

## NOTA CRÍTICA/CRITICAL NOTICE

### Homology, an (Un)Solved Problem

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*Homology, Genes, and Evolutionary Innovation*, by GÜNTER P. WAGNER.  
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The fact that Richard Owen's most original and persuading treatise on the subject matter of this notice [Owen (1849)] has recently been reedited in English [Amundson (2007)] and Spanish [Balari & Lorenzo (2012a)] is an eloquent piece of evidence that the homology concept seems to be in good shape, despite doubts cast upon it by the long shadow of Darwinism throughout the 20<sup>th</sup> century. It is a further piece of evidence on the same track that many such doubts may now be declared solved thanks to Günter Wagner's last book—published 165 years after its venerable “homolog”, which is a renewed and enlightened summary of his ideas on the matter since his groundbreaking articles of 1989, where the now popular “biological homology concept” was firstly introduced [Wagner (1989a), (1989b)]. For the sake of my point, let me start this notice by making a short detour and remembering another text written in 1971. I am referring to Gavin de Beer's very short (sixteen pages) but extremely beautiful reader on the then very challenging notion of homology, containing an expedient presentation of the concept and up-to-date information extracted from the fossil record and the individual unfolding of organisms corroborating the idea that superficial differences notwithstanding, species seemed to be massively made of the *same* component pieces [de Beer (1971)]. From a definitional point of view, the question seemed to be not particularly problematic, for a large consensus had existed since Richard Owen's characterization in 1843 that homologs were “the same organ in different animals under every variety of form and function” [Owen (1843), p. 379]. So far so good, but the curious fact about de Beer's booklet was that after twelve pages as seemingly clear and unproblematic as the concept itself, it ended with four demolishing pages that projected all kinds of shadows upon the ultimate reality of the category, as if after all it was but an

artifact conveniently installed in the biologists' jargon but with no real biological import. By the time of de Beer's passing away, just a few months after publishing the pamphlet, the "homology" question was, as he aptly entitled it, "an unsolved problem".

Gavin de Beer probably would not have even considered the issue — like most of his contemporaries, were not for the fact that besides a champion of the Evolutionary Synthesis and a guardian of the Darwinian orthodoxy, he was also a leading embryologist, and one early committed to the then counter-current idea of exploring the doings of individual development among the causal factors feeding species evolution [de Beer (1940), Gould (1977)]. Otherwise, evolutionary biologists were not particularly sensitive to the question of the component parts of phenotypes around the mid 20<sup>th</sup> century, for the new Darwinian universe was one where no major entities beyond populations and genetic sequences were felt necessary for explanatory purposes [Dawkins (1976), Hull (1980), Ghiselin (1997)]. Moreover, their focus was put on "adaptations", a category defined on functional grounds and regarding which the question of the structural boundaries within bodies was not particularly demanding [Lewontin (1978)]. Adaptations, mostly conceived of as external surrogates of competing allelic sequences, were at most organismal components in a rather fuzzy sense,<sup>1</sup> a conclusion that obviously run against the Owenian project of deciphering the organization of bodies as combinations and reconfigurations of a few basic building blocks. So de Beer's conflict, atypical but at the same time symptomatic of the prevailing idea of nature throughout the 20<sup>th</sup> century, was probably one between a Dr. Jekyll aware of the motivation of incorporating the generative foundations of agreeing parts of organisms within the evolutionist's agenda, and a Mr. Hyde prompted to disdain them as alien to the biologist's evolutionarily grounded worldview.

