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“Cladistic Analysis or Cladistic Classification?”:

A Reply to Ernst Mayr¹

Some time ago Ernst Mayr sent me a manuscript, which has recently been published (Mayr, 1974). It is a critique of phylogenetic systematics, but it is flawed by misunderstanding, conceptual imprecision, and inconsistency. And the paper as a whole is burdened with detailed discussion of peripheral issues. Mayr nevertheless purports to defend truly biological thought against mere formalism, breadth of vision against narrow-mindedness and limited experience, and sound tradition against unwarranted innovation. With the great authority that Mayr wields within the scientific world, much confusion may result. I therefore set aside my reluctance to write a paper devoted solely to rebuttal. But I do not intend to discuss each of Mayr's assertions that could be refuted; to do so would make my presentation at least as long as his. I restrict my discussion to a few basic concepts.

1.

After his introductory remarks, Mayr fully evaluates the epistemological and methodological legitimacy, and practical effectiveness, of the procedures of phylogenetic systematics, which aims to determine the chronological sequence of speciation events in lineages of phylogenetic descent, by evaluating the heterobathmy of characters and reconstructing a phylogenetic tree, or cladogram (Schlee, 1971).

Mayr asserts that phylogenetic systematics (his “cladistic analysis”), which proceeds with these methods, is or should be an indispensable preparatory step in every taxonomic work. But he rejects one other purpose of phylogenetic systematics—to

convert the cladogram into a hierarchic system. According to Mayr, such a system, based on the chronological sequence of speciation events in evolutionary lineages, is unsound, unrealistic, and unscientific; for it ignores the fact, so Mayr continues, that sister-groups often evolve along paths divergent adaptogenetically and ecofunctionally. Because phylogenetic systematics gives the same hierarchical rank to sister-groups (even if they represent different adaptive levels), Mayr concludes that the phylogenetic system contains no information about adaptogenesis in divergent sister-groups. The phylogenetic system, Mayr contends, arises from three scientifically impermissible circumstances: (1) that phylogenetic systematics is assumed to be the best possible systematics; (2) that well known terms (phylogeny, relationship, and monophyly) are arbitrarily redefined; and (3) that divergent adaptogenetic evolution in sister-groups is neglected. Mayr's argument about scientific permissibility is discussed below (sections 3–5).

2.

Mayr's opposing viewpoint is his “evolutionary systematics” (p. 95). This, too, begins with the construction of a cladogram, but does not produce a hierarchic system directly from the cladogram. Instead, it considers both phylogenetic (“cladistic”) and, in particular, adaptogenetic (ecofunctional) information. Thereby it preserves, according to Mayr, the information of adaptogenetic divergence in the evolution of sister-groups. As a result, “evolutionary systematics,” according to Mayr, satisfies much better than phylogenetic systematics the requirements of a scientific system: to permit the most useful generalizations and explanations (Mayr's “predictions” [p. 96]). Mayr considers this format of “evolutionary systematics” its “theory” (p. 96). But it seems to me that he thereby confuses the concept of a sci-

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entific theory with that of a schedule, or format, of taxonomic activity. I doubt, therefore, if Mayr's "evolutionary systematics" is really based on scientific theory—a doubt that has been expressed often, perhaps most clearly by Johnson (1970), who is himself an advocate of "evolutionary systematics."

Mayr's epistemological imprecision stands out clearly in his desire to build his "evolutionary" system in a "synthetic" (p. 95) manner according to two different viewpoints: phylogenetic and, also, adaptiogenetic (ecofunctional). With this system, built according to two different viewpoints, a user can never know of a particular group (taxon) if it is based and defined phylogenetically or adaptiogenetically (ecofunctionally). This circumstance, contrary to Mayr's belief, reduces the information content of his "evolutionary" system (see below).

The logical demand for strict uniformity of viewpoint in the arrangement of systems (already established although not always followed by Aristotle), is neither mentioned nor refuted by Mayr. He would, perhaps, reject this demand as formalistic, for he elsewhere rejects other logical demands. But rejecting a logical demand is not in itself a valid scientific refutation, and is at best a reckless practice—even outside the sciences.

3.

I will now consider the particular objections enumerated above, with which Mayr contests the scientific permissibility of phylogenetic systematics.

"The cladists are sincerely convinced that their theory produces the best classifications" (p. 96). This assertion, with which Mayr introduces his refutation of this alleged claim of the "cladists," is false, as is evident by examination of Mayr's citation (Hennig, 1971): I have maintained only that the phylogenetic system, as a general reference system, has a certain logical priority; and this statement is not the same as Mayr's assertion. As for the

question of what animal system is the best, I don't believe that it can be posed so generally (as Günther has pointed out, "the system of cook books is the best for the purpose of a cook book"). For the scientifically best system, Mayr, nevertheless, states several criteria, among which the best "explanatory, predictive, and heuristic properties" (p. 94) and an "efficient information storage and retrieval system" (p. 94) may be the most important. But I raise a question about the significance of the concept of "prediction," which seems to me a purely formal and meaningless metaphor, adopted by Mayr from a special group of biological theories to which no theory of biological systematics belongs. Indeed, the concept of predictions plays no further role in Mayr's presentation—except to figure in some very general assertions ("The number of evolutionary statements and predictions that can be made for many holophyletic groups . . . [that is, the monophyletic groups of phylogenetic systematics] is often quite minimal" [p. 96]). And it seems to me that Mayr, contrary to his stated purpose, agrees with my opinion of the logical priority of the phylogenetic system: "The synthetic or evolutionary method of classification . . . agrees with cladistics in the postulate that as complete as possible a reconstruction of phylogeny must precede the construction of a classification" (p. 95) and "Hennig is quite right when he states: 'phylogenetic research as biological science is possible only if it adopts the discovery of the genealogical relation of species as its first objective'" (p. 97).

