PHYLOGENETIC SYSTEMATICS[1]

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Since the advent of the theory of evolution, one of the tasks of biology has been to investigate the phylogenetic relationship between species. This task is especially important because all of the differences which exist between species, whether in morphology, physiology, or ecology, in ways of behavior, or even in geographical distribution, have evolved, like the species themselves, in the course of phylogenesis. The present-day multiplicity of species and the structure of the differences between them, first becomes intelligible when it is recognized that the differences have evolved in the course of phylogenesis; in other words, when the phylogenetic relationship of the species is understood.

Investigation of the phylogenetic relationship between all existing species and the expression of the results of this research, in a form which cannot be misunderstood, is the task of phylogenetic systematics.

The problems and methods of this important province of biology can be understood only if three fundamental questions are posed and answered: what is phylogenetic relationship, how is it established, and how is knowledge of it expressed so that misunderstandings are excluded?

The definition of the concept "phylogenetic relationship" is based on the fact that reproduction is bisexual in the majority of organisms, and that it usually takes place only within the framework of confined reproductive communities which are genetically isolated from each other. This is especially true for the insects, with which this paper is mainly concerned. The reproductive communities which occur in nature we call species. New species originate exclusively because parts of existing reproductive communities have first become externally isolated from one another for such extended periods that genetic isolation mechanisms have developed which make reproductive relationships between these parts impossible when the external barriers which have led to their isolation are removed. Thus, all species (= reproductive communities) which exist together at a given time, e.g., the present, have originated by the splitting of older homogeneous reproductive communities. On this fact is based the definition of the concept, "phylogenetic relationship": under such concept, species, B, is more nearly related to species, C, than to another species, A, when B has at least one ancestral species source in common with species C which is not the ancestral source of species A [Hennig (8)].

"Phylogenetic relationship" is thus a relative concept. It is pointless (since it is self-evident) to say, as is often said, that a species or species-group is "phylogenetically related" to another. The question is rather one of

[1] The survey of the literature pertaining to this review was concluded in 1963.

knowing whether a species or species-group is more or less closely related to another than to a third. The measurement of the degree of phylogenetic relationship is, as the definition of the concept shows, "recency of common ancestry" [Bigelow (1)]. A phylogenetic relationship of varying degree exists between all living species, irrespective of whether we know of it or not. The aim of research on phylogenetic systematics is to discover the appropriate degrees of phylogenetic relationship within a given group of organisms.

The degree of phylogenetic relationship which exists between different species, and thus also the results of research on phylogenetic systematics, can be represented in a visual form which is not open to misinterpretation as is a so-called phylogeny tree (dendrogram). To be able to discuss this, not only the species but also all of the monophyletic groups included in the diagram, must be given names. "Monophyletic groups" are small or large species-groups whose member species can be considered to be more closely related to one another than to species which stand outside these groups [Hennig (8)]. When a phylogeny diagram, conforming to this postulate, has been rendered suitable for discussion by the naming of all of the monophyletic groups, then the diagram can be discarded and its information may be expressed solely by ranking the names of the groups:

A. Myriopoda
B. Insecta
  B.1 Entognatha
    B.1a Diplura
    B.1b Ellipura
      B.1ba Protura
      B.1bb Collembola
  B.2 Ectognatha

Such arrangement of monophyletic groups of animals according to their degree of phylogenetic relationship is called, in the narrower sense, a phylogenetic system of the group in question. Such a system belongs to the type called a "hierarchical" system. Since "system" in the wider sense means every arrangement of elements according to a given principle, the phylogeny tree, too, can be termed a phylogenetic system. Phylogeny diagrams and arrangement of the names of monophyletic groups in a hierarchical sequence are merely different but closely comparable forms of presentation whose content is the same. Therefore, everything which can be said about the methods of phylogenetic systematics (see below) applies irrespective of whether the results sought by the use of these methods are expressed only as a phylogeny tree or, as a phylogenetic system in the narrower sense, in a hierarchically arranged list of the names of monophyletic groups.

In some cases, a hierarchical arrangement of group names, that is, a phylogenetic system in the narrower sense, is to be preferred to a phylogeny tree. One can, for instance, in a catalogue or check-list of Nearctic Diptera, give expression to all that one thinks is known about the phylogenetic rela-

tionship of all Nearctic species of Diptera in a form which can in no way be misinterpreted, without using a single phylogeny tree.

However, considerable difficulties arise because systems of the hierarchical type have also been used in biology with intentions other than of expressing the phylogenetic relationship of species. Long before the advent of the theory of evolution, "systematics" existed as the branch of biological science which had adopted as its aim an orderly survey of the plurality of organisms. Naturally, the principle of classification in systematics could not then be the phylogenetic relationship of species, which was still unrecognized, but only a morphological resemblance between organisms. This morphological systematics also used the hierarchical type of system to express its results although Linnaeus already held the view that morphological resemblances between organisms corresponded to a multidimensional net. Numerous attempts have also been made to introduce other types of system, which differ from the hierarchical, into biological systematics [see Wilson & Doner (21)]. But they have not been successful.

Today, there are still many authors who consider that the purpose of biological "systematics" is to classify organisms according to their morphological resemblance, and who use a system of the hierarchical type to this end. It is hardly surprising that misunderstandings and serious errors can be produced by this formal identity between morphological and phylogenetic systems.

The source of danger in the formal identity between systems based on such different principles of classification is that, in a hierarchical system, each group formation relates to a "beginner," which is linked in "one-many relations" with all of the members of that group and only those [Gregg (3)]. In morphological systems, the "beginner" which belongs to each group is a formal idealistic standard ("Archetype") whose connections with the other members of the group are likewise purely formal and idealistic. But, in a phylogenetic system, the "beginner" to which each group formation relates is a real reproductive community which has at some time in the past really existed as the ancestral species of the group in question, independently of the mind which conceives it, and which is linked by genealogical connections with the other members of the group and only with these. One could, without difficulty, adduce many examples from the literature in which the formal beginner ("Archetype") of a group, conceived according to the principles of morphological systematics, has been erroneously taken, with all of the consequences of such an error of logic, as the real beginner (ancestral species) of a monophyletic group.

