

A HIERARCHICAL THEORY OF SYSTEMATICS

by STEPHEN W. WOOD

University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, UK

Received 27 April 1994, 11 August 1994

ABSTRACT: Beatty (1982) claims that the pattern philosophy of the cladistic method is antagonistic to evolutionary theory. I show that the pattern philosophy is consistent with evolution if one takes into account the nature of hierarchical systems, as elucidated by Allen and Starr (1982). A surprising correspondence is revealed between the hierarchy theory of Allen and Starr (1982) and the pattern philosophy of Rieppel (1988). Rieppel (1988) describes two complementary approaches to systematics, called taxic and transformational. These are respectively equivalent to the linguistic and dynamic approaches to hierarchical systems described by Allen and Starr (1982).

* * *

Despite its widespread usefulness, the underlying justification of the cladistic method is in dispute, particularly with regard to its relation to the theory of evolution. In particular, the pattern or transformed cladistic philosophy, as opposed to the original phylogenetic philosophy, is said to be antagonistic to the theory (Beatty 1982). I argue that the pattern cladistic philosophy is consistent with evolution if one takes account the nature of hierarchical systems, as elucidated by Allen and Starr (1982). The pivotal concept in this result is that of complementarity, the biological significance of which was first discussed by Pattee (1978). The concept has been found to be relevant in systematics along an independent route by Rieppel (1988, 1991).

The principal weapon used by the transformed cladists against the phylogenetic school is the distinction between pattern and process (Nelson and Platnick 1981). I find another distinction much more constructive, the distinction between taxic and transformational approaches. Eldredge (1979) invented these terms to describe two approaches to process analysis. Rieppel (1988), following Patterson (1982), expands the original meaning of the terms and gives a clear description of both taxic and transformational approaches to pattern analysis. The taxic approach to pattern analysis is classification, the production of the general reference system. The transformational approach to pattern analysis is phylogenetics, the reconstruction of evolutionary history. Rieppel (1988: 159) describes the patterns of classification as atemporal and acausal, in contrast to the dynamics of the causal processes of evolution: 'Classification emphasises discontinuity and the subordinated hierarchy of types and subtypes. The type is a logical construct, a group diagnosed by homologies at their correct level of inclusiveness ... By its logical construction, the hierarchy of types is static, i.e. ahistorical ... By its abstraction from specific form and function, the hierarchy of types is acausal: it abstracts from the causes (structural and functional) of similarity versus dissimilarity and change, but remains restricted to the representation of formal, i.e. topological relations of similarity.'

Taxic homology as an element of being in the midst of becoming

According to Allen and Starr (1982: 37) a hierarchy is 'a system of communication.' Viewed simply, communication is flow of information and the information relevant to systematics is homology. Roth (1988: 2) discusses a definition of homology which covers both taxic and transformational concepts

* * * *

Evolutionary Theory 10: 273-277 (August, 1994).

The editors thank S.P. Rachootin and O. Rieppel for help in evaluating this paper.

© 1994, The University of Chicago.

of homology (Patterson 1982): 'The fundamental property of homology, according to Van Valen (1982) is "continuity of information." This is, to my mind, the most succinct, comprehensive and ideologically neutral definition of homology yet proposed.' Roth emphasises the two aspects of homology at different points in her discussion:

(1) 'According to modern evolutionary views ... the information in homologs is primarily genetic, and continuity is provided by genealogy' (Roth 1988: 2-3). Here homology is used in the transformational sense, expressed as a set of instructions inherited from a common ancestor.

(2) 'Phylogeny has components of both continuity and change. We identify the elements of continuity as homologies; the change is called evolution' (Roth 1988: 16). The taxic sense of this description of homology can be expressed as a constant thread of meaning sustained in the midst of change, as an element of invariance, of being in the midst of becoming (Rieppel 1988).

