multituberculates lacked the biological resources to successfully compete with them, and as the placentals radiated into more and more of the niches within this zone, the multituberculates were crowded into extinction.

REFERENCES

CLEMENS, W. A. 1963. Wealden mammalian fossils. Palaeontology, 6:55–69.

JEPSEN, G. L. 1949. Selection, "orthogenesis" and the fossil record. Proc. Amer. Philos. Soc., 93:473–500.

KERMACK, K. A. 1963. The cranial structure of the triconodonts. Philos. Trans. Roy. Soc. London (B), 246:83–103.

KERMACK, K. A., P. M. LEES, AND F. MUSSETT. 1965. *Aegialodon dawsoni*, a new trituberculosectorial tooth from the Lower Wealden. Proc. Roy. Soc. (B), 162:535–554.

MARTIN, C. J. 1902. Thermal adjustment and respiratory exchange in monotremes and marsupials; a study in the development of homoeothermism. Philos. Trans. Roy. Soc. London (B), 195:1–37.

PATTERSON, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana: Geol., 13:1–105.

ROBINSON, K. W. 1954. Heat tolerances of Australian monotremes and marsupials. Aust. J. Biol. Sci., 7:348–360.

SHARMAN, G. B. 1961. The embryonic membranes and placentation in five genera of diprotodont marsupials. Proc. Zool. Soc. London, 137:197–220.

SIMPSON, G. G. 1937. Skull structure of the Multituberculata. Bull. Amer. Mus. Nat. Hist., 73:727–763.

VAN VALEN, L., AND R. E. SLOAN. 1966. The extinction of the multituberculates. Syst. Zool., 15:261–278.

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Comments on Homology and Analogy

One of the most fundamental concepts of systematic biology is that of homology. This follows from the belief that an understanding of homology is essential for a meaningful approach to phylogeny. Because of this central position, it is natural that much controversy has arisen over definitions, usages, and recognition of homologous features. The pages of this journal have been the sounding board for several of the recent discussions of homology. While emphasizing the differences found in the various philosophies, the papers also point to some of the confusion still surrounding the uses of the different terms. The discussion which follows attempts to single out certain aspects of the conflict in the hope of contributing toward consistency in terminology.

1.—*As a definition*, no particular definition of homology is better than any other definition of homology. That is, as long as a word (e.g., homology) is defined correctly (lack of circularity, etc.), then one definition is not intrinsically "better" as a definition. (I do not imply, of course, that *any* redefinition of a word may be used once the word has been introduced; there should be some "priority" of subject matter included in definitions of a word.) Thus, I do not agree with those who assert that homology has nothing to do with similarities of features. It may—if so defined. This distinction of what is to be included in a definition is especially important with reference to "analogy." For example, Ghiselin (1966:129) states that "Analogy is simply a word used to express the idea that specified entities for which there is evidence of homology, such as similarity, are not in truth homologous." That other, equally valid notions of analogy exist will be mentioned later.

2.—Much of the discussion of homology is centered around the "operational" nature of the definition. "Operational" in this context usually refers to the ease of recognizing the given entities as homologous or nonhomologous. Curiously, the more mechanical—less human—are the methods for determining homology, the more operational is the definition; at least this is the implication. Some authors even suggest that the commonly used, phylogenetic definition of homology is nonoperational (Sokal and Camin, 1965:179). But most, if not all, definitions will be operational, if only to a slight degree. Of course, few phylogeneticists will argue that theirs is the most operational definition. Despite the continued misunderstanding about the conceptual versus the operational basis of homology still prevalent in some papers (e.g., Inglis, 1966; van der Klaauw, 1966), it cannot be stressed too strongly that the "meaning of a word has nothing whatever to do with the practical problem of identifying the things which may happen to fit the definition" (Ghiselin, 1966:127). *Simply stated, it is irrelevant whether a definition is operational or not.*

In apparent contrast to some typologists or to some numerical pheneticists, most phylogeneticists should not be upset over the dichotomy between the *concept* of homology and the basis by which features are recognized as being homologous. A phylogenetic definition of homology, like the "biological" definition of species, simply emphasizes the importance of the evolutionary processes that have produced the homologies, or the species. Hence, a particularly important point to grasp is that the concept of homology framed in nonevolutionary terms has little or no meaning for biology. This does not argue that a nonevolutionary definition of homology is invalid as a definition; rather it suggests that a nonevolutionary aproach will fail to give us as accurate a picture of historical (biological) events as the evolutionary definition will.

