4 April 1968

Dr. Russell B. Stevens
National Research Council
2101 Constitution Avenue
Washington, D. C. 20418

Dear Sir:

Please find enclosed the devised version requested.

Very truly yours,

George F. Estabrook

GFE:gm

DDDr. Reyment's comments are very relevant and appropriate, but I would like to share some further considerations with you. I do not feel that biology is a branch of statistics. Statistical Analysis is not the only mathematical technique which might be useful in systematics. To assume that it is is to eliminate, a priori, from consideration many of the advances of modern mathematics which might not only serve to analyze biological information but also to make more precise the basic principles of systematics. I would urge that an open mind be kept towards such branches of mathematics as combinatorial analysis, logic, and information theory.

I would like to emphasize Dr. Reyment's admonition that care be taken before employing a given statistical technique. We must be very careful that we do not make biology fit the statistics, but make sure that statistics fits biology. Dr. Reyment pointed out that certain statistical techniques tend to frown on redundancy. One of the effects of a principle component analysis, for example, is to summarize variation more efficiently by eliminating redundancy, i.e., correlations between the descriptors. However, many practicing taxonomists accept the idea that taxa are established with correlated characters. It is the redundancy in the descriptors which enables us to delimit, and later describe, taxa.

As biologists our primary concern whould be with the advancement of biology. Toward this end, mathematics may be used to help us to a firmer understanding of the principles of biology, as well as to help us process data. Thus, before any mathematical technique is used to analyze data it is essential that the biologist knows and accepts what biological principles the mathematical techniqqe assumes to be in force. Care should be taken that the mathematics should be appropriate to its biological application, rather than making mathematics a "bed of Procrustes" for the biology it is designed to serve.

Taximetrics Laboratory

Armory 101

13 July 1967

Dr. Russell B. Stevens
National Research Council
2101 Constitution Avenue
Washington, D. C. 20418

Dear Dr. Stevens:

The answer to your three questions concerning the Systematics Conference are as follows:

1. I am sending the rough notes of my participation in the informal discussion herewith.

2. You have already received my manuscript for my participation.

3. My manuscript has no illustrations.

The discussion in which I participated and which you have circled has been numbered for your convenience.

Sincerely,

David J. Rogers
Professor of Biology

DJR:gm

COMMENTS DURING DISCUSSION: (refers to discussion on line 67, page 5 of "Sequence of Speakers.")

"The problems brought up in this discussion (on molecular systematics) sound very similar to those faced for many years by the rest of us 'non-molecular' taxonomists. Such statements as - 'if we just had a little more data along these lines', or 'when such and such a piece of hardware (equipment) is available', etc., etc. indicate that using the information gained in this field provides the same difficulties we have had right along. Therefore, we hope the molecular people will join us in our search for taxonomic metholologies, where we worry about more scientific methods of using the information gained by various techniques.

"Along these lines, I have heard this panel using the work 'quantitative' as though it had some special meaning in relationship to molecular taxonomic characters. The question is: why are characters in molecular toxonomy more 'quantitative' than the 'number of petals', or 'the number of vertebrae', or 'fish scale counts', etc."

There were some other statements I made at about the same time, but since I didn't write them down, I have forgotten what was said. Perhaps they should just be eliminated.

DISCUSSION # 63

I believe my comments here were directed to those statements made by Peters in his discussion. I think that the gist of my comments are as follows:

"I disagree with Dr. Peters when he says that information retrieval systems should not deal with the 'trivia' of taxonomy. I firmly believe that hardware systems definitely should be employed to relieve the taxonomist of the need to shuffle the trivia of taxonomy around."

Other than this statement, I do not recall any others that I might have been made.

SEQUENCE OF SPEAKERS - SYSTEMATICS CONFERENCE

I. Wednesday, June 14 (Sibley, Chairman)

1. Dr. A. G. Norman (welcome)
2. Dr. Charles Sibley
3. F. A. STAFLEU - AN HISTORICAL REVIEW OF SYSTEMATIC BIOLOGY
4. M. T. GHISELIN - PRINCIPLES AND CONCEPTS OF SYSTEMATIC BIOLOGY
5. Discussion by Hermann Gisin
6. Discussion by David L. Hull
7. (Informal discussion involving James S. Farris and Ghiselin)
8. W. H. WAGNER - CONSTRUCTION OF A CLASSIFICATION
9. Discussion by H. H. Ross (delivered by Robert T. Allen)
10. Discussion by M. P. Starr
11. (Informal discussion involving Cronquist, Wagner and Farris)

II. Thursday, June 15 (Usinger, Chairman)

12. ROBERT ORNDUFF - SYSTEMATICS OF POPULATIONS IN PLANTS
13. Discussion by K. L. Chambers
14. Discussion by H. J. Thompson
15. (Informal discussion involving Cronquist)

16. D. W. TINKLE - SYSTEMATICS OF POPULATIONS IN ANIMALS

    17. Discussion by R. F. Inger

    18. Discussion by Allen Keast

19. (Informal discussion involving Beschel, and Blair)

20. A. R. KRUCKEBERG - ECOLOGICAL ASPECTS OF THE SYSTEMATICS OF PLANTS

    21. Discussion by Calvin McMillan

    22. Discussion by P. V. Wells

23. (Informal discussion involving Beschel, Kruckeberg, Sibley and P. Raven)

24. R. K. SELANDER - ECOLOGICAL ASPECTS OF THE SYSTEMATICS OF ANIMALS

    25. Discussion by L. B. Brower

    26. Discussion by B. C. Clarke

27. (Informal discussion involving Blair, Selander, Alexander, and L. L. Short)

III. Thursday, June 15 (Morris Goodman, Chairman)

28. JOZEF DE LEY - MOLECULAR DATA IN MICROBIAL SYSTEMATICS

    29. Discussion by Manley Mandel

    30. Discussion by A. W. Ravin

31. (Informal discussion)

32. JUAN H. HUNZIKER - MOLECULAR DATA IN PLANT SYSTEMATICS

    33. Discussion by Bert G. Brehm

    34. Discussion by Otto T. Solbrig

35. (Informal discussion involving Hunziker, Sibley, Brehm, Cronquist and Low)

36. H. C. DESSAUER - MOLECULAR DATA IN ANIMAL SYSTEMATICS

    37. Discussion by Margoliash

    38. Discussion by Throckmorton

39. (Informal discussion involving Clarke, Selander, Throckmorton, Farris)

IV. Friday, June 16 (Blackwelder, Chairman)

40. WALTER BOCK - COMPARATIVE MORPHOLOGY IN SYSTEMATICS

    41. Discussion by W. L. Stern

    42. Discussion by David B. Wake

43. (Informal discussion involving Bock, Wake, Sokal, and Farris)

44. M. J. LITTLEJOHN - SIGNIFICANCE OF ISOLATING MECHANISMS

    45. Discussion by Frank Blair (delivered by Bobbi Low)

    46. Discussion by Eviatar Nevo

47. (Informal discussion involving P. Raven, Littlejohn, Gottlieb)

48. R. D. ALEXANDER - COMPARATIVE BEHAVIOR IN SYSTEMATICS

    49. Discussion by P. A. Johnsgaard

    50. Discussion by P. H. Raven

V. Friday, June 16 (Cronquist, Chairman)

51. HARLAN LEWIS - COMPARATIVE CYTOLOGY IN SYSTEMATICS

    52. Discussion by R. C. Jackson

53. Discussion by W. H. Lewis

54. (Informal discussion involving Gottlieb, Lewis, Beschel and ?)

55. R. A. REYMENT - BIOMETRICAL TECHNIQUES IN SYSTEMATICS

56. Discussion by E. C. Olson

57. Discussion by R. R. Sokal

58. (Informal discussion involving Estabrook and ?)

59. WILLIAM BOSSERT - COMPUTER TECHNIQUES IN SYSTEMATICS

60. Discussion by D. J. Rogers

61. Discussion by F. James Rohlf

62. Discussion by James A. Peters

63. (Informal discussion involving Gilmartin, Cronquist, Cutler, Peters and Rogers)

64. E. O. WILSON - SUMMARY OF THE CONFERENCE

VI. Evening, Friday, June 16 (Sibley, Chairman)

65. ERNST MAYR - THE ROLE OF SYSTEMATICS IN BIOLOGY

VII. Evening, Thursday, June 15 (Sibley, Chairman)

66. "Molecular Systematics - A view of the Future"

Brehm

DeLey

Dessauer

Goodman

Hunziker

Mandel

Margoliash

Ravin

Solbrig

Throckmorton

67. (Informal discussion involving Sokal, Rogers, Farris, Wilson, Cronquist, Clarke, Howden, and Tihen(?))

