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The Armored Dinosaurs

by Peter Makovicky

Kenneth Carpenter (ed.)
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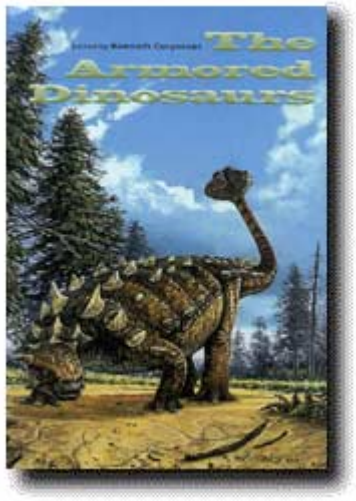
The Armored Dinosaurs, the newest in a series of paleontological offerings from Indiana University Press, is one of a recent wave of books dedicated to dinosaur paleontology. Unlike other such volumes, which are either broader in their coverage of dinosaur-related subjects or concentrate on very popular fields such as dinosaur eggs and babies, **The Armored Dinosaurs** is dedicated to the least studied of the major dinosaurian clades, Thyreophora. Thyreophora comprises Stegosauria and Ankylosauria and a handful of stem taxa, but despite their public appeal, fossils of these animals are comparatively rare. That this group is ripe for more attention is clear: prior to the publication of this volume, only a single cladistic analysis with three ingroup taxa was available for stegosaurs, and before 1998 none was available for ankylosaurs. Recent years have seen a revival in the study of Thyreophora, especially fueled by the description of a number of new ankylosaurian taxa by the book's editor Ken Carpenter and various colleagues.

The book, which has its roots in the symposium on ankylosaurs convened at the 58th Annual Meeting of the Society of Vertebrate Paleontology, goes some way toward correcting decades of neglect. The book's twenty-one chapters range widely in subject matter, ranging from paleontological history, descriptive and functional anatomy, ichnology, and developmental aspects to phylogeny. One new ankylosaur and a new stegosaur are described in separate chapters, and several known taxa such as **Euoplocephalus** are reviewed. Not surprisingly, the taxonomic distribution of chapters is skewed towards the more diverse and better-known ankylosaurs.



Although not a functional anatomist, I enjoyed the two chapters on jaw mechanics in **Scelidosaurus** by Paul Barret and in the advanced ankylosaurid **Euoplocephalus** by Rybczynski and Vickaryous, respectively. The feeding mechanics of ankylosaurs had received scant attention historically, and important details were probably overlooked because the teeth, which are unusually small for such large animals, were considered near-vestigial

structures. The two chapters also indicate that thyreophoran jaw mechanics were not uniform and that a detailed and comparative study across Thyreophora promises to be a fruitful field for future studies.

The two descriptive chapters on the primitive stegosaur **Hesperosaurus** and the ankylosaur **Cedarpelta,** both written by Ken Carpenter in collaboration with different co-authors, offer exciting new data on these groups. The description of **Hesperosaurus** is accompanied by what is only the second cladistic analysis of stegosaurs yet published. The basal **Hesperosaurus** and far more derived **Stegosaurus** are both from the Morrison Formation, and the near contemporaneous age of these disparate taxa suggest we have only scratched the surface of stegosaurian diversity. Much work remains to be done on the systematics of this understudied clade. The **Cedarpelta** remains include the first disarticulated cranial elements known for ankylosaurs, and these show that much of the cranial ornamentation of these animals was derived from the skull bones themselves, rather than deriving exclusively from osteoderms as previously thought. This latter point is further developed in a chapter by Vickaryous and colleagues. In an elegant study, in which ossification patterns in extant lizards were used as the comparative basis, the authors showed that highly fused and ornamented ankylosaur skulls display osteological correlates of both osteodermal ornamentation, and ornamentation derived from the dermal skull bones themselves. Osteoderms account for structures such as ossified eyelids and the pavement of scutes on the skull roof, but the dermal skull bones form structures such as horns above the orbits and on the cheeks. Being able to segregate these characters, many of which are important for ankylosaurian taxonomy, into distinct categories creates a potential for doing some very exciting systematic and character evolutionary research within the clade. Another interesting chapter by Coria and Salgado provided conclusive evidence for ankylosaurs in Argentina, strengthening the case for an influx of Laurasian dinosaur clades into South America late in the Cretaceous. For those working on thyreophoran anatomy and systematics, valuable reviews are provided in chapters such as Galton's redescription of the brain of **Stegosaurus** and Penkalski's review of **Euplocephalus** specimens.

