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# Typology versus transformation in the origin of birds

## Kevin Padian and John R. Horner

**The questions of bird ancestry and the evolution of typically 'avian' features appear never-ending. This is true in the press but not in the scientific trenches, where the methods of comparative biology are productively used to settle many major questions, including the origin of birds. Opponents of the view that birds evolved from dinosaurs tend to use typological characterizations of 'reptiles' and 'birds'; although they accept evolution, their approaches do not use the transformational approaches of phylogenetic systematics, against which hypotheses of evolutionary change in function, physiology and behavior should be tested. 'Typologists' also tend to depend on knowledge of how evolutionary processes must work, rather than on comparing independent patterns of evidence. Both typological and transformational approaches can be evolutionary, but the utility of typology is limited because it stresses taxonomic gaps rather than mosaic transitions.**

If the pages of many science journals, weeklies and newspapers are to be believed, several long-standing and perennially interesting questions in dinosaur biology remain endlessly controversial, if not completely intractable. Did birds evolve from dinosaurs? Were dinosaurs warm-blooded? Did they take care of their young? Surprisingly, much of the debate over these questions, however engaging to the press, is rooted less in evidence than in methodology. It reduces to a disagreement about the appropriate methods and philosophical approaches to evolutionary questions, and to the persistence of a pre-evolutionary philosophy that still invests much thinking about evolutionary problems.

### Are birds dinosaurs? (And how do we know?)
Not all workers agree that birds evolved from Mesozoic theropod dinosaurs [1,2]. But to most scientists in the relevant fields, these objections do not test or falsify the hypothesis that birds evolved from dinosaurs because they are not based on testable hypotheses and ignore standard methods of approaching questions of relationship [3]. Why? The

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systematic biology community has resoundingly accepted phylogenetic systematics (cladistics) as the means of determining evolutionary relationships, and if an analysis does not use this method, the hypothesis is not generally considered adequately tested.

Phylogenetic systematics has been the standard method for determining evolutionary relationships for over two decades [4,5]. Cladistics groups organisms only by new features that are identified in the descendants of a common ancestor; therefore, the order of evolution that cladistics establishes is not based on overall similarities, degree of ecological differentiation, or ideas about adaptive value or necessity. Repeated independent cladistic analyses all conclude that the closest relatives of birds comprise a small group of theropod dinosaurs (velociraptorines, dromaeosaurines and troodontids) [6–10]. No cladistic analysis has produced a different result. And no opponent of the bird–theropod hypothesis has done a full cladistic analysis of the question.

Opponents to the cladistic view rely on other kinds of knowledge. The theropod dinosaurs in question were too large, too late in time, could not climb trees, lacked postulated 'key features,' could not pass through an allegedly necessary gliding phase, or were physiologically incapable of performing birdlike functions [1,11,12]. These are all propositions that have been answered on their own terms, whether functional, stratigraphic, or metabolic [10]; but the important point is that none was based on any evidence of relationship, so they do not really test the question of bird origins [10]. No alternative hypothesis has withstood cladistic testing; and, in fact, there have not been any specific alternative hypotheses for >20 years. No other method of phylogenetic analysis has been proposed and argued to supplant cladistics, which is why the field, as a whole, remains unconvinced by these objections.