Here I draw attention to a distinction that might be made between the concept of system and that of classification. Let me begin with an example. If an archaeologist discovers potsherds in a tomb, he might begin by ordering, or classifying, them in some way: according to their material (clay or metal), their color, their decorations, etc. Subsequently, he might attempt to reconstruct the original vessels (vases, urns, etc.), of which the potsherds are

fragments. This reconstruction is another kind of ordering. One might call it a system, but one need not call it a classification. For another example, I refer to the rivers of Europe. These may be classified according to their navigability, water management, the conditions they offer for the settling of organisms, etc. But one might seek to determine the drainage (Danube, Rhine, Elbe, etc.) to which each belongs, in order to construct a different kind of system of rivers. Similarly, the construction of a cladogram in accordance with the principles of phylogenetic systematics results in a system rather different in principle from various kinds of possible classifications. Although my original perception of this distinction was somewhat unclear, I have nevertheless avoided speaking of phylogenetic "classification," preferring instead phylogenetic "system"—but I have sometimes used "classification" under the influence of English usage.

A peculiar defect in Mayr's work, one which jeopardizes the whole of what he presents a fundamental contribution, is that he disputes (p. 100) the conversion of a cladogram into a hierarchical system: "As valuable as the cladistic analysis is, it does not automatically provide a classification" (p. 123), and "The basic postulate of the cladistic theory, a complete congruence of a cladogram and classification, can be satisfied only by making numerous assumptions and redefinitions and by ignoring numerous facts of evolution and phylogeny (broadly defined)" (p. 100).

These assertions are simply false. They would be correct if "classification *sensu* Mayr" were inserted in the two sentences in place of "classification." Then, neither Mayr nor I would dispute their truth. Mayr here confuses the aims of "cladists" with those of "evolutionists" (with respect to the construction of systems), although he previously described correctly the differences between the two. And he reproaches the "cladists" because they proceed differently than he wishes. Through this remarkable solipsism, Mayr presumes to re-

fute the "cladists." It is a type of argument that he uses also in other places in his paper.

In actuality, the conversion of a cladogram into a hierarchical system is possible without a single additional assumption or the redefinition of any of the concepts used in constructing the cladogram. The conversion is a purely formal operation. Given the cladogram of Mayr's Fig. 1a, for example, the following hierarchy results:

- Taxon (B + C + D)
 - I. Taxon B
 - II. Taxon (C + D)
 - 1. Taxon C
 - 2. Taxon D

Why I often prefer a hierarchical system to a cladogram also needs brief discussion (sections 6-7).

4.

The logical priority of the phylogenetic system, as a general reference system, arises from its foundation in a biological theory with unambiguously defined central concepts. Mayr, however, objects to what he terms "arbitrary decisions, involving a redefinition of well known terms" (p. 100) and I respond as follows:

a. *Phylogenesis*, a term coined by Haeckel more than 100 years ago, has never before been unambiguously defined. The Greek word roughly means origin of phyla (groups of common descent). According to evolutionary theory, phyla originate by successive cleavage events within organismic communities of reproduction. Phylogenetic systematics defines phylogenesis in this unambiguous sense. Mayr considers this definition erroneous, and adds, as a second "set of factors" the "amount and nature of evolutionary change between branching points" (p. 95). But these companion phenomena of phylogenesis, which vary more or less in different sister-groups, are discussed in the literature under the terms adaptogenesis and anagenesis (or aramorphosis), about which, however, there is some ambiguity of meaning. Because he

senses, perhaps, that these are logically secondary epiphenomena of phylogenesis, Mayr calls his recommended theory of systematics "evolutionary" rather than phylogenetic.

b. *Relationship* is a term that in English as well as German means either form relationship or genealogical (blood) relationship. Mayr defends this ambiguity even for the practice of biological systematics, thereby disregarding the need for unambiguously defined terms and precise concepts. Thus, it seems to me that Mayr's position is logically indefensible: one cannot work logically with ambiguous terms, the meaning of which is not determinable in any given case of usage. Phylogenetic systematics defines the term relationship unambiguously as genealogical (blood) relationship. But "unambiguous" describes an attitude that Mayr dismisses as "highly specialized" (p. 102); and Mayr's dismissal places his argument beyond the realm of reasonable discussion.

c. *Monophyly*, as treated by Mayr, shows how much he engenders confusion rather than clarity by his disregard of the need for unambiguous definitions of scientific terms. Mayr, on his part, defends the "traditional definition" of (p. 99) of monophyly and asserts that I have caused much confusion by defining the term precisely. In actuality, the "traditional definition" of monophyly, as Mayr understands it (descent from a common ancestor), is meaningless. When Mayr asserts that "groups that are not composed of descendants of a common ancestor are artificial and of low predictive values" (p. 95), this assertion is itself meaningless: any two species whatever are descendants from a common ancestor (according to this "traditional definition," any group whatever is "monophyletic"). The definition becomes clear and usable only when the additional statement is added that species of a monophyletic group have an ancestor (stem species) in common only to themselves.