The main objection that de Beer generically raised against the project of identifying and positing homologies as units of evolutionary change revolved around the question of how the homology concept could possibly advance, given the prodigality of misleading examples, beyond its soft Darwinian or historical interpretation — "community of descent from a representative structure in a common ancestor", and towards a hard core biological one — already latent in Owen's writings [Balari & Lorenzo (2012b), pp. 51-57], based on the identification of shared genes and patterns of embryological origins underlying the structures of concern, which according to him ought to "provide the key to the problem" on mechanistic grounds [de Beer (1971), p. 15]. Let us briefly review a couple of particular cases to get the flavor of de Beer's point [for similar cases more recently raised with a similar argumentative mood, see Butler & Saidel (2000)]:

[1] The common frog (*Rana fusca*) does not develop a lens if the optic cup is cut out before the relevant embryological event; contrarily, the edible

frog (*Rana esculenta*) develops the *undoubtedly* homologous structure (de Beer's emphasis) even if the optic cup is removed at the corresponding developmental stage. Thus, the developmental mechanism differs completely in each specific scenario, yet the structures attained are notwithstanding the *same*.

[2] The moth *Triphaena* has grey and dark variants, but the way the latter attain their dark coloration is quite different in populations from the Scottish islands of the Orkneys and the Hebrides, respectively. Thus, developmental mechanisms differ again in a context of *agreeing* phenotypic qualities.

It is with great pleasure that readers may learn in the pages of Günter Wagner's book how to solve such recalcitrant de Beerian puzzles by their own, guided by the author's expertise both as a gifted philosopher and first rank scientist. As for the second case, for example, a rather simple piece of conceptual clarification seems to be enough to show that it is not so defying after all, illustrating at the same time how some philosophical care may prove crucial in matters biological. According to Wagner:

In morphology, we can distinguish between two kinds of entities. On the one hand there are *character identities* — for example, forewings and hind wings of insects. On the other hand there are various *character states* that insect wings can assume; the forewing can be a wing blade or a elytra or even a haltere (as in the enigmatic insect order Strepsiptera), and the hind wing can be a wing blade or a haltere. A wing blade can also have a different shape, structure, and color [Wagner (2014), p. 54].

Obviously enough, the homology concept applies to characters — i.e. entities where conditions of individuality are met at the genetic, developmental and functional levels of analysis [Wagner (2014), pp. 54-58], and not to states — as actually entailed in Owen's definition above. So the case of de Beer's moths does not seem to question in any relevant sense the homology concept, for it simply happens that he focused on “the wrong level to attach statements of homology” [Wagner (2014), p. 57]. Regarding this particular case, the only entity that corresponds to “the proper level of analysis” [Wagner (2014), p. 57] to attach them is the scales that cover most of the moth's body, regardless the great range of variation that scales exhibit in terms of form (hair-like, blade-like, and so on) and color (grays, browns, blacks, and so on). As for the parameter of concern here, particular colors obtain from the melanin with which scales are pigmented, as well as from structural properties like the way they are stacked and scattered: Namely, black coloration obtains due to high densities of melanin — a means specific of black variants, but also structurally due to the thickness of the adwing or lower side of the scales — by means of a structural pattern common to blue and red variants [Prum, Quinn & Torres (2006), Stavenga, Leertouwer & Wilts (2014)]. So there is not a single and exclusive means for attaining a specific coloration, which makes the expectation reasonable that the same color (say, black) may

be generated through not completely identical means in different species, a fact which is however tangential to the homology question. “States are still variants of the same thing” [Wagner (2014), p. 71]: Thus, different colored scales or identically colored scales but by different generative means, are still scale variants.<sup>2</sup>

The elaboration of this “character identity/character state” distinction is one of the main distinguishing features of Wagner’s contribution to the clarification of the homology concept, which paves the way to an important extra category that he also puts forward in the book: Namely, the “variational modality” concept [Wagner (2014), pp. 58-65]. It refers to sets of character states clustered together and in a non-overlapping way relatively to alternative sets: e.g. the fins of teleost fishes — four radials attached to the shoulder girdle plus a complex of dermal bones/rays, relatively to the limbs of tetrapods — one bone attached to the body and a set of two distal bones plus a number of endochondral long bones/digits. According to Wagner’s relevant conceptualization, the corresponding clusters are inaccessible from the complementary pattern of developmental origins and organizational distribution, yet they represent two alternative instantiations of an identical character (the vertebrate limb) at a “macro-state” level of analysis, so to speak: “Variational modalities reflect ‘deep’ differences between instances of the same character” [Wagner (2014), p. 126].<sup>3</sup> I turn to this important “variational modality” concept in my discussion below.