Failure to accept the evolutionary-oriented concept of homology has led Sokal and Sneath (1963:70) to coin the phrase "operational homology." To them features are operationally homologous when "they are very much alike in general and in particular." Supposedly, convergent characters are nonexistent under the concept of operational homology for "if the characters are recognized to be convergent (i.e., *superficially* similar) they would be coded as different characters and therefore would not contribute to the measure of similarity" (Sokal and Camin, 1965:183; italics theirs). Clearly, the action of calling given features operationally homologous will depend solely on an arbitrary decision of what features are or are not "superficially similar."

The methods of operational homology are susceptible to many of the same shortcomings faced by the phylogenetic approach. For example, there is the danger of both methods calling homologous structures (in the sense of common ancestry) that have changed radically with time nonhomologous. Furthermore, structures exist that are almost identical morphologically but that cannot be traced back to a common ancestor; here either method might incorrectly reach a decision of homology.

When examining structures the follower of operational homology asks the question, are these structures similar? Once having arrived at a decision to call the features similar, the numerical pheneticist designates the features as operationally homologous. On the other hand, the phylogeneticist would ask the question, are these structures the *same* structure (i.e., do they have a common ancestor)? This latter question has been asked since the time of Owen (although these workers were not concerned with a common ancestor). There has been a difference of opinion as to what Owen meant by the phrase "the same organ in different animals under every variety of form and function." To some (Bock, 1963:269) this definition has been taken to imply features of "natural groups," that is, truly homologous features (descent from common ancestor). Sokal and Sneath (1963:71) are of the opinion that Owen's definition, and particularly the words "the same organ," is quite close to their concept of operational homology. The differences of opinion seem to lie in the interpretation of the word "same," Bock taking a literal meaning of the word, Sokal and Sneath interpreting "same" as identical to their usage in the concept of operational homology. In Sokal and Sneath's terminology the "same" features would be those which are *similar*. Owen, to the contrary, almost certainly does not imply similarity since he says, "every variety of form. . . ." Hence, centered in this controversy

