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# Importing the Homology Concept from Biology into Developmental Psychology

**ABSTRACT:** To help introduce the idea of homology into developmental psychology, this article presents some of the concepts, distinctions, and guidelines biologists and philosophers of biology have devised to study homology. Some unresolved issues related to this idea are considered as well. Because homology reflects continuity across time, developmental scientists should find this concept to be useful in the study of psychological/behavioral development, just as biologists have found it essential in the study of the evolution and development of morphological and other characteristics. © 2012 Wiley Periodicals, Inc. *Dev Psychobiol*

**Keywords:** homology; development and evolution

## INTRODUCTION

Ever since Richard Owen defined “homology” in 1843 as referring to “the same organ in different animals under every variety of form and function” (p. 374), the concept has proven to be fundamental for biologists. Evolutionary biologists in particular have found the concept to be of central importance; Charles Darwin (1871), for example, argued effectively in *The descent of man* that only “descent from a common progenitor” (p. 31) could explain the many homological “correspondence[s] . . . between man and the higher animals” (p. 14) such as “the similarity of pattern between the hand of a man or monkey, the foot of a horse, the flipper of a seal [and] the wing of a bat” (p. 31). More recently, evolutionary theorists (e.g., de Beer, 1958; Griffiths, 2007; Wagner, 2007) have stressed that although such homologous body parts can appear similar to one another in some respects, homologues arise as a result of a process of *copying*, so their

relationship is best characterized as one of sameness, not primarily as one of similarity. In particular, homologues are versions of the same thing because they are present in animals that are descendants of a common ancestor that possessed that very same feature. As Wagner put it, “Sameness, then, by the definition of homology, does not refer to similarity of structure or function as such, but to historical continuity. . . . In other words, the homology concept can be applied to anything that forms a lineage” (p. 473). If we take “lineage” to mean “descent in a line from a common progenitor” (Merriam-Webster online dictionary), the homology concept should be relevant to both descent from a common ancestor and to descent from common progenitor *cells*, that is, to development.

Therefore, although modern developmental psychologists have not typically made use of the homology concept, it could prove to be as valuable for developmentalists as it has been for evolutionists. Particularly because the homology concept has been helpful to biologists in their attempts to recognize phenotypic characters across discrete species, developmental psychologists who are interested in identifying instances of the same behavioral processes across potentially discontinuous developmental stages might benefit from exploring how biologists think about these issues. Given that behavioral processes might appear similar even if they do not share common developmental origins or that very different superficial appearances might mask

Received 14 October 2011; Accepted 10 January 2012

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Contract grant sponsor: National Science Foundation

Contract grant number: BCS-1023899

Contract grant sponsor: Dalhousie University.

Published online in Wiley Online Library  
(wileyonlinelibrary.com). DOI 10.1002/dev.21015

underlying similarities that are rooted in common developmental origins (C. Moore, this issue), thinking about psychological development in terms of homology might yield important insights.

Homology has been called “one of the most important concepts in biology” (Brigandt & Griffiths, 2007, p. 633), and as a result, “no other fundamental concept in biology has generated as much discussion” (Hall, 2003, p. 413). Because theorists have been concerned with some form of this issue for centuries (Höbfeld & Olsson, 2005), there has been a proliferation of ideas associated with the phenomena of homology (Griffiths, 2007). Consequently, regardless of whether developmental psychology might best be served by *importing* the kinds of homology concepts characteristic of evolutionary or developmental biology, or instead by elaborating its own concept of homology, it will be important to first become familiar with some of the conceptions, distinctions, and guidelines biologists and philosophers of biology have developed as they have studied these phenomena.

## HOMOLOGY AT DIFFERENT LEVELS OF ANALYSIS

Among the most important insights of these theorists is that homology can be detected at several levels of analysis (Hall, 2003; Striedter & Northcutt, 1991). Homology of structures (the first of four levels of analysis I will consider here) can be observed both across and within organisms. Such *morphological* homologies across different species—so-called “taxic” homologies—reflect descent from a common ancestor that also had this feature. For example, the similarity of a dog’s femur and a human’s femur reflects descent from an ancestor of both animals that possessed such a structure itself. In addition, morphological homologues can exist within a single organism. For example, adjacent segments of a lobster’s tail or a primate’s vertebral column are said to be “serial” homologues (Rutishauser & Moline, 2005). Because serial homologues cannot be explained simply by the existence of a copy of the trait in an ancestral organism, their existence indicates that an evolutionary account of homology must be supplemented with a developmental account (Griffiths, 2007; P. E. Griffiths, personal communication, January 7, 2012).