To some extent, the vagueness of the

traditional definition, that a group is "monophyletic" if its members have a common ancestor, is recognized by Mayr himself, who adds the qualification that "the component species, owing to their characteristics, are believed to be each other's nearest relatives" (p. 104). But the value of his addition is annulled by the ambiguity of the term "nearest relatives." If one understands "nearest relatives" in the genealogical sense (rather than the form sense), then the only difference between Mayr's definition and that of phylogenetic systematics is their relative clarity of formulation.

At the present time, some systematists wish to use the term "monophyletic" to refer to groups that I termed paraphyletic. Mayr cites Ashlock, who introduced the term holophyletic for groups that are monophyletic in the phylogenetic sense (groups whose members have an ancestor in common only to themselves). Ashlock wished to use the term "monophyletic" in referring both to holophyletic and paraphyletic groups. A typical paraphyletic group is that of "animals" in a classification contrasting man and "animals"; another is "invertebrates" in a classification contrasting vertebrates and "invertebrates." To term such groups ("animals" and "invertebrates") "monophyletic" merely renders the term useless. Ashlock's attempts (1) to associate paraphyletic and holophyletic (monophyletic) groups under a common definition (Ashlock's "monophyletic"), and (2) to contrast them with "polyphyletic" groups, on the basis of certain supposed similarities and differences in the structure of genealogical relationships, I expect on theoretical grounds will founder hopelessly.

A categorical distinction exists between monophyletic groups (Ashlock's holophyletic), whose members possess a stem species common only to themselves, and non-monophyletic groups (paraphyletic and polyphyletic), whose members always possess a common stem species but not one common only to themselves.

A distinction between the terms paraphyletic and polyphyletic is possible only

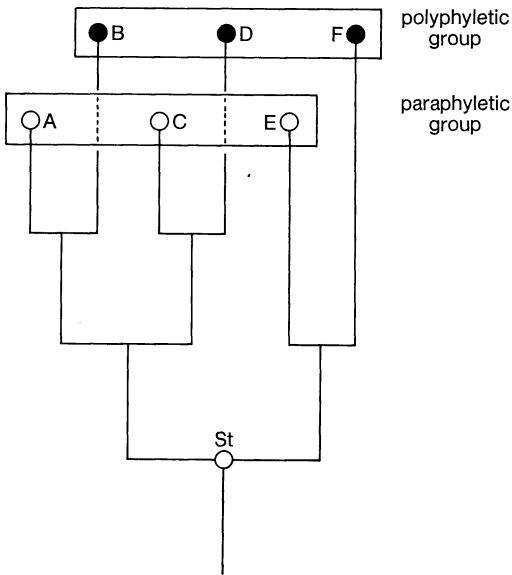


FIG. 1.—Polyphyletic and paraphyletic groups. Species A, C, E agree in primitive (plesiomorphous) characters; species B, D, F in derived, but convergently evolved characters.

at the methodological level. For example, an investigator may discover that a certain monophyletic group had previously been subdivided into two or more non-monophyletic subgroups. If so, the investigator may determine that one of two possible errors had been committed (fig. 1): a subgroup may have been formed on the basis of convergence (such groups have customarily been termed polyphyletic); or a subgroup may have been formed on the basis of symplesiomorphic agreement (such groups have sometimes been termed "polyphyletic," sometimes "monophyletic"). Both types of groups, those based on convergence (what I consider polyphyletic groups) and those based on symplesiomorphy (paraphyletic groups), are similar, for the members of each group-type lack a stem species common only to themselves. As the figure shows for groups of either type, there need be no difference between them in the structure of their genealogical relationships. The terminological distinction between paraphyletic and polyphyletic groups is valid, therefore, only when attention is drawn to the

particular kind of mistake made in the process of character analysis that led to the formation of the groups. From this standpoint, the terms paraphyletic and polyphyletic are not used for indicating differences in the genealogical relationships between taxa (groups). In view of the confusion already caused by Ashlock, and the acceptance of his suggestions by Mayr and Weidner, terminological clarity can best be preserved by rejecting Ashlock's compromise, and accepting the concept of monophyly as defined by phylogenetic systematics. For the moment, however, one could, perhaps, speak of monophyletic (holophyletic) groups.

Contrary to Mayr's assertion, the definition of the concept of monophyly does not first become important during the conversion of a cladogram into a hierarchic system, but rather during the construction of the cladogram (during "cladistic analysis," i.e., the determination of the chronological sequence of branching points and the relative recency of common ancestry). A "cladogram" that does not explicitly indicate the monophyletic (holophyletic) groups, is no cladogram of the phylogenetic system. If Mayr does not understand this aspect of cladograms, then I would consider specious his appreciative remarks about the value of "cladistic analysis": his assertion, "There is little argument between cladists and evolutionary taxonomists about the cladogram" (p. 98), would be untenable.

5.

