

The Semaphorontic View of Homology

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ABSTRACT

The relation of homology is generally characterized as an identity relation, or alternatively as a correspondence relation, both of which are transitive. We use the example of the ontogenetic development and evolutionary origin of the gnathostome jaw to discuss identity and transitivity of the homology relation under the transformationist and emergentist paradigms respectively. Token identity and consequent transitivity of homology relations are shown to be requirements that are too strong to allow the origin of genuine evolutionary novelties. We consequently introduce the concept of compositional identity that is grounded in relations prevailing between parts (organs and organ systems) of a whole (organism). We recognize an ontogenetic identity of parts within a whole throughout the sequence of successive developmental stages of those parts: this is an intra-organismal character identity maintained throughout developmental trajectory. Correspondingly, we recognize a phylogenetic identity of homologous parts within two or more organisms of different species: this is an inter-species character identity maintained throughout evolutionary trajectory. These different dimensions of character identity—ontogenetic (through development) and phylogenetic (via shared evolutionary history)—break the transitivity of homology relations. Under the transformationist paradigm, the relation of homology reigns over the entire character (–state) transformation series, and thus encompasses the plesiomorphic as well as the apomorphic condition of form. In contrast, genuine evolutionary novelties originate not through transformation of ancestral characters (–states), but instead through deviating developmental trajectories that result in alternate characters. Under the emergentist paradigm, homology is thus synonymous with synapomorphy. *J. Exp. Zool. (Mol. Dev. Evol.)* 324B:578–587, 2015. © 2015 The Authors. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* published by Wiley Periodicals, Inc.

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Primed by his friend Charles Darwin, T. H. Huxley delivered his famous Croonian Lecture on the vertebrate skull in front of the Royal Society of London on June 17, 1858. In the course of his lecture, he made it clear (Huxley, 1858, p. 382):

“That there is nothing really aberrant in nature; that the most widely different organisms are connected by a hidden bond; that an apparently new and isolated structure will prove, when its characters are thoroughly sifted, to be only a modification of something which existed before. . .”

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This quote from Huxley aptly captures the transformationist approach to comparative morphology and phylogeny reconstruction. To identify anatomical structures (organs, organ systems), and to arrange those in a graded series of abstract form relations was standard fare in pre-Darwinian comparative (idealistic) morphology (Gegenbaur, 1859). With the advent of evolutionary thought, such graded series of form relations came to be read as historical (evolutionary) transformation series: “The survey of such a series thus reveals a *process*, which involves the transformation of one and the same organ in different organisms” (Gegenbaur, 1870, p. 6; emphasis added; see also Rieppel, 2011). A graded transformation series that links the ancestral with the descendant condition of form through a series of intermediate stages is governed by the relation of homology, i.e., it comprises organs or organ systems that are *homologous*.

The original definition of homology goes back to Richard Owen (1843, p. 379) and reads: “(Gr[reek]. *homos*; *logos*, speech) The same organ in different animals under every variety of form and function.” In the context of evolutionary theory, “the same but different” implied the historical transformation of organs or organ systems of common evolutionary origin. What appears to be new, or at least different, in the descendant is nothing but the evolutionary transformation of a homologous structure already present in the ancestor in the primitive condition of form. In contemporary phylogenetics, morphological characters or character states are organized in such transformation series (i.e., the “transformational characters” of Sereno, 2007, p. 573), which then need to be polarized to distinguish the primitive (plesiomorphic) from the derived (apomorphic) condition.

Since the ancestral and descendant condition of form of homologous organs (organ systems) may drastically differ from one another, the study of development (ontogeny) has classically been used in the attempt to trace relations of homology. Influenced by his friend Ernst Haeckel, who had famously drawn a parallel between ontogeny and phylogeny, Gegenbaur’s (1870, p. 80) definition of homology accordingly reads: “the relation between two organs that are of common origin, which therefore have developed from the same embryonic rudiment (*Anlage*).” For example: the anteriormost gill arch in agnathans and jaws in gnathostomes trace back to the same embryonic rudiments. Their homology is thus established, minimally as a “latent homology” (Hall, 2003, p. 420f). Despite the striking dissimilarity in terms of form and function, the homologous ancestral structure that transforms into the descendant structure is still identified, as is required by the transformationist paradigm. Under that paradigm, nothing genuinely new is generated through evolution; everything that exists is a transformation of something that existed before. For this failure to address and explain the emergence of genuine evolutionary novelties, the Modern Synthesis of evolutionary theory has drawn criticism from evolutionary developmental biologists and philosophers of

biology alike (e.g., Love, 2006, 2008; Wagner, 2007; Brigandt and Love, 2010, 2012; Wagner and Lynch, 2010; Hall and Kerney, 2011).

