# ON EPIDERMAL INSULATION IN SMALL DINOSAURS

Boris Sorkin
3211 Ave I, apt. 5K
Brooklyn, NY 11210

ABSTRACT: The question is addressed of whether epidermal insulation was present in small dinosaurs. Using information about the integument of large dinosaurs provided by its fossilized impressions and by examining the types of integument present in small and large extant endotherms, it is demonstrated that epidermal insulation was extremely unlikely to have been plesiomorphic in Dinosauria, while very small adult size was plesiomorphic within the group. Furthermore, it is argued, on the basis of the probable phylogenetic relationships between various small dinosaurs and the large ones for which integument impressions are known and the evolutionary trends in those dinosaur lineages that included small members, that epidermal insulation evolved, in the form of feathers, only once within the group, in advanced theropod ancestors of the *Archaeopteryx*. Such distribution of epidermal insulation in Dinosauria is explained by showing that insulating feathers could only have evolved in animals adapted for flight and by postulating that some factor (presumably the lack of pre-existing structures that could evolve into hair) prevented evolution of pelage in dinosaurs.

* * *

Thermal physiology of dinosaurs has been the subject of much debate among paleontologists throughout 1970's and 80's and remains so into the 90's (see the results of the 1980 AAAS Symposium published accompanying Bakker 1980; Farlow 1990, Farlow et al. 1995; Paul 1988b, 1991, 1996; Reid 1987, 1990; Ruben 1995, Ruben et al. 1996; Spotila et al. 1991). The traditional view maintained that dinosaurs were physiologically similar to extant Reptilia, having low resting and maximum exercise metabolic rates and relying upon external heat sources and heat sinks or high thermal inertia for thermoregulation. However, many features of dinosaur morphology, bone histology, paleoecology and paleogeographic distribution suggest that they were endotherms like extant birds and advanced mammals (See Bakker 1980 and Paul 1988b for the most detailed reviews of evidence pro and con the latter view; also see Ricqles 1980 for the most detailed treatment of the correlation between bone histology and thermal physiology in amniotes). It is the opinion of the author of this article that evidence available to date is sufficient to demonstrate that all members of the Dinosauria were fully endothermic animals, relying upon their high resting metabolic rates for maintaining constant body temperature and capable of maintaining high levels of aerobic exercise metabolism. However, he is well aware of the fact that this view is currently accepted only by a minority of paleontologists.

If they were endothermic, dinosaurs needed some form of thermal insulation to thermoregulate successfully. Living mostly in relatively warm climates, large dinosaurs were sufficiently insulated by the low skin surface area to body volume ratio (as are extant "pachyderms" and

* * * *

Evolutionary Theory 11: 279-287 (July,1998)

The editors thank J.O. Farlow, J. Ruben, and two other referees for help in evaluating this paper.

some other tropical ungulates). However, smaller ones needed epidermal insulation to maintain constant body temperature (Paul 1988b). Therefore if strong evidence can be presented against the presence of hair or feathers in any small dinosaurs, it would either indicate that they were not endothermic or at least that they were in some ways different from all extant small endotherms. Thus the answer to the question whether or not epidermal insulation was present in small dinosaurs is crucial to our understanding of dinosaur physiology and the bioenergetic evolution of amniotes as a whole, yet it has received little attention so far. The only researchers to address the issue in some detail are Bakker (1980) and Paul (1988b). This paper addresses the above question from the perspective different from that of all previous treatments of the issue.