"Neglect of the dual nature of evolutionary change" (p. 105). Mayr states that I have "created enormous confusion" (p. 104) with my unambiguous definition of monophyly, which, Mayr asserts, "ignores, indeed it quite deliberately conceals, the most interesting aspect of evolution and phylogeny" (p. 104), namely that of radiative and divergent adaptiogenesis. This definition, of course, is the basis for groups such as Archosauromorpha, which include crocodiles and birds (as well as various

fossil groups related to them). Mayr considers this particular group “useless” (p. 104). But in my opinion information about the possible amount of adaptogenetic divergence of sister-groups is here even better expressed than in the usual classifications, particularly those that do not indicate even that crocodiles and birds are sister-groups: e.g., Class Reptilia (Order Crocodylia, Order . . ., Order . . .), Class Aves.

With his criterion (“neglect of the dual nature of evolutionary change”), Mayr would have reason to reject groups such as Chordata, which include divergent adaptogeneses (e.g., Tunicata and Aves), and Mammalia, which also include divergent adaptogeneses (e.g., Monotremata and Proboscidea). Reflections along these lines, which could be continued indefinitely, demonstrate that Mayr’s weak and vague conceptual constructs are scientifically ineffective because of their ambiguity.

Of Mayr’s arguments, there remains only the unfounded assertion that “To give them [e.g., crocodiles and birds] the same categorical rank . . . may be logically impeccable, but is simply wrong biologically” (p. 122). Here, as elsewhere, “Mayr betakes himself beneath his level in his polemic against phylogenetic systematics” (Löther, 1972:237).

6.

“Evolutionary systematics,” as propounded by Mayr, also makes use of a hierarchic system. For construction of this system, Mayr considers, besides the branching sequence of phylogeny, a second “set of factors” (or “variables” [p. 95]), namely the “amount and nature of evolutionary change between branching points.” And Mayr contends that the system of “evolutionary systematics” consequently has a much higher information content than that of phylogenetic systematics. Let us now check if this contention is true. According to current publications, the phylogeny of recent Sauropsida is as shown in Figure 2, which may be converted to a hierarchy thus:

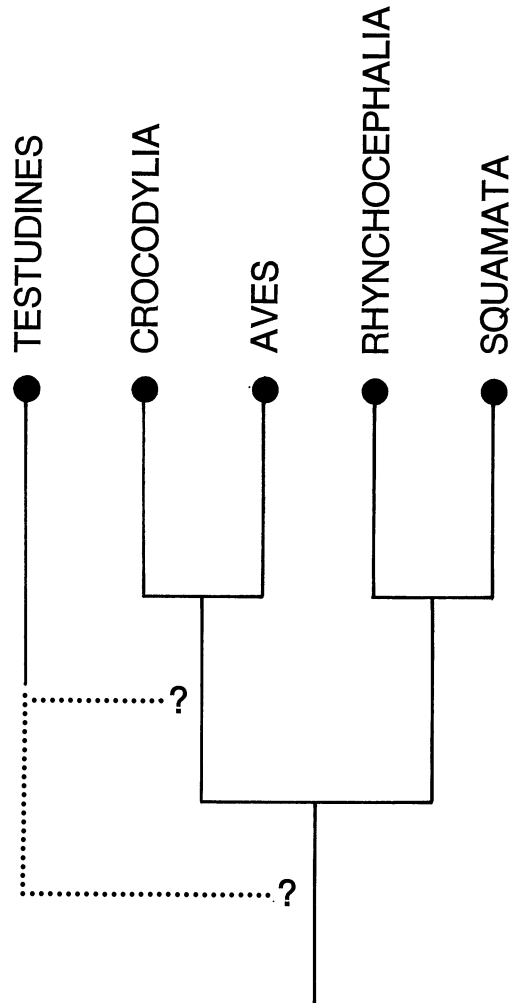


FIG. 2.—Phylogeny of Sauropsida according to recent authors. The phylogenetic relationships of Testudines are unclear.

- I. Testudines
- II. Archosauromorpha
 - A. Crocodylia
 - B. Aves
- III. Lepidosauria
 - A. Rhynchocephalia
 - B. Squamata

The information content of this hierarchy arises from its absolutely reliable reflection of the known branching sequence of the cladogram; the branching sequence can be

retrieved from the hierarchy just as accurately as from the cladogram. In addition, the hierarchy also indicates the uncertain interrelationships of the major groups (Chelonia, Archosauromorpha, Lepidosauria). For example, if the chelonians prove to be the sister-group of the remaining Sauropsida, the hierarchy, of course, could be modified to express this new information:

- I. Testudines
- II. Sauropsida *sensu stricto*
 - A. Archosauromorpha
 - 1. Crocodylia
 - 2. Aves
 - B. Lepidosauria
 - 1. Rhynchocephalia
 - 2. Squamata

The "evolutionary" system of the Sauropsida has never been specified by Mayr, but let us assume that it is similar to the system commonly found in textbooks:

- Class Reptilia
 - 1. Order Chelonia
 - 2. Order Rynchocephalia
 - 3. Order Squamata
 - 4. Order Crocodylia
- Class Aves

If we wish to rewrite this hierarchy as a cladogram, it would appear as in Figure 3. This "cladogram," of course, is false, as shown by comparison with the original (Fig. 2). I conclude, therefore, that the "evolutionary" system of the Sauropsida may contain little or no information about the branching sequence of the original cladogram—even though Mayr asserts that this first "set . . . of factors: phylogenetic branching" (p. 95) is, or should be, contained in the system. For other groups the "cladogram" that might be rewritten from an "evolutionary" system, according to the same principles and without adding information, would correctly represent part of the branching sequence of the original cladogram; but without additional information we could not identify the part correctly represented.

