

Altriciality and the Evolution of Toe Orientation in Birds

João Francisco Botelho¹  · Daniel Smith-Paredes¹ · Alexander O. Vargas¹

Received: 3 November 2014 / Accepted: 18 June 2015
© Springer Science+Business Media New York 2015

Abstract Specialized morphologies of bird feet have evolved several times independently as different groups have become zygodactyl, semi-zygodactyl, heterodactyl, pamprodactyl or syndactyl. Birds have also convergently evolved similar modes of development, in a spectrum that goes from precocial to altricial. Using the new context provided by recent molecular phylogenies, we compared the evolution of foot morphology and modes of development among extant avian families. Variations in the arrangement of toes with respect to the anisodactyl ancestral condition have occurred only in altricial groups. Those groups represent four independent events of super-altriciality and many independent transformations of toe arrangements (at least four zygodactyl, three semi-zygodactyl, one heterodactyl, one pamprodactyl group, and several syndactyl). We propose that delayed skeletal maturation due to altriciality facilitates the epigenetic influence of embryonic muscular activity over developing toes, allowing for repeated evolution of innovations in their morphology.

Keywords Altricial · Anisodactyl · Heterodactyl · Pamprodactyl · Precocial · Syndactyl · Zygodactyl

Introduction

Many of the locomotor adaptations that allow extant birds to explore different niches occur in the feet. Modifications of the feet allow birds to be fast runners, to climb and perch

trees, to swim under and above the water surface, to hunt and fish, and to walk in the mud and over aquatic vegetation, among other abilities. Toe orientations in the foot can be described in six main types: *Anisodactyl* feet have digit II (dII), digit III (dIII) and digit IV (dIV) pointing forward and digit I (dI) pointing backward. From the basal anisodactyl condition four feet types have arisen by modifications in the orientation of digits. *Zygodactyl* feet have dI and dIV oriented backward and dII and dIII oriented forward, a condition similar to *heterodactyl* feet, which have dI and dII oriented backward and dIII and dIV oriented forward. *Semi-zygodactyl* birds can assume a facultative zygodactyl or almost zygodactyl orientation. *Pamprodactyl* feet have all four digits pointing forward. Finally, the partial fusion of two or more digits produces *syndactyl feet* (Fig. 1).

Birds have also been classified according to their morphology upon hatching and the level of parental care thereafter, in a spectrum that varies from precocial to super-altricial (Fig. 2a) (Starck 1993; Starck and Ricklefs 1998; Nice 1962). *Precocial* birds show active locomotion at hatching and follow their parents for food and/or protection (Fig. 2b); this is considered to be the ancestral condition to Neornithes (Tullberg et al. 2002; Birchart et al. 2013). *Semi-precocial* birds show active locomotion but are fed in the nest and leave it only in case of danger. Birds in the *altricial* spectrum hatch with poor motor activity and are totally dependent on their parents. They are locomotorily inactive and stay in the nest for long periods. Altricial birds can be subdivided in *semi-altricial*, *altricial* and *super-altricial* following morphological characteristics of hatchlings. Semi-altricial birds hatch with feathers and eyes open, altricial birds hatch with feathers, but eyes closed (Fig. 2c), and super-altricial birds hatch without feathers and eyes closed (Fig. 2d).

The independent evolution of similar traits in related lineages, despite different ecological demands and functional

✉ João Francisco Botelho
joaofranciscobotelho@gmail.com

¹ Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Facultad de Ciencias de la Universidad de Chile, Las Palmeras 3425, 7800003 Santiago, Chile

Fig. 1 The diversity of foot morphology. Illustration of bird foot diversity modified from Cuvier *Le Règne Animal* (Cuvier 1836), **a**: buzzard; **b**: woodpecker; **c**: trogon; **d**: kingfisher; **e**: swift

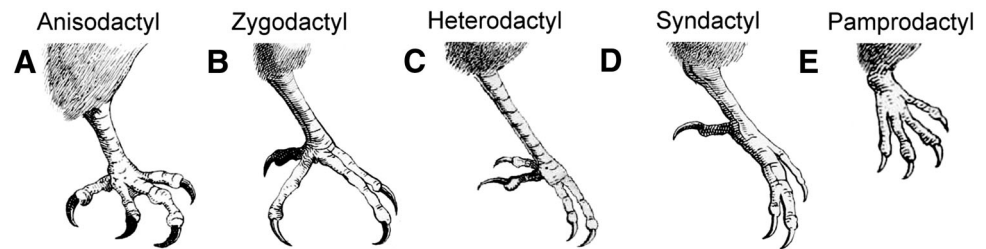
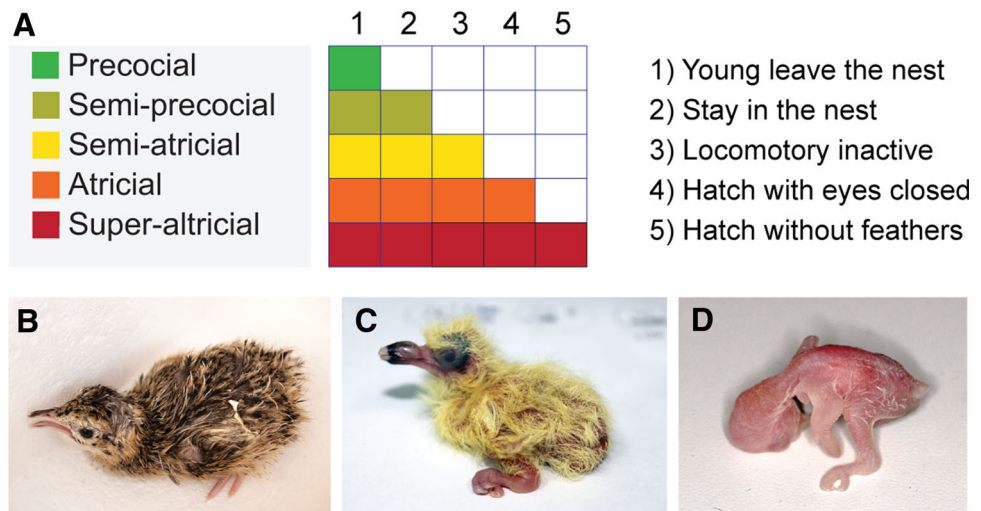


