed.) Butterworth's Sci. Publ., London. 198 pp. (2nd ed. 1964.)

———. 1971. Application of numerical methods to tropical forests. Pp. 195–204, *in* G. P. Patil, E. C. Pielou & W. E. Waters (editors), "Statistical Ecology." Vol. 3. Pennsylvania State Univ. Press, University Park.

GROENEWOUD, H. VAN. 1965. Ordination and classification of Swiss and Canadian coniferous forests by various biometric and other methods. Ber. Geobot. Inst. ETH Stiftung Rübel 36: 28–102.

HAIRSTON, N. G. 1969. On the relative abundance of species. Ecology 50: 1091–1094.

———, F. E. SMITH & L. B. SLOBODKIN. 1960. Community structure, population control and competition. Amer. Naturalist 94: 421–425.

———, J. D. ALLAN, R. K. COLWELL, D. J. FUTUYMA, J. HOWELL, M. D. LUBIN, J. MATHIAS & J. H. VANDERMEER. 1968. The relationship between species diversity and stability: An experimental approach with protozoa and bacteria. Ecology 49: 1091–1101.

HANDLER, P. 1970. Biology and the Future of Man. Oxford Univ. Press, London. 936 pp.

HARPER, J. L. 1960. The Biology of Weeds. Blackwell Sci. Publ., Oxford. 256 pp.

———. 1964. The nature and consequence of interference among plants. Pp. 465–482, *in* S. J. Geerts (editor), "Genetics Today." Pergamon Press, New York.

———. 1967. A Darwinian approach to plant ecology. Jour. Ecol. 55: 247–270.

———. 1969. The role of predation in vegetational diversity. Brookhaven Symp. Biol. 22: 48–62.

HESLOP-HARRISON, J. 1964. Forty years of genecology. Advances Ecol. Res. 2: 159–247.

HETT, J. M. & O. L. LOUCKS. 1971. Sugar maple (*Acer saccharum* Marsh.) seedling mortality. Jour. Ecol. 59: 507–520.

HILL, M. O. 1973. A unifying notation and its consequences. Ecology 54: 427–432.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG & J. A. TOSI, JR. 1971. Forest Environments in Tropical Life Zones. Pergamon Press, Inc., Elmsford, New York. 747 pp.

HOPKINS, B. 1970. Vegetation of the Olokemji Forest Reserve, Nigeria. The plants on the forest site with special reference to their seasonal growth. Jour. Ecol. 58: 765–825.

HORN, H. S. 1971. The Adaptive Geometry of Trees. Monogr. Populat. Biol. 3. Princeton Univ. Press, New Jersey. 144 pp.

HUMPHREY, A. R. 1962. Range Ecology. Ronald Press Co., New York. 234 pp.

HUNGATE, F. P. (editor). 1966. Radiation and Terrestrial Ecosystems. Proc. Hanford Symp. Pergamon Press, Elmsford, New York. 1675 pp.

HUTCHINSON, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415–427.

———. 1969. Eutrophication, past and present. Pp. 17–26, *in* "Eutrophication: Causes, Consequences, Correctives." Natl. Acad. Sci. Natl. Res. Council. Publ. 1700. Washington, D.C.

——— & V. T. BOWEN. 1947. A direct demonstration of the phosphorus cycle in a small lake. Proc. Natl. Acad. U.S.A. 33: 148–153.

IVERSEN, J. 1969. Retrogressive development of a forest ecosystem demonstrated by pollen diagrams from fossil mor. Oikos (Suppl.) 12: 35–49.

JACKSON, W. A. & R. J. VOLK. 1970. Photorespiration. Annual Rev. Pl. Physiol. 21: 385–432.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturalist 104: 501–528.

———. 1972. Whither tropical ecology? Pp. 281–296, *in* J. A. Behnke (editor), "Challenging Biological Problems." Oxford Univ. Press, New York.

JEFFERS, J. N. R. (editor). 1972. Mathematical Models in Ecology. Blackwell Sci. Publ., Oxford. 398 pp.

JOHNSON, P. L. (editor). 1969. Remote Sensing in Ecology. Univ. of Georgia Press, Athens. 244 pp.

JORDAN, C. F. 1971. A world pattern in plant energetics. Amer. Sci. 59: 425–433.

KADLEC, J. A. 1971. A partial annotated bibliography of mathematical models in ecology. Analysis of ecosystems IBP. Univ. of Michigan, Ann Arbor. Unnumbered.

KOZLOVSKY, D. G. 1968. A critical evaluation of the trophic level concept: Ecological efficiencies. Ecology 49: 48–60.

KOZLOWSKI, T. T. (editor). 1968. Water Deficits and Plant Growth. 2 Vol. Academic Press, New York.

KRUCKEBERG, A. R. 1969. The implications of ecology for plant systematics. Taxon 18: 92–120.

LAMBERT, J. M. & M. B. DALE. 1964. The use of statistics in phytosociology. Advances Ecol. Res. 2: 59–99.

——— & W. T. WILLIAMS. 1966. Multivariate methods in plant ecology VI. Comparison of information analysis and association analysis. Jour. Ecol. 54: 635–664.

LANGFORD, A. N. & M. F. BUELL. 1969. Integration, identity and stability in the plant association. Advances Ecol. Res. 6: 83–135.

LEOPOLD, A. & S. JONES. 1947. A phenological record for Sauk and Dane Counties, Wisconsin, 1935–1945. Ecol. Monogr. 17: 81–122.

LEWONTIN, R. C. 1970. The meaning of stability. Pp. 13–23, *in* "Diversity and Stability in Ecological Systems." Brookhaven Natl. Lab. Symp. Biol. 22.

——— & W. K. BAKER. 1970. Editor's Report. Amer. Naturalist 104: 499–500.

LIETH, H. 1970. Phenology in productivity studies. Pp. 30–56, *in* D. E. Reichle (editor), "Ecological Studies, Analysis and Synthesis." Springer-Verlag, Berlin.

———. 1972. Über die Primärproduktion der Pflanzendecke der Erde. Angew. Bot. 46: 1–37.

——— & G. M. MOORE. 1971. Computerized clustering of species in phytosociological tables and its utilization for field work. Pp. 403–422, *in* G. P. Patil, E. C. Pielou & W. C. Waters (editors), "Statistical Ecology." Vol. 1. Pennsylvania State Univ. Press.

LIKENS, G. E. 1972. Eutrophication and aquatic ecosystems. Pp. 3–13, *in* G. E. Likens (editor), "Nutrients and Eutrophication." Amer. Soc. Limnol. Ocean., Inc.

LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23: 399–418.

LIVINGSTON, B. E. 1948. Some conversational autobiographical notes on intellectual experience. Ecology 29: 227–241.

LOUCKS, O. L. 1970. Evolution of diversity, efficiency and community stability. Amer. Zoologist 10: 17–25.

———. 1972. Systems methods in environmental court actions. Pp. 419–473, *in* B. C. Patten (editor), "Systems Analysis and Simulation in Ecology." Vol. II.

MAAREL, E. VAN DER. 1969. Ordination models in phytosociology. Vegetatio 19: 21–46.

MACARTHUR, R. H. 1972. Geographical Ecology. Harper and Row, Publ., New York. 269 pp.

MAJOR, J. 1958. Plant ecology as a branch of botany. Ecology 39: 352–363.

———. 1969. Historical development of the ecosystem concept. Pp. 9–22, *in* G. M. Van Dyne (editor), "The Ecosystem Concept in Natural Resource Management." Academic Press, New York.

MARGALEF, R. 1968. Perspectives in Ecological Theory. Univ. of Chicago Press, Chicago. 111 pp.

MARTIN, P. S. 1963. The Last 10,000 Years. A fossil pollen record of the American Southwest. Univ. of Arizona Press, Tucson. 87 pp.

MCINTOSH, R. P. 1962. Raunkaier's "Law of frequency." Ecology 43: 533–535.

———. 1967. The continuum concept of vegetation. Bot. Rev. 33: 130–187.

———. 1970. Community, competition and adaptation. Quart. Rev. Biol. 45: 259–280.

MCMILLAN, C. 1960. Ecotypes and community function. Amer. Naturalist 94: 245–255.

MCNAUGHTON, S. J. & L. L. WOLFE. 1970. Dominance and the niche in ecological systems. Science 167: 131–139.

MORAL, R. DEL & C. H. MULLER. 1970. The allelopathic effects of *Eucalyptus camaldulensis*. Amer. Midl. Naturalist 83: 254–282.

MULLER, C. H. 1970. The role of allelopathy in the evolution of vegetation. Pp. 13–31, *in* P. R. Ehrlich (editor), Biochemical Coevolution. Oregon State Univ. Press, Corvallis.

NATIONAL SCIENCE BOARD REPORT. 1971. Environmental Science. Challenge for the Seventies. Natl. Sci. Board.-Natl. Sci. Foundation. Washington, D.C.

NELSON, D. J. & F. C. EVANS (editors). 1969. Symposium on radioecology. Proc. Second Natl. Symp. May 15–17, 1967. U.S. Atomic Energy Commission. 774 pp.

NOONEY, G. G. 1965. Mathematical models, reality and results. Jour. Theor. Biol. 9: 239–252.

ODUM, E. P. 1953. Fundamentals of Ecology. (Ed. 1.) W. B. Saunders Co., Philadelphia. 546 pp. (Ed. 2, 1959); (Ed. 3, 1971.)

———. 1964. The new ecology. BioScience 14: 14–16.

———. 1968. Energy flow in ecosystems. A historical review. Amer. Zoologist 8: 11–18.

———. 1969. The strategy of ecosystem development. Science 114: 262–270.

———. 1972. Ecosystem theory in relation to man. Pp. 11–23, *in* J. A. Wiens (editor), "Ecosystem Structure and Function." Oregon State Univ. Press, Corvallis.

Odum, H. T. 1971. Environment, Power and Society. Wiley-Interscience, New York. 331 pp.

——— & R. F. Pigeon (editors). 1970. A Tropical Rain Forest. A study of radiation and ecology at El Verde, Puerto Rico. Div. Techn. Inform. U.S. Atomic Energy Commission.

Ogle, C. J. 1970. Pollen analysis of selected *Sphagnum* bog sites in Puerto Rico. Pp. B-135–B-150, *in* H. T. Odum & R. F. Pigeon (editors), "A Tropical Rain Forest." Div. Techn. Inform. U.S. Atomic Energy Commission.

Olson, J. S. 1958. Rates of succession and soil change on southern Lake Michigan sand dunes. Bot. Gaz. (Crawfordsville) 119: 125–170.

O'Neill, R. V., J. M. Hett & N. F. Sollins. 1970. A Preliminary Bibliography of Mathematical Modeling in Ecology. Oak Ridge Natl. Lab. IBP. 97 pp.

Orloci, L. 1972. On objective functions of phytosociological resemblance. Amer. Midl. Naturalist 88: 28–55.

Paine, R. T. 1971. The measurement and application of the calorie to ecological problems. Advances Ecol. Syst. 2: 145–162.

Patil, G. P., E. C. Pielou & W. E. Waters. 1971. Statistical Ecology. 3 Vols. Pennsylvania State Univ. Press, University Park.

Patten, B. C. (editor). 1971. Systems Analysis and Simulation in Ecology. Vol. 1. Academic Press, Inc., New York. 610 pp.

——— & M. Witkamp. 1967. Systems analysis of cesium 134 kinetics in terrestrial microcosms. Ecology 48: 813–824.

Pearsall, W. H. 1964. The development of ecology in Britain. Jour. Ecol. 52(Suppl): 1–12.

Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York. 286 pp.

Platt, R. B. & J. F. Griffiths. 1964. Environmental Measurement and Interpretation. Reinhold Publ. Corp., New York. 235 pp.

Pomeroy, L. R. 1970. The strategy of mineral cycling. Annual Rev. Ecol. Syst. 1: 171–190.

Poore, M. E. D. 1967. The concept of the association in tropical rain forest. Jour. Ecol. 55: 46–74.

Preston, F. W. 1962. The canonical distribution of commonness and rarity, II. Ecology 43: 410–432.

Reichle, D. E. (editor). 1970. Analysis of Temperate Forest Ecosystems. Springer-Verlag, New York. 304 pp.

——— & S. I. Auerbach. 1972. Analysis of ecosystems. Pp. 260–280, *in* J. A. Behnke (editor), "Challenging Biological Problems." Oxford Univ. Press, New York.

Reiners, W. A., I. A. Worley & D. B. Lawrence. 1970. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52: 55–69.

Rice, E. L. 1971. Some possible roles of inhibitors in old-field succession. Pp. 128–132, *in* "Biochemical Interactions Among Plants." U.S. Natl. Committee for IBP. Natl. Acad. Sci., Washington, D.C.

Richards, P. W. 1952. The Tropical Rain Forest. Cambridge Univ. Press, New York. 450 pp.

———. 1963. What the tropics can contribute to ecology. Jour. Ecol. 51: 231–241.

Riley, G. A. 1972. Patterns of production in marine ecosystems. Pp. 91–110, *in* J. A. Wiens (editor), "Ecosystem Structure and Function." Oregon State Univ. Press, Corvallis.

Rodin, L. E. & N. I. Bazilevich. 1965. Production and Mineral Cycling in Terrestrial Vegetation. Translated by G. E. Fogg. Oliver & Boyd, Edinburgh. 288 pp.

Rorison, J. H. (editor). 1969. Ecological Aspects of the Mineral Nutrition of Plants. Blackwell Sci. Publ., Oxford. 484 pp.

Rosen, R. 1972. Review of: Trends of General Systems Theory. G. J. Klir (ed.), Wiley-Interscience, New York. Science 177: 508–509.

Ross, H. H. 1962. A Synthesis of Evolutionary Theory. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 387 pp.

Schultz, A. M. 1969. A study of an ecosystem: The arctic tundra. Pp. 77–93, *in* G. M.

Van Dyne (editor), "The Ecosystem Concept in Natural Resource Management." Academic Press, New York.

Schultz, J. P. 1960. Ecological studies on the rain forest in Northern Suriname. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Reeks 53, No. 1. Amsterdam.

Schultz, V. & A. W. Klement, Jr. (editors). 1963. Radioecology—Proceedings of the First National Symposium on Radioecology. Sept. 10–15, 1961. Reinhold Publ. Co., New York, and AIBS. 774 pp.

Sears, P. B. 1935. Deserts on the March. Oklahoma University Press, Norman. 231 pp.

———. 1969. Plant ecology. Pp. 124–131, *in* J. Ewan (editor), "A Short History of Botany in the United States." Hafner Publ. Co., New York.

Slobodkin, L. B. 1968. Aspects on the future of ecology. BioScience 18: 16–23.

Smith, R. F. 1970. The vegetation structure of a Puerto Rican rain forest before and after short term gamma irradiation. Pp. D-103-D-140, *in* H. T. Odum & R. F. Pigeon (editors), "A tropical Rain Forest." Div. Techn. Inform. U.S. Atomic Energy Commission.

Southern, H. N. 1970. Ecology at the crossroads. Jour. Ecol. 58: 1–11.

Spurr, S. M. 1964. Forest Ecology. Ronald Press Co., New York. 352 pp.

Stauffer, R. C. 1960. Ecology in the long manuscript version of Darwin's *Origin of Species* and Linnaeus' *Oeconomy of Nature*. Proc. Amer. Philos. Soc. 104: 235–241.

Steere, W. C. (editor). 1958. Fifty Years of Botany. McGraw-Hill Book Co. Inc., New York. 638 pp.

Sulzberger, C. L. 1972. To reach for other stars. New York Times. News of the Week in Review. June 11.

The Institute of Ecology. 1972. Man in the living environment. Report of the Workshop on Global Ecological Problems. 267 pp.

Tukey, H. B., Jr. 1970. Leaching of metabolites from foliage and its implications in the tropical rain forest. Pp. H-155–H-160, *in* H. T. Odum & R. F. Pigeon (editors), "A Tropical Rain Forest." Div. Techn. Inform. U.S. Atomic Energy Commission.

Van Dyne, G. M. (editor). 1969*a*. The Ecosystem Concept in Natural Resource Management. Academic Press, New York. 383 pp.

———. 1969*b*. Implementing the ecosystem concept in training in the natural resource sciences. Pp. 327–367, *in* G. M. Van Dyne (editor), "The Ecosystem Concept in Natural Resource Management." Academic Press, New York.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771–780.

Wadsworth, R. M. 1968. The Measurement of Environmental Factors in Terrestrial Ecology. Blackwell Sci. Publ., Oxford. 324 pp.

Walter, H. 1971. Ecology of Tropical and Subtropical Vegetation. Oliver and Boyd, Edinburgh. 539 pp.

Waterman, T. H. 1965. The problem. Pp. 3–23, *in* T. H. Waterman & H. J. Morowitz (editors), "Theoretical and Mathematical Biology." Blaisdell Publ. Co., New York.

Watt, K. E. F. (editor). 1966. Systems Analysis in Ecology. Academic Press, New York. 276 pp.

———. 1968. Ecology and Resource Management. McGraw-Hill, New York. 450 pp.

———. 1970. Review of: Van Dyne, G. M. (ed.) The Ecosystem Concept in Natural Resource Management. Academic Press, New York. Science 168: 1079–1080.

Weaver, J. E. 1954. North American Prairie. Johnson Publ. Co., Lincoln, Nebraska. 348 pp.

Webb, L. J., J. G. Tracey, W. T. Williams & G. N. Lance. 1970. Studies in the numerical analysis of complex rain-forest communities. V. A. comparison of the properties of floristic and physiognomic structural data. Jour. Ecol. 58: 203–232.

Weiser, C. J. 1970. Cold resistance and injury in wood plants. Science 169: 1269–1278.

Wells, P. V. 1970. Vegetational history of the Great Plains: A postglacial record of coniferous woodland in Southeastern Wyoming. Pp. 185–202, *in* W. Dort, Jr. & J. K. Jones, Jr. (editors), "Pleistocene and Recent Environments of the Central Great Plains." Univ. Kansas Press, Lawrence.

Went, F. W. & N. Stark. 1968. Mycorrhiza. BioScience 18: 1025–1029.

West, R. J. 1964. Inter-relations of ecology and Quaternary Paleobotany. Jour. Ecol. 52(Suppl.): 47–57.

Wetzel, R. G. 1965. Techniques and problems of primary productivity measurements in higher aquatic plants and periphyton. Pp. 249–267, *in* C. R. Goldman (editor), "Primary productivity in aquatic macrophytes." Mem. 1st. Ital. Idrobiol. 18. Suppl., Univ. California Press, Berkeley.

Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Sci. 25: 17–31.

———. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23: 41–78.

———. 1962. Classification of communities. Bot. Rev. 28: 1–239.

———. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207–264.

———. 1970. Communities and Ecosystems. Macmillan Co., New York. 158 pp.

———. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.

——— & P. P. Feeney. 1971. Allelochemics: Chemical interactions between species. Science 171: 757–770.

——— & G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Jour. Ecol. 56: 1–25.

——— & ———. 1972. Evolution of natural communities. Pp. 137–156, *in* J. A. Wiens (editor), "Ecosystem Structure and Function." Oregon State Univ. Press, Corvallis.

Wilimovsky, N. J. & H. N. Wolfe (editors). 1966. Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Commission. 1248 pp.

Williams, W. T. 1971. Principles of clustering. Annual Rev. Ecol. Syst. 2: 303–326.

Wilson, R. E. & E. L. Rice. 1968. Allelopathy as expressed by *Helianthus annuus* and its role in old field succession. Bull. Torrey Bot. Club 95: 432–448.

Witkamp, M. 1971. Soils as components of ecosystems. Annual Rev. Ecol. Syst. 2: 85–110.

Wolfe, J. M. 1949. Microclimates and macroclimates of Neotoma. Ohio Biol. Surv. Bull. 41. 267 pp.

Woodwell, G. M. & D. B. Botkin. 1970. Metabolism of terrestrial ecosystems by gas exchange techniques: The Brookhaven approach. Pp. 72–85, *in* D. E. Reichle (editor), "Analysis of Temperate Forest Ecosystems." Springer-Verlag, New York.

——— & R. H. Whittaker. 1968*a*. Primary production in terrestrial ecosystems. Amer. Zoologist 8: 19–30.

——— & ———. 1968*b*. Effects of chronic gamma irradiation on plant communities. Quart. Rev. Biol. 43: 42–55.

Young, H. E. (editors). 1968. Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. Univ. Maine Press, Orono. 245 pp.

25 years of botany

PLANT SYSTEMATICS
1947–1972[1]

PETER H. RAVEN[2]

A hundred years ago this month, at 10:00 in the morning on August 14, 1872, Asa Gray and his wife reached the summit of Grays Peak in the Rockies. Returning to Georgetown, Colorado, at 8:00 PM, the Grays caught the train for Dubuque, Iowa. The following evening, August 15, at 8:00 PM, Gray delivered his address as outgoing president of the AAAS. He chose as his theme "*Sequoia* and its history," giving a fine exposition of his original and perceptive views on the differentiation of northern floras. Gray was 61 years old, and within a year John Torrey had died, Gray had retired, and Charles Sprague Sargent had founded the Arnold Arboretum. It was 13 years since the publication of the *Origin of Species*, seven since the end of the Civil War, and three since the completion of the transcontinental railroad. The Republican incumbent president, Ulysses S. Grant, had been nominated for a second term in Philadelphia that June, and his Democratic opponent, Horace Greeley, selected by his party at their convention in July, was starting to campaign vigorously.

Fifty years ago this summer Harvey Monroe Hall was performing his first transplant experiments for the Carnegie Institution of Washington in the Sierra Nevada of California. The Morton Arboretum was established in Lisle, Illinois. The economy was rising and all seemed well with the world. It was nearly 20 years since the "rediscovery" of genetics and four since the end of World War I. Of particular interest to plant systematists was the development of the squash technique for chromosomes by J. Belling and the experimental verification of O. Winge's 1917 hypothesis of hybridization followed by polyploidy as a method for the origin of species by R. E. Clausen and T. H. Goodspeed, published in 1925.

Twenty-five years ago, the Marshall Plan was proposed, the newly founded United Nations decided to establish independent Jewish and Arab states in

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[1] Of necessity, this paper is limited to a consideration of the major trends of the period, and it has not been possible to mention a great many significant systematic studies. It is particularly biased toward the inclusion of workers in the United States, and especially those who have been active for a major portion of the 25 years under consideration.

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Palestine, and the economy was again rising after a world war. The dominant theme in systematic botany was biosystematics. This synthetic field was flourishing as the methods and concepts of genetics and cytogenetics were being applied to taxonomic problems. A whole new crop of graduate students, many of them recently returned from service in the armed forces, was eagerly reviewing the published works of Gote Turesson (*e.g.* 1922, 1930), G. Einar du Rietz (1930), Jens Clausen, David D. Keck, and William H. Hiesey (1940), J. W. Gregor, and W. B. Turrill in genecology; those of such authors as E. B. Babcock, A. F. Blakeslee, D. G. Catcheside, R. E. Cleland, F. Fagerlind, A. Gustafsson, A. Muntzing, and Karl Sax in genetics and cytogenetics; and comprehensive works by zoologists such as Julian Huxley (1940), T. Dobzhansky (1941), and Ernst Mayr (1942), which were to revolutionize the whole field of systematics. They were studying with talented and original teachers such as Edgar Anderson and G. Ledyard Stebbins, who had already made great contributions to the field and were to make many more in the quarter century we are considering.

In retrospect, it seems clear that the taxonomists of the 1940's were anxious to adopt criteria for recognizing species that were objective and operational. In the floras that were available to them, they had examples of extremely variable species concepts, with students such as P. A. Rydberg, J. K. Small, and E. L. Greene espousing especially narrow limits for species, a tendency that threatened to make the taxonomy of many groups arbitrary and incomprehensible to all but a few specialists.

In 1935, Karl M. Wiegand was moved to write, "Is it not our duty to science . . . not to clutter up our subject with endless names and half-baked concepts which seem only to confuse and to cause resentment and to pass the buck? The science of taxonomy stands too low now in the estimation of general workers" (Wiegand, 1935). If the chemists had the periodical table of the elements, why could taxonomists not have repeatable units also? Thus in his 1949 presidential address to the American Society of Plant Taxonomists, W. H. Camp argued, "Were classical taxonomy a science it would have its basic unit—"the species"—adequately defined . . . [by a] functional and usable definition. . . . The new system of nomenclature will have to be cut of a different cloth from the old and tailored so as to express, in descriptive terms, a vast array of most dynamic and involved genetic systems. . . . Some of us have hoped that the change would be gradual, and so avoid an open conflict between classical systematics and biosystematy. . . ." The millennium was clearly at hand.

The Ascendency of Biosystematics

The exciting studies that had been and were being made by students such as those named above, and others such as J. T. Baldwin, Jr., R. E. Clausen, T. H. Goodspeed, Irene Manton, and E. R. Sears, of the relationships between chromosomes in artificial and natural hybrids and polyploids were revitalizing the field of plant taxonomy. They inspired a whole generation of students to extend these methods to additional groups and to other regions of the world. Just 25 years ago, E. B. Babcock's monumental study of the genus *Crepis* (Babcock, 1947) appeared as the culmination of an outstanding research career and as an example of the rich rewards awaiting those who would apply the methods of cytogenetics to the study of plant populations. Like T. H. Goodspeed's treatment of *Nicotiana* (the culminating volume of which did not appear until 1954) and A. F. Blakeslee's life-long study of *Datura* (the summary volume appeared in 1959), this monograph of *Crepis* and the series of papers that had led up to it served as a model for many of the plant systematists who have been active in the past 25 years.

Other important workers were concentrating on broad questions concerning the nature and relationships of populations in the field and their evolutionary history. By the start of our period, Edgar Anderson had already been active for two decades, contributing important work on hybridization in the field and its meaning, on the evolution of cultivated plants, and on the nature of species. Anderson was much concerned with the use of mass sampling in dealing with natural variation, as were N. C. Fassett and W. H. Camp. Their outlook had a strong influence on the students of the late 1940's and 1950's also. At Berkeley, Herbert Mason was concerning himself with taxonomic philosophy and plant geography, while carrying out monographic work on the Polemoniaceae.

Important works by some of the scientists already mentioned appeared soon after 1947. Anderson's (1949) "Hybridization of the habitat," his (1948) book, *Introgressive Hybridization*, and his (1953) article of the same name were widely respected and influential works that summed up many of his earlier studies and concepts. Jens Clausen's (1951) *Stages in the Evolution of Plant Species* has been widely recognized as one of the most capable short summaries of plant evolution ever written. Irene Manton's (1950) *Problems of Cytology and Evolution in the Pteridophyta* was an important contribution not only for the study of ferns but also for vascular plant taxonomy as a whole.

What has undoubtedly been the most influential single book in plant systematics of this century, G. L. Stebbins' *Variation and Evolution in Plants*, also appeared in 1950. In this volume Stebbins captured and summarized the major concepts of biosystematics and plant evolution exceptionally well. His book has provided in many cases the framework into which subsequent experimental work and observations have been fit. Only in the past decade, with the rising importance of mathematics and chemistry, including plant physiology, in understanding and interpreting plant populations, has the book begun to seem less comprehensive; yet it will probably remain a classic and required reading for all students of the field for years to come.

Those who were active professionals or in graduate school in the late 1940's and the early 1950's, then, were presented with a whole series of challenges and questions by the conceptual framework, epitomized by Stebbins' *Variation and Evolution in Plants*, that had been built up mainly since World War I as a result of the mutual influence of systematics, genetics, and ecology. Many outstanding workers accepted these challenges and have made strong contributions to the field, both by means of their own published work and through the students they have instructed. Although it is invidious to single out individuals among those still active, a very few will be mentioned to illustrate the nature of this period in the history of systematic botany.

First, it should be noted that some of the workers and groups mentioned as contributing to the development of biosystematics 25 years ago have remained active right up to the present. The Department of Plant Biology of the Carnegie Institution of Washington, located at Stanford, California, provides an outstanding example. Although Jens Clausen has died and Hiesey and Keck now have retired, the group is still very active and continues to produce outstanding results. Olle Björkman, with the collaboration of David Fork and Malcom Nobs, has turned toward an elucidation of the biochemical basis of adaptation, the modern version of genecology (Langlet, 1971). Workers in other laboratories, among them Dwight Billings and Harold Mooney, have also made strong contributions to this field, but the Carnegie Institution laboratories stand out as a model of what can be achieved with sustained support.

Reed C. Rollins, who began his taxonomic work before World War II, made original contributions to guayule research during the war and then returned to the systematic study of crucifers in the period we are considering. In addition to his broadly based monographic studies of the family, he has, often in collaboration with his students and other associates, produced a series of interesting papers on the genetics and population structure of these plants, especially *Lesquerella* and *Leavenworthia*. Like Lincoln Constance, with whom he initiated his graduate work at Washington State College in Pullman, Rollins has influenced dozens of students and has often turned to the consideration of broader questions of systematics.

Among the more productive biosystematists whose professional careers began during the past 25 years have been Fritz Ehrendorfer, Verne Grant, Charles B. Heiser, Jr., Harlan Lewis, Spenser Smith-White, David Valentine, and W. H. Wagner, Jr. All began to publish in the late 1940's, and all have continued mainly to investigate plant populations from the standpoint of genetics, cytogenetics, and experimental hybridization. Each man has taken a particular direction, however, and these directions have often been maintained by their students. Thus Ehrendorfer, Lewis, and Smith-White are perhaps best known for their studies of chromosomal evolution, but each of them has also been concerned with the evolution of floras from a cytological point of view. Lewis has also produced an outstanding taxonomic monograph of the genus *Clarkia* (Lewis & Lewis, 1955), and his development of the theory of saltatory speciation has been an important trend of the period. Wagner has devoted most of his considerable energies to studies of chromosomal evolution in ferns, but has likewise approached their study from a number of other directions. Recently he has been much concerned with the development of numerical methods for evaluating hypothetical phylogenies. Heiser has not only made outstanding contributions to the biosystematics of *Helianthus* but has also contributed much to our understanding of the evolution of cultivated plants, particularly Solanaceae. Like Jonathan Sauer, T. W. Whitaker, and Hugh Cutler, all associated with Edgar Anderson, Heiser has been particularly interested in the association of plants and man.

David Valentine has had an important influence on plant systematics, mainly through his very careful analyses of barriers to hybridization in groups such as

Primula. In order to understand the evolution of vascular plants, it will be necessary to have a great deal more information of this kind, which often lies at the interface of systematics and development. Developmental and molecular biologists have learned a great deal through the analysis of interspecific hybrids in animals, and the further extrapolation of these methods, which are still evolving, to plants, will probably produce very interesting results during the next 25 years.

Verne Grant has, during the period under discussion, written several important books that have extended the tradition established by Stebbins' *Variation and Evolution in Plants* in 1950. Grant's books include *The Origin of Adaptations* (1963), *The Architecture of the Germplasm* (1964), and *Plant Speciation* (1971). He is also well known as a student of the biosystematics of the Polemoniaceae and of the genus *Gilia.* Grant played perhaps the decisive role in the reawakening of interest in pollination biology in the United States, his early papers in the field (*e.g.* Grant, 1950) having attracted a great deal of interest. He has continued his activity in pollination biology to the present, having been joined by a number of other students over the past 20 years.

Evaluation of Biosystematics

An evaluation of the current status of biosystematics was provided by the proceedings of a symposium entitled "Biosystematics at the Crossroads," held at the XIth International Botanical Congress in Seattle in 1969 and published in full in Taxon, Vol. 19, No. 2 (April 1970). In his introductory remarks, Ehrendorfer clearly outlined the trends discussed here: the feeling of great optimism in the 1940's, gradually giving way to many doubts about the generality of the standard biosystematic approaches and concepts by the 1960's. Nevertheless, the contributors to the symposium made it clear that as the study of the process of evolution in plant populations, biosystematics is still flourishing. I believe that one of the reasons that its practitioners may today feel a certain pessimism is that the methods of biosystematics have not solved the problems of what might be called "classical taxonomy." In the late 1940's, many workers felt that if extensive breeding programs were carried out, they would completely elucidate the nature of species in the groups being studied. Many of us are engaged in studies of the process of evolution at one level or another, but we have been conditioned to report our results in terms of taxonomic categories: genera, species, and subspecies. Perhaps the most important discovery of the 25 years being reviewed is that biosystematic studies do *not* lead to an unequivocal definition of the taxonomic units in most groups: they contribute to an understanding of the populations and the processes by which they have changed and are changing, but they do not dictate the taxonomic decisions that must be made in the light of this information.

The reasons for this discrepancy have been stated well by F. Merxmüller (1970: 144) when he wrote, "But what I still hardly understand is why it is exactly the biosystematists who press for a strongly generalized and fixed definition of that phase of evolution known as 'species': they should be in the best position to appreciate the manifold variety of evolutionary processes and their widely inadequate investigation." In 1940, Clausen, Keck, and Hiesey could write confidently about ecotypes as definite races with particular characteristics, which in turn made up ecospecies, well-integrated genetic-physiological entities within which gene exchange was still possible. Although ecospecies were never quite said to be equivalent with taxonomic species, the clear implication was that if they were studied sufficiently, this would prove to be the case. Experimental procedures were suggested to test for the existence of ecotypes, ecospecies, and coenospecies in nature, and many students took up these methods. The dilemma they had to confront in fitting their results into the taxonomic system is well illustrated by David D. Keck's opening remarks in his analysis of trends in systematic botany (Keck, 1957).

As a result of the large quantity of experimental work done on plant populations in the past 25 years, we can conclude without hesitation that evolution has not produced a series of equivalent units in different groups. Terms such as "ecospecies" and "coenospecies" have very rarely been used to discuss the results found in certain groups, because the requisite conditions have not been met. Ecotypes had been revealed as heterogeneous entities rather than stable building blocks even before World War II (*cf.* Langlet, 1971: 699–700), but the desire for stable, repeatable units has remained a powerful one to the present. In consequence of this, the kinds of studies that have traditionally been called biosystematic are now seen more clearly as studies of the process of evolution (*cf.* Stebbins, 1970) and are no longer being expected to provide automatic taxonomic decisions. The concept of a "general purpose taxonomy" has grown up in the past 20 years in the face of biosystematics, along with a realization that taxonomic species are not necessarily equivalent with the theoretical constructions of the biosystematists of the past. A valuable discussion of the nature of species and other taxonomic units has been provided by Davis and Heywood in their outstanding book on plant taxonomy (Davis & Heywood, 1963, especially pp. 89–103), and there has been a healthy development of the idea in the literature of the past decade. In the taxonomy of certain animal groups, the so-called "biological species concept" is still widely applied, but this is largely because there is not available for these groups the wealth of experimental work that has been carried out for vascular plants. It is still possible in dealing with them to make assumptions about such little-tested concepts as "gene flow" and "genetic discontinuity," reasoning from morphology, and then to use this information in a circular way to validate the concept. In the face of actual information, available for many plant groups, this can often no longer be done.

Floras and Data

What seems to have happened during the past 25 years is the acceptance of many new kinds of data, mostly derived from studies of a "biosystematic" nature, by those who are setting up and using the general purpose taxonomy of vascular plants. This can be illustrated by reference to a few of the excellent floristic works that have appeared during the period in question. In 1950, the eighth, centennial, edition of Asa Gray's great manual of the plants of the northeastern quarter of the United States and adjacent Canada appeared (Fernald, 1950). Neither in it nor in Steyermark's outstanding *Flora of Missouri* (1963) can there be found much evidence of the biosystematic ferment of the preceding decades. For example, formae are still recognized as if they were significant units worthy of formal taxonomic recognition. In the 1950's there was still a tendency to regard biosystematic studies as a West Coast phenomenon that did not affect the mainstream of taxonomy. In 1951 the third volume of Leroy Abrams' *Illustrated Flora of the Pacific States* appeared, with a very limited biosystematic input, especially in those groups that had been studied by Clausen, Keck, and Hiesey. By 1960, when the fourth and concluding volume appeared (Abrams & Ferris, 1960), the biosystematic influence was more evident. Munz and Keck's *A California Flora* (1959) is replete with references to biosystematic studies of the groups concerned, as are subsequent floras of the western United States. It is now not possible to write a flora within the limits of the United States or in northern Europe without frequent recourse to such studies, as illustrated by the floras of the British Isles (Clapham, Tutin & Warburg, 1962), the Carolinas (Radford, Ahles & Bell, 1968), Texas (Correll & Johnston, 1970), and tropical Florida (Long & Lakela, 1971). Meanwhile, journals such as *Brittonia* and *Watsonia* form convenient vehicles for the publication of articles on the application of biosystematic methodology to particular taxonomic problems.

Perhaps the most significant influence upon the conduct of systematic botany during the past 25 years, however, has been the organization of the *Flora Europaea* project and the appearance of the first two volumes of the flora itself (Tutin *et al.*, 1964, 1968). In two respects, *Flora Europaea* seems to indicate the future direction of floristic work and the way in which we shall arrive ultimately at a broadly based general purpose taxonomy. First, it is the reponsibility of a committee which has attempted to sift all of the available information and to provide the best possible contemporary account of the plants of Europe. We have clearly passed the point where a flora is regarded as the product of one individual's imagination, with his own views and prejudices predominating, regardless of the overall views of the botanical community. Many taxonomic decisions are essentially arbitrary, and if the resulting taxonomy is to be generally useful, it must incorporate our collective wisdom from the start. Second the editors of *Flora Europaea* have, by the development of an elaborate series of guidelines and by holding frequent meetings and conferences, attempted to investigate carefully the meaning of a general purpose taxonomy and to achieve consensus on some of its properties. What sorts of infraspecific taxa are to be recognized? How are hybrids to be treated taxonomically? What are the general principles for the treatment of apomictic or polyploid complexes?

A very significant event for the handling of taxonomic information took place in 1962 with the publication of the *Atlas of the British Flora* (Perring & Walters, 1962). This book consists of a series of computerized maps of the ranges of the plants of Britain, based upon specimens and observations, arranged in a predetermined grid system and printed automatically. With the publication of this volume, systematists began to wonder about the handling of other classes of information by computer. The Flora North America Program, organized in 1966 by the American Society of Plant Taxonomists and developed over a six-year period with the aid of grants from the National Science Foundation, is now ready to begin the preparation of a data bank of information about the vascular plants of North America north of Mexico. From this bank will be generated a concise flora of the region, comparable with *Flora Europaea* and building upon its conceptual advances. In addition, the data bank can be extended easily to include other kinds of organisms and other sorts of information, can be queried for correlations between the features it includes, and can be continually updated to allow the generation of complete or partial concise floras of the entire region or any part of it on demand. A project organized in this way can provide a means for utilizing efficiently the masses of specimens and literature pertaining to the plants of the area and can help overcome the problem caused by the apparent finality of a printed flora in the past. In view of the fact that the systematic collections of the United States will double their size within the next 25 years, and there appears to be no real prospect for indexing the flood of literature our system is producing, these appear to be very high priorities indeed for the next quarter century.

TRENDS IN SYSTEMATIC STUDIES

One kind of question concerns the future of biosystematics. If it has, during the past 25 years, truly begun to decouple itself from the sort of preoccupation with the naming and recognition of taxonomic units that characterized the 1940's and 1950's, we may very well agree with G. L. Stebbins (1970) that the future is very bright indeed. As long as biosystematists orient their work predominantly around the recognition of such units, they will be less able to study the process of evolution effectively. A host of new tools in the analysis of the process of evolution has become available in the period 1947–1972, and an army of well-prepared students is starting to employ them in productive ways. The remainder of this paper will be devoted to the consideration of such trends.

In 1947, chemical methods were utilized only sparingly in systematics, and early efforts such as those of Mez in serology were widely discredited. Ralph E. Alston and B. L. Turner published in 1963 one of the landmark books of the past 25 years, *Biochemical Systematics*. It was no longer possible for the practicing taxonomist to ignore the importance of chemical data to the understanding of systematic problems, and the number and variety of chemical studies has grown significantly in the past decade. Chemosystematists were, however, confronted immediately with the same sorts of problems that plagued the biosystematists earlier. What is the purpose of discovering chemical information about plants? If it is to produce a better taxonomic system or a better classification of a particular group, then it has a very limited goal indeed. Although these aims are laudable and clearly worthwhile, they will teach us very little about chemical evolution or the role that specific molecules play in nature. As long as the chief goal of a particular chemosystematic study is the elucidation of some systematic hypothesis, it will be unlikely that broader relationships will be perceived. This is of course an obvious point, and plant physiologists, ecologists, and molecular biologists are carrying out an array of interesting investigations on questions that are not primarily systematic.

These investigations include such subjects as the role of specific molecules in plant–herbivore relationships and in disease resistance in general; plant–plant inhibition on a community basis; and the adaptive significance of the variation in particular enzymes within and between populations. While none of these questions are directly related to formal taxonomy, the kind of understanding that information concerning them has to contribute to the process of evolution is intimately connected with such application. Chemical data can and will continue to be applied to systematic questions, but they are of much greater interest in the larger context of population biology.

A second landmark book of the period also appeared in 1963—Robert R. Sokal and P. H. A. Sneath's *Principles of Numerical Taxonomy.* As a discipline, numerical taxonomy has received a very unfortunate title and, to some extent, initial orientation. The kinds of comparative analytical methods that its practitioners have developed are very powerful indeed, but they will ultimately be shown to have their greatest utility in questions that are not directly taxonomic. It is strange that the methods of numerical taxonomy have met with such resistance, especially in view of the fact that most taxonomists believe that they are basing their classifications upon the similarities and differences of organisms. There is clearly no better way to analyze these similarities and differences than by the sorts of procedure that have been developed under the banner of "numerical taxonomy," and if precise determinations of such parameters are required, their use is mandatory. Nevertheless, it is not practical to apply the methods of numerical taxonomy to a very large sample of the world's organisms, and we are once more left with the necessity of choosing our examples carefully to illustrate some general principle. Such questions as the comparative rates of evolution of different sets of characteristics of the same organisms, or the relative differences between species in different groups, can be approached only by the methods of numerical taxonomy. It seems likely that the use of these methods for purely taxonomic purposes is superfluous in most instances, even though, paradoxically, only they are adequate to produce precisely the results that the taxonomist thinks he is seeking.

The Next 25 Years

The past 25 years has been a critical period in the history of systematic botany. I believe that it will be remembered as the one in which the consequences of the mid-19th Century discoveries of Charles Darwin and Gregor Mendel finally caught up with the taxonomists. As a result of this period of intense interaction, I think that students of population biology have begun to realize that their work should not be conducted primarily because of the taxonomic conclusions that may be derived from it. For their part, I think taxonomists have learned that they are the keepers of a general purpose system of classification which provides a crude method of information retrieval and a means for communicating information about organisms (see discussion in Ornduff, 1969). No one kind of evidence, no one hypothesis, regardless of how attractive and novel it may seem, should be allowed to disrupt the taxonomic system in a particular group; all can and should contribute to it. Thus, systematic botany has emerged clearly as what Lincoln Constance (1964) has so aptly called "an unending synthesis."

In the next 25 years, students of the population biology of organisms will continue forging an integrated system in which ecology and genetics will be seen as but two elements in the relationship between populations and their environment. Numerical analyses like those begun by Sewall Wright and R. A. Fisher will form the cornerstone of population biology and will be vastly expanded in scope and elegance. Conceptual models of ever increasing predictive value and generality will be constructed as our knowledge of the structure of the natural world grows. Taxonomists will continue to study the cytogenetics, breeding systems, chemistry, and anatomy of their organisms, aided by such modern tools as the amino acid analyzer and the scanning electron microscope. The taxonomic system as such will be seen more and more as a byproduct of investigations of the population biology of organisms, and its derivation will be seen less and less as a prime goal of these investigations. The materials collected by taxonomists will continue to play an important role in the formulation of the new generalities of population biology. Collective studies by groups of specialists will become increasingly important; a good example is provided by the recent symposium volume on Umbelliferae (Heywood, 1971).

The kinds of detailed tools and methods that have undergone such a spectacular development during the period we are considering will continue to be applied only to a very small fraction of the World's organisms. To date, they have had little effect outside of temperate North America and northern and central Europe. Although they will doubtless become more common during the next 25 years in such areas as Australasia, southern Africa, the Soviet Union, Mexico, and Argentina, there are vast regions of the world where they will probably never be used to any great extent. By the end of the next 25 years, the population of tropical South America, the region with the most poorly known and undiscovered plant species in the world, will have more than doubled from its present level of 160 million people; little if any undisturbed tropical lowland forest will survive when this meeting is repeated in 1997.

These facts suggest two major conclusions: First, it is obvious that systematists of whatever stripe should participate more and more in applied efforts of a practical nature. We will, if we continue to ask for the support of society, need to become more responsive to its needs. The world is getting to be a smaller and smaller place, even for systematists. Second, there are scientific repercussions. We tend to go on investigating the plants of temperate North America and Europe as if we would eventually build up a coherent picture of their biosystematics and then move on to the plants of other areas of the world. The problem is that if we ever wish to have biosystematic, or chemical, or any other kind of specialized informaton on the plants of lowland Amazonia to compare with that gained in temperate regions, we shall have to begin to gather it at once. There have been significant programs of exploration in the tropics: for example, those carried out by such students as José Cuatrecasas, R. A. Schultes (also known for his outstanding work on drug and medicinal plants), and A. C. Smith (who has also contributed much to our knowledge of primitive angiosperms). Of special value have been the Brazilian and Guyana Highland expeditions sponsored by the New York Botanical Garden. All of these efforts, however, have been concerned mainly with collecting specimens. It is, in fact, not necessary to have the basic taxonomy worked out before moving to other kinds of studies, and in a number of cases if we continue to assume that it is, we shall lose the opportunity forever. We seem unable to identify collective priorities, and yet, by not doing so, we are denying many kinds of information to those who may repeat this meeting in another 25 years. It would seem far better to begin to make these decisions actively and deliberately, rather than passively.

The very existence of such efficient information retrieval devices as computers means that they will be much more widely used in the future for biological information. The numbers of species involved, the numbers of their characteristics that might be studied and recorded—these indicate clearly that some way must be found to rationalize the flood of information and specimens that is inundating our small force of systematic botanists. Unless we use the aids that are available to us, we shall be stymied by the sheer magnitude of the problem and all but cut off from significant future progress in the field. We would like to operate as if we lived in a world that was standing still for us, but it is not. The next 25 years will be even more challenging than those we have just been through, but potentially even more rewarding.

If this challenge is to be met, systematists will do well to remember the century-old words of Asa Gray (1872: 21), delivered in the address mentioned in the opening paragraph of the present paper:

> "Organic nature—by which I mean the system and totality of living things, and their adaptation to each other and to the world—with all its apparent and indeed real stability, should be likened, not to the ocean, which varies only by tidal oscillations from a fixed level to which it is always returning, but rather to a river, so vast that we can neither discern its shores nor reach its sources, whose onward flow is not less actual because too slow to be observed by the *ephemerae* which hover over its surface, or are borne on its bosom."

The methods appropriate for studying and describing a river are very different from those suitable for dealing with an ocean, and the fuller realization of the nature of populations of living organisms has perhaps been the most important philosophical advance made by systematic botanists during the past quarter-century.

BIBLIOGRAPHY

ABRAMS, L. 1951. Illustrated Flora of the Pacific States. Vol. 3. Stanford Univ. Press, Stanford, California.

——— & F. S. FERRIS. 1960. Illustrated Flora of the Pacific States. Vol. 4. Stanford Univ. Press, Stanford, California.

ALSTON, R. E. & B. L. TURNER. 1963. Biochemical Systematics. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Anderson, E. 1948. Hybridization of the habitat. Evolution 2: 1–9.

———. 1949. Introgressive Hybridization. John Wiley & Sons, Inc., New York.

———. 1953. Introgressive hybridization. Biol. Rev. 28: 280–307.

Avery, A. G., S. Satina & J. Rietsema. 1959. Blakeslee: The Genus *Datura.* Ronald Press Co., New York.

Babcock, E. G. 1947. The genus *Crepis,* I and II. Univ. California Publ. Bot. 21, 22: 1–1030.

Camp, W. H. 1951. Biosystematy. Brittonia 7: 113–127.

Clapham, A. R., T. G. Tutin & E. F. Warburg. 1962. Flora of the British Isles. Cambridge Univ. Press.

Clausen, J. 1951. Stages in the Evolution of Plant Species. Cornell Univ. Press, Ithaca, New York.

———, D. D. Keck & W. M. Hiesey. 1940. Experimental studies on the nature of species. I. The effect of varied environments on western North American plants. Carnegie Inst. Washington Publ. 520: 1–452.

Clausen, R. E. & T. H. Goodspeed. 1925. Interspecific hybridization in *Nicotiana.* II. A tetraploid glutinosa-Tabacum hybrid, an experimental verification of Winge's hypothesis. Genetics 10: 279–284.

Constance, L. 1964. Systematic botany—An unending synthesis. Taxon 13: 257–273.

Correll, D. S. & M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

Davis, P. H. & V. H. Heywood. 1963. Principles of Angiosperm Taxonomy. Oliver & Boyd, Edinburgh and London.

Dobzhansky, T. 1941. Genetics and the Origin of Species. Columbia Univ. Press, New York.

DuRietz, G. E. 1930. The fundamental units of biological taxonomy. Svensk Bot. Tidskr. 24: 333–428.

Ehrendorfer, F. 1970. Introduction to "Biosystematics at the crossroads." Taxon 19: 137–139.

Fernald, M. L. 1950. Gray's Manual of Botany. Ed. 8. American Book Co., New York.

Goodspeed, T. H. 1954. The Genus *Nicotiana.* Chronica Botanica, Waltham, Massachusetts.

Grant, V. 1950. The flower constancy of bees. Bot. Rev. 16: 379–398.

———. 1963. The Origin of Adaptations. Columbia Univ. Press, New York.

———. 1964. The Architecture of the Germplasm. John Wiley, New York.

———. 1971. Plant Speciation. Columbia Univ. Press, New York and London.

Gray, A. 1872. *Sequoia* and its history. Salem Press, Salem, Massachusetts. 22 pp.

Heywood, V. H. (editor). 1971. The biology and chemistry of the Umbelliferae. Bot. Jour. Linn. Soc. 64(Suppl.): 1–438.

Huxley, J. (editor). 1940. The New Systematics. Oxford Univ. Press.

Keck, D. D. 1957. Trends in systematic botany. *In* "Survey of Biological Progress." 3: 47–107. Academic Press Inc., New York.

Langlet, O. 1971. Two hundred years genecology. Taxon 20: 653–722.

Lewis, H. & M. E. Lewis. 1955. The genus *Clarkia.* Univ. California Publ. Bot. 20: 241–392.

Long, R. W. & O. Lakela. 1971. A Flora of Tropical Florida. University of Miami Press, Coral Gables, Florida.

Manton, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge Univ. Press, Cambridge.

Mayr, E. 1942. Systematics and the Origin of Species. Columbia Univ. Press, New York.

Merxmüller, H. 1970. Provocation of biosystematics. Taxon 19: 140–145.

Munz, P. A. & D. D. Keck. 1959. A California Flora. Univ. California Press, Berkeley and Los Angeles.

Ornduff, R. 1969. The systematics of populations of plants. Pp. 104–128, *in* "Systematic Biology." Natl. Acad. Sci., Washington, D.C.

Perring, F. H. & S. M. Walters. 1962. Atlas of the British Flora. Thomas Nelson and Sons, Ltd., London.

Radford, A. E., H. E. Ahles & C. R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. Univ. North Carolina Press, Chapel Hill.

Sokal, R. R. & P. H. A. Sneath. 1963. Principles of Numerical Taxonomy. W. H. Freeman & Co., San Francisco and London.

Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

———. 1970. Biosystematics: An avenue towards understanding evolution. Taxon 19: 205–214.

Steyermark, J. A. 1963. Flora of Missouri. Iowa State Univ. Press, Ames.

Turesson, G. 1922. The genotypical response of the plant species to the habitat. Hereditas 3: 211–350.

———. 1930. The selective effect of climate upon the plant species. Hereditas 14: 99–152.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters & D. A. Webb (editors). 1964. Flora Europaea. Vol. 1. Cambridge Univ. Press.

———, ———, ———, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (editors). 1968. Flora Europaea. Vol. 2. Cambridge Univ. Press.

Wiegand, K. M. 1935. A taxonomist's experience with hybrids in the wild. Science 81: 161–166.

25 years of botany

PALEOBOTANY

1947–1972

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In trying to condense the products of hundreds of paleobotanists over the past 25 years one must be a ruthless editor. I hope that the reader will accept what is offered as representative of the kinds of progress that have been made rather than a definitive summary. It should be understood that a great many important contributions cannot be mentioned, and I have tried to conform to the guidelines of this symposium as an informational source for teachers of botany; accordingly, I have selected developments that should be informative and attractive to students of plant evolution. It has been a great period, the past quarter century, and paleobotany with all of its shortcomings may be very proud of it. We have made some exciting, even monumental, contributions to our knowledge of the evolution of life on the earth; much is presently in progress and it is safe to prophesy that equally important gains will appear in the next two decades. For the most part it seems appropriate to present the story in chronological order.

SOURCES OF INFORMATION

For those who may wish to probe more deeply into certain aspects of paleobotanical progress during the past 25 years it may be helpful to note the chief bibliographic sources that are available. These may be divided into two categories: a general encyclopaedic work covering all phases of paleobotany and periodical publications designed to summarize year to year developments.

As to the first, in February of 1960 the Paris publishing house of Masson et Cie announced its intention to issue an eight volume (later enlarged to nine volumes) work, *Traité de Paleobotanique*, under the general editorship of Prof. Edouard Boureau. The first part to appear was actually Vol. III in the series, dealing with the Sphenophyta and Noeggerathiophyta; this came out in 1964. Two more volumes have appeared as follows: Vol. II, Bryophyta, Psilophyta, Lycophyta in 1967; Vol. IV, Filicophyta in 1970. It is Boureau's intention to deal with all genera of fossil plants that have been described. A considerable number of paleobotanists are involved in the project, and the three volumes that have come out to date are thorough, well organized, and beautifully illustrated. The only regret that one might have about this great undertaking is the rather high cost.

As to the periodical bibliographic publications, two are of special interest to

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ANN. MISSOURI BOT. GARD. 61: 179–202. 1974.

American botanists. In 1956 the International Organization of Paleobotany initiated a *World Report on Palaeobotany*, also under the editorship of Prof. Boureau (1956–1971). These reports appear approximately every two years, the most recent one, No. 8 having been published in 1971. They include an address list of paleobotanists and a "Bibliography" starting with "Generalities" which is followed by publications listed according to geologic ages.

A second periodical publication, *Bibliography of American Paleobotany*, is issued each year by the Paleobotanical Section of the Botanical Society of America. This includes lists of publications, work in progress, and personal information. For further details concerning these two periodicals, see notations in the Bibliography section under E. Boureau and A. D. Watt.

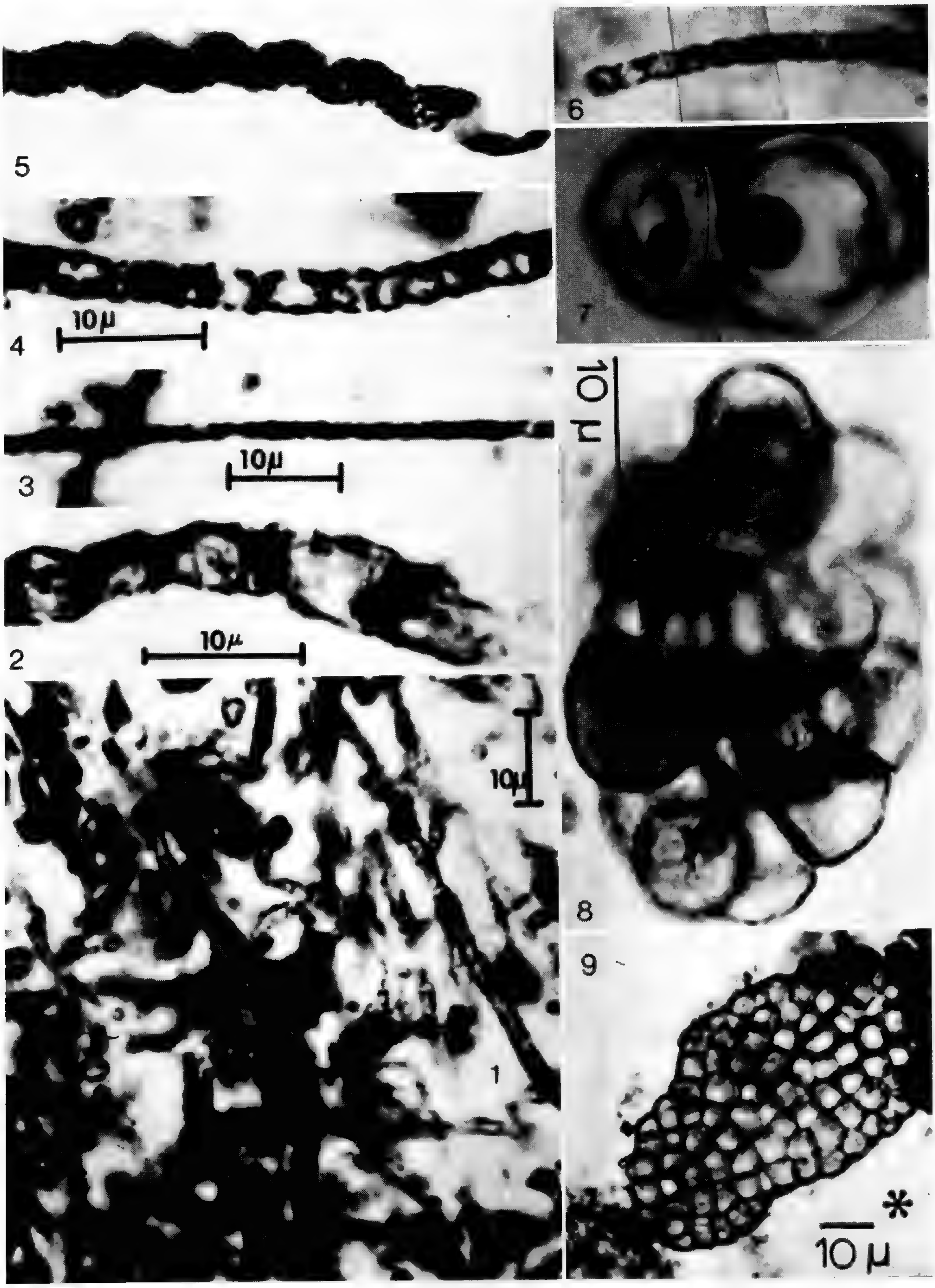
PRE-DEVONIAN PLANTS

There has been considerable interest in recent years in the origin of life on Earth, and paleobotanists have accomplished much in revealing early records of life as they are preserved in the rocks.

The fossil record drops off rather abruptly below the base of the Cambrian (about 600 million years ago); several groups of animals are known to have existed in Pre-Cambrian times, and these have been reported by Glaessner (1961) and have been rather widely introduced into textbooks. Although we know very little about vascular plants below the Devonian, there is an extensive literature dealing with algae or presumed algae that goes well back into the Pre-Cambrian, but much of this conveys information that is not very satisfactory to the student of plant evolution. As to the earliest evidence of plant life, certainly the most significant development is the recent work on the two-billion-year-old Gunflint chert of Ontario (Figs. 1–4). This contains unicellular and filamentous thallophytes that are structurally preserved. The flora was first reported in 1954 by Tyler and Barghoorn, and the detailed report, recording eight new genera, appeared in 1965 (Barghoorn & Tyler, 1965).

A few other Pre-Cambrian discoveries, which are indicative of what is going on, may be mentioned briefly. Barghoorn and Schopf (1966) have reported "bacterium-like, rod-shaped organisms" from the 3.1-billion-year-old Fig Tree Series of South Africa, and Schopf and Barghoorn (1967) have described "spheroidal microfossils . . . interpreted as probably representing the remnants of unicellular alga-like organisms" from the same source. Engel *et al.* (1968) have reported filamentous and sphaeroidal structures from a slightly lower level, dated as 3.2 billion years old. From the somewhat younger Bitter Springs Formation of Australia, dated at approximately 1 billion years, we have a more diverse and well-preserved algal flora (Barghoorn & Schopf, 1965; J. W. Schopf, 1968); 30 new taxa including 24 new genera have been described (Figs. 5–9). Most of the plants are referred to the blue-green algae, but a few are simple chlorophytes—unicellular, nucleated cells.

At this point a prophecy and a question seem appropriate. Investigations are in progress now that will certainly reveal much more about these Pre-Cambrian thallophytic plant remains. As to the question—Why did it take so long for vascular plants to become established on the land in late Silurian times (about



FIGURES 1–9.—1–4. Microorganisms from the Gunflint Chert of Ontario (from Barghoorn and Tyler, 1965).—5–9. Microorganisms from the Bitter Springs Formation of Australia (from J. W. Schopf, 1972).

400 million years ago), when it now seems clear that the cellular level was reached over two billion years ago?

THE EARLIEST LAND VASCULAR PLANTS AND LIFE IN THE DEVONIAN

I hope that the reader will regard the emphasis on Devonian paleobotany as not just a bias of the present reporter; it was a great time in plant evolution: vascular plants became established on the land and diversified into numerous pteridophytic lines; the progymnosperms come in strong in the Upper Devonian, and the first seed plants make their appearance. It was actually a long span of time, some 60 million years, and although much of great evolutionary importance went on, I think the rapidity of evolution may have been overemphasized by some writers.

Although we have only the vaguest speculations concerning the nature of the presumed algal ancestors of vascular plants, our knowledge of primitive land plants has increased considerably. To the best of my knowledge the only unquestioned Silurian vascular plant is *Cooksonia*, which was first described by Lang in 1937 on fossils from the Downtonian (Upper Silurian-basal Devonian) of Wales. He described two species, and in the axes of one of them he was able to demonstrate annular tracheids. Obrhel (1962) has described *Cooksonia* specimens from the Silurian of Czechoslovakia. More recently Edwards (1970*a*) has described *Cooksonia caledonica* from Scotland as a small, dichotomous, naked (no spines or other emergences) plant with axes under 2mm in diameter and a height of a few cm. Ananiev and Stepanov (1969) have reported specimens from Siberia which they assign to *C. hemispherica* Lang that have a near-monopodial habit; their illustrations show a plant with a slender main axis giving off dichotomizing branches in a spiral phyllotaxy, and some of these side branches bear terminal sporangia. An undescribed plant occurs in Lower Devonian rocks on the Gaspé coast that seems quite similar to this.

One of the most impressive and problematical features of the early Devonian plants is the diverse way in which the sporangia are borne. The genus *Gosslingia* is unique in this respect, and it has become much better known through the work of Dianne Edwards (1970*b*). In a recent restoration, based on an abundance of well-preserved specimens, it appears as a rather profusely branched plant, dichotomous to almost monopodial, attaining a height of some 50 cm, and with sporangia borne along the axes on very short stalks. Spores have been found in the sporangia, and the axis contained an elliptical protostele composed of scalariform and reticulate tracheids.

New early Devonian deposits are being discovered, and more information continues to come out of the classical ones. It is indeed precarious to ever decide that a fossil locality is "worked out" unless every vestige of rock is taken away. At Rhynie there are several interesting developments. Following two studies by Merker (1958, 1959), Pant (1962) has presented a careful analysis of the axes attributed to *Rhynia gwynne-vaughanii* and has shown that there are close structural similarities between them and the gametophytes of *Psilotum*. His investigations suggest that the "hemispherical projections" and "adventitious branches" as described by Kidston and Lang (1917) may be young sporophytes. In making

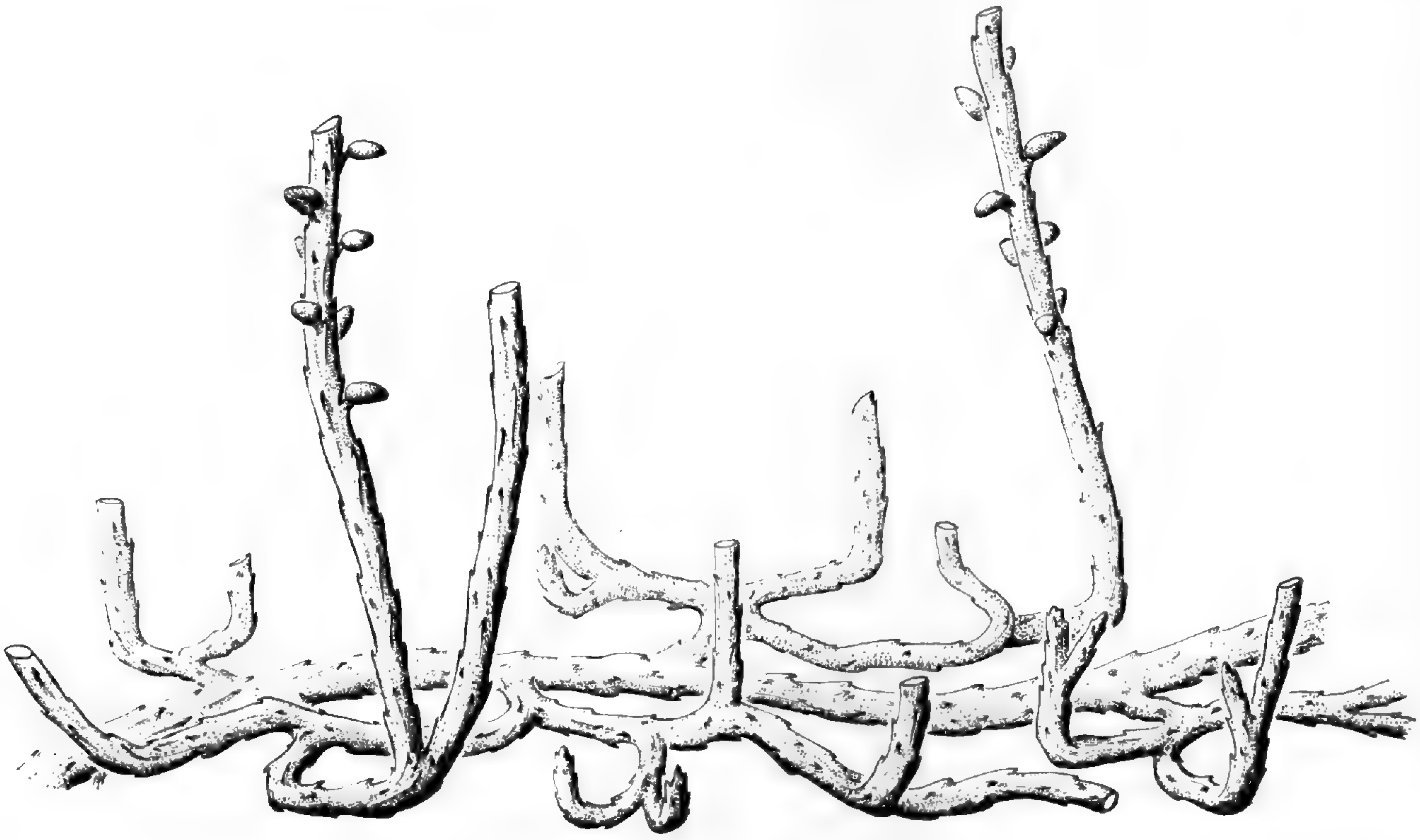


FIGURE 10. Restoration of *Kaulangiophyton akantha* Gensel and Kasper, from the early Devonian of northern Maine (from Gensel, Kasper & Andrews, 1969).

this comparison Pant admitted that it was based on indirect evidence, since he did not identify clearly defined reproductive structures (*i.e.* gametangia). But more recently Lemoigne (1968, 1969) has published results of his examination of the axes of *R. gwynne-vaughanii,* and he gives photos of structures that certainly look like perfectly good archegonia in longitudinal section. These studies may well stimulate further interest in the gametophytes of such living genera as *Psilotum, Lycopodium, Botrychium, Helminthostachys,* and *Ophioglossum.*

The nature of the sporangiate organs of another of the "well-known" members of the Rhynie flora, *Asteroxylon,* has long been in doubt. In 1964 Lyon published a short note showing a part of an *Asteroxylon* axis with sporangia borne terminally on short stalks which are scattered among the leaves. A student of Lyon's has made a more detailed study which hopefully will appear soon, but it may be noted that the sporangiate stalks are much less numerous than the vegetative leaves and the two do not seem to be interrelated. There is some comparison with *Kaulangiophyton akantha* (Gensel *et al.,* 1969) from the Trout Valley flora (Fig. 10) of northern Marine, but the emergences of the latter are very different from those of *Asteroxylon.* Banks (1968: 79) now classifies *Asteroxylon* as a lycopod, but it seems to me this stretches the lycopod concept too far; plants like *Asteroxylon* and *Kaulangiophyton* stand apart; they do not fit at all closely into any of the established taxa.

Dr. A. G. Lyon has kindly given me permission to mention a new plant from Rhynie that is presently under study in his laboratory. It is small, with terminal sporangia and axes only a few mm in diameter that bore emergences in the form of unicellular hairs. More will be heard about the Rhynie flora in the next two decades.

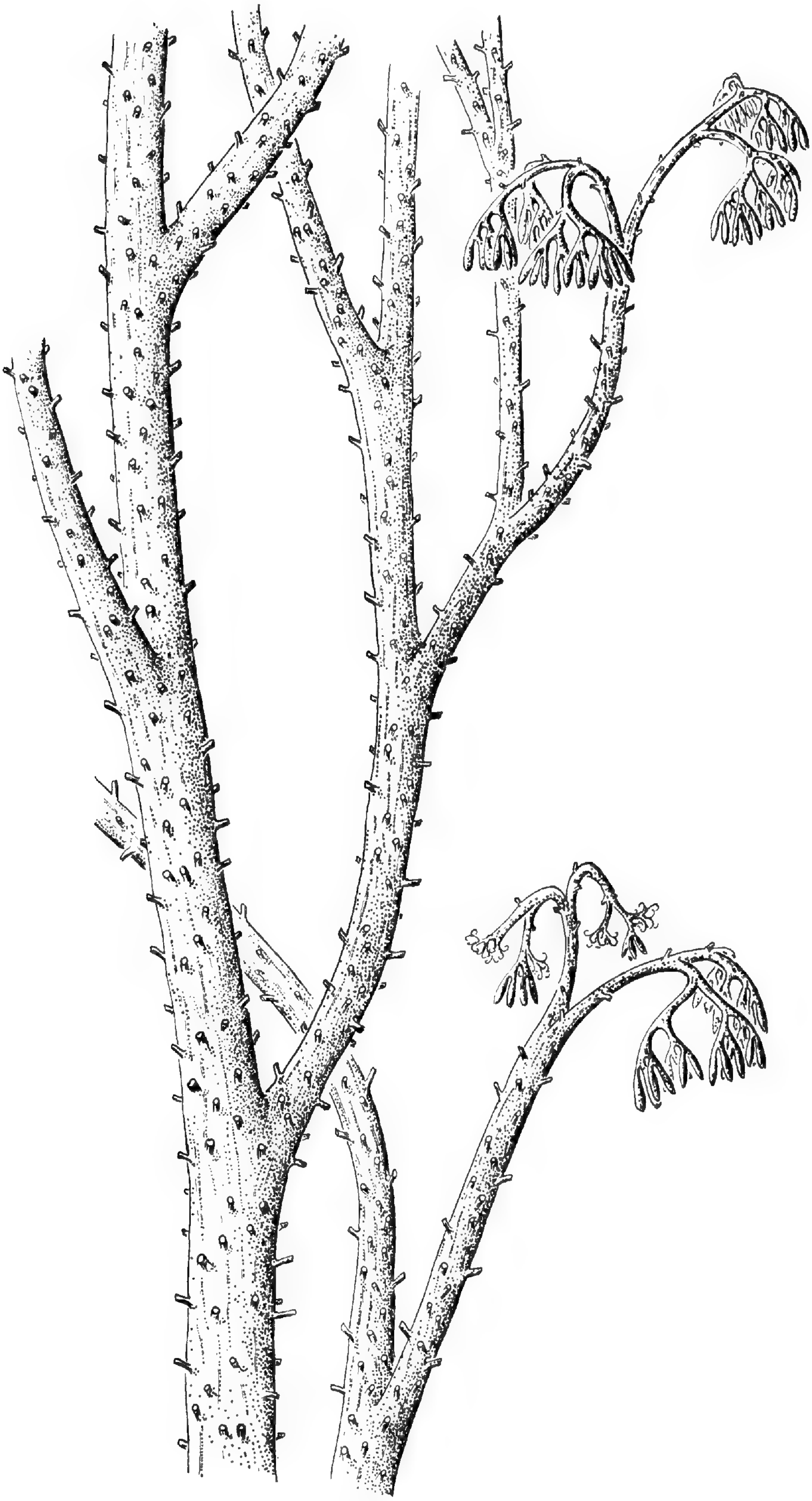


Figure 11. *Psilophyton princeps* Dawson from the Lower Devonian of New Brunswick, Canada (redrawn from a figure by Hueber, 1967).

A few words must be included concerning *Psilophyton princeps*, a primitive early Devonian plant from the Gaspé, and in a sense the "type" of our concept of a psilophyte, which was described by the Canadian geologist-botanist J. W. Dawson in 1859. Although this attracted little attention at the time, it was "revived" after the discovery of the Rhynie plants, and in recent decades a restoration drawing of the plant has found a place in many textbooks. However, it has been realized for some time that Dawson's concept actually combined three different plants. Resulting from their extensive knowledge of early Devonian plants, and much searching through museums for Dawson's original collections, Hueber and Banks (1967) presented a revised description of *P. princeps* (Fig. 11). This was followed by a more detailed account by Hueber in the same year. The genus is now defined as including plants with a pseudomonopodial main axis and dichotomizing branches, the axial system being naked or bearing different types of emergences; the branches may bear terminal paired sporangia in rather dense clusters. The type species, *Psilophyton princeps*, is distinguished by having peg-shaped emergences. Dawson's *Psilophyton princeps* var. *ornatum* (Fig. 12) has been given a new generic name by Hueber (1971), *Sawdonia ornata.* This too is found along the Gaspé coast, and the same plant has been described independently by Ananiev and Stepanov from Siberia; the illustration used here is taken from their recent study (1968). The plant is characteristically spiny, bore its sporangia laterally, and quite clearly is not congeneric with the revised *P. princeps* of Hueber and Banks. Thus the biology of these important land plants is considerably clarified, although the naming falls a little short of complete success. Ananiev and Stepanov have chosen to retain the binomial *Psilophyton princeps* for the original "var. *ornatum*" which Hueber (1971) now calls *Sawdonia ornata.*

Perhaps I may be excused a brief mention of work that is presently going on in my own laboratory, since it seems to fit very well into the charge we have been given to predict progress in the next 20 years. For several years we have been studying an early Devonian flora in northern Maine. We initially became involved in the project to try to aid geologists in determining the age of the beds which are probably either upper Lower Devonian or lower Middle Devonian. Most of the plants indicate the former but one is a little more suggestive of early Middle Devonian age. It is important to note that, in many places, age determinations of these early Devonian horizons are by no means as precise as we would like to have them.

As to the Maine flora itself, *Kaulangiophyton,* mentioned above, is one of the better known members. A description of another, also a new genus, is in press; it seems important in that it gives a clue to the earliest stage in the development of a megaphyll. And during the past winter we have been studying a collection of some four or five species of *Psilophyton* which differ in the nature of their emergences (if present) and in the size of the sporangia; the results should contribute to our knowledge of the evolution of these early and very simple vascular plants. Field work will go on again this summer and hopefully for several more seasons. It is significant that this wealth of information is coming from a small patch of sedimentary rocks in the forests of northern Maine, an area

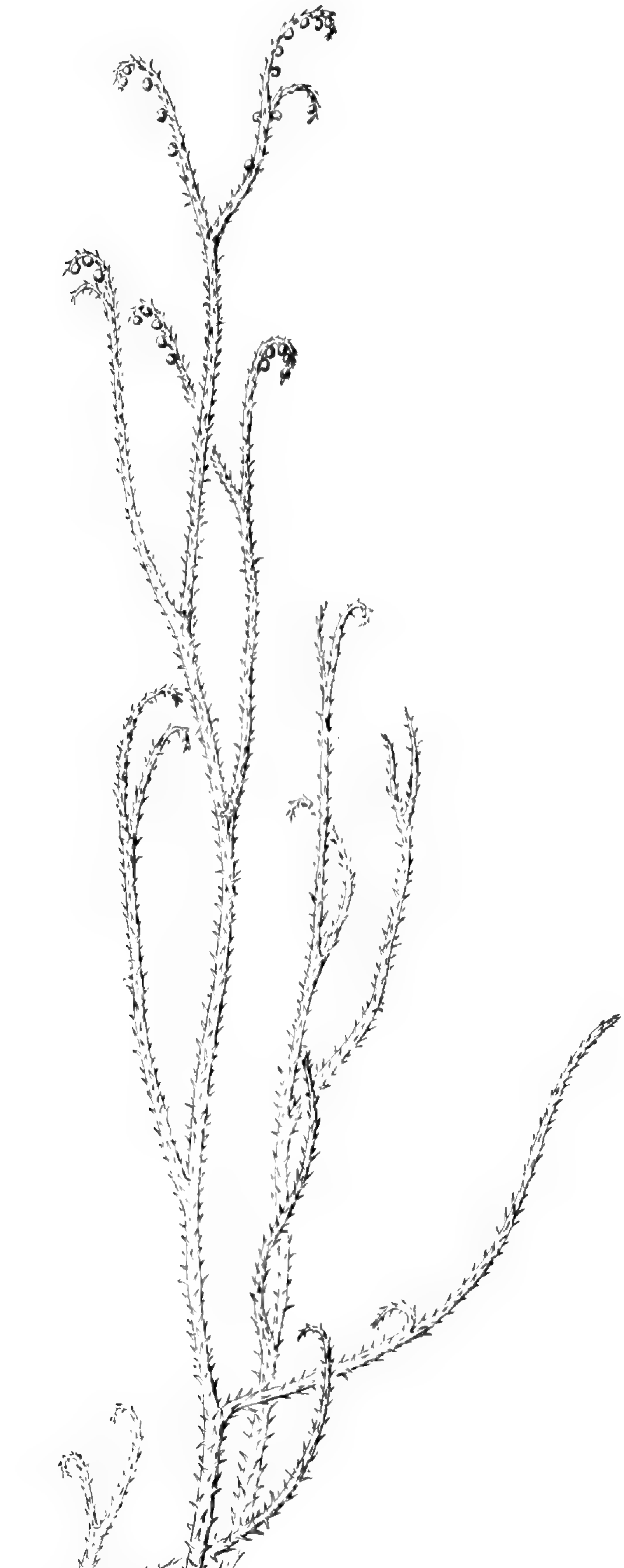


FIGURE 12. *Sawdonia ornata* (Dawson) Hueber, formerly known as *Psilophyton princeps* var. *ornatum* Dawson (from a restoration drawing by Ananiev & Stepanov, 1968).

that was not previously regarded as a likely place to look for fossil plants. How many more such localities will turn up in the next 20 years? It is very possible that there will be quite a few.

At this point I would like to note that Harlan Banks (1968) has done a fine job of bringing together much of the more important, recent discoveries dealing with Devonian plants and early vascular plant evolution. In particular, he has revised our classification of the more primitive early Devonian plants and brought considerable order out of chaos, but discoveries since 1968 indicate that his classification will require modifications in the not too distant future.

Some indications of the increasing complexity of plants by Middle Devonian times may be illustrated by two examples from a quarry in eastern Belgium. *Pseudosporochnus nodosus* (Leclercq & Banks, 1962) is somewhat larger than most of the earlier Devonian plants and shows some differentiation between axes and foliar appendages, but the precise morphology of the latter is still problematical. This is perhaps best regarded as a primitive fern in the broadest sense, but, like other Middle Devonian plants, the clearly defined pteridophytic groups of later times are not readily recognized.

Calamophyton bicephalum (Leclercq & Andrews, 1960) is unique in the morphology of its sporangiate organs; because of a slight tendency for the appendages, foliar or fertile, to be arranged in whorls, it was thought to be a primitive articulate, but the evidence is not very convincing. Both of these plants (*P. nodosus* & *C. bicephalum*) were collected by Prof. Suzanne Leclercq from an old quarry in Goé in eastern Belgium; they are beautifully preserved, and they represent but a portion of her extensive collections. It is safe to predict that Goé will contribute much more to our knowledge of the plant life of this period.

Closing the Gap between Pteridophytes and Seed Plants

All things considered, I believe the most important contribution that paleobotanists have made, during the past quarter century, to our knowledge of plant evolution is a series of discoveries that give us some real clues to the origin of the gymnosperms; the gap in our knowledge between the pteridophytes and the earliest seed plants remains, but it is a much narrower one than it was 25 years ago. This takes us to the Upper Devonian and basal Carboniferous; let's start with two "advanced pteridophytes" and work up in both time and structural complexity. *Tetraxylopteris schmidtii* was first described by Beck (1957) as a plant in which the stems were to 2.5 cm in diameter and bore spirally arranged, radially symmetrical fronds or branches which in turn bore "opposite to subopposite and decussate lateral axes of three orders." The stem has a cruciform primary xylem strand with some secondary wood and a fibrous cortex, foreshadowing pteridosperm features. In 1967 Bonamo and Banks described the fertile parts, which consist of a branch system bearing opposite and decussately arranged, upcurved "sporangial complexes"; the sporangia are abundant, 2–5 mm long and contain spores of one kind which vary in size from 73–176 μ. The second plant, *Rhacophyton ceratangium* Andrews and Phillips (1968) is from the Upper Devonian of West Virginia. It probably attained a height of a meter or two, had a main stem that rarely branched, and bore spirally arranged fronds, flattened but non-

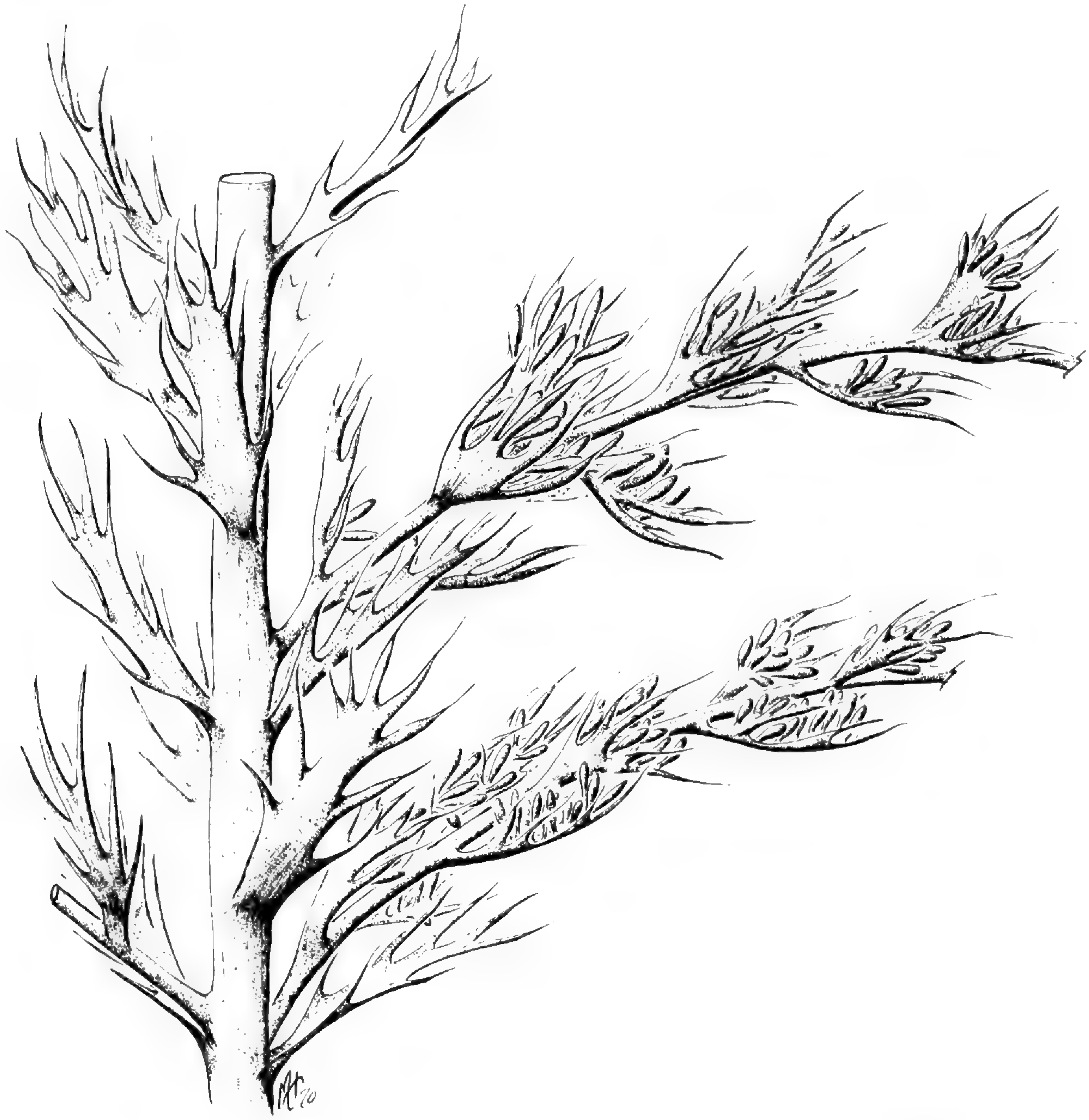


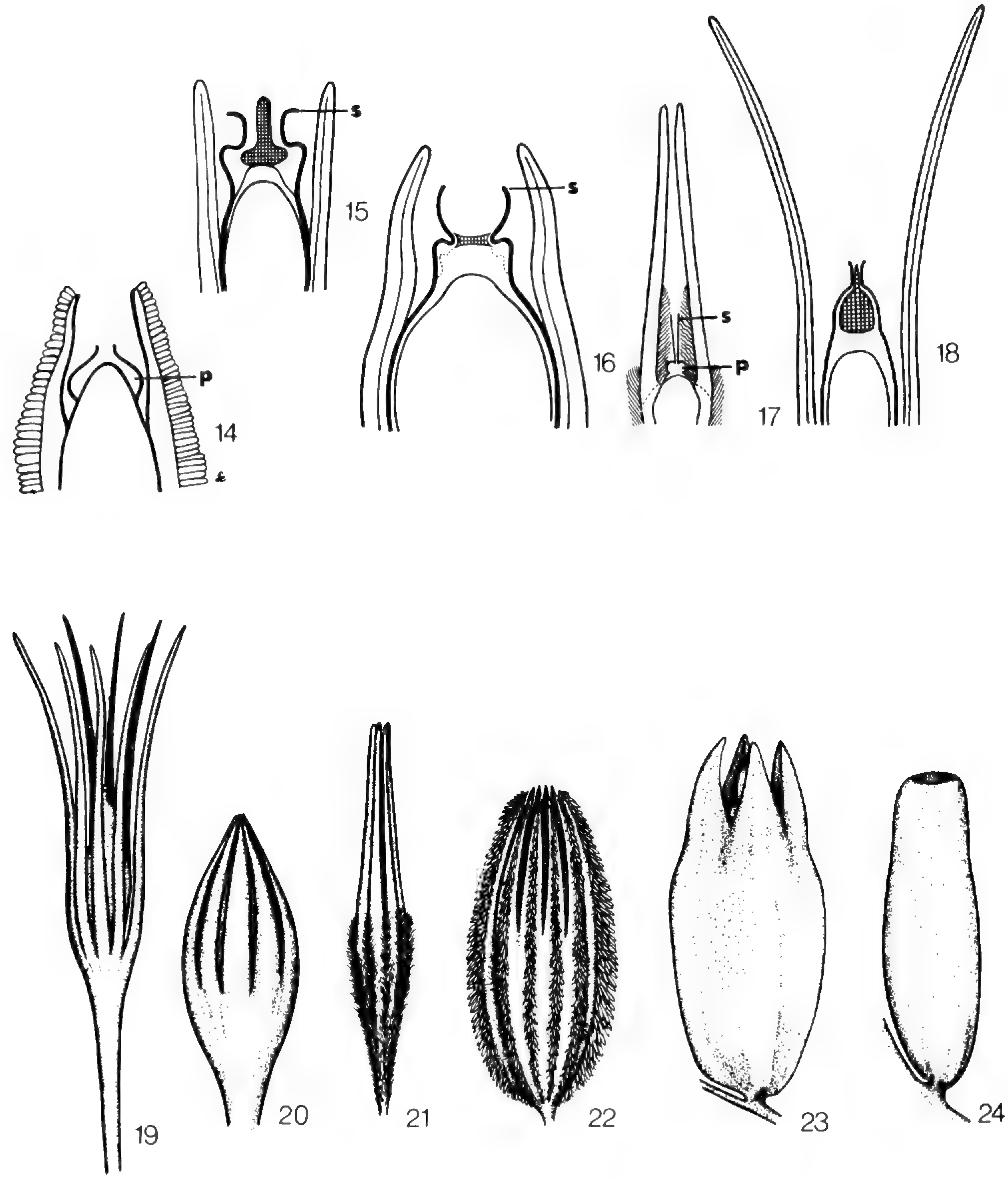
FIGURE 13. *Archaeopteris macilenta* Lesquereux; a portion of the penultimate axis with the basal part of two ultimate branches bearing spirally arranged sterile and fertile leaves (from Phillips, Andrews & Gensel, 1972).

laminate. The stems have some secondary wood and the fertile fronds bear a series of pairs of dense sporangial clusters; the sporangia are exannulate with a unique terminal beak and contain spores 50–60 μ in diameter; it was homosporous. Heterospory did make its appearance before this time and in this connection Chaloner (1970: 367) says, "While we have no clearly heterosporous vascular plants older than Middle Devonian, we have in the largest (greater than 200 μ) Emsian spores evidence of increasing size developed by that stage." Emsian is of upper Lower Devonian age.

Next in the sequence that I am outlining is a group of plants that Beck has gathered together under a new taxon, the Progymnospermopsida. The best known of these at present is *Archaeopteris* (Fig. 13) an Upper Devonian plant that has certainly been studied more intensively by several investigators than most living plants. Briefly, it is a genus of large plants with trunks to five feet in diameter in which the wood is typically gymnospermous (the petrified stems have long been known under the generic name *Callixylon*); the ultimate branch systems are modified into bipinnate pseudofronds which terminate in wedge-shaped leaves that are entire or variously divided and which were formerly called pinnules. The distinctive features here, and probably for the progymnosperm group, are: stems with gymnospermous wood (strong cambial activity), a "fernlike" appearance in the morphology of the ultimate branches, and heterosporous reproduction. Chester Arnold laid much of the foundations of our knowledge of this group of plants with his studies of *Callixylon* anatomy and *Archaeopteris* frond morphology, and in 1939 he demonstrated heterospory for a species from Pennsylvania. In 1960 Beck established the fact of organic connection between the *Callixylon* ("gymnosperm") stem and the *Archaeopteris* (pteridophytic) frond. In 1966 Carluccio *et al.* showed that the presumed bipinnate frond is actually a modified branch system and that the "pinnules" should be regarded as leaves. In 1965 Pettitt demonstrated heterospory for a Canadian species of *Archaeopteris*, and during the past two years we (Phillips, Andrews & Gensel, 1972) have been studying two species from West Virginia, both of which are heterosporous.

It seems most expedient at this point to jump the gap and consider certain studies of primitive basal Carboniferous seeds (Fig. 14–24), and this takes us to a monumental series of investigations by Albert Long that began about 1960. Long initiated a careful search in the volcanic ash deposits of southern Scotland and, with a bare minimum of facilities at his disposal, has given us some of paleobotany's most important results of the present century. Of the many new seeds that he has described, *Genomosperma kidstonii* (Calder) Long is of special interest; the nucellus is free from the "integument," the latter consisting simply of eight filaments that are separate down to the base, and there is no micropyle as the filaments flare outward. In another seed, *Genomosperma latens* Long, the eight integumentary lobes are fused for about one third of their length and come together at the distal end to form a rudimentary micropyle. These two, and other Carboniferous seeds, indicate quite clearly that the integument has evolved from the fusion of a ring of telomes or free filaments surrounding the megasporangium. This does not come as a complete surprise, since several botanists have previously suggested such a sequence of events, as is shown in Figures 19–24.

These Lower Carboniferous seeds display another interesting feature that seems to have been correlated with the primitive stage of development of the integument. The distal part of the nucellus was variously modified into a structure called a *salpinx* that served as a pollen collecting structure prior to the evolution of the micropyle and the pollen drop mechanism. Some of Long's seeds are remarkably well preserved; in *Deltasperma fouldenense* Long, the gametophyte with its archegonia is preserved and pollen grains are present in the pollen chamber. We also have some information on the plants that bore these seeds, but more is needed. In 1961 he described vegetative remains of petrified stems and leaves which he regards as a primitive pteridosperm. The



FIGURES 14–24.—14–18. Early Carboniferous Pteriodosperm seeds, showing modifications of the distal end of the nucellus to form pollen chamber (p) and salpinx (s).—14. *Physostoma elegans* Williamson.—15. *Hydrasperma tenuis* Long.—16. *Eurystoma angulare* Long.—17. *Salpingostoma dasu* Gordon.—18. *Genomosperma kidstonii* (Calder) Long (from Andrews, 1963).—19–24. Some Pteridosperm seeds, showing stages in the degree of fusion of the integument lobes and the development of the microphyle.—19. *Genomosperma kidstoni* (Calder) Long.—20. *Genomosperma latens* Long.—21. *Salpingostoma dasu* Gordon.—22. *Physostoma elegans* Williamson.—23. *Eurystoma angulare* Long.—24. *Stamnostoma huttonense* Long (from Andrews, 1963).

stem is protostelic with some secondary wood; the leaves are dichotomously forked organs with little development of a lamina.

The most recent contribution to this chapter of paleobotanical research is the report of a seed-bearing organ from the Upper Devonian by Pettitt and Beck

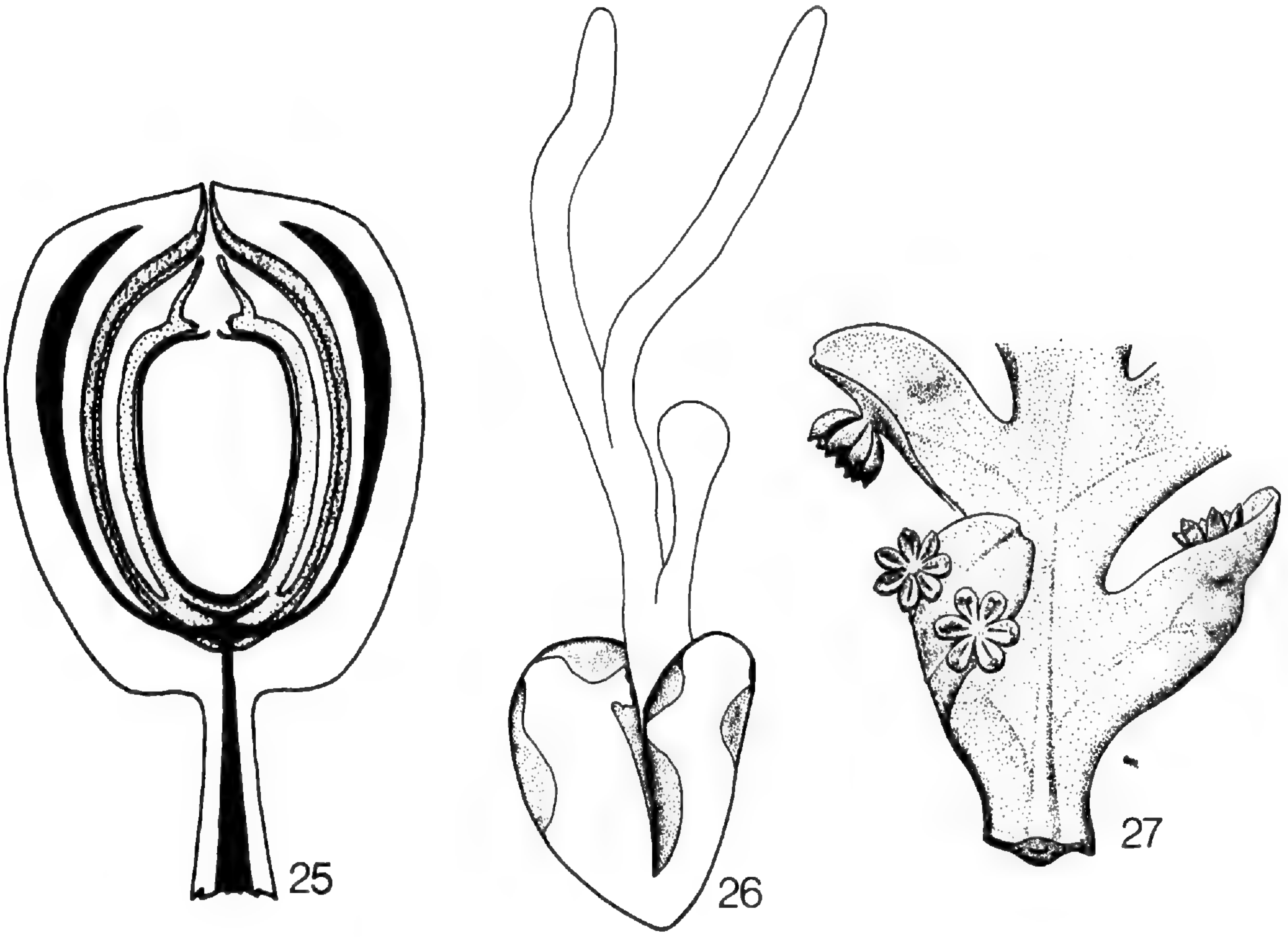
(1968). The fossil, *Archaeosperma arnoldii*, is a two-seeded fructification; the spiny integument of each seed is distally lobed, and the two seeds are partially enclosed by branch endings that form a primitive cupule.

It may be helpful to summarize very briefly these developments in our knowledge of the pteridophyte-gymnosperm transition. In a "pre-Progymnosperm" such as *Rhacophyton*, we find some cambial activity, homospory, clearly defined differentiation into axis and frond, and distinctly modified sporangia. Does the elongated distal end of the sporangium foreshadow the salpinx of Lower Carboniferous seeds? In *Archaeopteris* we find a clear combination of pteridophyte and gymnosperm features: strong cambial activity and advanced pteridophytic (heterosporous) reproduction. And, already at the top of the Devonian and at the base of the Carboniferous, we have a most remarkable series of fossils that afford critical information on the evolution of the integument and modification of the distal part of the nucellus (megasporangium). We now need information on the origin of the telomic lobes that fused together to form the integument. I shall be surprised if we do not know a good deal more about this within the next decade.

THE UPPER CARBONIFEROUS—AMERICAN COAL-BALL STUDIES

Significant results continue to pour forth from the numerous investigators of American coal-balls, petrifactions found in the Upper Carboniferous coals of the Central States.

It is especially impressive when scattered parts can be put together to give us a new whole, a case in point being a plant that typifies the new pteridosperm family Callistophytaceae (Fig. 25–30) proposed by Stidd and Hall (1970*a*), and the preservation of the several organs is superb. The stems were originally described under the name *Callistophyton poroxyloides* by Delevoryas and Morgan (1954); they are rather small, being to 2 cm in diameter with a parenchymatous pith, peripheral primary vascular bundles, and well-developed secondary wood that is typically pteridospermous (*i.e.* the tracheids bear several rows of closely compacted bordered pits, and the rays are several cells wide at the periphery of the wood). Fiber strands and secretory cavities are present in the outer cortex; conspicuous stalked glands are borne on the young stems and leaves. The pollen organs (*Callandrium callistophytoides*) of the plant were borne on the abaxial side of laminate fronds; they consist of 6–7 exannulate sporangia that are fused at the base and contain monosaccate, bladdered pollen (Stidd & Hall, 1970*b*). The seeds, originally described by Eggert and Delevoryas (1960) under the name *Callospermarion pusillum*, were borne terminally on elongate stalks; they have a three-layered integument that is free from the nucellus and a simple pollen chamber in which pollen has been found that is identical with the pollen borne in the *Callandrium* sporangia. All of these fossils come from the classic Berryville, Illinois, coal-ball locality; they are not all found in organic connection but, in addition to the evidence from the pollen cited above, the fertile leaves and seeds contain secretory cavities that are closely comparable to those present in the stem (Stidd & Hall, 1970*a*). The most recent bit of evidence has been contributed by Rothwell (1972), who has found a pollen grain with a branched pollen tube



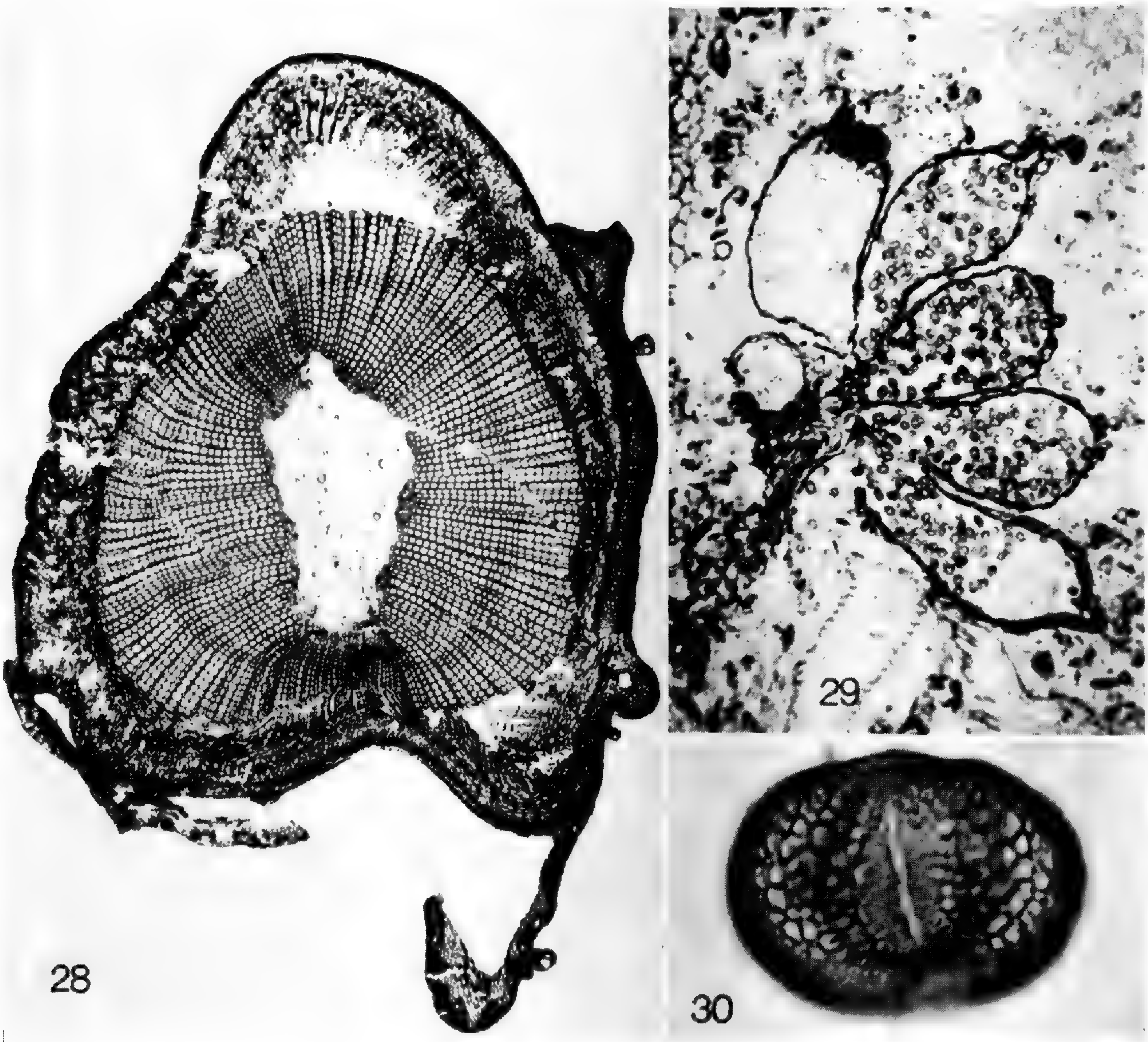
FIGURES 25–27. The new pteridosperm family Callistophytaceae.—25. Longitudinal section through the ovule of *Callospermarion pussilum* (from Stidd & Hall, 1970*a*).—26. Pollen grain with branched tube (from Rothwell, 1972).—27. Reconstruction of part of fertile frond (from Stidd & Hall, 1970*b*).

in one of the seeds of the plant; it was not determined whether the pollen tube was haustorial or siphonogamous (a sperm-carrying pollen tube), but it does suggest a more advanced microgametophyte than is known for previously described pteridosperms. Other features, in summary, that are distinctive are: axillary branching, exannulate, synangia borne on a laminate frond, noncupulate seeds, and bladdered pollen. It seems to me that Stidd and Hall are justified in establishing a new family of pteridosperms on these characters.

Based on a careful study of well-preserved specimens of the lycopod *Paurodendron fraiponti* (Leclercq) Fry, Phillips and Leisman (1966) have given us an informative restoration of the plant. This adds to our knowledge of Pennsylvanian herbaceous lycopods, and it is regarded as being most closely allied to the selaginelloid line.

Compression and petrifaction fossils of stems and fertile foliage of the Marattiaceous tree fern *Psaroniuu* have long been known as a dominant element of the Upper Carboniferous landscapes. Studies by Morgan (1959) and more recently by Stidd (1971) afford a splendid restoration-picture of representative species of this important Upper Carboniferous tree-fern group.

One of the most complete sequences in plant evolution that the fossil record has produced is the one that culminates with the lycopod seed *Lepidocarpon* in the Upper Carboniferous. Beginning with a primitive stage in heterospory in



FIGURES 28–30. The new pteridosperm family Callistophytaceae.—28. Cross section of the stem (*Callistophyton poroxyloides*) (from Delevoryas & Morgan, 1954).—29. Longitudinal section through synangium of *Callandrium callistophytoides* (from Stidd & Hall, 1970*b*).—30. A pollen grain enlarged (from Stidd & Hall, 1970*b*).

the Upper Devonian, we have a series of cones or parts of cones in which the megaspores per sporangium decrease in numbers and increase in size, until one functional one is reached in *Lepidocarpon*, in which the sporangium is enclosed by the sporophyll. A significant and essentially final link in that series is presented by Maxine Abbott (1963) in *Lepidocarpopsis semialata*, in which the sporangium is about half enclosed by the lamina (alation of the pedicel). Finally, Ramanujam and Stewart (1969) have described a *Lepidocarpon* cone with a well-preserved apex in which ontogenetic stages are demonstrated that fit nicely into the racial sequence. A further note may be added here relative to ontogenetic studies in paleobotany; these have been carried out perhaps more often than might be realized, in dealing with stem apices, the axes of the Carboniferous Marattiaceous ferns, and the primary body of the arborescent lycopods and articulates. Delevoryas (1964) has summarized some of the more important studies.

GLOSSOPTERIS AND ANTARCTIC FLORAS

Very few genera of plants have attracted as much attention over the years as *Glossopteris*, the dominant element in the Gondwana flora and of special importance during the past quarter-century because of the great interest in continental drift. In spite of studies by many investigators it has refused to yield satisfactory information concerning its natural affinities. In a series of contributions starting in 1952, Mrs. Plumstead has described several types of reproductive structures attached to the basal part of the leaf. It seems very likely that some of these are seed organs and others are pollen bearing, but they are all known as impressions and clear-cut morphological details have not been forthcoming. There is now a new source of hope on the horizon, and for reasons noted below it is quite possible that we will know a good deal more about *Glossopteris* and other members of its flora in the next 20 years.

Glossopteris has been known from Antarctica for some time, having been discovered there by Scott's expedition. Resulting from several seasons of paleobotanical exploration in Antarctica, J. M. Schopf reported a deposit of petrified peat from a Permian coal bed on Mount Augusta in Central Antarctica in 1970. We have only a brief report on this to date, but the preservation seems comparable to that of the north hemisphere coal-balls, and there is a considerable amount of the material available, if somewhat difficult to transport. He has also discussed at some length (1971) the probable sequence of events in the mineralization process, a subject that has remained shrouded in obscurity in spite of the many studies of petrified plant materials over the past 150 years.

Before leaving the Permian it is fitting to mention Mrs. Neuburg's studies of fossil mosses. Although several significant papers have appeared that extend our knowledge of the history of the bryophytes, her investigations of mosses from the Lower and Upper Permian sediments of the Kuznetzk, Tungas, and Pechora basins in the U.S.S.R. stand out as a real landmark. In her chief study (Neuburg, 1960) she described 14 species, including 12 new species and 9 new genera. Eleven species are placed in the Bryales or are closely related to that order; the other three are placed in the Protosphagnales and are either primitive sphagnums or the immediate progenitors of the Sphagnales.

Lacey (1969) has prepared a compact and useful summary of our knowledge of the fossil bryophytes, and in the second volume of the *Traité de Paleobotanique* Jovet-Ast (1967) gives a definitive and beautifully illustrated review.

THE CYCADS AND SOME NOTES ON THE TRIASSIC

We have several reports centering around the cycads or possible cycads that bring renewed interest to that group. Mamay (1969) has given a preliminary report on two reproductive organs from the Lower Permian: "new genus A" consists of an axis bearing two rows of seeds and is presumed to have borne distally a *Taeniopteris* type leaf; "new genus B" is laminar, with a slightly modified, foliar blade partly enveloping the ovules like the marginal indusia of some ferns. Mamay notes that the latter is "morphologically intermediate between *Spermopteris* [see below], with its undifferentiated lamina, and the modern *Cycas* megasporophyll, with its elaminar fertile base." He discusses two possible evolutionary series that might have followed from "new genus B": first, loss of the lamina could have resulted in a typical *Cycas* megasporophyll; second, continued development of the lamina, ultimately enclosing the ovules, could have resulted in an angiospermous carpel. *Spermopteris* was described by Cridland and Morris (1960) as a fossil with *Taeniopetris* foliage bearing a row of seeds on the abaxial surface on each side of the midvein. It is from the Upper Pennsylvanian of Kansas and was referred to the pteridosperms. In this context it is appropriate to mention Taylor's (1970) description of a well-preserved microsporangiate cone, *Lasiostrobus polysacci*, found in an Upper Pennsylvanian coal-ball in Illinois. It seems most likely that it should be referred to the Coniferales, but it is possible that it is the cone of a cycad.

In Triassic times the cycad lines (Cycadales and Bennettitales) appear in the full zenith of their racial development. But the Triassic in North America has not been a notably productive age for paleobotany; very fragmentary remains have been reported occasionally from the Connecticut River Valley and in years gone by the coal mines of Virginia and North Carolina produced some plants. The recent discovery of a very rich deposit in a shale quarry in central North Carolina gives promise of much new information; the assemblage includes numerous ferns and cycads in a fine state of preservation; for example, in an introductory article on the flora Delevoryas (1970) describes a nearly complete new cycad, including the stem, foliage, and a probable pollen cone.

The Origin of the Angiosperms and Tertiary Paleobotany

There have been no startling discoveries that clarify the origin of the flowering plants, and I know of no reason to prophesy that this will be accomplished in the near future. In 1960, Scott, Barghoorn, and Leopold gave a useful summary and appraisal of presumed pre-Cretaceous angiosperm fossils, concluding that most or all of them are doubtful, and I interpret their conclusions to be that the group probably originated in mid-Mesozoic times. In a rebuttal article under the same title ("How old are the angiosperms") Axelrod (1961) gives his views in favor of a late Paleozoic origin. We simply need more evidence, but the advanced stage of development attained by the cupule (progenitor of the carpel?) in early Carboniferous times, as shown by Long's studies, might be a point in favor of Axelrod's opinion.

Certainly the most tantalizing apparent pre-Cretaceous angiosperm, and the most difficult bit of evidence to brush aside, is Roland Brown's (1956) *Sanmiguellia lewisii* from the Triassic of Colorado. This is based on impressions of characteristically pleated, palm-like leaves borne on a slender stem. If they had been found in a Cretaceous or Tertiary deposit, no one would question their identification as a palm. The stratigraphy is unquestioned, but unfortunately the fossils are only impressions. Hopefully the future will yield some structurally preserved *Sanmiguellia* and thus settle this most interesting and vexing discovery. [Since this was written more recent studies cast doubt on the validity of assigning *Sanmiguellia* to the Palmae (see Taxon 21: 134. 1972).]

Young workers such as Dilcher are using improved techniques to extract more information from the fossil record. I think the studies that he and his students have under way with the Tertiary floras of Tennessee promise a new and very productive era in Tertiary paleobotany. There are numerous Eocene-age clay deposits in western Tennessee that are being actively mined, and some of them produce a remarkable wealth of fossil material. In a single pit one may find whole leaf compressions, lignitic seeds, fruits, and wood, as well as pollen. Of the clay pit at Puryear, Berry (1916: 47) wrote: "This is the most remarkable leaf-bearing clay that I have ever seen at any geologic horizon." When I lived in St. Louis, I used to take students there to dig, and they readily shared Berry's enthusiasm. Dilcher initiated his investigations in this area with a contribution dealing with some remarkably well-preserved epiphyllous fungi (1965) which are referred to the Erysiphales and Microthyriales. Several other papers have appeared, and two studies are in press, which he has kindly allowed me to read in manuscript. As an example of the kind of information that the leaf compressions are yielding, Dilcher finds that in leaves presently known as *Dryophyllum tennesseensis* (a common leaf type in the clay pits of both Tennessee and Kentucky, with probable affinities with the Fagaceae) the trichomes borne on different leaves "vary from long loose tufts of 4–5 hairs to short compacted tufts to star-shaped clusters of hairs." . . . Thus the gross morphology of this fossil leaf has remained constant while the nature of the trichomes has changed through Middle Eocene time. Variations in the cuticular features of other forms is also becoming evident as work with other fossil leaves progresses." The several clay pits in the general area are known to cover a span of about seven million years in the Middle Eocene. It seems safe to predict that this region alone will contribute some exceptionally accurate and detailed information on the floristics, evolution, and climate of the Eocene.

In 1933 Reid and Chandler produced their classic *Flora of the London Clay*, a monumental study of pyritized seeds and fruits found in Eocene deposits along the south England coast. Miss Chandler has added three more contributions dealing with other English Tertiary floras (1961, 1962, 1963) plus a summary volume in 1964. The summary volume includes a useful review of recent work as well as studies in progress by continental paleobotanists.

In reference to what may be expected in the next 25 years, Miss Chandler makes a special point of noting the need for constant observation of fossiliferous localities—frequent visits by paleobotanists and perhaps aided by local collectors. One may encounter a point of diminishing returns, but this should not lead to abandoning the site. Hamshaw Thomas once told me that his colleagues said he was wasting his time when he started digging at Cayton Bay in Yorkshire, but he found the Caytoniales, and a great many other things have come from there in recent decades. Tom Harris and his students have turned up many new plants in the Yorkshire beds, and he is presently at work on the fourth and fifth volumes of his great summary account of the Yorkshire Jurassic plants—a splendid source of information on plants of that age.

Finally, I have chosen to add a few words on recent studies of amber (fossil resin) because it is a unique botanical product of some economic importance; it may contain fossil plants and animals, and there is much that remains to be learned about it. Jean Langenheim (1964, 1969) has produced two studies that are especially informative dealing with the chemistry, botanical origin, and fossil contents of ambers. Although amber, in the broad sense, occurs at many localities from the Carboniferous on, it has been found chiefly in Cretaceous and Tertiary deposits. The Cretaceous ambers are probably derived mostly from coniferous trees, whereas the Tertiary ambers come, at least in part, from a considerable number of angiosperms. Langenheim's 1964 paper, which is a very readable account, deals in particular with the classic Baltic deposits, probably of early Tertiary age, and the Chiapas amber of southern Mexico. Insects and numerous other animal groups have been found entombed in the fossil resin, and the classic works of Conwentz (1886, 1890) reveal the remarkable flowers preserved in the Baltic amber. There is much that remains to be learned about amber such as the chemistry of different resins, pollen content, and correlation with the plants that produced it.

Some Mesozoic and Tertiary Plant Studies in the Soviet Union

Several colleagues have kindly aided me in sorting out the more important contributions of the past quarter century, and I am grateful to them for informing me of studies that might well have escaped my attention. There is a language problem with the rather voluminous Soviet literature, and like many of my colleagues I try to keep up with publications falling within my own research area. It has not been possible for me to obtain translations of all of the important studies, and I am, therefore, especially thankful to Dr. V. A. Samylina and Dr. S. G. Zhilin (Komarov Botanical Institute, Leningrad) for literature summaries of Mesozoic and Tertiary studies in their country. It is possible here to note only a few of the highlights in the abundant Soviet paleobotanical literature of recent decades; a much more complete listing may be found in the eight published numbers of the *World Report on Paleobotany* (Boureau, 1956–71).

Rich Triassic floras are known in the U.S.S.R in the Pechorsk Basin, the Donbass, the Urals, Taimyr, the Tungussk Basin, and several other areas. This is especially encouraging in view of the relative paucity, world-wide, of our knowledge of the vegetation of the Triassic. A summary work on these floras has recently been published under the title *Paleozoic and Mesozoic Floras of Eurasia and the Phytogeography of this Time* by V. A. Vakhrameev, I. A. Dobruskina, E. D. Zaklinskaya, and S. V. Meyen (1970).

Several comprehensive works dealing with Jurassic plants have appeared, among the more important being studies by Vakhrameev (1962, 1964, 1966, 1967) and Vakhrameev and Doludenko (1961).

V. A. Samylina is responsible for several important studies of Arctic and Cretaceous floras (1963, 1968). An especially significant treatment of the Tertiary floras is the *Oligocene Flora of Mt. Ashutas in Kazakhstan.* This is based on collections made in 1928 by Maria F. Neuburg. The study was initiated before the Second World War by I. V. Palibin and his students K. K. Shaparenko and A. V. Yarmolenko; the last two were killed in the war, and Palibin died in 1949, the work being completed by Krishtofovich and others in 1956.

P. I. Dorofeev is well known for his numerous studies of Tertiary seeds and fruits (1960, 1963; Dorofeev & Tiulina, 1962).

A great encyclopaedic work that deserves special mention is the *Fundamentals* *of Paleontology* (15 volumes in all) of which two volumes are devoted to fossil plants: one includes the Algae and Pteridophytes, and the other deals with Gymnosperms and Angiosperms, both being under the editorship of V. A. Vakhrameev, G. P. Radchenko, and A. L. Takhtajan (1963). In this category it is appropriate to mention Takhtajan's recent book *Flowering Plants, Origin and Dispersal,* an excellent text that is fortunately available in an English edition (1969).

Finally, I would mention the works of A. N. Krishtofovich, probably the greatest name in Soviet paleobotany at the time of his death in 1953. Some of his better-known works, of which he was either author or editor, actually appeared a few years later, including his textbook *Paleobotany* (1956*a*) and a *History of Paleobotany in the USSR* (1956*b*).

BIBLIOGRAPHY

ABBOTT, M. L. 1963. Lycopod fructifications from the Upper Freeport (No. 7) coal in southeastern Ohio. Palaeontographica 112B: 93–118.

ANANIEV, A. R. & S. A. STEPANOV. 1968. Finds of sporogenous organs of *Psilophyton princeps* Dawson emend. Halle in the Lower Devonian of the South-Minusunsk trough. Pp. 30–46, *in* "New Materials on the Stratigraphy and Paleontology of the Lower and Middle Paleozoic of Western Siberia." Vol. 202.

——— & ———. 1969. The first finding of *Psilophyton* flora in the Lower Devonian Salairskij Ridge (West Siberia). Trudy Tomsk. Gosud. Univ. Kujbyšev 203: 13–28.

ANDREWS, H. N. 1963. Early seed plants. Science 142: 925–931.

——— & T. L. PHILLIPS. 1968. *Rhacophyton* from the Upper Devonian of West Virginia. Jour. Linn. Soc. Bot. 61: 37–64.

ARNOLD, C. A. 1939. Observations of fossil plants from the Devonian of eastern North America. IV. Plant remains from the Catskill Delta deposits of northern Pennsylvania and southern New York. Contr. Mus. Paleont. Univ. Michigan 5: 271–314.

———. 1968. Current trends in paleobotany. Earth-Sci. Rev. 4: 283–309.

AXELROD, D. I. 1961. How old are the angiosperms? Amer. Jour. Sci. 259: 447–459.

BANKS, H. P. 1968. The early history of land plants. Pp. 73–107, *in* E. T. Drake (editor), "Evolution and Environment." Yale Univ. Press.

———. 1970. [Introduction to:] Major evolutionary events and the geological record of plants. Biol. Rev. 45: 317–454. [Contains articles by W. G. Chaloner, C. B. Beck, J. Pettitt, J. Muller.]

BARGHOORN, E. S. & J. W. SCHOPF. 1965. Microorganisms from the Late Precambrian of Central Australia. Science 150: 337–339.

——— & ———. 1966. Microorganisms three billion years ago from the Precambrian of South Africa. Science 152: 758–763.

——— & S. A. TYLER. 1965. Microorganisms from the Gunflint chert. Science 147: 563–577.

BECK, C. B. 1957. *Tetraxylopteris schmidtii* gen. et sp. nov., a probable pteridosperm precursor from the Devonian of New York. Amer. Jour. Bot. 44: 350–367.

———. 1960*a*. Connection bewteen *Archaeopteris* and *Callixylon.* Science 131: 1524–1525.

———. 1960*b*. The identity of *Archaeopteris* and *Callixylon.* Brittonia 12: 351–368.

———. 1962. Reconstructions of *Archaeopteris,* and further considerations of its phylogenetic position. Amer. Jour. Bot. 49: 373–382.

———. 1971. On the anatomy and morphology of lateral branch systems of *Archeopteris.* Amer. Jour. Bot. 58: 758–784.

BERRY, E. W. 1916. The Lower Eocene floras of southeastern North America. U.S. Geol. Sur. Prof. Pap. 91. 481 pp.

BONAMO, P. M. & H. P. BANKS. 1967. *Tetraxylopteris schmidtii*: its fertile parts and its relationships within the Aneurophytales. Amer. Jour. Bot. 54: 755–768.

BOUREAU, E. 1956–71. World Report on Palaeobotany. *in* Regnum Veg. 7(1956), 11(1958), 19(1960), 24(1962), 35(1964), 42(1966), 57(1968), 78(1971).

———. 1964–70. Traité de Paleobotanique. Vol. 2. Bryophyta, Psilophyta, Lycophyta. 845 pp. 1967.—Vol. 3. Sphenophyta, Noeggerathiophyta. 544 pp. 1964.—Vol. 4. Filicophyta. 519 pp. Masson et Cie, Paris. 1970.

Brown, R. W. 1956. Palmlike plants from the Dolores formation (Triassic) southwestern Colorado. U.S. Geol. Sur. Prof. Pap. 274-H: 205–209.

Carluccio, L. M., F. M. Hueber & H. P. Banks. 1966. *Archaeopteris macilenta*, anatomy and morphology of its frond. Amer. Jour. Bot. 53: 719–730.

Chaloner, W. G. 1970. The rise of the first land plants. Biol. Rev. 45: 353–377.

Chandler, M. E. J. 1961. The Lower Tertiary floras of Southern England. I. Paleocene flora, London Clay flora (Supplement). Brit. Mus. (Nat. Hist.) 354 pp., 34 pls.

———. 1962. The Lower Tertiary floras of Southern England. II. Flora of the Pipe-clay series of Dorset (Lower Bagshot). Brit. Mus. (Nat. Hist.) 176 pp., 29 pls.

———. 1963. The Lower Tertiary floras of Southern England. III. Flora of the Bournemouth beds; the Bascombe and the Highcliff sands. Brit. Mus. (Nat. Hist.) 169 pp., 25 pls.

———. 1964. The Lower Tertiary floras of Southern England. IV. A summary and survey of findings in the light of recent botanical observations. Brit. Mus. (Nat. Hist.) 151 pp., 4 pls.

Conwentz, H. 1886. Die Flora des Bernsteins. Vol. 2. Die Angiospermen des Bernsteins. Danzig. 140 p., 13 pls.

———. 1890. Monographie der Baltischen Bernsteinbäume. Danzig. 151 p., 18 pls.

Cridland, A. A. & J. E. Morris. 1960. *Spermopteris*, a new genus of pteridosperms from the Upper Pennsylvanian series of Kansas. Amer. Jour. Bot. 47: 855–859.

Dawson, J. W. 1859. On fossil plants from the Devonian rocks of Canada. Quart. Jour. Geol. Soc. London 15: 477–488.

Delevoryas, T. 1964. Ontogenetic studies of fossil plants. Phytomorphology 14: 299–314.

———. 1970. Plant life in the Triassic of North Carolina. Discovery 6: 15–22.

——— & J. Morgan. 1954. A new pteridosperm from Upper Pennsylvanian deposits of North America. Palaeontographica 96B: 12–23.

Dilcher, D. L. 1965. Epiphyllous fungi from Eocene deposits in western Tennessee, U.S.A. Palaeontographica 116B: 1–54.

——— & G. E. Dolph. 1970. Fossil leaves of *Dendropanax* from Eocene sediments of southeastern North America. Amer. Jour. Bot. 57: 106–113.

——— & B. Mehrotra. 1969. A study of leaf compressions of *Knightiophyllum* from Eocene deposits of southeastern North America. Amer. Jour. Bot. 56: 936–943.

Dorf, E. 1964. The petrified forests of Yellowstone Park. Sci. Amer. 210: 106–113.

Dorofeev, P. I. 1960. On paleocarpological methods in paleobotany. Paleont. Žurn. 1: 128–141.

———. 1963. The Tertiary floras of western Siberia. Bot. Inst. Komarov, Leningrad. 316 pp., 50 pls.

——— & L. N. Tiulina. 1962. Miocene flora of Mammoth Hill on the Aldan. Probl. Bot. 6: 46–54.

Edwards, D. 1970*a*. Fertile Rhyniophytina from the Lower Devonian of Britain. Palaeontology 13: 451–461.

———. 1970*b*. Further observations on the Lower Devonian plant, *Gosslingia breconensis* Heard. Phil. Trans. Roy. Soc. London 258B: 225–243.

Eggert, D. A. & T. Delevoryas. 1960. *Callospermarion*—a new seed genus from the Upper Pennsylvanian of Illinois. Phytomorphology 10: 131–138.

Engel, A. E. J., C. C. Engel, G. O. W. Kremp & C. M. Drew. 1968. Alga-like forms in Onverwacht Series, South Africa: oldest recognized lifelike forms on Earth. Science 161: 1005–1008.

Fry, W. L. 1954. A study of the Carboniferous lycopod, *Paurodendron*, gen. nov. Amer. Jour. Bot. 41: 415–428.

Gensel, P. G., A. E. Kasper & H. N. Andrews. 1969. *Kaulangiophyton*, a new genus of plants from the Devonian of Maine. Bull. Torrey Bot. Club 96: 265–276.

Glaessner, M. F. 1961. Pre-Cambrian animals. Sci. Amer. 216(3): 72–78.

Hall, J. W. & B. M. Stidd. 1971. Ontogeny of *Vesicaspora*, a late Pennsylvanian pollen grain. Palaeontology 14: 431–436.

Höeg, O. A. 1967. Ordre Incertae Sedis des Barinophytales. Pp. 400–433, *in* "Traité de Paleobotanique." Vol. 2.

Hueber, F. M. 1967. *Psilophyton*: the genus and the concept. Pp. 815–822, *in* D. H. Oswald (editor), "International Symposium on the Devonian System, Calgary." Vol. 2.

———. 1971. *Sawdonia ornata*: a new name for *Psilophyton princeps* var. *ornatum*. Taxon 20: 641–652.

——— & H. P. BANKS. 1967. *Psilophyton princeps*: the search for organic connection. Taxon 16: 81–160.

JOVET-AST, S. 1967. Bryophyta. Pp. 17–186, *in* E. Boureau (editor), "Traité de Paleobotanique." Vol. 2.

KIDSTON, R. & W. H. LANG. 1917. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part I. Trans. Roy. Soc. Edinburgh 51: 761–784.

KRYSHTOFOVICH, A. N. 1956*a*. Paleobotany. Leningrad. 650 pp.

———. 1956*b*. Paleobotanica. I. Bot. Inst. Komarov, Leningrad. 171 pp., 61 pls.

LACEY, W. S. 1969. Fossil Bryophytes. Biol. Rev. 44: 189–205.

LANG, W. H. 1937. On the plant-remains from the Downtonian of England and Wales. Phil. Trans. Roy. Soc. London 227B: 245–291.

LANGENHEIM, J. H. 1964. Present status of botanical studies of ambers. Bot. Mus. Leafl. 20: 225–287.

———. 1969. Amber: a botanical inquiry. Science 163: 1157–1169.

LECLERCQ, S. & H. N. ANDREWS. 1960. *Calamophyton bicephalum*, a new species from the Middle Devonian of Belgium. Ann. Missouri Bot. Gard. 47: 1–23.

——— & H. P. BANKS. 1962. *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with cladoxylalean affinities. Palaeontographica 110B: 1–34.

LEMOIGNE, YVES. 1968. Observations d'archegones portes par des axes vascularises du type *Rhynia gwynne-vaughani* Kidston et Lang. Existence de gametophytes vascularises chez des Psilophytales du Devonian. Bull. Mens. Soc. Linn. Soc. Bot. Lyon 37: 148–149.

———. 1969. Contribution à la connaissance du gametophyte *Rhynia gwynne-vaughani* Kidston et Lang: probleme des protuberances et processus de ramification. Bull. Mens. Soc. Linn. Soc. Bot. Lyon 38: 94–102.

LONG, A. G. 1960*a*. On the structure of *Calymmatotheca kidstoni* Calder (emended) and *Genomosperma latens* gen. et sp. nov. from the Calciferous Sandstone Series of Berwickshire. Trans. Roy. Soc. Edinburgh 64: 29–44.

———. 1960*b*. *Stamnostoma huttonense* gen. et sp. nov.—a pteridosperm seed and cupule from the Calciferous Sandstone Series of Berwickshire. Trans. Roy. Soc. Edinburgh 64: 201–215.

———. 1961. *Tristichia ovensi* gen. et sp. nov., a protostelic Lower Carboniferous pteridosperm from Berwickshire and East Lothian, with an account of some associated seeds and cupules. Trans. Roy. Soc. Edinburgh 64: 477–492.

———. 1966. Some Lower Carboniferous fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules, and carpels. Trans. Roy. Soc. Edinburgh 66: 345–375.

LYON, A. G. 1964. The probable fertile region of *Asteroxylon mackiei* K. and L. Nature 203: 1082–1083.

MAMAY, S. H. 1969. Cycads: fossil evidence of late Paleozoic origin. Science 164: 295–296.

MEEUSE, A. D. J. 1963. From ovule to ovary: a contribution to the phylogeny of the megasporangium. Acta Biotheor. 16: 127–182, Addendum 3 pp.

MERKER, H. 1958. Zum fehlenden Gliede der Rhynienflora. Bot. Not. 111: 608–618.

———. 1959. Analyse der Rhynien-Basis und Nachweis des Gametophyten. Bot. Not. 112: 441–452.

MORGAN, J. 1959. The morphology and anatomy of American species of the genus *Psaronius*. Illinois Biol. Monogr. 27. 108 pp.

NEUBURG, M. F. 1958. Permian true mosses of Angaraland. Jour. Palaeontol. Soc. India 3: 22–29.

———. 1960. Leafy mosses from the Permian deposits of Angarida. Trudy Geol. Inst. Leningrad 19: 1–104.

OBRHEL, J. 1962. Die Flora der Pridoli-Schichten (Budnany-Stufe) des mittelbohmischen Silurs. Geologie 11: 83–97.

PANT, D. D. 1962. The gametophyte of the Psilophytales. Pp. 276–301, *in* P. Maheshwari (editor), "Proceedings of the Summer School of Botany, Darjeeling, 1960." New Delhi.

PETTITT, J. M. 1965. Two heterosporous plants from the Upper Devonian of North America. Bull. Brit. Mus. (Nat. Hist.), Geol. 10: 83–92.

——— & C. B. BECK. 1968. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America. Contr. Mus. Paleontol. Univ. Michigan 22: 139–154.

PHILLIPS, T. L., H. N. ANDREWS & P. G. GENSEL. 1972. Two heterosporous species of *Archaeopteris* from the Upper Devonian of West Virginia. Palaeontographica 139B: 47–71.

——— & G. A. LEISMAN. 1966. *Paurodendron*, a rhizomorphic lycopod. Amer. Jour. Bot. 53: 1086–1100.

PLUMSTEAD, E. P. 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. Trans. Geol. Soc. S. Africa 55: 281–328.

———. 1956. On *Ottokaria*, the fructification of *Gangamopteris*. Trans. Geol. Soc. S. Africa 59: 211–236.

———. 1958. Further fructifications of the Glossopteridae and a provisional classification based on them. Trans. Geol. Soc. S. Africa 61: 51–76.

RAMANUJAM, C. G. K. & W. N. STEWART. 1969. A *Lepidocarpon* cone tip from the Pennsylvanian of Illinois. Palaeontographica 127B: 159–167.

REID, E. M. & M. E. J. CHANDLER. 1933. The London Clay flora. Brit. Mus. (Nat. Hist.). 561 pp., 33 pls.

ROTHWELL, G. W. 1972. Evidence of pollen tubes in Paleozoic Pteridosperms. Science 175: 772–774.

SAMYLINA, V. A. 1963. The Mesozoic flora of the lower course of the Aldan River. Paleobotanika 4: 57–139.

———. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. Jour. Linn. Soc. Bot. 61: 207–218.

SCHOPF, J. M. 1965. Anatomy of the axis in *Vertebraria*. Geology and Paleontology of the Antarctic, Antarctic Research Series 6: 217–228. American Geophysical Union.

———. 1970. Petrified peat from a Permian coal bed in Antarctica. Science 169: 274–277.

———. 1971. Notes on plant tissue preservation and mineralization in a Permian deposit of peat from Antarctica. Amer. Jour. Sci. 271: 522–543.

SCHOPF, J. W. 1968. Microflora of the Bitter Springs Formation, late Precambrian, Central Australia. Jour. Paleontol. 42: 651–688.

———. 1969. Recent advances in Precambrian paleobiology. Grana Palynol. 9: 147–168.

——— & E. S. BARGHOORN. 1967. Alga-like fossils from the early Precambrian of South Africa. Science 156: 508–512.

SCOTT, R. A., E. S. BARGHOORN & E. A. LEOPOLD. 1960. How old are the angiosperms? Amer. Jour. Sci. 258A: 284–299.

SCHWEITZER, H.-J. 1966. Die Mitteldevon-Flora von Lindlar (Rheinland). 1. Lycopodiinae. Palaeontographica 118B: 93–112.

———. 1967. Die Oberdevon-Flora der Bareninsel I. *Pseudobornia ursina* Nathorst. Palaeontographica 120B: 116–137.

SIEGEL, S. M. & C. GIUMARRO. 1966. On the culture of a microorganism similar to the Precambrian microfossil *Kakabekia umbellata* Barghoorn in NH_3-rich atmospheres. Proc. Natl. Acad. Sci. U.S.A. 55: 349–353.

——— & B. Z. SIEGEL. 1968. A living organism morphologically comparable to the Precambrian genus *Kakabekia*. Amer. Jour. Bot. 55: 684–687.

STIDD, B. M. 1971. Morphology and anatomy of the frond of *Psaronius*. Palaeontographica 134B: 87–123.

——— & J. W. HALL. 1970*a*. The natural affinity of the Carboniferous seed, *Callospermarion*. Amer. Jour. Bot. 57: 827–836.

——— & ———. 1970*b*. *Callandrium callistophytoides*, gen. et sp. nov., the probable pollen-bearing organ of the seed fern, *Callistophyton*. Amer. Jour. Bot. 57: 394–403.

TAYLOR, T. N. 1970. *Lasiostrobus* gen. n., a staminate strobilus of gymnospermous affinity from the Pennsylvanian of North America. Amer. Jour. Bot. 57: 670–690.

TYLER, S. A. & E. S. BARGHOORN. 1954. Occurrence of structurally preserved plants in Pre-Cambrian rocks of the Canadian shield. Science 119: 606–608.

VAKHRAMEEV, V. A. 1962. Jurassic floras of the Indo-European and Siberian botanical-geographical regions. Comm. Strat. Congr. Geol. Int. Coll. Jurass. Luxembourg, 1962: 1–27.

———. 1964. Jurassic and early Cretaceous floras of Eurasia and the paleofloristic provinces of this period. Trans. Geol. Inst. Acad. Sci. U.S.S.R. 102.

———. 1966. The late Cretaceous floras from the USSR Pacific coast, their stratigraphic range and peculiarities of composition. Izv. Akad. Nauk S.S.S.R., Ser. Geol. 3: 76–87.

———. 1967. Results of the investigation of Mesozoic floras of the U.S.S.R. (1917–1967). Bot. Žurn. (Moscow & Leningrad) 52: 1713–1722.

——— & M. P. DOLUDENKO. 1961. Flora of the Upper Jurassic and Lower Cretaceous of the Burinsk Basin and its stratigraphic significance. Trudy Geol. Inst. Akad. Nauk S.S.S.R. 54: 1–136.

———, G. P. RADCHENKO & A. L. TAKHTAJAN. 1963. Principles of Paleontology.—Handbook for paleontologists and geologists of the U.S.S.R. Vol. 14. Algae, Bryophyta, Psilophytales, Lycopodiales, Equisetales, Filicales. 698 pp. Vol. 15. Gymnospermae, Angiospermae. 743 pp. Moscow.

WATT, A. D. (editor). Bibliography of American Paleobotany. Paleobotanical Section, Botanical Society of America. [Initially: Report of the Committee on Paleobotany. Nat. Research Council. 1929–1951.]

WOLFE, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño 20: 83–110.

SOME PALEOBOTANICAL TEXTBOOKS

ANDREWS, H. N. 1961. Studies in Paleobotany. John Wiley Co., New York. 487 pp.

ARCHANGELSKY, S. 1970. Fundamentos de Paleobotanica. Univ. Nacional de la Plata, La Plata. 347 pp.

BANKS, H. P. 1970. Evolution and Plants of the Past. Wadsworth Publishing Co., Belmont, California. 170 pp.

DELEVORYAS, T. 1962. Morphology and Evolution of Fossil Plants. Holt, Rinehart and Winston, New York. 189 pp.

EMBERGER, L. 1944. Les Plantes Fossiles dans leurs Rapports avec les Végétaux Vivants. Masson et Cie, Paris. 492 pp.

KRÄUSEL, R. 1950. Versunkene Floren. Waldemar Kramer, Frankfurt am Main. 152 pp.

MÄGDEFRAU, K. 1956. Pälaobiologie der Pflanzen. Ed. 3. Gustav Fischer, Jena. 443 pp.

NĚMEJC, F. 1968. Paleobotanika. Vol. 3. Československá Akademie Ved, Praha.

25 years of botany

PALEOPALYNOLOGY

1947–1972[1]

ALFRED TRAVERSE[2]

It is probably a significant indication of the dynamic youthfulness of "palynology" that one must always begin with definitions. The subject is defined in only the more recent and more exhaustive dictionaries, and there is much uncertainty still about what it does and does not include. As originally introduced by Hyde and Williams (1944), the word palynology was meant to cover all aspects of study of pollen and spores (spores at least primarily of embryophytic plants). At the time, this meant mostly what had previously been called "pollen analysis" or "pollen statistics" of glacial, post-glacial, and recent sediments. Von Post's paper in 1916 on Swedish post-glacial pollen analysis as an indicator of vegetational history is generally accepted as the beginning point of this subject, and the early history is well summarized by Erdtman (1943), Manten (1967), and others. "Palynology" now covers such diverse matters as "mellito-palynology" (the study of pollen in honey) and studies of air-borne pollen and spores as causative agents in human allergic disease.

For the purposes of the present paper I shall quickly shave palynology down to include only fossils—hence the word "paleopalynology" in the title. However, this still leaves an unmanageably large and heterogeneous subject. The reason is pragmatic—everybody interested agrees that all fossil embryophytic spores and pollen are within the pale, but in practical palynology all resistant-walled "organic" (C-H-O) plant microfossils (usually but not always less than $200\,\mu$ in maximum dimension) are termed "palynomorphs" because they are about the size of spores and pollen. The organic requirement eliminates diatom frustules and the whole new and exciting field of nannofossils (coccoliths and discoasters), as all of these objects are mineral and hence are destroyed in palynological maceration. The basic rationale of such maceration is the concentration of organics by selective destruction of mineral matter in the sample and, finally, the selective destruction of relatively nonresistant organic matter, mostly by oxidation. The process concentrates spore and pollen shells (exines) because

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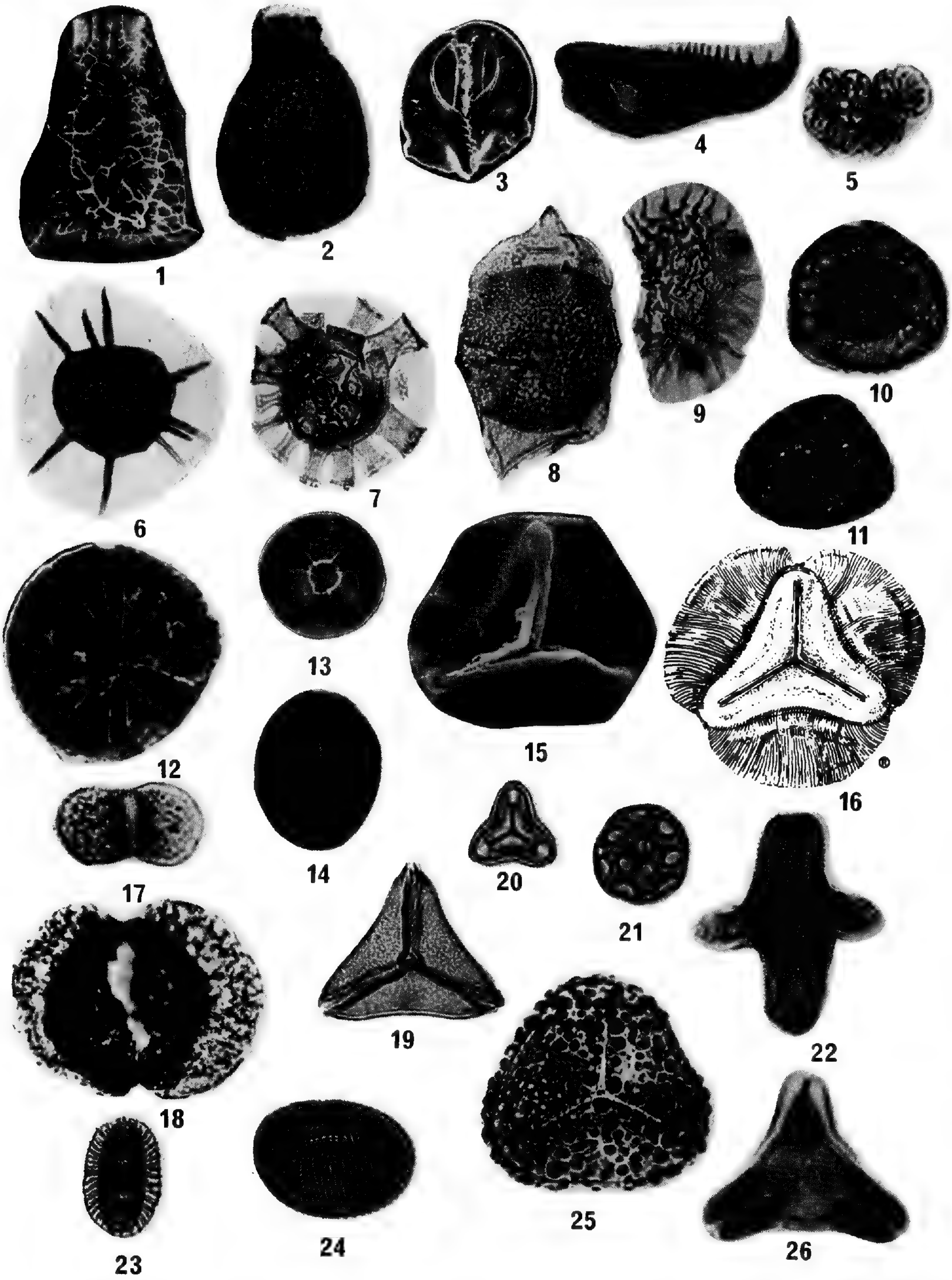
[1] The author acknowledges critical reading of the manuscript and helpful suggestions of H. T. Ames, Associate Editor of the *Catalog of Fossil Spores and Pollen.* Some of the illustrations of microfossils were kindly provided by C. J. Felix (Sun Oil Co.), R. W. Hedlund (Amoco Production Co.), Jan Jansonius (Imperial Oil Ltd.), W. A. M. Jenkins (Imperial Oil Ltd.), and J. B. Urban (University of Texas, Dallas), as noted in the captions.

[2] Catalog of Fossil Spores and Pollen, Deike Building, Pennsylvania State University, University Park, Pennsylvania 16802.

ANN. MISSOURI BOT. GARD. 61: 203–236. 1974.



Figures 1–26.—Photomicrographs, scanning electron micrographs, and a line drawing of palynomorphs of various sorts and geologic ages. All major categories of palynomorphs are included: chitinozoans, scolecodonts, colonial algae, an acritarch, dinoflagellates, spores, and pollen. Magnification varies but is mostly ca. 500 ×.—1. Chitinozoan: *Herochitina* sp., Upper Ordovician, England. Scanning electron micrograph by W. A. M. Jenkins. Length ca. 200 μ.—2. Chitinozoan: *Kalochitina multispinata* Jansonius, Upper Ordovician, Oklahoma. Photomicrograph by R. W. Hedlund. Length ca. 150 μ.—3. Scolecodont: *Xanthoprion albertensis* Jansonius & Craig. Dorsal view of partial apparatus. Scanning electron micrograph by J.

they are composed of "sporopollenin," a fantastically inert C-H-O compound. However, as an illustration of the difficulty of definition, some people would not agree with me in eliminating diatoms and nannofossils, and others would object to my including within the pale chitinozoans and scolecodonts and microforaminiferal inner tests, all of which are animal fossils, albeit consisting of chitin or pseudochitin (C-H-O-N compounds) and hence resistant to palynological maceration. (I would include them for the frankly pragmatic reason that they are in "our" size range and occur in our preparations.) Fungal spores and spore aggregates often have chitinous walls. They often occur in our preparations and are generally included in our subject, though chemically and phylogenetically they are about as strange bedfellows of pollen exines as are scolecodonts (worm jaws!). The < 200 μ suggestion made above is not much good either. Chitinozoans, for example, pay no attention to this limit. Some pollen, many pre-pollen, and (by definition, in paleopalynology) all megaspores are bigger than 200 μ but are still recognized by even the more supercilious palynologists as within their

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Jansonius. Length ca. 350 μ.—4. Scolecodont: *Arabellites* sp., Upper Ordovician, Oklahoma. Photomicrograph by R. W. Hedlund. Length ca. 150 μ.—5. Colonial alga: *Botryococcus* sp., Oligo-Miocene, New South Wales, Australia. Photomicrograph. Length ca. 40 μ.—6. Acritarch: *Baltisphaeridium* sp., Upper Ordovician, Oklahoma. Photomicrograph by R. W. Hedlund. Diameter ca. 100 μ.—7. Dinoflagellate cyst: *Hystrichokolpoma unispinum* Williams & Downie, Lower Cretaceous, Ellef Ringnes Island, Arctic Canada. Photomicrograph by C. J. Felix. Diameter ca. 85 μ.—8. Dinoflagellate cyst: *Deflandrea granulifera* Manum, Upper Cretaceous, Ellef Ringnes Island, Arctic Canada. Photomicrograph by C. J. Felix. Length ca. 120 μ.—9. Colonial alga: *Pediastrum* sp., Upper Pleistocene, Black Sea. Photomicrograph. Length ca. 50 μ.—10. Spore: *Hymenozonotriletes lepidophytus* Kedo, Uppermost Devonian, Pennsylvania. Photomicrograph. Diameter ca. 70 μ.—11. Spore: *Hymenozonotriletes famenensis* Kedo, Uppermost Devonian, Pennsylvania. Photomicrograph. Diameter ca. 70 μ.—12. Spore: *Emphanisporites robustus* McGregor, Upper Devonian. Photomicrograph by R. M. Hedlund. Diameter ca. 65 μ.—13. Spore: *Knoxisporites stephanephorus* Love, Upper Mississippian, Oklahoma. Photomicrograph by C. J. Felix. Diameter ca. 55 μ.—14. Spore: *Calamospora* sp., Uppermost Devonian, Pennsylvania. Photomicrograph. Diameter ca. 70 μ.—15. Spore: *Reinschospora speciosa* (Loose) Schopf, Wilson & Bentall, Upper Mississippian, Iowa. Scanning electron micrograph by J. B. Urban. Diameter ca. 65 μ.—16. Spore: *Reinschospora speciosa* (Loose) Schopf, Wilson & Bentall, Carboniferous. Line drawing by R. Potonié (Potonié & Kremp, 1954; 139) adopted as trademark of *Catalog of Fossil Spores and Pollen*.—17. Pollen grain: *Pityopollenites pallidus* Reissinger emend. Nilsson, (al. *Vitreisporites* and *Caytonipollenites*), Upper Triassic, Texas. Photomicrograph. Length ca. 30 μ.—18. Pollen grain: *Platysaccus nitidus* Pautsch, Upper Triassic, Texas. Photomicrograph. Length ca. 55 μ.—19. Pollen grain: *Expressipollis ocliferius* Khlonova, Upper Cretaceous, Ellef Ringnes Island, Arctic Canada. Photomicrograph by C. J. Felix. Diameter ca. 65 μ.—20. Pollen grain: *Expressipollis accuratus* Khlonova, Upper Cretaceous, Ellef Ringnes Island, Arctic Canada. Compare with Figure 19 *vis à vis* the heterogeneity of forms referred to the same form genera of dispersed spores. Photomicrograph by C. J. Felix. Diameter ca. 30 μ.—21. Pollen grain: *Kuylisporites lunaris* Cookson & Dettmann, Middle Cretaceous, Lougheed Island, Arctic Canada. Photomicrograph by C. J. Felix. Diameter ca. 40 μ.—22. Pollen grain: *Aquilapollenites trialatus* Rouse, Upper Cretaceous, Alaska. Photomicrograph by C. J. Felix. Length ca. 95 μ.—23. Pollen grain: *Wodehouseia spinata* Stanley, Upper Cretaceous, Alaska. Photomicrograph by C. J. Felix. Length ca. 50 μ.—24. Spore: *Schizaeoisporites* sp., Middle Cretaceous, Oklahoma. Photomicrograph by R. W. Hedlund. Length ca. 50 μ.—25. Spore: *Trilobosporites sphaerulentus* Phillips & Felix, Lower Cretaceous, Louisiana. Photomicrograph by C. J. Felix. Diameter ca. 80 μ.—26. Pollen grain: *Nudopollis* sp., Paleocene, Gulf Coast, U.S.A. Photomicrograph by R. W. Hedlund. Diameter ca. 30 μ.

purview, as are dinoflagellate cysts, other microplanktonic cysts (acritarchs), some colonial algae, various other algal microfossils, and a veritable hash of organic, microscopic things (see Figs. 1–26). The stratigraphic range of the whole spectrum is Pre-Cambrian to recent (see Fig. 27). All of this is by way of getting it out on the table that "paleopalynology" is not really a subject with some sort of agreed boundaries like "megafossil paleobotany," but a series of techniques—an art applied to a diversity of small objects, many of which were produced by plants of some sort.

FOSSIL POLLEN AND SPORE STUDIES, 1916–1946

Von Post was not the first to study either extant or fossil spores and pollen—the first published drawing of a modern pollen grain seems to have been by Nehemiah Grew in the 1600's, and there were many studies in the 19th century (see Wodehouse, 1935). Fossil pollen and spores were studied by various people in the mid-1800's, and the first published photomicrograph of a fossil spore, now known as *Reinschospora* sp., appeared in 1884 (see Traverse, Ames & Spackman, 1970; also Figs. 15–16 of the present paper illustrate this species). Nevertheless, von Post's 1916 paper does provide a watershed between the more or less casual interest in pollen analysis which preceded and the rather great expansion of practical application which followed. In the three decades which followed 1916, most of the developments had to do with Quaternary studies, as pollen analysts in many parts of the world (especially Europe) perfected methods, built reference collections, and established standard sections which enabled laboratories to trace vegetational history and to date, often with remarkable accuracy, samples or sections of unknown age. Faegri and Iversen's (1964) fine little text on pollen analysis provides a good overview of the status of the subject.

Various paleobotanists and coal petrologists had suggested that analysis of the abundant spores and pollen in coals and associated sedimentary rocks could be employed for correlation of coal beds, a matter of some importance to coal geology. Doubtless the expansion of interest in this subject was conditioned to some extent by the success of the Quaternary pollen analysts. Raistrick and Simpson (1933) in England, Naumova (1939) and Luber (see Luber & Valts, 1941), and Kosanke (1943, 1950) in the United States were among the earliest coal petrologists-paleobotanists systematically to apply the study of fossil spores to this problem, and the work was backed up by the beginnings of careful and extensive study of fossil pollen and spore morphology, taxonomy, and stratigraphic distribution. In this early period of pre-Quaternary work there were a few persons who were of special importance—Potonié (1934) in Germany, Schopf and Wilson in America (Schopf, Wilson & Bentall, 1944), Naumova (1939) and Malyavkina (1949) in the Soviet Union, Cookson (1947) in Australia. In mentioning these, one is of course slighting dozens of others who also played a significant role.

As can be seen from Hopping's (1967) discussion of the activities of a single company, Royal Dutch/Shell, the petroleum exploration people had realized the potential importance of pollen/spore studies in the 1930's, but it was with the end of World War II that petroleum-sponsored work began in earnest, at first

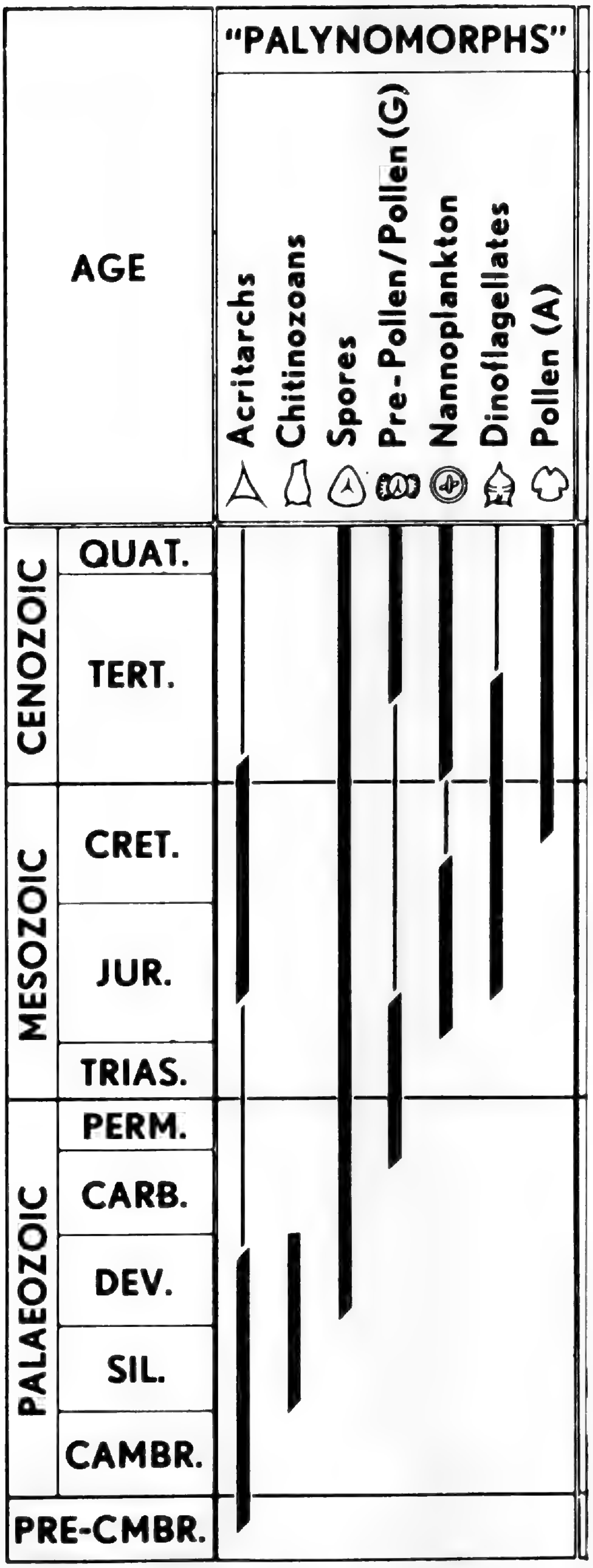

FIGURE 27. Stratigraphic range of major palynomorphs (Hopping, 1967). Note that the range of dinoflagellates has now been extended to the Silurian and that "nannoplankton" are excluded from palynology per discussion in the text.

chiefly by Shell and Standard of New Jersey (Carter, Esso, Creole, etc.). As one of the few pollen-spore researchers trained in the late 1940's, I well remember being interviewed by both Esso (about 1948) and California Standard (1950) when they were beginning to expand their operations in this area. Esso was (mildly) interested in my services for work in Venezuela. It was in that country, in the Maracaibo Basin, that Shell first made big money from palynology by its application to the stratigraphic problems of largely nonmarine (and hence "nonfossiliferous") sediments. Kuyl, Muller, and Waterbolk (1955) have summarized the scope of Shell's early and very successful work in Venezuela.

The onset of the 1950's was a "Grenzhorizont" for palynology. It was then that the subject reached a threshold of rapid expansion worldwide, stimulated in part by petroleum interests, in part by the increase of basic paleobotancal research on plant microfossils. I recall that my Ph.D. thesis (1951) was one of the earliest if not the earliest pre-Quaternary palynologcal doctoral dissertations in North America—before that time only L. R. Wilson at the University of Massachusetts (later at New York University and at the University of Oklahoma) and his students, Robert M. Kosanke (University of Illinois, later with U.S. Geological Survey, Denver) and Aureal T. Cross (University of West Virginia, later with Pan American Petroleum in Tulsa and now at Michigan State University) offered formal instruction in paleopalynology in North America. In other countries, this was likewise a time of rapid expansion of interest. For example, Potonié (1951) and Thomson and Pflug (1953) in Germany, Cookson (1953) and Couper (1953) in the ANZAC countries, and Samoilovich (1953) and Bolkhovitina (1953) in the Soviet Union made fundamental contributions. Most of these palynologists were supported by government geological surveys, and it must be emphasized that despite the greater cash outlay of the petroleum companies for palynological work and the stimulation this was to the whole field, relatively little of their research was published at the time.

PALEOPALYNOLOGY, 1951–71

THE PALYNOLOGICAL EXPLOSION

The big expansion of interest in palynology, which seemed to reach critical mass about 1951, continued throughout the 1950's and well into the 1960's. Several criteria for measurement of this are available. One is the number of oil company laboratories in the world—this went from a handful in 1951 to hundreds by the mid-1960's and has been slightly on the decline since then. Figure 28 shows the shape of the expansion for one of the large petroleum company complexes. In the Soviet Union, Neustadt (1967) reported that there were 70 palynological laboratories all over the Soviet Union (Fig. 29).[3] In 1951 there seem to have been perhaps a dozen or less, mostly in Moscow and Leningrad. Whereas only two or three universities in North America offered formal instruction in paleopalynology in 1951, and probably not more than a dozen worldwide, at least 50 universities and colleges in the United States and Canada were giving

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[3] According to H. Leffingwell (personal communication, 1972), Neustadt reports over 100 Soviet paleopalynological laboratories in 1971.

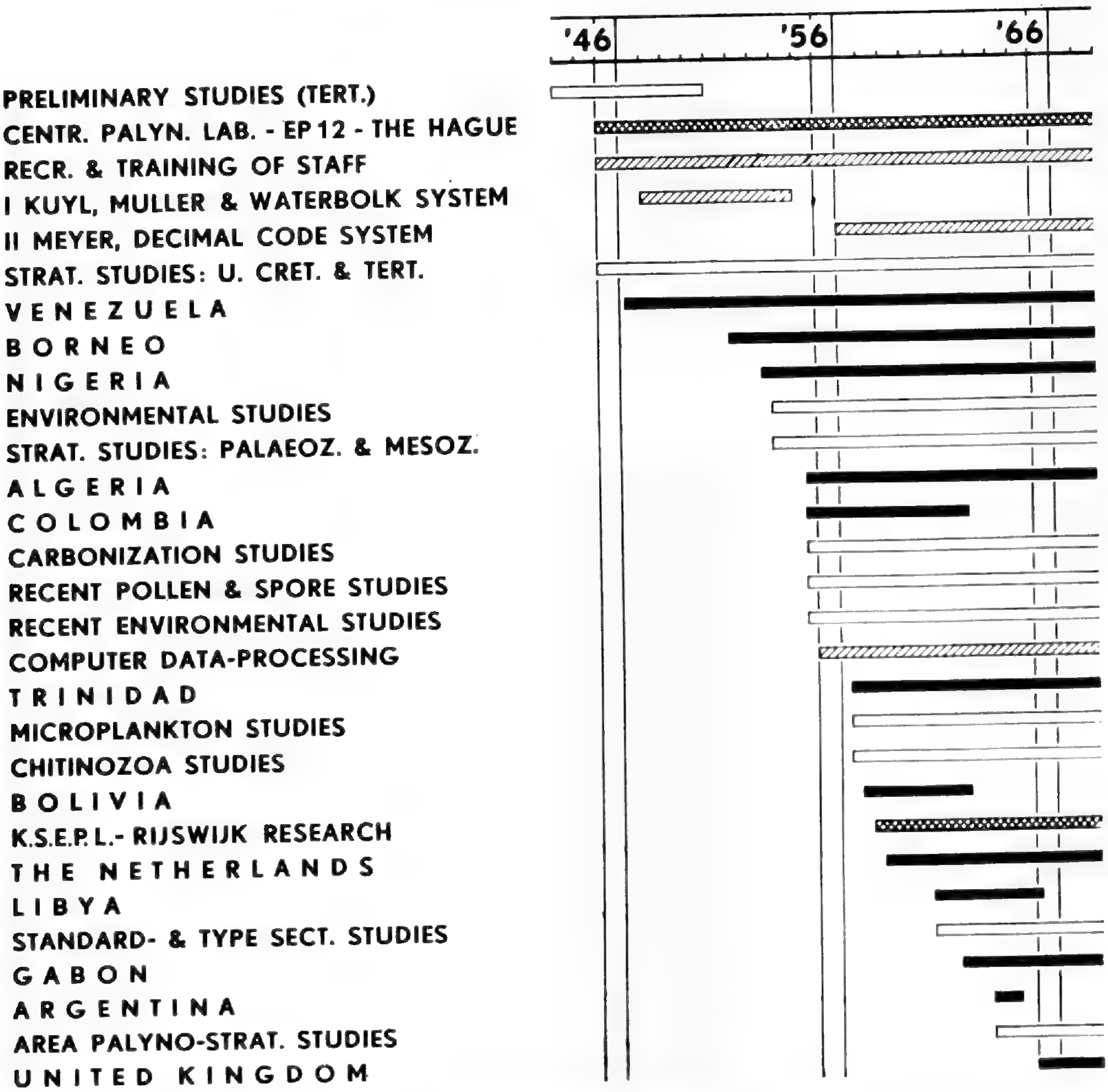

FIGURE 28. Rapid expansion of paleopalynological effort in Royal Dutch/Shell in mid-1950's (Hopping, 1967).

an introductory course in palynology in 1971. By extrapolation from data presented by Manten (1968), it appears that roughly 30,000 palynological papers were published worldwide from 1916 to 1971. Of these, approximately 22,000 have appeared since 1951—about 70% of the total. (Manten estimated that roughly two-thirds of the papers have been in the area of paleopalynology, and that this comprises about 3% of all earth science publication during the period.) As can be seen from Fig. 30, the massive acceleration of activity is clearly a feature of the early 1950's. I have the impression that while activity will remain at a high level, the period of exponential expansion is behind us. For some time the most important feature of paleopalynology will be characteristic of a maturing branch of science—systematic organization of the field and its subject matter. Among other things, this will surely involve a larger percentage of basic contributions of palynology to paleobotany than has been true during the pioneering phases of the subject.

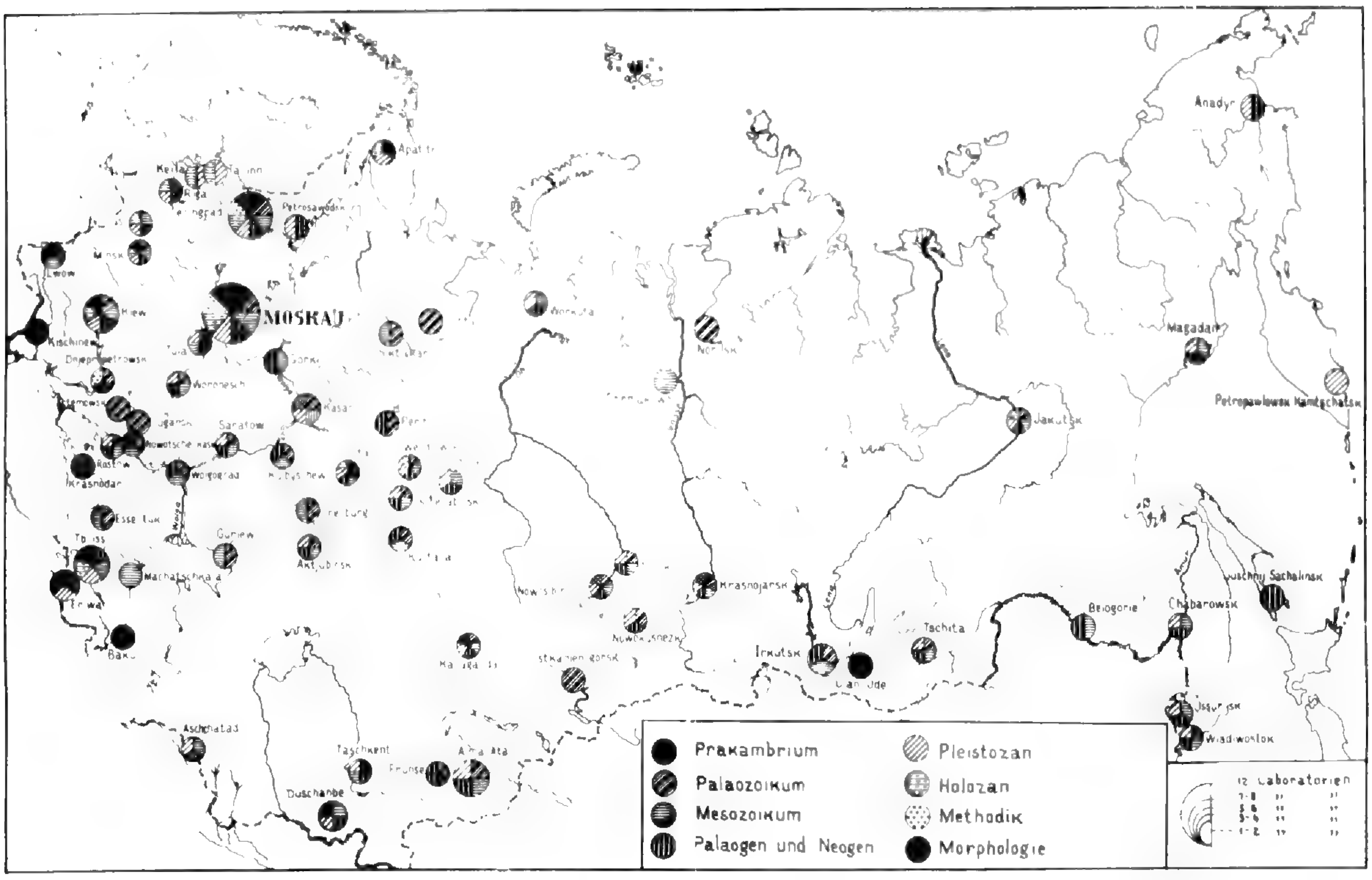

FIGURE 29. Geographic location of about 70 Soviet paleopalynological laboratories reported by Neustadt in 1967. By 1971, according to Neustadt, there were over 100.

SCIENTIFIC ORGANIZATION IN PALEOPALYNOLOGY

In the early days of pollen/spore analysis there was minimal formal organization of research people in the field. In North America, people who would now be called palynologists met with small groups of their colleagues and presented papers under the auspices of the Paleobotanical Section of the Botanical Society of America (PSBSA) or with the geological societies (see Traverse, 1960). In the late 1920's and into the 1940's American pollen-spore analysts exchanged information in more or less informal meetings and later by means of a mimeographed newsletter, the *Pollen and Spore Circular*, edited at first by Paul B. Sears (1943–1954) then of Oberlin College, later of Yale University; subsequently by Sears, L. R. Wilson, and C. J. Heusser. Some persons whose interests were pre-Quaternary were among those who exchanged information in the *Circular*, but it had a glacial–post-glacial cast for most of its run. In February 1953, Stanley Cain of the University of Michigan organized a meeting at Yale of palynologists from (mostly) the northeastern part of the United States. Sessions were chaired by Sears and E. S. Deevey, Jr. This meeting became known as the "First National Pollen Conference." A "Second National Pollen Conference" met in December, 1953, in Boston, under sponsorship of the American Association for the Advancement of Science. Later, in 1956, Kathryn Clisby, an associate of Sears, hosted the "Third National Pollen Conference" at Oberlin College, attended by about 50 persons working on various aspects of palynology. I was at that time an officer in PSBSA and was instrumental in having the Section host the Fourth and Fifth National Pollen Conferences as part of the sectional programs in 1957 and 1958. It seemed to me, at the time, desirable to

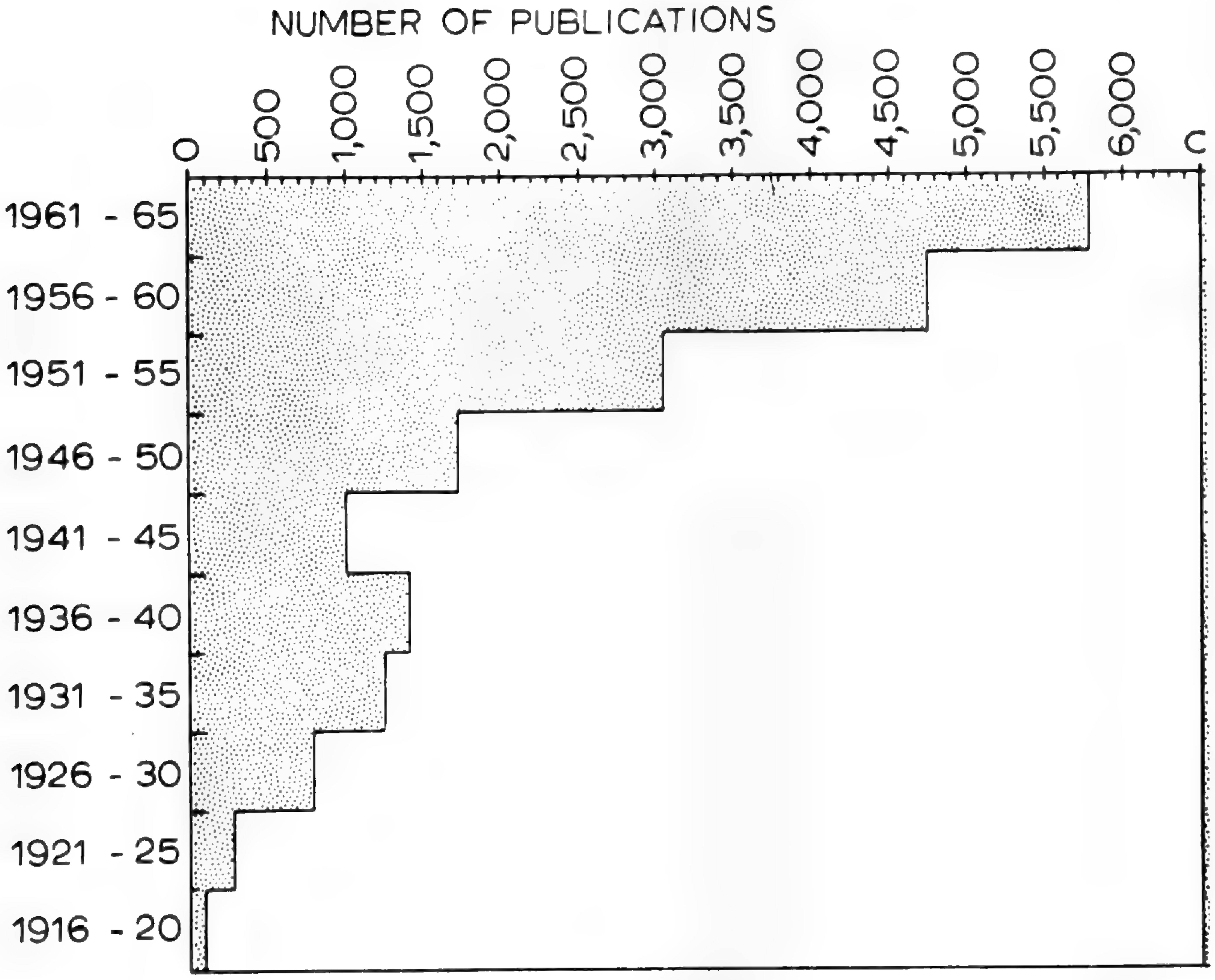

FIGURE 30. Volume of palynological publication per five-year period, 1916–1965 (Manten, 1968). Over two-thirds of these publications are paleopalynological.

keep all of paleobotany under one roof and that PSBSA offered an acceptable vehicle for the growing demand for palynological organization. However, as more and more people poured into palynological research, this position became less and less tenable. For one thing, by the late 1950's a majority of palynologists were persons who did not regard themselves as paleobotanists, were geologically trained, and were interested in palynology primarily as a geological tool. Also, some megafossil specialists were understandably nervous that the hypertrophied palynological tail would soon wag their dog.

Meanwhile, on the world scene, an international palynological meeting had been held semiformally at Stockholm in 1950 as part of the VIIth International Botanical Congress, with G. Erdtman as host. Numerous significant discussions were held regarding palynological systematics and other matters. More formal organization of palynology was clearly in the wind, and several more or less international sessions occurred during the 1950's. The First International Conference on Palynology was held at the University of Arizona in 1962, attended by about 100 palynologists from most of the world, and dealt with a broad spectrum of palynological subjects, emphasizing paleopalynology. Soviet palynologists were not able to attend, although they published a collection of papers which had been intended for presentation at the conference. An International

Committee was established at Tucson which led to the organization of the Second International Conference on Palynology, held at Utrecht, Netherlands, in 1966. This conference was considerably larger than the Tucson meeting, and the program of papers included contributions on all aspects of palynology, with heavy emphasis on paleopalynology. Before and during this conference there were further moves toward formal international organization of palynology. An abortive attempt on the part of certain Indian palynologists to begin a world association of palynology failed at this time, but the International Committee set up at Tucson became somewhat more formal, looking forward to the Third International Conference, which was to take place in Novosibirsk, U.S.S.R., in 1971. The Utrecht Conference in 1966 was pivotal in many ways, both from the point of view of revealing important trends in paleopalynological research and as regards professional organization.

Soon after the conference, H. J. Sullivan of Pan American Petroleum Corporation (now Amoco), Tulsa, reported that a questionnaire sent to North American palynologists indicated an interest in forming an American society, and eventually about 35 of us assembled in Tulsa in December 1967, and formed the American Association of Stratigraphic Palynologists. AASP is restricted to neither the U.S.A. nor to stratigraphically oriented palynologists, though the membership of about 300 includes mostly paleopalynologists residing in North America. AASP has held five annual conventions through 1972, with an average attendance of about 100. There have been varied programs of papers and field trips. National groups in other countries have also been active, two of them apparently rivalling AASP in degree of organization and vigor—the Indian Palynological Society, and the organization of Soviet palynologists, which is certainly the world's largest and which has sponsored large and important All-Union palynological conferences (see Neustadt, 1967).

The Indian society grew out of a symposium held in 1964 in Lucknow, attended by over 100 Indian palynologists (Reports, *Palynological Bulletin*, 1: 60, 1965). The society was inaugurated during a session of the Indian Science Congress in Calcutta in 1965 and includes members not only from India but from all over the world. Other national and regional palynological groups have organized somewhat less formally in France (according to Streel, 1972, the French group is involved primarily with "neopalynology," also called actuopalynology—that part of palynology which is not paleopalynology), the Netherlands, Great Britain, and Scandinavia. Palynological meetings have also been organized by regional and national groups in other places—for example, Mexican palynologists sponsored a "Primer coloquio sobre palinología en México" in October 1971. National organizations have several times sponsored palynological symposia—one example was the "Symposium on Palynology of the Late Cretaceous and Early Tertiary" sponsored by the Coal Division of the Geological Society of America in San Francisco in 1966 (*cf.* Kosanke & Cross, 1970).

Just as AASP, despite its name, represents all facets of paleopalynology, another nomenclaturally over-modest organization is C.I.M.P. (Commission Internationale de Microflore du Paléozoique), also sometimes referred to as I.C.M.P. from the anglicization of the name. It started (Streel, 1972) to provide a forum for works on Paleozoic paleopalynological problems but has become in fact the Western European regional paleopalynological society, with interests transcending both stratigraphic and national bounderies. C.I.M.P. has always had membership and participation from outside of Western Europe and has been very active in sponsoring meetings, publications, and special work groups to cope with stratigraphic and taxonomic problems (see Alpern, 1967).

The Third International Conference on Palynology, held in Novosibirsk in 1971 was not well attended by non-Soviet palynologists but was nevertheless a large and impressively diverse meeting. The field trips (Leffingwell & Norris, 1971, reports to AASP) were especially well planned and instructive. At the meeting the loosely organized international apparatus which had planned the Utrecht and Novosibirsk conferences was still further formalized, although once again an abortive attempt to create an international society on the spot was foiled. The permanent organization set up is the International Commission for Palynology (ICP) which has a 12-member Council headed by N. F. Hughes and M. Muir of Great Britain as president and secretary, respectively. At present, the only things certain about international organization are that the Fourth International Conference on Palynology is scheduled to be held in India in 1976; that the ICP Council has actually been constituted, with a president and secretary; and that ICP will have a difficult time producing a constitution and program which will be acceptable to all points of view in the palynological world community. At the moment, a truly worldwide palynological association still does not exist, at least in part because of division of opinion as to whether it should be independently organized or should be an association of national societies.

PUBLICATIONS

At the palynological "Grenzhorizont" in 1951 there were no specifically palynological journals, as I recall clearly both from trying to get papers published and from searching for papers in everything from the *American Midland Naturalist* to the *Geologiska Föreningens i Stockholm Förhandlingar.* (Fortunately, G. Erdtman began in 1927 publishing in that journal and widely distributing, a regular, very thorough, bibliography of papers on pollen statistics, later on palynology as a whole.) The two decades which transformed the field, 1951–1971, have seen a great change in publications. G. Erdtman's *Grana Palynologica* first appeared in 1954 and has been published ever since. Recently the editorship passed to B. Gullvåg, and the name changed to *Grana*, but it is still fundamentally the same journal, appearing thrice yearly and covering all aspects of the subject but with emphasis over the years on the nonpaleo side.

In 1956 the French Service de Palynologie of the Muséum National d'Histoire Naturelle, Paris, began publishing an annual bibliography of palynology, and it appeared also in 1957 and 1958. In 1959 the Muséum next announced the establishment of the new journal, *Pollen et Spores*, with M. Van Campo as director. At first the periodical came out twice a year, but it is now published thrice yearly. All aspects of palynology are treated. From the beginning, *Pollen et Spores* also has published a yearly bibliography of world palynology. Erdtman had continued his regular "Literature on Palynology," originally published in the Stockholm geological journal mentioned above, in *Grana Palynologica*, but when *Pollen et Spores* began to include similar bibliographies as part of each year's production, Erdtman ceased his separate effort which had served the field so well, with *Literature on Palynology* XIX, 1958.

Following the Second International Conference, the Dutch publishers, Elsevier, introduced a new journal, *Review of Palaeobotany and Palynology.* The first five fat volumes all appeared in 1967 and contained papers presented at the Conference. Since that time, the journal has appeared on a somewhat more modest scale of one to two volumes a year. Despite the title, the *Review* has been almost exclusively palynological with heavy emphasis on paleopalynology and, with *Grana* and *Pollen et Spores*, has become an indispensable part of any palynological library. Unfortunately, the three of them combined cost about $100 per year.

One of the bona fide collector's items in palynology is an original set of the mimeographed *Pollen and Spore Circular* mentioned above. Americans interested in pollen analysis (mostly Quaternary), cut off from the rest of the (as we would now say) palynological world by the war, first began circulating it in 1943, with Paul Sears, then of Oberlin College, as editor. Seventeen numbers were issued in fairly regular succession to 1949, then a last one in 1954, announcing that the circular would be incorporated in the American Museum of Natural History's *Micropaleontologist* (later to become *Micropaleontology*). However, that was really the end of the *Circular.* It is a fascinating mirror of the primitive phase of palynology when it was dominated by Quaternary pollen analysis. Withal, it was in issue number 8, October 1944, that Hyde and Williams proposed the name "palynology." Many other ideas (the importance of marine palynology, for example) which have become of central interest to modern palynology are discussed in the *Circular*, with the refreshing simplicity that one often finds in older scientific publications.

The *Pollen and Spore Circular* could well have become a permanent and important journal, but it was a little too early in the field. As a result, there is still no American palynological periodical. However, the American Association of Stratigraphic Palynologists have struck an agreement with the Louisiana State University for publication of the proceedings of the AASP annual meetings, including most of the papers presented, to be published in LSU's *Geoscience and Man* series. The papers of the first annual meeting (1968) have already appeared in *Geoscience and Man* Vol. 1, those of the second annual meeting (1969) in Vol. 3, and those of the third annual meeting (1970) in Vol. 4. AASF also publishes a quarterly *Newsletter*, occasional *Contributions* volumes (most recently, a bibliography of dinoflagellate work), and an annual membership directory.

In India, the Palynological Society began in 1965 publishing two periodicals, the *Palynological Bulletin* and the *Journal of Palynology.* In 1972, it was announced that these two journals have been merged as *Journal of Palynology, New Series.*

In 1951 it was understood that the numbers of fossil spore and pollen taxa described, though already large, was only a patch on the total potentially available fabric. It was apparent that something must be done eventually to keep track of the ballooning corpus of new taxa. One of the things which did happen was the creation at the Pennsylvania State University in 1957 of the *Catalog of Fossil Spores and Pollen* (Fig. 31), the history of which has been discussed by Traverse *et al.* (1970). G. Kremp and W. Spackman were the founding editors, A. Traverse is the present editor, and H. T. Ames has been associate editor throughout the history of the project. At present, 38 regular volumes have been published or are in press, plus three index volumes and two translation volumes. The *Catalog* presents the original descriptive and illustrative material for each taxon covered plus commentary and supplemental information. It is an indispensable taxonomic-nomenclatural tool for systematic palynologists. The *Catalog* has as yet only covered about 6,000 taxa of the perhaps 15,000 which have been described, but the 6,000 represent most of the systematically critical forms. There is also a *Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien*, published by Eisenack (1964, 1967), of which Volume 1 on dinoflagellates and its supplement have so far appeared. (Downie and Sarjeant, 1964, published a bibliography of literature on dinoflagellates which is a useful adjunct to the Eisenack catalog.)

In 1951 there were very few textbooks available in the general area of palynology, and these carried a heavy emphasis on pollen morphology of extant plants and Quaternary-Recent pollen analysis: Wodehouse's (1935) *Pollen Grains*, Erdtman's (1943) *Introduction to Pollen Analysis*, Faegri and Iversen's (1950), *Textbook of Modern Pollen Analysis.* Each of these had its merits, but none dealt much with paleopalynology. A paleopalynological text in English finally appeared in 1969, Tschudy and Scott's *Aspects of Palynology.* The book is a compilation of articles by various authors, mostly on paleopalynology, arranged stratigraphically. It is very useful indeed to students, despite some minor deficiencies noted elsewhere (Traverse, 1970). Erdtman's (1969) *Handbook of Palynology* has an excellent article by Sarjeant on fossil phytoplankton but is otherwise not too useful to the paleopalynologist. For the Russian-reading paleopalynologist, a three-volume textbook, *Paleopalinologia*, edited by Pokrovskaya (1966) provides a thorough grounding in the subject, including one whole volume of stratigraphically arranged illustrations of fossil spores and pollen. Kremp (1965) got out a compilation of terms used in palynology, *Morphologic Encyclopedia of Palynology*, which, though no longer comprehensive, is a good tool in using the literature. Erdtman's (1952, 1957, 1965) three-volume set of books on spore/pollen morphology is an important source of primary information for the identification of modern spores/pollen, but no substitute for a good reference collection of the real thing. Kapp (1969) has published a semipopular work on identification of spores/pollen which faces an uncertain market—it would seem that persons who have an interest in something as relatively recondite, plus the necessary equipment to develop the interest, will quickly need something more advanced.

In these two decades there has also appeared all over the world a very considerable library of monographs on paleopalynology, hard-bound and soft-bound,

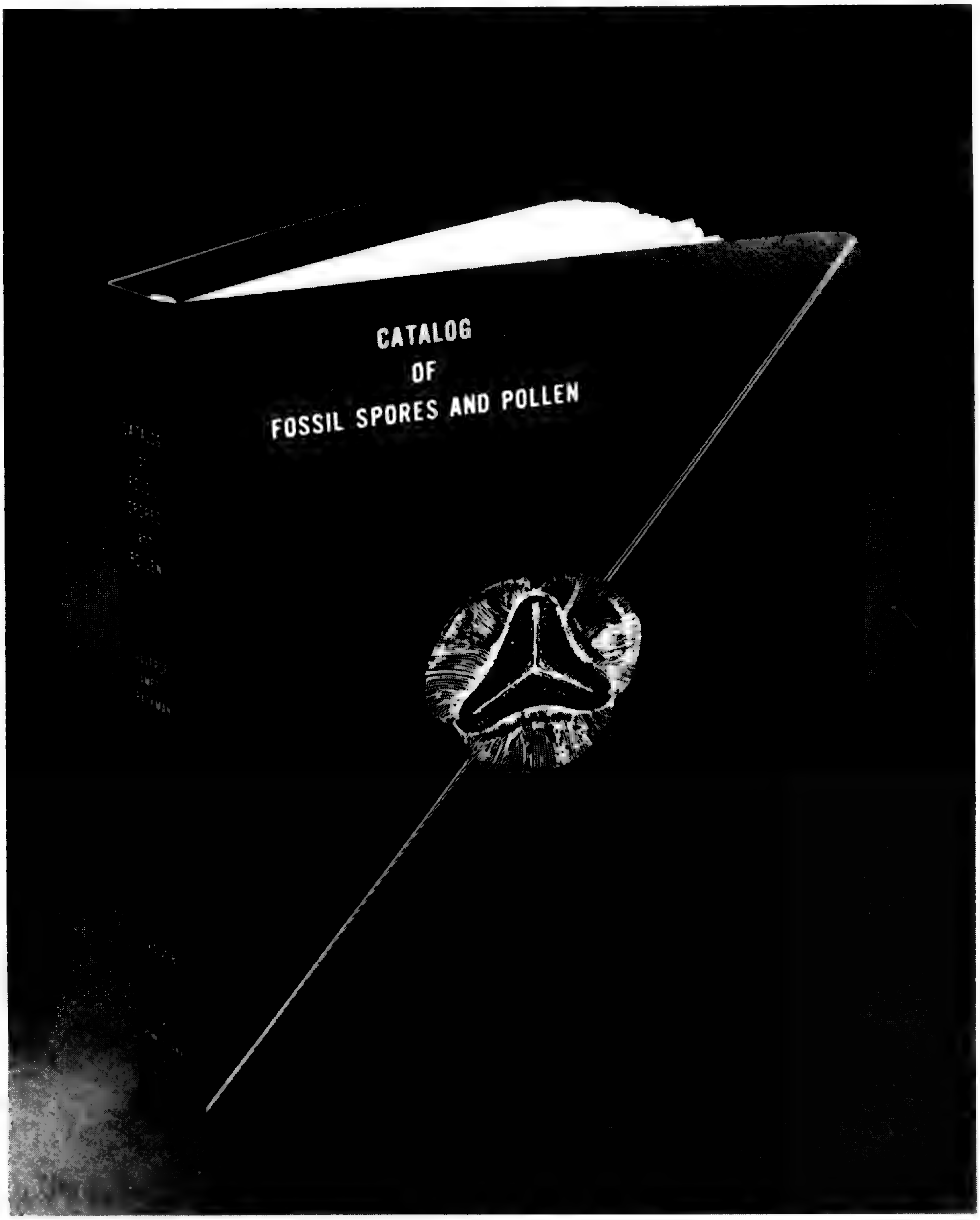

Figure 31. Sample volume of *Catalog of Fossil Spores and Pollen*, a compendium of paleopalynological systematics. Over 40 volumes have been published in the compendium series. The "CFSP" trademark on the cover represents *Reinschospora speciosa* (Loose) S.W.B., the first fossil spore for which a photomicrograph was published, by Reinsch in 1884. See also Figs. 15–16 of the present paper.

big and small, good and not so good—so that no matter where in the stratigraphic column he works, a paleopalynologist has not only his boxes of reprints but also at least a book or two he can show friends to establish that the subject "is for real." It is likely, however, that the book will be in the Cyrillic alphabet because

(Manten, 1968) about a quarter of all paleopalynological literature and a larger fraction of the longer works is from the Soviet Union. (English contributions are about a third of the total literature, German about a sixth, French about a tenth.)

Research in Paleopalynology: Raw Material for the Explosion, 1951–71

Something like 8,000 palynological titles had already appeared, perhaps 30% of all the literature of the subject, by 1951. But most of it was either not paleopalynology or was Quaternary pollen analysis. I recall as an early pre-Quaternary palynological graduate student that in the late forties I could enjoy the euphoria of feeling I was "on top of" the significant Western literature in the subject. After 1951 this quickly became impossible, and it has become progressively more impossible at an accelerating rate down to the present. The general expansion of knowledge in the field, resulting in part from the discovery that paleopalynology is a valuable stratigraphic tool, has forced paleopalynologists to specialize either stratigraphically or topically.

CARBONIFEROUS PALYNOLOGY

Stratigraphically speaking, the first segment of the column to come into its own in paleopalynology was the Carboniferous, a direct result of emphasis on coal studies in Europe and America. Already by 1951 this field was well along toward maturity. Potonié, Ibrahim and Loose (1932), Schopf, Wilson and Bentall (1944), and Kosanke (1950), three of the fundamental contributions in the field, had already appeared and had a lasting effect on nomenclature and taxonomy. Not long thereafter came the sure sign of maturity—cataloging and organization of taxa of Carboniferous spores by Potonié and Kremp (1954, 1955, 1956*a*, 1956*b*). Guennel (1952) had made a simple but significant contribution to progress by introducing the concept of miospore-megaspore, selecting the 200 μ boundary as the dividing point. "Megaspore" in practical palynology now meant, arbitrarily, all spores/pollen over 200 μ in largest dimension, whatever their botanical function—miospore meant all spores and pollen below 200 μ, whether they were functionally megaspores, microspores, isospores, pollen, or pre-pollen. After Potonié and Kremp's taxonomic contribution, Carboniferous palynology had come of age, and there has been worldwide and steady expansion of information in the field since then—for example, Guennel's (1958) beautifully illustrated monograph on the Pottsville coals of Indiana and, more recently, the thorough, extensive, and significant *Miospores in the Coal Seams of the Carboniferous of Great Britain*, by Smith and Butterworth (1967). Also worthy of special note are a series of monographs on Carboniferous—that is, Lower Gondwana—spores/pollen of central Africa, by Bose, Kar, and Maheshwari (1966–1969).

DEVONIAN PALYNOLOGY

The early occurrences of spore-bearing embryophytes in the fossil record has always been of great interest, not only to paleobotanists but to practical stratigraphic palynologists as well.

As late as the early 1950's it was assumed the Lower Devonian was about

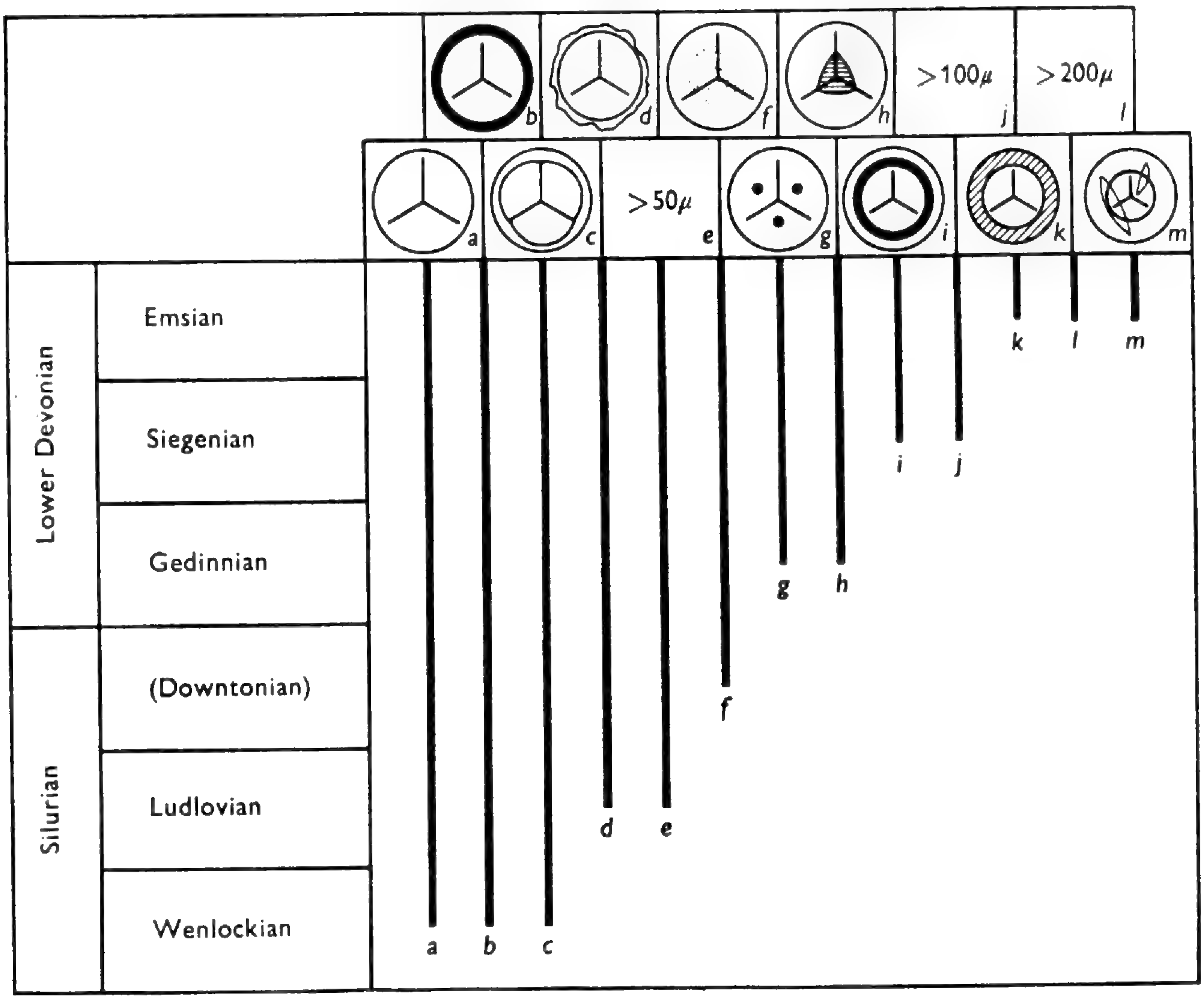

FIGURE 32. Regular appearance of morphologically new spore types in Silurian-Devonian time (Chaloner, 1970). The earliest forms were small, simple triletes ("a"). Note the advance toward megaspory—the 50 μ boundary was crossed in the Siegenian and the 200 μ line in the Emsian.

the oldest rock from which we could hope to extract spores, and there really had been only a few studies of pre-Carboniferous palynomorphs. In 1959, Hoffmeister described simple trilete spores from Lower Silurian rocks of Libya. Such spores—*Ambitisporites* and *Punctatisporites*—probably represent plants at the bryophytic level of evolution. Similar simple spores found in tetrads are now known to occur all the way to the base of the Silurian (see Gray & Boucot, 1971). In the 1950's and 1960's there has been a concentrated effort worldwide to elucidate Devonian palynofloras and their significance to plant evolution and to palynostratigraphy. Chaloner (1967, 1970*b*) has summarized this story—and the outlines are now clear (see Fig. 32). Simple, small trilete spores of a very limited number of types in Lower Silurian time were succeeded by more sculptured and somewhat larger types by Lower Devonian. During the Devonian there was explosive development of morphological diversity, for example, development of biform and even bifurcate appendages. Increasing numbers of larger spore types also developed, until by Upper Devonian there were many kinds of spores across the 200 μ size line, presumably mostly functional megaspores, and a clear harbinger of the seed habit. Chaloner (1967) has pointed out that clearcut palynological evidence on the regular origin of the various morphological specializations and megaspory through the Silurian and Devonian strongly supports the monophyletic origin of embryophytic vascular plants in early Silurian time. The Silurian-Devonian has become one of the really "hot" areas of palynology, and it is difficult to select those who can be given the lion's share of the credit, but certainly among the leaders have been McGregor (1960, 1961) of Canada, Richardson (1964) and Owens (1970) of Great Britain, Streel (1967) of Belgium, and Kedo (1957) of the U.S.S.R. Streel and Wagner (1970) have edited a C.I.M.P. volume which deals in part with the highly significant contribution paleopalynology is making to clarification of the boundary problem at the Devonian-Carboniferous interface.

PERMO-TRIASSIC PALYNOLOGY

If we used the concept of "Mesophytic" instead of Mesozoic, the boundary would be somewhere in the Permian—it is in this period that the spores/pollen of the more primitive vascular plant groups are replaced by those of presumed or known coniferophytes, ginkgophytes, cyadophytes, and perhaps gnetaleans. Bisaccate, monosulcate-asaccates, and striate pollen forms characterize the palynofloras, though trilete spores are still very important. Some of the pollen also displays trilete marks like those of spores—such grains are called "prepollen," and as Chaloner (1970*a*) has shown, the trilete mark remained the germination suture for some time in geological history. The distal sulcus of primitive gymnosperms functioned as the exitus for the pollen tube, which was at first haustorial, and only later assumed also the function of release of the fertilizing genetic material.

Although the broad outlines of the modernization of vascular plant floras at the Paleophytic-Mesophytic interface were known twenty years ago, most of the details have been sketched in as a result of comparatively recent work. In the Permian, Hart (1965), Wilson (1962), Klaus (1963), Bharadwaj (1962), and Samoilovich (1953) perhaps deserve special mention as helping to elucidate the story, though many others have contributed. A glance at a recent compendium of Permian spores/pollen generic names by Hart (1972) reveals that a large majority of the names are attributed to palynologists in the Southern Hemisphere, especially Indians (Hart himself is now in Louisiana, but most of his Permian work deals with South Africa's Karroo rocks). Thereby hangs a tale—the spores/pollen floras of the Permo-Carboniferous of the Southern Hemisphere (Lower Gondwanas of India) and the synchronous palynofloras of the Northern Hemisphere are as distinct from each other as are the megafossil floras of the two areas. The spate of Southern Hemisphere generic names, especially for bisaccate striate pollen, is partly a result of the sheer numbers of Lower Gondwana papers from India, and partly will probably turn out to be a case of liberal "splitting."

During the Triassic there is progressive modernization of the palynoflora: the striates lose importance, and center stage is taken by coniferous bisaccates and by other gymnospermous pollen—for example, that of the *Classopollis* complex (pollen of *Cheirolepis*) and even of the Caytoniales (*Vitreisporites* =

Caytonipollenites). Nearly all of the story is known from works published worldwide during the last fifteen years by Klaus (1960) of Austria, Balme (1970) and de Jersey (1964) of Australia, Malyavkina (1964) of the USSR, Mädler (1964) of Germany, Scheuring (1970) of Switzerland, and Visscher (1966) of the Netherlands.

JURASSIC-CRETACEOUS PALYNOLOGY

Upper Triassic spore/pollen floras, those of the Carnian-Rhaetic stages, are dominated by fern spores, pollen of conifers, and other advanced gymnosperms. This is essentially a "Jurassic type" palynoflora and, indeed, continues into Lowest Cretaceous time. One of the great events of evolutionary history then occurs in the upper part of the Lower Cretaceous at the Aptian-Albian interval, which is the "Mesophytic-Cenophytic" boundary, if such terms are used. This event is, of course, the origin of the angiosperms—known for over a century from megafossil evidence to occur at this level. Palynology has not affected the gross picture much, but it has provided far more data than were previously available—millions of specimens instead of a few thousand. As has been documented by Muller (1970) and by Doyle (1969), small, simple, smooth to weakly sculptured tricolpate pollen appears worldwide at about the same Aptian-Albian level. This is a basic dicot type. However, primitive ranaleans have monocolpate pollen, as did possible gymnosperm ancestors of the flowering plants—hence the joker is that "angiosperm" pollen recognized at the Aptian-Albian level is higher dicot pollen. At present we are not sure whether monocolpate pollen with angiosperm-like sculpturing found lower in the section is angiosperm or gymnosperm. However, Kemp (1968) has noted that monosulcate *Clavatipollenites* pollen from Cretaceous (Barremian) rocks just below the Aptian are enough like simple tricolpate forms, from stratigraphically just above, in wall structure and sculpturing to suggest that they are ancestral angiosperm forms. Muller (1970) is less cautious than Kemp about the *Clavatipollenites* story and would hence push the origin of the angiosperms to the Upper Jurassic on this evidence. One type of monocolpate pollen (trichotomosulcate) is especially interesting as possibly showing a route by which tricolpates could evolve from monocolpates, though there are symmetry problems (Chaloner, 1970*a*) with this solution. At one time there was excitement about apparently tricolpate *Eucommiidites* (formerly *Tricolpites*) pollen from Jurassic rocks, fossils first described by Erdtman (1948). Couper (1956), however, showed that these are gymnosperm pollen which are only apparently tricolpate, two of the three "colpi" being in reality lateral slits, not true colpi. All other pre-Cretaceous "angiosperm" pollen finds have suffered similar deflation, which is certainly significant in view of the thousands of samples and millions upon millions of specimens which have been investigated. However, it is probable that it will require application of new approaches and techniques to pre-Cretaceous palynofloras in the coming decades to make significant contributions to elucidation of flowering plant origin.

The course of angiosperm evolution through the Cretaceous, as revealed by pollen floras, is now quite well understood as a result of these two decades of work (see Fig. 33). The story is reminiscent of the Devonian, with increase in

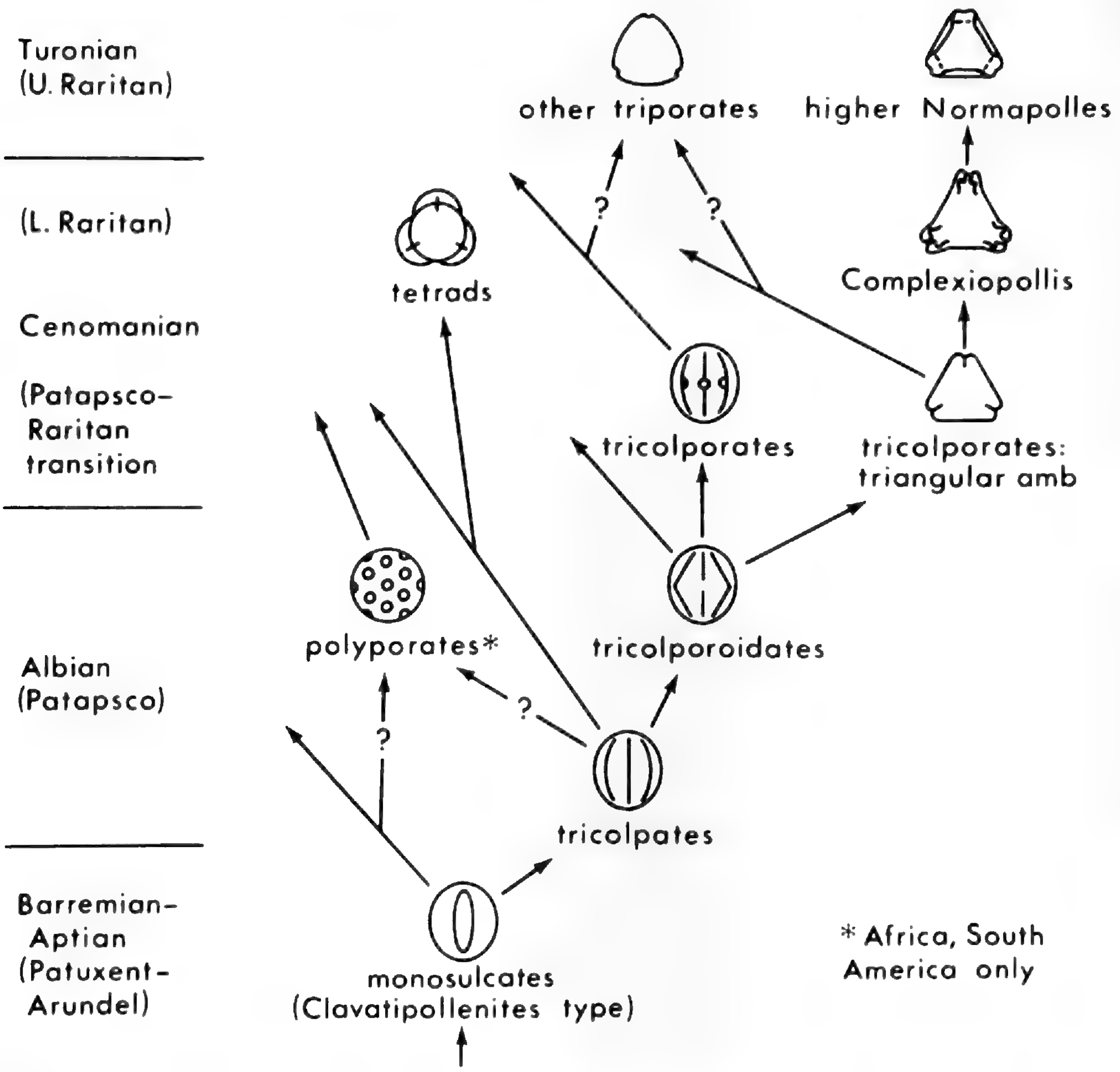

FIGURE 33. Evolution of major angiosperm pollen types during the Cretaceous (Doyle, 1969).

size of forms and increasing diversity of morphology and sculpturing upwards in the section from the Aptian-Albian (Doyle, 1969; Muller, 1970). Triporate grains appear in the Cenomanian. One enormously important development of Upper Cretaceous time was the Normapolles group of triporate forms with very complex pore structure and other morphological variations. These continue into the lower part of the Tertiary—the Early Paleogene, but they had their greatest "vogue" in Late Cretaceous time, and further study of the group will doubtless reveal still more about the phytogeography and evolution of the antique angiosperms. For example, pollen of the chiefly Southern Hemisphere family, the Proteaceae, are possibly Normapolles-derived.

Study of two unusual genera of Upper Cretaceous pollen has been especially productive in showing something of floral trends in the Upper Cretaceous-Lower Paleogene—*Wodehouseia* (Stanley, 1961*a*) and *Aquilapollenites* (Rouse, 1957; Stanley, 1961*b*; Khlonova, 1961). For example, Normapolles forms are more characteristic of eastern North America and Europe, whereas *Wodehouseia*-

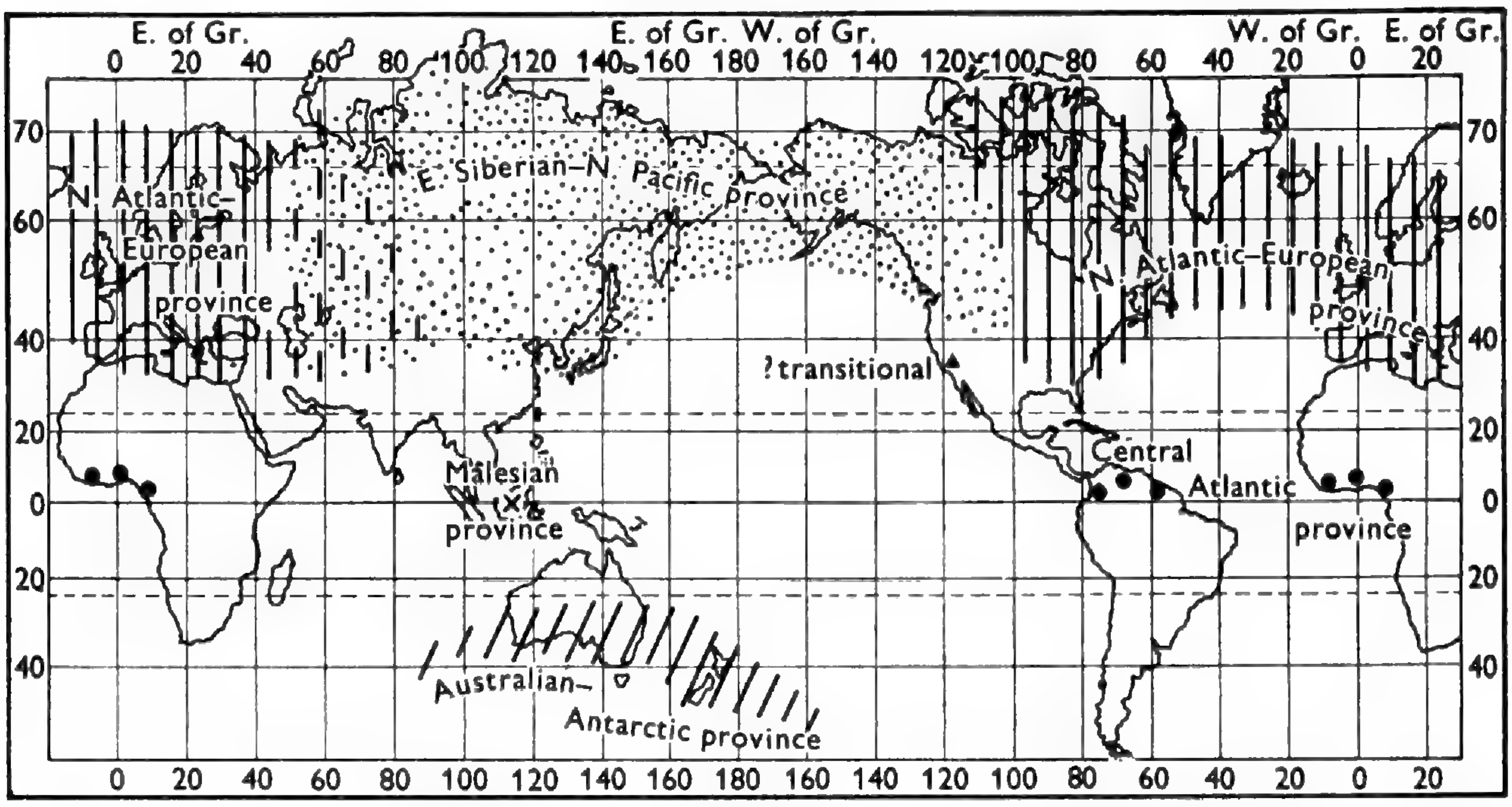

FIGURE 34. Palynofloristic provinces of the Maestrichtian (Uppermost Cretaceous), showing the *Aquilapollenites*-rich province (dotted pattern) and the Normapolles-rich province (vertical lines) (Muller, 1970).

Aquilapollenites forms are rare. *Aquilapollenites* spp. are especially characteristic of western North America and northeastern Asia (see Fig. 34).

There is also other evidence of marked divergence of regional angiosperm floras in the Upper Cretaceous—for example in Cretaceous palynofloras of Australia and New Zealand (Balme, 1964).

Soviet palynologists such as Malyavkina (1949), Samoilovich (1961), Bolkhovitina (1953), and Khlonova (1960) have contributed greatly to the field of Cretaceous palynology. Malyavkina's work especially has not received the attention it deserves, and its reexamination (for example in Vols. 38–40 of the *Catalog of Fossil Spores and Pollen*) is at present pointing out that this is particularly unfortunate nomenclaturally, because many of her names may require either the conservation or overturning of competing names, some of which are very familiar. The comprehensiveness of Soviet works in the Upper Mesozoic is for the most part matched in the western countries only in unpublished company reports.

TERTIARY PALYNOLOGY

The first fossil pollen grains ever observed, in the 1840's, were from a Tertiary coal in Germany, and Potonié's contributions in the late 1920's and early 1930's were also concerned primarily with Tertiary coals and other Tertiary sediments of Germany. It is significant that one of the first major breakthroughs in the practical application of palynology by the petroleum industry was in Tertiary rocks of Venezuela (Kuyl, Muller & Waterbolk, 1955). And yet, Tertiary palynology has not so far been quite as productive of excitement as have Devonian, Cretaceous, or Permo-Triassic spores/pollen efforts. At least part of the problem is systematic; in the Quaternary extant genera, even species, can be recognized without too many problems. In the Cretaceous and below everybody has agreed that form genera must be employed for taxonomy of spores/pollen, and the relationship of these to natural taxa is still mostly unknown, except in the somewhat unusual circumstances of spores/pollen found in sporangia/pollen sacs. In the Tertiary the problem is complicated. With progressive modernization of floras through the Cenozoic, there is increasing evidence of relationship to modern taxa. An example is the probably Upper Oligocene Brandon lignite of Vermont. Traverse (1955) referred many of the pollen forms to extant genera and later (1957) defended the practice, but Potonié (1967) has attacked this as unwarranted and unsound. Indeed, many of the Traverse forms which have been of interest to other palynologists have been transferred by them to this or that artificial form genus: *Alangium barghoornianum* Traverse to *Alangiopollis barghoornianus* Krutzsch, and so forth. This is not the place to rewarm this by now hoary argument, but it does indicate the magnitude of the nomenclatural-taxonomic problem. A famous and talented palynologist from Australia once wrote me that she was so upset by the difficulties that she proposed to leave the whole area of work to others. Most palynologists now feel that the problem is solved by the nearly universal present use of form-taxa names—but unquestionably the problem is still with us, and it has handicapped Tertiary palynology.

The European Tertiary work which Potonié began has been carried on by Thomson and Pflug (1953) in Germany, by Kedves (1969) in Hungary, and by many others. In Japan a series of palynologists have described many Tertiary palynofloras—K. Takahashi (1961) has been perhaps the most prolific writer.

In America many of the largest Tertiary areas still remain to be definitively investigated, though one of the earliest and best American contributions to paleopalynology was Wodehouse's (1933) work on the Eocene Green River shale. Stanley (1965) and Leffingwell (1970) have published on the lower Paleocene Fort Union Group of the Dakotas, and Elsik (1968), Nichols and Traverse (1971), and others on the upper Paleocene Wilcox of Texas. Many other deposits have been described in more or less detail—for example, some of those of the Pacific Northwest by Rouse, Hopkins, and Piel (1970) and Piel (1971), but the Tertiary of North America is prevailingly still very much open country awaiting settlement.

Beginning in 1962, Krutzsch in East Germany began a comprehensive effort to systematize the Tertiary spores/pollen taxa of Europe. This ambitious encyclopedic work has proceeded through seven numbers so far but would still seem not more than half-done. Several of the large Soviet atlases which have contributed much to our understanding of world palynofloras have treated Tertiary palynofloras (for example, Pokrovskaya, 1956; Boitsova, 1956).

Tertiary palynology of the past quarter-century has provided considerable information about angiosperm evolution during the last sixty million years, such as the first appearance of grasses in the Oligocene and their subsequent diversification; the first appearance of composites in the Miocene; and a harbinger of the onset of the Pleistocene in middle latitudes, the explosive increases in *Artemisia* spp. pollen.

QUATERNARY PALYNOLOGY

This is where it all began with von Post in 1916: "pollen analysis" and "pollen statistics" meant Quaternary spores/pollen studies. Since paleopalynology as a pre-Quaternary subject came into its own as a geologically oriented tool in the later 1940's and the 1950's, this older aspect of paleopalynology has grown more and more distinctive. In approach and application it has developed as quite a separate field, although some people have worked or work in both Quaternary and pre-Quaternary fields (for example, L. R. Wilson in America, A. Horowitz in Israel). Quaternary spores/pollen analysis of peats, lake deposits, and the like was already mature in 1946, especially in Europe, as a result of work by Erdtman, Faegri, Iversen, Godwin, their students, and many others. In America the technique was applied with success by Sears, Deevey, and others (see, for example, Wright & Frey, 1965). In both Europe and America the interdisciplinary connections have been largely with archeology, anthropology, and plant ecology, whereas those of pre-Quaternary paleopalynology are with geological fields—especially stratigraphy and sedimentology. The breakthroughs in Quaternary research of recent years have been partly on the quantitative side—for example, the absolute pollen frequency (APF) method described by Davis (1966) for the more accurate measurement of vegetation by study of the pollen content of sediments and the introduction of computer-based analysis of pollen data (for example by Walker, 1969). Partly also the advances in this field stem from study of a broader range of sediments than previously, including fluvial and marine sediments (for example, by Rossignol, 1969, and by A. Martin, 1968), and sediments even of arid regions (P. Martin, *et al.*, 1961).

Indeed, some of the greatest advances in Quaternary palynology of the last quarter-century have been made in studies of fluvial and marine sedimentation of pollen which were not oriented to "classical" pollen analysis (see discussion below), which is not to deprecate the very considerable amount of work which has gone on in this field. For example, in England the famed Cambridge University Sub-Department of Quaternary Research under the direction of H. Godwin was founded at the beginning of the past quarter-century, and from it have flowed dozens of highly significant contributions on pollen analysis as they bear on the vegetational and archaeological history of Great Britain. In recognition of the importance of this work, the American Association of Stratigraphic Palynologists, prevailingly pre-Quaternary, has used a basic pollen diagram of the Godwin group as the cover design for its convention program each year since the first convention in 1968.

RECENT SEDIMENTATION OF POLLEN, SPORES, AND OTHER PALYNOMORPHS

In the early years of pollen analysis a prevailing basic assumption was that spores/pollen reached their destination in the sediment prevailingly through the air. In the sediments of peat bogs and lakes (and coals and shales derived from them), which were mostly being studied, this was essentially correct. As practical application of palynology to stratigraphic geology came into the picture in the 1950's, the assumption became less tenable. Spores/pollen in the shales and siltstones which were now being investigated seemed (in retrospect not very surprisingly) to be sedimented as other particles with similar physical properties. In 1954 Hoffmeister's now famous patent statement (Patent no. 2,686,108) for the Standard of New Jersey group claimed that ancient shorelines could be detected by plotting the amount of fossil spores and pollen per gram of sediment and the ratio of large forms to small forms. (7500 p.g. and a 1:4 ratio indicated an ancient shoreline.) Muller (1959) of Shell several years later published the results of work in the Orinoco delta and vicinity which showed that while Hoffmeister's claims were too precise and by no means invariably true, it was certainly correct that pollen and spores are sedimented as silt particles responding to current patterns—the smaller particles being carried in currents farthest offshore before sedimentation. Wind distribution was for the most part only a minor factor in palynomorph sedimentation. In work going on at about the same time as Muller's publication but not published until 1966, Traverse and Ginsburg extended the study to marine sediments of Great Bahama Bank, a shallow basin with no streams or normal clastic sedimentation. Here pollen was shown to behave as a very sensitive indicator of water turbulence, being deposited in quiet water, remaining suspended in relatively turbulent water. Results with similar implications were obtained by Cross *et al.* (1966) in the Gulf of California. These and other studies of pollen sedimentation have had considerable impact on palynological thinking.

MARINE PALYNOLOGY

In addition to the basic contributions to understanding pollen sedimentation derived from study of recent marine sediments, the general area of "marine palynology" has also greatly expanded in recent years. Stanley (1969), one of the leaders of the field, has summarized the results. Investigation of recent and Pleistocene marine sediments in various parts of the world by Koroneva, Stanley, Groot, and others has contributed to understanding of world climatic history as well as to the natural history of the oceans. Study of cores of rock recovered from the marine environment on the continental shelves has for some time played a big role in oil exploration in several parts of the world. The palynologic floras contained in such cores are often rich in marine, "non-pollen" microfossils, such as acritarchs and dinoflagellates, in addition to spores/pollen. In very recent times sediment from the cores taken in many parts of the world's oceans in connection with investigation of sea floor-spreading have been dated with marvelous precision by nannofossils, study of which some would include under palynology. (Inasmuch as nannofossils—mostly coccoliths and discoasters—consist of $CaCO_3$ and are hence chemically inorganic, I am excluding them from this history even though they are paleobotanic. Their study has been one of the most dynamically developing areas of paleontology for about a decade.)

NON-POLLEN STUDIES

Working definitions of paleopalynology with respect to what is included in the field force some hard decisions. If fungal spore walls, which are not biologically homologous or chemically identical to walls of pollen and embryophytic spores (chitin as against sporopollenin) are included, how can dinoflagellate cysts, which are chemically similar and possibly even biologically comparable to spore exines, be excluded? Accepting the pragmatic approach that the category "palynologic fossils" or "palynomorphs" includes all microfossils which are chemically organic (sporopollenin, chitin, pseudochitin, cellulose, waxy) and which commonly occur in palynologic maceration residues, those which are neither pollen nor embryophytic spores can be called "non-pollen." They are palynologically and stratigraphically very important because they occur in environments throughout the stratigraphic column in which spores and pollen are rare or absent, and they are also abundant far below the first certain appearance of embryophytic spores in the Lower Silurian.

DINOFLAGELLATES, ACRITARCHS, "HYSTRICHOSPHAERIDS"

At the opening of the period we are considering and, indeed, until the early 1960's, all sorts of organic-walled fossil microplankton were called "hystrichosphaerids." Despite pioneer work on these fossils by Deflandre, Wetzel, Eisenack, and others, not a great deal was known about them biologically, though their value stratigraphically was already recognized (see historical summary in Evitt, 1970). Evitt (1961) showed that the morphology of many of the most common of these puzzling fossils agreed closely with the general morphology of dinoflagellates. Wall (1965) put the capstone on this suggestion by succeeding in germinating some of the "hystrichosphaerids," yielding normal dinoflagellates of already-named species. Thus it was shown that many erstwhile "hystrichosphaerids" were really the cysts of dinoflagellates. Evitt (1963) proposed calling the remaining hystrichosphaerids "acritarchs." Since that time many additional hystrichosphaerids have been advanced (demoted?) to the dinoflagellates. Dinoflagellates apparently do not occur before Silurian time, but more ancient acritarchs with dinoflagellate-like features suggest either that the group is older, though non-cyst parts of the life cycle are not known, or that these older acritarchs are related, probably ancestral forms. Still others, such as the abundant acritarchs in Lower Paleozoic and even pre-Cambrian rocks are presumably unrelated (see *Paleopalinologia*, by Pokrovskaya, 1966, for summary and abundant illustrations from work of B. V. Timofeev). Also, there are the *Tasmanites* and *Leiosphaeridia* sort of "acritarchs" which Wall (1962) has suggested are algal—but "another kettle of algae." For a time there was a little excitement that the early Paleozoic and late Pre-Cambrian acritarchs represented evidence for polyphyletic origin of land plants, but this has faded away. However, the enrichment of our knowledge of acritarchs has greatly enhanced stratigraphic work with the older formerly "nonpalyniferous" rocks in the last decade and promises to do even more in that direction in the future. The Evitt-Wall solution of the "hystrichophaerid problem" of twenty years ago has laid the foundation for the still increasing field of fossil dinoflagellate studies. General expansion of interest in fossil phytoplankton also has stimulated great expansion of research with Paleozoic and older acritarchs—for example, by Cramer (1970). Schopf (1969) has effectively summarized much of this work.

CHITINOZOANS AND SCOLECODONTS

In palynological maceration residues of lower Paleozoic sedimentary rocks one frequently finds organic-walled microfossils other than phytoplanktonic acritarchs. Most common are chitinozoans, presumably pseudochitinous in chemical composition, and scolecodonts, presumably chitinous. Chitinozoans are flask-shaped, often bear more or less spiny processes, and range in size from that of a large spore to half a millimeter or so. Because of their thick walls and large size, chitinozoans often do not transmit light very well, and the scanning electron microscope (SEM) has proven a boon in studying them. Although first observed long ago, the history of their study is largely a matter of the last fifteen years. Although there is no doubt that chitinozoans are animal remains, their phylogenetic position is still regarded as doubtful. Their stratigraphic range is Upper Cambrian to Devonian, with a few stragglers farther up the column—pretty much the range of graptolites. Jenkins (1970), in a general review of chitinozoans, noted this fact and other hints from morphology and chemical composition and suggested that chitinozoans might be reproductive bodies of graptolites. Jansonius (1970) and Combaz (1967) have contributed greatly to systematic understanding of this interesting and stratigraphically important group of nonbotanical palynologic fossils.

Scolecodonts are the chitinous external covers of the mouth parts of ancient ancestors of modern polychaete marine annelid worms. As Jansonius (1971) has pointed out, scolecodont taxonomy is unfortunately very complicated because one individual worm had a variety of mouth parts, each with its own characteristic scolecodont. Nevertheless, Jansonius and others have shown in recent years that the problems are not insuperable and that scolecodonts can be very useful for stratigraphic work, especially in the pre-spore part of the section.

OTHER PALYNOLOGIC "HASH"

One of the present apparent frontiers for paleopalynologists is the great variety of "non-pollen" material which occurs in palynologic macerations. Marine "hash" such as scolecodonts, chitinozoans, acritarchs, and dinoflagellates are only part of the picture. The chitinous inner tests of foraminfera (microforams) in palynological preparations were investigated in the 1950's, but only a few studies are in the literature (see Traverse & Ginsburg, 1966; Cohen & Guber, 1968). Microforams could be the subject of much more study, as could all sorts of other microscopic animal and algal remains. But even in nonmarine rocks, there is a great variety of leaf cuticle fragments, tracheary fragments, insect parts, and other "junk" which will doubtless be systematically investigated in the future.

CARBONIZATION STUDIES AND OTHER TECHNIQUES

It long has been noticed (*cf.* Kuyl *et al.*, 1955) that fossil spores and pollen become progressively darker in color the deeper the origin of the original samples in a series of strata. Originally yellow by transmitted light, exines become orange, brown, and finally black. The effect is obviously due to coalification (= carbonization)—enrichment of carbon through loss of hydrogen and oxygen—and the effect is also seen in rock which has been metamorphosed even without deep burial. Gutjahr (1966) pointed out that what happens is akin to the coalification of coals and suggested that as fixed-carbon content of coals can be used to predict petroleum-natural gas occurrence in the area of the coals, so the degree of carbonization of fossil spores could be similarly used. More recently, others have substituted reflectance measurements (higher reflectance by reflected light ± = deeper color by transmitted light) for color determination because reflectance is susceptible of much greater precision in measurement. (Gijzel (1967) noted that the series of metamorphic changes in fossil spores could also be observed by fluorescence microscopy.) Although the technique was first applied to fossil spore exines, it is now being applied more widely to plant fragments in sedimentary rocks (phytoclasts) as a precise measure of the metamorphic history of the rocks.

It would be impossible to ignore the impact on paleopalynology in the last twenty years of electron microscope studies—at first, clarification of exine structure by transmission electron microscope studies of ultra-thin sections (*e.g.* Pettit & Chaloner, 1964); more recently, the much greater application of the scanning electron microscope (SEM), especially useful for study of more or less opaque bodies (*cf.* Jenkins, 1970—SEM photos of chitinozoans). Although SEM pictures are striking and doubtless reveal fine surface features which are often obscure by light microscopy, it must be remembered that SEM pictures display only the surface. I do not believe with some enthusiasts that SEM will replace the light microscope in paleopalynology, even if the price of the equipment (currently about 25 times the cost of a good light microscope) is dramatically reduced. There is even danger (Chaloner, 1968) of parallel systems of taxa being described by light microscopy and SEM—the two instruments must be used in conjunction with each other. Refinements of light microscopy also have made a contribution to paleopalynological research in this period—for example, phase contrast microscopy and differential interference contrast (Nomarski) microscopy.

Doubtless still other technical breakthroughs will have as dramatic effect as SEM in coming decades; for example, automated microscopes for spores/pollen identification are technically possible.

PALYNOLOGIC SYSTEMATICS

Every branch of biological science has had its difficulties with taxonomy and nomenclature—paleontology's problem is the worst because of the additional, vertical, or time dimension to the record, the difficulty in defining generic and specific concepts for fossils, the problem of the interface of fossil groups with extant forms, and the problem of artificial versus natural classifications. Paleopalynology's difficulties in this area are especially thorny because a majority of its practitioners are not by orientation or training biologists and because some of the subject matter is governed by botanical rules, some by zoological rules—in some cases jurisdication might even be debated. Indeed, the nomenclatural problems have seemed so severe to some palynologists that they have advocated use of alphanumeric code designations for spores/pollen instead of names (this is widely done in industrial laboratories—see Hopping, 1967: 30–34). Others have suggested more formal new approaches which would remove paleopalynological nomenclature from the realm of Linnean-style binominal system (see Hughes, 1964; Hughes & Moody-Stuart, 1969). (The mainstream of paleopalynological systematics, however, has remained firmly linked to that of botanical nomenclature, and it is worth noting that it was a group of American paleopalynologists who were mostly responsible for getting the erstwhile "Paleobotanical Appendix" of the *International Code of Botanical Nomenclature* incorporated into the main body of the *Code* at the 1959 International Botanical Congress in Montreal. This had the salutary effect of removing any implication that plant fossils are somehow leprous.)

As is true of so much of palynology, the systematic development of the field is almost entirely a product of the post-World War II era. Potonié and Kremp summarized the Paleozoic genera in 1954–1956. Potonié began his very useful series of *Synopsis der Gattungen der Sporae dispersae* volumes in 1956. These books are now five in number. With their various collateral publications, they cover the whole gamut of fossil spore/pollen genera. The *Catalog of Fossil Spores and Pollen* (CFSP), discussed earlier in this paper, began in 1957 to republish the original protolog materials, with supporting information and commentary, for genera and species of fossil spores and pollen. CFSP now has covered about 6,000 of the most significant forms. With the *Catalog* and Potonié's *Synopsis* in hand, a paleopalynologist in 1972 is in infinitely better condition systematically than we were in the late 1940's, however true it is that both *Catalog* and *Synopsis* have many lacunae and other faults. Cataloging of other palynologic fossils (dinoflagellates by Eisenack, 1964, 1967; Chitinozoans by Combaz, 1967) is far behind that of pollen and spores.

Coordinate with his *Synopsis*, Potonié has proposed and developed a system for the artificial classification of fossil spores and pollen—the "turma" system (from *turma*, a Roman military term—a squadron). The idea originally came from Ibrahim (1933), but was first formally proposed by Potonié in 1952. The system consists of a hierarchy of suprageneric units based on morphology and entirely outside the provisions of the *International Code of Botanical Nomenclature.* (The system is for form genera of spores and pollen, and form genera cannot be assigned to higher categories by definition of the *Code.*) The largest units are two Anteturmae, Sporites and Pollenites, which paradoxically are not strictly morphological but functional. (As spores and pollen cannot always be distinguished morphologically, some fossils can show up in both Anteturmae.) Anteturmae are subdivided to Turmae, Subturmae, Infraturmae. The system is much used in paleopalynological papers—especially for Paleozoic palynofloras where the principal other live option is alphabetical listing. The system becomes progressively less useful as one moves up the column because of the increasingly large number of spores/pollen which do have phylogenetic reference points, until in the Lower Tertiary the system becomes quite useless. Potonié's system, which has been refined and expanded by others (for example, Dettmann, 1963), does have the advantage over, say, alphabetical listing that one can come to know where to look in a monograph for spores with certain features—for example, trilete, zonate spores will be in the subturma Zonotriletes.

It seems clear that careful study, compilation, and monographing of the various groups of genera is what is needed to bring order to paleopalynological nomenclature. Some of this has been going on, as I have already noted—for example, by Potonié with his *Synopses*, Krutzsch with his *Atlas* of Tertiary spores and pollen of Europe, Smith and Butterworth for British Carboniferous palynomorphs. Much more is needed, and, it is to be hoped, this will be a hallmark of the next generation of paleopalynology. It seems evident that one approach will be the use of computer-based techniques for information storage and retrieval, and indeed much has already happened along this line. Hughes (1969) has underlined the importance of handling systematic data in paleopalynology in a more standardized and rational manner—which would also greatly help computer-based efforts. Kremp (1970, 1971) has for several years headed a project supported by several American oil companies for computer storage of bibliographic and nomenclatural data from most of the paleopalynological literature and has also been seeking international cooperation for computer-based storage and retrieval of paleopalynological data. Beginning about 1967 the Joint Committee on Paleontological Information, sponsored by the American Geological Institute and funded in part by the National Science Foundation, has sponsored meetings to discuss all aspects of this set of problems. In October 1971, an international meeting of persons interested in this work assembled at Tucson, Arizona, jointly sponsored by the University of Arizona and the American Association of Stratigraphic Palynologists.

Germeraad (*cf.* Germeraad & Muller, 1970) of the Netherlands spoke on computer processing of coded morphological data. Tralau (1971) of Sweden described the thorough, computer-based bibliographic techniques of the Swedish Museum of Natural History. Others described various approaches to computer-based systematics being used in their laboratories or proposed for the future. Traverse and Ames, for example, described a project underway at Pennsylvania State University to use computer-based techniques for manipulation of the extensive systematic data already in the *Catalog of Fossil Spores and Pollen* and for design and production of future volumes of the *Catalog* in the service of systematic paleopalynology. Kremp reported on his recent trip to palynological laboratories around the world, with special emphasis on the Soviet Union. This was in connection with Kremp's continuing efforts to bring into being an international consortium for palynological information storage and retrieval by computer and other techniques (see Kremp & Methvin, 1969). It seems clear that this sort of effort will be characteristic of paleopalynology in the last quarter of the twentieth century.

CONCLUSION

The study of fossil spores and pollen has advanced from the status of an infant first cousin of mainstream paleobotany in the immediate post-World War II years to that of a vigorous and practically independent art in 1971. There are now about 300 practitioners of the art of paleopalynology in North America, perhaps 200 in India and 500 in the Soviet Union, and probably about 2,500 worldwide. Paleopalynology now clearly overshadows megafossil paleobotany in numbers of trained people and in economic importance.

It has been noted by others that most major taxa of fossil spores and pollen have probably already been described (however poorly) and that few big surprises are left. This has led some paleopalynologists to feel that their subject is in the beginnings of senescence. But this fails to recognize the bewildering complexity of a subject with something like 15,000 described taxa and new ones being added all the time (even if not often representative of important new groups any more). We are just on the threshold of the thorough systematic description and compilation of the as yet only partly digested cud of paleopalynology. Cataloging and monographing of systematic palynology on a mammoth scale awaits if we are to understand the data we have amassed. Furthermore, there are large areas of research, such as the sedimentation of palynomorphs, their microstructure, their evolutionary sequences, and environmental interpretation (to name only a few) which have really only been touched. Providing that funding remains available, I look for flowering of the field now that it has reached maturity. Whether funding does continue at a high level will depend in large measure on whether paleopalynology remains an important stratigraphic tool for private (mostly petroleum) and governmental geological enterprises. That is an economic question on which it is difficult to prophesy. Although there is some grumbling about oil company secrecy and applied paleopalynology's domination of the field, the tremendous amount of palynological information which is available in monographs, journals and books worldwide is a direct result of the economic potential of stratigraphic palynology.

BIBLIOGRAPHY

ALPERN, B. 1967. La C.I.M.P. lutte pour une meilleure efficacité stratigraphique en palynologie. Rev. Palaeobot. Palynol. 1: 69–74.

BALME, B. E. 1964. The palynological record of Australian pre-Tertiary floras. Pp. 49–80, *in* L. M. Cranwell (editor), "Ancient Pacific floras; the Pollen Story." 10th Pacific Congress Ser., Univ. Hawaii.

———. 1970. Palynology of Permian and Triassic strata in the Salt Range and Surghar Range, West Pakistan. Pp. 305–453, *in* B. Kummel & C. Teichert (editors), "Stratigraphic boundary problems: Permian and Triassic of West Pakistan." Univ. Kansas Dept. Geol. Spec. Pub. 4.

BHARADWAJ, D. C. 1962. The miospore genera in the coals of Raniganj stage (Upper Permian), India. Palaeobotanist 9: 68–106.

BOITSOVA, E. P. (editor). 1956. Atlas of Miocene spore-pollen complexes of various regions of the USSR. Materials of VSEGEI N.S. Paleont. and Strat. 13. 461 pp. [In Russian.]

BOLKHOVITINA, N. A. 1953. Spore-pollen character of Cretaceous deposits of the central provinces of the USSR. Acad. Sci. USSR, Inst. Geol. Sci. Trudy 145 (Geol. Ser. 61). 184 pp. [In Russian.]

BOSE, M. N., R. K. KAR & H. K. MAHESHWARI. 1966–1969. Palaeozoic sporae dispersae from Congo I–II, VII–X. Mus. Roy. Afrique Cent. Ann. Sci. Géol. 53, 60, 63. 249, 116, 168 pp.

CHALONER, W. G. 1967. Spores and land-plant evolution. Rev. Palaeobot. Palynol. 1: 83–93.

———. 1968. British Pre-Quaternary palynology: a historical review. Rev. Palaeobot. Palynol. 6: 21–40.

———. 1970*a*. The evolution of miospore polarity. Geosci. Man 1: 47–56.

———. 1970*b*. The rise of the first land plants. Biol. Rev. 45: 353–377.

COHEN, A. D. & A. L. GUBER. 1968. Production of pollen-sized "microforaminifera" from "normal" foraminifera. Micropaleontology 14: 361–362.

COMBAZ, A. (editor). 1967. Les Chitinozoaires. Comm. Int. Microflore Paleozoique (C.I.M.P.) Microfossiles organiques du Paleozoique. 1, 2. 96, 43 pp.

COOKSON, I. C. 1947. Plant microfossils from the lignites of Kerguelen Archipelago. B.A.N.Z. Antarctic Res. Exped. 1929–1931, Repts. Ser. A. 2: 127–142.

———. 1953. Difference in microspore composition of some samples from a bore at Comaum, South Australia. Austral. Jour. Bot. 1: 462–473.

COUPER, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geol. Surv. Paleont. Bull. 22: 1–77.

———. 1956. Evidence of a possible gymnospermous affinity for *Tricolpites troedssonii* Erdtman. New Phytol. 55: 280–285.

CRAMER, F. H. 1970. Distribution of selected Silurian acritarchs. An account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa. Rev. Esp. Micropalent. Num. Extraord. 1. 203 pp.

CROSS, A. T., G. G. THOMPSON & J. B. ZAITZEFF. 1966. Source and distribution of palynomorphs in bottom sediments, southern part of Gulf of California. Marine Geol. 4: 467–524.

DAVIS, M. B. 1966. Determination of absolute pollen frequency. Ecology 47: 310–311.

DETTMANN, M. E. 1963. Upper Mesozoic microfloras from south-eastern Australia. Proc. Roy. Soc. Victoria 77(1). 148 pp.

DOWNIE, C. & W. A. S. SARJEANT. 1964. Bibliography and index of fossil dinoflagellates and acritarchs. Geol. Soc. Amer. Mem. 94. 180 pp.

DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. Jour. Arnold Arbor. 50: 1–35.

EISENACK, A. 1964 & 1967. Katalog der fossilen Dinoflagellaten, Hystrichospären und Verwandten Mikrofossilien. Band I. Dinoflagellaten. E. Schweizerbart'sche Verlagsbuchhandlung. 895 pp. and (1967) supplement.

ELSIK, W. C. 1968. Palynology of a Paleocene Rockdale lignite, Milam County, Texas. Pollen Spores 10: 263–314; 599–664.

ERDTMAN, G. 1927–1958. Literature on Palynology. [1927–44: as Literature on Pollen-statistics and Related Topics.]

———. 1943. An Introduction to Pollen Analysis. Chronica Botanica, Waltham, Massachusetts. 239 pp.

———. 1948. Did dicotyledonous plants exist in Early Jurassic time? Förh. Fören. Geol. Stockholm 70: 265–271.

———. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms. (An introduction to palynology I.) Almquist and Wiksell, Stockholm. 539 pp.

———. 1957. Pollen and Spore Morphology and Plant Taxonomy: Gymnospermae, Pteridophyta, Bryophyta (illustrations). (An introduction to palynology II.) Almquist and Wiksell, Stockholm. 151 pp.

———. 1965. Pollen and Spore Morphology and Plant Taxonomy: Gymnospermae, Bryophyta (text). (An introduction to palynology III.) Almquist and Wiksell, Stockholm. 191 pp.

———. 1969. Handbook of Palynology. Hafner, New York. 486 pp.

EVITT, W. R. 1961. Observations on the morphology of fossil dinoflagellates. Micropaleontology 7: 385–420.

———. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs. Proc. Natl. Acad. U.S.A. 49: 158–164; 298–302.

———. 1970. Dinoflagellates—a selective review. Geosci. Man 1: 29–141.

FAEGRI, K. & J. IVERSEN. 1950. Text-book of Modern Pollen Analysis. E. Munksgaard, Copenhagen. 168 pp.

——— & ———. 1964. Textbook of pollen analysis. Ed. 2. Hafner, N.Y. 237 pp.

GERMERAAD, J. H. & J. MULLER. 1970. A computer-based numerical coding system for the description of pollen grains and spores. Rev. Palaeobot. Palynol. 10: 175–202.

GIJZEL, P. VAN. 1967. Palynology and fluorescence microscopy. Rev. Palaeobot. Palynol. 2: 49–79.

GRAY, J. & A. J. BOUCOT. 1971. Early Silurian spore tetrads from New York: earliest New World evidence for vascular plants. Science 173: 918–921.

GUENNEL, G. K. 1952. Fossil spores of the Alleghenian coals in Indiana. Indiana Geol. Surv. Rep. Progress 4. 40 pp.

———. 1958. Miospore analysis of the Pottsville coals of Indiana. Indiana Geol. Surv. Bull. 13: 1–101.

GUTJAHR, C. C. M. 1966. Carbonization measurements of pollen-grains and spores and their application. Doctoral "Proefschrift," Univ. Leiden. 29 pp.

HART, G. F. 1965. The Systematics and Distribution of Permian Miospores. Witwatersrand Univ., Johannesburg. 252 pp.

———. 1972. Permian Genera. [Compilation informally distributed to participants in Paleozoic palynology short course, Louisiana State University, 5 January 1972.]

HOFFMEISTER, W. S. 1954. Microfossil prospecting for oil. U.S. Patent 2,686,108. 4 pp.

———. 1959. Lower Silurian plant spores from Libya. Micropaleontology 5: 331–334.

HOPPING, C. A. 1967. Palynology and the oil industry. Rev. Palaeobot. Palynol. 2: 23–48.

HUGHES, N. F. 1964. Einige Vorschläge zur Angabe der Daten und der Klassifikation in der Sporologie. Fortschr. Geol. Rheinland Westfalen 12: 39–44.

———. 1969. Suggestions for better handling of the genus in palaeo-palynology. Grana Palynol. 9: 137–146.

——— & J. C. MOODY-STUART. 1969. A method of stratigraphic correlation using Early Cretaceous miospores. Palaeontology 12: 84–111.

HYDE, H. A. & D. A. WILLIAMS. 1944. Right word. Pollen Analysis Circular 8: 6.

IBRAHIM, A. C. 1933. Sporenformen des Aegerhorizonts des Ruhr-Reviers. Diss., Tech. Hochsch., Berlin. 47 pp.

JANSONIUS, J. 1970. Classification and stratigraphic application of Chitinozoa. Proc. N. Amer. Paleont. Conv. G: 789–808.

———. 1971. Scolecodonts: I. Descriptive terminology and revision of systematic nomenclature; II. Lectotypes, new names for homonyms, index of species. Bull. Canad. Petrol. Geol. 19: 251–302.

JENKINS, W. A. M. 1970. Chitinozoa. Geosci. Man 1: 1–21.

JERSEY, N. J. DE. 1964. Triassic spores and pollen grains from the Bundamba Group. Geol. Surv. Queensland Pub. 321: 1–21.

KAPP, R. O. 1969. How to Know Pollen and Spores. Wm. C. Brown, Dubuque, Iowa. 249 pp.

KEDO, G. I. 1957. Spores from hypersaline Devonian deposits of the Pripyat Basin and their stratigraphic significance. *In* "Paleontology and stratigraphy of the BSSR." BSSR Acad. Sci., Coll. 2: 3–43. [In Russian.]

KEDVES, M. 1969. Palynological studies on Hungarian Early Tertiary deposits. Akadémiai Kiadó, Budapest. 84 pp.

KEMP, E. M. 1968. Probable angiosperm pollen from the British Barremian to Albian strata. Palaeontology 11: 421–434.

KHLONOVA, A. F. 1960. Specific composition of the pollen and spores in deposits of the Upper Cretaceous of the Chulymo-Eniseisk basin. Acad. Sci. USSR, Siberian Div., Trudy Inst. Geol. Geoph. 3. 104 pp. [In Russian.]

———. 1961. Spores and pollen of the upper half of the Cretaceous of the West-Siberian depression. Acad. Sci. USSR, Siberian Div., Trudy Inst. Geol. Geoph. 7. 100 pp. [In Russian.]

KLAUS, W. 1960. Sporen der karnischen Stufe der ostalpinen Trias. Jahrb. Geol. Bundesanstalt (Wien) Sonderbd. 5: 107–184.

———. 1963. Sporen aus dem südalpinen Perm. Jahrb. Geol. Bundesanstalt 106: 229–363.

KOSANKE, R. M. 1943. The characteristic plant microfossils of the Pittsburgh and Pomeroy coals of Ohio. Amer. Midl. Naturalist 29: 119–132.

———. 1950. Pennsylvanian spores of Illinois and their use in correlation. Illinois State Geol. Surv. Bull. 74. 128 pp.

——— & A. T. CROSS (editor). 1970. Symposium on palynology of the Late Cretaceous and Early Tertiary. Geol. Soc. Amer. Spec. Pap. 127. 396 pp.

KREMP, G. 1965. Morphologic encyclopedia of palynology. Contr. 100, Program in Geochronology. Univ. Arizona. 185 pp.

———. 1970. Towards computerization of palynology—paleobotany: a progress report on a fact-finding trip. Interim Report 1, Dept. Geosciences, Univ. Arizona. 200 pp.

———. 1971. Morphographic and other information in palynologic-paleobotanic data banks. Interim Report 2, Dept. Geosciences, Univ. Arizona. 17 pp.

——— & J. G. METHVIN. 1969. Computer techniques in palynology-palaeobotany can stimulate fruitful research on a world scale. Pp. 161–171, *in* J. Sen Memorial Volume, Bot. Soc. India.

KRUTZSCH, W. 1962. et seq. Atlas der mittel- und jungtertiären dispersen Sporen- und

Pollen- sowie der Mikroplanktonformen des nördlichen Mitteleuropas. VEB Deutscher Verlag der Wiss., Berlin.

Kuyl, O. S., J. Muller & H. T. Waterbolk. 1955. The application of palynology to oil geology with reference to western Venezuela. Geol. Mijnbouw 17: 49–75.

Leffingwell, H. A. 1970. Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) formations of the type Lance area, Wyoming. Pp. 1–64, *in* R. M. Kosanke & A. T. Cross (editors), "Symposium on palynology of the Late Cretaceous and Early Tertiary." Geol. Soc. Amer. Spec. Pap. 127.

Luber, A. A. & I. E. Valts. 1941. Atlas of microspores and pollen of the Paleozoic of the USSR. Trudy VSEGEI 139. 107 pp. [In Russian.]

Mädler, K. 1964. Die geologische Verbreitung von Sporen und Pollen in der deutschen Trias. Beih. Geol. Jahrb. 65. 147 pp.

Malyavkina, V. S. 1949. Index of spores and pollen, Jurassic-Cretaceous. Trudy VNIGRI N.S. 33, Gostoptekhizdat, Moscow. 138 pp. [In Russian.]

———. 1964. Spores and pollen from Triassic deposits of the West-Siberian Lowland. Trudy VNIGRI 231. 293 pp. [In Russian.]

Manten, A. A. 1967. Lennart von Post and the foundation of modern palynology. Rev. Palaeobot. Palynol. 1: 11–22.

———. 1968. A short history of palynology in diagrams. Rev. Palaeobot. Palynol. 6: 177–188.

Martin, A. R. H. 1968. Pollen analysis of Groenlevi Lake sediments, Knysna (South Africa). Rev. Palaeobot. Palynol. 7: 107–144.

Martin, P., J. Schoenwetter & B. C. Arms. 1961. The Last 10,000 Years. Geochronology Labs., Univ. Arizona. 119 pp.

McGregor, D. C. 1960. Devonian spores from Melville Island, Canadian Arctic Archipelago. Palaeontology 3: 26–44.

———. 1961. Spores with proximal radial pattern from the Devonian of Canada. Geol. Surv. Canada Bull. 76: 1–11.

Muller, J. 1959. Palynology of recent Orinoco delta and shelf sediments. Micropaleontology 5: 1–32.

———. 1970. Palynological evidence on early differentiation of angiosperms. Biol. Rev. 45: 417–450.

Naumova, S. R. 1939. Spores and pollen of the coals of the USSR. Trans. 17th Int. Geol. Cong. (1937) 1: 353–364.

Neustadt, M. I. 1967. Stand der palynologischen Untersuchungen in der U.S.S.R. Rev. Palaeobot. Palynol. 4: 15–43.

Nichols, D. J. & A. Traverse. 1971. Palynology, petrology, and depositional environments of some Early Tertiary lignites in Texas. Geosci. Man 3: 37–48.

Owens, B. 1970. Recognition of the Devonian-Carboniferous boundary by palynological methods. Pp. 349–364, *in* M. Streel & R. H. Wagner (editors), "Colloque sur la Stratigraphie du Carbonifère." Cong. Colloq. Univ. Liège 55.

Pettit, J. M. & W. G. Chaloner. 1964. The ultrastructure of the Mesozoic pollen Classopollis. Pollen Spores 6: 610–620.

Piel, K. M. 1971. Palynology of Oligocene sediments from central British Columbia. Canad. Jour. Bot. 49: 1815–1920.

Pokrovskaya, I. M. 1956. Atlas of Oligocene spore-pollen complexes of various regions of the USSR. Mater. VSEGEI, Paleont. Strat., N.S. 16. 312 pp. [In Russian.]

——— (editor). 1966. Paleopalinologia. Trudy VSEGEI, N.S. 141, Nedra, Leningrad. 3 vols. 351 pp., 446 pp., 366 pp. [In Russian.]

Potonié, R. 1934. Zur Mikrobotanik der Kohlen und ihrer Verwandten. Arbeiten Inst. Paläobot. Petrog. Brennsteine (Preussischen Geol. Landesanst.) Vol. 4–5. 212, 101 pp.

———. 1951. Revision stratigraphisch wichtiger Sporomorphen des mittel-europäischen Tertiärs. Paleontographica, Abt. B. 91: 131–151.

———. 1952. Zur Systematik isolierter Sporen fossiler Pflanzen. Pp. 158–173, *in* G. Erdtman (editor), "Palynology. Aspects and prospects. III." Svensk Bot. Tidskr. 46.

———. 1956. Synopsis der Sporae dispersae, I. Beih. Geol. Jahrb. 23. 103 pp.

———. 1958. Synopsis der Sporae dispersae, II. Beih. Geol. Jahrb. 31. 114 pp.

———. 1960. Synopsis der Sporae dispersae, III. Beih. Geol. Jahrb. 39. 189 pp.

———. 1966. Synopsis der Sporae dispersae, IV. Beih. Geol. Jahrb. 72. 244 pp.

———. 1967. Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien. Forschungsber. Landes Nordrhein-Westfalen 1761. 310 pp.

———. 1970. Synopsis der Sporae dispersae, V. Beih. Geol. Jahrb. 87. 222 pp.

——— & G. Kremp. 1954. Die Gattungen der paläozoischen *Sporae dispersae* und ihre Stratigraphie. Geol. Jahrb. 69: 111–194.

——— & ———. 1955. Die *Sporae dispersae* des Ruhrkarbons, Teil I. Palaeontographica, Abt. B. 98: 1–136.

——— & ———. 1956*a*. Die *Sporae dispersae* des Ruhrkarbons, Teil II. Palaeontographica, Abt. B. 99: 85–191.

——— & ———. 1956*b*. Die *Sporae dispersae* des Ruhrkarbons, Teil III. Palaeontographica, Abt. B. 100: 65–121.

———, A. Ibrahim & F. Loose. 1932. Sporenformen aus den Flözen Ägir und Bismarck des Ruhrgebietes. Neues Jahrb. Mineral. Geol. Paläont. Beilageband, Abt. B. 67: 438–454.

Raistrick, A. & J. Simpson. 1933. The microspores of some Northumberland coals and their use in the correlation of coal seams. Inst. Min. Eng. Trans. 85: 225–235.

Richardson, J. B. 1964. Middle Old Red Sandstone spore assemblages from the Orcadian Basin, north-east Scotland. Palaeontology 7: 559–605.

Rossignol, M. 1969. Une séquence climatique du pléistocène dans la région de la Mer Morte (Israël). Pollen Spores 11: 603–614.

Rouse, G. E. 1957. The application of a new nomenclatural approach to Upper Cretaceous plant microfossils from western Canada. Canad. Jour. Bot. 35: 349–375.

———, W. S. Hopkins, Jr. & K. M. Piel. 1970. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Pp. 213–246, *in* R. M. Kosanke & A. T. Cross (editors), "Symposium on palynology of the Late Cretaceous and Early Tertiary." Geol. Soc. Amer. Spec. Pap. 127.

Samoilovich, S. R. 1953. Pollen and spores from Permian deposits of the Cherdynsk and Aktyubinsk Pre-Urals. Trudy VNIGRI 75: 5–92. [In Russian.]

———. 1961. Pollen and spores of western Siberia: Jurassic-Paleocene. Trudy VNIGRI 177: 1–659. [In Russian.]

Scheuring, B. W. 1970. Palynologische und palynostratigraphische Untersuchungen des Keupers in Bölchentunnel (Solothurner Jura). Schweiz. Paläont. Abh. 88. 119 pp.

Schopf, J. M. 1969. Early Paleozoic palynomorphs. Pp. 163–192, *in* R. H. Tschudy & R. A. Scott (editors), "Aspects of Palynology." Wiley-Interscience, New York.

———, L. R. Wilson & R. Bentall. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. Illinois Geol. Surv. Rep. Invest. 91: 1–73.

Sears, P. B., et al. 1943–1954. The Pollen and Spore Circular [Nos. 1–8 as Pollen Analysis Circular]. 1–18. [Mimeographed newsletter, distributed privately.]

Smith, A. H. V. & M. A. Butterworth. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. Palaeont. Assoc. (London) Spec. Pap. Palaeont. 1. 324 pp.

Stanley, E. A. 1961*a*. A new sporomorph genus from northwestern South Dakota. Pollen Spores 3: 155–162.

———. 1961*b*. The fossil pollen genus *Aquilapollenites*. Pollen Spores 3: 329–352.

———. 1965. Upper Cretaceous and Paleocene plant microfossils and Paleocene dinoflagellates and hystrichosphaerids from northwestern South Dakota. Bull. Amer. Paleont. 49: 177–384.

———. 1969. Marine palynology. Oceanogr. Mar. Biol. Ann. Rev. 7: 277–292.

Streel, M. 1967. Associations de spores du Devonien inférieur et leur signification stratigraphique. Ann. Soc. Geol. Belgique 90: 11–54.

———. 1972. Newsletter sent to members of C.I.M.P.

——— & R. H. Wagner. 1970. Colloque sur la stratigraphie du Carbonifère (CIMP). Cong. Colloq. Univ. Liège 55. 551 pp.

Takahashi, K. 1961. Pollen und Sporen des westjapanischen Alttertiärs und Miozäns (Teil II). Mem. Fac. Sci. Kyushu Univ., Ser. D (Geol.). 11: 279–345.

Thomson, P. W. & H. Pflug. 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. Palaeontographica, Abt. B. 94: 1–138.

Tralau, H. 1971. A computerized information system in palynology and palaeobotany. Swedish Nat. Hist. Mus., Stockholm. 4 pp.

Traverse, A. 1951. The pollen and spores of the Brandon lignite, a coal in Vermont of Lower Tertiary age. Ph.D. Thesis, Harvard Univ. 205 pp.

———. 1955. Pollen analysis of the Brandon lignite of Vermont: U.S. Bur. Mines Rep. Invest. 5151: 1–107.

———. 1957. The nomenclatural problem of plant microfossil species belonging to extant genera. Micropaleontology 3: 255–258.

———. 1960. P.S.B.S.A. The oldest organization of paleobotanists in the world. Pl. Sci. Bull. 6(3): 1–4.

———. 1970. [Review of:] Handbook of Palynology, by G. Erdtman: Aspects of Palynology, by R. H. Tschudy and R. A. Scott, ed. Amer. Sci. 58: 443–445.

——— & R. Ginsburg. 1966. Palynology of the surface sediments of Great Bahama Bank, as related to water movement and sedimentation. Marine Geol. 4: 417–459.

———, H. T. Ames & W. Spackman. 1970. The *Catalog of Fossil Spores and Pollen*—history and status. Rev. Palaeobot. Palynol. 10: 165–173.

Tschudy, R. H. & R. A. Scott (editors). 1969. Aspects of palynology. Wiley-Interscience, New York. 510 pp.

Visscher, H. 1966. Palaeobotany of the Mesophytic III. Plant microfossils from the upper Bunter of Hengelo, the Netherlands. Acta Bot. Neerl. 15: 316–375.

Walker, D. 1969. Computer assisted pollen identification-instruction manual. Multilithed report, Res. School Pacific Studies, Canberra, Australia. 21 pp.

Wall, D. 1962. Evidence from recent plankton regarding the biological affinities of *Tasmanites* Newton 1875 and *Leiosphaeridia* Eisenack 1958. Geol. Mag. 99: 353–362.

———. 1965. Modern hystrichospheres and dinoflagellate cysts from the Woods Hole region. Grana Palynol. 6: 297–314.

Wilson, L. R. 1962. Plant microfossils from the Flowerpot Formation. Oklahoma Geol. Surv. Circ. 49: 1–50.

Wodehouse, R. P. 1933. Tertiary pollen II. The oil shales of the Eocene Green River Formation. Bull. Torrey Bot. Club 60: 479–524.

———. 1935. Pollen Grains. McGraw-Hill, New York. 574 pp.

Wright, H. E., Jr. & D. G. Frey (editors). 1965. The Quaternary of the United States. 7th Congress of Int. Assoc. Quat. Res., Princeton Univ. 922 pp.

HISTORY OF BOTANY
1947–1972
WITH A BIBLIOGRAPHIC APPENDIX[1]

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Today we have heard a series of papers on the developments that have transpired in the past 25 years in the several major disciplines of botany. The recounting of events, highlights, and the work of individuals that have brought their respective fields to their present state of knowledge is in fact the basic materials for the history of botany as a distinct discipline. In a broader context, the endeavor of science, by its nature, is progressive and directive; building on what came before, discarding what is unsound in the light of new information, and finding new approaches or new theories of explanation. History, on the other hand, is reportive and analytical; the good and the bad, the successful and the unsuccessful, as well as the progressive and the retrogressive all deserve consideration. The historian of science faces a dilemma. Should he make value judgments about the course of history saying this line was "good" or that one "bad" or "retrogressive"? Too often it has been shown that the bias of a particular time changes, and what was thought "good" at one time is thought later or by someone else to not be as "good."

Further complications of interpretation arise in the breadth of approach made to the study of the history of science or to a particular science. For example, the history of botany, or mycology, or radiation botany could be considered by its students as only consisting of the events and concepts within that science—what is termed internal history. On the other hand, the student might consider the events in the science and its concepts in the broader stage of human activities as they relate directly or indirectly to the history of his science—what is termed external history. How should the historian of botany interpret the changes that have taken place in his science? As a series of sudden overthrows of established theory, procedure, and persons by the new challengers; as a series of revolutions as proposed by Thomas Kuhn (1970)? Or should he interpret the historical

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framework as a more gradual evolutionary series of changes in conceptualization, as is the more traditional opinion? These are the kinds of questions that concern the historian of science today. Many of these concerns have emerged during the past 25 years, during which time the history of science as a discipline has grown and become a viable independent field of study in this country. As bio-historians and botanists we should be prepared to be examined by historians and philosophers of science, to be asked difficult questions about why we approach our studies in the manner we do, and to learn to appreciate the value of critical external as well as self-examination. Our work can be interesting and exciting, and at the same time it can be scholarly and enlightening.

HISTORY OF BOTANY AS A DISCIPLINE

The history of botany as a discipline is now stronger, more active, and better recognized than at any time in the past. Our recounting of key events, developments, and publications in this field should provide sufficient evidence for such a belief. Since the founding of our country, most of the papers and books on the history of botany have been concerned with the history of the oldest of the plant science disciplines, namely, taxonomy and plant exploration. Much of this history has been written by taxonomists themselves. Within the past 50 years, and certainly within the past 25 years, the history of botany has broadened to include the histories of all of the botanical disciplines and more and more is being written by botanists of these other disciplines; the majority, however, are still being written by taxonomists. Historians of science and others have also begun writing botanical history. As this essay unfolds the present-day prominent writers and their fields should become apparent. If our paper sounds biased toward a history of taxonomic botany, it will be understood, not only because of the large amount of botanical history literature from that group, but also because of our strong ties to that discipline. Our approach provides some reasons why we should be studying the history of botany and gives some of the highlights that have come about in the field of botanical history in North America in this quarter century. Not being able to mention every important event or to cite every paper published, we have appended an extensive selective bibliography with the anticipation that it may be a useful reference tool for those who wish to explore the disciplines of the history of science, biology, and especially botany in either a general or specific manner. The arrangement of the bibliography has presented its problems, especially in that some categories are quite arbitrary and considerable overlap exists from one category to another. However, we believe that this arrangement will prove useful for teachers.

Why should botany students and teachers, or for that matter any botanists, be concerned with the history of their science? Two important reasons suggest themselves: insight and understanding. Insight is the quality brought into the methods of explanation and discovery that comes only from the perspective of history. By looking to the past, one can develop a better sense of the present. For example, the very detailed historical analysis of cellular respiration written by Keilin (1966), one of the major workers on that problem, provides an exciting perspective for understanding the present and suggests ways that science develops.

His approach makes valuable contributions to the teacher who must explain modern cellular respiration. The second reason, understanding, is particularly relevant to those of us who teach and learn. If one needs to understand some aspect of botany, one way, a way we think is useful, is to trace the history of the understanding of that subject. It will start at the beginning in a situation where the facts are put together and a hypothesis suggested. Upon this simple base, new experiments and observations are made, and step by step the superstructure is built. False starts, dead ends, and bursts of understanding occur, but all of these add to the excitement of understanding how the current solution to the problem came into being. This "case history" method was used successfully by Conant (1957). His approach still has much to recommend today. Science students are frequently surprised at the difficulties that appear along the way to current understanding as much as they are with the bursts of genius. It is valuable for them to realize both of these aspects. People and how they think are just interesting to other people. Thus, history can inject humanity into beginning botany that can be obtained in no other way. For example, in two recent beginning botany texts, persons are introduced as individuals (Cronquist, 1971; Jensen & Salisbury, 1972). The historians and philosophers of science add another reason for studying the history of botany. Their approach is to attempt to understand the way concepts have developed in relation to the basic philosophical framework of the science of botany and its broader relationships with the biological and physical sciences. Thus, the history of botany has an intrinsic interest all its own. Perhaps more botanists should develop this approach and interest!

Histories of Various Disciplines

Those wishing to approach the study of botany from the historical perspective or anyone wanting to learn what has occurred in the history of botany must naturally become aware of the events and work that have come forth. For example, no fewer than 15 papers on the history of botany of the United States have appeared between 1814 and 1947 (Ewan, 1969: 153). In the past 25 years, since 1947, or beginning the last half of the twentieth century, summaries of the botanical history in the United States or in North America are much more plentiful than previously and are a part of the information explosion that has affected all fields of learning. Many papers, summaries, and treatises have been written as individual efforts. Other accounts have come about because of a special meeting, committee, or symposium that was held for a special occasion, such as the one today. In fact had it not been for symposia of the kind we are having today, some botanical disciplines, such as anatomy, morphology, ecology, or paleobotany would have little or virtually no written history.

Three major events in the past 25 years have provided the stimulus for bringing together in book form a series of papers on the history of botany in the United States. First, a series of essays published in 1955 were prepared as part of the recognition of the Centennial of the California Academy of Sciences (Kessel, 1955). The central theme of that volume was the historical treatment of the systematics of living organisms and covered the development of various areas of cryptogamic botany, the systematics of gymnosperms and angiosperms, and plant geography.

Second, and of particular interest to this audience, was the celebration of the Golden Jubilee of the Botanical Society of America meeting with the AIBS in 1956 at the University of Connecticut, Storrs. Six invited papers were presented on the progress and achievements of the past 50 years in phycology, mycology, taxonomy, paleobotany, morphology, and physiology. These presentations and a series of special invitational papers of broad and general interest were published in volumes 43 and 44 of the *American Journal of Botany* and 40 of these papers were reprinted constituting a book, *Fifty Years of Botany* (Steere, 1958). This collection of papers was designed to enable intelligent nonbotanists to understand and to appreciate what botany is and what botanists were doing. The early history of the Botanical Society of America was also reviewed at that time by Tippo (1956), and a special feature was the awarding of Certificates of Merit to fifty persons who were judged to have made outstanding contributions in botanical science (Meyer, 1956). Since then, additional Certificates of Merit to outstanding botanists are awarded each year by the Botanical Society.

Third, and in the tradition of former International Botanical Congresses, it was proposed by the Historical Section of the Botanical Society of America, in particular by Professor Jerry Stannard, then secretary of the section, that a *Short History of Botany in the United States* be prepared for the Eleventh Congress meeting at the University of Washington, Seattle, in 1969. This book was prepared under the editorship of Professor Joseph Ewan (1969). Thirteen areas of special interest or disciplines were treated, with information on important developments and trends, principal investigators, and significant dates. Most of the histories extended to the present, and therefore now provide good backgrounds for current research and teaching. An additional five disciplines—genetics, cytology, ecology, horticulture, and medical botany—were treated in this volume that were not included in previously mentioned ones. The addition of these disciplines is a reflection that the scope of the history of botany was expanding. It is of further interest, and perhaps of significance to point out, that in this symposium today we have for the first time had a special paper devoted to the discipline of the history of botany. This event certainly reflects the growing interest in this field, the role of a few key individuals in this country who are interested in this field of study, and the role that the Botanical Society of America has played in fostering the history of botany in the United States.

A brief examination of the number of histories of the various disciplines of botany that have been considered at special symposia, or the collected works resulting from them, and an examination of titles in our representative bibliography reveals that, as mentioned earlier, the history of taxonomy and plant exploration has led the way. By the nature of their work, always building on and revising past work, taxonomists are concerned with collections of plants and their data, biographies of the individuals who explored and obtained plants, dates of collections and publications, travel narratives, diaries, letters, and other associated materials. Lincoln Constance, George H. M. Lawrence, and Reed Rollins have given much to the understanding of the history and conceptual framework of taxonomy as a discipline. Professor Joseph Ewan, as a contributor to the history of taxonomy, has combined biography and exploration in his many works. A masterpiece of this quarter-century in the history of botanical exploration is Susan Delano McKelvey's *Botanical Exploration of the Trans-Mississippi West* (1955). In this one work can be traced in meticulous detail the history of trained botanists and others in the western half of the United States from 1790 to 1850. Botanical exploration, biography, and evaluations of historically important plant collections have been subjects for scholarship of others such as Samuel Wood Geiser, Jeannette E. Graustein, Rogers McVaugh, Elmer D. Merrill, Harold William Rickett, Andrew Denny Rodgers, III, Ronald L. Stuckey, and John H. Thomas.

Genetics, too, has been building a sizable amount of literature on its history within the past 25 years. Although perhaps some would argue that it is not a part of our fraternity—it is not represented in this symposium, and many universities have separate departments of genetics—we believe it is a subject for the historian of botany. Perhaps fostered by the histories of plant hybridization by Roberts (1929, reprinted 1965) and Zirkle (1935), information in the field of the history of genetics has increased significantly. A further highlight was the celebration of the Golden Jubilee of Genetics, in honor of the fiftieth anniversary of the rediscovery of Mendel's work. At this meeting, held at The Ohio State University, Columbus, in 1950, under the sponsorship of the AIBS, 26 papers surveying the progress of genetics and exemplifying the status of problems of that day were presented. These papers were published as *Genetics in the 20th Century* under the editorship of L. C. Dunn (1951). The Gregor Mendel Symposium in Brno, Czechoslovakia, in 1965, added further stimulus to the writing of the history of genetics (Milan, 1966; Stern & Sherwood, 1966). The history of genetics, like that of taxonomy, has largely been written by the geneticists themselves; particularly noteworthy are the many contributions of the botanist Conway Zirkle.

On the other hand, some of the more specialized fields, such as anatomy, morphology, paleobotany, phytogeography, and certain areas of cryptogamic botany, have had little written of their history. Most of what has been written has been as a response to the three special events discussed earlier. However, it is surprising that little has been written on the history of ecology, a discipline much in the forefront of botany today, as well as in the forefront of countless other either related or nonrelated disciplines. Ecology is as old as some of the other basic botanical disciplines. Perhaps this paucity of papers reflects upon the difficulty of analyzing this multifaceted discipline.

Role of the Botanical Society of America

As alluded to above, the Botanical Society of America has played some role in fostering the history of botany as a discipline by creating an Historical Section. At the business meeting of 26 August 1963, a committee was formed to investigate the possibility and advisability of such a section, and the following year on 23 August at the University of Colorado, Boulder, the tenth section, the Historical Section, was created (Stannard, 1965). The stated purposes of this section were the promotion of general interest and encouragement of research and dissemination of knowledge in the history of botany, the establishment of closer relations between botanists and historians of science and medicine engaged in research in or the teaching of the history of botany, and the arrangement of suitable programs dealing with the history of botany in connection with annual meetings of the Botanical Society of America. The first session of contributed papers was held at the University of Illinois, Urbana, in 1965, and since then the Historical Section has held a session for contributed papers at each yearly meeting of the Society. Some years papers have been few and attendance low, but enthusiasm has been high, and what we need are more people interested in botanical history presenting papers and contributing. Membership in this section is now at 225 individuals.

In addition to the Historical Section, the archives of the Botanical Society of America, through 1954, were deposited in the History of Science collection at the University of Texas in 1964 (Leech, 1966). These valuable records and other botanical records there provide one source of primary materials for botanists and others seeking historical information. The Botanical Society of America is also providing botanical historians important information that is published in the *Plant Science Bulletin.* Although a committee was appointed in 1925 to consider the inauguration of a leaflet of botanical notes and news of benefit to teachers, amateurs, and others, this suggestion remained fallow for 30 years before coming to fruition in January 1955, when the first issue of the *Plant Science Bulletin* appeared with Harry J. Fuller as editor. Although at first not particularly interested in special events of botanical history, biographies of noted botanists, or book reviews (Fuller, 1955), the *Bulletin* has in recent years been publishing this type of information.

BIOGRAPHICAL APPROACH

Biographies and bibliographies of individual botanists have long been a major form of recording botanical history. These biographies and bibliographies appear in books or as small articles in botanical or other journals. In the 1940's we saw the results of what one man, neither a trained historian nor botanist, did for the history of botany. Mr. Andrew Denny Rodgers, III, of Columbus, Ohio, and a lawyer by profession, left the practice and devoted his full time to the writing of biographies of botanists. Seven biographies appeared from his pen from 1940 until 1952 (Rodgers, 1940, 1942, 1944*a*, *b*, 1949, 1951, 1952). His books are unique in that not only does each volume focus on one person (three in one book), but each also develops the history of that facet of botany for which the individual was a leader. Since 1965 all of Mr. Rodgers' books, except two, have been issued in facsimile editions by the Hafner Publishing Company. Presenting these life stories of American botanists has also provided a single thread of the development of botanical science in the United States. As a result of Mr. Rodgers' writings more is known about American botanists than about any other group of American scientists. His books are readable, scholarly, and authentic, and they have become "classics" for the significant documentation and evaluation of American botanical history. In the course of his research, Mr.

Rodgers discovered and preserved important collections of manuscript source materials which might otherwise have been lost. In recognition of his accomplishments and their value to botany in the United States, the Botanical Society of America, at its Golden Jubilee celebration in 1965, awarded him a Certificate of Merit, one of only 50 awarded to living botanists. Mr. Rodgers' pioneering research has laid the foundation for disciplined, scholarly study of the history of American botany.

Research has in the past quarter century seen the continued production of full-length book biographies, analyzing the person and his accomplishments in the context of the period in which he worked. Our bibliography lists 22 additional titles, most of which have been produced since Mr. Rodgers' last book in 1952 (see references in Appendix, Category VII, B). A few examples are: (1) The historian Dupree's life of Asa Gray, the leading American botanist of the nineteenth century, which deals not only with botanical history and exploration, but also with the history of science, American intellectual and social history, philosophy and its relation to science, theology, and the history of higher education. (2) Graustein's life of Thomas Nuttall, which brings him into focus as a thorough scholar and pioneer naturalist of scientific explorations into the American wilderness. (3) Ewans' John Banister, which presents a collection of Banister's own works that documents his place in the growth and knowledge of the natural history of the Atlantic seaboard for the seventeenth and eighteenth centuries. And (4) Sutton's life of Charles Sprague Sargent, which also concerns the development of the Arnold Arboretum and the American National Forests. University presses have usually provided the publication outlet for these biographies.

Countless numbers of biographical sketches (with or without bibliographies) or obituaries of contemporary botanists appear in many botanical journals. Twenty of these journals are mentioned in our bibliography (see references in Appendix, Category V). Biographical information must also be sought in state academy journals, state and local historical society journals, university bulletins, and special memorial papers. Much of this kind of information, especially that in journals other than botanical ones, is lost to botanists because no reasonably complete index currently lists these kinds of papers.

OTHER APPROACHES

Within the past quarter century we have seen the assembling of chronologies for botanists, for certain disciplines, and for periods in the history of botany. In this approach, according to Ewan (1970*a*), relationships emerge from the juxtaposition of the events that are brought together. These events, from the lives of individuals and their discoveries or accomplishments, allow us to outline botanical history and to think horizontally in time instead of the usual manner of thinking vertically. This technique has been developed to its fullest extent in this country by Joseph Ewan. His broadest botanical chronology in the *Short History of Botany in the United States* (Ewan, 1969: 1) spans time from ca. 300 B. C. to 1968 and gives a plethora of details that characterizes the trends and growth from all the plant sciences in the United States. Otherwise, Ewan's chronologies have been prepared for early American botanists—William Baldwin, John Bartram, William Bartram, John Banister, Stephen Elliott, John Lyon, Humphrey Marshall, and Thomas Nuttall. Other examples of chronologies are those for the field of plant pathology (Parris, 1968), and the recent bibliographies of botany for the states of Louisiana (Ewan, 1967) and for New Jersey (Fairbrothers, 1964, 1966).

The writing of the history of botany for each state has long been a standard approach. State botanical histories have usually been published in state academy journals, university bulletins, or as a chapter in a state or regional flora. An excellent example of the latter is the history of botanical explorations in the intermountain region in the recent *Intermountain Flora* by James Reveal (1972). Much of this type of historical information, however, is buried or even lost in the melieu of scientific, botanical, and popular literature. No bibliography has yet been compiled listing the titles of the histories of botany for each state. Such a bibliography would be a valuable working tool for future botanical historians. Within the past 25 years we have noted no fewer than 15 histories or compilations of biographical sketches of botanists and plant collectors for various states or regions (see references in Appendix, Categories V, VII). One book, *History of Botany in West Virginia* by Weldon Boone (1965*a*), must be singled out, for it attempts to integrate all aspects of the development of botany within the state—the various disciplines, botanical contributions of approximately 500 individuals in the form of their biographies and bibliographies, and the development of botany in the various universities. Written in a simple thorough style, Boone's is a scholarly work that may well serve as a good model of the history of botany in a state, which can be used by both the amateur and professional.

Probably no single botanist has contributed more to botanical history in the past 25 years than Professor Joseph Ewan of Tulane University, New Orleans. Beginning his biographical and historical investigations in 1933 as a research assistant under the botanist, W. L. Jepson, at the University of California, Ewan has authored over 110 short articles, reviews, and book-length monographs in the history of botany (Ewan, 1970*b*). His researches integrate botany and history, span all of time, and cross lines of endeavors—biographies, plant exploration, bibliographies, chronologies, and histories in several disciplines—taxonomy, phytogeography, and horticulture. Written in authoritative, scholarly, and interesting style, no historian of botany should be without access to his works, and we expect many more essays from his prolific pen.

SOURCES FOR INFORMATION

Within the past 25 years, several new journals (10 are listed in Table 1) have been established which are sufficiently interested in historical matters to publish biographical sketches, articles on botanical exploration, or evaluations of botanical history. Among these, mostly taxonomic journals, are *The Michigan Botanist, Sida, Taxon,* and *Huntia.* The *Journal of the History of Biology,* founded in 1968, contains articles mostly written by historians of science and is concerned with the emergence of ideas and the penetrating and critical analyses of changing concepts and altered methods of experimentation and observation. This analytical approach has sound scholarship and is to be commended; however, to date

Table 1. Scientific journals that have been established within the past 25 years that contain papers or information on American botanical history—evaluations, perspectives, biographical sketches, exploration, book reviews, and bibliographies of individuals and/or disciplines.

Taxon International Association for Plant Taxonomy, Utrecht, Netherlands. J. Lanjouw, original editor; now edited by Frans A. Stafleu.	1951
Regnum Vegetabile: A Series of Publications for the use of Plant Taxonomists International Association for Plant Taxonomy, Utrecht, Netherlands. J. Lanjouw, original editor; now edited by Frans A. Stafleu.	1953
Plant Science Bulletin Botanical Society of America, Tampa, Florida. Harry J. Fuller, original editor; now edited by Robert W. Long.	1955
British Journal for the History of Science The British Society for the History of Science, 393 Cowby Road, Oxford. M. P. Crosland, editor.	1962
History of Science: An Annual Review of Literature, Research, and Teaching W. Heffer & Sons Ltd., Cambridge, England. A. D. Crombie and M. A. Hoskin, editors.	1962
The Michigan Botanist The Michigan Botanical Club, Ann Arbor, Michigan. Edward G. Voss, editor.	1962
Sida: Contributions to Botany Privately published, Dallas, Texas. The late Lloyd Shinners founder and editor; now edited by William F. Mahler and John T. Thieret.	1962
Huntia: A Yearbook of Botanical and Horticultural Bibliography The Hunt Botanical Library and Carnegie Institute of Technology [now called Hunt Institute for Botanical Documentation], Carnegie-Mellon Universiy, Pittsburgh, Pennsylvania. George H. M. Lawrence, original editor.	1964
Bibliography of the History of Medicine National Library of Medicine, Bethesda, Maryland.	1966
The Journal of the History of Biology Belknap Press of Harvard University, Cambridge, Massachusetts. Everett Mendelsohn, editor.	1968

no papers pertaining strictly to botanical subjects have been reported in this journal. The *Journal of the Society for the Bibliography of Natural History,* founded in 1936 and published in England, serves a valuable function in the history of biology, but no journal of its scope is published in the United States.

Several journals that were publishing articles on botanical history in the United States have been discontinued shortly before or within the past 25 years. Among those were *Torreya* (as a separate journal in 1945), *Asa Gray Bulletin* in 1961 (replaced essentially by *The Michigan Botanist*), and the privately published journals, the *American Botanist* in 1947 and *Leaflets of Western Botany* in 1966. *Chronica Botanica,* founded in 1935 and edited by Frans Verdoorn through 1954, was an international journal devoted to botanists and their activities. Begun in the Netherlands, Verdoorn carried on his historical studies and editorial work in Waltham, Massachusetts, from 1937 until 1957, when he moved back to the Netherlands.

If twentieth century botanical history is to be as well recorded and documented as botanical history has been in past centuries, we must save letters, diaries, photographs, field notebooks, and laboratory records, and properly house them in institutions designed and devoted to the keeping of such records. Biographies, bibliographies, chronologies, and indexes will need to be prepared and published in order that the analytical historians may assimilate and correlate the facts and events that made twentieth century botany. It seems to us that a great need does exist for a journal devoted solely to the biography and bibliography of American botanical history. Such a journal should be most welcomed by taxonomists, but those in all other fields of botanical science would have a place to record their histories. *Huntia* published on a regular basis could help fulfill this role.

Elmer D. Merrill's imaginative planning in 1946 for the facsimile lithoprint reproductions of certain rare, much sought for, and very expensive or out of print botanical publications began an industry which has burgeoned since then, and especially in the past decade (Ewan, 1970*a*). Merrill saw to the reprinting of several early extremely rare classic American floras, such as Gronovius' *Flora Virginica*, Walter's *Flora Caroliniana*, and several of Rafinesque's rare books. The reprinting of works dealing with botanical history has been no exception. For example, we have already mentioned in passing the reprinting of five of Mr. Rodgers' books. The Hafner Publishing Company in New York City has probably led in the publishing of facsimile reprint editions. The *Classica Botanica Americana* series is one of their most comprehensive reprint endeavors. Now projected as seven volumes with two supplements, these are reprints of American botanical classics, mostly floras, selected for their critical reference value and historical importance (see references in Appendix, Category VI). Edited by Professor Ewan, each original is prefaced with biographical and bibliographical commentary that orients and assists the user in the significance of the work and in understanding unfamiliar procedures in its composition (Lubrecht, 1967). Only volumes two and three remain to be published of the original projected series.

A few other significant highlights in the past 25 years must be mentioned to help round out the story. On 10 October 1961, the Carnegie Institute of Technology formally opened to scholars and the public the Rachel McMasters Miller Hunt Botanical Library in Pittsburgh, Pennsylvania. Financed by the Hunt Foundation, this library set out on a five-fold research program in the history of botany: (1) completion of the *Catalogue of Botanical Books in the Library of Rachel McMasters Miller Hunt* (Quinby, 1958; Stevenson, 1961), which has already been completed in two volumes covering 764 titles and is fully described with biographical and bibliographical aids for the books dated through 1800, although many more books and special collections (*e.g.* Adanson and Linnaeus) have been added, (2) activation of the Hunt Facsimile Series (several of which have been published), (3) establishment of the Hunt Monograph Series, (4) activation of a project whose objective is the production of a comprehensive and analytical catalogue of all of the works in systematic botany and allied subjects published during the period 1735–1850, the *Bibliographia Huntiana*, and (5) the publication of a yearbook, *Huntia*, to serve as a medium for studies in the area of botanical and horticultural bibliography (Lawrence, 1962, 1964). Two volumes of *Huntia* have appeared and more are anticipated. Noteworthy of mention is *B-P-H* (*Botanico-Periodicum-Huntianum*) (Lawrence, Bucheim, Daniels & Dolezal, 1968), a compendium of information listing abbreviations for citations on all periodical publications that regularly contain (or have contained) articles dealing with the plant sciences and botanical literature and with the persons who have contributed to botany and its literature. The Hunt Library's research program has been one of essentially making available valuable "tools" for the historian of botany and the preservation of records—such as manuscripts, letters, illustrations used in books, and photographs of botanists. The research at the Hunt Library, begun under the directorship of George H. M. Lawrence, well known for his work in taxonomy and horticulture, is now, after 10 years, under the recent new leadership of George S. Daniels, and the Library has changed its name to the Hunt Institute for Botanical Documentation of Carnegie-Mellon University. Other earlier established libraries having significant amounts of botanical materials continue to serve the historian of botany. Some of these institutions are now organized into the Council on Botanical and Horticultural Libraries (see C B H L Newsletter, numbers 1 and 2, 1972).

A few other "tools" bear mention. For reference to biographical information on botanists, no one should be without access to the 3-volume, *Biographical Notes Upon Botanists* (Barnhart, 1965). These data, originally accumulated on over 44,000 cards by Dr. John Hendley Barnhart, bibliographer of the New York Botanical Garden, were made available by G. K. Hall in 1965. This index provides references to information about botanists, mostly taxonomists and horticulturalists, from all over the world from the earliest times to the late 1940's. Other reference "tools" made available in recent years that are valuable for the study of the history of botany are the fifteen folio volumes of the *U. S. D. A. Botany Subject Catalog* (1958). This original card file of 315,000 references was amassed by Alice C. Atwood and Marjorie Warner and their successors over a period of fifty years in Washington, D.C. Leading bio-historians and editors have judged this work as the best single "tool" in this country for searching botanical references through the year 1952 (Ewan, 1965). The reprinting of Max Meisel's (1924–1929) *Bibliography of American Natural History* in 1967, Ida Langman's (1964) *Selected Guide to the Literature of the Flowering Plants of Mexico*, and Frans Stafleu's (1967) *Taxonomic Literature: A Selective Guide to Botanical Publications with Dates, Commentaries and Types* should not go unnoticed.

In the past 25 years we have seen an amazing proliferation of materials for studying the history of botany. Not only the papers, journals, or books of which we have spoken, but also important is the ease of reproducing by photocopy or microform data from published papers, manuscripts, letters, or herbarium labels that we did not have 25 years ago. The use of the computer in storing and retrieving information should develop into an asset for the study of the history of botany. Today, facsimiles and reprints of classical works or collections of reprints of important papers are available, often in reasonably priced paperback editions. Many of these editions contain valuable interpretative introductions and supplements. Another development that is no less striking is the appearance of inexpensive methods of fine color reproduction which makes possible better graphic presentation of original drawings of the past, such as those of Ewan (1968) on William Bartram. The "tools" and literature available to the historian of botany today are indeed much greater than those 25 years ago.

THE FUTURE

What do we need or will we need for the future? As Professor Ewan (1970*a*) has noted, we have the pressing need to search for records, save these records before they are lost, compile information retrieval aids, and write interpretive histories. Biographies of botanists will continue to be written. Hopefully, more analytical histories of the disciplines and trends in the development of ideas and concepts will be prepared. We will need journals that will publish these papers. As has been alluded to above, we will need more "tools," such as indexes to biographies, textbooks, book reviews, chronologies, manuscripts, bibliographies, and certain kinds of specific botanical histories, *e.g.* those of botany in various states, botanical societies, herbaria, and botanical gardens. Many fruitful ideas needing attention and study in the history of botany have already been outlined by Stannard (1966). The future is indeed bright with prospects for a bountiful harvest to those who will plow the field of the history of botany.

BIBLIOGRAPHIC APPENDIX

An asterisk appears with those references that are cited in the text, most of which are listed in categories III and IX. The complete citation for those references that conclude with "see Ewan, 1969"; "see Kessel, 1955"; or "see Steere, 1958," are found in category III.

I. HISTORY OF SCIENCE—GENERAL

*CONANT, J. B. (editor). Harvard Case Histories in Experimental Sciences. 2 Vols. Harvard Univ. Press, Cambridge, Massachusetts. 639 pp.

DANIELS, G. H. 1968. American Science in the Age of Jackson. Columbia Univ. Press, New York. 282 pp.

GILLISPIE, C. C. 1960. The Edge of Objectivity. An Essay in the History of Scientific Ideas. Princeton Univ. Press, Princeton, New Jersey. 562 pp.

*KUHN, T. 1970. The Structure of Scientific Revolutions. Ed. 2. International Encyclopedia of Unified Science 2. No. 2. Univ. Chicago Press, Chicago, Illinois. 210 pp.

REINGOLD, N. (editor). 1964. Science in Nineteenth-Century America. A Documentary History. Hill and Wave, New York. 339 pp.

SARTON, G. 1952. A History of Science; Ancient Science Through the Golden Age of Greece. Harvard Univ. Press, Cambridge, Massachusetts. 646 pp.

———. 1957. Six Wings; Men of Science in the Renaissance. Indiana Univ. Press, Bloomington. 318 pp.

———. 1959. A History of Science; Hellenistic Science and Culture in the Last Centuries B. C. Harvard Univ. Press, Cambridge, Massachusetts. 554 pp.

STANLEY, G. F. G. (editor). 1966. Pioneers of Canadian Science. Symposium Presented to the Royal Society of Canada in 1964. Univ. Toronto Press, Toronto, Ontario. 146 pp.

STEARNS, R. P. 1970. Science in the British Colonies of America. Univ. Illinois Press, Urbana. 760 pp.

TATON, R. (editor). 1963–1966. History of Science. Translated by A. J. Pomerans. 4 Vols. Basic Books, New York. 552, 667, 623, and 638 pp.

II. HISTORY OF BIOLOGY—GENERAL

BODENHEIMER, F. S. 1958. The History of Biology; An Introduction. W. Dawson and Sons, London, England. 465 pp.

CARLSON, E. A. 1967. Modern Biology; Its Conceptual Foundations. George Braziller, New York. 327 pp.

CAULLERY, M. 1966. A History of Biology. Translated by J. Walling. Walker and Co., New York. 148 pp.

COLEMAN, W. 1971. Biology in the Nineteenth Century: Problems of Form, Function, and Transformation. John Wiley and Sons, New York. 187 pp.

GABRIEL, M. L. & S. FOGEL. 1955. Great Experiments in Biology. Prentice-Hall, Englewood Cliffs, New Jersey. 317 pp.

GARDNER, E. J. 1972. History of Life Science. Ed. 3. Burgess Publishing Co., Minneapolis, Minnesota. 464 pp.

LANHAM, U. 1968. The Origins of Modern Biology. Columbia Univ. Press, New York. 273 pp.

RITTERBUSH, P. C. 1964. Overtures to Biology; The Speculations of Eighteenth-Century Naturalists. Yale Univ. Press, New Haven, Connecticut. 287 pp.

ROOK, A. (editor). 1964. The Origins and Growth of Biology, based on *Moments of Discovery* edited by G. Schwartz and P. W. Bishop. Penguin Books, Baltimore, Maryland. 403 pp.

SIRKS, M. J. & C. ZIRKLE. 1964. The Evolution of Biology. Ronald Press, New York. 376 pp.

SMITH, P. & R. J. C. V. TER LAAGE. 1970. Essays in Biohistory and Other Contributions Presented by Friends and Colleagues to Frans Verdoorn on the Occasion of his 60th Birthday. Regnum Veg. 71. 426 pp.

STENT, G. S. 1969. The Coming of the Golden Age. A View of the End of Progress. Natural History Press, Garden City, New York. 146 pp.

III. HISTORY OF BOTANY—GENERAL

*EWAN, J. (editor). 1969. A Short History of Botany in the United States. Hafner Publishing Co., New York and London. 174 pp.

———. 1969. "Calendar of events," pp. 1–25, and "Early history" [of botany in the United States], pp. 27–48 + 1 fig., 3 tab. [See Ewan, 1969].

*———. 1970*a*. Opportunities in botanical history. Taxon 19: 825–830.

*———. 1970*b*. Ewan Bibliography 1928–1969 [with] Analytical Index of Names and Topics. Typewritten, dittoed. 26 pp. + Supplement I, 1970–. 1 p. [A copy may be seen at the New York Botanical Garden Library].

*[FULLER, H. J.]. 1955. Editorial platform. Pl. Sci. Bull. 1(1): 2.

*KESSEL, E. L. (editor). 1955. A Century of Progress in the Natural Sciences, 1853–1953: Published in Celebration of the Centennial of the California Academy of Sciences. California Acad. Sci., San Francisco. 807 pp.

*LAWRENCE, G. H. M. 1962. The Hunt Botanical Library. Pl. Sci. Bull. 8(2): 1–3.

*———. 1964. Genesis and revelations. Huntia 1: 1–4.

*LEECH, J. H. 1966. Botanical Records [of the Botanical Society of America]. Pl. Sci. Bull. 12(2): 8.

MACLEOD, A. M. & L. S. COBLY (editors). 1961. Contemporary Botanical Thought, A Series of Lectures Arranged by the Botanical Society of Edinburgh. Quadrangle Books, Chicago, Illinois. 197 pp.

*MEYER, B. S. 1956. Awards of certificates of merit at the fiftieth anniversary meeting [of the Botanical Society of America]. Amer. Jour. Bot. 43: 859–861. [See also Pl. Sci. Bull. 2(4): 1–2. 1956, and Steere, 1958: 14–32.]

RODGERS, A. D., III. 1957. Botanical history. Amer. Jour. Bot. 44: 186–188. [See also Steere, 1958: 467–470.]

SACHS, J. VON. 1890. History of Botany (1530–1860). Translated by H. E. F. Garnesy, revised by I. B. Balfour, Clarendon Press, Oxford. 568 pp. [Reprint edition, Russell and Russell, New York. 1967.]

SMITH, C. E., JR. 1957. A century of botany in America. Bartonia 28: 1–31.

*Stannard, J. 1965. Historical Section of the Botanical Society of America. Pl. Sci. Bull. 11(1): 5–6.

*Steere, W. C. (editor). 1958. Fifty Years of Botany: Golden Jubilee Volume of the Botanical Society of America. McGraw-Hill Book Co., Inc., New York. 638 pp.

*Tippo, O. 1956. The early history of the Botanical Society of America. Amer. Jour. Bot. 43: 852–858. [See also Steere, 1958: 1–13.]

A. ANATOMY AND MORPHOLOGY

Arber, A. 1950. The Natural Philosophy of Plant Form. Cambridge Univ. Press, Cambridge, England. 247 pp.

Carlquist, S. 1969. "Morphology and anatomy," pp. 49–57. [See Ewan, 1969.]

Cheadle, V. I. 1956. Research on xylem and phloem—progress in fifty years. Amer. Jour. Bot. 43: 719–731. [See also Steere, 1958: 95–117.]

Eames, A. J. 1957. Some aspects of progress in plant morphology during the past fifty years. Amer. Jour. Bot. 44: 100–104. [See also Steere, 1958: 606–614.]

Sinnott, E. W. 1956. Botany and morphogenesis. Amer. Jour. Bot. 43: 526–531. [See also Steere, 1958: 118–129.]

B. CRYPTOGAMIC BOTANY: BRYOLOGY, LICHENOLOGY, MYCOLOGY, PLANT PATHOLOGY, PHYCOLOGY, PTERIDOLOGY

Ainsworth, G. C. 1965. Historical introduction to mycology. Pp. 3–20, Vol. 1, *in* G. C. Ainsworth & A. S. Sussman (editors), "The Fungi; An Advanced Treatise." 3 Vols. Academic Press, New York. 748, 805, 738 pp.

Baker, K. F. 1965. A plant pathogen views history. Pp. 36–70, *in* "History of Botany. Two papers presented at a symposium held at the William Andrews Clark Memorial Library, December 7, 1963." The Clark Memorial Library, Univ. California, Los Angeles [and] The Hunt Botanical Library, Carnegie Institute of Technology, Pittsburgh, Pennsylvania.

———. 1969. "Plant pathology and mycology," pp. 82–88. [See Ewan, 1969.]

Bessey, E. A. 1955. "Mycology," pp. 225–265. [See Kessel, 1955.]

Bryson, V. (editor). 1959. Microbiology Yesterday and Today. Institute of Microbiology, Rutgers, The State Univ. [New Brunswick, New Jersey]. 122 pp.

Dawson, E. Y. 1966. A hundred years of marine botany in the United States. Pp. 295–301, *in* "Marine Botany; An Introduction." Holt, Rinehart and Winston, New York. 371 pp.

Doetsch, R. N. (editor). 1950. Microbiology: Historical Contributions from 1776 to 1908. Rutgers Univ. Press, New Brunswick, New Jersey. 233 pp.

Horsfall, J. G. 1956. The fight with the fungi—or the rusts and rots that rob us, the blasts and the blights that beset us. Amer. Jour. Bot. 43: 532–536. [See also Steere, 1958: 50–60].

Keitt, G. W. 1959. History of plant pathology. Vol. 1, pp. 61–97, *in* J. G. Horsfall & A. E. Dimond (editors), "Plant Pathology: An Advanced Treatise." 3 Vols. Academic Press, New York. 674 pp.

Manton, I. 1955. "Pteridology," pp. 301–321. [See Kessel, 1955.]

Papenfuss, G. F. 1955. "Classification of the algae," pp. 115–224. [See Kessel, 1955.]

———. 1957. Progress and outstanding achievements in phycology during the past fifty years. Amer. Jour. Bot. 44: 74–81. [See also Steere, 1958: 554–569.]

*Parris, G. K. 1968. A Chronology of Plant Pathology. Johnson and Sons, Starkville, Mississippi. 167 pp.

Raper, K. B. 1957. Microbes—man's mighty midgets. Amer. Jour. Bot. 44: 56–65. [See also Steere, 1958: 33–49.]

Rudolph, E. D. 1969. "Bryology and lichenology," pp. 89–96. [See Ewan, 1969.]

Smith, G. M. 1956. The role of study of algae in the development of botany. Amer. Jour. Bot. 43: 537–543. [See also Steere, 1958: 537–543.]

Steere, W. C. 1955. "Bryology," pp. 267–299. [See Kessel, 1955.]

———. 1971. A review of Arctic bryology. Bryologist 74: 428–441.

Taylor, W. R. 1969. "Phycology," pp. 74–81. [See Ewan, 1969.]

Tryon, R. 1952. A sketch of the history of fern classification. Ann. Missouri Bot. Gard. 39: 255–262.

———. 1969. "Pteridology," pp. 97–102. [See Ewan, 1969.]

Van Niel, C. B. 1955. "Classification and taxonomy of the bacteria and bluegreen algae," pp. 89–114. [See Kessel, 1955.]

WALKER, J. C. 1969. History of plant pathology. Pp. 14–46, *in* "Plant Pathology," Ed. 3. McGraw-Hill Book Co., New York. 819 pp. [Previous editions 1950 and 1957.]

WESTON, W. H. 1957. Mycology during the past fifty years. Amer. Jour. Bot. 44: 82–87. [See also Steere, 1958: 570–580.]

WHITFORD, L. A. 1968. Notes on the history of freshwater phycology. Jour. Phycol. 4: 169–173.

C. GENETICS AND CYTOLOGY

BABCOCK, E. B. 1949. The Development of Fundamental Concepts in the Science of Genetics. Portugaliae Acta Biol., Sér. A. [Reprinted Amer. Genetic Assoc. 1950.] 50 pp.

CARLSON, E. A. 1966. The Gene: A Critical History. W. B. Saunders, Philadelphia and London. 301 pp.

CLELAND, R. E. 1958. Cytology: The study of the cell. Amer. Jour. Bot. 43: 870–881. [See also Steere, 1958: 130–152.]

CREW, F. A. E. 1966. The Foundations of Genetics. Pergamon, Oxford, England. 202 pp.

*DUNN, L. C. (editor). 1951. Genetics in the 20th Century: Essays on the Progress of Genetics During its First 50 Years. The Macmillan Co., New York. 634 pp.

———. 1965. A Short History of Genetics: The Development of the Main Lines of Thought, 1864–1939. McGraw-Hill Book Co., New York. 261 pp.

———. 1965. Ideas about living units, 1864–1909: A chapter in the history of genetics. Perspectives in Biology and Medicine 8: 335–346.

——— ET AL. 1965. Commemoration of the publication of Gregor Mendel's pioneer experiments in genetics. Papers read at the annual general meeting April 23, 1965. Proc. Amer. Philos. Soc. 109: 189–248.

FORD, E. B. 1969. Ecological genetics. Pp. 173–195, *in* R. Harre (editor), "Scientific Thought 1900–1960. A Selective Survey." Clarendon Press, Oxford, England. 277 pp.

GLASS, B. 1965. A century of biochemical genetics. Proc. Amer. Philos. Soc. 109: 227–236.

GOLDSCHMIDT, R. 1950. Fifty years of genetics. Amer. Naturalist 84: 313–340.

GRANT, V. 1956. The development of a theory of heredity. Amer. Sci. 44: 158–179.

HAYES, H. K. 1963. A Professor's Story of Hybrid Corn. Burgess Publishing Co., Minneapolis, Minnesota. 237 pp.

HUGHES, A. A. 1959. A History of Cytology. Abelard Schuman, New York and London. 158 pp.

LANGLET, O. 1971. Two hundred years of genecology. Taxon 20: 653–722.

*MILAN, S. (editor). 1966. G. Mendel Memorial Symposium 1865–1965. Proc. Symp. (Brno), August 1965. Czechoslavak Acad. Sci., Prague. 311 pp.

MOORE, J. A. 1972. Readings in Heredity and Development. Oxford Univ. Press, New York. 329 pp.

OLBY, R. C. 1966. Origins of Mendelism. Schocken Books, New York. 204 pp.

PETERS, J. A. (editor). 1959. Classic Papers in Genetics. Prentice-Hall, Englewood Cliffs, New Jersey. 282 pp.

PROVINE, W. B. 1971. The Origins of Theoretical Population Genetics. Univ. Chicago Press, Chicago, Illinois. 201 pp.

PUNNETT, R. C. 1950. Early days of genetics. Heredity 4: 1–10.

*ROBERTS, H. F. 1929. Plant Hybridization Before Mendel. Princeton Univ. Press, Princeton, New Jersey. 374 pp. [Facsimile edition, Hafner Publishing Co., New York. 1965].

SHULL, G. H. 1952. Beginnings of the heterosis concept. Pp. 14–64, *in* John W. Gowen (editor), "Heterosis: A Record of Researches Directed toward Explaining and Utilizing the Vigor of Hybrids." Iowa State College Press, Ames. 552 pp. [Facsimile edition, Hafner Publishing Co., New York and London. 1964.]

SINGLETON, W. R. 1950. Some highlights on the first half century of genetics. Sci. Monthly 71: 401–407.

*STERN, C. & E. R. SHERWOOD (editors). 1966. The Origin of Genetics. A Mendel Source Book. W. H. Freeman and Co., San Francisco, California. 179 pp.

STURTEVANT, A. H. 1965. A History of Genetics. Harper and Row, New York. 165 pp.

TATUM, E. L. 1959. A case history in biological research. Chance and the exchange of ideas played roles in the discovery that genes control biochemical events. Science 129: 1711–1715.

TAYLOR, J. H. (editor). 1965. Selected Papers on Molecular Genetics. Academic Press, New York and London. 649 pp.

*Zirkle, C. 1935. The Beginnings of Plant Hybridization. Univ. Pennsylvania Press, Philadelphia and Oxford Univ. Press, London. 231 pp.

———. 1951. Gregor Mendel and his precursors. Isis 42: 97–104.

———. 1952. Early ideas on inbreeding and cross breeding. Pp. 1–13, *in* J. W. Gowen (editor), "Heterosis: A Record of Researches Directed Toward Explaining and Utilizing the Vigor of Hybrids." Iowa State College Press, Ames. 552 pp. [Facsimile edition, Hafner Publishing Co., New York and London. 1964.]

———. 1964. Some oddities in the delayed discovery of Mendelism. Jour. Heredity 55: 65–72.

———. 1969. "Plant genetics and cytology," pp. 58–66. [See Ewan, 1969.]

———. 1969. Plant hybridization and plant breeding in eighteenth century American agriculture. Agric. Hist. 43: 25–42.

D. ECOLOGY AND PHYTOGEOGRAPHY

Brewer, R. 1960. A brief history of ecology. Part I.—Pre-nineteenth century to 1919. Occas. Pap. Adams Center Ecol. Stud. 1, 18 pp.

Egler, F. E. 1951. A commentary on American plant ecology, based on the textbooks of 1947–1949. Ecology 32: 673–695.

Ewan, J. 1969. "Plant geography," pp. 115–123. [See Ewan, 1969.]

Eyre, S. R. (editor). 1971. World Vegetation Types. Columbia Univ. Press, New York. 264 pp.

Good, R. 1955. "Plant geography," pp. 747–765. [See Kessel, 1955.]

Hazen, W. E. (editor). 1972. Readings in Population and Community Ecology. Ed. 2. W. B. Saunders, Philadelphia, Pennsylvania. 421 pp.

Sears, P. B. 1956. Some notes on the ecology of ecologists. Sci. Monthly 83: 22–27.

———. 1956. Botanists and the conservation of natural resources. Amer. Jour. Bot. 43: 731–735. [See also Steere, 1958: 359–366.]

———. 1969. "Plant ecology," pp. 124–131. [See Ewan, 1969.]

Whittaker, R. H. 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. Amer. Jour. Bot. 44: 198–206. [See also Steere, 1958: 340–358.]

E. ECONOMIC BOTANY AND HORTICULTURE

Arber, A. 1938. Herbals, Their Origin and Evolution. Ed. 2. The University Press, Cambridge. 325 pp. [Facsimile edition, Hafner Publishing Co., New York. 1970.]

Avery, G. S., Jr. 1957. Botanic gardens—What role today? An "Operation Bootstraps" opportunity for botanists. Amer. Jour. Bot. 44: 268–271. [See also Steere, 1958: 536–544.]

Coats, A. M. 1969. The Plant Hunters; Being a History of the Horticultural Pioneers, Their Quests and Their Discoveries from the Renaissance to the Twentieth Century. McGraw-Hill Book Co., New York. 400 pp.

Crabb, R. A. 1947. The Hybrid-Corn Makers: Prophets of Plenty. Rutgers Univ. Press, New Brunswick, New Jersey. 331 pp.

Fulling, E. H. 1956. Botanical aspects of the paper-pulp and tanning industries in the United States—an economic and historical survey. Amer. Jour. Bot. 43: 621–634. [See also Steere, 1958: 508–535.]

Hedrick, U. P. 1950. A History of Horticulture in America to 1860. Oxford Univ. Press, New York. 551 pp.

Hodge, W. H. 1957. More plants for man. Amer. Jour. Bot. 44: 65–67. [See also Steere, 1958: 504–507.]

Hyams, E. 1969. Great Botanical Gardens of the World. Photography by William MacQuitty. The Macmillan Co., New York. 228 pp.

Kingsbury, J. M. 1961. Knowledge of poisonous plants in the United States—brief history and conclusions. Econ. Bot. 15: 119–130.

Klose, N. 1950. America's Crop Heritage: The History of Foreign Crop Introduction by the Federal Government. Iowa State College Press, Ames. 156 pp.

Lawrence, G. H. M. 1965. Herbals, their history and significance. Pp. 1–35, *in* "History of Botany. Two papers presented at a symposium held at the William Andrews Clark Memorial Library. December 7, 1963." The Clark Memorial Library, Univ. California, Los Angeles, [and] The Hunt Botanical Library, Carnegie Institute of Technology, Pittsburgh, Pennsylvania. 70 pp.

———. 1969. "Horticulture," pp. 132–145. [See Ewan, 1969.]

Manks, D. S. 1965. Some early American horticultural writers and their works: I. John Adlum and William Cobbett. Huntia 2: 59–110.

——— (editor). 1967 [1968]. Origins of American horticulture. Pl. & Gard. 23(3): 1–89.

Moldenke, H. N. & A. L. Moldenke. 1952. Plants of the Bible. Chronica Botanica. Waltham, Massachusetts. 328 pp.

Salaman, R. N. 1949. History and Social Influence of the Potato. Cambridge Univ. Press, Cambridge, England. 685 pp.

Stearn, W. T. 1965. The origin and later development of cultivated plants. Jour. Roy. Hort. Soc. 90: 279–341.

Wallace, H. A. & W. L. Brown. 1956. Corn and Its Early Fathers. Michigan State Univ. Press [East Lansing, Michigan]. 134 pp.

Weatherwax, P. 1954. Indian Corn in Old America. The Macmillian Co., New York. 253 pp.

F. EVOLUTION

Daniels, G. (editor). 1968. Darwinism Comes to America. Blaisdell Publishing Co., Waltham, Massachusetts. 137 pp.

Ghiselin, M. T. 1969. The Triumph of the Darwinian Method. Univ. California Press, Berkeley and Los Angeles. 287 pp.

Greene, J. C. 1959. The Death of Adam; Evolution and Its Impact on Western Thought. Iowa State Univ. Press, Ames. 388 pp.

Zirkle, C. 1959. Evolution, Marxian Biology, and the Social Sciences. Univ. Pennsylvania Press, Philadelphia. 527 pp.

G. MEDICAL BOTANY

Berman, A. 1956*a*. Neo-Thomsonianism in the United States. Jour. Hist. Med. Allied Sci. 11: 133–155.

———. 1956*b*. Social roots of the 19th century botanico-medical movement in the United States. Pp. 561–565, *in* "Actes du VIII° Congrès International d'Histoire des Sciences."

———. 1956*c*. A striving for scientific respectability: Some American botanics and the nineteenth-century plant materia medica. Bull. Hist. Med. 30: 7–31.

———. 1957. The botanic practitioners of 19th-century America. American Professional Pharmacist. October. [6 pp.].

———. 1958. The heroic approach in 19th century therapeutics. Univ. Mich. Med. Bull. 24: 419–427.

Raper, K. B. 1952. A decade of antibiotics in America. Mycologia 44: 1–59.

Schwarz, J. & G. L. Baum. 1957. A critical review of medical mycology in the United States 1946–1956. Mycopathol. Mycol. Appl. 8: 271–326.

Stannard, J. 1966. Dioscorides and renaissance materia medica. Pp. 1–21, *in* M. Florkin (editor), "Analecta Medico-Historia Materia Medica in the XVI Century." Vol. 1. Pergamon Press, Oxford, England. 84 pp.

———. 1969. "Medical botany," pp. 146–152. [See Ewan, 1969.]

Youngken, H. W., Jr. 1956. Botany and medicine. Amer. Jour. Bot. 43: 862–869. [See also Steere, 1958: 442–455.]

H. PALEOBOTANY AND PALYNOLOGY

Arnold, C. A. 1969. "Paleobotany," pp. 103–108. [See Ewan, 1969.]

Just, T. 1957. Fifty years of paleobotany, 1906–1956. Amer. Jour. Bot. 44: 93–99. [See also Steere, 1958: 590–605.]

Terasmae, J. 1967. A review of Quaternary paleobotany and palynology in Canada. Geol. Surv. Canada Pap. 67–13. 12 pp.

I. PHYSIOLOGY

Hendricks, S. B. 1969. "Plant physiology," pp. 67–73. [See Ewan, 1969.]

Hill, R. 1971. The growth of our knowledge of photosynthesis. Pp. 1–14, *in* Joseph Needham (editor), "The Chemistry of Life. Eight Lectures on the History of Biochemistry." Cambridge Univ. Press, London. 214 pp.

*KEILIN, D. 1966. The History of Cell Respiration and Cytochrome. Cambridge Univ. Press, Cambridge. 416 pp.

KREBS, H. A. 1970. The history of the tricarboxylic acid cycle. Perspect. Biol. Med. 14: 154–170.

MEYER, B. S. 1957. Recent trends in plant physiology. Ohio Jour. Sci. 57: 322–331.

STEWARD, F. C. 1970. From cultured cells to whole plants: The induction and control of their growth and morphogenesis. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 175: 1–30.

STUDHALTER, R. A. 1955. Tree growth I. Some historical chapters. Bot. Rev. 21: 1–72.

WEEVERS, T. 1949. Fifty Years of Plant Physiology. Scheltema and Holkema, Amsterdam, Netherlands. 308 pp.

WENT, F. W. 1957. Fifty years of plant physiology in the U.S.A. Amer. Jour. Bot. 44: 105–110. [See also Steere, 1958: 615–628.]

J. TAXONOMY, SYSTEMATICS, CLASSIFICATION, AND NOMENCLATURE

CAIN, A. S. 1959*a*. Deductive and inductive methods in post-Linnaean taxonomy. Proc. Linn. Soc. London 170: 185–217.

———. 1959*b*. The post-Linnaean development of taxonomy. Proc. Linn. Soc. London 170: 233–244.

CONSTANCE, LINCOLN. 1955. "The systematics of the angiosperms," pp. 405–483. [See Kessel, 1955.]

———. 1958. Plant taxonomy in an age of experiment. Amer. Jour. Bot. 44: 88–92. [See also Steere, 1958: 581–589.]

———. 1964. Systematic botany—an unending synthesis. Taxon 13: 257–273.

EWAN, J. 1969. Historical problems for the working taxonomist. Taxon 18: 194–203.

FLORIN, R. 1955. "The systematics of the gymnosperms," pp. 323–403. [See Kessel, 1955.]

GIBBS, R. D. 1963. History of chemical taxonomy. Pp. 41–88, *in* T. Swain (editor), "Chemical Plant Taxonomy." Academic Press, London and New York. 543 pp.

HELLER, J. L. 1964. The early history of binomial nomenclature. Huntia 1: 33–70.

HEISER, C. B., JR. 1969. "Taxonomy," pp. 110–114. [See Ewan, 1969.]

HOPWOOD, A. T. 1959. The development of pre-Linnaean taxonomy. Proc. Linn. Soc. London 170: 230–234.

KECK, D. D. 1957. Trends in systematic botany. Surv. Biol. Prog. 3: 47–107.

LAWRENCE, G. H. M. 1951. History of classification, pp. 13–41, *in* "Taxonomy of Vascular Plants." The Macmillan Co., New York. 823 pp.

PACLT, J. 1960. The "Classes" of Rafinesque and the modern biosystematics. Taxon 9: 47–49.

ROLLINS, R. C. 1952. Taxonomy today and tomorrow. Rhodora 54: 1–19.

———. 1957. Taxonomy of the higher plants. Amer. Jour. Bot. 44: 188–196. [See also Steere, 1958: 192–208.]

SHINNERS, L. H. 1962. Evolution of the Gray's and Small's Manual ranges. Sida 1: 1–31.

STAFLEU, F. A. 1959. The present status of plant taxonomy. Syst. Zool. 8: 59–68.

———. 1969. A historical review of systematic biology. Pp. 16–44, *In* C. G. Sibley (chairman), "Systematic Biology: Proceedings of an International Conference Conducted at The University of Michigan, Ann Arbor, Michigan, June 15–16, 1967, Sponsored by the National Research Council." Natl. Acad. Sci. Publ. 1962. Washington, D.C. 632 pp.

———. 1971. Linnaeus and the Linnaeans. The Spreading of Their Ideas in Systematic Botany, 1735–1789. Regnum Veg. 79. 386 pp.

VOSS, E. G. 1952. The history of keys and phylogenetic trees in systematic biology. Jour. Sci. Lab. Denison Univ. 43: 1–25.

WEATHERBY, C. A. 1949. Botanical nomenclature since 1887. Amer. Jour. Bot. 36: 5–7.

V. BOTANICAL EXPLORATION, COLLECTIONS, HISTORIES OF BOTANY IN REGIONS OF STATES, SHORT BIOGRAPHIES WITH REGIONAL INTEREST

For short biographies and bibliographies of recent botanists, consult the following selected journals: American Fern Journal, American Midland Naturalist, Journal of the Arnold Arboretum, Bartonia, Brittonia, The Bryologist, Castanea, Bulletin of the Ecological Society of America, Huntia, Madroño, The Michigan Botanist, Annals of the Missouri Botanical Garden, Mycologia, National Academy of Science Biographical Memoirs, Plant Science Bulletin, Rhodora, Sida, Journal of the Society for the Bibliography of Natural History, Taxon, Bulletin Torrey Botanical Club.

Andre, J. E. 1971. The history of systematic botany in Tennessee: 1770–1942. M. S. Thesis, Univ. Tennessee, Knoxville. 118 pp.

Barkley, F. A. 1947. Texas plant collectors as represented in Texas herbaria. Amer. Midl. Naturalist 38: 638–670.

Bartram, W. 1791. Travels Through North & South Carolina, Georgia, East and West Florida, . . . James & Johnson, Philadelphia, Pennsylvania. [Reprinted with Editor's Note by Mark Van Doren, pp. 5–6. Dover Publications, New York. 414 pp.]

Beidleman, R. C. 1956. The 1818–1820 Arkansas journey of Thomas Nuttall. Arkansas Hist. Quart. 15: 249–259.

———. 1960. Some biographical sidelights on Thomas Nuttall, 1786–1859. Proc. Amer. Philos. Soc. 104: 86–100.

Boewe, C. 1958. The manuscripts of C. S. Rafinesque (1783–1840). Proc. Amer. Philos. Soc. 102: 590–595.

———. 1961. Rafinesque and Dr. Short. Filson Club Hist. Quart. 35: 28–32.

*Boone, W. 1965*a*. A History of Botany in West Virginia. McClain Printing Co., Parsons, West Virginia. 196 pp.

———. 1965*b*. History of botany in West Virginia. Proc. West Virginia Acad. Sci. 37: 207–212.

Browne, E. T. 1965. Botany in Kentucky since 1914. Trans. Kentucky Acad. Sci. 25: 77–82.

Cantelow, E. D. & H. C. Cantelow. 1957. Biographical notes on persons in whose honor Alice Eastwood named native plants. Leafl. W. Bot. 8: 83–101.

Christensen, E. M. 1967. The growth of botany in Utah determined from botanical literature (1945–1964). Proc. Utah Acad. Sci. 44: 367–396.

Coats, A. M. 1969. The Plant Hunters. Being a History of the Horticultural Pioneers, Their Quests and Their Discoveries from the Renaissance to the Twentieth Century. McGraw-Hill Book Co., New York. 400 pp.

Core, E. L. 1970. The botanical exploration of the southern Appalachians. Pp. 1–65, *in* Perry C. Holt (editor), with assistance of Robert A. Patterson, "The distributional history of the biota of the southern Appalachians Part II. Flora." Res. Div. Monogr. 2. Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 414 pp.

Davis, R. B. 1955. The Abbe Correa in America, 1812–1820. Trans. Amer. Philos. Soc. 42: 87–197.

Ewan, J. 1955. "San Francisco as a mecca for nineteenth century naturalists, with a roster of biographical references to visitors and residents," pp. 1–63. [See Kessel, 1955.]

———. 1960. Bernard M'Mahon (c. 1775–1816), pioneer Philadelphia nurseryman, and his American Gardener's Caldendar. Jour. Soc. Bibl. Nat. Hist. 3: 363–380.

———. 1961. The scientist on the frontier. Pp. 81–101, *in* J. F. McDermott (editor), "Research Opportunities in American Cultural History." Univ. Kentucky Press, [Lexington]. 205 pp.

———. 1965*a*. French naturalists in the Mississippi Valley. Pp. 159–174, *in* John Francis McDermott (editor), "The French in the Mississippi Valley." Univ. Illinois Press, Urbana. 245 pp.

———. 1965*b*. Letters from Charles Sprague Sargent to Reginald Sommers Cocks, 1908–1926. Jour. Arnold Arbor. 46: 1–44; 122–159; 324–361; 411–444.

*———. 1967 [1968]. [Chronological] Bibliography of the botany of Louisiana. South. Louisiana Jour. 7: 1–83.

———. 1971. History of botanical collecting in southern Florida. Pp. 3–9, *in* R. W. Long & O. Lakela "A Flora of Tropical Florida: A Manual of the Seed Plants and Ferns of Southern Peninsula, Florida." Univ. Miami Press, Coral Gables, Florida. 962 pp.

*Fairbrothers, D. E. 1964. An annotated [chronological] bibliography of the floristic publications of New Jersey from 1753–1961. Bull. Torrey Bot. Club 91: 47–56; 141–151.

*———. 1966. An annotated [chronological] bibliography of the floristic publications of New Jersey from 1962–1965. Bull. Torrey Bot. Club 93: 352–356.

Friesner, R. C. 1952. The pioneer period in the study of the Indiana flora. Butler Univ. Stud. Bot. 10: 144–152.

———. 1953. Rafinesque and the taxonomy of Indiana vascular plants. Butler Univ. Stud. Bot. 11: 1–4.

Goldie, J. [1967.] Diary of a Journey through Upper Canada and some of the New England States 1819. Privately published, [Toronto, Ontario, Canada]. 65 pp. [Foreword by William Spawn, pp. vii–x.]

GRAUSTEIN, J. E. 1951. Nuttall's travels into the Old Northwest. An unpublished 1810 diary. Chron. Bot. 14: 1–88, 11 pls., 9 text figs.

———. 1961. The eminent Benjamin Smith Barton. Pennsylvania Mag. Hist. Biogr. 85: 423–438.

HARTUNG, S. A. 1957. A history of the botanical exploration of South Dakota. Proc. South Dakota Acad. Sci. (1956). 35: 111–115.

JARCHO, S. 1958. Biographical and bibliographical notes on Cadwallader Colden. Bull. Hist. Med. 32: 322–334.

JONES, G. N. & G. D. FULLER. 1955. Principal collectors of vascular plants in Illinois. Pp. 527–535, *in* "Vascular Plants of Illinois." Univ. Illinois Press, Urbana. 593 pp.

KALM, PETER. 1770. Travels into North America; Containing its Natural History, and . . . . Translated into English by John Reinhold Forster. William Eyres, Warrington. [The English version reprinted and revised from the original Swedish, with a translation of new material from Kalm's diary notes, edited by Adolph B. Benson + Introduction xviii pp., Dover Publications, Inc., New York.] Vol. 1, 401 pp.; Vol. 2, 402–797 pp.

LANGE, E. F. 1956. Pioneer botanists of the Pacific Northwest. Oregon Hist. Quart. 57: 109–124.

LEMMON, K. 1968. The Golden Age of Plant Hunters. Phoenix House, London. 229 pp.

MAGUIRE, B. 1958. "Highlights of botanical exploration in the New World," pp. 209–246. [See Steere, 1958.]

MARKLE, M. S. 1967. The history of plant taxonomy and ecology in Indiana. Proc. Indiana Acad. Sci. (1966). 76: 142–150.

*MCKELVEY, S. D. 1955. Botanical Exploration of the Trans-Mississippi West, 1790–1850. Arnold Arboretum, Jamaica Plain, Massachusetts. 1144 pp.

MCCLINTOCK, E. 1967. Early plant explorers in the West. Jour. California Hort. Soc. 28: 114–121; 152–160.

MCVAUGH, R., S. A. CAIN & D. J. HAGENAH. 1953. Farwelliana: An account of the life and work of Oliver Atkins Farwell, 1867–1944. Cranbrook Inst. Sci. Bull. 34. 101 pp.

———. 1970. Botanical results of the Michigan Geological Survey under the direction of Douglass Houghton, 1837–1840. Michigan Bot. 9: 213–243.

———. 1972. Botanical exploraton in Nueva Galicia, Mexico, from 1790 to the present time. Contr. Univ. Michigan Herb. 9: 205–357.

MEIJER, W. 1970. The flora and vegetation of Kentucky as a field for research and teaching. Castanea 35: 161–176.

MERRILL, E. D. & S. Y. HU. 1949. Work and publications of Henry Muhlenberg, with special attention to unrecorded or incorrectly recorded binomials. Bartonia 25: 1–66.

———. 1954. Botany of Cook's Voyages and unexpected significance in relation to anthropology, biogeography and history. Chron. Bot. 14: 161–384.

MILLER, H. S. 1970. The herbarium of Aylmer Bourke Lambert: Notes on its acquisition, dispersal, and present whereabouts. Taxon 19: 489–656.

MORTON, C. V. 1967. Freeman and Curtis' account of the Red River expedition of 1806, an overlooked publication of botanical interest. Jour. Arnold Arbor. 48: 431–459.

MUSSELMAN, L. J. 1969. Samuel H. Watson, pioneer botanist of southern Wisconsin. Michigan Bot. 8: 35–37.

———. 1969. The botanical activities of Thomas J. Hale, 1858–1862. Michigan Bot. 8: 181–185.

OVERLEASE, W. R. 1966. Dr. William Darlington as a botanist. Torch [Bull. West Chester State Coll.] 94: 6–12.

PENNELL, F. W. 1950. Historic botanical collections of the Amercan Philosophical Society and the Academy of Natural Sciences of Philadelphia. Proc. Amer. Philos. Soc. 94: 137–151.

