7　Homologizing as kinding

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Homology is a natural kind concept,[1,2] but one that has been notoriously elusive to pin down. There has been, and continues to be, sustained debate over the nature of correspondence (e.g. whether homology is an all-or-nothing relation or whether it admits of degrees) and the units of comparison (e.g. whole organisms, traits as morphological outcomes, behavioural activities, biochemical mechanisms, developmental processes, or certain properties of traits).

With some notable exceptions,[3,4] the continued debate over its meaning within history and philosophy of biology over the last 25 years has focused on defining *homology* rather than on its use in practice. The aim of this chapter is to reverse this trend and to concentrate instead on the practices of *homologizing*. I define "homologizing" to be a concept-in-use. Practices of homologizing are kinds of rule following, the satisfaction of which demarcates a category – that of being a homologue. Identifying, explaining, discovering, and understanding are exchanges that connect practice to concept through the performance of a rule by practitioners.[5] I contend that these practices of homologizing are constitutive of natural kinding activities[6] and that it is the activity that precipitates what recently has been called "homology thinking"[7]. If homologizing is a kind of kinding, then consideration of the nature of the comparative practices used in its discovery, tracking, and identification not only clarifies its meaning, its use, and the progression of the concept of homology, but also provides further understanding of the processes and progression of natural kinds and kinding practices in general.

A record of comparative investigations and the identification of sameness of form in different animals (e.g. iterations of structure, segmentation, dorsal/ventral polarity) has been observed and documented since Andreas Vesalius's[8] *De humani corporis fabrica*. These illustrated volumes generated knowledge of biological kinds through the comparative practices used in their production.[9] The extensive anatomical and physiological collections of John Hunter[10] and Richard Owen[11] exemplified making, displaying, and tracking the sameness of form in different organisms. These curated collections, their identification of type specimens, and the meticulous descriptions of these served as the ontological corpus and epistemic estate required for adjudicating whether a particular organism belongs to, or lays outside of, a particular kind.

In the following, I suggest that homologizing can be understood as a set of kinding activities that have shaped, and continue to shape, the meaning and use

of *homology*. Investigation into historical as well as current comparative practices reveals the diversity of these natural kind-generating and natural kind-discovering practices, the nature of correspondence, the units of comparison, and the continuing impact of these practices on the concept *homology*.

1 Early comparative practices from Vesalius to Darwin

Scientific understanding in the late Renaissance was shaped by the practice approach of the Flemish anatomist Vesalius. Cadavers and their active dissection were his pedagogical tools. His *De fabrica* recorded the anatomical details gleaned from the operating theatre. Depictions and representations of these begin with the elaborate frontispiece facing the book's title page. Vesalius includes implicit representations of serial repetition in the form and structure of bones and muscles as indicated in the illustrations of the *Fabrica* using Greek letters. The same Greek letter was used to indicate the ribs or ulnae in the skeleton of the same organism. This referential naming of parts facilitated their description as *the same part*. Vesalius also presents other animals as comparative epistemological subjects to aid understanding of human anatomy. Representations of a dog and human skull alongside each other are shown twice within the *Fabrica*. And the dissection of a pig by putti surgeons is featured in his historiated capitals. Much of Vesalius's text relies on descriptions taken from observed dissections of animals. Underlying the use of illustrations and descriptions of the dissection of animals as proxies for those of humans seems to be an unstated assumption that there is (at least in use) a unity of form that makes knowledge of animal skeletal, vascular, and organ orientation extendable to that of humans. That pigs and dogs were dissected and represented in the *Fabrica* suggests an implicit comparative approach to the study of anatomical structure across organisms.

Evidence for the explicit structural equivalence between the features of different animals can be found 12 years after Vesalius's work, in Pierre Belon's anatomical illustrations.[12] These detailed sketches compare the position and arrangement of the bones of a human with those of a bird. What was of particular significance in these sketches was how Belon arranged the bones of both the bird and the human skeleton in the same upright position. The skeleton of the bird was shown in an unnatural position that mirrored the upright standing position of the human skeleton: its head, neck, and spinal column forming a straight line and the forelimbs hanging down on either side of the body ventrally splayed. This intentional arrangement emphasized the positional equivalence and corresponding topology of the bones of each animal and their similar skeletal relationships.[13] Vesalius's anatomical studies and Belon's comparative anatomical illustrations and descriptions were augmented by the detailed compendia of Gessner, Aldrovandi, Johnstone, and Faber.

But the representational and descriptive approaches used in these were transformed by the experimental investigations of a group referred to as *le compagnie* in the Paris Academy of Sciences.[14] Claude Perrault, Louis Gayant, Jean Pecquet, and Joseph-Guichard Duverney extended and reformed biological natural kinding practices within their studies of comparative anatomy and physiology.[15] For Perrault and the rest of the Paris *compagnie*, natural kinding was a communal

rather than a solitary activity. Descriptions and representations were produced by a company of collective actors. Led by Perrault, the *compagnie* worked collaboratively on their projects of anatomical and physiological observation.[16] This collaboration was necessary, according to Perrault,[17] to ensure scientific accuracy and understanding. Although dissections and observations were augmented with reflection and reason, the guiding rule was that empirical knowledge trumped analytical knowledge. Accordingly, each specimen was treated as novel rather than as a token of a particular preconceived type.[18]

Dissection was directed, observed, and interpreted by committee in an attempt to resolve a more accurate picture – and one without assumptions of Cartesian mechanical philosophy of nature or unification of organic form.[19] This is exemplified in the discussion of a small spotted African cat, the *Chat-pard* (see Figure 7.1). Debate over the kindhood of the animal, whose features bore resemblance to multiple organisms familiar to the *compagnie*, was retained in the published description.[20] Despite all observing the same animal and investigative dissection, they concluded different causes for the apparent mixture of comparatively similar features to local European species. Whilst some described the cat as a mélange, there was disagreement over the different species which might have mated resulting in the birth of the apparent hybrid. Others speculated over its possible sterility or whether it might have been a castrate due to the defective and imperfectly formed organs of generation and the notable accumulation of fat that was revealed upon dissection.[21] The *compagnie* was unable to decide from the empirical evidence which of the several causal accounts were *the* cause of the apparent hybridity, morphological, and physiological similarities. The decision of the *compagnie* was that the causal explanation outstripped the empirical evidence. As a result, the Chat-pard was treated as a unique specimen whose categorization was unresolved. In the description of the animal, empirical descriptions citing similarities and differences of the parts of the Chat-pard with other species are retained but its full classification with regard to other known species remained an open question.[22]

