Letters

Pseudo-homeosis in avian feet

Galis *et al.*'s analysis of the evolutionary constraints on vertebrate autopodal (manus–foot) development [1] includes questionable assertions of homeotic changes of digit identity (changes of identity of one digit into another) in the avian foot. The first example concerns the totipalmate condition that defines pelecaniform birds wherein all four pedal digits comprise a common foot web, with digit I being more forwardly directed than is typical of most birds where it is directed posteriorly. The authors state: 'The fourth toe has moved forward', but, in fact, it is the first toe. The other example is the foot of piciform birds, wherein both digits I and IV are directed posteriorly to produce a zygodactylous (yoke-toed) condition. Such a foot is well adapted for perching (puffbirds, etc.), climbing (woodpeckers), and running (roadrunners, etc.). The authors' state: 'In all cases, the extra opposed digit has been obtained by changing the form of the second digit into that of the first, opposable, digit'. In fact, in all zygodactylous avian feet, it is merely that digit IV has been repositioned. In the heterodactylous foot of trogons, a similar yoke-toed foot involves reversing digit II. There has never been any question concerning the identity of the digits in any of the above cases [2]: they correspond to their appropriate trochleae, connected with fidelity by their appropriate ligaments. Interestingly, owls, ospreys, touracos and mousebirds have a temporary or facultatively zygodactylous foot in which the fourth toe can be held either anteriorly or posteriorly during perching [2]. Galis *et al.* [1] offer no arguments to support their implication of homeotic changes in the evolution of the avian foot.

Galis *et al.* [1] make the important point that evolutionary changes early in limb development are extremely constrained because of negative pleiotropic effects of deleterious mutations: 'Not only is the stage itself conserved, but also certain characters that are determined during that stage'. Thus, the lack of any homeotic changes in the feet of birds is the expected, and renders similar changes in the identity of all three manal digits extremely unlikely [3].

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Response from Galis, van Alphen and Metz

The letter by Feduccia [1] primarily concerns a semantic question – how does one define homeotic transformation and structural identity. It is tangential to the central theme of our review [2]. According to Bateson [3], who coined the term, homeotic transformations are transformations in which a structure partially or wholly changes into a different structure. He applied the term to describe how antennae of insects were partially transformed into legs (Antennapedia mutations). Similarly, he mentioned how cervical and lumbar vertebrae can undergo homeotic transformation into thoracic vertebrae by acquiring so-called cervical and lumbar ribs. Homeotic transformations can be complete in that all characters are transformed, but, more commonly, they are partial and not all morphological characters are changed. Recent molecular data have shown that, in the case of the Antennapedia mutation and the cervical and lumbar ribs, not only is the end result a homeotic change, but the developmental pathway for the transformed structure is also changed partly, or wholly, into that of the structure whose identity is taken over (co-option of pathways).

However, as Feduccia correctly indicated, we should have written that the identity of digit IV has changed to that of I in the case of the parrots, cuckoos and woodpeckers [2]. When we wrote for the pelican 'the fourth toe has moved forward', we actually meant fourth in a numerical sense and not in the sense of digit IV. We apologize for the ambiguity.

For our central hypothesis, it is immaterial whether the digit changes are homeotic, or which digits were involved, as long as the changes do not occur during the sensitive phylotypic period, but thereafter. However, we believe that, in the case of the above-mentioned birds, and the koala and the chameleons, (some of) the morphological characteristics (including position) of one digit have changed into that of another and therefore warrant the term homeotic change. We even think that it is probable that part of the developmental pathway of the digit has been changed into that of digit I, with two opposable digits as a result. However, more research is necessary for a full appraisal of the type of the transformation.

More attention should be paid to the occurrence of homeotic shifts in birds, whether complete or superficial, because it bears on the hypothesis of Wagner and Gauthier [4] of a homeotic digit shift of digits I,II,III in theropods into II,III,IV in birds. The occurrence of full homeotic shifts elsewhere would make this hypothesis more likely. To make this hypothesis really believable, one has to come up with a good adaptive scenario. Regardless of the likelihood of this particular digit shift, we think that, in general, the occurrence of homeotic digit shifts in birds and other tetrapods is less constrained than are polydactyly mutations, because of the differences in timing during development.

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