This dangerous difference between a formal morphological (typological) hierarchical system and the equally hierarchical system of phylogenetic systematics, would not arise if the degree of morphological resemblance were an exact measurement of the degree of phylogenetic relationship. But this is not the case. Furthermore, there is yet no definition of the concept of morphological resemblance which is not open to theoretical objection, nor any

method which can be accepted as the one and only method which achieves a satisfactory determination of more than the threshold of morphological resemblance, that is, the degree of resemblance between relatively similar species which agree in very many characters.

In these circumstances, the dangers which arise from the formal identity of phylogenetic and morphological systems will be avoided if agreement can be reached on whether or not the branch of biological science known simply as systematics will, in future always try to express the morphological resemblance of organisms or their phylogenetic relationship in the system in which it works.

It has often been stated, in defense of a system of morphological resemblance, that this has historical primacy over endeavors to express phylogenetic relationship in a system, because the morphological system had already existed as the aim of "systematics" before the advent of the theory of evolution. Even today, this reasoning is often augmented with the argument that the theory of evolution was established with the help, among other things, of the system of graduated morphological resemblances between organisms, and that therefore one is prescribing a circle if, in reverse, one wishes to take the theory of evolution and the notion of the phylogenetic relationship of organisms which follows from it as the theoretical starting-point of their classification in a system [Sokal (17); Blackwelder, Alexander & Blair (2)]. This "ebenso halt-wie heillose Einwand" [Günther, in discussing the work of Sokal (12)], has already been so often refuted that one can only attribute, to authors who persist in asserting it today, a lack of information.

It is certainly correct that the classification of organisms according to their morphological resemblance has led to the theory of evolution. This was possible only because the morphological differences between organisms are the result of a historical (phylogenetic) development and because, at least in rough terms, very similar organisms are, in fact, generally more closely related than are very different ones. It was therefore inevitable that the classification of organisms according to their morphological resemblance, in association with certain features of their ontogenetic development and their geographical distribution, would sooner or later lead to the discovery of their successive degrees of phylogenetic relationship and thus to the theory of evolution.

However, there are historical origins not only of the morphological differences between organisms in the narrower sense, but also differences in their physiological functions, their ways of behavior and, in addition to these physical ("holomorphological") attributes, differences in their distribution in geographical and ecological space. Since it has been recognized and, moreover, become widely known, that there are not the same degrees of agreement and difference in the various holomorphological and chorological resemblances which connect organisms, the way is open for establishing the phylogenetic relationship itself of organisms as the principle of classification, instead of successive degrees of resemblance in a single category of charac-

ters: for, only from the phylogenetic relationship is it possible to establish direct connections with all other thinkable kinds of agreement and difference between organisms. The demand for a phylogenetic system is thus not so much a renunciation of pre-phylogenetic resemblance, systematics, but its consequential further development.

The claim of the phylogenetic system to elevation into the universal reference system of biology has a logical, even if not historical, foundation, and arises because few areas of research can be conceived which do not bear fruit and lead to more profound conclusions through a knowledge of the phylogenetic relationship of its objects, and which cannot, in turn, lead to the discovery of hitherto unknown relationships in the course of mutual exchange of information. This is not true to the same extent for any other system built on any other principle of classification. Other systems may also have their value as knowledge; but this value is, in each case, restricted to answering particular questions.

The logical primacy of the phylogenetic system also arises because it alone provides all parts of the field studied by biological systematics with a common theoretical foundation [Kiriakoff (14)]. It is true that phylogenetic relationship exists only between different species, and species are not the simplest elements of biological systematics. These are not even the "individuals," but the individuals in given short periods of their lifetime ("semaphoronts"). The first and basic task of systematics is to establish that different individuals, or rather "semaphoronts," belong to particular species. The difficulty within this task rests in the fact that the species, which exist in nature as real phenomena independent of the men who perceive them, are units which are not morphologically but genetically defined. They are communities of reproduction, not resemblance. Of course, the morphological resemblance between members of a species is not unimportant for the practical establishment of specific limits. But it has only the significance of an auxiliary criterion whose capabilities of use are limited. This is because the definition of the phylogenetic relationship between species, as well as the definition of the species-concept, is deduced from the fact that the reproduction of species generally takes place only within the framework of defined communities which cannot be unqualified communities of resemblance if, in the demand for a phylogenetic system, biological systematics has acquired for all its spheres of activity a common aim, that is, the discovery and recording of the "hologenetical" connections which exist between all organisms. In contrast with this, morphological resemblance-systematics, though not denying the modern genetic species-concept, employs different principles of classification above and below the specific level.

It would, of course, be meaningless to extol the need for a phylogenetic system, however well founded it might be theoretically, if this demand could not be put into practice. There is, in fact, a widespread notion that phylogenetic systematics, at least in those groups of animals for which no fossil finds are available, possesses no method of its own, but can only interpret the

