The Chemotaxonomy of Plants

P. M. Smith

CONTEMPORARY BIOLOGY

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First published 1976
by Edward Arnold (Publishers) Limited
25 Hill Street, London W1X 8LL

Boards edition ISBN: 0 7131 2544 6
Paper edition ISBN: 0 7131 2545 4

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Printed in Great Britain by
J. W. Arrowsmith Ltd.,
Bristol, England

Preface

Chemotaxonomy is a field of scientific investigation which has attracted students and researchers from diverse academic disciplines. Taxonomists and chemists represent obvious end points of the spectrum of interests now brought to bear on the application of chemical evidence to taxonomic studies. In some ways taxonomists and chemists are very different kinds of scientist, and the philosophical meeting ground between them is small and inadequately explored. Yet, if the hybrid subject of chemotaxonomy is to manifest full hybrid vigour, the chemist and the taxonomist must begin to understand each other better.

In most first degree courses it is inappropriate or impossible to pursue both disciplines beyond an elementary level. Often the aspiring taxonomist may have little time and perhaps less taste for elementary chemistry in the early stages of his career. Nevertheless, he must understand something of the strengths and limitations of chemical methodology and data, if he wishes eventually to evaluate chemotaxonomic evidence relating to the organisms which he studies. Similarly the chemist who realizes that his techniques or results have a taxonomic or evolutionary relevance is seldom trained to appreciate the different demands and approaches of the biological subject.

It is hoped that this book may enable chemists and taxonomic biologists to glimpse possible areas where they may cooperate with mutual profit. To this end, facts and methods of chemistry and taxonomic principles are both gently introduced, and then integrated. Copious references are cited to facilitate subsequent penetration into either chemical or taxonomic literature.

Chemotaxonomic facts are used to illustrate principles and problems in chemotaxonomy, but no attempt is made to discuss chemosystematics *in extenso*. *Chemotaxonomy*—the subject of the book — is here regarded as the practice by which is produced *chemosystematics*—a body of chemical evidence and the classifications in which it is employed. Evolutionary significance of chemical data is considered when relevant, but taxonomic and phylogenetic problems are regarded as distinct, if sometimes related, matters. Functions of chemical characters are discussed.

Though chemotaxonomy has been well provided with research-orientated texts in the past, often in the form of symposium reports or multi-author, multi-level compilations (e.g. *Chemistry in Botanical Classifications*, ed. Bendz and Santesson 1973), I have felt for some time that a more introductory, homogeneous and relatively inexpensive treatment was needed, especially for students. The various past reviews have not been particularly accessible to the embryo chemotaxonomist, and much relevant material has been widely scattered. Alston and Turner's *Biochemical Systematics*[12] had an introductory, even pioneering function, but progress since 1963 has been rapid. Multi-volume encyclopaedias of chemosystematic data, such as Hegnauer's monumental *Chemotaxonomie der Pflanzen*[221] and Gibbs' *Chemotaxonomy of Flowering Plants*[179] have little discussion of taxonomic principles and problems. They are primarily reference books. Several excellent handbooks on chemical procedures are available (e.g. Harborne[209]), so it has not in general been thought necessary to include the minutiae of analytical methods in the present work.

I am grateful to various people for helping me to write about chemotaxonomy. I thank particularly Dr P. H. Davis, Dr R. O. D. Dixon and Professor G. L. Stebbins for reading draft material; Professor A. J. Willis for his careful editorial scrutiny, suggestions and encouragement; and Edward Arnold Ltd, for their calm efficiency. Finally and fundamentally, I thank my wife and family for their forebearance.

Edinburgh, 1975 P. M. S.

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Contents

PART I

Possibilities and Problems

I

Introduction

Taxonomy is the theory and practice of classification, and **chemotaxonomy** incorporates the principles and procedures involved in the use of chemical evidence for classificatory purposes. **Chemical Systematics** is the study of the chemical variation in a diversity of organisms, and of their relationships. This book does not aim to give accounts of the systematics of any group of plants but rather to introduce and illustrate the ways in which chemical data may be used with profit to taxonomists. Most taxonomists strive to produce **natural classifications**, that is, classifications based on consideration of as many features of the organisms as possible, which it is *hoped* will reflect their evolutionary relationships. Features used in a classification are termed **taxonomic characters**. All sources of taxonomic evidence are scanned in the search for taxonomic characters, and among the richest have been the fields of morphology, anatomy, cytology, ecology and genetics. The widespread use of chemical data as taxonomic characters marks a recent extension of the range of recognized sources of taxonomic evidence—a range which has been widening for several hundred years.

