Integumentary Status: It's Complicated: Phylogenetic, Sedimentary, and Biological Impediments to Resolving the Ancestral Integument of Mesozoic Dinosauria

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Introduction

Were the First Dinosaurs Fuzzy?

The discovery of non-squamous integument in heterodontosaurid and neornithischian specimens have led to the inference of the possibility that filamentous structures (quills or "fuzz") homologous to avian feathers were present in the most recent common ancestor of Dinosauria (Mayr et al. 2016). However, initial attempts at maximum-likelihood ancestral state reconstruction analyses (Barrett et al. 2015) found that the ornithischian filaments were best interpreted as having evolved convergently from those in theropods. Subsequently, new hypotheses of the basal relationships of Dinosauria and its immediate outgroups as well as additional discoveries of skin impressions within dinosaurs encourages a re-examination of this situation.

Complications in Assessing Fossil Integument

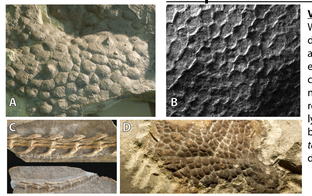


Fig. 1 *Squamous integument in dinosaurs. A,* Triceratops *(photo by author); B,* Edmontosaurus *(Bell 2014); C,* Concavenator *(Ortega et al. 2010); D,* Tyrannosaurus *(Bell et al. 2017)*

Varieties of Squamous Integument: Not All "Scales" are The Same

While preserved filamentous integument is largely in the form of carbonized remains, our record of dinosaurian scales are mostly as external molds and/or casts. Thus, no histological information is available in these to confirm that they all have comparable internal structures. Regularly patterned examples such as in ceratopsids (Fig. 1A), hadrosaurids (Fig. 1B), and some theropods and ornithischians (Fig. 1C) are convincingly interpreted as epidermal scales homologous to those of extant non-avian diapsids. Alternatively, the reticulae and scutae of avian hindlimbs--and potentially other regularly "scales" in dinosaurs--are interpreted as being secondarily derived from feathers (Dhouailly 2009). Furthermore, irregularly shaped tubercles on some dinosaurs (Fig. 1D) might concievably be cracked heavily keratinized skin, as in extant crocodilians (Milinkovitch et al. 2013) and *Loxodonta* (Martins et al. 2018) rather than serially-homologous developmental units. Without additional independant data, however, homology statements about this integument is problematic.

How Confident are We in "0"? Difficulties in Assessing the Absence of Filaments

Preservation of filamentous integument even in Lagerstätten is variable (Fig. 2A, B). Thus, failure to see filamentous remains is not convincing evidence of their absence, even on the same horizon of the same formation.

Additionally, decay processes may remove part or all of the integumentary structures prior to burial (Fig. 2B).

Furthermore, the sedimentary conditions that favor filamentous preservation are rare, while those that favor mere impressions are more common. Consider the rarity of fur for Cenozoic mammals outside of Lagerstätten such as Messel and the Green River Formation.

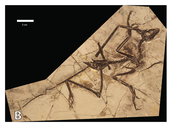


Fig. 2 *Variability in preservation of integument. A-B,* Anchiornis *(Pei et al. 2017) with and without preserved feathers; C,* Procyon *missing fur (photo © Jenna Hewitt)*

New Ancestral State Reconstruction Analysis

A new database was assembled in Mesquite 3.51 (Maddison and Maddison 2018), with 75 dinosauromorph taxa and Pterosauria and Pseudosuchia as outgroups. Taxa were selected either because integument has been observed in them or to represent the oldest represented of a clade in order to calibrate the branch lengths. Three alteranetive tree toplogies were used:

- Saurischia (Theropoda and Sauropodomorpha are more closely related to each other than either is to Ornithischia);
- Ornithoscelida (Theropoda and Ornithischia are more closely related to each other than either is to Sauropodomorpha); and
- Phytodinosauria (Ornithischia and Sauropodomorpha are more closely related to each other than either is to Theropoda)