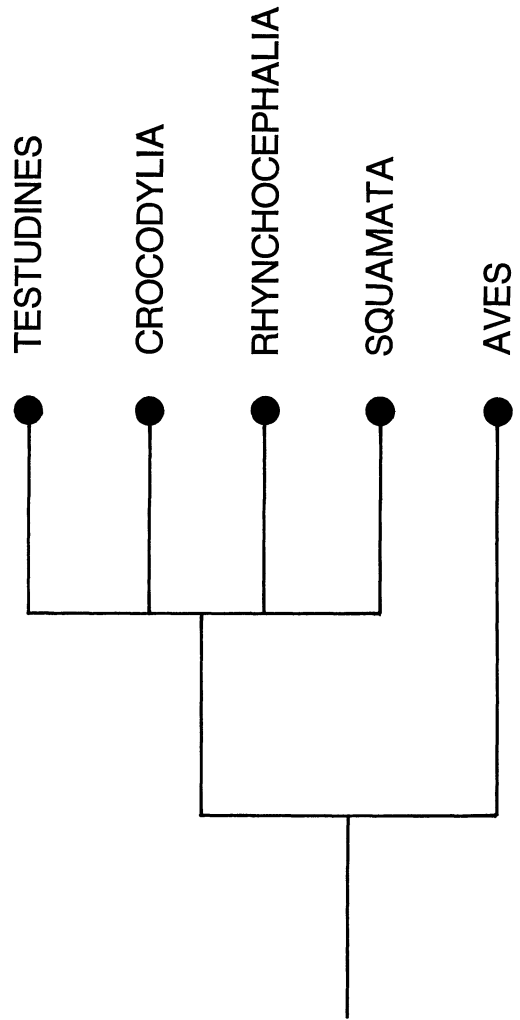


FIG. 3.—"Cladogram" resulting from the attempt to reconstruct a "phylogenetic tree" from the "evolutionary" classification of Sauropsida into classes and orders.

If the "evolutionary" system contains no reliable information about the first "set of factors" that it allegedly contains, what then is the status of the second "set of factors" ("amount and nature of evolutionary change between branching points")? According to Mayr, this second set of factors is extraordinarily complex. It includes, for example, even the "role a higher taxon plays in the economy of nature" (p. 122). But here I would ask, what objective stan-

dard, actually or potentially binding on all systematists, may be used to convert these many things of the highest qualitative diversity into a quantitative value (for this is what is involved in the last resort), thereby to determine the coordination and subordination of groups in the “evolutionary” system?

This standard of measurement is nowhere to be found in the literature, not even in Mayr’s works. Mayr does not give us even the rudiments of a practicable and teachable method (there is, of course, an extensive literature on this issue, but I will not pursue it further here).

If one asks wherein the “amount and nature of evolutionary change” is truly expressed, then the answer can be only in terms of the “amount and nature” of the manifold differences of the most diverse kinds that occur between organisms. If we wish to introduce into a hierarchic system information about the nature and amount of these differences, then we are concerned not with the process of phylogenesis and evolution, but with the results of that process (see above: adaptiogenesis as an epiphenomenon of phylogenesis). If we wish to build a hierarchic system with this result, then it becomes irrelevant if the result was produced through phylogenesis (evolution) or through a sudden act of creation. Mayr must sense this because he repeatedly appeals to Aristotle, and reproaches phylogenetic systematics for adopting “Aristotle’s downward classification” (p. 105). But I think that Aristotle, even if equipped with our present knowledge of the differences (in the broadest sense) among organisms—but without knowledge of the processes of phylogenesis—would have to reach the same results as Mayr and his adherents: according to the estimation of “amount and nature” of these differences. And Aristotle, too, would not have any binding objective standard of measurement for assessing differences of *Gestalt*. The term “evolutionary systematics” is, therefore, misleading, and I think Mayr’s system is better termed “Aris-

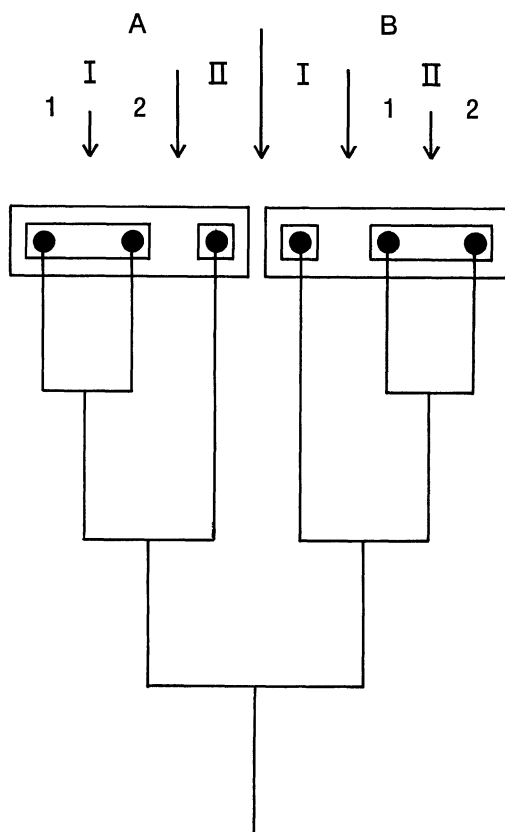


FIG. 4A.—The phylogenetic system of insects. The hierarchical division of subgroups is derived from the branching sequence of the phylogenetic tree (the tree can be reconstructed from the hierarchal system).