### Typology versus transformationism
The philosophical problem at the root of this methodological impasse is an old one (Fig. 1). Typology began as a pre-evolutionary idea that treats all organisms in a named group as if they share the same physiological and structural features [13]. It reinforces the perceived gaps between groups and makes it harder to distinguish transitional features and forms. Typology is associated with the works of Linnaeus, which divided living organisms into discrete groups, innocent both
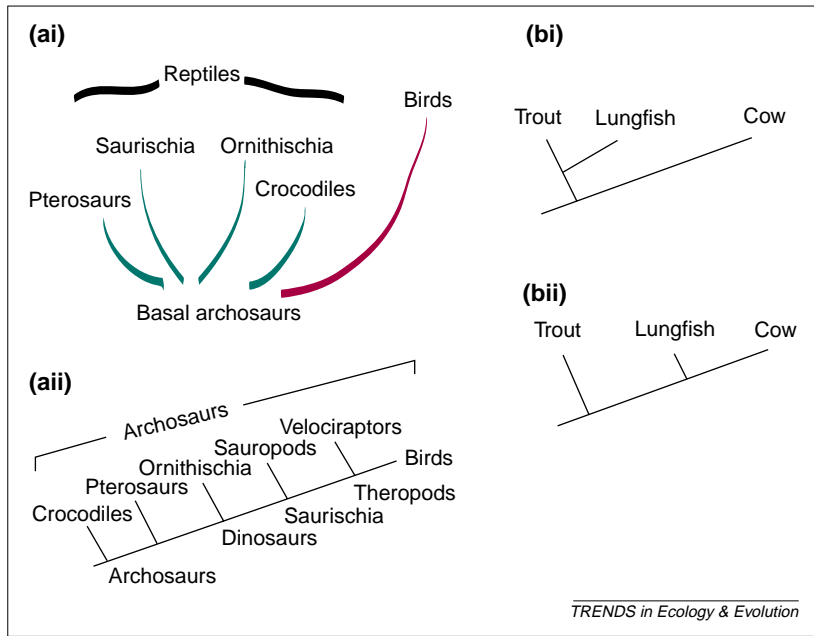
**Fig. 1.** Typological versus transformational perspectives. (a) A typological approach (ai) sees 'reptiles' and 'birds' more or less as Linnean categories that are difficult to bridge. Relationships are not rigorously analysed, so transitional features are explained away. A transformational approach (aii) considers the sequence of acquisition of derived characteristics to link forms successively. From the total matrix of characters considered, the timing and sequence of characters connected with physiology can be mapped and analysed. (b) A typologist sees a lungfish as being more closely related to a trout than to a cow (bi), because they are both 'fish' of aquatic habit. A transformationist sees the lungfish as being more closely related to the cow (bii), because they share physiologically important structures, inherited from a closer common ancestor, that the trout lacks.



**Fig. 2.** Waterhouse Hawkins' designs for the dinosaur statues accompanying the Crystal Palace Exhibition at Sydenham in 1854, under the direction of Richard Owen. Note that although dinosaurs were clearly perceived as reptiles, their upright stance reveals Owen's recognition that they were unlike any other reptiles, living or extinct.

of fossil organisms and of the idea of evolution. Although typological thinking can accept evolution (as Richard Owen did even whilst combating the darwinists on its material mechanisms), it contrasts with transformationism, which links the differences among related organisms successively through evolution [4,5]. Cladistics is the current method of consensus for transformational analysis, although by itself cladistics can only assess relationships. It cannot encompass hypotheses of functional, ecological and physiological change, although its patterns can test hypotheses based on such evidence.

Nowhere is the contrast between typology and transformation as clear as in the time-honored division between 'birds' and 'reptiles'. What could present a clearer dichotomy than a lizard and a warbler – one a cold-blooded creeper, the other a warm-blooded flyer? But include dinosaurs in the mix and the typology breaks down.