No skin impressions giving a clear indication of the type of the integument have been found around the skeletal remains of small dinosaurs, except for the theropod recently discovered in China. The significance of that find will be discussed later in the paper. Those known for a number of large ones, specifically for members of Ceratopsidae (Lull 1933), Hadrosauridae (Lull and Wright 1942), Abelisauridae (Bonaparte 1985), and Tyrannosauridae (Dale Russel personal comment cited in Paul 1988b), show that their skin was covered with small non-overlapping scales. It has been argued that the absence of hair or feathers in large dinosaurs does not contradict the presence of such structures in small ones since large extant endotherms (mammals) living in warm climates lack hair as well (Bakker 1980; Paul 1988a, 1988b). However, unlike large dinosaurs, extant "pachyderms" do not have scales either. Also, various birds with virtually naked heads and necks, such as condors or cassowaries, do not develop scales over those portions of their skin. In fact, a reversal from hair or feathers in small dinosaurs to the <u>unspecialized</u> reptilian scales in their large descendants (as opposed to the large bony scales that formed the armor of ankylosaurs and some other herbivorous dinosaurs) would hardly present any selective advantage over the thick naked skin of extant "pachyderms", and is therefore unlikely. Notably, when scales are present in animals that possess hair or feathers, they are either highly specialized defensive structures (armor of pangolins and armadillos) or are restricted to either areas of skin subjected to high abrasion (feet and tail of small mammals, lower segments of birds' legs) or to swimming organs (beaver's tail, penguin's flippers).

Paul (1988a) raises the possibility of large arctic dinosaurs (and presumably small ones from all latitudes) being covered with both scales and epidermal insulation, by pointing out that some arctic birds (ptarmigans) have both scales and feathers over the lower segments of their legs (Johnsgard 1983). To begin with, the integument of scales certainly precluded large dinosaurs (and, as already shown, their small ancestors as well) from possessing an insulating coat of hair, since in mammals hairs on the areas of skin covered with scales are so thin that they have virtually no insulating value. As to the retention of scales in an animal insulated by feathers, while anatomically possible, it is highly improbable. In the presence of feathers, an animal (especially a large, thick-skinned one) no longer needs scales to protect its skin and scales would certainly interfere with formation of insulating coat. Therefore, if non-avian dinosaurs evolved epidermal insulation in form of feathers, scales would almost certainly have been lost from insulated areas of their skin, as they were in birds. The retention of scales on the lower segments of arctic ptarmigans' legs despite the presence of feathers is probably due to the fact that those areas of a bird's skin are subjected to high abrasion and in the case of arctic ptarmigans lack the protection of feathers during the summer (Johnsgard 1983).

Thus it is extremely unlikely that any dinosaur, large or small, ancestral to one for which impressions of scaly skin are known possessed hair or feathers. This means that the smallest of all dinosaurs, with adult body weight less than 200 g (Paul 1988b), *Marasuchus lilloensis* (Sereno and Arcucci 1994), being the least derived and possibly the common ancestor of the Dinosauria (Paul 1988b, the species is considered to be synonimous with *Lagosuchus talampayensis*) and thus ancestral to all dinosaurs for which skin impressions are known, almost certainly lacked epidermal insulation. We must therefore conclude that at least some small dinosaurs were either ectothermic or were somehow able to compensate for the high rate of heat flow through their skin surfaces. Possible adaptations compensating for the absence of epidermal insulation in small endotherms will be discussed later in the paper.

Yet at least for some dinosaurs epidermal insulation must have presented a selective advantage, for it evolved at least once in the members of Dinosauria, as evidenced by the impressions of soft contour feathers on the Berlin specimen of *Archaeopteryx lithographica*. In order to understand why epidermal insulation did evolve in the archaeopterygid-avian lineage while being absent in small primitive dinosaurs, we must first establish how early did it appear within that lineage and whether it could evolve in other dinosaur lineages.

As already shown, ancestors of the dinosaurs for which impressions of scale-covered skin are known almost certainly did not possess epidermal insulation. This was probably true of taxa at least up to the family rank. Indeed, it is most unlikely that two dinosaurs, similar enough in their skeletal morphology to be placed within the same family, could be as different in their physiology and soft anatomy as a small amniote possessing epidermal insulation and one lacking it (even if all small dinosaurs were endothermic the above differences must have been substantial between furred or feathered ones and those lacking epidermal insulation). So, if a particular dinosaur family was ancestral to one, for whose members skin impressions showing an integument of scaly skin are known, then it is extremely unlikely that any members of either family possessed pelage or feathers.

Even if a particular family or a higher ranking taxon of Dinosauria was not directly ancestral to one, which included species known to have been scale-covered, the pattern of its evolution can sometimes be used to show that epidermal insulation probably had not evolved in its members.

