AN IMPROBABLE VIEW OF TERTIARY DINOSAURS

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To many of us the fact that dinosaurs are no longer around is a supreme frustration - we would give anything to see them. I have come across a few dinosaurologists who prefer dinosaurs as a case of detective work rather than field work, to them I say "tisk-tisk". Others note that had dinosaurs not gone extinct we would not be around to see them anyway, and to them I say "details, details"!

D. Dixon is one of the discontented, and in The New Dinosaurs - An Alternative Evolution he explores how dinosaurs might have evolved if they, and some other Mesozoic creatures, not bought the farm circa 65 Myr ago. This book is patterned after his look at what may befall Earth's future fauna in After Man - A Zoology of the Future. In his forward for the new volume D. Morris says that Dixon's modern dinosaurs left him "rarely disappointed". I am afraid that I was disappointed more often.

Indeed, I found The New Dinosaurs to be persistently frustrating, to an extent beyond what I can detail in this review. Dixon claims that his dinosaurian extrapolations are based on evolutionary principles, yet he came up with a menagerie of creatures that have little to do with the real dinosaurs of the Mesozoic, and are often wholly implausible. I believe this came about because Dixon has a superficial understanding of dinosaur and pterosaur biology, and of their actual evolutionary patterns - i. e. he is not familiar with the technical literature, a necessity since the popular literature remains incomplete and sometimes obsolete (it is interesting that two who have praised the book, Morris, and H. Gee in Nature [335: p. 505, 1988] are not dinosaurologists). In addition, he wants to make archosaurs more mammalian than is appropriate.

Just as some artists believe that good abstractionists should be able to execute first-class realistic works, Dixon shows how well he understands real dinosaurs by his restorations of "modern" dinosaurs that have changed little since the Mesozoic. Take his Megalosaurus modernus (a genus that did not last past the Jurassic). His restoration is a bland, amorphous rendition little better than a Zallinger or Parker effort of decades past, and lacks the very short, heavy forearm of the genus. Dixon simply misses the wonderful structural form that marks the skulls and skeletons of the great theropods. Dixon clearly did not carefully study the technical literature on the domeheaded pachycephalosaurs, because if he had he would have restored "Numbskull" with the bizarrely broad bellies and tail bases that they have, plus their very short forelimbs. Pterosaur necks could not assume the egret-like folded posture he shows for "parasos" and "sifts". His various sauropods are also lackluster, and his grasp of dinosaur detail is simply inadequate, as shown by feet that are too plantigrade, have too many hooves on the hands of sauropods, and have too few claws on their hindfeet. He draws the titanosaur "rajapahnat" as if it were a brachiosaur. In making these mistakes Dixon is, admittedly, often no worse than other artists, but that is no

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excuse.

Likewise, Dixon's understanding of Mesozoic dinosaur and pterosaur evolution is deficient. He shows dinosaurs evolving randomly from assorted thecodonts, contrary to the emerging consensus that all dinosaurs, and perhaps pterosaurs too, share a common ancestor above the level of thecodonts. He is unaware that teratosaurs have been shown to be chimeras made up of thecodont and theropod skulls and teeth mixed in with prosauropod skeletons. He shows theropods in the obsolete dichotomy of small gracile coelurosaurs and big "megalosaurs", and claims that the latter were failing at the end of the Cretaceous. Not so. The big theropods repeatedly evolved from smaller forms (allosaurs-tyrannosaurs from ornitholestians for example), and at the end of the Cretaceous there were an array of big tyrannosaurs, allosaurs, abelisaurs and dryptosaurs. Perhaps worst of all, Dixon has the tailless pterodactyloid pterosaurs continuing in a healthy radiation up to the end of the Cretaceous, when in fact they appear to have been in drastic decline in the latter part of that period. With basic mistakes like these, it is not surprising that Dixon makes erring speculations on post K-T dinosaurs.