When Owen established the Dinosauria in 1842, he knew that they were not typical reptiles because they were so large, yet terrestrial, had five hip vertebrae and had to stand upright – they could not sprawl [14]. Even in mid-Victorian restorations, made before complete skeletons were known, dinosaurs can always be recognized by their erect posture (Fig. 2). Owen's typological view of evolution could not allow dinosaurs to be as advanced physiologically as mammals and birds. But he recognized that they were far more like these animals than any other reptiles have ever been [15].
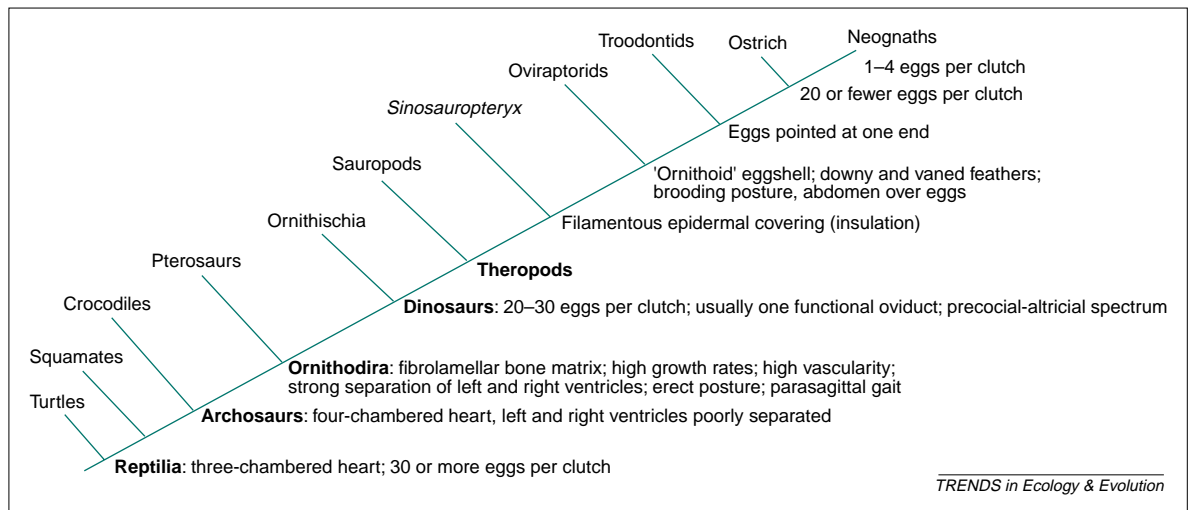
Typology ceased to be a guiding principle of biology once evolution (transmutation) was generally recognized after the publication of Darwin's *Origin of Species* in 1859. But the model of dinosaurs as essentially large, typical reptiles recapitulates the old typology. Because birds evolved from dinosaurs, the features of 'warm-bloodedness' and all that it entails must have evolved somewhere along the line. A typological view emphasizes the primitive similarities of dinosaurs to other reptiles (e.g. they did not fly and they lacked feathers). A transformationist view asks what derived features demonstrate warm-bloodedness (e.g. care of young), and tries to reconstruct the sequence of their appearance in an evolutionary lineage, so that the evolution of these features in birds can be understood. Which approach is more productive, and under what circumstances?

**What is the debate about?**

Some typologically oriented workers, who work almost exclusively on living organisms, suggest that transformationists rely too much on phylogeny when considering paleophysiology [16]. They charge that, because extinct dinosaurs are considered more closely related to birds than to crocodiles, dinosaur workers are predisposed to conclude that birds are better metabolic models than are crocodiles. But this is a mistake, they say, because the early members of clades are likely to be more similar to each other than to highly derived later members. This is possible, of course; but how would we know, and what specific features are we talking about? For example, typologists also say that the classic cladistic formulation that the lungfish is phylogenetically closer to the cow than to the trout raises problems for interpreting physiology, because the trout and lungfish share more (primitive) characters (Fig. 1). But lungfish share physiologically important features with all tetrapods (not only the admittedly extreme example of cows). They have internal choanae, functional lungs, fleshy limbs, and the ability to survive seasonal dryness. We do not know whether the first tetrapods were physiologically more like living lungfish than like living tetrapods, but they could do things that ancient and living trout relatives cannot. These features turned out to be directly related to the ability

**Fig. 3.** Cladogram mapping some of the features discussed in the text on a phylogeny established upon other characters from the skull, vertebrae, girdles and limbs (see [10]). Birds (ostrich and neognaths, here) are a subgroup of dinosaurs; many metabolic and behavioral features associated with the advanced physiology of birds first appeared in other dinosaurs. This transformational approach clarifies which features are really peculiar to birds (e.g. flight feathers, small egg clutches) and which are not (e.g. eggs pointed at one end); many nonavian dinosaurs hence should have had many 'avian' physiological and behavioral properties.