Dr. Rogers

JUL 11 1967

NATIONAL RESEARCH COUNCIL

NATIONAL ACADEMY OF SCIENCES NATIONAL ACADEMY OF ENGINEERING

2101 CONSTITUTION AVENUE WASHINGTON, D.C. 20418

DIVISION OF BIOLOGY AND AGRICULTURE

July 3, 1967

Memorandum to Participants, Systematics Conference

From: Russell B. Stevens R.B.S.

Subject: Proceedings Volume

If a proceedings volume is to be prepared promptly, it is absolutely essential that I have manuscripts from all participants who spoke either formally or informally at the recent conference on systematic biology. True, we do have the information on tape, but it would be prohibitively expensive of time and money to transcribe the entire 11 reels -- at best we can afford to do this only for the informal discussions and to clarify points here and there that are otherwise unclear.

Attached is a crude tabulation of the sequence of speakers at the conference, on which I have encircled your name where, so far as I can tell, there is a manuscript still due. If it is already in the mails on its way to this office, well and good. If not, please bend every effort to see that I have it immediately. Please, in any event, respond to the following three questions:

1. At those points where I have indicate that you joined the informal discussion, do you have any written material on which your remarks were based (even very rough notes will make transcription from the tapes quicker and more precise)?

2. If you have not already sent your manuscript for a formal paper or commentary, when can I expect to receive it?

3. Whether your manuscript is already in my hands or not, in those cases where slides were projected during the presentation, are there illustrations that are needed to make the published version understandable? If so, when can I expect to have them.

RBS:rvm

CONFERENCE: International Conference on Systematic Biology, University of Michigan
Ann Arbor, Michigan

DATE: June 14, 15, 16, 1967

DISCUSSANTS:

Dr. W. Frank Blair
Department of Zoology
University of Texas
Austin, Texas 78712

Dr. Bert G. Brehm
Biology Department
Reed College
Portland, Oregon 97202

Dr. Lincoln Pierson Brower
Department of Biology
Amherst College
Amherst, Massachusetts 01002

Dr. Kenton L. Chambers
HERBARIUM Department of Botany
Oregon State University
Corvallis, Oregon

Dr. Bryan Clarke
Department of Zoology
University of Edinburgh
West Mains Road
Edinburgh 9, Scotland

Dr. Russell F. Doolittle
Department of Biochemistry
University of California, San Diego
Post Office Box 109
La Jolla, California 92038

Dr. Hermann Gisin
Muséum d'Histoire Naturelle
Ville de Geneve
Geneve, Switzerland

Dr. Morris Goodman
Department of Anatomy
Wayne State University
1400 Chrysler Freeway
Detroit, Michigan 48207

Dr. David L. Hull
College of Letters & Science
University of Wisconsin
3203 Downer Avenue
Milwaukee 11, Wisconsin

Dr. Robert F. Inger
Program for Environmental Biology
National Science Foundation
Washington, D. C. 20550

Dr. R. C. Jackson
Department of Botany
University of Kansas
Lawrence, Kansas 66045

Dr. Paul A. Johnsgard
Department of Zoology and Physiology
University of Nebraska
Lincoln, Nebraska 68508

Dr. Allen Keast
Department of Biology
Queens University
Kingston, Ontario
Canada

Dr. Walter H. Lewis
Director of the Herbarium
Missouri Botanical Garden
2315 Tower Grove Avenue
St. Louis, Missouri 63110

Dr. Manley Mandel
Texas Medical Center
University of Texas
Houston 25, Texas

Dr. E. Margoliash
Department of Molecular Biology
Abbott Laboratories
North Chicago, Illinois 60064

DISCUSSANTS, continued

Dr. Calvin McMillan
Department of Botany
University of Texas
Austin, Texas 78712

Dr. Eviatar Nevo
Saar
Galil Maarair
Israel

Dr. Everett C. Olson
Committee of Paleozoology
Walker Museum
University of Chicago
Chicago, Illinois 60637

Dr. Peter Raven
Division of Systematic Biology
Stanford University
Stanford, California

Dr. Arnold W. Ravin
Department of Biology
University of Rochester
River Campus Station
Rochester, New York 14627

Dr. D.J. Rogers
Department of Botany
Colorado State University
Fort Collins, Colorado 80521

Dr. F.J. Rohlf
Department of Entomology
University of Kansas
Lawrence, Kansas 66045

Dr. H.H. Ross
Section of Faunistic Surveys & Insect Identification
Illinois Natural History Survey
Natural Resources Building
Urbana, Illinois 61801

Dr. Robert R. Sokal
Department of Entomology
University of Kansas
Lawrence, Kansas

Dr. Otto T. Solbrig
Department of Botany
University of Michigan
Ann Arbor, Michigan 48104

Dr. Mortimer P. Starr
Department of Bacteriology
University of California, Davis
Davis, California 95616

Dr. William Stearn
Smithsonian Institution
Washington, D.C. 20560

Dr. H.J. Thompson
Department of Botanical Sciences
University of California, Los Angeles
Los Angeles, California 90024

Dr. Lynn H. Throckmorton
Department of Zoology
University of Chicago
1101 East 57th Street
Chicago, Illinois 60637

Dr. David B. Wake
Department of Anatomy
University of Chicago
1025 East 57th Street
Chicago, Illinois 60637

Dr. Philip V. Wells
Botanical Garden
Department of Botany
University of California, Berkeley
Berkeley, California 94720

CONFERENCE: International Conference on Systematic Biology, University of Michigan
Ann Arbor, Michigan

DATE: June 14, 15, 16, 1967

SPEAKERS:

Dr. Richard D. Alexander
Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104

Dr. Walter Bock
Department of Biological Sciences
Columbia University
New York, N.Y. 10027

Dr. William Bossert
The Biological Laboratories
Harvard University
Cambridge, Massachusetts 02138

Prof. Dr. J. De Ley
Lab. voor Microbiologie
Casinoplein, 21
Gent, Belgium

Dr. Herbert C. Dessauer
Department of Biochemistry
Louisiana State University Medical Center
1542 Tulane Avenue
New Orleans, Louisiana 70112

Dr. Michael T. Ghiselin
Systematics - Ecology Program
Marine Biological Laboratory
Woods Hole, Massachusetts

Dr. Juan H. Hunziker
Genética II
Facultad de Ciencias Exactas y Naturales
Universidad de Buenos Aires
Perú 222
Buenos Aires, Argentina

Dr. A.R. Kruckeberg
Department of Botany
University of Washington
Seattle, Washington 98105

Dr. Harlan Lewis, Dean
College of Letters and Science
University of California, Los Angeles
Los Angeles, California 90024

Dr. Murray J. Littlejohn
Department of Zoology
University of Melbourne
Parkville N. 2, Victoria
Australia

Dr. Robert Ornduff
Department of Botany
University of California, Berkeley
Berkeley, California 94720

Dr. Richard A. Reyment
Geologiska Institutionen (Biometriska Laboratoriet)
Stockholms Universitet
Stockholm 45
Sweden

Dr. Robert K. Selander
Department of Zoology
University of Texas
Austin, Texas 78712

Dr. F.A. Stafleu
106 Lange Nieuwstraat
Utrecht, Netherlands

Dr. Donald W. Tinkle
Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104

Dr. Warren H. Wagner, Jr.
University of Michigan
Botanical Gardens
1800 North Dixboro Road
Ann Arbor, Michigan 48105

Dr. E.O. Wilson
The Biological Laboratories
Harvard University
16 Divinity Avenue
Cambridge, Massachusetts 02138

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$113.83

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2101 CONSTITUTION AVENUE, WASHINGTON, D.C.
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David J. Rogers Date 6-12, 1967

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INTERNATIONAL CONFERENCE
ON
SYSTEMATIC BIOLOGY

June 14-16, 1967

The University of Michigan
Ann Arbor, Michigan

TESSENE NO 5 6/23

Kluge - 764-6219

Stafleu - 6/14 - history
"Logical" class. - Theophr.
"Natural" genera -
Brunfels, Fuchs - alphabet genera in herbals
Principles
contigent - vs. logical
infinite gradient in org. contrary to tax.
Clash between abstract logic + "facts" of biologicals.
Phanerogamists end of 18th cent.
Caesalpino 1st botanist. many ways class - which characters direct the class
"Fundamental" chars. nutrition + ———
1st consistent aprioristic class.
"Deduction"?? was used -
32 groups of fl. plants.
1680 Magnol - French - plea for combination of characters - erected family -
Ray contemporary, 1682, of Magnol -
pragmatist - morph. criteria largely -
assigned genera.
Tournefort, 1700 pragmatist - order large no. org.
18th Cent. - explosion of pl. received spec. + knowledge.
Linneaus - ...