Fig. 2 The diversity of developmental modes. **a**: The mode of development is classified in a spectrum that goes from precocial to super-altricial following behavioural and morphological characteristics; **b**: *Nothoprocta perdicaria* (Tinamidae), a precocial new-hatching; **c**: *Columba livia* (Columbidae), an altricial new-hatching; **d**: *Melopsittacus undulatus* (Psittacidae), a super-altricial new-hatching. **a** modified from (Starck and Ricklefs 1998)



contexts, could indicate the existence of developmental constraints channelling their independent evolution (Alberch 1982; Arthur 2001). To explore this possibility, it is necessary to examine the underlying developmental mechanisms. We have recently shown that the development of an opposable dIV in the foot of the zygodactyl budgerigar requires embryonic muscular activity (Botelho et al. 2014). The same is true for the opposable hallux of the chicken foot (Botelho et al. 2015). Importantly, the change in orientation of these digits occurs at stages of immature cartilage, before chondrocyte terminal differentiation. This suggests a developmental window, before cartilage maturation and ossification, in which these transformations are possible. It is also well known that the timing of skeletal maturation is correlated with the developmental modes of birds, with a delayed onset of ossification in altricial forms (Starck 1993). With this information in mind, we explored how the evolution of specialized feet in birds could be related to that of developmental modes. To this effect, we made use of the important new evolutionary context provided by exhaustive molecular phylogenies of modern birds, that only recently have become available (Hackett et al. 2008; Yuri et al. 2013; Ericson et al. 2006; Kimball et al. 2013; McCormack et al. 2013; Jarvis et al. 2014). We found a previously overlooked yet striking

correlation between variations in the arrangement of toes and the altricial mode of development. We discuss how developmental constraints may have driven the repeated evolution of modified feet in modern birds.

Modes of Development and Foot Morphology in the New Avian Molecular Phylogenies

Precocial and Semi-precocial Birds are Anisodactyl

Palaeognathae (tinamous and ratites) and Galloanseres (chickens, ducks, and allies) are the most basal clades of extant birds and all of them conserve the ancestral precocial condition (Fig. 3). The remaining extant birds comprise a clade called Neoaves, where the precocial mode of development is still present in several families like grebes (Podicipedidae), sandgrouses (Pteroclididae), most shorebirds (Charadriiformes), Gruiformes sensu stricto and loons (Gaviidae). The semi-precocial mode of development evolved several times in Neoaves, as for example, in kagus (Rhynchotidae), the hoatzins (Opisthocomidae), and some shorebirds. All precocial and semi-precocial birds are anisodactyl.

