METHODS AND PRINCIPLES OF SYSTEMATIC ZOOLOGY

E. Mayr, E. G. Linsley & R. L. Usinger

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ERNST MAYR

Curator of the Whitney-Rothschild Collections
The American Museum of Natural History

E. GORTON LINSLEY

Associate Professor of Entomology and Chairman
Department of Entomology and Parasitology
University of California

ROBERT L. USINGER

Associate Professor of Entomology
University of California
Alternate Member, International Commission on Zoological Nomenclature, Paris 1948

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PREFACE

The authors have long felt the need for a treatise on the principles and methods of taxonomy. Such a work should be useful not only as an adjunct to teaching but also as a reference work for the practicing taxonomist and as a source of information to the general biologist. An analysis and full statement of the often disputed principles on which the taxonomic method is based are urgently needed. We share the view of O. W. Richards (1947) that "it is less the findings of taxonomy than its principles and methods which need to be taught" and understood. We believe that taxonomy is an important branch of biology which deals not only with the identification and classification of natural populations but with objectives that go well beyond these fundamental activities.

The teaching of taxonomic theory and method has been a seriously neglected phase of biology. Most formal courses in systematics have concentrated upon the end products of taxonomic research and have not provided the student with a means for critically evaluating these end products or for tracing the steps by which they were attained. An understanding of taxonomic theory and practice is essential not only to the beginning and the practicing taxonomist but to all those who draw upon the results of his studies. This is true to a greater or lesser extent for all biological sciences, but in particular for such fields as ecology, population genetics, comparative morphology, anthropology, comparative physiology, and applied biology. Sound taxonomy is a prerequisite to intelligent conclusions in all these fields.

At the present time there is no book available that deals comprehensively with the principles and methods of taxonomy. Available works are merely commentaries on the International Rules, or they deal with selected phases of taxonomic theory with occasional reference to taxonomic practice.

The treatment in this book of certain phases of systematic zoology has necessarily been restricted because of limitations of space. Collecting techniques, for example, are so diversely specialized in each group of animals and so completely covered in separate works that they are not discussed in detail. A full discussion of the phyla and classes of animals is considered beyond the scope of this work, although a listing is presented (Table 2).

Nomenclature, although strictly a means to an end, has occupied a disproportionate part of the time and energy of taxonomists. One reason for this is that the subject is inherently complex and that revisions of the Rules become necessary from time to time, since the practicability of the Rules, like that of any other code of law, can be tested only by application. A more fundamental reason is that a basic philosophy or theory underlies the Rules of Nomenclature. This theory has not only tended to change in the course of years (as, for instance, with respect to the significance of types), but some of it could not be fully understood until the principles of taxonomy themselves were more clearly understood (*e.g.*, treatment of infraspecific names). We feel, therefore, that a presentation of the Rules of Nomenclature would be incomplete which does not deal with the history of the field, or which omits a discussion of the basic principles. We have attempted to present both these aspects. On the other hand, it is not the purpose of this book to enter into nomenclatural controversies. Since at this writing there is no edition of the International Rules of Zoological Nomenclature which is accurate or up to date, we hope that the simplified review of the Rules in Part 3 of our book may prove to be especially useful. At the same time, the treatment is open to the criticism that it is an unofficial version of a highly technical and, at the moment, controversial subject. It has been our aim to make nomenclature comprehensible to the practicing taxonomist, leaving it to nomenclaturists to analyze the voluminous proceedings of the International Commission and to debate the various issues of the moment.

In attempting to bring together the more important elements of modern taxonomic theory and practice, we have, of necessity, selected our materials primarily from the point of view of the student of living animals and have chosen illustrative examples with preference from our own work. The problems of the paleontologist, microbiologist, and botanist have been taken into consideration as far as practicable, but the materials of these groups are often sufficiently different to require different approaches to the solution of taxonomic problems. Nevertheless, there is much common ground of theory and method shared by the workers in these diverse fields, and it is to be hoped that at some time in the not too distant future all biological taxonomy may be viewed as a single cohesive field. If this book, by focusing attention on the problems of the systematic zoologist, serves as a step in that direction, one of its goals will have been achieved. If it also assists in stimulating a more critical evaluation of taxonomic theory and methods and in a wider dissemination of knowledge concerning them, the authors will feel that their labors have been justified.