Bufon + Adanson - 1st "systematists", premises a diagnostic class - identif.
Bufon opposed to Linnaeus - Hist. Natural.
original thoughts
1. sp. had physical identity. species has a natural existence.
2. comparing species as present today and in the past -
3. Biological species concept.
4. Time element in systematics.
3. Phylogenetic concept established.
Biol. knowledge dissociated from physics
Moved tax. from definition to description.
Lack of "empirical" proof - practicality.
Bufons thought of "stream of life" but reality
Adanson - no apriori value of characters.
origin of species by hybridization + also of mutants.
Cuvier - 1812 - 1st big zool. system. Fixity of species.
Lamarck —

Ghiselin, M. T. - Principles of
2 Concepts -
1. Natural system
JS Mill 1874 - "Logic".
quote Gilmour's definition. = a phenomenalist -
" Sneath - not true "natural".
= overall similarity! ???

Herb Wagner 6/14 - Construction of Classif.

Ornduff 6/15

- Taximetrics Laboratory

June 20, 1967

Dr. Russell B. Stevens
Division of Biology and Agriculture
National Academy of Sciences
2101 Constitution Avenue
Washington, D.C. 20418

Dear Dr. Stevens:

Enclosed please find a copy of my discussions at the International Conference on Systematic Biology just passed. This paper is to follow Dr. William Bossert's presentation entitled "Computer Techniques in Systematics."

Sincerely yours,

David J. Rogers
Professor of Botany

DJR/ch

Enc.

Discussion by David J. Rogers following
Dr. William Bossert's paper entitled

COMPUTER TECHNIQUES IN SYSTEMATICS

Given at the
International Conference on Systematic Biology
Ann Arbor, Michigan

June 13 - 16, 1967

Perhaps the most significant implications of Dr. Bossert's presentation were intellectual ones. The computer system does not rise or fall, be successful or unsuccessful on the basis of a method of using it. There have been sufficient number of papers denouncing the computer in taxonomy to indicate a wide-spread misunderstanding about the computer as an instrument. The stored program of the computer is the set of instructions provided to the device by the operator. If the operator provides inadequate instructions, or his data are not properly prepared for the particular program, then the device carries out a poor set of operations. The opposite is equally true. If the stored program is a good one, and the data properly structured, one may anticipate good results.

But the computer has the attribute of forcing us to be more logical, more scientific in our methodology than has been required in the pre-computer days. It is essential that we know beforehand precisely what is needed in order that we achieve the desired results. The various kinds of usages of the computer must be understood, otherwise there will be the results that we have seen--poor reflections of our ideas about what the computer ought to have given us. If statistical taxonomic methods are not the most appropriate procedures for doing taxonomic work on the computer, it behooves us to look for the difficulty with the author of the program, not the wiring or circuitry of the machine. From this it should be evident that the computer is a tool, a very complex tool different in most respects from any other tools, but an outgrowth of our needs for ever faster computational capabilities. The primary limitation to the use of the computer is our own ingenuity.

Programming for computers is a very recent profession. In biological circles, it has been thought that anyone who wished to use the computer could take a few courses in programming languages, and proceed with his work. For some purposes, and some areas, this is true, but for the more complex tasks, such as classification, the aid of a mathematician and programmer are essential, and the biologist will be well-served to enlist the aid of people who are professionally trained in these areas. It is unlikely that the biologist will have sufficient time to cope with the very large body of skills being developed in either the programming or the hardware of computers. To get the maximum benefit from any one machine (or at least the larger and latest generation), much time, effort and energy must be expended to keep abreast. We may eventually be able to instruct a computer using colloquial English, but this is not possible at the moment.

Dr. Bossert has indicated that the computer may be used for keys. He demonstrated one key which had been made up to aid in the identification of Polynesian ants. Perhaps it will eventually be a practical matter to keep such programs in the memory of a computer, available for instant service, but there is not very much likelihood that this will be a compelling sales pitch to those who must provide the financial support for the work. Would it not be better to have the computer go to work with the description of the unknown, and, without the man-machine interaction demonstrated by Dr. Bossert, give the best possible set of determinations for the unknown ant? I think there are more immediate needs for computers than that demonstrated.

If the demonstration were intended only to show the potential flexibility of computer systems, this is different, but I hope the impression is not given that we will make this our primary use of the hardware.

The potentiality of one, or a few, large central computers for biological information retrieval was mentioned. (I assume these will be located in Colorado, or perhaps even in Kansas, but certainly not in either Cambridge or Berkeley, considering the present concern for geographic spread of public funds.) The need for a large information system for biology can hardly be overstressed. Much practical information about biological subjects is demanded daily, and the present method of providing answers either to the lay public or to more strictly scientific endeavors is not necessarily the most satisfactory. The design and operation of such a system, however, will require much strenuous effort by numbers of biologists and allied librarians, computer designers and programmers. To be worth much we, as taxonomists, must be centrally located in the operations, and must contribute to its development. The central question is, therefore, whether we are willing to give up some of our own research to achieve such goals.

There is no reason to believe that the computer cannot serve the biological community in much the same way the computers are used in business operations. That is, such things as accounting for specimens, inventories of collections, and clerical work with large quantities of repetitive drudgery. Such operations have been proposed by others, and it is not necessary to bring them up here.

Two large projects are potential users of computers as aids to more efficient operations. These are the taxonomic work to be done in Hawaii under the auspices of the International Biological program and the proposed, though not yet operative, Flora of North America. Both of these operations would be well-advised to establish a set of procedures for automatic data processing to aid them in accomplishing their goals in a reasonable and useful time limit. In these cases, a number of options are open to the workers, in terms of programs available to store, sort, and keep abreast of incoming raw data, and to take the raw data through various correlations necessary for proper interpretation. These types of programs can be adopted to the projects, given a little lead time.

We are just entering the age of computer-aided taxonomy. Our own fully computerized classification (Irwin & Rogers, Mem. N.Y. Bot. Gard. 16:71-120. 1967) has just appeared. To our knowledge, this is the first case of a group of plants being subjected to a computer analysis, and this followed by actual taxonomic reporting. Others, more sophisticated, will certainly be appearing. We look forward to the valuable aid we can derive from computers.

INTERNATIONAL CONFERENCE ON
SYSTEMATIC BIOLOGY

June 14 - 16, 1967

RACKHAM LECTURE HALL
THE UNIVERSITY OF MICHIGAN

Outlines and Abstracts

PRINCIPLES AND CONCEPTS OF SYSTEMATIC BIOLOGY

Michael T. Ghiselin
Marine Biological Laboratory
Woods Hole

In modern usage, "natural system" distinguishes between systems which correspond to empirical relationships and those which do not. Confusion has arisen through failure to distinguish between: 1) the evidence for naturalness, and 2) the truth of a proposition that a system is natural, and also between: 1) the evidence for relationships, and 2) the implications of the formal classification system.

"Overall similarity" in an objective sense presupposes a finite number of "unit characters," which in turn result from an equivocation. "Character" has been used to designate: 1) organs or parts, and 2) attributes. The failure to make this distinction underlies many disputes over "non-adaptive characters" and "single character classifications." Identifying taxonomic "characters" with genes or nucleotides causes serious misconceptions.

A metaphysical preference for intrinsic properties has caused some systematists to overlook the significance of relational properties. This oversight is largely responsible for deemphasis of: 1) phylogeny, 2) populations, 3) paleontology, 4) biogeography, 5) synecological relationships, 6) evolutionary trends, and 7) laws of nature. The result has been an erroneous view of both what a classification system may accomplish and the possible kinds of inductive support for evolutionary hypotheses.

THE CONSTRUCTION OF A CLASSIFICATION

W. H. Wagner, Jr.

Botanical Gardens
The University of Michigan

How are most classifications actually constructed? In the vast majority of cases, we simply inherit past classifications and modify them, adding here, subtracting there. Classifications were originally constructed on the basis of a few conspicuous characters, and were gradually changed by successive workers. Most active taxonomists are really not much concerned with the theory and philosophy behind the construction of classification; they merely do their work and hope for the best. Most workers who have dealt with the problems have usually had some special "iron in the fire" - expressing phenetic relationships, expressing fossil records, and so on. Nevertheless, the problems of constructing classifications are very serious ones, and of importance to biology. Any value that the present discussion may have lies in its attempt to see the whole picture: What are the problems? What, if anything, can or should be done about them?

We are confronted with a series of dilemmas, and the past dozen or so years have produced a great deal of argument, especially in the pages of such journals as Systematic Zoology and Taxon. What is homology? How can characters be quantified, if at all? Should characters be considered equal in significance, or should they be weighted? We cannot delve into these problems in detail, of course - the problems of actual construction of a classification are by themselves nearly overwhelming.

The rationale or concept which underlies the system determines its ultimate form. Early classifications aimed mainly at identification - either to categorize organisms according to their usages, or for pigeon-holing purposes. A latter-day variation is the goal of purely phenetic classification or assortment only, based upon all available data, all characters counted as equal in importance. Modern "biological" classifications, on the contrary, emphasize evolution. Concepts of primitiveness and specialization play a role, and some characters are more important than others in showing relationships. Even evolutionary taxonomists are not agreed, however, on whether the classification should express levels or lines. This is a special problem for plants, where parallelism and convergence have yielded pteridophytes, gymnosperms and angiosperms. Another question has to do with whether the chronology of the evolutionary branchings should be considered or not in setting up taxonomic categories.