The Armored Dinosaurs is largely geared toward specialists and serious dinosaur enthusiasts. A couple of chapters, such as the first chapter by David Norman and Carpenter and Galton's entry "Othniel Marsh and the myth of the eight spiked Stegosaurus" make for some pretty dry reading if one is not a passionate student of the history of paleontology. On the other hand, one advantage of edited books is that they provide an opportunity to deviate from the standardized journal formats, and allow for focus on particular aspects of a given subject matter. Several papers including ones by Ford and Kirkland, Molnar, and Blows on ankylosaurian armor patterns may not entice general readers, but they hold a wealth of information that is relevant to the taxonomy and systematics of this clade.

As with all edited volumes, chapters vary in both scope and quality, and some of the entries probably would not have made the cut in a professional journal. One such entry is Blow's "Possible stegosaur dermal armor from the Lower Cretaceous of southern England" dealing with isolated elements from various Wealden localities. The identity of the described dermal elements is so tentative, that it borders on the uninformative, and no useful

information on taxonomic diversity can be extracted from this chapter.

The aspect I found most disappointing about the book, was its lack of rigorous systematics-based approaches to character evaluation and phylogenetic conclusions. In a chapter revising the small nodosaur Struthiosaurus austriacus, Pereda-Suberbiola and Galton conclude that this animal is a small, primitive nodosaur that shows a pedomorphic reduction in body size relative to its larger, more derived, but mostly older cousins. Heterochrony is essentially a phylogenetic concept, so one would expect that characters indicative of heterochronic change should show transformations to states that are seen in juveniles of outgroup taxa. No such analysis is presented by the authors, and indeed the conclusions that **S. austriacus** is both primitive and pedomorphic relative to its larger cousins seem somewhat incongruous.

Most distressing was the final chapter on ankylosaurian systematics by the editor Ken Carpenter. The systematic nature of the title prompted me to read this chapter first, but my initial interest quickly turned to dismay. Discouraged by his efforts to achieve well resolved trees using global parsimony analyses, and unconcerned as to whether this problem is due to missing data or homoplasy, Carpenter appeals to Geraat Vermeij's controversial paper (Paleobiology 25: 431-433) to argue for a "compartmentalized" approach to ankylosaur systematics. This compartmentalized approach amounts to little more than constraining the monophyly of clades he views as stable and for which he chooses a set of diagnostic characters prior to analysis. In a time where systematists are increasingly working toward creating super-trees, Carpenter instead decides to restrict his analyses to "mini-trees". Obviously, the notion of testing phylogenetic hypotheses through the addition of taxa and characters is completely ignored, and the reference list reveals a surprising absence of systematic literature: only a single paper in **Systematic Biology** is cited. In his various analyses of these constrained and small data sets, Carpenter proceeds to make some inexplicable errors such as including a taxon with all question marks, and using bootstrap analyses or the distance-based neighbor-joining algorithm rather than parsimony anlysis, although he remains under the impression that he is conducting the latter. Fortunately, for those interested in ankylosaur systematics, a global parsimony analysis was recently published by Matt Vickaryous and colleagues. (Canadian Journal of Earth Sciences 38: 1767-1780).

My misgivings aside, **The Armored Dinosaurs** is the best volume around on thyreophorans, and a must-have for any serious student of dinosaurs. It provides a lot of detailed, new information on various aspects of thyreophoran anatomy and biology. It, furthermore, presents some novel approaches and much-needed reappraisals, and even its shortcomings serve their purpose: namely to define future research efforts within Thyreophora.