Building on the work of Vesalius, Belon, Ruini, Perrault, and the *compagnie*, the most famous and arguably most influential discussions on comparative anatomy were the debates between Georges Cuvier and Étienne Geoffroy Saint-Hilaire at the *Muséum National d'Histoire Naturelle, Jardin des Plantes* in Paris.[23] Cuvier and Geoffroy held different views on what they believed to be the significant relationships among corresponding traits in different animals. The centrality of positional continuity formed the foundation of Geoffroy's theory of homology, the keystone of which he called the *principe des connexions*. Cuvier's conception of homology focused on whether interdependent structures share a common functional goal or purpose in different animals. Whereas Cuvier relied on kinding organisms into four *embranchements* (*Articulata, Mollusca, Radiata*, and *Vertebrata*), Geoffroy's reliance on an abstracted notion of a universal body plan meant that the kinds of organs in different animals depended ultimately on their relative topological position. Cuvier's body plans were discrete and fixed. There were no transformations and no intermediates between the four *embranchements*. For Geoffroy, the universal body plan was almost infinitely flexible, producing a continuum of intermediate transformations and modifications to this body plan.
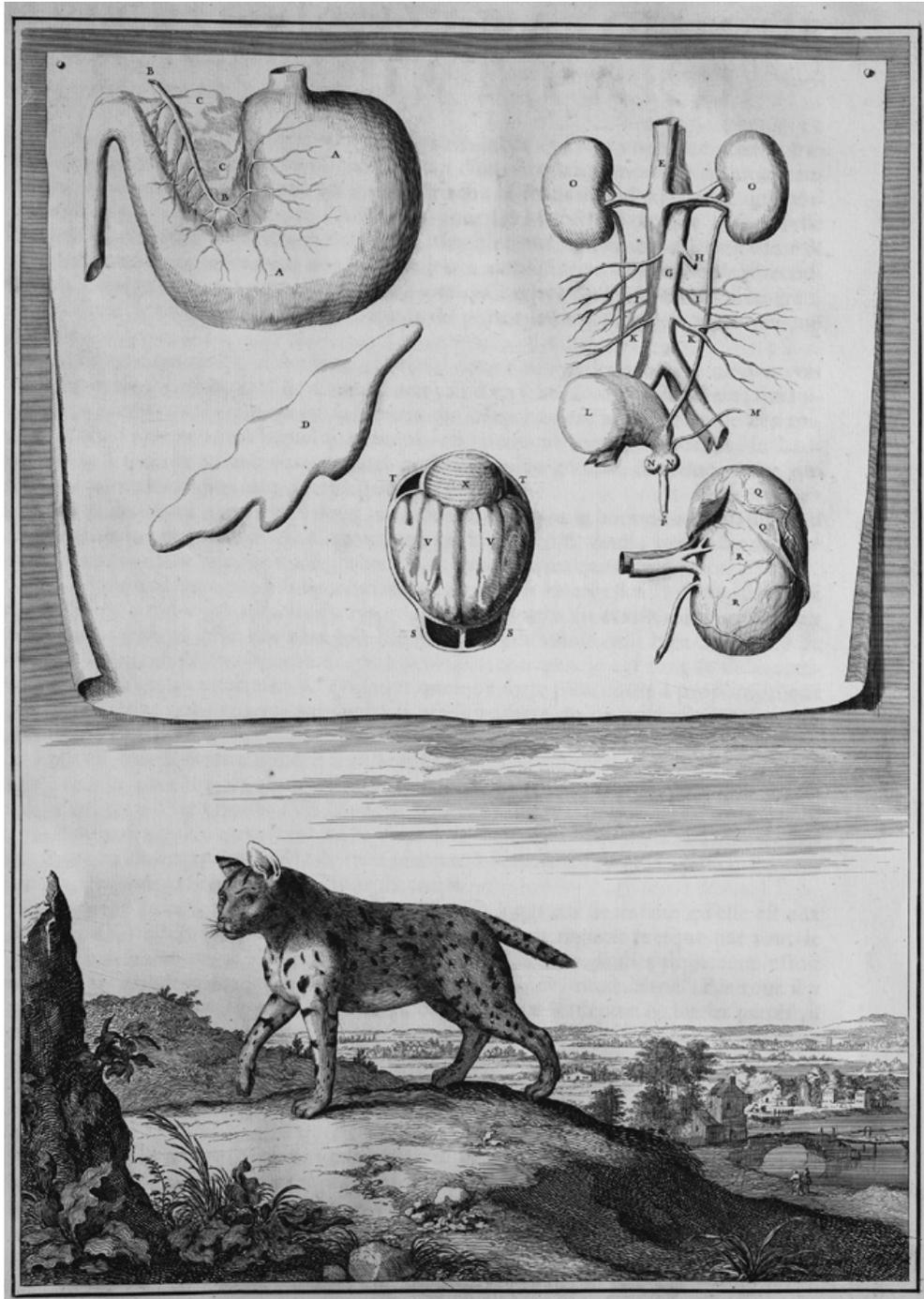
Figure 7.1 The Chat-pard. Perrault, C. (ed.) (1676) *Mémoires pour servir à l'histoire naturelle des animaux*. Paris: Imprimerie royale. Reproduced with kind permission from the Linda Hall Library of Science, Engineering, and Technology.