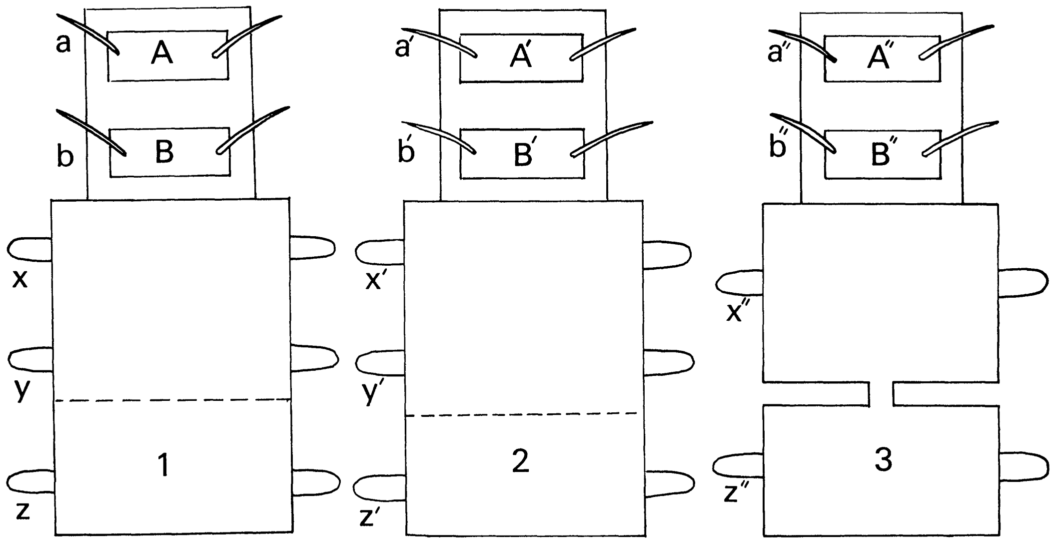

FIG. 1.—Hypothetical organisms showing certain labelled structures, modified after Inglis, 1966:227. See text for explanation.

over Owen's definition we find one of the major problems surrounding the concept of homology—that of similarity *versus* non-similarity. The view held by most phylogeneticists, and the view taken here, is that the concept of homology does not imply any notion of similarity. Merely citing the homologies of the middle ear bones of mammals with certain elements of the visceral arches of fish should suffice to show that "similarity" has a meaningless connection with homology. Because of these differences I reject the remark of Inglis (1966: 221) that the terms homology (*sensu* common ancestor) and operational homology are absolute equivalents. Although the methodologies are quite frequently very similar, the *concepts* expressed by the terms and the implications stemming from their use are not the same.

3.—In addition to the confusion over conceptual and practical aspects of homology, the methods employed to recognize homologies remain an important problem. Inglis (*op. cit.*:226–227) points out the method probably most commonly used to establish homologies, i.e., that of circular sequences (this method has been employed at least since the time of Geoffroy St. Hilaire). Unfortunately, some problems arise with circular sequences, but they were not discussed by Inglis. Figure 1 (modified after Inglis' Figure 2, p. 227) illustrates three hypothetical organisms with certatin labelled structures. According to Inglis (*op. cit.*:226–227) structure a of organism 1 would be homologous to structure a′ of organism 2 because they occur in the same position on plates A and A′. One must assume in turn that plate A is homologous to plate A′, and we do this because they occupy the same relative position on the anterior segment. Furthermore, the anterior segments of organisms 1 and 2 are assumed to be homologous because they have plates showing similar positional relationships and because they stand in the same relationship to the remainder of the body. The circularity of the comparison can be carried further, but it is hardly necessary to do so.

Continuing, Inglis compares the anterior segment of organisms 1 and 2 with that of organism 3. At first, all three anterior segments would appear to be homologous, but the circularity of the comparison is broken and cannot be extended beyond the anterior segment since the posterior portion of organism 3 differs from those of organisms 1 and 2. Inglis concludes from this comparison that the anterior region of organism 3 is not homologous with the anterior regions of organisms 1 and 2 and is, therefore, homoplasious.

In the main the method of circular sequences is probably valid for many comparisons, but Inglis leaves open the question of how far it is necessary to carry the comparison. If it is necessary to carry the circularity as far as possible, then it is obvious that the sequence will be broken unless, of course, the organisms being compared are identical. Other difficulties pose problems for this method. For example, if we assume that organism 3 underwent segmentation (in the region of the dotted line on organisms 1 and 2) and at the same time lost appendage y'', then a new picture emerges. Using the circular comparison of Inglis, appendages x'' and z'' on the anterior segment of organism 3 would not be recognized as homologous with the corresponding features on organisms 1 and 2 when, in fact, they are homologous. Unique structural modification is common in most, if not all, groups of organisms, and a strict adherence to the method of circular comparison suggested by Inglis is not adequate for establishing correct homologies. I am not suggesting that his methodology is wholly incorrect. But it is evident that a break in circularity of the comparison does not necessarily warrant the assumption of homoplasy instead of homology.

