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Abstract: It is a summer day on the pampas of central Argentina some five million years ago. Soon the head drops to the level of the grass, and the creature moves forward a few meters, then raises its head again to re new the surveillance. In preparation, it lowers its head to a large rock close to its feet, rubbing its deep beak there to sharpen the bladelike edges. In rocks from 55 million to 45 million years old in North America, Europe and Asia, large carnivorous birds are represented by the family Diatrymatidae-- which, according to my colleague Herculano M. F. Alvarenga of the University of Sao Paulo in Brazil, developed characteristics similar to those of the phorusrhacolds. After the emergence of the Panamanian land bridge, placental dogs and cats of the families Canidae and Felidae dispersed into South America from North America.

The Terror Birds of South America

These huge, swift creatures were the dominant carnivores of the continent for millions of years, until competitors drove them into extinction

It is a summer day on the pampas of central Argentina some five million years ago. A herd of small, horselike mammals are grazing peacefully in the warm sun. None of the animals is aware of the tall, vigilant creature standing 50 meters away in he high grass. Most of the watcher's, trim, feathered body is concealed by he vegetation. Its eyes, set on the sides of a disproportionately large head perched on a long and powerful neck, are fixed on the herd. The head moves from side to side in short, ra pid jerks, permitting a fix on the prey without the aid of stereoscopic vision.

Soon the head drops to the level of the grass, and the creature moves forward a few meters, then raises its head again to re new the surveillance. At a distance of 3t. meters, the animal is almost ready to attack. In preparation, it lowers its head to a large rock close to its feet, rubbing its deep beak there to sharpen the bladelike edges.

Now the carnivore bristles its feathers and springs. Propelled by two long, muscular legs, it dashes toward the herd. Within a few seconds it is moving at 70 kilometers an hour. Its small wings, useless for flight, are extended to the sides in aid of balance and maneuverability.

The herd, stricken with fright, bolts in disarray as the predator bears down. The attacker fixes its attention on an old male lagging behind the fleeing animals and quickly gains on it. Although the old male runs desperately, the attacker is soon a t its side. With a stunning sideswipe of its powerful left foot, it knocks

the prey off balance, seizes it in its massive beak and, with swinging motions of its head, beats it on the ground until it is unconscious. Now the attacker can swallow the limp body whole--an easy feat, given the creature's meter-long head and half-meter gape. Content, the gorged predator returns to its round nest of twigs in the grass nearby and resumes the incubation of two eggs the size of basketballs.

Eating Machines

MEET THE TERROR BIRDS, the most spectacular and formidable group of flightless, flesh-eating birds that ever lived. They are all extinct now, but they were once to the land what sharks are to the seas: engines of destruction and awesome eating machines. In their time, from 62 million years to about 2.5 million years ago, these creatures became the dominant carnivores of South America. Yet they ultimately declined as a result of competition from other carnivores.

The terror birds are members of a group ornithologists call phorusrhacoids. The first phorusrhacoid to be described scientifically--in 1887 by Argentine paleontologist Florentino Ameghino--was a fossil that he named *Phorusrhacos longissimus*. (*Phorusrhacos* is the genus; *longissimus* the species. Taxonomists go on to classify living and extinct organisms in increasingly larger groups: family, order, class, phylum, kingdom and, sometimes, domains.) The fossil came from the Santa Cruz Formation in Patagonia, the southernmost region of Argentina; the formation is about 17 million years old.

Ameghino and other researchers reconstructed the appearance of the birds from their fossil remains and their behavior from what creatures that might be living relatives do. The investigators initially interpreted the flesh-eating habits of the phorusrhacoids as an indication that they were related to modern eagles and hawks. Not all paleontologists agreed, and the issue was debated over the next 12 years. Charles W. Andrews of the British Museum resolved the controversy in 1899, concluding that among all living and extinct groups, the phorusrhacoids were most closely related to the South American seriema birds, which could also be regarded as the structural ancestors of the phorusrhacoids. Seriemas live today in the grasslands of northern Argentina, eastern Bolivia, Paraguay, and central and eastern Brazil. Seriemas and phorusrhacoids are classified as members of the order Gruiformes, which includes cranes and rails and their kin.

