Census of Dinosaur Skin Reveals Lithology May Not Be the Most Important Factor in Increased Preservation of Hadrosaurid Skin

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Census of dinosaur skin reveals lithology may not be the most important factor in increased preservation of hadrosaurid skin

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A global census of published records of dinosaur skin from the Mesozoic, cross-referenced against a more detailed lithological dataset from the Maastrichtian of North America, clarifies why most examples of fossilized dinosaur skin come from hadrosaurids. Globally, more published specimens of hadrosaurids exhibit preserved skin than any other major clade of dinosaur. North American Maastrichtian hadrosaurid fossils are 31 times more likely to have skin preserved than coeval dinosaur remains. This does not arise from collection methodology, the large population size of hadrosaurids, or the gross lithology of their depositional environment. The reason that so many hadrosaurid fossils have skin is still elusive, but was likely something intrinsic to hadrosaurids that originated early on in the clade, perhaps the possession of tougher or thicker skin. The database of published examples of fossilized dinosaur skin assembled here will assist the continued development of a much needed common terminology and taxonomic framework for dinosaur skin.

Key words: Dinosauria, hadrosaurid, skin, exceptional preservation, soft tissue fossils, Mesozoic, North America.

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Introduction

Although the first described impression of dinosaur skin (Hitchcock 1841) predates the term Dinosauria, we still have a poor understanding of dinosaur skin and the taphonomic processes that act to preserve such a labile tissue in the fossil record (Schweitzer 2011). What limits understanding is not a lack of material, but instead a lack of synthesis of the many specimens already examined (Kim et al. 2010). Though others have summarized important fossils with skin (Lull and Wright 1942; Wegweiser et al. 2006; Carpenter 2007; Kim et al. 2010), these lists were never intended to be comprehensive.

Fossilized skin (Fig. 1) is crucial for fleshing out the biology of dinosaurs and other prehistoric vertebrates (Czerkas 1997). It often reveals external morphologies and possibly even coloration that is impossible to obtain from skeletal elements alone (Horner 1984; Czerkas 1992; Briggs et al. 1997; Lingham-Soliar and Plodowski 2010). Exceptional 3D preservation of skin around fossilized bones can help reconstruct muscle mass (Manning 2008) and indicate an organism's proficiency in behaviors like running and swimming (Osborn 1912; Caldwell and Sasso 2004). Scale patterns are also useful in taxonomic identification and systematics (Negro 2001; Evans and Wang 2010; Bell 2012), and skin impressions contained in footprints can be used to reconstruct ancient sediment characteristics, facies, and stride mechanics (Lockley 1989; Gatesy 2001; Platt and Hasiotis 2006).

Most of what is known about the morphology and taphonomy of dinosaur skin comes from several exceptionally preserved hadrosaurid fossils (Czerkas 1997; Carpenter 2007). Some authors suspect that, compared to other dinosaurs, a larger proportion of hadrosaurids show preserved skin, and that it is exceptional not to find large areas of preserved skin when encountering an articulated hadrosaurid skeleton (Brown 1916; Maryańska and Osmólska 1984; Lyson and Longrich 2011). However, this bias has never been sufficiently quantified or explained. Exceptional preservation of soft tissues involves a whole suite of factors, some of which might influence the pattern of increased skin preservation found in hadrosaurids (Schweitzer 2011; McNamara et al. 2012). The prevalence of fossilized hadrosaurid skin in collections may not arise from a larger proportion of hadrosaurid fossils containing preserved skin but from the relatively high abundance of hadrosaurids in the fossil record compared to other dinosaurs (Hall et al. 1988). Or more hadrosaurid fossils could contain preserved skin because hadrosaurids occurred preferentially in an environment that was conducive to exceptional preservation of skin (Hall et al. 1988). Wegweiser et al. (2006) believe this environment involved rapid burial in nearshore marine sands with interplay between fresh and marine water both inhibiting decay and promoting formation of pyrolusite. However, Carpenter (2007) finds rapid burial most important in a riverine environment after the carcass goes through a period of desiccation. Detailed site stratigraphy has led others (Maryańska and Osmólska 1984) to suggest that a large proportion of hadrosaurid fossils contain preserved skin because of some intrinsic factor possessed by hadrosaurids like thicker or tougher skin.