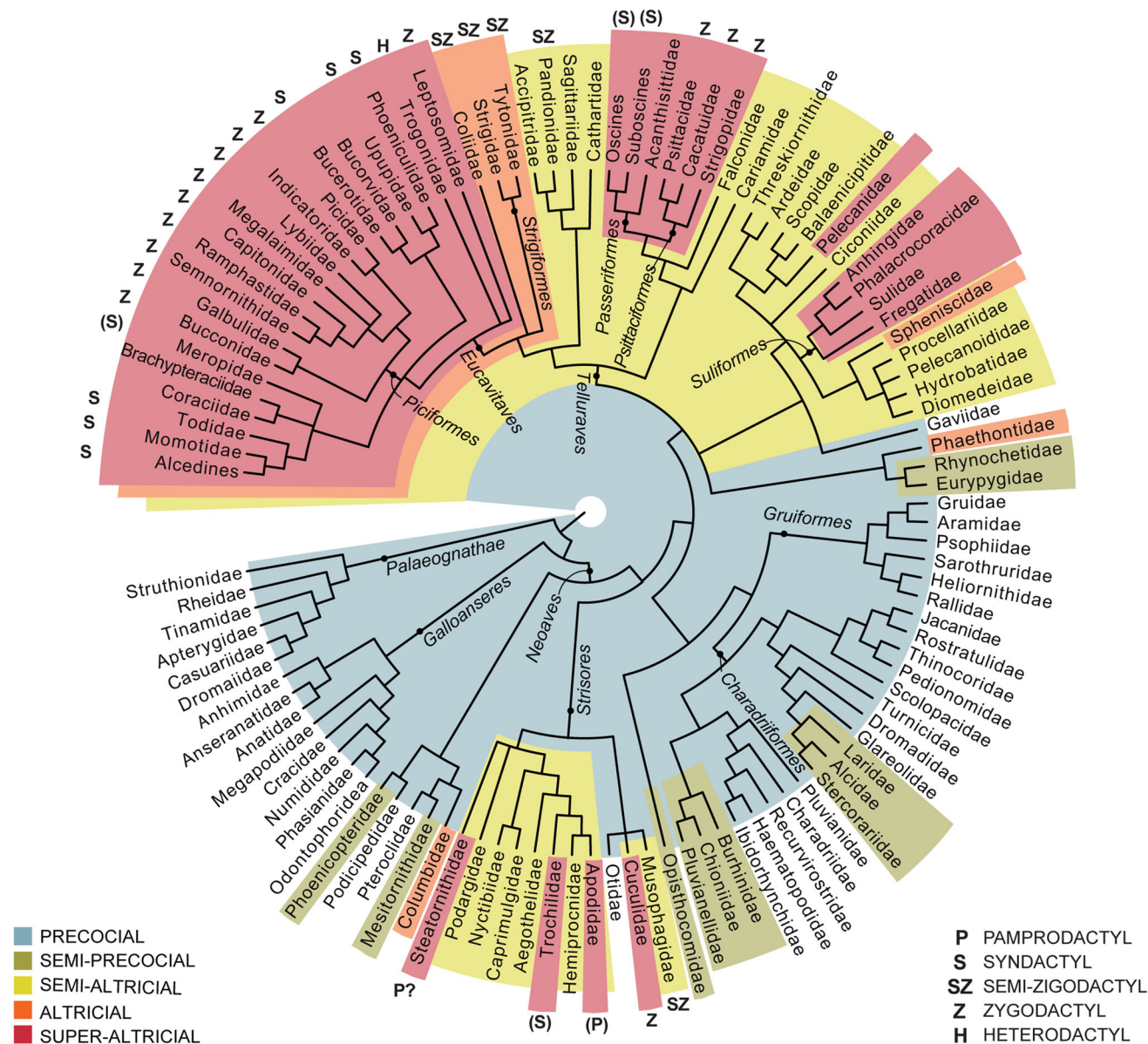


Fig. 3 The phylogenetic distribution of developmental modes and foot morphologies. A coherent phylogeny based on (Hackett et al. 2008; Yuri et al. 2013; Ericson et al. 2006; Kimball et al. 2013; McCormack et al. 2013; Jarvis et al. 2014) of extant bird families

Zygodactyl and Heterodactyl Birds are Super-Altricial

Zygodactyl feet are present in cuckoos (Cuculidae), the courel (Leptosomidae),¹ parrots (Psittaciformes), woodpeckers, toucans, barbets, jacamars and allies (Piciformes) (Fig. 3). This foot morphology has evolved at least four

¹ The courel (*Leptosomus*) is sometimes described as semi-zygodactyl (Forbes 1880), but modern observations of live nestling and adults show that it is fully zygodactyl, even when not perched (Goodman 2001; Forbes-Watson 1967).

depicting the mode of development and the morphology of foot. Passeriformes have been presented as Acanthisittidae, Suboscines and Oscines, as they comprise more than half of total bird families and are uniform in relation to both traits

times independently associated to three independent origins of super-altriciality. Non-zygodactyl fossil representatives of stem Cuculidae (Baird and Vickers-Rich 1997; Mayr 2006; Mourer-Chauviré et al. 2013), Leptosomidae (Mayr 2008a), Psittaciformes (Mayr et al. 2010; Mayr 2011; Ksepka and Clarke 2012; Mayr et al. 2013) and Piciformes (Mayr 2009) are known, which confirms their independent evolution. A zygodactyl extinct family, called Zygodactylidae, is considered sister group of Passeriformes (Mayr 2008b). Trogons (Trogonidae) are the only extant heterodactyl birds and, as all Eucavitaves, are super-altricial (Fig. 3).

Semi-zygodactyl Birds are Altricial or Semi-altricial

Semi-zygodactyl birds are able to facultative abduct dIV, reaching a zygodactyl or semi-zygodactyl position. Turacos (Musophagidae), ospreys (Pandionidae), owls (Strigiformes), and mousebirds (Coliidae) are semi-zygodactyl. Musophagidae and Pandionidae are semi-altricial, whereas Strigiformes and Coliidae are altricial (Fig. 3). Semi-zygodactyly in extant birds is inferred to have evolved at least three times: in the independently semi-altricial turacos and osprey, and the common ancestor of owls and mousebirds. Semi-zygodactyl forms are closely related to fully zygodactyl clades, which suggests semi-zygodactyly may be an intermediate stage towards the evolution of full zygodactyly. This is also suggested by fossil raptor-like stem Psittaciformes, which are believed to have been semi-zygodactyl (Mayr et al. 2010, 2013). However, the developmental mode of these extinct forms currently cannot be determined.

Pamprodaactyl Birds are Super-Altricial

Apodini swifts (Apodidae) represent the only uncontroversial pamprodaactyl clade.² Swifts are Strisores (Mayr 2010), a clade composed mainly by semi-altricial anisodactyl families (Fig. 3). Super-altriciality is inferred to have evolved at least twice inside Strisores: in Apodiformes (swifts and hummingbirds) and oilbirds (Steatornithidae) (Fig. 3). Pamprodaactyly in swifts and the peculiar morphology of the oilbird foot evolved associated to those two independent origins of super-altriciality. Interestingly, the fossil *Eurofluvioviridaves* was first classified in Strisores (Mayr 2005), but later dismissed as *incertae sedis* based on the morphology of its zygodactyl feet (Nesbitt et al. 2011).

Syndactyl Birds are Super-Altricial

Syndactyly occurs as different grades of fusion of proximal phalanges of two or three toes in several passerine families (Passeriformes) (Clark 1981; Raikow 1987), most kingfishers (Alcedines), todies (Todidae), motmots (Motmotidae), bee-eaters (Meropidae), jacamars (Galbulidae), wood-hoopoes (Phoeniculidae), hoopoes (Upupidae), hornbills (Bucerotidae) (Maurer and Raikow 1981; Raikow 1985; Cracraft 1971b), trogons (Trogonidae) and some hummingbirds (Trochilidae) (Mayr 2003; Maurer and Raikow 1981). The trait is highly plastic, but restricted to super-altricial birds. Except for Trochilidae

and Passeriformes, all syndactyl species are Eucavitaves, and the trait could be a synapomorphy for the clade (Kimball et al. 2013), secondarily lost by clades as Bucconidae and some Coraciidae (Fig. 3).