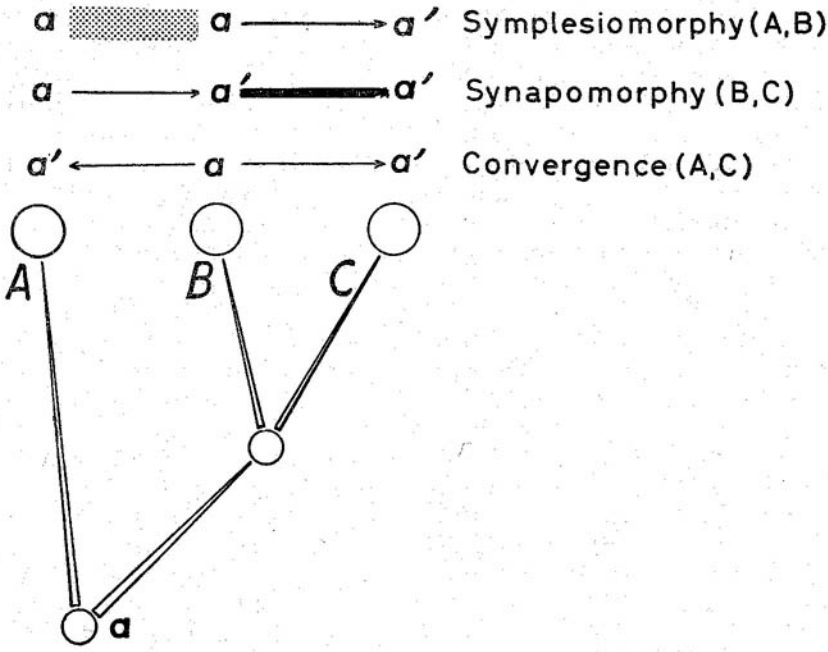

FIG. 1. The three different categories of morphological resemblance. *a* plesiomorph; *a'* apomorph expression of the morphological character *a*. Agreement may rest on sympleisiomorphy (*a*-*a*), synapomorphy (*a'*-*a'*) or convergence (*a'*-*a'*).

results of morphological systematics according to the principle that the degree of morphological resemblance equals the degree of phylogenetic relationship. This notion is false. The fundamental difference between the method of morphological and phylogenetic systematics is that the latter breaks up the simple concept of "resemblance." (Fig. 1).

It is a consequence of the theory of evolution that the differences between various organisms must have arisen through changes of characters in the course of a historical process. Therefore it is not the extent of resemblance or difference between various organisms that is of significance for research into phylogenetic relationship, but the connection of the agreeing or divergent characters with earlier conditions. It is valid to distinguish different categories of resemblance according to the nature of these connections.

The division of the concept of resemblance into various categories of resemblances probably began, in the history of systematics, with the introduction of the concept of convergence. Often this concept was linked with the distinction between analogous and homologous organs. Convergence is, in fact, commonly manifested by similar organs having arisen in adaptation to the same functions from different morphological foundations in different

organisms. But there are also cases where virtually complete agreement in the form of homologous organs rests on convergence. "Convergence" means resemblance between the characters of different species which has evolved through the independent change of divergent earlier conditions of these characters. It shows how species which differed from one another are ancestors of species which have become similar to one another. If one associates in a group the species whose resemblance rests on convergence, then this is not a monophyletic but a polyphyletic group. There are few authors today who would specifically support the inclusion of demonstrably polyphyletic groups in a system. "Convergence" and "polyphyletic groups" are concepts which presuppose acceptance of the theory of evolution. Therefore, some systematists think they are already working with a "phylogenetic system" when, in

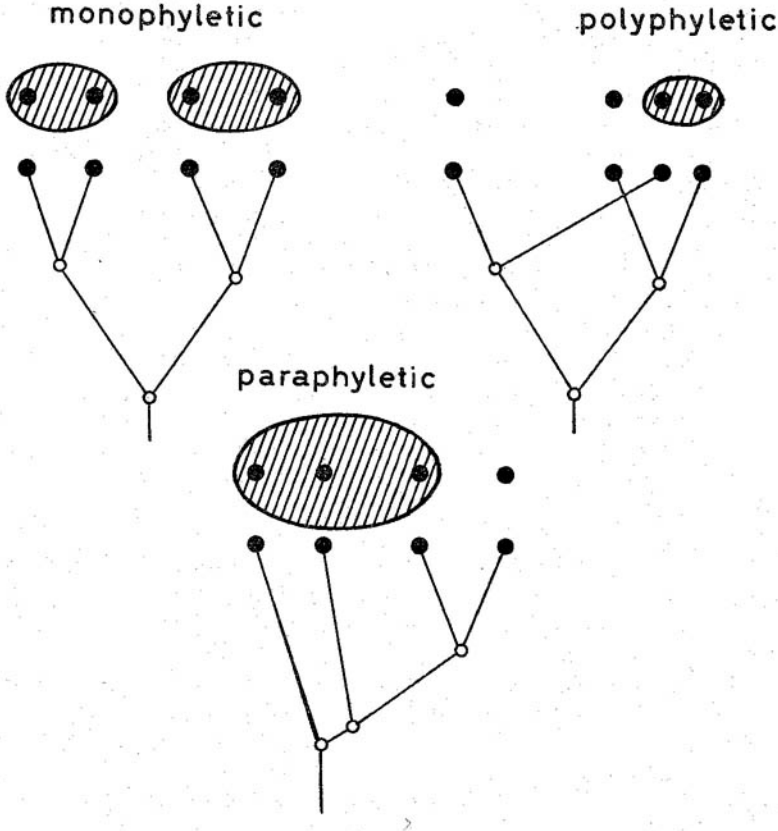

FIG. 2. The three different categories of systematic group formations corresponding to the resemblance of their constituents resting on synapomorphy (monophyletic groups), convergence (polyphyletic groups), or symplesiomorphy (paraphyletic groups). For comparison with Figure 1.

their evaluation of morphological resemblance, they exclude convergence and thus polyphyletic groups from their system.

But even when purged of convergence, morphological resemblance is still not a satisfactory criterion for the degree of phylogenetic relationship between species. It still does not provide one with exclusively monophyletic groups, such as a phylogenetic system demands. This arises from the fact that characters can remain unchanged during a number of speciation processes. Therefore, it follows that the common possession of primitive ("plesiomorph") characters which have remained unchanged cannot be evidence of the close relationship of their possessors.

