Studium Integrale Journal 27 (2020), 68-77 – Zusätzliches Online-Material für

Vogelmerkmale bei Dinosauriern
Vorläuferstadien oder Konvergenzen?

www.si-journal.de/ jg27/heft2/dino-voegel.pdf

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Dieses PDF-Dokument enthält einige zusätzliche Texte, Anmerkungen und die komplette Literaturliste

Zitate zu schrittweisem Erwerb von Vogelmerkmalen

Hauptaussage: Vogelmerkmale erscheinen einzeln nach und nach schon vor der Entstehung der Vögel bei Dinosauriern.

• „In summary, a great many skeletal features that were once thought of as uniquely avian innovations—such as light, hollow bones, long arms, three-fingered hands with a long second finger, a wishbone, a backward-pointing pelvis, and long hind limbs with a three-toed foot—were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees“ (PADIAN & CHIAPPE 1998, 44).

• „Preliminary analysis of character evolution suggests that the major avian osteological characters were acquired during the early evolution of maniraptoran dinosaurs” (XU 2006, 4).

• „However, nearly every single character that at one time was thought to make something a ‘bird’ is now known to occur progressively earlier in theropod evolution. Therefore, ‘bird’ is a colloquial term that lacks a meaningful taxonomic or scientific basis as it has no precise phylogenetic meaning“ (TURNER et al. 2012, 14).

• „When placed together on a family tree, these fossils show that many anatomical components of the modern-bird flight apparatus evolved piecemeal over tens of millions of years of dinosaur evolution, for reasons unrelated to flight“ (BRUSATTE 2017, 793).

• „Indeed, if we look at theropod history across the whole of the Triassic, Jurassic and Cretaceous, we see a gradual, cumulative acquisition of bird-like features, ranging from wishbones and a pneumatised skeleton to complex feathers, a reduced, three-fingered hand, an enlarged sternum (breastbone) and tiny size. … „... a robust and well-supported model showing a prolonged, directional trend in size reduction in the theropod lineage leading to birds: a trend that is continuous across 50 million years of theropod history, and which shows the animals at successive nodes becoming ever-smaller as we get closer to birds in the phylogeny. … Then there’s the fact that, as we get closer to birds in the phylogenetic tree, we see an increasingly elaborate plumage, a more bird-like system of body and hindlimb orientation linked to a shift in the centre of gravity, a stiffer, slimmer tail, and a number of behaviours that involve a degree of climbing (BIRN-JEFFERY et al. 2012) and gliding (Dyke et al. 2013)“ (NAISH 2014).

• „... most of the 30 or more characteristics that distinguished the small, flying *Archaeopteryx* from ground-dwelling, carnivorous dinosaurs (theropods) emerged much earlier“ (BENTON 2014, 508).

• „Birds evolved significantly faster than other theropods, but they are indistinguishable from their closest relatives in morphospace. Our results demonstrate that the rise of birds was a complex process: birds are a continuum of millions of years of theropod evolution, and there was no great jump between