It is well-nigh impossible to acknowledge sources in a book of this kind, which has grown out of the accumulated contacts and experiences of the three authors throughout their lives. Suffice it to say that our early teachers in Germany and at the University of California and our

colleagues at The American Museum of Natural History and in the Biosystematists Discussion Group at the University of California and at Stanford University have done much to shape our thinking along the lines expressed in this book. We also acknowledge the role of several generations of students at the University of California, who have unwittingly provided opportunity to test the clarity and effectiveness of portions of the manuscript during its formative stages. Their response has been most helpful.

Formal acknowledgment of quoted material is made through literature citations. Special thanks are due to several colleagues who generously gave of their time to read portions of the manuscript. Their detailed suggestions and criticisms were carefully considered and were in most cases adopted. To these readers should go a large share of credit for accuracy of statements. On the other hand, the authors individually and collectively assume the responsibility for the errors which undoubtedly will be discovered. The following persons read the chapters indicated: R. E. Blackwelder (1 to 17); E. Dougherty (10 to 16); Alden H. Miller (1 to 9); C. F. W. Muesebeck (1 to 17); C. W. Sabrosky (1 to 17); M. A. Cazier (4, 5, 8, and 9); G. G. Simpson (7); L. M. Klauber (7); H. Levene (7), and R. F. Smith (7).

Finally, we wish to express our sincere thanks to the secretaries, who meticulously typed the various drafts of the manuscript and helped in checking the bibliography and in various other tasks connected with the preparation of this work.

Ernst Mayr
E. Gorton Linsley
Robert L. Usinger

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CONTENTS

PART 1

TAXONOMIC CATEGORIES AND CONCEPTS

CHAPTER 1

TAXONOMY, ITS HISTORY AND FUNCTIONS

Taxonomy, or systematics, is the science of classification of organisms. The term *taxonomy* is derived from the Greek τάξις, arrangement, and νόμος, law, and was proposed by de Candolle (1813) for the theory of plant classification. *Systematics* stems from the Latinized Greek word *systema*, as applied to the systems of classification developed by the early naturalists, notably Linnaeus (*Systema naturae*, 1735). In modern usage both terms are used interchangeably in the fields of plant and animal classification.[1]

Taxonomy is built upon the basic fields of morphology, physiology, ecology, and genetics. Like other scientific disciplines it is a synthesis of many kinds of knowledge, theory, and method, applied in this case to the particular field of classification. Its potentialities and its limitations are largely those of the basic fields whose raw materials it utilizes.

The first step in the resolution of any kind of biological knowledge is the classification of phenomena in an orderly system. This means ultimately the naming, description, and classification of all plants and animals. Something of the diversity of organic nature and the magnitude of this task may be indicated by the following figures. There are now known more than one-third of a million species of plants, sixty times as many as at the time of Linnaeus (Merrill, 1943). Every year about 4,750 new species of plants are described. Including synonyms and subspecies, more than 1 million names were proposed for phanerogams and cryptogams between 1753 and 1942.

The number of known species of animals is much greater than that of plants and has been estimated at about 1 million (Table 1). Including subspecies, there are probably more than 2 million named forms of animals, and new ones are being described at the rate of about 10,000 per year. For the insects alone, Metcalf (1940) calculates that 1½ million names are already applied. Accepting an estimate of 3 million probable insect species (Silvestri, 1929), and assuming that each species has on the average five distinct developmental or morphological phases, 15 million descriptions will eventually be required to characterize the stages of all insect species! When we superimpose the necessity for arranging 3 million species in a framework of higher categories express-

[1] For different usage see Mason (1950).

ing inferred natural relationships, and analyzing the population structure of the species concerned, something of the magnitude of the task facing just one group of taxonomists may be seen.