Institutional abbreviations.—AMNH American Museum of Natural History, New York, USA; LACM Natural History Museum of Los Angeles County, Los Angeles, USA; YPM PU, Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, USA.

Material and methods

In order to quantify the increased preservation of skin among hadrosaurids and understand which taphonomic factors might be most responsible for this pattern of preservation, research followed two paths. To quantify the patterns of skin preservation across different clades, lithologies, and time periods, literature from around the world was examined for dinosaur specimens with preserved skin. This reveals how many skin examples are known but it does not show how common skin preservation was compared to typical fossilization of only hard parts. For this reason, a large lithological dataset of dinosaur specimens from the Maastrichtian of North America (Lyson and Longrich 2011) was reexamined and cross-referenced against the literature search of skin examples to calculate, for the North American Maastrichtian, the ratio of dinosaur fossils without preserved skin to those with preserved skin among different taxa, lithologies, and collection methodologies.

Global literature search.—For the literature search, 180 examples of dinosaur skin published from 1841 to 2010 were found, and details of skin morphology, geological formation, geologic age, preservation mode, and lithology were recorded (SOM: table 1S in Supplementary Online Material at http://app.pan.pl/SOM/app59-Davis_SOM.pdf). Clade and species names follow Weishampel et al. 2004, except for specimens published after 2004, which are entered as their authors described them. Also, the membership of Hadrosauridae follows Prieto-Márquez (2010b) in that Hadrosauridae is split into two main clades, Saurolophinae and Lambeosaurinae. Time period dates and spellings follow those of the Geological Society of America (Walker and Geissman 2009).

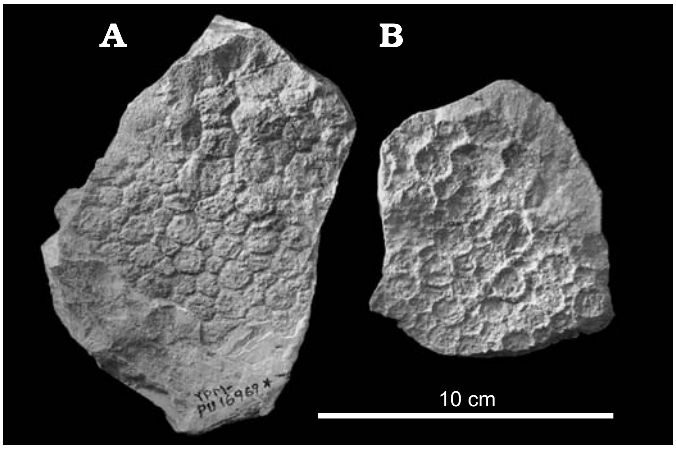

Fig. 1. Part (**A**) and counterpart (**B**) skin of hadrosaurid *Kritosaurus* sp. (YPM PU 016969) showing the typical dinosaurian morphology of non-imbricating, polygonal tubercles. Courtesy of the Peabody Museum of Natural History, Yale University, New Haven, USA.

Schweitzer (2011) lists three possible modes of preservation available for Mesozoic dinosaur skin: impressions, compressions, and casts. Impressions are 2D imprints in sediment like footprints that contain no traces of original skin material or diagenetically altered skin (Herrero and Farke 2010). The impression itself is visibly and chemically no different than the sediment underlying it and sand grains must be visible in the scale pattern (Schweitzer 2011). Compression fossils are 2D imprints of skin preserved as carbonaceous films distinct from the underlying sediment (Ji and Bo 1998). This film can be formed from altered skin material or bacterial mats (Schweitzer 2011). Lastly, casts are formed when bacteria precipitate minerals directly onto decaying skin preserving detailed 3D skin structures (Chiappe et al. 1998). While this terminology is useful, it is hard to apply on a specimen-by-specimen basis. Impressions can be as detailed as casts and need not have visible sand grains, as many are formed in fine sediments like muds and silts (Hitchcock 1841, 1858, 1865). Multiple forms of preservation seem possible in one specimen (Brown 1935; Manning et al. 1997) and few authors undertake the necessary chemical analysis to discriminate between simple impressions and mineralized skin. Even Schweitzer (2011) mentions a mummified *Edmontosaurus* specimen (LACM 23503) that does not fit neatly into any of her three modes of preservation. For these reasons, any designation of a specimen's preservation mode should be taken with caution unless considerable chemical analysis has been performed.