- A. Entognatha
 - I. Ellipura
 - a. Protura
 - b. Collembola
 - II. Diplura
- B. Ectognatha
 - I. Archaeognatha
 - II. Dicondylia
 - a. Zygentoma
 - b. Pterygota

totelean” (Crowson, 1970) or “typological” systematics.

Discussion about the relative merits of phylogenetic and Aristotelean systems are presently hampered and confused by two circumstances. The first circumstance is that the principles of phylogenetic systematics are frequently illustrated by reference

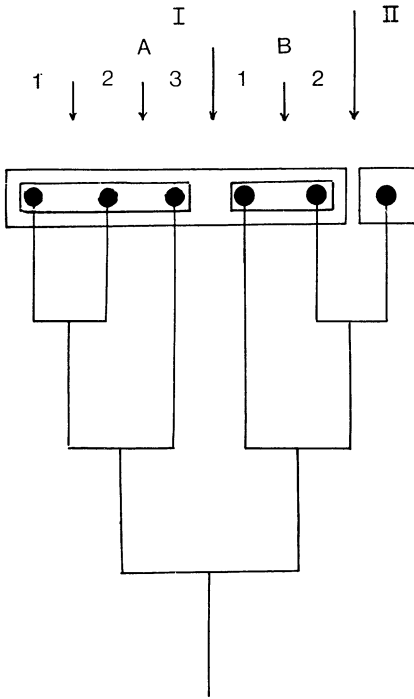


FIG. 4B.—Classification of insects (after Grassé, 1949, in *Traité de Zoologie*).

- I. Apterygota
 - A. Entotropha
 - 1. Protura
 - 2. Collembola
 - 3. Diplura
 - B. Ectotropha
 - 1. Archaeognatha
 - 2. Zygentoma
- II. Pterygota

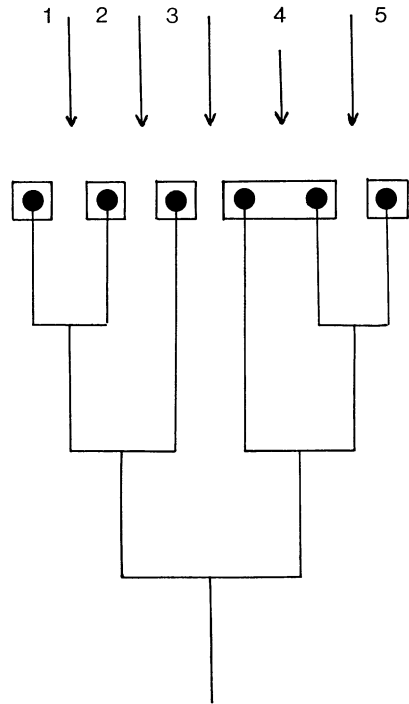


FIG. 4C.—Classification of insects (after, Weber, 1954, in *Grundriss der Insektenkunde*). 1-5, "Sub-classes."

- 1. Collembola
- 2. Protura
- 3. Diplura
- 4. Thysanura
- 5. Pterygota

to Amniota or Sauropsida. These illustrations are convenient, because everyone has an intuitive concept associated with the names of the vertebrate groups, but use of these illustrations has certain disadvantages. For example, to conclude that the group "Reptilia" must be dissolved and that crocodiles and birds must be associated in one group (Archosauromorpha) of the phylogenetic system strikes many as shocking and absurd; for the "amount and nature of evolutionary change" (or, as others have said, the "magnitude of anagenetic steps") appears to separate birds so distinctly from all "reptiles" (including crocodiles) that it seems pure formalism, and perfectionism

transcending any reasonable purpose, to neglect these facts in a hierarchical system. But let us note that the group Archosauromorpha is not at all "useless" (p. 104), as Mayr asserts. But it is all too easy to argue with a single extreme case. Fig. 4A-E shows some of the systems proposed for insects in various texts and handbooks. They are similar in attempting to represent in a hierarchy the morphological divergence of groups, the "amount and nature of evolutionary change," or "magnitude of anagenetic steps." Their differences arise from the different ways in which the different authors evaluate these phenomena (see length of arrows; it may be remarked here that the system in fig. 4E is not false in

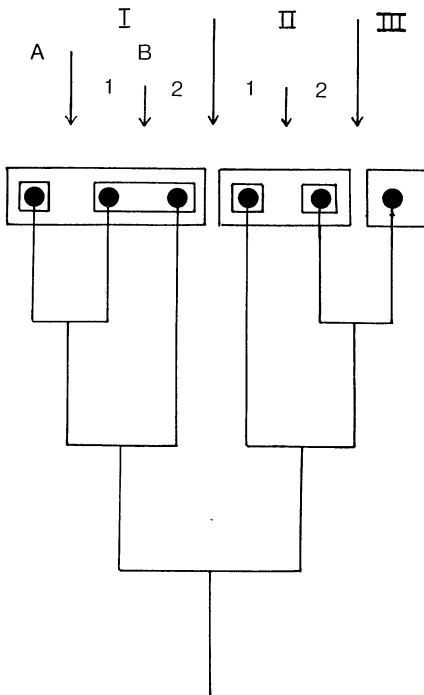


FIG. 4D.—Classification of insects (after Beier, 1969, *Handbuch der Zoologie*). SbCl, subclass; SpO, superorder; O, order; SbO, suborder.