The objectives of taxonomy can only be achieved by sustained cooperative effort. Furthermore, the ability of the individual taxonomist to contribute to this effort depends on the breadth of his training as well as on his native talent. The complexities of modern systematics, its dependence on related fields, the refinement of modern techniques, and the magnitude of the literature have made it inevitable that the days of

TABLE 1. ESTIMATED NUMBER OF KNOWN SPECIES OF RECENT ANIMALS (Mayr)

Protozoa	30,000	Linguatula	70
Mesozoa	50	Chelicerata	35,000
Porifera	4,500	Crustacea	25,000
Coelenterata	9,000	Other arthropods (excl. insects)	13,000
Ctenophora	90	Insecta	850,000
Platyhelminthes	6,000	Mollusca	80,000
Acanthocephala	300	Pogonophora	1
Rotifera	1,500	Bryozoa	3,300
Gastrotricha	175	Brachiopoda	250
Kinorhyncha	100	Echinodermata	4,000
Nematomorpha	100	Phoronidea	4
Nematoda	10,000	Chaetognatha	30
Priapulida	5	Hemichordata	80
Nemertina	750	Tunicata	1,600
Entoprocta	60	Fishes	20,000
Annelida	7,000	Reptiles and amphibians	6,000
Echiuroida	60	Birds	8,590
Sipunculoidea	250	Mammals	3,200
Tardigrada	180		
Onychophora	65	Total	1,120,310

One of the objects of this tabulation is to indicate the relative size of the various groups of animals. Even the smallest phyla have therefore been included, because they are quite important from the points of view of phylogeny and comparative anatomy. The number of species of birds is based on an accurate count. All other figures are estimates, subject to two sources of error. Only 60, 50, or 40 per cent (or even less) of the existing species have as yet been described in many animal groups. On the other hand, in the less-known groups of animals, many populations have been described as full species which appear to be merely subspecies of widespread polytypic species. The two sources of inaccuracy thus cancel each other to some extent.

the untrained taxonomist are limited. The amateur will always play a most important role in assembling much of the raw material with which the taxonomist works, but he needs a broad background and special training if he is to make direct taxonomic contributions of the quality which will be required in the future. Even the trained taxonomist can no longer cover the entire field in any major group of plants or animals.

Greater specialization has been the inevitable consequence of the tremendous growth of our knowledge of living things.

HISTORY OF SYSTEMATIC ZOOLOGY

The history of taxonomy may be divided into a number of periods. These in turn correspond loosely to the various levels of taxonomy (alpha taxonomy, beta taxonomy, gamma taxonomy, see below). Definitions of these periods facilitate the understanding of the progress that has been made in the field. The complexity of taxonomy must be kept in mind when studying its history. Progress in the taxonomy of various animal groups (and in the study of animals from different regions) has been very uneven. Taxonomy is most advanced in the most popular groups (birds, butterflies, mammals, some genera of beetles), while in others it may still be on an elementary level. It is most advanced in the North Temperate Zone and lagging behind in the tropics and other distant places. Consequently the three historical periods here outlined are not strictly consecutive but largely overlapping.

First Period—the Study of Local Faunas. The history of taxonomy is almost as old as man himself. Natives of even the most primitive tribes may be excellent naturalists, with specific names for local trees, flowers, mammals, birds, fishes, and the more conspicuous (or most edible) invertebrates. A tribe of Papuans in the mountains of New Guinea was found to have 137 specific names for 138 species of birds. Only one species was confused with another. Often the nomenclature of such tribes is clearly binominal, with a generic and a specific name (Bartlett, 1940).

Several early Greek scholars, notably Hippocrates (460–377 B.C.) and Democritus (465–370 B.C.) included animals in their studies. However, only fragments of the works of these earlier authors are in existence. Apparently it was Aristotle (384–322 B.C.) who brought together the knowledge of his time and formulated it into the beginnings of a science. Aristotle did not propose a formal classification of animals, but he provided the basis for such a classification in his statement that "animals may be characterized according to their way of living, their actions, their habits, and their bodily parts." He referred to such major groups of animals as birds, fishes, whales, and insects, distinguishing among the last both mandibulate and haustellate types and winged and wingless conditions, and utilizing certain terms for lesser groups, such as Coleoptera and Diptera, which persist today. Aside from these larger groupings, his categories, according to Nordenskiöld (1928) were but two in number, the *genos* and the *eidos*, "the latter corresponding to the individual animal form—horse, dog, lion—the former to all combinations of a higher degree." The Aristotelian philosophy—it can scarcely be called a system—sufficed for the students of animals for nearly two thousand years. It is only in the works of the immediate predecessors of Linnaeus that we find more than probing attempts at animal classification.