There are two living seriema species, the red-legged seriema (*Cariama cristata*) and the black-legged, or Burmeister's, seriema (*Chunga burmeisteri*). These birds reach a height of 0.7 meter. They are light-bodied, long-legged and long-necked. Their wings are small relative to their body, and the birds resort to spurts of short-distance flight only when pressed. They are excellent runners, able to attain speeds in excess of 60 kilometers an hour. Seriemas build twig nests, four to six meters above the ground, in low trees. The young, usually two, become fledglings in about a month, whereupon they leave the nest to live and hunt in the nearby grasslands. Like most carnivorous animals, seriemas are territorial. Their call has been described as eerie and piercing.

Seriemas eat insects, reptiles, small mammals and other birds. Under favorable conditions, they will attack larger game. They seize their prey in their beaks and beat the animal on the ground until it is limp enough to be swallowed whole. This feeding strategy is also practiced today by the roadrunner (*Geococcyx californianus*) of the southwestern U.S. and the secretary bird (*Sagittarius serpentarius*) of Africa.

Seriemas are placed in the family Cariamidae, which now is restricted to South America. About 10 fossil species have been found there, the oldest being from the Middle Paleocene epoch (some 62 million years ago) of Brazil. Relatives of this group are represented by two fossil families: the Bathornithidae, which appear in beds 40 million to 20 million years old in North America, and the Idiornithidae, found in certain European rock formations 40 million to 30 million years old. Some scientists believe these families are so closely related that they should all be grouped in the family Cariamidae.

Trading Flight for Speed

MOST OF THE TERROR birds were considerably larger than their living relatives. The creatures ranged in height from one to three meters (just shy of 10 feet). The earliest known members are virtually as specialized as the latest, indicating that they originated before their first appearance in the fossil record.

About a dozen genera and 25 species of terror birds have been recognized. The relation among them is still not clear. They were classified in 1960 by Bryan Patterson of the Museum of Comparative Zoology at Harvard University and Jorge L. Kraglievich of the Municipal Museum of Natural and Traditional Science of Mar del Plata in Argentina. This classification ordered the terror birds in three families that, in comparison to families of mammals, include animals of medium, large and gigantic size. Other workers, basing their view on the period of greatest diversity among terror birds, achieved between five million and three million years ago, recognize two families--gigantic and medium--as well as two subfamilies. Some researchers place all the fossils in one family.

In the three-family system the gigantic forms are members of the family Brontornithidae. Fossils of this family have been found in beds ranging in age from 27 million to 17 million years. A heavy, ponderous build characterized the birds; the leg bones were fairly short, the beaks massive. This evidence suggests that the birds were cumbersome runners, slower afoot than the members of the other two families.

Next comes the family Phorusrhacidae. Its members ranged between two and three meters in height. Fossils have been found, in rocks ranging in age from 27 million to three million years. The third family, Psilopteridae, comprised quite small members; most of them stood no more than one meter in height. Their known fossils range from 62 million to two million years in age. Within this family is the oldest known phorusrhacid, *Paleopsilopterus*, which was found in Brazil. Members of these last two families were lightly built, swift runners.

They were the members that became the dominant running carnivores of their time, and they held that status for millions of years.

The fact that phorusrhacoids came in several sizes indicates that the adults were capable of preying on a wide variety of animals, from rodents to large herbivores. Although some of the adult herbivores were as big as some adult phorusrhacoids, the birds could easily have preyed on the young ones. Phorusrhacoids newly out of the nest would certainly have had different food needs because they were smaller; they probably hunted rodents and other small vertebrates, much as their living seriema relatives still do.