Often, a given species can be phylogenetically more closely related to a species which possesses a particular character in a derivative ("apomorph") stage of expression than to species with which it agrees in the possession of the primitive ("plesiomorph") stage in the expression of this character. Therefore, a resemblance which rests on symplesiomorphy is of no more value in justifying a supposition of closer phylogenetic relationship than is a resemblance which has occurred through convergence. If, in a system, one associates in a group species whose agreement rests on convergence, a polyphyletic group is thereby formed, as has been established above and is generally recognized. If one associates species whose agreement rests on symplesiomorphy, then a paraphyletic group is formed (Fig. 2). Paraphyletic groups among insects are the "Apterygota" and Palaeoptilota (= Palaeoptera), if one considers the closer relationship of the Odonata with the Neoptera as established. Paraphyletic vertebrate groups are the "Pisces" and the "Reptilia."

The supposition that two or more species are more closely related to one another than to any other species, and that, together they form a monophyletic group, can only be confirmed by demonstrating their common possession of derivative characters ("synapomorphy"). When such characters have been demonstrated, then the supposition has been confirmed that they have been inherited from an ancestral species common only to the species showing these characters.

It must be recognized as a principle of inquiry for the practice of systematics that agreement in characters must be interpreted as synapomorphy as long as there are no grounds for suspecting its origin to be symplesiomorphy or convergence.

The method of phylogenetic systematics, as that part of biological science whose aim is to investigate the degree of phylogenetic relationship between species and to express this in the system which it has designed, thus has the following basis: that morphological resemblance between species cannot be considered simply as a criterion of phylogenetic relationship, but that this concept should be divided into the concepts of symplesiomorphy, convergence, and synapomorphy, and that only the last-named category of resemblance can be used to establish states of relationship.

The differences between the phylogenetic system and all other systems

which likewise classify species on the basis of their morphological resemblance, are as follows: (*A*) Systems which employ the simple criterion of morphological resemblance. Such systems include polyphyletic, paraphyletic, and monophyletic groups. (*B*) Systems which employ the criterion of morphological resemblance, but fail to consider characters whose agreement rests on convergence. In such systems, polyphyletic groups are excluded but paraphyletic as well as monophyletic groups are admitted. (*C*) Phylogenetic system. Characters whose agreement rests on convergence or symplesiomorphy are not considered. Therefore, polyphyletic and paraphyletic groups are excluded and only monophyletic groups admitted.

The systems named under (*B*) have also often been termed phylogenetic systems in the literature [e.g., Stammer (18); Verheyen (20)]. But it is thereby overlooked that the paraphyletic groups admitted in these "pseudophylogenetic" or "cryptotypological" systems [Kiriakoff (14)] are similar in many respects to polyphyletic groups. No one would think of considering polyphyletic groups in studies concerned with the course and eventual rules of phylogenesis (zoogeographical studies, for instance, belong here), since they have no ancestors solely of their own and therefore no individual history. Exactly the same holds true, however, for paraphyletic groups. The sole common ancestors of all of the socalled "Apterygota," for instance, were also the ancestors of the Pterygota, and the beginning of the history of the Apterygota was not the beginning of an individual history of this group, but the beginning of the individual history of the Insecta, which were at first Apterygota in the morphological-typological sense. Also, the concept of "extinction" is different in paraphyletic and monophyletic groups. Only monophyletic groups can become "extinct" in the sense that from a particular point in time no physical progeny of any member of the group have existed. But if, however, one says that a paraphyletic group has become "extinct," this can only mean that after a particular point of time no bearers of the morphological characters of this group have existed. But physical progeny of many of its members may, with changed characters, continue to live. Monophyletic and paraphyletic groups thus cannot be compared with each other in any question concerning their history. Failure to take account of this fact and invalid uncritical comparison of paraphyletic and monophyletic groups has led to some false conclusions in studies about the "Grossablauf der phylogenetischen Entwicklung" [Müller (15)], and the history of the distribution of animals.

From the premise that morphological agreement only confirms a supposition that the species concerned belong to a monophyletic group when it can be interpreted as synapomorphy. is derived for the practical work of the systematist, the "Argumentation plan of phylogenetic systematics" (Fig. 3). This plan shows that in a phylogenetic system which must contain only monophyletic groups, every group formation, irrespective of the rank to which it belongs, must be established by demonstration of derivative ("apomorph") characters in its ground plan. But it also shows clearly that in two