Indeed, Wagner (1989) has defined structures as homologous “if they share a set of developmental constraints” (p. 62), highlighting the possible utility of the idea of homology for developmental scientists. Wagner’s definition allows us to make sense of serial homology and also allows us to identify a third type of morphological homology. In addition to recognizing

taxic and serial homology, biologists—at least since Bertalanffy (1934, as described in Höbfeld & Olsson, 2005)—also recognize “homology between sexually differentiated parts (e.g., penis and clitoris, or testis and ovary), or between different generations in a complex life cycle (e.g., parthenogenetic and sexual generations of parasitic insects)” (Wagner, 1989, p. 62). Testes and ovaries, for instance, are considered homologous, because both types of gonad develop from the same collection of primordial cells, namely the genital ridge present both in embryos that develop into male fetuses *and* in embryos that develop into female fetuses. Because this type of morphological homology is neither taxic (across species) nor serial (within a single organism), we can refer to it instead as “developmental-origin” homology.

There is tension in biology between homology for developmental phenomena and homology for evolutionary phenomena (B. K. Hall, personal communication, December 5, 2011), and it is possible that developmental psychology would benefit more from importing one of these sets of ideas than the other. However, because developmental psychologists utilize a variety of methods in their efforts to understand human behavioral development—including both longitudinal studies of individuals (Singer & Willett, 2003) and comparative studies of nonhuman populations (Lickliter, 2000)—the ideas associated with either developmental homology or with evolutionary homology might have some value for us. Moreover, because of the close relationship between development and evolution and the need to build a unified theory of biology that integrates development into our understanding of evolution (Moore, 2008b), it seems worthwhile at present to remain open to the possibility that either or both the developmental and/or evolutionary senses of homology could be used to illuminate human psychological development.

In addition to detecting various types of morphological homology, we can also detect homology at a second level of analysis, namely at the level of DNA (Fitch, 2000). *Genetic* homologies can be of at least two different subtypes, analogous to taxic and serial morphological homologies, respectively. Orthologues are genes that are similar or identical across species. These are taxic-style molecular homologies; they reflect the workings of normal reproductive processes wherein copies of DNA sequences are transmitted to descendants across generations. In contrast, paralogues are identical or similar gene sequences within single genomes. These are serial-style molecular homologies; they arise when gene sequences are duplicated within a genome, as appears to have happened, for example, when the first diploid cells evolved with homologous *pairs* of chromosomes.

At a third level of analysis, we can detect *behavioral* homologies. These have been the focus of much less study than structural or molecular homologies, in part because some theorists hold that behavior cannot be appropriately subjected to homological analysis; for instance, Atz (1970) concluded that “the application of the idea of homology to behavior is operationally unsound and fraught with danger” (p. 69). But recent work in philosophy suggests that there are no insurmountable obstacles in using the homology concept to consider psychological phenomena, under certain circumstances (Clark, 2010; Ereshefsky, 2007; Love, 2007). Because homologous structures are homologous independently of their functions—for example, bat wings, whale flippers, and dog legs are homologous even though they serve the differing functions of flying, swimming, and walking, respectively—theorists interested in identifying behavioral homology should likewise focus on behaviors per se rather than on what a behavior’s adaptive purpose might be; such an approach should allow discovery of behavioral homologies. Moreover, thinking in this way should encourage attention to the *development* of behavior, in contrast to the typical approach of evolutionary psychologists who, by focusing on the adaptive functions of psychological traits, have often ignored those traits’ ontogenies (Buller, 2005; Ereshefsky, 2007).

It is unfortunate that one of the more influential attempts to use the concept of homology to understand behavior was that of Lorenz (1958), whose evolutionary perspective led him to invoke a now-discredited notion of “inherent” behavior (p. 68) and thereby short-circuit the very questions of interest to developmental scientists (Lehrman, 1953; see also Griffiths, this issue). In spite of this regrettable historical use of the homology concept, there do not appear to be any theoretical barriers to using this concept while studying behavior as an emergent product of a complex, dynamic system (Striedter, 1998; for more on the dynamic systems approach that understands behavior in this way, see Blumberg, 2005; Gottlieb, 1991, 2007; Johnston & Edwards, 2002; Lewkowicz, 2011; Lickliter & Honeycutt, 2003; Michel & Moore, 1995; Moore, 2002, 2008a; Oyama, 2000; Robert, 2004; Thelen & Smith, 1994).