Following these debates, Richard Owen applied both Cuvierian and Geoffroyian kinding approaches and practices to his ordering and reordering, and in describing the contents of the Hunterian Museum of the Royal College of

Surgeons in Lincoln's Inn Fields.[24] Owen used the London museum (where he acted as assistant curator[25]) and its contents in explaining organic order and form. Hunter had initially organized the collection to reflect a natural classification of organs and parts according to their physiological functions. Hunter divided his preparations into different sections, each containing a series of specimens of various anatomical parts of different animals grouped together to display either a general morphology or particular physiological function (e.g. those containing organs of motion, digestion, circulation, respiration, or reproduction). Specimens were arranged within each section from most rudimentary to most complex to display the comparative features of organs in different stages and from different organisms.[26]

From 1826 to 1830 Owen catalogued 13,000 specimens within the collection. Of these, there was one he was particularly intrigued by: a preserved pearly nautilus without its shell (see Figure 7.2). Representations and descriptions of comparative kinds pepper Owen's *Memoir on the Pearly Nautilus*.[27] He uses the words "analogy" and "analogous" on nearly every other page. Unlike in his later work, "analogy" and "precisely analogous" are used consistently to mean continuity of structure.[28] Owen also speaks of the "affinity" and "parallelism" and "non-analogy".[29] His investigations on the nautilus led him to conclude, *pace* Geoffroy, that there was not a "simple and unbroken series, plan of composition, or a principle of unity".[30] Here Owen follows Cuvier. But later, he relies on a more Geoffroyian notion, stating that

> [i]t will be seen how considerable are the external differences between the Pearly Nautilus and the higher Cephalopods; nevertheless, its general plan of organization renders its claim to rank with them indisputable; and as its locomotive apparatus is confined to the head, the received denomination of the class remains undisturbed by its admission.[31]

Following his *Memoir on the Pearly Nautilus*, Owen published formal definitions of the two kinds of comparative concepts in use in order to distinguish them from one another and avoid confusion between them. He identifies the cause of the sameness of analogous organismal traits in terms of the common functions they serve: "Analogue: . . . A part or organ in one animal which has the same function as another part or organ in a different animal".[32] Owen's definition of homology contains no such causal explanation: "Homologue: . . . The same organ in different animals under every variety of form and function".[33] Owen's definition of homologues as "the same organs" is intended to capture their topological orientation and structural correspondence in different organisms. Homologous organs, such as the wing of a magpie and the foreleg of a hedgehog, were identified in terms of their corresponding topological location within the magpie and the hedgehog in relation to their other features (e.g. the position of the humerus and its attachment by ligaments to the ulnae and radii of each animal). In contrast, the biological concept of analogy was defined in terms of the functional sameness of two organs in different organisms. For instance, the wings of a blow fly are
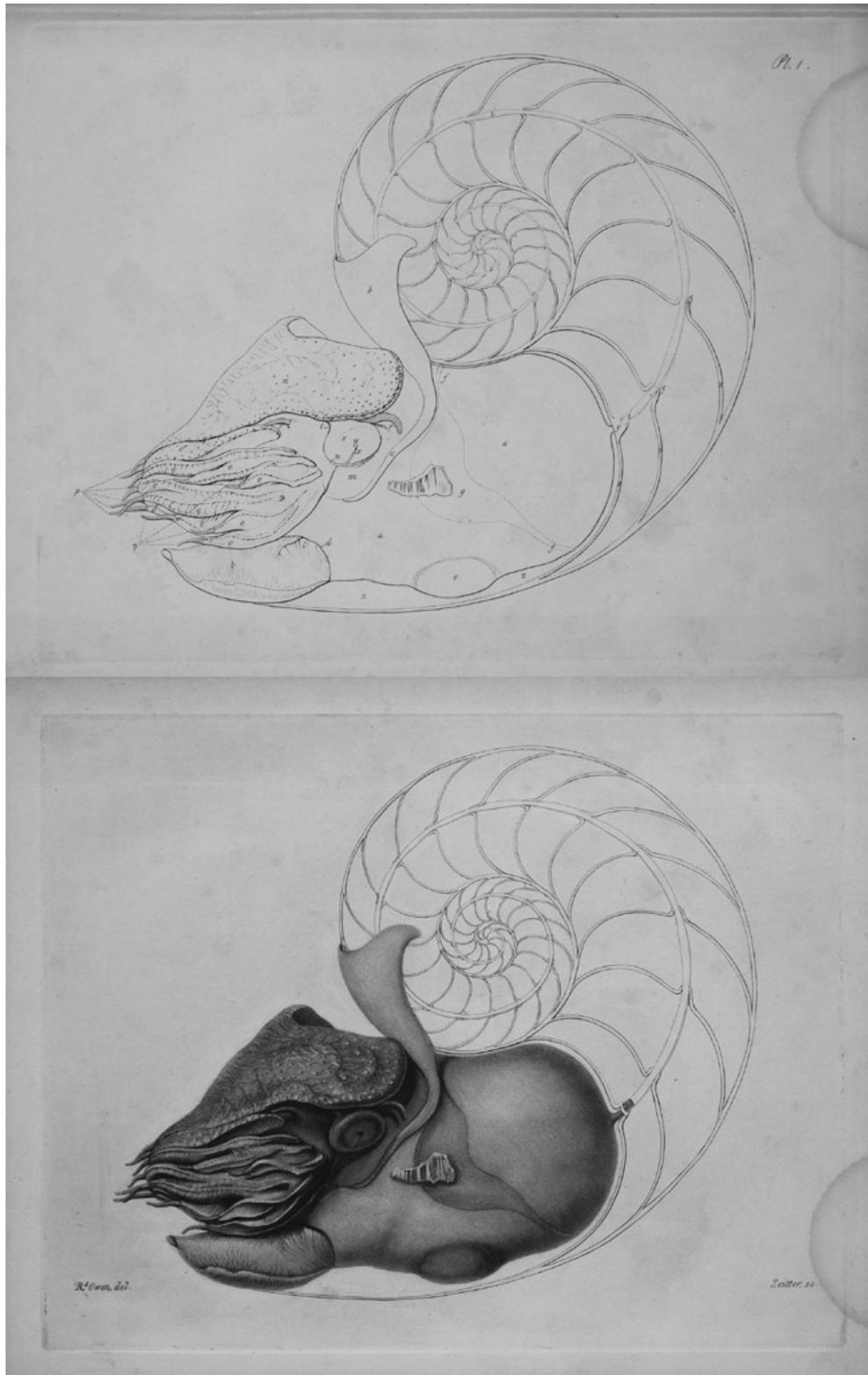
Figure 7.2 Pearly Nautilus. Owen, R. (1832) *Memoir on the Pearly Nautilus*. London: Richard Taylor, plate 1. Reproduced with kind permission from the Linda Hall Library of Science, Engineering, and Technology.

analogous to the wings of a hummingbird. These are identified as such because of their similar functional role in enabling the animal to manoeuvre itself around an aerial environment.