- I. SbCl Entognatha
 - A. SpO Collembola
 - B. SpO Diplura
 - 1. O Diplura [sic]
 - 2. O Protura
- II. SbCl Ectognatha
 - O Thysanura
 - 1. SbO Machilinea
 - 2. SbO Lepismatinae
- III. SbCl Pterygota

the sense of phylogenetic systematics, but only incomplete: it omits some of the information about relationships of particular groups). Similar examples could be cited for most animal groups. And as long as there is no objective and generally binding standard of measurement, by which we may measure the “amount and nature of evolutionary change” or “magnitude of anagenetic steps,” and thereby demonstrate that one of the proposed systems is more correct than the others, there can and will be no generally accepted Aristotelean (“evolutionary”) system.

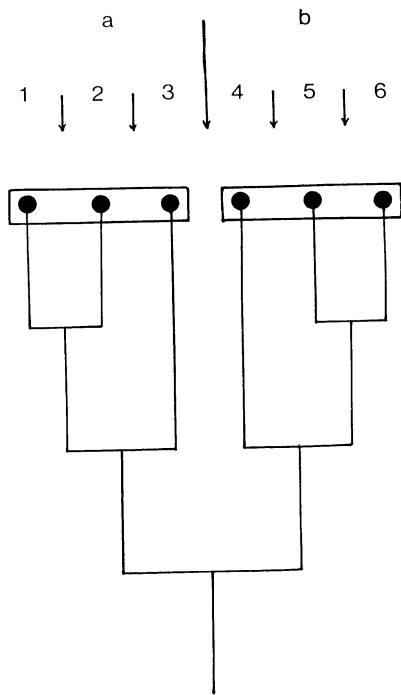


FIG. 4E.—Classification of insects (after Renner, 1971, in *Zoologisches Praktikum*). a, b, unranked groups; SbCl, subclass.

- a. Entotropha
 - 1. SbCl Diplura
 - 2. SbCl Protura
 - 3. SbCl Collembola
- b. Ectotropha
 - 4. SbCl Archaeognatha
 - 5. SbCl Zygentoma
 - 6. SbCl Pterygota

Indeed, if in the history of systematics there has been a certain progress in the direction of a generally accepted system (at least for some groups), this is the gradual progress toward a phylogenetic system.

The second circumstance that engenders confusion can likewise be recognized from Fig. 4A–E. In the Aristotelean system, just as in the phylogenetic system, the limits of the groups (taxa) always coincide with branching points of the cladogram. It requires little thought to perceive why this must be so. Accordingly, we can establish, even for a system that originated before the theory of descent, that the limit of a group

always coincides with one or another branching point of the cladogram—insofar as we know it today. The difference between a system that originated before the theory of descent, and one built in accordance with Mayr's recommended principles, consists only of our knowledge that the differences between groups arose in the course of a phylogenetic process (in connection with cleavage of species). But if Mayr's principles are followed, this additional knowledge is without any significance for the theory and methods of biological systematics: the differences between birds and crocodiles, and the differences between crocodiles and other "reptile" groups, remain the same—equally great or small, equally significant or insignificant in any conceivable respect—regardless if (1) we regard the differences as the results of a sudden act of creation, or (2) recognize them as consequences of the fact that in the course of phylogenesis different branches of the phylogenetic tree prove of different significance for the origin of present discontinuities in the form- and life-diversity of organisms. We thus return to the conclusion already reached that the term "evolutionary" system is misleading, and that there is no fundamental distinction between an "evolutionary" system and a pre-Darwinian, or Aristotelean, system.

With the demonstration (Fig. 1) that there is no distinction between paraphyletic and polyphyletic groups with respect to the genealogical relationships of their components, it also becomes illogical to argue that an "evolutionary" system differs from a pre-Darwinian system in the elimination of polyphyletic groups from the pre-Darwinian.

7.

So far we have considered systems in the form of simple hierarchies. Further information could be introduced by textual exposition at the various hierarchical levels of either a phylogenetic or Aristotelean system. Such textual exposition is normally included, for example, in checklists with

distributional notes. But a phylogenetic system can be augmented through such notes and thereby serve as a source of information more easily, I think, than an Aristotelean system, which is determined already in its construction by an obscure combination of qualitatively different viewpoints. On this matter, too, I will only hint here at further considerations.

Mayr asserts that phylogenetic systematics is impractical because there are sometimes not enough characters available to determine the interrelationships of all the species of a particular group. This is true. Therein lies, however, a stimulus for further study. Indeed, unresolved problems of relationship, uncovered by phylogenetic systematics, have already led to successful goal-oriented studies (e.g., by Schlee, Zwick, et al.).