The emergentist paradigm is perhaps best captured by the frequently cited definition of an ‘evolutionary novelty’ offered by Müller and Wagner (‘91, p. 243): “A morphological novelty is a structure that is neither homologous to any structure in the ancestral species nor homonomous to any other structure of the same organism.” In Wagner and Lynch (2010, p. R49), the definition of an “evolutionary novelty” reads: “a novel body part that is neither homologous to any body part in the ancestral lineage nor serially homologous to any other body part of the same organism.” In the context of phylogenetics, Sereno (2007, p. 574) among others called such evolutionary novelties *neomorphic* characters “that do not have comparable, recognizable transformational states.” He did recognize, however, that his distinction of transformational and neomorphic characters would “doubtless raise objections from those who contend that *all* characters must come from, or vanish into, something” (Sereno, 2007, p. 575). Similarly, and in the context of evo-devo research, Brigandt and Love (2012, p. 418) emphasized that “[e]mpirically, even for those structures that appear to be qualitatively novel, there are always precursors or homologous features at lower levels, such as tissues, cells, or gene expression patterns.” This observation is certainly the reason why, for Hall and Kerney (2012, p. 435), “[t]he identification of novelty is often a matter of first setting an investigative framework within the biological hierarchy.” In a similar sense, Love (2006, p. 327) requires the identification of “targets of explanation” when it comes to the explanation of the origin of evolutionary novelties. It is the antecedent identification of the vertebrate jaw as an evolutionary novelty that defines the “problem domain” and the consequent “problem agenda” (Love, 2008, p. 876, 879) for research into its origins.

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There exists a distinct tension between the transformationist and the emergentist paradigm: the recognition of genuine (de novo: Sereno, 2007, p. 575; see also Wagner, 2014, p. 132) evolutionary novelties with no homologous correspondent in the ancestral lineage as a problem agenda of evolutionary developmental research, coupled with the recognition that such evolutionary novelties develop from embryonic rudiments (*Anlagen*) shared with the ancestral lineage (see also Wagner, 2014, p. 126). We propose to articulate and analyze this tension from a perspective which one of us called “*the semaphorontic view of homology*” (Assis, in press). In the following, we will first introduce Willi Hennig’s concept of the semaphoront and discuss its relation to homology. We use the gnathostome jaw as an example to examine the understanding of evolutionary novelties under the semaphorontic view of homology. Subsequently, we address the

issues of the identity of homologues and the consequent transitivity of homology relations that have traditionally been invoked by biologists and philosophers alike. Our main finding is that ontogenetic identity relations maintained throughout developmental trajectories are not transitive with phylogenetic identity relations maintained throughout evolutionary trajectories. However, our discussion also shows how and why the understanding and judgment as to whether a structure is or is not an evolutionary innovation depends on the adoption of one of two alternative viewpoints on homology: that of the emergentist or the transformationist paradigm. In other words, assessments of evolutionary novelty are pre-conditioned by theoretical commitments rather than decided empirically on a case-by-case basis.

THE SEMAPHORONT

The concept of the semaphoront was first introduced by Hennig ('47, p. 276) as “the character-bearer [*Merkmalsträger*]. . . the individual organisms within a short time-span of their life, during which they do not themselves change and hence also do not change their relations to others.” The technical term *semaphoront* Hennig introduced in his *Grundzüge* of 1950, defined as “an individual during a very small temporal duration (not “a point in time”) of its life” (Hennig, '50, p. 9). Another, refined definition appeared in the English version of his textbook, published in 1966: “[. . .] we should not regard the organism or the individual as the ultimate element of the biological system. Rather it should be the organism or the individual at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its life” (Hennig, '66, p. 6) These definitions reveal that for Hennig, the concept of the semaphoront had a metaphysical as well as an epistemological dimension.

The metaphysical dimension is revealed by Hennig's commitment to a process philosophy. Hennig ('50, p. 5) followed the philosophers Nicolai Hartmann and Ludwig von Bertalanffy when he interpreted an organism as a dynamic, processual system, i.e., a “system of causal interactions” (Hennig, '50, p. 5, 23). He used the semaphoront to slice through this processual system to obtain a time-slice of theoretically minimal, but heuristically suitable thickness, i.e., a character-bearer that represents the organism at different stages of its life cycle (Rieppel, 2007).