The botanists were far ahead of the zoologists during this period, since they were the first to break away from the Aristotelian tradition and describe and classify local plants. From Brunfels (1530) and Bauhin (1623) there has been a continuous refinement of concepts and techniques (*e.g.*, Tournefort and Plumier). The contemporary writings of zoologists

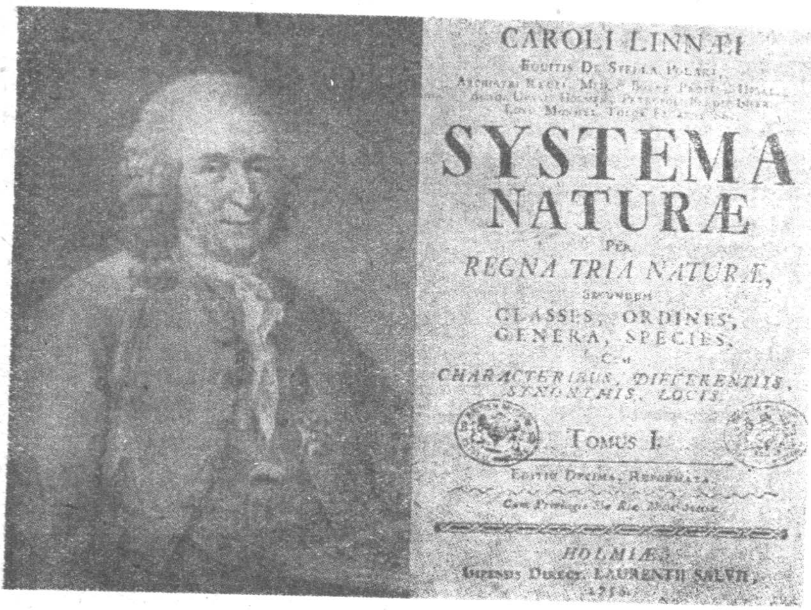

FIG. 1. Carolus Linnaeus (1707–1778) and title page from the foundation work in systematic zoology.

(*e.g.*, Gesner, Aldrovandi, and Belon) were, on the whole, still dominated by Aristotelian concepts and showed only rudiments of a consistent nomenclature and of principles of classification. Of all the earlier authors, the one who had the greatest influence on Linnaeus was John Ray (1627–1705), who recognized the difference between the genus and the species and who, through evaluation of both similarities and dissimilarities in animals, arrived at a more natural higher classification than did those who had gone before him (Raven, 1942).

The type of taxonomy that is based on the study of local faunas reached its peak in the great Swedish naturalist Linnaeus (1707–1778), whose contributions were so influential on subsequent students that, with much justification, he has been called the father of taxonomy. In the tenth edition of his great work *Systema naturae* (1758) (Fig. 1), the binominal system of nomenclature was for the first time consistently applied to animals, and this work became the foundation of systematic zoology. In addition to his new system of nomenclature, the work of Linnaeus was characterized by clear-cut species diagnoses and by the adoption of a hierarchy of higher categories: genus, order, class. The methods of Linnaeus were by no means wholly original, but his eminently practical system was quickly adopted, expanded, and elaborated because of his great personal prestige and the influence of his students. It dominated taxonomy for the next century, and most of the essentials of the Linnaean method are still components of modern taxonomy.

It is generally assumed that Linnaeus accepted the doctrine of fixity of species, *species tot sunt, quot formae ab initio creatae sunt.* Indeed, despite certain evidence to the contrary (Ramsbottom, 1938), systematic concepts of the Linnaean period were static concepts. Higher classification was largely mechanical and showed what we now recognize to be natural relationships only in cases where fundamental characters happened to be selected. The thinking of this period was characterized by the concepts of classical typological taxonomy. The species was the nondimensional species of the local naturalist. The particular importance of this period for the history of taxonomy is that at that time biology consisted almost entirely of taxonomy, and nearly all the eminent biologists of that day were taxonomists.