REVEAL, J. 1972. Botanical explorations in the Intermountain Region. Pp. 40–72, *in* A. Cronquist, A. H. Holmgren, N. H. Holmgren & J. L. Reveal, "Intermountan Flora: Vascular Plants of the Intermountain West, U. S. A." Vol. 1. Published for the New York Botanical Garden by Hafner Publishing Co., New York and London. 270 pp.

RICKETT, H. W. 1947. The Royal Botanical Expedition to New Spain 1788–1820 as described in documents in the Archivo General de la Nación [México] now translated and collated. Chron. Bot. 11: 1–86, pl. 44–52.

———. 1950. John Bradbury's explorations in Missouri Territory. Proc. Amer. Philos. Soc. 94: 59–89.

RITTENHOUSE, J. L. & E. G. VOSS. 1962. Douglass Houghton's botanical collections in

Michigan, Wisconsin, and Minnesota on the Schoolcraft Expedition of 1832. Michigan Bot. 1: 61–70.

ROBBINS, C. C. 1960. David Hosack's herbarium and its Linnaean specimens. Proc. Amer. Philos. Soc. 104: 293–313.

RODGERS, A. D., III. 1969. Foreword, 4 pp. not numbered, *in* William S. Sullivant, "Icones Muscorum, or Figures and Descriptions of most of those Mosses peculiar to North America which have not yet been figured." S-H Service Agency, New York. 361 pp. [facsimile of the 1874 edition.]

RUDD, V. 1954. Botanical contributions of the Lewis and Clark expedition. Jour. Washington Acad. Sci. 44: 351–356.

SHERFF, E. E. 1964. An annotated list of my botanical writings: A bibliographic list, with notations of observed errata, needed emendations, and additions of taxa described too late for inclusion in the original publications. Published by the author for the Earl Edward Sherff Botanical Library, Illinois Wesleyan University, Bloomington, Illinois. 48 pp.

SHETLER, S. G. 1969. The herbarium: Past, present, and future. Proc. Biol. Soc. Washington 82: 687–758.

SMITH, C. E., JR. & J. W. THIERET. 1959. Thomas Nuttall (1786–1859): An evaluation and bibliography. Leafl. W. Bot. 9: 33–42.

———. 1962. Henry Muhlenberg—botanical pioneer. Proc. Amer. Philos. Soc. 106: 443–460.

SPRY, I. M. 1963. The Palliser Expedition: An Account of John Palliser's British North American Expedition, 1857–1860. St. Martin's Press, New York. 310 pp.

STAFLEU, F. A. 1968. Rafinesque's Caratteri and Florula Ludoviciana. Taxon 17: 296–299.

STETSON, S. P. 1949. The traffic in seeds and plants from England's colonies in North America. Agri. Hist. 23: 45–56.

STUCKEY, R. L. 1966*a*. The botanical pursuits of John Samples, pioneer Ohio plant collector (1836–1840). Ohio Jour. Sci. 66: 1–41.

———. 1966*b*. Thomas Nuttall's 1816 Ohio valley plant collections described in his "Genera" of 1818. Castanea 31: 187–198.

———. 1967*a*. Daniel Steinhauer, early Ohio plant collector and his correspondence with the botanist Schweinitz. Bartonia 36: 1–24.

———. 1967*b*. The "lost" plants of Thomas Nuttall's 1810 expedition into the Old Northwest. Michigan Bot. 6: 81–94.

———. 1968. Biography of Thomas Nuttall: A review with bibliography. Rhodora 70: 429–438.

———. 1969. An overlooked plant name (*Aesculus maxima*) of Daniel Drake and his lost herbarium. Castanea 34: 185–192.

———. 1970. Type specimens of flowering plants described from Long's Expedition to the source of the St. Peter's River in 1823. Michigan Bot. 9: 41–47.

———. 1971*a*. C. S. Rafinesque's North American vascular plants at the Academy of Natural Sciences of Philadelphia. Brittonia 23: 191–208.

———. 1971*b*. The first public auction of an American herbarium including an account of the fate of the Baldwin, Collins, and Rafinesque herbaria. Taxon 20: 443–459.

SWEM, E. G. 1957. Brothers of the Spade: Correspondence of Peter Collinson, of London, and of John Custis, of Williamsburg, Virginia, 1734–1746. Proc. Amer. Antiq. Soc. 58: 17–190.

THOMAS, J. H. 1969. Botanical explorations in Washington, Oregon, California and adjacent regions. Huntia 3: 5–66 [issued only as a preprint].

WEATHERWAX, P. 1971. Charles Clemon Deam: Hoosier Botanist. Indiana Mag. Hist. 67: 197–267.

WHITTLE, T. 1970. The Plant Hunters; Being an Examination of Collecting with an Account of the Careers and the Methods of a Number of Those Who Have Searched the World for Wild Plants. Chilton, Philadelphia, Pennsylvania. 281 pp.

WISLIZENUS, A. 1848. Memoir of a Tour to Northern Mexico Connected with Colonel Doniphan's Expedition in 1846 and 1847. 30th Congress, 1st Session, Miscellaneous [Document] No. 26. 141 pp. + maps. [Reprinted with Foreword by Jack D. Rittenhouse, pp. V–X. Calvin Horn Publisher, Inc., Albuquerque, New Mexico.]

VI. CLASSICA BOTANICA AMERICANA SERIES

Classica Botanica Americana Series Volumes 2 and 3 have not appeared.

Ewan, J. 1967. Editor's Introduction, pp. [i–]xii, *in* H. Marshall, "Arbustrum Americanum: The American Grove, or, an Alphabetical Catalogue of Forest Trees and Shrubs, Natives of the American United States, Arranged According to the Linnaean System, . . ." 174 pp., and "Catalogue Alphabetique des Arbes et Arbrisseaux, . . ." 278 pp. + approbation, privilege, errata. Hafner Publishing Co., New York and London. [Facsimiles of the 1785 and 1788 editions.] CBA Vol. 1.

———. 1967. Editor's Introduction, pp. i–lii, *in* W. Darlington, "Memorials of John Bartram and Humphrey Marshall." Hafner Publishing Co., New York and London. 585 pp. [Facsimile of the 1849 edition.] CBA Suppl. 1.

———. 1967. Editor's Introduction, pp. i–xl, *in* C. S. Rafinesque, "Florula Ludoviciana: or, A Flora of the State of Louisiana. Translated, revised, and improved from the French of C. C. Robin." Hafner Publishing Co., New York and London. 178 pp. [Facsimile of the 1817 edition.] CBA Vol. 5.

———. 1969. Editor's Introduction, pp. i–lxix, *in* W. Darlington, "Reliquiae Baldwinianae: Selections from the Correspondence of the late William Baldwin, M. D., Surgeon in the U.S. Navy. With occasional notes, and a short biographical memoir." Hafner Publishing Co., New York and London. 346 pp. + corrigenda. [Facsimile of the 1843 edition.] CBA Suppl. 2.

———. 1969. Editor's Introduction, Vol. 1, pp. i–xvii; Vol. 2, pp. i–xvii, *in* J. Torrey & A. Gray, "A Flora of North America: Containing Abridged Descriptions of all the Known, Indigenous and Naturalized Plants Growing North of Mexico, Arranged According to the Natural System." 2 Vols. Hafner Publishing Co., New York and London. 711 pp. and 504 pp. + index. [Facsimile of the 1838–1843 edition.] CBA Vol. 4.

———. 1971. Editor's Introduction, Vol. 1, pp. [i–]xxxvii, *in* S. Elliott, "A Sketch of the Botany of South-Carolina and Georgia." Hafner Publishing Co., New York. Advertisement vi, 606 pp. + plates and preface, vii, 743 pp. + glossary 14 pp. [Facsimile of the 1816–1824 edition.] CBA Vol. 6.

———. 1971. Editor's Introduction, Vol. 1, pp. [i–]xxxvii, *in* T. Nuttall, "The Genera of North American Plants [and a Catalogue of the Species, to the Year 1817]. 2 Vols. Hafner Publishing Co., New York. 312 pp. and 254 pp. + index of the genera, eratum [sic], additions. [Facsimile of the 1818 edition.] CBA Vol. 7.

VII. BIOGRAPHIES

A. COLLECTIVE

Chardon, C. E. 1949. Los naturalistas en la America Latina. Vol. 1. Caribe, Cuidad Trujillo, Dominican Republic. 386 pp.

Ewan, J. 1950. Rocky Mountain Naturalists. Univ. Denver Press, [Denver, Colorado]. 358 pp.

Geiser, S. W. 1948. Naturalist of the Frontier. Ed. 2. Southern Methodist Univ. Press, Dallas, Texas. 296 pp.

———. 1958–1959. Men of Science in Texas, 1820–1880. Southern Methodist Univ. Press, Dallas, Texas. (From Field & Lab. 26: 86–139. 1958. 27: 20–48; 111–160; 163–256. 1959).

Gillispie, C. C. (director). 1970–. Dictionary of Scientific Biography. Charles Scribner's Sons, New York. 4 vols. to date. 624, 628, 624, 622 pp.

Humphrey, H. B. 1961. Makers of North American Botany. Ronald Press, New York. 265 pp.

[Leroy, J. F. (editor).] 1957. Les Botanistes Français en Amérique du Nord avant 1850. Colloques Internationaux du Centre National de la Recherche Scientifique, Paris. 360 pp.

Reifschneider, O. 1964. Biographies of Nevada Botanists 1844–1963. Univ. Nevada Press, Reno. 165 pp.

B. INDIVIDUAL(S)

Berkeley, E. & D. S. Berkeley. 1963. John Clayton: Pioneer of American Botany. Univ. North Carolina Press, Chapel Hill. 236 pp.

——— & ———. 1965. The Reverend John Clayton, a Parson with a Scientific Mind:

His Scientific Writings and other Related Papers. Edited, with a short biographical sketch. Published for the Virginia Historical Society, Univ. Press Virginia, Charlottesville. 170 pp.

——— & ———. 1969. Dr. Alexander Garden of Charles Town. Univ. North Carolina Press, Chapel Hill. 379 pp.

Childs, A. R. 1947. The Private Journal of Henry William Ravenel 1859–1887. Univ. South Carolina Press, Columbia. 428 pp.

Clements, E. S. 1960. Adventures in Ecology: Half a Million Miles . . . from Mud to Macadam. Pageant Press, New York. 244 pp. [Concerns life and work of Frederick Clements.]

Cutright, P. R. 1968. Meriwether Lewis: Naturalist. Reprint from Oregon Hist. Quart. [51 pp.]

———. 1969. Lewis and Clark: Pioneering Naturalists. Univ. Illinois Press, Urbana. 506 pp.

*Dupree, A. H. 1959. Asa Gray: 1810–1888. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts. 505 pp.

Ewan, J. 1952. Frederick Pursh, 1774–1820, and his botanical associates. Proc. Amer. Philos. Soc. 96: 599–628.

*———. 1968. William Bartram: Botanical and zoological drawings, 1756–1788, reproduced from the Fothergill Album in the British Museum (Natural History). Mem. Amer. Philos. Soc. 74: [i–]x, 1–180.

——— & N. Ewan. 1963. John Lyon, nurseryman and plant hunter, and his journal, 1799–1814. Trans. Amer. Philos. Soc., n. s. 53(2): 1–69.

*——— & ———. 1970. John Banister and his Natural History of Virginia. Univ. Illinois Press, Urbana. 485 pp.

*Graustein, J. E. 1967. Thomas Nuttall, Naturalist: Explorations in America 1808–1841. Harvard Univ. Press, Cambridge, Massachusetts. 481 pp.

Harper, F. 1958. The Travels of William Bartram. Naturalists' Edition. Yale Univ. Press, New Haven, Connecticut. 727 pp., 29 pl. + maps.

Harvey, A. G. 1947. Douglas of the Fir. Harvard Univ. Press, Cambridge, Massachusetts. 290 pp.

Herbst, J. 1954. New Green World: John Bartram and the Early Naturalists. Hastings House Publishers, New York. 272 pp.

McVaugh, R. 1956. Edward Palmer: Plant Explorer of the American West. Univ. Oklahoma Press, Norman. 430 pp.

Merrill, E. D. 1949. Introduction, pp. 1–64, *in* "Index Rafinesquianus: The Plant Names Published by C. S. Rafinesque, with Reductions, and a Consideration of his Methods, Objectives, and Attainments." Arnold Arboretum of Harvard University, Jamaica Plain, Massachusetts. 296 pp.

Robbins, C. C. 1964. David Hosack, Citizen of New York. Mem. Amer. Philos. Soc. 62. 246 pp.

———. 1968. John Torrey (1796–1873): His life and times. Bull. Torrey Bot. Club 95: 514–645.

*Rodgers, A. D., III. 1940. "Noble Fellow": William Starling Sullivant. G. P. Putnam's Sons, New York. 361 pp. [Facsimile edition, Hafner Publishing Co., New York. 1968.]

*———. 1942. John Torrey: A Story of North American Botany. Princeton Univ. Press, Princeton, New Jersey. 352 pp. [Facsimile edition, Hafner Publishing Co., New York. 1965.]

*———. 1944*a*. American Botany 1873–1892: Decades of Transition. Princeton Univ. Press, Princeton, New Jersey. 340 pp. [Facsimile edition, Hafner Publishing Co., New York. 1968.]

*———. 1944*b*. John Merle Coulter: Missionary in Science. Princeton Univ. Press, Princeton, New Jersey. 321 pp.

*———. 1949. Liberty Hyde Bailey: A Story of American Plant Sciences. Princeton Univ. Press, Princeton, New Jersey. 506 pp. [Facsimile edition, Hafner Publishing Co., New York. 1965.]

*———. 1951. Bernhard Eduard Fernow: A Story of North American Forestry. Princeton Univ. Press, Princeton, New Jersey. 623 pp. [Facsimile edition, Hafner Publishing Co., New York. 1969.]

*———. 1952. Ervin Frink Smith: A story of North American plant pathology. Mem. Amer. Philos. Soc. 31: i–x, 1–657.

*Sutton, S. B. 1970. Charles Sprague Sargent and the Arnold Arboretum. Harvard Univ. Press, Cambridge, Massachusetts. 382 pp.

Williams, L. O. (editor). 1963. Homage to Standley: Papers [by various individuals] in Honor of Paul C. Standley. Chicago Nat. Hist. Mus., [Chicago, Illinois]. 115 pp.

VII. EDUCATIONAL AND POPULAR

Anderson, E. 1952. Plants, Man, and Life. Little, Brown and Co., Boston, Massachusetts. [Reissued by Univ. California Press, Berkeley, 1967.] 245 pp.

Asimov, I. 1964. A Short History of Biology. Doubleday, Garden City, New York. 182 pp.

Blinn, W. C. 1968. The Search for Explanation: Studies in Natural Science. Vol. 3. Michigan State Univ. Press, [East Lansing]. 409 pp.

Blunt, W. 1950. The Art of Botanical Illustration. Collins (New Naturalist Series), London, England. 304 pp.

*Cronquist, A. 1971. Introductory Botany. Ed. 2. Harper and Row, New York. 885 pp.

Delaunay, A. 1969. History of Biology. Leisure Arts Ltd., London, England. 104 pp.

Eifert, V. S. 1965. Tall Trees and Far Horizons: Adventures and Discoveries of Early Botanists in America. Dodd, Mead and Co., New York. 301 pp.

*Jensen, W. A. & F. B. Salisbury. 1972. Botany: An Ecological Approach. Wadsworth Publishing Co., Belmont, California. 748 pp. + index.

Moore, R. 1961. The Coil of Life; The Story of Great Discoveries in the Life Sciences. A. Knopf, New York. 418 pp.

Savage, H., Jr. 1970. Lost Heritage [Wilderness America Through the Eyes of Seven Pre-Audubon Naturalists]. William Morrow and Co., New York. 329 pp.

Taylor, G. R. 1963. The Science of Life; A Picture History of Biology. McGraw-Hill Book Co., New York. 368 pp.

IX. REFERENCES AND "TOOLS"

*Atwood, A. C., M. Warner, and others. 1958. United States Department of Agriculture Botany Subject Index. 15 Vols. G. K. Hall and Co., Boston, Massachusetts. 15,040 pp.

*Barnhart, J. H. 1965 [1966]. Biographical Notes upon Botanists. 3 Vols. G. K. Hall and Co., Boston, Massachusetts. 1658 pp.

*Ewan, J. 1965. Reference tools for the botanists. Stechert-Hafner Book News 20: 33–35. [See also chapter 5, pp. 55–60, *in* Lubrecht, 1967.]

Kerker, A. E. & H. T. Murphy. 1968. Biological and Biomedical Resource Literature. Purdue University, Lafayette, Indiana. 226 pp.

*Langman, I. K. 1964. A Selected Guide to the Literature on the Flowering Plants of Mexico. Univ. Pennsylvania Press, Philadelphia. 1015 pp.

*Lawrence, G. H. M., A. F. G. Bucheim, G. S. Daniels & H. Dolezal (editors). 1968. B-P-H: Botanico-Periodicum-Huntianum. Hunt Botanical Library, Pittsburgh, Pennsylvania, 1063 pp.

*Lubrecht, H. (editor). 1967. Early American Botany: With a Miscellany of other Botanical Rarities. Stechert-Hafner, Inc., New York. 63 pp.

Lurie, E. 1953. Some manuscript resources in the history of nineteenth-century American natural science. Isis 44: 363–370.

*Meisel, M. 1924–1929. Bibliography of American Natural History. The Pioneer Century, 1769–1865. 3 Vols. Published by the author, New York. 244, 741, 749 pp. [Facsimile edition, Hafner Publishing Co., New York. 1967.]

Miller, G. (editor). 1964. Bibliography of the History of Medicine of United States and Canada, 1939–1960. Johns Hopkins Univ. Press, Baltimore, Maryland. xvi + 428 pp.

*Quinby, J. (compiler). 1958. Catalogue of Botanical Books in the Collection of Rachel McMasters Miller Hunt. Vol. 1. Printed Books 1477–1700. . . . Hunt Botanical Library, Pittsburgh, Pennsylvania. lxxxiv + 517 pp. [For Vol. 2, see Stevenson, 1961.]

Sarton, G. 1952. Horus: A Guide to the History of Science; A First Guide for the Study of the History of Science with Introductory Essays on Science and Tradition. Ronald Press, New York. 316 pp.

Smith, C. R. & W. M. Reid. 1972. Guide to the Literature of the Life Sciences. Ed. 8. Burgess Publishing Co., Minneapolis, Minnesota. 166 pp.

*Stafleu, F. A. 1967. Taxonomic Literature; A Selective Guide to Botanical Publications with Dates, Commentaries and Types. Regnum Veg. 52. 556 pp.

*Stannard, J. 1966. Early American botany and its sources. Pp. 73–102, *in* Thomas R.

Buckman (editor), "Bibliography & Natural History, Essays Presented at a Conference Convened in June 1964." University Kansas Libraries, Lawrence. 148 pp.

*STEVENSON, A. (compiler). 1961. Catalogue of Botanical Books in the Collection of Rachel McMasters Miller Hunt. Vol. 2, Part 1. Introduction to Printed Books 1701–1800; Part 2. Printed Books 1701–1800. Hunt Botanical Library, Pittsburgh. ccxliv; ix + 655 pp. [For Vol. 1, see Quinby, 1958.]

STUCKEY, R. L. 1970. Index to biographical sketches and obituaries in publications of the Ohio Academy of Science, 1900–1970. Ohio Jour. Sci. 70: 246–255.

SWIFT, L. H. 1970. Botanical Bibliographies: A Guide to Bibliographic Materials Applicable to Botany. Burgess Publishing Co., Minneapolis, Minnesota. 804 pp.

THORNTON, J. T. & R. I. J. TULLY. 1971. History and biography of biology. Pp. 311–330, *in* R. T. Bottle & H. V. Wyatt (editors), "The Uses of Biological Literature." Ed. 2. Archon Books, Hamden, Connecticut. 379 pp.

NOTA BENE

This bibliographic appendix has been prepared with those who are beginning to use historical approaches in their teaching and/or research in mind. Thus, some very selected works by European authors or about mainly European history that peripherally relate to American botany are included (*e.g.* Sarton, 1952, 1957, 1959; Taton, 1963–1966; Sachs, 1890). The annual "Critical bibliography of the history of science and its cultural influences," published as part of *Isis* by The History of Science Society, should be consulted for further in-depth study of particular topics or periods. The in-progress *Dictionary of Scientific Biography* (Gillispie, 1970–) contains more original analytical and original material about the botanists covered than the title might indicate.

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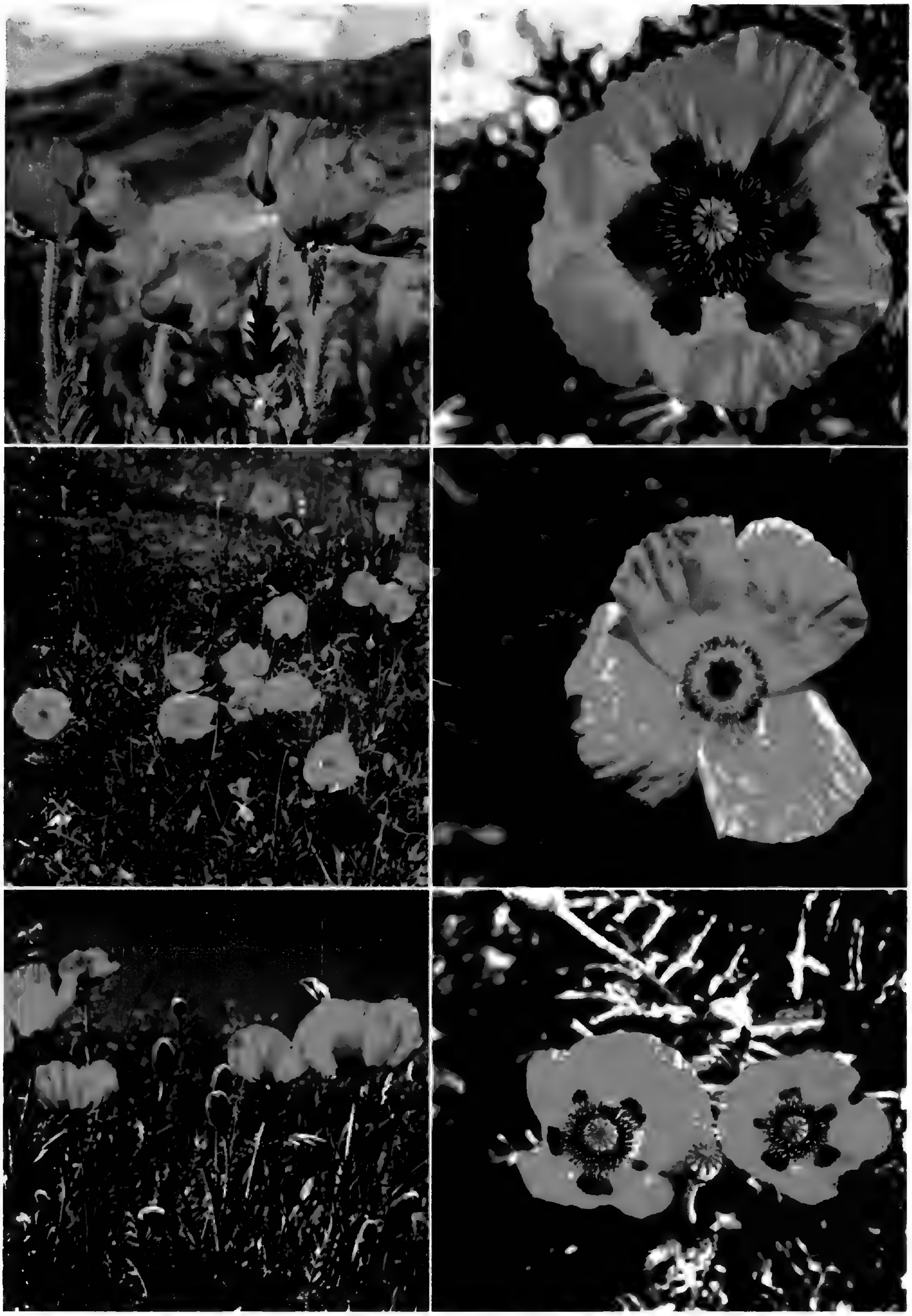

FIGURE 1. Top: *Papaver bracteatum* Lindl.; middle: *P. orientale* L.; bottom: *P. pseudo-orientale* (Fedde) Medw.

ANNALS
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BIOSYSTEMATIC STUDIES IN *PAPAVER* SECTION *OXYTONA*[1]

Peter Goldblatt[2]

Abstract

Intensive field study, combined with cytological and chemical analysis of *Papaver* section *Oxytona* has resulted in the re-evaluation of species in the group. The section is treated as comprising three species, *P. bracteatum*, diploid ($2n = 14$), *P. orientale*, tetraploid ($2n = 28$) and *P. pseudo-orientale*, hexaploid ($2n = 42$). Different major alkaloids characterize each species, and past confusion about alkaloid chemistry is clarified. A detailed taxonomic treatment with full synonymy, distribution data and listing of exsiccatae is provided.

The genus *Papaver* comprises about 100 species, found primarily in temperate regions of the Northern Hemisphere, one species being indigenous to southern Africa. The genus, which was subdivided into 9 sections (Fedde, 1909), contains numerous annual and biennial species as well as a number of perennials falling in three sections: *Scapiflora*, *Pilosa*, and *Oxytona* (*Macrantha*). *Papaver* is of major economic importance, one reason being that several of the annual species are major agricultural weeds but more important because most, if not all species, contain a variety of alkaloids some of which have considerable medicinal value.

The economically valuable alkaloids are those structurally related to morphine, which include codeine and thebaine as well as morphine itself. These alkaloids are known to occur in quantity in only two sections: section *Papaver* (= *Mecones*) in two species, *P. somniferum*, widely cultivated for its alkaloid extract opium, and *P. setigerum* (also treated as *P. somniferum* var. *setigerum*), and in section

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[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

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Oxytona. Reports in the literature for section *Oxytona* indicate that some forms only of *P. orientale* and *P. bracteatum* contain significant amounts of thebaine, while other reports mention isothebaine or oripavine as major alkaloids with the morphine relative thebaine absent or present in traces.

A superficial review of alkaloid literature for *Papaver* section *Oxytona* reveals reports of isothebaine and oripavine in *Papaver bracteatum* (Kisselev & Konovalova, 1948) and of isothebaine, bractavine, and other alkaloids (Heydenreich & Pfeifer, 1965, 1966). Other workers have reported thebaine only in the same species (Neubauer & Mothes, 1963; Böhm, 1965; Sharghi & Lalezari, 1967) or thebaine with traces of other alkaloids, *e.g.* "alkaloid E" (Böhm, 1967) and alpinigenine (Lalezari, Shafiee & Nasseri-Nouri, 1973). Reports for plants identifed as *Papaver orientale* are equally conflicting: recent reports include those of Dawson and James (1956) and Kleinschmidt (1961) who found isothebaine with small traces of thebaine in this species; Nemekova, Preininger, and Santavy (1966) confirm this with a report of isothebaine as the dominant alkaloid in *P. orientale*. Ping Cheng (1972) also reports isothebaine in *P. orientale* but together with the accompanying alkaloid orientalidine. In marked contrast to these records are the reports of the absence of isothebaine in *P. orientale* (Konovalova, Yunussoff & Orechoff 1935), who find nearly equal quantities of oripavine and thebaine in wild material from the Transcaucasus. The occurrence of oripavine and thebaine has been confirmed by Stermitz and Rapoport (1961). The literature to date thus suggests that these two species, *P. orientale* and *P. bracteatum*, are far more chemically heterogeneous than most plants; alternatively it is possible that plants used in some of the cited alkaloid studies were simply incorrectly determined as to species within section *Oxytona*.

Recently section *Oxytona* has become a subject of detailed chemical and agronomic study as commercially exploitable amounts of alkaloids have been recorded in certain cultivated races (Neubauer & Mothes, 1963). Following the rising interest in the section, a survey of the systematics revealed a very confused situation, and one important fact emerged, namely no detailed work on wild plants had ever been undertaken. Alkaloid reports, with few exceptions, were made from long cultivated material, and systematic studies were largely or entirely made on cultivated material and herbarium specimens. With the current importance of the group, field investigation seemed called for, and with the support of the Agricultural Research Service of the U. S. Department of Agriculture a study of this nature was initiated. The author has now spent two collecting seasons in Iran and a short period in Turkey, where the species occur, although not in the U.S.S.R., where they are also found. Observations obtained in Iran and Turkey appear significant and merit publication at this time, although the author hopes to be able to extend this study to the U.S.S.R. and to verify and elaborate on the observations reported here.

OBSERVATIONS

Initial observations on live populations led to the hypothesis, subsequently confirmed by cytological and chemical studies, that three species of *Papaver* section *Oxytona* occur in Iran and Turkey. The morphology of the section and of these three species is dealt with in detail in the taxonomic treatment. However, for the following discussion of ecology, cytology and chemistry, the species and their morphology are briefly mentioned.

1. *Papaver bracteatum* Lindl.: one species conforming closely to Lindley's original description and illustration occurs in Iran in the Alborz Mountains north of Tehran and also in the west in Iranian Kurdistan. It is relatively uniform in important taxonomic characters and is recognized by its robust habit, numerous large floral bracts, dark red, marked petals and, before flowering, by the erect oblong bud with short, appressed, broad-based bristles on the calyx (Figs. 1 & 7).

Synonym: *P. lasiothrix* Fedde.

2. *Papaver orientale* L.: a slender plant, identified with Linnaeus' species, occurs in northwestern Iran and northeastern Turkey. It has pale orange flowers, light petal markings (or no markings at all), and no floral bracts, while the buds droop characteristically and have slender spreading bristles on the calyx (Figs. 1 & 7).

Synonyms: *P. paucifoliatum* (Trautv.) Fedde; *P. orientale* var. *paucifoliatum* Trautv.; *P. orientale* var. *parviflora* Busch.

3. *Papaver pseudo-orientale* (Fedde) Medw.: a third species is found often associated with moist conditions and is widespread in Iran and Turkey. Though not commonly recognized in the literature, it is a very distinct plant in the field. It is variable, but can be recognized by its erect buds with slender spreading calyx bristles, deep orange flowers often with heavy black markings, and frequently bracteate flowers (Figs. 1 & 7).

Synonyms: *P. intermedium* DC.; *P. bracteatum* var. *pseudo-orientale* Fedde.

1. Ecology and Phenology

All three species grow in montane regions, usually above 1800 meters. However, each is found in a different characteristic habitat, and the ranges of each seldom overlap.

Papaver bracteatum shows a preference for comparatively dry situations, often occurring on stony slopes from 1,500 to 2,500 m frequently with a depauperate cushion type vegetation. It is found in two quite separate areas, the Alborz Mountains north and northwest of Tehran and in Kurdistan in western Iran. In the latter area plants are found at comparatively low altitudes, occasionally from 1,500 m but usually from 1,700 to 2,000 m and seldom above this. Consequently flowering in this area is earlier than in the Alborz and is usually at a peak at the end of May. The Alborz populations which occur above 1,800 m only begin to flower after mid-June and continue at higher elevations until late July. A third group of plants widely separated from both Iranian areas (Fig. 9) occurs on the north slope of the Caucasus in Russia. This is probably the type locale for the species.

At only one of many localities for *Papaver bracteatum* were other members of the section found; this was in the western Alborz in the area known as

Shuran, where the ranges of *P. orientale* and *P. bracteatum* meet. Even here *P. bracteatum* showed a preference for drier conditions and was usually on a south slope, while *P. orientale* was more common on the far moister north slopes. Several hybrids were noted at a few places where populations were in close proximity (*Goldblatt 747, 985–987*). These plants were recognized by an intermediate flower color, lightly marked petals, absence of bracts, and peduncular leaves set high up near the flower. The hybrids were found only in situations ecologically intermediate between conditions preferred by the parent species. The hybrids exhibit a high degree of pollen sterility with more than 95% of the grains collapsed. The remaining pollen, which does stain with lacto-phenol and cotton blue, appears normal though it does show a greater size variation than is usual.

Papaver orientale shows a marked preference for alpine conditions and has not been found below 1,800 m either in Turkey or Iran. It occurs in moister situations than *P. bracteatum* and usually grows on well watered, open mountain slopes, though is also found in sheltered places on screes below cliffs. Generally plants in the latter situations are more robust and those in exposed areas are smaller. *Papaver orientale* seldom blooms before the end of June and at higher altitudes continues flowering into late August.

It has been found together with *Papaver bracteatum* at one locality—already mentioned—and at two sites with *P. pseudo-orientale*, one in the mountains near Khalkhal, north Iran, and another near Siah Chesmeh, Iran near the Turkish border. In the latter cases the overlap of ranges was at the lower limit of *P. orientale* which flowers earlier than *P. pseudo-orientale* at these sites. The separation of flowering times is not complete and plants believed to be hybrids were found near Siah Cheshmeh. Again, the few hybrids are intermediate in appearance between the parents, though they are often difficult to distinguish from *P. orientale*, which they resemble more (*Goldblatt 1148–1152*). The flowers are intermediate in color between *P. orientale* and *P. pseudo-orientale* and lack markings, and the plants themselves are slender and have few peduncular leaves. Pollen of these plants is most unusual: between 85–95% is aborted, but a small percentage is unusually large, 8–12-colpate (compared to tricolpate in both parents) and apparently fertile, staining heavily with lacto-phenol and cotton blue. The cytology of these plants is discussed in a later section.

Papaver pseudo-orientale is usually found in moist situations at altitudes of between 1,500 and 2,000 m. It is most commonly found along stream banks, irrigation ditches or seepage areas, growing amongst comparatively luxuriant herbaceous vegetation in quite marked contrast to the rather stunted growth of drier adjacent areas. The species is widespread, occurring in northwestern Iran and throughout the eastern portion of Turkey, and flowers from mid-June in some areas to late July in others. Populations are quite small and plants usually scattered; this is in contrast to *P. bracteatum* and *P. orientale*, which are found in large numbers at some sites. The hybrids found where *P. pseudo-orientale* and *P. orientale* occur together have already been mentioned.

REPRODUCTION

Like most species of *Papaver*, the flowers of all three species of section *Oxytona* are large and very conspicuous. The petals, which are crumpled in the bud, unfold after the calyx valves are shed, and by the time the flower is open the anthers have dehisced and shed quantities of pollen on the surface of the stigmatic disc. The pollen remains on the stigmatic areas until this becomes receptive, but pollen can easily be removed by wind or by insect visitors.

The brightly colored flowers attract numerous insects, the major visitors being pollinivorous beetles and many species of bees which visit to gather pollen. Though the visitors may remove much of the pollen of a flower, they also bring pollen, and in this way the pollen of a wide range of plants other than *Papaver* finds its way to the stigma. Clearly the visitors mentioned could accomplish cross-pollination. However, no data is available on self-compatibility in *Oxytona* species, except for Bullis' (1955) report of both self-compatibility and incompatibility in "oriental poppies." The capsules of members of section *Oxytona* regularly produce copious amounts of seed.

Information on other members of the genus indicates that cross-pollination is the norm (Fryxell, 1957), but differences of opinion exist as to whether plants will set fertile seed by their own pollen if cross-pollination does not occur. Fryxell reports most members of the Papaveraceae, including *Papaver*, are self-incompatible. He found three species of *Papaver*, including *P. rhoeas*, to be self-incompatible, while *P. somniferum* was self-compatible. McNaughton and Harper (1967) found *P. rhoeas* as well as the four other native British species (all annuals) highly self-fertile. The present author can confirm the self-compatibility of *P. rhoeas* and *P. somniferum* and report this condition also in *P. atlanticum*, a perennial species.

2. Cytology

A. CHROMOSOME CYTOLOGY AND CYTOGENETICS

Cytological observations on a large number of individuals from many populations have provided one line of independent evidence on the taxonomy of section *Oxytona*. Chromosome counts were obtained from anther squashes or from root tips of seedlings grown from seed collected in the wild. A squash method was used on the root tips after pretreatment in 0.05% colchicine for four hours (for full description see Goldblatt, 1972).

The results of this study, set out in Table 1, show the three species recognized in this treatment are quite distinct from one another as regards ploidy level. The base number, $x = 7$, is the same as that for most species of *Papaver*. While the chromosomes of all species are similar in size and morphology and much like those of most other species of *Papaver*, all individuals of *P. bracteatum* examined proved to have a diploid number of $2n = 14$ (Fig. 2). *Papaver orientale* is apparently a tetraploid species with $2n = 28$, while *P. pseudo-orientale* with $2n = 42$ is hexaploid.

The cytological evidence obtained from Turkish and Iranian plants strongly supports the proposed taxonomy with each species exhibiting a different level

TABLE 1. Chromosome number and major alkaloids in *Papaver* section *Oxytona*. All vouchers are the collections of the author and are to be housed at the U.S. National Arboretum (NA) and Missouri Botanical Garden (MO).

Species	Haploid chromosome number	Dominant alkaloid	Other significant alkaloids	Collection data
P. bracteatum	$n = 7$	thebaine	alpinigenine	Damavand, N. Polour, Iran, *797–802*
	$= 7$	thebaine	alpinigenine	Damavand, S. Polour, Iran, *803–813*
	$= 7$	thebaine	alpinigenine	Rineh, Iran, *724–726*
	$= 7$	thebaine	alpinigenine	Chalus road, Khakak, Iran, *703*, *704*, *814*, *815*
	$= 7$	thebaine	alpinigenine	Near Khakak, Iran, *706–707*
	$= 7$	thebaine	alpinigenine	Shuran, Iran, *742*, *744*, *746*, *990*, *991*
	$= 7$	thebaine	—	Kanemat, Iran, *791–794*
		thebaine	—	Marivan-Saqqez, Iran, *860–872*
	$= 7$	thebaine	—	Sanandaj-Marivan, Iran, *851–857*, *1064–1084*
	$= 7$	thebaine	—	Saqqez-Baneh, Iran, *879–888*
	$= 7$	thebaine	—	Mahabad-Sardasht, *902–920*
P. orientale	$n = 14$	oripavine	traces thebaine and/or isothebaine	Khalkhal Pass, Iran, *733–736*, *741*, *762*, *763*, *769*
	$= 14$	oripavine	thebaine	Shuran, Iran, *748*, *749*
		oripavine	isothebaine	Shuran, Iran, *997*
		oripavine	—	Shuran, Iran, *980–984*
	$= 14$	oripavine	traces thebaine and isothebaine	Siah Cheshmeh, Iran, *1153–1155*
	$= 14$	oripavine	traces thebaine	Zinjinab, Iran, *778–781*
	$= 14$	oripavine	isothebaine	Mts near Takht-i-Soleiman, Iran, *786–788*
	$= 14$	oripavine	unidentified alkaloid and occasional traces thebaine	Guleh Khaneh, Iran, *782–785*, *1005–1014*
	$= 14$	oripavine	traces thebaine	Kars, Turkey, *1001*, *1001A*
	$= 14$	oripavine	isothebaine	Tahir Pass, Turkey, *1000*, *1000A*

Table 1 continued.

Species	Haploid chromosome number	Dominant alkaloid	Other significant alkaloids	Collection data
P. pseudo-orientale	$n = 21$	isothebaine	several others including trace oripavine	Zanjan Pass, Iran, *712–714*, *716*, *718*
	not known	isothebaine	others including trace oripavine	Qotur, Iran, *752–758*
	not known	isothebaine	thebaine and oripavine	Siah Chesmeh, Iran, *766–769*
	$= 21$	isothebaine	thebaine and oripavine	Qushi Pass, Iran, *1017–1024*
	$= 21$	isothebaine	not identified	Oshnaviyeh, Iran, *1025–1035*
	$= 21$	isothebaine	not identified	Mianeh-Firuzabad, Iran, *952–955*
		isothebaine	alpinigenine	Mianeh-Firuzabad, Iran, *956–957*
	$= 21$	isothebaine	not identified	Khakhal Pass, Iran, *1189–1192*
	not known	isothebaine	thebaine and oripavine	Horasan-Sarikamiş, Turkey, *1002*, *1002A*
	$= 21$	isothebaine	thebaine and oripavine	Hamur, Turkey, *999*
Hybrids				
P. bracteatum × *P. orientale*	not known	thebaine and oripavine		Shuran, Iran, *747*, *985–987*
P. orientale × *P. pseudo-orientale*	not known	isothebaine	oripavine	Siah Chesmeh, Iran, *1148–1152*

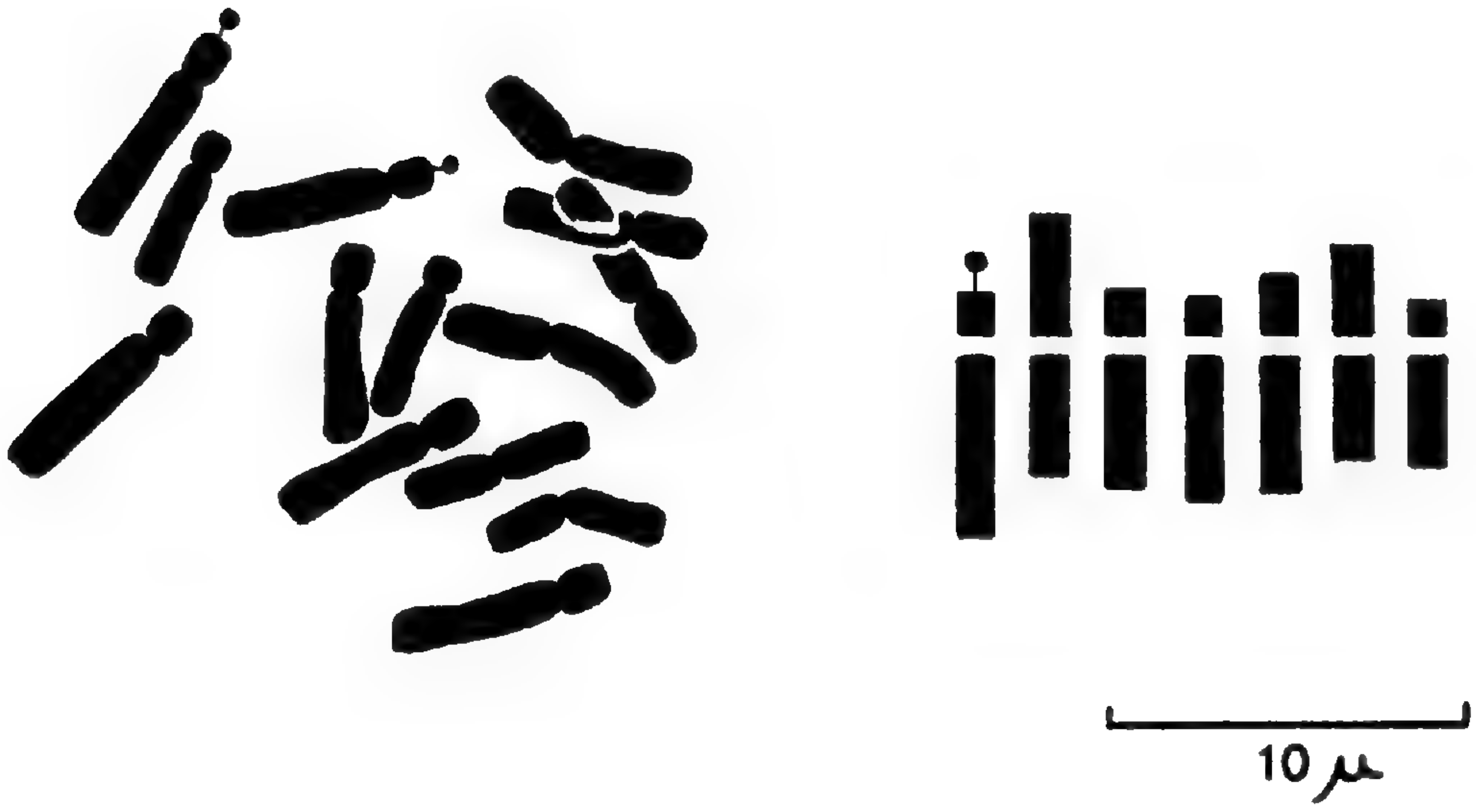


FIGURE 2. Mitotic metaphase and idiogram of the karyotype of *Papaver bracteatum*.

of ploidy. Nevertheless reports on the cytology of wild plants from the U.S.S.R. would be most welcome particularly in view of the occurrence of several unusual forms in this area.

The chromosome numbers as recorded here are supported by previous reports (Table 2) only in so far as the chromosome counts can be related to a properly identified specimen. Thus the diploid number of $2n = 14$ for *P. bracteatum* confirms the reports of Yasui (1936) and Böhm (1965), and $2n = 42$ for *P. pseudo-orientale* confirms the reports of Kawatani and Asahina (1959) and Ernst (1965) when the corrected taxonomy is taken into account. As already mentioned the taxonomy has in the past been too conflicting for determinations in this section to be accepted without recourse to examination of vouchers or descriptions given of the subject material. Thus the majority of cytological records in section *Oxytona* must, in the light of current studies, be regarded as doubtful, owing to incorrect species determination. In addition it should be noted that none of the previous counts were made from wild material, which makes these results even more difficult to accept.

The differences in ploidy among the species of section *Oxytona* suggest reasons why interspecific hybrids have predominantly sterile pollen. Meiosis has however not been observed in any of the naturally occurring hybrids and no chromosome counts are available for these plants.

The diploid number of $2n = 42$ along with the fact that *Papaver pseudo-orientale* is intermediate in many features between *P. bracteatum* and *P. orientale* suggests that *P. pseudo-orientale* may be an allohexaploid species which evolved from hybrids between *P. bracteatum* and *P. orientale*. The naturally occurring hybrids found in northern Iran were, as might be expected, intermediate in many ways to the two parents but not particularly like *P. pseudo-orientale*, especially as regards their small size. The author hopes to continue to investigate the origin of *P. pseudo-orientale* in the future.

CYTOGENETICS

Although several records exist of the artificial production of hybrids between *Papaver somniferum* and both *P. orientale* and *P. bracteatum* (Ljungdahl, 1922;

TABLE 2. Previous cytological records for section *Oxytona*[a]

Species	Reported chromosome number	Author and specimen data
P. bracteatum	$n = 7$	Yasui, 1936, 1937*a*, *b*; no voucher, description and photo adequate for determination
	$2n = 14$	Günther & Böhm, 1968; no voucher cited, description and illustration adequate.
P. pseudo-orientale		
(as *P. bracteatum*)	$2n = 42$	Ernst, 1965; *Ernst 729B* (DS) ex hort.
(as *P. orientale*)	$2n = 42$	unpublished; voucher seen at Kew, ex hort., Bot. Dept., J. & K Univ., India.
(as *P. orientale*)	$2n = 42$	Kawatani & Asahina, 1959; description and alkaloid data sufficient for determination.
(as *P. orientale*)	$2n = 42$	Günther & Böhm, 1968; description indicates redetermination probably correct.
Of uncertain identity:		
"*P. orientale* var. *olympia*"	$2n = 28$	Snoad, 1952; no specimen data.
"*P. orientale*"	$2n = 28$	Krishnaswami *et al.*, 1968; no specimen data.
"*P. orientale*"	$n = 21$	Tahara, 1915; no specimen data.
"*P. orientale*"	$n = 21$	Ljungdahl 1922; no specimen data.
"*P. orientale*"	$n = 21$	Yasui, 1921; specimen data insufficient.
"*P. orientale*"	$2n = 42$	Castiglia, 1955; no specimen data.
"*P. orientale*"	$2n = 42$	Kawatani & Ohno *in* Asahina *et al.*, 1957; no specimen data.
"*P. bracteatum*"	$2n = 42$	Kawatani & Ohno *in* Asahina *et al.*, 1957; no specimen data.
"*P. pseudo-orientale*"	$2n = 42$	Kawatani & Ohno, 1965; no specimen data.

[a] In view of the revised taxonomy proposed here, all determinations are questionable unless verified by voucher, illustration or description published with the chromosome count.

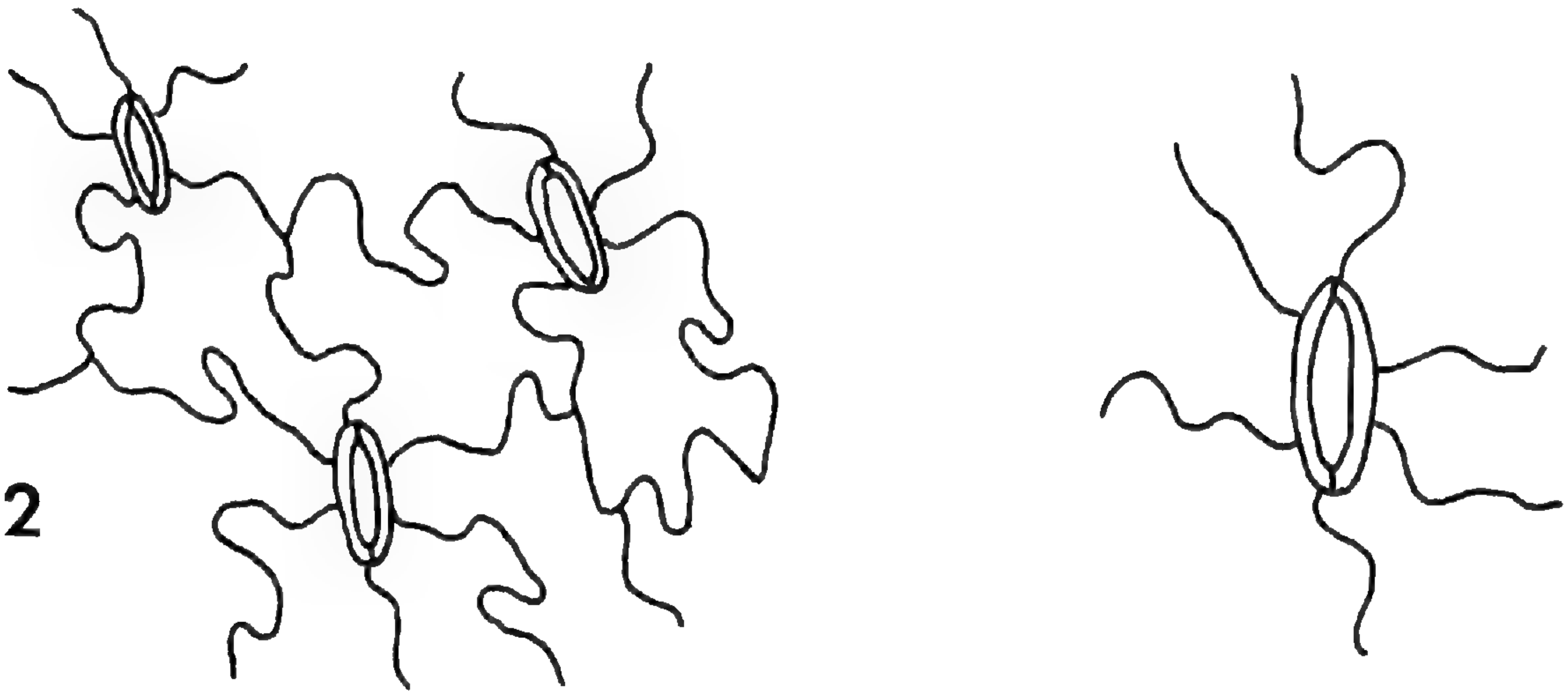
Yasui 1921, 1936; Kawatani & Asahina, 1959; Böhm, 1965), the only known hybrids between members of section *Oxytona* were made by Yasui (1936). Yasui described hybrids between *P. bracteatum* and what she called *P. orientale*, her plant being hexaploid ($2n = 42$). Yasui also crossed *P. somniferum* to a tetraploid oriental poppy she believed to be a spontaneous *P. bracteatum* × "*P. orientale*" hybrid. In view of the cytological data now known for the section, there is a suspicion that this so-called hybrid may have in fact been true *P. orientale*. Yasui's *P. bracteatum* × "*P. orientale*" hybrids were viable, but all exhibited very low fertility. Chromosome pairing in these hybrids is noteworthy: 13 bivalents and 2 univalents formed, indicating pairing homology within the 21 chromosomes of the hexaploid parent.

B. STOMATA AND POLLEN

Although at the morphological level the diploid *Papaver bracteatum* is the largest and most robust species, studies at the cellular level have indicated its diploid nature. A comparison of the epidermis of young live plants of the three species of section *Oxytona* reveals a marked difference in both epidermal and guard cell size (Fig. 3). The length of the ellipsoid stomata provides the best measure of comparison. Providing sufficient stomata are measured and averaged,

1

2



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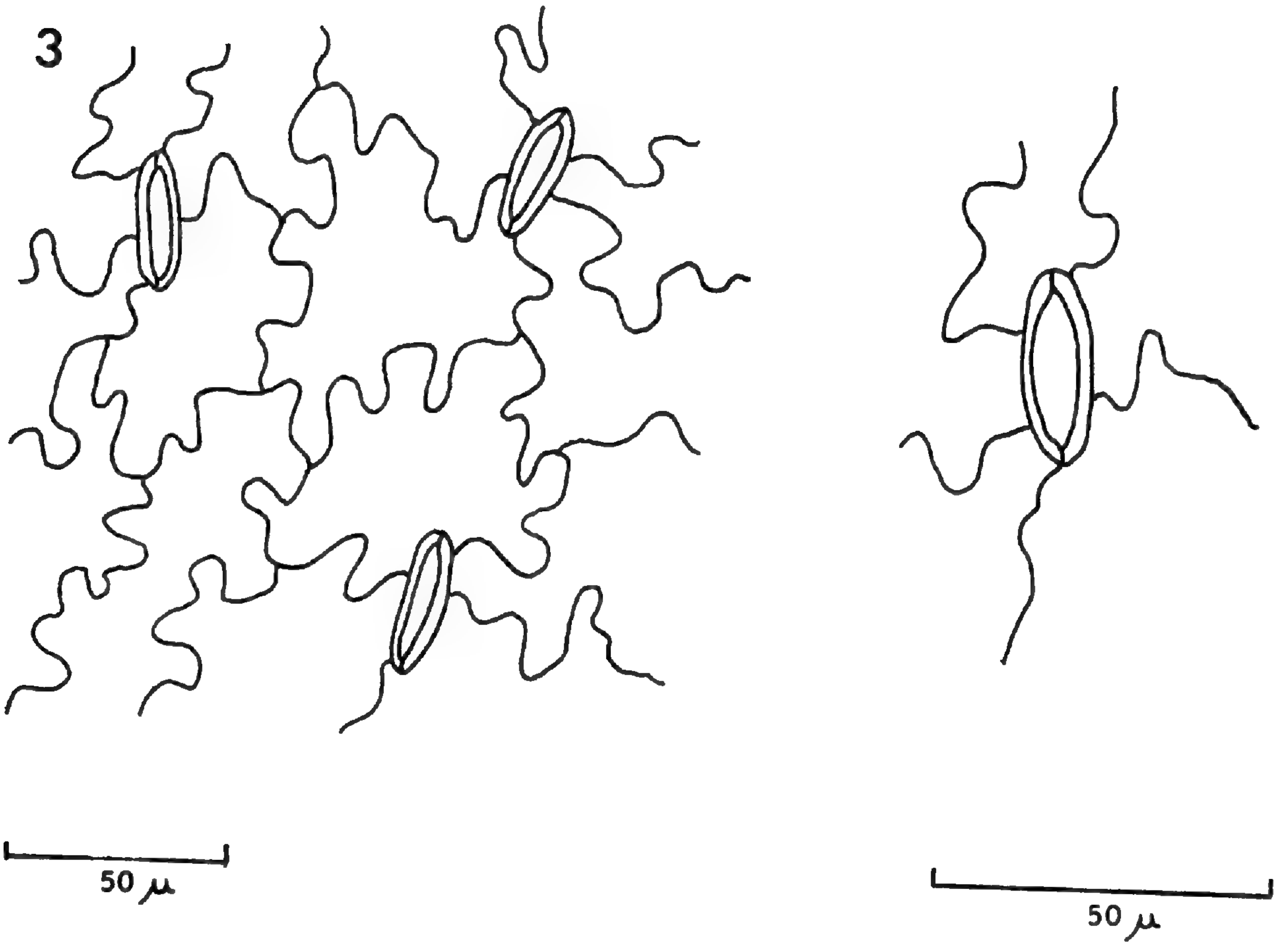

TABLE 3. Range and mean of both stoma length and pollen diameter in *Papaver* section *Oxytona.*

Species	Ploidy	Range and mean stoma length, μ		Range and mean pollen diameter, μ	
P. bracteatum	2*n*	20–32	$\overline{26}$	24.3–27.1	$\overline{25.5}$
P. orientale	4*n*	32–45	$\overline{36}$	26.4–28.2	$\overline{27.4}$
P. pseudo-orientale	6*n*	43–60	$\overline{50}$	27.8–30.1	$\overline{28.8}$

species can even be identified by epidermal characters. The data in Table 3 were obtained by making impressions of the lower epidermis of live, young, comparatively hairless leaves following the method described by Payne (1970). Dry herbarium material can also be used but is more difficult to manage, both because of the shrunken nature of the leaves and because mature plants are heavily setose.

A similar indication of ploidy can be obtained from pollen, though this is somewhat more variable in size than stomata (Table 3). The pollen, described by Erdtman (1943: 115) is quite thin-walled and is tricolpate, although occasionally 4-colpate grains occur in *P. pseudo-orientale*, the hexaploid species. Data shown in Figure 4 were obtained from grains mounted in glycerin jelly. Measurements are given only for the recent plant collections of the author where chromosome number was known. Older pollen samples from herbarium specimens did not match figures obtained for newer collections. In every case samples indicated a lower level of ploidy than expected for the species concerned and it is clear that for *Papaver*-type pollen, grains expand differentially in an aqueous-glycerin jelly medium depending on their age. This phenomenon has not to the author's knowledge been recorded, and reasons for it are not known. Failure of fossil pollen to expand as much as herbarium pollen has however been well documented, and the differential expansion observed here between recent pollen of varying age may be a comparable occurrence.

3. ALKALOID OCCURRENCE

As part of a broader study of section *Oxytona* being conducted under contract to the Agricultural Research Service of the U. S. Department of Agriculture, Dr. I. Lalezari and co-workers at the University of Tehran have been making analyses of alkaloids found in section *Oxytona.* These results are presented here with the permission of Lalezari and his team, who will be publishing their methods and findings in much greater detail elsewhere.

The results of alkaloid analysis (Table 1) can be summarized briefly. All populations of *Papaver bracteatum* sampled yield thebaine, either exclusively

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FIGURE 3. Epidermal features of: 1. *Papaver bracteatum* (diploid); 2. *P. orientale* (tetraploid); 3. *Papaver pseudo-orientale* (hexaploid).

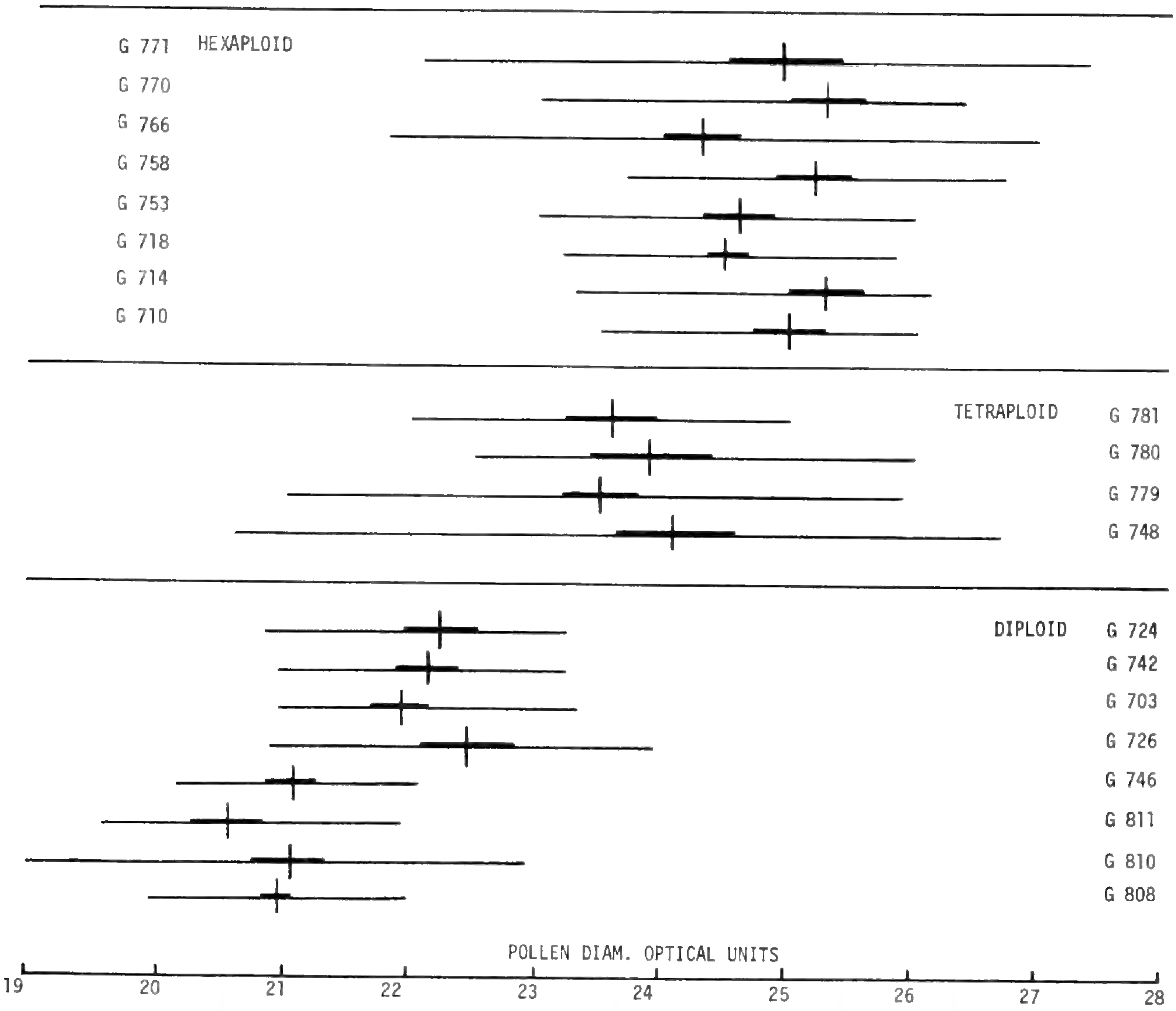

FIGURE 4. Mean, range and standard error round the mean of the diameter of samples of 50 pollen grains, each from selected collections of *Papaver* section *Oxytona*. Diploid samples are *P. bracteatum*, tetraploids all *P. orientale*, and hexaploids are *P. pseudo-orientale*.

as in the Kurdistan plants, or with small amounts of alpinigenine (Lalezari *et al.*, 1973) in the plants from the central Alborz mountains from all tissues of the plant. *Papaver orientale*, all too few populations of which have been examined, has what has been identified as oripavine as a major or dominant alkaloid, though others are also present, *e.g.* isothebaine in some individuals, traces of thebaine in others, as well as several unidentified alkaloids. The degree of alkaloid variation is unexplained, but is not linked to any morphological feature. *Papaver pseudo-orientale* is consistently found to have a predominance of isothebaine with smaller quantities of thebaine and oripavine and a characteristic range of other trace alkaloids. Occasionally either thebaine or oripavine are not detected, but this may be due to technique rather than a reflection of variation.

Like the cytological observations, the alkaloid data consistently support the taxonomy used here and in turn suggest that previous alkaloid accounts are unreliable with respect to species determination. As soon as more material, especially from Turkey and the U.S.S.R., can be analysed, it will be possible to ascertain how the observations thus far noted extend to other populations. Once the whole range has been sampled, it should be possible to infer from earlier alkaloid records the correct identifications of species previously tested. To reclassify species at present, according to recorded alkaloids is tempting but should be done only tentatively. Nevertheless it is almost certain that *P. bracteatum* and *P. orientale* have frequently been misidentified in most alkaloid reports and that these species are not as chemically heterogeneous as previously thought (Stermitz, 1968: 170).

4. Affinities of Section *Oxytona*

The occurrence of morphine type alkaloids in section *Papaver* (*Mecones*) and *Oxytona* has prompted suggestions of a close relationship between these groups. *Papaver somniferum*, which has the unusual diploid number of $2n = 22$, has been crossed several times with "*P. orientale*" (Ljungdahl, 1922; Yasui, 1921, 1937*a*; Kawatani & Asahina, 1959) and also with *P. bracteatum* (Yasui, 1937*b*; Böhm 1965). This has been seen as further evidence of the close relationship between these sections (Sansome & Philp, 1939). However it should be borne in mind that it is now known that many species of *Papaver* with similar or different chromosome numbers can artificially be hybridized, and this fact by itself cannot be seen as any indication of taxonomic affinity.

The present author finds any suggestion of relationship between sections *Papaver* and *Oxytona* difficult to accept, and the similarity of alkaloids in some species only of these two sections is seen as coincidental.

The closest relationship of section *Oxytona* probably lies in the morphologically similar section *Pilosa*. The latter group consists of small, perennial plants most of which are branched to some extent—this character presumably ancestral to the scapose habit of *Oxytona* species. Three species of section *Pilosa*, *Papaver oreophilum* Rupr., *P. lateritium* C. Koch and *P. monanthum* Trautv., all occurring in the Caucasus region, are particularly similar in appearance to *P. orientale*, and the latter and *P. monanthum* are almost indistinguishable. *Papaver monanthum* is in fact unbranched and also lacks cauline leaves on the flowering stalk. The last mentioned character is the only one which can be used to distinguish *P. monanthum* from some forms of *P. orientale*—so close is the similarity. The author doubts whether *P. monanthum* really belongs in section *Pilosa*, and it should be included in section *Oxytona*. Examination of live material and chemical study is clearly needed to verify this suggestion.

5. Horticultural Note

There seems little doubt that Tournefort (1718), who travelled in eastern Turkey in 1701, first brought the "oriental poppy" to the attention of botanists. In his travelogue, what is here treated as *Papaver pseudo-orientale* is recorded from the region near Erzerum. His illustration and description make this determination fairly certain. Tournefort must also be credited with the introduction of the "oriental poppy" to Europe. Commelin (1706), Linnaeus (1748), and other early eighteenth century botanists all grew it and credited Tournefort with its introduction. The examination of these early illustrations and especially herbarium specimens such as those in the Sloane Collection, a Miller collection in the Banks Herbarium, and Linnaeus' own specimen in the Linnaean Herbarium reveals that *P. orientale* was definitely the plant brought to Europe by Tournefort. Thus it seems that Tournefort must have collected seed of a different species from the one he saw and described in his writings, unless he actually brought seed of both *P. orientale* and *P. pseudo-orientale* to Europe.

The first record of *Papaver pseudo-orientale* growing in Europe known to this author is the illustration in Curtis' *Botanical Magazine* t. 57 (1788), where a good painting of a plant identified as *P. orientale* appears. There is no indication of the origin of the plant. De Candolle was the first botanist to regard this species as distinct from *P. orientale*, and he described it as *P. intermedium*, noting its similarity to both *P. bracteatum* and *P. orientale*. During the nineteenth century *P. pseudo-orientale* was however still largely confused with *P. orientale*, and most references to the later name refer in fact to *P. pseudo-orientale*. This is still the case today, and most plants named *P. orientale* turn out to be *P. pseudo-orientale*. In spite of the numerous cultivars of the oriental poppy in existence, it is often possible to relate most forms of the oriental poppy to *P. pseudo-orientale*, while true *P. orientale* is seldom encountered.

Papaver bracteatum was introduced to Europe only in 1818 when Fischer, curator of the Imperial Botanical Garden at Leningrad, collected seed, probably from the Caucasus and distributed the species to western Europe where Lindley described it in 1821. Although *P. bracteatum* is the largest and most striking of the three oriental poppies, it did not for some reason get into general cultivation, though it was maintained at several botanical gardens. Today it is rarely found in gardens though some cultivars offered in nurserymen's catalogs are undoubtedly *P. bracteatum*.

TAXONOMIC TREATMENT

TAXONOMIC HISTORY

The section *Oxytona* is one of the three sections of *Papaver* comprising perennial species, and it is limited in its distribution to the higher altitudes of central and eastern Turkey, north and northwestern Iran, and the Caucasus and trans-Caucasus regions of the U.S.S.R. A total of six species had been assigned the section (Table 4) up to 1909. With the exception of Fedde's (1909) monograph on the family, the section has only once been treated over its entire range (Medwedev, 1918). There are however several regional treatments most of which include all species, and a comparison of these with Fedde's and Medwedev's systems is revealing.

Fedde himself recognized four species and three varieties (Table 4). Two of the latter, *P. orientale* var. *proliferum* and *P. bracteatum* var. *monopetalum*, were monstrosities and can thus be ignored, leaving five taxa: *P. orientale*, *P. bracteatum* and its variety *pseudo-orientale*, *P. lasiothrix*, and *P. paucifoliatum*. Subsequently regional treatments have varied considerably even when the same taxa as recognized by Fedde occur within the given region. Considering only the more recent treatments (Table 5): Popov (1937) in *Flora of the U.S.S.R.* recognized five species, all of the taxa of Fedde excluding the monstrosities, with *P. bracteatum* var. *pseudo-orientale* recognized as a species under the name

TABLE 4. Summary of the taxonomic history of *Papaver* section *Oxytona* showing taxa described prior to 1909 and Fedde's treatment in his monograph of Papaveraceae. Illegitimate names are in quotes.

Species	Author	Collection Data
P. orientale	Linnaeus, 1753	Orient, *Tournefort*
P. bracteatum	Lindley, 1821	Caucasus, *Fischer*
"*P. intermedium*"	De Candolle, 1836	cult. Geneva
P. orientale var. *paucifoliatum*	Trautvetter, 1876	Armenia, *Radde*
P. pollakii	Kerner, 1888	Iran, *Pollak*
"*P. orientale* var. *parviflorum*"	Busch, 1904	Caucasus, *Brotherus* & *Aucher-Eloy*

Monographic Treatment by Fedde (1909)

Section *Oxytona* (as *Macrantha*)
1. *P. orientale* L.
2. *P. bracteatum* Lindl. var. *bracteatum*
   var. *pseudo-orientale* Fedde
3. *P. lasiothrix* Fedde
4. *P. paucifoliatum* (Trautv.) Fedde

P. intermedium DC., a name unfortunately illegitimate as it is a later homonym. Grossheim (1950), dealing with the same geographic region as Popov, recognized five taxa: three species, *P. bracteatum*, *P. paucifoliatum*, and *P. orientale*, with *P. intermedium* and *P. lasiothrix* now varieties of *P. orientale*.

Cullen (1965) in *Flora of Turkey* also recognizes five taxa, the same four species as Fedde; Cullen however divided *P. orientale* into two varieties, recognizing var. *parviflorum* Busch (1905), while disregarding *P. pseudo-orientale* (*P. intermedium*) and placing plants matching this species (as circumscribed

TABLE 5. Comparison of selected taxonomic treatments of section *Oxytona*, 1918–1966.

1. Medwedev, 1918, On . . . *Papaver pseudo-orientale*
   1. *P. orientale*
   2. *P. pseudo-orientale*
   3. *P. bracteatum*
2. Popov, 1937, *Flora of the U.S.S.R.*
   1. *P. bracteatum*
   2. *P. lasiothrix*
   3. *P. intermedium* (including *P. pseudo-orientale*)
   4. *P. orientale*
   5. *P. paucifoliatum*
3. Grossheim, 1950, *Flora Caucasus*
   1. *P. bracteatum*
   2. *P. orientale* var. *orientale*
      var. *intermedium* (*P. pseudo-orientale*)
      var. *lasiothrix*
   3. *P. paucifoliatum*
4. Cullen, 1965, *Flora of Turkey*, and 1966, *Flora Iranica*.
   1. *P. orientale*
      var. *orientale*
      var. *parviflorum* (only Turkey)
   2. *P. bracteatum*
   3. *P. lasiothrix*
   4. *P. paucifoliatum* (only Turkey)

here) partly in *P. bracteatum* and partly in *P. orientale*. Cullen's treatment in *Flora Iranica* (1966) is similar, although neither *P. paucifoliatum* nor *P. orientale* var. *parviflorum* are listed as being recorded from Iran.

The first point of contention in the above is in the treatment of *Papaver pseudo-orientale* (*P. intermedium* DC.). Apart from confusion over the correct name at specific level, this entity has been regarded either as a species, a variety (of *P. orientale* or *P. bracteatum*), or has been included in *P. bracteatum*. A second issue centers around the correct treatment of taxa closely allied to *P. orientale*, namely *P. paucifoliatum*, which is either recognized as a distinct species, ranked as a variety or entirely ignored, and *P. orientale* var. *parviflorum*, which is sometimes recognized but usually treated as synonymous with *P. paucifoliatum*, as it should be, being a nomenclatural synonym. Here, *P. paucifoliatum* is regarded as conspecific with *P. orientale* and is discussed under that species in the taxonomic treatment. Although *Papaver lasiothrix* has never presented a problem, field observations have led to a new understanding of this species, a taxon recognized by most authors, but which is now reduced to synonymy in *P. bracteatum*. The first of these three issues is dealt with below, while the others are discussed under the appropriate species.

Field observations have suggested an answer to the important question of species limits in the section and led to the recognition of only three distinct species in section *Oxytona*. The misunderstanding over *Papaver pseudo-orientale* (*P. intermedium* DC.) is solved by field observations on the variability of this taxon, and the reasons for the confusion surrounding it have become quite clear. It is robust, tall, deep orange ("scarlet") flowered, and some individuals bear up to four small bracts. Thus authors giving overdue weight to the bract as a taxonomic character have tended to regard it as a variety of *P. bracteatum* or to include it in this species. *Papaver bracteatum* is however generally even more robust, has larger bracts and has crimson-red flowers with quite different markings. Even when plants are dry, the pigments remain distinct and the differences become even more pronounced; only non-flowering specimens can cause any confusion. Other workers have seen a greater relationship of *Papaver pseudo-orientale* with *P. orientale*, for these two species are similarly colored and both can have self-colored flowers. The small size of the bracts in *P. pseudo-orientale* leads these to be overlooked at times, or these tiny bracts are credited as characters of *P. orientale*.

The whole question of the validity of *Papaver pseudo-orientale* was discussed at length by Medwedev (1918), and this paper agrees entirely with his conclusions. The previous paragraph is in fact almost a summary of Medwedev's findings.

Morphology and Critical Taxonomic Characters

The three species of section *Oxytona* are relatively similar in morphology and cannot be confused with other species of *Papaver*. All species are perennial, producing each year a rosette of long, pinnately dissected, deeply incised leaves. The basal leaves have a long petiole, and the whole leaf is covered in multicellular, white bristles. There is some variation in the leaves in the group,

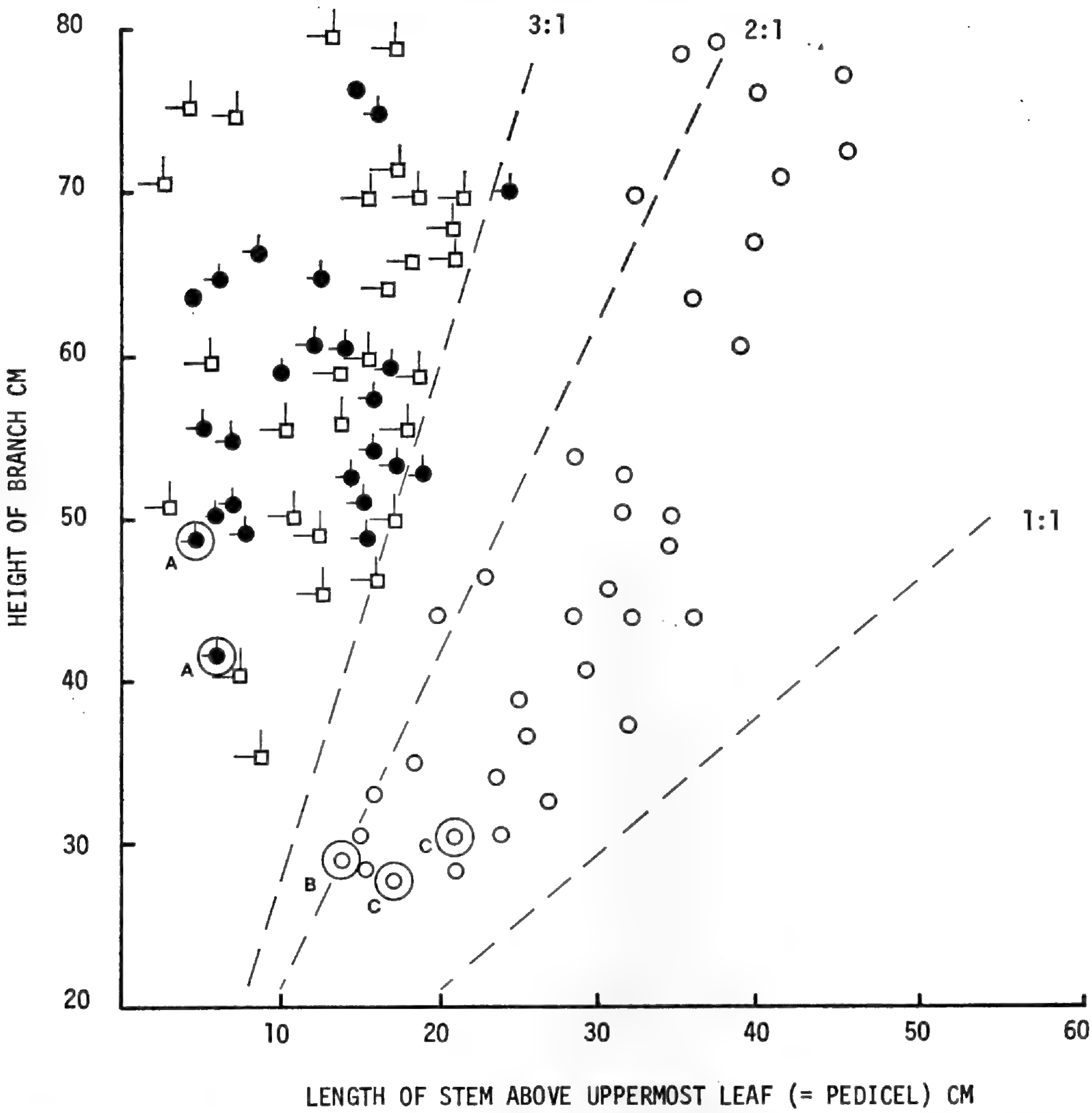

FIGURE 5. Comparison of height of flowering stem to length of pedicel, *i.e.* distance above last cauline leaf, in *Papaver* section *Oxytona*. *Papaver bracteatum* and *P. pseudo-orientale* fall in one group with the uppermost leaf inserted on the upper third of the stem; in *P. orientale* the uppermost leaf is inserted at about the midline or below this. Dotted lines represent ratio of stem to pedicel. See Figure 6 for explanation of symbols.

those of *P. orientale* often being recognizably different in being less dissected and somewhat narrower, but this distinction is not consistent.

The flowering stems or branches are produced annually, and these emerge not long after the leaves. They only begin to elongate when the leaves are fully developed. Each stalk is simple to the base (very rarely do branched individuals occur) and is heavily covered with white bristles, which are outspread below and most often appressed above. The stalk bears a solitary flower and several cauline leaves, the upper ones having shorter petioles or becoming sessile. The position of the insertion of the leaves is an important taxonomic feature (Fig. 5): *Papaver bracteatum* and *P. pseudo-orientale* have the upper-

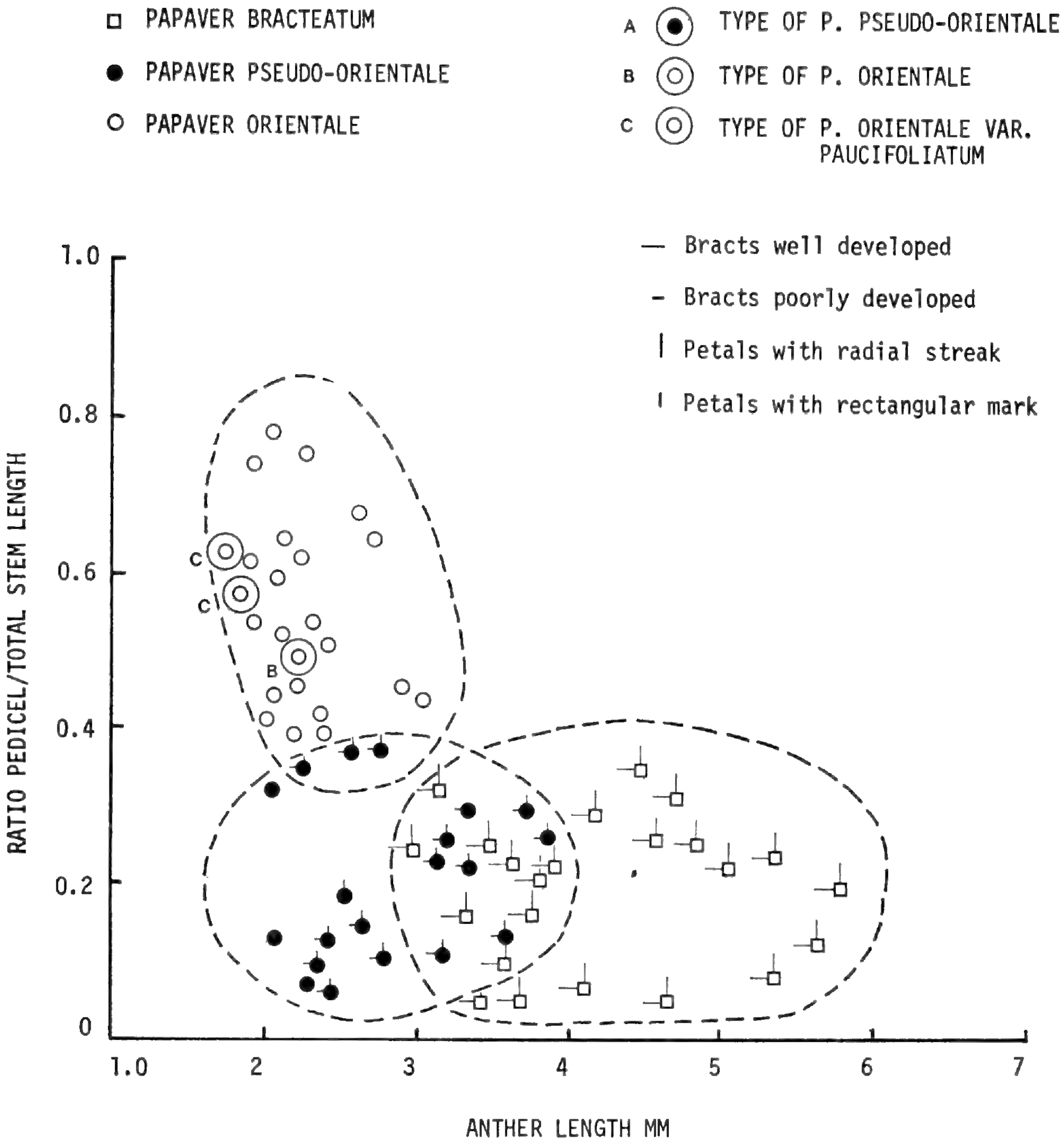

FIGURE 6. Comparison of ratio of pedicel:branch height to anther length. The intermediate position of *Papaver pseudo-orientale* is evident and can be demonstrated using several other characters such as ovary size, number of stigmatic rays, leaf length etc.

most leaf on the upper third of the stalk, sometimes just under the flower, while in *P. orientale* the uppermost leaf or leaves, as three are often grouped close together, is around the midline. This character is useful taxonomically as it provides a good means of distinguishing *P. pseudo-orientale* from *P. orientale* if floral features are inadaquate.

Bracts are found in two species, always in *Papaver bracteatum* and in some individuals of *P. pseudo-orientale*. These structures are located immediately outside the calyx and are appressed to it in the bud. They are however not shed when the flower opens. In *P. bracteatum* there are 3–8, but usually 5–7, bracts ranging in size and shape from the large incised outermost ones (up to 10 cm and leaf-like) to small inner entire ones (1.5 cm long and calyx-like).

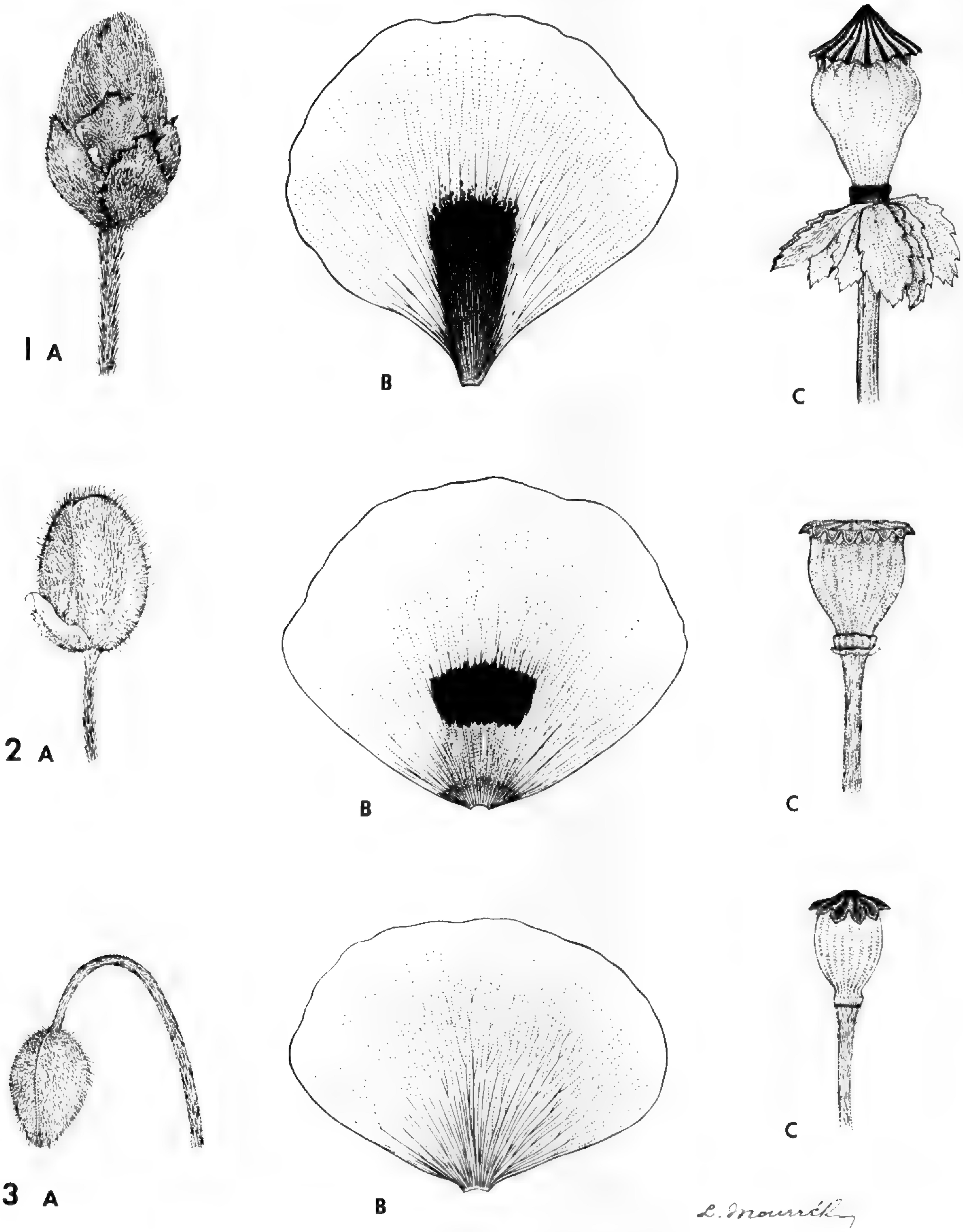

FIGURE 7. Critical taxonomic characters of: 1. *Papaver bracteatum*; 2. *P. pseudo-orientale*; 3. *P. orientale* (A. Bud; B. Petal; C. Mature capsule).

The margins of the inner bracts are membranous but are seldom entire for any length, being irregularly incised.

The flower buds are often characteristic, in the nature of the calyx bristles and in development. Buds of *Papaver bracteatum* are erect throughout their growth, and are distinct not only because of the large bracts over the lower half of the calyx but also because of the rather broad-based, appressed hairs on the calyx valves. When near maturity, buds of *P. bracteatum* often become markedly oblong in contrast to the round to oval buds in the other bracteate species, *P. pseudo-orientale*. The buds of *P. pseudo-orientale* are also erect, but can always be recognized by the slender spreading calyx hairs. In *P. orientale* the buds are pendulous during their development, and the stem only straightens just before the flower opens. The buds of this species are oval, often tapering towards the distal end, a distinctive feature.

The flowers, if normally developed, have two or three calyx valves and correspondingly, four or six petals. The lower numbers are characteristic of *Papaver orientale* and the higher of *P. bracteatum*. This feature is however very variable and appears to depend on external conditions to a large extent. The stamens are numerous and inserted in a spiral. Though variable in size, the anthers do give an indication of species, *P. bracteatum* having by far the largest and *P. orientale* the smallest (Fig. 6). Anther color varies little, being various shades of purple. The pollen, however, may be dark or pale purple or yellow. All three shades were observed in *P. orientale* though yellow may be the most common. The other species have a uniformly dark-colored pollen.

The petals have already been mentioned as providing the easiest guide to identification. Though size is rather uniform (the smallest petals are encountered in *Papaver orientale*) the color and markings are most distinctive (Figs. 1 & 7). In *P. bracteatum* the flowers are deep blood red with square or more usually long blackish stripes from the base to midline. The petals of *P. pseudo-orientale* are often described as scarlet, but the author perfers deep orange or vermillion, and are often marked with a dark rectangular blotch (less often square) well above the base. In some cases petals of *P. pseudo-orientale* lack markings, and then other features must be examined to determine identity. *Papaver orientale* usually has self-colored orange petals, but individuals with white or pale bluish marks can be met with, more often in the northern Turkey populations.

The gynoecium of section *Oxytona* is quite typical of *Papaver* with a large ovary capped by a flat disc on which are several radiating stigmatic rays. Like anther size, the oval shaped ovary and also the number of rays is variable but does indicate species to some extent. *Papaver bracteatum* has the largest ovary and most rays, *P. pseudo-orientale* is intermediate, and *P. orientale* lowest on the scale. As the capsule develops, the size differences remain, and shape, particularly in *P. bracteatum*, becomes distorted, with the disc often becoming conical or concave. The capsules become hard and woody as they ripen and seeds are released through pores which develop under the stigmatic rays.

DESCRIPTION OF SECTION *OXYTONA* BERNH.

Papaver section **Oxytona** Bernh., Linnaea 8: 843. 1833.

Papaver sect. *Macrantha* Elkan, Tent. Monog. Papaver. 13. 1839.
Calomecon Spach, Hist. Nat. 7:9. 1839.

Plants perennial, herbaceous, with a persistent tap root. *Leaves* many, arranged in a basal rosette, basal leaves petiolate, pinnatifid to pinnatisect, segments irregularly dentate and acuminate; covered with large white multicellular bristles. *Stems* arising from ground level, solitary (in young individuals) to many, unbranched (except in rare cases), erect rigid, densely covered with white bristles spreading below and usually appressed above, rarely spreading to apex. *Cauline leaves* similar to basal, becoming smaller above, uppermost often sessile. *Flowers* solitary, at apex of stem; bracteate or ebracteate. *Calyx* caducous, 2- or 3-valved, herbaceous, bearing bristles or hairs on outer surface. *Petals* 4 or 6 in 2 whorls, outer petals larger; transversely obovate, orange to deep red. *Stamens* many, *filaments* linear spathulate, constricted at apex; *anthers* narrowly rectangular to linear, yellow to dark purple. *Pollen* spheroidal, tricolpate (rarely tetracolpate); exine reticular. *Ovary* obovate, topped by a flat to conical stigmatic disc; stigma rays 10–25, softly pubescent. *Capsule* ovoid, woody, dehiscing though pores below stigma rays; seeds many, small, reniform. *Basic chromosome number* $x = 7$.

KEY TO SPECIES

1 Flowers bracteate.
  2 Flowers dark red; bracts 3–8; calyx bristles broadly triangular at base, appressed .... 1. *P. bracteatum*
  2′ Flowers orange (orange red; "scarlet"); bracts 1–4; calyx bristles slender throughout, subpatent .... 3. *P. pseudo-orientale*
1′ Flowers ebracteate.
  3 Cauline leaves not extending to upper third of stem; buds drooping; petals usually unmarked or with pale violet to white marks .... 2. *P. orientale*
  3′ Cauline leaves extending to upper third of stem; buds erect, occasionally drooping; petals usually with broadly rectangular black marks, occasionally unmarked .... 3. *P. pseudo-orientale*

1. **Papaver bracteatum** Lindl., Coll. Bot. *t.*23. 1821. TYPE: grown at Chelsea Physic Garden, London, from seed from the Caucasus region, Herb. Lindley s.n. (K, lectotype).

P. orientale var. *bracteatum* (Lindl.) Ledebour, Fl. Ross. 1: 91. 1842; Trautvetter, Act. Hort. Petr. 11: 495. 1873.
Calomecon bracteatum (Lindl.) Spach, Hist. Nat. Veg. Phan. 7: 9. 1839.
P. lasiothrix Fedde *in* Engl., Pflanzenr. 4: 366. 1909. TYPE: Lur Valley, Bornmüller *6094* (lectotype, not seen).
P. pulcherrimum Fisch. *ex* Steud., Nom., ed. 2. 1: 266. 1840, nom. nud.

Plants large (largest in section *Oxytona*), to 1 m high, with up to 15 flowering stems. *Leaves* to 45 cm long, pinnatisect, cut almost to midrib to compound, margins irregularly dentate to bidentate. *Stems* heavily setose, bristles spreading below, usually appressed above. *Cauline leaves* several (5–7), uppermost inserted on upper third of stem. *Floral bracts* 3–8, 1.5–3 cm long, irregularly dentate to entire with membranous comb-like margin (ranging from leaf-like to calyx-like). *Bud* erect during development, oval, often becoming oblong before open. *Calyx* usually 3-valved, bristles comparatively thick, appressed, to 5 mm long with broad triangular base. *Petals* 6, rarely 4, to 8 cm long, dark red with dark marking usually longer than wide, and running to base. *Filaments* to 1.5 cm long; *anthers* linear, (2.8–)3–5.5 mm long, dark purple. *Pollen* 24–27μ diameter. *Ovary* ovoid 1.2–2 cm high; disc flat, concave or conical, rays 12–24. *Capsule* up to 3 cm wide and to 4 cm high. *Somatic chromosome number* $2n = 14$. (Fig. 7: 1.)

DISTRIBUTION: north Iran in Alborz Mountains and Iranian Kurdistan and northern slopes of Caucasus Mountains U.S.S.R. (Fig. 9).

HABITAT: exposed semi-arid slopes (1,500–)1,700–2,500 m., occasionally in more sheltered gullies or near temporary streams or irrigation ditches; often in very dense stands and the dominant species amongst cushion-like *Astragalus*, *Thymus*, various thistles, and *Ferula* sp.

Papaver bracteatum is a very distinct representative of section *Oxytona* and, unlike the other two species recognized in Iran, is remarkably unvaried in its important taxonomic features. It can readily be recognized by its large floral bracts which range from 3–8 in number and by its large dark red flowers and robust habit, though size does tend to vary in different localities and especially from season to season. The only possible species which could be confused with *P. bracteatum* is *P. pseudo-orientale*, if bracts alone are used for identification. Individuals of the latter may occasionally be more heavily bracteate than usual. However, flower color and markings are always reliable as the flower color of the two species is quite different, even in the most atypical individuals.

Although diploid, *Papaver bracteatum* is the most robust species of the section and this is evident in almost all macroscopic characters (Figs. 5 & 6) so that ovary size, number of stigmatic rays, petal and anther length, leaf size, and stem thickness can all be used to aid determination. However, most of these characters are too variable and do overlap with those of *P. pseudo-orientale* as does the latter with *P. orientale*. The general phenotypic plasticity known in *Papaver* thus precludes the use of any of these features alone for determination purposes.

As mentioned in the discussion of taxonomic history, most authors have recognized *Papaver bracteatum* as distinct even though some have included bracteate forms of *P. pseudo-orientale* in *P. bracteatum*. Cytological differences, characteristic alkaloid patterns, and field observations of morphology and ecology will not support any treatment other than the restricted interpretation of *P. bracteatum* followed here.

THE IDENTITY OF *PAPAVER LASIOTHRIX*

The author is at odds with all treatments of section *Oxytona* concerning *Papaver lasiothrix*. The original reason for suspicion of the validity of this species was the observation in the Alborz Mountains of Iran that among several large populations of *P. bracteatum* in the area were plants which according to all treatment should be called *P. lasiothrix*. The only point of difference between these was that the bristles on the upper peduncle are outspread instead of appressed as in the majority of plants in the area (Fig. 8). In every other respect plants were identical. It would clearly be incorrect to recognize the individuals with outspread hairs as a different species, thus doubt arose as to the validity of *P. lasiothrix*. Subsequent observations in several areas revealed a few individuals of *P. pseudo-orientale* and even one individual of *P. orientale* with this character.

An examination of the specimens cited in the description of *Papaver lasiothrix* changed the suspicion to certainty. Four collections are cited, and with the exception of the peduncular bristles two match *P. pseudo-orientale*, one matches

FIGURE 8. Buds of *Papaver bracteatum* with outspread "lasiothrix" type bristles.

P. bracteatum, and one is probably *P. orientale*. One collection in particular illustrates the situation—*Sintenis 5989* from the Gümüşane region of Turkey. The collection was widely distributed with specimens at many European herbaria, and some plants of the collection have spreading, others appressed bristles. Material at Paris comprises two plants, and only one has outspread hairs. There is no reason to believe that *Sintenis 5989* is a mixed collection of two species, and the observation in the Alborz Mountains of the variability of the disposition of bristles in *P. bracteatum* shows that it is quite possible for the bristles of one species in a small area to vary in their disposition. In fact Faberge (1942) in genetic studies on *Papaver* section *Scapiflora* has shown that in this section spreading or appressed peduncular bristles are inherited in a simple Mendelian manner. This may also be the case in section *Oxytona*. Population counts on *P. bracteatum* in the Alborz showed a ratio of 53 plants with outspread to 130 with appressed bristles—fairly close to a simple 3:1 ratio.

Papaver lasiothrix is treated here as a synonym of *P. bracteatum* as the description relates best to the specimen cited from the Alborz Mountains, *Bornmüller 6094*. Bract size (though not number) and petal color and marking make it almost impossible to choose any other of the syntypes as a lectotype.

IRAN

GILAN: Shuran, dry slopes ca. 2,000 m, *Goldblatt 742, 744, 746* (NA).

KORDESTAN: near Baneh, *Goldblatt 1096–1121* (NA); between Baneh and Saqqez, *Goldblatt 879–888*(NA); 44 km from Marivan on road to Saqqez, *Goldblatt 860–872* (NA); Kanemat, between Marivan and Saqqez, *Goldblatt 791–794* (NA); 89–90 km from Sanandaj on

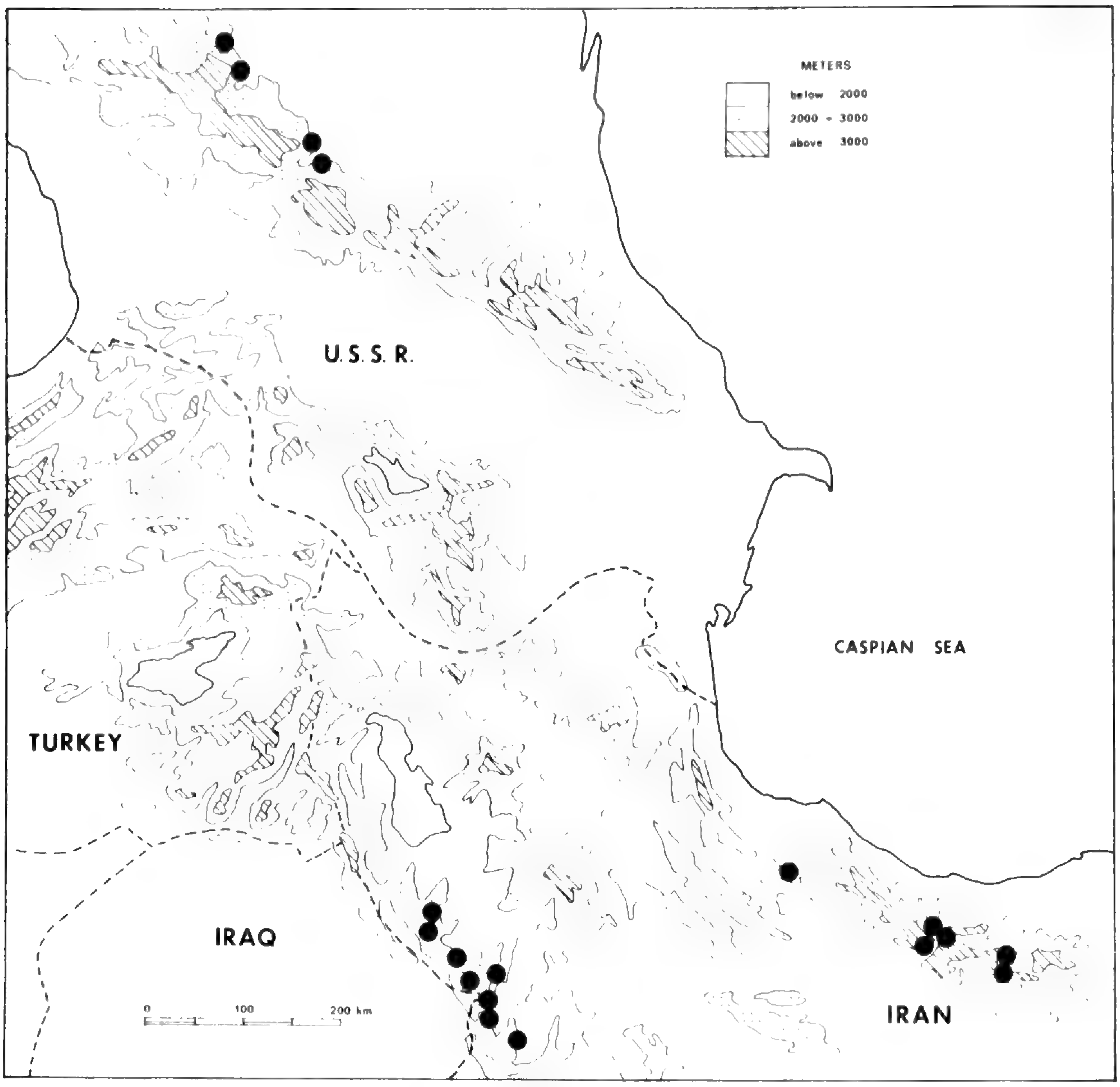

Figure 9. Distribution range of *Papaver bracteatum*.

road to Marivan, *Goldblatt 851–857, 1064–1084* (NA); *Lamond 4552* (E); *Wright & Brent 520–502* (K); 50 km from Sardasht on road to Mahabad, *Goldblatt 902–920* (NA); 30 km S. Mahabad, *Goldblatt 921–926* (NA).

Tehran: Allamul, Chalus road, *Archibald 2410* (K); Chalus Pass, north slope, *Andersen & Petersen 242* (E), *Furse & Synge 402* (K), *Goldblatt 703, 704, 814, 815* (NA), *Rechinger 843* (LD, S, K, US), *Trott 859* (CAM, K); Chalus road, Pol-e-Zanguleh, *Rechinger & Rechinger 6334a* (E, US); Gach Sar, north slopes, *Furse 2717* (K); Lar Valley, *Trott 87* (CAM, K); Mt. Damavand, *Hewer 1494* (E, K), *Goldblatt 797–813* (NA), *Hohenacker 340* (BM, G), *Kotschy 340* (BM, G, MO, P), *Schmid 6146* (E); Mt. Damavand, 6 km SW Rineh, *Goldblatt 724–726* (NA), *Grant 16553* (MO).

U.S.S.R.

Russia: foothills Beschtau, Ciscaucasus, *Hohenacker s.n.* (BM, CAM, K, M, MO, MPU); Patigorsk, *Richter s.n.* (BM); Beschtau mountains, *Karelini s.n.* (S).

Without Precise Locality.

Caucasus, *Schapp s.n.* (LD), *Count Puschkin* (BM).

2. **Papaver orientale** L., Sp. Pl. 508. 1753. TYPE: cult. Uppsala, Herb. Linn 669/10 (LINN, lectotype).

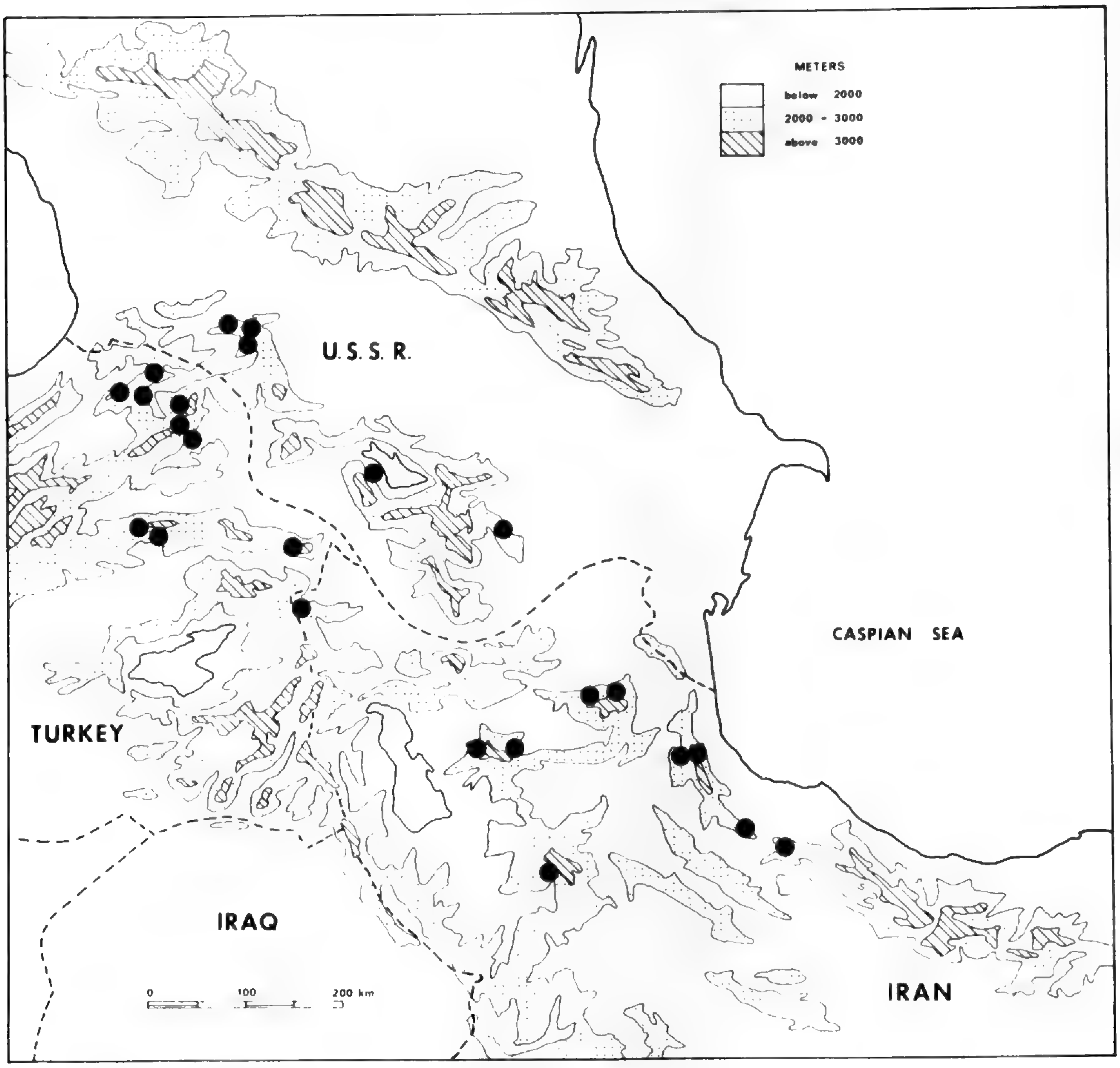

FIGURE 10. Distribution range of *Papaver orientale*.

Calomecon orientale (L.) Spach., Hist. Nat. Veg. 7: 9. 1839.
P. grandiflorum Moench, Meth. 247. 1794, nom. illeg., superfl. pro *P. orientale* L.
P. spectabile Salisb., Prod. 377. 1796, nom. illeg., superfl. pro *P. orientale* L.
P. orientale var. *paucifoliatum* Trautv., Act. Hort. Petr. 4: 345. 1876. TYPE: Lake Tabischuri, Georgia S.S.R., Radde 73 (L, lectotype).
P. paucifoliatum (Trautv.) Fedde *in* Engl., Pflanzenr. 4: 366. 1909.
P. orientale var. *parviflorum* Busch *in* Fl. Cauc. Crit. 3: 42–43. 1904, nom. illeg., superfl. pro *P. orientale* var. *paucifoliatum* Trautv.

Plants medium, comparatively slender, 30–70 cm (occasionally to 1 m) high, bearing 1–4 flowering stems. *Leaves* to 35 cm long, serrate to occasionally pinnatisect, usually not deeply cut, margins dentate. *Stems* setose, bristles spreading below, appressed above. *Cauline leaves* 2–3, rarely inserted above middle of stem. *Floral bracts* absent. *Bud* pendulous during development. *Calyx* usually 2-valved, bristles slender, subpatent. *Petals* usually 4, rarely 6, pale orange, occasionally with pale blue or white rectangular marking above the base. *Filaments* to 1 cm long; *anthers* oblong, 1.8–3 mm long, yellow or pale violet. *Pollen* 26–28.2μ diameter. *Ovary* 0.8–1.5 cm long, ovoid with slightly convex disc; stigmatic rays 8–15. *Capsule* to 2 cm long, disc flat at maturity. *Somatic chromosome number* $2n = 28$. (Fig. 7: 3.)

DISTRIBUTION: northwestern Iran, northeastern Turkey and transcaucasian U.S.S.R. (Fig. 10).

HABITAT: comparatively moist alpine slopes above 2,000 m on open mountain slopes occasionally somewhat lower in sheltered gullies or at base of rocks; a component of a sub-alpine–alpine herbaceous flora comprising several Gramineae, *Delphinium, Paeonia, Galium, Campanula* etc.

Papaver orientale is the only species in section *Oxytona* which can be regarded as truly alpine. Though it can be found at its lowermost limits growing together with *P. pseudo-orientale* in moist, sheltered areas, it is more common on open, well watered slopes at altitudes above 2,000 m. It can be found in bloom in late June at low elevations, but at high altitudes on open slopes flowering continues until August. It is the smallest species in the section, though *P. monanthum*, which occurs in Turkey and Transcaucasia and which should perhaps be placed in the section, is yet smaller.

The typification of *Papaver orientale* has presented a problem. This is due to the appearance of the type material—a plant grown at Uppsala by Linnaeus, and now in the Linnaean Collection in London. The specimen is incomplete as the base is missing, thus the point of insertion of the uppermost cauline leaf with respect to the base cannot be exactly calculated—it is somewhere between midline and upper third of the stem. This makes determination on the usual characters impossible. What can be determined is that bracts are lacking, and circumstantially from Linnaeus' omission of this from the description and the present appearance of the flowers, that they were unmarked. The anthers range from 2–2.3 mm long, and the plant is generally slender, with leaves only lightly covered with bristles and not strongly incised. All these characters may be found in extreme forms of what is treated here as *P. pseudo-orientale* but seldom all together, while the whole appearance and combination of characters are typical of *P. orientale* as circumscribed here.

This view is supported by a comparison of plants then in cultivation in Europe (see note on horticultural history). The illustration published by Commelin (1706) is probably *Papaver orientale* and is certainly of an unmarked bractless plant, while herbarium material grown during Linnaeus' time at the Chelsea Garden and now in the Banks Herbarium is undoubtedly the tall slender *P. orientale*. The typification is thus not entirely satisfactory, but the weight of evidence does favor the interpretation followed in this treatment. A glance at the two histograms illustrated here (Figs. 5–6) shows graphically the position of *P. orientale* and indicates that without new evidence, typification as suggested here should be followed.

Papaver orientale is at times difficult to distinguish from *P. pseudo-orientale* with which it may share a habitat. This is due to the variability of both species, and the extreme forms of both tend to resemble one another. Typically *P. orientale* has drooping buds; a pale orange flower, without marking or with very pale marks above the base of the petals; no floral bracts; small, yellow to pale purple anthers; no cauline leaves on the upper half of the stem. Extreme forms may however have dark blue marked petals, darker purple anthers and a cauline leaf higher up the stem. This approaches less typical examples of *P. pseudo-orientale*, a species which may lack petal marking, often lacks floral bracts, and thus such individuals become difficult to distinguish.

The situation is complicated in the field by the presence of hybrids where the ranges of *Papaver orientale* and *P. pseudo-orientale* overlap. In such localities, two of which were found in Iran, *P. orientale* is always the earlier flowering species and is usually in fruit by the time *P. pseudo-orientale* blooms. Nevertheless exceptions to the temporal isolation do occur, and this would explain the occurrence of hybrids (see earlier discussion).

Papaver paucifoliatum (*P. orientale* var. *paucifoliatum*), and consequently its nomenclatural synonym *P. orientale* var. *parviflorum*, is here tentatively regarded as a synonym of *P. orientale*, even though the type of this taxon comes from Transcaucasus and living material has not been examined by the author. This decision was taken because forms closely matching those of the type collection of *P. paucifoliatum* were found among populations of *P. orientale* in Iran (Fig. 5) particularly those individuals from higher altitudes (*Goldblatt 980, 981*). *Papaver paucifoliatum* is not distinguishable from these high altitude forms of *P. orientale*, and even recognition at the varietal level would seem unnecessary. Field studies in the U.S.S.R. are needed however to confirm the present observations.

NOMENCLATURAL NOTE

Papaver orientale has frequently been confused with *P. pseudo-orientale* in the past and all literature references to *P. orientale* may refer to either or both. Three superfluous synonyms exist for *P. orientale*: *P. grandiflorum* Moench, *P. spectabile* Salisb., and *P. orientale* var. *parviflorum* Busch. Fortunately none have found their way into the literature. In none of the three cases did the authors indicate reasons for using new names; the suspicion exists that they had in mind variant forms which they wished to describe, but in the former two cases there are no descriptions nor are types cited. In the case of *P. orientale* var. *parviflorum* Busch wished to recognize a smaller-flowered, fewer-leafed form of *P. orientale*—but in citing *P. orientale* var. *paucifoliatum* Trautv., Busch invalidated his var. *parviflorum*.

IRAN

AZERBAIJAN: Khalkhal, on pass to Caspian, 2,000–2,500 m, *Goldblatt 733–736, 959–979* (NA); Kuh-e-Sahand, above Zinjanab, *Cowan & Darlington 1850* (K), *Goldblatt 778–781* (NA); Kuh-e-Sahand, near Guleh Klaneh, E of Tabriz, *Goldblatt 782–788* (NA); Qotur Su, Kuh-e-Sabilan, SE Meshkinshar, *Lamond 4653* (E); Radar road, Kuh-e-Sabilan, *Lamond 4731* (E); hills 12 km S Siah Cheshmeh, 2,300 m, *Goldblatt 1153–1155* (NA).

GILAN: Gilan mountains, *Aucher Eloy 4045* (BM, FI, G, K); Shuran, moist north slopes at 1,900 m, *Goldblatt 748, 749, 980–984* (NA).

TURKEY

AĞRI: between Eleskirt and the Tahir Pass, *Tariman VI* (Herb. Tariman); E side of Tahir Pass, 19 km from Eleskirt towards Horasan, *Davis 47162* (E, MO); Tahir Pass, *Goldblatt 1,000* (MO), *Tariman VII* (Herb. Tariman).

KARS: near Ağri Dağ, *Tariman IX* (Herb. Tariman); Ardahan-Camliçatak, *Tariman XIa* (Herb. Tariman); Ardahan district, *Holmberg 2514* (LD), *2560* (LD, S); Kars, *Goldblatt 1001* (MO); Kisir dağ, 2,300 m *Davis & Hedge 30489* (BM); SW side of Kisir dağ, *Davis & Hedge 30487* (BM, E); Yalnizçam-Dağlari, *Davis & Hedge 32509*; Ziyaret dağ, Yalnizçam Dağlari ab Yalnizçam, *Davis & Hedge 30317* (E, K).

U.S.S.R.

ARMENIA: subalpine meadows near lake Gokca (Sevan), *Schelkovnikov & Kara Murza s.n.* (US).

AZERBAIJAN: Karabagh, *Szoviks 281* (CAM, P); Swant Georg, *Hohenacker s.n.* (G, K, P).

GEORGIA: Mt. Tzchra-Tzcharo, *Kozlowsky s.n.* (TGM); Borzhom, Tzchra-Tzcharo, *Grossheim & Schischkin s.n.* (BM, K, LD, NY, UC); near Lake Tabischuri, *Radde 73* (LE), *Brotherus & Brotherus 50* (BM, B, CAM, FI, G, P, S); source of Chrami R., 1,550 m, *Doluchanov, Mandenova & Shchian s.n.* (TGM).

WITHOUT PRECISE LOCALITY.

Iran, *Kotschy s.n.* (FI); Mountains of Kurdistan *Layard s.n.* (US); Armenia, *Szoviks s.n.* (FI, S, US); Orient, *Tournefort* (BM) identification not certain.

3. **Papaver pseudo-orientale** (Fedde) Medw., Bull. Mus. Cauc. 11: 204. 1918.

P. bracteatum var. *pseudo-orientale* Fedde *in* Engl., Pflanzenr. 4: 365. 1909. TYPE[3]: "Szanschak Gumuschkhane," *Sintenis 5989* (B, lectotype; BM, E, FI, K, P, S isotypes).

P. intermedium DC., Mém. Soc. Phys. Genève 7: 301. 1836, nom. illeg., non *P. intermedium* Becker, Fl. Frankf. 1: 386. 1828. TYPE: ex hort. Geneva, De Candolle (G, lectotype).

Plants medium to large, 40–60 cm high, rarely to 80 cm, bearing to 10 flowering stems. *Leaves* to 45 cm long, deeply pinnatisect to sub-compound, margins irregularly dentate. *Stems* setose, bristles spreading below, appressed or rarely spreading above. *Cauline leaves* 5–6, uppermost inserted on topmost third of stem. *Floral bracts* absent or present, small, 1–4, margins irregularly dentate or entire. *Bud* erect during development, usually oval. *Calyx* 2- or 3-valved, bristles slender and subpatent. *Petals* 4 or 6, deep orange "scarlet," usually with heavy black rectangular markings near the base. *Filaments* to 1.3 cm long; *anthers* linear (1.7–)2.0–3.5 mm long, dark purple. *Pollen* 27.8–30.1μ diam. *Ovary* (1.2–)1.5–1.8(–2.0) cm long, ovoid with slightly convex disc; stigmatic rays 9–19. *Capsule* up to 2.5 cm long with a flat disc. *Somatic chromosome number* $2n = 42$ (Fig. 7: 2).

DISTRIBUTION: northwestern Iran, central and eastern Turkey, and southern Transcaucasus (Fig. 11).

HABITAT: usually in moist places at altitudes of 1,600–2,200 m; either amongst rocks, where seepage occurs, or along streams or ditches; the populations have a scattered distribution and the dense stands common in *Papaver orientale* and *P. bracteatum* are not found in *P. pseudo-orientale*.

Papaver pseudo-orientale has had a rather checkered taxonomic history. Since its description by Fedde as a variety of *P. bracteatum*, it has been raised to species rank by Medwedev (1918), was recognized by Popov (1937) (as *P. intermedium* DC.), and then reduced again to varietal rank this time in *P.*

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[3] *Sintenis 5989* was collected in the region of Gümüşane near Ilya Dağ not, as might be though from the words "Argyri dagh," Mt. Ararat. (Cullen, 1963).

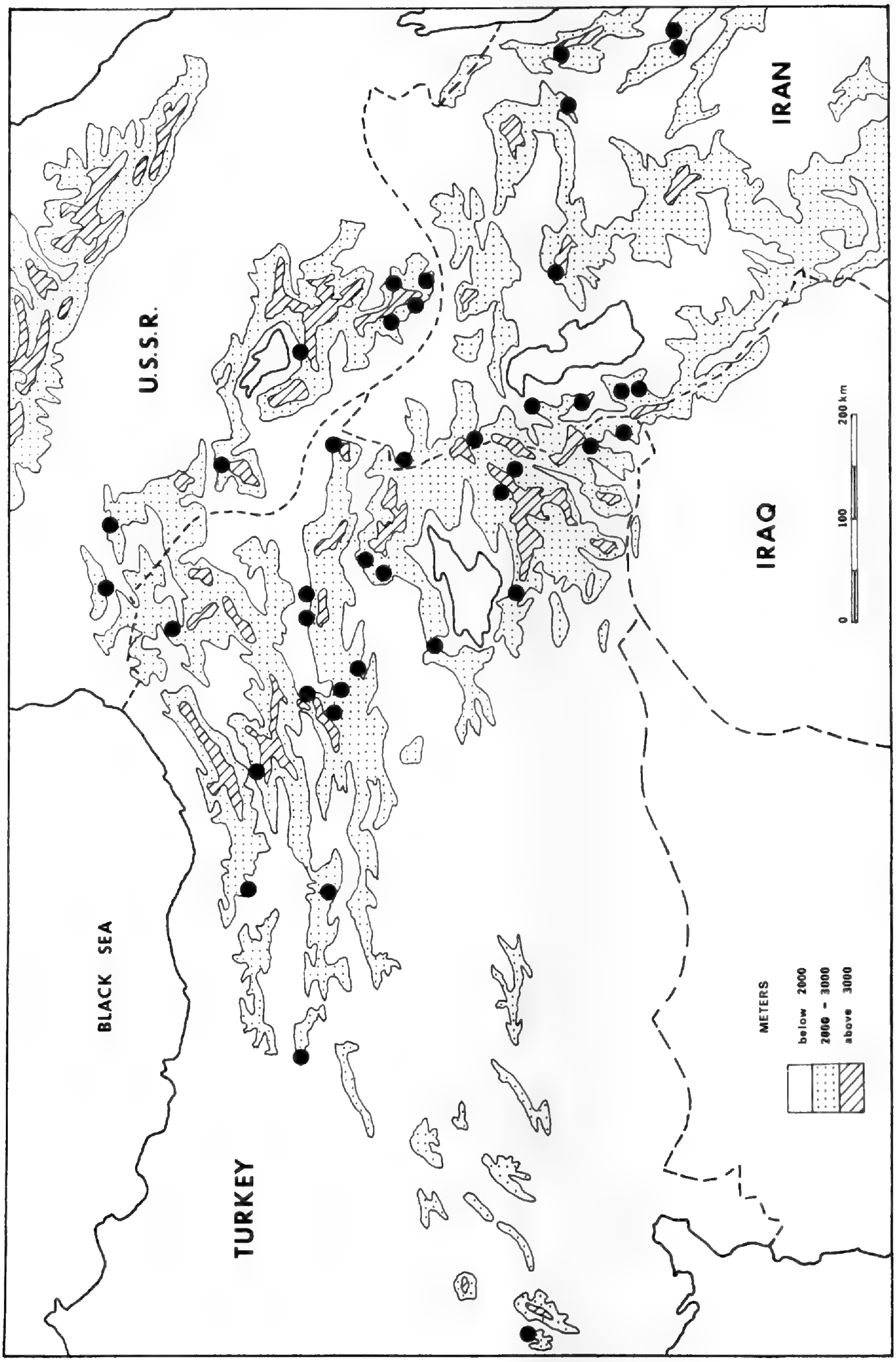

FIGURE 11. Distribution range of *Papaver pseudo-orientale*.

orientale (Grossheim, 1950). In the *Flora of Turkey* (1965) and *Flora Iranica* (1966) Cullen reduced the taxon to synonymy completely, and herbarium specimens of *P. pseudo-orientale* are cited both under *P. orientale* and *P. bracteatum.*

The reason for this lack of unanimity is clearly the variation of the important characters in the species. As already noted, a tendency to regard bracts as very significant would result in the inclusion of *P. pseudo-orientale* in *P. bracteatum,* while greater regard for color and calyx bristles might mean the inclusion of *P. pseudo-orientale* in *P. orientale.*

As shown here *Papaver pseudo-orientale* is cytologically and chemically distinct, has marked environmental preferences and, although somewhat intermediate in morphology between *P. bracteatum* and *P. orientale,* must be recognized as of equal rank with these two.

IRAN

AZERBAIJAN: Bandeshur Chai, below Sivik, *Cowan & Darlington 2349* (K); hillsides below Gilas, *Cowan & Darlington 2496* (E, K); between Mianeh and Firuzabad 1,700 m, *Goldblatt 952–955* (NA); Khalkhal pass on road to Caspian, 2,000 m, *Goldblatt 1189–1192* (NA); Mishou Dagh, *Gilliat-Smith 2537* (K); 25 km from Rezayeh towards Oshnavyeh, *Goldblatt 1025–1035* (NA); 26 km from Rezayeh towards Serow, *Lamond 4155* (E); Qotur, stream sides near station, *Goldblatt 752–758* (NA); Qushi Pass, near Paska, 1,800 m, *Goldblatt 1017–1024* (NA); between Zanjan and Manjil, Tarom Pass, 42 km from Tashvir, *Lamond & Iranshar 3633* (E); pass between Zanjan and Manjil, *Goldblatt 712–714, 716, 718* (NA); Zinjanab, *Gilliat-Smith 2537* (K).

TURKEY

AĞRI: 5 km S Hamur on road to Tutak, *Goldblatt 999* (MO); 3–5 km from Tutak to Hamur, *Davis 44039* (E, K).

ÇORUH: Artvin-Ardahan, Ardanuç, Kordevan dağ 1,450 m, *Davis & Hedge 30112* (BM).

ERZERUM: Erzerum, *Zorab 824* (K); Erzerum-Hamamderesi, *Tariman I* (Herb. Tariman); between Hinis and Basinler, 1,950 m, *Davis 46277* (K, MO); 10–15 km from Hinis, *Tariman IV* (Herb. Tariman); Ispir, *Tariman II* (Herb. Tariman); Tekman, *Tariman III* (Herb. Tariman).

ERZINCAN: Kesis dağ, above Çimin, 2,500 m, *Davis & Hedge 31811* (BM, K).

GÜMÜŞANE: "Szanschak Gümüschkhane," *Sintenis 5989* (B, BM, DS, E, FI, G, K, LD, P); Darsosdagh, *Sintenis s.n.* (LD).

HAKKARI: Sat Daği near Varegoz, *Davis 45720* (K, MO); Yüksekova-Şemdinli, 26 km, *Davis 45111* (E, K); 15–20 km from Yüksekova toward Bakjirge, *Davis 45693* (K, MO).

KARS: Iğdir-Cilli, *Tariman VIII* (Herb. Tariman); 36 km S. Ardahan, *Tariman XI* (Herb. Tariman); along Aras R. between Horasan and Sarikamiş, *Goldblatt 1002* (MO); Kinsatowal, Ardahan district, *Holmberg 2559* (LD, S).

MUŞ: Varto, *Tariman V* (Herb. Tariman).

NIĞDE: Andirmussen Dağh, *Siehe 482* (BM, E); Hasan Dağ, *Whittall 147* (K).

SIVAS: mtns. N of Sivas, 1,800 m, *Maunsell s.n.* (BM).

VAN: 30 km from Başkale towards Hoşap, *Davis 45924* (E, MO) Başkale, Ispiriz Dağ, *Davis & Polunin 23665* (BM, K); 15 km N Satak, *Davis & Polunin 22985* (BM, HUJ, K); Yedi Khilissa near Van, *Deyrolle s.n.* (GH, LD, MPU).

U.S.S.R.

ARMENIA: Mt. Agmagan, *Vessilov 9007* (WIR), *Zedelmejer & Gejdeman s.n.* (LE); Erevan-Natchichevan, *Karjagin & Safiev s.n.* (GH); Daralagher near Alagher, *Safiev s.n.* (S); near Ordubad, Sich Iurdy 1,800–2,000 m, *Schelkovnikov & Kara-Murza s.n.* (LE); near Elenovka, *Schelkovnikov & Kara-Murza s.n.* (HUJ).

GEORGIA: Achalzich, *Meffert 342* (A); Bakuriana, Tiflis Prov., *Kozlowsky s.n.* (TGM); Djavakhetia, Jetuoli, *Sosnovsky, Mandenova & Kutkateladje s.n.* (TGM).

WITHOUT PRECISE LOCALITY

Armenia, *Aucher Eloy 371* (MO, MPU, G, P), *Simon 24* (P); Kurdistan, *Brant s.n.* (CAM); "Perse," *Belanger 380* (P).

EXCLUDED SPECIES

Papaver pollakii Kerner, Wien. Gartenz. 13: 272. 1882.

This species was very superficially described by Kerner from material grown from seed from Iran and cannot be identified from the description alone. In the absence of the type which, though believed to be at the Botanical Institute of the University of Vienna, has not been seen, determination is impossible, and the species must be excluded.

LITERATURE CITED

ASAHINA, H., T. KAWATANI, M. ONO & S. FUJITA. 1957. Studies of poppies and opium. Bull. Narcot. 20: 25.

BÖHM, H. VON 1967. Über *Papaver bracteatum* Lindl. III Mitteilung: Charakteristische Veränderung des Alkaloidspektrums während der Pflanzenentwicklung. Pl. Med. 13: 215–220.

———. 1965. Über *Papaver bracteatum* Lindl. II. Mitteilung. Die Alkaloide des reifen Bastards aus der reciproken Kreuzeng dieser Art mit *Papaver somniferum* L. Pl. Med. 13: 234–240.

BULLIS, C. R. 1955. Golden green blotches in oriental poppies. Bull. Amer. Iris Soc. 137: 9–11.

BUSCH, N. 1905. Papaveraceae. *In* N. Kuznetsov (editor), "Flora Caucausica Critica." 3: 42–43. Iur'evie.

CASTIGLIA, E. 1955. Sulla poliploidia istologica nei vegetali. Caryologia 7: 420–437.

COMMELIN, C. 1706. Horti Medici Amsteladamensis Plantae Rariores et Exoticae. Leiden.

CULLEN, J. 1963. The Turkish collections of Paul Sintenis. Notes Roy. Bot. Gard. Edinburgh 25: 31–39.

———. 1965. Papaveraceae. *In* P. H. Davis (editor), "Flora of Turkey." 1: 221–223. Edinburgh.

———. 1966. Papaveraceae. *In* K. H. Rechinger (editor), "Flora Iranica." 34: 12–13. Graz.

DAWSON, R. F. & C. JAMES. 1956. Alkaloids of *Papaver orientale* L. I. Qualitative detection and occurrence. Lloydia 19: 59–64.

ERDTMAN, G. 1943. An Introduction to Pollen Analysis. Chronica Botanica. Waltham, Mass.

ERNST, W. R. 1965. Documented chromosome numbers. Madroño 18: 125.

FABERGE, A. C. 1942. Genetics of the *Scapiflora* section of *Papaver*. I. The garden Iceland poppy. Jour. Genet. 44: 169–193.

FEDDE, F. 1909. Papaveraceae. *In* A. Engler (editor), "Das Pflanzenreich," 4: 364–366. Leipzig.

FRYXELL, P. 1957. Mode of reproduction in higher plants. Bot. Rev. (Lancaster) 23: 135–233.

GOLDBLATT, P. 1972. Chromosome cytology in relation to classification in *Nerine* and *Brunsvigia* (Amaryllidaceae). Jour. S. African Bot. 38: 261–275.

GROSSHEIM, A. A. 1950. Flora Caucasica. IV: 93–94. Moscow & Leningrad.

GÜNTHER, K. F. & H. BÖHM. 1968. Kritische Bemerkungen zu *Papaver bracteatum* Lindl. Oesterr. Bot. Zeit. 115: 1–5.

HEYDENREICH, K. & S. PFEIFER. 1965. Bractavin, ein neues Papaveralkaloid. Pharmazie 20: 521.

——— & ———. 1966. Über Alkaloide der Gattung *Papaver*. II. Mitteilung: Isolierung von Orientalinon, Salutaridin und Oreophilin aus *Papaver bracteatum* Lindl. Pharmazie 21: 121–122.

KAWATANI, T. & H. ASAHINA. 1959. Characters and alkaloids of the artificial interspecific F_1 hybrid between *Papaver orientale* L. (♀) and *P. somniferum* L. Jap. Jour. Genet. 34: 353–362.

——— & T. OHNO. 1965. Chromosome numbers in *Papaver*. Kokuritsu Eisei Shikenjo. Tokyo. (Bull. Natl. Inst. Hyg. Sci. Tokyo). 83: 127–133.

KISELEV, V. V. & R. A. KONOVALOVA. 1948. Ob Alkaloidakh Dikorstushchikh Vidov Maka. Zhurnal Obshchei Khimii 18: 142–150.

KLEINSCHMIDT, G. 1961. Untersuchungen über die Alkaloid verteilung in in der Organen von *Papaver orientale* L. in Laufe der Vegetationsperiode. Archiv. Pharm. (Berlin) 294: 254–258.

KONOVALOVA, R. A., S. YUNUSSOFF & A. P. ORECHOFF. 1935. Über Alkaloide der *Papaver*-arten. I. Mitteilung. Alkaloide von *Papaver armenicum* & *Papaver orientale*. Ber. Deutsch. Chem. Ges. 68: 2158–2163.

KRISHNASWAMI, S., S. MUTHULINGAM & V. S. RAMAN. 1968. Cytomophological observations in garden populations of *Papaver*. S. Indian Hort. 16: 51–55.

LALEZARI, I., A. SHAFIEE & P. NASSERI-NOURI. 1973. Isolation of alpenigenine from *Papaver bracteatum*. Jour. Pharm. Sci. 62: 1718.

LINNAEUS, C. 1748. Hortus Uppsaliensis. 136. Stockholm.

LJUNGDAHL, H. 1922. Zur Zytologie der Gattung *Papaver*. Svensk. Bot. Tidsk. 16: 103–116.

MCNAUGHTON, I. H. & J. L. HARPER. 1964. Biological flora of the British Isles. *Papaver* L. Jour. Ecol. 52: 767–793.

MEDVEDEV, J. S. 1918. On a new poppy, *Papaver pseudo-orientale*. Isv. Kavkazsk. Mus. (Ann. Caucas. Dus.) 11: 204–207. [In Russian.]

NEMEKOVA A., V. PREININGER & F. SANTAVY. 1966. Isolierung und Identifizierung der Alkaloide aus *Papaver orientale* L., *Papaver rhoeas* L. und anderen Papaverarten. Deutsche Akad. Wiss. Kl. Chem. Geol. Biol. 3: 319–323.

NEUBAUER, D. VON & K. MOTHES. 1963. Über *Papaver bracteatum*. I Mitteilung. Ein neuer Weg zur Gewinnung von Morphinanen aug pflanzlicher Rohstoffbasis. Pl. Med. 11: 387–391.

PAYNE, W. W. 1970. Helicocytic and allelocytic stomata: Unrecognized patterns in the dicotyledonae. Amer. Jour. Bot. 57: 140–147.

PING CHUAN CHENG. 1972. Cultivation and analysis of *Papaver bracteatum* Lindley. Unpublished MS. thesis, University of Mississippi.

POPOV, M. G. 1937. Papaveraceae. *In* V. L. Komarov (editor), "Flora of the U.S.S.R." 7: 470–474. Jerusalem. [Translated, 1970.]

SANSOME, F. W. & J. PHILP. 1939. Recent Advances in Plant Genetics. Ed. 2. London.

SHARGHI, H. & I. LALEZARI. 1967. *Papaver bracteatum*, a highly rich source of thebaine. Nature 213: 1244.

SNOAD, B. 1952. Chromosome counts of species and varieties of garden plants. John Innes Hort. Inst. Appendix, 42nd Ann. Rep. 1951: 47.

STERMITZ, F. R. 1968. Alkaloid chemistry and the systematics of *Papaver* and *Argemone*. Recent Advances Phytochem. 1: 161–183.

——— & H. RAPOPORT. 1961. Biosynthesis of opium alkaloids. Alkaloid interconversions in *Papaver somniferum* & *P. orientale*. Jour. Amer. Chem. Soc. 83: 4045.

TAHARA, M. 1915. The chromosomes of *Papaver*. Bot. Mag. Tokyo 29: 254–256. [In Japanese.]

TOURNEFORT, J. P. DE. 1718. A Voyage into the Levant (transl. J. Ozell.). 2: 207–208. London.

YASUI, K. 1921. On the behavior of chromosomes in the meiotic phase of some artificially raised *Papaver* hybrids. Bot. Mag. Tokyo. 35: 154–167.

———. 1936. Cytogenetic studies in artificially raised interspecific hybrids of *Papaver* IV. Interspecific hybrids of *P. orientale* L. and *P. bracteatum* Lindl. Cytologia 7: 535–542.

———. 1937*a*. Cytogenetic studies in artificially raised interspecific hybrids of *Papaver* VI. The trigenomic hybrids of *Papaver*. Cytologia. Jubilee Vol.: 1101–1112.

———. 1937*b*. Cytogenetic studies in artificially raised hybrids of *Papaver* VII. *P. somniferum* L. × *P. bracteatum* Lindl. Cytologia 8: 331–334.

ECOLOGICAL DIFFERENTIATION IN SOME CONGENERIC SPECIES OF COSTA RICAN FLOWERING PLANTS[1]

William C. Burger[2]

Initial work for a new flora of Costa Rica disclosed a number of difficult taxonomic problems in the Piperaceae, Chloranthaceae, and Moraceae families. Herbarium studies indicated that there were very closely related taxa in a number of genera. These closely related taxa could be interpreted either as species complexes or as single variable species. Field work in Costa Rica showed that many of these closely related taxa do not grow together. They may grow in the same general geographic area, but these closely related populations are usually found in different habitats or at different altitudinal levels. These observations have been very important in making taxonomic decisions, but they may also be important in recognizing processes of population differentiation and speciation in the wet tropics.

Delimitation of taxa in the neotropics is often based on rather few herbarium collections with little biological or ecological data. Such is the case in this study where estimates of affinity are based primarily on similarity or dissimilarity in vegetative and floral characters. Palynological, cytological, or biochemical data are not presently available for these species.

The data are based on plants collected in Costa Rica and the adjacent provinces of western Panama. While this may seem to be a very small area from which to make general speculations, it is rather well sampled when compared to other wet tropical areas. Not only does the area of Costa Rica and westernmost Panama have the benefits of decades of botanical exploration, but it also represents an area of isolated highlands with considerable endemism. This area is a minor but natural phytogeographic region, though its lowland species are often widespread.

Despite the small area there is a great altitudinal range (0–3800 m) and the patterns of rainfall are very different in different parts of the region. The deciduous forest formations of the northern Pacific lowlands can have less than 20 mm of rainfall during the dry season (December through April), while on the Caribbean side of the mountains, as little as 30 km away, the rainfall averages over 50 mm in the dryest month of the year. However, the rainfall data alone can be misleading, especially at higher elevations. Turrialba on the Caribbean slope has an average annual rainfall of around 2400 mm, not much greater than some areas on the Pacific slope, such as Puriscal. The dry season on the Pacific slope, however, is much more severe and lacks the frequent cloudiness and misting of Turrialba and the Caribbean slope. These seasonal differences in cloud-cover and in rainfall affect the vegetation, and one can

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Ann. Missouri Bot. Gard. 61: 297–306. 1974.

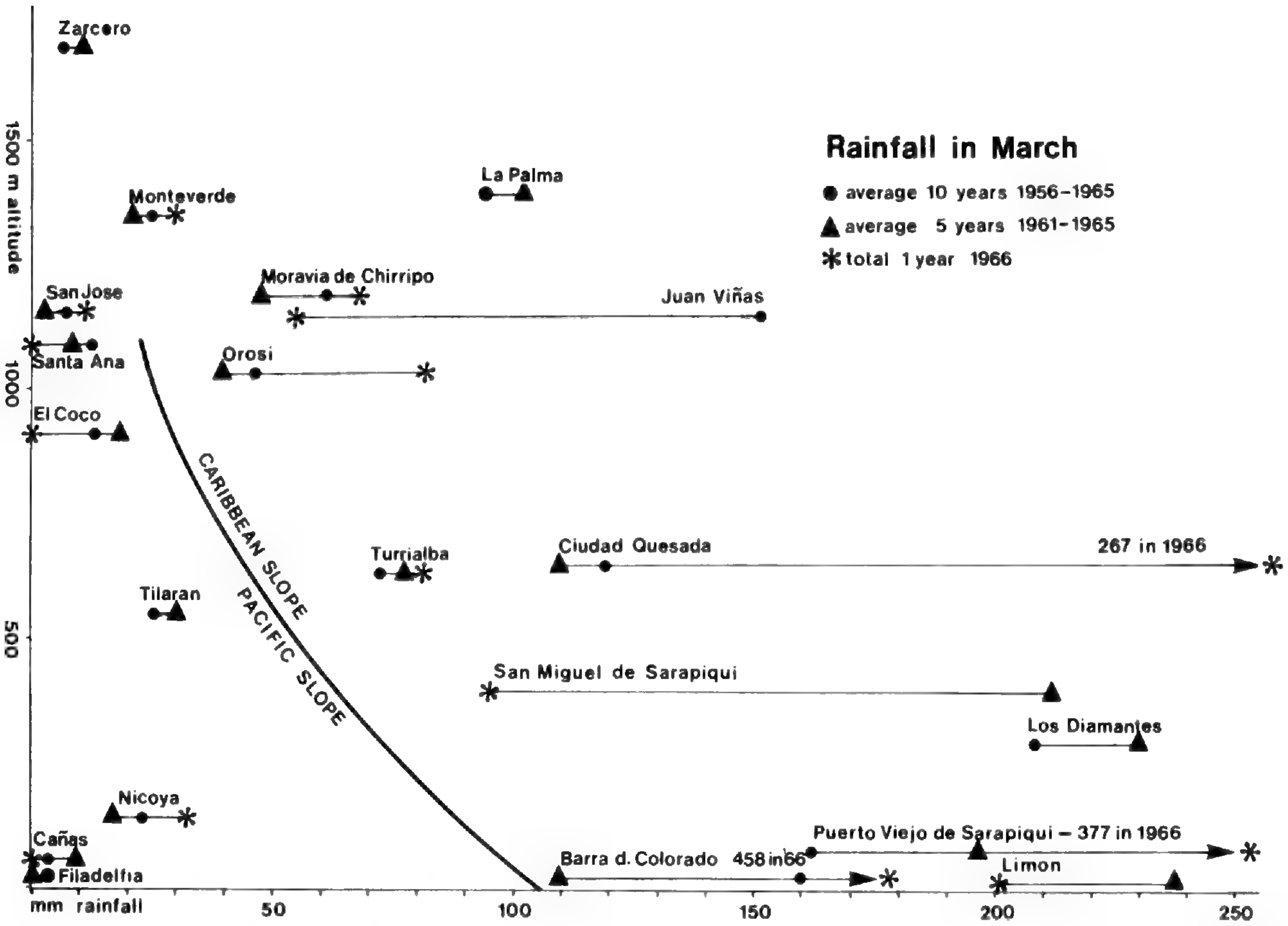

FIGURE 1. Rainfall in March at various altitudinal levels on the Caribbean and Pacific slopes of central and northern Costa Rica. The ordinate represents altitude in meters. The abscissa presents rainfall in millimeters for the month of March in the latter half of the dry season.

see striking differences over a distance of only a few kilometers in some areas. Relative humidity and evaporation data are not available. These would be more meaningful than simple rain-gauge readings.

An understanding of the topography and rainfall patterns is essential to any analysis of species distributions in Costa Rica. The life-zones depicted in the *Mapa Ecologico* (Tosi, 1969) give a good representation of the kinds of vegetation to be found in Costa Rica. However, precise use of the life-zone system is very difficult with museum specimens collected over a hundred-year period. Instead, I have used altitude and slope based on the geographical data found with the specimens to estimate the kind of environment in which the material was collected. By graphing altitude (ordinate) against rainfall in March at the height of the dry season (abscissa) it is apparent how different the Caribbean and Pacific slopes are (Fig. 1) in northern and central Costa Rica. (The Pacific slope of southern Costa Rica receives much more rainfall than the northern half and is not included in these graphs.) The plant collections are primarily from these same areas, and the resultant figures of distribution may not hold true for a few of these species which grow in other areas of Central America. The purpose of the graphs is simply to show how some closely related species are separated by altitude and slope in Costa Rica. The graphs are based on rainfall data from the *Anuario Meteorlogico 1966* (1967) of the Servicio Meteorologico Nacional of Costa Rica.

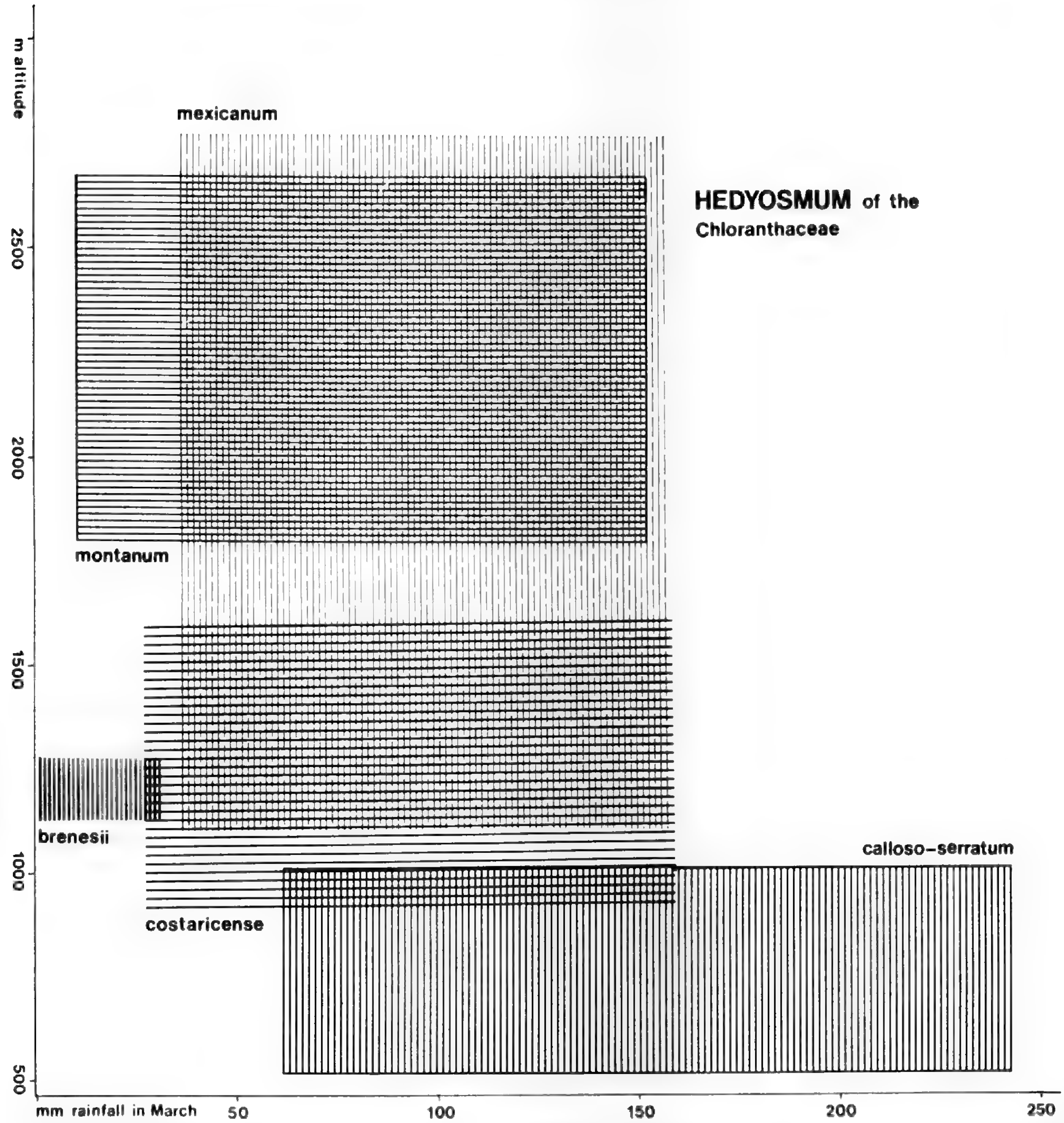

FIGURE 2. Distribution of the species of *Hedyosmum* in Costa Rica plotted against altitude in meters (ordinate) and rainfall for March in millimeters (abscissa). The boxed areas of *H. montanum* and *H. calloso-serratum* represent plants that were thought to be conspecific.

OBSERVATIONS

The genus *Hedyosmum* of the Chloranthaceae presents a series of distributions that is characteristic of many genera in Costa Rica (Fig. 2). These distributions are characterized by the fact that the very different species (from a morphological point of view) often share the same habitat, while those that appear to be very similar and were even thought to be conspecific do not grow together. *Hedyosmum mexicanum* Cordemoy, with its capitate female inflorescence, is the most easily distinguished species in Costa Rica. It ranges from 1100 to 2800 m elevation in many of the same habitats as *Hedyosmum montanum* Burger and *H. costaricense* Wood. *Hedyosmum costaricense*, with leaves having many secondary veins, is likewise easy to identify and shares

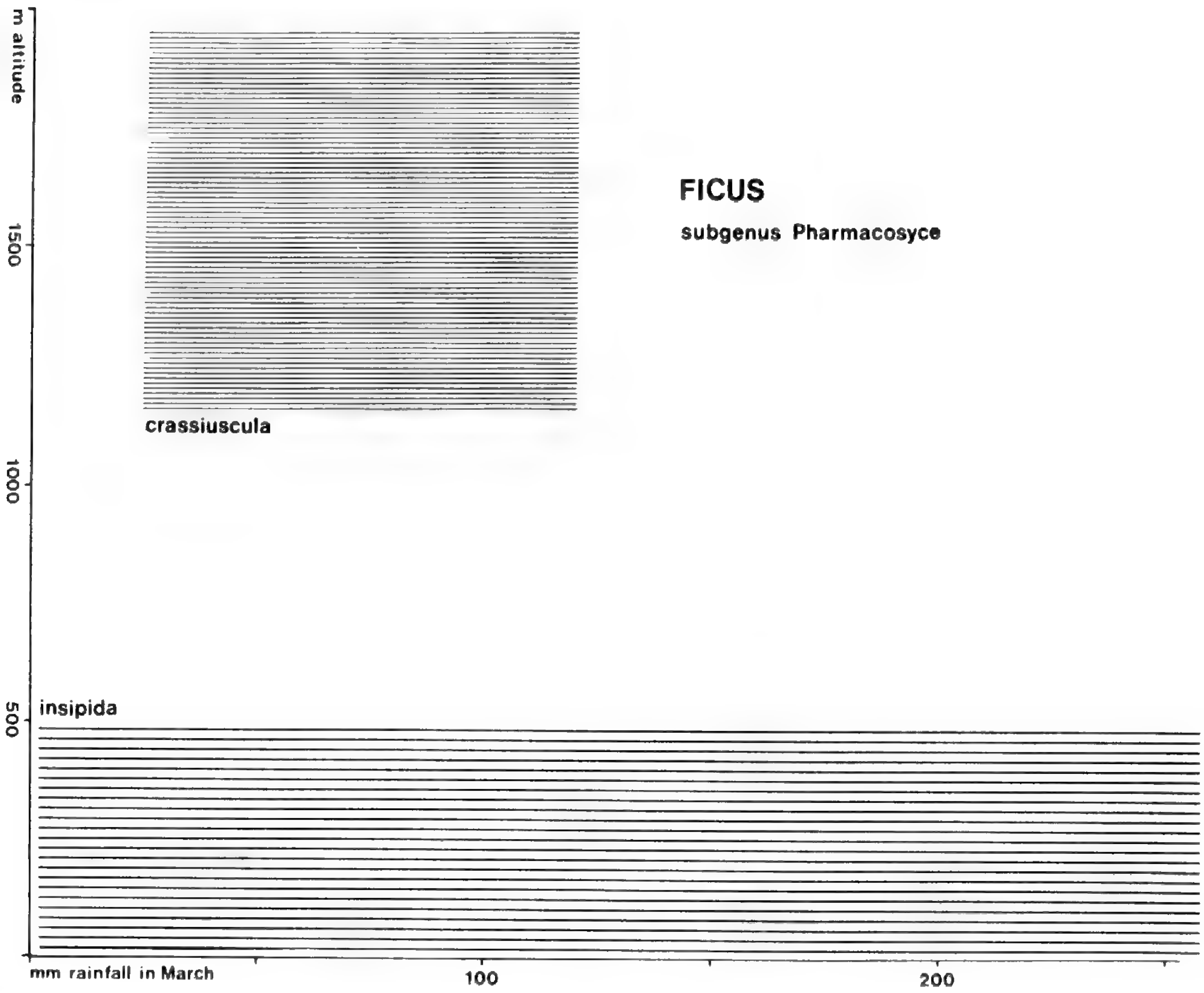

Figure 3. Distribution of *Ficus crassiuscula* and *F. insipida* in Costa Rica, plotted against altitude in meters (ordinate) and rainfall in March (abscissa).

some of its habitat with two other species of the genus in Costa Rica. *Hedyosmum brenesii* Standley is unusual in having monoecious plants and shares a small part of its range with *H. costaricense.* Material that is here referred to two species, *H. montanum* and *H. calloso-serratum* Oersted, was long referred to a single species: *H. calloso-serratum.* In Costa Rica, after over a hundred years of botanical collecting, we still lack material of either of these two closely related species in the altitudinal range of 1000 to 1800 m, though together they range from 500 to 2800 m elevation. The differences between the two taxa are subtle but consistent and correlate with their separate distributions. These two species are closely related to *H. scaberrimum* Standley of western Panama, and the relationships of these three species in that area are not clear because of the paucity of collections. It may be that the three form a complex or *artenkreis* with only the more differentiated extremes reaching central Costa Rica. In any event, in Costa Rica the most closely related taxa of this genus do not grow together.

Examples of very closely related species that do not share the same habitat can also be found in *Ficus* of the Moraceae. DeWolf authored the treatment of *Ficus* in the Flora of Panama (Woodson and Schery 1960) and Woodson, who had also surveyed the species, was in close agreement with DeWolf's species

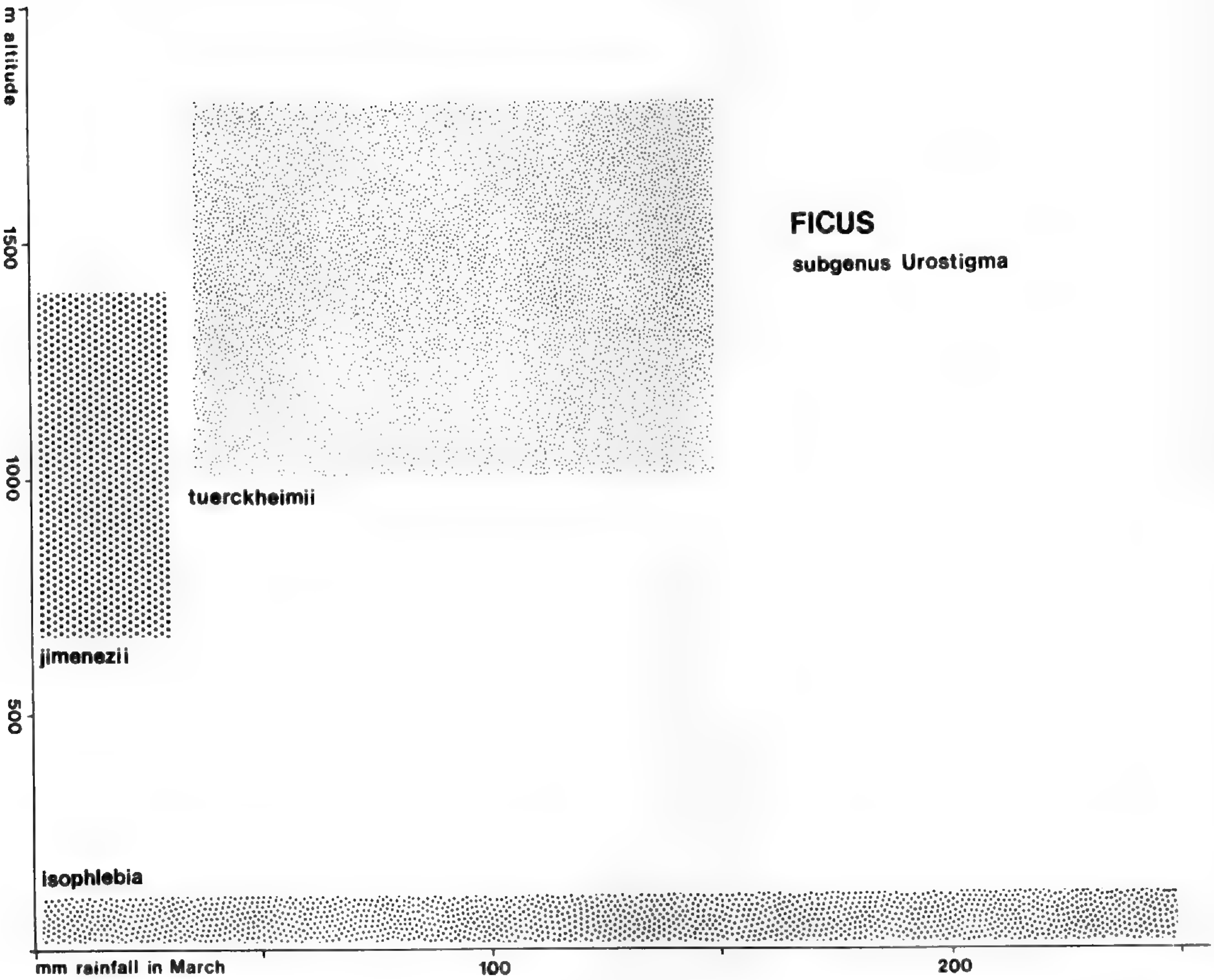

FIGURE 4. Distribution of *Ficus isophlebia, F. jimenezii,* and *F. tuerckheimii* in Costa Rica plotted against altitude in meters (ordinate) and rainfall in March (abscissa).

delimitation. In the decade since that treatment was published some species have come to be known by twice as many collections as were previously available. Most of the species-concepts delimited in the *Flora of Panama* (Woodson & Shery, 1960) have held up well under the scrutiny of the new material, but a few appear to have been made too broad. There are two such groups, one in each of the two subgenera. In the subgenus *Pharmacosyce, Ficus crassiuscula* Warburg was placed into synonymy under the wide-ranging *F. insipida* Willdenow. Close examination of material referable to *F. crassiuscula* shows that it grows only above 1100 m in Costa Rica and western Panama. While in our area, *F. insipida* has not been collected above 500 m elevation (Fig. 3). In the subgenus *Urostigma,* DeWolf considered a trio of names synonymous: *F. isophlebia* Standley, *F. jimenezii* Standley, and *F. tuerckheimii* Standley. Plotting the known collections of these three species in our area shows again that they do not share the same habitat (Fig. 4). William Ramirez has shown (1970*a*) that *F. isophlebia, F. jimenezii,* and *F. tuerckheimii* have different species of pollinators as do *F. insipida* and *F. crassiuscula.* Dr. Leslie Holdridge, a forest ecologist who knows these plants in the field, recognizes all as distinct (personal communication). The work of DeWolf, however, points out the very close relationships of these species. Here again, as in *Hedyosmum*, the very closely related species do not live in the same habitat.

In the genus *Sorocea*, also of the Moraceae, there are four species in the area of Costa Rica and western Panama. *Sorocea cufodontisii* Burger is very closely related to *S. pubivena* Hemsley and is endemic to the wet evergreen lowland forests of southern Costa Rica and adjacent Panama in the Pacific lowlands. A reexamination of my earlier concept of *S. pubivena* (Burger *et al.*, 1962) leads me to believe that it does not grow along the Pacific slopes in this area. These two species are thus isolated geographically by the central mountain ranges. *Sorocea trophoides* Burger is also closely related to *S. pubivena* but occurs at higher elevations. *Sorocea affinis* Hemsley, which grows in some of the same areas as *S. pubivena*, differs more from that species than the others and may be adapted to sites of better drainage. Again, the pattern is similar: the more closely related species do not grow in the same general habitat, more distantly related species do.

These patterns of congeneric distribution are best seen in genera with many species. This is the case in *Piper* with about 93 species in Costa Rica and western Panama (Burger, 1971). One particularly difficult complex of closely related taxa is that of *Piper hispidum* Sw. and its allies. From an analysis of herbarium material it was evident that there was a pattern of associated morphological characters, but the differences between these taxa were very subtle and seemed to be unimportant. I postulated that different populations were slightly different morphologically and all together formed a mosaic complex with some local differentiation. I also assumed that these were all plants of forest edges and similar open habitats. My hypotheses, however, proved quite incorrect after study in the field—Some of these taxa were found only on the darkest forest floor, while others grew at the open forest edge. The subtle morphological differences were consistent and were correlated with geography and ecology and, more important, many of these very closely related taxa did not grow together nor could I find intermediate plants or intermediate populations. For this reason my complex of scarcely distinguishable populations were recognized as biological units defined by subtle but consistent morphological traits correlated with specific habitats.

These examples in *Piper* are not as clearly separate as are the examples from *Hedyosmum*, *Ficus*, and *Sorocea*. The simple charts used here would not distinguish some of these closely related species of *Piper* because they are, in part, separated geographically.

The very closely related genus *Pothomorphe*, often considered synonymous with *Piper*, is represented by two species in Costa Rica. *Pothomorphe peltata* (L.) Miq. ranges from near sea level to about 700 m elevation, while *P. umbellata* (L.) Miq. ranges to 2000 m elevation and is only rarely encountered below 700 m. Both species are plants of open weedy sites in moist or seasonally wet areas.

DISCUSSION

The significance of these observations would be questionable were it not for the fact that these patterns occur in several unrelated groups. The Amentiferae (*sensu* Engler), to which they belong, are an admittedly artificial alliance of plant families. Many of these families are probably unrelated at the ordinal level. The Chloranthaceae and Piperaceae are probably related to the Ranales, while the relationships of Moraceae are thought to be with the Hamamelidales. The fact that genera in these unrelated families exhibit similar patterns of distribution as regards intrageneric morphological affinity is, I believe, significant.

An objection to the interpretations made here might be that the morphological differences used to separate taxa are ecologically induced and we are only dealing with ecotypes. If this latter interpretation were true, we would expect to see clines within the range of these species. *Hedyosmum montanum*, for example, ranges from 1800 to 2800 m elevation but is quite uniform throughout this range; likewise, the closely related *H. calloso-serratum* shows no ecologically correlated variation in its 500 to 1000 m range. In fact, the lack of clinal variation is a characteristic of many tropical species (Ashton, 1969). It is this lack of clinal variation together with relatively more uniform populations that allow us to identify these closely related taxa. (There are, of course, many tropical plant species that vary greatly. In the genera *Urera* and *Myriocarpa* of the Urticaceae variation is often so great that species delimitation is quite arbitrary and about 10% of the specimens cannot be identified with certainty.)

That all these examples might be interpreted as subspecies does not negate the thesis of ecological differentiation as an important factor in producing the great number of species to be found in the wet tropical forest. Whether species or subspecies, these taxa are presently separate. Evidence from *Ficus* suggests that some of these closely related taxa are, in fact, genetically isolated. Trees of *Ficus tuerckheimii* have been planted in the parks of San José, Costa Rica. This is about 15 km outside of the closest natural occurrence of the species and within the ecological range of *F. jimenezii* which grows in San José and the Meseta Central. William Ramirez (1970*b*) observed these trees of *F. tuerckheimii* for two years and found only six matured figs (syconia) during that time. They had been entered by one of the pollinating species of *F. tuerckheimii*. The pollinating wasps of *F. jimenezii* were never observed to enter the figs of *F. tuerckheimii* despite the fact that these wasps occur in the area.

The species discussed and represented here have very precise and rather narrow ecological boundaries. Are these boundaries real? A great many species of the tropics do have wide ranges and they do not seem to have such precise boundaries. Our question concerns only a small percentage of closely related species. Some of these taxa are rare as evidenced by the poor representation in herbaria which may be giving us a false concept of their ecological amplitude. The smaller trees and shrubs such as *Piper* and *Hedyosmum* are much better represented in collections than the larger trees such as *Ficus*. Of Costa Rica's 93 species of *Piper*, 34 have an altitudinal range of less than 900 meters. In the case of *Hedyosmum montanum* we have 14 collections representing 11 collection areas. Of these, four areas range between 2100 and 2800 m altitude with the remaining seven areas from between 1800 and 2100 m. In *Hedyosmum calloso-serratum* (in a narrow sense) we have 21 collections representing 15 areas. Of these, 11 areas are between 600 and 1000 m elevation and four areas from 500 to 600 meters. At the lower elevations at least, the samples fall off sharply, though these lower areas have been frequently visited by collectors. Thus, while sharp altitudinal and ecological boundaries may not be common, they are a real phenomenon in some species and do not appear to be an artifact of poor collecting.

How do these species maintain precise boundaries when their disseminules must certainly be transported over considerable distances and well beyond the population's perimeter? This question is especially interesting in *Ficus* subgenus *Urostigma* where most species begin as epiphytes by having their sticky seeds transported by animals. Why is it that we have no collections of *Ficus tuerckheimii* from the seasonally drier areas around San José in the area of *F. jimenezii*? Trees of *F. tuerckheimii* planted in San José show that the species can grow and mature outside of its native habitat. The pollinating wasps reached these trees so that mature seeds were set (Ramirez, 1970*b*). The only answers that suggest themselves are in the areas of seedling mortality and competitive exclusion in early stages of growth. There are no data available to support or deny these suggestions.

I do not wish to give the impression that closely related taxa never grow together but rather that this is an exceptional situation. In *Piper* a closely related complex of species (*P. biseriatum* C. DC., *P. cenocladum* C. DC., *P. fimbriulatum* C. DC., *P. imperiale* (Miq.) C. DC., and *P. obliquum* R. & P.) often grow together on the dark floor of wet lowland evergreen forests.

The observations presented in this paper contradict the generalization of Federov (1964) that the tropical wet forest possesses series of closely related species growing together. The Costa Rican material indicates that though closely related species appear to grow within the same small geographic area they do not usually grow together within the same habitat. Species of birds that are very closely related and cannot invade each other's territory have been called parapatric sister species (Mayr, 1969).

The evidence of closely related parapatric plant species in Costa Rica can be most easily explained by assuming that effective genetic isolation has evolved over relatively small geographical distances. The alternative is to postulate archipelagos, refugia, or similar devices providing larger scale geographic isolation. Costa Rica's small area (equivalent to the State of West Virginia) and its very diverse epiphytic flora argue, I believe, against major climatic or geological changes in the recent past.

Costa Rica is well known for the richness of its orchid flora with over a thousand species. This extraordinary diversity is found in other epiphytic plants representing a wide range of families. Diversity in plants especially sensitive to desiccation implies that there have been no major contractions of Costa Rica's wet forest formations in the recent past. The central mountain chain provides some isolation between the Caribbean and Pacific slopes. The Pacific lowlands of northern Costa Rica have a very severe dry season and support a vegetation different from that found elsewhere in the country. The Pacific lowlands of southern Costa Rica have a much less severe dry season, and this area supports evergreen forest. There is considerable endemism in this part of Costa Rica, from about the western slopes of the General Valley to the Osa Peninsula and the highlands of Chiriquí, Panama. The Caribbean slopes and lowlands are more uniform as regards climate, and the vegetation is essentially continuous. The areas of higher altitudes are rather small and perhaps insufficient in area to support theories of refugia during major climatic changes. I prefer to assume that major fluctuations in sea level or climate have not contributed significantly to the plant diversity of Costa Rica. Most of the species discussed previously in this paper are endemic to Costa Rica and adjacent Panama, and I believe they have arisen without the influence of major geological or climatic events.

If refugia did exist and did provide large scale geographic isolation for the development of these closely related species, other equally puzzling questions arise. Why do these species remain separate yet closely adjacent after the postulated isolation? And how is it that this isolation produced two species differing so precisely in their ecological requirements? The hypothetical climatic and geographic changes necessary for large-scale isolation raise as many serious questions as they attempt to solve.

Unfortunately, we are only describing an assumed phenomenon. Our interpretations are based on the assumptions that our samples are large enough and that our morphological taxa do indeed represent genetically isolated populations. If these interpretations are valid, we are faced with a situation which can be simply explained by a very hypothetical process: speciation or the initiation of genetic isolation over very small (10 km) distances. Ecological and genetic studies in the land snail *Partula taeniata* suggest that striking divergence can take place between adjacent populations in the absence of geographical barriers (Clarke & Murray, 1969). The plants discussed here do not lend themselves to genetic analysis but they exhibit some of the same phenomena seen in *Partula*. Additionally, biologists may have overemphasized the effect of gene flow on the processes of population differentiation (Endler, 1973).

The relative rarity of hybridization and clinal variations, the great number of species with relatively uniform populations, and the frequency of species with narrow ecological boundaries reflect an evolutionary strategy common in the wet tropics. We are most familiar with plants of environments with wide climatic fluctuations. In these genetic diversity or adaptive pliability is probably more important than adaptive precision. In a very uniform environment precision of adaptation, I believe, is more often a successful strategy. Chance and biological parameters, more than temperature and rainfall, determine reproductive success. Janzen (1967) has ably discussed the higher fidelity of animals and plants to spatial and temporal habitats set off by minor differences. In these more uniform environments it is adaptation to a particular habitat that may determine survival and not the ability to withstand a set of extremes. It is in this context that speciation over small distances in areas of ecological gradients appears to take place. While we may not understand how genetic isolation has been achieved over these small distances, I believe that the evidence from very closely related parapatric plants species indicates that speciation has indeed occurred over small distances in Costa Rica.

SUMMARY

A number of problems involving very closely related species in several genera of Costa Rican flowering plants have been resolved because, though almost sympatric, the species actually do not grow together. These parapatric sister-species or species-groups are found in unrelated families and may represent a general phenomenon. A simple explanation for the origin of these closely related species-pairs and species-groups is that they have become adapted to slightly different habitats and that this has provided small but effective spatial isolation. It seems possible that under the selection pressures found in the wet tropics relatively short periods of isolation and equivalently small distances may be sufficient to develop new co-adapted gene complexes. In turn, these may be easily destroyed by hybridization with the result that gene-flow between formerly sympatric and interbreeding, but now separate, populations quickly becomes detrimental to both. This provides a simple explanation, without refugia and without major geological changes, for these ecologically isolated, morphologically only slightly different taxa that show no evidence of gene-exchange.

LITERATURE CITED

ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. Biol. Jour. Linn. Soc. 1: 155–196.

BURGER, W. C. 1971. Flora Costaricensis, Piperaceae. Fieldiana: Bot. 35: 5–227.

———, J. LANJOUW & J. G. WESSELS BOER. 1962. The genus *Sorocea* St. Hil. Acta Bot. Neerl. 11: 428–477.

CLARKE, B. & J. MURRAY. 1969. Ecological genetics and speciation in land snails of the genus *Partula*. Biol. Jour. Linn. Soc. 1: 31–42.

ENDLER, J. A. 1973. Gene flow and population differentiation. Science 179: 243–250.

FEDEROV, A. A. 1964. The structure of the tropical rain forest and speciation in the humid tropics. Jour. Ecol. 54: 1–11.

JANZEN, D. 1967. Why mountain passes are higher in the tropics. Amer. Naturalist 101: 233–244.

MAYR, E. 1969. Bird speciation in the tropics. Biol. Jour. Linn. Soc. 1: 1–17.

RAMIREZ, W. 1970*a*. Taxonomic and biological studies of neotropical fig wasps. Univ. Kansas Sci. Bull. 49. 44 pp.

———. 1970*b*. Host specificity of fig wasps. Evolution 24: 680–691.

TOSI, J. A., JR. 1969. Republica de Costa Rica, Mapa Ecologico. Centro Cientifico Tropical, San José.

WOODSON, R. E. & R. W. SCHERY. 1960. Flora of Panama. Ann. Missouri Bot. Gard. 47: 146–165.

EVOLUTION OF SYSTEMATIC CHARACTERS IN THE FERNS[1]

INTRODUCTION

THOMAS N. TAYLOR[2] AND JOHN T. MICKEL[3]

For many years studies on living and fossil ferns have progressed with relatively little communication between researchers. This situation has been partially alleviated recently by the organization of the Pteridology Section of the Botanical Society of America. This symposium is one of the first fruits of such cooperation and coordination, and we hope that additional forms of interaction at all levels will be developed.

It has been more than ten years since sections of the Botanical Society of America have engaged in a symposium with ferns as the principal theme. In the introduction to the published volume resulting from that symposium—*Origin and Evolution of Ferns*—it was noted, "A symposium such as this could not have been possible ten years ago. It is obvious that most of the significant advances reported in each of the papers have taken place very recently. It is encouraging, for that reason, to believe that within the next ten years we can expect similar strides, and that we will be much closer to understanding just what a fern is, where it came from, and how it got that way." The ten years since those comments were made have passed, and during that time a number of significant advances have been made that have greatly altered ideas about ferns, and possibly more importantly, have directly influenced future research paths in pteridology. But of potentially far greater significance is the fact that we have seen both neo- and paleopteridologists cross traditional and functional boundaries in the application of new research techniques in pteridological research. Some of the approaches in one field will be of only passing interest to those of the other because of inherent limitations, but it is vital that both areas better understand the progress and limitations of the other field. This symposium provides an appropriate opportunity to review the current level of information and future research directions in pteridological research.

In modern ferns we have a valuable research tool in chromosome counts. Such studies are of particular value in examining hybridization and in supporting genetic and familial relationships. We have found great aneuploid series in certain groups such as Gleicheniaceae and Dennstaedtiaceae; groups that today have only scattered fragments of the series. Additional counts will assist in refining certain taxonomic problems. Promising studies are being made on karyotyping and other detailed studies of the chromosomes. The study of population biology is not generally thought of as a systematic character, but it

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[1] "Evolution of Systematic Characters in the Ferns," papers presented at a jointly sponsored symposium of the Paleobotanical and Pteridological Sections of the Botanical Society of America and the American Fern Society held at Amherst, Massachusetts, in June 1973, under the chairmanship of Thomas N. Taylor.

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appears likely that it will prove helpful in interpreting variation patterns and increase our overall appreciation of the genetic potential within ferns.

Fern systematics has relied heavily on reproductive features in the past Distinctions between the eusporangium and leptosporangium have broken down, and distinctive types such as that with an apical annulus, appear to have arisen independently in separate groups of ferns. Although one may no longer depend entirely on this feature, future research on the sporangium in coming years should provide information about sporangial variation and its systematic value.

Fern spores display remarkable variation and have been extremely helpful in systematic studies. In many cases particular spore morphologies are distinctive for families or genera, or in some instances individual species. Spore sizes and abortion have been useful in studies of hybridization and polyploidy, and in some cases they have led to the discovery of unknown reproductive variations in ferns. A broad detailed survey of spores is still needed to better understand variation patterns and to see which ones are meaningful taxonomically. Wall ultrastructure and development, including the organization and significance of the perispore, are areas of investigation that deserve critical examination. The extrapolation of these results would be of great value for paleobotanical studies where developmental approaches are not feasible.

Great strides have been made in recent years on the diversity and evolution within the heterosporous ferns. Links between homosporous and heterosporous ferns are still conjectural, but as research in this area continues many relationships will be clarified in the next several years.

Systematic chemical studies in the ferns are still in their infancy. Flavanoid chemistry appears quite promising and has been useful in studying hybridization and closely related species. Additional work on anteridogens and their activity will be helpful, and together with a detailed analysis of all chemicals in ferns, might be helpful in broad phylogenetic considerations.

The general organography of ferns is not as clear cut as previously thought. Current work with both living and fossil ferns is helpful in interpreting the variation in these organs. Detailed morphological and developmental studies are shedding light on the nature and significance of branching patterns and the evolution of the leaf. Anatomical studies are stressing stele organization and variation, apices and development, and various aspects of leaf structure and architecture. One of the few families in which good living and fossil material has been critically examined anatomically is the Marattiaceae. The detailed work on *Psaronius* has been very enlightening in showing diversity in the fossil members of this group.

In attempting to identify the precursors of ferns or in linking modern taxa with fossil ferns, there are many obstacles to overcome. Apparently, there are no true ferns in the Devonian, or more pointedly, their morphology and anatomy differ in enough features to make recognition by modern fern characters difficult at this time.

In attempting to construct a phylogeny of the ferns, there are two basic problems that deter us from placing all groups with confidence. First, there is the lack of a complete fossil record. There is little that can be done in this area except to continue looking, especially for the early ferns of perhaps Mississippian age, and the transitions to modern ferns in the early Mesozoic. The second concerns the lack of complete information on all ferns, especially the modern taxa. Broad studies are needed for almost all features of ferns. Studies on petioles, venation patterns, stomata, organ development, spores, mucilage ducts, and chemistry of the mucilage are all promising areas for future research. In recent years several aspects of the gametophyte phase have been elucidated, but still only a relatively small percentage of ferns are known in which the gametophyte has been critically examined. Different reproductive mechanisms have been found, and more work will undoubtedly show we have not yet exhausted the possibilities. Various aspects of fern chemistry, physiology, and genetics are areas that need concentrated effort.

The papers included in this symposium reflect our own biases and interests, and present only a fragmentary survey of the variety of potential approaches that might be included in a volume such as this. With the diversity of approaches available for studies of both modern and fossil ferns, it appears quite probable that our understanding of ferns will be further enhanced in the next few years. Another symposium on this same topic five years from now will have even greater advances to report.

THE SIGNIFICANCE OF CHROMOSOME NUMBERS IN FERNS[1]

Donald M. Britton[2]

Abstract

The importance of chromosome numbers in ferns is assessed. Some of the distinctive basic numbers ($x = 29$, 37, 39, 41 etc.) give unity to their respective genera. Evolutionary studies should be made in conjunction with geographical studies, and karyotype studies have been undertaken with the promise of advances from some new techniques. The synthesis of many different lines of evidence from many disciplines remains the best hope of achieving the goal of an evolutionary classification.

Any discussion about the significance of chromosomes in the study of pteridophytes starts with Manton's book of 1950. This book was large enough, inclusive enough, critical enough, and dogmatic enough to have had a tremendous impact on the cytogenetics of the pteridophytes. It represents a bench mark as far as the study of fern chromosomes is concerned. It is worthwhile to note that Manton had worked previously on the Cruciferae and thus approached the ferns with the training and bias of a professional cytogeneticist of higher plants. My background and bias is similar, and accordingly I accept the tenets of cytogenetics whether the organism is a moss, an insect, man, or a fern. Chromsomes stain similarly, look similarly, and behave similarly in a broad spectrum of plants and animals. I stress this point, because one should not look for bizarre attributes of chromosomes in the pteridophytes. Chromosomes as we know them must have a long history, and although one can find scholarly works discussing whether the basic chromosome number of the angiosperms was 7 for the primitive woody members or possibly 8 or 6 for the angiosperms as a whole, one cannot find references to where those chromosomes came from or indeed how a chromosome has evolved. Indeed, the molecular biologists are busy building models of chromosomes today which will package perhaps one meter of expanded DNA double helix into "sausages" of 5–10 microns. Undoubtedly, the most important part of the chromosome for its kinetics is the centromere or kinetochore, and so there has been much speculation as to the structure and origin of this region of the chromosome.

However, the cytotaxonomist accepts chromosomes as they are, or as they appear under the light microscope, as valuable aids for the understanding of species relationships. I do not want to present the old debate of classical taxonomy on one side ranged against modern biosystematics on the other. This debate has been well assessed by Heslop-Harrison (1953) and Bennett (1964), and my side of the debate has been well championed by Darlington (1956), Löve (1964), Stebbins (1971), and Grant (1971) among others. Nevertheless, it should be obvious to impartial observers that the controversy continues at

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the working level today. There are still monographs and floras being published in which chromosome numbers may or may not be listed. If they are listed, the information is sometimes added much as one would characterize a species as either annual or perennial. One still sees the statement that "chromosome number is just another character," which is apt to send the cytotaxonomist to the medicine cabinet for another tranquilizer! There is of course sufficient variation in nature, and with the evolution of many bizarre systems antagonists of the biosystematic approach can find much "grist for the mill." Examples that come to mind are the complex heterozygotes of *Oenothera*, unipolar spindles in the fly *Sciara*, and *Claytonia virginica* with recorded chromosome numbers of $2n = 12$ to $2n = 190$ with aneuploid increments of not necessarily even numbers. Perhaps one should mention that star member of the Pteridophyta, *Ophioglossum reticulatum* with $n =$ ca. 630 and $2n = 1260$. Critics are immediately apt to say what difference does a chromosome make with such a superfluity as this?

Although the cytogeneticist considers that chromosomes *are* important and that a karyotype is a visual representation of the blueprint of the plant, he accepts the evidence of the molecular biologist that much of the DNA he is observing is redundant or nonsense DNA. He also accepts the facts that even given the same chromosome number, the amount of DNA can vary markedly as shown in *Vicia*, with DNA values from 17 to 100 (Martin, 1968) or *Pinus* 75 to 139 Miksche, 1967). Admitting that the DNA amounts are variable and that much of this DNA is expendable we are still able to make great use of chromosomes.

If one considers that the first extensive, accurate list of chromosome numbers was in Manton (1950), then lists have appeared regularly since (Chiarugi, 1960; Fabbri, 1963, 1965; Ornduff, 1967, 1968, 1969; Moore, 1970, 1971, 1972). In the two decades post Manton (1950) the chromosome numbers of pteridophytes have become rather well sampled. Indeed, other than those in South America and the Chinese mainland, a broad cross-section of genera and species of the world have been examined. Walker (1972) estimated that 60% of say 300 plus genera have been sampled, but perhaps only 15% of say 12,000 species.

What have these chromosome numbers told us? The first impression one gets is of high numbers. Polyploidy has been a common phenomenon in the history of the present day ferns. This is perhaps not unexpected if we are looking at the last remnants of long lines of descent. In fact we should be impressed that three northeastern North American species of *Osmunda* are uniformly $n = 22$ and have had apparently this chromosome number for perhaps 200 million years (Klekowski, 1970).

We should also be impressed by the stability of some chromosome numbers in spite of their large number and in spite of redundant DNA. Gametic numbers occur such as 36 in *Asplenium*, 37 in *Polypodium*, 41 in *Dryopteris*, and 69 in *Cyathea*, for example.

Fern cytotaxonomists are fortunate indeed to have such distinctive chromosome numbers with which to work and speculate. A gametic number such as 12 as found in *Pinus*, *Solanum*, and *Lilium* does not impart much information regarding the inter-relationships of these genera. It is a further hindrance when one attempts to derive a basic chromosome number. For example, in tomatoes is $x = 12$, or $x = 6$? Even $x = 6$ is subject to division by two, so that a few might base the series on a palaeobasic $x = 3$. Stable chromosome numbers such as 29, 37 and 41 in ferns are not quite as susceptible to arithmetic manipulations.

The most worthwhile attribute of these numbers is to give unity to a genus. It is intellectually satisfying to find that a genus such as *Dryopteris* s. str., with a common ground plan or phenotype, has also a common basic chromosome number, $x = 41$. With this simple fact, one can then debate the position of the over-named taxa which I will simply refer to as the Oak and Beech ferns. Undoubtedly, it does not work for all genera, but it is extremely useful nevertheless. Even if it is not a solution when one is faced with $n = 29$ or $n = 30$ in *Cheilanthes*, it can be a point of departure for a further examination of the taxonomy of the genus.

Wilce (1972) presents the conservative taxonomic view for the retention of the genus *Lycopodium* with the statement, "I cannot consider a difference in chromosome number sufficient basis for any genus." Also, "to leave *Lycopodium* whole is to maintain a genus that anyone can recognize at a glance, an attribute not to be discarded lightly." Was this not true at one time for the genus *Polypodium*? I would think that one of the strongest cases against such an arrangement is the attempt to treat different genera somewhat equally, or is this being idealistic? If one recognizes segregate genera such as *Aspidotis*, *Phyllitis*, and *Camptosorus* on grounds other than the chromosomal evidence, then surely one is forced to conclude that gametic numbers of 136, 132, 78, 34, 24, and 23, which indicate very ancient dichotomies, should also receive some recognition.

But you may say, what about *Thelypteris* where basic chromosome numbers are known from $x = 27$ to $x = 36$ in an almost unbroken sequence? Smith (1971) has shown for 25 species in the section *Cyclosorus* at least, that x is uniformly 36. It would seem that with further comparative studies of species that much of the seeming diversity might be resolved.

As for higher plants so for ferns, the decision as to whether for example *Dryopteris intermedia* and *D. maderensis* are in fact conspecific rests on whether or not the two species can freely interbreed to give fertile offspring. One critical step in this procedure for the cytogeneticist is whether one sees 41 bivalents with normal pairing and normal crossing-over or not, in the F_1 hybrid. Crosses such as this are difficult, or at least demanding, and have not even been attempted as yet in genera such as *Botrychium* due to the technical difficulties of germinating the spores. However, the recent success of Whittier (1972) would suggest that a crossing program might be possible. A program involving *Botrychium multifidum*, *B. dissectum*, *B. obliquum*, *B. oneidense*, and *B. ternatum* would certainly help to resolve the problem as to whether one should recognize one species or up to five species in northeastern North America (Wagner, 1960).

The cytotaxonomist experiences quite a thrill in uncovering hidden variability at the chromosomal level. For example in *Asplenium trichomanes* (Britton, 1953) and *Pellaea glabella* it was unexpected on morphological grounds that cytotypes of $2x$ and $4x$ would be found. In Table 1, I have shown some paired species from northeastern North America. These are clear examples of a $2x$

TABLE 1. Diploid and tetraploid taxa pairs in eastern North America.

2X	4X
Botrychium lunaria	*B. minganense*
B. lanceolatum	*B. matricariaefolium*
Woodsia ilvensis	*W. alpina*
W. oregana	*W. cathcartiana*
Cystopteris protrusa	*C. fragilis*
Dryopteris intermedia	*D. spinulosa*
D. assimilis	*D. campyloptera*
D. goldiana	*D. celsa*
Asplenium trichomanes	*A. trichomanes*
Pellaea glabella	*P. glabella*
Polypodium virginianum	*P. virginianum*

and 4*x* situation without aneuploidy. I have not attempted in this table to decide which of the tetraploids might be considered autotetraploids, segmental allotetraploids, or genomic alloploids. It is probable that we have a complete range of these conditions represented in the table. The criterion for deciding on homology has been chromosomal pairing. Wagner (1971) has discussed some of the difficulties in interpreting bivalents and univalents in *Dryopteris*, and recently Klekowski (1973) has raised the issue of homologous versus homoeologous pairing. One should not forget that if one is to emulate the models of genomic allopolyploidy as found in cotton, tobacco, oats, and wheat, that the essential proof of the scheme rests on the artificial resynthesis of the species. We have yet to achieve this level of sophistication with ferns except in a couple of instances. The cytogeneticist before studying the chromosomes is unable to predict which species and genera will be uniform in chromosome number and which will show variation. As mentioned before *P. glabella* and *A. trichomanes* show variation in ploidy as does *Dryopteris assimilis* (2*x*) when compared with *D. campyloptera* (4*x*). Here we have little morphological variation and yet polyploidy. Conversely, we may be confronted with a great deal of morphological variation as in *Pteridium aquilinum*, *Athyrium filix-femina*, and *Botrychium dissectum* and yet find cytological uniformity. The situation is not peculiar to our flora, as it has been commented on by Walker (1966) for Jamaica.

Returning to the flora of northeastern North America, one finds fewer clear-cut examples of 4*x* and 6*x* situations than one finds in the tropics. Two reasonably clear-cut examples are shown in Table 2.

Often one has to look outside the floristic region for the related species (Table 3). This is another *major* contribution of chromosome studies, I feel. It forces workers to think of related species and their evolution and to be less provincial

TABLE 2. Tetraploid and hexaploid taxa pairs in eastern North America.

4X	6X
Dryopteris cristata	*D. clintoniana*
Cystopteris fragilis	*C. laurentiana*

TABLE 3. Diploid and tetraploid pairs with one member absent from northeastern North America.

2X	4X
Europe	*Phyllitis scolopendrium*
Europe	*Asplenium ruta-muraria*
Western North America	*Gymnocarpium dryopteris*
Dryopteris abbreviata (Europe)	*D. filix-mas*
C. acrostichoides	*Cryptogramma crispa* (Europe)

in their outlook. The cytogenetic approach can then join hands with plant geography (Britton & Soper, 1966) and consider the various entities on a world-wide basis (*e.g.* Tryon, 1969; Hultén, 1958, 1962).

Vida (1972) says that there are 85 species of ferns in *Flora Europaea*, and then he goes on to present some speculative charts for the evolution of species within *Polypodium, Polystichum, Dryopteris, Asplenium, Cheilanthes*, and *Cystopteris*. These genera also occur in our flora, where Fernald (1950) has described 28 genera and 83 species of ferns. Accordingly, the list of the more exciting genera for evolutionary schemes would include the European ones as well as *Botrychium, Woodsia, Pellaea, Gymnocarpium*, and *Phegopteris*.

A further contribution of cytogenetics has been in the study of hybrids. I think we have largely dispelled the concept of F_1s, backcrosses, and F_2 segregates as far as species crosses are concerned. The meiotic irregularities and the aborted spores of such plants as × *D. triploidea* Wherry (*Dryopteris intermedia* × *spinulosa*) would seem to indicate that these plants are evolutionary dead-ends. Also, even after acknowledging what seems like an endless enumeration of such hybrids as have been found or synthesized in the European Aspleniums, *e.g.* diploid *Asplenium trichomanes* × various other species, then again tetraploid *A. trichomanes* × the same species of *Asplenium*, one is still left with a very finite number of possible combinations. For example with *Dryopteris* in a given swamp in southern Ontario, if one finds *D. intermedia* (2*x*), *D. spinulosa* (4*x*), *D. cristata* (4*x*), and *D. clintoniana* (6*x*), it is quite probable that one could find six hybrids involving these four entities. A checkerboard fan would arrive at this by visualizing a 4 × 4 table yielding 16 combinations (Britton, 1965). He would subtract 4 for selfs giving 12 combinations and then divide by two for reciprocal crosses. Answer—6 hybrids. A non-checkerboard fan might say the first species could cross with each of the other three, the second with each of the other two and the third with the last one giving 3 plus 2 plus 1 interspecific combinations. Unless one is to admit the presence of an undetected other species in the swamp or at its edge, *e.g. D. marginalis* or *D. goldiana*, or decide that spores have been blown in, then six hybrids should be the magic number. In my discipline, this has more reality than trying to match a given plant with some aberrant or monstrous type such as *Polypodium amorphum*, whose chromosomes are unknown and which has never been recollected (Lang, 1969).

The first step in a study of the cytogenetics of a species is the accurate determination of the chromosome number. Unfortunately, this is as far as we have proceeded in many cases, and given the technical difficulties of the material even this has not been achieved in some cases (Britton, 1964). The second step is to obtain a karyotype. This has not been a popular pastime of cytogeneticists with ferns. Large numbers, small chromosomes, and slowly dividing root-tips are all deterrents, and only the Japanese workers have attempted the painstaking job of comparing karyotypes of different species (Kawakami, 1970, 1971; Takei, 1969; Tatuno & Yoshida, 1966, 1967; Tatuno & Kawakami, 1969; Tatuno & Okada, 1970; Tatuno & Takei, 1969). They have concluded that the present day basic numbers (X) are in fact derived from what they call b numbers (palaeobasic numbers?). For example in *Osmunda* where $n = 22$ and x is 22, they consider that b is 11, *i.e.* present-day Osmundas are ancient tetraploids. In *Asplenium* $x = 36$, but they consider that $b = 12$. It is logical to conclude that the present basic numbers in the ferns, which are high in comparison with angiosperm basic numbers, are derived from lower numbers. At the same time, the small size of some of the fern chromosomes and their large numbers make this type of study technically difficult to verify. One might also ask why the chromosomes should be so stable as to have resisted changes such as inversions, translocations, duplications, and deletions which would prevent identifying four or six of each kind of chromosome? New techniques showing fluorescent bands (Vosa, 1971) or Giemsa bands (Evans *et al.*, 1971; Lee *et al.*, 1972) may be of assistance in identifying individual chromosomes. However, the studies of Kurabayashi (1958) on *Trillium* would suggest that polymorphism will present limitations to the use of this technique for precisely identifying each individual chromosome.

I am less enthusiastic about the use of chromosome numbers for grand schemes of phylogenetic relationships. The distinctive numbers such as 37 for *Polypodium* can perhaps be used for evidence of polyphyletic lines, but is this not merely pushing the problems of origin further back into the hands of our paleobotanist friends? Walker (1966) has a phylogenetic scheme for the Hymenophyllaceae based on X numbers of 6, 7, 8, 9, 11, and 13. Each is considered as a different line and we are faced with six origins instead of one! The very fact that we have distinctive gametic numbers such as 29, 37, and 41 makes their inter-relationship and origin obscure. For example in *Marattia* and *Tectaria* the $n = 39$ could have arisen in different ways. As Walker (1966) suggests it may be an example of an aneuploid drop ($n = 40$ to $n = 39$), whereas others have suggested that 39 is three sets of 13. It is unlikely that we will be able to reconstruct the phylogeny of these different numbers. At best, a phylogenetic scheme will not be based on arithmetic manipulations of basic chromosome numbers. Instead, these numbers can be used as ancillary evidence that the scheme offered is not negated by the chromosomal evidence. However, since chromosomal increase by polyploidy and chromosomal decrease by translocations and loss of centromeres are both acceptable to cytogeneticists. I see few stringent restrictions for the speculative phylogenist!

I feel that the best hopes we have for the future are the comparative studies and the synthesis of many different lines of evidence. It is not just the chromosomes, but *all* the available evidence that should be considered. New evidence becomes available all the time. We now have phytochemical studies (Widén

& Britton, 1971 *a*, *b*), SEM studies (Britton, 1972 *a*, *b*), isozyme studies, fluorescent bands on chromosomes, and DNA hybridization studies to mention a few of the newer ones. Tomorrow who knows?

Literature Cited

Bennett, E. 1964. Historical perspectives in genecology. Scott. Pl. Breed. Stat. Rec. 1964: 51–115.

Britton, D. M. 1953. Chromosome studies on ferns. Amer. Jour. Bot. 40: 575–583.

———. 1964. Chromosome numbers of ferns in Ontario. Canad. Jour. Bot. 42: 1349–1354.

———. 1965. Hybrid wood ferns in Ontario. Michigan Bot. 4: 3–9.

———. 1972*a*. Spore ornamentation in the *Dryopteris spinulosa* complex. Canad. Jour. Bot. 50: 1617–1621.

———. 1972*b*. The spores of *Dryopteris clintoniana* and its relatives. Canad. Jour. Bot. 50: 2027–2029.

——— & J. H. Soper. 1966. The cytology and distribution of *Dryopteris* species in Ontario. Canad. Jour. Bot. 44: 63–78.

Chiarugi, A. 1960. Tavole cromosomiche delle Pteridophyta. Caryologia 13: 27–150.

Darlington, C. D. 1956. Chromosome Botany. George Allen and Unwin, London.

Evans, H. J., K. E. Buckton & A. T. Sumner. 1971. Cytological mapping of human chromosomes. Results obtained with quinacrine fluorescence and acetic saline Giemsa technique. Chromosoma 35: 310–321.

Fabbri, F. 1963. Primo supplemento alle Tavole Cromosomiche delle Pteridophyta di Alberto Chiarugi. Caryologia 16: 237–335.

———. 1965. Secondo supplemento alle Tavole Cromosomiche delle Pteridophyta di Alberto Chiarugi. Caryologia 18: 675–728 .

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. American Book Co., New York.

Grant, V. 1971. Plant Speciation. Columbia Univ. Press, New York and London.

Heslop-Harrison, J. 1953. New Concepts in Flowering Plant Taxonomy. Heinemann, London.

Hultén, E. 1958. The amphi-atlantic plants. Kongl. Svenska Vetenskapsakad. Handl. s.4, 7(1).

———. 1962. The circumpolar plants. I. Kongl. Svenska Vetenskapsakad. Handl. s.4,8(5).

Kawakami, S. 1970. Karyological studies on Aspleniaceae. Bot. Mag. (Tokyo) 83: 74–81.

———. 1971. Karyological studies on Pteridaceae I. Karyotypes of three species of *Pteris*. Bot. Mag. (Tokyo) 84: 180–186.

Klekowski, E. T., Jr. 1970. Populational and genetic studies of a homosporous fern—*Osmunda regalis*. Amer. Jour. Bot. 57: 1122–1138.

———. 1973. Sexual and subsexual systems in homosporous pteridophytes: A new hypothesis. Amer. Jour. Bot. 60: 535–544.

Kurabayashi, M. 1958. Evolution and variation in Japanese species of *Trillium*. Evolution 12: 286–310.

Lang, F. A. 1969. A new name for a species of *Polypodium* from northwestern North America. Madroño 20: 53–60.

Lee, C. L. Y., J. P. Welch & E. J. T. Winsor. 1972. Banding patterns in human chromosomes; production by proteolytic enzymes. Jour. Heredity 63: 296–297.

Löve, A. 1964. The biological species concept and its evolutionary structure. Taxon 13: 33–45.

Manton, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Univ. Press, Cambridge.

Martin, P. G. 1968. Differences in chromosome size between related plant species. *In* W. J. Peacock & D. Brock (editors), "Replication and Recombination of Genetic Material." Australian Acad. Sci., Canberra.

Miksche, J. P. 1967. Variation in DNA content of several gymnosperms. Canad. Jour. Genet. Cytol. 9: 717–722.

Moore, R. J. (editor). 1970. Index to plant chromosome numbers for 1968. Regnum Veg. 68: 10–15.

———. 1971. Index to plant chromosome numbers for 1969. Regnum Veg. 77: 6–7.

———. 1972. Index to plant chromosome numbers for 1970. Regnum Veg. 84: 8–12.

Ornduff, R. 1967. Index to plant chromosome numbers for 1965. Regnum Veg. 50: 8–25.

———. 1968. Index to plant chromosome numbers for 1966. Regnum Veg. 55: 4–12.

———. 1969. Index to plant chromosome numbers for 1967. Regnum Veg. 59: 14–18.

Smith, A. R. 1971. Systematics of the neotropical species of *Thelypteris* section *Cyclosorus*. Univ. California Publ. Bot. 59: 1–136.

Stebbins, G. L. 1971. Chromosomal Evolution in Higher Plants. E. Arnold, London.

Takei, M. 1969. Karyological studies in Polypodiaceae I. Karyotypes of a few species of the genus *Lemmaphyllum* and *Pyrossia* in Japan. Bot. Mag. (Tokyo) 82: 482–487.

Tatuno, S. & S. Kawakami. 1969. Karyological studies on Aspleniaceae I. Karyotypes of three species in *Asplenium*. Bot. Mag. (Tokyo) 82: 436–444.

——— & H. Okada. 1970. Karyological studies in Aspidiaceae I. Bot. Mag. (Tokyo) 83: 202–210.

——— & M. Takei. 1969. Karyological studies in Hymenophyllaceae I. Chromosomes of the genus *Hymenophyllum* and *Mecodium* in Japan. Bot. Mag. (Tokyo) 82: 121–129.

——— & H. Yoshida. 1966. Karyologische Untersuchungen über Osmundaceae I. Chromosomen der Gattung *Osmunda* aus Japan. Bot. Mag. (Tokyo) 79: 244–252.

——— & ———. 1967. Chromosomes of the genus *Osmundastrum* and *Plenasium* in Japan. Bot. Mag. (Tokyo) 80: 130–138.

Tryon, R. M. 1969. Taxonomic problems in the geography of North American ferns. BioScience 19: 790–795.

Vida, G. 1972. Cytotaxonomy and genome analysis of the European ferns. Symp. Biol. Hung. 12: 51–60.

Vosa, C. G. 1971. The quinacrine fluorescence patterns of the chromosomes of *Allium carinatum*. Chromosoma 33: 382–385.

Walker, T. G. 1966. A cytotaxonomic survey of the Pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh 66: 169–237.

———. 1972. Paper presented to International Symposium on the Phylogeny and Classification of the Filicopsida. London.

Wagner, W. H., Jr. 1960. Periodicity and pigmentation in *Botrychium* subg. *Sceptridium* in the northeastern United States. Bull. Torrey Bot. Club 87: 303–325.

———. 1971. Evolution of *Dryopteris* in relation to the Appalachians. *In* "The Distributional History of the Biota of the Southern Appalachians. Part II. Flora." Virginia Polytechn. Inst. & St. Univ. Res. Div. Monogr. 2.

Whittier, D. P. 1972. Gametophytes of *Botrychium dissectum* as grown in sterile culture. Bot. Gaz. (Crawfordsville) 133: 336–339.

Widén, C. J. & D. M. Britton. 1971*a*. Chemotaxonomic investigations on the *Dryopteris cristata* complex in North America. Canad. Jour. Bot. 49: 1141–1154.

——— & ———. 1971*b*. A chromatographic and cytological study of *Dryopteris filix-mas* and related taxa in North America. Canad. Jour. Bot. 49: 1589–1600.

Wilce, J. H. 1972. Lycopod spores, I. General spore patterns and the generic segregates of *Lycopodium*. Amer. Fern Jour. 62: 65–79.

REPRODUCTIVE BIOLOGY AND EVOLUTION IN THE PTERIDOPHYTA

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In flowering plants many of the diverse characteristics utilized in systematics to determine phylogenetic relationships represent direct adaptations to specific methods of pollination or reproduction. In turn, each of these specific methods can determine to a large extent the total amount of inbreeding and outbreeding occurring and thus control population variability, evolutionary potential, and geographical distribution of the species. These phenomena and influences are well known and have been discussed extensively in the literature.

In ferns many of the diverse characteristics utilized in systematics to determine phylogenetic relationships relate to the production of spores and include the size, shape, position and development of the sorus, the sporangia, and the spores contained within. The reproductive mechanisms, however, which determine genetic diversity and evolutionary potential, are held in a free-living independent gametophyte generation, a generation which, with the exception of its morphology, has been largely ignored.

The initial modern studies on reproductive biology in ferns were done by Edward J. Klekowski, Jr., in the middle 1960's (Klekowski & Baker, 1966; Klekowski & Lloyd, 1968). Since that time numerous studies have appeared on a variety of species and phenomena by a limited number of workers (Cousens & Horner, 1970; Duckett, 1970, 1972; Ganders, 1972; Holbrook-Walker & Lloyd, 1973; Klekowski, 1969*a*, 1969*b*, 1970*a*, 1970*b*, 1970*c*, 1971*a*, 1971*b*, 1972*a*, 1972*b*, 1973*a*, 1973*b*, 1973*c*, 1973*d*; Lloyd, 1973*a*, 1973*b*, 1974; Lloyd & Klekowski, 1970; Saus, 1973; Schedlbauer & Klekowski, 1972).

Homosporous ferns for the most part produce hermaphroditic haploid gametophytes, arising from a single haploid spore by a series of mitotic divisions. As a result, gametes from a single gametophyte will be identical genetically, barring mutation. Self-fertilization, *i. e.* fusion of sperm and egg from a single gametophyte (intragametophytic selfing) will produce a zygote which is completely homozygous. Thus, in ferns it is possible to produce completely homozygous individuals in a single generation, a condition rarely achieved in flowering plants even after many generations of inbreeding. Due to the complexities of the free-living gametophyte and the genetic system of ferns, it has been necessary to utilize specific terminology to describe their mating systems. Those terms that will be used in this paper are: (1) *intragametophytic selfing*: fusion of sperm and egg from a single gametophyte, usually resulting in complete homozygosity of the resultant zygote; (2) *intergametophytic selfing*: fusion of sperm and egg from different gametophytes but both having arisen from a single sporophyte; this is analogous to inbreeding in flowering plants and results in a zygote with less heterozygosity than the parental sporophyte; (3) *intergametophytic crossing*: fusion of sperm and egg from different gametophytes, each originating from a

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different sporophyte; this is analogous to outbreeding in flowering plants; (4) *intergametophytic mating*: fusion of sperm and egg from different gametophytes but origin of gametophytes not specified.

Because of the unique ability of fern gametophytes to form completely homozygous zygotes it is possible to screen sporophytes for deleterious recessive genes (genetic load). Data of this type, when used in conjunction with gametophyte and gametangia ontogeny, chromosome studies, and analysis for apogamy and vegetative reproduction, has allowed us to sample populations of plants and determine their mating systems and the degree of genetic heterozygosity for deleterious lethals. With data of this type it is now possible to extrapolate further to predictions of population variability and evolutionary potential of taxa and to correlate in some cases specific mating systems with specific ecological requirements.

In the following discussion I wish to cover four specific areas of fern reproductive biology which are important and significant in evolution. These areas are (1) levels of genetic load which have been found in natural populations of ferns; (2) homoeologous chromosome pairing; (3) specific studies utilizing ferns from a variety of habitats in Hawaii to illustrate the correlations which can be made between mating systems, subsequent genetic heterozygosity, and habitat selection; and (4) allelopathic compounds and antheridogen.

Unfortunately, time does not allow me to cover equally important facets of fern biology such as apogamy and hybridization (see DeBenedictis, 1969, for review of literature on apogamy in ferns).

1. Genetic Load

Sampling for deleterious recessive genes in sporophytes is a relatively simple procedure involving the isolation of 30 or more prothalli from a single sporophyte before the attainment of sexual maturity, growing these prothalli to maturity, analysing them for the hermaphroditic condition, and watering to insure an aqueous medium for the transference of sperm to egg. More specific genetic tests have been devised (pairs/isolates test) to provide additional support for the genetic basis of the results (Klekowski, 1971*a*). Interpretation of the data from the isolate cultures is somewhat more difficult. In general, lack of sporophyte production on any hermaphroditic gametophyte, with supporting evidence from the pairs/isolates test, or visible signs of sporophytic abortions or malformations, has been used as indicative of homozygous deleterious recessive gene combinations. From data of this type it is possible to determine in individual sporophytes heterozygosity for recessive lethals and the frequency of such sporophytes in given populations. Utilizing other morphological criteria, such as gametangia sequence of development and placement, presence or absence of polyembryony and antheridogen, and length of generation time, it is then possible to extrapolate with a fair degree of accuracy to the primary mode of mating system utilized in nature by the species and the expected resulting degrees of heterozygosity.

Genetic load studies which have been published on ferns from natural populations indicate that about 16 species of the more or less 10,000 species of

TABLE 1. Genetic load studies in ferns from natural populations. Given as percent of gametophytes bearing recessive sporophytic lethal genes, per sporophyte sampled.

Species	Genetic load (mean)	Source
Ceratopteris thalictroides	0.0–6.0%	Klekowski, 1970*a*
Cibotium chamissoi	26.6–90.0 (59.0)%	Lloyd, 1974
Dicranopteris linearis	20.0–65.0 (36.6)%	Lloyd, 1974
Microsorium scolopendria	0.0–10.0 (7.2)%	Lloyd, 1974
Nephrolepis exaltata	0.0%	Lloyd, 1974
Onoclea sensibilis	6.0–41.0 (26.0)%	Ganders, 1973
O. sensibilis	0.0–45.0 (13.7)%	Saus, 1973
Osmunda regalis	5.0–100.0 (59.5)%	Klekowski, 1970*b*
Pteridium aquilinum subsp. *aquilinum*		
var. *decompositum*	6.0–72.0 (31.0)%	Klekowski, 1972*a*
var. *latiusculum*	14.6–28.0 (21.3)%	Klekowski, 1972*a*
var. *pubescens*	47.1–100.0 (64.2)%	Klekowski, 1972*a*
P. aquilinum subsp. *caudatum*		
var. *arachnoideum*		
Galapagos	0.0–19.0 (9.0)%	Klekowski, 1972*a*
Peru	67.5%	Klekowski, 1972*a*
Costa Rica/Honduras	23.6–40.0 (30.1)%	Klekowski, 1972*a*
var. *esculentum*	82.0–87.8 (84.9)%	Klekowski, 1972*a*
Sadleria cyatheoides	44.0%	Holbrook-Walker & Lloyd, 1973
S. souleyetiana	44.0%	Holbrook-Walker & Lloyd, 1973
Thelypteris palustris	30.0–92.4 (40.0)%	Ganders, 1973
Woodwardia fimbriata	0.0%	Klekowski, 1969*b*

Pteridophyta have been investigated (Table 1). However, population studies sampling large numbers of sporophytes have been done only on *Ceratopteris thalictroides* from Hawaii, *Cibotium glaucum* from Hawaii, *Onoclea sensibilis* from Ohio, and *Osmunda regalis* from Massachusetts. Mean levels of genetic load which have been found in sporophytes in nature vary from 0.0% in *C. thalictroides* and *Nephrolepis exaltata* from populations in Hawaii to over 59.0% in *Cibotium chamissoi* and *Osmunda regalis*. The possible significance of these levels will be discussed below. The mean genetic load for all species studied to date, if such a figure has any significance, is about 29.4%.

Frequency of genetic load in sporophytes of ferns is dependent upon a large number of factors including polyploidy, mutation rate, mating system, population size, habitat diversity, and natural selection. Mating system has a large influence on levels of genetic load. Populations with high frequencies of intergametophytic mating can be shown to consistently express genetic load, whereas populations with primarily intragametophytic mating express little or none. Lloyd (1974) has shown in *Nephrolepis exaltata* that 100% of the sporophytes tested from recent lava flows on Hawaii exhibited no genetic load. Characteristics of gametangia ontogeny, with large numbers of antheridia being produced before archegonia and continuously throughout archegonial production, indicates that the mating system for this species is probably one of intragametophytic selfing.

Klekowski (1970*a*) has shown that presence of antheridia in the interior

TABLE 2. Genetic load in *Cibotium chamissoi* relative to gametophyte gametangia ontogeny.

Ontogeny	Per cent of sporophytes exhibiting ontogeny	Genetic load (mean)
Male to hermaphroditic	30.0%	26.6–30.0 (27.8)%
Male and Female to hermaphroditic	20.0%	83.7–90.0 (86.9)%
Female to hermaphroditic	50.0%	40.0–83.7 (65.1)%

surface position prior to and during initiation of archegonia in *Ceratopteris thalictroides* can be correlated with the lack of genetic load in one Hawaiian population of this species. In species with gametangia sequences from female to hermaphroditic most genetic studies have indicated the presence of genetic load: in *Onoclea sensibilis* the mean genetic load is 13.7% (Saus, 1973); in *Sadleria cyatheoides*, 44.0% (Holbrook-Walker & Lloyd, 1973); and in *Dicranopteris linearis*, 36.6% (Lloyd, 1974). The most striking evidence for the significance of mating system and gametangia ontogeny in the level of genetic load comes from recent work on *Cibotium glaucum* (Lloyd, 1974). This is the dominant understory species in the mature rainforest on the slopes of Mauna Loa in Hawaii. Investigations of the reproductive biology of this species indicate that different sporophytes from the same population will exhibit different levels of genetic load and that these levels are correlated with the sequence of gametangia ontogeny expressed by their gametophytes (Table 2). For example, sporophytes which produce gametophytes which undergo a male to hermaphroditic ontogeny exhibit a 26.6–30.0 (mean = 27.8) % genetic load; whereas sporophytes which produce gametophytes with a female to hermaphroditic ontogeny exhibit a 40.0–83.7 (mean = 65.1) % genetic load. Sporophytes which produce gametophytes which are initially unisexual and male and female have higher levels varying from 83.7–90.0 (mean = 86.9) %. Thus, these data indicate that fewer recessive deleterious genes are found in those sporophytes which produce gametophytes which have higher probabilities of intragametophytic selfing due to their gametangia sequence; conversely, gametangia sequences favoring intergametophytic mating are produced by gametophytes from sporophytes with higher frequencies of recessive deleterious genes.

However, the correlations of mating system, gametangia ontogeny, and genetic load as presented above are too simplistic. For example, *Onoclea sensibilis* exhibits a gametangia sequence which heavily favors intergametophytic mating, with the archegoniate stage lasting from 40 to about 85 days before hermaphroditism is attained. In addition, Näf *et al.* (1969) have documented the possible production of an antheridogen by gametophytes of this species. In dense cultures younger prothalli from later germinating spores will precociously produce antheridia. Some of these gametophytes remain male throughout their life span (Lloyd, 1971; Saus, 1973). Although the species appears to have high probabilities of intergametophytic mating, the genetic load found in sporophytes is relatively low (mean = 13.7%). In *Microsorium scolopendria* a similar situation is encountered. This species produces gametophytes with a gametangia sequence from female to hermaphroditic with the archegoniate stage lasting from 14 to 59 days. However, genetic load is low (0–10%, mean = 7.2%). In this latter species one must consider population size as well as gametangia ontogeny. Five plants forming the entire population were sampled from a lava flow dated from 1750 on the island of Hawaii. It is not unlikely that initial establishment of the species on the flow was by spores blown in by the wind, germinating to produce gametophytes which were most likely sufficiently isolated from one another to prevent intergametophytic mating. Thus, sporophytes resulting from these gametophytes would be the result of intragametophytic selfing and therefore homozygous and without deleterious recessive genes. Other sporophytes found here could be the product of the initial or subsequent introductions or more than likely of spores produced by the original pioneer. If the latter is true, lethals present in these plants would most likely be the result of accumulated mutations. In *Ceratopteris thalictroides*, the original population tested by Klekowski (1970*a*), in which he found no genetic load, was relatively small, consisting of plants found in only a few taro patches on the island of Oahu. Lloyd (1973*a*) has found that sexual reproduction in this population ceases between ten and 13 months after establishment and that a significant amount of reproduction takes place by vegetative budding. In a larger population of the same species from Kauai (probably introduced there from Oahu) Klekowski has found recessive deleterious genes in 55.5% of the sporophytes tested which varied from 0.0–7.5 (mean = 3.0) % (unpublished personal communication). In *Osmunda regalis*, Klekowski (1970*b*) found that the largest population tested had the highest genetic load. In addition, this species generally exhibits gametangia ontogeny from male to hermaphroditic yet exhibits high levels of genetic load. He has concluded that *O. regalis* has a gametophyte morphology which promotes intragametophytic selfing when gametophytes are sparse and intergametophytic mating when they are abundant.

A further influence on genetic load in natural populations is the availability of habitats for gametophyte establishment, prolonged growth, and survival. In general, longer lived gametophytes tend to favor intergametophytic mating whereas shorter generations favor intragametophytic selfing (Klekowski, 1969*a*). Klekowski (1972*a*) has shown in *Pteridium aquilinum* that plants from the Galapagos Islands exhibit a mean genetic load of 9.0%, whereas plants of the same species from Hawaii exhibit a mean genetic load of 31.0%. He interpretes this to be perhaps a response of the latter populations having greater genetic diversity brought about by more favorable, diverse mesic habitats with subsequent establishment of intergametophytic mating and interlocus heterozygosity. The Galapagos Islands, on the other hand, are more xeric and less diverse, a situation which would favor more shortened gametophyte generations, less genetic diversity, and apogamy. The populations of *P. aquilinum* occurring there probably arrived by spores from South America and probably initially produced sporophytes by intragametophytic selfing. Thus, they are more depauperate genetically, with a greater probability of an intragametophytic mating system and the resulting lowered genetic load.

2. HOMOEOLOGOUS CHROMOSOME PAIRING

One of the significant new hypotheses to come out of the study of fern biology during this century has been the recent documentation of homoeologous chromosome pairing in *Ceratopteris* by Edward Klekowski, Jr., of the University of Massachusetts, and its possible relationship to the high levels of polyploidy found within the Pteridophyta (Klekowski & Baker, 1966; Klekowski, 1972 *b*, 1973*c*, 1973*d*). He has related the evolution of polyploidy in homosporous ferns to suspected high frequencies of intragametophytic selfing due to the homothallic hermaphroditic nature of most gametophytes as a means of storing genetic diversity by duplicated alleles regardless of the subsequent homozygosity of sporophytes produced by the mating system. His data clearly indicate that ferns with an obligate intergametophytic mating system (*e. g.* heterosporous ferns) have chromosome numbers (mean $n = 13$) more nearly approaching those of flowering plants, whereas homosporous ferns have numbers which average considerably higher (mean $n = 54$). In addition, 40% of homosporous ferns show additional polyploidy over base numbers which themselves may be of polyploid origin. For example, in *Osmunda*, which has a haploid number of 22, Tatuno and Yoshida (1966, 1967) have shown that this probably represents an ancient tetraploid condition based on $x = 11$. From these studies and others it can be concluded that polyploidy is a major phenomenon present in homosporous ferns and that taxa with duplicated chromosome sets have had the greatest evolutionary potential (Klekowski, 1973*c*).

Duplicated chromosome sets allow for the storage of genetic material even in homzygous ferns. Mutations can occur in one allele without affecting another or required physiological processes, thus producing interlocus heterozygosity. In ferns which normally undergo intragametophytic selfing, recombination could occur by occasional intergametophytic crossing producing heterozygous sporophytes, followed by meiosis.

If, however, homoeologous chromosome pairing (pairing between duplicated chromosomes within polyploid sets) is occurring, species which normally undergo intragametophytic selfing can produce heterozygous spores from homozygous spore mother cells (if interlocus heterozygosity is present) rather than the expected homozygous spores produced by homologous pairing. Therefore, polyploidy, followed by mutation, serves to store genetic diversity; homoeologous pairing, when present, serves to release that variability even in ferns which frequently undergo intragametophytic selfing. This theory can be extrapolated to include most apogamous ferns which produce spores by meiosis.

Klekowski's evidence for homoeologous pairing has come from his initial observations of morphological variation in homozygous families of sporophytes to marker genes and cytological manifestations of paracentric inversions and translocations in completely homozygous sporophytes. These latter aberrations would not be visible in sporophytes with homologous pairing. This phenomenon has been documented only in *Ceratopteris*, and whether it occurs in any other species remains to be seen.

3. REPRODUCTIVE BIOLOGY AND HABITAT SELECTION

Recent studies on Hawaiian ferns have brought to light several distinct correlations between reproductive biology, habitat preference, and geographical distribution in *Sadleria* spp. (Holbrook-Walker & Lloyd, 1973). In this genus it has been possible to characterize the mating system of three of the four species and to relate these mating systems in some cases to specific abilities (or lack of) of the species to colonize lava flow habitats. Of the four species (all of which are endemic to Hawaii) *S. cyatheoides* is the most widely distributed in terms of ecology and geography and is the only species found as a colonizer on new lava flows. This species is characterized by an intergametophytic mating system with gametangia ontogeny (initially bigametophytic or female to hermaphroditic) which allows for possible intragametophytic selfing (hermaphroditism and polyembryony) with time. As plants found on lava are sometimes widely distributed they probably initially result from single spore introductions and the obligate intragametophytic selfing following. The second most common species, *S. pallida*, is never found as a colonizer and usually only occurs in relatively dense populations in stable mature forest vegetation complexes. Mating system studies in this species indicate that it may have a nearly obligate intergametophytic mating system due to the non-synchronous production of archegonia and antheridia. In our studies only 4% of the isolate culture and 25% of the composite culture gametophytes produced sporophytes, indicating that their was at least minimal overlap of the two gametangia in some gametophytes. Morphological studies indicated that archegonia production ceases with the initial production of antheridia or shortly thereafter. This hiatus in gametangia production appears to be significant as one possible cause for restricting the species to areas with high gametophyte densities, in other words, to habitats with a significant number of other mature sporophytes present.

A third species, *Sadleria squarrosa*, is restricted to extremely wet, deeply shaded steep banks and is rarely found scattered throughout the rain forest. Gametophytes of this species were found to be intolerant of light intensities used in our culture conditions (ca. 250 ft.c.). Lowering of the light intensity to less than 100 ft.c., however, allowed gametophytes to more normally complete their ontogeny. Similar phenomena were observed in gametophytes of *Onocleopsis hintonii*, a species found in only a few dark, wet canyons in southern Mexico and Guatemala (Lloyd, 1971). Conversely, gametophytes of the taro-patch-inhabiting *Ceratopteris thalictroides*, a habitat with high temperatures and light intensities, grow best and produce sporophytes at a more rapid rate at 500 ft.c. or greater and at temperatures above 33° C. At temperatures of 18° C. spore germination and gametophyte growth is greatly retarded (Lloyd, unpublished).

From these studies it is apparent that the gametophyte generation has as specific habitat requirements and responses as the sporophytes which produced them.

Further studies on Hawaiian ferns have elucidated trends in mating system and subsequent heterozygosity for genetic load between species found as dominants on lava flows and those found as dominants in mature rain forest

TABLE 3. Genetic load studies in Hawaiian sporophytes: mean percent of gametophytes bearing recessive lethal genes per population.

Species	Number gametophytes studied	Mean percent bearing lethal genes
Nephrolepis exaltata (pioneer lava)	100	0.0%
Microsorium scolopendria	110	7.2%
Sadleria cyatheoides	75	44.0%
Dicranopteris linearis	60	36.0%
Sadleria souleyetiana	75	44.0%
S. pallida	75	96.0%[a]
Cibotium chamissoi	270	59.0%

[a] Lack of sporophyte production probably due to non-synchronous gametangia production.

(Lloyd, 1974). Tables 3, 4, and 5 summarize these data. The dominant species found as a pioneer on lava is *Nephrolepis exaltata,* appearing as soon as 4.5 months after a flow. This habitat is almost uniformly depauperate in terms of soil, diversity, and other higher plants. Studies on *N. exaltata* indicate a mating system with high probabilities of intragametophytic selfing and no genetic load. Furthermore, this species reproduces profusely by vegetative stolons, is incapable of tolerating shade, and after establishment of tree cover will die out. Other species found in this habitat, which have been tested, also show little genetic heterozygosity for deleterious recessive genes, although their mating systems can be variously characterized as intra- or intergametophytic. On the other hand, dominants in the mature rain forest (*Cibotium chamissoi, Sadleria pallida*) can be characterized by much higher levels of genetic load and by intergametophytic mating systems.

Population size has been shown to affect heterozygosity by reducing the opportunities for intergametophytic mating. In some pioneer species on lava, such as *Microsorium scolopendria,* this is apparently the case. In others, however, such as the dominant *Nephrolepis exaltata,* the population consists of hundreds of plants. In the mature rain forest, density of *Cibotium chamissoi* is very high. As plants of this species produce large numbers of spores simultaneously when fertile it appears that gametophyte densities are probably also very high, thus increasing probabilities for intergametophytic mating which is reflected in the higher levels of heterozygosity for recessive deleterious genes.

Two factors may play a part in the intragametophytic mating system found

TABLE 4. Genetic load of dominant species relative to pioneer and non-pioneer habitats in Hawaiian ferns.

Habitat	Genetic load (mean)
Pioneer lava flows	0.0–44 (17.0)%
Intermediate forest (young)	10–59 (37.2)%
Mature rain forest	44–59 (51.5)%[a]

[a] Data for *Sadleria pallida* are not included.

TABLE 5. Age of appearance of species, vegetation type, and probable mating system of Hawaiian ferns.

Species	Pioneer habitats 1971–1950–1850–1750	Intermediate forest	Mature forest	Mating system
Nephrolepis exaltata	———————			Intragametophytic
Microsorium scolopendria	———			Intra/intergametophytic
Psilotum nudum	—	———		Probably intragametophytic
Polypodium pellucidum	———————	— — — — —	— —	Probably intragametophytic
Sadleria cyatheoides	— — — — ———	———		Intergametophytic
Dicranopteris linearis	— — — — —	———		Intergametophytic
Cibotium chamissoi	— — —	———————	———	Intergametophytic
Sadleria pallida			———	Intergametophytic
S. souleyetiana			———	Intergametophytic
S. squarrosa			— — —	Probably intragametophytic

in *Nephrolepis exaltata.* The first would relate to shortening the gametophyte generation to facilitate reproduction in what appears to be a harsh xeric environment. The second factor relates to the actual genotype of the plants, which by the process of intragametophytic selfing should be relatively homozygous. In the first instance, the harsh environment of the barren lava flow is restricted to the edaphic factor as soil profiles are lacking. Nearly all sporophytes observed were growing in shallow to deep, wet, cool crevices. With the moderate rainfall in these regions it would appear that these crevices would provide gametophytes with substantial moisture for a lengthy growing season. However, if this is the case, one would expect to find more variety in the species found in this habitat. The second factor, that of genetic homozygosity, deserves more consideration. In this case, intragametophytic selfing can be seen as a mechanism whereby this species can maintain favorable gene combinations which are opportunistic for pioneering and survival on lava flows.

4. Allelopathic Compounds and Antheridogen

Recently, Davidonis and Ruddat (1973) and Petersen and Fairbrothers (1973) have discovered allelopathic compounds produced by sporophytes which detrimentally affect gametophyte growth and development. Davidonis and Ruddat observed that gametophytes of *Thelypteris normalis* would not grow under sporophytes of that species. They determined that the roots of this species were releasing two groups of allelopathic compounds, thelypterin A and B, which were biologically active. Thelypterin A was characterized as a secondary amine-containing heterocyclic molecule with an anionic function. Further experiments utilizing gametophytes of *Pteris longifolia* and *Phlebodium aureum* indicated similar responses to the compounds.

Petersen and Fairbrothers have shown that gametophytes of *Osmunda* spp. are allelopathic to gametophytes of *Dryopteris* spp. by halving the growth rate and cell size of the latter. Both of these studies have attempted to relate ecological advantages in the production of these compounds by the elimination of competitive sporophytes.

Antheridogen has been reported in several species of unrelated ferns, including *Onoclea sensibilis* (Näf *et al.*, 1969), *Ceratopteris thalictroides* (Schedlbauer & Klekowski, 1972), *Pteridium aquilinum* (Döpp, 1950), *Anemia phyllitidis* (Näf, 1959), and *Lygodium japonicum* (Näf, 1960). Antheridogen functions in precociously initiating antheridia on slower growing and later germinating spores and gametophytes of the same species. This phenomenon has been interpreted as a mechanism for increasing the probabilities of intergametophytic mating by increasing the number of intergametophytic sperm present in any spatially dense gametophyte colony. In some cases antheridogen has been shown to precociously induce antheridia formation on gametophytes of unrelated ferns. For example, antheridogen A, released by *Pteridium,* affects gametangia ontogeny in many species of Adiantaceae, Davalliaceae, Aspidiaceae, Blechnaceae, and in one species of Dennstaedtiaceae (Voeller, 1964). The biological significance of this, if any, has yet to be shown conclusively.

TABLE 6. Gametophyte characteristics and predicted mating system.

Intragametophytic	Intergametophytic
Male to hermaphroditic gametangia ontogeny	Female to hermaphroditic; unisexual; heterosporous
Archegonial necks curved toward antheridia	Archegonial necks curved away from antheridia
Simple polyembryony absent	Simple polyembryony present
Underground gametophytes	Superficial gametophytes
Antheridogen absent	Antheridogen present
Generation time short	Generation time long
Genetic load absent	Genetic load present
Apogamy present	Apogamy absent
Vegetative reproduction present	Vegetative reproduction absent
Low recombinational index	High recombinational index
Low hybridization index	High hybridizational index
Narrow ecological tolerance	Wide ecological tolerance

CONCLUSIONS

We have seen from the above discussion that there are numerous parameters affecting reproduction, diversity, and evolution in ferns. These parameters vary from polyploidy, which stores genetic variability, to the mating system, which either releases some of this variability by intergametophytic mating and recombination or perpetuates homozygosity by intragametophytic selfing. Factors directly affecting mating systems in ferns are gametangia ontogeny, production of antheridogen, and genetic load. Genetic load in itself can be used not only as an indicator of heterozygosity in natural populations but can function in supporting intergametophytic mating by eliminating products of self-fertilization. Basic to the level of heterozygosity found in spores produced by a single sporophyte, however, is the presence or absence of homoeologous chromosome pairing during meiosis.

Table 6 indicates features of gametophyte biology which favor particular mating systems. Table 7 summarizes those features which would create under theoretical conditions maximum homozygosity and maximum heterozygosity in natural populations. From these summaries it can be seen that features yielding maximum heterozygosity in sexually reproducing ferns under ideal conditions include large population size, intergametophytic crossing, polyploidy, high mutation rate (assuming non-deleterious mutations), and homoeologous chromosome pairing. Characteristics favoring homozygosity include small populations, intragametophytic selfing, low polyploidy and mutation rate, and homologous pairing. It is doubtful if either of these two theoretical conditions are achieved in nature by any sexually reproducing species. It is more likely that most ferns fall somewhere in between.

Characteristics of the mating system can also influence species patterns. For example, the most distinct species in *Sadleria* (*S. squarrosa*) probably possesses an intragametophytic mating system. Other species in this genus (which have been characterized as having intergametophytic mating systems) show partial

TABLE 7. Characteristics yielding maximum homozygosity and maximum heterozygosity in natural populations of ferns.

Homozygosity	Heterozygosity
Intragametophytic selfing mating system	Intergametophytic crossing mating system
Apogamy present	Apogamy absent
Vegetative reproduction present	Vegetative reproduction absent
Small population size	Large population size
Low polyploids	High polyploids
Homologous chromosome pairing	Homoeologous chromosome pairing
Genetic load absent	Genetic load present
Low mutation rate	High mutation rate

intergradation from one taxon to the next. These patterns may have been brought about by interspecific hybridization which is facilitated by intergametophytic mating systems. *Dryopteris* in the Appalachian Mountains has evolved a number of distinct taxa through hybridization (Wagner, 1970), and work by Cousens and Horner (1970) indicate that these species may also possess intergametophytic mating systems.

Species with intragametophytic mating systems which have maintained the possibilities for intergametophytic crossing can present diversity patterns similar in many respects to those of apomictic flowering plant species which are occasionally sexual. Intragametophytic selfing, like apomixis, is a built-in mechanism for perpetuating specific genotypes. The intrinsic properties of the intragametophytic mating system, like those of apomixes, may in fact far exceed those of intergametophytic mating.

In conclusion I wish to state that it is only through understanding the basic causal factors for genetic diversity and reproduction in ferns that we will ever understand their mode of speciation and evolution. Specifically, they are those factors which are operable from the spore mother cell of the parental sporophyte, through the gametophyte, to establishment of the young sporophytic progeny. During this portion of the life-cycle, dissemination of spores takes place, genetic diversity of progeny is determined, and hybridization and apogamy occur. We are rapidly becoming aware that gametophytes require specific culture conditions for optimum growth. There are numerous parameters of gametophyte biology which have as yet not been discovered, and it is likely that many of these will be uncovered only through the investigation of gametophyte populations in nature.

LITERATURE CITED

COUSENS, M. I. & H. T. HORNER. 1970. Gametophyte ontogeny and sex expression in *Dryopteris ludoviciana*. Amer. Fern Jour. 60: 13–27.

DAVIDONIS, G. H. & M. RUDDAT. 1973. Allelopathic compounds, Thelypterin A and B in the fern *Thelypteris normalis*. Planta 111: 23–32.

DEBENEDICTIS, V. M. 1969. Apomixis in ferns with special reference to sterile hybrids. Unpublished doctoral dissertation, Univ. of Michigan, Ann Arbor.

DÖPP, W. 1950. Eine die Antheridienbildung bei Farnen fördernde Substanz in den Prothallien von *Pteridium aquilinum* (L.) Kuhn. Ber. Deutsch. Bot. Ges. 63: 139–147.

DUCKETT, J. G. 1970. Sexual behaviour of the genus *Equisetum*, subgenus *Equisetum*. Bot. Jour. Linn. Soc. 63: 327–352.

———. 1972. Sexual behaviour of the genus *Equisetum*, subgenus *Hippochaete*. Bot. Jour. Linn. Soc. 64: 87–108.

GANDERS, F. R. 1972. Heterozygosity for recessive lethals in homosporous fern populations: *Thelypteris palustris* and *Onoclea sensibilis*. Bot. Jour. Linn. Soc. 65: 211–221.

HOLBROOK-WALKER, S. & R. M. LLOYD. 1973. Reproductive biology and gametophyte morphology of the Hawaiian fern genus *Sadleria* (Blechnaceae) relative to habitat diversity and propensity for colonization. Bot. Jour. Linn. Soc. 67: 157–174.

KLEKOWSKI, E. J., JR. 1969*a*. Reproductive biology of the Pteridophyta. II. Theoretical considerations. Bot. Jour. Linn. Soc. 62: 347–359.

———. 1969*b*. Reproductive biology of the Pteridophyta. III. A study of the Blechnaceae. Bot. Jour. Linn. Soc. 62: 361–377.

———. 1970*a*. Reproductive biology of the Pteridophyta. IV. An experimental study of mating systems in *Ceratopteris thalictroides* (L.) Brongn. Bot. Jour. Linn. Soc. 63: 153–169.

———. 1970*b*. Populational and genetic studies of a homosporous fern—*Osmunda regalis*. Amer. Jour. Bot. 57: 1122–1138.

———. 1970*c*. Evidence against self-incompatibility and for genetic lethals in the fern *Stenochlaena tenuifolia* (Desv.) Moore. Bot. Jour. Linn. Soc. 63: 171–176.

———. 1971*a*. Ferns and genetics. BioScience 21: 317–322.

———. 1971*b*. Evidence for a duplicated locus in the fern *Osmunda regalis*. Jour. Heredity 62: 367–370.

———. 1972*a*. Evidence against genetic self-incompatibility in the homosporous fern *Pteridium aquilinum*. Evolution 26: 66–73.

———. 1972*b*. Genetical features of ferns as contrasted to seed plants. Ann. Missouri Bot. Gard. 59: 138–151.

———. 1973*a*. Genetic load in *Osmunda regalis* populations. Amer. Jour. Bot. 60: 146–154.

———. 1973*b*. Genetic endemism of Galapagos *Pteridium*. Bot. Jour. Linn. Soc. 66: 181–188.

———. 1973*c*. Sexual and subsexual systems in homosporous pteridophytes: a new hypothesis. Amer. Jour. Bot. 60: In Press.

———. 1973*d*. Homoeologous chromosome pairing in *Ceratopteris*. Amer. Jour. Bot. 60 (4, suppl.): 31.

——— & H. G. BAKER. 1966. Evolutionary significance of polyploidy in the Pteridophyta. Science 153: 305–307.

——— & R. M. LLOYD. 1968. Reproductive biology of the Pteridophyta, I. General considerations and a study of *Onoclea sensibilis* L. Jour. Linn. Soc. Bot. 60: 315–324.

LLOYD, R. M. 1971. Systematics of the onocleoid ferns. Univ. California Pub. Bot. 61: 1–94.

———. 1973*a*. Systematics of the genus *Ceratopteris* (Parkeriaceae), I. Sexual and vegetative reproduction in Hawaiian *Ceratopteris thalictroides*. Amer. Fern Jour. 63: 12–18.

———. 1973*b*. Facultative apomixis and polyploidy in *Matteuccia orientalis* (Hook.) Trev. Amer. Fern Jour. 63: 43–48.

———. 1974. Mating systems and genetic load in pioneer and non-pioneer Hawaiian Pteridophyta. Bot. Jour. Linn. Soc. In Press.

——— & E. J. KLEKOWSKI, JR. 1970. Spore germination and viability in Pteridophyta: Evolutionary significance of chlorophyllous spores. Biotropica 2: 129–137.

NÄF, U. 1959. Control of antheridium formation in the fern species *Anemia phyllitides*. Nature 184: 798–800.

———. 1960. On the control of antheridium formation in the fern species *Lygodium japonicum*. Proc. Soc. Exp. Biol. 105: 82–86.

———, J. SULLIVAN & M. CUMMINS. 1969. New antheridogen from the fern *Onoclea sensibilis*. Science 163: 1357–1358.

PETERSEN, R. L. & D. E. FAIRBROTHERS. 1973. Allelopathy: gametophytic chemo-antagonism between *Dryopteris* and *Osmunda* or supporting the "weakest link" hypothesis. Amer. Jour. Bot. 60 (4, suppl.): 32.

SAUS, G. L. 1973. Reproductive biology of the fern *Onoclea sensibilis* L. Unpublished master's thesis, Ohio Univ., Athens.

SCHEDLBAUER, M. D. & E. J. KLEKOWSKI, JR. 1972. Antheridogen activity in the fern *Ceratopteris thalictroides* (L.) Brongn. Bot. Jour. Linn. Soc. 65: 399–413.

TATUNO, S. & H. YOSHIDA. 1966. Karyological studies on Osmundaceae. I. Chromosomes of the genus *Osmunda* in Japan. Bot. Mag. (Tokyo) 79: 244–252.

——— & ———. 1967. Karyological studies on Osmundaceae. II. Chromosomes of the genera *Osmundastrum* and *Plenasium* in Japan. Bot. Mag. (Tokyo) 80: 130–138.

VOELLER, B. R. 1964. Antheridogen in ferns. Natl. Rech. Sci. (Paris) 123: 665–684.

WAGNER, W. H., JR. 1970. Evolution of *Dryopteris* in relation to the Appalachians. *In* "The distributional history of the biota of the southern Appalachians, Part. II." Virginia Polytechn. Inst. & St. Univ. Res. Div. Monogr. 2.

STRUCTURE OF SPORES IN RELATION TO FERN PHYLOGENY[1]

WARREN H. WAGNER, JR.[2]

Only in the past quarter of a century have the spores of ferns been used extensively in elucidating systematic relationships. Surprisingly, F. O. Bower (1923–28) made but little use of spores. In his volume I, "Criteria of Comparison," there was no chapter on spores *per se*, and he devoted only a few pages to the subject (pp. 258–272). The trend toward utilizing spore structure was illustrated by Copeland (1947) who used them in characterizing the taxa in *Genera Filicum*. Since then there has been a veritable explosion in the interest in fern spores. The advent of more critical optical equipment, especially the scanning electron microscope, has provided a strong boost to palynological studies in general, especially at the level of species, varieties, and hybrids. For the investigation of spores taken from dried plants on herbarium sheets, the technique of using gummed tape, as described by Martin and Drew (1969), has proved to be especially valuable.

Fern spores have actually been objects of study for well over a century, but many of the earlier papers are overlooked or ignored. Of course some represent only minor contributions, but one of them, the important article by E. Hannig (1911), pioneered the research on the development of the perispore and on the systematic significance of this, somewhat controversial, structure. (Alston's later [1956] application of data from the perispore to classification was long presaged by Hannig.) Among other notable early workers were Fischer (1892), Fischer von Waldheim (1864), and Tchistiakoff (1874), each of whom gave contributions to the knowledge of the morphology and development of fern spores.

Studies of spores of ferns of given localities have been popular for many years. C. B. Weaver in 1895 made one of the earliest of such investigations, "A Comparative Study of the Spores of North American Ferns," in which he illustrated 59 species. In 1935, McVaugh made a similar study of ferns of northeastern United States. Reed's 1953 book on the species of Maryland and Delaware is notable for illustrating not only the plants but their spores as well. More recently, Oliver (1968) described the spores of ferns of Indiana, and Maloney (1961a, 1961b) those of Minnesota.

In other parts of the world we have the works, for example, of Knox (1951) involving British ferns, Sladkov (1959*a*, 1959*b*, 1959*c*, 1961, 1968) on Russian ferns, and Sorsa (1964) on Scandinavian ferns. Especially valuable for the general systematist are the investigations of Selling in Hawaii (1944, 1946), Tschudy and Tschudy in Venezuela (1965), and in particular Harris's book

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(1955) on New Zealand fern spores. Tardieu-Blot's reports (1964, 1965, 1966) on Madagascar are notable for the excellence of the illustrations.

With all of this information now available for geographical areas, there is little surprise that fern systematists have been encouraged to utilize the comparative aspects of spores in arriving at conclusions. Further stimulation to the palynological investigation of ferns by systematists has been occasioned by the appearance of a number of general works such as that by Brown (1960*a*, *b*) on techniques of preparation, Foster (1956) on microscopy, Kremp (1965) on nomenclature, and especially the book by Erdtman (1957) on pollen and spore morphology of gymnosperms, pteridophytes, and bryophytes. As a result of the interest engendered in spore structure in relation to fern relationships, we have witnessed numerous reports on specific taxonomic groups.[3] For example, the genus of woodferns, *Dryopteris*, has been the focus of special attention because of its unusually interesting cytogenetic and evolutionary aspects. Of the students of spore structure in special groups, Nayar and his co-workers (see bibliography) have been exemplary, and they have contributed numerous substantial reports on various critical genera and species-groups.

The present paper is concerned with painting in a broad picture of the structure of spores in relation to fern phylogeny. I wish to examine trends in various characters as well as their relationship to broad phylogenetic questions. The emphasis is upon homospores rather than the highly specialized heterospores, and the terminology used here is mainly traditional. For a fairly conservative use of terminology the reader is referred to Harris (1955: 12–25). Fern spores are usually either tetrahedral or bilateral in over-all form, the laesurae triradiate or linear respectively. The wall layers are produced by elaboration of the exine or exospore, although there may also be a distinguishable outer layer in ferns, somewhat different in nature from the exine, which is referred to as perine or perispore (illustrated best in the dryopteroid and asplenioid ferns). The protoplast contains a single nucleus until the time of germination, and there are proplastids and sometimes chloroplasts present as organelles. Storage materials are visible, usually in the form of droplets. The spores are mostly transparent as seen under the compound light microscope, so it is possible to make out the major structures fairly well. Optical interference, however, often makes it difficult to assess precisely the structure of the surface, and for this reason critical observations on the surface configuration are made best with the scanning electron microscope.

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[3] To illustrate the nature and range of recent work, the following may be noted: Botrychioideae: *Botrychium*, Haeggstrom & Nieml (1964–65). Ophioglossoideae: *Ophioglossum*: Nakamura and Shibasaki (1959); Sladkov (1959*a*). Osmundaceae: Bobrov (1966). Polypodioideae: Kawasaki (1968); N. Pal and S. Pal (1964); S. Pal and N. Pal (1970); *Polypodium*, Evans (1968). Schizaeoideae: Bolkhovitina (1959, 1962); Selling, *Schizaea* (1944). Anemioideae: *Anemia*, Mickel (1962). Adiantoideae: *Cheilanthes*, Knobloch (1966, 1969); *Pteris*, Sladkov (1957, 1959*b*, 1961). Dryopteridoideae: "Davalliaceae," Braggio (1966); *Dryopteris*, Britton (1968, 1972*a*, 1972*b*); Crane (1955, 1960); Kanamori (1969); Mitui (1972*a*, 1972*b*); Reed (1954); *Polystichum*, Daigabo (1967); *Bolbitis*, Hennipman (1970); *Cystopteris*, Blasdell (1963); Hagenah (1961). Asplenioideae: Bir (1966–67*a*); Wagner (1952, 1966). Azollaceae: Fulvio (1961).

TABLE 1. Evolutionary trends in spore structure which seem probable on the basis of present evidence.

Character	Primitive	Derivative
a. Number	256 or more	128, 64, 32, 16, 4
b. Diameter	25–70 microns	70 or more microns
c. Division type	Meiospore	Mitospore
d. Shape	Tetrahedral	Globose
	Tetrahedral	Bilateral
e. Differentiation	Homospores	Heterospores
f. Variation	Narrow	Wide
g. Exine thickness	1 micron	2 or more microns
h. Exine sculpture	Finely sculptured	Coarsely sculptured
	Finely sculptured	Smooth
	Non-ridged	Parallel-ridged
	Unisculptate	Bisculptate
i. Equator elaboration	Weak	Pronounced
j. Laesura	Flush or nearly so	Raised or ridged
k. Perine	Absent	Present
	Corrugated	Smooth
	Cristate	Spinulate
	Cristate	Tuberculate
l. Color *en masse*	Tan to yellow	Black
m. Organelles	Proplastids	Chloroplasts
n. Amount of food	Moderate	Abundant
o. Resting stage	Present	Absent
p. Survival	Months to years	Weeks to days
q. Germination time	1 week or more	1 day or less
r. Germination medium	Mineral only	Organic
s. Germination pattern	Linear	Triradiate

Any determination of what constitutes a primitive state in the structure of fern spores must be based upon homologies. If, for example, the "perispore" of one taxon has one origin, and the "perispore" of another has another, any phylogenetic conclusions about the perispores of these plants are likely to be erroneous; we cannot say that one is derived from the other, or that one is evidence of affinity to the other. The fact is that fern spores are extremely simple structures with relatively few characters; parallel evolution has probably occurred repeatedly (see below), as well as convergent evolution. The fossil record of ferns is relatively poor. What we know of it suggests that the tetrahedral type of spore is the most primitive (this type was dominant in the Devonian and the Carboniferous). If we compare spore structure in classes of homosporous plants outside of the ferns, we find that once again the tetrahedral spore is the most prevalent. Again, comparison within the ferns shows the tetrahedral condition to be most widespread. Out of 25 taxa at the level of subfamily, the bilateral spore is dominant in 6, occurs approximately equally with the tetrahedral in 2, and is in the minority or is entirely absent in 17.

Using such bases for judgment as given above, the ancestral fern spore may be described tentatively as follows: Tetrahedral, 25–60 microns in diameter, produced by meiosis, 256 or more per sporangium, undifferentiated into heterospores and showing but little inter-spore variation, the exospore ca. 1 micron thick, minutely sculptured or smooth, with but a single pattern and the equator a simple angle, perispore absent. As seen *en masse* the spores appear yellow to tan and contain proplastids (not chloroplasts). Metabolites are visible within as droplets or small bodies, and the spore is capable of remaining viable to periods of months to years under natural conditions. Germination requires several weeks and is either amorphous at first or unipolar.

Such a description as that above should not be taken in any way as a final declaration of what the original fern spore was like. We must recognize other alternatives, at least as real *possibilities*. Such evolutionary phenomena as reversals and parallelisms have very probably occurred repeatedly and may perhaps have altered the real trends sufficiently as to obscure them. New evidence may change the whole pattern.

Table 1 summarizes a number of evolutionary trends in spore structure which, at present, seem probable on the basis of our evidence. At this point it is hard to imagine what adaptive value bilateral spores may have over tetrahedral, or indeed perispore *vs.* its absence, or most of the other trends. In this regard, the subject of possible adaptive "syndromes" will be discussed below.

Bower (1923: 264) dealt with the trend in spore number per sporangium in considerable detail. When we discover only 32 or 16 spores per sporangium, it may be the result of two processes—the assumption of the apogamous life cycle (discussed later) or an actual diminution in spore number as a result of reduction in number of spore mother cells and the number of archesporial divisions leading up to meiosis. The number 64 is certainly the most widespread in ferns; but such primitive assemblages as Ophioglossaceae, Marattiaceae, and Osmundaceae have much higher numbers, suggesting that reduction to 64 had adaptive significance in evolution. When there are only 4 spores per sporangium, this is associated with megaspory.

Although no statistical analysis has been made that brings together all the published data, the many reports on spore size in the literature (*e.g.* Harris, 1955; Selling, 1946; Tschudy & Tschudy, 1965) strongly suggest that spore dimensions over 70 microns are derivative. "Standard" fern spores run between 25 and 60 microns. Several factors may be responsible for increase in spore size, of which two are considered below. Typical ferns produce their spores by meiosis in spore mother cells with $2n$ or sporophytic number. However, there are several specializations related to apogamy, in which there are modifications of the cytokinetic origin. In the most common apogamous condition (meiotic apogamy), the sporophyte is cytogenetically a "hybrid," with failure of chromosome pairing at meiosis. Restitution nucleus formation takes place, however, prior to meiosis, thus doubling the chromosome number and making normal sporogenesis possible. The spores have then the same chromosome number as the sporophyte. As a rule, apogamous spores are more irregular than sexual, as shown in Figure 7 and as discussed by Kanamori (1971). Another form of apogamy, which is much less common, involves mitospores. There is no interjection of a restitution nucleus stage, and sporogenesis is entirely mitotic (Evans, 1969).

As indicated, of the two basic spore shapes, the tetrahedral appears to be

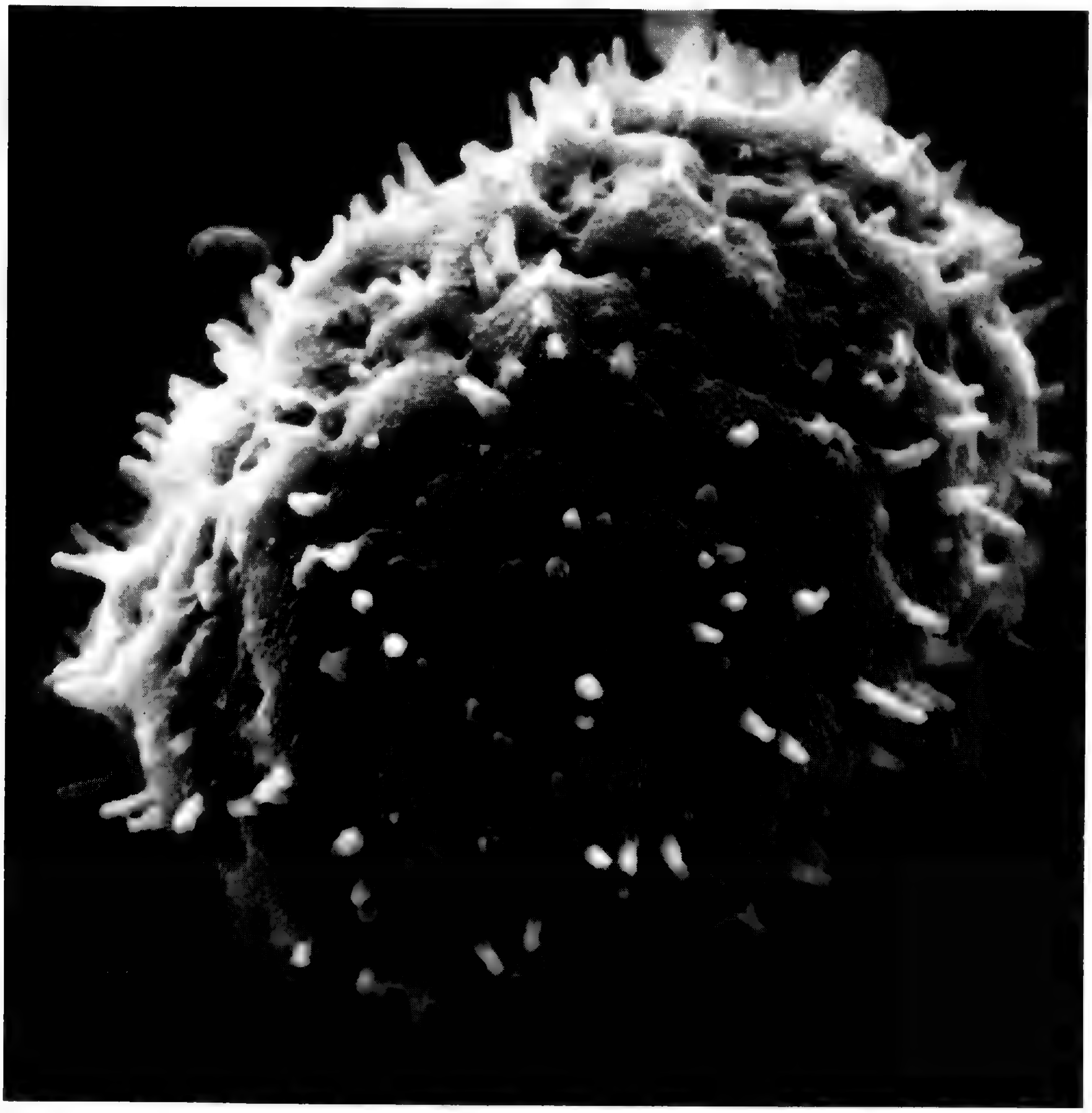

Figure 1. Bisculptate spore of *Arthromeris himalayanum* (Polypodioideae). Nepal, *Fleming*, 1961 (MICH).

the most primitive. The trilete and monolete patterns of the laesurae correspond to these shapes and result presumably from the manner of cytokinesis involved in their morphogenesis. Studies of the origins of different over-all shapes have been carried out by Marengo (1954, 1959, 1962). Usually one condition or the other—tetrahedral or bilateral—is fixed for a given genus, but intermediates may occur, especially in connection with hybridity or apogamy. Nayar (1967) has found various intermediate types in the somewhat controversial genus *Loxogramme*, and Selling (1946) reported that in Hawaiian *Botrychium*, *Ophioglossum*, *Cibotium*, *Pteris*, *Coniogramme*, and *Adiantum*—all basically tetrahedral-spored taxa—bilateral spores were found "often" to "very rarely"; conversely in *Marattia*—basically bilateral-spored—he encountered tetrahedral spores, "rarely."

No one seems to question that the heterosporous condition is specialized in pteridophytes. It is difficult to imagine reverse evolution when so many factors are involved—endosporic gametophyte development, food storage, fast germination in wet conditions, as well as the extreme size differences. Heterospory should not be regarded as a mere size difference, but instead a profound alteration of the spore apparatus in which the differentiation of two sexes is complete. Alice Tryon and Vida (1967) speak of "incipient heterospory" in *Platyzoma* which McLean Thomson showed had small spores, ca. 32 per sporangium, and large spores, 16 per sporangium (Bower, 1923). Other deviations from uniformity or constancy in spores are usually related to cytogenetic upsets. Most fern spores are fairly uniform and produce a more or less steep normal curve of size distribution. However, hybrids derived from two or more species and which have not undergone polyploidization tend to have extremely variable spores (Wagner & Chen, 1965; Kanamori, 1969).

The exospore is the most valuable source of data thus far in working out evolutionary relationships at the species and generic level. The architecture of the exospore (exine) is extremely diverse, and Gullvåg (1966) has presented a selective review of the fine structure of pollen grains and spores that is pertinent to its study. Pettitt (1966) has made valuable contributions based upon his investigations of exine structure as revealed by light and electron microscopy. It is evident that very thick-walled spores (*i.e.* layers of 2–6 or more microns thickness) are unusual and probably derivative. Certain genera (*e.g.* *Cyathea*, *Pityrogramma*, *Pteris*) possess individual species with strikingly thick exospores (Nayar & Devi, 1966; Tardieu-Blot, 1965). The most widespread exine sculpturing in ferns seems to be either very finely ornamented or essentially smooth. Massive, coarse sculpturings appear to be specialized.

Three features found in the exospores of certain ferns are almost unquestionably derivative—one involving the entire sculpture pattern, another the spore equator, and another the laesura. Figures 1 and 2 show scanning electron microscope photographs of *Arthromeris* and *Drymoglossum*, genera in the Polypodioideae in which there are actually two patterns, one upon the other. This condition, which I call "bisculptate," involves in these examples spines and pyramids, respectively, these superimposed on different basic patterns. Figure 3 shows photographs of different SEM views of the spores of a species of *Pityrogramma*, one of a number of genera in which certain species display remarkable elaboration of the equatorial region to produce one or more massive, rounded ridges (so-called "spare tires") around the circumference. Strongly raised or wall-like laesurae are rare (for an example, see Tschudy & Tschudy, 1965; p. 31, figs. 51–52) in ferns and most likely specialized.

Perispore or perine has been and still remains a somewhat controversial subject. Classically the term has been applied to the type of spore covering found in dryopteroid, blechnoid, and asplenioid ferns—corrugated, sac-like, easily destroyed envelopes (*cf.* Nayar & Devi, 1964*b*; Tarieu-Blot, 1966). The perispore begins its formation after the spore has reached full size and the exospore has completed its development; the first evidence of its formation is a brownish, undulate surface covering. The lines of the crests soon become evident as dull, darker areas (Wagner, 1952). In the fossilized state, the perispore

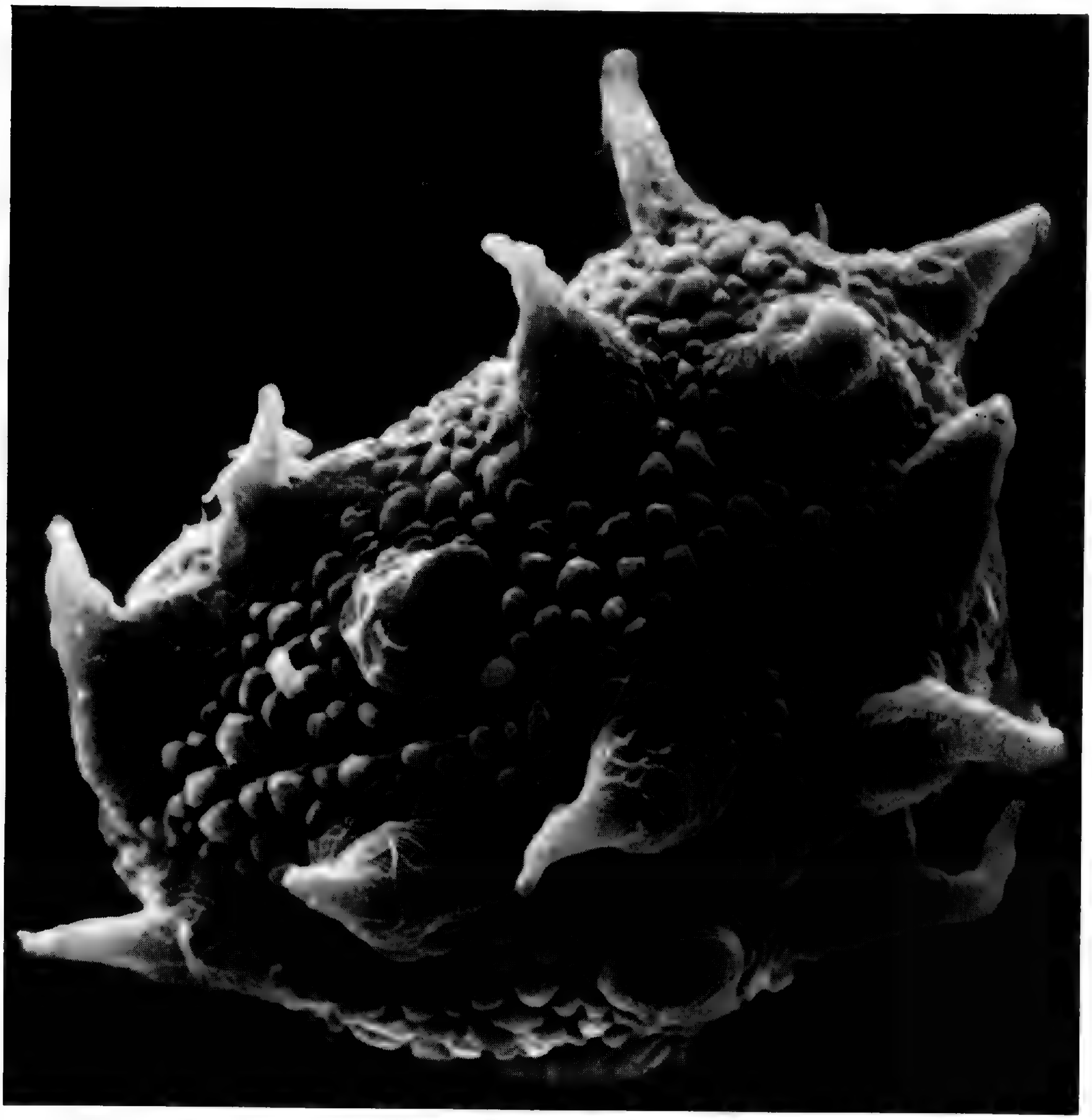

FIGURE 2. Bisculptate spore of *Drymoglossum piloselloides* (Polypodioideae). Philippines, *Mendoza*, 1953 (MICH).

is absent (Selling, 1946), leaving only the exospore. "Typical" perispores occur in Dryopteridoideae, Blechnoideae, and Asplenioideae, and there are many variations—smooth, tuberculate, cristate, reticulate, spinate. The commonest form, however, looks like the covering of a shrunken prune (*cf.* Tschudy & Tschudy, 1965), and this seems to be the basic type. Some of the best early studies of the perispore were those by Hannig (1911), who was also one of the earliest forerunners to exploit its presence in conjunction with systematics. Pettitt (1966) finds that at least in *Asplenium adiantum-nigrum* "the outer layer . . . or so-called perispore appears, ultrastructurally, to resemble a true exine layer," and he proposes that "there is clearly a need for a full comparative developmental investigation into the formation of these wall layers." On the contrary, the studies of Lugardon (1965) and Hennipman (1970) caused them to recognize a perispore, at least in species of *Blechnum* and *Bolbitis*.

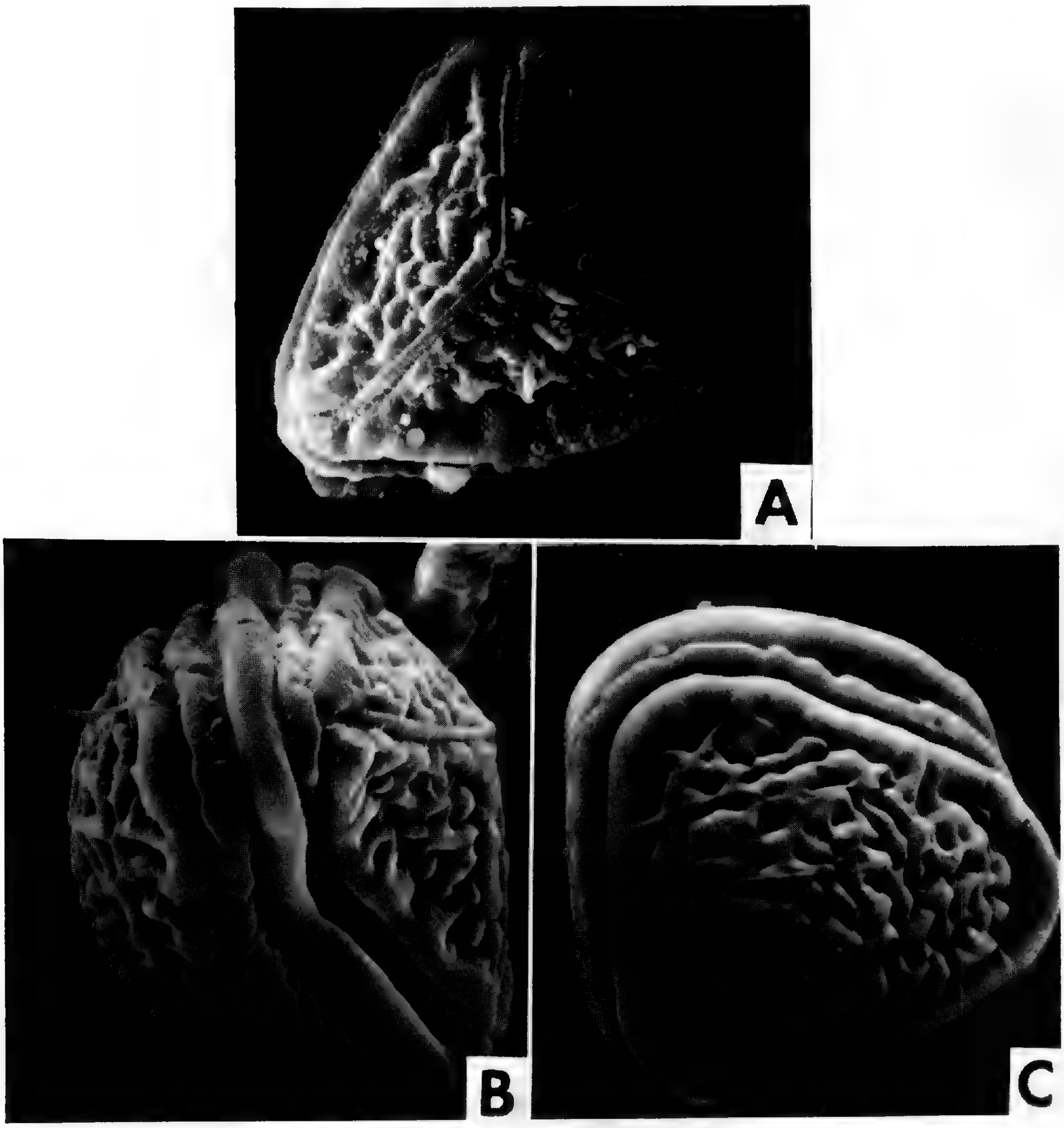

FIGURE 3. Equatorial elaboration shown in three views of spores of *Pityrogramma calomelanos*. Bolivia, *Rusby 130* (MICH).

In any event, the presence of the typical sac-like structure known as the perispore, whatever our ultimate conclusions as to its distinction from the typical spore wall layer or exospore may be, must be considered a specialization. Structures of this sort, so clearly differentiated from the underlying exospore layer, are, except in the indicated subfamilies, extremely rare or absent. The most elaborate perisporial structure known to me is that of *Athyrium klotschii*, a species widespread in tropical America. In this species not only are the ridges extremely tall and sharp, but in the depressions, complex vermiform masses of wall material are formed (Fig. 4).

Further research is decidedly needed on the nature of the perispore, and as an introduction to the problems the discussions of Kremp (1965) and Hennipman (1970) are commended.

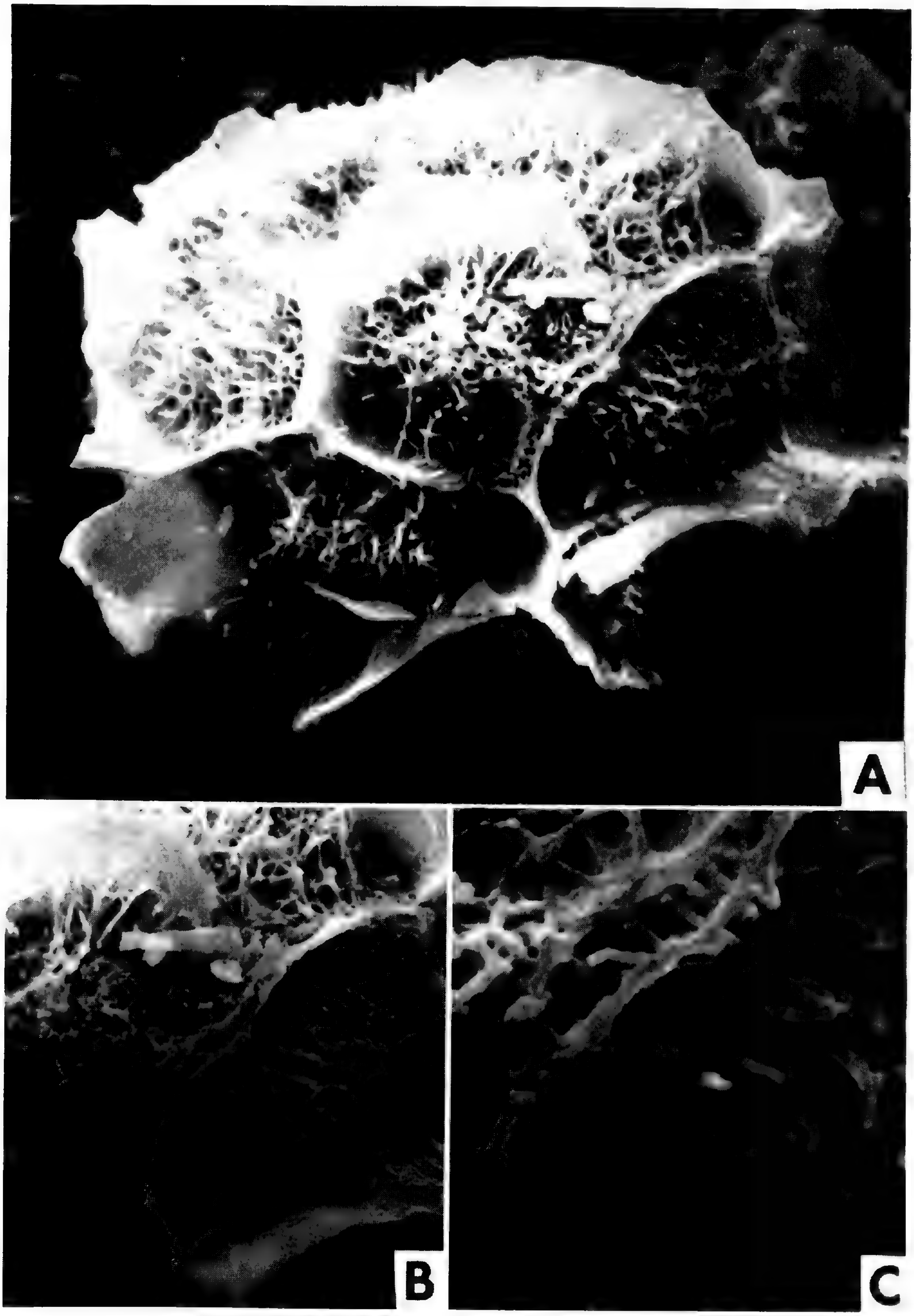

Figure 4. Perispore seen at 1500 (A), 4000 (B), and 12,000 (C) times magnification. *Athyrium klotschii*, Bolivia, *Rusby 394* (MICH).

Another characteristic—the metabolite—is also greatly in need of investigation. In general, palynologists are interested in the "shell" and not the organism within; most techniques designed to elucidate the nature of the wall, in fact, tend to destroy the protoplast. Some spores tend to be so "full" of oil drops and other materials that they become optically difficult and the configuration of the wall becomes obscure as seen under the light microscope. The fine structure of primary storage products of the green-spored *Equisetum fluviatile* and the non-green-spored *Blechnum spicant* were examined by Gullvåg (1969), who noted some important differences. Among the comparative data we need on metabolites are the following: (a) chemistry, (b) amount relative to the volume of the protoplast, and (c) form of the inclusions. It might be noted that certain species of both lycopods and of ferns, the spores of which germinate underground, have been found to be especially flammable, igniting easily and producing sheets of fire when scattered in the air and lighted with a burning match, suggesting that they may possess distinctive oils (*cf.* Tulloch, 1965).

The pigmentation of spores may be caused by at least two different factors, namely (a) wall color, or (b) contained chlorophyll. Normally fern spores are yellowish to brown as seen *en masse*. Black spores are relatively rare. Often hybrid perisporial ferns show blackish or deep brown sori and spores, apparently as a consequence of abortion and irregular, sometimes massive, development of the perispore. One of the genera or subgenera of thelypterid ferns—*Amphineuron* Holttum (1971; 45)—is described as having "sporae fere nigrae." The only member of this group which I have studied myself (*A. gretheri* from Rota, Marianas Islands, Wagner, 1948) had spores which were jet black. Green spores are known in several widely separated taxonomic groups, including Osmundaceae, Hymenophyllaceae, and Grammitidaceae, as discussed by Lloyd and Klekowski (1970). These spores not only have chlorophyll present, but they lack a resting period, germinating immediately in the proper environment. Their walls are thin, and the spores tend toward the globular form. They will be considered below.

Nayar and Kaur (1968) have given us a fine and detailed review of spore germination in homosporous ferns. They conclude the original ferns probably had what is called the "Amorphous type" of germination in which cell divisions occurred in all directions (*e.g.* in Marattiaceae, Matoniaceae, and members of Schizaeoideae). A plate of cells could evolve from an amorphous mass of cells by suppression of divisions in any one of the planes. One of the most distinctive germination patterns involves the "*Hymenophyllum* type," in which the germling is triangular, arising in a tripolar manner (Stokey, 1940; Atkinson, 1960). Although this could have arisen from the rather rare "Amorphous type," the possibility should also be entertained that, because of the specialized nature of the filmy-fern life habit, it arose from the "*Osmunda* type" or the "*Cyathea* type," both of which form "germ filaments," linear filaments of cells, in germination.

So far we have dealt largely with what might be called "purely morphological trends," these more or less divorced from their functional or ecological aspects. The structure of spores in relation to fern phylogeny must ultimately be tied to their adaptive significance, or lack of it. I am of the opinion that when we observe repeated parallelisms and convergences, these are usually of biological significance and tend to improve the survivability of a given line of evolution. What is the adaptive value of few spores per sporangium, of bilateral over-all shape, or of the sac-like perispore? About these we know little or nothing. In regard to other trends, however, there do appear to be fairly convincing correlations that indicate adaptations.

One of these is, of course, heterospory (*cf.* Piérart, 1961). With the gametophytes endosporic and parasitic, and the megaspores provided with much food, heterospory permits rapid fertilization (there being no need to "grow" a gametophyte), and there is abundant food already available for the developing embryo. This condition, so well known in Marsileaceae, Azollaceae, and Salviniaceae, enables species to exist in drought habitats where the ponds dry up. Sporadic rains and formation of pools enable these plants to go through their reproductive cycle. The phenomenon of apogamy also seems to be correlated with dry habitats. In apogamy, the number of spores per sporangium is halved, and through either restitution nucleus formation or direct mitotic division, the chromosome number of the spores is the same as that of the sporophyte (interestingly, triploidy is one of the commonest genome situations in apogameons). It is observed especially in Adiantaceae in such genera as *Pteris*, *Pellaea*, and *Cheilanthes*, and because of the ability to produce a sporophyte by direct proliferation from the gametophyte, it enables the plant to reproduce by spores but without dependence upon free water. All that is required is a humid environment, and water for the sperms to swim in may be lacking. These plants occur most commonly in well drained habitats or dry, often rocky, cliffs.

As noted earlier, large spore size, *i.e.* size that is amplified well beyond the normal for the given species or species-group, is evidently derivative. There do seem to be at least two biological correlations involved in large spores, these unrelated to one another. The first and best-known is the change in spore size associated with multiplication of the basic chromosome number due to doubling one or more times (*e.g.* Bir, 1966–67*b*; Blasdell, 1963; Kanamori, 1971; Wagner, 1970). Where normal spores are produced by these polyploids, their cytogenetic constitution appears to be either $A^1A^1A^2A^2$ (*i.e.* autopolyploids in which different pairing factors enable normal meiosis) or $A^1A^1B^2B^2$ (*i.e.* allopolyploids with different pairing factors). Most taxa at the subfamily-family level are known to have polyploids. The polyploids in *Ophioglossum* are noted for their huge numbers—up to $2n$ over 1200! Only, no polyploids have yet been reported in Osmundaceae. The other correlation involving large spores is the one detected by Sherwin Carlquist in his studies of loss of dispersibility in the Hawaiian flora. Carlquist (1966) found that unusually large spores occurred in certain taxa (Schizaeoideae, Hymenophylloideae, Adiantoideae, Blechnoideae) in members which occurred in the rainy, high forest of the islands of the Hawaiian archipelago. According to his theory, the production of unusually large spores counteracts the wide scattering of spores to unsuitable low, dry areas (or out to the high seas). The spores thus tend to fall near by, on the same or adjacent high rain-forest ridges.

The possible biological significance of chlorophyllous spores has been analyzed by Lloyd and Klekowski (1970). These spores, which are found in Osmundaceae, Grammitidoideae, Hymenophylloideae, as well as *Onoclea* and *Matteuccia* in the Dryopteridoideae, are characterized by thin walls, a more or less globose outline, short viability, and quick germination. Rather than proplastids they contain chloroplasts. I am impressed by two correlations—one in space, the other in time. Green spores occur in the rain forest (grammitids, filmy-ferns) in the tropics, where they are produced, presumably, year-round. Green spores also occur in the temperate zones (osmundas, onocleoids), but here they are produced in the spring only—the period of maximum rain. In both situations, the large amount of available moisture is evident. Thus the spores will not be damaged by the environment (as they would in drier places or times), and there is no need for resistance. This type of spore apparatus allows for immediate germination, and there is no resting stage.[4]

A type of spore which has long baffled the experimental morphologist is characterized by its nearly ungerminable behavior in culture. Only recently have techniques been developed to germinate *Botrychium* spores, for example. In the laboratory of Dean P. Whittier (Vanderbilt University, Nashville, Tenn.) great strides are being made toward germinating spores of this type and growing their gametophytes (Whittier, 1972, 1973). Nevertheless, it is clear these spores, which are found in Botrychioideae, Ophioglossoideae, certain Schizaeoideae (and also lycopods), have a distinctive behavior under natural conditions, as well as under culture conditions involving purely mineral media. The walls seem to be very resistant and the contents, as seen under the light microscope, commonly show a profusion of oil droplets (*cf.* Tulloch, 1965). Germination in nature apparently requires fungal symbiosis. Germination-resistant spores are correlated with buried habitats, lacking light, and having suitable fungal components for forming mycorhizal relationships. By making the necessary evolutionary changes, germination becomes delayed so long as to enable the spore to percolate into the soil, and there establish symbiosis. This explains why so many of the gametophytes of grapeferns, adder's-tongues, and clubmosses are found 1–5 cm below the soil surface. They obviously did not sink to those levels after germinating at the surface.

Any adaptive correlation for bilateral spores is at this point difficult to detect. However, there is one group of bilateral spores which may prove to be adaptive, although this is not yet clear. It involves the type of spore so common in Poly-

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[4] In studies of times of spore release in pteridophytes of the Great Lakes area, which I have been carrying out in collaboration with Royce H. Hill, we find that not only the osmundas (3 spp.) and onocleoids (2 spp.), but the equisetums as well (9 spp.) tend to discharge their spores in April and May (June in northern Michigan). The fact that horsetails and scouring-rushes, which also have chlorophyllous spores, tend to release them at the same time reinforces, we believe, our conclusion of the adaptive significance. Further reinforcement comes from an examination of the spores produced in the driest season of the year (August, September): The latest spores to be produced by pteridophytes of Michigan are those of 4 out of 10 species of *Botrychium* (all members of subgenus *Sceptridium*), and all 11 species of *Lycopodium*. These, of course, represent the taxa which possess mycorhizal gametophytes which are more or less subterranean, and which are *slowest* to germinate.

podioideae and Dryopteridoideae in those members which may be termed "dry epiphytes." These include such genera as *Polypodium*, *Pyrrosia*, *Davallia*, *Humata*, and *Nephrolepis*, the species of which tend to grow in dry tree-canopy in epiphytic situations in tropical regions, usually in the rain shadow or at middle or low elevations. They may grow also on rock cliffs. As can be shown in a comparison of polypodioid ferns (Nayar & Devi, 1964*a*) and davallioid ferns (Tardieu-Blot, 1964; Braggio, 1966) there are some remarkable resemblances between the spores, especially the types with shallowly tuberculate or mamillate sculpture. This may constitute a case of convergence, as the relationships of the polypodioid ferns are with families lacking the typical perispore, while the davallioids are evidently derived from dryopteroids with the typical perispore. Thus the davallioids may have lost or greatly reduced this structure, the end-result being a spore strikingly similar to the unrelated, but ecologically similar, polypodioids.

In an interesting statistical analysis, Ito (1972) found that in eastern Asia and northern Oceania there is a correlation between the ratio of monolete:trilete spores (m:t ratio) and geography. The values of m:t increase in accordance with the latitude and altitude in the northern hemisphere, according to his results, the trilete ferns being more abundant in the warmer regions, the monolete in the colder regions. In the Philippine Islands m:t = 1.27, but in eastern Himalaya m:t = 2.25, and in Japan m:t = ca. 2.71. Following his procedures (*i.e.* eliminating "fern allies," heterosporous ferns, and hybrids), I find in Hawaii (with a total of 128 native ferns) that the ratio m:t = 1.66, roughly equal to his ratio from the Bonin Islands and the Ryukyu Islands. However, in the state of Michigan with 63 species, and fairly representative of the north-central region of North America, I find a ratio of 1.74, considerably lower than I had expected. Part of the reason for this result is the unusually rich representation of ophioglossoids in the Great Lakes region. And this also points up the critical importance of taxonomic interpretation in arriving at conclusions of this type. Phytogeographers will recognize immediately the enormous relative increase in representation southward of groups such as cyatheoids, (Cyatheoideae), filmy-ferns (Hymenophylloideae), and dwarf polypodies of the rainforest (Grammitidoideae)—all groups with mainly or exclusively tetrahedral spores. Using Harris's (1955) data, the ratio for New Zealand (152 spp.) is m:t = 0.97.

Many fern taxa, especially in the temperate zones, are characterized by extremely variable spores, variable both in their shapes and their sizes. The majority of these spores lack protoplasts and are patently abortive, unable to germinate or reproduce the fern. A few of the spores do, however, contain protoplasts and will form gametophytes (Morzenti, 1962; DeBenedictus [née Morzenti], 1969), and in some instances the percentages of germination are surprisingly high, reaching as much as 36 per cent (Whittier & Wagner, 1971), even though, in practically all examples investigated, the ferns involved are interspecific hybrids. Taxa with the majority of their spores abortive are correlated in occurrence with an association of two species of close relationship which are capable of forming hybrids. Interspecific hybrids have been found

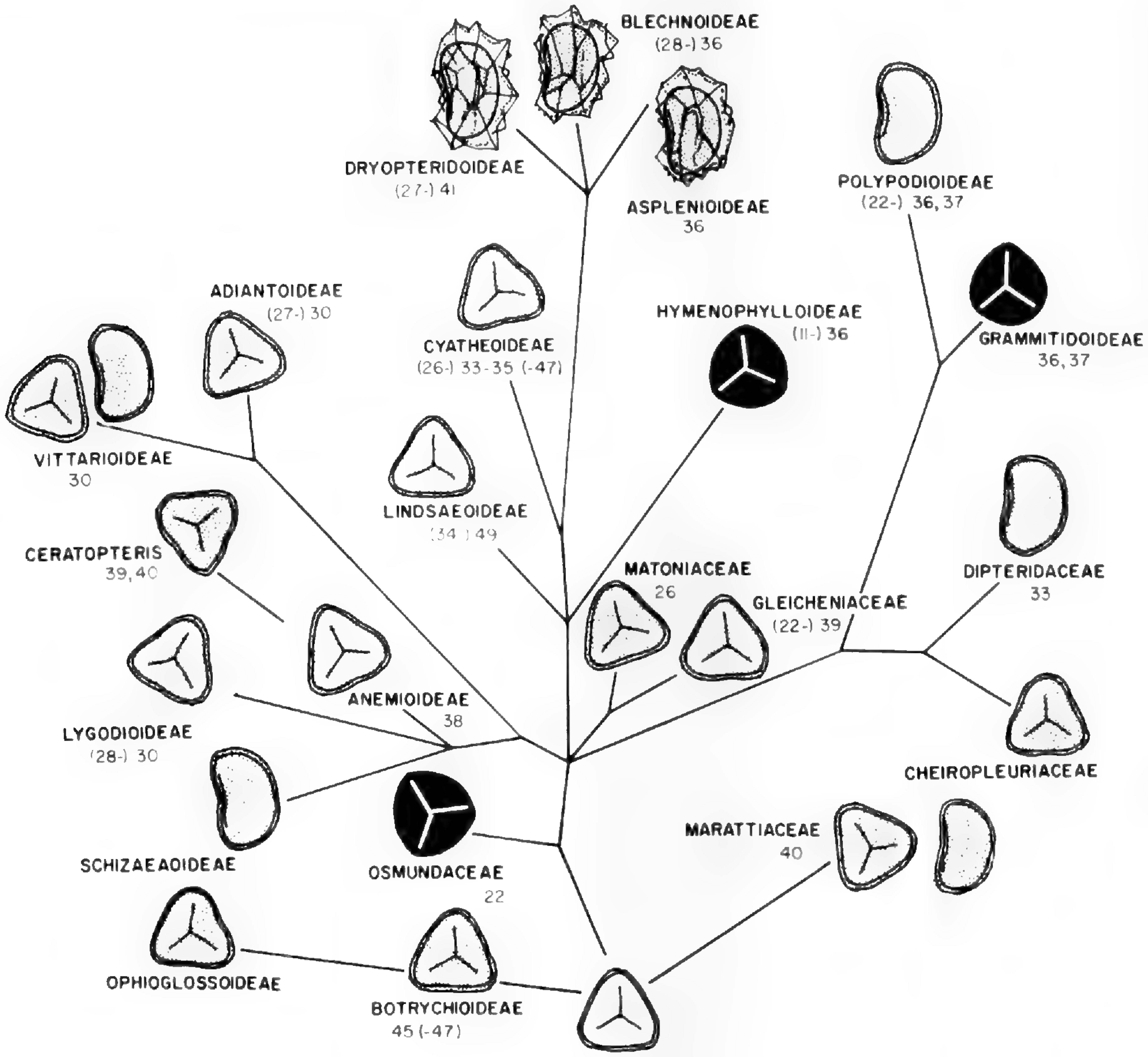

Figure 5. Correlation of spore types with phylogenetic groupings of families and subfamilies of ferns. Chlorophyllous spores shown in black; perinous spores with angular covering. Possible basic chromosome numbers shown in parentheses under the taxa.

in practically all subfamilies of ferns, but they seem to be relatively rare in tropical epiphytes. Presumably sterility barriers arise due to accumulated genetic differences between the parents, but they may also be adaptive to the extent that they oppose breakdown of the respective fitnesses of the parental species by the prevention of sloppy combinations of characters.

Spores and Over-all Phylogeny

That the spores may be useful in solving controversial problems of relationship is unquestioned. In my own research, I have found them especially useful (*e.g.* Wagner, 1952); in the Hawaiian genus *Diellia*, associated by many authors with the lindsaeoid ferns, the spores showed convincingly that the relationships were elsewhere. As in all systematic data, however, it is imperative that the evidence from this one source be correlated with that from other sources. In recent years the study of spore abortion has become a valuable tool in detecting taxa of hybrid origin (Kanamori, 1969, 1971; Morzenti, 1962; Reed, 1954; Wagner, 1954, 1966, 1970; Wagner & Chen, 1965; Wagner & Whitmire, 1957). This use of spores is limited to the level of species-groups closely related enough to make viable hybrids. At the level of genus, family, and higher, spore abortion is of no significance. In the overall phylogeny of ferns we ask questions like, "What are the relationships of the genus *Loxogramme*?" The genus *Cheiropleuria*? These and a number of other genera have been controversial as to their evolutionary position. It is interesting to note that Nayar (1963) investigated spore morphology in *Loxogramme*—a genus regarded by many as more or less intermediate between the bilateral-spored polypodioids and the tetrahedral-spored grammitids—and discovered one species, *L. lanceolata*, in which both spore types exist as well as all transitions between. As regards the genus *Cheiropleuria*, associated with polypodioid ferns by various authors in spite of its many deviant characters, the spore is so different that close relationship is very improbable (*cf.* Nayar & Devi, 1964*a*).

The broad outlines of correlation of some of the major spore characteristics with presumed phylogenetic relationships are now fairly well known, and are illustrated in Figure 5. The diagram shows that in general a given taxon at the level of subfamily has mainly or exclusively one type or the other—tetrahedral or bilateral. The tetrahedral type is the most prevalent. Bilateral spores are scattered in unrelated groups, indicating parallel evolution. Likewise, green spores are scattered and arose, no doubt, by parallel evolution and do not indicate affinity. Some of the groups, such as Gleicheniaceae and Cyatheoideae, show dominantly tetrahedral spores, but there are bilateral-spored members. Others, such as Vittarioideae and Marattiaceae, have fairly equal representation of both types. In Marattiaceae, genera centering around *Angiopteris* have tetrahedral spores, while those around *Marattia* and *Danaea* have bilateral. In Vittarioideae, there is some suggestion that the genera which exist in the wettest forest possess the tetrahedral type of spore and those which occur in dry forest as "dry epiphytes" (see above) have evolved the bilateral spore; this is an hypothesis that can be tested.

Some Problems in the Use of Spores

We have already indicated above some of the problems that are met in the study of spores. Caution must be observed in regard to a variety of spore characters, and there are the ever-present problems of confusing directions of evolution, reversals, parallelisms, and misinterpreting the extent of variability. As pointed out earlier, there are two entirely different factors that may produce large spores—selection for "precinctiveness" in montane rainforests and polyploidy. (In my original studies of Hawaiian fern spores (Wagner, 1961), I thought that the large spores of the higher rainforests resulted from polyploidy; not until I actually studied the chromosomes did I realize that some other factor was operative.)

In regard to the shape of the spores there may be reversals. At least in one case, that of *Thelypteris*, a genus or genus-group all of the relatives of which possess bilateral spores, there is the suggestion of reversal in a small species-

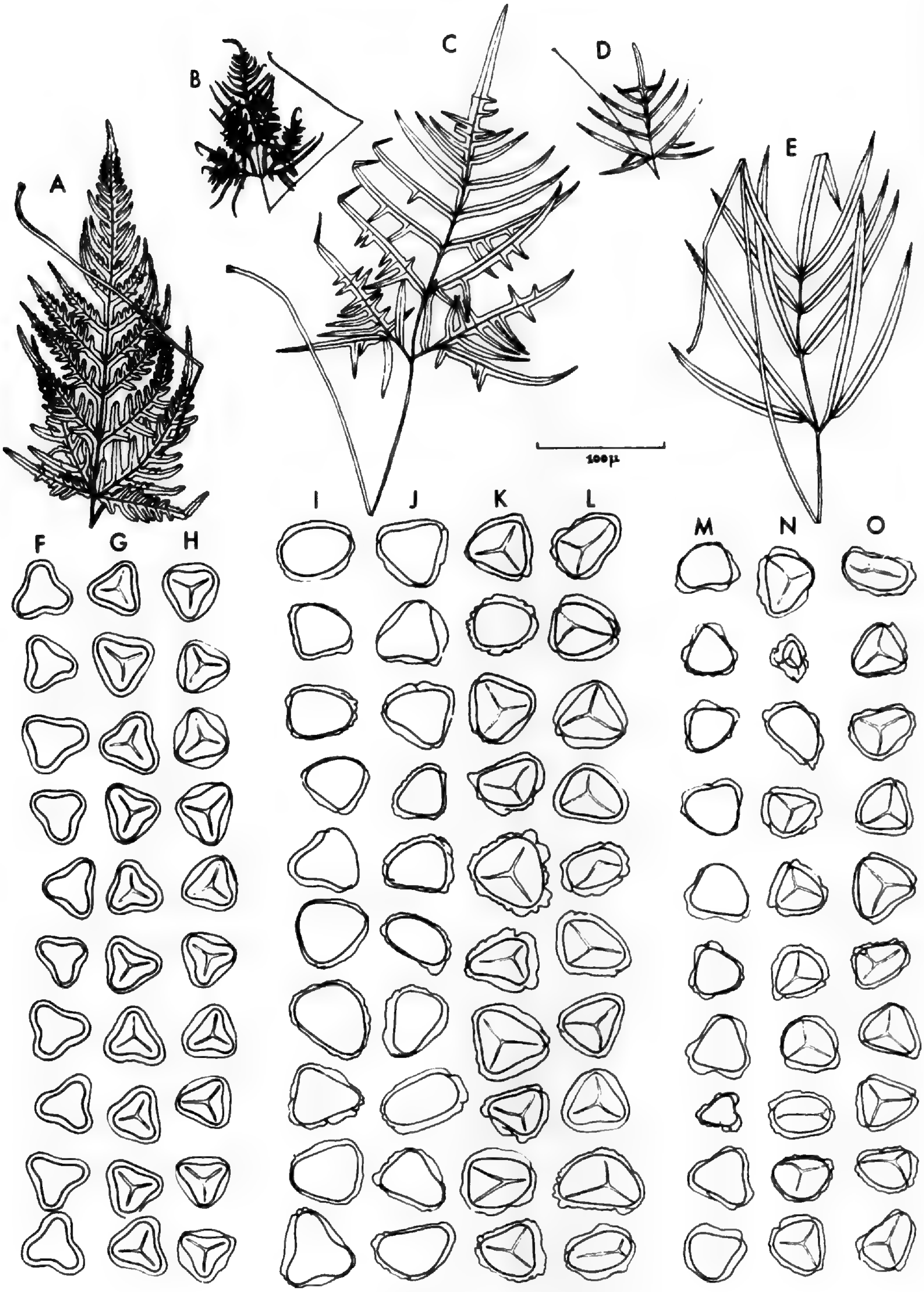

FIGURE 6. Spore tracings (left hand columns drawn without the laesurae) of sexual and apogamous Hawaiian ferns. *Pteris irregularis*—sexual species: A, frond; F–H, spores. *P. cretica*—apogamous species: E, frond; M–O, spores. *P.* × *hillebrandii*—apogamous hybrid: B, C, D, frond variations; I–L, spores.

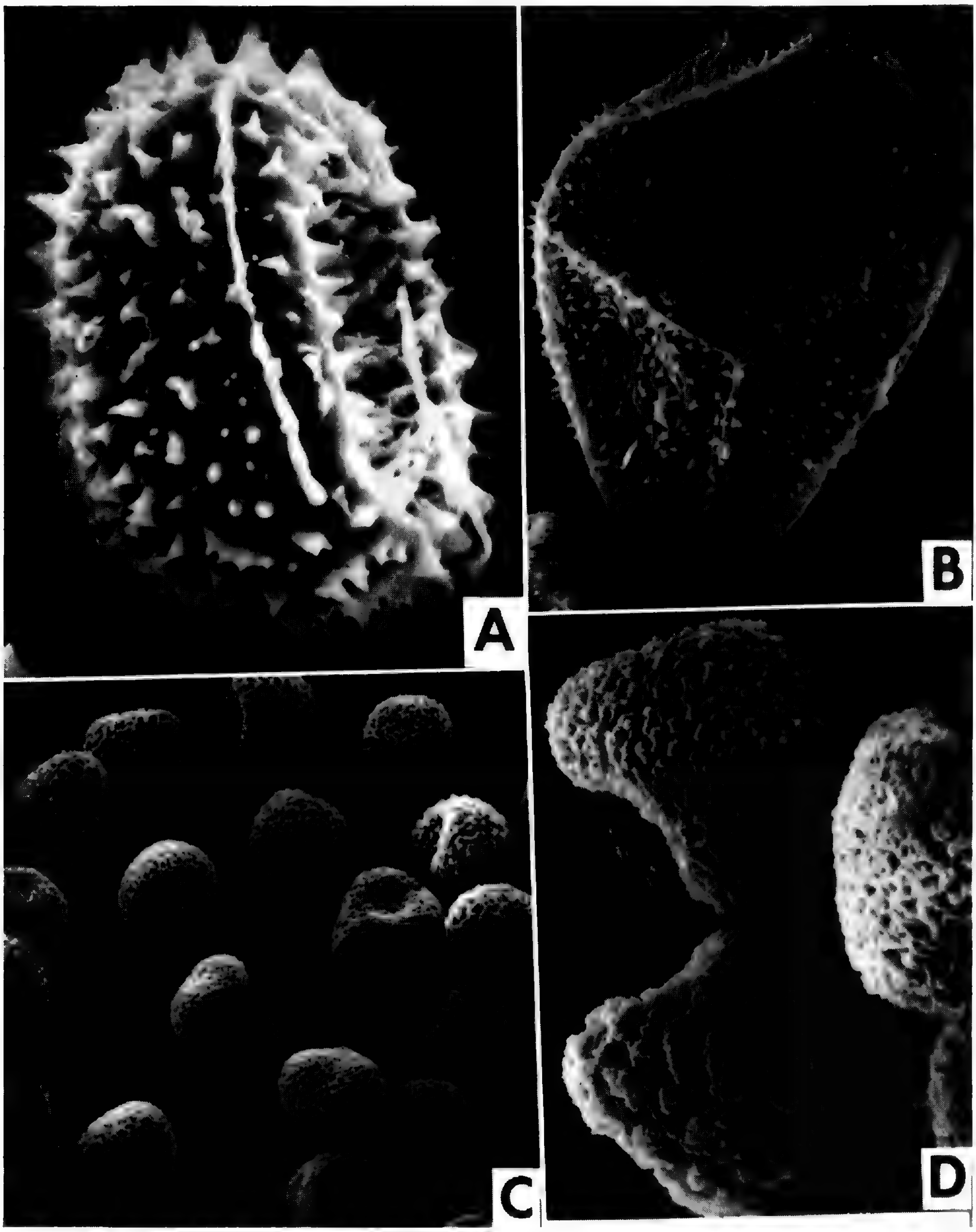

Figure 7. Spores.—A. *Thelypteris* sp. India, *Chand 4692* (MICH).—B. *Thelypteris* (*Trignospora*) *ciliata*. Hainan, *Lau 5306* (MICH).—C–D. *Botrychium dissectum*. Michigan, *Wagner 9101* (MICH).—C. Seen at 600×.—D. Seen at 1800×.

cluster which Holttum (1971) has recently designated *Trigonospora*. Figure 7 shows a typical thelypteroid spore (A) in comparison with the spore of *Thelypteris* (*Trigonospora*) *ciliata* (B).

The problem of the homologies of the perine or perispore alluded to above has been exacerbated recently by the report of Lloyd (1969) of a "winged perispore" in *Polypodium chnoodes*. Nayar and Devi (1964*a*: p. 363, fig. 84) found what is apparently a similar structure in the spores of *Pyrrosia nummularifolia*. Also, in what is presumably a single species, one of the best known fern species in the world, the fragile-fern, *Cystopteris fragilis*, there are evidently two wholly different spore forms, one of which has the typical perispore of dryopteroid ferns ("*C. dickieana*"), the other the characteristic spinate structure of the genus as a whole (*cf*. Blasdell, 1963; Hagenah, 1961). In *Davallia*, *Humata*, *Nephrolepis*, genera of obviously dryopteroid affinities, the spores resemble those of polypodioid ferns, as discussed earlier. Does this mean that they have lost the perispore? Or is it actually present in vestigial form?

The problem of variability can usually be met when dealing with living ferns, but single fossil spores can conceivably be misleading. To illustrate this point, one need only remove the contents of a single sporangium of certain species of grapeferns, *Botrychium*, and compare the different wall patterns. Figure 7, C and D, shows what we find in the common evergreen grapeferns of the eastern United States (*cf*. Sladkov, 1968).

In addition to the parallelisms already discussed, one additional one should be noted for its very striking character. This one, discovered by Sladkov (1959*b*), involved two wholly different genera, *Botrychium* (Ophioglossaceae) and *Cryptogramma* (Adiantaceae). As he shows (1959*b*: table 1, fig. 2), their spores are remarkably similar in size, shape, form of the laesurae, and sculpture. It would be easy indeed to confuse them.

CONCLUSIONS

In spite of relatively simple structure, spores in ferns may potentially provide a goldmine of systematic evidence, both at the level of species and higher. The variables, as discussed here, include such characters as number per sporangium, size, cytokinetic origin, general shape, heterospory, variability, nature of the exospore including its sculpture, equator, and laesura—the perispore, pigmentation, organelles, metabolites, resting stage, survivability, and germination. We have attempted to trace here some of the trends in spore morphology in relation to fern phylogeny. For some of the observed trends, we have also examined possible adaptive values. With new information, it is possible that some of the trends dealt with here will be found to be mistaken, and that, in fact, the direction of change has been the reverse of that postulated. There may be parallelisms and (or) convergences. There may even be evolutionary reversals. Accordingly we must observe due caution in utilizing spores for making phylogenetic conclusions.

Assuming that in general our deductions have been correct, the broad outlines of spore structure in relation to fern phylogeny are now drawn. There is a good overall correlation of spore type with the family-subfamily levels of classification. Among the different characters of fern spores, over two dozen probable trends can be distinguished. Not only should we be concerned with testing these with all the evidence that we can marshal, but we should also ask the basic question of what are the reasons that these changes have come about biologically.

LITERATURE CITED

ALSTON, A. H. G. 1956. The subdivision of the Polypodiaceae. Taxon 5: 23–25.

ATKINSON, L. R. 1960. A new germination pattern for the Hymenophyllaceae. Phytomorphology 10: 26–36.

BIR, S. S. 1966–67*a*. Role of spore morphology in the taxonomy of the family "Aspleniaceae." Palynol. Bull. 2–3: 3–11.

———. 1966–67*b*. Correlation between spore-size and polyploid-level in the Himalayan Asplenioid and Athyrioid ferns. Jour. Palynol. 2–3: 41–48.

BLASDELL, R. F. 1963. A monographic study of the fern genus *Cystopteris*. Mem. Torrey Bot. Club. 21(4): 1–102.

BOBROV, A. E. 1966. The spore morphology of Osmundaceae. Bot. Žurn. (Moscow & Leningrad.) 51: 1452–1460.

BOLKHOVITINA, I. A. 1959. Morfologia spor semeistva Schizaeaceae i isotira semeistva v geologischeskom proshlom. Paleontol. Žurn. 1: 121–131. [The morphology of the spores of the family Schizaeaceae and the history of the family in the geological past.—Translated by Stanwyn G. Shetler. March, 1960.]

———. 1962. History of the Schizaeaceae family in the geological past on the basis of spore studies. Pollen & Spores 4: 334–375.

BOWER, F. O. 1923, 1925, 1928. The Ferns. Vol. 1. The Criteria of Comparison. 359 pp. Vol. 2. The Eusporangiatae and other relatively primitive ferns. 344 pp. Vol. 3. The Leptosporangiate Ferns. 306 pp. Cambridge Univ. Press.

BRAGGIO, G. 1966. Morfologia delle spore e sistematica delle Davalliales. Webbia 21: 725–767.

BRITTON, D. M. 1968. The spores of four species of spinulose wood ferns (*Dryopteris*) in eastern North America. Rhodora 70: 340–347.

———. 1972*a*. Spore ornamentation in the *Dryopteris spinulosa* complex. Canad. Jour. Bot. 50: 1617–1621.

———. 1972*b*. The spores of *Dryopteris clintoniana* and its relatives. Canad. Jour. Bot. 50: 2027–2029.

BROWN, C. A. 1960*a*. What is the role of spores in fern taxonomy? Amer. Fern Jour. 50: 6–14.

———. 1960*b*. Palynological Techniques. Published by the author. Baton Rouge, Louisiana. vi + 188 pp.

CARLQUIST, S. 1966. The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. Brittonia 18: 310–335.

COPELAND, E. B. 1947. Genera filicum. Chronica Botanica Co., Waltham, Massachusetts. xvi + 247 pp., 10 pl.

CRANE, F. W. 1955. Comparative study of diploid and tetraploid spores of *Dryopteris dilatata* from Britain and Europe. Watsonia 3: 168–169.

———. 1960. A key to American *Dryopteris* species based on characters of the perispore. Amer. Fern Jour. 50: 270–275.

DAIGOBO, S. 1967. Variation of spore size in the Japanese *Polystichum polyblepharum* group. Jour. Jap. Bot. 42: 207–210.

DEBENEDICTUS, V. M. M. 1969. Apomixis in ferns with special reference to sterile hybrids. Doctoral Dissertation, Univ. Michigan.

ERDTMAN, G. 1957. Pollen and Spore Morphology/Plant Taxonomy. Gymnospermae, Pteridophyta, Bryophyta. (An introduction to Palynology. II.) Almqvist & Wiksell, Stockholm. 151 pp.

EVANS, A. M. 1968 [1969]. Interspecific relationships in the *Polypodium pectinatum-plumula* complex. Ann. Missouri Bot. Gard. 55: 193–293.

FISCHER, H. 1892. Beiträge zur Morphologie der Farnsporen. Jahresber. Schles. Ges. Vaterl. Cult. 1891. Breslau.

FISCHER VON WALDHEIM, A. 1864. Ueber die Entwicklung der Farnsporen. Jahrb. Wiss. Bot. 4: 349–382, pls. 1–4.

FOSTER, F. G. 1956. Microscopy of fern spores. Educational Focus 26: 7–13.

FULVIO, E. DI. 1961. On the epispore of the American species of *Azolla* with special reference to *A. mexicana* Presl. Kurtziana 1: 299–302.

GULLVÅG, B. M. 1966. The fine structure of pollen grains and spores: A selective review from the last twenty years of research. Phytomorphology 16: 211–227.

———. 1969. Primary storage products of some pteridophyte spores—a fine structural study. Phytomorphology 19: 82–92.

Haeggstrom, C.-A. & A. Nieml. 1964/1965. On the spores of *Botrychium boreale* Milde and *B. lunaria* (L.) Sw. Memoranda Soc. Fauna Fl. Fenn. 41: 65–70.

Hagenah, D. J. 1961. Spore studies in the genus *Cystopteris.* I. The distribution of *Cystopteris* with non-spiny spores in North America. Rhodora 63: 181–193.

Hannig, E. 1911. Über das Vorkommen von Perisporien bei den Filicineen nebst Bemerkungen über die systematische Bedeutung derselben. Flora 103: 321–346.

Harris, W. F. 1955. A Manual of the Spores of the New Zealand Pteridophyta. New Zealand Dept. Sci. Indust. Res. Bull. 116: 1–186.

Hennipman, E. 1970. Electron and light microscopical observations on the perine of the spores of some *Bolbitis* species (Filices). Acta Bot. Neerl. 19: 671–680.

Holttum, R. E. 1971. Studies in the family Thelypteridaceae III. A new system of genera in the Old World. Blumea 19: 17–52.

Ito, H. 1972. Distribution of monolete and trilete ferns in Asia and northern Oceania. Jour. Jap. Bot. 47: 321–325.

Kanamori, K. 1969. Studies on the sterility and size variation of spores in some species of Japanese *Dryopteris.* Jour. Jap. Bot. 44: 207–217, pls. 14–17.

———. 1971. Studies in the sterility and size variation of spores in some apogamous ferns. Jour. Jap. Bot. 46: 146–151, pls. 6–7.

Kawasaki, T. 1968. On the external figures of spores in the Polypodiaceae and their phylogenetic significance (8). Bull. Tokyo Gakugei Univ. 20: 106–115.

Knobloch, I. W. 1966. A preliminary review of spore number and apogamy within the genus *Cheilanthes.* Amer. Fern Jour. 56: 163–167.

———. 1969. The spore pattern in some species of *Cheilanthes.* Amer. Jour. Bot. 56: 646–653.

Knox, E. M. 1951. Spore morphology in British ferns. Trans. Proc. Bot. Soc. Edinburgh 35: 437–449.

Kremp, G. O. 1965. Morphologic Encyclopedia of Palynology. Univ. Arizona Press, Tucson. xiii + 185 pp., 38 pl.

Lloyd, R. M. 1969. Occurrence of a winged perispore in a New World species of *Polypodium.* Brittonia 21: 80–82.

——— & E. J. Klekowski, Jr. 1970. Spore germination and viability in Pteridophyta: Evolutionary significance of chlorophyllous spores. Biotropica 2: 129–137.

Lugardon, B. 1965. Structure des parois de la spore de *Blechnum spicant* (L.) Roth. Pollen & Spores 7: 409–428, pls. 1–7.

Lukose, N. G. 1964. New species of *Schizaea* spore from the Upper Mesozoic of Kashmire, India. Nature 204: 566–567.

Maloney, N. A. 1961*a.* Comparative morphology of spores of the ferns and fern allies of Minnesota. Doctoral thesis, Univ. Minnesota. Minneapolis, Minn.

———. 1961*b.* Comparative morphology of spores of the ferns and fern allies of Minnesota. Diss. Abstr. 22: 1805.

Marengo, N. P. 1954. The relationship of the cytoplasmic inclusions to the establishment of tetrahedral symmetry in the spore quartet of *Osmunda regalis.* Bull. Torrey Bot. Club 81: 501–508.

———. 1959. The cytokinetic origin of the monolete spores of *Polypodium virginianum.* Bull. Torrey Bot. Club 86: 259–263.

———. 1962. The cytokinetic basis of tetrahedral symmetry in the spore quartet of *Adiantum hispidulum.* Bull. Torrey Bot. Club 89: 42–48.

Martin, P. & C. M. Drew. 1969. Scanning electron photomicrographs of S.W. pollen grains. Jour. Arizona Acad. Sci. 5: 147–176.

McVaugh, R. 1935. Studies on the spores of some northeastern ferns. Amer. Fern Jour. 25: 73–85.

Mickel, J. T. 1962. A monographic study of the fern genus *Anemia*, subgenus *Coptophyllum.* Iowa State Jour. Sci. 36: 349–452.

Mitui, K. 1972*a.* Spore ornamentations of Japanese species of *Dryopteris.* Bull. Nippon Dental Coll. Gen. Educ. 1: 99–110, pls. 1–6.

———. 1972*b.* On the spore ornamentation of *Dryopteris yakusilvicola.* The Cell (Japanese) 4: 42–44.

MORZENTI, V. M. 1962. A first report on pseudomeiotic sporogenesis, a type of spore reproduction by which "sterile" ferns produce gametophytes. Amer. Fern Jour. 52: 69–78.

NAKAMURA, J. & T. SHIBASAKI. 1959. Diagnostic characters of fern spores. (I) Ophioglossaceae, Helminthostachyaceae and Osmundaceae. Res. Rep. Kochi Univ. 8: 1–11, pls. 1–8.

NAYAR, B. K. 1963. Spore morphology of *Loxogramme*. Grana Palynologica 4: 388–392.

———. 1967. Morphology of the spores and prothallus of *Christiopteris tricuspis*. Amer. Fern Jour. 57: 15–27.

———. 1969. A comparative study of the spore morphology of *Ceratopteris*, *Anemia*, and *Mohria*, and its bearing on the relationships of the Parkeriaceae. Jour. Indian Bot. Soc. 48: 246–256.

——— & S. DEVI. 1963. Spore morphology of some Japanese Aspidiaceae. Pollen & Spores 5: 355–372, pls. 1–3.

——— & ———. 1964*a*. Spore morphology of Indian ferns. III. Polypodiaceae. Grana Palynol. 5: 342–395.

——— & ———. 1964*b*. Spore morphology of Indian ferns. Aspleniaceae and Blechnaceae. Grana Palynol. 5: 222–246.

——— & ———. 1965. Spore morphology of Indian ferns. IV. Grammitidaceae. Grana Palynol. 6: 121–127.

——— & ———. 1966. Spore morphology of the Pteridaceae. I. The Pteridoid ferns. Grana Palynol. 6: 476–502.

——— & S. KAUR. 1963. Spore morphology of some Indian members of the Lomariopsidaceae. Pollen & Spores 5: 87–94.

——— & ———. 1968. Spore germination in homosporous ferns. Jour. Palynol. 4: 1–14.

———, P. LATA & L. P. TIWARI. 1964. Spore morphology of the ferns of Western tropical Africa. Pollen & Spores. 6: 544–582.

OLIVER, J. C. 1968. A study of spore characteristics of the ferns of Indiana. Amer. Fern Jour. 58: 5–12.

PAL, N. & S. PAL. 1964. Factors in the classification of ferns with special reference to Polypodiaceae. Bull. Bot. Soc. Bengal 18: 35–43.

PAL, S. & N. PAL. 1970. Spore morphology and taxonomy of Polypodiaceae. Grana 10: 141–148.

PETTITT, J. M. 1966. Exine structure in some fossil and recent spores and pollen as revealed by light and electron microscopy. Bull. Brit. Mus. (Nat. Hist.) Geol. 13: 221–257, pls. 1–21.

PIÉRART, P. 1961. L'évolution de la mégaspore. Bull. Soc. Roy. Bot. Belgique 93: 7–26.

REED, C. F. 1953. The Ferns and Fern-allies of Maryland and Delaware including District of Columbia. Reed Herbarium. Baltimore, Md. xviii + 286 pp.

———. 1954. Spores, sporangia and indusia of the genus *Dryopteris* in North America, north of Mexico. Bartonia 27: 47–56.

SELLING, O. H. 1944. Studies in the recent and fossil species of *Schizaea*, with particular reference to their spore characters. Acta Horti Gothob. 16: 1–212.

———. 1946. Studies in Hawaiian pollen statistics. Part I. The spores of the Hawaiian pteridophytes. Special Publ. Bernice Pauahi Bishop Mus. 37: 1–87, pl. 1–7.

SLADKOV, A. N. 1957. Polymorphism of spores in Cretan *Pteris*. Doklady (Proc. Acad. Sci. USSR) 117: 232–235.

———. 1959*a*. The spores of the adder's-tongue ferns growing in the USSR. Key for identification of spores (p. 109). Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 64: 97–111. [Translated by L. Kelso.]

———. 1959*b*. Morphological features of the spores of the ferns of the sub-family Pterideae Diels of the flora of the USSR. Doklady (Akad. Nauk USSR) 125: 81–84.

———. 1959*c*. The morphological similarity of different spores of species of *Cryptogramma* R. Br. and *Botrychium* Sw. Doklady (Akad. Nauk USSR) 125: 85–87.

———. 1961. Spory nastayashchikh paporotynikov podsmeistva Pterideae Diels flory S.S.S.R. Soobshch. I. Ryad Pterideae—Gymnogramminae. (Spores of true ferns of the subfamily Pterideae Diels in the flora of the U.S.S.R. Communication I. Series. Pterideae—Gymnogramminae. Vestn. Moskovsk. Univ., Ser. Biol. 6: 45–52.

———. 1968. Spore polymorphism of some *Botrychium* Sw. Vestn. Moskovsk. Univ., Ser. 6., Biol. 23: 121–123.

SORSA, P. 1964. Studies of the spore morphology of Fennoscandian fern species. Ann. Bot. Fenn. 1: 179–201, pls. 1–4.

STOKEY, A. G. 1940. Spore germination and vegetative stages of the gametophytes of *Hymenophyllum* and *Trichomanes*. Bot. Gaz. (Crawfordsville) 101: 759–790.

TARDIEU-BLOT, M. L. 1964. Sur les spores de Davalliaceae et Vittariaceae malgaches. Pollen & Spores 6: 537–543.

———. 1965. Sur les spores d'Adiantaceae, Aspleniaceae, Thelypteridaceae, et Athyriaceae de Madagascar. Pollen & Spores 7: 319–338.

———. 1966. Sur les spores de fougères malgaches: Filicales (fin), Marattiales, Ophioglossales (1). Pollen & Spores 8: 75–122.

TCHISTIAKOFF, J. 1874. Développement des sporanges et des spores chez les fougères. Les spores des Marattiacées. (2^e mémoire). Ann. Sci. Nat. Bot., Sér. 5. 19: 219–286.

TRYON, A. F. 1971. Structure and variation in spores of *Thelypteris palustris*. Rhodora 73: 444–460.

——— & G. VIDA. 1967. *Platyzoma*: A new look at an old link in ferns. Science 156: 1109–1110.

TSCHUDY, R. H. & B. D. TSCHUDY. 1965. Modern fern spores of Rancho Grande, Venezuela. Acta Bot. Venez. 1: 9–71.

TULLOCH, A. P. 1965. The oxygenated fatty acids from the oil of the spores of *Lycopodium* species. Canad. Jour. Chem. 43: 415–420.

WAGNER, W. H., JR. 1948. A new fern from Rota, Mariana Islands. Pacific Sci. 2: 214–215.

———. 1952. The fern genus *Diellia*: Its structure, affinities, and taxonomy. Univ. California Pub. Bot. 26(1): 1–212.

———. 1954. Reticulate evolution in the Appalachian Aspleniums. Evolution 8: 103–118.

———. 1961. Spore studies and speciation in the ferns of Hawaii. *In* "Symposium on Plant Biosystematics in the Pacific Basin." 10th Pacific Science Congr. Abstr. of Papers, pp. 135–136. Honolulu.

———. 1966. New data on North American oak ferns, *Gymnocarpium*. Rhodora 68: 121–138.

———. 1970. Evolution of Dryopteris in relation to the Appalachians. Pp. 147–192, *in* P. C. Holt (editor), "The Distributional History of the Biota of the Southern Appalachians. Part II: Flora." Virginia Polytechn. Inst. & St. Univ. Res. Div. Monogr. 2.

———. 1971. The southeastern adder's-tongue, *Ophioglossum vulgatum* var. *pycnostichum*, found for the first time in Michigan. Michigan Bot. 10: 67–74.

——— & K. L. CHEN. 1965. Abortion of spores and sporangia as a tool in the detection of *Dryopteris* hybrids. Amer. Fern Jour. 55: 9–29.

——— & R. S. WHITMIRE. 1957. Spontaneous production of a morphological distinct fertile allopolyploid by a sterile diploid of *Asplenium ebenoides*. Bull. Torrey Bot. Club 84: 79–89.

———, D. R. FARRAR & K. LIM CHEN. 1965. A new sexual form of *Pellaea glabella* var. *glabella* from Missouri. Amer. Fern Jour. 55: 171–178.

WEAVER, C. B. 1895. A comparative study of the spores of North American ferns. Proc. Iowa Acad. Sci. 3: 159–161.

WHITTIER, D. P. 1972. Gametophytes of *Botrychium dissectum* in axenic culture. (Abstract). Amer. Jour. Bot. 59(no. 6, part 2): 677.

———. 1973. Spore germination and early gametophyte development in *Psilotum* in axenic culture. (Abstract). Amer. Jour. Bot. 60(no. 4, supplement): 33.

——— & W. H. WAGNER, JR. 1971. The variation in spore size and germination in *Dryopteris* taxa. Amer. Fern Jour. 61: 123–127.

CRETACEOUS SALVINIACEAE[1]

JOHN W. HALL[2]

Whereas other major groups of vascular plants developed a highly sophisticated level of heterospory by the late Paleozoic, with the ultimate in reduction to one megaspore per sporangium and the assumption of the seed habit or its close approximation, these feats were not accomplished by the ferns until the late Mesozoic. A possible exception is the Lower Carboniferous coenopterid *Stauropteris burntislandica* P. Bertrand in which there are two relatively small (170 μ) megaspores in each sporangium according to Surange (1952). *Stauropteris oldhamia* Binney, from the Upper Carboniferous, however, is homosporous. If *Stauropteris burntislandica* is accepted as a bonafide fern it might be said that heterospory was reinvented by the ferns in the Mesozoic with a second incarnation on a much higher plane.

The Mesozoic record of the heterosporous ferns is based almost exclusively on dispersed megaspores and microspores or the unique structures (massulae) which contain the microspores. There is not a single occurrence of Cretaceous vegetative material of these plants reported in the published literature. One, possibly two, late Cretaceous occurrences of vegetative remains of species in the Salviniaceae have been called to my attention, the most convincing being that of *Salvinia* from the late Cretaceous of Mexico (R. Weber, personal communication). In spite of the fact that they grew in aquatic environments, which are actually basins of deposition, they, like so many other aquatics, are seldom represented in the vegetative condition. A notable exception is the well-known *Azolla primaeva* (Penhallow) Arnold from the Eocene of British Columbia (Arnold, 1955).

The rapid rise of palynology during the past two decades has been responsible for bringing to light the spores of fossil Salviniaceae. In 1965 there appeared the first two accounts of *Azolla* from the Cretaceous. Hills and Weiner (1965) described megaspores and massulae of *A. geneseana* Hills & Weiner from the uppermost Cretaceous of Alberta, and Stanley (1965) described massulae of *A. cretacea* Stanley from deposits of comparable position in South Dakota. Since that time numerous accounts have been published on Cretaceous Salviniaceae, most of them being based on material from the Edmonton Formation in Canada and the Hell Creek Formation in Montana and the Dakotas—the areas from which the original records were made. It is, I believe, a unique situation that palynology alone provides the basis for a phyletic interpretation of a distinctive group of plants. Furthermore, I believe there is an answer to the question of the origin of the unique megaspores and massulae of this family. The Jurassic yields no evidence of recognizable precursors of these ferns; the Marsileales appear just

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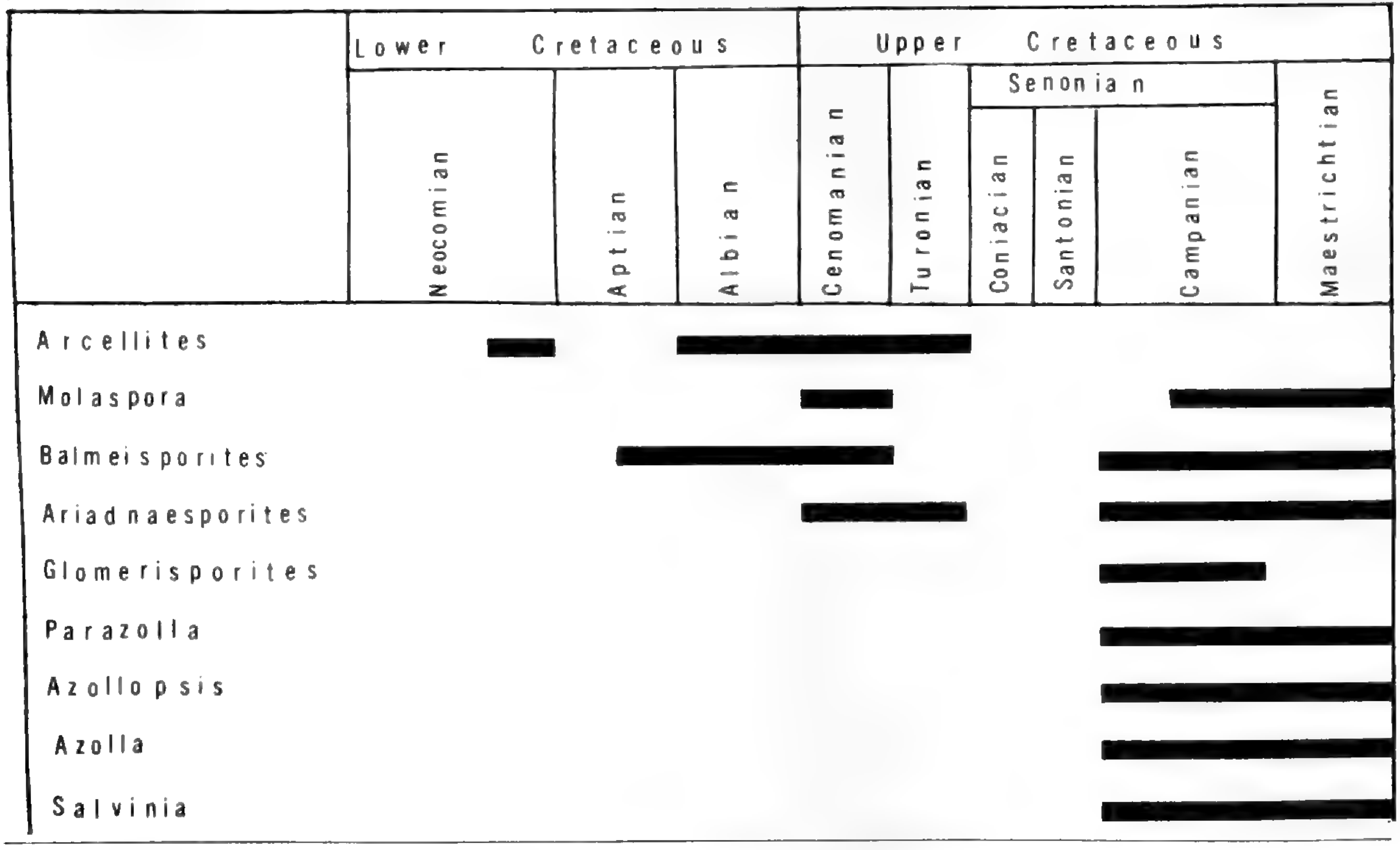
TABLE 1. Genera of heterosporous ferns and their known Cretaceous stratigraphic range.



as suddenly and as mysteriously as do the contemporaneously arising angiosperms, in the lower Cretaceous (Hughes, 1958). The Salviniales are younger and may first have occurred in mid-Cretaceous, in the Cenomanian, at the earliest. Recognizable species of *Azolla* and *Salvinia* occur in the latest Cretaceous, their earliest occurrence being in the Campanian and Maestrichtian Stages respectively, in the Upper Cretaceous sequence (Table 1).

The uniqueness of the megaspores and massulae of *Azolla* and *Salvinia* makes possible their recognition in fossil deposits. It is no overstatement to say that megaspores of *Azolla* are the most complex of any heterosporous plants. While the individual microspores themselves may be quite simple in structure and sculpture, the massulae in which they occur are only slightly less ornate than the megaspores.