The epistemological dimension is rooted in Hennig's critique of the practice of describing separate “species” for larvae and imagoes of holometabolous insects. The leading German limnologist of the time, August Thienemann, had argued that separate species descriptions, and corresponding identification keys, should be developed for larvae, pupae and imagoes of aquatic insects, so that non-specialists such as water hygienists would be enabled to readily identify any potential water pests (e.g., Thienemann and Krüger, '37; Thienemann was the first to distinguish oligotrophic [healthy] from eutrophic [undesirable] waters: Blackbourne, 2006, p. 232). Hennig ('43) retorted that the

natural system of greatest theoretical relevance to comparative biology is the phylogenetic system, one that represents the successive species lineage splitting events through time. But since there could be only one phylogenetic process, there could also be only one phylogenetic system, a system that had to provide a unifying perspective on biodiversity. The semaphoront thus serves as a tool to capture organisms at different stages of their life cycle, providing character-bearers suitable for phylogeny reconstruction.

The fact that Hennig ('50, p. 5) conceptualized the organism as a “system of causal interactions” has important theoretical, and metaphysical, consequences. The theoretical consequence is that although the semaphoront slices through the organism that is a processual system, the series of semaphoronts representing that organism at different stages of its life cycle is causally integrated and interconnected. This in turn has the metaphysical consequence, which Hennig ('50, p. 114, '66, p. 81) drew from the work of the philosopher Theodor Ziehen (1934) that the (self-) identity of the organism is preserved through time and change (metamorphosis).

Following Zimmerman's ('37, '43) concept of “character phylogeny” (see also Donoghue and Kadereit, '92), Hennig ordered the characters gleaned from semaphoronts of the organisms under comparison into transformation series: “[d]ifferent characters that are to be regarded as transformation stages of the same original character are generally called homologous. [. . .] Naturally, in determining homologies we are limited to erecting hypotheses – such as that particular characters a, a', a” belong to a phylogenetic transformation series” (Hennig '66, p. 93–94). The phylogenetic continuity of causal integration and interdependence underlying phylogenetic transformation series individuates homologues just as the ontogenetic causal integration and interdependence of a series of semaphoronts individuates the organism that they represent.

Some authors, including Hennig ('66), Platnick ('79) and Patterson ('82) did not see a difference between character and character states, in contrast to others who did, such as Wiley ('81). In a recent analysis of the relation of homology in terms of evolutionary transformation series, Wagner (2014, p. 54) emphasizes the distinction of *character* and *character states* in relation to the issue of character identity. The transformation series as a whole represents the character; the various conditions of form comprised by the transformation series are the different (transformational) states of that character. An evolutionary transformation series thus represents a homologue (homologous character); the states comprised by a transformation series represent this homologue in two or more organisms under a different condition of form, and possibly also of different function (homologous character states): “the same but different” again. It is therefore not similarity, but the continuity of causal integration and interdependence underlying a transformation series that individuates the homologue. A homologue, on

Wagner's (2014) account, is subject not to a similarity relation, but to the identity relation: "the identity of a morphological character is not tied to similarity; rather, it is tied to the historical continuity of descent" (Wagner, 2014, p. 53). On that account, homologues form evolutionary lineages. Wagner (2014) invokes "character identity" as individuating homologues, the latter maintained through transformational stages by the genealogical continuity of the underlying genetic "character identity networks" (ChIN: Wagner, 2014, p. 97; see also Wagner, 2007).

But just as the concept of the semaphoront can be applied to an individual organism and its successive stages in a complex life cycle, so can the concept of the semaphoront also be applied to parts of an individual organism (organs and organ systems) and their successive developmental stages. And in that context again, it is the causal integration of the developmental process that maintains the (self- or character) identity of organs and organ systems through developmental change. It is the application of the concept of the semaphoront to parts of an organism that provides the platform for the development of a semaphorontic view of homology, which one of us—paraphrasing Hennig's definition of the semaphoront ('66, p. 6; see above)—formulated as follows (Assis, in press):

"[. . .] we should not regard the [*part*] or the [*organ*] as the ultimate element of [*homology*]. Rather it should be the [*part*] or the [*organ*] at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its [*ontogeny*]."