nonbirds and birds in morphospace, but once the avian body plan was gradually assembled, birds experienced an early burst of rapid anatomical evolution“ (BRUSATTE et al. 2014, 2386).
• „In general anatomical terms, birds are a continuum of millions of years of theropod evolution. There is no great jump between nonbirds and birds in morphospace. Instead, those features that today combine to set birds apart from other vertebrates—feathers, wishbones, air sacs, and hundreds more—evolved piecemeal in Mesozoic theropods“ (BRUSATTE et al. 2014, 2389).
• „What was once seen as a rapid adaptive radiation, in which *Archaeopteryx* rapidly acquired 30 or more avian apomorphies, is now seen as a stepwise process of more than 50 million years“ (PUTTICK et al. 2014, 1497).
• „Recent discoveries of spectacular dinosaur fossils … demonstrate that distinctive bird characteristics such as feathers, flight, endothermic physiology, unique strategies for reproduction and growth, and a novel pulmonary system originated among Mesozoic terrestrial dinosaurs. ... The iconic features of extant birds for the most part evolved in a gradual and stepwise fashion throughout archosaur evolution“ (XU et al. 2014).
• „Thus, there is no sharp line demarcating bird and nonbird—the distinction has become entirely arbitrary“ (WITMER 2002, 6).
• „Currently, Aves is without a character-based definition; the last notable attempt—more than half a century ago—employed three skeletal features (the presence of a furcula, retroverted pubes, and a reversed hallux) and the presence of feathers (de Beer 1954). However, these features no longer define Aves, being either present in non-avian dinosaurs (furcula, feathers) or absent in basalmost birds (retroverted pubis, reversed hallux)“ (O'CONNOR & ZHOU 2015, 334). Die Autoren sehen aber Möglichkeiten für eine biologische Definition der Vögel: Besitz eines Kropfes und Verlust des rechten Ovariums.
• „… many features that are commonly associated with birds, flight, and arboreal life, such as the thin-walled bones, the furcula, the long forelimbs, the sideways-flexing wrist, and feathers, evolved in animals other than birds and for purposes other than flight; they were later exapted for other functions“ (DE RICQLÈS et al. 2003, 373).
• „… many of the traits that are considered uniquely avian among extant amniotes actually arose before the origin of birds themselves“ (MAKOVICKY & ZANNO 2011, 10).
„The fact that scientists are having a difficult time distinguishing the earliest birds from their closest dinosaur relatives illustrates just how bird-like some non-bird dinosaurs were (…), and how the transition between non-bird dinosaurs and birds was gradual“ (BRUSATTE et al. 2015, 889).

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Zitate zum verbreiteten Auftreten von Konvergenzen

• „Homoplasy is **common** among theropod dinosaurs" (XU & POL 2013, 327). Fallbeispiel: „Lee & Worthy (2012) found that the deinonychosaurian status of *Archaeopteryx* is supported by more synapomorphies but that these characters are more homoplastic than those supporting the avialan affinities of *Archaeopteryx* (which are fewer but less homoplastic)" (XU & POL 2013, 327).
• „An accurate phylogeny is the basis for understanding avian origins, but coelurosaurian systematics is plagued by large amounts of missing data and **prevalent** homoplasies, …" (XU et al. 2009, 434).
• „Convergent evolution and mosaicism in character evolution among paravians is **commonplace**" (TURNER et al. 2012, 137).
• „This uncertainty is due to real observed homoplasies; suites of derived characters shared with other different clades of coelurosaurs whose distributions cannot be resolved without some reversals or convergences" (HOLTZ 2001, 116).
• „Considering the distribution and combination of morphological characters in the fossil record it goes clear that many or even most characters considered typical of birds, like reduction of teeth, reduction of manual claws, the horny bill, the pygostyle, reduction of the fibula etc., evolved more than once" (PETERS 2002, 353).
• „... the fact that avian features have arisen **repeatedly** and independently in theropod evolution now seems to be an inescapable conclusion" (WITMER 2002, 5).
• „The distribution of „avian" characters strongly suggests evolution in the maniraptoran clade was **highly homoplastic**" (O'CONNOR & SULLIVAN 2014, 4).

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Zitate zu Konvergenz Zahnverlust / Schnabel

„The loss of teeth must have appeared several times in the evolutionary history of birds because it has independently occurred in extant birds as well as more basal birds such as *Confuciusornis* and *Gobipteryx*" (ZHOU & ZHANG 2006, 368).
„Minimally, there are six lineages of Avialae that show evidence of tooth reduction, with four lineages exhibiting complete tooth loss. … Among avialaen [sic!] lineages exhibiting tooth reduction or loss, a rhamphotheca has also independently evolved …" (MEREDITH et al. 2015, 1)

„The known fossil record shows that the tooth reduction happened independently on multiple lineages of Cretaceous ornithuromorphs“ (WANG & ZHOU 2017, 13). Man beachte, dass mehrfache Konvergenz alleine innerhalb der Ornithuromorpha angenommen wird.
„At least seven transitions to edentulism occurred independently in theropod dinosaurs, all presumably accompanied by the appearance of a horny beak“ (WANG et al. 2017a, 10930).
„Teeth have been reduced or lost independently several times in various lineages of early avian evolution [e.g., *Sapeornis*, *Zhongjianornis*, Confuciusornithidae, Enantiornithes and Ornithurae]“ (ZHENG et al.2011, 15905).
„Tooth reduction occurred in many avian lineages and led to complete edentulism in Confuciusornithidae, the enantiornithine *Gobipteryx*, the basal ornithuromorphs Archaeorhynchus, Zhongjianornis, and Schizooura, as well as in Neornithes (Mayr 2017, 71; unter Bezugnahme auf Louchart and Viriot 2011).

