Keeping Grounded: Podathecae, Feature Scales, and Feathers — Tracks, Simple-minded Cladistic Thinking, and the Insulated Ancestral State Condition in the Avemetatarsalia

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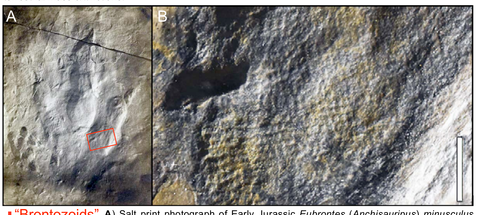
Abstract

A simple-minded, cladistic hypothesis posits that the avemetatarsalian ancestral state conditions for integument were filamentous insulation and pebbly reticulae on the podothecae (PRP), based on organically preserved remains. The Early Jurassic ichnite *Anomoepus* reveals PRP and filaments distal to proximal tail scutellate scales, supporting an origin of these bird-like features at the Triassic origin of dinosaurs, providing the group is monophyletic.

Ichnocladistic analysis of silesaur (*Atreipus*) and chirotheroid tracks shows that PRP originated prior to the Dinosauria/Pterosauria node, and are possibly primitive for Pseudosuchia+Avemetatarsalia. This is inconsistent with the argument that dinosaur/bird PRP are modified feathers, which would require feather origins at the Archosauria node or earlier. We instead default to the hypothesis that these scales are simply homologous to reptile scales.

Apomorphies of their respective clades, derived from the ancestral PRP condition for Pseudosuchia+Avemetatarsalia, are: 1) coarse autopod scales of extant crocodyliforms (a semiaquatic adaptation), evidenced by PRP in the terrestrial crocodyliform track *Batrachopus*; 2) angular scales of phytosaurs seen in the ichnite *Apatopus*, plausibly also a semi-aquatic adaptation; and 3) proportionally large, polygonal pedal scales of the track *Otozoum* observed in undoubted sauropod footprints and neosauropod integument.

Maximum likelihood models favoring a scaly ancestral state condition for avemetatarsalian integument rely on negative evidence from large dinosaurs. However, their size and thermoregulatory needs (analogous to nearly hairless low-latitude megafauna) plausibly drove filament reduction. Instead, we hypothesize that at least sauropods and hadrosaurs, actually retained filament homologues as their median feature 'scales' (MFS) composed of conjoined filaments. Indeed, hadrosaur MFS have been described as, "…evocative of rhinoceros horns … composed of an arrangement of hair-like keratinized tubules …" (**1**). If borne out by desperately needed additional analysis, recoding of sauropods and hadrosaurs as having 'reduced filaments,' as opposed to scales only, would reverse the maximum likelihood outcomes. The primitively present, filamentous integument in pterosaurs+dinosaurs was a key innovation that allowed them thrive in polar regions and survive multiple episodes of Mesozoic, volcanic winter-induced, terrestrial mass extinctions.



"Brontozoids" **A**) Salt print photograph of Early Jurassic *Eubrontes* (*Anchisauripus*) *minusculus* podotheca from Deane (1861) (2); **B**) Detail (red box in A) of reticulate scales (from 3).

The long-recognized similarity between the avian podotheca and autopod "pebbly" squamation in dinosaurs (6-8) is a consequence of inheritance of a primitive condition from at least the level of the Archosauriformes, and, not an avian apomorphy of modified feathers (e.g., 9).

Microraptor *Gallus*

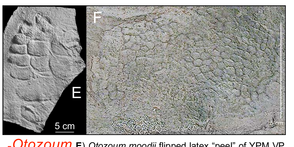
C) Podotheca, scutellate scales, and reticulate scales of Early Cretaceous non-avian dinosaur *Microraptor gui* (from 4); **D**) Podotheca, scutellate scales (scutella), and reticulate scales of *Gallus gallus* (from 5).