Obviously, hair or feathers could not evolve in those groups, all members of which were large, since the presence of those structures would not have conferred any selective advantage for them (they were already sufficiently insulated by the low surface to volume ratio). Furthermore, in many dinosaur lineages only the most primitive members were small enough to be advantaged by the evolution of epidermal insulation. If those small dinosaurs did indeed evolve an insulating coat of hair or feathers, why did none of their descendants remain small to take advantage of this feature? The only explanation would be that all ecological niches which small members of the dinosaur lineages exhibiting such pattern of evolution could fill disappeared or were filled with superior competitors immediately after epidermal insulation evolved in the early members of those lineages. Since such a coincidence is extremely improbable, the lack of adaptive radiation into the ecological niches of small dinosaurs in many dinosaur lineages whose most primitive members were quite small strongly suggests that epidermal insulation did not evolve in those lineages.

However, some dinosaur taxa within Ornithischia (Heterodontosauria, Hypsilophodontidae, and Pachycephalosauria) and Theropoda [Ornitholestidae, Caenagnathidae (sensu Paul 1988b), and Ornithomimidae] did produce adaptive radiations into the ecological niches of small dinosaurs. One might hypothesize that those radiations resulted from the evolution of epidermal insulation in the members of the above taxa, while in the rest of dinosaur lineages, whose members lacked it, there was a strong selective pressure for evolution of large size to achieve thermal insulation through low surface to volume ratio. However, family Hypsilophodontidae within Ornithischia and family Ornitholestidae within Theropoda were ancestral to Iguanodontidae-Hadrosauridae (Galton 1972) and Tyrannosauridae [Based on Paul 1988b, although Paul advocates a somewhat different relationship between ornitholestids, allosaurids, and tyrannosaurids; Holtz (1994) failed to refute Paul's (1988b) arguments for the monophyly of Allosauria sensu Paul 1988b, although he is probably correct in arguing against the allosaurid ancestry for Tyrannosauridae] respectively for which impressions of scale-covered skin are known and therefore their members could not have possessed hair or feathers. Thus the above hypothesis is falsified and there is no reason to postulate evolution of epidermal insulation in any dinosaur lineage, unless there is positive evidence that its members actually possessed hair or feathers.

Using the above concepts, it can be shown with a fair degree of certainty that epidermal insulation evolved only once in the members of Dinosauria, in advanced theropod ancestors of the *Archaeopteryx*. But in the *Archaeopteryx* and its avian descendants insulation is provided by feathers, which also function as wing and tail airfoil components. [Aerodynamic function of wing feathers in *Archaeopteryx* was challenged by Ostrom (1974), but reaffirmed by Feduccia and Tordoff (1979).] In order to understand the evolution of epidermal insulation in dinosaurs we must establish which of those two functions of feathers was the original one.

Parkes (1966) presented a very strong argument for the original function of feathers being that of airfoil components by pointing out that, on the one hand, there is only a small structural difference between a large scale and a structure of any aerodynamic properties (an elongated scale can already serve as an airfoil component). On the other hand, there is a very large structural difference between even such a scale and a structure of any thermoinsulating properties, since in order to function as a thermal insulator an epidermal structure must already have fairly long and fine filaments to trap air between them (the basis of functioning of all types of epidermal insulation). Intermediates between a scale and the above described structure do not have insulating properties to any greater degree than a scale. Therefore, while it is conceivable that natural selection produced a flapping feather from a scale, it is most unlikely that it produced a thermoinsulating feather-like structure from a scale precursor.

Parkes' argument is further strengthened by considering the probable nature of the integument of the theropod ancestor of the *Archaeopteryx* in which feathers first evolved. The fact that members of both Ornithischia (Hadrosauridae, Ceratopsidae) and Theropoda (Abelisauridae, Tyrannosauridae) are known to have been covered with small non-overlapping scales strongly suggests that this type of integument was plesiomorphic in Dinosauria and was probably present in all dinosaurs, except for those, of course, that did possess epidermal insulation. It is hard to imagine how feathers could possibly evolve from such structures. On the other hand, it is probable that the distal segments of theropod limbs were protected by large overlapping scales, as are the legs of extant birds (Paul 1988b). Such structures are perfect precursors for evolution of flapping feathers, especially if one takes into consideration the strong probability that powered bird flight evolved not from passive gliding, but from the flapping movements of the fore limbs serving to orient an arboreal theropod during interbranch leaps (Paul 1988b). Even a small increase in the surface area of the forelimb provided by the elongation of the protective scales would have improved its ability to orient itself in the air and thus presented a selective advantage (Caple et al. 1983). The initial fraying of those elongated scales would have also been advantageous by increasing the drag of the forelimbs, which would have further improved stirring ability. (Neither of the above changes would have been adaptive for the evolution of gliding.)