Zitate zu unübersichtlichen Verwandtschaftsverhältnissen

• „… the increase in specimen data has complicated rather than clarified the problem of identifying the avian sister-group, revealing a mosaic of ‘avian’ morphologies inconsistently distributed among purportedly closely related clades of non-avian dinosaurs. … Basal birds themselves possess disparate morphologies and do not provide a clear picture of the plesiomorphic avian taxon: *Archaeopteryx* strongly resembles troodontids such as *Anchiornis* and *Xiaotingia* (Turner et al., 2012; Xu et al., 2011), while the robust skull of sapeornithiforms most strongly resembles those of recently discovered basal oviraptorosaurs such as *Caudipteryx* (Ji et al., 1998) and of the scansoriopterygid *Epidexipteryx*“ (O’CONNOR & SULLIVAN 2014, 4).
• „As a result of the high amount of homoplasy that characterizes derived maniraptoran evolution, the identity of the avian sister taxon remains debated despite the rapid accumulation of morphological data“ (O’CONNOR & SULLIVAN 2014, 23).
• „Each of these clades [Dromaeosauridae, Troodontidae, Deinonychosauria] possesses a different combination of avian characters distributed amongst the included taxa, …“ (O’CONNOR et al. 2011, 45).
• „Inferred relationships between theropod clades are complex and have changed dramatically over the past thirty years with the emergence of cladistic techniques“ (HENDRICKX et al. 2015, 1). „Though one might expect few major changes in theropod relationships in the future, large portions of theropod phyletic history remain obscure; …“ (HENDRICKX et al. 2015, 34).
• „The discovery of numerous small-sized paravian theropods in the Late Jurassic and Early Cretaceous of China in the past decades have greatly enhanced our understanding of basal paravian anatomy and evolution. However, they also provided sometimes confusing evidence of widespread convergence and parallel evolution in this clade, …“ (RAUHUT et al. 2018, 83).

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Anmerkungen

1 „In truth, birds *are* dinosaurs—they are one of the many subgroups that can trace their heritage back to the common ancestor of dinosaurs … You can think of it this way: birds are dinosaurs in the same way that bats are an aberrant type of mammal that can fly“ (BRUSATTE 2017, 53).

2 Z. B.: „The origin of birds is now one of the best understood major transitions in the history of life“ (BRUSATTE et al. 2015, R888).

3 „Instead the morphospace we produced was a mess: birds were interspersed among a bigger cloud of dinosaurs. There was no clear separation between them, indicating that the transition was so slow as to be imperceptible“ (BRUSATTE 2017, 55).

4 Allerdings ist gerade dieses bedeutsame Merkmal diesbezüglich umstritten: Manche Forscher halten Formen mit flächigen Federn für Vögel (ggf. sekundär flugunfähig). Und ob man (bei anderen Gattungen) haarartige Anhänge überhaupt als Federn interpretieren soll, ist stark theorieabhängig und nicht offensichtlich. Vergleiche dazu die genauere Analyse von JUNKER (2017).

5 Wichtig für starke Beweglichkeit des Handgelenks (beim Flug und Falten der Flügel am Boden)

6 Die Homologieverhältnisse sind hier aber umstritten, vgl. die Übersichtsarbeit von ULLRICH (2008).

7 Diese Fortsätze stabilisieren den Brustkorb und spielen eine Rolle bei der Einatmung. Siehe https://en.wikipedia.org/wiki/Uncinate_processes_of_ribs

8 Although virtually all recent analyses put Dromaeosauridae or Troodontidae (or the two together as Deinonychosauria) as the sister group of Aves, neither is truly the ancestor, and hence known forms like *Deinonychus* or *Troodon* can only go so far as models for the true avian ancestor“ (WITMER 2002, 16).