It may be preferable to use a term such as megaspore apparatus when referring to the complex female gametophyte-producing-structure, for it includes much more than the so-called exine of most spores. In *Azolla* each mature leptosporangiate, exannulate sporangium bears one megaspore apparatus in a sporocarp. This has a swimming apparatus composed, in living species, of 3 or 9 floats attached to a columella[3] and a conspicuously hairy perispore around the actual megaspore or exine (Fig. 1). A number of ontogenetic and cytological studies have shown that perispore and swimming apparatus are derived from a sporangial periplasmodium composed of abortive megaspore and tapetal nuclei

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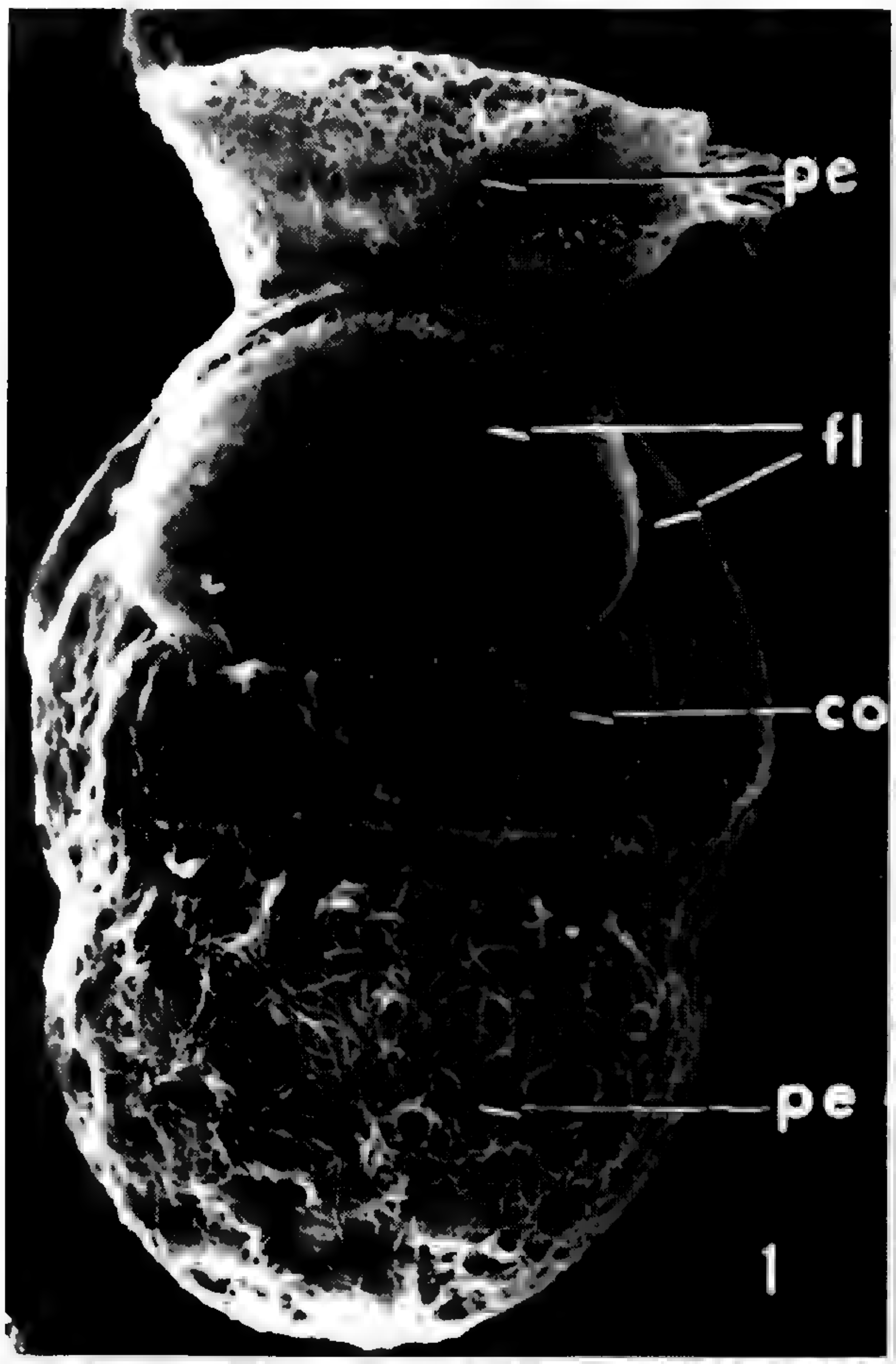
[3] There is some controversy about the use of the term columella. Kempf (1969*b*) uses the term gula, though I feel that this term should be reserved for proximal extensions of the exospore only. Hills (1967) has called this structure a trifolium. I prefer the term acrolamella, proposed by Tschudy (1966) for the fossil material, even though it is synonymous with the columella in this sense.



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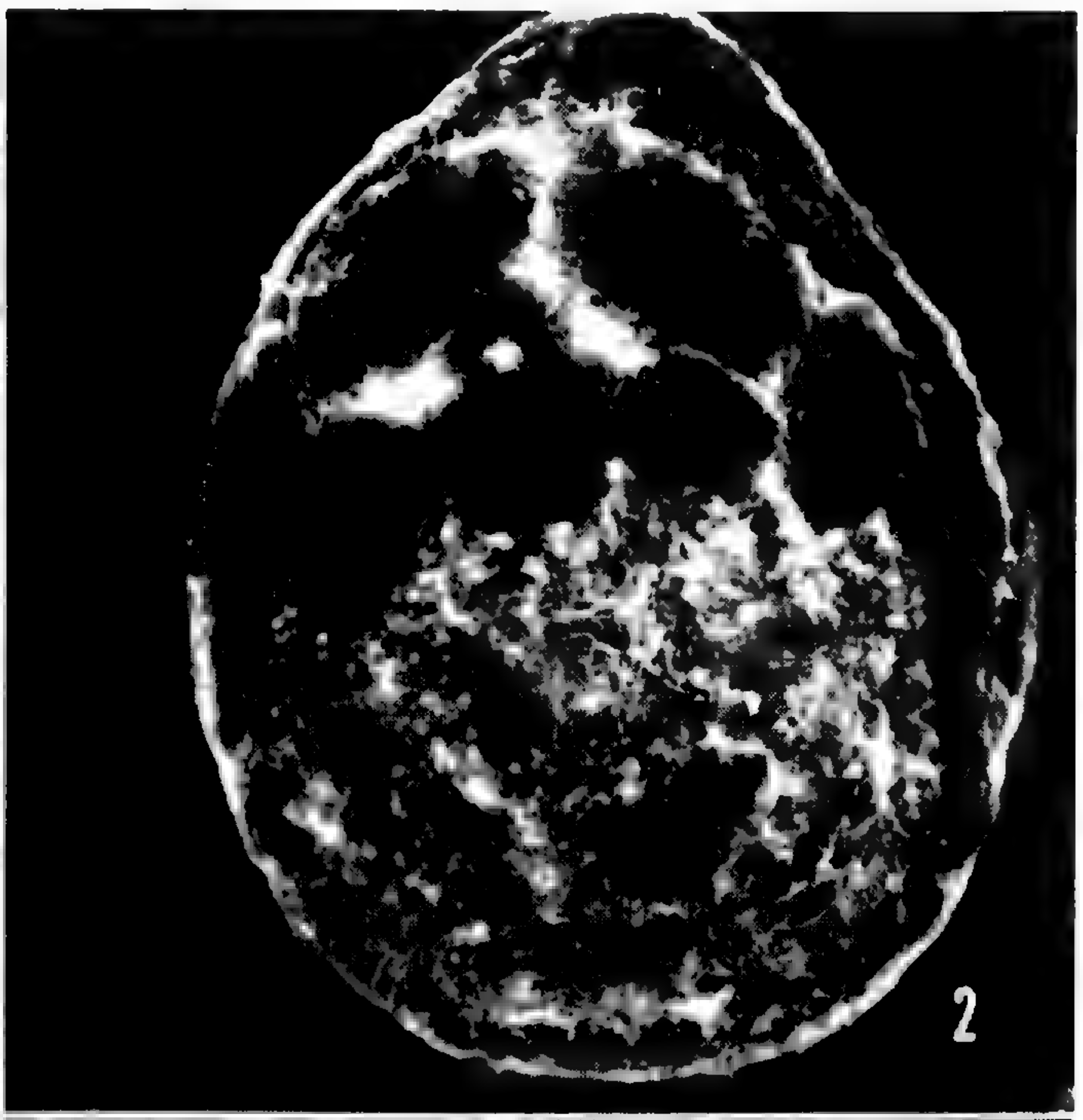

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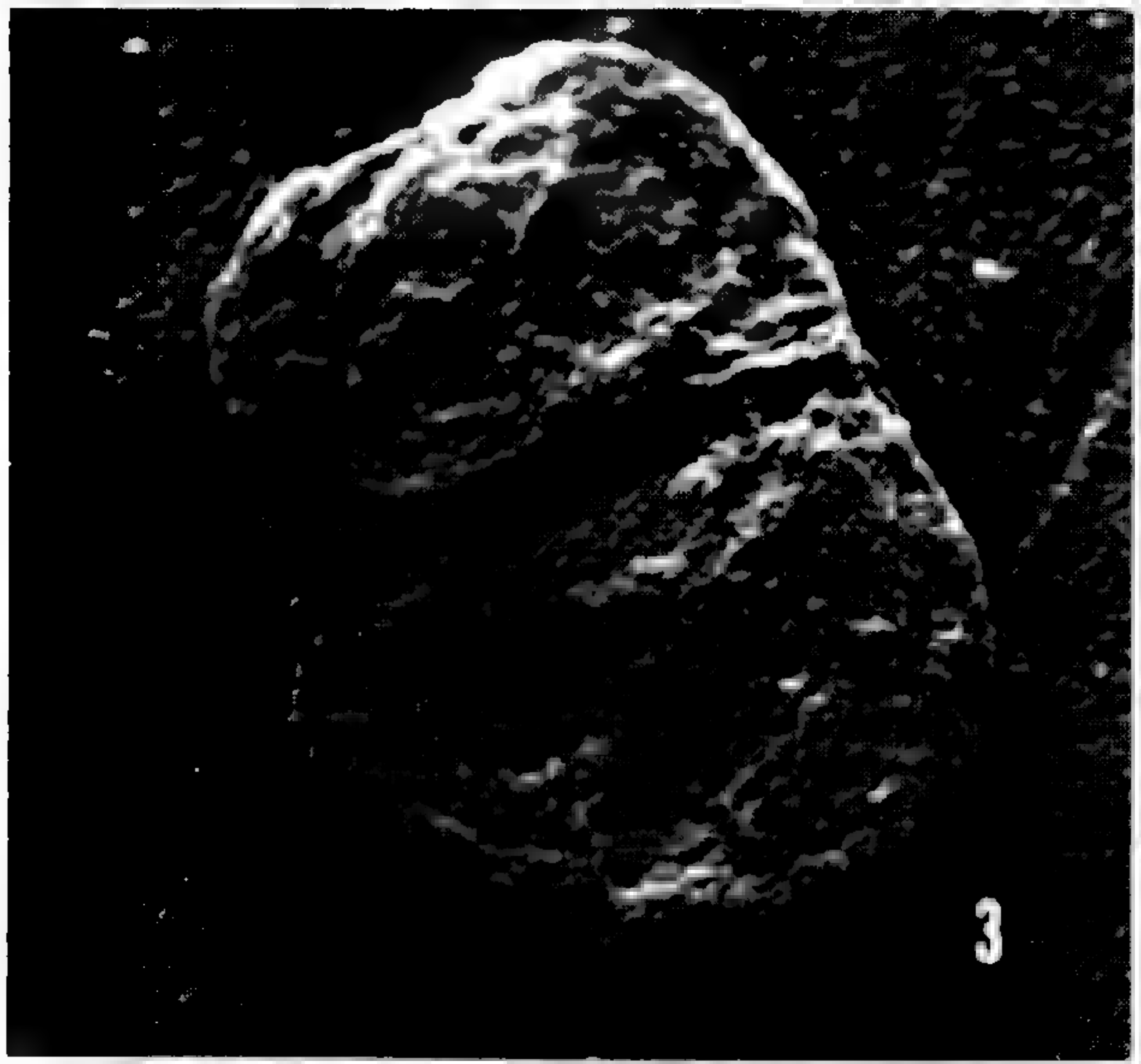

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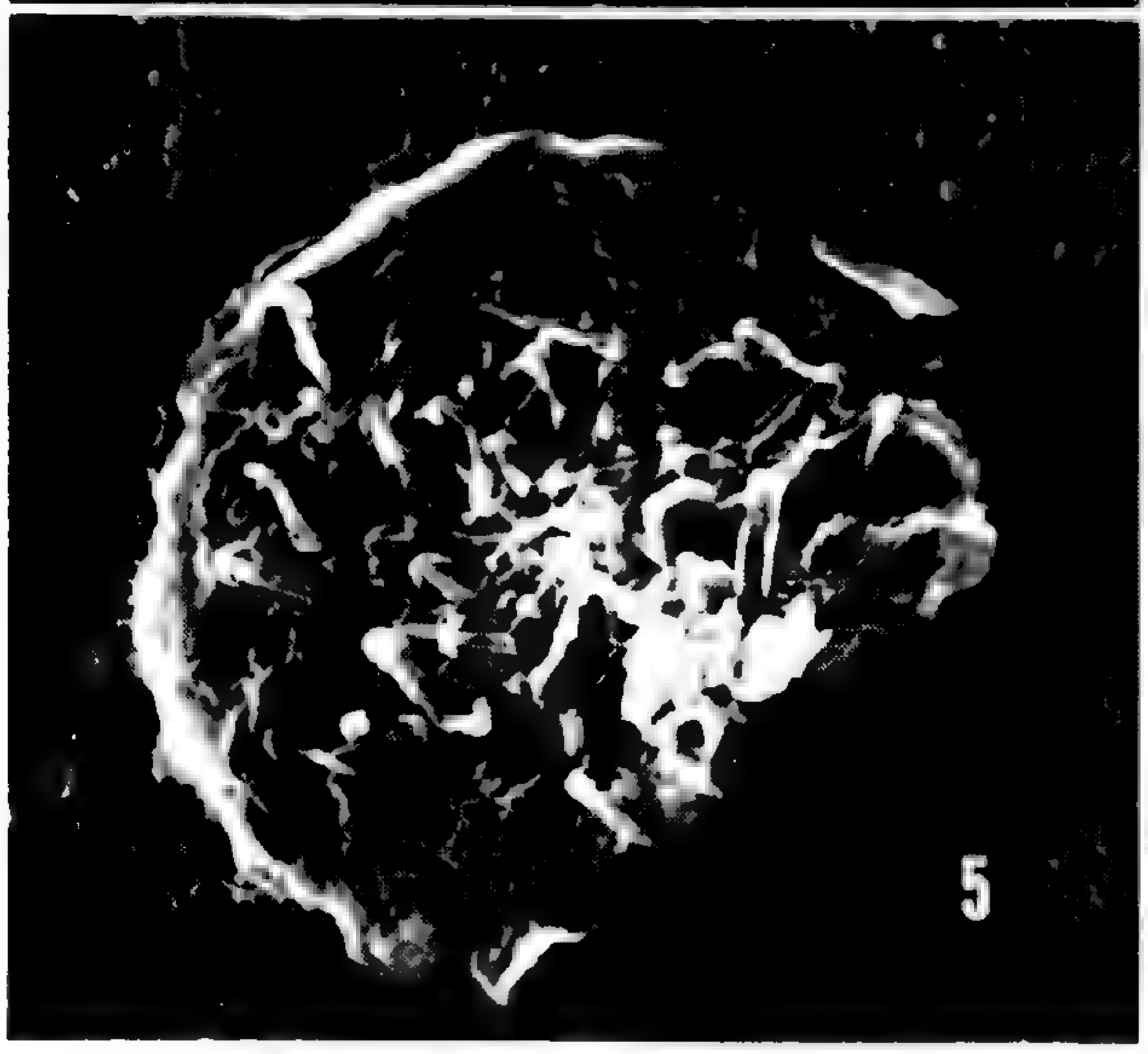

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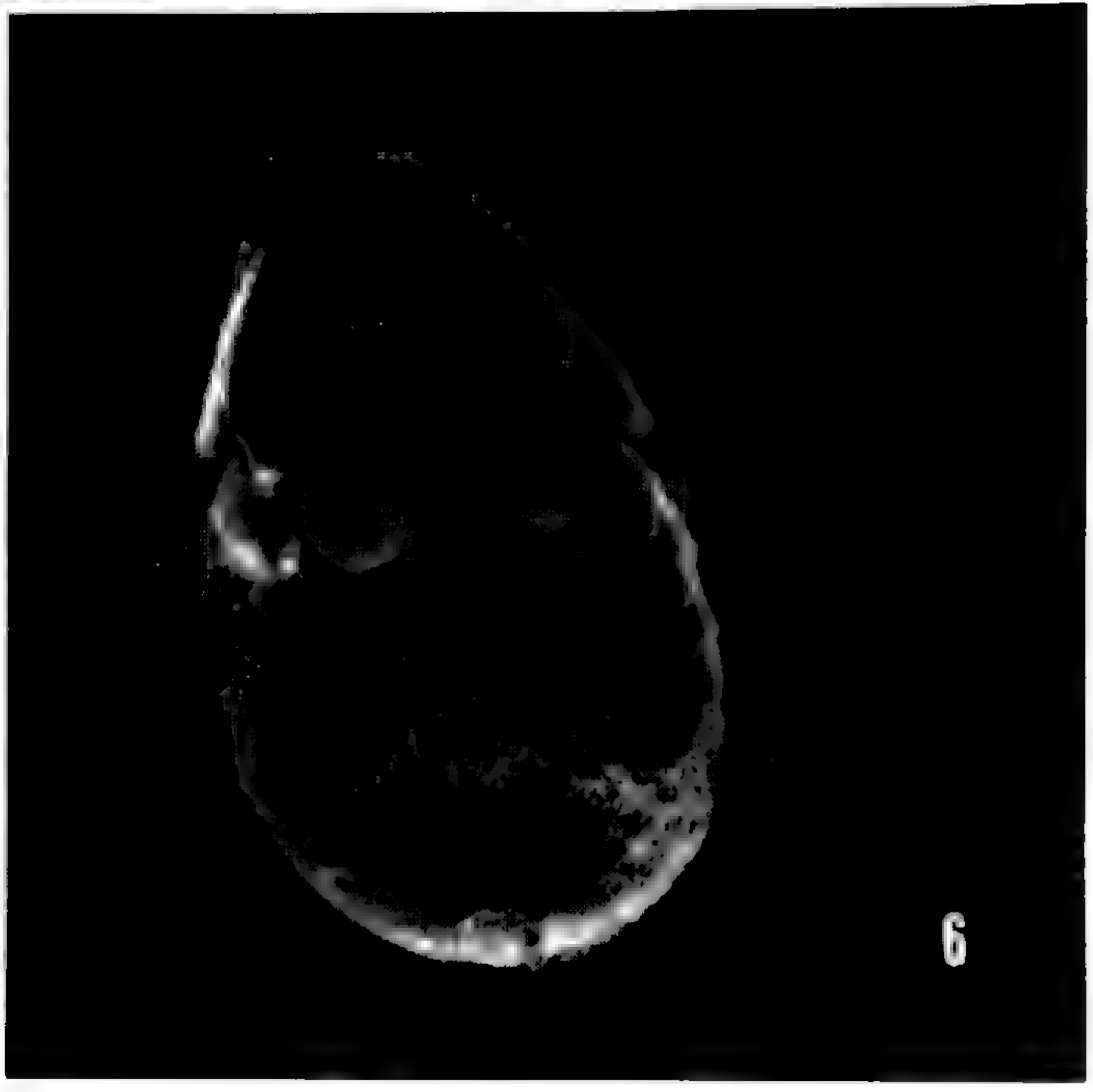

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(Bonnet, 1957; Duncan, 1940). Each of the three floats in A. *filiculoides* Lam. seems to be associated with an abortive nucleus of the tetrad that produces the functional megaspore, according to Bonnet (1957). Massulae develop in a comparable way, with the exception of lacking massive nuclear abortion. There are commonly four massulae per sporangium. Instead of the simple hairs found in the megaspore perispore, anchor-shaped glochidia are formed on the massular surface. These serve well to attach massulae to perispore. There is not a constant number of microspores per massula; each massula may have 4–10 or more, in the living species. Massulae of *Salvinia* and of *Azolla* section *Rhizosperma* lack glochidia.

There are five genera of Cretaceous Salviniaceae: *Azolla*, *Salvinia*, *Azollopsis*, *Parazolla* and *Glomerisporites*.[4] The last three are exclusively fossil. The stratigraphic range of these and of four other genera referable to the heterosporous ferns is shown in Figure 34.

Arcellites and *Molaspora* are most surely megaspores of marsileaceous plants (Ellis & Tschudy, 1964; Hall, 1963). *Balmeisporites* megaspores share some structural features of *Arcellites* but are of fairly small size in our North American deposits (Bergad, 1973). In my opinion, *Ariadnaesporites* may be considered a precursor of the salviniaceous megaspore. The remaining five genera are clearly salviniaceous, though the fossil species differ in some rather significant respects from the modern ones.

The genus *Azollopsis* occupies a key position with regard to the identification of salviniaceous precursors and to the phyletic derivation of the Cretaceous species of *Azolla*. There are two species of *Azollopsis* from North America (Hall, 1968), one from the Campanian and one from the Maestrichtian stages. Neither is abundant in our deposits. Stough (1968) has found a third species in Chile. The megaspores are distinctive. Each has large numbers of small pseudovacuolate, spherical floats loosely (or sometimes firmly) entangled in a mesh of long perisporial hairs (Figs. 7–8). When the floats and hairy perispore are

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[4] Assignment of *Glomerisporites* to the Salviniales is based on unpublished work in my laboratory. This is such an important genus phyletically that a brief summary of its characteristics is given here prior to a detailed account to be published later.

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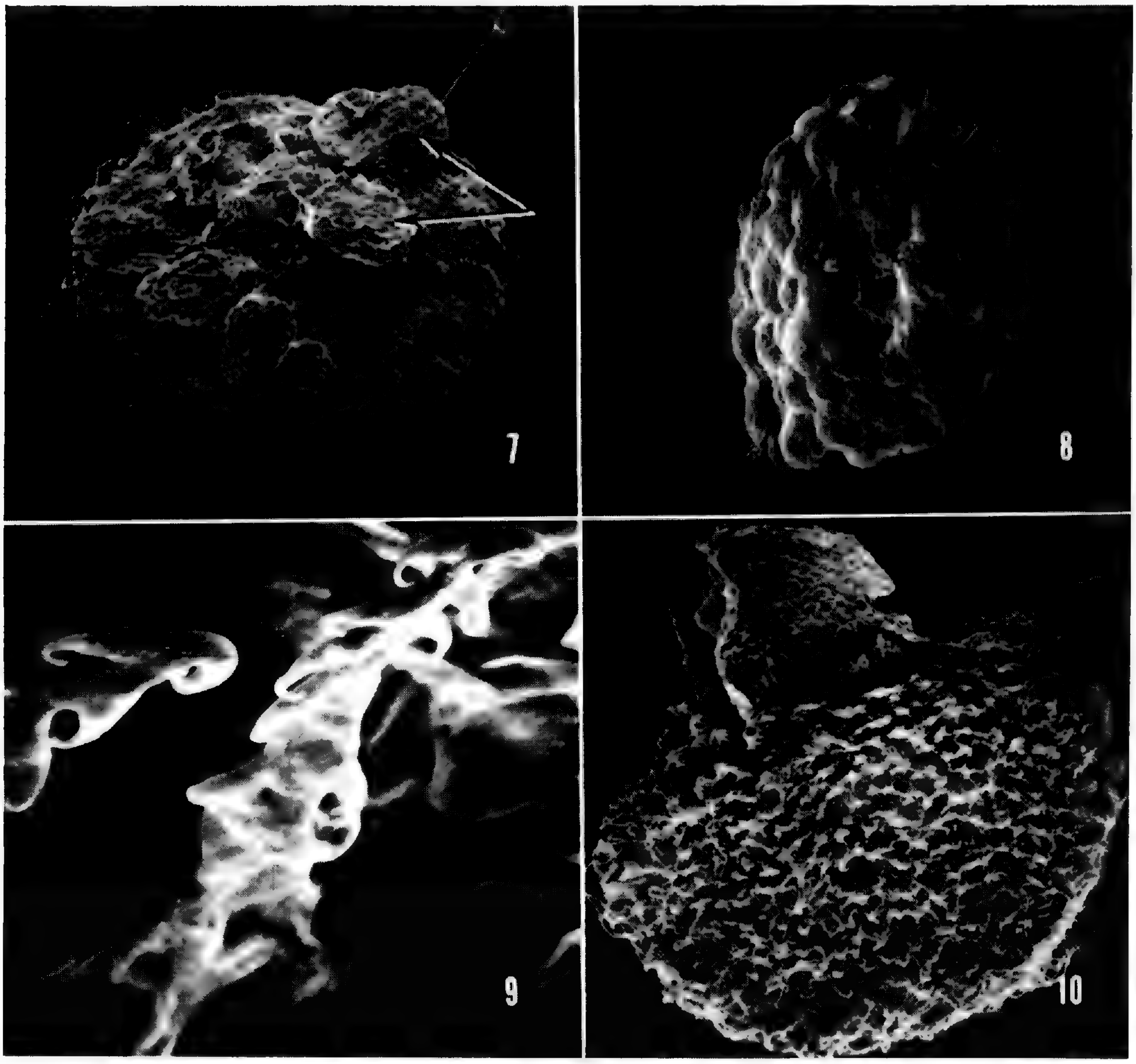
FIGURES 1–6. Scanning electron microscope photographs of *Azolla*.—1. Intact megaspore of *A. mexicana* Presl. pe, perispore; fl, floats; co, columella. The upper, flared portion of the perispore consists of hairs which are continuous with those of the lower part of the perispore, through the inner, hollow portion of the columella (not seen in this surface view). Only the hairs of the lower portion of the perispore, around the exospore, can be seen. St. Louis Park, Minn. × 78.—2. *A. distincta* Snead. Two rows of floats (dark objects) at proximal end of megaspore. Hell Creek Fm., Montana. × 157.—3. *A. primaeva* (Penhallow) Arnold. Megaspore with one apparent float at proximal end. Allenby Fm., Eocene, British Columbia. × 150.—4. *A. barbata* Snead. Megaspore with massulae attached at upper and lower left. Floats indistinct at proximal end slightly above and to right of uppermost massulae. Hell Creek Fm., Montana. × 150.—5. *A. gigantea* Bergad and Hall. Massula with anchor-shaped glochidia. Hell Creek Fm., North Dakota. × 250.—6. *A. montana* Hall and Swanson. Megaspore with irregularly arranged floats. Cap-like columella at proximal end. Hell Creek Fm., Montana. × 115.



Figures 7–10. Scanning electron microscope photographs of *Azollopsis tomentosa* Hall.—7. Megaspore with two massulae attached (arrows). Hell Creek Fm., North Dakota. × 85.—8. Intact megaspore with numerous floats. Hell Creek Fm., Montana. × 90.—9. Portions of multi-barbed glochidia of massulae. Hell Creek Fm., North Dakota. × 1670.—10. Megaspore with floats and hairy perispore removed. Short proximal tripartite acrolamella, rough-reticulate sculptured perine and remnants of a few hairs. Hell Creek Fm., North Dakota. × 157.

removed, a proximal acrolamella is revealed (Fig. 10). The distribution of the floats appears to bear no direct relationship to the position of the acrolamella; that is, they are arranged around the body of the megaspore as well as around the proximal end of the megaspore. In intact spores, the proximal end of the spore usually cannot be identified. Massulae are often attached to the megaspores (Fig. 7). The massulae have stout multibarbed glochidia (Fig. 9). Each massula is nearly the same size as a float. Microspores have the characteristic salviniaceous psilate sculpture and short laesurae.

Azollopsis megaspores seem to represent a situation in which considerably fewer abortive nuclei were involved in the formation of each float than in 3-float megaspores of extant *Azolla* (Hall, 1968). This assumption is based in part on the situation to be described in *Glomerisporites*, but even if it is not valid, there is an inverse relationship between float size and float number among salviniaceous megaspores that is well exemplified by *Azollopsis*.

Azollopsis represents a relatively primitive condition, one in which there are numerous uniformly distributed floats. Its relationship to the Salviniaceae is confirmed by its massulae with their glochidia. Two investigators have, in fact, assigned isolated massulae of this type to the genus *Azolla* (Srivastava, 1968; Stough, 1968).

The multifloat megaspores of *Azollopsis* provide a basis for understanding megaspores of *Glomerisporites*. These were described from the Senonian of the Netherlands by Dijkstra (1949) as ***Triletes pupus*** Dijkstra—an appropriate specific name relating to a thick matting of hairs which obscures the megaspore and its acrolamella.

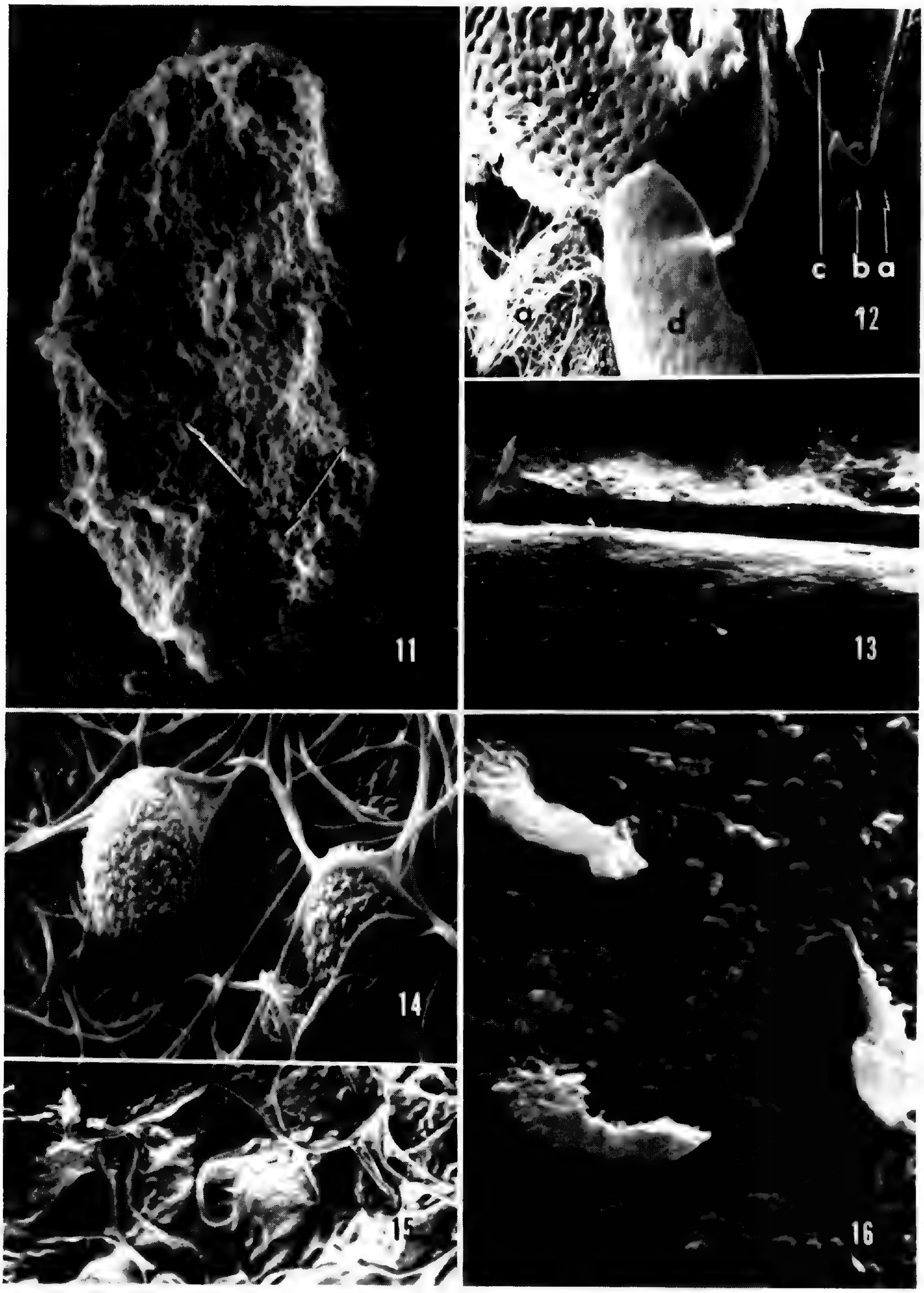
What Dijkstra did not see was the great number of small floats enmeshed in the hairs, nor did he find the microspores. The dry spores of *Glomerisporites* show no evidence of floats at low magnification in reflected light (*cf.* Fig. 11), and these were the conditions under which Dijkstra looked at his material. Without knowing that multifloat salviniaceous megaspores, as in *Azollopsis*, did exist, I believe the spore-like floats of *Glomerisporites* would not have been understood, so much like spores are the floats.

Because *Glomerisporites* has not yet been redescribed, a brief description follows.

The megaspores are oval to elliptical in outline (Fig. 11). The body is completely covered by a hairy perispore layer so that in intact spores one cannot distinguish proximal and distal ends. Removal of the hairs reveals a proximal, tripartite acrolamella and the outer layer of the perispore (the so-called sculptured perine) (Fig. 12). Hairs are attached at closely spaced intervals. The hair bases have an irregular surface, but the hairs themselves are smooth distally. The hairs are solid, though the hair base itself is hollow. The outer surface of the sculptured perine, among the hair bases, is granular to warty (Fig. 16).

Numerous small floats are enmeshed in the hairs. It is possible that some floats are attached to hairs, but most of them are free (Fig. 14, 20, 21). Each float is spherical to sub-spherical, 19–30 μm in diameter, hollow, inaperturate, and has an irregularly rugulate to granulose sculpture (Fig. 21). Floats are not confined to the proximal end of the megaspore, though they may be concentrated there (Figs. 17–19).

The megaspore wall is two-layered. The inner exine (megaspore proper) is illustrated in Figure 12. The arrow "c" points to the inner face of the exine, which is psilate, as is also the outer face of the exine (d). The inner face of the sculptured perine is foveolate (b). Each fovea marks the position of a hair base on the outer face of the sculptured perine. Thus, the hair bases are hollow. The letter "a" relates to the outer layer of the perine, and in this view only the hairs can be seen. Figure 13 shows the outer surface of the exine and a cross section of the sculptured perine after removal of the hairy perine. There is one broken hair base at the left, and the granular-warty aspect of the outer sculptured perine can be seen. Figures 17–19 show cross sections of the megaspore at



FIGURES 11–16. Scanning electron microscope photographs of *Glomerisporites pupus* (Dijkstra) Potonié from the Aachenian (Senonian) of the Netherlands.—11. Intact megaspore with two microspores attached (arrows). × 105.—12. Wall of megaspore, dissected and fractured to reveal constituent layers. A, outer hairy perispore (perine). B, inner surface of sculptured perispore (perine). The outer surface of this layer is shown in Fig. 16. The inner surface is foveolate, each fovea marking the position of an attached hair on the outer surface. C, exospore (megaspore proper), smooth on both inner and outer (D) surfaces. × 150.—13.

different levels. Figure 19 is through a central region. The exine has separated from the perine on the right, but is in contact with it at the left and at the bottom of the figure. Its psilate inner and outer faces can be noted. The vacuolate appearance of the sculptured perine is seen in Figures 18–19. The former section (Fig. 18) is taken near the proximal end of the megaspore, which was cut slightly obliquely and shows a portion of the trilete laesurae at the top of the illustration. At this magnification the surface structure of the sculptured perine cannot be seen. Figure 17 is a section through the acrolamella (columella). Its tripartite construction is obvious as is the fact that it is an extension of the sculptured perine. Floats seem most numerous in this level, but the hairy perispore with its floats was trimmed away from the illustrations in Figures 18–19 so that the number of floats at these levels is less than real.

So spore-like are the floats that the question may well be raised—are they not spores? There are several answers to this question, the most important being the occurrence of actual microspores of different structure attached to the megaspore. Furthermore, the floats are inaperturate (no known heterosporous fern has inaperturate microspores), and they are imbedded deep within the hairy perispore, a position they could not have achieved unless they developed there.

The microspores are borne singly, not in massulae. Each has a structure reminiscent of a megaspore (Figs. 24, 26). There is a hairy layer (perispore) particularly prominent at the distal end of the spore and a pseudovacuolate, foveolate, pseudoacrolamella at the proximal end (Fig. 25). The perisporial hairs are coiled (Fig. 15), perhaps functioning as glochidia. A single exospore (microspore-proper) lies at the base of the pseudoacrolamella, above the pseudovacuolate base (Fig. 24). Figures 22–23 are cross sections through, respectively, the distal base and the proximal spore-bearing region. The exospore is psilate and trilete, like the individual microspores in massulae of *Azolla*, etc.

Glomerisporites represents the ultimate in simplicity of floats; each float probably represents one abortive, plasmodially-derived spore. Their large number, small size and simple structure attest to this interpretation. A maximum in float number, under these conditions, would be found in *Glomerisporites*. Thus, in terms of its megaspores, this genus represents perhaps the most primitive of the recognizable members of the Salviniaceae.

The microspores of *Glomerisporites* are more complex than the individual microspores of other salviniaceous genera. It should be reemphasized that they are not borne in massulae, but singly. In my opinion, it is possible to interpret these microspores as simple massulae: they have coiled hairs (glochidia) like those of massulae of *Azolla circinata* Oltz and Hall and a psudovacuolate structure throughout. In reality, then, their principal difference from a true massula is in

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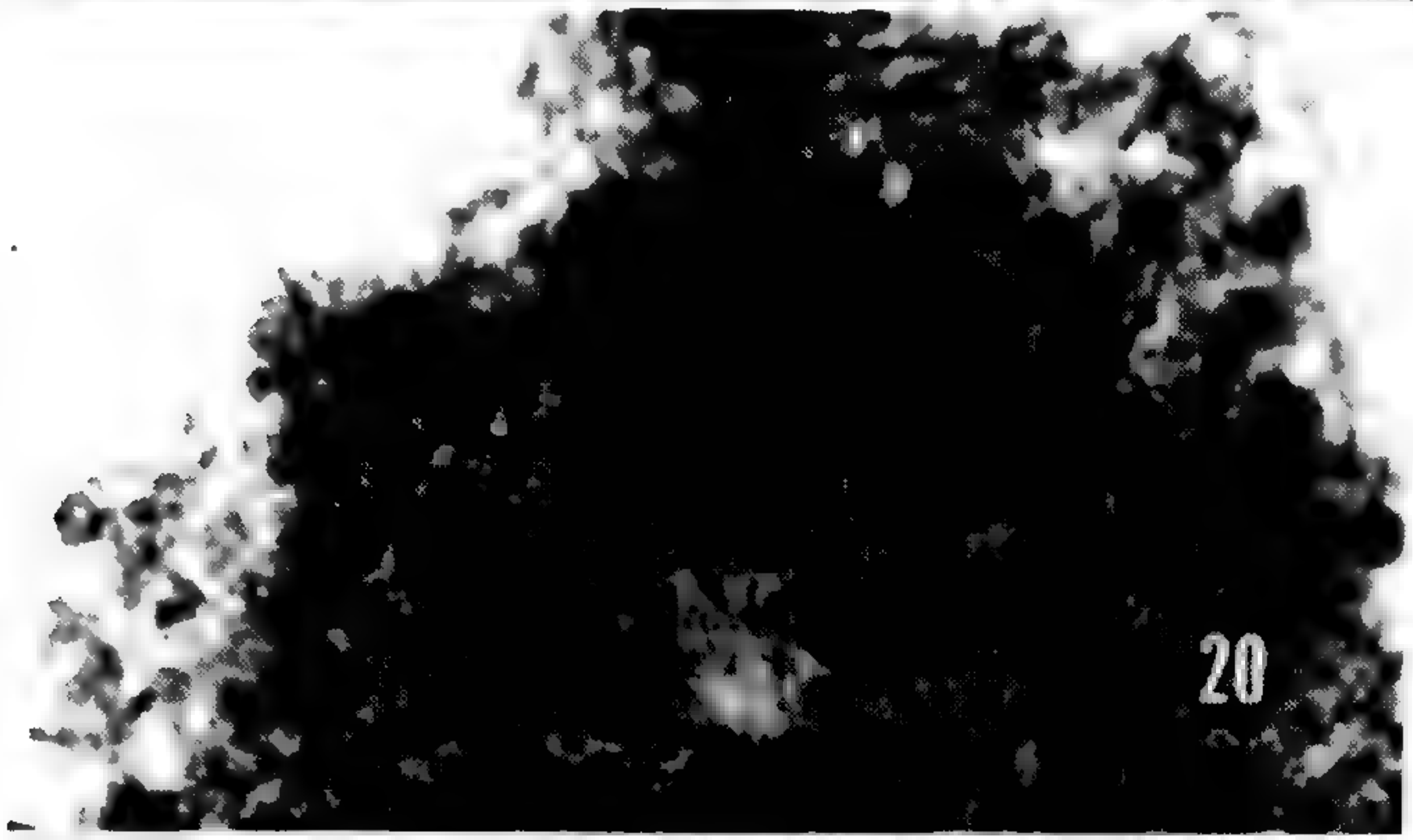
Section of perispore and surface of exospore. Hairy perispore removed. One hair base in upper left. Rough surface of sculptured perine, smooth outer surface of exospore. Perispore slightly pulled away from exospore. × 1140.—14. Floats enmeshed in perisporial hairs. × 725.—15. Coiled hair-tip on surface of microspore. × 655.—16. Sculptured perispore of megaspore with several hair bases. × 2300.


17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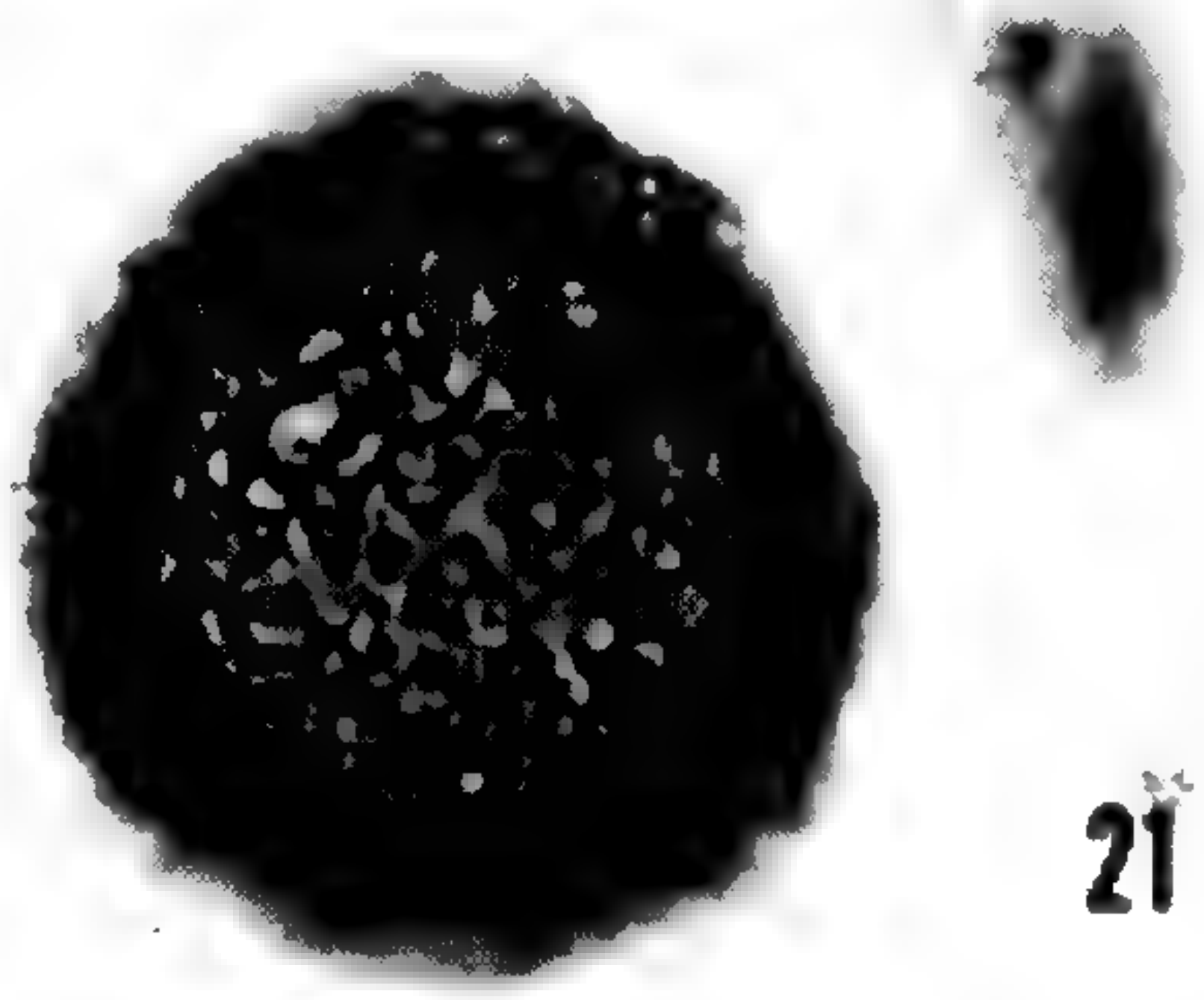
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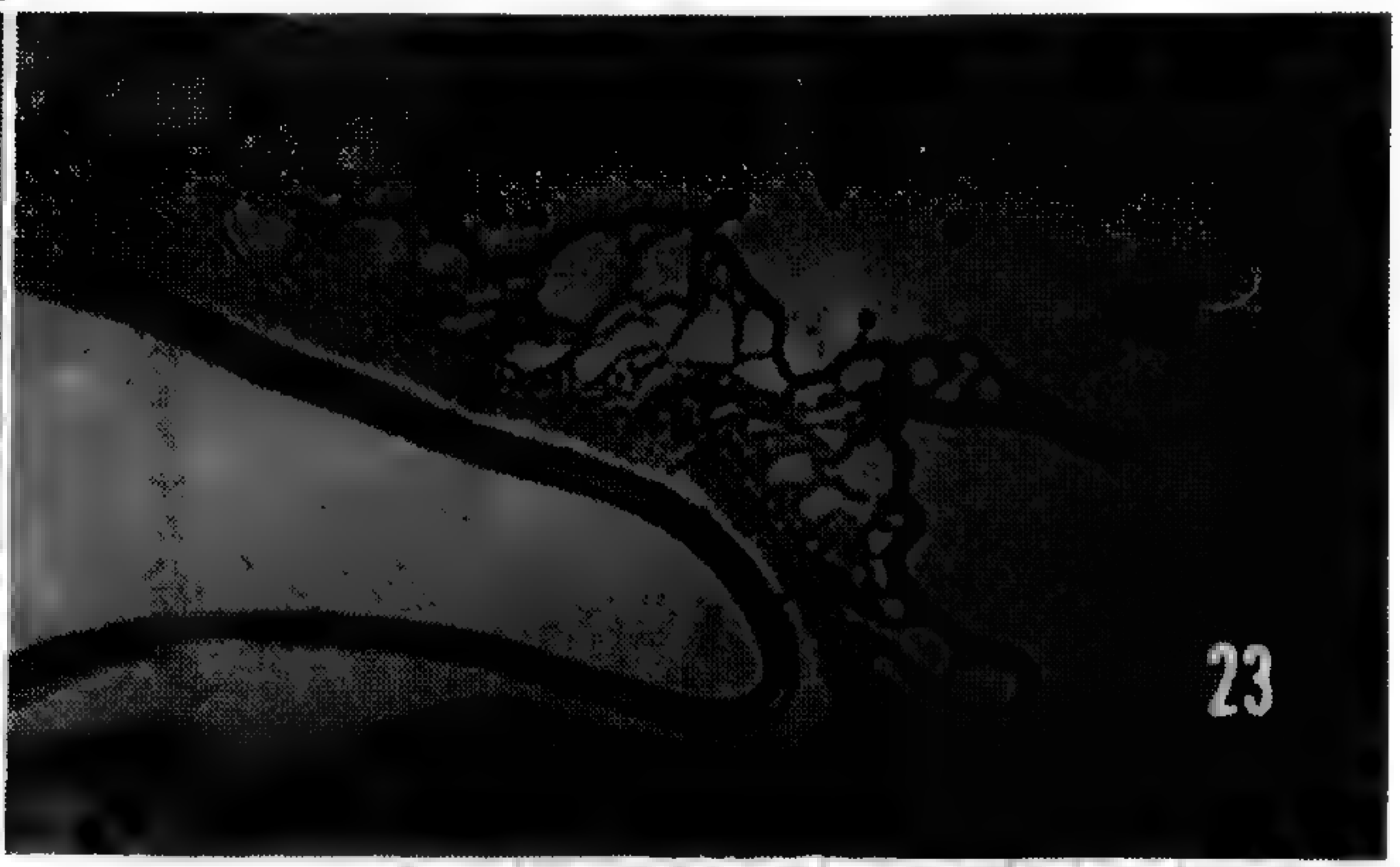
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their possession of only one spore. I would like to think that this is just the kind of situation one would prefer to find in a primitive massula.

Ariadnaesporites is another genus which might be included in the Salviniaceae, and I should like to make this claim. The evidence is not yet fully at hand, but I have some megaspores in which there are what are interpreted as small floats enmeshed in the hairs which surround a long acrolamella. These floats are not numerous, nor do they occur in all megaspores. Their mere presence is responsible for my opinion as to relationship.

If my assumption is correct, *Ariadnaesporites* provides a very fine precursor to salviniaceous heterospory and extends the stratigraphic record of this group. It has been demonstrated by Tschudy (1966) and by Hall (1967), later by Gunther and Hills (1971) that the megaspores and microspores of *Ariadnaesporites* are structurally comparable, and that there is no sharp size difference between the two kinds of spores. The microspores commonly occur in clusters, held together by long perisporial hairs. *Ariadnaesporites* extends back to the Cenomanian (Fig. 34).

A trend in reduction of float number from the megaspores of *Glomerisporites* to those of *Azollopsis* and thence to *Azolla* seems to have occurred. The genus *Azolla* may now be considered.

This is by far the best represented member of the family, with some 20 species having been described, though this may be twice as many as should have been. Some species are based solely on megaspores, others solely on massulae, a few on the basis of both.

In all megaspores of Cretaceous *Azolla* there are about 24 floats confined to a proximal swimming apparatus and associated with a proximal columella. The Eocene *A. primaeva* (Penhallow) Arnold apparently has only one float (Fig. 3). The floats of the Cretaceous megaspores may be arranged in two or more regular or irregular tiers. Hairs often enmesh the floats, and the columella may partly obscure them. Three species based on megaspores can be illustrated: *A. montana* Hall, *A. distincta* Snead, and *A. barbata* Snead (Figs. 2, 4, 6).

Massulae may conform to the traditional picture of the type with anchor-shaped glochidia. Such a one is *A. gigantea* Bergad & Hall, with especially large glochidia (Fig. 5). *Azolla cretacea* is another such species. Massulae attached to *A. barbata*, however, have small, coiled glochidia. Coiled glochidia also occur in the isolated massulae of *A. circinata* (Figs. 27–29), for which megaspores

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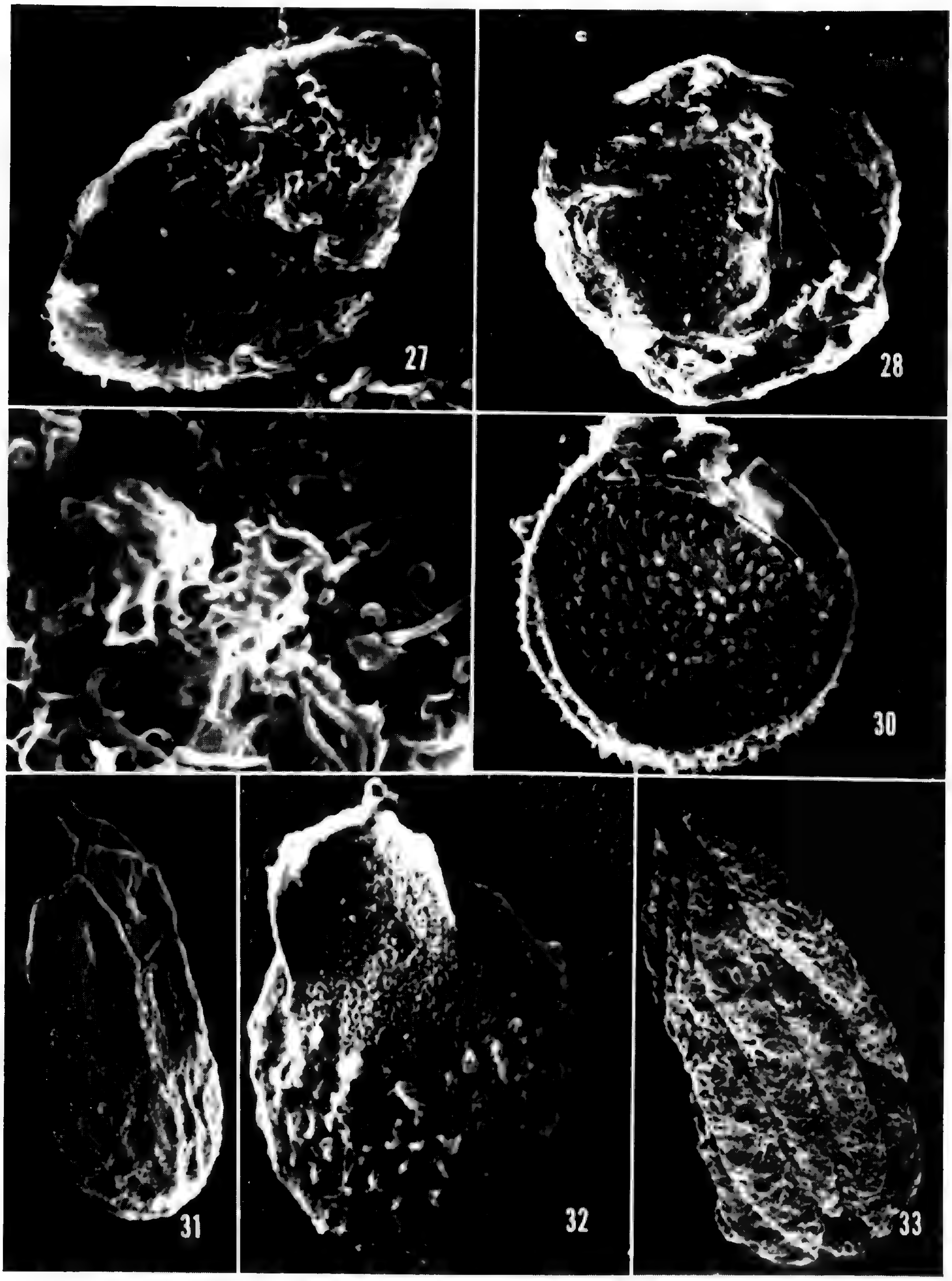
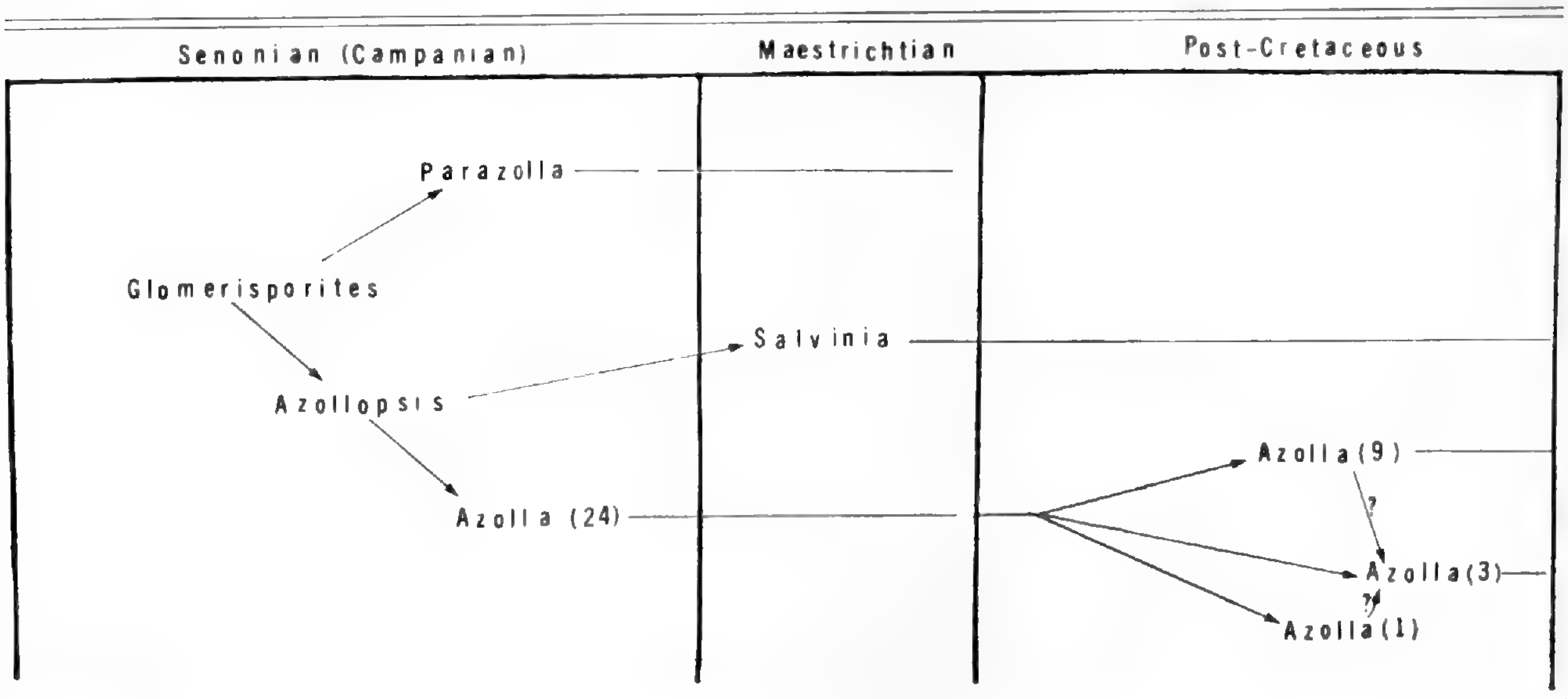
FIGURES 17–26. *Glomerisporites pupus* (Dijkstra) Potonié.—17–19. Cross sections of megaspore. (All × 312.—17. Proximal end; tripartite acrolamella, numerous perisporial hairs and small floats.—18. Apex (proximal end) of exospore, cut somewhat obliquely at the level of laesurae.—19. Mid-portion of spore; exospore separated from perispore except at bottom and left.—20. Mass of floats enmeshed in hairs separated from the megaspore. × 250.—21. Single floats. × 1000.—22–23. Cross sections of microspore at distal end (Fig. 22) and proximal end (Fig. 23). Pseudovacuolate appearance of perispore is apparent. × 1000.—24. Intact microspore; pseudoacrolamella surrounds a single exospore (microspore proper). × 250.—25. Pseudoacrolamella, faint outline of exospore, coiled hairs of microspore. × 425.—26. Intact microspore, scanning electron microscope photograph. × 250.



FIGURES 27–33.—27 and 29. *Azolla circinata* Oltz and Hall.—27. Intact, somewhat corroded massula. × 400.—29. Enlargement of another massula, coiled glochidia. × 1120. Hell Creek Fm., Montana.—28 and 30. *Salvinia spinata* Bergad and Hall.—28. Partially dissected megaspore, with hairy perispore and spiny sculptured perispore. × 115.—30. Sculptured perispore; hairy perispore removed. × 200. Hell Creek Fm., Montana.—31–33. *Parazolla* sp.—31. Intact megaspore. × 53.—32. Megaspore after removal of hairy perispore and floats. × 140.—33. Cluster of massulae. Hell Creek Fm., Montana. × 70.

TABLE 2. Suggested phylogeny of salviniaceous megaspores. Numbers in parentheses refer to floats.



are as yet unknown. Sweet (Personal communication) suggests that these may be the massulae of certain species of *Azollopsis*. The anchor-shaped glochidium occurs as early as the Campanian, attesting to its persistence from the time of appearance of the earliest *Azolla*.

Salvinia would seem to be a logical genus to discuss next. The existence of megaspores of *Salvinia* in the Cretaceous is somewhat equivocal. Three species have been described [one by R. D. Bergad and myself (1971)]. *Salvinia* megaspores lack floats. The proximal end of the megaspore has three flap-like extensions of the perispore which overarch the laesurae of the exospore. There are no true floats, according to Kempf (1969*a*). The Cretaceous megaspores called *Salvinia* also lack floats, but they do not have the proximal flaps either, being essentially elliptical in shape and covered with a pseudovacuolate perispore (Figs. 28, 30). Massulae of *Salvinia* are unknown from the Cretaceous. Both bonafide megaspores and massulae of *Salvinia* do occur in the late Paleocene or early Eocene (Jain & Hall, 1969).

One last Cretaceous genus remains. This is *Parazolla*, a name I created (Hall, 1969) but one not fully recognized by some workers who merge its species with *Azolla*.

The megaspores are quite large (Figs. 31–32). There is a proximal cluster of elongate, often grooved and interlocking floats in one or two regular or irregular tiers. In one species the perispore hairs are firmly attached to the wall, but in a second they can be removed to show the acrolamella (Fig. 32). Coiled hairs occur at the juncture of floats and body; these kinds of hairs do not occur in megaspores of any species of *Azolla*. Whereas the megaspores may resemble some species of *Azolla*, the massulae, which have been found attached, do not. These are elongate and banana-shaped. Clusters of them have been found, as in Figure 33, probably the contents of one sporangium. One species has massulae with glochidia which terminate in a spherical knob. In another species glochidia seem to be lacking. Size and shape of the massulae and characters of the glochidia are not matched by any species of *Azolla*, in my opinion.

As yet we have not been able to match all species of *Azolla* with the appropriate kind of massula. This is the most variable of the Cretaceous genera. On the basis of megaspores, with good substantiation from the massulae, a phyletic scheme for Cretaceous Salviniaceae can be proposed, as in Table 2.

What is so striking about evolution of the Salviniaceae is its sudden burst of appearance and almost equally sudden decline. *Glomerisporites*, *Azollopsis*, *Azolla*, and *Parazolla* all first occur in the Campanian. All but *Azolla* came to virtual extinction by the close of the Cretaceous. There is only one record of *Azollopsis* from the Paleocene (Jain & Hall, 1969), and it could have been reworked. Thus, it seems to me that this family which, up to a decade ago was known from the fossil record only in the Tertiary and only in examples directly comparable with extant species, has had a long history, is much more diverse than commonly believed, and is represented today by remnants of a formerly existing highly successful group of ferns.

LITERATURE CITED

ARNOLD, C. A. 1955. A tertiary *Azolla* from British Columbia. Contr. Mus. Paleontol. Univ. Michigan 12: 37–45.

BERGAD, R. D. 1973. North American species of the Cretaceous megaspores *Balmeisporites* and *Monophyllosporites*. Micropaleontology 19: 53–67.

——— & J. W. HALL. 1971. A Cretaceous *Azolla* massula with large glochidia. Bot. Gaz. (Crawfordsville) 132: 237–239.

BONNET, A. L-M. 1957. Contribution à l'étude des Hydropteridées. III. Recherches sur *Azolla filiculoides* Lamk. Rev. Cytol. Biol. Vég. 23: 1–88.

DIJKSTRA, S. J. 1949. Megaspores and some other fossils from the Aachenian (Senonian) in South Limburg, Netherlands. Meded. Geol. Stichting, N.S. 3: 19–32.

DUNCAN, R. E. 1940. The cytology of sporangium development in *Azolla filiculoides*. Bull. Torrey Bot. Club 67: 391–412.

ELLIS, C. H. & R. H. TSCHUDY. 1964. The Cretaceous megaspore genus *Arcellites* Miner. Micropaleontology 10: 73–79.

GUNTHER, P. & L. V. HILLS. 1970. Heterospory in *Ariadnaesporites*. Pollen & Spores 12: 123–130.

HALL, J. W. 1963. Megaspores and other fossils in the Dakota Formation (Cenomanian) of Iowa, U.S.A. Pollen & Spores 5: 425–443.

———. 1967. Two new species of *Ariadnaesporites*. Pollen & Spores 9: 563–568.

———. 1968. A new genus of Salviniaceae and a new species of *Azolla* from the late Cretaceous. Amer. Fern Jour. 58: 77–88.

———. 1969. Studies on fossil *Azolla*: Primitive types of megaspores and massulae from the Cretaceous. Amer. Jour. Bot. 56: 1173–1180.

HILLS, L. V. 1967. *Ariadnaesporites*, *Capulisporites* or *Caudaspora*: a discussion. Pollen & Spores 9: 553–562.

——— & N. WEINER. 1965. *Azolla geneseana*, n.sp., and revision of *Azolla primaeva*. Micropaleontology 11: 255–261.

HUGHES, N. F. 1958. Palaeontological evidence for the Age of the Wealden. Geol. Mag. 95: 41–49.

JAIN, R. K. & J. W. HALL. 1969. A contribution to the early Tertiary fossil record of the Salviniaceae. Amer. Jour. Bot. 56: 527–539.

KEMPF, E. K. 1969*a*. Elektronenmikroskopie der Sporodermis von Mega und Microsporen der pteridophyten Gattung *Salvinia* aus dem Tertiär und Quartär Deutschlands. Palaeontographica 136B: 47–70.

———. 1969*b*. Elektronenmikroskopie der Megasporen von *Azolla tegelienis* aus dem Altpleistozän der Niederlande. Palaeontographica 128B: 167–179.

Srivastava, S. K. 1968. *Azolla* from the Upper Cretaceous Edmonton Formation, Alberta, Canada. Canad. Jour. Earth Sci. 5: 915–919.

Stanley, E. A. 1965. Upper Cretaceous and Paleocene plant microfossils and Paleocene dinoflagellates and hystrichosphaerids from northwestern South Dakota. Bull. Amer. Paleontol. 49(222): 177–384.

Stough, J. B. 1968. New Late Cretaceous Palynomorphs from Southern South America. Univ. Kansas Paleontol. Contr. 32: 1–7.

Surange, K. R. 1952. The morphology of *Stauropteris burntislandica* P. Bertrand and its megasporangium *Bensonites fusiformis* R. Scott. Philos. Trans., Ser. B 237B: 73–91.

Tschudy, R. H. 1966. Associated megaspores and microspores of the Cretaceous genus *Ariadnaesporites* Potonié 1956 emend. U.S.G.S. Prof. Pap. 550D: D76–D82.

PHYTOCHEMICAL ASPECTS OF FERN SYSTEMATICS

DAVID E. GIANNASI[1]

ABSTRACT

The use of chemical data in fern systematics follows three main approaches: physiological studies, protein studies, and comparisons of secondary metabolite distributions. Physiological studies are useful at generic and higher taxonomic levels. These investigations include work on: (1) fern antheridogens and the differential response of various fern families to antheridial induction by these hormones, (2) the phenol glucosylation pathway, in which vascular plants possess the ability to glucosylate exogenously administered phenolic compounds, while non-vascular plants do not, and (3) differences in *D*-methionine metabolism in vascular and non-vascular plants. Protein work in ferns is limited and consists mainly of serological and electrophoretic studies. Secondary metabolites remain the largest body of chemical data available for chemosystematic research and are most effectively used at generic and lower taxonomic levels. Studies of acylphloroglucinol compounds in *Dryopteris* and some recent work with flavonoids in the fern genera, *Gymnopteris* and *Hemionitis*, are described as examples of chemosystematic studies employing secondary metabolites.

The development of new analytical techniques, such as paper and gas chromatography, and electrophoresis, has done much to expand the use of phytochemical data in plant studies (Alston, 1969; Alston & Turner, 1963). While this type of chemical information has been employed extensively in gymnosperm and angiosperm systematics, its use in fern systematics is still relatively recent. Yet, even a cursory look at the types of chemical constituents produced by ferns clearly shows great potential for such studies (Berti & Bottari, 1968). From the literature available, chemosystematic research on ferns appears to follow three major approaches:

(1) Physiological studies: examination of the effects on physiological and biosynthetic pathways in ferns and their allies, upon addition of natural or synthetic substances to the growing plant.

(2) Protein studies: systematic comparisons of proteins in ferns using various serological and/or electrophoretic techniques.

(3) Secondary metabolites: comparison of compounds which accumulate in the tissues of ferns and apparently are not involved in primary metabolic pathways, but differ qualitatively and/or quantitatively enough in structural variation as to be useful in systematic studies.

Within the limits of this discussion we will endeavor to examine several examples of each of these three approaches.

PHYSIOLOGICAL STUDIES

One of the more significant physiological works is that by Voeller on sex hormones in ferns (Voeller, 1971; Voeller & Weinberg, 1969; Weinberg & Voeller, 1969). Working with *Pteridium aquilinum*, Voeller succeeded in isolating and purifying a sex hormone, which was subsequently named Antheridogen-A. As described by Voeller (1971) and other earlier workers, some of the fern gameto-

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TABLE 1. Antheridial and germination responses to fern hormones.[a]

	Antheridial formation			Germination responses				
	Antheridogen		GA$_3$[b]	Light	Dark	Dark/Antheridogen		Dark/GA$_3$[b]
Family	A	B				A	B	
1. Aspidiaceae	+	–	–	+	(+)	+	–	–
2. Pteridaceae	+	–	–	+	(+)	+	–	–
3. Adiantaceae	+	–	–	+	–	+	–	–
4. Blechnaceae	+	–	–	+	–	+	–	–
5. Davalliaceae	+	–	–	+	–	+	–	–
6. Polypodiaceae	(+)[c]	–	–	+	(+)	(+)	–	–
7. Cyatheaceae	–	–	–	+	–	–	–	–
8. Osmundaceae	–	–	–	+	–	–	–	–
9. Schizaeaceae	–	+	+	+	–	–	+	+

[a] This table is a summarization of data taken from Voeller's papers.

[b] GA$_3$—gibberellic acid.

[c] Indicates that only one species gave a positive reaction in an otherwise negatively reacting family.

phytes under axenic culture grow faster than others and produce this hormone which in turn induces antheridial formation in the remaining, slower-growing gametophytes. Antheridogen-A was also found to induce production of an intragametophytic inhibitor in the larger hormone-producing gametophytes. This inhibitor stops antheridial formation in these large gametophytes which then become archegoniate. A second hormone, Antheridogen-B, was also found, and its physiological affects as well as spore germination responses to light, darkness, and gibberellic acid were also examined.

In his review of this work, Voeller (1971) clearly emphasizes the potential for physiological and morphogenetic studies of plant growth using ferns, especially since the distinct gametophytic stage can be grown easily in axenic culture under controlled conditions.

Of more immediate systematic interest, however, is the fact that not all ferns react to the antheridogens and different growth regimes in the same way (Table 1). Thus gametophytes of the first five families all produce antheridia in response to Antheridogen-A, while, with the exception of *Polypodium feei* (Polypodiaceae), the last four families show no response to the hormone. Antheridogen-B, in contrast, induces antheridia only in the Schizaeaceae. Similarly, the presence of gibberellic acid, GA$_3$, induces antheridial formation, but again only in the Schizaeaceae. However, Antheridogen-B and GA$_3$ induce different numbers of sperm in the antheridia of the same species.

In terms of the germination studies the spores of all ferns germinate in light. Most of the fern spores fail to germinate in the dark with the exception again of *Polypodium feei*, and *Polystichum munitum* (Aspidiaceae) and *Pteridium aquilinum* (Pteridaceae). However, if fern spores are grown in the dark but in the presence of Antheridogen-A, germination will occur in those species which normally show antheridial induction by Antheridogen-A. Similarly, spores of the Schizaeaceae are the only ones which germinate in the dark in the presence of Antheridogen-B or GA_3. These results match those observed for antheridial induction in the families tested. Though incomplete, this work clearly shows the potential of systematic distinctions between families based on hormone physiology.

Using another approach, Glass and Bohm (1970), have tested for the phenol glucosylation reaction in ferns. It is known that angiosperms and gymnosperms possess the ability to absorb and glucosylate simple phenolic compounds when exogenously administered to the plants. Such abilities are apparently lacking in lower plant groups such as the algae, fungi, and bryophytes.

These workers selected the fern *Pityrogramma calomelanos* and *Psilotum nudum* for their feeding experiments. After administering large, exogenous quantities of the phenols, quinol and catechol, to these plants, large amounts of quinol and catechol glucoside were recovered from the plants. While only the two plant species were examined, the phenol glucosylation pathway does appear to be characteristic of vascular plants.

Since this synthetic ability appears in *Psilotum*, the authors conclude that this reaction pathway probably evolved quite early in plants, since *Psilotum* is considered to be an example of a primitive tracheophyte. However, if, as Bierhorst (1972) suggests, *Psilotum* is in fact a highly modified fern, then the occurrence of the phenol glucosylation reaction in *Psilotum* does not necessarily indicate an ancient evolutionary origin for this chemical reaction.

The next question is whether the reaction is present in other fern allies. Unfortunately, the authors did not test the lycopsids, but they do state that *Equisetum arvense* does possess this glucosylation pathway. This lack of data on the lycopods again leaves the phylogenist adrift.

Such a question is in fact raised in some recent work by Pokorny, Marčenko and Keglević (1970). These workers examined methionine metabolism in several species from each class of plants in the plant kingdom to determine if the metabolic pathways and/or metabolites derived from methionine metabolism were of systematic interest.

Radioactively labelled *L*- and *D*-methionine-methyl-^{14}C were administered under identical conditions in parallel experiments. The pathways of the two racemic forms of methionine during their metabolism to other amines and acids were examined using a combination of chromatography, electrophoresis, and radioactivity counting. The following points were discovered.

(1) The *L*-isomer of methionine is metabolized in the same way in all plants.

(2) The *D*-isomer, in contrast, can be metabolized in two different ways:

A. Algae, fungi, some lichens, and liverworts can convert the *D*-form into the *L*-form via deamination of the *D*-form, followed by racemization to the *L*-form, or, by direct *L*-specific reamination to the *L*-form.

B. Most higher plants (and some mosses) lack these pathways and the *D*-form is instead acylated to a malonyl conjugate of methionine with retention of the *D*-form.

(3) The fungi and lichen, though unable to form N-malonyl conjugates of methionine, can form N-acetyl conjugates of the *D*-form.

(4) The lycopods and some mosses are able to form both N-malonyl and N-acetyl conjugates and thus appear to be a transition series between vascular and non-vascular plants.

(5) While in vascular plants the major portion of the radioactive label appears in the N-malonyl-*D*-methionine conjugate, the non-vascular plants, in contrast, concentrate the radioactive label in non-conjugated acidic and neutral amine compounds. Again, some mosses and the lycopods seem to be transitional, accumulating the label in both conjugated and non-conjugated forms.

Such data certainly invite some speculation as to how close the relationship is between the mosses and the "primitive" tracheophytes. Unfortunately, *Psilotum* was not examined, and again the phylogenist is left in the dark as to its methionine synthesis and thus its probable phyletic position. The large scale phyletic implications of this type of physiological data are, however, quite clear.

PROTEIN STUDIES

Systematic studies of ferns using proteins seem to be rather rare in the literature. However, a recent and very elegant study by Petersen and Fairbrothers (1970) on spore proteins in *Osmunda* deserves discussion. The problem involved whether or not *Osmunda claytoniana* is more closely related to *O. regalis* or to *O. cinnamomea*. Various systematists have favored one or the other of these relationships, while others favor neither and have raised all three taxa to distinct subgeneric or generic status. Using protein data the authors attempted to determine which of these possibilities is most probable. Comparisons of protein data were also made with *Matteuccia struthiopteris* and *Onoclea sensibilis* as well as *Dryopteris marginalis*.

The authors employed standard serological methods and more recently developed techniques, such as immunodiffusion, electrophoresis and immunoelectrophoresis, to ensure that their results were not due to the use of any one method. Further, they tested several different types of protein extraction methods to determine the full range of serological and electrophoretic reactions. Thus, they tested:

1) the crude protein extract from spores,
2) non-delipified extract in which lipid contaminants remained,
3) delipified extracts with all lipids removed, and
4) a protein extract partially purified by precipitation with ammonium sulfate.

Of these, the delipified protein extract gave the most clear-cut and consistent serological and electrophoretic results. Crude and non-delipified extracts were found to contain too many contaminants for good serological and electrophoretic resolution. Ammonium sulfate precipitation of protein extracts increased serological precipitation but decreased resolution of protein bands during electrophoresis. Further, there was some question as to whether protein precipitation for ammonium sulfate-treated extracts resulted from the increased concentration of just a few proteins or actually represented a true measure of all protein affinities between the taxa.

The results of this work using delipified protein extracts and both serological precipitates and electrophoretic band patterns, clearly show that *Osmunda clay-*

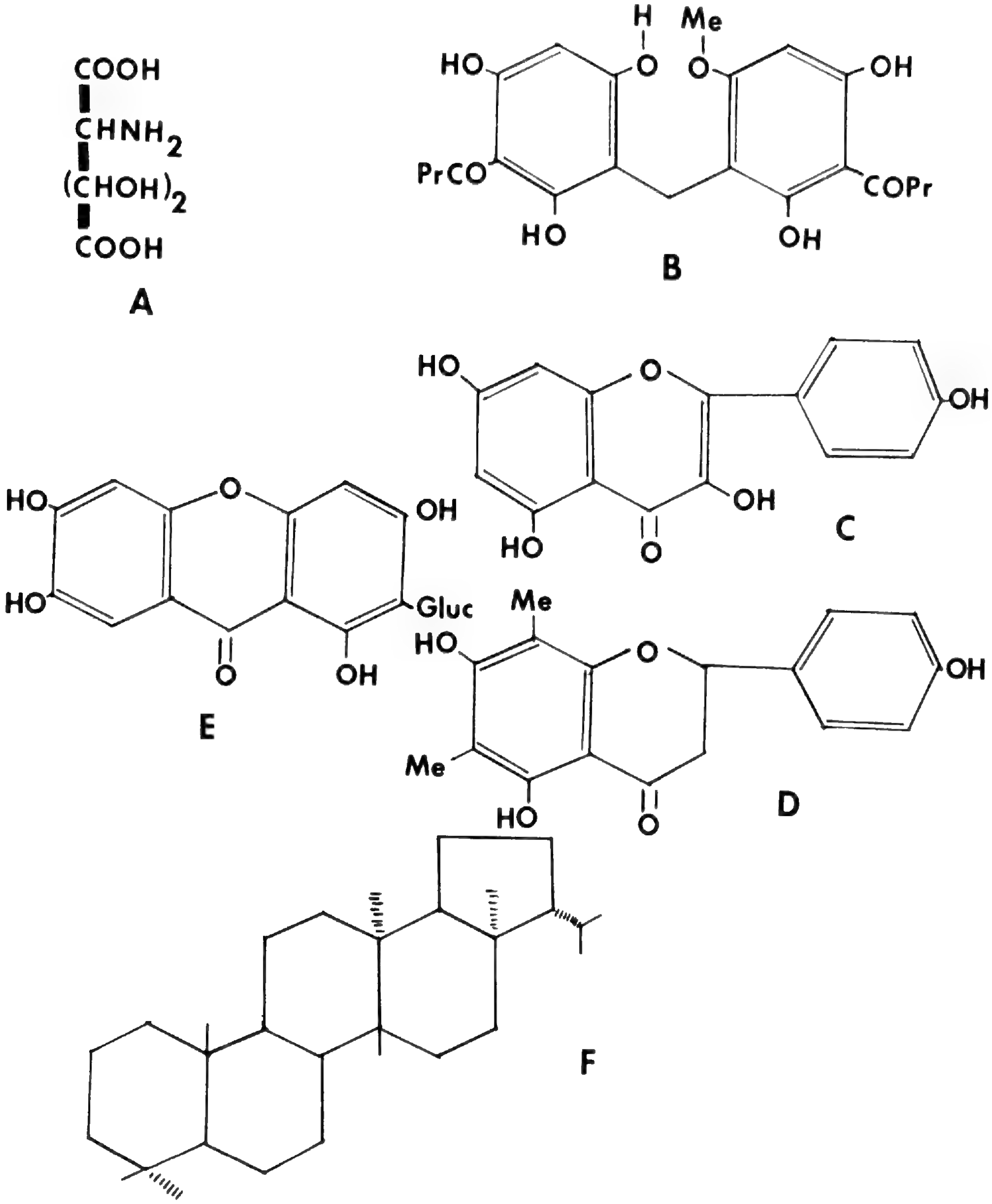

FIGURE 1. Structures and identities of some secondary metabolites.—A. 3, 4-dihydroxyglutamic acid.—B. Phloraspin, an acylphloroglucinol compound; Pr = propyl unit.—C. Kaempferol, a flavonol aglycone.—D. Farrerol, a C-dimethyl flavanone.—E. Mangiferin, a C-glucosyl xanthone.—F. Fernane, a triterpenoid; dotted constituents are in a plane opposite to that of the paper.

toniana is, in fact, more closely related to *O. cinnamomea*, and *O. regalis* is more closely related to *O. claytoniana* than to *O. cinnamomea*. The protein data further suggest that none of these taxa are worthy of subgeneric or generic rank.

Concerning generic comparisons, the authors found that *Osmunda* had greater protein affinities with *Matteuccia struthiopteris* and *Onoclea sensibilis* than with

Dryopteris. *Dryopteris marginalis*, in contrast, did show much protein affinity with *Matteuccia* and *Onoclea*.

While limited in scope, this work does set a detailed and rigorous testing model for further study of protein affinities in ferns.

SECONDARY METABOLITES

While the physiological and protein studies show great potential in fern systematics, secondary metabolites probably represent the largest body of chemical data available for fern studies. These secondary metabolites (Bú Lock, 1961) accumulate in various tissues of plants. The range of variation in these secondary metabolites has recently been reviewed (Berti & Bottari, 1968), although the reader should consult Hegnauer (1962) for data published previous to 1961.

As an example, free amino acids such as 3, 4-dihydroxyglutamic acid (Fig. 1A) are often species-specific, in this case, to *Struthiopteris* [= *Matteuccia*] *filicastrum* (Berti & Bottari, 1968). Although a number of ferns have been screened for free amino acids, few phyletic conclusions above the generic level may be drawn from the data available (Panvisavas, Worthen & Bohm, 1968).

In the case of alkaloids, their presence in *Lycopodium* is well known (Hegnauer, 1962), although they appear to be absent in *Selaginella* and *Isoetes*. Similarly, a general survey for alkaloids in ferns indicates that they are absent from this group, too (Panvisavas, Worthen & Bohm, 1968). Thus, the systematic use of alkaloids would seem to be restricted to *Lycopodium*.

Triterpenoids have also been examined and identified in ferns, but the investigations have only begun since 1960, and it is too early to determine their systematic significance (Berti & Bottari, 1968). An example, fernane, is shown in Fig. 1F.

Another group of fern constituents, the acylphloroglucinol compounds (Fig. 1B), have been found only in the genus *Dryopteris*, where these compounds have been used extensively in chemosystematic and phylogenetic studies (Widén, 1971; Widén & Britton, 1971*a*, 1971*b*, 1971*c*).

One of the more interesting works in this series on *Dryopteris* is that on the *D. cristata* complex in North America (Widén & Britton, 1971*c*). The complex consists of a series of diploid species which have given rise to tetraploid and hexaploid derivatives. The evolution of these taxa from each other has been documented cytologically, and the acylphloroglucinol patterns in each taxon confirms its putative cytological origin. *Dryopteris cristata* itself is apparently derived from genomic contributions from *D. ludoviciana* of the *D. cristata* complex and another unknown diploid ancestor which has many characters in common with *D. spinulosa* of the *D. dilatata* complex. This hypothetical ancestor has been described and informally named "*D. semicristata*" or "*D. pseudospinulosa*."

Examination of the chemistry confirms the similarities between *Dryopteris ludoviciana* and *D. cristata*. The chemistry also indicates that *D. spinulosa* of the *D. dilatata* complex is quite similar to *D. cristata* and that the hypothesized ancestor probably contributed genomes to both species. Correlation between chemical and cytological data is very good; and since the identity of the compounds is known, the full value of the work is realized.

Flavonoids represent another large group of so-called secondary metabolites which have been used in chemosystematic studies, like those in *Dryopteris*. Unlike the acylphloroglucinol compounds, however, the flavonoids are not restricted to one genus but occur throughout the ferns as well as the fern allies (Hegnauer, 1962; Berti & Bottari, 1968). Like other fern constituents, though, large flavonoid surveys of the pteridophytes are lacking, and the systematic and phyletic value of flavonoids above the generic level remains undetermined as yet (Harborne, 1967).

Certainly, at the generic level and below, the flavonoids have proven to be most useful. The classic paper on the phenolics of *Asplenium* (Smith & Levin, 1963) still remains as an example of integration of cytological and chromatographic pattern data. Unfortunately, these authors did not identify the phenolics in *Asplenium*, and much chemical data of potential systematic interest is unavailable. Recently, however, Smith and Harborne (1971) have reexamined some of the compounds described in the earlier work. These first compounds were not flavonoids, but were mangiferin glycosides (Fig. 1E) which are xanthones.

Other early chromatographic studies also used only spot patterns (Scora & Wagner, 1964). However, the publication of several texts in recent years make the identification of flavonoids much easier; and thus there is little excuse for not including some identification of the compounds along with the pattern data (Mabry, Markham & Thomas, 1970; Jurd, 1962). Indeed, the importance of structural identification of flavonoids was emphasized in some recently completed work on the fern genera, *Gymnopteris* and *Hemionitis*, done by myself and Dr. John Mickel at the New York Botanical Garden.

These two genera have been maintained on the basis of their leaf morphology and marginal leaf venation. *Hemionitis* has palmate venation, and the fronds of most species are generally palmately lobed, while the architecture in *Gymnopteris* is generally pinnate. The two genera are also separated on the basis of whether the veins are free (*Gymnopteris*) or netted (*Hemionitis*). These characters, however, are not reliable, and distinctions break down upon close examination.

Examination of the flavonoids by two-dimensional paper chromatography shows that most of the species have their own specific profile (Table 2). However, it should also be noted that if these species are arranged in a manner based on their chemical similarity, regardless of their generic assignations, we find that two groups exist. It is immediately apparent that these chemical groupings cut across generic lines. The question then arises as to whether there actually is a structural homology between the compounds characterizing each group, and indeed there is.

Looking at Group II first, it is characterized by the presence of two or more of the compounds, 9–12 (Fig. 2A). Ultraviolet spectral analysis and comparison with authentic flavonoid samples, as well as published data (Mabry, Markham & Thomas, 1970; Jurd, 1962), show compounds 9 and 11 to be quercetin-3-

TABLE 2. Flavonoid distribution and spore types in *Gymnopteris* and *Hemionitis*.

Taxon	Flavonoid compounds																Spore Type[a]
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Group I																	
H. palmata	+	+			+	+	+	+									T
H. pinnatifida	+		+	+				+								+	T
H. levyi		+	+	+				+							+	+	T
G. rufa	+	+		+		+											T
Group II																	
H. elegans									+	+	+	+	+	+			C
H. arifolia				+					+			+					C
G. subcordata									+	+		+					C
G. bipinnata									+	+							C
G. vestita									+	+							C
G. tomentosa									+	+	+	+					C

[a] Spore types: T—tuberculate; C—crested.

rutinoside and 3-monoglucoside, respectively. Compounds 10 and 12 are kaempferol-3-rutinoside and 3-monoglucoside. All four of these pigments are typical flavonol glycosides (*cf.* Fig. 1C for kaempferol aglycone).

Group I, however, lacks these typical flavonols; and instead, the taxa in this group are characterized by possessing two or more of compounds 1–3 (*cf.* Fig. 2B), which, although not fully characterized, do appear to be different glycosides of a methylated flavonol aglycone (Mabry, Markham & Thomas, 1970). These data certainly suggest that the separation of these two genera on the aforementioned morphological grounds is unnatural.

Quite independently, Dr. Mickel had examined the spores of these same taxa using the scanning electron microscope. The micrographs showed two major spore types, those which were covered with spines or tubercles and those which have a series of crests or ridges on the surface.

When compared with the chemical data, all species of Group I with the methylated flavonol glycosides (compounds 1–3) have the tuberculate spores, while all species of Group II, with the more typical flavonols (compounds 9–12), have the crested spores (Table 2). The chemical and palynological data agree perfectly, and the arrangements cut across previous generic parameters. This has led to a recombination of the two genera and a redefinition of the genus *Hemionitis* (Mickel, 1973). In this case, both chemical and spore data have radically altered the disposition of these genera. Complete details of this work will be described in a subsequent paper.

CONCLUSIONS

The study of chemical phylogeny in the ferns, then, is most crucial, considering their phyletic position as the earliest vascular plants. Certainly, the methionine metabolism experiments indicate some metabolic similarities between the mosses and the lycopods, though much more proof is obviously needed to prove any direct relationship.

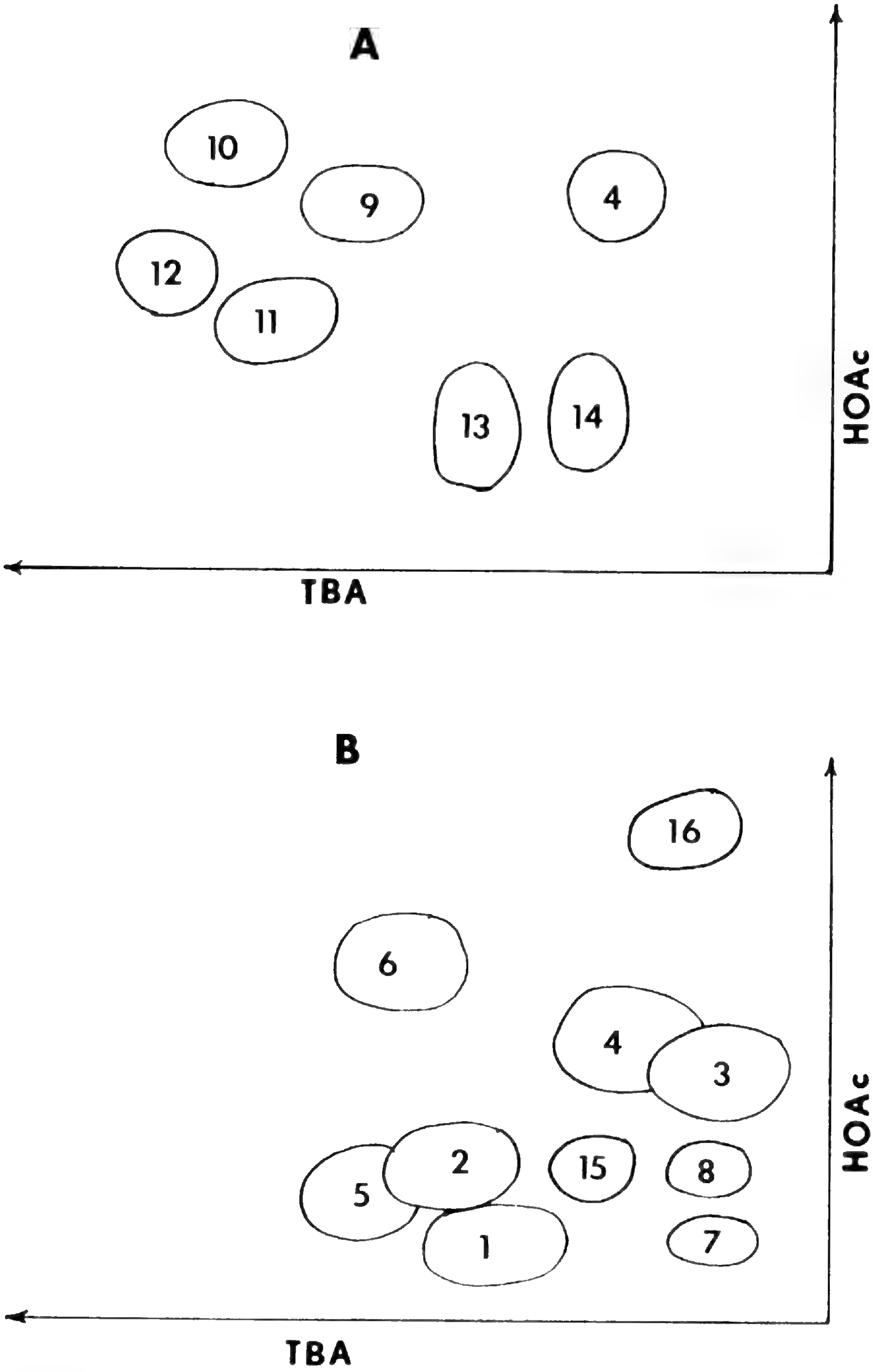

FIGURE 2. Chromatographic patterns of flavonoids in *Gymnopteris* and *Hemionitis*; TBA = *tert*-butanol: acetic acid: water (3:1:1 v v); HOAc = acetic acid: water (15:85 v/v).—A. Composite chromatogram of flavonoids found in species in Group II (Table 2).—B. Composite chromatograms of flavonoids found in species in Group I (Table 2).

Of the three approaches discussed, each has its own strong points as well as its shortcomings. At the present time the use of secondary metabolites is perhaps the most profitable group of compounds to work with. Procedures for the identification of these compounds are available; and methods can be learned by the taxonomist, or, more profitably, by teamwork between the taxonomist and chemist. To date, however, surveys of this type are still incomplete; and only limited phyletic conclusions can be drawn. The physiological approach is probably more useful at the family level or higher, since it provides a direct comparison of primary metabolic processes. The techniques and equipment needed for such studies, though, are usually beyond the scope and training of most taxonomists.

Protein studies probably represent the truest approach to chemical phylogeny, since the proteins represent the primary translation products of the DNA code. Serology illustrates the first step in the systematic use of proteins. But again, the most valuable portion of this data, the amino acid sequence, still is not available for the ferns, though some limited information is available for angiosperms (Boulter, 1973). However, techniques and equipment are not sufficiently developed to allow for the rapid analysis of a large number of taxa (Turner, 1971).

Perhaps the ultimate use of molecular data to date may be found in the use of DNA annealing-hybridization comparisons between plants species (Voeller, 1971). DNA helices may be dissociated by heating and will reassociate upon cooling. Dissociated DNA strands can be mixed with similarly treated DNA from another taxon, the degree of relationship being determined by the percentage of hybrid renaturation. However, such techniques are quite complicated and, like previous biochemical approaches, require quite some expertise.

More important, perhaps, is the need for a scientific standard in which there is as careful and complete a selection as possible from all plant groups to be examined, regardless of the technique. This would do much to fill many of the empty holes in many phylogenetic schemes.

LITERATURE CITED

ALSTON, R. E. 1967. Biochemical systematics. Pp. 197–305, *in* T. Dobzhansky, M. K. Hecht & W. C. Steere (editors), "Evolutionary Biology." Volume 1. New York.

——— & B. L. TURNER. 1963. Biochemical Systematics. New Jersey.

BERTI, G. & F. BOTTARI. 1968. Constituents of ferns. Pp. 590–685, *in* L. Reinhold & Y. Livschitz (editors), "Progress in Phytochemistry." Volume 1. London & New York.

BIERHORST, D. W. 1971. Morphology of Vascular Plants. New York.

BOULTER, D. 1973. Flowering plant proteins. Pp. 30–60, *in* L. P. Miller (editor), "Phytochemistry." Volume 2. New York.

BÚ LOCK, J. D. 1961. Intermediary metabolism and antibiotic synthesis. Advances Appl. Microbiol. 3: 293–342.

GLASS, A. D. M. & B. A. BOHM. 1970. The phenol glucosylation reaction in ferns. Phytochemistry 9: 2197–2198.

HARBORNE, J. B. 1967. Comparative Biochemistry of the Flavonoids. New York.

HEGNAUER, R. 1962. Chemotaxonomie der Pflanzen. Band 1. Basel.

JURD, L. 1962. Spectral properties of flavonoid compounds. Pp. 108–155, *in* T. A. Geissman (editor), "Chemistry of the Flavonoid Compounds." New York.

MABRY, T. J., K. R. MARKHAM & M. B. THOMAS. 1970. The Systematic Identification of Flavonoids. New York, Heidelberg, Berlin.

MICKEL, J. T. 1974. A redefinition of the genus *Hemionitis*. Amer. Fern Jour. 64: 3–12.

Panvisavas, R., L. R. Worthen & B. A. Bohm. 1968. The distribution of free amino acids and alkaloids in selected species of ferns. Lloydia 31: 63–69.

Petersen, R. L. & D. E. Fairbrothers. 1971. North American *Osmunda* species: A serological and disc electrophoretic analysis of spore proteins. Amer. Midl. Naturalist 85: 437–457.

Pokorny, M., E. Marčenko & D. Keglević. 1970. Comparative studies of *L*- and *D*-methionine metabolism in lower and higher plants. Phytochemistry 9: 2175–2188.

Scora, R. W. & W. H. Wagner, Jr. 1964. A preliminary chromatographic study of Eastern American *Dryopteris*. Amer. Fern Jour. 54: 105–113.

Smith, D. M. & J. B. Harborne. 1971. Xanthones in the Appalachian *Asplenium* complex. Phytochemistry 10: 2117–2119.

——— & D. A. Levin. 1963. A chromatographic study of reticulate evolution in the Appalachian *Asplenium* complex. Amer. Jour. Bot. 50: 952–958.

Turner, B. L. 1971. Implications of the biochemical data: A summing up. Pp. 549–558, *in* J. B. Harborne, D. Boulter & B. L. Turner (editors), "Chemotaxonomy of the Leguminosae." New York.

Voeller, B. R. 1971. Developmental physiology of fern gametophytes: Relevance for biology. BioScience 21: 266–270.

——— & E. S. Weinberg. 1969. Evolutionary and physiological aspects of antheridium induction in ferns. Pp. 77–93, *in* J. E. Gunckel (editor), "Current Topics in Plant Science." New York.

Weinberg, E. S. & B. R. Voeller. 1969. External factors inducing germination of fern spores. Amer. Fern Jour. 59: 153–167.

Widén, C.-J. 1971. Chemotaxonomic investigations on *Dryopteris fragrans*. Canad. Jour. Bot. 49: 989–992.

——— & D. M. Britton. 1971*a*. A chromatographic study of *Dryopteris dilatata* in North America and eastern Asia. Canad. Jour. Bot. 49: 247–258.

——— & ———. 1971*b*. A chromatographic and cytological study of *Dryopteris filix-mas* and related taxa in North America. Canad. Jour. Bot. 49: 1589–1600.

——— & ———. 1971*c*. Chemotaxonomic investigations on the *Dryopteris cristata* complex in North America. Canad. Jour. Bot. 49: 1141–1154.

COMPARATIVE ANATOMICAL STUDIES OF THE FERNS[1]

RICHARD A. WHITE[2]

ABSTRACT

The renewal of interest in systematic problems of the ferns has recently encouraged increased interest in comparative anatomical studies of the ferns. Three current examples are discussed in some detail: comparative morphology of fern shoot meristems, comparative anatomy of vascular tissue, and comparative studies of stomata patterns and ontogenies. Broad survey anatomical studies of critical problem taxa are suggested as preferable to narrow detailed studies unrelated to systematic problems. Professional taxonomists and systematists are useful resources for the identification of significant problems. The use of more recent taxonomic schemes and of techniques related to Wagner networks and trees is suggested as a means of handling the data and applying it to the solution of systematic problems.

Anatomical studies of the ferns have had a long and historically significant place in the professional literature. Through the years since the early work of the Europeans and F. O. Bower numerous fern species have been examined and described. Anatomical studies in particular, played a large part in the conclusions concerning fern systematic relationships and evolution drawn by Bower and Jeffrey (for example) and their contemporaries. Relatively recently anatomical data have emerged once again as important to an accurate understanding of relationships and evolution among fern groups (*e.g.* Holttum & Sen, 1961; Tryon, 1970; Lucansky, 1974*a*, *b*; McAlpin, 1971; McAlpin & White, 1974). With a few major exceptions the period between the early 20th century and today's renewed emphasis on comparative and systematic anatomical studies is filled with numerous examples of detailed anatomical and morphological descriptions of fern species, with relatively little regard being paid to systematic or evolutionary considerations.

Detailed anatomical investigations can, of course, serve several useful purposes including the addition of new knowledge about particular taxa and the useful application of these kinds of data to problems of relationships among fern taxa. I believe a primary current intellectual challenge to lie in the use of broad but detailed comparative anatomical studies as they apply to important problems of fern systematics and evolution. I hope to indicate here some of the more obvious areas of anatomical research currently being investigated and in need of both a more thorough study and a broader, comparative application to fern systematics.

Three examples of kinds of comparative studies might be used to illustrate this point: (1) shoot meristem organization and activity, (2) vascular (stelar) patterns, and (3) stomatal patterns.

SHOOT MERISTEM ORGANIZATION

In general, most current thinking about fern shoot meristem organization is based on early descriptions of individual species. The generalization held most

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frequently is that the meristematic organization of shoots in eusporangiate ferns is a small cluster of cells to a few apical cells and that the structure of the shoot meristem of typical leptosporangiate fern consists of a relatively large tetrahedral apical cell from which all the shoot tissues are derived (*e.g.* see Clowes, 1961). In the mid 20th century a new perspective was introduced which shifted emphasis from specific cellular detail to more generalized functional zones (Wardlaw, 1944, 1965). This approach was subsequently broadened to include additional species as experimental and comparative studies of ferns became more common (*e.g.* Steeves, 1963; Sussex & Steeves, 1967; White, 1971). Preceding and then paralleling this rather new approach to fern shoot anatomy was a growing awareness of a basic zonal organization in shoot meristems of seed plants, and some attempts have been made to harmonize the patterns (*e.g.* see Gifford & Corson, 1971; Hagemann, 1964; DeAlbertis & Paolillo, 1972). The validity of these studies has been further supported by recent studies of a broad range of fern taxa, representing both eusporangiate and leptosporangiate species (McAlpin, 1971; McAlpin & White, 1974). On the basis of detailed, histological study of a reasonable sample of plants representing species from approximately 25 fern genera, a broader, more functional interpretation of fern shoot apices is now possible. Briefly, all the species which were examined fit into a zonal pattern which consists of two major zones which compose the promeristem: surface initials and subsurface initials. The former zone is characterized by relatively large cells which remain undifferentiated and divide in two planes. Anticlinal divisions produce cells which remain in the surface layer, while periclinal divisions produce cells which compose the subsurface layer. As a result of continued periclinal divisions, a multilayered subsurface group of cells is produced. The cells of this second zone are smaller and less vacuolate than the surface cells, but they possess similar staining characteristics. Active cell division in these subsurface cells maintains the group and displaces cells to the periphery of the apex. These peripheral cells then begin cellular differentiation in the peripheral (organogenic) zone surrounding the lateral and basal regions of the promeristem. The structure of the promeristem is similar in both eusporangiate and leptosporangiate ferns, and it is general enough to encompass the diversity of tissue patterns which eventually develop in various fern shoots. With the demonstrated general occurrence of such an organization in fern shoot tips, an emphasis on developmental phenomena related to shoot and lateral primordial ontogeny is possible.

VASCULAR TISSUE PATTERN

Another area of fern anatomy which is receiving renewed interest is the reexamination of vascular (stelar) patterns. The importance of the vascular tissue as a unified tissue system (the stele) was recognized in the late 19th century (*e.g.* Tiegham & Douliot, 1886), and the stele became a primary consideration for comparative anatomists shortly after that. The establishment of the classical protostele, siphonostele, and dictyostele evolutionary sequence in fern steles was extended to include the eustele of seed plants (Jeffrey, 1899, 1902). Basically this sequence is read from the primitive protostele, through the siphonostele pattern (characterized by pith) with the dictyostele representing a siphonostele dissected by leaf gaps and finally the eustele representing a very highly dissected siphonostele. Clearly, the fern patterns feature very importantly in such an evolutionary sequence. From a fairly early period, however, a different interpretation, that the vascular strands in seed plants are discrete sympodia and that the "gaps" seen in the typical dicot or gymnosperm primary stem vascular pattern are not equivalent to fern gaps, was presented in the literature (*e.g.* DeBary, 1884). Recently, based on extensive survey studies, more emphasis is being given to the sympodial nature of the vascular systems in dicotyledons, monocotyledons, and gymnosperms; and a derivation of the vascular patterns in these groups from basic fern types is presented as unlikely. Rather, based on comparative studies of extant taxa and on fossil studies, it appears these patterns may be derived directly from protostele progenitors and have by-passed the classical siphonostele stage completely. There has been considerable very recent research done on the vascular systems of dicots, monocots, and gymnosperms; but the sympodial interpretation has not yet become a part of standard text presentations (for a current introduction to this topic for seed plants see Balfour & Philipson, 1962; Beck, 1970; Benzing, 1967*a*, *b*; Devadas & Beck, 1971, 1972; Namboodiri & Beck, 1968*a*, *b*, *c*; Tomlinson, 1970; Weidlich, 1973; Zimmerman & Tomlinson, 1972). With this new burst of activity in vascular tissue anatomy in the seed plants, there has been a renewed study of fern stelar patterns and an application of the data to systematic problems. A recent example of such a study concerns the tree ferns. Over the years since Bower's early studies, the systematic relationship has been problematical among the various tree fern genera and *Metaxya* and *Lophosoria* and between the two fern families, the Dicksoniaceae and the Cyatheaceae. First, the paleotropical species were examined and anatomical studies played a role in the systematic conclusions which were drawn (*e.g.* Holttum & Sen, 1961). More recently a new classification of neotropical Cyatheaceae has provided the basis for several extended anatomical studies (Tryon, 1970; Gastony, 1973). Anatomical studies of the vascular tissue of plants representing the genera considered to be included in the Cyatheaceae (Tryon, 1970) have provided data which support the basic ideas of the Tryon system. The vascular patterns of *Metaxya* and *Lophosoria* are distinct from each other and from the other genera of the tree ferns. These other genera (*Sphaeropteris*, *Alsophila*, *Nephelea*, *Trichipteris*, *Cnemidaria* and *Cyathea*) have several differences among them, but basically they form a natural grouping based on stelar characteristics (Lucansky, 1974*a*, *b*; Lucansky & White, 1974). A natural next step is to examine, in a similar way, presumed closely related families such as the Dicksoniaceae and Dennstaedtiaceae. These studies are currently underway. The data from intensive studies of the vascular tissue alone do not provide the basis on which systematic (or taxonomic) conclusions are based. In conjunction with all the other data characteristically used for such decisions, however, stelar anatomy is a potentially powerful tool. This recent trend toward intensive but broad survey studies, in which the size and nature of the sample is considered carefully, represents a positive direction for comparative anatomical studies. These studies and others among the ferns (*e.g.* Bierhorst's work on fern relationships, Bierhorst, 1971*a*) as well as those already mentioned among the seed plants represent a decided, problem-oriented improvement over the descriptive anatomical studies of more or less randomly selected fern species. In my opinion, there are still too many examples in the current literature of the latter type of study.

Stomata Patterns and Ontogeny

Although fern stomata, including unusual patterns, have been described in the literature for a long time (*cf.* DeBary, 1886), stomata patterns and their ontogeny have recently become the subject of renewed investigation. The current literature is full of descriptive studies of mature stomata types from among both seed plants and the ferns (for a recent descriptive survey of the literature see Fryns-Claessens & Cotthem, 1973), but few have drawn phylogenetic conclusions (*e.g.* Stebbins & Khush, 1961). Of particular interest here, however, are studies of fern stomata. Many of the recent studies are of particular and small groups of ferns, and although there is considerable overlap of the genera studied by various workers, the results (and particularly the terminology) are frequently not easily compared (*e.g.* Cotthem, 1970*a*, *b*; Thurston, 1969). The early terminology (ranunculaceous, cruciferous, caryophyllous, and rubiaceous) was obviously associated with flowering plants (Vesgue, 1890). A newer, perhaps more neutral system was developed (anomocytic, anisocytic, diacytic, and paracytic), and in addition to application to dicotyledons and other seed plants (Metcalfe & Chalk, 1950), it was also applied to the ferns (*e.g.* Cotthem, 1970*a*). As more and more species were surveyed new stomata types were described, and the "nomenclature" became quite elaborate (*e.g.* see Pant, 1965; Payne, 1970; Cotthem, 1970*b*, 1971; Fryns-Claessens & Cotthem, 1973). On top of this burst of descriptive studies, it became increasingly clear that similar mature patterns could be derived by different ontogenetic pathways and that in some cases parallel ontogenies could result in different mature stomata patterns. With this "caveat" in mind studies of stomata ontogeny became important. But still repetitive studies are reported of similar material, and in some cases different workers come to different conclusions (for examples, see Inamdar, 1970; Inamdar, Patel & Bhatt, 1971; Maroti, 1965, 1966). One major example of a stomatal ontogeny problem which apparently has not yet been resolved to everyone's satisfaction, despite several recent studies, is that concerned with the so-called "floating stomates" (adestostomy) which are characteristic of *Anemia* (*e.g.* see Mickel & Lerstern, 1967; Pant & Khare, 1972). The literature is replete with small samples of stomata studies of various species representing lower vascular plants (*e.g.* Pant & Strivastava, 1962; Pant & Mehra, 1964), the eusporangiate ferns (*e.g.* Maroti, 1960, 1965; Pant & Khare, 1969; Inamdar, 1970), and various leptosporangiate ferns (*e.g.* Inamdar, Patel & Bhatt, 1971; Kondo, 1962; Kondo & Toda, 1956), but the major summary and comparative study of mature fern stomata types remains that of Cotthem (1970*a*). Of particular interest to a topic to be considered later are the descriptions provided of stomata types and ontogeny for *Psilotum* and *Tmesipteris* (*e.g.* Maroti, 1961; Paliwal & Kakkar, 1967; Pant & Mehra, 1963; Pant & Khare, 1971). The point of mentioning the studies of fern stomata (both mature types and ontogenetic patterns) is to illustrate several points: (1) such studies represent renewed interest in this character; (2) the reports, with a few exceptions, are limited to a few species; (3) there is considerable variation in terminology among the various reports; (4) no one has yet done a careful and well sampled study among critical genera so that the data could be applied to particular systematic problems. With regard to point 4 above, there are two such critical areas that immediately come to mind—problems to which stomata ontogeny data, carefully obtained from a broad sample of relevant species, could be usefully applied (in addition to all other relevant data).

One of these problems relates to the earlier mentioned interrelationship among the fern families, Cyatheaceae, Dicksoniaceae, and others putatively closely related. Careful, detailed studies of stomatal ontogeny in a broad sample of relevant taxa would add useful data to that already being accumulated by other anatomical and morphological investigations of stelar pattern ontogeny, sporangial ontogeny, indument development, and gametophyte development. With all of these data in hand, a most valuable comparative study will then be possible of this important assemblage of fern families. Similar kinds of broad data collecting for other easily recognized problem-families in fern systematics would, in my opinion, lead to more fruitful results than detailed character analyses of isolated taxa.

A second problem area in fern systematics (or at least associated with fern systematics) relates to the still controversial conclusions to which Bierhorst has come concerning *Psilotum* and *Tmesipteris*. The data he has accumulated to support his position that these taxa are ferns associated with other clearly identifiable ferns (*e.g.* Stromatopteridaceae, Schizeaceae, Hymenophyllaceae) are impressive (*e.g.* Bierhorst, 1965, 1966, 1967, 1968*a*, *b*, 1969*a*, *b*, 1971 *a*, *b*). His current work also provides a new perspective related to the morphology of the Hymenophyllaceae (see paper in this symposium). In order to resolve these problems, additional ontogenetic data are needed, and certainly stomatal ontogenies represent an area in need of current study. To my knowledge, no one other than Bierhorst has seriously or clearly considered all the data and carefully tested his contentions regarding relationships among members of this complex group of taxa.

In addition to these three areas of comparative anatomy of the ferns in which renewed interest is evident in the literature (shoot meristem organization, vascular tissue patterns and stomata ontogeny), there are other areas which are still somewhat neglected. Additional studies of fern leaf ontogeny are needed to broaden the sample upon which our current understanding of leaf development depends (*e.g.* Gaudet, 1964; Lersten, 1965; Pray, 1960, 1962). New comparative studies of root origins, ontogeny, and mature structure, and careful comparative studies of soral (*cf.* Bierhorst, 1971b) and sporangial development are two examples of other areas which with proper study may still provide a wealth of comparative data which could be useful in the resolution of systematic problems.

ANALYSIS AND USE OF DATA

One of the major difficulties or obstacles to actually increasing the application of comparative anatomical studies to broader problems of fern systematics may lie in identifying the critical problem areas in the first place or in how to apply descriptive data to the analysis once the "problem" group has been chosen.

Briefly, I would suggest that both of these kinds of problems are solvable. The first difficulty may be met by close cooperation with other workers in the field, *e.g.* with researchers specifically concerned with taxonomic or systematic problems of particular fern groups. Recently, the results of a comparative anatomical study of vascular patterns have been applied to a proposed systematic scheme for the genera of the tree ferns (Cyatheaceae). The initial scheme of relationships among the genera was established (Tryon, 1970), and then the additional anatomical data were compared to the scheme (Lucansky, 1974*a*, *b*; Lucansky & White, 1974). Similarities and differences were noted, areas of agreement were discussed, and areas which might need additional data before final conclusions could be drawn were mentioned (Lucansky & White, 1974). On the basis of such cooperative projects, corollary problems have been identified, and anatomical studies are currently underway of closely related fern families (*e.g.* Dicksoniaceae and Dennstaedtiaceae). The initial identification of the problem and recognition of it as biologically significant was primarily the work of a professional fern systematist. Cooperative interaction with comparative anatomists has led to a broader understanding of the biology of the group and laid the groundwork for more extensive anatomical study.

It is quite possible when morphological and anatomical data are accumulated to apply these data to systematic and phylogenetic problems in assemblages of plants. The degree of accuracy which results, of course, depends on how complete the data are. One approach to handling a broad accumulation of comparative data is the Wagner Divergence-Index technique (*e.g.* Wagner, 1964, 1966, 1969) or one of the even more quantitative derivatives of this basic technique (*e.g.* Farris, 1966, 1970; Kluge & Farris, 1969; Lundberg, 1972). The basic result of using such techniques is a scheme which relates groups relative to each other based on similarities and differences which are quantified by use of a numerical scale. In its simplest form the scale is developed on an analysis of characters which are determined to be general or unspecialized (numerical value = 0) in the group, versus those which are present in only some members of the group and are considered more specialized or derived (numerical value = 1). Intermediate conditions may be given intermediate values (*e.g.* numerical value = 0.5). This basic technique (and its various modifications) provides a framework against which comparative systematic data may be played and from which "networks" and "trees" may be constructed which reflect relationships among the taxa. In view of the relatively sparse paleobotanical data usually available for particular groups, it is most likely that Wagner "networks" rather than trees are more accurate and appropriate (Lundberg, 1972). On the other hand, where paleobotanical data are relatively abundant, such as for the fern family, Osmundaceae, phylogenetic trees may be developed (*e.g.* Miller, 1971).

With the philosophical groundwork fairly well established (*e.g.* Hennig, 1966; Wagner, 1969), and the techniques described in some detail (*e.g.* Farris, 1970; Lundberg, 1972; Whiffen & Bierner, 1972), this approach should become more commonly used in botanical systematic research.

A current renewal of interest in systematic problems related to the ferns has led to an increase in the number of comparative anatomical and morphological studies of this group. Three examples have been mentioned, and there are others which could have been described. In order that maximum systematic value be obtained from comparative anatomical studies, I feel broad survey studies should be made (with careful samples) of major problem groups. Professional taxonomists and fern systematists should be a resource for the identification of significant problems and the quantitative and philosophical approaches reflected in the Wagner divergence-index (or Wagner networks and trees) should be useful for the application of the data to the problem.

LITERATURE CITED

BALFOUR, E. E. & W. R. PHILIPSON. 1962. The development of the primary vascular system of certain dicotyledons. Phytomorphology 12: 110–143.

BECK, C. B. 1970. The appearance of gymnospermous structure. Biol. Rev. Cambridge Philos. Soc. 45: 379–400.

BENZING, D. H. 1967*a*. Developmental patterns in stem primary xylem of woody Ranales. I. Species with unilacunar nodes. Amer. Jour. Bot. 54: 805–813.

———. 1967*b*. Developmental patterns in stem primary xylem of woody Ranales. II. Species with trilacunar and multilacunar nodes. Amer. Jour. Bot. 54: 813–820.

BIERHORST, D. W. 1965. Older gametophytes and young sporophytes of *Schizaea melanesica.* Bull. Torrey Bot. Club 92: 475–488.

———. 1966. The fleshy, cylindrical, subterranean gametophyte of *Schizaea melanesica.* Amer. Jour. Bot. 53: 123–133.

———. 1967. The gametophyte of *Schizaea dichotoma.* Amer. Jour. Bot. 54: 538–549.

———. 1968*a*. Observations on *Schizaea* and *Actinostachys* spp., including *A. oligostachys,* sp. nov. Amer. Jour. Bot. 55: 87–108.

———. 1968*b*. On the Stromatopteridaceae (fam. nov.) and the Psilotaceae. Phytomorphology 18: 232–268.

———. 1969*a*. On *Stromatopteris* and its ill-defined organs. Amer. Jour. Bot. 56: 160–174.

———. 1969*b*. Leaf development in *Schizaea* and *Actinostachys.* Amer. Jour. Bot. 56: 860–870.

———. 1971*a*. Morphology of Vascular Plants. MacMillan, New York.

———. 1971*b*. Soral and pinnule ontogeny in *Gleichenia linearis.* Amer. Jour. Bot. 58: 417–423.

CLOWES, F. A. L. 1961. Apical Meristems. Blackwell's, Oxford.

COTTHEM, W. VAN 1970*a*. Comparative morphological study of the stomata in the Filicopsida. Bull. Jard. Bot. Natl. Belgique 40: 81–239.

———. 1970*b*. A classification of stomatal types. Bot. Jour. Linn. Soc. 63: 235–246.

———. 1971. Vergleichende morphologische Studien über stomata und eine neue Klassifikation ihrer Typen. Ber. Deutsch. Bot. Ges. 84(5/4): 141–168.

DEALBERTIS, J. & D. J. PAOLILLO, JR. 1972. The concept of incipient vascular tissue in fern apices. Amer. Jour. Bot. 59: 78–82.

DEBARY, A. 1884. Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns (English translation). Clarendon Press, Oxford.

DEVADAS, C. & C. B. BECK. 1971. Development and morphology of stelar components in the stems of some members of the Leguminosae and Rosaceae. Amer. Jour. Bot. 58: 432–446.

——— & ———. 1972. Comparative morphology of the primary vascular systems in some species of Rosaceae and Leguminosae. Amer. Jour. Bot. 59: 557–567.

FARRIS, J. S. 1966. Estimation of conservatism of characters by constancy within biological populations. Evolution 20: 587–591.

———. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83–92.

Fryns-Claessens, E. & W. van Cotthem. 1973. A new classification of the ontogenetic types of stomata. Bot. Rev. (Lancaster) 39: 71–138.

Gastony, G. J. 1973. A revision of the fern genus *Nephelea*. Contr. Gray Herb. 203: 81–148.

Gaudet, J. J. 1964. Morphology of *Marsilea vestita*. I. Ontogeny and morphology of the submerged and land form of the juvenile leaves. Amer. Jour. Bot. 51: 495–502.

Gifford, E. M., Jr. & G. E. Corson, Jr. 1971. The shoot apex in seed plants. Bot. Rev. (Lancaster) 37: 143–229.

Hagemann, W. 1964. Vergleichende Untersuchungen zur Entwicklungsgeschichte des Farnesprosses. I. Morphogenese und Histogenese am Sprosscheitel Leptosporangiater Farne. Beitr. Biol. Pflanzen 40: 27–64.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana.

Holttum, R. E. & U. Sen. 1961. Morphology and classification of the tree ferns. Phytomorphology 11: 406–420.

Inamdar, J. A. 1970. Development of stomata in some *Ophioglossum* species. Ann. Bot. (London) 34: 975–982.

———, R. C. Patel & D. C. Bhatt. 1971. Structure and development of stomata in some leptosporangiate ferns. Ann. Bot. (London) 35: 643–651.

Jeffrey, E. C. 1899. The morphology of the central cylinder in the angiosperms. Trans. Roy. Canad. Inst. 6: 599–636.

———. 1902. The structure and development of the stem in the Pteridophyta and gymnosperms. Philos. Trans., Ser. B. 195: 119–146.

Kondo, T. 1962. A contribution to the study of the fern stomata. Res. Bull. Fac. Educ. Shizuoka Univ. 13: 239–267.

——— & H. Toda. 1956. A contribution to the study of fern stomata with special reference to their development and structure. Res. Bull. Fac. Educ. Shizuoka Univ. 5: 60–80.

Kluge, A. G. & J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.

Lersten, N. 1965. Histogenesis of leaf venation in *Trifolium wormskioldii* (Leguminoseae). Amer. Jour. Bot. 52: 767–774.

Lucansky, T. W. 1974*a*. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. I. *Metaxya* and *Lophosoria*. Amer. Jour. Bot. 61: 464–471.

———. 1974*b*. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. II. Squamate genera. Amer. Jour. Bot. 61: 472–480.

——— & R. A. White. 1974. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. III. Nodal and petiole patterns; summary and conclusions. Amer. Jour. Bot. 61: (in press).

Lundberg, J. G. 1972. Wagner networks and ancestors. Syst. Zool. 21: 398–413.

Maroti, I. 1960. Histologische Untersuchung der Marattiaceae-Blätter mit besonderem Hinblick auf die Epidermis. Acta Biol. (Szeged 1955+) 6: 71–89.

———. 1961. Untersuchung der Entwicklung der Epidermis des Psilotinae- und des Filicinae-Blattes und der Entwicklung der Stomas. Acta Biol. (Szeged 1955+) 7: 43–67.

———. 1965. Vergleichende anatomische Untersuchungen am den Blattern der Ophioglossaceae. Acta Biol. (Szeged 1955+) 11: 55–71.

———. 1966. Development of the Tmesopsida and Pteropsida leaves and histogenesis of the epidermis. Acta Biol. (Szeged 1955+) 12: 37–60.

McAlpin, B. W. 1971. Shoot organization in the Filicales: the promeristem. Thesis, Duke Univ.

——— & R. A. White. 1974. Shoot organization in the Filicales: the promeristem. Amer. Jour. Bot. (in press).

Metcalfe, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

Mickel, J. T. & N. Lersten. 1967. Floating stomata (adestostomy) in ferns: distribution and ontogeny. Amer. Jour. Bot. 54: 1181–1185.

Miller, C. N., Jr. 1971. Evolution of the fern family Osmundaceae based on anatomical studies. Contr. Mus. Paleontol. Univ. Michigan 23: 105–169.

Namboodiri, K. K. & C. B. Beck. 1968*a*. A comparative study of the primary vascular system of conifers. I. Genera with helical phyllotaxis. Amer. Jour. Bot. 55: 447–457.

——— & ———. 1968*b*. A comparative study of the primary vascular system of conifers. II. Genera with opposite and whorled phyllotaxis. Amer. Jour. Bot. 55: 458–463.

——— & ———. 1968*c*. A comparative study of the primary vascular system of conifers. III. Stelar evolution in the gymnosperms. Amer. Jour. Bot. 55: 464–472.

Paliwal, G. S. & L. Kakkar. 1967. The stomata of *Tmesipteris tannensis* Bernh. Curr. Sci. 36: 412–413.

Pant, D. D. 1965. On the ontogeny of stomata and other homologous structures. Pl. Sci. Ser., Allahabad 1: 1–24.

——— & P. K. Khare. 1969. Epidermal structure and stomatal ontogeny in some eusporangiate ferns. Ann. Bot. (London) 33: 795–805.

——— & ———. 1971. Epidermal structure of Psilotales and stomatal ontogeny of *Tmesipteris tannensis* Bernh. Ann. Bot. (London) 35: 151–157.

——— & ———. 1972. Epidermal structures and stomatal ontogeny of *Anemia* sp. Ann. Bot. (London) 36: 809–821.

——— & B. Mehra. 1963. Development of stomata in *Psilotum nudum* (L.) Beauv. Curr. Sci. 32: 420–422.

——— & ———. 1964. Development of stomata in some fern allies. Proc. Natl. Inst. Sci. India 30B: 92–98.

——— & G. K. Strivastava. 1962. The genus *Isoetes* in India. Proc. Natl. Inst. Sci. India 28: 242–280.

Payne, W. W. 1970. Helicocytic and allelocytic stomata: unrecognized patterns in the Dicotyledonae. Amer. Jour. Bot. 57: 140–147.

Pray, T. R. 1960. Ontogeny of the open dichotomous venation in the pinna of the fern *Nephrolepis*. Amer. Jour. Bot. 47: 319–328.

———. 1962. Ontogeny of the closed dichotomous venation of *Regnellidium*. Amer. Jour. Bot. 49: 464–472.

Stebbins, G. L. & G. S. Khush. 1961. Variations in the organization of the stomatal complex in the leaf epidermis of monocotyledons and its bearing on their phylogeny. Amer. Jour. Bot. 48: 51–59.

Steeves, T. A. 1963. Morphogenetic studies on *Osmunda cinnamomea* L. The shoot apex. Indian Jour. Bot. 42: 225–237.

Sussex, I. M. & T. A. Steeves. 1967. Apical initials and the concept of the promeristem. Phytomorphology 17: 387–391.

Thurston, E. L. 1969. Taxonomic significance of stomatal patterns in the ferns. Amer. Fern Jour. 59: 68–79.

Tiegham, P. van & H. Douliot. 1886. Sur la polystelie. Ann. Sci. Nat. Bot., Sér. 7. 3: 275–322.

Tomlinson, P. B. 1970. Monocotyledons—Towards an understanding of their morphology and anatomy. Advances in Botanical Research 3: 207–292.

Tryon, R. M. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 1–53.

Vesque, J. 1890. De l'emploi des caracteres anatomiques dans la classification des végétaux. Bull. Soc. Bot. France 36: xli–lxxvii.

Wagner, W. H., Jr. 1964. The evolutionary patterns of living ferns. Mem. Torrey Bot. Club 21: 86–95.

———. 1966. Modern research on evolution in ferns. Pp. 164–184, *in* W. A. Jensen & I. G. Kavaljian (editors), "Plant Biology Today: Advances and Challenges." Ed. 2. Belmont, Calif.

———. 1969. The construction of a classification. Pp. 67–99, *in* "Systematic Biology Publication 1692." Natl. Acad. Sci. Wash., D.C.

Wardlaw, C. W. 1944. Experimental and analytical studies of pteridophytes. III. Stelar morphology: the initial differentiation of vascular tissue. Ann. Bot. (London) 8: 173–188.

———. 1965. The organization of the shoot apex. *In* "Encyclopedia of Plant Physiology." 15: 966–1076. Springer-Verlag, Berlin.

Weidlich, W. 1973. The anatomy and morphology of the vascular system in the stems of *Nymphaea* (Abstr.) Amer. Jour. Bot. 60: 42.

Whiffin, T. & M. W. Bierner. 1972. A quick method for computing Wagner trees. Taxon 21: 83–90.

White, R. A. 1971. Experimental and developmental studies of the fern sporophyte. Bot. Rev. (Lancaster) 37: 509–540.

Zimmerman, M. H. & P. B. Tomlinson. 1972. The vascular system of monocotyledonous stems. Bot. Gaz. (Crawfordsville) 133: 141–155.

EVOLUTIONARY TRENDS IN THE MARATTIALES

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Abstract

The structure of living and fossil marattiaceous ferns is compared organographically. Stelar structure exhibits a basic pattern in all genera in spite of modifications correlated with size and symmetry. Fronds exhibit gross morphological and anatomical differences but can likewise be interpreted as specializations associated with size and form, and genera can be related to one another in an evolutionary sequence. Living genera with dorsiventral stems and once pinnate or palmate fronds are considered derived from fossil forms with radially symmetrical stems and large, highly branched fronds. Primitive fronds had small pinnules which became modified into large laminar units in the living genera. Evidence from fossil and living genera is cited in support of these conclusions. The problem of sporangial aggregation is discussed in light of transformations in pinnule morphology. The linear sorus in the Pennsylvanian age *Eoangiopteris* is considered to have been produced on pinnatifid areas of *Psaronius*-type fronds. Other regions of the frond, or perhaps different fronds or plants, bore radially symmetrical synangia identified as *Scolecopteris iowensis*. The significance of this interpretation is the possible insight provided relative to the evolution of large laminar units and concomitant sporangial aggregation and distribution. *Senftenbergia* is rejected as a marattiaceous fructification.

The Marattiales is a distinct group of ferns restricted to tropical areas and consequently known to most North Americans only through occasional contact in conservatories or herbaria. The order is considered primitive among living ferns and, primarily because of their eusporangiate development, usually placed close to the Ophioglossales in taxonomic schemes. Most of the detailed studies of living genera were undertaken in the early years of this century, largely under the stimulus provided by the occurrence of fossil marattiaceous plants in Carboniferous strata. In recent years our knowledge of the fossil forms has accumulated in the virtual absence of further work with the extant genera so that once again we are in a position of lacking comparative data from the living representatives.

Seven extant genera have been described: *Angiopteris*, *Marattia*, *Archangiopteris*, *Protomarattia*, *Macroglossum*, *Christensenia*, and *Danaea*. Of these, *Angiopteris*, *Marattia*, *Danaea*, and *Christensenia* are the best known. Relatively little is known of *Archangiopteris* and *Macroglossum*, which contain only six species between them. No anatomical studies have been undertaken on *Protomarattia*, and it would be helpful to know how this genus compares with the other genera. (Copeland, 1947, in his *Genera Filicum* follows Christensen and Tardieu and places *Protomarattia tonkinensis* in synonymy with *Archangiopteris tamdaoensis*.)

The group is usually characterized as consisting of large, coarse, sappy ferns, the latter feature being a function of numerous mucilage canals and tannin cells in the fundamental tissue. The vascular anatomy, at least in the larger stems, is very complex, consisting of several interconnected cycles composed of small meristeles. Stems of some genera—*Angiopteris*, *Marattia*, and *Macroglossum*—are short, erect, tuberous and occasionally up to two feet in diameter. The remaining genera have trailing, mostly dorsiventral stems. All possess large

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fleshy stipules at the base of the petioles, and all genera exhibit circinate vernation. Fronds range in size from 6 m long with petioles 10 cm or more in diameter and supporting a lamina that may be four or five times pinnate, to much smaller once pinnate fronds. An even simpler frond is present in *Danaea simplicafolia* where the frond consists of a single blade. *Christensenia*, perhaps the most aberrant genus, has a palmate frond with radially symmetrical sori scattered over the abaxial surface of the pinnules. Sporangia are massive and are either free or fused into synangia depending upon the genus. All sori are linear except for the radial synangium of *Christensenia*. Gametophytes of five genera are known and are generally large, thick, dorsiventral, and similar to thallose liverworts in appearance.

Fossils attributed to the Marattiales occur abundantly in Carboniferous strata and consist almost entirely of various organ and form genera that represent the different parts of the plant designated by the genus *Psaronius*. *Psaronius* was one of the dominant plants of the Pennsylvanian period, and much of the fern foliage found on the spoil banks of North American coal mines was produced by this plant. There are a few reports of *Psaronius*-type plants from the Devonian (Dawson, 1871), but these reports need confirmation utilizing modern techniques before they can be accepted. *Psaronius* was abundant during the upper Carboniferous in Europe and America and ranged into the Permian of Europe. Mesozoic representatives of the group include six compression genera of sterile and fertile frond portions. Nothing is known about other parts of the plants, nor is there any anatomical information about the fronds. The laminar portions of most species are large, imparting an aspect similar to the fronds of living species.

In the strict sense *Psaronius* is a genus established in 1832 for structurally preserved fern stems, but has since come to indicate the entire plant in much the same way that *Lepidodendron* denotes one of the arborescent lycopods. *Psaronius* was a tall graceful tree fern, larger than the contemporary seed ferns but smaller than the giant lycopods. Growth began as a small sporeling (Stidd & Phillips, 1968) on the forest floor, where it must have encountered the usual problems other plants experience in becoming established in a forest. Like many ferns, and in particular the marattialean ferns, it was at first protostelic and with increase in size became siphonostelic and eventually developed a complex polycyclic dictyostele of unrivaled complexity in the plant kingdom. New cycles were added within the older cycles at successive heights as the plant grew upward. The entire complex stem was produced by the apical meristem, and even though it obtained a diameter of eight inches or more near the top of the tree, the tissues were all primary. Obviously a stem 50 feet tall, eight or more inches in diameter at the top, and supporting a crown of a dozen or more fronds, each of which was three meters or more in length, would need substantial supportive tissue in order to remain erect. This is particularly true when one remembers that the stem was only 1–2 mm in diameter at the base. Of course such a strange plant never existed, not even among the most bizarre fossil forms. The problem of support was solved by *Psaronius* in a unique way even more remarkable than the secondary growth mechanisms devised by arboresent monocots. Increase in circumference, and consequent supportive tissue, was accomplished in *Psaronius* by the development of a layer of roots enveloping the stem. The root layer reached enormous proportions near the base of the plant, where the stem was very small, and diminished upward, giving a normal conical symmetry to the trunk. Individual roots of the root mantle were produced adventitiously at higher and higher levels as the stem increased in height. Roots originated primarily from the outer vascular cycle and passed outward to the stem surface. As the root apex approached the stem surface the subepidermal parenchyma of the stem began to proliferate and formed a tissue continuous with the cortex of the emerging roots. Subsequent roots arising at higher levels grew outward and downward over the previous roots and were also incorporated into the parenchyma matrix of the root mantle. In this way the stem increased in diameter by the addition of successive layers of roots forming a root mantle that was in actuality an integral part of the stem. Eventually the inter-root parenchyma failed to keep pace with new roots at the exterior, and the latter were not incorporated into the parenchyma matrix, thus forming the so-called free root zone.

The apex of the stem bore one or more whorls of large fronds with the characteristics of the form genus *Pecopteris*. Foliage of this genus has pinnules broadly attached at the base, parallel sides, and a single midvein entering the base of the pinnule. Lateral veins exhibited different forking patterns or were not forked at all. Fructifications were always synangiate and usually borne in two rows, one on either side of the midvein and directly beneath a lateral vein. Sporangia were massive, exannulate, and with one or two exceptions formed a radially symmetrical synangium. It was largely the presence of these fructifications in Carboniferous strata that was responsible for the widespread conviction that the Marattiales was well represented in the fossil record. With the discovery of the seed ferns, opinion for a time wavered (notably by Kidston, 1925) as to whether the fructifications were marattiaceous or represented the microsporangiate organs of pteridosperms. Today there is no question that the fructification genus *Scolecopteris* was borne on *Psaronius* fronds and that the genera *Eoangiopteris* and *Cyathotrachus* are marattiaceous. With a few exceptions then, the dozen or so genera described from the Carboniferous Period are in reality different parts of the plant designated by the name *Psaronius*. Consequently, a consideration of the relationships between the extant and extinct marattiales condenses primarily to the problem of how *Psaronius* is related to the seven extant genera. In spite of some obvious differences I am impressed by the similarities between *Psaronius* and the living genera, and the following organographic comparison reflects that bias.

STEMS

Psaronius stems were tall and were built up of multiple cycles of broad strap-shaped meristeles embedded in the fundamental tissue. The complexity of the polycyclic dictyostele at higher levels in the plant defies comprehension by the casual observer. In extant genera such as *Angiopteris* the compactness of the stem plus the more dissected condition of the vascular tissue into smaller bundles makes interpretation equally difficult. If, however, one looks at the

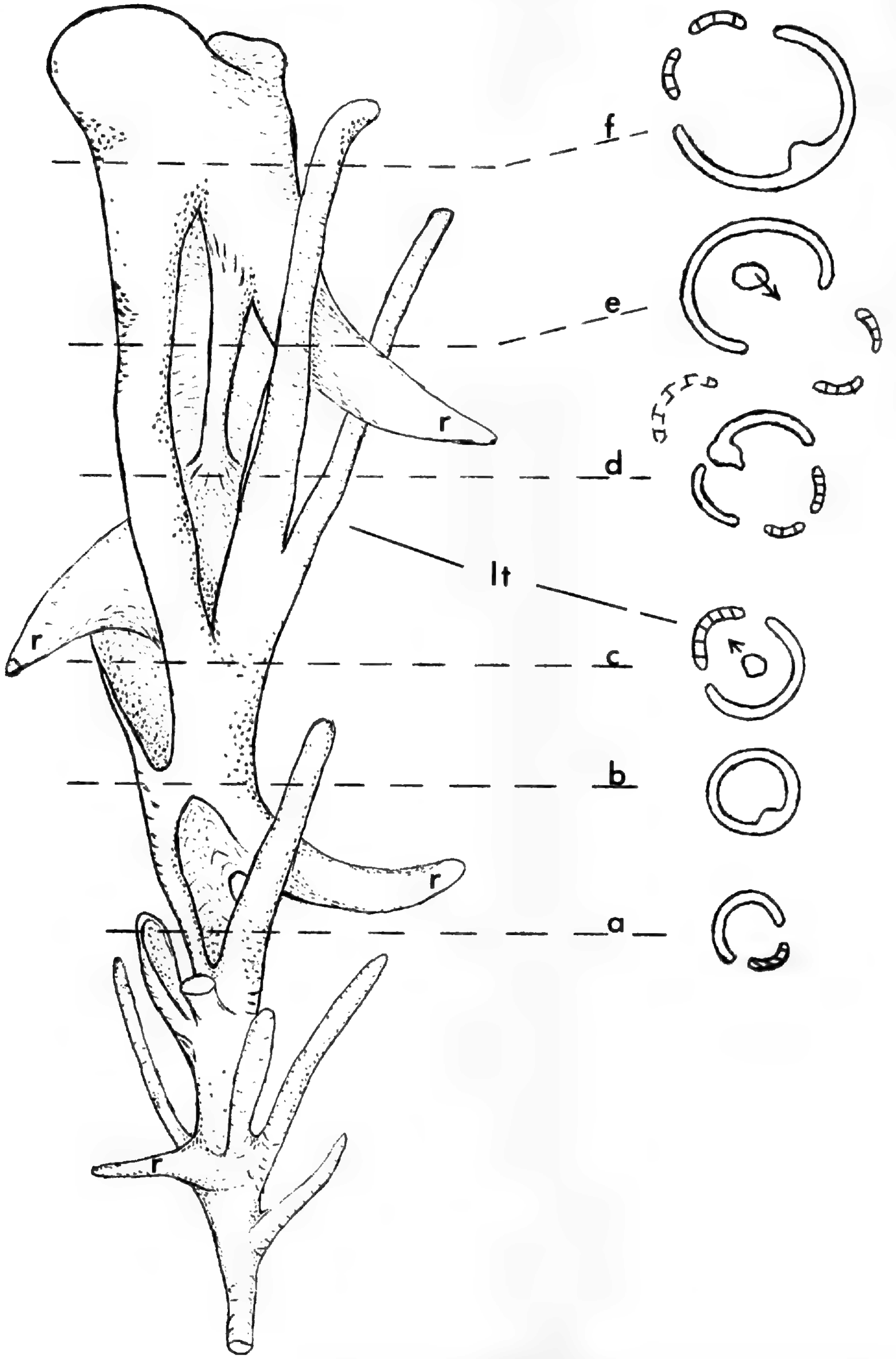

FIGURE 1. Drawing of the stelar system of the young sporophyte of *Danaea alata* (from West, 1917). Cross section diagrams supplied based upon description by West. Hatched segments are leaf traces.

vascular system near the base of the plant before the bewildering array of meristeles of older stems develops, the basic nature of the vascular system is readily understood. Figures 1 and 2 show the vascular systems of *Psaronius* and *Danaea* sporelings. The cross sections of the *Danaea* stem have been supplied based upon the description of West (1917). In both genera a siphonostelic condition soon develops (Figs. 1a; 2a–b), and the first leaf gaps are closed by simple refusion of the edges of the gap (Fig. 2d). Eventually at higher levels, (Figs. 1b; 2g) gap-closure leaves a small amount of vascular tissue projecting to the inside. This tissue separates from the stele and at successively higher levels is found closer and closer to the next leaf gap in the phyllotactic sequence. This strand of vascular tissue represents the beginning of another vascular cycle inside the original siphonostele and has been called a commissural or medullary strand in the extant Marattiaceae and simply an internal strand or cycle in *Psaronius.* The internal cycle approaches the next leaf gap (Figs. 1c; 2h) and fuses with the edges of the gap near their point of convergence (Figs. 1d; 2i). In this way the internal cycle contributes to the closure of the leaf gap and subsequently separates and moves across the pith toward the gap created by the next leaf trace (Figs. 1e–f; 2j–k). Repetition of these events results in the internal cycle following an upward spiral course, anastomosing with the outer cycle at the top of each leaf gap. Eventually the internal strand becomes siphonostelic as the stem continues to increase in diameter, and only a portion of the strand is given off to the leaf gaps of the outer cycle. This of course creates gaps in the now tubular inner cycle. Some vascular tissue is eventually left to the interior of the second cycle when the vascular gap is closed by the free margins. This tissue functions and develops essentially as its predecessor (the second cycle at its origin), and a third internal cycle is created. In large stems of *Psaronius*, *Angiopteris*, and *Marattia*, many such cycles arise one inside the other and a complex polycyclic dictyostele results. Such a stelar structure may perhaps be comprehended by visualizing a series of perforated cones stacked one inside the other, each connected to the outer one at its point of origin and where gaps in outer cones are filled by contributions from inner cones.

Stem vasculature then, constitutes one of the distinctive characters of the Marattiales. Stelar anatomy of such complexity might be expected to exhibit considerable variability. For example in an account of the vascular anatomy of *Angiopteris* by Blomquist (1922) the term "commissural strand" is not used in the sense employed by most authors. The behavior of Blomquist's "commissural strand" is a good example of how a slight variation in vascular configuration masks the basic stelar pattern. In reality the specimen described by Blomquist exhibits the same basic stelar structure and development common to all genera. Many differences in stelar structure in the group are correlated with differences in size and symmetry between genera. Genera with larger stems (*Angiopteris, Marattia*) develop complex polycyclic steles, while those with small stems (*Danaea*, *Christensenia*, *Archangiopteris*) have less complex steles with only 2–3 cycles. Species with dorsiventral stems often have the stelar structure modified accordingly. The most extreme example is the genus *Christensenia* which has a strongly dorsiventral stem with leaves arising from the dorsal surface.

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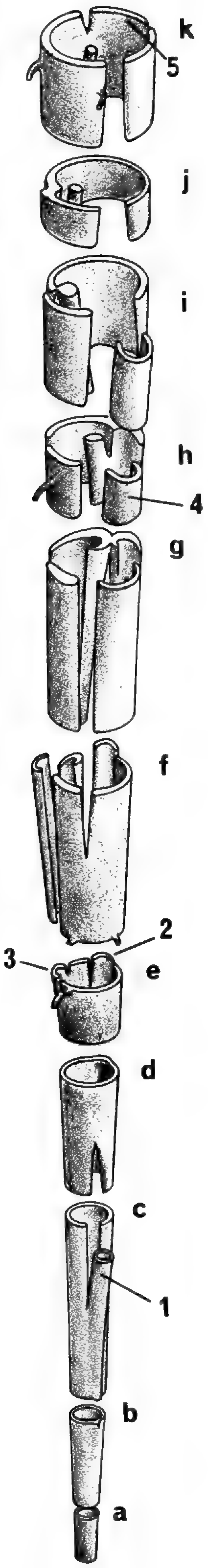
FIGURE 2. Vascular system of young sporophyte of *Psaronius.* 1–5 are leaf traces. From Stidd and Phillips, 1968.



The stem is dicyclic with a single internal vascular strand which follows an alternating course between the upper and lower edges of the outer cycle rather than the normal spiral course traversed by internal cycles in radially symmetrical stems. A very remarkable feature of the stele is the formation of gaps on the lower face of the outer cycle even though no leaf traces arise from the lower surface. This was interpreted by Farmer and Hill (1902) as evidence that the dorsiventral stem of *Christensenia* has been derived from a radially symmetrical ancestor.

FRONDS

Marattialean ferns possess megaphylls in the fullest sense of the term. The largest, most highly divided fronds occur in *Angiopteris*, *Marattia*, and *Psaronius*. The remaining genera have smaller once pinnate fronds with the exception of the palmate condition in *Christensenia*. *Macroglossum* fronds are once pinnate but up to 4 meters long and therefore perhaps the largest of the once pinnate fronds. *Danaea* is usually once pinnate, but one species, *Danaea simplicafolia*, has an even simpler frond with a single laminate blade (Fig. 7). *Psaronius* fronds were large, 3–4 times pinnate, and had many small, broadly attached pinnules imparting a lacey appearance to the frond. In contrast to the extant genera, there is no evidence that *Psaronius* had stipules.

A very interesting relationship exists between the vascularization and the size of the frond in the extant Marattiaceae. *Angiopteris*, which has the largest and most complex stem anatomy, also has the most complex vascular anatomy of the frond. Large petioles (Fig. 3a) have four or more concentric cycles of vascular bundles. The number of cycles is successively reduced as the distal end of the petiole and main rachis is approached (Fig. 3a–d). The vascular configurations in Figure 3b–d are repeated in primary pinna rachises, with the most complex configuration (Fig. 3b) present at the base of the pinna rachis. *Marattia* usually has a simpler vascular configuration at the base of the petiole (Fig. 3f) consisting of two or three vascular cycles. These are diminished distally in the rachis (Fig. 3g–h) in the same manner as in *Angiopteris* (Fig. 3b–d). This is accomplished by reduction of the inner cycle (Fig. 3b, f) to a single horizontally elongated strand (Fig. 3c, g) and finally by a series of fusions and separations of the horizontal strand with the bundles of the outer cycle at top-center (Fig. 3d, h) an open horseshoe configuration results as in Figure 3n. The smaller and less pinnate frond of *Danaea* has a simple vascular configuration in the petiole corresponding to more distal regions of the larger fronds of *Angiopteris* and *Marattia*. Either of two vascular arrangements (Fig. 3j or n) may be present in *Danaea* petioles.

The method of vascular supply to departing pinnae is a distinctive feature in the Marattiales. In all genera the vascular supply to pinnae is augmented by contributions from the vascular tissue in the interior of the main rachis. This is illustrated in Figure 3k, o where the vasculature is relatively simple. The bulk of the vascular tissue of the pinna comes from the bundles of the outer cycle. When an internal strand is present (Fig. 3k), vascular strands are constricted from the arms of the internal strand which contribute both to the bundles of the

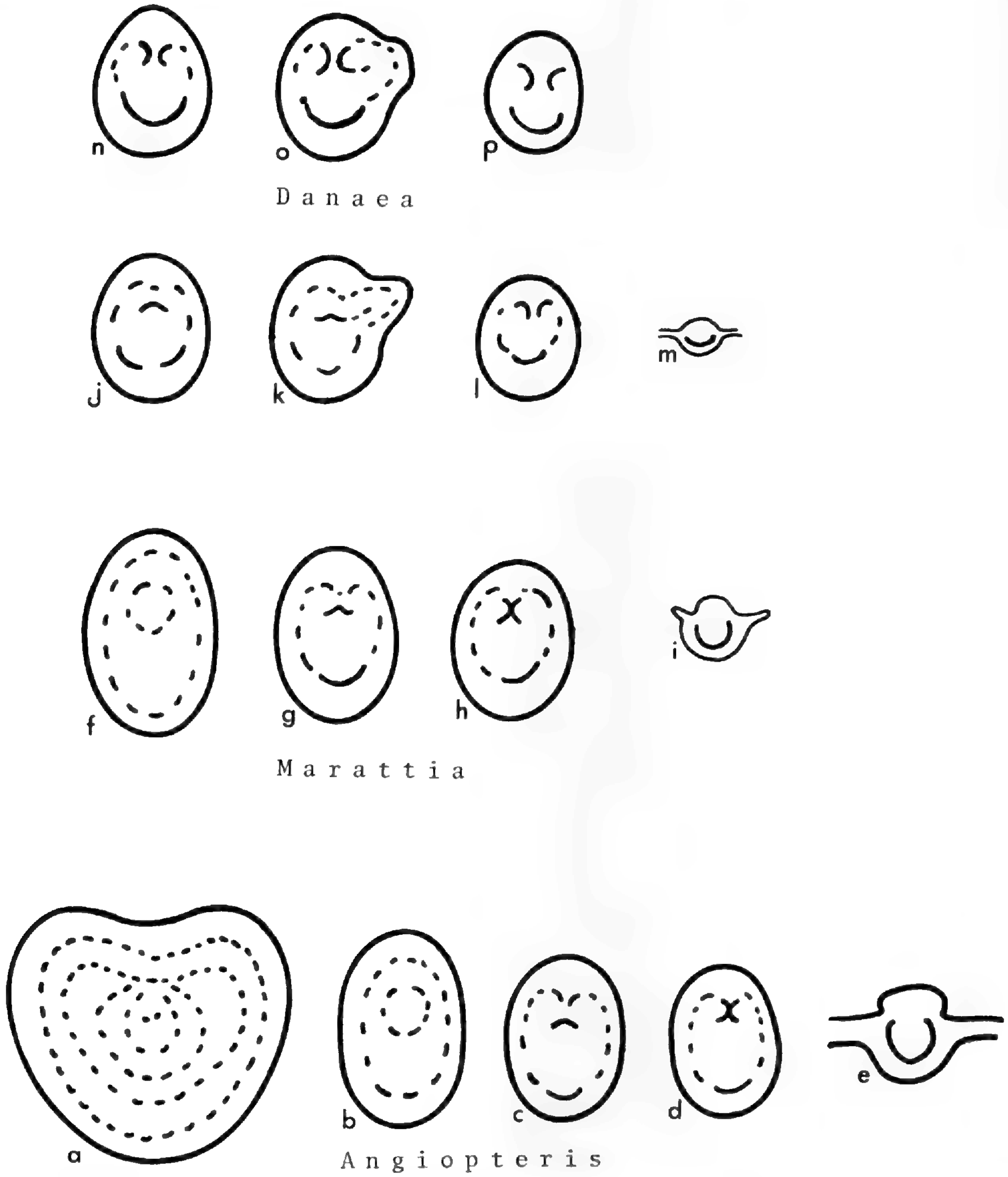


FIGURE 3. Transverse sections of frond members at selected levels of three extant genera. Solid outer line, edge of axis; broken lines, vascular bundles.

departing pinna and to the gap region created by the departure of bundles from the outer cycle. The internal strand in the frond functions in the same way as the internal cycle in the stem, *i.e.* it shifts from side to side along the length of the rachis, contributing vascular tissue to pinnae and closing pinnae gaps. It is not uncommon for the internal strand to divide and for the resulting halves to fuse with the two adaxial strands of the outer cycle. This results in a simpler vascular configuration with the bundles arranged as in a horseshoe but with the open ends slightly curved toward the center. When the bundles are arranged in this way (Fig. 3o), a contribution to the pinna vasculature is made by the abaxially directed end of the incurved arm of the horseshoe. In this case (West, 1917) no bundles were observed to contribute to pinna gap closure.

The vascular configurations of the three genera illustrated in Figure 3 represent the range of vascular arrangements known among the extant Marattiaceae. The petioles of *Christensenia*, *Macroglossum*, and *Archangiopteris* have an outer ring of vascular bundles surrounding one or a few inner bundles, corresponding to the arrangement in other genera shown in Figure 3c, g, k. In the palmate frond of *Christensenia* this arrangement of bundles may be repeated at the base of the axes that support the large pinnules (Bertrand & Cornaille, 1902). This bundle arrangement is commonly transformed into the horseshoe configuration at more distal levels in the pinnule where the midrib is reduced in diameter.

Psaronius fronds were for the most part more highly branched than the living genera and bore many small pinnules attached broadly at the base. Adjacent pinnules are commonly fused together at the frond extremities resulting in a pinnatifid condition. Like the stem, the vascular tissue in the frond is composed of large continuous strands. At the base of the petiole the most common configuration consisted of an outer continuous strand enclosing a smaller internal strand (Fig. 4L). As in the living forms this vascular configuration is converted to the horseshoe configuration within the rachis and further interconversions between the two basic forms may occur throughout the length of the rachis. Primary, secondary, and tertiary pinna rachises usually have the horseshoe vascular configuration.

Pinna trace formation is augmented by contributions from internal vascular tissue as has been described for the living genera. When the vascular strand of the parent rachis is open at the top and no internal strand is present (Fig. 4F), the pinna vascular supply receives a small strand of vascular tissue from the recurved end of the adaxial hook of the parent rachis (Fig. 4A–E). In addition pinna gap closure is aided by further contributions from the same source. When an internal strand is present, as a result of fusion and subsequent separation of the enrolled arms of the vascular strand, pinna trace formation and gap closure is augmented by constrictions from the lateral extremities of the internal strand (Fig. 4 G–K). In this case the internal strand functions in a manner similar to the inner cycles in the stem except for the difference imposed by the bilateral symmetry of the frond.

At first glance the differences in the vascular system of *Psaronius* and the extant genera appear quite distinct. If, however, one connects the individual bundles in the living forms with a continuous line, the similarity with the vascular tissue in *Psaronius* is evdent. The paths traversed and shifting of protoxylem positions of the individual bundles in the living genera is often made understandable by comparing with the changes in configuration of the continuous

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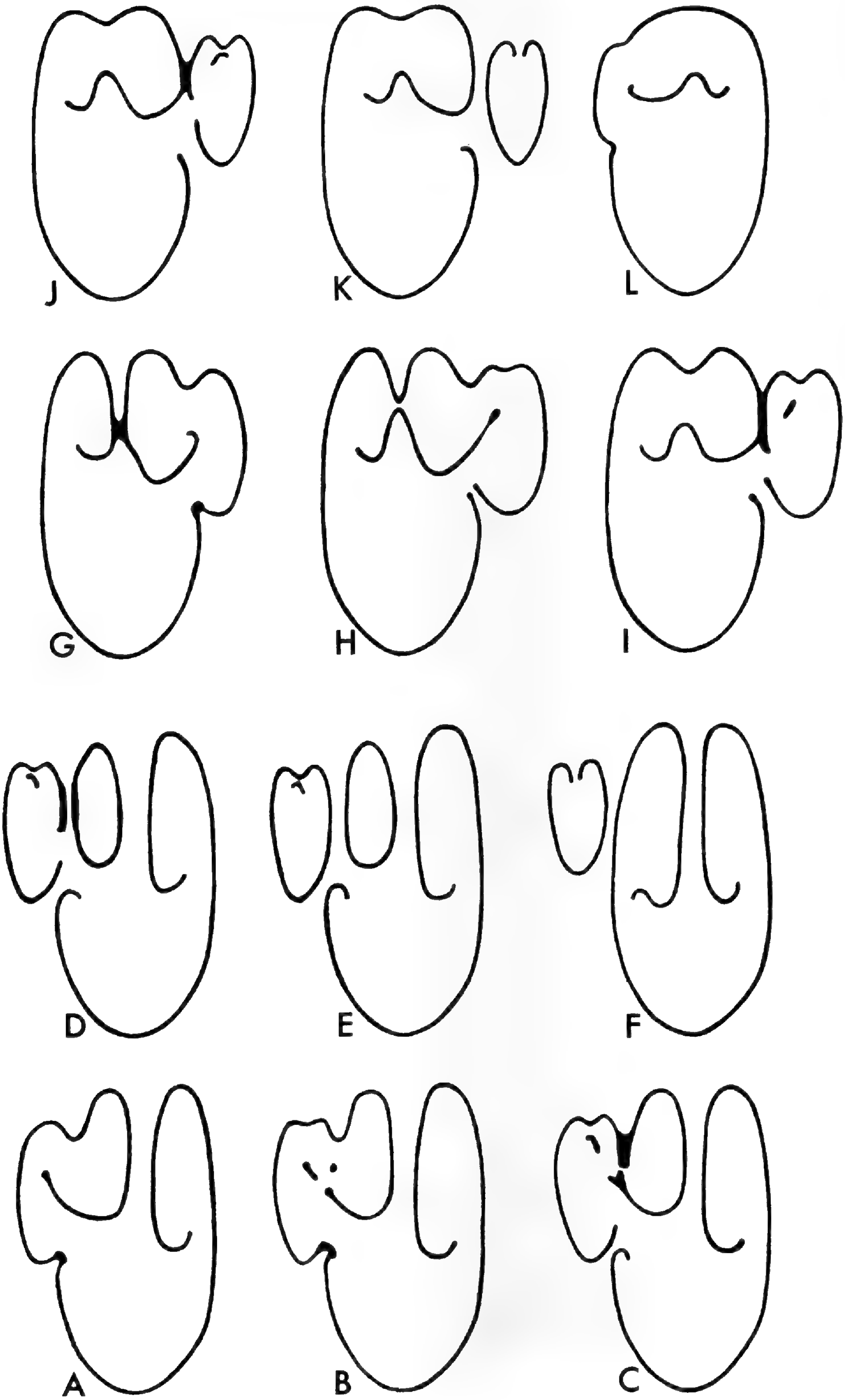
FIGURE 4. Selected transverse sections of rachis vascular system of *Psaronius* frond showing different vascular configurations and stages in pinna trace emission. A, most proximal level; L, distal.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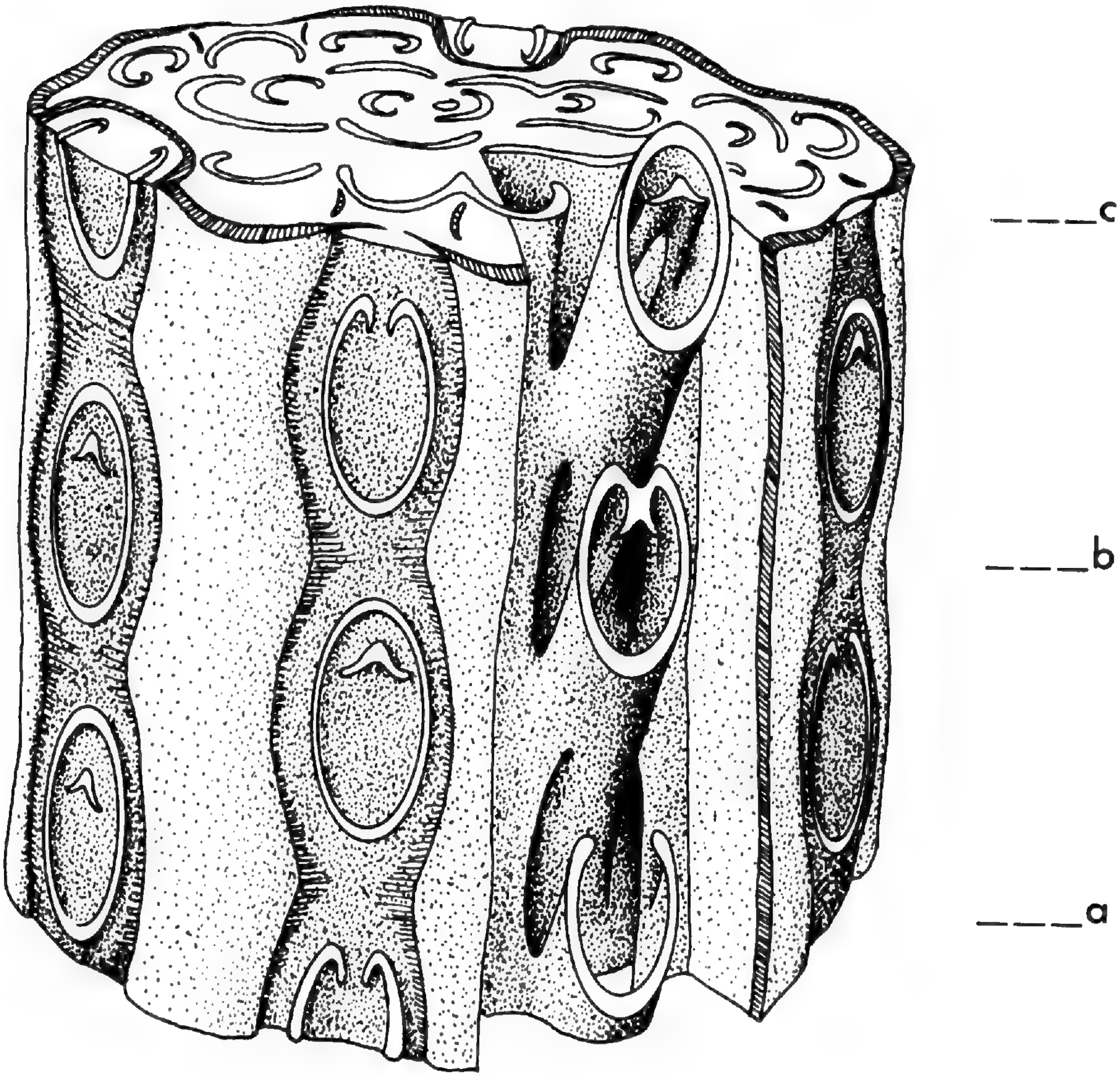


FIGURE 5. Segment of *Psaronius* stem showing origin of leaf traces (cut away portion). Levels a, b, c show three traces at successively greater distances from stem and different stages in the origin of the internal vascular strand at base of petiole.

vascular strands in *Psaronius*. For example, the following description of the course of vascular bundles in the petiole of *Christensenia* (Gwynne-Vaughan, 1905) is readily understandable to anyone familiar with how an internal strand is formed in *Psaronius* fronds: "These (vascular bundles) are arranged in a curve of the form of a widely open arch with its concavity facing directly towards the apex of the rhizome. The two terminal strands of the arch are somewhat larger than the rest, and as they pass upwards they approach the median plane of the petiole. As they do so they also curve inwards, and at the same time turn round so that their protoxylems face away from each other towards the sides of the petiole. This rotation is sometimes continued until at a point still further up their protoxylems face almost directly towards the median plane." There is no obvious reason why vascular bundles should rotate and shift positions as described here. However, if one conceives these bundles as segments of a once continuous vascular strand as in *Psaronius*, their otherwise peculiar behavior is explicable. Figure 5 depicts the way in which the internal strand is formed at the base of the *Psaronius* petiole. The internal strand (sometimes several separate bundles) in the living genera is formed in the same way, but because the vascular tissue consists of individual bundles this was not always clear to earlier workers.

There are of course some differences between the vascular system of *Psaronius* and the living forms. One of the most inexplicable is the origin of so-called "accessory bundles" from normal bundles situated in the abaxial region of the petiole. These accessory bundles traverse the intervening ground tissue and join with the terminal bundles of the outer cycle (Gwynn-Vaughan, 1905). They may also form inner cycles in *Angiopteris* and *Marattia*. There is nothing about the vascular system of *Psaronius* fronds that provides any clues about the nature of these bundles. They are regarded therefore as a development peculiar to the living forms and perhaps in some way associated with the dissected nature of the vascular system.

How then should the similarities between *Psaronius* fronds and those of the extant genera be regarded? Certain features of *Psaronius* such as the integrated root mantle appear too specialized to allow *Psaronius* to be regarded as directly ancestral to the living forms. Nevertheless, comparative analysis of the living forms has caused some previous workers to regard the less compound fronds and dorsiventral stems as derived from plants with radially symmetrical stems and highly compound fronds. Since *Psaronius* has both radially symmetrical stems and large, highly compound fronds, and preceded the living forms in time, it is reasonable to conclude that *Psaronius* represents the ancestral form in at least some of its characters. If these assumptions are correct, the following changes in marattialean frond architecture may have occurred. Based upon certain theoretical considerations (Stidd, 1971) the primitive marattialean "frond" was probably a non-planated branching system possessing a radially symmetrical vascular system. The vascular system in such a frond probably resembled the vascular system of the stem in that internal cycles followed a spiral course in connection with pinna emission and gap closure. By the time *Psaronius* had evolved, the frond was distinctly planated and internal vascular tissue followed-suit, shifting from side to side in a bilaterally symmetrical fashion in connection with pinna emission. The vascular tissue in *Psaronius*, perhaps in response to its large size, consisted of a continuous strand of xylem and phloem in contrast to the distinct individual bundles in the living forms. The bundles in the living forms, however, are arranged in a definite manner that reflects the ancestral continuous strands as in *Psaronius*.

A second trend involved the fusion of small, individual pinnules borne on an ultimate pinna rachis into large laminar units. In such units the resulting midrib corresponds with, or is homologous to, the ultimate pinna rachis in the antecedent condition. Repetition of this process would result in decreasingly compound fronds, ultimately producing a simple frond with one blade (pinnule?) as in *Danaea simplicafolia*. A harbinger of this trend is the common pinnatifid condition near the extremities of *Psaronius* (*Pecopteris*) fronds. Apparently there is sufficient plasticity in the ontogenetic pathways controlling frond development in the Marattiales to allow frond axes to produce either discrete units (additional pinnae or individual pinnules) or solid laminar structures. An in-

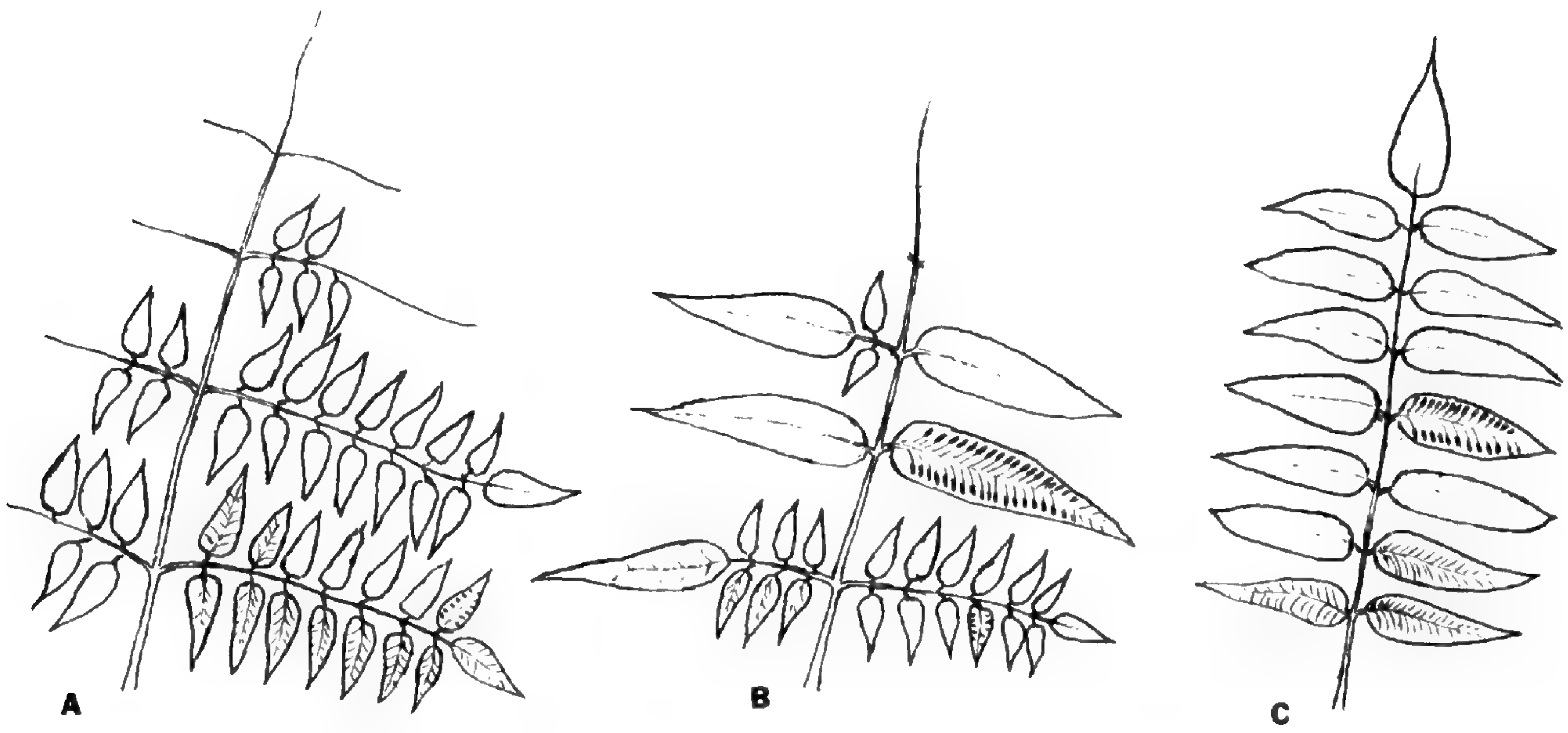


FIGURE 6. Diagrammatic drawings showing transformations in frond morphology of *Angiopteris lygodiifolia* (See Asama, 1960).—A. normal frond development at Koshiki islands, 31°, 40′ N latitude, 22.5° C mean temperature.—B–C. altered fronds when grown at Sendai, 37° 15′ N latitude, 17.7° C mean temperature.

teresting example of this is the observations recorded by Asama (1960) on the transformations in frond structure of *Angiopteris lygodiifolia* when transplanted 6 degrees northward, where growth conditions were less favorable. Under these conditions, plants with normal bipinnate fronds (Fig. 6a) produced fronds reduced in size and in some instances with fewer pinnae (Fig. 6b) each of which had fewer pinnules. Other fronds eliminated one order of branching and were once pinnate (Fig. 6c). In these fronds a pinnule was produced on the main rachis which corresponded in position to a pinna with pinnules in the normal bipinnate fronds. These changes were attributed by Asama to the reduced temperature which effected the fronds in early ontogenetic stages. *Cyathea boninsimensis* was also moved northward along with *Angiopteris* but underwent no noticeable changes in frond structure. The transformations exhibited by *Angiopteris lygodiifolia* are of the same type as the postulated evolutionary changes depicted in Figure 7. It is conceivable that the changes in frond morphology outlined in Figure 7 were stimulated by the changing post-Pennsylvanian climatic conditions.

An interesting aspect of marattialean frond structure is the vascular anatomy at different levels in the frond. If the evolutionary trends suggested here are correct, then one might expect that where, in essence, a pinna rachis is converted into a pinnule midrib, the vascular configuration of the original pinna rachis might be retained. Information of this type is limited in the living forms and is a point that needs further investigation. One example, however, that illustrates the contention here and suggests the conservative nature of the vascular system is the arrangement of vascular bundles in the frond of *Christensenia.* Bertrand and Cornaille (1902) found that at the base of the pinnule an internal bundle is present, surrounded by an outer ring of bundles (Fig. 7). This configuration corresponds to that of Figure 3j and is the vascular arrangement

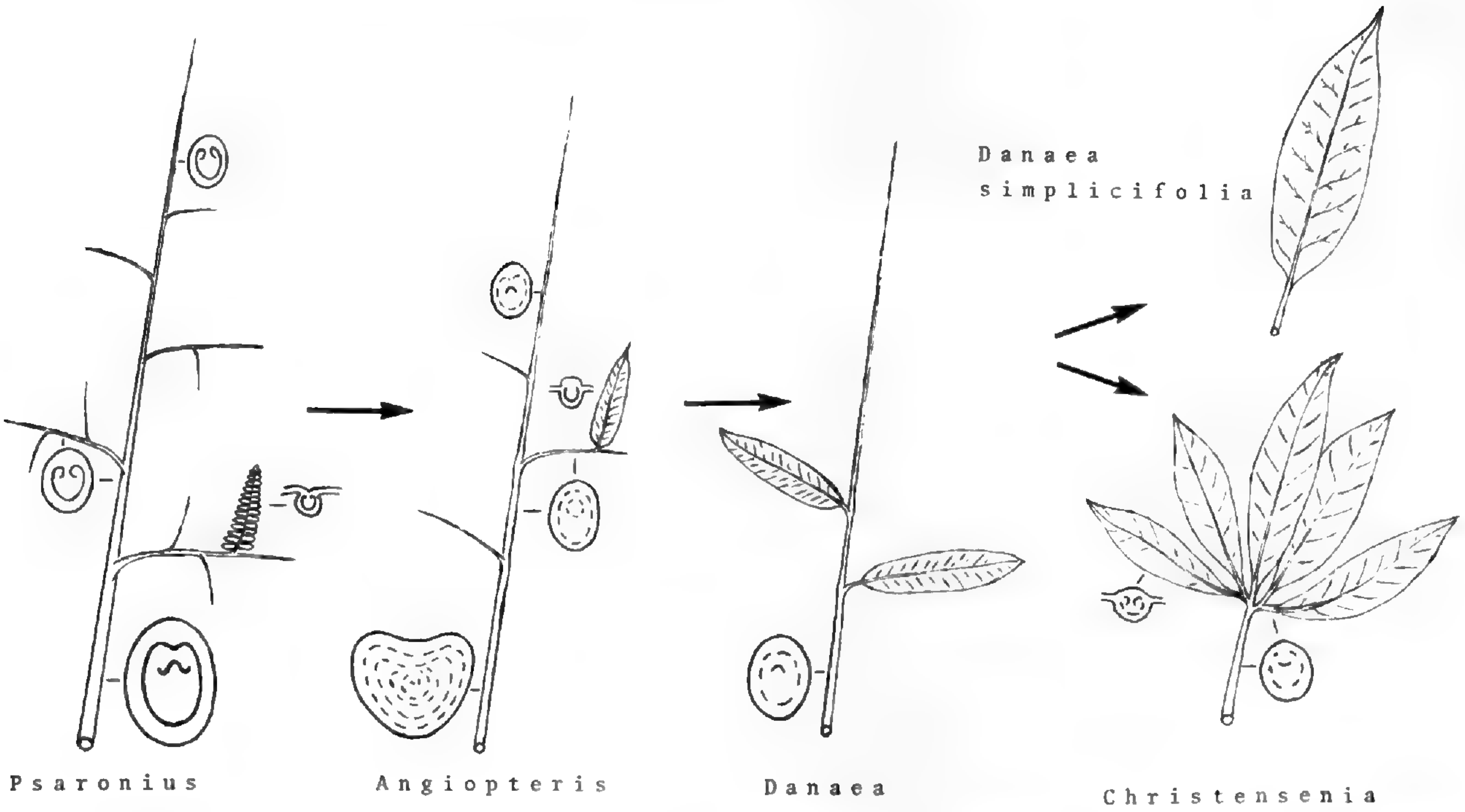
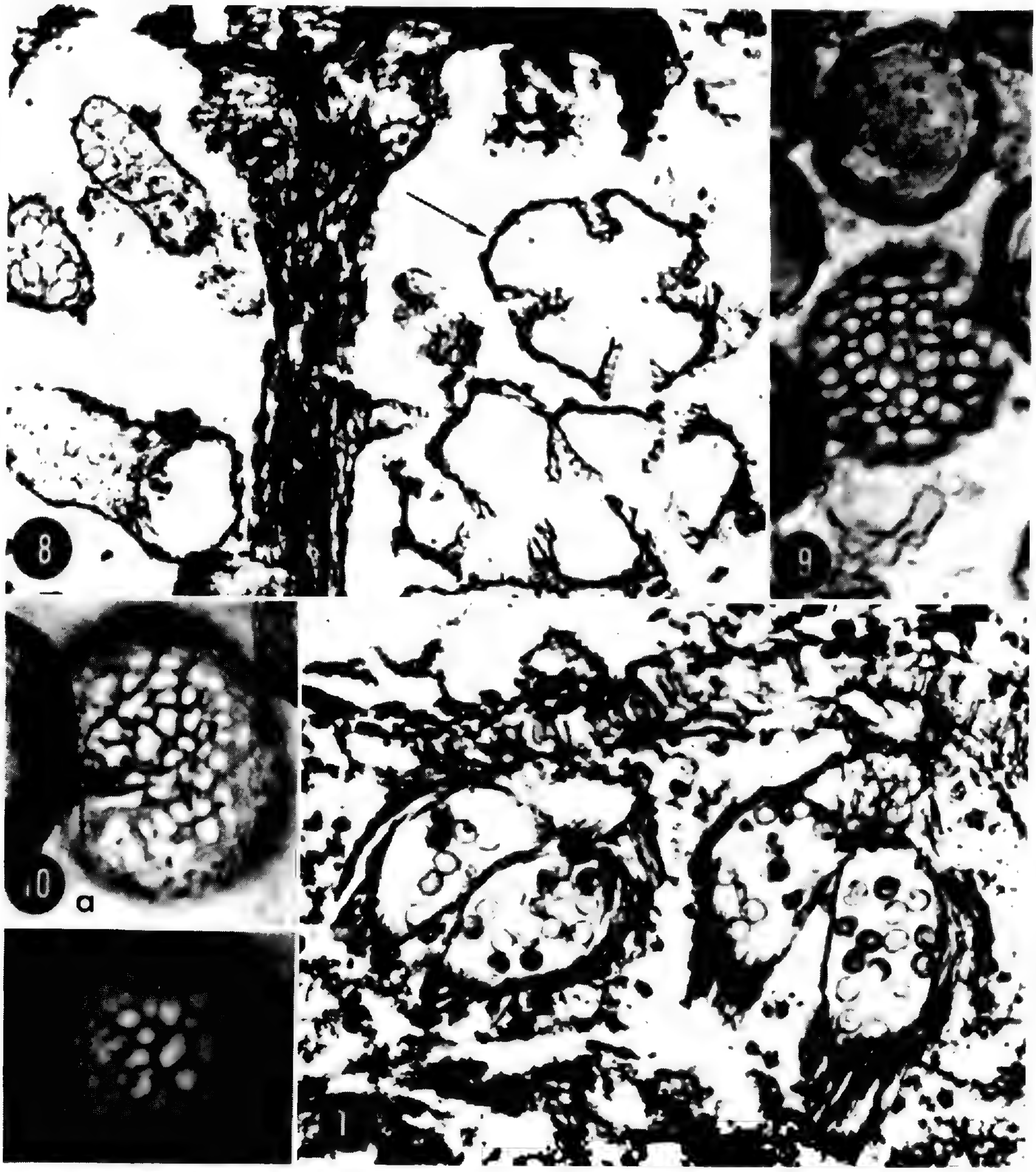


FIGURE 7. Schematic diagrams showing postulated evolutionary changes in marattialean frond morphology and anatomy.

that is normally present in a nonlaminate pinna rachis. Furthermore, the vascular configuration at the base of the pinnule is converted to a horseshoe arrangement of bundles toward the middle of the pinnule (Fig. 7). This is precisely the transformation that normally occurs in a pinna rachis or petiole in the genera with more highly branched fronds and is in distinct contrast to the terete vascular strand that traverses a pinnule of such a frond. It appears that although the morphology of the frond has changed drastically, the vascular anatomy has changed more slowly so that the midrib of the derived pinnule reflects its former state as a pinna rachis.

FRUCTIFICATIONS

Accepting for the moment the evolutionary trend in frond structure outlined in Figure 7, one might ask how soral distribution was affected by the appearance of large laminate pinnules concomitant with fewer branching orders. My initial thoughts were that fusion of small pinnules laterally would have brought their sori into close proximity and fusion of circular sori (*Scolecopteris*) might have resulted in the linear sori so predominate in the living genera. A similar sequence of events was suggested by Mamay (1950); *Scolecopteris iowensis*, which sometimes has two series of circular sori on each side of the pinnule midrib, was considered to have produced the linear sorus of *Eoangiopteris* by fusion of two sori borne on the same lateral vein. Any such scheme, however, presents certain spatial and geometric problems involving orientation of the resulting linear sorus in relation to the midrib and pinna rachis. Such schemes also ignore developmental aspects of the production of large laminar units replacing a series of individual small pinnules borne along an ultimate pinna rachis. Again the changes in frond morphology observed by Asama in *Angiop-*



FIGURES 8–11. Sporangia and spores of *Eoangiopteris* and *Scolecopteris iowensis*.—8. Paradermal section of pinnule of *E. andrewsii* through synangial receptacles on left, midrib in center, and sporangia on right. Note the radially symmetrical synangium at arrow. × 50.—9. Spores of *E. andrewsii*. × 500.—10a–b. Spores of *S. iowensis* × 500.—11. Longitudinal section through two synangia of *S. iowensis* attached to pinnule above. × 50.

teris are pertinent to the question of soral arrangement. When a pinna rachis with individual pinnules is transformed into a large, wide foliar unit (enlarged pinnule), the sori have the same relative distribution and arrangement on the enlarged, derived pinnule as on the smaller antecedent pinnules, *i.e.* near the edge of, and at right angles to, the margin. The transformation occurs abruptly without passing through a series of intermediate stages. If the evolution of the Marattiales proceeded by quantum steps of this sort, we would not expect to find a complete series of intermediate forms in the fossil record.

With these considerations in mind, it seems reasonable that the fossil fructifications *Scolecopteris iowensis* (Fig. 11) and *Eoangiopteris* (Fig. 8) represent a transformation of foliar and fructification units similar to the morphological changes observed in *Angiopteris lygodiifolia.* It is unfortunate that we know so little about the plants that bore *S. iowensis* and *Eoangiopteris*, but the pinnule structure and anatomy of the ultimate pinna rachis indicate *Psaronius* as the parent plant. It is possible that the two fructifications in question were borne on the same plant and perhaps even on the same frond. The similarities between *Scolecopteris iowensis* (radial sorus) and *Eoangiopteris* (linear sorus), inspite of the difference in symmetry, are striking and were well summarized by Mamay (1950): "Referring back to the description of *Scolecopteris iowensis*, a radial sorus, and *Eoangiopteris andrewsii*, a linear sorus, certain similarities may be noted between the two fructifications. Individual sporangia of the two are similar in size, shape, and their dehiscence mechanisms. The tissues comprising the pedicel of *S. iowensis* and the receptacle of *E. andrewsii* are alike. The spores of the two compare closely in gross morphology, size, and sculpturing of the exine. The chief difference between the two lies in the radial aspect of one as opposed to the linear aspect of the other." If the suggestion outlined above is correct, the difference between radial and linear sori are just what one might expect if the respective fructifications were borne on a plant undergoing changes in frond morphology. Further considerations, in part based upon study of the type material, can be interpreted in support of the suggestion that the two fructifications represent one taxon. First, the fertile pinnule of *Eoangiopteris* is slightly larger than most fertile pinnules of *Scolecopteris.* In this regard it should be noted that the "midrib" of *Eoangiopteris* is described as having a U-shaped vascular bundle. All species of *Scolecopteris* have a small terete vascular bundle traversing the midrib, and it is the pinna rachis bearing the pinnules that has a U-shaped vascular bundle. The interpretation suggested here is that *Eoangiopteris* represents an enlarged pinnule derived from ontogenetic fusion of smaller pinnules and that the "midrib" is in reality the former ultimate pinna rachis. Accordingly, the transformed midrib contains a U-shaped vascular strand reflecting its former status. Secondly, not all the sori of *Eoangiopteris* are linear. Figure 8 shows a radial sorus near the tip of a pinnule adjacent to a linear sorus. Such a sorus is scarcely distinguishable from *S. iowensis* and is further evidence that *S. iowensis* and *Eoangiopteris* are not generically distinct. The similarity of spore size and wall structure is a third reason for considering *S. iowensis* and *Eoangiopteris* as merely different forms of the same structural unit. *Scolecopteris iowensis* spores (Fig. 10a, b) are distinctly larger than other spores in the genus but only slightly larger than those of *Eoangiopteris* (Fig. 9). The spores of both are thick walled and have distinct pits in the exine. These features readily separate *S. iowensis* from other species of *Scolecopteris* and support the contention that *S. iowensis* and *Eoangiopteris* are conspecific. According to this interpretation then, one would expect to find in the same biological species, sporangia borne in the three ways exhibited by *S. iowensis* and *Eoangiopteris*, *i.e.* either in a single or double series on either side of the midrib or in linear synangia as in *Eoangiopteris.* Figure 12 illustrates some of the possible ways

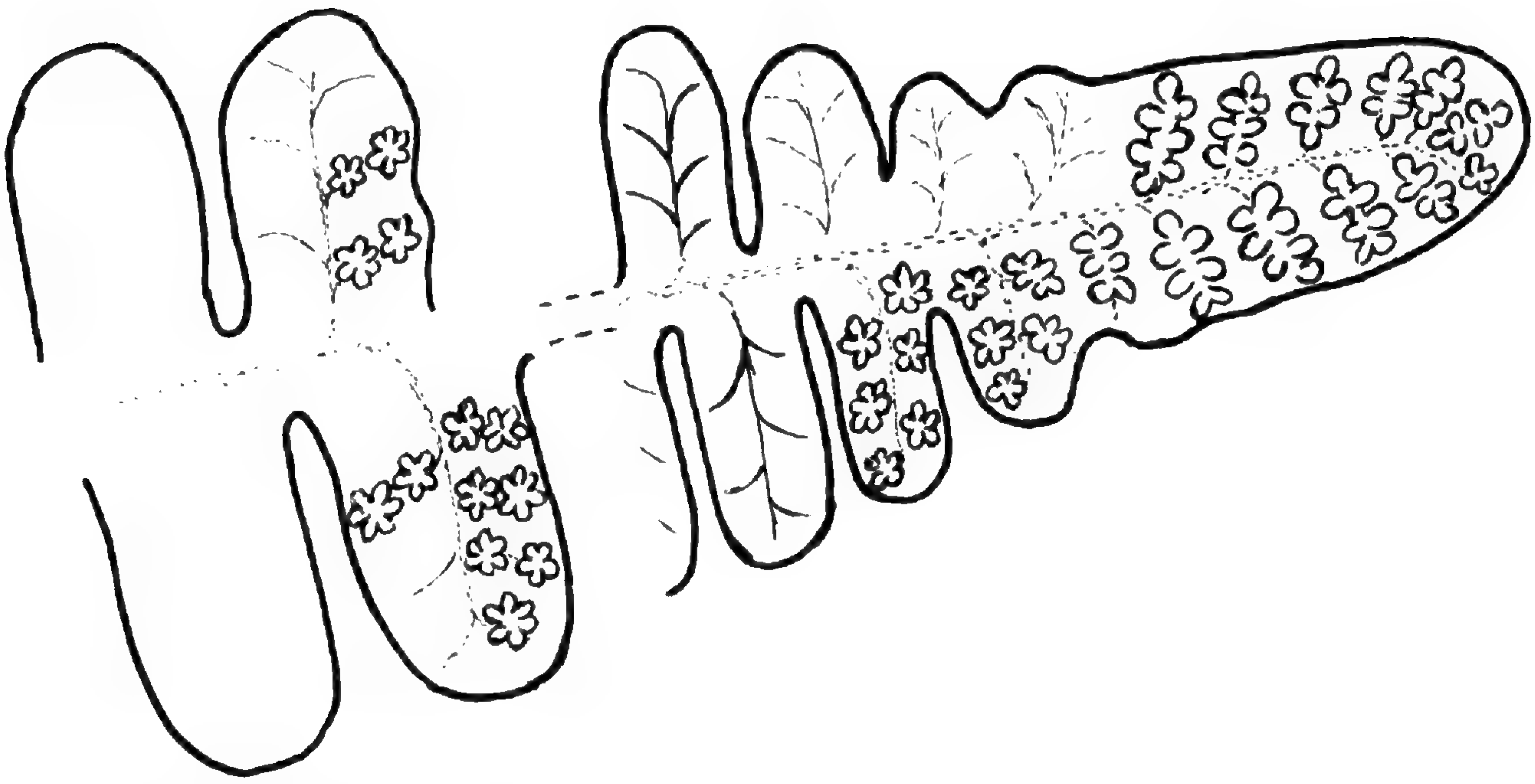


FIGURE 12. Sketch showing hypothetical distribution of *Scolecopteris iowensis* and *Eoangiopteris andrewsii* on *Pecopteris* foliage. Double and single series of synangia on each side of midvein of *S. iowensis* at left and middle respectively. *E. andrewsii* on terminal pinnule at right.

sporangia might be aggregated and is offered only as an aid in visualizing the suggestions made above. It is recognized that the possibilities represented in this sketch might not occur on one portion of a frond nor even necessarily on the same plant. The significance of this suggestion is the insight provided concerning possible sporangial aggregation and pinnule fusion in a species of Carboniferous age.

DISCUSSION

One of the most obvious problems in a consideration of the evolution of the marattialean ferns is the fact that there are few clues as to how the group might have originated. From its very first appearance in the Carboniferous *Psaronius* possesses a very distinct, even unique, morphology and anatomy. It is very difficult, on the basis of our current information, to detect evolutionary relationships *within* the genus. We need to know more about the Devonian specimens attributed to *Psaronius*. We need more information about the plant or plants that bore *S. iowensis* and *Eoangiopteris*. The genus *Radstockia* (Taylor, 1967) is an intriguing compression fossil known in this country from the famous Mazon Creek locality. The linear synangia appear nearly identifical to those in the living genus, *Marattia*. The occurrence of a Carboniferous form with such striking similarities to an extant genus and contemporaneous with the genus *Psaronius* suggests the existence in Carboniferous time of marattialean forms much more like the living forms than *Psaronius*. We may hope that future discoveries provide more information about the plant that produced the fertile regions of *Radstockia*.

Psaronius then is perhaps best regarded as an early representative of the Marattiales which was well adapted for survival in the Carboniferous swamp forests. The geologic and consequent environmental changes which accompanied the Permian and later periods were too drastic for *Psaronius* and most other species of the period. Many were highly specialized and adapted to the unique environment of the time and grew and multiplied in great numbers. This is reflected in the frequency with which they are encountered as fossils. What we learn of these plants greatly increases our understanding of the various taxa that they represent but as often as not more questions are raised than answered. The modern survivors of the fossil forms were in most cases probably not derived from the dominants but more likely from plants less well adapted to the prevailing conditions and therefore less numerous. The latter were able to adapt to the changing conditions of subsequent environments. The rare occurrence of *Radstockia* indicates that other marattialean forms were present but were much less numerous than the dominant *Psaronius* and are consequently much more poorly represented in our fossil collections. Unfortunately, if this conjecture is true, the critical specimens needed to determine the phylogeny of the Marattiales are perhaps forever beyond our grasp. The presence of *Radstockia* and *Psaronius* in Carboniferous strata presents us with two contemporaneous fossil forms with distinct differences in morphology and synangial type. Each appears too specialized to be ancestral to the other genera, and we therefore must await future discoveries to resolve the ancestry of the group.

What then can be said about the evolution of the Marattiales and upon what bases are relationships to be determined? The answer to the second part of the question is that at present one must rely on the classic methods of comparative morphology and anatomy. In such an attempt we are confronted with at least two fossil members and six or seven living genera. The fossil members *Psaronius* and *Radstockia* are each specialized in their own way; *Psaronius* with a tall erect stem and unique supporting root mantle and *Radstockia* with unknown stem but with linear synangia much more specialized than the radial synangia of *Psaronius*. Bierhorst (1971) has suggested that in the Marattiales the free sporangiate condition is derived from a synangiate one. The occurrence of linear synangia as in *Radstockia* contemporaneously with *Psaronius* is evidence that both conditions had evolved by Carboniferous time and is not helpful in deciding which was the primitive condition. If the contention is correct that the linear synangium of *Eoangiopteris* is a modification and fusion of radially symmetrical synangia in response to morphological changes in the laminar surface of the frond, then we see a rare instance of how a developmental aspect of one species provides clues to pathways which may have occurred in the evolution of the larger group. Sporangial aggregation has apparently evolved in different ways in descendant genera. In *Macroglossum*, *Archangiopteris*, and *Danaea* linear synangia represent one extreme, while in *Christensenia* the radial sorus was retained and became scattered over the surface of the large laminar units. *Christensenia* is regarded as highly modified from the ancestral condition in its vegetative anatomy and morphology but has retained the presumed primitive type of synangium. The trend in frond morphology outlined in Figure 7 is not to be interpreted as suggesting that the illustrated genera were derived from each other. Rather it is intended to illustrate broad evolutionary tendencies in frond morphology which probably occurred within as well as between genera. Some evolutionary trends in the Marattiales are summarized in Table 1.

TABLE 1. Some evolutionary trends in the Marattiales.

Character	Primitive	Derived
Stem anatomy.	Protostelic—Siphonostelic; strap-shaped vascular bundles.	Polycyclic, dictyostelic; small individual vascular bundles.
Stem morphology.	Erect, radially symmetrical.	Prostrate, bilaterally symmetrical.
Roots.	One root/leaf.	Root mantle in *Psaronius*; no association between roots and leaves.
Frond morphology.	Large, highly divided; small pinnules.	Large pinnules, once pinnate or less.
Frond anatomy.	Many bundles.	Few vascular bundles.
Fructifications.	Radially symmetrical sorus, free sporangiate.	Linear sorus, synangiate.

One of the problems in assessing evolutionary trends in the Marattiales is determining the effects of size on form and anatomy. For instance, the broad strap-shaped vascular bundles in *Psaronius* may indicate an adaptation to the large size of the plant and not a primitive condition as indicated in Table 1. Large fronds of a given taxa tend to be more highly divided than small fronds. Size and form are so closely correlated in the Marattiales that size alone is perhaps a primary evolutionary factor and consequent anatomy and morphology secondary.

A concluding note on the classification and taxonomy of the Marattiales is in order. Certain French workers have for some time contended that the fructification genus *Senftenbergia* is borne on *Pecopteris* foliage which was in turn borne on the arborescent trunks known as *Megaphyton* (Dalinval, 1960). *Megaphyton* is a *Psaronius*-type stem distinguished by the presence of two rows of leaf scars on opposite sides of the stem. Moreover, the vascular system of the leaf scar shows various stages of division indicating that the frond bifurcated near its base. *Senftenbergia* is a very unmarattiaceous type sporangium that has been allied with the Schizeaceae because of its apical annulus. Also, sporangia are not grouped into sori as in the Marattiales. The contention that *Senftenbergia* represents the fertile regions of *Megaphyton* is such an unlikely possibility that such a conclusion must have strong supporting evidence and in my opinion has not been provided. Recent work by Jennings and Eggert (1972) casts serious doubt on either a marattiaceous or schizaeaceous affinity of *Senftenbergia*. Their evidence suggests that *Senftenbergia* belongs to an *Ankyropteris*-type plant.

The Marattiales appear then as a distinct group of plants with sufficient similarity to be included in one family in spite of the gross differences in habit, for example, between the fossil *Psaronius* and the living *Christensenia*. The same structural plan is present in all members, and the extremes in morphology and anatomy are for the most part readily interpretable as specializations of a basic type. But as in so many other taxa, despite a good fossil record, the ancestral type remains a mental concept.

LITERATURE CITED

ASAMA, K. 1960. Evolution of the leaf forms through the ages explained by the successive retardation and neoteny. Sci. Rep. Tôhoku Univ. Ser. 2, Geol., Spec. Vol 4: 252–280.

BERTRAND, C. E. & F. CORNAILLE. 1902. Étude sur quelques caractéristiques de la structure des Filicinées actuelles. Trav. & Mém. Univ. Lille. X. Mém. 29.

BIERHORST, D. W. 1971. Morphology of Vascular Plants. Macmillan Company, New York.

BLOMQUIST, H. L. 1922. Vascular anatomy of *Angiopteris evecta.* Bot. Gaz. (Crawfordsville) 73: 181–199.

DALINVAL, A. 1960. Classification et répartition verticale des Pecopteridées dans le bassin houiller du Nord de la France. Bull. Soc. Géol. France, Sér. 7. 2: 573–580.

DAWSON, J. W. 1971. On new tree ferns and other fossils from the Devonian. Quart. Jour. Geol. Soc. 27: 269–276.

FARMER, J. B. & T. G. HILL. 1902. On the arrangement and structure of the vascular strands in *Angiopteris evecta* and some other Marattiaceae. Ann. Bot. (London) 16: 371–402.

GWYNNE-VAUGHAN, D. T. 1905. On the anatomy of *Archangiopteris Henryi* and other Marattiaceae. Ann. Bot. (London) 19: 259–271.

JENNINGS, J. R. & D. A. EGGERT. 1972. *Senftenbergia* is not a schizaeaceous fern. Amer. Jour. Bot. 59: 676. [Abstract.]

KIDSTON, R. 1925. Fossil plants of the Carboniferous rocks of Great Britain. Geol. Surv. Gr. Brit. Mem. Paleontol. 2: 523–670.

MAMAY, S. H. 1950. Some American Carboniferous fern fructifications. Ann. Missouri Bot. Gard. 37: 409–476.

STIDD, B. M. 1971. Morphology and anatomy of the frond of *Psaronius.* Palaeontographica, Abt. B, Paläophytol. 134: 87–123.

——— & T. L. PHILLIPS. 1968. Basal stem anatomy of *Psaronius.* Amer. Jour. Bot. 55: 834–840.

TAYLOR, T. N. 1967. On the structure and phylogenetic relationships of the fern *Radstockia* Kidston. Palaeontology 10: 43–46.

WEST, C. A. 1917. A contribution to the study of the Marattiaceae. Ann. Bot. 31: 316–414.

VARIABLE EXPRESSION OF THE APPENDICULAR STATUS OF THE MEGAPHYLL IN EXTANT FERNS WITH PARTICULAR REFERENCE TO THE HYMENOPHYLLACEAE[1]

David W. Bierhorst[2]

Abstract

Leaf-branch relationships and certain aspects of leaf ontogeny are described in representatives of 15 of the hymenophyllaceous genera (sens. Copeland). A series is discussed from leaves which are non-appendicular, *i.e.* which are direct continuations of stems, to others which are appendicular, *i.e.* which are bilateral and dorsiventral and different from stem apices from their inception. The results are discussed in a broader context of leaf determination and megaphyll phylogeny in the Filicales.

Any attempt at this point on the writer's part to synthesize or to accept a strict definition of a leaf would artificially limit the overall consideration of the spectrum of organ types which are now recognizable among ferns and fern-like plants as leaves. Much of this range (in form, structure, and ontogeny) now appears to exist among the extant Filicales which is a prime thesis of this presentation.

Stem-like features of certain clearly recognizable filicalean fronds have long been recognized. These are the occasionally radially organized petiolar steles at the bases of fronds (Hymenophyllaceae, Stromatopteridaceae, Psilotaceae), indeterminate growth of fronds (Lygodiaceae), delayed organ determination, *i.e.* retention of dual ontogenetic potentials (Osmundaceae), and presence of a stem-like apical cell in the leaf, at least during early stages of development (Osmundaceae). More recently, stem-like features of the leaf primordia of *Stromatopteris*, *Gleichenia*, and *Actinostachys* have been described (Bierhorst, 1968*a, b*, 1973) as well as stem-like steles at the bases of petioles in *Gleichenia*. In addition, the frond nature of what has been called "aerial shoot" in *Tmesipteris*, although in part long-known (Sykes, 1908), has recently been brought to attention (Bierhorst, 1968*b*). Most significantly, the non-appendicular nature of the frond of *Gonocormus* (*Trichomanes*), *Stromatopteris*, *Tmesipteris*, and *Psilotum* has been brought out, along with evidence that fronds of *Gleichenia* and *Actinostachys* may similarly be interpreted (Bierhorst, 1973).

Much of the above information supports the basic conclusion that filicalean fronds are megaphylls, that is phylogenetically derived from branch trusses, and it is generally significant that leaves with characters suggestive of stems all fall within families with an overall preponderance of primitive features.

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Ann. Missouri Bot. Gard. 61: 408–426. 1974.

There are also strong indications of morphological reversals in the basic trend from stem systems to fronds. The species in the Psilotaceae which was formerly considered to exhibit the most primitive morphology of its family, *Psilotum nudum*, now seems to show the most advanced. A very parallel trend also appears within the genus *Schizaea* in which one undescribed Fijian form (possibly a form of the very polymorphic S. *dichotoma*) exhibits a decussately dicotomous instead of a pinnate frond.

Two features of fern fronds are to be emphasized presently. One is the lack of (or at least long delayed) determination which is so pronounced in the Psilotaceae and Stromatopteridaceae and now appears in the Hymenophyllaceae. The other is the non-appendicular status of fronds now extended to various members of the Hymenophyllaceae and the transition of this status to one which is completely appendicular.

A major purpose in undertaking further studies of the Hymenophyllaceae was to clarify the apparently anomalous morphological status of *Gonocormus* (*Trichomanes*). Several New Caledonian collections of this peculiar "genus" were described (Bierhorst, 1973), and these bore what were obviously non-appendicular fronds. It was tempting to compare *Gonocormus* at the time to genera of other families with suggestively similar features, namely *Psilotum*, *Tmesipteris*, *Stromatopteris*, *Gleichenia*, and *Actinostachys*. Such a comparison, however, did not seem proper until *Gonocormus* was first placed in a proper comparative context within its own family, and hence more parallel information was sought.

Materials and Methods

All materials used were fixed in the field in a CRAF solution and later transferred to glycerine-alcohol for storage.

Below are listed the species studied, their source of origin, and collection numbers. PNG = New Guinea, S = Surinam, FG = French Guiana, NC = New Caledonia, F = Fiji.

- *Hymenophyllum* (*Mecodium*)
  - *H. badium* PNG *147, 153, 166*
  - *H. crispatum* PNG *258*
  - *H. polyanthos* PNG *227*
  - *H. javanicum* PNG *282*
  - *H. longifolium* PNG *171A*
  - *H.* sp. PNG *134*
- *Hymenophyllum* (*Amphiterium*)
  - *H. laminatum* PNG *136A, 179*
  - *H. geluense* PNG *171B*
  - *H.* sp. PNG *371B*
- *Hymenophyllum* (*Meringium*)
  - *H. holochilum* PNG *142*
  - *H. acanthoides* PNG *237, 259, 260, 275, 277, 278, 281, 298, 307*
  - *H. gorgonium* PNG *154, 131*
  - *H. bontocense* PNG *355*
- *Trichomanes* (*Macroglena*)
  - *T. meifolium* PNG *130, 280*; NC *573*
- *Trichomanes* (*Nesopteris*)
  - *T. grande* PNG *48, 60, 65, 67, 317*
  - *T. harveyi* F *119*
- *Trichomanes* (*Callisopteris*)
  - *T. apiifolium* PNG *350*
- *Trichomanes* (*Crepidopteris*)
  - *T. gracillimum* PNG *20, 137, 309*
  - *T. humile* PNG *42, 325*
  - *T. alternans* F *126*
  - *T.* sp. PNG *133A*
- *Trichomanes* (*Gonocormus*)
  - *T.* sp. PNG *128, 144, 148, 149, 261, 275, 333*
- *Trichomanes* (*Vandenboschia*)
  - *T. aphlebioides* PNG *45*
  - *T. giganteum* PNG *356*
- *Trichomanes* (*Cephalomanes*)
  - *T. atrovirens* PNG *50, 51, 55, 56, 64, 314, 324, 326, 328*
  - *T. asplenioides* PNG *318, 327*
  - *T. australicum* F *73*
- *Trichomanes* (*Microtrichomanes*)
  - *T. digitatum* PNG *132, 133B, 136B*
  - *T. francii* NC *576*

Trichomanes (*Selenodesmium*)
  T. obscurum PNG *90, 95, 96, 112, 177*
  T. dentatum F *30*; NC *460*
  T. sp. PNG *66, 100, 105, 145, 151, 152, 270, 272, 292, 305, 342*

Trichomanes (*Microgonium*)
  T. beccarianum PNG *348*
  T. motleyi S *81, 136, 183*

Trichomanes (*Crepidomanes*)
  T. venulosum PNG *61, 194*

Trichomanes (*Didymoglossum*)
  T. montanum S *103, 140, 141*

Trichomanes sens. strict.
  T. pinnatum FG *44, 46*
  T. sp. FG *121*

Trichomanes (*Feea*)
  T. diversifrons FG *176*

DESCRIPTIONS

The New Caledonian *Gonocormus* specimens studied showed a rootless body with a system of filamentous, hairy running stems. The runners bore distichously arranged lateral stems which in turn grew as the parental ones. In addition, vertical branches were produced which fell outside of the basic ½-cladotaxy of the runner system. The vertical branches dichotomized soon after their production, and of the two new apices formed, one became a new runner and one a "leaf." The ambiguity lies in the different designations of what a leaf is in *Gonocormus* (see Copeland, 1933). The apex which forms the "leaf" branches apically in a plane at right angles to the stem dichotomy below, and of the two new apices formed, in some collections the one on the abaxial side with respect to the original parental runner forms blade after its radially symmetrical apex assumes a linear form. The sister apex on the adaxial side branches as did its mother apex, and the process of branching and blade formation may continue until 5 or 6 blades with their planes more or less parallel to each other are produced. A leaf of this type, from which three blades have been removed, is illustrated for a New Guinea collection in Figure 5, the axes extending vertically in the photograph. In the less flabellate and more pinnate leaves, the leaf apex frequently drops off a series of these "proliferation" apices (P, Fig. 6) which may or may not produce new blades or whole "leaves."

The species designation in this context is not possible at present. According to Copeland (1933) there may be only one species or 5 or more of *Gonocormus*. Extreme variability and overlap in size and leaf form have not, and cannot be here, reconciled in a satisfactory system designating specific circumscriptions.

New Guinea collections, numbering 9 being described, varied considerably among themselves, but all differed in one particular way from the New Caledonian ones. In the New Guinea ones, the branches which formed leaves were not on the upper side of a runner, but all fell within the ½-cladotaxy of the laterally placed stems. After this was observed, more of the original New Caledonian material was examined, and in a few cases the leaf-bearing branch was also to be lateral.

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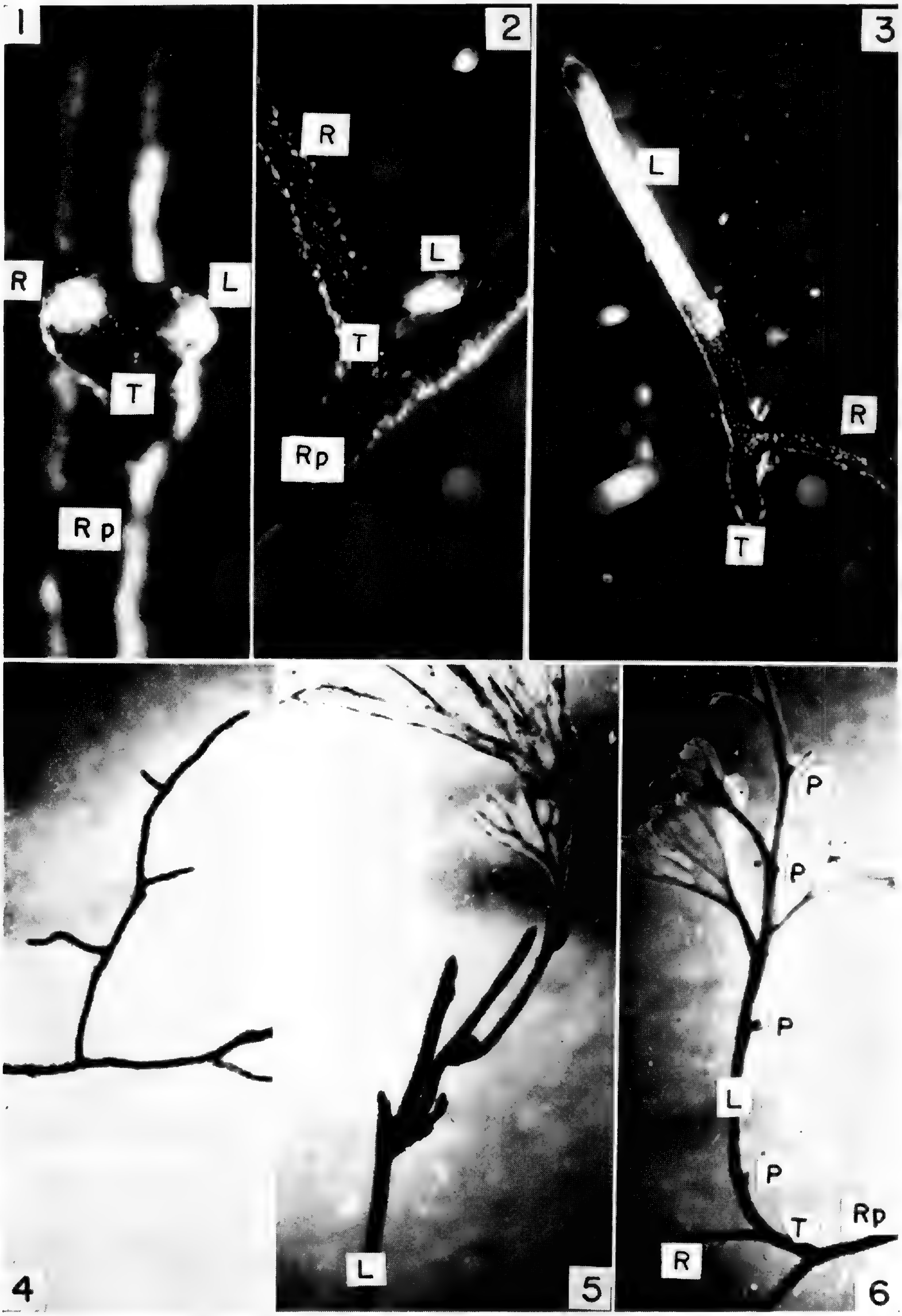
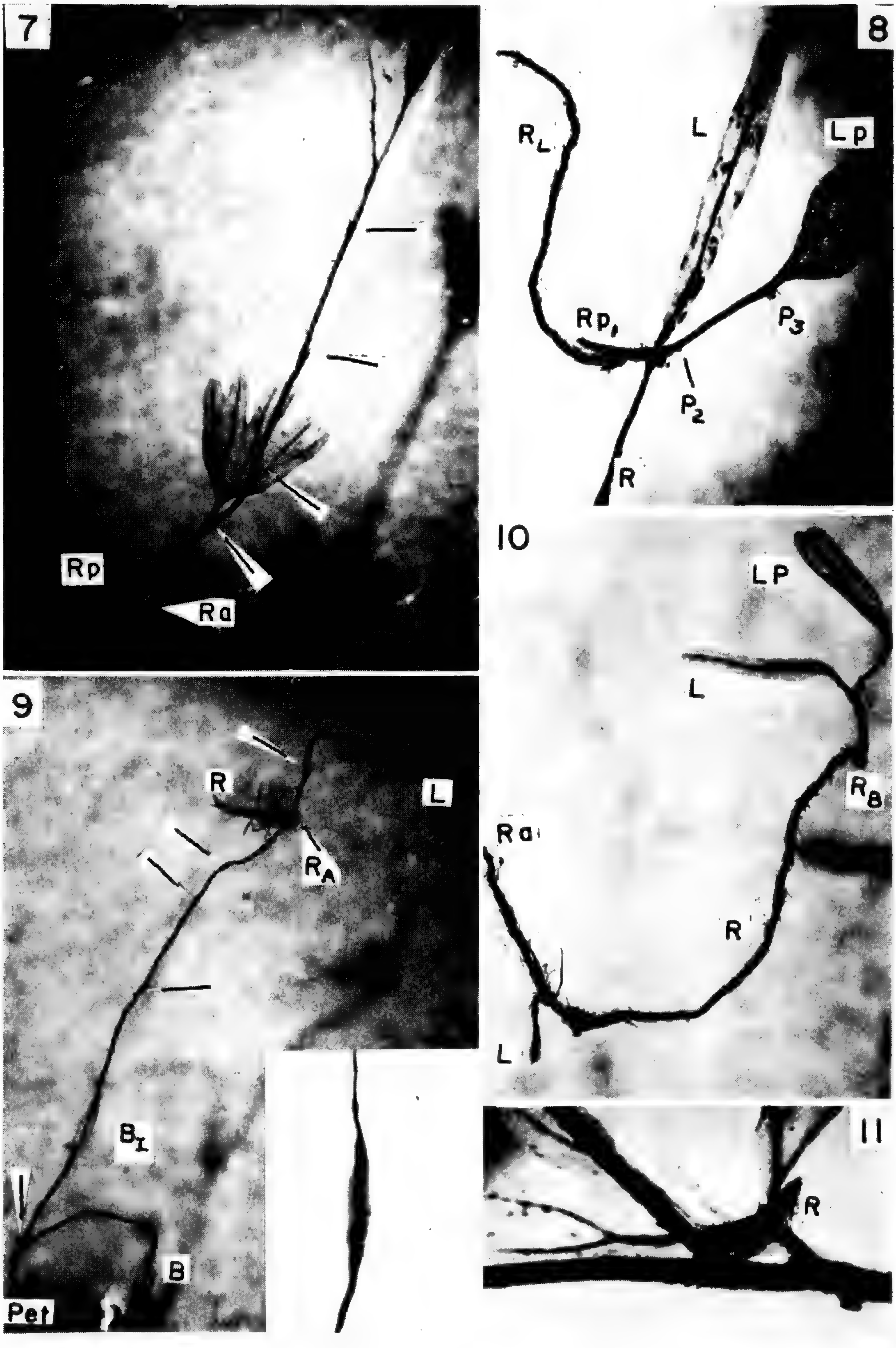
FIGURES 1–6. *Trichomanes* (*Gonocormus*).—1–3. Successively older stages in the development of the phylliferous lateral stem. 1–2, PNG *128*, × 21; 3, PNG *144*, × 18.—4. A runner stem, horizontally oriented, bearing two laterals; the upper one again bearing alternate runners. PNG *275*, × 4.8.—5. One leaf several times compounded by "proliferations." Three blades



have been removed. PNG *144*, × 7.—6. A portion of the runner, Rp, bearing a branch, T, which has bifurcated to produce runner, R, and leaf, L. P indicates "proliferation" apices which have not grown out. PNG *149*, × 7.—Rp = parental runner; T = trunk of a leaf-bearing branch; R = runner; L = leaf.



Figures 7–11. *Trichomanes* (*Gonocormus*).—7. An entire fertile leaf and its apparent attachment to the parental runner, Rp. Ra is the apex of the runner which forms the second

The formation of lateral branches on a runner is quite regular. Although on branching two apices of equal size are formed, one remains medianly situated at the apex of the runner (illustrated for *Crepidomanes*, = *Trichomanes* sens. lat., which shows identical branching, Fig. 12). The lateral apex branches in the vertical plane (Fig. 1) to produce two identical apices. The upper of these then forms "leaf," while the lower forms a new runner (Fig. 2, 3, 6). Or one or both of the two apices may remain dormant (Fig. 7, Ra). In the specimen shown in Figure 4, a branch runner is shown oriented vertically in the photograph, which again shows alternate, 2-ranked runner branches. At all but one point of branching, a dormant apex was seen at the base on the upper side. In a very few instances a lateral branch such as the one shown in Figure 1 formed two new runners rather than one runner and one leaf.

A further deviation from the pattern described above was found in one of the New Guinea collections in which proliferation apices well up on a "leaf" grew into new runners (Fig. 11) instead of new blades. In the same collection, new runners were observed arising from single cells on the lower sides of veins of old partly decayed laminae.

The most peculiar and most diminiative *Gonocormus* collection was PNG *171*, also from New Guinea (Fig. 7–10, note magnifications) in which the broadest lamina (lower one on the fertile "leaf," Fig. 7) was approximately 3 mm across with most others in the range of 0.5–1 mm and in which the runners were mostly between 90 and 170 μ in diameter! Much of the morphology of PNG *171* was similar to that of other collections. That is, a runner branched laterally, and lateral branches performed as described and illustrated in Figures 1–3. In Figure 7, Rp is a parental runner bearing a lateral branch. The branch dichotomized. An arrested apex was left behind (Ra), while its sister apex formed the "leaf." The broader blade at the base formed first. The first proliferation apex continued upward, leaving behind 4 arrested proliferation apices (at pointers) then formed the upper blade with the sorus. In Figure 10, a runner, R, with its older end broken off at R_B, produced blade L and a blade LP from its first proliferation. Runner R also produced two more lateral branches, one of which produced another leaf, L at lower right, and the other which is just below the runner apex Ra and too small to be indicated. Also in PNG *171*,

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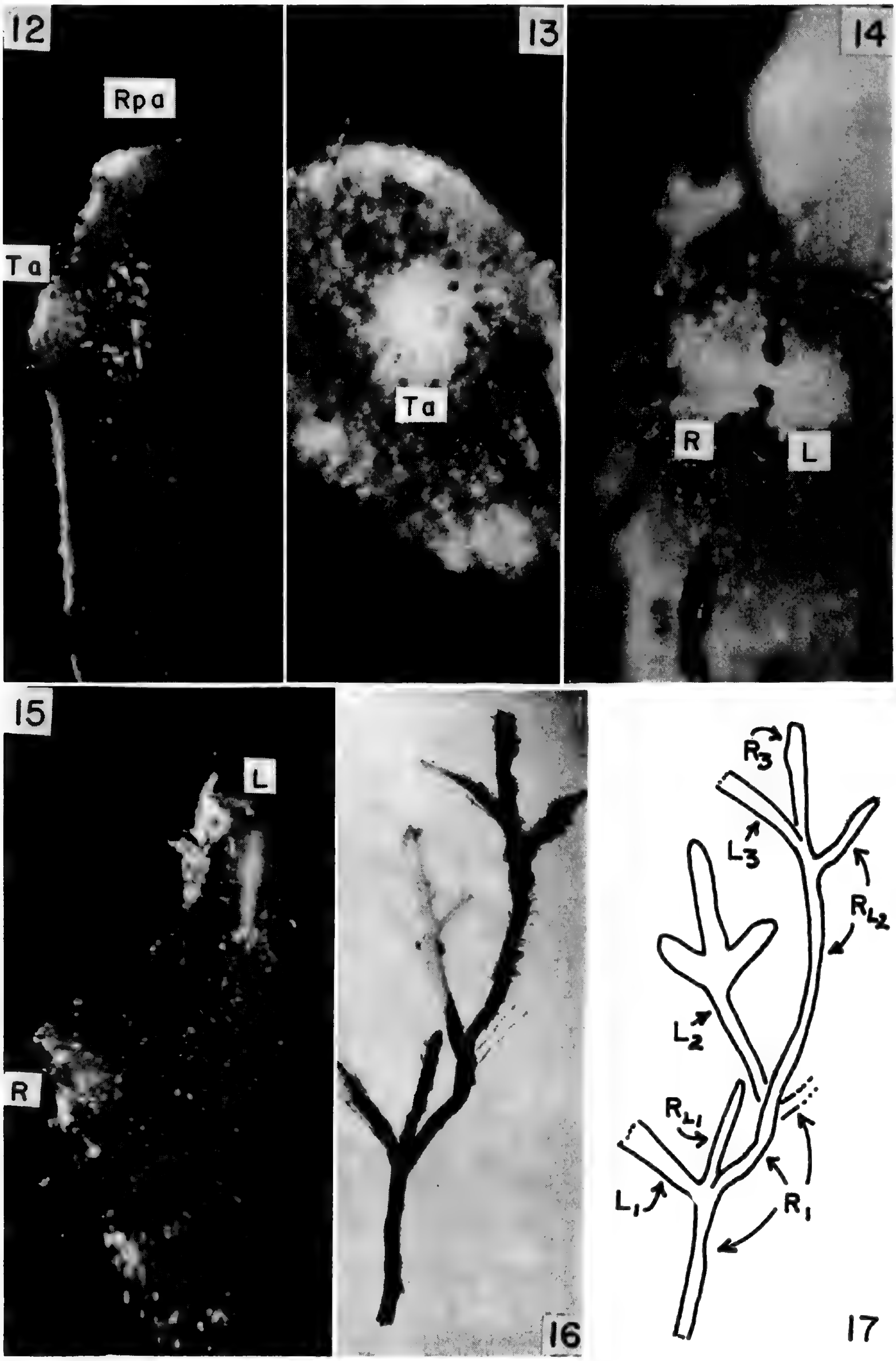
member of the bifurcation of the short branch which bears the leaf. Four "proliferation" apices are pointed out. × 6.1.—8. A unit such as shown in Fig. 1–3 and 6, but terminal on a runner, R, rather than lateral. L = first blade; L_P = blade of first proliferation; P_2 and P_3 = second and third proliferations upon the first; Rpl = a runner from the first proliferation which bore a lateral runner, R_L. × 8.—9. What began as a "leaf." Pet is its petiole; B = first lamina. Lower pointer indicates the apex of the first proliferation of the first proliferation of the original "leaf." B_I is an intercallary blade, enlarged in inset, produced by the first proliferation before it went on to form runner with lateral apices, pointers. The apex of the runner was broken off at R_A. It had produced a lateral truss (equivalent to the one in Fig. 3); R = its runner, L = its leaf. × 8.—10. A runner, broken off at R_B, produced a lateral truss (L = its first blade; Lp blade from its first proliferation) and another one, L. Ra = runner apex. × 8.—11. A runner, R, arising from a proliferation well up upon a frond whose major axis lies horizontally in the figure. × 9.6.—7–10, PNG *171*; 11, PNG *275*.



FIGURES 12–17. *Trichomanes* (*Crepidomanes*) *venulosum*.—12. A runner tip, Rpa, and a lateral truss primordium, Ta. PNG *61*, × 100.—13. Face view of truss primordium. PNG

the phylliferous unit (as illustrated in Fig. 3 for another collection) was occasionally terminal rather than lateral upon a runner (Fig. 8). In the figure, blade L was the first formed lamina; Lp is the blade of the first proliferation. The apex of the first proliferation before producing blade Lp produced three other proliferation apices; the second and third, P_2 and P_3, remained arrested. The first, however, formed a runner, Rp_1, which in turn produced a lateral runner, R_2.

Another peculiarity of PNG *171* was its ability to change a lamina apex back into a runner apex. The specimen in Figure 9 is what began as a "leaf" (Pet designates the petiole which forms the trunk of the truss). The blade B formed first. The first proliferation apex formed the rest of the specimen. It dropped off a proliferation apex (lower pointer), formed a lamina, B_I (enlarged in inset), and grew on while leaving behind three more proliferation apices (next 3 pointers). It, now acting as a runner apex, produced a lateral branch (again of the usual *Gonocormus* type as shown in Fig. 3) before the apex became arrested (R_A). The lateral branch forked to produce runner R and leaf L with one proliferation apex (upper pointer).

Among the other Hymenophyllaceae studied, *Crepidomanes*, *Microgonium*, and *Didymoglossum* (all three = *Trichomanes* sens. lat.) were most similar to *Gonocormus* in that they are rootless and possess thin running stems which branch alternately in the horizontal plane, although in *Microgonium* the arrangement is less regular and frequently seems to approach helical.

Crepidomanes is illustrated in Figures 12–17. A runner apex, Rpa in Fig. 12, and a lateral branch apex, Ta (also shown in face view in Fig. 13), are shown. The equivalent of the trunk of the phylliferous branch of *Gonocormus*, *i.e.* T in Figs. 1–3 and 6, is almost non-existant as the apex Ta bifurcates earlier (Fig. 14). This is also true of *Microgonium* and *Didymoglossum*. The leaf apex L may be designated as such only due to its position, since the dichotomy is always in the vertical plane and the upper of the two apices regularly forms leaf while the lower forms a new runner. A somewhat later stage appears in Figure 15, where the leaf apex now has developed a linear form and the prismatic layer is readily visible.

At maturity the system appears as in Figure 16 with an explanatory diagram in Figure 17. Runner R_1, which is broken off at dotted lines, produced lateral branch 1, which bifurcated to form leaf L_1 and runner R_{L1}. R_1 also produced lateral branch 2, which similarly bifurcated to form leaf L_2 and runner R_{L2}. R_{L2} continued growth and produced branch 3.

In *Crepidomanes* the lateral branches of the smallest runners generally

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194, × 130.—14. A lateral truss has bifurcated to form a runner apex, R, and a leaf, L. PNG *194*, × 130.—15. An older stage than in Fig. 14. The leaf L now shows a linear apical meristem. PNG *61*, × 95.—16. A runner with lateral trusses. PNG *61*, × 6.25.—17. Explanatory diagram for Fig. 16. The runner, R_1 which is broken off at dotted lines, produced truss 1 which bifurcated to form leaf L_1 and runner R_{L1}. Truss 2 was next produced by R_1 which next produced leaf L_2 and runner R_{L2} which in turn produced truss 3 with its leaf L_3 and runner R_3.

produce no leaves. They frequently, however, leave behind at their point of attachment an arrested apex on their upper side.

In mature portions of *Didymoglossum* and *Microgonium* the runner apex which is formed by the bifurcation of a lateral branch is most often non-functional, but by careful dissection it can be seen as a minute area of white tissue, 4 or 5 cells across, completely hidden by hairs on the upper side of and at the base of what appears to be petiole.

Microtrichomanes (= *Trichomanes* sens. lat.) like the other "genera" described above has a very thin runner with a series of lateral branches. The branches, however, are arranged spirally to irregularly, and the plant bears roots which, like all hymenophyllaceous roots, are endogenous in origin. Externally the roots are quite difficult to distinguish from running stems since they are of similar size, bear similar hairs, and the calyptra is very diminutive.

Lateral branches in *Microtrichomanes* originate much as do those of *Crepidomanes* and others described above. They grow out from the runner each as a short, broad cone rather than a cylinder, and they bifurcate. The plane of bifurcation is at right angles to that in *Gonocormus*, *Crepidomanes*, *et al.* and therefore produces one apex toward the tip of the runner and one away, rather than one on the upper and one on the lower side. Of these new apices, the one away from the runner apex forms leaf after its radial symmetry shifts to bilateral symmetry. Very shortly after the bifurcation, the leaf apex is also slightly larger than its sister apex which may remain dormant, grow out as a new runner, or bifurcate to produce a second leaf and another apex which also has variable potential.

The "genera" *Crepidopteris* (= *Trichomanes* sens. lat.), *Amphiterium*, *Meringium*, and *Mecodium* (all three = *Hymenophyllum* sens. lat.) and morphologically very similar to each other in terms of those characteristics considered in the present context. Each bears easily recognizable roots, and a running stem with lateral branches in a fixed cladotaxy which is spiral in *Amphiterium* and spiral to irregular in *Mecodium* and *Crepidopteris*. In *Meringium* the arrangement is 2-ranked with the two rows somewhat above the lateral position and therefore separated from each other by less than 180°.

The lateral branches of these four "genera" branch in the same plane as do those in *Microtrichomanes*, and of the two new apices formed the abaxial one usually forms leaf and adaxial one remains stem which may grow out as a new runner or more often remain dormant. Several times in *Amphiterium* and *Meringium* the apex in the leaf position has been seen to form a new runner instead of a leaf, and in these cases its sister apex in its apparent axil remained dormant. In one case both apices formed runners. In addition, the bud in the apparent axillary position occasionally bifurcated again to produce another leaf and another stem apex. In each of these four genera, as in others described, the young leaf apex is very similar in form and structure to the stem apices of the rest of the body until bilaterality sets in.

A still more significant variation observed in *Amphiterium* and *Meringium* is the occasional transformation of the tip of a long runner directly into a leaf.

Macroglena (= *Trichomanes* sens. lat.) shows also a creeping stem, but it is not so thin. It bears spirally arranged appendages which superficially appear to be leaves with near axillary buds. The manner in which these appendages originate and the parallelisms with other hymenophyllaceous "genera" allow these to be designated as branches of the stem. *Macroglena* bears prominent single apical cells on all of its apices, and the primordia are relatively large. This allowed for more detailed ontogenetic analysis down to the cell-lineage level than was possible for genera with minute apices without apical cells such as *Gonocormus* and *Microgonium.*

The apex of a runner in *Macroglena* possesses an apical cell with three cutting faces. An equal division of the apical cell initiates a new runner apex and the apex of a phylliferous branch (what has been called a leaf). When the two apices are separated by aproximately 6–8 cells, their form is still identical, but one may be designated as the future leaf-producing structure (L in Fig. 18) by its position in the cladotaxy (formerly called phyllotaxy) and the other as runner apex (S).

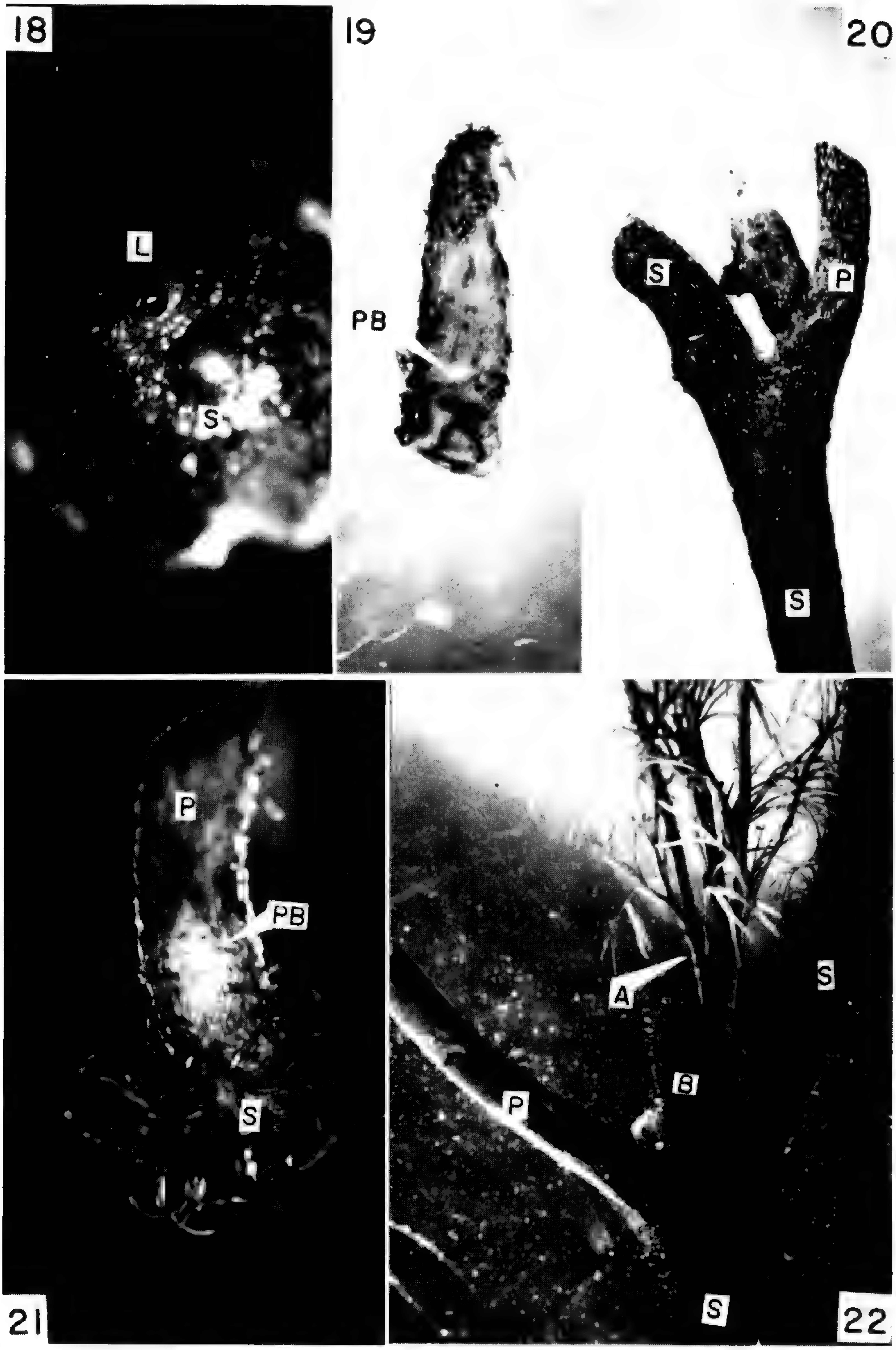
At about this stage, the shape of the future leaf-producing structure changes slightly; it becomes slightly longer in the direction at right angles to the line between it and its sister apex (the new runner apex). The apical cell is still triangular in top view, but one linear prismatic series of cells eminates from it down one of the narrow sides and two down the other. Soon thereafter a single, curved division wall of the apical cell cuts off one of its corners and establishes one cutting face where there were two, and the bilateral apical cell is oriented with its long axis (as viewed from above) directed toward the apex of the running stem.

It is close to this stage when the apex of the future phylliferous structure divides to leave behind an apex on its adaxial side. One such apex is shown situated on the adaxial side of what appears to be petiole of a young leaf in Figure 19 (PB) and on a slightly older structure in Figure 21. In the specimen shown in Figure 20 the seeming epipetiolar bud has grown out and also has produced one root.

The "epipetiolar" bud in *Macroglena*, according to its ontogeny and also by extrapolation of parallel information from other hymenophyllaceous forms, is then considered to be the sister apex of the leaf apex with both structures borne at the tip of a short lateral branch.

The "genera" *Cephalomanes, Selenodesmium, Nesopteris, Callisopteris, Trichomanes* (sens. strict.), and *Feea* (all = *Trichomanes* sens. lat.) have similar leaf-branch relationships. They each have relatively stout upright to tilted stems bearing closely crowded foliar appendages in a spiral order (divergence ca. 120°). They all bear roots and what are seemingly axillary, or near-axillary, buds.

In these forms the stem steles are radially organized protosteles. The trace to what has been called a leaf is similar, and from it the bud trace arises. Petiolar strands become more dorsiventral and therefore more leaf-like in the traditional sense farther up. In those "genera" with thin, creeping stems the information is not comparable. Very delicate forms often have only 1–3 tracheids



FIGURES 18–22.—18–21. *Trichomanes* (*Macroglena*) *meifolium*.—18. The stem apex bifurcated to form a "leaf," L, and a new stem apex, S. × 83.—19. An entire leaf bearing

in the stele. Larger creeping forms mostly show dorsiventral steles throughout their axial systems (see Bower, 1926).

Trichomanes sens. strict. is illustrated in Figures 23–25. One entire plant stock with petioles, roots and hairs removed appears in Figure 23. The axis was overtopped twice (aborted apices at SA) by lateral apices. BP indicates a lateral branch which grew out and later aborted. The tip of the specimen in Figure 23 is shown enlarged in Figure 24. A comparable photograph of another species appears as Figure 25 in which BP designates the lateral buds which are clearly not axillary.

The origin of the buds which appear epipetiolar was observed in *Trichomanes* sens. strict. and in *Feea*. They originate from the leaf apex just as they do in *Macroglena* and just as do the "proliferation" apices in *Gonocormus*. In fact, the same kind of bud origin has been described in *Psilotum*, *Stromatopteris*, *Gleichenia*, and *Actinostachys* (Bierhorst, 1968*b*, 1973).

Buds in similar positions occur in dennstaedtioid genera, but they have been described as originating on the stem (Bierhorst, 1973) and not from the leaf apex. In conjunction with the present studies, several grammitid genera were examined in which buds appear on the sides of the petioles near the base. These also were of stem origin and therefore not comparable.

Vandenboschia (*Trichomanes*) *aphlebioides* differed from the other hymenophyllaceous forms studied. The species has a relatively stout stem which creeps upward on tree trunks. Leaves are borne in subopposite pairs, but leaves of successive pairs are not within the same orthostichy, and the phyllotaxy approaches spirodistichous. In the axil of each leaf (Fig. 22) or commonly above the axil on the stem (S) is a bud (B). Toward the stem on the bud, but slightly out of direct alignment between the stem and the center of the bud, is the aphlebia (A) which has a linear attachment to the bud and is branched in a fan-like manner.

The leaf apex appears much like that of *Macroglena* at an early stage in development. Its apical cell has three cutting faces when young, but soon after the primordium is recognizable as a distinct bump, the apical cell has two cutting faces. The leaf primordium soon comes to be situated down the side of the domeshaped stem apex, but growth of the stem tissue below pushes the primordium upward and changes its orientation so that it becomes reoriented forward and falls on the broad flat end of the stem tip. The bud originates above the leaf primordium on the stem and therefore does not seem to have the same origin as buds in seemingly comparable positions in other hymenophyllaceous forms.

On the flat, distal face of the bud, several cells toward the parental stem from the apical cell of the bud, a single line of cells bulge, divide, and act as a

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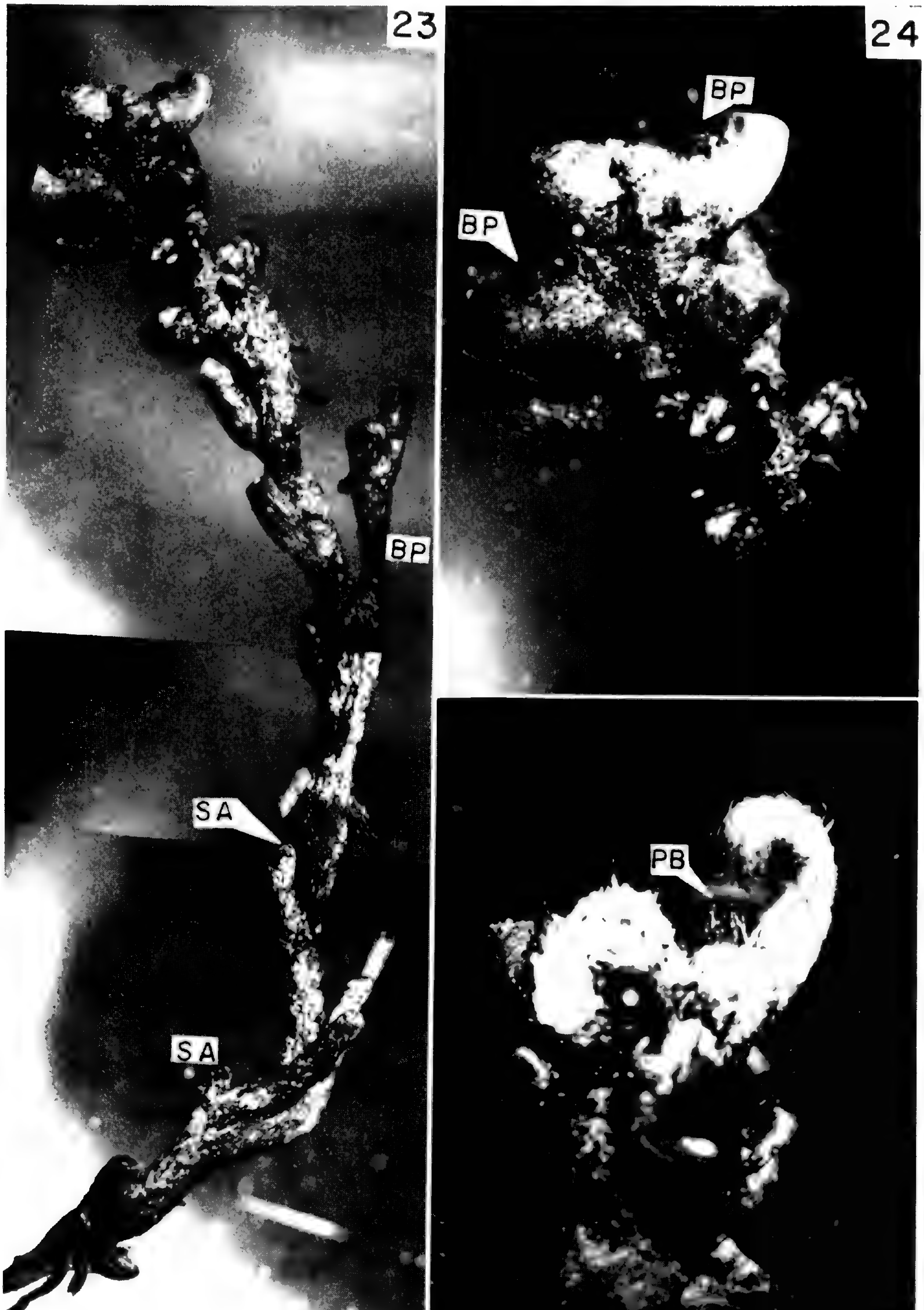
a petiolar apex, PB. × 13.5.—20. A stem, S, bearing a "petiole," P, with a bud. The bud has produced one root. × 10.—21. A stem, S, bearing a petiole, P, upon which is a bud, PB. × 21.—22. *Trichomanes* (*Vandenboschia*) *aphlebioides*. Stem, S, bears branch, B, which produced a leaf, P = its petiole, and an aphlebia, A. × 3.3.



FIGURES 23–25.—23. *Trichomanes* (sens. strict.) sp. Entire stock of one old plant. The apex of the near-vertical stem aborted twice at SA and was overtopped in each case by a lateral

linear meristem. The meristem, oriented circumferentially on the bud, soon divides itself to establish the branches of the aphlebia. This kind of origin would be quite unique among all fern leaves, if the aphlebiae were to be called leaves. Interpretation of aphlebiae in this case requires further information.

The buds of *Vandenboschia aphlebioides* occasionally grow as new running stems, but generally they remain dormant. They produce one or two leaves which originate in a manner similar to those on the runners. Leaves on lateral buds, however, mostly remain arrested in the primordial stage.

Another species of *Vandenboschia* studied was a terrestrial plant with more tufted leaves and without aphlebiae. The stem was essentially short-creeping. Phyllotaxy was similar but less regular and seemed to approach spiral. Buds were distinctly epipetiolar, but insufficient material was available to determine their origin.

Discussion and Conclusions

In discussions of the phylogeny of megaphylls, the following morphological changes are generally enumerated: overtopping, planation, and webbing. These are sufficient to characterize a sequence of mature forms in the general way, but webbing must be referred to the origin of a marginal meristem and the sequence of ontogenies involved in overtopping must be considered. In addition, the order of events, their degree of concomitance and their degree of fixation (therefore their capacity to revert) must be argued *separately* for the various megaphyllous taxa.

When overtopping has reached its ultimate, the overtopped branch truss has been reduced to appendicular status at its very inception. This end point has been reached in all extant seed plants and many ferns in which a leaf primordium is totally distinct from the stem apex upon which it is borne. It is dorsiventral from its inception. Evidence from plants with such leaves has been responsible for the interpretation (Wardlaw's concept) that the fundamental leaf features, *i.e.* the external and histological dorsiventrality, are causally related to the initial subordinance of the leaf primordium (or its presumptive site) to the stem apex and/or the relative positions of the two. The suggestion of Steeves (1963), based in part on Kuenert's work and more recently supported by differences in the protein spectrum between leaf primordia and stem apices and by changes in the spectrum with increasing age of leaf primordia (Caponetti *et al.*, 1972), that specific leaf-determining substances accumulate in a primordium to the point where one of its ontogenetic options is lost is not necessarily in contradiction to the above interpretation.

Those ferns which bear non-appendicular fronds, *i.e.* those which are direct continuations of stems, certainly contradict Wardlaw's concept. If the concept were broadened by suggesting that a primordium developed into a leaf as a

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branch. FG *121*, × 3.—24. Tip of the specimen in Fig. 23. BP = petiolar bud. × 5.6.—25. *Trichomanes* (sens. strict.) *pinnatum*, stem tip. PB = petiolar bud on young leaf. FG *44*, × 9.8.

consequence of its position relative to all other components of the plant body (without specifying any particular geometry such as that exhibited by *Dryopteris aristata* and other species like it), then the scope of the concept, however vague, would embrace the non-appendicular fronds of the Hymenophyllaceae and the Gleicheniaceae, since their geometrical relationships are quite fixed. On the other hand, the irregular, or apparently irregular, interrelationships among parts of the somata in the Psilotaceae and Stromatopteridaceae might seem to contradict.

At this point, it might be desirable to entertain Steeves' suggestion in a context divorced from geometrical considerations. But even then, there remain at least two genera, *Psilotum* and *Gonocormus*, in which leaf determination is never complete and in which the frond apex can cease to produce frond and proceed to produce typical stem.

If specific leaf-determining substances do exist, there are clues as to their possible nature. In a number of primitive ferns in which a leaf primordium is very difficult to distinguish from a stem apex, *i.e.* the Psilotaceae, Stromatopteridaceae, *Actinostachys* (young plants only), and various Hymenophyllaceae, the first indication of the selection of the leaf development pathway is the presence of a distinct region of cell elongation below the now-recognizable leaf apex. In the Stromatopteridaceae, *Actinostachys*, and the Hymenophyllaceae, this occurs before differential growth initiates the circinate coil and may precede the transition from an apical cell with three cutting faces to one with two. Into this is read the possibility that substances involved in cell elongation, auxin and/or gibberlins, may be involved in leaf determination in ferns. If indeed cell elongation factors are involved, they may be of either primary or secondary significance with respect to the protein spectrum changes as described by Caponetti *et al.* in *Osmunda*.

As for those morphological changes involved during the phylogeny of the filicalean frond, the following interpretations are presented. This basically represents a further refinement of the theory of double megaphyll phylogeny as presented by Bierhorst (1971, 1973) so as to embrace new information on the Hymenophyllaceae. Although changes are postulated in a definite sequence, it must be allowed (and expected) that during the phylogenetic history of forms which led up to the extant Filicales the changes were occasionally somewhat out of sequence and all changes were to some extent concomitant. It must also be assumed that, although the longtime trend postulated is unidirectional, there were frequent reversals to somewhat more primitive morphology as has certainly taken place in some extant taxa.

The morphological starting point in this theory is a plant with creeping and upright stems, exhibiting dichotomous branching, but not necessarily symmetrical. Ultimate upright axes were eventually determinate, *i.e.* ceased to grow with mature tissue replacing meristematic tissue. Certain ultimate axes became determinate before others, and their positions were irregular throughout the upright truss. It is assumed before determination that all apical meristems throughout the soma had the same developmental potential. In other words, any apex in the horizontal system could grow into an aerial axis, a lower branch of an aerial axis if close to the substratum could grow into a horizontal stem, or an apex high in the aerial system if accidentally buried could revert to a horizontal stem. It is also assumed that all dichotomies were not necessarily equal at their inception. The starting point conforms in general to a rhyniophyte, although, of course, attribution of developmental potentials of apical meristems represents an extrapolation of information from extant ferns.

It is postulated that lamina formation began very early from plants such as the indicated starting point. Such an increase in photosynthetic surface has occurred in all vascular plant lines and in the same manner: by the introduction of a linear meristem. In ferns and fern-like plants and, in particular, in the Filicales, linear meristems of leaves are derived ontogenetically by modifications of radially symmetrical apical meristems. It is assumed that linear meristems which produced some laminar tissue appeared at the tips of ultimate units in a dichotomous truss before (or along with) any other major morphological (phylogenetic) changes occurred and at a relatively late stage in ontogeny before determination.

(The tendency of ultimate determination of branch units as well as linear meristem formation may well have preceded vascular plant origin and therefore represent ancestral algal characters.)

In that line which led ultimately to the Filicales planation is interpreted to have begun in some of the minor branch trusses of an aerial or more or less upright system, at first better expressed near distal ends and later (phylogenetically) more proximally. The orientation of the planated trusses must have been coplanar throughout an entire upright aerial branch system.

Linear meristem activity is interpreted to have been expressed progressively earlier in the ontogeny of subtrusses of the major aerial systems. When this is expressed before a final division of an apical meristem, as in the extant ferns, the result is webbing of ultimate units and establishment of multiveined ultimate laminar units.

A monopodium with pinnate branching (at first a pseudomonopodium or dichopodium) is assumed to have been established early within the major aerial truss which now might be called a pre-frond. Among extant Filicales pinnate branching and dichotomous branching completely intergrade, and therefore the feature at least in many genera is not yet fixed. The entire sequence of ontogenetic intermediates exists in two genera, *Schizaea* and *Gleichenia*, and the author suspects *Lygodium*. In *Gleichenia* the series seems to be best read from pinnate to dichotomous and is expressed in the first one or two ramifications of the frond. Clearly pseudodichotomous (= pinnate) branching occurs where the frond apex ceases to grow and is overtopped by two pinnae from below. In this case there is a clear remnant of the frond apex with or without several arrested pinnae in the fork of the seeming dichotomy. In other cases in *Gleichenia*, however, the overtopping pinnae are much more precocious, and a series could be shown in which they develop closer and closer to the apex of the frond. The end point is a true ontogenetic dichotomy.

In *Schizaea dichotoma* the leaf at maturity appears equally dichotomous. Ontogenetically, however, a complete series exists between dichotomy and clearly lateral branching. Apical cells of new frond branches originate as sister cells of other apical cells (= true ontogenetic dichotomy) or from one to 7 cell generations removed from another apical cell.

In the apparently equally dichotomous frond ("aerial shoot") of *Psilotum nudum*, the lower set of bifurcations are pseudodichotomies of the *Gleichenia* type in which the new apical cells arise lateral to another apical cell which ceases to function. In the ontogeny of the more distal "dichotomies" of *P. nudum*, the apex of the trunk below continues while the second limb of an apparent dichotomy develops from a lateral primordium (Roth, 1963).

It can be postulated that cladotaxy, *i.e.* the fixed arrangement of prepinnae upon a prerachis (or prepinnules upon a prerachule as the order of branching dictates), occurred early in the phylogenetic history of the Filicales and that this branching character was also expressed in the insertions of prefronds upon running stems and even running stems upon running stems but in no case to the exclusion of equal apical branching. In various lines within the Filicales, then, one or another branching pattern may predominate or be exclusively expressed. The major reason for extending the branching trend to the entire soma rather than restricting it to prefronds lies in the fact that this is essentially the state which exists in most of the extant, primitive Filicales. If, however, one adheres to Bower's interpretation that an upright stem with spiral phyllotaxy is primitive within the Filicales then there is an apparent contradiction. Bower's interpretation, however, stems from another interpretation that the Osmundaceae forms the main phylogenetic trunk of the Filicales, but since his ideas were published much new information has been assembled all indicating that the Osmundaceae essentially stand alone and may well have been independently derived from all other Filicales.

The phylogenetic process of megaphyllization (planation plus webbing) is assumed to have worked its way from the more distal minor trusses of an aerial stem system toward the major trunks of the system and progressed toward the horizontal stem. Or in other words, modifications in meristems are assumed to have taken place earlier and earlier in the ontogeny of the prefrond. The first foliarized units of the prefrond were then the pinnae, and they are considered megaphylls of one order.

The entire frond (or prefrond) at this point has not evolved to the state of the leaf in any strict definition which one would like to impose. This is essentially the state at which it still exists in several extant filicalean genera. Such a frond arises directly from an apex which has stem-like organization, *e.g. Psilotum, Tmesipteris, Stromatopteris, Gleichenia, Actinostachys, Osmunda*, and a number of Hymenophyllaceae. This apex may be lateral in position, falling within a more or less fixed cladotaxy, *e.g. Stromatopteris* (young plants only), *Gleichenia, Actinostachys*, and Hymenophyllaceae, or it may be terminal on a longer creeping stem, *e.g. Psilotum, Tmesipteris*, and several Hymenophyllaceae. The stem or stem-like apex which develops into the frond may do so directly or it may dichotomize one or more times to leave behind apices with various developmental potentials before it finally commits itself to a frond developmental pathway. The final dichotomy of the phylliferous branch apex or frond apex

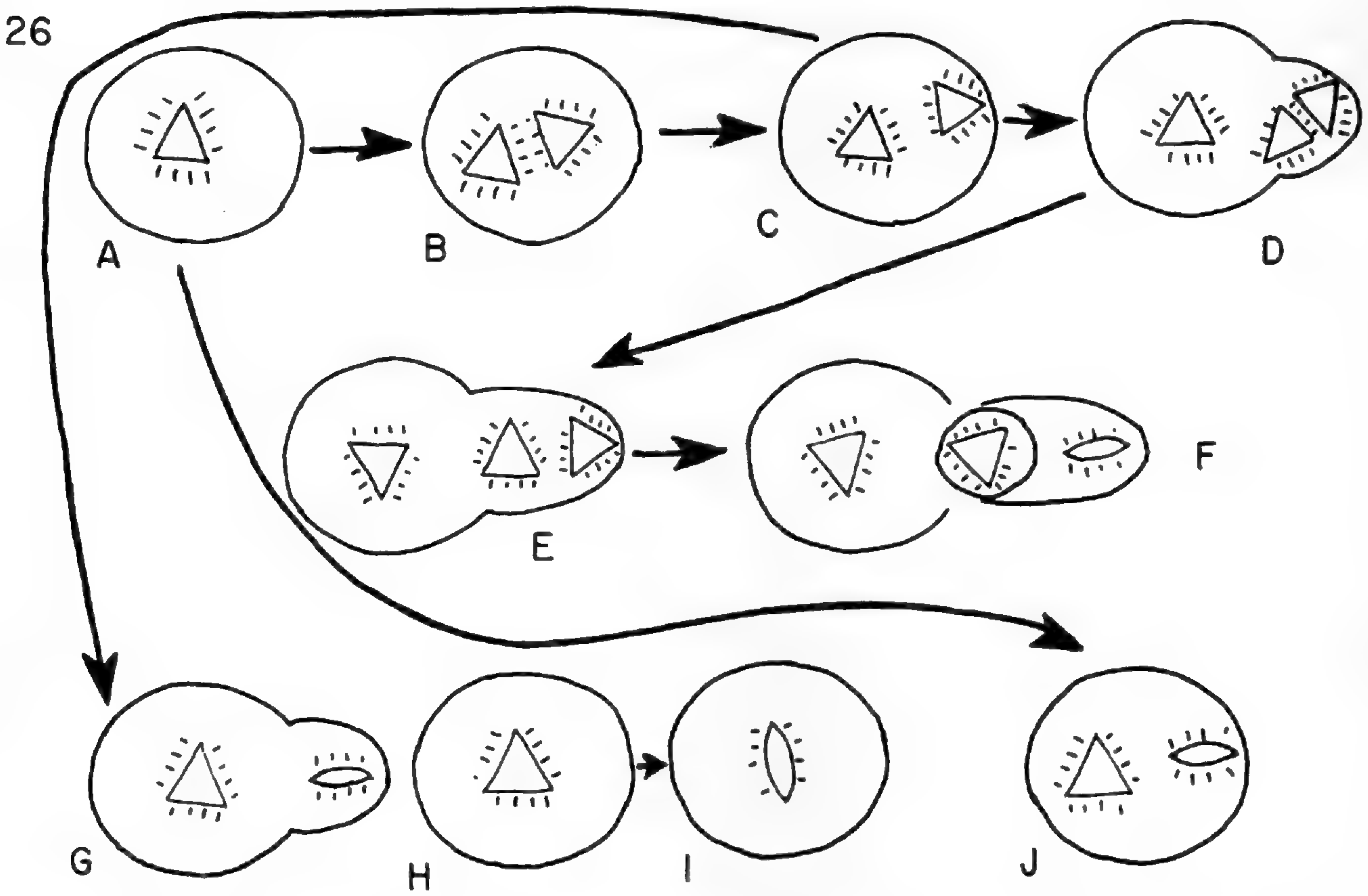

Figure 26. Diagrams showing certain aspects of frond ontogeny in various ferns. Explanation in text.

(the designation here is subjective) may result in a bud which is pseudoaxillary (*Stromatopteris*, *Gleichenia*, some Hymenophyllaceae) or apparently quite epipetiolar (*Actinostachys*, *Psilotum*, *Stromatopteris*, some Hymenophyllaceae). In at least two genera, *Psilotum* and *Gonocormus* (*Trichomanes*), a series of such buds may be produced. (Occasional proliferation apices reported in *Trichomanes* sens. strict. and *Feea* may be of the same nature, but their ontogenetic origin is not known). It is significant also that in several of these genera, an apex in a definite position in the plant body which would ordinarily be expected to develop into a frond occasionally develops into a running stem (*Psilotum*, *Gonocormus*, and *Stromatopteris*). It is also of significance that in those genera which seem to produce incompletely appendicularized fronds, as evidenced by their terminal positions on recognizable branches or by the occurrence of a basal branch derived from the sister apex of the frond apex, generally express classical radial stem anatomy at least in part within their fronds.

The final stages in appendicularization as they exist within the extant Filicales might be illustrated as in Figure 26, which depicts diagrammatically several types of ontogenetic sequences in frond formation. The various sequences in each case begin with a stem apex with an apical cell with three cutting faces and exhibiting more or less symmetrical growth (A or H). (Please allow for the fact that certain filiform stems of the Hymenophyllaceae do not bear a single apical cell.) A lens-shaped apical cell represents both it and the linear prismatic series emanating from its two cutting faces or just a linear meristem in those cases where an apical cell is not present or not recognizable.

The end point, *i.e.* the most specialized state, in appendicularization (A and J) has been reached when the leaf meristem originates from a lens-shaped apical cell upon the dome of the stem apex. The primordium is thus bilateral and dorsiventral from its inception. This is apparently the condition which exists in most filicalean ferns insofar as is known.

Less specialized is the sequence illustrated by A, B, C, and G in which the leaf primordium at first shows an apical cell with 3 cutting faces and then shifts to one with two. This occurs in some species of *Actinostachys*, *Gleichenia*, and *Osmunda*. In the first two of these, the apical transformation occurs early in the life of the frond. In *Osmunda* it may be early or in one species not until just before the terminal pinna is formed.

Sequence A, B, C, D, E, and F represents an ontogenetic sequence of a still less appendicularized frond, *i.e.* more primitive. Two new apical cells both with 3 cutting faces are formed (B), one becomes lateral in position (C), it divides and two similar ones are formed (D) (this division plane is variable), one of these shifts over to the leaf type (far right in F). This type of sequence appears in *Stromatopteris*, at least two species of *Actinostachys*, at least two species of *Gleichenia*, and in several Hymenophyllaceae. In *Gonocormus* the divisions may be repeated in the formation of the "proliferations." Also, the morphological unit composed of the two apices on the right in F may occasionally develop directly from an individual apex of a long stem (*Stromatopteris* and some Hymenophyllaceae).

Series H and I (or A and I) represents the condition where the frond develops directly from the apex of a long stem. This occurs in *Psilotum*, although the apical cell remains triangular throughout the growth of the frond, and in *Tmesipteris* where the apex also remains radially symmetrical but only until just before the terminal pinna is formed. Also in *Psilotum*, the frond apex frequently leaves behind one to 10 small, apparently lateral apices near its base in a manner considered equivalent to the branching in D, E, and F.

LITERATURE CITED

BIERHORST, D. W. 1968*a*. Observations on *Schizaea* and *Actinostachys* spp., including *A. oligostachys*, sp. nov. Amer. Jour. Bot. 55: 87–108.

———. 1968*b*. On the Stromatopteridaceae (fam. nov.) and the Psilotaceae. Phytomorphology 18: 232–268.

———. 1971. Morphology of Vascular Plants. New York.

———. 1973. Non-appendicular fronds in the Filicales. Bot. Jour. Linn. Soc. 67(Suppl.): 45–57.

BOWER, F. O. 1926. The Ferns. Vol. 2. London.

CAPONETTI, J. D., W. H. HARVEY & A. E. DEMAGGIO. 1972. Changes in soluble proteins of cinnamon fern leaves during development. Canad. Jour. Bot. 50: 1479–1483.

COPELAND, E. B. 1933. *Trichomanes*. Philippine Jour. Sci. 51: 119–280.

ROTH, I. 1963. Histogenese der Luftsprosse und Bildung der "dichotomen" Verzweigungen von *Psilotum nudum*. Advancing Frontiers Pl. Sci. 7: 157–180.

STEEVES, T. A. 1963. Morphogenetic studies of fern leaves. Bot. Jour. Linn. Soc. 58: 401–415.

SYKES, M. G. 1908. The anatomy and morphology of *Tmesipteris*. Ann. Bot. (London) 22: 63–89.

EVOLUTION OF VEGETATIVE MORPHOLOGY IN COENOPTERID FERNS[1]

Tom L. Phillips[2]

Abstract

Salient features of the vegetative morphology of *Clepsydropsis, Dineuron, Metadineuron, Diplolabis, Metaclepsydropsis, Zygopteris, Ankyropteris, Psalixochlaena, Tubicaulis, Anachoropteris, Apotropteris, Grammatopteris, Catenopteris,* and *Botryopteris* are summarized. Trends in xylary evolution include examples of tracheidal zonation of solid protosteles (*Diplolabis, Grammatopteris*), increased parenchymatization of vitalized protosteles (*Tubicaulis, Zygopteris*), siphonostely with and without leaf gaps (*Botryopteris, Anachoropteris,* and *Apotropteris*), and secondary xylem (*Zygopteris*). Simple scalariform thickenings and multiseriate scalariform bordered pitting are primitive types. A distinction in foliar and cauline anatomy occurs in the earliest well known representatives of each of the coenopterid families. Branching is dichotomous (Etapteroideae), axillary (*Ankryopteris* species), lateral (*Psalixachlaena*), and effected by shoots on fronds (*Anachoropteris, Botryopteris*). Circinate vernation, pinnate and planated frond divisions, and laminate pinnules occur in each family including form genera *Pecopteris, Sphenopteris,* and *Alloiopteris*. Vegetative morphology supports recognition of coenopterids as true ferns.

Considerations of the evolutionary changes and the significance of coenopterid ferns based on vegetative morphology are indicative of our general knowledge of coenopterids—incomplete, limited in scope, and changing. An excellent review by Eggert (1964) and a comprehensive treatment of genera of the Coenopteridales by Andrews and Bureau (1970) give an overview of the diversity and familial groups of coenopterid ferns. In this paper additional observations from more recent studies on vegetative morphology are integrated with the objectives of stressing the evolution of stelar and frond morphology, particularly branching, and to suggest that vegetative genera within the Botryopteridaceae, Anachoropteridaceae, and allied genera such as *Catenopteris* are the Paleophytic representatives of true ferns and the ancestral complex for some filicalean families. More importantly, in the context of this symposium is the objective of summarizing the salient features of vegetative fern morphology of these late Paleozoic ferns, regardless of their eventual taxonomic dispositions.

Discussions of stelar evolution and frond morphology are naturally centered on better known species of *Zygopteris, Ankyropteris, Anachoropteris,* and *Botryopteris* which provide insight for interpretations of other taxa; the mixed natural and artificial assemblages allied with these genera provide a variable basis for evolutionary suppositions, but such family groupings do bring together similar vegetative morphologies, at least to the extent that they are known. Assignments of most coenopterid genera to families based on foliar anatomy are

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tentative at best as is treatment of a partially known Paleozoic plant as a particular type of coenopterid fern.

Coenopterids *are*, for the most part, *ferns* which span the late Devonian through Permian time between the recognizable beginnings of fern-like morphology and the earliest-appearing extant filicalean familes (Gleicheniaceae and Osmundaceae). The tendency to assign fern-like Devonian plants as well as problematic genera such as *Stauropteris* and *Rhabdoxylon* to the Coenopteridales should not obscure the basic fern characters of the coenopterids as a whole. When Seward (1910) proposed recognition of the Coenopterideae for apparently generalized (common) Paleozoic ferns which differed from existing genera of the Filicales (and from the Marattiales), the recognition of Paleozoic pteridosperms was at hand, and real doubt existed concerning identification of the true ferns of the Carboniferous.

Each of the higher taxa represented by *Zygopteris*, *Ankyropteris*, *Botryopteris* and *Anachoropteris*, respectively, extend into the Permian. The earliest stratigraphic appearances of zygopterid ferns are probably the isolated phyllophores of *Clepsydropsis* in the Upper Devonian of Thuringia (East Germany), and genera considered here include the Mississippian *Metaclepsydropsis*, *Diplolabis*, *Clepsydropsis*, *Metadineuron*, and *Dineuron* and the Pennsylvanian-Permian *Zygopteris* assemblages. The Botryopteridaceae include *Botryopteris* with ten species; the oldest is *B. antiqua* from the Visean (Mississippian) of Scotland and France. The earliest appearance of the Anachoropteridaceae is the Westphalian A of western Europe. Among the vegetative genera considered here in the Anachoropteridaceae are *Psalixochlaena*, *Anachoropteris*, *Tubicaulis*, and *Apotropteris*. *Ankyropteris*, *Grammatopteris*, and *Catenopteris* are also discussed.

In general, the Mississippian Period seems to have been the most formative period of coenopterid vegetative evolution and diversification. Such an interpretation is based largely on the comparative morphology of Visean forms with those from the lower Westphalian A (Great Coal-Ball Horizon) of western Europe. The zygopterids with earlier geologic occurrences in the Devonian and early Mississippian seem to have evolved a specialized frond morphology and vitalized protosteles early in the Mississippian. By contrast, the Botryopteridaceae represented only by the Visean age *Botryopteris antiqua* and a species of *Grammatopteris* (*G. bertrandii*) described by Corsin (1937) from France are contemporaries with diverse zygopterid genera; by early Westphalian A time there are distinct phyletic lines of *Botryopteris*, several morphological lines of *Anachoropteris* and *Tubicaulis*, and numerous other coenopterid genera. The time gap between known Visean ferns and those of the Westphalian A apparently presents a major hiatus in the evolution of laminate foliage in coenopterids. Considerable diversification of coenopterids occurred in late Mississippian and early Pennsylvanian times, continuing into the middle Pennsylvanian. Additional genera appear in the Upper Pennsylvanian (Stephanian).

FERN MORPHOLOGY

Coenopterids are, with some exceptions, true ferns with megaphyllous leaves, foliar-borne sporangia, adventitious root systems, and circinate vernation. Cauline anatomy is typically protostelic with the occurrence of a siphonostele as early as the Westphalian A–B boundary and with several siphonostelic forms in the Middle and Upper Pennsylvanian. Secondary xylem occurs in *Zygopteris* (Dennis, 1972). Roots are typically diarch. Uniseriate multicellular hairs occur in all groups, and zygopterid ferns exhibit branched, vascularized, flattened appendages called aphlebiae on stems and/or fronds and in some cases prominent scales or long spine-like hairs. Foliar members have bilateral symmetry (with a second lateral plane of symmetry in zygopterid phyllophores); laminate foliage is probably the rule rather than the exception in Pennsylvanian time, and the evolutionary development of laminate foliage probably had occurred in all such groups by early to middle Pennsylvanian time. Circinate vernation occurs in each of the basic frond types (anachoropterid, botryopterid, and zygopterid).

Several vegetative features have characterized the coenopterids as primitive and/or different from modern ferns and have somewhat confusedly become part of the traditional concept of coenopterids in general. These are the supposed lack of distinction between stem and frond, the peculiar geometrical shapes of and/or orientations of petiolar traces (foliar xylem), and the multiseriate scalariform to elliptical and circular bordered pitting.

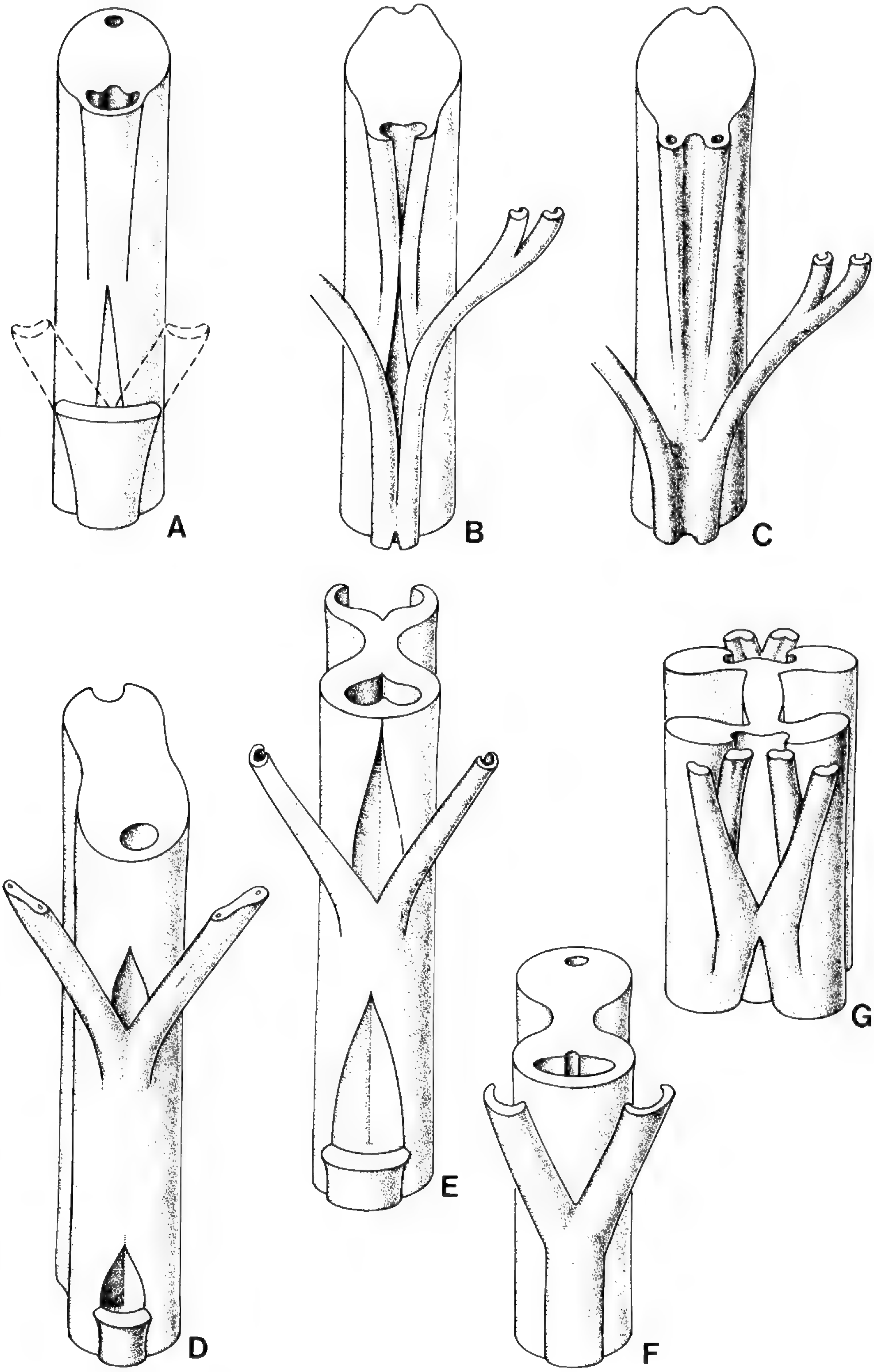
At this point the heterogeneity of coenopterids must be emphasized because the frond morphology differs markedly between zygopterid-types and those of the Botryopteridaceae and Anachoropteridaceae. The last two families seem to embody the generalized vegetative anatomy (and sporangial morphology) to consider seriously as filicalean; the zygopterid ferns constitute the largest group and for the most part seem to become quite specialized and sufficiently distinct as to warrant recognition at the ordinal level.

ANATOMY OF FOLIAR MEMBERS

The systematic use of cross-sectional foliar (non-laminate) anatomy led to initial grouping of most coenopterids into families and lower ranks, because foliar members are the common anatomically identifiable portions. Emphasis on anatomy retarded the recognition of coenopterid compressions, although numerous fertile compressions of zygopterids have been identified by means of sporangial morphology (also see Nemejc, 1936).

The basic C-shaped configuration of cross-sectional foliar xylem characterizes most ferns, with an adaxial opening in the C in practically all ferns except those of the Anachoropteridaceae in which the C is inverted (inversicatenalean). Consequently, a variety of inversicatenalean forms have been grouped with *Anachoropteris* to form the Anachoropteridaceae. The protoxylary groups of such foliar strands are adaxial and/or lateral as in catenalean types, and too much emphasis has been placed simply on inverted vascular configurations. The *Anachoropteris-Tubicaulis* complex of species seems to share numerous vegetative similarities with *Botryopteris*, and whether these reflect parallel or convergent evolution is not clear.

The Botryopteridaceae evolved the basic C-shaped foliar xylem, oriented as in modern ferns (catenalean), with an attached median xylary arm effecting an omega cross-sectional shape in several species of *Botryopteris*. Since the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monotypic Botryopteridaceae are the only family of coenopterid ferns with catenalean petiolar xylary configurations, similar C-shaped foliar types may be added to the family, such as *Catenopteris simplex*, but genera such as *Grammatopteris* and *Catenopteris* are treated herein as a separate artificial group.

ZYGOPTERIDACEAE

Significant recent studies have been completed on the vegetative morphology of zygopterid ferns from the Lower Carboniferous of France (Galtier, 1963, 1964, 1966*a*, *b*, 1970), from the Pennsylvanian of the U.S.A. (Dennis, 1972), and from the Lower Permian of East Germany (Barthel, 1968, 1970). These contributions have been emphasized in the discussion of vegetative morphology.

The zygopterid ferns include considerable diversity of form, and because of the paucity of stems among the late Devonian and Mississippian genera, the anatomy and branching of foliar members have been used to subdivide the family. The rachis of zygopterid ferns is commonly referred to as a phyllophore (Fig. 1), emphasizing its different anatomy from the typical C-shaped vascular strand of ferns and its somewhat axial relationship to the pinnae and their adaxial orientation toward it. Phyllophores exhibit lateral parenchymatous zones (peripheral loops) adjacent to protoxylem. Peripheral loops (Fig. 7) are entirely or partially surrounded by xylem. Pinna traces depart from the lateral xylary areas of peripheral loops as ring-shaped or crescent-shaped strands (Figs. 5, 8) which in turn have lateral traces (Fig. 6). Two frond morphologies separate the Clepsydroideae and Etapteroideae. Phyllophore xylem of the Clepsydroideae is typically hour-glass–shaped in cross-section and bears a row of alternating pinnae on each side; peripheral loops remain closed (permanent) in pinna formation, and metaxylem tracheids of members exhibit simple scalariform pitting. In the Etapteroideae phyllophore xylem strands range in cross-sectional shape from the simple ellipsoidal forms, *Metadineuron* and *Dineuron* (Figs. 1A–C, 2, 3), to the clepsydroid outlines of *Diplolabis* and *Metaclepsydropsis* (Fig. 1E–F, 5, 7). The H-shape of *Etapteris* (Fig. 1G, 9–10) relates geometrically as a bar with adaxial and abaxial arms or antennae which constitute a radial expansion from a clepsydroid configuration, without increase in size of the peripheral loops. Phyllophores of the Etapteroideae have temporary peripheral loops with extensive openings at pinna emission; fronds are quadriseriate with two rows of laterally borne pinnae on each side. Pinna emission usually involves a common trace at some stage of each pinna-pair, and traces show C-shaped curvature. Metaxylem tracheids have multiseriate scalariform or circular bordered pitting.

Further branching of zygopterid fronds is not well documented anatomically,

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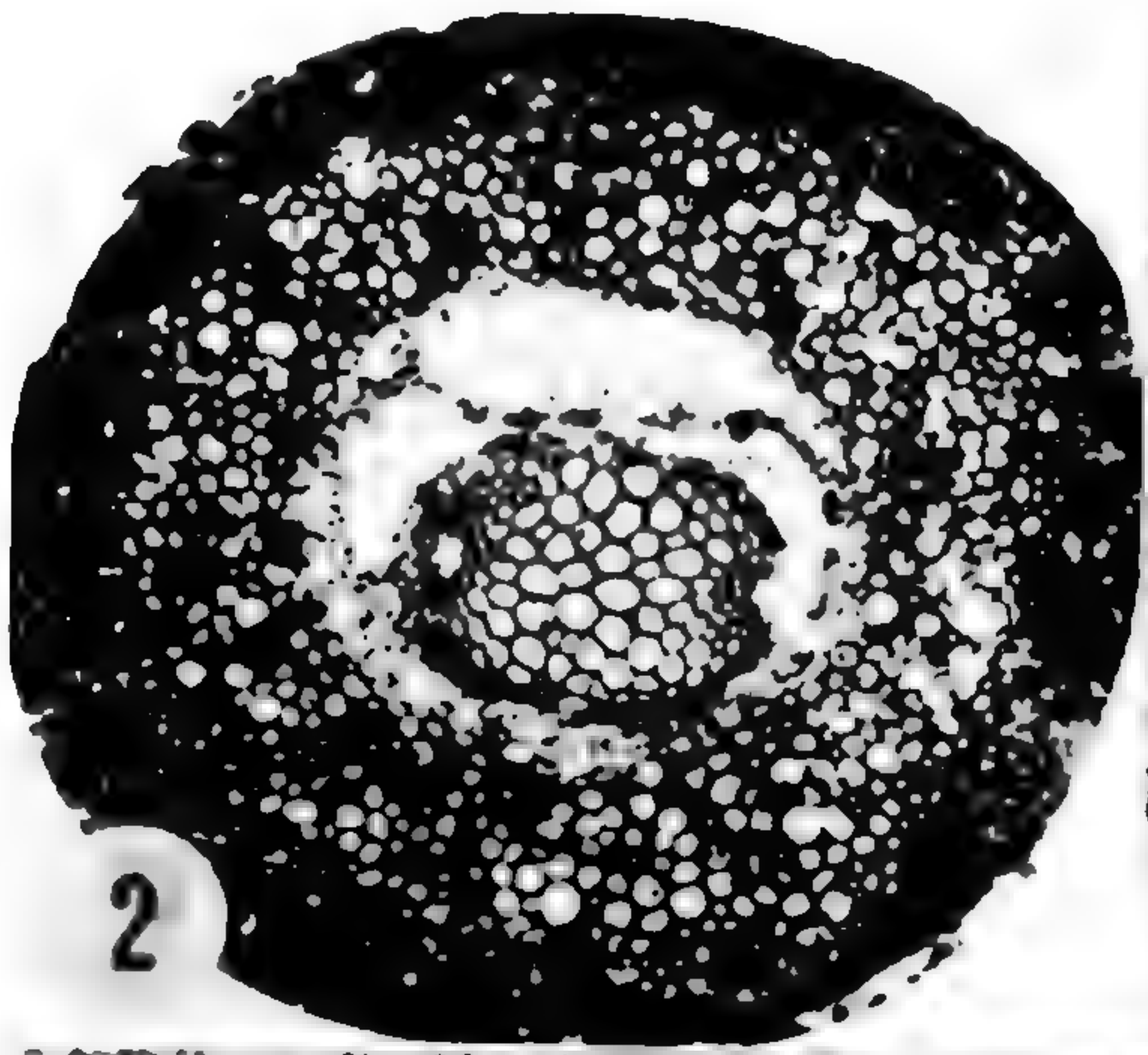
FIGURE 1. Xylary reconstructions of phyllophore (rachis) branching in "zygopterid" ferns.—A. *Metadineuron ellipticum*.—B–C. *Dineuron pteroides* alpha and beta (A–C redrawn from Galtier, 1964).—D. *Rhacophyton zygopteroides* (redrawn from Leclercq, 1951).—E. *Diplolabis roemeri*.—F. *Metaclepsydropsis duplex*.—G. *Etapteris scottii* (E–G redrawn from Posthumus, 1924).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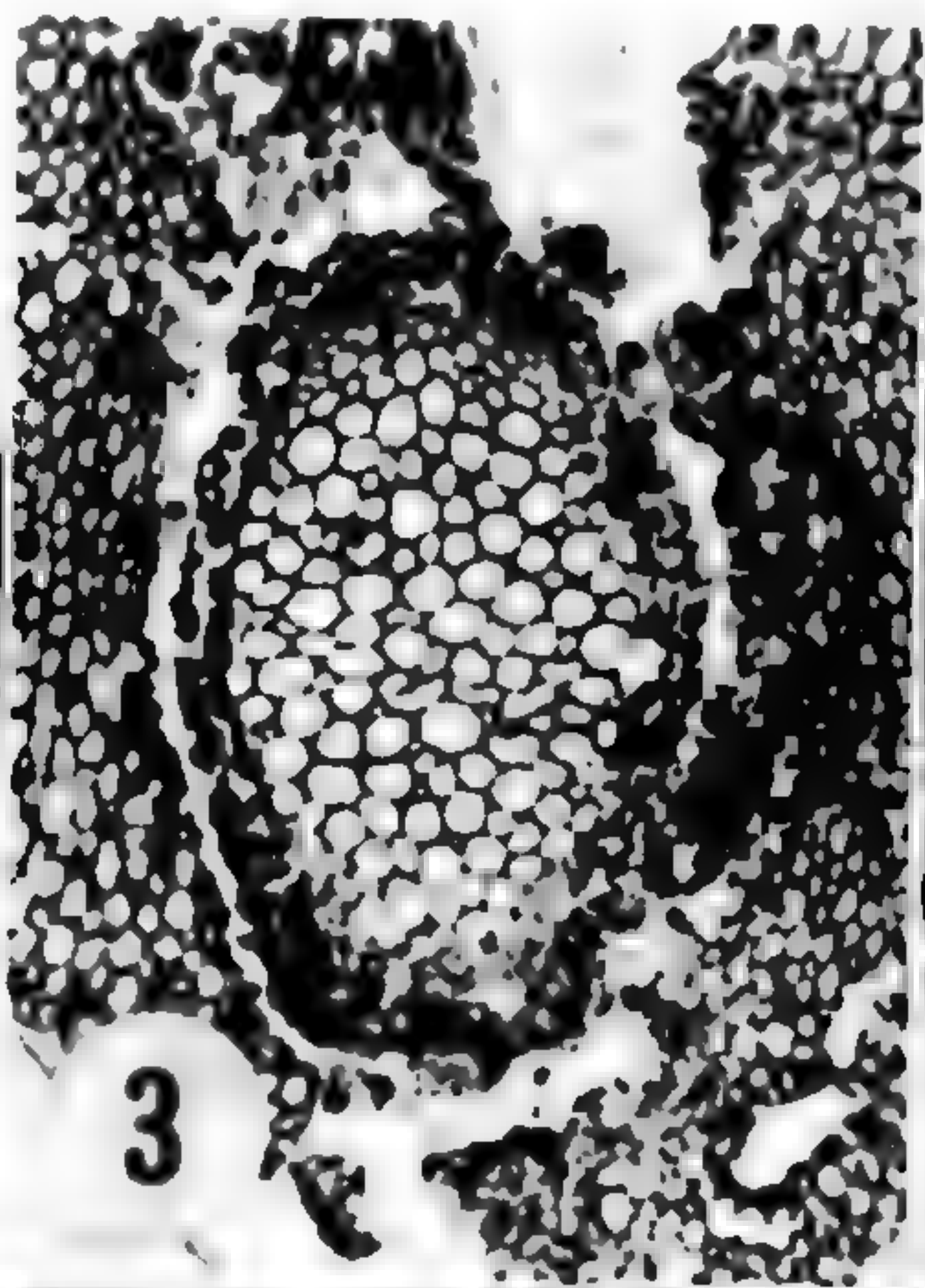
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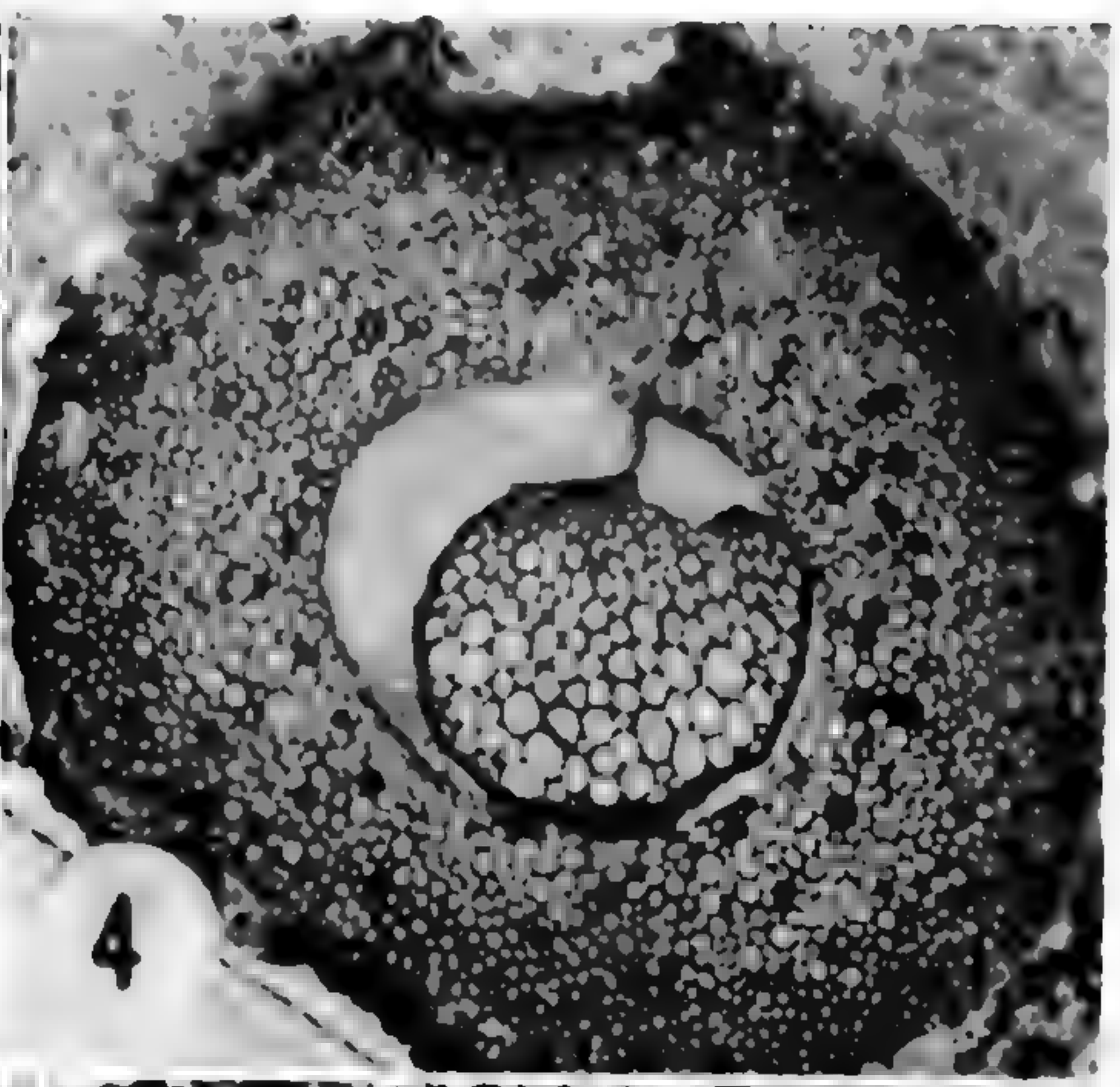
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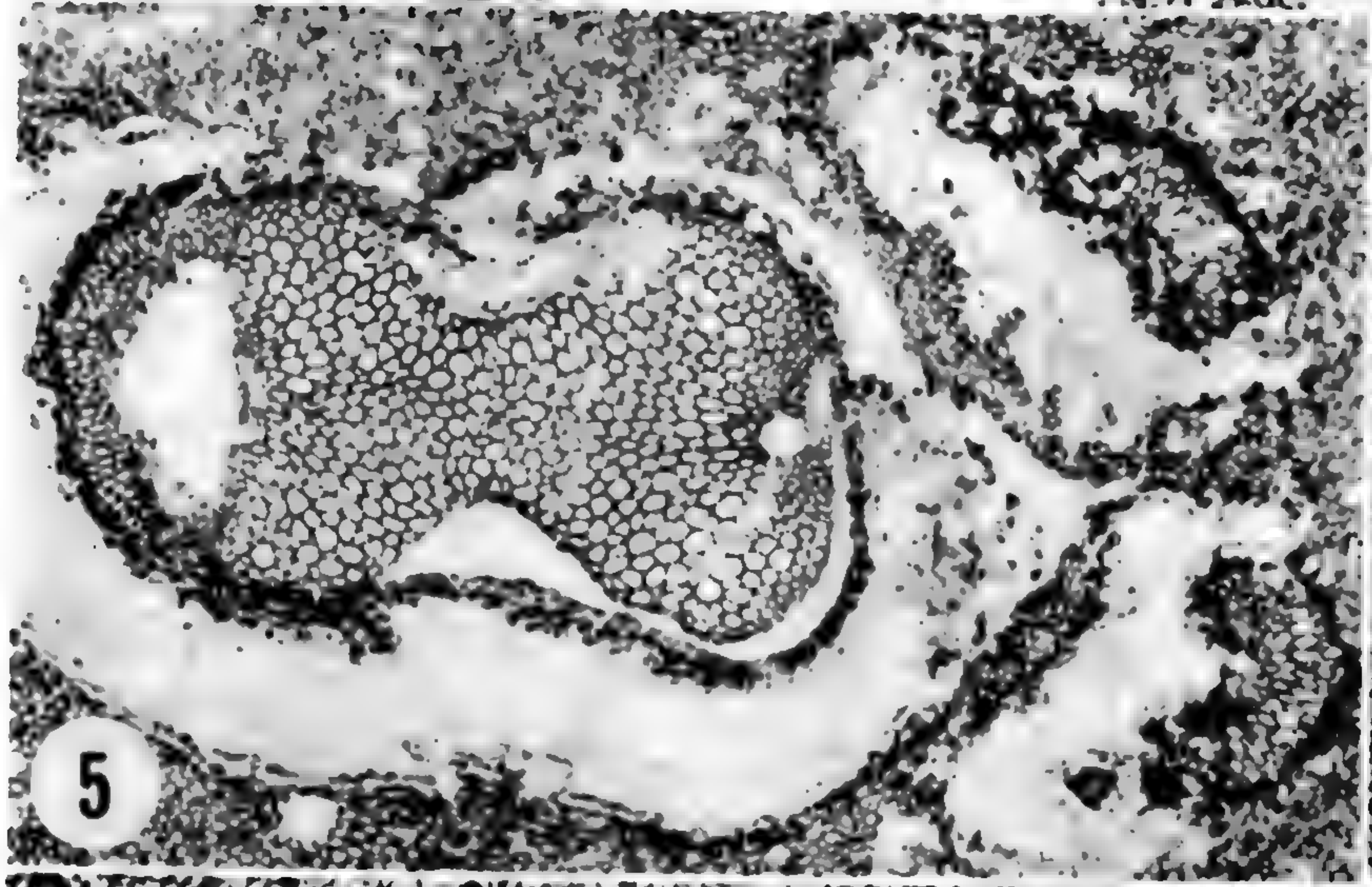
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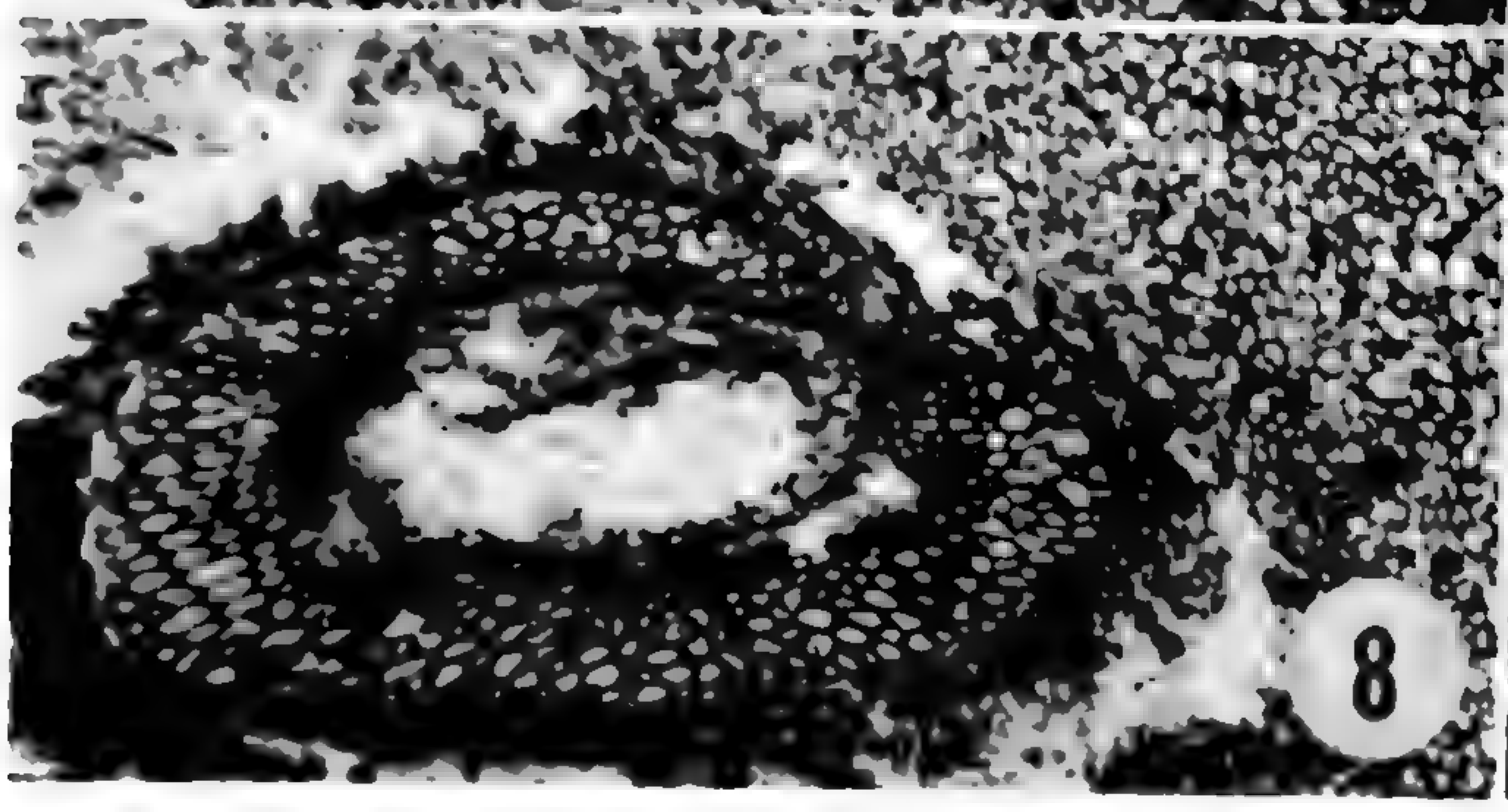
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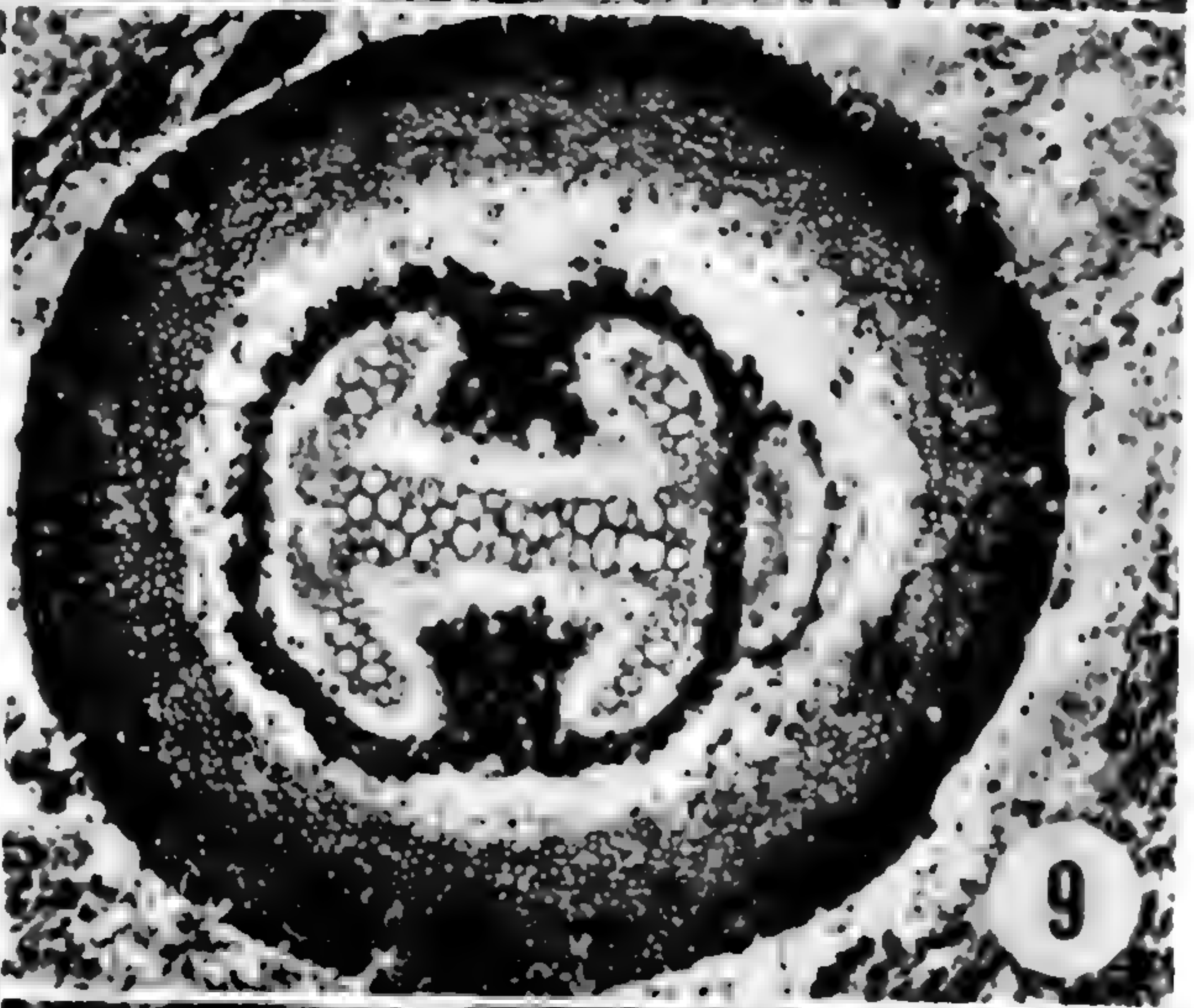
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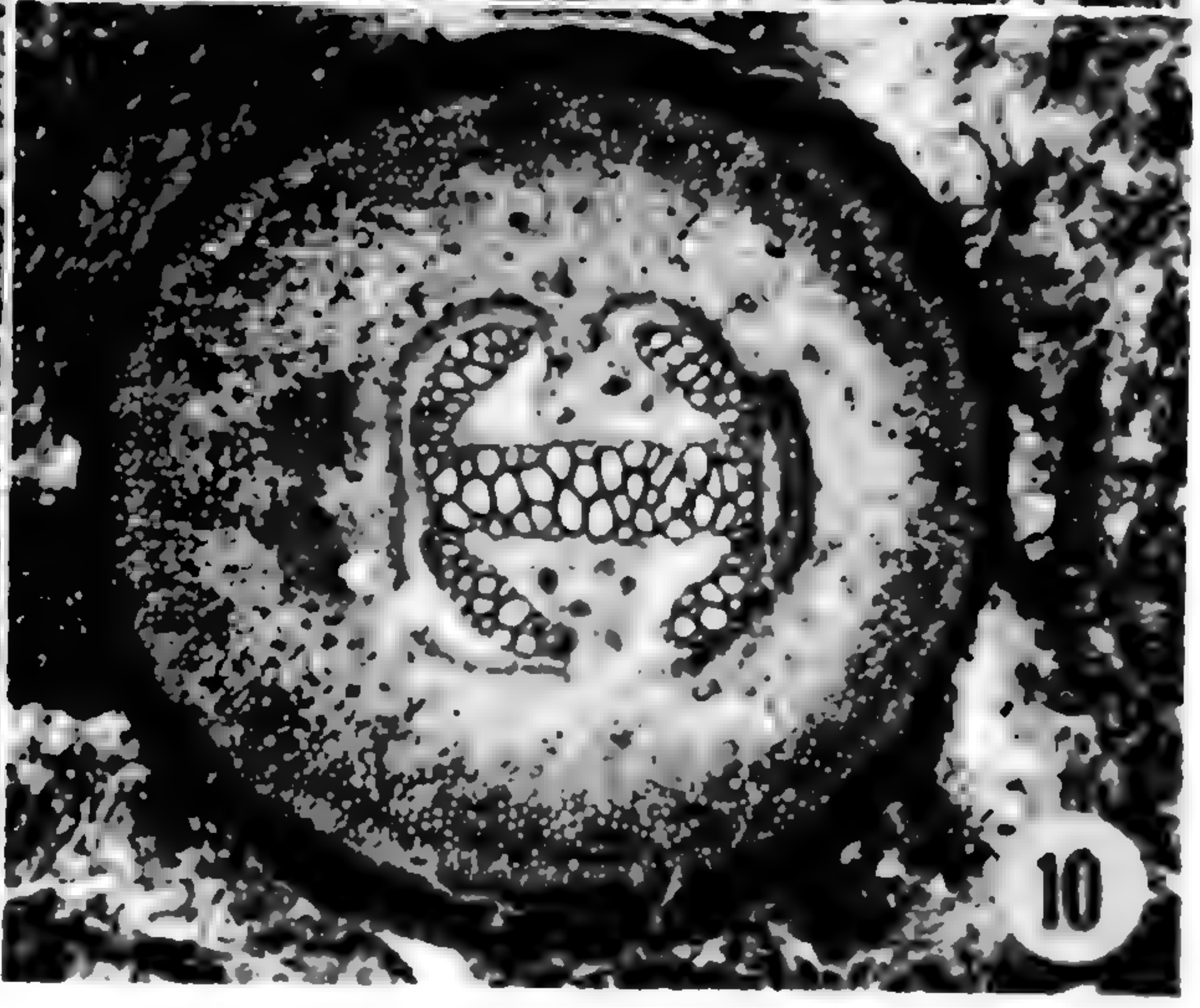
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but fertile pinna anatomy in *Biscalitheca* (Phillips & Andrews, 1968), *Notoschizaea* (*Alloiopteris*) (Fig. 21) and compression foliage of *Nemejcopteris* indicate that pinnate, biseriate divisions occurred in the more distal portions of etapteroid fronds and laminate pinnules were present in Pennsylvanian and Permian age representatives (Barthel, 1968; Nemejc, 1936).

CLEPSYDROIDEAE

The supposed evolutionary relationship between the late Devonian and early Mississippian *Clepsydropsis* forms and the Etapteroideae has been "primitive" and "derived" with considerable speculation regarding evolutionary changes of phyllophores and pinna emission (Sahni, 1918; Leclercq, 1931). In a more recent study of *Clepsydropsis* Galtier (1966*b*) has summarized anatomical details of eleven species, most of which have closed pinna traces and are typically biseriate. A newly described species, *C. leclercqii* from the lower Visean of France, may be regarded as an intermediate or transitional form between the Clepsydroideae and Etapteroideae with clepsydroid xylem, permanent peripheral loops, crescent-shaped pinna traces, and quadriseriate with quite a long undivided pinna trace below the dichotomy to a pinna-pair. The clepsydroid phyllophore xylem strand is 8 × 2 mm long with scalariform metaxylem and a massive pinna trace which extends more than 5 cm prior to division into a pair of shallow C-shaped xylem strands. *Rhacophyton* (Fig. 1D) has been considered to have another intermediate type of phyllophore anatomy between clepsydroid and etapteroid type fronds (Leclercq, 1951, 1954; Andrews & Phillips, 1968), with clepsydroid phyllophore vascular strands, secondary xylem, an opening in the peripheral loop with pinna emission, and both biseriate sterile and quadriseriate fertile pinnae. The pinnae derived from the phyllophore of zygopterid ferns exhibit xylary anatomy different from that of the phyllophore, but in *Rhacophyton* the clepsydroid phyllophore anatomy is repeated in the pinnae. It is interesting to note that such speculative evolutionary intermediates as *Rhacophyton* have secondary xylem present in the presumed phyllophores. *Clepsydropsis* is an organ genus of foliar members without stems, but the petioles of *Asterochlaenopsis* and *Austroclepsis* were assigned to *Clepsydropsis* by Sahni at one time.

ETAPTEROIDEAE

Within the Etapteroideae are both small and massive phyllophores (Figs. 1A–C, E–G) and some of the largest coenopterid ferns. *Metadineuron* and

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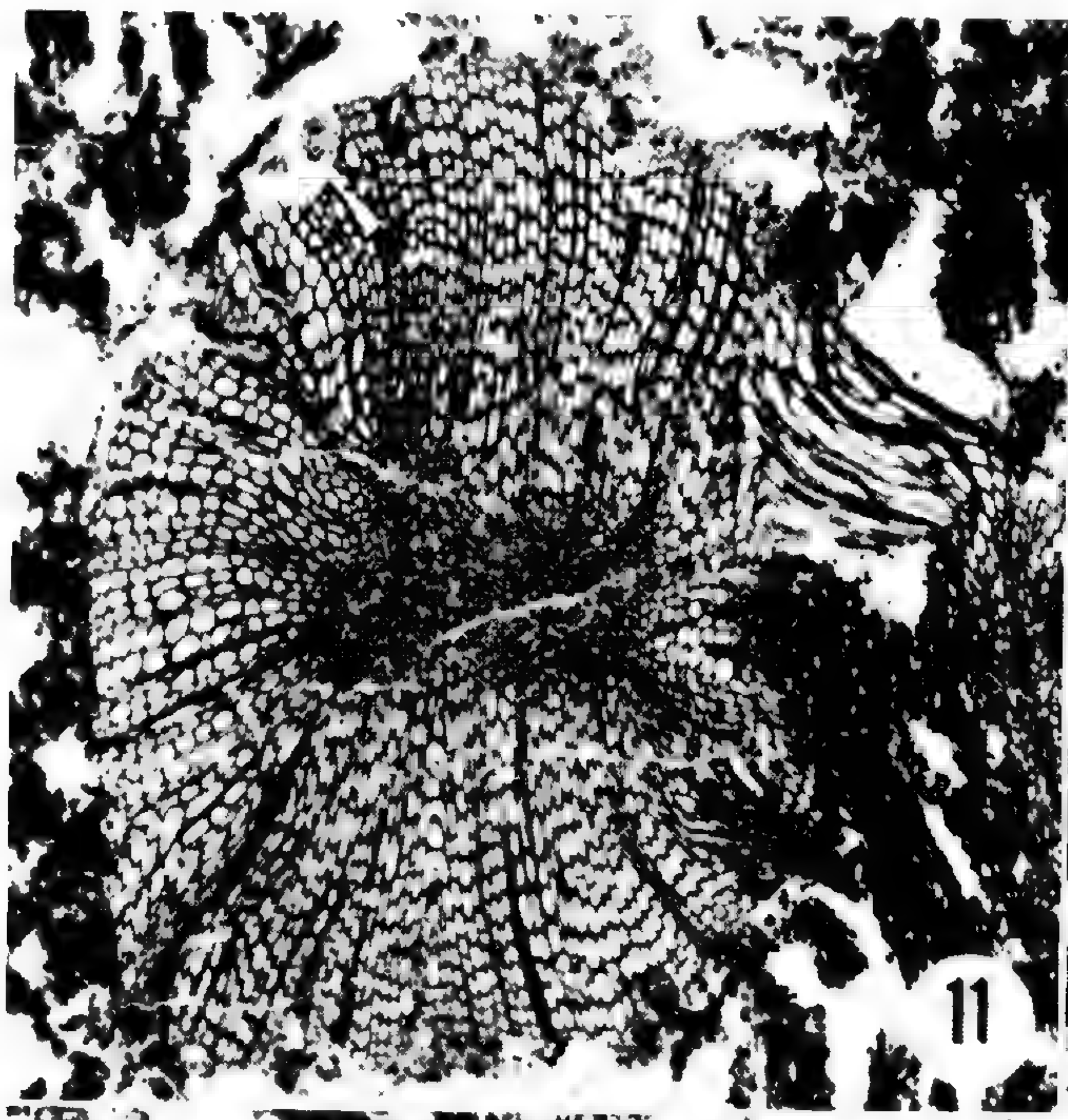
FIGURES 2–10.—2. *Metadineuron ellipticum*, x.s. phyllophore. Visean, Scotland. Kidston Coll. Hunterian Museum, Glasgow. × 20 (from Galtier, 1970).—3. *Dineuron pteroides*, x.s phyllophore. Visean, France. Montpellier Coll. × 20. (from Galtier, 1970).—4. *Botryopteris antiqua*, x.s. foliar member. Visean, France, Montpellier Coll. × 15 (from Galtier, 1970).—5–6. *Metaclepsydropsis duplex*, x.s. phyllophore and pinnae traces. Visean, Scotland. × 10.—7–8. *Diplolabis roemeri*, x.s. phyllophore and pinna trace. Visean, Scotland. × 10.—9. *Etapteris scotti*, x.s. phyllophore and pinnae traces. Mineral Coal, Kansas. × 10.—10. *Etapteris* sp., x.s. phyllophore and pinnae traces. Calhoun Coal, Illinois. × 10.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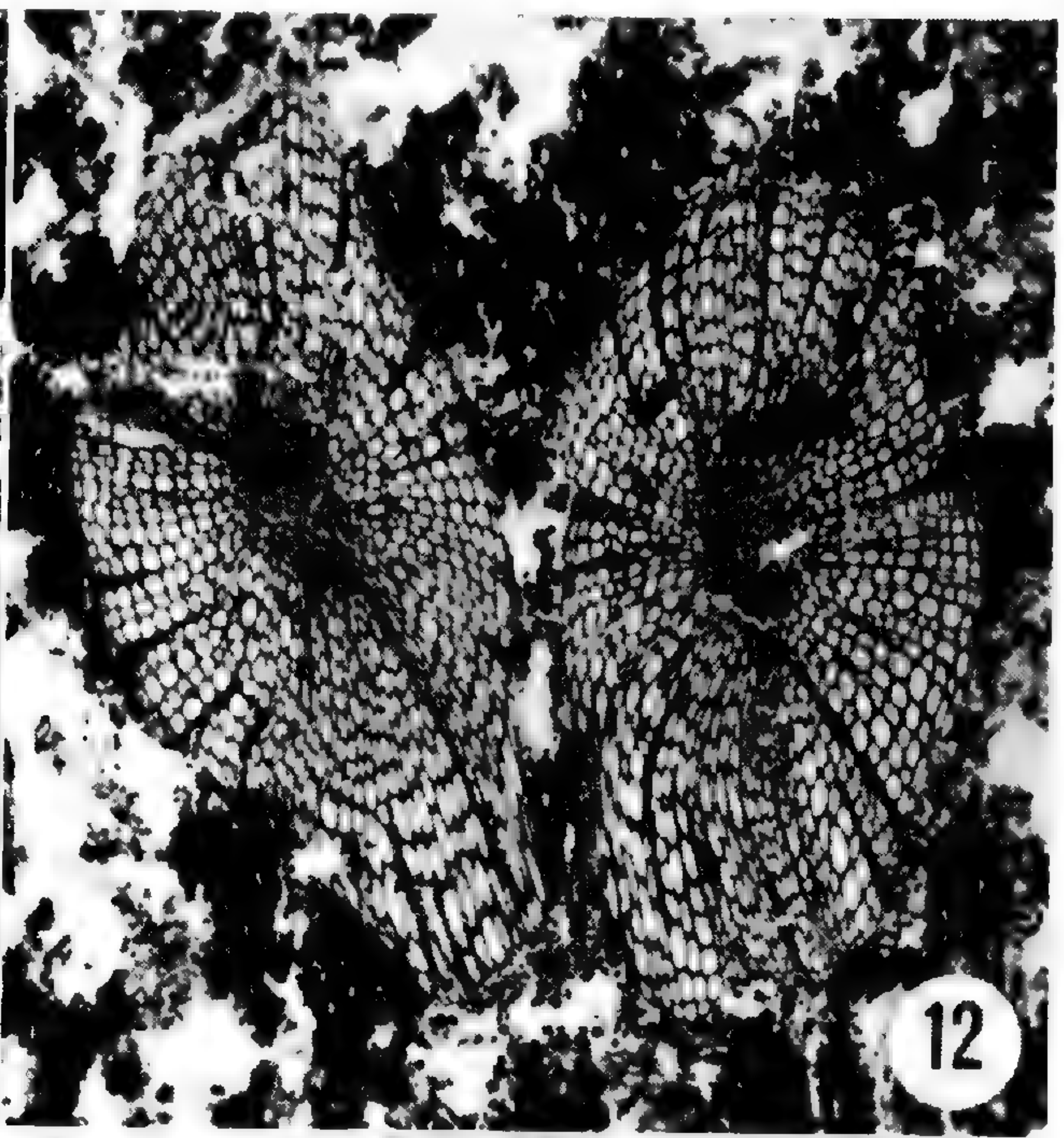
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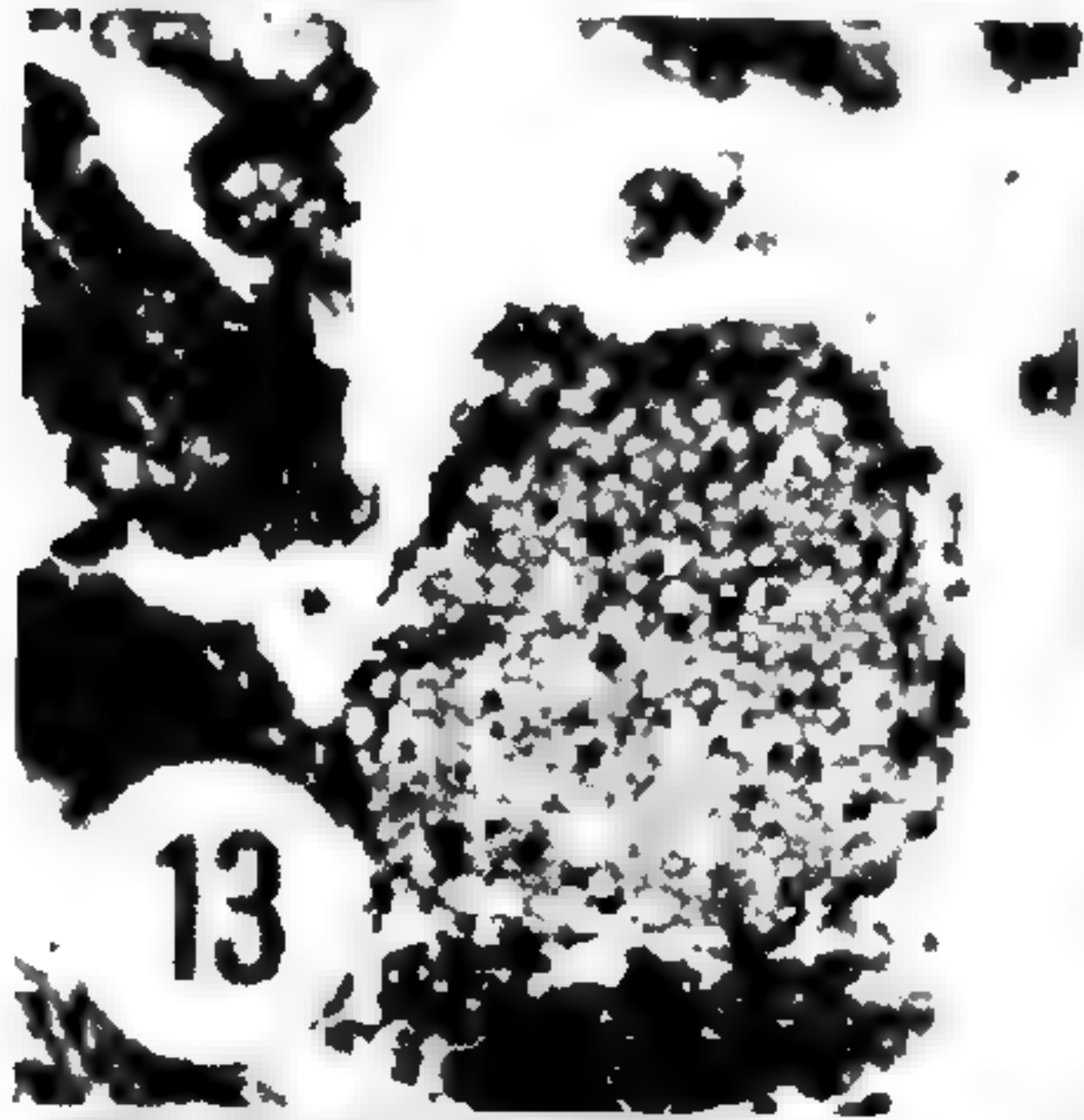
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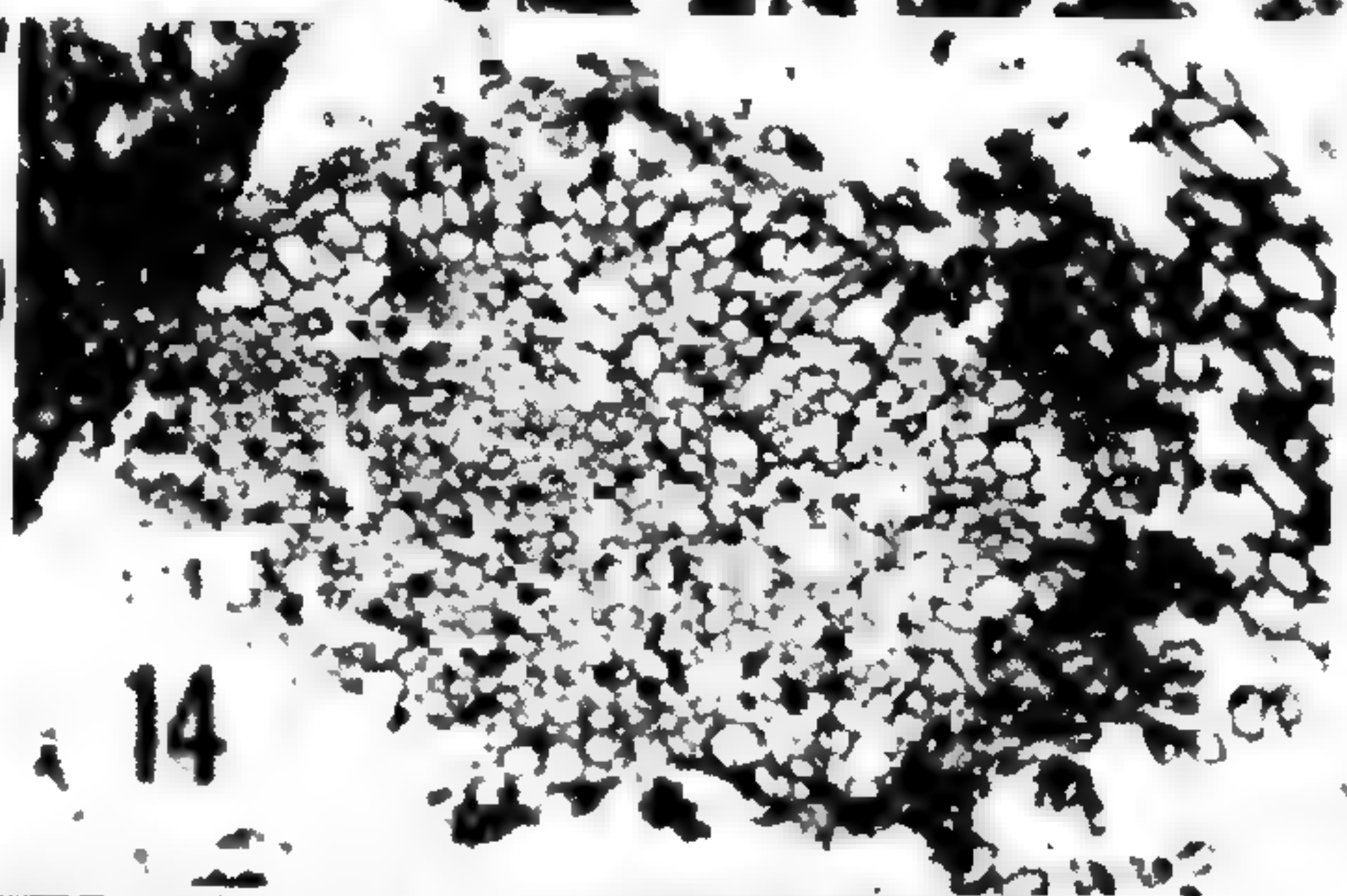
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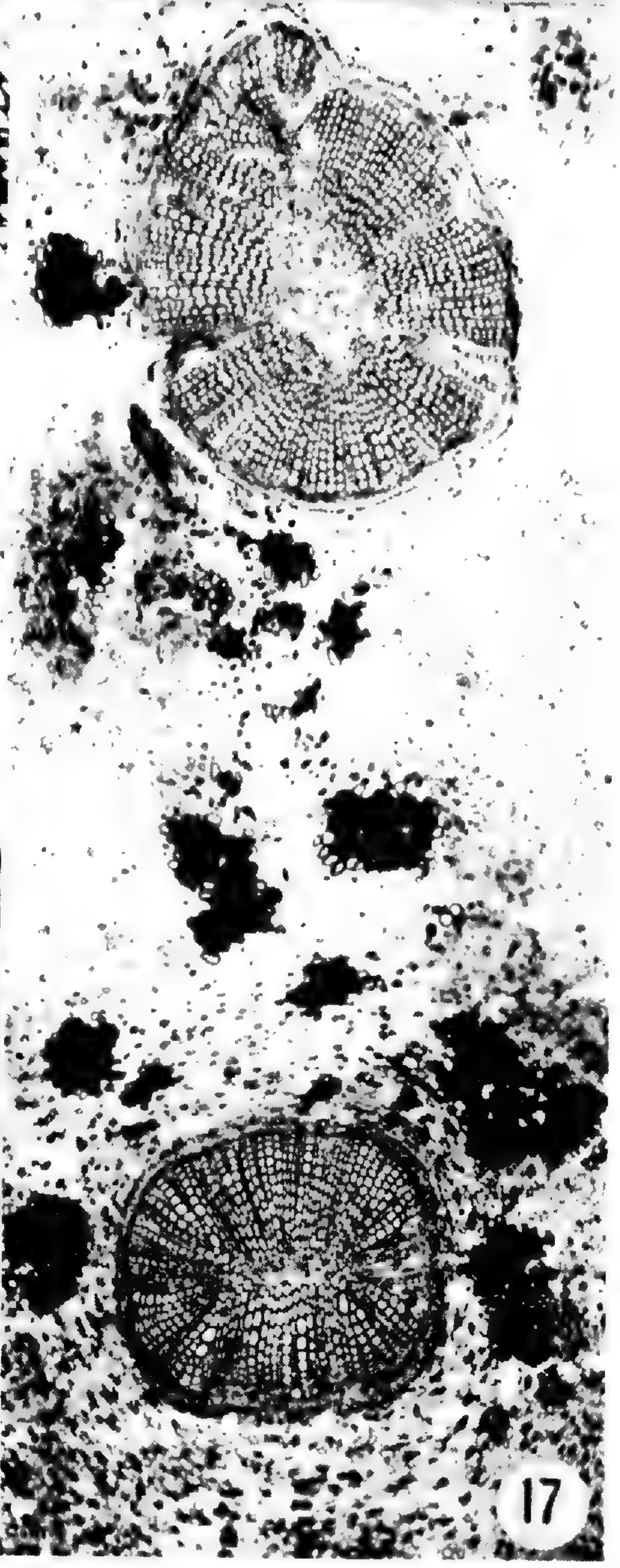
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Dineuron (Figs. 1A–C) are smaller phyllophore types with ellipsoidal xylem strands and with no known stems. *Metadineuron* (based on *Dineuron ellipticum* of Kidston, 1908) conforms to the pattern of pinna emission in *Metaclepsydropsis*, although dichotomy of the pinna trace into two pinna supplies has not yet been demonstrated (Galtier, 1964). *Dineuron*, which was previously thought to compare well with etapteroid types of phyllophores, exhibits a somewhat different kind of pinna emission than previously supposed. Within *D. pteroides* are two types of pinna emission which could be from the same frond (Figs. 1B, C). In one, the peripheral loops open, then close and reopen with separate C-shaped pinna traces departing from each margin of the opened loop; in the second type, a pair of small peripheral loops individually emit C-shaped pinna traces. The pinna traces are quite small compared to the phyllophore axis. The additional feature in pinna trace formation and emission of *Metadineuron* and *Dineuron* (Fig. 1B) shared with other etapteroid genera is the common trace stage or temporary union of xylem of the pinna-pair (Figs. 1E–G, 5–10).

Zygopteris primaria from the Permian had an erect habit with branching unknown (Sahni, 1932*a*); other species of *Zygopteris* are rhizomatous and dichotomously branched (Figs. 12, 15) with distantly spaced leaves in two lateral rows. *Metaclepsydropsis, Diplolabis, Ankyropteris corrugata*, and *Nemejcopteris* also have rhizomatous habits with dichotomous branching. Aphlebiae occur on the rhizomes and lower part of the petioles in *Zygopteris* and *Ankyropteris*, and all around the base of the frond and at bases of quadriseriate pinnae in *Nemejcopteris* (see Holden, 1930; Baxter, 1951).

Anatomically one of the unusual features of *Zygopteris* is the presence of secondary xylem (Scott, 1912*a*; Holden, 1955; Andrews, 1942), an interpretation which has been questioned by Baxter (1952) on pertinent points. In a study of American *Zygopteris* stems Dennis (1972) has presented quite convincing evidence of the secondary origin of the outer xylem. Primary xylem near the apex lacks radial files of larger tracheids (Figs. 13–14), there is a basipetal increase in the number of tracheids in radial files, and uniseriate rays are demonstrable in both tangential (Fig. 15) and radial section (Fig. 16). The lateral meristem that produced secondary xylem in *Zygopteris* was apparently active in younger regions of the stem and did not persist.