Finally, at a fourth level of analysis, *ontogenetic* homologies identify developmental processes that are the same, regardless of whether or not the phenotypes they contribute to are homologous. Thus, homology can entail the sharing of common developmental *processes* (Striedter & Northcutt, 1991) instead of—or in addition to—the sharing of common evolutionary origins, the sharing of common developmental origins in particular cell populations, or the sharing of common

developmental resources (e.g., genetic factors, nutritional factors, educational factors, etc.). Moreover, as was the case with morphological homologies, ontogenetic homologies can theoretically be detected across organisms (as in taxic or developmental-origin homology) or within an individual organism (as in serial homology). Clearly, the concept of homology could provide a variety of theoretical tools that might be of use to developmental psychologists.

It is important to note here that homologies at these various levels of analysis may be independent of one another. This is true for genes that contribute to the development of bodily structures, for neural circuits that contribute to conceptual structures, for conceptual structures that contribute to behaviors, and so on. Thus, homologous genes can contribute to the development of nonhomologous phenotypes (Griffiths, 2006), and nonhomologous genes can contribute to the development of homologous phenotypes (de Beer, 1971; Hall, 1992; Wagner, 2007; Wray & Abouheif, 1998). Likewise, nonhomologous neural circuits can underlie homologous behaviors or psychological processes (Ereshefsky, 2007), and nonhomologous behaviors can be subserved by homologous neural circuits (Bergeron, 2010). Finally, homologous *processes* can lead to the development of nonhomologous phenotypes, and nonhomologous developmental processes can lead to the emergence of homologous phenotypes (Hall, 1992, 2007). Specific examples of each of these types of independence are described in the articles cited in this paragraph. As a result of this state of affairs, it will be imperative for developmental psychologists using homology concepts to specify the levels of analysis on which they do and do not consider behavioral phenomena to be homologous.

To summarize, homology can be identified at the morphological, genetic, behavioral, and/or ontogenetic levels (and possibly at other levels as well). Furthermore, it should be possible to identify psychological or behavioral homologies across different species (taxic), across two individuals in the same species (developmental-origin or taxic), and within an individual at a given developmental moment (serial). Finally, in addition to being able to identify behavioral/psychological homologies, we might also be able to identify homologies in the developmental *processes* responsible for the emergence of behaviors or psychological states.

## HOMOLOGY ACROSS TIME

Developmentalists are particularly interested in time as a variable. Therefore, it can be useful to consider how biologists think about homology across time. To this

end, it is helpful to first think about taxic morphological homology, because since the 19th century, this type has been a primary focus of biologists. An instructive example is the relationship between a human arm and a bird wing, which are homologous as forelimbs because birds and people descended from a common tetrapod ancestor that had forelimbs itself. Interestingly, the forelimb of our tetrapod ancestor is just as much a homologue of a human arm as a bird wing is of a human arm; the fact that the comparison is made across species that lived hundreds of millions of years apart is unproblematic for evolutionary biologists, because taxic homology is based on shared ancestry that can be revealed through fossil and gene analysis (B. K. Hall, personal communication, December 5, 2011). For the same reasons, the forearms of *Australopithecus africanus* and of modern human beings are homologues, because animals of both species descended from a common ancestor with homologous forearms. But note that in this case, human beings are direct descendants of *A. africanus*.

By analogy, then, it should be unproblematic to consider primordial cells and the structures that develop from them to be noncontemporaneously homologous to one another. That is, if we recognize testes and ovaries as “developmental-origin” homologues, and we also recognize *H. sapiens* and *A. africanus* arms as taxic homologues, we should also consider the relationship between the genital ridge in an embryo and the gonad it develops into *in that same individual later in life* to be a kind of “developmental-origin” homology, too. However, even though biologists consider our arms to be homologous with the forelimbs of our ancestors (for evolutionary reasons) and they consider testes to be homologous with ovaries (for developmental reasons), it remains unconventional to consider adult morphological structures to be homologous with the primordial structures from which they develop (at least in part because of the tension described earlier between developmental and evolutionary accounts of homology). Nevertheless, even though biologists do not refer to this kind of relationship as a form of homology, it is likely to be of interest to developmental scientists. Many developmental psychologists, for example, are engaged in trying to identify behaviors, emotional states, or cognitive structures that normally develop from earlier-appearing behaviors, states, or structures, and recognizing these as homologues could be informative.