Troodontids    Ostrich    Neognaths
                                      1–4 eggs per clutch
Oviraptorids                          20 or fewer eggs per clutch

*Sinosauropteryx*            Eggs pointed at one end

Sauropods          'Ornithoid' eggshell; downy and vaned feathers;
                   brooding posture, abdomen over eggs

Ornithischia       Filamentous epidermal covering (insulation)

Pterosaurs         **Theropods**

Crocodiles         **Dinosaurs**: 20–30 eggs per clutch; usually one functional oviduct; precocial-altricial spectrum

Squamates          **Ornithodira**: fibrolamellar bone matrix; high growth rates; high vascularity;
                   strong separation of left and right ventricles; erect posture; parasagittal gait

Turtles            **Archosaurs**: four-chambered heart, left and right ventricles poorly separated

                   **Reptilia**: three-chambered heart; 30 or more eggs per clutch

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of early sarcopterygians to survive on land, which is why we need to use, rather than discount phylogeny.

The same workers [16] note that living birds have neither teeth nor a long bony tail, although some Mesozoic birds did; therefore, in these features, dinosaurs more closely resemble crocodilians than they do living birds. But if basal birds had teeth and a long bony tail, why were they not also like crocodiles, even though they had feathers (as we now know the closest dinosaurs to birds did)?

*Snouts and lungs*
Other workers rely on key features or 'Rosetta stones' that they invoke to dispel the idea that dinosaurs had any avian or mammalian physiological features. For example, nasal turbinates (delicate bones situated in and subdividing the nasal cavity) are said to have a 'functional association' with high lung ventilation rates and endothermy in living birds and mammals [17]. But many living birds and mammals lack these structures, they have never been shown to be essential to endothermy, and it has not been shown that dinosaurs did not have them or could not have had them (or something like them). Respiratory turbinates do not fuel lung ventilation rates, tidal volumes or gas exchange efficiency in the lungs. Their main function appears to be to recover exhalant moisture, but there are other ways in which animals can conserve, store and recover water [18]. Moreover, such structures neither have to be ossified, nor readily preserved in the fossil record. This 'key feature' argument uses an association with specific taxa, rather than with physiological causality, to tie dinosaurs to cold-blooded reptiles, as Owen did [15].

The same workers have also argued that dinosaurs must have had a simple one-chambered lung, inflated by a hepatic piston attached to the apron of the pubis, as in crocodiles [11,12]. But the pelvic configurations are completely different in crocodiles and theropod dinosaurs, and the assumed attachment point for the hepatic piston muscle (for which there is no evidence) on the theropod pubis was actually occupied by other

muscles – as a phylogenetic analysis of archosaur pelvic evolution shows [19]. Beyond this, a multi-chambered lung is distributed broadly in reptiles; one-chambered lungs are found only in small animals or those with very low metabolic rates, and, within reptiles, are clearly secondarily derived, rather than primitive [20]. This is why the typological argument fails: phylogenetic distributions of structures must be respected in framing evolutionary hypotheses. Typologists claim that it would not be possible to evolve an avian lung from their reconstruction of a dinosaurian lung without rupturing the internal musculature [11]. If so, then birds could not have evolved, because no known group of animals fits their hypothesized reconstruction, or provides a model of a lung from which the avian lung could have evolved.