Among the anatomically better known zygopterid genera are *Metaclepsydropsis, Diplolabis*, and particularly *Zygopteris*. The protostelic anatomy of these genera may be compared along with that of *Ankyropteris corrugata*. Each has a stellate central core of xylem with peripheral protoxylem groups and is surrounded by larger tracheids showing at least some degree of radial alignment. *Diplolabis* from the Visean of Scotland has a solid protostele composed

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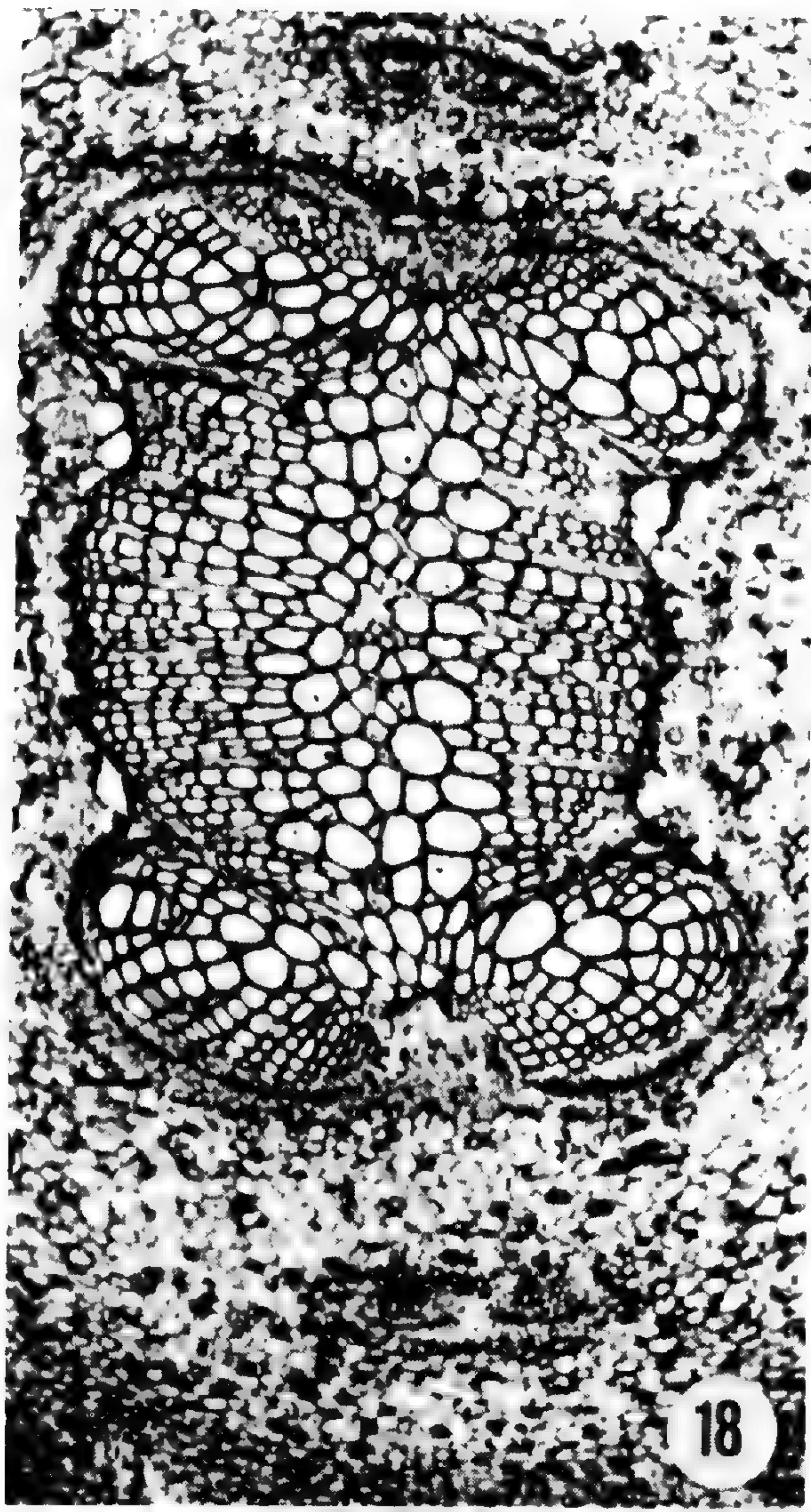
FIGURES 11–17. *Zygopteris* anatomy.—11–12. *Z. illinoiensis*, x.s. xylem of rhizome below and above dichotomy. Herrin Coal, Illinois. × 10.—13–14. *Zygopteris* sp. x.s. primary xylem near apex of rhizome. Calhoun Coal, Illinois. × 25.—15–16. *Zygopteris* sp. tangential and radial sections of secondary xylem of rhizome showing rays. Calhoun Coal, Illinois. × 10, × 25.—17. *Zygopteris* sp. x.s. rhizome and phyllophore trace (below) with secondary xylem. Calhoun Coal, Illinois. × 10 (figures 13–17 from Dennis, 1972).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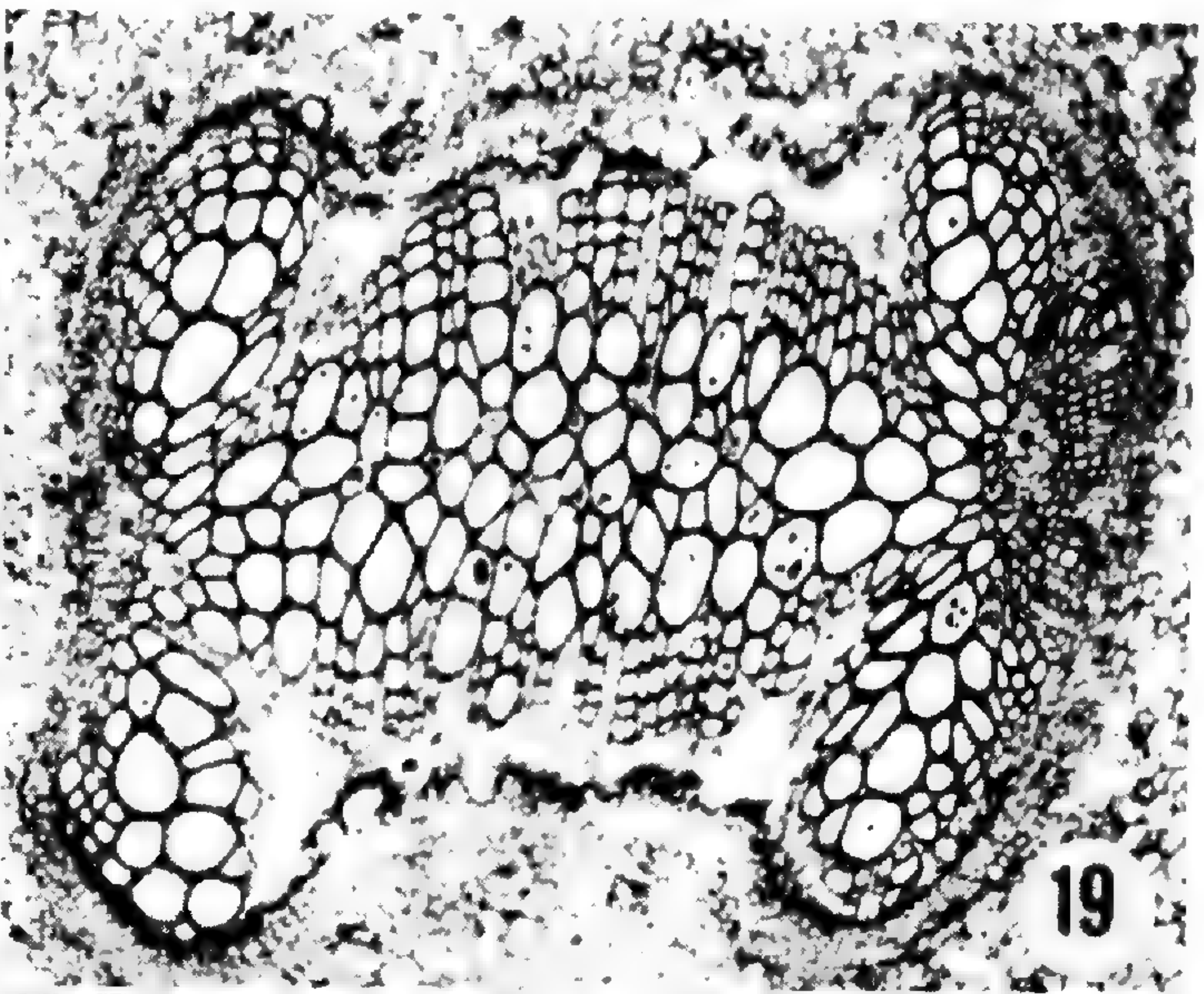
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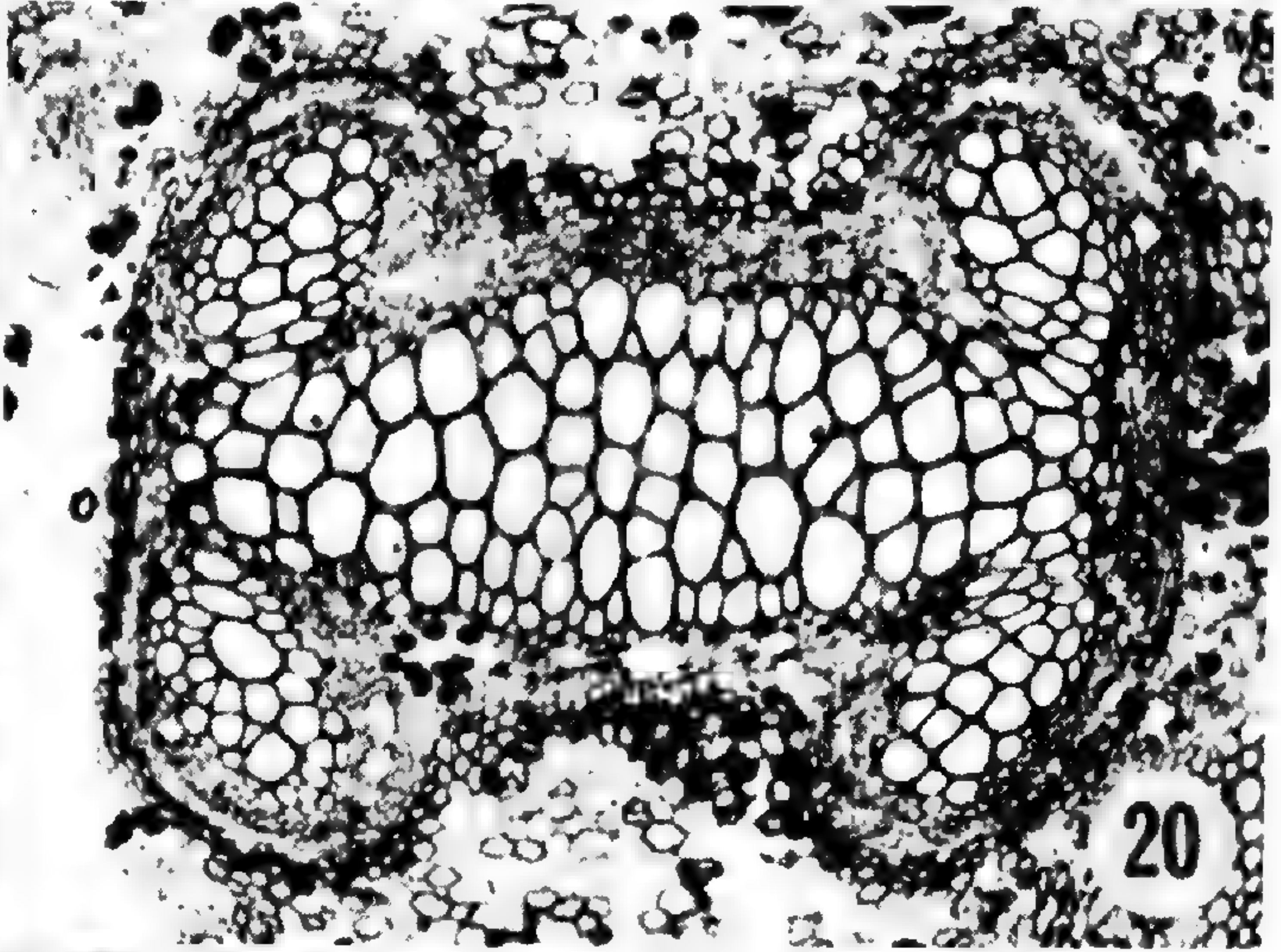
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Figures 18–20. *Zygopteris* sp. phyllophore trace at higher levels with diminishing amount of secondary xylem. Calhoun Coal, Illinois. × 25 (from Dennis, 1972).—21. *Notoschizaea robusta*, x.s. pinnules. "Baker" Coal, Kentucky. × 25.

of an inner zone of shorter- and smaller-diameter tracheids (Gordon, 1911*a*). Of the same age, *Metaclepsydropsis* indicates that the mixed protostele occurred early in zygopterid evolution (Gordon, 1911*b*); the inner primary xylem of the rhizome consists of tracheids and parenchyma as it does in the lower Westphalian A species *Ankyropteris corrugata* (Holden, 1930) and Pennsylvanian species of *Zygopteris* (Scott, 1912*a*; Andrews, 1942; Baxter, 1952; Dennis, 1972). An increase in stelar parenchymatization in Middle and Upper Pennsylvanian species of *Zygopteris* is suggested by Dennis (1972).

Petiolar trace formation and emission in these taxa is quite similar. There is an oval bipolar (two protoxylem groups) trace which originates in the outer xylem of *Diplolabis* and *Metaclepsydropsis*, from both inner and outer xylem in *A. corrugata,* and from strictly the inner (primary) xylem in *Zygopteris*. Traces take on an elongate bar-shaped configuration; protoxylem groups divide to form a tetrapolar petiolar strand; peripheral loops appear, and in *Zygopteris* antennae develop. Along the course of the petiolar trace in *Zygopteris* there may be a variable amount of secondary xylem (Fig. 17) which diminishes upwardly and the antennae become distinct (Figs. 18–20); aphlebia-pair traces are emitted at this level (Fig. 18). More prominent antennae develop at higher levels, and pinna trace emission begins (Figs. 9–10).

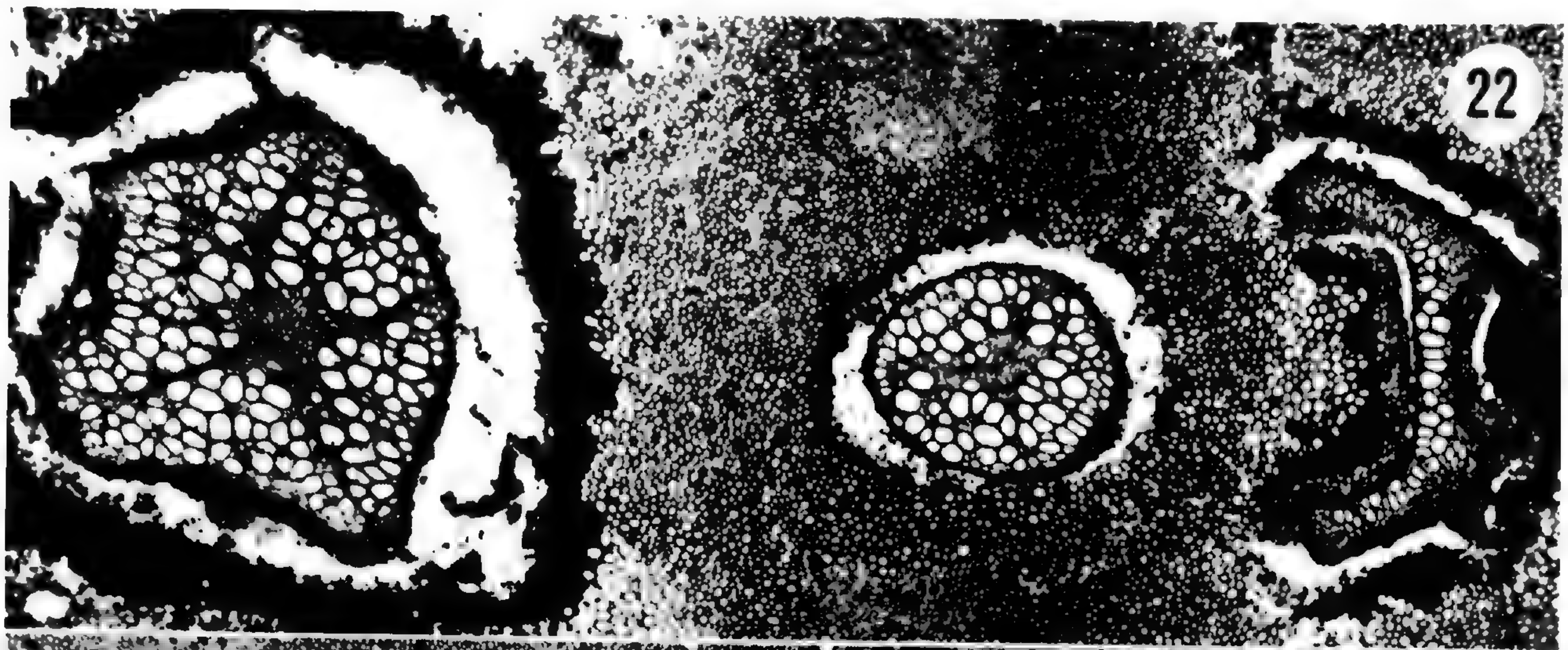
The best known zygopterid assemblage from compression studies is *Nemejcopteris (Pecopteris) feminaeformis*, a *Zygopteris*-like plant known from the Lower Permian of East Germany (Barthel, 1968). The creeping dichotomous rhizome was up to 6 mm in diameter and densely pilose with spine-like hairs up to 3 mm long. Quadriseriate phyllophores were erect upon the rhizome. Evidence of roots was lacking. The phyllophore also had long stiff hairs and attained diameters up to 7 mm with preserved lengths of 40 cm; the tip of the phyllophore exhibited circinate vernation. At the base of each pinna pair are aphlebiae. Pinnae are once pinnately branched and bear laminate pinnules of the *Pecopteris* type. Sterile foliage similar to that of *Nemejcopteris* is widely distributed in the Stephanian and Lower Permian (Barthel, 1968).

ANKYROPTERIS

The genus *Ankyropteris* includes two groups of species; those known only from foliar members and those with both stems and petioles. The earliest occurrences of isolated foliar members are in the Upper Mississippian of Arkansas (Taylor & Eggert, 1967) and the Namurian of Poland (Corsin, 1952), and the isolated foliar members have been compared in detail by Baxter (1951) and Corsin (1952). The earliest stratigraphic records of species with known stems and petioles are all Lower Pennsylvanian (*A. hendricksii, A. grayi, A. corrugata*). *Ankyropteris glabra* from the Middle and Upper Pennsylvanian of the U.S.A. is one of the most completely known Paleozoic ferns and differs slightly from *A. grayi* (lower Westphalian A of England) which has shorter internodes and more mixed parenchyma and tracheids in the center of the stem. *Ankyropteris scandens* from the Lower Permian is apparently quite similar to *A. grayi.*

The earliest known shoots of *Ankyropteris* indicate three habits. *Ankyropteris hendricksii* (Read, 1938) from Oklahoma has very closely spaced petioles and densely packed ramentum and roots which give a "false stem" aspect to the erect habit. *Ankyropteris corrugata* exhibits a rhizomatous or climbing habit with dichotomous branching, unassociated with leaves. *Ankyropteris grayi* and *A. glabra* were probably upright climbing plants, and *A. glabra* is often found preserved alongside *Psaronius* stems and their root mantles.

The morphology of *A. glabra* is best known, and with the above mentioned differences may serve as an anatomical representative of the group, although comparable details of frond morphology are not known for other species (Baxter, 1951; Andrews, 1956; Eggert, 1959*a*, 1963; Eggert & Taylor, 1966). The stele is a pentarch actinostele with an inner network of mixed parenchyma and small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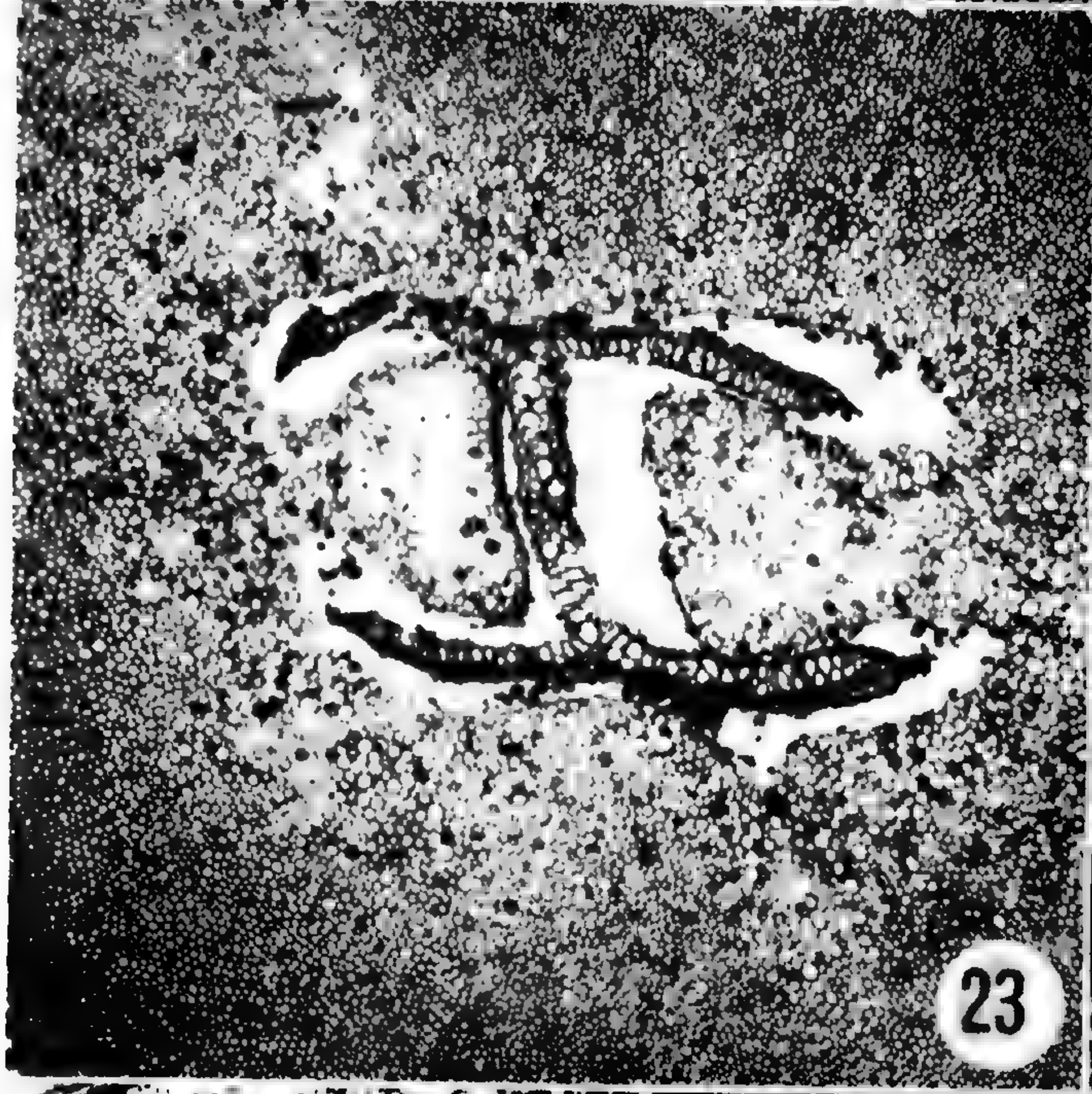
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diameter scalariform tracheids, surrounded by scalariform metaxylem elements (Fig. 22). Branching is axillary with either a common trace giving rise to the terete axillary stele and the di-upsilon phyllophore trace (Baxter, 1951) or with the branch stele arising from the stem above the point of petiole trace departure (Andrews, 1956). Development of axillary branches in *A. glabra* normally took place, resulting in several successive orders of stems and petioles which were progressively smaller and simpler in structure with determinate growth (Eggert, 1959*a*). The stem system and petiolar bases (see fig. 14 in Eggert, 1959*a*) are cloaked with numerous aphlebiae and multicellular uniseriate hairs. Despite the H-shaped zygopterid phyllophore and peripheral loops of *A. glabra* (Fig. 23) the frond was biseriate and quite similar to modern ferns in its pinnately compound, planated pinnae with small laminate pinnules of a *Pecopteris* type. The primary pinnae are supplied from the adaxial antennae and are slightly turned toward the stem; their xylem stages have adaxial antennae (Figs. 25, 27) and small abaxial lobes. These in turn bear secondary ultimate pinnae with terete xylem strands which bear the pinnules (Fig. 26). Basalmost pinnule-pairs are slightly larger and have a somewhat undulating margin like those shown by Eggert and Taylor (1966) in the fertile foliage. A scale-like aphlebia occurs on the adaxial side of the petiole at the base of each pirmary pinna (Eggert, 1963). The vascular configuration of the rachis of *Ankyropteris glabra* changes distally (Fig. 24); it resembles that of the European *A. westfaliensis* which, by parallel, may be the distal part of the rachis of *A. grayi* (Scott, 1912*b*; Eggert, 1963).

Ankyropteris glabra has been regarded as the first recognizable member of an extinct family which combines somewhat zygopterid anatomy (shared with *Ankyropteris* species, *Asterochlaena*, *Asterochlaenopsis* and *Austroclepsis*) with planated biseriate laminate fronds (Eggert & Taylor, 1966).

ANACHOROPTERIDACEAE

Among genera included in the Anachoropteridaceae with abaxial curvature of petiolar xylem strands are *Tubicaulis* (Figs. 37–42), *Anachoropteris* (Figs. 44–50), *Psalixochlaena* (Figs. 28–36), and *Apotropteris* (Figs. 54–55). *Tubicaulis* and *Anachoropteris* occur from lower Westphalian A to Permian; *Psalixochlaena* is known only from the lower Westphalian A of western Europe; and *Apotropteris* is known only from the Upper Pennsylvanian of the U.S.A.

Solid and mixed protosteles are exhibited by the genera, and siphonosteles are known from current studies. Stelar evolution within the Anachoropteridaceae has followed two general pathways with the retention of a solid protostele in one phyletic line of *Tubicaulis* as well as the Pennsylvanian species *Psalixochlaena cylindrica*, *Anachoropteris clavata*, and some stems of *Apotropteris minuta*.

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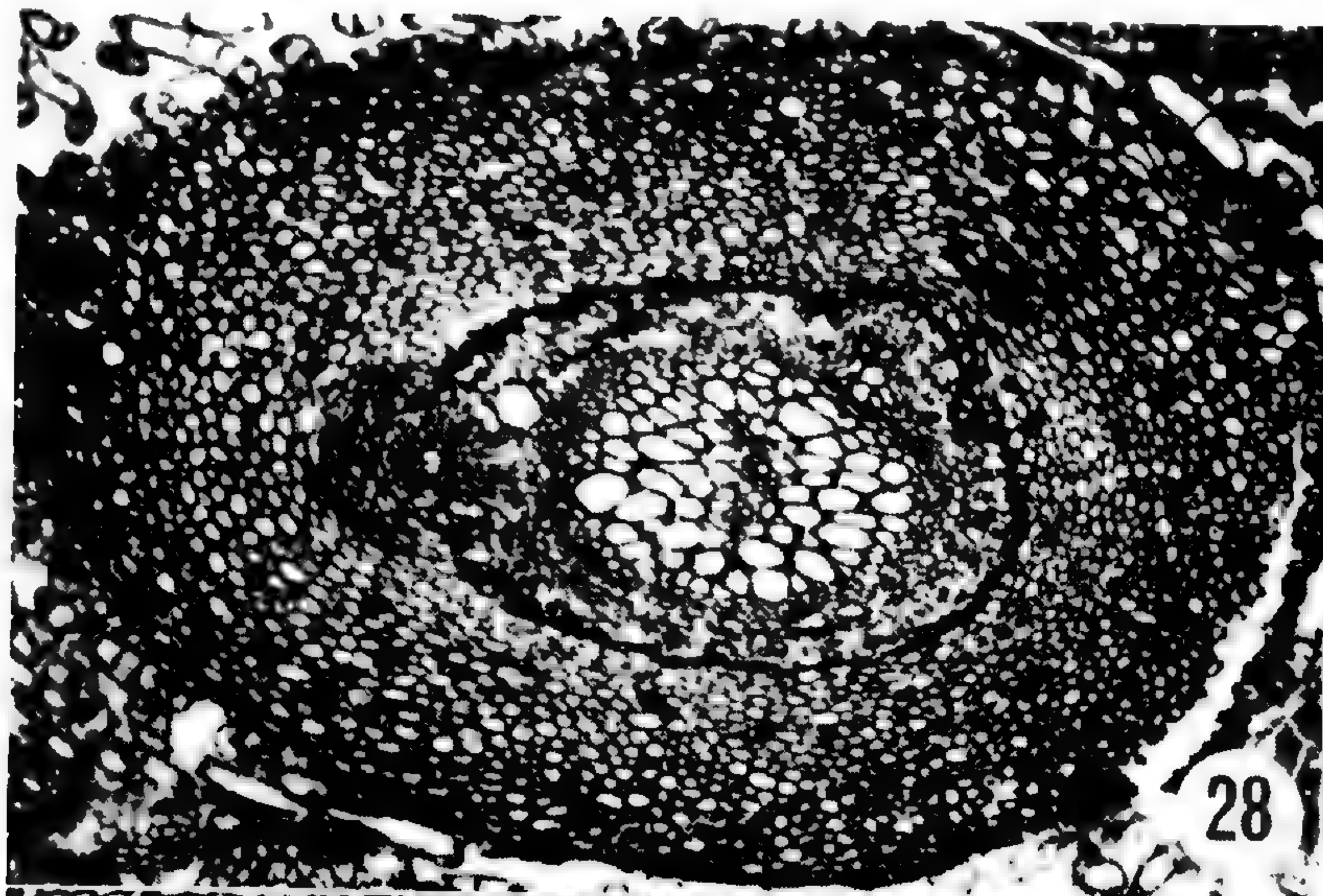
FIGURES 22–27. *Ankyropteris glabra* stem and frond anatomy. Herrin Coal, Illinois. × 10. Adaxial face of all foliar cross-sections is oriented to left except Fig. 23.—22. Stem and axillary branch steles with petiolar trace at right.—23. Petiole x.s.—24. Rachis x.s. distal.—25. Pinna x.s.—26. Pinnules in paradermal section.—27. Pinnae and laminate pinnules x.s.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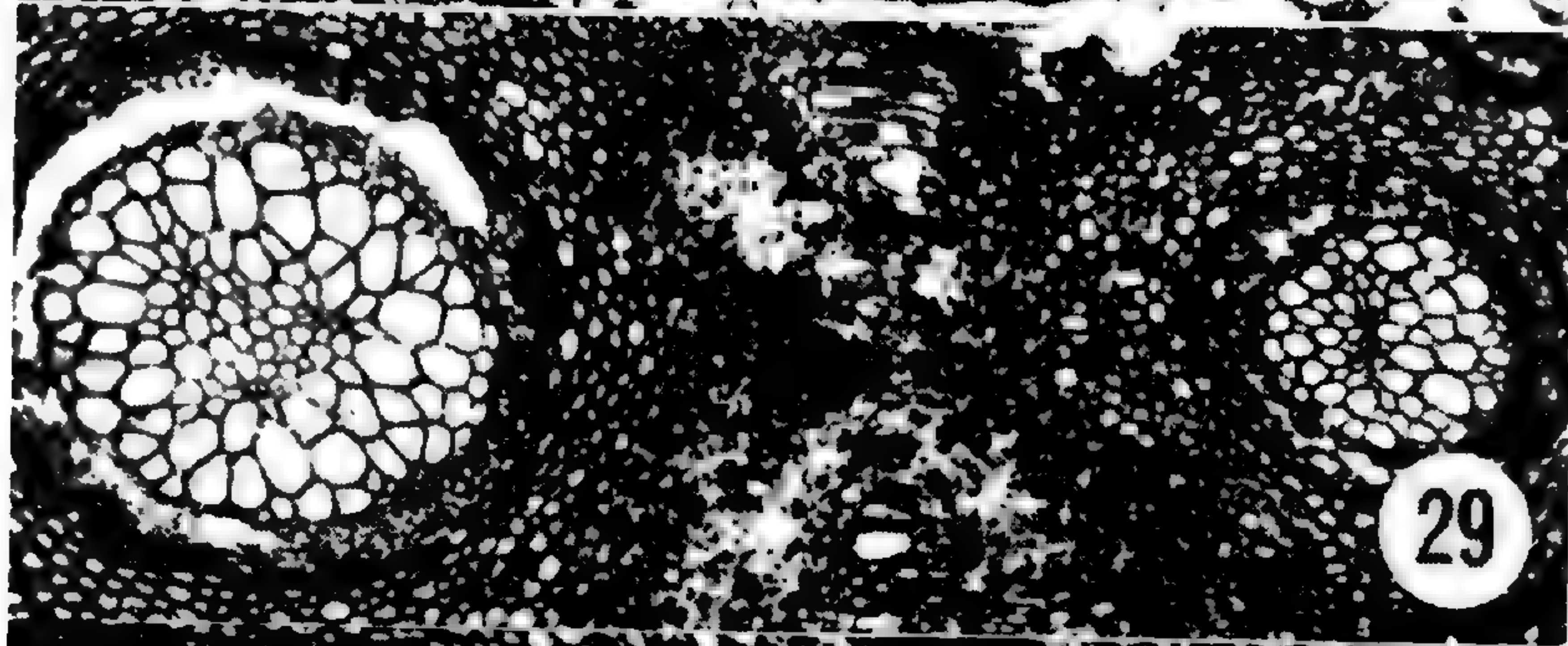
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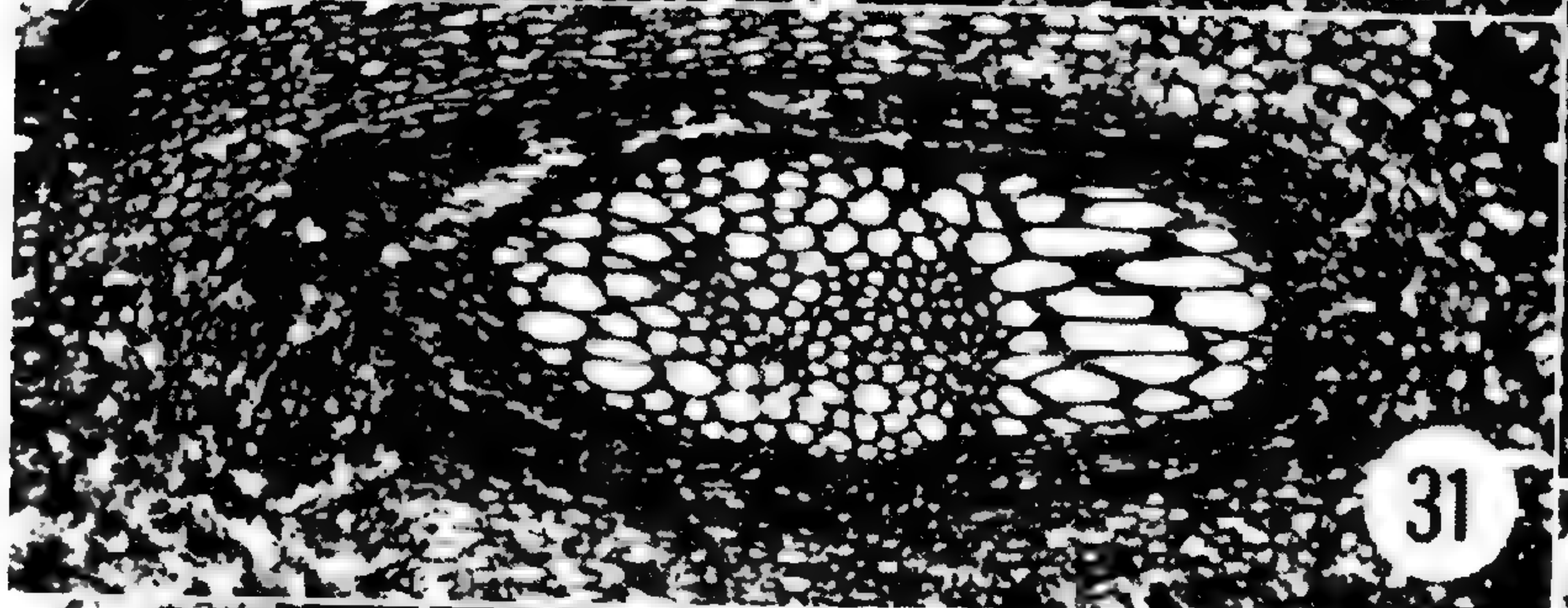
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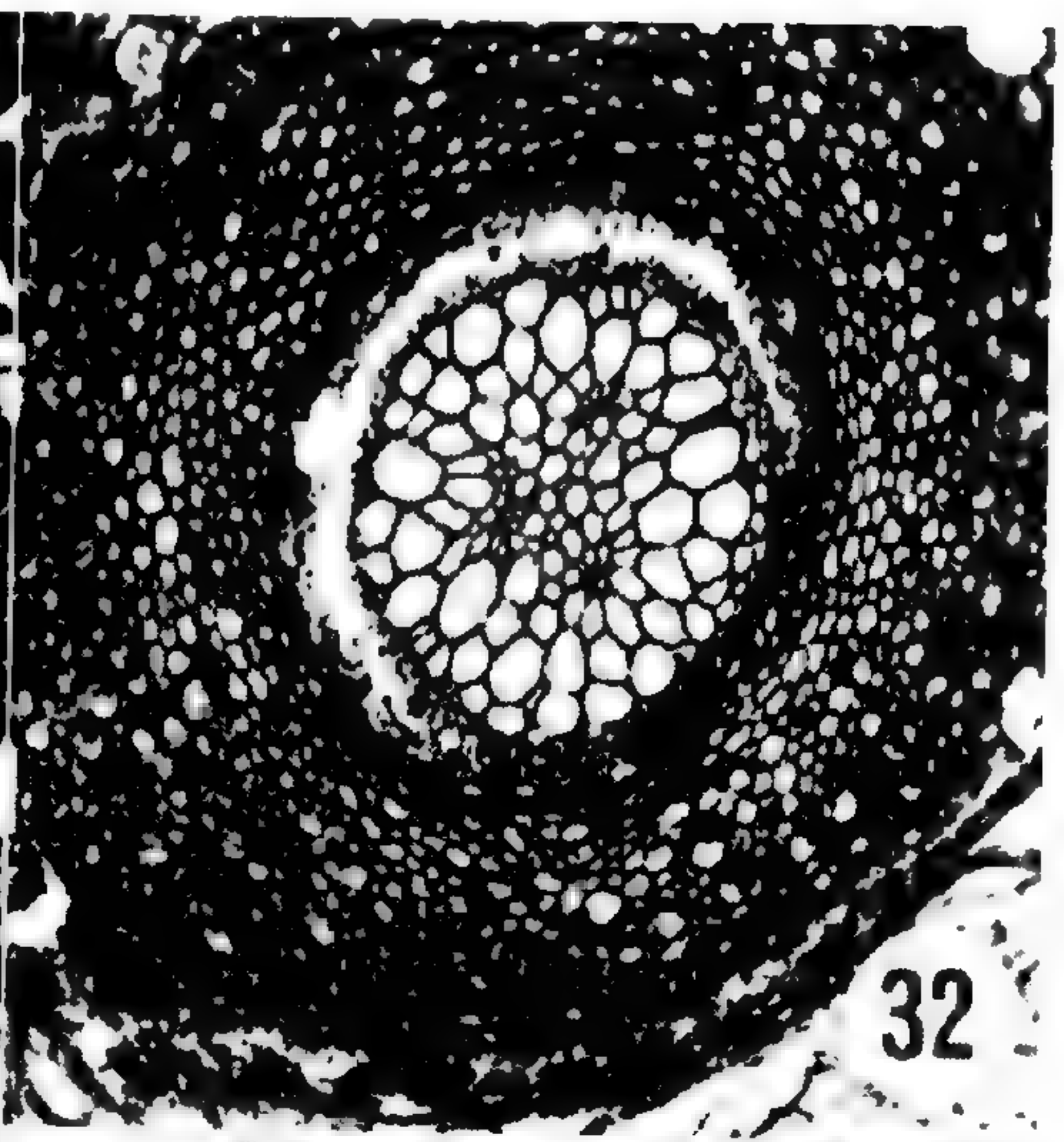
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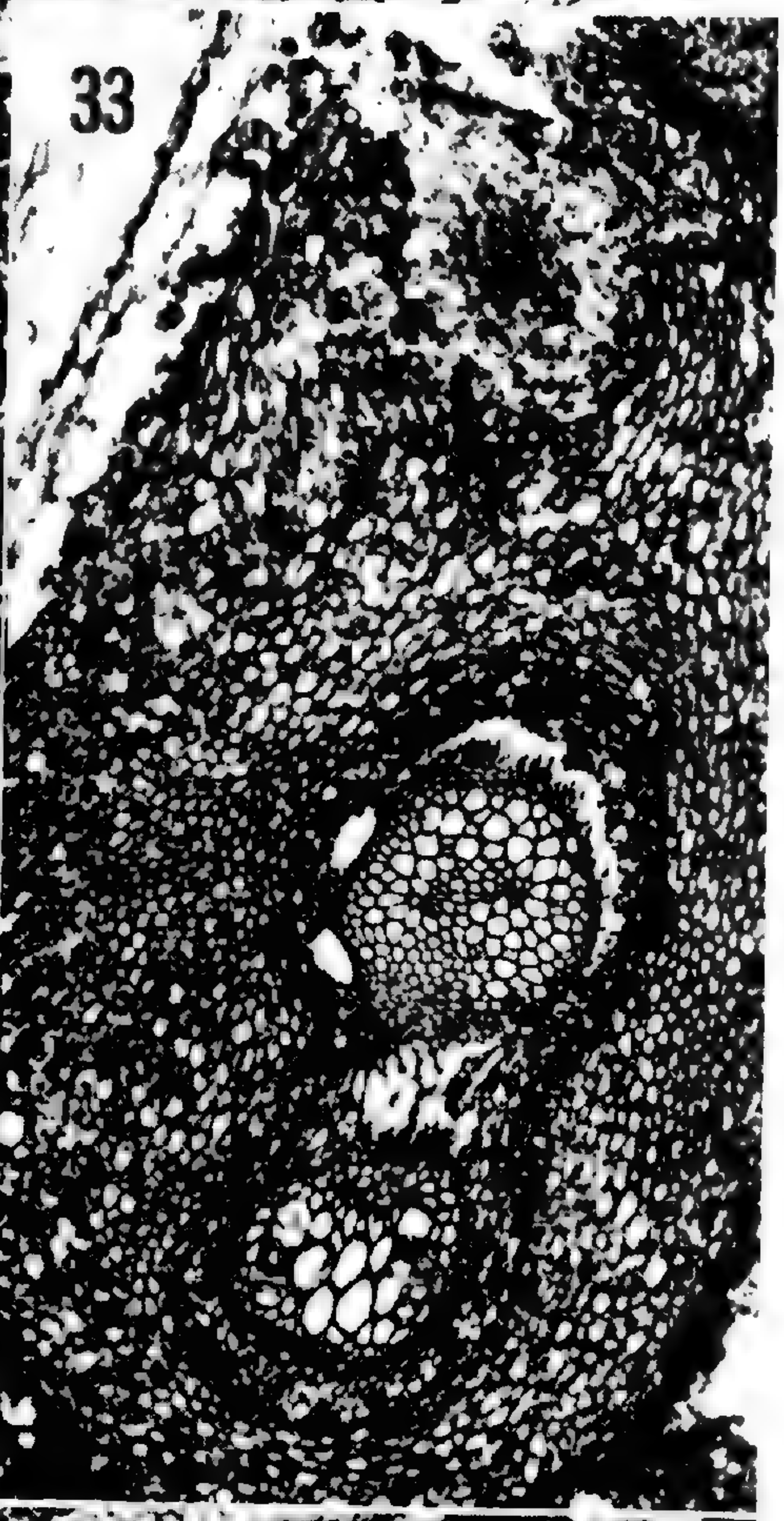
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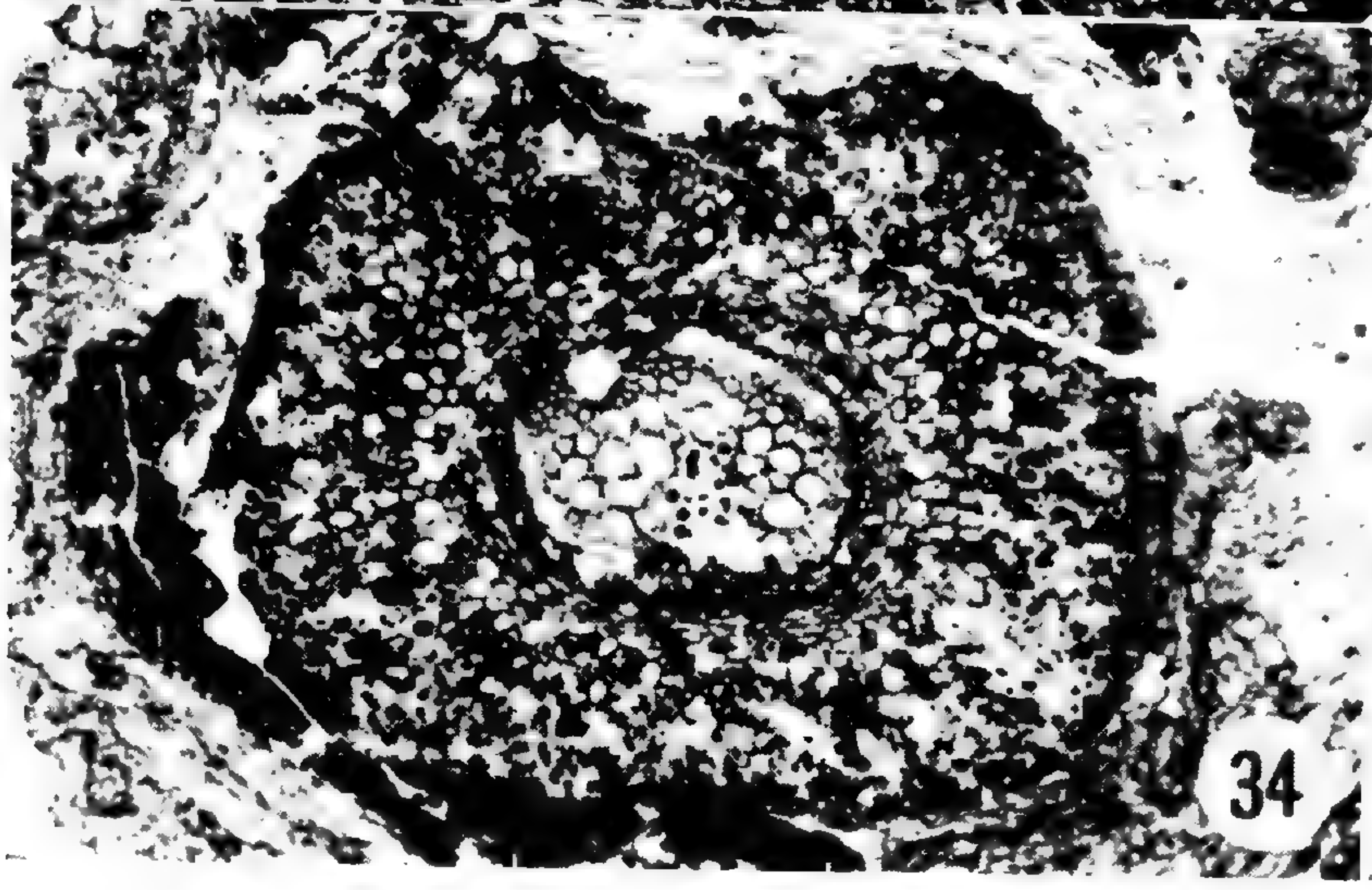
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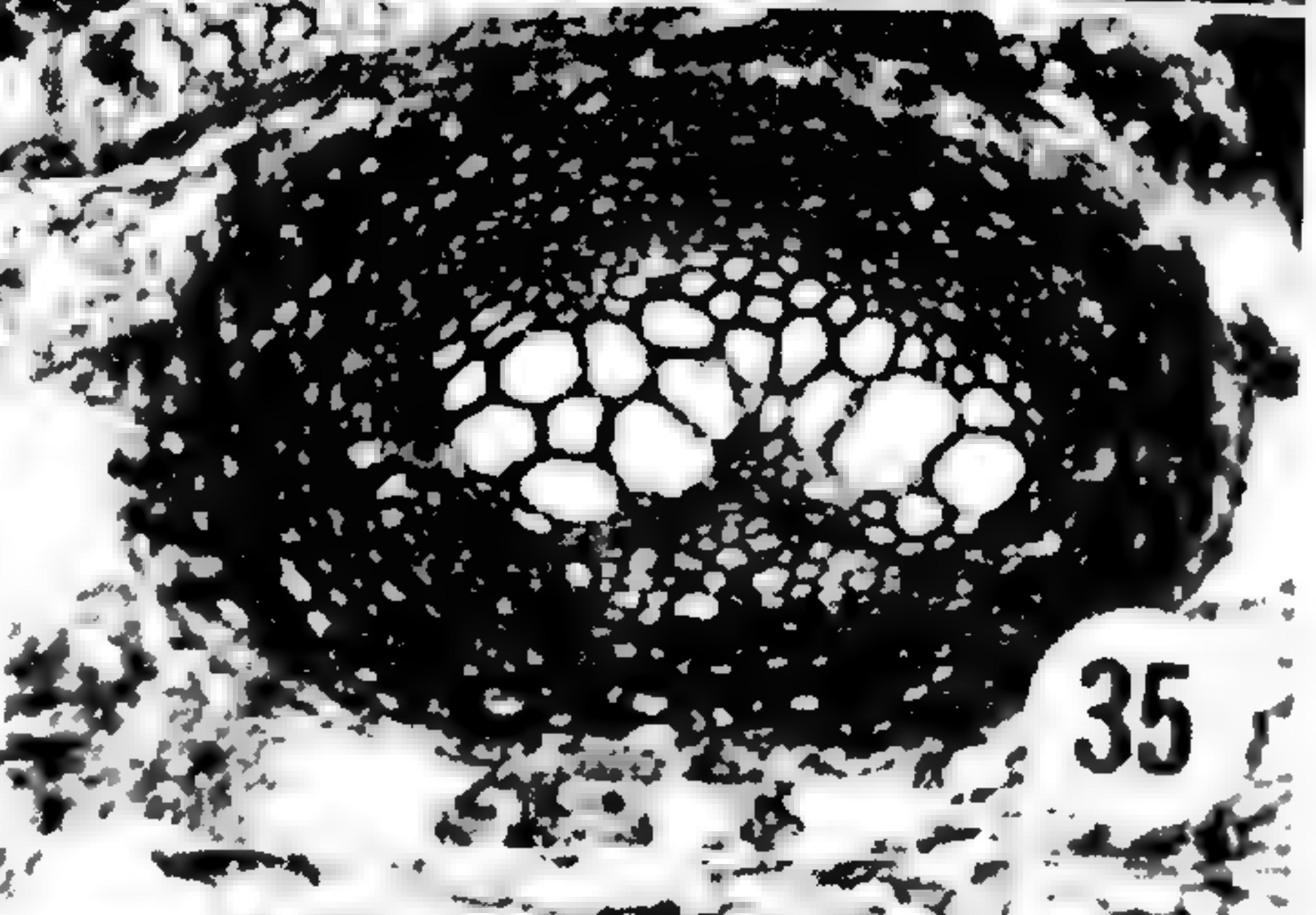
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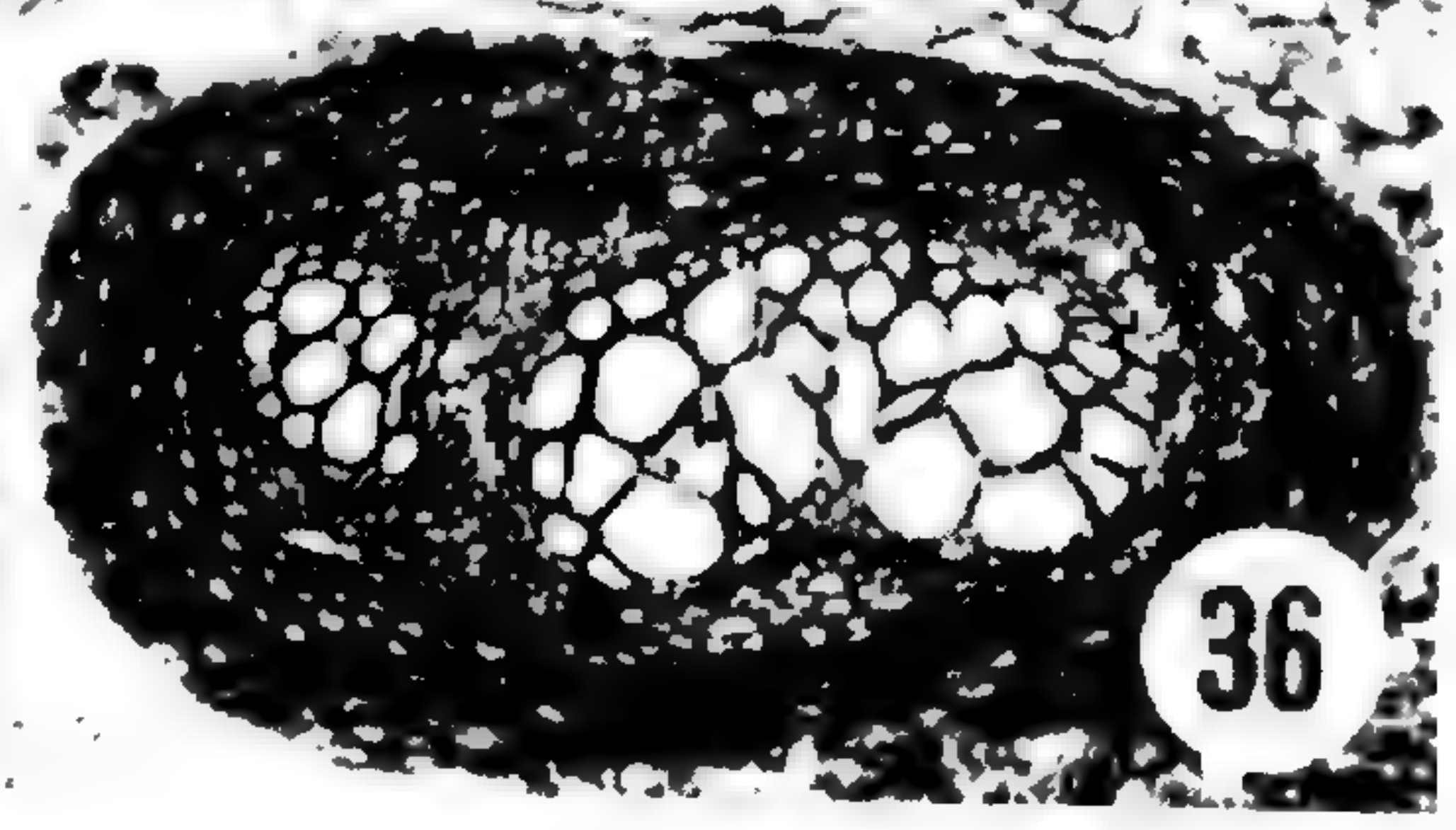
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Vitalization of the protostele with abundant parenchyma approaching a "mixed pith" in *Tubicaulis africanus* is a generally demonstrable trend in one phyletic line of *Tubicaulis* from the lower Westphalian A to the ?Upper Permian; parenchyma may be quite abundant in some older middle Pennsylvanian *Tubicaulis* stems (Fig. 40). A second evolutionary line leads to siphonostelic forms which occur in Middle Pennsylvanian forms of *Tubicaulis* and *Anachoropteris* and in larger stems of *Apotropteris minuta*; the appearance of a sclerotic or parenchymatous pith is transitory in some stems and apparently a mature feature of others (Figs. 52–55). Stelar anatomy will be discussed further with branching and foliar characters in appropriate groups of species of the Anachoropteridaceae.

PSALIXOCHLAENA—RHIZOME WITH SHOOTS

Branching of the larger stems (Fig. 28) of *Psalixochlaena cylindrica* is unequal with smaller lateral branches bearing the spirally arranged petioles (Figs. 31, 33), *i. e.* the rhizome bears shoots. The rhizome, its branch, and the first petiole are in the same plane in *Psalixochlaena*, and frequently only one petiole is developed on a lateral shoot (Figs. 32–33). Early (basalmost) stages of stem branching are identical to those of petiolar trace emission of some specimens (Figs. 29–30), and both types of branching are cross-sectionally similar to petiole emission in many *Botryopteris* species (Fig. 30, and see Holden, 1960, fig. 3, pl. 9). Holden (1960) established the abaxial curvature of the foliar strand at slightly higher levels (Figs. 34–36) and pointed out the similarity to foliar members of *Apotropteris* (Figs. 54–55). Foliar branching is apparently pinnate and circinate vernation was established by Holden (1960).

Typically, in anachoropterid foliar members with distinct protoxylem groups there are two protoxylem groups on the adaxial face and usually additional ones on each margin or side of the strand. The latter protoxylem groups follow pinna emission patterns and are decurrent with the nearest adaxial ones.

TUBICAULIS—STEMS WITH INVERTED C-SHAPED PETIOLAR XYLEM

Tubicaulis is an organ genus for terete, exarch protostelic stems without secondary xylem and with inverted C-shaped petiolar xylem traces (Mamay, 1952; Holden & Croft, 1962); *Anachoropteris* is an organ genus for isolated foliar members with inverted U- to C-shaped, to involuted xylarly strands.

Interconnections between *Tubicaulis* and *Anachoropteris* were first established (Hall, 1961) with a demonstration of the transition from typical *Tubicaulis* petioles to foliar anatomy of the *Anachoropteris involuta* type (Figs. 40–43E). Hall (1961) also reported the occurrence of a lateral bud on a foliar member of the *A. involuta* type (Fig. 48). By priority, specimens showing *Anachoropteris* anatomy are assigned to that genus, but it is not clear if the phyletic line of

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FIGURES 28–36. *Psalixochlaena cylindrica* stem and frond anatomy. x.s. Halifax Coal, lower Westphalian A, England. × 25.—28. Stem.—29–30. Rhizome with lateral shoot trace (right).—32–33. Rhizome (Fig. 32), lateral shoot from rhizome and leaf trace (bottom).—34–36. Foliar members.


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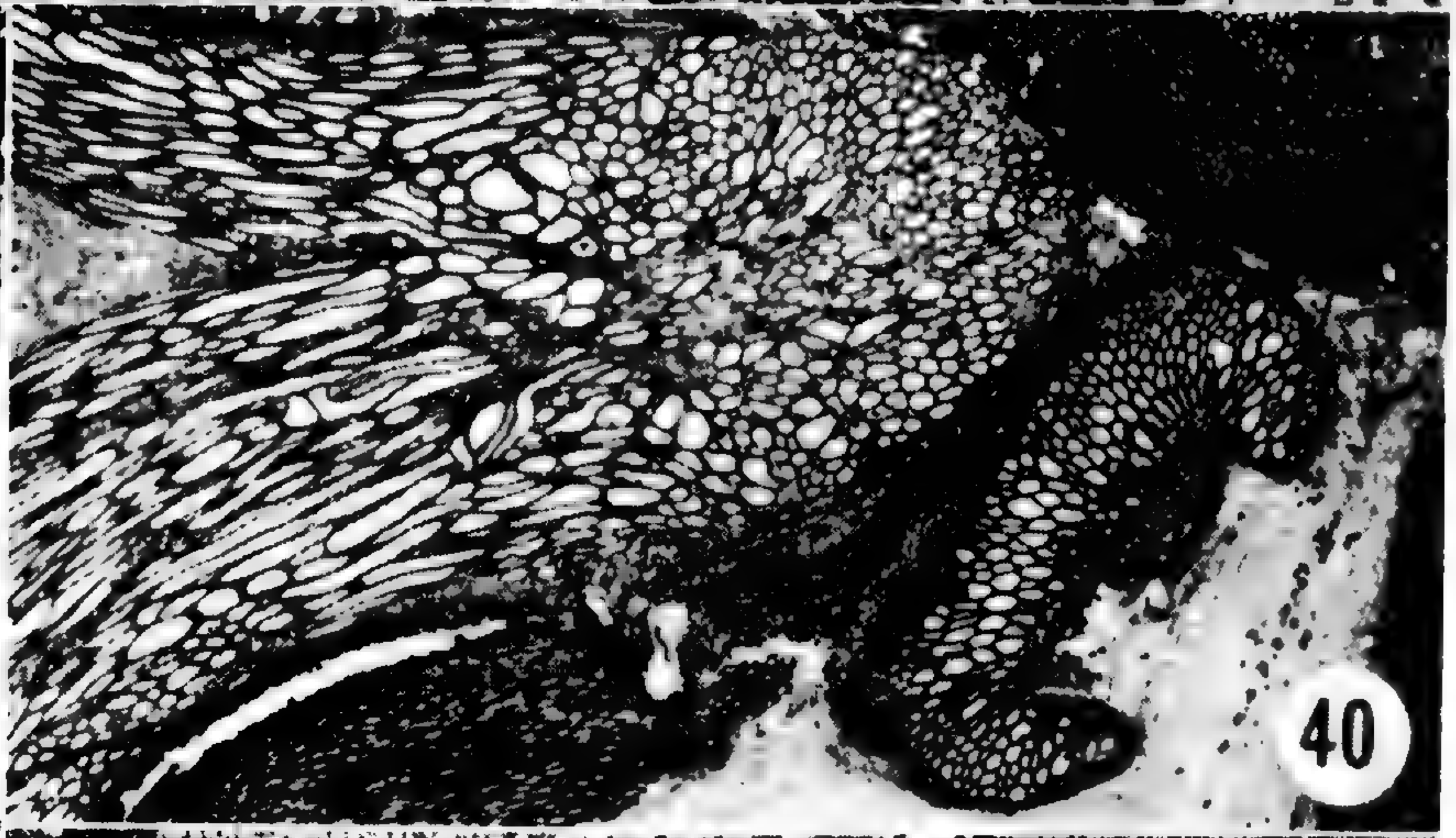
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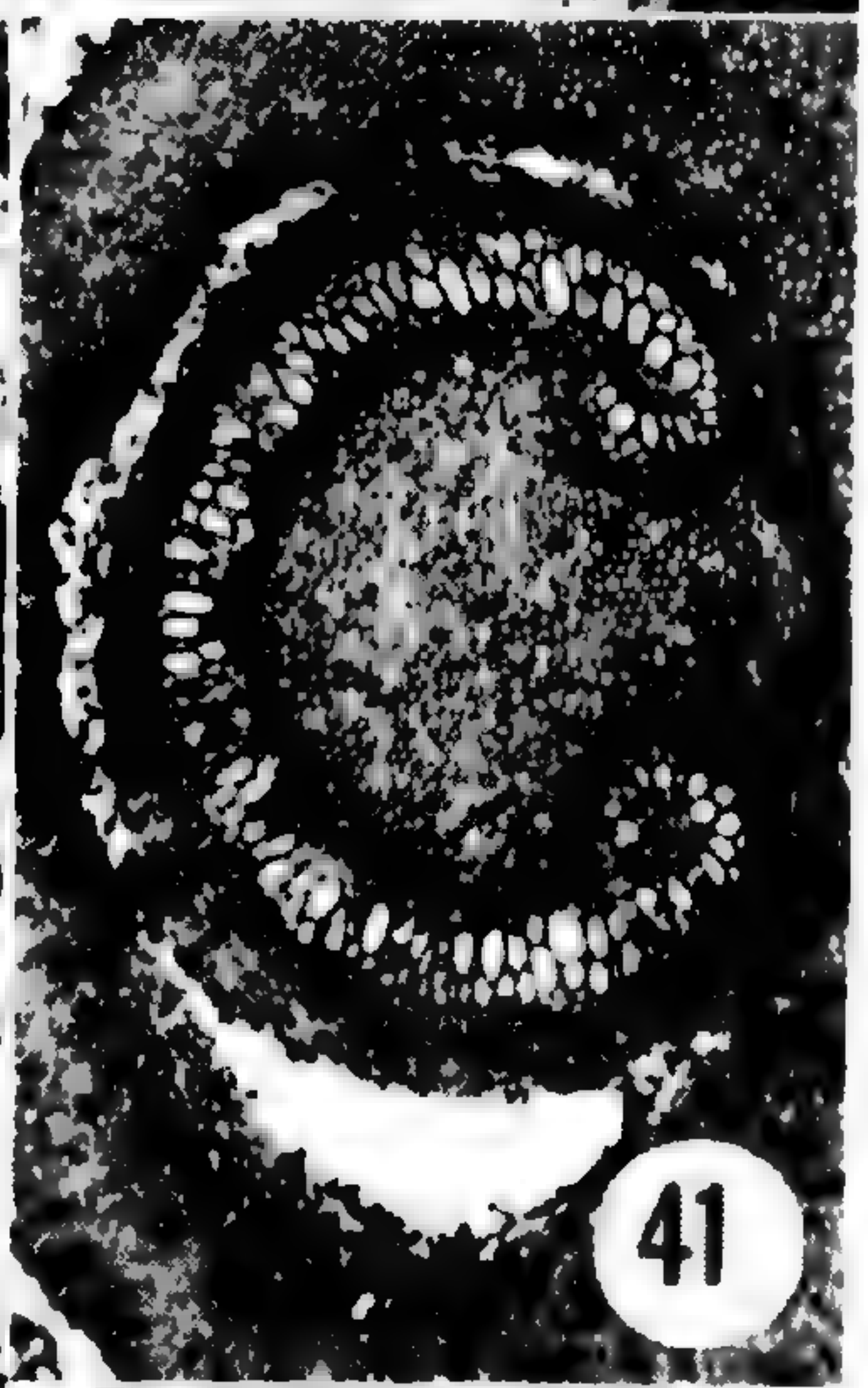
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Tubicaulis species with vitalized protosteles are the only ones bearing *Anachoropteris* fronds or where generic limits will ultimately fall among such assembled plants. *Tubicaulis* stems with vitalized protosteles also occur on *Anachoropteris* fronds. Vegetatively, there are fairly coherent branching patterns and types of stelar anatomy to summarize for specimens showing both *Tubicaulis* and *Anachoropteris* morphology.

With the same stem and petiolar organization there are at least two major evolutionary lines of *Tubicaulis* (Eggert, 1959*b*) from the lower Westphalian A to the Permian, and each exhibits the same kinds of diversity in habit and size. The stelar characters of the two groups are mixed protosteles with multiseriate scalariform metaxylem pitting compared to solid protosteles with reticulate to multiseriate circular bordered pitting (*T. sutcliffia*, *T. berthieri*, and *T. solenites*). Among the seven named species of *Tubicaulis* there are also marked differences in size, habit, and cortical anatomy. Some *Tubicaulis* species were erect to semi-erect; others were epiphytic to scrambling. An epiphytic habit for *T. scandens* was suggested by Mamay (1952), who summarized other data on *Tubicaulis* as have Eggert (1959*b*) and Holden and Croft (1962). Permian species, *T. africanus* from Tanganyika and *T. solenites* from East Germany, have the largest stem diameters (4.5–14.0 cm) and their steles are 3.5–6.0 mm in diameter.

Tubicaulis stems with mixed protosteles, suggesting progressive increase in parenchymatization of the xylem, are an unnamed species from the lower Westphalian A of England (Millay, 1970), several Middle Pennsylvanian species (Figs. 37–40) including *T. multiscalariformis* (Delevoryas & Morgan, 1952), *T. stewartii* from the Upper Pennsylvanian (Eggert, 1959*b*) and *T. africanus* from the Permian (Holden & Croft, 1962). Vertical anastomosing strands of parenchyma partially divide tracheidal groups, and abundant parenchyma may appear in the center as a "mixed pith" with scattered tracheids; there are interconnections with parenchyma extending to the outer xylary margin (Holden & Croft, 1962).

ANACHOROPTERIS—FOLIAR MEMBERS AND BRANCHING

Anachoropteris is based on a foliar member (*A. pulchra*) with abaxial curvature and an inrolled (involute) vascular strand differing from the C-shaped xylem of *Tubicaulis* species. More than a dozen species have been described (Corsin, 1937; Graham, 1935; Hoskins, 1930) ranging from *A. williamsonii* in the lower Westphalian A to *A. involuta* types in the Lower Permian. Two series of species are recognized (Corsin, 1937). The *A. robusta* series includes numerous distinct foliar members with variously arched to U- and almost

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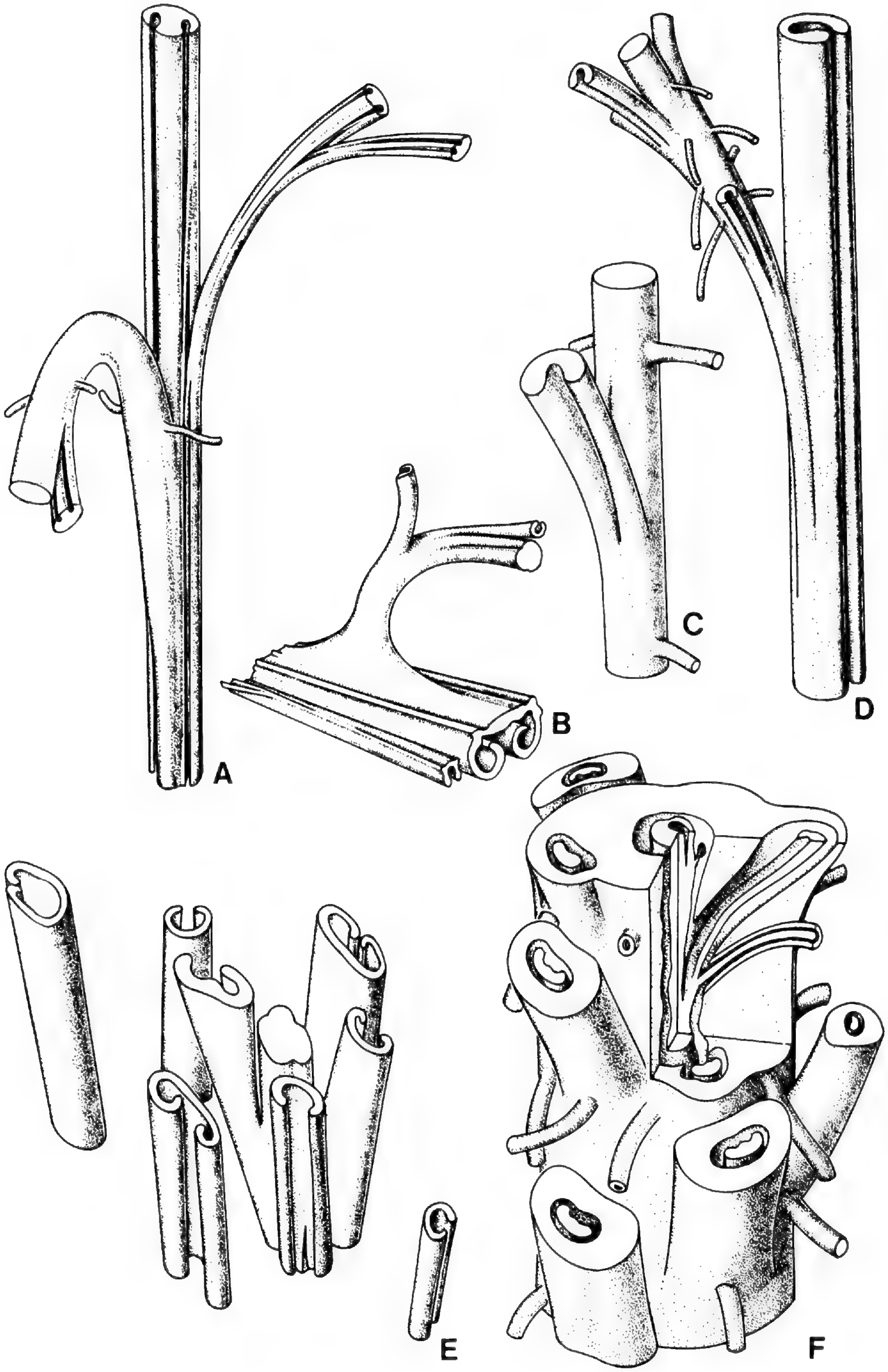
FIGURES 37–42. *Tubicaulis* and *Anachoropteris* anatomy. × 10.—37. Stem and petiolar traces x.s. Lower Cherokee Group, Iowa.—38–39. Longitudinal and cross-section of rhizome with petiolar traces. Herrin Coal, Illinois.—40–42. Rhizome stele and petiolar strands in x.s. at successively higher levels to the *Anachoropteris involuta* type foliar member (Fig. 42). Murphysboro Coal Equivalent, Indiana.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C-shaped vascular strands in cross-section; the *A. involuta-A. williamsonii* series includes those species with inrolled xylary margins and is a heterogeneous group of taxa with very similar cross-sectional anatomy. Within the *A. involuta* group there are at least three distinct branching types in the development of shoots on fronds. Pinnately compound fronds bear protostelic shoots laterally (Fig. 48) and adaxially (Figs. 43B, 47); foliar branching is also dichotomous with pinnate lateral divisions, and siphonostelic to protostelic shoots are formed by dichotomy of the frond (Fig. 51).

Pinna trace formation in *A. involuta* type fronds consist of lateral extramarginal development of C- to O-shaped pinna traces (Figs. 44–45). In addition to the C-shaped to involuted foliar xylem configurations exhibited by the *Tubicaulis* type petioles and *A. involuta* foliar members (Figs. 39–42), there are other configurations which ontogenetically continue from the involuted stage in a somewhat different anachoropterid frond. The fronds which exhibit dichotomous branching and bear siphonostelic shoots exhibit an involute xylary strand in part and, also have stages with the inrolled arms laterally joined to form a closed xylary configuration with inwardly projecting arm tips which, at higher levels, form a bar-shaped inner xylem strand (Figs. 46, 49).

Laminate pinnules with sporangia have been described in one species with *Anachoropteris* foliar anatomy, and the genus *Sermaya* is the basis for a new family (Eggert & Delevoryas, 1967).

Anachoropteris clavata has a U-shaped xylary strand with expanded club-like abaxial arms (Graham, 1935). The stem has a solid protostele. The study of this Middle and Upper Pennsylvanian species by Delevoryas and Morgan (1954*b*) provided the first evidence of the stem of *Anachoropteris*, established the actual abaxial curvature or inverted orientation of the petiolar trace to the stem, and was the first report of shoots on foliar members in the Anachoropteridaceae (Fig. 43D). Shoots also occur on foliar members of the *Anachoropteris involuta* type, and there is a parallel with *Botryopteris* in the kinds of branching, with both lateral and adaxial protostelic shoots (Figs. 43, 47–48, 50). *Anachoropteris involuta* type fronds also exhibit dichotomies with one member of the division becoming a siphonostelic shoot (Figs. 51–53). The siphonostele trace is formed by closure of the arched xylary portion associated with involute foliar anatomy, and a massive development of tracheids takes place around a sclerotic pith which corresponds histologically to inner ground tissue usually seen within such foliar xylem strands. The extent of such siphonostelic anatomy

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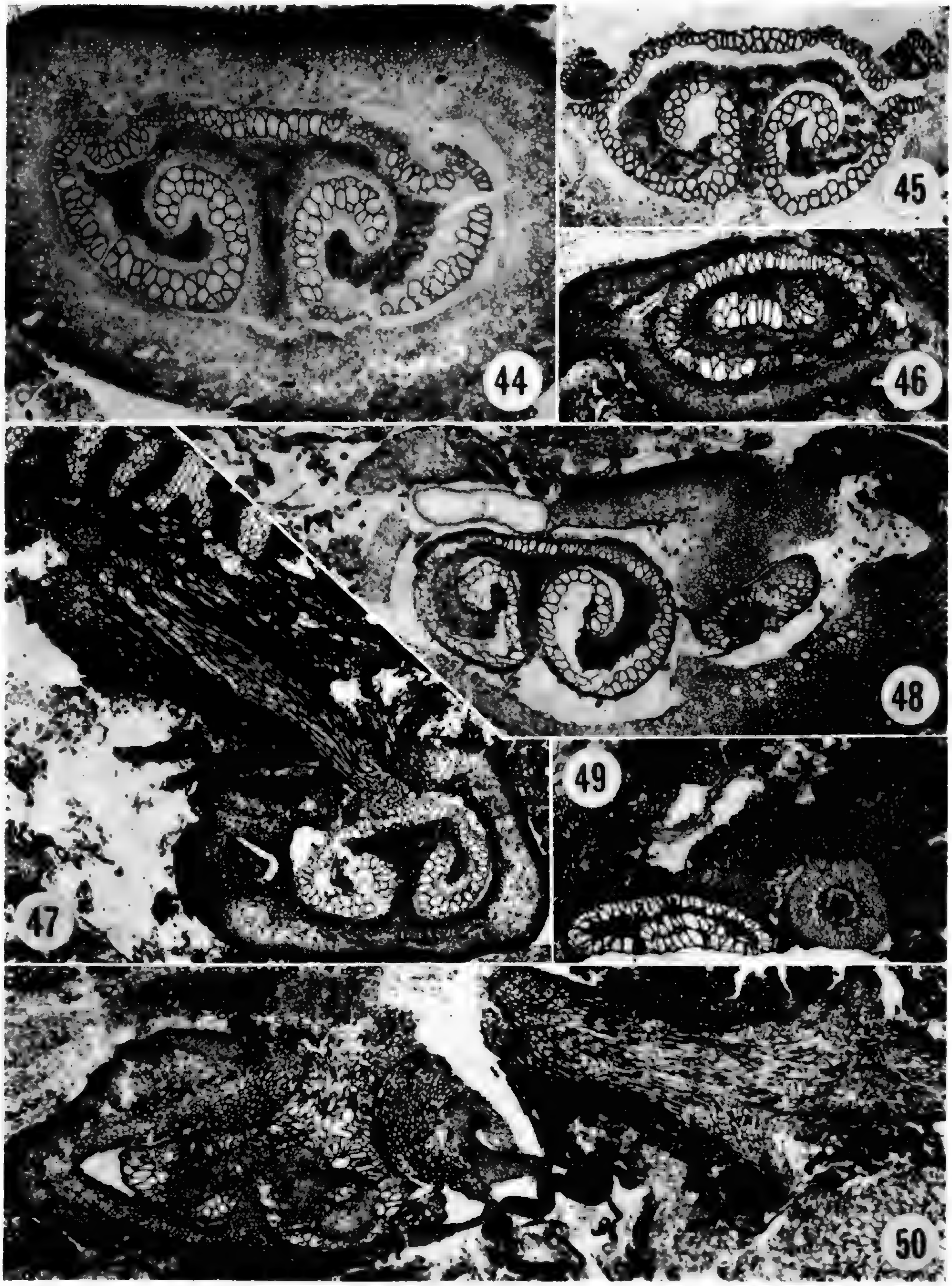
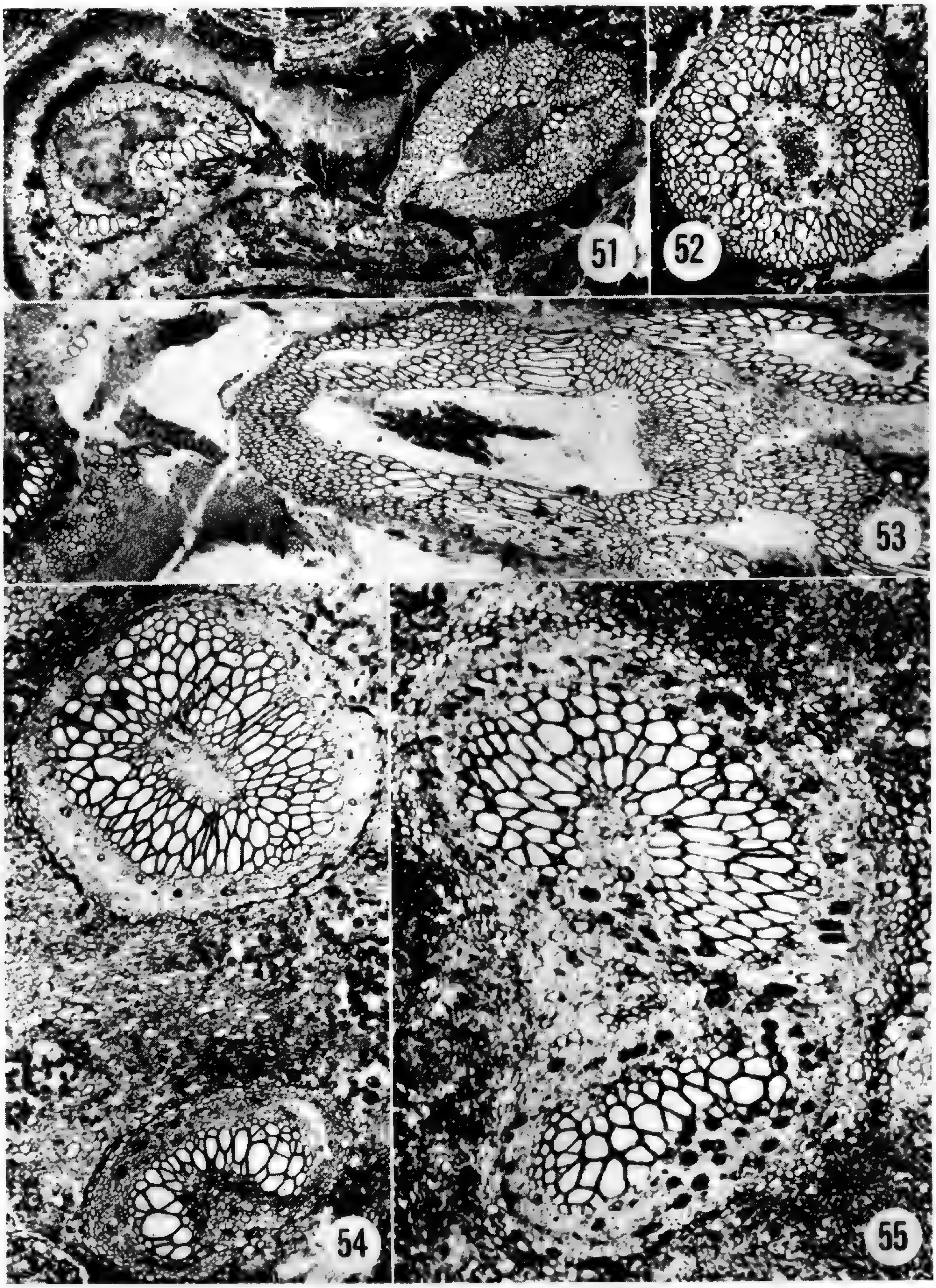
FIGURE 43. Xylary reconstructions of branching in Pennsylvanian age coenopterid ferns.—A. *Botryopteris* sp. with adaxial shoot and lateral pinna on foliar member.—B. *Anachoropteris* sp. with adaxial shoot (roots deleted) and lateral pinna on foliar member.—C. *Apotropteris minuta* with petiolar trace departure from stem (redrawn from Morgan and Delevoryas, 1954).—D. *Anachoropteris clavata* with lateral shoot on foliar member (redrawn from Delevoryas and Morgan, 1954*b*).—E. Stem (roots deleted) of *Tubicaulis* sp. bearing petioles of *Anachoropteris involuta* type (redrawn from Hall, 1961).—E. Portion of shoot of *Catenopteris simplex* with cortical tissues represented (redrawn from Phillips and Andrews, 1966).



FIGURES 44–50. Branching of anachoropterid foliar members. × 10.—44–45. *Anachoropteris involuta* with pinna trace formation, x.s. Parker Coal, Indiana. × 10.—46. Foliar member with closed elliptical xylem strand and internal xylary band. Herrin Coal, Illinois. × 10.—47. *Anachoropteris* sp. foliar member with lateral (left) pinna trace, x.s. and adaxial cauline trace, l.s. Herrin Coal, Illinois.—48. *Anachoropteris pulchra* foliar member in x.s. with lateral (right) pinna trace, in turn with cauline trace. Calhoun Coal, Illinois.—49. Foliar member and derived siphonostelic trace (right), x.s. Herrin Coal, Illinois.—50. *Anachoropteris* sp. foliar member, x.s. with adaxial shoot of *Tubicaulis* type in l.s. Herrin Coal, Illinois.



FIGURES 51–55. Siphonostelic stems of anachoropterid ferns.—51. Dichotomous branching of foliar member with closed foliar xylary strand (left) and siphonostelic trace. Herrin Coal, Illinois. × 10.—52. Siphonostele x.s. Herrin Coal, Illinois. × 25.—53. Oblique section of siphonostelic stage of *Tubicaulis* stem with petiolar traces. × 10.—54–55. *Apotropteris minuta* x.s. with siphonostelic stems (above) and leaf traces. Leaf gap in Fig. 55. Calhoun Coal, Illinois. × 25.

is apparently variable; a number of leaf traces pass off without effecting leaf gaps, and higher up there is a transition to a typical mixed protostele of the *Tubicaulis* type in some specimens. All the reported cases of shoots upon foliar members of *Anachoropteris* (Delevoryas & Morgan, 1954*b*; Hall, 1961) and those demonstrated herein also include pinna trace formation from the same foliar members.

APOTROPTERIS—SIPHONOSTELIC SHOOTS

Apotropteris minuta is an Upper Pennsylvanian fern originally described (Morgan & Delevoryas, 1954) as having a solid protostele in which a vertical indentation or groove occurs in the xylem above leaf trace departure (Fig. 43C). The foliar xylem is similar to that of *Psalixochlaena*. Small specimens of *Apotropteris minuta* are protostelic, and somewhat larger ones have a small pith (Figs. 54–55). There is a gradation of forms with a leaf gap (Fig. 55) and without a leaf gap. In the latter a decurrent funnel of parenchyma, adaxial to the leaf trace, joins the pith at a level below leaf trace departure. The indentation of xylem upon leaf trace departure reported by Morgan and Delevoryas (1954) may have been simply a leaf gap.

GRAMMATOPTERIS AND *CATENOPTERIS*—*INCERTAE SEDIS*

Some of the Paleozoic ferns suggest basic filicalean organization in the geometry of their foliar xylem and provide interesting parallels in stelar anatomy as possible prototypes, but not necessarily the actual progenitors, of extant families such as the Osmundaceae. *Grammatopteris*, *Catenopteris*, and a recently discovered Upper Pennsylvanian fern fall into the above category, and it seems desirable to treat them together as an *incertae sedis* group.

GRAMMATOPTERIS

Grammatopteris is known from stelar and leaf trace anatomy in *G. rigollotii* and *G. baldaufii* from the Stephanian and Lower Permian of Europe and has been reported also from the Visean of France, based on isolated foliar members assigned to *G. bertrandi* (Corsin, 1937). The foliar xylem in *Grammatopteris* is essentially a bar-shaped metaxylem strand in cross-section with adaxial protoxylem groups near each margin. The lack of curvature of the foliar xylem places this genus between the Anachoropteridaceae and Botryopteridaceae; stelar and cortical anatomy with the bar-shaped petiolar xylem traces of *G. baldaufii* have been considered as a possible link with the Osmundaceae (Miller, 1971). The solid protostele of the Lower Permian *G. baldaufii* exhibits broader shorter tracheids in the center surrounded by typical tracheids, a type of protostelic anatomy which occurs in some Upper Permian Osmundaceae (Thamnopteroideae) (Miller, 1971). Features of the anatomy of *Grammatopteris baldaufii*, which have also merited comparisons with the Osmundaceae are the distinct indentations in the stelar xylem, apparently relating to leaf trace departures, and scattered nests of sclerenchyma within the middle cortex as well as thick-walled cells in the outer cortex. Compared to the interpretation given to *G. baldaufii* by Sahni (1932*b*), the revised description of Renault's *G. rigollotii* differs markedly (Corsin, 1937). The solid protostele of *G. rigollotii* consists of a mixture of large and small tracheids with multiseriate bordered pitting, and the surrounding zone of tracheids in radial rows were interpreted as secondary xylem (Corsin, 1937). The tendency for identations along the xylary margin in *G. rigollotii* (as in *G. baldaufii*) was interpreted as undulations of the secondary xylem around departing leaf traces. The tracheidal diameters of the central primary xylem and those of the leaf trace xylem were larger than tracheids of the secondary xylem which surrounds the protostele and portions of departing leaf traces (see Corsin, 1937: 19, fig. 2).

CATENOPTERIS—C-SHAPED FOLIAR XYLEM

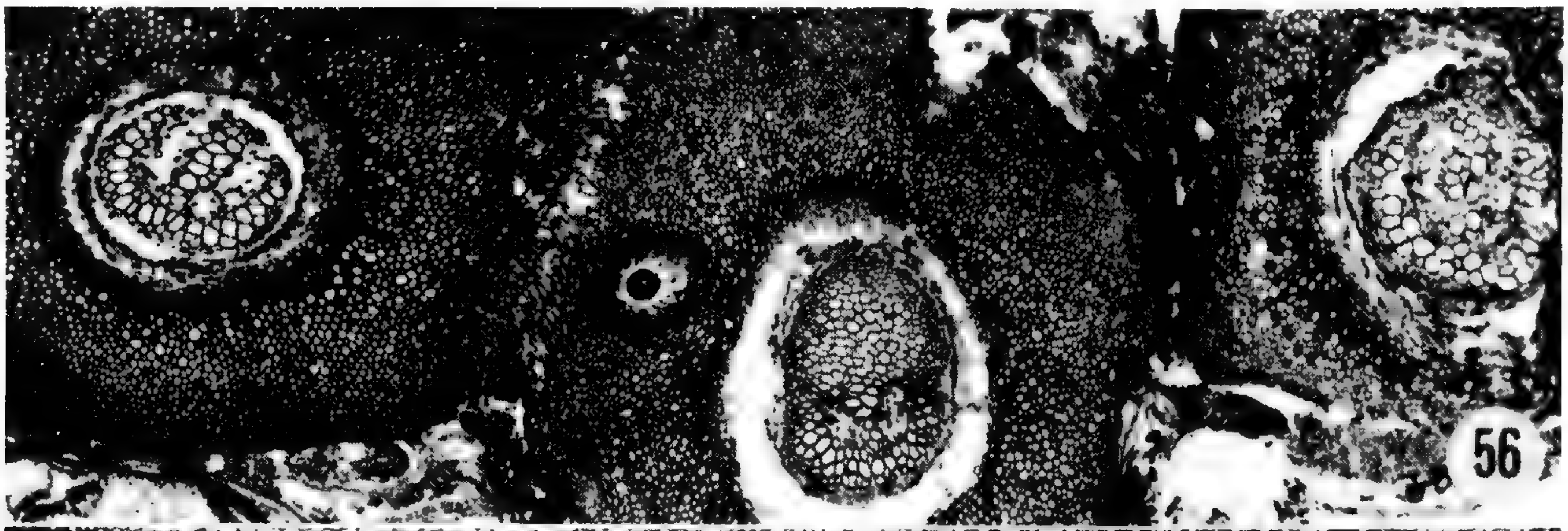
Catenopteris simplex is a small protostelic fern with adaxially curved shallow C-shaped foliar xylem similar to that of modern ferns such as *Osmunda* (Fig. 43E). Adaxial to each leaf trace is a decurrent lens of parenchyma extending down into the solid protostele which has scalariform metaxylem (Phillips & Andrews, 1966). In addition to roots from the stem a root occurs on the abaxial face of each leaf trace. *Catenopteris* in the Upper Pennsylvanian has been the only known coenopterid fern until recently with a simple catenalean C-shaped foliar xylem strand. Another fern with C-shaped foliar xylem and a siphonostelic stem has been discovered recently from the Upper Pennsylvanian of Indiana. To the extent that sectioning has progressed a leaf gap apparently occurs above leaf trace departure.

BOTRYOPTERIDACEAE

BOTRYOPTERIS—WHOLE PLANT GENUS

Among coenopterid genera with numerous species, *Botryopteris* with more than ten appears to be a natural assemblage and a prime example of a genus through geologic time (Visean to Permian) with diverging coherent phyletic lines. Vegetative species have been based on stratigraphically disjunct forms emphasizing changes in anatomy and geometry. For example, *B. tridentata* is separable from *B. ramosa* largely on the basis of its siphonostelic stem (Figs. 79–80) at the Westphalian A-B boundary; *B. ramosa* occurs in the lower Westphalian A. At higher stratigraphic horizons *B. tridentata* foliar members have more prominent adaxial xylary ridges than *B. ramosa* (Figs. 63–65F, G).

Botryopteris is known from over 30 stratigraphic horizons in the Pennsylvanian of the U.S.A., western Europe and the Donetz Basin of the U.S.S.R., and the same species occur across these areas in coal balls and other petrifactions of stratigraphically similar ages. *Botryopteris tridentata* is known from the U.S.S.R. (Snigirevskaya, 1961, 1962), West Germany (Felix, 1886), and across the U.S.A. from Kentucky to Kansas. The recent study by Galtier (1971) of the type material of *B. forensis* from France (Renault, 1875) allows recognition of the same species in the U.S.A., described under the names of *B. americana* (Figs. 56, 65D–E, 73), *B. trisecta* (Figs. 65H, 69, 70), and in part specimens assigned to *B. globosa* (Graham, 1935; Mamay & Andrews, 1950; Delevoryas & Morgan, 1954*a*; Murdy & Andrews, 1957; Phillips 1961, 1966; Phillips & Rosso, 1970).



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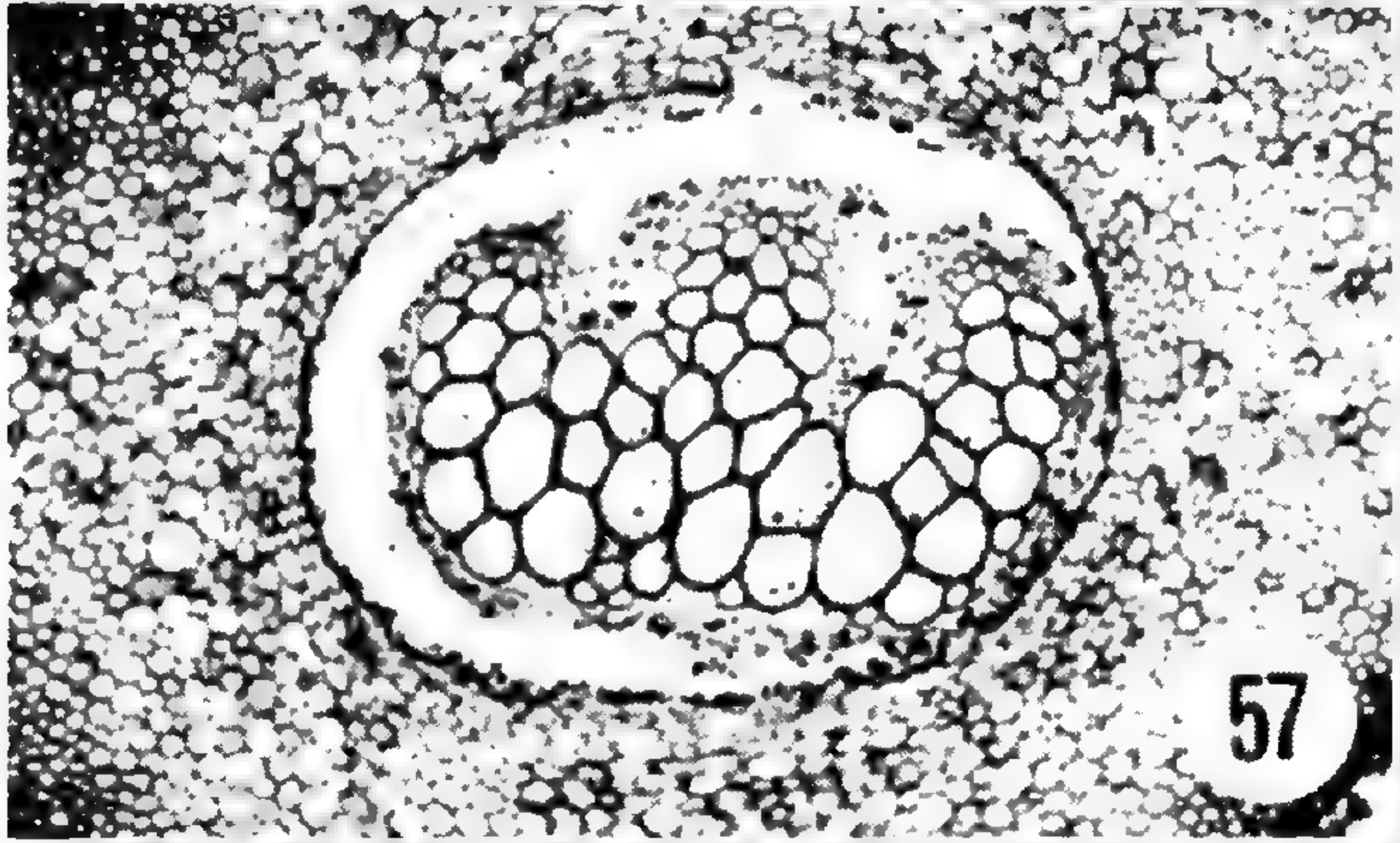

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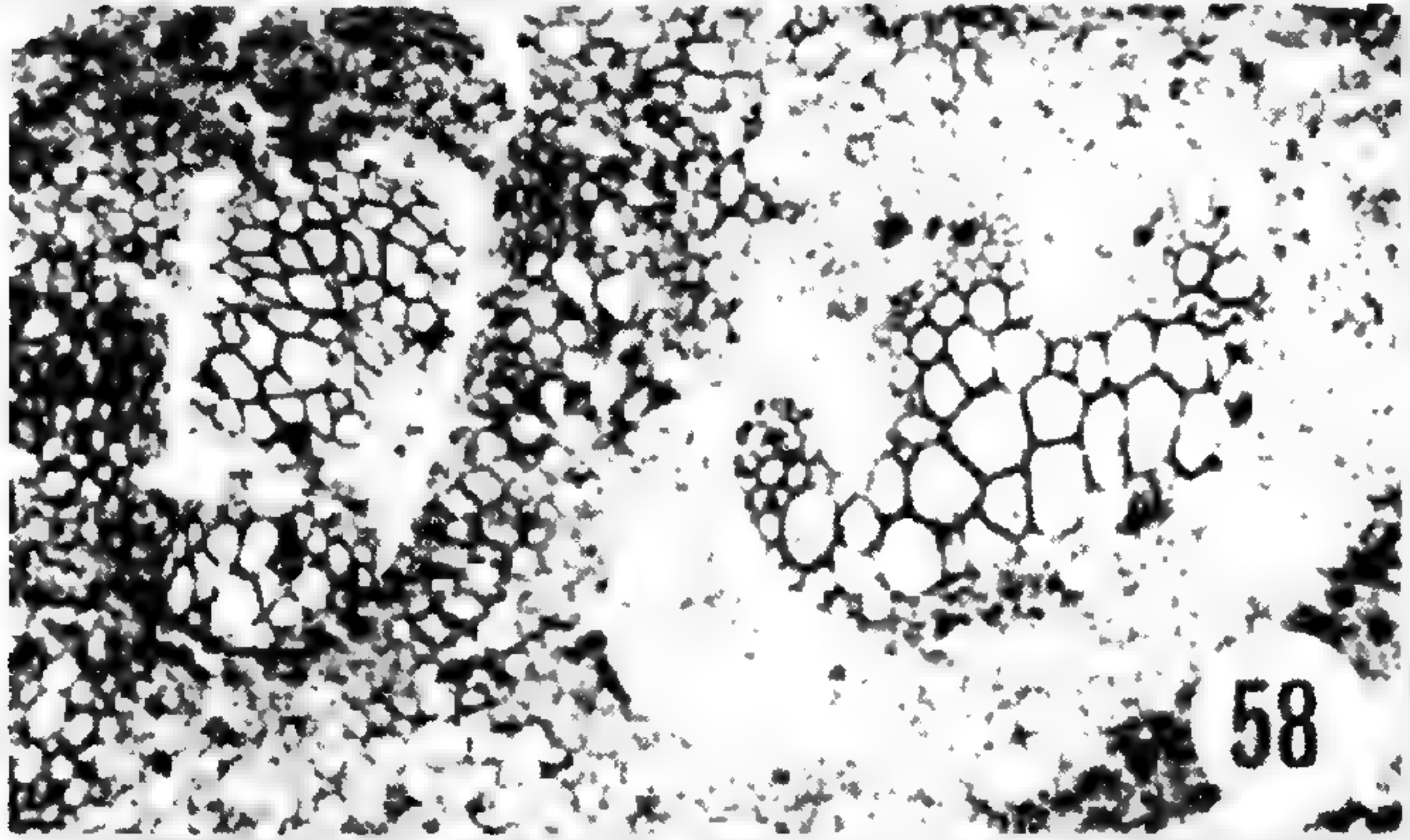

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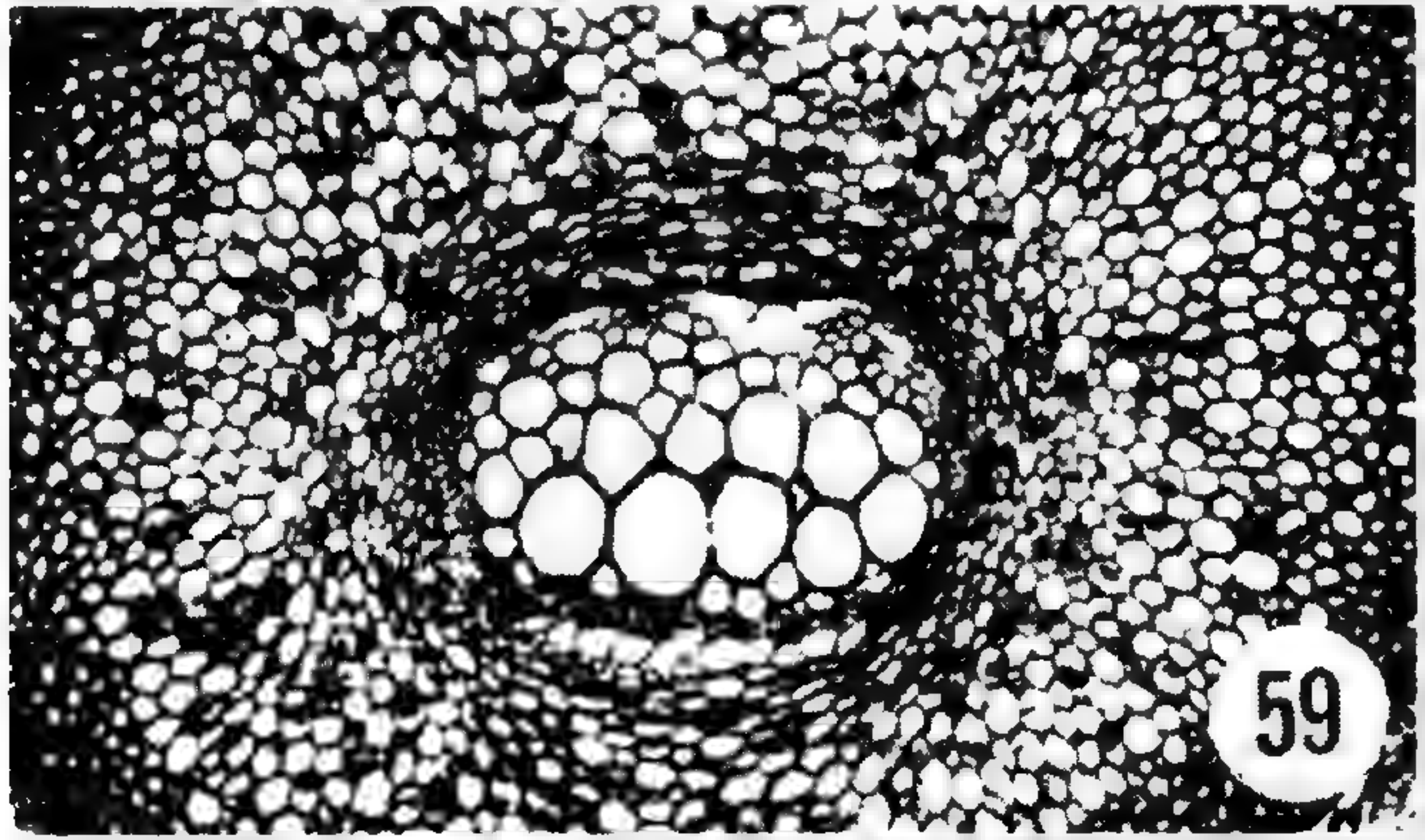

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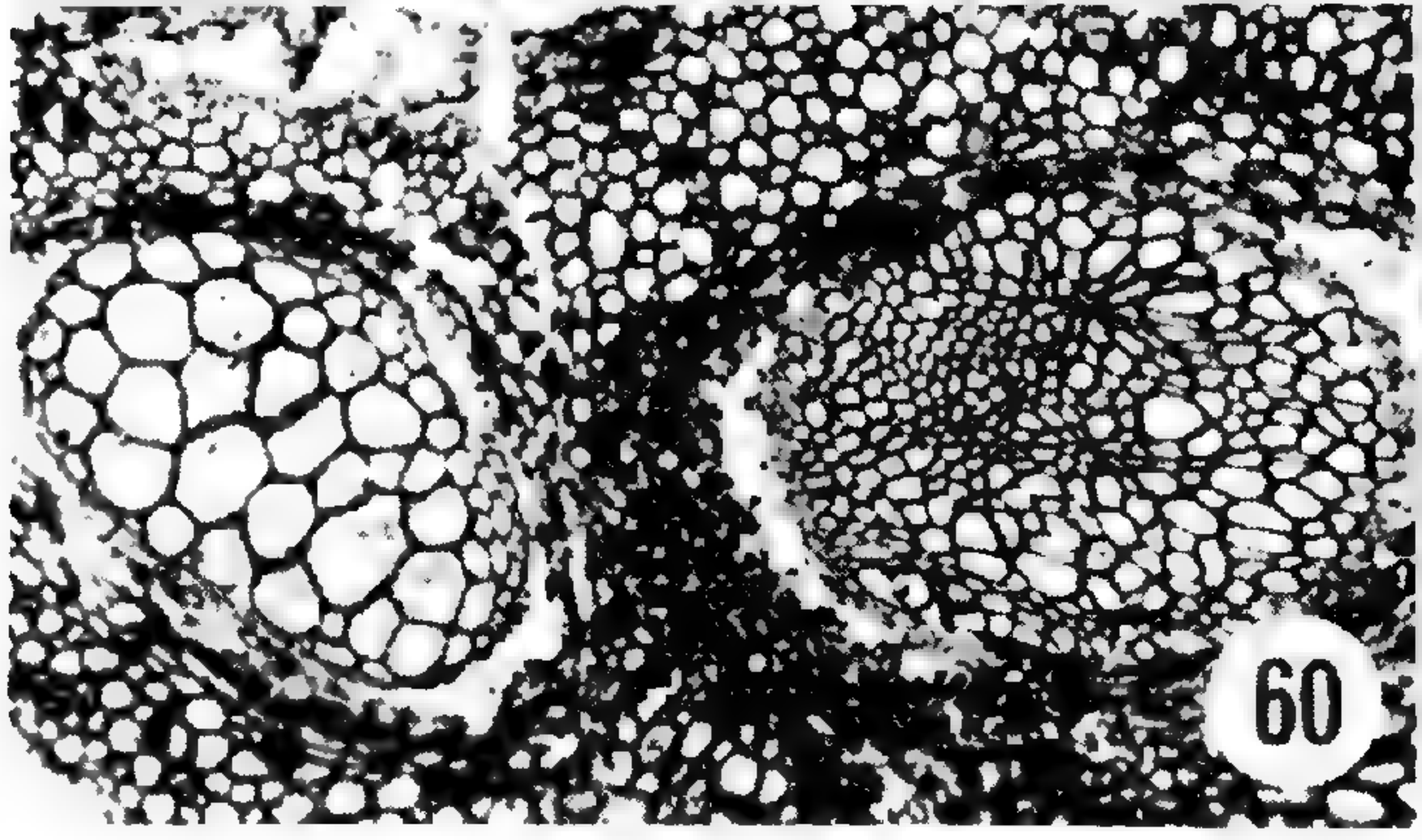

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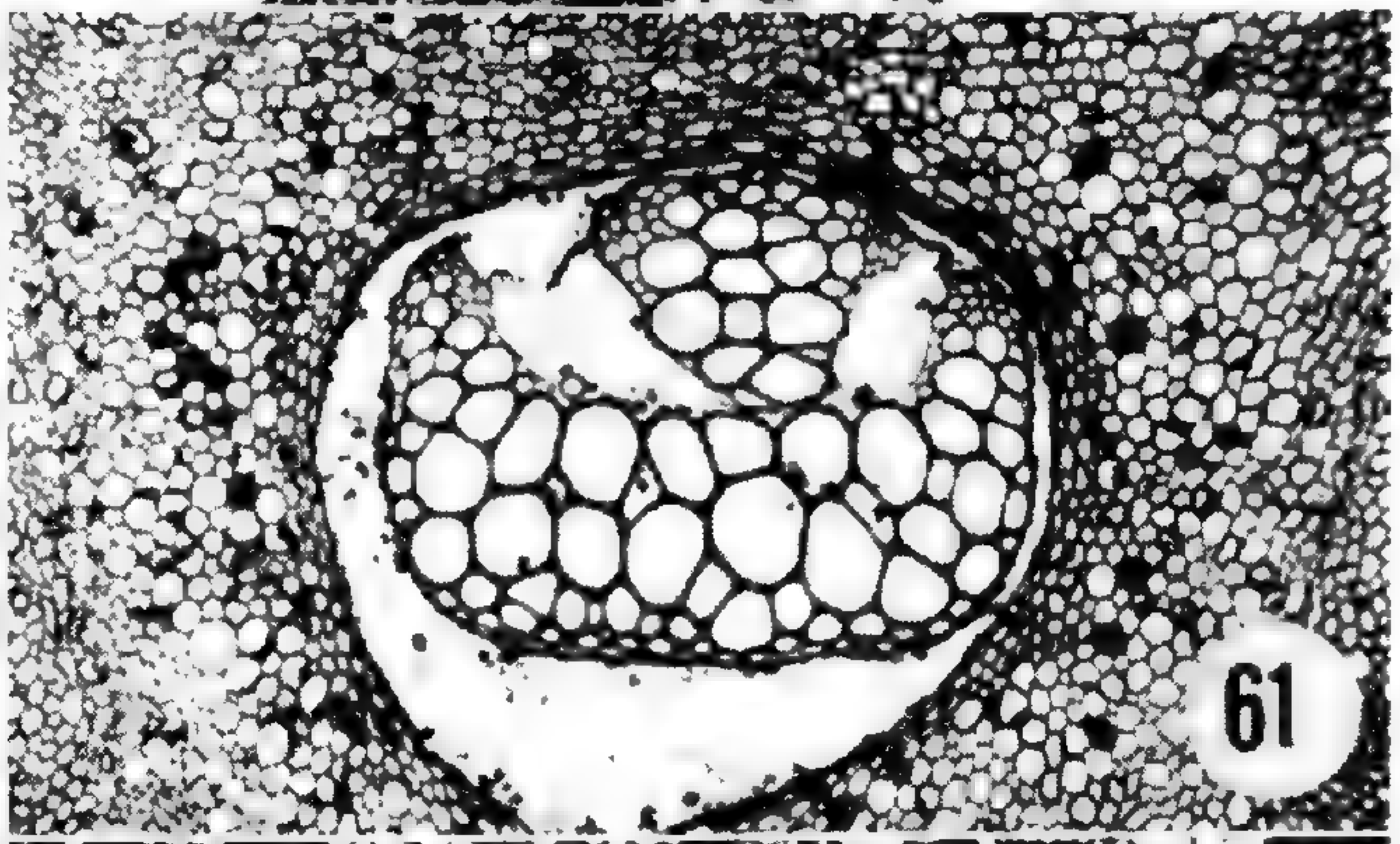

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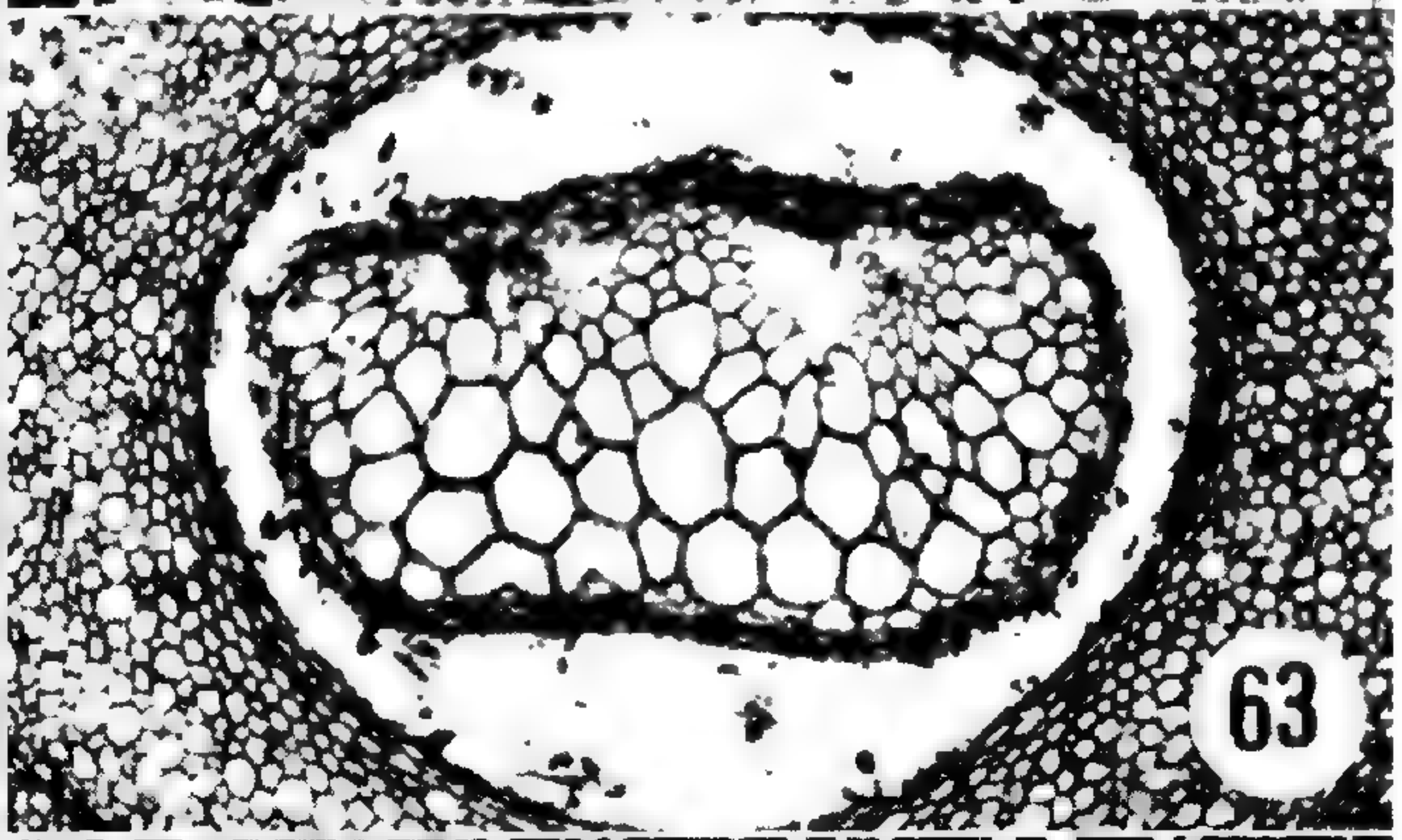

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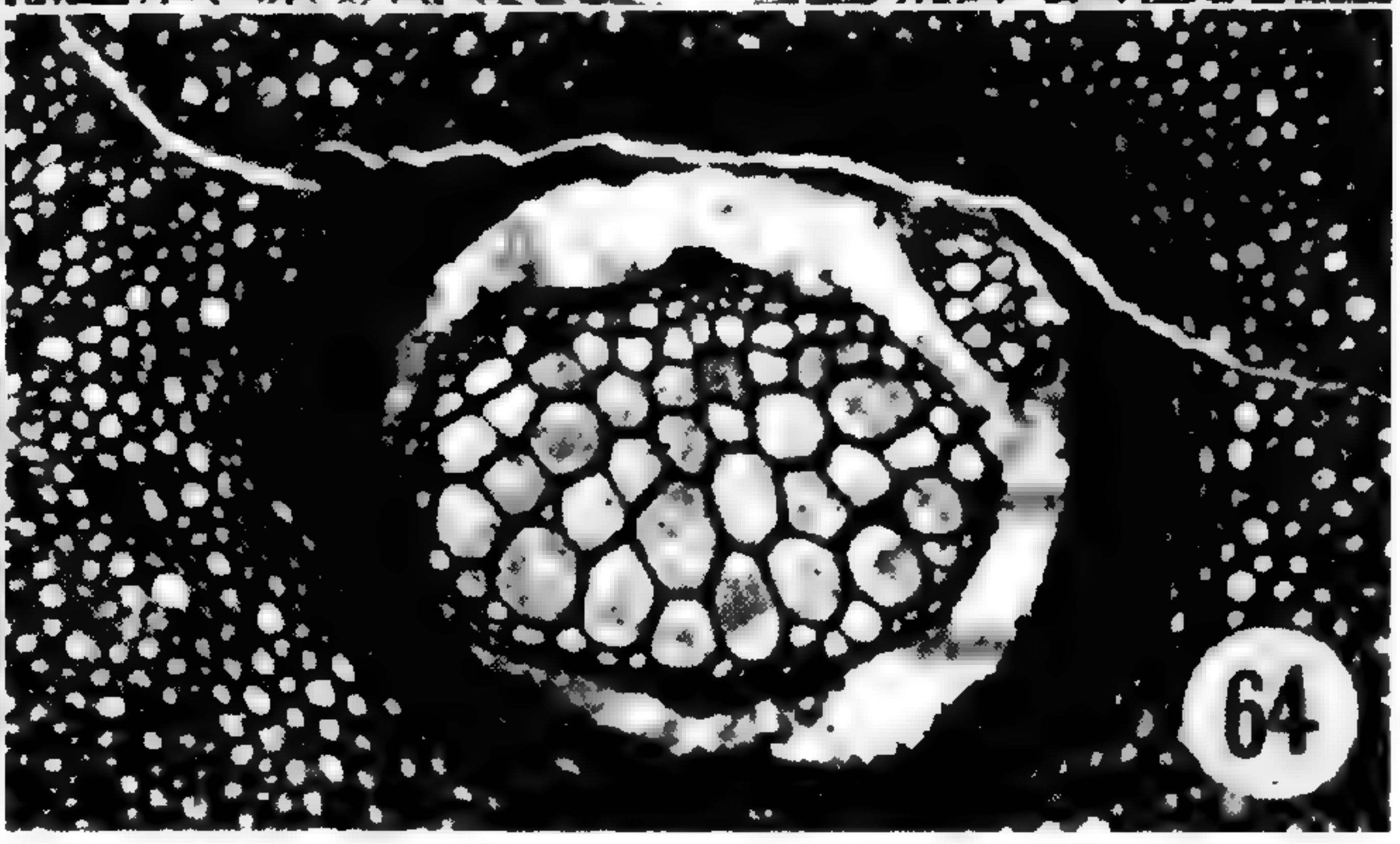

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Three divergent phyletic lines of *Botryopteris* evolved between the earliest appearing Visean assemblages of *B. antiqua* (Fig. 60), and the lower Westphalian A species, *B. hirsuta* (Fig. 59), *B. ramosa* (Fig. 64), and *B. mucilaginosa* (Fig. 62). These three specific epithets are convenient designations for the phyletic lines; a fourth, anatomically simpler, line parallels these and is designated the "pseudoantiqua" line (Fig. 66). The *B. hirsuta* line includes *B. forensis* and intermediate forms which have not been described yet (Figs. 57–58); in the *B. mucilaginosa* line is an undescribed Middle Pennsylvanian species (Fig. 61) and also the Stephanian *B. renaultii* (Corsin, 1937); *B. tridentata* is allied with *B. ramosa.*

The common anatomical features of the foliar members of *Botryopteris* are the somewhat elliptical vascular strand in cross-section with protoxylem located always medianly on the adaxial face and at some stage with lateral adaxial protoxylem groups which are associated with lateral divisions. The evolutionary changes in foliar xylem configurations from a *B. antiqua* type are the progressive decurrence of lateral protoxylary groups to a median group of protoxylem and the elaboration of xylem geometry (cross-sectional) into three adaxial ridges and finally into three adaxial xylem arms (Figs. 56–64). The appearance of adaxial xylary ridges or arms establishes an adaxially curved strand in most species of *Botryopteris*, but the primitive ellipsoidal configuration occurs across the Pennsylvanian in the "pseudoantiqua" line (Figs. 66–68).

Bilateral symmetry, pinnate branching, circinate vernation, sporangia-bearing, laminate pinnule-bearing, and phyllotactic arrangement of foliar members on shoots collectively attest the foliar interpretation given them. Apart from the bearing of fronds, *Botryopteris* stems are not known to branch, with the possible exception of *B. mucilaginosa* (Kraentzel, 1934). Shoots occur on the fronds in *Botryopteris* and effect vegetative propagation.

Branching patterns of the fronds of *Botryopteris* provide distinctions among the three divergent lines. Fronds are pinnately branched and have both pinnae and shoots. In the *B. mucilaginosa* line the shoots are borne adaxially (Figs. 43A, 72, 77) as in some *Anachoropteris involuta* types (Fig. 43B). In the other phyletic lines shoots are lateral, occurring along various orders of the frond except in laminate and fertile portions; the shoots occupy positions comparable to pinnae or at the bases of foliar members. The details of lateral cauline trace formation differ in the *B. hirsuta* and *B. ramosa* lines (Fig. 65); minor differences occur within each concomitant with changes in xylary configurations.

Frond morphology in *Botryopteris forensis* consists of a pinnately compound

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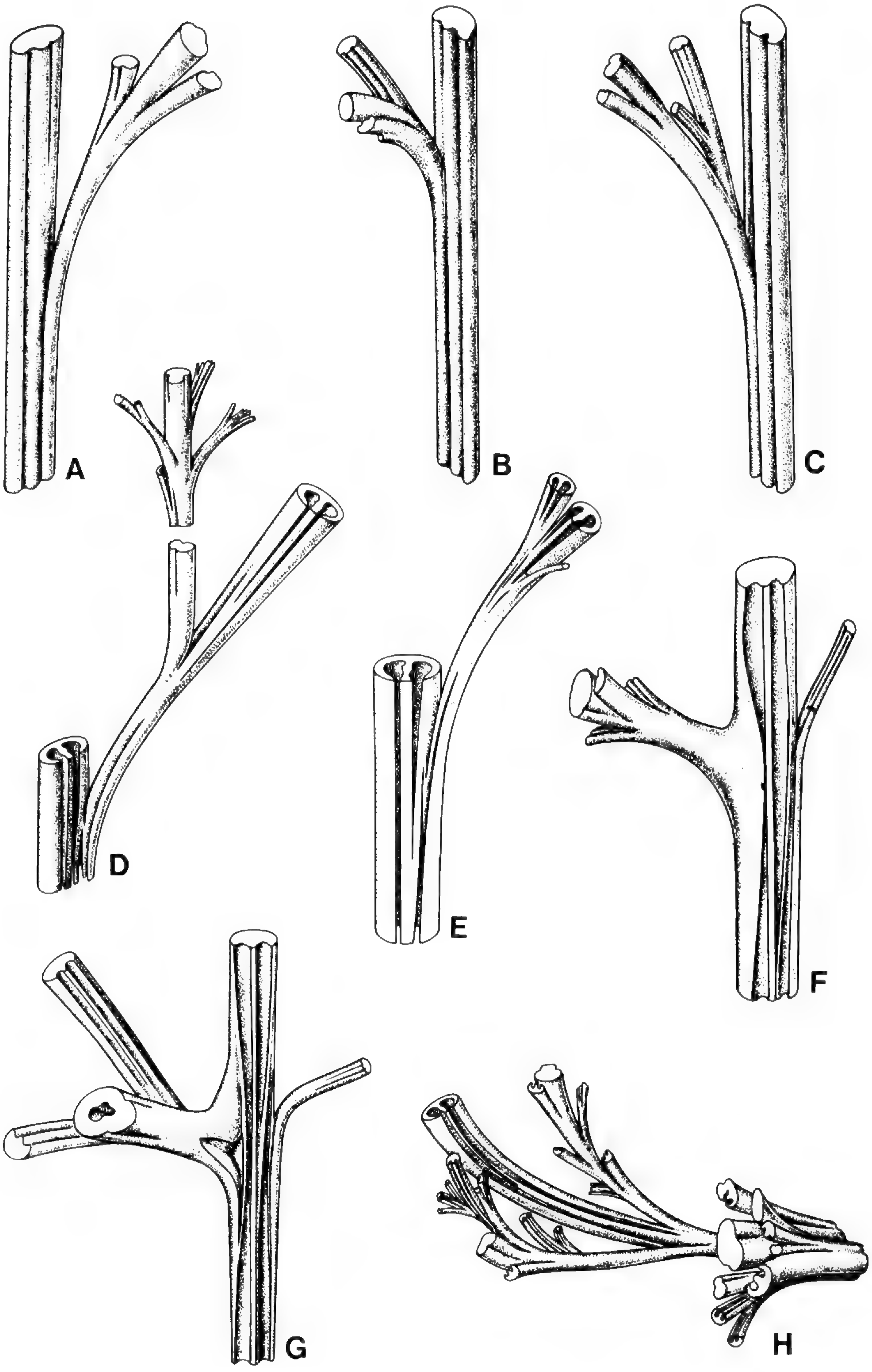
FIGURES 56–64. Foliar members of *Botryopteris* in x.s. × 25 except Fig. 56.—56. *B. forensis* with rachis (right), primary pinna (left) with shoot bearing petiolar trace. Calhoun Coal, Illinois. × 10.—57. *Botryopteris* sp. Pottsville Group, Kentucky.—58. *Botryopteris* sp. with trace. Westphalian A-B boundary, West Germany.—59. *B. hirsuta*, lower Westphalian A, England.—60. *B. antiqua* with cauline trace (right). Visean, Scotland.—61. *Botryopteris* sp. Herrin Coal, Illinois.—62. *B. mucilaginosa*, lower Westphalian A, Belgium.—63. *B. tridentata.* Mineral Coal, Kansas.—64. *B. ramosa* with pinna trace, lower Westphalian A, England.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foliar system with lower orders of pinnae slightly turned out of the plane of the rachis and clearly planated distal divisions with laminate pinnules (Delevoryas & Morgan, 1954*a*); strongly three-dimensional branching occurs in fertile pinnae complexes and foliar members on shoots at frond bases. Such densely branched non-laminate pinnae are adaxially oriented toward their parent foliar members, and with spatial limitations around the main rhizome (Fig. 65H) the diminutive fronds on lateral shoots at the petiolar bases are extremely compacted. Fertile pinnae complexes are often borne singly at the base of a primary pinna which immediately terminates in a crozier.

Frond branching in *Botryopteris antiqua* (Long, 1943; Surange, 1952; Holden, 1962; Galtier, 1969, 1970), *B. hirsuta* (Long, 1943), and *B. forensis* (Phillips, 1961) shows considerable variation in the relationship of shoots to pinnae. The typical branching patterns involving lateral cauline trace formation may be compared in Figures 65A–D. The variations in *B. antiqua* (Galtier, 1970) include possibilities for deriving the patterns in all the phyletic lines. In *B. antiqua* the shoot is supplied with a cauline trace from a foliar member, and the first petiole is oriented with respect to foliar member bearing the shoot as a pinna would be; in *B. forensis*, except for shoots at petiolar bases, the shoot is similarly derived but at the base of a pinna (Figs. 65D, 73), and its first petiole is also oriented as a pinna. Stratigraphically between the two types are intermediate stages which exhibit a common trace (Figs. 65B–C, 74–75) from a foliar member, resulting in a stem and in a foliar member which may be regarded as either the first petiole of the stem or as the pinna which bears the shoot (Fig. 76).

In the *Botryopteris hirsuta* line, the gross organization does not seem to have changed between *B. antiqua* and *B. forensis*; the "pseudoantiqua" line apparently exhibited the same type of morphological organization, but it is not as well known. Evolutionary changes in the *B. hirsuta* line include lamina development (Galtier, 1970; Delevoryas & Morgan, 1954*a*), changes in pitting from multiseriate scalariform to multiseriate elliptical to circular bordered pitting (Phillips, 1970), and apparently an increase in the overall dimensions of stems and leaves. The largest rhizomes of *B. forensis* are about 1 cm in diameter and frond bases are up to 8 mm wide. Elliptical to circular bordered pitting seems to have occurred geologically in foliar members first; multiseriate scalariform bordered pitting is characteristic of the stems of *B. antiqua* and is regarded as the primitive type in *Botryopteris* as it is in one line of *Tubicaulis* species (Eggert, 1959*b*). Laminate pinnules also occur in the *B. ramosa* line (Fig. 81), and some orders of the frond in the "pseudoantiqua" line developed winged margins (alations) (Fig. 67). Compression specimens of sterile laminate pin-

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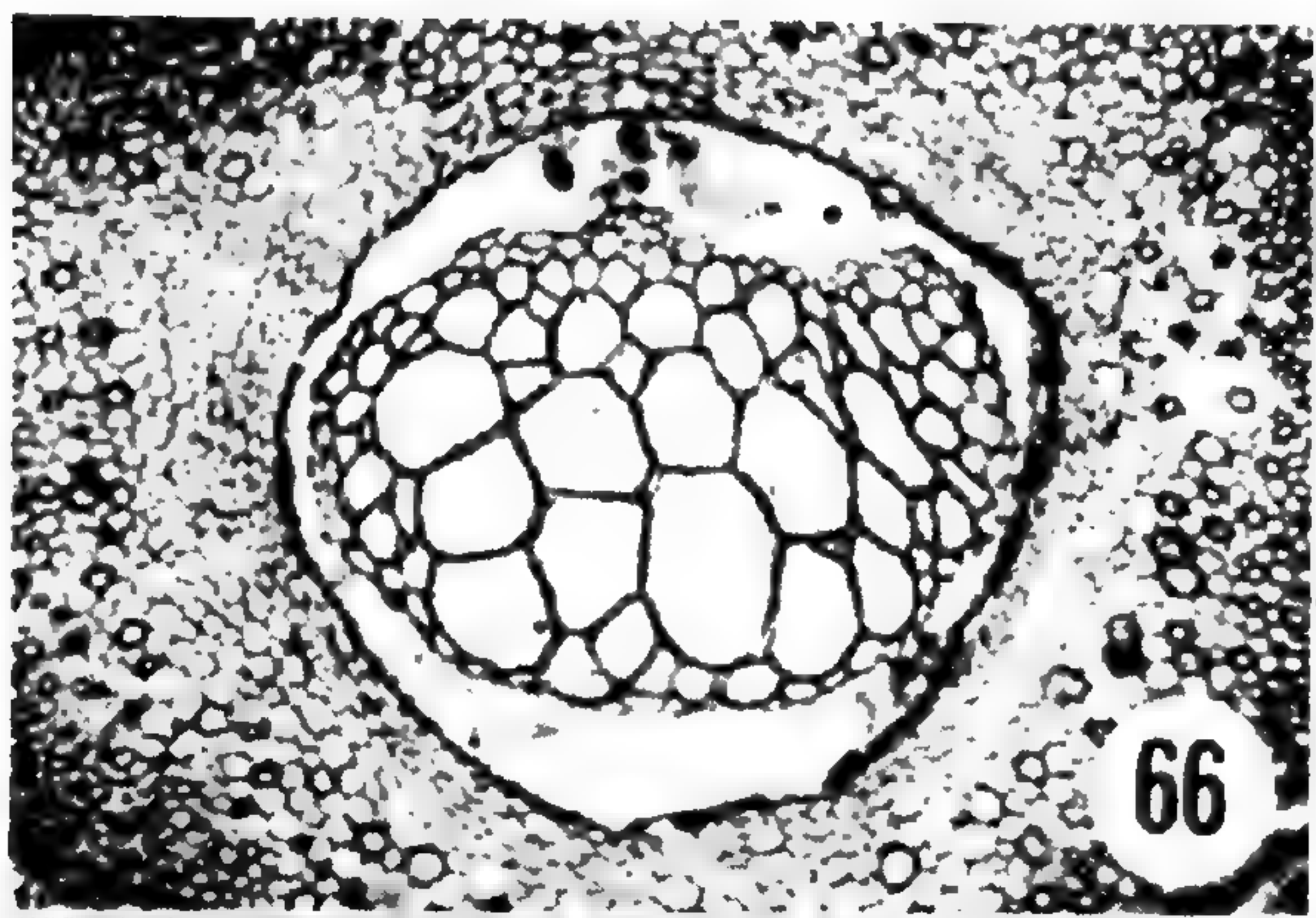
FIGURE 65. Xylary reconstructions of branching in *Botryopteris* with shoots and pinnae on foliar members.—A. *B. antiqua.*—B. *B. hirsuta.*—C. *Botryopteris* sp.—D. *B. forensis.*—E. *B. forensis*, all foliar.—F. *B. ramosa.*—G. *B. tridentata* with siphonostele.—H. *B. forensis* (= *B. trisecta*) with prostrate rhizome bearing three petiolar traces, each with cauline traces or lateral shoots. Drawings modified, in part, from Phillips (1961, 1970).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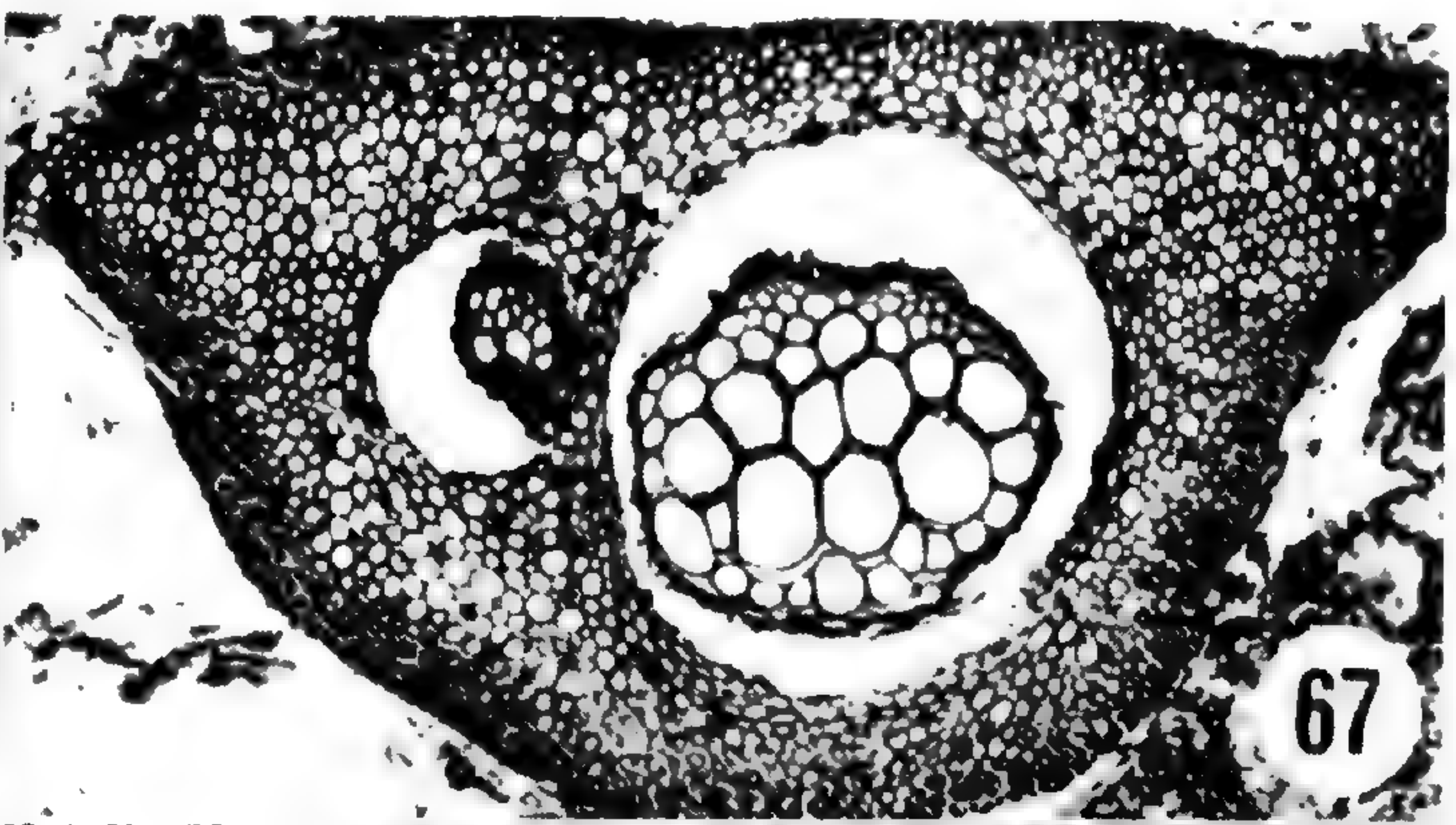
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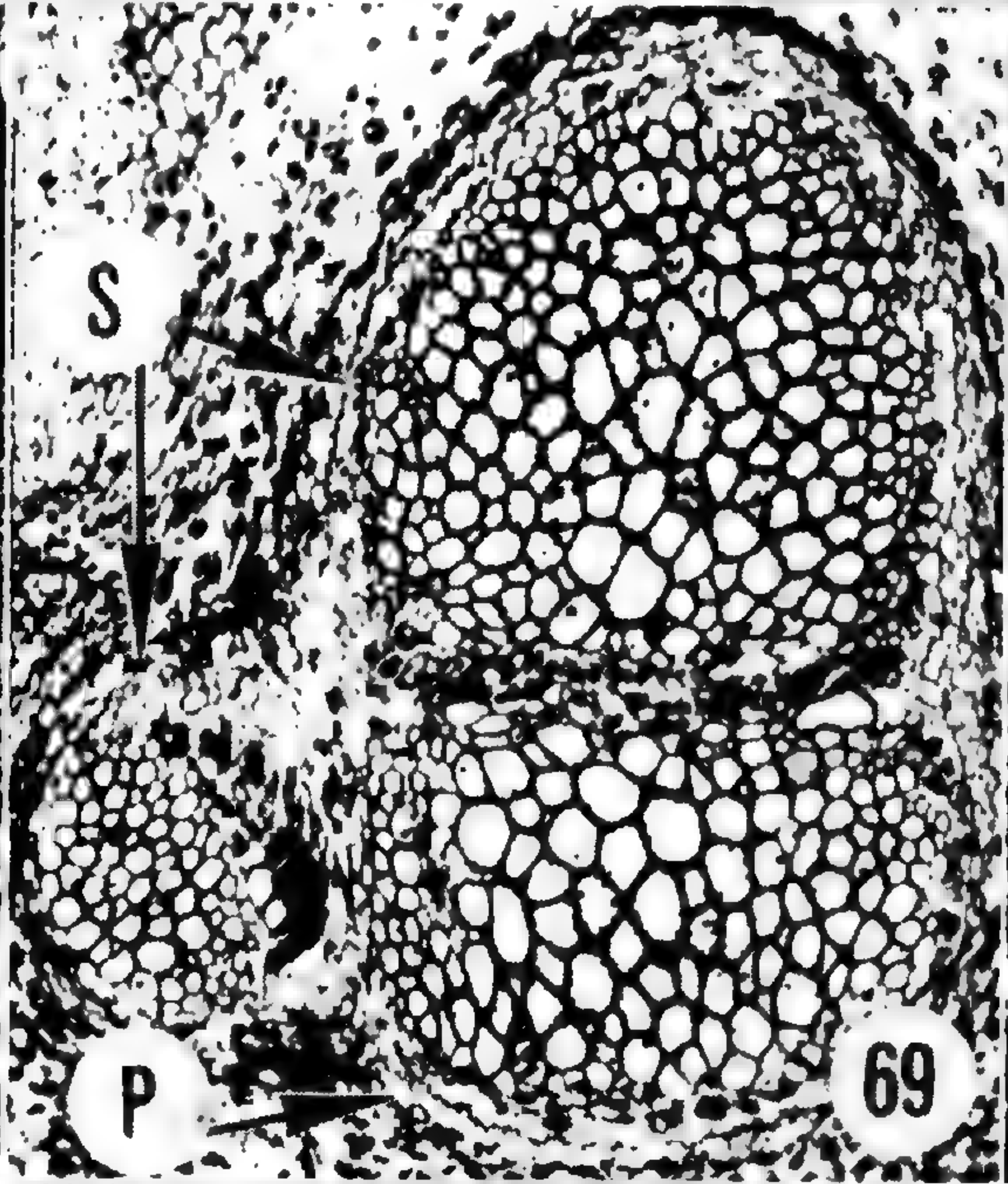

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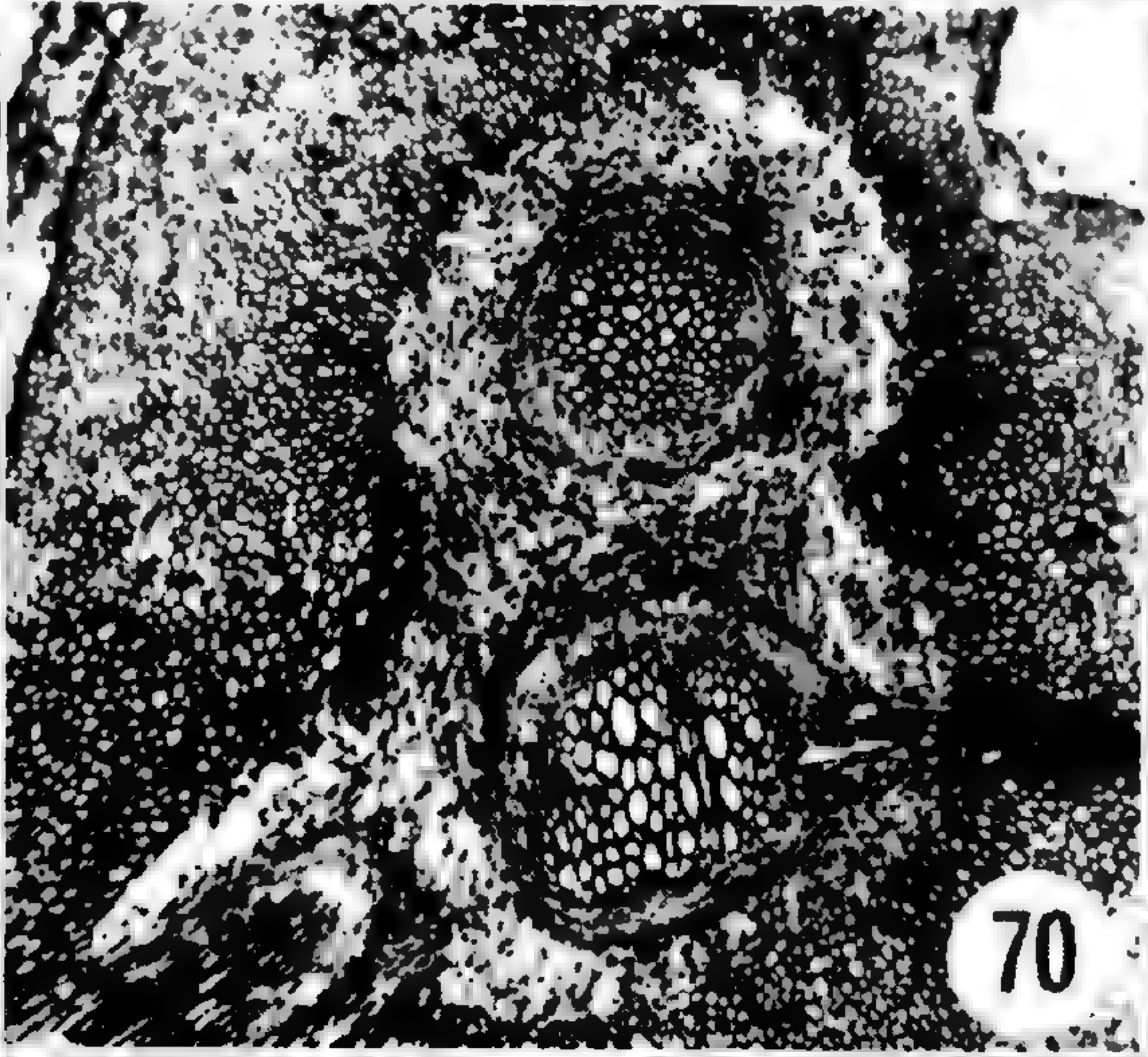
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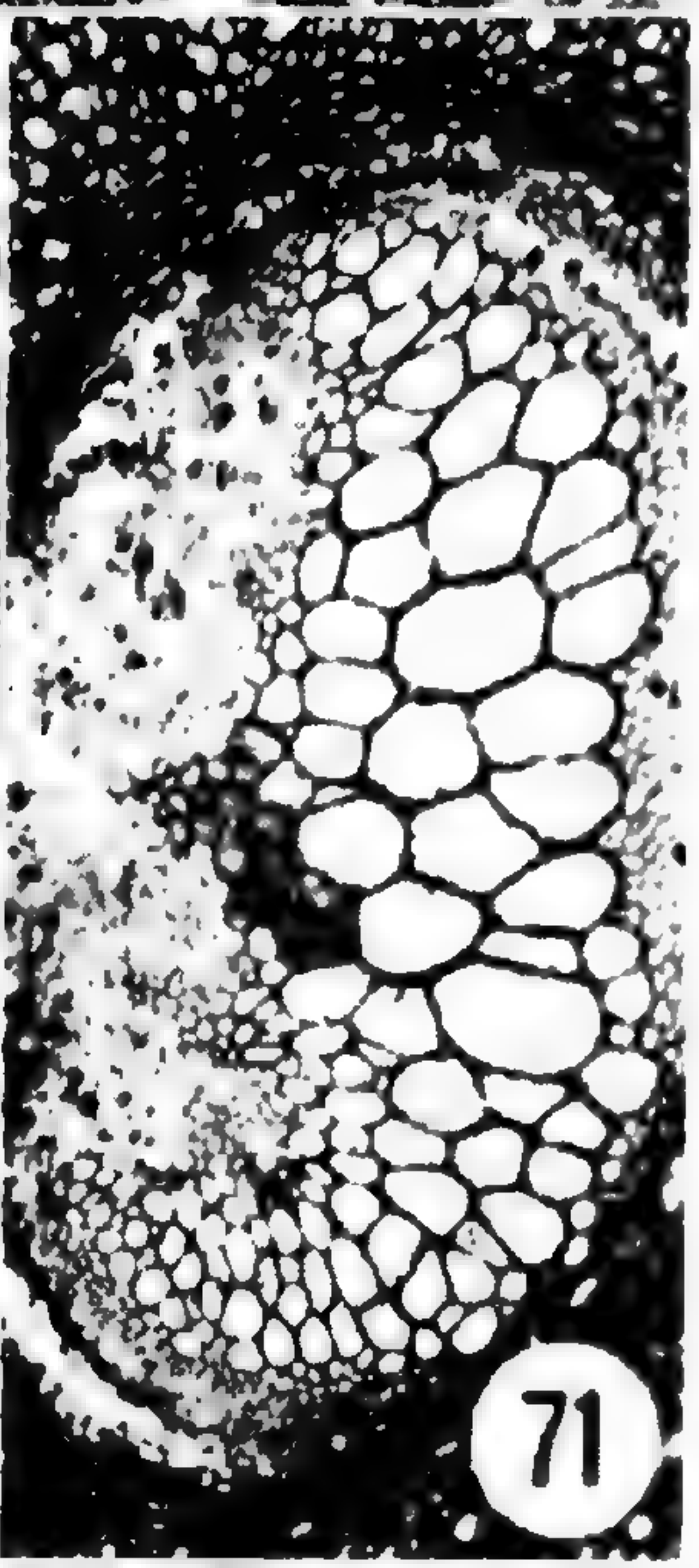
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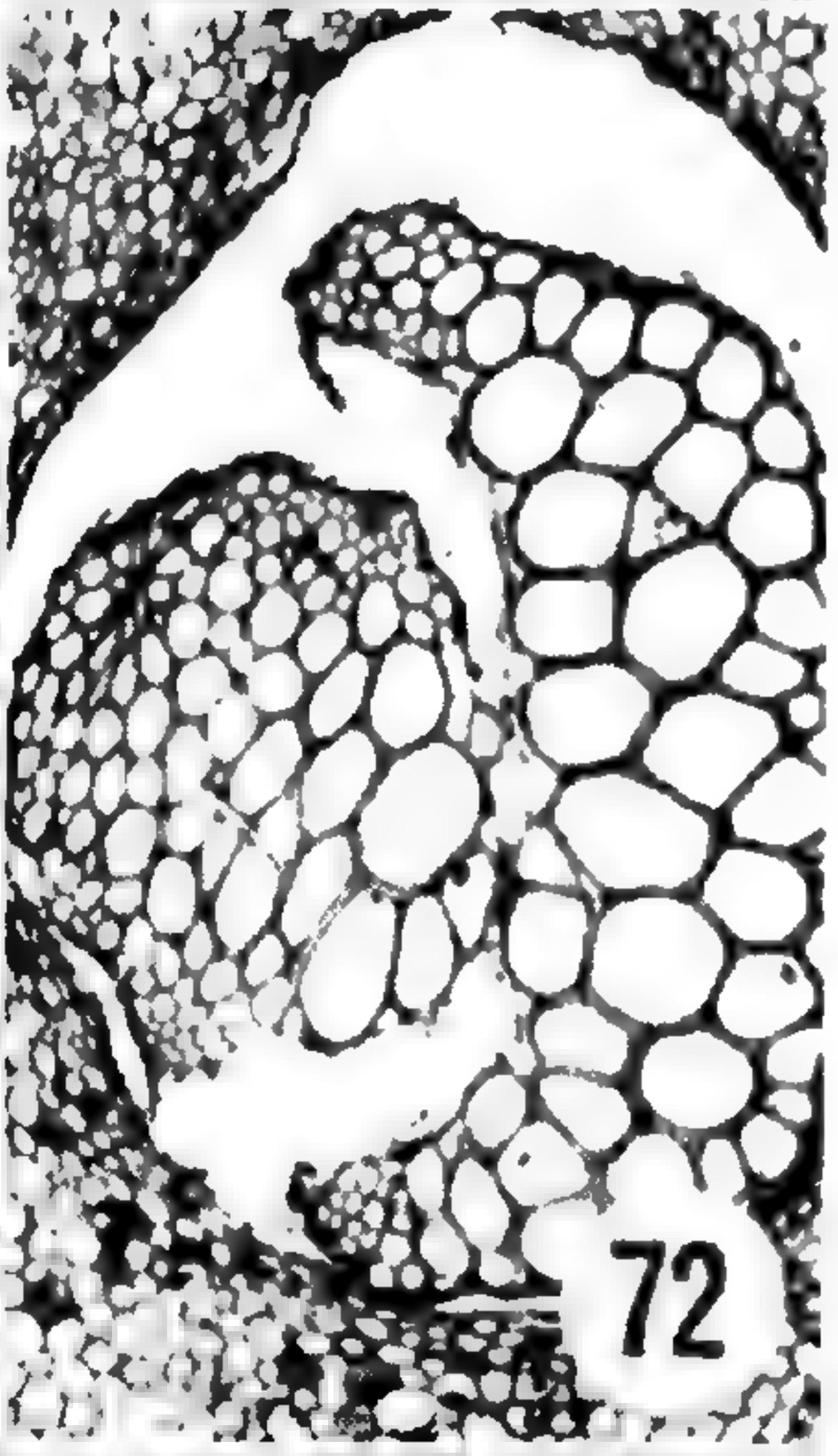
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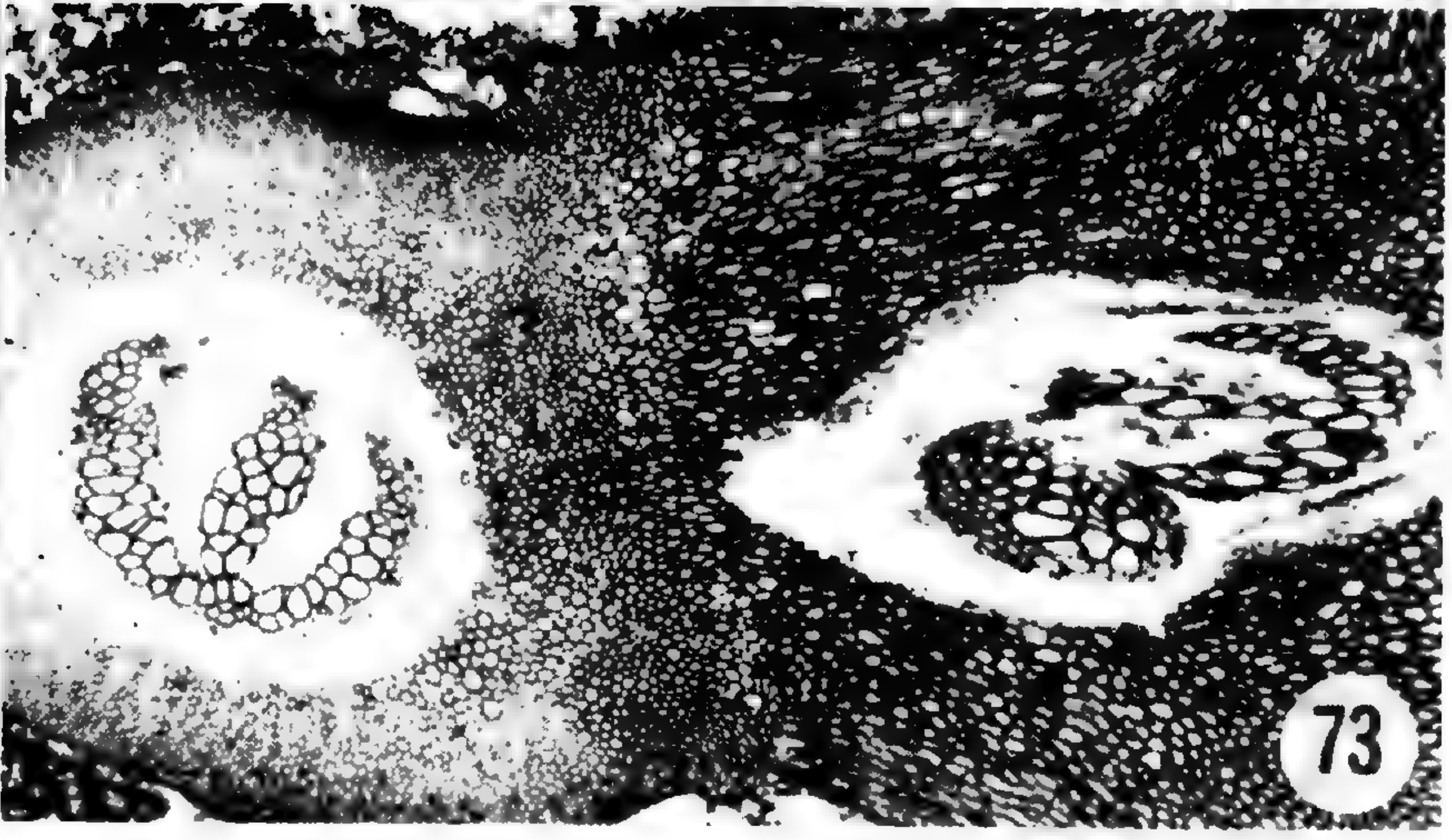
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nules of *Botryopteris* have been reported from the Permian of the Döhlen Basin by Barthel (1970); the foliage is referred to as *Sphenopteris burgkensis.*

Botryopteris stems have terete solid protosteles except *B. tridentata* and bear spirally arranged fronds and diarch roots. The habit in the *B. hirsuta* line (based on *B. antiqua* and *B. forensis*) is a prostrate rhizome with semi-erect apex, as in *Osmunda*, with fronds spaced less closely than in *Tubicaulis.* The same habit is postulated for the *B. ramosa* and "pseudoantiqua" lines. The *B. mucilaginosa* group may have been erect, climbing plants. The stem cortex of the *B. mucilaginosa* line contains distinct clusters of elongate, thick-walled cells with peculiar deposits.

In *B. forensis* (*B. trisecta* of Mamay & Andrews, 1950; Phillips, 1961, 1966) the occurrence of lateral stems on petiolar bases results in a dense "false stem" composed of hundreds of foliar members, their divisions and parent stems around the main rhizome and its fronds (Fig. 65H). This aggregation is up to 15 cm across. In *B. forensis*, *B. antiqua* (Phillips, 1970), and the "pseudoantiqua" line the petiolar traces from the main rhizome (Figs. 68–70) bear one or two lateral cauline traces which in turn bear fronds with compact foliar divisions. Some of the larger lateral shoots may in turn have lateral shoots at their petiolar bases, but this is exceptional.

The evolutionary interpretations of frond morphology in *B. forensis* and the *B. hirsuta* line as a whole are that the frond has evolved from a branch system, having achieved a distinction between cauline and foliar morphology in *B. antiqua.* There has been a progressive planation of foliar branching, achieved in part by *B. antiqua* fronds (Galtier, 1970), and lamination occurred in the *B. hirsuta* stage and was well developed in higher stratigraphic forms (Fig. 57; Delevoryas & Morgan, 1954*a*). The dense, three-dimensional non-laminate branching of fronds on lateral shoots at petiolar bases and in fertile pinna complexes of *B. forensis* may be indicative of primitive branching patterns in forms ancestral to *Botryopteris.* Shoots on fronds throughout the genus probably have evolutionary significance in that the morphogenetic flexibility of apical organization for either foliar or cauline development is consistent with a megaphyllous origin in which the expressions of foliar and cauline morphology are distinct but intermixed. Vegetative propagation is a functional significance of frond-borne shoots in *Botryopteris* as has been suggested in *Anachoropteris* by Hall

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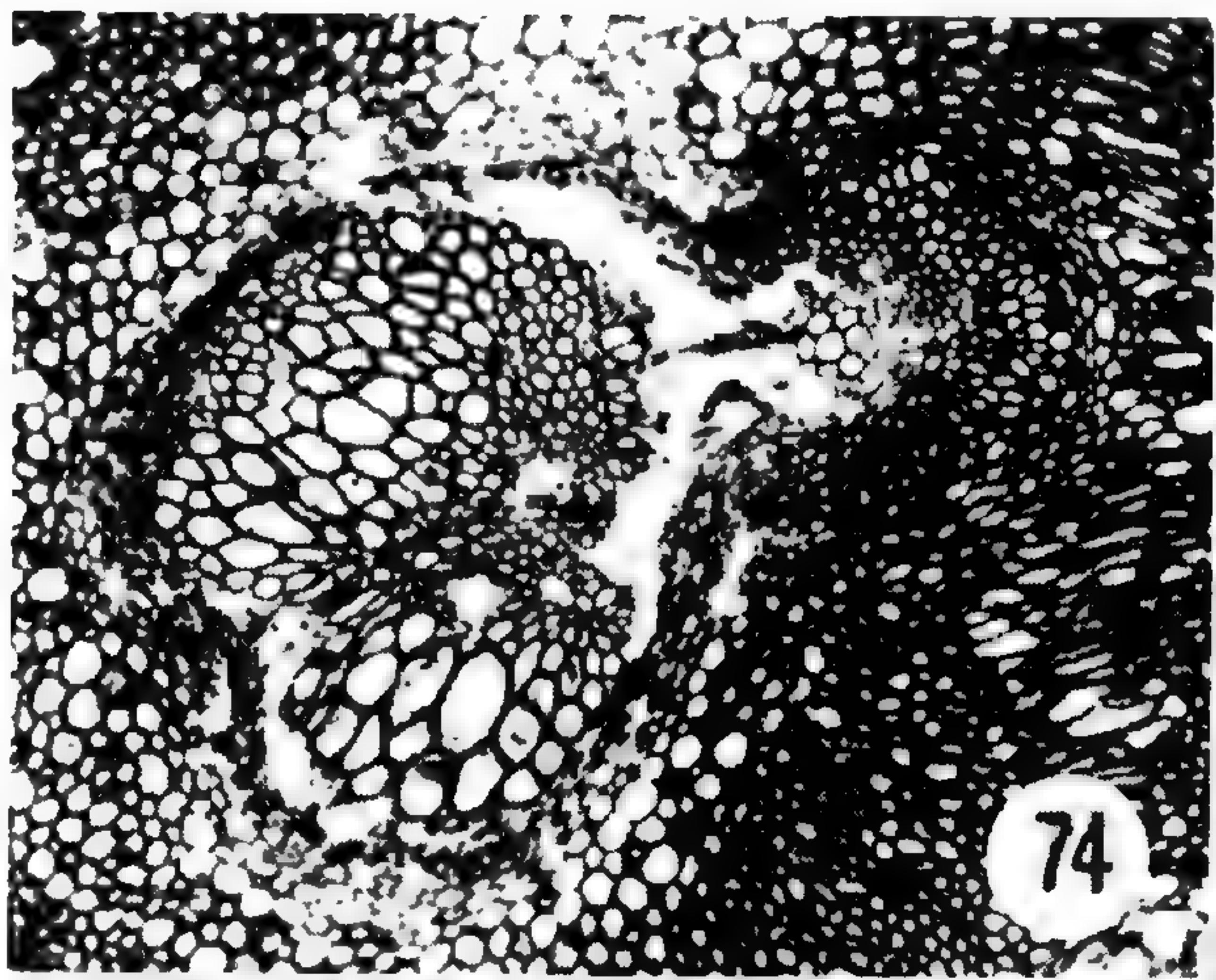
FIGURES 66–73. *Botryopteris* anatomical sections.—66–67. Foliar members of "pseudoantiqua" line. Parker Coal, Indiana and Pottsville Group, Kentucky. × 25.—68. Oblique tangential section of rhizome of "pseudoantiqua" line showing petiolar trace (F) and its lateral cauline trace (S) below and main rhizome stele and petiolar traces at top. Herrin Coal, Illinois. × 10.—69. *B. forensis* (= *B. trisecta*), cross-section of stele of rhizome with petiolar trace (P) and its lateral cauline trace. Cauline steles (S). Calhoun Coal, Illinois. × 10.—70. *B. forensis* (= *B. trisecta*), cross-section of rhizome stele (above) with petiolar trace bearing branch trace (left) and incipient branch trace and root (right). Calhoun Coal, Illinois. × 10.—71. *B. tridentata* foliar member x.s. at level of lateral incipient cauline trace formation. Mineral Coal, Kansas. × 25.—72. *Botryopteris* sp. foliar member x.s. at level of adaxial incipient cauline trace formation. Herrin Coal, Illinois. × 25.—73. *B. forensis*, foliar member (left) with its pinna bearing a cauline trace. Calhoun Coal, Illinois. × 10.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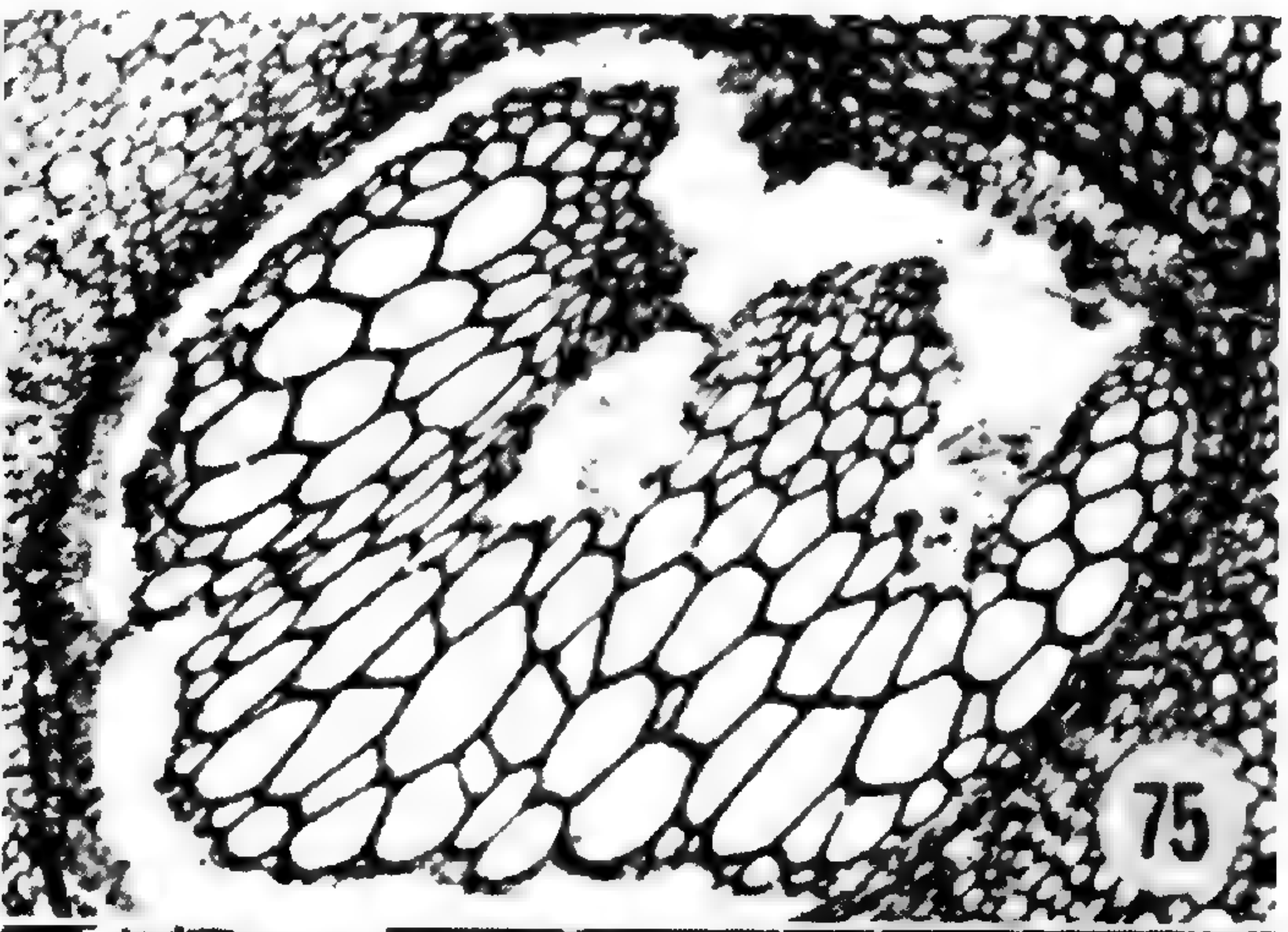
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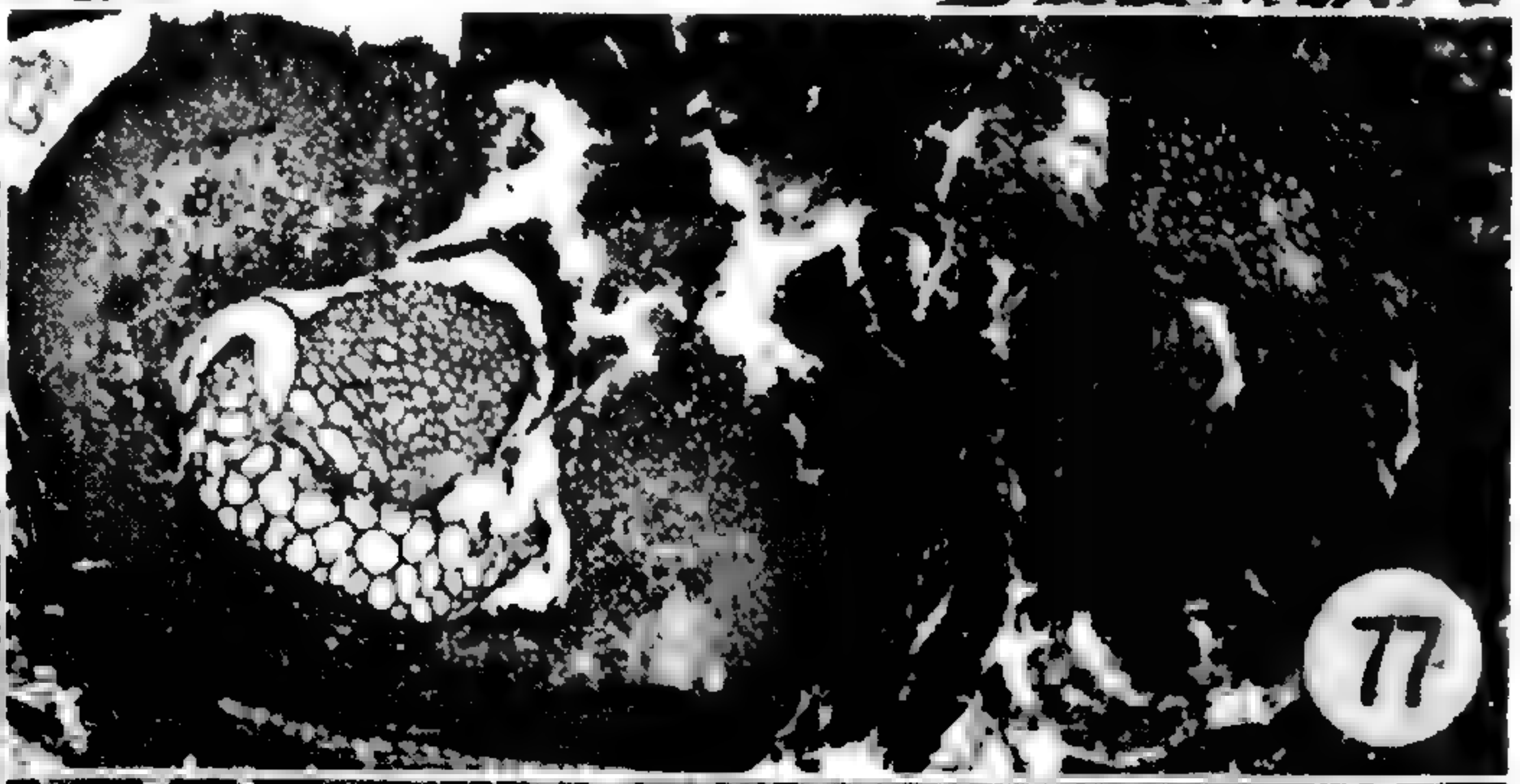
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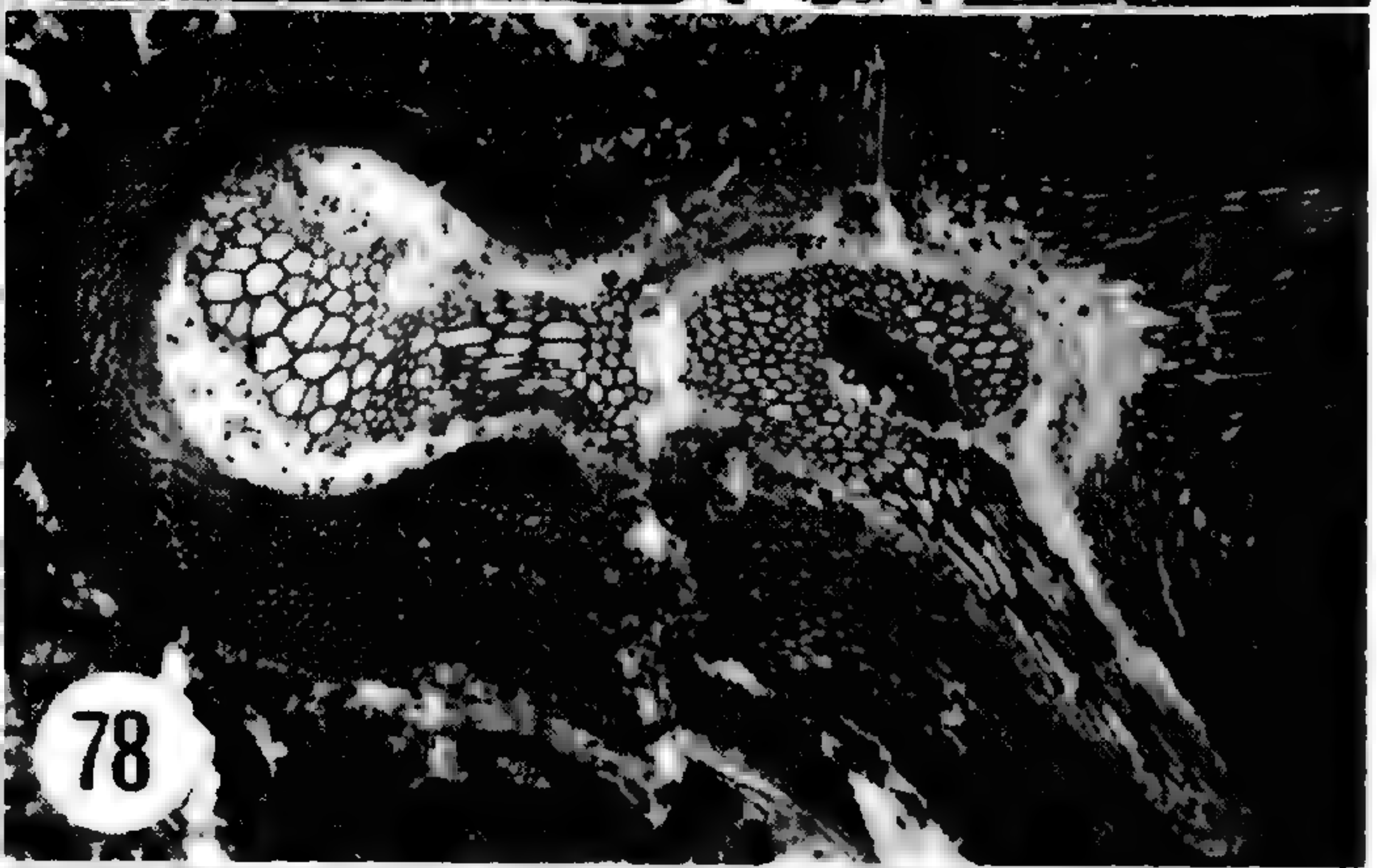
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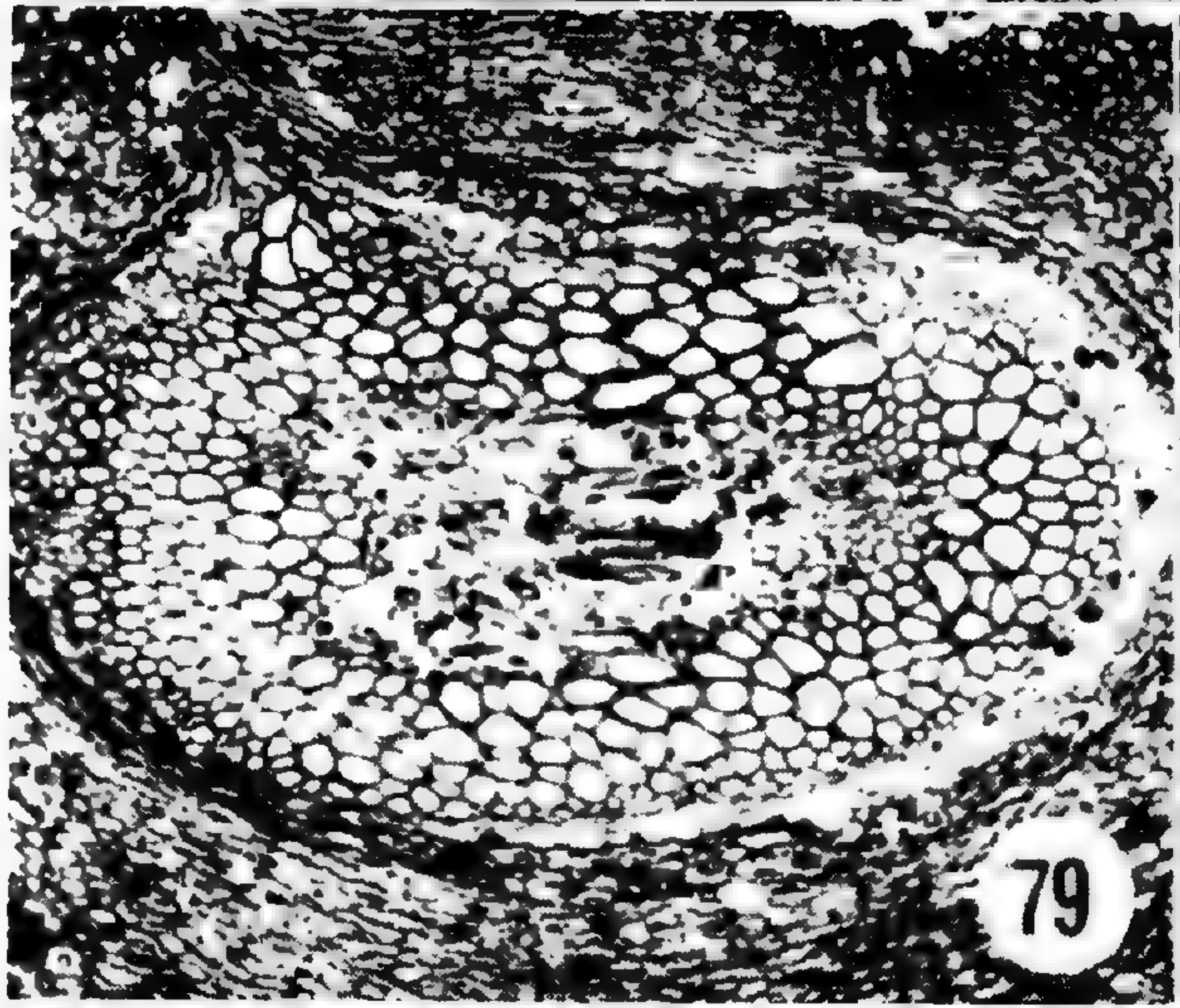
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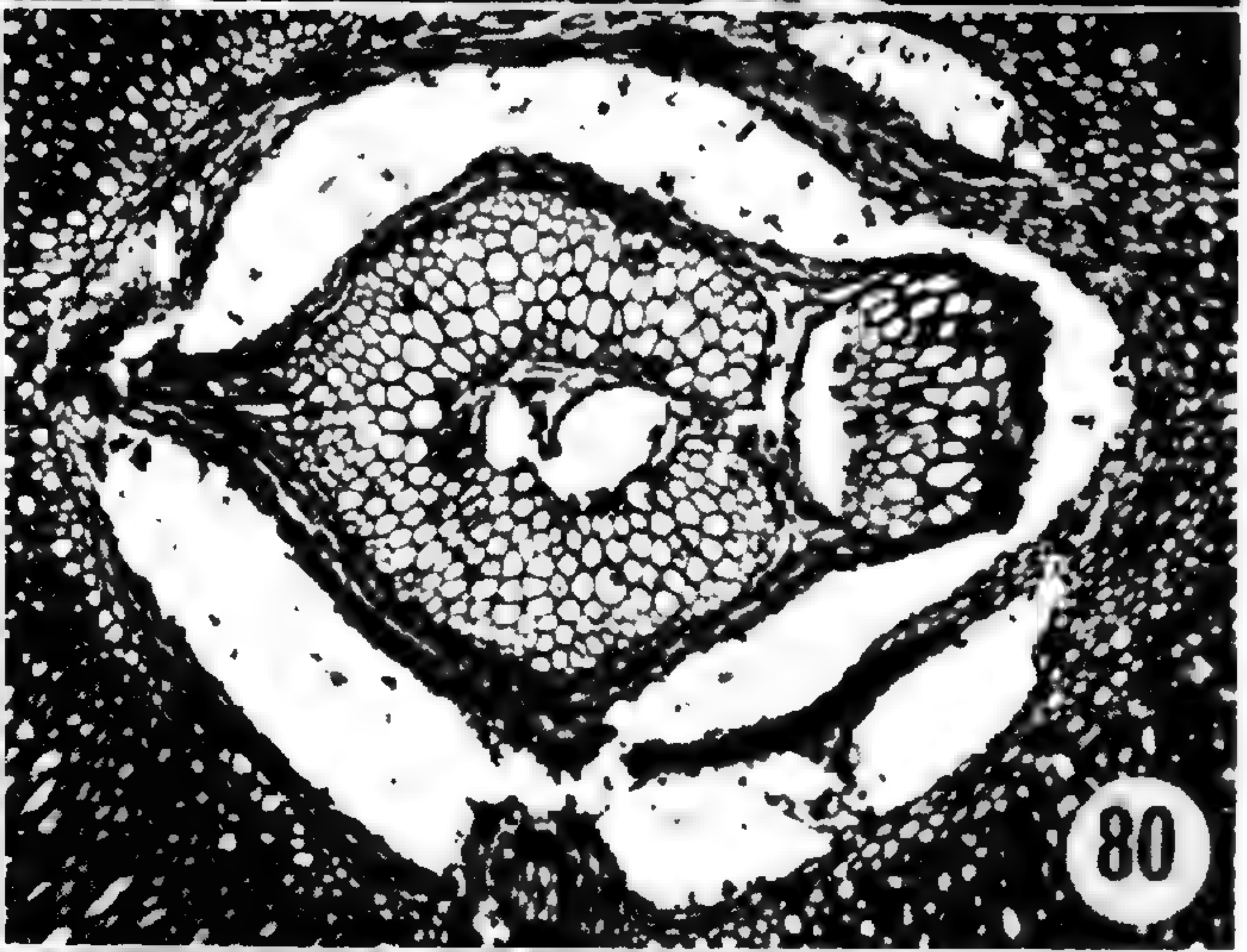
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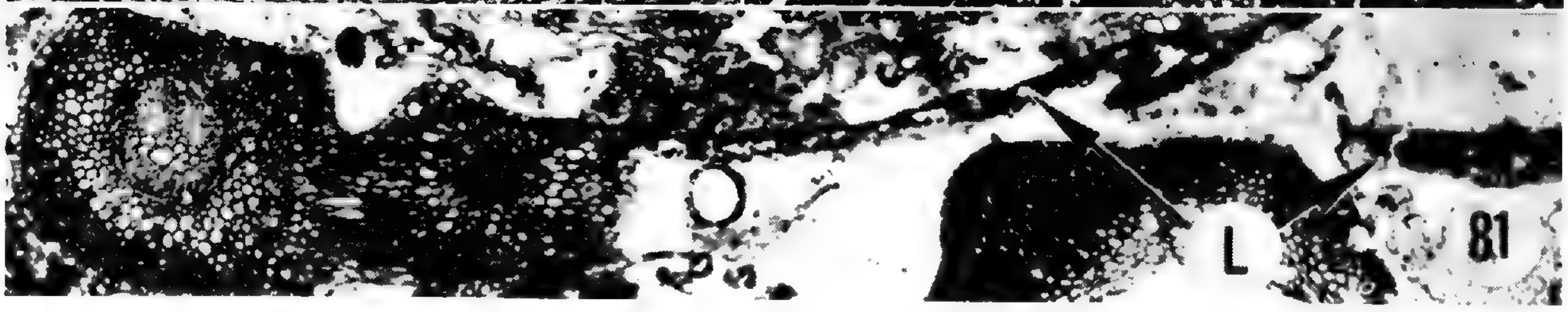
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(1961). Most of the shoots or "buds" on fronds of *Botryopteris*, except those on petiolar bases, and in *Anachoropteris* are small with less than six petioles and with very limited growth except for the basalmost petiole. Such "buds" functioned probably only under conditions of frond damage and/or availability of a rooting substrate. In both genera large (main) rhizomes have developed from such foliar borne shoots (Phillips, 1961; Fig. 53).

The main rhizome is known in each phyletic line except the *B. ramosa* group, and knowledge of cauline anatomy there is exclusively from shoots borne on fronds. Felix (1886) first described the siphonostele of *B. tridentata*, and it was not until comparable American specimens (Fig. 79) were found that his discovery was appreciated as the earliest geologic ocurrence of siphonostely in coenopterids (Westphalian A-B boundary). *Botryopteris tridentata* extends stratigraphically to the Bevier Coal, being particularly abundant in swamp floras rich in cordaites. The siphonostelic trace is formed by a progressive differentiation of tracheids along a lateral foliar arm (Figs. 63, 71) which upwardly arches around to form a circle in which a sclerotic pith appears (Fig. 78); there is no protostelic stage in the foliar-borne siphonosteles. In lower stratigraphic occurrences of *B. tridentata* a few specimens bear protosteles as in *B. ramosa*. Leaf gaps are lacking from many stems, borderline in some (Fig. 80), and clearly present in others. It appears likely that the leaf gap developed after the siphonostele in *B. tridentata* and that leaf gaps and their degree of expression are the result of increasing developmental influences of the frond on stelar differentiation through geologic time. Delicate laminate pinnules with stomata occur in *B. tridentata* by early Middle Pennsylvanian time (Fig. 81).

SUMMARY

The Zygopteridaceae appear in late Devonian time, the Botryopteridaceae in the Visean, the Anachoropteridaceae in the lower Westphalian A and all families extend into the Permian.

Stelar morphology in coenopterid ferns is typically protostelic with solid protosteles in all groups. Vitalized protosteles occur earliest (Visean) in the zygopterid ferns and are the characteristic type. *Zygopteris* exhibits secondary xylem and shows a trend of increased parenchymatization of the protostele between Middle and Upper Pennsylvanian. Vitalized protosteles are not known in the Botryopteridaceae in which evolved the earliest known coenopterid

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FIGURES 74–81. *Botryopteris* anatomical sections.—74. *B. hirsuta*, x.s. common trace at level of distinction between cauline trace (above) and foliar supply, lower Westphalian A, England. × 25.—75. *Botryopteris* sp. Xylem of foliar member with incipient departure of lateral common trace (left). Pottsville Group, Kentucky. × 25.—76. *Botryopteris* sp. Foliar member (below) with attached stem (left) and foliar member from common trace. Pottsville Group, Kentucky. × 10.—77. *Botryopteris* sp. Foliar member (left) with adaxial cauline trace; stem at right, x.s. Herrin Coal, Illinois. × 10.—78. *B. tridentata*, x.s. Foliar member with attached siphonostelic stem bearing a petiole trace. Murphysboro Coal Equivalent, Indiana. × 10.—79–80. *B. tridentata*, x.s. siphonostele with incipient leaf trace formation (Fig. 79) and departure with minute leaf gap. Mineral Coal, Kansas. × 25.—81. *B. tridentata*, pinnae and laminate pinnules (L) x.s. Mineral Coal, Kansas. × 25.

siphonostele (Westphalian A-B Boundary). The Anachoropteridaceae exhibit the most diverse stelar evolution with a general trend toward increased parenchymatization of the mixed protostele, approaching a mixed pith, and the evolution of siphonosteles in both Middle and Upper Pennsylvanian genera. Siphonosteles occur in *Anachoropteris* and *Apotropteris*. Siphonosteles may be transitory or mature features in *Anachoropteris* and occur in larger stems of *Apotropteris*. In both *Botryopteris tridentata* and *Apotropteris minuta* leaf gaps may be present or lacking. Additional evolutionary possibilities are suggested by *Grammatopteris* and *Catenopteris*. Tracheidal zonation with short broad tracheids in the center in *G. baldaufii* may represent a stage leading to a mixed pith or siphonostele as in the Osmundaceae. Corsin's interpretation of *G. rigollotii* could indicate another example of secondary xylem development as in *Zygopteris*. *Catenopteris simplex* with decurrent adaxial parenchyma inserted well into the solid protostele could lead to pith development by an overlap of decurrent parenchyma. The existence of siphonostelic anatomy, leaf gaps, and a catenalean C-shaped foliar xylem strand by early Late Pennsylvanian is indicated by a recently discovered fern from Indiana.

In general, mature secondary thickenings of the metaxylem fall into three categories in the coenopterids. Simple scalariform tracheids occur in the Clepsydroideae, *Ankyropteris* and *Catenopteris*. Multiseriate, scalariform and elliptical to circular bordered pitting occur in the Etapteroideae, Anachoropteridaceae and Botryopteridaceae; the scalariform bordered pitting is considered primitive and the best evolutionary sequence is found in *Botryopteris*.

Roots are diarch.

Cauline branching is predominately dichotomous in the Etapteroideae, axillary in species of *Ankyropteris*, and apparently rare in *Tubicaulis*, *Anachoropteris*, and *Botryopteris*. *Psalixochlaena* rhizomes bear lateral shoots. Shoots occur frequently on fronds of *Botryopteris* and less frequently on *Anachoropteris* fronds. Shoots are borne laterally and adaxially in both genera; shoots also occur by dichotomy of the frond in *Anachoropteris* and at petiolar bases in species of *Botryopteris*. Shoots on fronds were probably important as a means of vegetative propagation and their occurrences in coenopterids are paralleled by modern ferns (McVeigh, 1937), particularly by dennstaedtioid (Arnold & Daugherty, 1964; Troop & Mickel, 1968) and related tropical ferns.

Fronds are biseriate except in the Etapteroideae, and known branching is pinnate except for the primary pinna-pair of the Etapteroideae and certain dichotomous anachoropterid fronds. Planated pinna systems occur in all the coenopterid groups, although there is a common tendency to have primary pinnae (and some higher orders) turned slightly out of the rachis plane. The zygopterids constitute the greatest exception. Repetitive three dimensional branching occurs in some non-laminate fertile pinnae complexes of *Botryopteris* and pinnae on shoots at petiolar bases. Laminate pinnules occur in all familial groups in the Pennsylvanian with identified form genera of foliage including *Pecopteris*, *Sphenopteris*, and *Alloiopteris* (see also Nemejc, 1936).

Aphlebiae and scales are restricted to the zygopterid ferns, and multicellular uniseriate hairs occur in all families.

Coenopterid vegetative morphology supports the increased recognition and appreciation of these Paleozoic ferns as true ferns with distinctions in their cauline and foliar morphology at their earliest presently known stratigraphic occurrences.

LITERATURE CITED

ANDREWS, H. N. 1942. Contributions to our knowledge of American Carboniferous floras. I. *Scleropteris*, gen. nov., *Mesoxylon*, and *Amyelon*. Ann. Missouri Bot. Gard. 29: 1–18.

———. 1956. A note on the nodal anatomy of *Ankyropteris glabra* Baxter. Ann. Missouri Bot. Gard. 43: 379–380.

——— & E. BOUREAU. 1970. II Classe des Coenopteridopsida. Pp. 3–117, *in* E. Boureau (editor), *"Traité de Paléobotanique,* 4(1). *Filicophyta."* Masson, Paris.

——— & T. L. PHILLIPS. 1968. *Rhacophyton* from the Upper Devonian of West Virginia. Jour. Linn. Soc. Bot. 61: 37–64.

ARNOLD, C. A. & L. H. DAUGHERTY. 1964. A fossil dennstaedtioid fern from the Eocene Clarno formation of Oregon. Contr. Mus. Paleontol. Univ. Mich. 19: 65–88.

BARTHEL, M. 1968. *"Pecopteris" feminaeformis* (Schlotheim) Sterzel und *"Araucarites" spiciformis* Andrae in Germar—Coenopterideen des Stephans und Unteren Perms. Paläontol. Abh. 2B: 726–742.

———. 1970. Alte und neue wertvolle Funde fossiler Pflanzen aus dem Rotliegenden. Wiss. Zeitsch. Humboldt-Univ. Berlin, Math.-Naturwiss. Reihe 19: 268–274.

BAXTER, R. W. 1951. *Ankyropteris glabra*, a new American species of the Zygopteridaceae. Amer. Jour. Bot. 38: 440–452.

———. 1952. The coal-age flora of Kansas. II. On the relationships among the genera, *Etapteris, Scleropteris* and *Botrychioxylon*. Amer. Jour. Bot. 39: 263–274.

CORSIN, P. 1937. Contribution à l'études des fougères anciennes du groupe des Inversicatenales. G. Sautai, Lille. 247 pp.

———. 1952. Une fougère nouvelle, l'*Ankyropteris bertrandi* P. C., du Namurien de Haute-Silésie. Palaeobotanist 1: 126–145.

DELEVORYAS, T. & J. MORGAN. 1952. *Tubicaulis multiscalariformis*: a new American coenopterid. Amer. Jour. Bot. 39: 160–166.

——— & ———. 1954*a*. Observations on petiolar branching and foliage of an American *Botryopteris*. Amer. Midl. Naturalist 52: 374–387.

——— & ———. 1954*b*. A further investigation of the morphology of *Anachoropteris clavata*. Amer. Jour. Bot. 41: 192–198.

DENNIS, R. L. 1972. Studies of Paleozoic ferns: *Zygopteris* from the Middle and Upper Pennsylvanian of the United States. Ph.D. dissertation. University of Iowa, Iowa City. 145 pp.

EGGERT, D. A. 1959*a*. Studies of Paleozoic ferns. The morphology, anatomy, and taxonomy of *Ankyropteris glabra*. Amer. Jour. Bot. 46: 510–520.

———. 1959*b*. Studies of Paleozoic ferns: *Tubicaulis stewartii* sp. nov. and evolutionary trends in the genus. Amer. Jour. Bot. 46: 594–602.

———. 1963. Studies of Paleozoic ferns: The frond of *Ankyropteris glabra*. Amer. Jour. Bot. 50: 379–387.

———. 1964. The question of the phylogenetic position of the Coenopteridales. Mem. Torrey Bot. Club 21: 38–57.

——— & T. DELEVORYAS. 1967. Studies of Paleozoic ferns: *Sermaya*, gen. nov. and its bearing on Filicalean evolution in the Paleozoic. Palaeontographica 120B: 169–180.

——— & T. N. TAYLOR. 1966. Studies of Paleozoic ferns: On the genus *Tedelea* gen. nov. Palaeontographica 118B: 52–73.

FELIX, J. 1886. Untersuchungen über den inneren Bau westfälischer Karbonpflanzen. Abh. Geol. Spezialkarte Preussen Thüring. Staaten 7: 153–225.

GALTIER, J. 1963. Structure et ramification du phyllophore chez un *Dineuron* du Carbonifère inférieur. Naturalia Monspel., Sér. Bot. 15: 83–92.

———. 1964. Anatomie comparée et affinités de deux Zygoptéridacées du Carbonifère inférieur. Compt. Rend. Hebd. Séances Acad. Sci. 259: 4764–4767.

———. 1966*a*. Un phyllophore de *Clepsydropsis* à ramification quadrisériée. Compt. Rend. Hebd. Séances Acad. Sci. 263: 232–235.

———. 1966*b*. Observations nouvelles sur le genre *Clepsydropsis*. Naturalia Monspel., Sér. Bot. 17: 111–129.

———. 1969. Observations sur les structures foliaires et caulinaires de *Botryopteris antiqua* Kidston. Compt. Rend. Hebd. Séances Acad. Sci. 268D: 3025–3028.

———. 1970. Recherches sur les végétaux à structure conservée du carbonifère inférieur français. Paleobiol. Continentale 1(4): 1–221. Montpellier.

———. 1971. La fructification de *Botryopteris forensis* Renault (Coenopteridales du Stéphanien français): Précisions sur les sporanges et les spores. Naturalia Monspel., Sér. Bot. 22: 145–155.

GORDON, W. T. 1911*a*. On the structure and affinities of *Diplolabis römeri* (Solms). Trans. Roy. Soc. Edinburgh 47: 711–736.

———. 1911*b*. On the structure and affinities of *Metaclepsydropsis duplex* (Williamson). Trans. Roy. Soc. Edinburgh 48: 163–190.

GRAHAM, R. 1935. Pennsylvanian flora of Illinois as revealed in coal balls. II. Bot. Gaz. (Crawfordsville) 97: 156–168.

HALL, J. W. 1961. *Anachoropteris involuta* and its attachment to a *Tubicaulis* type of stem from the Pennsylvanian of Iowa. Amer. Jour. Bot. 48: 731–737.

HOLDEN, H. S. 1930. On the structure and affinities of *Ankyropteris corrugata*. Philos. Trans., Ser. B 218: 79–113.

———. 1955. On the occurrence of secondary thickening in palaeozoic ferns. Jour. Linn. Soc. Bot. 55: 271–278.

———. 1960. The morphology and relationships of *Rachiopteris cylindrica*. Bull. Brit. Mus. (Nat. Hist.) Geol. 4: 51–69.

———. 1962. The morphology of *Botryopteris antiqua*. Bull. Brit. Mus. (Nat. Hist.) Geol. 5: 361–380.

——— & W. N. CROFT. 1962. The Morphology of *Tubicaulis africanus* sp. nov. a fossil fern from Tanganyika. Bull. Brit. Mus. (Nat. Hist.) Geol. 7: 199–211.

HOSKINS, J. H. 1930. Contributions to the coal measure flora of Illinois. Amer. Midl. Naturalist 12: 154–163.

KIDSTON, R. 1908. On a new species of *Dineuron* and of *Botryopteris* from Pettycur, Fife. Trans. Roy. Soc. Edinburgh 46: 361–371.

KRAENTZEL, G. 1934. Étude monographique de *Botryopteris mucilaginosa* nov. sp. Ann. Soc. Géol. Belgique 58: M51–M76.

LECLERCQ, S. 1931. Sur l'évolution des *Etapteris*. Ann. Soc. Géol. Belgique 55: 51–59.

———. 1951. Étude morphologique et anatomique d'une fougère du Dévonien Supérieur: Le *Rhacophyton zygopteroides* nov. sp. Mem. Ann. Soc. Géol. Belgique 9: 1–62.

———. 1954. An upper Devonian Zygopterid showing clepsydropsoid and etapteroid features. Amer. Jour. Bot. 41: 488–492.

LONG, A. G. 1943. On the occurrence of buds on the leaves of *Botryopteris hirsuta* Will. Ann. Bot. (London), n.s. 7: 133–146.

MCVEIGH, I. 1937. Vegetative reproduction of the fern sporophyte. Bot. Rev. (Lancaster) 3: 457–497.

MAMAY, S. H. 1952. An epiphytic American species of *Tubicaulis* Cotta. Ann. Bot. (London), n.s. 16: 145–163.

——— & H. N. ANDREWS, JR. 1950. A contribution to our knowledge of the anatomy of *Botryopteris*. Bull. Torrey Bot. Club 77: 462–494.

MILLAY, M. A. 1970. A *Tubicaulis* from the British coal measures. Amer. Jour. Bot. 57: 757.

MILLER, C. N., JR. 1971. Evolution of the fern family Osmundaceae based on anatomical studies. Contr. Mus. Paleontol. Univ. Michigan. 23: 105–169.

MORGAN, J. & T. DELEVORYAS. 1954. An anatomical study of a new coenopterid and its bearing on the morphology of certain coenopterid petioles. Amer. Jour. Bot. 41: 198–203.

MURDY, W. H. & H. N. ANDREWS, JR. 1957. A study of *Botryopteris globosa* Darrah. Bull. Torrey Bot. Club 84: 252–267.

NEMEJC, F. 1936. A revision of the Carboniferous and Permian floras of the coal districts of Central Bohemia. II. Sphenopterides: A. Coenopteridae. Palaeontographica Bohemiae 16: 5–56.

PHILLIPS, T. L. 1961. American species of *Botryopteris* from the Pennsylvanian. Ph.D. thesis, Washington Univ., St. Louis, Missouri. 77 pp.

———. 1966. Upper Carboniferous species of *Botryopteris*. Amer. Jour. Bot. 53: 630.

———. 1970. Morphology and evolution of *Botryopteris*, a Carboniferous age fern. 1. Observations on some European species. Palaeontographica 130B: 137–172.

——— & H. N. ANDREWS. 1966. *Catenopteris simplex* gen. et sp. nov., a primitive pteridophyte from the upper Pennsylvanian of Illinois. Bull. Torrey Bot. Club. 93: 117–128.

——— & ———. 1968. *Biscalitheca* (Coenopteridales) from the Upper Pennsylvanian of Illinois. Palaeontology 11: 104–115.

——— & S. W. ROSSO. 1970. Spores of *Botryopteris globosa* and *Botryopteris americana* from the Pennsylvanian. Amer. Jour. Bot. 57: 543–551.

POSTHUMUS, O. 1924. On some principales of stelar morphology. Recueil Trav. Bot. Néerl. 21: 111–296.

READ, C. B. 1938. A new fern from the Johns Valley shale of Oklahoma. Amer. Jour. Bot. 25: 335–338.

RENAULT, B. 1875. Recherches sur les végétaux silicifiés d'Autun et de Saint-Etienne. Étude du genre *Botryopteris*. Ann. Sci. Nat. Bot., Sér. 6. 1: 220–240.

SAHNI, B. 1918. On the branching of the zygopteridean leaf. Ann. Bot. (London) 32: 369–379.

———. 1932*a*. On the structure of *Zygopteris primaria* (Cotta) and on the relations between the genera *Zygopteris*, *Etapteris*, and *Botrychioxylon*. Philos. Trans., Ser. B 222: 29–45.

———. 1932*b*. On a Paleozoic tree-fern, *Grammatopteris baldaufi* (Beck) Hirmer, a link between the Zygopterideae and the Osmundaceae. Ann. Bot. (London) 46: 863–877.

SCOTT, D. H. 1912*a*. On *Botrychioxylon paradoxum*, sp. nov., a Palaeozoic fern with secondary wood. Trans. Linn. Soc. Bot. 7: 373–389.

———. 1912*b*. On a Palaeozoic fern, the *Zygopteris grayi* of Williamson. Ann. Bot. (London) 26: 39–69.

SNIGIREVSKAYA, S. N. 1961. The genus *Botryopteris* in the coal balls from the Donetz Coal Basin. Žurn. Bot. (Moscow & Leningrad) 46: 1329–1335.

———. 1962. The morphology and systematization of the genus *Botryopteris*. Paleontol. Žurn. 2: 122–132.

SURANGE, K. R. 1952. The morphology of *Botryopteris antiqua* with some observations on *Botryopteris ramosa*. Palaeobotanist 1: 420–434.

TAYLOR, T. N. & D. A. EGGERT. 1967. Petrified plants from the upper Mississippian (Chester series) of Arkansas. Trans. Amer. Microscop. Soc. 86: 412–416.

TROOP, J. E. & J. T. MICKEL. 1968. Petiolar shoots in the Dennstaedtioid and related ferns. Amer. Fern Jour. 58: 64–70.

SYSTEMATIC CHARACTERS OF DEVONIAN FERNS[1]

Stephen E. Scheckler[2]

Abstract

Several groups of fern-like plants occur in the Middle and Upper Devonian and are probably evolved from the Trimerophytina of Banks. The branching systems of these plants are predominantly three-dimensional and are deceptively similar. All the plants are characterized by mesarch development of their primary xylem, but certain histological details permit their separation into at least three major groups—Progymnospermopsida, Cladoxylopsida, and Coenopteridopsida. The first group is somewhat better known anatomically than the others and is the least fern-like, probably evolving towards the gymnosperms. The second class is anatomically distinct from most other plant groups. The Devonian plants placed in Coenopteridopsida, with the exception of *Rhacophyton*, are mostly problematic. Utilizing data from these plants, several criteria are suggested as having value in the determination of the relationships of Devonian fern-like plants. In order of increasing value they are: cortical and epidermal histology, form of the primary xylem, presence (or absence) of secondary wood, and the structure of the protoxylem strands. The application of these criteria suggests that some, but not all, Devonian plants placed in Cladoxylopsida and Coenopteridopsida find their closest relationship with Carboniferous coenopterid ferns. No Devonian plant seems to be more closely related to modern ferns.

At present no Devonian plant is recognized as unequivocally related to the modern ferns. A number of Middle and Upper Devonian plants seem to be related to some Carboniferous coenopterid ferns, however. Our understanding of the relationships of the Devonian fern-like plants has been greatly aided by Banks' (1968) reclassification of Psilophytales into three new subdivisions: Zosterophyllophytina, Rhyniophytina, and Trimerophytina. The zosterophyll group is probably related to younger lycopods and is of no concern to a discussion of Devonian ferns. Trimerophytina is thought to have evolved from the more ancient and simple plants placed by Banks in Rhyniophytina. Plants at the trimerophyte level of organization are assumed to be the evolutionary source of the fern-like plants which radiated during Mid to Late Devonian time.

Trimerophytina currently includes four Lower Devonian genera: *Trimerophyton*, *Psilophyton*, *Pertica*, and *Dawsonites* (Banks, 1968; Kasper & Andrews, 1972). *Dawsonites* is a form genus for detached sporangia of the type borne by *Psilophyton*. Branching from the main axes of *Trimerophyton*, *Psilophyton*, and *Pertica* is pseudomonopodial, but the laterals divide isotomously, *i.e.* dichotomously or trichotomously, and form "tufts" of branchlets (Hopping, 1956; Hueber, 1968; Andrews, Kasper & Mencher, 1968; Kasper & Andrews, 1972). Some laterals of *Pertica* and *Psilophyton forbesii* (Fig. 13) terminate in pairs of sporangia. Other laterals are sterile and still others seem to be "mixed." Judging from morphology, fertile and sterile branches are homologous. Anatomy is known for *Psilophyton* (Fig. 1) and consists of an elliptical primary xylem strand and

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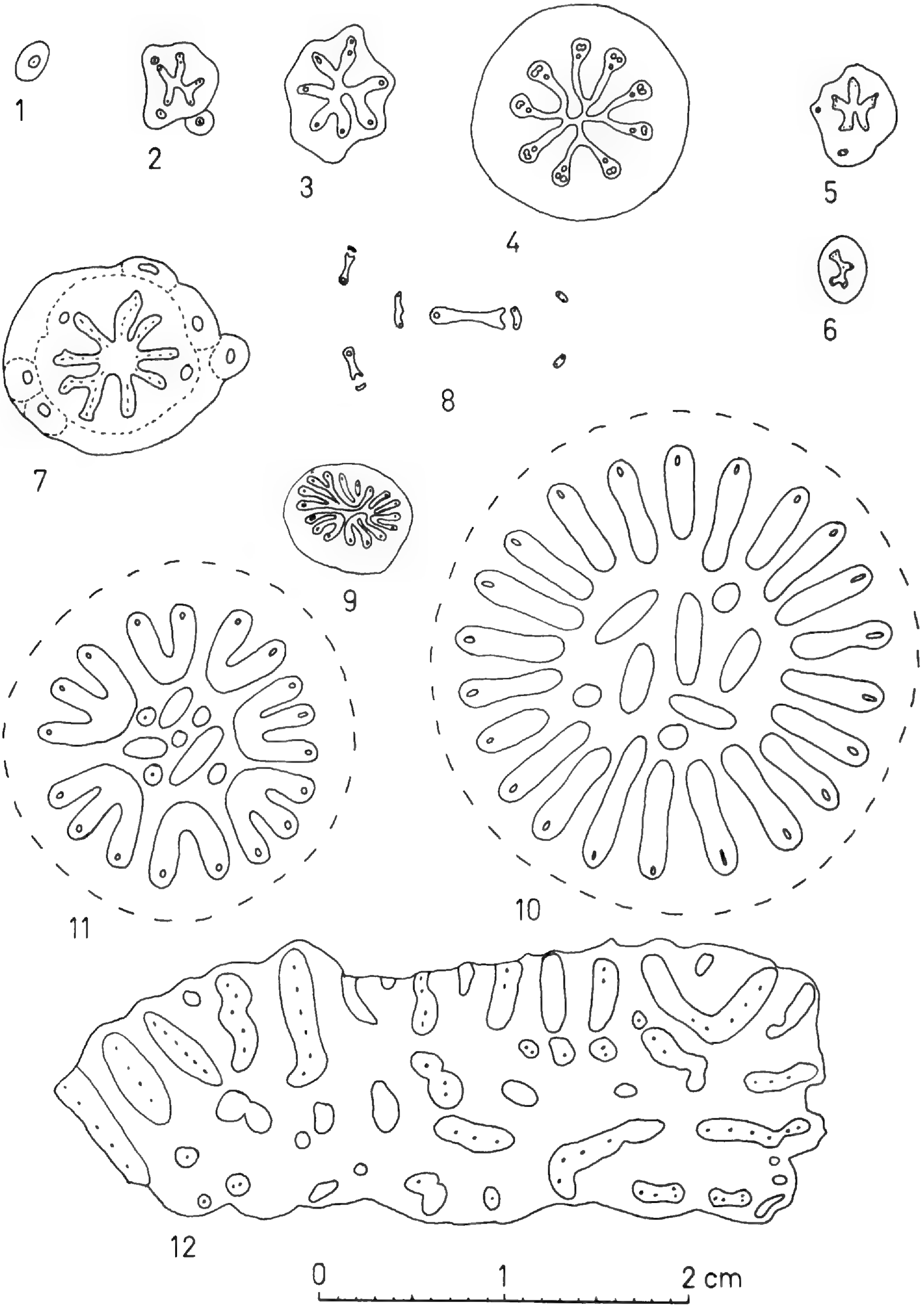
a well preserved outer cortex (Hueber & Banks, 1967; Hueber, 1968). Maturation of the xylem strand was mesarch to centrarch. From a plexus of Lower Devonian plants at the trimerophyte level of evolution it is suggested that the progymnosperms, cladoxylaleans, "coenopterids," and possibly some presphenopsids evolved (Banks, 1968; Skog & Banks, 1973). Each of these groups has similar morphology, but differences in their anatomy permit identification. Illustrations of many of these plants are found in Boureau (1970).

Progymnospermopsida was erected by Beck (1960*a*) for plants with fern-like reproduction but gymnospermous secondary tissues. Two groups of progymnosperms occur in the Middle and Upper Devonian, Aneurophytales and Archaeopteridales. The aneurophyte-type is the older and includes plants with the simplest morphology. Branching is helical or decussate except for the ultimate appendages, which dichotomize. One species, *Protopteridium minutum*, seems quite fern-like and had once been classified here. It has since been transferred to another genus, *Cathaiopteridium*, by Obrhel (1966) and is no longer considered a progymnosperm. Branching in some of the younger archaeopterid-type plants is two-ranked, and the ultimate appendages are webbed and more obviously leaf-like. Sporangia are borne on some leaves in Archaeopteridales and on larger portions of the branching system in Aneurophytales. Despite the morphological resemblance of some progymnosperms to ferns, their vascular anatomy is distinctly that of a gymnosperm. This, along with some other features, has led to the conclusion that progymnosperms are neither ferns nor related to them, but are ancestral to younger gymnosperms (Beck, 1964, 1970, 1971; Namboodiri & Beck, 1968; Scheckler & Banks, 1971*a*).

Cladoxylopsida forms a distinctive group of Middle Devonian to Lower Carboniferous plants. The group is characterized by dissected xylem and is well summarized by Leclercq (1970). Only the Devonian plants are known morphologically. The Middle Devonian genus *Pseudosporochnus* is the most completely known. Leclercq and Banks (1962) demonstrated the probability that at least one species, *P. nodosus*, was a small tree which bore a crown of branches at its summit (Fig. 18). Major branches divided equally into a number of lesser branches and all bore helically arranged leaves. The leaves divided in one plane and were either sterile or bore pairs of sporangia at their tips. The anatomy of the branches (Figs. 10–11) consists of an outer system of radially oriented bundles and an inner system of elliptical or terete strands (Leclercq & Lele, 1968). Protoxylem strands are mesarch, and those near the periphery of the outer xylem bundles developed cavities called peripheral loops.

Branches of the Middle Devonian *Cladoxylon scoparium* also divided equally and bore helically arranged ultimate appendages (Kräusel & Weyland, 1926). Fan-shaped organs (Fig. 17) replaced some ultimate appendages and bore terminal sporangia. Although the precise morphology of the fan-shaped fertile organs and the ultimate appendages is still not well understood, the two types of organs seem to be homologous (Leclercq, 1970). The xylem of *C. scoparium* consists of numerous interconnected strands much like that of *C. dawsonii* (Fig. 9).

Calamophyton had long been thought of as a pre-sphenopsid but was shown



FIGURES 1–12. Outlines of typical cross sections of some Devonian fern-like plants. Where known, the positions of protoxylem strands are indicated by dots or small circles.—1. *Psilophyton* sp. (from Hueber & Banks, 1967).—2. *Ibyka amphikoma* (from Skog & Banks, 1973).—3. *Arachnoxylon kopfii* (from Read, 1938).—4. *Asteropteris noveboracensis* (modified from Dawson, 1881).—5. *Iridopteris eriensis* (from Arnold, 1940).—6. *Stenokoleos bifidus* (from Matten & Banks, 1969).—7. *Langoxylon asterochlaenoideum* (from Stockmans, 1968).—8.

to have cladoxylalean anatomy (Leclercq & Schweitzer, 1965). Morphologically, this Middle Devonian plant is similar to *Pseudosporochnus* and *Cladoxylon scoparium* but differs by having recurved fertile organs which recall the sporangiophores of younger sphenopsids. Banks (1968) questioned whether anatomy would outweigh the morphology of the fertile organs, and *Calamophyton* continues to be treated as an early sphenopsid (Bierhorst, 1971; Skog & Banks, 1973).

Two other cladoxylaleans, both Upper Devonian, are also known from morphology. One has been referred to the genus *Cladoxylon* and branched dichotomously (Leclercq, 1970; 139). The other is a new plant discovered by me. A detailed description will be published elsewhere, but the new plant differs from other Devonian Cladoxylales by branching pseudomonopodially and by possessing an actinostele in proximal branches.

All other Devonian cladoxylaleans are known only from petrifactions. Two are described here. *Xenocladia* is known only from fragments. Evidently this Middle Devonian plant represented a portion of a large trunk like that possessed by *Pseudosporochnus* (Arnold, 1952). *Xenocladia* (Fig. 12) differs from other Cladoxylales by its size and the large number of protoxylem strands found in some bundles. Many of the xylem strands of the Upper Devonian *Cladoxylon dawsonii* (Fig. 9) are connected at the center of the axis. Protoxylem strands are found only at the tips of the strands (Read, 1935).

Astralocaulis (= *Schizopodium* Harris) is often compared with Cladoxylales. The genus may have been misinterpreted, however, and is currently under investigation (Hueber, 1971). For this reason it will not be described here.

Several Devonian plants (*Arachnoxylon*, *Reimannia*, *Iridopteris*, and *Asteropteris*) with lobed xylem strands have been placed into Coenopteridopsida (Banks, 1968). To this list might be added *Ibyka*, *Langoxylon*, and *Stenokoleos*. The chief feature relating these plants to the Carboniferous coenopterid ferns is the resemblance of some of their protoxylem strands to peripheral loops. Noteworthy also, however, is the similarity of some to the Lower Carboniferous genus *Protoclepsydropsis* (Long, 1967). The value of *Reimannia* has been greatly diminished by the findings that similar three-lobed xylem strands occur in several other Devonian plants (*e.g. Stenokoleos*, *Triloboxylon*, *Proteokalon*, and *Actinoxylon*). The existence of *Reimannia* as a natural taxon is seriously in doubt, and it will not be considered any further here.

Ibyka has been recently described from petrifactions and compressions as a possible Middle Devonian precursor to sphenopsids (Skog & Banks, 1973). I include this plant here because of its anatomical similarity to the others. *Ibyka* branched helically except for its ultimate appendages and fertile organs, which dichotomized (Fig. 14). The fertile organs were not well preserved but

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Rhacophyton zygopteroides primary xylem of fertile frond (from Leclercq, 1951).—9. *Cladoxylon dawsonii* (from Read, 1935).—10. *Pseudosporochnus nodosus* first order branch (from Leclercq & Lele, 1968).—11. *Pseudosporochnus nodosus* third order branch (from Leclercq & Lele, 1968).—12. *Xenocladia medullosina* (from Arnold, 1952).

seem to be homologous to ultimate appendages. A typical cross section (Fig. 2) shows a five- or six-armed actinostele from which traces depart helically.

Arachnoxylon (Fig. 3) is known only from Middle and Upper Devonian petrifactions (Arnold, 1935; Read, 1938; Banks, 1964, 1968). It differs from the petrified axes of *Ibyka* by its larger size and greater number of arms. Traces have not been described for *Arachnoxylon*, but from the protoxylem arrangement of Read's specimen (Fig. 3) one can guess that they were helical.

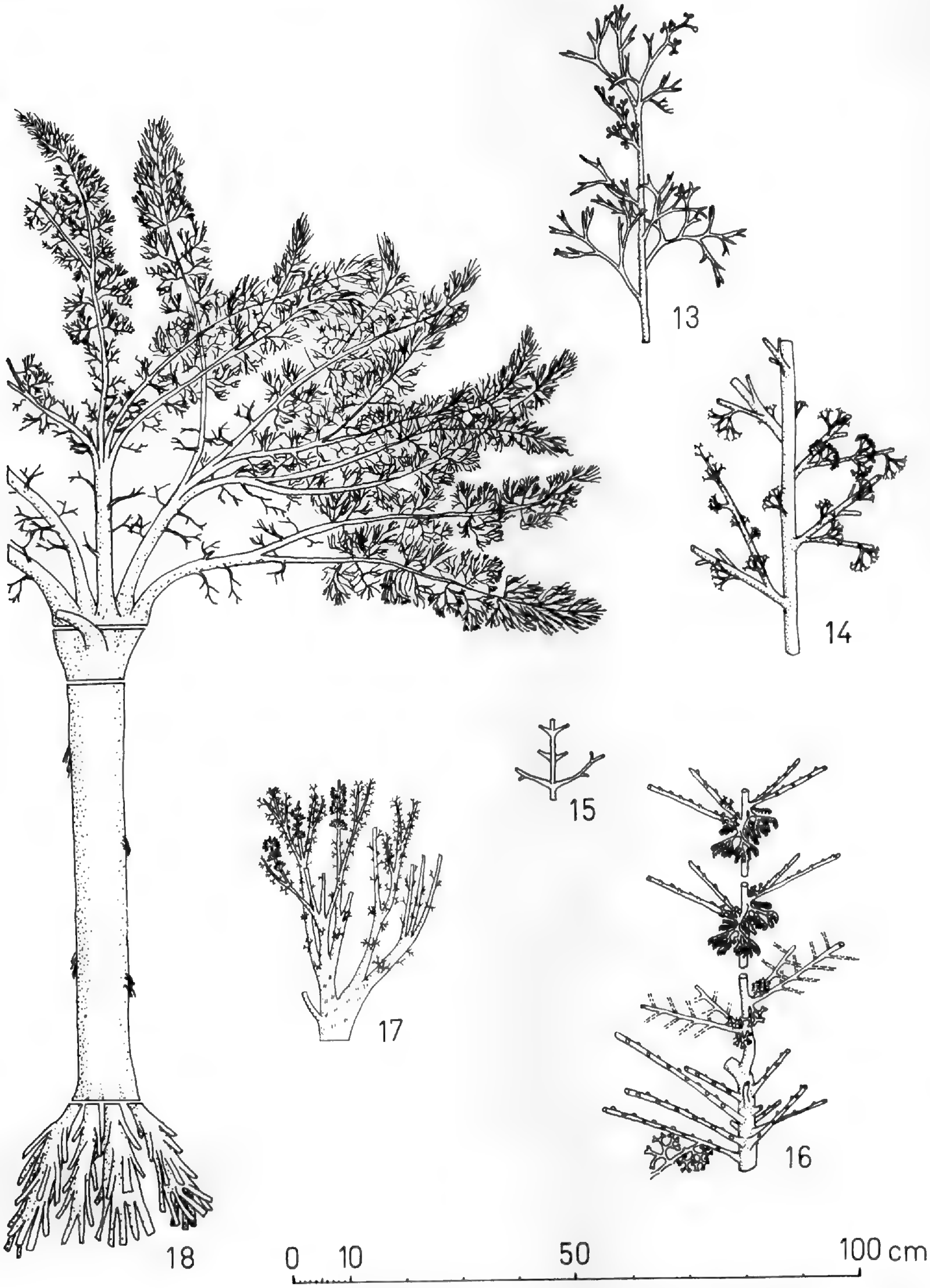
Asteropteris (Fig. 4) is also known from Middle and Upper Devonian petrifactions (Banks, 1964). Its xylem strand is similar to those of *Arachnoxylon* and *Ibyka* but is larger, has more lobes, and bears whorled traces to appendages. The traces are bilobed at first but develop four protoxylem poles distally (Bertrand, 1913; Dawson, 1881).

Langoxylon (Fig. 7) occurs in the Middle Devonian and has a large actinostele. Appendages are numerous and probably depart helically (Stockmans, 1968). *Langoxylon* differs from the previous genera by having many protoxylem strands in the arms of the actinostele.

Iridopteris (Fig. 5) is a poorly known Middle Devonian petrifaction genus (Arnold, 1940). Its xylem strand is bilaterally symmetrical unlike the others and it seems to bear two sizes of appendages. The larger is supplied by an elliptical trace with two peripheral protoxylem strands. The other type of appendage is supplied with a small centrarch trace. Protoxylem strands are located at the margins of the actinostele and differences in their arrangement suggest a helical departure of the smaller appendages. Frequently the protoxylem strands are paired and aligned tangentially.

Stenokoleos was first described from rocks thought to be Mississippian, but the genus is known also from the Upper and possibly Middle Devonian (Matten, 1968; Matten & Banks, 1969). The Upper Devonian species, *S. bifidus*, bears distichous pairs of appendages, which bear two-ranked laterals (Fig. 15). The xylem strand of the main axis is highly variable, and one of several possible shapes is shown in Figure 6. Traces to the appendages are three-lobed at first. The protoxylem strands of *Stenokoleos* are paired and tangentially aligned at the tips of the arms supplying appendage traces. Matten and Banks (1969) drew attention to the similar departure of traces in *Stenokoleos*, *Tristichia*, and *Tetrastichia*. The latter two genera are presumed to be pteridosperms, but seeds have not been found attached. The departure of traces of the three genera is also remarkably similar to some parts of the Carboniferous coenopterid *Stauropteris* (Surange, 1952; Emberger, 1968).

The Upper Devonian genus *Rhacophyton* represents another type of coenopterid fern. In this type (etapteroid) the peripheral loop opens during the departure of a trace. The other Devonian plants thought to be coenopterids have a different type of peripheral loop (clepsydroid) which remains closed. Two species of *Rhacophyton* are well known from both compressions and petrifactions, *R. zygopteroides* and *R. ceratangium* (Leclercq, 1951, 1954; Andrews & Phillips, 1968). The two differ mainly by the morphology of their pinnules and fertile appendages. *Rhacophyton* (Fig. 16) has a large stem which bears fronds in a crowded helix. Vegetative fronds are twice pinnate, and the pinnules



FIGURES 13–18. Reconstructions of the known branching of some Devonian fern-like plants.—13. *Psilophyton forbesii* (from Andrews, Kasper & Mencher, 1968).—14. *Ibyka amphikoma* (from Skog & Banks, 1973).—15. *Stenokoleos bifidus* (from Matten & Banks, 1969).—16. *Rhacophyton zygopteroides* (from Leclercq, 1951).—17. *Cladoxylon scoparium* (from Kräusel & Weyland, 1926).—18. *Pseudosporochnus nodosus* (from Leclercq & Banks, 1962).

are bifurcate. Fertile fronds are four-ranked and more complex. Their primary pinnae divide at the base and are subtended by a pair of pendulous organs, which bear the sporangia. The xylem of the stem of *R. zygopteroides* is stellate, that of the frond (Fig. 8) is bipolar. *Rhacophyton ceratangium* is said to have a bipolar xylem strand in all parts. Externally *Rhacophyton* resembles the branching systems of some progymnosperms placed in Aneurophytales (Andrews & Phillips, 1968; Bierhorst, 1971). The anatomy of the frond of *Rhacophyton* is so similar to some other coenopterid ferns, however, that it would be difficult to deny an affinity.

If it becomes better known, the Middle Devonian genus *Protocephalopteris* may prove to be related to *Rhacophyton*. Despite similarities in their reconstructions (Schweitzer, 1968), however, *Protocephalopteris* is based on only a few small fragments, while *Rhacophyton* is far better known.

The preceding descriptions show that a large number of Middle and Upper Devonian plants have some of the characters of primitive ferns, *i.e.* reproduction by spores, branching systems that resemble fronds, and mesarch xylem strands. Identification of the "true" affinities of these plants is difficult, but study of their anatomy suggests that it is possible. Several anatomical criteria are here suggested as useful in the determination of relationship of the Devonian fern-like plants. In order of increasing value they are: histology of the cortex and epidermis, form of the primary xylem, presence of a vascular cambium, and the structure of the protoxylem strand.

Cortical histology affects the appearance of some compressed axes. Specimens of *Pseudosporochnus nodosus* have a distinctive pattern of sculpturing. Leclercq and Banks (1962) attributed the sculpturing to the presence of "nests" of sclereids in the cortex. Tangential sections of the cortex of a newly collected petrifaction referable to *Pseudosporochnus* show that the "nests" of sclereids occur in the same pattern seen on compressions. Other compressed axes show a different type of pattern dominated by longitudinal ridges. The anatomy of these axes suggests that the ridges are due to the multi-stranded xylem rather than to the distribution of different types of cells in the cortex. Hairs are present on compressed axes of *Ibyka* and a petrified axis of *cf. Pseudosporochnus* and demonstrate that they can be recognized in either type of preservation. The features just described can be useful in separating specimens of a plant from others in the same collection (Leclercq & Banks, 1962; Skog & Banks, 1973).

Some progymnosperms (Aneurophytales) and the plants described earlier as Devonian coenopterids have lobed xylem strands. Other progymnosperms (Archaeopteridales) and Cladoxylales have primary xylems consisting of several discrete strands. The multi-stranded type of primary xylem has been suggested as evolving by dissection of an actinostele (Harris, 1929; Arnold, 1952; Namboodiri & Beck, 1968; Skog & Banks, 1973). If this evolutionary sequence is valid, it should be possible to cite examples of Devonian plants whose actinosteles contain abundant xylem parenchyma. Three plants with this type of primary xylem are listed here: my new plant with cladoxylalean anatomy, *Proteokalon* (Aneurophytales, see Scheckler & Banks, 1971*b*), and one presumed early coenopterid. This suggests that the dissection of an actinostele occurred several times in Devonian plants. The parallel development of a multi-stranded xylem from an actinostele indicated by these plants suggests that classifications based solely on numbers of xylem strands in an axis are unrealistic.

Several Devonian Cladoxylales (*Xenocladia, Cladoxylon dawsonii,* and my new plant) have aligned cells that resemble secondary xylem at the margins of some xylem bundles. The only "cladoxylalean" in which vascular rays have been illustrated is *Cladoxylon kidstoni* (Solms-Laubach, 1910: Taf. 3, Fig. 13). The specimen upon which the species was based was only doubtfully referred to *Cladoxylon,* however (Seward, 1917: 205–207). Numerous tangential and radial sections of *Xenocladia,* an Upper Devonian *Cladoxylon,* and my new plant clearly demonstrate that vascular rays were absent from the aligned cells of these plants. In agreement with Leclercq (1970), I interpret the aligned cells to be metaxylem. Additional support for this interpretation comes from the structure of the walls of the outer cells of the xylem bundles of several Devonian Cladoxylales. Both the aligned cells of *Xenocladia* and the late metaxylem elements of other, smaller axes have thicker walls and fewer pits than the inner, early metaxylem tracheids. These cells appear fiber-like and may prove to be a distinctive anatomical character of Cladoxylales and related plants. Progymnosperms differ from the Devonian Cladoxylales by possessing a vigorous vascular cambium that produced remarkably gymnospermous secondary xylem and secondary phloem (Beck, 1970; Scheckler & Banks, 1971*a, b*). The aligned tracheids present in some axes of *Rhacophyton* (Leclercq, 1951; Andrews & Phillips, 1968) have not been shown to have vascular rays and may also be metaxylem.

Closed (clepsydropsoid) versus open (etapteroid) peripheral loops may be fundamental to the classification of Coenopteridopsida (Leclercq, 1954). The closed peripheral loop has been defined as a rod of parenchyma surrounded by tracheids of the protoxylem (Leclercq, 1970). This type of protoxylem structure has been illustrated for *Clepsydropsis* and for some of the Carboniferous Cladoxylales (Bertrand, 1935; Galtier, 1966). It occurs also in *Stenokoleos* (Beck, 1960*b*; Matten & Banks, 1969), *Cladoxylon dawsonii,* and another Devonian plant with an actinostele. The protoxylem tracheids of the peripheral loop are not disorganized. The lack of nearby xylem parenchyma cells outside of the peripheral loop suggests that the parenchyma of the loop should not be interpreted as cavity parenchyma or tyloses as Bierhorst (1971) has done. Parenchyma near the tip of a xylem arm of *Triloboxylon* (Aneurophytales, Scheckler & Banks, 1971*a*) is deceptively similar to a peripheral loop, but the protoxylem strands of the genus are independent of it. A different type of protoxylem structure occurs in some other Devonian plants and seems to have been confused with a peripheral loop. The protoxylem strands of *Ibyka,* a petrified specimen of *cf. Pseudosporochnus,* and my new cladoxylalean disintegrate and form lacunae that superficially resemble peripheral loops. The interiors of the lacunae differ by being filled with disorganized protoxylem tracheids instead of parenchyma (see Skog & Banks, 1973).

The peripheral loops of *Rhacophyton* and some other coenopterids (*e.g. Dineuron, Metaclepsydropsis* and others—see Boureau, 1970) differ from those just described by opening during the departure of traces. Whether this type of loop was filled with parenchyma or some other cells, it forms an easily recognized structure that serves to relate these fern-like plants.

Utilizing the criteria outlined above, a number of observations and interpretations can be made regarding Devonian "ferns." The presence of a well developed vascular cambium in Devonian progymnosperms relates them with younger gymnosperms, but not with ferns. The inability to demonstrate vascular rays in *Rhacophyton* and Cladoxylopsida suggests that the aligned cells present on some axes of each should not be used as evidence against their affinity to other fern-like plants.

The presence of two distinct types of protoxylem structure in some members of both Cladoxylales and the Devonian coenopterid-like plants suggests that each assemblage may contain unrelated plants. Skog and Banks (1973) suggested that *Ibyka* and some of the Middle Devonian Cladoxylales formed a plexus from which evolved sphenopsids. The presence of protoxylem lacunae in *Ibyka* and many sphenopsids was viewed by them as significant to their argument. Protoxylem lacunae, however, are not unique to Sphenopsida and are found in representatives of the ferns, gymnosperms, and angiosperms (Boureau, 1970; Bierhorst, 1971). The closed parenchymatous peripheral loop, on the other hand, does seem to be unique to some cladoxylalean plants and some Devonian and Carboniferous coenopterid-like plants.

The demonstration that at least three fern-like plants which had abundant xylem parenchyma in their primary xylem strands existed in the Devonian suggests that dissected xylem may have arisen in several groups of early plants. If so, this might mean that not all plants with cladoxylalean anatomy were necessarily related. Nor were they necessarily unrelated to other plants with actinosteles. Although the data are premature, I make the tentative suggestion that the Devonian and Carboniferous plants with closed, parenchymatous peripheral loops will ultimately be found to be related. The other plants, with protoxylem lacunae, are possibly parallel in their anatomy and some, as Skog and Banks (1973) suggest, may be related to the sphenopsids.

The points raised in the preceding discussion of Devonian "ferns" are summarized as follows:

1. Trimerophytina of Banks, from the Lower Devonian, is the most likely source for the fern-like plants found in younger strata. Trimerophytes and their presumed derivatives, Progymnospermopsida, Cladoxylopsida, Coenopteridopsida, have mesarch xylem strands and many branch pseudomonopodially.
2. Some progymnosperms have simply organized branching systems that resemble those of other fern-like plants. Anatomy, however, suggests that they were ancestral to younger gymnosperms.
3. Plants with cladoxylalean anatomy form a distinct group from the Middle Devonian to Lower Carboniferous. Their relationships with other groups of plants are obscure.
4. Some of the Middle and Upper Devonian plants with lobed xylem strands

may be related to Carboniferous coenopterid ferns. Many have protoxylem strands that resemble peripheral loops.

5. *Rhacophyton* has similar morphology to some progymnosperms but its anatomy demonstrates its affinity with Zygopteridaceae.

6. Cortical histology and the presence of hairs can sometimes be determined from either compressed or petrified axes and offer valuable clues to the identity of specimens.

7. The possibility that multi-stranded vascular systems could have evolved by dissection of actinosteles is supported by the presence of xylem parenchyma in the primary xylem strands of three, apparently unrelated, Devonian plants.

8. Longitudinal sections of *Xenocladia*, *Cladoxylon* sp., and a new plant show that vascular rays are absent from the aligned cells of these Devonian plants. The aligned elements are interpreted as metaxylem. They and the late metaxylem elements of other cladoxylalean axes have thicker walls and fewer pits than early metaxylem tracheids and are fiber-like. In contrast, vascular rays are obvious in the wood of progymnosperms. The aligned tracheids of *Rhacophyton* have not been demonstrated to have vascular rays and might also be metaxylem.

9. The peripheral loops of *Clepsydropsis* and related coenopterids remain closed during the departure of traces and consist of a rod of parenchyma surrounded by protoxylem tracheids. This type of protoxylem structure occurs also in some Devonian and Carboniferous Cladoxylales and in some Devonian plants with actinosteles. Other Cladoxylales and actinostelic plants have a different type of protoxylem structure which resembles a peripheral loop. In these plants, however, the protoxylem strands distintegrate and form lacunae.

10. Those Devonian and Carboniferous plants with parenchyma-filled peripheral loops may be related to some coenopterid ferns. The other plants, with protoxylem lacunae, may be related to Sphenopsida or other groups.

Literature Cited

Andrews, H. N. & T. L. Phillips. 1968. *Rhacophyton* from the Upper Devonian of West Virginia. Jour. Linn. Soc. Bot. 61: 37–64.

———, A. Kasper & E. Mencher. 1968. *Psilophyton forbesii*, a new Devonian plant from northern Maine. Bull. Torrey Bot. Club 95: 1–11.

Arnold, C. A. 1935. Some new forms and new occurrences of fossil plants from the Middle and Upper Devonian of New York State. Bull. Buffalo Soc. Nat. Sci. 17: 1–12.

———. 1940. Structure and relationships of some Middle Devonian plants from western New York. Amer. Jour. Bot. 27: 57–63.

———. 1952. Observations on fossil plants from the Devonian of eastern North America. VI. *Xenocladia medullosina* Arnold. Contr. Mus. Paleontol. Univ. Michigan 9: 297–309.

Banks, H. P. 1964. Putative Devonian ferns. Mem. Torrey Bot. Club 21: 10–25.

———. 1968. The early history of land plants. Pp. 73–107, *in* E. T. Drake (editor), "Evolution and Environment: a symposium presented on the occasion of the 100th anniversary of the foundation of Peabody Museum of Natural History at Yale University." Yale Univ. Press, New Haven.

Beck, C. B. 1960*a*. The identity of *Archaeopteris* and *Callixylon*. Brittonia 12: 351–368.

———. 1960*b*. Studies of New Albany Shale plants. I. *Stenokoleos simplex* comb. nov. Amer. Jour. Bot. 47: 115–124.

———. 1964. The woody, fern-like trees of the Devonian. Mem. Torrey Bot. Club 21: 26–37.

———. 1970. The appearance of gymnospermous structure. Biol. Rev. Cambridge Philos. Soc. 45: 379–400.

———. 1971. On the anatomy and morphology of lateral branch systems of *Archaeopteris*. Amer. Jour. Bot. 58: 758–784.

BERTRAND, P. 1913. Étude du stipe de l'*Asteropteris noveboracensis*. Pp. 909–924 *in* XIIe Sess. Congr. Géol. Internat. Compt. Rend. Ottawa, Canada.

———. 1935. Contribution à l'étude des Cladoxylées de Saalfeld. Palaeontographica, Abt. B, Paläophytol. 80: 101–170.

BIERHORST, D. W. 1971. Morphology of Vascular Plants. Macmillan Co., New York.

BOUREAU, E. (editor). 1970. Traité de Paléobotanique. IV. Fasc. I. Filicophyta. Masson et Cie, Paris.

DAWSON, J. W. 1881. Notes on new Erian (Devonian) plants. Quart. Jour. Geol. Soc. London 37: 299–308.

EMBERGER, L. 1968. Les Plantes Fossiles dans leur Rapports avec les Végétaux Vivant. Ed. 2. Masson et Cie, Paris.

GALTIER, J. 1966. Observations nouvelles sur le genre *Clepsydropsis*. Naturalia Monspel., Sér. Bot. 17: 111–132.

HARRIS, T. M. 1929. *Schizopodium davidii* gen. et sp. nov.—A new type of stem from the Devonian rocks of Australia. Philos. Trans., Ser. B 217: 395–410.

HOPPING, C. A. 1956. On a specimen of "*Psilophyton robustius*" Dawson, from the Lower Devonian of Canada. Proc. Roy. Soc. Edinburgh B 66: 10–28.

HUEBER, F. M. 1968. *Psilophyton*: the genus and the concept. Pp. 815–822, *in* D. H. Oswald (editor), "International Symposium on the Devonian System." Vol. 2. Alberta Society of Petroleum Geologists, Calgary, Canada.

———. 1971. *Astralocaulis*: a new name for *Schizopodium* Harris. Taxon 20: 640–641.

——— & H. P. BANKS. 1967. *Psilophyton princeps*: the search for organic connection. Taxon 16: 81–85.

KASPER, A. E. & H. N. ANDREWS. 1972. *Pertica*, a new genus of Devonian plants from northern Maine. Amer. Jour. Bot. 59: 897–911.

KRÄUSEL, R. & H. WEYLAND. 1926. Beiträge zur Kenntnis der Devonflora. II. Abh. Senckenberg. Naturf. Ges. 40: 115–155.

LECLERCQ, S. 1951. Étude morphologique et anatomique d'une fougère du Dévonien Supérieur le *Rhacophyton zygopteroides* nov. sp. Ann. Soc. Géol. Belgique 9: 1–62.

———. 1954. An Upper Devonian zygopterid showing clepsydropsoid and etapteroid features. Amer. Jour. Bot. 41: 488–492.

———. 1970. III. Classe des Cladoxylopsida Pichi-Sermoli, 1959. Pp. 119–177, *in* E. Boureau (editor), "Traité de Paléobotanique. IV. Fasc. I. Filicophyta." Masson et Cie, Paris.

——— & H. P. BANKS. 1962. *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with cladoxylalean affinities. Palaeontographica, Abt. B, Paläophytol. 110: 1–34.

——— & K. M. LELE. 1968. Further investigation on the vascular system of *Pseudosporochnus nodosus* Leclercq et Banks. Palaeontographica, Abt. B, Paläophytol. 123: 97–112.

——— & H. J. SCHWEITZER. 1965. *Calamophyton* is not a sphenopsid. Bull. Acad. Roy. Belgique, Cl. Sci. 51, 11: 1395–1403.

LONG, A. G. 1967. Some specimens of *Protoclepsydropsis* and *Clepsydropsis* from the Calciferous Sandstone Series of Berwickshire. Trans. Roy. Soc. Edinburgh 67: 95–107.

MATTEN, L. C. 1968. A Middle Devonian flora from New York. Amer. Jour. Bot. 55: 723. Abstract.

——— & H. P. BANKS. 1969. *Stenokoleos bifidus* sp. n. in the Upper Devonian of New York State. Amer. Jour. Bot. 56: 880–891.

NAMBOODIRI, K. K. & C. B. BECK. 1968. A comparative study of the primary vascular system of conifers. III. Stelar evolution in gymnosperms. Amer. Jour. Bot. 55: 464–472.

OBRHEL, J. 1966. *Protopteridium hostinense* Krejči und Bemerkungen zu den übrigen Arten der Gattung *Protopteridium*. Čas. Mineral. Geol. 11: 441–443.

READ, C. B. 1935. An occurrence of the genus *Cladoxylon* Unger, in North America. Jour. Washington Acad. Sci. 25: 493–497.

———. 1938. Some Psilophytales from the Hamilton Group in western New York. Bull. Torrey Bot. Club 65: 599–606.

SCHECKLER, S. E. & H. P. BANKS. 1971*a*. Anatomy and relationships of some Devonian progymnosperms from New York. Amer. Jour. Bot. 58: 737–751.

——— & ———. 1971*b*. ***Proteokalon*** a new genus of progymnosperms from the Devonian of New York State and its bearing on phylogenetic trends in the group. Amer. Jour. Bot. 58: 874–884.

SCHWEITZER, H. J. 1968. Pflanzenreste aus dem Devon Nord-Westspitzbergens. Palaeontographica, Abt. B, Paläophytol. 123: 43–75.

SEWARD, A. C. 1917. Fossil Plants. A textbook for students of botany and geology. III. Pteridospermeae, Cycadofilices, Cordaitales, Cycadophyta. Cambridge Univ. Press, Cambridge.

SKOG, J. E. & H. P. BANKS. 1973. *Ibyka amphikoma*, gen. et sp. n., a new protoarticulate precursor from the late Middle Devonian of New York State. Amer. Jour. Bot. 60: 366–380.

SOLMS-LAUBACH, H. 1910. Über die in den Kalksteinen des Culm von Glätzisch-Falkenberg in schlesien erhaltenen structurbietenden Pflanzenreste. IV. *Völkelia refracta*, ***Steloxylon*** *ludwigii*. Zeitschr. Bot. 2: 529–554.

STOCKMANS, F. 1968. Végétaux MésoDévoniens récoltés aux confins du Massif du Brabant (Belgique). Mém. Inst. Roy. Sci. Nat. Belgique 159: 1–49.

SURANGE, K. R. 1952. The morphology of ***Stauropteris burntislandica*** P. Bertrand and its megasporangium *Bensonites fusiformis* R. Scott. Philos. Trans., Ser. B 237: 73–91.

PHYLETIC LINES IN THE MODERN FERNS[1]

JOHN T. MICKEL[2]

Before we can begin to discuss the overall phyletic lines of the ferns, we must ask ourselves the rather old and trite but nevertheless crucial question, "What is a fern?" From what we know of the fossil record there were no true ferns in the Devonian, but there was a great array of now extinct groups of so-called ferns in the Carboniferous. How do we circumscribe the group, and is there any reason to question the naturalness of this taxon? Traditionally we define it as any megaphyllous plant reproducing by spores. From the great diversity of plants that we have seen placed in "the ferns" in the fossil record it seems quite possible that some groups could well have arisen separately from Devonian or Carboniferous ancestors before we would have called them true ferns. I am not proposing that we answer the question at this moment, nor am I certain that we can answer it at this point in time, but I want to keep the question open as we address ourselves to the overall view of the evolutionary lines as seen in the modern ferns.

Another major difficulty that must be mentioned before we can begin is that morphologically we are still in somewhat of a mess regarding the characters of the ferns. In an attempt to prepare an objective way of producing a phylogeny with the aid of computerization, the systematic characters of the ferns were examined rather closely. A broad comparison is extremely difficult or impossible at this time. What are the characters? We actually know little about any of them. In the first place in many cases we cannot make comparisons between the taxa. We may have information on certain characters for certain taxa, but it generally is difficult to compare the information we have between major groups of ferns. Secondly, we do not know what we are looking for in all characters. For example, in most descriptions of ferns their vestiture is described as consisting of hairs or scales and only rarely with any sort of qualifiers, such as clathrate scales or acicular hairs. In some cases the same type of scale or hair is described as being present in totally different and unrelated groups of ferns, yet no detailed study has been made to see whether in fact the two are really the same.

We have virtually no information on another aspect of vestiture, namely the paraphyses. What types are there? What is their importance to the plant? What is their phylogenetic significance? There are many other characters in just this same state of non-recognition. The work of Bower along these lines was extremely important, but the work is far from finished. We are still in the crosier stage of morphological and phylogenetic study in the ferns.

The study of phyletic lines in ferns has taken into consideration in the past virtually exclusively the modern ferns and ignored the fossil ferns. The reasons for this are good ones. The ferns of the Paleozoic are extremely diverse and

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bizarre by modern standards with only the slightest traces of our modern groups represented in them. How they can be tied into our modern ferns is still quite up in the air (or more correctly down in the ground). The ferns suffer from the same gap that the angiosperms do, namely the fossil ferns of the Cretaceous and onward are essentially those of modern times without offering us any real assistance as to which came first or which are most primitive. Prior to the Cretaceous ferns disappear down the dark tunnel of the Jurassic and Triassic and appear on the far side in unrecognizable forms, leaving us with no guide as to the relationships and origins of our modern groups of ferns. We strongly hope that more evidence will be forthcoming from the fossil record for this time period, but for the moment we must turn our attention to the modern ferns for evidence on fern phylogeny, supplemented only sparingly with glimpses of the past.

In the past 50 years we have seen a number of phylogenetic schemes presented for the ferns. Bower's scheme (1923–28) placed great stress on the position of the sorus, marginal vs. dorsal, with only rare instances of changing from one to another, as in his "phyletic slide" found in the pteroid ferns. We now know that this does not faithfully represent all the diversity within the ferns, the shift from marginal to dorsal sori occurring several times, thus necessitating modification of Bower's tenets.

A great flush of fern phyletic fervor arose in the 1940's. Ching (1940) made a classic move in splitting the traditional Polypodiaceae into 33 families in five phylogenetic lines. The splitting itself was extreme and often ill-founded, the relationships were often based on speculation rather than solid evidence, and his five phyletic lines ended with nebulous ancestry, such as "extinct ancestral stock." In a relatively unknown paper Dickason (1946) made a plea for more solid evidence in phyletic deliberations and made a rather thoughtful analysis of the characters to be studied. Soon thereafter Holttum (1947, 1949) presented a more lengthly consideration of fern phylogeny in which he greatly recondensed the bulk of the classic Polypodiaceae into a large Dennstaedtiaceae. Although Copeland (1947) considered many relationships of the genera and families of ferns, he did not present these in a formal phylogenetic scheme.

Phylogenies have also been produced based on other grounds than strictly morphological, such as Mehra's (1961) phyletic lines based on chromosome numbers. Most recently Nayar (1970) has offered a fern phylogeny in which there has been no attempt at all to justify postulated relationships.

In the present paper I would like to present a very brief view of the modern ferns to lay out somewhat our knowledge of the relationships of the major groups, show the problems and areas of weakness in our knowledge, and propose questions that should be faced in the near future as we try to gain a clearer picture of fern phylogeny.

In this symposium Dr. Stidd has shown us in some detail the morphology of the Marattiaceae and its fossil record in the Carboniferous. In the Marattiaceae we stress especially the peculiar sorus structure (the synangium) and the stipules, large fleshy outgrowths from the leaf that often function as propagules. These stipules are often compared with those of the Osmundaceae

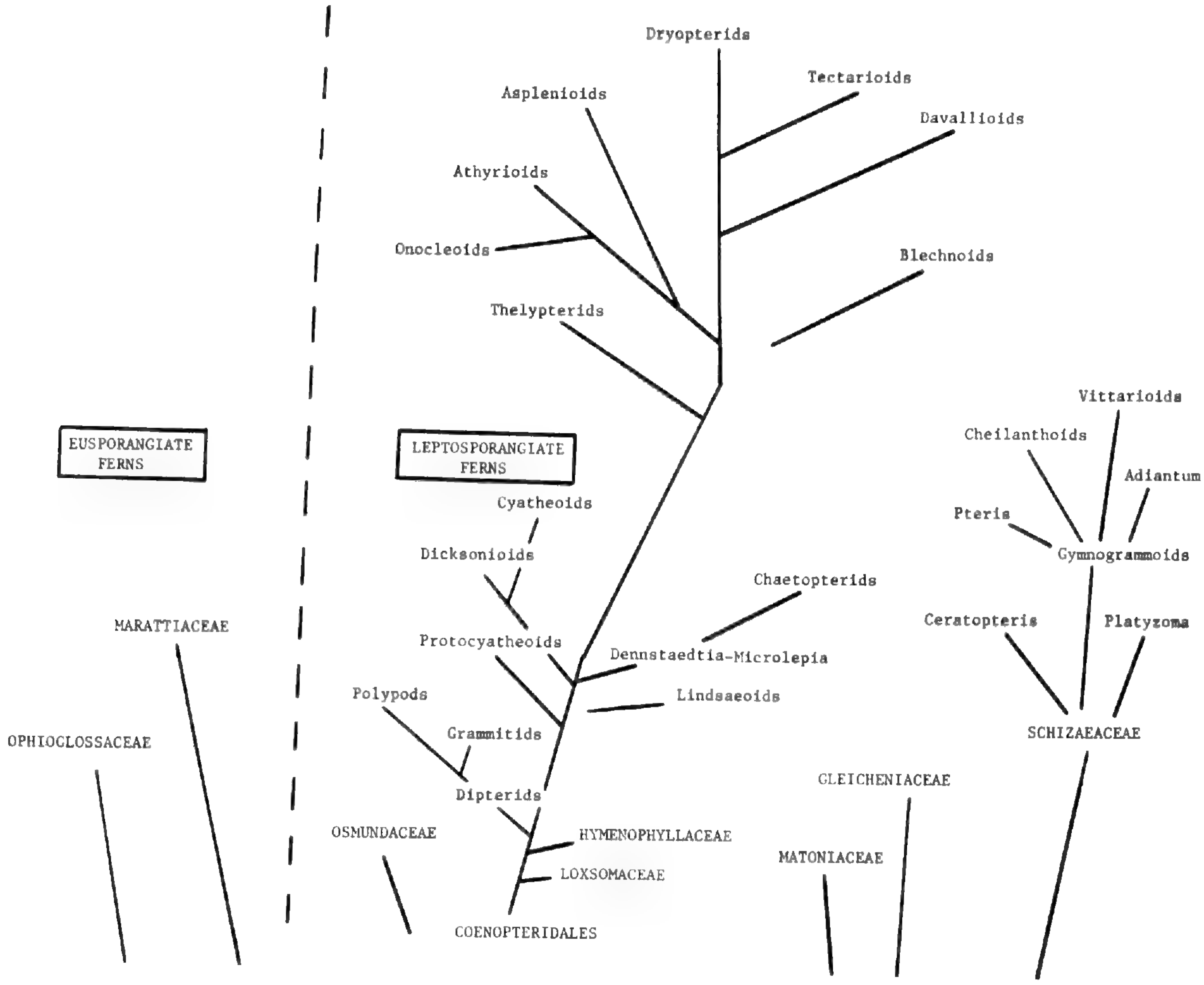

FIGURE 1. Phyletic diagram showing presumed relationships of the major groups of the Filicopsida.

and the Ophioglossaceae. A detailed comparative study would help in this matter, but it would seem that stipules in the Marattiaceae are quite different from the stipular sheaths of the Ophioglossaceae and the flared leaf bases of the Osmundaceae.

The Marattiaceae are plants that are fleshy and lack strengthening tissue. The stele is distinctive in its polycyclic dictyostele. The indument is composed of scales, but they are unlike any scales of the Filicales and are essentially amorphous. A detailed comparison of indument types in the ferns as a whole would be well worth the time. The plants contain abundant mucilage ducts, and the flesh of the plant turns pink when exposed to the air. Is this the same mucilage as in the Cyatheaceae and a few other ferns? Another feature that cements the relationships of the fossil *Psaronius* and the modern Marattiaceae is the distinct root anatomy that is common to both. Its stele contains radiating arms of xylem and phloem as opposed to the diarch protostele of virtually all other ferns.

In the Ophioglossaceae we again have soft fleshy plants without any substantial strengthening tissue. The unique features of this family include its very large sporangia, its fertile stalk of unknown origin (Is it an ancient dichotomy? Could it be a branch? Is it a fused pair of pinnae?), its subterranean rhizome and gametophyte, and its mycorrhizal relationship in both gametophyte and sporophyte.

Quite possibly the Ophioglossaceae have an origin distinct from the rest of the ferns and probably the Marattiaceae also have arisen independently. This possibility should be given serious consideration rather than accommodating all the so-called ferns into one phyletic line and trying with great imagination to derive the characters of the leptosporangiate ferns from our modern eusporangiate representatives.

Of the leptosporangiate ferns the Osmundaceae stands part perhaps farther than most groups. It has distinct sporangia with the small lateral patch annulus, a distinctive stele recognizable in the fossil record, and is distinctly primitive in its gametophytes, sex organs, spore number and leaf anatomy. It seems to stand alone, although closer to the true ferns than to the eusporangiate ferns. Miller (1967) has given us a detailed picture of evolution within the Osmundaceae itself.

The Playiogyriaceae (*Plagiogyria*) is also distinct and primitive. For lack of any place else to put it, it is probably more closely related to the Osmundaceae than to any other group. Its pneumatophores on the petiole base are of uncertain function and origin and significance.

The main line of the ferns began with probably large leaves, marginal sori with both inner and outer indusia, creeping rhizomes, and a siphonostele. Most likely the modern protosteles are reduced from siphonostelic predecessors. Very early in the line there arose a side line with elongated receptacles. This includes the small group Loxsomaceae and the better known filmy ferns, Hymenophyllaceae. In this line the stele condition has been reduced with size to a protostele. The larger members of the Hymenophyllaceae have a distinct siphonostele.

Within the main line of the ferns we find a diversity of sporangial types, ranging from the oblique complete ring to the vertical interrupted annulus. In looking for fossil ancestors we are fortunate in having in the Coenopteridales (*e.g. Anachoropteris* and *Botryopteris*) a generalized type of sporangium from which any type of modern annulus can be evolved in a theoretical way.

Farther up the line we find the familiar tree ferns, basically with tall trunks, but we also find trunkless forms which are probably the more primitive. Within the tree ferns proper we have two large groups, the Dicksoniaceae, with hairs and marginal clam-like sori, and the Cyatheaceae, with an indument of scales and dorsal sori. Tryon (1970) has dealt with the latter in some detail and described the probable relationships of the subgroups of cyatheoid ferns.

At this point it becomes important to mention the diversity of stomatal types in the ferns. As has been pointed out by various authors (Kondo, 1962; Thurston, 1969; Cotthem, 1970), the stomata can be of some phyletic importance. In this symposium White has pointed out that the mature stomatal configuration cannot be used in determining the developmental type of stomate. Although this may be true in some cases, a great deal of systematic information can be gained from observation of mature stomates. Kondo (1962) pointed out the basic types of stomates, based on the number of divisions necessary to convert a stomatal initial into a stomate. Type 1 divided an epidermal cell directly into a stomate (two guard cells), Type 2 required a division of subsidiary cell first, and Type 3 involved division to form two subsidiary cells. Basically the primitive ferns have Type 1 without any subsidiary cells, the most specialized have Type 3, and the intermediate ones have either Type 2 or a mixture of Types 2 and 3. Different types may be of diagnostic value for particular groups, but the overall trend fits any phyletic scheme, *i.e.* everyone agrees that those with Type 1 are primitive and that those with Type 3 are specialized. There is one additional type of stomate that is especially impressive in its configuration and the groups that have it. This is what Kondo called Type X. Thurston (1969) and Cotthem (1970) have pointed out the groups that have Type X. According to Bower's view (1923–28), these would fall into at least three different unrelated groups of ferns. On the contrary, it is quite possible that all are related (Mickel, 1973). There is no particular evidence to dispute this hypothesis, and it makes a great deal of sense to place them together. The groups that have Type X stomates include the dicksonioid tree ferns, the protocyatheoids (*Lophosoria* and *Metaxya*), Loxsomaceae, the dipterids (*Dipteris* and *Cheiropleuria*), and at least one primitive member of the Polypodiaceae (*Christiopteris*). Most likely the Protocyatheaceae form an independent side line not directly connected with the tree ferns. Similarly, the dipterids form another line prior to that and lead directly into the Polypodiaceae. Their stomata as well as their stele, venation, sori, and chromosome numbers support this hypothesis.

In the ferns in general venation patterns have evolved from free to netted. Within the Polypodiaceae sens. str., in contrast, it is clear that the primitive condition is netted and only the more specialized groups have free veins.

In the polypod line of evolution there was an early divergence that led to the Grammitidaceae, which are distinct in their green tetrahedral spores, long hairs, and ribbon-like gametophytes. Precise relationships between the grammitids and polypods are not fully understood, and there remain a few odd genera, such as *Hyalotricha* and *Loxogramme*, whose familial dispositions are not clear-cut.

Close to the dicksonioid tree ferns are the dennstaedtioid ferns. These are characterized by their large fronds, marginal cup-like sori, creeping rhizome clothed with hairs, and often polycyclic siphonostele. In the dennstaedtioids the petiole anatomy varies greatly and can be used as a taxonomic tool. Within *Dennstaedtia* itself nearly all the species can be distinguished on the basis of the stelar configuration of the petiole (Keating, 1968). A more extended study of petiole anatomy in the ferns is needed. Keating's study was based on petiole anatomy near the base of the petiole. A more thorough study is needed to determine the value of such anatomical studies through the length of the petiole. In some cases the petiole strand may divide as it goes up the petiole, whereas in other cases it may fuse in its ascent. Just what part is the most diagnostic and in which fern groups it is helpful are yet to be determined.

Within the Dennstaedtiaceae we see another example of Bower's "phyletic slide" in which the sorus may shift from the margin to a dorsal position. We can see a morphological series from *Dennstaedtia* with its marginal sorus to *Paesia* with its reduction of the inner indusium, *Pteridium* in which the inner indusium is nearly gone, *Hypolepis* with no inner indusium but still a marginal sorus in *H. repens* to *H. nuda* in which the sorus is in a nearly medial dorsal position.

This slide can also be seen in the closely related *Dennstaedtia* (marginal) to *Microlepia* and *Saccoloma* with the sorus moving back from the margin about a millimeter. In fact, the prime difference between *Dennstaedtia* and *Microlepia* is the sorus position, and a more complete study of this complex is needed to fully determine the generic limits.

One character that can be observed only in living material is a peculiarity in growth habit in certain members of the Dennstaedtiaceae. In *Pteridium* and some species of *Hypolepis* (Mickel, 1973) the lowest pair of pinnae may develop to maturity before the crosier will continue and produce the next pinna pair. The function and taxonomic significance of this character is not at all understood.

Another character visible generally only on living material is the branching habit of the plants. Within the dennstaedtioid ferns the branching is predominantly epipetiolar; that is, the branches arise from the petiole of the leaf rather than from the stem. In some cases it is only a matter of a few millemeters out on the petiole, but it may be as much as 15 cm away from the stem. This feature is perhaps best developed and most conspicuous in *Hypolepis* in which regularly two or up to four branches develop as a major part of the stem system. Branching seems to be largely epipetiolar in most of the primitive ferns of the main line of ferns. This includes the filmy ferns, dipterids, dennstaedtioids (Mickel, 1973; Troop & Mickel, 1968). This is reminiscent of the peculiar branching of *Botryopteris* and *Anachoropteris* of the Carboniferous, and whether or not there is a direct connection in evolutionary line, the consistency of the branching habit in this line of ferns is certainly significant and must be explained. It is possible that this type of branching is a remnant of branch origin of megaphylls.

Arising from the dennstaedtioids the aspidioid ferns appear to emerge, characterized by dorsal sori, bilateral spores with a well-developed perine, and a rhizome indument of scales rather than hairs. Trends in these directions are seen within the dennstaedtioids, and a good transition is seen in the genus *Monachosorum*. A great deal of diversity is seen within the aspidioid ferns, and details of their interrelationships await careful scrutiny.

The Schizaeaceae are held together largely by the sporangium with its apical annulus, which we are told by Eggert in this symposium, is not to be trusted. Within the family there are three distinct elements—*Lygodium*, *Schizaea-Actinostachys*, and *Anemia-Mohria*, each of which might possibly be considered for family rank. *Anemia* has distinct erect fertile pinnae and spores with ridges; the spores are well-known and easily recognized in the fossil record. The climbing habit of *Lygodium* and the grass-like fronds of *Schizaea* and *Actinostachys* set them apart as extremely divergent elements. The Carboniferous genus *Senftenbergia*, which has long been touted as the ancient element of the Schizaeaceae, has been found on zygopterid foliage and therefore seems to be a coenopteridalean fern. Apparently this type of sporangium has evolved more than once and cannot be used as a definitive character for the Schizaeaceae. This does not mean necessarily that the modern members of the family are unrelated, but rather that we must use caution in ascribing schizaeaceous affinity to all fossil ferns bearing sporangia with apical annuli.

One of the most serious questions regarding the phylogenetic position of a large block of ferns involves the relationships of the Adiantaceae. Often these are placed in the main line of the ferns close to the Dennstaedtiaceae on the basis of the marginal sori in many of the genera. It seems more likely, however, that the Adiantaceae belongs closer to the Schizaeaceae. If this is so, the gymnogrammoid group of the Adiantaceae would appear to be the most primitive. They have sori that run along the veins but lack an indusium. This is much like those of *Anemia* in the Schizaeaceae, where there is no distinct sorus but the sporangia are situated on the veins. Furthermore, some of the gymnogrammoids, such as *Jamesonia* and *Eriosorus*, have hairs rather than scales on the rhizome, which is generally considered to be a primitive character. In the cheilanthoid ferns the sori are restricted more and more to near the margin, and in some the margin is differentiated and reflexed to protect the sorus. If the Adiantaceae were derived from the Dennstaedtiaceae, we would expect that somewhere there would be a remnant of the inner indusium, but there is no sign of it.

The genus *Pteris* seems to be largely a wet-forest representative of the generally xeric Adiantaceae. It differs in certain details from the rest of the group, but there is no question of its inclusion in this family.

In *Adiantum* the gymnogrammoid sorus has been restricted to an area very close to the margin, with the margin then reflexed as a false indusium; thus, the sorus is located on the underside of the false indusium. Many species of the genus have distinctive epidermal idioblasts. These idioblasts are a uniform feature of the vittarioids, which are epiphytic representatives of the Adiantaceae. The sori are gymnogrammoid in some genera, such as *Antrophyum* and *Hecistopteris*, but are linear near the margin in *Vittaria*.

The Parkeriaceae (*Ceratopteris*) is distinct in its vegetative morphology due to the aquatic habitat, but it appears to be somewhat intermediate between the Schizaeaceae and the Adiantaceae. Its spores closely resemble those of *Anemia*. The genus *Platyzoma* also shares characters of the two families, (A. Tryon 1961, 1964) and would appear to have as much right to family status as does *Ceratopteris*. It would appear to be an evolutionary offshoot with peculiar habit, anatomy, and incipient heterospory and cannot be considered part of the Adiantaceae itself.

The forking ferns, Gleicheniaceae and Matoniaceae, appear to have much in common, such as the brittle woody petioles and rhizomes, pectinate pinnae, and distinctive sori. The stele in the Gleicheniaceae is generally a vitalized protostele but is often a siphonostele. In the Matoniaceae it is a polycyclic siphonostele. The Gleicheniaceae are often credited as the ancestors of the Polypodiaceae sens. str. There is little evidence to support this view, and the stomatal evidence mentioned above is to the contrary.

The heterosporous water ferns present a major problem since we have little to go on regarding their origin. The Salviniaceae especially has a well known fossil record, thanks to the work of Hall and his associates (Hall, 1969; Jain & Hall, 1969; Hall & Bergad, 1971; Jain, 1971). The record goes back to the Lower Cretaceous, but again disappears down the black hole of the Triassic-Jurassic. We hope that in the coming years there will appear the link to the modern or other major groups of ferns.

Finally we have purposely ignored the position of the especially difficult problem of *Psilotum* and *Stromatopteris*. Bierhorst (1968, 1969) has postulated relationships between these and has included them in the ferns. *Stromatopteris* certainly does have peculiar morphology with no clear distinction between stems, roots and leaves, and it may be related to *Psilotum*. The question, however, is whether these are in fact ferns. What is their relationship to the rest of the ferns? Are they related at all to the other ferns or did they arise independently from preferns? The answers are not easy to come by.

In looking at the overall picture of the ferns, we must address ourselves to many of the questions posed here before a definitive phylogeny of the ferns will be possible. However, this does not preclude the construction of new phylogenetic schemes since these act as hypotheses and stimuli for further research. If we were to withold our phylogenetic theorizing until all the information were available, research would be more diffuse and the final picture would be even slower in emerging. Let us use these phylogenies to help us direct our future studies on the phylogeny of the ferns.

LITERATURE CITED

BIERHORST, D. W. 1968. On the Stromatopteridaceae (fam. nov.) and on the Psilotaceae. Phytomorphology 18: 232–268.

———. 1969. On *Stromatopteris* and its ill-defined organs. Amer. Jour. Bot. 56: 160–174.

BOWER, F. O. 1923–1928. The Ferns (Filicales). 3 Vols. Cambridge, England.

CHING, R. C. 1940. On natural classification of the family "Polypodiaceae." Sunyatsenia 5: 201–268.

COPELAND, E. B. 1947. Genera Filicum. New York.

COTTHEM, W. VAN 1970. Comparative morphological study of the stomata in the Filicopsida. Bull. Jard. Bot. État 40: 81–239.

DICKASON, F. G. 1946. A phylogenetic study of the ferns of Burma. Ohio Jour. Sci. 46: 73–108.

HALL, J. W. 1969. Studies on fossil *Azolla*: primitive types of megaspores and massulae from the Cretaceous. Amer. Jour. Bot. 56: 1173–1180.

——— & R. D. BERGAD. 1971. A critical study of three Cretaceous salviniaceous megaspores. Micropaleontology 17: 345–356.

HOLTTUM, R. E. 1947. A revised classification of the leptosporangiate ferns. Jour. Linn. Soc., Bot. 51: 123–158.

———. 1949. The classification of ferns. Biol. Rev. 24: 267–295.

JAIN, R. K. 1971. Pre-Tertiary records of Salviniaceae. Amer. Jour. Bot. 58: 487–496.

——— & J. W. HALL. 1969. A contribution to the early Tertiary fossil record of the Salviniaceae. Amer. Jour. Bot. 56: 527–539.

KEATING, R. C. 1968. Trends of specialization in the stipe anatomy of *Dennstaedtia* and related genera. Amer. Fern Jour. 58: 126–140.

KONDO, T. 1962. A contribution to the study of the fern stomata. Res. Bull. Shizuoka Univ. Fac. Educ. 13: 239–267.

MEHRA, P. 1961. Cytological evolution of ferns with particular reference to Himalayan forms. Proc. 48th Ind. Sci. Congr. 2: 1–24.

MICKEL, J. T. 1973. The classification and phylogenetic position of the Dennstaedtiaceae. Jour. Linn. Soc., Bot. In press.

Miller, C. N. 1967. Evolution of the fern genus *Osmunda*. Contr. Mus. Paleontol. Univ. Michigan 21: 139–203.

Nayar, B. K. 1970. A phylogenetic classification of the homosporous ferns. Taxon 19: 229–236.

Thurston, E. L. 1969. Taxonomic significance of stomatal patterns in the ferns. Amer. Fern Jour. 59: 68–79.

Troop, J. E. & J. T. Mickel. 1968. Petiolar shoots in the dennstaedtioid and related ferns. Amer. Fern Jour. 58: 64–70.

Tryon, A. F. 1961. Some new aspects of the fern *Platyzoma microphyllum*. Rhodora 63: 91–102.

———. 1964. *Platyzoma*—a Queensland fern with incipient heterospory. Amer. Jour. Bot. 51: 939–942.

Tryon, R. M. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 3–53.

A RECONSIDERATION OF *SPONDIAS MOMBIN* L. (ANACARDIACEAE)[1]

Thomas B. Croat[2]

Abstract

Spondias radlkoferi J. Donn. Sm. is considered distinct from *Spondias mombin* L. It differs chiefly in flowering precociously about one month later than S. *mombin*, in having fewer styles and a fruit which is green at maturity with an oblong endocarp, in having a trunk with a smooth periderm, and in forming droplets of viscid, cloudy sap when slashed. It is most easily recognized by the villous pubescence of its parts.

The genus *Spondias* as treated by Blackwell (1967: 363–367) in the *Flora of Panama* consists of two species, S. *purpurea* L. and S. *mombin* L. Field work done on Barro Colorado Island indicates that another taxon, S. *radlkoferi* J. Donn. Sm., must be segregated from S. *mombin* L.

The occurrence of the segregate taxon was first brought to my attention by Dr. Dennis Knight (University of Wyoming). After he sampled a number of *Spondias* by slashing the trunks, he concluded that two taxa were involved since part of the trees sampled produced small droplets of viscid, cloudy sap shortly after having been slashed, while others did not. He believed the plants to be otherwise quite similar. Robin Foster (Duke University), in the course of his phenological studies on Barro Colorado Island, noted other features which separate *Spondias* into two species. He noted that one group of trees flowers about one month later than do others and that the latter group develop fruits which are elongate and green at maturity. The other *Spondias* trees produce fruits which are more globose and turn yellow, then orange at maturity.

It was not surprising to discover that at least some native Panamanians were already familiar with part of these differences and had called the green-fruited *Spondias* "jobo verde." Mr. James Zetek wrote, in a recently discovered letter at the Field Museum, to Paul Standley on May 6, 1936 from Barro Colorado Island: "Here we have a mombin that resembles the yellow mombin, but it never gets yellow, it stays green all the time." He also added, "The trunk of the green one is smooth compared to that of the yellow."

Recent studies have confirmed the observations of Zetek, Knight, and Foster. Other characters have also been found which further delimit *Spondias mombin* L. and S. *radlkoferi* J. Donn. Sm.

Spondias radlkoferi is readily distinguished from S. *mombin* both in the field and in the herbarium. The former usually flowers about a month later than S. *mombin*, though sufficient overlap occurs in their flowering periods to allow hybridization. Plants of both species may be common in mixed populations on Barro Colorado Islands. However, while they are without question

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Ann. Missouri Bot. Gard. 61: 483–490. 1974.

closely related species, there is no strong evidence of hybridization. Characters used to separate the two species are numerous and consistent.

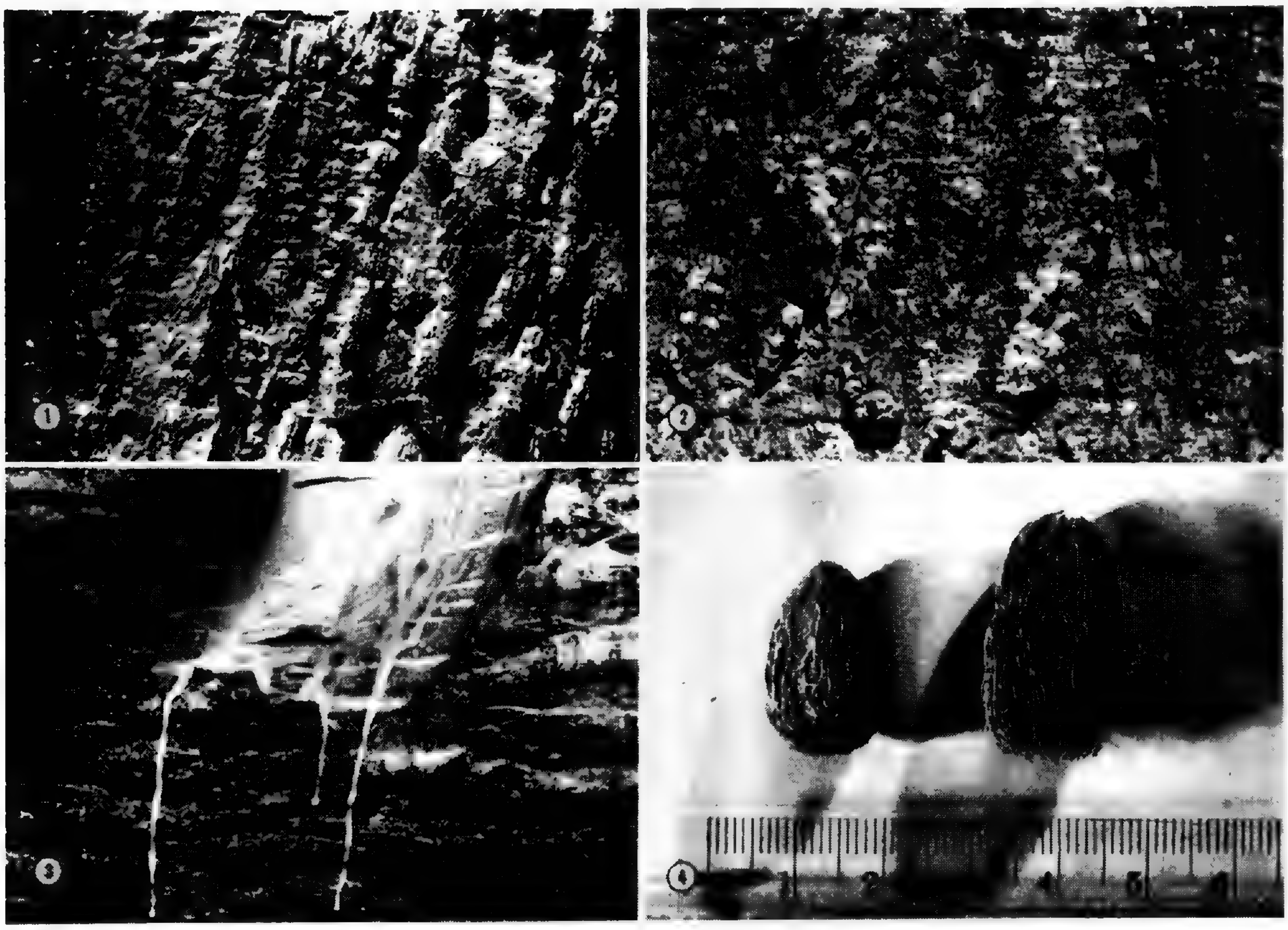
One of the most striking differences between the two species is the precocious flowering of *Spondias radlkoferi.* Although S. *mombin* flowers, on average, about one month earlier than S. *radlkoferi,* it generally has fully developed leaves at time of flowering. *Spondias radlkoferi* begins to flower at about the time new leaves are developing.

No doubt as a consequence of its later flowering, fruits of *Spondias radlkoferi* mature later. Moreover they are somewhat larger. The appearance of their fruit later in the rainy season when food has become slightly more scarce perhaps explains their lack of an attractive color. Whereas S. *mombin* turns orange at maturity and is sweet and tasty, S. *radlkoferi* fruits remain green at maturity and, although edible, they are not sweet and tasty. Their peak of fruiting activity (October-November) comes at a time when competition for food is greatest, so the species has perhaps lost its ability to produce colored fruits or never developed it in the first place. Because of the 3-stylar condition of its flowers, in contrast to the 5-stylar condition of S. *mombin* (discussed later), it is suggested that S. *radlkoferi* has been derived from S. *mombin* and probably has lost its ability to produce colored fruits because the serious competition for food in the late dry season has made attractive fruits unnecessary.

On Barro Colorado Island, larger trees produce the bulk of all animal food. Phenological studies made in central Panama (Croat, 1969) indicate that the peak of the fruiting season for medium- to large-sized trees occurs in April and then tapers off until a low is reached in November when fruit is always very scarce. Since the peak of fruiting for *Spondias radlkoferi* usually occurs during October and November when fruit is most scarce, the species has no difficulty getting an abundance of animals to disperse even its uncolorful, not-so-tasty fruits. The fact that it is apparently as abundant as S. *mombin,* which has attractive, tasty fruits, attests to this.

There are several other good field characters which may be used to separate the two closely related species. The appearance of the bark of the trunk and larger branches offers one of the most characteristic features. While there is some variability from tree to tree, *Spondias radlkoferi* has a trunk with a relatively smooth surface with paper-thin strips of grayish periderm oriented vertically (Fig. 1). The intervening brownish areas are roughened but not raised. In S. *mombin,* the thin grayish strips of periderm are missing and are replaced by much thicker, coarse sections of periderm 1–2 cm wide which are considerably raised from the intervening areas of the trunk (Fig. 2). These thick, irregular patches may contain further elevated, somewhat rounded projections to 7–8 mm high. The intervening area of the trunk is flat but variously fissured in an irregular vertical pattern. Occasionally the lowermost part of the trunk may lack the raised warty strips of periderm. Instead this area usually has a more or less continuous pattern of broad, shallow depressions.

The inner bark of both species is similar. Though quite variable from tree to tree, the inner bark is pink to reddish with whitish, narrowly wedge-shaped areas protruding inward from the periphery (Fig. 3). The surface of the inner



FIGURES 1–4. Comparison of *Spondias mombin* and *Spondias radlkoferi*—1. *S. radlkoferi*, bark showing broad strips of thin periderm.—2. *S. mombin*, bark showing coarse sections of raised periderm.—3. *S. radlkoferi*, slash of trunk showing milky sap flowing from fallen tree.—4. Endocarps of *S. mombin* (left) and *S. radlkoferi* (right).

bark of *Spondias radlkoferi* forms minute, whitish, viscid droplets, easily visible within 30–60 seconds after slashing. Generally the droplets do not increase greatly in size nor do they coalesce or form a stream of sap. However, felled trees may form abundant, runny sap (Fig. 3). In contrast, *S. mombin* shows no evidence of whitish, viscid sap and does not form the small droplets on the inner bark after it has been slashed.

Another distinguishing field character is the appearance of the old fruit endocarps, which generally lie in great abundance beneath trees of both species for most of the year. While some animals, particularly rodents such as the agouti (*Dasyprocta punctata*) and other frugivores, carry many of the fruits away and bury them (Smythe, 1970), monkeys eat the fruit covering in the tree, dropping the inedible endocarp directly to the ground. These weathered endocarps alone are adequate for determination of the tree. The endocarps of *Spondias mombin* are obovoid, 2–2.5 cm long, whereas those of *S. radlkoferi* are oblong, usually 3 cm or more long (Fig. 4).

Those features distinguishing the two species on herbarium specimens are many and varied. The most easily observed definitive character is that of pubescence, although after a number of specimens are examined the color of a dry specimen is adequate for determination. Specimens of *Spondias radlkoferi* dry blackened, while those of *S. mombin* dry greenish. *Spondias mombin*

TABLE 1. Field characters separating *Spondias mombin* L. and *S. radlkoferi* J. Donn. Sm.

S. mombin	*S. radlkoferi*
Bark very coarse, deeply fissured the intervening corky periderm hard and prominently raised.	Bark not deeply fissured, the strips of periderm paper-thin, smooth.
Slash not producing cloudy, viscid droplets on inner bark.	Slash producing cloudy, viscid droplets within 30–60 seconds on inner bark.
Old endocarps (persisting on ground beneath tree for most of the year) obovoid.	Old endocarps oblong.
Leaves generally fully developed at time of flowering (ca. 1 month earlier than *S. radlkoferi*).	Leaves usually young at time of flowering.
Mature fruits orange, sweet, and tasty.	Mature fruits green, edible but not very tasty and reported by some to be more acidic.

is sometimes nearly glabrous, but any pubescence consists of short, puberulent trichomes. The species is reasonably uniform throughout its range in this respect, but the trichomes are longer in Mexico. *Spondias radlkoferi* is sparsely to densely villous, especially on the veins of the lower leaf surface and branches of the inflorescence. Trichomes are crisped or straight and are usually curly or at least recurved near the middle.

Although the inflorescence of *Spondias radlkoferi* occurs precociously or nearly so, its flowers do not differ greatly from those of *S. mombin*. The most easily distinguished difference is the generally glabrous pedicel and calyx. This contrasts sharply with the usually densely pubescent branchlets of the inflorescence. Costa Rican and other Central American specimens often have some pubescence on the pedicel, but the trichomes are sparse and long. The pedicel and calyx of *S. mombin* are usually moderately to densely short-puberulent.

In addition there are characters not so easily observed such as shape of the flower buds (ovoid in *Spondias radlkoferi* vs. round to obovoid in *S. mombin*), length of the calyx lobes (much deeper in *S. radlkoferi*), and thickness of the disk. The disk of *S. radlkoferi* is ca. 2.3 mm wide and broader than the width of the stylar clump, whereas the disk of *S. mombin* is only about 1 mm wide and narrower than the stylar clump.

Finally there are significant differences in the number of styles for the two species. *Spondias mombin* generally has 5 styles, less frequently it may have up to half of the flowers with 4 styles and rarely do flowers have only 3 styles. On the other hand, *S. radlkoferi* generally has flowers with 3 or 4 styles (in actual counts of ca. 50 flowers, 60% were 4-stylar and 40% were 3-stylar), very rarely with 5 styles.

There are strong indications that the 3- and 4-stylar condtions have arisen directly from the 5-stylar condition. Analysis of the number of styles on both flowers and juvenile fruits from the same plants invariably shows more fruits with 5 styles than flowers with 5 styles. Since there is no reason to believe that a flower with 5 styles is more apt to produce fruit than one with 3 or 4, I believe the 4-stylar condition in flowers is often the result of fusion of 2 styles. In a few rare cases the fourth style was seen in the process of pulling apart on a maturing fruit. This is clear evidence that many of the 4-stylar flowers (and for the same reason, the 3-stylar flowers) are the result of a fusion of styles. It is not certain whether fusion of the styles in this manner is detrimental. Both *Spondias mombin* and *S. radlkoferi* appear to have 5-locular fruits, and thus the united styles apparently function as 2 separate styles. The fact remains, however, that the degree of style fusion is more advanced in *S. radlkoferi* than in *S. mombin.*

The characters used in the key were selected because they are usually the easiest to observe on dried herbarium specimens. They are no more definitive however than a variety of other characters. Table 1 lists other sets of contrasting characters useful in separating the two species in the field.

KEY

Plants glabrous or pubescent parts of plant merely puberulent (the trichomes short and straight); leaves not drying blackened, usually fully developed at time of flowering; blades with a prominent submarginal collecting nerve; calyx pubescent .... *Spondias mombin* L.

Plants villous to velutinous (the trichomes not straight or if so long and very dense); leaves usually drying blackened, usually not fully developed at time of flowering; blades lacking a submarginal nerve; calyx glabrous .... *Spondias radlkoferi* J. Donn. Sm.

Spondias mombin L., Sp. Pl. 371. 1753.—"Hogplum."

S. lutea L., Sp. Pl., ed. 2. 613. 1762.
S. lutea L. var. *maxima* Engl. *in* Mart., Fl. Bras. 12(2): 374. 1876.
S. lutea L. var. *glabra* Engl. *in* Mart., Fl. Bras. 12(2): 374. 1876.

Tree mostly 10–30 m tall, to 60 cm d.b.h.; periderm gray, deeply and coarsely fissured, the raised segments hard, rough, the inner margin irregular; inner bark variously colored, usually with triangular patches of red or tangerine alternating with white; at least the youngest branchlets puberulent. *Leaves* imparipinnate, alternate, to 60 cm long (to 70 cm on juveniles); petiole and rachis usually finely puberulent; leaflets mostly (3–)9–17, opposite or subopposite; petiolules 6–9(–14) mm long; blades oblong to ovate, usually acuminate, acute to rounded and asymmetrical at base, 3–20 cm long and 1.5–7 cm wide, usually ± glabrous except for puberulence on midribs and major veins above and below; reticulate nerves prominulous, the margin minutely revolute with a prominent submarginal nerve; the larger leaflets with the midrib arched. *Panicles* terminal, to 60 cm long; branches, peduncles, pedicels and calyces usually puberulent; *flowers* 5–7 mm wide, 5-parted, globular to obovoid in bud; pedicels 1–5 mm long, usually articulate near the base; calyx shallow, the lobes short, triangular, sharply acute, usually minutely puberulent, the margins ciliate; petals white, acute and inflexed-apiculate at apex, somewhat reflexed at anthesis; stamens 10, exserted, 1.5–3 mm long, alternating with the fleshy, undulate segments of the disk; disk fleshy, undulate-lobed, to ca. 1 mm wide, the width of one side less than the width of the clump of styles; styles usually 4 or 5 (rarely 3), much shorter than stamens at anthesis, the stigma linear, on the dorsal surface near apex. *Fruit* oblong to obovoid, 2.5–3 cm long, yellow to orange at maturity; mesocarp to 6 mm thick, fleshy, sweet and tasty; endocarps obovoid, 2–2.5 cm long, hard, covered by a tough, coarse, fibrous matrix.

Flowering principally from March to June (rarely earlier), but most abundant in April and May. Fruits are mature from July to October, mostly in August and September. Leaves are lost during the early part of the dry season beginning in December and January and are replaced before flowering commences.

Throughout tropical America. Introduced in tropical Africa. In Panama principally from tropical moist forest in the Canal Zone and the Provinces of Bocas del Toro, Colón, Panamá and Darién; also known from premontane moist forest in Panamá Province (Farfan Beach), tropical dry forest in Coclé and premontane wet forest in Chiriquí (Progresso).

Since S. *mombin* and S. *radlkoferi* were lumped in the *Flora of Panama* (Blackwell, 1967: 363–367), the following list of exsiccatae from Panama is published here for clarification.

PANAMÁ. BOCAS DEL TORO: Forest above railroad station 7.5 mi., *Croat & Porter 14622* (MO). CANAL ZONE: Along K-2 Highway N of Cocolí, *Croat 9169* (MO). Gaillard Highway on road to treatment plant, *Croat 14015* (MO). Along road between Gatún locks and Fort Sherman, *Croat & Porter 15383* (MO). Road C2c on Cerro Luisa, *Croat 10770* (MO). U.S. Army Tropic Test Center, Miraflores Bridge, *Dwyer & Robyns 3* (MO). Farfan Beach, roadside thicket adjacent to beach, *Dwyer et al. 4688* (MO, F). Summit Garden, *Croat 14481* (MO). Along canal near Gamboa gate to Pipeline Road, *Croat 14836* (MO). Curundu Survival School area, *Tyson & Dwyer 4457* (MO). Miraflores Lake near water plant, *Tyson 3553* (MO). Albrook, U.S. Army Tropic Test Center side, *Dwyer & Robyns 61* (MO). Near Fort Clayton, *Croat 14462* (MO). Victoria Fill near Miraflores Locks, *P. H. Allen 1762* (MO, F). West of Gamboa, *Haines 571* (MO, F). Edge of lake below spillway on Miraflores Dam, *Stern et al. 1* (MO). Opposite motor pool at Fort Davis, *Lazor & Blum 5413* (MO). Balboa, *Zetek 3611* (MO). Barro Colorado Island, shore of large cove between Slothia Island and Colorado Point, *Croat 6043* (MO); eastern side of Peña Blanca Peninsula, *Croat 5357* (MO); Donato Start, *Croat 5895* (MO); shoreline of Gigante Bay north of Burrunga Point, *Croat 8432* (MO); laboratory clearing near dock, *Croat 10751* (MO); forest north of clearing, *Croat 14090* (MO); Lutz Trail 500, *Croat 11698* (MO); Barbour Trail 700, *Croat 11827* (MO); without further locality, *Carpenter 52* (F, MO); *Zetek 3611* (MO, F). CHIRIQUÍ: Progresso, *Cooper & Slater 207* (MO, F). COCLÉ: Santa Clara Beach, *Croat 9599* (MO). COLÓN: Buenavista, *Holdridge 6390* (MO). DARIÉN: Río Pirre 2–5 mi. above El Real, *Duke 5079.* Trail between Pinogana and Yavisa, *Allen 272* (MO). Santa Fé, *Duke 8400* (MO). Río Pirre, *Croat & Porter 15485* (MO). PANAMÁ: Sajalices, Capira, *E. A. Lao 62* (MO). Pedro Gonzales, Perlas Islands, *P. H. Allen 2598* (MO). Coronado Beach 6 mi. E of San Carlos, *Croat 14260.* Las Lajas, Las Cumbres, S. A. *Sandoval 15* (MO). 1 mi. E of El Llano, *Croat 14484* (MO).

Spondias radlkoferi J. Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 194. 1891.

S. *nigrescens* Pittier, Contr .U. S. Natl. Herb. 18: 75. 1914.

Tree to 30 m tall, to 75 cm d.b.h.; periderm not deeply fissured, the surface with thin, narrow strips of periderm; inner bark similar to S. *mombin* except producing whitish, viscid droplets within a short time after being cut; younger branches glabrate to sparsely crisp-villous to densely villous, becoming glabrate. *Leaves* imparipinnate, alternate, to 54 cm long, usually sparsely crisp-villous on petiole, rachis, upper midrib and lower surface of leaflets, especially on younger leaves; leaflets mostly 7–19; blades ovate to oblong-elliptic or oblong, abruptly long acuminate, acute to subcordate and markedly inequilateral at base, 2.5–16 cm long and 1.8–6 cm wide, the margins ± revolute, usually ciliate, usually lacking a submarginal nerve. *Flowers* 5-parted, usually bisexual, rarely pistillate, the first open flowers usually appearing with the new leaves in terminal and upper axillary panicles to 55 cm long; axes and rarely pedicels sparsely to densely crisp-villous; pedicels glabrous or less often pubescent, articulate usually 0.5–2.5 mm below the calyx (the articulation sometimes obscured by bracteoles); flower buds usually ± pyriform; calyx cupulate, the lobes thick, prominent, rounded to blunt-triangular, ca. 1 mm long, usually glabrous throughout; petals ± oblong-elliptic, acute and inflexed-apiculate at apex, 3-nerved (including marginal nerve), 2.3–4.3 mm long, white or greenish-white, recurved at anthesis; stamens 10, 1.7–2 mm long, in 2 series, exserted at anthesis; disk to 2.3 mm wide, fleshy, undulate-lobed, the width of one side more than the width of the clump of styles; ovary subglobose, pubescent; styles usually 3 or 4 (rarely 5), usually free and shorter than the stamens at anthesis in bisexual flowers, the stigmatic surfaces linear, on the dorsal surface near the apex; female flowers rare, the styles to ca. 2 mm long, ca. twice as long as the stamens, united below the middle, the stigmatic surface ovate, turned inward. *Fruit* 3–3.5 cm long, minutely pubescent when immature, oblong to obovate and green at maturity; mesocarp thin, green with a ± unripened flavor, faintly sweet to acidic; endocarp oblong, nearly as long as fruit, hard, covered by a tough, coarse, fibrous matrix.

Plants often flower 4–6 weeks later than *S. mombin* on Barro Colorado Island, but since their flowering periods overlap, they may be seen flowering together. Flowers occur mostly April to July, especially May and June. Fruits mature from September to December, especially October and November.

Southern Mexico (Veracruz, Chiapas, Campeche), throughout Central America, into Colombia and Venezuela. In Panama known principally from tropical moist forest in the Canal Zone and Panamá Province (El Llano) but also known from tropical moist forest in Bocas del Toro and from premontane wet forest in Chiriquí (Finca Linda to Boquete).

MEXICO. CAMPECHE: Tuxpena, *Lundell 894* (F, MO). CHIAPAS: Escuintla, Calculata, *Matuda 16668* (F). VERACRUZ: Fortuno, Coatacoalcos River, *Llewellyn Williams 8694* (MO). YUCATAN: *Gaumer 24069, 24070* (both F); Southeast Kancabonot, *Gaumer 23885* (F).

GUATEMALA. ALTA VERAPAZ: Near Alta Verapaz-Petén border, *Steyermark 45214* (F). CHIRIQUIMULA: Caracol Mts. 1.5 mi. N of Quezaltepeque, *Steyermark 31408* (F). IAZBAL: Valley of Río Motaqua, *Steyermark 38348* (F). PETÉN: Camino Melchor K 32, 250 m, *Aquilar 37* (F). QUETZALTENANGO: Between Colomba and Coatepeque, 850 m, *Steyermark 52128* (F). RETAHULEU: Region of Ajaxa E of Santa Cruz Mulua, 330 m, *Standley 88210* (F). SAN MARCOS: Volcán Tajumulco, 1300–1500 m, *Steyermark 37141* (F). PROVINCE UNKNOWN: Río Dulce, *Wilson 409* (F).

BELIZE. Corozal-San Antonio Road, *Gentle 130* (F), *Lundell 424* (F), *5017* (F, MO), *Wm. C. Meyer 190* (F). Honey Camp, Orange Walk, *Lundell 116* (F).

HONDURAS. ATLANTIDA: Forest back of Ceiba, *Yuncker et al. 8592* (F). CORTES: La Lima, *Williams & Molina 14467* (F). Río Lindo, *Molina 5668* (F). MORAZAN: Road between El Jicarto and El Pedregal, *Standley 14505* (F). Quebrada de la Pita near Zamarano, *Williams & Molina 14083* (F). Río Yeguare, 960 m, *Williams & Molina 13248* (F). Vicinity of Zamarano, *Standley 13051* (F).

NICARAGUA. Region of Braggman's Bluff, *Englesing 232* (F).

EL SALVADOR. *Allen & van Severen 6890* (F).

COSTA RICA. ALAHUELA: La Garita Dam, *Lent 1148* (F). GUANACASTE: Catalina, *H. E. Stork 2763* (MO). Comelco Ranch, 7 km NW of Bagaces, *E. R. Heithaus 119* (MO). Finca la Pacifica, 2 mi. N of Canas, *Gentry 842, 843* (both MO).

PANAMA. BOCAS DEL TORO: Bocas del Toro, *Dunlap 504* (MO). CANAL ZONE: Barro

Colorado Island, *Aviles 10* (MO), *Croat 4912, 4929, 6040, 6453, 6838, 9046, 9101, 9283, 10082, 10218, 10227, 10294, 10320, 10328, 10836, 11157, 11682, 12580, 14404a* (all MO), *Dwyer 1458* (MO), *Ebinger 392* (F), *Foster 861, 1652* (both MO), *Knight 69–31* (MO), *Shattuck 82* (F, MO), *Starry 106* (MO), *107* (F), *Zetek 3414, 3584, 3645* (all F, MO), *3854, 4998* (both MO). Gaillard Highway near Gamboa, *Croat 14476* (MO). Gaillard Highway near Summit Garden *Croat 14830* (MO). Road to Gamboa airport *Croat 14841* (MO). Along canal near gate to Pipeline Road, *Croat 14837* (MO). Pipeline Road near gate, *Croat 16681* (MO). 2 mi. E of El Llano, *Tyson 1757* (MO). CHIRIQUÍ: Finca Lerida to Boquete, ca. 1300–1700 m, *Woodson et al. 1109* (MO). PANAMÁ: Vicinity of El Llano, *Duke 5869* (MO).

VENEZUELA. Without exact locality, *Birschel s.n.* (F).

LITERATURE CITED

BLACKWELL, W. H. 1967. Anacardiaceae. *In* R. E. Woodson Jr. & R. W. Schery, "Flora of Panama." Ann. Missouri Bot. Gard. 54: 351–379.

CROAT, T. B. 1969. Seasonal flowering behavior in central Panama. Ann. Missouri Bot. Gard. 56: 295–307.

SMYTHE, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Naturalist 104: 25–35.

CIENFUEGOSIA CAV. EXTENDED TO MADAGASCAR

Paul A. Fryxell[1]

My earlier revision of the genus *Cienfuegosia* (Fryxell, 1969) did not recognize any representatives of that genus on the island of Madagascar, although reference was made (p. 198) to Ulbrich's statement that *C. hildebrandtii* Garcke occurred there. No basis was known then, nor is known now, for Ulbrich's assertion.

However, an examination of the description and illustration of *Hibiscus humbertianus* Hochr. in the *Flore de Madagascar* (Hochreutiner, 1955) suggested the possibility that this species was a *Cienfuegosia.* Consultation of the original description revealed that Hochreutiner had acknowledged but rejected this possibility. In his later treatment he does not mention this similarity, but in placing it in *Hibiscus* states only (Hochreutiner, 1955: 68), "Espèce très distincte, ne ressemblant en rien aux autres espèces de la section [*Spatula* Hochr.] et même du genre." The examination of authentic material confirms Hochreutiner's statement that this species is poorly accommodated in *Hibiscus* and also confirms his earlier suspicion that a placement in *Cienfuegosia* might be correct.

Hochreutiner rejected a placement of *Hibiscus humbertianus* in *Cienfuegosia* for two reasons: (a) *H. humbertianus* has a 5-lobed stigma and a 5-celled fruit, whereas these structures are typically 3–4-merous in *Cienfuegosia*; and (b) *H. humbertianus* lacks the black punctiform glands ("gossypol glands") in the calyx that are prominent in many species of *Cienfuegosia.* However, *Cienfuegosia drummondii* (A. Gray) Lewton has a (4–)5-merous gynoecium, and several species have the gossypol glands restricted in distribution from certain plant parts, including absent from the calyx (or nearly so) in *C. hildebrandtii* Garcke and *C. hearnii* Fryx. The transfer of *H. humbertianus* to *Cienfuegosia,* therefore, does not unduly stretch the generic boundary of *Cienfuegosia.* Characters that support such a transfer include the following:

1. *Style and stigmas.* The style is single or very slightly divided apically and surmounted by five capitate stigmas. Hochreutiner notes a resemblance to *Thespesia* in reference to the undivided style, but the stigmas in *Thespesia* are decurrent rather than capitate. The style and stigma characters of *Hibiscus humbertianus* are similar to those found in species of *Cienfuegosia* sect. *Paraguayana* Fryx. and *Cienfuegosia* sect. *Friesia* Fryx., except that all except one (*C. drummondii* (A. Gray) Lewt.) of the eight species included in these two sections have three stigmas rather than five. In *Hibiscus,* on the other hand, the styles are typically free above with the five capitate stigmas widely separated.

2. *Foliar nectaries.* The leaves each bear a nectary near the base of the midrib on the abaxial surface. In this respect, and in general leaf conformation, *Hibiscus humbertianus* is similar to species of *Cienfuegosia* sect. *Garckea* Fryx.

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Such nectaries are found in most species of the eight genera that comprise the tribe Gossypieae, in which *Cienfuegosia* is included (Fryxell, 1968). In *Hibiscus* they occur (to my knowledge) only in species of sect. *Furcaria* DC. (e.g. *H. furcellatus* Lam.), sect. *Azanza* DC. (e.g. *H. tiliaceus* L.), and sect. *Lilibiscus* Hochr. (e.g. *H. rosa-sinensis* L.). None of these sections could accommodate the species in question.

3. *Gossypol glands.* The tribe Gossypieae is distinguished from other tribes of the Malvaceae (and indeed from other angiosperms) by the possession of gossypol glands (Lukefahr & Fryxell, 1967; Fryxell, 1968). These structures are lacking in *Hibiscus.* Although they are sometimes obscure in *Cienfuegosia* (especially in species of sect. *Friesia*), they may be demonstrated in all species. In *H. humbertianus* these glands are present in abundance on the leaf lamina, although they may be obscured by pubescence. (They are best observed on the undersurface of young leaves.) A few also occur on the petals, although they are not prominent because they are not dark-pigmented.

Additional characters to support the correctness of this transfer (cf. Fryxell, 1968) may be sought in chromosome number, in embryo morphology, and in phytochemical tests for the presence of gossypol, a substance that has been shown to occur in all species of *Cienfuegosia* tested (Lukefahr & Fryxell, 1967). As yet, material for the evaluation of these characters is not available.

Cienfuegosia humbertiana (Hochr.) Fryxell, comb. nov.

Hibiscus humbertianus Hochr., Candollea 5: 9. 1932. [Type: *Humbert & Swingle 5468* (P.)] Fl. Madag. 129 Fam. Malv. 66. *t. 28. f. 3–7.* 1955.

Small *shrub* with glabrescent, cicatricose, woody twigs. *Leaves* small (5–10 mm long), ovate or sometimes reniform to trilobed, basally truncate, serrate (the teeth sometimes spinescent), with coarse stellate pubescence on undersurface (the hairs 3–4-armed, the arms 1 mm long, spiniform) together with very fine, simple hairs (0.1–0.2(–0.3) mm long) with recurved, sharp tips (uncinate hairs), the fine pubescence predominating on the upper surface, both surfaces with "pitted" appearance resulting from the presence of sunken gossypol glands. *Petioles* exceeding lamina, densely covered with fine, uncinate hairs. *Stipules* subulate, 1 mm long, rigid, sometimes persistent even after leaf abscission. *Pedicels* axillary, solitary, 1.5–2 cm long, articulated near apex, densely covered with fine, uncinate hairs. *Involucral nectaries* lacking. *Involucre* of ca. 9 bracteoles; bracteoles distinct, spatulate, ca. 3 mm long, obtuse to acute, invested with fine uncinate hairs and a few coarser hairs. *Calyx* ca. 6 mm long, 5-lobed, ca. half-divided, with pubescence similar to that of under leaf surface. *Petals* white, obovate, 12 mm long, 6–7 mm broad, glabrous, with a very few (0–10) translucent gossypol glands scattered in lower half that are best observed with transmitted light. *Androecium* glabrous, pallid; filaments ca. 2 mm long. *Style* undivided, glabrous, exceeding staminal column by ca. 3 mm; stigmas 5, capitate, nearly distinct or coalescent into a single structure. *Capsule* globose, ca. 6 mm in diameter, 5-celled, with both fine uncinate pubescence and coarse stellate hairs (the latter sometimes simple). *Seeds* unknown.

Specimens examined:
MADAGASCAR: Delta de la Linta (Côte Sud-ouest), alt. 1–10 m, *Humbert & Swingle 5468* (P). Ambovombe, *Decary 3445* (P); *Decary*, 1925 (P).

The taxonomic placement of *C. humbertiana* within *Cienfuegosia* presents problems. Its possession of foliar nectaries, its leaf conformation, its shrubby growth habit, its articulate peduncles, and its African distribution, all suggest a placement in sect. *Garckea*. However, its capitate stigmas, its pentamerous gynoecium, its lack of involucral nectaries, and its spatulate involucral bracteoles suggest a placement in sect. *Paraguayana*. The combination of these several characters suggests its removal from both of the above sections and the establishment of a new section, as does the unique and specialized indumentum of *C. humbertiana*, its pallid corolla, and, to some degree, its isolated geographical occurrence. The distinctive uncinate hairs that occur in abundance in this species are similar in form to the recurved spines of the fruits of *Triumfetta* series *Uncinatae* (Lay, 1950), although they are much smaller. The combination of characters noted above, moreover, is anomalous not only for these two sections, but for the respective subgenera to which these sections belong: *Cienfuegosia* subgen. *Articulata* Fryx. and *C.* subgen. *Cienfuegosia*. Because these two subgenera are discrete cytologically with $n = 11$ and 10, respectively (Fryxell, 1969; Wilson & Fryxell, 1970), the chromosome number of *C. humbertiana* (as yet unknown) will have considerable bearing on its taxonomic placement.

In view of the above uncertainties, it is felt best to leave *C. humbertiana* incertae sedis for the present with the possibility acknowledged that a distinct subgenus may need to be erected to accommodate it when it becomes more fully known.

LITERATURE CITED

FRYXELL, P. A. 1968. A redefinition of the tribe Gossypieae. Bot. Gaz. (Crawfordsville) 129: 296–308.

———. 1969. The genus *Cienfuegosia* Cav. (Malvaceae). Ann. Missouri Bot. Gard. 56: 179–250.

HOCHREUTINER, B. P. G. 1955. Flore de Madagascar et des Comores. 129ᵉ Familie—Malvacées. 170 pp.

LAY, K. K. 1950. The American species of *Triumfetta* L. Ann. Missouri Bot. Gard. 37: 315–395.

LUKEFAHR, M. J. & P. A. FRYXELL. 1967. Content of gossypol in plants belonging to genera related to cotton. Econ. Bot. 21: 128–131.

WILSON, F. D. & P. A. FRYXELL. 1970. Meiotic chromosomes of *Cienfuegosia* species and hybrids and *Hampea* species (Malvaceae). Bull. Torrey Bot. Club 97: 367–376.

STUDIES OF BIGNONIACEAE 11: A SYNOPSIS OF THE GENUS *DISTICTIS*.

Alwyn H. Gentry[1]

Abstract

The genera *Wunschmannia* and *Anomoctenium* are united with *Distictis*. Necessary new combinations are *D. staminea* (Lam.) A. Gentry, *D. stipularis* (Mart. *ex* DC.) A. Gentry, and *D. scabriuscula* (Mart. ex DC.) A. Gentry. A new species, *D. steyermarkii* A. Gentry, related to the former members of *Anomoctenium*, is also described. A synopsis of the species of *Distictis* is included.

Distictis Mart. *ex* Meissn., Gen. 1: 300; 2: 208. 1840.

Phaedranthus Miers, Proc. Roy. Hort. Soc. London 3: 182. 1863.
Macrodiscus Bur., Monogr. Bignon. 46, *pl. 11.* 1864.
Wunschmannia Urb., Symb. Antill. 5: 494. 1908.
Anomoctenium Pichon, Bull. Soc. Bot. France 92: 226. 1946.

As usually delimited, *Distictis* has contained only three species. To these I have recently added a fourth by synonymizing *Phaedranthus* with *Distictis* (Gentry, 1973). Further study reveals that two more genera, *Wunschmannia* and *Anomoctenium*, should also be united with it.

As thus constituted, *Distictis* is characterized by scandent habit, six-angled, ribbed branchlets without interpetiolar glandular fields and often with foliaceous pseudostipules; 3(–5)-fid tendrils; terminal few- to several-flowered inflorescences; cupular, more or less truncate, usually glandular calyces; pubescent, tubular-campanulate or widely tubular, white or cream to deep red-violet corollas; sometimes exserted stamens; ecolpate pollen; more or less oblong, puberulous (very slightly puberulous but conspicuously lepidote in *D. lactiflora*) ovaries with the ovules several-seriate in each locule; and elliptic-oblong capsules, acute at the ends, with convex woody non-echinate valves, a flat septum, and seeds in two rows with the bodies brown, irregularly ridged, and usually somewhat papillose or puberulous.

A synopsis of the nine species which should be included in *Distictis* follows.

1. **D. lactiflora** (Vahl) DC., Prodr. 9: 191. 1845.

Bignonia lactiflora Vahl, Symb. Bot. 3: 80, *t. 66.* 1794. TYPE: St. Croix: *West s.n.* (C).
B. rigescens Jacq., Hort. Schoenbr. 2: 44, 5. 210. 1797. TYPE: Caracas(?) (location doubtful, not seen).
Distictis rigescens (Jacq.) DC., Prodr. 9: 191. 1845.
Macrodiscus rigescens (Jacq.) Bur., Mon. Bignon. 46, *pl. 11.* 1864.
Bignonia odorata Bello, Anal. Soc. Esp. Hist. Nat. 10: 293. 1881. TYPE: Puerto Rico (not seen).
Macrodiscus lactiflorus (Vahl) Bur. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894.

This is the best known species of the genus. It is reported from most of the islands of the West Indies and was chosen as the lectotype of the genus by

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Sandwith (1962: 454). *Distictis rigescens* was only provisionally separated from *D. lactiflora* by A. de Candolle (1845: 191) and Schumann (1894: 216). Britton (1925: 193) was apparently the first to definitely unite the two species.

2. **D. gnaphalantha** (A. Rich.) Urb., Feddes Repert. 14: 310. 1916.

Bignonia gnaphalantha A. Rich. *in* Sagra, Cuba 11: 105. 1850. TYPE: Cuba (not seen).
Macrodiscus gnaphalanthus (A. Rich.) Baill. *ex* Durand & Jackson, Index Kewensis, Suppl. 1: 259. 1903.
Distictis rhynchocarpa Urb., Symb. Antill. 9: 253. 1924. TYPE: Cuba: Oriente, *Ekman 1388* (not seen).
D. gnaphalantha subsp. *rhynchocarpa* (Urb.) Borhidi & Muñiz, Bot. Közlem. 58: 176. 1971.

Endemic to Cuba. *Distictis rhynchocarpa* was united with *D. gnaphalantha* by Borhidi and Muñiz (1971). Although they regarded it as a subspecies, it seems likely that it is at most a variety. The emarginate leaves used to separate it are often not constant, even on a single plant, in closely related *D. lactiflora.*

3. **D. laxiflora** (DC.) Greenm., Proc. Amer. Acad. Arts 33: 486. 1898.

Bignonia laxiflora DC., Rev. Bign. 21 (Biblioth. Universelle Genève). 1838, nom. nud.
B. cinerea DC., Rev. Bignon. 21 (Biblioth. Universelle Genève). 1838, nom. nud.
Pithecoctenium cinereum DC., Prodr. 9: 195. 1845. SYNTYPES: Mexico, *Mairet s.n.* (G-DC); Mexico, Oaxaca, *Andrieux 221* (G-DC).
P. laxiflorum DC., Prodr. 9: 195. 1845. TYPE: Mexico, Oaxaca, *Andrieux 220* (G-DC)
Distictis cinerea (DC.) Greenm., Proc. Amer. Acad. Arts 33: 487. 1898.

Mexico to Nicaragua (the Nicaraguan collections possibly from cultivated plants?). Standley (1926), the first to unite *P. cinereum* and *P. laxiflorum*, used the latter name.

4. **D. buccinatoria** (DC.) A. Gentry, Brittonia 25: 237. 1973.

Pithecoctenium buccinatorium DC., Prodr. 9: 195. 1845. TYPE: Mexico, *Mairet s.n.* (G-DC).
Bignonia buccinatoria Mairet *ex* DC., Prodr. 9: 195. 1845, nom. nud., pro syn.
Pithecoctenium buccinatorium var. *exsertum* DC., Prod. 9: 195. 1845. TYPE: Mexico, *Mairet s.n.* (G-DC).
Bignonia ghiesbreghtii Heller, Linnaea 30: 45. 1859. TYPE: Mexico, Toluca, *Heller 390* (not seen).
Phaedranthus buccinatorum [*sic*] (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 182. 1863.
P. lindleyanus Miers, Proc. Roy. Hort. Soc. London 3: 182. 1863, nom. nud.
P. exsertus (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 183. 1863.
P. cinerascens Miers, Proc. Roy. Hort. Soc. London 3: 183. 1863, nom. nud.

Endemic to Mexico; widely cultivated elsewhere. The reasons for synonymizing *Phaedranthus* with *Distictis* have been discussed elsewhere (Gentry, 1973).

The merger of *Phaedranthus* with *Distictis* makes advisable reconsideration of *Sererea* Raf. against which it has been conserved. *Sererea*, the oldest of these three names, was nominally based on *Bignonia heterophylla* Willdenow, an illegitimate name change for *B. kerere* Aublet. As interpreted by Sandwith (1955), Rafinesque's genus is actually based on Lindley's (1829) description and plate of his "*B. cherere.*" The plant figured by Lindley is apparently

Distictis buccinatoria and only distantly related to Aublet's (1775) *B. kerere*, which belongs to the modern *Pachyptera*. Sandwith successfully proposed *Phaedranthus* for conservation against *Sererea* on this basis.

However, I do not think that Rafinesque's genus can be definitively linked to *Phaedranthus* at all. The generic description, though following Lindley for the most part, is certainly inadequate to distinguish between the species figured by Lindley and that of Aublet. "Cal. urceol. 5dent. cor. tubul. limbo plano 5part. lac. (*sic*) obcord. obliquis subeq. stylo clavato, stig. obt. antheris sagittatis lobis divarcatis" describes *Distictis buccinatoria* and *Pachyptera kerere* about equally well. Nor does Rafinesque's description of his single species, *Sererea heterophyla* (*sic*) throw much light on the matter. Neither species has a 5-dentate calyx (sometimes remotely denticulate in *D. buccinatoria*). Neither species ever has simple leaves, even in part. Neither has sagittate anthers. Both species normally have racemose rather than paniculate inflorescences. The habitat, "Guyana," applies to *P. kerere* but not *D. buccinatoria*. The description of the flowers ("4 inches long, base yellow limb scarlet") fits *D. buccinatoria* rather than *P. kerere* (though a red-flowered variety of *P. kerere* is also known). All other characters agree with both species and indeed with the majority of genera of Bignonieae. Merrill's (1949) consideration of *Sererea* as synonymous with yet another genus, *Pithecoctenium*, underlines the inadequacy of its circumscription.

If *Sererea* is not rejected, then conservation of *Distictis* against it might be in order. Although the case for conservation of *Distictis* (9 species, at least 3 with some horticultural importance) is stronger than that successfully argued for *Phaedranthus* (a single horticulturally important species), conservation seems unnecessary in view of the confused status of *Sererea*.

Alternatively, if Rafinesque's genus is considered based on *B. kerere*, the conservation of *Pachyptera* against *Sererea* might be considered. Willdenow, Lindley, and Rafinesque all thought they were describing Aublet's plant, and nomenclaturally at least, the type species of *Sererea*, *S. heterophylla*, is a superfluous synonym of *Pachyptera kerere*. *Pachyptera* contains four species, at least two of some horticultural importance, and is also better known than *Phaedranthus*.

Under the circumstances, I see no way to definitively assign Rafinesque's inadequate generic description either to *D. buccinatoria* or to the Aublet plant upon which it was nominally based. The outright rejection of *Sererea* under either Article 69 or Article 70 of the *Code* appears in order.

WUNSCHMANNIA Urb.

In creating his monotypic genus *Wunschmannia* for Lamarck's *Bignonia staminea*, Urban (1908) separated it from *Macrodiscus* (*i.e. Distictis*) on the basis of its more strongly bilabiate corolla and exserted (or subexerted!) stamens. The close relationships of the single specimen of *Wunschmannia* (*Buch 352* (MO) cited by Urban) examined by me with *Distictis* is obvious on the basis of its 6-angled, ribbed branchlets, leaf form, terminal inflorescence, subfoliaceous pseudostipules, truncate, cupular calyx, sometimes with linear glandular fields descending from its rim, and strongly pubescent corolla. Although I have seen no fruiting material, Urban tentatively described the capsule as oval and both Lamarck and Plumier described it as hard and oval, which accords well with *Distictis.* I find the similarities of the two genera more impressive than their differences, especially since the very similar *Phaedranthus*, which likewise has been separated from *Distictis* largely on the basis of exserted stamens, has proven congeneric with *Distictis.* An equivalent variation in corolla shape and degree of zygomorphy is found in such other genera as *Tecoma* and *Adenocalymma.*

The reduction of *Wunschmannia* to *Distictis* adds a fifth species to that genus.

5. **D. staminea** (Lam.) A. Gentry, comb. nov.

Bignonia staminea Lam., Encyc. 1: 421. 1783. TYPE: (not seen—illustration by Plumier in Pl. Am. *t. 56, fig.* 2; original at P).
Wunschmannia staminea (Lam.) Urb., Symb. Ant. 5: 494. 1908.

Apparently endemic to Haiti. Lamarck's name was based on a Plumier drawing and, as noted by Urban, could hardly be identified with any other plant. In addition to the toothed calyx (a common error of the period) and simple tendril noted as inconsistencies by Urban, the figuring of the flower as emerging from the end of a leaf in the position of a tendril proves the poor quality of the Barmann illustration. The original Plumier drawing is much better, and I have accepted Urban's identification of the Buch specimen with Lamarck's plant.

An additional point of interest is the superficial similarity of this species with the monotypic *Dolichandra*, a reputed member of the Tecomeae from southern Brazil, Uruguay, and Argentina.

ANOMOCTENIUM Pichon

Sandwith (1965) accepted *Anomoctenium* as a distinct genus, comparing it with *Pithecoctenium, Distictella*, and *Amphilophium*, and characterizing it by six-angled branchlets with detachable ribs, dendroid trichomes, corolla tube with evident rows of glands at base of lobes without, a non-echinate sharply acuminate, very convex, pubescent or subtomentose capsule with the acumen remaining with the valves at dehiscence, and seeds in two rows, smaller and more narrowly transversely oblong than in *Pithecoctenium*, with membranous wings veined with brown and with a darker brown, rough, irregularly ridged, papillose or pubescent body and leaving a long and narrow hilum scar on the septum. Although adequately separated from *Pithecoctenium* and *Distictella* on the basis of the listed characters, *Anomoctenium* seems much closer to *Distictis* which was, surprisingly, omitted from Sandwith's discussion. Indeed the above description of *Anomoctenium* applies almost equally well to *Distictis.* Only dendroid trichomes and glands at the bases of the corolla lobes are out of place is *Distictis.* In addition the two genera share usually trifid (to several-branched) tendrils, foliaceous pseudostipules, terminal inflorescences, often with leaf-like bracts, and have very similar corollas, calyces, and general appearance. Both genera are reported to have ecolpate pollen (Urban, 1916: 773; Sandwith, 1965: 412).

The otherwise unique fruit of *Anomoctenium*, emphasized by Sandwith in separating that genus from *Pithecoctenium* and *Distictella*, is just that of *Distictis*. Even the seeds of *Anomoctenium* with their ridged, more or less papillose or papillose-puberulous bodies are the same as those of *Distictis*. Although I have not microscopically examined the fruit of *D. lactiflora* (Vahl) DC., it has the same general form as that of *Anomoctenium*. The fruit of *D. buccinatoria* (DC.) A. Gentry, though not acuminate, is of the same shape as that of *Anomoctenium*, similarly convex and woody-valved, pubescent, and with the midrib very inconspicuous or not evident. Its seeds also have a rather wrinkled body, somewhat papillose toward the center. The fruit of *D. laxiflora* (DC.) Greenm. (*Pringle 6724*, MO), still more like that of *Anomoctenium*, is acutely narrowed at both ends, with convex, woody, pubescent valves with a slightly wrinkled surface and inconspicuous midrib. Its seeds have an irregularly wrinkled, slightly papillose-puberulous body. The fruit of *D. gnaphalantha* (A. Rich.) Urb. (*Wright 3050*, MO) is also like that of *Anomoctenium*, even to an acuminate tip, a yellowish indumentum when young, and the presence of scattered warty glands. I have examined only immature seeds of *D. gnaphalantha*, and these also have the characteristic wrinkled body but seemingly lack papillae or pubescence.

We are thus left with only dendroid trichomes and corolla glands as possible characters for separating *Anomoctenium* from *Distictis*. Neither character appears adequate for generic segregation, since genera such as *Amphilophium* and *Arrabidaea* have some species with dendroid and some with simple trichomes, while corolla glands similar to those of *Anomoctenium* are present in some species of *Anemopaegma* and *Pachyptera* but absent in others. There seems no justification for retention of *Anomoctenium*, and I accordingly reduce it to *Distictis*, to which must be added the following three species.

6. **D. stipularis** (Mart. ex DC.) A. Gentry, comb. nov.

Pithecoctenium stipulare Mart. ex *DC*., Prodr. 9: 194. 1845. TYPE: Brazil: Bahia, *Martius 2079* (M).

P. frutescens DC., Prodr. 9: 196. 1845. TYPE: Brazil: *Lhotsky s.n.* (G-DC).

Anemopaegma nigrescens Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 125. 1896. SYNTYPES: Brazil: Espírito Santo, *Sellow 398* (not seen). Brazil: Rio de Janeiro, *L.* [= Luschnath?] no. *313* (not seen).

Anomoctenium stipulare (Mart. *ex* DC.) Pichon, Bull. Soc. Bot. France 92: 227. 1945.

Distictella nigrescens (Bur. & K. Schum.) J. C. Gomes, Arch. Jard. Bot. Rio de Janeiro 12: 150, *t. 4.* 1953.

Eastern Brazil.

7. **D. granulosa** Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 179. 1896.

Pithecoctenium uleanum Kranzl., Notizbl. Bot. Gart. Berlin-Dahlem 6: 377. 1915. TYPE: Brazil: Rio Branco (Terr. Roraima), *Ule 7706* (K).

Distictella granulosa (Bur. & K. Schum.) Sprague & Sandw., Kew Bull. 1932: 89. 1932.

Anomoctenium granulosum (Bur. & K. Schum.) Sandw. Kew Bull. 19: 156. 1965.

Colombia (*Haught 2209*, MO) to the Guianas and in Amazonian Brazil.

8. **D. scabriuscula** (Mart. *ex* DC.) A. Gentry, comb. nov.

Pithecoctenium scabriusculum Mart. *ex*. DC., Prodr. 9: 197. 1845. TYPE: Brazil: Rio Paraíba (formerly Rio Parahyba), *Prince Vidensis s.n.* (Wied-Neuwied) (BR).

Eastern Brazil.

An undescribed species closely allied with the former members of *Anomoctenium* is the ninth member of the expanded genus.

9. **D. steyermarkii** A. Gentry, sp. nov.

Frutex scandens. *Ramuli* 6-angulati, pubescentes, sine consociebus glandularum in nodis inter petiolos. *Pseudostipulae* foliaceae. *Folia* bifoliolata, interdum cirrho 3-partito, foliolis plus minusve suborbiculatis, confertim dendroideo-pubescentibus. *Inflorescentiae* floribus in racemis bracteatis terminalibus dispositis, bracteis linearibus ad 10 mm longis. *Calyx* cupulatus, truncatus, puberulus, consociebus glandularum linearibus. *Corolla* lobis albis tuboque intus luteo extus cremeo, tubulo-campanulata, dense pubescens in tubo extus atque in lobis. *Stamina* thecis divaricatis, 4 mm longis. *Pistillum* stylo dense pubescenti, ovario ellipsoideo, tomentoso. *Capsula* elliptica, acute, puberula.

Vine, the branchlets inconspicuously 6-angled with wide detachable ribs, dendroid-pubescent, the nodes without interpetiolar glandular fields; pseudostipules minutely foliaceous, dendroid-pubescent, to 3 mm by 3 mm. *Leaves* 2-foliolate, often with a tendril; leaflets ovate to suborbicular, obtuse, cordate, 4–8 cm long and 3–7 cm wide, chartaceous, secondary veins 3–5 on a side, densely dendroid-pubescent below, scabrous above with simple and dendroid trichomes, drying olive; tendril trifid; petiolules 0.6–2 cm long, petiole 1–3 cm long, dendroid-tomentose like the petiolules. *Inflorescence* a few-flowered, bracteate, terminal raceme, its branches dendroid-pubescent, the bracts linear, to 10 mm long and 2 mm wide. *Calyx* cupular, truncate, 4–7 mm long and 6–7 mm wide, dendroid-puberulous, with several linear glandular fields descending from rim. *Corolla* with lobes white and tube yellow within and cream without; tubular campanulate, 6.5–7.5 cm long and 1.7–1.9 cm wide at mouth of tube, the tube 5–6 cm long, the lobes 1.2–1.7 cm long, with linear glandular fields at base without; densely dendroid-pubescent without and on lobes within, the tube within mostly glabrous, with gland-tipped trichomes at level of stamen insertion. *Stamens* didynamous, the anther thecae divaricate, each 4 mm long, the longer filaments 2.8–2.9 cm long, shorter filaments ca. 2.0 cm long, the staminode 6 mm long; insertion 1.1–1.4 mm from base of corolla tube. *Pistil* 4.7–4.9 cm long; style densely dendroid-pubescent; ovary ellipsoidal, 3–4 mm long and 2 mm wide, somewhat contracted at base, tomentose, the ovules ± 6-seriate in each locule; disk annular, 1 mm long and 2–3 mm wide. *Capsule* elliptical, acute at both ends, 8–11 cm long and 3–3.5 cm wide, ca. 1.5 cm thick, the valves woody, convex, dendroid-puberulent, with numerous cup-shaped glands, especially along the slightly impressed midrib; seeds 1.1–1.4 cm long and 3–3.9 cm wide, the wings hyaline-membranous, distinctly demarcated from the puberulous body.

HOLOTYPE: Venezuela. Distrito Federal: Steep, seaward, forested slopes with *Manilkara bidentata*, between Osma and Todasana, alt. 100 meters. Low vining over shrubs; flowers delicately fragrant; corolla tube creamy without, yellow within to orifice; lobes white without and within; leaflets membranous, yellow green below, 24 Nov 1971 *Steyermark & Brewer Carias 105274* (MO; isotype, VEN).

This striking plant is apparently endemic to extreme northern Venezuela and adjacent Colombia, having been collected only from the Distrito Federal and Trujillo in Venezuela and Norte de Santander in Colombia.

Additional collections examined:

VENEZUELA. DISTRITO FEDERAL: Dry seaward slopes, 0.6 km W of Oritapo, 7 km E of Osma, Dept. Vargas, alt. 50 m, 11 Mar. 1973, *Steyermark & Carreño Espinosa 106874* (MO, VEN); selva seca tropofila, entre Los Caracas y Todasana; sprawling low, leaves membranous, yellow-green below with raised nerves, flower buds yellow green, alt. 100 m, 30 Apr. 1967, *Steyermark & Bunting 98243* (VEN). TRUJILLO: Alrededores de Escuque, en matorrales a la orilla del rio, 10 Jan. 1929, *Pittier 13129* (US, VEN).

COLUMBIA. NORTE DE SANTANDER: Between Chinacota and La Esmeralda, alt. 1000–1300 m. 19 Mar. 1927, *Killip & Smith 20877* (US).