To see the possible value of this approach, consider Anderson’s (2007, 2010) Massive Redeployment Hypothesis, which posits that neural circuits that serve a particular function have sometimes been exapted during evolution such that they are now used to serve both the original function and a later-appearing function. For

example, Penner-Wilger and Anderson (2008) have marshaled evidence consistent with their hypothesis that “one of the functional circuits originally evolved for finger representation has since been redeployed to support the representation of number and now serves both functions” (p. 2446). In particular, regions of the parietal lobe that are associated with representations of the fingers are also activated in number processing tasks, and experimental disruption of left angular gyrus functioning interferes both with tasks requiring the representation of numbers and with tasks requiring the representation of the fingers. One of the more interesting consequences of this sort of “neural re-use” (Anderson, 2010) would be that two functions that share neural resources (e.g., number and finger representation) would both be expected to be characterized by the same kinds of computational attributes. Thus, this perspective would specifically predict that there would be observable similarities between the two functions.

Although Anderson (2010) focused on the potential *evolutionary* re-use of neural circuits rather than on the potential re-use of neural circuits in development, it remains possible that neural circuits are re-used in development in a way that gives rise to homologous psychological characteristics (Moore & Moore, 2010). For example, a neural circuit that subserves a specific function normally seen in juvenile organisms might typically be re-used later in life in a new behavioral context. If some distinctive juvenile behavior reflects a distinctive aspect of the neural structure(s) underlying it, it becomes possible to test specific hypotheses regarding aspects of the later-developing behavior, on the grounds that the juvenile and mature behaviors are noncontemporaneous homologues. Similarly, recognizing *contemporaneous* behavioral homologues in a person could be of value to psychologists; if two different behaviors typically seen in human adults are both thought to make use of a particular neural circuit, a search for common features in those adult behaviors would be warranted.

## IDENTIFYING BEHAVIORAL HOMOLOGY

In the 1950s, Adolf Remane described three specific criteria—initially developed by Geoffroy Saint-Hilaire in the 18th century—that could be used to recognize morphological homologues (Griffiths, 2007); these criteria will be helpful to psychologists interested in behavioral homology as well. Following Saint-Hilaire, Remane recommended first looking at the relative (spatial) position of the body parts in question in the arrangement of two organisms. When seeking behavioral homologues, Ereshefsky (2007) and Love (2007)

suggest taking a similar approach involving looking for behaviors' relative (temporal) positions in an overall behavioral pattern. The second criterion requires evaluation of the extent to which a bodily structure is "special." In explaining this criterion, Griffiths (2007) noted that if a morphological characteristic "cannot be explained by the role of a part in the life of the organism," it is special in the way Saint-Hilaire and Remane meant; "The fact that in the vertebrate eye the blood supply to the retina lies between the retina and the source of light is a famous example of a 'special quality' " (p. 648). Applied to behavior, this criterion has been used to identify, for example, "the web weaving behaviors of different spider taxa as distinct behavioral homologies" (Ereshefsky, 2007, p. 665). Finally, the third criterion entails the tracing of a bodily structure through evolutionary intermediates. Here, too, behavioral homology could be ascertained if particular behaviors within or across organisms could be linked to one another either in ontogenetic or phylogenetic time.

## THE POTENTIAL UTILITY OF HOMOLOGY THINKING FOR DEVELOPMENTAL PSYCHOLOGY

Importing the concept of homology from biology into developmental psychology could facilitate our understanding of how various psychological phenomena are related to one another. Speaking generally, Matthen (2007) noted that

Homology thinking is adopted in a particular domain because it is thought to be the best theoretical approach to the explanation of a certain set of features in that domain, given empirical facts about it. For example, it is adopted as a way of identifying a dog's physical gesture as one of submission . . . because grouping these things together with others of common origin explains their morphology, system connectivity, functional role, and adaptive function better than alternative taxonomical approaches. (p. 677)

More specifically, homology thinking could be particularly helpful to developmental psychologists interested in addressing questions such as whether or not developmentally early-appearing and developmentally late-appearing psychological characteristics can properly be considered versions of "the same" attribute.