Owen's formal definitions of these comparative kind concepts can be seen in some sense as codification of the earlier kinding practices of comparative anatomists and physiologists as they drew from the kinding approaches, methods, and activities of Cuvier's theory of *embranchements*, Geoffroy's *principe des connexions*, Hunter's curating and ordering practices, and the anatomical illustrations and descriptions of Vesalius, Belon, Ruini, and Perrault. However, Owen did not believe that Cuvier's teleological point of view sufficiently explained the same topological correspondence of organs' positions across a variety of different animals:

> After the publication of the 'Memoir on the Pearly Nautilus', . . . the question of the condition or law of special homologies pressed itself upon me, more especially in connection with the task of arranging and cataloguing the osteological part of the Hunterian Museum. As my observations and comparisons accumulated, with *pari passu* tests of observed phenomena of osteogeny, they enforced a reconsideration of Cuvier's conclusions to which I had previously yielded assent.[34]

To rectify what he found (in the course of his kinding and homologizing activities) to be an omission, he augmented Cuvier's account with Geoffroy's notion of the universal body plan – what Owen called the "archetype". For Owen, "archetype" referred to a common plan or structural arrangement. Studying and cataloguing the bones of the Hunterian was catalyst for his re-examination and the later postulation of not just the archetype as an ideal plan of structure for all vertebrates, but for three different kinds of homologizing: *general, special*, and *serial homology. General homology* was the comparison of two or more organs as the same where their sameness to each other was caused by their relationship to the same organ in the archetype.[35] *Special homology* was defined as the comparison of the same organs within two different organisms. This relationship does not include the comparison to the same organ in the archetype, but consists in "the correspondence of a part or organ [as] determined by its relative position and connections, with a part or organ in different animals".[36] The third kind of homology Owen specified was s*erial homology*, which was the sameness between different parts or organs within the same organism (these parts are thought to possess the same basic structure). Serial homologues arose from the repetitive construction and development of an iterative part (e.g. the vertebrae or the leaves of a plant).

Although intended to identify the identity of two organs, the notion of sameness Owen employed was not meant to imply the material identity of two organs. After Owen formalized the definitions of homology and analogy, attempts to provide a causal explanation of the sameness of homologues became a widespread endeavour. Comparative embryological studies of the morphological features of many organisms' early anatomy lead both Ernst Haeckel[37] and Charles Darwin[38]

to reconceive Owen's concept of homology in terms of the historical continuity of traits over generations of ancestors and descendants. But whereas Haeckel's historical notion of homology was based on the theory of recapitulation, Darwin's was based on the theory of descent with modification.

Darwin was, however, keen to distance himself from the idealism of Owen and Geoffroy and their particular use of the archetype. Avoiding this idealist notion meant that in order to integrate Owen's concept of homology into his theory of evolution, Darwin needed to make some alterations to its meaning and reference.

Owen's special homology made no reference to the archetype. But it also provided no causal explanation of the topological correspondence of organs in different animals. It was merely a description of their same correspondence. The only kind of homology characterized by Owen that had a causal explanation within its definition was that of general homology – the sameness of two corresponding organs in different animals to each other was caused by their same relationship to the same organ in the archetype.

Although Darwin sought to avoid these commitments to idealism, he does not rely on Owen's notion of special homology (which does not refer to the archetype) for the basis of his own account of homology. It was instead Owen's general homology that Darwin used. Looking at the role homology plays in Darwin's theory reveals why. For Darwin, homology is not just a description but a causal explanation; organs correspond to each other *because* they both correspond to the same common cause – a shared ancestor. Darwin's concept makes use of the same form of explanation as Owen's general homology but interprets the archetype differently – in terms of the historic notion of a shared common ancestor rather than the idealist notion of the archetype:

> [S]uppose that the ancient progenitor, the archetype as it may be called, of all mammals, had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class.[39]

The historical notion of Darwin's "ancient progenitor" replaces Owen's idealist "archetype". According to Darwin's historical notion of homology, the traits of two different organisms are not homologous because of their shared function or form – which may differ greatly – and not because of their position or orientation. These traits are homologous because they have both been inherited (and modified) from the same trait in an ancestor common to them both.

2 Homologizing as monophyleticizing

Darwin's historical notion has been revised and reconceived in terms of an historical-analytic conception of homology since its inception, and later in terms of a particular kind of phylogenetic relationship.[40] These later conceptions include restrictions on both the meaning of homology and its application. In one of the most restrictive forms, it limits the meaning of *homology* as referring only to

traits that are inherited through a monophyletic lineage – the result of a continuous unbroken linear inheritance from one shared ancestor possessing the ancestral trait to all (and only) its descendants: "[H]omology . . . is defined not in terms of similarity, correspondence, or ancestry but in terms of monophyly".[41]

One of the most widely used approaches in comparative biology and classification relying on the monophyletic understanding of homology is *cladism*.[42] Cladism conceives of evolution as a series of speciation events over evolutionary time, represented as the branchings of a bifurcating tree. According to cladists a natural group is a branch of this phylogenetic tree called a *clade*. A clade is a group of individuals related by a continuous common phylogenetic lineage. Cladists, as well as other phylogenetic approaches to homology which conceive of homologizing as monophyleticizing, tend to take what I dub an "all-or-nothing" approach to homology – either the trait is inherited through a monophyletic lineage, and so is a homologue, or it is not. All traits that are not the result of monophyletic lineages are grouped together and referred to collectively as "false homologies" or "homoplasies", a sort of ersatz kind or comparative class made up of things excluded from the class of kinds which is of interest, that is, homologies. "Homoplasy [is defined] as the possession by two or more taxa of a character derived not from the nearest common ancestor but through convergence, parallelism, or reversal".[43]

Homoplasy can refer to the analogical similarity or sameness of corresponding traits due to inheritance from multiple ancestors through parallel or convergent evolution. But it also refers to structural correspondences of traits between organisms that have inherited the trait from more than one ancestor (i.e. are polyphyletic), as well as traits inherited through a broken lineage from a shared ancestor (e.g. recurrent traits that do not occur in every generation).