The Evolution of Modified Digits Coincides Repeatedly with the Altricial Spectrum

The new molecular phylogenies allow unprecedented resolution on the number of times birds have independently evolved changes in developmental mode and foot morphology. Some convergence was suspected (Fain and Houde 2004), but morphological phylogenies have often resulted in clades of birds with similar developmental mode and foot morphology (Wetmore 1934; Livezey and Zusi 2007). Recent molecular phylogenies have revealed that many of these clades were polyphyletic, pointing to numerous events of convergent evolution for both traits. In this context, it is striking that modified digits have repeatedly coincided with the evolution of developmental modes within the altricial spectrum. The correlation works one-way only: All birds with these foot specializations are altricial, but not all altricial birds carry these specializations. This suggests that altriciality is necessary, but not sufficient: modified digits are allowed within altriciality, but also require for additional factors. Remarkably, we found no reference in the literature to the possible link between the evolution of altriciality and foot specializations. This may be because without the molecular phylogenies, the correlation is less striking: Fewer independent events are inferred, that could be dismissed as coincidental. Also, no reasonable hypothesis of a mechanism had come into focus that could link developmental mode and toe modifications. Evolutionary explanations of foot morphology focused mostly on direct selection of adaptive foot morphology, never on developmental modes.

Embryonic Muscular Activity and Evolution of Toe Orientation

We have recently researched the developmental mechanisms underlying digit orientation in birds, producing information that allows for a reasonable hypothesis linking developmental mode and toe modifications (Botelho et al. 2014, 2015). A good example of toe orientation development is the opposable hallux (dI) common to most birds. The hallux is opposable chiefly because of the twisted shape of its metatarsal. In early theropod ancestors, the foot is very similar but the hallux was a non-opposable digit with a straight metatarsal. In Galliformes, torsion of metatarsal I occurs by embryonic muscular activity on the

² The parakeet genus *Micropsitta* (Psittaciformes) and the oilbird (Steatornithidae) are considered pamprodaactyl by some authors, but their hallux seems to point medially, not forward (Collins 1983).

metatarsal, whose skeletal maturation is evidently delayed with respect to other digits, consisting almost entirely of immature cartilage (Botelho et al. 2015).

Skeletal maturation rates among birds vary importantly with developmental mode. A major characteristic of altricial birds is that late embryonic development is slowed down, followed by fast post-hatching growth rates (except for the Aequornithes, who do not have modifications in digit orientation) (Starck 1993) (Fig. 4a). The differences are particularly remarkable in the skeleton. Precocial and altricial birds begin ossification at similar stages, around HH32. Nevertheless, when altricial species hatch, large parts of the skeleton are still cartilaginous, while the skeleton of precocial hatchlings is mostly ossified (Starck 1993, 1998; Grady et al. 2014) (Fig. 4b). The slowing down of skeletal differentiation in altricial birds begins around the second half of the embryonic period (HH35) precisely when the musculoskeletal system controlling the toes is functional and digit orientation is being defined (Fig. 4a). Metatarsophalangeal articulations mature later, finishing cavitation at HH38 (Winslow and Burke 2010; Ray et al. 2015). The development of zygodactyl feet in budgerigars (Psittaciformes) is caused by the action of asymmetrical forces, due to the loss of an intrinsic muscle of the foot (Botelho et al. 2014) (Fig. 4c). Intrinsic muscles individually control the extension, flexion, adduction or abduction of toes. During the early embryogenesis of budgerigars, the dorsally placed *musculus extensor brevis digiti IV* degenerates, and in the absence of this muscle, the ventrally placed *musculus abductor digiti IV* abducts the embryonic dIV until it reaches a zygodactyl orientation. The same asymmetric muscular arrangement is present in the convergently zygodactyl Pici (Swierczewski and Raikow 1981). A similar yet different case of muscular asymmetry is seen in the opposable dII of heterodactyl trogons. Unlike dIV of zygodactyl birds, which shifts its position towards lateral until it points backwards, the dII of heterodactyl trogons shifts towards medial until it points backwards. Accordingly, in this case, it is the *musculus abductor brevis digiti II* that is present, and the *musculus adductor brevis digiti II* that is lost (Maurer and Raikow 1981). Importantly, budgerigars pharmacologically paralyzed *in ovo* develop anisodactyl feet (Botelho et al. 2014).

We propose that the observed correlation between altriciality and foot morphology could be explained considering that the action of foot muscles can modify the orientation and shape of skeletal elements in a more radical way when exerted over the immature embryonic skeleton of altricial birds. This could be because the development of embryonic articulations is plastic during a specific stage or “window” that is more prolonged in the generally slowed-down development of the skeleton of altricial birds (Fig. 4b). Intrinsic foot muscle organization is highly

variable (Pitsillides 2006) in extant birds (Hudson 1937, 1948; Maurer and Raikow 1981; Swierczewski and Raikow 1981; Raikow 1985, 1987; Berger 1960; George and Berger 1966). Missing or reduced muscles generate asymmetric forces over individual digits. However, these asymmetric forces can only transform the orientation of the digits if the skeleton and joints upon which they are acting is plastic during enough time. In this scenario, a transition from semi-zygodactyly to full zygodactyly may not require any further re-arrangements of musculature, which would be already asymmetrical in semi-zygodactyl birds: Rather, full zygodactyly may come about upon a change in the duration of the period of skeletal plasticity, as suggested by the fact that semi-zygodactyl birds are not super-altricial, but altricial or semi-altricial (Fig. 3). Zygodactyly, heterodactyly, and pamprodactyly would have evolved in every super-altricial clade where asymmetric forces were acting on toes. A similar case is provided by the evolution of the hallux during the dinosaur-bird transition. Muscular connectivity in this digit is inferred to have been essentially the same in theropod dinosaurs. A subsequent delay in skeletal maturation, related to pedomorphosis, could have triggered actual torsion by extending the window of developmental plasticity (Botelho et al. 2015).