Transformational approaches, by contrast, use hypotheses of both pattern and process to reconstruct evolution; for example, the metabolic transition from 'reptilian' to 'avian' status. For many workers, dinosaurs were not exactly like either extant ectotherms or extant endotherms [21]. The question is to determine in what respect dinosaurs might have been like the ectotherms and endotherms that we know, and how they might have been different from anything known today. Phylogeny tells us that birds evolved from small theropods (Fig. 3), and that dinosaurs had a circulatory system that was more like that of birds than like those of other reptiles, with a fully developed double-pump system and well-separated left and right chambers [21]. Small forms would have had higher mass-specific standard or basal metabolic rates than would large forms. Given that dinosaurs also had fast-growing fibrolamellar bone, and a cardiovascular system capable of supporting its growth, they could not have been merely large 'good reptiles' ([21], *pace* [16]). In fact, Mesozoic dinosaurs grew at rates comparable to those of large birds and mammals: hadrosaurs reached 7 m length in seven years [22], and giant sauropods achieved sub-adult sizes in ~12 years [23]. But even the largest extinct crocodiles still grew at reptilian rates, taking up to 50 years to reach 8–9 m [24].

*Lessons from the bones*

To some workers, the presence of growth lines, which are found in nearly all dinosaur bones, suggests that dinosaurs could not sustain growth in the face of fluctuating climates, hence demonstrating that they were not endothermic [25]. But this again is typological reasoning. First, growth lines are not all alike; some are mere pauses in deposition and some comprise rings of avascular bone that interrupt 'normal' tissue. Furthermore, they are found in the long bones of all tetrapod groups, including living and extinct mammals and birds that are undoubtedly endothermic and, in these animals, they indicate nothing more than endogenous rhythms of growth [26]. Many of today's dinosaurs (birds) do not have growth lines for a simple reason: they reach adult size in six to eight weeks, before growth lines would be deposited, and they sustain rapid growth until they reach full size. Even some small birds deposit growth lines that are decidedly not annual [27,28]; and large birds such as the rhea and ostrich, which deposit typical fibrolamellar tissue, reach adult size in less than a year, too short to reflect an annual growth line.

The types of tissue deposited in the bones of extinct animals are the most direct evidence of basal metabolic rates, because they directly reflect growth rates [29]. The sustained deposition of fast-growing bone tissues, as displayed by mammals, birds and other dinosaurs, must reflect sustained high basal metabolic rates; no other physiological explanation appears plausible. Crocodiles and their ancient relatives, as far back as their mid-Triassic division from the dinosaurian lineage, do not sustain the growth of this kind of bone tissue ([30], but see [21]). Assessments of ancient growth rates and regimes should be tied to measurements of tissue growth in living animals, and should be based on complete samples from many bones at different ontogenetic stages [31,32]. These data, in a phylogenetic context, provide more meaningful models of comparative rates of growth and underlying basal metabolic rates than do single typological features, such as the simple presence or absence of growth lines.

*Reproduction and behavior*

The tendency to see dinosaurs as merely large conventional reptiles induces similarities to be drawn with lizards and crocodiles. For example, like living reptiles, dinosaurs are said to have been '*r*-strategists', because they laid more eggs than do birds. True, small birds typically lay one to four eggs per clutch, and large mammals typically have eight or fewer offspring, whereas large dinosaurs ranged into the low 20s. But crocodiles lay 30–80 eggs in a clutch, rodents produce ~12 offspring at monthly intervals, and the ostrich typically broods a mean of 19 eggs. The ostrich loses 75% of its eggs to predation, in spite of intense parental care [33], and the rate scarcely could have been lower in Mesozoic dinosaurs. Small birds have smaller clutches in part because most hide their nests in trees, brush, or pits, away from most predators. The shape of carnivorous dinosaur eggs, pointed at one end, is shared only with birds, as are specific features of their shell microstructure [34], to say nothing of the presence of several kinds of feather and forms of keratin that are otherwise peculiar to birds and never found in other reptiles [35–37]. Some birds even retain two functional ovaries, as did some Mesozoic dinosaurs.