The dual concepts of homology are summarised below:

Homology	Continuity	Information
Transformational	Genealogy	Set of instructions
Taxic	Constancy	Meaning

Continuity of developmental information as a causal explanation of taxic homology

Van Valen (1982: 305) introduces his novel concept of homology as follows: 'All homologies involve a continuity of information. In fact homology can be defined in a quite general way, as correspondence caused by a continuity of information.' The concept embraces both historical and repetitive homology (evolutionary and iterative homology, Ghiselin 1976): 'They are aspects of a single phenomenon, caused by continuity of developmental information' (Van Valen 1982: 308). Van Valen's concept is clearly transformational. He disqualifies Nelson's concept of homology, that of correspondence *per se*: 'Nelson ('70) denied the existence of homology itself' (Van Valen 1982: 305). Independently of Patterson (1982) he has understood the equivalence of idealistic and evolutionary concepts of homology (see also Wood, in prep.). According to Owen (1843: 379) a homologue is 'the same organ in different animals under every variety of form and function.' Van Valen (1982: 307) asks: 'What does the same mean? To Owen ... it meant being a variant of the same part of the idealistic archetype from which a group of organisms was created to deviate each in its own way. We retain a similar notion in the latest common ancestor of the group, as Darwin noted, so continuity of information is retained for homologs. However, it also applies to Owen's view directly: Information was continuous, in God's mind, from the archetype to its various imperfect manifestations.' Patterson (1982) has shown though, that Owen's (1846) concept of special homology is taxic, whereas his general and serial concepts of homology are transformational (cf. Van Valen 1982: 307, note 2).

Homology is defined as 'correspondence caused by continuity of information' (Van Valen 1982: 305). Correspondence is more than resemblance and 'more than position is involved' (Van Valen 1982: 305, note 1). A point of correspondence *per se* (Nelson 1970), an element of being in the midst of becoming (Rieppel 1988), a constant thread of meaning sustained in the midst of change - is a taxic homology. Thus transformational homology, which Van Valen has defined, is taxic homology caused by continuity of developmental

information. The postulation of continuity of information is a causal explanation for a taxic homology which turns it into a transformational homology.

The taxic approach results in an acausal description of the phylogenetic hierarchy

In the transformational approach, a homologue originates in a low-level holon (generally conceived as a species) and becomes fixed, characterising that holon. As the ancestral entity diversifies, splitting into an ever-growing number of descendant entities, the homologue characterises a holon at a higher level in the phylogenetic hierarchy. In the transformational approach, information flows from low-level holons to high-level holons.

In the taxic approach, a homology is assigned to a high-level holon. The function of cladistics is to assign each character state its correct level of inclusiveness (Rieppel 1988: 159). A hypothesis of homology is only generated by applying a state to a high-level holon. A homology defines a component of a cladogram (Nelson 1979), and can be said to be transmitted to the lower-level holons contained within that component. Continuity of information, in the taxic sense, therefore flows from high-level to low-level holons.

The transformational approach provides a time axis, and thus the velocity of information flow. When we view information in the transformational approach we find that it flows from low-level to high-level holons. The direction of causation in the transformation must therefore originate with the low-level holon. When we view information in the taxic approach we find that it flows in the opposite direction, from high-level to low-level holons. Within a unified model this would imply that time also flows in the reverse direction, or that backwards (future) causality is involved. Within the complementarity paradigm, however, the taxic approach can be most fruitfully viewed as acausal (Rieppel 1988: 159), that 'causality as it is normally employed has no meaning' (Allen and Starr 1982: 64).

In the transformational approach secondary losses, such as the loss of legs in snakes, appear to be a genuine part of the evidence of relationship, because they represent changes occurring within low-level holons, namely species. The reverse view of absences is found in the taxic approach, that they cannot be used as evidence of relationship. They are either the result of the absence of information (primary absence) or discontinuity of information flowing from high-level holons (secondary absence or loss). This latter case is an example of homoplasy, called reversal. Parallelism is another form of homoplasy, where information is transmitted from two or more discontinuous sources.

The taxic approach results in an atemporal description of the phylogenetic hierarchy

The complementarity principle in hierarchy theory can be summarised as follows (cf. Allen and Starr 1982: 264). Deriving from the observer-observed duality, the principle demands a rate-independent analysis and a rate-dependent analysis. The rate-independent analysis is linguistic in its nature, and refers to the observer-dependent aspects of the phenomenon. The rate-dependent, dynamical mode of analysis is associated with observer-independent aspects of the phenomenon. Greater precision in one complement is gained by confounding or comprising the other complement. Neither complement is sufficient, but both complements are necessary for a full account of phenomena.