This species is most closely related to *Distictis scabriuscula*, and the Pittier collection was tentatively determined by Sandwith in 1958 as *Pithecoctenium scabriusculum* with the note, "I place this collection—also *Alston 7095*—here provisionally, awaiting further evidence, and more Brazilian material and fruit." *Killip & Smith 20877* was determined by Dugand as *Pithecoctenium* cf. *scabriusculum*, probably by matching it with the sheet determined by Sandwith. Since Sandwith (1965: 410) later gave the range of *P. scabriusculum* as "extra-hylean eastern Brazil" without mentioning the Pittier collection from Venezuela at all, it appears likely that he subsequently changed his mind about identifying it with that species. The additional collections now available have convinced me that the differences between *D. steyermarkii* and *D. scabriuscula* are constant and that the Venezuelan and Colombian plant merits specific recognition. In addition to its geographic disjunction, *D. steyermarkii* differs from *D. scabriuscula* especially in its conspicuously cordate leaflets and smaller (4–7-mm-long), thinner, less pubescent calyx in contrast to the truncate to asymmetrically subcordate leaflets and thick, 7–9-mm-long (fide Bureau & Schumann, 1896–97; 171), densely pubescent calyx of the latter. *Distictis steyermarkii* is also characterized by small, foliaceous pseudostipules, lack of which is a key specific character for *D. scabriuscula* as interpreted by Bureau and K. Schumann (1896–97: 164.).

The new species is noteworthy for its dense indumentum of dendroid trichomes. In fact it appears almost vegetatively indistinguishable from similarly pubescent *Amphilophium paniculatum* var. *molle* (Schlecht. & Cham.) Standl. (also known as *A. macrophyllum* H.B.K.) thus emphasizing the relationship with *Amphilophium* noted by Sandwith. The fruit agrees in general form with the more blunt-ended one of *Amphilophium paniculatum* (L.) H.B.K. especially in the pubescent seeds but is also similar to that of other species of *Distictis*. Its calyx and flower are more like those of *Ceratophytum* or *Anemopaegma* than like those of *Distictella* or *Pithecoctenium*, the other two genera with which Sandwith compared *Anomoctenium*.

LITERATURE CITED

AUBLET, M. 1775. Histoire des Plantes de la Guiane Française. 2.

BORHIDI, A. & O. MUÑIZ. 1971. Combinationes novae florae Cubanae I. Bot. Közlem. 58: 175–177.

BRITTON, N. 1925. Bignoniaceae. Pp. 191–201 *in* Sci. Surv. Porto Rico & Virgin Isl. 6.

BUREAU, E. & K. SCHUMANN. 1896–97. Bignoniaceae. *In* C. F. P. von Martius, "Flora Brasiliensis." 8(2).

CANDOLLE, A. DE. 1945. Bignoniaceae. Pp. 142–248, *in* "Prodromus." 9.

GENTRY, A. 1973. Generic delimitations of Central American Bignoniaceae. Brittonia 25: 226–242.

LINDLEY, J. 1829. Bot. Reg. *t. 1301.*

MERRILL, E. 1949. Index Rafinesquianus.

SANDWITH, N. 1955. Nomina generica conservanda proposita. Taxon 4: 43–47.

———. 1962. Notes on Bignoniaceae XXV: Proposed lectotypes of certain genera. Kew Bull. 15: 453–457.

———. 1965. Notes on Bignoniaceae XXVIII: The identity of *Anemopaegma nigrescens.* Kew Bull. 19: 409–414.

SCHUMANN, K. 1894. Bignoniaceae. Pp. 189–252, *in* A. Engler & K. Prantl, "Natürlichen Pflanzenfamilien." 4(3b).

STANDLEY, P. 1926. Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23.

URBAN, I. 1908. Nova genera et species III. Symb. Ant. 5: 287–531.

———. 1916. Uber Ranken und Pollen der Bignoniaceen. Ber. Deutsch. Bot. Ges. 34: 728–759.

JACQUEMONTIA OVALIFOLIA (CONVOLVULACEAE) IN AFRICA, NORTH AMERICA, AND THE HAWAIIAN ISLANDS[1]

Kenneth R. Robertson[2]

Abstract

Jacquemontia ovalifolia (Choisy) Hallier f. is one of the most broadly distributed species of the genus. A study of herbarium material from throughout its range lead to the recognition of three subspecies: subsp. *ovalifolia* from Africa, subsp. *obcordata* (Millspaugh) Robertson from Mexico and the West Indies, and subsp. *sandwicensis* (A. Gray) Robertson from the Hawaiian Islands. The species is probably of American origins and was dispersed at an unknown time by unknown means to Africa and Hawaii. The nomenclatural histories of the species and subspecies are reviewed, and a complete taxonomic treatment is presented.

While preparing a revision of the New World species of *Jacquemontia* Choisy, taxonomic and nomenclatural difficulties were encountered with what has been called *J. subsalina* Britton or *J. obcordata* (Millspaugh) House, and it became clear that the problems could be resolved only by studying this taxon and its relatives on a world-wide basis, namely Africa, Mexico and the West Indies, and the Hawaiian Islands.

NOMENCLATURAL HISTORY

African Populations

Vahl (1798) described a plant collected by von Rohr supposedly in "India Occidentali" as *Convolvulus ovalifolius*; the type and an isotype are conserved in Copenhagen (Fig. 3). This specimen is discordant with any known American plant. Monachino (1958) realized this from an examination of the type and concluded that it was instead from the Hawaiian Islands. Verdcourt (1963) considered the von Rohr collection identical with plants from Africa, although he stated that the type specimen probably was from Trinidad. In comparing the von Rohr collection with material from the West Indies, Mexico, the Hawaiian Islands, and Africa, I concur with Verdcourt that the type of *Convolvulus ovalifolius* Vahl belongs to the same taxon as the African plants. Julius von Rohr collected primarily in the West Indies and northwestern South America during the late Eighteenth Century; however, Junghans (1961) notes that von Rohr did collect a few plants in Danish Guinea [now Ghana] and that there are

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[1] Extracted, rewritten, and augmented from a dissertation submitted to the Department of Biology and the Faculty of the Graduate School of Washington University, St. Louis, in partial fulfillment of the requirements for the degree Doctor of Philosophy. The scanning electron photomicrographs of pollen were taken by Dr. Umesh Banerjee of the Arnold Arboretum on an Advanced Metals Research High Resolution Scanning Electron Microscope Model 900 located at Harvard University. Microfisches are cited by the method of Hepper (1968). All specimens cited have been examined, unless otherwise indicated.

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Ann. Missouri Bot. Gard. 61: 502–513. 1974.

seven such specimens extant at Copenhagen. It seems very likely that the von Rohr collection of *C. ovalifolius* is from Danish Guinea.

Unfortunately, West (1793) had previously used *Convolvulus ovalifolius* for another plant (referred by Vahl to *C. quinquepartitus* Vahl = *Jacquemontia havanensis* (Jacquin) Urban), attributing the description to Vahl (see also Urban, 1898, and Monachino, 1958); thus, *C. ovalifolius* Vahl is illegitimate. Choisy (1834) transferred this species to *Ipomoea*; nomenclaturally, *I. ovalifolia* Choisy must be regarded as a new name with the same type as *C. ovalifolius* Vahl. *Convolvulus coeruleus* Schumacher, published in 1827, is earlier than *I. ovalifolia* Choisy but is itself a later homonym of *C. coeruleus* Sprengel (1824), which is a taxonomic synonym of *J. pentantha* (Jacquin) G. Don. Later, Welwitsch (1858) described *Ipomoea oleracea* based on plants collected by himself in Angola. This name is clearly a synonym of *Jacquemontia ovalifolia*.

American Populations

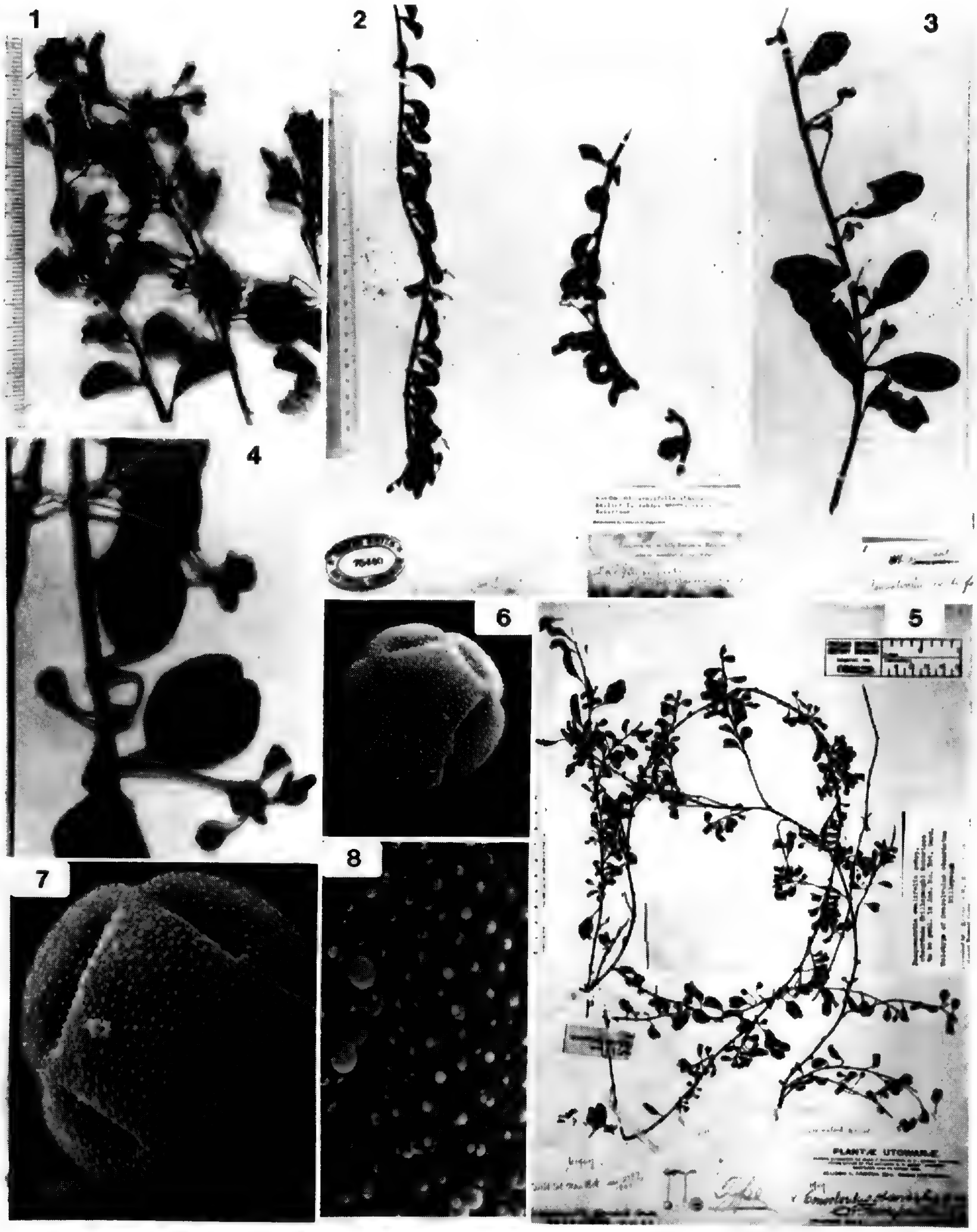
Based on Vahl's incorrect allocation of the von Rhor collection to the West Indies, later authors such as Choisy (1834, 1845) listed the species as occurring there. Actually, related plants are found on certain islands in the Caribbean and in eastern Mexico and were gathered early by Pavón, Sessé and Mociño, and Wullschlägel. These collections mostly were referred to *Jacquemontia* (*Convolvulus*, *Ipomoea*) *ovalifolia*. The American plants do differ from the African ones and can be recognized as a distinct taxon. Millspaugh (1900) described a new species, *Convolvulus obcordatus*, from material he collected in Yucatán, Mexico (Fig. 5). This name was transferred to *Jacquemontia* by House (1921), who considered the Mexican plants distinct enough from the West Indian plants to represent a separate species. Evidently unaware of Millspaugh's name, Britton (1925) delimited *J. subsalina* from Puerto Rico.

Hawaiian Populations

Early explorers to the Hawaiian Islands (named the Sandwich Islands by their discoverer Captain James Cook) such as Menzies and the Beechey and Wilkes Expeditions encountered similar plants, and Hooker and Arnott (1832), Choisy, and others referred these to *Jacquemontia* (*Convolvulus*, *Ipomoea*) *ovalifolia*. Asa Gray (1862), working with material from the U. S. Exploring Expedition, described *J. sandwicensis* for the Hawaiian plants (Fig. 2). Since then, this specific name generally has been applied to them. The African and American populations were even included under *J. sandwicensis* by Hallier (1918).

RELATIONSHIPS AND DISCUSSION

The plants considered here have been placed in four genera: *Convolvulus* L., *Ipomoea* L., *Jacquemontia* Choisy, and *Montejacquia* Roberty. Such a diverse treatment is not uncommon in the Convolvulaceae where generic limits are notoriously ill-defined. The following attributes indicate that these plants are properly included within *Jacquemontia*: 2-armed trichomes; smooth pollen



FIGURES 1–8. *Jacquemontia ovalifolia.*—1. Subsp. *obcordata*, detail of branch with mature capsules (*Moore 2129*).—2. Type of *J. sandwicensis* A. Gray.—3. Type of *Ipomoea ovalifolia* Choisy.—4. Portion of a densely pubescent plant of subsp. *sandwicensis* (*Webster et al. 13986*).—5. Type of *Convolvulus obcordatus* Millspaugh.—6–8. Scanning electron photomicrographs of acetolyzed pollen grains of subsp. *obcordata* (*Moore 2129*).—6. Polar view, × 500.—7. Equatorial view, × 1000.—8. Detail of pollen, a colpus to the left, 4 Ubisch bodies attached to the margin of the colpus, note the numerous punctae and spinules, × 2500.

with 15 colpi, 5 at each pole, 5 equatorial (Figs. 6–8); 2-locular and 4-ovulate ovaries; bilobed stigmas, the lobes flattened and shortly ellipsoidal or clavate; capsular fruit (Fig. 1); glabrous seeds with minute wings on the outer margins; and a base chromosome number of 9 (one count by Jones, 1968).

The current practice in regional floras is to treat plants from the different geographical areas as distinct species (Verdcourt, 1963; Adams, 1972; Degener & Degener, 1956). From a careful study of herbarium material from all three regions, and from comparisons to other species of the genus, I conclude that only one species should be recognized, *Jacquemontia ovalifolia* (Choisy) Hallier f., with three subspecies, subsp. *ovalifolia* in Africa, subsp. *obcordata* in the West Indies and Mexico, and subsp. *sandwicensis* in Hawaii. This species has the broadest distribution of any species of the genus.

Within the genus, *Jacquemontia ovalifolia* may be distinguished by its ability to root at the nodes; blue to white, subrotate to shallowly campanulate corollas; elliptic to circular leaves with indented apices and noncordate bases; 2-armed and T-shaped trichomes; usually 2–4-valvate capsules; and minutely areolate and narrowly winged seeds. The only clearly related species is *J. serpyllifolia* (H.B.K.) Urban, an endemic of the serpentine hills and palm barrens in the western part of Cuba. These two species constitute a distinct section of the genus (to be described in a later paper).

The geographical distribution of this species is perplexing, and it can probably never be known if the species was dispersed from one region of the world to another by natural means or by man. The total range does not seem to follow old exploration, merchant, slave trade, or missionary routes. Until it can be shown otherwise, it is presumed that the species is indigenous to the three areas. The genus is mostly American with the greatest diversity of forms in the West Indies, although the majority of species occur on the American mainland. No species is restricted to Africa. The African representatives of the genus are *Jacquemontia ovalifolia*, *J. tamnifolia* (L.) Grisebach, which also is found in the New World from Virginia to Dominica, Paraguay, Argentina, and Brazil, and *J. paniculata* (Burmann f.) Hallier f., which ranges from Africa and Madagascar to southeastern Asia, tropical Australia, and New Caledonia. *Jacquemontia ovalifolia* is the only species of the genus in Hawaii. Although widespread in its distribution in Caribbean America and Africa, this species is never very abundant there, while in Hawaii it is both ubiquitous and common. The comparative lack of competition in the isolated oceanic situation of the Hawaiian Islands may account for its plentifulness. It can be speculated that the species is of American origins, perhaps in the West Indies where its only related species, *J. serpyllifolia*, occurs, and it was dispersed at an unknown time by unknown means to Africa and Hawaii.

The broad distribution of this species within each geographic area in which it occurs suggests that it must have a fairly efficient means of short-range dispersal. The seeds have a hard coat, as do many Convolvulaceae, and would probably pass intact through a bird's digestive system. Also, the seeds are small enough to be carried in mud on birds' feet. Morphologically, the seeds of the different subspecies of *Jacquemontia ovalifolia* do not differ significantly from one another or indeed from the other species of the genus, which are certainly not dispersed primarily by water. However, water is the agent used in theories presented to account for the long-range dispersal of this species to the Hawaiian Islands. The seeds of subsp. *sandwicensis* reportedly sink in sea water, and Guppy (1906) suggested that the original colonizing seeds might have rafted to Hawaii from North America in crevices of a drifting log. Ridley (1930) speculated that perhaps the ancestor of the Hawaiian *Jacquemontia* had buoyant seeds, and Carlquist (1967) adds that this plant is probably in a stage of transition with respect to loss of dispersibility. It seems to me that there is very little case for long-range dispersal of *J. ovalifolia* by water; birds could be the vector for both short- and long-range dispersal. The morphological distinctiveness of the plants from the three geographical areas indicates that reintroductions from one area to another do not occur frequently, if ever.

TAXONOMIC TREATMENT

Jacquemontia ovalifolia (Choisy) Hallier f., Bot. Jahrb. Syst. 16: 543. 1892.

Ipomoea ovalifolia Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. Based on *Convolvulus ovalifolius* Vahl, *non* Vahl *ex* West.

? *J. ovata* Owerin *ex* Regel, Gartenflora 9: 271. *pl. 300.* 1860. Plants grown from seeds collected in Chili, no specimens known; illustration taken as the type.

Montejacquia bifida (Velloso) Roberty, Candollea 14: 33. 1952, *pro parte.* Roberty included an incredible variety of plants, representing at least half a dozen species in two genera, in this species.

Annual or perennial *vines*; stems slender, woody at base, primary stems numerous, mostly prostrate, radiating from thick rootstocks and forming mats, many short, lateral branches produced, the stem apices prostrate or ascending; rooting at occasional nodes with plants sometimes arising from such nodes. *Indumentum* of 2-armed, T-shaped trichomes; stems, leaves, inflorescence branches, and sepals glabrate to densely pubescent. *Leaves* shortly petiolate, the blades elliptic to subcircular, the apices obtuse to obcordate, the margins entire, slightly undulate, the bases obtuse to cuneate. *Inflorescences* few-flowered axillary cymes or the flowers rarely solitary, the peduncles erect; bracts small, linear or obovate. *Flowers* white or bluish, 5-merous; sepals unequal, quincuncially imbricate, the outer 2 mostly elliptic with obtuse apices, the middle one asymmetric, the inner 2 shorter and narrower with acute apices, all persistent in fruit; corolla tubes faintly 5-toothed, subrotate to shallowly campanulate; stamens unequal, included, the lower part of the filaments flattened, adnate to the corolla tube, glandular pubescent, and constricted around the ovary and base of the style; pollen smooth, spheroidal, 15-colpate with 5 colpi circumpolar at each pole and 5 equatorial colpi perpendicular to and alternate with the polar colpi, the tectum punctate with numerous suprategullar spinules; gynoecium of 2 united carpels, the ovary 2-locular, 4-ovulate, subglobose to cylindrical, a small disc enclosing the base, the style exceeding the stamens, the stigma lobes flattened, shortly clavate or ellipsoidal. *Capsules* subglobose, 4-seeded (or fewer by abortion), splitting into 2 primary and 4 or more secondary segments. *Seeds* trigonous in cross section, the outer face rounded and humped, asymmetically parabolic in longitudinal section; seed coat minutely areolate and sometimes faintly ruminate, the outer 2 margins narrowly and irregularly winged.

Subtropical regions of the world with three geographically separated subspecies: subsp. *ovalifolia* in Africa, subsp. *obcordata* from Mexico and the West Indies, and subsp. *sandwicensis* in the Hawaiian Islands.

Key to the Subspecies of *Jacquemontia ovalifolia*

1. Plants quite small, leaf blades usually 7–20 mm long and 6–18 mm wide, corolla tubes 7–10 mm long; Mexico and the West Indies .... 1. subsp. *obcordata*
1. Plants larger, leaf blades usually 18–50 mm long and 10–30 mm wide, corolla tubes 8–15 mm long; Africa or Hawaii 2
    2. Pubescence nearly absent, occasional trichomes found on young parts, leaf blades elliptic, the apices obtuse or retuse; Africa .... 2. subsp. *ovalifolia*
    2. Pubescence tomentose to glabrescent, leaf blades broadly elliptic to circular, the apices strongly retuse or obcordate, rarely obtuse; Hawaii .... 3. subsp. *sandwicensis*

1. **Jacquemontia ovalifolia** subsp. **ovalifolia**.

Convolvulus ovalifolius Vahl, Eclog. Amer. 2: 16. 1798, *non* Vahl *ex* West, Bidrag Beskr. Ste. Croix, 271. 1793. TYPE: Guinea [now Ghana], without locality, *von Rohr s.n.* (C—Herb. Vahl [IDC 2201. 13: III. 4], Fig. 3; isotypes, C [IDC 2201. 13: III. 5; photo A], W). Vahl incorrectly attributed this collection to the West Indies.

C. coeruleus Schumacher, Beskr. Guineiske Pl., 101. 1827; evidently preprinted from Kongel Danske Vidensk. Selsk. Naturvindensk. Math. Afh. 3: 121. 1828, *nec* Sprengel *in* L., Syst. Veg., ed. 16. 1: 593. 1824, *nec* Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12: 254. 1845. TYPE: Guinea [now Ghana], without locality, *Thonning 62* (C—Herb. Schumacher [IDC 2203. 25: II. 3. photo MO]; isotypes, C [IDC 2203. 25: II. 1,2]).

J. coerulea (Schumacher) Choisy *ex* G. Don, Gen. Syst. 4: 283. 1838.

Ipomoea oleracea Welwitsch, Ann. Conselho Ultramarino 1: 589. 1859. TYPE: Angola, dist. Angola, in periodically flooded dry places in the region of the sea shore, July 1858, *Welwitsch*, presumably LISU, not seen. Verdcourt cited *Welwitsch 6252* (BM) as an isotype. I have examined three sheets of this number from BM, and none were collected in July 1858.

Stems to 3 m long, the apices usually ascending. *Pubescence* sparce, mostly confined to young plant parts and mature peduncles. *Leaves* to 9.5 cm long; petioles 0.3–3 cm long but usually 0.5–1.2 cm long; blades elliptic, the apices obtuse or retuse, the bases cuneate, to 7 cm long and 4.5 cm wide but commonly ⅓–⅔ that size, slightly fleshy. *Inflorescences* 1–4.5 cm long, usually not exceeding the leaves, the lower bracts to 13 mm long and 5 mm wide but usually much smaller. *Flowers* bluish; outer 2 sepals elliptic or obovate, obtuse to slightly acute, 6–8 mm long and 4–6 mm wide, the middle sepal falcate, acutish, 5–6 mm long and 2–3 mm wide, the inner 2 narrowly ovate, acute, 5–6 mm long and 2 mm wide; corolla tubes 8–12 mm long; filaments 5–8 mm long, constricted around the style 1.5–3 mm from the base, the anthers 1–1.5 mm long; ovaries ovoid or cylindrical, 1–1.5 mm long, the styles 6–7 mm long, the stigma lobes 1–2 mm long. *Capsules* globose, 5 mm in diameter. *Seeds* 2.5–3 mm long. Flowering from January to August (October).

Africa south of the Sahara Desert—the Gold Coast, Portugese West Africa, and British East Africa (Fig. 9). Little is known of habitat perferences; plants have been collected from sandy beaches and the margins of seasonal or permanent lakes at altitudes from sea level to ca. 1000 m.

SPECIMENS EXAMINED

ANGOLA. **Luanda:** without localities, *Gossweiler 165* (K); Jan 1854, *Welwitsch 6252* (BM); Jul 1854, *Welwitsch 6252* (BM); Aug 1858, *Welwitsch 6252* (BM); without date, *Welwitsch 6252* (G). **Moçâmedes:** Damaraland, Moçâmedes, *Höpfner 21* (G); ad ripas fluminis Bero, *Welwitsch 6121* (BM).

GHANA: Accra, *Dalziel 8* (K); Accra, behind beach, *Irvine 668* (K); Agric. Res. Station, Nungua, Accra Plains, *Rose-Innes GC30064* (K); without localities, *Isert s.n.* (C), *Thonning 62* (C), *von Rohr s.n.* (C, W, type).

TOGO: Prope Lomé, *Warnecke 254* (BM, BR, G, L).

KENYA. **Baringo:** Lake Baringo, *Bickford EAH11062* (K); SW shore of Lake Baringo, in patches near shore, *Verdcourt 3579* (BR). **Kilifi:** Haluabagula camp, N of Dakatcha, *Dale K1073* (K).

SOMALI REPUBLIC: Galwin, *Ciferri 105* (K).

TANZANIA. **Mpwapwa:** Dry floor of seasonal lake, Gombo Lake, *Burtt 4630* (K); Lake Kimagaii, *Hornby & Hornby 706* (K).

UGANDA. **Bunyoro:** Shore of Lake Albert, near Kibero, *Bagshawe 1422* (BM, US).

MADAGASCAR: Côte orientale, anno 1853, *Boivin s.n.* (G).

Hallier (1918) also reports this taxon from Sierra Leone (collected by Afzelius).

2. **Jacquemontia ovalifolia** subsp. **obcordata** (Millspaugh) Robertson, stat. et comb. nov.

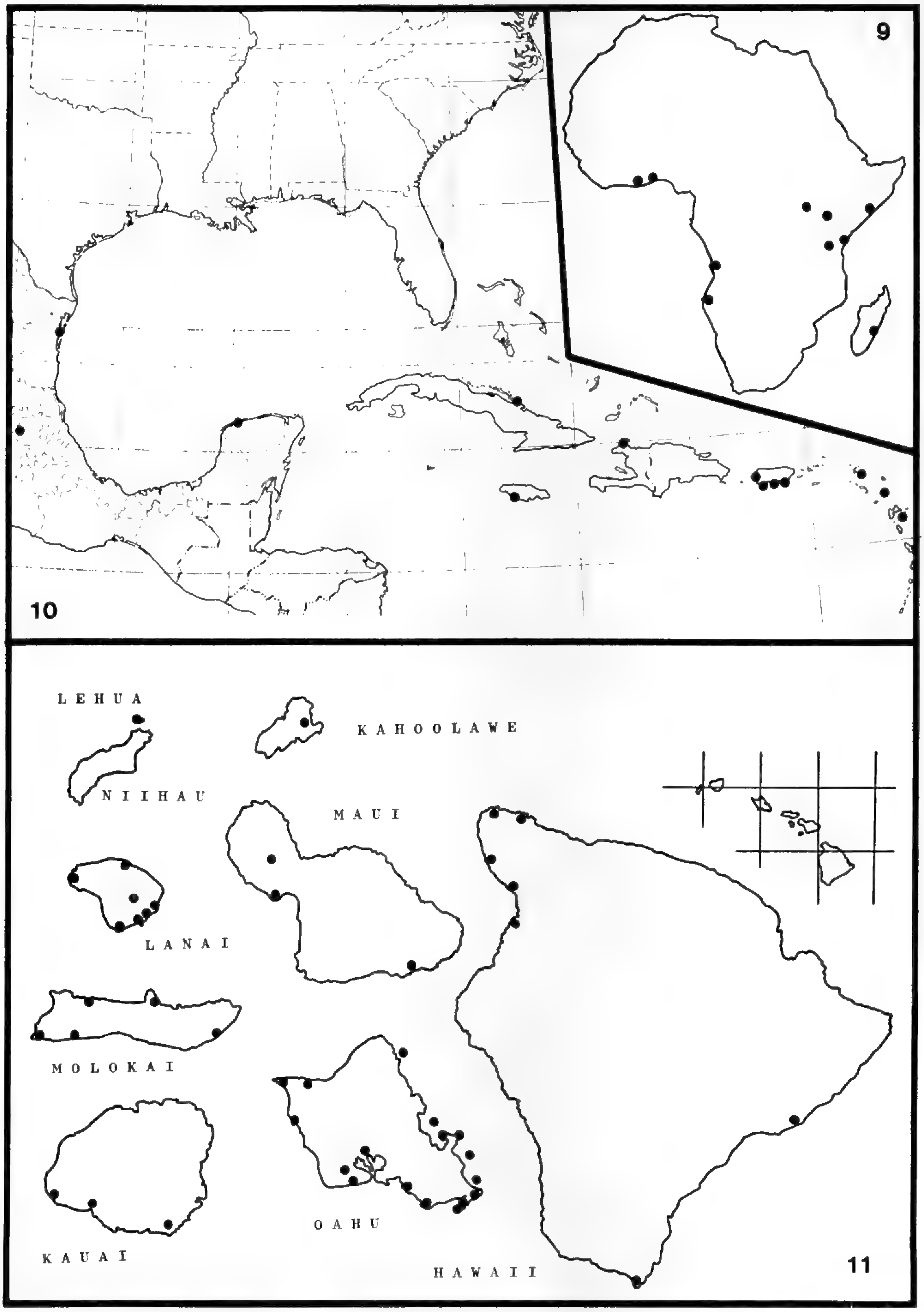
Convolvulus obcordatus Millspaugh, Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 88. 1900. TYPE: Mexico, Yucatán, along the railroad about 8 km S of Progresso, 5 March 1899, *Millspaugh 1707* (F, Fig. 5).

J. obcordata (Millspaugh) House, New York State Mus. Bull. 233–234: 63. 1921.

J. subsalina Britton *in* Britton & Wilson, Sci. Survey Porto Rico & Virgin Isl. 6: 106. 1925. TYPE: Puerto Rico, Ponce, coastal marsh between Ponce and Santa Isabel, 18 March 1915, *Britton & Brown 5515* (NY, photo MO; isotypes MO, NY).

Stems prostrate, to 2 m long. *Pubescence* sparce, mostly confined to young plant parts, petioles, and peduncles. *Leaves* to 5.5 cm long, usually much smaller; petioles 0.5–1.2 cm long, rarely to 2.5 cm; blades elliptic to subcircular, the apices retuse to obcordate, the bases cuneate, to 3 cm long and 2.6 cm wide, mostly ¼–⅔ that size, fleshy. *Inflorescences* 6–29 mm long, rarely exceeding the leaves; bracts linear, small. *Flowers* white to blue or lavender; outer 2 sepals ovate, elliptic, or broadly elliptic, obtuse to acutish, 2.5–4 mm long and 2–2.5 mm wide, the middle sepal asymmetrically ovate, obtuse to acutish, 2.5–3 mm long and 2 mm wide, the inner 2 narrowly ovate to ovate, acute, 2.5–3.5 mm long and 1.5–2 mm wide; corolla tubes 7–10 mm long; filaments 4–7 mm long, constricted around the style 2 mm from the base, the anthers 1–1.5 mm long; ovaries ovoid to globose, 1 mm long, the styles 4–5 mm long, the stigma lobes 0.75–1.25 mm long. *Capsules* globose, 4–5 mm in diameter. *Seeds* 2–2.5 mm long. Flowering from October to May, most frequently collected in February and March. Chromosome number, $2n = 18$ (Jones, 1968; as *J. subsalina*).

Eastern Mexico, the Greater Antilles, and a few of the limestone Caribbees (Fig. 10). This subspecies is usually found in saline or alkaline soils near the coast, sometimes in marshes, around the edges of ponds, or along railroad tracks. Its occurrence is sporadic, and most populations evidently consist of only a few plants.



FIGURES 9–11. Distribution of *Jacquemontia ovalifolia.*—9. Subsp. *ovalifolia.*—10. Subsp. *obcordata.*—11. Subsp. *sandwicensis.*

Illustration: Britton (1930), as *J. subsalina*; Robertson (1971; to be published in a later paper).

SPECIMENS EXAMINED

MEXICO. **Hildago:** Distr. Metztitlán. San Cristobal to main body of Laguna de Metztitlán, altitude 1200 m, *Moore 2129* (GH). **Tamaulipas:** San José Island in Laguna Madre, *LeSueur 369* (F, GH, US). **Yucatán:** Progresso, *Millspaugh 1707* (F, type). **State not known:** Nueva España, *Pavón s.n.* (G); *Sessé et al. 444* (*1641*) (F).

ANTIGUA. Freetown, *Box 1154* (F, IJ, MICH, US); Ffryes near Bethesda, *Box 1374* (MO, US); presumably from Antigua, *Wullschlägel 361* (M).

CUBA. **Camagüey:** Ganado, Cayo Sabinal, *Shafer 865* (F, NY, US).

HAITI. **Nord Ouest:** Vicinity of Port de Paix, *Leonard & Leonard 11739* (US), *15266* (NY, US).

JAMAICA. **St. Elizabeth:** Pedro Bluff, *Harris 9812* (UCWI).

MARIE GALANTE. Bord de mer sur la route qui longe la mer entre Capesterre en Grand Bourg, altitude 2 m, *Quentin 161 Duss 438* (A) [mixed collection?]; *Questel 746* (US), *1467* (US), *1492* (US); *Stehlé 1942* (US).

PUERTO RICO. **Guánica:** Guánica Lake, *Sargent 8* (GH). **Guayama:** Aguirre, *Britton et al. 6026* (F, NY, US); vicinity of Salinas, *Britton et al. 6046* (F, NY, US). **Mayaguez:** Moist plain near Boquerón, *Britton & Britton 9252* (NY); plain, Boquerón, *Britton & Britton 9385* (GH, NY); vicinity of Boquerón, *Britton et al. 8873* (NY); Boquerón Swamp, *Velêz 1831* (NY); cultivated ground, Ensenada, *Britton et al. 8323* (NY, US). **Ponce:** Between Ponce and Santa Isabel, coastal plain, *Britton & Britton 5515* (F, MO, NY, US), *7339* (NY), saline plain, *Britton & Britton 9451* (NY, US).

ST. BARTHÉLEMY. Grande Saline, *Questel 373* (NY, US).

Subspecies *obcordata* has also been reported from St. John's in the Virgin Islands (Jones, 1968, as *J. subsalina*).

3. **Jacquemontia ovalifolia** subsp. **sandwicensis** (A. Gray) Robertson, stat. et comb. nov.

J. sandwicensis A. Gray, Proc. Amer. Acad. Arts 5: 336. 1862. LECTOTYPE: Sandwich Islands [Hawaii], Oahu, "*Herbarium of the U. S. Exploring Expedition under the command of Capt. Wilkes*" (US 75440, Fig. 2; isolectotypes NY, fragment GH). Gray saw all the duplicates cited; the specimen at US is selected as the lectotype because it is the best specimen and also that institution is the depository of material from the Wilkes Expedition.

Ipomoea ovalifolia var. *pubescens* Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. LECTOTYPE: Sandwich Islands [Hawaii], *Gaudichaud 26* (G); selected by Choisy in DC., Prodr. 9: 357. 1845.

I. ovalifolia var. *tomentosa* Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. LECTOTYPE: Sandwich Islands [Hawaii], *Gaudichaud 27* (G); selected by Choisy in DC., Prodr. 9: 357. 1845.

J. ovalifolia var. *tomentosa* Hillebrand, Fl. Hawaiian Isl. 318. 1888. TYPE: Hawaii, southern shore of Molokai, *Hillebrand* (destroyed in B).

Convolvulus sandwicensis (A. Gray) Bentham & Hooker *ex* Drake, Ill. Fl. Isl. Maris Pacifici. 245. 1892.

J. sandwicensis var. *tomentosa* fo. *hosakai* Degener & Degener, Fl. Hawaiiensis. Family 307. 1956. TYPE: Hawaii, Kawaihae, Waimea, *Hosaka 2024* (BISH, not seen).

Stems prostrate, to 3 m long. *Pubescence* quite variable, stems, leaves, peduncles, and sepals with densely overlapping trichomes to merely pubescent, rarely glabrescent; some plants with all parts (except the corolla) canescent. *Leaves* to 6 cm long; petioles 5–15 mm long; blades elliptic to circular, the apices retuse or obcordate, the bases cuneate to attenuate, to 4.8 cm long and 3.2 cm wide, mostly ⅓–⅔ that size, often thick and/or fleshy. *Inflorescences* 2–4.5 cm long, rarely reaching 9.5 cm, usually exceeding the leaves; lower bracts

3–8 mm long, linear to obovate. *Flowers* pale blue to almost white; outer 2 sepals broadly ovate, broadly obovate, or broadly elliptic, 5–8 mm long and 4–6 mm wide, the middle sepal asymmetrically ovate or falcate, obtuse to acutish, 5–6 mm long and 2–5 mm wide, the inner 2 narrowly ovate, acute to acuminate, 4–6 mm long and 2–3 mm wide, the sepals enlarging with the fruit; corolla tubes 10–15 mm long; filaments 5–12 mm long, constricted around the style 2–3 mm from the base, the anthers 1–2 mm long; ovaries ovoid, 1.5 mm long; styles 7–13 mm long, the stigma lobes 1–1.25 mm long. *Capsules* enclosed by the accrescent sepals, quadrangular-globose, 4–6 mm in diameter. *Seeds* 2–3 mm long, sometimes without winged margins. *Flowering* all year, most frequently collected from December to July.

Hawaii, all islands (except Niihau) in the major eastern group (Fig. 11). Subspecies *sandwicensis* is usually found near the ocean, particularly on the leeward side of the islands, in arid habitats such as dry plains, rocky slopes, and barren lava flows; the substrata are clay, coral, coral sand, and volcanic ash and cinders. According to Fosberg (1951) this taxon is one of only two strand plants of American affinities in the Hawaiian Islands (the other is *Lycium carolinianum* (Walter).

Illustrations: Pope (1929: 184); Degener & Degener (1956: Family 307); photograph in Carlquist (1970).

The abundance of trichomes on the leaves, inflorescence branches, and calyces varies greatly, and the full range between glabrescent and tomentose (Fig. 4) exists not only on the same island but also within the same population and even on some individual plants. Degener and Degener (1956) use the combination *Jacquemontia sandwicensis* var. *tomentosa* (Choisy) Hillebrand for plants with densely castaneous indumentum, but Hillebrand considers *Ipomoea ovalifolia* var. *tomentosa* Choisy a synonym of the glabrescent form and is clearly describing a new variety based on a different type. Plants with canescent indumentum have been called *J. sandwicensis* var. *tomentosa* fo. *hosakai* Degener & Degener. Because of the variability in indumentum density, I do not recognize any infrasubspecific taxa. The situation in *J. ovalifolia* subsp. *sandwicensis* seems analogous to that in *Conocarpus erectus* L., the buttonwood mangrove of tropical America and West Africa, in which there can be a full continuum between glabrous and densely pubescent leaves even on the same branch (Semple, 1970). Pope (1929) notes two flower colors in subsp. *sandwicensis*, light blue and bright blue.

The native name *pauohiiaka* means "skirt of Hiiaka," and legend has it that the Goddess Pele bestowed this name upon the plant. Degener and Degener relate this fable: ". . . when the Goddess returned from a protracted morning's fishing, she discovered that this plant had grown over her baby sister, Hiiaka, whom she had left on the beach, to protect her from the sun."

The leaves and other plant parts of subsp. *sandwicensis* have been used as a tea and in folk medicine for a variety of ailments, and the rootstocks are edible (Degener & Degener, 1956; Nagata, 1971; Pope, 1929). This plant showed positive tests with six reagents used to detect alkaloids (Swanholm *et al.*, 1959).

Specimens Examined

Hawaii. **Hawaii:** Between loran station and Upolu Airport, *Baldwin 27296* (L); along coast, Halawa, Kohala, *Degener 7143* (GH, NY); near Puako, *Degener & Degener 31644* (A); coastal rocks between Mahukona and Kawaihae, *Degener & Degener 31645* (A); arid barren range between Kawaihae and Waimea, *Degener & Wiebke 3362* (NY, UC, US); among rocks and ash along coast, Kalae, *Degener et al. 24361* (L, M, NY, US); Kaene Point, sand dunes near sea level, *Webster et al. 13847* (GH); S Kohala Distr., 2 mi. SE of Kawaihae, altitude ca. 500 ft, *Webster et al. 13986* (GH), *13987* (GH). **Kahoolawe:** E end, above Kanopou Bay, bare wind-swept ground, altitude 200–300 m, *Bryan & Christophersen 731* (NY, UC); without locality, *Remy 420* (GH). **Kauai:** In sand, Mana Airport, *Alexander & Kellogg 5277* (UC, US); in littore Koloa, *Faurie 1044* (G); Waimea, altitude 300 m, *Hochreutiner 3622* (G). **Lanai:** On rocks and clay above low sea cliffs, Kalaeahole, *Degener & Degener 24214* (L); arid clay, rock coast, Hulope Bay, *Degener & Degener 24215* (NY, US); bare clay, arid soil, Puu Ulaula, *Degener & Degener 28623* (A, M, W); red lava cinders along coast, near Manele, *Degener & Degener 30110* (NY); coastal rocks, Kaunola Bay, *Degener & Degener 30756* (NY, W); from grassy area to windy bare clay, Kuahua Culch, altitude 800 ft, *Degener & Degener 30757* (A, NY, W); dry roadside, road 1 km N of Koele, *Fosberg 12519* (A); Manele, *Munro 232* (MO). **Lehua:** Crusty volcanic ash near lighthouse at summit of Island, *Carlquist 2255* (GH, IJ, UC). **Maui:** Windy coast, Kaupo, *Degener & Degener 27778* (L, UC); on barren hills near McGregor, *Degener & Wiebke 3361* (NY, UC); arid aeolian deposits, on way to Iao Valley, *Wiebke & Topping 3359* (NY, UC, US); along bank above beach near Paia, *Yuncker 3451* (US); without localities, *Topping 7138* (NY, US), *7144* (NY), *Wawra 1923* (W), *U. S. Exploring Expedition under the command of Capt. Wilkes* (US, fragment GH). **Molokai:** Arid rocky plain near Kolo, *Degener 7139* (NY); extremely arid region near sea W of Moomomi, *Degener 7140* (A, NY); along coast in arid regions, Kaa, *Degener 7141* (CAS, MO, NY, US); Ka Law o Ka Laau, *Forbes 65* (NY); without locality, *Forbes s.n.* (NY); bare slopes above shore, Pohakuloa, Honoulimaloo, altitude 10 m, *Fosberg 13413* (F); eroded places in dry flat volcanic soil NE of Puu Ula, *Fosberg 29574* (NY); sand flat, Moomomi sand dunes, altitude 10 m, *Fosberg & Fosberg 13433* (F, MO); West, open, dry ground, *Hitchcock 15123* (US); West, sand dunes along coast, *Hitchcock 15127* (US); Moomoni Beach, *Rock 14051* (A), *Rock s.n.* (A, GH, US). **Oahu:** Kaena Point, altitude 5 m, *Christophersen 1042* (NY); on sand and coral back of beach, Honouliuli, Barbers Point, *Cowan 794* (UC); near coast on arid plain, Makapuu Point, *Degener 2062* (UC, US); near ocean, Mokuleia Beach, Waialua, *Degener & Degener 23615* (BM, NY); arid rocky clay plain overlooking the sea, Makapuu Head, *Degener et al. 7142* (GH, MO, NY); along arid coast, Lahilahi [Mauna], *Degener et al. 10412* (CAS, GH, KANU, L, MO, NY, US); Pearl City, *Forbes 1532* (MO); Mokapu Peninsula, Pyramid Rock, Heeia Flats, Heleloa, *Fosberg 10578* (US); side of gully near ocean, Ulupau Head, Mokapu Peninsula, altitude 2 m, *Fosberg 10902* (F); eroded slope, Mokulua, S islet, Kaiua, altitude 15 m, *Fosberg 12889* (A, F, UC, US); thin coral sand on basalt, Kaohikaipu Island, Waimanalo Bay, altitude 3 m, *Fosberg 14057* (F); sandy coral soil on raised reef, Kapapa Island, Keneohe Bay, altitude 2 m, *Fosberg & Egler 14012* (F, US); calcareous sandstone, Mokuauia Island, Laie Bay, altitude 4 m, *Fosberg & Egler 14162* (A, CAS, F, US); Diamond Head, *Heller 2095* (BM, F, GH, MO, NY, UC, US, W); Macrae, *Herb. Hillebrand 395* (GH); Honolulu, Fort Shafter, *Hitchcock 13851* (US); coral plain near beach, Ewa, Barbers Point, *Hosaka 1353* (F, W); top of bluffs above Hanauma Bay, altitude 50–100 ft, *Hutchinson & Obata 2846* (F, NY, UC, US); without locality, *Mann & Brigham 619* (F, G, GH, MO, NY, US); Honolulu, *Meebold 8373* (M); Koko Head, *Meebold 24963* (M); Koko Head region, 6 Aug 1930, *Neal s.n.* (UC); Waimanalo, *Pickering & Seamster 3358* (F); Waialua, anno 1911, *Rock s.n.* (GH); Mokuleia Beach Park, foremost sandy dunes, *von Royen 10198* (A); Koko Head, wind-swept volcanic stone slope near sea, *van Steenis 20401* (L); Koko Head Crater, *Topping 3032* (NY); beside road up Mokapuu Head, *Wilbur 502* (US); without locality, *Herb. U. S. Exploring under the command of Capt. Wilkes* (US, fragment GH, type). **Island Unknown:** *Chamisso 163* (F); *Gaudichaud 26* (G), *27* (G), *245* (G); *Hillebrand s.n.* (US, W).

Literature Cited

Adams, C. D. 1972. Flowering Plants of Jamaica. Mona, Jamaica. [*J. obcordata*, 605.]

Britton, N. L. 1925. *Jacquemontia subsalina*. *In* N. L. Britton & P. Wilson, Sci. Survey Porto Rico & Virgin Isl. 6: 106.

———. 1930. *Jacquemontia subsalina*. Addisonia 15: 37. *pl. 499*.

Carlquist, S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. Bull. Torrey Bot. Club. 94: 129–162. [*J. sandwicensis*, 138, 139.]

———. 1970. Hawaii, a Natural History. Garden City, New York. [Photograph of *J. sandwicensis*, 273.]

Choisy, J. D. 1834. Convolvulaceae orientales. Mém. Soc. Phys. Genève 6: 385–502. *6 pls.* [Reprinted with separate pagination, 1–120. *I. ovalifolia*, 449 (67).]

———. 1845. Convolvulaceae. *In* A. P. de Candolle, "Prodromus" 9: 323–462. [*I. ovalifolia*, 357.]

Degener, O. & I. Degener. 1956. Flora Hawaiiensis. Family 307: *Jacquemontia sandwicensis.*

Fosberg, F. R. 1951. The American element in the Hawaiian flora. Pacific Sci. 5: 204–206.

Gray, A. 1862. Characters of new or obscure species of plants of monopetalous orders in the collection of the United States South Pacific Exploring Expedition under Captain Charles Wilkes, U.S.N. With occasional remarks, &c. Proc. Amer. Acad. Arts 5: 321–352. [*J. sandwicensis*, 336.]

Guppy, H. B. 1906. Observations of a Naturalist in the Pacific between 1896 and 1899. Vol. 2. Plant dispersal. London and New York. [*Jacquemontia*, 365, 366.]

Hallier, H. 1918. Ueber Aublet's Gattungen unsicherer order unbekannter Stellung und über pflanzengeschichtliche Beziehungen zwischen Amerika und Afrika. Meded. Rijks-Herb. 35: 1–33. [*J. sandwicensis*, 7, used for African, Hawaiian, and American populations.]

Hepper, F. N. 1968. A standard citation of microfiches. Taxon 17: 604.

Hooker, W. J. & W. G. Arnott. 1832. The botany of Captain Beechey's voyage. Part. 2. London. [*C. ovalifolius*, 90, 91.]

House, H. D. 1921. Necessary changes of certain plant names. New York State Mus. Bull. 233–234: 60–69.

Jones, A. 1968. Chromosome numbers in *Ipomoea* and related genera. Jour. Heredity 59: 99–102. [*J. subsalina*, 100.]

Junghans, J. 1961. Thonning's and Isert's collections from "Danish Guinea" (Ghana) in West Tropical Africa. Bot. Tidsskr. 57: 310–355; 1962, 58: 82–122.

Millspaugh, C. F. 1900. Plantae Utowanae. I. Catalogue of the species. Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 1–110. [*C. obcordatus*, 88.]

Monachino, J. 1958. *Convolvulus ovalifolius* Vahl. Revisita Soc. Cubana Bot. 15: 81–83.

Nagata, K. M. 1971. Hawaiian medicinal plants. Econ. Bot. 25: 245–254. [*J. sandwicensis*, 250.]

Pope, W. T. 1929. Wayside Plants of Hawaii. Honolulu. [*J. sandwicensis*, 184–187.]

Ridley, H. N. 1930. The Dispersal of Plants throughout the World. Ashford, England. [*J. sandwicensis*, 302.]

Robertson, K. R. 1971. A revision of the genus *Jacquemontia* (Convolvulaceae) in North and Central America and the West Indies. Ph.D. dissertation, Washington University, St. Louis, Missouri. [See Diss. Abstr. 32: 2037B.]

Schumacher, H. C. F. 1827. Beskrivelse af Guineiske Planter. København. [Evidently preprinted with separate pagination from Kongel Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 3: 21–248. 1828; 4: 1–236. 1829; *C. coeruleus*, 101 (3: 131).]

Semple, J. C. 1970. The distribution of pubescent leaved individuals of *Conocarpus erectus* (Combretaceae). Rhodora 72: 544–546.

Sprengel, K. P. J. 1824. Caroli Linnaei, Systema Vegetabilium. Ed. 16. Vol. 1. [*C. coeruleus*, 593.]

Swanholm, C. E., H. St. John & P. J. Scheuer. 1959. A survey of alkaloids in Hawaiian plants. I. Pacific Sci. 13: 295–305. [*J. sandwicensis*, 297.]

Urban, I. 1898. I. Bibliographia Indiae Occidentalis botanica. Symb. Antill. 1: 1–195. [H. West, 174–176.]

Vahl, M. 1798. Eclogae Americanae. Vol. 2. København. [*C. quinquepartitus*, 14; *C. ovalifolius*, 16.]

Verdcourt, B. 1963. Convolvulaceae. *In* C. E. Hubbard & E. Milne-Redhead (editors), "Flora of Tropical East Africa." London. [*Jacquemontia*, 33–37.]

Welwitsch, F. M. J. 1858 [1859]. Apontamentos phytogeographicos sobre a flora da provinca de Angola no Africa equinocial servindo de relatorio preliminar ácerca da exploração botanica da mesme provincia. Ann. Conselho Ultramarino 1: 527–592. [*I. oleracea*, 589.]

West, H. 1793. Bidrag til Berskrivelse over Ste. Croix. København. [*C. ovalifolius*, 271.]

NOTES ON SOME CRITICAL CHARACTERS IN *COLUMNEA* CLASSIFICATION[1]

Brian D. Morley[2]

Recent workers including Stearn (1969) and Wiehler (1970) have commented on reassessment of some of the sections within *Columnea* sens. lat. The following notes are based on my own attempts at improving *Columnea* classification, and are intended as an evaluation of some of the critical characters employed in the classification.

Columnea belongs to the tribe Columneeae, subfamily Gesnerioideae of the Gesneriaceae. The Columneeae comprises approximately 396 species of which about 160 belong to *Columnea* sens. lat., the next largest genera being *Episcia* Mart. and *Drymonia* Mart. with approximately 35 species each (Wiehler, 1970). Estimates of the size of *Columnea* sens. lat. vary from 100 plus (Stearn, 1969) to 200 (Willis, 1966). Since *Columnea* was described by Linnaeus in 1753 many new species have been discovered and described with the result that the known variation now exceeds those limits defined by Linnaeus and sometimes borders on those of *Alloplectus* Mart.

Experimental observations on *Columnea* have accumulated in the past 20 years particularly from the disciplines cytology (Eberle, 1956; Fussell, 1958; Sherk, 1960), plant breeding (Sherk & Lee, 1967) and anatomy (Wiehler, 1970). A beginning has also been made on field studies of wild populations in relation to their breeding systems and patterns of variation (Morley, 1968, 1971). These data have not yet been incorporated into the classification of *Columnea* sens. lat. partly because more experimental work is required on larger species samples.

Critical Characters

Four main types of attribute were used by Hanstein (1865), Bentham and Hooker (1876: 993), and Fritsch (1893–94) to classify *Columnea* sens. lat. These characters were a) corolla morphology, b) calyx morphology, c) leaf anisophylly, and d) leaf vestiture. Each of these characters can be examined on the basis of present knowledge of their variation and their likely evolutionary significance. The possession of a berry fruit serves to distinguish *Columnea* sections from most *Alloplectus*, which have capsular fruits. The Caribbean "*Alloplectus*" species may, for example, relate to sect. *Stygnanthe* or *Collandra* in *Columnea* by having berry fruits. More observations on fruit

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Ann. Missouri Bot. Gard. 61: 514–525. 1974.

FIGURE 1. Diagrams of corolla morphology, all vestiture omitted. Bar scales = 1 cm.—a. *Columnea aureonitens* Hook. (sect. *Collandra*), cult. Glasnevin.—b. *C. calotricha* Donn. Sm. (sect. *Stygnanthe*) (after A. J. M. Leeuwenberg (1958), The Gesneriaceae of Guiana, Fig. 15, p. 385).

characters in *Columnea* and *Alloplectus* are required in cultivation and the field.

1. *Corolla morphology.*—Because *Columnea* is monophyletic on the basis of fruit characters but corolla morphology is diverse, corolla shape is systematically significant and is stressed in the Fritsch and other treatments of the genus. As Macior (1971) has pointed out the "flower as a functional reproductive unit, is an essential link in plant breeding systems," and, "selection pressure on this link in the breeding system must have a profound influence on speciation and consequently on the principles of systematics of the plant angiosperms, and even of their pollen vectors." Corolla diversity on *Columnea* sens. lat. is best explained as being the result of past and continuing natural selection pressures exerted by pollen vectors.

While corolla shape is systematically significant it is possible that as a taxonomic suite of characters the attribute could be misleading. We do not yet know whether morphologically similar corollas denote a common evolutionary past or whether convergent evolution might have created similar corollas in species with different origins, as has been suggested in other gesneriads. Increased knowledge of the pollen vectors of *Columnea* will help resolve the question. Little is known about pollination in *Columnea* sens. lat., and it remains to be seen if species are vector specific and which particular species of animal carry out pollination. It may be that the unusually shaped corollas of some columneas such as *C. incarnata* Morton (sect. *Pentadenia*) are adapted to visits by a particular vector such as bats. The changes in corolla morphology which can be brought about by hybridization (Sherk, 1960; Saylor, 1971) should also be remembered, especially as some sections of *Columnea* are genetically crossable.

Pollen-vector selection-pressure on sympetalous corollas determines the amount of dissection and zygomorphy of the organ. This in turn may influence other parts of the flower as is the case in *Columnea* sens. lat. where stamen mechanism changes with increased zygomorphy. Actinomorphy is usually accepted as a less elaborated condition than zygomorphy, and plants with zygomorphic corollas are regarded as derived for the evolution of that organ. Corolla shape in *Columnea* sens. lat. ranges from almost actinomorphic to strongly bilabiate.

i) The most actinomorphic corollas are those of species in sections *Collandra* and *Stygnanthe* (see Figs. 1a–b), these sections being otherwise distinguished by leaf length. The species have corollas which are relatively tough and waxy in texture and which are normally coarsely sericeous or adpressed hairy. It is held (Knuth, 1909: 237) that waxy corolla tissues like those found in *Collandra* and *Stygnanthe* and numerous other columneas are part of an ornithophilous pollination syndrome affording protection to the flowers from the sharp probing bills of feeding birds and rigidity against the buffeting of wing beats. The unfused corolla lobes in *Collandra* and *Stygnanthe* are only several millimetres long, are weakly spreading, and often partly restrict entry to the mouth of the corolla. The corolla tube is usually cylindrical and more or less sigmoid curved in profile, sometimes slightly bulging in the middle, but never ventricose. Like all columneas the proximal end of the tube is more or less gibbous. Some workers suggest that such corollas are hummingbird pollinated, pollen being deposited at the root of the bill, but I have yet to see bird visits.

Because of the narrow throat of sect. *Collandra* and *Stygnanthe* corollas the protandrous stamens, after dehiscence, must make room for the receptive stigma if selfing is to be avoided. The stamen filaments coil up and retract the anthers into the corolla tube, where they can often be found in a moist fungus infected mass. This stamen mechanism can also be seen in corollas of species in sections *Stenanthus* and *Ortholoma*, where the mouth of the corolla is also narrow.

Unlike most cultivated columneas, *C. sanguinea* (sect. *Collandra*) often sets fruit without artificial pollination, and this could indicate that at least some species in *Collandra* are autogamous especially as other collandras such as *C. aureonitens* Hook. also set fruit without artificial pollination in cultivation. *Columnea sanguinea* is a tetraploid.

ii) Increased zygomorphy is seen in the corollas of species in sections *Trichantha, Pterygoloma, Stenanthus* and *Ortholoma* (see Figs. 2a–d), as slight differences in the length of the free corolla lobes, differences in the relative posture of posterior and anterior lobes the anterior often becoming reflexed, and sometimes by swelling of the corolla tube to a ventricose condition. The pollen vectors of all these sections are not known.

Section *Trichantha* differs from *Stenanthus* and *Ortholoma* in lacking a ventricose corolla tube and sometimes possessing conspicuous appendages of unknown function between the corolla lobes: appendages in the sinuses of the corolla lobes are also known in species from sect. *Collandra, C. dissimilis,* and species in sect. *Columnea* has been observed to possess vestigial appendages. Sections *Stenanthus* and *Ortholoma* differ in leaf vestiture. Section *Pterygoloma* corolla shape is intermediate between that of *Trichantha* and *Columnea.* The corolla vestiture of these sections consists of long scattered hairs and is pilose unlike the vestiture of sects. *Collandra* and *Stygnanthe.*

The anthers of the above sections, and those of all columneas, are adherent in two pairs but not fused. Sometimes regarded as a diagnostic character of *Columnea* sens. lat., adherence is by no means a constant feature. Adherence is found when the normal developmental processes of the flower allow its expression, but in poorly developed flowers or ones in the first flush of the season

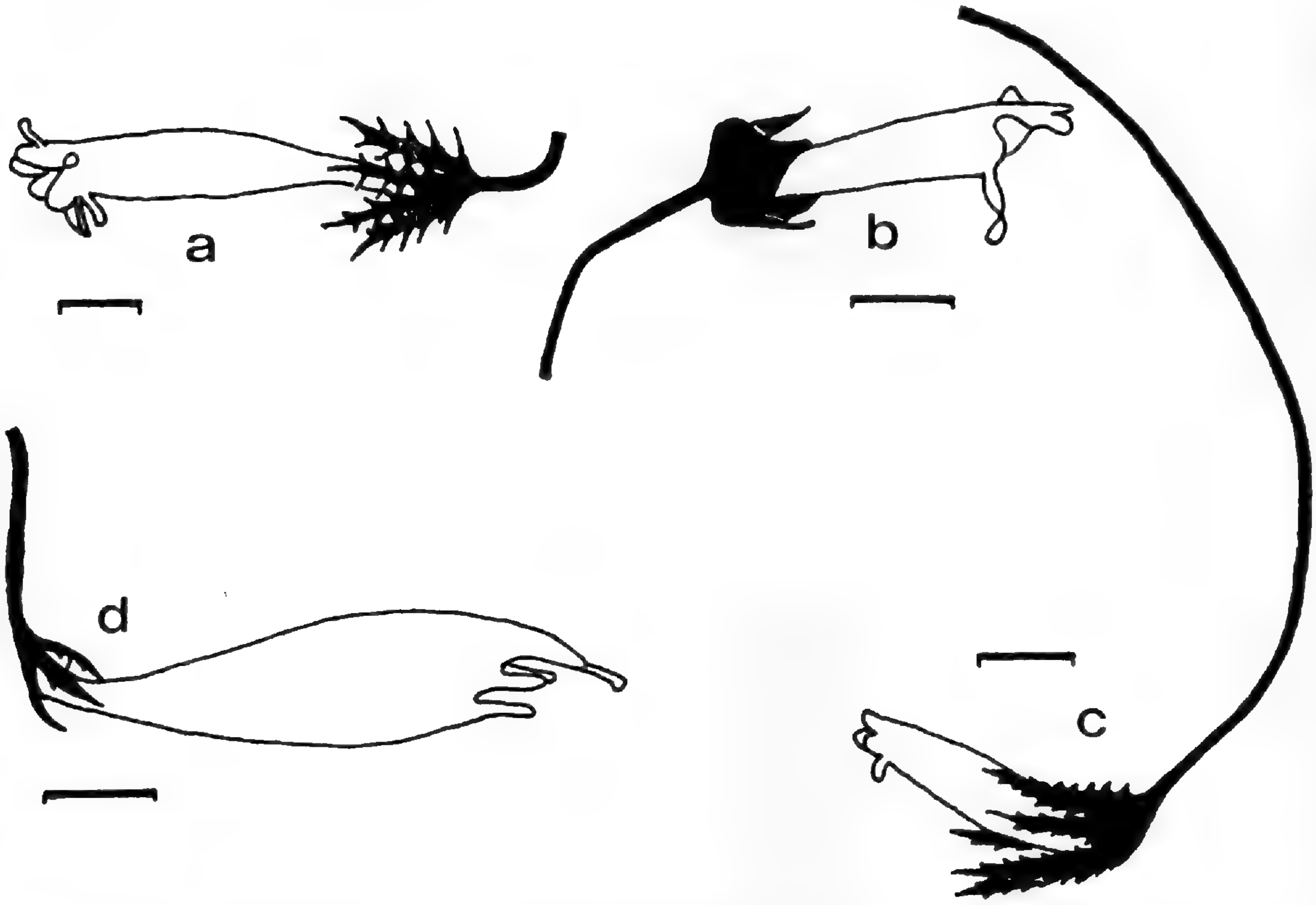

FIGURE 2. Diagrams of corolla morphology.—a. *Columnea elegans* (Rose *ex* Morton) Morton (sect. *Trichantha*) (after Bot. Mag. *t.5428* (1864)).—b. *C. jamaicensis* Urban (sect. *Pterygoloma*), cult. Glasnevin.—c. *C. grata* Morton (sect. *Stenanthus*) (after *Oersted 9288*, Naranjo, Costa Rica (c).—d. *C. mira* Morley (sect. *Ortholoma*) (after Dwyer *et al. 7236*, Cerro Jefe, Panama (MO)).

examples are found of free anthers, anthers adherent in twos and threes, or anthers adherent in a linear series of four. The utility of adherence is seen during hummingbird pollination when a more compact and larger surface area of pollen is presented for dusting on the vector than would be available from four free anthers. Adherence also confers more rigidity to the otherwise flexible filaments and assists economical pollen transfer. With minor alterations in detail anther adherence occurs widely in Gesneriaceae.

iii) Extreme zygomorphy exists in sections *Columnea*, *Cryptocolumnea*, and *Pentadenia* (see Figs. 3a–e). The two posterior lobes of the corolla are fused together for much of their length, and the two lateral lobes are variously connate to the posterior lobes. The laterals spread to either side of the corolla or may become reflexed above the posterior lobes. The reflexed or spreading and often narrow anterior lobe of the corolla is the least fused of the five lobes.

Section *Pentadenia* species differ from both *Cryptocolumnea* and *Columnea* in often having long-pedicellate flowers, a corolla tube which is notably ventricose instead of narrowly funnel shaped, and sometimes free corolla lobes which are longer than the corolla tube.

Hummingbirds are known to pollinate some species in sect. *Columnea* (Morley, 1966), and because of similar corolla morphology are presumed to pollinate species in sect. *Cryptocolumnea*. Hummingbirds were the only pollen vectors

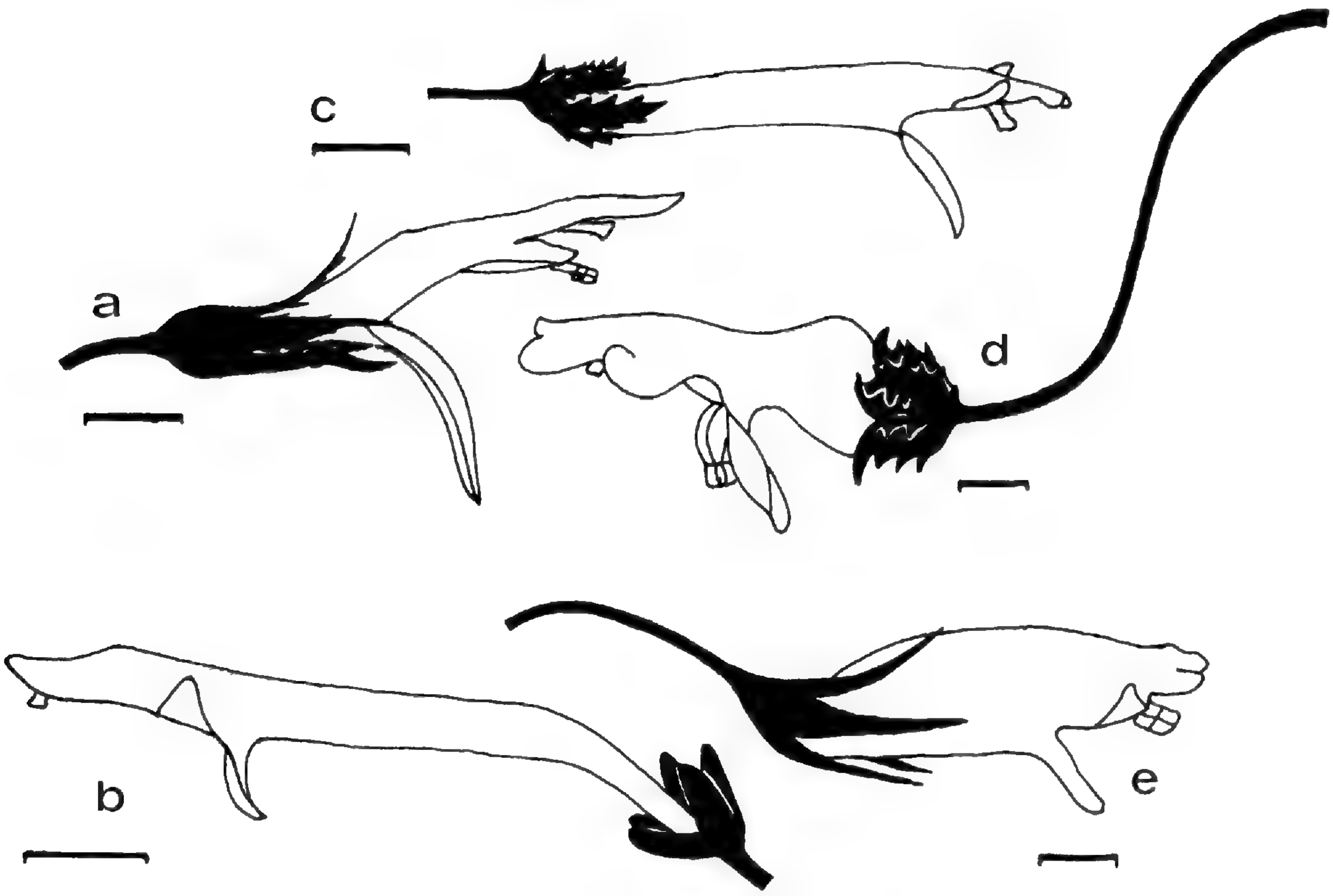

FIGURE 3. Diagrams of corolla morphology.—a. *Columnea fawcettii* (Urban) Morton (sect. *Columnea*), cult Glasnevin.—b. *C. tulae* Urb. var. *tulae* (sect. *Columnea*), cult. Glasnevin.—c. *C. wilsonii* Wiehler (sect. *Cryptocolumnea*), cult. Kew.—d. *C. aurantiaca* Decne. *ex* Planch. (sect. *Pentadenia*) (after Fl. Serres 6: 45, *t*.552 (1845)).—e. *C. dictyophylla* Donn. Sm. (sect. *Pentadenia*) (after *Killip & Garcia* 33895, Colombia (US).

seen to visit the flowers of Jamaican columneas (sect. *Columnea*), which were the basis for the observations. There are two endemic and therefore resident species of hummingbird in Jamaica, both of which are capable of pollinating columneas. *Trochilus polytmus*, the Streamertail, is the commoner of the two species and the one which was observed to carry out pollination on *C. hirsuta*, *C. urbanii* and two natural interspecific hybrids between *C. urbanii* and *C. rutil*ans (Morley, 1971): *Anthracothorax mango*, the Jamaican Mango, is the other bird. The Vervain Hummingbird, *Mellisuga minima* occurs in Hispaniola and Jamaica and is probably too small to work the flowers of columneas in Jamaica (see Table 1).

While the flowers of *Columnea brevipila*, for example, have corolla tubes which are longer than the average bill length of *Trochilus polytmus*, the nectar may still be accessible if lapped with the tongue, for this organ in *T. polytmus* is almost twice as long as the bill. Birds with bills shorter than the corolla tubes of flowers they are visiting may still bring about pollination.

Trochilus polytmus in Jamaica was polytropic and was seen to visit any nectariferous flower including *Asclepias* (Asclepiadaceae) *Hedychium* (Zingiberaceae), and *Elleanthus capitatus* (Orchidaceae) see Pijl and Dodson (1969: 95). Flower color in sect. *Columnea* is briefly described by Morley (1973). Jamaican hummingbirds were seen to fly at all levels in the forest canopy and

TABLE 1. Correlation between bill length and corolla tube length in Jamaican hummingbirds and columneas. Bill length was obtained from a sample of skins at the British Museum; corolla tube length from a large sample of herbarium sheets (Morley, 1968); jam. = *C. jamaicensis*, hir. = *C. hirsuta*, faw. = *C. fawcettii*, rut. = *C. rutilans*, arg. = *C. argentea*, urb. = *C. urbanii*, sub. = *C. subcordata*, his. = *C. hispida*, bre. = *C. brevipila*.

Bill length (cm)		Corolla tube length (cm)								
		jam.	hir.	faw.	rut.	arg.	urb.	sub.	his.	bre.
T. polytmus	1.8	2.1	1.9	1.9	1.7	2.4	1.7	2.1	1.5	2.2
A. mango	2.5									
M. minima	0.9									

both terrestrial and epiphytic columneas were visited. There was some evidence for hummingbirds remembering a food source.

The vestiture of corollas in sects. *Columnea*, *Cryptocolumnea*, and *Pentadenia* is usually pilose, although species such as *C. nicaraguensis* Oerst. and *C. linearis* Oerst., both in sect. *Columnea*, have sericeous corollas. The behavior of the stamens after dehiscence in these sections, and also *Pterygoloma*, does not involve a direct horizontal withdrawal into the corolla. Instead, anterior corolla dissection allows the filaments to swing through a small vertical arc away from the receptive stigma, after which the withered stamens often dry up resting on the anterior lip. The filaments also coil up a little. Deflection of the anthers from the ripening stigma greatly increases the chances of outcrossing particularly by the activity of pollen vectors such as hummingbirds with bill and head dimensions which correlate with the spatial arrangement of *Columnea* genitalia.

To summarise, the corolla morphology in *Columnea* sens. lat. has a diversity some of the components of which are a) corolla vestiture, b) length of tube, c) width of tube, d) curvature of the tube walls, e) length of the unfused portion, f) relative degree of lobe fusion with one another, g) relative posture of lobes, and h) staminal withdrawal mechanism.

The sections of *Columnea* as shown by corolla morphology must be regarded as parts of the same evolving biological system (see Morley, 1973). The relationship between corolla length and dissection shows a continuum throughout the genus, but it should be remembered that such a correlation involves only two of the several variables which characterise the flowers of these plants, and shows nothing of the development of ventricose as opposed to funnel shaped corolla tubes amongst columneas. The shape of *Alloplectus* corollas could indicate that collandras have common ancestry with alloplecti, and by the same argument columneas sensu stricto could have had stenanthoid or ortholomoid ancestry. However, corolla morphology may have no "phylogenetic" significance, and a trait such as ventricose corolla may be produced by selection for visits by a particular pollen vector. Corolla morphology should be regarded as an integrated system of attributes having the greatest relevance to the reproductive biology of columneas.

2. *Calyx morphology.*—The sepals have been used in *Columnea* classification at sectional, specific, and infraspecific level. The use of the sepals is undisputed

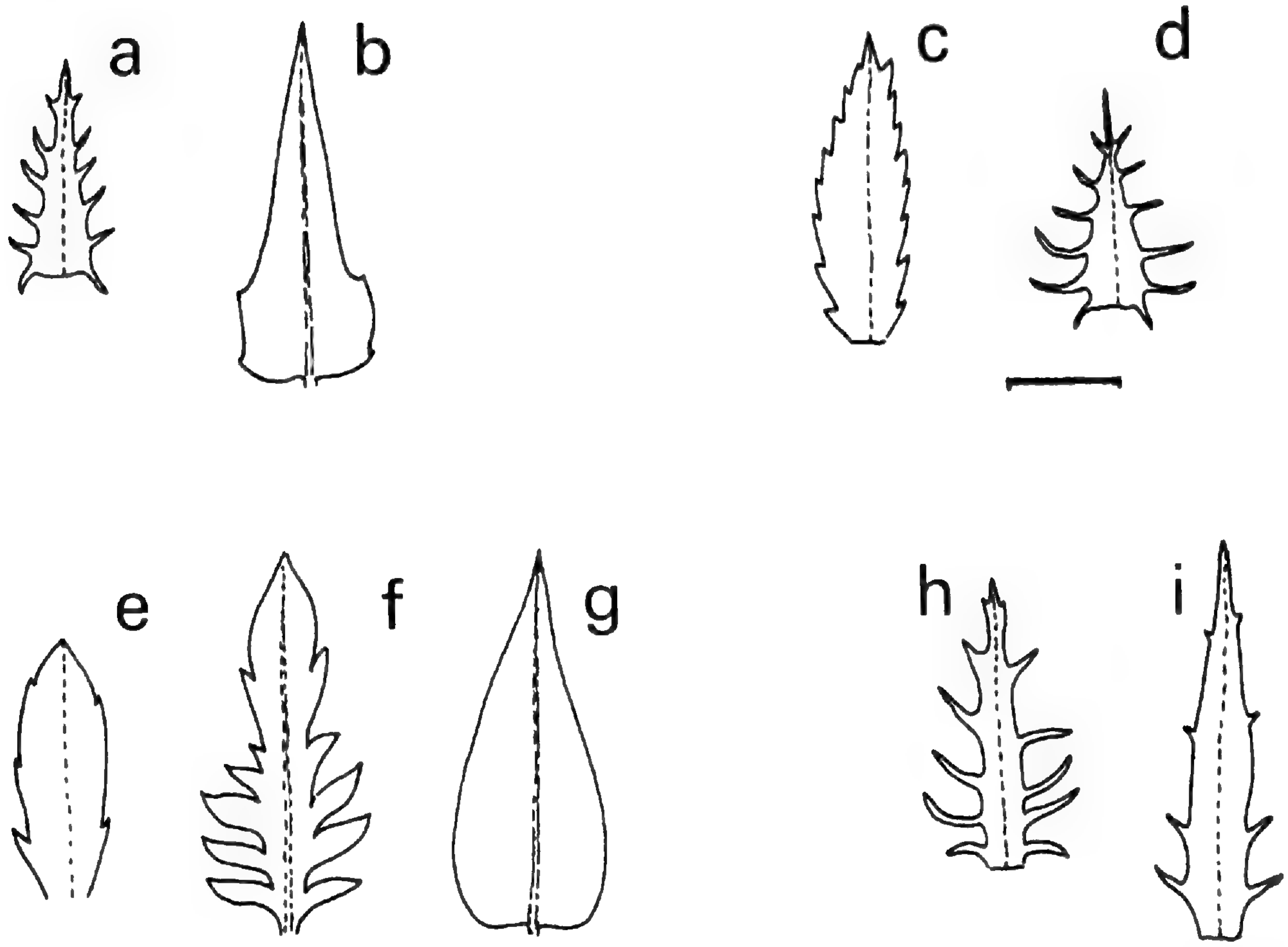

Figure 4. Sepal shapes.—a. *Columnea arguta* Morton (sect. *Columnea*).—b. *C. allenii* Morton (sect. *Columnea*).—c. *C. crassa* Morton (sect. *Collandra*).—d. *C. florida* Morton (sect. *Collandra*).—e. *C. tincta* Grisebach (sect. *Columnea*).—f. *C. rutilans* Swartz (sect. *Columnea*).—g. *C. nicaraguensis* Oersted (sect. *Columnea*).—h. *C. moorei* Morton (sect. *Trichantha*).—i. *C. illepida* Moore (sect. *Trichantha*). Bar, scale = 1 cm.

at and below species rank despite the variation of sepal shape and toothing which accompanies the geographical distribution of some species such as *C. scandens* (sect. *Columnea*) (Morton, 1944; Morley, 1972). At species rank sepal characters largely correlate with other taxonomic and geographic criteria to provide useful distinguishing characters between such species as *C. allenii* and *C. arguta* (both sect. *Columnea*) and *C. florida* and *crassa* (both sect. *Collandra*) (see Figs. 4 a–d).

Species in sect. *Collandra* have sometimes been noted to possess pectinate sepals, but some species in the group such as *C. consanguinea* have almost entire sepals. The possession of pectinate sepals is supposed to be one of the distinguishing characters between sect. *Stenanthus* and *Ortholoma*, yet in *Stenanthus* not all species exhibit well developed pectinate sepals (*e.g. C. grata*), and the absolute distinctions between poorly pectinate (*C. grata*), pinnatifid (*C. rutilans*, sect. *Columnea*), and strongly subulate toothed sepals (*C. arguta*, sect. *Columnea*) are slight.

Although not strictly a morphological character, sepal color must be mentioned. Red sepal colors have been seen to attract hummingbirds to columneas in sect. *Columnea* in Jamaica. *Trochilus polytmus* was seen to attempt to feed from the red calyces of *C. hirsuta* which had lost corollas and had set no fruit

(Morley, 1968). Red sepals may help to make the flowers more conspicuous to bird pollen vectors especially in species with yellow corollas such as *C. sulfurea*, sect. *Columnea*. The red, reddish, or bronze flower vestiture found in sect. *Collandra* species having otherwise small dull yellow corollas may also attract pollinators. Elaboration of the sepal margin by teeth increases the area of pigment containing-tissue, especially if teeth are pectinate and also covered with long red hairs: to support this notion species having pectinate sepals also have red sepals (*e. g. C. sanguinolenta*, sect. *Stenanthus*, and *C. major*, sect. *Trichantha*). The red pigment found in flowers and leaves of some columneas is a 3-desoxyanthocyanin, called columnin.

Sepal color may also serve to attract fruit dispersal agents. At fruiting time the white, pink, red, or magenta berries of columneas are about 1 cm. diameter, and when surrounded by brightly colored sepals, possibly with an elaborated margin such as in *C. rutilans* (sect. *Columnea*), the fruits are made more conspicuous for dispersal agents than if the sepals are green or chaffy and withered. The fruits are widely presumed to be bird dispersed, but no observations of the process have yet been made: secondary agents are ants (Morley, 1968). Ridley (1930: 392, 410, 418) notes that the combination of red and white colors is often associated with bird dispersal of fruits, and this color combination is more or less expressed in a majority of columneas studied. Fruits may be white or pink with red sepals (*e. g. C. schiedeana*, sect. *Columnea*) or red with pale chaffy sepals (*C. tulae*, sect. *Columnea*). In *C. harrisii*, sect. *Columnea*, having green sepals at flowering time, there is a slight development of red pigmentation after the corolla withers and before the fruit reaches maturity, indicating that sepal coloring in at least this species is correlated with fruiting time. Species such as *C. florida*, sect. *Collandra*, do not have a red-white combination of fruiting colors, the sepals being colored orange and fruits yellow to orange. The berries of Jamaican columneas are slightly sweet to human taste but very seedy, and the matrix of the berry sticky.

In summary calyx characters are useful at species level but questionable at sectional level, partly because variation of sepal characters can be as great within sections as between. It is suggested that sepal shape, margin type, and color have the dual role of attracting pollen vectors during flowering, and later helping attract fruit dispersal agents.

3. *Leaf anisophylly*.—Leaf anisophylly has been used as a reliable taxonomic character in *Columnea* classification, because herbarium sheets give an impression that the character provides a morphological discontinuity between species. This is so with certain species but cannot be said for all columneas.

Sherk (1960) explained variation of anisophylly in *C. nicaraguensis* and *C. verecunda* (both sect. *Columnea*) as due to genetic heterozygosity for leaf size and shape on the basis of selfing experiments, hence implying some genetic basis for the taxonomic character anisophylly. My observations on species with weakly anisophyllous shoots, and which thus resemble some of the species studied by Sherk, show that phenotypic variation can destroy the value of anisophylly as a taxonomic character.

In all columneas the arrangement of leaves about the axis partly depends

TABLE 2. Alterations of leaf anisophylly with shoot inclination in *Columnea*. Leaf pair ratio (LPR) is an expression of the amount of anisophylly obtained by dividing the length of the short leaf into that of the longer for each pair (an LPR = 1.0 is isophyllous).

	Average leaf pair ratio		Sample number of nodes	
Species	Erect	Horizontal	Erect	Horizontal
C. rutilans	1.4	2.0	11	11
C. fawcettii	1.5	1.9	14	14

on inclination of the shoot to a source of light and partly on the genotypic length and breadth of the leaf of the particular species. Variation of leaf dimensions I regard as due to polygenic inheritance. Alterations of leaf posture are seen to be brought about by resupination of petioles in agreement with the observations of Goebel (1900: 113) and Hill (1939). An axis oriented parallel to a source of light has leaves arranged in a radial leaf mosaic around the axis, but one oriented at right angles to a source of light has leaves in a dorsiventral "frondlike" leaf mosaic which is often apparent in herbarium specimens. Simultaneous with changes in the leaf arrangement about the axis are changes altering the final expression of leaf length and breadth of pairs of leaves at nodes where leaf expansion is still active. The changes of leaf size appear to be related to axis orientation and how pairs of decussate leaves can be best arranged for maximum light interception. Table 2 shows the effect of axis orientation on anisophylly for two pairs of shoots of well grown *C. fawcettii* and *C. rutilans* (both sect. *Columnea*) in cultivation in a controlled environment. Care was taken to sample nodes of comparable age, as LPR in Jamaican species was found to stabilize only after the tenth node had been produced. The average LPR for *C. fawcettii* is 1.9 based on a sample of 68 herbarium specimens, figures which indicate that in nature the shoots are horizontally pendent when mature as is confirmed in the field. *Columnea rutilans* had an LPR of 2.5 in nature based on 48 herbarium specimens, a figure larger than the LPR achieved in experiment.

Columnea microphylla (sect. *Columnea*) with leaves less than 1.0 cm long is always isophyllous (LPR = 1.0) irrespective of whether shoots are pendulous or prostrate because pairs of leaves are small enough to find accommodation at each node without lamina overlap. Anisophylly is also less marked in narrow leaved species such as *C. crassifolia* and *C. linearis* (both sect. *Columnea*) as might be expected because narrow leaves can also be accommodated in both erect and horizontal shoot positions without lamina overlap if slight resupination occurs. It is in large leaved species such as *C. purpurea* (sect. *Collandra*) or *C. wilsonii* (sect. *Cryptocolumnea*) that some physical change in the size of leaves at each node must occur if lamina overlap is to be avoided: there seems to be strong genetic control over leaf anisophylly in large leaved species on the basis of constancy of anisophylly in these plants. In comparison with *C. microphylla* the LPR of *C. sanguinea* (sect. *Collandra*) is 6.0–6.5. The taxonomic significance of this reasoning is that as LPR approaches unity, the effects of phenotypic variation may be enough to spoil that anisophylly which has a genetic

TABLE 3. Leaf pair ratio in Jamaican columneas showing sample size and standard deviation. Sample size refers to number of herbarium specimens from which a single node was examined; and hir. = *C. hirsuta*, faw. = *C. fawcettii*, rut. = *C. rutilans*, arg. = *C. argentea*, sub. = *C. subcordata*, urb. = *C. urbanii*, har. = *C. harrisii*, bre. = *C. brevipila*, his. = *C. hispida*, jam. = *C. jamaicensis*, pro. = *C. proctorii*.

Species	hir.	faw.	rut.	arg.	sub.	urb.	har.	bre.	his.	jam.	pro.
Mean LPR	1.8	1.9	2.5	1.5	3.5	1.3	3.6	1.2	3.3	1.5	3.5
Sample size	43	68	48	11	14	27	9	17	6	21	16
Standard deviation	0.5	0.6	0.9	0.4	1.0	0.3	1.2	0.2	1.5	0.3	1.2

component and which is being used as a taxonomic character. Table 3 shows LPR for Jamaican columneas and the amount of variation of values for each species all of which belong to sect. *Columnea* except *C. jamaicensis* (sect. *Pterygoloma*). It is suggested that any *Columnea* having leaf dimensions of this magnitude will behave in the same way despite its geographical origin or taxonomic affinity.

It may be useful to speculate on correlation between leaf size and ecological adaptation in columneas, although little ecological work has been carried out on this group with versatile terrestrial and epiphytic preferences. Large leaved species with laminas 20–30 cm long have leaves which are relatively thin in proportion to area, which implies a possible susceptibility to wilting from transpiration losses. If Wiehler's observations of 1970 are general for all columneas, the fact that large leaved species have smaller more numerous epidermal cells per square centimetre than small leaved suggests that large leaved species also have more stomates per unit area. This would support the notion that large leaved species are susceptible to transpiration losses resulting in serious wilting. While needing much investigation, the habitat requirements of large leaved species may approximate to sheltered niches, where leaves suffer little wind damage, moist niches where transpiration can be made good by water uptake or where transpiration will be minimal, and perhaps shady niches where light intensity requires large surface areas in leaves for photosynthesis to proceed satisfactorily. These conditions are indicated on some herbarium sheets. Large leaved taxa require relatively thick axes (10–15 mm diameter) to support the foliage, and such heavy plants may be better fitted to terrestrial niches, although herbarium sheet data indicate that a number of large leaved taxa are regularly epiphytic.

Small leaved species with laminas to 3.0 cm long have leaves thicker in proportion to area and also have fewer larger epidermal cells. These attributes suggest that small leaved species are found in more dry, windy, sunlit epiphytic habitats, where water stress can be offset by the development of succulence in the leaves, and where the thin axes having a pendulous or drooping habit both weigh little and support the leaves. These conclusions are borne out by field observations and herbarium sheet data. Wiehler (1970) found water storage tissues in *Columnea* leaves and Morley (1968) found that in Jamaican columneas all of which possess water storage in the leaves, the thickness of storage tissue is closely related to altitudinal distribution and wetness of habitat in at least *C. hirsuta* and *C. fawcettii* (sect. *Columnea*) (Morley, 1972.) Specialised ecological adaptation can be interpreted from the habit and foliage of species such as *C. allenii* or *C. arguta* (sect. *Columnea*), both being well suited to an epiphytic niche, and they show a narrow tolerance to water and temperature regime experienced in cultivation in support of their being ecologically specialized. In contrast, one finds that *C. sanguinea* (sect. *Collandra*) seems able to accommodate to a range of water and temperature regimes in cultivation, perhaps indicating less ecological specialization.

Conclusions on leaf anisophylly are that when LPR is large the character is sufficiently stable for the definition of groups. This is the same as saying that long, broad leaves are a useful character is the classification of columneas.

4. *Leaf vestiture.*—There are four types of hairs in columneas studied, a) multicellular sharply pointed, b) multicellular gland-tipped, c) multicellular slender, and d) glandular papillae. This largely agrees with Wiehler (1970), who does not recognise the different thickness of hair types a) and c), the latter being found only on corollas and some leaves of species with densely sericeous vestiture. The walls of the cells are refractive and clear or brownish, but the cell cavity may be clear or filled with various amounts of the red pigment columnin.

There are large numbers of possible combinations and permutations of different hair types, in various postures and with various densities on the adaxial and abaxial leaf surfaces, which are not necessarily the same. It has been found that particular vestitures characterize particular species with the greatest accuracy in herbarium studies, and inheritance of posture, density, and type of hair is documented for some species (Morley, 1971): in hybrids the vestiture characters may show heterosis.

As stomates are confined to the abaxial leaf surface in the columneas so far examined, adaxial leaf vestiture cannot serve to reduce transpiration. It has been suggested that vestiture may reduce the amount of light entering the leaf, or even increase light admitted. Colored leaf vestiture may serve to attract pollinators to the flowers of species in sections *Ortholoma* and *Collandra*, perhaps in conjunction with the red blotching on the undersides of leaves of species in the above sections and also *Cryptocolumnea* and *Pentadenia*. Seen from below the foliage, where the flowers tend to hang and from which direction birds generally approach the flowers, the red pigmentation on leaves of species such as *C. sanguinolenta* (sect. *Stenanthus*) or *C. sanguinea* (sect. *Collandra*) is most conspicuous.

Leaf vestiture has been used to distinguish between sections *Stenanthus* and *Ortholoma*, but when the same attributes which define these sections appear in *C. florida* and *C. pectinata* (sect. *Collandra*), it is given the importance of denoting only specific difference; clearly such use of characters is arbitrary. This does not detract from the usefulness of leaf vestiture at species level.

CYTOLOGY AND GENETICS

An interesting relationship exists between the corolla morphology and interfertility data so far available for *Columnea* sens. lat. (Morley, 1973). Hybrids between species in sect. *Collandra* and *Stenanthus* form stainable pollen, but sect. *Collandra* species will not produce hybrids forming stainable pollen when crossed with sect. *Columnea* species. Sections *Trichantha* and *Pterygoloma* (Saylor, 1971) are both compatible with sect. *Columnea*, but *Trichantha* and *Pterygoloma* produce no stainable pollen when crossed. Section *Trichantha* crossed with *Ortholoma* species and crossed with *Stenanthus* species both result in hybrids which form stainable pollen. Hybrids between *Columnea* and *Cryptocolumnea* sections form stainable pollen. Such breeding relationships suggest that section *Collandra* and *Columnea* are the most genetically dissimilar, with sections *Ortholoma, Trichantha, Stenanthus* and *Pterygoloma* genetically intermediate. This is precisely what is shown by corolla morphology where *Collandra* and *Columnea* corollas occupy opposite poles of a scatter diagram for corolla length against corolla dissection, and the remaining sections occur in between the two (Morley, 1973). This relationship may suggest that corolla morphology is taxonomically reliable as a character and is more than simply an indicator of the type of pollinator visiting a species.

Literature Cited

Bentham, G. & Hooker, J. D. 1876. *Columnea. In* "Genera Plantarum." Vol. 2.

Eberle, P. 1956. Cytologische Untersuchungen an Gesneriaceen I. Chromosoma 8: 285–316.

Fritsch, K. 1893–94. Gesneriaceae. *In* A. Engler & K. Prantl, "Die natürlichen Pflanzenfamilien." 4(3b): 133–185.

Fussell, C. P. 1958. Chromosome numbers in Gesneriaceae. Baileya 6: 117–123.

Goebel, K. 1900. Organography of Plants. Oxford.

Hanstein, J. 1865. Die Gesneraceen des Königlichen Herbariums und der Gärten zu Berlin. . . . II. Abschnitt . . . . Drittes Stück. Linnaea 34: 225–446.

Hill, A. W. 1939. Resupination studies of flowers and leaves. Ann. Bot. (London), n.s. 3: 871–888.

Knuth, P. 1909. Handbook of Flower Pollination. Vol. 3. Oxford.

Macior, L. W. 1971. Coevolution of plants and animals—Systematic insights from plant-insect interactions. Taxon 20: 17–28.

Morley, B. D. 1966. *Columnea* and aspects of its evolution. Science notes and news (Jamaica) 2(4): 13–14.

———. 1968. Biosystematics of *Columnea* in Jamaica. Thesis, University of the West Indies, Mona, Jamaica.

———. 1971. A hybrid-swarm between two hummingbird pollinated species of *Columnea* in Jamaica. Bot. Jour. Linn. Soc. 64: 81–96.

———. 1972. The distribution and variation of some gesneriads in Caribbean islands. Pp. 239–257, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography and Evolution." London.

———. 1973. Ecological factors of importance to *Columnea* taxonomy.

Morton, C. V. 1944. The West Indian species of *Columnea*. Contr. U. S. Natl. Herb. 29: 1–15.

Pijl, L. van der & Dodson, C. H. 1969. Orchid Flowers, their Pollination and Evolution. Coral Gables, Florida.

Ridley, H. N. 1930. The Dispersal of Plants throughout the World. Ashford.

Saylor, W. R. 1971. Gesneriad cross roads. Gloxinian 21: 30.

Sherk, L. C. 1960. Cytogenetic studies in *Columnea* L. Thesis, Cornell University, Ithaca.

——— & Lee, R. E. 1967. Interspecific hybridization in the genus *Columnea* (Gesneriaceae). Baileya 15: 89–96.

Stearn, W. T. 1969. The Jamaican species of *Columnea* and *Alloplectus*. Bull. Brit. Mus. Nat. Hist. (Bot.) 4: 181–236.

Wiehler, H. 1970. Studies . . . . in the Gesneriaceae-Gesnerioideae. Thesis, Cornell University, Ithaca.

Willis, J. C. 1966. A dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge. Pp. 265–281, *in* V. Heywood (editor), "Taxonomy and Ecology." London.

NOTES

CASEARIA BELIZENSIS STANDLEY, A SYNONYM OF *LAETIA PROCERA* (POEPPIG) EICH. (FLACOURTIACEAE)

Laetia procera (Poeppig) Eich. was considered by Robyns (Ann. Missouri Bot. Gard. 55: 130. 1968) to range from the Guayanas and northern Brazil to Panama. Recent investigations at the Missouri Botanical Garden have shown that the species also includes *Casearia belizensis* Standley described from British Honduras (Field Mus. Publ. Bot. Ser. 12: 412. 1936. Type: *Schipp 1314*). Material identified as the latter species has been collected all along the Caribbean Coast of Central America from Belize south. The Central American material is identical with that of South America.

Investigations of the flowers of the type specimen of *Casearia belizensis* as well as others collected in Central America have shown no evidence of staminodia, a feature common to *Casearia* and lacking in *Laetia*, so *C. belizensis* Standley should be considered synonymous with *Laetia procera* (Poeppig) Eich.—*Thomas B. Croat & Ronald L. Liesner, Missouri Botanical Garden.*

DIPHYSCIUM ROTUNDATIFOLIUM (MUSCI), A NEW SPECIES FROM TAIWAN

Diphyscium rotundatifolium Wang & Lin, sp. nov.

Plantae gregariae, parvae, ad 1.2 cm altae, fusco-virides, non nitidusae, ad bases rhizoideis, fuscis densis. *Caules* simplices, erecti, ca. 0.5 cm longi, dense foliosi. *Folia* sicca e apicibus et marginibus incurvata, humida erecto-patentia vel leviter curva, inferiora minora, superiora majora, oblongo-spathulata vel e basibus leviter angustis oblonga, apicibus manifeste rotundatis, interdum retusis, truncatis, mucronatis vel rare acuminatis, ca. 2.3–6.5 mm longa, rare ad 8.5 mm, ca. 0.75–1.25 mm lata, paginis undulatis, marginibus fere integris, laminis usque 2-cellulato-crassis, sed ad bases 1-cellulato-crassis, nervis simplicibus, distinctis, infuscatis, prope apice vel ad apices evanescentibus, vel longe excurrentibus, postice valde convexis. *Cellulae* rotundato-hexagonae, in sectione transversali humille mamillatae, chlorophyllose, ca. 11.3 μ in diam., ad bases rectangulares, ca. 11.3–14.1 μ latae, ca. 56.4–98.7 μ longae, laxae et hyalinae.

Dioicum (?). *Folia perichaetii* intima minuta, tenella et hyalina, laxe areolata, ovato-lanceolata, apice inciso, superne brevissimo-ciliata, ca. 1 cm longa, nervo excurrenti. *Gynoecia* terminalies, archegonis ca. 14, 0.6 mm longis, 37 μ latis, sine antheridis, paraphysibus densis et in juventuto moniliformibus vel in maturitate filiformibus. *Seta* brevissima, ca. 0.2 mm longa. *Theca* immersa ovata, asymmetrica, ca. 4 mm longa, 1.8 mm lata, versus orificium angustatum, ca. 0.84 mm in diam. *Endostomium* pallidum, membranaceum, carinato-plicatum, minute papillosum, ad 0.66 mm altum. *Sporae* sphaericae, ca. 10.7–17.5 μ in diam., luteo-virides, papillis densis et minutis. Caetera ignota.

Plants gregarious, small, to 1.2 cm high, dark-brownish-green, not glossy, with dark-brownish rhizoids at bases. *Stems* simple, erect, about 0.5 cm long,

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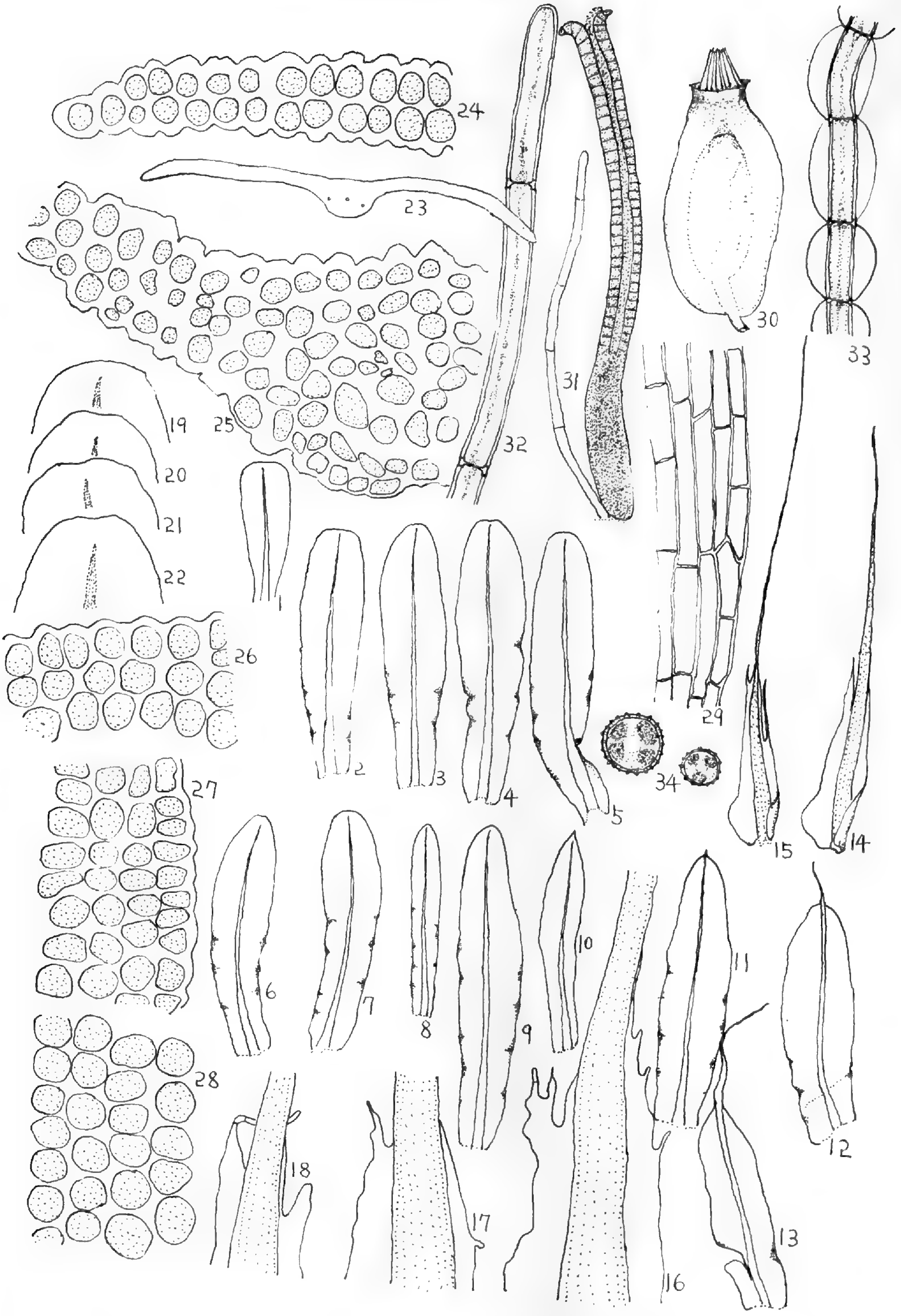
FIGURES 1–34. *Diphyscium rotundatifolium.*—1–13. Leaves, × 12.5.—14–15. Inner perichaetial leaves, × 12.5.—16–18. Apices of inner perichaetial leaves, × 63.—19–22. Leaf apices, × 32.—23. Leaf in cross section, × 87.—24–25. Leaves in cross sections, × 710.—26.



Apical cells of leaf, × 710.—27. Marginal cells of leaf, × 710.—28. Central cells of leaf, × 710.—29. Basal cells of leaf, × 710.—30. Capsule, × 12.5.—31. Archegonium and paraphysis, × 180.—32–33. Paraphyses, × 710.—34. Spores, × 710.

densely foliate. *Leaves* involute from apices and margins when dry, erect-spreading or slightly curved when moist, smaller below and larger above, oblong-spathulate or oblong from slightly narrow bases, with obviously rounded apices, sometimes retuse, truncate, mucronate or rarely acuminate, about 2.3–6.5 mm long, rarely to 8.5 mm, about 0.75–1.25 mm wide, undulate on surfaces, almost entire at margins, in 2-celled layers, but 1-celled layer at bases; costa simple, distinct, brown in color, excurrent, percurrent or ending below apex, on back strongly convex. *Leaf cells* rounded-hexagonal, with low mamillae on both surfaces, chlorophyllose, about 11.3 μ in diam., rectangular at bases, about 11.3–14.1 μ wide and 56.4–98.7 μ long, lax and hyaline.

Dioicous (?). Inner *perichaetial leaves* small, delicate and hyaline, laxly areolate, ovate-lanceolate, incised at the apex, with simple short cilia above, ca. 1 cm long including aristate point; costa strong, excurrent, with arista twice as long as the length of blade. *Gynoecia* terminal, with about 14 archegonia, about 0.6 mm long, 37 μ wide, with dense paraphyses, moniliform when young, thread-like when mature. *Antheridia* not seen. *Seta* extremely short, about 0.2 mm long. *Capsule* immersed, ovate, asymmetric, about 4 mm long and 1.8 mm wide, narrow toward mouth, about 0.84 mm in diam. *Peristome* single, teeth none, endostome pale, membranous, with longitudinal plaits, covered with minute papillae, to 0.66 mm high. *Spores* spherical, about 10.7–17.5 μ in diam., yellowish-green, densely and minutely papillose. Calyptra, lid and annulus not seen.

TAIWAN. NANTOU: Luku Hsiang, Chitou, on moist soil (?). alt. 1150–1750 m, *S. H. Lin*, Nov. 12, 1971 (holotype TUNGH, no. 1267).

In examining this new species, we have found no antheridia or male plants, thus it may be dioicous. The shape of the paraphysis, mingled with archegonia in the female organs, is rather peculiar. Each cell of a paraphysis is surrounded by a swelling membrane which is bubble-like when the cell is short or young, spindle-like as the cell continues to grow, and finally ruptures when the cell extends its length to some extent.

Diphyscium rotundatifolium is easily distinguished from other members of the genus *Diphyscium* by its oblong-spathulate leaves, the rounded leaf apices, the conspicuous mamillae on both leaf surfaces, the almost entire leaf margins, and the few short cilia being poorly developed above the apices of the inner perichaetial leaves. It is similar to *D. fulvifolium* Mitt. in many ways. However, so far as we know, although the apex, size, and shape of the leaves on the same plant of this genus often have rather wide ranges of variation as shown in Figs. 1–13, and the intergradation among vegetative leaves and between vegetative and perichaetial leaves appears evidently, the noticeable difference between the two species is still in the characteristics of the leaves. On the whole, the apex of *D. rotundatifolium* is significantly rounded whereas that of *D. fulvifolium* is obviously mucronate. In addition, *D. rotundatifolium* has longer leaves and larger spores.

The new species, *Diphyscium rotundatifolium*, may sometimes be confused with *D. foliosum*, which is widely distributed in the Northern Hemisphere. As has been mentioned, however, *Diphyscium rotundatifolium* has the characters of oblong-spathulate or spathulate leaves, which are variously pointed but often rounded at the apex, and short and poorly developed cilia of the inner perichaetial leaves, whereas *D. foliosum* has linear-lanceolate or narrowly lingulate leaves, which are also variously pointed but often acuminate apically, and long and well developed cilia of the inner perichaetial leaves.—*Chung K'uei Wang & Sang-hsiung Lin, Department of Biology, Tunghai University, Taiwan, Republic of China.*

NOTES ON *RHYNCHOSPORA* (CYPERACEAE)

Rhynchospora watsonii

With the inclusion of the genus *Dichronema* in *Rhynchospora* the following combination becomes necessary for the Central American sedge flora:

Rhynchospora watsonii (Britt.) Davidse, comb. nov.

Dichronema watsonii Britt., Bull. Torrey Bot. Club 15: 101. 1888.
Rhynchospora radicans (Schlecht. & Cham.) Pfeiffer var. *watsonii* (Britt.) Kuekenthal, Bot. Jahrb. Syst. 75: 311. 1951.

Rhynchospora argentea Standl.

Endemic to Panama, this species has long been known only from the type collection (Svenson, Ann. Missouri Bot. Gard. 30: 312. 1943). This was an immature specimen; consequently, the fruit has never been described. Recent collecting in Panama has uncovered a number of new specimens of this species, allowing me to provide the following expanded description.

Rhynchospora argentea Standl., Contr. U.S. Natl. Herb. 18: 87. 1916.

Perennial; loosely caespitose, with short, slender rhizomes mostly less than 2 cm long but occasionally longer; each rhizome segment expanded at its apex thus forming a corm-like base which produces a new leafy shoot; rhizome system persistent after disintegration of the aerial shoots, forming a tangled mass in older, well-developed plants. Roots conspicuous and well-developed, 2–3 mm thick, brown, usually 1–2(–3) per rhizome segment. Scales covering rhizome segments, grading into cataphylls at the base of the aerial shoots. Cataphylls 1–13 cm long, stramineous to brown, upper ones becoming green, margin membranous. Leaves strictly basal, 20–90 cm long and 1–3 cm wide, acuminate, many-nerved, grayish-white on the upper surface, glabrous, margins scabrous above, smooth or nearly so below, narrowed below into a keeled petiole 5–15 cm long. Culm central, one per shoot, 20–75 cm long, shorter than the leaves, 3-angled, smooth below, scabrous above, without leaves. Inflorescence sparse, compound-corymbose with (0–)1–3 major rays bearing corymbs with few, loosely or densely arranged spikelets; bracts 5–18 mm wide and 5–20 cm long, margins scabrous, lower bracts with well-developed closed sheaths to 6 cm long, upper bracts increasingly smaller and without closed sheaths; bracteoles setaceous. Spikelets solitary, short pedicellate to nearly sessile, lanceolate, 6–8 mm long, whitish, flowers 6–9, the lower ones perfect, mostly maturing 1–3 achenes, the upper 2 or 3 staminate. Glumes 10–13, membranous, 1-nerved, whitish, glabrous; the basal 3 or 4 empty, broadly lanceolate, 2.1–6.0 mm long, acute, apex with a short mucro ca. 0.5 mm long; upper glumes mostly 6.0–6.5 mm long, broadly acute. Stamens 3, anthers 3–4 mm long; style branches 2, ca. 1/10 the length of the undivided portion. Achenes biconvex, lenticular, grayish-brown, 2.5–2.7 mm long, 2.3–2.6 mm wide, 1.5–1.8 mm thick; achene body nearly orbicular in surface view with a rim around the entire circumference; surface of achene finely reticulate; style base elongate triangular, 2.0–2.4 mm long and 1.2–1.4 mm wide at its base, slightly narrower at its base than the apex of the achene, indistinctly reticulate, grayish-white. Hypogymous bristles 5 or 6, slightly shorter than achene and style base.

The following Panamanian collections have been examined (all MO):

PANAMÁ: Cerro Campana, *Croat 22794, 17160.* Along road into Santa Rita, *Kennedy 2745.* Road to Carti from Panamerican Highway near El Uano, *Kennedy, Dressler & Mahler 2413.* 3 mi. NE of Altos de Pacora, *Liesner 513.* COLÓN: Ca. 2–3 mi. up Río Guarche, *Kennedy & Foster 2148.* Santa Rita Ridge, 1 mi. from Boyd-Roosevelt Highway, *Croat 15320.* CANAL ZONE: Quebrada Lopez, *Allen 2129.*

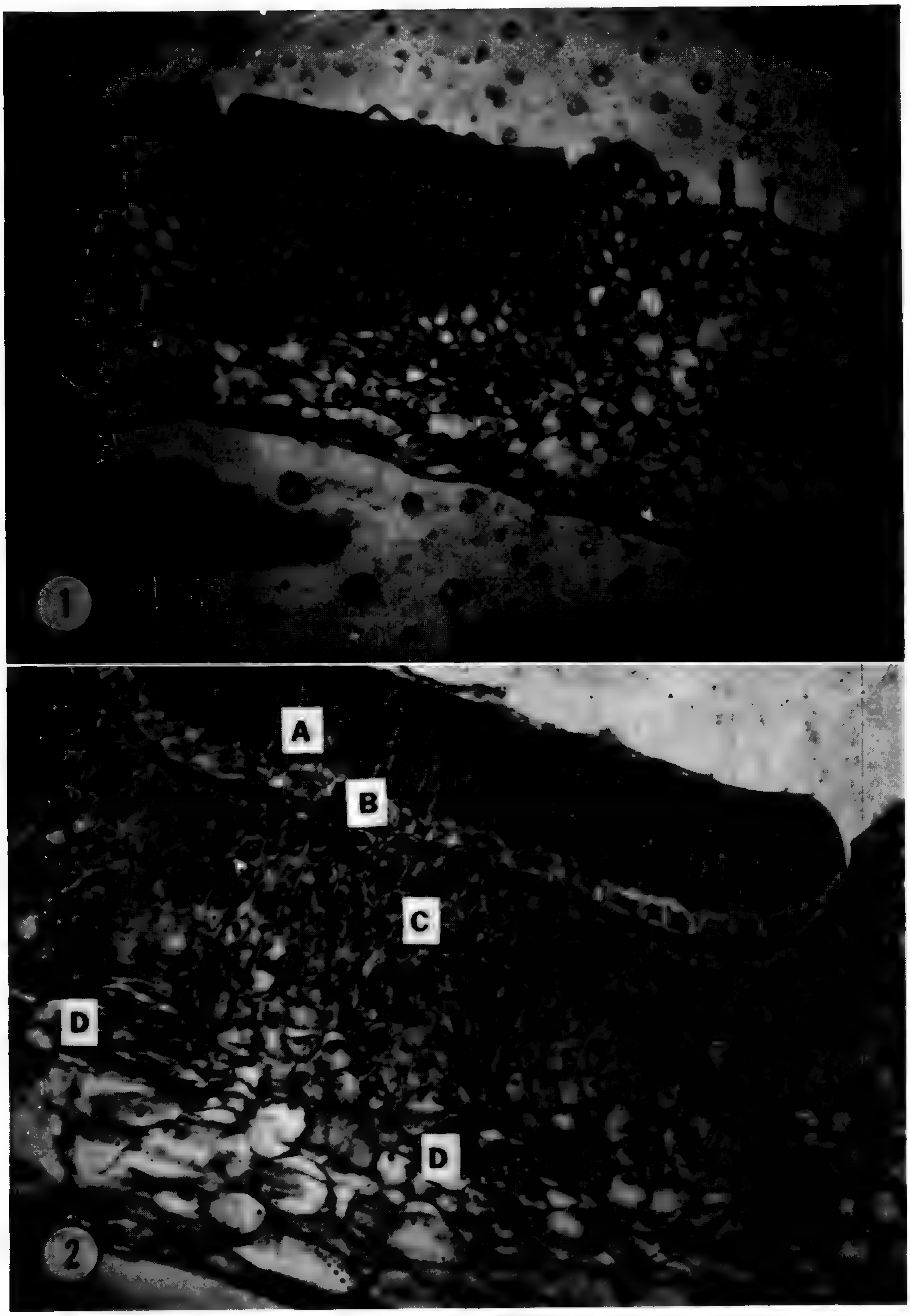
The rhizome system is striking in well-developed plants reminding one, on a smaller scale, of the pachymorph rhizomes of many bamboos.—*Gerrit Davidse, Missouri Botanical Garden.*

ANATOMIC CONSIDERATIONS OF THE CALYX OF *ADENOCALYMMA COMOSUM* (CHAM.) A.P. DC.

This investigation was motivated by the occurrence of patelliform glands on the calyx of the species of *Adenocalymma* Mart. *ex* Meisn. According to R. J. Siebert (Ann. Missouri Bot. Gard. 35: 123–136. 1948), the presence of glands in the Bignoniaceae is a characteristic of great value for the separation of taxa within the family. For a better understanding (and possibly for future taxonomic use), I decided to study the structure of these glands, and also the anatomy of the calyx. *Adenocalymma comosum* (Cham.) A.P. DC. was chosen for two reasons: it is the type species of the genus and material is easily obtained in the State of Guanabara, Brazil.

The material used for this study corresponds to herbarium sheet *D. Sucre 6600* in the Rio de Janeiro Botanical Garden Herbarium (RB), collected in the Serra do Mendanha, State of Guanabara.

Fresh material was used for microchemical tests. Structural observations were made on fresh material fixed in FPA. This material was submitted to the usual dehydration methods and paraffin impregnation. Blocking and cutting with a rotating microtome (thickness of 14 μ) followed the Jung method. The material was stained with safranin-fast green and mounted in Canada balsam. The presence of sugar was confirmed by Fehling's solution (D. A. Johansen, *Plant Microtechnique*, New York & London, 1940). Using a binocular Zeiss microscope, the most important details were recorded in microphotography.



Figures 1–2. The calyx of *Adenocalymma comosum.*—1. Transverse section showing a patelliform gland. 57 ×.—2. Details of the calyx: A. Secretory cells of the gland. B. Quadrangular cells which unite the gland to the calyx. C. Parenchymatous cells of the mesophyll arranged similarly to palisade tissue, with the large nuclei apparent. D. Vascular bundles consisting essentially of sieve-tube members. 110 ×.

In transverse section, the calyx presents an abaxial epidermis consisting of rectangular or approximately isodiametric cells, with the greater diameter in the periclinal direction. The protective cuticle is thin. A dense covering of simple, uni- or multicellular hairs was observed, these either uniseriate, branched, or articulated. The presence of glandular hairs and stomata as well as patelliform glands at the base of the narrow lobes was also recorded. The adaxial epidermis consists of rectangular cells with a greater diameter in the periclinal direction, covered by a thin cuticle. Capitate glandular hairs were also observed. These trichomes, as well as the stomata, will be described separately when considering the epidermis. The region situated between the epidermis (mesophyll, see K. Esau, *Anatomia Vegetal*, Barcelona, 1959) consists of various layers of parenchyma cells. The thicker sections correspond to the region of the most developed vein or to the edges of the patelliform glands. These parenchymatous elements have irregular forms, and their walls are somewhat thickened with few intercellular spaces. Submerged in this tissue are the vascular bundles, consisting of spiraled xylem vessels and phloem elements (sieve-tube members and companion cells) wrapped by a parenchymatous sheath.

In frontal view, the abaxial epidermis of the calyx of *Adenocalymma comosum* (Cham.) A.P. DC. presents 4–6-sided, polygonal shaped cells with straight walls. The stomata are of the paracytic type. The adaxial epidermis in frontal view is made up of 5–6-sided cells, also approximately polygonal in shape, which are larger than those of the abaxial epidermis.

The simple hairs observed on the adaxial surface exhibit verrucose thickenings on the smooth cuticle. The unicellular hairs are usually elongate, sometimes with a curved tip (uncinate hair). They present verrucose thickenings on the cuticle of the basal cell. The bicellular hairs have, as a rule, verrucose thickenings on the cuticle of both the basal and apical cells. The pluricellular hairs have from 3 to 10 cells. All except the basal cell are provided with verrucose thickenings on the cuticle. They may be uniserate, branched, or articulated. The form and arrangement of the cells also varies.

The glandular hairs that occur on this epidermis are capitate. In transverse section, they present a bicellular base located in the plane of the epidermis and connected to the bilcellular "head" by a connecting cell (J. C. T. Uphof, Plant hairs. *In* K. Linsbauer, "Encyclopaedia of Plant Anatomy, Vol. 4, Histology." Berlin. 1962). In frontal view, a total of 12 cells can be seen. The capitate glandular hairs which occur on the abaxial epidermis are made up of a unicellular base, a unicellular "head" and one or two connecting cells. The patelliform glands are located in depressions on the epidermis. In frontal view, they are discoid in shape with a reticulate-thickened cuticle that becomes even more evident at the edge of the gland. In longitudinal section, they are made up of elongate cells, arranged like palisade tissue (secretory cells, E. Haberlandt, *Physiological Plant Anatomy*, London, 1928), some of them transversally divided. They have dense cell contents, large nuclei, and conspicuous nucleoli. They are connected to the calyx by quadrangular cells with conspicuous intercellular spaces. The protective cuticle is broken in some places, as a result of the expelling of excreted substances (see Haberlandt, *op. cit.*, and Esau, *op. cit.*).

In the region of gland implantation the epidermal cells of the calyx and also those of the mesophyll exhibit some modifications. These cells are much smaller than the others, with thin walls, dense cellular contents, and a well defined nucleus. The parenchymatous elements of the thin walled mesophyll are arranged in 3 or 4 layers, like palisade cells. Here, the vascular bundles consist essentially of sieve-tube elements that separate concentrated sugar solutions. Upon submitting the sections to Fehling's solution, the formation of abundant cupric oxide precipitate was observed, indicating the presence of sugars, not only in the cells of the glands, but also in the palisade cells of the mesophyll.

Due to their morphology and reaction of Fehling's solution (indicative of sugar presence), I conclude that the patelliform glands of the calyx of *Adenocalymma comosum* (Cham.) A.P. DC. carry out the function of nectaries.

I would like to thank Carlos Toledo Rizzini and Cecilia G. Costa for their guidance, Jorge Fontella Bereira for his help, Dorothy Dunn de Araujo for the translation, and laboratory technician Walter dos Santos Barbosa for his help in developing the photographs. This research received the support of the Conselho Nacional de Pesquisas (CNPq).—*Rose Claire Laroche, Instituto de Conservação da Natureza, Caixa Postal 3545, ZC 1600, Rio de Janeiro, G.B., Brazil.*

GIBSONIOTHAMNUS (SCROPHULARIACEAE) IN PANAMA

The species of the recently described genus *Gibsoniothamnus* L. Wms. (Fieldiana, Bot. 32: 211. 1970) are rarely collected and apparently highly endemic. Besides the three Panamanian species described here and *G. epiphyticus* (Standl.) L. Wms. of Costa Rica, the genus contains three species—*G. cornutus* (Donn. Sm.) A. Gentry, *G. mimicus* (Standl. & Steyerm.) L. Wms., and *G. moldenkeanus* (Standl.) L. Wms.—of Guatemala and adjacent Mexico.

The familial placement of this genus and its ally *Schlegelia* remains a matter of some conjecture as noted by Monachino (Phytologia 3: 102–105. 1949), Williams (Fieldiana, Bot. 32: 211. 1970) and Gentry (Fieldiana, Bot. 34: 55. 1971), among others. The four previously known species of *Gibsoniothamnus* were all described under *Clerodendron* in the Verbenaceae. One of these same species had also been described under *Schlegelia* of the Bignoniaceae. *Schlegelia* itself was described twice, first in Gesneriaceae (later transferred to Bignoniaceae) and again in Scrophulariaceae as *Dermatocalyx*; *Schlegelia* and *Dermatocalyx* were treated separately in such works as Bentham & Hooker's *Genera Plantarum* (1876), Baillon's *Histoire des Plantes* (1888, 1891), Engler and Prantl's *Natürlichen Pflanzenfamilien* (1894), and Standley's *Flora of Costa Rica* (Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1105, 1128. 1938).

Williams described *Gibsoniothamnus* in the Scrophulariaceae, pointing out that it has even more in common with that family than does *Schlegelia* and interpreted the new genus as evidence linking *Schlegelia* with Scrophulariaceae rather than Bignoniaceae. On the basis of a study of its placentation, Leinfellner (Oesterr. Bot. Zeit. 121: 13–22. 1973) likewise interprets *Schlegelia* itself as agreeing better with Scrophulariaceae than with Bignoniaceae. The ovary of *Gibsoniothamnus* is completely bilocular with a single central placenta in each locule and clearly fits Scrophulariaceae better than Bignoniaceae. Its small angulate seeds lack foliaceous cotyledons and are completely unlike the seeds of Bignoniaceae but quite acceptable for Scrophulariaceae. On the other hand the woody habit, opposite leaves and close relationship to *Schlegelia* which has been traditionally treated as Bignoniaceae suggest that family. The calyces of several species of *Gibsoniothamnus* closely resemble those of *Capsicum chacoense* Hunz. and its allies and have led to confusion with Solanaceae, as has a superficial similarity to some species of *Witheringia*. *Gibsoniothamnus* also resembles some species of *Lisianthus* (Gentianaceae) to some extent. As an indication of the problems involved, it might be noted that specimens of *G. latidentatus* in the Missouri Botanical Garden herbarium have been referred to at least the five different families mentioned above (Verbenaceae, Scrophulariaceae, Bignoniaceae, Gentianaceae, and Solanaceae) during routine curatorial work, surely some kind of a record in taxonomic confusion.

The Panamanian collections of *Gibsoniothamnus* belong to the following three new species.

1. **Gibsoniothamnus allenii** A. Gentry, sp. nov.

Frutex epiphyticus. *Ramuli* acute tetragoni, glabri. *Folia* elliptica, acuta, late cuneata, subcoriacea vel coriacea, plerumque glabra, integra, margine revoluto, venis secundariis super impressis, infra acute elevatis, domatiis axillaribus ciliatis. *Flores* in bracteatis fasciculis dispositi, bracteis subulatis plus minusve glabris. *Calyx* cupulatus, 5-dentatus, plerumque glaber, dentibus subulatilinearibus 4–6 mm longis. *Corolla* tubulosa, extus glabra, intus lepidota, lobis sparsim ciliatis. *Stamina* quatuor. *Pistilum* 1.6 cm longum, ovario sphaerico, placentatione axili. *Fructus* baccatus, sphaericus, calyce expanso ⅔ obtectus, seminibus numerosis, parvis.

Epiphytic *shrub* 1–2 mm tall. *Branchlets* acutely tetragonal, the angles slightly winged, glabrous. *Leaves* elliptic, 2–8 cm long and 1–3 cm wide, acute, the base broadly cuneate, coriaceous or subcoriaceous, mostly glabrous, sometimes with a few trichomes on median nerve below, with well-developed ciliate axillary domatia below, gland-dotted below, especially toward base, the margins entire, more or less revolute, drying dark above, olive below, secondary veins 1–3 on each side, impressed above, usually raised below, the basal pair ascending more strongly, tertiary veins not evident; petiole 4–10 mm long, glabrous or rarely with a few trichomes. *Inflorescence* a bracteate fascicle, the bracts subulate, 3–8 mm long, mostly glabrous or inconspicuously lepidote, often with a few trichomes mostly along edges or at tip, pedicels to 1.7 cm long at anthesis, to 3 cm long in fruit, glabrous or very slightly lepidote toward apex. *Calyx* cupular, 5-setate, glabrous or with a few scattered trichomes or lepidote scales, 3–4 mm long (not including teeth) and 3–4 mm wide, the setae linear, 4–6 mm long. *Corolla* magenta, tubular, 1.7–1.9 cm long and 2–3 mm wide, the 5 lobes rounded, ca. 2 mm long; glabrous without, sparsely ciliate on lobes, stalked lepidote within on lobes and upper part of tube, pubescent at level of stamen insertion. *Stamens*

4, ca. 1.3 cm long, the staminode 2–3 mm long; insertion 4–5 mm from base of corolla tube. *Pistil* 1.6 cm long, style 1.5 cm long, stigma capitate, ovary depressed globose, 1 mm long, 1.5 mm in diameter, bilocular, the ovules 4–7 seriate on a single central placenta in each locule. *Fruit* a spherical berry to at least 5 mm in diameter, the lower ⅔ covered by the expanded calyx which reaches (without teeth) 4 mm by 8 mm in fruit, the seeds numerous, small, angulate.

Panama. coclé: Top of Cerro Pilon, flowers magenta, 13 Apr. 1971 (fl, frt), *Gentry 758* (mo, holotype).

This species is only known from the premontane rain forest like zone above El Valle, Panama.

Panama. coclé: Vicinity of El Valle de Antón: epiphytic shrub, flowers rose, N rim (wet), 21 May 1939 (fl), *Allen 1824* (mo). Vicinity of La Mesa, 1000 m, epiphytic shrub, much branched, the branches 2 m long, stems square, flowers pinkish lavender, 12 Apr. 1941 (fl, frt), *Allen 2385* (mo). El Valle de Antón, epiphytic shrub, 2 m, flowers dark purple, 1000 m, 16 Mar. 1946 (fls), *Allen 3414* (mo).

This species was included with *G. epiphyticus* of Costa Rica by Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 168. 1940) under his *Clerodendron epiphyticum* on the basis of a fragmentary Panamanian collection (*Allen 1824*), bearing a single partially destroyed calyx. Additional material shows that the plant of central Panama differs from that of central and northern Costa Rica in such important characters as glabrous (rather than pubescent) young branchlets, pedicels, calyces, and leaves, and strongly tetragonal (rather than subterete) stems with the raised margins more or less winged.

2. **Gibsoniothamnus pterocalyx** A. Gentry, sp. nov.

Frutex epiphyticus vel scandens. *Ramuli* plus minusve teretes, glabri. *Folia* elliptica, acuta, cuneata, chartacea vel subcoriacea, glabra, integra, margine plano, venis secundariis leviter elevatis super et infra, interdum domatiis axillaribus. *Flores* axillares, singulares vel gemini, pedicellis glabris. *Calyx* (in fructu juveni) cupulatus, 5-dentatus, glaber, dentibus subulati-linearibus, 5–6 mm longis atque alis in calyce extensis. *Corolla, stamina,* et *pistillum* ignota. *Fructus* juvenis baccatus, subglobosus, basi calyce expanso tectus.

Woody *epiphyte* or liana. *Branchlets* irregularly terete to subangulate, glabrous. *Leaves* elliptic, acute, cuneate at base, chartaceous to subcoriaceous, glabrous above and below, sometimes with ciliate domatia in axils of lower secondary nerves, gland-dotted below, the margin entire, very slightly or not at all revolute, drying dark olive above, light olive below, secondary veins 2–3 on each side, very inconspicuously raised above and below, the basal pair not noticeably more strongly ascending, tertiary veins not evident; petiole ca. 5 mm long, glabrous. *Inflorescences* of 1–2 axillary flowers, the pedicels glabrous, 2–2.5 cm long (in young fruit). *Calyx* (in young fruit) cupular, 5-setate, glabrous or very slightly lepidote, 2 mm long (not including teeth) and 3 mm wide, the teeth linear, laterally compressed, 5–6 mm long, extending down the calyx as 5 conspicuous lateral wings. *Corolla, stamens,* and *pistil* unknown. Young *fruit* a subglobose berry, 3 mm in diameter, its base covered by the patelliformly expanded calyx.

Panama. chiriquí: Woody epiphyte or liana, calyx greenish white, fruits green; denuded premontane rain forest between Pinola and Quebrada Seco on Chiriquicito-Calder Trail, 21 Apr. 1968, *Kirkbride & Duke 1020* (MO, holotype).

Known only from the rather unsatisfactory type collection, this species is nevertheless well demarcated by its winged, glabrous calyces, laterally compressed calyx teeth, relatively thin leaves with the secondary veins not impressed above or conspicuously raised below, and more or less terete branchlets. Its one or two flowered inflorescences, if constant, are another conspicuous distinguishing characteristic.

3. **Gibsoniothamnus latidentatus** A. Gentry, sp. nov.

Frutex vel arbor parva, saepe epiphyticus. *Ramuli* acute tetragoni, plus minusve glabri. *Folia* elliptica, acuta, late cuneata, coriacea, plerumque glabra, integra, margine revoluto, venis secundariis super impressis, infra acute elevatis. *Flores* in bracteatis fasciculis vel paniculis valde contractis dispositi, bracteis subulatis strigosis, pedicellis glabris. *Calyx* cupulatus, 5-dentatus, plus minusve glaber, dentibus anguste triangularibus, acutis, 2–4 mm longis. *Corolla* tubulosa, 2.2–3.2 cm longa, extus glabra, intus lepidota, lobis ciliatis. *Stamina* quatuor. *Pistilum* 2.6 cm longum, ovario sphaerico, placentatione axili. *Fructus* baccatus, sphaericus, calyxe expanso inclusus, seminibus numerosis, parvis.

Shrub or small tree to 5 m, sometimes climbing, often epiphytic. *Branchlets* acutely tetragonal, the angles slightly winged, glabrous or with a few appressed simple trichomes at uppermost nodes. *Leaves* elliptic, 4–10 cm long and 2–4.5 cm wide, acute, the base broadly cuneate, coriaceous, glabrous above, mostly glabrous below, sometimes with a few trichomes along main veins and in axils of lateral nerves, without domatia, gland-dotted below, especially toward base, the margin entire, revolute, drying dark above, olive below, secondary veins 2–3 on each side, impressed above, sharply raised below, the basal pair ascending most strongly, tertiary veins not evident; petiole 5–13 mm long, sparsely strigose or glabrate. *Inflorescence* a bracteate fascicle or strongly contracted panicle, the bracts subulate, 1–2 mm long, sparsely strigose, peduncles 0–5 mm long, pedicels elongating to 2.5 cm at anthesis and 4 cm in fruit, glabrous, or slightly lepidote. *Calyx* cupular, 5-dentate, glabrous or very sparsely lepidote or strigose, 12–16 mm long (including teeth) and 5–6 mm wide, the teeth narrowly triangular, acute, 2–4 mm long. *Corolla* magenta, tubular, 2.5–3.2 cm long and 3–4 mm wide, the 5 lobes rounded, ca. 2 mm long, glabrous without, the lobes ciliate, stalked lepidote within on lobes and upper part of tube. *Stamens* 4, anthers very slightly divergent, the thecae 1–1.5 mm long and almost 1 mm wide, the filaments 1.8–2.0 cm long, the staminode 4–5 mm long; insertion 6–7 mm from base of corolla tube. *Pistil* ca. 2.6 cm long, style 2.4–2.5 cm long, stigma subcapitate, ovary globose, 1.5–2 mm in diameter, glabrous, bilocular, the ovules 5–8 seriate on a single central placenta in each locule. *Fruit* a spherical fleshy berry to at least 7 mm diameter, completely enclosed by the expanded calyx which reaches 18 mm by 10 mm in fruit; seeds numerous (ca. 30), small, angulate.

PANAMA. PANAMÁ: Cerro Jefe to Altos de Pacora; shrub along road near Cerro Jefe; flowers tubular, magenta, 15 Apr. 1971 (fl) *Gentry 759* (MO, holotype).

This species has been collected only near the summit of Cerro Jefe in the premontane rain forest life zone.

PANAMA. PANAMÁ: Cerro Jefe, summit, 2900 ft., epiphyte, shrub to 4 ft., flowers fuschia-colored, waxy, 12 Mar. 1967 (fl), *Dwyer et al. 7293* (MO); forest edge and road bank, shrub 15 ft., perianth china purple, berry green, 29 Jul. 1967 (frt), *Dwyer & Gauger 7351* (MO); shrub 1.5 m, pedicels and calyces red-violet, 23 Jun. 1972 (frt), *Croat 17343* (MO); vine, 19 Jul. 1967 (frt), *Kirkbride & Crebbs 27* (MO).

Gibsoniothamnus latidentatus is easily recognized by its triangular (not linear-subulate) calyx teeth. It is probably most closely related to *G. allenii* which likewise has winged-tetragonal branchlets, but it differs from that species in lacking axillary domatia, in a usually less congested inflorescence, in longer pedicels, and in the usually larger calyx which completely covers the fruit as well as in its triangular calyx teeth.

One additional specimen which is probably referable to *Gibsoniothamnus* remains unidentified. This is *Duke 15657*, from Cerro Pirre, Darién Province. It includes only a twig, unattached leaves and part of a single fruit. The leaf texture is relatively thin and the stems are not tetragonal, indicating possible relationship with *G. pterocalyx*.

The Costa Rican and Panamanian species of *Gibsoniothamnus* can be readily separated by the following key.

1. Branchlets more or less terete or subangulate.
   2. Calyx pilosulus, the teeth compressed parallel to the calyx, sometimes continued as lines on calyx, inflorescence a fascicle of several flowers; secondary veins impressed above, conspicuously raised below; Costa Rica .... *G. epiphyticus*
   2. Calyx glabrous, the teeth laterally compressed, continued as wings on calyx; inflorescence of 1 or 2 flowers; secondary veins slightly or not at all raised above and below; Panama .... *G. pterocalyx*
1. Branchlets sharply tetragonal with the angles conspicuously raised.
   3. Calyx teeth linear-subulate; pedicels to 1.7 cm at anthesis and 3 cm in fruit; leaves with axillary domatia; calyx covering lower two thirds of fruit, to 4 mm long (not including teeth) in fruit .... *G. allenii*
   3. Calyx teeth triangular; pedicels to 2.5 cm at anthesis and 4 cm in fruit; leaves without domatia; calyx completely covering fruit, 10–15 mm long (not including teeth) in fruit .... *G. latidentatus*

—Alwyn H. Gentry, Missouri Botanical Garden.

EASTERN POPPIES

". . . We observ'd in the Fields about this City a very fine Species of *Poppy*, which the *Turks* and *Armenians* call *Aphion*, as they do the *common Opium*: yet they do not extract Opium from the Kind we now speak of; but by way of delicacy they eat the Heads of it when they are green, tho very acrid, and of a hot Taste.

". . . Each Stalk commonly supports but one Flower, the Button whereof, which is eighteen or twenty lines long, is cover'd with a Cup consisting of two or three membranous Leaves, hollow, whitish towards the edge, bristling with Hairs. They fall when the Flower blows, and then you perceive that is consists of from four to six Leaves, two inches and a half long, and three and a half broad, rounded like those of other Poppies, and of the Colour of the wild Poppy, more or less deep, with a great spot, which is also more or less obscure. . . . This fine Species of Poppy is mightily pleas'd with the King's Garden, nay, and with *Holland* too, where we have communicated it to our Friends. M. *Commelin*, a very able Professor of Botaniks at *Amsterdam*, has publish'd the Figure of it." (*A Voyage into the Levant* . . . . By M. Tournefort . . . Chief Botanist to the late *French* King, *&c.* London. 1718.)

The plant which Tournefort described from near Artze-rum (or Erzerum) has been identified as *Papaver pseudo-orientale* (Fedde) Medw. The plate published by C. Commelin (*Horti Medici Amstelædamensis.* 1706) was drawn by P. Sluyter and has been identified as *P. orientale* L. A portion of this plate is reproduced on the banner of this issue of the ANNALS.—*Editor.*

THE SEVENTH ANNUAL JESSE M. GREENMAN AWARD

The 1974 Greenman Award was presented to Ihsan A. Al-Shehbaz, University of Baghdad, for the publication "The biosystematics of the genus *Thelypodium* (Cruciferae)" (Contr. Gray Herb. 204: 3–148. 1973.)

The Award of $200 is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the best paper in plant systematics based in a doctoral dissertation published during the *previous* year. Papers published in *1974* are now being considered for the 1975 award. Reprints of such papers should be sent to Alwyn H. Gentry, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110 U.S.A., *before* 1 May 1975.—*Editor.*

The previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 60, No. 3, pp. 573–980, and Vol. 61, No. 1, pp. 1–263, were issued on 3 July 1974 and 8 August 1974, respectively.

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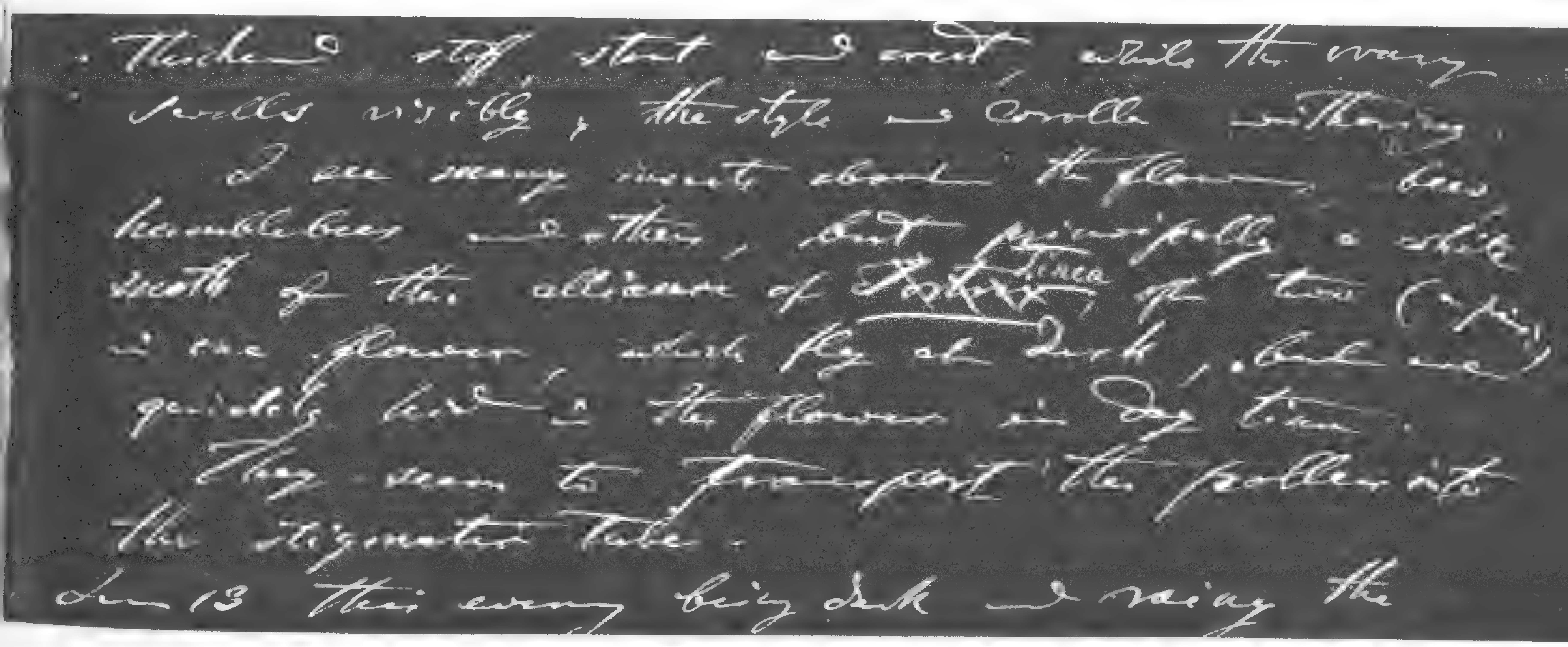

thickened, stiff, stout and erect, while the ovary
swells visibly, the style and corolla withering.
I see many insects about the flowers, bees,
humblebees and others, but principally a white
moth of the alliance of ~~Tortrix~~ Tinea, [illegible] two (in pairs)
in one flower, which fly at dusk, but are
quietly hid in the flowers in day time.
They seem to transport the pollen into
the stigmatic tube.
Jun 13 this evening being dark and rainy the

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The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden. Papers originating outside the Garden will also be accepted. Authors should write the editor for information concerning preparation of manuscripts and page charges.

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ANNALS
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ANGIOSPERM BIOGEOGRAPHY AND PAST CONTINENTAL MOVEMENTS[1]

PETER H. RAVEN[2] AND DANIEL I. AXELROD[3]

The isolation of land areas by sea-floor spreading, the uplift of new cordilleras, the emergence of new archipelagos and the disappearance of old ones, and the shifting positions of (some) land-masses have both created and destroyed environments to which biota have responded. In this sense, changing physical environments governed by plate tectonics have had a major role in evolutionary history. Plate tectonic theory thus provides a more reliable basis for analyzing changes in land-sea relations and changes in climates, and hence for interpreting problems of evolution and distribution, than has been available earlier. The reappraisal of the nature of the earth's crust by plate tectonic theory does not require any modifications of previously established major principles of evolution. However, it does demand that we recognize certain new principles of biogeography (McKenna, 1973). Lands may be rafted across latitudinal belts of climate which may lead to *a*) widespread impoverishment of the biota (India), *b*) new opportunities for change (arid flora of Australia), or *c*) lead even to the total decimation of a rich biota (Antarctica). Since moving plates may carry ancient biota

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We are grateful for the support, individually received, of varied grants from the National Science Foundation which have provided us with a background sufficiently diverse and complementary to have aided immeasurably in the present study. Carla Lange has provided expert and efficient bibliographical help during all aspects of the preparation of the paper.

Reprints of this paper may be obtained by sending $3.50 to BIOGEOGRAPHY, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

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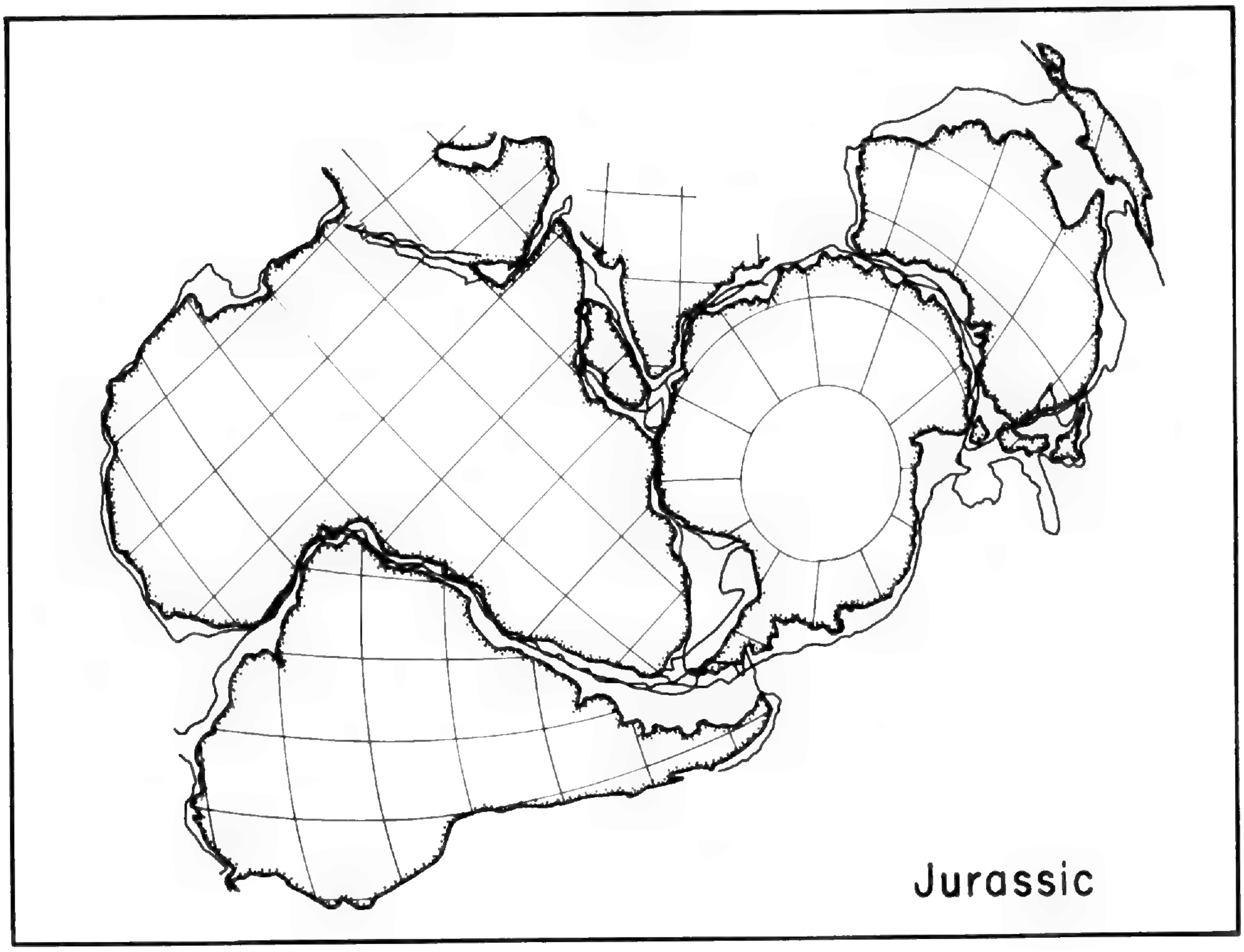

FIGURE 1. Fit of the Gondwana continents during the Jurassic, prior to breakup (after Smith & Hallam, 1970).

far from the area in which they lived, reconstructions of ancient biotic zones and climates must take cognizance of such changes

In the present paper, we examine the distributions of flowering plants, present and past, and attempt to interpret them in the light of newly available geological evidence. Although the field is vast, and we have been unable to provide a comprehensive survey of the available facts, we believe that an overview of angiosperm distributions in the light of geological history as now suggested by plate tectonic theory will be useful in suggesting new hypotheses and new directions for future research.

First, we shall review geological evidence as it pertains to certain areas that we believe were of prime importance to the evolution of flowering plants. Second, we shall review our current state of knowledge about the biogeography and history of the vertebrates of South America, critical for understanding the possibilities for migration between South America and other continents prior to the Miocene. Third, we shall attempt to interpret, insofar as possible, the timing of evolutionary radiation in the angiosperms so as to ascertain relative ages for some of the taxa. Fourth, we shall review the present distributions of the orders, families, and some infrafamilial groups of angiosperms, with selected references to the paleobotanical literature where we believe these to be useful. Fifth, we shall outline the broad patterns of angiosperm migration in the past, and interpret

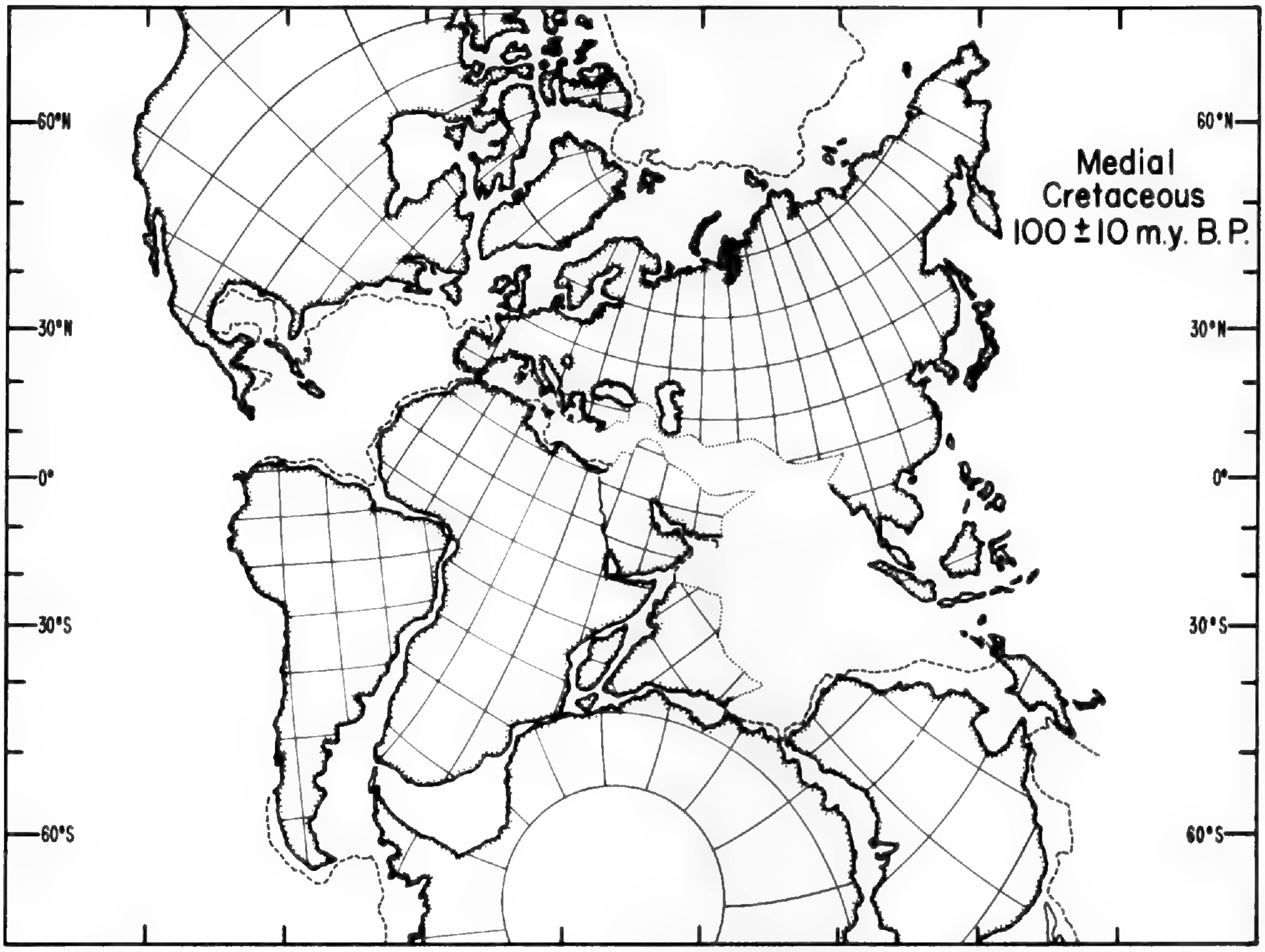

FIGURE 2. Relative positions of Laurasia and Gondwanaland in the medial Cretaceous (~ 100 ± 10 m.y. BP) (from Smith, Briden & Drewry, 1973). Note that the connection between South America and Antarctica was linear, having been deformed to make the Scotia Arc since the Cretaceous (Dalziel *et al.*, 1973).

the relationships between these patterns and the age of the respective taxa. Finally, we shall address ourselves to the question of the place of origin of the angiosperms in the light of this knowledge.

GEOLOGICAL BACKGROUND

OPENING OF THE INDIAN OCEAN

We start with a Jurassic Gondwanaland configuration like that presented by Smith and Hallam (1970; Fig. 1) or Tarling (1972). The formation of the Indian Ocean began with the rotation of Africa (with India) away from South America and the movement of Antarctica (with Australia) into a more polar position. The opening of the South Atlantic, reviewed below, began 125–130 m.y. BP. Sediments recently drilled from the ocean floor west of Australia indicate that the eastern Indian Ocean is about 150 m.y. old (Heirtzler *et al.*, 1973, footnote 13). If India was ever immediately adjacent to Australia, it separated at this time and moved westward for 80 m.y. As reviewed below, India certainly remained connected to Madagascar and Africa until at least 100 m.y. BP. Current evidence does not indicate with any degree of certainty the time of separation of Africa-Madagascar-India from Antarctica. However, in view of the configuration of the Indian Ocean 75 m.y. BP (Laughton *et al.*, 1973; Fig. 3), more or

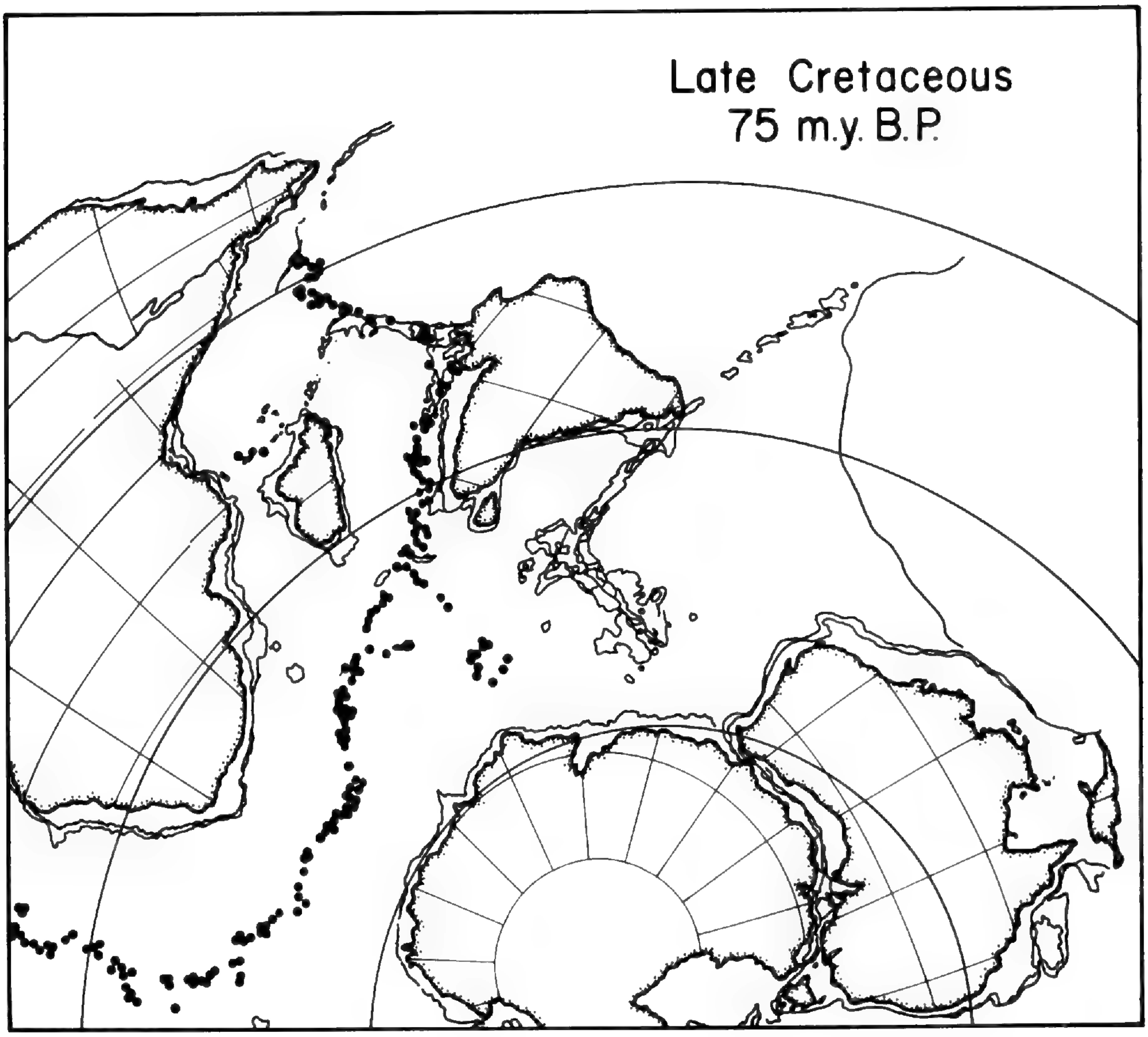

FIGURE 3. Relations between East and West Gondwanaland in the Late Cretaceous (~ 75 m.y. BP), according to McKenzie and Sclater (1971).

less direct migration between Africa and Australia *via* East Antarctica was possible into mid-Cretaceous time (Fig. 2, Smith *et al.*, 1973; see also Jones, 1972). Even if the land masses were somewhat more separated at that time, plant migration would have been easy *via* volcanic islands on mid-ocean ridges. Epicontinental seas apparently had spread around the southern and eastern coast of Africa to Madagascar by the earliest Cretaceous (Dingle, 1973), but Madagascar and India were still attached and formed a more or less continuous bridge to Antarctica and Australia into the mid-Cretaceous (Fig. 2). The initial rifting of Africa from South America, at about the start of the Cretaceous, presumably sets a limit for the earliest date for the separation of Africa-Madagascar-India from East Antarctica. See Addendum, Sclater and Fisher (1974).

Madagascar has not moved significantly relative to mainland Africa (Green, 1972; Kent, 1972), and evidently has been separated from it for as much as 100 m.y. (Simpson *et al.*, 1972; see also references summarized in McKenna, 1973). Thus many of the plants and animals of Madagascar apparently reached it across a water barrier after the mid-Cretaceous, as hypothesized by Darlington (1957).

On the other hand, the presence of sauropods in the Upper Cretaceous of Madagascar, with the genus *Laplatasaurus* reported in India and Madagascar in addition to South America, and the presence of carnosaurs also in the Upper Cretaceous of Madagascar (Charig, 1973) negates Simpson's (1973) view that Madagascar has been separated from the mainland of Africa since the Permian. A modern review of the sauropods would be highly desirable. It is possible, as reviewed by Cracraft (1973*c*) that India and Madagascar remained joined longer than Madagascar and Africa.

Another event of biogeographic significance is the separation of New Zealand and New Caledonia from Australia, 80 m.y. BP (summary in Raven & Axelrod, 1972). Evidently the entire Campbell Plateau region, including New Caledonia and New Zealand, had reached approximately its present position by Paleocene time, and only subsequently did Australia begin to separate from Antarctica (Houtz *et al.*, 1973; Hayes & Ringis, 1973). Normal oceanic crust began to form between the Australian and Antarctic continents about 55 m.y. BP (Weissel & Hayes, 1972; Kennett *et al.*, 1972), with the separation of the continental margins of Australia and Antarctica taking place 49 m.y. BP (McGowran, 1973). More or less direct migration through the Tasmanian area may have been possible for perhaps another 10 m.y., especially since the South Tasman Rise is now known to be continental (Houtz *et al.*, 1973; Kennett *et al.*, 1973). Present features along the Scotia Arc developed from a linear Late Cretaceous trend (Anonymous, 1972; Adie, 1972; Dalziel *et al.*, 1973), though the initial break between the Antarctic Peninsula and Tierra del Fuego, if they were ever joined (Katz, 1973), probably occurred before the Late Cretaceous (Dalziel *et al.*, 1973). The water around Antarctica was cool temperate by Late Oligocene time (Hayes *et al.*, 1973), and glaciation in Antarctica is now known to have begun at least 20 m.y. BP (Hayes *et al.*, 1973), if not earlier, with a major increase in the icecap to continental extent about 4–5 m.y. BP. There may also have been episodes of glaciation in Paleogene time (Margolis & Kennett, 1971; Denton, Armstrong & Stuiver, 1971: 271–278). More or less direct migration *via* Antarctica between Australia and South America may have continued well into the Oligocene, and was certainly possible in Eocene time (Raven & Axelrod, 1972).

It is unlikely that any portion of Southeast Asia or Indonesia was once a part of Gondwanaland and moved north, since paleontological and geological evidence contradicts such a pattern of drift (Tarling, 1972; Audley-Charles *et al.*, 1972; Stauffer & Gobbett, 1972; Ridd, 1972; Griffiths & Burrett, 1973). Not until mid-Miocene time was the migration of Asian plants and animals into Australasia relatively direct (Raven & Axelrod, 1972; Audley-Charles *et al.*, 1972).

India, which commenced its northward motion about 100 m.y. BP, now appears to have collided with Asia by the Middle Eocene (Powell & Conaghan, 1973), and there are mammal faunas of obviously Laurasian character in the Lower Upper Eocene of the Murree Hills (Ranga Rao, 1971, 1972). The extensive crustal shortening and fracturing of the region, as well as the upthrust of the Himalayas, belongs to the second phase of development of the region, commencing in the Miocene and reaching its strongest phase in Plio-Pleistocene time (Gansser, 1964, 1966; Laughton *et al.*, 1973; McKenzie & Sclater, 1973; Powell &

Conaghan, 1973). The presumed Lower Eocene Deccan Intertrappean floras reviewed by Lakhanpal (1970) may represent mixtures of groups that have come from the north (such as, perhaps, Datiscaceae) with those that were derived from the south, and the flora of peninsular India was progressively enriched from mid-Tertiary time onward with northern, predominantly tropical groups of angiosperms, such as Dipterocarpaceae (Axelrod, 1971).

To summarize for the lands around and east of the Indian Ocean, the following estimates are the last dates at which more or less direct migration may have been possible: 1) between West Gondwanaland and Australia, 110 ± 10 m.y. BP; 2) between Africa and Madagascar, about 100 m.y. BP; 3) between Australia-Antarctica and New Zealand or New Caledonia, 80 m.y. BP; 4) between Australia and South America *via* Antarctica, 45 m.y. BP. Direct communication between West Gondwanaland and India may have ceased about 100 m.y. BP, and direct communication between India and Asia was initiated about 45 m.y. BP.

CONNECTIONS OF AFRICA WITH OTHER CONTINENTS

The Atlantic Ocean began to open with the rotation of Africa and South America away from North America in the Early Jurassic (180 m.y. BP; Dietz & Holden, 1970; Pitman, Talwani & Heirtzler, 1971; Pitman & Talwani, 1972; Phillips & Forsyth, 1972; Walper & Rowett, 1972; Dewey *et al.*, 1973). Prior to this, Africa was also broadly connected with southwestern Europe (Smith, 1971). Beginning 148 m.y. BP and continuing until 80 m.y. ago, Africa rotated counterclockwise relative to Europe (Dewey *et al.*, 1973). During the interval 80–53 m.y. BP Africa continued its counterclockwise motion but also moved westward relative to Europe, with compressive components indicating connections until 63 m.y. BP, following which relative motion was almost entirely east-west strike-slip (Dewey *et al.*, 1973). In the Early Paleocene, Africa and Europe were connected *via* Spain. Africa may also have been connected broadly with Asia through Arabia at this time (Cooke, 1972). From the Early Paleocene (63 m.y. BP) into the Upper Eocene (53 m.y. BP), Africa and Europe seem to have become more widely separated (Dewey *et al.*, 1973, figs. 16–17), with convergence resulting in direct connection some 17 m.y. ago (Cooke, 1972; Hallam, 1973*a*; Dewey *et al.*, 1973). Following reestablishment of direct connections between Africa and Eurasia, many northern groups of plants and animals reached Africa, and many African taxa—for example, proboscideans and catarrhine primates—entered Eurasia.

RELATIONS WITHIN LAURASIA

As recently summarized by McKenna (1973), the European Plate (including Greenland) began to separate from the North American Plate in the Late Cretaceous (~ 81 m.y. BP; Laughton, 1971; Smith, 1971; Heirtzler, 1973), with spreading rapid until the Late Eocene and still continuing. Both the North American Mid-Continent Seaway and the Asian Turgai Strait divided the Laurasian landmass, and the Bering Strait was at a higher paleolatitude (~ 75°N) than at present. By 50 m.y. BP, direct migration was still possible across the North Atlantic, and the North American Mid-Continent Seaway had disappeared by 60 m.y. BP. Since the Bering Strait was at a higher latitude, migration between Eurasia and North America across the North Atlantic was probably the main route of communication between these landmasses. Direct overland migration across the North Atlantic was possible for land vertebrates until 49 m.y. BP (McKenna, 1972), but cool temperate conifer-hardwood forests continued to occupy Iceland during the Neogene, providing an interrupted pathway between America and Europe into the early Quaternary (Schwarzbach & Pflug, 1957). Migration *via* the Bering Straits became relatively more important for land vertebrates as the North Atlantic widened and as the latitude of the Bering Straits decreased.

RELATIONS OF SOUTH AMERICA WITH AFRICA

In the South Atlantic, separation seems to have commenced 125–130 m.y. BP (Maxwell *et al.*, 1970b; Wright, 1971; Francheteau & Le Pichon, 1972; Mascle & Phillips, 1972; Phillips & Forsyth, 1972; Heirtzler, 1973; Francheteau, 1973; Anonymous, 1973; Larson & Ladd, 1973). The final marine connection associated with the spreading apart of Africa and South America took place slightly less than 100 m.y. BP (Reyment, 1969, 1972; Reyment & Tait, 1972; Douglas *et al.*, 1973), with the continents remaining in near contact along strike-slip faults until at least 90 m.y. BP (Le Pichon & Hayes, 1971; Grant, 1971, 1972), when northeast Brazil (Sergipe) and Africa (Gabon) were separated by only a narrow strait. At the close of the Cretaceous, about 800 km probably separated Africa and South America at their closest points. However, they were still linked by numerous islands which existed along the Mid-Atlantic Ridge and its flanks at that time (*e.g.* see Klerkx & de Paepe, 1971; Addendum: Anonymous, 1974).

RELATIONS BETWEEN NORTH AND SOUTH AMERICA

Relationships between the American continents during the Cretaceous Period are of great biogeographic interest. Many extant groups of organisms originated and expanded greatly during this period, and the opportunities they had for migration between the Americas have long been a subject of discussion.

North and South America have converged at least from the mid-Cretaceous to the early Cenozoic (Dietz & Holden, 1970; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972). In the following remarks, however, they will be considered to have remained in their present positions, which represents a minimum estimate of distance, and therefore of ease of migration.

During most of the Cretaceous, about 3,000 km seems to have separated the southern continental margin of North America (in Oaxaca) from the continental margin of South America (the Guyana Shield; Fig. 4; Dengo, 1973). This exceeds the present distance (about 2,500 km) between Freetown, Sierra Leone, and Recife, Brazil. South America was joined to Africa until somewhat less than 100 m.y. BP, while North America was moving to the northwest; therefore, 3,000 km must be a minimum distance even if North and South America were still moving apart (*cf.* Freeland & Dietz, 1971), at least for the Early Cretaceous.

It is well established that the entire Atlantic and Gulf Coastal Plain, including Florida, was submerged in the Late Jurassic and continued to receive sediment

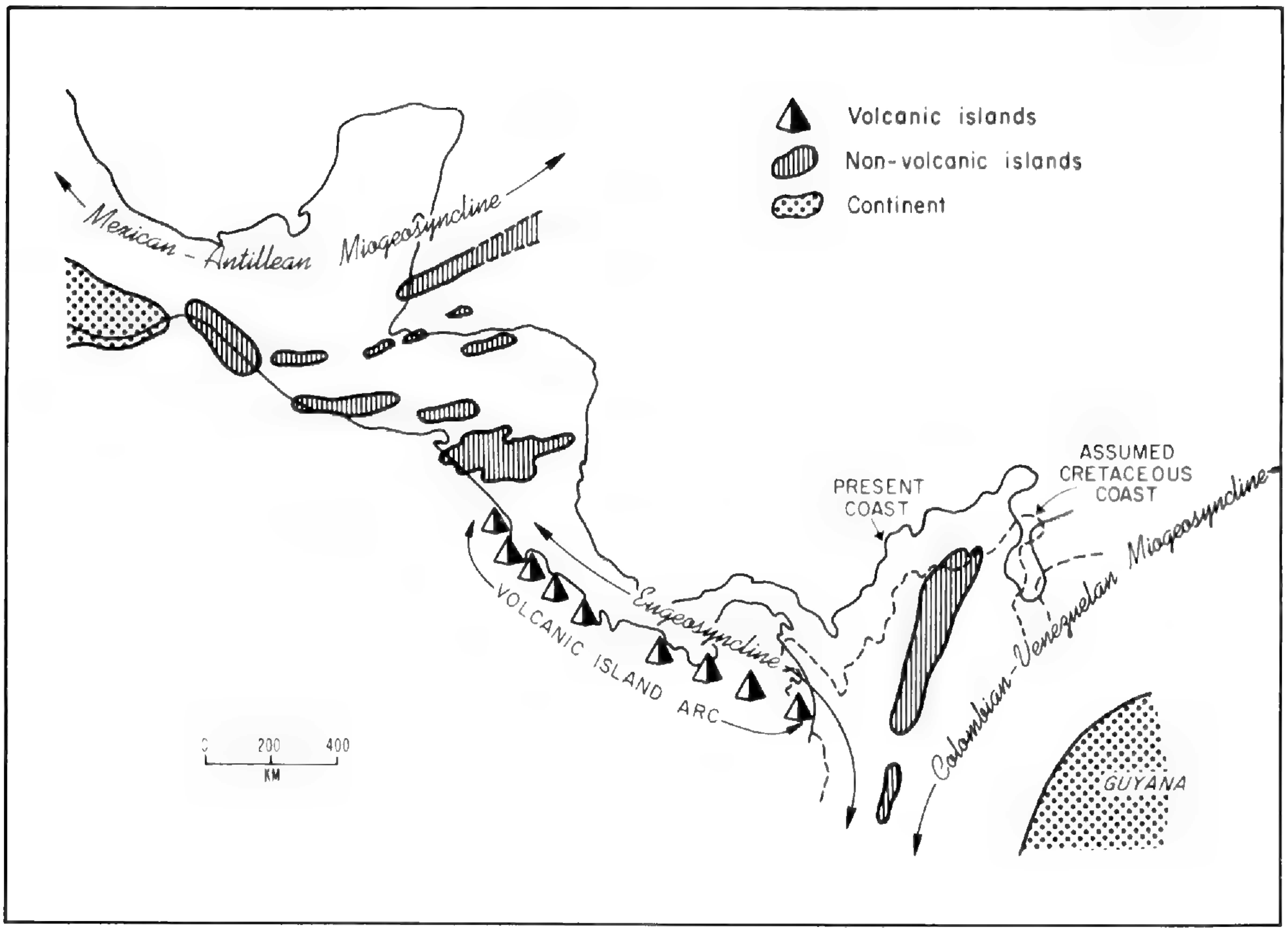

FIGURE 4. Paleogeographic relations between Central and South America in the Late Cretaceous (after Dengo, 1973).

from the Appalachians during Cretaceous and most of Tertiary time (King, 1951; Rodgers, 1970). By the Late Jurassic the distance between land at the southeastern margin of the Appalachians and the small islands along the chain of the Greater Antilles, probably was at least 1,000 km. This diminished only in the Oligocene when portions of the Coastal Plain, including Florida, began to emerge for the first time since the Jurassic (Cooke, 1945; James, 1961; Wilhelm & Ewing, 1972).

In the Late Cretaceous (Fig. 4), scattered and perhaps large continental islands were in the region of Nuclear Central America, including the Maya Mountains of Belize (Dengo & Bohnenberger, 1969) and the northern Cordillera Central in Colombia, itself probably an island. They were linked by scattered, small volcanic islands at the present site of southern Central America (Fig. 4). There also may have been a chain of scattered volcanic islands along the Greater Antilles and Lesser Antilles, leading to the continental margin of South America.

In evaluating whether this interrupted arc was an important dispersal path between North and South America, the distribution of land to the north must be borne in mind. As noted above, the southeastern margin of the Appalachians comprised the southeasternmost exposed land in North America throughout Cretaceous and Paleocene time and was separated by some 1,200 km of ocean from the volcanic islands of the Greater Antilles. The portion of North America nearest the Greater Antilles might have been an island near Honduras, itself a minimum of 650 km from Jamaica and Cuba. Apart from sea-drift moving northward, scattered small islands in the Bahaman area would have enabled some long-distance migration *via* island stepping stones.

A general period of uplift at the close of the Cretaceous resulted in Nuclear Central America and the northern Andes somewhat approaching their modern configuration. From then until the start of the Miocene, migration between North and South America would have been *via* volcanic islands spanning some 1,300 km between northern Nicaragua and northern Colombia. Following the Late Eocene uplift of Yucatán, and the Oligocene uplift of the southern Atlantic Coastal Plain, interrupted migration could have occurred between North and South America *via* the West Indies. On geological grounds, this has not been as important at any time as has migration *via* Central America, and it has never been more direct than it is at present. Uplift of southern Central America that commenced in the Miocene, and continuing volcanism, gradually led to the union of North and South America about 5.7 m.y. BP.

Since the final separation of South America and Africa took place about 100 m.y. BP, and the present distance between them is about 2,500 km, it can be calculated that in the Early Eocene, South America was about equally distant from Africa and North America. Earlier, opportunities for immigration from Africa were greater; later, the connection with and possibility for immigration to North America became more direct.

The Caribbean and its Borderlands.—The geologic history of this region is exceedingly complicated and not well understood, yet it seems desirable to present a general digest of events there so that some of the historical relations of biota in the region can be evaluated more accurately.

The Caribbean Sea and Gulf of Mexico formed during the period 180–105 m.y. BP as North America moved away from South America and Africa (Freeland & Dietz, 1971, 1972; Malfait & Dinkelman, 1972; Phillips & Forsyth, 1972; Walper & Rowett, 1972). Caribbean crust probably formed *in situ*, and not as an extension of the older Pacific crust (Phillips & Forsyth, 1972; Kesler, 1973). Freeland and Dietz (1972) indicate that the formation of the Caribbean Sea began about 135 m.y. BP. By the end of the Early Cretaceous, it had opened to its maximum extent, with North and South America farther apart than at present (Freeland & Dietz, 1971, fig. 6; Malfait & Dinkelman, 1972, fig. 1; Phillips & Forsyth, 1972). The Caribbean then began to close slowly as South America moved northward relative to North America, reaching a climax in the Middle Eocene, and marked by major tectonism on both its northern and southern margins (Freeland & Dietz, 1972; Mattson, 1972).

In the region of the Greater Antilles, small islands were in the area of Cuba by the Late Jurassic (Khudoley & Meyerhoff, 1971, fig. 22). The Cayman Ridge, extending westward from the Sierra Maestra of Cuba towards Guatemala, exhibits a geology that suggests it may have been land in Paleocene to Lower Eocene time (Heezen, Dreyfus & Catalano, 1973), this then facilitating migration to Cuba and indirectly the other Antilles. The Bahamas seem to have been subsiding since initiation of drift between Africa and North America (Dietz *et al.*, 1970*a*, 1971; Sheridan, 1971). Most existing islands east or south of Cuba are no older than Upper Cretaceous. Their origin probably resulted from intense crustal movements beginning in Late Aptian or Early Albian times, perhaps contemporary with the initial rifting of South America from Africa. By the Late Turonian, a chain of small- to medium-sized volcanic islands was in the area of the Greater Antilles and Lesser Antilles (*e.g.* Proto-Hispaniola, Bracey & Vogt, 1970; Puerto Rico, Mattson, 1973). However, most of the islands in both chains attained their present size and outlines only in the late Neogene.

Jamaica formed in the Early Cretaceous as a series of small volcanic islands that were uplifted substantially in the latest Cretaceous (Robinson & Lewis, 1971). However, no part of Jamaica seems to have been above sea level between Middle Eocene and the early Middle Miocene (Robinson & Lewis, 1971). This means that all of the plants and animals on Jamaica were derived by long-distance overseas dispersal since then. In this light, it is noteworthy that Jamaica has only 4 endemic genera and 784 endemic species of angiosperms (Adams, 1972), or about 27% of the native flora. By contrast, Cuba, which has not been submerged, has 41 endemic genera and about 50% endemic species (Liogier, 1962), and Hispaniola, which is younger than Cuba but has also not been submerged, has 26 endemic genera and about 33% endemic species (Howard, 1973).

In the Late Cretaceous, the Sierra Madre Occidental of Mexico was elevated and marine transgression limited to the area from Veracruz north. There was elevated land and mountains south to the present area of Oaxaca (*cf.* Malfait & Dinkelman, 1972, fig. 1; Kesler, 1973), which does not seem to have reoriented significantly relative to the mainland of Mexico since Precambian time (Kesler & Heath, 1970).

Nuclear Central America is a Paleozoic orogenic belt extending from the Isthmus of Tehuantepec to northeastern Nicaragua (Kesler, 1971), and possibly Cuba (MacGillavry, 1970). Lateral faulting in the region does not suggest great displacement during Tertiary time (Kesler, 1971; G. Dengo, personal communication). However, some paleomagnetic evidence suggests approximately 1,000 km of northeastward displacement of Jamaica since Aptian and Albian time (Steinhauser *et al.*, 1972). Clearly, the geologic history of the region is still far from completely understood. The area from southern Mexico to northeastern Nicaragua, the Nicaraguan bank, and possibly Cuba was uplifted in the Late Cretaceous and subsequently to form what has probably remained a peninsula from Mexico to northern Nicaragua (Mills *et al.*, 1967; Dengo, 1973). The portions of Nuclear Central America that were land before the latest Cretaceous are established only for certain areas, *e.g.* the Maya Mountains of Belize (Hall & Bateson, 1972) and Honduras (Mills *et al.*, 1967). A large portion of Yucatán may have been emergent in Late Eocene time (G. Dengo, personal communication), establishing essentially the modern configuration between Cuba and Central America.

Southern Central America, extending from central Nicaragua south to the Atrato lowland in Colombia, has an oceanic basement of Senonian age overlain by younger sedimentary and volcanic rocks (Dengo, 1969). The earliest deformation is latest Cretaceous, but major uplift occurred only in Late Miocene and Pliocene times. Scattered volcanic islands existed prior to the Oligocene

(Dengo, 1967, 1968, 1969; Case, 1973), but there was no substantial land area (McBirney & Williams, 1965; Malfait & Dinkelman, 1972).

At the start of the Cretaceous, a broad zone of northern Venezuela (Bell, 1971) and much of Colombia (Schuchert, 1935; Liddle, 1946; Jenks, 1956) was subsea. Alvarez (1971) has shown that the Guajira Peninsula of Colombia was receiving sediment from a landmass to the north, perhaps at the present site of the Nicaraguan Rise. In latest Cretaceous time, the Cordillera Central of Colombia (Campbell & Bürgl, 1965; Alvarez, 1971; Anderson, 1972) and the Cordillera de la Costa of Venezuela (Bell, 1971), together with Trinidad (Barr & Saunders, 1971), emerged above the sea, the latter a large island or group of small ones (Liddle, 1946). There is evidence a landmass of considerable size, "Paría," extending from Aruba to Tobago and even Barbados, was uplifted in early Tertiary time and resulted in deposition of thick sediments to the south (Schuchert, 1935; Edgar, Ewing & Hennison, 1971). The Cordillera Oriental was elevated in late Neogene time, and reached its full height during the Pleistocene (summary in Alvarez, 1971), giving the land area of northwestern South America its present configurations. The complex history of the Sierra Nevada de Santa Marta has been treated by Tschanz *et al.* (1974).

From the Early Oligocene onward, volcanic islands along the present axis of Central America gradually coalesced into continuous land. About 10–12 m.y. ago there was evidently an intermittent land connection to Panama from the north (Whitmore & Stewart, 1965; Malfait & Dinkelman, 1972), which finally coalesced to join North and South America about 5.7 m.y. BP (Simpson, 1950; Kaneps, 1970; Haffer, 1970; Graham, 1972*a*; Emiliani, *et al.*, 1972).

Summary.—Judging from the geology of the region, and the relative motions of the plates, South America was more accessible to immigration from Africa than from North America until after the Early Eocene. Subsequently, more and more insular connections with North America were established, culminating with a direct land connection only 5.7 m.y. BP. Clearly, the history of South American biota has been one of evolution in isolation of an initial West Gondwanaland stock shared with Africa. To South America have come many cool temperate Australasian plants and animals, essentially overland until the Eo-Oligocene, and by overseas long-distance dispersal subsequently. South America contributed increasingly to the flora of tropical and subtropical North America during the Tertiary, it received immigrants from temperate North America only as the Cordillera rose in the late Neogene, at which time it also contributed montane tropical taxa to Central America.

SUMMARY OF PLATE TECTONIC EVENTS

The following events have had great importance for the patterns of evolution and distribution of organisms: (1) Direct migration last possible between North America, Europe, and Africa, 180 m.y. BP. (2) Direct migration last possible between West Gondwanaland (Africa + South America) and Australasia for warm-temperate and subtropical plants and animals, 100 ± 10 m.y. BP. (3) Direct migration between Africa and Madagascar, and probably also India, last possible, about 100 m.y. BP (possibly more recent; evidence ambiguous). (4)

Overland direct migration last possible between South America and Africa, nearly 100 m.y. BP. (5) Direct migration between Australia and New Caledonia–New Zealand, 80 m.y. BP. (6) Last direct connection between Africa and Eurasia prior to the Miocene, ~ 63 m.y. BP. (7) Direct migration possible across the North Atlantic for plants throughout the Tertiary, but for land animals until 49 m.y. BP, when the Bering Straits became more and more important as a migration route. (8) South America equally distant from North America and from Africa, ~ 50 m.y. BP. (9) India abuts against Asia, ~ 45 m.y. BP. (10) More or less direct migration possible between South America and Australia *via* Antarctica until approximately 38 m.y. BP. (11) Reestablishment of direct connection between Africa and Eurasia, 17 m.y. BP. (12) More or less direct migration first possible between Asia and Australasia *via* New Guinea, ~ 15 m.y. BP. (13) Direct land connection between North and South America, 5.7 m.y. We shall now proceed to consider existing and past patterns of distribution among vertebrates and flowering plants in relation to these events.

BIOGEOGRAPHY OF SOUTH AMERICAN VERTEBRATES

Although we shall devote our attention chiefly to vascular plants, we shall first review the present state of understanding of vertebrate history in South America. We do this for precisely the same reasons that the entomologist Darlington (1957) selected the vertebrates as the primary material for his volume on zoogeography. Vertebrates, both Recent and fossil, are better known than any other group; the patterns of distribution that they display should parallel those found in other groups of organisms, and it should be simpler to look among the vertebrates for solutions to many outstanding problems that are evident in the distribution of other organisms. Furthermore, the basic hypotheses and the amount of evidence that were utilized in Darlington's (1957) synthesis are now so out of date it is necessary to review the facts again in a more modern context. Our remarks supplement the reviews presented by Cracraft (1973*b*, 1973*c*).

In preparing the present paper, we have consulted a number of treatments of invertebrates and cryptogams, such as those presented in the two volumes on biogeography and ecology in South America (Fittkau *et al.*, 1968, 1969), and find their patterns of distribution to accord, in general, with those of the vertebrates and vascular plants upon which we shall focus here. A particularly elegant analysis of an exactly parallel pattern has been presented by Edmunds (1972) for the mayflies, and Schlinger (1974) has recently provided interesting new information on the insects associated with *Nothofagus*.

We shall now analyze the paleobiogeography of each of the groups of vertebrates in turn.

FISHES

The dominant freshwater fishes of Africa and South America are characoids and siluroids, both derived from ancestral forms that dispersed directly between these continents when they were united (Myers, 1966; Roberts, 1973, Fig. 1, 3). In South America, the characoids gave rise to the endemic gymnotids, and in Africa cyprinoids subsequently entered from the north (Gosline, 1972), probably at least in part in Neogene time. There are thus no gymnotids in Africa and no cyprinoids in South America. The non-ostariophysan primary freshwater fish families of South America, Lepidosirenidae, Osteoglossidae, and Nandidae, are all shared with Africa. No primary freshwater fishes of North American origin extend south of Lago Nicaragua, and none has reached South America (Myers, 1966), contrary to the elaborate scheme proposed by Darlington (1957). The dominant cichlids and poeciliids of Central America are secondary freshwater fishes that disperse across saltwater barriers. The cichlids probably were derived from South American forms, whereas the poeciliids may have been derived from North American cyprinoids. Both evidently have been radiating in Central America through most of Neogene time. No primary freshwater fish from South America reached Central America until these lands were connected, about 5.7 m.y. BP. Subsequently, a few genera of characoids extended their range north into Mexico, and one (*Astyanax*) reached the Rio Grande (Myers, 1966). The evidence from the distribution of freshwater fishes is in full accord with our present understanding of the relationships between Africa, South America, and North America.

AMPHIBIANS

Caecilians, recently reported from the Late Paleocene of Brazil (Estes & Wake, 1972), almost certainly dispersed overland between South America and Africa in the Cretaceous or earlier, and also spread between Africa and Asia. Salamanders are a Laurasian group, with plethodontids having reached South America from North America after the establishment of a direct land connection between them in the late Neogene.

Frogs may have originated in Gondwanaland, though the suggestion must remain speculative (Laurent, 1972; Estes & Reig, 1973: 48; Reig, 1973). At any rate, South America together with Africa (= West Gondwanaland) has clearly been the primary area from which most, if not all, modern lines of anurans have been derived (Savage, 1973). Pipidae almost certainly dispersed directly between Africa and South America. They are known from the Late Cretaceous of both regions, and from the Early Cretaceous of Israel (Laurent, 1972; Estes & Reig, 1973). Bufonidae (including Atelopidae) may also have done so (Cracraft, 1973*b*). Since *Heleophryne* of southern Africa is a leptodactylid (Lynch, 1971), it seems reasonable that the group dispersed directly between South America and Africa prior to their separation, and also across Antarctica to Australia (Darlington, 1957: 166; Lynch, 1971). However, Cracraft (1973*b*) points out that relationships with the Northern Hemisphere pelobatids and phylogenetic lines within the leptodactylids must be understood better before definite conclusions can be drawn.

Savage (1973) contends that one of the genera of Leptodactylidae (*Eleutherodactylus*) reached North America prior to the Pliocene. Savage (personal communication) has pointed out that *Eleutherodactylus* sens. lat. is an excellent candidate for overwater dispersal, with an encapsulated, land-laid egg, like the widely distributed ranid *Cornufer* (*Platymantis*), which has reached Fiji. There are approximately a hundred species of *Eleutherodactylus* in the West

Indies, and at least three derivative endemic genera—*Sminthillus*, *Syrrhophus*, and *Tomodactylus*—are north of South America.

Leiopelmidae, known as fossils in the Mesozoic of South America (Estes & Reig, 1973), occur today only in northwestern North America and New Zealand. Dispersal to New Zealand need not be explained *via* Antarctic connections. Since this group is known from the Early Jurassic, it may have spread directly between any of the continents (see Fig. 1), and may have arrived in North America much earlier than suggested by Estes and Reig (1973: 47).

Hyla is evidently a South American derivative of leptodactylid stock (Savage, 1973: 414). The Central American hylids are derived from South America, whereas the Nearctic hylids are more closely related to Eurasian taxa (Duellman, 1970). The recent record of *Hyla* from the Early Oligocene of Saskatchewan (Holman, 1969, 1972) implies sweepstakes dispersal from South to North America at least that early, whereas contemporary Central American hylids evidently came later. Although *Hyla*, using some current concepts, would seem to have migrated from South America to Australia directly (Raven & Axelrod, 1972), Tyler (1971) and Savage (1973: 356) have recently allied Australasian forms currently referred to *Hyla* to leptodactylids. This implies their independent derivation from other leptodactylids in Australia.

Bufo, first known from the Paleocene of Brazil (Estes & Reig, 1973), also seems to have been derived from leptodactylid stock in South America (Blair, 1972), spreading by sweepstakes dispersal to North America (Blair, 1972, Fig. 18-1). The presence of fossil bufonids in the Eocene of Europe (R. Estes, personal communication) implies their arrival in North America at least that early, even though the first fossils are from the Lower Miocene. The ancestors of the African groups, which are distinctive, might have arrived by rafting in the Paleocene across a much narrower South Atlantic (*cf.* Laurent, 1972), as we shall discuss below for primates and caviomorph rodents. Blair (1972) has emphasized the similarity between *Bufo* species in Africa and South America. *Rana* reached South America very recently, *via* North America from Eurasia (Darlington, 1957: 170).

To summarize, caecilians and several groups of anurans seem clearly to have migrated overland between South America and Africa in the Cretaceous. *Hyla* probably reached North America from South America by the Early Oligocene at least, and a number of other groups were exchanged between these two continents in the Miocene and more recently. There is no evidence that any amphibians passed directly between North and South America between Lower Jurassic and Early Oligocene times, although the presence of bufonids in the Eocene of Europe suggests that they may have done so.

REPTILES

The four families of dinosaurs recorded from the Upper Cretaceous of South America all occur in North America, and only one has been recorded definitely from Africa (Charig, 1973). These relationships have been used to argue that migration between North and South America must have been relatively direct at that time, and that migration between South America and Africa very indirect

(Colbert, 1952; Darlington, 1957; Charig, 1973). Of these four families, however, one is doubtful in South America and a second has been doubtfully recorded from Madagascar. Ceratopsidae, abundant in North America, are known in South America only from a single fragment of a lower jaw from the Upper Cretaceous of Argentina, which is very doubtfully assigned to this family (Colbert, 1948). Hadrosaurs, abundant in North America at the same time, have not been found in the Southern Hemisphere. Finally, at the generic level, as among the nearly cosmopolitan sauropods, there is as strong an indication of connection between South America, Africa/Madagascar, and India as between East Asia and North America (Charig, 1973).

This analysis of dinosaur distribution, therefore, does not support the notion of direct migration between North and South America in the Mesozoic, which agrees with the known positions of Africa and South America in Early Cretaceous time. There is, however, ample evidence of links between South America, Africa, India, and Madagascar, probably until Upper Cretaceous (Charig, 1973; Colbert, 1973). Cetiosaurinae are known from the Jurassic of Australia, Coeluridae (Charig, 1973), Megalosauridae (Colbert & Merrilees, 1967), and Iguanodontidae (E. H. Colbert, personal communication) from the Early Cretaceous. The presence of these large dinosaurs certainly indicates terrestrial connections between Australia and other parts of the World at that time (Colbert, 1973). However, all of these families existed in the Jurassic, and they might have arrived in Australia prior to the close of that period.

Among the turtles (Simpson, 1943), the pelomedusids evidently dispersed between South America and Africa when these were linked or close to one another, and fossils are known from both regions, as well as from the Northern Hemisphere (Darlington, 1957). Land tortoises (Testudininae) and Chelydridae may have reached South America from North America in the Miocene or more recently, and the Emydinae, basically a northern group, probably did the same. Most other groups are basically northern or southern. Before the arrival of the predominant northern groups of turtles in South America in Neogene time, there were meiolaniids and chelyids, both of which may have reached Australia *via* Antarctica (Raven & Axelrod, 1972). There is no evidence for dispersal of turtles between North and South America prior to Miocene time.

Of the lizards, Iguanidae first appear in the fossil record in the Upper Cretaceous of Brazil (Estes & Price, 1973). The diversity of Paleocene iguanids there suggests that the evolution of the family took place primarily in South America (Tihen, 1964; Estes, 1970). They appear in North America, which they probably reached by sweepstakes dispersal, in the Eocene. The presence of two relict genera on Madagascar suggests that iguanids passed from South America to Africa-Madagascar in the Cretaceous (Estes & Price, 1973). The occurrence of a third endemic genus on Fiji and Tonga seems to be related to long-distance trans-Pacific dispersal, presumably *via* archipelagos, since it is closely related to the American genus *Iguana* (R. Estes, personal communication).

Gekkonidae probably also dispersed more or less directly between South America and Africa during the Cretaceous (Cracraft, 1973*b*). Teiidae seem to have been in both North and South America in the Late Cretaceous (Estes, 1970) and probably spread to North America by sweepstakes dispersal at that time.

However, the only Recent teiid north of Mexico, *Cnemidophorus*, which undoubtedly came from South America, first appears in the North American fossil record in the Early or Middle Miocene (Estes, 1963; Estes & Tihen, 1964; Tihen, 1964). For Amphisbaenidae, now known chiefly from South America and Africa, the Paleocene fossil record in Eurasia and North America suggests a route from Africa to Europe and then to North America. Summarizing, teiids seem to have reached North America from South America by sweepstakes dispersal in the Upper Cretaceous, iguanids in the Eocene, and many other groups of lizards in the Miocene and subsequently.

Aniliid and boid snakes extend back to the Late Cretaceous (Estes, Berberian & Mesozoely, 1969; Estes, 1970), and more primitive snakes are in the Early Cretaceous (Hoffstetter, 1959). The boa *Madtsoia*, if correctly identified, is known from the Upper Cretaceous of Madagascar and the Paleocene-Eocene of Patagonia (Del Corro, 1968). Hence, some boids and possibly other primitive snakes dispersed more or less directly between Africa and South America. Tertiary boids known from North America may have arrived *via* Europe, and snakes must have reached Eurasia prior to the Early Paleocene. Colubroid snakes, which have diversified in the main Eurasian landmass (Rabb & Marx, 1973), reached South America from North America in the Miocene (Hoffstetter, 1967), and have undergone extensive radiation there subsequently. Their diversity in South America in itself seems to be insufficient evidence to postulate an antiquity there greater than the Miocene, contrary to the arguments of Raab and Marx (1973). The early evolution of tropical American colubroid stocks may have taken place in southern North America (= Central America), where Savage (1966) has demonstrated the presence of a substantial endemic element, presumably of some antiquity, among the reptiles. As for Australasia, it is unlikely that any snakes, except possibly seasnakes, reached the area prior to the Miocene, because the Australian snake fauna consists of groups not known to have been in existence prior to the Tertiary.

MAMMALS

As summarized by Clemens (1968, 1970), marsupials are known from the Albian (> 110 m.y. BP; but see Cox, 1973) to the Early Miocene of North America, the Early Eocene to Miocene of Europe, and are also reported from the Upper Cretaceous of Peru (Grambast *et al.*, 1967; Sigé, 1971). They have persisted to the present in South America, and *Didelphis* colonized North America in the Pleistocene, subsequent to the formation of a land connection, reestablishing marsupials in the north after an absence of some 20 m.y. The predominantly southern distribution of marsupials renders it probable that they originated in West Gondwanaland, dispersing directly to Australia (Raven & Axelrod, 1972; Keast, 1972; Cox, 1973). Didelphoids had reached North America by the Upper Cretaceous and were in Europe at least by the Early Eocene. Fossil marsupials are not known from Africa but may be expected there. They spread between North and South America either by sweepstakes dispersal (more likely if they were spreading near the end of the Cretaceous) or *via* Africa and Europe (which can only be confirmed if and when fossil marsupials are discovered in the Cretaceous of Africa and Europe; Cox, 1970; Fooden, 1972). If the Mongolian

Deltatherium proves to be a marsupial (Butler & Kielan-Jaworowska, 1973), the group would then be demonstrated to have been present in Eurasia in Santonian-Campanian time.

Monotremes, like dinosaurs, presumably reached Australasia overland *via* India in the Lower Cretaceous or even Jurassic. Although inferential and some direct evidence suggests the presence of prototherians (monotremes), metatherians (marsupials), and eutherians (placentals) in West Gondwanaland before the separation of Africa and South America, eutherians do not appear to have been in the region early enough for direct migration to Australasia, as discussed below.

One family of notoungulates, Arctostylopidae, is known only from the Upper Paleocene of Mongolia and the Upper Paleocene and Lower Eocene of North America (Simpson, 1945; M. C. McKenna, personal communication). Since other families of the group are exclusively South American, and it seems most likely that notoungulates ancestral to Arctostylopidae reached North America by sweepstakes dispersal from South America by the close of the Paleocene, thence *via* the Bering Straits to Asia. However, an indirect route from West Gondwanaland *via* Eurasia to North America is not precluded.

How the condylarths passed between North and South America is unknown (Kurtén, 1973). The group is not known from African fossils and presents an enigma comparable with that of the marsupials.

Darlington (1957), following Simpson (1945), places the Metacheiromyidae with the edentates, and says that the nearly complete skeletons of *Metacheiromys* are "among the most important of all fossil mammals," because they show that "early in the Tertiary, edentates were in North America, from where they may have reached South America" (Darlington, 1957: 383). Emry (1970) has since shown that the Metacheiromyidae are not edentates but members of the Pholidota. The edentates are therefore an exclusively austral group that spread to North America in the Pliocene.

Among other groups of mammals, caviomorph rodents and platyrrhine primates appear in the fossil record of South America in the Early Oligocene (Patterson & Pascual, 1972). Perhaps the ancestors of both groups arrived by rafting and island-hopping from Africa (Hoffstetter, 1972): in the Early Oligocene South America appears to have been about equally distant from North America and from Africa. Since a platyrrhine primate reached Jamaica in the Pliocene or Pleistocene over a water barrier of about 600 km, perhaps a gap of about twice that distance from Africa to South America was crossed in the Eocene. Hystricomorphous and hystricognathous rodents are known from the Eocene of Europe and North America (Wahlert, 1973), and there is one additional recent record of a hystricognathous rodent from the Eocene of North America (Wood, 1972). Otherwise, living hystricomorphous rodents occur in Eurasia (Old World porcupines only), Africa, and South America, with a Pleistocene invasion of North America by one group of New World porcupines, *Coenodon*. The New World hystricomorphous rodents, almost entirely South American, are all caviomorphs, a group that does not occur in the Old World. The known Eocene North American hystricomorphous and hystricognathous rodents clearly are not ancestral to the caviomorphs (Wood, 1972; Wahlert, 1973, and personal communication), and presumably evolved in North America from a mammalian fauna that was shared with Europe. Thus the derivation of the caviomorph rodents in South America may have been from ancestral forms that arrived from Africa, as mentioned above, and hystricomorph rodents provide no evidence for direct migration between North and South America until the Late Pliocene. The same is true for platyrrhine primates, which seem to have reached Central America and the West Indies only in Pliocene time, and subsequently.

Marsupials and condylarths might have dispersed between North and South America in the Cretaceous (Keast, 1972), but the evidence is not strong and the assumption is based mainly upon contemporary geography. The extensive exchange of mammalian faunas between North and South America which began about 5 m.y. BP is, of course, well established (Simpson, 1947*a*; Patterson & Pascual, 1972; Savage, 1973). However, there is no evidence for an earlier "intense exchange of land mammals" (Darlington, 1957: 365), and none would be expected from the geological history of Middle America. Before the extinct *Cyonasua* group of extinct procyonids arrived in South America in the Middle Pliocene, Arctostylopidae provide the only convincing case for direct dispersal between North and South America, although marsupials and condylarths might also have crossed the gap between these two continents. These facts argue compellingly for the absence of any direct, or even relatively direct, connection for mammals between North and South America until latest Neogene time.

It appears probable that the original mammalian stocks of South America (condylarth-ungulates and edentates) were derived from an Early Cretaceous mammal fauna shared with Africa (Hoffstetter, 1972). Unfortunately, nothing is known about the Cretaceous mammals of Africa, and we have only fragmentary knowledge about those in the South American Cretaceous. The earliest known African Tertiary mammals, from the Late Eocene, are highly endemic and all proboscideans (Coryndon & Savage, 1973; Cooke, 1973).

BIRDS

Although birds disperse readily across many sorts of barriers and have a poor fossil record, their patterns of distribution accord with those of other groups (Darlington, 1957; Cracraft, 1973*b*, *c*). Cracraft (1973*b*, *c*) has suggested that such families as Struthionidae, Musophagidae, Coliidae, Pteroclididae, Columbidae, Psittacidae, and Eurylaimidae and indeed such orders as Columbiformes, Galliformes, Psittaciformes, and Cuculiformes, may have radiated from West Gondwanaland, and the ratites as a whole may also have done so (Raven & Axelrod, 1972; Cracraft, 1973*c*). A number of important Oriental and otherwise cosmopolitan families of birds, such as Psittacidae and Columbidae, are especially well developed in Australasia. South America is a rich center of diversity for the latter two families and many others which apparently diversified there during the Late Cretaceous and Tertiary.

The absence of living or fossil ratite birds in North America and the presence of a distinctive tropical North American (including Central American) bird fauna, perhaps including such families as Motmotidae, Todidae, Cracidae, Trochilidae, and Thraupidae (Mayr, 1946, 1964; Bond, 1948; Cracraft, 1973*c*), reemphasize the wide separation of North and South America in Paleogene times. In attempting to minimize this relationship, Darlington (1957: 279–287) confused the issue by assuming that Central America was an island lying between North and South America.

Although no confirmation is possible on the basis of present fossil evidence, the primary radiation of the birds as a group may well have taken place in West Gondwanaland, with migration to the Northern Hemisphere from Africa to Europe by the Late Jurassic. Judging from the pattern found in many other groups and discussed later in this paper, numerous phylogenetic lines became extinct in Africa after its separation from South America, and this, together with its ready access to Eurasia, may account for the low degree of endemism in Africa noted by Cracraft (1973*b*), as may the impact of spreading aridity (see p. 608).

Summary.—Direct dispersal between Africa and South America prior to Santonian time (80–85 m.y. BP) is evident for many tropical groups which basically have a West Gondwanaland pattern of distribution. These include characoid and siluroid primary freshwater fishes, as well as the fish families Lepidosirenidae, Osteoglossidae, and Nandidae; caecilians and at least two families of anurans, Pipidae and Leptodactylidae; pelomedusid turtles; iguanid and amphisbaenid lizards; boid snakes; several groups of dinosaurs; and ratite birds. It is probable that the condylarth-ungulate and edentate stocks of South America were derived from a Cretaceous mammal fauna shared with Africa, and that the primary radiation of anurans, birds, marsupials, snakes, and lizards also took place on this large tropical landmass.

Direct migration between Africa and Eurasia was possible at various times during the Cretaceous and Paleocene, and direct migration between Europe and North America was easily possible for vertebrates until the Early Eocene (~ 49 m.y. BP). However, it is uncertain whether such animals as marsupials, amphisbaenid lizards, boid snakes, and various dinosaurs passed between North and South America *via* Africa and Europe, or directly. A better understanding of the fossil record, and a clarification of the affinities of extinct members of these groups, may lead to the solution of this problem for at least some of the groups. At any rate, present evidence suggests that the following groups of vertebrates probably did pass *via* sweepstakes dispersal between North and South America by the times indicated: (1) teiid lizards, Late Cretaceous; (2) arctostylopid mammals, Upper Paleocene; (3) the genus *Bufo* and iguanid lizards, Eocene; (4) the frog genus *Hyla*, Early Oligocene. Marsupials and condylarths may have dispersed between the two continents in the Cretaceous, but otherwise the five groups mentioned above constitute the only likely instances of dispersal by land vertebrates between North and South America in Cretaceous and Paleogene times.

Considering the rich and varied vertebrate faunas of North and South America, the small amount of interchange certainly accords with the geological evidence that suggests a very wide separation of the Americas in Cretaceous and Paleogene time. In the Miocene and subsequently, interchange between the two continents of the Western Hemisphere accelerated and led eventually to the development of a Latin American fauna. The rich and endemic flora and fauna of South

America, however, evolved principally during its period of isolation from both Africa and North America, a span of some 70 m.y. between the Santonian (Upper Cretaceous) and the late Neogene. West Gondwanaland, a large landmass lying in tropical latitudes and more or less united until about 90 m.y. BP, seems to have been the primary seat of evolution and radiation of many groups of plants and animals, with intermittent migration to the north *via* Africa; a cool temperate connection to Australasia until about 45 m.y. BP; and an increasingly effective direct interchange between South America and North America during approximately the last 10 m.y.

THE BIOGEOGRAPHY OF ANGIOSPERMS

In the light of the geological evidence reviewed above, and the patterns of evolution and migration that can be seen among living and fossil vertebrates, we shall now review the patterns of distribution among the flowering plants. In order to establish the relevance of certain dates to the history of the groups concerned, we shall first briefly review what is known about the timing of major differentiation among the angiosperms.

THE AGE OF THE ANGIOSPERMS

Although the group might be considerably older, and have existed in low numbers (Axelrod, 1952*b*, 1970), undoubted monosulcate angiosperm pollen is first known from the Barremian of England, Maryland, and Argentina (Couper, 1964; Archangelsky & Gamero 1967; Kuprainova, 1967; Kemp, 1968; Doyle, 1969; Muller, 1970; Brenner, 1974; Wolfe *et al.*, 1975). Such pollen is characteristic of the Annonales ("woody Ranales") and Nymphaeales among the dicots and of the monocots, which were definitely distinct by Aptian time (Samylina, 1968; J. A. Doyle, 1973). Tricolpate pollen, characteristic of all dicots other than Annonales and Nymphaeales, is first reported from the Hauterivian to Barremian of the U.S.S.R. (Bolchovitina, 1953; Pokrovskaya, 1964; Voronova, 1966); these records have not been reconfirmed, as far as we are aware, in the more recent literature. It is next recorded from Barremian-Aptian beds in the Northern Negev of Israel (Brenner, 1974), and from the Aptian of Brazil (Muller, 1966; Brenner, 1974), the U.S.S.R. (Yedemskaya, 1960; Panova, 1964; Voronova, 1966; Khlonova, 1971; Orlova-Turchina, 1971; Papulov, 1971), and the U.S.A. (Hedlund & Norris, 1968; J. A. Doyle, personal communication). The information available at present is indecisive about the place of origin of plants with tricolpate pollen (Jones & Kremp, 1973; R. E. Jones, personal communication). An origin in tropical West Gondwanaland, attractive on ecological grounds, would be consistent with these data (Brenner, 1974). Tricolpate pollen does not appear in the record in Arctic North America until Cenomanian time, this certainly being in accordance with

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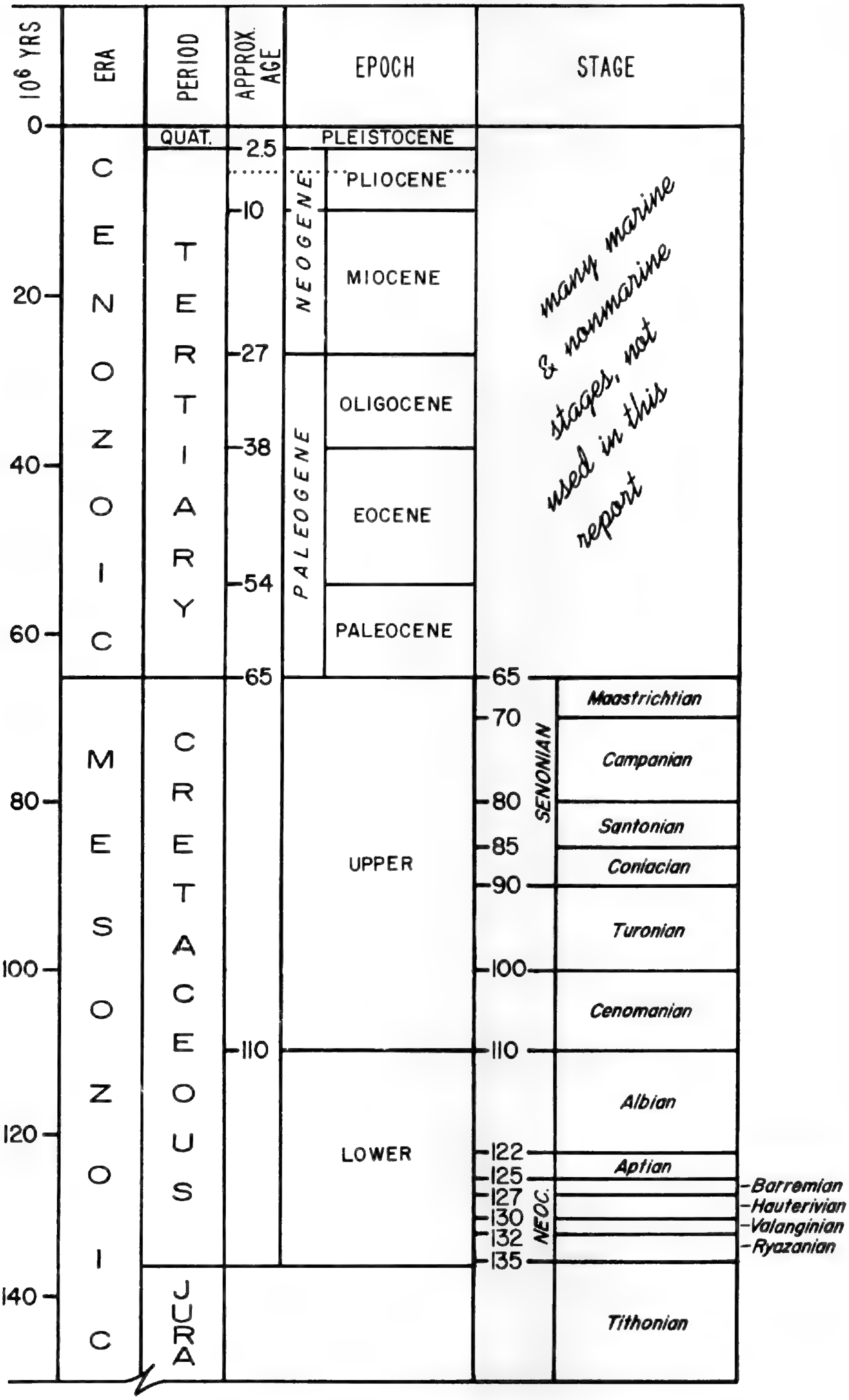
FIGURE 5. Geological time scale since the Jurassic. The ages of most of the Epoch/Stage boundaries are correct to within 1–2 million years, as judged from radiometric dates. Some authorities (Berggren, 1972; Kaneps, 1970; Van Couvering & Miller, 1971) have shown that the Miocene-Pliocene boundary in the *marine* section may be as young as 5.5 m.y.; see dotted line). For Cretaceous time see Addendum: Baldwin *et al.* (1974). Neoc. = Neocomian.



10⁶ YRS
ERA
PERIOD
APPROX. AGE
EPOCH
STAGE
0
20
40
60
80
100
120
140
CENOZOIC
MESOZOIC
QUAT.
TERTIARY
CRETACEOUS
JURA
2.5
10
27
38
54
65
110
PLEISTOCENE
NEOGENE
PALEOGENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
UPPER
LOWER
many marine & nonmarine stages, not used in this report
65
70
80
85
90
100
110
122
125
127
130
132
135
SENONIAN
NEOC.
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Ryazanian
Tithonian

the notion of a northward migration of early angiosperms from middle latitudes (Hughes, 1961, 1973; Doyle, 1969; Brenner, 1974), as suggested earlier on the basis of megafossil evidence by Axelrod (1959). See Hopkins (1974) in Addendum.

Among the few putative pre-Aptian megafossil records of angiosperms is *Onoana*, from the Hauterivian of northern California (Chandler & Axelrod, 1961), which is very likely a gynospermous seed (Wolfe *et al.*, 1975; M. E. J. Chandler, personal communication).

Chandler (1958) recorded a structure of uncertain affinity that she regarded as an angiosperm fruit from the Valanginian of France, but the specimen has not been traced since World War II and its identity is uncertain (M. E. J. Chandler, personal communication). Various pre-Campanian palmlike leaves such as the Jurassic *Propalmophyllum* and the Triassic *Sanmiguelia* are not now generally regarded as palms (Read & Hickey, 1972; Scott *et al.*, 1972; Moore, 1973; Doyle, 1973). An example of a pre-Cretaceous fossil which exhibits certain angiosperm-like tendencies (reduction in seed size, pappus-like parachute) is Upper Jurassic *Problematospermum* (Krassilov, 1973).

There are few suggestions of Aptian (122–125 m.y. BP) angiosperm diversity in the available record. Krassilov (1967, 1973) has assigned fruits from the Aptian of Primorye in the Far East of the U.S.S.R. to *Onoana*, but his description "probably many seeded, and spiny" (1973: 172) suggests they represent a very different taxon. Krassilov simply interprets it as a primitive angiosperm and apparently associates with it Upper Cretaceous staminate heads with pollen of the *Tricolpopollenites* type which is not recorded before the basal Albian.

By Upper Albian time (110–113 m.y. BP), diverse angiospermous floras existed, as shown for the Potomac Group (Wolfe *et al.*, 1975); the Dakota flora, that from the Cheyenne Sandstone (Lesquereux, 1891; Berry, 1922; most, if not all, of the generic determinations are incorrect); and other contemporary floras. Small tricolpate pollen with a psilate or finely reticulate sculpturing becomes abundant in the Middle Albian at many widely scattered localities at middle latitudes (Brenner, 1974), but was already widespread by Aptian time, as we have seen. On present evidence, it appears reasonable that primitive members of the Annonales and of one or more groups of monocotyledons were in existence by Neocomian time, at the latest. The tricolpate pollen which appears in the record in the Aptian may be compared with that characteristic of some modern families, but the picture is blurred (Doyle, 1969; Muller, 1970). In any event, such groups as Annonales, Theales, Berberidales, and Hamamelidales, or their immediate precursors, as well as some monocots (see also Samylina, 1968: 216; Doyle, 1973), might logically be considered to have existed before the close of the Lower Cretaceous and possibly considerably earlier.

Although more diversity appears in the pollen record in the Cenomanian, it is in general not until the Turonian and Senonian that angiosperm pollen becomes more abundant than the spores of ferns and the pollen of gymnosperms, with a concomitant great increase in angiosperm diversity. The number of modern angiosperm families recorded for the Cenomanian has apparently been greatly exaggerated by superficial comparisons of leaves and fruits with those of modern taxa (Penny, 1969; Muller, 1970). By Maastrichtian time, however, a number of modern genera and families were definitely present (Muller, 1970; Wolfe *et al.*, 1975; Wolfe, 1974). These include *Nypa* (Arecaceae), *Ctenolophon* (Linaceae), Proteaceae, Myrtaceae, *Ilex* (Aquifoliaceae), Poaceae, Sapotaceae, *Nothofagus* (Fagaceae), *Pachysandra* or *Sarcococca* (Buxaceae; Srivastava, 1972), *Ascarina* (Chloranthaceae), *Anacolasia* (Olacaceae), *Alnus* (Betulaceae), *Guarea* (Meliaceae; Graham, 1962), and *Symplocos* (Symplocaceae), as judged by very strict criteria (Muller, 1970). It is reasonable to infer the existence of some modern families by Turonian time (90–100 m.y. BP) and at least several orders in the Cenomanian, with some even earlier. By the Paleocene, *Alyxia* (Apocynaceae), *Betula* (Betulaceae), *Barringtonia* (Lecythidaceae), *Brownlowia* (Tiliaceae), *Bombax* (Bombacaceae), *Crudia* (Caesalpinaceae), and *Liquidambar* (Hamamelidaceae) were in existence, as were very many other living genera (*e.g.* see Brown, 1962).

This pattern of appearance of angiosperms in the lowland record suggests that the primitive members of several extant orders and perhaps even a few families were already in existence by the close of the Early Cretaceous, 110 m.y. BP. Many more were in existence when essentially direct interchange was still possible between Africa and South America, 90 m.y. BP, and a great many by the Paleocene when these two continents were only about 800 km apart and linked by numerous volcanic islands. Most modern angiosperm families were in existence before the connection between Africa and Eurasia was severed in the Paleocene, about 63 m.y. BP. All but the most recently derived families had originated when direct migration between Australia and South America was still possible, ~ 45 m.y. BP, although this path was used only by cool-temperate organisms. Many of the ancient angiosperms and animals of Australasia presumably did not come by this temperate pathway from South America prior to the Cenomanian, but directly from West Gondwanaland *via* India and Antarctica (see Fig. 2). Similarly, the ancient tropical and subtropical flora and fauna of South America was shared with Africa, and has been enriched only in the later Neogene and more recently with temperate North American taxa in ever-increasing numbers. It now remains to consider the patterns of distribution seen among living angiosperms in the light of these deductions.

REVIEW OF EXISTING GROUPS

We have had no opportunity to investigate the great majority of angiosperm orders in detail, but offer the following comments, arranged according to the system of Thorne (1968), to illustrate the major patterns that do exist in the group. In the following notes, we have used especially *Die Natürlichen Pflanzenfamilien* (Engler & Prantl, 1887–1915) and *Das Pflanzenreich* (Engler, 1900–1953), Airy Shaw (1966), and Hutchinson (1959). The following more local works have also been very useful: Burbidge (1963), Standley (1920–1926), Muñoz Pizarro (1966), Thorne (1965), Guillaumin *et al.* (1965), and Hillebrand (1888).

No extensive effort has been made to review the paleobotanical literature, especially since the identification of Cretaceous and Paleogene angiosperms with modern forms presents so many difficult problems. We do, however, mention a few records when they appear to be of special interest in relation to the distribution of patterns being discussed. In this connection, the bibliography assembled by Graham (1973*b*) has been especially helpful. In the following pages, the orders of dicots are presented first, in alphabetical order, followed by the orders of monocots.

DICOTYLEDONEAE

Annonales.—Illiciaceae, Schizandraceae, Magnoliaceae, Calycanthaceae, and Saururaceae seem clearly to be Laurasian families, originating in the Northern Hemisphere and in some cases spreading southward subsequently. This implies a Miocene or more recent dispersal of Magnoliaceae from North into South America (Lozano Contreras, 1972), where *Talauma* and *Magnolia* are the only genera. Magnoliaceae have seeds with sarcotestas, which are eaten by birds, and the seeds are easily dispersed. Aristolochiaceae likewise appear to be Laurasian, but the *Aristolochia* line is well represented in South America, where many species of *Aristolochia* as well as the related endemic genera *Holostylis* and *Euglypha*, occur. Relatively early sweepstakes dispersal from North America probably accounts for this. Judging from the distribution of their possibly more primitive relatives, Saururaceae, the pantropical Piperaceae may also have had a Laurasian origin, perhaps reaching South America *via* Africa. Piperaceae are reported from the Eocene of Argentina (Menéndez, 1972).

A number of families of Annonales are common to Africa and South America, with most also extending to tropical Asia. Especially in view of their antiquity, it seems probable that some of them migrated more or less directly between South America and Africa when they were in closer contact. These families include Canellaceae (well represented in West Indies), Myristicaceae, Siparunaceae, and Annonaceae. On the other hand, Gyrocarpaceae and Hernandiaceae, easily dispersed judging from present distributions, may not be so ancient, although their modern distributions link Africa and South America.

Annonaceae, which evidently did migrate directly between Africa and South America (Smith, 1973), apparently radiated extensively in tropical Asia by Paleogene time. Indeed, they radiated to such an extent that Takhtajan (1969) was misled into considering the family primarily disjunct between Asia and South America. The incisive studies of Walker (1971, 1972) have clearly shown this family to have a West Gondwanaland distribution. The two temperate North American genera, *Asimina* and *Deeringothamnus*, are more closely related to African genera such as *Hexalobus* and *Uvariastrum* than to any South American genus. Their ancestors doubtless reached North America from Africa *via* Europe by Early Eocene time or earlier. All other genera of Annonaceae found north of Panama are probably Neogene or more recent arrivals from South America. Annonaceae are well represented in the Eocene of southern England (Chandler, 1964) and reported from the Eocene of Argentina (Menéndez, 1972), as well as from the Paleocene of Egypt (Chandler, 1954) and Colombia (Hammen & García de Mutís, 1966).

Judging from the complex interrelationships of American and Old World genera, Monimiaceae s. str. seem to have spread directly between Africa (where four genera, three endemic, and about 40 species occur on Madagascar and the Mascarenes, but none at the present day on the mainland) and South America, and seem to have evolved early enough to have reached Australasia more or less directly. Monimiaceae are known from the Senonian of Europe (Rüffle, 1965), and reported from the Upper Cretaceous of Argentina (Menéndez, 1972).

Lauraceae, much more poorly represented in Africa than in South America or tropical Asia at present, presumably also dispersed directly between South America and Africa. The family is reported from the Upper Cretaceous of Argentina (Menéndez, 1972). *Ocotea* has hundreds of species in tropical America and a few in Africa; *Beilschmeidia* also occurs on both continents. Much extinction took place among the Lauraceae of Africa, as judged from the contemporary occurrence of four genera in the Canary Islands. One of these, *Persea* (Kopp, 1966), consists of two subgenera in the Western Hemisphere, of which subg. *Persea* seems to be North American, subg. *Eriodaphne* South American. *Persea* is known in North America from at least Eocene times onward (MacGinitie, 1941), and wood very similar to that of this genus is known from the Eocene of Patagonia (Romero, 1970). *Persea* (with *Machilus*, *Nothophoebe*, and *Alseodaphne*; Kostermans, 1952), is an old Laurasian genus, but subg. *Eriodaphne* evidently was South American and may have spread north of Panama only in the Miocene or more recently, where it came in contact with subg. *Persea*. Although *Persea* is not now found on the mainland of Africa, it thrives on the Canary Islands, and it seems reasonable to assume that the ancestors of subg. *Eriodaphne* reached South America *via* Africa more or less directly by Paleocene time. *Umbellularia* and *Sassafras* (the latter included in *Persea* by Kostermans, 1964) are ancient offshoots of the *Persea* line which survive with restricted ranges in North America, and, in the case of *Sassafras*, in Asia also. *Litsea* and *Lindera* are Laurasian genera represented today by a few species in the North American region. All other American genera of Lauraceae seem to have reached Central and North America and the West Indies from South America, commencing in Paleogene time, and with fossils of leaves very similar to those of *Ocotea*, *Nectandra*, and *Beilschmeidia* in North America by the Middle Eocene (MacGinitie, 1969; Dilcher, 1973*b*).

Drimys, the sole representative of Winteraceae in South America, may have dispersed from Australasia to South America *via* an Antarctic route prior to the full separation of Australia from Antarctica (Raven & Axelrod, 1972). Direct connections have been overemphasized, however, by the lumping of *Drimys* with the Australasian genus known as *Tasmannia*. Whereas *Tasmannia* has a gametic chromosome number $n = 13$, *Drimys*, like other genera of Winteraceae that have been studied, has $n = 43$ (Raven & Kyhos, 1965; Ehrendorfer *et al.*, 1968). Since a species of the otherwise Australasian genus *Bubbia* occurs in Madagascar, an alternative hypothesis is that *Drimys* was derived from a West Gondwanaland stock of Winteraceae which subsequently became extinct on the mainland of Africa. The single species of *Bubbia* in Madagascar should be compared with *Drimys*. As L. J. Hickey (personal communication) has pointed out, however, the pollen of Winteraceae is specialized within Annonales, and the fossil record of the family begins in the Early Oligocene. In view of this, the simplest assumption would be that the Antarctic dispersal route for Winteraceae to the New World is correct, and that the species of *Bubbia* on Madagascar reached it from the east by long-distance dispersal. Its fruits are fleshy and perhaps it is readily dispersed.

Chloranthaceae are known from four genera: *Hedyosmum*, which has about 40 species in tropical America and the West Indies and one in Hainan(!); *Ascarina*, with 8 species in Malaysia, Polynesia, and New Zealand; *Ascarinopsis*, one species, Madagascar, related to *Ascarina*; and *Chloranthus*, with about 15 species in East Asia and Indomalaysia. The family appears to be Laurasian in origin, and it is logical to presume that the ancestors of *Ascarinopsis* reached Madagascar by long-distance dispersal from the east. *Hedyosmum* may have differentiated in tropical Laurasia and spread to North America and then to South America perhaps in later Neogene time.

Other families of Annonales are more restricted in distribution, either to Australasia—Degeneriaceae, Eupomatiaceae, Himantandraceae, Austrobaileyaceae, Amborellaceae, Trimeniaceae, Idiospermaceae (Blake, 1972)—or to South America—Lactoridaceae, Gomortegaceae—or to both—Atherospermataceae (Schodde, 1970). Another restricted group, probably deserving recognition as a distinct family, is the Monimiaceae–Hortonioideae of Ceylon. It probably was derived from West Gondwanaland stock, and may have survived during the passage of India northward to Asia (= "Noah's ark" distribution; Axelrod, 1971, 1972*c*; McKenna, 1973). We know of only one other vascular plant—*Schumacheria* (Dilleniaceae)—that we think might have survived in India during its northward passage from Africa, but Schuster (1972) has proposed that several genera of liverworts may have been transported to Eurasia in this manner. For Winteraceae, Chloranthaceae, and the common ancestors of Thorne's (1968) suborders Magnoliineae (Magnoliaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae) and Laurineae (Austrobaileyaceae, Chloranthaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Atherospermataceae, Siparunaceae, Calycanthaceae, Lactoridaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Gyrocarpaceae, Idiospermaceae) a warm-temperate or tropical route from West Gondwanaland to Australasia seems probable, as it does for Monimiaceae s. str. Atherospermataceae may have originated in the more temperate latitudes of Australasia, reaching South America secondarily *via* Antarctica.

Asterales.—No fossil pollen of the vast family Asteraceae is known prior to the uppermost Oligocene, despite extensive search (Germeraad *et al.*, 1968; Leopold, 1969; Becker, 1969; Muller, 1970), and pre-Miocene records are exceedingly few. The Cretaceous *Palaeanthus* (Newberry, 1896) is probably a cycadophyte and certainly not a composite (T. Delevoryas, personal communication; A. Cronquist, personal communication). No Asteraceae have what appears to be a distribution achieved by direct migration between Australia and southern South America, suggesting with other evidence no more than a mid-Oligocene age for the family. The migrations of Asteraceae, consisting of many very readily dispersed genera, must therefore be seen in the light of present geography. Primitive Heliantheae and Mutisieae, the most generalized tribes, are concentrated in northern South America, which may be a likely place of origin for the family. Considering that the family is in the Lower Miocene in New Zealand (Couper, 1960), northern South America, Nigeria, and eastern Asia, and rapidly increases in abundance in all areas (Germeraad *et al.*, 1968), and that the tribe Cichorieae appears in the Upper Miocene in nearly all areas that have been sampled, dispersal must have been extremely rapid (Raven, 1973*b*). Asteraceae have rapidly produced many genera and species in response to the worldwide expansion of semiarid and subhumid habitats in Neogene time and subsequently. If Calyceraceae are closely related to Asterales, this provides additional evidence suggestive of a South American origin for Asteraceae, but might not accord with a postulated derivation for both from Dipsacales.

Balanopales.—The affinities of the single family Balanopaceae, which is confined to the warmer portions of Australasia, are obscure (Wolfe, 1974; R. F. Thorne, personal communication). Its ancestors may have reached this region in mid-Cretaceous time, or earlier.

Batidales.—The single genus is widespread along warm shores.

Berberidales.—Menispermaceae seem to have a West Gondwanaland pattern at the present day, but if *Pycnarrhena*, an Asian genus of about 25 species of which one reaches Australia, is primitive, the origins of the family could be Laurasian, as suggested by J. A. Wolfe (personal communication). The family is in the Eocene of Europe (Chandler, 1964) and the Early Oligocene of Oregon (Scott, 1954). The other families of the order are without doubt Laurasian, with Sargentodoxaceae, Ranunculaceae, Berberidaceae, and Papaveraceae either restricted there or represented by only scattered species in the Southern Hemisphere that are closely related to northern relatives. The major puzzle in the distribution of Berberidales is the presence of two endemic genera (*Boquila* and *Lardizabala*) of the chiefly East Asian Lardizabalaceae in Chile. Perhaps Lardizabalaceae were in Africa in the Cretaceous, for their present distribution is truly relict; otherwise a very early and unlikely long-distance dispersal to South America, followed by extinction in North America, must be postulated. The order certainly seems to have originated in Laurasia.

Bignoniales.—Bignoniaceae, better represented in South America than in Africa or Asia, seem to have existed when more direct migration between Africa and South America was possible, judging from their present distribution. Although *Neosepidacea* is endemic to New Guinea and Queensland, Bignoniaceae are very poorly represented in Australasia, where they may not have arrived prior to the Miocene. Most of the North American representatives of the family have probably come from South America except *Catalpa*, *Campsis*, and possibly *Chilopsis.* Crescentieae consist of 3 or 4 genera of Central America; the 9 genera endemic to Madagascar with *Kigelia*, endemic to continental Africa, seem to have been derived independently from Tecomeae (A. Gentry, personal communication). The herbaceous genera *Argylia* (Andes) and *Incarvillea* (Asia) are closely related but anomalous in the family; their distribution recalls that of Lardizabalaceae.

Pedaliaceae are primarily African, with some representation, including the endemic *Trapella*, in tropical Asia and one species of *Josephina* reaching Australia. Martyniaceae, on the other hand, are South American, with the monotypic *Martynia* endemic to Mexico. Myoporaceae appear to be primarily Australasian, though the monotypic *Bontia* is West Indian, and *Leucophyllum*, currently referred to Scrophulariaceae, is North American (S. Tomb, personal communication). The African *Oftia* is discordant in the family (Takhtajan, 1969; S. Tomb, personal communication), and better referred to Scrophulariaceae (Dahlgren & Rao, 1971). The West African *Zombiana*, mentioned by Dahlgren and Rao (1971) as an obscure genus of Myoporaceae, is in fact a synonym of *Rotula* (Boraginaceae; Heine, 1963). Myoporaceae presumably achieved their disjunct distribution by Paleogene trans-Pacific dispersal.

Scrophulariaceae are Laurasian, with well developed elements in Africa. Despite a proliferation of species in some genera in Australasia (the *Veronica*-complex) and in South America (*Calceolaria*, *Jovellana*, *Angelonia*, a few other small endemic genera), the family, which consists of many readily dispersed plants, a number of them of moist habitats, appears to be a fairly recent arrival in both areas. Scrophulariaceae were not represented, as far as known, in the Paleogene of England (Chandler, 1964). Some genera, such as *Lamourouxia* (Ernst, 1972), apparently originated in tropical North America and subsequently spread to South America. There are no evident connections between the Scrophulariaceae of Africa and those of South America, except in widespread weedy genera, implying that the family may not have been in existence when these continents were in closer proximity.

Plantaginaceae are presumably basically Laurasian and are widespread, but an endemic monotypic genus, *Bougueria*, is in the Andes. Orobanchaceae are likewise Laurasian, although *Orobanche* has attained a nearly cosmopolitan distribution. Lentibulariaceae are extremely widespread herbs of wet places for which it is not possible at present to postulate a place of origin.

The pollen of Acanthaceae is, curiously, not known from the fossil record until Neogene time (Muller, 1970), although fruits from the Eocene of England are referred to *Acanthus* (Chandler, 1964). Judging from the distribution of some genera, Acanthaceae must often be easily dispersed, even though they are very poorly represented in Polynesia and not known as native plants in the Hawaiian Islands. Despite the existence of very few small endemic genera, Acanthaceae definitely seem to be newcomers in Australasia. The family is well represented in Africa (including Madagascar), South America, and tropical Asia, suggesting some antiquity. Their pollen appears in the first two of these areas in the Miocene but in Asia not until the Mio-Pliocene (Germeraad *et al.*, 1968). Some groups, such as the Thunbergioideae, are confined to the Old World; others, such as *Mendoncia* and *Justicia*, are common to Africa and South America. The curious genus *Oplonia* (Stearn, 1971) is common to tropical America and Madagascar. Moderately large genera such as *Carlowrightia* in North America seem to provide evidence of an early Laurasian element.

Gesneriaceae consist of two subfamilies. The African and Eurasian, mainly tropical Asian, Cyrtandroideae include some genera that reached Australasia (*Boea*, *Didymocarpus*) and one which is in Australia and the Pacific Islands (*Cyrtandra*). The principally South American Gesnerioideae include the small genera *Coronanthera*, *Rhabdothamnus*, and *Fieldia*, which are Australasian. *Rhabdothamnus* and probably also *Coronanthera* are very distinctive within the family in terms of their flavonoids (Lowry, 1973), possibly suggesting a relict status and not a direct derivation from South American forms, at least in recent time. *Fieldia* is not closely related to the other two genera but allied to a group of small Chilean genera. Its Paleogene ancestors probably entered Australasia by a cool-temperate path across Antarctica. Gesneriaceae were probably in existence when Africa and South America were in closer contact, while the major groups of the family differentiated subsequently.

Summarizing, Bignoniales seem to have originated when Africa and South America were closer, perhaps in early Paleogene time. The same may be said for the ancestors of Myoporaceae, Bignoniaceae and Gesneriaceae, whereas the other families, including Scrophulariaceae, Pedaliaceae, and Martyniaceae, may have appeared subsequent to the wider separation of Africa and South America. Myoporaceae can be compared with the most primitive elements in Scrophulariaceae, and these two families probably had a common ancestor early in the differentiation of Bignoniales.

Campanulales.—Campanulaceae are widely distributed and evidently easily dispersed. The geography of the family suggests a Paleogene age, as exemplified by Cyphioideae in Africa and South America. In general, Campanuloideae appear to be a Laurasian–African group, Lobelioideae southern. Pentaphragmataceae are tropical Asian, Goodeniaceae are essentially Australasian and perhaps not directly related to Campanulaceae (Carolin, 1960; Raven, 1975).

Capparales.—Capparaceae have a West Gondwanaland–tropical Asian distribution, and are known from the Eocene of southern England (Chandler, 1964). If *Oceanopapaver* of New Caledonia is correctly assigned here (Thorne, 1968: 60), when and how it reached Australia is problematical. It is the only strongly distinctive endemic member of the entire superorder Cistiflorae in Australasia. Moringaceae, with a single genus and about a dozen species, are mainly African but extend to India. Resedaceae are mainly North African and Mediterranean and extend eastward to Central Asia and India; they presumably reached South Africa by long-distance dispersal. The family seems to be introduced in the Western Hemisphere, judging from the relationships of the species (Abdallah, 1967; Raven, 1971). Brassicaceae are cosmopolitan in temperate regions, and occur in New Zealand by Oligocene time (Raven, 1973*b*). They appear to be a Laurasian group, but are well represented in South America. Unusual genera are scattered throughout the world, and members of the family are apparently easily dispersed. Whether the order originated in West Gondwanaland or Laurasia is problematical, but the pattern for the whole Cistiflorae suggests the former.

Casuarinales.—The single family is Australasian and known from the Tertiary of South America. It presumably crossed Wallace's line in Neogene time (Raven & Axelrod, 1972). It is one of the few "Amentiferae" in the Southern Hemisphere, and is known from Middle Eocene fossils in Australia (Lange, 1970) and Miocene ones in Argentina (Frenguelli, 1943). Maastrichtian pollen records (Couper, 1960; Raven & Axelrod, 1972) from New Zealand are not definitively assignable to this genus (Mildenhall & Harris, 1971; Wolfe, 1974). The evidence for a relationship with Hamamelidales seems convincing.

Chenopodiales.—Although the pattern has been obscured by the ready dispersal mechanisms of some families, it is clear that the Chenopodiales (Centrospermae) differentiated in West Gondwanaland when Africa and South America were in closer contact (Turner, 1973). Caryophyllaceae have an essentially Laurasian distribution, although they have spread repeatedly into different southern continents. All of the other families are basically southern. Fossil pollen of Caryophyllaceae first appears in the Oligocene (Muller, 1970), although *Hantsia*, from the Eocene of southern England, has been assigned to this family (Chandler, 1964).

Phytolaccaceae may have been in existence when Africa and South America were in more or less direct contact, judging from the existence of the endemic South African *Lophiocarpus*; other families appear to have been more recent in origin. Other primarily South American families are Nyctaginaceae, Cactaceae (the North American Cactaceae must be derived, Buxbaum, 1969, and there is no fossil record; Brown, 1959), Portulacaceae, Halophytaceae, and perhaps Polygonaceae, reported from the Upper Cretaceous of Argentina (Menéndez, 1972), and extremely well developed in Laurasia. Basellaceae consist of five genera, of which only *Basella* is found in the Old World, with two species in tropical Africa and three in Madagascar. This pattern suggests an origin in South America followed by long-distance dispersal to Africa. Basically African families are Aizoaceae and Didiereaceae (Madagascar).

Chenopodiaceae and Amaranthaceae are now so widespread in semiarid regions it is difficult to suggest the area of their early evolution. The Australian family Gyrostemonaceae, consisting of five genera and about 15 species of trees, shrubs, and herbs, many in temperate areas, probably is derived from phytolaccaceous ancestors that reached Australia *via* Antarctica and a cool temperate route. Other Chenopodiales appear to be relatively recent arrivals in Australia, where Polygonaceae probably arrived partly by this southern route (*Muehlenbeckia*), partly from the north, and other groups probably appeared in Oligocene time or more recently by relatively long-distance dispersal, radiating in the expanding desert and semiarid regions there (Raven & Axelrod, 1972).

In summary, the common ancestor of Chenopodiales seems to have been present, possibly with ancestral Phytolaccaceae, when Africa and South America were still in relatively close proximity—perhaps in early Paleogene time. The phytolaccaceous ancestors of Gyrostemonaceae must have reached Australia early, just as the ancestors of *Stegnosperma* must have reached North America early. Most families of the group differentiated in South America, Africa, and Laurasia (Caryophyllaceae), after these areas were well separated. This agrees with Muller's (1970: 438) suggestion that Chenopodiales commenced their main differentiation by Paleocene-Eocene time. A rather distinctive pollen of this order marks the basal Paleocene in the Atlantic Coastal Plain (J. A. Wolfe, personal communication).

Cistales.—Flacourtiaceae have a West Gondwanaland–tropical Asian distribution (to southern England in the Eocene, including the tropical African *Oncoba*; Chandler, 1964), are evident newcomers in Australasia, and may have reached Central and North America only in Neogene time. *Cochlospermum* (Cochlospermaceae) has a similar distribution. The second genus, *Amoreuxia*, is presumably basically South American, and probably entered Central and North America in Neogene time. Dipentodontaceae and Scyphostegiaceae are tropical Asian, Peridiscaceae Brazilian, Bixaceae basically South American, Malesherbiaceae western South American, and Achariaceae South African. Violaceae are readily dispersed, but many center in South America and Laurasia, with some species of *Rinorea* and *Hybanthus* in Africa and Asia. The monotypic *Decorsella* is West African, whereas *Melicytus* and *Hymenanthera* are Australasian, as is *Agatea*. Perhaps Violaceae differentiated in South America after its separation from Africa and spread widely subsequently. *Viola* is especially widespread.

Cistaceae are Laurasian, with the ancestors of *Crocanthemum* presumably having reached South America in the Miocene or more recently. Datiscaceae are also clearly Laurasian. Turneraceae have an African–South American distribution, with some genera having reached Central and North America in Neogene time or more recently. Caricaceae are similar in their pattern of distribution, but the endemic genus *Jarilla* may have a relatively great antiquity in Mexico, where its ancestors probably arrived from South America. Begoniaceae are also similar, but evidently easily dispersed in tropical and subtropical regions.

Passifloraceae are chiefly African, with some genera represented in tropical Asia and a few species even reaching Australasia, where they are clearly recent arrivals (Wilde, 1972). The large genus *Passiflora* is mainly American, and three other genera exclusively so. Cucurbitaceae (Jeffrey, 1962) are well represented in South America, Africa, and tropical Asia, implying antiquity. They have also reached Australia, where there is a moderate representation of genera. Temperate North American and Eurasian genera probably are derived from Laurasian ancestors, such as those represented in the Paleogene of southern England (Chandler, 1964). The North American Paleocene *Vitis lobata* (Knowlt.) Brown (1962) is clearly Cucurbitaceae (J. A. Wolfe, personal communication). Loasaceae are best represented in South America. However, *Kissenia* is in South-West Africa and near the mouth of the Red Sea, and several genera, some endemic, are in Central and North America. The family probably dispersed between South America and Africa when these continents were closer. Judging from its diversity, it may have reached North America in Early Miocene time, or earlier.

To summarize for Cistales, the primary differentiation of the families seems to have taken place in West Gondwanaland in Upper Cretaceous time. There are a number of taxa common to Africa and South America, with a number of small, endemic families on each of these continents and a few in tropical Asia. Datiscaceae and Cistaceae are primarily Laurasian, with wood of the former reported from the Eocene of India (Lakhanpal, 1970). Their ancestors presumably reached Eurasia from Africa in Paleogene time. Cistales are mainly represented in Australasia by widespread taxa.

Cornales.—Rhizophoraceae have their greatest diversity in the Old World tropics. Of the non-mangrove genera, *Cassipourea* occurs in South America, Africa, Madagascar, and Ceylon, and one species of the mainly African and Asian *Anisophyllea* is in South America—implying a West Gondwanaland history.

The tribe Rhizophoreae itself, abundantly represented by fossil pollen, had originated by the Eocene, possibly in Southeast Asia, and then spread to tropical America (in the Eocene) and Africa (Germeraad *et al.*, 1968: 281–2). *Bruguiera* is reported from the Eocene and Oligocene of England (Chandler, 1964).

Vitaceae are mainly Laurasian and African, with a few widespread tropical genera in South America. Despite the endemic monotypic *Clematocissus*, they do not appear to be of great antiquity in Australasia. Vitaceae are reported from the Eocene of India (Lakhanpal, 1970). Nyssaceae are Laurasian, Garryaceae North American. Alangiaceae consist only of the African and tropical Asian *Alangium* (which reaches Australia). *Alangium* was widespread in the Tertiary throughout Laurasia (Eyde, 1972*b*). The South American *Metteniusia* should not be referred to Alangiaceae (Eyde, 1968, contrary to Hutchinson, 1959). *Alangium* probably does not belong to Cornales (Eyde, 1968). Cornaceae are chiefly Laurasian, with the monotypic *Afrocrainia* in East Tropical Africa; all other non-Laurasian genera referred to the family may belong to other groups (Thorne, 1973*b*). The subfamily Mastixioideae was richly represented in the Paleogene of Europe (Chandler, 1964) and western North America (Scott, 1954; *in* Chandler, 1964: 58; MacGinitie, 1969: 129). *Griselinia* of South America and New Zealand probably does not belong to Cornales and might be closer to Escalloniaceae (= Saxifragaceae sens. lat.; Philipson, 1967). *Corokia*, of New Zealand and Polynesia, is referred by Airy Shaw (1966: 285) and by Eyde (1966) to the Escalloniaceae also, where it is certainly more at home on phytogeographic grounds. Haloragaceae are cosmopolitan, centering in Australia in terms of diversity. *Gunnera* (Gunneraceae; Thorne, 1973*b*), easily dispersed in view of its occurrence on the Hawaiian Islands, seems at present also to be southern, but its pollen is reported from the Maastrichtian of the western United States (Leffingwell, 1966; Chmura, 1973). Hippuridaceae are circumboreal waterplants, also found in southern South America.

In the suborder Araliineae, Araliaceae are evidently easily dispersed and well represented on islands, including the Hawaiian Islands. The family is reported from New Zealand in the Lower Eocene (Couper, 1960). There are several endemic genera in Australasia and also in Polynesia (*e.g. Pterotropia, Cheirodendron*). Araliaceae are well represented in Laurasia, especially tropical Asia. They are more diverse in South America than in Africa. *Dendropanax* has been reported from a number of localities in Laurasia in the early Tertiary (Dilcher & Dolph, 1970; Dilcher, 1973*b*; Leopold & MacGinitie, 1972). Araliaceae had reached Australasia by the mid-Eocene (Couper, 1960), possibly by a combination of long-distance dispersal and migration across India-Antarctica in the Late Cretaceous or Early Tertiary. Araliaceae seem almost certainly to have been in existence when more or less direct migration between South America and Africa was possible, and, if it is correctly placed here (Airy Shaw, 1966), the New Caledonian *Phelline* also might be derived from ancestors that reached Australasia very early.

In the Apiaceae, Hydrocotyloideae definitely have a West Gondwanaland distribution (*e.g.* Mathias & Constance, 1965). Saniculoideae and Apioideae (possibly with the exception of *Oreomyrrhis*; Raven, 1973*b*) are chiefly Laurasian but have a strong representation in Africa, probably mostly achieved since the Miocene, and a lesser one in South America. The numerous South American species of *Eryngium* may have been derived from tropical North American ancestors in Neogene time and more recently. In Australasia, where they are probably recent arrivals (Raven, 1973*b*), Apioideae have evolved rapidly to produce a series of distinctive taxa.

Summarizing for Cornales, Rhizophoraceae, Araliaceae s. str., and Apiaceae-Hydrocotyloideae seem to have been in Africa and South America when these continents were closer together, whereas Cornaceae and Vitaceae, also relatively ancient families, might have been more or less confined to Laurasia at that time and reached the Southern Hemisphere subsequently.

Dipsacales.—Caprifoliaceae are Laurasian, with recent incursions into the southern continents, including that of *Sambucus* to Australia. The monotypic Adoxaceae are also Laurasian. Valerianaceae are Laurasian, but they have proliferated in South America, where they are probably not very old. Dipsacaceae are Eurasian, Calyceraceae South American. In general, the order is Laurasian, very poorly developed in Africa, and virtually absent in Australasia. If Calyceraceae belong with this order, their ancestors may have reached South America *via* Africa, where the order is poorly represented, or by early long-distance dispersal from North America. Since such a great age for the family appears unlikely, they might better be associated with Asterales, as is traditional. Takhtajan (1969) has placed them in a separate order, next to Asterales.

Ebenales.—Ebenaceae are perhaps basically an African family, with *Diospyros* having reached Laurasia presumably by Paleocene time at the latest (Chandler, 1964) and migrating throughout Eurasia and North America. Since the North and South American species of *Diospyros* are related respectively to Eurasian and African groups, not to one another, a Cretaceous West Gondwanaland history is implied. *Oncotheca* of New Caledonia, sometimes considered to be ebenaceous, may better be referred to Theales (Takhtajan, 1969). *Diospyros* is common to Africa and South America, with a few species related to Asian ones also in Australasia.

Sapotaceae, with about 128 genera, are viewed by Aubréville (1973) as consisting of 17 groups, six of Laurasian and eleven of Gondwanaland distributions. They are known from the Eocene of Europe (Chandler, 1964; Krutzsch, 1967) and from the Oligocene of the eastern United States (Traverse, 1955). An origin in West Gondwanaland appears most probable, almost certainly before the close of the Cretaceous; both the *Manilkara* group and the pentasepalous group are common to Africa and South America. The Australian species appear to have been derived in the Neogene or more recently from tropical Asia, although *Amorphospermum* (1 sp.) and *Niemeyera* (2 sp.) are endemic genera of tropical Australia related to *Chrysophyllum*. The relationships of the genera on New Caledonia and other Pacific Islands are probably ultimately with those of tropical Asia. Exchange between Africa and tropical Asia evidently took place in or before the Paleocene, and plants of this family appear to have been relatively well dispersed since.

Symplocaceae evidently have a Laurasian distribution, probably having entered Australasia (including New Caledonia) in the Miocene or subsequently. The family is absent from Africa, but well represented in South America. The South American species of *Symplocos* may be derived from a complex that existed in tropical North America prior to the linking of North and South America. However, the genus might be older and thus have reached South America *via* Africa. Styracaceae are best represented in Asia but with *Styrax* in North America in the Eocene and secondarily reaching South America, presumably in the Neogene. The affinities of the Brazilian *Pamphila* should be investigated in the context of the family before drawing definite conclusions about its paleobiogeography. *Afrostyrax* of West Tropical Africa has been placed with *Hua* in Huaceae and considered of sterculiaceous affinity (Chevalier, 1947; Airy Shaw, 1966: xxi; Takhtajan, 1969), but other authors such as Hutchinson (1959) and Hepper (1963, and personal communication) retain it in Styracaceae. Lissocarpaceae are tropical South American.

To summarize, Sapotaceae and Ebenaceae seem to have a West Gondwanaland distribution, while Symplocaceae are apparently Laurasian. On the balance, the order may have originated in West Gondwanaland.

Ericales.—Ericaceae seem to have a Laurasian-West Gondwanaland distribution (*e.g.* Stevens, 1970). The common ancestor of *Gaultheria* and *Pernettya* probably arrived in southern South America relatively early, by long-distance dispersal, and then spread from there, as did *Acaena*. Empetraceae, like *Gaultheria-Pernettya*, are probably Laurasian and recent arrivals in the Southern Hemisphere. Epacridaceae, judging from their diversity, seem to be a group of some antiquity in Australasia; the earliest fossil record, however, is from the Upper Eocene (Couper, 1960). The bipolar dichotomy between Ericaceae and Epacridaceae may represent divergence from a tropical alliance of West Gondwanaland. Epacridaceae, including the tribe Styphelieae, are reported from the Early Eocene of southern England (Chandler, 1964), but these records should be reexamined critically in the context of the living members of the family.

Euphorbiales.—Euphorbiaceae are extremely widespread and easily dispersed. They are mainly tropical in distribution, and may have been common to Africa and South America when these continents were much closer. A number of genera, a few of them endemic, occur in Australasia, and *Poranthera* and *Ricinocarpos* are especially distinctive (Airy Shaw, 1966). The oldest known fossils of Euphorbiaceae are Paleocene (Chandler, 1954; Muller, 1970). The occurrence of the related families Aextoxicaceae in Chile, Pandaceae in West Tropical Africa, and Didymelaceae in Madagascar makes the origin of Euphorbiaceae in West Gondwanaland seem likely. Koch (1972) compared fruits from the latest Cretaceous of Greenland with those of the West Indian *Picrodendron*, often considered a distinct family but grouped by Thorne (1968) with Euphorbiaceae; however, Koch (personal communication) has subsequently withdrawn his suggestion of affinity. Dichapetalaceae, with two endemic genera in tropical South America, one on Madagascar, one (*Tapura*) common to South America and Africa, and a fifth (*Dichapetalum*) found in all three main tropical regions of the world, were almost certainly present in Paleogene time when Africa and South America were much closer.

Buxaceae are an ancient group, with *Sarcococca* Asian, *Pachysandra* Laurasian, *Buxus* Laurasian and ranging also into tropical and southern Africa and Madagascar (including *Notobuxus*). *Pachysandra* or *Sarcococca* is known from fossil pollen in the Maastrichtian. *Styloceras* of South America has traditionally been grouped with the African *Notobuxus* in a tribe Stylocereae, but Airy Shaw (1966) separated it as a distinct although related family. Buxeae are clearly Laurasian, but the group also seems to have been in West Gondwanaland when more or less direct migration between South America and Africa was possible. *Simmondsia*, a genus of uncertain affinity and probably autochthonous in the southwestern United States and adjacent Mexico, appears best referred to a monotypic family Simmondsiaceae (Airy Shaw, 1966: 1040). Thymelaeaceae are best represented in Africa but have some antiquity in Laurasia (cf. *Dirca*, *Daphne*, *Thymelaea*, *Aquilaria*, *Lagetta*: also in the Eocene of southern England; Chandler, 1964) and in Australia, where three endemic genera (*Phaleria*, *Pimelea*, *Drapetes*) occur. The family is certainly older than the present Oligocene limit of its fossil occurrence (Muller, 1970). Such genera as *Lophostoma*, *Lasiadenia*, and *Daphnopsis* are basically South American.

Summing up for Euphorbiales, the group has considerable antiquity both in West Gondwanaland and in Laurasia, and a temperate element evolved very early. The rich representation of Thymelaeaceae in Australasia, South America, and Africa suggests differentiation of the order by the Upper Cretaceous.

Fagales.—The Fagaceae are primarily Laurasian, and the genus *Quercus* has spread to South America probably in the Pliocene or more recently. How *Nothofagus* reached the Southern Hemisphere is unknown (Raven & Axelrod, 1972), but it is represented by abundant pollen in the Maastrichtian of Australia, New Zealand, and southern South America. In Africa, *Quercus* occurs today in the Atlas Mountains and adjacent areas, a region which it had already reached in the early Quaternary. Post-Eocene woods of Fagaceae (derived from sites in the Anti-Atlas?) are recorded near Tindouf in Spanish Morocco (*in* Aubréville, 1970). The absence of Fagaceae in the high mountains of north-central Africa (Hoggar, Tibetsi) today may be explained by expanding dry climate which eliminated earlier forests from the region. Furthermore, montane pathways comparable to the American Cordillera do not now provide a route into lower latitudes. There are no reliable records of Cretaceous or Paleogene Fagaceae either in India (see Lakhanpal, 1970: 685) or in Africa south of the Mediterranean region. The pollen record of *Nothofagus* and other now austral genera reported from the Cretaceous of Nigeria (Puri, 1965) is based on a sample of drilling mud carried in from another region (Prof. A. T. Cross, written communication, Sept. 1972), and hence is not valid. Pollen of *Nothofagus* about 10,000 years BP in sediments in the Cape Flats of South Africa is thought to have been blown from South America (Schalke, 1973). A mid-Cretaceous migration of an ancestral group from southern (montane) Eurasia into Australasia *via* Africa-India seems required to account for the presence of *Nothofagus* in austral regions. At that time ancient highs on the Precambrian basement terrain, now largely reduced by erosion, may have afforded a route for entry into the temperate Southern Hemisphere. The existence of the distinctive *Nothofagus* by Maastrichtian time suggests an origin for the family at least by early Senonian time or earlier—pending a review of Turonian and Cenomanian fossils that have been referred here.

Betulaceae are Laurasian, and *Alnus* has reached South America in the late Miocene or more recently. Wood of the tribe Coryleae occurs in the latest Campanian (~ 72 m.y. BP) of California (Page, 1970), with pollen of *Alnus* known from the Maastrichtian onward (Wolfe, 1974).

Gentianales.—Of the three subfamilies of Loganiaceae (Thorne, 1968), Buddleioideae are mainly African, the genus *Buddleia* itself widespread in Laurasia, with its arrival in South America probably Neogene. Desfontainioideae have *Anthocleista* in Africa and Madagascar, *Desfontainia* and *Potalia* in South America, and *Fagraea* in tropical Asia, extending to Polynesia and Australia—clearly a West Gondwanaland nuclear group. Loganioideae are mainly African and Laurasian, but one species of the African *Mostuea* occurs in Brazil. The genus *Logania*, with about 25 species, is Australasian, and *Labordia*, with about 25 species also, is endemic to Hawaii. The general distribution indicates that at least some Loganiaceae are relatively easily dispersed, and we therefore assume that *Logania* is not necessarily ancient in Australasia.

Among related groups segregated as families by Hutchinson (1959), Antoniaceae have three genera in South America, one in Malaysia, and the monotypic *Usteria* in West Tropical Africa, again a West Gondwanaland pattern. The herbaceous Spigeliaceae are widespread in tropical regions and may be relatively easily dispersed. Strychnaceae are tropical Asian, but *Scyphostrychnos* is tropical African and *Strychnos* African, South American, and tropical Asian, just entering Australasia. The loganiaceous complex as a whole, and the elements called Desfontainioideae, Antoniaceae, and Strychnaceae, probably existed when more direct dispersal was possible between Africa and South America; this may have been the case for the genus *Strychnos* also. In spite of the endemic *Logania*, the family (sens. lat.) is apparently represented mainly by recent arrivals in Australasia and Polynesia.

The huge, widespread family Rubiaceae (Verdcourt, 1958), despite the presence of at least three small endemic genera in Australia and a good representation in Australia, New Caledonia, and even Hawaii, seems to consist mainly of recent arrivals in Australasia and Polynesia. Many rubiaceous genera have attained very wide distributions owing to ready dispersability. However, family differentiation certainly took place when Africa and South America were closer, with subgroups apparently having differentiated subsequently. Rubiaceae are well represented in tropical Asia, and there are a few primarily temperate genera, including especially those of the tribes Rubieae (Galieae) and Thelygoneae. Most genera of Central and North America and the West Indies presumably have come from South America in Neogene time and more recently.

The Apocynaceae sens. lat. (including Asclepiadaceae) have a distribution pattern similar to that of Rubiaceae. Despite the presence of a few small endemic genera in Australasia, the family does not appear to be old there; most of the genera have been derived since Miocene from related tropical Asian taxa. The subfamilies and some of the tribes of Apocynoideae and Plumerioideae probably existed when South America and Africa were closer together, and the same might even be true for Asclepiadoideae. Although there are a few temperate genera—*Apocynum*, *Asclepias*—most genera of Central and North America and the West Indies have evidently come from South America in Neogene time or more recently.

Gentianaceae may be a Laurasian group, but are well represented in Africa and in South America, mainly by unrelated genera. Menyanthaceae also appear to be Laurasian, but have achieved a wide representation in Australasia; apparently, like many water plants, they are very readily dispersed.

Fossils of these families are not known before Paleocene time (Muller, 1970). Gentianales were therefore in existence when Africa and South America were closer, and the families Loganiaceae and Rubiaceae, together with some of their subdivisions, also seem to have been present. The order evidently has reached Australasia only secondarily.

Geraniales.—Linaceae are old, with pollen of *Ctenolophon* recorded from Maastrichtian time (~ 70 m.y. BP). This genus, sole member of the subfamily Ctenolophonoideae, occurs in West Tropical Africa and Southeast Asia. In the subfamily Ixonanthoideae, *Klainedoxa*, *Desbordesia*, and *Phyllocosmus* are in tropical Africa; *Oxonanthes* in tropical Asia to New Guinea; *Irvingia* in Africa and tropical Asia; *Allantospermum* in Madagascar and Borneo; *Ochthocosmus* in tropical America; and *Cyrillopsis* in northern Brazil. They clearly are differentiates of an old West Gondwanaland plexus. Houmirioideae are mainly tropical American, but with one species of *Sacoglottis* in West Africa, to which its ancestors probably drifted. Finally, Linoideae have a number of genera in Asia, some reaching Australasia but none are endemic there; *Hugonia*, with about 40 species, shared between tropical Africa, Madagascar, and Asia; *Aneulophus* endemic in West Tropical Africa; two genera, *Hebepetalum* and *Roucheria*, endemic to South America; and the cosmopolitan *Linum*. Differentiation of the four major groups of Linaceae, often regarded as families, must have occurred when Africa and South America were closely joined, but too late for direct migration into Australia, where they are poorly represented. This is in accordance with the fossil evidence (*e.g.* Germeraad *et al.*, 1968: 275–6).

Ancistrocladaceae occur in West Tropical Africa and again from India and Ceylon to Southeast Asia. Two of the genera of Erythroxylaceae are endemic to Africa, whereas *Erythroxylum* itself is well represented in tropical America and on Madagascar, occurring in all three main tropical regions. It probably dispersed directly between Africa and South America in early Paleogene time.

Zygophyllaceae also have a West Gondwanaland distribution, with some genera reaching Asia and a few Australia. The North American endemics *Sericodes*, *Viscainoa*, and *Morkillia* suggest a considerable antiquity for the family there. *Viscainoa* and *Morkillia* are related to one another, whereas *Sericodes* is related to *Larrea*. In the light of this, Porter (1974) has suggested a North American origin for *Larrea*, with subsequent dispersal to South America and the evolution of three additional species there. On the other hand, the arguments of Hunziker *et al.* (1973) for a southern origin appear convincing also, and the family must ultimately be derived from the south. According to Porter (1974), two genera related to *Larrea* are southwest African (*Neoluederitzia*, *Sisyndite*), two South American (*Metharme*, *Plectocarpa*), and one (*Sericodes*) North American. *Viscainoa* and *Morkillia* seem to be derived from a tropical American complex that includes *Guaiacum*, *Porlieria*, and *Bulnesia*, as well as the Chilean *Pintoa*, probably following a Paleogene arrival in North America (Porter, 1974). *Fagonia* is highly disjunct and evidently easily dispersed. Other genera of Zygophyllaceae north of Panama are apparently recent arrivals from South America. The preceding families, constituting the suborder Linineae, certainly differentiated in West Gondwanaland prior to the Maastrichtian.

In the next suborder, Geraniineae, most of the family radiation seems to have occurred later, with Oxalidaceae, including the genus *Biophytum*, shared between South America, Africa, and Asia. However, Geraniaceae and Balsaminaceae are primarily Old World families, Tropaeolaceae South American. The most generalized Geraniaceae, the Vivianoideae, are South American. In the suborder Limnanthineae, the only family, Limnanthaceae, is confined to western North America and is probably autochthonous.

In the suborder Polygalineae, Malpighiaceae are confined to South America, with secondary extensions to Central and North America and the West Indies, except for the subtribes Aspidopteryginae (7 genera, 79 species) in Africa and Asia, with one widespread tropical species just reaching tropical Queensland; and Sphedamnocarpinae (6 genera, 45 species), also in Africa and Asia, with one species of *Rhyssopteris* native in northeastern Queensland. Since these two subtribes are related respectively to the New World subtribes Mascagniinae and Banisteriinae (Niedenzu, 1928), the introduction of at least two separate New World lines into the Old World, probably Africa, is suggested (W. R. Anderson, personal communication). In context, the family scarcely seems old enough to have passed more or less directly between South America and Africa, so one may perhaps visualize mid-Tertiary or Early Neogene long-distance dispersal across the South Atlantic. Both of these groups consist of plants that have winged fruits. The probability of older long-distance dispersal of the ancestors of Aspidopteryginae and Sphedamnocarpinae seems enhanced by the occurrence of one species each of *Heteropterys* and *Stigmaphyllon*, both with winged fruits and belonging to two different Neotropical genera, in West Africa; presumably their ancestors were dispersed across the South Atlantic quite recently (W. R. Anderson, personal communication).

Polygalaceae are common to South America, Africa, and tropical Asia, with the basically tropical genus *Polygala* secondarily widespread in temperate regions. The other Central and North American genera evidently were derived from South America, and *Securidaca* leaves and pollen are in the Early Miocene of Oregon (Wolfe, 1962). Trigoniaceae are in tropical South America, Madagascar, and Malaysia—an ancient relationship. Vochysiaceae, except for *Erismadelphus*, a large forest tree of tropical West Africa, are confined to tropical America. Polygalineae seem to have radiated in West Gondwanaland, but have scarcely reached Australasia. An evident exception is the well developed Australian genus *Comesperma* (Polygonaceae), closely related to if not identical with the South American *Bredemeyera*, which probably reached Australia by a cool-temperate southern route. The North American representatives of Polygalineae consist of a few temperate genera from Eurasia with some South American additions presumably dating from the Miocene or more recently.

Hamamelidales.—Most families of this ancient and archaic group are entirely Laurasian: Trochodendraceae, Tetracentraceae, Eupteleaceae, Cercidiphyllaceae, Eucommiaceae, Platanaceae. In the Hamamelidaceae itself, the subfamilies Liquidambaroideae, Disanthoideae, Rhodeleioideae, and Exbucklandioideae are exclusively Laurasian. In the subfamily Hamamelidoideae most genera are Laurasian, and especially tropical Asian, with *Distyliopsis* in New Guinea; *Trichocladus* is endemic to tropical East and South Africa, and *Dicoryphe* is restricted to Madagascar and the Comoros. The monotypic genera *Neostrearia* and *Ostrearia* (Smith, 1958) are endemic to tropical Queensland. These two genera are quite distinct from one another and closely related to the Malaysian *Embolanthera* and *Maingaya* (Smith, 1958; P. K. Endress, personal communication) and to the African *Trichocladus.* They therefore would seem to be Miocene or more recent arrivals in Australia from Asia. The relationship postulated between the Australian genera and *Dicoryphe* of Madagascar by White (1936: 61) is not borne out by a reexamination of their characteristics (P. K. Endress, personal communication).

Hamamelidales may have originated in eastern Asia–Western North America (Wolfe, 1974) by early Upper Cretaceous time, but seem to have reached West Gondwanaland before the close of the Period. Aubréville (1970) mentions wood of Hamamelidaceae from the Saharan region from the close of the Cretaceous, and L. J. Hickey (personal communication) has suggested that the record of *Araliaephyllum* from the Cretaceous of Argentina (Menéndez, 1972) may refer to a hamamelid. The existence of the distinctive endemic *Dicoryphe* in Madagascar might reflect Paleocene or earlier migration of Hamamelidaceae—Hamamelidoideae to Africa from Laurasia. Alternatively, the group might have differentiated in West Gondwanaland, a possibility that will be clarified only with additional fossil evidence.

Lamiales.—Hydrophyllaceae are principally North American, with *Hydrolea* widespread through tropical America, Africa, and Asia. *Codon* consists of two South African species. The South American Hydrophyllaceae, with the possible exception of *Hydrolea,* all appear to have been derived in Neogene time and more recently from North America. If *Codon* is truly related to other members of the family, its distribution is extremely unusual.

Boraginaceae are mainly Laurasian and have reached the southern lands repeatedly, producing a few endemic genera—*Embadium, Halgania,* and *Omphalolappula* in arid portions of Australia, for example. *Wellstedia,* representing a distinct subfamily, indicates some antiquity for the Boraginaceae in Africa, as do the Ehretioideae in South America. Judging from the excellent representation of ehretioid genera in the Eocene of southern England (Chandler, 1964), and the presence of several genera in Africa (*Poskea* is better referred to Scrophulariaceae), the subfamily may have spread to South America *via* Africa by Paleogene time. Lennoaceae are North American. Hoplestigmataceae consist of two species of African trees, perhaps related to Boraginaceae.

In Verbenaceae, Chloanthoideae are mainly Australian shrubs, with some representation in Madagascar and possibly East Africa, according to Airy Shaw (1966). Stilboideae are entirely South African. Phrymatoideae are Laurasian, Nyctanthoideae tropical Asian, Caryopteridoideae Asian. Symphorematoideae are mainly tropical Asian, with *Congea* also in tropical Africa and South America. Avicennioideae consist of the widespread mangrove genus *Avicennia*. Both Verbenoideae and Viticoideae are widespread in tropical Asia, Africa, and South America, with an appreciable Laurasian element also, and a few endemic genera of Verbenoideae in Australasia. The distinctive, monotypic Lithophytoideae occur in semiarid southern Mexico (D'Arcy & Keating, 1973). Callitrichaceae are widespread water plants. Lamiaceae include the Australian Prostantheroideae and seven other subfamilies which are perhaps basically Laurasian but well represented in Africa and South America. Ocimoideae may have spread relatively early—perhaps in Paleogene time—between Africa and South America, with Hyptidinae (South America) and Plectranthinae (Old World) having evolved subsequent to the wider separation of these continents (R. M. Harley, personal communication). *Tetrachondra* (the only genus of Tetrachondroideae) occurs in southernmost South America and New Zealand.

The order Lamiales, and probably ancestral Verbenaceae and Boraginaceae-Ehretioideae, seem likely to have been in existence when Africa and South America were closer. An unusual feature of the order is the strong development of endemic subfamilies of Verbenaceae and Lamiaceae in Australia. Rather than suggesting a very early arrival there, which would be inconsistent with the apparent age of the group, this pattern may imply a Paleogene arrival with subsequent extensive radiation as subarid and semihumid habitats expanded in Australia (Raven & Axelrod, 1972).

Leitneriales.—A single species of the southeastern United States. Pollen of *Leitneria* has been reported from the Oligocene of southern England (Chandler, 1964) and seeds from the Oligocene of Siberia (Dorofeyev, 1963).

Malvales.—Fossils of Sterculiaceae and Tiliaceae are well represented in the Eocene of both Europe and the United States, with Sterculiaceae extending to the Paleocene and perhaps even Maastrichtian in North America (Chandler, 1964; Krutzsch, 1967; L. J. Hickey, personal communication). The European records include pollen of the tropical Asian Tiliaceae—Brownlowieae (Krutzsch, 1967). Tiliaceae are in the Indian Eocene (Lakhanpal, 1970). Judging by the strong representation of these families also in both South America and Africa, it seems reasonable on the basis of present evidence to assume that they were in all four continents by early Paleogene time, having spread between Europe and Africa and across a narrow Atlantic Ocean between Africa and South America. The remarkable endemic sterculiaceous genera *Fremontodendron* (California, Arizona, Baja California) and *Cheirostemon* (*Cheiranthodendron*; southern Mexico, Guatemala) are probably derived from an older Laurasian element, whereas other genera doubtless entered from South America starting in Eocene time. The subfamily Byttnerioideae of Sterculiaceae is well represented in Australia. *Keraudrenia* and *Rulingia* of this group are common to Australia and Madagascar, which they probably reached by long-distance dispersal around the Indian Ocean.

Ancestral Byttnerioideae probably reached Australia *via* a temperate Antarctic route from South America.

Bombacaceae have distinctive pollen, which has not been found before the Paleocene (Muller, 1970). They are represented in Australia only by a species of the widespread tropical genus *Bombax* and one of the primarily Mascarene and African *Adansonia.* This suggests that the single species of *Adansonia* reached that continent by long-distance dispersal in the Tertiary, contrary to our earlier view (Raven & Axelrod, 1972). Like the two families just discussed, Bombacaceae are well represented in both Africa and South America, probably passing between them by Paleogene time across a narrower Atlantic Ocean. The presence of the North American endemic *Nephropetalum* (Texas, adjacent Mexico), considered in the context of the family, suggests that the pattern for Bombacaceae might be essentially similar to that proposed for Sterculiaceae and Tiliaceae, but the apparent absence of Bombacaceae in the Eocene London Clay (Chandler, 1964), in contrast to the other two families, might lend more credence to the notion of an African–South American origin for the group. In any case, Bombacaceae were in western North America by the earliest Middle Eocene (Leopold & MacGinitie, 1972) and have been reported frequently in the North American region from that time onward (*e.g.*, Graham & Jarzen, 1969; Langenheim, Hackner & Bartlett, 1967).

A southern origin is very likely for Elaeocarpaceae, best represented in South America, southeast Asia, Madagascar, and by several endemic genera in Australia, but the family is absent on the mainland of Africa. Wood of Elaeocarpaceae is reported from the Paleocene of Patagonia and from the Tertiary of India (Petriella, 1972; Lakhanpal, 1970), and fruits are reported from the Eocene of southern England (Chandler, 1964). Since the family is represented only by the widespread and common Asian genera *Elaeocarpus* (2 species) and *Sloanea* (1 species) in Madagascar, it probably reached Madagascar by long-distance dispersal around the Indian Ocean. *Sloanea* occurs in Australia only in the northeastern tropics, and probably spread from Asia to America by long-distance trans-Pacific dispersal. *Aristotelia*, on the other hand, may have spread between Australasia and temperate South America *via* an Antarctic route, or, in view of its fleshy fruits, been carried by birds.

Malvaceae are so well represented all over the world that it is difficult to analyze their distribution. They are reported from doubtful Upper Cretaceous macrofossils (Muller, 1970), but their pollen first appears in the fossil record in the Lower Eocene (Muller, 1970), and in New Zealand by the Middle Eocene (Couper, 1960). Connections between the floras of Africa and South America are indicated by the tribe Gossypieae (*e.g.* Fryxell, 1969), but *Gossypium* and some other genera of the tribe are so easily dispersed they even occur on oceanic islands, including Hawaii. The distinctive Australasian *Plagianthus* probably came *via* a temperate Antarctic route, and in general the family does not appear old enough for more or less direct dispersal between Africa and South America.

Considering present distributions and the available fossil record, it appears most likely that the primary radiation of Malvales took place in Africa + South America in Maastrichtian time or earlier, although the alternate possibility of a primary radiation in the north cannot yet be excluded. First Sterculiaceae, then Tiliaceae and Bombacaceae, and finally Malvaceae reached Eurasia and then North America, with direct dispersal from South to North America increasing in importance throughout the Tertiary. Elaeocarpaceae have remained almost entirely a southern group. Sphaerosepalaceae, a family of two genera and some 14 species which are endemic to Madagascar, is of such uncertain affinities (*cf.* Airy Shaw, 1966), that it should not be taken into account in arguments about the phytogeography of the order (see also Theales).

Myricales.—The single family Myricaceae appears to be Laurasian, but *Myrica* also occurs in Africa and South America (where it may be relatively recent). *Canacomyrica* consists of a single New Caledonian species; it may have no direct relationship to Myricaceae (R. F. Thorne, personal communication), but is at least a very distinct subfamily (Leroy, 1949). Macrofossils of Myricaceae are reported from the Upper Cretaceous (Muller, 1970).

Myrtales.—Myrtaceae are perhaps the oldest family in the order (Muller, 1970), possibly extending back to Cenomanian time (Penny, 1969). Unfortunately, the identification of early Normapolles-type pollen with particular families is problematical (Wolfe, 1974). The original differentiation between the subfamilies Myrtoideae and Leptospermoideae evidently took place from an ancestral stock that occupied West Gondwanaland (Myrtoideae) and Australasia (Leptospermoideae). Myrtoideae are better represented in South America than in Africa at present, and abundant in tropical Asia, where they have been joined in the Miocene and more recently by some Australasian Leptospermoideae. If the Miocene record of *Eucalyptus* in Patagonia (Frenguelli, 1953) is reconfirmed, then Leptospermoideae would be seen to have reached South America *via* Antarctica. Various South American Myrtoideae have reached Central and North America and the West Indies, where most living genera of the family seem to be newcomers. The family is known from the Eocene of Europe (*e.g.* Szafer, 1964; Krutzsch, 1967) and Colorado (MacGinitie, 1969). Pollen of *Metrosideros* is known from the Maastrichtian of New Zealand (Couper, 1960), and macrofossils are reported from Argentina (Menéndez, 1972), also in the Upper Cretaceous.

Melastomataceae evidently evolved too recently to reach Australasia more or less directly, and in that region they are evident newcomers and poorly represented. They are abundant and diverse in South America, well represented in Africa and tropical Asia, and have a few temperate genera in Laurasia (Meijer, 1972). They are evidently easily dispersed, but the original stock seems to have been in existence in Paleogene time, when Africa and South America were relatively close. Probable pollen has been reported from the Paleocene of Colombia Hammen & García de Mutís, 1966).

Lythraceae are best represented in South America, where a number of endemic genera occur, some of which (*Cuphea* is a notable example) have radiated extensively in Central America, the West Indies, and southern North America after what may have been a late Paleogene arrival in North America. There are several endemic genera in Africa, but no close relationships with those of South America, implying their long isolation. The family is well represented in Laurasia, with genera such as *Decodon*, *Lythrum*, *Lagerstroemia*, and probably *Ginorea* having evolved in temperate or subtropical areas there. Lythraceae are known from the Eocene onward in both Eurasia and in India (Graham & Graham, 1971; Eyde, 1972*a*). The pattern of distribution in Lythraceae is strikingly like that in Melastomataceae, suggesting the ancestral forms were probably present in West Gondwanaland and Eurasia early, but not early enough to have reached Australia until Neogene time. Some genera are widespread aquatics.

Oliniaceae and Penaeaceae are African but not necessarily properly placed in this order (see Rao & Dahlgren, 1969); Crypteroniaceae, Punicaceae, and probably Trapaceae are Laurasian. Onagraceae seem to be chiefly Laurasian, but two of the least specialized genera, *Fuchsia* and *Ludwigia*, center in South America(–Africa?). *Fuchsia* had reached New Zealand by the Middle Miocene (Couper, 1960; Jenkins, 1971; Raven, 1973*a*), probably by long-distance trans-Pacific dispersal (Raven, 1973*a*). Early connections between North and South America are suggested by this family.

For Combretaceae (Exell & Stace, 1966, 1972), the subfamily Strephonometoideae (1 genus, 7 species) is tropical West African. In the second subfamily, Combretoideae, there are two tribes, of which the Laguncularieae consist of two widespread littoral genera, *Laguncularia* and *Lumnitzera*, and the endemic Australasian *Macropteranthes*. The second tribe, Combreteae, consists of three subtribes: (1) Pteleopsidinae (1 genus, 10 species, tropical Africa); (2) Combretinae, including three endemic African, one South American, one Asian, one African and Asian (*Quisqualis*), and one pantropical (*Combretum*) genus; and (3) Terminaliinae, including three American; one African; one Asian; one African and Asian; and two pantropical (*Terminalia, Conocarpus*) genera. Of the Terminaliinae, *Bucida*, with nine species, is largely centered in the tropical North American area. Combretaceae appear to provide evidence of early links between Africa and South America, both in Combretinae (even two sections of *Combretum* are common; Exell & Stace, 1972) and Terminaliinae. They are clearly newcomers to Australasia, and *Bucida* may or may not have originated in tropical North America.

Summarizing for Myrtales, the order itself and the family Myrtaceae specifically seems to be old enough to have dispersed more or less directly to Australia by a subtropical route before the full opening of the Indian Ocean. Melastomataceae, Lythraceae, and Combretaceae seem to have existed when South America and Africa were much closer. Onagraceae are mainly Laurasian, but early in South America. Myrtales apparently had become common to West Gondwanaland and Laurasia by the close of the Cretaceous, with the differentiation of families occurring in both areas. The geographical relationships accord with a pre-Eocene period of differentiation, as suggested by Muller (1970).

Nepenthales.—*Nepenthes*, the sole genus of this order, is found in tropical East Asia (and northern Australia), New Caledonia, Ceylon, the Seychelles, and Madagascar. It occurs in open habitats (see Rauh, 1973), and its small seeds are easily dispersed, so that its scattered range around the Indian Ocean may not reflect any great antiquity, any more than does its spread to northern Queensland, despite the arguments of Dejardin *et al.* (1973: 383). It is doubtless originally tropical Laurasian in origin.

Nymphaeales.—This group of widespread water plants might have originated either in West Gondwanaland or Laurasia. Leaves attributed to Nymphaeaceae are reported from the Upper Cretaceous of Argentina (Menéndez, 1972), and from the Paleocene of the Rocky Mountains and Great Plains (Brown, 1962). Remains attributed to the group are also in the Albian of the U.S.S.R. and Maryland (Samylina, 1968).

Oleales.—The three genera of Salvadoraceae all occur in Africa and tropical Asia. In the Oleaceae (Johnson, 1957), the subfamily Oleoideae has a Laurasian distribution but is very well represented in Africa, with *Notelaea* and *Nestegis* Australasian. In the second subfamily, Jasminoideae, *Menodora* (Steyermark, 1932) is in South America and South Africa, as well as North America, with one species common to South America and Africa. One species of the African and Asian *Schrebera* is known from Peru (P. S. Green, personal communication). *Jasminum* is entirely introduced in the New World (Green, personal communication). Oleaceae have considerable antiquity both in Africa and in Laurasia, where several temperate genera have evolved. They were probably not present in Africa when direct dispersal to South America was possible. This analysis implies that *Notelaea*, *Nestegis* (*Gymnelaea*), and other Australasian Oleaceae probably are to be regarded as immigrants in the Oligocene or more recently (P. S. Green, personal communication). The presence of *Nestegis* in Hawaii attests to its powers of dispersal.

Pittosporales.—The six families of the suborder Brunineae are all African, the three of suborder Pittosporineae Australasian, although *Pittosporum* ranges to Africa, Madeira, and into the Pacific as far as the Hawaiian Islands. If these groups are really homogeneous and related, the order might have considerable antiquity and may have spread more or less directly between Australia and Africa. The six families of Brunineae are placed in four different unrelated orders by Takhtajan (1969). Cronquist (1968), by placing most of Thorne's (1968) Pittosporales in Rosales, implies that there might not be a direct relationship between Thorne's subgroups. The third suborder, Daphniphyllineae, consists of a single genus of tropical Asia which may or may not belong with this group of families. The North American Stegnospermaceae, placed in this order by Hutchinson (1959), have betacyanins and belong in the Chenopodiales (Mabry, Taylor & Turner, 1963). Clearly, the Pittosporales need intensive study.

Plumbaginales.—Plumbaginaceae, first known from the fossil record in the Upper Miocene, are evidently easily dispersed, judging from their nearly cosmopolitan distribution.

Primulales.—Myrsinaceae and Primulaceae seem to have been West Gondwanaland–Laurasian counterpart families, with each having extended its range into the area of the other subsequent to their initial radiation. Myrsinaceae probably have considerable antiquity in the Asian tropics and are known from the Eocene of southern England (Chandler, 1964). *Tapeinosperma* is Australasian. The Central and North American Myrsinaceae and the South American Primulaceae presumably date from Neogene time or more recently. Theophrastaceae may have differentiated from primulalean stock in tropical North America and then spread to South America as opportunities for migration between the continents became greater. *Clavija* is, however, a predominantly South American genus of this close-knit family, but the most advanced in the family morphologically (W. G. D'Arcy, personal communication), indicating that it may be derived from ancestors that spread to South America in or shortly before Neogene time.

Proteales.—Of the three subfamilies of Proteaceae (Johnson & Briggs, 1963 and personal communication), the most generalized, Persoonoideae, is confined to Australasia; Proteoideae to Australasia and Africa; and Grevillioideae to Australasia (reaching Fiji), Africa, and South America. It seems logical to assume that the early diversification of the family took place in warm, moist, equable forest climates in the Australasian region (Johnson & Briggs, 1963 and personal communication; Venkato Rao, 1971) from ancestors that arrived there in the mid-Cretaceous from West Gondwanaland. *Proteacidites* is a pollen type widely distributed in the Southern Hemisphere in early Upper Cretaceous time (Muller, 1970). A derivation of Proteaceae and the possibly related Laurasian Elaeagnaceae (Cronquist, 1968) from Myrtales (Cronquist, 1968) is clearly contradicted by the anatomical evidence (Eyde, 1975) and is not supported by what is known of the relative ages of the groups either. The first unequivocal records of Proteaceae pollen in the fossil record are from the Santonian (~ 82 m.y. BP) of Australasia, including New Zealand (Couper, 1960; Muller, 1970). Proteaceae and Myrtales may be derived from common rosid ancestors no later than Early Cenomanian time (~ 110 m.y. BP; J. A. Doyle, personal communication). The pollen of Proteaceae is first known in South America from the Middle Maastrichtian (~ 68 m.y. BP) of Patagonia (S. Archangelsky, personal communication). There are no unequivocal records of Proteaceae from the Northern Hemisphere (J. A. Wolfe, personal communication; D. L. Dilcher, personal communication; Tschudy, 1971).

Some members of the subfamilies Proteoideae and Grevilleoideae seem to have migrated more or less directly from Australasia to West Gondwanaland following their presumed origin in Australasia, but only Grevilleoideae exist in South America at present. South American members of this subfamily belong to six distinct alliances (Johnson & Briggs, 1963, and personal communication)—(1) *Orites*, (2) *Lomatia*, (3) *Oreocallis* and *Embothrium*, (4) *Euplassa–Gevuina*, (5) *Roupala*, and (6) *Panopsis*. *Orites*, *Lomatia*, *Gevuina*, and *Oreocallis* are shared between Australasia and South America. The first three groups may have originated in Australasia and migrated to South America *via* Antarctica, even though *Oreocallis*, in the South American portion of its range, is confined to the northern Andes. If this reasoning is correct, then *Oreocallis*-like ancestors probably gave rise to *Embothrium* in South America. Pollen similar to that of *Lomatia* and pollen similar to that of some species of *Embothrium* is known from the Lower Paleocene of Patagonia (S. Archangelsky, personal communication).

The last three groups listed above include all the South American representatives of the tribe Macadamieae. Two species of this primarily Australasian group occur in Africa. One belongs to a monotypic genus, *Brabeium*, which occurs in relatively moist, sheltered habitats in South Africa. The second occurs in Madagascar and has been referred to the otherwise Australasian and tropical Southeast

Asian genus *Macadamia* (Capuron, 1963), but it actually represents an undescribed genus related to certain Australian genera and to the Asian *Heliciopsis*. *Macadamia*, *Brabeium*, and *Panopsis* constitute a closely related group within the Macadamieae (Johnson & Briggs, 1963, and personal communication). The South American *Panopsis* has an entirely tropical distribution and seems a most unlikely candidate to have spread between Australia and South America *via* Antarctica. In the light of the present distribution pattern, relationships, and the inferred antiquity of the group, it seems possible that the ancestors of *Panopsis* migrated directly between South America and Africa, where *Brabeium*, a member of the same lineage, survives. *Roupala*, on the other hand, which extends to southern Mexico at present, is directly related to an Australasian genus (Johnson & Briggs, personal communication), and it is difficult to ascertain the probable route of the plants of this alliance between Australasia and South America. Even though *Gevuina* is common to Australasia and South America, *Euplassa* is closely related, in some ways more primitive, and confined to South America. If the line that gave rise to *Euplassa* came to South America *via* Africa, as would be inferred from its ecology and relationships, it is now extinct in Africa, and the same might be true of the ancestors of *Roupala*. The tribe also includes *Heliciopsis*, the only exclusively Asian genus of Proteaceae, the ancestors of which presumably came from Australia in the Miocene. Our current understanding of the relationships within Proteaceae suggests that the ancestors of the Mascarene species of "*Macadamia*" came from Australia, but the timing of their arrival is uncertain.

In summary, the initial diversification of Proteaceae seems to have taken place in Australia, and then various groups seem to have migrated out by different routes and at different times: Macadamieae (Grevilleoideae) and Proteoideae to Africa in the Upper Cretaceous; at least one line of Brabeieae to South America and Africa in the Upper Cretaceous or Paleocene (tropical groups) and three to five lines of other Grevilleoideae *via* Antarctica (temperate groups), at least one by Maastrichtian time; *Macadamia*, *Helicia*, and the ancestors of *Heliciopsis* across Wallace's line in the Miocene or subsequently; and *Roupala* into the North American region at about the same time. *Gevuina* may be a genus that originated in South America and then migrated to Australia *via* Antarctica subsequently.

Rafflesiales.—Hydnoraceae exhibit an African–South American disjunction, one of the two genera being found in each region. Rafflesiaceae are basically a Laurasian family which reached South America and Australasia probably in the Miocene or more recently (*Pilostyles*), and, probably by long-distance dispersal, South Africa (*Cytinus*). Both families consist of fleshy parasites.

Rhamnales.—Elaeagnaceae are Laurasian, with one species just reaching the northern tip of Australia. Rhamnaceae are so well represented both in tropical and temperate regions that it is difficult to trace the history of the family. A number of genera of Rhamnaceae, some endemic, occur in Australasia.

Rosales.—In the large saxifragalean alliance, the elements of which are often accorded family status, the subfamilies Penthoroideae, Saxifragoideae, Ribesioideae, Lepuropetaloideae, Parnassioideae, Pterostemonoideae, and Hydrangeoideae (Stebbins, 1972) are essentially Laurasian, with many genera having reached South America in Neogene time or more recently. Vahlioideae and Montinioideae are African groups, Francooideae, Columellioideae, and Phyllonomoideae are South American. Escallonioideae are South American and Australasian, presumably having migrated between the two areas *via* Antarctica, and *Tetracarpaea* (Tetracarpaeoideae; monotypic; Tasmania) may be a derivative of this line in Australasia. The Laurasian *Itea* and the African *Choristylis* constitute the Iteoideae. Brexioideae are shared between East Africa and the islands in the western Indian Ocean (*Brexia*, *Roussea*) and New Zealand (*Ixerba*), presumably reflecting ancient dispersal between these areas before the major opening of the Indian Ocean. Eremosynoideae, consisting of a single Australian annual species, are very distinctive in the Saxifragaceae s. lat.

Chrysobalanaceae have a distribution that suggests direct migration between South America and Africa, as well as to Asia and eventually Australia. Rosaceae are mainly Laurasian, but the existence of the ancient and archaic *Quillaja* and *Kageneckia* in South America; the Neuradoideae in Africa; and three isolated woody genera of the tribe Sanguisorbeae—*Margyricarpus*, *Tetraglochin*, and *Polylepis*—in South America with other comparable genera in Africa including *Bencomia* of the Canary Islands, suggest connections between South America and Africa. *Acaena* presumably evolved from primitive Sanguisorbeae in South America and later spread widely around the Antarctic region (Moore, 1972; Raven, 1973*b*). *Hesperomeles* is a genus of Maloideae which evidently originated in tropical North America and migrated into northwestern South America in Neogene time. Relationships of the South American *Quillaja* and *Kageneckia* to one another and to various northern genera are of interest; if they are related to the North American *Vauquelinia*, *Lyonothamnus*, and *Lindleya* (Banwar, 1966), a very early example of sweepstakes dispersal of their ancestors to South America would be inferred. No related genera are found in Africa.

Connaraceae have a West Gondwanaland pattern, and seem to have migrated between Africa and South America in Paleogene time, and to Asia; they are poorly represented in Australasia. In the Fabaceae, both Mimosoideae and Caesalpinioideae have distributions like Connaraceae, whereas Fabodeae have radiated more extensively in Laurasia. Although the family is easily dispersed and offers perplexing patterns of distribution, it may well have originated or at least undergone its primary radiation and differentiation into three subfamilies in West Gondwanaland (R. M. Polhill, personal communication). The subsequent history of the family has been marked by frequent interchange between Northern and Southern Hemispheres, and the gradual accumulation of a strong representation of all three subfamilies in Australasia, probably commencing in Paleogene times. There are no reliable Cretaceous records of Caesalpinioideae (Germeraad *et al.*, 1968; J. A. Wolfe, personal communication). *Hymenaea* (Caesalpinioideae), which is spread easily in sea drift and is common to tropical Asia, Africa, and South America, had become established in Chiapas, Mexico, by the close of the Oligocene and was producing amber (Langenheim, 1967). It also occurs on many islands in the West Indies. The tribe Cynometreae, to which *Hymenaea* belongs, provides evidence of close links between Africa and South America (Langenheim, 1973).

Crassulaceae have had their principal radiation in Africa, but are also well developed in Laurasia, with some nearly cosmopolitan. Scarious calyces that have been compared with those of *Dudleya* are reported from the Eocene of California (MacGinitie, 1969); their identity needs to be confirmed. Droseraceae are so widespread that it is especially difficult to trace their history; their pollen does not appear in the fossil record until the Miocene (Leopold, 1969), but *Aldrovandra*, a widespread aquatic of Eurasia and tropical Australasia, was represented by two species in the Eocene of southern England (Chandler, 1964). Podostemonaceae have a West Gondwanaland distribution, with extensions to tropical Asia. Stylidiaceae are Australasian, with secondary extensions to temperate South America and tropical Asia. Their distribution, and that of the Australian Cephalotaceae, does not accord well with Thorne's (1968) placement of these families in his Rosales. Coriariaceae, despite the fact that they are best represented in New Zealand, may be Laurasian, possibly exhibiting the sort of pattern discussed by Raven (1973*a*) for *Fuchsia*. *Coriaripites* is recorded from the Maastrichtian of Alberta (Srivastava, 1970), but the single existing New World species of *Coriaria* might nevertheless have spread north from South America following long-distance transport from New Zealand *via* Tahiti. Diapensiaceae and Crossosomataceae are definitely Laurasian, Greyiaceae southern African.

One of the suborders of Rosales, Cunoniineae, deserves special attention. Cunoniaceae not only have a West Gondwanaland distribution (but without extensions into Asia), they are apparently old enough to have spread more or less directly to Australasia by a subtropical route. Even the genus *Cunonia*, admittedly loosely held together, is found in South Africa and New Caledonia. On the other hand, the very distinctive pollen grains of Cunoniaceae appear in the record in New Zealand only in Lower Miocene time (Couper, 1953). Paleocene wood of Cunoniaceae is known from Patagonia (Petriella, 1972). Pollen very similar to that of the South American genus *Lamanonia* is reported by Hickey (1974) from the Early Tertiary Golden Valley formation of North Dakota, indicating an early arrival in the north, presumably by sweepstakes dispersal. Among the rest of the group, Brunelliaceae are South American, Davidsoniaceae northeast Australian, Eucryphiaceae Australasian–South American, Corynocarpaceae restricted to the southwest Pacific and Medusagynaceae, probably better referred to Theales, confined to the Seychelles. Staphyleaceae evidently represent an ancient Laurasian derivative of this suborder, which otherwise has remained mainly southern.

The pattern of distribution in Rosales suggests that the group may have been in existence before the major opening of the Indian Ocean. The ancestors of the Saxifragaceae s. lat., including Brexioideae, and Cunoniaceae seem to have differentiated very early. Of later origin, but in existence in Paleogene time, when Africa and South America were much closer, were the Chrysobalanaceae, Connaraceae, Mimosoideae, Caesalpinioideae, Podostemonaceae, and perhaps Rosaceae and Faboideae. A number of the other groups originated early enough to migrate more or less directly between South America and Australasia *via* a cool temperate East Gondwanaland (Antarctic) route.

Rutales.—Since Rutaceae are well represented in South America, Africa, Eurasia, and Australasia, they may have originated early enough for more or less direct migration to Australia. Paleocene wood is known from Patagonia (Petriella, 1972), and the family is well represented in the Eocene of southern England (Chandler, 1964). Simaroubaceae probably also migrated more or less directly between Africa, South America, and Asia, where the temperate *Ailanthus* evolved. Whether the ditypic endemic *Cadellia* and the related monotypic endemic *Guilfoylia* in Australia are ancient elements seems doubtful in view of their ecology. The presence of the endemic *Holacantha* and *Recchia* in Mexico and the adjacent United States suggests the pattern found in Zygophyllaceae. On the other hand, Simaroubaceae are represented by three genera in the Hawaiian Islands and the family is presumably readily dispersed. Surianaceae consist of a single species widespread on tropical shores. Wood of *Suriana* has been reported from the Eocene of Wyoming (Kruse, 1954). Cneoraceae include one species of *Cneorum* in the Mediterranean region, one in Cuba, as well as the closely related monotypic *Neochamaelea* in the Canary Islands.

Meliaceae are tropical Asian, African, and South American, and clearly newcomers in Australasia. *Guarea*, common to tropical America and Africa, was present by the Maastrichtian in North America (Graham, 1962), presumably having arrived *via* Africa and Europe. There are many North American Tertiary records of *Cedrela* from the Paleocene onward. Meliaceae are also well represented in the Paleogene of southern England (Chandler, 1964). Burseraceae share this pattern of distribution, but the presence of perhaps half of the species of *Bursera* in Mexico, Central America, and the West Indies suggests that they may have some antiquity both in North and in South America. Amber in the Eocene London Clay is thought to have been produced by burseroids (Langenheim, 1969), and the family is reported from the Eocene of North America (MacGinitie, 1969). Fruiting structures similar to those of *Bursera* are well represented in the Paleogene of southern England (Chandler, 1964).

Anacardiaceae have a pattern of distribution similar to Simaroubaceae, with *Euroschinus* and *Rhodosphaera* endemic in Australia, *Cyrtocarpa*, *Comocladia* and several other genera endemic to Central America, southern North America, and West Indies. The mainly South American *Tapirira* is known from the Oligo-Miocene Chiapas amber of southern Mexico (Langenheim, 1964). Anacardiaceae are reported from the Cretaceous of Argentina (Menéndez, 1972) and are represented in the Paleogene of southern England (Chandler, 1964) and Oregon (Scott *in* Chandler, 1964: 58). Sapindaceae are again similar, but well represented in Australasia, and reliably known from North America in the Eocene. Pollen of Sapindaceae appears in New Zealand in Paleocene time (Couper, 1960). The family is well represented in the Paleogene of southern England (Chandler, 1964). Juglandaceae and Rhoipteleaceae, constituting the suborder Juglandineae, are Laurasian, and Juglandaceae reached South America only in late Neogene time (Brown, 1946). Cenomanian records of Juglandaceae (Muller, 1970) are very doubtful, but the evolutionary line leading to this family had diverged by the Early Campanian (~ 80 m.y. BP; Wolfe, 1974). *Rhoiptelea* is known from Maastrichtian pollen (Wolfe, 1974).

Of the remaining families related to Sapindaceae, Sabiaceae are predominantly Asian and tropical American. *Meliosma* (Beusekom, 1971) is in tropical Asia and tropical America, but was widespread throughout Laurasia in Paleogene time. Of the three species of subg. *Kingsboroughia*, two are Asian, and the third, *M. alba* (Schlechtend.) Walp., disjunct in southeast Asia and southern Mexico. Paleogene and Neogene fossils representing this subgenus occur in North America and Europe, as well as in Japan (Beusekom, 1971). In subg. *Meliosma*, sect. *Meliosma* is entirely southeast Asian, but sect. *Lorenzanea* is South American. The genus *Ophiocaryon* is also endemic in South America. North American Tertiary fossil leaves which are compared by Beusekom (1971) with sect. *Lorenzanea* may all belong to sect. *Meliosma*, as do the most of North American fossils. Beusekom (1971) has considered sect. *Lorenzanea* (as well as the genus *Ophiocaryon*) as autochthonous American taxa, but that does not solve the problem of how they reached South America. Presumably this distribution could have been achieved most easily *via* Africa, where the family is not now represented, but where it may well be found in the fossil record. Thus *Meliosma* subg. *Meliosma* may have reached Mexico by two routes, one *via* Africa, the other by way of Beringia or, more probably, the North Atlantic. If a critical evaluation of the North American fossils definitely establishes the existence of sect. *Lorenzanea* in North America, then very early and unlikely long-distance dispersal to South America might be postulated; how *Ophiocaryon* or its ancestors arrived in South America would still pose a difficult problem.

Melianthaceae are African, the monotypic Akaniaceae, Australian. Aceraceae are Laurasian. Hippocastanaceae are also Laurasian, *Billia* evidently having migrated into Colombia in Pliocene time or more recently. Breitschneideraceae are Chinese.

Much of the primary differentiation of Rutales seems to have taken place in Africa–South America, with long-standing connections to Eurasia. It appears possible that at least Rutaceae and Sapindaceae, and probably Simaroubaceae and Anacardiaceae, had appeared early enough (Turonian?) for more or less direct migration to Australia. Several families of Rutales include relict genera in the North American region, suggesting early differentiation in semiarid sites in Laurasia.

Salicales.—The single family, with three genera, is clearly Laurasian.

Santalales.—Celastraceae are widely distributed in temperate and tropical regions, including Australasia, and evidently relatively easily dispersed. They are reported from Cretaceous macrofossils (Muller, 1970), but not known from fossil pollen until the Upper Miocene. They show no obvious patterns of distribution linked with continental movements. The related Stackhousiaceae are essentially Australasian. Icacinaceae are well represented in Africa, South America, and tropical Asia, and evidently dispersed between Africa and South America when they were much closer. There are at least four endemic genera in Australasia, and pollen is reported from the Upper Cretaceous of New York State (Scott & Barghoorn, 1957), with fruits known from the Paleocene of Egypt (Chandler, 1954), and from the Eocene of Europe (Reid & Chandler, 1933; Chandler, 1964; Krutzsch, 1967) and of Oregon (Scott, 1954). *Onoana*, a putatively icacinaceous plant from the Early Cretaceous, has been discussed on p. 560. Cardiopteridaceae are tropical Asian, Medusandraceae tropical West African, Myzodendraceae temperate South American and parasitic.

Olacaceae, including some genera, are common to South America and Africa, extending into tropical Asia, as in Icacinaceae. The living North American Olacaceae may have come from South America or be derived from Laurasian ancestors. The family was in Europe (Chandler, 1964; Krutzsch, 1967) and in Oregon (Scott *in* Chandler, 1964: 58) in the Eocene. Curiously, pollen of the *Anacolosidites* type is known from the Paleocene of Australia (Harris, 1965). The pollen is very distinctive and resembles that of *Anacolosa*, *Cathedra*, and *Ptychopetalum*, a group that appears to have had a West Gondwanaland–Asian history. It is known from the Maastrichtian of North America (Srivastava, 1970), the Paleocene of Victoria, Nigeria, and northern Asia, and from Borneo, but it is not in the Caribbean region until the Paleocene–Eocene transition (Germeraad *et al.*, 1968). This pollen type has since become less abundant in all areas. This suggests that despite their occurrence in Australia, which is confined to the principally recent Asian arrivals *Olax* and *Ximenia*, Olacaceae migrated to Australia more or less directly before the close of the Cretaceous, then became extinct.

Opiliaceae are common to tropical South America and Africa, and also reach tropical Asia. Santalaceae are widely distributed in tropical and temperate regions, including Australasia. Loranthaceae (Barlow & Wiens, 1971) appear to be basically a south temperate group which evolved in South America and Australasia, and then spread north through Asia and then southward into Africa in the Tertiary. In contrast, Viscaceae (Wiens & Barlow, 1971) appear to be a Laurasian group which has spread southward into Africa, South America, and Australia. This pattern would imply the evolution of *Korthalsella* in tropical Asia and of *Phoradendron* and *Dendrophthora* in tropical North America. Eremolepidaceae (Wiens & Barlow, 1971) are South American, with secondary spreading into Central and North America presumably in the Miocene and more recently. This family may be derived from Santalaceae.

Balanophoraceae may not be directly related to the other families in the order (R. F. Thorne, personal communication). The subfamily Lophophytoideae is South American, the subfamilies Balanophoroideae and Helosidoideae South American, African, and tropical Asian, and with extensions into Central America and tropical North America probably no older than the Miocene. *Balanophora* (Hansen, 1972) is tropical Asian, with one species extending from West Africa to Tahiti and another found in Rarotonga, so dispersal may not be difficult in this group. *Langsdorffia* is common to tropical America and New Guinea (Geesink, 1972). The subfamilies Mystropetaloideae and Sacrophytoideae are African, whereas the two genera of Dactylanthoideae are found one each in New Caledonia and New Zealand. Balanophoraceae, which may be a heterogeneous group bound together by only a superficial similarity (Airy Shaw, 1966: 114), seem nevertheless to have had a West Gondwanaland–tropical Asian history. The related Cynomoriaceae are Eurasian.

Santalales evidently radiated in West Gondwanaland, migrating in the Upper Cretaceous to tropical Asia, and very likely reaching Australasia early, judging from the representation of Santalaceae, Icacinaceae, and Balanophoraceae, as well as the endemic Stackhousiaceae, there.

Sarraceniales.—The three genera of Sarraceniaceae occur, respectively, in western North America, eastern North America, and the Guianas. The direction and timing of their migration between North and South America is unknown.

Solanales.—Solanaceae, evidently easily dispersed and often with berries, occur widely in tropical and temperate regions. The geography of the family provides no indications of great antiquity, although the ancestors of *Duboisia*, *Anthotroche*, and *Anthocercis* presumably reached Australasia *via* Antarctica from South America in Paleogene time. Indeed, the weak representation of Solanaceae in Africa—if not due to Neogene extinction—would seem to indicate major differentiation in South America in isolation, although there are several distinctive Laurasian elements. Solanaceae are known as fossils from the Eocene (Muller, 1970). Convolvulaceae are widespread but exhibit no apparently ancient patterns. Polemoniaceae and Fouquieriaceae are groups that differentiated in semiarid North America bordering the tropics, with Polemoniaceae reaching South America probably in the Miocene or more recently and Eurasia perhaps in the Pleistocene. The ancestors of *Cobaea* may have differentiated in tropical North America, whereas *Cantua* and *Huthia* must have differentiated from *Bonplandia*-like ancestors following relatively early long-distance dispersal to South America (Grant, 1959). The pollen of this family first appears in the fossil record in the Miocene (Leopold, 1969). Differentiation of families of Solanales may have occurred after the wide separation of Africa and South America.

Tamaricales.—Frankeniaceae are readily dispersed in alkaline situations and along shores. Perhaps they are from a South American, or South American–African homeland; *Beatsonia* is endemic on St. Helena and *Hypericopsis* in Iran. About 50 species of the widespread *Frankenia* are recognized in Australia. Tamaricaceae are clearly Eurasian.

Theales.—Dilleniaceae (Stebbins, 1972) are best developed in diversity and number of species in Australasia, with good representation also in South America and in tropical Asia. The Hibbertieae are Australian, but one species of *Hibbertia* is in Madagascar and *Schumacheria*, perhaps the most archaic and unspecialized genus in the family (Dickison, 1967*a*, *b*), is in Ceylon. The ancestors of *Schumacheria* might have been carried northward with the Indian Plate, as suggested for *Hortonia* (Axelrod, 1971). If the very primitive monotypic *Didesmandra* of Borneo is referable to Hibbertieae, as suggested by G. L. Stebbins (personal communication), the occurrence of *Hibbertia* in the Eocene London Clay might not seem so anomalous. On the other hand, *H. coriacea* Baill., the only species of the genus in Madagascar, occurs in open coastal woods (Rauh, 1973) and is closely related to West Australian species. It is reasonable to assume it reached Madagascar by long-distance dispersal. Dillenieae and Acrotremeae are basically tropical Asian, with *Dillenia* also reported from the Eocene London Clay (Chandler, 1964). Tetracereae are South American but with a few species of *Tetracera* in the Old World tropics, including Africa, and reported from the Eocene London Clay (Chandler, 1964) and several Eocene to Early Oligocene floras on the Pacific Coast (see MacGinitie, 1937: 148). Thus the Dilleniaceae appear to be a very old family, with tribal differentiation having followed the opening of the Indian Ocean and the separation of South America from Africa.

Paeoniaceae, Actinidiaceae, Stachyuraceae, and Pentaphylacaceae are clearly northern groups. Only one section of *Saurauia* (Actinidiaceae; Hunter, 1966) is found in the New World, and it is inferred that the South American species (about 40) were derived from North American ancestors starting in mid-Tertiary time. *Saurauia* seems clearly to be a Paleogene arrival in North America from Eurasian sources. Theaceae also seem basically to be a northern group, but the Bonnetioideae are disjunct between South America, especially the Guyana Highland, and Malaysia, where the genus *Ploiarium* occurs. *Ternstroemia* has two African species, in addition to many in America and Asia (Hepper, 1968). *Melchiora* and the peculiar and isolated monotypic *Ficalhoa* are endemic to Africa.

Aquifoliaceae are widely distributed, but most diverse in Laurasia. The genus *Ilex*, known from Maastrichtian pollen (Muller, 1970), may have migrated more or less directly between South America and Africa, but evidently is easily dispersed, judging from its presence on Hawaii and New Caledonia. The New Caledonian *Phelline*, on the other hand, may belong with Araliaceae (Airy Shaw, 1966), or elsewhere. Marcgraviaceae, Caryocaraceae, Quiinaceae are South American, with evidently recent incursions into Central America. *Clethra*, the only genus of Clethraceae, consists of two sections (Sleumer, 1967). Of these, sect. *Clethra* is Laurasian, with 23 species in eastern Asia and two in the eastern United States. Sect. *Cuellaria* has two subsections, one consisting of a single species of Madeira and Tenerife (Bramwell, 1972), the second of 37 species in tropical America, about half each north and south of Panama. Leaves of sect. *Cuellaria* occur in the Lower Eocene Chalk Bluffs flora of California (MacGinitie, 1941, as *Laurophyllum litseaefolia* MacGinitie) and in the Miocene of southern California (Axelrod, 1939). This pattern suggests either the former presence of sect. *Cuellaria* on the African or Eurasian mainland, or very unlikely long-distance dispersal from the Americas to the Macronesian Islands; in any event, its occurrence in South America seems clearly to be secondary and derived from tropical North America in or perhaps even before Neogene time.

Cyrillaceae are basically North American, known from the fossil record as far back as the Upper Cretaceous (Thomas, 1960), but reported from the Paleogene of southern England also (Chandler, 1964). Two of the genera include single species which occur in South America and probably spread there in the Miocene or more recently.

Scytopetalaceae and Dioncophyllaceae are West Tropical African, Sarcolaenaceae and Sphaerosepalaceae (see also discussion under Malvales) confined to Madagascar, Medusagynaceae to the Seychellas, and Strasburgeriaceae to New Caledonia. Dipterocarpaceae are mainly tropical Asian, with one species (of *Vateria*) in the Seychelles and the very distinctive genera *Monotes* and *Marquesia*, constituting one of the two subfamilies, in tropical Africa. Hypericaceae s. lat. (Clusiaceae) are well represented both in the remnants of West Gondwanaland and in tropical Asia, being known from fruits in the Eocene of India (Lakhanpal, 1970). *Symphonia* and *Vismia* common to Africa, Madagascar, and South America, which *Symphonia* at least reached by long-distance dispersal (Germeraad *et al.*, 1968: 277–8). *Rheedia* is common to tropical America and Madagascar, and *Hypericum* has become widespread in temperate regions. *Montrouziera* is endemic to New Caledonia, which, especially in view of its relationship to *Symphonia*, its ancestors probably reached by long-distance dispersal. Lecythidaceae have had a similar history but remained wholly tropical in distribution. The differentiation of major groups within the family seems to have followed the separation of Africa and South America. Thus Lecythidaceae–Lecythidoideae are entirely American; Barringtonioideae, widespread in Old World tropics; Napoleonoideae, West Tropical Africa; Foetidoideae, Mascarene region; and Asteranthoideae (monotypic), Brazil. Elatinaceae are widespread waterplants.

Summarizing for Theales, both West Gondwanaland and tropical Laurasia appear to have been important sites of evolution, with the Dilleniaceae apparently reaching Australasia *via* a warm temperate to subtropical pathway in the mid-Cretaceous, as did the ancestors of Strasburgeriaceae and perhaps *Oncotheca*, if it belongs in this order (Takhtajan, 1969). Hypericaceae may also have reached Australasia very early. A number of thealean lines originated in or have become confined to the Northern Hemisphere, but the Theaceae proper have differentiated both in West Gondwanaland and in Laurasia, judging from the presence of the endemic Bonnetioideae in South America, and the occurrence of a few species of Theaceae in Africa at the present time (Hepper, 1968). The South American Marcgraviaceae, Quiinaceae, and Caryocaraceae and the African Scytopetalaceae, Dioncophyllaceae, and Sarcolaenaceae may be autochthonous, having differentiated after the separation of Africa and South America. Hypericaceae, on the other hand, have a pattern of distribution which suggests more or less direct dispersal between the two continents.

Urticales.—Moraceae and Urticaceae differentiated in South America, Africa, and Laurasia, but are poorly represented in Australasia. Ulmaceae were derived from the same stock in Laurasia, and *Ulmus*-like pollen occurs in the Rocky Mountain Maastrichtian (Wolfe, 1974). Barbeyaceae, consisting of a single species of Arabia and northeastern Africa, are a group of uncertain affinities (R. F. Thorne, personal communication). There are likewise temperate genera of Moraceae and Urticaceae that have differentiated in Laurasia. Although early records of fossil Moraceae are badly in need of review, the geographical distribution of the family suggests that it was in existence early enough to have been dispersed more or less directly between Africa and South America (Axelrod, 1972*c*).

MONOCOTYLEDONEAE

Alismales.—The widespread water plants of the Butomaceae, Alismataceae, and Hydrocharitaceae are well represented in Laurasia and in Africa. Easily dispersed, they present no evidence either for early migration to Australasia or for direct connections between Africa and South America, where their representation is poorer than in Africa.

Arales.—Araceae appear to have a West Gondwanaland–Laurasian distribution that has been interrupted by much extinction in Africa. Pollen is reported from the Paleocene of Colombia that may be *Spathiphyllum* (Hammen & García de Mutís, 1966). The tribes Pythonieae, Philodendreae, Colocasieae, Dieffenbachieae, and Richardieae link Africa and South America, several extending to Asia also. *Philodendron* sect. *Meconostigma*, now confined to South America, is reported from the Middle Eocene of Tennessee (Daghlian & Dilcher, 1971; Dilcher, 1973*b*). There are a number of temperate Laurasian genera, and the family may be relatively old in Australasia, at least as judged from the presence of the distinctive endemic genus *Gymnostachys*. Lemnaceae and Typhaceae are widespread waterplants. Sparganiaceae are Laurasian and probably recent arrivals in Australasia.

Arecales.—The palms probably originated in West Gondwanaland, with subsequent decimation in Africa and migration to Eurasia and ultimately Australasia, where several arecoid alliances have proliferated (Moore, 1973*a*, 1973*b*). Authentic palm fossils go back to the basal Campanian (~ 80 m.y. BP; Read & Hickey, 1972; Scott *et al.*, 1972; Moore, 1973), following which coryphoid palms, fairly uniform, soon became frequent. Palms are known from the South American Senonian (Menéndez, 1969; Muller, 1970), and from the central Patagonian Danian (~ 64 m.y. BP), a warm temperate period (Romero, 1968). The genus *Nypa* was in existence and widespread in the Maastrichtian (Germeraad *et al.*, 1968; Tralau, 1964, 1968; Muller, 1970). Most Central American and Mexican palms seem to be recent arrivals from South America, whereas most coryphoid palms in North America probably are Laurasian elements (H. E. Moore, Jr., personal communication). *Pseudophoenix*, most distinctive of the North American palms, may have arrived in Paleogene time from South America, but the direction and time of arrival of many other palms in the North American region is problematical. There is no sign of great antiquity for the palms of Australasia or of the Pacific (H. E. Moore, Jr., personal communication), although they appear in both New Zealand (Couper, 1960) and Australia (McWhae *et al.*, 1958: 133) in the Eocene.

Commelinales.—Bromeliaceae are South American, with probably Miocene and more recent extensions into Central and North America and the West Indies. The single species of *Pitcairnia* on the seacliffs of West Africa undoubtedly reached them by long-distance dispersal. Rapateaceae are another primarily South American group, but the monotypic semiaquatic genus *Maschalocephalus* is confined to West Africa, which its ancestors probably reached in Neogene or later times by long-distance dispersal. It is closely similar to other members of the tribe Monotremeae (Carlquist, 1966). Xyridaceae are easily dispersed and widely distributed, especially in the tropics; the few Australian species of *Xyris* may have arrived recently. Pontederiaceae are easily dispersed waterplants centering in South America and Africa, but with *Monochoria* ranging more widely and *Pontederia* in North America. It is difficult to say whether the family existed or not when more or less direct communication between Africa and South America was possible; there are four common genera and one endemic to each continent.

Philydraceae are Australasian, one genus ranging into Southeast Asia. Much of the diversity of Juncaceae is in South America, but the widespread temperate *Juncus* and *Luzula* probably differentiated in Laurasia. The Antarctic genera probably originated in southern South America and then spread by long-distance dispersal. Cyperaceae are now so widespread and numerous that their distribution is difficult to analyze. They are well represented in South America, Africa, tropical Asia, and Australasia, and have numerous temperate genera also. The most primitive subfamily, Mapanioideae, exhibits a West Gondwanaland–Laurasian range, and it is especially well represented in the Guyana Highlands (Maguire, 1971).

Commelinaceae are well represented in the West Gondwanaland continents and in Asia, but are apparently readily dispersed (Brenan, 1966; Tomlinson, 1966; Jones & Jopling, 1972). The same suggestion might be made for such genera as *Murdannia, Floscopa,* and *Aneilema.* Although the remarkable *Cartonema* is restricted to northern Australia, the family does not in general appear to have any great antiquity there. All genera north of Panama, except perhaps *Thyrsanthemum* and a few others, may have been derived from South America in Neogene time and subsequently. *Mayaca,* the only genus of Mayacaceae, has about 10 primarily South American species and one in Angola, a distribution that can be explained most easily by long-distance dispersal. Eriocaulaceae are waterplants well represented in Africa and South America, with *Eriocaulon* more widespread. North American representatives, including the endemic *Lachnocaulon,* have probably been derived from South America. Flagellariaceae occur in tropical Asia, with *Flagellaria* ranging to Africa and Australia, and *Joinvillea* to the Pacific. Restionaceae are reported from Eocene fossil pollen in Europe (*e.g.* Chandler, 1964; Krutzsch, 1967), but the environment does not seem to have been suitable, and these records should be carefully reviewed. They probably passed between Africa and Australasia by long-distance dispersal in Paleogene time, reaching southern South America subsequently, also by long-distance dispersal (Cutler, 1972; Raven & Axelrod, 1972), but in any case are probably no older than the Maastrichtian at most (Doyle, 1973). Centrolepidaceae are basically Australasian and Subantarctic in distribution.

Among the Poaceae, the ancient and archaic Bambuseae, although pantropical and well represented on Madagascar, are very poorly represented in continental Africa and virtually absent from Australia. Many of the more specialized groups of the family probably originated in Laurasia following migration from Africa into Eurasia, whereas many archaic and unspecialized grasses are confined to, or radiated from, Africa. The relatively unspecialized olyrioid grasses are mainly South American, whereas other lines of grasses seem to have radiated principally from Asia. Very few especially unspecialized or unusual grasses occur in Australasia (*Micraira* is one exception), where the family is probably not an ancient element. The bamboos found north of Panama, except for the Laurasian *Arundinaria* and *Yushania* (McClure, 1973), probably arrived in the Neogene time or more recently from South America. Some of the South American bamboos may be found to be related to those of Africa and Madagascar, and their ancestors may have migrated between these continents when they were closer together. It is difficult on phytogeographic grounds to accept a direct relationship between the primarily South American *Guadua* and the Asian *Bambusa,* as proposed by McClure (1973, see comment by R. E. Holttum, pp. v–viii), although Lardizabalaceae have a similar distribution. Grass pollen has not been detected in New Zealand prior to the Pliocene (Couper, 1960), possibly because of a wider forest cover on the east side of the South Island prior to the uplift of the main range. Pollen of the family is first reported from the Maastrichtian of West Africa (Muller, 1970; Doyle, 1973), but grasses do not become frequent in the fossil record until the Lower Eocene, probably correlated with the rise of grazing mammals and the origin of non-bambusoid tribes of grasses (J. Muller, personal communication).

In summary, most of the families of this order seem to have differentiated in the Guyana Shield area of South America, as suggested by R. F. Thorne (personal communication). It is difficult to be sure which if any of the families of the order existed early enough for direct dispersal to Africa, although the bambusoid grasses are likely candidates. Some alliances reached Australasia a very long time ago, judging from the existence of Philydraceae, Centrolepidaceae, and especially Restionaceae, but the facility with which modern members of the order seem to be spread by long-distance dispersal makes it difficult to know when and how their ancestors may have reached Australia, especially if the Paleogene pollen records of Restionaceae in Europe are correct.

Cyclanthales.—Cyclanthaceae are South American, and have spread northward probably in the Miocene and more recently. They may have originated from a common West Gondwanaland stock with Arecaceae, which is consistent with their reported occurrence in the Paleocene of India (Sahni & Surange, 1953; Lakhanpal, 1970).

Liliales.—Following the analysis of Huber (1969), Liliaceae of Thorne (1968) would be divided into eight orders. Among the smaller ones, Dioscoreales (Dioscoreaceae, Stenomeridaceae, and Trichopodaceae) are Laurasian and African, but there are a number of South American species of *Dioscorea* (including *Epipetrum*). *Dioscorea* might have spread more or less directly between Africa and South America (Ayensu, 1972) or reached South America early by sweepstakes dispersal from the north. Roxburghiales (Roxburghiaceae, Trilliaceae) are Laurasian. Taccales (Taccaceae) are evidently Laurasian, and especially east Asian, but a few species of *Tacca* occur in Africa and Madagascar, and a few others occur in South America. Since the genus is also in Hawaii, it seems unwise to attribute this pattern of distribution to great age. In Haemodorales (Haemodoraceae), the Conostylideae are Western Australian, Haemodoreae South American and African, with *Haemadorum* (mainly Western) Australian and one species in Malaysia. The North American *Lophiola* seems not to belong with the conostylid Haemodoraceae, but rather with the colchicoid Liliiflorae, near *Aletris* (Huber, 1969). Velloziales (Velloziaceae) are confined to South America and Africa (Ayensu, 1973), and they evidently existed when these continents were close together. If the close relationship between Velloziaceae and Bromeliaceae postulated by Huber (1969) is confirmed, it might be possible to think of the group as a whole as having originated in West Gondwanaland, with subsequent differentiation of Bromeliaceae after the wider separation of South America and Africa. On the other hand, Taccaceae and Haemodoraceae, said by Huber to be related, appear to have differentiated respectively in the north and in the south.

In the Orchidales, the saprophytic Burmanniaceae are evidently easily dispersed and nearly cosmopolitan. We can say nothing useful about their distribution, except that they are predominantly tropical. Nearly the same statement can be made for the vast and readily dispersed family Orchidaceae, which unfortunately lack a useful fossil record (Schmid & Schmid, 1973). The two least specialized subfamilies, Apostasioideae and Cypripedioideae, however, are Laurasian, and mainly east Asian, this possibly suggesting their area of origin. Orchidaceae are much better represented in South America and tropical Asia than in Africa, and more diverse and abundant on Madagascar than in continental Africa, a frequent pattern.

One of the major hypotheses of Huber (1969) is the separation of the asparagoid Liliiflorae (as Asparagales). Eight family groups are recognized, and these will now be reviewed in turn:

(a) Asparagaceae alliance: Ripogonaceae (*Ripogonum*), Australasia, Smilacaceae (*Smilax*, *Pseudosmilax*, *Heterosmilax*), evidently easily dispersed, with *Smilax* on Hawaii, but perhaps Laurasian. Philesiaceae (*Lapageria*, *Philesia*), temperate South American. Luzuriagaceae, mainly Australasian, but with *Luzuriaga* in Chile and New Zealand, and the monotypic *Behnia* endemic to southeastern Africa. Ruscaceae, Laurasian and North African. Convallariaceae, Laurasian with the two species of *Drymophila* endemic to eastern Australia and Tasmania. Dracaenaceae (*Dracaena*, *Sansevieria*), Old World tropics, especially Africa, the Canaries, one species of *Dracaena* just reaching northern Australia. Nolinaceae, drier portions of North America. Asparagaceae, widespread in warmer and drier portions of Old World, and one species native to Australia. Herreriaceae, one genus in Madagascar, another one or perhaps two in South America. This alliance appears to be widespread and of some antiquity. Only Herreriaceae, however, seem to have been involved in more or less direct dispersal between Africa and South America, which makes it seem likely that the ancestors of Luzuriagaceae may have reached Australia *via* Antarctica from South America, and those of *Ripogonum* and *Drymophila*, both with fleshy fruits, from the warmer parts of the Old World by long-distance dispersal. This is almost certainly the case for the few Australian species of the widespread genera *Smilax*, *Dracaena*, and *Asparagus*. *Behnia*, which likewise has a berry like all Luzuriagaceae, is probably derived from ancestors that reached Africa by long-distance dispersal also.

(b) Asteliaceae alliance: Asteliaceae consist of the primarily Australasian *Astelia* and *Milligania* (the former evidently easily dispersed and ranging out into the Pacific to Hawaii), and with one species in southern South America, together with *Cordyline*, which is widespread in the Asian and American tropics, as well as northern Australia and New Zealand, where it first appears in the fossil record in the Lower Miocene (Couper, 1953). *Cohnia*, with three species, occurs in the Mascarene Islands and on New Caledonia; it has berries and probably reached the Mascarene Islands by long-distance dispersal from the east. Dianellaceae are likewise Australasian, with the berry-fruited *Dianella* ranging to tropical Asia, Madagascar, and Hawaii, and the capsule-fruited *Excremis* South American, possibly having reached that continent by way of an Antarctic route. Hypoxidaceae seem to center in Africa, and to have spread to Asia and eventually the

New World from there. *Hypoxis*, of which most species occur in Africa, and *Curculigo* are widespread. If the relationship between Velloziaceae and Hypoxidaceae discussed by Ayensu (1973) is genuine, then the case for an African origin would be strengthened. The monotypic and distinctive South African *Lanaria* is likewise allied by Huber (1969) with this group. The families of this alliance seem to suggest long-standing connections between Africa and Australasia, but it is difficult to say why if they are so old they are so poorly represented in South America.

(c) Tecophilaeaceae alliance: *Walleria* and *Eriospermum*, each assigned by Huber (1969) to its own family, are African. In the Tecophilaeaceae, *Cyanella* is South African, three other genera Chilean, and the monotypic Californian *Odontostomum* probably also correctly referred here according to Huber. Old connections between Africa and South America seem to be indicated, but how and when the ancestors of *Odontostomum* reached California is uncertain.

(d) Xanthorrhoeaceae alliance: Australasian, diverse and probably ancient.

(e) Asphodelaceae alliance: Many genera, widespread but much better represented in the Southern Hemisphere; both tropical and temperate (Antarctic?) connections between South America and the Old World seem to be represented in this group, and the Johnsonieae are evidently of considerable antiquity in Australia, as are the distinctive genera *Sowerbaea* and *Bartlingia.*

(f) Phormiaceae alliance: Australasian, probably ancient. Pollen of *Phormium* is known from the Middle Eocene onward in New Zealand (Couper, 1960).

(g) Agavaceae alliance: Subhumid to arid portions of the North American region, except for the East Asian *Hosta.* Presumably an ancient Laurasian group.

(h) Amaryllidaceae-Hemerocallidaceae alliance: Hemerocallidaceae consist only of the Eurasian *Hemerocallis*, with about 20 species. Alliaceae are mainly South American, with some genera in North America, especially western North America, and *Allium* widespread in the Northern Hemisphere. Agapanthaceae are South African. Hyacinthaceae consist of three tribes, the western North American Chlorogaleae, the African Bowieeae, and the African-Mediterranean Scilleae, with *Camassia* endemic to North America and the monotypic *Fortunatia*, closely related to the Old World *Scilla*, in Chile, which its ancestors must have reached by long-distance dispersal. Amaryllidaceae in the strict sense are African, South American, and Laurasian, with several groups having genera in both Africa and South America. Eustephieae are entirely South American, and Hippeastreae are South American and Laurasian. The impression is of a group that has considerable antiquity both in South America and in Africa, and doubtless dispersed between these continents when they were much closer than at present. This alliance has evidently also been represented in Laurasia for a very long time. The disjunction in range between the Alliaceae–Brodiaeeae in North and South America is unusual.

For Asparagales (Huber, 1969) as a whole, West Gondwanaland seems clearly to have been the primary site of evolution, with Laurasia involved probably before the close of the Cretaceous. The ancestors of elements among the families related to Asteliaceae, Xanthorrhoeaceae, Asphodelaceae, and Phormiaceae seem to have reached Australasia early, whereas elements in the groups related to

Asparagaceae, Asteliaceae, Tecophilaeaceae, Asphodelaceae, and Amaryllidaceae–Hemerocallidaceae suggest old connections between Africa and South America. The kind of disjunctions in range between North and South America that occurs in Alliaceae—Brodiaeeae and Tecophilaeaceae is unusual among angiosperms as a whole and suggests ready dispersibility for these plants.

