Not deconstructing serial homology, but instead, the a priori assumption that it generally involves ancestral anatomical similarity: An answer to Kuznetsov's paper

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REVIEW

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Not deconstructing serial homology, but instead, the a priori assumption that it generally involves ancestral anatomical similarity: An answer to Kuznetsov's paper

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Abstract

I am very thankful to Kuznetsov for his comments on our recent paper about serial structures published in this journal. I hope this is just the beginning of a much wider, and holistic, discussion on the evolution of serial homologous structures, and of so-called "serial structures" in general, whether they are truly serial homologs or the secondary result of homoplasy. Strangely, Kuznetsov seems to have missed the main point of our paper, what is particularly puzzling as this point is clearly made in the very title of our paper. For instance, he states that "Siomava et al. claim that the serial homologues are false because they are ancestrally anisomeric (dissimilar)' and that" Siomava et al., (Siomava et al., Journal of Morphology, 2020, 281, 1110–1132) expected that if serial homology was true, then the serial homologs would be identical at the start and then only diverge. " However, our paper clearly did not state this. Instead, we stated that (a) serial homology is a real phenomenon, and (b) ancestral dissimilarity is actually likely the norm, and not the exception, within serial homology. In particular, our paper showed that, as clearly stated in its title and abstract, within the evolution of serial homologues these structures "many times display trends toward less similarity while in many others display trends toward more similarity, that is, one cannot say that there is a clear, overall trend to anisomerism." Serial homology is therefore a genuine and much widespread phenomenon within the evolution of life in this planet. It is clearly one of the most important issues—and paradoxically one of the less understood, precisely because of the a priori acceptance of long-standing assumptions that have never been empirically tested, some of them repeated in Kuznetsov's paper—within macroevolution and comparative anatomy.

KEYWORDS

anatomy, anisomerism, convergence, evolution, homologs, polysomerism, scientific misunderstandings, serial homology, similarity

First of all, I should explain that I am very thankful to Kuznetsov for his comments about our recent (2020) paper, published just after some weeks after its publication. This was precisely the intention of our paper, to promote discussions about serial homology in particular, and awareness and interest about the anatomical evolution of so-called "serial structures" in general, either if they are truly serial homologs or the secondary result of homoplasy, that is, of convergence or parallelism. Interestingly, and showing the difficulty of undertaken such discussions in academia in general, most points raised by Kuznetsov do not reflect a true difference of opinion, or about

evidence supported by empirical data, but instead misunderstandings, a common phenomenon in science and elsewhere.

For instance, Kuznetsov states that "the organs do not arise from organs, and therefore their genetic basis, and hence homology, can be changed in zygote singularity.. thus, the morphological homology is not static." Of course homology is not static: this is actually one of the main points of our paper. That is, structures that are serial homologs, such as the vertebrae, can either become more similar or more different, within different evolutionary stages. We all know that homology is not static, as the flippers of dolphins, wings of birds, and upper limbs of humans are clearly homologous. We have shown another examples regarding serial homology in previous papers. For instance, the fifth ceratobranchial of zebrafishes bears teeth and ossifies earlier than other ceratobranchials, and the muscles associated with it also develop earlier, than those related with other ceratobranchials (which are clearly serial homologos of the fifth ceratobranchial), in cypriniforms, linked to the evolution of a "second (pharyngeal) mouth" in these fishes (Diogo, Hinits, & Hughes, 2008). So we clearly agree with Kuznetsov about this major point.

Another misunderstanding is that in Kuznetsov's comment about our paper he uses a genetic/developmental definition of homology, while we clearly stated in our paper that we were following instead the historical definition of homology. This is clear when he states that "the organs do not arise from organs, and therefore their genetic basis, and *hence* homology." He equates a similar genetic basis with homology. This is very different from a historical definition of serial homology, and Kuznetsov does not only fails to explain why he used a developmental definition but also to understand—seemingly—that we are not following such a definition. As we explain in our paper, using a historical definition of homology, there is no serial homology of the pectoral and pelvic appendages as a whole, and thus also of the upper and lower limbs of tetrapods as a whole, as shown by the empirical data compiled in a recent paper (Diogo, 2020; see below).