As for case [1] above, as a matter of fact it had already been raised by Hans Spemann, one of the founder fathers of modern embryology, in 1915, in a paper where he concluded that organs undoubtedly the same — like the lens of a variety of amphibian species’ eyes, were however discontinuous from the point of view of their developmental origins [Spemann (1915)]. Specifically, Spemann experimentally settled then that lens formation was in some species dependent on the inductive effect of the eyecup, but that in other species it was not. This was presented as an intriguing fact, which did not however question the identity of lenses despite the lack of an across-the-board lens generation means. It nevertheless pointed, as underscored by de Beer, to the conflicting conclusion of disconnecting the homology question from developmental considerations. A century after Spemann’s original observations, Wagner accepts the challenge of these defying cases and in a curious tour the force, admits that “*we can safely assume that some level of variation in the developmental mechanisms of homologous characters is the rule rather than the exception*” [Wagner (2014), p. 90; the emphasis is from the original]. Note that such a stance entails a non-trivial modification of Owen’s original definition above, which should now read as follows:

Homolog [Wagner's extended version].— The same organ in different animals under every variety of form, function and developmental mechanism. [the wording is mine]

Obviously enough, this definition does not suggest that a particular organ may be obtained by an unrestricted array of means. It makes in any event clear that different developmental means may lead to the same organic structure. So in the end, is it or is it not development the ultimate foundation of the sameness relation underlying collections of homolog candidates? Wagner's not uncontroversial [see below], but extremely elegant position is that it is: Namely, that complementarily to the range of variation in the developmental mechanisms of homologs, a core of uniformity also exists that guarantees *character identities*, in the sense introduced above. From this point of view the case of lenses is straightforward, for it is a well established fact that the inductive signals that ultimately transform cell populations — e.g. two lateral patches of embryonic skin — into organs — e.g. lenses, are rather unspecific, in the sense that they basically act as a perturbing stimulus that can be easily replaced by natural or artificial surrogates. The role of such signals is that of inciting cells to enter into one among the different possible fates originally accessible to them. So putting all the pieces together, it becomes clear that “*the information for character identity is within the cells that react to the signal and not in the inductive signal itself*” [Wagner (2014), p. 93; the emphasis is from the original]. In other words, it is “within” that the foundations of identities (i.e. of homologies) must be found. In this respect, the idea that Wagner puts forward in the book, building upon previous suggestions by Jean Deutsch [(2005)],<sup>4</sup> is that “character identity networks” (ChINs) exist at the genetic level, which interface between the positional information provided by inductive signals, on the one side, and downstream “realizer” genes in charge of character states differentiating among collections of homologs, on the other side. In between, variational modalities reflect “developmental modalities that lead to different and persistent variational tendencies” [Wagner (2014), p. 127]. In any event, it is ChINs that Wagner deems ultimately responsible to the individuality of organs and their identity across species: i.e. of homologies.

In a nutshell, the previous paragraphs offer the core of Wagner's up-to-date and high-tech approximation to the problems traditionally raised by the homology concept. Obviously enough, Wagner's beautifully written four hundred and twenty five pages are full of important qualifications of the framework and excellent illustrations of each and every of the author's points. It is fair to conclude that the concept relies now on much more solid grounds than before — and it is worth remembering that it has been pointed out as “the central concept of all biology” [Wake (1994), p. 268]. So Wagner's cannot be appraised but as a major advancement in our present under-