The reason why phylogenetic systematics is not satisfied merely with a cladogram in the sense of Mayr, to represent the results of studies in branching sequence in a particular group, but prefers a hierarchical system, may be made clear with one final consideration. A hierarchical system has many advantages. It can be clearly set out in a small space; for the birds, for example, it would take up the same space as Wetmore's checklist. It would allow anyone quickly and clearly to recognize the gaps in our knowledge: species of unknown interrelationships could be listed in alphabetical order under their appropriate monophyletic group; groups of doubtful monophyly could be placed in brackets or indicated with question marks (these, of course, are purely technical devices). But we should consider the value of this system, in the simple form of a checklist, as (1) an information source and (2) a stimulus for studying yet unresolved branching sequences of the phylogenetic tree. Can a "traditional," or Aristotelean, system, built according to Mayr's recommendations, have the same value as an information store and as a stimulus for new studies? I am afraid that a catalogue of the 300,000 species of beetles, even if it could be constructed on the principles of Mayr's recommended

Aristotelean system, would in practice be an information source only for those coleopterists who constructed it.

8.

Apart from his unsubstantiated critique of the fundamental questions discussed above, which Mayr believes adequate to refute phylogenetic systematics, he also critically treats at length some questions of secondary importance for his theme. Only some of these will be discussed here. For example, he reproaches me for "a purely formalistic species definition" (p. 109) and refers to a note on the deviation rule given by Schlee (1971:28). Hitherto I have assumed that the biological species concept, used by me since 1950, does not essentially differ from that of Mayr (Hennig, 1950, 1966). The concept is, of course, based on study of Recent species. But if one believes that, despite all difficulties and restrictions in particular cases (of which we are well aware), the Recent species of any complete checklist conform to the biological species concept, then this should be the case also for any species known for example from Miocene fossils (naturally, it is impossible in practice to set out a complete checklist of this kind, including both fossil and Recent species, but it must be admitted as a conceptual possibility). Three and only three possible genealogical relationships are conceivable between, for example, the Miocene and Recent species of a monophyletic group: (1) A Miocene species has no descendants in the Recent fauna; (2) A Miocene species has one descendant species in the Recent fauna; (3) A Miocene species has two or more descendant species in the Recent fauna. In case (2), it is possible that the Recent (descendant) species either does or does not differ in recognizable characters from the Miocene species. For neither possibility could it be decided if the Miocene and Recent specimens belong to the same or different biological species (this is of no importance if we are interested only in the genealogical relationships in a particular context; for the specimens in either

case represent the same taxon, irrespective of whether or not the Miocene species and its Recent descendants belong to the same community of reproduction and are thus conspecific in the sense of the biological species concept). Now because we know (1) that in Recent species subpopulations that originated only a relatively short time ago differ slightly from one another, and because (2) that morphological distinctions between different Recent species can often be determined only with difficulty (*Drosophila*, *Phlebotomus*), we may assume that in most if not all cases the Recent descendants of a particular species from the geological past will be slightly different, irrespective of whether they today form one species or many species. The deviation rule and the illustrative figure with which we are here concerned (Hennig, 1950: fig. 25) are, therefore, not false in this sense. The presentation by Schlee, which Mayr criticizes so vehemently, has no other purpose than to show this. Not only Mayr's critique, but also the conclusion of Peters, upon which Mayr bestows much approval, completely miss this point.

9.

Mayr considers, also, if we should speak of the persistence of a "stem species A" alongside a daughter "species C" (pp. 109-110) during the cleavage of an ancestral species. Phylogenetic systematics prefers to accept the daughter species, B and C, as given, and to consider the stem-species (A) that gave rise to both. Mayr does not note that his consideration is in reality a dispute about words (neither he nor anyone else knows the gene-pool of any stem-species before and after its cleavage). So we deal here simply with different descriptions of the process and results of speciation; that of the "cladists" is methodologically better (Günther, 1962:279).

Mayr attempts to invalidate the "cladistic principle of dichotomy," noting that phylogenetic cleavages may conceivably occur also in a multiple or radiative manner. But in refutation of this objection, also raised by

Darlington, other authors have already argued that, even when a strictly dichotomous branching of the phylogenetic tree cannot be demonstrated, an investigator need never conclude that multiple speciation has in fact occurred (although it might have). Mayr (p. 110) takes notice of, but does not seem to understand, this refutation. Moreover, the principle that every monophyletic group has only one sister-group, although not strictly verifiable empirically, has a high heuristic value: it challenges the investigator to study carefully every case where no dichotomy has yet been demonstrated.

10.

Mayr's section entitled "The mode of origin of higher taxa" (pp. 111-113) is based on confusion of the "cladistic approach" with that of "evolutionary systematics," and inspires Mayr, as the final proof of his error, to reproach the "cladists" with the "phyletic tree" drawn by Throckmorton (1965) for the *Drosophilinae* (Mayr's fig. 5). This "phyletic tree" is formed according to the principles of "evolutionary systematics" and is therefore a proof of the conclusion (see above) that a tree-like drawing not founded on the concepts (monophyly, relationship) defined by phylogenetic systematics is not a cladogram of the phylogenetic system. Hence, Mayr's argument on this point is epistemological nonsense. Besides, I doubt that even Mayr, much less Throckmorton, would argue that the species *Drosophila tripunctata*, standing at the apex of this "phyletic tree," is really the stem species of all other taxa shown there, as Mayr's "evolutionary systematics" implies.

Many of Mayr's remaining sections contain questions about the *modus operandi* of the "cladists," and are answered in the works of the various representatives of phylogenetic systematics. Moreover, Mayr's

"evolutionary systematics" in no case is spared the incidental difficulties of phylogenetic systematics, which Mayr so emphatically draws to our attention. Mayr's criticisms of phylogenetic systematics therefore seem to me unsound. His indisputably great achievements lie in another field.

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