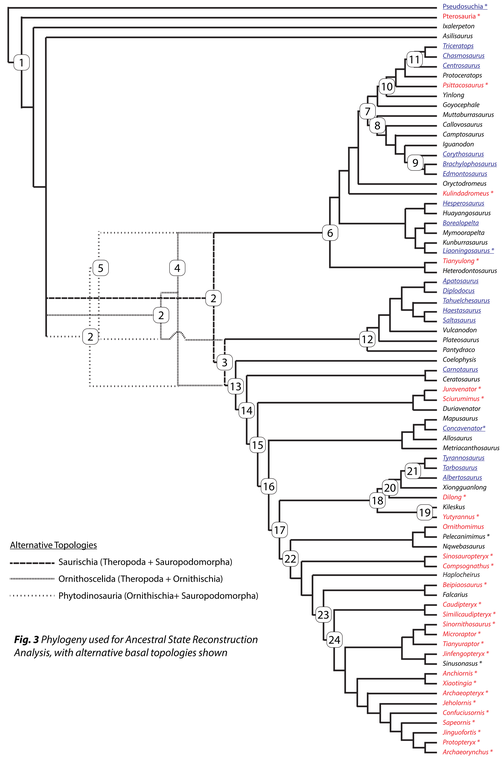
(Baron et al. 2017a, b; Langer et al. 2017). The topologies are shown in Fig. 3.

Previous analyses treated "scales" and "filaments" as two alternative states of the same character. While this might be true for an individual patch of skin, observation of the shared presence of squamous and filamentous integument on the same individual (as in modern birds or *Kulindadromeus* [Godefroit et al. 2015]) indicates this is an inappropriate approach. Instead, these are treated as two separate characters. The lack of any taxon in this set that demonstrably lacks squamation makes the analysis of the presence of scales meaningless; this study examines the likelihood of the presence or absence of filamentous integument (without distinguishing between quills, plumulose fuzz, or pennaceous feathers.

Three alternative scenarios were examined: under the assumption that pterosaurian pycnofibers are not homologous to dinosaurian filaments; under the assumption that pycnofibers and dinosaurian filaments are homologous; and a final set where only taxa preserved in Lagerstätten depostions are scored as either "present" or "absent" (and other taxa are scored as "unknown").

The data were analyzed using "maximum likelihood" in BayesTraits V3.0 (Meade and Pagel 2016). Results are shown in Fig. 3

Ancestral State Reconstruction Analysis



Alternative Topologies

Saurischia (Theropoda + Sauropodomorpha)

Ornithoscelida (Theropoda + Ornithischia)

Phytodinosauria (Ornithischia+ Sauropodomorpha)

Fig. 3 *Phylogeny used for Ancestral State Reconstruction Analysis, with alternative basal topologies shown*

Taxon with observed integument, without filaments

Taxon with observed integument, filaments

Taxon without observed filaments

Taxon preserved in Lagerstätte *

KEY

Dinosaurian Filaments not Homologous to Pterosaur Pycnofibres

Dinosaurian Filaments Homologous to Pterosaur Pycnofibers

Only specimens preserved in Lagerstätten Recorded as 0 or 1

Very unlikely to have filaments (0-20%)

Unlikely to have filaments (20-40%)

Ambiguous (40-60%)

Likely to have filaments (60-80%)

Very likely to have filaments (80-100%)

TABLE 1: LIKELIHOOD OF FILAMENTS AS ANCESTRSAL STATE FOR VARIOUS SELECTED CLADES (%)

	SAURISCHIA			ORNITHOSCELIDA			PHYTODINOSAURIA		
1) Ornithodira	3.3	100	74.0	4.0	100	74.0	3.3	100	73.7
2) Dinosauria	33.3	100	51.5	32.6	100	50.3	28.9	100	49.1
3) Saurischia	14.5	100	47.1						
4) Ornithoscelida				67.4	100	50.5			
5) Phytodinosauria							35.3	100	53.4
6) Ornithischia	71.3	100	55.6	75.4	100	55.7	71.5	100	55.7
7) Cerapoda	29.8	100	54.4	32.7	100	54.4	29.9	100	54.5
8) Ornithopoda	19.9	25.0	50.0	21.0	25.0	50.0	20.0	25.0	50
9) Hadrosauridae	0.4	1.0	50.0	0.5	1.0	50.0	0.4	1.0	63.0
10) Ceratopsia	60.5	100	62.8	63.0	100	62.9	60.7	100	67
11) Ceratopsidae	0.4	1.0	50	0.5	1.0	50	0.4	1.0	50
12) Sauropodomorpha	15.8	21.0	50	16.8	21.0	50	15.9	21.0	50
13) Theropoda	39.2	100	45.4	42.9	100	45.4	39.4	100	45.3
14) Averostra	37.7	100	42.9	42.0	100	43.0	37.9	100	42.8
15) Orionides	88.6	100	39.2	90.0	100	39.3	88.6	100	39.3
16) Avetheropoda	66.2	100	27.0	69.1	100	27.0	66.3	100	27.0
17) Coelurosauria	98.3	100	68.8	98.5	100	69.0	98.3	100	69.1
18) Tyrannosauroidea	91.0	100	74.1	92.1	100	74.2	91.0	100	74.4
19) Proceratosauridae	92.8	100	73.7	93.1	100	73.8	92.8	100	73.9
20) Pantyrannosauria	62.1	100	73.7	65.0	100	73.8	62.3	100	73.9
21) Tyrannosauridae	0.3	1.0	50.0	0.5	1.0	50.0	0.4	1.0	50
22) Maniraptoriformes	97.8	100	61.1	98.0	100	61.2	97.8	100	61.3
23) Metornithes2	98.7	100	76.8	98.8	100	76.9	98.7	100	77.1
24) Pennaraptora	99.3	100	81.0	99.4	100	81.2	99.3	100	81.3