standing of nature. It was not however the author's ambition to solve the question from root to branch and in just one assault, as he actually admits by pointing out some of the questions that he has decided to put aside for the time being, which jointly boil down to the question whether the same homology concept that applies to morphological characters also applies to behaviors, proteins, genes and gene regulatory networks [Wagner (2014), p. 1]. For the sake of his own practical needs, Wagner's decision of concentrating just on the morphological level somehow entails that solving subtleties at the corresponding levels of analysis may be safely driven by ignoring the rest. I understand this as a practical and justifiable move that undoubtedly has benefited the book. But it also raises some non-trivial questions regarding Wagner's otherwise elegant theory of homology, as I presently explain. Before that, I also want to comment another loose end — unless my own understanding of some critical passages of the book is not fair enough, which in my opinion projects the shadow of a doubt into the overall new conceptual map that the book opens. For the sake of clarity, I divide the rest of this notice into two sections, respectively devoted to what I will refer to as the “intension” and the “regression” problem.

### I. THE INTENSION PROBLEM

In his 1849 monograph Richard Owen left a note of dissent relatively to a particular aspect of Étienne Geoffroy Saint-Hilaire's prior identifications of parts of different animals [Geoffroy (1830)], which the latter directed under less restricted criteria and with more across-the-board results than the former. Specifically, it was one of Geoffroy's conclusions that insect limbs and vertebrate limbs were the same organ, as they clearly showed an “analogous” pattern of organization [Geoffroy (1820)].<sup>5</sup> Owen reacted to his antecessor's claim, for while he admitted that similarly organized parts of invertebrates existed answering similar purposes than their putative vertebrate correlates, yet he contended that the external versus internal character of the respective skeletons was a bridge wide enough as to prevent deeming the corresponding organs homologous [Owen (1849), pp. 4-5; pages are from Amundson's (2007) edition]. It is somehow perplexing that the question has not been definitely settled 165 years later, and it is perhaps even more disturbing that it is not completely clear whether the question remains open for conceptual or empirical reasons. The aim of this short section is to explain the broad implications of this particular case taking advantage of Wagner's elaborated theory of homology, which notwithstanding probably finds one of the limits to its explanatory potential in similarly defying cases.

An important contribution regarding the “Geoffroy-Owen affaire” can be found in a recent paper by Neil Shubin, Cliff Tabin and Sean Carroll [Shubin, Tabin & Carroll (2009)], a follow-up of the authors’ ground breaking article of 1997 [Shubin, Tabin & Carroll (1997)]. Shubin, Tabin and Carroll defend that while fish fins and tetrapod limbs are undoubtedly the same organ (i.e. *bona fide* homologs), as they are clearly molded by shared genes and signaling machinery, vertebrate and insect limbs are also homologs, but in a more unconventional and deeper sense: Namely, they share primitive developmental machinery devoted to making things protrude from the body wall. So the authors’ conclusion is in part pro-Owenian — vertebrate and insect limbs are not homologs as organs, and also in part pro-Geoffroyan — vertebrate and insect limbs are homologs as protrusions. I confess not being absolutely convinced of this Salomonic solution, namely for one thing: It purports the non-trivial transformation of the classical homology concept into a “homology as” concept. The peril of this new concept is clear: It entails the introduction of a perspectival or intensional dimension (i.e. a natural semantics of sorts) into the workings of development and evolution.<sup>6</sup> So the odd implication of the concept boils down to the fact that according to it, it seems to make a difference to otherwise purely mechanical developmental events whether they work at one or another semantic level, to which no clear natural correlate is declared.<sup>7</sup>