During most of the age of mammals (the past 66 million years or so), phorusrhacoids thus occupied the role of fleet-footed carnivores in South America. They were able to assume this role by giving up the greatest virtue of being a bird--the power of flight. The door to dominance as carnivores opened to the phorusrhacoids when their predecessors in that role--small, bipedal dinosaurs known as coelurosaurs--disappeared in the dinosaur extinction 66 million years ago. Paleobiologists call such a transition an evolutionary relay.

The forms of the terror birds and the coelurosaurs were quite similar: trim, elongated bodies; long, powerful hind limbs; long necks; large heads. Many coelurosaurs had reduced anterior limbs, indicating that the animals captured, killed and processed prey primarily with the hind limbs and mouth, as the phorusrhacoids did. Coelurosaurs apparently used their long tail as a balance while running; phorusrhacoids probably used their reduced wings for the same purpose. Different strategies and appendages were thus employed to serve the same functional purpose.

Land Bridges Taken

TERROR BIRDS and their relatives are also known outside South America. Their distribution is the key to the intriguing bio-geographic history that accounts for the gradual ending of the terror birds' reign as South America's primary carnivores.

In rocks from 55 million to 45 million years old in North America, Europe and Asia, large carnivorous birds are represented by the family Diatrymatidae--which, according to my colleague Herculano M. F. Alvarenga of the University of Sao Paulo in Brazil, developed characteristics similar to those of the phorusrhacoids. Diatrymatidae family members attained heights of about two meters. Like the phorusrhacoids, they had massive skulls and large claws. Their legs, however, were relatively shorter and sturdier, suggesting that they were more methodical and cumbersome in their movements, much as the brontornithids were.

A reported phorusrhacoid, *Ameghinornis*, is known from the Phosphorites du Quercy rocks, 38 million to 35 million years old, in France. This animal was the size of a living seriema and was apparently capable of brief flight.

The Antarctic is also the scene of similar fossils. Two isolated footprints, 18 centimeters in length, are known in rocks about 55 million years old on the Fildes Peninsula of King George Island in West Antarctica. The three-toed bird was big, broad and elongated, either a ratite (a rhea or an ostrich or one of their relatives) or a phorusrhacoid.

The anterior part of a phorusrhacoid's beak was collected from rocks (dated to 40 million years ago) of the La Meseta Formation on Seymour Island, which is on the south side of the Antarctic Peninsula. The proportions of the beak indicate that the bird was more than two meters tall.

Finally, a formidable phorusrhacoid named *Titanis walleri* is known from rocks in northern Florida aged 2.5 million to 1.5 million years. The estimated height of the bird is more than three meters. This record is the youngest yet found and represents the last of the known terror birds.

A scenario for this pattern of phorusrhacoid distribution can be constructed from the premises that these flightless birds required overland routes for dispersal and that the fossil record accurately reflects their occurrence in space and time.

Both biological and geologic evidence show that a continuously dry land bridge united North and South America about 59 million years ago. It ran by way of the Greater and Lesser Antilles, providing an opportunity for dispersal for various groups of terrestrial vertebrates. Among them were a seriema and a phorusrhacoid (probably a *Psilopteridae*) that dispersed north.

Fifty-five million to 45 million years ago a land corridor between North America and Europe that included what is now Ellesmere Island provided another route by which the phorusrhacoids could steadily disperse. One group that appeared to have used the route was indeed *Amegabornis*. A note of caution is in order here: the supposition presumes that the phorusrhacoid group was already present in North America. No fossils of that age have yet been found there.

From at least 45 million years ago, perhaps as much as 70 million, a body of land united southernmost South America and West Antarctica. The supposition of a land connection at this time is supported by a group of marsupials, an armadillo and the southern beech in the same rock beds as the phorusrhacoid on Seymour Island. Together the land bridge and the cool, temperate climate of the time account for the presence of terror birds in West Antarctica 40 million years ago.

Eventually the land bridges uniting South America with North America and Antarctica disappeared. South America remained an island continent until the appearance of the Panamanian land bridge 2.5 million years ago. The bridge formed as a result of the continued tectonic uplift of the northern Andes region, probably associated with a worldwide drop in sea level of as much as 50 meters resulting from the buildup of the polar ice caps. The final connection of the bridge was completed in the area of what has become southern Panama and northern Colombia.