Understanding the study of homology as monophyleticizing commits proponents to a linear view of causation. A linear view of biological causation is a continuous causal chain that links genes to developmental schedules to phenotypes.

> The traditional idea of homology visualizes a linear series of changes whereby an ancestral trait has been transformed into a descendent one. . . . By this idea different homologues may appear differently modified on different phylogenetic branches, but each descendent homologous trait has at its core a single ancestral trait.[44]

Traits are the outcomes of the linear inheritance of instructional programs for building phenotypic traits. Homologues are the phenotypic outcomes of the same genes that code for these traits which are vertically inherited from one generation to the next in an unbroken ancestor-descendent lineage. Using *kind* as a verb, this sets up a clear dichotomy between concepts and activities that kind unbroken (monophyletic) lineages and those that kind broken lineages. Restricting homology to an all-or-nothing relationship means that different organisms either share a common ancestor and are therefore homologues, or they do not and are not homologues. Homology does not come in degrees, and partial homology is disallowed.

Opposition to the inclusion of partial homology as a kind of homology (rather than as a kind of homoplasy) has been sustained with few challengers.[45] Partial homology has been vociferously objected to as a threat to the Modern Synthesis: "Partial homology is incompatible with standard evolutionary views, according to which structures are either homologous or not".[46] The anti-partial homology consensus is broad. It includes not just neo-Darwinians but some proponents of developmental systems perspectives.[47] Even if partial homology is accepted with regard to the comparison of genes, it is widely believed that "[p]artial homology does not occur with morphological characters".[48] In the remaining sections I present empirical evidence that calls into question both the opposition to the inclusion of partial homology as a kind of homologizing and the claim that doing so would amount to a contravention of evolutionary theory.

3 Multi-modular traits and mosaic origins

Some complex traits may be the result of multiple (and discontinuous) lineages of inheritance or what could be called *mosaic* origins. What I mean by *mosaic* origins is that different sub-features of the same trait can evolve independently of others. They may change in diverse ways to the other sub-features, evolve at different rates, or utilize different resources in their construction. These discrete features may be weakly linked to other features of a particular part of an organism. Because they are weakly linked, one feature of the trait may dissociate from it and may then be used in association with a different trait. This re-configurability of modular features (as subunits of traits) constitutes a highly conserved core capacity of organisms.[49]

The possibility of dissociating these modular units and their subsequent rearrangement into novel combinations by the organism to serve other purposes further increases the organism's ability to vary its growth to meet new needs. Variation can then be understood to be the organization and reorganization of modular parts. Mosaic traits are organized into complex systems in their development, effectively "choreographed" by the organism "through [different] causal factors giving rise to morphological associations".[50] Different features of the same trait capable of independent variation may have different developmental pathways and may be responsive to different genetic and extra-genetic resources but remain coordinated by the organism. For instance, cranial and jaw bone development in rats varies at different rates of growth. In the early development of the rat pup these exist as separate and independent structures. However, in the adult rat they form a mosaic complex trait. These two previously separate bones are now used by the organism in a coordinated way so that the length of the jaw correlates with the growth of the skull. Linking the two structures provides the organism the means to accommodate the new feeding behaviour it learns after weaning. Instead of requiring morphological structures that allow it to suckle milk from its mother, the coordinated growth of its jaw and skull enables it to masticate solid food.[51]

Another example of the mosaic construction of organismal traits from diverse sources is the construction of plant leaves from different histogenic layers of the meristem:

> [Each histogenic] layer of the meristem makes a [different] contribution to the formation of leaves. In dicots, the L1 layer contributes only to the epidermis, whereas the L2 and L3 layers contribute to the internal tissues of the leaf. The contributions of individual layers are not strictly lineage dependent, however. A cell from one layer occasionally invades a neighbouring layer, where it contributes to lateral organs in a manner characteristic of the new layer rather than the original layer, demonstrating its lack of commitment.[52]

The initiation and determination of the organism's leaves are the product of diverse cellular, genetic, and environmental resources and the organization and reorganization of the organism's patterns of development. These include its hormonal changes, rates of cell division, changes in the plant's polarity, position in relation to other leaves, and environmental influences (e.g. sun exposure, submersion underwater). Understanding traits as mosaics requires treating them as the product of the heterogeneous construction of self-organizing and reorganizing organisms. Accordingly, traits are the product of contingent processes, the novel recombination of sub-features or units, and the organism-directed choreography of distributed genetic, behavioural, and environmental resources.

4 From linear to multidimensional thinking

Homology, as typically defined, is sameness that is due to common descent from a shared ancestor. Since Darwin, it is not this definition which was the subject of the debates but the meaning and use of the concept of homology, the criteria used for identifying instances of homology, and how homology is to be distinguished from analogy. Many of these debates seem to centre on whether the common descent from a shared ancestor is broken or unbroken.[53] Broken ancestry refers to the absence of the sameness in some generations, for example, recurrent traits[54] or latent phenotypes.[55] Unbroken ancestry requires the sameness to appear in every generation.[56] Standard monophyletic and all-or-nothing accounts of homology only regard inheritance from unbroken lineages as candidates for homologizing.