Similarly, there is a huge misunderstanding when Kuznetsov stated that "if Siomava, Fuentes, and Diogo (2020) will succeed in their deconstructing activity, the serial homology will come out of explicit use as already did its senior cousin, the general homology". We are *not* deconstructing the notion of serial homology, which is a real and very important phenomenon, and is actually the central subject of a book being written by me, which is precisely entitled "Serial Homology". Our Siomava et al. (2020) paper is instead deconstructing, as the title explicitly shows, the a priori *assumption* that serial homology generally involves ancestral similarity. This is the main problem, not the notion of serial homology: by always assuming a priori, without testing this empirically, that "serial structures" were ancestrally similar, researchers failed to see not only that (a) many times true serial homologs were not ancestrally anatomically similar, but also that (b) structures assumed to be "serial homologs" such as the pectoral and pelvic appendages were not only very different ancestrally but are even very likely not truly serial homologs.

This is the main take-home message of our paper, and not at all, as argued by Kuznetsov, to deconstruct the notion, and deny the existence, of serial homology. This sentence of Kuznetsov in particular clearly shows that he completely missed the main message of our paper: "Siomava et al. (2020) claim that the serial homologs are false because they are ancestrally anisomeric (dissimilar)." Instead, we stated that serial homology is real and that it often involves ancestrtal dissimilarity, and that this is one of the most important and less understood issues within macroevolution and comparative anatomy, precisely because of the a priori acceptance of old, long-standing wrong ideas about it without testing them against empirical evidence.

Another misunderstanding, which involves some personal - and odd - comments, is that we are not "aware" about the historical discussion between the "syntropistic" and "antitropist" theories. For instance, Kuznetsov states "Diogo and Molnar (2014), being unaware of the antitropist theory, state that not even one pelvic thigh muscle has a clear 'topological equivalent' in the pectoral region and arm". This is a very strange comment, as (a) Kuznetsov never personally asked any of us if we are aware or not about these issues, and (b) of course we are aware of them, as attested by the fact that we have discussed them in detail in many previous works, including books (see, e.g., Figures 1–3). This is the central part of my research for the last two decades, and also crucial in the way I teach medical students, which are always confused about why the big toe is "medial" and the thumb is "lateral", or why the forearm is said to be "flexed" when moving anteriorly while the leg is said to be also "flexed" when moved posteriorly. This is shown in Figures 1–3, which are adapted from two of the works in which we discussed this in detail, which are precisely aimed for medical students and their professors: our Diogo and Molnar (2016) paper and our Diogo et al., 2016 book: so, how could we not know about this? In fact, as we explained in those works, Vicq-d'Azyr's (1774) assumption that the ulna and tibia "corresponded" to each other simply has to do with the fact that Vicq d'Azyr, and other scientists that followed his idea, did not account for the external and internal rotations of the upper and lower limbs during the ontogeny of humans (Figure 3), contrary to what happens in animals such as birds and salamanders (Figure 2).

A similar point is when Kuznetsov states that, regarding, the skeleton of the lamprey *Petromyzon marinus*, shown in our paper, when "turning the photo of this specimen upside down and accurate labeling of morphological details reveals that it is the axial skeleton of a shark or ray … this mistake invokes a doubt on the morphological importance of all the other mentions by Siomava et al. (2020) of the gradual changes of lengths, angles of inclination, and so forth, of wings, appendages, bristles, vertebrae, ribs, teeth, digits, myomeres, feathers, and hairs considered in the paper." Really? Even if this would be the case, would this put in question "all" the numerous other examples we refer to, in our paper? Actually, the mention to the lamprey skeleton is a mere detail in our paper, which if it would not have been included, would not change at all the general patterns we have found, and the overall conclusions of the paper. Moreover, as we clearly state in our paper, "we inspected the image of a lamprey skeleton (*Petromyzon marinus* (NC62070)) that we identified from the available gallery of the Smithsonian Institution (Frey, n.d.)". Therefore, if there would be a mistake, it would involve a mistake made by the Smithsonian Institution, in the first place. And, clearly, this would be a