By far the greatest problem in constructing classifications has to do with application of categories. Hierarchial inflation has made many systems unwieldy and difficult to use, where species-groups have been raised to genera, genera to families, families to orders, and so on. The problem of the evolutionary continuum enters here, because much of categorization is based upon gaps in the record. The year-by-year changes in classification systems have discouraged many biological workers, especially those in applied fields, about taxonomy, and the fact is that the instability of taxonomy is its chief drawback.

What, if any, agreements can we reach, after surveying the state of affairs and the problems in the construction of classifications? A few of these may be enumerated below:

1. Characters have different values in classification. Some are highly correlated with others and are thus guidelines to evolutionary relationships, because they do not commonly undergo parallel changes and are not subject to irregular fluctuations.

2. A classification should be constructed only to express evolutionary relationships, including those of all organisms from all levels in time. The <u>time</u> of the branching of a line, or the <u>place</u> of origin is immaterial.

3. There is, at present, no objective way to solve the problem of uniform application of categories. Stability in classification is, however, of major importance to biology. One way some stability may be achieved is as follows:

a. Accepting the idea that construction of a classification should take into account tradition, consistency, and usefulness.

b. Setting up of boards or panels of competent biologists who would review proposed classifications at all levels and pass upon their acceptability in terms of the above criteria.

THE SYSTEMATICS OF POPULATIONS IN PLANTS

Robert Ornduff

Department of Botany
University of California

The terms systematics and population are briefly reviewed as they have been used by biologists. Phenomena that exist at the population level are briefly catalogued; some of the most interesting of these are relegated to other symposiasts. The origin of the Conflict of Categories (sensu lato) is discussed in light of the following: (1) the conflict arose because of the difficulties in expressing complex population phenomena in the traditional taxonomic terminology and because of strong disagreement as to the validity of superimposing "biological" criteria on a basically morphological terminology, (2) parallel terminologies have been constructed which have supposedly expressed these population phenomena in precise terms, but (3) these parallel termonologies and their associated concepts are likewise oversimplifications of conditions and relationships within and among populations. Because of the strong influence that descriptive terminologies and preconceptions have in shaping investigative methodologies, certain evolutionarily important properties of populations may be overlooked, consciously ignored, or underemphasized. Evolutionists and taxonomists are often interested in modal population conditions, but it is suggested that the uncommon aberrant individual or condition has a greater prospective evolutionary role than might be supposed. Intensive population studies in the field are encouraged to determine whether or not this is true. It is also suggested that many of the emergent characteristics ascribed to species are present at the population level as well. If, indeed, the systematist is a student of evolution, he should divest himself of some of the terminological and conceptual straightjackets and approach evolutionary problems with a truly open mind.

SYSTEMATICS OF POPULATIONS IN ANIMALS

Donald W. Tinkle

Museum of Zoology
The University of Michigan

If systematics is broadly defined (e.g. Simpson, 1961) then any comparative study of populations that provides information on relationships or on evolutionary processes may be included within the scope of this discipline.

This study focuses attention primarily on the behavior, the structure, the demography and the reproductive rates of a Texas and Colorado population of *Uta stansburiana* living under quite different climatic regimes. An attempt is made to provide an explanation for the differences in the above by reference to the operation of natural selection at the individual level and to the presumed evolutionary history of the two populations.

The Colorado population belongs to the race *U. s. stansburiana* and the Texas population to the *U. s. stejnegeri*. These two races differ in a number of quantifiable characteristics. The Colorado population represents what is evidently the primitive stock in the genus as a whole while *stejnegeri* is of the advanced stock. The present northern restriction of *stansburiana* is evidently a recent phenomenon as isolated relict populations of the same stock occur hundreds of miles to the south of the present range of this race.

In the Texas populations, both sexes are highly aggressive and this aggression can be shown to improve the fitness of individual females, i.e. increase the probability that they will leave greater numbers of surviving offspring than less aggressive ones. The Colorado lizards are much less aggressive and tend to form social hierarchies. These behavioral differences are explained by the differences in the demographic properties of the two populations.

Associated with the differences in aggression are a strong sexual dimorphism and low frequency of distant emigration in Texas and a weak sexual dimorphism and high frequency of emigration in Colorado. Such differences are presumably genetically based and may be explained by differences in breeding structure of the population and in adult life expectancy. However, the explanation is also complicated by the fact that almost all representatives of primitive stocks in the genus lack sexual dimorphism.

There are also differences in mating, courtship and copulatory behavior between the two populations. Although the evolution of such differences must be understood in terms of selection within each local population, they might, fortuitously, serve as partial premating isolating mechanisms if the populations should become sympatric.

The Colorado lizards have a lower reproductive rate and lower mortality rate than those in Texas. However, because no satisfactory means exist for selection to adjust the birth rate to the death rate, explanations for the difference were found in differences in size at sexual maturity and the social structure of the two populations.

Taxonomy and ecology may be powerful allies in the study of evolutionary problems at the population level. Unfortunately, the necessary precision of information on the ecological parameters of reptile populations is almost totally lacking as are detailed studies of microsystematics of single species.

ECOLOGICAL ASPECTS OF THE SYSTEMATICS OF PLANTS

A. R. Kruckeberg

Department of Botany
University of Washington

I. Introduction

A. Need for inclusion of evolution and taxonomy in "mix".
B. Search by systematist for causal bases for relationship, grouping, affinity, etc., leads to environmental phenomena. Sources of systematic discontinuity arose, in part, from ecological discontinuities.

II. Areas of Mutual Concern at the Ecology-Systematics Interface

1. Operational interactions vs. disparate interests.
2. Kinds of feedback that might exist between the two.
3. Generalizations of mutual applicability.
4. Interactions at various hierarchical levels of both systematics and ecology.

III. Examination of Some Interactions Between Ecology and Systematics, or Between Ecologists and Systematists

A. Evolutionary Studies

1. Ecological basis of adaptation and selection.
2. Systematics and ecotypic variation: Genecology and systematic units; contemporary work in genecology (physiological, edaphic, etc.).
3. Ecology and Isolating Mechanisms: External factors, e.g. edaphic.
4. Ecological aspects of biotic isolation: Both during vegetative stages and reproductive stages; e.g., competition, chemical inhibition, mutualisms. Interrelationships of competition and succession to speciation. Interference studies by John Harper and associates. Prey-predator relationships, especially herb-herbivore (animal and mechanical); morphological and biochemical indicators of herb-herbivore interactions. Pest pressure as a factor in coevolution. Chemical inhibition and systematics.
5. Ecological aspects of reproductive isolation. Distinction between isolation during vegetative versus reproductive phases. Pollination ecology. Ecology and dispersal types.
6. Ecology, the Disturbed Habitat and Hybridization. Introgression and allopolyploidy - their ecological stimuli or repressors. Need for adequate ecological documentation of causes of natural hybridity. Some examples: C. V. Muller and oaks, B. Briggs and <u>Ranunculus</u>, Brayton and Mooney on <u>Cercocarpus</u>. Ecological aspects of polyploidy, especially alloploidy.
7. Ecology and the Diversification of Genera and Families.

Significance of ecological pressures and stimuli; i.e., do all species have their genesis in response to ecological differences? Ecological life-history approach: British work, Cole on Eriogonum (Mooney's student). Need for coordinated ecological life-histories of selected genera. Origin of floras and limiting ecological factors (e.g., phosphate in Australia, Ca/Mg and serpentine floras). Coevolution (pland-animal-microbe) and higher categories, or adaptive radiation.

B. Ecological Data in Taxonomy

1. Problem of niche in plants.
2. Levels of taxonomic hierarchy and ecological data (e.g., ordinal vs. species level).
3. Kinds of ecological characters available.
4. Ecological data and purpose of a particular taxonomy.

IV. Conclusions

A. Present status of rapport between ecology and systematics.
B. Greater interplay needed: ecological life-histories, floristics, evolutionary ecology, ecological bases for discontinuities, etc.

ECOLOGICAL ASPECTS OF THE SYSTEMATICS OF ANIMALS

Robert K. Selander

Department of Zoology
University of Texas

Ecological data are now widely employed in descriptive systematic research at all levels of classification, and ecology is, of course, an essential aspect of all research in population and phylogenetic systematics.

Although the "biological" species definition is entirely genetical, the species problem is both genetical and ecological, since, in a sense, full speciation requires the attainment by populations of both reproductive (genetical) isolation and ecological isolation (compatibility). Competitive replacement of genetically isolated but ecologically incompatible populations illustrates this dual aspect of the speciation process.

Rate and extent of adaptive radiation at the species level are determined largely by the availability of unoccupied, exploitable ecological niches and the opportunity for the development of genetical isolation of populations. At the intrapopulation level, adaptive radiation into unoccupied subniches is achieved through polymorphic and continuous ecological variation.

