References

1 Sloan, C.P. (1999) Feathers for *T. rex*? *Nat. Geogr. Mag.* 196, 98–107
2 Feduccia, A. (1999) *The Origin and Evolution of Birds* (2nd edn), Yale University Press
3 Galis, F. (2001) Digit identity and digit number: indirect support for the descent of birds from theropod dinosaurs. *Trends Ecol. Evol.* 16, 16
4 Wagner, G.P. and Gauthier, J.A. (1999) 1,2,3=2,3,4: a solution to the problem of the homology of the digits in the avian hand. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5111–5116
5 Drossopoulou, G. *et al.* (2000) A model for anteroposterior patterning of the vertebrate limb based on sequential long- and short-range Shh signalling and Bmp signalling. *Development* 127, 1337–1348
6 Burke, A.C. and Feduccia, A. (1997) Developmental patterns and the identification of homologies in the avian hand. *Science* 278, 666–668
7 Hinchliffe, R. (1997) The forward march of the bird–dinosaurs halted? *Science* 278, 596–597
8 Müller, G.B. and Alberch, P. (1990) Ontogeny of the limb skeleton in *Alligator mississippiensis*: developmental invariance and change in the evolution of archosaur limbs. *J. Morphol.* 203, 151–164
9 Feduccia, A. (1999) 1–2–3=2–3–4: accommodating the cladogram. *Proc. Natl. Acad. Sci. U. S. A.* 96, 4740–4742

Digit homology of birds and dinosaurs: accommodating the cladogram

Response from Galis

When hypothesizing evolutionary transitions, scientists attempt to construct the most parsimonious scenario. As Feduccia states[1], most scientists agree that the scenario in which birds descend from dinosaurs is the most parsimonious. However, this scenario faces one major hurdle – the mismatch of the digits. When we assume that birds are derived from theropod dinosaurs and that the digits of birds are II–III–IV, there are two possible hypotheses: (1) avian ancestors had digits II–III–IV or (2), as was proposed by Wagner and Gauthier[2], there has been a homeotic shift from digits with identity I–II–III to digits with identity II–III–IV. On the basis of the present fossil record, the second hypothesis is the most probable.

Feduccia claims that the gap at the position of digit I in the embryonic hand of an eight-day chick argues against a homeotic shift. I disagree. Let us compare the situation to that in vertebrae. In homeotic changes of vertebrae, two half somites that would normally develop into a given vertebra develop the identity of a neighbouring vertebra instead. Therefore, for a homeotic change of digits, the initial Anlagen of digits should form normally, as occurs in somites. Subsequently, the Anlage of digit II is expected to develop with the identity of digit I, digit III with the identity of digit II, etc. In the embryonic wings of ducks, ostriches, terns, chicks, penguins and gulls prechondrification-Anlagen of four, or possibly five, digits are formed[3–10]. In the chondrification phase of all these species, digit II has shifted half of the way, or even wholly, towards the position of digit I. In the hand of a gull (Fig. 1a), digit II clearly lies in the position of digit I in the foot (Fig. 1b) (Refs 3,4), digits III and IV have hardly shifted and there is a gap between digits II and III. Subsequently, digit II develops an identity that is similar to that of theropod digit I, III of II and IV of III, in agreement with a homeotic shift.

To analyse the plausibility of a homeotic shift further, it is useful to compare the vertebral situation. The most common homeotic changes occur in vertebrae at the border of a region[11]. For example, in ~5% of humans, the first lumbar vertebra changes into a thoracic one. Importantly, such a change is often accompanied by a homeotic change of the last lumbar vertebra into a sacral one[11]. This leaves the normal number of lumbar vertebrae, but the lumbar region starts one vertebra lower. Presumably, all lumbar vertebrae have shifted identity. Therefore, in the vertebral column, at least, identity shifts of serial structures do occur.

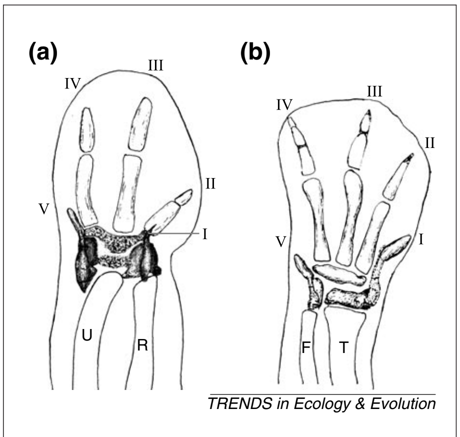

Fig. 1. Embryonic hand (a) and foot (b) of the gull, *Larus canus*. Note that the position of digit II in the hand is approximately in the position of digit I in the foot. Holmgren and others[3–5,8] claim to recognize digit I in some bird species, but this is disputed, at least for the chicken[10]. Abbreviations: F, femur; R, radius; T, tibia; U, ulna. Reproduced, with permission from Ref. 3.

Thus, in addition to the independence of the determination of digit number and identity demonstrated by Drossopoulou *et al.*[12,13], there is indirect support for a homeotic shift from the early development of vertebrae in several bird species. As long as no fossils of theropods are found with four digits and the first one reduced, the hypothesis of Wagner and Gauthier[2] provides us with the most probable explanation for the digit identity of birds and theropods.

Frietson Galis
Institute of Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300RA Leiden, The Netherlands.
e-mail: galis@rulsfb.leidenuniv.nl

References

1 Feduccia, A. (2001) Digit homology of birds and dinosaurs: accommodating the cladogram. *Trends Ecol. Evol.* 16, 285–286
2 Wagner, G.P. and Gauthier, J.A. (1999) 1,2,3=2,3,4: a solution to the problem of the homology of the digits in the avian hand. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5111–5116
3 Holmgren, N. (1933) On the origin of the tetrapod limb. *Acta Zool.* 14, 185–295
4 Holmgren, N. (1955) Studies on the phylogeny of birds. *Acta Zool.* 36, 243–328
5 Sieglbauer, F. (1911) Zur Entwicklung der Vogel extremität. *Z. wiss. Zool.* 97, 262–313
6 Leighton, V.L. (1894) The development of the wing of *Sterna wilsonii*. *Am. Nat.* 28, 761–774
7 Rosenberg, F.T. (1911) Beiträge zur Entwicklungsgeschichte und Biologie der Colymbidae. *Z. wiss. Zool.* 97, 199–217
8 Steiner, H. (1922) Die ontogenetische und phylogenetische Entwicklung des Vogelflügelskelettes. *Acta Zool.* 3, 307–360
9 Burke, A.C. and Feduccia, A. (1997) Developmental patterns and the identification of homologies in the avian hand. *Science* 278, 666–668
10 Hinchliffe, J.R. (1984) 'One, two, three' or 'Two, three, four': An embryologist's view of the homologies of the digits and carpus of modern birds. *Proc. Int. Archaeopt. Conf.* Eichstatt, pp. 185–197
11 Bardeen, C.R. (1904) Numerical vertebral variation in the human adult and embryo. *Anat. Anz.* 25, 97–519
12 Drossopoulou, G. *et al.* (2000) A model for anteroposterior patterning of the vertebrate limb based on sequential long- and short-range Shh signalling and Bmp signalling. *Development* 127, 1337–1348
13 Galis, F. (2000) Digit identity and digit number: indirect support for the descent of birds from theropod dinosaurs. *Trends Ecol. Evol.* 16, 26

http://tree.trends.com 0169–5347/01/$ – see front matter