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Leathery-Winged Harpies

If TV, film, and overzealous internet users have taught me anything, it's that the prehistoric world was harsh and brutal, and everyday existence was a life-or-death struggle. These terrible landscapes would be unrecognizable to our modern eyes, and only the biggest, nastiest animals survived. Consider, for example, the giant birds that stalked the Earth as recently as two million years ago. Taller than basketball players, they kicked and stabbed small, defenseless mammals to death. The ancestors of our pet cats and dogs wielded sabre teeth and bone-crushing jaws that they used to hunt giant elephants and rhinoceros, themselves armed with tusks and horns that would shame their mightiest modern relatives. The world was even more ferocious before these birds and mammals existed. During the span of time known as the Mesozoic (245–65 million years ago, or "Ma"), terrible reptiles ruled the day and predator-prey arms races were more intense than the Cold War. Gangs of carnivorous dinosaurs attacked their enormous herbivorous relatives, contesting their switchblade claws and armor-piercing teeth against the spikes, clubs, shields, and armored hides of their quarry. The Mesozoic oceans were just as deadly, teeming with giant, snaggle-toothed marine reptiles that render Moby Dick as intimidating as Flipper. Even the planet itself had a bad attitude in this Age of Reptiles. Angry volcanoes perpetually smoked, continents ripped themselves to pieces, and gigantic meteorites collided with the Earth, thowing enough dust and ash into the skies to block out the sun and cause cataclysmic extinction events.

The skies of this terrible age were no less formidable. They were dominated by a group of lanky grotesques, strange hybrids of birds and bats with a decidedly reptilian flavor. Their oversize heads were bristling with ferocious teeth or else bore savage beaks, each used to spear fish from primordial seas. Their outstretched membranous wings attained dimensions rivaling the wingspans of small aircraft, but were supported by lank, undermuscled limbs and tiny bodies. They were weak, flimsy, and pathetic animals, barely able to power their own locomotion and reliant on cliffs and headwinds to achieve flight. They were virtually helpless when grounded, barely able to push or drag themselves about, and completely at the mercy of any carnivorous reptile that fancied chewing on their hollow, twiglet-like bones. These creaky beasts were an archaic first attempt by vertebrate animals to achieve flight before graceful birds and nimble bats inherited the skies later in Earth's history. Given their obvious physical ineptitude, it's hardly surprising these creatures, the pterosaurs, collectively bought the farm at the end of the Mesozoic, along with any dinosaur that was not lucky enough to have evolved into a bird.

But That's All Hokum

Of course, the world and animals described above are nothing but caricatures of reality, the sort of landscape you may expect to find in Arthur Conan Doyle's *The Lost World* or similar-grade fiction. The popular view of primordial Earth as violent and totally unfamiliar is probably entirely untrue, a construct of poor scientific communication, overdramatic media representation, and romantic storytellers. In reality, ancient animals were no less sophisticated or intelligent, nor more freakish and savage, than those alive today. Paleontological research has probed deeply into the exotic and strange natures of many ancient animals to reveal that they merely represent "extreme" variants of anatomies and behaviors we see in our modern, familiar species. Such research has not made animals like the long-necked sauropods or giant theropod dinosaurs any less spectacular, but they are certainly not as mysterious and enigmatic as they once were.

Pterosaurs, which translates from Greek to "winged lizards," have suffered more than most in their depiction as ancient savages. All that remains of these animals are their fossil bones, oddly proportioned skeletons that have proved difficult to comprehend and continue to cause frequent controversies among those who study them. The pterosaur's ability to fly, combined with bizarre anatomy, often gigantic size, and an old-fashioned attitude that extinct animals were inherently inferior to modern species, resulted in them being perceived as crude, biological hang gliders, which were rather useless at

Fig. 1.1. Two *Rhamphorhynchus*, fish-eating pterosaurs of the Late Jurassic, doing what pterosaurs do best.

Fig. 1.2. The major pterosaur bauplans of the 130–150 species currently known. See chapters 9–25 for the identities of each animal.

everything but remaining airborne. Constant, often unwarranted, comparisons with birds and bats has cast pterosaurs as evolutionary also-rans, vertebrates that took the bold first stab at powered flight but were ultimately only the warm-up act for later, more sophisticated fliers.

Thankfully, these attitudes have slowly changed. Most modern pterosaurologists perceive pterosaurs as successful, diverse animals with interesting and intricate life histories, and in this book we'll discover the evidence for this change in attitude. We'll see that, while pterosaurs were undeniably very well adapted for powered flight (fig. 1.1), they were also skilled walkers, runners, and swimmers. They lived in diverse habitats across the globe and fueled their active lifestyles with prey caught in distinct, dynamic ways. They grew from precocial beginnings to adulthood and invested heavily in social and sexual display before becoming old and, in some cases, sick and arthritic. We'll meet numerous pterosaur groups (fig. 1.2) and over one hundred species spread across a dynasty spanning almost the entire Mesozoic, beginning in the Triassic period (245–205 Ma), thriving in the Jurassic (205–145 Ma), before ending at the very end of the Cretaceous, 65 Ma.

Our overview of pterosaurs is split into three parts. We'll start with an assessment of their general paleobiology, looking at their anatomy, locomotion, and other generalities of their lifestyles. Then, beginning with chapter 9, we'll meet, chapter by chapter, the diverse array of pterosaur groups currently recognized by pterosaur researchers, or "pterosaurologists." Finally, in the last chapter, we'll ponder their evolutionary story and try to ascertain why the skies of modern times are not full of membranous, reptilian wings in the way they once were.