Ecological studies are important in the phyletic weighting of characters and in the detection of convergence, but of greater significance is their contribution to an understanding of adaptation and radiation. The recent rapprochement of ethology and population ecology is producing major advances in knowledge of the interaction of selection pressures in the evolution of functionally correlated complexes of characters and of the ultimate ecological basis of systems of social organization.

MOLECULAR DATA IN MICROBIAL SYSTEMATICS

J. De Ley

Laboratory of Microbiology
State University
Gent, Belgium

The orthodox classification of bacteria is based on rather few phenotypic features, expressing only a very small fraction of the genome. Numerical taxonomy covers about one-third of the genome. Molecular bacterial systematics now pivots around three centers.

1. DNA base composition, conveniently expressed as % GC. This approach is now in its constructive phase and should be used in conjunction with numerical analysis. Data on some 2000 bacteria, involving some 120 genera are known. The data are summarized and their impact on bacterial taxonomy is discussed. When complete, this method will be a powerful tool for identification and classification. It is urged that the description of every new strain or isolate should be accompanied by its % GC value.

2. DNA homology, determined by DNA-DNA or DNA-RNA hybridizations. The advantages and shortcomings of each method are briefly outlined. The methods consist in determining the similarity of nucleotide sequences amongst different strains. These techniques have been used in the study of relationships within and between several groups of bacteria: *Pseudomonas*, *Xanthomonas*, *Mycoplasma*, some *Pasteurella* species, some Enterobacteriaceae, Azotobacteriaceae, Rhizobiaceae. In each case the taxonomic conclusions depart considerably from the orthodox classification, because complete genomes are compared and not some arbitrary small phenotypic fraction.

3. The size of the bacterial genome, expressed as the molecular weight of the chromosomal DNA.

MOLECULAR DATA IN PLANT SYSTEMATICS

Juan H. Hunziker

School of Exact and Natural Sciences
University of Buenos Aires
Buenos Aires, Argentina

Systematic biology of the present decade is characterized by among other things, a continuously growing emphasis on molecular systematics. Some recent important articles, reviews and books have appeared covering various general aspects of chemotaxonomy.

Systematics based on small molecular weight compounds such as alkaloids, flavonoids, betacyanins, terpenoids, amino and fatty acids, carbohydrates, quinones, etc. already have received considerable attention and adequate treatment in excellent books. On the other hand, macromolecular data such as proteins (except for serology) have not been used much in plant systematic and evolutionary research despite their usefulness and promising future in these areas. Because of this and due to limitations of time and space the present review will deal exclusively with protein data.

Recent progress in the study of the biochemistry and biophysics of proteins has introduced new concepts and techniques that can be successfully used in the interpretation of phylogenetic relationships. Proteins are regarded as the means of transfer of information between the genetic code of DNA and the complicated processes of development and function of the organism. According to present evidence the order of amino acids of a protein is genetically determined being, through RNA, a direct translation of the genetic information encoded in a structural gene. If we assume that organisms are related to each other proportionally to their genetic similarity it is valid to assume that the degree of relationships among these organisms is proportional to the similarity of their proteins. Sibley has thoroughly discussed the use of proteins as a source of phylogenetic information and its rational foundation.

Hall and collaborators have presented evidence based on electrophoresis that amphiploid plants have, in regard to their seed protein composition, a more or less complete addition of the proteins of the parental species. These results provide a very important new tool for the study of the origin of amphiploids, which consists of the study and comparison of the electrophoretic spectra of amphiploids and parental species. In plants where amphiploidy has played such an important role in speciation this method might constitute an important tool to elucidate the origin of complex allopolyploids and it is at present being used by Hall and Johnson to solve the intricate history of the origin of hexaploid wheat and its relatives.

Several recent papers on serology, immunoelectrophoresis of global proteins of specific organs such as leaf, seeds, grains, etc. and different molecular forms of specific enzymes (isozimes) will be discussed in relation to their taxonomic and evolutionary significance.

Protein electrophoretic data obtained by the author on the *Hordeum murinum* complex will be discussed with special emphasis on the origin of tetraploid *H. leporinum*. The importance of protein band data for the interpretation of meiotic pairing in interspecific hybrids will be stressed, on the basis of results obtained in hybrids between tetraploid *Agropyron tilcarense* and hexaploid *A. scabriglume* and tetraploid *H. jubatum* and hexaploid *H. parodii*. In the first case a correlation between meiotic chromosome homology and protein band homology has been found. In the second case a correlation has been found between lack of chromosome homology and lack of close protein band homology. On account of the latter information the possibility of genic asynapsis causing failure of the chromosomes to pair is disregarded.

Protein band data on several *Agropyron* polyploid species will be discussed with special reference to their significance when integrated to morphological, cytogenetic and ecological information.

The importance of protein data on the study of geographically isolated populations of the *Agropyron scabriglume* hexaploid complex will be briefly discussed. Within this complex there are geographic races that being morphologically undistinguishable have undergone chromosome repatterning. There are several situations: in some cases the populations are chromosomically identical and the seed proteins have identical band patterns (Taff, San Martin); in other cases being chromosomically identical they present some slight differences in the grain proteins. (Tupungato, Balcarce). Finally, as in the case of El Carancho and Balcarce populations, chromosomal differences of at least 5 reciprocal translocations (a chain or ring of 12 chromosomes can be observed in most cells at first metaphase) and 2 paracentric inversions are not coupled by differences in the protein patterns, these showing an exact correspondence in all 18 protein fractions that can be obtained from the seed proteins. These data suggest that a similar genetic material is present in both populations but extensive chromosome repatterning has occurred as to reduce fertility to about 20% in the hybrids.

Evidence will be presented to show the lack of influence of extremely different environmental conditions on the reproducibility of results with proteins from mature grains. Seed samples of *A. tilcarense* and *A. attenuatum* from their original habitats (2500 m. above sea level, 23° South Lat. and 3400 m., 15° South Lat. respectively) and from cultures at warmer environments (sea level and 34° South Lat.) have yielded identical electrophoretic patterns.

Finally, the future role of protein electorphoretic band data as an analytical tool in such important evolutionary and taxonomic aspects such as studies of polymorphism, polytypic and semispecific differentiation, cryptic speciation (sibling species groups) will be discussed. Its usefullness in the analysis of chromosome pairing in meiosis of interspecific hybrids (asynapsis, etc.) and in the study of the origin of ancient amphiploids will also be considered.

MOLECULAR DATA IN ANIMAL SYSTEMATICS

Herbert C. Dessauer

Department of Biochemistry
Louisiana State University
School of Medicine

Flordin has said, "The study of biochemical characteristics...is more difficult to accomplish than direct observation of morphological characters. Nevertheless, had naturalists started from there rather than from morphological observation, they would have been bound to conceive the idea of evolution of animals." Characteristics available for analysis include: A listing of metabolites and enzymes associated with a metabolic pathway; physicochemical, immunological and sequence data on proteins; and melting point, hybridization and sequence data on nucleic acids. To properly interpret such evidence one must have knowledge of methodology used to obtain the data as well as an understanding of biochemical theory.

Molecular data focuses attention upon mechanisms of evolution at the level of gene structure and function. Sources of variation are analyzed in terms of gains, losses and substitutions of single nucleotide or larger segments of DNA. Changes are detected as alterations in protein structure or synthesis. The problem of identifying the homology of such genetically related structures is no less difficult at the molecular level than at the morphological level. Relatedness of different polypeptides within an individual organism as well as homologies of polypeptides of divergent species must be determined.

Molecular evidence demonstrates the dynamic nature of the biological species. Largely because of variations in activities of control genes, stage of development and physiological state affect tissue composition. As individuals of a population exhibit heritable differences in their genetic complement, the biologist is forced to appreciate the population rather than the typological nature of the species. Frequencies of individual proteins of an allelomorphic series reflect gene representation within populations and can serve in quantitative descriptions of populations. Comparisons of such frequencies in adjacent populations show the extent of inbreeding; frequencies in different populations over the range of the species may indicate clines of gene flow. Features of molecular structure that individuals of a species have in common are useful in identifying the organism.

The distribution of complex molecules and metabolic pathways make sense only when organized according to natural groupings and analyzed in light of evolutionary theory. The fundamental similarity in protein and nucleic acid structure, protein synthesis, information storage in nucleotides and the genetic code offers strong evidence for the relatedness of all forms of life. Procaryota are distinct from Eucaryota in their apparent lack of a requirement for sterols. In their adaptation to ingestive life and subsequent development of a highly integrated metabolism, animals have lost many fundamental metabolic pathways but have acquired a number of highly specialized synthetic capatilities. Collagen and chitin distribution follow the divergence of the chordata and arthropod lines. Metabolic pathways for biosynthesis of bile salts, urea and for the catabolism of purines can serve to identify major vertebrate taxa.