Parts of organisms (organs or organ systems) at different developmental stages can thus be understood as different semaphoronts of those parts. Homology relations may then obtain between semaphorontic parts of two or more organisms throughout different developmental stages of those parts in these same organisms. On the semaphorontic view of homology, two different dimensions of identity relations obtain for parts (organs and organ systems) and their corresponding homologues. The first is the relation that ties together different developmental stages of a homologue within an organism, e.g., from precursor *anlagen* through to the fully differentiated organ, an identity that is anchored in the continuous causal integration of the developmental (ontogenetic) process. The second dimension is the relation that ties together homologues at successive developmental states as character states of a character transformation series across species, an identity that is anchored in the continuous causal integration of the evolutionary (phylogenetic) process. The first dimension is an intra-organismal character identity maintained throughout developmental change; the second dimension is an inter-species character (-state) identity maintained throughout evolutionary change.

In line with this, two questions might be raised: (1) why is the semaphorontic definition productive for evolutionary biology?

and (2) is it substantially different than the character-state/character equation? With respect to the first question, the semaphorontic view of homology reinforces the importance of ontogenetic evidence in support of homology hypotheses and evolutionary relationships (Assis, in press). The view also develops novel resources for solving the transitivity problem for identity-based theories of homology, as we demonstrate in the penultimate section of this paper. With respect to the second question, the semaphorontic view is not in disagreement with Wagner's distinction between character states and characters. Rather, it identifies another crucial distinction residing within Wagner's and others' views on homology: a distinction between the ontogenetic and phylogenetic states of a homologous character. Again, recognizing this distinction provides the resources for solving the problem of transitivity that arises with a strong conception of homology built on identity relations (Wiley, 2008, following Ghiselin, 2005), with important consequences for the understanding of evolutionary novelties, consequences we will discuss immediately after the presentation of an illustrative empirical case.

AN EMPIRICAL EXAMPLE

We have chosen the origin of the gnathostome jaw as an empirical example to illustrate the application of the semaphorontic view to homology assessment, and its theoretical consequences. The example is based on the work of Shigeru Kuratani and his collaborators (e.g., Shigetani et al., 2002, 2005, ; Kuratani, 2004, 2005, 2012; Kuratani et al., 2012), who compared the pharyngula and post-pharyngula larval (ammocoete) stages of the lamprey *Lethenteron japonicum* with gnathostome development (e.g., Kuratani et al., 2004). The ammocoete oral apparatus comprises the upper and lower lips, and a pair of muscular flaps, the velum. This oral apparatus is compared to that of gnathostomes, in particular the primary upper (palatoquadrate) and lower (Meckel's cartilage) jaws, their associated musculature and innervation patterns. At the pharyngula stage, both lamprey and gnathostome show the same fundamental "tripartite configuration of the rostral-most [neural] crest-derived ectomesenchyme" (Kuratani et al., 2001), indicating homology amongst the parts. The anteriormost compartment of the rostral ectomesenchyme lies in a preocular position. Behind the optic vesicle lies the trigeminal ectomesenchyme, which is subdivided into a postocular (pre-mandibular) and a mandibular compartment, in accordance with the partitioning of the trigeminal nerve into an ophthalmic and a maxillary-mandibular division. The mandibular compartment of the ectomesenchyme corresponds to the mandibular arch domain, as it is from this compartment of the ectomesenchyme that the gnathostome jaw (palatoquadrate and Meckel's cartilage) develops.

Rathke's classic account of the development of the gnathostome jaw distinguished two anterior visceral arches (the mandibular and hyoid arch) from the succeeding branchial

arches. The serial patterning of the visceral/branchial arches is controlled by a hierarchically structured “*Hox* code” which fails to be expressed in the mandibular arch domain. The latter is thus specified by its “*Hox*-default” position. The dorsoventral patterning of the visceral/branchial arches is specified by *Dlx*-family genes. The ectomesenchyme located in the premandibular (postoptic) domain of gnathostomes is *Dlx*-negative, and develops into the trabeculae cranii that floor the prechordal neurocranium on either side of the head (Kuratani et al., 2012; Shigetani et al., 2005; and references therein).