Other special cases in the evolution of bird feet are also consistent with skeletal plasticity under embryonic musculature. For instance, the hallux of penguins has secondarily become non-opposable, with a non-twisted, straight metatarsal (Botelho et al. 2015). However, unlike dinosaurs, this digit has secondarily lost its musculature, lacking both *flexor hallucis longus* and *flexor hallucis brevis* (George and Berger 1966; Hudson 1937; Raikow 1985). This is consistent with the absence of muscular activity, which will lead to a straight, non-twisted morphology, as proven by pharmacological paralysis in the chicken (Botelho et al. 2015). In this context, syndactyly emerges as another characteristic possibly related to the loss of intrinsic muscles of the foot. Experimental evidence shows that lack of movement often leads to the fusion of elements (Hall and Herring 1990; Murray and Drachman 1969; Pitsillides 2006). Syndactyly could be direct or indirectly related to the reduction of movements in the proximal phalanx, as Upupiformes, Alcediniformes, Passeriformes and Trochilidae have lost most of the intrinsic musculature of the foot, specially the abductors (Zusi and Bentz 1984; Maurer and Raikow 1981; Swierczewski and Raikow 1981; Raikow 1987; Hudson 1937). Non-syndactyl clades closely related to syndactyl birds usually present shallow *incisures intertrochlearis lateralis* and small divarication angles between digits, already indicating the presence of modified muscles of the foot.

The case of Passeriformes may be intriguingly more complex. As was mentioned above, Passeriformes lacks all

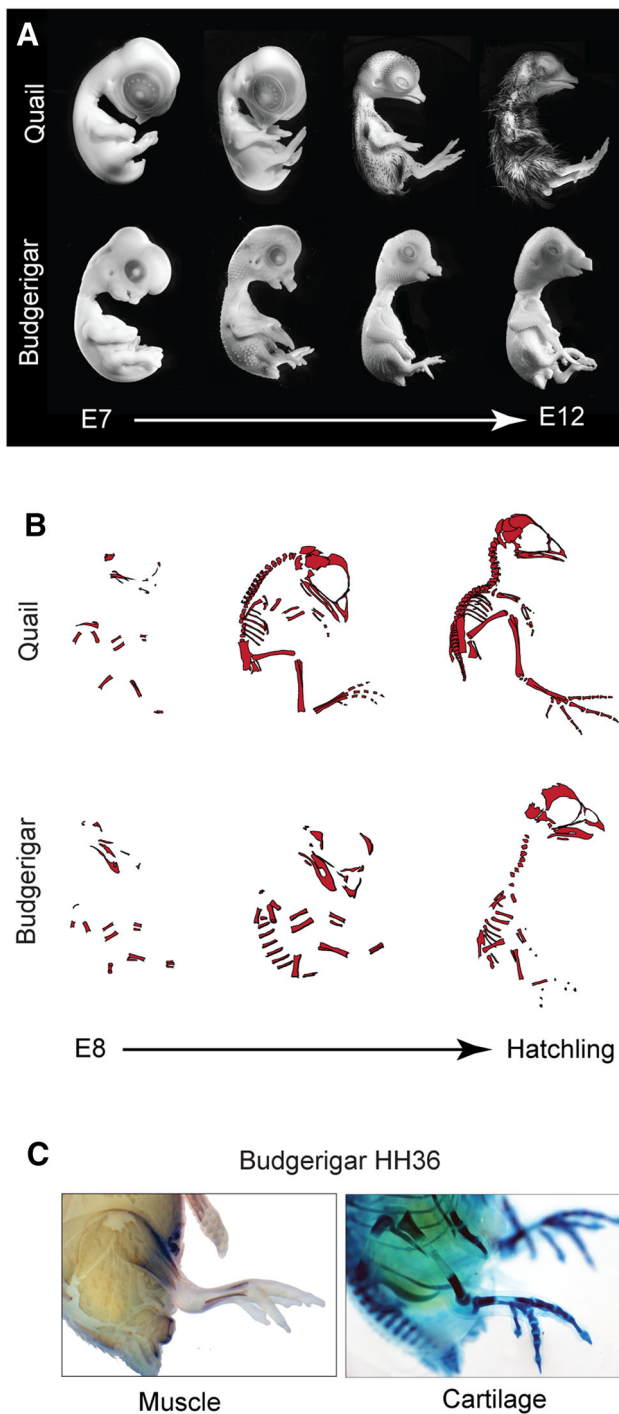


Fig. 4 The altricial mode of development and its relation to skeletal plasticity. **a:** Comparison between the two contrasting developmental modes of the precocial and anisodactyl quail (*Coturnix japonica*) and the super-altricial and zygodactyl budgerigar (*Melopsittacus undulatus*); **b:** comparison of ossification progress during embryonic time between quail and budgerigar. The skeletons of both species begin to ossify around the same stage. Upon hatching time, precocial birds are almost completely ossified, locomotory active and able to feed alone, while altricial birds are poorly ossified, locomotory inactive and unable to feed by themselves; **c:** Budgerigar embryos stained with antibody against myosin and Alcian Blue at HH36 showing, respectively, muscles and cartilages interacting before the development of zygodactyly

zygodactyl, bringing forth a scenario in which these ancestors could have first lost the *musculus extensor brevis digiti IV*, becoming zygodactyl, but then further lost the *musculus abductor digiti IV*, becoming once again anisodactyl or syndactyl. Anisodactyly in Passeriformes may thus be secondarily acquired from a zygodactyl ancestor by the absence of intrinsic muscles controlling digit IV. Altricial birds that are known to have symmetric intrinsic muscles of the foot, like pigeons, are anisodactyl (Cracraft 1971a).

