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## The hand of birds revealed by early ostrich embryos

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**Abstract** The problem of resolving the homology of the digits of the avian hand has been framed as a conflict between paleontological and embryological evidence, the former thought to support a hand composed of digits I, II, III, because of similarity of the phalangeal formulae of the earliest known bird *Archaeopteryx* to that of Mesozoic pentadactyl archosaurs, while embryological evidence has traditionally favored a II, III, IV avian hand. We have identified the critical developmental period for the major features of the avian skeleton in a primitive bird, the ostrich. Analysis of digit anlagen in the avian hand has revealed those for digits/metacarpals I and V, thus confirming previous embryological studies that indirectly suggested that the avian hand comprises digits II, III, IV, and was primitively pentadactyl.

The identity of the digits of the avian tridactyl hand was first addressed in 1821 and has been hotly debated since then (Meckel 1821; Holmgren 1955). Early avian embryos have three central digital condensations and a condensation for a reduced digit/metacarpal V which disappears late in development; typically a condensation for digit/metacarpal I is absent. By incubating, preparing and comparing bracketed embryos of a paleognathous bird, the ostrich, we identified the critical period for digital anlagen, providing the first direct and demonstrable evidence to support previous embryological studies that implied that the avian hand comprises digits II, III, IV (Burke and Feduccia 1997; Hinchliffe 1997).

A deep split between neognathous and paleognathous birds is evidenced by Lower Cretaceous fossils of the paleognaths *Ambiortus* and *Otogornis* from Mongolia and China (Kurochkin 1999). Because paleognaths are the most likely primitive living birds, their embryology presents an opportunity to test hypotheses of skeletal homology obscured by derived modifications in other taxa.

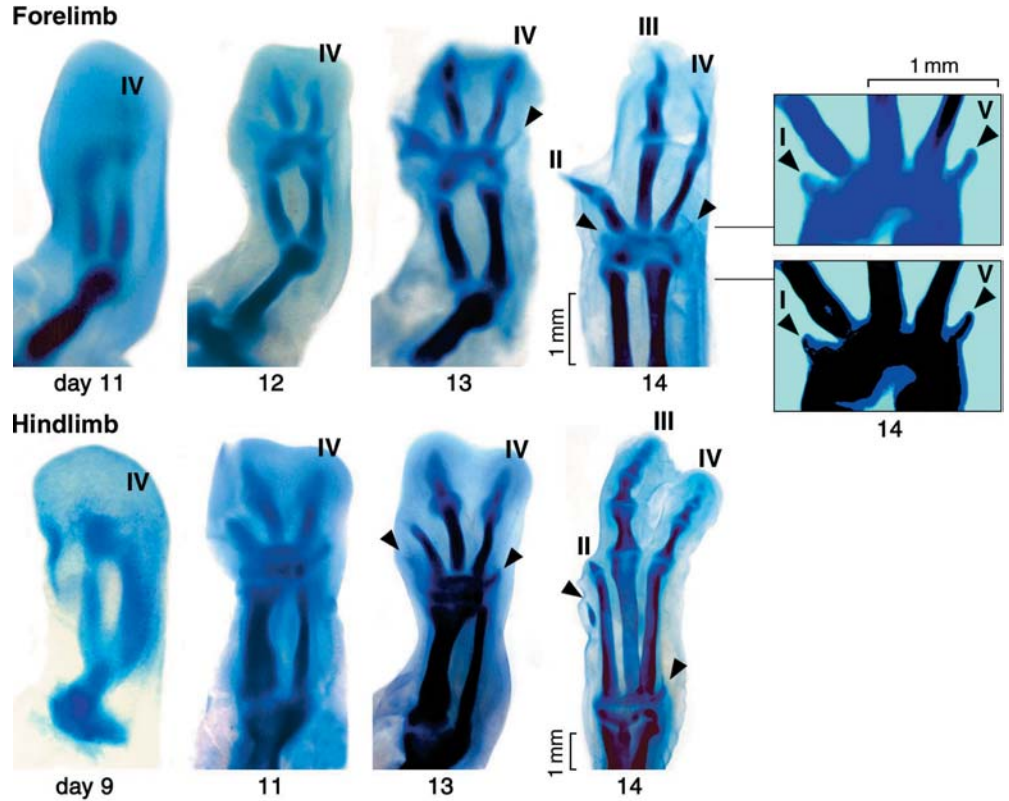
We bracketed ostrich embryos, concentrating on the period of development of major skeletal features. We incubated ostrich eggs and obtained embryos at 1-day intervals representing the period of early appendicular skeleton development, days 8–14 (or 15), (with two embryos at 10 and 14–15 days). Embryos were fixed in 10% formalin, stained with alcian blue, and cleared in a glycerol/potassium hydroxide series. We also studied embryos at 17, 18, 20, 22, 28 days of incubation.