9 „According to this story, the development of flight was chaotic, with different dinosaurs experimenting with different airborne behaviors using different airfoil and feather arrangements (see the figure), until ultimately only modern birds survived“ (BRUSATTE 2017, 792).

10 Although some paravians like *Microraptor* may have been able to power themselves through the air, the authors found that not all paravians had this ability. Nor was the common ancestor of paravians and birds clearly a lift-producing flapper. Coupled with the many morphological differences among winged paravians and early birds, this suggests that powered flight may not have been a singular innovation of the lineage that led to modern birds, but a behavior that many different groups of small, feathered, winged paravians achieved independently“ (BRUSATTE 2017, 793).

11 Die Merkmalskombination aus einfachen Federn, befiederten Beinen, kurzen Vorderextremitäten und Merkmalen, die auf ein Bodenleben hinweisen, ist evolutionstheoretisch unerwartet. Vgl. PICKRELL (2017): „The distribution and type of feathers on its body are not consistent with the currently preferred scenario about the evolution of bird feathers and flight. That scenario assumes that long pennaceous feathers on arms and legs originated with arboreal four-winged gliders such as *Microraptor*.“ Für einen Bodenstart eines schnellen Läufers sind befiederte Beine nachteilig; für den Baumstart passen die kurzen Vorderextremitäten und das Leben auf dem Waldboden nicht. Weitere Diskussion: Zu *Anchiornis*: JUNKER (2018a); zu *Serikornis*: JUNKER (2018b).

12 „*Protopteryx* retains a feather type that has never before been described: It lacks barbs or rami at the proximal end“ (ZHANG & ZHOU 2000, 1957). Ähnlich waren noch lange Schwanzfedern von *Confuciusornis* ausgebildet. „ Such a feather structure, including those of some long tail feathers of *Confuciusornis* (Fig. 1C) and at least four other enantiornithines, is different from those of all other known fossil and modern feathers“ (ZHANG & ZHOU 2000, 1957).

13 „In combination with the wide distribution of proximally ribbon-like pennaceous feathers and elongate broad filamentous feathers among extinct theropods, this find suggests that early feathers were developmentally more diverse than modern ones and that some developmental features, and the resultant morphotypes, have been lost in feather evolution“ (XU et al. 2010, 1338).

14 „Aside from feathers the bill is surely the most quintessentially birdlike feature of the avian body.“

15 Nur die Küken des Hoatzin haben kleine Zähne, die sie einsetzen, um aus dem Ei zu schlüpfen und die sie danach abwerfen (https://theconversation.com/how-did-dinosaurs-evolve-beaks-and-become-birds-scientists-think-they-have-the-answer-84633).

16 MARTYNIUK (2012, 43) schreibt weiter: „A tooth protruding from the beak, relegating the keratin itself to essentially the gums, would have rendered the beak useless anyway. Teeth protruding from a beak would have been a redundancy, an expense that would not have been evolutionarily advantageous."

17 Der Schnabel ist rhynchokinetisch ausgebildet.

18 „Derived members of this clade are characterized by … an edentulous premaxilla and dentary tip, suggesting the presence of a rostral rhamphotheca; …" (LAUTENSCHLAGER et al. 2013, 20657).

19 „Formed by midline fusion of the clavicles, the furcula is marked by considerable structural diversity (…), varying widely in terms of interclavicular angle, profile curvature (U- to V-shapes), anteroposterior curvature, and development of the hypocleideum and articular facets or epicleideum;…" (CLOSE & RAYFIELD 2012, 1).

20 Die Funktionen der Furkula können nach BOCK (2013, 1236) je nach Art unterschiedlich sein: „(a) serving as the site of origin for the cranialmost muscle fibers of the m. pectoralis; (b) maintaining a space for the passage of the esophagus and trachea; (c) acting as a spring maintaining the distance between the right and left shoulders of the pectoral girdle; (d) storing energy of the major flight muscles; (e) serving as protection for the cranial end of the bird's trunk in some diving birds; and (f) assisting in respiration during flight."

21 „1. occupy a similar, mid-ventral position in the pectoral apparatus; 2. fail to co-exist within the same individual (no vertebrate, fossil or living, has both clavicles and a furcula); and 3. develop via intramembranous ossification, a mode of skeletogenesis that is otherwise atypical for the postcranial skeleton" (HALL & VOCKARYOUS 2015, 440).