A major attribute of molecular data is that it can be used to obtain quantitative estimates of genetic relationships, largely void of personal opinion. DNA-hybridization has given quantitative meaning, in terms of DNA-complementarity, to taxonomic levels such as genus, family, order and class. Sequence differences in a series of homologous proteins can be translated in terms of "mutation distances" which represent direct measures of relatedness of a particular homologous gene. "Mutation distances" between the cytochromes C alone, a molecule of only 104 residues, has allowed a calculation of genetic relatedness of categories above the family level that is in amazing agreement with currently accepted ideas. Molecular data capable of quantitative assessment are most extensive for primates. This includes: extent of serological correspondence of albumins and other proteins, sequence differences between hemoglobin polypeptides as well as some evidence on DNA complementarity.

Quantitative estimates of evolutionary rates are possible by combining measures of divergence with evidence from the fossil record. Biophysical methods allow precise dating of times of divergence of fossil ancestors. Studies presently available indicate that chemical evolution has proceeded at different rates. Some polynucleotide sequences of DNA have evolved rapidly but others apparently have remained unchanged through eons of time. As much as 80% of the DNA of mammals of distant relationship will not hybridize in recombination studies. However, about 20% is a "mammalian fraction," apparently common to all mammals. This fraction includes a "smaller vertebrate fraction" shared by mammals, birds and fishes. Apparently the "mammalian fraction" has retained a fairly uniform sequence of nucleotides for 200 million years. Rates of evolution of proteins also appear to vary. Cytochrome C actin and insulin appear to be more conservative structures than the hemoglobin polypeptides. Vertebrate transferrins may represent a remarkably variant protein. Furthermore, rates of evolution of an homologous protein may be rapid in one taxon and slow in another. The alpha-globin chain varys little among most primates but has undergone a sharp divergence of structure in the baboon. Although transferrins exhibit extreme variability among most snakes, they appear to be more conservative proteins among lizards.

What pressures in the environment of an animal have led to the choice of a particular structural variant of a protein by natural selection? Evidence available is meager but suggests close correlations between ecological factors and properties of specific proteins: (1) temperature with stability of LDH's and collagens; (2) oxygen availability with hemoglobin affinities for oxygen and with the tissue distribution of LDH isozymes; (3) wave length of light in environment with position of absorption maxima of rhodopsins; (4) succeptibility to disease with hemoglobin structure and with the occurrence of specific proteins in human leprosy and murine typhoid; (5) toxic materials in environment with the presence of specific esterases.

COMPARATIVE MORPHOLOGY IN SYSTEMATICS

Walter J. Bock

Department of Biological Sciences
Columbia University

Introduction

Systematics of the higher categories has always rested upon a foundation provided by comparative morphology with a resulting intertwining of the goals and fortunes of the two disciplines. Morphology was studied as a guide to classification and rarely as morphology; hence, comparative morphology remained a shallow conceptual area within biology characterized by notions such as "anyone can compare," and "morphological study only requires the ability to observe." The near total eclipse of comparative morphology after 1900 was inevitable and requires no further comment. After a long dormancy, morphology has become an active center of study with, however, much of the work done for the sake of morphology. Development of new concepts and approaches are resulting in a morphology that differs sharply from classical comparative morphology. The emerging synthesis may be called evolutionary morphology and is characterized by the comparative study of the biology of morphological features in accordance with the principles of evolutionary biology. Evolutionary morphology is simply comparative morphology catching up with the New Systematics.

In this talk, I would like to outline some of the theoretical concepts developed within evolutionary morphology and illustrate how they may be applied to practical problems of systematics. My examples are restricted to vertebrates and largely to birds, but I believe that the conclusions are broadly valid. I make no distinction between morphology and anatomy as done in plants and insect -- all structural features will be considered under the same heading.

Theoretical concepts

The concepts of the form, function and biological role of morphological features must be defined clearly and separated from one another. And the factors of the environment must be delimited. The synerg or link between the feature and environmental factors is formed by the biological role and the selection force. Adaptation is dependent upon the nature of the synerg, not simply the form and function of the feature and the properties of the environmental factor. The degree of adaptation can be related to the amount of energy required for the successful operation of the synerg.

All features possess simultaneously adaptive and paradaptive aspects. Adaptive aspects are those responsible for the feature being favored by selection. Paradaptive aspects are those dependent upon, resulting from, or under the control of chance-based evolutionary mechanisms and phenomena. Recognition of both adaptive and paradaptive aspects of features is dependent upon studies of functional and biological morphology.

Comparisons must be divided into horizontal (between numbers of different phyletic lineages) and vertical (between members of the same phyletic lineage) ones. The differences observed and interpretations reached in each type of comparison are not equivalent nor can they be interchanged at will. Vertical differences are mainly adaptive while horizontal ones are mainly paradaptive although the correlation is not so simple. Recognition of this distinction forms the basis of multiple pathways of adaptation.

Relative value or weighing of taxonomic characters may be approached via the concept of paradaptation. Features that are valuable taxonomically are those possessing paradaptive aspects for which the probability of unique occurrence is high; such features would be assigned much weight. Ascertaining these probabilities is again dependent, in part, upon studies of functional and biological morphology.

Many other concepts, such as homology, monophyly, physiological adaptation, preadaptation, experimentation and mosaic evolution, have been clarified further within the domain of evolutionary morphology, but time does not permit discussion of these interesting developments.

Practical applications

The strength and weakness of comparative morphology lies in the wealth of available information. Older work is excellent descriptively, but one must know the foundations upon which the comparisons and conclusions rest; many of the ideas used are no longer acceptable. It is erroneous for current workers to cite conclusions from the older literature without knowing their basis. Although regrettable, the use of the available morphological information is not a simple or obvious matter.

The grounds for ascertaining homologues must be investigated as well as checking whether the same term really conotes homologous structures in different groups. The os prominens in hawks and owls, for example, is not homologous as an enlarged sesamoid bone in the wing.

Work in functional morphology has been hampered by a lack of clear definition of concepts and by a sadly insufficient amount of experimental study. Most functional observations are still deductions from the observed morphological form. This is a valid and necessary procedure, but frequently suffers from an unsound deductive base. At present, a plague of vague and erroneous functional statements bedevil morphological work to the extent that it may be better to say nothing than to add to the existing morass. Considerable information for the formulation of functional conclusions is available from other biological disciplines; morphologists must make greater use of this data.

Inclusion of a functional analysis, even a simple one, can often allow more meaningful conclusions. Study of the ratite skull using the same morphological features as in earlier works, but with a simple functional interpretation permitted sounder taxonomic results. An analysis of the mechanism of tetrapod cranial kinesis yielded the conclusion that this feature could never be regained during tetrapod evolution; the knowledge that a kinetic group cannot evolve from an akinetic group may be helpful in unraveling tetrapod phylogeny.

The application of the concept of paradaptation to weighing taxonomic characters is still in its infancy because of a deficiency of functional studies.

Many features of low weight can be demonstrated, but few good examples of features of high taxonomic value because of uniquely occurring paradaptations can be cited. The presence of an osseous arch on the radius of owls may be one example. Another may be the complex of features in the ratite skull, including the bony palate. The patterns of jaw musculature in the cardueline finch *Coccothraustes* and the ploceid *Amblyospiza*, which possess very similar bills, may be another example of uniquely occurring paradaptations.

Interpretations of the presumed genetical or evolutionary, or taxonomic meaning of morphological differences has been more firmly established. With recognition of the distinction between vertical and horizontal comparisons, the causal basis for these differences can be judged better. Moreover, many vertical morphological differences can be shown to be the result of physiological (somatic) adaptation and hence not to the result of any genetical change. Some examples are the formation of the secondary articulation of the avian skull, the mammalian jaw articulation, and modifications in the size of the nasal (salt) gland in birds. Whether a strong correlation exists between the degree of morphological difference and taxonomic difference is open to question with the available evidence suggesting that the correlation is weak at best.

Conclusions

The emergence of evolutionary morphology is establishing a firmer and more sophisticated theoretical basis for systematic study of the higher categories. Earlier notions that "anyone can study morphology" and "anyone can compare" are no longer tenable with the necessary training for morphological study becoming highly rigorous. It may be safely predicted that morphology will remain as a major cornerstone of biological classification because of the combination of the advantages afforded by structural features and the impetus being generated by evolutionary morphology.

SYSTEMATIC SIGNIFICANCE OF ISOLATING MECHANISMS

M. J. Littlejohn

Department of Zoology
University of Melbourne

If we may consider the terms systematics and taxonomy as synonymous then the subject can be approached at three levels: alpha: the delimiting and naming of taxa; beta: the phylogenetic arranging of taxa; and gamma: the analysis of basic evolutionary mechanisms, rates and trends. The significance of reproductive isolating mechanisms at these three levels will be examined, although not necessarily in the above order.