Amniotes share a stereotyped, early developmental pattern of stylopod (humerus/femur) and zeugopod elements (radius/tibia and ulna/fibula), characterized by Y-shaped condensations (Müller and Alberch 1990; Burke and Feduccia 1997). Postaxial elements form a “primary axis”, an array that identifies, in sequence, ulna–ulnare–distal carpal IV – and ultimately digit IV – and equivalent hindlimb elements. At the highly conserved primary axis stage it is virtually impossible to distinguish bird from reptile, or fore- from hindlimb elements (Feduccia 1999). Thus, most embryological studies have reached the same conclusion; that the bird hand comprises digits II, III, IV, but lack of direct evidence from the embryo for the presence of a digit/metacarpal I, combined with the prevalence of the current dogma concerning a bird–theropod nexus and similarity of the phalangeal formulae of the earliest known bird *Archaeopteryx* to that of primitive archosaurs, has led to the conclusion that birds and theropod dinosaurs have similar hands (Shubin 1994).

Both fore- and hindlimbs of ostrich conform to the highly conserved amniote limb developmental pattern. While condensations for DI (digit I) and DV (CI, CV, condensations) are present, the middle three digits (DII, DIII, DIV) already show their putative adult morphology, by day 14–15. Figure 1 shows the transition from primary axis stage (far left) to stages with all condensations of hand and foot. Pedal condensations for vestigial metatarsals I and V are non-diffuse, as is the hand condensation for DV. The region for putative CI has progressed beyond the level of mesenchymal condensation to chondrogenesis, so that the stained region represents the

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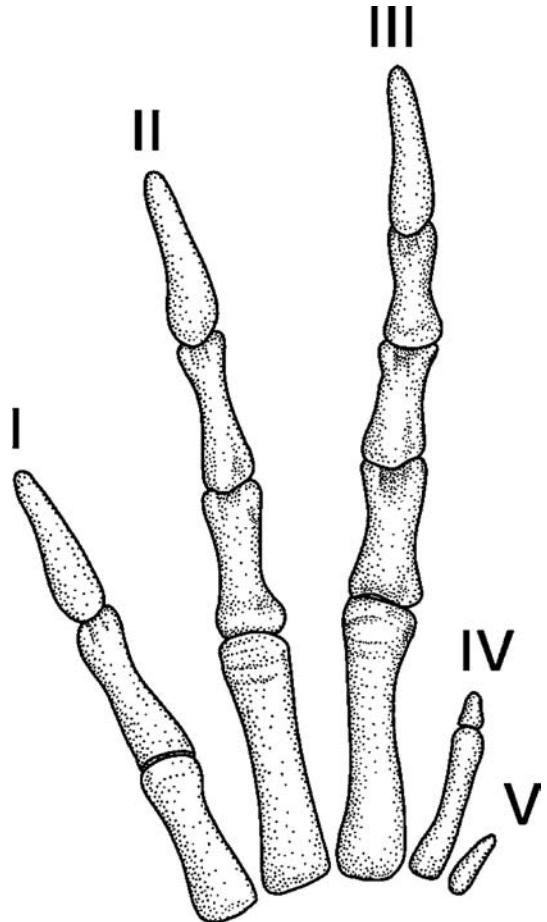
**Fig. 1** Comparison of right hand views of manus (*top row*) and pes (*bottom row*) development in *Struthio*, dorsal views, days 8–14 (or 15). *Arrows* point to condensations for digits I and V in manus and metatarsals I and V in pes; days given below each specimen. High contrast photos of enlargement of area of condensation for DI and DV, *far right*. Images are not to scale



chondroblastema for DI. By day 14–15, CV appears as a mildly staining feature but is present as a cartilaginous bar, with condensed cells at its base. A similar highly condensed central cylinder is visible in the condensation for DI, but is not as well developed as that of DV. By day 17, the transitory condensation for DI has disappeared, but the other four digits exhibit no position change and DV remains as a small, dark-staining cartilage sliver, but with visible osteogenesis.

Identification of the preaxial nubbin as the anlage for DI is supported by: (1) its location in the anatomical position where putative digit I/metacarpal I should appear; (2) its morphological similarity to the anlage for DV; (3) the fact that it extends distally beyond the base of other developing manal metacarpals and digits; and (4) the fact that the larger, centrally located digits would be asymmetrically skewed postaxially, if they represented digits I, II, III.

We discovered that within the 42-day incubation period for ostrich, most of the major skeletal features develop between days 8 and 15. By day 20 the ostrich embryo represents a small adult in most skeletal features. Because most avian phylogenetic studies using bird embryos have relied on embryos in the second half of development, usually at or near hatching, these studies have used



**Fig. 2** The hand of the primitive Late Triassic basal theropod *Herrerasaurus*, illustrating the trend in theropods towards the reduction and eventual elimination of digits IV and V. The hand of theropods therefore comprises digits I, II, III

embryos that exhibit a morphology of the specialized adult (McGowan 1984), with misleading results.

Although a homeotic frame shift has been proposed in the supposed theropod lineage leading to birds (Wagner and Gauthier 1999), evolutionary changes in early limb development are extremely constrained because of negative pleiotropic effects of deleterious mutations (Galis et al. 2001; Feduccia 2002), and the presence of a first digit in the early embryo argues for a primitive avian pentadactyl hand, with adult digits II, III, IV. Such a pattern follows the typical pattern of symmetrical reduction in amniotes, unlike the highly derived I, II, III hand of theropods (Fig. 2).

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