While the premandibular (postoptic) and mandibular arch domains respectively of the trigeminal ectomesenchyme can be considered to be homologous morphological structures (homologous tissues: Compagnucci et al., 2013, p. 444) at the pharyngula stage of the lamprey and gnathostomes, the entire trigeminal ectomesenchyme is *Dlx*-positive in the lamprey, whereas the premandibular (postoptic) compartment is *Dlx*-negative in gnathostomes. Subsequent development of the trigeminal ectomesenchyme is divergent in the lamprey and gnathostomes. The premandibular (postoptic) ectomesenchyme, which in gnathostomes gives rise to the trabeculae cranii, in the ammocoete larva gives rise to mucocartilaginous structures in the upper lip (see de Beer '37, p. 44). The ectomesenchyme of the mandibular arch domain, which in gnathostomes gives rise to the jaws, in the ammocoete larva gives rise to mucocartilaginous structures in the lower lip and velum. And unlike the gnathostome trabeculae, which derive from prechordal ectomesenchyme, the trabeculae of the lamprey develop from anterior parachordal mesoderm (see Kuratani, 2004, fig. 6; Kuratani et al., 2012).

On a semaphorontic account, and given a causal integration of developmental processes, there obtains ontogenetic character identity (a form of semaphorontic or intra-organismal identity maintained throughout developmental trajectories) of the premandibular (postoptic) ectomesenchyme and the upper lip skeleton in the lamprey, as well as ontogenetic character identity of the premandibular (postoptic) ectomesenchyme and the trabeculae cranii in gnathostomes. Similarly for the mandibular arch domain ectomesenchyme: it is ontogenetically identical with the skeletal structures of the lower lip and velum in the ammocoete larva, and with the jaws in gnathostomes respectively. There also obtains, at the pharyngula stage, phylogenetic character identity (a form of ancestral or inter-species identity maintained throughout evolutionary trajectories) of the premandibular (postoptic) and mandibular arch domains respectively of the trigeminal ectomesenchyme in the lamprey and gnathostomes. At the genetic level, however, the premandibular (postoptic) domain of the ectomesenchyme is *Dlx*-positive in the lamprey, *Dlx*-negative in gnathostomes. Problems of homology, i.e., of phylogenetic identity at the morphological level come into focus in post-pharyngula stages. What does it mean to say that the mucocartilaginous structures in the upper lip of the

ammocoete larva are homologous (i.e., phylogenetically identical) with the trabeculae cranii in gnathostomes, as would have to be the case if derivation from common embryonic rudiments (*Anlagen*) is the key to homology?

On the latter criterion, the jaws of gnathostomes would have to be homologous in the phylogenetic dimension with mucocartilaginous structures in the lower lip and velum of the ammocoete larva. Kuratani and his collaborators reject such morphological homologies. Given heterotopic effects in *Dlx*-family gene regulation, they speak of a “loss” (Kuratani 2004: 339, 342), an “obliteration” (Kuratani, 2005, p. 439), or a “disruption” (Shigetani et al., 2005, p. 335) of homology relations. The consequence is that the gnathostome jaw qualifies as an evolutionary novelty *sensu* Müller and Wagner ('91): homologous throughout gnathostomes, it has no homologue in the ancestral lineage (Kuratani, 2004, p. 342). A transformationist approach to the study of the origin of the gnathostome jaw is further rejected on the grounds that there obtains no ‘primitive’ condition of the anteriormost branchial arch in any adult agnathan, extant or fossil, from which the gnathostome jaw could seamlessly be derived. The reason is that the branchial arch skeleton in all adult agnathans is always specialized, i.e., adapted to specific modes of life (Kuratani, 2005, p. 489).

IDENTITY AND TRANSITIVITY OF THE HOMOLOGY RELATION

The conclusion to a “loss,” “obliteration,” or “disruption” of relations of homology through heterotopic effects in development is predicated on the way homologues are conceptualized. Owen’s definition (see above) renders homologues “the same but different” in two or more organisms. On that account, mucocartilaginous structures in the lower lip and velum of the ammocoete larva and the jaws of gnathostomes could well qualify as ‘the same but different.’ Elsewhere, Owen characterized homologues as namesakes: “A ‘homologue’ is a part or organ in one organism so answering to that in another as to require the same name” (Owen, 1866: xii). The question then arises as to whether the names of homologues are proper names or general names (natural kind terms)? Alternative conceptualizations of homologues as individuals or natural kinds have been discussed by Brigandt (2007, 2009) and Assis and Brigandt (2009).