Linnaeus was not only the classical representative of this first period of taxonomy, his work also heralded the coming of the second period. Although Linnaeus in his earlier writings (*e.g.*, *Fauna suecica*, 1746) exemplified the local naturalist, he became more and more cosmopolitan in his later publications, utilizing the discoveries of naturalists in faraway countries. Still, his philosophy remained that of the student of local faunas, except that the *Systema naturae* was the product of the joint labors of many local naturalists.

Second Period—the Acceptance of Evolution. Evolutionary thought was already widespread in the eighteenth century (Maupertuis, Buffon, Lamarck, and many others), but it owes its firm foundation to the second period in the history of taxonomy, the period of exploration. This movement started modestly during the previous period and reached a grand climax during the middle of the nineteenth century. It was characterized by an intense interest in the faunas of faraway places, in magnificent world voyages and expeditions, and in the accumulation of vast numbers of specimens from all over the world, which permitted the monographic treatment of genera and families. Charles Darwin (1809–1882) was the naturalist on one of these expeditions (Voyage of the Beagle) and worked up some of its results. He became the world's leading specialist of the Cirripedia (barnacles) and wrote a monograph of this group that was authoritative. It was largely on the basis of his experiences as a traveling naturalist and taxonomist that Darwin conceived the theory of evolution. Combined with the reading of Malthus's *Essay on Population*, it also gave him an answer to the problem of the cause of evolution, the theory of natural selection. It is more than a coincidence that another traveling field naturalist, Alfred R. Wallace (1823–1913),

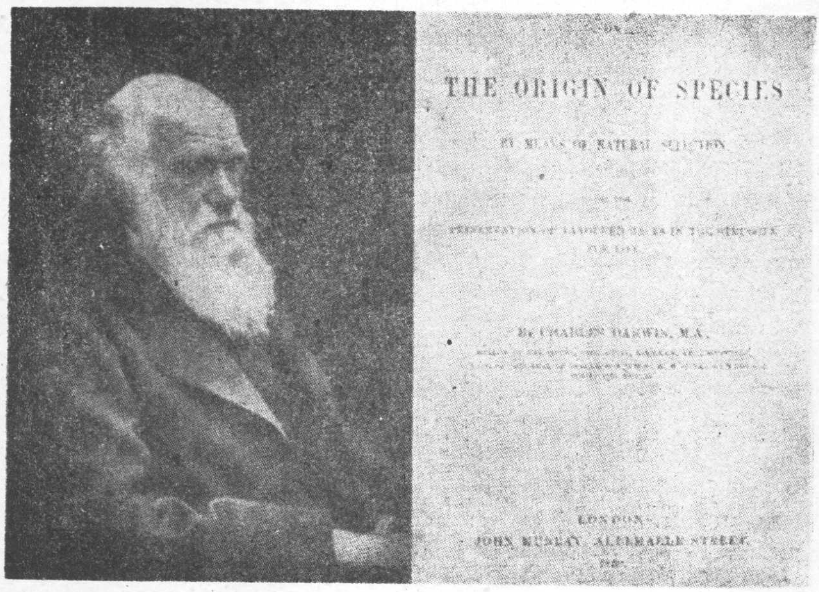

FIG. 2. Charles Robert Darwin (1809–1882) and title page from the foundation work in evolutionary theory.

came simultaneously to the same conclusions. The views of both men were jointly presented in 1858 to the Linnaean Society in one of the most dramatic episodes in the history of science. That Darwinism was to a large extent based on taxonomic work is perhaps one of the reasons why it did not actually alter taxonomic arrangements very basically, as has been pointed out by Dobzhansky (1951).

The publication of Darwin's *On the Origin of Species* (1859) (Fig. 2) resulted in a tremendous stimulation of biological thought and work. The decades immediately following 1859 were principally taken up by the question, Is evolution a fact? Or, stated differently, Are all the living organisms descendants of common ancestors? The interest of this period was preeminently phylogenetic. The chief effect of the acceptance of the theory of evolution on taxonomy has consequently been a greater preoccupation with phylogeny.