As for Wagner’s position on the issue, it is difficult to guess what his actual stance is. Shubin, Tabin and Carroll’s findings and conclusions are early introduced in the book [Wagner (2014), p. 36], but they seem to lose any relevance thereafter. This fact may be interpreted as if for Wagner deep homologies (e.g. homologs as protrusions) do not pertain to the same level of analysis of morphological characters (e.g. limbs and so on) on which he focuses the book. But according to my reading, the Geoffroy-Owen case could have offered a nice field of exploration for Wagner’s “variational modality concept” [see above], maybe as an extension of the whole fascinating chapter that he devotes to the prototypal cases of variational modalities: i.e. fish fins and tetrapod limbs [Wagner (2014), Ch. 10]. The closer Wagner approximates to the question is probably in his analysis of eye development networks [Wagner (2014), pp. 102-111], where he decides the question in an Owenian mood, for despite the amount of shared genes found both in vertebrate and insect eye development, he nevertheless concludes that the networks these genes respectively belong to “are so different that it is a more likely conclusion that these genes regulatory networks were assembled independently during the evolution of eyes” [Wagner (2014), p. 111].<sup>8</sup> So it is also tempting to conclude that Wagner’s opinion on the limb issue is also Owenian, for despite a certain common genetic background, vertebrate and insect limb development clearly splits by “the details of [the] molecular and functional interactions” of the whole array of genes committed to the task [Wagner

(2014), p. 111; note that Wagner's quote refers to the case of eyes]. So insect limb probably is not an extra variational modality of the same homological class to which fish fins and tetrapod limb belong. Moreover, within Wagner's framework the case does not seem to deserve the introduction of a further conceptual distinction, for it simply amounts to the pervasive phenomenon of sharing and reusing developmental resources in the most disparate organic structures (or "molecular convergence"; Wagner [p.c.]).

If the above paragraph faithfully reflects Wagner's actual position on the issue, then one may preliminarily conclude that the intension problem is probably neutralized within his theory.<sup>9</sup> However, it is not at all clear that Wagner's homological theory is really powerful enough to solve such issues in the absence of a corresponding theory at the genetic level, for the book's statements on such delicate matters rely on claims on similarities among gene regulatory networks,<sup>10</sup> which are however not grounded on a clear metric. So it seems that only a theory of morphological homologies *cum* an associated homological theory at the ChIN level may ultimately prove strong enough to decide whether a certain array of organic structures are plain homologs, variational modalities or nothing at all, defying Wagner's ambition of obtaining clean answers while avoiding theorizing on homologies at levels other than observed morphologies. This leads me to the next problem I want to briefly comment.

## II. THE REGRESSION PROBLEM

It is my conclusion in the previous section that Wagner's theory of morphological homologies is committed to converge with a worked out enough theory of ChIN homologies in order to eventually provide better grounded statements regarding particular identity relations among body parts of the same or different organisms.<sup>11</sup> From his short comments in Chapter 3 one may conclude that he is perfectly aware of this, but the truth is that the book leaves the question mostly undetermined. What Wagner positively asserts in this *in passim* section basically boils down to the following statements:

[1] The degree to which similarity of gene regulatory networks is indicative of homology depends on how unlikely it is to find two genes that interact in two unrelated tissues,

and

[2] Similarity of a gene regulatory network of some tissues, even one in which multiple genes are involved per se, is not strong evidence for homology [Wagner (2014), p. 113].



The additive effect of these statements is an inconclusive stance on the question of how the molecular composition and organizational pattern of interacting genes in specific developmental contexts may solve the question of the putative identity of the resulting morphologies. It is fair to clarify that it is precisely Wagner's intention to underscore such a perplexing situation. On the one hand, he seems to favor the idea that similarities at the genetic level are indicative of homology on probability grounds; but on the other hand, he is also aware that on strictly biological grounds the logic of probability is easily defied and defeated. What is curious, even somehow ironic about this problem is that it looks as a repetition at the genetic level of analysis of the same problems that historically defied the application of the homological method by its precursors in the late 18<sup>th</sup> and early 19<sup>th</sup> centuries. It is also interesting that judging from his insightful reflections on the case of eye development, Wagner seems to privilege a view reminiscent of Geoffroy's *principe de corrélation des formes*, but now applied at establishing ChIN identities attending to the similarity of the interactive patterns among the dedicated genetic resources. But as commented above, it precisely was what at the time was felt as flawed results of such formal principle that motivated the introduction of supplementary criteria—like histological and embryological ones in the case of Owen [Padian (2007)], also leading to unclear solutions in many cases. The point of my comment is that a regression problem of sorts seems to arise once the suggestion is made that the composition and organization of ChINs may prove the definitive judge to solve questions of morphological sameness. In any event, the promise seems to be open by Wagner's book that such a problem may eventually be circumvented by properly worked out inter-ChIN isomorphism criteria capable of deeming homologous (or not) sets of structures at the morphological level.<sup>12</sup>