Conclusion

Evolutionary changes in the orientation of digits are generally approached from an adaptive perspective (Bock and Miller 1959; Mayr 2009; Zelenkov 2007; Collins 1983). Some of these hypotheses seem very appropriate, but others are non-satisfactory. Exclusively adaptive perspectives are unable to explain why some perching birds are anisodactyl, while others are zygodactyl, or why only some swifts are pamprodactyl. Indeed, foot usage—perching, running, walking, hunting, swimming, etc.—could not be statistically ascribed to specific ecological habits, beyond a basic separation between terrestrial and aquatic birds (Mitchell and Makovicky 2014; Bell and Chiappe 2011). The altricial-precocial spectrum, in the same way, cannot be confidently associated to ecological attributes (Ricklefs 1984). As an alternative to adaptive explanations based only on “ultimate causes” (Mayr 1961), we propose that developmental mechanisms (“proximate causes”) (Caponi 2012; Laland et al. 2011) are important drivers in the evolution of foot morphology, leading to the observed pattern of repeated convergence among independent lineages of altricial birds.

Developmental and metabolic changes have been pointed out as crucial to the evolution of birds (Balanoff et al. 2013; Grady et al. 2014). Importantly, it has been argued that birds are paedomorphic dinosaurs (Bhullar et al. 2012) which led to radical transformations in several juvenile

intrinsic musculature controlling digits II, III and IV, and are either anisodactyl or syndactyl (a vestigial *musculus abductor digiti IV* is still present in some Passeriformes (George and Berger 1966)). Interestingly, molecular phylogenies place the zygodactyl Psittaciformes as the extant sister clade to Passeriformes, and another zygodactyl group, the fossil Zygodactylidae, is considered the extinct sister clade of Passeriformes (Mayr 2008b). This suggests that the ancestors of Passeriformes could have been

characteristics: the loss of teeth, large brains and eyes, fusion of bones, etc. The notion that super-altriciality prolongs the plasticity of the embryonic skeleton under embryonic muscular activity suggests that similar changes in developmental rates may also be an important driver for the evolution of differences amongst extant birds. This provides a link between heterochronic changes and previous arguments for the evolutionary relevance of the epigenetic mechanism of embryonic muscular activity (Muller 2003; Newman and Muller 2005; Newman et al. 2013). Further ontogenetic investigations shall contribute to the comprehensive understanding of the causes of modern avian diversification.

Acknowledgments We are thankful to Macarena Faunes, Jorge Mpodozis, Sergio Soto-Acuña, Mauricio Cornejo, Vitor Piacentini and Gonzalo Marín for the useful commentaries on the manuscript. Daniel Nuñez-Leon kindly provided some bird photos.

Compliance with Ethical Standards

Funding This Project was funded by FONDECYT (1150906).

References

- Alberch, P. (1982). Developmental constraints in evolutionary processes. In J. T. Bonner (Ed.), *Evolution and Development* (pp. 313–332). Berlin: Springer.
- Arthur, W. (2001). Developmental drive: An important determinant of the direction of phenotypic evolution. *Evolution and Development*, 3(4), 271–278.
- Baird, R. F., & Vickers-Rich, P. (1997). *Eutreptodactylus itaboraiensis* gen. et sp. nov., an early cuckoo (Aves: Cuculidae) from the Late Paleocene of Brazil. *Alcheringa: An Australasian Journal of Palaeontology*, 21(2), 123–127. doi:10.1080/03115519708619179.
- Balanoff, A. M., Bever, G. S., Rowe, T. B., & Norell, M. A. (2013). Evolutionary origins of the avian brain. *Nature*, 501(7465), 93–96. doi:10.1038/nature12424.
- Bell, A., & Chiappe, L. M. (2011). Statistical approach for inferring ecology of Mesozoic birds. *Journal of Systematic Palaeontology*, 9(1), 119–133.
- Berger, A. J. (1960). Some anatomical characters of the Cuculidae and the Musophagidae. *The Wilson Bulletin*, 72(1), 60–104.
- Bhullar, B. A., Marugan-Lobon, J., Racimo, F., Bever, G. S., Rowe, T. B., Norell, M. A., et al. (2012). Birds have paedomorphic dinosaur skulls. *Nature*, 487(7406), 223–226. doi:10.1038/nature11146.
- Birchard, G. F., Ruta, M., & Deeming, D. C. (2013). Evolution of parental incubation behaviour in dinosaurs cannot be inferred from clutch mass in birds. *Biology Letters*, 9(4), 20130036. doi:10.1098/rsbl.2013.0036. ISSN: 1744-957X.
- Bock, W. J., & Miller, W. D. (1959). The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. *American Museum Novitates*, 1931, 1–45.
- Botelho, J. F., Smith-Paredes, D., Nuñez-Leon, D., Soto-Acuña, S., & Vargas, A. O. (2014). The developmental origin of zygodactyl feet and its possible loss in the evolution of Passeriformes. *Proceedings of the Royal Society B: Biological Sciences*. doi:10.1098/rspb.2014.0765.
- Botelho, J. F., Smith-Paredes, D., Soto-Acuña, S., Mpodozis, J., Palma, V., & Vargas, A. O. (2015). Skeletal plasticity in response to embryonic muscular activity underlies the development and evolution of the perching digit of birds. *Scientific Reports*. doi:10.1038/srep09840.
- Caponi, G. (2012). *Réquiem por el Centauro: Aproximación epistemológica a la biología evolucionaria del desarrollo*. México: Centro de Estudios Filosóficos y Sociales Vicente Lombardo Toledano.
- Clark, G. A. (1981). Toe fusion in oscines. *The Wilson Bulletin*, 93(1), 67–76.
- Collins, C. T. (1983). A reinterpretation of pamprodactyly in swifts: A convergent grasping mechanism in vertebrates. *The Auk*, 100(3), 735–737.
- Cracraft, J. (1971a). The functional morphology of the hind limb of the domestic pigeon, *Columba livia*. *Bulletin of the AMNH. Bulletin of the American Museum of Natural History*, 144, 172–267.
- Cracraft, J. (1971b). The relationships and evolution of the rollers: Families Coraciidae, Brachypteraciidae, and Leptosomatidae. *The Auk*, 88(4), 723–752.
- Cuvier, G. (1836). *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée* (Vol. 3). Paris: Louis Hauman et Comp., libraires-éditeurs.
- Ericson, P. G., Anderson, C. L., Britton, T., Elzanowski, A., Johansson, U. S., Källersjö, M., et al. (2006). Diversification of Neoaves: Integration of molecular sequence data and fossils. *Biology Letters*, 2(4), 543–547. doi:10.1098/rsbl.2006.0523.
- Fain, M. G., & Houde, P. (2004). Parallel radiations in the primary clades of birds. *Evolution*, 58(11), 2558–2573.
- Forbes, W. A. (1880). On the anatomy of *Leptosoma discolor*. *Proceedings of the Zoological Society of London*, 48(3), 465–475. doi:10.1111/j.1469-7998.1880.tb06585.x.
- Forbes-Watson, A. D. (1967). Observations at a nest of the cuckoo-roller *Leptosomus discolor*. *Ibis*, 109(3), 425–430. doi:10.1111/j.1474-919X.1967.tb04015.x.
- George, J. C., & Berger, A. J. (1966). *Avian myology*. New York: Academic Press.
- Goodman, S. (2001). Family leptosomatidae (Cuckoo-roller). In J. Hoyo, A. Elliot, & J. Sargatal (Eds.), *Handbook of the birds of the world. Mousebirds to hornbills* (Vol. 6, pp. 390–395). Barcelona: Lynx Edicions.
- Grady, J. M., Enquist, B. J., Dettweiler-Robinson, E., Wright, N. A., & Smith, F. A. (2014). Evidence for mesothermy in dinosaurs. *Science*, 344(6189), 1268–1272.
- Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J., et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320(5884), 1763–1768. doi:10.1126/science.1157704.
- Hall, B. K., & Herring, S. W. (1990). Paralysis and growth of the musculoskeletal system in the embryonic chick. *Journal of Morphology*, 206(1), 45–56. doi:10.1002/jmor.1052060105.
- Hudson, G. E. (1937). Studies on the muscles of the pelvic appendage in birds. *American Midland Naturalist*, 18(1), 1–108.
- Hudson, G. E. (1948). Studies on the muscles of the pelvic appendage in birds II: The heterogeneous order falconiformes. *American Midland Naturalist*, 39(1), 102–127.
- Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., et al. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, 346(6215), 1320–1331.
- Kimball, R. T., Wang, N., Heimer-McGinn, V., Ferguson, C., & Braun, E. L. (2013). Identifying localized biases in large datasets: A case study using the avian tree of life. *Molecular Phylogenetics and Evolution*, 69(3), 1021–1032. doi:10.1016/j.ympev.2013.05.029.