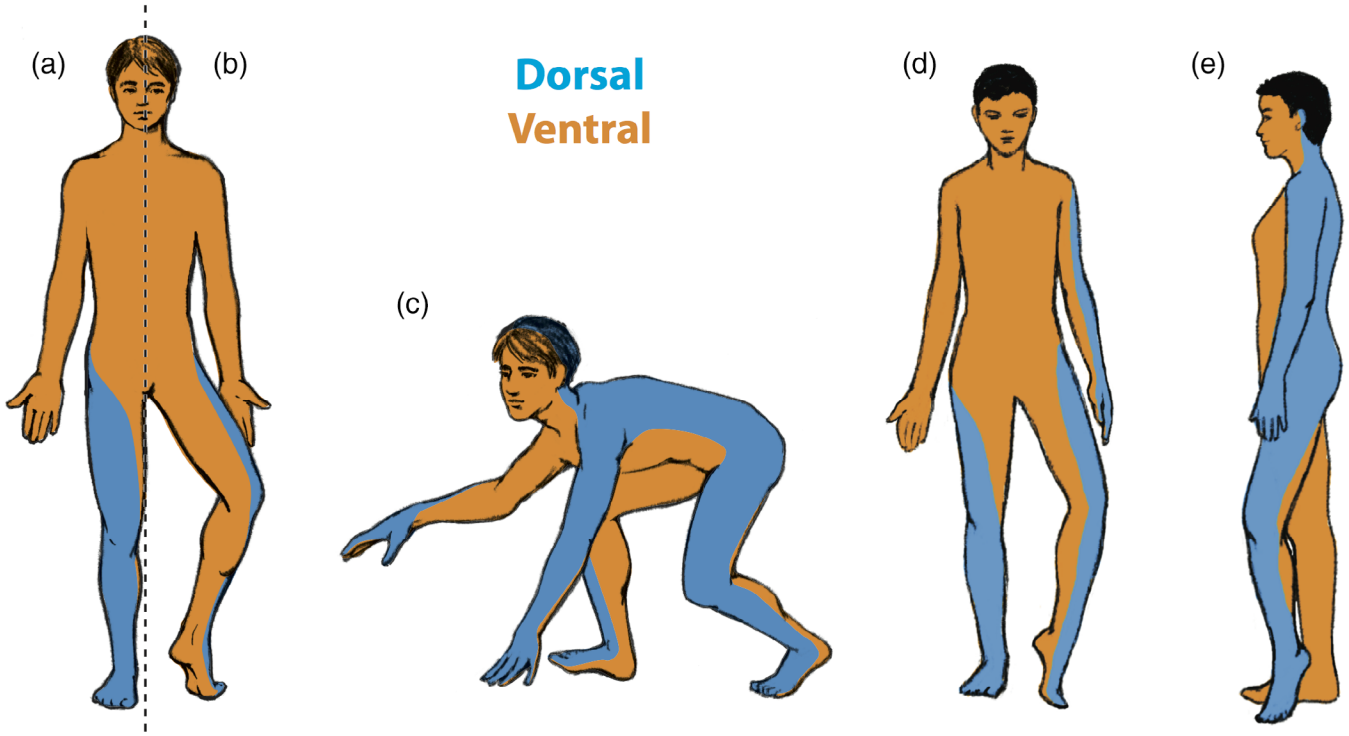

FIGURE 1 Diagram showing the "human standard anatomical position" (a), the re-defined anatomical position with the lower limb rotated laterally almost 180° (b), and other positions that emphasize the evolutionary and developmental history of the human body (c–e). In b, the flexor (ventral) musculature of both upper and lower limbs faces anteriorly, reflecting the true topological correspondence between the elements of the limbs. C shows a quadrupedal crouched posture similar to that of salamanders (see Figure 2), emphasizing our ancestry as tetrapods. Developmentally ventral structures (orange) mainly face superiorly. (d, e) Show the left limbs in a position similar to that of an early embryo (see Figure 3a), with ventral limb structures facing medially, while the right limbs are in standard anatomical position (modified from Diogo & Molnar, 2016)