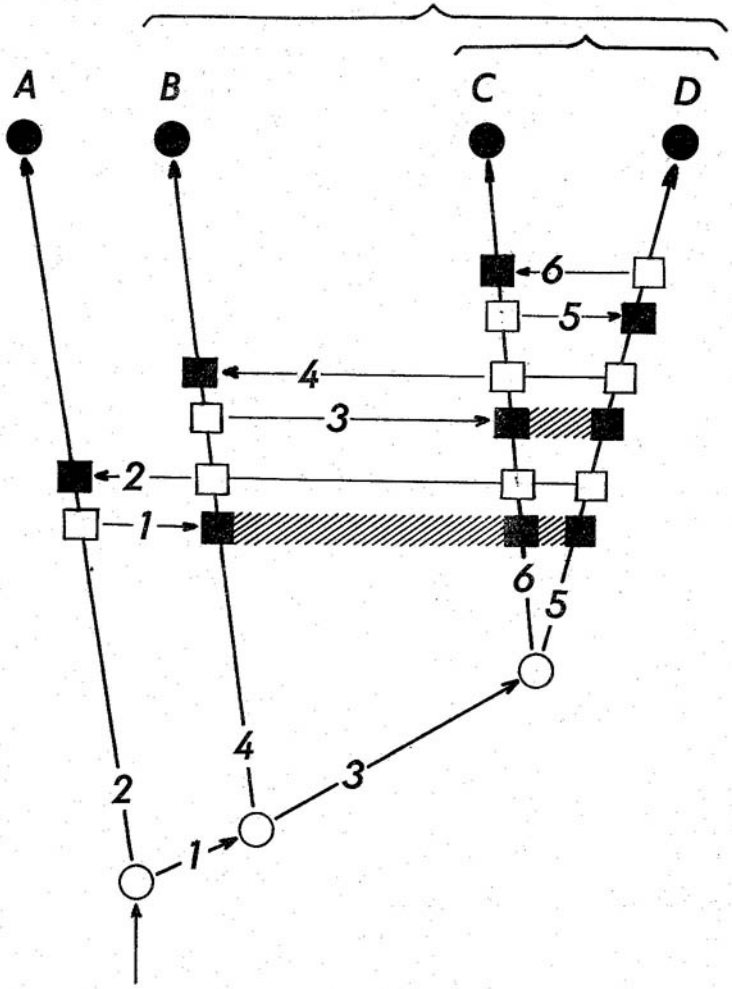

Fig. 3. Argumentation plan of phylogenetic systematics. □ plesiomorph, ■ apomorph expression of characters. Equal numbers indicate how sister-group relations are established by the distribution of relatively plesiomorph (white) and relatively apomorph (black) characters ("heterobathmy of characters"). Adapted from Hennig (11).

monophyletic groups which together form a monophyletic group of higher rank and are therefore to be termed "sister-groups," one particular character must always occur in a more primitive (relatively plesiomorph) condition in one group than in its sister-group. For the latter, the same is true in respect to other characters. This mosaiclike distribution of relatively primitive and relatively derivative characters in related species and species-groups [Spezialisationskreuzungen, Heterobathmie der Merkmale: Takhtajan (19)] is a fact which has long been known. But one still finds it occasionally mentioned in the literature as a special peculiarity of some groups of animals that the classification of their constituent groups cannot be achieved in a definite sequence, because there are no solely primitive and no solely derivative species or species-groups. In a phylogenetic system there can indeed be no solely primitive and no solely derivative groups. The possession of at least one derivative (relatively apomorph) ground-plan character is a precondition for a group to be recognized at all as a monophyletic group. But it also follows from this that this same character in the nearest related group must be present in a more primitive (relatively plesiomorph) stage of expression. The exclusive presence of relatively plesiomorph characters is indicative of paraphyletic groupings: these are to be found only in pseudophyletic (see above under *B*) and purely morphological systems (see above under *A*), but not in phylogenetic systems. Heterobathmy of characters is therefore a precondition for the establishment of the phylogenetic relationship of species and hence a phylogenetic system.

It is sometimes said that the aims of phylogenetic systematics are not only practically but also theoretically unattainable, because the comparison of species living in a given time-horizon, such as the present, cannot in any way reveal their phylogenetic relationship which refers to a completely different dimension. This view is false. Just as two stereoscopic views of a landscape, which themselves assume only a two-dimensional form, together contain exact information about the third spatial dimension, so the mosaic of heterobathmic characters in its distribution over a number of simultaneously living species contains reliable information about the sequence in which the species have evolved from common ancestors at different times. The study and use of the methods which serve to reveal this information needs, it is true, a far greater amount of knowledge and experience than some systematists are willing to employ. The theoretical foundation and refinement of these methods forms a special chapter in the theory of phylogenetic systematics which can only just be touched upon in the present brief paper.

It is sometimes alleged that consideration of as many characters as possible which have so far not been studied is a prerequisite for the progress of phylogenetic systematics. In particular, the restriction of entomological systematics to comparatively easily recognizable characters of the external skeleton which lie open to view is often not highly regarded. This has some justification. The phenomena of convergence (particularly in its variant known under the name "parallel development"), reversed development of

characters and paedomorphosis, which leads to pseudoplesiomorph conditions, make the establishment of true synapomorphy difficult. The more complex is the mosaic of heterobathmic characters which we have at our disposal in a chosen group of species, the more surely can their phylogenetic relationship be deduced from it.

Consideration of new and hitherto unobserved characters can, however, represent progress only if these are analyzed with the special methods of phylogenetic systematics. Thus, it is also necessary to distinguish between plesiomorph and apomorph expressions of characters in the internal anatomy and chemical structure, physiology, and serology and when considering different ways of behavior. Symplesiomorphy must be excluded just as much as convergence. If this is not observed, then consideration of however many characters leads, at best, only to a more precise determination of the overall similarity of the bearers of all of these characters, but not to a more precise establishment of their degree of phylogenetic relationship.

This becomes particularly obvious in animal groups such as the insects in which the life of the individual is subject to the phenomenon of metamorphosis. This is the cause of the incongruences which are so often discussed between larval, pupal, and imaginal classification in morphological and pseudophylogenetic systematics. A theoretically acceptable solution of such "incongruences" is possible only in phylogenetic systematics. It can indeed be the case that particular instances of synapomorphy, and therefore of monophyletic groups, can be recognized only in the larval or pupal stages and others only in the imaginal stage. But this is not a true incongruence, for the phylogenetic system does not try to classify organisms according to their degree of resemblances, but species according to their degree of phylogenetic relationship. It does not matter therefore which stage of development is used to establish relationship on the ground of synapomorphy. A monophyletic group remains such even if it can be established only with the characters of a single stage of development [for more detailed exposition see Hennig (11)].

The fact that not resemblance as such, but only agreement in a particular category of characters is significant for the study of phylogenetic relationship, also makes it possible for phylogenetic systematics to adduce for its purposes features other than physical (holomorphological) characters. Such nonholomorphological characters are the life history and geographical distribution of species. Phylogenetic systematics can, for instance, proceed from the plausible hypothesis that species which show a clearly derivative ("apooec") life history, and for which a certain relationship is probable on other grounds, form a monophyletic group. This is, for instance, often true with parasites. However, hypotheses of this kind must always be verified by close morphological studies, for it is particularly with similar life histories that adaptive convergence is common.