22 „Because the architecture of the dinosaur shoulder is so dramatically different form that of *Archaeopteryx* as well as modern birds, it seems unlikely that any of these structures could have articulated or functioned in a manner similar to the bird furcula or the hypertrophied furcula of the first bird, *Archaeopteryx* (Martin 1991), which is a large, flat, U-shaped structure lacking the hypocleidium …" (FEDUCCIA 1999, 77).

23 „There no longer remains doubt that the furcula of birds is homologous to the clavicles of tetrapods. Both phylogenetic and developmental data strongly support this conclusion" (NESBITT et al. 2009, 874).

24 „But we still don't know whether the furcula represents the interclavicle, a neomorph or fused clavicles" (HALL & VICKARYOUS 2015, 450).

25 Ähnlich sehen TYKOSKI et al. (2002, 728, 732). „Given the abundant missing data with respect to basal theropods, the furcula may yet prove apomorphic for Theropoda" (TYKOSKI et al. 2002, 732).

26 NESBITT et al. betrachten diese Deutung bei den Alvarezsauriden wegen deren schlechter Erhaltung als möglich: „… alvarezsaurids are known from a few largely incomplete specimens making the absence of a furcula possibly a result of taphonomic processes" (NESBITT et al. 2009, 872). CHIAPPE et al. (2002, 102) geben aber zu bedenken: „The scapula, coracoid, and sternum are well known in both *Mononykus* and *Shuvuuia*. Portions of the scapulocoracoid and coracoid are preserved for *Alvarezsaurus* and *Patagonykus*, respectively. None of the available specimens of these taxa preserves a furcula. The fact that some of these (e.g., MGI 100/977) are exquisitely preserved and articulated suggests that this element was probably absent in Alvarezsauridae, …"

27 So bei den Ornithomimosauria. „No unambiguously recognizable clavicle or furcula has been found in any ornithomimid even though well-preserved completely articulated specimens are known from many taxa. … It is unclear if the furcula was never preserved, if it was not ossified, or if it did not form at all. The absence of a furcula would be interpreted as a secondary loss following the phylogeny presented here" (NESBITT et al. 2009, 872).

28 It is difficult to say unequivocally whether the furcula arose many times independently or was lost more than once, and for which taxon or taxa its presence is diagnostic. This is because our current knowledge of the

distribution of clavicular elements among non-avian theropods is incomplete, no clear consensus with regards to hypotheses of theropod phylogeny“ (TYKOSKI et al. 2002, 730f.). Vgl. auch MAKOVICKY & CURRIE (1998, 147): „Rather, the known patchy distribution of the furcula within theropods is most parsimoniously interpreted either as a number of independent evolutions of clavicular fusion (…), or as a large number of independent losses of a plesiomorphic feature. Because clavicles are of dermal origin, the absence of a furcula may reflect an unossified, and perhaps juvenile stage, or simply be due to non-recovery or misidentification.“

29 „If this is a pervasive characteristic of flightless birds, why would one expect to find a fully developed furcula in flightless bipedal dinosaurs?“ (FEDUCCIA 1999, 265).

30 „Paired fibroadipose tissue structures called rectricial bulbs lie on both sides of the pygostyle and predominantly attach to the pygostyle lamina; the calami of the rectrices are imbedded in this tissue, except for the medial pair which attach directly onto the dorsodistal end of the pygostyle (Baumel, 1988). Spiraling around the surface of each bulb is a striated muscle, the rectricial bulb muscle“ (WANG & O'CONNOR 2017, 290f.)

31 „… the pygostyle, rectrices, rectricial bulbs, and bulbi rectricium musculature form a specialized fanning mechanism“ (GATESY & DIAL 1996, 2037). „The rectrices form a flight surface that is tightly coupled with the wings during aerial locomotion“ (2037f.).

32 „This sophisticated tail complex plays a significant role in avian flight. … Because the tail complex functions as an integrated whole, the uropygium and integument are morphologically correlated and one can be used to predict the other (Felice and O'Connor, 2014). Furthermore pygostyle morphology can be used to predict flight or foraging style in both extinct and extant birds (Felice, 2014). These results support the hypothesis that pygostyle and rectricial morphology co-evolve (Clark et al., 2006)“ (WANG & O'CONNOR 2017, 291).