Most taxonomists are interested in the relationships of the organisms which they study, as well as in the best ways to classify them. It is very difficult to produce a natural classification without being aware of the possible affinities of the species or other groups which are recognized. Chemical taxonomy, like any other contributory discipline, will provide evidence for or against schemes of relationship between the taxonomic groups (taxa) which it helps to define. The

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extent to which chemical data may be useful in suggesting or testing schemes of relationship will therefore be considered in the chapters which follow.

To speak of relationship without qualifying the meaning further is to introduce a vagueness which has characterized certain work in the field of chemical taxonomy. There is the relationship between all plants which have descended from a common ancestor which we describe as **evolutionary** or **phylogenetic relationship**. There is also a relationship between plants in terms of some shared feature or features, regardless of the reason for the sharing, based simply on the resemblances which they show in the features studied. Such relationships based upon perceived similarities are described as **phenetic.** Chemical analyses might show that certain plant species were all very similar in terms of the polysaccharides stored in their seeds. This would reveal a phenetic relationship but not necessarily a phylogenetic one. Many workers in chemical taxonomy have become interested in the problems of plant evolution and in many cases the aim of their studies seems not to be the provision of chemical evidence for better classification, but to shed light upon the phylogeny of the plant taxa with which they work. These different purposes are not always stated clearly. Our knowledge of the origin and evolution, i.e. the phylogeny, of many plant groups is so sparse that we must welcome any further knowledge from chemical analysis of living plants which may reinforce other comparative phenetic studies and the impoverished fossil record. As with comparative morphology, that main-stay of phylogenetic speculations, the evidence of the chemist and biochemist must be scrutinized with great care.

The distinctions between phenetic, phylogenetic and natural classifications are fully discussed in recent taxonomic works[118,230,233].

The principles, procedures and results of investigations into the chemical variation of plant taxa are therefore applied mainly for two different purposes: first, to provide taxonomic characters which may improve existing plant classification, i.e. a strict taxonomic purpose, and second, to add to knowledge of phylogeny or evolutionary relationship. An introduction to chemotaxonomy must explore the potential contribution and usefulness of chemical evidence to both.

Perhaps a brief word on the status of the two purposes of chemotaxonomy would be appropriate here. Phylogeny and evolution have always been compellingly interesting to biologists, and it is noteworthy that the fascination of the subject has recently diverted many chemists and biochemists from their orthodox enquiries.

Knowledge of phylogeny in any group aids genetic manipulation of the species in the group for human gain, particularly important when the group in question includes cultivated plants. The classification of plants, or of any other objects, seems to be a basic human behaviour pattern which we cannot avoid—we have an urge to classify. So necessary is the recognition of the entities in our environment to our survival, to efficient communication and to optimal exploitation of resources, that our art or science of taxonomy by which we achieve this recognition must be a fundamental reason for our success as a species.

THE PLACE OF CHEMISTRY IN TAXONOMY AND SYSTEMATICS

Studies of chemical variation have been suggested to be one of the principal growing points in the field of taxonomy and systematics. Reasons why chemotaxonomy seems so exciting at present will be reviewed in the next chapter. Here we should relate the subject to the other activities of taxonomists in order to place it in perspective.

Figure 1.1 is a 'taxonomic flow chart' which shows that though chemotaxonomy has become such a large and useful treasury of new facts for the taxonomist, it must not be thought of as a replacement for his traditional work. At best it is a major source of new characters and information. All other sources of taxonomic evidence still exist and are still producing new ideas and facts which cannot be ignored. Chemical facts are not vital to the continuation of improvement in taxonomy, except in the case of bacteria and some other microorganisms, but are extremely helpful and stimulating. The taxonomic contributions of cytology and of genetics, both still comparatively new fields, have been enormous. It is likely that chemical taxonomy or chemotaxonomy, by whatever name it is finally known, will make at least an equally great impact on our ideas of classification, and of phylogeny.