For example, several researchers (Starkey, Spelke, & Gelman, 1983; Wynn, 1992, 1995; Xu & Spelke, 2000) have concluded that infants can represent and process

numerical information using a capacity that is not fundamentally different than that found in adults. Stating this explicitly, Xu and Spelke wrote "the capacities to represent approximate numerosity found in adult animals and humans . . . develop in human infants" (p. B1). However, other researchers (Allen & Bickhard, in press; Simon, 1997) have argued that what can appear in infants to be adult-like competence in the number domain might in fact be something quite different, much as smiling in human neonates looks like smiling in adults even though these are widely regarded as being two very different kinds of responses (Dondi et al., 2007; Messinger & Fogel, 2007).

Similar questions must be asked about infants' competences in other domains as well (e.g., Nadel, 2011). Although neonatal imitation (Meltzoff & Moore, 1977) might appear to be similar to imitation in adults or older children, such behaviors need not necessarily be closely related to one another (Suddendorf, this issue). Likewise, a number of laboratories (Moore & Johnson, 2008, 2011; Quinn & Liben, 2008; Schwarzer, Freitag, & Buckel, 2010) have reported data consistent with the possibility that infants in their first year of life can perform mental rotations like those observed in adults (Shepard & Metzler, 1971) and children (Levine, Huttenlocher, Taylor, & Langrock, 1999). But whether or not the performances of infants in mental rotation tasks should be understood as manifestations of the same psychological character that is observable in older populations remains an open question. Importing homology thinking into developmental psychology would draw attention to the utility of Remane's criteria for identifying behavioral, developmental-origin (i.e., within-individual) homologues and could thereby provide tools for theorists to use in resolving these kinds of questions.

For the same reasons, homology thinking could also be useful in addressing the opposite situation, namely how to identify behavioral homologues that, like some of their morphological counterparts, do *not* appear similar to one another. For example, Tomasello (2003) has argued that syntax might best be thought of as a form of joint attention, in which case these behaviors might be developmental-origin homologues, notwithstanding the obvious differences in how they appear in individuals (see also C. Moore, this issue). Because homologues are better characterized as the *same* than as similar (Griffiths, 2007; Wagner, 2007), the best way to support an argument that two behaviors are homologous is to establish the kind of relational criteria Remane identified, "such as position in a behavioral pattern, uniqueness in function, or continuity in an evolutionary sequence" (Ereshefsky, 2007, p. 672). Of course, if the arguments presented here are sound, it should also be possible to support an argument that two behaviors

are homologous by establishing continuity in a *developmental* sequence.

### SOME POTENTIAL PROBLEMS ASSOCIATED WITH THE CONCEPT OF BEHAVIORAL HOMOLOGU

One challenge facing psychologists interested in identifying behavioral homologies is that homology has traditionally been understood to describe the relationship between certain characters, *irrespective of the states* those characters are in. Morphological homologues, for instance, are discrete characters that are the same structure across different species (Brigandt, 2007; Fitch, 2000; Wagner, 2007), but in those different species, they can sometimes be in extremely different states. To use an example from Wagner (2007), many insects have characters that can be identified as forewings and hindwings, respectively. However, the *states* that these characters are in can vary radically. So, whereas butterflies' forewings and hindwings are both wing blades, houseflies' forewings are wing blades but their hindwings have evolved into halteres (an alternate state that serves the function of helping to balance flies during flight); in contrast, beetles' wing blades are their *hindwings*, whereas their *forewings* have evolved into elytra (a different alternate state that provides a protective cover for the hindwings when the insect is not flying). Thus, halteres are homologues of butterflies' and beetles' hindwings, and elytra are homologues of houseflies' and butterflies' forewings, even though neither halteres nor elytra appear to be particularly wing-like. So, the fact that characters can be in any of several (potentially continuously) varying *states* means that the characters themselves can be thought of as abstractions across those states. The distinction between characters and states is important because, as Wagner notes, it "removes the confusion that is inherent . . . between parts, such as wings and legs (character identities), and attributes of parts, such as size, shape and colour (character states)" (p. 475).