If the names of homologues are proper names, then homologues are individuals (for a characterization of homologues as individuals see Brigandt, 2009, p. 87). According to Wagner (2014, p. 70), “a homologue [...] behaves like an entity that forms lineages of descent”; homologues consequently are “individuals”, not “sets or classes” (see also Ghiselin, 2005). The relation of homology (in which homologues take part) is then governed by the identity relation; for instance, Wagner (2007, p. 473; see also Wagner, 2014) characterized homology as “character identity.” Identity in the strong sense is transitive (Wiley, 2008): if A is identical to B, and B is identical to C, then A

is also identical to C. Brigandt (2002, p. 391) on good grounds rejected the equation of the sameness of homologues (as in ‘the same but different’) with numerical or token-identity, but instead characterized the relation of homology as one of correspondence.

But correspondence, just as identity, has been claimed to be transitive as well (Ghiselin, 2005, p. 96). Either way, the transitivity of the relation of homology *qua* character identity has important consequences, if the relation of homology is also symmetrical—as it indeed is (if A is homologous with B, then B is also homologous with A). Call the mandibular arch domain of the ectomesenchyme in the lamprey A_1 , the mucocartilaginous structures in the ammocoete lower lip and velum A_2 : on the semaphorontic view, A_1 is (ontogenetically, through development) identical with A_2 . Call the mandibular arch domain of the ectomesenchyme in gnathostomes B_1 , the gnathostome jaw B_2 : on the semaphorontic view, B_1 is (ontogenetically, through development) identical with B_2 . On morphological grounds, A_1 is (phylogenetically, through shared evolutionary history) homologous with B_1 . If the homology relation is an identity relation that is transitive and symmetrical, A_2 must also be homologous with B_2 . Ghiselin (2005, p. 98) attributes any “dissatisfaction” with this counterintuitive conclusion to “a propensity to conceptualize taxa as classes,” rather than individuals of which homologues are parts. In line with this, Wagner (2014, p. 91) highlights the important caveat that “character identity arises at a certain stage of development and not earlier.” This could imply that the character identity of the gnathostome jaw (B_2) is not yet established by the mandibular domain ectomesenchyme at the pharyngula stage, rendering its non-homology—at both ontogenetic and phylogenetic levels—with skeletal structures in the lamprey lower lip and velum (A_2) unproblematic. Conversely, if the identity of the gnathostome jaw had been established at the pharyngula stage, its non-homology with the lamprey lower lip and velum would require the “disruption” of character identity during development, as was concluded by Shigetani et al. (2005, p. 335).

COMPOSITIONAL IDENTITY AS AN ALTERNATIVE TO TRANSITIVITY

An alternative is to ask (see also Brigandt, 2002) whether numerical (or token) identity is simply too strong to be applied to what Winther (2006, p. 471) has identified as *compositional* biology, one “that is based on the notion of parts and wholes, as well as their respective functions and capacities,” such as the capacity of the mandibular arch domain ectomesenchyme to develop into jaws in gnathostomes (see also Winther, 2011). Correspondingly, we introduce the notion of *compositional* identity: identity that is grounded in *relations* prevailing between parts of a whole, rather than in numerical self-identity. For compositional biology—so concerned with parts as well as wholes—and especially for evolutionary studies in compositional biology, it is important to understand part-part relations as well as the more traditional part-whole relations.

For example, in the semaphorontic view of homology, it is not just the organism at different developmental stages between which one can pick out identity relations (these would be Hennig’s temporal-part-to-whole relations); it is also the different developmental stages of parts (organs or organ systems) of an organism between which one can pick out identity relations (these would be temporal-part-to-part relations). Likewise, as Wagner’s distinction between homologous characters and character states shows, studies in comparative morphology are not limited to comparisons among whole organisms of different species at different points in the evolutionary trajectory. It is also possible to pick out just a part of these organisms of different species—a homologous character—and then to compare instances of this part—a character state—at different points in the evolutionary trajectory. To put the point in other words, to do this kind of comparison is to treat a part of an organism (a character state) like its own Hennigean temporal-part of an evolutionary-rather-than-developmental whole (a homologous character). Just as identity holds between Hennigean temporal-parts and the whole organism throughout development, so too does identity hold between character states and the homologous character throughout evolution.