A particularly great importance for phylogenetic systematics is presently often ascribed to parasites and to monophagous and oligophagous plant-feeders which are to be equated with them from the standpoint of phylogenet-

ic method. The theoretical justification for this is supplied by the so-called parasitophyletic rules. Particularly important among these is the so-called "Fahrenholz rule," which supposes a marked parallelism between the phylogenetic development of parasitic groups of animals and their hosts in the majority of cases. If this is correct, then it might be concluded from the restriction of a monophyletic group of parasites to a particular group of host species that the latter, too, form a monophyletic group. But it can easily be shown that this conclusion would be correct only if one could assume that the ancestral species of the host group was attacked by one parasite species and that thereafter each process of speciation in the host group has been accompanied by one speciation process in the parasites. Clearly, this precondition is only rarely fulfilled, since the evolution of parasites often seems to be retarded in comparison with that of their hosts, both in respect to character changes and speciation. The result of this is that paraphyletic host groups can also be attacked by monophyletic groups of parasites. Moreover, it happens that parasites can transfer secondarily (without being passed from ancestors to progeny in the course of speciation) to host species which offer them similar conditions of life. This, too, is often seen as an indication of close phylogenetic relationship between host species which are exclusively attacked by particular parasite species or a monophyletic group of parasites. But this assumption would be valid only if one could assume that the "degree of resemblance" of different species and the "degree of their phylogenetic relationship" corresponded closely with each other. As has been shown, this is not the case. Resemblance can also be based, for instance, on symplesiomorphy, and this cannot be assumed to establish phylogenetic relationship. Since one cannot assume that parasites distinguish, in their choice of host range, the categories of resemblance connections (symplesiomorphy, synapomorphy and convergence) whose differences are important for phylogenetic systematics the greatest care is necessary in attempting to draw conclusions about the phylogenetic relationship of their hosts from the occurrence of monophyletic groups of parasites. The importance of parasitology for phylogenetic systematics is considerable. But on the grounds given it is not so great as is sometimes supposed. In particular there is still no really satisfactory clarification of this whole complex of questions.

The geographical distribution of organisms is also of restricted though not to be underestimated importance for phylogenetic systematics. This can often proceed from the hypothesis that parts of a group which are restricted to a defined, more or less separated, part of the total range, whose ancestors may be assumed to have arrived from other regions, form a monophyletic group. This is particularly valid for the fauna of the marginal continents (Australia and South America), whose ease of accessibility has been different at different periods of the earth's history, and for some islands (e.g., Madagascar, New Zealand). One can, for instance, proceed on the working hypothesis that the Marsupialia of Australia form a monophyletic group, and then seek either to sustain or refute this hypothesis with the morphological

methods of phylogenetic systematics. With groups of animals with disjunctive distribution, one may proceed on the hypothesis that both parts of the range (Australia and South America in the case of pouched mammals) have been settled by monophyletic subgroups and that between these a sister-group relationship exists. Extensive investigations of the phylogenetic development of animal groups (e.g., Hofer on the Marsupialia) often in themselves remain fruitless, since they do not proceed from a working hypothesis of this kind and as a result contain no statements which serve to answer the questions which first come clearly to light in such an hypothesis. This is often of even greater importance in studies of the history of the settlement of geographical space. Discussions about the earlier existence of direct land connections between now separate regions [Madagascar and the Oriental Region, Günther (5); New Zealand and South America, Hennig (12)] have somewhat the same significance as have attempts to sustain or refute hypotheses about the monophyletic, paraphyletic, or polyphyletic character of particular groups of animals. The inadequacy of morphological or pseudophyletic systems is shown here with particular clarity.

A special chapter in the theory of phylogenetic systematics which can only be touched upon here, is the position of fossils in the system [Hennig (9)]. Despite a widely held opinion, establishing the phylogenetic relationships of fossil animal forms is usually more difficult than that of recent species. The cause of this is that in fossil finds, usually only a small, often extremely small, section is available from the character structure of the whole organism. But, since the methods of phylogenetic systematics have a numerical character insofar as the certainty of their conclusions grows as the number of characters at their disposal increases (see above), it follows necessarily that the reliability with which relationships can be established cannot usually be as great with fossils as with recent species. In the sphere of the lower categories of the system, the species and their subunits, palaeosystematics is, in addition, at a decisive disadvantage because it can never observe its objects alive, and can therefore only solve its problems with the help of relatively unreliable morphological criteria. It is true that the systematics of recent organisms also satisfies itself mainly with morphological criteria to help it establish the limits of species. However, there is always the possibility, in principle, of testing in important cases, that individuals of similar or different appearance actually belong to one or to different reproductive communities by observation of their life in nature or by breeding and crossing experiments. In species with seasonal and sexual dimorphism and those in which the life of the individual contains a metamorphosis, systematics depends upon such methods. But, in palaeontology, they cannot be employed. Here systematics can establish the specific limits only with a much lower degree of accuracy than with recently known organisms. It would, however, be completely false to deduce from this, as is sometimes done, that palaeontological systematics operates with other concepts (e.g., a different species-concept) and other methods. It differs from the systematics applicable to recent animal forms

only in the lesser degree of certainty and accuracy with which it is able to apply itself.

This applies to inquiry into specific limits just as it does to establishing the degree of the phylogenetic relationship between species. If the purpose of systematics does not consist exclusively of conducting a survey of the animal forms which have existed on the earth at any time, then palaeontology must also try to relate its objects to the phylogenetic system of recent organisms, that is to include them in this system. But this can be meaningful and fruitful only if the limits of the knowledge it can supply are known very precisely and are clearly expressed in each particular case.