A vital point that Dixon misses is just how conservative the evolution of dinosaur and pterosaur groups often was. For example, some of the small Late Cretaceous ornithopods were little different from those of the Triassic and Jurassic. Although specialized in some regards, the Late Cretaceous segnosaurs were still prosauropodian in basic form. All dinosaurs were erect-gait, terrestrial animals with substantial tails. Of the many thousands of dinosaur trackways known, not one shows a hopping gait. Although some of the small, longer-fingered theropods could climb fairly well, no dinosaur was truly arboreal. None was truly aquatic, marine, or a burrower. Pterosaurs always retained much the same design, with a short humerus, three short innner fingers, a very long wing finger, and four short, small clawed toes. Pterosaurs always seem to have been essentially semi-aquatic too, and there never was a truly predatory species. Even Quetzalcoatlus had a beak and neck that were too slender and weak for scavenging; it was instead a three meter tall animal pursuing a crane-like lifestyle. In their 170 Myr dinosaurs and pterosaurs did achieve a spectacular variation in form and habitat preference, but never to the degree seen in mammals and birds during the last 65 Myr. One reason for the archosaur's relative constancy of form is the basic phenomenon of adaptive entrenchment, in which changes in a lineage's form and genetics cannot breach the limits presented by the original body design and genetic makeup. So while organisms are remarkably plastic, they are not infinitely so.

The key question is, therefore, why should one expect dinosaurs and pterosaurs to suddenly experience the incredible explosion in new forms that Dixon paints in only 65 Myr? Especially when dinosaurs had already filled most large-animal roles - unlike Tertiary mammals, which started out with no large species. Why would dinosaurs and pterosaurs suddenly become burrowers, hoppers, tree-snake-like "wyrms", penguin- and manatee-mimicking "glubs" and "plungers", "arbosaurs", and so on, when they had failed to do so during 170 Myr in the Mesozoic? Dixon offers no convincing or detailed explanation for this idea, probably because there is none. It should be remembered that we have samples of a diverse array of Mesozoic habitats, from polar regions to dune deserts. Only eroding highland areas are entirely missing. The modern world flora and climate is more diverse than it was in the Mesozoic, and very probably would support a higher

diversity of dinosaur species and forms. Dixon just goes much too far with the idea.

The radiation of modern pterosaurs in the book is particularly implausible. Whether the failing pterosaurs would have made it much past the K/T boundry is very dubious. Even if they did, there is no reason to doubt that they would have followed the same pattern as before, in which pterosaurs never filled many roles often assumed by birds, and never lost flight (in this regard Dixon seems unaware of the controversy continuing to surround pterosaur biology; they may have been less "birdy" and bipedal than Padian has suggested). That pterosaurs would take it upon themselves to adopt many bird-type roles, when birds were already around to do that anyway, is hardly likely. That a pterosaur would become a polar, penguin-like "plunger" is hardly tenable. I have no doubt that true moas and kiwis would have evolved on New Zealand, not wingless, rodent-headed(!) pterosaurs doing much the same thing. Flamingos, not a "cribrum" pterosaur, would be flamingos. There never have been true flying predators as big as "harridan", not in the Mesozoic, nor after. Since pterosaurs were always eaters of fish and other water-life, or insects, the grass- and other plant- eating "flarp", "kloon", "wandle", and "lank" appear to be well outside the bounds of their entrenched adaptative potential.

Indeed, the "lank" is perhaps the worst beast in the book. That pterosaurs would beat their dinosaurian cousins into evolving into giraffes, of all things, complete with hooves and reticulated orange-brown color pattern, is unbelievable. It may be significant that Dixon made a similar mistake in his previous book by creating flightless island bats, something that has never happened - and this leads to the question of why bats would not have gone ahead and filled their nocturnal sonar hunting role in a dinosaur-dominated world.

By the same token, it is very probable a dinosaurian modern world would see the trees filled with birds, mammals, snakes and tree frogs little different from what we really have. Dixon's "arbosaurs" would find it just as impossible to get a foothold in the trees as dinosaurs did in the Late Cretaceous. So, woodpeckers would peck on old trees, not "naugers". This and some of the other "arbosaurs" are anatomically reasonable extrapolations, but that a long-limbed dinosaur (the "treehopper") would run as oddly on the ground as does a sifakas lemur is difficult to swallow. So are the gliding "gimp", "scaly glider" and "flurrit". The snake-like "treewyrm" flies right in the face of the entrenched biology of dinosaurs. Likewise, the idea that dinosaurs would suddenly end up looking like cuddly pandas ("taddy") and koala bears ("tubb") ignores the fact that it is mammals, not archosaurs, that have such evolutionary potential.

Small sand-burrowing theropods did not evolve in the Mesozoic - the stiff, bird-like bodies of theropods were not even close to being suitable for such a transformation - so we can confidently say that "sandle" and "wyrm" would not pop up from modern desert dunes.