The 'whole' taxonomist, a hypothetical person, includes in his research some work in all the departments mentioned in the flow chart (Fig. 1.1). In most cases, the taxonomist is unable through lack of time, knowledge or skill to produce evidence of all the different types personally. Instead he will try to integrate all available evidence in his final conclusions about the classification and the evolutionary relationships of the group of plants concerned. Many scientists produce contributory taxonomic evidence almost as a by-product of their own work—on cytology or genetics, for

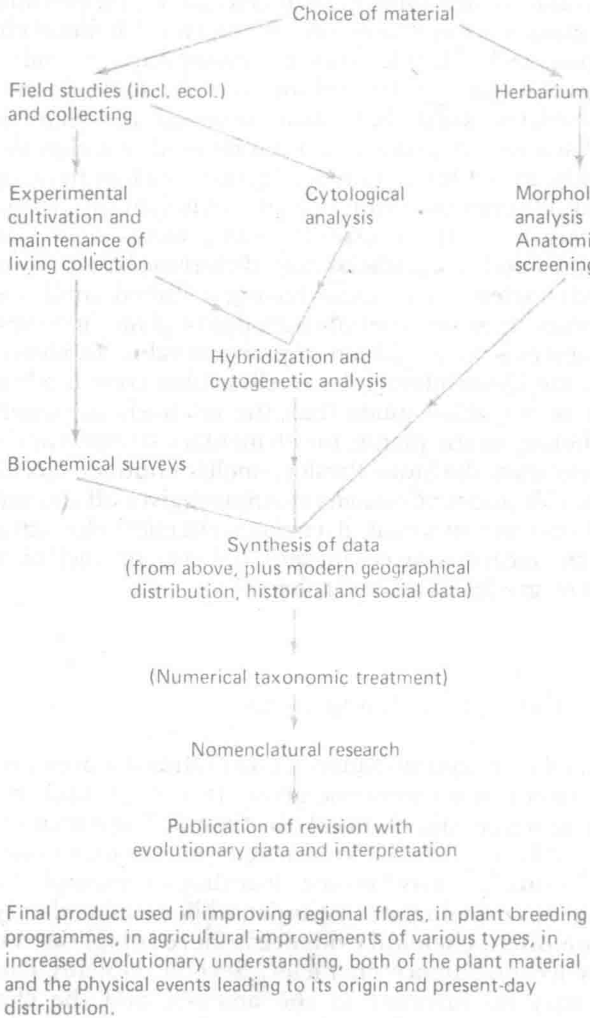

Fig. 1.1 A taxonomic 'flow chart'.

example. In the case of chemical evidence, the situation is often one where chemists or biochemists furnish chemical facts, which are then available for a taxonomist to consider subsequently. It would be profitable if both parties involved knew of the needs and problems of the other.

As a contributory discipline in both taxonomic and evolutionary studies, chemotaxonomy is now very important. Chemical characters have provided valuable clues to unsuspected or only half-suspected evolutionary relationships and in some cases have removed problems which have lain unsolved for many years. Chemical characters of plants can often be used in a classification almost or quite as readily as familiar features such as those of leaf arrangement, chromosome number and indumentum. In future, chemical characters will be essential components in systems of natural classification. In **artificial classifications**, based on one or only a few characters, and usually having a limited application in keys for identification, or in defining groups of plants in commerce, chemical features have long been of practical value. In identifying members of the Umbelliferae, the smells arising from the crushed foliage may be a quicker guide than the relatively homogeneous gross morphology of the plants, for elementary students and Early Man. *Sison amomum*, the Stone Parsley, smells of nutmeg mixed with petrol, while Coriander (*Coriandrum sativum*) gives off the smell of bed-bugs. These are practical, if curious, chemical characters. In commerce, chemical characters underly the taste or smell of different varieties or grades of tea and tobacco.

INFORMATION FROM MOLECULES

What form does chemical evidence take? Often it is presented as a statement that a given taxonomic group (taxon, pl. taxa) does or does not contain a certain chemical constituent. The distribution of the constituent becomes better known as a wider range of plants are analysed. Eventually it may become clear that, for example, certain species in a genus contain the constituent, while certain other species do not. More often, chemical evidence is more complicated than a single presence or absence character. Several or many chemical substances may be involved in the analysis, and the chemical characters may consist of the different *combinations* in which these are found to occur. More rarely, the character may be quantitative, i.e. one group may consistently contain much more of a substance than another group.