For this study, all published specimens found exhibiting impressions, compressions, and/or casts of skin as defined above (Schweitzer 2011) were included, whether found in isolation (Hall et al. 1988), associated with skeletal material (Brown 1916), or within footprints (Currie et al. 1991). Excluded from the database are the following dermal structures: osteoderms, even though they form from and within skin and replicate scale morphology (Carpenter 1998); keratinous structures such as beaks (Norell et al. 2001); feathers (Vinther et al. 2010); other integumentary structures of uncertain affinity (Zheng et al. 2009); and soft tissues such as gut traces (Dal Sasso and Maganuco 2011). Because feathers were not considered, the entire clade Aviale (sensu Padian 2004) was excluded from this analysis, leaving a paraphyletic Theropoda, hereafter referred to as “Theropoda”. It is likely that this exclusion did not remove many specimens but records of pedal scales do exist for Mesozoic birds and their kin (Williston 1898; Czerkas and Yuan 2002; You et al. 2006) and should be included in future analyses. In this study, one skin example is counted as including all the records of skin associated with an individual organism or with a particular footprint. Though Sternberg’s famous *Edmontosaurus* mummy (AMNH 5060) includes many individual fragments of skin and has been published on numerous times (Matthew 1909; Osborn 1909, 1911, 1912; Sternberg 1909a, b), it would only count as one example of skin preservation in this analysis. This has the potential to introduce a bias, as one dinosaur can leave many individual footprints over its lifespan but only one carcass capable of fossilization. Though impressions of skin in footprints share many similarities with impressions from other parts of the body, they were analyzed separately owing to their separate formation mechanisms (single impactor vs. stationary decaying body, respectively).

North American Maastrichtian lithological dataset.—Results from the first analysis on the global literature search for dinosaur skin were used to determine which specimens in Lyson and Longrich’s (2011) North American Maastrichtian dataset showed skin preservation. Lyson and Longrich (2011) studied 343 specimens of associated remains (two or more bones from the same specimen within 1 m of each other) from 43 public institutions and recorded elements preserved, gross lithology, geologic formation, and year of collection. Footprints were not considered. Lithology was determined from directly examining matrix still adhering to specimens, the literature, or museum staff and records. Lyson and Longrich (2011) also recorded collection methodology for each specimen, showing whether it was collected in a selective manner where only the most complete specimens were excavated or whether it was part of an exhaustive collection where all diagnostic material regardless of completeness was collected. The specimen data were subjected to logistic regression in the R Statistical software package (R Development Core Team 2011) to determine what effects the predictor variables of lithology, collection methodology, and taxonomy had on the likelihood of skin preservation. The 95% probability level was used to evaluate significance.

Results

A thorough review of the literature revealed 180 published examples of preserved skin from both footprints and body fossils. Preserved skin was found throughout most of the major clades of dinosaurs (SOM: tables 1S, 2S) from the 0.3 mm diameter pebble basement-scales of embryonic titanosaurs (Chiappe et al. 1998) to the 125 mm midline feature-scales of *Gryposaurus* (Parks 1919). Published skin examples were found in 14 countries in Asia, Europe, and the Americas. Most skin examples came from the USA (66), Canada (34), or Greenland (21). Preserved skin was found from the Late Triassic to the end of the Mesozoic with most (88) skin found in the Late Cretaceous and no examples found in the Middle Jurassic. Throughout the literature, hadrosaurids had more body fossil skin examples than any other clade both in total number and in examples per species. However, few footprints contained preserved hadrosaurid skin (2); “theropods” had 15 times as many footprints with skin as hadrosaurids did (SOM: table 2S). Though the genus *Edmontosaurus* accounted for 25% of the skin preserved for hadrosaurids (SOM: table 1S), skin examples were spread over the diversity of the clade with at least 14 species in Asia and North America exhibiting some skin preservation (Prieto-Márquez 2010b).

The North American Maastrichtian (Lyson and Longrich 2011) dataset included 343 body fossil specimens with 22 displaying skin preservation (SOM: table 3S). A greater proportion of hadrosaurid fossils retained skin compared to other dinosaurs, with 25% of hadrosaurid specimens showing examples of skin. Logistic regression of the North American Maastrichtian data showed that hadrosaurids were 31 times more likely to preserve skin than other coeval dinosaurs with high significance ($p = 2.39E\text{-}05$; Table 1). Both gross lithology ($p = 0.35$) and collection methodology ($p = 0.08$) showed no significant increase in odds for preserving skin (Table 1).