Likewise the stiff-bodied and rigid-tailed small ornithopods (that is why they had ossified rods astride their vertebrae) would not have turned into flexible swimmers like "water glub" and "glub". Of these the latter is the worse design, because ornithopod legs were much more powerful than the arms and would not have been lost.

The carcass imitating "springe" is an animal of pure fantasy.

Dixon also shows how little he understands dinosaurs in his restorations of more plausible forms. For example, just about all his

ornithopods have the tail bent sharply up at the tail base. Actually, in ornithopods the tail-base vertebrae either sweep gently downwards or emerge nearly straight from the hip; they could not bend sharply upwards (it was dromeosaur tails that could do that). Dixon shows "balaclav" with an enormous fifth-finger claw, but digit V is always the most reduced in dinosaurs. The thumb is the digit with a large weapon. The finger claws of predatory dinosaur were always manipulative rather than killing weapons because arms are not as powerful as jaws or legs, so finger-poking "northclaw" does not make the grade. Such errors plague most of Dixon's "postulations".

For example, the "taranter" looks too much like a glyptodont, with a spherical body and brickwork armor, rather than an ankylosaur with the low-slung, extraordinarily broad body and more loosely spaced armor typical of these dinosaurs.

Nor do I approve of Dixon's slow, scavenging tyrannosaur "gourmand". Even 12-ton T. rex had limbs that were, bone for bone, almost identical to the swift ostrich-mimic dinosaurs, and the limb-segment ratio of its leg was about the same as that of a horse. Such things suggest speed. The fantastic biting power and binocular vision of tyrannosaurs were clear-cut killing adaptations, and field biologists have shown that pure land scavengers are energetically implausible. Dixon also misses the beautiful structure of tyrannosaur heads.

Dixon misses other opportunities: for example, the heads and bodies of the sickle-clawed dromaeosaurs and troodonts were often elegant and graceful, but not in this book. The face of "northclaw" looks more like that of a mad Irishman than a dinosaur.

But what really irks me is how Dixon ignores the true appearance of large dinosaurs. We have skin impressions and even "mummies" for a number of ceratopsians, ornithopods (hadrosaurs especially), sauropods, and theropods. They always show a rich and wonderful topography of mosaic-pattern scales. Bony ridges, bosses and the like show that large scales and hornlets usually adorned their heads. Hadrosaurs are known to have had either a horny or skin frill running atop their spinal column, and skin folds draped over their shoulders. I am one who believes that all dinosaurs were avian and mammalian in basic design and physiology, and small dinosaurs may well have been insulated. But the big species had a reptilian veneer of scales and horns. None of this shows up in Dixon's work. Instead, his big dinosaurs look like unscaled or furry mammals. His hadrosaurs have no frills, skin folds, or the delightful scales. The "monocorn" ceratopsid has a smooth-surfaced head and unmuscled, plain-edged frill that is not only out of tune with the superb, hornlet-adorned heads of real ceratopsids, but is not nearly as interesting either. The skin is drawn as being elephantine, rather than correctly ceratopsid. Scaly big dinosaurs were probably living through long, cold polar nights, so there is no need to make large modern dinosaurs dwelling in temperate areas so furry.

Modern polar dinosaurs would need heavy insulation, and here Dixon contradicts himself. Believing that dinosaurs could not cope with the arctic tundra, he puts only birds there (why not big mammals?). Yet he constructs high-mountain dinosaurs such as the "balaclav" and "mountain leaper" living in conditions just as harsh.

Dixon's misunderstanding of dinosaur biology also shows up when he gives hadrosaurs ("sprintosaurs"), ceratopsids, etc. elongated limbs too much like those of gracile ungulates. Actually, the limbs of Mesozoic hadrosaurs and ceratopsids were already well designed for high-speed travel, and many of these species lived in open habitats

rather than forest. So plains-dwelling dinosaurs would have elongated their limbs only a little, if at all. Besides, various species of grazing rhinos show that stout limbs are good for life on the plains. On the other extreme, sauropods had truly elephantine limbs that were unsuitable for running, contrary to the book's fast Tertiary sauropods of South America. Also too like mammals are the shoulder and thigh muscle patterns in the quadrupeds. Like many artists, Dixon often draws quadrupedal dinosaurs with the shoulder joint set high on the chest in the mammalian manner, rather than in the low position where it really was.