Subject to these conditions, the value of fossil finds lies in enabling one to interpret character agreements in recent species when this cannot be done solely from a knowledge of these recent forms. There are, in the recent fauna, monophyletic groups which agree in certainly derivative (apomorph) characters with other diverse groups which are just as surely monophyletic. Some of these agreements must therefore rest on convergence. But it is often impossible to decide with certainty which of these agreements are based on convergence and which are to be considered as true synapomorphy. The possibility of decision in such cases depends on a knowledge of the sequence in which the characters in question evolved. This is sometimes clarified by fossils. An example of this kind is supplied by the sea urchins (Echinoidea).

The Cidaroidea, which are shown to be a monophyletic group by their peculiar spine formation, agree completely with most other recent sea urchins in their possession of a rigid corona. The more primitive expression of this character, a flexible corona, is present only in the Echinothuridae. On the other hand, the Echinothuridae agree completely, in their possession of external gills, with the sea urchins which do not belong to the Cidaroidea. This is likewise a derivative character. This character distribution allows no decision on the question of whether the Cidaroidea or the Echinothuridae are more closely related to the bulk of recent sea urchins. One of the two derivative characters, the external gills or the rigid corona, must thus have evolved through convergence at least twice independently. The oldest fossil Cidaroidea, which are shown to belong to this group by their spine formation, possess a flexible corona. This is decisive evidence that the rigidity of the corona in recent Cidaroidea and in the remaining recent sea urchins (except the Echinothuridae) has evolved through convergence. Concerning the external gills, there are no reasons to suggest convergent evolution. Their presence in recent sea urchins which do not belong to the Cidaroidea may therefore be regarded as synapomorphy. However, it must also be said that they have often been lost secondarily. In other cases, only fossil finds make it possible to establish which expression of a character should be regarded as plesiomorph in a group and which as apomorph.

The importance of fossils thus lies, not so much in the fact that they reduce the morphological gap between different monophyletic groups of the

recent fauna, but in that they help to make it possible to decide the categories of resemblance (symplesiomorphy, synapomorphy, or convergence) to which particular agreements of character belong.

Still greater is the value of fossils for determining the age of animal groups. But in this context it should be realized that age determinations have a meaning only in monophyletic groups, since only they have a history of their own (see above). It can be difficult, however, to demonstrate the relationship of a fossil to a given monophyletic group of animals. As has been shown above, heterobathmy of characters is characteristic for nearly related monophyletic groups. Therefore, it often happens that one of two sister-groups can be established as a monophyletic group only by a few apomorph characters which are difficult to verify or only present at a particular stage of metamorphosis. For the distinction of the two groups and the identification of the species belonging to them, this has no significance, because plesiomorph characters can also be employed for diagnosis, though they must be left out of consideration in establishing the monophyly of a group. One can, for instance, recognize at once that a recent arthropod species belongs to the Myriopoda from its possession of homonomous body segmentation with jointed appendages on more than three of its trunk segments, although both are plesiomorph characters and cannot be used to justify the supposition that the Myriopoda are monophyletic. But this is not the case with fossils. One cannot assume without qualification that fossils, especially from the early Palaeozoic, belong to the Myriopoda if they possess a homonomous segmentation and jointed appendages on more than three trunk segments. Both are plesiomorph characters which must also have been present in the common ancestors of the Insecta and Myriopoda. To demonstrate that fossils in fact belong to the Myriopoda, one must demonstrate in them those apomorph characters in the ground plan of the group which suggest its monophyly, i.e., the absence of ocelli and compound eyes. Such demonstration is often very difficult, since these characters are not preserved for us in the fossils. If, in this case, one proceeds uncritically, and classifies fossils on the basis of plesiomorph characters which suffice as diagnostic characters for the certain recognition of all recent species of a monophyletic group, then it can happen that the group will become a paraphyletic group solely through its acquisition of fossils. This can then become the source of all the errors which necessarily arise if one compares monophyletic and paraphyletic groups with one another in phylogenetic studies (see above).

When, however, it has been firmly established that a fossil belongs to a given monophyletic group, that fossil can then be of importance not only for determining the minimum age of the group to which it belongs, but also for determining the minimum age of related groups, of which no fossil finds are available. The existence of *Rhyniella praecursor* in the Devonian not only proves that Collembola, the group to which *Rhyniella* belongs, already occurred then, but from our relatively certain knowledge of the phylogenetic relationships of the principal monophyletic groups of insects it follows that at

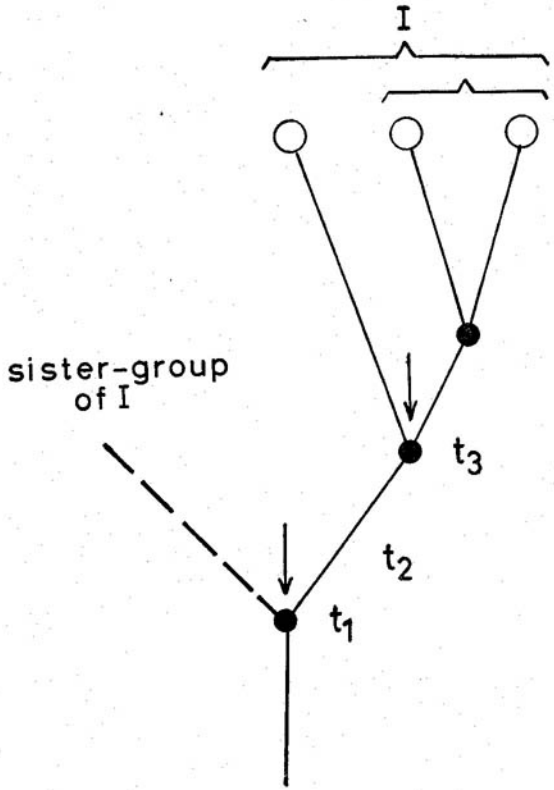

FIG. 4. The three different meanings of questions about the "age" of an animal group.

t_1 age of origin (separation of group I from its sister-group),
t_2 first appearance of the "typical" characters of group I,
t_3 age of division (last common ancestor of all recent species of group I)

the same period the Protura, Diplura, and Ectognatha must also have existed, although, of course, not in the form of their present-day progeny.