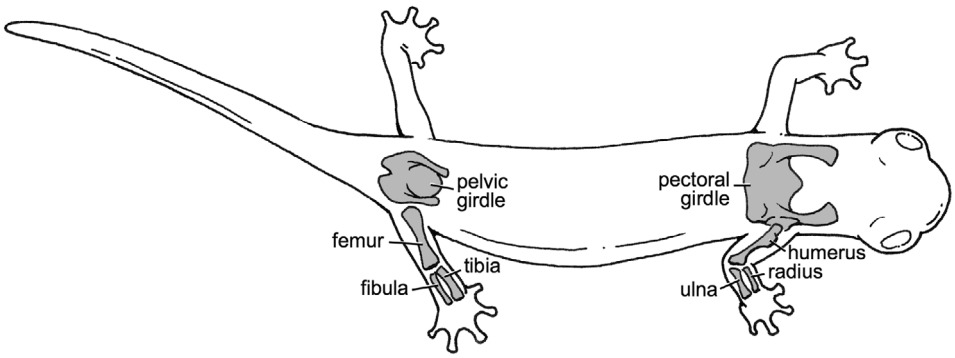

FIGURE 2 Limb anatomy of a salamander, representing the ancestral tetrapod body plan and showing topological correspondences between the fore- and hindlimb bones: humerus/femur, tibia/radius, fibula/ulna, and "thumb"/"big toe." Note that the ventral (flexor) muscle compartments of both limbs face ventrally (modified from Diogo & Molnar, 2016)

very, very, rare and exceptional mistake, from such an institution. Clearly, Siomava had no reason, a priori, to put in doubt the identification by one of the most prestigious institutions in the planet. Furthermore, this is the only image taken from the online collection of any institution, in our paper, all the others are from our own work, or from published works from other authors, so saying that in case there was indeed a simple mistake with this figure would put in doubt the "all the other mentions" is a rather odd, and completely unjustified, and again rather tendentious, statement, in particularly when the work of our lab is consensually considered, worldwide, to be of the highest quality, rigor, and accuracy within the field of anatomy. As the senior author of the paper, and the leader of our lab, and former advisor of Siomava's work, I can affirm, without any doubt that the work of Siomava, a brilliant, young, Belarus female is of the highest quality, and Kuznetsov's general statement is clearly a very unfortunate, completely unwarranted suggestion.

Similarly, Kuznetsov states that he is "concerned" about the "kind of a quantitative approach to morphology, which is represented on Figure 2 of Siomava et al. (2020). It shows the numbers of muscles or muscle groups, which are presumably shared by the fore and the hind limbs in different gnathostome vertebrate groups … in fact, this is not a quantitative but a numeric approach to morphology." He argues that