Ernst Haeckel (1866), more daring and speculative than Darwin, introduced (Fig. 3) the method of representing phylogeny by means of trees or branching diagrams (see Chap. 8). Although his formalized diagrams resemble but little those that are in use today, the method itself was useful and stimulating, and it provided the taxonomist with a graphic means for expressing supposed relationships. The search for facts to improve the designs of phylogenetic trees dominated biology during the second half of the nineteenth century and led to a boom in the fields of comparative systematics, comparative morphology, and comparative embryology. In taxonomy, in particular, it spurred the search for "missing links" and "primitive ancestors." These efforts were not wasted but led to a far-reaching understanding of the animal forms and to the establishment of a natural system that is still considered essentially valid.

This was an exciting period in the history of taxonomy. Not only were new species and genera discovered daily, but with reasonable frequency even new families or orders. The reward of such exciting discoveries attracted the keenest minds to the field of taxonomy. Alas, the wealth of nature is not inexhaustible, and the period of major new discoveries in the higher animals was over well before the end of the nineteenth century. Those who were anxious to describe new orders, families, and genera had difficulty discovering them. As an alternative choice they resorted to the splitting of the existing categories. Some splitting was justified and led to an elucidation of classification by doing away with heterogeneous, polyphyletic groups. In other cases, however, it led to a disintegration of natural categories. It appears, in retrospect, as the most retrogressive period in the history of taxonomy. Few of the splitters were good biologists, nor did they understand the proper function of the taxonomic categories. Part of the disrepute into which taxonomy fell during the latter part of the nineteenth and early twentieth century was caused by the activities of those who unnecessarily split well-known and well-founded taxonomic categories, thereby hopelessly concealing natural affinities.

Third Period—the Study of Populations. While the preceding period was dominated by the study of evolution of the higher categories, with a great interest in ancestral forms or missing links (such as *Amphioxus* or *Peripatus*), the most recent phase in the history of taxonomy is characterized by a study of the evolution *within* species. The typological concept of the species, which was already shaky in the preceding period, was abandoned and replaced by a dynamic, polytypic concept. Interest reverted to the fauna of local areas and to the study of variation within