Another often employed criterion of homology is commonness of embryonic origin. Some authors have even included a statement as to embryonic origin in their definition of homology (for example, see Smith, 1967). This is unfortunate for several reasons, not the least important of which is the inclusion of criteria for *recognizing* what is homologous in the *definition* of homology. Moreover, on purely biological grounds, embryological data present considerable problems pertaining to the determination of homologies. First, at what point in the developmental process do two or more structures become homologous? To carry the argument to its extreme, Is a common origin from a single germ layer sufficient to term two structures homologous? Certainly, in some sense the epidermis and nervous system have a common embryonic origin. Second, nonhomologous features can have quite similar, if not identical, developmental histories. For instance, a small bony process can be found on the external side of metacarpal II of the carpometacarpus of birds. The process has arisen independently in families of several different orders and cannot be accounted for by common ancestry. By definition, then, the process is nonhomologous in these orders. The process is merely an ossification of cartilage and associated connective tissue, and the development is most certainly the same for all families possessing this feature. Here, commonness of embryonic origin does not indicate homology. Third, homologous features can have different developmental histories as has been clearly demonstrated by de Beer (1958). The pelvic girdle and appendages of fishes have shown a remarkable amount of migration in different lines and may now arise from different somitic constituents. Other examples of homologous features that have different embryonic origins are the lens of the eye of different species of *Rana*, the gut of Chordates, and the ganglia of the trigeminal nerve. These examples are intended simply to show that homology of features "does not necessarily imply similarity of genetic factors or of ontogenetic processes" (de Beer, 1958:153). Clearly, developmental data must be interpreted with care when determining homologies.

4.—The word "analogy" has received much attention, and there have been many different opinions as to how it should be defined. Some believe analogy should refer to similarity of function of structures whether they are homologous or not (Smith, 1967; Boyden, 1943); some would restrict a definition to nonhomologous structures showing similarity of function (Simpson, 1961; many textbooks; original conception of Owen); while a third group would prefer to define analogy in terms of the logical opposite of homology, nonhomology, and eliminate any connotation of similarity in structure or function (Bock, 1963; Ghiselin, 1966).

It can be said without hesitation that the vast majority of uses of analogy have included some statement as to similarity of function. This idea is so firmly established in the minds of most biologists that I think it would be futile to try to eliminate similarity in function from the definition. Contrarily, the question of whether to include an appendage of nonhomology in the definition has other, more important consequences. If homology is to be regarded as descent from a common ancestor, then it would seem wise to include the logical opposite (i.e., nonhomology) in the definition of analogy. That homologous features are likely to be similar in function (more correctly, biological role) is not startling, and it does not seem necessary to emphasize this fact. Nonhomologous features that have become similar in structure due to a similar interaction with the environment are more interesting, and it is to these features that the term analogy perhaps should be restricted.

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REFERENCES

Bock, W. J. 1963. Evolution and phylogeny in morphologically uniform groups. Amer. Nat., 97:265–285.

Boyden, A. 1943. Homology and analogy: a century after the definition of 'homologue' and 'analogue' of Richard Owen. Quart. Rev. Biol., 18:228–241.

de Beer, G. R. 1958. Embryos and ancestors. Oxford Univ. Press, Oxford. 197 pp.

Ghiselin, M. T. 1966. An application of the theory of definitions to systematic principles. Syst. Zool., 15:127–130.

Inglis, W. G. 1966. The observational basis of homology. Syst. Zool., 15:219–228.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 pp.

Smith, H. M. 1967. Biological similarities and homologies. Syst. Zool., 16:101–102.

Sokal, R. R., and J. H. Camin. 1965. The two taxonomies: areas of agreement and conflict. Syst. Zool., 14:176–195.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. Freeman, San Francisco. 359 pp.

van der Klaauw, C. J. 1966. Introduction to the philosophic backgrounds and prospects of the supraspecific comparative anatomy of conservative characters in the adult stages of conservative elements of vertebrata with an enumeration of many examples. Verhandelingen der Koninkluke Nederlandse Akademie van Wetenschappen, 57(1):1–196.

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