Readers may judge by themselves whether my comments point to minor or major shortcomings of Wagner's theory. In my opinion, they are probably good pieces of evidence that Wagner has taken the question up until the limit to which it might be currently taken. And a limit, I dare to add, where few before reading the book could even think that the question was ready to be debated yet.

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## NOTES

<sup>1</sup> Amundson [(2005), p. 240] aptly refers to the resulting view on homology as the “homology as residue” concept.

<sup>2</sup> A note of disclaim is in order here: I am applying Wagner’s ideas to de Beer’s objection by my own, so any fault in the analysis is of my exclusive responsibility.

<sup>3</sup> Actually so deep that Wagner concludes that the novelties that differentiate between modalities at this level may eventually be deemed new organs “nested within” the shared identity (Wagner [2014], p. 318).

<sup>4</sup> Namely, Deutsch’s ingenious interpretation of comparative data from three insect species — flies, beetles and butterflies. In all three species, the appendage of the second thoracic segment behaves as a default element, which shows up in mutants where the action of genes modeling the specificity of the third segment is repressed. So according to Deutsch the respective appendages of the second segment must be deemed homologs—i.e. the same organ, despite the fact that it is a wing in flies, an elytra in beetles and a characteristically colored wing in butterflies.

<sup>5</sup> “Analogy” is the word that Geoffroy specifically used to refer to natural identities (i.e. homologies).

<sup>6</sup> My point is thus reminiscent to Jerry Fodor and Massimo Piattelli-Palmarini’s criticism of classical Darwinian adaptationism [Fodor & Piattelli-Palmarini (2010)]. It may be worth remembering that from Brentano on, “intensionality” is customarily thought of as a hallmark of the mind. Fodor and Piattelli-Palmarini’s main conceptual objection to Darwinism boils down to the metaphysical shortcoming of deeming nature a mindful entity, as according to the model it makes a difference whether traits are selected *as* adaptations for one *or* another concurrently particular benefit [see Richards (2005) and (2012), for the particular case of Darwin]. It is my point that some versions of the homological project similarly treat identities (or lack thereof) as in the eye of the beholder, which cannot be other than nature itself.

<sup>7</sup> A footnote of qualification (as it relates only indirectly to Wagner’s book) is in order here. What I specifically mean is that a distinction like the one between a “protrusion” and a “limb” seems to correspond to a conceptual hierarchy rather than to a *bona fide* organic hierarchy. To be fair, Shubin, Tabin and Carroll do offer a precise definition of “protrusion”: Namely, “outgrowth of the body wall that [is] patterned along three axes — the proximodistal, anteroposterior and dorsoventral axes” [Shubin, Tabin & Carroll (2009), p. 821]. So it names a superordinate category comprising organs like limbs, horns, and so on. Their point is that the category is coextensive with the expression of a certain array of common genetic sequences. It is my point, however, that the distinction remains conceptual (in other words, it is just in the beholder’s eye) in that no a clear biological correlate is actually suggested. Fair enough, Shubin, Tabin and Carroll mention some candidate genes. But in the absence of a theory grounding the rationale of telling them apart from the factors specifically

acting in the development of specifically different kinds of appendages, concluding that “protrusion” names more than a concept seems, to say the less, premature. For example, one of the genes referred to by Shubin, Tabin and Carroll is *Distall-less* (*Dll*). But *Dll*, like most genes, is a very unspecific resource, also recruited for example in developmental tasks like pigment production in some insect wing spots [Wagner (2014), pp. 191ff]. So lacking a more articulate theory on superordinate genetic circuitries acting in agreement with ChINs, the claim that *Dll* (or similar genes) belongs to one such circuitry that brings about protrusions does not seem particularly justified relatively to just claiming that it is a gene with a high propensity of being recruited in the machinery for making the most disparate characters, limbs among them — thus parsimoniously avoiding intermediates categories like “protrusion”.