33 „Distinct from that of sapeornithiforms, the pygostyle in confuciusornithiforms is more strongly co-ossified, proportionately longer and more robust“ (WANG & O'CONNOR 2017, 295). „The sapeornithiform pygostyle is relatively smaller and poorly co-ossified compared to most other Early Cretaceous pygostylians. … Compared to sapeornithiforms, the pygostyle is proportionately longer in confuciusornithiforms and enantiornithines … Differences in pygostyle morphology between these four groups correspond to consistent differences in tail plumage. *Sapeornis* has been interpreted as having a strongly graded fan consisting of approximately eight pennaceous feathers“ (WANG & O'CONNOR 2017, 304).

34 Als älteste Art der Ornithuren mit „modernem“ Pygostyl gilt *Hongshanornis longicresta*) O'CONNOR et al. 2010).

35 „It also had robust transverse processes on the proximal caudal vertebrae that would have served as attachment sites for the large caudofemoralis muscles that were the primary hind limb retractors“ (RASHID et al. 2014, 2).

36 „However, morphological differences between these phylogenetically separated taxa indicate these co-ossified structures cannot be considered equivalent to the avian pygostyle…. Although pennaceous tail feathers are present in oviraptorosaurs, the absence of a pygostyle lamina or a similar dorsal ridge makes the development of rectricial bulbs or equivalent structures in this clade unlikely. … fusion in the distalmost caudals of non-avian theropods should be described as pygostyle-like and a true pygostyle should be regarded as a synapomorphy of the Pygostylia (Aves)“ (WANG & O'CONNOR 2017, 303).

37 „Oviraptorosaur caudal osteology is unique among theropods and is characterized by posteriorly persistent and exceptionally wide transverse processes, anteroposteriorly short centra, and a high degree of flexibility across the pre-pygostyle vertebral series“ (PERSONS et al. 2014, 553). Oviraptorosaurs do not fit neatly into any stage of this sequence, … “ (S. 562; dort werden weitere anzunehmende Konvergenzen beschrieben).

38 „However, no fossil directly elucidates this important skeletal transition“ (O'CONNOR et al. 2015, 114).

39 „There is a clear-cut distinction between avians that lack a pygostyle and those that have it, and the latter are usually classified in the Pygostylia“ (MAYR 2017, 45).

40 „Nevertheless, little is known about how the abbreviation of the tail took place without relevant fossils documenting that transition“ (WANG & ZHOU 2017, 6).

41 The rectricial bulbs and rectricial fan appear to have coevolved with the ploughshaped pygostyle early in the evolution of the Ornithuromorpha (WANG & O'CONNOR 2017, 289)

42 „The consistent co-occurrence of short pygostyle morphology with clear aerodynamic tail fans in the Ornithuromorpha, the Sapeornithiformes, and now the Pengornithidae strongly supports inferences that these features co-evolved with the rectricial bulbs as a 'rectricial complex.' Most parsimoniously, rectricial bulbs are plesiomorphic to Pygostylia and were lost in confuciusornithiforms and some enantiornithines, although morphological differences suggest three independent origins“ (O'CONNOR et al. 2015, 114).

43 „If the presence of rectricial bulbs represents the plesiomorphic condition in enantiornithines, as suggested by the basal position of the Pengornithidae [10], it is unclear why more derived enantiornithines would have abandoned this feature in favor of a more robust pygostyle with purely ornamental rectrices. This supports an alternative scenario in which rectricial bulbs and pygostyle reduction evolved independently in sapeornithiforms, pengornithids, and ornithuromorphs (Figure 3). This is supported by morphological differences in the pygostyle: …“ (O'CONNOR et al. 2015, 117).

44 „For *Zhongornis haoae* (and for other juvenile Mesozoic avians), this indicates that lack of a pygostyle does not necessarily indicate an intermediate species in the long- to short-tailed evolutionary transition“ (RASHID et al. 2018, 8).

45 Dies wird beispielhalt im Einzelnen in diskutiert; detaillierter in JUNKER (2019).

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