Recent research into developmental recombination, facilitated variation, phenotypic plasticity, niche construction, and cultural inheritance has forced hard questioning of the widespread assumption that evolution is, for the most part, unbroken and consistently linear.[57] These also pose new challenges to the standard account of homology when viewed through the lens of comparative practices:

> The possible role of phenotypic plasticity in the evolution of phenotypic novelties may offer an excellent system in which to apply both the experimental and the comparative methods to tackle the intimately related problems of homology and the origin of new traits.[58]

I contend that practices of kinding in comparative biology are reshaping the conception(s) of homology. A turn to a multidimensional approach to evolution has meant concepts defined within the linear approach require not just a pragmatic rejigging of methodological practices but a retuning[59] of homological conceptualization too. If alternative routes of inheritance (e.g. horizontal, vertical, and diagonal) and the inheritance of extra-genetic (e.g. behavioural, ecological, epigenetic, and microbiotic) resources are taken seriously, then morphological traits can be conserved and their continuity maintained across successive generations in spite of basic changes to developmental and genetic resources.[60] The same gross morphological traits may be present in two different organisms, but each may be the result of different developmental pathways and genetic resources. An organism may recombine some of its phenotypic features in a novel way or make use of new genetic or extra-genetic resources and variations within its environment. This means that novel phenotypes may be the result of the rearrangement and reorganization of old phenotypes and old resources linked together in new ways. Mary Jane West-Eberhard calls this *combinatorial evolution*:

> Combinatorial evolution raises the possibility that derived traits may often contain elements of more than one ancestral trait, and that what was formerly seen as a *de novo* modification actually involves the recombined expression of preexisting traits.[61]

Rather than following a single continuous unbroken linear route, evolution progresses intermodally[62] – involving different modes or routes of inheritance in conveying heritable resources. Recognition of the plasticity of developmental processes and phenotypes alters our natural biological kinding concepts by changing how we homologize. How we evaluate causes of evolutionary variation in the judgement of homology affects how we track historical continuity, what is included in the mechanisms of inheritance, which relationships between traits of organisms are attended to in comparison of potential homologues, and what lineage-based conception of species result from our homologizing.[63]

The standard, linear homology thinking kinds the traits of organisms in each generation in virtue of their unbroken lineage of inheritance. In contrast, what I'll dub "multidimensional homology thinking" takes the traits of organisms to not always be the result of unbroken lineages; they can also be the result of discontinuous and reticulate lineages of inheritance. Multidimensional homology thinking about the heterogeneous causes of traits takes traits to be the result of different developmental processes and reorganizing activities of both vertically and horizontally inherited genetic, epigenetic, developmental, behavioural, and ecological resources. That is, it takes the causes of homologous traits to be located not just in the continuity of genetic ancestral lineages, but in the continuity of epigenetic, environmental, and cultural lineages too (recognizing these do not necessarily coincide). Viewed in this way, the conservation of traits over generations might be due to the developmental pathways, the cellular connections, the use of other phenotypic capacities or resources, or certain generative systems of pattern formation which are conserved.

5 Retuning homology in response to homologizing practices

I began this chapter laying out some of the longstanding debates within comparative and evolutionary biology, the meaning and use of homology, and the origins of this kind of kinding. The concepts used within comparative biology and the activities of natural kinding have a history of being revised and retuned in response to comparative research practices. The remaining sections of this chapter aim to show that this is an ongoing process by providing evidence of the current retuning of homology to incorporate partial and mixed homologizing.

If we want to compare mosaic traits, our standard monophyletic view of homology seems ill-equipped. Homologizing depends on tracking descent from a common ancestor – a shared common cause. But if the traits in two different organisms we are seeking to compare are mosaic – each the result of fragmented discontinuous lineages or the result of multiple origins – how is this possible? Taking seriously multidimensional evolutionary lineages seems to call into question the assumption that homology is always an all-or-nothing kind of natural kind. But how can we reconceive the homology of traits if traits are the result of intermodal constructive processes of biological organization, developmental reorganization, and evolution? Can there be a homological relationship between two or more mosaic traits?

I contend that comparing the morphological traits or developmental pathways of two different organisms may reveal not one but multiple causal sources of continuity. The conservation of homologous traits, especially complex traits, may be the result of multiple distributed resources. Novel traits may be the result of reshuffling and new linkages between the already-present features of traits or the result of novel timing. These features may be used by each organism being compared in correspondingly different ways. The use of these resources in particular ways by both organisms ensures the continuity of the particular phenotypic traits being compared as homologues. If the resources or developmental pathways being compared are due to some shared common resources or pathways, then they are homologues. Understanding homologizing in this way just means that although homologizing by monophyleticizing does pick out all-or-nothing natural kinds, they are not the only kind of natural kind that homologizing can identify. A mixed (intermodal) approach to homologizing tracks the multiple ancestral origins of the different parts that make up a single derived trait.[64]

Recognizing the role of modular re-configurability in development and multidimensional evolution ultimately affects how we circumscribe the units of comparison and provides empirical evidence to challenge the conceptual opposition to partial homology – in particular, the suspicion that it contravenes our understanding of evolution. If our understanding of evolution has shifted from a linear to a multidimensional view, then this demands a shift in our homology thinking that relies on this same evidence. The upshot? Partial homology – far from being incompatible with evolutionary theory – may provide an invaluable addition to our suite of natural biological kind concepts.

6 Homologizing, holobionts, and typification

I initially described homologizing as a kind of natural kinding activity. But as the abbreviated history of comparative anatomy and physiology from Vesalius through Perrault's *compagnie*, Owen, Darwin, and revisions to the evolutionary synthesis have shown, homologizing as a set of activities exists within nested practices, empirical investigations, and protocols for the interpretation of these. These practices and protocols constrain the overarching meta-conceptual system that specifies how the category of homologues fits with the categories specified by other concepts (e.g. species, lineage, traits).