Adopting the compositional view entails that, with ontogenetic identity *in general*, the relevant wholes are whole organisms, while the relevant parts are the time-slices or temporal parts of those wholes—i.e., Hennig’s original semaphoronts. The ontogenetic identity *of homologous parts* of an organism is thus an identity relation that holds not between the whole organism and its temporal parts, but rather that homologous part and its temporal part-parts—i.e., the various states of just a fly’s wing throughout the development of the fly. With phylogenetic identity *in general*, the relevant wholes are higher taxa (like clades), while the relevant parts are the smaller taxa contained within the higher taxa (like species). The phylogenetic identity *of homologous parts* is thus an identity relation that holds not between whole clades and the species they contain, but rather it is a relation that holds between one part (in Wagner’s terms: character) possessed (or not) by organisms throughout the clade and that part’s particular instantiations (again, in Wagner’s terms: character states) in different species within the relevant clade. So, a particular human arm has a part-to-part *ontogenetic identity* from embryonic stages to adulthood and through senescence; human arms also share a certain part-to-part *phylogenetic identity* with seal flippers, bat wings and other tetrapod forelimbs. Ontogenetic identity comes from shared developmental history whereas phylogenetic identity comes from shared evolutionary history; what the semaphorontic view helps to illustrate is that both shared and divergent developmental tracks are nested within evolutionary history, which is how we end up with confusing situations like the one detailed in this paper, where A_1 and B_1 share a certain, limited phylogenetic identity but then diverge developmentally, producing non-

homologous ontogenetic states (A_2 and B_2) from their homologous precursors.

It is crucial to realize that the identity of one temporal part of an organism with the whole organism—or the identity of a character state with the homologous character—does not imply the identity of that part with others within the whole. To illustrate this point consider identical twins. These are organisms which share a genetic identity; and they each have a personal identity that persists throughout organismal changes in development. Yet identical twins do not share one personal identity. The fact that they share a genetic identity does not mean that they are semaphoronts of the same organism, sharing personal identity as well. Hence, we need a conception of identity that allows us to make clear that we are picking out identity relations among parts across wholes, rather than that conception of numerical identity which holds between all of a thing and only itself.

Our notion of compositional identity ought not to be confused with the Composition as Identity thesis (as formulated in Baxter, '88a, '88b; Lewis '91) from analytic philosophy. Whereas the Composition as Identity thesis deals with part-whole relations (defining numerical identity of a whole in terms of composition by its parts), our notion of compositional identity deals with part-part relations, i.e., defining identity relations between parts of an organism through different developmental stages, or parts of different organisms throughout different evolutionary trajectories. In the notation defined above, there prevails an ontogenetic form of compositional identity between A_1 and A_2 , since these represent two semaphoronts (*qua* parts of an organism) of the same developmental (ontogenetic) transformation series. The same holds of B_1 and B_2 , which are ontogenetic semaphoronts of the same developmental sequence. The compositional identity of a part of an organism that is maintained in two (or more) different developmental stages of this part is thus rooted in ontogenetic relations.

Turning to the putative homology of A_1 with B_1 , it can be stated that A_1 and B_1 are *ontogenetically similar* phylogenetically homologous semaphoronts, i.e., semaphoronts whose character identity is grounded in phylogenetic relations, i.e., in their common evolutionary origin. In other words, there is a phylogenetic form of compositional identity between A_1 and B_1 . In contrast, A_2 and B_2 are *ontogenetically dissimilar* and phylogenetically non-homologous semaphoronts, i.e., semaphoronts that have differentiated along distinct and different developmental (ontogenetic) trajectories. The fact that character identity between developmental stages of the same part of an organism is grounded in ontogenetic relations, whereas character identity between a homologous part of two or more organisms is grounded in different, i.e., phylogenetic relations, breaks the transitivity of homology relations relative to ontogenetic relations. An ontogenetic form of compositional identity holds between A_1 and A_2 as well as between B_1 and B_2 , but this form of compositional identity is not transitive with the phylogenetic

form of compositional identity that holds between A_1 and B_1 . Such transitivity would necessitate the homology of the gnathostome jaw with the mucocartilaginous structures in the lower lip and velum of the ammocoete oral apparatus. To deny the homology of A_2 and B_2 means to acknowledge the fact that although A_2 and B_2 both derive from similar, indeed homologous embryonic precursors (A_1 and B_1), they subsequently undergo radically divergent development that leads to the emergence of novel structures in both lampreys and gnathostomes.