A cooling of world climates at the time shrank tropical habitats and expanded the savannas. Grassland environments were established on the land bridge. After a time, a continuous corridor of savannas extended from Argentina to Florida. The reciprocal dispersal of terrestrial fauna made possible by these conditions is now known as the Great American Interchange. It represents the best-documented example

in the fossil record of the intermingling of two long-separated continental biotas. Among the participants were the terror birds. One phorusrhacoid lineage survived beyond 2.5 million years ago in South America, and individuals dispersed north to give rise to *Titanis* in Florida.

Against this background, one can begin to see why a group of large, flightless birds rose to the top of the food pyramid in South America and why they finally lost that position. The answer lies in the historical development of the terrestrial fauna of South America.

Recall that for most of the past 66 million years South America was, as Australia is today, an island continent. As a consequence of the groups that inhabited each of these continents 66 million years ago, the role of terrestrial mammal carnivores was filled in South America by marsupials and the role of large herbivores by placentals. This marsupial-placental combination was unique among continental faunas; both roles were filled by marsupials in Australia and by placentals in North America, Europe and Asia.

The group of South American marsupials that evolved to fill the place that placental dogs and cats eventually held on the northern continents is called borhyaenoid. Its doglike members are further grouped into three families. They ranged in size from that of a skunk to that of a bear. One specialized family, the thylacosmilids, had characteristics similar to those of the placental saber-toothed cats. It is particularly significant that all these animals were relatively short-legged and that none showed marked adaptation to running. These were the mammal occupants of the carnivore niche in South America.

Gone to the Dogs

ALSO IN THIS NICHE were large terrestrial or semiterrestrial crocodiles of the family Sebecidae. They had deep skulls; their limbs were positioned more under the body than those of aquatic, flat-skulled crocodiles, and their laterally compressed teeth had serrated cutting edges, much like those of carnivorous dinosaurs. The other occupants of the carnivore niche were the terror birds. Thus, from about 66 million to about 2.5 million years ago, the role of terrestrial carnivores in South America was shared at various times, but not equally, by marsupial mammals, sebecid crocodiles and phorusrhacoid birds.

From about 27 million to 2.5 million years ago, the fossil record shows a protracted decrease in the size and diversity of the doglike borhyaenoids and a concurrent increase in the size and diversity of the phorusrhacoids. Consequently, by about five million years ago, phorusrhacoids had completely replaced the large carnivorous borhyaenoids on the savannas of South America. (The smaller ones, which were not competitive with the terror birds anyway, also became extinct before the Panamanian land bridge appeared.) This transition demonstrates another relay in the evolutionary history of the phorusrhacoids whereby they successfully replaced their marsupial counterparts, the borhyaenoids. Just why the phorusrhacoids were able to do so is unclear, but their superior running ability would certainly have been an advantage for capturing prey in the savanna environments that first came into prominence about 27 million years ago.

After the emergence of the Panamanian land bridge, placental dogs and cats of the families Canidae and Felidae dispersed into South America from North America. Because all the large marsupial carnivores of South America were by then long extinct, the only competition the dogs and cats had was from the phorusrhacoids. It proved to be a losing battle for the birds.

The Riddle Remains

THUS IT WAS that the phorusrhacoids reached their peak in size and diversity just before the interchange, gradually declining thereafter because of the competition with the dogs and cats. Only one lineage survived beyond 2.5 million years in South America; it is the one that dispersed to Florida, where it is represented by Titanis. This was the only South American carnivorous animal to disperse northward. Its success there at coexisting with the advanced placental carnivores was brief, why that was so is a major riddle. Perhaps the resident placental carnivores were too well established for the phorusrhacoids to find a permanent niche.

The fate of the phorusrhacoid relatives in North America and Europe between 55 million and 45 million years ago is also linked to the appearance of advanced placental carnivores. During that time on the northern continents, the large mammalian carnivores were the creodonts. This primitive group of placentals resembled the marsupial borhyaenoids in that they lacked special running abilities and had rather small brains. The phorusrhacoid relatives on these continents disappeared with the appearance of advanced placental mammals beginning about 45 million years ago.