For the colchicoid Liliiflorae, grouped by Huber (1969) as Liliales s. str., Melanthiaceae are Laurasian except for *Nietneria* of northern South America. Calochortaceae, consisting of a single genus, are western North American and Mexican. Liliaceae s. str. (Tulipeae) are Eurasian and secondarily North American. Colchicaceae are Eurasian and African, with several small genera in Australia and Tasmania (which they probably reached independently by long-distance dispersal) and one (*Uvularia*) in North America.

Iridaceae probably were in existence when South America and Africa were closer, and they have had their principal radiation on these continents. Some genera are Eurasian—*Hemerodactylus*, *Belemcanda*, *Gladiolus*, *Crocus*, for example—and *Iris*, a Eurasian genus, has reached North America at least twice. Primitive Iridoideae, as well as some Sisyrinchioideae, are shared between Africa and South America, also implying the origin of these subfamilies by Paleogene time, and probably a more recent origin for the third subfamily, the basically African Ixioideae (P. Goldblatt, personal communication). No genera or even tribes are common to Africa and South America, in spite of misconceptions to this effect based on faulty taxonomic treatments (P. Goldblatt, 1971). *Sisyrinchium*, *Tigridia*, and the ancestors of the endemic *Rigidella* were evidently recent arrivals in North America. The Australasian Sisyrinchieae have probably been derived from South America *via* Antarctica, as might the ancestors of *Patersonia* (Aristeae) and those of the New Caledonian *Campynemanthe* (Huber, 1969) and the Tasmanian *Isophysis* (*Hewardia*). How the single endemic species of the otherwise African *Dietes* reached Lord Howe Island is problematical. One of the most remarkable Iridaceae is the saprophytic *Geosiris* of Madagascar, which is relict and implies antiquity.

The Liliales s. str. (colchicoid Liliiflorae) do not appear, on the basis of present distributions, to be as old as the Asparagales (sensu Huber, 1969). Only Iridaceae seem to be old enough to have migrated more or less directly between South America and Africa (Paleocene?), with the other groups all more recent.

Despite the fact that many of the members of this large array of families and perhaps orders are easily dispersed, it does appear likely that ancestral forms related to this order existed when more or less direct migration into Australia for warm temperate plants was possible. Pollen of the group appears in New Zealand about 70 m.y. BP (Couper, 1960). Primitive Liliaceae, Amaryllidaceae, Haemodoraceae–Haemodoreae, Iridaceae, and Velloziaceae seem to have existed when South America and Africa were more closely linked, whereas most of other groups may not yet have originated. The major differentiation of the complex as a whole may perhaps have been in West Gondwanaland, but Roxburghiales, Taccales, the colchicoid Liliiflorae (Liliales s. str.), and Orchidales seem to have had their primary radiation in Laurasia, as do many smaller groups. Early migration to Australia is suggested for the ancestors of some groups, notably the

Xanthorrhoeaceae alliance, the Phormiaceae alliance, the Johnsonieae, and the Asteliaceae alliance, all asparagoid Liliiflorae (Asparagales); and for the ancestors of Haemodoraceae–Conostyloideae. Other groups appear to have arrived in Australia more recently, by long-distance dispersal, or (as in Iridaceae) *via* Antarctica from South America. The kinds of disjunction in range between North and South America in Brodiaeeae and Tecophilaeaceae are unusual for angiosperms as a whole and, together with other evidence, suggest that many members of the Liliiflorae are very easily dispersed.

Najadales.—A single genus of widespread waterplants.

Pandanales.—Pandanaceae are now widespread in the Old World tropics, but are not necessarily old in Australasia. The order has affinity with Cyclanthaceae and Arecaceae and may have a Cretaceous age.

Triuridales.—Triuridaceae occur in South America, Africa, and Asia and are herbaceous saprophytes. The species north of Panama and in Australasia are clearly recent arrivals, and the plants of this unique and specialized family appear to be easily dispersed. The genus *Sciaphila* has nearly the entire range of the family.

Zingiberales.—Musaceae almost certainly antedate the separation of South America from Africa, with clear-cut endemic genera in both areas and no ready means of dispersal. *Musa* ranges to tropical Asia. A *Heliconia*-like stem with attached lamina occurs in the Paleocene of India (Trivedi & Berma, 1972). Most species of *Heliconia* are tropical American, but one is Melanesian (Green, 1969), possibly having crossed the Pacific by long-distance dispersal as has been hypothesized for other fleshy-fruited genera such as *Fuchsia* (Raven, 1973*a*) and *Coriaria.* Lowiaceae, acaulescent herbs represented by a single genus *Orchidanthera,* are endemic to Malaya and Borneo.

Zingiberaceae are mainly confined to Africa and tropical Asia, but *Renealmia* (Zingibereae) and *Costus* (Costeae) are common to Africa and South America. The other genera of Costeae are also South American, except *Tapeinocheilos* which ranges from tropical Asia to Australia. The family is recorded from the Eocene of southern England (Chandler, 1964) and India (Prakash, 1972: 80), and the Early Eocene of North America (Hickey, 1974). The family probably was common to Laurasia and West Gondwanaland very early. Cannaceae are South American, but spread to Laurasia by Early Tertiary time, judging from the occurrence of leaves probably referable to this family in the Eocene of North America (Berry, 1916, 1924) and the Soviet Union (Gorbunov, 1962), and in the latest Oligocene of Montana (Becker, 1969).

In the Marantaceae one of the two tribes, Phyrnieae, is found in Africa and tropical Asia, except for *Calathea* of South America; the other, Maranteae, is South American, except for *Thalia,* one species of which occurs in tropical Africa and in tropical America, the other ten being confined to tropical America. Marantaceae seem to have existed prior to the separation of South America and Africa, and these seem clearly to have had 3-locular ovaries and therefore to have been referable to the tribe Phrynieae. The family is recorded from the Eocene of southern England (Chandler, 1964). *Calathea* and the Maranteae seem to have evolved in South America after its separation from Africa, and *Thalia geniculata* L. has probably been carried back to Africa by long-distance dispersal.

Zosterales.—What has been said for Alismales can be repeated for most of this order, Potamogetonaceae, Posidonaceae, Zannichelliaceae, and Zosteraceae. The presence of two endemic genera related to *Triglochin* in Australia and one in southern South America is interesting, and the ancestors of Juncaginaceae (Scheuchzeriaceae)–Juncaginoideae may have had a relatively long history in Australia. Aponogetonaceae are Asian and African, but known from the Upper Cretaceous of Patagonia (Selling, 1947), indicating their antiquity and past history.

ANGIOSPERM BIOGEOGRAPHY

We shall now review the patterns of distribution just discussed in the light of plate tectonic events reviewed earlier to see what can be learned about the age and pattern of dispersal of various angiosperm groups. A major obstacle in such considerations is posed by the possibility that some of the recognized orders are "unnatural;" *i.e.* did not have a common ancestor which gave rise to the families presently included in the order. Nonetheless, students of angiosperm phylogeny are converging on standard definitions of the orders, and the current evidence supports most of the groupings; exceptions will be discussed at the appropriate points. We shall now consider some of the characteristic patterns of angiosperm distribution that have been perceived in our review.

DISPERSAL BETWEEN AFRICA AND SOUTH AMERICA

General.—Explanations for the taxa to Africa and South America have fallen in one of three groups: 1) long-distance dispersal; 2) land bridges; 3) sea-floor spreading. For example, some plant geographers assert that all of the links between the far-flung tropical lands of the western Pacific and America, or between America and Africa, can be explained by long-distance dispersal. While in no way denying the importance of such dispersal (Axelrod, 1952*a*; Iltis, 1967; Sauer, 1969; Raven, 1963, 1973*a*, 1973*b*; Bowden *et al.*, 1971; Johnson & Bowden, 1973), we feel that many of the presumed examples are more readily explained in terms of sea-floor spreading (Axelrod, 1970, 1972*a*).

In his excellent and detailed analysis of the relationships between Africa and South America, Thorne (1973*b*) did not take into sufficient account the differing ages and rates of evolution of the taxa involved; the gradual opening of the Atlantic, with opportunities for migration between Africa and South America being greater at any time in the past than they are now; and the high degree of impoverishment of the African flora by climatic change during the Neogene and Quaternary.

Much of the confusion involved in discussions concerning the dispersal of plants and animals between Africa and South America stems from the natural desire to find one absolute answer to the question of long-distance dispersal *vs.* direct migration. Thus Thorne (1973*b*) and Iltis (1967) have attempted to ascribe all close similarities in the floras of South America and Africa to long-distance dispersal. The question is, however, a relative one.

As we have already seen, these continents parted company about 100 m.y. BP. Sea-floor spreading data show that in Early Paleocene time (~ 64 m.y. BP), they were about 800 km apart. This is a third more than the distance between Yucatán and Jamaica, which has in about 15 m.y. acquired a flora of some 2,888 species of angiosperms, representing 996 genera (Adams, 1972), a number of species of *Eleutherodactylus*, four species of *Hyla*, many lizards, some snakes, an extinct primate, an octodont rodent, and various other animals (Darlington, 1957). If such exchange had taken place between Africa and South America into the Paleocene, today we would be unable to distinguish its results from those of direct overland migration.

Islands have probably been present in the position of Hawaii for at least 70 m.y. (Dalrymple *et al.*, 1973), yet they were farther from the present position of North America in the past because the latter has been moving west from the mid-Atlantic ridge. They are now about 3,900 km from North America, the closest source area. At least 272 flowering plant immigrants have become established in the Hawaiian Islands (Fosberg, 1948), including such families as Apocynaceae, Aquifoliaceae, Araliaceae, Arecaceae, Asteraceae, Campanulaceae, Celastraceae, Cucurbitaceae, Cyperaceae, Euphorbiaceae, Fabaceae, Gesneriaceae, Goodeniaceae, Hydrangeaceae, Lamiaceae, Liliaceae (*Smilax*, *Cordyline*), Loganiaceae, Myrsinaceae, Myrtaceae, Orchidaceae, Piperaceae, Poaceae, Rhamnaceae, Rubiaceae, Rutaceae, Sapindaceae, Sapotaceae, Theaceae, Thymelaeaceae, Urticaceae, and Violaceae. Many of these are, of course, from source areas other than North America, and farther removed from Hawaii. This does not mean that long-distance migration to Hawaii was entirely over open tracts of water of such magnitude. The numerous archipelagos of the Southwest Pacific no doubt provided important stepping stones in the past, the high islands having been since eroded to wave level, and thence transported subsea by sea-floor spreading (Axelrod, 1972*a*: fig. 25).

Aside from the fact that it is easier to become established on new volcanic islands in the ocean than on a continent with an existing flora, the plants of Hawaii illustrate very clearly the potentialities of long-distance migration. The distance of the Hawaiian Islands from the nearest mainland is about 60 per cent greater than the present distance between Africa and South America. Yet these figures should not be taken to prove or disprove the mode of dispersal of a single group, or of all groups, between distant lands. In our analysis of the floras of Africa and South America, we have tried to identify those groups for which a sufficient antiquity was plausible or demonstrated, and for which the representation on the two continents indicated more or less direct migration in Paleocene or earlier times. At these times, there would have been numerous islands along the Mid-Atlantic Ridge that would have served as stepping stones between Africa and South America.

Steenis (1962), on the basis of much more limited geological information than we have at our disposal today, once called on land bridges to explain the fundamental relations between the tropical flora of America and that of Southeast Asia–Malaysia. More of the genera and families of tropical South America are common to Southeast Asia–Malaysia than to Africa (Thorne, 1973*a*). Since the

Paleocene separation of Africa from Eurasia, migration, *via* the North and Central Atlantic and the Bering Straits, has been much more direct between tropical America and Eurasia than between Africa and either other continent. Although the problem of migration of tropical plants through the north is a difficult one, some migration of such plants by such a route apparently has certainly taken place, and the climates in the north were definitely warmer in the past (Wolfe, 1972; Smith *et al.*, 1973; McKenna, 1973; Thorne, 1973*a*, 1973*b*). On the other hand more or less direct migration between South America and Africa provided a simpler possibility for exchange between the Old and New World tropics into Paleogene times and must also be given serious consideration.

The earlier belief of Thorne (1973*b*), Smith (1973), and others, that separation of Africa–South America had been completed before the appearance of present seed plant floras of the world, and possibly earlier than that of the Jurassic gymnosperms, is supported neither by botanical nor by geological evidence. The gradual isolation of tropical Africa from South America by progressive sea-floor spreading during the Late Cretaceous and Tertiary preceded the origin of many new taxa (genera, tribes, families) in each area (Axelrod, 1970; 1972*a*). That the distinctness of the tropical flora on opposing shores of the Atlantic increased during the Cenozoic is demonstrated by the presence of essentially identical pollen floras in the Late Cretaceous of Brazil and Gabon (Freake, 1966), and very similar ones in Colombia and Nigeria (Hoeken-Klinkenberg, 1964), as compared with the marked differences between them today. Brenner (1974) groups northern South America and Africa in a single floristic province in the Upper Cretaceous. Even in the Early Tertiary, Krutzsch (1967) considers South America, Africa, and India to constitute a single province from the standpoint of palynology. Numerous islands afforded ready migration across the opening Atlantic into the Early Tertiary. As these commenced to subside, and as the ocean basin deepened and widened, long-distance dispersal gradually became more important.

The breakup of West Gondwanaland by sea-floor spreading led to the increasing distinctness of the floras and faunas of Africa and South America. Relations of this sort are inferred for such groups as mites, land mollusks, fresh-water fish and insects, liverworts, and other alliances that are common to South America–Africa, and to other tropical regions, as summarized recently by various authorities (*in* Fittkau *et al.*, 1968, 1969). At the same time, there was an increasing tendency for the marine faunas of the Caribbean region to become distinct from those of the Mediterranean region (see Hallam, 1973*a*; Douglas *et al.*, 1973; papers in symposium volumes edited by Mindelmiss, Rawson & Newall, 1971; Hughes, 1973; and Keast, Erk & Glass, 1973, for example). The marked differences between the American–African tropical floras are due in large measure to their evolution in isolation (Axelrod, 1970), as well as to widespread extinction in Africa (Axelrod, 1972*a*, 1972*c*).

At the generic level, a recent review of the relationships between Africa and South America has been provided by Thorne (1973*b*). At least 111 genera of Africa and Madagascar are limited to Africa–Madagascar and America, representing fewer than 2.5 per cent of the genera of both continents. However, as can be seen repeatedly in the preceding pages, any genus or other group old enough to have spread directly between Africa and South America would also have had direct access to Eurasia. Therefore, it is not particularly meaningful to limit comparisons only to those taxa restricted to Africa and America. Interestingly, about 45 endemic genera in Africa–Madagascar have more than 100 species (Thorne, 1973*b*). Clearly, most of these originated since the separation of Africa and South America. On the other hand, some relatively old—*e.g. Guarea, Caperonia*—and some recent—*e.g. Aspilia, Coreopsis, Chrysocoma*—genera are represented by large numbers of species on both continents. This clearly implies that opportunities for evolutionary bursts may be recurrent for genera of woody plants—though not for the placental mammals which evolved into new genera. In some cases, as Velloziaceae (Ayensu, 1973), older taxonomies have given mistaken impressions about the representation of intrafamilial groups on the two continents (see also Johnson & Briggs, 1963; Cutler, 1972). Statistical analyses of floras are interesting, but can be judged adequately only in the context of the careful examination of individual groups.

Direct Migration.—The groups noted below presumably migrated between Africa and South America during or prior to the Paleocene, judging from what is known or can be inferred about their history and from their present patterns of distribution. After the Paleocene, the floras of Africa and South America became largely distinct, and the evidence suggests only limited migration between these continents from the Eocene onward (Germeraad *et al.*, 1968). The profound differences between the floras of Africa and South America led Engler (1905) to reject the notion of any connection in the past. Some long-distance dispersal has occurred throughout the Tertiary, however, and doubtless is still occurring. The age of genera such as *Solanum* and *Gossypium*, both represented on Hawaii, which is some 60 per cent farther from the nearest source area than Africa is from South America, cannot be dated from the original separation of these continents, as proposed by Hawkes and Smith (1965). The notion that either long-distance dispersal or direct migration is responsible for all the African–South American similarities is in error. Virtually all of the groups listed are also known or presumed to have reached Eurasia by the Early Paleocene, and many are well developed in Eurasia and/or North America at present:

Annonales, including Annonaceae, Canellaceae, Myristicaceae, Siparunaceae, Monimiaceae s. str., and Lauraceae (including *Ocotea* and *Beilschmeidia*).
Arales, Araceae (several tribes).
Arecales, Arecaceae (several subgroups).
Berberidales, Menispermaceae.
Bignoniales, Bignoniaceae, including Tecomeae, with Bignonieae s. str. and other tribes arising subsequently; Gesneriaceae, with the split between Cyrtandroideae (Old World) and Gesnerioideae occurring subsequently.
Capparales, Capparaceae.
Chenopodiales, possibly Phytolaccaceae, the other families evidently having evolved more recently after the separation of Africa and South America. Basellaceae and Portulacaceae–Calandrineae are also common to both continents, but may have evolved more recently.

Cistales, Flacourtiaceae (including Oncobeae, Banareae, Homalieae), Cochlospermaceae (*Cochlospermum*), Turneraceae, Caricaceae, Cucurbitaceae (including Anguriinae; Jeffrey, 1962).

Commelinales, Poaceae (bambusoid grasses only).

Cornales, Rhizophoraceae, Araliaceae, Apiaceae–Hydrocotyloideae.

Ebenales, Ebenaceae (*Diospyros*), Sapotaceae (including *Manilkara* and pentasepalous groups; Aubréville, 1973), Styracaceae.

Ericales, Ericaceae [including Andromedeae (Gaultherieae)].

Euphorbiales, Euphorbiaceae, Dichapetalaceae (including *Tapura* and *Dichapetalum*), Thymelaeaceae, Buxaceae–Stylocereae.

Gentianales, Loganiaceae–Desfontainioideae, Loganioideae; Antoniaceae; Strychnaceae (including *Strychnos*); Rubiaceae; Apocynaceae, including Apocynoideae and Plumerioideae; possibly Gentianaceae.

Geraniales, Linaceae (including subfamilies Ixonanthoideae and Linoideae), Erythroxylaceae (*Erythroxylum*), Zygophyllaceae, Oxalidaceae, Malpighiaceae, Polygalaceae, Vochysiaceae.

Liliales, Amaryllidaceae–Hemerocallidaceae, Asphodelaceae, Dianellaceae, and Herreriaceae, Tecophilaeaceae, Amaryllidaceae (several tribes), Haemodoraceae (including Haemodoreae), Velloziaceae, Iridaceae.

Malvales, Sterculiaceae, Tiliaceae, Bombacaceae.

Myrtales, Myrtaceae–Myrtoideae, Melastomataceae, Lythraceae, Combretaceae (including Combretinae and Terminaliinae).

Primulales, Myrsinaceae.

Proteales, Proteaceae, tribe Macadamieae.

Rafflesiales, Hydnoraceae.

Rosales, Chrysobalanaceae; Rosaceae–Sanguisorbeae; Connaraceae; Fabaceae–Mimosoideae and Caesalpinioideae, possibly including the tribes Swartzieae and Cynometreae, as well as *Macrolobium* and *Bauhinia*, among others; Podostemonaceae; Cunoniaceae.

Rutales, Rutaceae, Simaroubaceae, Meliaceae (including *Guarea*), Burseraceae, Anacardiaceae, Sapindaceae.

Santalales, Balanophoraceae, Icacinaceae, Olacaceae (including *Heisteria*), Opiliaceae.

Theales, Dilleniaceae, Theaceae (including *Ternstroemia*), Aquifoliaceae (*Ilex*), Hypericaceae (perhaps including *Rheedia* and *Vismia*), Lecythidaceae.

Urticales, Moraceae and Urticaceae.

Zingiberales, Musaceae (including Strelitzioideae), Zingiberaceae (including Costeae, *Costus*, and *Renealmia*), Marantaceae (including Phrynieae).

Probably a majority of families and many modern genera of seed plants had come into existence by the Paleocene. Many of these seem to have dispersed more or less directly between Africa and South America. There is also an almost complete floristic continuity at the family and often generic level between Africa and Southeast Asia, indicating the ease of migration between these two areas into early Paleogene time (Axelrod, 1960: 257–258), and again in the Neogene when the overland connection was restored, though by the later Miocene the links were chiefly those of drier climates.

A number of families not on the list above appear to have evolved more recently, or to be so easily dispersed that they may have spread between South America and Africa by long-distance dispersal, as of course may some of those listed above. These include: Cyperaceae, Juncaceae, Celastraceae, Convolvulaceae, Orchidaceae, Solanaceae, and Xyridaceae, for example, as well as the genera *Menodora* and *Fagonia*, among many others. In some taxa, a single species apparently has been carried from one continent to the other: Houmirioideae (Linaceae), *Thalia* (Marantaceae–Maranteae), Bromeliaceae, Rapateaceae, Cactaceae (two apparently derived species coexist with the original one in Madagascar; Guillaumet, 1972), *Maranthes* (Chrysobalanaceae; Prance, 1968). The occurrence of a single genus, *Codon*, of the predominantly North American Hydrophyllaceae, in South Africa, can most easily be explained in this manner, although alternative possibilities involving extinction in intermediate areas cannot be ruled out.

A very interesting case deserving special comment concerns *Parkia* (Fabaceae–Mimosoideae; Baker, 1973). Common to all three main tropical regions of the world and bat-pollinated in each, *Parkia* might have migrated more or less directly, although there is very little evidence that Mimosoideae could be so old. *Parkia* is pollinated by the exclusively Old World Megachiroptera in the Old World, by the cosmopolitan Microchiroptera in the New World (Baker, 1973). Evidently the Megachiroptera evolved well after the separation of Africa and South America, whereas *Parkia* probably evolved earlier.

Arid Areas.—When South America and Africa were in close contact, there must have been extensive arid areas, some of them edaphic, in the interior of the vast continent formed by their union (Axelrod, 1972*a*, *b*; Schuster, 1972). This has been demonstrated by the Cretaceous saline deposits of the Sergipe basin of Brazil and the Gabon basin of Africa by Allard and Hurst (1969) and is evident from the present geology of the areas concerned. Many of the endemic families and taxa of the two continents may have survived in, or later evolved in, such edaphic deserts, including unique xerophytic endemics in such families as Velloziaceae and Bombacaceae which link Africa and South America (Axelrod, 1970, 1972*b*). Much of the *primary* differentiation of Chenopodiales, producing such families as the American Cactaceae and Portulacaceae, and the African Didiereaceae and Aizoaceae, may well have taken place in such local edaphic settings.

Nonetheless, there is no evidence to support the contention of Engler (1914) that genera such as the following, which are scattered in arid regions around the Atlantic basin, owe the disjunctions in their ranges to the breakup of West Gondwanaland: *Menodora* (Oleaceae), *Fagonia* (Zygophyllaceae), *Thamnosma* (Rutaceae), *Pilostyles* (Rafflesiaceae), *Frankenia* (Frankeniaceae), *Lycium* (Solanaceae), and various Chenopodiaceae (*Atriplex*, *Chenopodium*, *Salsola*), and Fabaceae (*Acacia*, *Hoffmanseggia*, *Prosopis*). For the most part they are not isolates within their families, and they comprise only a very small proportion of the floras of the areas in which they occur, although *Acacia* is a clear exception.

Some occur in Australia (*Frankenia, Acacia, Lycium, Atriplex, Chenopodium, Suaeda*), in which the evolution of arid areas has taken place in complete isolation from all others (Raven & Axelrod, 1972). As pointed out by Raven (1973*a*), they must have attained both their disjunct east–west and north–south ranges by long-distance dispersal. As we have seen, those plants which may have occurred in these arid areas since the time of separation of Africa and South America have subsequently become distinct genera or even families. Long-distance dispersal between similar climatic regions in Africa and South America has probably occurred, but with decreasing probability, ever since separation (Simpson, 1952; Axelrod, 1952*a*; Raven, 1973*a*). As the continents separated, their climates would have become moister and more equable (Axelrod, 1972*b*), and hence the probability of long-distance dispersal between the contracting arid areas would have decreased. On the other hand, so much air-borne dust, doubtless including many seeds and small animals, is being blown westward from Africa that the sun is being dimmed over the Caribbean region and as much as 15 per cent of the solar energy reaching the surface of the tropical Atlantic may be lost (Anonymous, 1974). This condition clearly indicates the efficacy of winds for such intercontinental transport. Increasing opportunities for the evolution of rainforest and savanna taxa would have developed on these continents in Upper Cretaceous and Paleogene times, supporting Stebbins' hypothesis (1952) that taxa of rainforest environment may have been derived from those of drier areas.

In contrast to the relationships between the southern lands, migration between North America and Eurasia has been relatively unimpeded during most of the history of the flowering plants. The North Atlantic provided an overland pathway for plants of temperate forested regions until 49 m.y. BP and an interrupted one into the Miocene (*i.e. via* Iceland); the Beringian area has been equally important and the sole major land route since the Eocene. These pathways account for the sort of patterns discussed by Sharp (1966), Graham (1972), Hara (1972), Thorne (1973*a*), Wood (1973) and many others, but are not important for the plants of subhumid to semiarid habitats (Raven, 1971, 1973*a*). The sorts of differences between the pollen floras of eastern North America and Europe from the Cenomanian onward may be related to the relatively high latitude of the bridge between the two continents (Wolfe & Pakiser, 1971). As Kornaś (1972) has pointed out, the herbaceous species of the boreal coniferous forests are often circumpolar, but those of the deciduous woodland are older and hence generally are clearly separated taxonomically.

Many genera of woody plants are common to the Mediterranean region and California, playing conspicuous roles in the vegetation of both regions. These are reviewed by Raven (1971) and include *Acer, Arbutus, Cercis, Clematis, Cupressus, Fraxinus, Juniperus, Lonicera, Platanus, Populus, Prunus, Rhamnus, Rhus, Rosa, Rubus, Smilax, Staphylea, Stryax, Viburnum, Vitis*, and especially *Pinus* (with "closed-cone," fire-type species in each area) and *Quercus* (with a number of very important and conspicuous evergreen oaks in each region). The ties were even more numerous in Neogene times, with such genera as *Clethra, Ilex, Ocotea, Persea, Pistacia, Sabal*, and *Sapindus* present in each region (Axelrod, 1972*a*, 1973). Most of them are also found in the Eocene, and MacGinitie (1941) has also reported *Nerium* of the Mediterranean region from the Eocene of California. Many of these genera have been associated with the Arcto-Tertiary Geoflora and its derivatives since at least Paleogene time, and they have differentiated similar species in semiarid areas on the two sides of the Atlantic. Only in Late Miocene time did the semiarid plant communities of Eurasia (Takhtajan, 1969) and North America (Axelrod, 1950, 1958) approach their modern form.

As judged from current reconstructions which place eastern America and western Europe in latitudes suited to warm, seasonally dry climate, these taxa may have bridged the Atlantic during the Late Cretaceous to Early Eocene (Axelrod, 1972*c*, 1973). With scattered islands along the Mid-Atlantic Ridge and its flanks, east-west movement would be possible. On this basis, it is not surprising to find that the Azores still have a Mediterranean flora (*i.e. Erica, Ilex, Lavatera, Myrsine, Persea, Myrtus, Myrica, Rhamnus*); that the family Cneroaceae is restricted to the western Mediterranean–Canary Islands and Cuba; and that various genera (*Clethra, Pistacia, Persea, Myrica, Ilex,* etc.) in the subhumid parts of Mexico have representatives in the Neogene of California and in the Mediterranean region. All of these may be regarded as the surviving descendants of the more numerous links between the subhumid climates at the edge of the tropics on opposite sides of the Atlantic during the past. The rather numerous ties between the mediterranean regions north of the tropics (Raven, 1971) provide a marked contrast with the profound differences between sclerophyllous taxa in the regions of mediterranean climate in central Chile, Australia, and South Africa. This is wholly consistent with their much longer period of separation.

The Impoverished African Flora.—The distribution of the "primitive" woody ranalian angiosperms and other groups that reveal stronger ties between the American and Australasian tropical floras than the African, seems due largely to one factor: impoverishment of the African flora, chiefly during Neogene and later times. Down to the close of the Oligocene the African tropical flora probably was very diverse. This is implied in part by the rich flora that has survived on Madagascar which was a part of Africa until mid- or Late Cretaceous time. Furthermore, the Late Cretaceous and Paleogene rainforest vegetation of North Africa, covering what is now the Sahara Desert, included such families as Annonaceae, Celastraceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Fabaceae, Hamamelidaceae, Hypericaceae, Icacinaceae, Lauraceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae, Proteaceae, Rutaceae, Sterculiaceae, and Theaceae (Aubréville, 1970, 1971; Chandler, 1954). These also included *Nypa* (Chandler, 1954; Tralau, 1964), which is now extinct in Africa. Humid forest evidently clothed nearly all of Africa, except perhaps for the south, until Neogene time.

In discussing imbalance in the African flora, Richards (1973) notes that there probably is no large area of African rainforest where rainfall is distributed evenly through the year; even in its wettest parts there is a month or two of dry season, with precipitation as low as 100 mm. Since the richest part of the rainforest flora, and that which harbors most of the relicts, regularly occurs in areas with least drought, he infers spreading drought may have eliminated numerous taxa that lived there earlier. Axelrod (1972*a*) noted that the development and spread of dry climate over tropical Africa probably began near the close of the Oligocene, at which time upwarp of the continent commenced, and has continued to the present as the rift valleys continue to grow (see Baker, Mohr & Williams, 1972, for new geologic evidence). The altitude of eastern Africa has increased fully 8,000 feet above that of the Miocene (in Axelrod, 1972*a*: 50–51) and has brought to it a cooler and drier climate. This was supplemented by building a volcanic field from Ethiopia southward down the rift valleys, further increasing the rain-shadow effect and bringing greater drought and temperature extremes.

A second major factor that affected the African flora was the development of the Benguela Current, for it brings cold water and hence a drier climate to the West African coast. Since glaciation was initiated on Antarctica in the Early Miocene (Anonymous, 1973; Hayes *et al.*, 1973), cold water commenced to bathe the West African coast at that time, bringing to it a dry season of at least slight magnitude. Furthermore, in the Pliocene (~ 5 m.y. BP) glaciation on Antarctica was extensive so that the bottom of the Ross Sea was scraped by an ice sheet that extended 200–300 miles farther out than the present one (Hayes *et al.*, 1973). Whereas the Ross Ice Shelf now forms an apron of floating ice about 600 feet thick, the Pliocene ice sheet plowed across the sea floor that is 1,000 to 2,000 feet below sea level. Clearly, this would not only have brought a much drier climate to the tropical West African coast, it may also (in a global sense) account for the very dry climate of the Middle Pliocene, as recorded in California and elsewhere (Axelrod, 1948; Mudrey *et al.*, 1973).

Finally, fluctuations of Quaternary climate also had an important effect on the African tropical rainforest flora, with the drier phases being times of extinction of taxa that required more nearly ever-wet conditions (*e.g.* Langenheim, 1972). Wild (1968: 207) and others have reconstructed tentative vegetation maps of Rhodesia and other parts of Africa showing how vegetation could have differed from that of today if rainfall increased to approximately 150 per cent of present levels. The maps show that Rhodesian forests that are now isolated would have been sufficiently widespread to have been in contact with the main forest areas of the Congo and West Africa. This could explain the affinities of species and generic composition of the Rhodesian forests that are now isolated, but have West African relationships. Quaternary pluvials of only 50 per cent higher rainfall could also probably account for the distribution of middle and lower altitude riparian forest species which may have formed a more or less continuous forest at lower altitudes through much of tropical Africa. In this sense, their present isolated distributions are merely relict of their former wide occurrences along most river systems.

At the same time that spreading drought tended to impoverish and disrupt the African flora, other factors were operating that tended to preserve the richness of the South American and Australasian tropical floras. With respect to South America, it is recalled that the cold water from Antarctica that now flows north as the strong Humboldt Current is the chief cause of the Atacama Desert climate and probably also the barren desert slopes of the entire Pacific slopes of the Andes north of Santiago, Chile. From the Paleocene to Miocene, tropical to subtropical rainforest inhabited the present desert coast of Peru and Chile (review in Berry, 1938: 48). We infer that as the Humboldt Current gained strength during the Miocene and Pliocene, and as the subtropic high became more permanent, rainforest was replaced by savanna and then thorn scrub, and finally desert vegetation. Gerth (1941) commented on the progressively increasing severity of the South American climate as reflected by the changing floras of Upper Cretaceous, Paleogene, and Neogene times, However, the Andes commenced to rise in the later Pliocene and Quaternary. They then imposed an effective barrier between the moist climate suited to the rich tropical rainforest and savanna vegetation of Brazil and adjacent tropical lands east of the range, and that suited to the expanding aridity and to thorn scrub and desert vegetation to the west. Clearly, the tropical rainforest of South America would have become further impoverished if the Andes had not sheltered it from spreading drought on the west coast. That it has suffered some impoverishment in the east is clear from the record in northeast Brazil. A rich Pliocene rainforest is recorded in Bahia (Hollick, 1924), but today the fossil locality is in a region of thorn scrub. The aridity here results in large part from the cold water carried west from Africa by the Benguela-Brazil Current which is sufficiently cold to inhibit reef corals, and accounts in large part for the low precipitation and the presence of thorn scrub there.

There is now reliable evidence for widespread ice-age aridity in low tropical latitudes (Emiliani, 1971: 185). In South America, Bigarella and de Andre (1965) note that residual pediments occur at the foot of the Serra do Mar in east-central Brazil, in present-day very wet forested areas. Since pediments and pediplanes—which form under relatively dry to desert climates—can be traced widely over eastern Brazil, they conclude that climate was semiarid, not pluvial, as had generally been supposed, when sea level was lower. They suggest that world-wide aridity probably affected wide areas of the inner tropics during the cold phases of the Pleistocene. This evidence is nicely supplemented by the discovery that arkosic sands of late Wisconsin age occur in deep sea cores from the Guiana basin, whereas today fine muds derived from deep chemical weathering are being deposited there (Damuth & Fairbridge, 1970). This observation is consistent with the nature of a pollen flora of late Wisconsin age (12,000 years BP) recovered from the deep sea off Argentina which shows that semiarid vegetation (*Ephedra*, chenopods) was widespread, and "occurred when sea level was low, and when much of the present wide continental shelf was emerged and supported a steppe vegetation" (Groot & Groot, 1966). Measurements of kaolinite/quartz ratios in Caribbean cores likewise indicate that the Caribbean area was more arid during Pleistocene temperature minima (Bonati & Gartner, 1973), as do studies of foraminiferal assemblages in the Colombia Basin (Prell, 1973). The circulation of both the California and Peru currents into equatorial regions along the west coast of South America was intensified during glacial maxima (Thompson & Saito, 1973), this necessarily resulting in increased aridity onshore.

Furthermore, biological evidence from the lowlands of Colombia and Guyana (Wijmstra & Hammen, 1966), Brazil (Haffer, 1969, 1970; Vanzolini & Williams, 1970; Vanzolini, 1970), and the Galapagos Islands (Colinvaux, 1972) can best be interpreted in terms of widespread drought and forest restriction during the glacial ages (Vuilleumier, 1971). Evidence of various taxa indicate many areas of disjunction, hybridization, secondary sympatry, and introgression exist in Amazonia. Since these areas of secondary contact do not correspond to observable physical or ecological barriers, they must be related to historical factors. Inasmuch as these areas occur across Amazonia, which is now a relatively uniform habitat, Vuilleumier postulates that there must have been Pleistocene climatic changes that caused the fragmentation and re-expansion of the selva. The changes in the climate were presumably synchronous with those that also affected the montane forests in the lower Andes. She therefore visualizes the repeated alternation of distribution patterns during the Quaternary, with rainforests fragmented during the dry (glacial) periods and then expanding again during the humid (inter-glacial) phases. Thus, speciation of forest taxa was initiated or completed in isolated patches of fragmented forest. Secondary contract, with hybridization or reunion of populations that did not become reproductively isolated, occurred in periods of expansion. In this manner, Pleistocene climatic changes have had a major role in increasing the diversity in the inner tropics—a region that previously had been regarded as stable, an evolutionary enigma (Vuilleumier, 1971).

The phenomenon of ice-age aridity was not confined to South America. Pleistocene dune ridges (now stabilized) pass below sea level onto the continental shelf of northwest Australia. They evidently formed at a more arid, cooler time than now, when sea level was glacio-eustatically lowered and the Sahul Shelf was dry land (Fairbridge, 1953). From his study of birds in Timor and northern Australia, Mayr (1944) concluded that a dry savanna landscape on the Sahul Shelf during the glacial stages was required to permit migration of grassland birds. In New Guinea and adjacent Australia sea level was about 180 meters lower during the glacial ages, and hence more than adequate to unite Australia and New Guinea, and to extend Australia far to the northwest. Webster and Streten (1973) indicate that at these times cooler sea-surface temperatures, cooler trade winds, and the greatly expanded land surfaces gave the region a significantly drier climate than at present. This supports Mayr's inference (1969) that alternating climates during the Quaternary can largely explain much of the recent bird speciation in the tropics.

In West Africa (*in* Damuth & Fairbridge, 1970), Tricart reports that desert dunes from the Sahara dive below sea level at the coast. At the glacial maxima, the Sahara sands spread south into the Upper Nile and the Congo rivers. Radiocarbon dating of alluvial fills in the Nile and in the Congo indicate that these great tropical rivers were partly overwhelmed by desert sands and almost dried up during certain stages of the Wisconsin maximum (see Damuth & Fairbridge, 1970, for references). Bakker (1972), collating evidence provided by the late Pleistocene and Holocene lacustrine phases in the southern Sahara and in East Africa, showed that the lake levels changed practically simultaneously in the entire area. Evidence suggests desert-like conditions in the region during a time that was contemporaneous with the last maximum glaciation. He infers that the climate of the Sudan and Guinea was dry about 20,000 years ago—during the Wisconsin. By analogy, other glacial ages in the inner tropics were also dry. Bakker and Coetzee (1972), after a review of evidence of late Quaternary climate change in tropical Africa, conclude glacial-age climate was drier and interglacialage climate was wetter than at present, which agrees with evidence provided earlier on the bases of studies in more local areas (*i.e.* Livingstone, 1967: 50; 1968; 1971; Coetzee, 1967: 68, 81; Hamilton, 1972; Kendall, 1969). Bakker and Coetzee (1972) emphasize that during the arid and semiarid cooler phases the pattern of plant and animal distribution was greatly different than that of the present. The Sahara extended to the south, and in East and Central Africa mountain forests must have been very restricted and isolated. During winters in the glacial periods, intrusions of cool Benguela-South Equatorial Current waters occurred off northwest Africa, contributing greatly to spreading aridity in regions now tropical (Gardner, 1973). Dry types of woodland, savanna and grassland were widespread, and the main area of tropical rainforest may have been confined to local areas similar to that indicated for the Amazonian selva (Vuilleumier, 1971). Clearly, the evidence of recurrent, ice-age aridity in the tropics nicely explains many of the evolutionary problems posed by taxa in both the New and Old World tropics, as discussed recently in the symposium on *Speciation in Tropical Environments* (Lowe-McConnell, 1969) and also by Vuilleumier (1971).

The climatic vicissitudes of the Neogene (Benguela, Humboldt Currents triggering drought) and the Quaternary with several periods of ice-age aridity seem adequate to explain the impoverishment of the African flora, as well as the tropical American and presumably the Southeast Asian (and Indian) flora as well. This may well account for the elimination of taxa that may earlier have been in Africa, or America, and now survive only in Asia, or in equable insular regions that were less affected by these changes.

The several drought periods of the Quaternary not only impoverished the South American and African rainforests, but that of the area from Southeast Asia to Australasia as well, though probably in lesser degree owing to the more oceanic nature of the area. These periods of ice-age drought bring up the problem, chiefly discussed by archaeologists, geographers and botanists, as to whether tropical grasslands are man-made. The evidence of ice-age aridity in the tropics implies that at least some of them are native—not man-made—and are relicts of past climate (but see Wijmstra & Hammen, 1966). A strong indication of this is seen in the actual distribution of grasslands in the region stretching from New Guinea westward to Asia and northward into the Philippines: these are clearly controlled by terrain and climate, as judged from a study of tens of thousands of high altitude aerial photos of the entire region.

Survival and Extinction in Africa.—We have direct fossil evidence for the extinction of some plants, such as *Nypa* (Tralau, 1964), in Africa. Unfortunately, owing mainly to the general uplift of the continent from the Miocene onward, there are few Cretaceous or Paleogene rocks in which to search for fossils. For a number of plant groups there is, however, indirect evidence of extinction of at least some lines on the African mainland. For example, on Madagascar and its neighboring islands in the western Indian Ocean, groups such as ferns, palms, orchids, bamboos, Malpighiaceae, Celastraceae, and Bignoniaceae are much better represented than on the African mainland, a pattern which seems to be associated with the effects of spreading aridity and mass extinction on the mainland. As Dejardin *et al.* (1973) have stressed, the flora of Madagascar is in fact balanced with respect to such widespread tropical groups: it is the situation in continental Africa which is peculiar. In addition there are a number of taxa that link tropical America with Madagascar, but are absent on the mainland of Africa. These include Monimiaceae s. str., Trigoniaceae, Winteraceae, Chloranthaceae, Elaeocarpaceae, *Rheedia* (Hypericaceae), *Rhacoma* (Celastraceae), *Ravenala–Phenakospermum* (Musaceae), *Phenax* (Utricaceae), *Weinmannia* (Cunoniaceae), Herreriaceae, the ceroxyloid and chamaedoreoid palms (Moore, 1973*a*, 1973*b*), and the ferns *Adiantopsis*, *Trachypteris*, and *Ophioglossum palmatum* L. (Dejardin *et al.*, 1973). How did these disjunct distributions come about, and what may we infer from them?

Long-distance dispersal certainly has occurred, and is occurring, in the lands around the Indian Ocean. Thus we would postulate that some of the genera which provide links between the Australasian region and Madagascar such as *Hibbertia*, *Cohnia*, *Keraudrenia*, *Caesia* (also in South Africa), *Adansonia*, *Polypompholyx* (also in South America), and *Ascarinopsis–Ascarina*, as well as several other genera of such families as Asteraceae, Poaceae, and Cyperaceae, passed between Madagascar and Australasia in this manner. We base this contention upon the presence of the characteristic features of groups that have been dispersed by long-distance dispersal (Raven, 1963): unbalanced representation in the two floras, close relationship, occurrence in open habitats. There are also tropical Asian groups, such as *Nepenthes*, *Dillenia*, *Evodia*, *Dapania*, *Calophyllum*, *Rulingia* (also in Australia) and a number of other groups discussed by Dejardin *et al.* (1973), which seem to have reached Madagascar the same way, and which are presumed to be easily dispersed, judging from their present ranges. Some of the genera mentioned, incidentally, are represented on the Seychelles. Finally, groups such as *Fuchsia*, *Coriaria*, *Heliconia*, Myoporaceae, and Gesneriaceae–Gesnerioideae seem to have spread across the Pacific by long-distance dispersal. Some animals, and even iguanid lizards, may have done the same. It can clearly be seen that the disjunctions between Madagascar and tropical America could have been built up stepwise in the same way; the judgment of whether they were or not depends upon the analysis of particular taxa.

The groups linking Madagascar with tropical America differ in their overall distributions and patterns of relationship. Thus Trigoniaceae consist of two American genera, *Trigonia* (30 species) and *Lightia* (2 species), together with one monotypic genus each in Malaysia (*Trigoniastrum*) and in Madagascar (*Humbertiodendron*). Chloranthaceae appear to have reached Madagascar from the east, since the relationships of *Ascarinopsis* are with the Asian–Australasian–Polynesian *Ascarina*, and *Hedyosmum*, the only genus in America, presumably came independently from Eurasia. Elaeocarpaceae are represented in Asia and the Pacific Islands, tropical America, and on Madagascar, where there are two species of *Elaeocarpus* and one of *Sloanea*, large genera widespread in Asia (see p. 579). *Weinmannia* and the group of genera including the Mascarene "*Macadamia*" have similar patterns of distribution. For each of these groups, depending upon a detailed analysis of distribution, one could perhaps most logically suggest that they may have reached Madagascar from the east, and need never have been present on the mainland of Africa, but it is very difficult to be certain.

Other disjunct groups have ranges which strongly suggest extinction in Africa. These include *Rheedia*, with about 15 species in tropical America, about 12 on Madagascar, and one in the Comores; *Phenax*, with about 25 species in tropical America, 3 on Madagascar; *Ravenala–Phenakospermum*; Liliaceae–Herrerieae (Herreriaceae); the ceroxyloid and chamaedoreoid palms; *Rhacoma*; *Oplonia* (Acanthaceae); and *Oliganthes* (Asteraceae), all completely confined to Madagascar and the neighboring islands and tropical America at the present time. Animal groups with similar relationships are discussed by Paulian (1972: 11). For these groups, it seems likely in all cases that they were once present on the African mainland, and subsequently have become extinct there. Direct dispersal between Madagascar and tropical America seems a virtual impossibility, and the present ranges of these plants, together with a consideration of the climatic trends in Africa during the Tertiary and subsequently, appears to lend credence to a hypothesis of extinction on Africa in response to spreading drought.

For groups now more widespread, consideration of the relationships of the taxa involved may lead to an inference of whether they have become extinct on the mainland of Africa or not. For example, in Winteraceae, discussed on p. 563–4, long-distance dispersal is apparently not difficult, judging by the fact that *Tasmannia* has reached the Philippines since Miocene time. If the single species on Madagascar is in fact a *Bubbia*, an otherwise Australasian genus, then one might imagine that it reached Madagascar by long-distance dispersal. If on the other hand it is related to the exclusively New World *Drimys*, a possibility that has yet to be examined in detail, it might be a remnant of an ancient population of Winteraceae that extended across West Gondwanaland. Economy of logic at present suggests that Winteraceae may be an Australasian group that reached Madagascar by long-distance dispersal and America from Australia *via* Antarctica (Raven & Axelrod, 1972); but the alternate hypothesis also needs to be examined. For Proteaceae, discussed above, it appears very likely that ancestral Macadamieae, and specifically the ancestors of the group of four genera including *Brabeium* (South Africa), *Macadamia* (Australasia to southern tropical Asia, one supposed species in Madagascar), and the tropical South American *Panopsis* and *Roupala* (Johnson & Briggs, 1963), were once more widespread in Africa and migrated directly between Africa and South America. Monimiaceae s. str. have similar complex patterns of interrelationship involving the genera of Madagascar and neighboring islands and those of tropical America, strongly suggesting extinction on the mainland of Africa following direct migration between Africa and South America.

For Chloranthaceae, since the monotypic Mascarene genus *Ascarinopsis* is apparently not directly related to the American *Hedyosmum* but is similar to the Polynesian *Ascarina*, we suggest that the ancestors of *Ascarinopsis* reached Madagascar by long-distance dispersal from one of the other lands bordering the Indian Ocean. One may also argue by analogy that the apparently relict endemic taxa on Madagascar and neighboring islands, such as Didymelaceae, Medusagynaceae, Sphaerosepalaceae, Didiereaceae, Sarcolaenaceae, and dozens of genera and suprageneric taxa, may also have occurred at one time on the mainland of Africa, although this can be proved only if fossil evidence is found.

The geological evidence already reviewed, together with that from a history of the vertebrates, indicates little interchange of plants and animals between North and South America before Neogene time. For taxa that are well developed and apparently of some antiquity in South America, including some disjunct to Asia, the possibility exists that they have come *via* Africa and subsequently became extinct there. Again, such extinction can be proved only by fossil evidence from Africa, but the possibility needs to be weighed against others for the groups concerned, which have been reviewed in the pages above. These include Dipsacales (ancestor of Calyceraceae), Lardizabalaceae, Symplocaceae, Theaceae–Bonnetioideae, Rosaceae–Quillajeae s. str., Asteraceae–Mutisieae, the *Argylia–Incarvillea* line (Bignoniaceae), *Bambusa*, and *Meliosma* subg. *Meliosma*. For many of these groups, and for other disjuncts noted by Steenis (1962), the alternative hypotheses often seems no more likely than extinction in Africa: a very early arrival in North America followed by unlikely, very long-distance dispersal to South America, and sometimes by extinction in North America; or trans-Pacific long-distance dispersal. What we are urging here, as in the analysis of the affinities of the plants and animals of Madagascar and its neighboring islands with those of Latin America, is an awareness of the possibilities and an unprejudiced evaluation of the similarities.

The Cape Region of South Africa seems also to provide a refuge for certain plants and animals once more widespread in Africa, including *Brabeium*, the leptodactylid frog *Heleophryne*, and possibly the Proteaceae–Proteoideae and Restionaceae. That the African flora has been impoverished only recently is also implied by the history of the Canary Island laurel forest (Takhtajan, 1969: 203; Bramwell, 1972). Whereas this forest includes four genera of Lauraceae (*Apollonias, Laurus, Ocotea, Persea*), there are only five on the entire African continent. The Canary Island laurel forest inhabits middle altitudes (2,000 to 4,000 feet), chiefly on the north coast of the islands, where they are in the trade wind belt and hence are shrouded in fog during the hot summer months. A highly equable climate (see Axelrod, 1966: fig. 9) and ample fog-drip during summer help maintain the forest which clearly is a remnant of the much richer evergreen forest that covered parts of Europe and Africa in the Tertiary, and which is closely allied to the Afro-montane forest of the present day.

As judged from the fossil flora of southern Europe and north Africa, a similar forest persisted at sea level in southern Europe into the Late Pliocene (Depape, 1922; Bramwell, 1972), but it was eliminated there by colder glacial climates and by the spread of aridity over the Mediterranean and adjacent Africa during the drier inter-glacial ages. The persistence of laurel forest on the Canary Islands owes largely to fortuitous tectonic events. The low, semi-desert eastern Canary Islands (Fuerteventura, Lanzarote, Concepcion Bank) lie on the continental basement of Africa (Rona & Nalwalk, 1970). They are separated from it by a major northeast-trending strike-slip fault that has displaced the east Canary Island block 160 km southwestward from the Ifni gap, which it earlier occupied (Dietz & Sproll, 1970*c*). Apart from geologic evidence, the late Neogene remains of ratite birds on Lanzarote indicate that it was tied to Africa (Sauer & Rothe, 1972). Presumably as a result of movement of the east Canaries block, volcanism built up the western Canaries, composed of Tenerife, Gomera, Hierro, and La Palma which rest on oceanic crust. The oldest rocks are on Tenerife, and indicate volcanism from the Middle Miocene to Pliocene (16–4.5 m.y. BP). However, 80 per cent of the subaerial volcanism in the western Canaries is Pleistocene (2.0 m.y. and less), according to radiometric evidence (Abdel-Monem, Watkins & Gast, 1972). As the volcanos gradually increased in altitude, moist areas suitable for the forest came into existence. At levels above 2,000–2,500 feet a fog-deck now formed regularly during summer to provide favorable sites for persistence of the laurel forest that had earlier inhabited the lowlands nearby, but was disappearing there as precipitation decreased during the Pliocene.

The greater diversity of the Tertiary forest may be inferred from the geographic affinities of some of the taxa in the Canary laurel forest. For example, *Heberdenia*, *Drusa*, *Clethra*, and *Persea* are absent on the African mainland but have relatives in Latin America. In addition, there are the endemic genera *Visnea* (Theaceae), *Picconia* (Oleaceae), and *Bencomia* (Rosaceae), the latter belonging to a group that ties together Africa and South America, the tribe Sanguisorbeae.

As Richards has noted (1973), many of the species of the African rainforest are common and widely distributed, rather than rare and local as in the rainforests of America and southeast Asia. This situation finds a parallel in the flora of India, which also was left impoverished by spreading drought, and chiefly since the Oligocene (Axelrod, 1971). The Canary Islands, like Madagascar and to some extent the Cape Region of South Africa, provide refugia in which representatives of a formerly more widespread mesic African flora have survived in relative isolation and under the influence of an oceanic climate. These islands play for the ancient flora of Africa a role similar to that of New Caledonia and New Zealand with respect to the ancient flora of Australasia (Raven & Axelrod, 1972).

DISPERSAL BETWEEN WEST GONDWANALAND AND AUSTRALASIA

Geological evidence reviewed above suggests the possibility of more or less direct migration between Africa and Australasia up to the close of Early Cretaceous time—110 ± 10 m.y. BP (Fig. 2). Although both the geological evidence and that from the distribution of vertebrates is inconclusive about when the connection between Africa and Australasia was severed, even the reconstruction at 75 m.y. BP (Fig. 2) suggests that Madagascar and India would have served as a subtropical route of migration, perhaps somewhat interrupted, to Australasia into Late Cretaceous time. Once the migration of tropical alliances by this route was no longer possible, Australasia was connected with the rest of the world only by a cool-temperate pathway to South America *via* Antarctica. Darlington (1957, 1965), Martin (1972), and others have argued that this corridor, judging from the distribution of modern organisms in South America, was unsuitable for many of the South American–Australian disjuncts. This is chiefly because a number of them now have tropical or subtropical patterns of distribution on both continents, as for example some of Proteaceae, discussed above.

Among the angiosperms, it is likely that *the ancestors* of the following ancient and archaic groups reached Australia in mid-Cretaceous time by a subtropical to tropical route from Africa:

Annonales, including the ancestors of Winteraceae and Monimiaceae st. str. and the suborders Magnoliineae and Laurineae. The other suborders and families may have evolved later, or in the Northern Hemisphere.
Balanopales.
Campanulales perhaps, if Goodeniaceae are closely related to Campanulaceae.
Casuarinales, its ancestors.
Commelinales, including the ancestors of several endemic Australasian families—Philydraceae, Centrolepidaceae, and Restionaceae. *Cartonema*, a very distinct genus of Commelinaceae, may have come subsequently.
Cornales, including Araliaceae and Haloragidineae, as well as possibly *Phelline.*
Ericales, Epacridaceae.
Euphorbiales, including Thymelaeaceae and perhaps Euphorbiaceae.
Liliales, including the ancestors of the Xanthorrhoeaceae alliance, the Phormiaceae alliance, the Johnsonieae, the Asteliaceae, and Haemodoraceae–Conostyloideae.
Myrtales, Myrtaceae.
Pittosporales, as a part of Rosales (Cronquist, 1968).
Proteales.
Rosales, including Saxifragaceae subfamily Brexioideae and Cunoniaceae, in addition to ancestors of the endemic or sub-endemic Australasian taxa Eremosynoideae, Stylidiaceae, Cephalotaceae, Davidsoniaceae, Eucryphiaceae, and Corynocarpaceae, all of which are separately related to groups found outside of Australasia.
Santalales, including Santalaceae and Icacinaceae. The differentiation of Stackhousiaceae probably took place in Australasia after the early arrival of santalalian stock in the region. Olacaceae migrated to Australia by Paleogene time, became extinct, and re-entered subsequently.
Theales, including Dilleniaceae and possibly Hypericaceae, as well as the ancestors of Strasburgeriaceae and of *Oncotheca.*

An analysis of distribution patterns suggests that of Cronquist's (1968) six subclasses of dicots, only Magnoliidae and Dilleniidae–Rosidae (the distinction between them is becoming increasingly blurred; Eyde, 1974) were almost certainly in existence when more or less direct migration between West Gondwanaland and Australasia was possible. If the phytolaccaceous ancestors of Gyrostemonaceae came from South America *via* Antarctica, feasible considering the cool temperate Australian distribution of the group, and if the ancestors of Goodeniaceae–Brunoniaceae either did the same or reached Australasia subsequently by long-distance dispersal, then one could conclude from present distributions that neither Asteridae nor Caryophyllidae, nor their immediate ancestors, were in existence in mid-Cretaceous time. Although the relationships of Balanopaceae are obscure, *Nothofagus* and the Casuarinaceae probably provide an indication that Hamamelidae existed at that time, or soon after.

Among the monocots, Commelinales and Liliales are the only groups that seem likely, on the basis of present distributions, to have been in existence when more or less direct migration between West Gondwanaland and Australasia was possible. The monocots almost certainly originated in West Gondwanaland and many lines subsequently migrated to Australasia. It is very unlikely that any living genus of flowering plants is old enough to have migrated more or less directly between Australasia and West Gondwanaland, and there are at most only a few families involved in this pattern, which mainly concerns the ancestors of the groups we recognize as orders.

In general, the ease of migration to Australasia has decreased during the Late Cretaceous to Paleogene, only to increase again in Neogene time as the Australian plate neared Asia. Nevertheless, migration between Australasia and Africa *via* India and Madagascar probably was relatively direct, but with fairly long steps over water after the start of the Tertiary (65 m.y. BP). Among the taxa that seem, on the basis of their current representation, to be relatively old in Australia, but not as old as the mid-Cretaceous, are Araceae, Arecaceae (Eocene fossils), Celastraceae, Chenopodiaceae, Fabaceae–Faboideae, Loganiaceae, Oleaceae, Rhamnaceae, Rubiaceae, Smilacaceae, Sterculiaceae–Byttnerioideae, and Violaceae. Their ancestors may have arrived during Paleogene time, as probably also did those groups in which distinctive elements have evolved in Australasia: Bignoniales (Myoporaceae), Cornales (Haloragaceae), Chenopodiales (Gyrostemonaceae), Capparales (*Oceanopapaver*), Lamiaceae (Prostantheroideae), Liliales (Ripogonaceae), Verbenaceae (Chloanthoideae), and Malvaceae (*Plagianthus* group). *Canacomyrica*, a monotypic genus of New Caledonia which may be unrelated to Myricaceae (R. F. Thorne, personal communication), might also be placed in this list.

Nothofagus presents a special problem in its dispersal to Australasia. As suggested above (p. 573), the group of Fagaceae ancestral to *Nothofagus* may have spread to Australasia from the montane tropics by the mid-Cretaceous, using topographic highs on the Precambrian basement across Africa, India, and Antarctica which have since been largely reduced by erosion. The ancestors of the Australasian members of the suborder Magnoliineae (Himantandraceae, Eupomatiaceae, Degeneriaceae) may have done the same, since the only other member of the suborder is the essentially Laurasian Magnoliaceae. Similar problems are presented by many of the other groups in the list mentioned above, although their relatives in the Northern Hemisphere are often not clear. For example, the African Proteaceae and Restionaceae seem derived from Australasian progenitors; yet whence came the ancestors of the original Australasian stocks? In the absence of a more or less direct pathway from Asia into Australia in the mid-Cretaceous, we must postulate migration across Africa and India, followed by extinction, for many of these taxa.

Many plants and animals have certainly migrated between South America and Australasia *via* Antarctica (Raven & Axelrod, 1972), perhaps until Early Oligocene time. We emphasize, however, that this has not been the only possible route to Australasia during the history of the angiosperms. In Proteaceae, for example, some genera may have spread from Australasia to South America *via*

Antarctica, others went directly from Australasia to West Gondwanaland in the mid-Cretaceous (see discussion on p. 583–4), a duality of dispersal suggested earlier by Axelrod (1972*c*). Grevilleoideae have reached South America, probably by at least two different routes, and Africa; Proteoideae, Africa; and Persoonoideae, the most archaic of the three subfamilies, have remained in Australasia. If Restionaceae and Epacridaceae were truly present in the Eocene of southern England, they might have originated in Laurasia and reached Australasia by relatively long-distance dispersal. Restionaceae are evidently easily dispersed at present (Cutler, 1972), and it may be that their anatomically relatively homogeneous African representation arrived by long-distance dispersal across or around the Indian Ocean. Detailed consideration of individual families and other groups is necessary to determine their routes to and from Australasia.

For the vertebrates, there is no conclusive evidence that any group crossed Antarctica between Australasia and South America since Lower Triassic time (Colbert, 1972, 1973). Contrary to the view we expressed earlier (Raven & Axelrod, 1972), we now believe that the patterns observed among the vertebrates mostly suggest direct migration between West Gondwanaland and Australasia in the Jurassic and Lower Cretaceous. These groups include ratite birds, ceratodont lungfishes, osteoglossomorph fishes, rhynchocephalians (tuatara), leiopelmid frogs, and the ancestors of monotremes; all of these groups may have existed before the close of the Jurassic. Present evidence is inconclusive about the route by which meiolaniid and chelyid turtles reached Australasia, and about the route or routes whereby galaxiid fishes achieved their present Antarctic distribution.

Leptodactylid frogs seem certainly to have been present in West Gondwanaland, judging from present distribution and the occurrence of the endemic *Heleophryne* in Africa (Darlington, 1957; Cracraft, 1973*b*), and their occurrence in the Paleocene of India (Darlington, 1957). They may have reached Australasia directly *via* the subtropical route proposed above, although more comparative study of living and fossil anurans will be necessary before the question can be settled.

For marsupials, direct migration from West Gondwanaland to Australasia, with subsequent extinction in Africa, seems probable (Cox, 1970), and the age of the group appears compatible with such an hypothesis. Dispersal by this warm temperate to subtropical pathway answers Darlington's (1957, 1965) objections about the ecological requirements of marsupials. Further, the age of the dichotomy would be consistent with the great differences between Australasian and South American marsupials. Fossil evidence, especially from Africa, is highly desirable.

The distinctive placental mammals of West Gondwanaland may have originated after the marsupials (Lilegraven, 1969), and perhaps in Laurasia (Cracraft, 1973*b*), after the possibility of more or less direct migration between West Gondwanaland and Australasia had ceased. On this basis, the origin and composition of the mammal faunas of both South America and Australasia, as well as the relationships between them, would be neatly solved. The presence of a nearly complete (Dalziel *et al.*, 1973) land pathway between Australia and South

America would have presented an impassable filter bridge: cool temperate climate covered Antarctica from the latest Cretaceous onward (Raven & Axelrod, 1972).

Migration from West Gondwanaland to India and Australia by a warm temperate to subtropical route seems to provide a satisfactory solution for the anomalies in the distributions of dinosaurs we noted earlier (Axelrod & Raven, 1972). For example, the large dinosaurs from the Early Jurassic to the mid-Cretaceous of India indicate direct connections with Africa (Colbert, 1973), and Lower Cretaceous dinosaur faunas are in general of world-wide extent. Large sauropod dinosaurs, including the genus *Laplatasaurus*, are common to Argentina, India, and Madagascar in Late Cretaceous time. Dinosaurs entered Australia from other parts of the world in Upper Jurassic or Early Cretaceous time (Colbert, 1972), thus clearly demonstrating the efficacy of the warm temperate to subtropical West Gondwanaland–Australasian pathway, but unfortunately not telling us yet how long it persisted.

A major problem concerns the absence of not only marsupials but also monotremes, living and fossil, on New Zealand. We earlier inferred (Raven & Axelrod, 1972) that the arrival of marsupials in Australasia may have taken place subsequent to the separation of New Zealand from Australia–Antarctica (~ 80 m.y. BP), but this seems less probable in the light of the hypothesis advanced here. The dilemma is that many plants that do not seem to disperse across water gaps (*e.g. Nothofagus*, Proteaceae, austral gymnosperms) are well represented in the balanced flora of New Zealand, but there are few vertebrates. Ratite birds may be older, but why are there no living or fossil monotremes in New Zealand and why no reptiles, living or fossil, except *Sphenodon*? Although the question of direct Cretaceous land connections to New Zealand requires further study (Fleming, 1962, 1963; Gaskin, 1972), one or more shallow water gaps may have separated New Zealand and New Caledonia from Australia during the later Cretaceous. Current evidence indicates the Tasman Sea evolved by a process of seafloor spreading 60–80 m.y. BP (Hayes & Ringis, 1973). Hence, New Zealand and New Caledonia (Houtz *et al.*, 1973) were readily accessible only to the earliest immigrants.

Climate may also have been a critical factor. New Zealand, at latitude 60–70°S in the later Cretaceous (80 m.y. BP; Hayes & Ringis, 1973: fig. 7), would have had long dark nights and sustained low temperatures unsuited for most amphibians and reptiles, and probably early mammals as well. *Sphenodon* has extremely low body temperatures, ranging from a mean of 10.6°C (November) to 11°C (April), much lower than any other reptile (Bogert, 1953*a*, 1953*b*), and even lower than that reported for terrestrial salamanders (Brattstrom, 1963). Furthermore, tuatara has a lower metabolic rate than turtles and lizards. Its low metabolic rate and heat requirements may reflect its ancient Cretaceous (and earlier?) tolerance. On this basis, *Sphenodon* probably has survived in New Zealand because the area has had cool to cold temperate climates suitable for it continuously since the Cretaceous. Further, these climates could have been unsuited for other Cretaceous vertebrates, not only ectotherms, but endotherms (marsupials, monotremes) may not yet have been able to withstand the sustained low yearly temperatures of New Zealand. In view of their absence, *Sphenodon* has been isolated from predators and has therefore survived.

We agree with Cox (1970), Fooden (1972), and others that marsupials may have become extinct in Africa, as have many other groups as discussed above. The views we have presented here appear to some extent to vindicate Darlington's (1965) skepticism about the importance of Antarctica as a route of migration for a number of megathermous groups of organisms, although for many microtherms it has certainly been of extreme importance. It is not possible to agree with Keast (1973) and Cracraft (1973*a*) about the unimportance of West Gondwanaland-Australian migration up to the mid-Cretaceous. This pathway provides a much simpler explanation for the distribution of many groups of subtropical requirements. If India provided a bridge from Africa to Antarctica and Australasia prior to Cenomanian time (Fig. 2), then the conclusion of Jardine and McKenzie (1972) that a route from South America *via* Antarctica was the only plausible one for marsupials obviously is invalid.

In concluding this section, we recall the crucial role that Antarctica has had in the history of land plants from later Paleozoic time onward. Antarctica was centrally located with respect to other austral lands from the Permo-Carboniferous well into the Early Cretaceous (Figs. 1, 2). It is this central position that accounts for the similarity of the *Glossopteris* flora at localities that are now as widely separated as India, Australia, Argentina, and South Africa (Plumstead, 1962; Seward, 1941: 178). Its central position also explains the close relationships between the Triassic and Jurassic floras of these austral lands, for they all share many species of ferns, seed ferns, cycadophytes and austral conifers (Seward, 1941: Tables B, C, D). As discussed in detail above, India–Antarctica served as a major route for dispersal of early angiosperms of warm temperate to subtropical requirements from West Gondwanaland to Australia. Furthermore, it served as a major pathway the temperate evergreen dicots and austral gymnosperms whose nearest descendants are now isolated in the Tasman and Fuegian regions (Axelrod, 1960: 270; Raven & Axelrod, 1972), taxa whose close relationships are "agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes" (Hooker, 1853: 36).

As Antarctica moved to a more polar position during the Tertiary, forests were gradually eliminated there as temperatures were progressively lowered. Fossil floras from its borders (Snow Hill I., Seymour I.) and the Subantarctic Islands (Kerguelen, South Georgia, South Shetland, King George I.) suggest that forests were present on Antarctic into the middle Tertiary at least. Whether this is demonstrated by the pollen flora recovered at McMurdo Sound, Antarctica, (Cranwell *et al.*, 1960) is doubtful for it may have been carried there from distant lands: pollen of *Nothofagus* has been recovered from the modern peats of Auckland and Campbell islands, as well as Tristan and Gough! (Cranwell, 1963). Much of Antarctica seems to have been covered with a cool-temperate, evergreen forest into early Neogene time (Denton, Armstrong & Stuiver, 1971; Cracraft, 1973*c*). The leaf floras clearly indicate cold temperate equable climate like that now in southern Chile and southern New Zealand. By analogy with the zonation of vegetation in these regions today, with a slight rise in altitude on Antarctica during the middle Tertiary, fern-bush and then rosette (tussock-cushion) communities would soon have appeared, and then permanent ice fields at altitudes near 3000–4000 feet, reaching down as ice tongues to the sea—as other data now also indicate (Hayes *et al.*, 1973). With further chilling as the ice fields continued to grow, there was a progressive retreat of evergreen forest, evergreen scrub and tussock-cushion communities, followed by their eventual extinction.

DISPERSAL BETWEEN NORTH AND SOUTH AMERICA

General.—Some 100 m.y. BP, in Turonian (Upper Cretaceous) time, South America and Africa were still in more or less direct contact. Until about 50 m.y. BP (early Late Eocene), when most modern angiosperm families and many genera were in existence, South America was closer to Africa than to North America, and hence more accessible to immigration from Africa than from North America. Subsequently, and especially since the Early Miocene (~ 26 m.y. BP), dispersal between North and South America has increased progressively. In the late Neogene, about 5.7 m.y. BP, these two continents were connected by land for the first time.

Putting it differently, South America has progressively rafted the plants and animals of West Gondwanaland toward North America. Many of the phylogenetic lines involved had earlier entered Eurasia from Africa, and then North America. As a result, a number of orders and families, and even some genera—*Meliosma* and *Persea* may be examples—were reunited when South America finally became attached to North America.

The fossil record.—Fossil evidence will eventually provide reliable information about the arrival of South American plants in North America and North American plants in the south. Interpretations of plant fossils are fraught with difficulty, however, and many of the older determinations are inaccurate and therefore misleading (see, for example, Dilcher, 1973, 1974). In view of the monumental work by Berry on the Cretaceous and Tertiary floras of North and South America, it is not possible to estimate quickly the validity of his paleobotanical taxonomy. Nonetheless, while it is certain that many of his identifications are in error, it seems unwarranted to regard his work as wholly worthless. His general picture of relations between the tropical to subtropical floras of North and South America seems reasonable, as may be judged from the following summary statement (Berry, 1937: 36):

> "About 60 per cent of the genera, with over 100 species, are considered to have entered (the Gulf and Atlantic States) from equatorial America, either by way of Mexico, the Antilles, or as drift seeds and fruits.
>
> "The climatic conditions on the east and west coasts of the Mississippi embayment resulted in considerable differences in the floras along the two shores. Thirty-three genera with 37 species are confined to the western shore, and 148 genera with 354 species are confined to the eastern shore.

> The plants of the former show a greater resemblance to members of the contemporaneous floras of western North America and to the present day floras of central America; those of the latter are more closely allied to the present day floras of northern South America, and presumably entered the region, at least in part, by way of an extended Antilles."

The water barrier between North and South America was by no means an insurmountable obstacle for many plants. Sweepstakes dispersal readily accounts for the numerous taxa representing beach-jungle and mangrove vegetation in the Gulf and Atlantic States Eocene floras and provides a means for dispersal of taxa of more normal environments. In this connection, the present flora of the Indomalayan region provides an excellent basis for judging the efficacy of migration. The flora now reaches eastward from Assam-Malaya to New Guinea, the Solomons and northern Australia, and north into the Philippines, forming a rather unified floristic region. It has been dispersed rapidly over islands that are spread at least twice the distance from the northern shore of South America to North America in Paleogene-Cretaceous time. Since there were scattered islands between Central and South America (Fig. 4), effective migration seems assured. Further, the distance is far less than that involved in dispersal to Hawaii, discussed above.

Distribution maps of typical tropical South American families (see Vester, 1940) show quite clearly that a number of them enter Central America only marginally, finding their chief centers of distribution in the Amazonian basin and bordering inner tropical regions. This is consistent with northward dispersal to their climatic limits at the edge of the inner tropics in Central America. However, it remains for future work to determine which of these may have arrived by long distance dispersal during the early or middle Tertiary, or moved north when a volcanic gangplank was finally constructed between the Americas during late Neogene time.

Eocene records of possibly South American plants from North America include those of MacGinitie (1969), who reports *Lomatia* (Proteaceae), *Anacardites* (supposedly directly comparable with the South American *Schinopsis*; Anacardiaceae), *Athyana* (Sapindaceae; South America), from the Eocene Green River flora of northwestern Colorado and northeastern Utah. None of these are now regarded unambiguously as valid records. The supposed *Athyana* probably represents Anacardiaceae (J. A. Wolfe, personal communication); the *Lomatia* record is not Proteaceae (cf. Johnson & Briggs, 1963); *Anacardites* is not necessarily most closely related to *Schinopsis*.

Other records reviewed by MacGinitie (1969) include the primarily South American or South American and African genera *Beilschmiedia* and *Ocotea* (Lauraceae) and *Swartzia* (Fabaceae). Records of the subfamilies Caesalpinioideae and Mimosoideae of Fabaceae and of *Bursera* (Burseraceae) are very interesting in the light of discussion presented in the present paper.

One significant record of a basically South American plant is a species of *Philodendron* sect. *Meconostigma* in the Middle Eocene of Tennessee (Daghlian & Dilcher, 1971, 1973; Dilcher, 1973*b*). Plants of this section are now confined to subtropical South America and had been dispersed to North America at this early date. Dilcher (1973*a*) has shown that the Eocene floras of the Mississippi embayment existed under equable warm temperate to cool subtropical conditions, bordering on a seasonally dry to slightly moist temperature regime. *Dendropanax* (Araliaceae) is also reported from these deposits on the basis of a modern revision of the material, as are *Sabal* (Arecaceae), *Hura* (Euphorbiaceae), *Ficus* (Moraceae), *Ocotea* and *Nectandra* (Lauraceae), and *Podocarpus* (Podocarpaceae), all possibly austral groups (Dilcher, 1973*b*).

In a recent review, Leopold and MacGinitie (1972) consider that "Neotropical" elements were important in the Middle Eocene of the Rocky Mountain region and then became extinct by the Middle Oligocene. Among the genera they list are *Engelhardtia*, *Bernoullia*, *Thouinia*, and *Lindera*, which are tropical or warm temperate North American. Others which may have come from South America, with their times of first known appearance in North America, are:

Latest Paleocene—Cunoniaceae.
Early Eocene—*Annona* (Annonaceae), *Mabea* (Euphorbiaceae), *Luehea* (Tiliaceae), *Serjanea* (Sapindaceae), and *Oreopanax* (Araliaceae), all known from leaf fossils.
Earliest Middle Eocene—*Eugenia* (Myrtaceae) known from leaves; pollen of Sapotaceae and Bombacaceae.
Early Middle Eocene—*Apeiba* (Tiliaceae), leaves; pollen of *Ochroma* (Bombacaceae), *Guaiacum* (Zygophyllaceae), *Luehea* (Tiliaceae), Sapotaceae, tropical Meliaceae, *Iodes* and *Phytocrene* (Icacinaceae).
Late Eocene—Pollen of *Bombacopsis* (Bombacaceae).

On the basis of these records, Leopold and MacGinitie (1972) postulate a relationship of Middle Eocene Rocky Mountain flora with that of tropical America. Actually, many of the above records, and many others omitted here, can just as well be explained as survivors of an older, widespread subtropical Laurasian flora—a relation noted earlier by Berry (1937: 35). More reliable information from the fossil record will be necessary before it can be shown whether some or all of these taxa came from South America.

The analysis of the pollen flora of the Upper Oligocene San Sebastian Formation of Puerto Rico by Graham and Jarzen (1969; Graham, 1972) is of particular interest in interpreting the relationships between North and South America. Of the genera identified, *Podocarpus* (Podocarpaceae), *Acacia* (Fabaceae), *Aetanthus* (Loranthaceae), *Bombax* (Bombacaceae), *Brunellia* (Brunelliaceae), *Casearia* (Flacourtiaceae), *Catostemma* (Bombacaceae), *Chrysophyllum* (Chrysobalanaceae), *Corynostylis* (Violaceae), *Eugenia* (Myrtaceae), *Faramea* (Rubiaceae), *Guarea* (Meliaceae), *Jacaranda* and *Tecoma* (Bignoniaceae), *Marcgravia* and *Norantea* (Marcgraviaceae), *Pelliciera* (Theaceae), *Pleodendron* (Canellaceae), *Rauwolfia* (Apocynaceae) and *Tetrorchidium* (Euphorbiaceae) seem to be South American. This flora shows that by Upper Oligocene a number of South American taxa had crossed water barriers—most plausibly *via* Yucatan and Cuba—and entered Central America and the West Indies. The Cayman Ridge may have been largely above water in Early Paleogene time (Heezen, Dreyfus & Catalano, 1973), providing more direct access to Cuba from northern Central America, as did the probable Eocene elevation of Yucatan above the sea. Relationships set up then, and the more direct accessibility of Cuba to immigration in Paleogene time, presumably provide the foundation for Alain's (1958) belief in a direct land connection. Such a connection does not in fact seem to have existed since prior to the Cretaceous, if then. Jamaica was submerged from the Middle Eocene to the Middle Miocene. The notion of a Paleogene arrival of some South American taxa in the West Indies would be consistent with the prominence of such groups as Cactaceae (Buxbaum, 1969), Gesneriaceae (*Gesneria*, *Rhytidophyllum*), and Canellaceae there. *Columnea*, with 11 endemic species on Jamaica, and *Alloplectus* (Gesneriaceae; Morley, 1972) provide examples of the kinds of genera that may have reached the North American area, including the West Indies, early in Neogene time.

Graham and Jarzen (1969) also reported three temperate North American genera in Puerto Rico: *Liquidambar* (Hamamelidaceae), *Nyssa* (Nyssaceae), and *Fagus* (Fagaceae). Geological evidence, as currently interpreted, does not support the great elevation of Puerto Rico in the Upper Oligocene visualized by Graham and Jarzen (1969), as pointed out by Graham (1972). Much more geological work needs to be done in this complex area, but the question of the paleoclimatic conditions under which temperate forest elements might have existed in Puerto Rico during Paleogene time must be considered further. R. A. Howard (1973, and personal communication) has pointed out that there are apparent remnants of temperate vegetation on a number of Antilles today, an observation which might assist in the interpretation of the occurrence of these temperate trees in Puerto Rico in the Oligocene. On the other hand, these remnants might have been derived from plant associations that spread between the islands by long-distance dispersal and achieved even greater extent during the cool, dry conditions obtaining during the Pleistocene pluvials and discussed above. It is just conceivable that the pollen was carried to Puerto Rico from another source: Germeraad *et al.* (1968: 206) have indicated that pollen from wind-pollinated trees in tropical montane vegetation is often carried over considerable distances, but it is not known whether these genera were present in Mexico before the Upper Miocene.

Although the present land connection between North and South America is only about 5.7 m.y. old, islands have allowed stepwise migration of plants in Oligocene, Eocene and perhaps even earlier times (Fig. 4). The Antillean Chain, however, is a more direct and complete pathway for migration at present than it ever has been in the past. To judge from the floras (Howard, 1973) and faunas of the Lesser Antilles, relatively few organisms seem to have used that route between North and South America—apart from beach-jungle taxa. The faunas and floras of the West Indies have certainly been accumulated across water barriers, as clearly stated by Darlington (1938, 1957) and many earlier investigators, and supported by the patterns outlined by Howard (1973). In the case of Jamaica, this only commenced in the past 15 m.y. For about the past 9 m.y., opportunities for migration from island to island, and to the group as a whole, have been maximal, with the exception that the possible Early Paleogene elevation of the

Cayman Ridge above the sea, discussed above, may have enhanced opportunities at the time for immigration, still across water barriers, into Cuba.

Among the plants from the Upper Miocene Paraje Solo site in Veracruz, Mexico (Graham, 1972, 1973*a*, and personal communication), are pollen grains identified as those of *Podocarpus*, *Faramea*, *Fagus*, *Casearia*, *Liquidambar*, and *Guarea*, all reported from the Upper Oligocene of Puerto Rico (Graham & Janzen, 1969). In addition, there are members of the following families which appear to have been derived ultimately from South America: Polygonaceae (*Coccoloba*), Sapindaceae (*Matabya*), Thymelaeaceae (cf. *Daphnopsis*), Araceae (cf. *Spathiphyllum*), Chloranthaceae, Combretaceae, and Lecythidaceae. Other temperate elements include *Abies*, *Picea*, *Alnus*, *Celtis*, *Juglans*, *Myrica*, *Populus*, and *Ulmus*. By the Upper Miocene, therefore, elements of the temperate forest of eastern North America were well represented in the mountains of Veracruz (Graham, 1973*a*). In addition, a few grains of *Alnus*, *Juglans*, and *Myrica* have been found in the Miocene Gatun Formation of Panama.

As regards South America, *Juglans* was in Ecuador by the Uppermost Miocene (Brown, 1946), and other temperate North American genera for which documentation is available appear in northern South America in the Upper Pliocene and Pleistocene. *Alnus*, for example, appears suddenly at the start of the Middle Pleistocene in the Cordillera Oriental of Venezuela (Graham, 1972). Hammen (1972) records the appearance of *Alnus* (500,000 years ago) and *Quercus* (150,000 years ago) in northern South America following the Late Pliocene elevation of the mountains, together with the northward migration of such cool-temperate, southern genera as *Gunnera* and *Drimys*. These records support Chaney's (1936) view of a migration of temperate elements into Central America in Uppermost Neogene time, increasingly well documented by the studies of Hammen and Graham just reviewed. These studies suggest that at least a great majority of temperate North American plants did not appear south of the Isthmus of Tehuantepec until the Upper Miocene, at the earliest, whereas South American plants have become established in the tropical portions of the North American region from at least Eocene time onward, presumably by relatively long-distance dispersal over decreasing water barriers.

Evolution of a Latin American Biota.—Arguing from mammalian evidence, Simpson (1951: 407) reasoned that tropical North America would have been an important early site of evolution. His contention has been supported convincingly by Patterson and Pascual (1972), who point out that well over half the genera of Recent land mammals of northern origin in North America are found in the tropics, with about a quarter of the total only there—impressive figures when the present very limited extent of the North American tropics is taken into account. Considering that the tropics had a much greater extent in the Cretaceous and early Tertiary than at present, Patterson and Pascual seem almost certainly correct, although Whitmore and Stewart (1965) have argued that there was no tropical North American mammal fauna until the continent was physically joined with South America. Similarly, Darlington (1956), in part misled by erroneous notions of the relationship between Central America and North America in the Tertiary, contended that there was no truly tropical North American bird fauna. However, most ornithologists maintain that such a fauna did exist and was indeed an important source of origin of many groups (*e.g.* Mayr, 1946; Bond, 1948; Cracraft, 1973*c*). Halffter (1964, 1972) has argued cogently that most of the insects of the tropical, as well as the subtropical and semiarid, portions of North America are ultimately derived from South America. Rzedowski (1972, 1973) has similarly allied a majority of the genera of flowering plants of the semiarid and arid regions of Mexico with those of South America, in addition to the more obvious connections among tropical plants.

From his detailed analysis of the Central American herpetofauna, Savage (1966) concluded that there is a unique and important endemic tropical element in Central America that is more or less independent of the North and South American faunas. He also indicated that tropical North America was an important early site of evolution for this group. As in many groups, Central America from at least the Miocene onward has been invaded by many new taxa of South American origin.

Generalizing, it now becomes clear why biologists have long been able to speak of a Latin American fauna and flora as if it were a unified whole (Simpson, 1950). For most groups—fishes, birds, amphibians, reptiles, insects, and plants are no exception—tropical North America, including Central America and the West Indies, has been populated mainly by a biota that evolved in isolation in South America. In some cases—birds, mammals, reptiles, certain plants—taxa that originated in tropical North America have became widespread in the New World tropics. In general, however, many of the North American plants that invaded South America in Pliocene time and more recently have temperate requirements and remained at high elevations or developed in the high latitudes southward in South America. The Pliocene elevation of the Cordillera Oriental that made migration of northern plants into South America more direct cut off direct migration from the lowland tropical Amazon Basin into Central America, as T. Croat (personal communication) has suggested. This event isolated the lowland rainforest west of the northern Andes from that east of the Andes for the first time. The tropical South American biota, which for plants began reaching North America in numbers in Paleogene time—the vertebrates later—gradually invaded the lowland tropics there. The Neotropical faunal region is thus recognized by the presence of basically South American animals, which have in some instances (*e.g.* armadillo) penetrated northward even to the deserts of the southwestern United States.

Thus the tropical biota of South America have progressively taken over areas of appropriate climate in North America (including Central America and the West Indies), just as the tropical biota of Asia have taken over the lowlands of New Guinea and neighboring islands, as well as northern Australia, while old Australian plants predominate in the more equable highlands (Raven & Axelrod, 1972). The spread of plants from South to North America, earlier and far more extensive than that of the vertebrates until the formation of an actual land connection, is also reminiscent of the situation in Australasia. Wallace's line, which divides the fauna of Asia from that of Australasia, is usually regarded as one of the sharpest zoogeographic boundaries in the world; botanists, on the other hand, have tended to think in terms of an Assam-to-Fiji flora. This relationship has been discussed by Schuster (1972) and by Raven and Axelrod (1972), who relate it to the far greater dispersal powers of many plants than of vertebrate animals (Axelrod, 1952*a*). In America, it seems certain that modern types of tropical South American plants were established in numbers in the West Indies and southern North America by Paleogene time, but they were not followed in large numbers by vertebrates until after the late Neogene (5.7 m.y. BP) establishment of the Panamanian land connection. The biota of tropical North America, Central America, and the West Indies probably is comparable to the biota that would have developed in Australasia if a direct land bridge from Malaysia through Java to New Guinea and Queensland had been established in late Neogene time. Wallace's line would then presumably be much less distinct both for vertebrates and also for other groups of organisms.

In the light of the preceding discussion, we present the following list of plant families that probably spread from South to North America in Eocene time or subsequently:

Aizoaceae
Apiaceae–Hydrocotyloideae
Balanophoraceae
Basellaceae
Begoniaceae
Bixaceae
Bromeliaceae
Canellaceae
Cannaceae
Caryocaraceae
Chloranthaceae
Chrysobalanaceae
Cochlospermaceae
Combretaceae
Connaraceae
Coriariaceae
Cunoniaceae
Cyclanthaceae
Elaeocarpaceae
Eremolepidaceae
Erythroxylaceae
Fabaceae–Mimosoideae
Flacourtiaceae
Gesneriaceae
Gunneraceae
Gyrocarpaceae
Hernandiaceae
Lecythidaceae
Malpighiaceae
Marantaceae
Marcgraviaceae
Mayacaceae
Monimiaceae s. str.
Myristicaceae
Myrsinaceae
Opiliaceae
Passifloraceae
Podostemonaceae
Proteaceae
Quiinaceae
Siparunaceae
Spigeliaceae
Strychnaceae
Trigoniaceae
Triuridaceae
Tropaeolaceae
Turneraceae
Viscaceae
Vochysiaceae
Winteraceae
Zingiberaceae

Other families seem to have already been represented in the North American region by taxa derived from Eurasia when the other elements arrived from South

America. These judgments are made either on the basis of present patterns of distribution and endemism, on the fossil record, or both. The families include:

Acanthaceae
Anacardiaceae
Annonaceae
Apocynaceae
Aquifoliaceae—*Ilex*
Araceae
Araliaceae
Arecaceae
Asteraceae
Bignoniaceae
Bombacaceae
Capparaceae
Caricaceae
Caryophyllaceae—*Colobanthus*
Celastraceae
Commelinaceae
Cucurbitaceae
Ebenaceae
Euphorbiaceae
Fabaceae–Caesalpinioideae—only *Cercis* in north
Hypericaceae
Icacinaceae
Iridaceae—only *Iris* in north
Lauraceae
Lythraceae
Meliaceae
Menispermaceae
Moraceae
Myrtaceae
Olacaceae
Oleaceae—*Menodora*
Orchidaceae
Poaceae–Bambuseae
Polygalaceae
Portulacaceae–Calandrineae—except *Talinum*?
Rhamnaceae
Rosaceae—*Acaena*
Rubiaceae
Rutaceae
Sabiaceae—*Meliosma*
Santalaceae
Sapindaceae
Sapotaceae
Scrophulariaceae—*Calceolaria*
Simaroubaceae
Solanaceae—including *Solanum*
Sterculiaceae
Theaceae—for example *Ternstroemia*
Thymelaeaceae—only *Dirca* in north
Tiliaceae
Ulmaceae
Verbenaceae
Violaceae
Vitaceae

A few additional groups appear to have come principally from South America, but they are so well or distinctively represented by endemic elements in North America that they may well have arrived in North America by early Tertiary time: Cactaceae, Liliaceae–Allieae, Loasaceae, Martyniaceae, Nyctaginaceae, Tecophilaeaceae, Zygophyllaceae. Sarraceniaceae, with one endemic genus in the Guyanas and one each in eastern and western North America, might also be mentioned here, although their past history is totally unknown.

A few isolated, mainly small taxa of familial or infrafamilial rank (categories of Airy Shaw, 1966, used here) are now confined to tropical and subtropical North America, and chiefly to semiarid and arid regions:

Agavaceae—most subgroups
Canotiaceae
Crossosomataceae
Fouquieriaceae
Garryaceae
Goetzeaceae
Koeberliniaceae
Krameriaceae

Lennoaceae
Picrodendraceae
Plocospermataceae
Simmondsiaceae
Stegnospermaceae
Verbenaceae–Lithophytoideae

In addition, at least 68 genera of woody plants are endemic to the dry regions of Mexico and the adjacent southwestern United States (Rzedowski, 1962, 1973).

As compared with the past, the tropical area of North America is now extremely contracted. The taxa in the preceding list occur in semiarid or subhumid sites which are separated from similar arid sites in South America by the moist tropics. It is among the plants of semiarid or subhumid habitats that most of the endemics occur (Rzedowski, 1962, 1964, 1973), presumably because there has never been good opportunity for interchange between the biota of such areas in North and South America in the past (Raven, 1963).

The following taxa may not have been in South America prior to Late Miocene or Pliocene time and then may have spread there from North America as migration became more direct. The taxa marked by an asterisk (*) already seem to have been represented in South America when the new arrivals came from the north. An additional list of genera is given on p. 631–2.

Actinidiaceae—*Saurauia*
Apiaceae–Apioideae, Saniculoideae
Berberidaceae
Brassicaceae
Caprifoliaceae
Caryophyllaceae—except *Colobanthus*
Cistaceae
Crassulaceae
Cucurbitaceae*—*Cucurbita*
Cyrillaceae
Ericaceae*
Fagaceae*
Hippocastanaceae
Hypericaceae*—*Hypericum*
Juglandaceae—*Juglans*
Linaceae*—*Linum*
Lythraceae*—*Lythrum*
Magnoliaceae
Myricaceae
Papaveraceae
Poaceae–Festuceae, Triticeae
Primulaceae
Rafflesiaceae
Ranunculaceae
Rosaceae*
Saxifragaceae*—including all
    Saxifragoideae and Ribesoideae
Symplocaceae
Valerianaceae
Violaceae*—*Viola*

Many of these are montane plants that presumably expanded in the newly elevated mountains and temperate climates of South America, a trend that has persisted throughout Neogene time and up to the present.

Judging from their affinities, the following taxa may also have gone from North America to South America. They are so well represented there it seems probable that they are not very recent arrivals:

Boraginaceae
Clethraceae
Gentianaceae
Hydrophyllaceae
Loganiaceae—*Buddleia*
Onagraceae—*Fuchsia*
Plantaginaceae
Polemoniaceae
Scrophulariaceae
Theophrastaceae
Viscaceae

Even among these plants, there is little indication of a primary North American tropical element: most are derivative temperate groups. In addition, it is apparent that there are not so many primitive or generalized types of plants in the flora of North America as in South America. Furthermore, clusters of small families similar to those of North America occur in widely separated semiarid and subhumid regions around the world. Thus, in the Mediterranean Region are Biebersteinaceae, Cynomoriaceae, Globulariaceae, and Punicaceae; in the Cape Region of South Africa, Achariaceae, Aitoniaceae, Bruniaceae, Geissolomataceae, Grubbiaceae, Penaeaceae, Roridulaceae, and Stilbaceae; and in Chile and subandean South America, Aextoxicaceae, Calyceraceae, Gomortegaceae, Malesherbiaceae, and Nolanaceae.

DISJUNCTIONS BETWEEN NORTH AND SOUTH AMERICA

It is now clear that long-distance dispersal is involved in the range disjunctions between desert plants of the Monte of Argentina and neighboring areas and the Sonoran and Chihuahuan deserts of North America. The problem has been discussed by many authors, and recently reviewed by Solbrig (1972, 1973) and by Werger (1973). Even though dry areas do exist in the tropics, they only attained maximum extent in the drier phases of the mid-Pliocene and Quaternary. The meagre fossil record does not provide evidence for an arid corridor during the Tertiary (Graham, 1972), although more sampling should be done along the western sides of the continents. Prior to the Pleistocene, arid areas were much smaller, less severe, and more widely separated than they are at present. Hence, the concept of a "trans-tropic scrub" (Barbour, 1969), from which the present ranges of taxa such as *Larrea* may have developed, is unsupported by any evidence.

The idea that relatively long "jumps" are involved in the establishment of the North-South American desert disjuncts is in agreement with the observations that (1) they constitute only a small proportion of their respective floras, (2) the animals associated with them in their disjunct areas are almost entirely different, and (3) they are mainly self-compatible (Raven, 1963). In genera which seem to have migrated more or less directly between North and South America, bees and other associated insects are often closely related. *Cucurbita* (Hurd *et al.*, 1971), for instance, provides an excellent example of a genus in which migration to South America must have taken place nearly directly in Neogene times, as it has closely related oligoletic bees associated with it on the two continents. In general, however, the evidence concerning the bee faunas north and south of the tropics in the New World suggests an historic lack of direct dispersal between them (Hurd, 1972); no species of bee has a range similar to that of *Larrea*, for example. Virtually all plant taxa disjunct between the monte of Argentina and the Chihuahuan Desert of North America meet the criteria just enumerated and almost certainly attained their disjunct ranges by long-distance dispersal.

The data suggest strongly that most of the disjunctions in range of desert taxa developed in the Pliocene, and especially more recently, as land connections between North and South America were established and as the rising cordillera produced widespread "rain-shadow" effects. For plants of Mediterranean climates, the disjunctions may be mainly Pleistocene and Recent in age (Raven, 1963, 1971), although the vegetation types involved existed from the Middle Pliocene onward (Axelrod, 1948, 1973).

As outlined above (p. 609–11), ample evidence now indicates that semi-arid to arid climates were widespread in low tropical latitudes during the ice ages. On this basis, relatively rapid migration would have been greatly aided by the presence of open areas in the subtropics and tropics, in regions presently under a regime of moister climate and covered with rainforest. Coupled with the intense tectonism and accompanying erosion that caused the development of intermontane drier valleys and lee slopes, it seems clear that during the ice ages there were much broader connections across the low latitudes than exist today—which the record does show. These connections may have developed especially along the western sides of the Andes and of Central and North America, onshore from areas of cooler water, and fossil evidence should be sought in such regions. On the other hand, much of the savanna vegetation of northern South America east of the Andes may be Recent in origin (Wijmstra & Hammen, 1966) and may therefore not have functioned as dispersal routes during the Pleistocene, for which the evidence is ambiguous (Hammen, 1963).

The open and relatively dry areas that formed in now forested regions during the glacial ages may well account for many of the links that are found between the monte and the warm deserts of North America, as well as those between the steppe and grassland climates of the Americas. Furthermore, these widespread open environments in the deep tropics during the glacial ages provide a more reasonable ecological basis for the interchange of mammals, especially large grazing and browsing ones (horses, glyptodonts, ground sloths, camels) between the Americas than those which exist now (Stirton, 1950) or the ones which existed during Neogene time. The evidence reviewed for ice-age aridity in the tropics (p. 609–11) strongly suggests that they crossed *via* areas of open savannas and grasslands that reverted to rainforest as each glacial stage waned. Whereas the savannas of South America may have existed on a regional scale since Oligocene time (A. Graham, personal communication), the pampas of the far south, with their rich representation of festucoid grasses ultimately derived from North America, cannot be older than the Uppermost Miocene, a conclusion that is consistent with other evidence (Vuilleumier, 1971).

For bipolar disjuncts (Moore, 1972), suitable habitats have probably been available in the Southern Hemisphere for at least 5 m.y., and long-distance dispersal has clearly been involved. For montane species that have extended their ranges between the Americas by means of way-stations on mountaintops (Moore, 1972; Raven, 1973*b*), Pleistocene and more recent times have undoubtedly been the most favorable, with very long gaps between suitable habitats having existed earlier. Among the genera that may have reached South America in this manner from the Upper Miocene onward, and perhaps mainly during the Pleistocene or more recently are *Adenocaulon*, *Agrostis*, *Alnus*, *Anagallis* (*Centunculus*), *Anemone*, *Antennaria*, *Aphanes*, *Apium*, *Aster*, *Astragalus*, *Barbarea*, *Berberis*, *Cardamine*, *Carex*, *Clematis*, *Chrysosplenium*, *Deschampsia*, *Draba*, *Eleocharis*, *Empetrum*, *Epilobium*, *Erigeron*, *Festuca*, *Galium*, *Habenaria*, *Hypericum*, *Hypo-*

choeris (despite its present absence as a native plant in North America), *Juncus, Lathyrus, Linum, Luzula, Oenothera, Orobanche, Osmorrhiza, Poa, Polygonum, Potentilla, Potamogeton, Primula, Quercus, Ranunculus, Ribes, Rubus, Rumex, Salix, Sambucus, Sanicula, Saxifraga, Senecio, Trisetum, Urtica, Vicia, Viola,* and many other genera mentioned for example by Steenis (1972: 285–286). Moore (1972: 123–125) may have assigned too early a date to the arrival of some of these genera in the south, considering the past geological relationships between North and South America as now understood.

THE PLACE OF ORIGIN OF THE ANGIOSPERMS

Angiosperms could not have originated in the area that included Southeast Asia and northern Australasia to New Caledonia and Fiji, as earlier suggested by Smith (1967, 1970, 1973), Takhtajan (1957, 1969), and others. This region is a composite one geologically that came into existence only with the Miocene arrival of the Australian plate in the vicinity of Asia (Raven & Axelrod, 1972; Axelrod & Raven, 1972; Schuster, 1972). The persistence in Australasia of equable climates during the Tertiary, coupled with the increasing isolation of some of its components (*i.e.* New Caledonia, Fiji), has afforded some primitive angiosperms unusual opportunities for survival. The ancient unglaciated mountains of Southeast Asia, with their striking juxtaposition of temperate and tropical climates, are another such center of survival, as ably discussed by Takhtajan (1969) and Schuster (1972), and documented by the fossil record of the gymnosperms. Perhaps because many ancient and archaic angiosperms are adapted to moist, equable climates which would not have been likely over much of West Gondwanaland when Africa and South America were closely joined, and because of much extinction in Africa, they are better represented today in Australasia and Southeast Asia.

The *initial radiation* of the angiosperms certainly took place when direct migration was possible between South America, Africa, India, Antarctica and Australia, and *via* Africa to Laurasia, as is implicit in earlier investigations (*e.g.* Camp, 1947, 1952; Axelrod, 1952, 1960). In our present state of knowledge, North America does not appear to have been an important early site of differentiation of angiosperms, perhaps because of its limited access to tropical areas throughout its entire history. As to Australasia, our analyses indicate that it is an area to which various lines of angiosperms migrated following their origin elsewhere. In the interior of the vast continent formed by the union of Africa and South America would have been severe deserts (Axelrod, 1972*b*) and the sorts of semiarid transitional areas that have been especially important as centers of plant evolution (Axelrod, 1952*b*, 1960, 1967, 1970, 1972*b*; Stebbins, 1952, 1972). Because of this, and since Southeast Asia seems to be an area of survival rather than of origin, we agree with Camp (1947), Schuster (1972), and others that angiosperms may have originated in Gondwanaland, but we particularly suggest West Gondwanaland. It is significant in this connection that Brenner (1974) has traced the Barremian-Cenomanian spread of tricolpate pollen from the northern part of West Gondwanaland northward during a period of some 25 m.y. to temperate Laurasia and finally the Arctic regions. See Addendum, Hopkins (1974).

Many of the mesophytic types of angiosperms now so well represented among archaic and ancient groups, generally regarded as primitive (Bews, 1927), may have come into being as West Gondwanaland split. With the accompanying spread of more moderate climates to which they became adapted, they then migrated to other parts of the world where similar climates occurred. In addition, just as Takhatajan (1969) argued that Southeast Asia was a likely place of origin for the angiosperms because of its crucial position in terms of contemporary routes of dispersal, we would argue that West Gondwanaland was centrally located on routes of dispersal at the time when the primary evolutionary radiation of angiosperms was taking place, whereas Southeast Asia at that time, widely separated from Australasia, certainly was not. In other words, given the geography of the mid-Cretaceous (Fig. 2), Southeast Asia is a very unlikely cradle for the angiosperms, contrary to the arguments of Takhtajan (1969).

Reasoning from the present distribution of the Annonales, Smith (1970, 1973) suggested that angiosperms—except perhaps for Annonaceae—may not have been present in West Gondwanaland prior to the separation of Africa and South America. However, the evidence presented here has revealed the existence of many links, among Annonalean families as well as other groups, between the floras of Africa and South America. In addition, there is the well known discontinuity in range for many taxa between the American and Asian tropics (Vester, 1940; Steenis, 1962; Good, 1964; Thorne, 1973). This pattern has resulted in part from the extinction of many angiosperm families in Africa. The relatively weak representation of primitive angiosperms in South America (Smith, 1967) may likewise find its explanation in the Neogene climatic history of that continent, as noted above.

If the environmental stresses that occurred in the dry interior of West Gondwanaland favored origination of the special features that make angiosperms —closed carpels, insect-mediated pollination systems, vessels, drought-resistant leaves, abundant secondary metabolites—then many of the most primitive lines might have become extinct as humid conditions spread in this area (Axelrod, 1970). A number of the secondary mesophytic lines might have become extinct later, with the spread of dry climates over the African sector and the elevation of mountains during the Tertiary. For these reasons, primitive angiosperms might not be so well represented as we might expect in areas where they appear to have originated.

There is a considerable amount of evidence that the invasion of these new habitats was the decisive step in the initial radiation of angiosperms, and was accompanied by the extensive formation of new polyploids (Stebbins, 1950: 359–369; Raven, 1975). As Takhtajan (1969) has pointed out, most primitive angiosperms are not in the tropical lowland forests but in the temperate mountains near these forests. A great majority of the existing families of Annonales and Hamamelidales are of polyploid origin, and these polyploid lines have evidently changed in their characteristics very slowly (see Stebbins, 1950: 359–369, for discussion). In contrast with Annonales and Hamamelidales, the Theales, a very primitive group which is well represented in both regions, do not display such extensive polyploidy as Annonales or Hamamelidales.

Suggestions can be made as to the place of origin of some of the major groups of angiosperms above the family level. Modern distributions suggest that the monocotyledons originated in West Gondwanaland; nearly all groups appear to radiate from, or are well represented in, that area. The superorder Annoniflorae of Thorne (1968), including Annonales and Berberidales, is extremely well represented both in the remnants of Gondwanaland and in Laurasia, as we have just discussed. The pattern in most other groups would be more consistent with an origin in West Gondwanaland than one in Laurasia, and indeed the pattern tends to agree with Cracraft's (1973*b*) analysis of vertebrates in the Old World: the phyletic lines in tropical Asia are in most cases derived. Hamamelidiflorae, including Hamamelidales, Casuarinales, Fagales, and doubtfully Balanopales, may, however, be a group that differentiated very early in Laurasia. Although the Casuarinales and Balanopales are Australasian and there are two genera of Hamamelidaceae in Africa, the superorder appears to be primarily Laurasian. The relationships of Casurinales, and especially Balanopales, should be restudied, since they might be wind-pollinated derivatives of some other phylogenetic lines. For energetic reasons, and owing to intense herbivore pressure in the tropics (Heinrich & Raven, 1972), wind pollination has originated mainly in temperate regions. The wind pollinated members of Hamamelidales, Cistiflorae (Salicaceae), Urticales (Ulmaceae, Moraceae–Cannabinoideae), Rutiflorae (Juglandaceae, Myricaceae, Leitneriaceae), as well as many wind pollinated monocotyledons, have Laurasian distributions and doubtless originated there, where there is a much greater expanse of temperate lands than in the south. For wind pollinated plants, the warm tropics provide an almost impenetrable barrier (Heinrich & Raven, 1972), and Balanopaceae, Casuarinaceae, and *Nothofagus* are among the few well developed groups of wind pollinated dicotyledons south of the tropics. Ranunculanae (*sensu* Takhtajan, 1969) may also have originated in Laurasia, with Menispermaceae and Lardizabalaceae secondarily spreading to West Gondwanaland, presumably before the close of the Cretaceous. Most other major groups of angiosperms, however, seem to have had a long period of association with, if not their initial radiation in, West Gondwanaland.

In analyzing the history of any group, it is not possible to know where it originated; but we may learn where most of its early differentiation took place. For the angiosperms as a whole, and for both dicotyledons and monocotyledons, as well as for most of the major groups within these taxa, we suggest West Gondwanaland. This implies that the climatic changes that accompanied the breakup of this supercontinent, which commenced at about the time we first encounter angiosperms in the fossil record, may have been of critical importance in the evolution of the group and in the establishment of major lines within it. Africa–South America seems to be the homeland of the angiosperms, but it is a homeland devastated by subsequent geologic and climatic events, and one where access to temperate regions has been interrupted for most of the Late Cretaceous and Tertiary. Thus the primitive angiosperms, which may have spread initially into the equable, subtropical highlands, have survived in the greatest numbers in two regions where comparable habitats are ancient geologically and relatively well protected from immigration: Southeast Asia and Australasia.

SUMMARY AND CONCLUSIONS

West Gondwanaland was a primary area of evolution for many major groups, possibly including birds, marsupials, snakes, and anurans, but certainly many orders of angiosperms, and perhaps the earliest angiosperms themselves. The area included vast arid to subhumid tracts in tropical latitudes, terrain and edaphic conditions were diverse, and there was ample opportunity for rapid evolution. Opening the South Atlantic 125–130 m.y. BP, which signalled the spread of more mesic climates over much of the region, seems to have triggered the main evolutionary radiation and surge of angiosperms into the mesic lowland record ~ 110 m.y. BP. By the Paleocene, Africa and South America were separated by a gap of only ~ 800 km, populated with volcanic islands that aided east-west dispersal of tropical taxa.

The present-day amphi-Pacific tropical floristic similarities have resulted in many instances from massive extinction in Africa as a result of expanding aridity. This was brought on by increased elevation of Africa in the Neogene, by the appearance and gradual strengthening of the cold Benguela and Humboldt Currents during the Neogene, and by increased aridity over the inner African and American tropics during the glacial ages as the subtropic high pressure cells shifted equatorward and increased in strength. Many early "primitive" angiosperms were therefore eliminated from Africa and, in some instances, also South America, but have survived in tropical Southeast Asia and in northeast Australasia—areas of moist, equable climate relatively removed from the major vicissitudes of these Neogene and later climatic changes. The cyclic recurrence of aridity throughout the tropics during the glacial stages increased the areas of tropical savanna and grassland, and seems more nearly to explain the wide grasslands than repeated burning by early man.

The older biota of Australasia were acquired in or prior to medial Cretaceous time by more or less direct migration across Africa-Madagascar-India-Antarctica. These taxa of warm temperate to subtropical requirements included austral gymnosperms, a few orders and older families of flowering plants, and probably marsupials, dinosaurs, monotremes, ratite birds, ceratodont lungfishes, and osteoglossomorph primary freshwater fishes. Australasia remained open to immigration from South America by island stepping-stones for plants and animals of cool temperate requirements into the mid-Tertiary.

The general absence of land vertebrates from New Zealand–New Caledonia may reflect early isolation from Australia by a water gap. However, the cold climate and long dark nights that resulted from a high latitude position (60–70°S) may not have been suited yet for early mammals and most reptiles and amphibians. The very low body temperature and exceedingly low metabolic rate of *Sphenodon* may be symptomatic of the physiology of the group during Cretaceous and earlier times in cold latitudes.

We suggested earlier that separation of Australia–Antarctica in the Eocene resulted in the development and strengthening of the circum-Antarctic wind and current systems which have progressively increased the efficacy of long-distance dispersal across cold temperate austral regions, and this continues today. As Antarctica continued to move into deep freeze, increasing cold successively eliminated evergreen dicot forests (Middle Miocene?), fern-scrub, and finally cushion-plant and herbaceous communities, with the latter now surviving in modified form on the scattered subantarctic lands, marginal to their home in the Pliocene and earlier.

India had a rich tropical to subtropical flora during the Cretaceous. In view of its direct contact with Africa and thence to South America, it is expectable that India has yielded fossil plants that are now confined to South America. Numerous genera of moist tropical Africa are now common to Southeast Asia. They linked Africa-India with that region during the later Cretaceous and Paleocene, when rainforest and savanna vegetation occupied the Tethyan shores and all of southern Eurasia. As the Indian subcontinent was rafted north through different climatic belts many tropical taxa unique to it appear to have been eliminated, as were temperate austral alliances, including leptodactylid frogs and austral gymnosperms. Their elimination left India with a rather general flora, characterized by few endemics as compared with other tropical regions. Spreading aridity in the Neogene and Quaternary further obliterated links to other tropical regions, and confined rainforest and savanna vegetation to the east at the expense of expanding thorn scrub, semidesert, and finally desert vegetation.

Many of the plants and animals that spread from West Gondwanaland (Africa) to Eurasia seem to have migrated subsequently to North America. Prior to the opening of the North Atlantic, and continuing into the early Paleogene, this was over generally low to middle latitudes and seems to account for the paleotropical element there. Direct migration between Europe and eastern North America following the early Paleogene was by increasingly cooler temperate biota as the North Atlantic widened. Although the direct interchange of mammals was blocked by the Eocene, balanced floras of progressively lower temperature requirements spread across these narrow water barriers throughout the rest of the Tertiary. Beringia, at higher latitudes during the Cretaceous and Eocene than at present, became increasingly important as a pathway between Asia and western North America. Generally warm temperate and subtropical biota utilized Beringia during the Paleogene, with mixed deciduous hardwood forests and conifer forests present in the lowlands, respectively, in the Miocene and Pliocene.

A 2,500 km water gap separated North and South America during Cretaceous and Paleogene time. The presence of volcanic archipelagos between them enabled plants to move generally north through the Cretaceous and Tertiary, but migration for most animal groups became regular only after the late Neogene land bridge was finally constructed. This bridge also enabled temperate montane plants in Central America to migrate into northern South America, as well as montane andine taxa to move into Central America, greatly increasing diversity there. During the Quaternary there was major long-distance, transtropic migration between areas of desert, steppe, and mediterranean climates in the Americas.

There are certain broad parallels in the later history of angiosperm floras of the Eastern and Western Hemispheres. The tropical lowlands of Central America and the West Indies, which increased markedly in area from later Paleogene time onward, have been populated by a tropical South American flora which predominates northward over much of southern Mexico. This finds a parallel in a lowland flora of northern Australia–New Guinea which, although part of the Australian plate, has been populated almost exclusively by tropical taxa derived from the Asian tropics *via* the intervening islands. Also, the cordilleras of southern North America and of South America have been populated largely by temperate taxa derived from North America, as have the mountains of New Guinea by temperate Australasian taxa. During the latest Cenozoic there has been transtropic migration in each hemisphere, with a transfer of taxa from the colder boreal to austral areas.

Both in Australasia and in Africa remnants of the ancient flora have persisted on offshore islands separated from the mainland by seafloor spreading in the Upper Cretaceous and subsequently. The increasing isolation of these islands and their highly equable, oceanic climates have made them excellent sites for survival of ancient taxa.

It is amply clear that a restudy of the known Cretaceous and Paleogene floras of Africa–South America is a research project of highest priority. Previously described fossil floras should be intensively recollected, utilizing earth-moving equipment to secure adequate samples wherever possible. The taxa must be compared with those in the American, Malaysian, Australasian and African tropics and border areas, so that past links between these regions may be established wherever possible. The results should dispel at least some of our uncertainty about the early history of tropical floras, and of the angiosperms themselves.

LITERATURE CITED

ABDALLAH, M. S. 1967. The Resedaceae. A taxonomical revision of the family. Meded. Landbouwhoogeschool 67(8).

ABDEL-MONEM, A., N. D. WATKINS & P. W. GAST. 1972. Potassium-argon ages, volcanic stratigraphy, and geomagnetic polarity history of the Canary Islands: Tenerife, La Palma, and Hierro. Amer. Jour. Sci. 272: 805–825.

ADAMS, C. D. 1972. Flowering Plants of Jamaica. Univ. of the West Indies, Mona, Jamaica. 848 pp.

ADIE, R. J. (editor). 1972. Antarctic Geology and Geophysics. Universitetsforlaget, Oslo. 876 pp.

AIRY SHAW, H. K. 1966. J. C. Willis. A Dictionary of Flowering Plants and Ferns. Cambridge Univ. Press, Cambridge. xxii + 1214 + liii pp. Ed. 7.

ALAIN, HERMANO (E. E. LIOGIER). 1958. La flora de Cuba: Sus principales caracteristicas (y) su origen probable. Revista Soc. Cubana Bot. 15: 36–96.

ALLARD, G. O. & V. J. HURST. 1969. Brazil-Gabon geologic link supports continental drift. Science 163: 528–533.

ALLEN, C. K. 1945. Studies in the Lauraceae, VI. Preliminary survey of the Mexican and Central American species. Jour. Arnold Arbor. 26: 280–434.

ALVAREZ, W. 1971. Fragmented Andean belt of northern Colombia. Mem. Geol. Soc. Amer. 130: 77–96.

ANDERSON, T. A. 1972. Paleogene nonmarine Gualanday Group, Neiva Basin, Colombia, and regional development of the Colombian Andes. Bull. Geol. Soc. Amer. 83: 2423–2438.

ANONYMOUS. 1972. Scotia axis confirmed. Nature 240: 14–15.

———. 1973. Pacific drilling dates Atlantic opening. Science News 104: 278.

———. 1974. Sahara's far-flung dust dims Atlantic sunlight. Science News 105: 38–39.

ARCHANGELSKY, S. & J. C. GAMERRO. 1967. Spore and pollen types of the Lower Cretaceous in Patagonia (Argentina). Rev. Palaeobot. Palynol. 1: 211–217.

AUBRÉVILLE, A. 1970. La flore tropicale Tertiare du Sahara. Adansonia, n.s. 10: 9–14.

———. 1971. La Flore Saharo-Lybienne tropicale d'après Paul Louvet. Adansonia, n.s. 11: 583–592.

———. 1973. Géophylétique florale des Sapotacées. Compt. Rend. Hebd. Séances Acad. Sci. 276: 2641–2644.

AUDLEY-CHARLES, M. G., D. J. CARTER & J. S. MILSOM. 1972. Tectonic development of eastern Indonesia in relation to Gondwanaland dispersal. Nature Phys. Sci. 239: 36–39.

AXELROD, D. I. 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Washington Publ. 516: 1–129.

———. 1948. Climate and evolution in western North America during Middle Pliocene time. Evolution 2: 127–144.

———. 1950. Evolution of desert vegetation. Carnegie Inst. Washington Publ. 590: 215–306.

———. 1952*a*. Variables affecting the probabilities of dispersal in geologic time. Bull. Amer. Mus. Nat. Hist. 99: 177–188.

———. 1952*b*. A theory of angiosperm evolution. Evolution 6: 29–60.

———. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24: 433–509.

———. 1959. Poleward migration of early angiosperm flora. Science 130: 203–207.

———. 1960. The evolution of flowering plants. Pp. 227–307, *in* S. Tax (editor), "Evolution after Darwin. Vol. 1, The Evolution of Life." Univ. of Chicago Press.

———. 1966. A method of determining the altitudes of Tertiary floras. Paleobotanist 14: 144–171.

———. 1967. Drought, diastrophism and quantum evolution. Evolution 21: 201–209.

———. 1970. Mesozoic paleogeography and early angiosperm history. Bot. Rev. 36: 277–319.

———. 1971 [1974]. Plate tectonics in relation to the history of the angiosperm flora of India. Birbal Sahni Inst. Paleobot. Spec. Publ. 1: 5–18.

———. 1972*a*. Ocean-floor spreading in relation to ecosystematic problems. Univ. Arkansas Mus. Occas. Paper 4: 15–76.

———. 1972*b*. Edaphic aridity as a factor in angiosperm evolution. Amer. Naturalist 106: 311–320.

———. 1972*c*. Plate tectonics and problems of angiosperm history. XVII Internat. Zool. Congr., Thème 1. Biogéographie et liasons intercontinentales au cours du Mésozoïque. 16 pp.

———. 1973. History of the Mediterranean ecosystem in California. Pp. 255–277, *in* H. Mooney & F. di Castri (editors), "Ecological Studies, vol. 7. Mediterranean Type Ecosystems." Springer Verlag, Berlin and New York.

——— & P. H. RAVEN. 1972. Evolutionary biology viewed from plate tectonic theory. Pp. 218–236, *in* J. A. Behnke (editor), "Challenging Biological Problems. Directions toward their Solution." Oxford Univ. Press, New York.

AYENSU, E. S. 1972. Dioscoreales. *In* C. R. Metcalfe (editor), "Anatomy of the Monocotyledons VI." Oxford Univ. Press. 184 pp.

———. 1973. Phytogeography and evolution of the Velloziaceae. Pp. 105–119, *in* B. J. Meggers, A. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Institution Press, Washington, D.C.

BAKER, B. H., P. A. MOHR & L. A. J. WILLIAMS. 1972. Geology of the eastern rift system of Africa. Geol. Soc. Amer. Spec. Paper 136: 1–67.

BAKER, H. G. 1973. Evolutionary relationships between flowering plants and animals in American and African tropical forests. Pp. 145–159, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Institution Press, Washington, D.C.

BANWAR, S. C. 1966. Morphological and anatomical studies on the genus *Lyonothamnus*. Univ. California, Berkeley, Ph.D. Dissertation, Botany. University Microfilms, Ann Arbor, Michigan. 66–8267.

BARBOUR, M. G. 1969. Patterns of genetic similarity between *Larrea divaricata* of North and South America. Amer. Midl. Naturalist 81: 54–67.

BARLOW, B. A. & D. WIENS. 1971. The cytogeography of the loranthaceous mistletoes. Taxon 20: 291–312.

BARR, K. W. & J. B. SAUNDERS. 1971. An outline of the geology of Trinidad. Pp. 2–12, *in* J. F. Tomblin (editor), "Field Guides to the Geology of Trinidad." Internat. Field Institute. Guidebook to the Caribbean Island-Arc System. Amer. Geol. Institute.

BATESON, J. H. 1972. New interpretation of geology of Maya Mountains, British Honduras. Bull. Amer. Assoc. Petrol. Geol. 56: 956–963.

BECKER, H. F. 1969. Fossil plants of the Tertiary Beaverhead Basin in Southwestern Montana. Palaeontographica B 127: 1–142, *pl. 1–44*.

BELL, J. 1971. Tectonic evolution of the central part of the Venezuelan Coast Ranges. Mem. Geol. Soc. Amer. 130: 107–118.

BERGGREN, W. A. 1972. A Cenozoic time scale—some implications for regional geology and biogeography. Lethaia 5: 195–215.

BERRY, E. W. 1916. The Lower Eocene floras of southeastern North America. U. S. Geol. Surv. Prof. Pap. 91: 1–481.

———. 1922. The flora of the Cheyenne Sandstone in Kansas. U. S. Geol. Surv. Prof. Paper 127-I: 199–225.

———. 1924. The Middle and Upper Eocene floras of southeastern North America. U. S. Geol. Surv. Prof. Pap. 92: 1–206.

———. 1937. Tertiary floras of eastern North America. Bot. Rev. 3: 31–46.

———. 1938. Tertiary flora from the Río Pichileufu, Argentina. Geol. Soc. Amer. Spec. Pap. 12: 1–149.

BEUSEKOM, C. F. VAN. 1971. Revision of *Meliosma* (Sabiaceae), section *Lorenzanea* excepted, living and fossil, geography and phylogeny. Blumea 19: 355–529.

BEWS, J. W. 1927. Studies in the ecological evolution of angiosperms. New Phytologist Reprint 16.

BIGARELLA, J. J. & G. O. DE ANDRADE. 1965. Contribution to the study of the Brazilian Quaternary. Special Paper Geol. Soc. Amer. 84: 433–451.

BLAIR, W. F. (editor). 1972. Evolution in the Genus *Bufo*. Univ. Texas Press, Austin. 459 pp.

BLAKE, S. T. 1972. *Idiospermum* (Idiospermaceae), a new genus and family for *Calycanthus australiensis*. Contr. Queensl. Herb. 12: 1–12.

BOGERT, C. M. 1953*a*. Body temperatures of the tuatara under natural conditions. Zoologica 38: 63–64.

———. 1953*b*. The tuatara. Sci. Monthly 76: 163–170.

BOLKHOVITINA, N. A. 1953. Sporovo-pyl'tsevaya kharakteristika melovykh otlozheniy Nizhnesyrdar'inskogo podnyatiya (Severo-vostochnoye Priaral'ye). Dokl. Akad. Nauk SSSR 152(2): 392–395.

BONATI, E. & S. GARTNER, JR. 1973. Caribbean climate during Pleistocene ice ages. Nature 244: 563–565.

BOND, J. 1948. Origin of the bird fauna of the West Indies. Wilson Bull. 60: 207–229.

BOWDEN, J., P. H. GREGORY & C. G. JOHNSON. 1971. Possible wind transport of coffee leaf rust across the Atlantic Ocean. Nature 229: 500–501.

BRACEY, D. R. & P. R. VOGT. 1970. Plate tectonics in the Hispaniola area. Bull. Geol. Soc. Amer. 81: 2855–2860.

BRAMWELL, D. 1972. Endemism in the flora of the Canary Islands. Pp. 141–159, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

BRATTSTROM, B. H. 1963. A preliminary view of the thermal requirements of amphibians. Ecology 44: 238–255.

BRENAN, J. P. M. 1966. The classification of Commelinaceae. Jour. Linn. Soc. Bot. 59: 349–370.

BRENNER, G. J. 1974. Middle Cretaceous floral provinces and early migrations of angiosperms. *In* C. B. Beck (editor), "Origin and Early Evolution of Angiosperms." (In press.)

BROWN, R. W. 1946. Walnuts from the Late Tertiary of Ecuador. Amer. Jour. Sci. 244: 554–556.

———. 1959. Some paleobotanical problematica. Jour. Paleontol. 33: 120–124, *pl.* 23.

———. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U. S. Geol. Surv. Prof. Paper 375: 1–119, *pl.* 1–69.

BURBIDGE, N. T. 1963. Dictionary of Australian Plant Genera. Angus & Robertson Ltd., Sydney. xviii + 345 pp.

BURGER, D. 1968. Relationships of palynology to stratigraphy in the Lower Cretaceous of the Surat Basin in Queensland. Bur. Miner. Res. Geol. Geophys. Rec. 125 (Queensland).

BUTLER, P. M. & Z. KIELAN-JAWOROWSKA. 1973. Is *Deltatherium* a marsupial? Nature 245: 105–106.

BUXBAUM, F. 1969. Die Entwicklungswege der Kakteen in Südamerika. Monogr. Biol. 19: 583–623.

CAMP, W. H. 1947. Distribution patterns in modern plants and the problems of ancient dispersals. Ecol. Monogr. 17: 159–183.

———. 1952. Phytophyletic patterns on land bordering the South Atlantic basin. Bull. Amer. Mus. Nat. Hist. 99(3): 205–216.

Campbell, C. J. & H. Bürgl. 1965. Section through the Eastern Cordillera of Colombia, South America. Bull. Geol. Soc. Amer. 76: 567–590.

Capouron, R. 1963. Contributions à l'étude de la flore de Madagascar. XI. Présence à Madagascar d'un représentant du genre *Macadamia* F.v.M. (Protéacées). Adansonia n.s. 3: 370–373.

Carlquist, S. 1966. Anatomy of Rapateaceae—roots and stems. Phytomorphology 16: 17–38.

Carolin, R. C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanulales. Proc. Linn. Soc. New South Wales 85: 166–177.

Case, J. E. 1973. Geophysical data on Central American land bridge. Mexico City, July, 1973. Amer. Assoc. Adv. Sci.

Chandler, M. E. J. 1954. Some upper Cretaceous and Eocene fruits from Egypt. Bull. Brit. Mus. (Nat. Hist.), Geol. 2: 147–187.

———. 1958. Angiosperm fruits from the Lower Cretaceous of France and Lower Eocene (London Clay) of Germany. Ann. Mag. Nat. Hist., ser. 13. 1: 354–358.

———. 1964. The lower Tertiary floras of southern England. IV. A summary and survey of findings in the light of recent botanical observations. Bull. British Museum (Nat. Hist.), Geol. 12: 1–151, *pl. 1–4.*

——— & D. I. Axelrod. 1961. An early Cretaceous (Hauterivian) angiosperm fruit from California. Amer. Jour. Sci. 259: 441–446.

Chaney, R. W. 1936. Plant distribution as a guide to age determination. Jour. Washington Acad. Sci. 26: 313–324.

Charig, A. J. 1973. Jurassic and Cretaceous dinosaurs. Pp. 339–352, *in* A. Hallam (editor), "Atlas of Palaeobiogeography." Elsevier Scientific Publicating Co., Amsterdam.

Chevalier, A. 1947. La famille des Huaceae et ses affinités. Rev. Int. Bot. App. Agric. Trop. 27: 26–29.

Chmura, C. A. 1973. Upper Cretaceous (Campanian-Maastrichtian) angiosperm pollen from the western San Joaquin Valley, California, U.S.A. Palaeontographica B. 141: 89–171.

Clemens, W. A. 1968. Origin and early evolution of marsupials. Evolution 22: 1–18.

———. 1970. Mesozoic mammalian evolution. Annual Rev. Ecol. Syst. 1: 357–390.

Coetzee, J. A. 1967. Pollen analytical studies in east and southern Africa. *In* E. M. van Zinderen Bakker (editor), "Palaeoecology of Africa." 3: 1–146. A. A. Balkema, Cape Town.

Colbert, E. H. 1948. Evolution of the horned dinosaurs. Evolution 2: 145–163.

———. 1952. The Mesozoic tetrapods of South America. Bull. Amer. Mus. Nat. Hist. 99: 237–249.

———. 1971. Tetrapods and continents. Quart. Rev. Biol. 46: 250–269.

———. 1973. Continental drift and the distributions of fossil reptiles. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 395–412. Academic Press, London and New York.

——— & D. Merriless. 1967. Cretaceous dinosaur footprints from Western Australia. Jour. Roy. Soc. West. Australia 50: 21–25.

Colinvaux, P. A. 1972. Climate and the Galapagos Islands. Nature 240: 17–20.

Cooke, C. W. 1945. Geology of Florida. Florida Geol. Surv. Bull. 29.

Cooke, H. B. S. 1972. The fossil mammal fauna of Africa. Pp. 89–139, *in* A. Keast, F. C. Erk & B. Glass (editors), "Evolution, Mammals, and Southern Continents." State Univ. New York Press, Albany.

Coryndon, S. C. & R. J. G. Savage. 1973. The origin and affinities of African mammal faunas. *In* N. F. Hughes (editor), "Organisms and Continents through Time." Palaentol. Assoc. London, Spec. Pap. Palaeontol. 12: 121–135.

Couper, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zeal. Geol. Surv. Paleontol. Bull. 22: 1–77, 9 *pl.*

———. 1960. New Zealand Mesozoic and Cainozoic plant microfossils. New Zeal. Geol. Surv. Palaeont. Bull. 32: 1–87, *pl. 1–12.*

———. 1964. Spore-pollen correlation of the Cretaceous rocks of the Northern and Southern Hemispheres. Soc. Econ. Paleont. Mineral. Spec. Publ. 11: 131–142.

Cox, C. B. 1970. Migrating marsupials and drifting continents. Nature 266: 767–770.

———. 1973. Systematics and plate tectonics in the spread of marsupials. *In* N. F. Hughes (editor), "Organisms and Continents through Time." Palaeontol. Assoc. London, Spec. Pap. Palaeontol. 12: 113–119.

CRACRAFT, J. 1973*a*. Mesozoic dispersal of terrestrial faunas around the southern end of the world. XVII Congr. Internat. Zool., Theme No. 1. Biogéographie et liaisons intercontinentales au cours du Mésozoïque.

———. 1973*b*. Vertebrate evolution and biogeography in the Old World tropics: Implications of continental drift and palaeoclimatology. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 373–393. Academic Press, London and New York.

———. 1973*c*. Continental drift, paleoclimatology, and evolution and biogeography of birds. Jour. Zool. London 179: 455–545.

CRANWELL, L. C. 1963. *Nothofagus*: living and fossil. Pp. 387–400, *in* L. J. Gressitt (editor), "Pacific Basin Biogeography: a Symposium." Univ. Hawaii Press, Honolulu.

———, H. J. HARRINGTON & I. G. SPEDEN. 1960. Lower Tertiary microfossils from McMurdo Sound, Antarctica. Nature 186: 700–702.

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Thomas Nelson and Sons, Ltd., London. xi + 396 pp.

CUTLER, D. F. 1972. Vicarious species of Restionaceae in Africa, Australia and South America. Pp. 73–83, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

DAGHLIAN, C. P. & D. L. DILCHER. 1971. *Philodendron* leaves from Eocene sediments in Tennessee. Proc. Indiana Acad. Sci. 80: 95–96.

DAHLGREN, R. & V. S. RAO. 1971. The genus *Oftia* Adans. and its systematic position. Bot. Not. 124: 451–472.

DALRYMPLE, G. B., E. A. SILVER & E. D. JACKSON. 1973. Origin of the Hawaiian Islands. Amer. Sci. 61: 294–308.

DALZIEL, I. W. D., W. LOWRIE, R. KLINGFIELD & N. C. OPDYKE. 1973. Palaeomagnetic data from the southernmost Andes and the Arctandes. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 87–101. Academic Press, London and New York.

DAMUTH, J. E. & R. W. FAIRBRIDGE. 1970. Equatorial Atlantic deep-sea arkosic sands and ice-age aridity in tropical South America. Bull. Geol. Soc. Amer. 81: 189–206.

D'ARCY, W. G. & R. C. KEATING. 1973. The affinities of *Lithophytum*: A transfer from Solanaceae to Verbenaceae. Brittonia 25: 213–225.

DARLINGTON, P. J., JR. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol. 13: 274–300.

———. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley & Sons, Inc. xi + 675 pp.

———. 1965. Biogeography of the Southern End of the World. Harvard Univ. Press, Cambridge, Mass. x + 236 pp.

DEJARDIN, J., J.-L. GUILLAUMET & G. MANGENOT. 1973. Contribution à la connaissance de l'élément non endémique de la flore malgache (végétaux vasculaires). Candollea 28: 325–391.

DEL CORRO, G. 1968. La presencia de *Madtsoa* Simpson (Boidae) en el Eocene de Patagonia y en el Cretacio de Madagascar y algunos ejemplos de distribución disjuncta. Comm. Mus. Argent. Cíen. Nat. "Bernardino Rivadavia" Paleo. 1: 21–26.

DENGO, G. 1967. Geological structure of Central America. Studies in Tropical Oceanography 5: 56–73. Univ. Miami.

———. 1968. Estructura geológica, historia tectónica y morfológia de América Central. Centro Regional de Ayuda Técnica, A.I.D., México. 50 pp.

———. 1969. Problems of tectonic relations between Central America and the Caribbean. Trans. Gulf Assoc. Geol. 19: 311–320.

———. 1973. Estructura geológica, historia tectónica y morfológia de América Central. Ed. 2. Centro Regional de Ayuda Técnica, A.I.D., México. 52 pp.

——— & O. BOHNENBERGER. 1969. Structural development of northern Central America. Mem. Amer. Assoc. Petrol. Geol. 11: 203–220.

DENTON, G. H., R. L. ARMSTRONG & M. STUIVER. 1971. The late Cenozoic glacial history of Antarctica. Pp. 267–306, *in* K. K. Turekian (editor), "The Late Cenozoic Glacial Ages." Yale Univ. Press, New Haven.

DEPAPE, G. 1922. Recherches sur la flore Pliocène de la Vallée du Rhone. Ann. Sci. Nat. Bot., sér. 4. 10: 73–265.

Dewey, J. F., W. C. Pitman III, W. B. F. Ryan & J. Bonin. 1973. Plate tectonics and the evolution of the Alpine system. Bull. Geol. Soc. Amer. 84: 3137–3180.

Dickison, W. C. 1967*a*. Comparative morphological studies in Dilleniaceae, I. Wood anatomy. Jour. Arnold Arbor. 48: 1–29.

———. 1967*b*. Comparative morphological studies in Dilleniaceae, II. The pollen. Jour. Arnold Arbor. 48: 231–240.

Dietz, R. S. & J. C. Holden. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, Permian to present. Jour. Geophys. Res. 75: 4939–4956.

——— & W. P. Sproll. 1970. East Canary Islands as a microcontinent within the Africa-North America continental drift fit. Nature 226: 1043–1044.

———, J. C. Holden & W. P. Sproll. 1970*a*. Geotectonic evolution and subsidence of Bahama platform. Bull. Geol. Soc. Amer. 81: 1915–1928.

———, ——— & ———. 1970*b*. Geotectonic evolution and subsidence of Bahama platform: Reply. Bull. Geol. Soc. Amer. 82: 811–814.

Dilcher, D. L. 1963. Cuticular analysis of Eocene leaves of *Ocotea obtusifolia*. Amer. Jour. Bot. 50: 1–8.

———. 1973*a*. A paleoclimatic interpretation of the Eocene floras of southeastern North America. Pp. 39–59, *in* A. Graham (editor), "Vegetation and Vegetational History of Northern Latin America." Elsevier Scientific Publ. Co., Amsterdam.

———. 1973*b*. A revision of the Eocene flora of southeastern North America. Paleobotanist 20: 7–18.

——— & G. E. Dolph. 1970. Fossil leaves of *Dendropanax* from Eocene sediments of southeastern North America. Amer. Jour. Bot. 57: 153–160.

Dingle, R. V. 1972. Reply to Jones (1972). Nature Phys. Sci. 235: 60.

———. 1973. Mesozoic paleogeography of the southern Cape, South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 13: 203–213.

Dolianiti, E. 1955. Frutos de *Nipa* no Paleoceno de Pernambuco, Brazil. Min. Agr., Dept. Nac. Prod. Min., Div. Geol. Min. Bol. 158: 1–36.

Dorofeev, P. I. 1963. Tretichnyye flory Zapodnoy Sibiri [Tertiary floras of western Siberia]. Bot. Inst. Komarov. Akad. Wiss. 316 pp.

Douglas, R. G., M. Moullade & A. E. M. Nairn. 1973. Causes and consequences of drift in the South Atlantic. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 517–537. Academic Press, London and New York.

Doyle, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. Jour. Arnold Arbor. 50: 1–35.

———. 1973. Fossil evidence on early evolution of the monocotyledons. Quart. Rev. Biol. 48: 399–413.

——— & L. J. Hickey. 1972. Coordinated evolution in Potomac Group angiosperm pollen and leaves. (Abstract.) Amer. Jour. Bot. 59: 660.

Duellman, W. E. 1970. The hylid frogs of Middle America. Mongr. Mus. Nat. Hist. Univ. Kansas. 2. 753 pp.

Edgar, N. T., J. T. Ewing & J. Hennion. 1971. Seismic refraction and reflection in Caribbean Sea. Amer. Assoc. Petrol. Geol. Bull. 55: 833–870.

Edmunds, G. F., Jr. 1972. Biogeography and evolution of Ephemeroptera. Annual Rev. Entom. 17: 21–42.

Ehrendorfer, F., F. Kerndl, E. Habeler & W. Sauer. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon 17: 337–353.

Emiliani, C. 1971. The amplitude of Pleistocene climatic cycles at low latitudes and the isotopic composition of glacial ice. Pp. 183–197, *in* K. K. Turekian (editor), "The Late Cenozoic Glacial Ages." Yale Univ. Press, New Haven.

———, S. Gaertner & B. Lidz. 1972. Neogene sedimentation on the Blake Plateau and the emergence of the Central American isthmus. Palaeogeogr. Palaeoclimatol. Palaeoecol. 11: 1–10.

Emry, R. J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. Bull. Amer. Mus. Nat. Hist. 142: 455–510.

Engler, A. (editor). 1900–1953. Das Pflanzenreich. Pruess. Akademie der Wissenschaften, Berlin. No. 1–107.

———. 1905. Über floristische Verwandschaft zwischen dem tropischen Africa und Amerika, sowie über die Annahme eins versunkenen brasilianischen-äthiopischen Kontinents. Sitszungsber. Köngl. Pruess. Akad. Wiss. Phys. Math. Kl. 6: 179–231.

———. 1915. Über herkunft, alter und verbreitung extremer xerothermer Pflanzen. Sitzungsber. Köngl. Pruess. Akad. Wiss. Phys. Math. Kl. 6: 180–231.

——— & K. A. E. Prantl (editors). 1887–1915. Die natürlichen Pflanzenfamilien. Berlin.

Ernst, W. F. 1972. Floral morphology and systematics of *Lamourouxia* (Scrophulariaceae: Rhinanthoideae). Smithsonian Contr. Bot. 6: 1–63.

Estes, R. 1963. Early Miocene salamanders and lizards from Florida. Quart. Jour. Florida Acad. Sci. 26: 234–256.

———. 1970. Origin of the Recent North American lower vertebrate fauna: An inquiry into the fossil record. Forma et Functio 3: 139–163.

——— & L. I. Price. 1973. Iguanid lizard from the Upper Cretaceous of Brazil. Science 180: 748–751.

——— & O. A. Reig. 1973. The early fossil record of frogs. A review of the evidence. Pp. 11–63, *in* J. L. Vial (editor), "Evolutionary Biology of the Anurans." Univ. Missouri Press, Columbia.

——— & J. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. Amer. Midl. Naturalist 72: 453–472.

——— & M. H. Wake. 1972. The first fossil record of caecilian amphibians. Nature 239: 228–231.

———, P. Berberian & C. Meszoely. 1969. Lower vertebrates from the late Cretaceous Hell Creek Formation, McCone County, Montana. Mus. Comp. Zool. Harvard Univ. Breviora 337: 1–33.

Exell, A. W. & C. A. Stace. 1966. Revision of the Combretaceae. Boll. Soc. Brot. 2. 40: 5–25.

——— & ———. 1972. Patterns of distribution in Combretaceae. Pp. 307–323, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

Eyde, R. H. 1966. Systematic anatomy of the flower and fruit of *Corokia*. Amer. Jour. Bot. 53: 833–847.

———. 1968. Flowers, fruits, and phylogeny of Alangiaceae. Jour. Arnold Arbor. 49: 167–192.

———. 1972*a*. Note on geologic history of flowering plants. Brittonia 24: 111–116.

———. 1972*b*. Pollen of *Alangium*: Toward a more satisfactory synthesis. Taxon 21: 471–477.

———. 1975. Floral anatomy and the bases of angiosperm phylogeny. Ann. Missouri Bot. Gard. 62: (in press).

Fairbridge, R. W. 1953. The Sahul Shelf, northern Australia: its structure and geological relations. Jour. Roy. Soc. West. Australia 37: 1–33.

Fittkau, E. J., J. Illies, H. Klinge, G. W. Schwabe & H. Sioli (editors). 1968. Biogeography and Ecology in South America. Volume 1. Monogr. Biol. 18: i–xvi, 1–447.

———, ———, ———, ——— & ——— (editors). 1969. Biogeography and Ecology in South America. Volume 2. Monogr. Biol. 19: i–xi, 449–946.

Fleming, C. A. 1962. New Zealand biogeography. A paleontologist's approach. Tuatara 10: 53–108.

———. 1963. Paleontology and southern biogeography. Pp. 369–385, *in* J. L. Gressitt (editor), "Pacific Basin Biogeography." Bishop Museum Press, Honolulu.

Fooden, J. 1972. Breakup of Pangaea and isolation of relict mammals in Australia, South America, and Madagascar. Science 175: 894–898.

Fosberg, F. R. 1948. Derivation of the flora of the Hawaiian Islands. *In* E. C. Zimmerman, "Insects of Hawaii." 1: 107–119. Univ. Hawaii Press, Honolulu.

Francheteau, J. 1973. Plate tectonic model of the opening of the Atlantic Ocean south of the Azores. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 197–202. Academic Press, London and New York.

——— & X. Le Pichon. 1972. Marginal fracture zones as structural framework of continental margins in South Atlantic Ocean. Bull. Amer. Assoc. Petrol. Geol. 56: 991–1007.

Freake, J. R. 1966. A summary of results obtained during the 2nd W. African Micropaleontological Colloquium. Second W. African Micropal. Colloquium Proc. (Ibadan), p. 269.

Freeland, G. L. & R. S. Dietz. 1971. Plate tectonic evolution of Caribbean-Gulf of Mexico region. Nature 232: 20–23.

———. 1972. Plate tectonics in the Caribbean: a reply. Nature 235: 156–157.

Frenguelli, J. 1943. Restos de *Casuarina* en el Mioceno de El Mirador, Patagonia austral. La Plata Univ. Nac. Mus. Not. Paleont. 8(58): 349–354.

———. 1953. Restos del género "*Eucalyptus*" en el Mioceno del Neuquén. Not. Mus. La Plata 16: 210–213.

Fryxell, P. A. 1969. The genus *Cienfuegosia* Cav. (Malvaceae). Ann. Missouri Bot. Gard. 56: 179–250.

Gansser, A. 1964. Geology of the Himalayas. Interscience, London. xv + 289 pp.

———. 1966. The Indian Ocean and the Himalayas. A geological interpretation. Eclog. Geol. Helvet. 59: 831–848.

Gardner, J. V. 1973. Eastern equatorial Atlantic: sea-surface temperature and circulation response to global climatic changes during the past 200,000 years. Geol. Soc. Amer. Abstr. Prog. 1973 Meetings, Dallas, p. 629.

Gaskin, D. E. 1972. Reappraisal of the New Zealand Mesozoic with respect to sea-floor spreading and modern tectonic plate theory. XVII Congr. Internat. Zool., Thème 1, Biogéographie et Liaisons inter-continentales au cours du Mésozoïque. 23 pp.

Geesink, R. 1972. A new species of *Langsdorffia* from New Guinea (Balanophoraceae). Acta Bot. Neerl. 21: 102–106.

Germeraad, J. H., C. A. Hopping & J. Muller. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palynol. 6: 189–348.

Gerth, H. 1941. Die Tertiärfloren des südlichen Südamerika und die angebliche Verlagerung des Südpols während dieser Periode. Geol. Rundschau 32: 321–336.

Goldblatt, P. 1971. Cytological and morphological studies in the southern African Iridaceae. Jour. South Afr. Bot. 37: 317–460.

Good, R. D'O. 1964. The Geography of Flowering Plants. Wiley, New York. Ed. 3.

Gorbunov, M. G. 1962. Description of Tertiary plants of western Siberia. Trudy Sib. Nauchn.-Issl. Inst. Geol., Geogr. Min. Ser. 22: 327–360, *pls. 66–76.* [in Russian.]

Gosline, W. A. 1972. A reexamination of the similarities between the freshwater fishes of Africa and South America. XVII Congr. Internat. Zool., Thème 1. Biogéographie et liaisons inter-continentales au cours du Mésozoïque. 12 pp.

Graham, A. 1962. *Ficus ceratops* Knowlton and its affinities with the living genus *Guarea*. Jour. Paleontol. 36: 521–523, *pl. 90.*

———. 1972*a*. Some aspects of Tertiary vegetational history about the Caribbean Basin. Mem. Symp. I Congr. Latinoamer. Bot., pp. 97–117.

——— (editor). 1972*b*. Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publ. Co., Amsterdam. xii + 278 pp.

———. 1973*a*. History of the arborescent temperate element in the northern Latin American biota. Pp. 302–314, *in* A. Graham (editor), "Vegetation and Vegetational History of Northern Latin America." Elsevier Scientific Publ. Co., Amsterdam.

———. 1973*b*. Literature on vegetational history in Latin America. Pp. 315–360, *in* A. Graham (editor), "Vegetation and Vegetational History of Northern Latin America." Elsevier Scientific Publ. Co., Amsterdam.

——— & D. J. Jarzen. 1969. Studies in Neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

——— & S. Graham. 1971. The geologic history of Lythraceae. Brittonia 23: 335–346.

Grambast, L., M. Martínez, M. Mattauer & L. Thaler. 1967. *Perutherium altiplanense* nov. gen., nov. sp., premier mammifère Mésozoïque d'Amérique du Sud. Compt. Rend. Hebd. Séances Acad. Sci. 264: 707–710.

Grant, N. K. 1971. South Atlantic, Benue Trough, and Gulf of Guinea Cretaceous triple junction. Bull. Geol. Soc. Amer. 82: 2295–2298.

———. 1972. Comments on paper by X. Le Pichon and D. E. Hayes, "Marginal offsets, fracture zones, and the early opening of the south Atlantic." Jour. Geophys. Res. 77: 3171–3173.

Grant, V. 1959. Natural History of the Phlox Family. Vol. 1. Systematic Botany. Martinus Nijhoff, The Hague. xv + 280 pp.

Green, A. G. 1972. Seafloor spreading in the Mozambique Channel. Nature Phys. Sci. 236: 19–32.

Groot, J. J. & C. R. Groot. 1964. Quaternary stratigraphy of sediments of the Argentine basin—a palynological investigation. Trans. New York Acad. Sci., ser. 2. 26: 881–886.

——— & ———. 1966. Pollen spectra from deep-sea sediments as indicators of climatic changes in southern South America. Marine Geol. 4: 525–537.

Green, P. S. 1969. Notes on Melanesian plants: II. Old World *Heliconia* (Musaceae). Kew Bull. 23: 471–478.

GRIFFITHS, J. & C. BURRETT. 1973. Were South-east Asia and Indonesia parts of Gondwanaland? Nature Phys. Sci. 245: 92–93.

GUILLAUMET, J.-L. 1972. Les variations du genre *Rhipsalis* (Cactacées) à Madagascar. Adansonia, sér. 2. 12: 433–445.

GUILLAUMIN, A., R. F. THORNE & R. VIROT. 1965. Vascular plants collected by R. F. Thorne in New Caledonia in 1959. Univ. Iowa Stud. Nat. Hist. 20(7): 15–65.

HAFFER, J. 1969. Speciation in Amazonian forest birds. Science 165: 131–137.

———. 1970. Geologic-climatic history and zoogeographic significance of the Uraba region in northwestern Colombia. Caldasia 10: 603–636.

HALFFTER, G. 1964. Las regiones Neárctica y Neotropical desde el punto de vista de su entomofauna. Anais do Segundo Congresso Latino-Americano de Zoologia, São Paulo. 1: 51–61.

———. 1972. Éléments anciens de l'entomofauna Néotropicale: ses implications biogéographiques. XVII Congr. Internat. Zool., Thème 1. Biogéographie et Liaisons intercontinentales au cours du Mésozoïque. 40 pp.

HALL, I. H. S. & J. H. BATESON. 1972. Late Paleozoic lavas in Maya Mountains, British Honduras, and their possible regional significance. Bull. Amer. Assoc. Petrol. Geol. 56: 956–963.

HALLAM, A. 1973*a*. Distributional patterns in contemporary terrestrial and marine animals. *In* N. F. Hughes (editor), "Organisms and Continents through Time." Palaeontol. Assoc. London, Spec. Pap. Palaeontol. 12: 93–105.

———. 1973*b*. Provinciality, diversity and extinction of Mesozoic marine invertebrates in relation to plate movements. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 287–294.

HAMMEN, T. VAN DER. 1957. Climatic periodicity and evolution of South American Maastrichtian and Tertiary floras (A study based on pollen analysis in Colombia). Colombia Inst. Geol. Nac. Bol. Geol. 5: 49–91.

———. 1963. A palynological study on the Quaternary of British Guiana. Leidse Geol. Meded. 29: 125–180.

———. 1972. Historia de la vegetación y el medio ambiente del Norte Sudamérica. Mem. Symp. I Congr. Latino-Amer. Bot. 119–134.

——— & C. GARCÍA DE MUTÍS. 1966. The Paleocene pollen flora of Colombia. Leidse Geol. Meded. 35: 105–116.

HAMILTON, A. C. 1972. An interpretation of pollen diagrams from highland Uganda. *In* E. M. van Zinderen Bakker (editor), "Palaeoecology of Africa." 7: 45–149. A. A. Balkema, Capetown.

HANSEN, B. 1972. The genus *Balanophora* J. R. and G. Forster. A taxonomic monograph. Dansk Bot. Ark. 28: 1–188, *pl. 1–8.*

HARA, H. 1972. Corresponding taxa in North America, Japan and the Himalayas. Pp. 61–72, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography and Evolution." Academic Press, London and New York.

HARLAND, W. B. & E. H. FRANCIS (editors). 1971. The Phanerozoic time scale: a supplement. Geol. Soc. London Spec. Publ. 5. 356 pp.

———, A. G. SMITH & B. WILCOCK (editors). 1964. The Phanerozoic time scale. Quart. Jour. Geol. Soc. London: 120s (supplement). 458 pp.

HARRIS, W. K. 1965. Basal Tertiary microfloras from the Princetown area, Victoria, Australia. Palaeontographica B. 115: 75–106.

HAYES, D. E. & J. RINGIS. 1973. Seafloor spreading in the Tasman Sea. Nature 243: 454–458.

——— ET AL. 1973. Leg 28 deep-sea drilling in the southern ocean. Geotimes 18(6): 19–24.

HAWKES, J. G. & P. M. SMITH. 1965. Continental drift and the age of angiosperm genera. Nature 207: 48–50.

HEDLUND, R. W. & G. NORRIS. 1968. Spores and pollen grains from Fredricksburgian (Albian) strata, Marshall County, Oklahoma. Pollen & spores 10: 129–159.

HEEZEN, B. C., M. DREYFUS & R. CATALANO. 1973. The Cayman Ridge. Geol. Soc. Amer. Abstr. Prog. 1973 Meetings, Dallas, p. 705.

HEINE, H. 1963. Boraginaceae. Fl. West. Trop. Africa 2: 317–325.

HEINRICH, B. & P. H. RAVEN. 1972. Energetics and pollination ecology. Science 176: 597–602.

Heirtzler, J. R. 1973. The evolution of the North Atlantic Ocean. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 191–196. Academic Press, London and New York.

——— et al. 1973. Age of the floor of the eastern Indian Ocean. Science 180: 952–954.

Hepper, F. N. 1963. Styracaceae. Fl. West. Trop. Africa 2: 33–34.

———. 1965. Preliminary account of the phytogeographical affinities of the flora of West Tropical Africa. Webbia 19: 593–617.

———. 1968. The occurrence of *Ternstroemia* (Theaceae) in West Africa. Kew Bull. 21: 429–431.

Hickey, L. J. 1974. The stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. Mem. Geol. Soc. Amer. (in press).

——— & J. A. Doyle. 1972. Fossil evidence on evolution of angiosperm leaf venation. (Abstract.) Amer. Jour. Bot. 59: 661.

Hillebrand, W. 1888. Flora of the Hawaiian Islands. Reprinted by Hafner Publ. Co., New York and London, 1965. xcvi + 673 pp.

Hoeken-Klinkenberg, P. M. 1964. A palynological investigation of some Upper Cretaceous sediments in Nigeria. Pollen Spores 6: 209–231.

Hoffstetter, R. 1959. Un serpent terrestre dans le Crétacé inferieur du Sahara. Bull. Soc. Géol. France, sér. 7. 1: 897–902.

———. 1967. Observations additionelles sur les serpents du Miocéne de Colombie et rectification concernant la date d'arrivée des colubridés en Amérique du Sud. Comp. Rend. Sommaire Séances Soc. Géol. France 1967: 209–210.

———. 1972. Relationships, origins, and history of the ceboid monkeys and caviomorph rodents: a modern reinterpretation. Evol. Biol. 6: 323–347.

Hollick, A. 1924. A late Tertiary flora from Bahia, Brazil. Johns Hopkins Univ. Stud. Geol. 5: 1–136.

Holman, J. 1969. Lower Oligocene amphibians from Saskatchewan. Quart. Jour. Florida Acad. Sci. 31: 273–289.

———. 1972. Herpetofauna of the Calf Creek local fauna (Lower Oligocene: Cypress Hills Formation) of Saskatchewan. Canad. Jour. Earth Sci. 9: 1612–1631.

Hooker, J. D. 1853. Botany of the Antarctic Voyage of H. M. Discovery ships "Erebus" and "Terror" in the years 1831–43. Vol. 2: Flora Novae-Zelandiae. Pt. 1, Introductory Essay.

Houtz, R. E. et al. 1973. Geophysical results DSDP Leg 29: New Zealand, Tasmania, and magnetic quiet zone. Lamont-Doherty Geol. Observatory Contr. 1983.

Howard, R. A. 1973. The vegetation of the Antilles. Pp. 1–38, *in* A. Graham (editor), "Vegetation and Vegetational History of Northern Latin America." Elsevier Scientific Publ. Co., Amsterdam.

Huber, H. 1969. Die Samenmerkmale und Verwantschaftsverhältnisse der Liliifloren. Mitt. Bot. München 8: 219–538.

Hughes, N. F. 1961. Fossil evidence and angiosperm ancestry. Sci. Progr. 49: 84–102.

——— (editor). 1973. Organisms and Continents through Time. Palaeontol. Assoc. London, Spec. Pap. Palaeontol. 12: i–vi, 1–334.

Hunter, G. E. 1966. Revision of Mexican and Central American *Saurauia* (Dilleniaceae). Ann. Missouri Bot. Gard. 53: 47–89.

Hunziker, J. H., R. A. Palacios, A. G. de Valesi & L. Poggio. 1972. Evolución en el género *Larrea*. Res. I Congr. Latino-Amer. Bot., p. 191–192.

———, ———, ——— & ———. 1973. Species disjunctions in *Larrea*: Evidence from morphology, cytogenetics, phenolic compounds, and seed albumins. Ann. Missouri Bot. Gard. 59: 224–233.

Hurd, P. D. 1972. Evolutionary relationships between bees and *Larrea*. Origin & Structure of Ecosystems Newsletter 2(3): 38–41.

———, E. G. Linsley & T. W. Whitaker. 1971. Squash and gourd bees (*Peponapis*, *Xenoglossa*) and the origin of the cultivated *Cucurbita*. Evolution 25: 218–234.

Hutchinson, J. 1959. The Families of Flowering Plants. Ed. 2. Vols. 1 and 2. Clarendon Press, Oxford.

Iltis, H. H. 1967. Studies in the Capparidaceae, XI: *Cleome afrospina*, an African endemic with Neotropical affinities. Amer. Jour. Bot. 54: 953–962.

Jacobs, C., H. Bürgl & D. L. Conley. 1963. Backbone of Columbia. Mem. Amer. Assoc. Petrol. Geol. 2: 62–72.

James, C. W. 1961. Endemism in Florida. Brittonia 13: 225–244.

Jardine, N. & D. McKenzie. 1972. Continental drift and the dispersal and evolution of organisms. Nature 235: 20–24.

Jeffrey, C. 1962. Notes on Cucurbitaceae, including a proposed new classification of the family. Kew Bull. 15: 337–371.

Jenkins, D. G. 1971. New Zealand Cenozoic planktonic Foraminifera. New Zealand Geol. Surv. Palaeontol. Bull. 42.

Jenks, W. F. (editor). 1956. Handbook of South American geology. Mem. Geol. Soc. Amer. 65: i–xix, 1–378.

Johnson, C. C. & J. Bowden. 1973. Problems related to the transoceanic transport of insects, especially between the Amazon and Congo areas. Pp. 207–222, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Inst. Press, Washington, D.C.

Johnson, L. A. S. 1957. A review of the family Oleaceae. Contr. New South Wales Natl. Herb. 2: 395–418.

——— & B. G. Briggs. 1963. Evolution in the Proteaceae. Austral. Jour. Bot. 11: 21–61.

Jones, J. G. 1972. Significance of Upper Jurassic sediments in the Knysna Outlier (Cape Province). Nature Phys. Sci. 235: 59–60.

Jones, K. & C. Jopling. 1972. Chromosomes and the classification of the Commelinaceae. Bot. Jour. Linn. Soc. 65: 129–162, *2 pl.*

Jones, R. E. & G. O. W. Kremp. 1973. The earliest distribution of tricolpate angiospermous pollen. Jour. Arizona Acad. Sci. 8, Proceed. Suppl. 44–45.

Kaneps, A. G. 1970. Late Neogene Biostratigraphy (Planktonic Foraminifera), Biogeography and Depositional History. Columbia Univ., New York.

Katz, H. R. 1973. Contrasts in tectonic evolution of orogenic belts in the south-east Pacific. Jour. Roy. Soc. New Zealand 3: 333–362.

Keast, A. 1972. Continental drift and the evolution of the biota on southern continents. Pp. 23–87, *in* A. Keast, F. C. Erk & B. Glass (editors), "Evolution, Mammals, and Southern Continents." State Univ. New York Press, Albany.

———. 1973. Contemporary biotas and the separation sequence of the southern continents. *In* D. H. Tarling & S. K. Runcorn (editors), "Implications of Continental Drift to the Earth Sciences." Vol. 1: 309–343. Academic Press, London and New York.

———, F. C. Erk & B. Glass (editors). 1972. Evolution, Mammals, and Southern Continents. State Univ. New York Press, Albany.

Kemp, E. M. 1968. Probable angiosperm pollen from British Barremian to Albian strata. Palaeontol. 11(3): 421–434.

Kendall, R. L. 1969. An ecological history of the Lake Victoria basin. Ecol. Monogr. 39: 121–176.

Kennett, J. P. et al. 1972. Australian-Antarctic continental drift, palaeocirculation changes and Oligocene deep-sea erosion. Nature Phys. Sci. 239: 51–55.

———. 1973. Deep-sea drilling in the roaring 40s. Geotimes 18(7): 14–17.

Kent, P. E. 1972. Mesozoic history of the east coast of Africa. Nature 238:147–148.

Kesler, S. E. 1971. Nature of ancestral orogenic zone in Nuclear Central America. Bull. Amer. Assoc. Petrol. Geol. 55: 2116–2129.

———. 1973. Basement rock structural trends in southern Mexico. Bull. Geol. Soc. Amer. 84: 1059–1064.

——— & S. A. Heath. 1970. Structural trends in the southernmost North American Precambrian, Oaxaca, Mexico. Bull. Geol. Soc. Amer. 81: 2471–2476.

Khlonova, A. F. 1971. Palynological characteristics of Cretaceous layers in Siberia and the Far East. Akedemiya Nauk SSSR Sibirskoye Otdeleniye, Trudy Instituta Geologii i Geofiziki 138: 52–156. [In Russian.]

Khudoley, K. M. & A. A. Meyerhoff. 1971. Paleogeography and geological history of Greater Antilles. Mem. Geol. Soc. Amer. 129: i–xv, 1–199.

King, P. B. 1951. The Tectonics of Middle North America. Princeton Univ. Press, Princeton, N.J. xix + 203 pp.

Klerkx, J. & P. de Paepe. 1971. Cape Verde Islands: Evidence for a Mesozoic oceanic ridge. Nature Phys. Sci. 233: 117–118.

Koch, B. E. 1972. Fossil picrodendroid fruit from the upper Danain of Nugssauq, West Greenland. Meddel. Grønland 193(3): 1–33.

Kopp, L. E. 1966. A taxonomic revision of the genus *Persea* in the Western Hemisphere (*Persea*-Lauraceae). Mem. New York Bot. Gard. 14: 1–120.

KORNAŚ, J. 1972. Corresponding taxa and their ecological background in the forests of temperate Eurasia and North America. Pp. 37–59, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

KOSTERMANS, A. J. G. H. 1952. A historical survey of the Lauraceae. Jour. Sci. Res. (Indonesia) 1: 83–95, 113–127, 141–159.

———. 1964. Bibliographia Lauracearum. Ministry of National Research, Bogor, Indonesia. 1450 pp.

KRASSILOV, V. 1967. Early Cretaceous Flora of South Primorye and its Bearing on the Stratigraphy. Nauka Publ. House, Moscow. 248 pp. [In Russian.]

———. 1973. Mesozoic plants and the problem of angiosperm ancestry. Lethaia 6: 163–178.

KRUTZSCH, W. 1967. Der Florenwechsel im Alttertiär Mitteleuropas auf Grund von sporenpaläontologischen Untersuchungen. Ahh. Zentr. Geol. Inst. 10: 17–37.

KUPRAINOVA, L. A. 1967. Palynological data for the history of the Chloranthaceae. Pollen & Spores 9: 95–100.

KURTÉN, B. 1973. Early Tertiary land mammals. Pp. 437–442, *in* A. Hallam (editor), "Atlas of Palaeobiogeography." Elsevier Scientific Publishing Co., Amsterdam.

LAKHANPAL, R. N. 1970. Tertiary floras of India and their bearing on the historical geology of the region. Taxon 19: 675–694.

LANGE, R. T. 1970. The Maslin Bay flora, South Australia. 2. The assemblage of fossils. Neues Jahrb. Geol. Paläont., Monatsh. 8: 486–490.

LANGENHEIM, J. H. 1964. Present status of botanical studies of ambers. Bot. Mus. Leafl. 20: 225–287.

———. 1972. Botanical origin of fossil resin and its relation to forest history in northeastern Angola. Publ. Cult. Comp. Diam. Angola 85: 13–36.

———. 1973. Leguminous resin-producing trees in Africa and South America. Pp. 89–104, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Inst. Press, Washington, D.C.

———, B. L. HACKNER & A. BARTLETT. 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. Bot. Mus. Leafl. 21: 289–324.

LARSON, R. L. & J. W. LADD. 1973. Evidence for the opening of the South Atlantic in the Early Cretaceous. Nature 246: 209–212.

LAUGHTON, A. S. 1971. South Labrador Sea and the evolution of the North Atlantic. Nature 232: 612–617.

———, D. P. MCKENZIE & J. G. SCLATER. 1973. The structure and evolution of the Indian Ocean. *In* D. H. Tarling & S. K. Runcorn (editors), "Implication of Continental Drift to the Earth Sciences." Vol. 1: 203–212. Academic Press, London and New York.

LAURENT, F. 1972. La distribution des amphibiens et les translations continentales. 17th Internat. Zool. Congr., Monte Carlo. Thème 1, Biogéographie et liaisons inter-continentales au cours du Mésozoïque, 16 pp. + 4 figs.

LEFFINGWELL, H. A. 1966. Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) formations of the Type Lance Area, Wyoming. Geol. Soc. Amer. Spec. Pap. 127: 1–64.

LEOPOLD, E. B. 1969. Late Cenozoic palynology. Pp. 377–438, *in* R. H. Tschudy & R. A. Scott (editors), "Aspects of Palynology." Wiley-Interscience, New York.

——— & H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200, *in* A. Graham (editor), "Floristics and Paleofloristics of Asia and Eastern North America." Elsevier Publ. Co., Amsterdam.

LE PICHON, X. & D. E. HAYES. 1971. Marginal offsets, fracture zones, and the early opening of the South Atlantic. Jour. Geophys. Res. 76: 6283–6292.

LEROY, J.-F. 1949. De la morphologie florale et de la classification des Myricaceae. Compt. Rend. Hebd. Séances Acad. Sci. 229: 1162–1163.

LESQUEREUX, L. 1891. The Flora of the Dakota Group. U. S. Geol. Surv. Monogr. 17: 1–398, *pl. i–lxvi.*

LIDDLE, R. A. 1946. The Geology of Venezuela and Trinidad. Ed. 2. Paleontological Research Institution, Ithaca, N.Y. xlvii + 890 pp.

LILLEGRAVEN, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Paleont. Contr. Univ. Kansas 50: 1–122.

LIOGIER, E. E. (HERMANO ALAIN). 1962. Flora de Cuba. Vol. 5. Editorial Universitaria, Universidad de Puerto Rico, Río Piedras.

LIVINGSTONE, D. A. 1967. Post-glacial vegetation of the Ruzenwori Mountains in equatorial Africa. Ecol. Monogr. 37: 25–52.

———. 1968. A 22,000 year pollen record from Zambia. Geol. Soc. Amer. Spec. Paper 121: 177–178.

———. 1971. Speculations on the climatic history of mankind. Amer. Sci. 59: 332–337.

LLOYD, J. J. 1963. Tectonic history of the south Central-American orogen. Mem. Amer. Assoc. Petrol. Geol. 2: 88–100.

LOWE-MCCONNELL, R. H. (editor). 1969. Speciation in tropical environments. Biol. Jour. Linn. Soc. 1: 1–246 (Also published by Academic Press).

LOWRY, J. B. 1973. *Rhabdothamnus solandri*: Some phytochemical results. New Zealand Jour. Bot. 11: 555–560.

LOZANO CONTRERAS, G. 1972. Contribución al conocimiento de las Magnoliaceae de Colombia. Res. I Congr. Latino-Amer. Bot., p. 191–192.

LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 53: 1–238.

MCBIRNEY, A. R. & H. WILLIAMS. 1965. Volcanic history of Nicaragua. Univ. Calif. Publ. Geol. Sci. 55: 1–65, *pls. 1–3.*

MCCLURE, F. A. 1973. Genera of bamboos native to the New World (Gramineae: Bambusoideae). Smithsonian Contr. Bot. 9: i–xi, 1–148. [Edited by T. R. Soderstrom.]

MACGILLAVRY, H. J. 1970. Geological history of the Caribbean. Koninkl. Nederl. Akad. Wetensch Proc. B. 73: 64–96.

MACGINITIE, H. D. 1937. The flora of the Weaverville beds of Trinity County, California. Carnegie Inst. Wash. Publ. 465: 83–151.

———. 1941. A Middle Eocene flora from the central Sierra Nevada. Carnegie Inst. Wash. Publ. 534: 1–178.

———. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. Univ. Calif. Publ. Geol. 83: 1–140, *31 pl.*

MCGOWRAN, B. 1973. Rifting and drift of Australia and the migration of mammals. Science 180: 759–761.

MCKENNA, M. C. 1972. Was Europe connected directly to North America prior to the Middle Eocene? Evol. Biol. 6: 179–189.

———. 1973. Sweepstakes, filters, corridors, Noah's Arks, and beached Viking funeral ships in paleogeography. Pp. 291–304, *in* D. H. Tarling & S. K. Runcorn (editors), Implications of Continental Drift to the Earth Sciences." Academic Press, London and New York.

MCKENZIE, D. P. & J. G. SCLATER. 1973. The evolution of the Indian Ocean. Sci. Amer. 228(5): 62–72.

MCWHAE, J. R. H., P. E. PLAYFORD, A. W. LINDNER, B. F. GLENISTER & B. E. BALME. 1958. The stratigraphy of Western Australia. Jour. Geol. Soc. Australia 4(2): 1–161.

MABESOONE, J. M. & I. M. TINOCO. 1973. Palaeoecology of the Aptian Santana Formation (Northeastern Brazil). Palaeogeogr. Palaeoclimatol. Palaeoecol. 14: 97–118.

MABRY, T., A. TAYLOR & B. L. TURNER. 1963. The betacyanins and their distribution. Phytochemistry 2: 61.

MAGUIRE, B. 1971. On the flora of the Guyana Highland. Pp. 63–78, *in* W. L. Stern (editor), "Adaptive Aspects of Insular Evolution." Washington State Univ. Press, Pullman.

MALFAIT, B. T. & M. G. DINKELMAN. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Bull. Geol. Soc. Amer. 83: 251–272.

MARGOLIS, S. V. & J. P. KENNETT. 1971. Cenozoic paleoglacial history of Antarctica recorded in Subantarctic deepsea cores. Amer. Jour. Sci. 271: 1–36.

MARTIN, P. G. 1972. Marsupial biogeography in relation to continental drift. XVII Congr. Internat. Zool., Thème 1. Biogéographie et liaisons inter-continentales au cours du Mésozoïque.

MASCLE, J. & J. D. PHILLIPS. 1972. Magnetic smooth zones in the South Atlantic. Nature 240: 80–84.

MATHIAS, M. E. & L. CONSTANCE. 1965. A revision of the genus *Bowlesia* and its relatives. Univ. Calif. Publ. Bot. 38: 1–73.

MATTSON, P. H. 1972. Plate tectonics in the Caribbean. Nature 235: 155–156.

———. 1973. Middle Cretaceous nappe structures in Puerto Rican ophiolites and their relation to the tectonic history of the Greater Antilles. Bull. Geol. Soc. Amer. 84: 21–38.

MAXWELL, A. E., R. P. VON HERZEN, J. E. ANDREWS, R. E. BOYCE, E. D. MILOW, K. HSU, S. F. PERCIVAL & T. SAITO. 1970*a*. Initial Reports of the Deep Sea Drillings Project. Vol. III. Washington, U. S. Govt. Printing Office. 806 pp.

———. 1970*b*. Deep sea drilling in the South Atlantic. Science 168: 1047–1059.

MAYR, E. 1944. Timor and the colonization of Australia by birds. Emu 44: 113–130.

———. 1946. History of the North American bird fauna. Wilson Bull. 58: 1–41.

———. 1964. Inferences concerning the Tertiary American bird faunas. Proc. Natl. Acad. Sci. 51: 280–288.

———. 1969. Bird speciation in the tropics. Biol. Jour. Linn. Soc. 1: 1–17.

MEIJER, W. 1972. The genus *Axinandra*—Melastomataceae: A missing link in Myrtales. Ceylon Jour. Sci. (Biol. Sci.) 10: 72–74, *2 pl.*

MENÉNDEZ, C. A. 1969. Die fossilen Floren Südamerikas. Monogr. Biol. 19: 519–561.

———. 1972. Estudios paleobotánicos en la Argentina, avances, problemas y perspectivas. Mem. Symp. I Congr. Latino-Amer. Bot., p. 61–97.

MEYERHOFF, A. A. 1973. Diapirlike features offshore Honduras: Implications regarding tectonic evolution of Cayman Trough and Central America: Discussion. Bull. Geol. Soc. Amer. 84: 2147–2152.

——— & H. A. MEYERHOFF. 1972. Continental drift, IV: The Caribbean "Plate." Jour. Geol. 80: 34–60.

MILDENHALL, D. C. & W. F. HARRIS. 1971. Status of *Haloragacidites* (al. *Triorites*) *harrisi* (Couper) Harris comb. nov. and *Haloragacidites trioratus* Couper, 1953. New Zealand Jour. Bot. 9: 297–306.

MILLS, R. A., K. E. HUGH, D. E. FERAY & H. C. SWOLFS. 1967. Mesozoic stratigraphy of Honduras. Bull. Amer. Assoc. Petrol. Geol. 51: 1711–1786.

MINDELMISS, F. A., P. F. RAWSON & G. NEWALL (editors). 1971. Faunal Provinces in Space and Time. Geol. Jour. Special Issue 4. Seel House Press, London.

MOORE, D. M. 1972. Connections between cool temperate floras, with particular reference to southern South America. Pp. 115–138, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

MOORE, H. E., JR. 1973*a*. Palms in the tropical forest ecosystems of Africa and South America. Pp. 63–88, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Institution Press, Washington, D.C.

———. 1973*b*. The major groups of palms and their distribution. Gentes Herb. 11: 27–140.

MORLEY, B. 1972. The distribution and variation of some gesneriads on Caribbean Islands. Pp. 239–257, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

MUDREY, M. G., JR., S. B. TREVES, P. R. KYLE & L. D. MCGINNIS. 1973. Frozen jigsaw puzzle: First bedrock coring in Antarctica. Geotimes 18(11): 14–17.

MÜLLER, H. 1966. Palynological investigations of Cretaceous sediments in northeastern Brazil. Pp. 123–136, *in* "Proc. 2nd West African Micropaleontological Colloquium, Ibadan." Leiden.

MULLER, J. 1968. Palynology of the Pedawan and Plateau sandstone formations (Cretaceous-Eocene) in Sarawak, Malaysia. Micropaleontology 14(1): 1–37.

———. 1970. Palynological evidence on early differentiation of angiosperms. Biol. Rev. 45: 417–450.

MUÑOZ PIZARRO, C. 1966. Sinopsis de la Flora Chilena. Ed. 2. Univ. Chile. 500 pp.

MYERS, G. S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia 1966: 766–773.

NEWBERRY, J. 1896. Flora of the Amboy clays. Monogr. U. S. Geol. Surv. 26.

NIEDENZU, F. 1928. Malpighiaceae. *In* A. Engler (editor), "Das Pflanzenreich." IV. 141: 1–870.

ORLOVA-TURCHINA, G. A. 1971. Lower Cretaceous palynostratigraphy of the Crimea (Abstract). Third Internat. Palynol. Conference, Novosibirsk, USSR, Sect. 5.

PAGE, V. M. 1970. Angiosperm wood from the Upper Cretaceous of central California, III. Amer. Jour. Bot. 57: 1139–1144.

PAPULOV, G. N. 1971. Change of floras at the Early-Late Cretaceous boundary of the Urals as revealed by palynological evidence (Abstract). Third Internat. Palynol. Conference, Novosibirsk, USSR, Sect. 5.

PATTERSON, B. & R. PASCUAL. 1972. The fossil mammal fauna of South America. Pp. 247–309, *in* A. Keast, F. C. Erk & B. Glass (editors), "Evolution, Mammals, and Southern Continents." State Univ. New York Press, Albany.

PAULIAN, R. 1972. La position de Madagascar dans le double probleme du peuplement animal et des translations continentales. XVII Contr. Internat. Zool., Thème 1. Biogéographie et liaisons inter-continentales au cours du Mésozoïque. 23 pp.

PENNY, J. S. 1969. Late Cretaceous and Early Tertiary palynology. Pp. 331–376, *in* R. H. Tschudy & R. A. Scott (editors), "Aspects of Palynology." Wiley-Interscience, New York.

PETRIELLA, B. 1972. Estudio de maderas pertificadas del Terciario Inferior del area central de Chubut (Cerro Bororo). Revista Mus. La Plata, n.s. 6: 159–254, *pls. 1–8*.

PFEIFER, H. W. 1966. Revision of the North and Central American hexandrous species of *Aristolochia* (Aristolochiaceae). Ann. Missouri Bot. Gard. 53: 115–196.

———. 1970. A taxonomic revision of the pentandrous species of *Aristolochia*. Univ. Connecticut Publ. Series. 134 pp.

PHILIPSON, W. R. 1967. *Griselinia* Forst. fil.—Anomaly or link. New Zealand Jour. Bot. 5: 134–165.

PHILLIPS, J. D. & D. FORSYTH. 1972. Plate tectonics, paleomagnetism, and the opening of the Atlantic. Bull. Geol. Soc. Amer. 83: 1579–1600.

PINET, P. R. 1972. Diapirlike features offshore Honduras: Implications regarding tectonic evolution of Cayman Trough and Central America. Bull. Geol. Soc. Amer. 83: 1911–1921.

PITMAN, W. C., III & M. TALWANI. 1972. Sea-floor spreading in the North Atlantic. Bull. Geol. Soc. Amer. 83: 619–646.

———, M. TALWANI & J. R. HEIRTZLER. 1971. Age of the North Atlantic Ocean from magnetic anomales. Earth Planet. Sci. Letters 11: 195–200.

PLUMSTEAD, E. P. 1962. Fossil floras of Antarctica. Trans-Antarctic Exped., 1955–1958. Sci. Rept. 9. 154 pp.

POKROVSKAYA, I. A. 1964. Lower Cretaceous spore-pollen complexes of the Western Siberian Lowland. Atlas of Lower Cretaceous Spore-Pollen Complexes of Some Regions of the USSR. All-Union Sci. Res., Geol. Inst. (VSEGEI), n. s., 124: 82–101. [In Russian.]

PORTER, D. M. 1974. Disjunct distributions in the New World Zygophyllaceae. Taxon 23: 339–346.

POWELL, C. MCA. & P. J. CONAGHAN. 1973. Plate tectonics and the Himalayas. Earth Planet. Sci. Newsl. 20: 1–12.

PRAKASH, U. 1972. Paleoenvironmental analysis of Indian Tertiary floras. Geophytology 2: 178–205.

PRANCE, G. T. 1968. *Maranthes* (Chrysobalanaceae), a new generic record for America. Brittonia 20: 203–204.

PRELL, W. 1973. Evidence for Sargasso Sea-like conditions in the Colombia Basin, Caribbean Sea, during glacial periods. Geol. Soc. Amer. Abstr. Prog. 1973 Meetings, Dallas, p. 771.

PURI, G. S. 1965. Some plant microfossils from Nigeria. Proc. Central Afr. Sci. Medical Congr., Lusaka (Northern Rhodesia), 1963, pp. 391–404.

RABB, G. B. & H. MARX. 1973. Major ecological and geographic patterns in the evolution of colubroid snakes. Evolution 27: 69–83.

RANGA RAO, A. 1971. New mammals from Murree (Kalakot Zone) of the Himalayan foot hills near Kalakot, Jammu & Kashmir State, India. Jour. Geol. Soc. India 12: 125–134.

———. 1972. Further studies on the vertebrate fauna of Kalakot, India. Directorate of Geology Oil & Natural Gas Commission Dehra Dun India Spec. Paper 1: 1–22, *4 pl.*

RAO, V. S. & R. DAHLGREN. 1969. The floral anatomy and relationships of Oliniaceae. Bot. Not. 122: 160–171.

RAUH, W. 1973. Über die Zonierung and Differenzierung der Vegetation Madagaskars. Tropische und subtropische Pflanzenwelt 1: 1–146. Akad. Wissensch. Lit. Mainz.

RAVEN, P. H. 1963. Amphitropical relations in the flora of North and South America. Quart. Rev. Biol. 29: 151–177.

———. 1971. The relationship between 'mediterranean' floras. Pp. 119–134, *in* P. H. Davis, P. C. Harper & I. C. Hedge (editors), "Plant Life of South-west Asia." Bot. Soc. Edinburgh.

———. 1973*a*. Plant species disunctions: A summary. Ann. Missouri Bot. Garden 59: 234–246.

———. 1973*b*. The origin of the alpine and subalpine floras of New Zealand. New Zealand Jour. Bot. 11: 177–200.

———. 1975. Cytology and the bases of angiosperm phylogeny. Ann. Missouri Bot. Gard. 62: (in press).

——— & D. I. Axelrod. 1972. Plate tectonics and Australasian paleobiogeography. Science 176: 1379–1386.

——— & D. W. Kyhos. 1965. New evidence concerning the original basic chromosome number of angiosperms. Evolution 19: 244–248.

Read, R. W. & L. J. Hickey. 1972. A revised classification of fossil palm and palm-like leaves. Taxon 21: 129–137.

Reid, E. M. & M. E. J. Chandler. 1933. The London Clay Flora. British Museum (Natural History), London. 561 pp.

Reig, O. A. 1973. Discussion. Pp. 204–206, *in* J. L. Vial (editor), "Evolutionary Biology of the Anurans." Univ. Missouri Press, Columbia.

Reyment, R. A. 1969. Ammonite biostratigraphy, continental drift and oscillatory transgressions. Nature 224: 137–140.

———. 1972. The age of the Niger Delta (West Africa). 24th Internat. Geol. Congr., sect. 6: 11–13.

——— & E. A. Tait. 1972. Biostratigraphical data of the early history of the South Atlantic Ocean. Trans. Roy. Soc. London 264: 55–95.

Richards, P. W. 1973. Africa, the "odd man out." Pp. 21–26, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Institution Press, Washington, D.C.

Ridd, M. F. 1972. Southeast Asia a part of Gondwanaland?: Reply. Nature Phys. Sci. 240: 140.

Roberts, T. R. 1973. Ecology of fishes in the Amazon and Congo Basins. Pp. 239–254, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Institution Press, Washington, D.C.

Robinson, E. & J. F. Lewis. 1971. Field guide to aspects of the geology of Jamaica. *In* Internat. Field Institute Guidebook to the Caribbean Island-Arc System, pp. 2–39 (Jamaica Section). Amer. Geol. Inst.

Rodgers, J. 1970. The Tectonics of the Appalachians. Wiley-Interscience, New York. xii + 271 pp.

Romero, E. J. 1968. *Palmoxylon patagonicum* n. sp., del Terciaro Inferior de la Provincia de Chubut, Argentina. Ameghiniana 5: 417–432.

———. 1970. *Ulminium atlanticum n. sp.* tronco petrificado de Lauraceae del Eocene de Bahía Solano, Chubut, Argentina. Ameghiniana 7: 205–224.

Rona, R. A. & A. J. Nalwalk. 1970. Post-early Pliocene unconformity on Fuerteventura, Canary Islands. Bull. Geol. Soc. Amer. 81: 2117–2122.

Rüffle, L. 1965. Monimiaceen-Blätter im älteren Senon von Mitteleuropa. Geologie 14: 78–105.

Rzedowski, J. 1962. Contribuciones a la fitogeografía florística e história de México. Bol. Soc. Bot. Méx. 27: 52–65.

———. 1964. Relaciones geográficas y posibles origenes de la flore de México. Bol. Soc. Bot. Méx. 29: 121–177.

———. 1972. Contribuciones a la fitogeografía florística e histórica de México. II. Afinidades geográficas de la flora fanerogámica de deferentes regiones de la República mexicana. Anal. Esc. Nac. Ci. Biol. 19: 45–48.

———. 1973. Geographical relationships of the flora of Mexican dry regions. Pp. 61–72, *in* A. Graham (editor), "Vegetation and Vegetational History of Northern Latin America." Elsevier Scientific Publ. Co., Amsterdam.

Sahni, B. & K. R. Surange. 1953. On the structure and affinities of *Cyclanthodendron sahnii* (Rode) Sahni & Surange from the Deccan Intertrappean Series. Paleobotanist 2: 93–100.

Samylina, V. A. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. Jour. Linn. Soc. Bot. 61: 207–216.

Sauer, E. G. F. & P. Rothe. 1972. Ratite eggshells from Lanzarote, Canary Islands. Science 176: 43–45.

Sauer, J. 1969. Oceanic islands and biogeographical theory: A review. Geogr. Rev. 59: 582–593.

SAVAGE, J. M. 1966. The origins and history of the Central American herpetofauna. Copeia 1966: 719–766.

———. 1973. The geographic distribution of frogs: Patterns and predictions. Pp. 351–445, *in* J. L. Vial (editor), "Evolutionary Biology of the Anurans." Univ. Missouri Press, Columbia.

———. 1974. The Isthmian link and the evolution of Neotropical mammals. Contrib. Sci. Nat. Hist. Mus. Los Angeles County 260: 1–51.

SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geol. 15: 1–57, 8 appendices.

SCHLINGER, E. I. 1974. Continental drift, *Nothofagus* and some ecologically associated insects. Annual Rev. Entom. 19: 323–343.

SCHMID, R. & M. J. SCHMID. 1973. Fossils attributed to the Orchidaceae. Amer. Orchid Soc. Bull., Jan. 1973: 17–27.

SCHODDE, R. 1970. Two new suprageneric taxa in the Monimiaceae alliance. Taxon 19: 324–328.

SCHUCHERT, C. 1935. Historical Geology of the Antillean-Caribbean Region. John Wiley & Sons, Inc. xxvi + 811 pp.

SCHUSTER, R. M. 1972. Continental movements, "Wallace's line" and Indomalayan-Australasian dispersal of land plants: Some eclectic concepts. Bot. Rev. 38: 3–886.

SCHWARZBACH, M. & H. D. PFLUG. 1957. Das Klima des zungeren Tertiars in Island. Neues Jahrb. Geol. Paläontol., Abh. 104: 279–298.

SCOTT, J. A. 1972. Biogeography of Antillean butterflies. Biotropica 4: 32–45.

SCOTT, R. A. 1954. Fossil fruits and seeds from the Eocene Clarno formation of Oregon. Palaentographica 96B: 66–97.

——— & E. S. BARGHOORN. 1957. *Phytocrene microcarpa*—a new species of Icacinaceae based on Cretaceous fruits from Kreischerville, New York. Paleobotanist 6: 25–28.

———, P. L. WILLIAMS, L. C. CRAIG, E. S. BARGHOORN, L. J. HICKEY & H. D. MACGINITIE. 1972. "Pre-Cretaceous" angiosperms from Utah: Evidence for Tertiary age of the palm woods and roots. Amer. Jour. Bot. 59: 886–896.

SELLING, O. H. 1947. Aponogetonaceae in the Cretaceous of South America. Bot. Tidskr. 41: 182.

SEWARD, A. C. 1941. Plant life through the ages. Cambridge Univ. Press. 2nd ed. 607 pp.

SHARP, A. J. 1966. Some aspects of Mexican phytogeography. Ciencia 24: 229–232.

SHERIDAN, R. E. 1971. Geotectonic evolution and subsidence of Bahama platform: Discussion. Bull. Geol. Soc. Amer. 82: 807–810.

SIGÉ, M. B. 1971. Les Didelphoidea de Laguna Umayo (formation Vilquechico, Crétacé superieur, Pérou) et le peuplement marsupial d'Amérique du Sud. Compt. Rend. Hebd. Séances Acad. Sci. 273: 2479–2481.

SILVER, E. A. ET AL. 1972. USGS-IDOE Leg 4 Venezuelan borderland. Geotimes May 1972: 19–21.

SIMPSON, E. ET AL. 1972. Leg 25 DSPS. Western Indian Ocean. Geotimes Nov. 1972: 21–24.

SIMPSON, G. G. 1943. Turtles and the origin of the fauna of Latin America. Amer. Jour. Sci. 241: 413–429.

———. 1945. The principles of classification and a classification of the mammals. Bull. Amer. Mus. Nat. Hist. 85: 1–350.

———. 1947*a*. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Amer. 58: 613–688.

———. 1947*b*. Evolution, interchange, resemblance of the North American and Eurasian Cenozoic mammalian faunas. Evolution 1: 218–220.

———. 1950. History of the fauna of Latin America. Amer. Sci. 38: 361–389.

———. 1951. History of the fauna of Latin America. Pp. 369–408, *in* G. A. Gaitsell (editor), "Science in Progress." (7th Ser.) Yale Univ. Press, New Haven, Conn.

———. 1952. Probabilities of dispersal in geologic time. Bull. Amer. Mus. Nat. Hist. 99: 163–176.

———. 1956. Zoogeography of the West Indian land mammals. Amer. Mus. Novit. 1759: 1–28.

———. 1969. South American mammals. *In* E. J. Fittkau *et al.* (editor), "Biogeography and Ecology in South America." Monogr. Biol. 19: 879–909.

———. 1973. (Review of:) Biogeography and Ecology in Madagascar. R. Battistini and G. Richard-Vindard (Eds.). Monogr. Biol. 21. Science **180**: 1163–1164.

Sleumer, H. 1967. Monographia Clethracearum. Bot. Jahrb. Syst. 87: 36–175.

Smith, A. C. 1963. Summary discussion on plant distribution patterns in the tropical Pacific. Pp. 247–249, *in* J. L. Gressitt (editor), Pacific Basin Biogeography." Bishop Museum Press, Honolulu.

———. 1967. The presence of primitive angiosperms in the Amazon Basin and its significance in indication migrational routes. Atas Simpos. Biota Amaz. 4: 37–59.

———. 1970. The Pacific as a key to flowering plant history. Univ. Hawaii, Harold L. Lyon Arboretum Lecture 1. 26 pp.

———. 1973. Angiosperm evolution and relationship of the floras of Africa and America. Pp. 49–61, *in* B. J. Meggers, A. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative review." Smithsonian Inst. Press, Washington, D.C.

Smith, A. G. 1971. Alpine deformation and the oceanic areas of the Tethys, Mediterranean, and Atlantic. Bull. Geol. Soc. Amer. 82: 2039–2070.

——— & A. Hallam. 1970. The fit of the southern continents. Nature 225: 139–144.

———, J. C. Briden & G. E. Drewry. 1973. Phanerozoic world maps. *In* N. F. Hughes (editor), "Organisms and Continents through Time." Palaeontol. Assn. London, Spec. Paper Palaeontol. 12: 1–43.

Smith, L. S. 1958. New Species of and notes on Queensland plants—III. Proc. Roy. Soc. Queensland 69: 43–51.

Solbrig, O. T. 1972. New approaches to the study of disjunctions with special emphasis on the American amphitropical desert disjunctions. Pp. 85–100, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

———. 1973. The floristic disjunctions between the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the United States. Ann. Missouri Bot. Gard. 59: 218–223.

Shrivastava, S. K. 1970. Pollen biostratigraphy and paleoecology of the Edmonton formation (Maestrichtian), Alberta, Canada. Palaeogeogr. Palaeoclimatol. Palaeoecol. 7: 221–276.

———. 1972. Pollen genus *Erdtmanipollis* Krutzsch 1962. Pollen & Spores 14: 309–322.

Standley, P. C. 1920–26. Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23: i–vii, 1–1721.

Stauffer, P. H. & D. J. Gobbett. 1972. Southeast Asia a part of Gondwanaland? Nature Phys. Sci. 240: 139–140.

Stearn, W. T. 1971. A survey of the tropical genera *Oplonia* and *Psilanthele* (Acanthaceae). Bull. Brit. Mus. (Nat. Hist.), Bot. 4: 259–323.

Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York. 643 pp.

———. 1952. Aridity as a stimulus to evolution. Amer. Naturalist 86: 33–44.

———. 1972. Ecological distribution of centers of major adaptive radiation in angiosperms. Pp. 7–34, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

Steenis, C. G. G. J. van. 1962. The land-bridge theory in botany. Blumea 11: 235–542.

———. 1972. *Nothofagus*, key genus to plant geogrophy. Pp. 275–288, *in* D. H. Valentine (editor), "Taxonomy, Phytogeography, and Evolution." Academic Press, London and New York.

Steinhauser, P., S. A. Vincenz, S. N. Dasgupta. 1972. Paleamagnetism of some Lower Cretaceous lavas on Jamaica. Amer. Geophys. Union Trans. 53: 356–357.

Stevens, P. F. 1970. *Agauria* and *Agarista*: An example of tropical transatlantic affinity. Notes Roy. Bot. Gard. Edinburgh 30: 341–359.

Steyermark, J. A. 1932. A revision of the genus *Menodora*. Ann. Missouri Bot. Gard. 19: 87–176, *pl. 1–11*.

Stirton, R. A. 1950. Late Cenozoic avenues of dispersal for terrestrial animals between North America and South America. Abstr. Bull. Geol. Soc. Amer. 61: 1541–1542.

Szafer, W. 1958. Nowa flora Eocenska in Tatrach. Kwart. Geol. Warsaw 2: 173–176.

Takhtajan, A. 1957. On the origin of the temperate flora of Eurasia. Bot. Žurn. (Moscow & Leningrad) 42: 935–953. [In Russian, with English summary.]

———. 1969. Flowering Plants, Origin and Dispersal. Transl. by C. Jeffrey. Smithsonian Inst. Press, Washington, D.C. 310 pp.

TARLING, D. H. 1971. Gondwanaland, palaeomagnetism and continental drift. Nature 229: 17–21, 71.

———. 1972. Another Gondwanaland. Nature 238: 92–93.

THOMPSON, P. R. & T. SAITO. 1973. Equatorial Pacific climatic fluctuations during the last 500,000 years. Geol. Soc. Amer. Abstr. Prog. 1973 Meetings, Dallas, pp. 840–841.

THORNE, R. F. 1965. Floristic relationships of New Caledonia. Univ. Iowa Stud. Nat. Hist. 20(7): 1–14.

———. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 4: 57–66.

———. 1973*a*. Major disjunctions in the geographical ranges of seed plants. Quart. Rev. Biol. 47: 365–411.

———. 1973*b*. Floristic relationships between tropical Africa and tropical America. Pp. 27–47, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Smithsonian Inst. Press, Washington D.C.

———. 1973*c*. Inclusion of the Apiaceae (Umbelliferae) in the Araliaceae. Notes Roy. Bot. Gard. Edinburgh 32: 161–165.

TIHEN, J. 1964. Tertiary changes in the herpetofaunas of temperate North America. Senckenberg. Biol. 45: 265–279.

TOMLINSON, P. B. 1966. Anatomical data in the classification of Commelinaceae. Jour. Linn. Soc. Bot. 59: 371–395.

TRALAU, H. 1964. The genus *Nypa* van Wurmb. Kungl. Svenska Vetenskapsakad. Handl. ser. 4. 10: 1–29.

TRAVERSE, A. 1955. Pollen analysis of the Brandon lignite of Vermont. U. S. Bur. Mines, Rept. of Investig. 5151. 107 pp.

TRIVEDI, B. S. & C. L. VERMA. 1972. Occurrence of *Heliconites mohgaonensis* gen. et sp. nov. from the Early Eocene and Deccan Intertrappean Series, M. P., India. Paleontographica B. 139: 73–82.

TSCHANZ, C. M., R. F. MARVIN, J. CRUZ B., H. H. MEHNERT & G. T. CEBULA. 1974. Geologic evolution of the Sierra Nevada de Santa Marta, northeastern Colombia. Bull. Geol. Soc. Amer. 85: 273–284.

TSCHUDY, B. D. 1970. Palynology of the Cretaceous-Tertiary boundary in the Rocky Mountain and Mississippi embayment regions. Geol. Soc. Amer. Spec. Paper 127: 65–111.

———. 1971. Two new fossil pollen genera from Upper Campanian (Cretaceous) rocks of Montana. U. S. Geol. Surv. Prof. Paper 750-B: 53–61.

TURNER, B. L. 1973. Chemosystematic data: Their use in the study of disjunctions. Ann. Missouri Bot. Gard. 59: 152–164.

TYLER, M. J. 1971. Phylogenetic relationships of certain Neotropical toads with the description of a new genus (Anura: Bufonidae). Los Angeles County Mus. Contr. Sci. 216: 1–40.

UCHUPI, E., J. D. MILLIMAN, B. P. LUYENDKY, C. O. BOWIN & K. W. EMERY. 1971. Structure and origin of southeastern Bahamas. Bull. Amer. Assoc. Petrol. Geol. 55: 687–704.

VAN COUVERING, J. A. & J. A. MILLER. 1971. Late Miocene marine and non-marine time scale in Europe. Nature 230: 559–563.

VANZOLINI, P. E. 1970. Zoologia sistemática, geografia e a origem das espécies. Instituto de Geografia, Univ. São Paulo, Série Teses e Monografias 3: 1–56.

——— & E. E. WILLIAMS. 1970. South American anoles: The geographical differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. São Paulo 19: 1–298.

VENKATO RAO, O. 1971. Proteaceae. Botanical Monograph No. 6, Council of Scientific and Industrial Research, New Delhi.

VERDCOURT, B. 1958. Remarks on the classification of the Rubiaceae. Bull. Jard. Bot. Bruxelles 28: 209–290.

VESTER, H. 1940. Die Areale und areal Typen der Angiospermen-Familien. Bot. Archiv. 40: 203–275, 295–356, 530–577.

VORONOVA, M. A. 1966. Subdivision of Lower Cretaceous deposits in the northwestern part of the Dnieper-Donets depression on the ground of spore-pollen analysis. Pp. 80–86, *in* "The Importance of Palynologic Analysis for the Stratigraphic and Paleofloristic Investigations." Acad. Sci. USSR, Moscow. For the Second Internat. Palynol. Conf., Utrecht. [In Russian with English summary.]

VUILLEUMIER, B. S. 1971. Pleistocene changes in the flora and fauna of South America. Science 173: 771–780.

WAHLERT, J. H. 1973. *Protoptychus*, a hystricomorphous rodent from the Late Eocene of North America. Mus. Comp. Zool. Harvard Univ. Breviora 419: 1–14.

WALKER, J. W. 1971. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. Contr. Gray Herb. 202: 3–130.

———. 1972. Chromosome numbers, phylogeny, phytogeography of the Annonaceae and their bearing on the (original) basic chromosome number of angiosperms. Taxon 21: 57–65.

WALPER, J.L. & C. L. ROWETT. 1972. Plate tectonics and the origin of the Caribbean Sea and the Gulf of Mexico. Gulf Coast Assoc. Geol. Soc. Trans. 22: 105–116.

WEBSTER, P. J. & N. A. STRETEN. 1973. Aspects of late Quaternary climate in tropical Australasia. *In* D. Walker (editor), "Bridge and Barrier. The Natural and Cultural History of Torres Strait." Res. Pac. Stud., Dept. Biogeogr. Geomorph. Publ. BG/3: 39–60. Australian Nat. Univ. Press, Canberra.

WEEKS, L. A., R. K. LATTIMORE, R. N. HARBISON, B. G. BASSINGER & G. F. MERRILL. 1971. Structural relations among Lesser Antilles, Venezuela, and Trinidad-Tobago. Bull. Amer. Assoc. Petral. Geol. 55: 1741–1752.

WEISSEL, J. K. & D. E. HAYES. 1972. Magnetic anomalies in the southeast Indian Ocean. Antarct. Res. Serv. 19: 165–196, 1 map.

WERGER, M. J. A. 1973. Las disyunciones anfitrópicas en las floras xerofíticas norte y sudamericanas. Darwiniana 18: 9–18.

WHITE, C. T. 1936. Contribution to the Queensland flora, no. 5. Proc. Roy Soc. Queensland 47: 51–84.

WHITMORE, F. C., JR. & R. H. STEWART. 1965. Miocene mammals and Central American seaways. Science 148: 180–185.

WIENS, D. & B. A. BARLOW. 1971. The cytogeography and relationships of the viscaceous and eremolepidaceous mistletoes. Taxon 20: 313–332.

WIJMSTRA, R. A. & T. VAN DER HAMMEN. 1966. Palynological data on the history of tropical savannas in northern South America. Leidse. Geol. Meded. 38: 71–90.

WILD, H. 1968. Phytogeography in South Central Africa. Kirkia 6: 197–222.

WILDE, W. J. J. O. DE. 1972. The indigenous Old World passifloras. Blumea 20: 227–250.

WILHELM, O. & M. EWING. 1972. Geology and history of the Gulf of Mexico. Bull. Geol. Soc. Amer. 83: 575–600.

WILLIAMS, C. A. & D. MCKENZIE. 1971. The evolution of the north-east Atlantic. Nature 232: 168–173.

WOLFE, J. A. 1962. A Miocene pollen sequence from the Cascade range of northern Oregon. U. S. Geol. Surv. Prof. Paper 450C: 81–84.

———. 1972. An interpretation of Alaskan Tertiary floras. Pp. 201–233, *in* A. Graham (editor), "Floristics and Paleofloristics of Asia and Eastern North America." Elsevier Publ. Co., Amsterdam.

———. 1974. Fossil forms of Amentiferae. Brittonia 25: 334–335.

——— & H. M. PAKISER. 1971. Stratigraphic interpretations of some Cretaceous microfossil floras of the Middle Atlantic States. U. S. Geol. Surv. Prof. Paper 750B: 35–47.

———, J. A. DOYLE, V. M. PAGE & L. J. HICKEY. 1975. The bases of angiosperm phylogeny: fossil evidence. Ann. Missouri Bot. Gard. 62: (in press).

WOOD, A. E. 1972. An Eocene hystricognathous rodent from Texas: Its significance in interpretations of continental drift. Science 175: 1250–1251.

WOOD, C. E., JR. 1973. Morphology and phytogeography: The classical approach to the study of disjunctions. Ann. Missouri Bot. Gard. 59: 107–124.

WRIGHT, J. B. 1968. South Atlantic continental drift and the Benue Trough. Tectonophysics 6: 301–310.

———. 1971. Comments on "Timing of break-up of the continents round the Atlantic as determined by Paleomagnetism" by E. E. Larson and L. La Fontain, Earth and Planetary Science Letters 8 (1970) 341–344. Earth Planet. Sci. Lett. 10: 271–272.

YEDEMSKAYA, A. L. 1960. Sporovo-pyl'tsevyye kompleksy iz aptskikh i al'bskikh otlozheniy vostochnoy chasti severnogo Kavkaza. Byul. Mosk. O-va. Isp. Prirody, Otd. Geol. 35(6): 110–115.

ZIMMERMAN, E. C. 1963. Pacific Basin biogeography. A summary discussion. Pp. 477–481, *in* J. L. Gressitt (editor), "Pacific Basin Biogeography." Bishop Museum Press, Honolulu.

ZINDEREN BAKKER SR., E. M. VAN. 1972. Late Quaternary lacustrine phases in the southern Sahara and east Africa. *In* E. M. van Zinderen Bakker (editor), "Palaeoecology of Africa." 6: 15–27. A. A. Balkema, Cape Town.

——— & J. A. COTZEE. 1972. A reappraisal of late Quaternary climatic evidence from tropical Africa. *In* E. M. van Zinderen Bakker (editor), "Palaeoecology of Africa." 7: 151–181. A. A. Balkema, Cape Town.

ADDENDUM: ADDITIONAL ANNOTATED REFERENCES[4]

ANONYMOUS. 1974. DSDP drills into Gondwanaland's past. New Sci. 63: 4.—A submerged fragment of Gondwanaland, with rocks 150 m.y. old, was discovered some 1400 km east of South America and 800 km east of the Falkland Islands. Until 125–130 m.y. BP, this block linked Antarctica, South America, and Africa. Its weathered top surface is reported to indicate a seasonally arid climate at that time. The block had separated from Africa by 100 m.y. BP and settled to its present depth by 80 m.y. BP.

———. 1974. Deep drilling in the Southeast Pacific Basin. Geotimes Aug. 1974: 16–19.—First ice-rafted debris, indicating widespread Antarctic glaciation, from the Miocene.

AUBRÉVILLE, A. 1974*a*. Les origines des Angiospermes (1re partie). Adansonia II. 14: 5–27.—The proposal that the angiosperms originated all along a tropical belt across Laurasia made in this paper fails on two accounts: 1) a great displacement of the Permian equator, as shown in Fig. 2, is not currently accepted (Smith, Briden, & Drewry, 1973), and this forms the basis for Prof. Aubréville's argument; 2) nothing that happened so early could have affected the distribution of modern angiosperms, the first evidence of recognizable modern groups dating from the Upper Cretaceous, some 100 million years later.

———. 1974*b*. Origines polytopiques des Angiospermes tropicales (2e partie). Essais chorologiques. Adansonia II. 14: 145–198.—See above remarks.

BAKSI, S. K. 1973[1972]. On the palynological biostratigraphy of Bengal Basin. Pp. 188–206, *in* A. K. Ghosh *et al.* (editors), "Proceedings of the Symposium on Paleopalynology and Indian Stratigraphy." University Grants Commission and Botany Department, Univ. of Calcutta, Calcutta.

BALDWIN, B., P. J. CONEY & W. R. DICKINSON. 1974. Dilemma of a Cretaceous time scale and rates of sea-floor spreading. Geology 1974: 267–270.—This survey indicates better age control on the Cretaceous is needed; implications with respect to the breakup of lands, rates of spreading, age of the seafloor, and patterns of evolution are evident.

BROWN, K. S., JR. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part III. Ecology and biology of *Heliconius nattereri*, a key primitive species near extinction, and comments on the evolutionary development of *Heliconius* and *Eueides*. Zoologica (New York Zoological Society) 57: 41–69.

——— & O. H. H. MIELKE. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. Zoologica (New York Zoological Society) 57: 1–40.

CASE, J. E. 1974. Oceanic crust forms basement of eastern Panama. Bull. Geol. Soc. Amer. 85: 645–652.

CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. Palaeontology 3: 487–621.—Three very distinctive angiosperm woods definitely had Lower Greensand (Aptian) matrix attached to them; Baldwin, Coney, and Dickinson (1974) now estimate the Albian-Aptian boundary at about 120 m.y. BP.

CRAWFORD, A. F. 1974. A greater Gondwanaland. Science 184: 1179–1181.—Hypothesizes that Gondwanaland at its maximum extent included Tibet, the Tarim Basin block, and parts of northern China, and that the Himalayas are of intracontinental origin. Little evidence at present, and too early to have affected the distribution of flowering plants; in the Triassic, migration between *all* lands was possible (*Lystrosaurus*).

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Dalziel, I. W. D., M. J. de Wit & K. F. Palmer. 1974. Fossil marginal basin in the southern Andes. Nature 250: 291–294.—In the southern part of South America a marginal basin opened behind an active andesitic island arc in the earliest Cretaceous and closed again in the middle Cretaceous.

Dingle, R. V. & R. A. Scrutton. 1974. Continental breakup and the development of post-Paleozoic sedimentary basins around southern Africa. Bull. Geol. Soc. Amer. 85: 1467–1474.—Sedimentation off the southeastern coast of Africa dates from the earliest rift (~180 m.y. BP) between East and West Gondwanaland. Sedimentation on the west coast dates from the opening of the South Atlantic, 125–130 m.y. BP. Subsequent major sealevel movements are attributable to epeirogenic/eustatic events that were probably worldwide in scope.

Foster, F. J. 1974. Eocene echinoids and the Drake Passage. Nature 249: 751.—In the Eocene, warm water was sweeping north of Australia into the Indian Ocean; this was later blocked by the northward movement of Australia. Cold water from a current made possible by the breaching of the Drake Passage between South America and Antarctica began to flow through the seaway between Australia and Antarctica 36–41 m.y. BP, this probably dating the separation of South America and Antarctica.

Furon, R. 1972. Éléments de Paléoclimatologie. Librairie Vuibert, Paris.

Goin, C. J. & O. B. Goin. 1973. Antarctica, isostasy, and the origin of frogs. Quart. Jour. Florida Acad. Sci. 35: 113–129.—Although published in 1973, this article contains no references subsequent to 1965 and its conclusions are invalidated by modern geological evidence.

Griffiths, J. R. 1974. Revised continental fit of Australia and Antarctica. Nature 249: 336–338.

Hamilton, A. 1974. The history of the vegetation. Pp. 188–209, *in* E. M. Lind & M. E. S. Morrison, "East African Vegetation." Longman, London.—Reviews evidence for glacial aridity in East Africa, specifically 25,000 to 12,500 BP, at which time the vegetation belts on the mountains were depressed 800–1,000 m. Lowland forest was greatly reduced in extent and was virtually absent from Uganda. Abundant pollen of Chenopodiaceae around the Cherangani hills in Kenya suggests that the mountain was surrounded by semidesert vegetation during the period of aridity.

Hammen, T. van der. 1954. El desarrollo de la flora Colombiana en los periodos geológicos. I: Maestrichtiana hasta Terciario Mas Inferior (Una investigación palinológica de la formación de Guaduas y equivalentes). Bol. Geol. Bogotá 2: 49–106.

———. 1957. Climatic periodicity and evolution of South American Maestrichtian and Tertiary floras (A study based on pollen analysis in Colombia). Bol. Geol. Bogotá 5: 49–91.

———. 1960. Estratigrafía del Terciario y Maestrichtiano continentales y tectogenesis de los Andes colombianos. Bol. Geol. Bogotá 6: 67–128.

———. 1961. Late Cretaceous and Tertiary stratigraphy and tectogenesis of the Colombian Andes. Geol. en Mijnb. 40: 181–188.

——— & T. A. Wymstra. 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. Leisde Geol. Meded. 30: 183–241.

———, J. H. Werner & H. van Dommeln. 1973. Palynological record of the upheaval of the Northern Andes: A study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its High-Andean biota. Rev. Palaeobot. Palynol. 16: 1–122.—During the Early Pliocene, the central part of what is now the Cordillera Oriental was a tropical lowland, with small areas of savanna. The major ultimate uplift of the Cordillera took place during the Middle-Late Pliocene (4.5–2.5 m.y. BP). *Myrica* appears 3–2.3 m.y. BP, an open páramo-type vegetation about 2 m.y. BP. During the past 1.2 m.y., *Styloceras*, *Juglans* (>1 m.y. BP), *Alnus*, and *Quercus* appear in that order.

Herngreen, G. F. W. 1974*a*. Palynology of Albian-Cenomanian strata of borehole 1-QS-1-MA, State of Maranhão, Brazil. Pollen & Spores 15: 515–555.—Close similarities between the Albian pollen floras of West Africa, the Maranhão Basin of Brazil, and Peru are discussed.

———. 1974*b*. Middle Cretaceous palynomorphs from northeastern Brazil. Results of a palynological study of some boreholes and comparison with Africa and the Middle East. "Sciences Géologiques" (Bull. Serv. Carte Géol. Alsace-Lorraine), Strasbourg, France (in press).—Evidence for continuous and clearly recognizable pollen zones from eastern Brazil *via* Central and North Africa to the Middle East (Israel and Saudi Arabia) from the mid-Albian to the Upper Cenomanian is in agreement with a post-Cenomanian separation of South America and Africa. The rich and diverse pollen flora of this region is very distinct from that found in Europe and North America at the same time, and includes among others *Psilatricolpites*, *Retitricolpites*, *Psilatricolporites*, *Hexaporotricolpites*, *Cretacaeiporites*, and *Tetradites*, found in the Middle and Upper Albian of Brazil and West Africa. It is apparently more diverse than the contemporary flora of Laurasia, an observation consistent with an origin of angiosperms in West Gondwanaland.

HERRON, E. M., J. F. DEWEY & W. C. PITMAN III. 1974. Plate tectonics model for the evolution of the Arctic. Geology 1974: 377–380.—Extremely useful model consistent with the data presented in our paper.

HOPKINS, W. S. 1974. Some spores and pollen from the Christopher Formation (Albian) of Ellef and Amund Ringnes Island, and northwestern Melville Island, Canadian Arctic Archipelago. Geol. Surv. Canada Pap. 73-12.—The assemblage of pollen and spores from the Albian indicates a moist, warm-temperate climate, with angiosperms with small and simple tricolpate grains appearing in mid- to Late Albian times, considerably before the Cenomanian records mentioned on p. 555 but still consistent with the notion of a poleward migration of the group.

HOUVENAGHEL, G. T. 1974. Equatorial undercurrent and climate in the Galapagos Islands. Nature 250: 565–566.—Author shows that a dry climate in the Galapagos Islands could result from changes in the intensity of the southern trade windbelt.

HOWDEN, H. F. 1974. Problems in interpreting dispersal of terrestrial organisms as related to continental drift. Biotropica 6: 1–6.

HOWE, M. W. 1974. Nonmarine Neiva Formation (Pliocene?), upper Magdalena Valley, Colombia: Regional tectonism. Bull. Geol. Soc. Amer. 85: 1031–1042.—Evidence indicating major uplift of the Cordillera Central in Pliocene time, when the Cordillera Oriental was not a major feature in southern Colombia; its uplift may date from the Late Pliocene or Pleistocene.—See Hammen *et al.* (1973).

HUERTAS, G., G. & T. VAN DER HAMMEN. 1953. Un posible banano (*Musa*) fosil del Crétaceo de Colombia. Acad. Colomb. Ci. Rev. 9: 115–118.

KENNETT, J. P. ET AL. 1974. Development of the Circum-Antarctic Current. Science 186: 144–147.—Deepsea drilling south of Australia shows that the Circum-Antarctic current developed about 30 m.y. BP when final separation occurred between Antarctica and the continental South Tasman Rise.

LANGENHEIM, J. H., Y.-T. LEE & S. S. MARTIN. 1973. An evolutionary and ecological perspective of Amazonian Hylaea species of *Hymenaea* (Leguminosae: Caesalpinioideae). Acta Amazonica 3: 5–38.—As discussed on pp. 584 and 604, *Hymenea* provides evidence for Paleogene drift across the ocean from Africa and South America. The tribe Cynometreae and probably the Caesalpinioideae as a whole seem to be of African origin.

MANI, M. S. (EDITOR). 1974. Ecology and Biogeography in India. Dr. W. Junk, The Hague. —A useful collection of articles, the information in which should be assessed in terms of up-to-date chronologies of the movement of the Indian Plate. An article by Mani himself (pp. 614–647) is of particular interest in relation to the survival in India of biota of austral affinities and those which link India with Madagascar-Africa. The book contains very few references from 1970 and 1971, and none subsequently.

MARESCH, W. V. 1974. Plate-tectonics origin of the Caribbean Mountain System of northern South America: Discussion and proposal. Bull. Geol. Soc. Amer. 85: 669–682.

MARTIN, A. R. H. 1973. Reappraisal of some palynomorphs of supposed proteaceous ancestry. Spec. Pap. Geol. Soc. Austral. 4: 73–78.

MATHUR, Y. K. & K. MATHUR. 1972. Angiospermous pollen and associated fossils from the Mid-Cretaceous subsurface sediments of Rajasthan, India. Jour. Palynol. 8: 89–96.—Angiosperm pollen from Albian, Cenomanian, Turonian, and Coniacian sediments indicate a wide diversity of angiosperms by Albian time, and it is claimed that these Cretaceous floras are more diverse than most contemporary ones elsewhere.

MOORE, G. W. 1972. Crust and mantle of the Gulf of Mexico. Nature 238: 452–453.

——— & L. DEL CASTILLO. 1974. Tectonic evolution of the southern Gulf of Mexico. Bull. Geol. Soc. Amer. 85: 607–618.

MULLER, P. 1973. The Dispersal Centres of Terrestrial Vertebrates in the Neotropical Realm. 2 vol. Dr. W. Junk, The Hague.

Nagle, F. 1974. Blueschist, eclogite, paired metamorphic belts, and the early tectonic history of Hispaniola. Bull. Geol. Soc. Amer. 85: 1461–1466.—From pre-Cretaceous through Early Eocene time, Hispaniola was characterized by submarine basaltic and andesitic volcanism which ceased after the Paleocene or Early Eocene. Vertical uplift began during the Middle Eocene and has continued at least to Miocene time and perhaps to the present.

Parmenter, C. & D. W. Folger. 1974. Eolian biogenic detritus in deep sea sediments: A possible index of equatorial ice age aridity. Science 185: 695–697.—Confirms the pattern for glacial aridity in the tropics, specifically the southern Sahara.

Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. Acta Amazonica 3(3): 5–28.—Proposed relatively extensive refuge areas are highly consistent with those of Haffer (1969), Brown (1972), and Brown and Mielke (1972), but not as restricted as those proposed by Vanzolini (1970).

Primm, A. C., B. McGowran & S. Gartner. 1974. Early sinking history of Ninetyeast Ridge, Northeastern Indian Ocean. Bull. Geol. Soc. Amer. 85: 1219–1224.—The Ninetyeast Ridge, a portion of the Indian Plate, rapidly sunk beneath the sea by the Maastrichtian and was at ocean depth by the earliest Tertiary. Evidence consistent with its rapid northward movement is presented.

Sah, S. C. D. & R. K. Kar. 1973[1972]. Palynostratigraphic evaluation of the Lower Eocene sediments of India. Pp. 255–265, *in* A. K. Ghosh *et al.* (editors), "Proceedings of the Symposium on Paleopalynology and Indian Stratigraphy." University Grants Commission and Botany Department, University of Calcutta, Calcutta.

Sahni, A. & V. Kumar. 1974. Palaeogene palaeobiogeography of the Indian subcontinent. Palaeogeogr., Palaeoclimat., Palaeoecol. 15: 209–226.—Oldest mammal fossils from the Indian subcontinent are from the early Middle Eocene, and they were derived from Asia.

Santamaria, F. & C. Schubert. 1974. Geochemistry and geochronology of the southern Caribbean–Northern Venezuela plate boundary. Bull. Geol. Soc. Amer. 85: 1085–1098. —Hypotheses on the plate tectonics of the region which indicate a Late Cretaceous—early Tertiary period of intrusion and later metamorphism and a Late Eocene—Oligocene orogenic event, both reflected in the coast ranges of Venezuela. Fig. 13B shows volcanoes (Aves Ridge?) linking North and South America in the Late Cretaceous, as we have inferred.

Saunders, W. B., R. H. Mapes, F. M. Carpenter & W. C. Elsik. 1974. Fossiliferous amber from the Eocene (Claiborne) of the Gulf Coastal Plain. Bull. Geol. Soc. Amer. 85: 979–984.—Portions of the infrared absorption spectra of the amber are similar to those of *Shorea* (Dipterocarpaceae), but total spectrum is quite different and the identification seems as highly improbable chemically as it does botanically. We are indebted to J. L. Langenheim for her comments on this paper.

Savage, J. M. 1974. [Review of] Muller, 1973. Science 184: 685–686.

Schminke, H. K. 1974. Mesozoic intercontinental relationships as evidenced by bathynellid Crustacea (Syncarida: Malacostraca). Syst. Zool. 23: 157–164.—The relationships within this ancient group of freshwater Crustacea accord with what is now known about Mesozoic geography. *Notobathynella* of Australia and New Zealand is supposed to be less advanced than the two other related genera of Australasia, which also reach South America. This offshoot of the "*Chilibathynella*-group," now Asian, Australasian, and South American, presumably reached Australasia prior to the mid-Cretaceous, like many other groups. Movement was across an embryonic Indian Ocean, certainly not along a track such as that shown by Schminke in his fig. 5. This track did not exist until Miocene time, according to evidence from all other groups of organisms and available geological evidence.

Schnell, R. 1971. Introduction à la Phytogéographie des Pays Tropicaux. Les Problèmes Généraux. 2 vol. Gauthier-Villars, Paris. Géobiologie, Écologie, Aménagement.—A valuable and detailed source book on tropical vegetation and plant distribution.

Sclater, J. G. & R. L. Fisher. 1974. Evolution of the East Central Indian Ocean, with emphasis on the tectonic setting of the Ninetyeast Ridge. Bull. Geol. Soc. Amer. 85: 683–702.—Suggests that India separated from Enderby Land in Antarctica about 100 m.y.

BP, a conclusion consistent with the notion of a subtropical to warm temperate, possibly interrupted route of migration between Africa and Australia at that time.

THORNE, R. F. 1974. A phylogenetic classification of the Annoniflorae. Aliso 8: 147–209. —In this important and useful paper, Thorne reduces Idiospermaceae (Blake, 1972) to a subfamily of Calycanthaceae, Idiospermoideae. As mentioned on p. 564 and 616 of the present paper, it seems reasonable to assume that primitive members of Thorne's suborder Laurineae migrated between West Gondwanaland and Australasia across a narrower Indian Ocean, and that the same might have been true for the ancestors of Monimiaceae, one of the families of this suborder. If the relationships postulated by Thorne are confirmed, the ancestors of Calycanthaceae *sens. lat.* might have done the same, which would imply their former presence and extinction in Africa. Thorne also divides Nymphaeaceae into five taxa, of which Nelumbonaceae (one bitypic genus with an impressive fossil record), Cabombaceae (monotypic), and Nymphaeaceae—Barclayoideae (monogeneric) are Laurasian. Of the other two subfamilies of Nymphaeaceae, Euryaloideae include the Asian *Euryale* and the South American *Victoria* and Nymphaeoideae include the cosmopolitan *Nymphaea* (represented by only a few species in Australia), the Laurasian *Nuphar*, and the monotypic Western Australian *Ondinea.*

VENKATACHALA, B. S. & M. S. RAWAT. 1973[1972]. Palynology of the Tertiary sediments in the Cauvery Basin 1. Palaeocene–Eocene palynoflora from the sub-surface. Pp. 292–335, *in* A. K. Ghosh *et al.* (editors), "Proceedings of the Symposium on Paleopalynology and Indian Stratigraphy." University Grants Commission and Botany Department, Univ. of Calcutta, Calcutta.

WOPFNER, H., R. CALLEN & W. K. HARRIS. 1974. The lower Tertiary Eyre Formation of the southwestern Great Artesian Basin. Jour. Geol. Soc. Austral. 21: 17–51.—Documents increasing aridity from Eocene time onward, a trend consistent with the northward motion of the Australian plate.

INDEX

PLANT-ANIMAL COEVOLUTION: THE TWENTIETH SYSTEMATICS SYMPOSIUM

Gerrit Davidse[1]

The following papers were presented at the Twentieth Annual Systematics Symposium held at the Missouri Botanical Garden, 19–20 October 1973. The Symposium was attended by approximately 290 biologists from 29 states and Canada. Expenses for this event were in part provided by the National Science Foundation (Grant GB-36049), whose support is gratefully acknowledged. Friday, 19 October was devoted to informal conversation and discussion as well as individual study in the herbarium and library, whereas Saturday was taken up by the formal program of papers. Welcoming remarks were provided by the Director of the Missouri Botanical Garden, Dr. Peter H. Raven. Moderation of the papers and discussion was in the capable hands of Dr. Alan Covich, Washington University.

The Symposium was developed along an extremely broad, interdisciplinary theme, plant-animal coevolution. The object of this Symposium, at least in the broad sense, was to further our understanding of the processes and final products of evolution through a presentation and discussion of the results of researchers currently active in this field.

The possible interactions between plants and animals are numerous and diverse, and the possible approaches to elucidate such interactions are correspondingly varied. Therefore, a one-day Symposium dealing with coevolutionary studies must of necessity be of limited scope. Two main approaches were taken in the Symposium. On the one hand, plant-animal interactions were discussed on a broad community level to come to grips with some overall patterns and processes (Heithaus, Strong, Ayensu). On the other hand, plant-animal interactions which dealt with individual taxa such as genera and families and which involved primarily aspects of pollination and fruit dispersal (Macior, Gentry, Ramírez, Beattie) were examined.

Coevolutionary studies involve a great deal of synthesis of information from a large array of disciplines. Furthermore, such studies are clearly heavily ecologically oriented, since the numerous biological processes operative in biological communities must first be elucidated. This ecological theme is a constant focal point in all the Symposium papers. Finally, as is evident from the papers, coevolutionary studies are of great importance to systematics in providing causal hypotheses and explanations for the diversity now extant in the biological world. Therefore, the subject was a most appropriate one for a Symposium dedicated to systematics in its broadest sense.

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[1] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Ann. Missouri Bot. Gard. 61: 674. 1974.

THE ROLE OF PLANT-POLLINATOR INTERACTIONS IN DETERMINING COMMUNITY STRUCTURE[1]

E. Raymond Heithaus[2]

This paper is dedicated to the recent generation of studies on community structure that utilize systems analysis and energy flow but fail to mention, or mention only in passing, the reproductive parts of plants. Flowers and fruits are passed over because they usually represent an insignificant proportion of the standing biomass of most forests (Odum *et al.*, 1970; Fittkau & Klinge, 1973), however, we should not lose sight of the fact that for most plant species those metric tons of standing biomass are the product of the evolution of mechanisms to provide sufficient energy for the formation of propagules. Further, the formation of propagules often involves the coevolved behaviors of plants and animals. These interactions are even more difficult to express as energy gained or lost in an ecosystem. It appears that the "importance" of community subsets cannot always be measured in terms of calories.

One other expression of the importance of a set of interactions, such as plant-pollinator interactions, is its contribution to the determination of community structure. Community structure may be defined by several parameters, including species diversity and dominance patterns, trophic structure, or diversity of reproductive types. To simplify analysis, I will confine this discussion to the consideration of diversity at one trophic level, the consumers of nectar or pollen, and to one reproductive type, flowering angiosperms. The question to be considered is, how important are plant-flower-visitor interactions in determining the diversity of visitors and plants that rely on animals for reproduction?

This is an important question because there has been no clear demonstration that the structure of flower-visitor communities depends on the floral resources that are available. While it is obvious that animals such as bees are found where there is some nectar and pollen, it is not obvious that the structure of entire flower-visitor communities is largely a function of the number of flowers present and the way visitors partition the resource. There are at least three classes of theory explaining diversity differences among communities, and plant-pollinator interactions would be important in only one of these. One theory claims communities are not saturated with species and differences in diversity result from historical considerations (*e.g.* Whittaker, 1969). If flowering plant and flower-visitor species diversity are the result of historical accidents, then plant-pollinator

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[1] Peter H. Raven, Andrew Moldenke, and Patricia A. Heithaus contributed extensively to the work and ideas presented here. David Culver read an early manuscript of this paper. Robert Colwell kindly provided a computer program for the calculation of niche metrics. Portions of this study were supported by research grants to Peter H. Raven, OTS Pilot Studies Grant N70-58, a Grant-in-aid from the Society of the Sigma Xi, and the Department of Biological Sciences, Stanford University. I was supported by NSF Predoctoral Fellowships and an NIH Traineeship.

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Ann. Missouri Bot. Gard. 61: 675–691. 1974.

interactions are important as factors in speciation but not in regulation of community diversity.

Two other classes of theory are based on the existence of an equilibrium in the number of species in a community, but they differ in the proposed regulatory mechanisms. The predation theory (Paine, 1966; Janzen, 1970) asserts that predator regulation of prey populations may increase the diversity of prey species by preventing the dominance of any single prey species. Predation may also maintain low prey diversities depending on the selectivity of the predator (Harper, 1969; Paine & Vadas, 1969). Theoretically, predation could be an important factor in regulating plant (Janzen, 1970) and flower-visitor (Elton, 1973) diversity. In this case we would conclude again that the coevolution of these groups is significant in the process of species evolution but not for the determination of community structure.

Finally, the other equilibrium theory claims that species numbers are regulated by competition among members of a community (Klopfer & MacArthur, 1960; Levins, 1968; Vandermeer, 1970; MacArthur, 1970, 1972). MacArthur (1972) considers species diversity to be a function of three factors: (1) the diversity of resources available in a community, (2) the average portion of the resources used by each species (niche breadth), and (3) the average part of each species niche that is shared with other taxa (niche overlap). Increasing the diversity of resources can increase the number of consumer species in a community maintaining a competitive equilibrium in diversity. Consumer diversity can also be increased by increasing specialization (decreasing niche breadth) or by increasing the average niche overlap in a community. If competitive interactions are widely important in determining plant or flower-visitor species numbers, then the coevolution of these groups is important both as a factor in speciation and in the regulation of community structure.

The experimental measurement of competition in complex communities is nearly impossible. To answer the question of whether competitive interactions are important in regulating species diversity we need to test the accuracy of predictions made by the "competition theory" using real communities. That is, are differences in species diversity among communities accompanied by the predicted differences in resource diversity, average niche breadth, and average niche overlap? Raven and Moldenke initiated a program to study a series of plant flower-visitor communities in California (Moldenke, 1971) and Chile. My studies were an extension of this program and included four seasonal tropical communities in Costa Rica. Some patterns are emerging on a local scale, although results from broad geographical comparisons have not been fully analyzed. I will discuss these local patterns in the Costa Rican communities for the regulation of flower-visitor diversity and then for plants that are potentially competing for pollinator services.

THE FLOWER-VISITOR "COMMUNITY"

I will only summarize the techniques used in Costa Rica, since these are reported in detail elsewhere (Heithaus, 1973). Four communities were chosen;

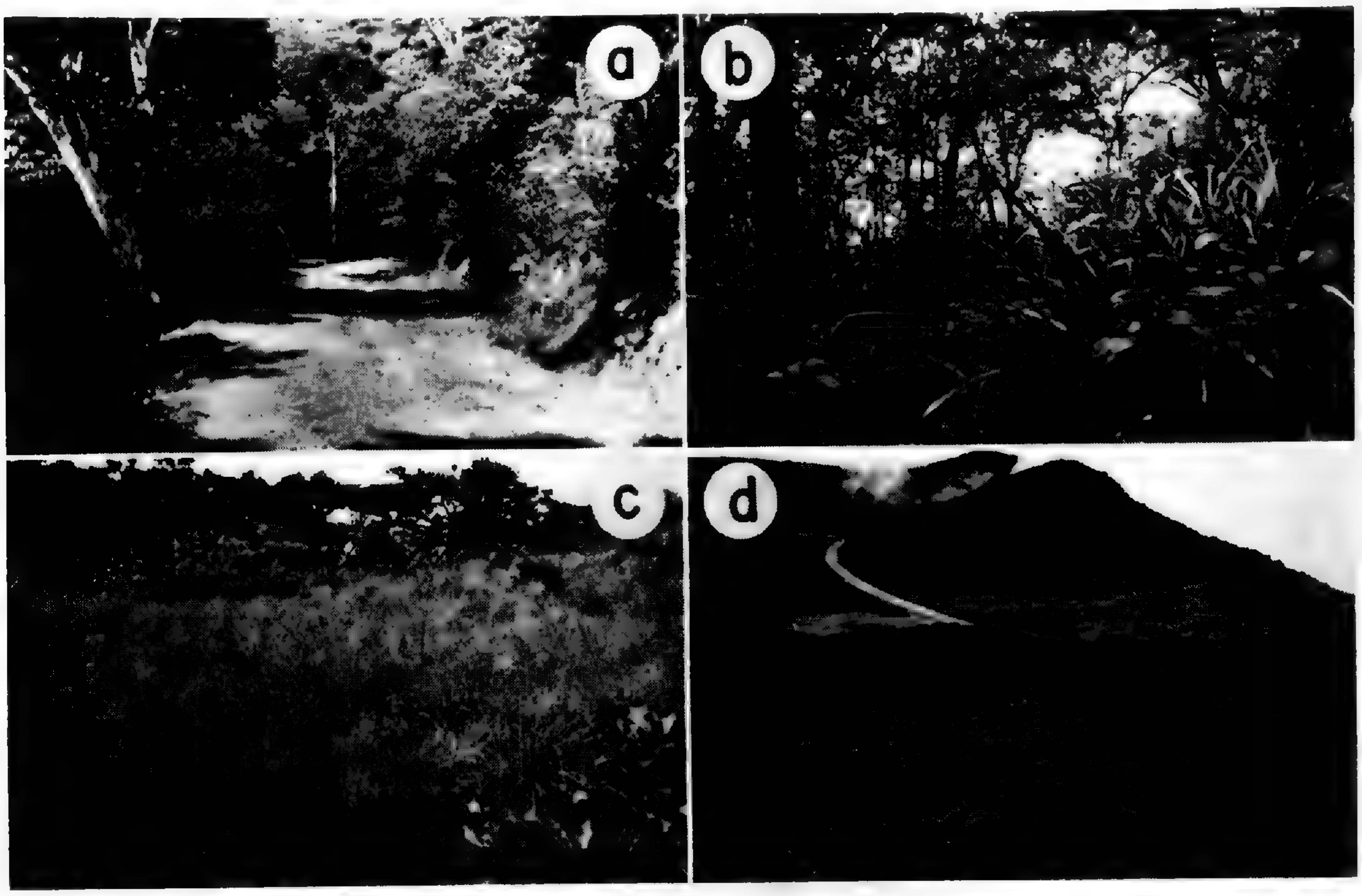

FIGURE 1. The four Costa Rican study areas.—a. Area E, a complex, lowland deciduous forest. The conspicuous tree at the end of the road is 25 m tall.—b. Area G, a "simple," lowland deciduous forest. Note the relatively open canopy. The shrub on the right, *Bromelia pinguin*, is 1.7 m tall.—c. Area S, a grassland "savanna." Note the figure in the center, among *Byrsonema crassifolia* trees.—d). Panorama of Area P, the montane wet rain forest site. The dominant shrubs are 2–3 m high.

three were in the Tropical Dry Forest life zone and one in the Montane Rain Forest life zone of Holdridge (1967). The communities differed in physical structure and plant diversity as seen in Figure 1. The lowland communities included a complex deciduous forest (Area E), a simple deciduous forest (Area G), and a grassland-savanna (Area S). The high altitude site (3335 m, Area P) was dominated by shrubs and was subject to frosts and occasional freezes. Monthly estimates of floral resources were made. These estimates took into account both the number and size of flowers found in quadrats and along transects. Flower visitors were observed at each site for at least one week each month. Where field identifications were reliable (*e.g.* hummingbirds and some butterflies) I did not collect the visitors, but insects were usually collected. Using over 20,000 observations of flower visitation, I calculated the niche breadth for flower visitation for each species and the pairwise niche overlap among the different species. Niche breadth and overlap were calculated using the method of Colwell and Futuyma (1971). Their method facilitates the comparison of trends in niche metrics over different communities because differences in the amount of resource and differences in resource spacing among communities are taken into account. We therefore have relatively independent estimates of niche breadth, niche overlap, and resource diversity in each of the communities. I will now discuss the observed relationship between flower-visitor diversity and each of these three parameters.

TABLE 1. The number of visitor species in the dry and wet seasons, and total visitor species numbers.

	Number of Species											
	Season											
	Dry				Wet				Total			
	Area				Area				Area			
Group	E	G	S	P	E	G	S	P	E	G	S	P
Coleoptera	42	15	5	3	80	33	12	6	107	37	12	8
Diptera[a]	22	8	7	20	35	15	7	25	46	16	9	37
Hymenoptera												
Bees	126	72	43	6	125	67	44	6	170	87	52	7
Wasps	62	47	20	1	89	49	22	6	112	6	31	7
Lepidoptera	56	25	18	13	123	46	27	4	138	51	31	6
Trochilidae	7	7	2	3	7	7	2	4	7	7	2	5
Miscellaneous	3	1	0	0	3	0	1	0	6	1	1	0
Total	318	175	95	46	462	217	115	51	586	260	138	69

[a] Diptera are represented only by the families Bombyliidae, Nemestrinidae, and Tachinidae.

DIVERSITY AND NICHE BREADTH

Over 900 species in seven major taxonomic groups were observed at flowers (Table 1). The breadth of taxa included in this analysis is important. Since we are concerned with potential competition for floral resources, we should logically consider all groups that are utilizing these resources. For example, we should not analyze niche metrics for bees alone, because competition with other groups, such as hummingbirds, can influence bee feeding-patterns. One advantage of the program initiated by Raven and Moldenke is the study of ecologically determined groups.

The problem of estimating niche breadth for rare species was avoided by calculating niche breadth for only those species represented by at least 12 individuals. Unfortunately, most flower-visitor species in Costa Rica were represented by only one to eleven individuals (Fig. 2), so the estimate of mean niche breadth is from a sample of the total species pool. There was no evidence, however, that rare species were actively excluded from visiting flowers also used by common species (Heithaus, 1973). Further, the proportion of species that were rare was nearly the same for all communities, so it is likely that the niche breadth estimates are reasonably used as indicators of community interactions.

As predicted by the competition theory, there was a decrease in the mean niche breadth (or increased specialization) of common flower-visitor as the number of species in the lowland communities increased (Fig. 3). In terms of the Colwell-Futuyma measure of niche breadth, this means that each lowland flower-visitor species tended to utilize a smaller proportion of the total available resource as the number of species in the community increased. The results from the seasonal lowland areas agree with those of Moldenke (1971), who found that

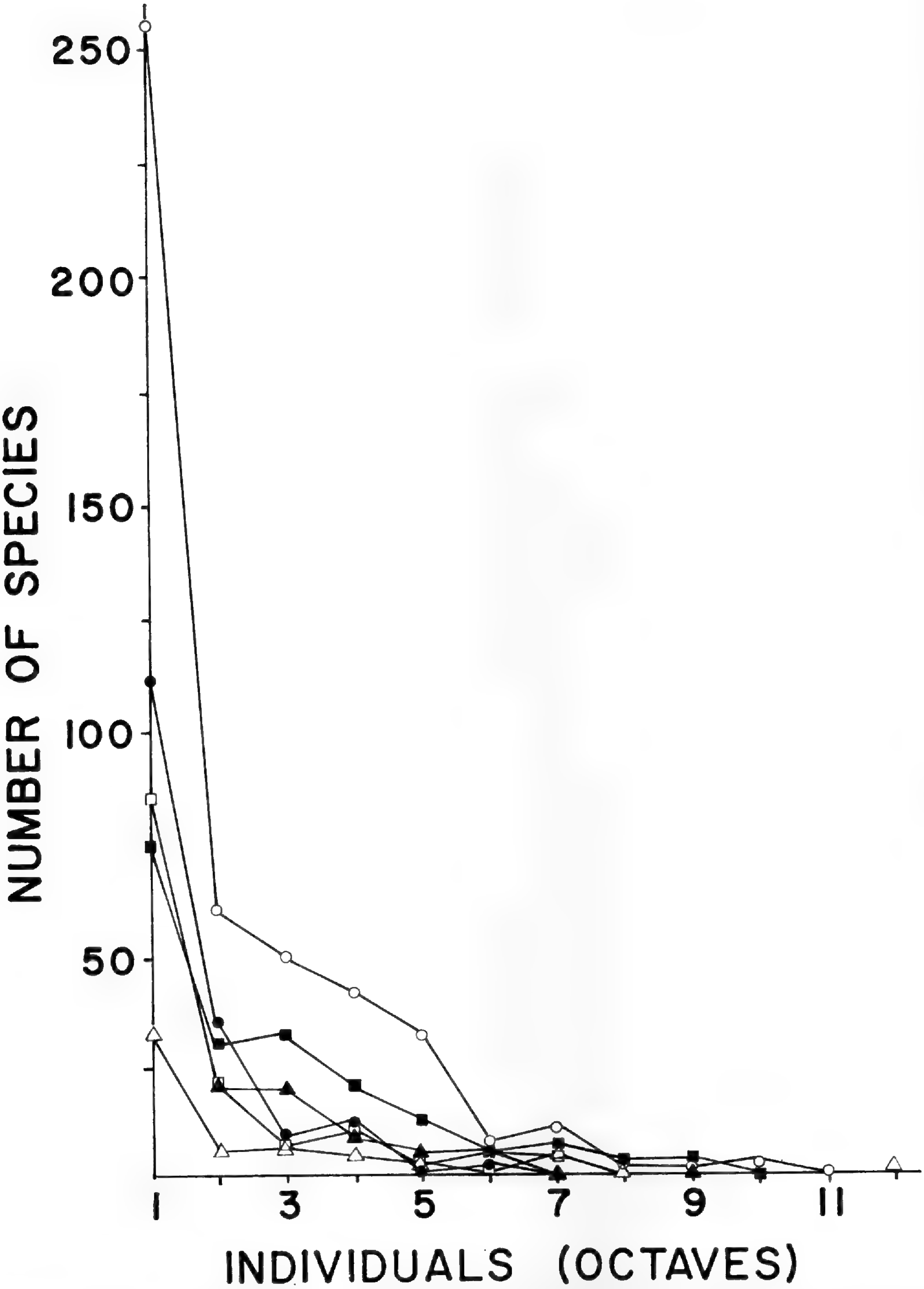

FIGURE 2. The distribution of individuals among species, plotted according to the method of Preston (1948). The number of individuals per species is given on a $\log_2$ scale; the upper bounds of "octaves" are in the series 2^0, 2^1, $2^2 \ldots 2^n$. The ordinate gives the number of species with at least 2^n individuals. ○ = Area E, wet season; ● = Area E, dry season; □ = Area G, wet season; ■ = Area S; △ = Area P.

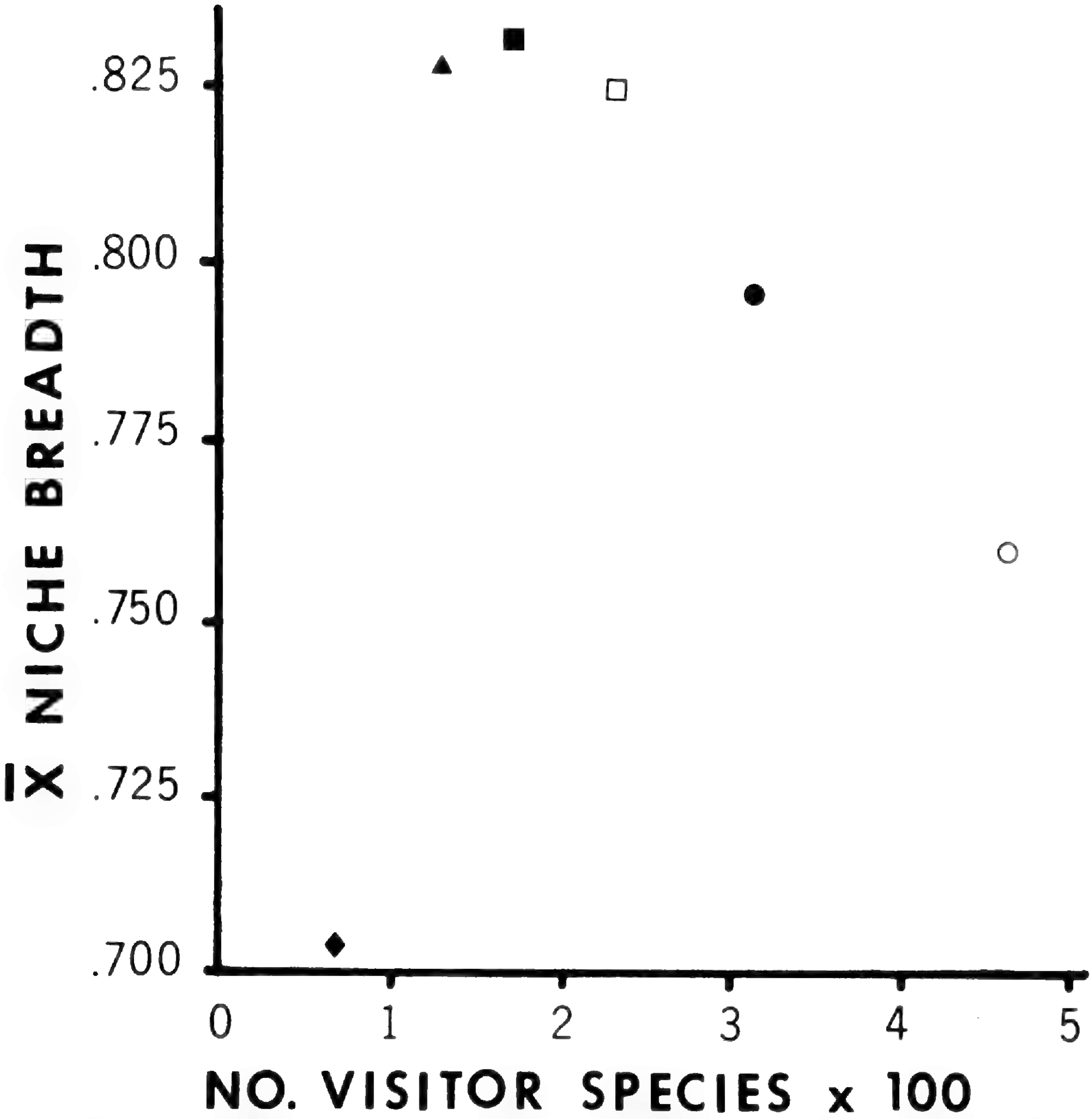

Figure 3. Correlation between the number of species and the mean niche breadth of common flower-visitor species in a community. ◆ = Area P; ▲ = Area S; ■ = Area G, dry season; □ = Area G, wet season; ● = Area E, dry season; ○ = Area E, wet season.

the proportion of oligolectic bees increased as species diversity increased among communities in California.

This pattern did not extend to the very different habitat of the shrubby Montane Rain Forest (Area P), as the niche breadths of flower-visitors tended to be much narrower than predicted. This may have resulted from a relatively constant temperature stress in the high altitude environment. The mean annual temperature near Area P was only 10.8°C, and the range in monthly means was 9.6°C to 11.8°C (Holdridge *et al.*, 1971). These low temperatures, with no real warm season, may have resulted in large energetic stresses on invertebrates, especially flower-visitors which need energy to fly from flower to flower (Heinrich, 1972). There is just one abundant generalist species in Area P, *Bombus ephippiatus*. The genus *Bombus* is able to regulate body temperature to a large degree. Most of

TABLE 2. Mean niche overlap values, the number of species-pairs values, and number of species.

Area	$\bar{X}$ Overlap	N[a]	No. Species[b]
S	.2871	91	138
G_{dry}	.2840	77	175
P	.1968	141	69
G_{wet}	.1966	50	217
E_{dry}	.1870	404	318
E_{wet}	.1644	636	462

[a] "N" = the number of species pairs used in calculating the mean overlap. Only species represented by more than 11 individuals were included in the niche overlap analysis.

[b] No. Species = the total number of flower visitor species in each area.

the remaining, relatively non-thermoregulating, species visit just one or two *Senecio* species. These are patchy and offer a large amount of resource per patch. Specialization on patchy resources could clearly be advantageous where temperatures are low (Heinrich & Raven, 1972). With many species utilizing a few, patchy resources it appears that temperature stress creates an environment that consists of a series of refugia for most flower-visitor species. That is diversity in Area P may depend more on the presence of concentrated resources than on changes in niche breadth. Cruden (1972) also found evidence for the restriction of bee activity at high altitudes. Therefore we can see that changes in niche breadth follow predictions within similar climatic zones, but they may differ from predictions as temperature stress becomes extreme.

NICHE OVERLAP

For the lowland communities there is a minor trend toward decreasing niche overlap with increased species packing (Table 2). This could be the result of the decrease in niche breadth that was observed with increasing species numbers. Increasing niche overlap is not an important mechanism for controlling species packing in the Costa Rican communities. This conclusion is consistent with the predictions of May and MacArthur (1972), which were based on MacArthur's model of regulation of diversity through competition. In this paper they assert that niche overlap should not increase greatly through broad ranges of environmental variation.

RESOURCE DIVERSITY

The number of visitor species in a study area each month was positively correlated with floral diversity. This relationship held for all communities when floral diversity was expressed as number of species (Fig. 4) (Pearson product-moment correlation, $r = .7588$, $P < .01$). The number of lowland visitor species was also positively correlated with floral resource abundance (Fig. 5) ($r = .5710$, $P < .01$), and this is precisely the relationship predicted by the competition theory of diversity regulation. Consumer diversity should increase with resource diversity. Area P did not follow this trend, because the number of visitor species

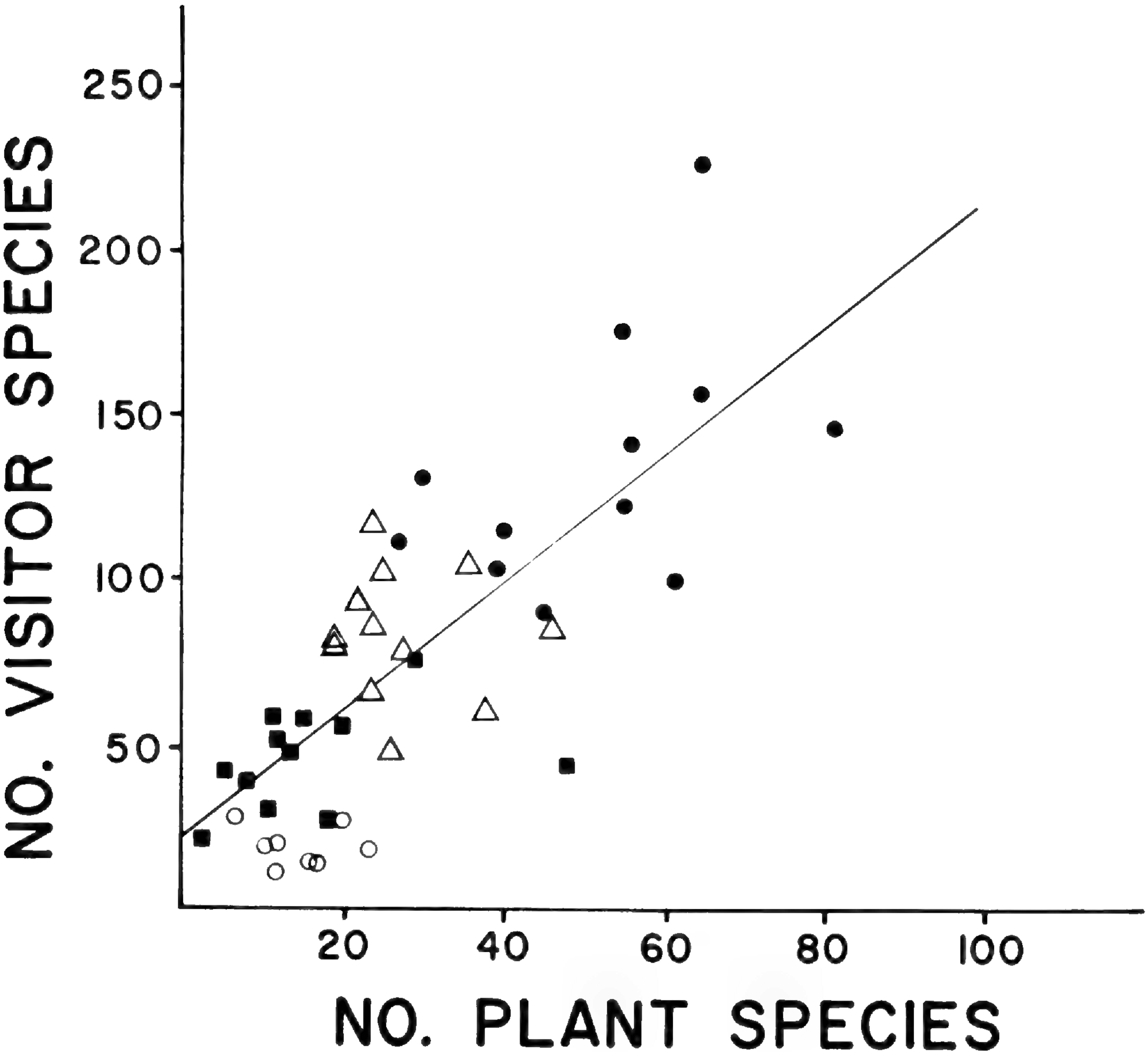

FIGURE 4. Correlation between the number of visitor species and plant species in monthly censuses in each area. ■ = Area S; ○ = Area P; △ = Area G; ● = Area E. The correlation is significant, r = .7588. P < .01.

was more closely associated with a few, often relatively uncommon, but patchy plants such as *Senecio oerestediana*.

In summary, the competition theory of diversity regulation generates predictions that are confirmed by observations in lowland, seasonal tropical communities. Niche breadth decreases as the number of species in a community increases, and species diversity increases with increasing resource diversity. Changes in niche overlap probably do not contribute to increased diversity, but the observed differences in niche overlap can be explained by differences in the average niche breadth in communities. Observations from a high altitude site do not confirm predictions based on the competition theory and data from lowland areas. Average niche breadth is much lower than predicted, and the number of visitor species is lower than predicted by the abundance of floral resources. Additional parameters, such as environmental severity, may be needed to supplement competition theory in explaining diversity differences in extreme environments. However, the competition theory is nicely supported by lowland community results,

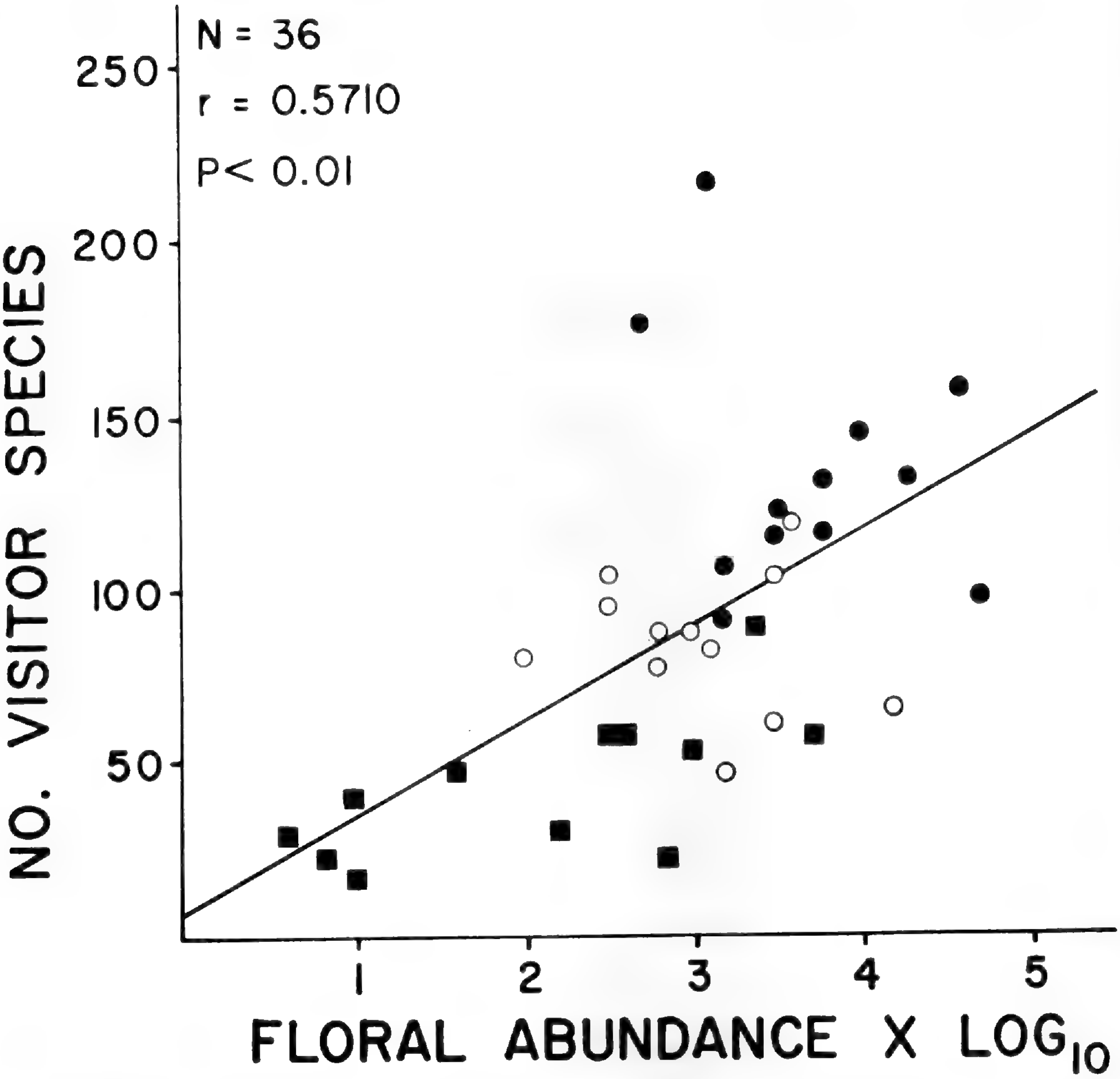

FIGURE 5. Correlation between the number of visitor species and floral abundance in monthly censuses in lowland areas. ■ = Area S; ○ = Area G; ● = Area E.

and the structure of these flower-visitor communities can be directly related to plant-animal interactions. Pollination systems are important at the community level of organization as well as at the level of species-species coevolution.

COMPETITION FOR POLLINATOR SERVICES

The idea that plants compete for pollinator services must be nearly as old as the observation that different flower types attract different visitors. The mechanisms of this competition have been studied in some systems with a few competing species (Free, 1968; Levin & Anderson, 1970; Levin, 1972*a*, 1972*b*). There have also been assertions that competition for pollinators is not confined to a few or closely related species, but that it is a major factor in the evolution of the timing of flowering within entire plant communities (Hocking, 1968; Croat, 1969; Mosquin, 1971). The implications of the latter claim are different than those arising from knowing that two, or a few, species are competing for polli-

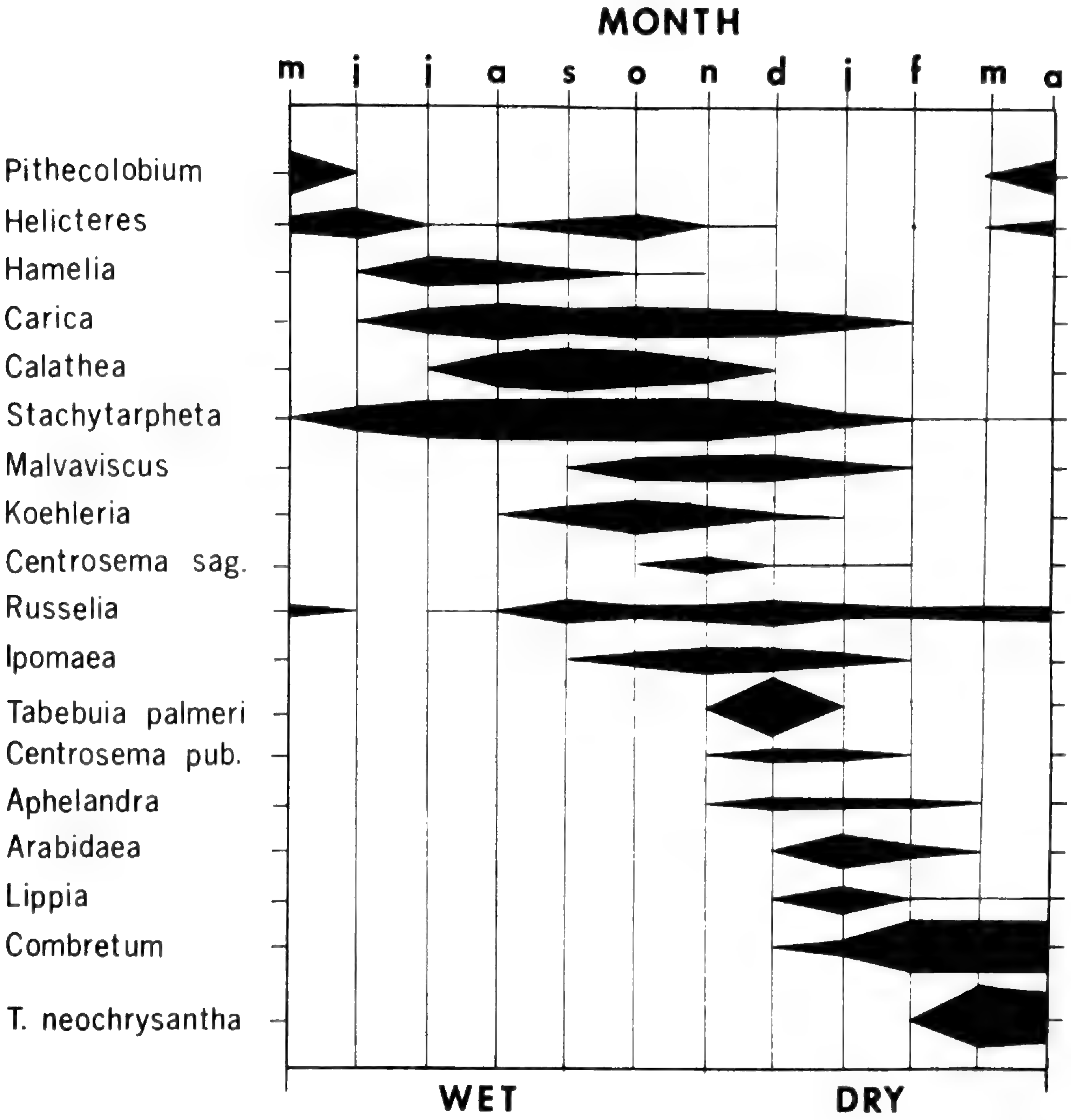

FIGURE 6. Temporal distribution of floral abundance of "butterfly-pollinated" plants. The vertical axis for abundance uses a $\log_{10}$ scale. The range of the wet and dry seasons is given.

nators. In two species systems competition for pollinators could result in subspeciation, in the extinction of one of the species, or selection for the displacement of flowering periods. If competition for pollinators operates on a community level, then it is possible that all potential flowering periods would be used in diverse communities. In such saturated communities no additional flowering plants could become established, if they required animal-mediated pollination. Claiming competition for pollinators on a community level therefore implies interactions. This is in contrast to the belief that present plant communities "could soak up many more species" (Whittaker, 1969; Ross, 1972), so the assertion of competitive displacement of flowering should be critically examined.

Naturally, experimental methods have not been used to determine that competition for pollinators affects large communities. Such techniques would be

TABLE 3. The number of species in flower and the distribution of flowering peaks[a] through time in a complex deciduous forest.

	Month											
Pollinator Syndrome	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
Large Bees:												
Number of Peaks	3	4	2	3	4	3	9	4	3	4	4	2
Number of Species	7	10	6	10	9	12	14	12	12	11	9	10
Small-medium Bees:[b]												
Number of Peaks	7	2	1	4	7	4	8	9	6	3	1	1
Number of Species	10	9	7	13	16	17	18	24	18	14	6	10
Wasps:												
Number of Peaks	3	2	0	0	1	1	2	0	2	2	0	1
Number of Species	4	2	0	2	2	4	3	0	2	3	1	3
Hummingbirds:												
Number of Peaks	1	1	1	1	3	2	4	6	3	1	2	1
Number of Species	4	3	3	6	7	8	9	10	10	8	4	7
Butterflies:												
Number of Peaks	2	2	2	3	3	2	2	2	3	0	0	3
Number of Species	3	6	5	10	9	9	10	8	9	7	5	6

[a] A "peak" = a month in which the floral abundance for a species is at or within 25 percent of its maximum.

[b] The distributions of numbers of "small and medium bee flower" species in bloom and peak flowering periods are the only distributions that differ significantly from an evenly spaced pattern (Chi-square Test).

impractical; so indirect evidence again has been used. This hypothesis was supported by Mosquin's (1972) studies of northern Canadian communities. Here, dominant species that offered large floral rewards appeared to "displace" the flowering periods of plants that offered less floral resource.

The remaining line of evidence that competition for pollinators involves whole plant communities comes from studies of flower phenology. A frequent pattern emerging from phenology is a temporal displacement of flowering for species with similar pollination syndromes, so that some species are blooming throughout the growing period (Croat, 1969; Mooney *et al.*, 1973; Heithaus *et al.*, 1973). I found similar "displacement" of flowering times in Area E, the complex, lowland, deciduous forest (the other communities have not yet been similarly analyzed). The flowering periods of "butterfly-pollinated" and "hummingbird-pollinated" plants are shown in Figures 6 and 7. I found nearly the same number of plant species in bloom and the same number of species reaching peak flower production each month. These distributions were not significantly different than ones predicted by assuming an "even" distribution of flowering through the year (Chi-square Test), except for the plants in the "small-medium sized bee syndrome" (Table 3).

One of the big problems with this analysis is the large amount of overlap in flowering periods. If competition for pollinators were important, nearly non-overlapping flowering periods would be expected. Secondly, the observed flowering pattern is also the one predicted by assuming that flowering periods are determined purely at random. Demonstrating the "displacement" of flowering periods is one problem, but linking the pattern to competitive interactions and explaining the overlap is quite a different one.

If we temporarily assume that competition for pollinators is important, we can generate at least two testable hypotheses. First, plants that bloom simultaneously should have different visitor species; or if the same visitors are attracted, then one or two plant species would probably "outcompete" the others (Levin & Anderson, 1970). To test this prediction I looked at visitation patterns among plants in two pollination syndromes—butterfly- and hummingbird-pollinated plants. These were chosen on the basis of the relatively small numbers of species involved and ease of analysis. Some generalist plants (those attracting and potentially pollinated by several vector types) were included in both syndromes. First I determined the total number of visits to flowers made by hummingbirds or butterflies, combining visits to all plant species. Secondly, two visitation characteristics were determined for each plant species in a syndrome: (1) the most common visitor species (primary visitor), and (2) the proportion of total visits received by the single plant species. Plants receiving fewer than 5 percent of the total visits for the syndrome were noted.

Butterfly-pollinated plants tended to have different primary visitors, if the plants were visited frequently. Sixty-eight percent (N = 22) of the infrequently visited plants shared primary visitors with a frequently-visited plant. Just two wet season plants were equally successful in attracting one "primary" pollinator species (Table 4). The butterfly was extremely abundant in the area, and there was no overlap in the less common butterfly species that visited these two plants, *Cordia* sp. 2 and *Tridax procumbens*. Thus, overlap in visitors was not extensive in this case. During the dry season only two commonly visited species (*Tridax*, *Melanthera aspera*) appeared to share visitor species (Table 5). Their "primary" visitor, *Eurema diara*, was extremely abundant, and again, there was little overlap in the less common butterflies that visited the two plants.

There were even fewer cases of overlap in common visitor species to hummingbird-pollinated plants (Fig. 7). As in butterfly-pollinated plants, when two plants were visited by the same "primary" visitor one, of them received fewer than five percent of the observed visits. This result is especially interesting when we consider the fine temporal adjustments flowering plants can make. Compared to potential differences in daily anthesis, differences in monthly flowering reflect a very coarse time scale. That we encounter so few exceptions to a prediction based on monthly flowering is impressive. It is fair to say that the prediction based on the hypothesis that these species are dividing the pollinator resources is supported by the analysis of visitation frequencies to simultaneously blooming plants.

Other predictions can be made. For example, if competition is important at the community level, then regulation of floral diversity may fit MacArthur's (1972) conceptualization. Floral diversity (although not necessarily plant diversity) would depend on the diversity of available pollinators, the average specialization of flowers, and the average "pollinator-niche"-overlap in a community.

TABLE 4. Visitation patterns to "butterfly-pollinated" plants.

	Month											
Plant Species	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
Casearea n. sp.	(Me)[b, c]											
Cordia sp.		Me										
Cordia pringlei		Hh[c]		Hh	Hh	Hh						
Matelea			(Hh)	(Hh)	(Hh)							
Hamelia			(Hh)	(Hh)	(Hh)							
Carica			NV[a]	NV	NV	NV	(Hh)	(Hh)	NV			
Lonchocarpus				NV								
Tridax	Me + Ed[c]	Me + Ed	Me + Ed	Me + Ed	Me + Ed	Ed			Py[c] + Ed	Py + Ed	Ed	Ed
Cordia polyceph.					Zo[c]	Zo	Zo					
Stachytarpheta		Ur[c]	Ur	Ur	Ur	Ur	Ur	Ur				
Hyptus						(Ur)	(Ur)		(Ur)			
Callicophyllum							Ad[c]	Ad	He[c]			
Melanthera								Ed	Ed	Ed	Ed	Ed
Licania									Af[c]			
Cupania									Vs[c]	Vs		
Lantana	(Hh)	(Hh)		(Hh)	(Hh)	(Hh)	(Hh)	(Hh)		(Ed)	(Ed)	(Ed)
Asclepias		Af		Af	Af	Af	Af	Af			Af	Af
Blechnum												(Ed)

[a] NV = not visited.

[b] ( ) indicate that less than 5 percent of all butterfly visits were to the plant listed.

[c] The most common butterfly visitors are indicated by the following abbreviations: Ad = ***Adelpha*** sp., Af = ***Anartia fatima***, Ed = ***Eurema diara***, He = ***Hesperiidae***, Hh = ***Heliconius hecale***, Me = ***Microtia elva***, Py = ***Pyrgus*** spp., Ur = ***Urbanus*** spp., Vs = ***Victorina stelenes***, Zo = ***Zopyrion*** sp.

TABLE 5. Visitation patterns to "Hunmingbird-pollinated" plants.

Plant Species	Month											
	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
Pithecolobium	NV[a]											NV
Helicteres	(Ar)[b, c]	(Ar)			(Ar)	(Ar)						(Ar)
Hamelia			As[c]	As								
Carica				NV	NV	NV	NV	He[c]	He	He		
Calathea				As + Pl[c]	As + Pl	As + Pl	As + Pl					
Stachytarpheta		Ar	Ar	Ar	Ar	Ar	Ar	Ar	Ar			
Malvaviscus						(Ar)	(Ar)	(Ar)	(Ar)			
Koehleria					Hy[c]	Hy	Hy					
Centrosema sag.							Ar + As					
Russelia	NV				NV	NV	NV	(As)	NV	NV	NV	NV
Ipomaea						(As)	(As)	(As)				
Tabebuia palmeri								NV	NV			
Centrosema pub.								NV	NV			
Aphelandra								NV	NV	NV		
Arabidaea									(Hc)[c]	(Hc)		
Lippia									(As)	(As)		
Combretum									As	As	As	As
T. neochrysantha											(Hc) + (As)	

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[a] NV = not visited.
[b] ( ) indicate that less than 5 percent of all hummingbird visits were to the plant listed.
[c] The most common hummingbird visitors are indicated by the following abbreviations: Ar = *Amazilia rutila*, As = *A. saucerotii*, Hc = *Heliomaster constantii*, He = *Hylocharis eliciae*, Hy = *H.* sp. 2, Pl = *Phaethornis longuemareus*.

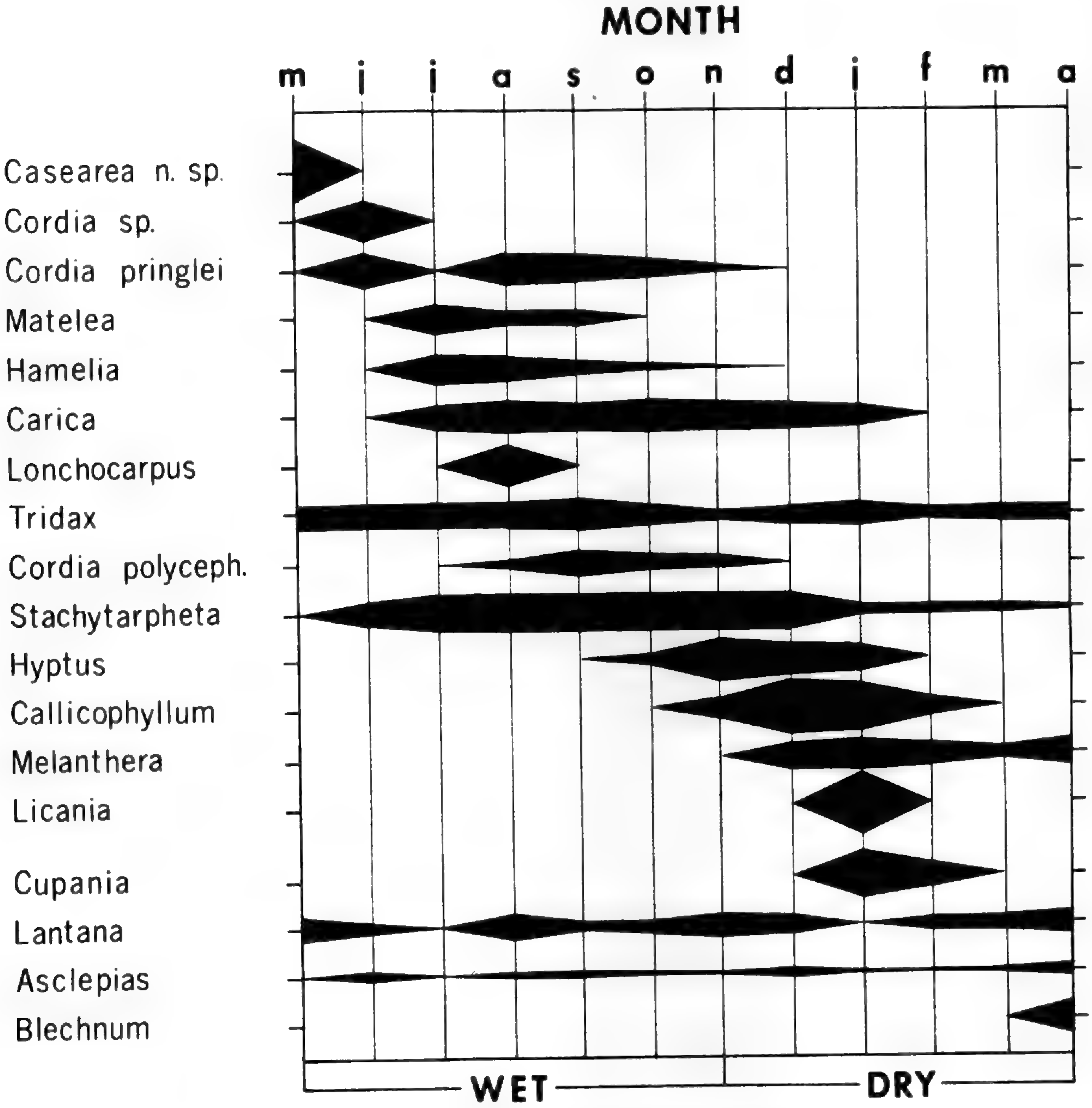

FIGURE 7. Temporal distribution of floral abundance of "hummingbird-pollinated" plants. The axis are as in Figure 6.

There are hints that this prediction will be confirmed. We have already noted the correlation between floral diversity and flower-visitor diversity. We must refine our analysis to distinguish the truly potential pollinators among nectar and pollen consumers. Further analysis of visitation to Costa Rican plants, combined with Moldenke's and Raven's studies, should allow an evaluation of this prediction.

To conclude, there is evidence from lowland Costa Rican communities that plant-animal interactions at flowers are very important to the determination of community structure. The diversity of flower-visitors is largely a function of competition for floral resources, and in turn, the diversity regulation through competitive interactions, diversity in these communities should be at equilibrium. We would not expect major increases or decreases in species diversity through "ecological" time. However, if this is essentially a positive-feedback system, where increased floral diversity increases flower visitor diversity, and increased pollinator diversity increases floral diversity, we must wonder whether there are any limits to diversity through evolutionary time. Perhaps limits to potential productivity would impose a ceiling on floral resource diversity, but for the present this remains an open question. At the very least we can conclude that plant-animal interactions at flowers are an important and interesting component of community structure and that these interactions deserve more attention in community studies.

Literature Cited

Colwell, R. K. & D. J. Futuyma. 1971. On the measurement of niche breadth and niche overlap. Ecology 52: 567–576.

Croat, T. B. 1969. Seasonal flowering behavior in Central Panama. Ann. Missouri Bot. Gard. 56: 295–307.

Cruden, R. W. 1972. Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. Science 176: 1439–1440.

Elton, C. S. 1973. The structure of invertebrate populations inside neotropical rain forest. Jour. Animal Ecol. 42: 55–104.

Fittkau, E. J. & H. Klinge. 1973. On biomass and trophic structure of the Central Amazonian rain forest ecosystem. Biotropica 5: 2–14.

Free, J. B. 1968. Dandelion as a competitor to fruit trees for bee visits. Jour. Appl. Ecol. 5: 196–178.

Harper, J. L. 1969. The role of predation in vegetational diversity. Brookhaven Symposia in Biology 22: 48–62.

Heinrich, B. 1972. Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. Jour. Comp. Physiol. 77: 49–64.

——— & P. H. Raven. 1972. Energetics and pollination ecology. Science 176: 597–602.

Heithaus, E. R. 1973. Species diversity and resource partitioning in four neotropical plant-pollinator communities. Ph.D. Thesis in Biological Sciences, Stanford University. 148 pp.

———, T. H. Fleming & P. A. Opler. 1973. Foraging patterns and resource utilization by several bat species in a seasonal tropical forest. In preparation.

Hocking, B. 1968. Insect-flower associations in the high Arctic with special reference to nectar. Oikos 19: 359–387.

Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica. 206 pp.

———, W. C. Grenke, W. H. Hatheway, T. Liang & J. A. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones; A Pilot Study. Pergamon Press, New York. 747 pp.

Janzen, D. J. 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturalist 104: 501–528.

Klopfer, P. H. & R. J. MacArthur. 1960. Niche size and faunal diversity. Amer. Naturalist 94: 293–300.

Levin, D. A. 1972*a*. Low frequency disadvantage in the exploitation of pollinators by corolla variants in *Phlox*. Amer. Naturalist 106: 453–460.

———. 1972*b*. The adaptedness of corolla-color variants in experimental and natural populations of *Phlox drummondii*. Amer. Naturalist 106: 57–70.

——— & W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. Amer. Naturalist 104:455–467

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton. 120 pp.

MacArthur, R. H. 1970. Species packing and competitive equilibrium for many species. Theor. Popul. Ecol. 1: 1–11.

———. 1972. Geographical Ecology. Harper and Row, Pub., New York. 269 pp.

May, R. M. & R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proc. Natl. Acad. Sci. U.S.A. 69: 1109–1113.

Moldenke, A. R. 1971. Studies of the species diversity of California plant communities. Ph.D. Thesis in Biological Sciences, Stanford University.

MOONEY, H. A., D. J. PARSONS & J. KUMONEROW. 1973. Plant phenological development in Mediterranean environments. *In* H. Lieth (editor), "Ecological Studies, Phenology and Seasonal Modeling." Springer-Verlag, Berlin. In Press.

MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22: 398–402.

ODUM, H. T., W. ABBOTT, R. K. SELANDER, F. B. GOLLEY & R. F. WILSON. 1970. Estimates of chlorophyll and biomass of the Tabonuco forest of Puerto Rico. Pp. 13–119, *in* H. T. Odum (editor), "A Tropical Rain Forest." U.S.A.E.C., Washington, D.C. 164 pp.

PAINE, R. T. 1966. Food web complexity and species diversity. Amer. Naturalist 100: 65–75.

——— & R. L. VADAS. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14: 710–719.

PRESTON, F. W. 1948. The commonness and rarity of species. Ecology 29: 254–283.

ROSS, H. H. 1972. The origin of species diversity in ecological communities. Taxon 21: 253–259.

VANDERMEER, J. H. 1970. The community matrix and the number of species in a community. Amer. Naturalist 104:73–79.

WHITTAKER, R. H. 1969. Evolution of diversity in plant communities. Brookhaven Symp. in Biology 22: 178–195.

THE INSECTS OF BRITISH TREES: COMMUNITY EQUILIBRATION IN ECOLOGICAL TIME[1]

DONALD R. STRONG, JR.[2]

ABSTRACT

The most widely accepted model of insect-plant interaction derives from the correlation between insect species richness and the relative number of recorded Quaternary fossil remains of British tree species (Southwood, 1961). The implications of this relationship are: 1) that community formation and the equilibration of insect species richness is a very slow process, taking at least 2 million years, 2) that introduced plant species will necessarily have relatively few associated insect species, 3) that insect communities are basically different from vertebrate communities in that saturation of species does not occur (Whittaker, 1969).

I present a model mutually exclusive to Southwood's, indicating that insects of British trees follow a species area relationship. The implications of this new finding are: 1) insect community formation and equilibration of species richness occurs at least within 300 years, 2) the insect diversity of introduced plants becomes a function mainly of the range of distribution of the plant within ecological time, 3) insect communities do not differ from vertebrate communities in terms of species saturation rate. The saturation occurs within ecological time for both groups.

Plant/insect interactions are apposite to general ecological thought because they provide the only uncontested example of non-equilibrium community biology; the number of insect species associated with tree species apparently can increase continually and without limit over long periods of geological time. This is suggested by Southwood (1961), who shows the number of insect species recorded from British trees to be positively and linearly correlated with the total number of Quaternary fossil records of the tree taxon. This implies community formation and any resultant equilibration of species number for these insects to be a very slow process, taking longer than the Quaternary or between 15,000 and 2 million years—depending upon "one of the most popular topics in all biogeography . . . . whether the whole fauna and flora of the British Isles immigrated in post-glacial times, or whether some fraction survived from an earlier time" (Deevey, 1949). Extremely protracted community development is logically necessary given the fact that there is no asymptote in Southwood's correlation and that native trees are on the same line as species introduced only 300 years ago. The Oaks provide a good example. *Quercus petraea* and *Q. robur* are native species that together have the richest associated insect fauna of any tree taxon in Great Britain (284 species), whereas *Quercus ilex*, introduced into Britain about 400 years ago has only 2 associated insect species. Southwood's correlation predicts that after another 14,600 to 2 million years in Britain *Q. ilex* will have many more species of insects associated with it, however by that time *Q. petraea* and *Q. robur* will also have acquired many more. But unless the relative abundance or distributions of these two taxa change, the difference between them in number

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[1] I thank Tom Ray for counting the 60 thousand-odd dots in Perring and Walters for this study.

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of associated insect species will remain constant. The non-asymptotic nature of the correlation implies that the rate of addition of insect species to the fauna of a tree taxon is independent of the number of insects already in that fauna. Perhaps within another million years, "saturation" (MacArthur, 1965) or "equilibrium" (MacArthur & Wilson, 1963) will have occurred for the insect biotas of the oldest or most perenially abundant tree species, and continued existence in the flora will not add any more insect species to their faunae. However Southwood's correlation gives no indication that these faunae will ever saturate. The correlation supports Whittaker's contention that similar generalizations may not apply to insect and bird communities: "Bird communities can thus be saturated, determinate in their evolution of diversity; but plant and insect communities may show indefinite, indeterminate evolutionary increase in diversity" (Whittaker, 1969).

However there is a problem with Southwood's correlation. It ignores the influence of present abundance of host taxa upon associated insect species richness. The general importance of present conditions in determining diversity has been well established by the species-area relationship. For many taxocenes of birds, reptiles, phanerogams, and invertebrates the number of species in a biota is a function of the present area supporting the biota, when geographically close and similar areas are considered. (See Simberloff, 1972, for review.) This relationship, $S = kA^z$ (Preston, 1960) where S = number of species, A = area of the region considered, k = a constant for the biota in question, and z = ratio of log species addition per log area addition, has been most often demonstrated to explain the difference in richness among the biotas of oceanic islands, but there is no reason that it should not be valid for "islands" on the mainland as well. Indeed, Janzen (1968) has suggested that host plants are islands in a sea of vegetation for phytophagous insects. Hence I reason that for the British insect/tree system the analogue of area, of "A" in the species-area relationship, should be the present range or breadth of distribution of a host tree taxon.

The idea that cumulative ancient host tree abundance determines species richness of associated insect faunae is an extension of the popular notion that the antiquity of a biota determines its species richness (Wallace, 1878; Wimpenny, 1941; Dunbar, 1960; Fischer, 1960; Zenkevitch, 1961; Sanders, 1968). This "geological time theory" of organic diversity proposes that the number of species in a biota tends to grow steadily through long periods of geological time. It is obvious that geological time theories and recent or ecological time theories are competing or alternative explanations of species richness. That a biotas's antiquity determines its species richness is in conflict with the idea that ecological conditions during recent times control richness. However both may operate, one being a major factor and the other being minor, or both may be of relatively equal importance, or finally one of the two may be shown to be overwhelmingly more important in determining species richness. By subtracting the amount of variation in insect richness attributable to variation in present day range from the total amount of insect richness variation it is possible to establish the proportion contributed by cumulative ancient abundance of the host taxon.

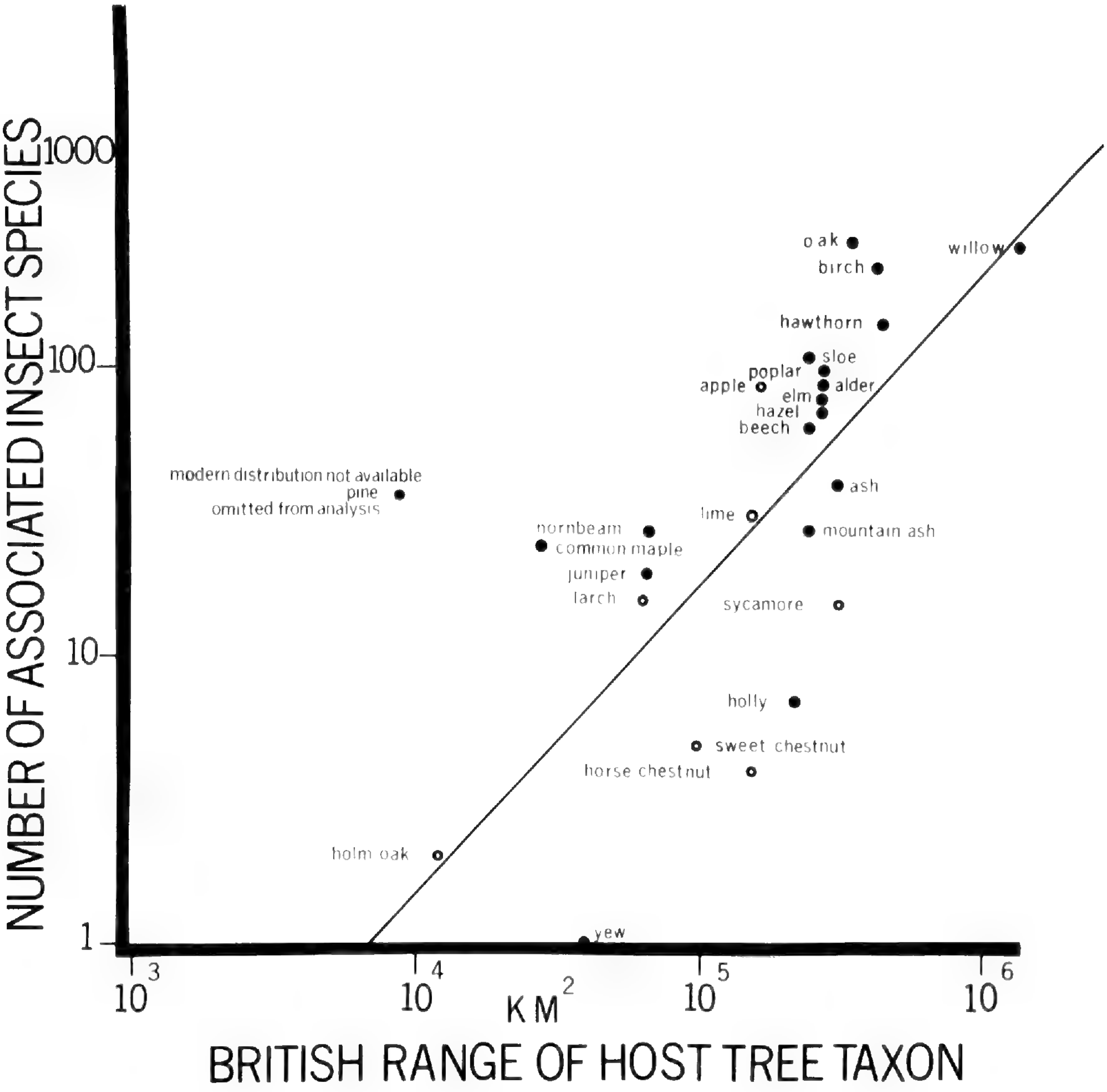

Figure 1. The number of insect species associated with British tree taxa, as a function of the present-day range in Britain of the tree taxa (Perring & Walters, 1962). Native species are indicated by closed points, introduced species by open circles. Apple is a mixed taxon, with both native and introduced elements in Britain. The slope of the regression line = 1.10. The correlation coefficient = .78, $p < .001$. The datum for pine is its inferred native range, Perring and Walters do not give its present distribution.

In Figure 1 I show the strong relationship between insect species richness and the present day range of British tree species. The host tree range data are taken from the dot maps of the *Atlas of the British Flora* (Perring & Walters, 1962). I used all modern records of host distribution from this source. Unfortunately the distributions of 4 tree species treated by Southwood's correlation are not given by Perring and Walters. I have included all host tree taxa for which there is distributional informaton in Perring and Walters. I computed the range of each host taxon as the sum of the ranges of sub-taxa listed in Perring and Walters. Some of these hosts are not taxonomically subdivided in Perring and Walters (*e.g. Corylus*, *Taxus*, *Fraxinus*, etc.) and others are (*e.g. Salix* with 18

TABLE 1. Data of origin, number of associated insect species, and present range of British tree taxa. The information of tree origin and associated insect species richness is from Southwood (1961), that for range of the tree taxa is from Perring and Walters (1962). For pine, only data of inferred "native" distribution are available; Perring and Walters do not give the modern distribution of this species.

Tree Taxon	Status	Number of associated insect species	Present range $\times$ 10 km^2
Quercus petraea & *robur* (oak)	Native	284	3593
Betula spp. (birch)	"	229	4217
Corylus avellana (hazel)	"	73	2885
Salix spp. (willow)	"	266	14,358
Alnus glutinosa (alder)	"	90	2931
Crataegus spp. (hawthorn)	"	149	4648
Fraxinus excelsior (ash)	"	41	3187
Pinus sylvestris (pine)	"	91	38 "native" range
Ilex aquifolium (holly)	"	7	2388
Taxus baccata (yew)	"	1	326
Prunus spinosa (sloe)	"	109	2564
Populus spp. (poplar)	"	97	2834
Ulmus spp. (elm)	"	82	2984
Fagus sylvatica (beech)	"	64	2639
Acer campestre (common maple)	"	26	277
Carpinus betulus (horn beam)	"	28	683
Juniperus communis (juniper)	"	20	624
Tilia spp. (lime)	"	31	1634
Sorbus aucuparia (mountain ash)	"	28	2446
Castanea sativa (sweet chestnut)	Introduced, 100 A.D.	5	986
Malus spp. (apple)	Native & introduced	93	1651
Qeurcus ilex (holm oak)	Introduced, 1580	2	129
Larix decidua (larch)	Introduced, 1629	17	608
Aesculus hippocastaneum (horse chestnut)	Introduced, ca. 1600	4	1692
Acer pseudoplatanus (sycamore)	Introduced, ca. 1250	15	3097

spp.). The insect data are from Southwood (1961). The data are given in Table 1.

Figure 1 shows a significant species-area relationship ($r = .78$, $p < .001$), hence broadly distributed tree taxa have more associated insect species than do narrowly restricted ones, and a new and very different interpretation from that forced by the Southwood correlation is needed. The most important change in thinking necessitated by Figure 1 is that the diversity of insect/host plant systems must now be regarded as asymptotic; the breadth of geographic distribution of British tree taxa sets an upper limit to the number of associated insect species, and the faunae of most if not all of the analyzed tree taxa are at that upper limit.

The regression of Figure 1 gives an indication of how rapidly the asymptote in species number (the saturation or equilibrium level) is reached. There are

5 introduced taxa in the analysis (sweet chestnut, holm oak, larch, horse chestnut, and sycamore) and two taxa of mixed (introduced and native) origin, apple and lime. There is no tendancy for the introduced taxa to fall below the regression line, which would be the case if the introduced (younger) host taxa were not yet saturated with insect species. Three of the introduced taxa are below the line and three are above. I have included lime as an introduced taxon, as most of its distributional records are contributed by native specimens; apple is not included as most of its distributional records are contributed by natives (Perring & Walters, 1962). A more powerful demonstration that the introduced species do not tend to fall below, or the natives above, the regression line is given by the non-parametric *Wilcoxon Two Sample Rank Test* of the regression residuals; the hypothesis that the residuals of introduced taxa are distributed about the regression line differently than are the natives is rejected by this test ($p > .14$, n.s., with both lime and apple included among the introduced taxa; $p > .12$, n.s. with lime but not apple included among the introduced species; $p > .05$, n.s. with neither apple nor lime included among the introduced species). Because introduced species do not fall below the regression line the asymptote for this system is reached in less than 350 years, as larch was introduced into Britain in 1629 (Southwood, 1961). A further example of how rapidly the equilibrium is reached is given by the case of pine, *Pinus sylvestris.* This tree is very widely distributed throughout the British Isles, but records are only available for the presumed "native distribution" of the species. Apparently British botanists feel its present distribution to be somehow irrelevant because this distribution is the result of man's activities. The number of associated insects shows the present, albeit anthropochorous, distribution to be highly relevant ecologically (Fig. 1). There are enough insect species associated with pine in Britain to allow it a range much broader than its native one. Most of the change in distribution of pine has probably been within the last 500 years, therefore the adjustment of insect species richness has also been within this period. This rapidity of accumulation of insect species on plant species suggests that instead of host transference of an insect species being a rare event Zwölfer & Harris, 1971), it is rather a common event that classical entomological methods rarely detect.

Though this analysis of the simple species-area regression strongly suggests that present distribution of host trees is by far the most important determinant of the number of species of associated insects, it has not ruled out the possibility that there is some small contribution to this richness from age and/or ancient abundance of the host taxon. I have tested this with multiple regression. With this technique one can assign proportional contributions to the variation of the dependent variable by the independent variables. The results of multiple regression of $\log_{10}$ number of insect species upon the independent variables "$\log_{10}$ host range" and "number of Quaternary remains" for each host taxon are given in Table 2. The meaning of the results is clear; although the fossil data does not add significant explanation of the variance in insect species number when $\log_{10}$ host range is the first variable treated by the analysis, $\log_{10}$ of host range does add significant explanation of the variance in insect species number when the

TABLE 2. Analysis of variance of multiple regression of range and number of fossil records upon associated insect species richness of British tree taxa.

Log$_{10}$ S Regressed on Log$_{10}$ Range of Host Taxon, and Number of Fossil Records

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.03	15.78 $p < .001$
Added by fossil record	1	.58	3.01 n.s.
Deviation about regression	21	.19	

Log$_{10}$ S Regressed on Log$_{10}$ Host Taxon Range, and Log$_{10}$ Number of Fossil Records

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.07	16.40 $p < .001$
Added by log$_{10}$ fossil record	1	.67	3.58 n.s.
Deviation about regression	21	.18	

Log$_{10}$ S Regressed on Number of Fossil Records, and Log$_{10}$ Host Taxon Range

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.03	15.78 $p < .001$
Added by log$_{10}$ range	1	2.38	12.43 $p < .001$
Deviation about regression	21	.19	

Log$_{10}$ S Regressed on Log$_{10}$ Number of Fossil Records, and Log$_{10}$ Host Taxon Range

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.07	16.40 $p < .001$
Added by log$_{10}$ range	1	2.58	13.79 $p < .001$
Deviation about regression	21	.18	

fossil data is the first variable treated in the analysis. This tends to rule out the geologic history of the host as having a significant effect upon the number of insect species associated with these tree taxa.

The objection might be raised that, since geological record insect species richness correlations are significant, the geological record explains as much of the variance in insect species richness as does host plant range. This is a statistical quibble, naïve of the biology of the system, and is incorrect for three reasons: 1) species-area relationships are known to be almost ubiquitously important in determining species richness, hence any other factors have to be weighed after the species-area effect has been accounted for. 2) My statistical analysis of the regression residuals of introduced *versus* native species, and my multiple regression analysis show cumulative ancient abundance of host taxa to have insignificant effect upon the insect species richness in comparison to host plant ranges. 3) The logic of the matter precludes giving fossil records of very different ages equivalent weight in the analysis as Southwood (1961) has. Figure 2 shows a hypothetical but not unrealistic diagram of fossil abundance of a host tree taxon as a function of the age of these fossils. Southwood's correlation would assign equal weight to records at the right- and left-hand end of the graph. The intermediate periods of lack of abundance of this hypothetical tree taxon would tend to lead to the extinction of associated insect species. There are many dramatic peaks and valleys in the actual fossil record diagrams of the host tree taxa (Godwin, 1956). If one argues that these are not the result of fluctuations in abundance but rather of differential fossilization or discovery rates among the host

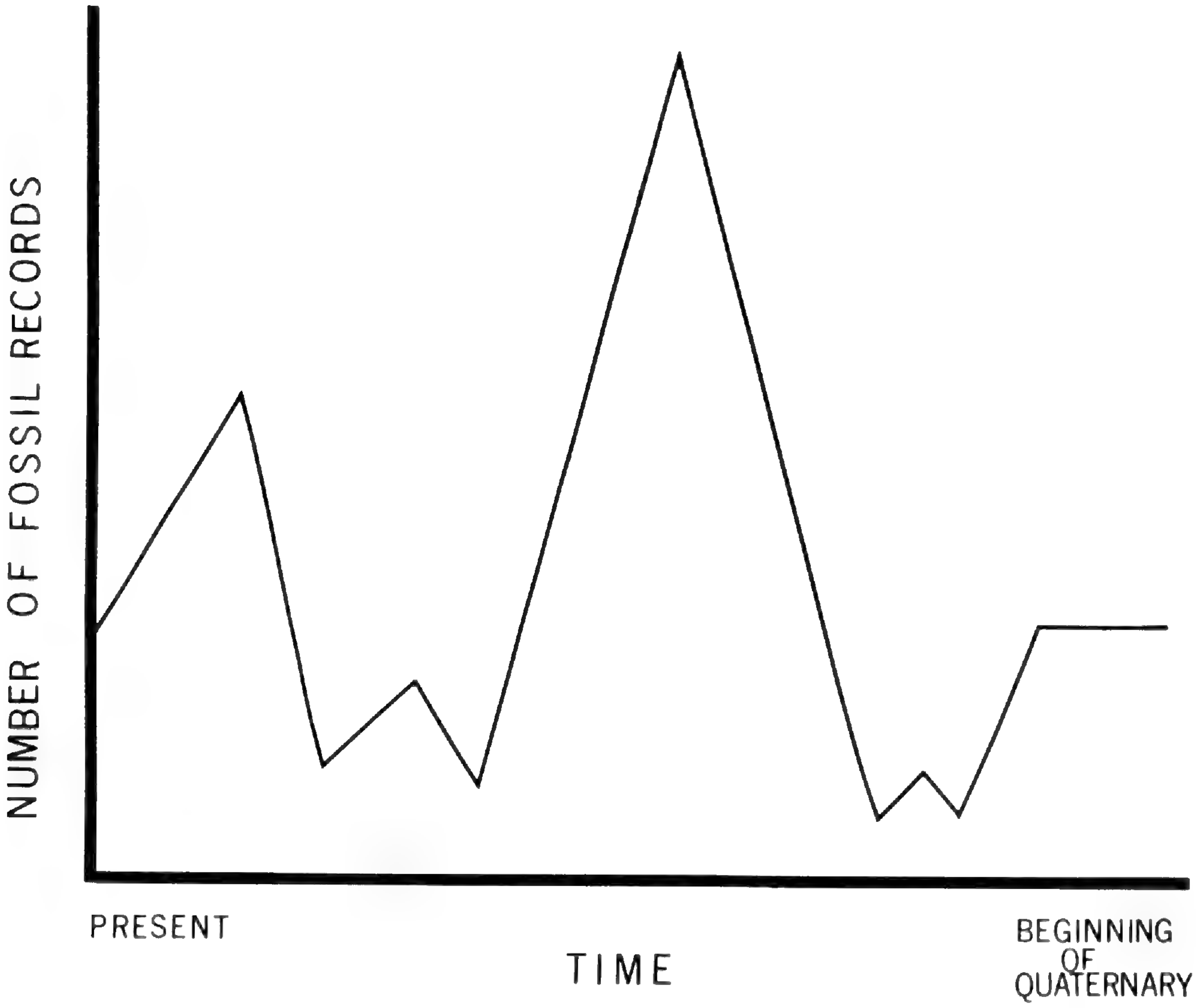

FIGURE 2. A graph of fossil discoveries as a function of age for a hypothetical host tree taxon. The cumulative number of Quaternary records for this taxon is the area under the curve. It is unreasonable to assume ancient and recent host tree abundance to contribute equally to extant insect species richness, because intervening periods of low abundance would lead to insect species extinction.

tree taxa, the entire basis of Southwood's correlation is vitiated; for his correlation to be causal, and not spurious, different numbers of fossil discoveries among the host taxa have to be an accurate history of relative abundance of once-living tree taxa. Carried to the extreme, the equal weighting of old and young fossil records is analogous to arguing that extinct plant species should have a number of extant associated insect species proportional to cumulative host plant abundance before extinction.

The above reasoning leads us to suspect that Southwood's correlation is fortuitous, highly unlikely but adventitious. The probability that this could happen is small but real (his $r = .85$, $p < .001$). It is likely that a contribution to this spurious correlation comes from the correlation between the number of fossil records of tree taxa and their present range. Figure 3 shows this relationship ($r = .53$, $p < .01$). I must stress that this does not compromise my earlier conclusion; causality of associated insect species richness derives from recent host plant range. Because the relative range of these trees has apparently not changed radically during the Quaternary in Britain the number of fossil records is correlated

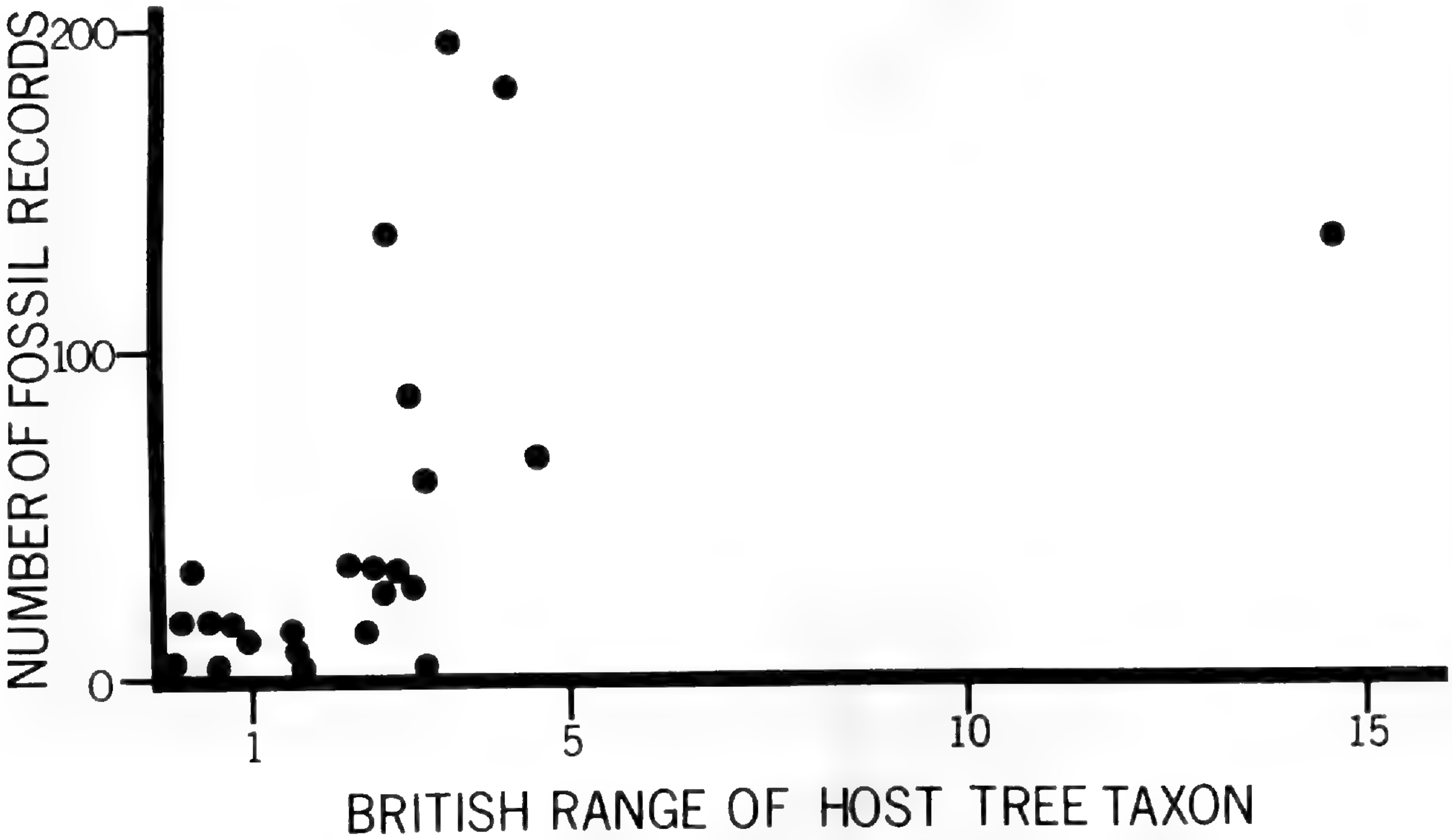

FIGURE 3. The number of fossil records of British tree taxa (Godwin, 1956) as a function of the present range of British tree taxa (Perring & Walters, 1962). The correlation is marginally significant ($r = .53$, $.01 > p > .001$). This correlation may contribute to the spurious correlation between the number of fossil records and the number of associated insect species of British trees (Southwood, 1961).

with range, hence number of fossil records is also correlated with the associated insect species richness. But the cumulative ancient host plant abundance does not cause the present day insect richness.

This system is different from the polynesian ant fauna (Wilson & Taylor, 1967) in that no secondary increase in species richness can be demonstrated after the species asymptote is first reached. The first equilibrium or saturation occurs within a few hundred years (perhaps much sooner?) for insects on British trees, and no discernable increase in richness follows. The conclusion of Ricklefs and Cox (1972), from Southwood's correlation, that "a history of abundance creates the opportunity for specialization" (leading to increased diversity) must then be withdrawn. Whittaker's (1969) idea that insect and bird communities are different, in that insect communities do not saturate whereas bird communities do, is incorrect as well. The British insect/tree information is the best data available, and the analyses in this paper indicate the saturation processes and rates to be strikingly similar for birds and insects.

This demonstration that insect species richness is a species-area phenomenon, independent of the effects of ancient host plant abundance and only a function of host range in ecological time, confirms MacArthur's (1965) suspicion of Southwood's correlation. MacArthur felt that the apparently non-asymptotic species accumulation suggested by the correlation could actually be asymptotic because "a single tree constitutes more than one habitat" (MacArthur, 1965: 518). This does not seem to be the reason however. The insect species asymptote is set by the geographic range of the host plant.

There are two possible mechanisms causing this species-area phenomenon, the number of distinct environments inhabited by the host species increases with range (Johnson & Raven 1973) and the effective population sizes of the insect species increase also with host range (Simberloff, 1973). Hence both increased habitat diversity and lowered insect species extinction rates may occur with greater host plant range. The only work to date that explores the role of decrease in extinction rate with increasing population size has been done with only very small islands, hence with only small populations (Simberloff, unpublished). Whether this extinction factor is significant over a range of "island sizes" as great as that covered by the ranges of the trees of Britain is questionable. It is probably more reasonable to consider each tree taxon as an archipelago than an island, because of the tremendous amount of discontinuity that must exist among trees, groves, and forests as well as among taxonomic subdivisions within the tree taxa. Given distributional discontinuities in host plant range, insect population sizes would not be as large as the entire range of the host, and insect species extinction rates would be expected to increase as a result. But on the other hand the discontinuities would cause isolation of subpopulations of the insect species, and sources of extinction that were contagious (disease, competition, heavy predation) would be prevented from spreading to effect the entire species.

The slope of the species-area regression line is equal to 1.1. This is the greatest slope ever reported for a species-area phenomenon. One explanation of this extreme value suggests itself—the data may be systematically biased to produce an overestimate of the slope. If the distribution of the more restricted host species were systematically overestimated and the distribution of the more wide ranging were systematically underestimated, the resultant slope would be an overestimate of the actual species-area slope. This type of bias is likely, given the nature of the data. Perring and Walters give only species presence or absence per 10 km^2; species with a single individual would be recognized as having a distribution not different from a species made up a solid forest 10 km^2. The other end of the host plant distributional range spectrum might also be biased by the data in Perring and Walters to overestimate the slope. Very broadly distributed trees perhaps are more dense where they do occur than are narrowly restricted species; this would give the species with greater range fewer dots per individual tree than narrowly restricted host taxa.

Finally it should be recognized that Southwood has proposed that both cumulative ancient abundance *and* present host plant distribution determine species richness of insects associated with trees; he has not proposed that the cumulative ancient abundance of host plants alone determines associated insect species number. He has pointed out that the relative abundance of Hawaiian tree species accounts for much of the variation in the species richness of their insect faunae (Southwood, 1960) and that a tree species will have a longer list of associated insect species in a country in which it is more abundant (Southwood, 1961). He however has never attempted to assess the relative magnitude of the contributions to associated insect species richness of the two factors. More important, he did not recognize that if the greatest contribution of this species richness were from cumulative ancient abundance, as his widely quoted correlation implies, the number of species in the system would not equilibrate and there would be no asymptote in species number through time. My analysis has established the system to be asymptotic by demonstrating the variation in insect species richness among tree taxa to be accounted for by a species-area phenomenon and by showing the contribution to the variation in insect species richness from cumulative ancient abundance of host tree taxa to be insignificant.

LITERATURE CITED

DEEVEY, E. S. 1949. Biography of the Pleistocene. Part I. Europe and North America. Bull. Geol. Soc. America 60: 1315.

DUNBAR, M. J. 1960. The evolution of stability in marine environments, natural selection at the level of the ecosystem. Amer. Naturalist 94: 129–136.

FISCHER, A. G. 1960. Latitudinal variation in organic diversity. Evolution 14: 65–80.

GODWIN, H. 1956. The History of the British Flora. Cambridge.

JANZEN, D. H. 1968. Host plants as islands in evolutionary and contemporary time. Amer. Naturalist 102: 592–595.

JOHNSON, M. P. & P. H. RAVEN. 1973. Species number and endemism: The Galapagos Archipelago revisited. Science 179: 893–895.

MACARTHUR, R. H. 1965. Patterns of species diversity. Biol. Rev. 40: 510–533.

——— & E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373–387.

PERRING, F. H. & S. M. WALTERS. 1962. Atlas of the British Flora. Nelson & Sons, Ltd., London.

PRESTON, F. W. 1960. Time and space and the variation of species. Ecology 41: 611–627.

RICKLEFS, R. E. & G. W. COX. 1972. Taxon cycles in the West Indian avifauna. Amer. Naturalist 106: 195–217.

SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Naturalist 102: 243–280.

SIMBERLOFF, D. S. 1972. Models in biogeography. *In* T. J. M. Schopf (editor), "Models in Paleobiology." Freeman, San Francisco.

———. 1973. Permo-Triassic extinction and the effects of area on biotic equilibrium. Jour. Geol. (in press).

SOUTHWOOD, T. R. E. 1960. The abundance of the Hawaiian trees and the number of their associated insect species. Proc. Hawaiian Entomol. Soc. 1959: 299–303.

———. 1961. The number of species of insects associated with various trees. Jour. Animal Ecol. 30: 1–8.

WALLACE, A. R. 1878. Tropical Nature and Other Essays. Macmillan, London & New York.

WHITTAKER, R. H. 1969. Evolution of diversity in plant communities. *In* G. M. Woodwell & H. H. Smith (editors), "Diversity & Stability in Ecological Systems." Brookhaven Symposium in Biology 22.

WILSON, E. O. & R. W. TAYLOR. 1967. An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. Evolution 21: 1–10.

WIMPENNY, R. W. 1941. Organic polarity. Quart. Rev. Biol. 16: 389–425.

ZENKEVITCH, L. A. 1961. Certain quantitative characteristics of the pelagic and bottom life of the ocean. Pp. 323–335, *in*: M. Sears (editor), "Oceanography." A.A.A.S., Washington, D.C.

ZWOLFER, H. & P. HARRIS. 1971. Host specificity determination of insects for biological control of weeds. Ann. Rev. Entomol. 16: 157–178.

PLANT AND BAT INTERACTIONS IN WEST AFRICA[1]

EDWARD S. AYENSU[2]

ABSTRACT

One of the most dramatic plant and animal relationships in the West African ecosystem is that which takes place between such frugivorus bats as *Epomophorus gambianus* and *Eidolon helvum* and the introduced neem tree, *Azadirachta indica.* While earlier studies on bat behavior were carried out by personal observation and ordinary photographic means, recently developed night vision equipment has allowed the author to make nocturnal observations previously not possible. New observations, using this equipment, have now been made on bats and their interaction with trees of the following species: *Mangifera indica, Anacardium occidentale, Ficus umbellata, Psidium guajava, Carica papaya, Kigelia africana, Spathodea campanulata, Parkia clappertoniana, Ceiba pentandra,* and *Adansonia digitata.* Observations are reported on the roosting characteristics of bats of the genus *Epomophorus.* The effect of feeding by bats on the fruits of various trees and the resulting dispersal of seeds on the coastal savannah-grassland, (Accra Plains) of Ghana, are discussed. The effect of introduced plants on the bat population and disadvantages to the West African ecosystem which are attributable to the plant and bat interactions are summarized.

Throughout the history of human societies bats have had an unchallenged notoriety in the realm of superstition and mythology. As the only known flying mammals, bats have for centuries been associated with various mysterious nocturnal activities. The Chinese are perhaps the only people who consider bats as objects of good luck and happiness. The Chinese word for bat is *fu* which signifies happiness (Allen, 1962). In many primitive societies bats have been associated with the dead, who are believed to possess souls that have the ability to fly freely at night when the living are asleep. In West Africa as well as in other regions of the world, several mythical stories about bats have been handed down from one generation to the next. Even today superstitious stories about bats are told to children. Bats are considered sinister, and their unexpected nightly visitations are believed to be signs of ill omen in some societies.

It is not unusual, therefore, that bats are looked upon from various perspectives in West Africa (Fig. 1). They are considered by many as animals with supernatural powers which should be avoided at all cost, especially at night because of their purported evil intentions. The West African Moslems, for example, place bats in the same category as pigs, because they are considered unclean; their peculiar roosting position is thought to make it easy for them to urinate on themselves. It should be noted that the Egyptians used sketches of bats as a symbol of a nursing mother, "for it is the only flying creature that has teeth and two nipples and nurtures its young with care" (Allen, 1962: 2). In southwest Ghana (Fig. 2) some of the people of Half Assini use the bat as the tribal totem. The clan therefore is forbidden to eat bats. Since bats often live near areas of

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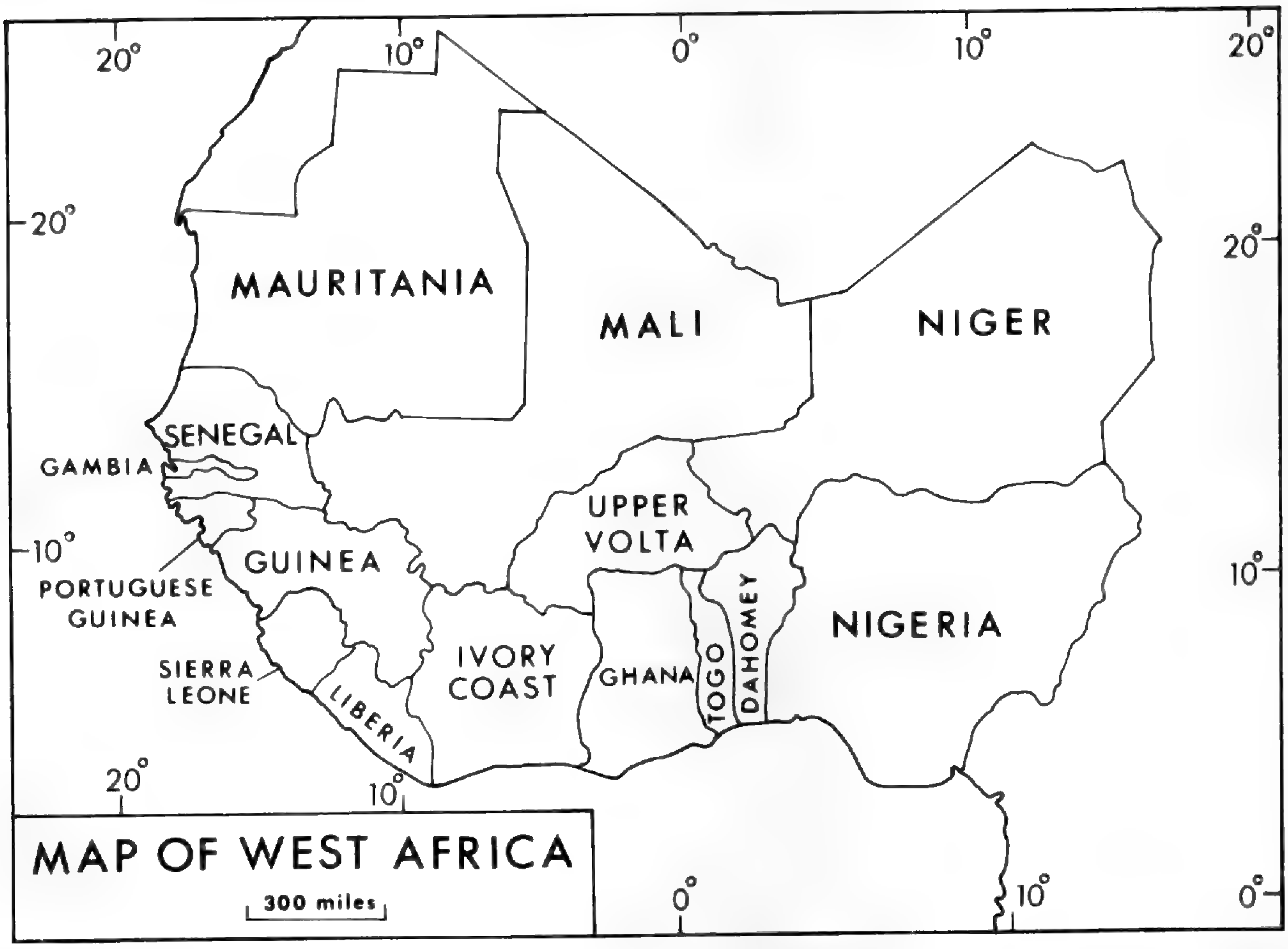

FIGURE 1. Political boundaries of West African countries where several genera of fruit bats occur.

human habitation, they are regarded as a public nuisance, because they roost on and in buildings and leave waste products on ceilings and in crevices. Bats are also considered destructive. In some areas fruits such as mangoes, guavas, and papayas are destroyed by bats during feeding. Besides their negative attributes these vegetarian bats (fruit bats) are a source of meat to some people in West Africa. In Ghana, for example, some of the Kwahus, the Ashantis, and the Brongs take bat meat as a significant source of protein in their diet apart from considering this meat a delicacy.

Several years ago I became acquainted with the fact that certain plants partly owed their continuous existence to the fact that their prinicipal pollinators were bats. Two plant biologists, Drs. Herbert G. Baker and B. J. Harris, were responsible for the renewed interest in the observation of the behavior of bats on plants in West Africa about the mid-1950's. Most of the studies of Baker and Harris were conducted in the vicinity of my high school (Achimota Secondary School) grounds. I was naturally familiar with the tree populations on which their studies were based, and I have since continued to observe the plant and bat interactions at the same site.

REVIEW OF PAST RESEARCH

The first description of bat visitation to flowers of the Baobab (*Adansonia digitata*) in Africa was by Jaeger (1943) in Senegal. But it was Baker and Harris who actually stimulated public awareness of pollination of flowers by bats in

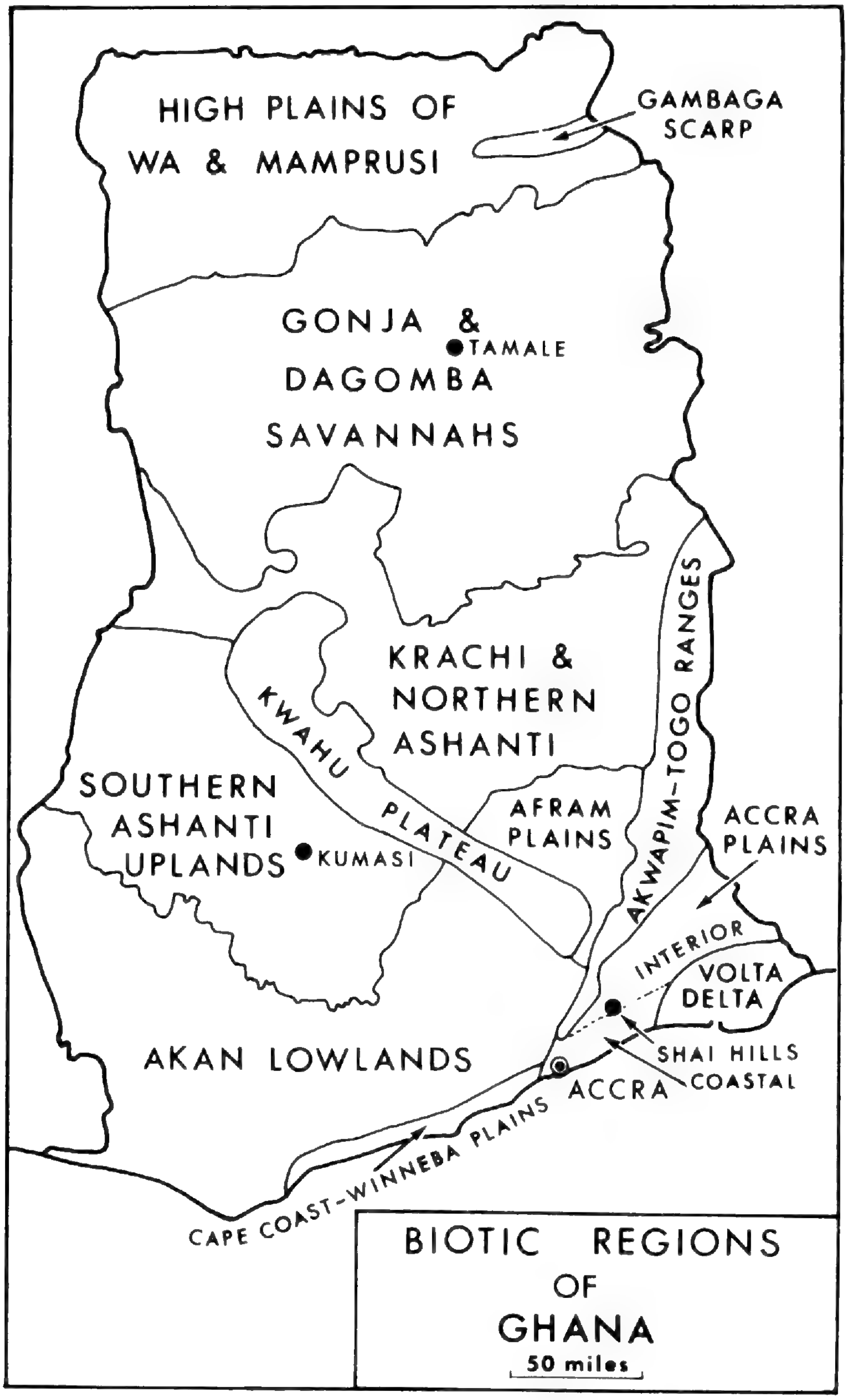

FIGURE 2. Biotic regions of Ghana.

this region. Their studies concerned four well known plants: *Parkia clappertoniana* (dawadawa), *Kigelia africana* (Sausage Tree), *Ceiba pentandra* (Silk-Cotton Tree or Kapok Tree), and *Adansonia digitata* (Baobab Tree).

Parkia clappertoniana is one of the characteristic tropical trees that loses its leaves during the dry season. In West Africa leaf fall in *Parkia* occurs from late October to early February. With the loss of leaves comes the production of red ball-like inflorescences, each containing about 2,000 flowers. The flowers are

FIGURE 3.—a. A colony of Gambian Fruit Bats, *Epomophorus gambianus* roosting in *Azadirachta indica*.—b. Large numbers of *Epomops franqueti* roosting on the east face of the Lilidze Mountain Range.

protandrous, *i.e.* anthers ripen before the stigmas. Baker and Harris (1957) and Harris and Baker (1959) reported that when the flowers first open they are deep red with ripe anthers (male condition), but by the following day the flowers become pinkish as the stigma (female condition) protrudes. With the opening of the flower by late afternoon and just before dusk, the fruit bats begin to visit the flowers. Baker and Harris noted that the first bats to visit the *Parkia* flowers were *Epomophorus gambianus.* These bats visit the trees for about twenty minutes, more or less restricting their visit to the upper part of the tree. The bats generally insert their snouts into the depressions on the upper part of the florescence where nectar collects. They often lap the nectar continuously for periods of fifteen to forty-five seconds at a time. The gentle flapping of their wings helps to maintain their balance, while the fur on the head, especially on the underside of the jaw, the throat and on the chest, collects pollen which is later transferred to the stigma of other flowers. Other bats that were observed to make subsequent visits included *Nanonycteris* and *Eidolon.*

Studies of the visitation to *Kigelia africana* (Sausage Tree) shows that when the flowers open, Dwarf Epaulet fruit bats (*Micropteropus pussilus*) often land at the lower lip of the flower and insert their heads in the floral cup to lap nectar (Harris & Baker, 1958). The flowers open at night and emit an unpleasant smell which presumably attracts the bats. It should be pointed out here that visitation is not confined to bats only. Hawk moths have been observed to be frequent visitors. Furthermore, the pollination of the Sausage Tree has been recorded in several areas where bats are not found. The flowers are constructed in such a way that the male (four stamens) and female (stigma) organs are somewhat confined to the basal part of the tubular flower. The pollinators become effective only when they reach the inner portion of the flower in search of nectar.

The Silk-Cotton Tree or the Kapok Tree (*Ceiba pentandra*) is one of the most interesting members of the Bombacaceae in West Africa. In their studies of bat pollination, Baker and Harris (1959) note that when the flowers of *Ceiba pentandra* open, visits to them are made by *Epomophorus gambianus* (Fig. 8a), *Nanonycteris veldkampi* (Fig. 8c), and *Eidolon helvum.* They observe, however, that of these three bat species, *Nanonycteris veldkampi* is somewhat the most important visitor, since these bats stay on the trees much longer in search of nectar.

Another bombacaceous species that was studied by Harris and Baker (1959) is *Adansonia digitata* (Baobab Tree). A plant indigenous to the savannahs of West Africa, the Baobab occurs in large numbers in the Shai Hills area of the Accra Plains (Fig. 5b). The trees are in bloom during March to May, and at night some fruit bats such as *Eidolon helvum* visit the trees for the soft floral parts and presumably feed on the stamens and nectar as well.

The observation of bat activities on the above plants by Baker and Harris using still cameras, synchronized to electronic flashguns, in the 1950's exerted a profound influence on the students and faculty of the Department of Botany, University of Ghana, in pollination studies. However, with the departure of these plant biologists, pollination observations declined, although on occasions there were bursts of intensive studies by other faculty members.

PERSONAL OBSERVATIONS

My initial observations of plant and bat interactions were confined to the same trees and localities where Baker and Harris conducted their research, using more or less similar photographic techniques.

FIGURE 4.—a. The development of coppice after heavy pruning of *Azadirachta indica.*—b. Many young plants of *Azadirachta indica* growing in the Accra Plains.

With the advent of night vision equipment, modified for extended viewing of bat activities on plants, I began, on a daily basis, an intensive study of several plants that are visited by the fruit bats. The first night vision equipment I used was the Starlight Scope (the snooper scope), originally designed for modern night warfare. I had the good fortune of learning the potentialities and limitations of this instrument at the U.S. Army Electronics Command, Night Vision Laboratory at Fort Belvoir, Virginia. This instrument operates on the principle of magnifying available low level ambient light by 8,000 times without the aid of any artificial light source. While this instrument provided a marked improvement over the still camera documentation of bat activities, its limitations became obvious when I made attempts to use it in dense forested areas where even star light or moon light was in short supply.