If basal birds can retain the large clutch size characteristic of basal reptiles and still have extended parental care (beyond that seen in lizards, snakes and crocodiles), it follows that such care could have evolved considerably before the common ancestor of living birds. Repeated examples of oviraptorids squatting on nests of eggs with (apparently feathered) forearms spread [38] leave no reasonable doubt that these animals were brooding the eggs, using their bodies to warm them. Although some workers claim that incubating is widely distributed among extant tetrapods [39], this is a typological confusion of primitive and derived features. The oviraptorid is not resting its anterior end on a nest mound like a crocodilian does, or wrapping its body around its eggs like a python does, but is sitting with its abdomen centred directly on top of a neatly arranged clutch of eggs, with its feet tucked beneath its body [38]. Furthermore, incubating (warming eggs by any means) is not the same as brooding (warming with body heat). Animals warm eggs using means other than body heat either because they cannot radiate sufficient body heat or because they are too large to sit on their nests without breaking the eggs. Therefore, an animal that sits on its nest is *prima facie* contributing heat.

**Why we need transformationism, not typology**

Formulations that see no reason to regard dinosaurs as anything other than typical reptiles are typological. That is, they are based on the assumption of no departure from the primitive condition, because these dinosaurs were not 'yet' birds. This is a perfectly good hypothesis, although the assumption of no departure is conservative, rather than parsimonious. But there are good reasons to think that Mesozoic dinosaurs were less like today's reptiles in many respects than like today's birds and mammals, even if they were not necessarily exactly like today's birds and mammals. There are no 'Rosetta stones' or 'magic bullets' of structure in fossil vertebrates that unequivocally constrain or indicate metabolism and physiology.

Presumed correlates of evolutionary structure and function are mapped on cladograms so that their distributions among taxa are clearly indicated; in this way, hypotheses about evolutionary processes and the order of appearance of certain key features can be assessed. Analyses of dinosaurian paleobiology are untested until they are compared to the evolutionary sequence that comprises the stepwise changes from basal dinosaurs to birds (Fig. 3). The 'typological' approach to inferring soft tissue anatomy, function, behavior and physiology [1,11,12,16,17,25,39] tends to force extinct animals into the reduced spectrum of

animals available to us today, without considering substantial evidence of mosaic change in related extinct forms. It lacks an evolutionary component, produces only conundrums, and explains very little.

By contrast, when paleobiological analyses incorporate patterns from ontogenies of ancient animals, and use features that are associated causally (not taxonomically) with results from experimental ontogeny and physiology, they provide parallel explanations of patterns [3–10,20,21,38]. For example, they show that many features typically considered 'avian' actually evolved much earlier on the dinosaurian tree, often in quite different functional, ecological and physiological contexts (Fig. 3).

### The utility of types and transformations

The typological approach is not always sterile or misleading. Useful ideas and generalizations are possible, as long as inferences do not require the assumption of no evolutionary change. For example, if a given crop insecticide is effective on several related insect species, it is reasonable to hypothesize that it will work on others. And, if a particular ontogenetic sequence entails specific embryonic stages in several related forms of a group, the sequence can be presumed typical of that group, subject to future survey and assessment. Exceptions to patterns do not deny the typical. However, if evolutionary change is being studied, the utility of typology is limited, and transformational studies are required.

In characterizing this debate as between typological and transformational thinking, we do not characterize opponents to the dinosaurian origin of birds as old-fashioned typologists akin to Linnaeus and Owen. Rather, we stress the consequences of their using primitive rather than derived features to analyse evolutionary change. The first is characteristic of typology, the second of transformationism. Cladistics, which is transformational, depends on discovering the nested sets of shared derived characters by which evolution is reconstructed, and by which Darwin suggested that classification be organized [40]. Cladistics is not the arbiter of all hypotheses, but a specific method by which patterns of evolutionary relationships can be derived. Hypotheses about the evolution of function, behavior, and so on, should be formulated independently, but if they do not match some well-corroborated hypothesis of relationships, the utility of such models is in question, because they are not supported by comparison to the evidence from evolutionary relationships [3,37].

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