For those interested in studying behavior, the distinction between characters and states presents a problem (albeit a potentially helpful problem in that it could help focus attention in a productive way). Before the homology concept could be usefully imported into psychology, it would be necessary to identify behavioral constructs that can appropriately be considered discrete "characters" capable of being in varying—and possibly quite distinct—states. Approaching behavioral phenomena in this way raises immediate questions. For example, an individual described as "fearful" could be construed either as having a particular character or as

being in a particular character state (e.g., a state that an emotional response system might be in), and it is not immediately clear which of these two ways of thinking would be more helpful (for more information on the use of homology thinking to apprehend affective phenomena, see Clark, 2010, this issue; Ereshefsky, 2007). Remaining cognizant of extant work on other types of homology could help psychologists as they think through such questions.

Another problem likely to face psychologists interested in identifying behavioral homologies will be how to limit the phenomena to which the concept can be applied. Taxic morphological homology exists only when the most recent common ancestor of two species itself has a character that can be identified in both descendant species. Developmental-origin homologies, too, can be identified when particular cell populations give rise to particular organs. However, because there are no discrete "generations" apparent in behavioral development, it will be necessary to identify a reference point in the development of any psychological character of interest, one that can serve as an analogue to a most-recent-common-ancestor in morphological evolution. The reference point identified will necessarily be somewhat arbitrary, but in the absence of such a reference point, any two psychological characters could arguably be called homologous on the grounds that the development of all of our psychological characters can ultimately be traced to a single progenitor zygote in a uterine environment. The fact that behavioral homologues and neural homologues can be independent of one another means that a reductionistic approach to behavior will not yield an easy solution to this problem.

### INTERDISCIPLINARY CO-EXPLORATION

Although work biologists and philosophers of science have already done on homology can be of help to developmental psychologists, developmental perspectives can also contribute to biologists' understanding of homology. Biologists' explanations of taxic morphological homology have typically sidestepped the question of how characters present in ancestors are transmitted—sometimes in a radically altered form—to their descendants (Griffiths, 2006); what has been missing is a developmental account of the presence of these characters. Serial homologies in particular require *both* developmental and evolutionary explanations, leading Griffiths (2007) to conclude that such explanations "are strictly complementary elements of a complete explanation. . ." (p. 651).

In fact, a developmental perspective arguably can be more valuable than an evolutionary perspective when

attempting to explain psychological phenomena, because there are behavioral characters that have not evolved (e.g., no direct selection pressures can be invoked that can provide a thorough explanation of how and why people interact with modern technologies in the ways they do). That is, although an evolutionary perspective can be of value as we try to understand the appearance of *some* characters, it is not sufficient for understanding the appearance of *any*, because all characters—behavioral and otherwise—develop. Because developmental explanations for complex organisms' characteristics are always necessary, and evolutionary explanations are never sufficient, we can expect advances in understanding when developmental theorists begin working to explain homology.

As Wagner has pointed out, “homology is an essential idea of biology, referring to the historical continuity of characters” (2007, p. 473). Because psychological characters are aspects of biology and because developmental psychologists study psychological characters across continuous developmental time, homology thinking might prove to be as revealing for developmental psychologists as it has been for biologists. Likewise, because homology is necessarily invoked, “consciously or unconsciously, . . . whenever we compare two or more biological units, whether those units are genes, cells, tissues, organs, structures, behaviour, or individuals” (Hall, 2003, p. 410), and because studying development necessarily entails comparing earlier- and later-appearing characters, homology could prove to be as fundamental for developmental psychology as it is for biology. The fact that homologues can be identified at many distinct levels of analysis means that communication among theorists from several disciplinary backgrounds will be necessary if importing homology thinking into developmental psychology is to be fruitful, but such an interdisciplinary approach to the study of homology stands a good chance of contributing in important ways to our understanding of the development of psychological characteristics.

## NOTES

This article was written with the support of a grant (BCS-1023899) from The National Science Foundation. Additional financial support for the Workshop on the Concept of Homology in Developmental Psychology was provided by Dalhousie University. I am grateful for the support and help provided in connection with this project by Chris Moore, George Michel, and Dawn Moore. Thanks are also extended to those theorists whose work I relied on while writing this article, including Michael Anderson, Ingo Brigandt, Jason Clark,

Marc Ereshefsky, Paul Griffiths, Brian Hall, Alan Love, Mohan Matthen, and Günter P. Wagner.

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