In determining the age of animal groups, another factor should be considered as well. In the history of a monophyletic group of animals, there are two points of time which are especially important (see Fig. 4): one is the time at which the group in question was separated from its sister-group by the splitting of their common ancestor (age of origin), and the other the time at which the last common ancestral species of all recent species of the group ceased to exist as a homogeneous reproductive community (age of division). The distinction between these two points of time is especially important in those groups whose recent species are distinguished from species of other groups by their agreement in a large number of derivative characters. One

must assume that these characters were already present in the last common ancestral species to whose progeny they have been transmitted unchanged or, in part, further developed. These characters must have evolved in the period between the two named points of time.

Speculation upon the age of a particular group of animals can have three appropriate but different meanings. The following may be intended: (*a*) When did the last common ancestral species of all the recent species of this group which have inherited their derivative characters from it, live? (question about the group's age of division). (*b*) When was the group separated from its sister-group? (question about the group's age of origin). (c) When, in the period between these two points of time, did species for the first time occur with the characters which justify their ascription to the "type" represented by the recent species?

It is seldom clear which of these three essentially different questions is intended when questions are asked about the age of fleas, lice, or other animal groups. This fact, in conjunction with the custom of seeing in phylogenesis mainly the emergence of particular "types" or "Baupläne" whose delimitation is dependent on subjective criteria, is the cause of endless and fruitless debate on the question of whether or not certain fossils should be considered "reptiles," "birds," "mammals," or "men," and when these groups evolved.

It might seem that questions about the age of animal groups lie outside the field of systematics. But this is not the case. The examples quoted should have shown that answering these questions has the same significance as systematically classifying fossils in particular groups, and that the meaning of an answer depends on the classificatory principle used in forming them.

The age of animal groups also has yet another significance for phylogenetic systematics, under some circumstances. It has been said above that the phylogeny diagram and the hierarchical system are closely corresponding kinds of presentation whose content is one and the same. The phylogeny tree presents, as the most important factor, the time dimension in which the degree of phylogenetic relationship between species or monophyletic groups of species is expressed by the sequence in which they have evolved from each common ancestral species (i.e., recency of common ancestry); in a hierarchical system this is shown by the sequence of subordination in the group categories. It is a justifiable aim to perfect the phylogeny diagram by giving, not only the relative sequence of origin of the monophyletic groups, but also the actual time of their origin. This detail of a perfected phylogeny diagram can also be reproduced in a hierarchical system by means of the absolute rank of its group categories. In a hierarchical system, not only are the names of the monophyletic groups quoted but they are also given a specific absolute rank (class, order, family, etc.). Some clearsighted authors [e.g., Simpson (16)] have quite correctly realized that the absolute rank which is attributed to a given group (e.g., family) does not generally mean that this group can be compared with any other of the same rank in any particular respect. Only

within one and the same sequence of subordination is it true that the lower ranks show a higher degree of phylogenetic relationship than the higher. This situation can be accepted without injury to the basic principles of phylogenetic systematics. It could be changed, without injury to these principles, only if the absolute rank of categories was linked to their time of origin, just as in geology the sequence of strata in different continents is made comparable by its correlation with specific periods of the earth's history (e.g., Triassic, Jurassic, Cretaceous). Some authors [e.g., Stammer (18)] think that one must take into account, when according absolute rank to systematic groups, their different rates of evolution which have led to greater or lesser morphological "differentiation." But it needs little reflection to see that this is incompatible with the theoretical foundations of phylogenetic systematics and necessarily leads to pseudophylogenetic systems. This should already have been shown by the fact that sister-groups must have the same rank in a phylogenetic system, entirely without regard for the way in which this rank is established; for sister-groups can, of course, have morphologically unfolded (i.e., diverged from the form of their common ancestors) with completely different rates of evolution.

Biological systematics can no more do without a theoretical foundation for its work than can any other science. The theory of phylogenetic systematics is a comprehensive and complex edifice of thought, which here can only be touched upon lightly, even in its most important aspects. In this edifice there is, as always, a logical arrangement of individual problems. In critical expositions, this logical order must be observed. It is not permissible, as sometimes happens, to confuse the critique for answering logically subordinate questions with the critique concerning the principles of the phylogenetic system. From a thoroughgoing theory of phylogenetic systematics, there arise necessarily some unexpected demands on the practical work of the systematist. If the theory as such is accepted in principle it is not permissible to refuse these demands or leave them unconsidered merely because they conflict with certain customary methods obtaining at the time when systematics had no theory. There are many problems in biology whose solution presupposes knowledge of the phylogenetic relationship of one or many species; that is a phylogenetic system of one or more groups of animals. To avoid false conclusions it is therefore especially important that every author of a system should make it easy to recognize whether, or rather to what extent, his system ought to meet the demands imposed by the theory of phylogenetic systematics. But even when these demands should be met in a system, according to the expressed wish of its author, there will always be differences of opinion over the actual relationships of some species or species groups. The person who requires a phylogenetic system as a premise for his own work, will then have to decide on which side lie the better arguments; the criteria for this must again emerge from the theory of phylogenetic systematics. Differences of opinion on matters of fact are not, however, a special defect of phylogenetic systematics but the universal mark of every science.

It is impossible in a short paper to treat even sketchily the extensive field of phylogenetic systematics with all of the questions of detail which are important for the practical work of the systematist. A more comprehensive account in Spanish and another in English, with detailed bibliography, are in the course of preparation. Excellent introductions on its theoretical and methodological foundations with many critical comments on recent systematic works are given in the writings of Günther (4, 6). A valuable study on the philosophical foundations of biological systematics has very recently been published by Kiriakoff (14).

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