Paraves

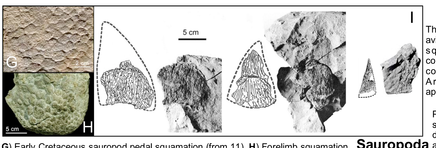
Theropoda

The long-recognized similarity between the avian podotheca and autopod "pappilous" squamation in dinosaurs (6-8) is a consequence of inheritance of a primitive condition from at least the level of the Archosauriformes and not an avian apomorphy of modified feathers e.g., (9).

Pedal squamation of *Otozoum* and sauropods are similar to each other but different from that of theropods and most archosaurs, including pterosaurs [sensu Nesbitt, 2011(14)], suggesting the polygonal pedal scale pattern is a synapomorphy for the Sauropodomorpha and that *Otozoum* was made by an early diverging sauropodomorph. These polygonal scales have delicate papillate edges.



Otozoum **E**) *Otozoum moodii* flipped latex "peel" of YPM VP 003411, (photo by D. Baird), left pes impression; **F**) Squamation detail on metatarsal-phalangeal pad of digits III-IV of F (from 10).



G) Early Cretaceous sauropod pedal squamation (from 11). **H**) Forelimb squamation, Early Cretaceous neosauropod *Haestasaurus becklesi* (from 12). **I**) Diplodocid "median spines", Howe Quarry, Late Jurassic Morrison Formation (from 13).

Sauropoda

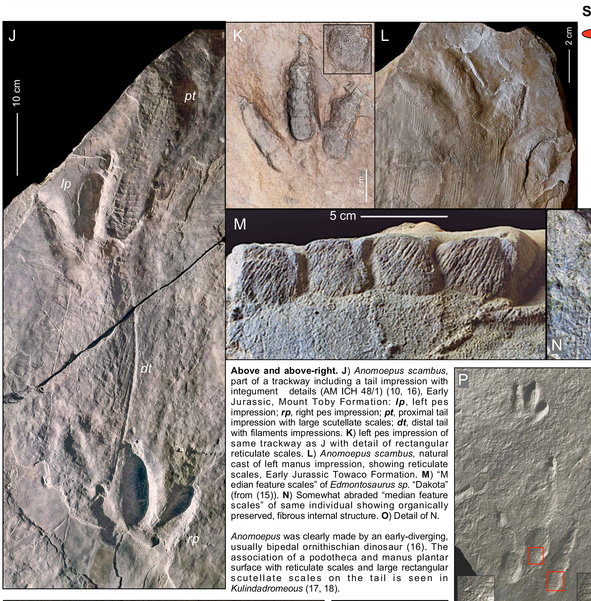
Sauropodomorpha

Polygonal pedal scales

Czercas (1992) (13) described dorsal median spines of a diplodocid sauropod that are similar to the "median feature scales" of some hadrosaurs (1, 15). They are organically preserved with a fibrous appearance comprised of, "… hypertrophied tubercles, about 2-3 mm in diameter, that reach to the apex of the spines and together form a fluted or combed texture of parallel lines" [p. 1069 (13)]. They do not have the structure of scales or keratinous horn and do not sheath an osteoderm.

We hypothesize these structures to be conjoined feather homolog filaments and that it is incorrect to code for an absence of feathers in analysis of ancestral state integument condition.

Saurischia



Above and above-right. **J**) *Anomoepus scambus*, part of a trackway including a tail impression with integument details (AM ICH 48/1) (10, 16). Early Jurassic, Mount Toby Formation: ***lp***, left pes impression; ***rp***, right pes impression; ***pt***, proximal tail impression with large scutellate scales; ***dt***, distal tail with filaments impressions. **K**) left pes impression of same trackway as J with detail of rectangular reticulate scales. **L**) *Anomoepus scambus*, natural cast of left manus impression, showing reticulate scales, Early Jurassic Towaco Formation. **M**) "Median feature scales" of *Edmontosaurus sp.* "Dakota" (from (15)). **N**) Somewhat abraded "median feature scales" of same individual showing organically preserved, fibrous internal structure. **O**) Detail of N.