Multidimensional kind thinking extends what has been referred to as the holobiont/hologenome theory[65] of evolution – a theory developed from investigative observations of symbiotic relationships. In particular, the heritability of microbial and genomic resources from the symbiotic relationships of corals and their microbial communities. From these investigative practices, it was the holobiont – not the species, organism, population – that was reconsidered to be the unit of selection.[66] Multidimensional kind thinking expands the hologenome theory augmenting genomic and hologenomic inheritance with other kinds of inheritance (e.g. epigenetic, behavioural, and cultural). Multidimensional kind thinking is a reconceptualization of natural kindhood, but it is both based on practice and may affect the tracking of future homological practices.

For instance, if mosaic and partial homologizing is possible, what does this mean for the typification of type species that relies on the identification of the presence or absence of homologous traits in identifying a specimen as representative of a new species and designating it as a holotype of that species by practitioners?[67] The *holotype* designation allows researchers to identify a specimen in question as being of the same new species as the holotype species by anatomical and physiological comparative methods of the specimen in question in relation to the holotype as the specimen designated as the name bearing representative of the new species.[68] If homology tracks the same traits due to shared ancestry/phylogeny, then it tracks routes of inheritance. If what counts as a potential route of inheritance shifts (as the holobiont theory of evolution and the multidimensional approach to inheritance suggest), then this may affect the typification of specimens. This would occur if typification of holotypes tracked the inheritance of multiple organisms – as in the case of holobionts.

This is not as far-fetched as it may sound. The designation of holotypes in the most recent edition of the International Code of Zoological Nomenclature extends eligibility of name-bearing types from those eligible in earlier editions. "Holotype" may refer not just to a single organism but also to "a colony of animals that exists in nature as a single entity, derived by asexual or vegetative multiplication from a single individual (e.g. a colony of cnidarians, such as corals), or part of such a colony".[69]

7 Partial homology, revisited

In the foregoing, I have suggested that what has been traditionally thought to be independently evolved structures may actually be the result of a combination of various ancestral traits synthesized together to form an amalgam trait in the descendant. In contrast to the standard all-or-nothing kind of homology thinking, I have offered multidimensional homology thinking. Multidimensional homology thinking would mean that when we compare these amalgam traits, we would attend to their various origins of their composite evolved structures tracking the diverse routes of inheritance. How might an application of this kind of homology thinking look in practice? I provide one example here.[70]

Both humans and octopi have camera eyes. Their eyes possess certain striking sameness or similarities of general structure and function. The camera eyes of octopi and humans both have lenses and retinae with photoreceptors. However, the photoreceptors of humans face the back of the eye, while those of octopi face the front.[71] Some of the ontogenetic origins of octopi and human eyes also differ. Whereas octopus photoreceptor cells differentiate from the epidermis, those of humans differentiate from the nervous system.[72] Because of these and other differences, octopi and human eyes are widely believed to have evolved independently rather than being inherited from a common ancestor.[73] They are thought to be analogues not homologues.

Conceiving of octopi and human eyes as analogues and not homologues offers a limited description of these similarities. There is much evidence suggesting the homology of the structural organization of visual systems in octopi and humans.[74] Vision in humans and octopi is the result of light on organs which are photosensitive. The retinae of both organisms use rhodopsin for photoreception. Rhodopsin is a type of opsin. Over 1,000 different opsin proteins have been found in different animals.[75] What is striking is that in each and every animal, the opsin is connected to the same 11-cis-retinal chromophore.[76] The 1,000+ opsins are grouped into five types or families, all of which are thought to share a distant common ancestor possessing multiple opsin types.[77] Apart from the deep homology of the opsins across a wide range of organisms, similarities in the neurological structure of the visual system of octopi and humans have also been found. Exposure to light produces a chemical change in both octopus and human retinae. This change produces voltages that are transmitted to the brain through a network of neurological events.[78] In addition to the structural similarities in the visual systems of octopi and humans, eye development in both (as well as a range of other organisms including fruit flies) is initiated by the Pax-6 gene.[79]

These findings reveal that distinguishing the eyes of octopi and humans as either homologous or analogous means ignoring certain aspects of their development or structure. If we used the multidimensional homology view, we would conceive octopi and humans as utilizing the same resources in the construction of eyes in different arrangements. Their eyes can be understood as homologous because the resources used in their construction are present in all bilateral organisms, all of which share a common ancestor. Although octopi and human eyes

initially appear to be analogous, it is perhaps more accurate to understand them as partially homologous due to their use of similar tissues, genes, cells, proteins, and organization of their visual systems, and partially analogous due to the different ontogenetic pathways which lead to the construction of similar outcomes. This parsing of comparative elements and the assessment of partial homology/partial analogy is not possible using an all-or-nothing account of homology.

The purpose of this chapter was to make a novel suggestion about the retuning of the natural kind concept *homology* in response to activities and practices of homologizing. In doing so, it provided an alternative to the standard all-or-nothing homology thinking – that traits are either completely homologous or not homologous at all. Instead, multidimensional homology thinking and homologizing furnish a method of tracking the conservation of morphological traits, mechanisms, and developmental pathways inherited by intermodal processes. Controversially, this retuning may mean that the sharp distinction Owen formulated between homology and analogy, and the cladists' homology and homoplasy, may not be possible (or desirable). Comparing two or more organismal traits as partially homologous and partial analogous may afford a more accurate description of their combinatorial origins and the intermodal routes of inheritance by which they have been evolutionarily conserved over generations.

Notes

1 Historical research for this project was begun during a Linda Hall Library of Science, Engineering & Technology Residential Fellowship in 2013. In addition to thanking the library for their generous grant funding, I also thank the History of Science rare books librarians Bruce Bradley, Cindy Rodgers, and Nancy Officer; consultant and professor of History of Science Bill Ashworth; digital projects technician Jon Rollins; fellowship program mentor, Donna Swisher; Vice President for Public Programs Eric Ward; and President Lisa Browar for access to the collection, help in locating texts, and discussions in the history of science.