- Ksepka, D. T., & Clarke, J. A. (2012). A new stem parrot from the Green River Formation and the complex evolution of the grasping foot in Pan-Psittaciformes. *Journal of Vertebrate Paleontology*, 32(2), 395–406. doi:10.1080/02724634.2012.641704.
- Laland, K. N., Sterelny, K., Odling-Smee, J., Hoppitt, W., & Uller, T. (2011). Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful? *Science*, 334(6062), 1512–1516.
- Livezey, B. C., & Zusi, R. L. (2007). Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society*, 149(1), 1–95. doi:10.1111/j.1096-3642.2006.00293.x.
- Maurer, D. R., & Raikow, R. J. (1981). Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Annals of the Carnegie Museum*, 50(18), 417–434.
- Mayr, E. (1961). Cause and effect in biology. *Science*, 134, 1501–1506.
- Mayr, G. (2003). On the phylogenetic relationships of trogons (Aves, Trogonidae). *Journal of Avian Biology*, 34(1), 81–88. doi:10.1034/j.1600-048X.2003.03042.x.
- Mayr, G. (2005). A *Fluvioviridavis*-like bird from the Middle Eocene of Messel, Germany. *Canadian Journal of Earth Sciences*, 42(11), 2021–2037.
- Mayr, G. (2006). A specimen of *Eocuculus* Chandler, 1999 (Aves, Cuculidae) from the early Oligocene of France. *Geobios*, 39(6), 865–872. doi:10.1016/j.geobios.2005.10.007.
- Mayr, G. (2008a). The Madagascan “cuckoo-roller” (Aves: Leptosomidae) is not a roller—Notes on the phylogenetic affinities and evolutionary history of a “living fossil”. *Acta Ornithologica*, 43(2), 226–230. doi:10.3161/000164508x395360.
- Mayr, G. (2008b). Phylogenetic affinities of the enigmatic avian taxon *Zygodactylus* based on new material from the early oligocene of France. *Journal of Systematic Palaeontology*, 6(3), 333–344. doi:10.1017/s1477201907002398.
- Mayr, G. (2009). *Paleogene fossil birds*. Berlin: Springer.
- Mayr, G. (2010). Phylogenetic relationships of the paraphyletic ‘caprimulgid’ birds (nightjars and allies). *Journal of Zoological Systematics and Evolutionary Research*, 48(2), 126–137. doi:10.1111/j.1439-0469.2009.00552.x.
- Mayr, G. (2011). Well-preserved new skeleton of the Middle Eocene *Messelastur* substantiates sister group relationship between Messelasturidae and Halcyornithidae (Aves, Pan-Psittaciformes). *Journal of Systematic Palaeontology*, 9(1), 159–171. doi:10.1080/14772019.2010.505252.
- Mayr, G., Rana, R. S., Rose, K. D., Sahni, A., Kumar, K., Singh, L., et al. (2010). *Quercypsitta*-like birds from the early Eocene of India (Aves, Psittaciformes). *Journal of Vertebrate Paleontology*, 30(2), 467–478. doi:10.1080/02724631003617357.
- Mayr, G., Rana, R., Rose, K., Sahni, A., Kumar, K., & Smith, T. (2013). New specimens of the early Eocene bird *Vastanavis* and the interrelationships of stem group Psittaciformes. *Paleontological Journal*, 47(11), 1308–1314. doi:10.1134/S0031030113110105.
- McCormack, J. E., Harvey, M. G., Faircloth, B. C., Crawford, N. G., Glenn, T. C., & Brumfield, R. T. (2013). A phylogeny of birds based on over 1,500 loci collected by target enrichment and high-throughput sequencing. *PLoS One*, 8(1), e54848. doi:10.1371/journal.pone.0054848.
- Mitchell, J. S., & Makovicky, P. J. (2014). Low ecological disparity in early Cretaceous birds. *Proceedings of the Royal Society B: Biological Sciences*, 281(1787), 20140608.
- Mourer-Chauviré, C., Tabuce, R., Essid, E. M., Marivaux, L., Khayati, H., Vianey-Liaud, M., et al. (2013). A new taxon of stem group Galliformes and the earliest record for stem group Cuculidae from the Eocene of Djebel Chambi, Tunisia. In U. B. Göhlich & A. Kroh (Eds.), *Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution*. Austria: Verlag Naturhistorisches Museum Wien.
- Muller, G. B. (2003). Embryonic motility: Environmental influences and evolutionary innovation. *Evolution and Development*, 5(1), 56–60.