Anomoepus was clearly made by an early-diverging, usually bipedal ornithischian dinosaur (16). The association of a podotheca and manus plantar surface with reticulate scales and large rectangular scutellate scales on the tail is seen in *Kulindadromeous* (17, 18).

P) *Atreipus milfordensis* Late Triassic Passaic Formation

Atreipus

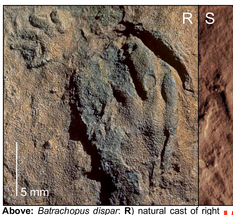
Anomoepus, Edmontosaurus

Ornithischia, Genasauria, Neornithischia, Cerapoda

Although we have not examined the specimens in person, the photographs of the abraded, "median feature scales" of *Edmontosaurus* look to us strikingly similar to the diplodocid dorsal median spines by Czercas (1992) (13). The hadrosaur "median feature scales" have been described in *Gryposaurus* as, "…evocative of rhinoceros horns … composed of an arrangement of hair-like keratinized tubules …" (1). The organically-preserved internal structures show that the median feature scales were not hollow, scale-like, or fleshy (e.g., (19)) based on *Edmontosaurus* and *Gryposaurus* (1, 13).

Rather than a completely new kind of integumentary structure we again hypothesize these structures to be conjoined feather homolog filaments and an absence of feathers should not be assumed for hadrosaurs in analysis of ancestral state integument condition, just as a (near) absence of filamentous hair in *Rhinoceros* does not indicate an absence of hair in the Perissodactyla or even the Rhinocerotidae.

The most parsimonious hypothesis is that the similar feature scales of sauropods and hadrosaurs are parallelisms, derived from filamentous or quill-like coverings along the back, primitive for the Dinosauria.



Above: *Batrachopus dispar*: **R**) natural cast of right manus pes impression, Early Jurassic McCoy Brook Formation; **S**) natural cast of right manus pes impression, Early Jurassic, Towaco Formation. Note reticulate scales on manus and pes imprints.

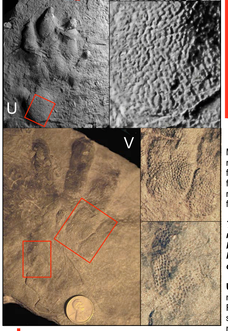
T) *Crocodylus johnsoni*, manus (above) and pes (below) (from (25).

Crocodylus

Batrachopus

Based on its reduced and clawless pedal digit IV and temporal distribution *Batrachopus* dispar was made by a crocodylomorph, and based on its abundance, a protosuchid. *Batrachopus* has reticulate scales on the manus and pes resembling those of avemetatrasalians as well as many chirothere tracks.

Interestingly, the autopodal squamation of extant crocodylomorphs does not resemble that in either the Avimetatarsalia or other archosaurs for which data exist. It is much coarser than in avemetatrasalians and not reticulate. This may be an apomorphy for the group, perhaps related to their semi aquatic habitus.



Chirotherium, Brachychirotherium

Paracrocodylomorpha, Loricata

Many chirothere ichnites have fleshy pads and reticulate autopodal squamation indistinguishable from the Avimetatarsalia. There is no evidence from fossils or inferences from phylogenetic bracket reasoning that any pseudosuchians had a filamentous integument.

The parsimonious inference is that autopodal reticulate scales and the podotheca evolved before feathers and their filamentous homologues, and therefore bird pedal scales could not have developed from feathers.

U) *Chirotherium barthi*: **Left**, natural cast of right manus pes impression, Middle Triassic, Moenkopi Formation (from (26); **Right**, details of reticulate scales (from (27). **V**) *Brachychirotherium* isp.; **Left**, natural cast of right pes impression, Late Triassic Passaic Formation; **Right**, details of reticulate scales

Silesauridae

Above: *Atreipus milfordensis* and *A. acadianus* were made by silesaurids based on the apomorphic reduction of pedal digit I that does not impress regardless of track depth, consistent with the tarsus of *Silesaurus* itself (20, 21). *Atreipus milfordensis* and *A. acadianus* was made by a trackmaker that had a podotheca with reticulate scales similar to that in theropods and basal ornithischians. Whether or not silesaurs had a filamentous integument is unknown, although the presence is suggested by phylogenetic bracket thinking with pterosaurs as an outgroup.