The likelihood of the bodies of theropod dinosaurs in which feathers evolved being covered with small non-overlapping scales makes the hypothesis of feather origin proposed by Regal (1975) extremely improbable. He suggested that feathers first evolved as shields against solar radiation and later attained their thermoinsulating and aerodynamic functions. But there is a large structural difference between a scale of dinosaur integument and one with any shielding properties and intermediates between the two structures would have presented no selective advantage over the former of the two. Also, Regal's hypothesis fails to explain why the evolution of insulating feathers seemingly coincided with the evolution of flight in dinosaurs.

Regal (1975) criticized the hypothesis that feathers evolved as airfoils by asking why the unfeathered ancestors of birds did not evolve membranous wings, like those of bats and pterosaurs, and by pointing to the lack of adaptive intermediates between a frayed scale and a contour feather. The first criticism was refuted by Paul (1988b), who pointed out that theropod dinosaurs were precluded from evolving flying membranes by possessing hip joints that allowed hind limb movement only in parasagittal plane, thus preventing the hind limb from splaying out to support such membranes. As to the second criticism, every stage of evolution of barbules and then hooks would have been selectively advantageous by allowing to rigidify the airfoil without increasing its weight [which would have certainly resulted from the reduction of fraying of the edges of airfoil scales proposed by Regal (1975) as an alternative to the evolution of barbules and hooks].

Support for the hypothesis that feathers evolved from large protective scales on the distal segments of theropod forelimbs comes from an embryological study by Zou and Niswander (1996). By blocking the BMP signaling (Bone Morphogenetic Proteins were thought to be involved in triggering programmed cell death in tetrapod embryos) in the hind limbs of chicken embryos they were able to induce, among other changes, the development feather-like structures in place of large scales (scuta). The homology of scuta and feathers demonstrated by the study is easily explained by postulating that as large protective scales on the forearms of arboreal theropods evolved into feathers, the potential was created for the development of the latter structure in place of the former on both fore and hind limbs. In latter case such potential is, of course, suppressed in the majority of those theropods' living descendants.

The alternative explanation, that avian scuta actually evolved from feathers, is extremely improbable. Even if the former structure had evolved in the members of theropod-avian lineage after the latter, surely natural selection could produce large scales from small ones (the reticula of birds) much faster than from feathers. (In living birds development of feathers in place of scuta can be induced by blocking a single signaling pathway only because extant members of theropod-avian lineage already possess the genetic information for developing either type of integumentary structure.) In fact, considering the similarity between the hind limbs of living birds and even the most primitive theropods, large protective scales on the distal segments of hind and, presumably, fore limbs were probably plesiomorphic for Theropoda, and could have even been present in the common ancestor of the Dinosauria since the foot of *Marasuchus* is already quite bird-like (digitigrade with long and narrow metatarsus). On the other hand, as already shown, insulating feathers were unlikely to have been plesiomorphic for Dinosauria or Theropoda. Thus, the homology of scuta and feathers, established by Zou and Niswander, can be explained by evolution of the latter from the former, not visa versa.

Thus it can be said with confidence that feathers initially evolved in theropod dinosaurs as airfoil components and only later attained their thermoinsulating function. This does not mean that no non-flying theropod possessed insulating feathers. Paul (1988b) has presented strong evidence for the members of theropod family Dromaeosauridae not only being flightless secondarily, but being descendants of flying theropods (birds?) more advanced than *Archaeopteryx* and therefore undoubtedly possessing insulating feathers. While the author of this article disagrees with Paul that the same was true of the Troodontidae, he does believe, based on troodontids' skeletal morphology, that this family diverged from the theropod-avian lineage after airfoil and probably insulating feathers evolved in it and therefore possessed the latter.