The historical development of concepts in this area, and their rather meagre factual support, have been well covered in recent reviews. Nevertheless, some seemingly important results and statements in the literature have perhaps been overlooked, not given their due emphasis, or may now be re-interpreted as a result of more recent publications.

Since speciation in bisexual organisms is achieved through the development of adequate reproductive isolation, this process is clearly of basic evolutionary significance, being second only to the mechanisms of adaptation and continuity of a genetic lineage through space and time. But in order to delimit the problem it will first be necessary to define some of the critical terms, such as the bisexual species, the speciation process, sympatry, and hybridization, particularly in view of some recent pointed criticisms of the basic dogma.

An understanding of the origin and subsequent evolution of reproductive isolation is thus the key to speciation in sexually reproducing organisms. This whole area is currently in a state of flux, but much more information of direct application is now becoming available. There has also been further conceptual maturation (although often re-directing us to the significance of statements in earlier works). Accordingly, this subject will be re-appraised and the classification of isolating mechanisms considered, according to their evolutionary origin and efficiency.

Results of recent research (principally on insects and vertebrates), in which techniques as objective and quantitative as possible were employed, will be briefly reviewed with emphasis on the following:

(1) the nature and effectiveness of isolating mechanisms operating between closely related sympatric species;
(2) the detection of sibling species;
(3) the assessment of potential reproductive isolation and stage of speciation in allopatric populations;
(4) the analysis of situations in which reproductive isolation has broken down, or failed to develop to an effective level.

Because they are the most distinctive and absolute characteristics of closely related species (although not necessarily so apparent to human sensory modes), the application of data on some types of isolating mechanisms to problems of phylogeny requires a considerable measure of caution. In this context, however, levels of genetic incompatibility may be one of the best measures of relationship, particularly at the generic and infra-generic levels.

Finally, an overall evaluation of the present position will be attempted, and possible future lines of research suggested.

ANIMAL BEHAVIOR AND SYSTEMATICS

Richard D. Alexander

Museum of Zoology
The University of Michigan

As with any other aspect of the phenotype, the study of behavior in its relationship to systematics concerns the nature, origin, maintenance, and adaptive significance of similarities and differences among organisms. Behavior, however, is in general that aspect of the animal phenotype which is simultaneously most directly selected and most complexly and indirectly related to the genotype. Behavior, furthermore, has traditionally been difficult to document and not as easily preserved as morphology. And men have tended to view animal behavior in human terms more extensively than they have other characteristics of animals.

For these various reasons, it is not surprising that systematists have neglected behavior and still do, nor that zoologists in general have allowed its study to lag, and to remain largely the province of human-oriented psychologists. Systematists have tended to accept admonishments that behavior cannot be used by them unless its ontogenetic and physiological bases are thoroughly understood, without wondering what it means that the same strictures should then be expected to apply to all aspects of the phenotype. Perceptive searches for predictability in the extent and nature of hereditary variations underlying behavioral variations have been discouraged by interminable arguments about the significance of the probable physiological and developmental backgrounds of a few behaviors in a few animals.

As William Morton Wheeler pointed out long ago, because "in the field of possible observation the ethological tend to outstrip the morphological characters" the usefulness of behavior in detecting relationships is potentially great. Moreover, because of its diversity and its special adaptive features, behavior can be indispensable, even to alpha taxonomy, sometimes to the extreme of being the only reasonable way of recognizing or distinguishing species, in both vertebrates and invertebrates.

The study of behavior, in turn, has suffered from its neglect by systematically-oriented zoologists, particularly because of the dearth of broad-scale comparative studies and a general failure to examine the adaptive significance of behavioral variations. Sometimes, properly oriented comparative study, even though relatively superficial, can more swiftly accelerate understanding and predictiveness about some rather complex aspects of behavior that it has generally lacked, a deficiency from which it has suffered extensively.

COMPARATIVE CYTOLOGY IN SYSTEMATICS

Harlan Lewis

College of Letters and Science
University of California, Los Angeles

Discussion will be limited to chromosomes.

Measurement and scoring of chromosomal traits.

- What the traits are.
- Difficulties and limitations.
    - Variation among organisms.
- Use of hybrids.

Application of cytological traits to systematics.

- As phenotypic traits equivalent to those of morphology, behavior, etc.
    - (If this is their only use they are not worth the trouble it takes to score them).
- As indicators of barriers to gene exchange.
    - (Operationally this is the principal value of comparative cytology in systematics).
    - Relation of chormosomal differences to barriers.
        - (1) affecting only rate of gene exchange (no taxonomic significance)
        - (2) preventing gene recombination (indicative of genetic discontinuity, not genetic difference)
    - Relation of barriers to systematics.
        - (covered by an earlier speaker, but I may wish to amplify)
- As indicators of phylogenetic relationship.
    - Some phylogentic sequences can be rigorously tested.
        - Polyploid sequences
        - Aneuploid sequences
    - Others can be reasonably inferred.
    - Relation of phylogeny to systematics.
- As indicators of mode of speciation.
    - Relation of the speciation process to systematics.

Biology is fed entirely by Mathematical statistics!!!

~~No need to argue the place of~~

Multivariate analysis encompasses much more than classical statistical procedures.

Biologic + statistical procedures for character selection

BIOMETRICAL TECHNIQUES IN SYSTEMATICS

R. A. Reyment

Biometrical Laboratory, Department of Geology
University of Stockholm
Sweden

Multivariate statistical analysis provides the most directly useful body of techniques for systematics, owing to the occurrence of many variables in most connections, although this part of statistics should not be applied blindly and to the exclusion of any other part. For the purposes of this paper, some biometrical techniques of use in systematics are regarded from the standpoint of arbitrary "models". The presentation in connection herewith is one of convenience and is not necessarily the statistically most logical.

Model I. The analysis of the properties of a single multivariate sample. This model is useful for studying the variability of a population and for examining certain kinds of growth and shape hypotheses.

Model II. Comparison of the properties of two multivariate samples. This model supplies approximate information on the agreement of growth directions and on comparative variability; it is useful on all levels of study in Systematics.

Model III. The simultaneous comparison of several multivariate samples. This model is the logical extension of Model II. Rejection of the hypothesis of equality of the universes would lead to a series of analyses of the Model II category.

Model IV. The identification model. This may be considered in two parts: (a) There are two or more known universes; it is desired to place a specimen, with the minimum chance of error, with the correct universe, assuming that the specimen actually comes from one of the universes. (b) It is not known definitely whether a specimen actually comes from one of k universes; it is desired to test to which of these universes the specimen is nearest, if it does not belong to any of them. The application of this approach in phylogenetic studies and in routine taxonomic analysis is obvious.

Model V. The classification model. A multivariate sample may be composed of more than one entity (heterogeneously constituted). The technique used is designed to bring out the eventual existence of "clusters" in the data.

Model VI. The population affinity model. This expresses the relatedness of multivariate samples from each of k universes in a manner permitting graphical representation. It is applicable to taxonomic problems, geographic and ecologic variation, chronologic shifts in morphometric variables and is also applicable to the analysis of rate of change in characters with respect to distance, some ecologic factor, or time.

Model VII. The population overlap model. This model studies the unlikeness between two or more populations, on the grounds of multivariate samples, by the use of some kind of discriminant function.

Model VIII. Correlation between sets of variables. This model analyzes the significance of the degree of correlation between two groups of variables. For example, the correlation between a set of morphologic variables and a set of ecologic variables.

Model IX. A prediction model. This model is of limited use in systematics and finds it main sphere of application in paleontology, where one may have good sets of measurements on a fossil form and wish to make use of these in predicting some measurement on an incomplete specimen.

COMPUTER TECHNIQUES IN SYSTEMATICS

William Bossert

The Biological Laboratories
Harvard University

The greatest impact of automatic computing in systematics has certainly been in the application of multivariate statistical methods to problems of classification and identification. A number of "packages" of statistical and taxonomic computer programs have been widely distributed. Most of these require little knowledge of automatic computers but considerable statistical sophistication for successful operation, particularly in the selection of method and the interpretation of the results. I feel that these two points are central to the continuing controversy over statistical taxonomy. Both proponents and opponents have at times ignored the variety of methods available, none of them appropriate for every problem, and also have been unwilling to admit that the solution was not always completed in the computer printout. My principle concern in this conflict is that too often computer taxonomy is identified with statistical taxonomy and the computer rises or falls in favor according to the success or failure of particular statistical applications.

Automatic computers can, in fact, do a great deal more than evaluate statistical formulas. I would like to sieze upon a recent statement by Blackwelder, "...Of course, computers can also be used as data recovery devises to store taxonomic information (assuming that there is a taxonomist anywhere with sufficient access to a computer to use it in day to day work)..." It leads to the consideration of two important developments in automatic computing. The first involves techniques for manipulating non-numeric (alphabetic, graphical) information. The second is the development of multiple access, time shared computing systems. A simple illustration of a computer program which makes use of these is given in the accompanying figure. In this illustration a computer has been programmed to lead a user in conversational fashion through a taxonomic key, here based on Wilson and Taylor. The user interacted with the program through a small teletypewriter connected by standard telephone lines to the computer. (A more meaningful illustration which properly exploits the potential for such interactions will be presented at the conference.) The central computer was carrying on twenty or thirty independent interactions simultaneously.