Not all kinds of chemical substance present in plants reveal information useful to the taxonomist. They are by no means all equal in the amount and value of taxonomic information conveyed. Part of this book is concerned with assessing the value of taxonomic evidence gleaned from the occurrence and distribution of the various kinds of chemical substances.

Unlike biochemists, taxonomists and evolutionists are only incidentally interested in molecules from the standpoint of how they may be synthesized, or what their function may be. Instead they are primarily concerned with the molecule as a carrier of information. Zuckerkandl and Pauling[514] have defined information-carrying molecules as **semantides**. Deoxyribonucleic acid (DNA) is now widely recognized as the physical basis of the genetic code—the information necessary to construct a new individual. This information is similar in similar organisms, and hence also in plants in similar species and similar genera. As the specification for an individual in all respects, DNA is a primary source of taxonomic information, as well as being the blue-print for development and differentiation. Evolutionists believe that similarity between organisms is normally proportional to the number of ancestors which they share, and to the age of their most recent common ancestor. Therefore DNA is also a primary source of information relating to phylogeny. Zuckerkandl and Pauling characterize it as a **primary semantide**. Ribonucleic acid (RNA) is a secondary source of this information (a **secondary semantide**) while the translation of the code into sequences of amino acids provides the taxonomist with **tertiary semantides** in the form of proteins. All chemical materials synthesized by an organism reflect the information in the semantide molecules to a greater or lesser degree. To varying extents all therefore contain useful information for taxonomy which may also have a bearing on phylogeny.

Other chapters examine the significance of the information in different types of naturally occurring substances, and comment on its value in studies of taxonomy or evolution in terms of its accessibility and ease of interpretation. Taxonomic information cannot always be readily extracted from the most obvious chemical sources. Improvements in analytical techniques have been so great in the recent past, providing so much of value to systematics, that taxonomists can look forward with high hopes of receiving more taxonomic or evolutionary evidence at present locked up in molecules. It will be freed completely only by substantial advances in technology and in methods of interpretation.

Further researches into techniques, and further use of available methods of analysis, will be most effective only if the aims and requirements of evolutionists and taxonomists are fully appreciated. They have not always been understood in the past. Chapter 3 attempts to define the kinds of chemical evidence most needed and also to emphasize the quite strict requirements necessary for chemical techniques and investigations if they are to gain acceptance by taxonomists in general. When the objectives and problems of taxonomists are better understood by technologists, perhaps 'purpose-built' techniques for chemical taxonomy will come forward. They are urgently needed.

CHEMICAL CHARACTERS, THE TAXONOMIC HIERARCHY, AND THE PLANT KINGDOM

How far may chemical evidence be useful throughout the Plant Kingdom? We have no reason to suppose that chemical evidence is limited in its applicability in any way to only part of the Plant Kingdom or to only part of the hierarchy of taxonomic categories. Numerous examples of taxonomically useful chemical facts can be cited in most groups of plants. Chemical evidence is of particular significance in the simplest organisms—the bacteria—and it has been used effectively in all more complex groups from the fungi to the most highly specialized angiosperms.

The identification, rather than the classification, of lichens has been considerably aided by the use of simple microchemical tests and crystallization reactions. Lichens form complicated organic molecules ('lichen substances') which produce colour reactions with simply applied test reagents such as potassium hydroxide and calcium hypochlorite. Some variation of the colour reaction within populations of certain species of lichen has been detected, and taxonomic problems arise from it.[109,139,197]

In the case of bacteria, the taxonomic characters provided by chemistry have long been vital to classification. These primitive organisms have so few structural features, even when viewed with the electron microscope, that their chemical properties have provided much of the evidence for delimitation of species, genera and higher categories. A glance through Bergey's fascinating *Manual of Determinative Bacteriology*[71] furnishes endless instances of the value of biochemical evidence in bacterial taxonomy. For example, the tribe Nitrobacterieae is defined largely on the ability of the members to gain energy from the oxidation of ammonia to nitrite or from nitrite to nitrate. Genera in this tribe are characterized partly by the rates at which they are able to carry out these oxidations.

Even in the bacteria, where the importance of chemical characters is well established, the newer concepts and techniques of chemo-

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