Which brings us to the matter of the recently discovered feathered theropod. The very fact of presence of insulating feathers in a theropod dinosaur does not disprove any of the above conclusions because that theropod could have diverged from the theropod-avian lineage after the evolution of airfoil and insulating feathers in it. However, if it's morphology would indicate that the above possibility is improbable, this find would falsify the hypothesis that feathers originally evolved as airfoil components and if the theropod in question was closely related to the probable ancestors of Tyrannosauridae or Abelisauridae then all of the above reasoning about the presence of epidermal insulation in dinosaurs is wrong. While firm conclusions about the phylogenetic position of the newly discovered theropod can not be reached until its detailed description is published, the author of this article, having the opportunity to examine photographs of the specimen at the 1996 annual meeting of the Society of Vertebrate Paleontology, believes that certain features of its morphology do suggest that it did not evolve its feathers independently from the *Archaeopteryx*, but inherited them from even more primitive fliers, ancestral to the "ancient bird".

So unless more information on the feathered theropod from China or new finds prove otherwise, available evidence strongly suggests that epidermal insulation was not plesiomorphic in Dinosauria, while very small adult size was, and evolved only once within the group in the form of feathers, which originally arose as airfoil components.

Several hypotheses can be proposed to explain the above described pattern of evolution of epidermal insulation in dinosaurs. One hypothesis would be that endothermy was apomorphic in Dinosauria and evolved only once in association with the evolution of flight. However, the author of this article finds this hypothesis extremely improbable because of the strength of available evidence for full endothermy in all dinosaurs. In fact, existence of small endotherms with no epidermal insulation is not as improbable as may appear. McNab and Auffenberg (1976) have shown that at body weights above 30 kg lizards and mammals have similar thermal conductance and even tropical mammals of that size invariably possess substantial pelage. This indicates that scale-covered amniotes can compensate for the lack of epidermal insulation. Moreover, small dinosaurs, while having maximum exercise and therefore resting metabolic rates as high or higher than those of similar sized advanced mammals (Bennett and Ruben 1979) as suggested by their highly cursorial limb morphology, may have thermoregulated at lower body temperatures, like monotremes and edentates, to avoid excessive energy expenditure on thermoregulation.

Therefore a more plausible hypothesis would be that while all small dinosaurs, being endotherms, would have been advantaged by the presence of epidermal insulation, some factor (presumably the lack of pre-existing structures that could evolve into hair) prevented evolution of pelage in them; while insulating feathers, being derivatives of airfoil ones, could only evolve in dinosaurs adapted for flight, such as the members of the archaeopterygid-avian lineage.

Yet another explanation of the pattern of appearance of epidermal insulation in Dinosauria would be that, while being endothermic, most small dinosaurs would not have been advantaged by its presence, possessing alternative means to effectively reduce heat loss, except for those theropod ancestors of the *Archaeopteryx* that already possessed airfoil feathers and all of their descendants. The latter evolved epidermal insulation in form of contour feathers rather than hair because natural selection was able to produce thermoinsulating feathers from pre-existing airfoil ones faster than it was able to produce pelage.

However, this explanation is the most improbable one. To begin with, while it is conceivable that small endothermic dinosaurs living in tropical climates were able to thermoregulate successfully in the absence of hair or feathers, it is hard to believe that the presence of these structures would have conferred no selective advantage for them. Moreover, the hypothesis fails to explain why epidermal insulation became advantageous for small members of only one dinosaur lineage.

Considering all of the above, the proposition that the Dinosauria were unable to evolve hair and only those dinosaurs that already possessed airfoil feathers could evolve insulating ones is the most probable explanation of why epidermal insulation was almost certainly absent in tiny *Marasuchus* and most of its descendants, evolving only once among them and in the form of feathers rather than pelage.

## LITERATURE CITED

Bakker, R. T. 1980. Dinosaur heresy-dinosaur renaissance: why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution. 351-462 in Thomas, D. K. and Olson, E. C. (eds), *A Cold Look at the Warm Blooded Dinosaurs*. AAAS, Washington D. C.