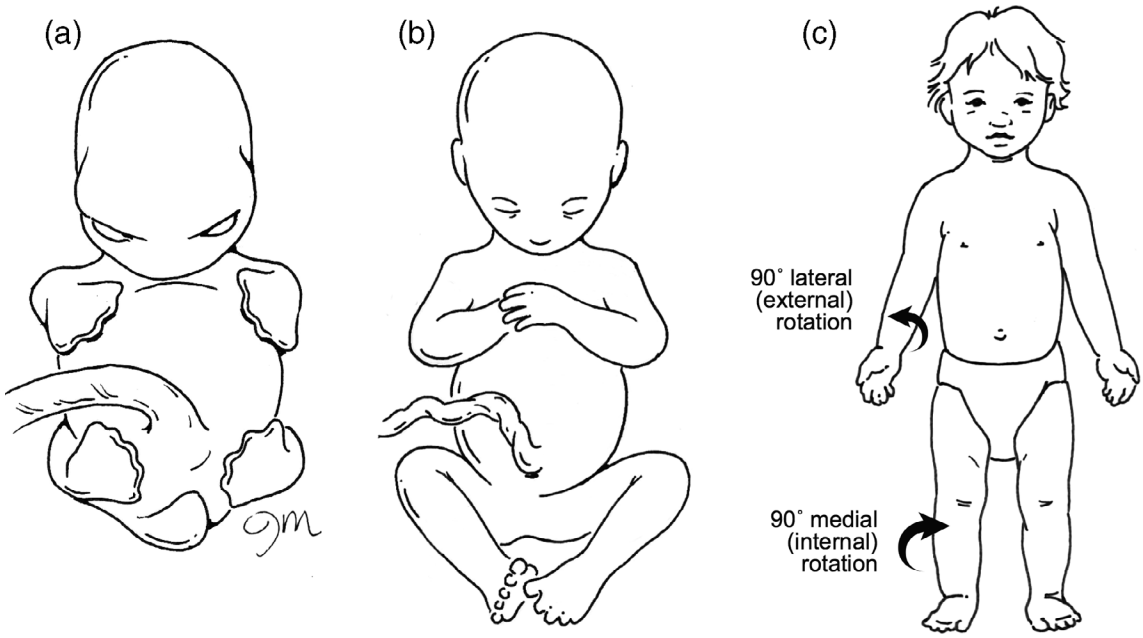

FIGURE 3 Stages of human embryology showing opposite rotations of upper versus lower limbs. (a) At about 19 weeks, the first digit of the upper limb (thumb) and lower limb (big toe) form on the cranial side of the developing limb, as they are in adult salamanders. (b) By about 23 weeks, the upper limb begins to rotate laterally and the lower limb begins to rotate medially. (c) At about 1 year, the limbs approach their adult configuration. In "human standard anatomical position" shown in this figure, the upper limb is rotated 90° laterally so that the thumb lies on the lateral side. (Note, however, that in normal standing posture the rotation of the upper limb is less than 90°.) In both normal standing posture and "human standard anatomical position" the lower limb is rotated 90° medially so that the big toe lies on the medial side (modified from Diogo & Molnar, 2016)

"obviously, these numbers entirely depend on the structural model adopted by the authors … the numbers would be entirely different if the authors adhered to the antitropist alternative of which they are unaware." Again, not only we are fully aware of this alternative, but what is shown in Figure 2 of our Siomava et al. (2020) paper, and the lack of correspondence of any proximal muscle of the upper versus lower limbs of any tetrapod in general, have nothing to do with a "syntropistic treatment" or an 'antitropist' treatment of the issue. No matter what 'treatment' is given, or how much people might try to force to see any similarity between these muscles in order to "fit the data" within their a priori assumptions, as the German romantics did, in reality there is not even a single topological equivalent, period. This is because the proximal muscles of the upper limb and the proximal muscles of the lower limb have evolved independently: fishes do not have them, so to assume a priori that they *have* to be similar, makes no sense at all. They were never similar—as shown in our detailed recent muscle reconstructions of early tetrapod fossils (Molnar, Diogo, Hutchinson, & Pierce, 2018, 2020), and continue to not be similar in living tetrapods, as shown by a huge number of comparisons between the upper and lower limbs of numerous tetrapods, including detailed developmental works and using other state-of-the-art techniques such as anatomical network analysis (e.g., Diogo & Molnar, 2014, 2016; Diogo & Ziermann, 2014, 2015; Diogo et al., 2016; Diogo, Esteve-Altava, Smith, Boughner, & Rasskin-Gutman, 2015; Diogo, Linde-Medina, Abdala, & Ashley-Ross, 2013; Diogo, Murawala, & Tanaka, 2014; Diogo, Nacu, & Tanaka, 2014; Diogo & Tanaka, 2014; Diogo & Wood, 2015, Diogo, Ziermann, & Linde-Medina, 2015; Diogo, Ziermann, Molnar, Siomava, & Abdala, 2018; Miyashita & Diogo, 2016; Sears, Capellini, & Diogo, 2015; Siomava, Shkil, Voronezhskaya, & Diogo, 2018; Ziermann, Freitas, & Diogo, 2017; Ziermann, Miyashita, & Diogo, 2014). Only the muscles related to the distal region, particularly the autopods, are similar, because of the secondary convergence—due to "gene piracy", as we explain—between the evolution of the tetrapod hand and foot. Our Diogo et al., 2016 book provides one of the most detailed, and recent, discussions on the topological correspondence of the muscles, arteries, veins, and nerves of the distal portions of the lower and upper limb, and about the lack of such correspondences not only in muscles but also in blood vessels and nerves of the proximal portions of these limbs, in humans.