The terror birds thus flourished in the absence of advanced placental carnivores, which have repeatedly shown themselves to be better competitors. The marsupial borhyaenoids and placental creodonts were, in essence and in comparison with the terror birds, second rate.

Though plausible, this argument is speculative. One cannot identify with certainty a single factor that explains the extinction of any group of animals now found only as fossils. In the case of the terror birds, their disappearance on two occasions in time correlates directly with the appearance of advanced placental carnivores. Were the advanced placentals more intelligent than the terror birds and so better adapted to capturing the prey that the birds had had to themselves? Did the fact that they had four legs give them an advantage over the two-legged phorusrhacoids in speed or agility? Did the placentals eat the phorusrhacoids' eggs, which were readily accessible in ground nests because of the birds' large size? Did the placentals prey on the vulnerable hatchlings?

It is intriguing to think what might happen to the mix of fauna if all big carnivorous mammals were suddenly to vanish from South America. Would the seriemas again give rise to a group of giant flesh-eating birds that would rule the savannas as did the phorusrhacoids and their bygone allies?

MORE TO EXPLORE

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PHOTO (COLOR): Terror bird prepared to eat a small, horselike animal (*Brachythrium*) that it has caught in a chase and stunned by holding the prey in its beak and beating it against the ground. The bird (*Andalgalornis*), which was as tall as a human, was one of many species-all now extinct-known as phosusrhacoids. They were the dominant terrestrial carnivores of South America until about two million years ago.



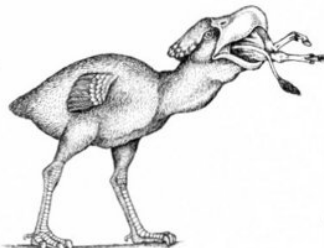
STALKING



RUNNING



STUNNING



EATING



GORGED

PHOTO (BLACK & WHITE): HUNTING TECHNIQUE of a terror bird was focused and deadly PHOTO (BLACK & WHITE): Living on the pampas of South America, the bird could stay hidden in the grass until it had drawn close to its prey. It would then dash toward its victim at speeds close to 70 kilometers an hour, seize the catch in its beak and stun it. It often ate its catch whole. Having no natural predators itself, it could then feed at leisure before returning to its nest.

HUNTING TECHNIQUE of a terror bird was focused and deadly. Living on the pampas of South America, the bird could stay hidden in the grass until it had drawn close to its prey. It would then dash toward its victim at speeds close to 70 kilometers per hour, seize the catch in its beak and render it unconscious by beating it against the ground. It often ate its catch whole. Having no natural predators itself, it could then feed at leisure before returning to its nest.



PHOTO (COLOR): LIVING RELATIVES of the phorusrhacoids are the seriema birds of South America: the redlegged (*Cariama cristata*) and the black-legged, or Burmeister's, seriema [*Chunga burmeisteri*]. The seriemas, considerably smaller at about 0.7 meter, hunt much as the terror birds did. Seriema nests are in low trees, but the terror birds

built nests on the ground,

PHOTO (COLOR, MAP): DECLINE OF TERROR BIRDS began when the Panamanian land bridge formed between North and South America some 2.5 million years ago, allowing North American mammals that could outhunt the terror birds to enter South America. Fossils of animals that migrated south or north have been found on both continents. Terror bird fossils are mostly in South America. A tip of a jaw was found in Antarctica.

PHOTO (COLOR): DOWNFALL OF THE TERROR BIRDS was apparently caused by the influx of many species of carnivores, particularly large dogs and cats (saber-toothed and jaguar), that crossed the Panamanian land bridge into South America. Greater intelligence, more speed and agility, or the ability to prey on terror bird eggs and hatchlings could explain how the migrants from North America displaced the long-established terror birds.

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By Larry G. Marshall

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