- Murray, P. D. F., & Drachman, D. B. (1969). The role of movement in the development of joints and related structures: The head and neck in the chick embryo. *Journal of Embryology and Experimental Morphology*, 22(3), 349–371.
- Nesbitt, S. J., Ksepka, D. T., & Clarke, J. A. (2011). Podargiform affinities of the enigmatic *Fluvioviridavis platyrhamphus* and the early diversification of Strisores (“Caprimulgiformes” + Apodiformes). *PLoS One*, 6(11), e26350. doi:10.1371/journal.pone.0026350.
- Newman, S. A., Mezentseva, N. V., & Badyaev, A. V. (2013). Gene loss, thermogenesis, and the origin of birds. *Annals of the New York Academy of Sciences*, 1289(1), 36–47.
- Newman, S. A., & Muller, G. B. (2005). Origination and innovation in the vertebrate limb skeleton: An epigenetic perspective. *Journal of Experimental Zoology Part B Molecular and Developmental Evolution*, 304(6), 593–609. doi:10.1002/jez.b.21066.
- Nice, M. M. (1962). Development of behavior in precocial birds. *Transactions of the Linnean Society*, 8, 1–212.
- Pitsillides, A. (2006). Early effects of embryonic movement: “A shot out of the dark”. *Journal of Anatomy*, 208(4), 417.
- Raikow, R. J. (1985). Locomotor system. In A. S. King & J. McLelland (Eds.), *Form and function in birds* (Vol. 3, pp. 57–147). London: Academic Press.
- Raikow, R. J. (1987). Hindlimb Myology and evolution of the old world suboscine passerine birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae). *Ornithological Monographs*, 41, 7–81.
- Ray, A., Singh, P. N. P., Sohaskey, M. L., Harland, R. M., & Bandyopadhyay, A. (2015). Precise spatial restriction of BMP signaling is essential for articular cartilage differentiation. *Development*, 142(6), 1169–1179.
- Ricklefs, R. E. (1984). The optimization of growth rate in altricial birds. *Ecology*, 65(5), 1602–1616. doi:10.2307/1939139.
- Starck, J. M. (1993). The evolution of avian ontogeny. In D. M. Power (Ed.), *Current Ornithology* (Vol. 10, pp. 275–366). New York: Plenum Press.
- Starck, J. M. (1998). Structural variants and invariants in avian embryonic and postnatal development. In J. M. Starck & R. E. Ricklefs (Eds.), *Avian growth and development: Evolution within the altricial-precocial spectrum* (pp. 59–88). New York: Oxford University Press.
- Starck, J. M., & Ricklefs, R. E. (1998). Patterns of development: The altricial-precocial spectrum. In J. M. Starck & R. E. Ricklefs (Eds.), *Avian growth and development (Oxford ornithology series)* (Vol. 8, pp. 3–30). New York: Oxford University Press.
- Swierczewski, E. V., & Raikow, R. J. (1981). Hind limb morphology, phylogeny, and classification of the piciformes. *The Auk*, 98, 466–480.
- Tullberg, B. S., Ah-King, M., & Temrin, H. (2002). Phylogenetic reconstruction of parental-care systems in the ancestors of birds. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 357(1419), 251–257. doi:10.1098/rstb.2001.0932.
- Wetmore, A. (1934). A systematic classification for the birds of the world, revised and amended. *Smithsonian Miscellaneous Collections*, 89(13), 1–11.
- Winslow, B. B., & Burke, A. C. (2010). Atypical molecular profile for joint development in the avian costal joint. *Developmental Dynamics*, 239(10), 2547–2557. doi:10.1002/dvdy.22388.
- Yuri, T., Kimball, R. T., Harshman, J., Bowie, R. C., Braun, M. J., Chojnowski, J. L., et al. (2013). Parsimony and model-based

analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology*, 2(1), 419–444. doi:[10.3390/biology2010419](https://doi.org/10.3390/biology2010419).

Zelenkov, N. V. (2007). The structure and probable mechanism of evolutionary formation of the foot in piciform birds (Aves: Piciformes). *Paleontological Journal*, 41(3), 290–297. doi:[10.1134/s0031030107030082](https://doi.org/10.1134/s0031030107030082).

Zusi, R. L., & Bentz, G. D. (1984). Myology of the purple-throated carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). *Smithsonian Contributions to Zoology*, 385, 1–70. doi:[10.5479/si.00810282.385](https://doi.org/10.5479/si.00810282.385).