Dinosauria

Q) Left and right tapejarid, azhdarchoid pterosaur pedes (from 22).

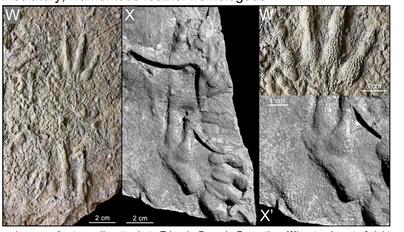
Pterosauria

Pterosaurs apparently had a podotheca with reticulate scales as seen in ctenochasmatid (23) and azhdarchoids (22, 24). At least ctenochasmids and have similar scales on the manus (23). Hone et al. (2025) (23) state, "… the structure of the surfaces of the hands and feet that contacted the substrate were largely uniform across the clade, despite the enormous differences in habitats, body sizes and temporal differences between the various lineages"

The structures are also similar to what is seen in Atreipus, Anomoepus, brontozoids, and birds, suggesting, that along with filamentous feather homologues, they are primitive at the level of the Avemetatarsalia. Only the feather homologues, however, are apomorphic for the group.

Avemetatarsalia, Ornithodira

Insulatory, filamentous feather homologues

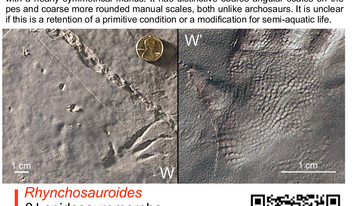


Apatopus

Apatopus lineatus Late Triassic Passaic Formation: **W**) natural cast of right impression of manus and pes; **X**) YPM VP 7731, natural cast of right impression of manus and pes and underlying *Brachychirotherium* isp.; **W'**) detail of manus of W; **X'**) detail of pedal pad for digit I in X.

Phytosauria

Apatopus combines a very primitive pes impression with a long digit IV with a nearly symmetrical manus. It has distinctive coarse angular scales on the pes and coarse more rounded manual scales, both unlike archosaurs. It is unclear if this is a retention of a primitive condition or a modification for semi-aquatic life.



Rhynchosauroides

? Lepidosauromorpha

Dimetropus, **Synapsida**

Z) Manus and pes of *Dimetropus leisnerianus* with distinctly creased skin without scales (from (28)).

Dimetropus, is assumed to be a synapsid track. It exhibits primitive amniote proportions with digits I-IV progressively longer laterally, and with a shorter digit V; the manus impression is as large as that of the pes. No scale impressions appear on the autopod planter surfaces. However, because the primitive state for amniote autopod integument is unresolved, this may not indicate a synapsid apomorphy. Scale-like structures are present on body impression linked to *Dimetropus leisnerianus* (29) but their homology with sauropsid scales is also murky.

Pseudosuchia, Suchia

Rounded reticulate autopodal scales; ?podotheca

Archosauria

Right: Y) *Rhynchosauroides hyperbates*: left manus (smaller) and pes (larger and fainter) impressions, Late Triassic Lockatong Formation. **Y'**) detail of plantar surface of manus impression.

Rhynchosauroides exhibits the primitive amniote condition of similarly proportioned manus and pes impressions with digit IV being the longest, with however, a distinctly smaller manus. The latter is plausibly a diapsid apomorphy. Squamation is similar on the manus and pes and is characterized in this ichnospecies by decidedly angular scales, grading from square to polygonal. Rounded reticulate scales characteristic of the Archosauria appear absent in this ichnogenus, which is plausibly a primitive feature.

Archosauriformes, Crurotarsi

Sauropsida, Diapsida, Crown Reptilia

Amniota*

* This framework cladogram is based on references 14 and 30-33.

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references