More recently the Astrophysics Research Corporation of California developed new night vision equipment known as "The Owl Eye." This instrument permits the investigator to obtain high resolution photography (still and movie as well as video tape recordings) at ambient light sources of less than one or two candle power. This portable instrument (about 12 lbs.) has the capability of amplifying available light at an average of 20,000 times. Furthermore, it provided four times the detail obtained from regular television screens. These new instruments have greatly aided our observation of plant and bat interactions without interrupting the natural behavior of bats during their nocturnal activities.

Mangifera indica (Mango Tree).—This species probably originated in the Indo-Burma region, and its wild members occur in the northeast hilly forests of India (Purseglove, 1968). Until the beginning of the 18th Century mangoes were unknown in West Africa. They were introduced to this region by the Portuguese and are now common throughout West Africa. The fruits are exceptionally popular not only in India but in every country where the trees have become naturalized. The mango trees have widely branched terminal panicles that are 10–60 cm long with 1,000–6,000 flowers borne on new growth. Quite often both male and hermaphrodite flowers occur in the same inflorescence. The sweet-scented flowers are in cymes, 5–8 cm in diameter. The sepals are usually five, free, and yellowish-green in color. The petals are also five, but they are twice as long as the calyx. The petals are generally creamy in color with 3–5 dark yellow ridges on the inner surface. The stamens are usually five, inserted on the outer margin of a five-lobed disc, and only one or sometimes two are fertile. The anthers turn from pink to purple at anthesis. The pistil is abortive in male flowers, but in the hermaphrodite flowers both stamens and pistils are fertile. The fruits are in fleshy cups, variable in size (2.5 cm long) and come in a variety of shapes. Some are rounded, ovoid-oblong, or laterally compressed. The color is variable, and includes mixtures of green, yellow, and red.

The flowers of mangoes usually begin to open during the early hours of the morning and continue to open throughout the morning, reaching a maximum around noon. The anthers begin to dehisce either during or shortly after flower opening (Makherje, 1953; Mallik, 1957). The stigmas are reported to be receptive from just before the bud opens until 72 hours after the flower has opened completely. During the day the principal visitors to mango inflorescences are insects that feed on the nectar secreted into the disc situated between the corolla and the androecium. Pollination of the flowers is effected by the insects during feeding. The interaction of mangoes and bats observed in West Africa occurs when the fruits begin to ripen. Bats seldom visit mango trees when the fruits are unripe. I do not know if the ripe fruits emit some compounds that serve as attractants (odors) to the bats, but I am inclined to think that at dusk the visual appearance of the fruits has little influence in attracting the bats from a distance until they are fairly close to the mango trees.

On several occasions during the fruiting seasons (October to November) I observed large numbers of *Epomophorus gambianus* (Fig. 8a) in the Botanic Garden of the University of Ghana, virtually covering every available space on the large mango trees planted on either side of one of the main walks. These bats are fairly large, about 15 cm long with a wing span of about 60 cm. As the bat approaches the fruit, its wings' flapping action is considerably reduced. When it lands on the branch holding the fruit, the bat immediately attacks the hanging fruit. The skin of the ripe mango is first torn off, and the bat begins to feed on the juicy pulp. The bat generally feeds on the mango until the free flow of the pulpy juices is reduced, whereupon it moves on to another ripe mango to continue feeding. Throughout my studies I did not observe a bat carrying a mango from the tree. However, the enthusiasm with which the bat attacks the fruits causes considerable damage to the mango tree. It is not uncommon to find that after a mango tree has been visited by a huge flock of bats, over one-third of all the fruits on the tree will find their way to the ground, mostly destroyed.

The interaction between bats and mango trees, in which the plant offers food to the bat and gets nothing but destruction in return, can hardly be described as a mutualistic interaction. Generally when a mango tree is in fruit, there are panicles of flowers on the same tree. It may seem reasonable to assume that during feeding the bats may inadvertantly pollinate some of the flowers. I think, however, the chances for effective pollination are greatly reducd. Firstly, since most of the panicles contain both male and hermaphrodite flowers, the chances are that the flowers left on the mango tree during the height of fruiting may be the male flowers. Secondly, under normal circumstances it is known that 65–85 per cent of the hermaphrodite flowers remain unpollinated during the day (8:00 a.m. to 12:00 noon), when the stigma is most receptive to pollen. By nightfall, when the bats are active, I would imagine that the receptivity of the stigma could be sharply reduced (*cf.* Mallik, 1957; Singh, 1962; and Free, 1970). The only interaction that can be described as mutually beneficial in this case is the pollination of the mango flowers by the insects during the daytime and the food they obtain in the form of secreted nectar.

The relationship between bats and mangoes as I observed them in West Africa can therefore be described as a one-sided interaction. A cooperative interaction could have been the case, if there were some evidence that the bats either effected pollination during their visitation to the mango trees or were able to carry the heavy fruits and seeds off to other areas to ensure propagation. It is very possible that some of the fruits that fall to the ground are carried away by rodents and larger mammals. So long as the bats do not destroy the seeds,

Figure 5.—a. A large supply of firewood obtained from the Neem Trees cleared in the Accra Plains.—b. *Adansonia digitata* growing on the Shai Hills overlooking a portion of the Accra Plains.

they may actually aid the dispersal by opening the outer covering and thus allowing the fleshy material to become more odoriferous and attractive to terrestrial dispersers.

Anacardium occidentale (Cashew Tree).—In the back yards of homes where the cashew nut trees grow I have observed, on occasions, the visitation of these trees by bats such as *Eidolon helvum, Epomophorus gambianus,* and *Micropteropus pusillus.* The Cashew plant is an evergreen tree of tropical American origin. It grows to the height of about 12 meters. The bats visit this plant when the fleshy, swollen, edible pedicel, known as the cashew apple, is ripe and juicy. The bats feed on the cashew apple in the same manner as they do on the mango fruits. The cashew fruit, which is attached to the apple, is often left in place and not eaten by the bats. Several fruits and "apples" are destroyed during feeding. In the New World, bats are probably the primary dispersal agent for cashews. They carry off part of the pedicel and drop the hard nut when they are eating on the fleshy part (Wilson, 1971).

Ficus umbellata (Fig Tree).—At the botanical garden of the University of Ghana stand two large fig trees that are regularly visited by *Eidolon helvum* when the plant is in fruit (Fig. 7a). The trees are about 40 feet in height and provide abundant shade. The fruits are about one inch in diameter, borne in clusters on the branches of the tree away from the leaves. The fruits are green with pale spots on them. *Eidolon helvum* feeds on the ripe fruits night after night until fruiting is completed. The fruits are often carried in the bats' mouths to other roosting sites. They also spit out the seeds in flight or swallow them only to be excreted later. The trees also serve as a suitable meeting place for both sexes, where mating takes place quite frequently. I observed feeding and mating on the same tree on five consecutive nights in November 1972.

Psidium guajava (Guava Tree).—This plant is a native of tropical America, where it occurs wild and is also cultivated. The date of its introduction to West Africa is uncertain, however, fruit bats have found the fruits to be an important food source. The fruit is a berry, often with persistant calyx lobes. The fruit comes in a variety of sizes, some are globose, ovoid, or pyriform. They are from 4 to 12 cm long. The exocarp is light green to bright yellow. When ripe, the mesocarp is fleshy and juicy, ranging from sweet to tart with a distinct musky flavor.

Apart from large plantations, guavas are found in the back yards of houses in towns and villages in West Africa. When the fruits are ripe, fruit bats such as *Eidolon helvum, Micropteropus pusillus, Nanonycteris veldkampi* (Fig. 8c), and *Epomophorus gambianus* (Fig. 8a), feed on them. When a guava tree is near the roof of a house that is covered with corrugated iron sheets, the bats create continuous commotion by plucking the guavas with their mouths and dropping them on the roof while feeding. Some of the bats, such as *Eidolon* and *Epomophorus,* are capable of carrying whole fruits when flying and are thus able to distribute the seeds in nearby areas.

Carica papaya (Papaya or pawpaw).—The country of origin of this plant is not known, since it has never been seen wild. However, some botanists think that it must have originated in an area from southern Mexico to Costa Rica. Today the papaya is found throughout the tropical and subtropical regions of the world. The fleshy ripe fruits are eaten by man, birds, and bats. The fruit is a berry which is from 10–30 cm long, sometimes even longer. On the average a fruit may weigh about one kilogram. Fruit bats such as *Eidolon helvum, Epo-*


a

mophorus gambianus, and *Nanonycteris veldkampi* first bite the exocarp off and then feed on the inner fleshy part of the fruit. If the bat eats deeply into the fruit, it is likely to come in touch with the many black or greyish seeds which are attached to the inner wall of ovary. Seeds of *Carica papaya* germinate quite easily in 2 to 3 weeks. The viability of the seeds is long, some lasting for 2 to 3 years.

Kigelia africana (Sausage Tree).—One of the well known trees of the savannah woodlands of West Africa, this tree grows as high as 50 feet and is easily recognized by the hanging racemes of large, dark red or purple flowers. Harris and Baker's (1959) observations of the visitation of the long faced fruit bat (*Micropteropus pusillus*) as it lands on the lower tip of the flower and thrusts its head inside the flower to lap nectar is confirmed. On leaving the flower the bat is dusted with pollen which could easily be deposited on the stigma of the same or the next flower and thus effect pollination.

Spathodea campanulata (African Tulip Tree).—This is a spectacular tree which has large bright-red flowers with the edges of the corrolla lobes colored yellow. The flowering heads appear in circular masses with packed buds. The buds on the outer portion of the head open together, surrounding the inner buds. For several years I have observed in the University of Ghana Botanic Garden several bat visits to the avenue of *Spathodea campanulata* in the same vicinity as *Mangifera indica*. At dusk, *Micropteropus pusillus* insert their heads in the cup-like flowers to lap large quantities of rather dilute nectar. On several occasions I observed that instead of the bats entering the corolla tube, they conveniently tear the basal part of the flower cup and thus obtain an easy flow of nectar which they lap rapidly.

Azadirachta indica (Neem Tree).—Without a doubt the most interesting interaction between plants and bats in West Africa is demonstrated by this plant, commonly known as the Neem or Margosa Tree, and the Epaulet bat, *Epomophorus gambianus* (Fig. 3a). The Neem was introduced to West Africa from India during the British colonial days some sixty years ago as an exotic forest tree, together with other plants such as *Cassia siamea*, *Cedrela mexicana*, *Gmelina arborea*, and *Tectona grandis* (Lane, 1958). The idea behind the introduction was to supplement the indigenous species with exotic species that might be useful in the economic activities of the West African countries. The British silviculturists carefully worked out various techniques for the establishment of the introduced species. These were based on the climatic conditions of the regions, soil types, and the conditions of the vegetation zones. Nurseries were established to raise the plants for transplanting. Generally after 9–12 months, the young plants were transplanted to selected areas within the countries. In Ghana, for example, the young trees were planted in both the high forest and the woodland-savannah zones. In the Accra-Achimota area a large acreage of Neem Trees

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FIGURE 6.—a. Leaves and fruits of *Azadirachta indica*.—b. Termite mound surrounding a Neem Tree in the Accra Plains.

Figure 7.—a. *Eidolon helvum* feeding on fruits of *Ficus umbellata*. Photograph taken through "The Owl Eye" night vision equipment.—b. A large flock of *Epomops franqueti* leaving their roost at dusk to feed.

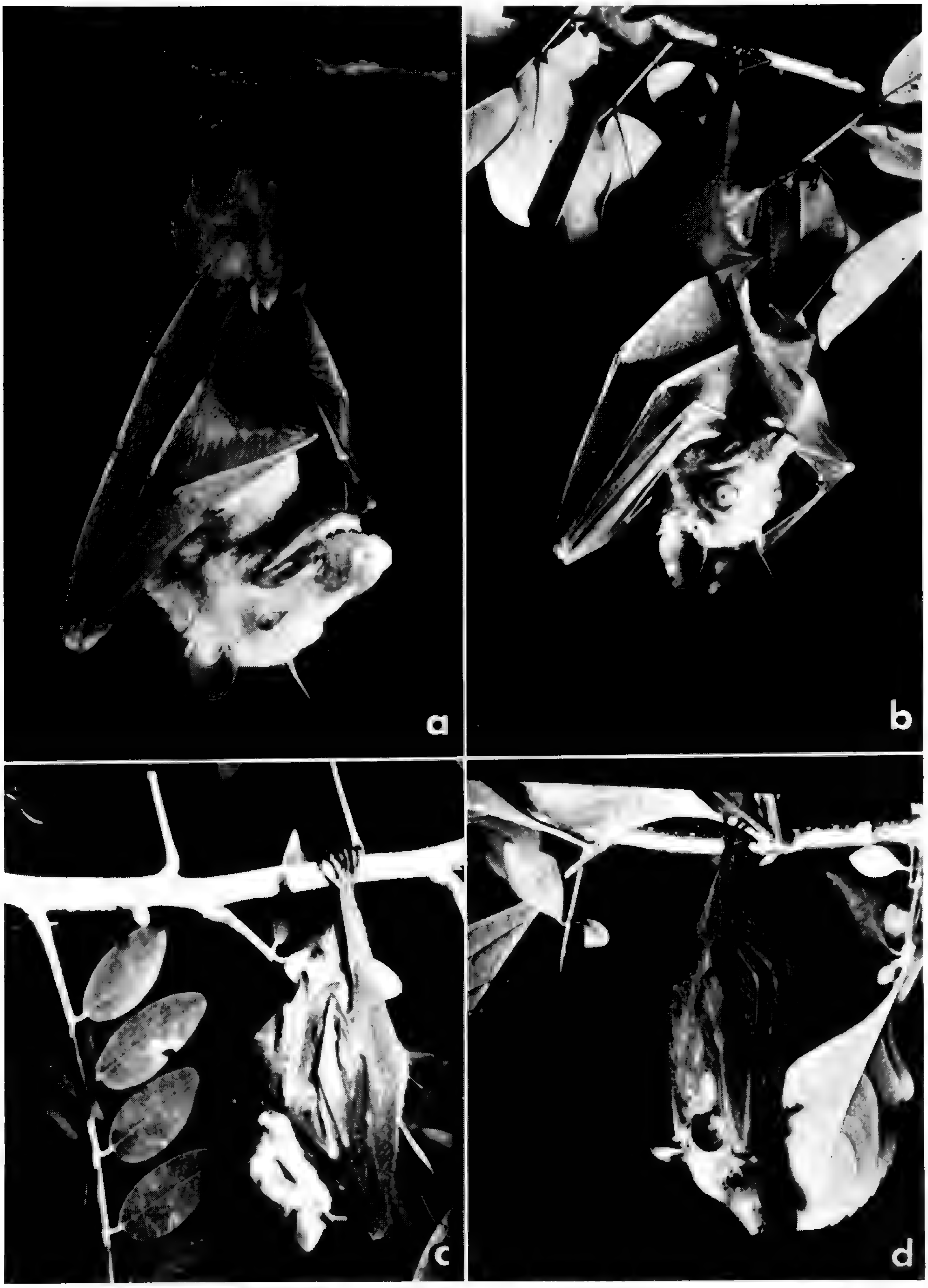

FIGURE 8. General morphology of West African bats.—**a**. *Epomophorus gambianus*.—b. *Epomops franqueti*.—c. *Nanonycteris torquata*.—d. *Megaloglossus woermanni*.

was planted. This plantation became a forest reserve after a number of years. The trees grow to 80 feet high and have a dense crown. The leaves are pinnate, glossy, and with slightly toothed margins (Fig. 6a). The flowers are white, small, and scented. After five years the plants begin to flower and fruit profusely. The majority of the seeds are viable and need no pregermination treatment. The ellipsoid fruits (Fig. 6a) are about 1.2 cm long with a fleshy outer coat and sweet juicy pulp.

Epomophorus gambianus are perhaps attracted to the Neem Tree more than any other West African fruit bat. *Eidolon helvum* also visit the Neem to feed on nectar and fruits. At dusk these bats leave their roosting places and converge in the forest reserve as well as the several acres of Neem Trees planted as "amenity" trees in towns and villages throughout the country. The bats feed for long periods; sometimes a flock will stay on a tree for at least one hour before flying away. During their departure, however, many of them carry neem fruits in their mouths and drop the seeds during flight before or after they have completed feeding on the fruit.

ROOSTING CHARACTERISTICS OF *EPOMOPHORUS*

It is generally observed that bats in West Africa have the tendency to roost on trees near villages and towns as well as the outskirts of these areas. One of the introduced tropical trees that has become a favorite roosting haven for the bats is the Neem. It seems that the bats use the Neem Tree for two separate functions: (a) during the day to roost in them and (b) at night to feed on the fruits. One interesting phenomenon is that although neem fruits are available on the tree on which the bats roost, they are not eaten. As soon as it is dusk the bats begin to fidget, especially when there are signs of encroachment of one's territory by another bat. The bats begin to hover around the tree for about 2 or 3 minutes, and then take off en masse to their selected feeding area. Intensification of the fidgeting behavior, which comes at sunset, provides the signal to which the bats respond in preparation for their flight to the feeding area. Similarly, the *Eidolon helvum* that roost in the palms in Ghana do not feed on the fruits of the same palm tree, but fly to another palm to feed. "This seems to be a general phenomenon. We noticed that the bats in Ghana did not roost in trees of *Ceiba* or *Parkia* that they pollinated or *Ficus umbellata* that they visited for fruit. But it is *most* interesting that they do not even eat neem fruit when this is available at their roost" (Dr. Herbart Baker, personal communication). A possible explanation of this peculiar behavior is that when the bats return to roost from feeding, they are most likely well fed, and therefore they need no more food during the roosting period. By dusk, however, the bats respond to their daily (circadian) biological clocks that "instruct" them to fly to their feeding grounds. This normal and natural behavior precludes the bats from remaining on the same tree to feed.

EFFECT OF FEEDING ON DISPERSAL OF SEEDS ON THE ACCRA PLAINS

In the mid-1950's the silviculturists in Ghana (then the Gold Coast) discussed the potentialities of planting *Azadirachta indica* on the Accra Plains to produce some form of an irrigated plantation. The Accra Plains forms a major part of the Ghana coastal savannah-grassland area which covers a sizable portion of the southeastern part of the country (Fig. 2). The northwestern part of the Plains is limited by the Akwapim escarpment to the northwestern side by the Volta River. The southern part of the Plains is bordered by the Atlantic Ocean, but more specifically the Gulf of Guinea. The rainfall is comparatively low, averaging 25–30 inches annually. Ecologically, the Accra Plains is most interesting in that it is quite different from the Guinea savannah or any other vegetation types of the coastal woodland-savannah composition, such as the Cape Coast-Winneba Plains. The Accra Plains is generally undulating for the most part, but on the northeasternmost part of the coastal section stand the prominent Shai Hills with a sizable population of *Adansonia digitata* (Baobab Trees). The vegetation of the rest of the Accra Plains is composed of grasses such as *Andropogon gayanus, Panicum maximum, Ctenium newtonii, Enteropogon macrostachyus, Microchloa kunthii, Setaria sphacelata,* and trees and shrubs such as *Sida cordifolia, Mimosa pigra, Waltheria indica, Elaeophorbia drupifera, Dichrostachys glomerata, Griffonia simplicifolia, Securinega virosa, Croton lobatus, Indigofera hirsuta,* and *Hoslundia oppositofolia.*

None of these trees, however, have become dominant on the Accra Plains. One of the spectacular features of the Plains is the many pronounced termite mounds (Fig. 6b), and these are usually colonized by shrubs and trees. With the introduction of *Azadirachta indica* planting near Achimota and the western edge of the Accra Plains, it was soon realized that the potential of this plant as plantation material was very high.

The original need for planting *Azadirachta* and *Cassia* was to have a wood supply available on a continuous basis (Fig. 5a). Firewood plantations were thus established on an eight-year-rotation system for *Azadirachta* and on a five-year-rotation system for *Cassia.* In the case of the Neem, the plots were arranged in such a way that when the first plantings were eight years old, the eighth-year plantings were one-year-old. At the end of the first eight years, the trees in plot one were cut almost to the ground, leaving about a foot of the tree stump on the ground. Since the Neem grows freely, such heavy pruning was considered necessary to reduce excessive coppice (Fig. 4a). After the initial plantings the project was not continued, but it soon became evident that sporadic seedlings of the Neem were appearing on the whole of the Accra Plains, with a high percentage of the seedlings appearing just outside the plantation and tapering towards the eastern part of the Plains up to the foot of the Shai Hills.

For several years I have wondered about the encroachment of Neem Trees on the Accra Plains. During my observations of the nocturnal flight patterns of bats from their roosts in and around the University of Ghana campus to the Achimota Forest Reserve (composed primarily of Neem Trees and Cassias) where they feed, it became obvious that from the forest reserve the bats flew across the Accra Plains and dropped neem seeds. It is now evident that substantial scattering of Neem Trees on the Accra Plains should be attributed to the dispersal of seeds by fruit bats. When the bats cross the Accra Plains, after

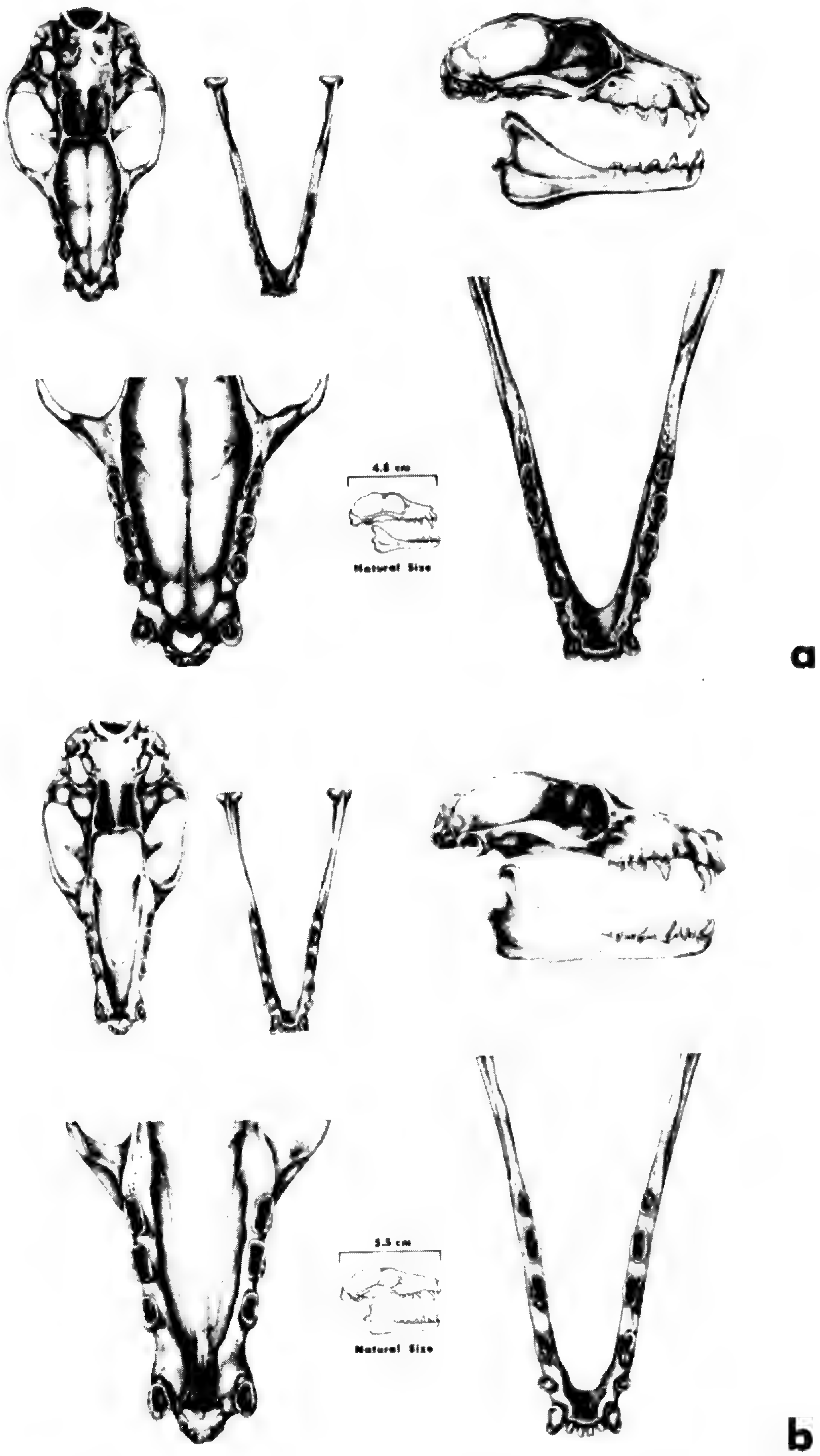

FIGURE 9. Cranial drawings of bats.—a. *Epomops franqueti* feeds principally on fruits. —b. *Epomophorus gambianus* feeds equally on fruits and nectar.

making several stops on the way, they reach the Shai Hills (Fig. 5b) and engage in another intensive feeding on the flowers of *Adansonia digitata* as well as on the fruits of *Azadirachta indica*. The bats return to their roosts in the early hours of the morning, quite often in small groups instead of the large flocks that leave the roost at dusk to feed.

EFFECT OF INTRODUCED PLANTS ON BATS

The question is often asked: On what kinds of food did the bats feed in West Africa before the introduction of exotic plants such as *Azadirachta indica, Mangifera indica, Carica papaya*, and *Psidium guajava*?

To answer this question meaningfully will require a brief review of the evolutionary trends in the feeding mechanisms of bats. In a recent paper Baker (1973: 147) pointed out that "the term 'co-evolution,' so freely used nowadays, may not be the most apt in describing the correlated development of flowering plants and flower-visiting animals over a period of time. The evolutionary pattern must be one of *demande et réponse* which, if prolonged, may produce a 'reciprocating' evolution, wherein changes in one kind of organism stimulate the selection of alterations in the morphology or behavior of another kind of organism, to be followed by a return influence in the first kind of organism. In such responsive or reciprocating evolution (at least insofar as it involves pollination relationships), it appears to be the animals that more often make the initial selective demands and the plants that show the most profound responses."

It is generally accepted that the earliest known bats (from middle Eocene to Oligocene) were insectivorous with dentitions similar to many recent members. The structural modifications of the teeth, the muzzle, and the tongue of fruit bats represent derived and specialized conditions. We can speculate that with the arrival of flowering plants, bats began to pursue insects that visited fruits and flowers. Consequently, some of the bats became interested in floral nectar and fruits, hence the process of structural modifications over an extended period of time. For further explanation see Baker (1973: 156).

In the absence of any definitive studies on this subject, we can only surmise that in West Africa, for example, bats were initially insectivorous (although this might have happened before the bats reached West Africa), but through time some became adapted to feeding on floral parts and nectar and some became totally frugivorous, thus feeding on fruits of all kinds. The dentition of West African fruit bats shows quite clearly that the sharp cusps of the molars have been suppressed and the crowns significantly broadened or in some cases clearly flattened. Such dental modifications are the result of constant crushing and mashing of fruits and nuts by bats to ensure smooth mastication of food. In a recent study Wilson (1973) presented a quantitative analysis of food preferences of several genera of bats. A comparison of skull shape and dentition on the one hand and the percentage of food preference on the other (Table 1) give some indication of correlation between muzzle morphology and feeding habit. Bats that feed principally on fruits, such as *Epomops franqueti* (Fig. 9a), *Eidolon helvum* (Fig. 10a), *Myonycteris torquata* (Fig. 11a), *Scotonycteris ophiodon*,

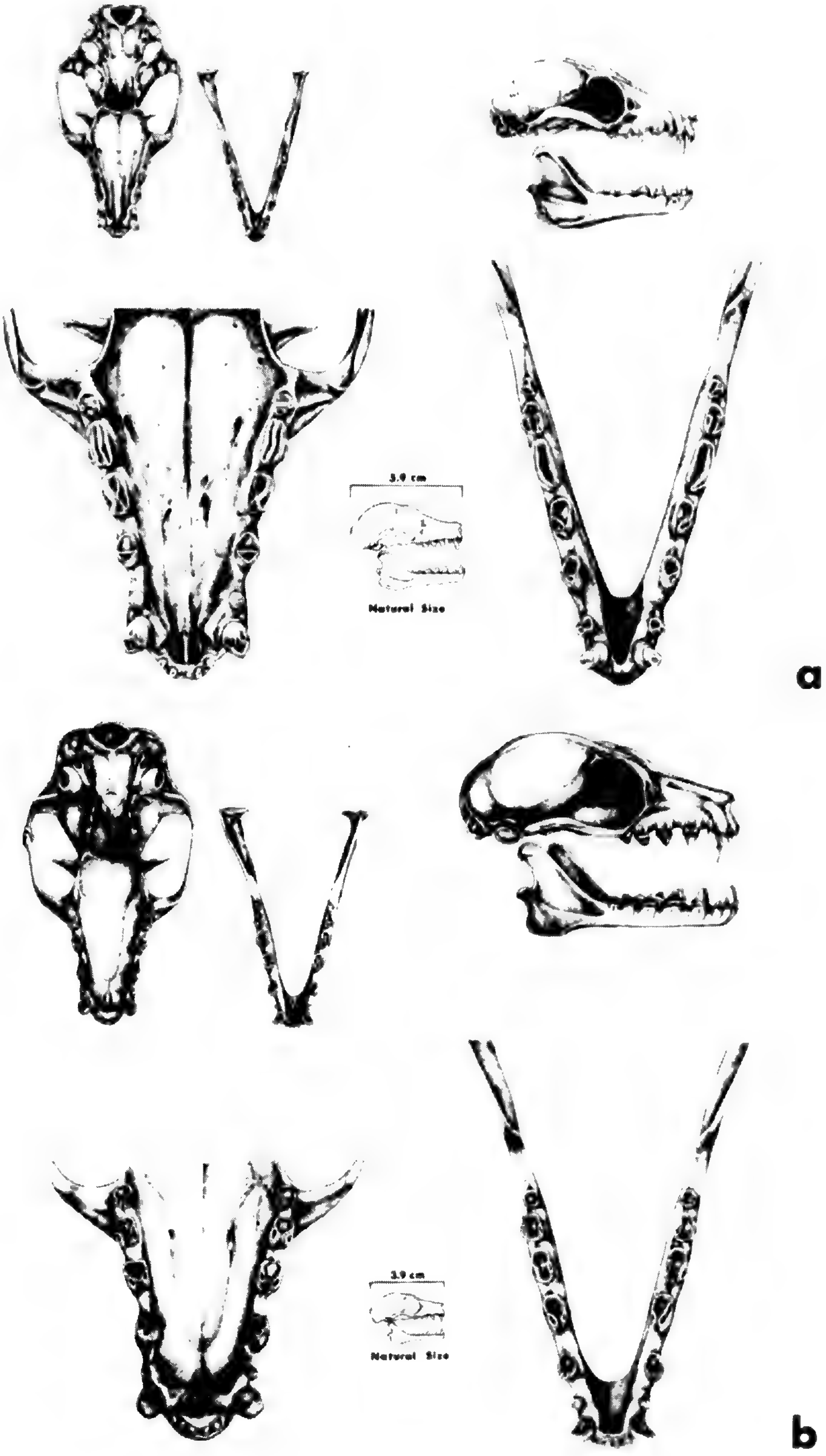

FIGURE 10. Cranial drawings of bats.—a. *Eidolon helvum* feeds principally on fruits.—b. *Rousettus aegyptiacus* feeds equally on fruits and nectar.

TABLE 1. Percentage food preference of West African fruit bat genera and New World *Desmodus*. Data from Wilson (1973: 16–18).

Genus	Fruit	Nectar	Foliage gleaning	Blood
Myonycteris	100	–	–	–
Eidolon	90	10	–	–
Epomops	90	10	–	–
Scotonycteris	90	10	–	–
Hypsignanthus	80	20	–	–
Micropteropus	80	20	–	–
Epomophorus	50	50	–	–
Rousettus	50	50	–	–
Megaloglossus	–	100	–	–
Nanonycteris	–	100	–	–
Desmodus	–	–	10	90

Hypsignanthus monstrosus (Fig. 11b), and *Micropteropus pusillus* (Fig. 12a), have short muzzles in comparison with predominantly nectar-feeders such as *Megaloglossus woermanni* (Figs. 8a, 13a). Bats that feed equally on fruits and nectar such as *Epomophorus gambianus* (Fig. 9b) and *Rousettus aegyptiacus* (Fig. 10b) have muzzle shapes that lie between the two extremes.

In contrast to the dentition of the frugivorous and nectarivorous bats is the highly modified dentition of the vampire bat (*Desmodus rotundus*) of the New World Tropics (Fig. 13b). The sharp but numerically reduced teeth are designed for slicing the surface of the skin to allow easy flow of blood which is its main diet.

It seems reasonable to assume that before the introduction of trees such as the neem, mango, cashew, papaya and guava, West African fruit bats lived on flowers and fruits native to this region, such as *Butyrospermum parkii* (Shea Butter Tree). This deciduous tree, which is common in the savannahs of West Africa, produces white flowers that are clustered at the ends of the shoots and one-seeded fruits about 4–5 cm long with fleshy pulp. The bats feed on this fleshy pulp, releasing the seeds that fall to the ground where, after the fleshy pulp decomposes, the seeds are gathered by man. After drying, the seeds are pressed locally for the fat (45–60 per cent) and protein (9 per cent). Most shea nuts are exported to a number of European countries where the extracted oil is used for production of soaps, candles, and cosmetics and as a constituent of chocolate fillings in creams (Purseglove, 1968).

We might assume that food was not so abundant as it is today and the population of fruit bats therefore not so dense as it is now. In the open skies of the Accra Plains it is not uncommon to observe large flocks of fruit bats covering a quarter of a square mile almost every evening. The availability of food in this savannah-woodland region has seemingly helped to increase the population of the fruit bats which in turn continues to ensure the progressive propagation of seeds such as those of the neem tree (Fig. 4b).

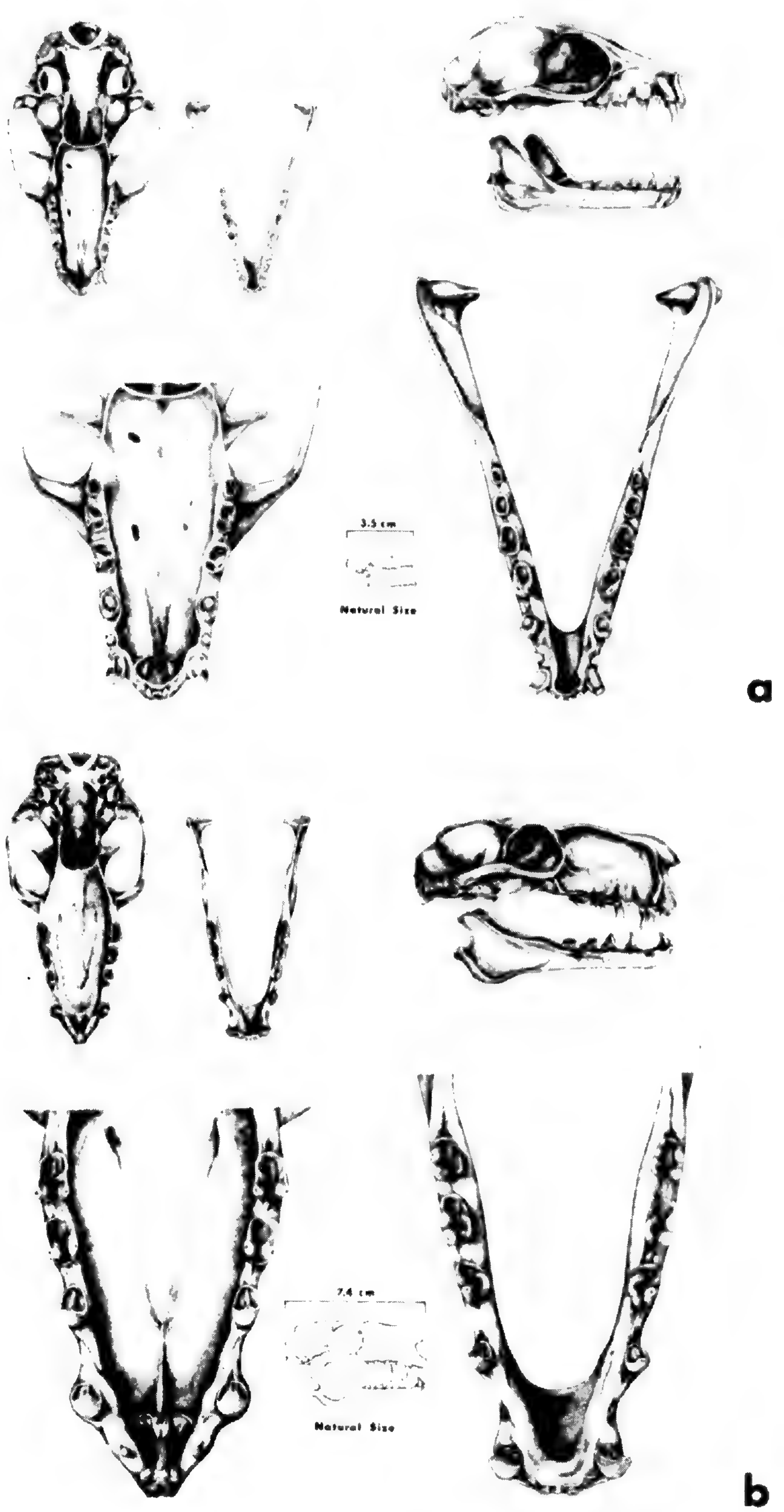

FIGURE 11. Cranial drawings of bats.—a. *Myonycteris torquata* feeds exclusively on fruits.—b. *Hypsignanthus monstrosus* feeds mostly on fruits.

ADVANTAGES AND DISADVANTAGES OF PLANT AND BAT RELATIONSHIPS

Some of my observations which deal with the interrelationship between plants and bats have been alluded to above. I will now attempt to classify the various interactions in a way that will demonstrate the effect of plants on bats and vice versa from both the positive and negative viewpoints.

Effect of bats on plants—positive aspects: Fruit bats have been instrumental in effecting the pollination of some flowering plants whose flowers open with maximum anthesis at dusk and at night while the stigma is also receptive to pollen during this period. Although moths, bees, beetles, and butterflies participate in various pollination activities, these bats have been found to be very important during their nightly visits to plants such as *Parkia clappertoniana.* Similarly, the fruit bats visit *Ceiba pentandra* in search of nectar and floral parts. In the process the conspicuous pollen grains of the flowers are carried on their fur from one flower to another on the same tree, thus promoting autogamy and geitonogamy, or they may carry pollen from one plant to another and effect allogamous pollination. Furthermore, the ten or so hours of pollinating activity by bees during the morning are supplemented at dusk by bats, for the flowers of the kapok tree remain open for some 20 hours. The flowers of *Kigelia africana* also open at night, and among its visitors are hawk moths and bats, such as *Nanonycteris veldkampi* and *Micropteropus pusillus.* Some members of *Kigelia* occur, although not naturally, in regions that have no fruit bats, and their flowers are pollinated either by moths or artificially by man. In areas where the bats occur in addition to the moths, there is ample evidence that the bats play an effective role in the pollination of *Kigelia africana.*

Another positive relationship between bats and plants is seed dispersal that takes place during feeding by frugivorous bats. The dispersal of neem fruits and seeds of the Accra Plains by *Epomophorus gambianus* and *Eidolon helvum* is a classic case of *mutualistic* existence between two organisms—the bat obtaining its sustenance from the ripe neem fruits while ensuring the continuous propagation of this plant.

Negative aspects: Tremendous enthusiasm is generally engendered by bats when they leave their roosts to go feeding. This often results in a considerable amount of fruit and floral destruction of the roost tree.

As I have indicated earlier in this paper, it is not uncommon to find over one-third of the ripe fruits underneath a mango tree after it has been visited by bats. I always ponder over the thought of what the economic consequences on the West African cocoa producing countries would be if the frugivorous bats were feeding on cocoa fruits. However, I do not know of any accounts of bat destruction of cocoa pods, except for Hicks' (1967) report that bats and birds caused the loss of 8.7% of cocoa pods in a New Guinea orchard.

Bats frequently select certain trees in which they roost over a period of several months, and their continuous roosting often results in sustained damage to these trees. For example, several royal palms in which bats roost in Ghana have been killed because of continuous urination by bats in the crowns of these trees. Henshaw (1970: 226), in discussing special environmental parameters for bats,

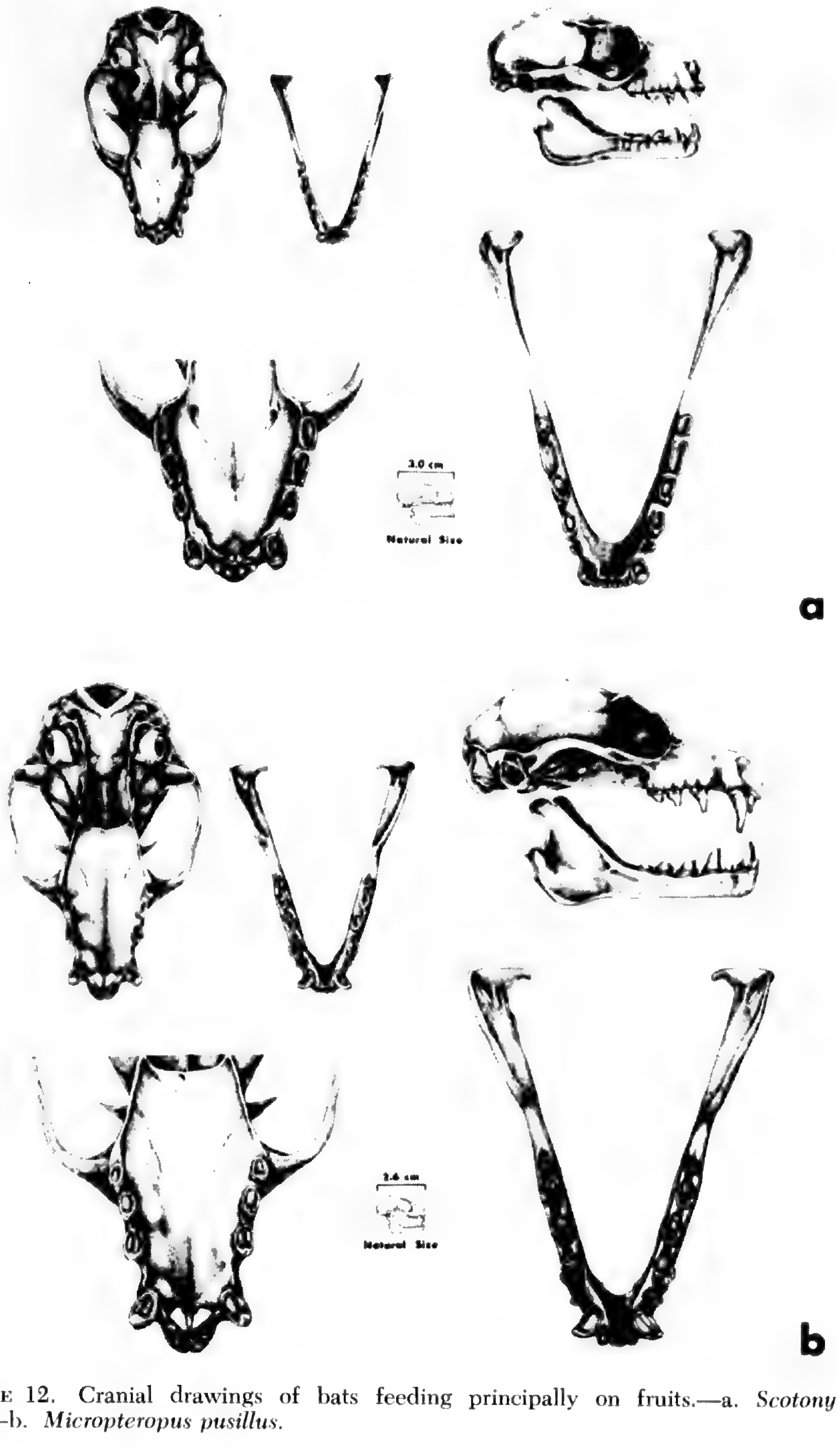

FIGURE 12. Cranial drawings of bats feeding principally on fruits.—a. *Scotonycteris ophiodon*—b. *Micropteropus pusillus*.

mentioned among other things that the microhabitats of some of the bats may provide "a number of potentially stressful environmental conditions for which animals may have produced physiological adaptations." He pointed out that the partial pressure of oxygen in caves which *Tadarida brasiliensis* inhabit may be lowered while the partial pressure of carbon dioxide may be raised, resulting in the concentration of ammonia. It seems reasonable to assume that the high concentration of ammonia, which results from bacterial decomposition of the urine in such an environment, frequently reaches toxic levels strong enough to kill the vegetation. I have also observed that the Neem Trees in which the bats roost often grow vegetatively for long priods when most other trees of the same species are flowering and fruiting. I presume that the high concentrations of toxic material may have some adverse effect on the flowering of the specific trees.

Effect of plants on bats—positive aspects: It is well known that the bats often live in dark caves and in crevices or roost on trees that have very dense foliage such as the neem and the palm trees. Even those bats that are tolerant of daylight tend to cluster in the darkest portion of a tree that has otherwise scanty foliage. The trees provide shelter for the bats most of the day as well as protection from their predators. By far the most important contribution of the plants to the existence of frugivorous bats is to provide them with food such as nectar, floral parts, fruits, and nuts. The availability of an abundant food supply will often improve the breeding conditions of the bats and thereby increase their numbers.

Adverse aspects: It is very possible that a continuous food supply may have an adverse effect in delineating the roosting areas of the bat population in some regions. For example, the trees in the area of the Lilidze Mountain Range (this mountain formation separates Ghana from Togo) on which some bats roost are so congested that large numbers of *Epomops* (Fig. 7b) have resorted to roosting on bare rock surfaces (Fig. 3b). These bats are therefore subjected to high solar radiation. However, they have devised a system of alternating roosting and flying throughout the day, while those bats roosting in trees at the same place continue to enjoy seemingly uninterrupted roosting during the same period. Notwithstanding, bats will often adapt to the optimum combination of food and roosting sites, no matter how adverse the roosting sites. If the rock roosts are sub-optimal, it will affect the reproductive effort of those bats using them, and natural selection will work to either better adapt them to the roosts, or lower their population size.

In evaluating the rapidly changing environment of the Accra Plains in response to the continuous dispersal of neem seeds by bats, I have considered the impact of *Azadirachta indica* on the native plant population and the rodent and other faunal organisms that inhabit this region. It seems clear to me that the progressive occupation of the Accra Plains by the Neem Trees—barring any major ecological catastrophe—may diminish or destroy the equilibrium between the native flora and fauna. Recent faunistic studies of parts of the eastern Accra Plains have shown that in areas where large populations of Neem Trees occur, native rodent populations have diminished considerably (Dr. Henry Setzer, per-

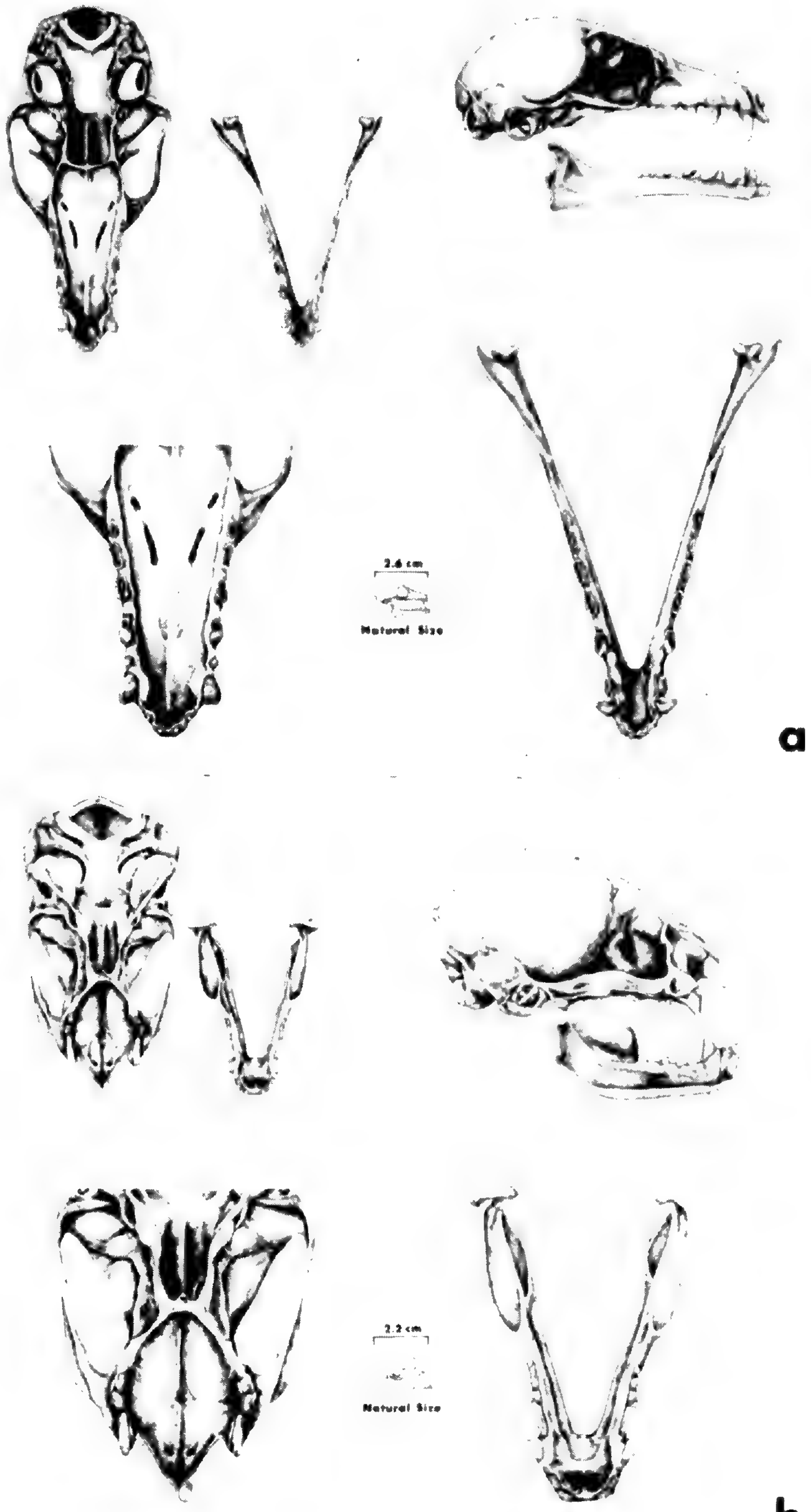

Figure 13. Cranial drawings of bats.—a. *Megaloglossus woermanni* feeds exclusively on nectar.—b. *Desmodus rotundus* feeds principally on blood.

sonal communication). It seems therefore that this phenomenal adaptation of the Neem Tree to the Accra Plains may eventually result in partial or total elimination of the native flora and fauna.

General Remarks

Plant and bat interaction on the Accra Plains offers an ideal situation for an intensive, quantitative study of this coastal-savannah ecosystem. The rate at which the original vegetation is being altered is certainly alarming, especially if we consider that it was only sixty years ago that *Azadirachta indica* was introduced to West Africa. The rapid adaptation of neem fruit as one of the major food sources of West African fruit bats is spectacular, and during the past five years population growth of fruit bats has seemed phenomenal.

It is of crucial importance that we understand the impact of the rapidly changing vegetation of the Accra Plains on the faunal elements native to this region. In addition, a systematic monitoring of what may eventually be an extreme population congestion of fruit bats in southeastern Ghana must be undertaken. Few quantitative data exist as to the influence West African fruit bats have on health and human welfare. It is therefore necessary that we amass all the information we can obtain from their activities in this region.

Literature Cited

Allen, G. M. 1962. Bats. New York.

Baker, H. G. 1973. Evolutionary relationships between flowering plants and animals in American and African Tropical forests. Pp. 145–159, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Washington.

——— & B. J. Harris. 1957. The pollination of *Parkia* by bats and its attendant evolutionary problems. Evolution 11: 449–460.

——— & ———. 1959. Bat pollination of the Silk-Cotton tree, *Ceiba pentandra* (L) Gaertn. (Sensu Lato), Ghana Jour. West African Sci. Assoc. 5: 1–9.

Free, J. B. 1970. Insect Pollination of Crops. London.

Harris, B. J. & H. G. Baker. 1958. Pollination in *Kigelia africana* Benth. Jour. West African Sci. Assoc. 4: 25–30.

——— & ———. 1959. Pollination of flowers by bats in Ghana. The Nigerian Field 14: 151–159.

Henshaw, R. E. 1970. Thermoregulation in bats. Pp. 188–232 *in* B. H. Slaughter & D. W. Walton (editors), "About Bats—A Chiropteran Biology Symposium." Dallas.

Hicks, P. G. 1967. Observations on the diseases and conditions of cocoa pods in Papua and New Guinea—Pod losses 1962–1965. Papua N. Guinea Agr. Jour. 19: 5–9.

Jaeger, P. 1945. Epanouissement et pollinisation de la fleur du Baobab. C. R. Acad. Sc. 220: 369.

Lane, D. A. 1958. The Planting of Exotic Forest Trees in Ghana. Accra.

Makherjee, S. K. 1953. The Mango—Its botany, cultivation, uses and future improvement, especially as observed in India. Econ. Bot. 7: 130–162.

Mallik, P. C. 1957. Morphology and biology of the Mango flower. Indian Jour. Hort. 14: 1–23.

Purseglove, J. W. 1968. Tropical Crops. Dicotyledons. Vols. I and II. London.

Sing, S. 1962. Studies on the morphology and viability of the pollen grains of mango (*Mangifera indica*) Hort. Adv. Saharanpur 5: 121–144.

Wilson, D. E. 1971. Food habits of *Micronycteris hirsuta* (Chiroptera: Phyllostomidae). Mammalia 35: 107–110.

———. 1973. Bat faunas: a trophic comparison. Syst. Zool. 22: 14–29.

COEVOLUTIONARY PATTERNS IN CENTRAL AMERICAN BIGNONIACEAE[1]

Alwyn H. Gentry[2]

The 600 species of the family Bignoniaceae are mostly large-flowered, wind-dispersed, woody, tropical plants. Division of the family into three major tribes —Tecomeae, Bignonieae, and Crescentieae—is based primarily on fruit morphology. In the neotropics the majority of the species are lianas, virtually all belonging to the Bignonieae. The neotropical Tecomeae and Crescentieae (excluding *Schlegelia*) are arborescent.

Bignoniaceae is one of the most important families of woody plants and the most important family of lianas in the Central American forest ecosystems I have studied. This is true no matter whether diversity, frequency of occurrence, or density is chosen as an index of importance (Gentry, 1972, and in preparation). The coevolutionary patterns found in such an important family are clearly very important to understanding the evolution of the adaptive strategies of the animals which interact with these plants. Several aspects of bignon biology indicate long histories of coevolution with various groups of animals. I will note separately some evolutionary diversifications in the family related to interactions with herbivores, frugivores, and pollinators.

Vegetative Interactions

Non-reproductive interactions of bignons with animals have led to the development of different kinds of defensive mechanisms against herbivores. Chemical defenses in the Bignoniaceae appear to be very effective. In the field the level of herbivore damage to bignons is generally low, and even when dried plants of this family are remarkably resistant to insects (Lewis, 1971). The wood of this family is much prized for construction because of its great durability. Beams of *Tabebuia* wood, known to have been exposed to the elements for 400 years, are still free of decay (Record & Hess, 1940). *Tabebuia guayacan* is one of the most durable woods of Panama with respect to terrestrial organisms, and the few sound trees remaining from the forest inundated over 50 years ago by Gatun Lake are mostly *T. guayacan* (Southwell & Bultman, 1971). Resistance to herbivores and wood-destroying insects is related to the presence of large quantities of lapachol in many species of the family (Sandermann & Dietrichs, 1957; Gentry, 1967). Other genera are presumably protected by such unidentified chemical

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[1] This paper is based on a section of a Ph.D. dissertation submitted to the graduate school of Washington University of St. Louis. I would like to thank John Dwyer, Walter Lewis, Alan Covich, Owen Sexton, Thomas Croat, Robert Colwell, Dan Janzen, Herbert Baker, and others for useful comments on earlier versions of the manuscript; Peter Raven's criticisms of the final version were especially helpful. Robert Dressler assisted greatly with identification of pollinators. Support for this study was provided by a National Science Foundation graduate fellowship, an NSF predoctoral dissertation improvement grant (GB-28496), and NSF grant GB-40103.

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Ann. Missouri Bot. Gard. 61: 728–759. 1974.

compounds as those associated with the strong onion or garlic odor of *Pachyptera* (*Pseudocalymma*) and the clove odor of *Tynnanthus*. *Tanaecium* is characterized by a strong almond (cyanide) odor and has been responsible for livestock poisoning in Colombia (Dugand, 1942). Yet despite the general effectiveness of their chemical defenses, bignons are host to such specialized herbivores as leaf-mining beetles of the buprestid genus *Hylaeogena*. Of the about 15 species of *Hylaeogena* known from Panama, all but one feed on various bignon lianas (Hespenheide, personal communication).

Most bignon species have a second system of protection from herbivores: ants. The presence of ants on a plant has been shown to be an effective deterrent to herbivores (Janzen, 1967*b*, 1972), and many bignons have specialized mechanisms for ant attraction. The large-pithed twigs of many Tecomeae are easily hollowed out and inhabited by ants. In Central America *Tabebuia palustris*, *T. rosea*, *Godmania aesculifolia*, and *Jacaranda copaia* often host ant colonies inside their twigs. The name *Tabebuia* was based upon the Tupian Indian words meaning "ant" and "wood" and refers to this phenomenon in some species of that genus. Most of the lianas of the Bignonieae attract ants through production of sugary secretions. In specialized species well defined secretory glands are concentrated at the nodes of young branchlets and sometimes at the petiole apex. Small ants regularly cluster around these glandular areas. Even in many species without discrete glands ants congregate at the nodes of young branches, where a sticky substance is produced. In general, species which attract ants through sugar-secreting glands (many Bignonieae) appear to be more advanced than those which attract them through easily-hollowed twigs (Tecomeae).

Coevolution and Seed Dispersal

Tribal division in the Bignoniaceae is largely based on fruit morphology (Fig. 1). The Tecomeae have capsules dehiscing perpendicular to the septum. The more advanced Bignonieae have capsules dehiscing parallel to the septum and (in the New World) a specialized replum. Seeds of both Tecomeae and Bignonieae are mostly winged and wind dispersed. Such minor tribes as Tourrettieae and Eccremocarpeae also have dehiscent capsules and winged seeds. The third important tribe, Crescentieae, has indehiscent fruits.

The differences in fruit morphology between the Crescentieae and the rest of the family are so pronounced that some authors (*e.g.* Lindley, 1847; Seemann, 1860) proposed their segregation as a separate family. However, an understanding of their seed dispersal ecology indicates that the Crescentieae are closely related to the Tecomeae (Fig. 2). The indehiscent fruit of Crescentieae is derived from the dehiscent fruit of Tecomeae through coevolution with frugivorous mammals.

Parmentiera is the non-missing link which provides the clues needed to understand the phylogeny of the Crescentieae. The fruits of *Parmentiera cereifera*, though fleshy and indehiscent, are superficially very similar to young fruits of *Tabebuia* and other *Tecomeae*. They have exactly the elongate-linear form of *Tabebuia* fruit; more significantly, the seeds are vestigially winged. The very

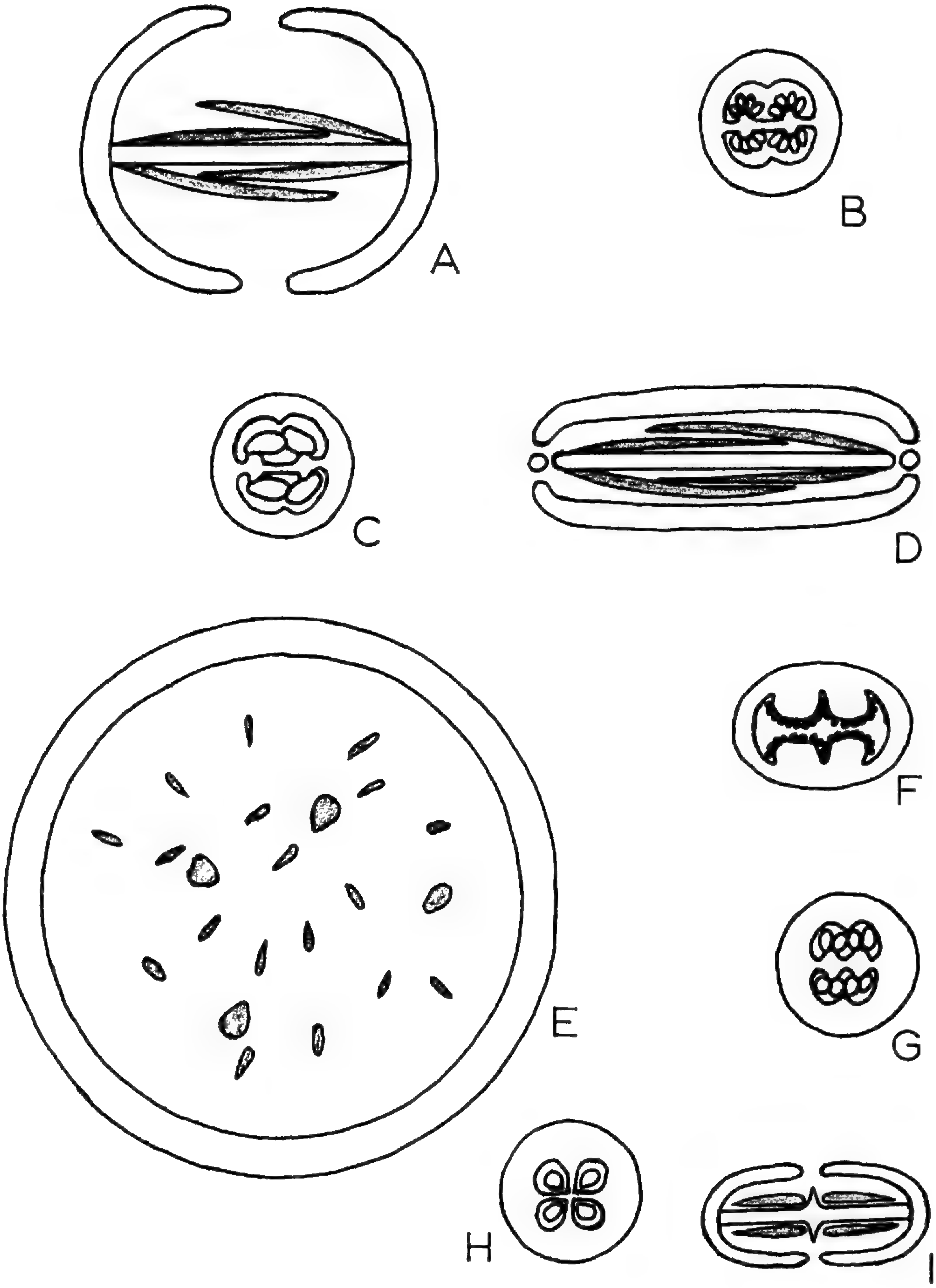


FIGURE 1. Fruit and ovary cross sections of Bignoniaceae (schematic).—A. Tecomeae fruit.—B. Tecomeae ovary.—C. Bignonieae ovary.—D. Bignonieae fruit.—E. Crescentieae fruit.—F–G. Crescentieae ovary.—H. Tourrettieae ovary.—I. Tourrettieae fruit.

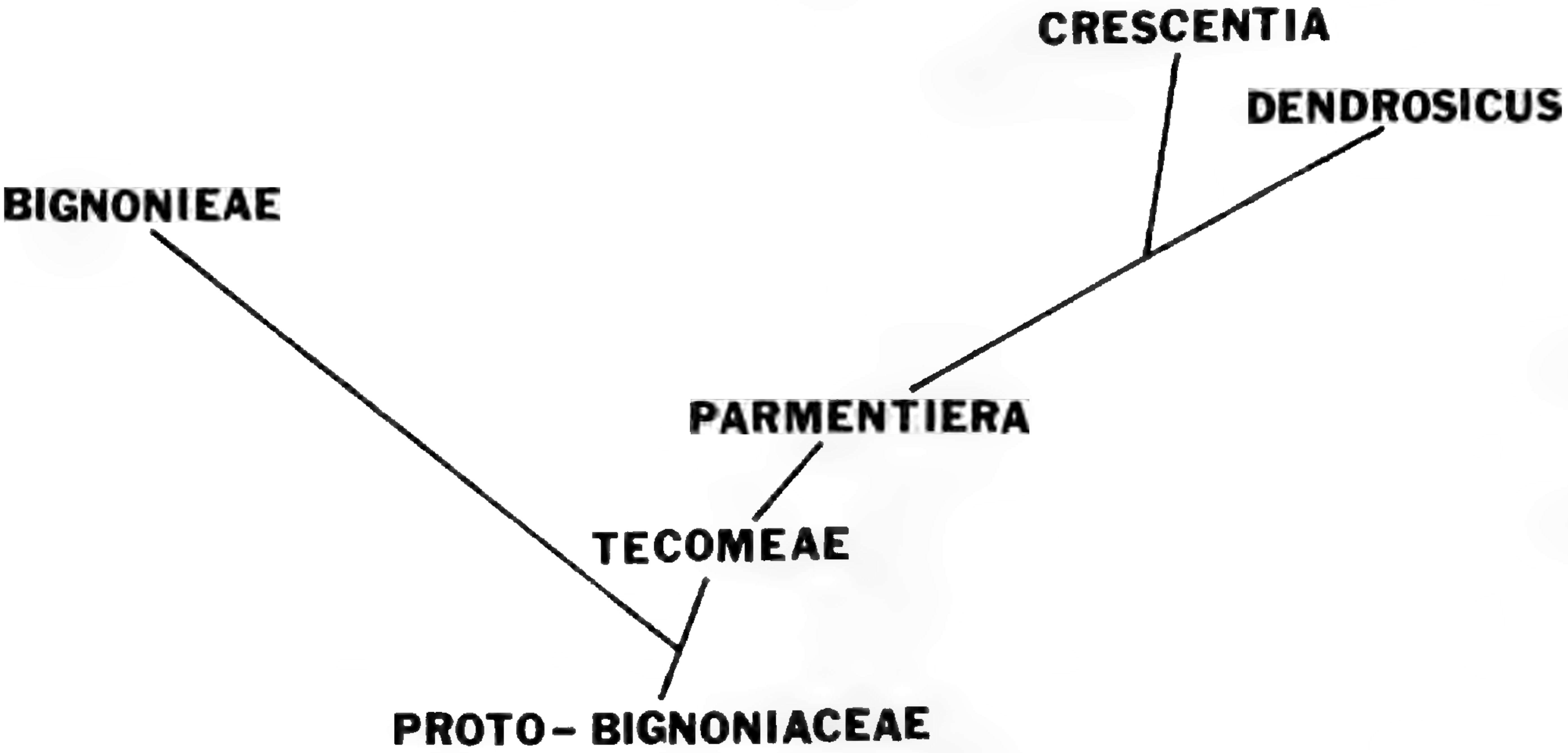


FIGURE 2. Phylogenetic relationships of the New World Crescentieae (*Parmentiera, Dendrosicus*, and *Crescentia*).

small seeds of *Parmentiera* are quite like immature *Tabebuia* seeds. It seems evident that *Parmentiera* has indeed been derived from a species of Tecomeae or proto-Tecomeae with dehiscent fruit and winged seeds.

It might be argued that it would be difficult for a species to make the critical change from dehiscent to indehiscent fruits, but an acceptable mechanism is readily available. It is well known that monkeys are extremely destructive of young fruits; I have seen most of the green fruits of a tree of *Tabebuia guayacan* stripped off by a troop of howler monkeys on Barro Colorado Island. Although some wind-dispersed plants cope with monkeys and other frugivorous mammals and birds by developing thickened or spiny fruits, an alternate evolutionary solution takes advantage of attraction of fleshy young fruits to frugivores and utilizes these animals as dispersal vectors. Neotenous maturation of seeds and selection for fleshier more edible fruits would lead from the dehiscent Tecomeae fruit to the fruit of *Parmentiera* with no evolutionarily awkward inadaptive gap. The succulent pulp of these fruits is avidly eaten by many mammals and they are often fed to cattle in Central America (Seemann, 1854; Standley, 1928). The central part of the *Parmentiera* fruit is fibrous-fleshy, and the seeds are situated between this core and the fleshy pericarp. Often the seeds and core remain uneaten. Probably the small mucilaginous seeds can also pass unharmed through a mammalian digestive system.

Other genera of New World Crescentieae have spherical or ellipsoid fruits with hard shells surrounding a soft pulp in which the seeds are embedded. The pulp is eaten by mammals and in some species by man. A series of additional evolutionary steps could easily produce these fruits from those of *Parmentiera*. Shortening and thickening of the fruit involves relatively little change and has taken place in such species of *Parmentiera* as *P. macrophylla* and *P. aculeata* (H.B.K.) Seem. I visualize *Dendrosicus* (*Enallagma*) and *Crescentia* as having developed the hard exocarps usually thought of as characteristic of the Crescentieae as a protection for the immature fleshy fruits. Most species of *Dendrosicus* are montane, and the fruit shell is relatively soft. However such protective exocarps would also make possible long distance dispersal of the whole fruit by water. Water dispersal would in turn select for harder, thicker exocarps; and the fruits of water-dispersed *Dendrosicus latifolius* have the hardest and thickest exocarps of the genus. This species is a well known plant occurring along sea coasts throughout the Caribbean region and also along the Pacific coast of Central America and Colombia. Its fruits are frequently found cast upon the beach, often with still viable seeds. The fruit of this speices is also eaten by mammals, notably pacas, and a balance appears to have been achieved whereby long distance dispersal of the fruit is by water and local dispersal of the seed by frugivores.

Crescentia must have evolved in a similar manner. I have seen apparently naturalized (possibly native?) trees of *Crescentia cujete* along the Caribbean coast of Costa Rica in an uninhabited swampy area south of Cauhita and have found occasional fruits with viable seeds cast up on the beach. *Crescentia amazonica* Ducke, which grows along the banks of the Amazon and Orinoco, is surely water-dispersed. Even the savannah species *C. alata* H.B.K. is readily dispersed during the rainy season in Guanacaste, Costa Rica, when the poorly drained savannahs often stand in water after a heavy rain. The fruits float, and naturally dispersed juvenile plants are relatively common along sandbars where the fruits are cast up by flood waters. The pulp of *Crescentia* is also eaten by mammals so that this genus, too, has a supplementary method of seed dispersal.

Schlegelia, a genus of lianas with mostly bird-dispersed fruits, has usually been included in the Crescentieae but is excluded from this discussion. It is only distantly related and may belong in the Scrophulariaceae.

An interesting sidelight to this story is the correlation between mammal dispersal and endemism in the Bignoniaceae. Wind-dispersed and water-dispersed species of *Tecomeae* and *Bignonieae* are typically wide-ranging, many occurring from Mexico to Argentina (Gentry, in preparation). The species of Crescentieae with chiefly water-dispersed fruits likewise have wide ranges—*Dendrosicus latifolius* from Mexico to Venezuela and Pacific Colombia and throughout the West Indies, *Crescentia amazonica* the length of the Amazon and Orinoco, *C. alata* from Mexico to Costa Rica, *C. cujete* throughout tropical America through the intervention of man, although its natural range is obscure. However the primarily mammal-dispersed species of Crescentieae tend to be highly endemic with very restricted ranges. Of the wind- and water-dispersed Panamanian–Costa Rican species of Bignoniaceae, 78% reach Venezuela (Gentry, Bignoniaceae in *Flora of Venezuela*, in preparation; several more species are to be expected) and 73% the Maya area (Seibert, 1940; Standley & Williams, 1974). None of the 7 exclusively animal-dispersed Costa Rican–Panamanian species reaches either the Maya area or Venezuela. Nor do any of the 9 animal-dispersed species of the Maya area reach Costa Rica or Panama. In fact none of the *ca.* 18 species of animal-dispersed Central American Crescentieae is found in more than two adjacent countries. Apparently animal dispersal in the Bignoniaceae occurs on a much more local basis than wind or water dispersal, and this has resulted in a prevalence of local species among animal-dispersed groups.

POLLINATION ECOLOGY

The most intricate interactions of bignons with animals are related to pollination ecology. Adaptations in floral morphology, flowering phenology, and seasonality are the raw materials which make possible the various pollination strategies of the different species of Bignoniaceae.

FLORAL MORPHOLOGY

The basic morphology of a bignon flower is represented in Figure 3A–D. The sepals are fused into a cupular calyx. The petals are fused into a tubular five-lobed corolla with two longitudinal folds in the floor of its tube. The part of the base of the tube which fits into the calyx is narrowed. The filaments of the four fertile stamens are fused to the corolla tube at the top of its narrower basal part. The filament bases and the corolla tube at the level of insertion are glandular pubescent. The filaments are bent so that the divaricate anthers are held together in two pairs in the roof of the tube with the thecae parallel to the axis of the flower. The two anterior stamens are longer, and their anthers are aligned in front of those of the posterior stamens. A fifth stamen is reduced to an inconspicuous posterior staminode. The ovary is within the calyx, and beneath it is a conspicuous nectar-producing disc. The style is held against the roof of the corolla tube with the stigma usually held just in front of the foremost pair of anthers.

The upper and lower lobes of the bilamellate stigma are spread apart in unpollinated flowers. When triggered by contact with a pollinator, the stigma lobes close. The reaction is not proof of pollination, since touching the inner surface of the stigma lobes with a stick or finger also causes them to close. However, lack of closing of the stigma lobes following the pollen-collecting activities of some kinds of flower visitors indicates that they have not come in contact with the stigma and can be used to rule them out as pollinators. The stigma is usually held in front of the anthers, with its receptive surface facing the mouth of the tube where pollen carried by an entering pollinator can readily lodge. When the pollinator backs out of the corolla covered with pollen from that flower, it only contacts the nonreceptive outer surface of the closed stigma.

There are at least eight major variations on this basic pattern among the 78 species of Bignoniaceae occurring naturally in Costa Rica and Panama (Table 1). Cultivated Old World species show two additional morphological types and are included here to point out similarities and differences with their New World counterparts. Observed pollinators of Bignoniaceae are closely correlated with the morphological types described above (Table 2). Each type of floral morphology has a distinctive pollinator spectrum with relatively little overlap.

ANEMOPAEGMA-TYPE.—Most species of bignon have a thin membranaceous corolla, an open mouth, and included anthers. I have termed this the *Anemopaegma*-type of morphology (Fig. 3A–F). There are many minor modifications

TABLE 1. Summary of floral morphology: comparison of morphology, phenology, and pollination syndrome by flower type and genus. ? = flowers not observed but presumed to belong here.

Flower Type	Pollination syndrome	Genus	Morphology	Associated phenology
Anemopaegma	Open-mouthed bee flowers	*Adenocalymma* *Anemopaegma* (See also Table 2)	Medium-sized, tubular-campanulate, thin-thick textured, throat ridges smaller, tube little compressed, color various	Type 2, 3, and 4
Tynnanthus	Bee/butterfly flowers	*Ar. florida* *Godmania* *Mussatia* *Tynnanthus*	Small, anthers subexserted, often bilabiate, mouth open, lobes reduced, color various	Type 3
Pithecoctenium	Xylocopid flowers	*Ceratophytum* *Distictella* *Paragonia* *Pithecoctenium*	Medium-sized, tubular-campanulate, thick textured, throat ridges reduced, tube not compressed, mouth open, color various	Type 3 (2)
Amphilophium	Pseudocleistogamous flowers	*Amphilophium*	Very bilabiate, mouth closed by fused lobes, very thick, without throat ridges, purple	Type 2
Cydista	Dorsally compressed bee flowers	*Phryganocydia* *Cydista* *Clytostoma* *Scobinaria* *Tabebuia* (pro parte)	Medium-sized, tubular-infundibuliform, usually thin, conspicuous throat ridges, tube compressed dorsally, often with nectar lines, color various	Mainly Type 5
Tanaecium	Hawkmoth flowers	*Tanaecium* *Tab. striata*?	Very long narrow corolla tube, thick texture, anthers subexserted, white	Type 3, but opens at night
Martinella	Hummingbird flowers	*Martinella* *Pyrostegia* *Tourrettia*?	Medium-sized, average texture, anthers sometimes exserted, tubular, deep violet/red orange	Type 3
Crescentia	New World bat flowers	*Crescentia* *Dendrosicus* *Parmentiera*	Medium-sized, thick textured, campanulate, cauliflorous, whitish	Type 1
Spathodea	Old World bird flowers	*Spathodea*	Large, thin, more or less exserted anthers, campanulate, orange red	Type 3
Kigelia	Old World bat flowers	*Haplophragma* *Kigelia*	Large, thick-textured, campanulate, exposed, dull-colored	Type 1

of floral morphology within this group. The flowers may be yellow, white, blue, or magenta, often with a contrastingly colored throat which may change in color after anthesis. The corolla may be variously pubescent, lepidote, or glabrous outside. Some species have relatively short, thin corollas. Others have longer, thicker-textured corollas. All are conspicuous, fragrant, and produce nectar.

TABLE 2. Panamanian species of Bignoniaceae with floral morphology, phenology, and observed visitors. Visitors include nonpollinators as interpreted in text for each type of floral morphology and phenology. Most observations of visitors published elsewhere or mentioned in text are omitted. Most species with recorded visitors were observed for from 1 to 5 hours; other species were mostly observed sporadically for from 15 minutes to an hour. Three species were not seen in the field at all and 4 others were not seen in flower as noted under the "visitors" column. Visitors include those observed in Costa Rica, Belize and South America; phenological observations were made in Panama and Ecuador.

	Morphological type	Phenological type	Observed visitors
BIGNONIEAE			
Adenocalymma apurense (H.B.K.) Sandw.	Anem.	3(2)	—
A. arthropetiolatum A. Gentry	Anem.	3	—
Amphilophium paniculatum (L.) H.B.K.	Amph.	2	see text
A. pannosum (DC.) Bur. & Schum.	Amph.	2	—
Anemopaegma chrysanthum Dugand	Anem.	2	—
A. chrysoleucum (H.B.K.) Sandw.	Anem.	2	—
A. orbiculatum (Jacq.) DC.	Anem.	5	Halictids, xylocopids, *Euglossa igniventris*
A. puberulum (Seib.) Miranda	Anem.	?	not seen
A. santa-ritense A. Gentry	Anem.	2	—
Arrabidaea candicans (L. Rich.) DC.	Anem.	3	Halictids, trigonids, skippers, small anthophorids
A. chica (H. & B.) Verl.	Anem.	3	see text
A. conjugata (Vell.) Mart.	Anem.	3	Anthophorids, skippers
A. corallina (Jacq.) Sandw.	Anem.	3	Anthophorids
A. mollissima (H.B.K.) Bur. & Schum.	Anem.	3	Anthophorids
A. florida DC.	Tynn.	3	see text
A. pubescens (L.) A. Gentry	Anem.	3	trigonids, *Eulaema*, skippers, *Xylocopa*
A. patellifera (Schlecht.) Sandw.	Anem.	3	see text
Callichlamys latifolia (L. Rich.) Schum.	Anem.	3?	halictids, trigonids, 6 euglossine spp.
Ceratophytum tetragonolobum (Jacq.) Spr. & Sandw.	Pith.	2	—
Clytostoma binatum (Thunb.) Sandw.	Cyd.	5	—
Cuspidaria floribunda (DC.) A. Gentry	Anem.	3?	not seen
Cydista aequinoctialis (L.) Miers	Cyd.	5	see text
C. diversifolia (H.B.K.) Miers	Cyd.	5	see Gentry (1974)
C. heterophylla Seib.	Cyd.	4(5)	—
Distictella magnoliifolia (H.B.K.) Sandw.	Pith.	2?	not seen in flower
Lundia corymbifera (Vahl) Sandw.	Anem.	3	small moth
L. puberula Pittier	Anem.	3?	—
Macfadyena uncata (Andr.) Spr. & Sandw.	Anem.	2	—
M. unguis-cati (L.) A. Gentry	Anem.	4	anthophorids?
Martinella obovata (H.B.K.) Bur. & Schum.	Mart.	3	see text
Mussatia hyacinthina (Standl.) Sandw.	Tynn.	3	skippers, trigonids

Table 2. (continued)

	Morphological type	Phenological type	Observed visitors
Onohualcoa verrucifera (Schlecht.) A. Gentry	Anem.	4	—
Pachyptera hymenaea (DC.) A. Gentry	Anem.	3(4)	—
P. kerere (Aubl.) Sandw.	Anem.	2	bluish *Euglossa* sp.
P. parvifolia A. Gentry	Anem.	?	not seen in flower
P. standleyi (Steyerm.) A. Gentry	Mart.	3?	—
Paragonia pyramidata (L. Rich.) Bur.	Anem./ Pith.	3	Wasps, halictids, *Trigona*, *Melipona*, anthophorids, xylocopids. (also see text).
Phryganocydia corymbosa (Vent.) Bur. ex Schum.	Cyd.	5	see text and Gentry (1974)
P. phellosperma (Hemsl.) Sandw.	Cyd.	2	—
Pithecoctenium echinatum (Jacq.) Baill.	Pith.	2(3)	see text
Pleonotoma variabilis (Jacq.) Miers	Anem.	2	—
Scobinaria japurensis (DC.) Sandw.	Cyd.	3	see text
Stizophyllum inaequilaterum Bur. & Schum.	Anem.	2	—
S. riparium (H.B.K.) Sandw.	Anem.	2	*Euglossa* aff. *igniventris*, *Trigona* sp.
Tanaecium jaroba Sw.	Tan.	?	—
T. nocturnum (Barb. Rodr.) Bur. & Schum.	Tan.	3?	—
Tynnanthus croatianus A. Gentry	Tynn.	3	see text
Xylophragma seemannianum (Kuntze) Sandw.	Anem.	3	*Euglossa* sp., *E. townsendi*, large anthophorid.
Tecomeae			
Godmania aesculifolia (H.B.K.) Standl.	Tynn. ?	3	halictids
Jacaranda copaia (Aubl.) D. Don	Anem.	3	—
J. caucana subsp. *sandwithiana* A. Gentry	Anem.	3	hummingbirds, medium-sized bees
Tabebuia chrysantha (Jacq.) Nichols.	Anem./ Cyd.	4	see Borrero (1972)
T. guayacan (Seem.) Hemsl.	Cyd./ Anem.	4	hummingbirds, medium-sized anthophorids
T. impetiginosa (Mart. ex DC.) Standl.	Anem.	4	anthophorids, trigonids, halictids, vespids, hummingbirds
T. ochracea subsp. *neochrysantha* (A. Gentry) A. Gentry	Anem./ Cyd.	4	several anthophorids, *Euglossa* sp., trigonids, halictids, wasps, hummingbirds.
T. palustris Hemsl.	Cyd./ Anem.	2	halictids
T. rosea (Bertol.) DC.	Anem./ Cyd.	3	*Xylocopa*, *Eulaema*, *Trigona*, small anthophorids
T. striata A. Gentry	prob. Tan.	?	not seen in flower.

TABLE 2. (continued)

	Morphological type	Phenological type	Observed visitors
CRESCENTIEAE			
Crescentia cujete L.	Cres.	1	see text
Dendrosicus isthmicus A. Gentry	Cres.	1(2)	—
D. kennedyi A. Gentry	Cres.	1(2)	not seen in flower
D. latifolius (Mill.) A. Gentry	Cres.	1(2)	unidentified bats (not seen to enter flower)
D. sessilifolia (Donn. Sm.) A. Gentry	Cres.	1	—
D. spathicalyx A. Gentry	Cres.	1	—
Parmentiera cereifera Seem.	Cres.	1	unidentified bats
P. macrophylla Standl.	Cres.	1	—
TOURRETTIEAE			
Tourrettia lappacea (L'Her.) Willd.	cf. Mart. ?	?	not seen

Anemopaegma-type flowers are pollinated mostly by large to medium-sized bees, mostly euglossines and anthophorids. These bees contact anthers and stigma chiefly with the top of the thorax. In addition to their pollinators, these flowers are often visited by nonpollinating nectar and pollen thieves. Small halictid and trigonid bees collect pollen but rarely, if ever, trigger the stigma. Butterflies are frequent visitors but remain entirely outside the tube and contact neither anthers nor stigma; often they only take moisture from the calyx or outside of the corolla. Hummingbirds are regular visitors but puncture the base of the corolla tube just above the calyx with their bills to steal nectar without making contact with anthers or stigma. Xylocopid bees are among the most frequent visitors to *Anemopaegma*-type flowers but are also nectar thieves. They slit the base of the corolla tube with their proboscis to obtain nectar and may slit open every flower of a plant.

The pollination spectrum for *Arrabidaea patellifera*, a typical *Anemopaegma*-type flower observed in Guanacaste, Costa Rica, (8 hours) and the Canal Zone (1 hour) included five species of anthophorids, four species of euglossines (*Eulaema polychroma*, *Euglossa variabilis*, *E. viridissima*, *Euplusia* sp.), all females, a single honey bee (*Apis mellifera*), and an unidentified medium-sized bee perhaps related to the xylocopids. Non-pollinating visitors included *Amazilia* hummingbirds, two species of large *Xylocopa*, small pollen-collecting bees (*Trigona* spp. (2) and a metallic green halictid), numerous butterflies (*Phoebis philea*, *P. sennae*, *Anteos clorinde*, a riodinid, and 6 species of skipper), three vespid wasps, a stratiomyid fly, and an unidentified fly. *Arrabidaea chica* may be chosen as a second example. The pollinator spectrum of a vine of *A. chica* observed in Ecuador (5 hours) was very similar and included euglossines (3 species of *Euglossa*), several genera of anthophorids, along with such non-pollinators as a large xylocopid (*Xylocopa*), small pollen-collecting bees (mostly halictids), vespid wasps, butterflies (hairstreaks and skippers), and hummingbirds (especially *Damophila julie*). (See Table 2 for pollinators of other *Anemopaegma*-type flowers.)

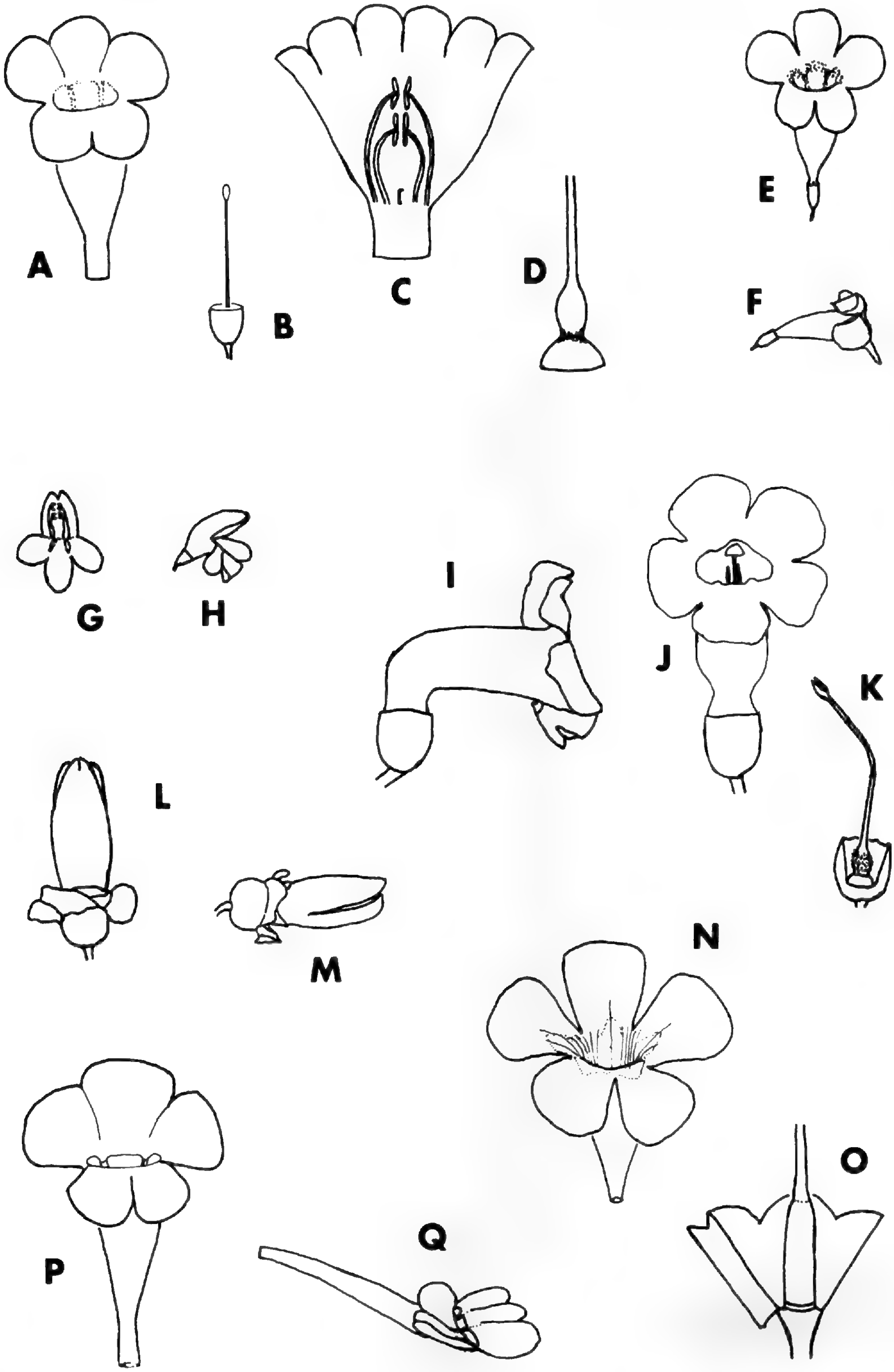
TYNNANTHUS-TYPE.—One of the modifications of the basic pattern is toward smaller, markedly bilabiate corollas with subexserted anthers. I have termed this the *Tynnanthus*-type of morphology (Fig. 3G–H). The corollas of these species are thin-textured and puberulous or lepidote outside. The corolla lobes tend to be almost valvate in bud. The flowers are very fragrant, variously colored, usually have open mouths, and produce nectar. *Tynnanthus, Arrabidaea florida*, and *Mussatia* have *Tynnanthus*-type flowers in Central America.

Tynnanthus-type flowers are visited by small bees (halictids and trigonids) and butterflies (mostly skippers). Both types of visitors make contact with the subexserted anthers and stigma and appear to be effective pollinators. The skippers partially enter the corolla tube and contact the anthers with the front edge of their wings or the top of their heads. The pollinator spectrum for a lavender-flowered plant of *Arrabidaea florida* growing on Pipeline Road, Canal Zone (ca. 5 hours of observations) includes two species of halictid, 2 species of trigonid, and 5 species of skippers. A white-flowered plant of the same species growing near the Summit Hills Golf Course, Canal Zone (ca. 6 hours of observation) had a pollinator spectrum including a halictid, 2 species of trigonid, 12 species of skipper, and a hairstreak (lycaenid). An *Epargyreus*-like skipper, several smaller skippers, and some unidentified small bees were observed to visit *Tynnanthus croatianus* near Madden Lake, Canal Zone, (½ hour of observation), and a skipper (*Pholisora* aff. *hayhurstii*) was observed on flowers of *Tynnanthus guatemalensis* in Belize (½ hour of observation). Skippers and small bees were observed at *Mussatia hyacinthina* in Venezuela (½ hour of observation).

PITHECOCTENIUM-TYPE.—An opposite modification of the basic floral morphology results in the *Pithecoctenium*-type flower (Fig. 3I–K). These species have thick, often gland-covered calyces and corollas greatly thickened, especially near the base. The tube is nearly closed near its base by a thickened, densely glandular pubescent ridge at the level of stamen insertion. The corolla tube is rather long, highly puberulous outside, has poorly developed throat ridges, and an open mouth. It is usually bent forward below the middle. The flower is white or cream-colored, has a conspicuous disc, and produces abundant nectar.

→

FIGURE 3. Floral Morphology.—A–F. *Anemopaegma*-type.—A–D. *Anemopaegma orbiculatum*.—A. Corolla in top view.—B. Calyx and pistil (stigma lobes closed).—C. Corolla split open to show stamen placement.—D. Ovary and disc.—E–F. *Arrabidaea candicans*.—E. Flower in top view.—F. Flower in side view.—G–H. *Tynnanthus*-type, *Tynnanthus croatianus*.—G. Flower in front view.—H. Flower in side view.—I–K. *Pithecoctenium*-type, *Pithecoctenium echinatum*.—I. Flower in side view.—J. Flower in bottom view.—K. Pistil, disc, and section through calyx.—L–M. *Amphilophium*-type, *Amphilophium paniculatum*.—L. Flower in top view.—M. Flower in side view.—N–Q. *Cydista* type.—N–O. *Cydista heterophylla*.—N. Corolla in top view.—O. Ovary and part of calyx.—P–Q. *Scobinaria japurensis*.—P. Corolla in top view.—Q. Corolla in side view.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Pithecoctenium, *Distictella*, and *Ceratophytum* are Central American genera with this corolla morphology.

Pithecoctenium-type flowers are pollinated by large anthophorids and xylocopids. I have observed an unidentified large bee (*Xylocopa*?) visiting flowers of *Pithecoctenium echinatum* in Belize (½ hour observation) and Paul Opler (personal communication) has recorded numerous visits by *Centris* sp. in Guanacaste, Costa Rica. Flowers with such thick calyces and corollas are apparently immune to nectar robbing by hummingbirds and xylocopids.

Paragonia is of special interest as being halfway between the *Anemopaegma*-type and the *Pithecoctenium*-type. In *Paragonia* the corolla is thicker than in the former but thinner than in the latter. I observed visits by two different species of *Xylocopa* to a *Paragonia pyramidata* vine blooming on the Osa Peninsula of Costa Rica (2 hours of observation, see also Table 2). One species penetrated the corolla base from outside in the usual manner, but the slightly smaller second species entered the flower as a legitimate pollinator. Presumably *Paragonia* represents an intermediate stage in the evolutionary conversion of xylocopid visitors from robbers to pollinators. Additional thickening of the calyx and corolla as in the *Pithecoctenium*-type flower entirely eliminates nectar thieves.

AMPHILOPHIUM-TYPE.—Further modification of the *Pithecoctenium*-type morphology would give rise to the *Amphilophium*-type flower (Fig. 3L–M). In these species the trend toward greater protection of the nectar is carried to such an extreme that the corolla never opens spontaneously and even the pollen is protected inside the flower. The corolla is tubular, extremely thick, and strongly bilabiate with the very thick upper lip formed by fusion of the two upper lobes and the slightly thinner lower lip formed by fusion of the three lower lobes. These two lips remain loosely fused at anthesis unless physically forced apart. In the herbarium the two lips are forced apart by lateral compression of the flower during pressing so that this unique adaptation has gone unremarked. There is a very pronounced ridge at the level of stamen insertion, and the base of the corolla tube below this is convoluted and apparently secretory. The disc is conspicuous and abundant nectar is produced. The calyx is also highly modified and consists of a very thick inner sleeve tightly appressed to the base of the corolla and a thin, loose, uneven, outer rim which is reflexed away from the corolla. The inner surface of the outer calyx and outer surface of the inner calyx are secretory and sticky. Such South American genera as *Glaziovia* have floral morphologies similar to *Amphilophium*.

The *Amphilophium*-type flower is a logical extension of the trend toward greater protection seen in *Paragonia* and *Pithecoctenium*. It has the thickest corolla of all the Central American Bignoniaceae, and its secretory double calyx attracts ants and wasps which presumably give further protection to the flower. The calyx of *A. pannosum* is so viscid that it can protect the flower by trapping small insects. *Amphilophium* pollinators are by necessity large and robust bees including *Megachile* sp., two species of large anthophorid (*Centris*?), and probably xylocopids which physically force the two lips of the unopened corolla apart in order to enter the flower.

Cydista-type.—A different modification on the basic *Anemopaegma*-type morphology results in the *Cydista*-type flower (Fig. 3N–Q). In this group the corolla tube is long, dorso-ventrally compressed, relatively funnel-shaped (rather than bell-shaped above a tubular base), and has a wide but narrow mouth. Many species have conspicuous nectar guide lines, these being usually a number of finely pencilled more or less parallel magenta or brick red longitudinal lines converging from the lobes onto the two longitudinal folds in the floor of the corolla tube. Most of these species have the tube glabrous or inconspicuously puberulous outside and relatively thin corollas. Most of the genera included here (*Cydista, Clytostoma, Phryganocydia*) are unusual in lacking a nectariferous disc. The pattern intergrades with the *Anemopaegma*-type from which it is rather arbitrarily separated; for example several species of *Tabebuia* are intermediate between these two morphological types.

The *Cydista*-type flower is, like the *Anemopaegma*-type, pollinated mostly by euglossine bees. However, visitors to most of these species, especially those lacking a nectariferous disc, are very infrequent (see phenology below). I have observed only *Trigona* spp. to visit *Cydista diversifolia*, and these small bees collected pollen without triggering the stigma (5½ hours of observation in Guanacaste, Costa Rica; ½ hour in the Canal Zone). I have seen *Euglossa* spp. (as well as *Trigona* sp.) visit *Phryganocydia corymbosa* in the Canal Zone (ca. 5 hours of observation) and near El Real, Darién Province (ca. 6 hours of observation). I have observed only a single *Exarete*(?) as a potential pollinator of *Cydista aequinoctialis* in ca. 15 hours of observation in the Canal Zone, although small halictids and trigonids visit the flowers. I have observed no visitors to *Cydista heterophylla* (1 hour of observation, mostly in the Canal Zone) and *Clytostoma binatum* (sporadic observation).

Scobinaria is of special interest in being intermediate in several respects between the *Cydista*-type flower and other groups. It is the only genus included here with a conspicuously pubescent corolla tube and the only one which vegetatively has interpetiolar glandular fields. Its corolla is somewhat thicker in texture and more strongly compressed than corollas of other species included here. It is likely that the dorsally compressed corolla of *Scobinaria* (which has a nectariferous disc) was evolved independently from the other *Cydista*-type flowers. Access to the *Scobinaria* flower is more limited than to other *Cydista*-type flowers. In Belize, I observed small non-pollinating halictids and trigonids unsuccessfully attempt to enter the *Scobinaria* corolla, while several larger *Euglossa* spp. forced their way into the corolla tube.

Tanaecium-type.—The *Tanaecium*-type is one of the most spectacular modifications of bignon floral morphology (Fig. 4A–B). These flowers have a relatively thick and rigid corolla which is white and has a greatly elongated narrow tube. The anthers are subexserted, and the thecae are long and flexuous. They have a conspicuous disc, abundant nectar, a heavy sweet aroma, and open in the evening. This corolla form has evolved separately in the Bigononieae (*Tanaecium*) and the Tecomeae (South American *Tabebuia* spp. and probably *T. striata*).

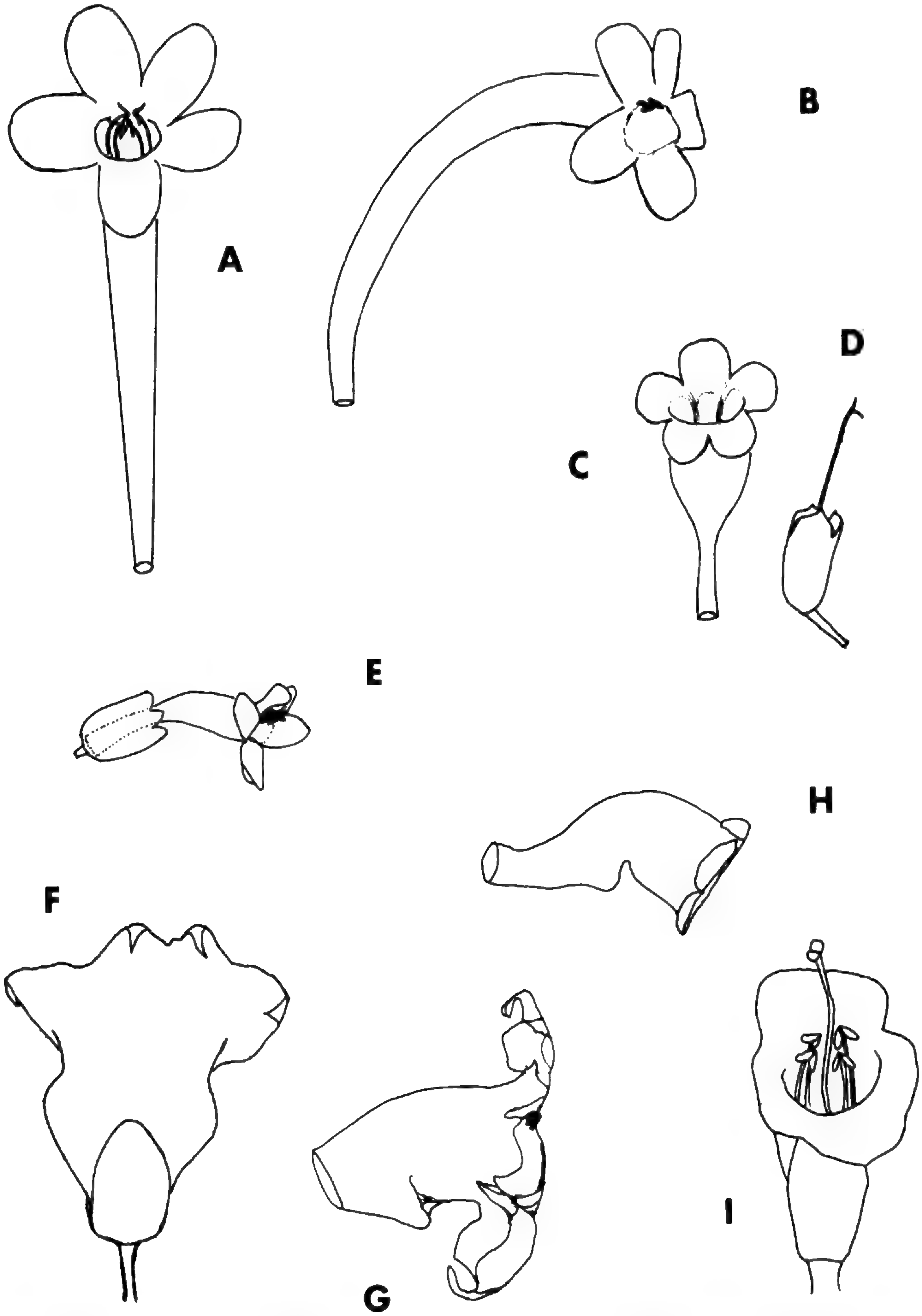


FIGURE 4. Floral Morphology (continued).—A–B. *Tanaecium*-type, *Tanaecium nocturnum*.—A. Corolla in bottom view.—B. Corolla in side view.—C–D. *Martinella*-type.—C–D. *Martinella obovata*.—C. Corolla in top view.—D. Calyx and pistil.—E. *Pachyptera standleyi*, Flower in side view. —F–I. *Crescentia*-type.—F–G. *Crescentia cujete*.—F. Flower in top view.—G. Corolla in side view.—H–I. *Dendrosicus latifolius*.—H. Corolla in side view.—I. Flower in bottom view.

Although I have observed no visitors to *Tanaecium*-type flowers, they fit the classic syndrome for hawk-moth pollination (Faegri & Pijl, 1966). Of all the potential pollen vectors available in Panama, only sphingid moths have long enough tongues to reach the nectar at the bottom of the long (to 17 cm), narrow tube of *Tanaecium.*

MARTINELLA-TYPE.—I have termed another morphological pattern the *Martinella*-type (Fig. 4C–E). These flowers are bright red-orange or deep red-violet (in *Tourrettia* only the calyx is red). The corolla is rather thick in texture, glabrous outside (except *Tourretia*), and has an open mouth, rather long tube, and often exserted or subexserted anthers. It is usually glabrous outside. The two corolla ridges are reduced or accentuated and very close together. The flower is odorless, has a conspicuous disc, and produces abundant nectar. The calyx is usually large and thin and encloses the base of the corolla tube very loosely. These flowers have evolved independently in the Bignonieae (*Martinella, Pyrostegia*) and in the *Tecomeae* (*e.g.* West Indian *Tabebuia* spp. and north temperate *Campsis*).

Martinella-type flowers are pollinated by hummingbirds. In contrast to their usual behavior at other bignon flowers, hummingbirds enter *Martinella*-type flowers from the front. I have observed the little hermit (*Phaethornis languimaris*) pollinate *Martinella obovata* on the Osa Peninsula (ca. 1 hour of observation) and on Santa Rita Ridge (½ hour of observation). This relatively small, short-billed hummingbird sticks its entire head into the campanulately expanded upper part of the tube and contacts the anthers with its forehead and the back of its head. I have also observed larger hummingbirds visit *Martinella*, but even though they approached the corolla from the front their bills were long enough to reach the nectar without contacting the anthers. Trigonids sometimes cut holes in flowers in bud, but I have not seen them visit mature flowers. I observed the approach to a flower of *Martinella* of a single *Euglossa* which left without entering the corolla. Cultivated vines of *Pyrostegia venusta* are often visited by hummingbirds, and its exserted anthers can make contact with both long and short-billed visitors. Red flowers and lack of odor are part of the standard syndrome for bird pollination. Reduction of pubescence probably relates to loss of odor production. The large loosely fitting calyx of several *Martinella*-type species probably serves to discourage puncture of the corolla base in the usual manner. The close-together corolla ridges of *Martinella* apparently act as a guide to direct the pollinator's bill to the basal nectar supply; in other species the more narrowly tubular flower serves this function.

Pachyptera standleyi has an interesting additional modification. Instead of being odorless its flowers have the same unpleasant garlic odor as the vegetative parts of the plant. Presumably this would act as a repellent to odor-sensitive insects but not to birds. I have observed no visitors to *P. standleyi*, but its narrowly tubular red corolla, subexserted anthers, and large inflated calyx are typical of hummingbird-pollinated species.

CRESCENTIA-TYPE.—The final pattern of New World bignon flowers is the *Crescentia*-type (Fig. 4F–I). These species are all members of the Crescentieae (*Crescentia, Parmentiera, Dendrosicus*). The corolla is white or off-white, glabrate, thick in texture, and usually has a transverse fold across the throat, behind which is formed a nectar-storing bulge. It is widely campanulate, with reduced lobes and subexserted anthers and stigma. These flowers have a characteristic musky odor, are more or less cauliflorous, and open at night. They have a very large disc and produce nectar copiously.

Crescentia-type flowers are bat-pollinated. I have observed several species of bats (especially *Glossophaga soricina*) visit *Crescentia alata* and *C. cujete*. The bats contact both anthers and stigma, receiving and carrying large quantities of pollen on the fur of their foreheads. While noctuid moths may also be visitors, they do not seem to make contact with the anthers. Trigonids and hummingbirds may penetrate unopened corollas during the day but are only nectar thieves. Night flowering, extremely copius production of nectar, an open rachitic branching pattern, and cauliflorous flowers are adaptations which clearly facilitate visits by bats.

KIGELIA-TYPE.—One of the additional morphological patterns shown by Old World bignons cultivated in Central America is the *Kigelia*-type. Such plants (*Kigelia* and *Haplophragma* in Panama) have very large, widely campanulate, dull-colored off-white or maroon flowers which are borne outside the canopy either flagelliflorously on long dangling leafless branches (*Kigelia*) or pincushion-style on thick-branched, stiff inflorescences projecting out from the canopy (*Haplophragma*). They have large discs, produce copious nectar, and have the same musky odor as *Crescentia*-type flowers. Like *Crescentia*-type flowers they have reduced corolla lobes, subexserted anthers and stigma, and open in the evening.

The *Kigelia*-type morphology is much like that of the *Crescentia*-type except for the much larger and differently presented flowers. These differences are related to evolution for pollination by Old World Megachiropteran bats (Harris & Baker, 1958; Pijl, 1956). Megachiropteran bats are generally larger than the Microchiropteran, New World, flower visiting bats and have a more poorly developed sonar system for navigation (Faegri & Pijl, 1966). These features correlate with larger flowers presented entirely outside the canopy as in the *Kigelia*-type of bignon. In cultivation in the New World these plants are rarely pollinated, although avidly visited by bats. Apparently their visitors are too small to make effective contact with anthers and stigma.

SPATHODEA-TYPE.—The second peculiarly Old World morphology is the *Spathodea*-type. Flowers of *Spathodea* are bright red, usually with a yellow border, glabrous, very large, widely campanulate, medium-textured, and have subexserted, flexuous anthers. The anthers and stigma are held loosely against the inner side of the corolla. The calyx is large and spathaceous. The flower has very little odor, a large disc, and produces abundant nectar.

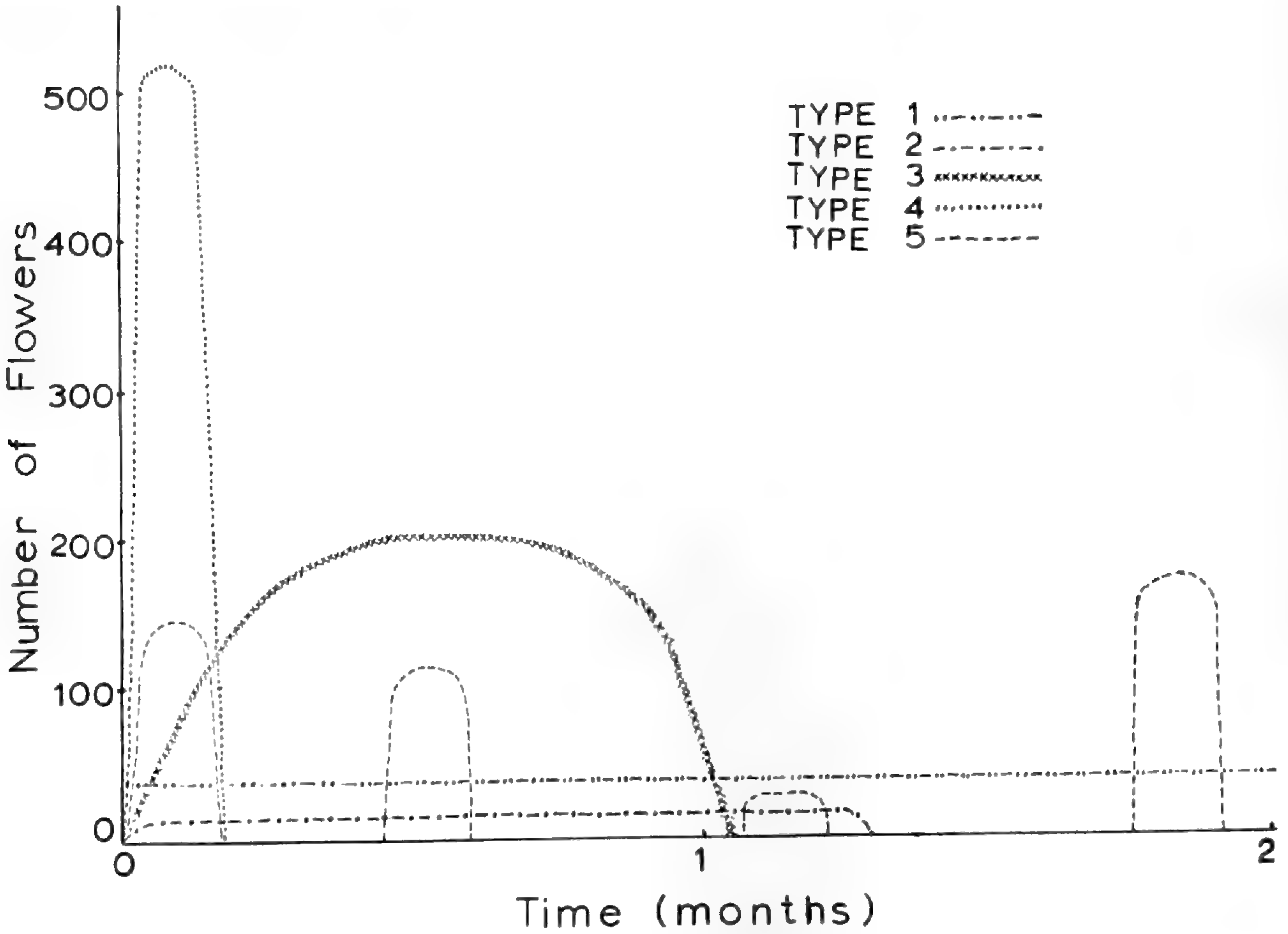


Figure 5. Schematic summary of phenology types.

The *Spathodea*-type flower is bird pollinated and is similar to hummingbird-pollinated New World species in such traits as red color, lack of fragrance, production of copious nectar, and subexserted anthers. However, it differs conspicuously in its open, bowl-shaped form and the position of its stamens. These differences correlate with lack of hummingbirds in the Old World and pollination by nonhovering birds (Faegri & Pijl, 1966). The reflexed spathaceous calyx makes a convenient perch from which non-hovering birds can reach the nectar inside the corolla tube.

Phenology

Different genera and species of Bignoniaceae exhibit strikingly different patterns of flowering phenology. These are related to different strategies of effecting pollination and can be broadly categorized into five major flowering types (Fig. 5, Table 3). Both Types 1 and 2 correspond to Janzen's (1971) trapline syndrome. I have tentatively separated them on the basis of different patterns of duration of flowering and different numbers of flowers produced. Type 4 and some species of Type 3 fall into the mass flowering syndrome as elucidated by Janzen (1967*a*; personal communication cited in Frankie *et al.*, 1973). Mass flowering has been subjectively defined and based mostly on general appearance of the flowering plant. In general, Type 3 species of Bignoniaceae (*e.g. Tabebuia rosea, Jacaranda caucana* subsp. *sandwithiana*, Fig. 8E) which bloom while deciduous would be classed as mass flowerers by many

TABLE 3. Summary of phenological types.

	1	2	3	4	5
Unit of attraction	single flower	single flower	mass of flowers and buds	mass of flowers	mass of flowers
Duration of flowering cycle	all year	3–8 weeks	3–10 weeks	few days	few days
Seasonality	little or none	little or none	strong: wet or dry season	dry season only	little or none
Flower presentation	single cauliflorous flowers	few flowered axillary inflorescence	large many flowered inflorescence	term. many flowered inflorescence	clustered axillary inflorescence
Anthesis	evening	very early morning	morning: after daybreak	mostly morning	very early morning
Duration of one flower	1 night	(1–)2 days	1 day	2 days	2–3 days
Synchronization with adjacent plants	none	little or none	only as to seasonality	near perfect	very strong
Number of flowering cycles in a year	one	probably one or two	one	either one or two	many
Number of flowers produced at a time at maturity	few to 40	mostly less than 10	many (to few thousand)	many (to 10,000)	few to many (variable)
Location of inflorescence	low; often near ground	below canopy; mostly pendent	mostly in canopy	canopy (leaves usually deciduous)	on young branchlets; low or high
Nectar production	copious	some	some	some	usually none

authors. Mass flowerers may bloom for a few days or several weeks and thus have very different patterns of flower production. While general appearance is perhaps more important than duration of flowering in terms of pollinator attraction, length of flowering and number of flowers produced are more important to the plant in terms of energy expenditure (*cf.* Heinrich & Raven, 1972). Because of this difference in viewpoint, I have used the term "cornucopia" species for Type 3 bignon and the term "big bang" species to refer to bignons with a Type 4 phenology. Most of my observations of phenological patterns were made in Panama, and a list of Panamanian species noting phenological type and observed pollinators is included in Table 2.

The Type 1 ("steady state") flowering pattern (Fig. 6) is correlated with *Crescentia*-type flowers and pollination by bats. The key feature of this phenological type is production of flowers almost every day throughout the reproductive life of a plant. Type 2 ("modified steady state") species (Fig. 7) are bee-pollinated. They differ from Type 1 species chiefly in shorter flowering periods.

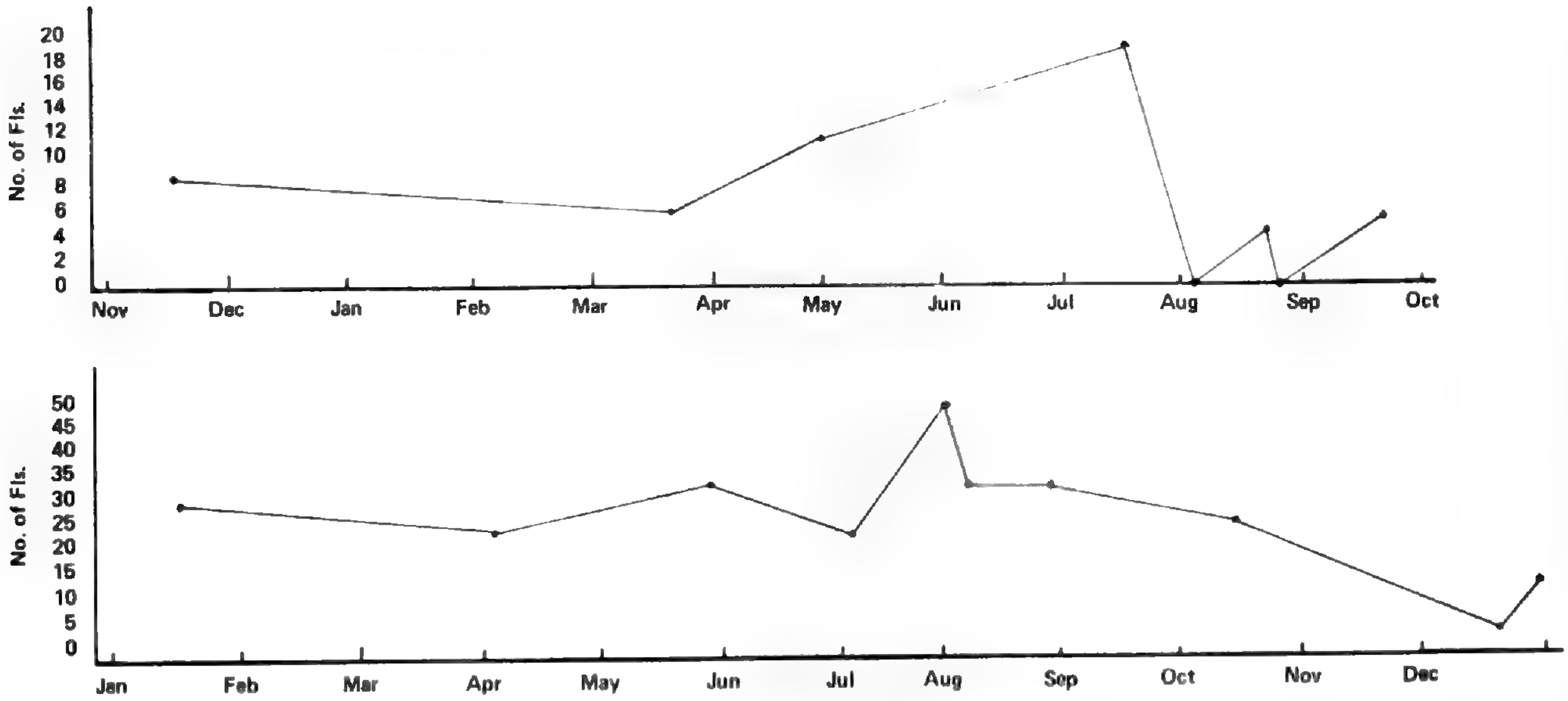


FIGURE 6. Examples of Type 1 ("steady state") phenology. Top. *Parmentiera cereifera* tree at end of "Boy Scout Camp Road" near Madden Lake, Canal Zone. Bottom. *Crescentia cujete* tree in Los Ríos, Canal Zone.

However flowering may be interrupted in some individuals of a Type 1 species, in which case this flowering pattern approaches that of Type 2. Another difference between bat-pollinated "steady state" species and the bee-pollinated species of Type 2 is in the larger numbers of flowers usually produced each day (or night) by the former. Of course diurnal differences in time of anthesis are also present between the two types. Although separation of Type 1 and Type 2 species is not clear cut in every instance, the flower production patterns of representative individuals of the two groups which I followed closely appear sufficiently different to merit their distinction.

Both "steady state" phenologies are associated with pollination by long-lived pollinators which establish fixed daily foraging routes (termed trapliners by Janzen, 1971). In comparison with other phenological types, "steady state" species open very few flowers at a time and bloom for a longer period. There is little seasonality or external synchronization of flowering and individual plants of "modified steady state" species are dependent on chance overlap of flowering periods to provide opportunity for cross-pollination.

Both of the strictly mangrove species of Bignoniaceae in Panama and Costa Rica (*Phryganocydia phellosperma* and *Tabebuia palustris*) have a modified form of Type 2 phenology. Plants of these species produce only one or two flowers at a time at sporadic intervals. Since these species grow in relatively dense stands, the population as a whole presumably fulfills the role of continual pollinator attraction.

The Type 3 or "cornucopia" phenology (Fig. 8) is the generalized Bignoniaceae flowering strategy and is shown by most temperate plants (Gentry, 1974). All hummingbird, hawkmoth, and bee/butterfly pollinated Panamanian and Costa Rican species have this phenology as do many bee-pollinated species. Type 3 species bloom for from a few weeks to over a month. The flowers usually last a single day. Flowering is seasonal, but flowering of individual plants of

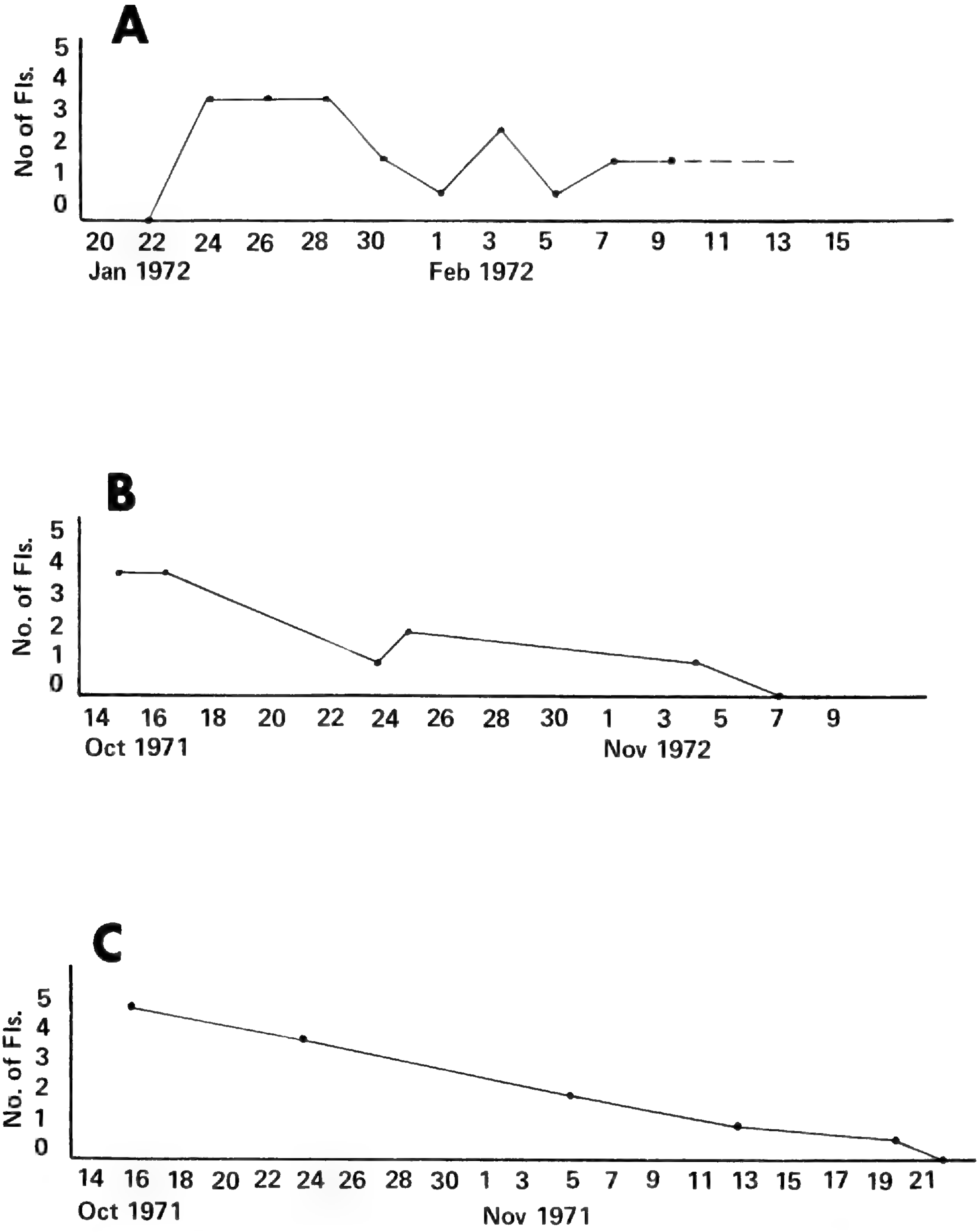


FIGURE 7. Examples of Type 2 ("modified steady state") phenology.—A. *Anemopaegma chrysoleucum* vine at junction of Ríos Espavé and Bayano, between Cañitas and Agua Clara; predicted from size classes of buds on first day of flowering, 26 Jan. 1972.—B. *Stizophyllum riparium* vine on Pipeline Road, Canal Zone; first observed in October 1971, but presence of mature fruit at that time indicates a flowering period beginning in September.—C. *Amphilophium paniculatum* vine at entrance to Pipeline Road, Canal Zone.

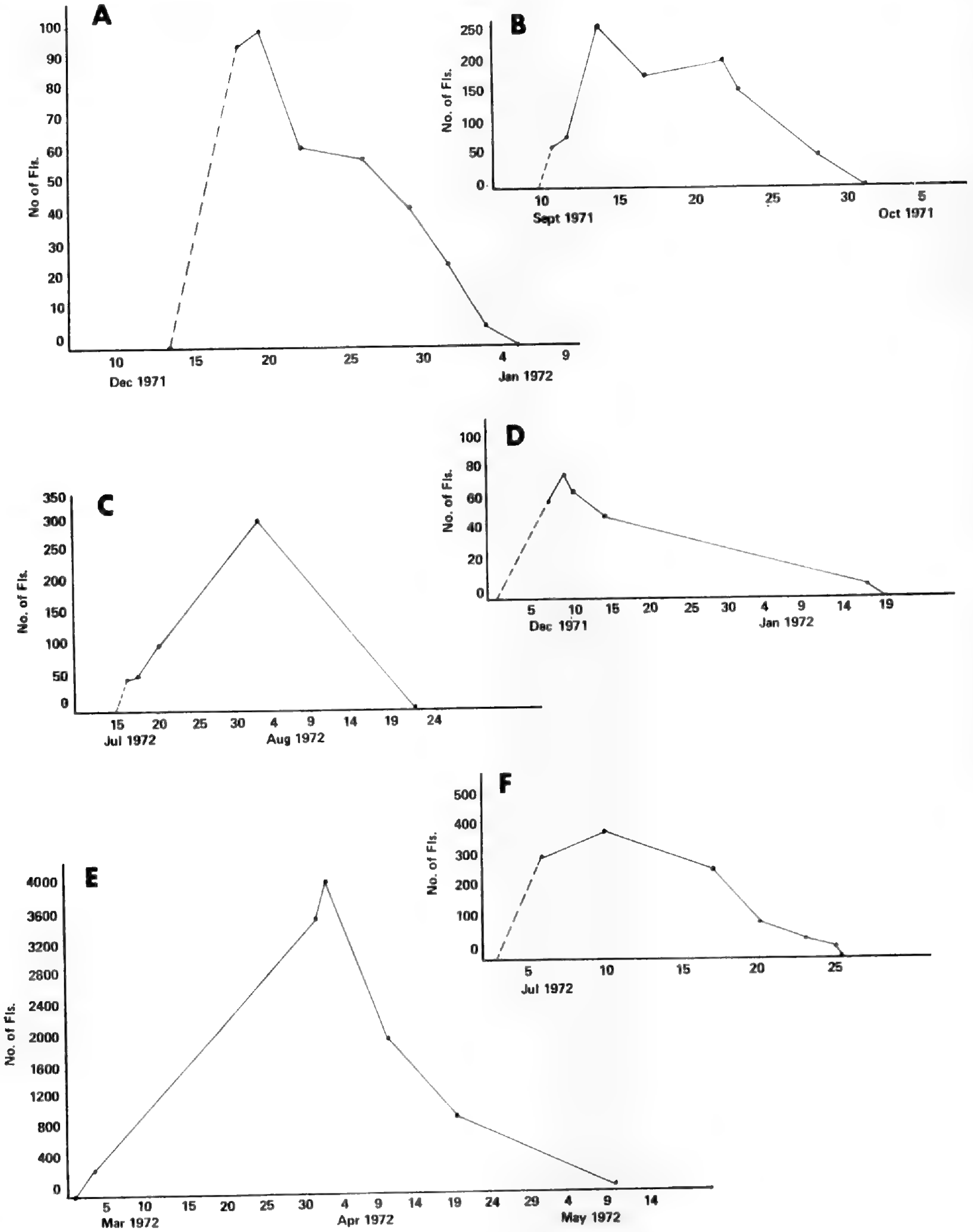


FIGURE 8. Examples of Type 3 ("cornucopia") phenology.—A. *Arrabidaea candicans* vine near Number 23, Pipeline Road, Canal Zone; the plant was rather immature with only a single flowering branch.—B. *Arrabidaea florida* vine on Pipeline Road, Canal Zone.—C. *Tynnanthus croatianus* vine on "Boy Scout Camp Road," Canal Zone.—D. *Tecoma stans* shrub at base of Sosa Hill, Canal Zone.—E. *Jacaranda caucana* subsp. *sandwithiana* tree cultivated at Summit Garden, Canal Zone.—F. *Arrabidaea patellifera* vine near Paraiso, Canal Zone.

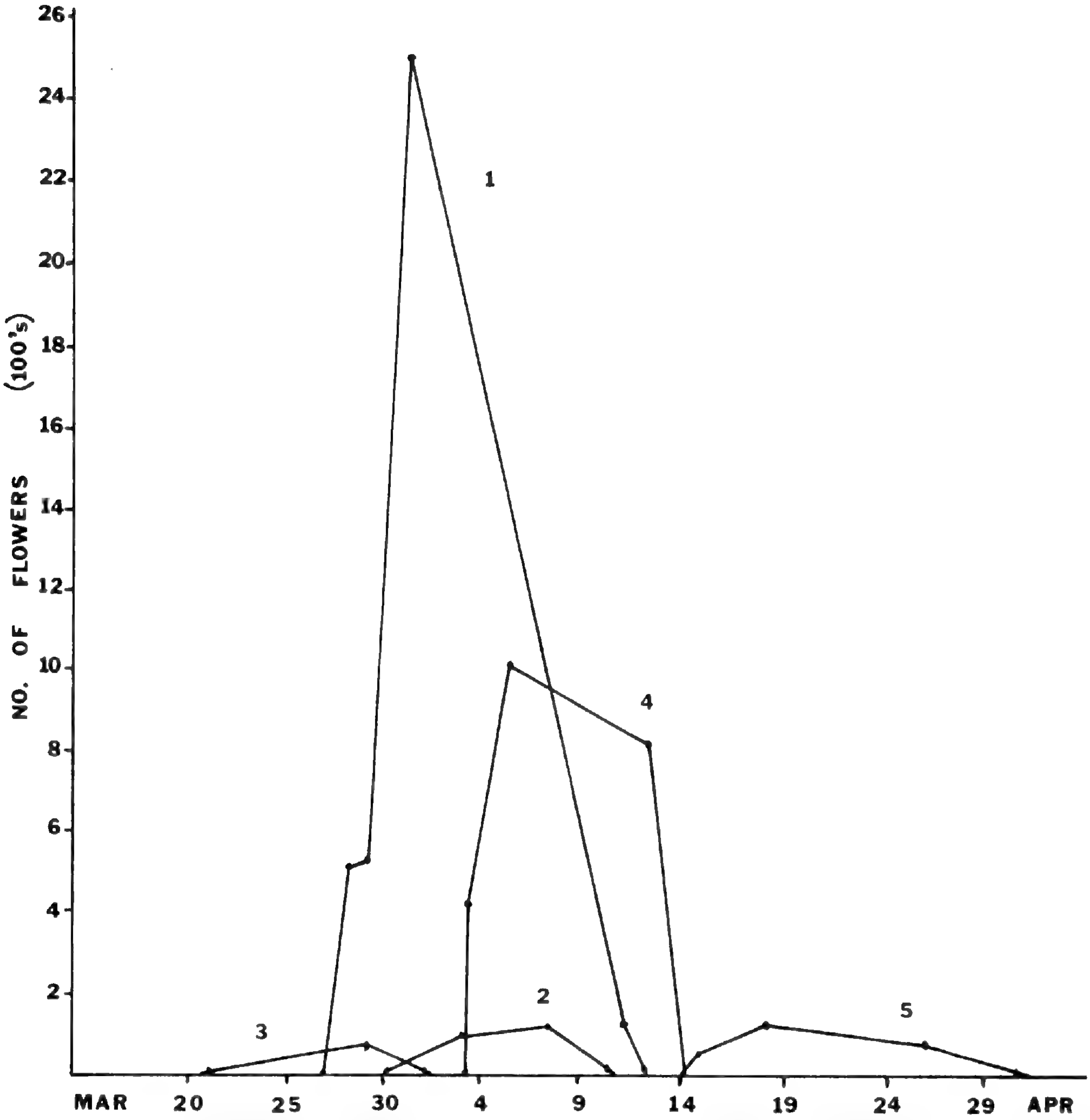


FIGURE 9. Phenology of several vines of Type 3 *Xylophragma seemannianum* illustrating overlap of flowering periods without synchronization. Vine 1—near beginning of pavement on Pipeline Road, Canal Zone; Vine 2—0.5 miles N of first gate on Pipeline Road, Canal Zone; Vine 4—near Paraiso, Canal Zone; Vine 5—near Summit Garden, Canal Zone.

a species is synchronized only as to season (Fig. 9). Dry season bloomers of Type 3 (Fig. 8A, D, E; Fig. 9) often flower while deciduous and appear to be "mass flowerers," while species flowering with their leaves can produce the same number of flowers over the same time span without appearing to be mass flowerers. *Paragonia pyramidata* is exceptional in having Type 3 flower production but lacking seasonality; perhaps it is significant that fruit set is less frequent for *Paragonia* than for most other Type 3 species.

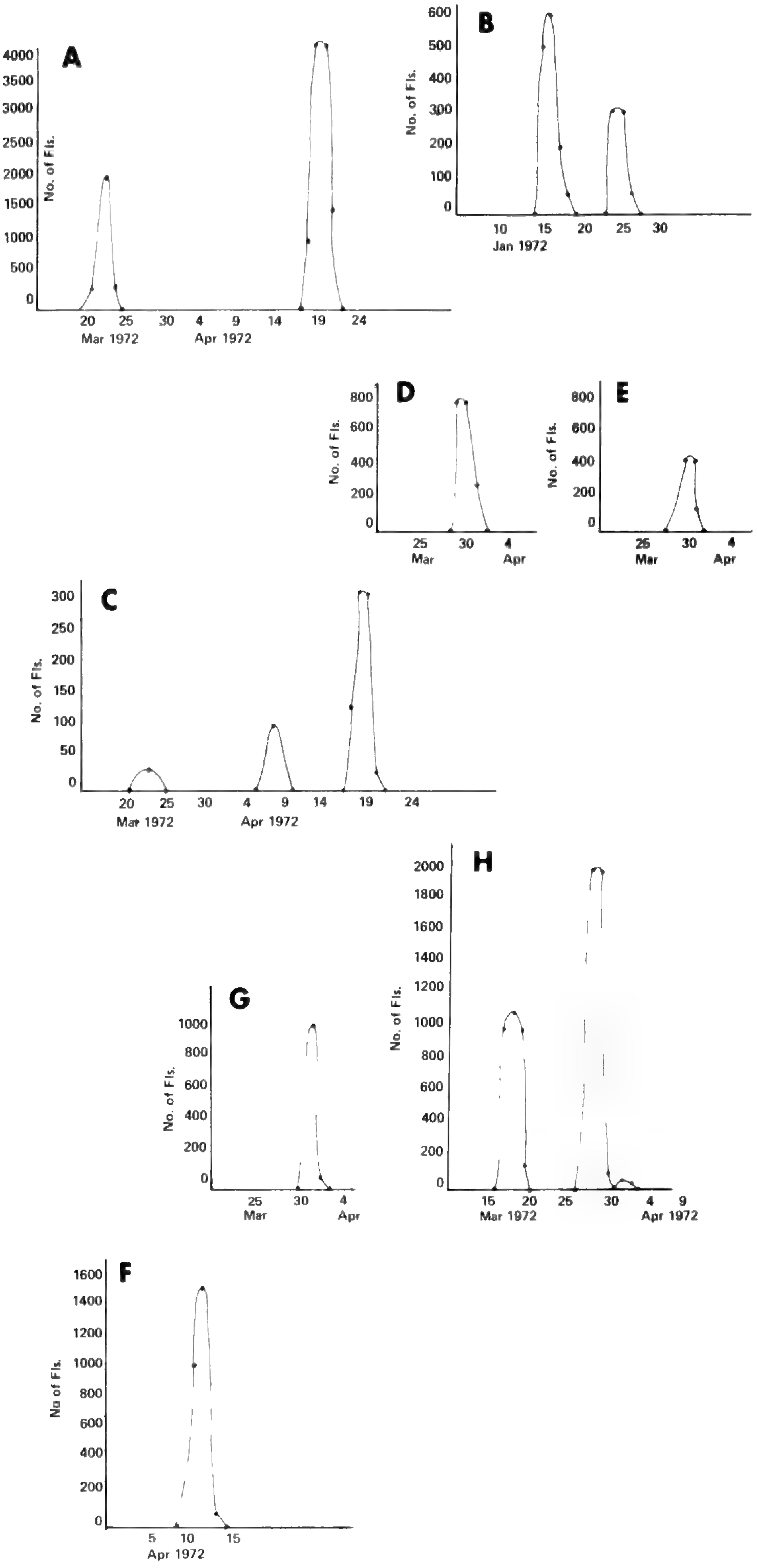
The Type 4 ("big bang") flowering type (Fig. 10) is characterized by a single brief highly conspicuous burst of mass flowering with the production of a great many flowers, each lasting about two days. All "big bang" species flower during the dry season. Blooming is highly synchronized between different individuals so that most of the plants of a species in a community bloom at the same time. Each flowering cycle is only a few days in duration. These plants seem to attract a generalized spectrum of pollinators, mostly bees, and appear to be an important source of both nectar and moisture for the insect members of a community during their brief burst of flowers.

Tabebuia guayacan epitomizes this phenological pattern with up to an estimated 10,000 flowers covering a single tree for four short days. Many observed trees of *T. guayacan* showed flowering curves as in Figure 10D–E; others bloomed twice during the dry season (Fig. 10A–B). One tree actually bloomed three times (Fig. 10C), but one of these blooming periods involved only a single lower branch. Trees of *Tabebuia ochracea* subsp. *neochrysantha* showed the similar pattern illustrated in Figure 10H. Vines of *Macfadyena unguis-cati* bloomed with the pattern shown in Figure 10F–G.

It is noteworthy that all of these plants are dry season bloomers (see Janzen, 1967, for additional discussion). It seems quite possible that only in the dry season can a tree or vine attract potential pollinators from a sufficient distance to achieve high pollinator density and hence good fruit set during such a short period of flowering. During the wet season potential pollinators presumably are under less stress and can utilize alternate, more long-lasting and dependable resources for nectar or moisture. Even though occasional individuals of the species utilizing the "big bang" flowering strategy do flower during the wet season, I have never observed these wet-season flowerings to produce fruit, although sometimes several plants will bloom together so that cross-pollination should be possible. It is also probable that synchronization of flowering between different trees, apparently related to water stress, is more precise during the dry season.

Plants of flowering Type 4 show an amazing coordination of flowering periods between the different individuals of a population. *Tabebuia guayacan* (Fig. 11), for example, synchronizes its flowering so that virtually all of the trees in an area bloom during the same few days of the year. *Tabebuia ochracea* subsp. *neochrysantha* shows the same phenomenon, as does *Macfadyena unguis-cati* to a lesser extent. This exact synchronization contrasts sharply with the relative asynchrony of a typical Type 3 flowerer like *Xylophragma seemannianum* (Fig. 9) (see also Croat, 1969).

Type 5 or "multiple bang" flowering (Fig. 12) appears to be the most specialized of all in many respects. The plants in this group, all vines, have numerous short flowering periods (ca. 3 days) scattered throughout the year. Each individual flower lasts two or three days. Synchronization between different individuals of a population is extremely good. For example, on 21 December 1971 a very noticeable percentage of the trees in the Canal Zone were covered with the purple flowers of vines of *Phryganocydia corymbosa* whereas on 20 December and 23 December not a single flowering *Phryganocydia* was evident. Flowering is usually not so conspicuous, however, and a plant often produces only a few flowers during a given flowering cycle. In addition to intraspecific synchronization of flowering periods, there is a marked tendency for all the


A
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20 25 30 4 9 14 19 24
Mar 1972
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B
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600
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200
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10 15 20 25 30
Jan 1972
D
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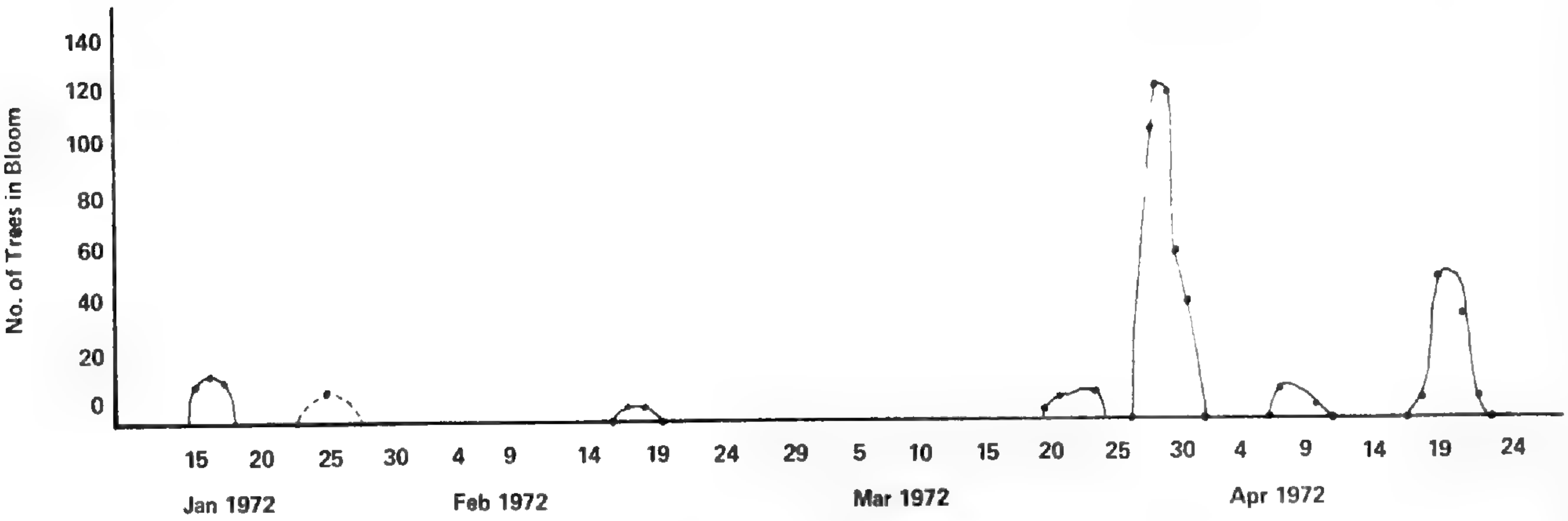

FIGURE 11. Synchronization of flowering in *Tabebuia guayacan.*

species exhibiting this flowering strategy to bloom at the same time (Fig. 12). There is a general lack of synchronization of different branches of the same plant, although each branch may bloom synchronously with other plants of the population.

I think that this type of reproductive behavior is triggered by vigorous vegetative growth so that all plants in an area may achieve synchronization through similar response to optimal growth conditions, *e.g.* a good rain. That moisture or possibly an associated temperature phenomenon (see Schulz, 1940) triggers flowering in plants of this group is indicated by some circumstantial evidence. For example, during the wet season and early dry season a *Cydista aequinoctialis* vine growing at Summit Gardens flowered once every few weeks in synchrony with other plants of the species in the vicinity (Fig. 12A–C), but with onset of the dry season it was subject to regular irrigation and during February and March bloomed almost every day in contrast to non-irrigated vines which bloomed hardly at all during this period.

One of the most interesting aspects of many "multiple bang" species is their lack of a nectariferous disc and apparently of nectar production as well. As might be expected, these species receive very few visits from prospective pollinators, and all such visits are very brief, being confined to penetration of only one or two flowers. Although small pollen-collecting bees do visit these flowers, their activity does not trigger the stigma so their value as pollinators seems to be nil. I interpret these species (*Cydista aequinoctialis, C. diversifolia, C. heterophylla, Phryganocydia corymbosa,* and *Clytostoma binatum*) as mimics of nectar-producing mass flowering species, including other Bignoniaceae, which are dependent for pollination on exploratory visits by nectar-seeking bees in-

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FIGURE 10. Examples of Type 4 ("big bang") phenology.—A. *Tabebuia guayacan* tree near Summit Gardens, Canal Zone.—B. *Tabebuia guayacan* tree cultivated at Summit Gardens, Canal Zone.—C. *Tabebuia gauyacan* tree at Madden Wye, Canal Zone.—D. *Tabebuia guayacan* tree near Gamboa airport, Canal Zone.—E. *Tabebuia guayacan* tree near grease pit just outside Gamboa, Canal Zone.—F. *Macfadyena unguis-cati* vine near Madden Dam, Canal Zone.—G. *Macfadyena unguis-cati* vine near Pedro Miguel, Canal Zone.—H. *Tabebuia ochracea* subsp. *neochrysantha* tree near Miraflores Lake, Canal Zone.

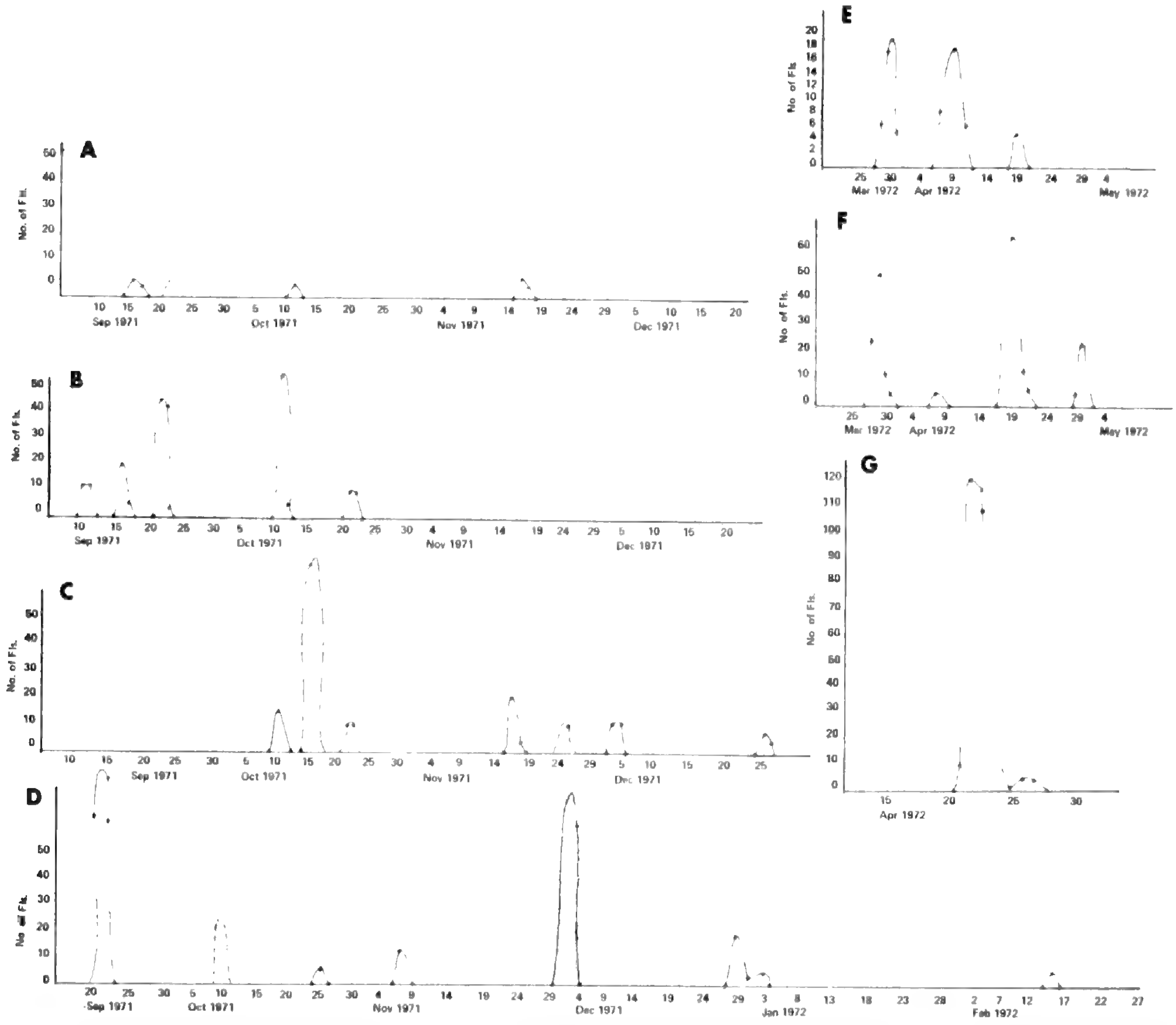

FIGURE 12. Examples of Type 5 ("multiple bang") phenology.—A. *Cydista aequinoctialis* vine at Summit Herbarium, Canal Zone.—B–C. *Cydista aequinoctialis* vines across highway from Summit Hills Golf Course.—D. *Phryganocydia corymbosa* vine near Number 23, Pipeline Road, Canal Zone.—E. *Anemopaegma orbiculatum* vine near Number 23, Pipeline Road, Canal Zone.—F. *Anemopaegma orbiculatum* vine just inside first gate on Pipeline Road, Canal Zone.—G. *Cydista heterophylla* vine near Summit Garden, Canal Zone.

vestigating apparent new nectar sources. Repeated but separated short bursts of flowering allow maximum exposure to naïve prospective pollinators of new flowers to be investigated; few flowers are wasted on bees which have already learned that they are unsuitable nectar sources. Conspicuous visual and olfactory stimuli aid in attracting first-time visitors. Physiologically the plant saves the energy it would have expended on nectar production, and it also avoids the destructive visits of such nectar-thieves as xylocopid bees and hummingbirds. In addition, the lack of repeated visits by foraging bees to flowers on the same plant assures a very high degree of cross-pollination should pollination be effected at all. That this reproductive strategy is eminently successful is evidenced by a tremendous abundance of young post-seedling plants and also the relative commoness of mature vines; *Phryganocydia corymbosa* and *Cydista aequinoctialis* are the two commonest species of Bignoniaceae in the Canal Zone. In fact it is possible that this strategy could only be successful in a very common species where there is a relatively high chance that a randomly foraging prospective pollinator will encounter two plants of the same species more or less in succession.

Not all of the plants with "multiple bang" flowering phenology are non-nectar producing mimics. *Anemopaegma orbiculatum* (Fig. 12E–F), for example, illustrates this flowering pattern while maintaining nectar production. It is subject to extensive corolla damage from nectar-robbing xylocopid bees and sets no more fruit than the species without nectar. Conceivably this is an intermediate step in development of the mimicking phenomenon.

Another variant is *Cydista heterophylla* (Fig. 12G) which apparently has only one or two flowering periods in a year and blooms only in the dry season. I have never actually seen a vine of this species undergo more than a single flowering period, but the occasional occurrence of fruit on a flowering vine indicates at least two such periods for some individuals. The flowering strategy of this species is perhaps closer to Type 4 than Type 5, although it is more closely related to the "multiple bang" flowerers.

DISCUSSION OF PHENOLOGY

These five major flowering phenologies correlate rather well with a whole syndrome of reproductive behavior as summarized in Table 3.

Intuitively the basic phenological pattern should be Type 3, in which a plant has a definite, prolonged, flowering season, blooming profusely and continually for a number of weeks. Although containing a number of heterogeneous elements, this phenological type is probably natural in the sense that it encompasses the putative ancestral pattern of the family. The type 3 pattern serves as a convenient base line for discussion of the other flowering types.

Selection for conservation of reproductive energy (*cf.* Heinrich & Raven, 1972) would favor production of few flowers, given adequate pollination of the consequently less attractive flowering plant. By utilizing the constant behavioral patterns of many of the larger long-lived tropical bees (Janzen, 1971), the plants of flowering Type 2 have been able to afford a dramatic reduction in the amount of energy expended on flower production. Further modifications are the tendency to prolongation of flowering and the elimination of seasonality. Both modifications provide a more constant nectar source through time for the pollinator and hence favor its increased utilization of this resource making it in turn a more reliable pollen vector. Many "modified steady state" species have high local population densities as along rivers or in swamps. Such a distribution of individual plants would make cross pollination more frequent.

The mass flowering strategy of species with Type 4 phenology makes possible a different utilization of the same group of pollinators. It depends upon attracting large numbers of bees by disruption of established behavior patterns. Given a suitable environmental trigger, through which individual plants of a species can coordinate flower production, it becomes energetically advantageous for such opportunistically pollinated plants to have shorter more synchronized flowering periods concentrating reproductive energy into a single burst of flowering. Even though it produced many fewer flowers than a species with Type 3 phenology, such a plant could be much more conspicuous during its short flowering period and divert many of the potential pollinators of an area to its munificient supply of nectar. This is exactly what happens with such species as *Tabebuia impetiginosa* and *T. ochracea* subsp. *neochrysantha*, where dozens or even hundreds of pollinators concentrate on these trees during their few short days of flowering. This phenomenon is certainly augmented by dry season flowering when general moisture shortage should force maximum utilization of a large new nectar supply, and the loss of leaves by many trees makes flowering plants more conspicuous and visible for greater distances (see also Janzen, 1967*a*).

Many Type 4 individuals have two flowering periods separated by a few weeks; in both of these they are coordinated with many other plants of the same species. I have actually observed one tree of *Tabebuia guayacan* to flower three times during one dry season, although during the first flowering period only a single branch was in bloom. It is quite possible that from such a phenomenon could be developed the Type 5 phenology wherein many plants of a species bloom synchronously for short periods which are less spectacular and scattered throughout the year. A more measured response to the same or a similar stimulus as that producing the Type 4 flowering burst could easily have led to the Type 5 phenology.

Alternately Type 5 phenology could be a modification of the Type 2 pattern. This idea is supported by the lesser flower production of Type 5 than of Type 4 plants, their lack of seasonality, and by the Type 5 phenology of a species of *Anemopaegma* (*A. orbiculatum*) while other species of the genus show Type 2 flowering. Under this hypothesis, development of a flowering response to some environmental trigger, probably related to rainfall, could give short synchronized flowering periods often with production of relatively few flowers at one time.

In either case, the significance of Type 5 phenology is in making possible yet another utilization of the same limited group of bee pollinators. The Type 5 species rely on the same mass attraction as the Type 4 species but by multiple flowering periods avoid putting all their eggs in one basket as do the Type 4 flowers. Very short flowering periods insure that a significant percentage of visits to Type 5 plants are by bees investigating the flowers as potential nectar sources for the first time. Hence loss of nectar production and reliance on mimicry of nectar-producing flowers becomes a reasonably effective as well as energetically advantageous pollination strategy. These species can thus make use of the same bees which pollinate species with "steady state" or "cornucopia" strategies, since the occasional investigative visits which suffice to pollinate these non-nectar producers interfere very little with established visitation patterns.

SEASONALITY

Seasonality of flowering is, of course, a well-known isolating mechanism making possible greater intracommunity diversity. In the Bignoniaceae it is important only to "cornucopia" and "big bang" species. Although the "big bang"

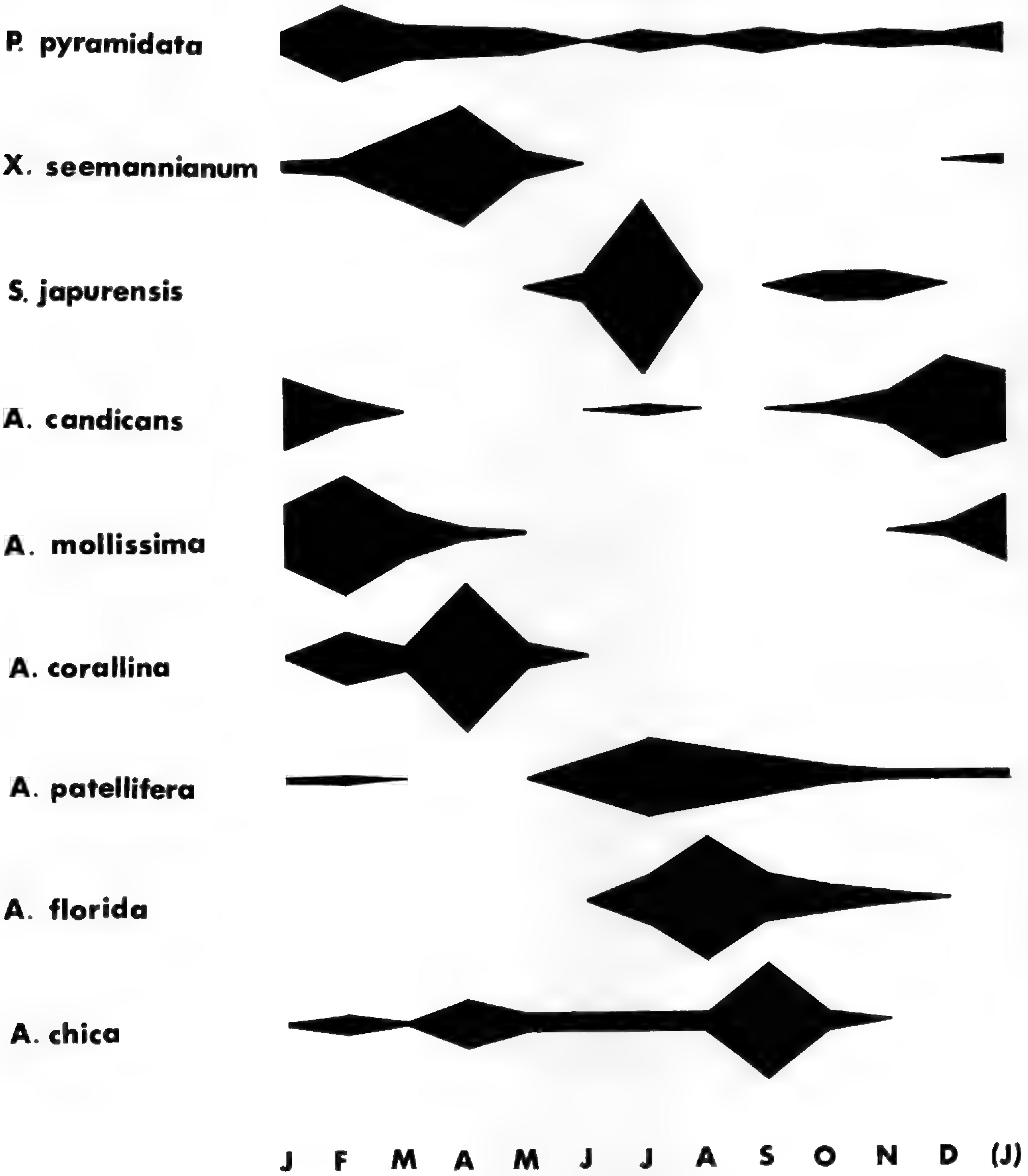

FIGURE 13. Seasonal distribution of commoner Type 3 nectar sources.

phenology implies a kind of seasonality in its restriction to the dry season, seasonality as a means of increasing diversity is only apparent in "cornucopia" species. The various species of *Arrabidaea* are the best examples with *A. candicans* flowering in early and mid dry season, *A. corallina* and *A. mollissima* in mid dry season, *A. patellifera* in early wet season, *A. chica* in early to mid wet season, *A. pubescens* in mid wet season, and *A. florida* in mid to late wet season in Panama. Each species of *Arrabidaea* has its flowering peak in a different month (see Gentry, 1974). As a whole such species, especially when taken in conjunction with Type 4 "big bang" species, provide an important and almost year round source of nectar for the pollinators of a community (Fig. 13).

SUMMARY

While interactions with herbivores and frugivores have been important in bignon evolution, pollinator interactions provide the most spectacular coevolutionary examples. I have attempted to make three points about coevolution between bignons and their pollinators.

1. The family has radiated in floral morphology to make use of nearly all the potential pollinators of a tropical community. As one of the more primitive families of Tubiflorae this radiation can be presumed to have been accompanied by, and in turn to some extent responsible for, the evolution of such animal specialists as flower bats, hummingbirds, hawkmoths, and long-tongued bees.

2. The majority of species of Panamanian Bignoniaceae are morphologically adapted for pollination by long-tongued bees. These plants have evolved different specializations in flowering phenology which correlate with the different behavioral patterns of their pollinators—steady state flowering with traplining behavior; big bang and multiple bang flowering with opportunistic behavior. Presumably the pollinator behavioral patterns coevolved with the bignon phenological specializations and with similar and concomitant specializations in other plant groups.

3. Among those genera of Bignoniaceae retaining the generalized cornucopia phenology, seasonality of flowering is important in making possible differential utilization of the same group of pollinators by different plant species. From the viewpoint of the pollinator, this seasonal sequence of flowering provides a year-round source of nectar to bignon-visiting pollinators.

The varied and often complex patterns of interaction shown by Bignoniaceae with different animals appear to have long coevolutionary histories. Understanding such interactions promises to be useful in working out evolutionary relationships within the Bignoniaceae. In addition such studies of taxonomically delimited subsets of diverse tropical ecosystems have great potential for elucidating the incredibly complex ecologies of these communities.

LITERATURE CITED

BORRERO, J. I. 1972. Explotación de las flores de Guayacán (*Tabebuia chrysantha*) por varias especies de aves e insectos. Biotropica 4: 28–31.

CROAT, T. B. 1969. Seasonal flowering behavior in Panama. Ann. Missouri Bot. Gard. 56: 295–307.

DUGAND, A. 1942. Dos nuevas Bignoniaceaes del valle del Magdalena. Caldasia 1: 29–35.

FAEGRI, K. & L. VAN DER PIJL. 1966. The Principles of Pollination Ecology. Pergamon, London.

FRANKIE, G. W., H. G. BAKER & P. A. OPLER. 1973. Tropical plant phenology: applications for studies in community ecology. *In* H. Lieth (editor), "Phenology and Seasonal Modeling." Springer-Verlag, Berlin (in press).

GENTRY, A. H. 1969. *Tabebuia* (Bignoniaceae) in Central America. Master's thesis submitted to the University of Wisconsin, Madison.

———. 1972. An Eco-Evolutionary Study of the Bignoniaceae of Southern Central America. Ph.D. thesis submitted to Washington University, St. Louis.

———. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica. 6: 64–68.

HARRIS, B. J. & H. G. BAKER. 1958. Pollination of *Kigelia africana* Benth. Jour. West Afr. Sci. Assoc. 4: 25–30.

HEINRICH, B. & P. H. RAVEN. 1972. Energetics and pollination ecology. Science 176: 597–602.

JANZEN, D. H. 1967*a*. Synchronization of sexual reproduction of trees within the dry sea-in Central America. Evolution 21: 620–637.

———. 1967*b*. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Univ. Kansas Sci. Bull. 47: 315–558.

———. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171: 203–205.

———. 1972. Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest. Ecology 53: 885–892.

LEWIS, W. H. 1971. Selective insect damage in a tropical herbarium collection. Ann. Missouri Bot. Gard. 58: 91–92.

LINDLEY, J. 1847. The Vegetable Kingdom. London.

PIJL, L. VAN DER. 1956. Remarks on pollination by bats in the genera *Freycinitia*, *Duabanga* and *Haplophragma*, and on chiropterophily in general. Acta Bot. Neerl. 5: 135–144.

RECORD, S. J. & R. W. HESS. 1940. American timbers of the family Bignoniaceae. Tropical Woods 63: 9–38.

SANDERMANN, V. W. & H. H. DIETRICHS. 1957. Untersuchungen über termitenrisistente Hölzer. Holz als Roh- und Werkstoff 15: 281–297.

SCHULZ, A. G. 1940. Las Bignoniaceas del Territorio del Chaco. Lilloa 5: 131–158.

SEEMANN, B. 1854. Botany of the Voyage of H.M.S. *Herald*. London.

———. 1860. Synopsis Crescentiacearum: an enumeration of all the Crescentiaceous plants at present known. Trans. Linn. Soc. 23: 1–22.

SEIBERT, R. J. 1940. The Bigononiaceae of the Maya area. Carnegie Inst. Washington Publ. 522: 375–434.

SOUTHWELL, C. R. & J. D. BULTMAN. 1971. Marine borer resistance of untreated woods over long periods of immersion in tropical waters. Biotropica 3: 81–107.

STANDLEY, P. C. 1928. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: 1–416.

——— & L. O. WILLIAMS. 1974. Bignoniaceae. *In* "Flora of Guatemala." Fieldiana Bot. 24(10): 153–232.

BEHAVIORAL ASPECTS OF COADAPTATIONS BETWEEN FLOWERS AND INSECT POLLINATORS

LAZARUS WALTER MACIOR[1]

Regardless of precisely where in geologic history entomophily originated and what the taxonomic affinities of the earliest insect-pollinated flowers were, it is becoming increasingly evident that any complete study of floral evolution must include investigations of pollen vector dynamics. Likewise any study of plant breeding systems involving insects must include information on the indispensable link of pollen transport, since genes flow between plants only within pollen grains. Pollinating insects exert selection pressure on every consequence of genetic recombination expressed in the form and function of entomophilous flowers. Pollination mechanisms, in turn, exert selection pressure on the intrafloral activity of insects. Thus there arises a reciprocal pattern in which flowers exploit the behavioral repertoire of insects, and insects exploit the genetic parameters of the expression of floral form. Considered as a transitory phenomenon, any pollination mechanism may be better characterized as a stage in the ever-changing function of sexual reproduction of angiosperms than as the final product of coadaptation. In this regard Vogel (1954), Leppik (1957*a*, 1957*b*, 1968), Pijl (1960, 1961), and other contemporary pollination ecologists have attempted to relate floral mechanisms on a functional basis rather than on one of phylogenetic origin. Their suggestions are likely to indicate a new direction for the evolutionary study of floral form. To understand the behavioral problems associated with a study of floral evolution it may be well to consider several specific investigations of floral mechanisms and their implications.

POLLEN FORAGING

The manner in which an insect forages for pollen is directly related to the way in which a flower discharges pollen from its anthers. Pollen readily available to any type of forager may be immediately eaten by syrphid flies and other relatively non-selective insects. Bees, which provision their nests with the pollen, carry it in corbicular or similar containers. Although no complex behavior is required to gather pollen on open, actinomorphic flowers, bumblebees have been observed foraging for it by vibrating their wings at a high frequency accompanied by a high-pitched buzzing sound. This behavior has been studied in detail on *Dodecatheon* (Macior, 1964, 1970*b*) and *Pedicularis* (Macior, 1968*a*, 1970*c*, 1973), flowers of which conceal pollen and release pollen only in response to such foraging behavior. The high-pitched sound is distinct from that produced by the insect in flight but closely resembles that emitted by bumblebees in the nest when it is disturbed (Hoffer, 1882). The foraging insect does not use the vibration sound as a warning on the flower as it does in the nest for it does not defend the forage source. Instead the behavior pattern is directed toward a

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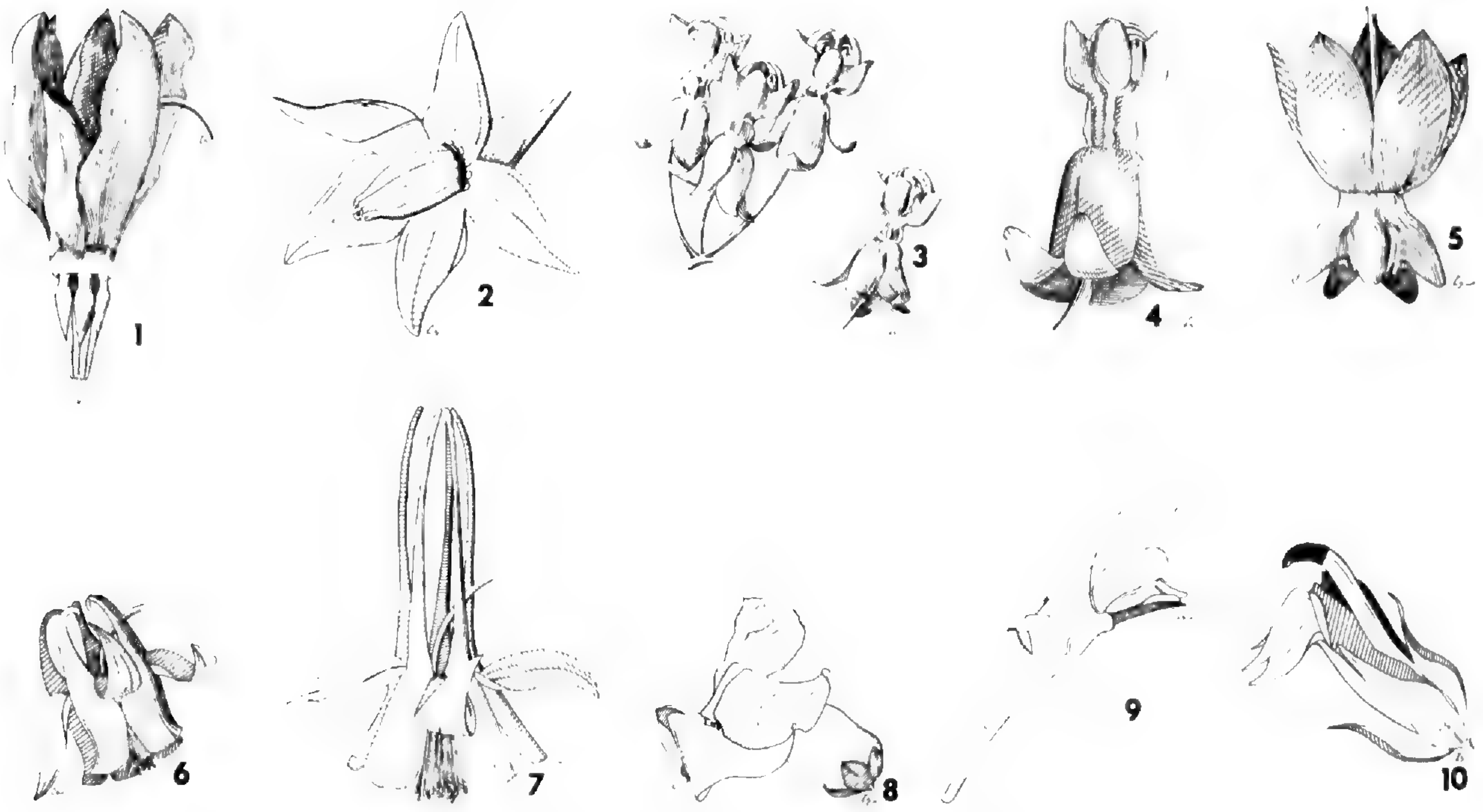
different end. In the nest queens are more likely to respond with the high-pitched vibration, but on flowers both queens and workers forage with it. It appears that an activity originally serving as a warning signal to nest intruders has become associated with pollen foraging.

The evolutionary response of pollen-sifting mechanisms is apparent in the structure of the stamens and pollen. Pollen leaves the anthers through well-defined openings and is not exposed on the surface of the anther. Deprived of their pollinators the flowers do not self-pollinate even though pollen eventually drops from the anthers as they dry. The pollen grains are small, generally in the range of 4–12 nm in diameter or length and lack sharp sculpturings. These characteristics must contribute to the ease with which the grains leave the anthers by vibration. The corolla form of pollen-sifting mechanisms varies considerably between taxa, but in every case it must be such that it does not impede wing vibrations. This excludes all corollas that confine the entire insect when it is foraging. In *Dodecatheon* (Fig. 1) and *Solanum* (Fig. 2) the petals are reflexed to expose a cone of connate, introrsely dehiscent anthers through the tip of which pollen is discharged on to the ventral side of a forager inverted on the cone. The corolla attracts pollinators but does not function during pollen discharge. In other functionally related floral mechanisms, however, the corolla assumes an integral function in pollen-vibration behavior of insects.

FLOWER CONSTANCY

The concept of flower constancy of pollinators has been suggested as a behavioral means of isolating plant species during sexual reproduction (Grant, 1950; Leppik, 1951; Manning, 1957; Linsley & MacSwain, 1958). Except for the behavior of monolectic bee species, flower constancy must be viewed as a relative term. Individual pollen foragers of the same insect species may carry from one to 6 types of pollen when working in the same plant community. Prior habituation in foraging behavior of individuals is undoubtedly as important as the relative availability of pollen from one or more plant species in the foraging area in determining the degree of flower constancy of any individual. Polylectic taxa such as bumblebees are very effective interspecific pollinators so that if behavioral isolation of plant taxa is to be maintained other causal agents must be found.

In three sympatric species of *Asclepias* (Figs. 3–5), which attach pollinia of different sizes to different respective parts of a forager's body, functional isolation is maintained by the different "lock-and-key" characters of pollinia and stigmatic fissures of the three flowers and by the positions of pollinial attachment. Nectar-foraging behavior of all pollinators is similar on all species except that in *A. syriaca* the lax pedicels often require the forager to work in an inverted position. Furthermore, since individual pollinators have been found to carry pollinia of all three milkweed species (Macior, 1965), flower constancy cannot be suggested as a mechanism of maintaining species integrity in the genus. Although this mode of species isolation may well have been instrumental, together with geographic isolation, in establishing these species, mechanical and genetic



FIGURES 1–10.—1. Flower of *Dodecatheon meadia*.—2. Flower of *Solanum dulcamara*.—3. Flower of *Asclepias verticillata*.—4. Flower of *Asclepias incarnata*.—5. Flower of *Asclepias syriaca*.—6. Flower of *Aquilegia vulgaris*.—7. Flower of *Aquilegia coerulea*.—8. Flower of *Antirrhinum majus*.—9. Flower of *Linaria vulgaris*.—10. Flower of *Lobelia siphilitica*.

isolation are most likely the mechanisms that maintain species integrity today. Flower constancy in relation to behavioral isolation of plant species is more appropriately applied where it can be demonstrated that the plant depends exclusively upon a reciprocally dependent pollinator as in *Ficus* (Galil & Snitzer-Pasternak, 1970; Ramirez, 1970), *Yucca* (Powell & Mackie, 1966), and perhaps *Habenaria* (Thien & Utech, 1970).

Behavioral isolation has been advanced as a cause for the diversity of floral form found in *Aquilegia* species (Grant, 1952). Considering the attraction of red flowers for hummingbirds, one may be tempted to conclude that selective behavior of such pollinators has actually isolated red-flowered species. If, however, there is any pollinator that will reverse such behavioral isolation in the same area, species integrity will be dissolved. This behavior pattern has been demonstrated experimentally in Wisconsin for *Aquilegia canadensis* grown together with other species and cultivars having widely divergent floral forms and colors (Macior, 1966). In the High Sierra of California Chase (1971) has demonstrated that the red-flowered *A. formosa* and the white-flowered *A. pubescens* are maintained mutually distinct neither by pollinator specificity nor by phenological isolation. Similar conclusions are drawn by Miller (1973) from a study of *A. elegantula* and *A. coerulea* in Colorado. Habitat preference of the plants is suggested as a prime isolating factor. In Wisconsin as in California pollen-foraging bumblebees, which ignore corolla form in gathering pollen from the exserted anthers, effectively cross-pollinate species with divergent floral form and color. Under experimental conditions one foraging individual may collect pollen on the red *A. canadensis* with short straight spurs, on the blue *A. vulgaris* (Fig. 6) with short curved spurs, and on the blue and white *A. coerulea* (Fig. 7) with very long straight spurs. Thus potential behavioral isolation based upon corolla selection pressure is reversed by pollen-foraging behavior. This is not to deny that foraging behavior has had an effect on the evolution of floral form and color, but such selective influence requires substantial observational and experimental evidence to support it before it can be accepted.

ZYGOMORPHY

If selective behavior of pollinators has been responsible for the evolutionary conversion of actinomorphic, polypetalous floral mechanisms into zygomorphic, sympetalous ones, one should be able to find the pollinator or pollinators that may have effected this conversion if they are still associated with the mechanisms. In the Labiatae and Scrophulariaceae most mechanisms are nototribic, that is, they transfer pollen on the dorsal side of the vector. Sternotribic flowers, as in the Leguminosae, use the ventral side of the pollinator. The general strategy of the mechanism appears to be the deposition of pollen in a specific location on the pollinator from which it is least likely to be removed during body grooming. That this operation is successful in nototribic flowers has been demonstrated in *Antirrhinum* (Fig. 8), *Linaria* (Fig. 9), and *Lobelia* (Fig. 10), even though the nectar-foraging bumblebees that pollinate them regularly remove some of the nototribically-deposited pollen by grooming (Macior, 1967). Such floral mechanisms need not be considered imperfectly adapted to such pollinators because the insects locate and regularly collect concealed pollen. If pollination is successful and pollinator interest is increased by the availability of pollen in addition to nectar in a mechanism that effectively eliminates other foragers, as these flowers do, the mechanism is highly efficient. Foragers do not completely remove pollen from the mid-dorsal and mid-ventral lines of the thorax. Residual pollen in these body positions has guaranteed successful and regular pollination. Foraging behavior has thus apparently exerted selection pressure in the direction of zygomorphy. Although pollen is concealed from the forager's visual and tactile perception, its foraging pattern exploits this concealment by foraging where other insects neither forage nor pollinate. One cannot conclude, however, that all zygomorphic mechanisms operate in the same general manner and that pollinators forage in only one way on the flowers. Precise field observations of pollinator behavior are likely to disagree with speculations about the operations of floral mechanisms based upon their form alone. It would not be generally suspected, for example, that insects enter the nototribic flower of *Antirrhinum* in an inverted manner so that its essential parts contact the ventral instead of the dorsal side of the thorax. These variants in behavior probably exert selection pressure leading to variants in zygomorphic mechanisms.

COROLLA PERFORATION

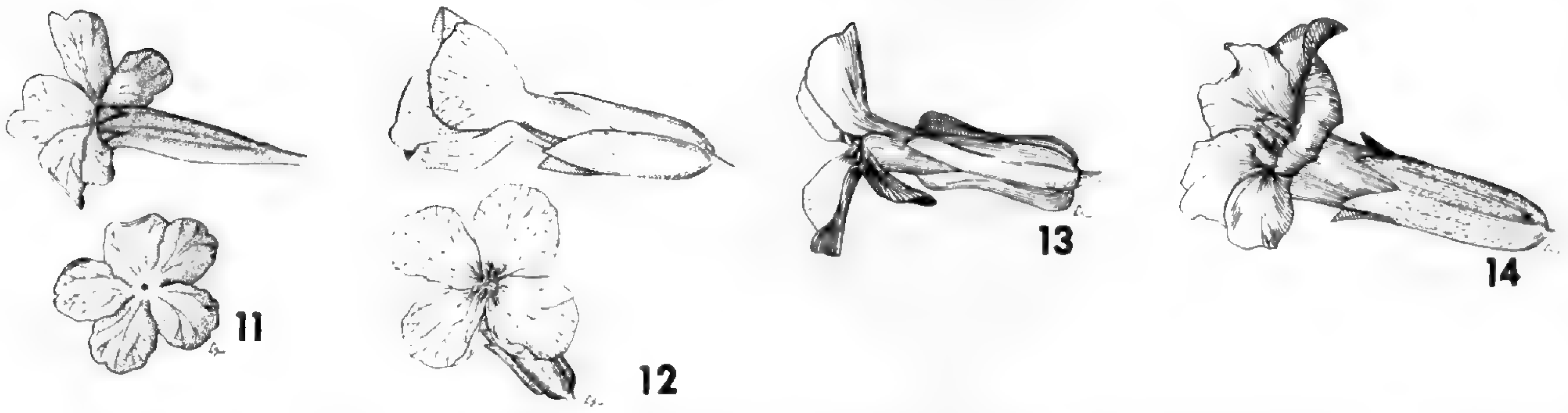
Corolla perforation by nectar-foraging insects is related to zygomorphy but probably originated prior to it, since actinomorphic sympetalous flowers are perforated along with zygomorphic flowers. Zygomorphic and some actinomorphic flowers conceal nectar in corolla spurs and tubes often perforated by bumblebees (*Bombus*) and carpenter bees (*Xylocopa*) that forage regularly in this manner. Although Müller (1879) considered this behavior deleterious to the pollination of the flower, other interpretations are possible. It has been shown that in *Dicentra cucullaria* (Macior, 1970*a*), as in *Vicia* and *Melampyrum* (Biliński, 1970), fertility is not reduced by nectar-foraging through perforations. Furthermore, it is also known that in *Aquilegia canadensis* (Macior, 1966) *Bombus affinis* queens that regularly perforate nectar spurs land first on the essential flower parts and effect pollination before climbing to the less stable spurs to perforate them. If, therefore, corolla perforation does not positively reduce effective pollination it may, in fact, be preadaptive in the sense that it retains forager interest in the flower, which in the future may accommodate the same insect species in its pollination when floral form diverges.

It has also been supposed generally that perforation behavior of insects is the result of the tongue's being too short to reach nectar through the ordinary corolla opening. In the Colorado Front Range, however, *Bombus occidentalis*, which regularly perforates corollas for nectar, has a longer mean tongue length than *B. mixtus*, which never perforates (Macior, 1974*a*). This suggests that perforating behavior is associated with shortness of tongues in nectar-foraging insects but that shortness of tongue is not necessarily associated with perforation behavior.

Considered as a continuing interaction between floral mechanisms and foraging pollinators, concealment and discovery of pollen and nectar provides that variation in degree of coadaptation which assures sufficient future evolutionary adaptability.

FLORAL MIMICRY

If convergent evolution of floral form has occurred between systematically unrelated angiosperm taxa, one may expect to find pollination mechanisms that resemble each other morphologically as already indicated by the flowers of *Dodecatheon* and *Solanum* or of *Linaria* and *Lobelia*. Yeo (1972) suggested that *Calluna vulgaris* and *Euphrasia micrantha* reflect a kind of Batesian mimicry in their flowers. The synchronously and sympatrically blooming pink flowers of *Primula angustifolia* (Fig. 11) and *Erysimum amoenum* (Fig. 12) are apparently mimics that share the same pollinators in the alpine tundra of Colorado (Macior, 1971) as do *Erysimum nivale* (Fig. 13) and *Polemonium viscosum* (Fig. 14). The sharing of pollinators in the same ecological context may indicate the origin of floral mimicry and at the same time suggest a mechanism for sympatric speciation. In a relatively stable pollination system any variation in floral mechanism is not likely to succeed in preferentially attracting pollinators. If, however, the variant resembles a mechanism already receiving substantial attention from pollinators, it may share these insects and at the same time increase its numbers relative to the total community. When the combined mimic and model populations are able to command preferential pollinator activity, the parent stock of the mimic may even be lost in the area. This may be the case with *Erysimum amoenum*, which is sometimes considered a color variant of *E.*



FIGURES 11–14.—11. Flower of *Primula angustifolia.*—12. Flower of *Erysimum amoenum.* —13. Flower of *Erysimum nivale.*—14. Flower of *Polemonium viscosum.*

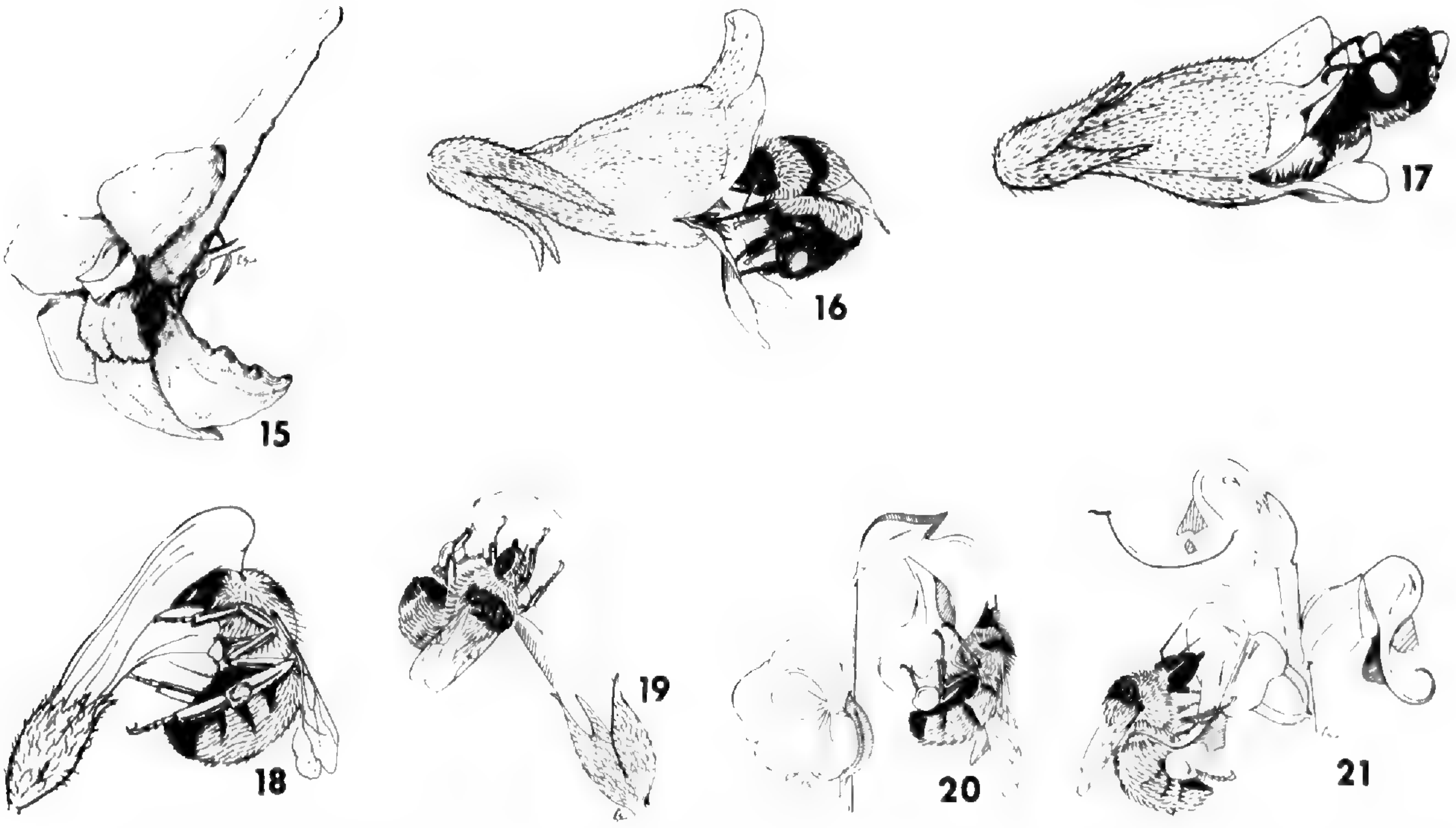
nivale on the alpine tundra, where it usually occurs dissociated from it geographically.

In any attempt to demonstrate mimicry relationships it is essential to study the ecological relationships of floral mechanisms in the field. Morphological comparisons between mechanisms removed from their functional associations are of little value. This is true even in studies of single mechanisms apart from their possible associations in mimicry. *Cypripedium acaule,* for example, is supposedly adapted structurally to prevent self-pollination by reason of the stigma's being placed in advance of the anthers along the pollinator's path through the flower. It has been found recently, however, that pollinators sometimes reverse direction in the flower when they encounter difficulty in squeezing through the exit and deposit pollen from the flower on its own stigma when traversing the labellum a second time before successfully exiting (Wright & Macior, unpublished data).

COMPETITION FOR POLLINATORS AND POLLINATOR SPECTRA OF FLOWERS

The concept of competition of plants for pollinators has received considerable attention in recent years. The management of plant populations for commercial seed production has emphasized the need for abundant pollinators in large, uniform stands of one crop plant (Free, 1970). Similar considerations have been given to large populations of native plants and their interactions with less abundant species in the same habitat. From such areas of interest has arisen the popular concept of competition. Unfortunately few, if any, studies have clearly demonstrated how many native pollinators are actually needed during the blooming period of one native species to provide adequate seed for replacement within and growth of the plant population. Consequently it is difficult, if not impossible, to measure the degree of competition that is taking place at any one time and place between plant species and its impact on the reproductive success of the population.

More information is also needed on the diversity of pollinator species associated with any given pollination mechanism. The classification of floral mechanism by their pollination syndrome has served to identify many mechanisms with one kind of pollinator. It has also obscured more subtle relationships that may exist with other foragers in the same flower. If, for example, one characterizes



Figures 15–21.—15. Flower of *Delphinium tricorne*.—16. Nototribic *Bombus* pollinator on *Penstemon gormanii*.—17. Sternotribic *Bombus* pollinator on *Penstemon gormanii*.—18. Nototribic *Bombus* pollinator on *Pedicularis bracteosa*.—19. Sternotribic *Bombus* pollinator on *Pedicularis bracteosa*.—20. *Bombus* pollinator vibrating pollen from *Pedicularis racemosa*. —21. *Bombus* pollinator vibrating pollen from *Pedicularis groenlandica*.

the nectariferous flower of *Delphinium tricorne* (Fig. 15) as a bumblebee flower on the basis of its commonest pollinator, its dominant purple-blue and ultraviolet corolla reflectance, its long nectar spur, and the coincidence of its blooming phenology with the foraging period of long-tongued bumblebee queens, one's attention may be diverted from the fact that the flower is also effectively and regularly pollinated by nectar-foraging hummingbirds (*Archilochus colubris*). To suggest that all foragers on the flower are successful pollinators, on the other hand, is to overlook the fact that many nectar and pollen foragers are ineffective as pollinators (Macior, 1974*b*). Furthermore it is entirely possible that one kind of pollinator may exhibit two distinctly different foraging behavior patterns on the same floral mechanism. *Penstemon gormanii* in the St. Elias Mountains (Yukon Territory), for example, is pollinated nototribically by nectar-foraging bumblebees (Fig. 16) and sternotribically by the same pollinators foraging for pollen (Fig. 17) (Macior, unpublished data). The corolla is relatively unrestrictive of pollinator types so that other insects forage on and pollinate the flowers. The occurrence of a rather broad spectrum of pollinators on what appears to be a partially selective mechanism may be interpreted as a floral strategy maintaining several avenues of future coadaptive evolution. It may also be indicative of present success in stringent environments where overspecialization for single pollinator types would place the plant at a competitive disadvantage, if pollinators were demonstrated to be scarce during its period of bloom. In any case it is imperative that studies of particular pollination mechanisms be based upon critical observations not only of the mechanisms themselves but of the entire ecological context in which they operate.

PEDICULARIS—A MODEL OF COADAPTIVE EVOLUTION

Many of the concepts of behavioral coadaptation considered thusfar may now be combined in a putative functional history of *Pedicularis* in North America. Based upon behavioral considerations of insects upon which all species studied to date are dependent for their pollination, such a history is likely to diverge from the speculations of Tsoong (1955, 1961) and Li (1951) on taxonomic and morphological grounds.

Dependence upon insect pollinators is reflected in the form and function of all mechanisms, which are zygomorphic. Whether they are nototribic, as in *P. canadensis* (Macior, 1968*b*), or sternotribic, as in *P. lanceolata* (Macior, 1969), however, depends upon the behavior of the insect. Some mechanisms, as in *P. bracteosa* (Figs. 18–19) (Macior, 1970*c*, 1973), function in both ways. Behavior, in turn, depends on the kind of forage collected. Nototribic galeate mechanisms yield both nectar and pollen. Sternotribic mechanisms yield pollen only, even if they are nectariferous. If two distinct foraging patterns of one pollinator type occur in the same species, they are found throughout its geographic range. If only one behavior pattern is found on a mechanism, it is not replaced by another pattern in a population geographically isolated from the first. All rostrate forms (Figs. 20–21) are nectarless and uniformly require pollen vibration foraging by bumblebees (Macior, 1968*a*, 1970*c*, 1973). They are apparently derived from nectariferous, galeate mechanisms through behavioral selection pressure.

Functional convergence of sympatric species unrelated to *Pedicularis* is suggested by bumblebees vibrating pollen from *Pedicularis groenlandica* and *Dodecatheon radicatum* alternately in the same habitat. The taxonomically unrelated plants share the same foraging individuals (Macior, 1968*a*, 1970*c*). Mutually synchronous anthesis, common pink flower color, concealed pollen in sifting mechanisms, and similar habit and habitat strongly suggest convergent evolution together with pollinator sharing. There is no evidence of a dearth of pollinators in these areas indicating possible competition for pollinators and reduced fertility of less successful competition.

Radiating evolution is suggested for pairs of *Pedicularis* species with similar mechanisms. Thus the galeate, endemic *P. rainierensis* is probably derived from the sympatric *P. bracteosa* subsp. *latifolia* in Washington State, while the rostrate *P. groenlandica* and *P. attollens* in California are most likely related in the same manner. With the evidence presently available it is impossible to determine the role that behavioral isolation may have played in segregating these mechanisms, but obligate dependence of these mechanisms upon insects for their successful operation indicates that they could not have evolved without animal pollinators.

NEW DIRECTIONS IN POLLINATION RESEARCH

Basic investigations of the pollination process have increased at a rapid rate over the past decade and promise to continue for some years to come. The impact of human intervention on the pollination ecology of natural areas through the introduction of cultivated plants and pollinators and the decimation of natural vegetation and native pollinators is being felt by researchers in both basic and applied science. Whether sufficient fundamental knowledge of the dynamics of pollination mechanisms is available when required for various applications will be determined not only by the number of researchers active in the field but also by the methods they employ in their investigations.

Our present knowledge of visual, olfactory, and taste perception of pollinators must be related experimentally to the structure and function of pollination mechanisms. Circumstantial evidence between spectral reflectance from corollas and insect vision, between chemical composition of nectars and pollinator taste perception, and other similar correlations is valuable as a starting point for testing the significance of such putative coadaptations. More precise observational techniques of pollinator behavior are also required to document the operation of contemporary pollination mechanisms and to avoid the observational errors of the past. Regional pollination surveys of relatively undisturbed native vegetation will provide suggestive information for experimental investigations of selected floral mechanisms. Most important of all, however, is the absolute need to support all theorizations about the functional and ecological significance of pollination mechanisms with adequate objective evidence lest what is provocative speculation with fragmentary documentation become accepted as established fact and preclude further investigation in a genuinely scientific manner.

LITERATURE CITED

BILIŃSKI, M. 1970. Wyniki obserwacji nad przegryzaniem kwiatów przez trzmiele—*Bombus* Latr. (Hym., Apoidea). Polskie Pismo Ent. 40: 107–123.

CHASE, V. C. 1971. Maintenance of species separation in two columbines— *Aquilegia formosa* and *A. pubescens*. Ph.D. dissertation. Stanford Univ., Stanford, California.

FREE, J. B. 1970. Insect Pollination of Crops. Academic Press, London.

GALIL, J. & Y. SNITZER-PASTERNAK. 1970. Pollination in *Ficus religiosa* L. as connected with the structure and mode of action of the pollen pockets of *Blastophaga quadraticeps* Mayr. New Phytol. 69: 775–784.

GRANT, V. 1950. The flower constancy of bees. Bot. Rev. 16: 379–398.

———. 1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens*. El Aliso 2: 341–360.

HOFFER, E. 1882. Ueber den sogenannten Trompeter in den Hummelnestern. Ent. Nachr. 8: 178–182.

LEPPIK, E. E. 1951. Sind Bienen und Hummeln Arstet? Orion 6: 707–709.

———. 1957*a*. A new system for classification of flower types. Taxon 6: 64–67.

———. 1957*b*. Evolutionary relationship between entomophilous plants and anthophilous insects. Evolution 11: 466–481.

———. 1968. Morphogenic classification of flower types. Phytomorph. 18: 451–466.

LI, H. 1951. Evolution in the flowers of *Pedicularis*. Evolution 5: 158–164.

LINSLEY, E. G. & J. W. MACSWAIN. 1958. The significance of floral constancy among bees of the genus *Diadasia* (Hymenoptera, Anthophoridae). Evolution 12: 219–223.

MACIOR, L. W. 1964. An experimental study of the floral ecology of *Dodecatheon meadia*. Amer. Jour. Bot. 51: 96–108.

———. 1965. Insect adaptation and behavior in *Asclepias* pollination. Bull. Torrey Bot. Club 92: 114–126.

———. 1966. Foraging behavior of *Bombus* (Hymenoptera: Apidae) in relation to *Aquilegia* pollination. Amer. Jour. Bot. 53: 302–309.

———. 1967. Pollen-foraging behavior of *Bombus* in relation to pollination of nototribic flowers. Amer. Jour. Bot. 54: 359–364.

———. 1968*a*. Pollination adaptation in *Pedicularis groenlandica*. Amer. Jour. Bot. 55: 927–932.

———. 1968*b*. Pollination adaptation in *Pedicularis canadensis*. Amer. Jour. Bot. 55: 1031–1035.

———. 1969. Pollination adaptation in *Pedicularis lanceolata*. Amer. Jour. Bot. 56: 853–859.

———. 1970*a*. The pollination ecology of *Dicentra cucullaria*. Amer. Jour. Bot. 57: 6–11.

———. 1970*b*. Pollination ecology of *Dodecatheon amethystinum* (Primulaceae). Bull. Torrey Bot. Club 97: 150–153.

———. 1970*c*. The pollination ecology of *Pedicularis* in Colorado. Amer. Jour. Bot. 57: 716–728.

———. 1971. Co-evolution of plants and animals—systematic insights from plant-insect interactions. Taxon 20: 17–28.

———. 1973. The pollination ecology of *Pedicularis* on Mount Rainier. Amer. Jour. Bot. 60: 863–871.

———. 1974*a*. Pollination ecology of the Front Range of the Colorado Rocky Mountains. Melanderia. 15. 59 pp.

———. 1974*b*. The pollination ecology of *Delphinium tricorne* Michx. (Ranunculaceae). (In press).

MANNING, A. 1957. Some evolutionary aspects of the flower constancy of bees. Proc. Roy. Phys. Soc. 25: 67–71.

MILLER, R. B. 1973. Maintaining species integrity in *Aquilegia*: are pollinators relevant? First Int. Congr. Syst. and Evol. Biol. Unpublished report.

MÜLLER, H. 1879. *Bombus mastrucatus*, ein Dysteleolog unter den alpinen Blumenbesuchern. Kosmos 5: 422–431.

PIJL, L. VAN DER. 1960. Ecological aspects of flower evolution. I. Phyletic evolution. Evolution 14: 403–416.

———. 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. Evolution 15: 44–59.

POWELL, J. A. & R. A. MACKIE. 1966. Biological interrelationships of moths and *Yucca whipplei*. Univ. California Publ. Entomol. 42: 1–59.

RAMIREZ, W. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24: 680–691.

THIEN, L. B. & F. UTECH. 1970. The mode of pollination in *Habenaria obtusata* (Orchidaceae). Amer. Jour. Bot. 57: 1031–1035.

TSOONG, P. 1955. A new system for the genus *Pedicularis*. Acta Phytotaxonomica Sinica 4: 103–147.

———. 1961. A new system for the genus *Pedicularis*. Acta Phytotaxonomica Sinica 6: 252–274.

VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. Bot. Stud. 1: 1–338.

YEO, P. F. 1972. Miscellaneous notes on pollination and pollinators. Jour. Nat. Hist. 6: 667–686.

COEVOLUTION OF *FICUS* AND AGAONIDAE

William Ramírez B.[1]

There are many kinds of wasps, representing several families which develop in the syconia of *Ficus*; however only species of the family Agaonidae act as pollinators. The other fig wasps are parasites either of the syconia or of the Agaonidae. Most of these parasites are unable to penetrate the syconia; they usually have very long ovipositors which allow them to pierce the fig wall and oviposit inside the fig.

Because the agaonids develop and spend most of their lives inside the figs, they responded more to the morphology of the syconial entrance (the ostiolum) and to the distribution, physiology, and morphology of the flowers than to the gross morphological changes suffered by other parts of the fig tree. The modifications found in the syconia and in the flowers of the different groups of figs as well as those found in the bodies of their symbiotic agaonids seem to be the result of mutual adaptations which favored their symbiotic association.

The female agaonid is winged and has structures which help her to carry pollen, to enter the fig through the ostiolum, and to oviposit in the female flowers inside the syconium. The males on the contrary are apterous and usually do not leave the fig in which they develop.

The syconium is a completely closed inflorescence with the flowers located in the internal wall (Figs. 3–4). The only access to the interior of the fig is a very complicated entrance called the ostiolum, which is covered with bracts (Figs. 1–2). There are three kinds of flowers in the fig: long-styled or true female flowers, which usually set seeds; gall flowers, which are short-styled female flowers where the wasps oviposit, and male flowers (Figs. 3–4).

The fig inflorescence is characterized by its high degree of protogyny, the male flowers maturing several weeks after the female. Another characteristic of *Ficus* is the high degree of synchronization in the development of the syconia; all the figs in a tree are pollinated at the same time and thereafter ripen together.

The developmental period of the syconium is divided into several phases (Galil & Eisikowitch, 1968): prefloral phase, which lasts from the time of appearance of the syconial buds to the maturation of the female flowers; the female phase, lasting no more than three days, which corresponds to that time when the female flowers are receptive for pollination and oviposition, during this period the ostiolar scales become loose to facilitate the entrance of the female agaonids; the interfloral phase, which lasts from the end of the pollination and oviposition phase to the maturation of male flowers and the eclosion of a new generation of wasps from the galls. The interfloral phase is usually very constant for each species of fig and seems to be determined by the developing agaonids inside the figs. This phase I have found to last from 15 to 100 days for different neotropical figs (Table 1). The male phase corresponds to the time when the male flowers

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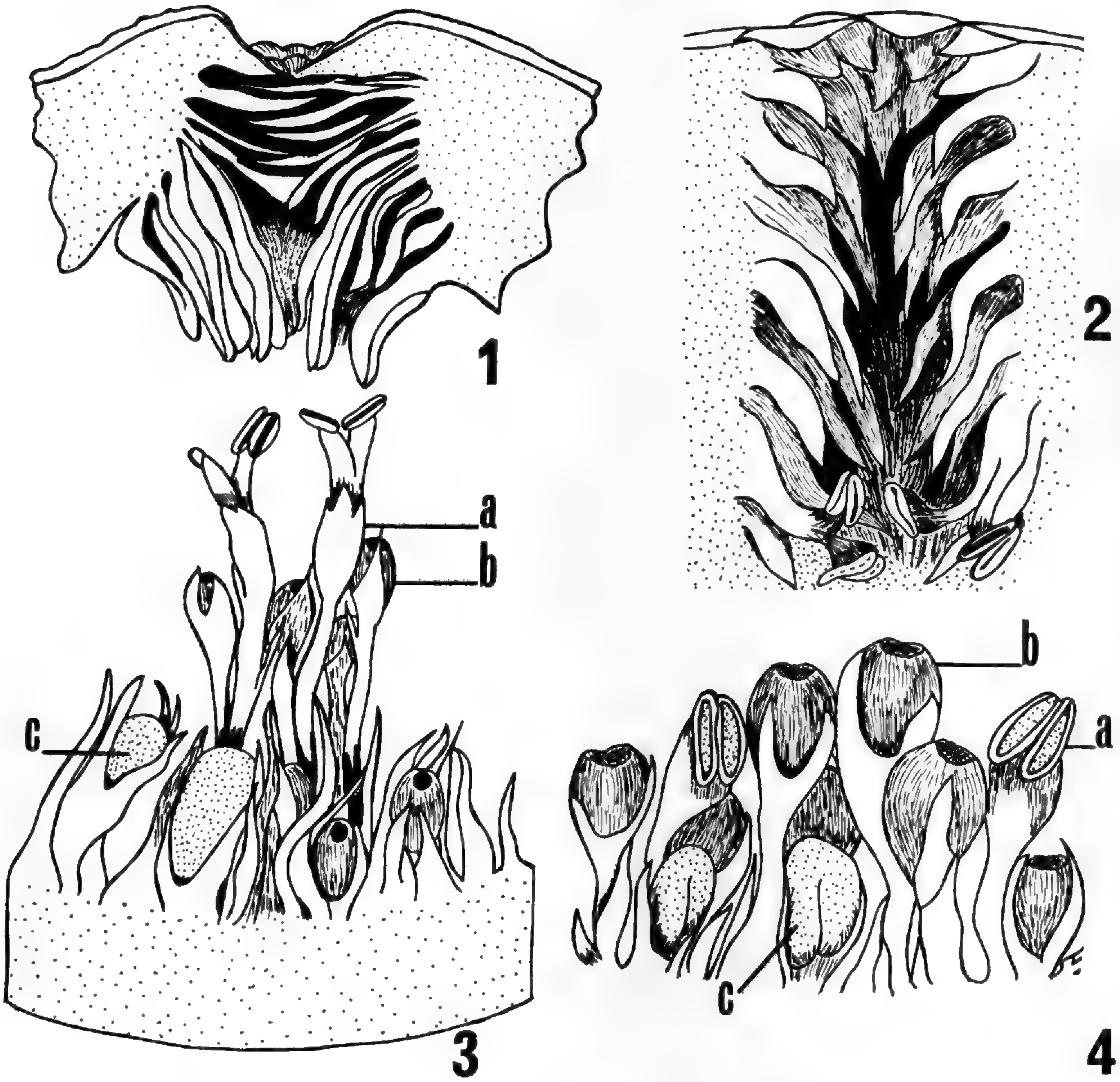
Ann. Missouri Bot. Gard. 61: 770–780. 1974.



FIGURES 1–4. Longitudinal section through the ostiola and the interior of four syconia at male phase.—1. Ostiolum of the Old World *Ficus carica* (after Grandi, 1920).—2. Ostiolum of the New World *Ficus maxima*.—3. Section through the interior of the syconium of *F. maxima* (a, male flower; b, gall flower, and c, mature seed).—4. Section through interior of a New World *Urostigma* fig (section *Americana*); a, male flower; b, gall flower, and c, mature seed.

mature. At this phase the female wasps eclose from their galls after copulation has occurred, search for the ripe anthers, and escape from the figs carrying pollen which they will take to other figs in the female phase.

The male phase lasts only a few hours and usually occurs during early morning in the Neotropics. Once the female agaonids and other fig wasps escape from the mature figs, the syconia become completely ripe, that is, soft and juicy, and the post-floral phase starts. In this phase the figs become edible for frugivorous vertebrates.

Thus, the syconia are traps entered by the female agaonids, which pollinate, oviposit and die inside the syconial cavity. The female wasps which escape from the male phase figs belong to the new generation; the apterous males usually

TABLE 1. Length of interfloral phases of different Neotropical species of *Ficus*. DeWolf (1960) considers that *F. insipida*,* *F. glabrata*,* and *F. crassiuscula** are one species (*F. insipida* Willd.); he also considers that *F. turbinata*** and *F. hensleyana*** are one species (*F. citrifolia* P. Mill.), and that *F. involuta**** and *F. obtusifolia**** are one species (*F. obtusifolia* H.B.K.).

Ficus	Number of days
*F. insipida**	15
F. nymphaeaefolia	20
F. myriacycea	23–28
F. trigonata	27
*F. turbinata***	28
F. maxima	27–30
*F. glabrata**	30
*F. hemsleyana***	27–30
F. oerstediana (= *F. perforata*)	30
F. tonduzii	31
F. bullenei	37
Ficus sp. (No. 4 of Venezuela) (Ramirez, 1970)	41–43
F. popenoi	43
*F. involuta****	43
*F. obtusifolia****	44–45
*F. crassiuscula**	50
F. lapathifolia	56
F. paraensis	60
F. torresiana	70
F. padifolia	100

die inside the fig after mating and gnawing an exit for the escape of their female siblings.

Association of Different Syconial Characters with some Morphological and Biological Characters

The *Ficus*-pollinating agaonid species have become completely adapted in their morphology and physiology to the species of fig in which they develop, while the syconial features of each *Ficus* species also exhibit a morphological and physiological adjustment to the corresponding pollinator species. The most striking cases of coevolution between *Ficus* and Agaonidae are explained below.

MONOECISM

This condition is found in those figs in which the true "female flowers," "gall flowers," and male flowers develop in the same syconium; thus the production of pollen, seeds, and wasps occurs in the same syconium (Figs. 3–4). The monoecious figs have two kinds of female flowers which differ mainly in the length of the styles and size of the stalks. The stalked flowers usually have short styles which are as long as or shorter than the length of the ovipositor of the symbiotic agaonid of the fig. The short-styled flowers are used for oviposition; however, these kinds of flowers may also function as true female flowers which are transformed into seeds if they are pollinated artificially or by the agaonid. The other kind of female flowers have styles which are usually much longer than the ovipositor of the agaonid; thus, the wasps are unable to oviposit in their ovaries. The long-styled female flowers usually become transformed into seeds if pollinated by the egg-laying wasps.

Monoecious figs: Subgenus *Urostigma*, subgenus *Pharmacosycea*, section *Sycomorus* (*sensu* Ramírez, 1974), and two species of section *Sycocarpus* (*F. microdictya* and *F. pritchardii*).

Associated characters of the agaonids: Presence of long ovipositors which are usually as long as or longer than the gasters. Such long ovipositors are necessary because the styles of gall flowers of monoecious figs are longer than those of dioecious figs.

Agaonids with long ovipositors: *Agaon, Alfonsiella, Allotriozoon, Blastophaga* groups E, F, G, the *Ceratosolen* which inhabit section *Sycomorus* (*sensu* Ramírez, 1974), and two species of section *Sycocarpus*, the megarhophalus group, *Dolichoris, Elisabethiella, Eupristina, Maniella, Paragaon, Pegoscapus, Pleistodontes, Tetrapus*, and *Waterstoniella*.

DIOECISM

This condition exists in those figs in which the long-styled female flowers (true "female flowers") are located in one kind of syconium the "seed fig," while the short-styled female flowers, the "gall flowers," and the male flowers grow in another kind of syconium, the "gall fig." The seed fig usually has no functional male flowers. The two kinds of syconia ("gall" and seed "figs") usually occur in the same tree but in some species (*e.g. F. carica*, the edible fig) the gall and seed figs are located in different trees. Both kinds of figs attract the egg-laying agaonids and are entered by them The long-styled female flowers of the seed fig are pollinated by the agaonids, and as rule most, if not all, become seeds because the wasps are unable to oviposit in their ovaries. In the gall fig, the agaonids are able to oviposit in the majority, if not all, the female flowers which therefore become transformed into psenocarps or galls. It is not known for sure if the gall flowers are receptive when they are artificially pollinated; although some seeds have been occasionally found in the gall figs of *F. carica.* The "gall figs" and "seed figs" are quite similar externally and are confused by the agaonids, although they show some differences, *e.g.* the gall figs are usually smaller, less colorful, less sweet and much drier at male phase than the seed figs. Gall figs are usually characterized by the presence of abundant sclerotic cells on the receptacular wall, and they become ripe much faster than the seed figs pollinated at the same time. It seems probable that the precocious maturity of the gall figs is due to the presence of the developing agaonids. Corner (1933) reports for *F. fistulosa* and *F. variegata* that the gall receptacles develop and ripen in two-thirds of the time required by the female receptacles which persist full-sized on the plant for a month or so longer.

Group of dioecious figs: Subgenus *Ficus* and subgenus *Sycomorus* (both *sensu* Ramírez, 1974) except section *Sycomorus* and two species of the section *Sycocarpus* which are monoecious.

Associated character of the agaonids: Presence of very short slightly projecting ovipositors, related to the short styles of gall flowers of all dioecious figs.

Agaonids with short ovipositors: *Blastophaga* groups A, B, C, and D and most *Ceratosolen*, except the pollinators of section *Sycomorus* (*sensu* Ramírez, 1974) and of *F. microdictya* and *F. pritchardii* of section *Sycocarpus*.

ENTRANCE OF POLLINATORS THROUGH OSTIOLE

A. *Syconial entrance with superficial interleafing bracts*: This type of entrance (as in Fig. 1) is found in most *Ficus* with the exception of section *Pharmacosycea* of subgenus *Pharmacosycea* (Fig. 2).

Associated characters of the agaonids: Breakage of the antennae and wings when the wasps enter the figs at female phase. The breakage of the structures mentioned probably facilitates the entrance into the figs; certainly the wasps tolerate this breakage as they enter among the tightly fitting bracts.

Wasps which break the antennae and wings: All agaonidae except those of genus *Tetrapus*. *Sycophaga sycomori* (Sycophaginae), a torymid that enters the fig, also breaks the antennae and wings when it passes through the interleafing superficial scales of its host *Ficus sycomorus*.

B. *Syconial entrance without superficial interleafing bracts*: This condition occurs only in New World section *Pharmacosycea* (Fig. 2) which is exclusively pollinated by *Tetrapus*.

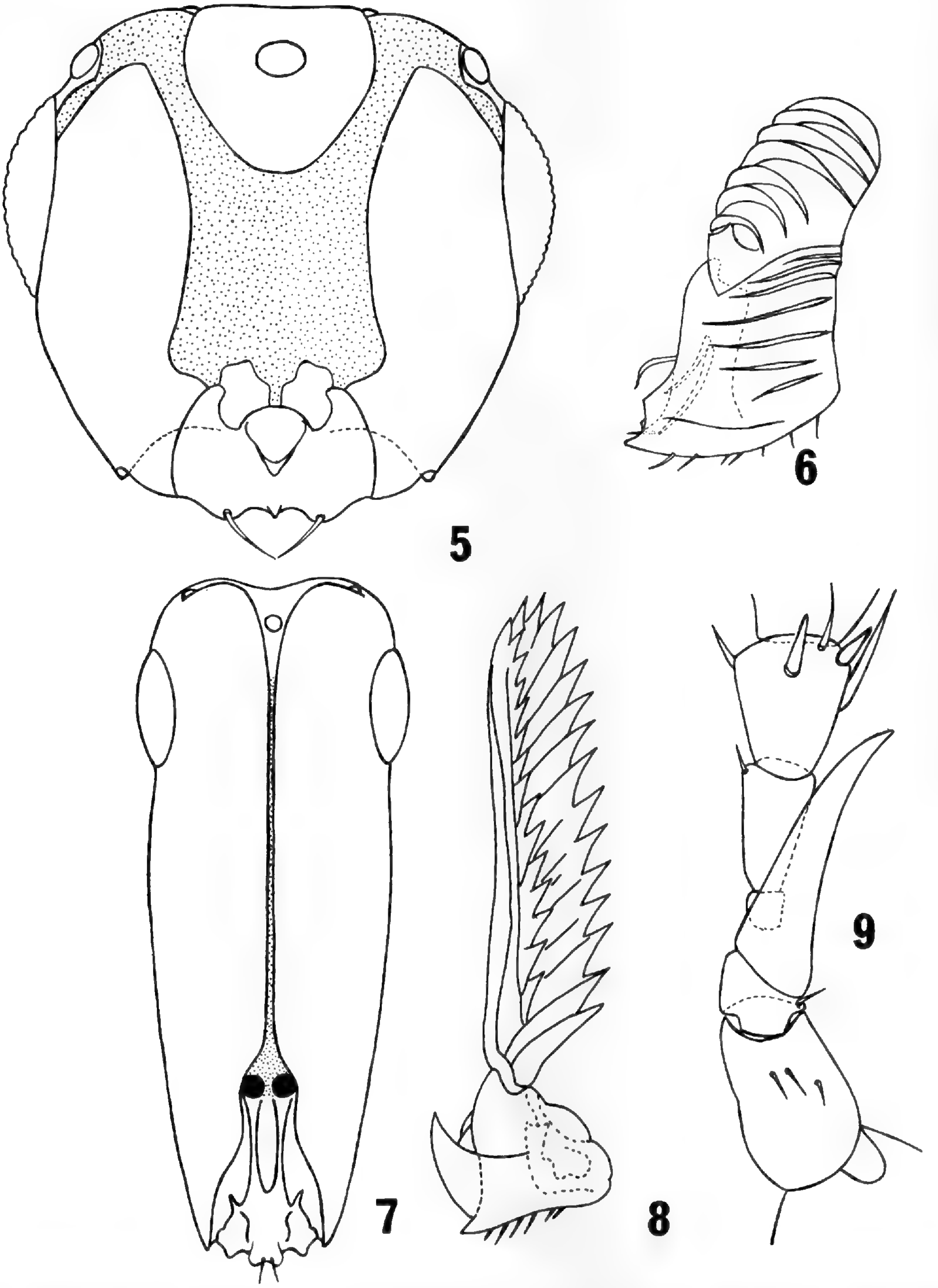
Associated characters of Tetrapus: They break neither the antennae nor the wings when they enter the figs at female phase.

C. *Syconial entrance with helicoidal bract arrangement*: The bracts of this type of ostiolum (Fig. 1) are imbricated and located in such way that they form a helicoidal entrance. The agaonids that penetrate figs with that type of ostiola have to turn around several times among the ostiolar bracts to reach the internal cavity of the syconium.

Groups of figs with helicoidal ostiolar entrance: Subgenera *Ficus* and *Sycomorus* (*sensu* Ramírez, 1974) and the sections *Americana, Conosycea, Leucogyne, Stilpphyllum,* and *Urostigma.*

Associated characters of the agaonids. A) Subquadrangular or subhemispherical flattened heads which are usually as long as broad across the eyes (as in Fig. 5); B) short mandibular appendages with lamellae (as in Fig. 6); short subhemispherical or subtriangular depressed scapes; D) usually long scale-like antennal processes (as in Fig. 9).

Groups of agaonids with the characters described: *Blastophaga* (subgenera, *Blastophaga, Eupristina, Parapristina, Pegoscapus,* and *Waterstoniella*), *Ceratosolen,* and *Liporrhopalum.* All the characters described above for the head characterize the megarrhopalus group and *Dolichoris vasculosae,* but their antennal processes are short and not scale like. *Dolichoris* is peculiar in having unidentate mandibular lamellae. *Sycophaga sycomori* (Sycophaginae) and the wasps of the tribe Sycoecini except *Seres armipes* have subquadrangular flattened heads and also enter figs with helicoidal ostiolar entrances.



FIGURES 5–9. Dorsal views of heads, mandibles and antennal process.—5. Head of *Maniella delhiensis*, the pollinator of *F. tsiella*, (section *Leucogyne*), a fig with helicoidal ostiolar entrance (as in Fig. 1).—6. Mandible of *Blastophaga amabilis*, the pollinator of *F. nymphaeaefolia* (section *Americana*), a fig with helicoidal ostiolar entrance.—7. Head of *Pleistodontes regalis* (after Grandi, 1952, Fig. IX, 1), the pollinator of *F. pleurocarpa* (section *Malvanthera*), a fig with tubular ostiolar entrance as in Fig. 2.—8. Mandible of *Tetrapus costaricanus*, the pollinator of *F. glabrata* (section *Pharmacosycea*), a fig with tubular ostiolar entrance.—9. Base of antennal flagellum of *Maniella delhiensis* showing the antennal scale-like process.

D. *Syconial tubular entrance*: This kind of ostiolum has the majority of the bracts pointing down, that is inflexed (as in Fig. 2) so that they form a long tubular ostiolar tunnel through which the wasps enter. Sections *Galoglychia* and *Malvanthera* have 2 or 3 interleafing superficial ostiolar bracts on top of the tubular tunnel. The wasps penetrate in a straight way, although they break the antennae and wings under the superficial bracts.

Groups of figs with tubular ostiolar tunnel: Sections *Galoglychia* and *Malvanthera* of subgenus *Urostigma* and section *Pharmacosycea* (Fig. 2) of subgenus *Pharmacosycea.*

Associated characters of the agaonids: Head usually long, in some agaonids more than one-half as long as broad across the eyes (Fig. 7); scapes long; antennal processes short, not scale-like, unsegmented; mandibular appendages long, usually with transverse rows of teeth (Fig. 8). The type of ostiolum mentioned seems also to be associated with the presence of odontoid spiniform processes on the front tarsi in *Pleistodontes* and *Tetrapus. Seres armipes* (subfamily Sycophaginae, tribe Sycoecini), a wasp that also penetrates a fig with long tubular ostiolar entrance, also has a long head and spiny processes on the front tibiae.

Groups of agaonids with the characters described: *Alfonsiella, Agaon, Allotriozoon, Elisabethiella, Paragaon, Pleistodontes*, and *Tetrapus.*

ESCAPE OF FIG WASPS FROM SYCONIA

A. *Dehiscence of the gall-fig at male phase*: This condition exists in the moraceous genus *Sparattosyce* in which the male inflorescences splits when ripe, thus exposing the male flowers to the wind that diseminates the pollen; the female inflorescences also splits when ripe. The dehiscence of the gall figs is a condition that permits the agaonids to escape at male phase.

Related characters of the agaonids: The males do not gnaw exits for the escape of the females from the figs at male phase.

Group of agaonids with the character described: The agaonids inhabiting section *Ficus* subseries *Dehiscentes* of Corner (1965), that is, those of *Blastophaga* group A.

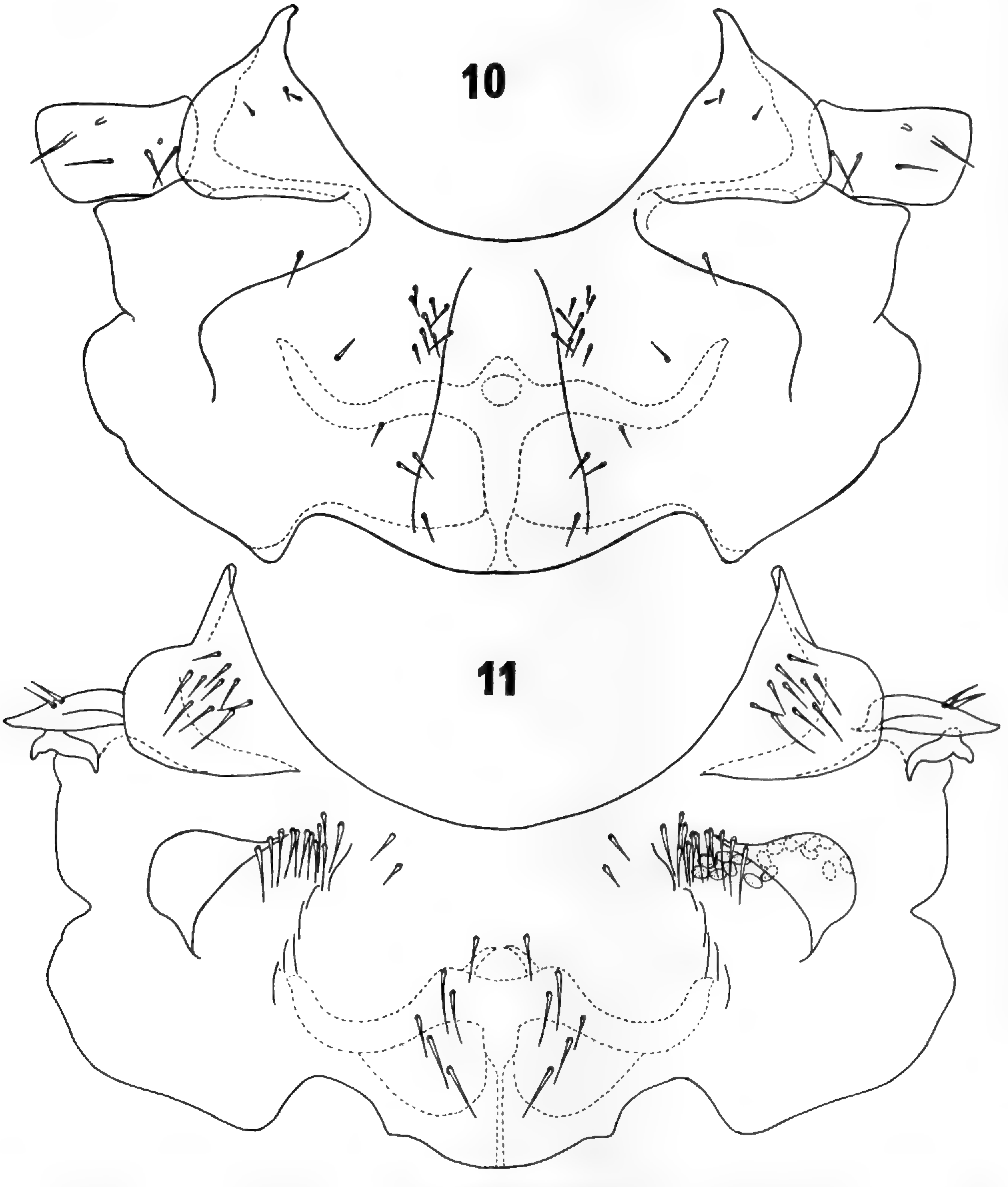
B. *Natural opening of the ostiolum at male phase*: In some groups of fig the ostiolar bracts become loose and form a natural exit for the escape of the agaonids as well as other sycophillous wasps.

Groups of figs with ostiola which open naturally at male phase: Sections *Ficus, Eriosycea* (both *sensu* Ramírez, 1974), *Kalosyce, Rhizocladus*, and probably *Sinosycidium.* It is not known if the figs of section *Paleomorphe* open the ostiola naturally.

Associated characters of the agaonids: The males do not gnaw exits for the escape of the females at male phase.

Groups of wasps with the character described: *Blastophaga* groups A and B, also probably *Liporrhopalum.*

C. *Ostiola which do not open at male phase*: In the majority of figs the ostiolar bracts do not open when the fig reaches maturity.



FIGURES 10–11. Mesosterna of *Blastophaga* wasps.—10. *Blastophaga psenes* (of *Blastophaga* group A), the pollinator of *Ficus carica* (section *Ficus*), a fig with abundant male flowers as in Fig. 3. Note the absence of corbiculae.—11. *Blastophaga malavarensis* the pollinator of *F. virens* (section *Urostigma*), a fig with male flowers as in Fig. 4. Note some grains of pollen in the right corbicula.

Groups of figs whose ostiola do not open naturally: Subgenera *Urostigma, Pharmacosycea, Sycomorus* (*sensu* Ramírez, 1974), and sections *Phaeopilosae* and *Sycidium* of subgenus *Ficus* (*sensu* Ramírez, 1974).

Associated characters of the agaonids: The males gnaw exits through the receptacular wall for the escape of the females. In most figs the males pierce the exit through the ostiolum.

Groups of agaonids which gnaw exits for the escape of the females: All the pollinators which inhabit the subgenera *Urostigma*, *Pharmacosycea*, and *Sycomorus* and the sections *Phaeopilosae* and *Sycidium* of *Ficus*.

MALE FLOWERS

Several characteristics of the figs' male flowers are associated with the amount of pollen produced and with the system of pollen transport used by the agaonids. The presence of numerous male flowers (about 35 or more per 100 gall flowers) and of long-stalked male flowers with large anthers from which the pollen comes out naturally is associated with the production of abundant pollen.

Groups of figs with the characteristics mentioned: Sections *Ficus*, *Kalosyce*, *Rhizocladus*, and probably *Sinosycidium* of subgenus *Ficus* (*sensu* Ramírez, 1974); section *Pharmacosycea* of the subgenus *Pharmacosycea* (Fig. 3); section *Malvanthera* and probably the series *Glaberrimae*, some subseries of series *Drupaceae*, *e.g.* *Zygotricheae*, *Crassirameae* of the section *Conosycea* (subgenus *Urostigma*).

Associated characters of the agaonids: Absence of corbiculae to carry pollen (Fig. 10), however, some *Waterstoniella* wasps, *e.g.* *B. masii* and the megarhopalus group, have minute sternal corbiculae. Also, abundant male flowers with large anthers are associated with the habit of eating pollen by the females when they eclose from their galls at male phase.

Groups of agaonids which eat pollen: *Blastophaga* group A, in the subgenus *Ficus*; *Tetrapus* in the section *Pharmacosycea* of the subgenus *Pharmacosycea*; *Pleistodontes* in the section *Malvanthera* and the megarhopalus group and *Waterstoniella* in the section *Conosycea* of the subgenus *Urostigma*.

Other groups of figs usually have few male flowers per 100 galls. The male flowers (Fig. 4) are usually short-stalked (if not sessile) and have small anthers from which the pollen does not come out after dehiscence without wasp activity.

Groups of figs with few male flowers per fig: Sections *Sycidium*, *Copiosae*, and *Paleomorphe* of the subgenus *Ficus* (*sensu* Ramírez, 1974); subgenus *Sycomorus* (*sensu* Ramírez, 1974); section *Oreosycea* (subgenus *Pharmacosycea*) and sections *Americana*, *Leucogyne*, *Stilpnophyllum*, *Urostigma*, and some subseries of section *Conosycea* (subgenus *Urostigma*).

Related characters of the agaonids: They usually have conspicuous corbiculae (Fig. 11), search for ripe anthers, extract the pollen from the thecal sacs, load their corbiculae with their front legs and so far as known do not eat pollen.

Agaonids with the characters mentioned: *Agaon*, *Alfonsiella*, *Allotriozoon*, *Blastophaga* groups B, C, D, F, and G; *Ceratosolen*, *Dolichoris*, *Elisabethiella*, *Eupristina*, *Liporrhopalum*, *Maniella*, *Parapristina* and *Pegoscapus*.

THE EVOLUTION OF AGAONIDAE IN DIFFERENT GROUPS OF *FICUS*

The Agaonidae are specific not only to the species level but also to different groups of figs. Some groups of figs are inhabited by a single agaonid group (genus or subgenus). Other groups of figs have more than one agaonid genus

TABLE 2. Suggested classification of the genus *Ficus* considering the fig wasps as taxonomists; with a list of the agaonid pollinators (modified from Hill, 1967) of each group, and the presence or absence of corbiculae.

				Corbiculae		
Subgenus	Section	Subsection	Agaonidae	Absent	Sternal	Coxal
Urostigma	*Urostigma*		*Blastophaga* Group E		+	+
	Leucogyne		*Maniella*		+	+
	Conosycea	*Conosycea*	*Blastophaga*		+	+?
			Megarhopalus group		+	
			Eupristina		+	+
			Waterstoniella	+		
			Waterstoniella		+	
		Dictyoneuron	*Waterstoniella*	+		
			Eupristina		+	+
		Benjamina	*Parapristina*		+	+
	Stilpnophyllum		*Blastophaga clavigera* (= *Blastophaga* Group G)		+	+?
	Malvanthera		*Pleistodontes*	+		
			Pleistodontes		+	+
	Galoclychia		*Agaon*		+	+
			Alfonsiella		+	+
			Allotriozoon		+	+
			Elisabethiella		+	+
			Paragaon		+	
	Americana		*Pegoscapus*		+	+
Pharmacosycea	*Oreosycea*		*Blastophaga* Group F		+	+
			Dolichoris		+	+
	Pharmacosycea		*Tetrapus*	+		
Ficus	*Ficus*		*Blastophaga* Group A	+		
	Rhizocladus		*Blastophaga* Group A	+		
	Kalosyce		*Blastophaga* Group A	+		
	Sinosycidium[a]					
	Eriosycea		*Blastophaga* Group B		+	
	Sycidium	*Scabrae*	*Blastophaga* Group B		+	
		Varinga	*Blastophaga* Group B		+	
	Phaeopilosae		*Blastophaga* Group C		+	
	Paleomorphe	*Paleomorphe*	*Liporrhopalum*		+	
		Copiosae	*Blastophaga* Group D		+	

Table 2. (*continued*)

Subgenus	Section	Subsection	Agaonidae	Corbiculae Absent	 Sternal	 Coxal
Sycomorus	*Adenosperma*		*Ceratosolen*		+	
	Neomorphe		*Ceratosolen*		+	
	Prostratae		*Ceratosolen*		+	
	Pungentes		*Ceratosolen*		+	
	Pseudopalmeae		*Ceratosolen*		+	
	Rivulares[b]				+	
	Sycocarpus		*Ceratosolen*		+	
	Sycomorus		*Ceratosolen*		+	

[a] Probably pollinated by a wasp of *Blastophaga*, Group A.

[b] Probably pollinated by a *Ceratosolen* wasp.

or subgenus; however, such agaonid groups are also peculiar to a single group of figs.

Table 2 shows a classification of the figs and their accompanying agaonids. Both are based on Ramírez (1974). The correspondence between groups of figs and of pollinators is evident.

Literature Cited

Corner, E. J. H. 1933. A revision of the Malayan species of *Ficus*: *Covelia* and *Neomorphe*. Jour. Malayan Branch Roy. Asiat. Soc. 9: 1–65.

———. 1965. Check-list of *Ficus* in Asia and Australasia with keys to identification. Gdns Bull., Singapore 21: 1–186.

DeWolf, G. P., Jr. 1960. *Ficus* (Tourn.) L. *In* R. E. Woodson Jr., R. W. Schery *et al.*, "Flora of Panama" 4, 2 (Chlorantaceae to Proteaceae). Ann. Missouri Bot. Gard. 47: 146–165.

Galil, J. & D. Eisikowitch. 1968. Flowering cycles and fruit types of *Ficus sycomorus* in Israel. New Phytol. 67: 745–758.

Grandi, G. 1920. Studio morphologico e biologico della *Blastophaga psenes* (L.). Boll. Lab. Zool. Gen. Agr. Portici 14: 63–204.

———. 1952. Insetti dei fichi Messicani, Malesi ed Australiani. Boll. Ist. Entomol. Univ. Bologna 19: 47–67.

Hill, D. S. 1967. Figs (*Ficus* spp.) and fig-wasps (Chalcidoidea). Jour. Nat. Hist. 1: 413–434.

Ramírez B., W. 1970. Taxonomic and biological studies of Neotropical fig wasps (Hymenoptera: Agaonidae). Univ. Kansas Sci. Bull. 49(1): 1–44.

———. 1974. Host specificity in *Ficus* and Agaonidae. Ph.D. dissertation (in preparation). University of Kansas.

FLORAL EVOLUTION IN *VIOLA*

ANDREW J. BEATTIE[1]

ABSTRACT

Pollination in *Viola* results both from sternotribic and nototribic pollinator responses, the frequencies of which vary according to the plant species. Syndromes of floral characters determine these frequencies, and each is adaptive to a group of pollinators, of variable taxonomic heterogeneity, characterised by particular morphology and behavior. Some syndromes elicit equal frequencies of sterno- and nototribic responses, while others elicit chiefly, or exclusively, one type, and coevolution with a single insect genus may be in progress. One effect of the differing syndromes is the partitioning of pollinator resources among simultaneously flowering species.

An evolutionary sequence for the floral syndromes is proposed which, in broad agreement with systematic conclusions, considers yellow-flowered, sternotribic Chamaemelanium violets as the most ancient and blue-flowered sterno- or nototribic violets of the sections *Rostellatae* and *Plagiostigma* as the most recently evolved. Species of the section *Melanium* (the pansies), in which cleistogamy is almost absent, appear to be an early offshoot leading to multicolored, nototribic flowers.

The "generalist" syndromes were probably vital to the success of the genus in (a) invading the northern and southern temperate zones and (b) adapting to widespread habitat disturbance by man. The basic structure of the violet flower is adaptive to a temperate pollinator complex to be found over very large geographic areas. Floral variations demonstrate adaptive radiation to many ecological conditions.

One of the interesting fields remaining in pollination biology is the creation of a synthetic theory of evolution that links the processes of differentiation of pollination systems as observed in living plant populations with the major trends of coevolution over very long periods of time. The evolution of pollination systems in individual angiosperm families has been the subject of several elegant studies such as Lewis and Raven (1961), Grant and Grant (1965), and Eyde and Morgan (1973). In most cases the sequencial stages in evolution have been typological; the data indicating only major changes in mode of pollination from one group of animals to another, for example from insects to birds. The actual processes of differentiation are still very poorly understood. The purpose of this paper is to suggest processes of change in the pollination systems of *Viola* and then to examine their operation both from contemporary and historical perspectives. Therefore, discussion will focus first on data from living populations and second on how this data may be applied to a phylogeny of pollination systems in the genus.

THE POLLINATION MECHANISM: CLASSICAL DESCRIPTION

This may be best described with reference to Figures 1 and 2. The proboscis of the pollinator, loaded with pollen from another flower, is inserted into the petal-spur via the furrow in the anterior petal. As the proboscis and adjacent structures slide under the style the pollen load accumulates at the opening of the stigmatic cavity, which acts as a scoop, like a snow-shovel. Simple extension of the proboscis is insufficient to obtain nectar so the head of the insect is pushed

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ANN. MISSOURI BOT. GARD. 61: 781–793. 1974.

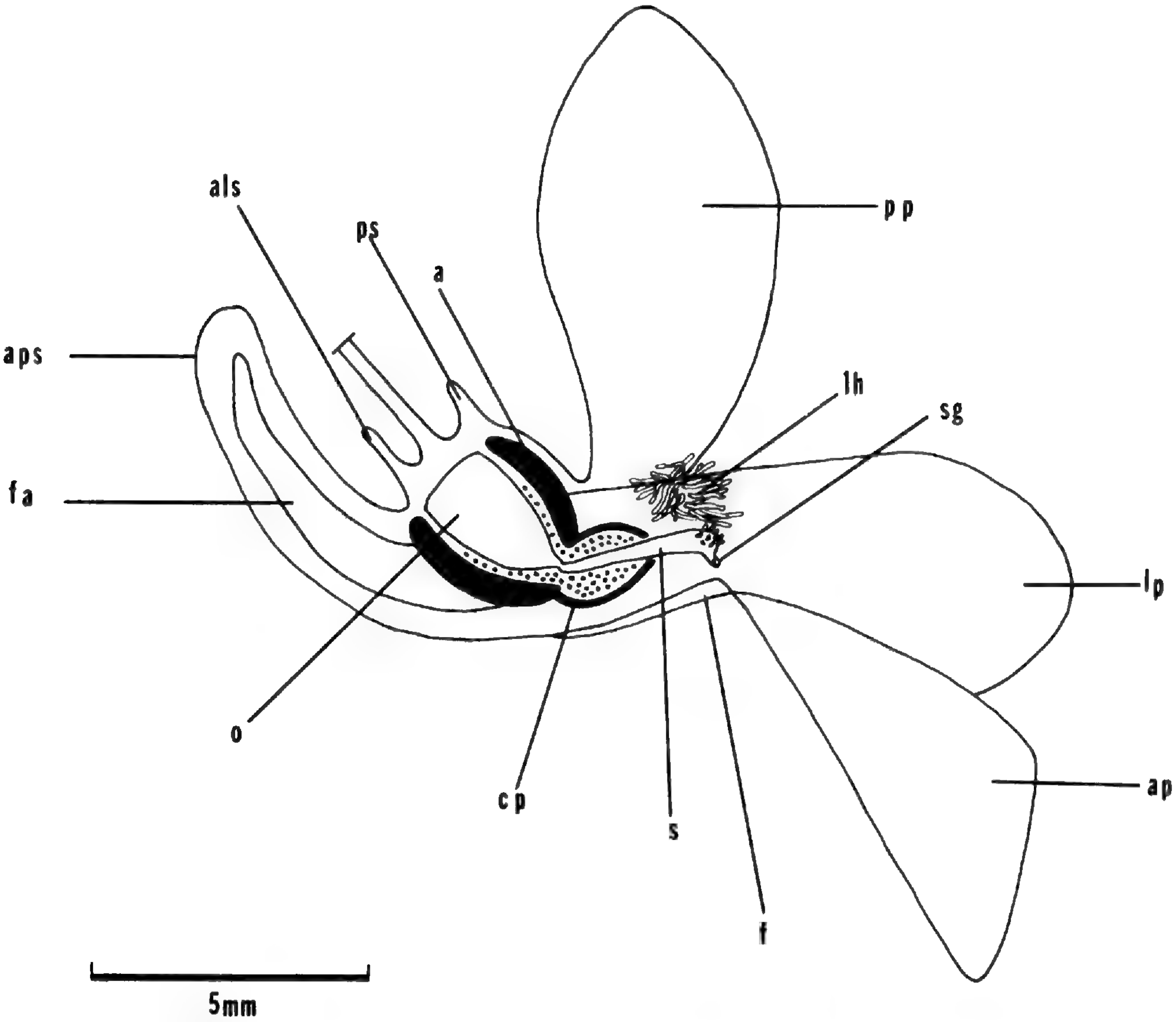

FIGURE 1. Diagrammatic half-flower of *Viola*. als: anterior sepal, ap: anterior petal, aps: anterior petal-spur, a: anther, cp: connective appendage, f: furrow in anterior petal, fa: filament appendage (nectary), lh: lateral hairs ("beards"), lp: lateral petal, o: ovary, pp: posterior petal, ps: posterior sepal, s: style, sg: opening of stigmatic cavity.

into the flower, below the style, raising it to a steep angle. This deflection acts as a lever to open the cone of connective appendages which contains the loose, powdery pollen. It is this opening in the appendages through which a new load of pollen cascades on to the pollinator, normally the dorsal surfaces of the proboscis and head. Simultaneously the old pollen load at the stigma-opening is pushed into the stigmatic cavity by the head of the pollinator. When the proboscis is withdrawn the style snaps back into place, closing the cone of appendages and, by a kind of suction, ingesting any pollen still remaining outside the stigmatic cavity. Figure 2 shows clearly that the classical view is that *Viola* is nototribe and adapted to long- and medium-tongued, nectar-seeking insects—especially bees.

THE POLLINATION MECHANISM: REVISED DESCRIPTION

It is curious that the great classical pollination biologist Christian Sprengel, having described the above mechanism, provided an illustration of a bee feeding in a completely different posture. And it is a fact that a large proportion of in-

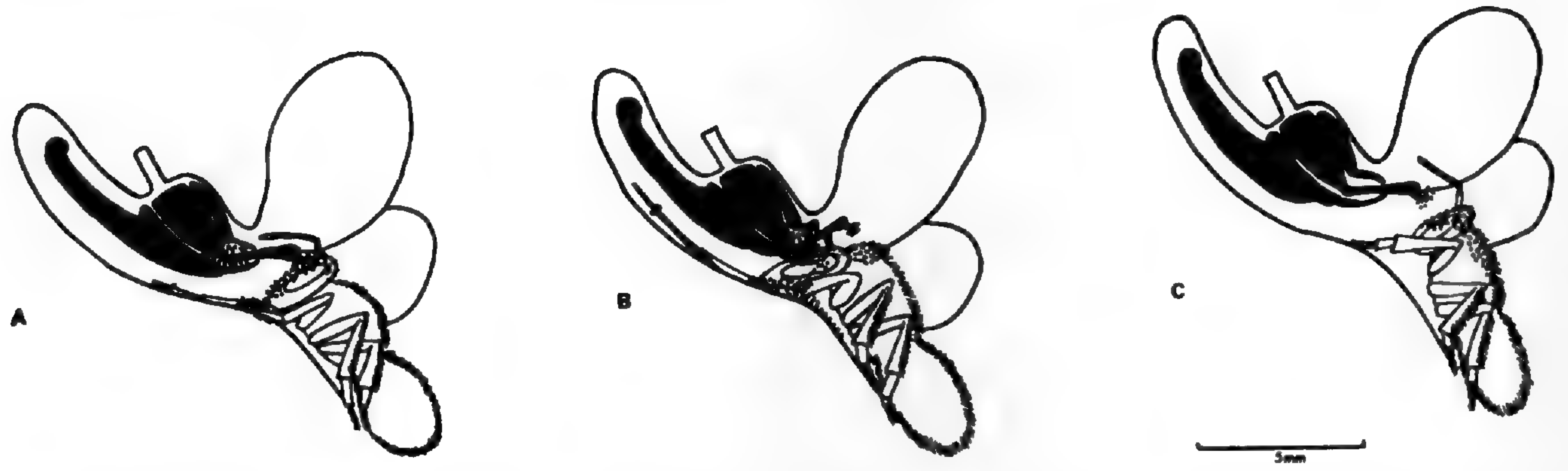

FIGURE 2. Diagram to show nototribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

sect visits involve not the "normal" or prone position as described, but the "upside-down" or supine position illustrated by Figure 3. Most solitary bees adopt the supine position while feeding. Usually the insect orients to the flower as before but prior to probing and feeding rotates so as to be virtually standing on its head. It can be seen from Figure 3 that the pollination mechanism operates exactly as before but *the flower is now sternotribe.* A further difference is that more of the insect receives pollen, it usually being scattered over the ventral surfaces of the proboscis, head, and thorax. Even the ventral abdomen becomes involved in bees with abdominal pollen scopae. Also the solitary bees which operate the pollination mechanism by the supine feeding position are frequently seeking, and getting, both nectar and pollen. A complete description of all the mechanisms and positions may be found in Beattie (1971).

STERNOTRIBY VERSUS NOTOTRIBY

All species of *Viola* so far investigated in the field experience pollination by several groups of insects and are said to exhibit a spectrum of pollinators and pollination effects. Thus, medium- and long-tongued, nectar-seeking insects tend

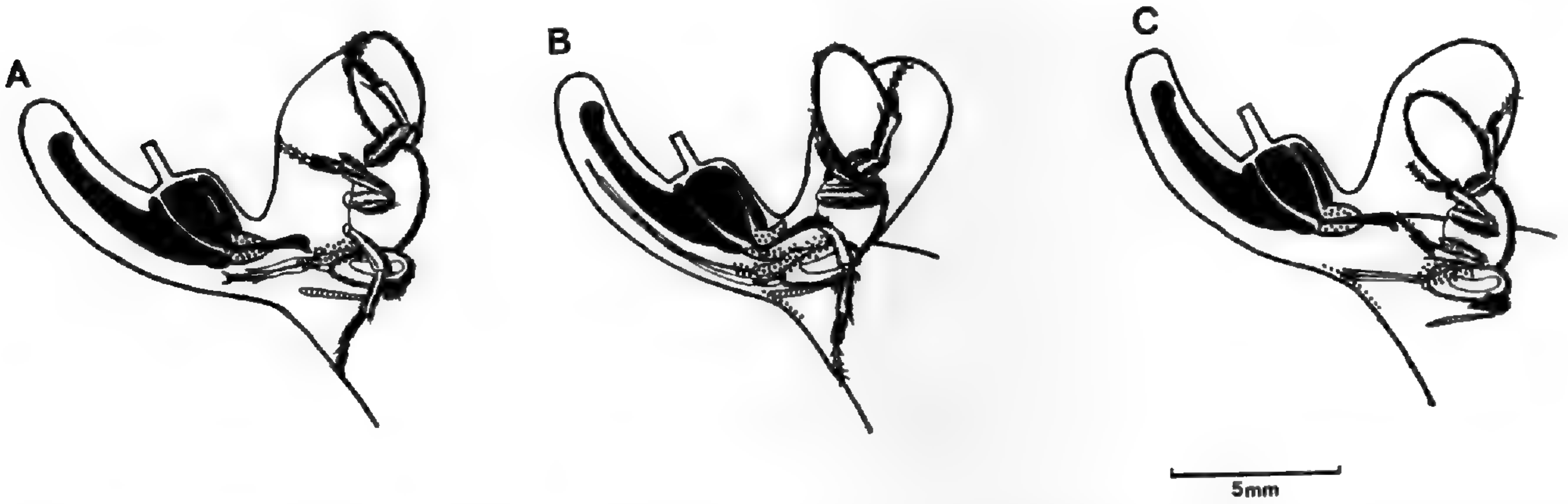

FIGURE 3. Diagram to show sternotribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

TABLE 1. Frequency of visits by bumblebees, solitary bees, syrphids, Bombyliids and Lepidopterans to each of twelve species of *Viola*; expressed as percentage of total number of visits taken from five populations of each species. ** = major group of pollinators, 20% or more of total visits. * = minor group of pollinators, 10–20% of total visits only. (Data for *Viola tricolor* taken from published lists.)

	Viola Species											
Visitor Species	*nuttallii*	*eriocarpa*	*striata*	*reichenbachiana*	*rostrata*	*hirta*	*adunca*	*blanda*	*papilionacea*	*fimbriatula*	*pedata*	*tricolor*
Bumblebees	0	0	19*	19*	0.5	40**	0	0	5	5	10*	93**
Solitary bees	84**	85**	50**	3	28**	40**	89**	87**	64**	95**	64**	0
Syrphids	3	8	28**	70**	15*	0	5.5	8	17*	0	4	0
Bombyliids	1	6	1	8	55**	20**	5.5	5	12	0	1	0
Lepidoptera	12*	1	2	0	1.5	0	0	0	2	0	21**	7
Sternotriby	84	85	50	3	28	40	89	87	64	95	64	0
Nototriby	16	15	50	97	72	60	11	13	36	5	36	100

to be systematic cross-pollinators, while short-tongued or pollen-gathering species tend to be chance cross- or self-pollinators. A glance at Table 1 will show that some violet species receive a majority of visits from just one or two groups (or "bands") of the spectrum, while others receive visits from several. For example, the major pollinators of *Viola nuttallii* are solitary bees, but butterflies may be occasionally important. *Viola striata*, on the other hand, may experience high frequencies of pollination visits by three insect groups: bumblebees, solitary bees, and syrphid flies.

As a consequence of the presence of variable pollination spectra most violet species receive a majority of visits from either sternotribic or nototribic pollinators. The data in Table 1 have been accumulated from prolonged observations of at least five populations of each species; the populations having been chosen on the basis of maximum ecological and geographic differences. Further data has not significantly altered the figures for percentage sternotriby,[2] consequently individual violet species can be characterized as being predominantly sternotribic, predominantly nototribic, or "generalist" (having approximately equal number of the two types of visits).

It is clear from pollination data published elsewhere (*e.g.* Beattie, 1972) that the habitat determines which groups of pollinators may be available to any violet species, and, therefore, habitat preferences exhibited by the plant species will determine to a great extent, the availability of sternotribe and nototribic pollinators. However, certain floral characters do have selective effects in *Viola* and inhibit visits from some groups while encouraging visits from others. Expressing this in more specific terms; the floral biology of individual species may be most adaptive to either sternotribic or to nototribic pollinators, with some intermediates. An interesting consequence of this is the partial partitioning of pollinator resources among sympatric, simultaneously flowering species. For example, *Viola striata* and *V. papilionacea* very frequently bloom together, but *V. striata* is clearly a generalist, while *V. papilionacea* is more sternotribic. The partioning is clearer between *V. rostrata*, which is nototribic, and *V. blanda*, which is sternotribic. These two species occur together in dense stands in the mesic forests of the Eastern U.S.A., and the assortative foraging of pollinators is easily observable.

FLORAL SYNDROMES

The fact that pollinators descriminate between resource species on the basis of obvious differences in the flowers—such as corolla color—has been appreciated by many workers (*e.g.* Levin, 1972). Descrimination of floral characters leading to sternotribic or nototribic visits appears to have a more subtle basis. With the exception of very occasional worker bumblebees, solitary bees are the only

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[2] By contrast with Grant and Grant (1965) there was no evidence for ecogeographical races where the same species is pollinated by different insect groups in different regions. For example, an altitudinal transect across the southwestern Rockies showed that *Viola nuttallii* was visited chiefly by solitary bees wherever it grew, with no increase in fly visitors according to altitude.

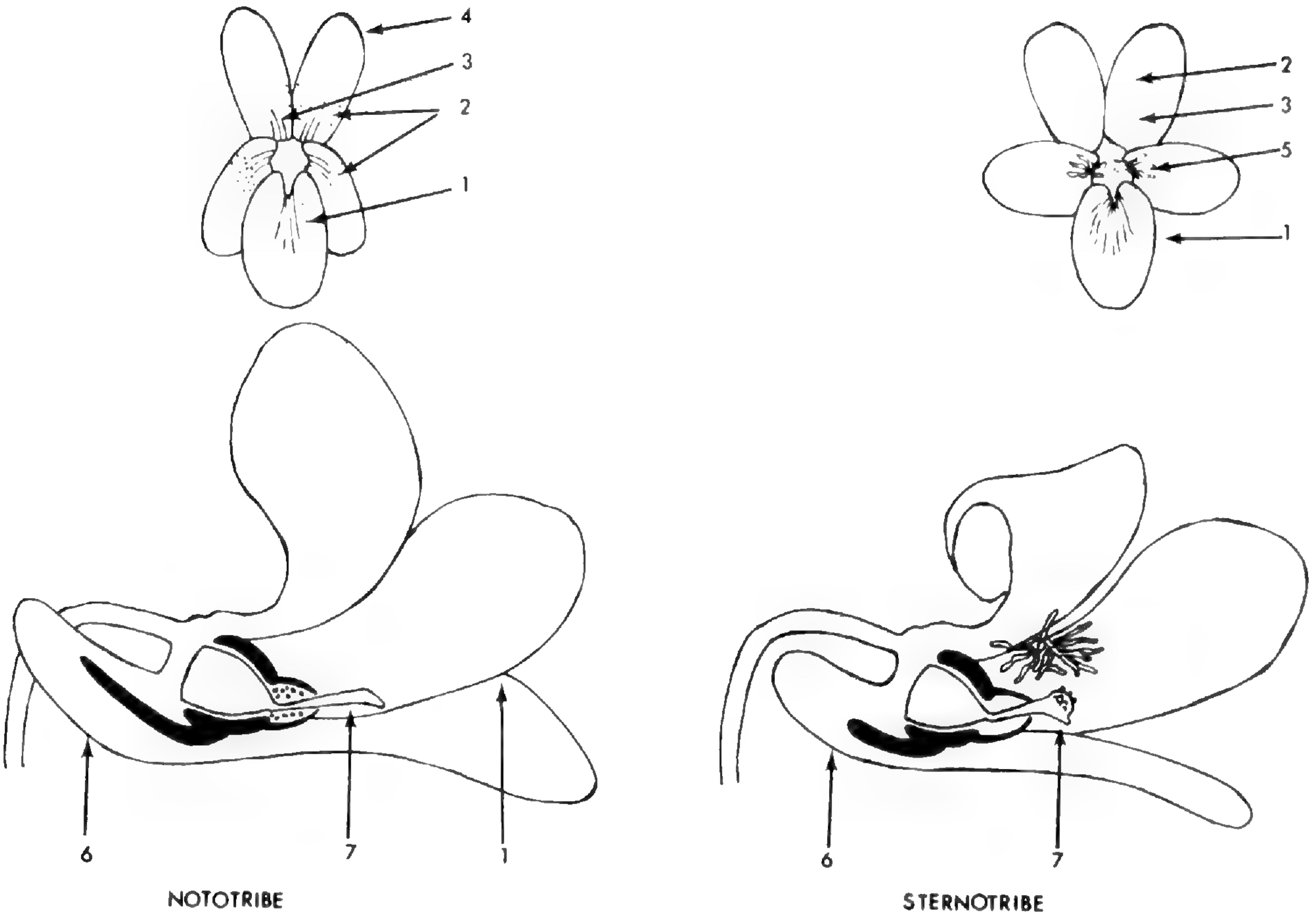


FIGURE 4. Characters of nototribe and sternotribe floral syndromes. For explanation see Table 2.

pollinators which visit sternotribically. Therefore, it is possible to say that sternotribic violet species are adapted for solitary bee pollination. However, since all species investigated so far are visited by solitary bees and are therefore to some degree sternotribic, it becomes of interest to discover what aspects of floral biology manipulate pollinators into nototriby and to ask if they are of evolutionary significance. Although no single floral character appears to be responsible for this, it is possible to identify a character complex, or syndrome, which is associated with nototriby. This syndrome does not exclude sternotribic pollinators but lowers the frequency of their visits. Each character may be more or less developed in nototribic violet flowers, but their combined function does effectively "screen out" many or most sternotribic pollinators. For example, in mixed populations of *Viola rostrata* and *V. papilionacea* sternotribic pollinators forage almost exclusively on the latter species.

Characters of the syndrome are listed in Table 2 and illustrated in Figure 4. Items 2 and 3 in Table 2 suggest high sensitivity to nectarguide patterns among nototribic visitors. This has been shown experimentally for butterflies by obscuring or altering color contrasts and guide lines. These insects fail to orient correctly to the corolla-tube and food source when the normal patterns are altered. The significance of the "beards" of hairs (Table 2, item 5) on the lateral petals is chiefly for sternotribic visitors which require them as footholds as they feed from an inverted posture. Item 9 in Table 2 has puzzled many students of *Viola*. The rostellum of many groups of species, especially in the South American

TABLE 2. Characters of nototribic and sternotribic flowers.

Nototribic	Sternotribic
1. Lateral petals overlapping anterior petal to form a composite "landing platform."	Petals various, usually no special association of anterior and lateral petals.
2. Color patterns and contrasts on all petals.	Petals more uniform in color.
3. Posterior petals with nectarguides.	Posterior petals without nectarguides.
4. Posterior petals held erect.	Posterior petals often reflexed.
5. "Beards" of hairs on lateral petals usually absent.	"Beards" present.
6. Nectar spur long and produced into a tube formed by the proximity of the genitalia to the anterior petal; nectar deeply hidden.	Nectar spur short with space between genitalia and anterior petal; nectar not deeply hidden.
7. Anterior petal furrow well developed.	Anterior petal furrow poorly developed or absent.
8. Nectar spur often horizontal or downward-curving.	Nectar spur upward-curving.
9. Style has simple form without a clearly differentiated rostellum.	Style has complex form with a clearly differentiated rostellum.

sections, shows astonishing variation of form with many kinds of bizarre protuberances. It is suggested that their function is to guide the proboscides and heads of sternotribic visitors beneath the rostellum and over the opening of the stigmatic cavity. Tactile guides such as these are required since the eyes of the sternotribic visitor are not in a position to observe the precise location of the passages leading to the nectar (see Fig. 3).

FLORAL SYNDROMES AND THE POSSIBILITIES FOR COEVOLUTION

There are a few clear cases of coevolution between flowers and pollinators in *Viola*. For example, the European *V. calcarata* and *V. cornuta* are both extreme nototribes adapted for hawkmoth pollination. Table 3 lists the frequencies of visits of individual insect genera to twelve violet species, and this data tempts speculation. *Viola nuttallii*, *V. eriocarpa*, *V. adunca*, *V. blanda*, and *V. fimbriatula* appear to be almost exclusively pollinated by solitary bees of the genera *Osmia*, *Andrena*, and members of the family Halictidae. The mean tongue-length of these bee visitors is 4–5 mm, and they are all 9.0 mm–10.0 mm in body-length—appropriate dimensions for the size of the flowers of the five violet species. The flowers do not have any clearly differentiated "landing platform," the styles are short with clearly differentiated rostellae, the corolla-tubes are lax, and the bunches of hairs ("beards") on the lateral petals are invariably convenient for the bees to cling to as they feed upside-down.

Viola striata appears to be a true generalist with many visits from *Osmia*, *Andrena*, *Halictids*, *Bombus*, and *Rhingia* (Table 3). *Viola papilionacea* is similar with frequent visits from all the above insects plus *Bombylius*. However, if we plot percentage pollination against the percentage of sternotribic visits for *V. striata* and *V. papilionacea* (Fig. 5), it appears that the former is relatively unaffected by an increase in nototribic visits, while the latter clearly experiences a drop in pollination as nototriby increases. The same pattern appears when

TABLE 3. Frequency of visits by individual genera of insects to each of twelve species of *Viola*; expressed as a percentage of the total number of visits taken from five populations of each species.

	Viola Species											
Visitor Species	*nuttallii*	*eriocarpa*	*striata*	*reichenbachiana*	*rostrata*	*hirta*	*adunca*	*blanda*	*papilionacea*	*fimbriatula*	*pedata*	*tricolor*
Osmia	49	9	11	0	5	27	72	5	16	53	0	?
Andrena	25	53	17	0	4	0	0	59	19	0	63	?
Other solitary bees	10	23	22	3	19	13	17	23	29	42	1	?
Bombus	0	0	19	19	.5	40	0	0	5	5	10	?
Rhingia	0	7	23	3	10	0	0	7	13	0	4	?
Bombylius	1	6	1	8	55	20	5.5	5	12	0	1	?
Lepidoptera	12	1	2	0	1.5	0	0	0	2	0	21	?
Other insects	3	1	5	67	5	0	5.5	1	4	0	0	?

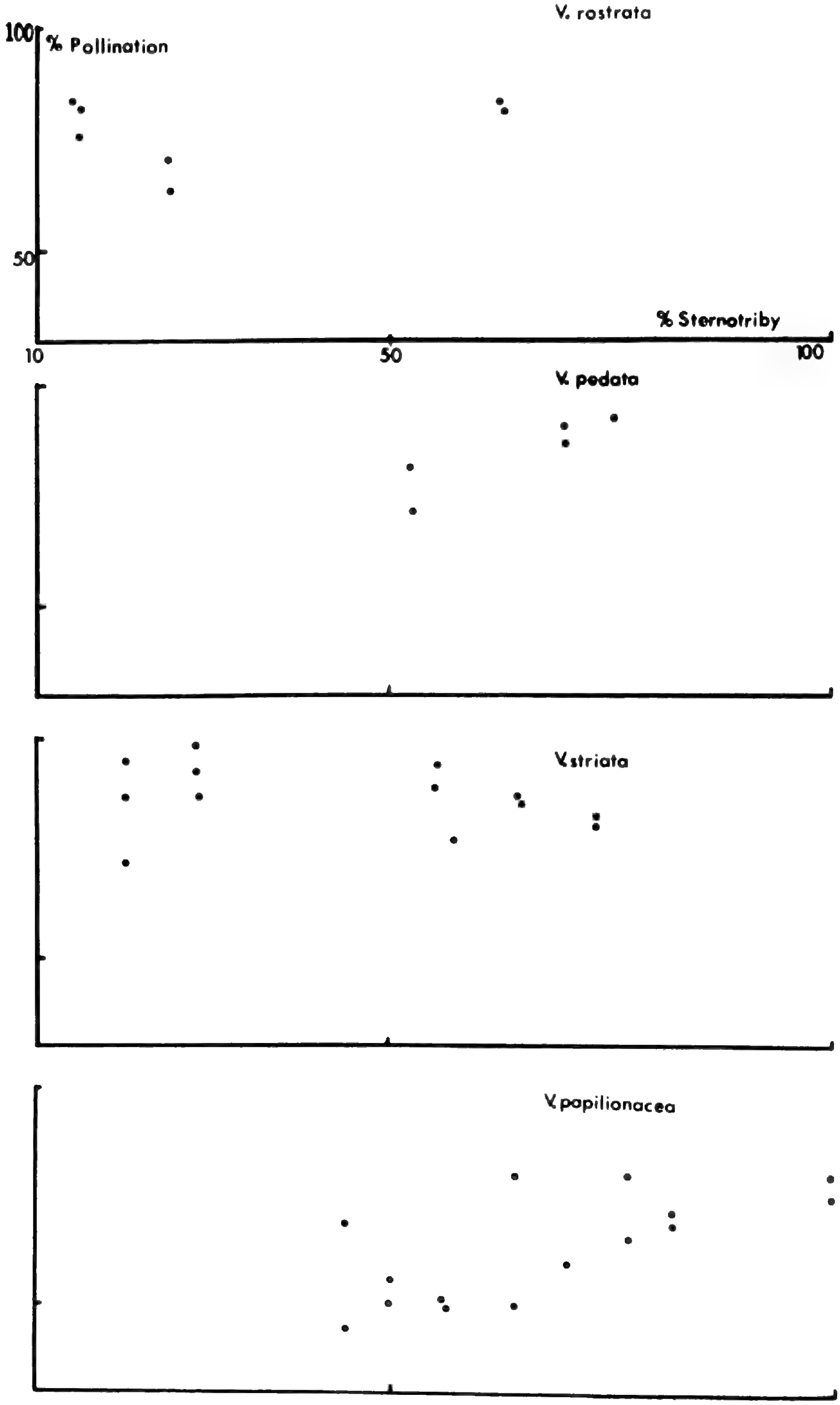
percentage seed-set is plotted against percentage sternotriby (not shown). This is evidence that *V. striata* is a true generalist being adapted to broad-spectrum pollination while, by contrast, *V. papilionacea* is not.

It is possible that because of its close resemblance to solitary bee-adapted species *Viola papilionacea* was once primarily pollinated by these insects. It still is in some habitats. However, today, probably as a result of several hundred years of habitat disturbance by man, its populations occur throughout a great variety of habitats including roadsides, backyards, and waste ground where prolific cleistogamous seed production and vegetative propagation enable it to spread like a weed. Many of its populations experience low frequencies of sternotribic pollination (Fig. 5) and highly variable pollinator "climates." At the same time its flowers show a remarkable degree of polymorphism, and it is tempting to suggest that the original floral syndrome is disintegrating in many habitats and the new morphs are being favored by different groups of pollinators in a process of disruptive selection. This is detected by a reduction in percentage pollination.

The nototribic species show adaptive radiation to special groups of pollinators. *Viola reichenbachiana* is pollinated chiefly by small syrphids and butterflies and may be coevolving with them towards complete nototriby. *Viola rostrata* is pollinated chiefly by *Bombylius* to which its flower is well adapted. The flowers of these species have a landing platform (poorly developed in *V. rostrata* because *Bombylius* hovers while feeding), bands of color contrast near the mouth of the corolla-tube, attenuated styles with simple rostellae, long petal-spurs, and deeply hidden nectar. When percentage pollination is plotted against percentage sternotriby for *V. rostrata* (Fig. 5), there is little variation in pollination efficiency. When the frequency of nototribic visits approaches 100%, pollination remains high, and it is reasonable to assume that the particular floral morphology of *V. rostrata* is the product of coevolution with the nototribic *Bombylius. Viola pedata*, on the other hand, appears to be in a position similar to *V. papilionacea* with decreasing pollination correlated with increasing nototriby. *Viola pedata* is apparently still primarily sternotribe, and yet the flowers exhibit many nototribic characters: there is a large landing platform, all petals exhibit color contrasts, the lateral "beards" are absent, the nectar-spur is long and the style, although unique in shape, is simple with no rostellum. The species is visited by nototribic hawkmoths such as the bumblebee mimic *Hemaris* and by large solitary bees. The behavior of these latter insects is particularly instructive; most attempt sternotribic feeding, but species of *Anthophora* and *Synhalonia* are forced to feed *nototribically* to get food. Consequently, we have evidence that *V. pedata* is in transition from sternotriby to nototriby and may experience reduced pollination as a result. The transition is suggested most strongly by the ambivalent responses of solitary bees.

PHYLOGENETIC CONSIDERATIONS

There have been several careful phylogenetic studies of the genus *Viola* (*e.g.* Clausen, 1927, 1929; Gershoy, 1928) with considerable agreement as to which


V. rostrata
100
% Pollination
50
% Sternotriby
10
50
100
V. pedata
V. striata
V. papilionacea

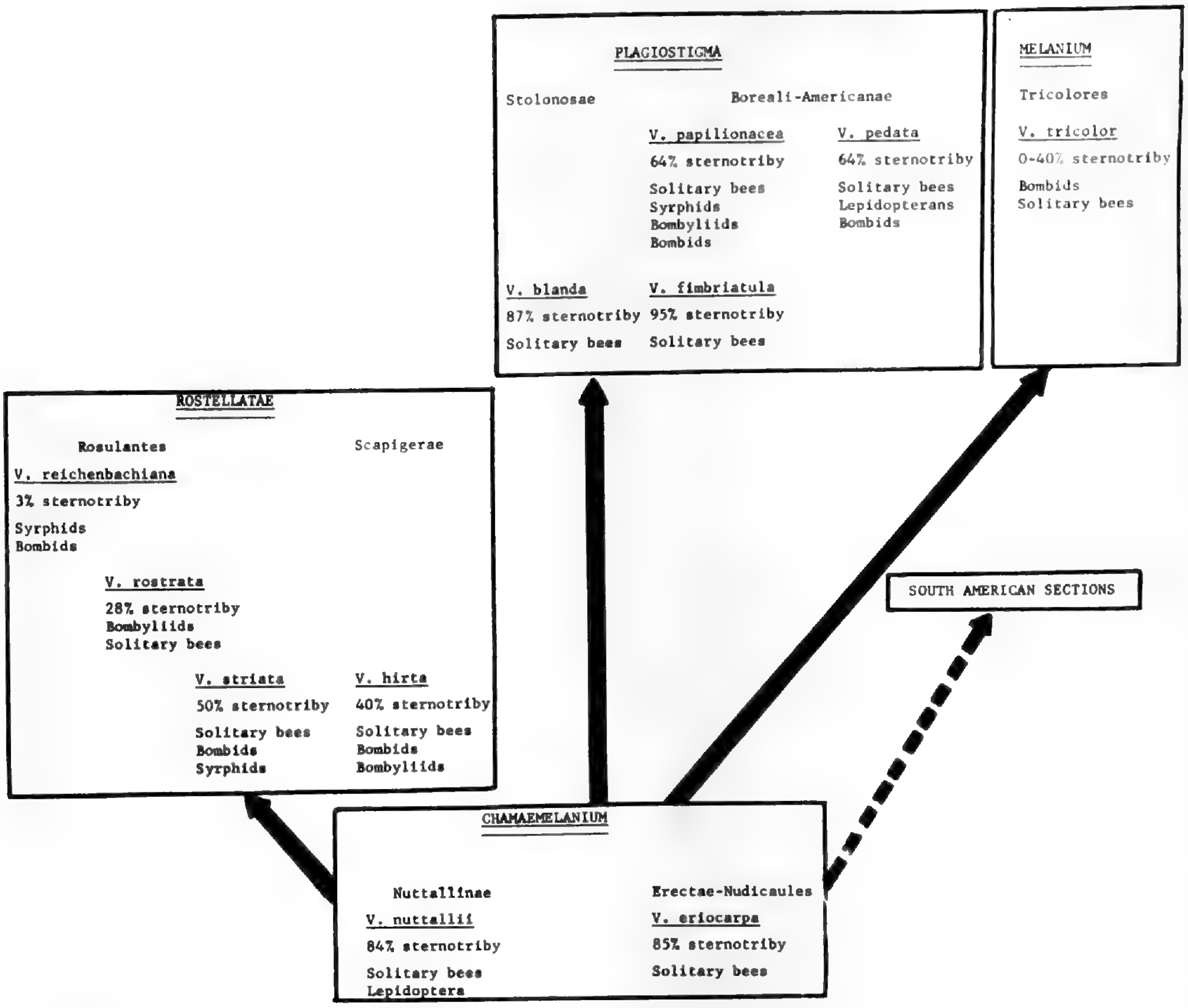


FIGURE 6. A proposed phylogeny of pollination systems in the genus *Viola*.

species are ancient and which are recently evolved. Species of the section *Chamaemelanium* are thought to be the oldest violets, and they are represented in this study by *V. nuttallii* and *V. eriocarpa*. These are yellow-flowered with similar floral morphologies and pollinated by solitary bees. Both species have been found to be approximately 85% sternotribic wherever they have been studied. If we assume this to be the primitive condition for *Viola*, we can trace the evolution of pollination systems through the other sections of the genus (see Fig. 6). Clausen (1927) believed that the section *Rostellatae* to be close to *Chamaemelanium* and derived from it. *Viola adunca* is representative of the Rostellate species closest to the ancestral condition; it exhibits 89% sternotriby. Indeed, Clausen said of this and other closely related species that if they were yellow-flowered they would be very like *Chamaemelanium* violets. The remain-

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FIGURE 5. Percentage pollination and percentage sternotriby for four species of *Viola*. Percentage pollination is the proportion of the total number of ovules in each sample which are matched by the presence of a compatible pollen grain in the stigmatic cavities of the flowers analysed. Percentage sternotriby is the proportion of the total number of insect visits to each sample which were of this type.

ing Rostellate violets studied showed a progressive decrease in sternotriby. *Viola striata* and *V. hirta* with 50% and 40% sternotriby respectively appear to be generalists, while *V. rostrata* (28%) and *V. reichenbachiana* (3%) represent lines of nototribic evolution. All these violets are blue-flowered; and with increasing nototriby there is a reduction or loss of lateral petal hairs, a tendency for the lateral and anterior petals to overlap, and a reduction in the differentiation of the stylar rostellum to produce a simple, non-papillate, terminal stigmatic opening (see Fig. 4).

The section *Plagiostigma* has many obviously sternotribic species such as *Viola blanda* (87%) and *V. fimbriatula* (95%). One suspects that if *V. papilionacea* was not as ecotypically variable as it is and was more restricted with respect to habitat—like *V. fimbriatula*—it would exhibit a higher degree of sternotriby than 64%. *Viola papilionacea* and *V. pedata* may represent early transitional stages from sternotriby to nototriby, suggesting (when considered with *V. rostrata* and *V. reichenbachiana*) parallel evolutionary trends in the sections *Plagiostigma* and *Rostellatae*. The *Melanium* violets are mostly nototribically pollinated by bumblebees, butterflies, and moths. *Viola tricolor* exhibits a nototribe floral syndrome and may be sufficiently representative of the section to suggest an early and direct evolution towards nototribic pollination (see Fig. 6).

THE PROCESS OF DIFFERENTIATION IN THE EVOLUTION OF POLLINATION SYSTEMS

The dual sets of stimuli presented by the *Viola* flower elicit both sternotribic and nototribic types of response. These provide a broad base of variation available for selection, which, as in the case of trends towards nototriby, may be sufficiently intense for the production of distinct floral syndromes. The field data suggest processes whereby new pollination systems may differentiate, by selection, from pre-existing systems. Furthermore, within the several hundred extant violet species we have the opportunity to examine an array of intermediate stages in the greatest detail. From the considerable adaptive radiation it is possible to build up a conjectural picture of possible steps in the evolution of violet pollination systems.

Selection sometimes operates by the gradual accumulation of floral characters more favorable to one group than another. This may be detected by a drop in pollination efficiency but does not necessitate complete discontinuities in pollination, either in time or space. Adaptive radiation may occur, perhaps originating with a generalist floral syndrome, in response to differential pollinator complexes, throughout a large geographic area.

The generalist syndrome may have had a special significance for *Viola*: the visitor species lists accumulated for North America closely resemble those of other workers (mostly unpublished) from Europe and parts of Asia. The pollinator complex of *Osmia/Andrena/Halictids/Bombus/Rhingia/Bombylius* and various Lepidoptera is apparently available to violet populations over a vast geographic area of the north temperate zone. Many violet populations receive visits from most of these insects (see Tables 1 and 3), and many floral morphologies permit some pollination as a result of their feeding activities (Beattie, 1971). Therefore, the basic floral structure is more or less adapted to a pollinator complex which has a wide geographic distribution. This being so, it is not surprising to find that the basic structure remains identical among the 350–400 known species—a violet flower is instantly recognisable despite enormous differences in vegetative structure such as vines, succulents and shrubs—and that variation is limited to detailed structure, presumably as a result of coevolution with particular groups of pollinators. This pattern of variation may have been of special adaptive significance during two major migrations of the genus in the northern temperate zones: First, outwards from its putative center of origin in the Central and South American, sub-tropical and tropical montane environments and second, from the southern-most limits of the final glaciation back to its contemporary northern-most limit of distribution.

It is interesting that adaptive radiation in the north temperate regions has exploited so many facets of the potential pollinator complex with so little change in reproductive structure. This may reflect a general paucity of pollen vectors in this region as compared to the tropics. Thus, the genus has radiated at comparatively little genetic and energetic "expense" and may also, therefore, maintain the option of reverse evolution should general shifts of pollinator climates occur. By contrast similar radiation among tropical plant groups, *e.g.* the Bignoniaceae, have required major reorganisations of floral structure accompanied by a higher frequency of specialisation of pollination systems.

In conclusion it seems that for many plant species the minority and majority pollinators are of equal interest, for together they constitute the variation available for selection of novel floral structures. By understanding their impact upon reproductive success, and by measuring it, we gain some insight into the processes whereby pollination systems evolve.

LITERATURE CITED

BEATTIE, A. J. 1971. Pollination mechanisms in *Viola*. New Phytol. 70: 343–360.

———. 1972. Insect visitors to three species of violet (*Viola*) in England. Ent. Mon. Mag. 108: 7–11.

CLAUSEN, J. 1927. Chromosome number and the relationship of species in the genus *Viola*. Ann. Bot. 41: 678–714.

———. 1929. Chromosome number and relationship of some North American species of *Viola*. Ann. Bot. 43: 741–764.

EYDE, R. H. & J. T. MORGAN. 1973. Floral structure and evolution in the Lopezieae (Onagraceae). Amer. Jour. Bot. 60: 771–787.

GERSHOY, A. 1928. Studies in North American violets. 1 General considerations. Vermont Agric. Exp. Sta. Bull. 279.

GRANT, V. & K. A. GRANT. 1965. Pollination in the *Phlox* Family. Columbia University Press.

LEVIN, D. A. 1972. Low frequency disadvantage in the exploitation of pollinators by corolla variants in *Phlox*. Amer. Naturalist 106: 453–460.

LEWIS, H. & P. H. RAVEN. 1961. Phylogeny of the Onagraceae. *In* "Recent Advances in Botany." Toronto Press, Toronto.

ECOLOGICAL ECONOMICS OF FORAGING AMONG COEVOLVING ANIMALS AND PLANTS

Alan Covich[1]

The papers presented in this symposium focus on the reciprocity between plants and their associated fauna. Some studies approach plant-pollinator interactions at generic or familial levels and treat distributions over broad expanses of evolutionary time (*e.g.* Beattie, Gentry, and Ramírez). Others examine selected habitats and community interactions on ecological time scales (*e.g.* Ayensu, Heithaus, Macior, and Strong). Generally, one goal is to document specific boundaries which allow definition of floral resources relative to specific faunal consumers. I want to relate some of these new findings to recent research on consumer "switching" between alternative food resources.

Early studies of pollination did not consider the gathering of pollen and nectar as generalized modes of foraging, but Robertson (1899) did recognize the similarity when he stated, "The relations of the host-bees to the flowers from which they get pollen are quite analogous to the relations of parasites to their hosts, of phytophagous insects to their food plants, or of predaceous insects to the insects upon which they feed . . . ." Pollination ecologists currently use terminologies and classifications for describing pollinator behavior which are different from those applied to predatory behavior, but there is a continued recognition of the general similarity between these distinct types of foraging. For instance, a pollinator which visits a single plant species for pollen and nectar is termed "monotropic," and Faegri and Pijl (1971) comment, similar to Robertson, that "its relation to the blossom is more or less on the lines of a host-parasite relationship." Michener (1954) has also noted that bees which collect pollen from a few kinds of flowers (termed "oligolecty") represent a "form of host specificity" (for a review of these terms see Linsley, 1959). Yet, there has been little attempted transfer of methodologies from related studies on selective predation to the techniques used for studying selective pollination. In the following discussion, I propose an extension of a measure that I have recently developed for determining "rate of resource substitutability" among selective consumers (Covich, 1972*a*) to studies of pollinator energetics.

Before discussing these points, I want to compare plant-pollinator and prey-predator interactions. By definition, a pollinator is a dispersal agent for highly specialized pollen grains which transmit genetic information and produce sexual recombination and heterozygosis. Being direct links in the reproductive pathways of many flowering plants, pollen transporters have a strong influence on floral evolution and are tightly coupled to development of complex morphological and biochemical adaptations. Predators also have a direct effect on their prey populations, but predation (in the strict sense) can have a less intense impact if non-reproductive individuals (immature, weakened, or senescent com-

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ponents of the prey population) are eliminated. A pollinator's energetic income is derived primarily by consumption of plant products (nectar, pollen, fruit) rather than individual plants. However, a wider definition of predation has developed which makes this difference between pollinators and predators less distinct. For example, the concept of predation used in a recent review (Mooney, 1972) covers a broad spectrum of herbivorous consumption, from grazing on plant parts such as leaves and stems to "seed predation," whether the consumption eliminates a reproductive individual from the prey (*i.e.* plant) population or not. Thus, it appears that pollination fits in the broad conceptual framework of predation but also has some important special characteristics that permit pollinator-foraging to be treated as a specific subset of consumer activity. That is, pollinators are usually nectar or pollen "predators."

Since Aristotle's time, observers have noted that certain bees initially visit individual plants of one species and later shift to other species rather than flying randomly to several different kinds of flowers (Proctor & Yeo, 1972). This selective feeding behavior is often termed "flower constancy" by pollination ecologists, but their measurements and definitions of constancy are quite varied. For example, two frequently used approaches for determining degree of constancy are: i) the following of individual insects (marked with dye or radioactive tracers) as they move from plant to plant and ii) the analysis of plant species visited by marking pollen or identifying pollen from particularly distinct species that comprise the pollen load gathered by an individual insect (Free, 1970). These values are usually expressed as percentages of intra- and interspecific visits or as percentages of "pure" and "mixed" pollen loads. There is, however, a lack of uniformity among researchers in their definitions of constancy so that comparisons among different complexes of species are difficult. For instance, V. Grant (1950) reexamined some data interpreted as "mixed" loads of *Apis millifera* and found that "every one was 95–99% pure . . ." and that "over half of the interspecific visits paid by species of bumble-bees results in pollen pellets which were at least 95% pure." Free (1970) also concluded that "determinations of pure loads is not an entirely satisfactory way of expressing constancy . . . ." A comprehensive review is presented by Faegri and Pijl (1971), who point out there has been some confusion between the terms "constancy" and "monotropy." They note that "both of them have been called 'flower constancy,' but they are entirely unrelated. A monotropic animal is (physiologically, physically, and/or ethologically) unable to utilize any other plant species . . . . Constancy is an *individual* quality in a polytropic (theoretically also in an oligotropic) animal which as a species is . . . able to, and does visit any of a number of plant species . . . . One might define constancy as an individual and (as the case may be), a temporary, monotropy in a polytropic species." They also stress the importance of perspective in defining constancy and delineate three distinct viewpoints: i) that of the flower, ii) the species of the animal pollinator, and iii) the individual visitor in relation to changes during its life history or a particular activity.

Many parallel difficulties are also encountered by ecologists dealing with selective predation in which marked predators are visually tracked or their stomach contents and fecal pellets are analyzed. For example, the uncertainty regarding the establishment of specific "search images" by selective predators (for reviews see: Dawkins, 1971; Royama, 1970) is similar to that encountered in operationally defining "flower constancy." The major sources of difficulty in measuring feeding selectivity in these types of research are: i) reliance on percentage values rather than fully expressed ratios or other types of relative and absolute index values, ii) inadequate definitions of "resources" and "availability" so that the result is often an absence of essential information on availability of consumed resources relative to other types of foods which were present but not consumed, iii) lack of uniform time spans over which initial data are collected and general failure to incorporate temporal variables, iv) assumed uniformity for qualitative and quantitative nutritional values among the alternative energy courses, and v) lack of information on previous feeding (*i.e.* hunger levels and conditioning effects).

These problems have been recognized by other researchers and are dealt with in a variety of ways by pollination ecologists. One example is a study by Synge (1947), who used pollen traps to study foraging by colonies of *A. mellifera* relative to changing availabilities of different flowers on an hourly and seasonal basis. She designed some feeding-choice experiments but was unable to account completely for observed differences in pollen collecting between different bee colonies and notes that "it would be interesting to offer them pollens that, though plentiful, they do not appear to use to any extent, such as those from *Tilia* and the Gramineae." I have not found any reference to further experimental work in which pollen resources have been identified and tested for their relative substitutability, but Gilbert (1972), using time-lapse videotape recording, reports some important data on feeding rates and preferences by *Heliconius* for pollen and pollen-sized glass beads relative to sucrose solutions. Another approach to defining resources has focused on the biochemical characteristics of nectar resources and exploitation by specific pollinators (*e.g.* Baker & Baker, 1973; Free, 1970; Percival, 1961). Other studies have considered the energetics of nectar exploitation and emphasized the importance of relative efficiencies among pollinators in determining flower constancy (*e.g.* Heinrich & Raven, 1972; Wolf, Hainsworth & Stiles, 1972). Energy expenditures by pollinators appear to be greatly affected by proximity of resources within a three-dimensional distribution (Heinrich, 1972; Levin & Kerster, 1973). A few ecologists have stressed the necessity to search for possibly unique foraging patterns and to consider the effects of varying abundances of alternative potential resources other than nectars (and for some species, direct consumption of pollen) which may require unusual definitions of floral resources. For example, Wickler (1968) points out, "Some plants, such as *Cassia* species, have even developed special nutritive sterile pollen in addition to the normal form . . . . Other flowers, those of orchids in particular, are equipped with protein-rich edible haris or other edible tissues . . . ." These examples of distinct viewpoints for considering precise relationships among pollinators and nutrient resources provide a good basis for avoiding the difficulties

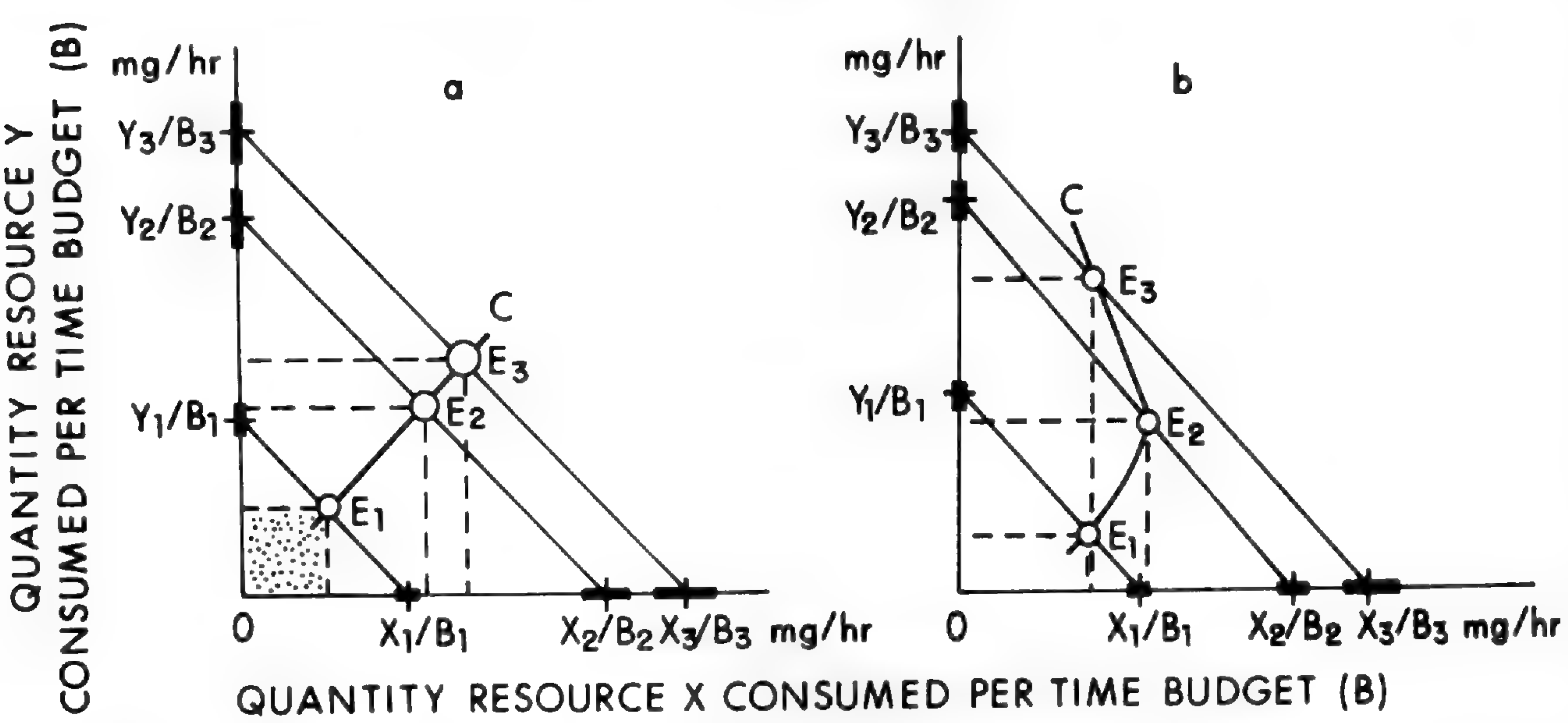

FIGURE 1. Results of hypothetical increases in feeding periods ($B_3 > B_2 > B_1$) when both resources (X, Y) are available at constant levels.—a. If equal proportions of X and Y are consumed per time budget, the resources are defined as "perfect substitutes" and the "consumption curve" (C) is positively sloped.—b. If changing proportions of X and Y are consumed per time budget so that X is preferred during short feeding periods (B_1) and Y is preferred during long feeding periods (B_3), the resources are "imperfect substitutes." The consumption curve (C) changes from positively to negatively sloped.

involved in defining "constancy," but additional techniques may supplement these approaches.

A wide spectrum of foraging "strategies" are reported in the ecological literature on selective predation (for reviews see: Royama, 1971; Schoener, 1971). Some of these concepts and related methodologies (particularly the "electivity" index of Ivlev, 1961) may be applicable to pollinator selectivity. The approach I propose is to define different classes of pollen and nectar resources and to measure their substitutability under varied sets of absolute and relative availabilities. The method is based on measurements of consumption rates in a series of one- and two-choice tests performed first in controlled laboratory conditions and then in manipulations of natural field populations. The consumer (*i.e.* the pollinator) is initially introduced to two potentially different types of food (*e.g.* equally concentrated nectars produced by two closely related species) which are readily available *ad libitum* and the quantities (volume, weight, or caloric content) of each that are consumed per unit time are recorded and graphed (*e.g.* Fig. 1a) on rectangular coordinates. The axes are scales of the quantities consumed of each of the different resources (X and Y) during a controlled feeding period termed the "time budget." The limits of resource exploitation by a particular consumer within any given series of time budgets can be observed experimentally. These limits are bounded by the "time budget line." The shape of this line is first defined by three points, one of which (Fig. 1a, E_1) is obtained by systematically repeating a series of two-choice tests of the consumer's selection of X + Y combinations so that an average combination (*e.g.* $E_1 = 4$ mg X/hr + 4 mg Y/hr) and the variance can be calculated for a given level of abundance and time budget. The variance is represented graphically by the diameter of the circle around each average equilibrial value. The other two points that define the time budget line are determined by a series of replicated one-choice tests in which the same time budget is expended in consuming first one food (X_1/B_1) and then the other (Y_1/B_1). These average maximal intercepts on the abscissa and ordinate, together with E_1 (the average total consumption of $\frac{X+Y}{B_1}$) denote the limits of the time budget line for a particular consumer given a specific level of abundances. Thus, during the time budget B_1 a consumer can select from any range of combinations from all Y_1 + no X_1 to all X_1 + no Y_1. The relative consumer preference is indicated by the ratio of $Y_1:X_1$. That is, if the E_1 combination has equal amounts of Y_1 and X_1 (and the ratio is therefore 1:1), then the consumer has equal preference for both resources at that level of food abundance and time (as in Fig. 1a). The area in the quadrant (or "resource space") selected for consumption is represented by the stippled square in Figure 1a. Note that it is possible for the consumer to select any combination within the restraints of the time budget (*i.e.* the triangular area bounded by $Y_1/B_1 - X_1/B_1 - 0$). The portion selected indicates the consumer's evaluation of the two resources. The slope of the time budget line is the rate of substitution of Y for X, *i.e.* to select more of Y some X must be given up (or "traded off"). A more detailed discussion of these relationships and the use of this method to define specific resources (either as "perfect" or "imperfect" substitutes, or as complements) is presented in another study (Covich, 1972*a*).

Two types of tests are required to complete the analysis. One is to run a series of consumption measurements using the same foods and abundances but increasing the time budgets (Figs. 1a and 1b). The other is a series in which the time budget is held constant (Figs. 2a and 2b), but the abundance of one food (or the other) is changed (either by changing absolute abundance, or relative distances between units of each food, or concentration of the food such as diluting one or the other nectars). Both of these types of experiments measure the consumer's response to changes in relative resource availability and yield sets of Y_n/B_n and X_n/B_n intercepts as well as E_n values. Thus, any point in "resource space" represents a possible equilibrial or mean combination of X + Y. Some combinations will be within and others outside the time-budgetary restraints for a particular consumer foraging on specific sets of available combinations. The series of points (Figs. 1 and 2: E_1, E_2, E_3) representing average consumption of X + Y combinations per time budget is connected by a line termed the "consumption curve" (C in Figs. 1 and 2).

Inasmuch as these two distinct types of changes (*i.e.* either length of time budgets or abundances of one alternative resource) are interrelated, their separate analysis is useful because patterns of feeding behavior may shift in distinct modes and are documented independently by shapes of the C curves. For example, if the total amount of time available for feeding increases and the consumer is not saturated differently by the two foods, then the expected C curve would have a continuously positive slope (Fig. 1a: C). If the resources are exploited in a consistent manner following an increased abundance of X, the slope

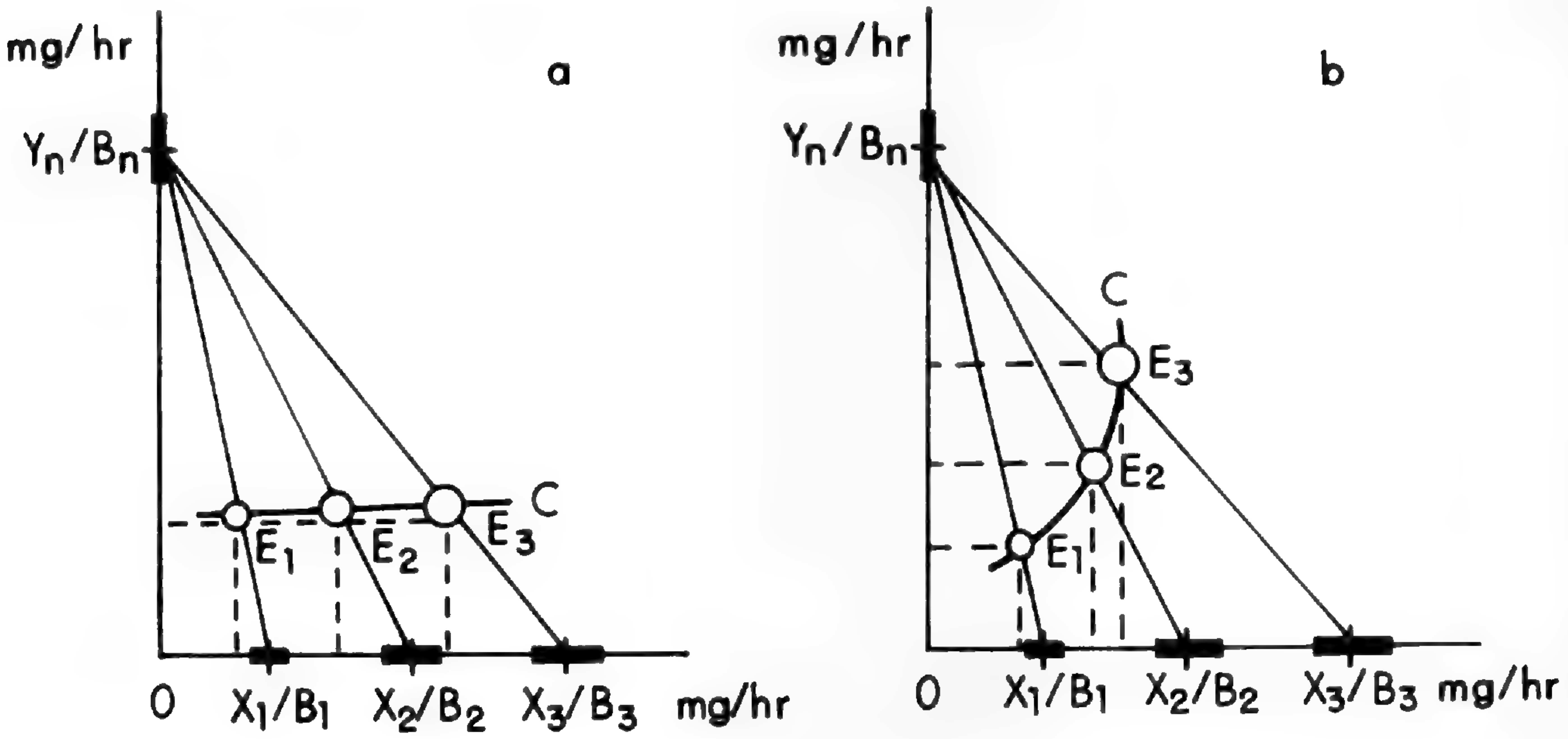

FIGURE 2. Results of hypothetical increases in availability of one resource ($X_3 > X_2 > X_1$) when the availability of an alternative resource remains constant ($Y_1 = Y_2 = Y_3 = Y_n$) and the feeding periods remain constant ($B_1 = B_2 = B_3 = B_n$).—a. If equal amounts of Y are consumed as increasing amounts of X are eaten, the two resources are defined as "poor substitutes" and the consumption curve (C) has zero slope.—b. If increased amounts of both Y and X are consumed as the availability of X increases, the two resources are defined as "complementary" and the consumption curve is positively sloped. Change in proportional consumption of Y and X indicates Y is preferred to X. These shifts in ratios of Y:X illustrate the definition of "subsidiary" resources and the concept of "time transfers."

of C will be zero and C will be a straight line horizontal to the X axis (Fig. 2a). Rapid saturation with resource X is depicted in Figure 1b (C) following an extended time budget and in Figure 2b (C) following an increased abundance of X. One important point is that a consumer may actually eat less of one resource following an increased time budget than when that resource was relatively hard to find during a short time budget (Fig. 1b, *cf.* X:Y in E_2 and E_3). This type of shift occurs, then, if the resources are "imperfect substitutes" (*i.e.* in Fig. 1b Y is strongly preferred to X during long feeding periods). Shifts in substitutability and degree of selectivity are known to occur as consumers become satiated at high levels of abundance or if their time budgets are long (*i.e.* low restriction on searching). Increased selectivity has been clearly observed in studies on consumption isoclines of silkworms (Ishikawa *et al.*, 1969), fish (Ivlev, 1961), and mice (Covich, in preparation; Holling, 1959). Alternative models of this effect are presented by Emlen (1968), Holling (1966), Marten (1973), and Rapport (1971) and reviewed by Pulliam (1974).

The most interesting relationship occurs among selective consumers with a strong preference for one resource when the strongly preferred resource has very low availability relative to a nonpreferred (but nutritionally adequate) food resource. This non-preferred food is termed a "subsidiary" resource because the consumer can exploit it and simultaneously continue to search for the rarer, more preferred "primary" resource. If the subsidiary resource increases to extremely high levels of abundance (as depicted in Fig. 2b: $X_3 > X_2 > X_1$), the "time cost" for finding and consuming this readily available resource (X) de-clines. Even if the time budget remains uniform (*i.e.* Fig. 2b: $B_1 = B_2 = B_3 = B_n$), more of X can be obtained with less time expended per unit X consumed (*i.e.* in Fig. 2b: $X_1/B_1 > X_2/B_2 > X_3/B_3$). The significant effect is that simultaneously more of the preferred resource (Y) can be obtained as a result of the consumer's ability to transfer time saved in searching for X to increased searching for Y. Therefore, even though the availability of the preferred primary resource remains at a constant low level (Fig. 2b: $Y_1/B_1 = Y_2/B_2 = Y_3/B_3 = Y_n/B_n$) and the time budget is constant, more of the primary resource (Y) can be included in equilibrial combinations (*cf.* E_1 to E_2 and E_3 in Fig. 2b). The proportion of Y:X in the combination shifts in response to increases in availability of the subsidiary resource (X). My current research focuses on this relationship, and I am investigating what degree of preference for primary resources and what level of abundance among subsidiary resources are necessary in order to predict complete elimination (on a local scale) of the primary resource.

Although these studies on selective consumption have focused on non-pollinators, components of some of these methods appear applicable to investigating pollinator selectivity. A generalized approach to measuring resource substitutability may help answer some questions which I feel have been generated by papers presented in this symposium. In the first paper, for instance, Heithaus proposes that we "refine our analysis to distinguish the truly potential pollinators among nectar and pollen consumers." He defines floral resources by observing which plants are in flower during a particular time, and his approach yields excellent results. The additional measurement of resource substitutability would provide another method for identifying resources independent of taxonomic relationships (*e.g.* unrelated species may produce nectars which are "perfect substitutes," or identical "resources," for some pollinators but perhaps because of differences in floral color, scent, or morphology, these resources may or may not be available to other pollinators). This supplemental information would be useful for interpreting some of his observations on foraging by butterflies in Costa Rica. For example, certain butterflies (*Anartia fatima*) have a uniform supply of nectar resources from milkweeds (*Asclepias*) throughout the year and switch to *Licania* during its brief peak abundance. It would be interesting to know if *Licania* nectar is strongly preferred to that produced by *Asclepias.* Also of importance would be the relative preference for *Cupania* and *Melanthera,* which are similarly seasonally available but not exploited by *Anartia.*

Beattie's study of *Viola* uses several methods for documenting the breadth of taxonomic diversity among pollinators. He is able to demonstrate that behavioral differences among pollen and nectar consumers determine which insects are significant pollinators. Apparently, the number of visits by pollinators may be misleading with regard to determining which species actually cross-fertilize the plants. Beattie stresses that data must be carefully obtained to distinguish differences between common species which consume resources but have little effect on the plant's productive potential, and relatively rare species whose consumption of resources may be slight but whose role in pollination is significant.

Beattie has previously considered related questions in his discussion of some analogies between pollinators and flower-predators. Beattie, Breedlove and Ehrlich (1973) note that, "Success at avoidance of insect predators . . . would appear to militate against the evolution of specialized insect pollinators. Both specialized predators and pollinators have many problems in common, particularly synchronizing with the food source . . . ." The evolution of specific synchrony between pollinators and avoidance of large population build-ups of predatory insects may be a common strategy based on supplying distinctly different ("poorly substitutable") resources to these two very different groups of consumers in distinct temporal modes of availability.

Rates of substitution may also be useful information for interpreting some of the plant-insect relationships discussed by Strong. He contends that the extension of an insect's host range (*i.e.* the "host transference" by stenophagous consumers) "is rather a common event that classical entomological methods rarely detect." That some highly selective insect consumers can rapidly shift among a restricted range of alternative food plants is well documented, but the frequency with which this switching occurs in nature is not well known. It would be impossible to document precisely the feeding behavior of numerous insects, but based on the data presented by Strong and Southwood, a few characteristics as well as exceptional species could be tested for the rate of substitutability. For example, the single species of Lepidoptera that is associated with native yews (*Taxus baccata* L.), or the one lepidopteran species currently associated with acacia (*Robinia pseudoacacia* L., introduced more than 300 years ago), might be interesting consumers to compare with regard to feeding selectivity. As Southwood (1973) suggests, the mechanism (or "degree of predilection") limiting the number of insect consumers of yew is probably a structural or biochemical one (such as phytoecdysone or the alkaloid "taxine"). The significance of these exceptions to the general relationships between numbers of insects and tree abundances may be considerable. But in addition to these exceptional instances of coadaptations, there is a more general set of interspecific competitive interactions among insects colonizing and exploiting plant resources. Some of these complex relationships occur over varied ecological and evolutionary time scales which may limit the usefulness of isolated studies of feeding selectivity. As Janzen (1973) points out, "All the parts of an individual plant are connected through the medium of its resource budget. Since this budget is subject to selection at the level of the individual plant, a species of insect colonizing it over evolutionary time will automatically compete with *all* other species of insect already established on the island (plant)."

In contrast to the breadth of the plant-animal associations discussed by Heithaus, Beattie, and Strong, the reciprocity among figs and fig wasps of the family Agaonidae is characterized by extremely narrow specialization. Ramírez presents a detailed account of these complex coadaptations which illustrate the limits on obligate mutualists. Neither the flowers nor the pollinators can reproduce without the other, and nearly each species of *Ficus* is pollinated by a distinct chalcidoid wasp (even the highly specific pollinating wasps serve as hosts to other species of wasps which are specialized to parasitize them). The inability of these chalcidoid wasps to switch to alternative fig flowers limits the reproductive distributional patterns of both these groups. Ramírez (1970) presents a possible link between dispersal of *Ficus* and fruit-eating bats. Not only is there a strong correlation between the distributions of figs and these bats, but Ramírez observes that bats do occasionally transport both the mature fig fruits and the wasps which are entrapped.

Ayensu presents an interesting case study in selective feeding by bats which illustrates some important general principles regarding resource definition. He notes that the neem tree (*Azadirachta indica*) was introduced to West Africa some 60 years ago without any idea of the rapidity at which it might spread and displace the indigenous vegetation. The seeds are dispersed by fruit eating bats (*Epomophorus gambianus*) which have become extremely numerous. Inability to predict these trophic dynamics probably occurred because the flexibility of bat feeding behavior was not understood. Perhaps more important, however, is the complexity of bat feeding which would have hindered the predictability of even a very good methodology for measuring resource substitution by bats. Ayensu notes that "although neem fruits are available on the tree on which bats roost, they are not eaten . . . . Similarly, the *Eidolon helvum* that roost in the palms in Ghana do not feed on the fruits of the same tree, but fly to another palm to feed." These are remarkable illustrations of the difficulties of defining resources and in measuring their absolute availabilities, and similar examples exist for other highly mobile consumers (*e.g.* Brown, 1969). Identification of food resources generally requires study of both temporal and spatial variables in a framework that incorporates distinct and rapid changes in consumer behavior.

The phenological classification proposed by Gentry relates directly to the general problem of food resource availability. As he points out, there are distinct types of blooming periodicity in Bignoniaceae, all of which require some expenditures of energy by plants in order to produce nectar and pollen for attracting pollinators. Of particular interest are the relationships between some of these distinct types of periodicity. Certain species (Gentry's "type 5") synchronize short periods of flower production and develop numerous blossoms that lack nectar. These flowers still attract sufficient insect pollinators from other species (types 1, 2, and 3), especially from those characterized by more prolonged production of large masses of flowers containing abundant nectar (type 4). Gentry proposes that the species lacking nectar are "mimics" of nectar-producing mass flowering species. The dynamics of this interesting hypothesis could be experimentally tested by manipulating the availabilities (*i.e.* flower frequency and spacing or nectar concentration) of co-occurring "model" species which produce the nectar. Pollinators have different energetic demands and conditioning thresholds which could be compared in terms of their effects on fertilization and seed production among both models and mimics. Field manipulations could be designed to answer questions such as: i) What is the lowest possible nectar availability (in type 4 flowers) which would allow a specific pollinator sufficient time and energy to search for other sources of nectar (some being type 5 flowers without nectar)? ii) Do pollinators learn to substitute markedly different nectar resources (or migrate to habitats with different flowers) if the proportion of type 4 to type 5 flowers is below their energetic demands?

The general significance of various types of "mimicry" is further discussed by Macior, who offers additional examples. His documentation of pollinator behavior with slow motion films is an effective method for recording actual expenditures within the limits of a given pollinator's time budget. As a result of his detailed studies, it is readily apparent that flower constancy (and resource substitutability) are relative measures in need of a high degree of precision.

Several other pollination ecologists (*e.g.* K. A. Grant, 1966; Yeo, 1968) have interpreted aspects of convergent floral evolution which relate directly to these reports by Gentry and Macior. For example, Grant (1966) notes that "the existence of common red coloration is of evolutionary significance in providing an instance of a situation in plants comparable to the phenomenon of Mullerian mimicry among animal species." Proctor and Yeo (1972) discuss several cases of floral evolution they consider to be "the result of *Mullerian mimicry*—in which a number of species of similar character and behavior, and of comparable abundance, have evolved a common 'adversitising style' to their mutual advantage . . ." and others that "are examples of *Batesian mimicry,* in which one organism obtains a one-sided advantage by imitating another organism more numerous than itself." This latter extension of the concepts of Batesian and Mullerian mimicry to include plant-pollinator interactions may cause some ecologists to object on the grounds that animals with aposematic coloration provide a signal to *repel* their predators (models typically are toxic or distasteful to specific consumers who learn to avoid them), whereas flowers evolve signals to *attract* their pollinators. Clearly, the consumers learn by distinct modes either primarily through negative reinforcement (for distasteful prey) among predators or through positive reinforcement (for nectar rewards) among pollinators. Yet, these two different types of evolutionary processes do have important linkages between them. For example, in regard to evolution of red coloration in both faunal prey and flowers, Cott (1940) notes, "The efficient reception of red light by the eye of diurnal birds is linked up with extensive use, by utterly unlike organisms and structures, of orange, vermilion, crimson, and scarlet, in typical bird-advertisements: and this, although their functions may be diametrically opposed—in the one case being attractive, in the form of flowers or fruit; in the other repellent, in the shape of dangerous or distasteful prey." Both among faunal Mullerian mimics and among convergently evolved red-colored flowers there is increased efficiency in learning by the associated consumers (predators or pollinators) as the number of species and individuals with the same coloration (or "signal") increases in abundance. Furthermore, as Raven (1972) suggests, these coevolving species are complexly integrated in terms of their energetic budgets so that the probability of outcrossing is maximized.

In the concluding discussion of the symposium, Dodson stated he felt evolution of floral coloration was sufficiently different from warning coloration in Batesian and Mullerian mimics to preclude extending these concepts to include convergence of flower color. He noted the general phenomenon of "deception" covers a wide range of specializations from "pseudo-copulation" among orchid flowers and male pollinators to common patterns of red-orange coloration in groups such as *Asclepias* and *Lantana.* For sake of definitional clarity, it may be necessary to consider some of these forms of deception as instances of "aggressive mimicry" (also termed "Peckhammian mimicry") to differentiate them from other distinct types of mimicry as Wickler (1968) suggests. The analogy between Batesian mimicry in animals and plants can, however, be useful in suggesting parallels for experimentally testing putative floral relationships. The significance of balanced proportions among model and mimics is now well documented (*i.e.* the consumer learns to recognize the palatable mimic very quickly if it is brightly colored and if there are relatively few distasteful models to frequently reinforce the relationships between the bright pattern of coloration and toxicity). I have previously suggested (Covich, 1972*b*) that non-toxic varieties of *Manihot esculenta* may be subject to less attack by herbivores when interplanted among toxic varieties containing cyanogenic glucosides. I am currently investigating these relationships in Mayan "milpas" where both toxic and nontoxic varieties of manioc are simultaneously cultivated. Model-mimic relationships have been tested among several species in ways (as reviewed by Brower, 1970; Rothschild, 1973) which may be partially applicable to laboratory and field experiments on floral nectar exploitation.

The participants in this symposium present a broad range of studies dealing with a diverse array of coevolving plants and animals. The large number of different methodological approaches reflect the heterogeneous nature of these multispecific interactions and the widely different questions being asked. Despite these distinctly varied interactions, some questions regarding selective herbivory and pollination can be broadly compared. To characterize some questions which need solutions, I review the concept of flower constancy and discuss some analogies with other concepts such as specific searching image, Batesian mimicry, and the analysis of consumer choice as measured by rate of resource substitution. These analogies do provide some interesting hypotheses, but testing them will require innovative field methods. Their successful development and application can be expected to yield considerable insight into population dynamics and the regulation of coevolving communities.

LITERATURE CITED

BAKER, H. B. & I. BAKER. 1973. Amino-acids in nectar and their evolutionary significance. Nature 241: 543–545.

BEATTIE, A. J., D. E. BREEDLOVE & P. R. EHRLICH. 1973. The ecology of the pollinators and predators of *Frasera speciosa.* Ecology 54: 81–91.

BROWER, L. P. 1970. Plant poisons in a terrestrial food chain and implications for mimicry theory. Pp. 69–82 *in*, K. L. Chambers, editor. "Biochemical Coevolution."

BROWN, R. G. B. 1969. Seed selection by pigeons. Behaviour 34: 115–131.

COTT, H. B. 1940. Adaptive Coloration in Animals. New York.

COVICH, A. P. 1972*a*. Ecological economics of seed consumption by *Peromyscus*: A graphical model of resource substitution. Trans. Connecticut Acad. Arts Sci. 44: 71–93.

———. 1972*b*. Cyanogenic glucosides in manioc; a predator-prey model for toxic food plants. Paper read at 18th Annual Symposium on Systematics, "Systematics in the Lowland Tropics." Missouri Bot. Gard., St. Louis.

Dawkins, M. 1971. Perceptual changes in chicks: another look at the "search image" concept. Animal Behav. 19: 566–574.

Emlen, J. M. 1968. Optimal choice in animals. Amer. Naturalist 102: 385–389.

Faegri, K. & L. van der Pijl. 1971. The Principles of Pollination Ecology. New York.

Free, J. B. 1970. Insect Pollination of Crops. New York.

Gilbert, L. E. 1972. Pollen feeding and reproductive biology of *Heliconis* butterflies. Proc. Natl. Acad. U.S.A. 69: 1403–1407.

Grant, K. A. 1966. A hypothesis concerning the red coloration in Californian hummingbird flowers. Amer. Naturalist 100: 85–98.

Grant, V. 1950. The flower constancy of bees. Bot. Rev. (Lancaster) 16: 379–398.

Heinrich, B. 1972. Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. Jour. Comp. Physiol. 77: 49–64.

——— & P. H. Raven. 1972. Energetics and pollination ecology. Science 176: 597–602.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canad. Entomol. 91: 293–320.

———. 1966. The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Canada 48: 1–86.

Ishikawa, S., T. Hirao & N. Arai. 1969. Chemosensory basis of host plant selection in the silkworm. Ent. Exp. Appl. 12: 544–554.

Ivlev, V. S. 1961. Experimental Ecology of the Feeding of Fishes. New Haven.

Janzen, D. H. 1973. Host plants as islands. II. Competition in evolutionary and contemporary time. Amer. Naturalist 107: 786–790.

Levin, D. A. & H. W. Kerster. 1973. Assortative pollination for stature in *Lythrum salicaria*. Evolution 27: 144–152.

Linsley, E. G. 1958. The ecology of solidary bees. Hilgardia 27: 543–599.

Marten, G. G. 1973. An optimization equation for predation. Ecology 54: 92–101.

Michener, C. D. 1954. Bees of Panama. Bull. Amer. Mus. Nat. Hist. 104: 1–175.

Mooney, H. A. 1972. The carbon balance of plants. Annual Rev. Ecol. Syst. 3: 315–346.

Percival, M. S. 1961. Types of nectar in angiosperms. New Phytol. 60: 235–281.

Proctor, M. & P. Yeo. 1972. The Pollination of Flowers. New York.

Pulliam, H. R. 1974. On the theory of optimal diets. Amer. Naturalist 108: 59–74.

Ramírez B., W. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24: 680–691.

Rapport, D. J. 1971. An optimization model of food selection. Amer. Naturalist 105: 575–587.

Raven, P. H. 1972. Why are bird-visited flowers predominately red? Evolution 26: 674.

Robertson, C. 1899. Flowers and insects. XIX. Bot. Gaz. (Crawfordsville) 28: 27–45.

Rothschild, M. 1973. Secondary plant substances and warning colouration in insects. *In* "Insect/Plant Relationships." Sym. Roy. Entomol. Soc. Lond. 6: 59–83.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). Jour. Animal Ecol. 39: 619–668.

———. 1971. A comparative study of models for predation and parasitism. Res. Popul. Ecol., suppl. 1. 91pp. Kyoto, Japan.

Schoener, T. 1971. Theory of feeding strategies. Annual Rev. Ecol. Syst. 2: 369–404.

Southwood, T. R. E. 1973. The insect/plant relationship—an evolutionary perspective. *In* "Insect/Plant Relationships." Sym. Roy. Entomol. Soc. Lond. 6: 3–30.

Synge, A. D. 1947. Pollen collection by honeybees (*Apis mellifera*). Jour. Animal Ecol. 16: 122–138.

Wickler, W. 1968. Mimicry in Plants and Animals. New York.

Wolf, L. L., F. R. Hainsworth & F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176: 1351–1352.

Yeo, P. F. 1968. The evolutionary significance of the speciation of *Euphrasia* in Europe. Evolution 22: 736–747.

PLANT GEOGRAPHIC STUDIES ON DIPTEROCARPACEAE IN MALESIA[1]

WILLEM MEIJER[2]

The primary lowland forest of tropical Southeast Asia west of Wallace's Line have the peculiar feature that they are dominated as regards the numbers of emergent trees and volume of timber by a single family, the Dipterocarpaceae. The timber produced by trees belonging to this family is often sold in the United States under the rather misleading name Philippine mahogany. Renewed interest in this family among scientists and environmentalists in the U.S.A. stems from the studies of military forest destruction in Vietnam, and the opening up of large new American timber concession holdings in Indonesian Borneo and Sumatra.

There is an awareness that the Dipterocarpaceae are a unique object for biosystematic and plant geographic study besides being the most valuable renewable natural resources of extensive areas of Southeast Asia (Foxworthy, 1946; Slooten, 1961; Ashton, 1969*b*; Jong & Lethbridge, 1967). They are, as regards sizes of trees, biomass and number of species, the most successful family among all Angiosperm families in Southeast Asia. The unexploited forests of Borneo and Sumatra represent a fortune of many billions of dollars in timber value.

From a purely scientific point of view, the Dipterocarpaceae are extremely interesting because they occur in areas which have had a relatively stable geology since the Cretaceous, probably the time of their origin. Since that time they have spread over Southeast Asia and over Africa; possibly they occur in disguised forms also in the American tropics as plants now considered to belong to Tiliaceae. In their leaf forms and indumentum they show Malvalean characters. The flowers of the African *Monotes* have short androgynophores, and their barks have slime ducts as in some Tiliaceae. The Dipterocarpaceae proper have resin canals in their woods and the flowers have calyx lobes which enlarge and develop into wings on the ripening fruit. Stamens occur in 5 whorls of 3 or in multiples of 15.

Because of the *dispersal* of the fruits by wind over distances in general not further than up to half mile, *we can use the Dipterocarpaceae as tracers of old land connections.* Because large areas of Malaya, Sumatra, and Borneo, the

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FIGURE 1. Flowering lowland dipterocarp forest north of Segama River, near Lahad Datu, Sabah. Note the usual distance between flowering trees belonging to the same species.

main center of the family, were until recently relatively undisturbed, we can study the patterns of distribution of species pretty closely. These patterns can be related to taxonomic affinities of species, their ecological adaptations, and their flower and fruit biology. Hopefully we can learn in this way something about speciation in tropical rain forests (Ashton, 1969*b*). However, there is little time left to tackle comprehensive biosystematic studies of this family because the rate of disappearance of primary rain forests in Southeast Asia is far outstripping the very feeble attempts made for botanical exploration.

A family like the Dipterocarpaceae needs to be studied in the field by keen alert young forest botanists who are technically well equipped with good documentation methods, who also know how to use tree climbers and who possess extreme perseverance. Differences between species of *Shorea*, now amounting to 164 species, are often very minute and their study can be tedious. A lot of sterile herbarium material stays a long time as undetermined in file cabinets. Rapid progress with their identification can only be made by specialized botanists who go out in the field and who at the costs of much sweat and labor get themselves familiar with these trees in all their stages, from seedling to adult, with flowers, fruits, sterile branches and fallen leaves (Fig. 1). This takes a lot of time and patience. Foresters are often not disposed to make such detailed careful field studies and after they get training they often tend only to look at the known species and pass by the unknown or fit them together with species they pretend to know. The local names are often very confused and a bad guide in genera with minute differences between species. A professional field taxonomist always quickly outgrows the local experience of so-called tree-experts. The knowledge about the dipterocarps of Indonesia has been accumulating very slowly though steadily by collections brought together by foresters and worked up by van Slooten, who was mainly an herbarium botanist. There are stories that when he once entered a forest in Borneo he could not recognize the Dipterocarps (Dilmy, personal communication). The herbarium collections often come from areas where in 100 square kilometers not more than 5–10 plants have been collected—like most of lowland Sumatra, an island about the size of California. That whole area has never had a full time professional field taxonomist who was specialized in the Dipterocarpaceae and without doubt, scores of species still have to be discovered there. I made a few expeditions in the lowland Dipterocarp forests of East Central Sumatra during 1955–1956, but I am sure that with my present experience I would get far more out of it.

Intensive work has been done during the last 15 years in former British Borneo, Sarawak, Brunei, and Sabah by Wood, Ashton, Anderson, and myself. From this resulted the description of 88 species new to science. There is no reason to believe that Sarawak is richer in Dipterocarpaceae than western Indonesian Borneo with collection density of seven specimens per 100 square kilometers. Consequently we can conclude that a lot more intensive field work should be done before we have a more complete picture of speciation and evolution in this family. It is hoped that the U.S.A. can assist Indonesia not only in exploiting its natural resources by logging big concession areas and buying about half of the Dipterocarp timber exports from Japan, but also in exploring and conservation. If no adequate botanical reserves are set aside in Borneo and Sumatra, we will be faced with irreparable loss of one of the most interesting and valuable gene pools of trees in the world. Intensive training courses and exploration work will be needed here as well as in the Philippines. Dipterocarp collections in the National Museum in Manila are totally unrepresentative. It is a fact that these forests can be exploited without bothering too much about the niceties of species identification though intensive research in Malaya by Symington (1943) and Desch (1957) and in Sabah by Wood and Meijer (1964) and Burgess (1966) certainly has assisted to standardize timbers and their uses on the buyers' markets (mainly Japan).

It is essential now to accompany the new opening up of forests in Indonesian Borneo (Kalimantan) and Sumatra with renewed field work on the Dipterocarps and to assure that areas are not being overlogged or swept away in conversion into useless grasslands, which already cover five million hectares in Sumatra (Dilmy, 1960). It has been shown in Sabah that lowland Dipterocarp forests can be logged selectively on a sustained yield basis and that this type of land-use is in many areas far preferable to so-called conversion into agricultural lands because the soils of tropical lowlands are not permanently productive without tree cover, except under irrigation. A strong case was made in Sabah for a permanent Forest Estate on the East Coast by a team of United Nations Special Fund researchers. Similar cases could be made in tropical America and tropical Africa.

SPECIATION AMONG DIPTEROCARPS IN BORNEO

Compared with other parts of Southeast Asia, Borneo is at present undoubtedly the center of development of the Dipterocarpaceae. Sarawak with about

247 species (Ashton, 1969) has about the same size as Malaya with 160 species (Symington, 1943). Sabah, about the size of Virginia but still not fully explored, has about 160 known species (Wood & Meijer, 1964), tiny intensively explored Brunei has 153 (Ashton, 1963). There is now growing evidence that the western part of Borneo has a greater species density for Dipterocarps than the Southeast and South. This can possibly be explained by longer geological stability. It is the so-called central core of Palaeozoic and early Mesozoic rocks, exposed since the Cretaceous. Other portions of that old Sunda Shield area are found in Malaya and Sumatra, and around that we find a mantle of late Mesozoic and Tertiary rocks in great geosynclinal formations (Kirk, 1968).

After an early phase of volcanism in the Upper Cretaceous, of which rocks are exposed in eastern Sabah, around Darvel Bay, there was another phase in the Miocene with uplifting of the ultrabasic mountains in the Labuk area (Kirk, 1968). During the same time there must have been a high mountain range along the Crocker range, the northern continuation of the watershed between Sarawak and Kalimantan, according to palynological data studied by J. Muller (1966).

The occurrence of Dipterocarpaceae in Africa, India, as well as Malesia, and their possible relationship with some rare or undescribed forms in Latin America suggest that the roots of this family go back to the area of the possible Gondwanic origin of pan-tropical lowland families. However, it seems too early to be sure about the center of origin of the various genera. Facts so far established are that in Borneo the fossil records of pollen and macro-fossils of the genus *Dipterocarpus* go back to the Oligocene (Muller, 1964, 1970), in Assam and India up to the Himalayan foothills to the Miocene (Lakhanpal, 1970). Fossils also have been found in the Tertiary of Egypt and Somaliland (Lakhanpal, 1970). Merrill (1923) reports Pliocene leaf prints of three species from Luzon identified with species now living in the Philippine Archipelago.