There are a few good ideas in Dixon's book. His dwarf island dinosaurs are fine, as is his idea of grass-grazing hadrosaurs. The "coconut grab" makes sense to this vertebrate paleontologist. The "zwim" is a nice little mammal, and there was a trend towards reduction of the arm in tyrannosaurs that would have led to their loss in another 10 or 20 Myr. The duckbills, ceratopsids, theropods and other running dinosaurs are correctly drawn with flexed limbs. I tend to agree that troodonts would not have become nuclear-weapon-deploying dinosauroids, since such dramatic increases in brainsize did not even begin to occur during their long evolution in the Cretaceous.

But such items are few and far between, and frankly, I think the book lacks the combination of discipline and imagination needed to pull off such a work. It does not take much inspirition to come up with Australian dinosaurs that bound like kangaroos and look like koala bears, African pterosaurs that just happen to look exactly like giraffes, Asian psuedo-pandas, South American equivalents of sabre-toothed marsupials and manatees, and so on. In these cases Dixon picked a mammal, and tried to squeeze a dinosaur or pterosaur into the same package. The evolutionary odds against such likenesses in place and form are at best very long; at worst they are anatomically impossible.

I was inspired to come up with a more plausible postulation of post K/T dinosaurs (Figure 1). It shows an extension of the North American Late Cretaceous fauna onto the western grasslands sometime in the Late Tertiary. The tyrannosaur's design is little changed - how could such fast, powerful predators be improved - although the arms are nearly lost, skull openings are further reduced and the stereoscopic vision is increased. The grazing, crested lambeosaurine retains its scales and frill, but has a longer, squarer beak. Well-developed posterior jaw muscles have prevented the eyes from shifting far back on the head, the tail is still substantial, and the legs remain those of a hadrosaur. It is postulated that the true ceratopsids have become extinct, to be replaced by a new radiation of rhino-sized protoceratopsid descendants better adapted for grasslands. They have developed an impressive array of horns and scale patterns. The furry little ornithopod has conservatively retained the body design that served them so well for some 200 Myr. One cannot see that it is now a rumen-equiped cud chewer (unlike the animals over 1000 kg, which cannot use and do not need rumens). The dinosaur's extremities are only slightly elongated for plains life. Overhead fly birds, not pterosaurs, and rodents churn up the ground.

One might wonder if mammals would have continued to be totally submissive in a dinosaur-dominated Tertiary. Primitive ungulates, carnivores and primates first appeared in the latest Cretaceous, and there is no a-priori reason that they could not have become increasingly successful, although the radiation of ungulates and carnivores would have been much slower. It is plausible that the relative domi-

nance of archosaurs and therians, both as predators and herbivores, may have varied from continent to continent, much as it really does between marsupials and placentals. Competition with large carnivores and ungulates could eventually have spurred an increase in dinosaur brainsize - after all, many sharks and rays have brains as big and complex as mammals'. Some of the primates might have evolved into homonids that cut apart dinosaur carcasses with their crude stone tools, before employing more advanced technology against the archosaurs.

I would not have so much of a problem with The New Dinosaurs if Dixon promoted it as wholly a work of science fiction, which it is, rather than a popular science book, which it certainly is not. Most of Dixon's dinosaurs are little more plausible than the faster-than-light starship Enterprise. But even then I find the Enterprise (as first presented in the original series) to be the more believable work of fiction, it looks just like what an interstellar battle-cruiser should look like. The "lank" does not look like what any pterosaur would ever look like.

Postscript: Having been the recipient of what I believe are two or three unjustifiably harsh reviews (and one fair one) of my book, Predatory Dinosaurs of the World, a few additional comments are appropriate. Being an author and illustrator myself, I understand and respect the tremendous effort that Dixon undertook in creating his book, especially the many color pieces whose quality is excellent. Dixon made a good faith effort to present his views to the public, and I confirm his right to do so. Since his book did not get suppressed by the increasingly pernicious peer review system, we all now have the opportunity to voice our views in support or otherwise of the concepts presented in The New Dinosaurs. The field can only benefit from such a free exchange of ideas - even improbable thoughts are often stimulating and revealing.

Fig. 1. A Late Tertiary tyrannosaur culls out a lambeosaurine grazer from a mixed herd that also includes large protoceratopsid descendants. A small ornithopod leaves the scene on the right, shovel-nose horned rodents peer from their burrows, and geese flock together in the distance. The locale is the western grasslands of North America.