CONCLUSIONS

Divergence is the fundamental developmental trajectory articulated in von Baer's (1828, p. 224) "Laws of Individual Development." The essence of von Baer's conception of embryonic development that he equated with a process of individuation of an organism has been aptly captured by Richards ('92, p. 59): "Embryological evolution, in von Baer's view, is a process of differentiation—a movement from the more homogeneous and universal to the more heterogeneous and individual." A group of related organisms will show similar early embryonic stages, but progressively deviate from one another during subsequent development as the more particular, or individual characteristics become differentiated. Viewed from the semaphorontic perspective, it is possible not only to talk about the individuation of the whole organism, but also about the individuation of parts of organisms through development. On that account, von Baerian differentiation results in the individuation of parts of organisms (organs and organ systems) through development which, as was stressed by Wagner (2014, p. 91), establishes character identity at a certain time in development, and not before.

On the classic, transformationist account, the vertebrate jaws (palatoquadrate and Meckel's cartilage respectively) evolved from the first visceral, i.e., mandibular arch (epi- and ceratobranchial respectively). This renders the gnathostome jaw a homologue of the first gill arch of agnathans. Such homology is rejected by Kuratani (2005, p. 489) not only because of divergent developmental trajectories in the lamprey and gnathostomes, but also because the first gill arch is always specialized in its own way not just in extant, but also in extinct agnathans. According to this argument, there does not exist, in any fully differentiated agnathan, a primitive condition of the first gill arch that could easily have transformed into the gnathostome jaw. Kuratani's (2005) argument in this respect recalls Remane's ('48, p. 258) rejection of the possibility of a "zero-value-ancestor" ("*Nullwertstahne*") on the grounds that a completely unspecialized, hence non-adapted organism would not be viable. Enough reason, then, to turn away from consideration of the transformation of fully differentiated ancestral into descendent structures, and to compare embryonic conditions of form instead.

Within the emergentist paradigm, and in accordance with von Baer's conception of development, the lamprey and

gnathostomes—both being vertebrates—share structural similarities at early developmental stages, i.e., at the phylotypic pharyngula stage (phylotypic “period” *sensu* Richardson, '95, '98). They all share a central nervous system, neural crest, a series of branchial arch primordia etc., at the pharyngula stage. At that early developmental stage, it is possible to identify a mandibular arch domain of ectomesenchyme, associated with the maxillary and mandibular divisions of the trigeminal nerve ($V_{2/3}$), that is ontogenetically similar and phylogenetically homologous in the lamprey and in gnathostomes. The subsequent development of the mandibular arch domain is radically divergent, however, in the lamprey and gnathostome, resulting in the individuation of ontogenetically dissimilar and phylogenetically non-homologous structures (i.e., different character identities) in both lineages: mucocartilaginous skeletal elements of the lower lip and velum in the ammocoete larva, jaws in gnathostomes. These then represent alternative characters, not character states forming a transformation series.

In sum: from the transformationist perspective, the gnathostome jaw must be a homologue of the first gill arch of agnathans, but this assumption is not borne out by the empirical situation described by Kuratani (2005). On an emergentist account such as Wagner's, both the mucocartilaginous skeletal elements in the ammocoete larva and jaws in gnathostomes must be evolutionary novelties, but this assessment downplays the ontogenetically similar and phylogenetically homologous developmental precursor states in both lineages. The semaphorontic view of homology, however, captures both the element of sameness (between A_1 and B_1) and that of difference (between A_2 and B_2), without falling afoul of the logical problem of transitivity.

With respect to the phylogenetic meaning of the characters, the mandibular arch domain of the ectomesenchyme is a synapomorphy of vertebrates (present in A_1 and B_1). The jaw (palatoquadrate and Meckel's cartilage) is a synapomorphy of gnathostomes (B_2), whereas the mucocartilaginous structures in the lower lip and velum of the lamprey ammocoete larva are a synapomorphy of lampreys (A_2). Under von Baerian differentiation, which results in the individuation of alternate non-homologous characters (different character identities) through deviation in development, homology thus is synonymous with synapomorphy. This is not the case in under the transformationist paradigm, where homology reigns over an entire transformation series (either linear or ramifying), thus encompassing both the plesiomorphic as well as the apomorphic character states (for further discussion see Brower and de Pinna, 2012; Nixon and Carpenter, 2012; Assis, 2013). Furthermore, if evolutionary novelties are defined as characters that have no homologue in the ancestral condition, then evolutionary novelties can only obtain under the emergentist paradigm of deviating developmental trajectories. Under the transformationist paradigm, evolutionary novelties so defined could not obtain.

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