Research in automatic computing seems directed largely to furthering these developments to the point of providing large central computer utilities to which users can gain access remotely through terminals ranging in complexity from a touch tone telephone to separate complete computers, and in which the user interacts with the computer in a manner and language suited to the problem rather than to the computer. I feel we should discuss the possibility of taking advantage of these developments in the establishment of one or more central computer taxonomic information stores. This would be technically and economically feasible by the early or middle 1970's. (I shall be able to estimate or at least set some limits on the costs involved.)

There is a significant gap between feasibility and justification, however. The cost will certainly be great enough that if the system is viewed solely as a taxonomic archive to be used by specialists for identification and classification purposes other methods might be preferable such as the card file proposed by Brown. To make sense the system must be recognized as a clearing house and store for information of biogeographical, ecological and behavioral importance, and there should be a regular flow of such information into the system from the users. In the computer the taxonomic record could be the basis for the development of theoretical structures in all of these areas.

Since the technical problems are being overcome and the potential of the product so great for the advancement of population biology, it is difficult for me to consider the many drawbacks to a project of this sort. Quite obvious are the conflicts between the exchange of information through the computer store and the traditional concepts of publication. This problem as it relates to the copyright laws is currently being considered by the United States Congress. I am more deeply worried about the many blocks which exist or might arise to hinder the essential communication between computer scientists and biologists in the course of the project. Neither group alone could produce a valuable system.

```
THIS PROGRAM SHOULD HELP YOU IDENTIFY A POLYNESIAN ANT.
THE SOURCE IS WILSON AND TAYLOR 1967.
THE KEY IS BASED ON THE WORKERS.  DO YOU HAVE A SPECIMEN BEFORE YOU?
NO
TYPE YES WHEN YOU ARE READY.
YES
IS THE GASTER ATTACHED TO THE MESOSOMA BY A WAIST CONSISTING OF TWO MORE OR
LESS REDUCED AND NODIFORM SEGMENTS?
NO
IS THE STING WELL DEVELOPED AND FUNCTIONAL?
NO
IS THE SEVENTH STERNITE ROLLED INTO A SHORT VENTRO-APICAL CONE WITH A ROUND
ORIFICE (WITH OR WITHOUT A CORONULA OF TINY HAIRS) THAT SERVES AS A NOZZLE
FOR A DEFENSIVE SPRAY?  DO NOT CONFUSE IT WITH THE CLOACAL ORIFICE, WHICH IS
MORE DORSAL AND NORMALLY HIDDEN.
NO
THE ANT IS DOLICHODERINE.
IS THE PETIOLE ARMED WITH TWO LARGE, LATERALLY DIRECTED HORN-LIKE SPINES?
NO
HOW MANY SEGMENTS ARE THERE TO THE ANTENNA?
12
IS THE JUNCTURE OF THE DORSAL AND BASAL FACES OF THE PROPODEUM OF THE WORKERS
(MINOR WORKERS IF POLYMORPHIC) DRAWN INTO AN ACUTE TOOTH-LIKE PROTUBERANCE?
YES
IS THE PETIOLAR NODE ARMED WITH A POSTERIOR MEDIAN TOOTH-LIKE PROTUBERANCE?
NO
THE SPECIES IS CAMPONOTUS FLAVOLIMBATUS.
WHERE WAS THE SPECIMEN COLLECTED?
SAMOA
GOOD, THE SPECIES SEEMS TO BE ENDEMIC TO SAMOA.
TYPE YES WHEN YOU ARE READY WITH ANOTHER SPECIMEN.
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Figure: A brief illustration of an interaction between a person (responses underlined) and a program to evaluate a taxonomic key (computer response without underline). The interaction was through a teletypewriter remotely connected to a multiple access computer system, the model SDS-940 at the Harvard Computing Center.

- Taximetrics Laboratory

May 8, 1967

Dr. William Bossert
The Biological Laboratories
Harvard University
Cambridge, Massachusetts 02138

Dear Dr. Bossert:

Thank you for sending the abstract. I am sending a copy of a paper you might be interested in reading.

Sincerely yours,

David J. Rogers
Professor of Botany

DJR/ch

Enc.: reprint: Use of
Computers in Studies
of Taxonomy + evolution
(Evolutionary Biology -
Vol. I).

THE COMPUTATION LABORATORY OF HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS 02138

May 2, 1967.

Dr. D. J. Rogers
Department of Botany
Colorado State University
Fort Collins, Colorado 80521

Dear Dr. Rogers:

I have enclosed an abstract of my presentation for the Systematic Biology Conference next month. As you can see, I hope to leave most of the arguments on Numerical Taxonomy to Reyment, Sokal and Olsen. The major point of my presentation will be to discuss the feasibility of large centralized Computer Taxonomic Information Units.

While I hope to have a complete manuscript for you as soon as possible, the details of the presentation are certainly open enough at the moment that I would appreciate any comments you care to make about it. I of course do not mean to suggest that we try to resolve controversies that may now exist, but even hope that I could expand on these areas of the presentation which might lead to stimulating discussion.

Sincerely,

William Bossert

William H. Bossert
Assistant Professor Biology
and Applied Mathematics

WHB/g
Encl.

COMPUTER TECHNIQUES in SYSTEMATICS

(Abstract, May 1, 1967.)

William Bossert

The greatest impact of automatic computing in systematics has certainly been in the application of multivariate statistical methods to problems of classification and identification. A number of "packages" of statistical and taxonomic computer programs have been widely distributed. Most of these require little knowledge of automatic computers but considerable statistical sophistication for successful operation, particularly in the selection of method and the interpretation of the results. I feel that these two points are central to the continuing controversy over statistical taxonomy. Both proponents and opponents have at times ignored the variety of methods available, none of them appropriate for every problem, and also have been unwilling to admit that the solution was not always completed in the computer printout. My principle concern in this conflict is that too often computer taxonomy is identified with statistical taxonomy and the computer rises or falls in favor according to the success or failure of particular statistical applications.

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1. Syst. Zool. 16:64, 1967

2. in press

3. Syst. Zool. 10:80, 1961

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Yale University New Haven, Connecticut 06520

PEABODY MUSEUM OF NATURAL HISTORY
Division of Vertebrate Zoology

Tel. 203-787-3131 Ext. 426

February 28, 1967

Dr. D.J. Rogers
Department of Botany
Colorado State University
Fort Collins, Colorado 80521

Dear Dr. Rogers:

The National Academy of Sciences of the United States is sponsoring an International Conference on Systematic Biology to be held at the University of Michigan, June 14, 15 and 16, 1967. The Program will include some 19 papers as indicated on the enclosed outline.

For each of the papers we wish to invite two Discussants who will read the paper or an abstract in advance and will then offer some comments on the paper during the Discussion Period following the presentation by the Speaker.

It is my pleasure and privilege to invite you to be a Discussant on the paper entitled "Computer Techniques in Systematics" to be presented by Dr. William Bossert.

If you can participate your travel expenses (jet economy fare) and subsistence during the Conference will be paid by the Academy.

I hope that you will be able to help us to make this Conference a success.

Sincerely yours,

Charles Sibley

Charles G. Sibley, Chairman
Organizing Committee

CGS:gfl

Copy to: R.B. Stevens
file

INTERNATIONAL CONFERENCE ON SYSTEMATIC BIOLOGY

June 14, 15, 16, 1967

University of Michigan
Ann Arbor, Michigan

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Preliminary Program

The following 19 papers have been tentatively scheduled for presentation over the period from 2:00 p.m. on June 14, to the evening of June 16.

- - - - -

1. An Historical Review of Systematic Biology.
2. The Principles and Concepts of Systematic Biology.
3. The Construction of a Classification.
4. The Systematics of Populations.
5. The Systematic Significance of Isolating Mechanisms.
6. The Ecological Aspects of the Systematics of Plants.
7. The Ecological Aspects of the Systematics of Animals.
8. Molecular Data in Microbial Systematics.
9. Molecular Data in Plant Systematics.
10. Molecular Data in Animal Systematics.
11. Round Table Discussion of Molecular Systematics, especially its Future Role.
    Moderator: C. G. Sibley
12. Comparative Physiology in Systematics.
13. Comparative Cytology in Systematics.
14. Comparative Morphogenesis in Systematics.
15. Comparative Behavior in Systematics.
16. Biometrical Techniques in Systematics.
17. Computer Techniques in Systematics.
18. Summary of the Conference.
19. "The Role of Systematics in Biology" (=after-banquet address by Ernst Mayr)