Toxic homologies can be shown to be part of the linguistic, non-dynamic, atemporal description of the phylogenetic hierarchy:

(1) A toxic homology is a signal transmitted between holons of the phylogenetic hierarchy: 'At departure, the signal represents a freezing of the infinitely rich dynamics of the transmitting holon as expressed by the medium of energy or matter of which the signal stream is made' (Allen and Starr 1982: 17-18). A toxic homology is abstracted from the dynamics of ontogeny and function (Rieppel 1988: 38).

(2) 'Although meanings can change, a single meaning has no dynamics of its own, in contrast to, say, a process or system' (Allen and Starr 1982:18). A toxic homology is the meaning of the holon. Groups defined by toxic homologies are thus types, i.e. non-dynamic and atemporal (Rieppel 1988: 159).

(3) 'In capturing the dynamics of the holon, the structure of the signal is a sign of the state of the holon; and signs have no rate or dynamics' (Allen and Starr 1982: 18). The toxic approach deals with the rate-independent, linguistic aspect of the phylogenetic hierarchy.

To discover a toxic homology, the observer must break into the system to give it meaning. The toxic approach must therefore take account of observer-observed duality. The transformational approach, however, deals with mechanistic models of evolutionary change. The latter can therefore be said to deal with the objective reality independent of the observer.

Summary

A full account of the phylogenetic hierarchy, in terms of both linguistic and dynamic descriptions, is provided jointly by the toxic and transformational approaches to systematics, complementary and yet incompatible. Classification, in the pattern philosophy of the cladistic method advocated by Rieppel (1988), provides an atemporal, acausal, i.e. linguistic description of the phylogenetic hierarchy.

References

- Allen, T. F. H. and Starr, T. B. (1982) *Hierarchy: Perspectives in Ecological Complexity*. University of Chicago Press, Chicago, London.
- Beatty, J. (1982) Classes and cladists. *Systematic Zoology* 31: 25-34.
- Eldredge, N. (1979) Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History* 13: 7-19.
- Ghiselin, M. T. (1976) The nomenclature of correspondence: a new look at "homology" and "analogy." In Masterton, R. B. Hodos, W. and Jerison, H. (eds.) *Evolution, Brain and Behaviour: Persistent Problems*, pp. 279-314. Lawrence Erlbaum, Hillsdale, New Jersey.
- Nelson, G. J. (1970) Outline of a theory of comparative biology. *Systematic Zoology* 19: 373-384.
- Nelson, G. J. (1979) Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's *Familles des Plantes* (1763-1764) *Systematic Zoology* 28: 1-21.
- Nelson, G. J. and Platnick, N. I. (1981) *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- Owen, R. (1843) *Lectures on Comparative Anatomy and Physiology of Invertebrate Animals*. Longman et al., London.
- Owen, R. (1846) *Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals*. Part I: Fishes. Longman, Brown, Green and Longmans, London.
- Pattee, H. H. (1978) The complementarity principle in biological and social structures. *Journal of Social and Biological Structures* 1: 191-200.

- Patterson, C. (1982) Morphological characters and homology. In Joysey, K. K. A. and Friday, A. E. (eds.) *Problems in Phylogenetic Reconstruction*, pp. 21-74. Academic Press, London.
- Rieppel, O. (1988) *Fundamentals of Comparative Biology*. Birkhäuser Verlag, Basel.
- Rieppel, O. (1991) Things, taxa and relationships. *Cladistics* 7: 93-100.
- Roth, V. L. (1988) The biological basis of homology. In Humphries, C. J. (ed.) *Ontogeny and Systematics*, pp. 1-26. British Museum (Natural History), London.
- Van Valen, L. M. (1982) Homology and causes. *Journal of Morphology* 173: 305-312.
- Wood, S. W. (in prep.) Richard Owen's three concepts of homology.