Bennett, A. F. and Ruben, J. A. 1979. Endothermy and activity in vertebrates. *Science* 206: 649-654.

Bonaparte, J. F. 1985. A horned Cretaceous carnosaur from Patagonia. *National Geographic Research*, 149-151.

Caple, G. R., Balda, R. P., and Willis, W. R. 1983. The physics of leaping animals and the evolution of preflight. *American Naturalist* 121: 455-476.

Farlow, J. O. 1990. Dinosaur energetics and thermal biology. 43-55 in Weishampel, D. B., Dodson, P., Osmolska, H. (eds), *The Dinosauria*. University of California Press, Berkeley.

Farlow, J. O., Dodson, P., and Chinsamy, A. 1995. Dinosaur Biology. *Ecology and Systematics* 26: 445-471.

Feduccia, A. and Tordoff, H. B. 1979. Feathers of Archaeopteryx: Asymmetric Vanes Indicate Aerodinamic Function. *Science* 203: 1021-1022.

Galton, P. M. 1972. Classification and Evolution of Ornithopod Dinosaurs. *Nature* 239: 464-466.

Holtz, T. R. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68(5): 1100-1117.

Johnsgard, P. A. 1983. *The Grouse of the World.* University of Nebraska Press, Lincoln.

Lull, R. S. 1933. A revision of the Ceratopsia. *Peabody museum of Natural History Memoirs*, III(3).

Lull, R. S. and Wright, N. E. 1942. Hadrosaurian dinosaurs of North America. *Geological Society of America Special Paper* 40.

McNab, B. K., and Auffenberg, W. 1976. The effect of large body size on the temperature regulation of the Komodo dragon, *Varanus komodoensis*. *Comparative Biochemistry and Physiology* 55A: 345-350.

Ostrom, J. H. 1974. Archaeopteryx and the Origin of Flight. *Quaterly Review of Biology* 49: 27-47.

Parkes, K. C. 1966. Speculations on the origin of feathers. *Living Bird* 5:77-86.

Paul, G. S. 1988. Physiological, migratorial, climatological, geophysical, survival and evolutionary implications of polar dinosaurs. *Journal of Paleontology* 62: 640-652.

Paul, G. S. 1988. *Predatory Dinosaurs of the World.* Simon and Schuster, New York.

Paul, G. S. 1991. The Many Myths, Some Old, Some New, of Dinosaurology. *Modern Geology* 16: 69-99.

Paul, G. S. 1996. The Status of Respiratory Turbinates in Theropods. *Journal of Vertebrate Paleontology* 16 (supplement to no. 3) 57A.

Regal, P. J. 1975. The Evolutionary Origin of Feathers. *Quaterly Review of Biology* 50: 35-66.

Reid, R. 1987. Bone and dinosaur "endothermy". *Modern Geology* 11: 133-54.

Reid, R. 1990. Zonal growth rings in dinosaurs. *Modern Geology* 15: 19-48.

Ricqles, A. R. de. 1980. Tissue structure of dinosaur bone: Functional significance and possible relation to dinosaur physiology. 103-140 in Thomas, D. K. and Olson, E. C. (eds), *A Cold Look at the Warm Blooded Dinosaurs.* AAAS, Washington D. C.

Ruben, J. A. 1995. The Evolution of Endothermy in Mammals and Birds: From Physiology to Fossils. *Annual Review of Physiology* 57: 69-95.

Ruben, J. A., Hillenius, W. J., Geist, N. R., Leitch A., Jones, T.

D., Currie, P. J., Horner, J. R., Espe, J. III 1996. The Metabolic Status of Some Late Cretaceous Dinosaurs. *Science* 273: 1204-1207.

Sereno, P. C., and Arcucci, A. B., 1994. Dinosaurian precursors from the middle triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* 14(1): 53-73.

Spotila, J. R., O'Connor, M. P., Dodson, P., Paladino, F. 1991. Hot and Cold Running Dinosaurs: Body Size, Metabolism and Migration. *Modern Geology* 16: 203-227.

Zou, H. and Niswander, L. 1996. Requirement for BMP Signaling in Interdigital Apoptosis and Scale Formation. *Science* 272: 738-741.