<sup>8</sup> This is however a controversial issue. See Shubin, Tabin & Carroll [(2009), pp. 818-820] for a review of the position contrary to Wagner’s. For a philosophical discussion, see Balari & Lorenzo [(2014), p. 13] and references therein.

<sup>9</sup> But to be fair, it is not completely clear that the issue is actually solved in the book. In the closing pages, Wagner himself raises the question whether it really makes sense “to say that the bird wing is not homologous to the bat wing *as wing* but homologous *as forelimb*”, yet simply to conclude that “while there is some useful truth in this observation, it is also intrinsically confusing” (Wagner [2014], p.421). In the end, he seems to waive that question by saying that the issue is only relevant concerning character states, but not character identities, thus at a level different from the one at which homologies are established.

<sup>10</sup> To wit, only one page and a half note is devoted to the question in the book [Wagner (2014), pp. 112-114]. According to Wagner [p.c.] this is justified, for the book is aimed at constructing a mechanistic explanation of homologies at the morphological level (i.e. what morphological homologies are), and not to operationalizing criteria for identifying them (i.e. how they can be recognized). I agree that this is a legitimate position. In any event, my point is that what it is auxiliary for Wagner’s interests, it is explanatorily central from the point of view of homologies at the ChIN level (i.e. what ChIN homologies are), on which morphological homologies are crucially dependent. So the former theory cannot aspire to full completion not being the latter satisfactorily articulated.

<sup>11</sup> An obvious point of reference is Abouheif’s (1999) model. However, Abouheif’s and Wagner’s frameworks are not fully convergent, for two main reasons. On the one hand, Abouheif trusts in historical criteria more than Wagner seems to deem necessary: “[The] historical or genealogical notion of homology [...] begs the question of what it is that has continuity of inheritance” [Wagner (2014), p. 270]. On the other hand, Wagner (despite the comments below in the main text) clearly trusts in inter-level correlations more than Abouheif does: “Homology among networks cannot always be taken as strong evidence to support homology among [...] morphological structures” [Abouheif (1999), pp. 211-212].

<sup>12</sup> It is fair to note that this “regression problem” is not exclusive of Wagner’s approach. It is also manifest, for example, in Shubin, Tabin and Carroll’s influential “deep homology” model, as the following definition clearly shows: “[...] Deep homology: Morphologically disparate organs whose formation (an evolution) depends on *homologous genetic regulatory circuits*” [Shubin, Tabin & Carroll (2009), p. 819; the emphasis is mine].

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## RESUMEN

El concepto de “homología” se ha mostrado históricamente muy resistente a ser explicado sobre unas bases mecanicistas. Esta nota introduce la reciente propuesta de Günter Wagner, con la que da respuesta a la intuición de que tal explicación debe estar conectada con el desarrollo. Apunta también dos posibles cabos sueltos de la teoría, aunque probablemente acomodables a este nuevo marco.

PALABRAS CLAVE: *homología, identidad, desarrollo, intensidad, isomorfismo.*

## ABSTRACT

The “homology” concept has historically proved very refractory to mechanistic explanations. This notice introduces Günter Wagner’s recent proposal, with which he fulfills the intuition that such an explanation is to be connected with development. The notice also deals with two possible loose ends of the theory, which are nevertheless presented as putatively resolvable within this new framework.

KEYWORDS: *Homology, Identity, Development, Intension, Isomorphism.*