Table 1. Increased odds of preserving skin from logistic regression of Maastrichtian lithology dataset. A p value of less than 0.05 is considered significant. Original data modified from Lyson and Longrich (2011).

Predictor variable	Increased odds of preserving skin	95% Confidence interval for odds	p
Hadrosaurids	31	8–217	2.39E-05
Selective collection	3	1–11	0.0831
Sandstone	3	0-57	0.3533

Discussion

Analysis of published specimens of dinosaur skin (SOM: table 2S) and a more detailed set of fossil specimens from the North American Maastrichtian (SOM: table 3S) demonstrates that more preserved dinosaur skin is found on hadrosaurids and that a greater proportion of hadrosaurid fossils contain preserved skin than in other dinosaurs. These biases could exist for several reasons. The number of skin examples known from a particular geologic period or formation is most certainly influenced by geological (rock record incompleteness), biological (dinosaur diversity) and human (variable study effort) filters. The number of skin examples per period does follow the general upward trend toward the end-Cretaceous of both the number of named formations in the USGS lexicon (Peters and Foote 2001) and the number of recognized dinosaur species (Wang and Dodson 2006), but rough comparisons to simple and redundant sampling proxies are inappropriate for understanding large biases like these (Benton et al. 2011). Comparing skin preservation among many species collected with varying intensities from similar formations in one geographic area and geological period like the North American Maastrichtian drastically reduces any possible large scale bias from human or geological sampling incompleteness.

Hadrosaurids were both diverse and abundant during the Late Cretaceous (Prieto-Márquez 2010a). If the likelihood of skin preservation were identical for all dinosaur individuals, more preserved skin might be attributed to hadrosaurids simply because there were more living hadrosaurids to begin with. This does not seem to be the case, at least in the North American Maastrichtian. Hadrosaurids were numerous (SOM: table 3S), comprising 23% of specimens in the Maastrichtian dataset, but ceratopsians were even more numerous, outnumbering hadrosaurids by more than two to one without preserving a single example of skin (Lyson and Longrich 2011). Hadrosauridae is also a large clade with many species but in the literature, the average number of preserved skin examples per species is five times higher in Hadrosauridae than in other dinosaurian clades (SOM: table 2S). This number would likely be even higher, but there is probably a publication bias against announcements of new examples of hadrosaurid skin, because so many cases have already been published.

It could be that hadrosaurids were more likely to preserve skin than other dinosaurs because, during life, hadrosaurids preferred an environment conducive to rapid burial and preservation of soft tissues (Wegweiser et al. 2006). Again, at least in the North American Maastrichtian, this does appear to be the case. Hadrosaurids, and dinosaurs in general, did not show any significant change in skin preservation whether they were buried in mudstone, representing a floodplain or lacustrine environment, or sandstone representing a fluvial environment (SOM: table 3S; Lyson and Longrich 2011). Collection bias also seems to have no significant effect as dinosaurs collected in a selective manner, where only the best specimens are excavated, were no more likely to retain preserved skin than those collected as part of a more exhaustive search where all specimens of taxonomic worth were retrieved (SOM: table 3S; Lyson and Longrich 2011).

Sampling effort, environment and lithology, and other extrinsic factors like population size and diversity do not explain the large number of preserved hadrosaurid skin examples. This does not mean that these factors do not affect skin preservation, and indeed all are seen as important (McNamara et al. 2012). But we must consider factors intrinsic to hadrosaurids to explain their *increased* propensity to preserve skin compared to other dinosaurs (Maryańska and Osmólska 1984). For example, hadrosaurids might have possessed thicker or more resistant integument than other dinosaurs, something that could explain their perceived lack of defensive adaptations (Ostrom 1964; Maryańska and Osmólska 1984). This conjecture must be evaluated by comparative study of dinosaur skin morphology and composition, which is outside the scope of this study. Although there are no known examples of skin from non-hadrosaurid Hadrosauroidea (SOM: table 1S), the multiple species of hadrosaurids preserving skin in both Saurolophinae and Lambeosaurinae suggest that whatever this intrinsic factor was, it originated early on in the evolution of the Hadrosauridae and was probably common throughout the clade and its varied habitats around the globe.

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