Preondactylus *silhouette by M. Witton, from PhyloPic.org*

Results & Discussion

Ancestral State Reconstruction Highly Sensitive to Outgroup Condition

Table 1 indicates the results of the analysis, representing the inferred likelihood of filaments being the ancestral state for the indicated node. Not surprisingly, the results are highly sensitive as to whether pterosaurian pycnofibers are considered homologous to dinosaurian filaments. When these are considered independant origins, filaments are found to be unlikely at the basal nodes within Dinosauria; likely at the base of Ornithischia through Ceratopsia; and very likely in Orionides (Megalosauroidea + Avetheropoda) and crownward. In contrast, when pycnofibers and feathers are considered homologs, filaments are very likely throughout Dinosauria with reversals in large-bodied in Ornithopoda, Ceratopsidae, Sauropodomorpha, and Tyrannosauridae (similar to results in differnt iterations in Barrett et al. 2015).

In the Lagerstätten-only analyses, the results were equivocal for the base of Dinosauria and most nodes within the clade. (As Hadrosauridae, Ceratopsidae, Sauropodomorpha, and Tyrannosauridae are not represented in these environments, they were recorded as "unknown".)

The status for the integument of the earliest dinosaurs therefore remains ambiguous under this methodology, and awaits more definitive understanding of the histology of pterosaur pycnofibers and/or additional well-preserved integument from throughout the diversity of dinosaurs.

No "General Theory" of Integument

Of consideration is the recognition that in extant animals the integument can be highly variable in even closely related forms. For instance, *Potamochoerus porcus* (Red River hog) and *Babyrousa* spp. (babirusa) are both tropical rainforest suids; the former has a typical mammalian pelage while the latter is virtually hairless (Fig. 4). Despite close phylogenetic affinity and similarity in habitat, they have radically different integuments: furthermore, from their skeletons alone it would be very difficult to establish that their body coverings were so radically different. Of course, mammalian fur is not homologous to dinosaurian filaments, but this difference in closely-related txa indicates that additional factors control the final expression of integument in the living animal beyond mere phylogenetic position.

Fig. 4 *Variability in integument in two closely-related taxa living in similar habitats. A,* Potamochoerus porcus *(photograph CC BY-SA 3.0 by Rufus46); b,* Babyrousa celebensis *(photo CC BY-SA 2.0 by Masteraah)*

Concluding Thoughts

The possibility that the ancestral dinosaur was fuzzy has been raised through the discovery of filaments outside of Theropoda. Unfortunately, at present, our ability to assess the likelihood of this condition is compromised by factors of variability in preservation; in our ability to clearly assess when filaments are lacking; and in the sensitivity of analytical techniques to the outgroup condition. Firm statements to the media and the general public that this issue has been solved or is even strongly supported one way or the other do not properly recognize the present ambiguity of the situation. Futhermore, paleoartists must recognize that our present understanding means that we are uncertain as to the distribution of filaments within Dinosauria, and thus nearly any artistic decision they choose will be speculative.

References (Extended Bibliography Available Online)

Baron et al. 2017a *Nature* **543**: 501-506
Baron et al. 2017b *Nature* **551**: E4-E5
Barrett et al. 2015 *Biology Letters* **11**: 20150229
Bell 2014 in *Hadrosaurs* (eds. Eberth & Evans)
Bell et al. 2017 *Biology Letters* **13**: 20170092
Dhouailly 2009 *Journal of Anatomy* **214**: 587-606
Godefroit et al. 2015 *Science* **345**: 451-455.
Langer et al. 2017 *Nature* **551**: E1-E3
Maddison and Maddison 2018 Mesquite 3.51
Martins et al. 2018 *Nature Communications* **9**: 3865
Mayr et al. 2016 *Palaeontology* **59**: 793-802
Milankovitch et al. 2013. *Science* **339**: 78-81
Meade and Pagel 2016 BayesTraits V3
Ortega et al. 2010 *Nature* **467**: 203-206
Pei et al. 2017 *Bulletin of the AMNH* **411**: 1-67

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