A number of widespread genera and species may have originated over the late Cretaceous or early Tertiary land connections reaching from Malesia to India. *Shorea*, *Dipterocarpus*, *Vatica*, and *Hopea* all range from Ceylon to Malesia. The following species reached out beyond Borneo:

Dipterocarpus grandiflorus—Burma, Thailand, Malaya, Sumatra, Borneo, Philippines.
Dipterocarpus gracilis—Burma, Thailand, Malaya, Sumatra, Java, Borneo, Philippines.
D. kerrii—Andamans, Burma, Thailand, Malaya, Borneo.
D. hasseltii—Siam, Malaya, Sumatra, Borneo, Philippines.
Anisoptera costata—Northwest Thailand, Malaya, Sumatra, eastern half of Borneo, Moluccas, New Guinea.
Shorea gratissima—Tenasserim, Siam, Malaya, Borneo.
Shorea guiso—Indochina, Siam, Malaya, Borneo, Philippines.
Vatica mangachapoi—Malaya (high hills in the North), Borneo, Philippines (all areas) according to Ashton (1964).

FIGURE 2. *Shorea maxwelliana* near Gravel pit, Sungai Manila Road, Sandakan, Sabah. Flowers and fruits were collected from this tree by the use of the native ladder construction. Authentic wood sample was taken for timber study.

At least 78 species occurring in Sumatra have been found also in Malaya and at least 55 species are shared between Sumatra and Borneo. The most prominent species shared among Malaya, Sumatra, and Borneo are *Dryobalanops aromatica*, the so-called camphor tree, *Dipterocarpus lowii*, *D. palembanicus*, *D. verrucosus*, and *Shorea leprosula*. Besides, there is a rather considerable group of species which seem to have spread from Borneo to Malaya and some beyond that to Thailand:

Dipterocarpus sarawakensis
D. humeratus
D. oblongifolius
D. acutangulus
Anisoptera laevis
Cotylelobium malayanum
Hopea dyeri
H. montana
H. nervosa
H. nutans
Shorea gratissima
S. faguetiana
S. lamellata
S. gibbosa
S. multiflora
S. kunstleri
S. teysmanniana
S. exelliptica
S. flava

Towards the east there are species which link Borneo with the Philippines, and most of these have their Bornean center in Sabah:

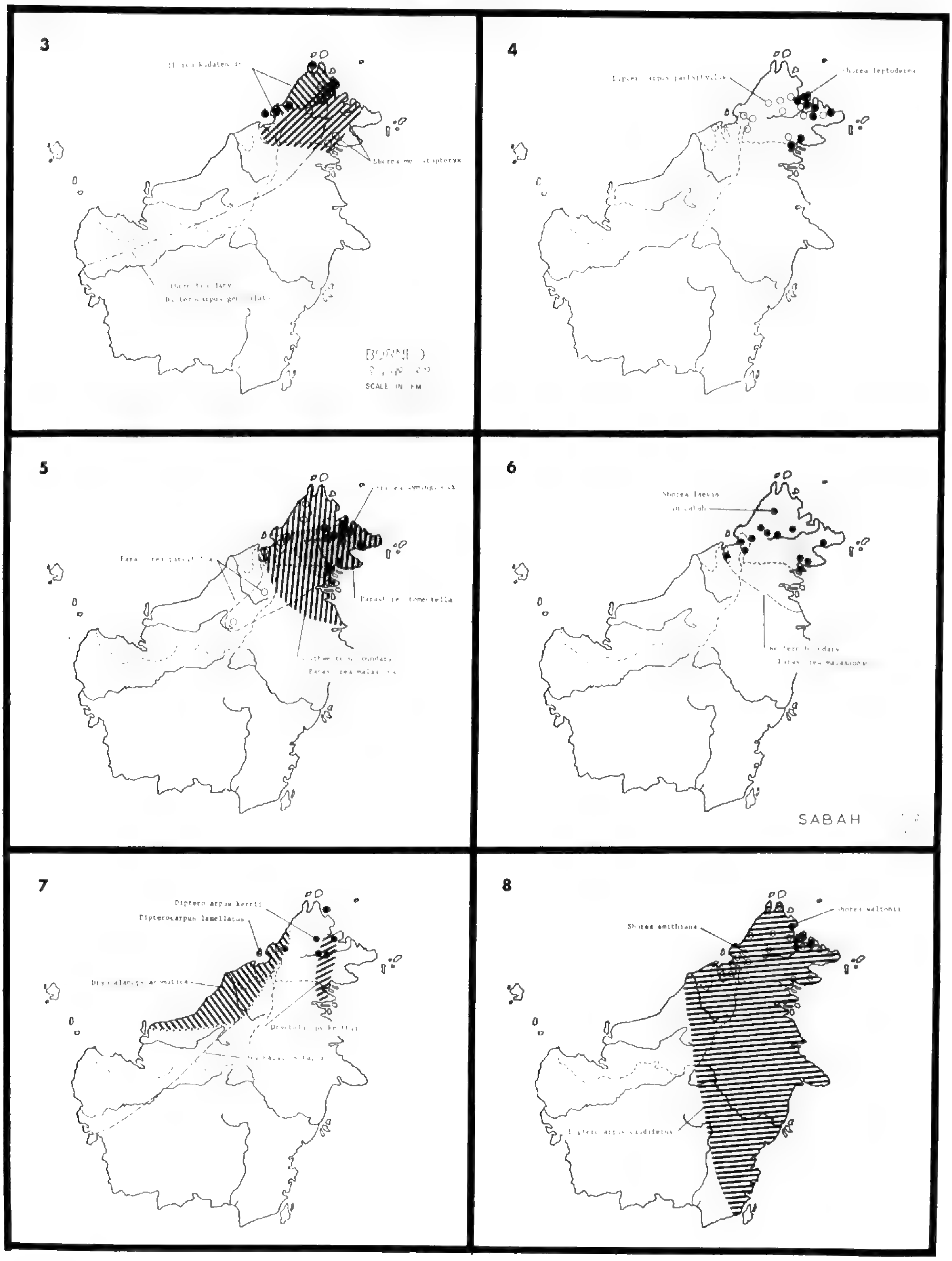
Dipterocarpus warburgii
Vatica mangachapoi
Parashorea malaanonan
Shorea almon
S. seminis

The farthest link between Borneo and islands east of it is through *Vatica papuana*. However, that could be a case of distribution of fruits in coastal drift. So far no experimental proof has been given for this, though *Vatica papuana* tends to grow on clayish soils at the inner side of mangroves. The very remarkable fact that the Ceylonese *Vateria copallifera* is narrowly related with *Vatica papuana* has been overlooked a long time (Meijer, 1972). There are also a number of species in Borneo which are endemic. Some of these seem to occur over the whole island, like *Shorea virescens*.

Others occupy more or less the northern half, others the southern, others only occur in the southeast (*Shorea smithiana*), still others only in the northeast. Quite a few species are restricted to the area northwest of the Crocker Range (*Shorea albida*, *Shorea slootenii*, *Dryobalanops rappa*, *Upuna borneensis*, and scores of others).

There are 8 species endemic to Sabah: *Vatica maritima*, *Shorea leptoderma*, *S. waltonii*, *S. symingtonii*, *S. hypoleuca*, *S. kudatensis*, *Hopea argentea*, and *Dipterocarpus pachyphyllus*. Most of these species are locally sufficiently abundant to be considered vigorous young species, like *Shorea waltonii*, *S. kudatensis*, and *Dipterocarpus pachyphyllus*.

Parashorea tomentella and *Dryobalanops lanceolata* occur mainly in Sabah and adjacent Indonesian Borneo, and within their distribution areas they are sufficiently common to form substantial volumes in the export timber market.



Figures 3–8. Examples of species distributions inside Borneo.—3, 4, 5, and 8. Areas of species centered in or around Sabah (lightly shaded in Fig. 6).—6. Scattered distribution of *Shorea laevis* in Sabah. Farther south in East Malasian Borneo this species is far more frequent. It also occurs in Malaya.—7. Only the scattered distribution of *Dipterocarpus kerrii* inside Sabah is illustrated.

Detailed analysis of vegetation types has shown that there is a lot of diversity according to ecological preferences. The most remarkable is the contrast in Dipterocarp flora between sandstone, shale, and basaltic areas dominated by a concentration of *Parashorea malaanonan, P. tomentella, Dryobalanops lanceolata,* and *Dipterocarpus caudiferus* and a group of species on ultrabasic hills where the constant combination of the most frequent species consists of *Shorea laxa, S. kunstleri, Dipterocarpus geniculatus,* and *D. lowii.* Even more remarkable is that in East Sabah these species are restricted to ultrabasic areas while they occur in Southwest Sabah and adjacent Brunei and Sarawak on other geological formations and sandy clayish soils derived from these.

A few species occur on the ultrabasic as well as on poor leached sandstone: *Shorea venulosa* and *Shorea multiflora.* Besides the edaphic-geological sorting of species there is variation in preferences according to drainage and altitudes (for examples, see Wood & Meijer, 1964), in a similar way as can be observed in Malaya and Sumatra. *Shorea platyclados* is the most prominent upper Dipterocarp-forest species in all three areas. *Shorea curtisii,* a mountain ridge species of Malaya and Sumatra, reaches into the southwest part of Borneo; *Shorea monticola* is a Crocker Range-Kinabalu species. Species like *Hopea pentanervia* and *Dryobalanops beccarii* are specialized to high level alluvium terraces with white sand and gravel along the upper Labuk River, in the Labuk delta, and around the Sook-plain. It is possible that all these white sands derive from an ancient Trusmadi, the second highest mountain in Sabah.

The conclusion is that Dipterocarps have evolved in Borneo in all parts of the island between sea level and 6000 feet altitude in all kinds of habitats, most vigorously below 3000 feet. The present distribution centers of species are located in all parts of the island (Figs. 3–8). It looks as if given time, species could evolve anywhere. Having 50 species together within one forest, 20 species of *Shorea* within 80 acres (Fox, 1967), it seems unlikely that speciation can be explained by adaptation to different niches. Poore (1968) has tried to check that hypothesis in Malaya, but Wong and Whitmore (1970) could not substantiate it. My own impression from detailed sampling work is also that within one forest type species can have overlapping niches, slightly better drainage may benefit one species more than another, but where gaps occur in the forests when old trees fall over or rot away, it is often first come, first served, and among the mixture of seedlings and saplings coming up the one in the best position as regards light conditions will finally fill the gap in the canopy.

The striking feature among some species with small areas is that they can often be traced to their still living ancestors, so-called parent species which have larger areas of distribution. I am pretty sure that *Parashorea malaanonan* is the parent species of *P. tomentella* and that *Shorea faguetiana* is the parent of *Shorea kudatensis.* Other examples are given in Meijer (1963). A detailed computer-taxonomy including data on phytochemistry, pollen structure, and wood anatomy could establish the taxonomic gaps between species and compare this with distribution areas. Ashton (1969) tried to explain speciation in Dipterocarps in the light of current theories of selection, adaptation, and genetic drift. He referred back to a thought-provoking paper by Federow (1966), who tried to explain speciation in tropical rain forests through non-adaptive differentiation of small populations. Federow (1966) asserted that individuals of a population of a tree in a tropical forest are often spatially isolated, self fertilization must then be the rule. This is substantiated by sample plot studies by Poore (1964) in Malaya in which a survey was made of 23 hectares of forest in which among 381 species, 157 only occurred once. Of course, only the large-sized trees could be enumerated, and according to my experience a tree rare or scattered in one site might be much more frequent elsewhere. According to Ashton (1969) "the nature of the problem lends itself to speculation rather than scientific inquiry." His scholarly treatment cannot hide the fact that we know very little about actual selection pressures and adaptation in the life of Dipterocarps, though it becomes more and more clear now that crown structures and leaf forms may have far more adaptive strategic value than was thought before (Brunig, 1970).

Also very little is known about pollination of dipterocarps. Ashton (1969) mentions the occurrence of the bees belonging to *Apis dorsata* in large nests in emergent trees of *Koompassia excelsa* in Malaya, Borneo, and Sumatra. In addition, we could mention the far greater frequency of occurrence of stingless bees belonging to the genus *Trigona* often living at the base of dipterocarp trees in nests made of resin of the trees. It is unlikely that pollinators can be very specific. Dipterocarp trees flower very infrequently at intervals of 3–5 or even 9 years. However, when they flower they flower in general gregariously, though different species often in different phases (Wood, 1955; Meijer, 1967, 1974), and that could create isolation mechanisms (Fig. 2).

Fruit dispersal might be responsible for restricted areas of species as demonstrated by Ashton (1969) for a whole series of species often restricted to particular water catchment areas in Sarawak (Northwest Borneo). However, that does not necessarily prove that such species originated simply because of their spatial isolation between rivers acting as barriers to their dispersal. Therefore, I am strongly inclined to question Ashton's contention that the breeding pattern of Dipterocarps conforms to the normal pattern of speciation among pan-mictic herbaceous flowering plants. Fosberg (1970) points out that the floristic wealth of the lowland tropical rain forest is far greater than might be expected, considering the apparent uniformity of the rain forest environment.

Ecological isolation of species might have played a role in a genus like *Dryobalanops* where each of the five Bornean species has its own ecological adaptive peak, but it looks different in *Shorea* with at least 150 species in Malaya, Sumatra and Borneo; 60 in Malaya alone. It is impossible to imagine that they all occupy different ecological niches. I am inclined to leave options open for the possibility of speciation by saltation as suggested by Steenis (1969), in which one tree becomes the founder of a new species. After all, when a Dipterocarp flowers there are hundreds of thousands of flowers open on the crown of a tree and the bees swarming around these flowers will in general pollinate flowers on the same tree (Fig. 2). Some of our plots give an idea of the scattering of flowering crowns of two closely related species of *Parashorea* within 10 acres of forest. In this case there is no evidence that the two species hybridize, though they flower at the same time.

I have found only one example of a dipterocarp hybrid—one between *Dipterocarpus confertus* and *D. stellatus*, mentioned in Wood and Meijer (1964) but overlooked by Ashton (1969) and Steenis (1969).

If a tree of *Parashorea malaanonan* underwent a mutation through radiation or any other cause which caused hairiness of leaves, longer size of stamens and a few other characters in a pleiotropic way, then this tree might become the center of a new species, provided there is sufficient isolation between progeny of this tree and those belonging to the mother species. In this connection it should be noticed that species which can be of very scattered occurrence in one area are sometimes in other localities very gregarious. Examples: *Shorea guiso* very common around Darvel Bay, scattered around Sandakan Bay, *Parashorea malaanonan* is very dominant on basaltic soils near Mostyn, Labah Datu District.

If we had more solid information on the migration rate of Dipterocarps, the rate with which the progeny of one tree can spread out to form a new population, we would have an idea of how long the areas of some of the endemic species in Sabah or Sarawak took to grow out from the "founder tree." In case we would assume that a dipterocarp can spread fruits and establish seedlings within a radius of one-eighth of a mile in 10 years' time, then it would take 8000 years to spread over a 100-mile radius. In case the large dipterocarp forests of Malesia are not wiped from the face of the earth within the next 20 years, we might still be able to collect more data on pollination, pollinators, exact phases and frequencies of flowering and fruiting, ecological adaptation of species and rate of dispersal and migration from a single tree as center. Meanwhile cytological studies as started by Jong and Lethbridge (1967) could give us more data on interspecific variation.

ISLAND HOPPING AND DISJUNCTIONS

Another way to study evolution in the dipterocarps is an analysis of disjunctions of genera and fragmentation of areas of species between the various islands and the Southeast Asian continent. The so-called Sunda shelf, including Malaya, Sumatra, and Borneo, has at least 25 species in common. One could be inclined to explain this by the fact that as recently as the Pleistocene these islands were connected. However, that depends on the length of the period of those land connections and the speed of migration of species. Far stronger differences are shown between Borneo and the Philippines in their dipterocarp floras. In the first place, the total number of species in the Philippines is only 52 (against around 300 in Borneo). The genus *Dryobalanops* represented with 5 species in Borneo is absent from the Philippines. Part of the species which the Philippines share with Borneo are most likely old, widespread: *Dipterocarpus grandiflorus*, *D. gracilis*, *D. hasseltii*, *Anisoptera costata*, *Shorea gratissima*, *S. guiso.* A few other shared species only occur in Borneo in areas adjacent to the Palawan and Sulu landbridges: *Dipterocarpus warburgii* and *Vatica mangachapoi.* This distribution is paralleled in other families, for example Flacourtiaceae.

It is, of course, possible that those with Eastern Borneo areas are relicts and were formerly far wider spread over the Sunda shelf. A case in point is *Vatica mangachapoi*, also reported from North Malaya (Ashton, 1969). We have to accept the fact that species may have died out. For example, in the genus *Hopea* there are no shared species except perhaps *Hopea philippinensis*, and it is unlikely that that one species is the source of the seven species of *Hopea* now known from the Philippines. The distribution of *Pentacme* with 2 species in the Philippines and others in Thailand shows that species must have died out in intervening areas. Much of the South China Sea between Indo-China, Borneo, and the Philippines might have been land sometime. In the genus *Parashorea*, which is represented in Sumatra by at least 6 species and in Malaya by 3, it looks as if the northeastern part of Borneo together with the Philippines forms a secondary center of speciation. Also within species distributions we can notice disjunctions.

Anisoptera costata, a species of forests below 3000 feet altitude, is in Sabah and Brunei of very scattered occurrence (Ashton, 1969; Wood & Meijer, 1964). Nowhere in Sabah have I ever seen this species otherwise than as very isolated trees. In the 10,000 acres Sepilok Forest Reserve widely explored over a period of 9 years with frequent Forest School field classes, we found only a few isolated trees. There are no other species of dipterocarp with their principal region of distribution in western Malesia which extend as far eastwards as *A. costata*. It thus must be a very old species, and Slooten (1952) assumes that the origin of this and other Dipterocarpaceae of Malesia was somewhere in the region now occupied by the South China Sea. Possibly *Anisoptera mindanensis* of the Philippines is the same species (Slooten 1952: 10). From all the evidence known so far, it looks as if *A. costata* is in Borneo a rather *senescent* species. It has a low rate of regeneration and consequently it is now very scattered and rare. How much its "non-occurrence" in West Borneo is real or due to lack of exploration has still to be seen.

The area of *Dipterocarpus kerrii* in Borneo is by no means a closed distribution pattern anymore (Fig. 7). In Sepilok Forest Reserve 15 miles west of Sandakan, we found one tree of this species within 10,000 acres, and maybe only on Jembongan Island is this species fairly common locally. It looks like a species on the way out. The same scattered occurrence can be noticed with *Dipterocarpus gracilis*. In Sabah it generally occurs as scattered individuals over the whole region. In Brunei it is very rare, only semi-gregarious in a few locations. In this case the senescence of this species could point to a former higher frequency during dry periods of the Pleistocene or earlier in the Pliocene as illustrated by Steenis (1961) and suggested by the former distribution of the mangrove genera *Aegialitis* and *Camptostemon* as shown by pollen analysis work of J. Muller (personal communication).

During the Pliocene these genera were fairly common in Borneo. Later on, *Aegialitis* disappeared and *Camptostemon* is now very rare in Borneo (Muller and Steenis *in litt.*). Possibly the contrasts between ultrabasic and sandstone Dipterocarp floras have to be explained also in terms of aggressive (strongly regenerating) versus non-aggressive species.

Parashorea malaanonan, *Dryobalanops lanceolata*, and *Dipterocarpus caudiferus* have not made much headway in Brunei and Sarawak—or have not reached there yet. Thus they left there ample space for *Dipterocarpus geniculatus*, *Shorea laxa*, and *Shorea kunstleri*, while in Sabah they invaded the new Tertiary deposits, especially the upper coastal marine platform before the forests on older geological formations got established on these. All these observations lead us to consider the possibility that gaps in distribution areas originated after periods in which one of the "older" widespread species were more gregariously distributed. Now assume we have the means to distinguish on the one hand new species with small areas and narrow taxonomic gaps from still living parent species and on the other hand "dying out" more isolated relict species.

The whole picture becomes one of increasing diversity in the course of evolution, new species branching off from parent species, at first narrowly related, but with age having larger areas and wider systematic gaps—some species dying out or becoming fragmented; genera like *Hopea*, *Shorea*, *Vatica*, *Anisoptera*, and *Dipterocarpus* hopping over from Borneo to the Philippines. A few species in such genera little or not changed from their Bornean parent population; others branching off forming new endemic species.

I hope that from all this it will be clear that all possible attempts have to be made to maintain the Dipterocarpaceae as natural resources of Southeast Asia on a sustained yield basis, to set aside virgin Jungle Reserves for their continuous scientific studies, and to finance this research substantially. It is far more important to preserve these trees as *living monuments* for all time too come, than to remain content with our scrappy herbarium records and merely throw up our hands about the barbaric destruction of these natural resources by the military, by lumber-jacks, and by shifting cultivators.

LITERATURE CITED

ASHTON, P. S. 1963. A Manual of the Dipterocarp Trees of Brunei State.

———. 1969*a*. A Manual of the Dipterocarp Trees of Brunei State and Sarawak.

———. 1969*b*. Speciation among tropical forest trees, some deductions in the light of recent evidence. Biol. Jour. Linn. Soc. 1: 155–196.

BRUNIG, E. F. 1970. Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. Trop. Ecol. 11: 26–43.

BURGESS, P. F. 1966. Timbers of Sabah. Sabah Forest Records 6, For. Dept. Sabah, Malaysia.

DESCH, H. E. 1957. Manual of Malayan timbers. Malayan Forest Records 15, vol. 1.

DILMY, A. 1960. The effect of fire used by early man on the vegetation of the humid tropics. Pp. 119–122, *in* "Symposium on the Impact of Man on Humid Tropics Vegetation."

FEDEROW, A. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. Jour. Ecol. 54: 1–11.

FOSBERG, F. R. 1970. The problem of isolation in the lowland tropical rain forest. Trop. Ecol. 11: 162–168.

FOXWORTHY, F. W. 1946. Distribution of the Dipterocarpaceae. Jour. Arnold Arbor. 27: 347–354.

FOX, J. E. P. 1967. An Enumeration of lowland Dipterocarp forest in Sabah. Malayan Forester 30: 263–279.

HILDEBRAND, F. H. 1952–1954. Series of Lists of Treenames. Sumatra.

JONG, K. & A. LETHBRIDGE. 1967. Cytological studies in the Dipterocarpaceae. I. Chromosome numbers of certain Malaysian genera. Notes Roy. Bot. Gard. Edinburgh 27: 175–184.

KIRK, H. J. C. 1968. The igneous rocks of Sarawak and Sabah. Geol. Sur. Borneo Region, Malaysia, Bull. 5.

LAKHANPAL, R. N. 1970. Tertiary floras of India and their bearing on the historical geology of the region. Taxon 19: 675–694.

MEIJER, W. 1963. Notes on Borneo Dipterocarpaceae. Acta Bot. Neerl. 12: 319–353.

———. 1967. Elements of Forest Botany in Sabah.

———. 1970. Regeneration of tropical lowland forest in Sabah, Malaysia, forty years after logging. Malayan Forester 33: 204–229.

———. 1972. Some taxonomic and nomenclatorial notes on *Vateria copallifera.* (Retz.) Alston. Ceylon Jour. Sci. 10: 76–79.

———. 1974. Field Guide for Trees of West Malesia. Univ. of Kentucky Book Store, Lexington.

MERRILL, E. D. 1923. Distribution of the Dipterocarpaceae. Philippine Jour. Sci. 23: 1–32.

MULLER, J. 1964. Palynological contributions to the history of Tertiary vegetation in N.W. Borneo. P. 371, *in* "Abstracts, Xth Int. Bot. Congress, Edinburgh."

———. 1966. Montane pollen from the Tertiary of N.W. Borneo. Blumea 14: 231–235.

———. 1970. Palynological evidence of early differentiation of Angiosperms. Biol. Rev. 45: 417–450.

POORE, M. E. D. 1968. Studies in Malaysian rain forest I. The forest on triassic sediments in Jengka Forest Reserve. Jour. Ecol. 56: 143–196.

SLOOTEN, D. F. VAN. 1952. Sertulum Dipt. mal. V. Reinwardtia 2: 1–68, Figs. 1–22.

———. 1961. Sertulum Dipt. mal. VII. Reinwardtia 5: 457–479.

STEENIS, C. G. G. J. VAN. 1961. Introduction. *In* M.S. van Meeuwen, H. P. Nooteboom & C. G. G. J. van Steenis, "Preliminary revisions of some genera of Malaysian Papilionaceae I. Reinwardtia 5: 420–429.

———. 1969. Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution in Speciation in Tropical Environments. Biol. Jour. Linn. Soc. 1: 97–133.

SYMINGTON, F. 1943. Forester's Manual of Dipterocarps. Malayan Forest Record 16.

WONG, Y. K. & T. C. WHITMORE. 1970. On the influence of soil properties on species distribution in a Malayan lowland Dipterocarp forest. Malayan Forester 33: 42–54.

WOOD, G. H. S. 1956. The Dipterocarp flowering season in North Borneo 1955. Malayan Forester 19: 195–201.

——— & W. MEIJER. 1964. Dipterocarps of Sabah.

SOLANUM AND ITS CLOSE RELATIVES IN FLORIDA[1]

W. G. D'Arcy[2]

Among the wide variety of plants received for determination by the University of Florida Agricultural Experiment Station, members of the genus *Solanum* and its close relatives *Lycianthes* and *Lycopersicon* appear from time to time. Prompted as an aid to identification of such materials, this paper includes 32 species known to have occurred in the state in the wild and in cultivation. Table 1 lists the Florida taxa with some of their characteristics. The assemblage is a good representation of the diversity in the group, yet members are recognizable by even unsophisticated workers as belonging to *Solanum* or a genus much like it. The taxonomic diversity of the Florida species facilitates their identification, especially of the introduced species, but some native groups are undergoing evolution, and their taxonomic distinctions are not so clear. To separate the taxa, Key No. 1 (p. 830) makes use of vegetative and floral characters, and Key No. 2 (p. 833) makes use of characters of the fruit.

METHODS

Living plants were studied in most counties of Florida during the years 1966–68, and many plants were grown in the greenhouse in Gainesville from seed collected during field visits. Seed from a number of non-Florida sources, particularly New Zealand, California, and the Antilles was grown out for comparison. Major North American and European herbarium holdings of *Solanum* specimens from Florida were studied either through loans or personal visits. Chromosomes of several taxa were counted using anther squash technique, and some of these counts were reported earlier (D'Arcy, 1969). The count of *Solanum racemosum* reported here was made from root tip squashes. In noting chromosome counts, usually only one recent report is cited although, there are sometimes more in the literature. Pollen was acetolysed according to the method of Erdtman (1952) using Florida material. Measurements are the range of ten normal grains from three different plants, or where fewer plants were available, from one or more flowers.

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TABLE 1. Some features of the Florida taxa of *Solanum*. The type species of a section is indicated by an asterisk following the name. An asterisk in the chromosome column indicates a count for Florida material.

Taxon	Florida occurrence	Florida range	Native range	Leaves	Fruit color	Corolla color	Anther length, mm	Pollen diameter, μ	Chromosomes n =
Subgenus *Solanum*									
Sect. *Solanum*									
S. americanum Mill.	common	widespread	widespread	toothed/entire	shiny black	white(purple)	0.9–1.4	17.0–20.0	12*
var. *baylisii* D'Arcy	rare	central	Old World	toothed/entire	black	white	2.5–4.0	21.0–24.0	12
S. nigrescens Mart. & Gal.	common	widespread	widespread	toothed/entire	dull black	white	2.5–2.9	21.0–23.5	12*
S. nigrum L.	rare	scattered	N. temperate	toothed/entire	dull black	white(purple)	2.2–2.8	28.0–35.0	36
S. villosum Lam.	extinct	panhandle	Old World		red		—	—	24
Sect. *Leiodendra*									
S. diphyllum L.	cultivated/escape	widespread	Mexico	entire	beige	white	ca. 2	14.0–16.5	12*
S. glaucophyllum Desf.	extinct	panhandle	Argentina	entire/sinuate	—	blue	3–6	—	12
Subgenus Brevantherum									
Sect. *Brevantherum*									
S. erianthum D. Don*	common	south	Caribbean	entire	yellow	white	ca. 3	16.0–19.5	12*
S. mauritianum Scop.	rare	central	Argentina	entire	yellow	deep blue	ca. 3	19.0–27.0	12
Sect. *Pseudo-Capsica*									
S. pseudocapsicum L.*	cultivated/escape	north	Brazil	entire/sinuate	red	white	2.5–3.0	—	12

TABLE 1. (*Continued.*)

Taxon	Florida occurrence	Florida range	Native range	Leaves	Fruit color	Corolla color	Anther length, mm	Pollen diameter, μ	Chromosomes $n =$
Subgenus *Leptostemonum*									
S. donianum Walp.	common	south	Caribbean	subentire	red	white	4.0–5.0	25.0–29.0	12*
Sect. *Acanthophora*									
S. ciliatum Lam.	common	widespread	Caribbean	angular lobed	red	white	ca. 6	24.0–30.5	—
S. mammosum L.*	cultivated	—	Tropical America	angular lobed	yellow	white	10–12	—	11, 12
Sect. *Aculeigerum*									
S. wendlandii Hook. f.*	cultivated	south	Central Amer.	rounded lobed	—	blue	8.0–10	19.0–23.5	12*
Sect. *Androceras*									
S. rostratum Dun.*	infrequent	scattered	Western U.S.	dissected	spiny	yellow	6–7/11–14	20.5–24.0	12
S. citrullifolium A.Br.	extinct	north-central	Mexico, Texas	dissected	spiny	purple	7/13	—	—
Sect. *Cryptocarpum*									
S. sisymbriifolium Lam.*	infrequent	north	Argentina	dissected	red	white	ca. 8	29.5–40.0	12
Sect. *Eriophyllum*									
S. jamaicense Mill.*	rare	central	Tropical Amer.	angular lobed	red	white	3.0–4.0	—	12
Sect. *Lasiocarpum*									
S. pseudolulo Heiser	cultivated	south	South America	angular lobed	red/orange	white	ca. 6	16.0–21.0	—
Sect. *Nycterium*									
S. tridynamum Dun.	cultivated	south	Mexico	subentire	brown	purple	5/12	—	12*

TABLE 1. (*Continued.*)

Taxon	Florida occurrence	Florida range	Native range	Leaves	Fruit color	Corolla color	Anther length, mm	Pollen diameter, μ	Chromosomes $n =$
Sect. *Persicariae*									
S. bahamense L.	common	south	Caribbean	subentire	orange	mauve	ca. 7	19.0–27.0	12*
var. *luxurians* D'Arcy	common	Key Largo	Key Largo	subentire	red	deep purple	6.0–7.0	—	12*
var. *rugelii* D'Arcy	extinct	south	—	subentire	—	—	4.0–6.0	—	—
S. racemosum Jacq.	rare	south	Caribbean	subentire	red	white	6.0–10	—	12
Sect. *Melongena* (including Sects. *Lathyrocarpum, Leprophora, Torva*).									
S. melongena L.	cultivated	widespread	India	angular lobed	black	purple	ca. 6	26.5–33.0	12
S. dimidiatum Raf.	infrequent	north	Southern U.S.	angular lobed	yellow	purple	6.0–8.0	25.0–30.0	36*
S. wrightii Benth.	cultivated	south	South America	angular lobed	—	purple to white	ca. 15	—	—
S. carolinense L.	common	widespread	Eastern U.S.	angular lobed	yellow	purple or white	6.0–11	25.0–29.0	12
var. *floridanum* Chapm.	scattered	north	Florida	dissected	yellow	purple or white	—	—	12*
S. elaeagnifolium Cav.	infrequent	scattered	Mexico, Texas	entire/sinuate	yellow	purple	6.0–8.0	27.0–31.0	12
S. torvum Sw.	rare	south	Tropical Amer.	angular lobed	yellow	white	9.0–12	21.5–34.0	12
Subgenus *Potatoe*									
Sect. *Petota*									
S. tuberosum L.*	cultivated	widespread	Chile	dissected	yellow	white	ca. 6	—	—
Sect. *Jasminosolanum*									
S. jasminoides Paxt.*	cultivated/escape	north	Brazil	rounded lobed	—	blue/white	ca. 4	—	12
S. seaforthianum Andr.	cultivated/escape	widespread	Central Amer.	rounded lobed	—	blue	2.5–3.5	17.0–21.0	12*

THE RELATED GENERA

Four genera of the Solanaceae have anthers that open by terminal pores; three of these and the close relative, *Lycopersicon*, can be separated in the following key. For generic descriptions and synonyms see D'Arcy (1973). The fourth genus with apical pores, *Triguera* of the Mediterranean region, is not of concern here.

1 Anther connectives strongly thickened and evident the whole length of the anther; inflorescence arising at a dichotomy of the stem .... *Cyphomandra*
1′ Anther connectives not thickened or conspicuous; inflorescence axillary, opposite a leaf, or lateral on a stem, seldom arising at a dichotomy of the stem.
  2 Anthers extended into sterile tips, dehiscence by ciliate, longitudinal slits; seeds pubescent .... *Lycopersicon*
  2′ Anthers opening by terminal pores, without sterile tips; seeds glabrous.
    3 Calyx with 5 main ribs or veins, the lobes mostly opening by splitting at the sutures; leaves often compound, toothed or lobed .... *Solanum*
    3′ Calyx with 10 main ribs or veins, the apex truncate and stretching to permit egress of flower and fruit, leaves simple, mostly entire .... *Lycianthes*

Cyphomandra is a primarily South American genus of 50–60 species. One species, *Cyphomandra crassifolia* (Ort.) Macbr. (= *C. betacea* Cav.), is cultivated in many parts of the world as the "tree tomato," but no Florida material has been seen. It has a pendulous inflorescence of whitish flowers and a red, juicy fruit. It is cultivated as a food crop in New Zealand.

Lycopersicon is closely related to sect. *Petota* of *Solanum* but differs in its pubescent seeds, different alkaloids and anthers which have sterile tips and dehisce by longitudinal slits. The yellow flowers and lowland rather than upland distribution also differ from species of sect. *Petota*, although they are not unknown in other groups in *Solanum*. *Lycopersicon* includes about seven species of Ecuador and Peru, as well as the cultivated tomato.

Lycianthes is closely related to *Solanum* and differs most obviously in the structure of its calyx. The primary calyx lobes or teeth are truncate and fused into an entire rim or "sleeve." The 10 vascular traces running through the calyx give rise to 1–10 teeth subtending this sleeve in one or two series. The species discussed here has less obvious teeth and a less obvious rim than most species of *Lycianthes*. The genus includes nearly 200 rare species in tropical America and Asia.

THE TAXONOMY OF *SOLANUM* IN FLORIDA

The genus *Solanum* is one of the largest in the plant kingdom. Some 3,500 species have been described, of which between a third and a half are sound. Although the genus is strongly centered in the New World, there are many species elsewhere. The most recent conspectus (D'Arcy, 1972) notes seven subgenera and 50 sections.

The Florida members of the group have long been known to botanists in both Europe and America. A third of the species had been described within 15 years of 1753, and only one, an introduction from South America, was named in this century. Few of these names were based on plants collected in Florida, and comparison of authentic specimens from different sources has revealed considerable redundance in names. Some of the Florida groups are discussed here in detail. The Florida species fall into four subgenera and 15 sections, and Table 1 lists the species in their sectional placement. One Florida element, *Solanum donianum*, is assigned to subgenus but not to section in the hope that later insight will clarify its relationships.

Section *Solanum*, or the *Solanum nigrum* complex as it is sometimes called, is taxonomically difficult. Dunal (1852), Jørgensen (1928), Bitter (1911–1923), Stebbins and Paddock (1949), Baylis (1958), Heiser (1955), and Edmonds (1968 1972) have made important contributions to the knowledge of this group, but the situation is still far from clear. The group includes both diploids and polyploids. *Solanum nigrum* L. sensu stricto is a hexaploid from northern Europe and Asia which is present in the northern United States. It is almost absent from the South. In the early years of this century seed was widely sold under the name "Wonderberry" (Heiser, 1969), and one of the three Florida collections of the species was taken in that era. *Solanum nigrum* is difficult to distinguish from *S. nigrescens*, but it is apparently not interfertile with it or with any of the other diploids (Stebbins & Paddock, 1949; Baylis, 1958). *Solanum villosum*, known in the New World only by the 1899 Curtiss collection from Pensacola, is a tetraploid which does not interact with other species in Florida. Material from North America formerly known as *S. villosum* is in reality *S. sarachoides* Sendt., a diploid species from Argentina which does not occur in Florida. *Solanum furcatum* Poir., a hexaploid of the Pacific coast, resembles some Florida collections of *S. nigrescens*, but pollen measurements verified that all such Florida collections are, in fact, *S. nigrescens*.

The diploids in sect. *Solanum* are widespread and plastic, and there is interfertility between those occurring in Florida. *Solanum americanum* is common. It is usually easily recognizable in fruit. The berry is shiny black, held erect and subtended by a strongly reflexed calyx. The plant does not root at the nodes, and the root is short and fibrous. Herbarium material is identifiable by the small anthers. The species is cosmopolitan and ranges as far north as Connecticut and Indiana in the eastern United States. Plants from the West Indies have shorter anthers, often less than 1.1 mm long, but are not otherwise separable. Edmonds (1968) recognized a glabrate and a puberulent variety in South America, but this difference is not taxonomically significant in Florida. Plants with large bushy habit (to 1 m × 1 m) with small leaves and some plants with minute leaves were found in various parts of the state, but their greenhouse-reared progeny were normal in appearance. *Solanum nigrescens* is also common in Florida. It differs from *S. americanum* in its dull, downward deflected fruits with applied calyces and in its elongate root system, which permits colonization of palm tree sheaths and cliff-sides. It is also somewhat salt tolerant and may be found beside beaches within reach of salt spray, these plants sometimes developing flowers much larger than their inland counterparts. The third diploid taxon identified in Florida is described here as *S. americanum* var. *baylisii*. It is similar in appearance to *S. nigrescens* but has longer internodes and narrower leaves. The anthers are in the size range of *S. nigrescens*. As it appears to hybridize more readily with *S. americanum*, it is described under *S. americanum* rather than *S. nigrescens*.

One Florida collection clearly resembles plants grown from seed received from Baylis in New Zealand under the name S. *gracile*, and several other Florida collections taken in the vicinity appear intermediate between the Baylis plants and S. *americanum*. This may be a transitional element in the Florida flora, adventive and soon becoming submerged in a native gene pool. A similar situation is surmised for S. *racemosum* (see below).

Some data supporting the interfertility and intersterility of the two common Florida species has been published by Stebbins and Paddock (1949), Baylis (1958), and Heiser *et al.* (1965). Intersterility apparently varies with strains from different areas. One series of observations seems to bear out hybridization on a local scale. In 1966, in and around a palm tree in front of McCarty Hall, University of Florida, were a few plants of S. *nigrescens*, while in lawns and flower beds nearby were scattered plants of the typical "citrus grove" grade of S. *americanum*. In autumn 1968, previously marked plants in the palm tree were still alive and showing their original characters. In the lawn near the tree were new plants resembling S. *nigrescens* in all respects except that the berries were shiny as in the nearby populations of S. *americanum*. While it is not certain which plants had provided the seed for these new plants, they appear to be hybrids between the two species. In Florida, California, and tropical America *Solanum americanum* and S. *nigrescens* are morphologically and ecologically distinct, but in other parts of the United States these distinctions are obscure, and in large areas of the Midwest, a relatively uniform intermediate is found. One may speculate that this is a hybrid between the two elements which has stabilized over time by repeated backcrosses and fine attunement of the product to selective conditions in the region. The diploids of sect. *Solanum* may be referred to as a "syngameon" consisting in Florida of two or three semi-species—"partially interbreeding, partially isolated, sympatric population systems" (Grant, 1963). For practical purposes, it is more useful to consider S. *americanum* and S. *nigrescens* as species, bearing in mind their close relationship but stressing the fact that two describably different biological units are present. As species they can be recognized with careful attention to detail, but as infraspecific taxa the magnitude of difference present is not apparent. The morphological and ecological differences underly pharmacological and physiological differences, and it is well for them to be distinguished as clearly as possible.

Section *Leiodendra* in Florida embraces two quite different species. *Solanum glaucophyllum* should probably be placed in a distinct subsection, but S. *diphyllum* is much like many species of sect. *Leiodendra* in Central and South America.

Section *Brevantherum* has been revised recently by Roe (1967*a*; 1972). It includes about 30 species of North and South America with three species native or naturalized in the Old World.

Section *Acanthophora* is under study by Michael Nee, University of Wisconsin. The two species discussed here are readily distinguished, but in South America a number of species present taxonomic difficulty. The $n = 11$ chromosome number reported for S. *mammosum* is anomalous in the genus. These plants contain alkaloids of possible medicinal use.

Section *Persicariae* appears to be confined to the Caribbean region, with about six species in the Antilles, and Florida. Only one specimen, the type collection of *S. anacanthum* (see under *S. racemosum*) has been seen from Central America. The group is identifiable by its slender, ventrally stellate-pubescent anthers, which in Florida species and some others are tightly coherent into a tube. Members of the group appear to be interfertile and widely distributed by birds, which provides opportunities for hybridization and introgression. *Solanum racemosum* appears to be a transitional element of the Florida flora, occasionally adventive but unable to establish colonies distinct from the native *S. bahamense* with which it seems to hybridize. These plants were considered by Dunal (1852) and Seithe (1962) to belong to sect. *Graciliflora* (1852), a later name than sect. *Persicariae* (1813). A search for material of its type species, *S. graciliflorum* Dun., at Paris, Montpellier, and Geneva failed to turn up specimens or drawings of the Javanese plants upon which the name was based.

Section *Melongena* is here considered to embrace sects. *Lathyrocarpum, Leprophora, Oliganthes*, and *Torva* (see D'Arcy, 1972). Only sect. *Leprophora* has characters (trichomes) different from the others in the group. Its type species, *S. elaeagnifolium* Cav., and the closely related *S. hindsianum* Benth. from Mexico form a pair of distinctive species, but their difference does not seem to be of sectional magnitude. Two elements of the Florida flora are interesting. Both *S. dimidiatum* and *S. carolinense* var. *floridanum* seem intermediate in many ways between *S. carolinense* and another species; in the first case the other species is *S. melongena*, and in the second case the other species is *S. sisymbriifolium*. Both elements have features suggesting hybridity: *S. dimidiatum* in its more-or-less sterile fruit, and *S. carolinense* var. *floridanum* in its irregular venation and leaf lobing (see Wagner, 1962). However, the pollen examined of these two taxa appeared quite normal.

DISTRIBUTION AND ORIGINS

The 30 species of *Solanum* occurring in Florida differ in their adaptability to Florida conditions, as is indicated by their frequency of occurrence and distribution in the state. Only seven species may be termed common in the state, and three of these, *S. bahamense*, *S. donianum*, and *S. erianthum* are located in the extreme south. These are Caribbean species: the first two are confined to the northern Antilles and mainland, and the third ranges to the South American coast and is naturalized in the Old World. All grow on limestone substrates. *Solanum ciliatum* is also a Caribbean species, but it ranges north into Georgia and occurs in Africa and other parts of the Old World. Winter conditions set the northern limits of these four species. *Solanum ciliatum*, probably because of its low habit and sturdy rootstock, is able to withstand more northerly temperatures than the three arborescent species. The other three common species are not of a Caribbean distribution. *Solanum carolinense* is a species found throughout the eastern deciduous forest of North America, becoming less plentiful in southern Florida. North of the coastal plain it dies to the ground and overwinters by means of its elongate, tuberous roots. *Solanum carolinense* has been reported from Brazil and occasionally from tropical countries, but apparently it is best adapted to seasonally cold climates. *Solanum americanum* and *S. nigrescens* are both near-cosmopolitan weeds of unknown origin, and they both range widely on both north and south bounds of Florida. In the tropics, *S. americanum* occurs from sea level to upper elevations, while *S. nigrescens* is absent from the lowlands. In temperate North America, *S. americanum* frequently behaves as an annual, but in Florida it overwinters, and its foliage survives mild frosts. These seven species would appear to be native elements successfully adapted to Florida conditions, although some are of southern and one is of northern affinity.

Presumably less well adapted to Florida conditions are those taxa of infrequent or local distribution, although this is not always corollary. *Solanum jamaicense* and *S. torvum* are both plentiful in the Caribbean region and are persistent in Florida as rare populations. *Solanum seaforthianum* is also native to the West Indies and is naturalized in south and central Florida. It is sometimes grown for ornament. The usually bright or shiny fruits of *Solanum* plants are assumed to be bird dispersed, and transport of fruits from the nearby Antilles to Florida probably accounts for the introduction of these species to the North American mainland, although escapes from cultivation account for many of the populations of *S. seaforthianum* in Florida. Winter temperatures impose a northern limit to the range of most West Indian introductions, but the central Florida rather than south Florida localities for *S. jamaicense* and the fact that these species are persistent but rare argue that winter temperatures are not the only feature of the environment limiting the distribution of these plants. *Solanum rostratum* and *S. elaeagnifolium* are species of the western plains of the United States and Mexico, and they occur in Florida as apparently persistent but quite local populations. Introduced from other continents, *S. mauritianum* and *S. sisymbriifolium* are successful in restricted distribution, the first in one central Florida county and the second scattered across the northern edge of the state. The four species just mentioned are found in both Florida and in Argentina, *S. rostratum* and *S. elaeagnofolium* presumably introduced southward and *S. mauritianum* and *S. sisymbriifolium* introduced northward, perhaps via the Old World. Although seemingly well established in local populations, these introductions have been unable to expand beyond scattered sites. In no case has a species of *Solanum* become common or widespread in the state without being well represented in neighboring territory. The expansion from well established local populations to a widespread range with frequent occurrence is apparently a major achievement which none of the sparingly introduced species of *Solanum* has managed.

In addition to those species which are well established in Florida, eleven taxa occur in the wild only in what seems to be a transitory fashion, and they probably require repeated introduction to maintain their presence. *Solanum glaucophyllum* and *S. villosum* were reported only at the beginning of the century from Pensacola, perhaps brought in by ships' ballast and unable to persist. *Solanum citrullifolium* was introduced by the University and vanished soon after. *Solanum racemosum* may be introduced from time to time from the Windward Islands, but it does not form colonies, and isolated plants presumably breed into the *Solanum bahamense* gene pool. *Solanum americanum* var. *baylisii* is presumed to disappear in similar fashion. Both of these taxa might persist in the absence of numerous individuals of such close relatives to hybridize with. *Solanum nigrum* is presumably reintroduced from cooler regions from time to time, but it has not become a part of the naturalized flora of the state. *Solanum tuberosum*, *S. jasminoides*, *S. pseudocapsicum*, and *Lycopersicon esculentum* are found in the wild, but they do not build up significant populations.

Six species are found in cultivation in the state but are not known to grow in the wild. Of these, *Solanum melongena* is an important crop plant in many parts of the state; and *Solanum wendlandii* is cultivated out-of-doors for ornament in the south, but it does not fruit. Four other species: *S. pseudolulo*, *S. wrightii*, *S. tridynamum*, and *Lycianthes rantonnei* are sold by nurseries and are probably planted out-of-doors. *Solanum ochraceo-ferrugineum* appears in plantings at Fairchild Tropical Gardens, presumably an adulterant of other plant materials from Central America. *Solanum topiro* Dun. (as *S. hyporrhodium* A. Br. & Bouché) was introduced to Florida in the 1950's as a curiosity and for experimental purposes, but the stock soon died out (see Schultes, 1958). There are no specimens at the University of Miami, where the work was done. It is likely that other species enter the nursery trade or appear in cultivation for scientific or horticultural purposes from time to time.

Lawrence (1960*a*, *b*) listed species of *Solanum* occurring in cultivation in the United States. *Solanum quitoënse* Lam. is noted as occurring in Florida. It is a stellate-tomentose herb closely resembling *S. pseudolulo*. Also listed are "*Solanum Donnell-Smithii* Coult." [= *S. lancaeifolium* Jacq. (D'Arcy, 1973)], a noxious vine with recurved spines from the Antilles and Central America, and *Solanum havanense* Jacq., an attractive shrub or vine with small, pale-blue flowers from Cuba. No Florida material of these species was seen.

Characters of the Florida Species

Of the 21 species of *Solanum* occurring in Florida outside of cultivation, 10 are perennial herbs, some of these short-lived; three are high climbing vines; and the others are woody—shrubs or trees. Only two of the herbs, *S. rostratum* and *S. americanum*, are sufficiently short-lived to sometimes behave as annuals; and only one species, *S. nigrescens*, sometimes occurs as an epiphyte. Two species have tuberous roots, but the woody, cigarette-like tubers of *S. carolinense* are quite different from the yam-like tubers of *Solanum tuberosum*, the common potato. Several of the herbs proliferate by sarmentose roots, and this enables some species to withstand periods of cold or drought. The pith of most species is solid but may be fistulose in *S. sisymbriifolium* and *S. tuberosum*. The genus *Lycianthes* consists mainly of vines or low herbs, but the species grown in Florida is a shrub. Most species of *Lycopersicon* are scandent herbs.

Hairs are simple in the subgenera *Solanum* and *Potato*; they are branched or stellate in subgenus *Brevantherum*, while in subgenus *Leptostemonum* they are stellate. Hairs with arms arising from one point are referred to as stellate (stellae); the continuation of the axis beyond this point being the midpoint, and if the arms (or radii) are more than 12, the hair is echinoid, if fewer than 12, it is pauciradiate. When the rays come off in one plane, the hair is porrect. When the arms come off the axis at more than one point, it is branched or dendritic. When the arms of porrect hairs are basally fused, the hair is termed scutellate, but such hairs are not well developed in any of the Florida taxa. Stellate hairs with stiff, multiseriate stalks are bristles, and these occur on the calyx of *S. jamaicense.* The bayonet hair, which has a larger basal cell and an elongate, narrower acicular terminal cell, is present in some species of *Solanum* in tropical America, but occurs in the Florida taxa only as an admixture to the otherwise stellate indumentum of *S. sisymbriifolium.* In some cases, *e.g.* sect. *Acanthophora,* plants at juvenile stages bear sessile, porrect hairs, but with maturity the plant bears hairs with reduced or obsolete arms, and the remaining midpoint remains as an apparently simple hair. Glandular or viscid species usually bear glands at the tips of the simple hairs or midpoints of stellate hairs.

Calyces provide useful information for recognizing species. In sects. *Cryptocarpum* and *Androceras,* the spiny calyx is accrescent, completely enveloping the fruit. In the first case, the calyx splits at maturity exposing a scarlet berry while in the second case it is persistent as part of the dispersal unit of the species. *Solanum seaforthianum* has an almost truncate calyx, the teeth umbonate and resembling that of species of *Lycianthes.* This calyx structure is almost unique in *Solanum.* In other cases, the five short calyx lobes split at the suture to yield teeth (lobes) of various length, which may reflex or remain applied to the fruit.

Anther shape is important in distinguishing subgenus *Leptostemonum* (from the Greek meaning slender anther). Here the anther tapers to a point, and the apical pores are small. In other subgenera, the pores are relatively large and may coalesce. Although *Solanum* anthers are sometimes reported to open by terminal pores which sometimes extend to become longitudinal slits, this is apparently an artifact of the herbarium sheet. In no case did this occur in any living anthers seen; rather, in many species, a line of weakness appears forming longitudinal slits distinct from the terminal pores. In sect. *Leptostemonum* such slits may appear in the basal third of the anther; in other groups the slits appear higher up. Pubescence on stamens is often consistent for sections, *e.g.* the ventral surface of anthers in sect. *Persicariae* and the ventral surface of filaments in sect. *Solanum.*

Fruits vary sufficiently to be diagnostic to species or even variety in many cases, and Key No. 2 separates the Florida taxa on the basis of fruit. Fruits in the genus are mostly juicy berries with eye-catching appearance, and the genus is generally assumed to be bird dispersed. The only cases for which the writer can personally vouch of birds eating *Solanum* fruits are the frequent feeding on berries of sect. *Solanum* by mockingbirds, which sometimes entered the Gainesville greenhouse, and greedy feeding on fruits of *Solanum pseudocapsicum* by chickens at an upland Panama farmstead. Some species are apparently dispersed by other vectors. The spiny fruits in sect. *Androceras* suggest mammal dispersal, and the persistent, capsule-like berries of *S. elaeagnifolium* and *S. tridynamum* suggest a mechanical, shaker sort of seed release. Not all *Solanum* berries are juicy: in sect. *Acanthophora* the flesh is a moist pulp with a large moist locule, and in *S. melongena* the seeds are embedded in moist pulp. The interesting fruit of *S. dimidiatum* is described below.

Seeds of most species of *Solanum* are discoid or lenticular and light colored. In *S. ciliatum*, however, they are conspicuously winged, and in *S. rostratum* they are black and not much compressed. Since neither of the species has juicy, bird-dispersed berries, the distinctive seed morphology is probably correlated with other modes of dispersal.

The prevailing chromosome base number in the genus *Solanum* and its close relatives is $x = 12$. Polyploidy is commonly reported in sects. *Solanum* and *Petota* but is infrequent in other groups. The aneuploid reports of $x = 11$ in *Solanum mammosum* and the hexaploid report of $x = 36$ in *S. dimidiatum* are therefore both of interest.

Key No. 1. Key to Florida species, not based on characters of fruit. * Plants not now known in the wild in Florida.

1 Anthers not opening by terminal pores, extended into sterile tips; flowers yellowish, mostly 6–9-merous; seeds pilose .... 32. *Ln. esculentum*

1′ Anthers opening by terminal pores, without sterile tips; flowers various colors, mostly 5-merous; seeds glabrous.

2 Mature plants mostly stellate pubescent.

3 Inflorescence a condensed cyme held above the leaves by a straight, erect, apically branched peduncle; leaves all entire; anthers not or only slightly thicker in the lower half; unarmed shrubs or trees.

4 Flowers purple; new growth with stipule-like minor leaves at the base of the petioles; pedicels deciduous near the middle .... 15. *S. mauritianum*

4′ Flowers white; stipule-like minor leaves absent; pedicels deciduous near the base.

5 Pedicels stout, 2–5 mm long; anthers ca. 3 mm long; ovary stellate-tomentose .... 10. *S. erianthum*

5′ Pedicels slender, 5–8 mm long; anthers 4–5 mm long; ovary with a few simple hairs .... 8. *S. donianum*

3′ Inflorescence not as above; leaves subentire or variously lobed; anthers much thicker in the lower half; plants often armed, their habit various.

6 Calyx accrescent and enveloping the fruit, at least when young; leaves dissected; plants copiously spiny.

7 Calyx persistent and tightly enveloping the mature fruit; seeds black; anthers strongly unequal.

8 Flowers yellow; pubescence eglandular, of stellate hairs .... 22. *S. rostratum*

8′ Flowers purple; pubescence glandular, stellate hairs few or absent .... 5. *S. citrullifolium**

7′ Calyx loosely enveloping the fruit and splitting at maturity; seeds yellowish; anthers equal .... 24. *S. sisymbriifolium*

6′ Calyx not enveloping the fruit; leaves mostly not dissected; spines various.

9 Anthers sessile, the tips curved outwards; flowers in a tight, short-stalked cluster on the stem .... 20. *S. pseudolulo**

9′ Stamens with filaments, the anther tips not curved outwards; inflorescence various.

10 Anther tube pubescent inside; corolla lobed to the base, the lobes linear lanceolate.

11 Flowers white; anthers more than 6 mm long; leaves mostly more than 8 cm long, the tips sharply pointed .... 21. *S. racemosum*

11′ Flowers purple or mauve; anthers mostly less than 7 mm long; leaves mostly less than 12 cm long, the tips blunt .... 2. S. *bahamense*

12 Inflorescence several branched; midpoints of stellate hairs conspicuous to the naked eye (extinct element) .... 2c. S. *bahamense* var. *rugelii**

12′ Inflorescence unbranched; midpoints of stellate hairs wanting or visible only with a lens.

13 Flowers deep colored; some stellate hairs of the inflorescence with midpoints as long as the arms; leaves mostly more than 2.5 cm wide .... 2b. S. *bahamense* var. *luxurians*

13′ Flowers pale colored; stellate hairs with no midpoints as long as the arms; leaves mostly less than 2.5 cm wide .. 2a. S. *bahamense* var. *bahamense*

10′ Anthers glabrous; corolla lobes mostly broader.

14 Anthers strongly unequal .... 26. S. *tridynamum**

14′ Anthers equal.

15 Stems with stout, recurving spines.

16 Leaves petiolate; calyx without bristles; peduncle once-branched; tree or shrub .... 25. S. *torvum*

16′ Leaves sessile, basally cuneate; calyx with bristles; peduncle unbranched, woody vine .... 12. S. *jamaicense*

15′ Stems with straight spines or none.

17 Anthers more than 12 mm long; flowers more than 5 cm across, fading with age; pedicel scars peltate, ca. 2 mm across .... 30. S. *wrightii**

17′ Anthers less than 10 mm long; flowers less than 5 cm across, not fading with age; pedicel scars sessile, inconspicuous.

18 Leaves lobed to near the middle with narrow lobes .... 3b. S. *carolinense* var. *floridanum*

18′ Leaves lobed less than halfway to the middle.

19 Leaves lanceolate, mostly less than 2 cm wide, silvery pubescent with both scutellate and stellate hairs .... 9. S. *elaeagnifolium*

19′ Leaves ovate or elliptical, mostly more than 2 cm wide, not silvery pubescent, scutellate hairs absent.

20 Ovary stellate pubescent on top; plants mostly few- (to 5-) flowered; leaf lobes rounded .... 16. S. *melongena**

20′ Ovary glabrous or with a few simple hairs; plants several- (4-or more) flowered; leaf lobes rounded or acute.

21 Filaments ca. 1.5 mm long; anthers 6–8 mm long; corolla 2–3.5 cm across; peduncle seldom branched; leaf lobes acute .... 3a. S. *carolinense*

21′ Filaments 2–4 mm long; anthers 8–12 mm long; corolla 3–4 cm across; peduncle branched; leaf lobes obtuse or rounded ..... 6. *S. dimidiatum*

2′ Mature plants with mostly simple or branched hairs or glabrous, stellate hairs rarely present.

22 Plants spiny; anthers much thicker in the lower half.

23 Leaf undersides with hook-like spines; glabrous vines ..... 29. *S. wendlandii**

23′ Leaves and stems with acicular spines; erect or sprawling pubescent herbs.

24 Calyx enveloping the fruit; leaves finely dissected ..... 5. *S. citrullifolium**

24′ Calyx not enveloping the fruit; leaves lobed but not dissected.

25 Corolla 14–20 mm across; anthers ca. 6 mm long; leaves glabrate except for sparse coarse hairs on the surface and margins ..... 4. *S. ciliatum*

25′ Corolla 30–40 mm across; anthers ca. 10 mm long; leaves copiously viscid-villous ..... 14. *S. mammosum**

22′ Plants unarmed (pointed enations of the stem sometimes present); anthers little thicker in the lower half.

26 Calyx truncate, not splitting at the sutures, the teeth or umbos small or wanting; plants glabrate.

27 Inflorescence a 1- to few-flowered fascicle; leaves entire ..... 31. *Ls. rantonnei**

27′ Inflorescence an open panicle; leaves lobed or entire.

28 Calyx teeth obtuse, small but distinct, and splitting at the sutures ..... 13. *S. jasminoides*

28′ Calyx teeth acute, small, not splitting at the sutures.

29 Leaves mostly deeply lobed, the margins not indurated ..... 23. *S. seaforthianum*

29′ Leaves entire, the margins indurated ..... 11. *S. glaucophyllum**

26′ Calyx with distinct lobes splitting at the sutures; plants pubescent to glabrous.

30 Leaves pinnate or deeply pinnate-lobed, scandent species.

31 Plants viscid-pubescent; pedicels articulated about half-way up ..... 27. *S. tuberosum*

31′ Plants glabrate; pedicels articulated almost at the base ..... 13. *S. jasminoides*

30′ Leaves toothed or entire but not divided below the middle; pedicels articulated at the base or not at all.

32 Inflorescence an open panicle; leaves lanceolate; the margins indurated ..... 11. *S. glaucophyllum**

32′ Inflorescence not a panicle; leaves mostly ovate, the margins not indurated.

33 Sterile portion of the peduncle as long as the pedicels, the inflorescence a sub-umbellate raceme; herbs ..... sect. *Solanum*

34 Anthers less than 1.7 mm long.

35 Plants copiously and persistently pubescent overall with short, erect hairs ..... 28. *S. villosum**

35′ Plants sparingly pubescent with appressed hairs ..... 1a. *S. americanum*

34′ Anthers more than 1.7 mm long.

36 Pedicels and peduncles remaining slender.

37 Internodes nearly as long as the leaves; leaves narrow .... 1b. *S. americanum* var. *baylisii*
37′ Internodes shorter than the leaves; leaves broader .... 17. *S. nigrescens*
36′ Pedicels and peduncles becoming stout .... 18. *S. nigrum*
33′ Sterile portion of the peduncle much shorter than the pedicels, or wanting.
38 Leaves narrow; peduncles 1–3-flowered, without out a conspicuous cicatrix; anthers more than 2.4 mm long .... 19. *S. pseudocapsicum*
38′ Leaves ovate or elliptic; peduncles several- to many-flowered, developing a conspicuous cicatrix; anthers less than 2.4 mm long .... 7. *S. diphyllum*

Key No. 2. Key to Florida species, based on fruit in living state. * Taxa not now known in the wild in Florida.

1 Not known to fruit in Florida .... *Ls. rantonnei*
S. bahamense var. *rugelii*
S. glaucophyllum
S. villosum
S. wendlandii
S. wrightii

1′ Known to fruit in Florida.
2 Fruit enveloped at least until near maturity by the spiny calyx.
3 Fruiting calyx with stellate hairs .... 22. *S. rostratum*
3′ Fruiting calyx with simple hairs .... 5. *S. citrullifolium*
2′ Fruit not enveloped by the calyx.
4 Fruits stellate-pubescent.
5 Fruits less than 15 mm across, yellow.
6 Fruits held above the foliage; pedicels stout; calyx teeth deltoid without filiform tips.
7 Pedicels articulating near the base .... 10. *S. erianthum*
7′ Pedicels articulating near the middle .... 15. *S. mauritianum*
6′ Fruits not held above the foliage; pedicels not stout; calyx teeth with filiform tips .... 9. *S. elaeagnifolium*
5′ Fruits more than 25 mm across, red or orange .... 20. *S. pseudolulo*
4′ Fruits glabrous.
8 Fruits pendulous in a much branched panicle.
9 Fruits less than 12 mm long; receptacle surmounted by a circular or 5-angled annular calyx .... 23. *S. seaforthianum*
9′ Fruits more than 12 mm long; receptacle surmounted by 2–4 remnants of calyx teeth .... 13. *S. jasminoides*
8′ Fruits not pendulous in a much branched panicle.
10 Pedicels articulating near the middle .... 27. *S. tuberosum*
10′ Pedicels not articulating near the middle.
11 Pericarp moist but not juicy, thick and white or green.
12 Fruit red, not shiny; pericarp white, less than 4 mm thick .... 4. *S. ciliatum*
12′ Fruit not red, sometimes shiny; pericarp white or green, mostly more than 4 mm thick.
13 Pericarp hard, green; endocarp stony .... 6. *S. dimidiatum*
13′ Pericarp soft, white; endocarp not evident.
14 Fruit yellow, often appendaged, spongy material absent adaxial to the seeds .... 14. *S. mammosum*

14′ Fruit black, or variously colored, seldom pure yellow, not appendaged, spongy material both abaxial and adaxial to the seeds .... 16. *S. melongena*

11′ Pericarp juicy, mostly thin and colored as the fruit wall.

15 Fruits red or orange.

16 Fruits held above the leaves in a branched cyme .... 8. *S. donianum*

16′ Fruits not held above the leaves, not in a cyme.

17 Pedicels slender, nodding; fruits less than 9 mm in diameter.

18 Fruits shiny, scarlet .... 21. *S. racemosum*
2b. *S. bahamense* var. *luxurians*

18′ Fruits shiny, orange .... 2a. *S. bahamense* var. *bahamense*

18″ Fruits dull, orange or beige .... 7. *S. diphyllum*

17′ Pedicels stouter, not nodding; fruit of various size.

19 Fruits more than 12 mm across .... 19. *S. pseudocapsicum*

19′ Fruits less than 12 mm across.

20 Calyx teeth filiform, calyx tomentose .... 12. *S. jamaicense*

20′ Calyx glabrate, teeth deltoid .... 24. *S. sisymbriifolium*

15′ Fruits not red or orange.

21 Fruits black.

22 Fruit shiny, held erect, seeds less than 12 mm across .... 1. *S. americanum*

22′ Fruit dull, held downwards against the stem; seeds large or small.

23 Pedicels and peduncles heavy; seeds 1.8 mm or more across .... 18. *S. nigrum*

23′ Pedicels and peduncles slender; seeds 1.8 mm or less across .... 17. *S. nigrescens*

21′ Fruits not black, rarely dark brown in extreme age.

24 Fruit greenish or yellowish in part, mostly brown.

25 Calyx teeth overtopping the fruit .... 26. *S. tridynamum*

25′ Calyx teeth shorter than the fruit .... 9. *S. elaeagnifolium*

24′ Fruit yellow.

26 Pedicels with mostly simple, glandular hairs, filiform and dark colored .... 25. *S. torvum*

26′ Pedicels stellate pubescent, not filliform or dark colored.

27 Calyx with sparse, yellowish, sessile, few-armed hairs .... 3. *S. carolinense*

27′ Calyx with dense, white, many-armed and scutellate hairs .... 9. *S. elaeagnifollium*

1. **Solanum americanum** Mill., Gard. Dict., ed. 8. 1768. AUTHENTIC SPECIMENS: herb. Sloane 295 (BM).

1a. var. **americanum**.

Solanum nodiflorum Jacq., Coll. 1: 100. 1788. Ic. Pl. Rar. 2: 17, *t. 326.* 1786. AUTHENTIC SPECIMEN: ex Jacquin, s.n. (BM; Bitter, Abh. Naturwiss. Vereine Bremen 23: 138. 1914, cited a specimen at W, not seen).

Solanum triangulare Lam., Illustr. 2: 18. 1794. TYPE: herb. Lamarck s.n. (P).

Solanum parviflorum Badaro, Giorn. Fis. dec. II 7: 364. 1824. TYPE: *Badaro* "1824" (G-DC).

Solanum subspathulatum Sendt. *in* Mart., Fl. Bras. 10: 45. 1846. TYPE: Brazil, *Sello s.n.* (P, ex hort. bot. Berol.).

Solanum indecorum A. Rich. *in* Sagra, Fl. Cuba 11: 121. 1850. TYPE: herb. Richard s.n. (P).

Solanum amaranthoides Dun. *in* DC., Prodr. 13(1): 55. 1852. TYPE: Brazil, *Gaudichaud 552* (MPU, P-holotype).

Solanum caribaeum Dun. *in* DC., Prodr. 13(1): 48. 1852. LECTOTYPE: Jamaica, collector unknown (G-DC, ex Kew).

Solanum fistulosum Dun. *in* DC., Prodr. 13(1): 49. 1852. LECTOTYPE: Brazil, herb. Richard s.n. (P[3]).

Solanum inops Dun. *in* DC., Prodr. 13(1): 55. 1852. TYPE: Mexico, *Berlandier 46* (G, G-DC–holotype, P).

Solanum nodiflorum var. *acuminatum* Dun. *in* DC., Prodr. 13(1): 46. 1852. LECTOTYPE: Brazil, *Vauthier 537* (P, ex herb. Drake).

Solanum nodiflorum var. *macrophyllum* Dun. *in* DC., Prodr. 13(1): 46. 1852. LECTOTYPE: Brazil, *Gaudichaud 521* (P).

Solanum nodiflorum var. *petiolastrum* Dun. *in* DC., Prodr. 13(1): 46. 1852. HOLOTYPE: Brazil, *Claussen 180* (P).

Solanum nodiflorum var. *puberulum* Dun. *in* DC., Prodr. 13(1): 46. 1852. TYPE: Mexico, *Berlandier 1904* (G-DC–lectotype, P).

Solanum oleraceum Dun. *in* DC., Prodr. 13(1): 50. 1852. TYPE: Cayenna, herb. Richard s.n. (G-DC–isolectotypes, MPU, P-lectotype).

Solanum ptychanthum Dun. *in* DC., Prodr. 13(1): 54. 1852. TYPE: Georgia, U.S.A., collector unknown (G-DC).

Solanum nigrum var. *nodiflorum* (Jacq.) A. Gray, Syn. Fl. N. Amer. 2(1): 288. 1878

Solanum nigrum var. *americanum* (Mill.) O. E. Schulz *in* Urb., Symb. Ant. 6: 160. 1909–10.

Solanum purpuratum Bitt., Fedde Rep. 13: 85. 1913. TYPE: Andros, Bahamas, *Small & Carter 8805* (P-holotype, US-isotype).

Solanum adventitium Polgar, Magyar Botanicai Lapok 24: 18, *t. 1.* 1925. TYPE: Hungary, *Polgar s.n.* (MPU).

Solanum merillianum Liou, Contr. Inst. Bot. Natl. Acad. Peiping 3: 455. 1935. TYPE: Hainan, *Tsang 412* (A).

Solanum photeinocarpum Nak. & Odash., Jour. Soc. Trop. Agr. 8: 54. 1836. TYPE: not seen (see Stebbins & Paddock, 1949).

Solanum americanum var. *nodiflorum* (Jacq.) Edmonds, Jour. Arnold Arbor. 52: 634. 1971.

Short lived or annual, unarmed *herb*, rarely to 1.5 m tall, glabrate or pubescent with simple hairs; stems terete to strongly angled, sometimes with tooth-like enations, green or purplish, not sarmentose. *Leaves* simple, small to large (2–20 cm long), mostly ovate, basally truncate or shallowly cuneate, the margins entire, undulate or dentate; minor leaves often present. *Inflorescence* lateral, several-flowered, umbellate or nearly so, the peduncle slender, unbranched, appressed pubescent; pedicels slender, appressed pubescent, deflexed in bud but erect and spreading in fruit. *Flowers* small, perfect, the calyx lobes deltoid to lanceolate, not accrescent; corolla white, blue or mauve, with or without a conspicuous eye, to 1 cm across; anthers 0.9–1.4(–2.1) mm long, stout, subequal; ovary glabrous, the style usually pubescent, mostly thicker in the middle. *Fruit* black, shiny, 4–8(–15) mm across, juicy; seeds 1.2–1.5 mm across. *Pollen*: 17–20 μ. *Chromosomes*: $n = 12$ (Edmonds, 1972; Baylis, 1958, as *S. nodiflorum*).

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[3] This specimen bears two labels. Although the label "Isle de France" is in Dunal's hand, the protologue refers also to the Richard label. The true source of this specimen is not evident.

Solanum americanum is distinct in its shiny, black berries, which are held erect at maturity, subtended by strongly recurved calyx lobes. The small anthers are another useful character. This species is quite variable in leaf shape, overall size and in pubescence, and a distinction between glabrate and pubescent varieties is not meaningful in Florida. *Solanum americanum* is known to hybridize with other diploid species in Florida, and intermediates, especially herbarium material, may be difficult to place. Meiotic chromosome counts were verified in this study using a variety of Florida material.

This is perhaps the commonest species of *Solanum* in the state, although it is rare in the panhandle. It is a conspicuous and unwanted invader of citrus fields in Central Florida where it grows to large size and luxuriant appearance. It is also perhaps the world's most widespread species of *Solanum*, occurring from Scandinavia to New Zealand and from sea level to over 3,000 m elevation in Central America.

The ripe berries of this species are apparently edible by humans, but there are cases on record of poisoning by unripe fruits and other green parts. "Black nightshade."

Representative specimens:

ALACHUA: Overgrown lot ca. 1 mi. S of Gainesville on Fla 441, *Burch 677* (MO). Vacant lot, downtown Gainesville, *Heiser 4044B* (IND). Railroad S of Gainesville, *Murrill* 1937 (MO). Gainesville, *Murrill* 1939 (MO). BAY: Panama City, *Ahles 10274* (UNC). BREVARD: Hammock along Indian River, *Small 8712* (NY). CHARLOTTE: In weedy citrus field, Fla 865 7 mi. S of Punta Gorda, *D'Arcy 1443* (FLAS). CITRUS: Beside American Legion beach, Crystal River, *D'Arcy 1542* (BIRM, FLAS, MO). COLLIER: Ca. 14 mi. SE of Naples along old Marco Road, *Deam 60788* (IND). Roadside near shallow swamp, land development E of Lake Trafford, *Long et al. 2751* (USF). COLUMBIA: Lake City, *Pickel 719* (FLAS). DADE: Infrequent by old rock pit in pineland, Silver Palm Drive and Naranja Road, W of Goulds, *Beckner 1967* (BIRM, FLAS, MO, UCWI). Swale in dune near picnic area, Key Biscayne, *Gillis 7677* (MO). Brickell Hammock, near US 1 and Rickenbacker Causeway, Miami, *Long & Andorfer 2828* (MO, USF). DESOTO: In roadside lawn S of Arcadia, *D'Arcy 1424* (FLAS). DIXIE: Beside public boat ramp W of Jena, Steinhatchee River, *D'Arcy 1525* (FLAS). ESCAMBIA: Beside culvert, US 98 at bridge over Pensacola Bay, *D'Arcy 2506* (BIRM, FLAS, MO). FRANKLIN: Empty lot in Eastpoint, *Kral 1988* (FSU). GILCHRIST: Hammock along Santa Fe River, Fla 77, *West & Arnold*, 1943 (FLAS). GLADES: On Indian mounds, S side of Fisheating Creek, *D'Arcy 1430* (FLAS). Open places W shore of Lake Okeechobee, Fisheating Creek to Three-Mile Canal, *Small 8216* (MO). HARDEE: E bank of Peace River, N of Fla 64, W side of Zolfo Springs, *Ward A-4* (FLAS, FSU). HENDRY: In city park, Clewiston, *Deam 58627* (IND). HERNANDO: Orange grove 4.5 mi. N of Brooksville, *Godfrey 57199* (FSU). HIGHLANDS: Along canal SW side of Highlands Hammock State Park ca. 7.5 mi. SW of Sebring, *Deam 64104* (IND). HILLSBOROUGH: Moist location, Tampa, *Ferguson* 1898 (MO). Disturbed undergrowth, Northgate, Tampa, *Lakela & Almeda 31345* (USF). Fencerow in pasture 7 mi. E of Tampa, *West*, 1949 (FLAS). HOLMES: US 90 under bridge over Choctawatchee River, *D'Arcy 2567* (FLAS). INDIAN RIVER: Behind foredune, N limit of Indian River Shores, *D'Arcy 2852* (FLAS, MO). Small fill island just S of Wabasso Island, in Indian River, *D'Arcy 3002* (FLAS, MO). Sandy banks of canal near coast, *Demaree 49402* (UNC). JACKSON: Behind food store, W side of Cottondale, US 90, *D'Arcy 2569* (FLAS, MO). Blue Springs, *West & Arnold*, 1937 (FLAS). JEFFERSON: Wacissa, *Murrill*, 1942 (FLAS). LAKE: Citrus grove 8 mi. S of Clermont, *D'Arcy 1337* (FLAS). LEE: Weed in field, Myers, *Hitchcock 239* (F, MO, NY). Near Fort Myers, *Standley 72* (MO). LEON: Bottomland, Tallahassee, *Godfrey 57953* (FSU). Edge of parking lot across from Florida State University, Tallahassee, *Windler & Windler 2731A, 2731B* (both FLAS, MO). LEVY: Waste places, Cedar Key, *Godfrey 52830* (DUKE, UNC). MADISON: Dried up pond, 14 mi. SE of Madison on Fla 53, *Mitchell 226* (FSU). MANATEE: Bradenton, *Cuthbert 1457* (FLAS). MONROE: In limestone at seaside, ca. 1 mi. E of Port Largo, Key Largo, *D'Arcy 2244* (BIRM, FLAS, MO). Roadside, Pine Crest, *Moldenke 867A* (MO). Hammock, Big Pine Key, *Seibert 1297* (MO).

Longboat Key, *Tracy 6829* (MO). OKALOOSA: Fort Walton Beach, *D'Arcy 2492* (FLAS, MO). Fort Walton Beach, *Ward 6404* (FLAS, MO). ORANGE: Overgrown grove, 2.5 mi. E of Ocoee, *Gale 151* (FLAS). PALM BEACH: Lantana Beach, *Heiser 4669* (IND). PASCO: Citrus grove, Fla 41, 3 mi. E of US 75, 1 mi. E of Blanton, *Beckner 1633* (FLAS). Margin of citrus grove, 10 mi. N of Pasco-Hillsborough line, *Wiggins 19596* (FLAS). PINELLAS: Road to Lutz from Tarpon Springs, *Cooley 5860* (USF). POLK: Near Fort Meade, *Jennings & Jennings 1919* (USF). Near Lakeland, *McFarlin 3920* (MICH). ST. JOHNS: Elkton, *Shinners 18004* (SMU). ST. LUCIE: Ditch W of Fort Pierce, *Beckner 2205* (FLAS). SANTA ROSA: Behind gas station, US 90 and Fla 87, ca. 4 mi. E of Milton, *D'Arcy 2500* (BIRM, FLAS, MO). SEMINOLE: Altamonte Springs, *Schallert 3103* (UNC). SUMPTER: 2 mi. W of Wildwood, *Ward 4278* (FLAS). TAYLOR: W side of Perry, *D'Arcy 2483* (FLAS, MO). Between Perry and Salem, *Heiser 4028* (IND). VOLUSIA: Ormond, *Deam 1636* (IND). WALTON: SW side of De Funiak Springs, *D'Arcy 2565* (FLAS). WITHOUT LOCALITY: *Chapman s.n.* (MO). *Rugel 44* (MO).

1b. **Solanum americanum** var. **baylisii** D'Arcy, var. nov. TYPE: Cultivated, New Zealand, *Momson*, 1953 (OTA-00419).—Differt varietate typice antheris longioribus, fructibus non nitidis, foliis dense albo-pubescentibus.

Solanum gracile sensu Baylis, Trans. Roy. Soc. New Zealand 85: 379. 1958, non Sendt. *in* Mart., Fl. Bras. 10: 13. 1846; nec Dun. *in* DC., Prodr. 13(1): 54. 1852; nec Small (1933).

This variety is distinct in its long internodes, generally white, conspicuous pubescence, deltoid rather than obtuse calyx nodes, and dull, downward deflected fruits. In most respects it is similar to S. *nigrescens*. Only one Florida collection clearly represents this taxon, but several collections from the same part of Central Florida which appear to be intermediate between this and typical var. *americanum* are taken as evidence that the closest relationship is with var. *americanum*.

Baylis (1958) reported a meiotic chromosome count of $n = 12$ for this taxon, and this count was confirmed using plants grown from New Zealand seeds. He also reported anthers 2.5–4 mm long.

The names S. *gracile* and S. *ottonis* Hylander have been used by some botanists for this taxon, but examination of type material showed these names to be synonymous with S. *nigrescens* Mart. & Gal.

HERNANDO: 1 mi. S of county line N of Chinsegut Hill, *Cooley & Eaton 6666* (USF).

2. **Solanum bahamense** L., Sp. Pl. 188. 1753. TYPE: not seen. Based on S. *bahamense spinosum petalis angustis reflexis* Dill., Hort. Elth. 364, *t. 271, fig. 350.* 1736.

2a. var. **bahamense**.

Solanum lanceifolium Salisb., Prodr. 134. 1796, non Jacq., Ic. Pl. Rar. 2: 11, *t. 329.* 1787. TYPE: Based on S. *bahamense* L.

Solanum subarmatum Willd., Enum. Hort. Berol. 1: 240. 1809. TYPE: Bahamas, herb. Willd. 4414 (B, not seen; IDC 7440-7, 111. 9.; BM, "*Catesby* ex Bahamas").

Solanum bahamense var. *lanceolatum* Griseb., Flora 5: 440. 1861. ?TYPE: (specimen at K labelled as type). Grisebach cited herb. Sloane *t. 145, fig. 3.*

Solanum bahamense var. *subarmatum* (Willd.) O. E. Schulz *in* Urb., Symb. Ant. 6: 222. 1909–10.

Solanum racemosum sensu Britt. & Wilson, Bot. Porto Rico & Virgin Isl. 6: 169. 1926 pro maj. parte, non Vahl.

Armed or unarmed *tree* or *shrub* to 4 m tall; stems sometimes with yellow or orange acicular spines 4–5 mm long. *Leaves* simple, broadly lanceolate, mostly 5–12 cm long, subentire, often basally dimidiate, coriaceous, above scabrous with dispersed, sessile stellate hairs mostly lacking midpoints, the veins to 15 on each side of the midvein. *Inflorescence* lateral, an unbranched, secund raceme to 12 cm long, the pedicels 1 mm long in flower, ca. 2 cm long and lax in fruit, articulating at the base. *Flowers* elongate, the calyx in bud sub-truncate, splitting at the sinuses before anthesis to form acuminate lobes to 6 mm long; the corolla usually mauve, 10 mm long, split nearly to the base into ensiform, reflexed lobes; stamens equal forming a slender tube to 14 mm long, the filaments connate for most of their length (1–2 mm), anthers ca. 7 mm long, coherent by lateral grooves and dense, long-armed stellate hairs within the tube; ovary with a few short, glandular, simple hairs, enclosed by the filament tube. *Berry* scarlet to pale orange, 4–7 mm across, shiny, juicy; seeds 3–7 mm across, compressed. *Pollen*: 19.0–27.0 μ. *Chromosomes*: $2n = 24$ (Roe, 1967*b*).

Solanum bahamense is distinct in its mauve or purple flowers, orange or red fruits and racemose, cernuous inflorescences. It is closely related to *S. racemosum* Jacq. and to several other similar species in the West Indies.

In Florida the species is common on the Keys and other coastal areas of the south. "Canker Berry."

Representative specimens:

BROWARD: Sand dunes at Dania Beach, *Beckner 1549* (FLAS, MO). Dune, Fort Lauderdale, *Davis*, 1933 (FLAS). In muck, edge of pineland, N of Floranada, *Fennell & Jones 838* (A). Hammock, Hugh Taylor State Park, *Lakela 29600* (USF). Lauderdale Beach, *Moldenke 261* (MO). DADE: Crocodile Point, Everglades National Park, *Craighead* 1959 (FLAS, GH). In shelter of low dunes, NE corner of Key Biscayne, *D'Arcy 2223* (ADW, C, FLAS, IJ, MO). Key Biscayne, *DeBoer 36* (USF). Clearing in thicket, Key Biscayne, *Gillis 7243* (MO). S of picnic area, Elliott Key, *Meagher & Utley 312* (USF). Bull Key, opposite Lemon City, *Small 620* (NY, US). Miami, *Tracy 9254* (MO). Coastal hammock, Key Biscayne, *West 1332* (USF). MARTIN: Tunney Estate, Hobe Sound, *Crevasse*, 1940 (FLAS). MONROE: West Summerland Key, *Aregood 106, 161* (both USF). Loggerhead Key, Dry Tortugas, *Atwater 14* (FLAS). Boca Chica Beach, Shark Key, *Barghoorn 92* (USF). Edge of pinelands on spoil bank, Big Pine Key, *Brizecky & Stern 218* (A, FLAS, US). Lignum Vitae Key, *Craighead* 1956 (USF). West Summerland Key, *D'Arcy 3030* (FLAS, MO). Big Pine Key, *D'Arcy 3031* (FLAS, MO). Ramrod Key, *D'Arcy 3039* (FLAS, MO). Crawl Key, *D'Arcy 3043* (FLAS, MO). In hammock, Little Torch Key, *D'Arcy 3045* (FLAS, MO). Bahia Honda Key, *D'Arcy 3121* (FLAS, MO, USF). Key West, *Farlow*, 1891 (USF). Infrequent, Marquesas Keys, *Lansing 2130* (NY). Little Torch Key, *Long et al. 2492* (USF). Beach strand area on Atlantic side of Bahia Honda Key, *Long et al. 2617* (USF). Key West, *Palmer 371* (MO). N end of Key Largo, *Webster & Samuel 10228* (IJ). SE hammock, Big Pine Key, *Thorne 15121* (FSU, IJ). PALM BEACH: Old field, Jupiter Island, *Cooley et al. 4814* (GH, USF). Wooded roadsides and clearings near Palm Beach, *Curtiss 5519* (FLAS, GH, MO). Crest of shore dunes, Boca Raton just N of Broward Co. line, *Lakela 28271* (FLAS, USF). Hypoluxa Island, *Muenschner & Muenschner 14093* (A, GH).

2b. var. **luxurians** D'Arcy, var. nov. TYPE: Key Largo, Florida, *D'Arcy 2234* (FLAS-holotype, MO-isotype).

Differt a varietate typica corollis ostrinis saturatis vice lilacinarum pallidinarum, acinis miniatis, puniceis seu igneis vice aurantiacorum dilutorum, foliis latioribus majisque, plantis grandioribus, necnon inflorescentiis, pilis stellatis radio mediano producto sparsis copiosisve instructis.

This variety is distinct in its deep blue-purple corollas, bright red fruits, broader and larger leaves, larger plants and the scattered to plentiful elongate midpoints on the stellate hairs of the inflorescence. It is restricted to Key Largo and neighboring islands in Florida. Plants of this variety maintain their identity as far west as Boca Chica Key, where most plants along the roadsides are var. *bahamense.* Each of the characters mentioned above may be found in some plants of the typical variety, but only in the Key Largo region do all characters occur together. Plants here are strikingly different in appearance from most *Solanum bahamense* of other areas. Plants of Palm Beach County, and some of those from the Bahamas, have similar leaves and resemble var. *luxurians* on the herbarium sheet, but they lack the hairs with long midpoints. Similar long midpoints are found on two related species of the Antilles, S. *drymophyllum* O. E. Schulz (Puerto Rico) and S. *polyacanthos* Lam. (Hispaniola), as well as on var. *rugelii* of Florida. Mitotic chromosomes of this variety were counted by J. Semple as $2n = 24$ using root tips from seed of *Austin 4364* (MO).

Representative specimens:

BROWARD-PALM BEACH: Coastal hammocks between Fort Lauderdale and Palm Beach, *Rehder 847* (A). DADE: Hammock on coral rock, Totten Key, *Cooley 9350* (FSU, USF). Miami, *Garber* 1877 (US). Elliott Key, *Meagher & Utley 312* (USF). Hammocks, Miami, *Small & Wilson* 1904 (US). Ca. 2 mi. below N end of Elliott Key, *Ward & Ward 1583* (MO). MONROE: Key Largo, *Austin 4364* (MO). Roadside, N Key Largo, *Brizickey & Stern 546* (FLAS). North Key Largo, *Cooley 9286* (USF). Thicket ca. 100 m from the sea, Key Largo, *D'Arcy 2234* (FLAS, IJ, MO, MPU). Borders of hammock, Boca Chica Key, *Godfrey 58147* (FSU). Rock Harbor, Key Largo, *Janish & Janish 487* (MO). Rocky coastal strand and hammock, North Key Largo, *Lakela et al. 31776* (USF). North Key Largo, *Long et al. 1763, 1765* (both USF). Newport, Key Largo, *Pollard et al. 173* (US). N end of Key Largo, *Thorne 15133* (US, USF).

2c. var. **rugelii** D'Arcy, var. nov. TYPE: Key West, Florida, *Rugel s.n.* (MO).

Solanum radula sensu Chapman, Fl. S. United States 348. 1860, non Vahl.

Differt inflorescentia ramosa, floribus parvis, pilis stellatis radio medianao producto copiosis instructis.

Three collections from the first half of the last century have strikingly branched inflorescences, smaller flowers and copious stellate hairs with elongate midpoints. Their appearance is suggestive of some pathological condition, but they may represent an element of the Florida flora extinguished when the dense tropical hammock was removed from Key West early in this century.

MONROE: Key West, *Blodgett* (NY). WITHOUT LOCALITY: *Chapman* (NY). *Rugel* 7 (MO, US).

3. **Solanum carolinense** L., Sp. Pl. 187. 1753. TYPE: herb. Linn. 246-37. (LINN).

3a. var. **carolinense.**

Solanum caule aculeato fruticoso . . . Clayton "ex herb. Gronovius," Hort. Cliff 61 (BM).
Solanum pleei Dun. *in* DC., Prodr. 13(1): 305. 1852. TYPE: United States, *Pleé 204* (MPU, "ex herb. mus. Paris").
Solanum carolinense var. *pohlianum* Dun. *in* DC., Prodr. 13(1): 305. 1852. TYPE: Brazil, *Dr. Pohl s.n.* (M).
Solanum occidentale Dun. *in* DC., Prodr. 13(1): 309. 1852. TYPE: Southwest America, collector unknown (MPU, "ex herb. Lambert 1819").

Usually armed, erect or spreading woody perennial to 60 cm tall; stem green or purplish, pubescent, mostly with yellow or orange acicular spines to 1 cm long; rhizomes with cylindrical tubers 4–10 mm thick and to 10 cm long. *Leaves* simple, to 15 cm long, elliptical to lanceolate, the margins entire or sinuate, rarely pinnatisect, the lobes 2–5 on each side, apically obtuse, above with inconspicuous, dispersed, sessile, pauciradiate stellate hairs, beneath with more abundant, sometimes short-stalked hairs, both sides mostly with spines on the major veins. *Inflorescence* lateral, an unbranched, secund raceme, the pedicels 5–10 mm long, articulating tardily at the base; the first flowers staminate; calyx 3–5 mm long in flower, 4–7 mm in fruit, lobed about ⅓ way down, mostly spiney; corolla mauve, blue or white, 2–3.5 cm across, lobed halfway down, the lobes deltoid; stamens connivent or separate, equal, the filaments stout, 1.5 mm long, the anthers 6–11 mm long, glabrous, elongate and tapering with small pores; ovary and style with sparse glandular simple hairs, the style of fertile flowers exserted, those of staminate flowers equalling the filaments. *Berry* ripening through white and green-mottled to yellow, 1–1.5 cm across, mucilaginous; seeds 2.5 mm across, compressed. *Pollen*: 25.0–29.0 μ. *Chromosomes*: $n = 12$ (*D'Arcy 1969*).

This species is distinct in its sarmentose, herbaceous aspect, its mostly sinuate, spiny leaves, deltoid corolla lobes, blue, mauve or white flowers and usually greenish fruits.

Solanum carolinense is one of the commonest species of *Solanum* in Florida, although it is less common in the south. It grows in shade or sun, in disturbed woodlands, pastures, beside culverts and around dwellings, and frequently performs as a noxious weed.

This species is probably native to the southeastern United States but has been reported from California, Idaho, Ontario, Haiti, and Brazil. In typical and other varieties, flowers may vary in color, and recognition of the forma *albiflorum* (O. Kuntze) Benke is of little utility and no taxonomic significance. In addition to the two varieties considered here, a var. *hirsuta* (Nutt.) D'Arcy[4] occurs in Georgia. This has long, shaggy pubescence and is not known from collections in this century, hence having some analogy with S. *bahamense* var. *rugelii*. Although there is a tendency to longer and denser pubescence as one moves west from the Atlantic coast to Missouri, S. *carolinense* is remarkably uniform throughout its range.

Solanum carolinense is reportedly poisonous to livestock, and the tubers contain crystals of calcium oxalate (Metcalfe & Chalk, 1950) and must be regarded as poisonous to humans. "Horse-nettle."

Representative specimens:

ALACHUA: Roadside by concrete bridge over Prairie Creek, Fla 234, *D'Arcy 1579* (FLAS, MO). 2 mi. W of Gainesville, *D'Arcy 1640* (FLAS, MO). Burnett's Lake, *Watson & Murrill*, 1939 (FLAS, GA, US). BAY: 3 mi. E of Lynn Haven along Fla 390, *Beckner et al. 1499* (FLAS, MO).

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[4] *Solanum carolinense* var. *hirsuta* (Nutt.) D'Arcy, nom. nov. Based on *Solanum hirsutum* Nutt., Jour. Acad. Nat. Sci. Philadelphia 7: 109. 1834; non Dun. Hist. Soc. 158. 1813; nec. Roxb., Hort. Beng. 17. 1813 [1814]. TYPE: Milledgeville, Georgia, *Boykin* (PHILA).—The only other collection seen of this taxon is from Columbus, Georgia, *Boykin* (NY), of the same era.

CALHOUN: Swamp along Stafford Creek 5 mi. N of Blountstown, *Ford 3387* (FLAS). CITRUS: Scrub near Lake Tsala Apopka, Inverness, *West & Arnold*, 1941 (FLAS). CLAY: Doctor's Inlet, *D'Arcy 12134* (MO). Doctor's Inlet, *Murrill*, 1939 (MO), 1941 (FLAS). COLUMBIA: Moist roadside along US 441 ca. 7 mi. S of Lake City, *Ward 3550* (FLAS). DADE: Without locality, *Moldenke*, 1930 (BUS). DUVAL: Jacksonville, *Barnhart 2002* (NY). Near Jacksonville, *Curtiss 4400* (MO). ESCAMBIA: Roadside, Pensacola, *Brinker 17* (MO). US 90 at bridge over Bayou Texar, Pensacola, *D'Arcy 2502* (FLAS). GADSDEN: River flats, Chatahoochee, *West*, 1931 (FLAS). HERNANDO: Richland, *McFarlin 5957* (MICH). HOLMES: Around abandoned houses, W side of Ponce de Leon, *D'Arcy 2566* (FLAS, MO). JACKSON: Disturbed area on bluffs, W side of Apalachicola River by US 90, *D'Arcy 2572* (FLAS, MO). Chipola River, *Knight*, 1940 (FLAS). Dry field, Marianna, *Moldenke 8360* (MO). JEFFERSON: Without locality, *Hitchcock*, 1898 (MO). Monticello, *Nolen 1928* (FLAS). LAFAYETTE: Suwannee River opposite Branford, *West & Arnold*, 1941 (FLAS). LAKE: Near Eustis, *Nash 928* (GH, MO). LEON: Tallahassee, *Rolfs 178* (FLAS, MO). LIBERTY: Picnic ground, Torreya State Park, *West & Arnold*, 1940 (FLAS). MADISON: N shore of Lotus Lake, Greenville, *Beckner 1884* (FLAS). OKALOOSA: Garbage dump, Fort Walton Beach, *D'Arcy 1495* (FLAS, MO). Sandy roadsides, Niceville, *Godfrey 56652* (FSU, GH). OKEECHOBEE: Near lake, Okeechobee City, *Moldenke 5432* (NY). PUTNAM: Palatka, *Hood*, 1940 (FLAS, MO). ST. JOHNS: Pineland N of E Palatka, *Godfrey 52635* (FSU). SANTA ROSA: Edges of cultivated land W of Allentown, *Ford 4160* (FLAS). SEMINOLE: Sanford, *Scudder 01* (FLAS). VOLUSIA: Beside culvert 1.5 mi. N of Brevard County Line, *D'Arcy 1628* (FLAS). WALTON: Near Eucheanna Church SE of De Funiak Springs, *West & Arnold*, 1954 (FLAS, GH). WASHINGTON: Under Dickenson Bridge over Choctawatchee River, W side of Caryville, *D'Arcy 2568* (FLAS, MO). Choctawatchee River W of Caryville, *Godfrey 60780* (FSU).

3a. **Solanum carolinense** var. **floridanum** Chapm., Fl. S. United States 349. 1860. TYPE: Florida, *Rugel 1843* (G-DC–holotype; isotypes K, MO, MPU, NY).

Solanum floridanum Shuttlw. *ex* Dun. *in* DC., Prodr. 13(1): 306. 1852, non Raf., Aut. Bot. 107. 1840.

Solanum godfreyi Shinners, Sida 1: 108. 1962. TYPE: Florida, *Godfrey 60037* (FSU, SMU).

This variety is distinguished by the deep lobing of its leaves. Usually, intermediates may be found between this variety and the typical within the same colony (see D'Arcy, 1970*b*). Some herbarium sheets are suggestive of *S. sisymbriifolium*, but that species has an accrescent calyx and red fruits.

Variety *floridanum* is restricted to north Florida and neighboring Georgia and is most commonly found between the Suwannee and Apalachicola Rivers and along the St. Johns River. It is found in habitats much like those of the typical variety with perhaps a tendency to grow in slightly moister sites.

The chromosome number found in this species is $n = 12$ (D'Arcy, 1969).

Representative specimens:

GEORGIA: LOWNDES: Dry wayside adjoining railroad tracks along Ga 84, 2.5 mi. W of Valdosta, *Krysiak*, 1970 (MO, left-hand specimen only). FLORIDA: CLAY: W side of Doctor's Inlet, *D'Arcy 1212A* (FLAS). Doctor's Inlet, *Murrill*, 1939 (FLAS). DUVAL: South Jacksonville, *Churchill*, 1897 (MO). Vacant lot, University and Santa Monica Boulevards, South Jacksonville, *Creager 476* (FLAS). Dry roadsides near Jacksonville, *Curtiss 4845* (US). Without locality, *Fredholm 5211* (GH). FLAGLER: Haw Creek near Deanville, *West*, 1942 (FLAS). FRANKLIN: Apalachicola, *Chapman s.n.* (MO). GADSEN: Quincy, *Foster 25* (FLAS). HERNANDO: Brooksville, *Phillips et al.*, 1938 (BUS). LEVY: Yankeetown, *Jarrish & Jarrish 348* (MO). Gulf Hammock near Wekiva River, *West & Arnold*, 1937 (DUKE, FLAS). PUTNAM: Canal bank E of East Palatka, *West & Arnold*, 1940 (FLAS). ST. JOHNS: Roadsides and waste places, *Reynolds*, 1877 (MO). St. Augustine, *Reynolds*, 1878 (FLAS, MO). Fla 214, 5.2 mi. E of Tocoi, *Ward 2100* (FLAS). 1.8 mi. N of Switzerland, *Wilmot & Murrill*, 1941 (FLAS). TAYLOR: Clearings of swampy woodland near Nuttal's Rise along Aucilla River, *Godfrey 60037* (FSU, SMU). Roadside near low hammock, Aucilla Wildlife Management Area, *McDaniel 4297* (FSU, UNC). WAKULLA: Bean patch in Newport, *D'Arcy 2484* (ADW, FLAS, MO). Moist clearing of deciduous woodland, Wakulla, *Godfrey 56815* (FSU, GH, SMU). Moist shady soil bordering marshes, St. Marks, *Godfrey 59554* (FSU). In apricis prope St. Marks, *Rugel 1843* (G-DC, K, MO, MPU, NY). Sandy roadside to St. Marks lighthouse, *Trott 154* (FSU, GH).

4. **Solanum ciliatum** Lam., Illustr. 2: 21. 1793 [1794]. TYPE: herb. Lamarck s.n. (P; photo IJ).

Solanum aculeatissimum sensu Britt. & Millsp., Bahama Fl. 382. 1920, Small, Man. Southeastern Fl. 1114. 1933; Backer & Bakhuizen, Fl. Java 2: 472, 474. 1965; Corr. & Johnst., Man. Vasc. Pl. Texas 1398. 1970; Long & Lakela, Fl. Trop. Florida 757. 1971, non Jacq., Coll. 1: 100. 1786.

Solanum pentapetaloides Roxb. *ex* Hornem., Hort. Hafn. Supp. 27. 1819. Based on *S. pentapetaloides* Roxb., Hort. Bengal 17. 1814, nomen nudum. TYPE: *Roxburgh s.n.* (P-Lam.).

Solanum ciliatum var. *arenarium* Dun. *in* DC., Prodr. 13(1): 242. 1852. LECTOTYPE: Brazil, *Gaudichaud 473*, 1836 (MPU ex G-DC).

Copiously armed, erect or spreading perennial *herb* to 80 cm; stems green or purplish, sparingly pilose with long simple hairs and armed with flattened, green, yellow or orange acicular spines to 15 mm long; sometimes spreading by rhizomes. *Leaves* broadly ovate or orbicular to 14 cm long, the margins sinuate to pinnatifid, apically acute to rounded, basally rounded to cordate, sparsely pilose above, glabrate beneath, manifestly ciliate on the margins with long simple hairs, armed with green spines on the veins above and beneath; petiole 2–5 cm long, mostly armed. *Inflorescence* lateral, few flowered, a congested cincinnus elongating in fruit, the first flowers staminate; pedicels 1 cm long, hispid with short, glandular simple hairs, sometimes armed, almost white in flower; calyx often spiny, 2–3 mm long, slightly accrescent, lobed ⅔ way down; corolla white, 14–20 mm across, deeply lobed, the lobes lanceolate; stamens equal, the filaments 1.5–2 mm long, glabrous, the anthers ca. 6 mm long, connivent or separate, elongate, narrowly conical with minute pores; ovary and style glabrous, style of perfect flowers exserted, those of staminate flowers equalling the filaments. *Fruit* 1.5–5 cm across, bright, matte orange-red, the pericarp white, fleshy, 1–2 mm thick, later drying chartaceous, locules moist or dry but without wet pulp; seeds flat, winged, 2–3 mm across (4.5–5.5 mm including wings), yellow. *Pollen*: 24.0–30.5 μ, irregular in size.

This species has been confused with S. *aculeatissimum* Jacq., which differs from S. *ciliatum* in a number of respects: the fruit is somewhat smaller and matures yellow, the seeds are not winged and are much smaller, the leaves are of a more symmetrical shape with smaller, sharper teeth or lobes, and the pubescence comprises dense, fine, glandular and eglandular simple hairs, scattered stellate hairs and larger, apparently simple hairs like those of S. *ciliatum*. *Solanum aculeatissimum* was lectotypified by a specimen at Vienna (see D'Arcy, 1970*a*). The two species appear to be distinct in range. Plants resembling S. *aculeatissimum* have been seen only from southern Africa, Mexico, and Paraguay, while almost all plants of this group seen from the Southeastern United States, from the Antilles and from Asia have been S. *ciliatum*. In South and Central America other closely related species occur and S. *ciliatum* is found only locally.

In Florida, *S. ciliatum* occurs in pastures, road shoulders and other disturbed habitats, usually in partial shade and most commonly in areas of former hardwood forest. *Solanum ciliatum* is plentiful in Central and North Florida, uncommon in the south and rare in the panhandle.

In various parts of the world this species is occasionally grown as an ornamental or curiosity, and in parts of tropical America it is used as a roach poison, attracting the common name "mata cucaracha." In the United States it is sometimes called a "cockroach berry." Its toxicity to humans is not known; the spininess may prevent ingestion by livestock.

Representative specimens:

ALACHUA: Weed in yard, S edge of Gainesville, *Carmaichael*, 1965 (FLAS). BREVARD: Waste ground, Okeechobee region, *Fredholm 5894* (GH). CHARLOTTE: Without locality, *Parrott 176* (DUKE). CITRUS: Along Withlacoochee River ca. 1.5 mi. E of Pineola, *Kral 1879* (FSU). CLAY: Hibernia, *Canby 1869* (GH). COLLIER: Cypress sloughs, Sunniland, *Craighead*, 1965 (USF). DADE: North Cross Hammock, Key Biscayne, *McAllister 263* (DUKE). DIXIE: Under oak trees in town of Horseshoe Beach, *D'Arcy 1524* (FLAS, MO). DUVAL: Without locality, *Fredholm 5235* (GH). FLAGLER: Swamp on Crescent Lake at St. Johns Park, *West*, 1942 (FLAS). FRANKLIN: Waste places Apalachicola, Herb. Chapman 3441b (NY, US). GLADES: Along Fla 78 3 mi. SW of Kissimee River, *Ward 1140* (FLAS). HAMILTON: 5 mi. NE of White Springs, *West*, 1946 (FLAS). HARDEE: In high hammock, Wauchula, *O'Neill* 1929 (FLAS). HENDRY: Devil's Garden Hammock, *Cooley 772* (USF). HERNANDO: In orange grove 4.5 mi. N of Brooksville, *Godfrey 57453* (FSU, GH). 2.5 mi. E of Brooksville, *Cooley 5497* (GH, USF). HIGHLANDS: Highlands Hammock county road, Sebring, *McFarlin 8070* (FLAS). HILLSBOROUGH: Sand barrens, Hillsboro River at the "Dam," Tampa, *Churchill*, 1923 (GH). INDIAN RIVER: Sebastian, *Rhoades*, 1935 (GH). LAKE: Waste places, near Eustis, *Nash*, 1894 (GH). LEE: Weed in waste places, Fort Meyers, *Hitchcock 240* (GH). LEVY: Gulf Hammock, *Watson & Murrill*, 1939 (FLAS). MARION: MacIntosh, *Miller 485* (US). OKEECHOBEE: 3 mi. N of Okeechobee, *West*, 1946 (FLAS). ORANGE: Vacant yard, Orlo Vista, *West*, 1929 (FLAS). OSCEOLA: Swamp 7 mi. S of St. Cloud, *Cooley 1036* (USF). PALM BEACH: Sandy roadside, 15 mi. W of Jupiter and 6 mi. S of Indiantown, *Atwater 562* (FLAS). PASCO: Hammock along ravine, Fla 41, 1 mi. E of US 75, 2 mi. W of Blanton, *Beckner 1642* (FLAS). PINELLAS: Dunedin, *Tracy 6834* (GH). POLK: 3 mi. E of Edwards Shores, S end of Lake Marion, *Conard*, 1964 (FLAS). PUTNAM: Moist open woodland along shores of Crescent Lake at Crescent City, *Godfrey 56905* (FSU, GH). ST. LUCIE: Pine barren, Fort Pierce, *Hunnewell 7449* (GH). SEMINOLE: Ca. 3 mi. N of Oviedo off Fla 419, *Ray 10868* (USF). SUMPTER: On limestone pile, US 75 ca. 1 mi. N of Hernando County line, *D'Arcy 2294* (FLAS). VOLUSIA: Hammock, Oak Hill, *Rhoades*, 1936 (FLAS).

5. **Solanum citrullifolium** A. Br., Ann. Sci. Nat. Bot., Sér. 3. 12: 356. 1849. TYPE: *A. Braun 201* (MO, ex Hort. Freiburg 1849).

Spiny *herb*, stems viscid with simple glandular hairs and copiously armed with acicular yellow spines to 6(–10) mm long. *Leaves* to 13 cm long, 1–2-pinnatifid, both sides with glandular simple hairs and with spines on the veins beneath with occasional stellate hairs; petiole sometimes as long as the lamina. *Inflorescences* terminal, later lateral, few flowered, the peduncle as long as the petioles, the pedicels becoming 10–12 mm long in fruit; calyx with lanceolate lobes ca. 5 mm long, in fruit densely spiny, accrescent and enveloping the fruit; corolla blue, 25–30 mm across; stamens unequal, the anthers attenuate with small pores, the longest 13 mm long, the 4 others 7 mm long; the style arcuate, long exserted. *Fruit* enclosed in the persistent accrescent calyx, ca. 8 mm across.

This species is similar and related to *S. rostratum*, which differs in its copious, eglandular, stellate pubescence, the coarser dissection of its leaves and its purple flower. Although first described from a plant in a European garden, S. *citrullifolium* is a native of Mexico. It is a rare adventive in Florida. To judge from label information, it was deliberately introduced for study by workers at the University of Florida, subsequently escaped, but did not persist in the state.

ALACHUA: Escape, Gainesville, *Murrill*, May 1939; June 1939 (both MO).

6. **Solanum dimidiatum** Raf., Aut. Bot. 8: 107. 1840, non Sendt. *in* Mart., Fl. Bras. 10: 1846. TYPE: not seen.

Solanum platyphyllum sensu Engelm. & Torr., Ann. Lyc. New York 2: 227. 1828, non Dun., Sol. Syn. 38. 1816.

Solanum mammosum sensu Engelm. & Gray, Boston Jour. Nat. Hist. 5: 254. 1845, non L.

Solanum ———— Torr. & Gray *in* Pope, Rep. Pacific R.R. Surv. 2: 172. 1854. Refers to *S. mammosum* Engelm. & Gray, non L.

Solanum torreyi A. Gray, Proc. Amer. Acad. 6: 44. 1862. TYPE: Texas, *Lindheimer 281* (A-lectotype; isolectotypes BM, K, LL, MO, P, SMU).

Solanum perplexum Small, Man. S.E. Fl. 1115, 1508. 1933. TYPE: Georgia, *Small* 1895 (NY).

Sparingly armed, sarmentose *herb* to 50 cm tall; young stems somewhat angled, tomentose with stalked, many-armed stellae bearing long midpoints, mostly with straight slender spines of various colors. *Leaves* mostly 8–12 cm long, ovate, sinuate lobed, the lobes and sinuses mostly rounded, above with dispersed sessile stellate hairs, beneath tomentose with sessile few-armed hairs, the veins often with spines to 10 mm long; petioles 1–4 cm long, often spiny. *Inflorescence* lateral, an erect, branched, several flowered panicle, the pedicels 1–3 cm long. *Flowers* showy, calyx 4–7 mm long, unarmed, deeply lobed, the lobes subulate tipped; corolla deep mauve or blue, 3–4 cm across, lobed less than ⅓ way down, the lobes deltoid; stamens connivent or separate, equal, the filaments 2–4 mm long, glabrous, the anthers 6–8 mm long, elongate and tapering, opening by small pores and tardily by longitudinal slits; ovary with minute, curved, glandular simple hairs, style basally pubescent, apically flattened and broadened. *Fruit* yellow, 1–3 cm across, not juicy, the pericarp thick, green, very hard, the endocarp forming a lignified capsule-like enclosure compressing the 6–12 maturing seeds; seeds twisted-lenticular. *Pollen*: 25.0–30.0 μ. *Chromosomes*: $n = 36 \pm 1$ (D'Arcy, 1969).

This species is distinct in its showy, deep-colored flowers and large, hard yellow fruits. It is apparently closely related on the one hand to *S. carolinense* and on the other hand to *S. melongena*, both species which may be found throughout the range of *S. dimidiatum*.

Solanum dimidiatum ranges from Texas and Oklahoma to Georgia and Florida. In Florida it occurs in scattered colonies on the red hills in the Tallahassee area and in single colonies in Gilchrist and Alachua Counties further south. In these sites it grows in disturbed habitats of former hardwood forest. The Gilchrist County population dominates about 30 acres of cornfield and pasture and is a noxious plague to the landowners. Here most reproduction is by underground runners, although farmers report volunteer seedlings in cut hay. The Alachua

County colony consists of a few plants along a sandy road where it persists in spite of road grading and sometimes extended drought. Little fruit is set here, in part due to damage by the ash-grey blister beetle (*Epicauta fabricia* (LeConte)), which feeds heavily on the flowers.

The species is interesting because of its reported chromosome numbers. The Gilchrist and Alachua County colonies referred to above have the haploid number $n = 36 \pm 1$ (D'Arcy, 1969), one of the first reports of polyploidy in the spiny, stellate-pubescent subgenus *Stellatipilum*. Hardin *et al.* (1972) reported $n = 18$ for a population in Oklahoma, and LaCour (1952) reported $2n = 24$ (as *S. torreyi*). Vouchers for the LaCour count are not known. The fruit of this species is also interesting, displaying signs of sterility. Instead of a mucilaginous fruit like the similar *S. carolinense* or a fleshy, soft fruit like *S. melongena*, this species has a hard, almost woody pericarp enclosing a stony endocarp. Fewer than 12 (sometimes no) seeds are produced, twisted and packed by constraint of the stony endocarp, but the inside of the carpel wall is sprinkled with pepper-like aborted ovules.

ALACHUA: Sandy road shoulder, dirt road between Fla 24 and Fla 26, 1 mi. W of US 75, *D'Arcy 1587* (FLAS). Old Rocky Point near Gainesville, *West & Arnold*, 1937 (DUKE). GILCHRIST: Ca. 2 mi. W of Bell on Fla 341, *D'Arcy 2477* (FLAS, MO). JACKSON: Without locality, *Chapman* (NY). JEFFERSON: Monticello, *Nolen* 1968 (FLAS). LEON: Tallahassee, *Godfrey 53226* (DUKE, FSU, GA, NY, SMU). Edge of thicket, Tallahassee, *Moldenke 1118* (MO). Apalachicola National Forest 10 mi. S of Tallahassee, *Redfern 350-2-55* (FSU). WAKULLA: Edge of farm field 3 mi. S of Crawfordsville, *Kral 4711* (FSU, SMU). In pinetis prope St. Marks, *Rugel 1843* (NY). Fla. 376, 0.3 mi. E of US 98, *Wooten 272* (FSU).

7. **Solanum diphyllum** L., Sp. Pl. 184. 1753. TYPE: ?*Patrick Browne*, herb. Linn. 248.5 (LINN).

Glabrate, unarmed, erect *shrub* 1(–3) m tall; stems green, angled; twigs sparingly puberulent with appressed simple hairs. *Leaves* elliptic, to 12 cm long, apically acute or acuminate, basally narrowed or short acuminate, the margins entire, glabrous except occasionally minutely puberulent along the major veins beneath; minor leaves orbicular, to 6 cm long. *Inflorescence* opposite the leaves, a short, congested cincinnus with a prominent cicatrix of pedicel scars; pedicels filiform, 8–12 mm long, pendant in fruit; calyx 1.2 mm long, slightly accrescent, deeply deltoid lobed; corolla white, 5–7 mm across, deeply lobed, the lobes lanceolate or obtuse, stamens equal, the filaments glabrous, the anthers 2 mm long, stout with large pores; ovary glabrous. *Fruit* 8 mm across, dull beige, yellow or orange, at maturity globose but 2-lobed by an apical sulcus before maturity; seeds compressed, 2–3 mm across. *Pollen*: 14.0–16.5 μ. *Chromosomes*: $n = 12$ (D'Arcy, 1969).

A native of Mexico, this species has been confused with other similar species of tropical America. It is usually completely glabrous, but some specimens bear minute trichomes on the leaf undersides which give an appearance of roughness rather than puberulence.

Solanum diphyllum is occasionally cultivated throughout the state as an outdoor foliage shrub and is sometimes spontaneous.

ALACHUA: Gainesville, *Beckner* 1970 (MO); *D'Arcy 3500* (FLAS, MO). HILLSBOROUGH: Open area, University of South Florida Botanical Gardens, Tampa, *Burch 4053* (USF). ORANGE: Orlando, *Burch & Silverman 3715* (USF). Near Orland, *Maxwell* 1970 (USF).

8. **Solanum donianum** Walp., Rep. Bot. Syst. 3: 54. 1844. TYPE: Based on S. *bahamense* Mill.

Solanum bahamense Mill., Gard. Dict., ed. 8. 1768, non L. TYPE: Based on S. *frutescens tomentoso flore albo . . .* Houst. mss.
Solanum stenorchis Dun. *in* DC., Prodr. 13(1): 270. 1852. TYPE: Based on S. *bahamense* Mill.
Solanum blodgettii Chapm., Fl. S. United States 349. 1860. TYPE: Key West, *Blodgett s.n.* (NY).
Solanum bahamense var. *subarmatum* sensu O. E. Schulz *in* Urb., Symb. Ant. 6: 223. 1909–10 pro parte, non Willd. Citation of *Curtiss 2199* (C, M).
Solanum decurtatum Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 20. 1943. TYPE: Mexico, *Lundell 2012*, not seen, fide Gentry and Standley (1974: 107).
[*Solanum frutescens tomentoso flore albo umbellato fructu parvo rubro* Houst. mss. TYPE: *Houston s.n.* (BM).]

Small *tree* or *shrub* to 3 m tall; juvenile stems with small, weak acicular spines, but plants otherwise unarmed; twigs articulating at the base, tomentose with stalked and sessile many-armed stellate hairs. *Leaves* 4–15 cm long, ovate, obovate or elliptic, entire, above with dispersed few- and many-armed stellate hairs, beneath with dense, stalked, many-armed hairs standing on papillae. *Inflorescence* lateral, an erect panicle or cyme, the tomentose, 5–8-mm-long pedicels articulating at the base leaving elevated scars; calyx 1–5 mm long, tomentose, truncate in bud, splitting into oblong, short acuminate lobes; corolla white, 6–11 mm across, deeply lobed, the lobes lanceolate and short acuminate apically; stamens equal, the glabrous filaments 1–2 mm long, the anthers connivent, 4–5 mm long, elongate, attenuate, opening by small pores, often drying dark; ovary with few short, glandular simple hairs. *Berry* globose or faintly 2-lobed, 4–7 mm across, shiny and red or rarely orange, overripe berries sometimes blackening (on the Lower Keys) apically with an umbonate stylar scar; seeds compressed, 2–3 mm across. *Pollen*: 25.0–29.0 μ. *Chromosomes*: $n = 12$ (Roe, 1967*b*, as *S. blodgettii*).

This species is often confused in the herbarium with *Solanum bahamense* from which it differs in many respects. The erect, branched inflorescence and the leaf undersides, tomentose with stalked, many-armed stellate hairs which stand on papillae arising from the leaf surface, are good distinctions. The flowers are always white, whereas in *S. bahamense* they are purplish or bluish. The structure of the hairs and the basal articulation of the twigs are unusual features.

This species grows in South Florida in full sun, usually on limestone. It is especially plentiful on the Lower Keys where it forms dense hedges ca. 1 m tall. *Solanum donianum* ranges from the Bahamas through the Florida Keys to the Yucatan and British Honduras.

Schulz's error in considering this species under *S. bahamense subarmatum* was discussed by N. L. Britton (1912). *Solanum bombense* Jacq. (Enum. Pl. Carib. 15. 1763) was described from Isla Tierra Bomba off Cartagena, Colombia, but has not been noted since. A type for this name has not been located, but there is at least a remote possibility that it applies to this Florida taxon.

Roe (1966, 1967*a*) discussed removal of this species from sect. *Brevantherum* where it was considered by Small (1933, as '*Verbascifolia*'). The relationships of *S. donianum* are obscure but may be with *S. punctulatum* Dun. of Jamaica which has scattered hairs on the leaves. It is clearly a member of subgenus *Leptostemonum*. "Blodgett's potato."

Representative specimens:

COLLIER: Plentiful along berm, Fla 29, ca. 1 mi. S of US 41, N of Everglades, *D'Arcy 2253* (FLAS, MO). South end of Big Cypress Swamp, *Jennings*, 1929 (USF). Marco Island, S of Marco Pass, *Lakela 29834* (USF). DADE: 4 mi. E of Homestead, *Godfrey 58124* (FSU). Royal Palm Hammock, *Hunnewell 5774* (A). In crevices of Miami oolite, SW of Homestead, *Lakela 26751* (USF). Edge of hammock S of Florida City, *Moldenke 748* (MO). In swamp, West Lake, *O'Neill* 1929 (FLAS). Everglades, Camp Jackson to Camp Longview, *Small*, 1911 (FLAS). LEE: Hammock about Deep Lake, *Small 9933* (A). MONROE: Limestone near inner edge of mangroves, Big Pine Key, *Conroy 161* (MO, FAU). US 1, Ramrod Key, *D'Arcy 3034* (MO). Buttonwood Head, Flamingo, *Eaton 1338* (A). Marly salt flats, Flamingo, *Godfrey 63369* (FLAS, FSU). Disturbed hammock edge and pinelands, Sugarloaf Key, *Long 2498* (USF). Key West, *Palmer 370* (MO); *Rugel 133* (MO). Hammocks, Key West, *Small 3754* (MO). Hammocks, Big Pine Key, *Small & Mosier* (BUS).

9. **Solanum elaeagnifolium** Cav., Icon. Pl. 3: 22, *t. 243*, p. 115. 1795. TYPE: *Cavanilles s.n.* (C, MA, P-Juss.).

Solanum leprosum Ort., Hort. Matr. Dec. 9: 115. 1800. TYPE: Chile, collector unknown (MPU ex hort. Matrit.).
Solanum obtusifolium Dun., Sol. Syn. 26. 1816. TYPE: Mexico, *Bonpland* (?P, not seen).
Solanum flavidum Torr., Ann. Lycium New York 2: 227. 1828. TYPE: Western United States, *James 309* (NY).
Solanum texense Engelm. & Gray, Boston Jour. Nat. Hist. 5: 227. 1845. TYPE: Texas, *Lindheimer 135* [= *Drummond 200*] (K, MO).
Solanum roemerianum Scheele, Linnaea 21: 767. 1848. TYPE: not seen; ? = S. *undatum* Roemer.
Solanum elaeagnifolium var. *leprosum* (Ort.) Dun. *in* DC., Prodr. 13(1): 291. 1852.
Solanum elaeagnifolium var. *obtusifolium* (Dun.) Dun. *in* DC., Prodr. 13(1): 291. 1852.
[*Solanum undatum* Roemer, ined., non Lam. TYPE: "ex herb. Roem." (BM)].

Greyish, often armed, erect or sprawling *herb* to 60 cm tall; stems scaly, often with orange or blackening, 2–5-mm-long, acicular spines; twigs with dense, subsessile scutellate-stellate hairs; long propagating rhizomes present. *Leaves* narrow, 1–10 cm long, sometimes spiny, the margins entire, sinuate or rarely pinnatifid, blue-green above with dispersed to dense subsessile scutellate hairs, beneath silvery with stalked and sessile stellate hairs. *Inflorescence* lateral or terminal, a mostly unbranched raceme or cincinnus; the pedicels congested in flower, 0.4–2.5 cm long, mostly spiny, pubescent, sometimes articulating at the base; calyx often spiny, 3–5 mm long, tomentose, splitting to form oblong lobes with filiform-subulate apices; corolla blue, violet or rarely white, ca. 3 cm across with a broad limb and deltoid lobes; stamens equal, the filaments 1–2 mm long, glabrous, the anthers 6–8 mm long, attenuate with small pores; ovary tomentose, the arms of the stellate hairs long and pointed upwards, the style with glandular, simple hairs. *Berry* globose, 1–1.5 cm across, dirty to bright yellow, sometimes persisting with viable seed for several years; seeds 3–4 mm across, flat to lenticular and irregular in outline within the same berry. *Pollen*: 27.0–31.0 μ. *Chromosomes*: $n = 12$ (Averett & Powell, 1972).

The greyish, scaly surface and showy flowers distinguish this species from all other Florida members of the genus except perhaps S. *tridynamum*, which has much broader leaves and strongly unequal anthers.

Solanum elaeagnifolium has long been a street weed on Key West but is otherwise rare in the state. It is native to the southwestern United States and northern Mexico and perhaps also to temperate South America. It is reported from across the southern United States and from the islands of the Caribbean.

Significant livestock losses have been reported in Texas from poisoning by this plant (Kingsbury, 1954). "White Horse-Nettle."

ALACHUA: Roadside, Gainesville, *Hartman*, 1944 (FLAS). DADE: Pasture, Miami, *Steffani*, 1945 (FLAS). ESCAMBIA: Waste ground, Pensacola, *Curtiss 5913* (F, FLAS, GA, GH, K, MO, UNC). MONROE: Key West, *Avery*, 1964 (FLAS). Key West, *Buswell*, 1937 (BUS). Key West, *D'Arcy 3024* (MO). Key West, *Small & Small 4949* (MO). ORANGE: Winter Park, *Hayward*, 1938 (MO).

10. **Solanum erianthum** D. Don, Prodr. Fl. Nepal 96. 1825. TYPE: *Nepal*, herb. Wallich 2616c (K).

Solanum racemosum Mill., Gard. Dict., ed. 8. 1768, non Jacq. TYPE: *Houston s.n.* (BM, right-hand specimen).
Solanum verbascifolium var. *adulterinum* G. Don, Gen. Syst. 4: 415. 1838. TYPE: herb. Wallich 2616h (K).
Solanum erianthum var. *adulterinum* (G. Don) Baker & Simmonds *in* Williams, Fl. Trinidad & Tobago 2(4): 264. 1953.

White-tomentose, unarmed *shrub* or *tree* to 10 m tall; twigs with stalked and sessile dendritic-echinoid and echinoid hairs. *Leaves* entire, to 20 cm long, ovate, felty tomentose with stalked echinoid stellate hairs. *Inflorescence* an erect, long-stalked many-flowered cyme, the pedicels stout, tomentose, 2–5 mm long, articulating nearly at the base; calyx 7–9 mm long in flower, slightly accrescent in fruit, tomentose, lobed halfway down with subequal deltoid lobes; corolla white, deeply lobed, ca. 1.5 cm across, the lobes broadly lanceolate; stamens subequal, the filaments 2 mm long, glabrous, narrowing upwards, the anthers 3 mm long, stout with large pores and ultimately with longitudinal slits; ovary stellate-tomentose, the style sparsely pubescent. *Berry* globose, 7–12 mm across, sparingly pubescent with mostly sessile echinoid hairs, dull yellow but seldom seen ripe, mucilaginous within; seeds slightly compressed, 1.5–2 mm across. *Pollen*: 16.0–19.5 μ. *Chromosomes*: $n = 12$ (Roe, 1967*b*).

This species is easily recognized by its large, felty leaves and cymes of white flowers. Closely related to S. *mauritianum*, it differs in its white rather than blue flowers and in its globose flower buds.

Solanum erianthum is a plentiful species in South Florida, growing on road shoulders, hammock edges and in old fields. Very large (to 12-m-tall) trees occur along the Tamiami Trail, Collier County. Occasional collections have been taken in Central Florida as far north as Polk, St. Johns, and Volusia Counties. This species is plentiful in the Caribbean area but is repalced by other species in South America. It is widespread in the Old World tropics.

This species was long known as *Solanum verbascifolium*, but Roe (1968) has shown S. *erianthum* to be the correct name. The type of S. *verbascifolium* L.

(LINN 248.1) is a close relative of S. *hartwegii* Benth. or S. *hispidum* Pers., both spiny Mexican shrubs not closely related to S. *erianthum.*

Pollen of this species is usually 3-colporate, but *Curtiss 5456* is an exception. Pollen was examined from all sheets except that at Kew (K), and it was in tetrads, 28 μ across. No other features of this collection seem in any way unusual. "Potato tree."

Representative specimens:

BROWARD: Canal bank near Andytown, *Burch 59* (MO). DADE: Dry hammock, Old Cutler Road ca. 15 mi. S of Miami, *Burch 42* (MO). Dry Rocky soil, Miami, *Hood,* 1910 (MO). INDIAN RIVER: Indian River, *Reynolds 11564* (MO). MARTIN: Roadside between Canal Point and Okeechobee, *Gaiser et al.,* 1945 (FLAS). MONROE: Rocky pineapple field, Key Largo, *Curtiss 5456* (A, FLAS, K, MO, NY). Hammock clearings, Key Largo, *Godfrey 53815* (FSU). Edges of mangrove swamp, 2.6 mi. N of Flamingo, *Godfrey 63386* (FSU, UNC). Key Largo, *Janish & Janish* 493 (MO). Key West, *Rugel 8, 216* (both MO). Pinelands, Big Pine Key, *Small & Small 5019* (MO). Edge of *Lysiloma* hammock, Pinecrest, 4 mi. W of Dade County line, *Ward 3311* (FLAS, UNC). Long Key, *Weber & Hawkins,* 1928 (FLAS). OKEECHOBEE: Low thicket, Okeechobee City, *Burger & West,* 1927 (FLAS). Roadside, Okeechobee City, *Moldenke 246* (MO). POLK: Lake Alfred, *McFarlin 5223* (MICH). PUTNAM: Esperanza, *Donnell Smith,* 1879 (US). ST. JOHNS: Picolata, *Canby,* 1858 (DUKE). ST. LUCIE: Road shoulder in mangrove swamp, 11 mi. S of N end of Huchinson Island, *Beckner 2237* (FLAS). SARASOTA: Osprey, *Smith,* 1901 (DUKE). VOLUSIA: Hammock W of Allandale, *West,* 1942 (FLAS).

11. **Solanum glaucophyllum** Desf., Cat. Pl. Hort. Par. 114: 396. 1829. TYPE: not seen.

Solanum angustifolium Lam., Illustr. 2: 18. 1797, non Mill., Gard. Dict., ed. 8. 1768. TYPE: not seen.
Solanum malocoxylon Sendt. *in* Mart., Fl. Bras. 10: 51. 1846. TYPE: not seen.
Solanum amygdalilfolium Steud. *ex* Sendt. *in* Mart., Fl. Bras. 10: 51. 1846. TYPE: not seen.
Solanum glaucum Dun. *in* DC., Prodr. 13(1): 100. 1852. LECTOTYPE: Argentina, *Baclé 43* (G-DC); syntype *Gaudichaud 1833* (P "ex h. imp. Bras. 1748").

Unarmed, glabrate, glaucous, paludal *shrub* to 2 m tall. *Leaves* narrow, 9–13 cm long and 1–2 cm wide, long acuminate at each end, sessile and slightly clasping the stem. *Inflorescences* numerous, terminal and lateral, several-flowered, racemes to 10 cm long, mostly unbranched; the calyx with short-deltoid teeth, splitting at the sinuses to form minutely ciliate lobes ca. 3 mm long; the corolla blue, 2–3 cm across, the lobes short and the limb broad; stamens equal, filaments ca. 1 mm long, glabrous, the anthers 3–6 mm long, stout with large pores and ultimately with longitudinal slits; the ovary glabrous. *Berry* 7–10 mm across, apiculate. *Chromosomes*: $2n = 24$ (Gerasimenko & Reznikova, 1968, as S. *glaucum*).

This species is distinctive in its narrow, thick, glabrous and somewhat glaucous leaves, and in the blue corollas which are glabrous except for a band of fine simple hairs outside near the margins.

A native of Argentina, this species is known in Florida from only two collections taken many years ago. Perhaps it was introduced with ships' ballast and has not persisted. It grows in paludal waste places. It causes a sometimes fatal disease of livestock known as *Enteque seco* or "dry weakness," and the vitamin D-like effects of its toxic principle were recently reported (Wasserman, 1974).

Use of this name is based on a specimen labelled "S. *glaucophyllum* Hort.

Paris Cat. Ann. 1829, p. 396" (MPU), which may be from the type collection, and on specimens labelled S. *glaucum* Dun. (G) but annotated as S. *glaucophyllum* by Georg Bitter. Material labelled S. *malocoxylon* and S. *angustifolium* Lam. (both G) was similarly annotated as S. *glaucophyllum*. In each case, the protologue agrees with the present concept of the species. Dunal in his original publication of S. *glaucum* cited an S. *glaucophyllum* Hort.

ESCAMBIA: Pensacola, 1899 *Curtiss 6500* (GH). Pensacola, 1901 *Curtiss 6862* (G-DC, GA, GH, MO, US).

12. **Solanum jamaicense** Mill., Gard. Dict., ed. 8. 1768. TYPE: *Houston*, Sloane Cat. 107 (BM).

Solanum brevipilum Dun., Hist. Sol. 193, *t. 2.* 1813. TYPE: ?St. Thomas, *Riedlé s.n.* (MPU).
Solanum cuneifolium Dun., Hist. Sol. 193, *t. 22.* 1813. TYPE: not seen.
Solanum heterotrichum Dun., Hist. Sol. 192, *t. 20.* 1813. TYPE: fragment "Dun. 1813" (MPU).
Solanum brevipilosum Dun. *in* DC., Prodr. 13(1): 199. 1852. LECTOTYPE: Brazil, *Salzman 384* (G-DC).
Solanum portoricense Dun. *in* DC., Prodr. 13(1): 374. 1852. TYPE: Porto Rico, *Riedlé s.n.* (B-W, not seen; IDC 7440. 301: II. 4).

Tomentose, armed, erect or scandent *shrub* to 3 m tall; stems tomentose with slightly ochraceous, stalked, many-armed stellate or dendritic hairs, armed with stout-based, ca. 5-mm-long recurved spines. *Leaves* thick and felty, 4–15 cm long, broad, mostly angular sinuate, basally acute or acuminate and subsessile, both sides tomentose, sometimes spiny. *Inflorescence* lateral, a short, congested raceme, the peduncle pubescent, the pedicels 2 cm long, villous; flowers small, the calyx 4 mm long with narrowly lanceolate lobes extending halfway down and bearing prominent dendritic or stellate bristles; corolla white, 8–11 mm across, lobed halfway down; stamens equal, the filaments very short (0.2 mm long), glabrous, the anthers 3–4 mm long, attenuate with large pores and sometimes ultimately longitudinal slits. *Berry* 5 mm across, globose, shiny red; seeds lenticular, orange, 1.5–2 mm across. *Chromosomes*: $n = 12$ (Heiser, 1956).

The triangular, subsessile leaf bases distinguish this species, as do the inconspicuous white flowers, bright red fruits and recurved spines.

Rare in Central Florida, this species ranges through the Antilles, Central America, and tropical South America, in some places becoming a noxious weed.

ORANGE: Cypress swamp near Boggy Creek settlement 6 mi. SE of Taft, *Nicholson 103* (US). OSCEOLA: East Lake, *McFarlin 5901* (MICH). Near St. Cloud, *Mulvania*, 1903 (NY).

13. **Solanum jasminoides** Paxt., Mag. Bot. 8, *t.* 5. 1841. TYPE: not seen.

Glabrate, unarmed climbing *vine*, rooting by runners. *Leaves* both entire and basally lobed on the same plant, 3–4 cm long, membranaceous; petioles 1–2 cm long. *Inflorescence* an open, many-flowered panicle, the pedicels ca. 1 mm long abscissing just above the base; calyx apically ciliate with umbonate teeth, later splitting briefly into 2-mm-long lobes; corolla mostly bluish white, 2 cm across, lobed ⅔ way down, the lobes narrowly obtuse with a prominently angled midvein, stamens subequal and alike, the filaments 1 mm long, villous within, the anthers 4 mm long, stout with large pores and longitudinal slits; ovary glabrous, the style glandular-villous in the lower half. *Chromosomes*: $n = 12$ (Gerasimenko & Reznikova, 1968).

LEON: Cultivated, Tallahassee, *Reese & Godfrey* (USF).

14. **Solanum mammosum** L., Sp. Pl. 187. 1753. TYPE: not seen.

Villous armed *herb* or *shrub* to 1.5 m tall; stems and twigs viscid-villous with long simple hairs, armed with yellow or green acicular spines which in age become flattened, recurved, woody, 2.5 cm long; stems fistulose. *Leaves* 6–20 cm long, broadly ovate, angular-lobed, basally truncate to cordate, both sides villous with long, simple glandular hairs, short-stalked glands and sessile, long-radiate stellae with ascending radii, armed with flattened acicular spines to 3 cm long; petioles 5–7 cm long, sparingly armed. *Inflorescence* lateral, a short, several-flowered raceme, the pedicels 5–12 mm long, becoming stout and somewhat longer in fruit; calyx unarmed, deeply lobed, the lobes 3–6 mm long, lanceolate; corolla violet, 3–4 cm across, lobed about halfway down; stamens equal, the filaments very short, the anthers 10–12 mm long, slender and tapering with small pores, ovary and style glabrous. *Fruit* orange or yellow, 4–7 cm long, ovoid, often with one or more 2-cm-long, rounded protrusions at the base and a nipple-like contraction at the apex; seeds compressed-lenticular, not winged, dark brown, 5–7 mm across. *Chromosomes*: $n = 12$ (Bell, 1965); 11 (Madhavadian, 1968; Heiser, 1971).

This species has fruit like no other species of *Solanum*. The glandular villous pubescence is composed of reduced stellate hairs in which the radii are fused with the leaf lamina and the mid-point remains as an apparently simple hair. The nature of this hair may be seen in seedlings. Similar hairs occur in S. *ciliatum*, but they are not so dense and are less commonly glandular.

Solanum mammosum is occasionally cultivated in Florida as a curiosity. The species is a native of tropical America where it is sometimes cultivated for medicinal properties or for reputed insecticidal properties. "Nipple fruit," "pig's ears."

15. **Solanum mauritianum** Scop., Delic. Insub. 3: 16, *t.* 8. 1788. TYPE: not seen.

Solanum auriculatum Ait., Hort. Kew, ed. 1. 1: 246. 1789. TYPE: not seen.

Foetid, tomentose, unarmed *tree* to 12 m tall, the pubescence white (Florida); twigs with long-stalked dendritic-echinoid and echinoid hairs; wood white, brittle. *Leaves* entire, to 60 cm long, ovate, felty tomentose, basally oblique, above shiny with subsessile, sub-echinoid stellate hairs, beneath tomentose with long-stalked sub-echinoid and echinoid hairs; minor leaves sessile, rounded, sometimes paired, deciduous. *Inflorescence* an erect, sometimes long-stalked many flowered cyme, the pedicels stout, tomentose, 2–5 mm long, longer in fruit, articulating at the middle or just below; calyx 3–4 mm long, slightly accrescent in fruit, lobed halfway down with subequal deltoid lobes; corolla deep blue-purple, 5–8 mm across, the lobes broadly lanceolate; stamens subequal, the filaments 1.5–2 mm long, glabrous, the anthers 3 mm long, stout with large pores and longitudinal slits; ovary stellate-tomentose, the style basally pubescent. *Berry* globose, ca. 10 mm across, dirty yellow, hispid, mucilaginous; seeds lenticular, 2 mm across. *Pollen*: 19.0–27.0 μ, quite irregular. *Chromosomes*: $n = 12$ (Krishnappa, 1968, as *S. auriculatum*).

This species is similar to *S. erianthum* but differs in its larger size, prominent but deciduous minor leaves, blue flowers, and strong odor. It is known in only one Florida locality, a subtropical ravine ca. 1 km long which contains a lush growth of many naturalized exotic species in Pasco County. Fertilizer leached from flanking citrus groves probably encourages growth, and trees of *S. mauritianum* here reach 12 m height.

Solanum mauritianum is a native of Uruguay (Roe, 1972) but has become widespread, occurring as a weed tree in the Old World tropics and in New Zealand. In the Florida plants, pollen is irregular and seed germination less than 10 per cent. "Ear-leaved nightshade."

The name *Solanum mauritianum* is based on plants grown in Italy from seed originating on Mauritius but obtained from a French source. Material of this species was grown at about the same time in England and Paris, and all may have been from the same stock. While type specimens cannot be located, the identity of *S. mauritianum* and *S. auriculatum* is clear from the description and plates supporting each name.

PASCO: Rim of ravine just W of Blanton on Fla 41 ca. 2 mi. E of US 75, *Beckner 1616* (FLAS). Naturalized in ravine flanked by citrus groves, Fla 41 2 mi. W of Blanton, *D'Arcy 1648* (FLAS, MO, US, WIS).

16. **Solanum melongena** L., Sp. Pl. 186. 1753. TYPE: herb. Linn. 248.28 (LINN).

Solanum esculentum Dun., Hist. Sol. 208. 1813. TYPE: Based on S. *melongena* L.

Erect, tomentose, sometimes armed perennial *herb* to 60 cm tall; twigs tomentose with whitish, stalked and sessile stellate hairs, glabrescent, sometimes with straight or curved stout spines. *Leaves* to 25 cm long, ovate, pinnatifid-lobed to entire, the margins mostly sinuate, above pubescent with mostly sessile stellate hairs, beneath tomentose; petioles to 6 cm long. *Inflorescence* a short, few-flowered raceme, the first flowers functionally staminate, a few later flowers perfect; pedicels 1–2 cm long, tomentose, sometimes articulating near the base, longer and much stouter in fruit; calyx ca. 12 mm long, lobed about halfway down, the lobes lanceolate, accrescent and splitting irregularly in fruit; corolla mauve, 3.5–5 cm across, lobed halfway down, the lobes deltoid to acute; stamens equal, the filaments 3–4 mm long, narrowing upwards, the anthers ca. 6 mm long, stout and attenuate with small pores, ovary tomentose apically, glabrescent, the style tomentose in the lower half. *Fruit* very large, to 40 cm long, ellipsoidal or ovoid with a moist fleshy pulp, purple-black (Florida), ultimately turning yellow, rose, green or brown; seeds compressed. *Pollen*: 26.5–33.0 μ, mixture of 3- and 4-colporate grains. *Chromosomes*: $n = 12$ (Carpinin *et al.* 1963).

This species is distinctive in its large fruit with a moist pulp several cm thick. A substantial acreage is devoted to this crop in various parts of the state, and the species is rarely cultivated for ornament. Ornamental plants may develop corollas 5 cm across. No escapes have been seen, and it is not known to winter over. *Solanum melongena* is a native of the Old World, perhaps India. "Egg plant."

Many synonyms have been published for this species, but the above noted name is the only such synonym which has gained (erroneous) currency.

HILLSBOROUGH: Cultivated, Tampa, *Burch & Chevalier 3708* (USF). Cultivated, University of South Florida Botanical Garden, Tampa, *Burch 6452* (USF).

17. **Solanum nigrescens** Mart. & Gal., Bull. Acad. Roy. Bruxelles 12(1): 140. 1845. TYPE: *Galeotti 1238* (P).

Solanum aloysiaefolium Dun. *in* DC., Prodr. 13(1): 73. 1852. HOLOTYPE: Bolivia, *d'Orbigny 1208* (P).
Solanum crenato-dentatum Dun. *in* DC., Prodr. 13(1): 54. 1852. LECTOTYPE: San Fernando, Chile, *Gay, s.n.* (P). PARATYPE: Mexico, *Berlandier 118* (G).
Solanum crenato-dentatum var. *ramossissimum* Dun. *in* DC., Prodr. 13(1): 54. 1852. TYPE: Louisiana, *Barbe*, 1839 (P).
Salanum gracile Dun. *in* DC., Prodr. 13(1): 54. 1852, non S. *gracile* Sendt. *in* Mart. Fl. Braz. 10: 13. 1846. TYPE: "Hort. Monsp. 1831" (MPU) (= S. *gracile* Otto *ex* Baxt. *in* Loud., Hort. Brit. Supp. 2: 673. 1839).
Solanum douglasii Dun. *in* DC., Prodr. 13(1): 48. 1852. TYPE: California, *Douglas 1833* (BM, G-DC, K, MPU, P).
Solanum nigrum var. *rigidum* Dun. *in* DC., Prodr. 13(1): 50. 1852. LECTOTYPE: specimen labelled manu Dunal "1841–1847" (P).
Solanum durangoense Bitt., Fedde Rep. 12: 82. 1913. TYPE: Mexico, *Palmer 101* (US).
Solanum approximatum Bitt., Fedde Rep. 12: 86. 1913. TYPE: Jamaica, *Nichols 89* (MO, US).
Solanum ottonis Hylander, Uppsala Univ. Ärsskr. 7: 279. 1945. New name for S. *gracile* Dun.

Perennial *herb*, to 3 m, sometimes epiphytic; stems glabrate to pubescent; often sarmentose. *Leaves* to 10 cm long but mostly much shorter, ovate to lanceolate, entire or toothed. *Inflorescence* a condensed, subumbellate raceme, 1- to several-flowered, the peduncle slender, appressed pubescent, pedicels slender, often thickening in fruit, appressed-pubescent, erect or deflexed in flower but always strongly deflexed in fruit. *Flowers* with the calyx lobes ovate, lanceolate or deltoid, not accrescent; corolla white or mauve, small (to 15 mm across), mostly with a conspicuous eye; anthers mostly 2.5–2.9 mm long. *Fruit* black or rarely green with dark purple marking, dull, 4–8 mm across; seeds 1.2–1.5 mm across. *Pollen*: 21.0–23.5 μ. *Chromosomes*: $2n = 24$ (Gerasimenko & Reznikova, 1968, as S. *douglasii*).

S. *nigrescens* may be recognized in the field by its rhizomes or adventitious roots, unbranched peduncles, deflexed fruiting pedicels, applied calyces, the usually reflexed corolla with a distinct eye, large anthers, and dull black fruits; but on the herbarium sheet some of these characters disappear and recognition is often difficult. In fresh material, leaves are somewhat more opaque and firmer in texture than S. *americanum*. The meiotic chromosome number ($n = 12$) was verified in this study using a variety of Florida material.

This species is under-represented in most herbaria. Although common, plants are usually scattered or isolated, and the major habitats are unattractive collecting areas. The plant occurs along railroad tracks (often weed treated), amongst dense weed growth along fencerows, rarely as an epiphyte in palm trees, saxicolous on the walls of phosphate pits, and frequently along the seacoasts where it grows on hummocks in salt marshes or on top of the middle or fore dunes. I have not seen a plant in a citrus grove, a favorite habitat for S. *americanum*. Although preferences are not clear, it would seem inclined to habitats of greater osmotic stress than S. *americanum*, and it does not depend to the same extent on recent disturbance. It is present throughout peninsular Florida but absent or nearly absent from the panhandle.

There is considerable geographic variation in this species. Thus California plants often have larger flowers, fuller inflorescences, and heavier pubescence than those of Florida; but many plants of each region can be matched with complete confidence. In Hispaniola, where the species occurs above 1,500 m elevation, plants are generally larger and many berries develop only a partial purple-black coloring. Plants from Panama usually have entirely green fruits. Seed from Hispaniolian and Californian plants when grown in the greenhouse matched the Florida plants.

It is likely that an earlier name will be found for this species; either because a type is found to support an earlier name for plants like those of California, Mexico, and Florida, or because a decision is evolved to include plants of S. *chenopodioides* Lam.[5] and S. *nigrescens* within the same species concept. *Solanum chenopodioides* and S. *pygmeum* are names for plants of northern Argentina and southern Brazil usually recognizable by smaller, sinuately lobed and thicker leaves than are usual on S. *nigrescens*, but some collections are difficult to assign between these species concepts. Some plants seen along the Indian River, Indian River County, were suggestive of S. *chenopodioides* but are considered variants of S. *nigrescens*. "Black nightshade."

Representative specimens:

ALACHUA: SE of LaCrosse, *Hargraves*, 1946 (FLAS). BAY: Homesteads, Apalachicola, from Herb. *Chapman 912*^{c} (NY). BROWARD: N of Long Island, *Moldenke 507* (NY). CITRUS: Picnic area near the sea, Western Island, W of Ozello, *D'Arcy 1568* (FLAS). COLLIER: Roadside S of Tamiami Trail, *Moldenke 874* (NY). DADE: Humbugus Prairie, *Small 5573* (NY). DIXIE: Beach 4 m from the sea and exposed to salt spray, Horseshoe Beach, *D'Arcy 1521* (FLAS). DUVAL: Pablo, *Lighthipe 385* (NY). FLAGLER: Grassy low ground 3 mi. E of Bunnell, *West et al.*, 1937 (FLAS). GADSEN: Front of grocery store, US 90, ca. 4 mi. W of Quincy, *D'Arcy 2574* (FLAS). HENDRY: Devil's Garden Hammock, *Cooley 797* (USF). HIGHLANDS: Among heavy palmetto undergrowth, N edge of Lake Placid, 1 mi. S of edge of Lake Placid, *Ward 2-8* (FLAS). INDIAN RIVER: Wooded dune bordering the ocean just N of Vero Beach, *Deam 60240* (IND). Indian River, *Palmer 369* (MO). LEE: Homestead, Sanibel Island, *Cooley 11850* (UNC).

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[5] *Solanum chenopodioides* Lam., Illustr. 2: 18. 1794. TYPE: Commerson, Buenos Aires (P; an examination of the suite of specimens at Paris (P) and Montpellier (MPU), leads to the conclusion that Lamarck was describing Commerson plants from Buenos Aires, and his mention of a Mauritius (or Île de Bon) specimen is irrelevant): includes S. *pygmeum* Cav., Icones 5: 23, *t. 439, f.* 2. 1799. TYPE: Laguna de Ballestero, pampas de Buenos Aires, *Nee iter s.n.* (MA); S. *sublobatum* Willd. *ex* R. & S. *in* L., Syst. Veg. 4: 664. 1819. TYPE: Buenos Aires, Herb. *Willd. 4336* (B, not seen; IDC 7440. 298 II. 2). This species often, but by no means always, blooms when very small, less than 15 cm tall.

LEON: Sandy hardwood clearing 2 mi. W of Tallahassee, *Godfrey 53610* (FLAS, GA, NY). LEVY: Just back of beach, Gulf side of island, Seahorse Key, 2 mi. SW of Cedar Key, *Ward 3249* (FLAS). MANATEE: Waste ground, Bradenton, *Cuthbert 1458* (FLAS). MONROE: Clearing in hammock, Key Largo, *Kral 12070* (FSU). NASSAU: In sand dunes beside parking lot, Amelia Beach, *D'Arcy 1670* (FLAS). ORANGE: Clarcona, *Meislahn 7* (US). OSCEOLA: St. Cloud, *Bitting 708* (F). PALM BEACH: Jupiter Island, S end, *Cooley 4800* (USF). PINELLAS: Cunningham Key, Fort DeSoto County Park, South Tierra Verde, *Lakela 26716* (USF). POLK: Without locality, *Ohlinger 454* (FLAS). PUTNAM: Hammock, Conservation Reserve, Welaka, *DeVall*, 1939 (FLAS). ST. JOHNS: In woods near beach, St. Augustine, *Small 2311* (NY). SARASOTA: Venice, *Rapp 1956* (FLAS). VOLUSIA: Sandy soil, Morelands', Glenwood, *Van Clef 1114* (FLAS).

18. **Solanum nigrum** L., Sp. Pl. 186. 1753. LECTOTYPE: Central Asia (LINN 248.18).

Erect, unarmed, sparingly pubescent *herb*; stems sometimes purplish. *Leaves* ovate, elliptical or lanceolate, to 10 cm long, entire to sinuate dentate; petiolate. *Inflorescence* a subumbellate raceme of few to 10 flowers, the peduncle stoutish to 4 cm long, pedicels thickening upwards, puberulent, deflexed in fruit; calyx lobed halfway, the lobes deltoid, applied to the berry in fruit, ultimately becoming free and somewhat reflexed; corolla white or purplish, to 12 cm across, anthers 2.2–2.8 mm long. *Fruit* a dull black globose juicy berry 4–8(–15) mm across; seeds 1.5–2.0 mm. *Pollen*: 24–35 μ. *Chromosomes*: $n = 36$ (Stebbins & Paddock, 1949; Baylis, 1958).

This species is difficult to distinguish from S. *nigrescens* and sometimes from other members of this section in Florida, especially when dried on the herbarium sheet. Living material is usually distinguishable by its weakly reflexed fruiting calyx and by the sturdy construction of the inflorescence. For dried material, the sturdy inflorescence is perhaps the most useful character, although it has not been possible to provide quantitative details of this feature. In general, the seeds are larger than those of S. *nigrescens*. Both peduncle and pedicel are much stouter and sometimes longer than other members of the group. The specimens cited below are the only collections clearly belonging to this species, but there may be others which have been misidentified as S. *nigrescens*. "Black nightshade."

DADE: In wet hammocks, Lake Jovita, *O'Neill 1927* (MO). ESCAMBIA: Waste ground Pensacola, *Curtiss 6863* (MO, NY, US). PINELLAS: Open shade of hammock on Cunningham Key, *Lakela 26719* (USF).

19. **Solanum pseudocapsicum** L., Sp. Pl. 184. 1753. TYPE: herb. Linn. 248.4 (LINN).

Glabrate, unarmed *shrub* to 2 m tall; stem glabrous or minutely puberulent. *Leaves* 2–12 cm long, elliptic or oblanceolate, mostly narrow, apically obtuse to acuminate, basally narrowed, margins entire or faintly sinuate, above mostly glabrous, beneath glabrous or puberulent with sparse dendritic hairs; petiole 5–20 mm long, mostly winged. *Inflorescence* axillary or lateral, a 1–3-flowered fascicle or subsessile congested raceme; pedicels 3–10 mm long, thickening in fruit; calyx 4–6 mm long, deeply lobed, the lobes deltoid to narrowly oblong or spatulate, the tips ciliate; corolla white, 1–1.5 cm across, deeply lobed, the lobes oblong, apically obtuse or acute; stamens subequal, the filaments stout, 1 mm long, the anthers 2.5–3 mm long, stout with large pores and longitudinal slits; ovary glabrous. *Berry* globose, orange-red, 12–18 mm across, minutely apiculate; not juicy or mucilaginous; seeds yellow, compressed-lenticular, 3 mm across. *Chromosomes*: $n = 12$ (Madhavadian, 1968).

This species is recognizable by its small white flowers which resemble those of S. *nigrum* or S. *americanum* and by the showy bright red berries which are displayed outside of the foliage. The dendritic hairs are distinctive. *Solanum pseudocapsicum* has been confused with S. *capsicastrum* Link *ex* Schau *in* Otto & Dietrich (Allg. Gartenz. 1: 228. 1833), which is copiously pubescent, pilose on the peduncles and calyx, and which has much smaller flowers with anthers only 2 mm long, and yellow fruit.[6]

Plants and cuttings of *Solanum pseudocapsicum* are widely offered for sale through novelty stores and other outlets before Christmas. They are usually sold in pots or cans when 25–50 cm tall and in both flower and fruit. Fruiting branches are sold in bunches along with cut flowers. The species is occasionally grown out-of-doors as an ornamental or for nursery stock, and it is sparingly naturalized on the southern Coastal Plain. Spontaneous plants are rare in Florida. The type locality for this species is Madeira, where it grows wild; it is also native to Brazil. "Jerusalem cherry."

ALACHUA: Cultivated and escaping, NW Gainesville, *D'Arcy*, 1968 (FLAS, MO, USF).

20. **Solanum pseudolulo** Heiser, Ciencia y Nat. 11: 5. 1968. LECTOTYPE: Cultivated, seed from Colombia, *Heiser 6343* (IND, photo MO).

Densely tomentose, erect, armed *shrub* or *tree*; stems stout, stellate-tomentose and copiously armed with green to orange brown or stramineous acicular spines 3–8 mm long. *Leaves* of juveniles to 60 cm long and 30 cm broad, smaller on older plants, broadly ovate, angular-sinuate, the lobes and apex acuminate, the sinuses rounded, basally cordate or truncate, oblique, velutinous and appearing ciliate above, loosely tomentose beneath, the hairs sessile, pauciradiate with elongate midpoints and long-stalked, pauciradiate to sub-echinoid, both sides copiously armed with acicular, green, sometimes purplish spines, the epidermis sometimes purplish; petiole 3–6 cm long, tomentose and spiny. *Inflorescence* becoming lateral, crowded, subumbellate and subsessile, several-flowered, pedicels 8–10 mm long, stout; calyx 7–10 mm long, lobed past halfway, ovate, apically acuminate; corolla white, campanulate, 2–3 cm across, thick and fleshy, lobed ¾ way down; stamens equal, the anthers sessile, basally imbedded in the corolla tube, 6 mm long and 3 mm across, abruptly narrowed to an outward curving beak with minute pores; style inserted at an angle, the ovary tomentose. *Fruit* a juicy, red, persistently tomentose, globose berry to 5 cm across. *Pollen*: 16.0–21.0 μ.

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[6] Details taken from the lectotype specimen: "Brasil, *Sellow*, ex herb. Berlin," labelled by Link (?), and "donné par le Museum Bot. de Berlin 1855" (P).

This species is distinct in its large, felty, spiny leaves, congested flowers and sessile anthers. The fruit is agreeably sweet and tart. Heiser reported light yellow, nearly white pulp, but the Florida plants seen had orange pulp.

Solanum pseudolulo is cultivated as a curiosity in the South Florida nursery trade.

Lawrence (1960*a*) noted cultivation of *S. quitoënse* Lam. in Florida, but no material of this species was seen. It is similar to *S. pseudolulo* but differs in having short but manifest anther filaments and in the purple suffusion of the leaves arising from pigment in the pubescence rather than in the leaf surface.

Representative specimens:

ALACHUA: Cultivated, Gainesville, *D'Arcy 2701C* (MO); *2701B, 2071D* (FLAS). CULTIVATED: Missouri Botanical Garden from seed of *D'Arcy 2701B, D'Arcy 3895* (MO, USF).

21. **Solanum racemosum** Jacq., Enum. Pl. Carib. 15. 1760; Sel. Stirp. Amer. 50, *t. 36.* 1762 TYPE: not seen.

Solanum igneum L., Sp., Pl., ed. 2: 270. 1762. TYPE: not seen.
Solanum anacanthum Dun. *in* DC., Prodr. 13(1): 183. 1852. TYPE: Mexico, *Pavon s.n.* (G).
Solanum racemosum Jacq. var. b, Duss, Fl. Phan. Ant. Franc. 414. 1897. TYPE: Based on *S. igneum* L.
Solanum ramosum Poir. *in* Lam., Encycl. 4: 281. 1796. Error for *S. racemosum.*

Shrub to 2 m tall, rarely spiny; twigs puberulent to villous with sessile stellate hairs. *Leaves* to 20 cm long, lanceolate or elliptical, apically acuminate, basally obtuse, mostly oblique, veins 12–20 on each side of the midvein, the margin subentire; petioles 5–20 mm long. *Inflorescence* terminal becoming lateral, an unbranched raceme 4–8 cm long, somewhat longer in fruit, the pedicels 8–15 mm long, in fruit longer and appearing cernuous and secund. *Flowers* elongate, the calyx 1.5–2 mm long with 5 deltoid undulate teeth; corolla white, ca. 1 cm long, deeply lobed, the lobes narrowly lanceolate; stamens equal, forming a coherent tube, the filaments united halfway up, the anthers 6–8 mm long, slender, slightly tapering, coherent by lateral grooves and ventral pubescence; ovary with a few stellate hairs. *Fruit* shiny red, globose, 6–8 mm across. *Chromosomes*: $n = 24$.

Very like *S. bahamense* to which it is closely related, this species differs in its white flowers, larger, longer leaves with more lateral veins and in its longer anthers. It is less commonly spiny, but spines may become copious, acicular or almost deltoid, and yellow to orange red. Chromosomes of this species were counted using root tips of *Howard 17730* (A) from St. Vincent, Windward Islands.

Solanum racemosum is a native of the Windward Islands, and it occurs in Florida only as an occasional adventive. It would appear to hybridize with *S. bahamense*, and the collections cited here all bear some characters seemingly derived from *S. bahamense*. The above description is taken from a range of Windward Island material at MO and IJ.

MONROE: Hammock growth and roadside areas ca. 10 mi. N of junction US 1 and Fla 905, Key Largo, *Long et al. 1773* (USF). Second growth hammock and limestone margins, Plantation Key, *Long 1989* (USF). Coastal strand and hammock ca. 5 mi. N of junction US 1 and Fla 905, Key Largo, *Long et al. 2809* (USF). PALM BEACH: Singer Island, E of N Palm Beach, *McCart 11049* (USF).

22. **Solanum rostratum** Dun., Hist. Sol. 234, *t. 24.* May 1813. TYPE: ex Hort. Monsp. (G, G-DC, MPU, P).

Solanum heterandrum Pursh, Fl. Amer. Sept. 1: 56, *t.* 7; 2: 731. Late 1813. TYPE: not seen, based on seed from Nuttall, Missouri River.
Androcera lobata Nutt., Gen. Amer. 1: 129. 1818. TYPE: Missouri River, *Nuttall s.n.* (MO-as *Solanum heterandrum*; G-DC). Nuttall cited *S. heterandrum* Pursh.
Nycterium rostratum (Dun.) Link, Enum. Hort. Berol. 1: 189. 1821.
Nycterium lobatum (Nutt.) Sweet, Hort. Brit., ed. 1. 301. 1826.
Nycterium flavum Lindl. *in* Donn, Hort. Cantabr., ed. 11: 76. 1826. TYPE: Based on *Solanum heterandrum.*
Nycterium luteum Steud., Nom., ed. 2. 2: 199. 1840. Nomen nudum.
Solanum propinquum Mart. & Gal., Bull. Acad. Bruxelles 12(1): 143. 1845. TYPE: Mexico, *Galeotti 1167* or *1205* (BR, not seen).
Solanum chrysacanthum Dun. *in* DC., Prodr. 13(1): 330. 1852. TYPE: Mexico, *Andrieux 191* (G-DC, MPU).

Densely armed, dissected *herb* to 1 m tall; pubescent with stalked, eglandular, nearly porrect, pauciradiate stellate hairs, copiously armed with straight, slender, yellow spines to 8 mm long and spine-like bristles. *Leaves* to 15 cm long, ovate to obovate, mostly 2-pinnatifid, the lobes 3–7 on each side of the midvein, apically obtuse to rounded, both sides pubescent with sessile, pauciradiate, stellate hairs bearing long midpoints, the undersides with some multi-radiate stellae, the major veins armed; petioles often as long as the leaves, mostly armed. *Inflorescence* lateral, an unbranched, 5–10-flowered raceme, the pedicels tomentose, 10–15 mm long; calyx 8–10 mm long, lobed nearly to the base, the lobes lanceolate, apically acuminate and unarmed, the basal portion tomentose and mostly spiny and bearing bristles, eglandular; corolla bright yellow, 25–30 mm across, lobed ¼–⅓ way down, the lobes deltoid, unequal; stamens dimorphic, the filaments 1.5–2.2 mm long, one anther 11–14 mm long, stout but tapering abruptly and arcuate upwards, the remaining 4 subequal, 6–7 mm long, slightly curved, the terminal pores small; ovary glabrous, the style filiform, apically circinnate, about as long as the long anther. *Fruit* enveloped in the accrescent, spiny persistent calyx, the calyx and fruit wall sometimes withering to release the seeds through gaps; seeds black, puck-shaped, not flat or lenticular as in most other species of *Solanum,* 2–2.5 mm across. *Pollen*: 20.5–24.0 μ. *Chromosomes*: $n = 12$ (Averett & Powell, 1972).

This species is similar to S. *citrullifolium* which also has spiny dissected leaves and strongly unequal anthers, but that species has glandular, simple hairs and blue flowers instead of eglandular, stellate hairs and bright yellow flowers as in *S. rostratum. Cnidoscolus stimulosus* (Michx.) Engelm. & Gray, Euphorbiaceae, is sometimes confused with *Solanum rostratum* in the herbarium. The *Cnidoscolus* has white flowers, palmately divided leaves, and lacks spines, although the dried stinging hairs do resemble juvenile spines.

A troublesome weed in regions where it is plentiful, S. *rostratum* is native to northern Mexico and the Great Plains of the United States. It has been introduced to the plains of Russia and to the West Indian Islands.

This species is a rare adventive in Florida, although it may form persistent local colonies. It may be expected in waste places.

Solanum rostratum and closely related species have been proposed at generic rank and as sect. *Androceras* (Nutt.) Marz. Three names for yellow flowered species of sect. *Androceras*, *S. angustifolium* Mill. (1768), *S. cornutum* Lam. (1794), and *Nycterium cardaminefolium* Vent. (1805) are earlier than *S. rostratum* but refer to another related species, probably what has been going under the name *S. macroscolum* Fern. (1900) from southern Mexico. Dr. Susan M. Coles, University of Birmingham, has examined the type of *S. angustifolium*. "Buffalo bur."

23. **Solanum seaforthianum** Andr., Bot. Rep. 8, *t. 504.* 1808. TYPE: not seen.

Glabrate, unarmed *vine*, high climbing to 6 m long, sometimes blooming as a juvenile and appearing as a small shrub; emergent growth with a few simple hairs, otherwise glabrous, stems mostly slender. *Leaves* 5–16 cm long, pinnatisect, the lobes 2–6 cm long, lanceolate to broadly elliptic, the terminal lobe the largest. *Inflorescence* a many-flowered pendent panicle 10–20 cm long, the pedicels 8–16 mm long, articulating almost at the base. *Flowers* showy, the calyx subtruncate, 2–3 mm long, tardily splitting; corolla blue, purplish, or white, 2–5 cm across, deeply lobed, the lobes lanceolate or obtuse; stamens subequal, the filaments 2 mm long, narrowing upwards, glabrous, the anthers stout, 2.5–3.5 mm long, opening by large pores which may coalesce and by longitudinal slits; ovary and style glabrous. *Berry* globose, 1–2 cm across, bright, shiny, scarlet, juicy; seeds ca. 3.5 mm across, much compressed. *Pollen*: 17.0–21.0 μ. *Chromosomes*: $n =$ 12 (Roe, 1967*b*).

This species is readily recognized by its climbing aspect, lobed leaves and large open panicles of flowers followed by red berries. The leaves somewhat resemble those of *S. jasminoides*, but in that species there are never more than one or two pairs of lobes at the base of the leaf and many of the leaves are entire. In *S. jasminoides* the corolla is lobed less than halfway down and the filaments are pubescent on the ventral surface.

Solanum seaforthianum is occasionally cultivated for ornament and is naturalized throughout the state. It is most commonly seen in citrus groves and hammocks in South and Central Florida and is rare in other districts. The species is a native of the West Indies, perhaps Cuba, and is locally naturalized in Central America.

HILLSBOROUGH: Cultivated, University of South Florida garden, from seed from Jalisco, Mexico, *Burch 5335* (USF).

24. **Solanum sisymbriifolium** Lam., Illustr. 2: 25. 1793 [1794]. TYPE: ?Argentina, *Commerson s.n.* (MPU, P-Lam).

Solanum balbisii Dun., Hist. Sol. 232, *t. 3D.* 1813. TYPE: manu Dunal (P-Bonpl.).
Solanum decurrens Balbis, Hort. Acad. Taurin. 17: 360. *t. 1.* 1810, non Vell. 1805. TYPE: "Jardin des Plantes" (MPU, P).
Solanum inflatum Hornem., Hort. Hafn. 1: 221. 1813. TYPE: *Horneman s.n.* (C).

Large, viscid-pubescent spiny *herb* to 60 cm tall; stems erect, stout, green, viscid with glandular simple hairs and bayonet hairs, and with scattered eglandular stalked multiradiate stellate hairs, copiously armed with orange, straight, acicular to stout, basally compressed spines to 15 mm long; sometimes spreading by long rhizomes; fistulose. *Leaves* to 40 cm long and 25 cm wide, smaller upwards, pinnatifid to pinnatisect, the lobes sinuate or angular with umbonate tips, above with mostly eglandular, apparently simple hairs and sessile, pauciradiate long-armed hairs, beneath with glandular hairs, the veins mostly villous and copiously armed; petioles 1–6 cm long, flattened above. *Inflorescence* a lateral unbranched raceme emergent from the foliage, the first flowers staminate or perfect, the pedicels 0.4–1.5 cm long, villous. *Flowers* showy, the calyx 5–6 mm long, armed, lobed ⅔ way down, the lobes lanceolate with conspicuous midveins; corolla white, light blue or mauve, ca. 3 cm across, lobed ⅓ way down; stamens equal, mostly separate, the filaments 1.5–2 mm long, narrowed slightly upwards, glabrate with a few glandular simple hairs, the anthers 8 mm long, somewhat attenuate with terminal pores and longitudinal slits; ovary with sparse, glandular simple hairs, the style glabrate. *Berry* bright shiny scarlet, juicy, 8 mm across, loosely enveloped until maturity by the calyx with its enlarged spines which ruptures to expose the fruit; seeds 3 mm across, compressed-lenticular. *Pollen*: 29.5–40.0 μ. *Chromosomes*: $n = 12$; $2n = 24$ (Gerasimenko & Reznikova, 1968).

With its robust habit, copious armament and dissected leaves this species is distinct from other species of *Solanum* in Florida. The accrescent calyx which loosely envelops the scarlet fruit until maturity is perhaps unique in the genus.

Solanum sisymbriifolium is uncommon in Florida, occurring along the northern reach of the state where it is to be found on railroads and along sandy, barren roadsides. The species is a native of Argentina but has long been cultivated as a curiosity in European gardens. A number of self-pollination trials suggest that this species is self-sterile.

ALACHUA: Roadside, Fairbanks, *Weber & West*, 1927 (FLAS). BAY: Roadside, Fountain, *West*, 1937 (FLAS). CITRUS: Along railroad, Inverness, *Burger*, 1927 (FLAS). DUVAL: Jacksonville, *Churchill 713* (MO). Waste places, Jacksonville, *Curtiss 2201* (MO), *5686* (FLAS, GA, GH, MO, NY, US). Near Jacksonville, *Curtiss 4401* (MO). Garbage grounds, Jacksonville, *Smith*, 1882 (GH). Chaffee Road near US 10, *Creager 684* (FLAS). ESCAMBIA: US 90 at bridge over Bayou Texar, Pensacola, *D'Arcy 2501* (FLAS, MO, USF). Pensacola, *Knight*, 1939 (FLAS). Sandy vacant lot, West Pensacola, *Godfrey 56695* (DUKE, FSU, GH). Near harbor, Pensacola, *Rolfs*, 1893 (F, FLAS). HERNANDO: Richland, *McFarlin 5956* (MICH). LEON: Near Tallahassee, Blanton, *O'Neill 6578* (MO, US). POLK: Bartow, *Buswell*, 1919 (BUS). ST. JOHNS: Sand along roadside, Matanzas Inlet, *Smith*, 1929 (NY). STA. ROSA: Beach of Pensacola Bay, *Brinker*, 1941 (MO). On berm, Fla 399 ca. ¼ mi. S of US 98 at Gulf Breeze, *D'Arcy 2507* (FLAS). In scrub at Pensacola Beach, *Godfrey 54579* (FLAS, FSU, GA). East Florida, *Palmer*, 1874 (MO). WALTON: Occasional on edge of sand pine woods, Mossy Head, *McDaniel 4853* (FSU). Railway embankment, S side of DeFuniak Springs, *D'Arcy 2563* (FLAS). WASHINGTON: Choctawatchee River W of Caryville, *Godfrey 60779* (FSU).

25. **Solanum torvum** Sw., Prodr. 47. 1788. TYPE: Jamaica, Swartz (?s, not seen).

Solanum ferrugineum Jacq., Hort. Schoenbr. 3: 46, *t. 334.* 1798. TYPE: not seen.
Solanum ficifolium Ort., Nov. Pl. Hort. Matrit. 116. 1800. TYPE: not seen.

Armed *tree* or *shrub* to 5 m tall; twigs tomentose with stalked dendritic and stellate hairs bearing short midpoints and long arms, sparingly to profusely armed with stout, flattened, straight or curved spines. *Leaves* ovate or elliptic, to 25 cm long, sinuate to pinnatifid, the sinuses mostly rounded, above scabridulous to velutinous with dispersed stellae bearing long midpoints, beneath tomentose, the veins sometimes armed. *Inflorescence* lateral, once-branched, a pair of short racemes, the peduncle and pedicels hispid with mostly glandular simple hairs, becoming woody in fruit, the pedicels 1–5 cm long, filiform, purplish; calyx 4–8 mm long, lobed halfway down, the lobes unequal, acute-acuminate with narrow tips; corolla glittering white, 15–25 mm across, lobed ⅛ way down; stamens subequal, the filaments ca. 2 mm long, glabrous, the anthers 9–12 mm long, elongate and attenuate with small pores and longitudinal slits; ovary with short, glandular simple hairs on top, the style basally pubescent. *Fruit* erect, subglobose, 10–15 mm across, glabrous, mucilaginous, yellow but seldom seen ripe. *Pollen*: 21.5–34.0 μ, irregular in size and shape. *Chromosomes*: $2n = 24$ (Roe, 1967*b*).

This species is distinct from other Florida members of the genus in its arborescent habit, stout, recurved spines, and its white flowers followed by grape-size berries.

A rare plant in the state, *Solanum torvum* has been collected only a few times in South Florida. It is a pan-tropical weed, which is plentiful in the Greater Antilles. In Central America it apparently hybridizes with several other similar species and material resembling the typical is not common. One of these, S. *ochraceo-ferrugineum* (Dun.) Fern., has appeared from time to time as a volunteer at Fairchild Tropical Garden (*Meagher 824* (FTG); *Read 1511* (FTG)). It differs in its mostly eglandular, stellate-pubescent pedicels and calyces and in other characters (see D'Arcy, 1973).

PALM BEACH COUNTY: Open area among pines collected one mile west of Rt 441 just north of Hillsborough Canal, flowers white, *Meagher 889* (MO).

26. **Solanum tridynamum** Dun. *in* Lam., Encycl. Supp. 3: 776. 1814. TYPE: Mexico, *Sesse & Mocino 1538*, *5367*, or *5367bis* (all MA).

Solanum amazonium Ker-Gawl., Bot. Reg. *t. 71.* 1815. TYPE: not seen.
Solanum obtusilobum Mart. & Gal., Bull. Acad. Bruxelles 12(1): 142. 1845. TYPE: Mexico, *Goleotti 1168* (P).
Solanum tridynamum var. *stylosum* Dun. *in* DC., Prodr. 13(1): 334. 1852. TYPE: Mexico, *Pavon s.n.* (G).
Solanum tridynamum var. *anoplocladum* Dun. *in* DC., Prodr. 13(1): 334. 1852. TYPE: cult. hort. Genèv. (G-DC).
[*Solanum polygamum* Sesse & Moc., ined. non Vahl. TYPE: Mexico, *Sesse & Mocino 1538*, or *5367bis* (MA).]

Mostly armed *subshrub* to 1 m tall; stem tomentose with stalked, pauciradiate stellate hairs and reddish-brown, acicular spines to 5 mm long. *Leaves* to 15 cm long, oblong, elliptical or lanceolate, often oblique, sinuate or sub-entire, pubescent with stalked pauciradiate stellae, more so beneath, the venation obscure above, prominent beneath. *Inflorescences* lateral, sparingly branched racemes, a few flowers opening at a time, the first few staminate; pedicels 1 cm long, articulating with a conspicuous scar at the base, often spiny, more so on perfect flowers. *Flowers* showy, the calyx ca. 12 mm long, lobed just beyond halfway down, the lobes filiform; corolla deep magenta or royal purple, 4–5 cm across, lobed about halfway down, the lobes deltoid with membranaceous margins; stamens dimorphic, the lower 2 much shorter, the filaments 1.5 mm long, stout, terete or slightly flattened, perhaps basally connate, the 3 upper anthers 12 mm long, circinate apically, the lower 2 5 mm long, connivent with the upper three, almost straight, all pores small, longitudinal slits not evident; style of perfect flowers much exceeding the anthers, apically circinate, blue or purple, that of the staminate flowers a pair of triangular flaps not exceeding the filaments. *Fruit* a brownish leather-like berry, sometimes long persistent on the plant and withering to expose the seeds, 12–15 mm across, the basal half enclosed by the accrescent calyx, the lobes of which exceed the fruit; seeds lenticular with wide margins, brownish, ca. 3 mm across. *Chromosomes*: $2n = 24$ (D'Arcy, 1969); $n = 12$ (Averett & Powell, 1972, as *S. amazonium*).

This species is distinctive in its showy purple flowers and strongly unequal anthers. The subentire or sinuate leaves distinguish it from *S. citrullifolium* which also has zygomorphic purplish flowers. The leaf of *S. tridynamum* somewhat resembles that of *S. elaeagnifolium* but lacks lepidote hairs and is much broader in outline. It is closely related to *S. vespertillio* Ait. of the Azores.

Solanum tridynamum is cultivated for ornament in South Florida, and the present stock seems to be a recent introduction. The species is a native of Mexico. It has long been known under the name *S. amazonium*.

DADE: Cultivated, Kendall, *Gillis 7014* (MO). Volunteer, Fairchild Tropical Garden, *Gillis 8530* (MO). (MISSOURI) Cultivated, Missouri Botanical Garden from seed from Miami, Florida, *D'Arcy 3901* (A, ADW, C, FLAS, MO, MPU, USF).

27. **Solanum tuberosum** L., Sp. Pl. 185. 1753. LECTOTYPE: herb. Linn. 248.12 (LINN).

Foetid, pubescent, unarmed *herb* to 1 m tall, stems weak, often villous, sometimes viscid. *Leaves* 10–13 cm long, pinnatisect with small lobes interstitial between the major lobes, the lobes elliptic to ovate, mostly pubescent. *Inflorescence* terminal, tardily lateral, an erect, sparingly branched, several-flowered panicle; pedicels 1–2 cm long, articulated part way up. *Flowers* with the calyx lobed halfway, 4–6 mm long, the lobes cuspidate; corolla white or purple, often drying yellow, the margin undulating, the lobes short; filaments broader than long, 1 mm long, the anthers stout, ca. 6 mm long with large terminal pores and longitudinal slits; ovary glabrous. *Fruit* yellow, globose or slightly apiculate, 1–3 cm across, mucilaginous or juicy.

This species is recognizable by its strong odor, weak stems, divided leaves, and by the articulation part way up the pedicels.

Cultivated as an important crop throughout the state, it is sometimes spontaneous around packing sheds and is rarely persistent in fields for a number of years. "Irish potato."

ALACHUA: Single plant in center of several-year abandoned potato field, Fla 121, ca. 2 mi. S of LaCrosse, *D'Arcy 1678* (FLAS).

28. **Solanum villosum** Mill., Gard. Dict., ed. 8. 1768. TYPE: not seen.

Solanum alatum sensu Small, Man. S.E. Fl. 1114. 1933, ?an Moench.

Erect, pubescent unarmed *herb* to 60 cm tall, branching at the base; stems villous with simple hairs. *Leaves* ovate, to 3 cm long, weakly toothed or entire, petiolate, ?viscous. *Inflorescence* a several-flowered subumbellate raceme, the peduncle villous, ca. 10 mm long, the pedicels 7–10 mm long, ?nodding; flowers white, resembling those of *S. americanum* but the calyces more pubescent. *Fruit* a red globose berry ca. 6 mm across; seeds lenticular, yellowish, ca. 2 mm long. *Chromosomes*: $2n = 48$ (Gerasimenko & Reznikova, 1968).

This species is distinct in its overall pubescence of weak, perhaps viscid hairs, and in its red fruits.

Solanum villosum is a weed of the Old World, and only one collection, has ever been encountered of this species in the Americas. It may have arrived as a waif on ships' ballast. Several specimens distributed in the past by American scientific supply companies under the name *S. nigrum* are of this species, but there is no label information indicating that they were collected in the New World.

ESCAMBIA: Waste ground, Pensacola, *Curtiss 6493* (GH, MO, UC).

29. **Solanum wendlandii** Hook. f., Bot. Mag. *t. 691.* 1887. TYPE: Cultivated. Kew Gardens, 28 July 1886 "plant received from Mr. Wendland, Botanic Gardens, Hanover" (K).

Glabrate, armed, climber or sprawling *shrub*; stems often with stout recurved spines. *Leaves* 15–18 cm long, the first leaves smaller and entire or 3-lobed, later leaves pinnatifid with broad rounded lobes, the veins mostly armed beneath, glabrous; petiole 5–8 cm long, mostly armed. *Inflorescence* a dense, pendulous panicle to 20 cm long, some flowers functionally staminate; pedicels 8–15 mm long, slender, articulating at the base. *Flowers* showy, the calyx 4–8 mm long, lobed ½ or ⅓ way down; corolla blue or mauve, the margin undulate with short, ca. 2-mm-long teeth; stamens subequal in length but one anther much longer than the others and bent to meet them at the same level, the anthers 8–10 mm long, elongate and little tapering, with both terminal pores and longitudinal slits; ovary glabrous. Not fruiting in Florida. *Pollen*: 19.0–23.5 μ. *Chromosomes*: $2n = 24$ (Roe, 1967*b*).

Solanum wendlandii is distinctive in its recurved spines on the undersides of the glabrous, mostly lobed leaves. The showy flowers and one bent anther are also good characters for recognition.

This species is occasionally cultivated for ornament in South Florida. The original source of the seed was Costa Rica, and it is not known to fruit elsewhere.

INDIAN RIVER: Cultivated, Vero Beach, *Lawson*, 1969 (MO).

30. **Solanum wrightii** Benth., Fl. Hongkong 243. 1861. TYPE: not seen.

Tree to 12 m tall, stellate pubescent, armed or not; stems sparingly hispid with long-stalked (1–2 mm) stellate hairs and often with straight tapering spines. *Leaves* to 35 cm long, broadly ovate, sinuate lobed, mostly basally oblique, above with dispersed, glandular simple or stellate hairs, beneath with sparse to dense stalked stellate hairs, often with straight yellow or green spines; petioles 5–8 cm long. *Flowers* showy, the calyx 12–15 mm long, deeply lobed, the lobes with slender, inrolled tips, hispid outside with mostly glandular simple hairs; corolla large, 5–9 cm across, opening deep purple and fading through blue to white over several days, lobed ⅓ way down, the lobes obtuse with sharp tips, the margins erose; stamens subequal, the filaments 2–3 mm long, stout, glabrous, the anthers ca. 15 mm long, initially coherent by lateral grooves, then free, with small pores and no longitudinal slits; ovary and style glabrate with a few short glandular simple hairs, in staminate flowers the style equalling the filaments. *Fruit* not seen, "almost rounded, the size of a golf ball" (Blatter & Mallard, 1954).

This species is distinctive in its large, fading flowers and large leaves. Plants are sometimes offered for sale in South Florida in cans when about 70 cm tall and in full bloom. A native of South America, S. *wrightii* is sometimes used as a street tree in India (Blatter & Mallard, 1954).

ALACHUA: Cultivated, University greenhouse, Gainesville, *D'Arcy 2701A* (MO).

31. **Lycianthes rantonnei** (Carr.) Bitt., Abhandl. Naturw. Ver. Bremen 24(2): 292–520. 1919, "Rantonnetii."

Solanum rantonnei Carr., Revue Horticole 1859: 135, *t. 32.* 1 March 1859. TYPE: not seen.
Solanum rantonnetii Carr. *ex* Lescuyer, Hort. Français, sér. 2. 1(9): 197, *t. 16.* 1859 [late 1859 or 1860], orth. mut.

Erect, unarmed *shrub* to 2 m tall; stems slender with prominent angles leading away from the nodes; twigs puberulent with mostly simple and some branched hairs, glabrescent. *Leaves* thin, apically acuminate, entire or weakly sinuate margined, sparingly pubescent, short petiolate. *Inflorescence* a terminal or axillary fascicle of 1–5 flowers; pedicels deciduous near the base, slender, 3–4 cm long; calyx 2–3 mm long, truncate with 1–5 small, sometimes umbonate apical teeth and 1–5 basal umbos or swellings alternating with the apical teeth; corolla deep blue purple with a well-defined yellow eye, 3.5–4 cm across, the limb broad and apically undulate; stamens alike, the filaments 1–3 mm long, stout, at the base sparingly dorsally pubescent, the anthers 2–4 mm long, stout with large terminal pores; style recurving over the anthers, ovary glabrous. *Fruit* (unknown in Florida) red, heart-shaped, 20–35 mm across. *Pollen*: 17.0–23.0 μ. *Chromosomes*: $2n = 24$ (Gerasimenko & Reznikova, 1968, as *Solanum rantonnetii*).

This species is distinct in its showy deep blue or purple flowers with a distinct yellow eye. The truncate calyx and basal swellings identify it as a species of *Lycianthes* rather than *Solanum*, but this feature is less apparent here than in most other species of *Lycianthes*.

Lycianthes rantonnei has long been erroneously known as *L. rantonnetii*, a change first made by Lescuyer in reviewing Carriere's original publication. Difficulties in dating the two French journals cited above were resolved by J. A. Leussink, International Association for Plant Taxonomy. As Carriere used the epithet *rantonnei* three times in his brief publication, it is clear that his formation was deliberate. W. T. Stearn, British Museum (N.H.), pointed out in conversation that formation of the Latin epithet on *Rantonneius* as chosen by Carriere rather than on *Rantonnetius* as chosen by Lescuyer preserves the French pronunciation of M. Rantonnet's name.

Lycianthes rantonnei is grown out-of-doors in the Tampa-St. Petersburg area where it is sold by nurseries in cans. Material seen had corollas 4 cm across and may represent a different introduction from that noted by Lawrence (1960): "Specimens of native material (Argentina and Paraguay) bear flowers scarcely 12 mm across, but all cultivated material otherwise identifiable with it bears flowers that are about 25 mm across and is presumed to be the selection introduced many years ago as var. *grandiflorum* and now designated as cv. 'Grandiflorum'."

BAKER: Cultivated, Glen St. Mary, *Hume*, 1923 (MO). PINELLAS: Cultivated, Clearwater, *Black 3* (FLAS).

32. **Lycopersicon esculentum** Mill., Gard. Dict., ed 8. 1768. TYPE: not seen.

Solanum lycopersicum L., Sp. Pl. 1753. TYPE: not seen.

Scandent, foetid *herb* to 60 cm tall, stems often viscid-pubescent with simple hairs. *Leaves* to 25 cm long, pinnatisect, usually with an alteration of large and small lobes, rarely simple. *Inflorescence* lateral, few flowered, racemose or subumbellate; peduncles to 7 cm long. *Flowers* mostly 6–8-merous, calyx lobed to near the base, the lobes lanceolate, accrescent and recurving in fruit; corolla greenish-yellow, 7–9 mm long, lobed to near the base, the lobes lanceolate; stamens equal, the anthers yellow, 11–14 mm long, narrowly oblong, tapering to a sharp, non-polleniferous point, coherent into a tube by intermeshed lateral and ventral hairs, opening introrsely by longitudinal slits; ovary with minute, erect simple hairs, the style basally pilose. *Fruit* a large, red, juicy berry, 2–8-loculed by proliferation of the placentae; seeds 2–3 mm across, compressed, thick margined, pilose. *Pollen*: 23.5–29.5 μ. *Chromosomes*: $2n = 24$ (many reports).

This species is recognizable by its unarmed, dissected, odorous foliage, its small yellow flowers and large, juicy fruit. It is an important crop plant in many parts of Florida. It is spontaneous throughout the state and naturalized in South Florida. Small fruited forms sometimes seen in the wild were all referable to this species. "Tomato."

The "Cherry Tomato," *Lycopersicon esculentum* var. *cerasiforme* (Dun.) Alef., is probably cultivated in the state from time to time. "It has thinner leaflets that are mostly smaller and usually less acuminate than in the typical material, the flowers are prevailing in longer clusters, and the red or yellow regular and globular fruit has fewer cells and is only about 2 cm in diameter" (Correll & Johnston, 1970).

OKALOOSA: Beside city garbage dump, Fort Walton Beach, *D'Arcy 2494* (MO).

LITERATURE CITED

AVERETT, J. E. & A. M. POWELL. 1972. Chromosome numbers in *Physalis* and *Solanum* (Solanaceae). Sida 5: 3–7.

BAYLIS, G. T. S. 1958. A cytogenetical study of the New Zealand forms of *Solanum nigrum* L., *S. nodiflorum* Jacq., and *S. gracile* Otto. Trans. Roy. Soc. New Zealand 85: 379–385.

BELL, C. R. 1965. Documented plant chromosome numbers. Sida 2: 169.

BITTER, G. 1911–23. [Series of many papers appearing in Fedde Rep. 10–19 and in Bot. Jahrb. Syst. 54–55. For a full bibliography see C. A. Weber, 1928. Ber. Deutsche Bot. Ges. 46 (Generalsvers. Heft 1): 148–156.]

BLATTER, E. & W. S. MALLARD. 1954. Some Beautiful Indian Trees. Ed. 2. Bombay Nat. Hist. Soc., Bombay.

BRITTON, N. L. 1912. Notes on species of *Solanum*. Bull. Torrey Bot. Club 39: 11.

CARPININ, J. M. ET AL. 1963. Cytogenetics of interspecific hybrid between *Solanum melongena* Linn. and S. *cumingii* Dunal. Philippine Jour. Sci. 92: 169–196.

CORRELL, D. S. & M. C. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, Texas.

D'ARCY, W. G. 1969. *In* Chromosome numbers of phanerogams 3. Ann. Missouri Bot. Gard. 54: 178–181.

———. 1970*a*. Jacquin names, some notes on their typification. Taxon 19: 554–560.

———. 1970*b* [1971]. Solanaceae studies I. Ann. Missouri Bot. Gard. 57: 258–263.

———. 1972 [1973]. Solanaceae studies II: typification of subdivisions of *Solanum*. Ann. Missouri Bot. Gard. 59: 262–278.

———. 1973 [1974]. Solanaceae *in* Woodson & Schery, Flora of Panama. Ann. Missouri Bot. Gard. 61: 123–456.

DUNAL, M. F. 1852. Solanaceae. *In* A. P. De Candolle, "Prodromus systematis naturalis regni vegetabilis." 13(1): 1–690. Paris.

EDMONDS, J. M. (née Gray). 1968. The taxonomy of the *Morella* section of the genus *Solanum* L. within South America. Ph. D. thesis, Univ. Birmingham (unpublished).

———. 1972. A synopsis of the taxonomy of *Solanum* sect. *Solanum* (*Maurella*) in South America. Kew Bull. 27: 95–114.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Stockholm.

FERNALD, M. L. 1900. Some undescribed Mexican phanerogams, chiefly Labiatae and Solanaceae. Proc. Amer. Acad. Arts 35: 570.

GENTRY, J. L., JR. & P. STANDLEY. 1974. Solanaceae. *In* "Flora of Guatemala." Fieldiana: Bot. 24 (10-nos. 1,2): 1–151.

GERASIMENKO, I. I. & S. A. REZNIKOVA. 1968. A cytological investigation of the genus *Solanum* L. Bot. Žurn. 53: 505–513.

GRANT, V. 1963. The Origin of Adaptations. Columbia University Press, New York.

HARDIN, J. W., G. DOERKSEN, D. HERNDON, M. HOBSON & F. THOMAS. 1972. Pollination ecology and floral biology of four weedy genera in southern Oklahoma. Southw. Naturalist 16: 403–412.

HEISER, C. B., JR. 1955. The *Solanum nigrum* complex in Costa Rica. Ceiba 4: 292–299.

———. 1956. *In* Documented chromosome numbers of plants. Madroño 13: 205–206.

———. 1969. Nightshades, the Paradoxical Plants. W. H. Freeman. San Francisco.

———. 1971. Notes on some species of *Solanum* (sect. *Leptostemonum*) in Latin America. Baileya 18: 59–65.

———, J. SORIA & D. BURTON. 1965. A numerical taxonomic study of Solanum species and hybrids. Amer. Naturalist 99: 471–488.

JØRGENSEN, C. A. 1928. The experimental formation of heteroploid plants in the genus *Solanum*. Jour. Genet. 19: 133–210.

KINGSBURY, J. M. 1954. Poisonous Plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, New Jersey.

KRISHNAPPA, D. G. 1968. Meiotic behavior in non-tuberiferous species of *Solanum*. Cellule 67: 163–173.

LA COUR, L. F. 1952. Chromosome counts of species and varieties of garden plants. Annual Rep. John Innes Hort. Inst. 42: 47–50.

LAWRENCE, G. H. M. 1960*a*. The cultivated species of *Solanum*. Baileya 8: 20–35.

———. 1960*b*. Additional notes on cultivated solanums. Baileya 8: 75–76.

MADHAVADIAN, P. 1968. Chromosome numbers in South Indian Solanaceae. Caryologia 21: 343–347.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. 2 vols. Oxford, London.

ROE, K. E. 1966. Juvenile forms in *Solanum mitlense* and S. *blodgettii* (Solanaceae) and their importance in taxonomy. Sida 2: 381–385.

———. 1967*a*. A revision of *Solanum* sect. *Brevantherum* (Solanaceae) in North and Central America. Brittonia 19: 353–373.

———. 1967*b*. Chromosome numbers in some Solanaceae. Sida 3: 153–155.

———. 1968. *Solanum verbascifolium* L., misidentification and misapplication. Taxon 17: 176–179.

———. 1972. A revision of *Solanum* section *Brevantherum* (Solanaceae). Brittonia 24: 239–278.

SCHULTES, R. E. 1958. A little known cultivated plant from northern South America. Bot. Mus. Leafl. 18: 229–244.

SEITHE, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. Bot. Zeit. 81: 261–335.

SMALL, J. K. 1933. Manual of the Southeastern Flora. University of North Carolina Press, Chapel Hill.

STEBBINS, G. L. & E. F. PADDOCK. 1949. The *Solanum nigrum* complex in Pacific North America. Madroño 10: 70–81.

WAGNER, W. H., JR. 1962. Irregular morphological development in hybrid ferns. Phytomorphology 12: 87–100.

WASSERMAN, R. H. 1974. Calcium absorption and calcium-binding protein synthesis: *Solanum malacoxylon* reverses strontium inhibition. Science 183: 1092–1094.

NOTE ADDED IN PROOF

After this paper was in press specimens were received of another species of *Cyphomandra*. This appears to be *C. uniloba* Rusby (Mem. Torrey Bot. Club 6: 90. 1896. Type: Bolivia, *Bang 1535* (MO)). It is a small tree with minutely pubescent, ovate leaves, the bases sometimes cordate; inflorescences at a dichotomy of the stem or obviously concaulescent above one, slender, branched, many-flowered, with a conspicuous cicatrix; flowers ca. 8 mm long, the petals thick, ovate, white, odorous. The minute but dense indumentum consists of short, several-celled, acicular hairs and short glandular hairs, the glands globose, apparently multicellular.

HILLSBOROUGH: Tub plant from nursery in Sarasota, USF Botanical Garden, Tampa, *Burch 6794* (MO). Tub plant from seed from Geo. Park Seed Co. as '*Cyphomandra fragrans*,' USF Botanical Garden, Tampa, *Burch 6795* (MO).

POLLINATION IN PIPERACEAE[1]

Kathleen Shea Semple[2]

Abstract

A study of four *Piper* species and one *Pothomorphe* species in Costa Rica showed that insects do visit some Piperaceae flowers and are probably involved in pollination. Due to the globular nature of the pollen it is not likely that wind or rain are significant pollination agents. The degree of self-pollination for the species studied has not been determined, although presumably some may occur because *Piper nigrum* has been found to be partially self-fertile.

The family Piperaceae is pantropical in distribution with *Piper nigrum* L., the source of black and white pepper, its best known representative. It has been thought that pollination in this family occurs by wind or rain because of the similarity of its minutely-flowered, spicate inflorescences to known wind-pollinated plants in the Amentiferae (Menon, 1949; Martin & Gregory, 1962). A pollination study of four *Piper* species and one *Pothomorphe* species in Costa Rica showed that insects as well as weather are involved in pollination in the Piperaceae.

The inflorescence characteristic of the Piperaceae may be described as a spike of closely packed minute flowers. Flowers of Costa Rican species are bisexual (Burger, 1971). Perianth parts are absent and a floral bract subtends each flower. The gynoecium is unilocular with one ovule and usually has a style with three to five stigmatic branches. There are four stamens, rarely two or six, attached to the base of the pistil. Anther filaments are short with bilobed anthers borne at the level of the stigmas (Burger, 1971). The fruit is drupaceous and fleshy or dry.

The flowers are protogynous, the stigmas being exserted several days before anther dehiscence. Anthesis proceeds from base to tip of a spike, taking about a week for all flowers to open (Menon, 1949). Pollen is held together in glutinous masses, parts of which are shed for up to five days after dehiscense. In *Piper nigrum* stigmas are exserted three to eight days ahead of another dehiscense, and receptivity lasts for up to ten days. According to Martin and Gregory (1962), in spite of differences in sexual expression, it is possible for the pollen of any spike to fertilize the entire spike if properly distributed.

Although Gentry (1955) reported high fruit set in a dioecious clone of black pepper with no staminate flowers visible, experimental evidence and growing experience show poor fruit set in the absence of staminate flowers (Menon, 1949; Martin & Gregory, 1962). Therefore it is assumed that for good fruit set pollination rather than apomixis occurs. In India it has been the belief that the agent of pollination in *Piper nigrum*, at least, is the monsoon rains (Menon, 1949).

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[1] Study done as a student in the Organization for Tropical Studies class, "Tropical Biology, an Ecological Approach," during the summer of 1971. I gratefully acknowledge the identification of the plant by Dr. William Burger, Field Museum of Natural History, and the identification of the bees by Dr. Alvaro Willie, University of Costa Rica. I thank Drs. John Vandermeer, Charles Schnell, Duncan Porter, and John Semple for their help and encouragement.

[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Ann. Missouri Bot. Gard. 61: 868–871. 1974.

Others have suggested that Piperaceae are wind-pollinated (Martin & Gregory, 1962), having small pollen, a feathery style, and many small flowers in spikate inflorescences. Martin and Gregory's paper (1962) is the only known previously published report of insects on Piperaceae inflorescences. In a study of *Piper nigrum* in Puerto Rico, spring tails (order Collembola) were commonly seen. Because of erratic fruit set they did not appear to be important in pollination and were more noted for disturbance and damage to the flowers and fruits. The conclusion is that the cultivated pepper is mostly self-pollinated with rain possibly increasing the efficiency of pollination. Previous unpublished Organization for Tropical Studies class reports have recorded bee and fly insect visitors on Piperaceae flowers (Hines, 1967; Weaver, 1968).

Materials and Methods

Five sites, including four species of *Piper* and one *Pothomorphe*, were selected for the pollination study at the Tropical Science Center Field Station, Rincón de Osa, Costa Rica: three sites on the edges of primary forest and two sites in secondary growth areas. The Piperaceae species observed were *Piper aduncum* L., *P. auritum* H.B.K., *P. friedrichsthalii* C. DC. *in* DC., *P. villiramulum* C.DC., and *Pothomorphe peltata* (L.) Miq. From 5–10 August 1971, each site was visited for a thirty-minute interval during the period of insect activity, from 6:00 to 9:30 a.m. Each site was visited at each time interval, allowing fifteen minutes to travel between sites. At each site twenty spikes were observed, the number for each species depending on its prevalence. The different pollinators were noted and the number of visits of each insect species was recorded during the half-hour interval.

Pollen was examined by scraping pollen off the bees' pollen baskets into a glassine envelope. In the lab pollen was transferred to a slide, stained with fuchsin glycerine jelly (Beattie, 1971), and examined under a microscope.

Results

Observations showed that insects do visit inflorescences of the Piperaceae species studied. Several species of *Trigona* bees were the most common visitors, and several small Coleoptera were next most numerous (Table 1). The most common *Trigonas* were *Trigona dorsalis* Smith, *T. latitarsis* Friese, and *T. perangulata* Cockerell. Also observed were *T. mexicana subobscuripennis* Schwarz, *T. nigerrima* Cresson, and halictid bees of the genera *Augochloropsis* and *Lasioglossum.* It appears that the *Trigona* bees do promote pollination, because they collect large amounts of pollen in their pollen baskets by working up and down the spikes collecting pollen, and they fly from spike to spike. Wind-pollination is unlikely because of the glutinous nature of the pollen. Pollen was present on the spikes for at least five days through numerous rain storms, indicating that it is not easily washed or blown away.

Trigonas did not differentiate among the Piperaceae species except that more than twice as many bees of each species visited *Piper auritum.* Perhaps *P. auritum* is preferred because it has longer spikes, from 12 to 30 cm long, and thus more pollen than the other species. Also it may be recognized by a distinctive "licorice-like" odor when the leaves are crushed.

Pollination activity appeared to be largely determined by weather conditions. The peak of activity, between 8:00 and 10:00 a.m., coincided with the period of greatest sunlight. Fewer bees were seen under cloudy conditions, and none were seen during rainfall, which usually started around noon. The first

TABLE 1. Periods of pollinator activity in Piperaceae during five days at Rincón de Osa, Costa Rica.

	Time of observation (a.m.)				
	6:00–6:30	6:45–7:15	7:30–8:00	8:15–8:45	9:00–9:30
Hymenoptera			Number of Visits		
Trigona dorsalis *T. latitarsis* *T. perangulata*	—	—	14	51	74
T. mexicana	—	—	12	2	17
T. nigerrima	—	—	6	9	15
Augochloropsis *Lasioglossum*	—	—	2	—	—
COLEOPTERA	2	9	17	40	15

bees appeared around 7:30 a.m. when most of the dew had evaporated. Up to six bees were observed on a spike at a time, moving up, down, and around the spike without seeming to follow any pattern. During activity peaks it was difficult to follow a single bee. However, bees were seen going from one *Piper* species to another, indicating no strong species constancy on single foraging trips.

The most common Coleoptera seen, but not identified, first became numerous at 6:45 a.m. and appeared throughout the observation period. These beetles seem to eat pollen and probably cause some pollination, although pollen does not stick well to their rather smooth bodies. The few halictid bees observed were not significant pollination vectors, but are of interest because they represent a potential source of pollinators.

Pollen samples from *Trigona* bees were examined with the aim of determining if the bees visit flowers other than those of the Piperaceae. The pollen consisted mainly of Piperaceae pollen, however scattered grains of non-Piperaceae pollen were also observed.

DISCUSSION AND CONCLUSIONS

The Piperales are one of the most primitive dicot groups, derived from and closely related to the Magnoliales (Takhtajan, 1969). In spite of the outward similarity of the *Piper* inflorescence to the wind-pollinated Amentiferae, the Amentiferae are thought to have evolved from quite different evolutionary lines. Because the Magnoliales are insect-pollinated, it does not seem unusual that a closely related group would also have insect pollinators.

The Piperaceae studied occur in a variety of secondary and edge communities subject to harsh environmental extremes. As colonizing species they have evolved a generalized reproductive strategy conducive to survival in uncertain environments. The strategy involves producing more flowers and fruits, with less energy needed for formation of each individual flower; hence, the loss of the perianth. The fruits are small and easily dispersed by wind or by falling to the ground.

Bats may also be important in dispersal, as indicated by studies showing that bats eat *Piper* fruit (Fleming, 1972). Because the flowers are not specialized, the agent of pollination does not visit the flower in a precise way, and there may be several types of pollinators, *i.e.* various species of small Hymenoptera, small Coleoptera, and probably Diptera. If pollinators are not available, there is evidence (Martin & Gregory, 1962) that self-fertilization may occur. In *Piper nigrum* self-fertilization yields good fruit and presumably self-fertilization may occur in other *Pipers* as well.

The protogyny of Piperaceae flowers encourages outcrossing, although the timing is not sufficiently different to prevent pollination of flowers on the same spike by each other (Martin & Gregory, 1962). If apomixis occurs, it is quite rare. In an embryological study by Kanta (1961) the ovules in 50 per cent of the ovaries of *Piper nigrum* collapsed due to lack of pollination, and only 10 per cent of all ovules developed healthy embryos, indicating high sterility. More research needs to be done to determine if this sterility is due to environmental or genetic factors and to determine if it occurs in other *Piper* species.

It is not known if self-pollination or outcrossing predominates in the family. P. A. Opler (personal communication) has suggested that *Trigonas* are especially adapted for the pollination of some self-compatible plant species. *Trigonas* may aid in distributing pollen within a single spike and occasionally in distributing pollen between plants. Studies have shown (Allard, 1965) that this combination of self-fertilization and occasional outcrossing is highly successful and characteristic of a large number of colonizing species. The genetic system allows for perpetuation of superior genotypes and the introduction of a low level of genetic variability important to long term survival.

LITERATURE CITED

ALLARD, R. W. 1965. Genetic systems associated with colonizing ability in predominantly self-pollinated species. *In* H. G. Baker & G. L. Stebbins (editors), "The Genetics of Colonizing Species." Academic Press, New York.

BEATTIE, A. J. 1971. A technique for the study of insect-borne pollen. Pan-Pacific Entomol. 47: 82.

BURGER, W. 1971. Piperaceae. Fieldiana Bot. 35: 5–227.

FLEMING, T. 1972. Ecology of bat-plant interactions in Costa Rica. Missouri Botanical Garden Systematics Symposium, October 20–21, 1972.

GENTRY, H. S. 1955. Apomixis in black pepper and jojoba. Jour. Hered. 46: 8.

HINES, D. M. 1967. Pollination biology in three species of *Piper*. Organization for Tropical Studies tropical biology class report.

KANTA, K. 1961. Embryolessness in *Piper nigrum* L. Phytomorphology 11: 304–306.

MARTIN, F. W. & L. E. GREGORY. 1962. Mode of pollination and factors affecting fruit set in *Piper nigrum* L. in Puerto Rico. Crop Sci. 2: 295–299.

MENON, K. K. 1949. The survey of pollu and root diseases of pepper. Ind. Jour. Agric. Sci. 19: 89–136.

TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Smithsonian Institution Press, Washington.

WEAVER, R. E. 1968. Studies in the pollination of Piperaceae. Organization for Tropical Studies botany course report.

STUDIES IN BIGNONIACEAE 12: NEW OR NOTEWORTHY SPECIES OF SOUTH AMERICAN BIGNONIACEAE[1]

Alwyn H. Gentry[2]

Abstract

Four new species of Bignoniaceae—*Distictella pauciflora* A. Gentry, *Jacaranda irwinii* A. Gentry, *Memora paucifoliolata* A. Gentry, and *M. croatii* A. Gentry—and the fruits of *Roentgenia bracteomana* (K. Schum. *ex* Sprague) Urb., *Cuspidaria weberbaueri* (Sprague) A. Gentry, and *Tynnanthus weberbaueri* Sprague are described. Confusion of the winged fruits of some species of *Tynnanthus* with *Cuspidaria* is noted, and *Cuspidaria ovalis Rusby* and *Cuspidaria schumanniana* O. Kuntze are transferred to *Tynnanthus*. *Jacaranda praetermissa* Sandw., *Jacaranda robertii* S. Moore, *Tabebuia eximia* (Miq.) Sandw., *Tabebuia elliptica* (DC.) Sandw., and *Tabebuia bureauvii* Sandw. are reinterpreted.

Several new species and a number of other important collections of South American Bignoniaceae have been discovered during routine curatorial work in the herbarium of the Missouri Botanical Garden and in consignments of specimens sent for identification by the New York Botanical Garden and the Instituto Botanico de Venezuela. Consultation of relevant material in most of the major European herbaria has also made possible a reinterpretation of several species of *Tabebuia*.

DISTICTELLA PAUCIFLORA A. Gentry, sp. nov.

Frutex scandens. Ramuli teretes, minute puberuli, sine consociebus glandularum in nodis inter petiolos. *Pseudostipulae* deficientes. *Folia* bifoliolata, interdum cirrho, foliolis anguste ellipticis vel lanceolato-ellipticis, acuminatis, confertim lepidotis. *Inflorescentio* pauciflora. *Calyx* campanulatus, truncatus, lepidotus, margine ciliato, consociebus glandularum linearibus. *Corolla* superne pallide lavandula, infra alba, tubulo-campanulata, dense puberula in tubo extus atque in lobis. *Stamina* thecis divaricatis, 4 mm longis. *Pistillum* stylo confertim strigoso-puberulo basi, ovario oblongo, dense strigoso. Capsula ignota.

Vine, the branchlets terete, minutely puberulous, the nodes without glandular fields; pseudostipules lacking. *Leaves* 2-foliolate, sometimes with a tendril; leaflets narrowly elliptic to lanceolate-elliptic, long acuminate, cuneate, 5.5–13 cm long and 1.5–4.2 cm wide, subcoriaceous to coriaceous, secondary veins 4–7 on a side, densely glandular-lepidote below, less so above, otherwise glabrous or with a few inconspicuous trichomes at extreme base of midvein above, the midvein and secondary veins slightly impressed above and raised below, drying brownish olive; tendril tip broken on type specimen; petiolules 0.3–0.7 cm long, petiole 1–2 cm long, lepidote and somewhat minutely puberulous like the petiolules. *Inflorescence* of type with one terminal flower and one flower in the axil of the uppermost leaf, ebracteate, the pedicels lepidote and papillose-puberulous, 1.8–2.3 cm long. *Calyx* campanulate, truncate, 8–9 mm long and 7–8 mm wide, lepidote and

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inconspicuously scurfy-puberulent, the margin somewhat ciliate, with several paired linear glandular fields descending from rim. *Corolla* pale lavender above, white below, tubular-campanulate, 5–6 cm long and 1.3–1.8 cm wide at mouth of tube, the tube 3.5–4.5 cm long, the lobes 1.3–2 cm long; densely puberulous without and on lobes within, the tube within mostly glabrous or very sparsely glandular-lepidote toward mouth and base, densely glandular-pubescent with 1–3-celled trichomes at level of stamen insertion. *Stamens* didynamous, the anther thecae divaricate, each 4 mm long, the longer filaments 1.9–2.1 cm long, shorter filaments 1.7–1.9 cm long, the staminode (broken) at least 2 mm long, insertion 7–10 mm from base of corolla tube. *Pistil* 3.6–3.7 cm long, the stigma lobes 2.5 by 1.5 mm, the style densely strigose puberulous at base, becoming sparsely puberulous 1.5 cm from base and glabrous in upper third, the ovary oblong, 4 mm long and 1.5 mm wide, densely strigose; disk in two distinct parts, the upper part truncate-conical, 1 mm long and 1 mm wide at top, 1.5 mm wide at base, the lower part annular-pulvinate, 1 mm long and 3 mm wide. *Capsule* unknown.

Holotype: VENEZUELA. BOLÍVAR: Region de Canaima, entre el hotel y el Salto Hacha, 6° 15′ N lat., 62° 47′ W long., alt. 400 m; vining low, corolla pale lavender above, white below; calyx pale green; leaves coriaceous, deep green above, dull green below, 18 Jul. 1972, *Steyermark 106343* (MO).

This species differs dramatically from all known species of the genus in its greatly reduced inflorescence. In its very narrow leaflets, it is equalled only by *D. angustifolia* (Schum. *ex* Spr.) Urb. from which it differs vegetatively (ex descri.) in its long-acuminate leaflets (obtusely acuminate in *D. angustifolia*), shorter petioles (1–2 cm; 2–3 cm in *D. angustifolia*) and petiolules (0.3–0.7 cm; 1–2 cm in *D. angustifolia*), and fewer secondary veins (4–7 on a side; 10–12 on a side in *D. angustifolia*). Its described flower color (pale lavender above) is also unique in this white-flowered genus. (*Distictis rosea* Kränzl., of which I have seen no specimen, has lavender flowers but is certainly not a *Distictella*; this is hardly surprising since Kränzlin's generic placement of his (supposedly) new species of Bignoniaceae seems almost random.)

Both in its reduced inflorescence and lavender flower color, *D. pauciflora* approaches *Distictis*, which differs from *Distictella* in characters of the fruit and in having a straight (not bent) corolla tube, angulate stems with detachable ribs, and the usual presence of pseudostipules. Nevertheless, *D. pauciflora* provides a link between these two genera. Should its fruit also prove to resemble that of *Distictis*, support would be given to a possible reunion of these two genera.

CUSPIDARIA WEBERBAUERI (Sprague) A. Gentry, Brittonia 25: 233. 1973.

This rarely-collected species was transferred from *Arrabidaea*, first to *Saldanhaea* by Sandwith (Kew Bull. 1968: 408. 1968) and then with that whole genus to *Cuspidaria* by Gentry (Brittonia 25: 231–233. 1973), on the basis of floral characters. Its fruit has remained unknown. As circumscribed by Sandwith (Kew Bull. 1953: 462. 1954: 22: 408. 1968) it contains two elements, a Peruvian and Colombian form with tannish leaf tomentum and a form with canescent leaves having prominulous veinlets (vegetatively much like *Arrabidaea candicans* (L.

Rich.) DC.) which occurs in Amazonian Brazil and Venezuela. A fruiting collection which appears referable to the canescent-leaved form of *C. weberbaueri* is included in the recent Brazilian collections of Ghillean Prance and associates. This specimen, *Prance et al. 13974* (MO), is from the vicinity of the Lábrea airport, forest on terra firme, Rio Purus, Rio Ituxi, State of Amazonas, Brazil. It is described as a liana with simple tendrils, 8 cm maximum diameter, fruit green, glaucous. The fruit is linear, terete, 29 cm long and 1.3 cm wide, puberulous, drying grayish, with scattered small lenticel-like glands. Each valve has a conspicuous median longitudinal furrow 2–3 mm wide and bordered by a slightly raised line on either side. The seeds are thin, flattened, bialate, 8–9 mm long and 3.7–4.6 cm wide, with the hyaline membranaceous wings sharply demarcated from the seed body.

The leaves of *Prance et al. 13974* are larger and more coriaceous and the branchlets more conspicuously lenticellate than in other collections of *C. weberbaueri* I have seen. However, similar changes often occur in fruiting specimens of Bignoniaceae, and I am fairly confident that the *Prance et al.* collection can be identified with the canescent form of *C. weberbaueri.* I suspect that this canescent-leaved plant may itself prove distinct from the tannish-pubescent Peruvian plant despite their strong floral similarities, but description of a new species seems premature until a more adequate series of herbarium specimens is available for analysis.

The fruit of the *Prance et al.* collection is of interest in being rather intermediate between those of the species formerly assigned to *Saldanhaea* and those of *Cuspidaria* sensu stricto. Though having the median furrow of *Saldanhaea* it is shorter than the fruit of *C.* (*Saldanhaea*) *lateriflora* (Mart.) DC. or *C.* (*Saldanhaea*) *floribunda* (DC.) A. Gentry and no longer than that of some species of *Cuspidaria* with winged fruits. This fruit further supports the merger of *Saldanhaea* with *Cuspidaria.*

TYNNANTHUS SCHUMANNIANUS (O. Kuntze) A. Gentry, comb. nov.

Cuspidaria schumanniana O. Kuntze, Rev. Gen. Pl. 3: 243. 1893.
C. ovalis Rusby, Descr. 300 New Sp. S. Amer. Pl. 120. 1920.

It has recently been discovered (Gentry, Brittonia 25: 231–233. 1973) that the winged fruit which had been considered the chief generic criterion of *Cuspidaria* is insufficient for generic definition. An additional example of the pitfalls of taxonomic over-reliance on this character is now at hand. *Cuspidaria ovalis*, a Bolivian species described from fruiting material in the absence of flowers, was placed in *Cuspidaria* because of its winged fruit-margins. It has seemed rather strange that the several collections of this species were all in fruit, a reversal of the usual predominance of flowering material in collections of Bignoniaceae. A re-examination of *Cuspidaria ovalis* shows that it vegetatively matches previously unidentified flowering specimens of *Tynnanthus* from the same region. Its transfer to *Tynnanthus* is thus necessary.

Coincidentally, yet another species of *Cuspidaria* was described from the same area of Bolivia, also from a fruiting collection. *Cuspidaria schumanniana* was described by Kuntze in 1893 but has been subsequently ignored. Although I have seen no specimen of *C. schumanniana*, its trifid tendril clearly identifies it with *Tynnanthus* rather than *Cuspidaria*, and its description matches *Cuspidaria ovalis*. Kuntze's name is older than Rusby's so the new combination in *Tynnanthus* is *Tynnanthus schumannianus*.

The description of this species can now be completed as follows: *Inflorescence* an axillary panicle, its branches puberulous with simple trichomes. *Calyx* cupular, truncate or minutely and evenly 5-denticulate, puberulous at least on denticulations and at base. *Corolla* pale yellow (after *Prance et al. 12484*), bilabiate, 5–6 mm long, split more than half its length, the 2 upper lobes almost fused, the 3 lower ones 1–2 mm long; puberulous without and on lower 3 lobes within, subpuberulous on anterior side of tube and at base of stamens. *Stamens* didynamous, the anther thecae ca. 1 mm long, divaricate, twisted near base and reflexed forward, insertion near base of corolla tube, staminode with a few short trichomes above base. *Pistil* 4–5 mm long, the style puberulous, the ovary conical, 1 mm long, 0.5 mm wide, densely puberulous; disc lacking.

Collections examined: BRAZIL. ACRE: Cruzeiro do Sul, Rio Jurua & Rio Moa, vicinity of Serra da Moa village, varzea forest; liana, calyx green, corolla pale yellow, flowers fragrant, young fruit green, 26 Apr. 1971, *Prance et al. 12484* (MO). Near mouth of Rio Macauhan (tributary of Rio Yaco), lat. 9 20′ S, long. 69 W, on Terra firma; vine (fruit), 11 Aug. 1933, *Krukoff 5454* (MO). AMAZONAS: Rio Purus, Rio Ituxi, vicinity of Lábrea, forest on terra firme; liana with trifid tendrils, fruit green, 4 Jul. 1971, *Prance et al. 13954* (MO). BOLIVIA. LA PAZ: Province of Larecaja, Copacabana, about 10 km S of Mapiri, alt. 850–950 m; vine (flowers), 8 Oct.–15 Nov. 1939, *Krukoff 11245* (MO). Mapiri, (fruit), Jul.–Aug. 1892, *Bang 1485* (GH, K, MO, NY, US; type of *C. ovalis*). Province of S. Yungas, basin of Rio Bopi, San Bartolome (near Calisaya), alt. 750–900 m; vine (fruit), 1–22 Jul. 1939, *Krukoff 10399* (MO).

The species appears restricted to northern Bolivia and adjacent Brazil.

Tynnanthus schumannianus keys out with *T. myrianthus* in the *Flora Brasiliensis* (Bureau & K. Schumann, Fl. Bras. 8(2). 1896) treatment because of its puberulous inflorescence, subtruncate or minutely 5-denticulate calyx, and 6-mm-long corolla. Its narrower elliptic or ovate-elliptic leaflets and almost complete vegetative glabrescence readily separate it from *T. myrianthus*. *Tynnanthus goudotianus* (Bur.) Bur. of Colombia, known only from the type collection, is very closely related to *T. schumannianus* but differs in an obliquely truncate calyx with a single posterior denticulation. Its fruit is unknown. *Tynnanthus weberbaueri* (see below) also has glabrous leaves but these are larger and dry yellowish beneath with contrasting reddish black main veins. The corolla of *T. schumannianus* (subpuberulous anteriorly) is intermediate between *T. goudotianus* and *T. weberbaueri*. *Tynnanthus guatemalensis* of northern Central America is likewise very close to *T. schumannianus*. It seems to differ constantly in a less strongly pubescent inflorescence, simple rather than trifid tendrils, thinner less intricately reticulate leaves with the midvein often somewhat puberulous, and the usual presence of a V-shaped interpetiolar ridge. Significantly, its winged fruit is just that of *T. schumannianus*. None of the characters separating *T. schumannianus*, *T. goudotianus*, and *T. guatemalensis* appear especially convincing, and they may eventually prove no more than geographical variants of a single wide-ranging species. However, in view of their large range disjunctions correlated with constant morphological differences, it seems best to consider them distinct, at least for the present.

TYNNANTHUS PANURENSIS (Bur.) Sandw., Kew Bull. 1953: 465. 1954.

Tynnanthus panurensis has been represented in herbaria only by Spruce's type collection from Santarem, Brazil. I would also refer *Klug 1942* (MO) from lowland Amazonian Peru (Dept. Loreto: Florída, Río Putumayo at mouth of Río Zubineta, alt. 200 m; forest) to this species. The *Klug* collection is described as a vine with the corolla cream-lilac. It differs from the type in having some simple trichomes on the inflorescence and in the slightly puberulous calyx which has a somewhat ciliate margin. The leaflets of the *Klug* specimen are also less asymmetric than in Spruce's plant although similar in membranaceous texture, main veins drying conspicuously darker beneath, and glabrous condition. The long, dark-drying petiole (8.5 cm) and terminal petiolule (4.5 cm) of the single intact leaf of the *Klug* collection also agree well with *T. panurensis* (described as petiole 10 cm long, terminal petiolule 3.5–4.5 cm long).

TYNNANTHUS WEBERBAUERI Sprague, Bot. Jahrb. (Syst.) 42: 176. 1909.

Tynnanthus weberbaueri was described from an altitude of 1000 m in the Department of Junín, Amazonian Peru. It is known only from the *Weberbauer* type collection. Its flowers are much smaller than those of *T. panurensis*, but vegetatively the two species are quite similar, especially in relatively large glabrous leaves which dry light (usually yellowish) below with contrasting darker main veins. *Tynnanthus weberbaueri* differs vegetatively from *T. panurensis* principally in subcoriaceous leaves and shorter petioles (3–4 cm long) and terminal petiolules (2–2.7 cm long). The first fruiting collection of this alliance is now at hand and must of course be identified on the basis of vegetative characters. This collection is *Forero, Coelho & Farias 6336* (MO) from the vicinity of Campinas at km 242–246 on the highway from Abuña to Rio Branco, State of Acre, Brazil. It is described as a vine with the fruit green. Its leaves are subcoriaceous with petioles 4–4.5 cm long and terminal petiolules 2.7–3 cm long. The *Forero et al.* collection thus appears to belong to *T. weberbaueri* rather than the lowland *T. panurensis*. The fruit of *T. weberbaueri* proves to be of the *Cuspidaria* type. It is a linear oblong, conspicuously 4-winged capsule, obtuse at both ends, 15–22 cm long, ca. 1.2 cm wide and 7–8 mm thick without the wings, to 2.3 cm wide with the 4–5-mm-wide wings flattened, drying brown to blackish, glabrous, the midrib not evident; seeds thin, flat, bialate, 0.6–0.8 cm long and 2.5–3.2 cm wide, the hyaline-membranaceous wings sharply demarcated from the seed body.

With the admission of the *Forero et al.* collection into *Tynnanthus weberbaueri* the range of that species overlaps with that of *T. schumannianus*. It might then be possible that Kuntze's *Cuspidaria schumanniana* (see above), described as a glabrous-leaved plant with winged capsules, should be referred to *Tynnanthus weberbaueri*. However, the 8-cm-long and 1–1.5-cm-wide capsule of

Kuntze's plant is clearly closer to *Cuspidaria ovalis* than to the larger capsule of *T. weberbaueri.*

MEMORA CROATII A. Gentry, sp. nov.

Frutex scandens. *Ramuli* teretiusculi, plerumque glabri, sine consociebus glandularum in nodis inter petioles. *Pseudostipulae* parvae, obovatae. *Folia* bipinnata vel tripinnata, vulgo cirrho simplici inter duas pinnas principales, foliolis anguste ellipticis vel late lanceolatis, plerumque glabris, puberulis supra in costa. *Inflorescentia* axillaris paniculata, ramulis lateralibus racemosis, bracteis minutis, bracteolis obovatis caducis. *Calyx* cupulatus, 5-denticulatus, vulgo aliquantum fissus, puberulus margine. *Corolla* flava, tubulo-campanulata, extus glabra, intus plerumque glabra. *Stamina* thecis divaricatis, 2.5 mm longis. *Pistillum* ovario lineari, glabro. *Discus* pulvinatus. *Capsula* linearis, valde compressa, glabra.

Liana, the branchlets subterete, mostly glabrous, often puberulous at nodes, drying brownish; without interpetiolar glandular fields, a straight ridge connecting opposite petioles; pseudostipules small (to 9 mm by 3 mm), obovate, narrowed at base, drying blackish, conspicuously glandular. *Leaves* bipinnate or tripinnate, usually with a simple tendril between two primary pinnae, sometimes ecirrhose with a third (terminal) primary pinna, this variously divided, each lateral primary pinna usually 5–9-foliolate with the lowermost pair of leaflets itself usually trifoliolate, the terminal pinna, if present, usually terminating in a second pair of 5–9-foliolate pinnae; leaflets narrowly elliptic to widely lanceolate, acute to acuminate, the base cuneate, 2–8(–10) cm long and 0.7–3(–3.5) cm wide, chartaceous, the main veins (especially midvein) somewhat raised below, midvein slightly raised above, mostly glabrous underneath, sometimes subpuberulous at extreme base of midvein, above puberulous on midvein, otherwise glabrous; drying olive to olive-brown; petiolules 0–5 mm long, rachises of primary pinnae 3–15 cm long, grooved on upper side, petioles 1–2.5 cm long, puberulous in grooves, especially along margins. *Inflorescence* an axillary panicle with 2–4 paired lateral branches, each branch racemose, inconspicuously lepidote, slightly puberulous at nodes, each pair of pedicels subtended by a pair of acute, narrowly triangular, caducous bracts, these ca. 1.5 mm long, pedicels 7–10 mm long with a pair of glandular obovate caducous bracteoles near middle of pedicel below each bud, these 3–4 by 2–3 mm. *Calyx* cupular, basically truncate, conspicuously 5-denticulate, usually one-sidedly split one-third the way to base, 8–9 mm long and 4–6 mm wide, the apiculations to almost 1 mm long, mostly glabrous, puberulous on margin, especially the teeth, eglandular or inconspicuously glandular, drying greenish. *Corolla* yellow, tubular campanulate, 4–5 cm long and 0.8–1.2 cm wide at mouth of tube, glabrous outside, mostly glabrous inside, slightly puberulous at level of stamen insertion and very slightly glandular-lepidote at base of lobes. *Stamens* didynamous, the anther thecae divaricate, 2.5 mm long, the longer filaments 2.3–2.5 cm long, shorter filaments 1.7–1.9 cm long, the staminode ca. 3 mm long, insertion 11–12 mm from base of corolla tube. *Pistil* 3.3–3.4 cm long; ovary linear, 3–4 mm long and 1 mm wide, glabrous; disc pulvinate, 1–1.5 mm long, 2.5 mm wide. *Capsule* linear, strongly and uniformly compressed, 35–39 cm long and 1.0–1.8 cm wide, the margin undulate, contracted between seeds, glabrous, slightly glandular lepidote, drying blackish, the midrib not evident; seeds not seen.

Holotype: PERU. LORETO: 7 km. NE of Río Nanay and Puerto Almendra; liana, flowers yellow, fruit green, immature, 23 Jul. 1972, *Croat 18335* (MO; isotypes F, K, NY, PMA, VEN, USM).

Known from lowland Amazonian Peru and adjacent Brazil.

Additional collections examined: PERU. LORETO: Prov. Maynas, la carretera a Zúngaro Cocha, cerca del Lago, al S.O. de Iquitos, alt. 125 m; trepadora flores amarillas, con los ápices del tubo naranja, 3 Nov. 1964, *Dodson 2899* (MO). BRAZIL. ACRE: Cruzeiro do Sul, Rio Jurua and Rio Moa, Estrada Alemanha, forest margins; liana, flowers yellow, 27 May 1971, *Maas et al. P13312* (MO).

Two collections from the Rio Curuquete (a tributary of the upper Rio Purus), State of Amazonas, Brazil (*Prance et al. 14349*, *14308*, both MO) are closely allied to this species. They differ chiefly in larger leaflets (9–17 cm by 3–8.8 cm) and in having the calyx conspicuously glandular below the apex and usually truncate without a split on one side. Additional collections are needed to determine whether these collections represent a distinct taxon.

Memora is taxonomically a very difficult genus. This new species is allied to *M. patula* Miers on the basis of its inflorescence but differs in its narrower, basically truncate, evenly denticulate, green-drying calyx, smaller bracts, and much narrower, undulate-margined fruit. In Sampaio's key, *M. croatii* is related to the very different *M. flavida* (DC.) Bur. & K. Schum. if its calyx is considered truncate and to *M. rondoni* A. Samp. (which from the description is probably actually closer to the very distinct *M. schomburgkii* (DC.) Miers), if the calyx is considered one-sidedly split.

MEMORA PAUCIFOLIOLATA A. Gentry, sp. nov.

Fruticulus. *Ramuli* teretiusculi, pilosi, sine consociebus glandularum in nodis inter petioles. *Pseudostipulae* foliaceae. *Folia* trifoliolata vel paripinnatim 4-foliolata, foliolis ovatis, apicibus obtusis, basaliter rotundatis, subcoriaceis, bullatis, pilosis. *Inflorescentia* racemosa, bracteata, rachi pedicellisque pilosis, floribus per bracteolas ellipticas subtentis. *Calyx* subspathaceus, intus lepidotus extus pilosus. *Corolla* flava, tubulo-infundibuliformis, extus glabra, intus plerumque glabra. *Stamina* thecis divaricatis, 3–4 mm longis. *Pistillum* ovario oblongo, glabro. *Discus* pulvinatus. *Capsula* lineari-oblonga, aliquantum lignosa, glabra, seminibus tenuibus, alis plerumque bruneolis.

Subshrub 2 m tall, branchlets terete, pilose, without interpetiolar glandular fields; pseudostipules foliaceous, suborbicular, to 1.2 cm long and 1 cm wide, resembling the leaflets. *Leaves* trifoliolate or paripinnately 4-foliolate (rarely 2-foliolate), without tendrils; leaflets ovate to rhombic-elliptic, obtuse, the base rounded but sometimes abruptly and shortly attenuate at extreme base, 3.5–8 cm long and 1.4–4.3 cm wide, subcoriaceous, rather bullate with the main veins conspicuously raised beneath, pilose throughout with simple trichomes, these especially conspicuous on margin and main veins, drying grayish olive; petiolules lacking or to 3 mm long (to 9 mm in terminal leaflet of 3-foliolate leaves), petiole 0.5–1.0 cm long, rachis of 4-foliolate leaves ca. 2 cm long, conspicuously pubescent. *Inflorescence* a bracteate terminal raceme (described as paniculate by the collectors), the flowers paired, adjacent pairs separated by 2–3 cm, each pair of flowers subtended by 2 narrowly elliptic, shortly apiculate, pubescent, caducous bracts, these to 12 mm long and 4 mm wide, rachis and pedicels pilose, each pedicel 8–10 mm long, with a pair of elliptic bracts subtending the flower in its upper third, these ca. 1 cm long and 0.5 cm wide, pubescent. *Calyx* subspathaceously split about half its length, the apex irregularly several-lobed, each lobe apiculate, 15–22 mm long and 7–9 mm wide, pilose-puberulous especially in lower third and on lobes, glandular-lepidote inside, usually with plate-shaped glands outside. *Corolla* yellow, tubular-infundibuliform, 5–6 cm long and 1.3–1.8 cm wide at mouth of tube, glabrous outside, inside mostly glabrous, pubescent below level of stamen insertion. *Stamens* didynamous, the anther thecae divaricate, 3–4 mm long; insertion ca. 10 mm from base of corolla tube. *Pistil* ca. 3.5 cm long, the ovary oblong, somewhat compressed, with 2 longitudinal grooves on each side, 2.5 mm long and 1 mm wide, 0.5 mm thick, glabrous; disc ca. 1 mm long and 4 mm wide. *Capsule* linear oblong, widest in middle third, tapering toward each end, 28–29 cm long and 2.4 cm wide at middle, ca. 5 mm thick, the valves uniformly and evenly flattened but rather woody, midrib not visible, glabrous, drying brownish-black; seeds thin, asymmetrically bialate, 1.3–1.4 cm long and 7.5–8 cm wide, the wings mostly brown, becoming gradually hyaline at extreme tips, not demarcated from seed body.

Holotype: BRAZIL. GOIÁS: Cerrado, ca. 10 km W of Cristalina, elev. 1200 m; subshrub ca. 2 m tall, the paniculate inflorescence ca. 1.5 m high; corolla yellow; fruit green, 4 Mar. 1966, *Irwin, Grear, Souza & Reis dos Santos 13438* (UB; isotypes MO, NY, to be distributed).

This species is known only from the type collection.

Vegetatively *M. paucifoliolata* is similar to its sympatric congener *M. axillaris* Bur. & K. Schum. Both are subshrubs of the cerrado and have pubescent, simply pinnate leaves, foliaceous pseudostipules, similar inflorescences, and calyces glandular-lepidote inside. *Memora paucifoliolata* differs most strikingly from *M. axillaris* in its conspicuous bracts and bracteoles. In *M. axillaris* bracts and bracteoles are absent or reduced to scales ca. 1 mm long. Furthermore the scale-like bracteoles of *M. axillaris* are very near the base of the pedicel rather than in its upper third. Calyces, pedicels, and inflorescence rachis of *M. axillaris* are all glabrous rather than pilose and the calyx is eglandular. The fruit of *M. axillaris* has much thinner valves than that of *M. paucifoliolata* and has a noticeably raised midline and an undulate margin; its seeds have much shorter more symmetrical wings. Vegetatively its rather bullate leaves with (always?) fewer leaflets seem a consistent character for separating *M. paucifoliolata* from *M. axillaris*. Two other species have the calyx conspicuously glandular-lepidote inside (the Axillares group of Sampaio (Anais Reunião Sul-Amer. Bot. 3: 149–170. 1938)). Of these *M. tridenticalyx* Samp. (from the description) differs in climbing habit, few-flowered racemes, minute bracts and bracteoles, different calyx apex, and glabrous leaves. *Memora peregrina* (Miers) Sandw. (including *M. cuspidata* Hassl.) is usually also a shrub but has much more highly divided almost glabrous leaves and reduced bracts and bracteoles.

Generic subdivision of *Memora* is quite artificial and depends upon the size of inflorescence bracteoles. In section *Pharseophora* the bracteoles reach the middle of the calyx or beyond it; in section *Eumemora* the bracteoles are lacking or fail to reach the middle of the calyx. Some bracteoles of *M. paucifoliolata* reach the middle of the calyx and others do not so its sectional placement is moot. However, its closest relationship is with *M. axillaris* and the rest of the Axillares group all of which belong in section *Eumemora*.

The epithet *paucifoliolata* denotes at the same time the species of *Memora* with the fewest leaflets per leaf and the convergence of that species with *Jacaranda paucifoliolata*, another simply pinnate subshrubby campos representative of a genus more noted for woody-trunked species with highly divided leaves.

ROENTGENIA BRACTEOMANA (K. Schum. *ex* Sprague) Urb., Ber. Deutsch. Bot. Ges. 34: 747. 1916.

To my knowledge the fruit of *Roentgenia bracteomana* (K. Schum. *ex* Sprague) Urb., the type species of the genus, has not been described. A fruiting collection (*Seibert 2146*, MO), from Madre de Dios, Peru, apparently is referable to this species, the fruit of which can thus be described as elongate-linear, compressed, ca. 44 cm long and 2.0–2.2 cm wide, the valves flat, subwoody, the midrib not noticeable, the margins slightly and gradually raised, uniformly brown, glabrous, appearing varnished under dissecting microscope, with scattered raised lenticellate spots. The very thin seeds are smooth, glabrous, uniformly brown, 1.4–1.7 cm long and 4.5–5 cm wide, with a small very indistinctly demarcated body and a linear hilum 1.7–2 cm long and 1–2 mm from the margin. The fruit of *R. bracteomana* is very like that of *Cydista aequinoctialis* (L.) Miers, raising further doubts (see Macbride, Publ. Field Mus. Bot. 13(95): 62. 1961) as to the validity of the separation of *Roentgenia* from *Cydista*. It is noteworthy that one of the two major characters supposedly separating *Roentgenia* from *Cydista*, that of trifid versus simple tendrils, breaks down in *Seibert 2146*. Of the three tendrils present on the collection, one is simple, one bifid at the extreme tip, and one trifid at the extreme tip—the latter two so minutely split that the division is hardly evident without a lens. The second major difference between *Roentgenia* and *Cydista* is in the pollen, that of the former being 12-colpate and that of the latter acolpate. Should such other characters of *Roentgenia* as the pattern of anomalous vascularization in its stem and the appearance of its fresh corollas prove as similar to *Cydista* as does its fruit, the two genera could be profitably reunited despite the difference in their pollen. Without such additional evidence from field study, however, union of the two genera seems premature.

JACARANDA IRWINII A. Gentry, sp. nov.

Frutex. Ramuli subpuberuli, subtetragoni. *Folia* imparipinnata, rhachidi puberula, exalata, foliolis 5–15, ellipticis, obtusis, subcoriaceis, punctatis, puberulis. *Inforescentia* floribus in panicula dichotome ramosa dispositis, ramulis bracteis foliaceis subtentis. *Calyx* campanulatus, 5-lobatus, lobis suborbicularibus, puberulus. *Corolla* lavandula, anguste tubulato-campanulata, extus peuberula, intus glabra pro parte maxima. *Stamina* quatuor, thecis duabus in quoque stamine. *Staminodium* 3.1–3.2 cm longum, ad apicems fissum, pubescens ad medium trichomatibus glandulosis. *Pistillum* ca. 3.5 cm longum, ovaria ovoideo glabro. *Fructus* ignotus.

Shrub to 3 m tall, with slender arching stems; twigs subpuberulous to glabrate, subtetragonal, drying brown. *Leaves* imparipinnately compound, the rachis 5–

20 cm long, puberulous, unwinged, grooved above, the leaflets 5–15, 1.0–1.3 cm apart, elliptic, obtuse, the base rounded, sessile or with petiolule to 4 mm long, subcoriaceous, 1–7 cm long, 0.5–3.4 cm wide, the secondary veins 3–7 on a side, inconspicuous above, prominulous below, the margins entire, revolute, glandular punctate above and below, puberulous above and below, glabrescent above, drying olive above and below, the main veins below yellowish or orangish. *Inflorescence* a narrow sparingly branched panicle, its dichotomously branched subdivisions subtended by elliptic or obovate-elliptic foliaceous bracts, these to 3.5 by 1.8 cm, puberulous and glandular punctate like the leaflets. *Calyx* campanulate, with 5 suborbicular lobes 2–3 mm in diameter, 6–7 mm long (with lobes) and 6–7 mm wide, puberulous and minutely lepidote, the lobes glandular. *Corolla* lavender-purple, narrowly tubular-campanulate, 5–6 cm long, 1.0–1.9 cm wide at mouth of tube, the tube 4.2–4.7 cm long, the lobes 6–9 mm long; puberulous with simple trichomes without, the lobes within very sparsely glandular lepidote and puberulous to almost glabrous, the tube glabrous within except for glandular trichomes at level of stamen insertion. *Stamens* didynamous, the anthers 2-thecate, the thecae divaricate, 2 mm long, the longer filaments ca. 1.8 cm long, the shorter filaments ca. 1.6 cm long, the staminode 3.1–3.2 cm long, bifid at tip, densely glandular pubescent near middle, the upper third glandular lepidote, also with a few gland-tipped trichomes near apex; insertion 12–13 mm from base of tube. *Pistil* 3.5 cm long; ovary ovoid, 1 mm long and 1 mm wide, glabrous; disk 1.5 mm long, 2 mm wide, pulvinate cupular, distinctly larger than the ovary. *Fruit* unknown.

Holotype: BRAZIL. BAHIA: Serra do Tombador; shrub to ca. 3 m tall, with slender arching stems, corolla lavender-purple; thin sandy soil on sandstone near margin of riacho, ca. 18 km E of Morro do Chapeu, elev. ca. 1100 m, 16 Feb. 1971, *Irwin, Harley, & Smith 32250*, (UB; isotypes MO, NY).

Jacaranda irwinii is especially remarkable in its once-compound leaves, foliaceous inflorescence bracts, and well-developed, almost suborbicular, calyx lobes. Its unique calyx serves to distinguish it at once from all other species of the genus. Although a few other species of *Jacaranda* (*e.g. J. praetermissa* Sandw. and *J. bracteata* Bur. & K. Schum.) also have foliaceous bracts, those of *J. irwinii* are of a different form. Only three other species, *J. racemosa* Cham, *J. egleri* Sandw., and *J. paucifoliolata* Mart. *ex* DC., have once-compound leaves. The former two are very different in habit and have narrower leaflets and linear bracts. *Jacaranda paucifoliolata* is evidently the closest relative of *J. irwinii* and likewise has foliaceous inflorescence bracts, but its leaves differ in fewer (usually 5–7), sessile, more or less obovate leaflets with the margins not at all revolute. The inflorescence bracts of *J. paucifoliolata* differ in being pointed and its calyx has acute, triangular lobes.

JACARANDA PRAETERMISSA Sandw., Kew Bull. 1954: 599. 1955.

This species has been previously known only from a few collections in Southern Piauí and a single collection from the Serra da Tabatinga in extreme northern Bahia. Several recent collections by New York Botanical Garden personnel from the Espigão Mestre west of Barreiras in western Bahia significantly extend the known range of this species. These collections are:

BRAZIL. BAHIA: Sandy cerrado, upper slopes of Espigão Mestre ca. 32 km W of Barreiras, elev. ca. 600 m, tree ca. 3 m by 5 cm, corolla violet, fruit green, mostly defoliated, 5 Mar. 1971, *Irwin, Harley & Smith 31539* (NY); serra 34 km W of Barreiras, elev. ca. 710 m, cerrado or cerradão, the soil clay or somewhat sandy, tree 3.5 m tall, 2 Mar. 1972, *Anderson, Stieber, Kirkbride 36433* (MO, NY); sandy campo with scattered trees and shrubs, ca. 100 km WSW of Barreiras, elev. ca. 760 m, small tree 3 m tall, fruit green, 6 Mar. 1972, *Anderson, Stieber, & Kirkbride 36677* (MO, NY).

In addition to the difference in collecting locality, these collections differ from typical *J. praetermissa* in having notably larger (to 12 mm long and 4 mm wide) almost foliaceous calyx lobes and larger (4–5 cm long and 3.5–4 cm wide) fruits with the apex rounded or minutely and bluntly apiculate rather than emarginate. Despite these differences it seems advisable to retain the Espigão Mestre collections in *J. praetermissa* pending further study.

Another collection from Bahia, *Luetzelburg 151* (M), is also referable here. However, its fruit is strongly emarginate, indeed almost heart-shaped, as described for *J. praetermissa*. It is also reminiscent in shape of the much larger fruit of *J. chapadensis* Barb. Rodr., known only from a leafless fruiting collection from Mato Grosso. If capsule size and the shape of its apex prove as variable within other species of this alliance as I am inferring for *J. praetermissa*, then it may be possible to reduce *J. chapadensis* to *J. brasiliana* (Lam.) Pers. and a re-evaluation of the differences (summarized by Sandwith in Kew Bull. 1953: 52–53. 1954) between *J. acutifolia* H.&B. and the widely cultivated *J. mimosifolia* D. Don might also be in order.

JACARANDA ROBERTII S. Moore, Jour. Bot. 45: 405. 1907.

This extremely interesting species is known only from the type collection (*A. Robert 675* from Sant' Anna da Chapada, Mato Grosso, Brazil) and has not been commented upon since its description. Moore's description was somewhat misleading. He described the leaflet as decurrent at the base and noted neither the irregularly serrulate margin and cordulate base of the leaflet nor the conspicuously winged rachis of leaf and pinnae which are among the most striking features of the plant.

Moore compared his species with *Jacaranda decurrens* Cham., emphasizing the decurrent leaflets of both plants. However, the leaflets of *J. robertii*, though sessile, are discrete and not at all continuous with the winged rachis of the pinna while in *J. decurrens* the leaflets and rachis wing are continuous. Although having only a single fertile anther theca per stamen and thus clearly belonging with *J. decurrens* in section *Monolobos*, *J. robertii* is vegetatively very different from all members of that alliance. On the other hand it is superficially very like *J. rufa* Manso of section *Dilobos*. Indeed, the present author would have assigned without further consideration the undesignated and misidentified (as *J. cuspidifolia*) MO isotype to that species had the single calyx of the mounted material not appeared much too short for *J. rufa*. Although further examination revealed that this calyx was merely broken and, except for its lesser pubescence could after all have belonged to *J. rufa*, dissection of a flower revealed that the stamens were monothecate! A careful comparison of the two species then revealed that the leaflets of *J. rufa* are distinguishable as being elliptic or rhombic-elliptic, widest at the middle and tapered to an acute (rarely subcordulate) base while those of *J. robertii* are ovate, widest below the middle, with a distinctly cordulate base. The leaflets of *J. rufa* are also generally more conspicuously serrate and more pubescent, and its corolla is quite different (tube glabrous within, not narrower above base, mostly glandular lepidote without). Nevertheless the resemblance of the two species remains striking, especially in light of the vegetative divergence of *J. robertii* from other species of section *Monolobos*. For the present it must be regarded as an interesting example of convergence with *J. rufa*, although it is remotely possible that hybridization between *J. rufa* (also collected by Roberts at Sant' Anna da Chapada) and a species (but which?) of section *Monolobos* could have given rise to this plant.

A second collection which is possibly related to this species is *Irwin et al. 25307* which is described as a simple and few-branched shrub ca. 1 m tall. This collection, from the Serra do Facao, State of Goiás, is in fruit only so that its placement is difficult to assess. Nevertheless, its winged rachises and numerous rather large leaflets are reminiscent of *J. robertii*. Its leaflets differ, however, in being coriaceous or subcoriaceous and entire with slightly revolute margins and rounded rather than cordulate bases.

It is to be hoped that other specimens of this taxon will come to light. I would anticipate that careful examinations of the sheets of *J. rufa* in major herbaria might reveal such additional specimens.

TABEBUIA EXIMIA (Miq.) Sandw., Lloydia 2: 213. 1939.

Tecoma eximia Miq., Linnaea 22: 803. 1849.

Tabebuia eximia has apparently not been interpreted since its inclusion (as *Tecoma eximia*) in the *Flora Brasiliensis* (Bureau & Schumann, 1896–97). Sandwith made the new combination in *Tabebuia* without comment in 1939. Miquel, in describing the species, related it to *T. serratifolia* (Vahl) Nichols. and *T. heptaphylla* (Vell.) Toledo (both of which he considered to be species of *Tecoma*). Bureau and Schumann, on the other hand, remarked a similarity between *T. eximia* and *T. atrovirens* (now regarded as a synonym of *Tabebuia elliptica* (DC.) Sandw.). The type collection of *T. eximia*, *Blanchet 3963* from Bahia, Brazil, is represented by duplicates at many of the major European herbaria, although I have seen no other collections of the species. (Bureau & Schumann list *Luschnath 26* as a second collection, but that gathering was probably destroyed at Berlin.) Examination of the holotype at Utrecht and the isotypes at Brussels, Copenhagen, Kew, and Paris reveals that in each case a detached branch with leaves is mounted alongside a leafless flowering branch. Considered as separate elements, the material with leaves is readily identifiable with *Tabebuia impetiginosa* (Mart. *ex* DC.) Standl. (*sensu lato* to include *T. heptaphylla* sensu Martius & DC., see Gentry, Ann. Missouri Bot. Gard. 62, in prep.), while that with flowers appears to match *T. umbellata* (Sond.) Sandw., a situation strongly suggestive of a mixed collection. Examination of yet another isotype, at Geneva, clinches the argument, since this sheet contains, in addition to the detached branchlet with mature leaves, a few young leaves attached to the flowering branchlet. The attached leaves are quite strongly stellate-pubescent and match young leaves of such collections of *T. umbellata* as *Hatschbach 6407* (K) but are completely different from the nearly glabrate leaves of *T. impetiginosa* making up the second element of the collection.

I propose to select the flowering branchlets and young leaves of *Blanchet 3963* as the type element for *Tecoma eximia* under Article 9 of the *Code of Nomenclature.* This makes *T. eximia* synonymous with *T. umbellata* (Sond.) Sandw. Through an amazing coincidence, however, both *Tecoma eximia* and *Tecoma umbellata* were published in the same volume of *Linnaea*, apparently on the same day. It is therefore necessary to choose one of these names for the plant in question. The choice, under Recommendation 7B, of the well known epithet *T. umbellata* rather than the relatively unknown and confusing *T. eximia* is obvious. The alternate procedure of outright rejection of *T. eximia* under Article 70 gives the same result more directly. However that alternative leaves open the possibility of later selection of a type element from the *Blanchet* collection with resultant additional confusion if *T. umbellata* were then to be rejected in favor of *T. eximia* as would still be theoretically possible.

TABEBUIA ELLIPTICA (DC.) Sandw., Candollea 7: 253. 1937.

Bignonia elliptica Cham., Linnaea 7: 686. 1832, non Thunb.
Tecoma elliptica DC., Prodr. 9: 220. 1845.
Tecoma atrovirens DC., Prodr. 9: 220. 1845.
Sparattosperma psammophilum Mart. *ex* DC., Prodr. 9: 203. 1845.
S. ellipticum (DC.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 362. 1897
Tabebuia atrovirens (DC.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 176. 1936.

This species was a source of confusion to Sandwith who first (Kew Bull. 1954: 598. 1955) suggested that *T. insignis* (Miq.) Sandw. might have to be reduced to *T. elliptica* and later (notes in K) noted the same possibility for *T. roseo-alba* (Ridley) Sandw. *Tabebuia elliptica* is indeed intermediate between *T. insignis* and *T. roseo-alba*, resembling the former in its 5-foliolate leaves and inflorescence and the latter in its calyx which is bearded on the upper margin. My first inclination was that *T. elliptica*—known only from the type (*Sellow s.n.* (K)) collected in Espírito Santo, Brazil, the type of *T. atrovirens* (*Blanchet s.n.* (G-DC)) collected in Bahia, Brazil, and the type of *Sparattosperma psammophilum* (*Wied.-Neuwied s.n.* (BR)) collected in Espírito Santo—might be a hybrid between *T. insignis* and *T. roseo-alba.* However two recent collections, sharing exactly the same combination of characters, indicate that it must be recognized as a good species. The additional collections I have examined are *Belém & Magalhães 799* (NY) from the mata litorânea, Rodovia Camacan-Canavieira, Bahia, described as a tree 10 m tall and 40 cm in diameter, the flowers white with yellow centers, and *Belém & Mendes 246* (NY) from restinga, Lagoa Abaeté, Salvador, Bahia, described as having white flowers. Gomes (Rev. Brasil. Biol. 11: 49–52. 1951) reported examining the pollen of yet another collection of this species which he designated only as "Herb. Mus. Nac. Rio de Jan. No. 21843." *Tabebuia elliptica* is evidently restricted to the narrow band of lowland forest along the eastern coast of Brazil.

TABEBUIA BUREAUVII Sandw., Kew Bull. 13: 442. 1959.

Tecoma dentata Bur. & Schum. *in* Mart., Fl. Bras. 8(2): 323. 1897.

Sandwith failed to note its resemblance to *T. umbellata* (Sond.) Sandw. when he transferred *Tecoma dentata* to *Tabebuia* as *Tabebuia bureauvii*. Since *Tabebuia dentata* Miers (Proc. Roy. Hort. Soc. 3: 199. 1863.) pre-empted the epithet *dentata* in *Tabebuia*, Sandwith's nomen novum was necessary in that genus. However, the chief difference between *T. bureauvii* and the closely related *T. umbellata*, which also occurs near Rio de Janairo, appears to be in the conspicuously serrate leafliets of the former. *Tabebuia bureauvii* has been regarded as endemic to Corcovado Mountain and is known from only three collections, two of them consecutive numbers (*12080* (K) and *12081* (C, P)) of Glaziou. *Tabebuia umbellata* is widespread in the eastern lowlands of Brazil. However, I have seen a specimen of *T. umbellata* (*Dusén 18146* (K)) from Paraná, Brazil, which has basally entire leaflets which are dentate at the tips. I strongly suspect, therefore, that the serrate leaflets of *T. bureauvii* should not be regarded as a valid specific character. Although I am unprepared to evaluate the significance of the exceptionally long ovary accorded to this plant by Bureau and Schumann, it seems likely that *T. bureauvii* will prove to be no more than a variety of *T. umbellata*.

A NEW SPECIES OF *MYRCIA* (MYRTACEAE) FOR PANAMA

Thomas B. Croat[1]

Abstract

Myrcia fosteri (Myrtaceae) is described as new. The species is closest to *M. fallax* (Rich.) DC. but differs in having smaller flowers, more prominently acuminate leaf blades and fruits which are globose to depressed-globose.

For a number of years a population of *Myrcia* (Myrtaceae) on Barro Colorado Island was observed by both myself and by Robin Foster, then a resident of the island. Plants collected over a period of several years were tentatively identified as *Myrcia gatunensis* Standley following Amshoff's treatment in the *Flora of Panama* (1958: 172–175). The species is closely related to and perhaps inseparable from *M. fallax* (Rich.) DC. After several years of field observations as well as herbarium and library studies, it is concluded that this *Myrcia* is a new species.

Myrcia fosteri, sp. nov.

Arbor parva 3–8 m; laminae lanceolatae ad ellipticae, abrupte caudatae-acuminatae, acutatae ad basim, 3–8 cm longae, 1–3(–3.5) cm latae; inflorescentiae racemos vel paniculas axillares 1–2.5 cm longos formantes; alabastra 1.5–2 mm longa; bacca globosa vel depressa-globosa, circa 5 mm longa, 6–8 mm diametro.

M. fallax (Rich.) DC. maxime simile sed ab hac specie differt floribus parvioribus, laminis plus abrupte acuminatis, et bassis globosis ad depressis-globosis.

Slender *tree* 3–8 m tall; trunk to ca. 7 cm dbh. *Leaves* opposite; petiole 2–6 mm long, sparsely to densely ± appressed-pubescent with short brownish trichomes; blade lanceolate to elliptic, abruptly caudate-acuminate, acute (rarely obtuse) at base, 3–8(–10) cm long, 1–3(–3.5) cm wide, lower surface inconspicuously pubescent throughout, the trichomes denser on midrib above and below, glabrescent above except midrib, pellucid-punctate, thin, the secondary veins not prominulous below on drying, the acumen often as much as ¼ the length of the blade, the margin entire and ± revolute especially near base. *Flowers* 5-parted, in axillary racemes or panicles 1–2.5 cm long; pedicels 1–1.5 mm long; buds 1.5–2 mm long; calyx to ca. 2.5 cm wide, the lobes short-triangular to rounded; axes of inflorescence, pedicels and hypanthium densely, erect to more commonly appressed-pubescent; petals orbicular, ca. 1.7 mm long, pellucid-punctate, white, soon falling; stamens numerous, to 3.5 mm long; ovary and lower half of style short-villous; ovary and style together to 5.5 mm long. Berry globose to depressed-globose, 6–8 in diameter, to ca. 5 mm long, turning blue-gray, finally blue-black at maturity; seed 1, ± globose, ca. 4 mm in diameter, smooth; seed coat thin, brown.

Holotype: *Croat 15147* (MO, 2059366); isotypes CAS, COL, DUKE, F, GH, K, MICH, NY, P, PMA, RSA, US, VEN.

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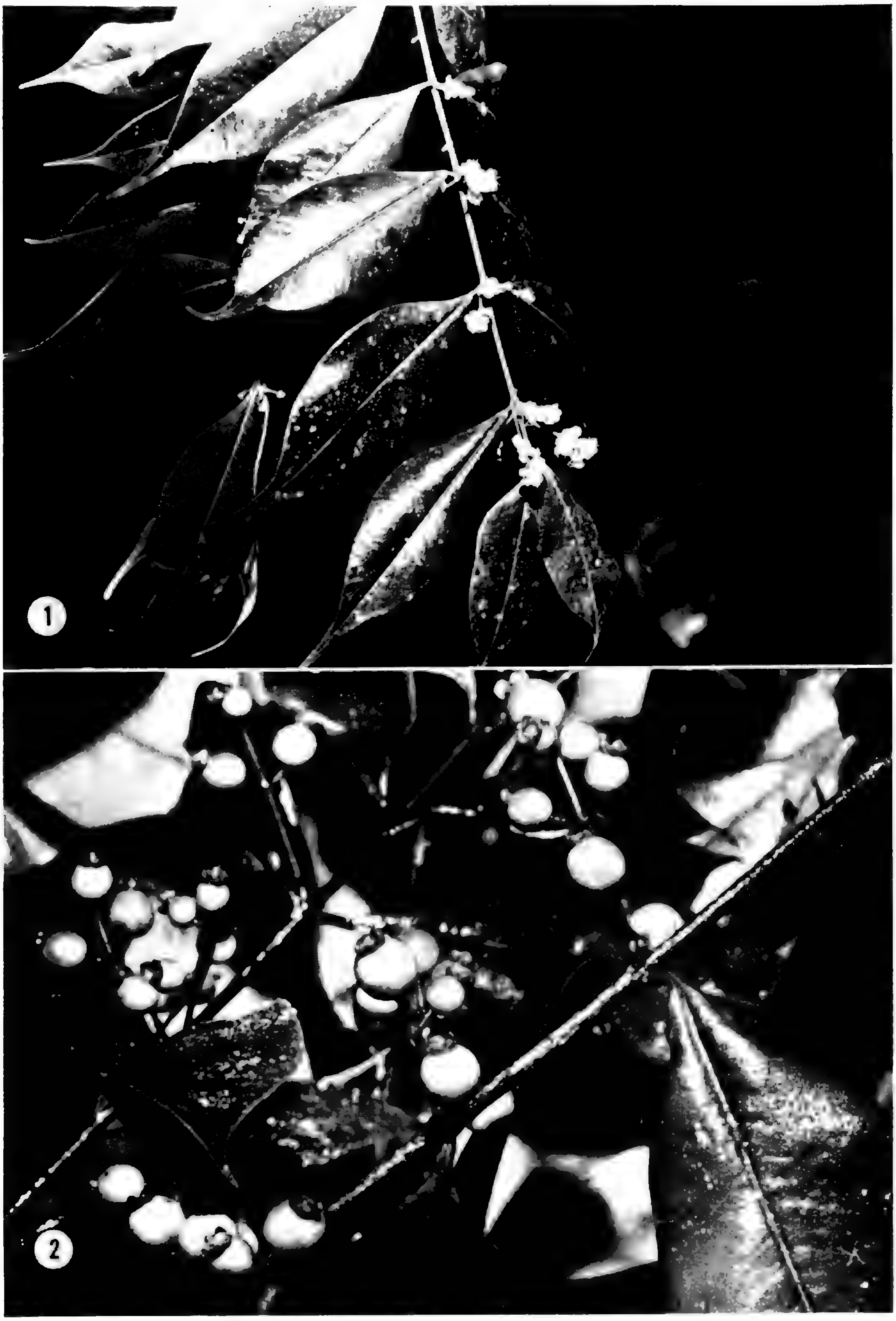
Ann. Missouri Bot. Gard. 61: 886–888. 1974.



FIGURES 1–2. *Myrcia fosteri* Croat.—1. Habit and flowers at anthesis, × .53—2. Full-sized but unripened fruit, × 1.36.

Flowers in late June and in July. Fruits mature in September and October. Known only from Panama in tropical moist forest on Barro Colorado Island and in the Province of Darién.

Myrcia fosteri Croat is most closely related to *M. fallax* (Rich.) DC. but differs from that species in having smaller flowers. Flowers buds are 1.5–2 cm long on *M. fosteri* and usually to 3 mm long on *M. fallax.* The leaf blades of *M. fosteri* are more abruptly acuminate than on *M. fallax* with the acumen as much as one-fourth the length of the blade (Fig. 1). *Myrcia fosteri* is also similar to *M. splendens* (Sw.) DC. It differs from both *M. splendens* and *M. fallax* in having a globose to depressed-globose fruit (Fig. 2), whereas both of the latter species have fruits which are ellipsoid-oblong at maturity.

The species is named for plant ecologist Robin Foster, an ardent student of the Barro Colorado Island Flora.

PANAMA. CANAL ZONE: Barro Colorado Island, *Dwyer 1415* (MO); Barbour Trail 2100, *Foster 1040* (DUKE, MO); Miller Trail 100–200, *Croat 14987, 15147, 17046* (all MO), *Foster 2371* (DUKE, MO), *Knight s.n.*, June 24, 1967 (MO); Wheeler Trail 600–700, *Croat 9228, 14861, 15244* (all MO), *Foster 1062* (DUKE, MO), *Starry 108* (MO). DARIÉN: Periaque camp, *Tyson, Dwyer, Blum & Duke 4756* (MO); Río Paca, *Stern, Chambers, Dwyer & Ebinger 719* (MO).

LITERATURE CITED

AMSHOFF, G. J. H. Myrtaceae. *In* R. E. Woodson, Jr. & R. W. Schery, "Flora of Panama." Ann. Missouri Bot. Gard. 45: 165–201. 1958.

NOTES

A NEW PANAMANIAN SPECIES OF *LOBELIA* (SECTION *TYLOMIUM*)[1]

Since most of the readily available specimens of Panamanian Campanulaceae had already been assembled and studied for the treatment of that family in the *Flora of Panama*, I was puzzled by Dr. Robert L. Dressler's inquiry as to the identity of a green-flowered lobeliad recently collected on the Atlantic Coast of Panama. Nothing like it was known from the area, and the promised arrival of Dressler's specimens was eagerly awaited. Before they came, an unidentified specimen of Dr. Thomas Croat was received from the Missouri Botanical Garden. Croat's collection came from the same general area and was clearly unlike any other Central American lobeliad. Its closest relative appears to be *Lobelia cirisifolia* Lam. of the Lesser Antilles. Dressler's fine specimens arrived some weeks later and together with Croat's form the basis of the following description.

Lobelia dressleri sp. nov.

Herba erecta, ca. 1 m alta. Caulis tenuiter puberulus demum glabrescens. Petioli glabri, 1–2 cm longi. Lamina foliorum elliptica, ca. 15–30 cm longa et 3–7.5 cm lata, glabra, serrulata. Flores 2.8–3.2 cm longi, 40–70 in racemi cylindrici terminali, 6–8 dm longi; bracteae ellipticae glabrae, ca. 2–10 cm longae. Pedicelli 1.2–3 cm longi, pubescentes patentes. Bracteolati supramedii glabri, lineari vel lanceolati serrulati, 6–10 mm longi et 1–2 mm lati. Hypanthium semiglobosum, glabrum vel pubescentum, 6–9 mm altum et 10–15 mm latum. Lobi calicis anguste triangulares, erecti, glabri, serrulati 5–8 mm alti et basi 2–4 mm lati. Corolla viridis glabra; tubus curvatus in dorso usque ad basim fissus et fenestratus. Filamenta ± connata et glabra. Tubus antherarum 4–6 mm longus, glaber; apices anterarum 5 penicellati. Capsula 8–12 mm alta et 10–15 mm lata.

Reportedly a suffruticose *herb* to 1 m tall with the stem basally to 5 cm in diameter, apparently unbranched or nearly so and inconspicuously spreading short-pubescent. Petioles glabrous 1–2 cm long. *Leaves* cauline, apparently numerous and rather evenly spaced along the stem, spreading-ascendent, thin papery to semichartaceous when dry, inconspicuously serrulate with appressed, incurved teeth, medially 1–3 per cm; blades elliptic, slightly broadest above the middle, acutely tapering both apically and basally, about 15–30 cm long and 3–7.5 cm wide, about 4–6-times as long as wide, glabrous on both the upper and lower surface. *Inflorescence* 6–8 dm long, about 40–70-flowered, narrowly cylindrical. Bracts elliptic, tapering to either end and somewhat broader above the middle, inconspicuously serrulate, glabrous, the upper about 2 cm long and 6–8 mm wide and the lowermost to 10 cm long and 3–4 cm wide. Pedicels stiff, straight, strongly divaricate except distally where upturned at anthesis and somewhat incurved in fruit, 1.2–2.8 cm long in flower and 2–3 cm long in fruit, about 1–1.5 mm in diameter, densely spreading short-pubescent and bearing a pair of linear to lanceolate, serrulate, glabrous bracteoles about three-fourths or more the distance from the base of the pedicel to the hypanthium, 6–10 mm

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long and 1–2 mm wide. *Flowers* 2.8–3.2 cm long including the hypanthium. Hypanthium at anthesis broadly hemispherical, glabrous or basally spreading short-pubescent, symmetrical or nearly so, 6–9 mm high and 10–15 mm in diameter and with a free calycine rim about 2 mm high. Calyx-lobes at anthesis triangular or deltoid, glabrous, inconspicuously serrulate, 5–8 mm long and 2–4 mm wide at base. Corolla light green, glabrous; the tube distally strongly curved ventrally, dorsally slit at first to within about 6–8 mm and eventually to within 1 mm of the base and with 2 conspicuous lateral fenestrae about 4–6 mm high; corolla-lobes all strongly arching ventrally, the 2 upper linear or linear-lanceolate, 10–15 mm long and about 2 mm wide, acute and the 3 lower lobes 8–12 mm long and 2 mm wide. Filament-tube glabrous, 15–20 mm long, connate except for basal 4–5 mm. Anther-tube 4–6 mm long, glabrous except for the dense tuft of white trichomes about 1 mm long at apex of each anther. *Capsule* somewhat depressed hemispheric, 8–12 mm high and 10–15 mm in diameter, about two-fifths superior terminating in the tapering 2–4 mm long conical base of the style. Seeds compressed, broadly oblong, about 0.8 mm long and 0.6 mm broad, shallowly pitted.

TYPE: Panama: Provincia de Colón, near Coclé del Norte; near beach. 18 August 1972. *Dressler 4206* (DUKE, holotype; PMA, isotype).

Other specimens examined: Panama: Provincia de Colón: Miguel de la Borda along beach. 24 April 1970. *Croat 10016* (DUKE, MO).

This species is named in honor of one of its collectors, Dr. Robert L. Dressler of the Smithsonian Tropical Research Institute. He has served as an apparently willing and certainly most amiable guide to countless visiting biologists who have depended upon him for an introduction to the biotic diversity of Panama. Dr. Dressler has not collected great numbers of specimens during his years of Panamanian residence, but what he collects has been done with a very discriminating eye and with great care. The type collection was unusually carefully prepared which is something of a rarity in this day when the average specimen made by a systematic botanist ought to shame even a molecular biologist.

This most distinctive species was found, like so many new Panamanian species, in an area within fifty miles of the Panama Canal Zone. It again emphasizes the need for extensive and intensive general collecting from throughout the neotropics, for contrary to the opinion held by many biologists, our herbaria and museums are not overflowing with countless overlooked specimens of these same undescribed species. Panama has doubtless had more than its share of biological exploration, but even so vast areas have never been adequately collected and much of it has not even been collected at all.

This species belongs to section *Tylomium* (Presl) Benth. & Hook. This species group is characterized by shallowly pitted seeds, non-bluish flowers (either red, purplish, white, or green), non-basal, conspicuously bracteolate pedicels and a stoutly herbaceous or subshrubby habit. The approximately twenty species of this section range about the Caribbean from the Greater Antilles south through the Lesser Antilles and perhaps onto Trinidad. On the mainland its species have been previously known only from northern Central America (Guatemala, Honduras, and probably Nicaragua).—*Robert L. Wilbur, Department of Botany, Duke University, Durham, North Carolina 27706.*

NOTES ON PANAMANIAN APOCYNACEAE

Since the publication of the account of the Apocynaceae for the *Flora of Panama* (Ann. Missouri Bot. Gard. 57: 59–130. 1970), a number of noteworthy additional collections have become available. These include several species new to Panama, two representing genera previously unreported outside Amazonia and another a genus new to North America, the first fruiting collection of several species, new species of *Prestonia, Mandevilla, Stenosolen,* and *Malouetia,* and some significant range extensions within Panama. All specimens referred to are at MO unless otherwise noted.

1. *Aspidosperma darienense* Woods. *ex* Dwyer, Ann. Missouri Bot. Gard. 53: 105. 1966. This species has been previously known only from the holotype collection, *Sexton & Knight s.n.*, from Darién Province between Río Chucunaque and Río Canglón. A second collection of *Aspidosperma* from the same general area matches the type. This collection, *Duke 8589,* from Darién Province along the Río Chucunaque between Río Membrillo and Río Subcuti, is in fruit, making possible the description of the fruit of *A. darienense.* The fruit is a woody follicle, in the form of an asymmetrically truncated circle (unequally convex-plane in Woodson's terminology) 6.5 cm in longest diameter and 4.7 cm in shortest diameter. It is smooth, flat with no midrib, conspicuously yellow puberulent, and lacks a stipe. The seeds are thin, flat, concentrically winged, 4.5 cm in shortest diameter, 6.2–6.5 cm in longest diameter with a 5-cm-long funicle. The tree is described as 8 inches d.b.h. with a fluted trunk. The fluted trunk supports Dwyer's placement of *A. darienense* in series *Nitida,* but the non-verrucose fruit separates it radically from other species of that series.

2. *Aspidosperma marcgravianum* Woods., Ann. Missouri Bot. Gard. 38: 170. 1951. A second species of *Aspidosperma* with fluted trunk also occurs in Panama. This species is represented by *Dressler 3440* with both flowers and young fruits. The collection was not named by Nowicke (Ann. Missouri Bot. Gard. 57: 84. 1970), although she discussed it under *A. darienense.* The specimen matches Venezuelan material of *A. marcgravianum* Woods. (e.g. *Steyermark 86928*) as well as the Brazilian type. *Aspidosperma marcgravianum* is closely related to *A. excelsum* Benth. but can be distinguished by its smoother lower leaf surface and stipitate fruit. In Panama, *A. marcgravianum* is a large tree, commonly reaching 30 meters in height. It has a conspicuously fluted trunk and is relatively common in the tropical wet forest life zone of Santa Rita Ridge, Colón Province.

3. *Aspidosperma cruentum* Woods., Amer. Jour. Bot. 22: 684. 1935. The commonest Panamanian species of *Aspidosperma* was treated by Woodson (Ann. Missouri Bot. Gard. 38: 192. 1951) and in the *Flora of Panama* as *A. megalo-*

carpon. Müll.-Arg. Woodson had not seen the type of *A. megalocarpon*, however. Gómez-Pompa (Inst. Méx. Rec. Nat. Renov. 94–99. 1966), after studying the type, pointed out that Woodson's interpretation was incorrect and that the name of *A. megalocarpon* should instead be applied to the plant treated by Woodson (Ann. Missouri Bot. Gard. 38: 178. 1951) as *A. stegomeris* (Woods.) Woods. The earliest name for the common Panamanian species is *A. cruentum*.

4. *Aspidosperma megalocarpon* Müll.-Arg. Linnaea 30: 400. 1860. The real *A. megalocarpon*, known from Veracruz, Mexico, to the Osa Peninsula, Costa Rica, has also been recently collected in Panama, bringing to four the known Panamanian species of *Aspidosperma*. The Panamanian collection of *A. megalocarpon* is *Croat 22450* from the Burica Peninsula of Chiriquí Province. This species can easily be told from *A. cruentum* by the conspicuous and more widely separated secondary veins of its leaves, its larger flowers, and by the loose, wrinkled surface of its essentially glabrous fruit.

5. *Laxoplumeria tessmannii* Mgf., Notizbl. Bot. Gart. Berlin-Dahlem 9: 981. 1926. Another significant addition to the Panamanian flora is the distinctive genus *Laxoplumeria*. This rarely collected genus has been previously known only from Amazonian Peru and Brazil, each of its three species being represented in herbaria by only one or two collections (see Monachino, Phytologia 3: 67–70. 1949). The Panamanian material (*Gentry 1607*) is in fruit only so that its specific identification must remain tentative. In Monachino's key its 2–5-cm-long petioles relate it to both *L. tessmannii* and *L. baehniana* Monachino. Its 10–12-cm-long (in fruit) inflorescence distinguishes it from the latter. I have seen no material of *L. tessmannii*, apparently known only from the Peruvian type collection, but a photograph of the type (Field Museum Neg. 4386) seems to match the Panamanian plant. Although *L. tessmannii* has a puberulous inflorescence while the Panamanian material does not, the inflorescence is probably glabrate in fruit. The only known fruiting collection of *L. baehniana* (*Krukoff 5720*, F, MO) has similar but shorter fruits 20–31 (–38 at NY *fide* Monachino) cm long; the fruit of *L. tessmannii* is unknown.

The Panamanian plant is a tall lactiferous tree reaching 25 meters in height with pendent follicles 40–50 cm long and 4–6 mm wide. The seeds are flat, pointed, 2.2–2.8 cm long and 3 mm wide, densely pubescent with long (ca. 1 cm), brown trichomes. Juvenile trees are reasonably abundant in the premontane wet forest area of Pipeline Road, Canal Zone, but only a single mature individual is known.

6. *Macoubea sprucei* (Muell.-Arg.) Mgf., Notizbl. Bot. Gart. Berlin-Dahlem 14: 179. 1938. *Macoubea* is another genus of Amazonian trees which has not previously been reported from Panama or North America. The Panamanian specimens, all in fruit, seem to match *M. sprucei*, which has been collected as far northwest as Panure on the Rio Uaupes, Brazil. Dr. F. Markgraf, who kindly identified the Panamanian plant, notes that "the unripe seeds have the many-grooved testa of *Macoubea* and the hemisyncarpous fruit is a character that sometimes occurs in this genus. I saw such a case in *M. sprucei* from Rio Urubu,

Brazilian Amazonia (*G. T. Prance et al. 3739* (NY)). This gap between Amazonia and Panama is large, and without flowers a determination is not absolutely certain." The four Panamanian collections, all from the tropical wet forest life zone of Panamá Province between kilometers 14 and 20 on the El Llano-Carti road, include *Kennedy, Dressler & Mahler 2411*, 13 Feb. 1973; *Kennedy 2518*, 20 Feb. 1973; *Liesner 1145a*, 26–27 Mar. 1973; and *Correa, Dressler, Carrasquilla &Mendieta 1847*, 20 Feb. 1973. The species is described as a tree 5–6 m tall with latex and a green fruit turning brown at maturity. The fruit is syncarpous, more or less spheroidal, separated into two halves by a shallow longitudinal groove. The only other genus of Panamanian Apocynaceae to have syncarpous fruits and opposite leaves is *Lacmellea*. Its furrowed fruit and much larger leaves readily distinguish *M. sprucei* from *Lacmellea*.

7. *Bonafousia undulata* (Vahl) A. DC., Prodr. 8: 359. 1844. This species was reported by Nowicke in the *Flora of Panama* on the basis of a single collection. It proves too be a locally common shrub in the tropical wet forest life zone of eastern Panama. Dr. Robert Dressler informs me that he has examined the type of *Stemmadenia nervosa* Standl. & L. Wms., which proves to be synonymous with *B. undulata*, extending the range of this species to Costa Rica. Additional collections examined include *Correa et al. 791*, *Dwyer & Gentry 9387*, *Correa & Dressler 645*, *Gentry 6577*, and *Duke 15271*, all from Santa Rita Ridge, Colón Province, and *Gentry 5812* from north of El Llano in Panama Province near the San Blas border. Most of these specimens had been incorrectly determined as *Ervatamia cumingiana* (DC.) Markgraf, and duplicates were presumably distributed under that name.

8. *Peltastes colombianus* Woods., Ann. Missouri Bot. Gard. 19: 378. 1932. Only three collections of this genus were reported by Nowicke, one from the Canal Zone and two from lowland Chiriquí Province. Additional collections including *Gentry & Dressler 1971* from Pipeline Road, Canal Zone, and *Gentry 5760* from Cerro Campana, Panamá Province, as well as sterile plants seen in various parts of eastern Panama close most of the supposed distributional gap between *P. isthmicus* Woods. and the earlier *P. colombianus*. When he separated the Central American plant as a new species on the basis of its geographical disjunction and larger corollas, Woodson (Ann. Missouri Bot. Gard. 23: 197. 1936) had seen only a single flowering specimen of it. The floral dimensions given by Nowicke for *P. isthmicus* included smaller flowers than those described by Woodson, and the recent collections cited above include yet smaller flowers (corollas 5–6 cm long in *Gentry & Dressler 1971*), well within the range of variation of the otherwise identical *P. colombianus*. Since both characters used to separate the two species break down, *P. isthmicus* should be regarded as a junior synonym of *P. colombianus*, another example of the unreliability of absolute flower size as a specific character for large-flowered species of sympetalae (*cf.* many Bignoniaceae).

9. *Odontadenia macrantha* (R. & S.) Mgf., Fl. Surinam. 4, pt. 1: 461. 1937. The fruit of this well known species was described by Woodson (Ann. Missouri

Bot. Gard. 22: 298. 1935, under *O. hoffmannseggiana*), but its description was omitted from the treatment in *Flora of Panama.* A recent collection (*Croat 16597*) from Pipeline Road, Canal Zone, is the first fruiting specimen from Panama. The follicles, noteworthy as being significantly thicker than the 1–2 cm diameter described by Woodson but according well with the 4 cm diameter recorded by Markgraf (Pulle, Fl. Surinam 4(1): 462. 1937), are stout, divergent at an angle of about 45 degrees, 14–15 cm long and about 4.5 cm in diameter. Another interesting note on this species is that its flowers have a strong and distinctive odor of cloves. Gaps in the conspicuously broken geographical distribution (noted by Woodson, Ann. Missouri Bot. Gard. 22: 274) of *O. macrantha* are lessened by several additional collections from Panama including, besides the Croat collection cited above, *Gentry 4798* from Pipeline Road Canal Zone, *Gentry 4980* from near the junction of the Ríos Espavé and Bayano in eastern Panamá Province, and *Gentry 4549*, the first Darién Province collection from near El Real.

It should be noted that the correct name of this species is *O. macrantha* rather than *O. grandiflora* (G. F. W. Mey.) Miq. This was first pointed out by Markgraf (Notizbl. Bot. Gart. Berlin-Dahlem 9: 461–462. 1926) and accepted by Macbride (Field Mus. Publ. Bot. 13(5): 444. 1959) and others but apparently overlooked by Woodson (N. Amer. Fl. 29: 168. 1938) and in the *Flora of Panama* treatment. Markgraf's argument is that *O. grandiflora* Miq. was based on a different type than *Echites grandiflora* G. F. W. Mey. so that the latter's transferal to *Odontadenia* by Kuntze made it a later homonym in that genus. The next oldest basionym for the species is*Echites macrantha* R. & S. which must be the name adopted in *Odontadenia.*

10. *Prestonia allenii* Woods., Ann. Missouri Bot. Gard. 27: 332. 1940. Known to Nowicke only from the type collection (*Allen & Alston 1855*) from El Valle, Coclé Province, additional collections indicate that this species is widespread though uncommon in the tropical wet forest life zone. It is now also known from Colón Province (*Dressler & Lallathin 9025*, Santa Rita Ridge) and Panamá Province (*Gentry 5575*, north of El Llano near San Blas border). A fruiting collection (*Lewis et al. 287*, 2–3 mi. S of Goofy Lake, road to Cerro Jefe) may be also referable to *P. allenii.* It has been determined as *P. ipomaeifolia* DC. but the old calyx lobes reach 21 mm in length. Unfortunately neither annulus nor squamellae are apparent so that it can only be related to *P. allenii* rather than *P. remediorum* Woods. or *P. wedelii* Woods. through tenuous characters of leaf pubescence and by its collection locality. The follicles of this specimen are like those of *P. ipomaeifolia*, stout, widely diverging, pubescent, 9 cm long and 1.5 cm in diameter at the widest point. This would constitute the first collection of mature fruit for any of these three large-calyxed species.

11. *Prestonia concolor* (Blake) Woods. *in* Standl. & Record, Field Mus. Publ. Bot. 12: 327. 1936. This species, previously known only from Belize (formerly British Honduras) and Guatemala, is recorded for the first time from Panama. The single Panamanian collection, *Gentry 2804*, is from the top of the fila above Almirante, Bocas del Toro Province, and was determined by Prof.

F. Markgraf of Zürich. In the *Flora of Panama* this species keys out between *P. exserta* and *P. obovata*, agreeing with the former in its short (5 mm) calyx lobes and with the latter in its thick concrescent nectaries. Woodson (Ann. Missouri Bot. Gard. 23: 299. 1936) keys it out with *P. obovata* from which he separates it by its shorter calyx lobes and simple (*i.e. racemose*) inflorescence, longer than the leaves. The leaves of *P. concolor* are most similar to those of *P. portobellensis* among the other Panamanian species. Besides flowers, the Panamanian collection contains fruits, previously unknown for this species. The follicles of *P. concolor* are long and slender, somewhat agglutinated when young, 37–38 cm long and 4–5 mm wide, subglabrous with a few very short, scattered, inconspicuous trichomes. The seeds are 1.0–1.2 cm long with a whitish coma ca. 4 cm long.

12. *Prestonia tysonii* A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, dense ferrugineo-tomentulosis. *Folia* ovata, abrupte acuminata, basi rotundata, supra hispido-velutina, subtus dense velutino-tomentosa. *Inflorescentia* densa, ferrugineo-tomentosa. Lobi *calycis* anguste ovati, acuti, 4–5 mm longi; squamellis triangularibus. *Corolla hypocrateriformis*, strigoso-velutina apice tubi et in lobis, tubo 5–6 mm longo, appendicibus epistaminalibus annulum faucis attingentibus. *Stamina* in parte superna faucis inserta. *Pistillum* 5 mm longum, ovario glabro, nectariis haud concrescentibus. *Follicula* 29–30 cm longa, ca. 5 mm lata, velutino-tomentosa.

Vine, the stems terete, densely ferruginous tomentose. *Leaves* elliptic-ovate to broadly ovate, shortly acuminate, the base rounded, 8–13 cm long and 4–9.5 cm wide, above hispid-velutinous with trichomes scattered over surface and congested on main veins, below densely and evenly velutinous-tomentose, the indument orangish tan, petioles 5–10 mm long, ferruginous tomentose. *Inflorescence* dense, subumbellate, ferruginous tomentose. *Calyx* lobes narrowly ovate, acute or shortly acuminate, 4–5 mm long and ca. 2 mm wide at base, appressed-velutinous, the squamellae triangular, blunt-tipped, pubescent without, 1 mm long. *Corolla* salverform, strigose-velutinous at top of tube and on lobes without, the tube 5–6 mm long and 1.5 mm wide at top, epistaminal appendages reaching the faucal annulus, ca. 2 mm long, the faucal annulus somewhat thickened. *Stamens* inserted in upper third of corolla tube, the anthers sagittate, 4 mm long, glabrous, the tips exserted. *Pistil* 5 mm long, ovary 1.5 mm long, glabrous, the nectaries separate, thin, petaloid, to 1 mm long. *Follicles* long and narrow, united at tips, 29–30 cm long, ca. 5 mm wide, velutinous-tomentose; immature seeds with coma ca. 2 cm long.

Holotype: PANAMA. PANAMA: Cerro Jefe in Clusia forest at 3000 ft., fruits united, vine, 27 Jan. 1966, *Tyson, Dwyer & Blum 3214* (MO).

This species belongs to Woodson's (Ann. Missouri Bot. Gard. 23: 276–367. 1936) section *Tomentosae* on the basis of its appendiculate, pubescent corolla and large calyx lobes. However, its long, narrow follicles, joined at the ends, are remarkably different from the short, stout, widely divaricate follicles of most other species of section *Tomentosae*. The only species known to me whose fruit even approaches that of *P. tysonii* is the very different *P. riedelii* (Muell.-Arg.) Mgf. which ranges from southern Peru and southern Brazil to Argentina.

Since the fruits of many species are unknown it is likely that other species of section *Tomentosae* may also be found to have narrow elongate follicles. *Prestonia tysonii* is also very unusual for the small size of its corolla. Its 5–6-mm-long corolla tube is less than half as long as that of all other species of section *Tomentosae* with the exception of *P. parviflora* Benth. of Cundinamarca, Colombia. Although *P. parviflora* is probably the closest ally of *P. tysonii*, it differs (*fide* Woodson's description) in elliptic leaves, shorter (1 mm) wholly included epistaminal appendages, acuminate corolla lobes, and stamen insertion at middle of the corolla tube. In Nowicke's treatment for the *Flora of Panama P. tysonii* keys out with *P. ipomaeifolia* DC., from which it is easily distinguished by its much smaller flowers and long, narrow follicles.

13. *Prestonia lenticellata* A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, puberulis, lenticellis prominentibus suberosis. *Folia* obovata, abrupte acuminata, basi anguste subcordata, supra glabrescentia, subtus puberula. *Inflorescentia* simplex, puberula. Calyx lobis lanceolatis, puberulis, 10–14 mm longis; squamellis triangularibus. *Corolla* hypocrateriformis, extus puberula, intus villosa in fauce, tubo 1.2–1.5 cm longo, appendicibus epistaminalibus annulum faucis superantibus. *Stamina* in parte superna faucis inserta. *Pistillum* 1.7–1.8 cm longum, ovario pubescenti, nectariis haud concrescentibus. *Follicula* ignota.

Vine, the stems terete, puberulous when young, glabrescent, with prominent raised corky lenticels when young, these coalescing and becoming suberous when older. *Leaves* obovate or obovate-elliptic, very abruptly short acuminate, broadly tapering to a narrowly subcordate base, 15–25 cm long and 9.5–18 cm wide, above mostly glabrescent, slightly puberulous near main veins, below puberulous with evenly scattered short trichomes, especially along the veins, the veins strongly raised below, lower secondary veins making 90 degree angle with midvein, uppermost veins a ± 60 degree angle, the secondary veins connected by an equally conspicuous continuous submarginal vein never more than 3 mm from margin, petioles ca. 1 cm long, puberulous. *Inflorescence* unbranched, 6–17-flowered, with subulate bracts to 8 mm long, the rachis and pedicels puberulous. *Calyx* lobes lanceolate, acuminate, 10–14 mm long and 3–5 mm wide, puberulous, the squamellae triangular, pointed or bifid, often serrate, 1.5–2 mm long. *Corolla* salverform, densely puberulous without, villous at top of throat within, the tube 1.2–1.5 cm long, epistaminal appendages exceeding faucal annulus, ca. 4 mm long. *Stamens* inserted toward top of corolla tube, the anthers sagittate, 5 mm long, pubescent, partially exserted. *Pistil* 1.7–1.8 cm long, ovary 1.5–2 mm long, densely pubescent, the nectaries separate, thick, ca. 2 mm long, slightly exceeding ovary. *Follicles* unknown.

Holotype: PANAMA: PANAMA: El Llano-Carti highway, about 16 km N of El Llano; vine, flowers yellow, crown white, 23 Mar. 1973, *Dressler 4303* (MO; isotypes PMA and to be distributed).

Additional collections examined: PANAMA. COLÓN: Santa Rita Ridge, flowers yellow, milky sap, 1 Mar. 1971, *Croat 13876* (MO). PANAMÁ: El Llano-Carti road, 16 km N of El Llano, 23 Mar. 1973, *Kennedy 2907* (MO, SCZ).

This species is known from three collections, all from the tropical wet forest life zone of eastern Panama.

This very distinctive plant appears to be intermediate between Woodson's (1936) sections *Annulares* and *Tomentosae*. It is easily distinguished from all species of section *Annulares* by its conspicuously puberulous corolla and thus keys to section *Tomentosae*. However, its not-at-all ferruginous, relatively inconspicuously puberulous leaves, stems and calyces are quite anomalous in section *Tomentosae*. Its macroscopic appearance is more that of section *Annulares*. On the basis of its exserted epistaminal appendages, simple many-flowered inflorescence, pubescent anthers, corolla dimensions, and nectaries surpassing the ovary, it keys to *P. calycina* Muell.-Arg. That species, known only from southern Brazil and adjacent Paraguay, is totally different in ferruginous pubescence on all parts and a glabrous ovary. In the *Flora of Panama* this species keys out with *P. ipomaeifolia*, from which it differs most obviously in its relatively sparse, non-rufescent tomentum. *Prestonia lenticellata* is easily separated, even vegetatively, from all species represented in the herbarium of the Missouri Botanical Garden by its large, almost bullate leaves and conspicuous, raised, corky lenticels.

14. *Forsteronia peninsularis* Woods., Ann. Missouri Bot. Gard. 22: 215. 1935. Several recent Panamanian collections agree with this species, previously known only from Guatemala and British Honduras. These include *Dwyer & Correa 8422* from Santa Rita Ridge, Colón Province, *Dressler & Williams 3960* from Cerro Campana, Panamá Province, *Duke 11894* from Loma Prieta, Los Santos Province, and *Foster 950* and *Croat 14000* both from Barro Colorado Island, Canal Zone. These specimens are noteworthy in their uniform notation of yellow flowers in contrast to the greenish-white flowers mentioned by Woodson (Ann. Missouri Bot. Gard. 22: 158) from British Honduras. This species has smaller leaves than either of the other two species of *Forsteronia* reported from Panama. In the generic key in *Flora of Panama* its thyrsiform inflorescence distinguishes it from *F. spicata* (Jacq.) G. Mey., while the presence of hairs in the axils of the veins beneath separates it from *F. viridescens* Blake. The nerve axils also differ from those of *F. spicata* in having sunken domatia rather than external tufts of trichomes and the base of the midvein above lacks the glands of the other two species.

15. *Rauvolfia sarapiquensis* Woods., Ann. Missouri Bot. Gard. 28: 271. 1941. A collection from Monte Rey, above Boquete, extends the range of this distinctive species, previously known only from two gatherings in adjacent Costa Rica, into Chiriquí Province. The field notes on *Croat & Porter 15705* note that the specimens are from a tree 7 m tall with greenish white flowers, growing in disturbed cloud forest. Its many-flowered, much-branched inflorescences and rather leathery leaves with very inconspicuous almost transverse secondary veins make the species unmistakable. The leaves are markedly like those of many species of Guttiferae.

The descriptions of the following three new species were provided by F. Markgraf of Zürich, current expert on the Apocynaceae. I have added short English descriptions and brief discussions of important characters for separating them from other Panamanian species. Several collections not seen by Markgraf are included in the listings of specimens cited.

16. *Mandevilla campanulata* Markgraf, sp. nov.

Frutex scandens glaber. *Folia* coriacea, glabra, elliptico-oblonga, apice longiuscule (8–10 mm) acuminata, basi cuneata, 8–11 × 2–2.5 cm; petiolus 5 mm longus; costa supra prope basin laminae glandulifera, ceterum eglandulosa, nervi laterales 10–11 paria, arcuati et arcuato-coniuncti, tertiarii subtus distincti, horizontales. *Inflorescentiae* axillares, alternae, semel dichotomae, pauciflorae, pedunculus 0.5–1 cm longus, ramuli bracteolis late ovato-acuminatis, 0.5 mm longis, 1 mm latis instructi. *Pedicelli* 1.5 cm longi. *Calycis* lobi glabri, breviter ciliati, ovati, obtusi, subpellucidi, 3 × 2 mm, squamellas complures latiusculas et longiusculas includentes. *Corolla* recta, subcampanulata, extus glabra, tubus pallide luteus, inferior 3.5 cm longus, prope basin 5 mm, prope faucem 2.5 mm latus, intus infra stamina pilosus, tubus superior 3.5 cm longus, in ore 1.4 cm latus, glaber, lobi patuli, late ovati, obtusi, 8 mm longi, 10 mm lati, glabri, flavi. *Antherae* in basi tubi superioris subsessiles, 5.5 × 1 mm, apice breviter acuminatae, basi truncatae, ad basin intus barbulatae. *Clavuncula* umbraculiformis, 2 mm alta, apice breviter apiculat et pilifer. *Stylus* 14 mm longus. *Ovarium* ovoideum, glabrum, 2 mm altum, 1.5 mm latum, bipartitum, squamis disci 5 subaequialtis papillosis circumdatum.

Vine; *leaves* coriaceous to subcoriaceous, glabrous, elliptic-oblong, long acuminate, the base cuneate, the midrib glanduliferous near the base of the blade. *Inflorescence* axillary, dichotomous, few-flowered. *Calyx* lobes glabrous, shortly ciliate, 3 mm long and 2 mm wide, the squamellae included. *Corolla* cream or white with a greenish to reddish base, straight, tubular campanulate above the narrowed 3.5–4-mm-long base, 7–8 cm long, glabrous outside, pubescent below the stamens inside. *Anthers* subsessile, inserted at the constriction in the middle of the tube, acuminate at apex and truncate at base. *Pistil* with clavuncle umbraculiform, 2 mm long, the style 14 mm long, the ovary ovoid, glabrous, 2 mm long and 1.5 mm wide, biparted, surrounded by 5 subequal squamellae. Fruit unknown.

Holotype: PANAMA. COLÓN: Santa Rita Ridge, 3 km N of Agua Clara rain gauge, lumber road, 19 Jan. 1973, *Dressler 4261* (Z; isotypes MO and to be distributed).

Additional collections examined: PANAMA. COLÓN: Santa Rita Ridge 4–5 miles from Trans-isthmian Highway, elev. 500–800 m, flowers cream with red base, fallen from canopy vine, 20 Sept. 1972, *Gentry 6104*. PANAMÁ: Road to Cartí, ca. 19 km from Pan-American Highway, vine, leaves dark green, calyx green, lower portion of tube pale green, upper portion and lobes white, flowers ca. 8 cm long, 20 Feb. 1973, *Kennedy 2520*. DARIÉN: Cerro Pavarando, inland from Jacqué, *Gentry s.n.* (collection of fallen corollas destroyed in Summit Herbarium fire).

The species is known from the tropical wet forest life zone of eastern Panama.

This species belongs to Woodson's section *Laxae* and is most closely related to the northern Andean species with truncate anthers (*M. equatorialis* Woods. and *M. versicolor* Woods. of Ecuador and *M. alboviridis* of Colombia).

The flower of *M. campanulata* is similar in shape to the flowers of these species but larger. The most closely related Panamanian species is *M. veraguasensis* (Seem.) Hemsl. with which *M. campanulata* would key out in the generic key in the *Flora of Panama*. However, the cuneate leaf base of *M. campanulata* is very different from the cordate one of other Panamanian species of *Mandevilla* so that it could not be placed to genus by use of the artificial key.

17. *Malouetia isthmica* Markgraf, sp. nov.

Arbor ad 10 m alta. *Ramuli* graciles, angulati, vix lenticellosi. Folia coriacea, opaca, 7–10 × 3–4 cm, glabra, elliptica, basi et apice acuminata, subtus secus costam conspicue foveolata; petiolus 0.5 cm longus. *Nervi* laterales 6–8 paria, arcuati, indistincte coniuncti, tertiarii indistincti. *Inflorescentiae* axillares, multiflorae, umbelliformes, pedunculus 0.5 mm longus, pedicelli adulti 6–8 mm longi, bracteis navicularibus 0.7 mm longis suffulti. *Calyx* campanulatus, usque ad basin fissus, lobi foliacei, ovato-oblongi, obtusi, apice recurvi, extus puberuli. *Corollae* albae tubus 7 mm longus, glaber, a basi 2 mm lata in faucem 1 mm latam, intus gibbosam sensim angustatus, lobi oblongi, obtusi, 6 × 2.5 mm, supra usque ad ⅔ pilosi. *Antherae* 1.5 mm exsertae, 2.5 mm longae, sessiles, in dorso connectivi setosae, apice acutae, basi obtusae et incurvae, retinaculo crasso ad clavunculam obtuse ovoideam agglutinatae. *Stylus* 6 mm longus. *Ovarium* globosum, dense pubescens, 7 mm altum, bipartitum, squamis disci glabris, partim connatis, 3 mm altis circumdatum. *Mericarpia* glabra, divergentia, cylindracea, follicularia, longitudinaliter rimosa, immatura ad 14 cm longa, ½ cm lata. *Semina* semicylindrica, apice et basi breviter rotundato-acuminata, in ventre plana et sulco longitudinali instructa, in dorso convexa et longitudinaliter rimosa et ibi pilis 4 cm longis villosa, immatura 35 × 4 × 2 mm.

Tree to 10 mm tall, the branchlets slender, angulate. *Leaves* coriaceous or subcoriaceous, 7–10 cm long and 3–4 cm wide, glabrous, elliptic, acuminate, cuneate at base. *Inflorescence* axillary, many-flowered, paniculate. *Calyx* campanulate, split to the base, the lobes foliaceous, ovate-oblong, obtuse, recurved at the apex, puberulous. *Corolla* white, glabrous, the tube 7 mm long, the lobes 6 mm long, pubescent. *Anthers* sessile, 2.5 mm long, exserted 1.5 mm, setose on the dorsal connective, the apex acute, the base obtuse and incurved. *Pistil* with the style 6 mm long, the ovary globose, densely pubescent, 7 mm long, biparted, the squamellae glabrous, partly connate, 3 mm long. *Mericarps* glabrous, divergent at more than a 90 degree angle, cylindric, follicular, longitudinally striate, to 38 cm long and 0.6 cm wide. Seeds semicylindrical, rounded acuminate at apex and base, the underside flat, the upper side convex, villous.

Holotype: PANAMA. CANAL ZONE: Navy reservation north of Gamboa, tree 7 m tall; flowers white, 28 May 1972, *Dressler 4194* (Z; isotypes MO, PMA, NY).

Additional collection examined: PANAMA. COLÓN: Santa Rita Ridge, tree 10 m, 1 Mar. 1971, *Croat 13874* (MO, Z, and to be distributed).

This species is known from two collections, one from the tropical wet forest and the other from the premontane wet forest life zone.

Malouetia isthmica belongs in Woodson's section *Tamaquarinae* and to the group with foliaceous, spreading calyx lobes (Ann. Missouri Bot. Gard. 22: 238–270. 1935). The other species of this small alliance are known from northern South America (mostly Amazonian Brazil) and the West Indies. This is the first species of section *Tamaquarinae* to be recorded from Panama or North America. Its conspicuously exserted anthers and slender terete fruit distinguish *Malouetia isthmica* from *M. guatemalensis* (Muell.-Arg.) Standl., the other Panamanian species of the genus.

18. *Stenosolen holothuria* Markgraf, sp. nov.

Frutex glaber. Ramuli graciles, teretes, albo-grisei. *Folia* cuiusque secundi paris magnitudine diversissima, omnia membranacea in sicco flavescentia. *Petiolus* 1–2 mm longus, lamina elliptica, basi sinuato-angustata, apice longe acuminata, maiores 65 × 22 mm, minores 20 × 7 mm. *Nervi* laterales arcuati, indistincte coniuncti, maiorum 6 paria, minorum 4 paria, tertiarii indistincti. *Inflorescentia* in bifurcatione ramulorum terminalis, brevis, uniflora. *Pedicellus* 5 mm longus. *Lobi* calycis 3 mm longi, 1 mm lati, ovato-lanceolati, glabri, intus glandulis paucis longiusculis instructi. *Corollae* albae, mox flavescentis tubus glaber, 10 mm longus, 1 mm latus, intus a fauce ad insertionem staminum setosus, lobi oblique securiformes, acuti, 5 mm longi, prope faucem 2 mm lati et supra nonnullis setis pilosi. *Stamina* 1 mm supra basin tubi filamentis brevissimis inserta, glabra, antherae sagittiformes, angustae, apice aristatae, loculis ad basin divergentibus, 3 mm longae, 0.3 mm latae. *Clavuncula* longiuscule (0.5 mm) cylindrica, apice incrassata et breviter apiculata, basi 5-corniculata. *Stylus* 0.5 mm longus. *Ovarium* ovoideum, glabrum, 1 mm altum, 0.6 mm latum, bipartitum, pluriovulatum. *Fructus* apocarpus, modice carnosus, mericarpium reclinatum, lanceolatum, verrucis ad 3–4 mm elongatis obtectum (ideo holothuriae non dissimile), immaturum 4 × 1 × 0.8 cm. *Semina* biseriata, ad 10, ellipsoidea, arillo longitudinaliter sulcato induta, immatura 7 × 5 × 3 mm.

Glabrous *shrub*, the branchlets slender, terete. *Leaves* membranaceous, elliptic, long-acuminate at apex, the base cuneate, 20–70 cm long and 0.7–2.2 cm wide, drying yellowish green. *Inflorescence* terminal, one-flowered. *Calyx* lobes 2–3 mm long and 1 mm wide, ovate-lanceolate, glabrous. *Corolla* with the tube 10–14 mm long and 1 mm wide, the lobes 5 mm long. *Stamens* inserted 1 mm above the base of the tube, glabrous, the anthers sagittiform, narrow, the apex aristate, the locules divergent, 3 mm long. *Pistil* with clavuncle 0.5 mm long, cylindric, thickened at apex and shortly apiculate, 5-corniculate at base, the style 0.5 mm long, the ovary ovoid, glabrous, 1 mm long and 0.6 mm wide, biparted. *Fruit* apocarpus somewhat fleshy, the mericarps lanceolate, 4 cm long, 0.8–1 cm wide, verrucose-echinate, the projections 2–4 mm long and recurved at the tip. *Seeds* biseriate, ellipsoid, arillate.

Holotype: PANAMA. DARIÉN: Tumaganti, 18 Sept. 1967, *Duke 14149* (Z; isotypes F, MO, NY).

Additional collection examined: PANAMA. DARIÉN: Río Pirre, Apr. 1966, *Duke & Bristan 8266* (MO).

This species is apparently restricted to Darién Province, Panama.

This species belongs to the group characterized by distinct lateral enlargements of the corolla lobes. Geographically, the species of this group occurring nearest to Panama is *Stenosolen eggersii* Markgraf of the coastal region of Ecuador (cf. Notizbl. Bot. Gart. Mus. Berlin-Dahlem 14: 177–178. 1938).

In flower *Stenosolen* resembles *Tabernaemontana* but can be separated by its usually one-flowered inflorescence and anthers inserted near the base of the corolla tube. The conspicuously verrucose-echinate fruit with numerous 2–4 mm long projections mostly recurved at the tips is unique among Panamanian Apocynaceae.

ACKNOWLEDGMENTS

I thank Dr. Robert Dressler for calling my attention to the Gómez-Pompa article on *Aspidosperma*. Dr. William D'Arcy has similarly called to my attention a paper by Stearn (Lloydia 29: 196–200. 1966) in which it is pointed out that the periwinkle commonly cultivated in Panama should be known as *Catharanthus roseus* (L.) G. Don rather than *Lochnera rosea* (L.) Reichenb. as used in the *Flora of Panama*.

—*A. H. Gentry, Missouri Botanical Garden.*

CHROMOSOME NUMBERS OF PHANEROGAMS. 5.[1]

Chromosome numbers of phanerogams are reported below together with voucher data and herbaria where collections are deposited. Unless indicated otherwise the chromosome records are based on the study of one plant. Haploid counts are from pollen mother cells, and diploid counts are from root tips unless otherwise indicated.

The authors responsible for counts are listed alphabetically. Citation should have the form: Doe, J. 1974. *In* Chromosome numbers of phanerogams. 4. Ann. Missouri Bot. Gard. 61:   .

Counts by PETER GOLDBLATT, Missouri Botanical Garden.

AMARYLLIDACEAE

Ixiolirion tataricum (Pall.) Herb. $2n = 24$. IRAN. Chalus Pass near Kandevan tunnel, *Goldblatt 705B* (MO).

EUPOMATIACEAE

Eupomatia laurina R. Br. $2n = 20$. NEW GUINEA. Busu R. near Lae, *Womersley s.n.* (NGF).

IRIDACEAE

Iris barnumae M. Foster & Bak. $2n = 20$. IRAN. Hills between Khoy and Shahpur, *Goldblatt 1243* (MO).

Anomalesia saccata (Klatt) Goldbl. $2n = 30$. SOUTH AFRICA. South of Bitterfontein, Namaqualand, *Goldblatt 1244* (BOL).

Gladiolus lapeirousioides Goldbl. $2n = 30$. SOUTH AFRICA. Kliprand-Loeriesfontein road. *Goldblatt 540* (BOL, NBG, PRE).

LEGUMINOSAE

Sophora gypsophila Turner & Powell var. *gypsophila.* $2n = 18$. MEXICO. Chihuahua (from the type locality) *Powell 2537* (MO).

LILIACEAE

Allium cf. stamineum Boiss. $2n = 16$. IRAN. Near Qotur at Turkish border, *Goldblatt 760* (MO).

Allium synthamanthum C. Koch. $2n = 16$. IRAN. Between Khoy and Qotur, *Goldblatt 764* (MO).

Allium scotostemon Wendelbo. $2n = 16$. IRAN. Chalus Pass, 6 miles N Kandevan tunnel, *Goldblatt 705* (MO).

Allium sp. $2n = 16$. IRAN. Near Qotur, at Turkish border, *Goldblatt 760* (MO).

Merendera trigyna (Adams) Woron. $2n =$ ca. 20. IRAN. North of Firuzkuh at entrance to pass, *Goldblatt 839A* (MO).

Muscari commosum Miller. $2n = 18$. IRAN. About 12 km south of Siah Cheshmeh, *Goldblatt 775* (MO).

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[1] The previous number in this series appeared in Ann. Missouri Bot. Gard. 57: 382–384. 1970.

Muscari tenuiflorum Taush. $2n = 18$. IRAN. Near Polour, *Goldblatt 1241* (MO).

PAPAVERACEAE

Glaucium oxylobum Boiss. $n = 6$. IRAN. Abandoned fields near Rudhen, *Goldblatt 702* (MO).

Papaver chelidoniifolium Boiss. & Buhse. $2n = 14$. IRAN. Forest near Masuleh, south of Fowmen, *Goldblatt 728* (MO).

SAXIFRAGACEAE

Astilbe papuana Schl. $2n = 14$. NEW GUINEA. Near Mt. Hagen, *Womersley s.n.* (NGF).

Counts by John C. Semple, Missouri Botanical Garden.

Seedlings were grown at either the Missouri Botanical Garden, Washington University, or the University of Missouri-St. Louis.

ROSACEAE

Cercocarpus montanus Raf. $2n = 18$. COLORADO. PARK CO. NE of Bailey, 26 Nov. 1972, *J. & K. Semple 796* (MO).—Seedling root tips.

SAPINDACEAE

Paulinnia turbacensis H.B.K. $2n = 24$. PANAMA. CANAL ZONE. Secondary forest near Boy Scout Road, 3 April 1971, *Semple 497* (MO).—Two plants. Seedling root tips.

COMBRETACEAE

Conocarpus erectus L. $2n = 24$. Seedling root tips. GALAPAGOS ISLANDS.

CONVOLVULACEAE

Ipomoea sinuata Ort. $2n = 30$. TEXAS. KLEBERG CO. E of Kingsville, 13 June 1971, *Semple 592* (MO).—Seedling root tips.

SOLANACEAE

Solanum bahmense L. var. *luxurians* D'Arcy. $2n = 24$. FLORIDA. MONROE CO. Key Largo, *Austin 4364* (MO).—Adventitious root tips from cutting of seedling.

Solanum drymophyllum O. E. Shulz. $2n = 24$. PUERTO RICO. Central Mountains, Aug. 1967, *D'Arcy 1712* (MO, FLAS).—Adventitious root tips from cutting of seedling.

Solanum persicifolium Dun. $2n = 24$. VIRGIN ISLANDS. TORTULA; Sept. 1967, *D'Arcy 2053* (FLAS).—Adventitious root tips from cutting of seedling.

COMPOSITAE

Bradburia hirtella T. & G. $n = 3_{II}$. TEXAS. FAYETTE CO. 0.5 miles S of junction of US 77 and Farm Road 153, 10 July 1970, *Lewis 7658* (MO). LEE CO. Giddings, 3.1 miles SW on US 77, 10 July 1970, *Lewis 7661* (MO).

Elephantopus carolinianus Raeusch. $2n = 22$. MISSOURI. FRANKLIN CO. Gray Summit, Arboretum, 3 Oct. 1972, *Shea 310* (MO).—Seedling root tips.

Grindelia lanceolata Nutt. $2n = 12$. Oklahoma. osage co. 7.6 miles N of Shilder, 21 Sept. 1973, *J. & K. Semple 911* (mo).—Seedling root tips.

Heterotheca latifolia Buckl. $n = 9_{II}$. Arkansas. sebastian co. Ft. Smith, IS-540 and Grand Ave., 22 Sept. 1973, *J. & K. Semple 925* (mo).

Heterotheca pilosa (Nutt.) Shinners. $n = 4_{II}$. Texas. dewitt co. 11 miles S of Cuero, 10 July 1970, *Lewis 7657* (mo).

Macheranthera scabrella (Greene) Shinners. $n = 4_{II}$ and $n = 3_{II} + 2_{I}$. Texas. presidio co. 13 miles SE of Redford on Hwy. 170, "Closed Canyon," *Averett 503B* (tex).—Buds from cultivated plants.

Macheranthera blephariphylla (Gray) Shinners. $n = 4_{II}$. Texas. presidio co. 13 miles SE of Redford on Hwy. 170, "Closed Canyon," *Averett 502* (tex).—Buds from cultivated plant.

Prionopsis ciliata (Nutt.) Nutt. (Syn. *Haplopappus ciliatus* Nutt.). $n = 6_{II}$. Kansas. butler co. US 77, 3 miles N of Kansas 96, 21 Sept. 1973, *J. & K. Semple 905* (mo). $2n = 12$. Kansas. butler co. El Dorado, 0.5 mile E of Kansas Turnpike, 21 Sept. 1973, *J. & K. Semple 904* (mo).—Seedling root tips. cowley co. Kansas Hwy. 15, 2.7 miles N of Oklahoma state line, 21 Sept. 1973, *J. & K. Semple 910* (mo).—Seedling root tips. Oklahoma. osage co. 1.0 mile N of Salt Creek on Oklahoma Hwy. 18 (S of Fairfax), 21 Sept. 1973, *J. & K. Semple 918* (mo).—Seedling root tips.

Spiracantha cornifolia H.B.K. $2n = 16$. Panama. canal zone. Summit Garden, 3 April 1971, *Semple 635* (mo).—Seedling root tips.

Counts by F. H. Utech, Missouri Botanical Garden.

Liliaceae

Polygonatum pubescens (Willd.) Pursh. $2n = 20$ and $n = 10$. Tennessee. sevier co.: Great Smoky Mountains Natonal Park, Laurel Run, 1.5 miles NNE of Cades Cove, elev. 2000 ft., 27 April 1972, *Utech 25* (mo). $2n = 20$. Virginia. smyth co.: Jefferson National Forest, N slope of Mt. Rogers, 15 miles ENE of Damascus on US Hwy. 58, elev. 3800 ft., 5 May 1972, *Utech 81* (mo). page co.: Shenandoah National Park, Skyland Area, Stony Man Cliffs, mile 41.5 of Skyline Drive, elev. 3000 ft., 12 May 1972, *Utech 121* (mo).

Maianthemum canadense Desf. $2n = 36$. Massachusetts. berkshire co.: N slope of Mt. Greylock, 7 miles SW of North Adams, elev. 2900 ft., 4 June 1972, *Utech 281* (mo). Quebec. gaspe-est: Mont-Ste.-Anne, 1.0 mile W of Perce, elev. 800 ft., 13 June 1972, *Utech 311* (mo). Mt. Albert, 28 miles SSW of Ste.-Anne-des-Monts on Hwy 299, elev. 2500 ft., 16 June 1972, *Utech 331* (mo). New Jersey. sussex co.: High Point State Park, Saw Mill Road, elev. 1000 ft., 16 May 1972, *Utech 131* (mo). $2n = 36$ and $n = 18$. North Carolina. avery co.: SSW slope of Grandfather Mountain, 1.0 mile NE from Linville on US Hwy 221, 4 May 1972, *Utech 71*.

Maianthemum dilatatum (Wood) Nels & Macbr. $2n = 36$. California. humboldt co.: Redwood forest on campus of Humboldt State University, Arcata, elev. 650 ft., 30 July 1972, *Utech 6101* (mo). Oregon. benton co.: Siuslaw National Forest, Mary's Peak, 25 miles WSW of Corvallis on Ore. Hwy 34. elev.

3500 ft., 8 August 1972, *Utech 5101* (mo). Washington. clallam co.: Olympia National Forest, Hurricane Ridge, 6 miles SSW of Port Angeles, elev. 1800 ft., 16 August 1972, *Utech 5161.*

Smilacina racemosa (L.) Desf. $2n = 36$. Oregon. linn co.: Willamette National Forest, Lost Prairie, South Santiam Hwy, 25 miles E of Cascadia, elev. 3300 ft., 7 August 1972, *Utech 5091* (mo). clatsop co.: Saddle Mountain State Park, 6 miles N of Necanicum, 6 miles N of US Hwy 26, elev. 1500 ft., 9 August 1972, *Utech 5112* (mo). Washington. chelan co.: Wenatchee National Forest, White Pine, 21 miles NW of Leavenworth, elev. 1800 ft., *Utech 5191* (mo).

Smilacina stellata (L.) Desf. $2n = 36$ and $n = 18$. Quebec. gaspe-est: Mont-Ste-Anne, 1.0 mile W of Perce, elev. 800 ft., 13 June 1972, *Utech 312* (mo). $2n = 36$. gaspe-ouest: Mont-St.-Pierre, 1.0 miles E of city, elev. 1000 ft., 15 June 1972, *Utech 322* (mo).

Streptopus amplexifolius (L.) DC. $2n = 32$. Oregon. jackson co.: Winema National Forest, Aspen Point, Lake of the Woods, 35 miles NW of Klamath Falls, elev. 4600 ft., 4 August 1972, *Utech 5021* (mo). clatsop co.: Saddle Mountain State Park, 6 miles N of Necanicum, 6 miles N of US Hwy 26, elev. 1800 ft., 9 August 1972, *Utech 5111* (mo).

Streptopus roseus Michx. $2n = 16$. Tennessee. sevier co.: Great Smoky Mountains National Park, Laurel Run, 1.5 miles NNE of Cades Cove, elev. 2000 ft., 27 April 1972, *Utech 24* (mo). North Carolina. swain co.: Great Smoky Mountain National Park, 2.0 miles S of Newfound Gap, elev. 4400 ft., 28 April 1972, *Utech 33* (mo). Pennsylvania. monroe co.: Tannersville Bog on Cranberry Road, elev. 1200 ft., 16 May 1972, *Utech 135* (mo).

A NEW *SPHAGNUM* FROM HIGH ALTITUDE COSTA RICA

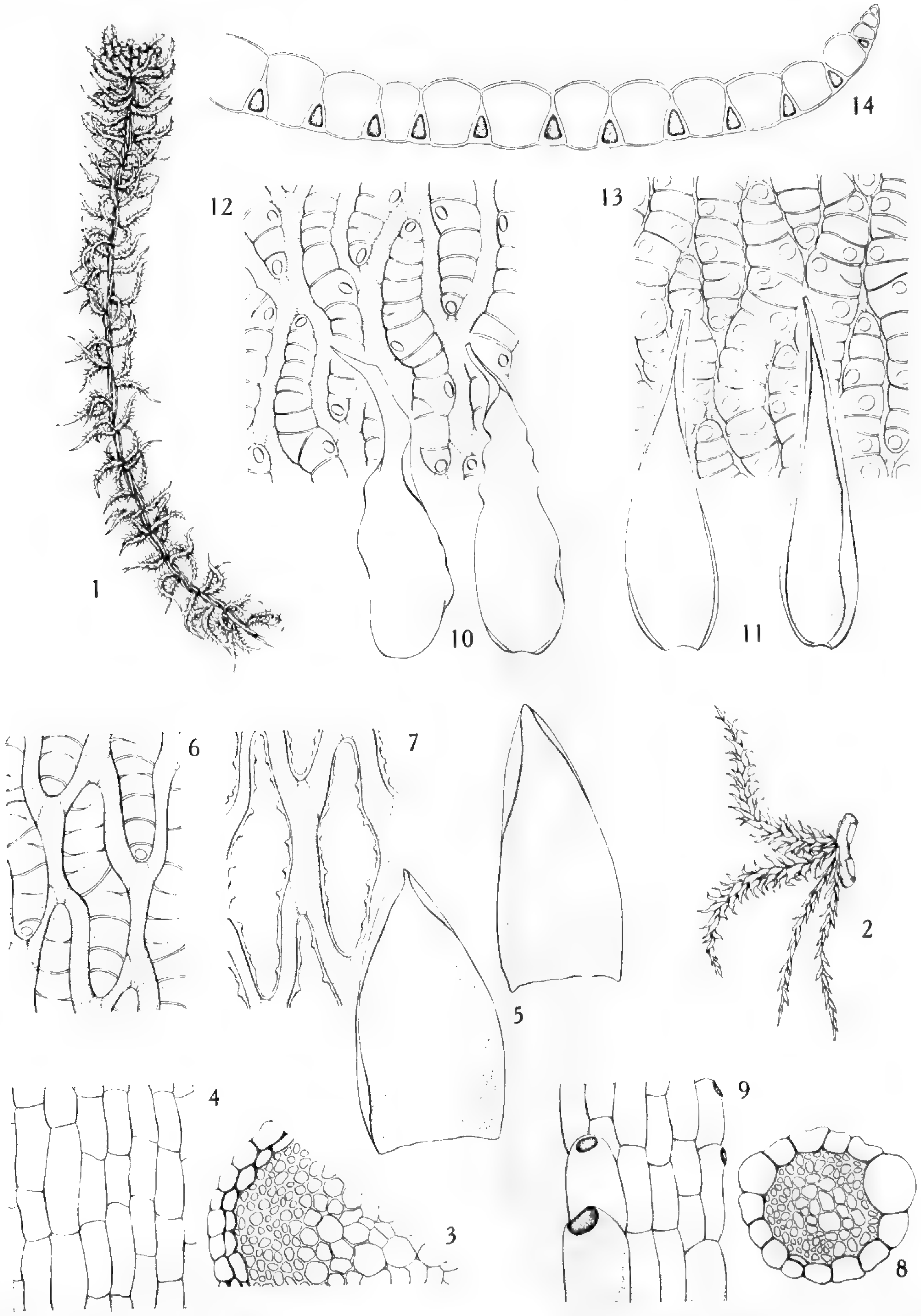
Sphagnum sancto-josephense Crum & Crosby, sp. nov.

Planta ± tenera, mollis, pallens. Epidermis caulina stratis 2 composita, a cylindro lignoso distincte diversa. Folia caulina ca. 1.4 mm longa, oblongo-ovata, acuta, ad apicem dorso superficie fibrosa; limbus deorsum non dilatatus. Folia ramulina 1.7–1.8 mm longa, anguste lanceolata, madida concava, sicca ± plana et valde undulata, fibrosa, dorso superficie pori pauci (2–3) et parvi, in angulis, atque interiore superficie pori multi (4–11), ± magni, rotundi; cellulae chlorophylliferae sectione transversali triangulae, interiore folii superficie inclusae.

Plants rather slender, in soft, loose, pale, yellowish-green tufts; terminal bud not noticeably differentiated; young pendent branches not in pairs. *Stems* yellowish; cortical cells moderately enlarged, thin-walled, in 2 layers, elongate-rectangular (3–4:1) in surface view, without pores or fibrils; wood cylinder yellowish.

→

Figures 1–14. *Sphagnum sancto-josephense.*—1. Habit, dry, × 1.—2. Fascicle, dry, × 3.—3. Stem in cross-section, × 117.—4. Stem cortex in surface view, × 117.—5. Stem leaves, wet, × 27.—6. Cells of stem leaf at middle of apical portion, outer surface, × 400.—7. Cells of stem leaf at middle of apical portion, inner surface, × 400.—8. Branch in cross-



section, × 117.—9. Branch cortex in surface view, × 117.—10. Branch leaves, dry, × 27.—11. Branch leaves, wet, × 27.—12. Cells of branch leaf in upper one-fourth, outer surface, × 400.—13. Cells of branch leaf in upper one-fourth, inner surface, × 400.—14. Branch leaves in cross-section, in upper one-fourth of leaf, × 400. [Drawings prepared by Constance Butley.]

Stem leaves ca. 1.4 mm long, somewhat concave, oblong-ovate, acute, not noticeably bordered; hyaline cells undivided, without membrane pleats, mostly resorbed on the inner surface, with fibrils and occasional end pores near the apex on the outer surface. *Branches* in fascicles of 4–5, with 2 or 3 spreading; cortex in 1 layer, the retort cells often 1 above the other, moderately large, with rather inconspicuous necks. *Branch leaves* flat and wavy when dry, concave, 5-ranked, and narrowly lanceolate when moist, 1.7–1.8 mm long, narrowly bordered by several rows of linear cells and entire except at the narrowly truncate apex; hyaline cells linear-rhomboidal, fibrillose, on the inner surface somewhat convex, with numerous (4–11), rather large and conspicuous, rounded pores with thin margins along the commissures (similar in size, number, and distribution throughout the leaf), on the outer surface nearly plane, with 2–4 small and inconspicuous, somewhat ringed, rounded or elliptic pores at ends and corners; green cells as seen in cross-section triangular, exposed on the outer surface, not reaching the inner surface, the lumen also triangular. Inflorescences and sporophytes unknown.

COSTA RICA: In a small bog, 3333 m alt., near the summit of Cerro de la Muerte, along the Pan-American Highway, 83° 45′ W, 9° 30′ N, *Marshall R. Crosby 2578A*, March 1, 1966 (holotype MICH; isotypes CR, MO).

This species (of the section *Cuspidata*) closely resembles *Sphagnum recurvum* P.-Beauv. and its numerous relatives because of leaves flattened and wavy at the margins when dry. A difference of basic importance is provided by the abundance of large, rounded pores on the inner surface of hyaline cells of branch leaves, easily discernible even on light staining. The fairly large, concave, acute stem leaves are distinctive too. The fact that the young pendent branches, as viewed between the rays of the capitulum, do not seem paired aids in distinguishing this from the S. *recurvum* group in the field.—*Howard Crum, Herbarium, University of Michigan, Ann Arbor, Michigan 48104* and *Marshall R. Crosby, Missouri Botanical Garden.*

REDUCTION OF *BOSLERIA* (SOLANACEAE)

Perhaps prompted by the occurrence of another endemic solanaceous genus in the region, *Oryctes* S. Wats., Aven Nelson described a puzzling collection as *Bosleria nevadensis* A. Nels. (Proc. Biol. Soc. Washington 18: 175. 1905). Examination of the type collection, *G. H. True 761* (RM) from Pyramid Lake, Washoe Co., Nevada, 9 June 1903, reveals it to be *Solanum sarachoides* Sendt., a species from the Argentine now naturalized through the northwestern states. The *True* collection agrees with Nelson's description. As *B. nevadensis* is the sole name published in *Bosleria* and its type species, the generic name *Bosleria* is a synonym of *Solanum*.—*W. G. D'Arcy, Missouri Botanical Garden.*

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 61, No. 2, pp. 264–538, was published on 11 October 1974.

GEORGE ENGELMANN'S NOTES ON THE POLLINATION OF *YUCCA*

The first published report of the extraordinary interaction between *Yucca* and the moths which pollinate it seems to be a letter dated June 1872 by George Engelmann in Bull. Torrey Bot. Club 3: 33. 1872. After discussing the structure and behavior of the *Yucca* flower, Engelmann noted simply: "Nocturnal insects are the agents [of pollination]—in our gardens at least, a white moth of the genus Tortrix."

In the next issue of the same journal (Bull. Torrey Bot. Club 3: 37. 1872) Engelmann noted several errors which had crept into his original letter, including " . . . you made me refer the moth in question to the *Genus Tortrix.* I undoubtedly said '*allied* to Tortrix.' " He then briefly described the feeding behavior of the young larvae.

Engelmann's voluminous notes and drawings, often scrawled on the backs of apothecary's prescription forms and in one case on the back of a letter from the tax collector stating that Engelmann's taxes were overdue, are preserved in the Missouri Botanical Garden Library. A folded sheet of foolscap bears the original observations on the pollination of *Yucca*:

> 1872. June 13th . . . .
>
> I see many insects about the flowers, bees, bumblebees and others, but principally a white moth of the alliance of *Tortrix* [crossed out] *Tinea*, often two (a pair!) in one flower, which fly at dusk, but are quickly [?] hid in the flower in day time.
>
> They seem to transport the pollen into the stigmatic tube. . . .
>
> July 16th. Capsules very much constricted, remain small, none full grown. Today [I] observed the first holes in them, where a larva of our [?] moth has gnawed through and escaped (into the ground?). Opening a capsule I find 4 or 5 more larvae in it and almost all the seeds eaten up.
>
> In the first days of July *Mr. Riley* found the Yucca in full bloom in Kirkwood [Missouri], fertilized by the moth—which by a peculiar appendage of the mandible (peculiar to the female, wanting in the male) gathers up the pollen, pushes it into the stigmatic tube and lays its egg (into it—no) [parentheses and "no" added later in pencil].

While Engelmann contributed subsequent papers on *Yucca*, none seems to be concerned with further observations on its pollination. Charles V. Riley continued to work and publish on *Yucca* pollination and summed up 20 years of research as "The *Yucca* moth and *Yucca* pollination" in Annual Rep. Missouri Bot. Gard. 3: 99–158, pl. 34–43. 1892. Kirkwood, Missouri, is also the area in which Phil Rau carried out observations in the late 1930's and early 1940's for his "Ecologico-behavior study" of *Yucca* plants and *Yucca* moths (Ann. Missouri Bot. Gard. 32: 373–394. 1945). An excellent recent bibliography on *Yucca-Yucca* moth interaction appears in J. A. Powell and R. A. Mackie, Biological interrelationships of moths and *Yucca whipplei* (Lepidoptera: Gelechiidae, Blastobasidae, Prooxidae) (Univ. California Publ. Entomol. 42. 59 pp. 1966).—*Editor.*

Angiosperm Biogeography and Past Continental Movements

Peter H. Raven and Daniel I. Axelrod

"The isolation of land areas by sea-floor spreading, the uplift of new cordilleras, the emergence of new archipelagos and the disappearance of old ones, and the shifting positions of (some) landmasses have both created and destroyed environments to which biota have responded. In this sense, changing physical environments governed by plate tectonics have had a major role in evolutionary history. Plate tectonic theory thus provides a more reliable basis for analyzing changes in land-sea relations and changes in climates, and hence for interpreting problems of evolution and distribution, than has been available earlier. The reappraisal of the nature of the earth's crust by plate tectonic theory does not require any modifications of previously established major principles of evolution. However, it does demand that we recognize certain new principles of biogeography. . . .

"In the present paper, we examine the distributions of flowering plants, present and past, and attempt to interpret them in the light of newly available geological evidence. Although the field is vast, . . . we believe that an overview of angiosperm distributions in the light of geological history as now suggested by plate tectonic theory will be useful in suggesting new hypotheses and new directions for future research."

Reprints of this exhaustive, 150-page-long review are available for $3.50, postpaid. It originally appeared in volume 61, number 3, of the ANNALS in 1974.

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