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3 Those that refer to practice directly include Hall, B. (1992) *Evolutionary Developmental Biology*. London: Chapman and Hall; Hall, B. (2003) 'Descent with Modification: The Unity Underlying Homology and Homoplasy as Seen through an Analysis of Development and Evolution', *Biological Reviews*, 78:3, pp. 409–433; Hall, B. (2012) 'Parallelism, Deep Homology, and Evo-Devo', *Evolution & Development*, 14:1, pp. 29–33; Love, A.C. (2007) 'Functional Homology and Homology of Function: Biological Concepts and Philosophical Consequences', *Biology and Philosophy*, 22:5, pp. 691–708; Brigandt, I. 'Typology Now: Homology and Developmental Constraints

Explain Evolvability'; Minelli, A. (1996) 'Segments, Body Regions and the Control of Development through Time', In: Ghiselin, M. and Pinna, G. (eds.) *New Perspectives on the History of Life*. San Francisco, CA: California Academy of Sciences, 55–61. Minelli, A. (2003) *The Development of Animal Form*. Cambridge: Cambridge University Press; Winther, R. G. (2009) 'Character Analysis in cladistics: abstraction, reification, and the Search for Objectivity', *Acta Biotheoretica*, 57:129–162; Ereshefsky, M. (2012) 'Homology Thinking', *Biology & Philosophy*, 27:3, pp. 381–400.

 4 See: Reeck, G. R., de Häen, C., Teller, D. C., Doolittle, R. F., Fitch, W. M., Dickerson, R. E., Chambon, P., McLachlan, A. D., Margoliash, E., Jukes, T. H., and Zuckerkandl, E. (1987) ''Homology' in Proteins and Nucleic Acids: A Terminological Muddle and a Way out of It', *Cell*, 50, p. 667, for a number of voiced concerns over the misuse and misapplication of the concept of homology in practice.

 5 The aim here is not to produce an account of homology as Wittgensteinian rule-following, although it shares some commonalities with his approach. See for instance, in Wittgenstein, L. (1973) *Philosophical Investigations*. (3rd edition) Translated by G.E.M. Anscombe. New York and London: Pearson, §202, "And hence also 'obeying a rule' is a practice. And to *think* one is obeying a rule is not to obey a rule. Hence it not possible to obey a rule 'privately': otherwise thinking one was obeying a rule would be the same thing as obeying it."

 6 See also: Kendig, C. (2015) 'What Is Proof of Concept Research and How Does It Generate Epistemic and Ethical Categories for Future Scientific Practice?' *Science and Engineering Ethics;* and the editor's introduction to this volume.

 7 The phrase "homology thinking" is used by Ereshefsky, M. (2012).

 8 Vesalius, A. (1543) *De Humani Corporis Fabrica*, Basel.

 9 The project of this chapter is to investigate the practices of homologizing and analogizing and their retuning. Working definitions of these as a starting point from which to depart are as follows: *Homologizing*: tracking of sameness in structure, sequence, or orientation in a variety of different organisms due to modification or deviation from a shared origin – my arm, a whale's pectoral fin, the wing of bat, the forelimb of horse. *Analogizing*: tracking of sameness of function due to similar purpose or goal or similar solutions to similar environments – the wings of a butterfly, humming bird, and a bat.

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17 Perrault, 'Advertissement', *Mémoires pour servir à l'histoire naturelle des animaux*.
18 Perrault, 'Advertissement', *Mémoires pour servir à l'histoire naturelle des animaux*.
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20 Perrault, C., *Mémoires pour servir à l'histoire naturelle des animaux*, pp. 49–52.
21 Perrault, C., *Mémoires pour servir à l'histoire naturelle des animaux*, pp. 49–52.
22 Perrault, C., *Mémoires pour servir à l'histoire naturelle des animaux*, pp. 49–52.
23 Geoffroy, Saint-Hilaire, E. and Cuvier, G. (1824–1847) *Histoire naturelle des mammifères*. Paris.
24 See in particular his mixed use of Cuvierian and Geoffroyian concepts in Owen (1832).
25 John Hunter founded the Hunterian museum in 1763.
26 Hunter, J., *The works of John Hunter F.R.S with notes*.
27 Owen, R. (1832) *Memoir on the Pearly Nautilus*. London: Richard Taylor.
28 This has led to confusion among some scholars as although Owen uses the word "analogy" here, the meaning is more similar to what Owen later (following his 1843 distinction) refers to using the word "homology".
29 Owen, R., *Memoir on the Pearly Nautilus*, p. 26.
30 Owen, R., *Memoir on the Pearly Nautilus*, p. 1.
31 Owen, R., *Memoir on the Pearly Nautilus*, p. 15.
32 Owen, R., *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals*, p. 374.
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37 Haeckel, E. (1866) G*enerelle Morphologie der Organismen*. Berlin: Reimer.
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41 Nelson, G., 'Homology and Systematics', p. 127.
42 See: Hennig, W. *Phylogenetic Systematics;* Nelson, G. and Platnick, N. (1981) *Systematics and Biogeography: Cladistics and vicariance*. New York: Columbia University Press; Patterson, C. (1982) 'Morphological Characters and Homology', In: Joysey, K.A. and Friday, A.E. (eds.) *Problems in Phylogeny Reconstruction*. London: Academic Press 21–74; and Lauder, G.V. (1994) 'Homology, Form, and Function', In: Hall, B. K. (ed.), *Homology*. San Diego: Academic Press, 151–196.
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44 West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*. Oxford: Oxford University Press, p. 485.

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61 West-Eberhard, M. J., *Developmental Plasticity and Evolution*, p.485.

62 The use of the adverb "intermodally" and the verb "intermodal" are my descriptions of the process, not West-Eberhard's. Their use is to qualify the kinds of evolutionarily relevant causal routes taken by inherited biological resources by analogy to intermodal logistics that utilize two or more modes of transportation to transfer cargo.

63 For further discussion of how this may alter conceptions of species see: Kendig, C., 'Towards a Multidimensional Metaconception of Species'.

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67 Thanks to Rasmus Grønfeldt Winther for urging me to explore the impact of homologizing practices on holotypes.

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Natural Kinds and Classification in Scientific Practice

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