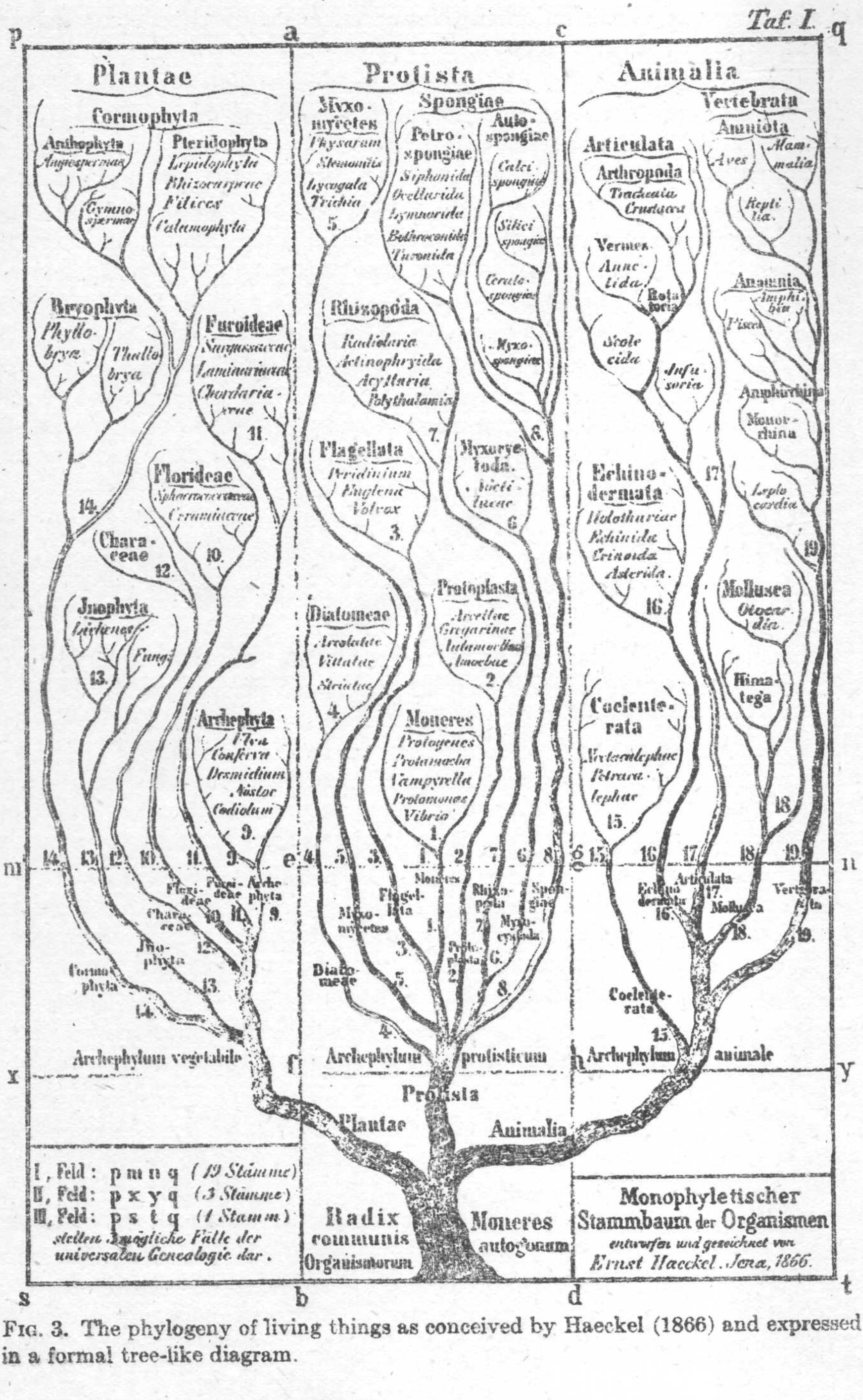

FIG. 3. The phylogeny of living things as conceived by Haeckel (1866) and expressed in a formal tree-like diagram.

populations and the slight differences between adjacent populations. The taxonomist is no longer satisfied to possess types and duplicates; he collects series and analyzes them quantitatively. This type of study was commenced almost simultaneously by ornithologists, entomologists, and malacologists in the second half of the nineteenth century.

The detailed history of this phase of taxonomy has not yet been written, but it would be well worth the attention of historians of biology. Although the study of populations reached its dominant position in systematics only within recent generations, its roots go back to the pre-Darwinian period. In ornithology, after the pioneer efforts of Schlegel, the systematic collecting of series was particularly in vogue among the American school, following the leadership of Baird (1854):

> As the object of the [Smithsonian] Institution in making its collections is not merely to possess the different species, but also to determine their geographical distribution, it becomes important to have as full series as practicable from each locality. . . . The number of specimens to be secured will, of course, depend upon their size, and the variety of form or condition caused by the different features of age, sex, or season. In gathering specimens of any kind, it is important to fix with the utmost precision the localities where found.

Among the malacologists are to be mentioned particularly Kobelt (1881), Gulick (1905), the Sarasins (1899), as well as Crampton, whose biometrical studies in the local geographical variation in the genus *Partula* (1916, 1932) have become classical.

The results of this work caused the abandonment of the typological species concept. Species were no longer considered as something fixed and uniform, but rather as polytypic, consisting of many subspecies and local populations, each differing from the others and each showing considerable variability within itself. Two facts, in particular, were outstanding. First, that the differences between subspecies and species were compounded of very numerous small variations; and second, that much of the local and geographical variation was closely correlated with the environment. The working and thinking of the leading taxonomists of this period was thoroughly modern and biologically correct, except in one respect. Most of them interpreted the close correlation between variation and the environment as indicating a direct effect of the environment. They were Lamarckians. In spite of this error they were essentially much closer to the truth than the early Mendelians.

It was during this period that the Mendelian rules were rediscovered (in 1900), an event which eventually led to the spectacular rise of the field of genetics. However, the early Mendelians emphasized the role of large mutations (De Vries and Bateson) and thought that they produced new species by a single step. They minimized the role of the environ-