This is what the empirical evidence, using a huge sample of different methods and perspectives, truly shows. We cannot just ignore these facts, in order to try to "fit facts into a priori just-so-stories". In reality, the fact that reseachers cannot avoid following a priori, long-standing assumptions, and to try to "fit data" within such assumptions, even when they clearly go against empirical data, is actually—and unfortunately—reflected in the very paper of Kuznetsov. For instance, he states: "the generation of paired appendages in the pelvic region, near cloaca, may be associated with their initial role of copulatory claspers in males … in the placoderms *Austroptyctodus* and *Incisoscutum* there is a series of three pairs of appendages: the pectoral fin, the pelvic fin, and the male clasper … one can imagine a quite *unusual* scenario that, at first, the pectoral fins arose near cloaca as

male claspers". *Quite unusual* scenario indeed, as there is no evidence at all to support it. That is, yes, one can "imagine" anything one wants, and make any just-so-story in order to fit a priori assumptions, but why not stick with what the empirical data truly shows, instead? There is no paleontological or developmental, evidence at all that the pectoral appendage came from the pelvic region. Moreover, paleontological data shows that the pectoral appendage arose in time before the pelvic one, not the other way round. In fact, in a recent paper written about at the same time in which we wrote ours, and at the same time that wrote a paper specifically about the upper and lower limbs (Diogo, 2020), Sleight and Gillis (2020) showed how developmental data does support instead the idea that the pectoral girdle comes very likely from the head, exactly as I defend in that upper-lower limb paper. A similar idea had been also defended in a paper by Nagashima et al., 2016, which had provided very strong developmental data to support it, which my colleagues and me had put forward three years before (Diogo et al., 2013). One can actually say that a consensus starts to slowly emerge—contrary to the a priori assumptions that have been accepted for so long without real evidence—, particularly within developmental biologists and evolutionary developmental biologists, about the fact that the origin of the pectoral girdle has nothing to do with that of the pelvic girdle (see, e.g., my 2020 review on this subject).

Having said that, Kuznetsov's account on the historical discussions between the "antitropist theory" and the "syntropist theory" is a great, and much needed, piece of work, and the type of historical framework that we clearly need in comparative anatomy, and that we are precisely trying to stimulate with the publication of our Siomava et al., 2020 paper. Such similar historical notes, about other issues concerning serial homology, have been given in our 2013 Diogo et al. paper, and in particular in Schmitt's, 2004 excellent book "Histoire d'une question anatomique", as noted in our Siomava et al. (2020) paper and as noted as well in Kuznetsov's paper. I am thus sincerely very thankful to Kuznetsov for his comments—even if they do include some misunderstandings—and historical notes, and hope that this is just the beginning of a much wider and holistic discussion on the evolution of serial homologous structures in particular, and of so-called serial structures in general, whether they are truly serial homologs or homoplasic ones.

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AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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