a 15-cm spider, is the living symbol of the demigod and bears the vernacular name *mengidarudkoel.* The English name alludes to the golden hue of its 3-m web.

SEE ALSO THE FOLLOWING ARTICLES

Archaeology / Marine Lakes / Reef Ecology and Conservation

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PANTELLERIA

SEE MEDITERRANEAN REGION

PANTEPUI

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Pantepui (*pan,* Greek for "all," and *tepui,* South American indigenous name for "table mountains") is a discontinuous biogeographical entity shaped by the assemblage of the flat-topped summits of the Guayana (northern South America) table mountains, or Guayana Highlands (Figs. 1 and 2), above 1500 m in altitude. These summits are isolated from each other and from the surrounding lowlands by spectacular vertical cliffs, and they hold a singular biota with unique adaptations and amazing levels of biodiversity and endemism. The origin of such biotic patterns is a still-unresolved evolutionary enigma.

THE TEPUIS

The indigenous (Pemón) word *tepui,* meaning "stone bud," has been adopted as a physiographical term to name the table mountains of the Guayana Highlands (e.g., Auyán-tepui). A typical tepui is a tabular mountain made of sandstones and quartzites (with occasional intrusive rocks, mostly diabases), with a more-or-less flat summit limited by a rim, and isolated from the surrounding lowlands by vertical escarpments in the upper part and steep talus slopes in the foothills (Fig. 3). To understand the origin of the tepuis, it is necessary to go back to the Cretaceous (145 to 65 million years ago), when Africa and South America were joined in the Gondwana supercontinent. The separation began around 80–100 million years ago and determined the initial opening of the Atlantic Ocean, which led to the formation of the huge Amazon and Orinoco basins, among others. By that time, the Guayana region was covered by extensive erosional plains modeled on the Precambrian sandstones and quartzites of the Roraima

FIGURE 1 Radar view of northern South America showing the placement of the Guayana highlands (GH) region, with respect to the Orinoco and Amazon basins, and the Andean range. (Image courtesy of NASA/JPL Caltech.)

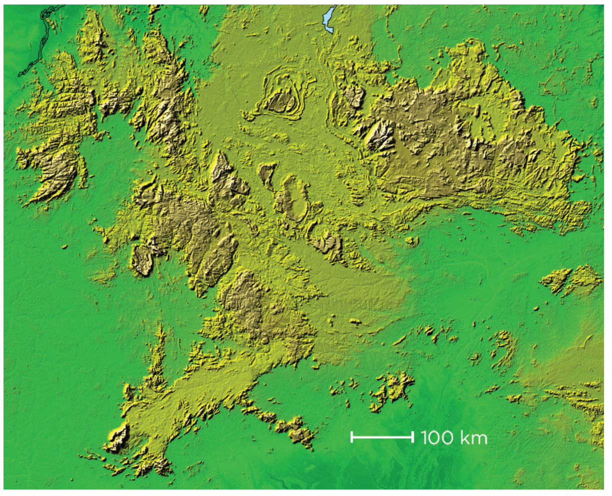

FIGURE 2 Close-up view of the Guayana highlands, showing this area's characteristic tabular topography, composed of several erosion surfaces and culminated by the tepuis. Lowlands (100–500 m altitude) are in green and yellow, whereas uplands and highlands (500–1500 and 1500–3000 m, respectively) are in light brown. (Image courtesy of NASA/JPL Caltech.)

FIGURE 3 View of the Upuigma-tepui, showing the typical flat summit (2100 m altitude and more than 1 km^2 in surface area), the vertical cliffs, the extensive forested slopes, and the basal level, which in this case is part of the so-called Gran Sabana, and is around 850 m in altitude. Note the characteristic savanna vegetation, spiked by clusters of "morichales" or gallery forests dominated by the palm *Mauritia flexuosa.* In the background, two other table mountains are present: the Angasima-tepui (left), at 2250 m in altitude, and the extensive Chimantá massif (right), composed of several tepuian summits between 2200 and 2700 m in altitude, attaining a total surface of more than 600 km^2. Photograph by the author.

group (1400–2300 million years ago). These sedimentary rocks began to be denuded by the incipient fluvial systems, in a process that is still ongoing. Weathering and erosion proceeded more easily on anticlines, where water penetration has been favored by an open fracture system. Synclines, however, are more resistant to erosion, and several of them have persisted as isolated topographical remnants: the tepuis.

More than 50 tepuis and tepuian massifs have been recognized as such, most of them in Venezuela—where they attain their maximum development—with a few representatives in Guyana and Brazil. The tepui summits are variable in both altitude and surface area, ranging from 1100 to 3014 m (typically 2000–2600 m) in maximum altitude and less than 1 to more than 1000 km^2 (typically 200–500 km^2) in area. The total Pantepui surface is ~5000 km^2 in area. The degree of physical isolation of these summits is also variable. The surrounding lowlands are situated between 100 and 1200 m elevation (commonly 100 to 400 m), and the vertical difference between them and the tepui summits ranges from 200 to 2400 m (usually 800 to 1800 m). Despite these numbers and the visual impression of the tepuian landscape, only ~20% of the tepui summits are really isolated topographically; the others are connected to the lowlands by extensive river valleys, ridges, or eroded walls.

BIOTA

The climate atop the tepuis is mild (10–18 ºC average annual temperature) and very humid (2500–3500 mm of total annual rainfall), which allows development of dense vegetation types, most of them unique and characteristic of Pantepui. Among forests, the more emblematic are the dense high-tepui forests dominated by *Bonnetia* (Theaceae), associated with diabase intrusions and watercourses. The more characteristic shrublands, exclusive of one single tepuian massif (the Chimantá), are organized around a few species of the endemic Asteraceae genus *Chimantaea* (Figs. 4–6). The typical tepui meadows are dominated by broad-leaved plants without gramineous morphology, such as *Stegolepis* (Rapateaceae) and *Xyris* (Xyridaceae). Grasses and sedges are minor elements atop the tepuis. Characteristic pioneer communities with cyanobacteria, fungi, and incrustant lichens grow on bare rock. Vascular plants, the best-known organisms of Pantepui, are commonly used to illustrate the biodiversity and endemism patterns of the tepui summits. So far, around 2500 species (630 genera and ~160 families) are known, of which 62% are endemic to the Guayana region, 42% are endemic to Pantepui, and 25% are local endemics (i.e., endemic to a single tepui or tepuian massif). Local endemism can reach up to 60% in some tepuis, which is comparable to the most isolated oceanic islands. There are 23 endemic genera (~4%) but not any endemic family. Most of the Pantepui vascular plant genera are of neotropical distribution (~70%), followed by paleotropical (~20%), cosmopolitan (~5%), and temperate (~5%) elements. Among neotropical affinities, 25% of the genera correspond to Guayana endemics, and 6% are shared with the tropical Andes; the rest are more widespread.

Among the animals, the most studied are birds, followed by frogs and reptiles, and then mammals. Around 100 species of birds have been described in Pantepui, of

FIGURE 4 Inflorescences of *Stegolepis ligulata* (Rapateaceae) from the summit of the Apakará-tepui (Chimantá massif), around 2200 m in altitude. This species is endemic to the summits of the Chimantá massif, where it dominates the broad-leaved meadows. Photograph by the author.

FIGURE 5 *Chimantaea mirabilis* (Asteraceae) from the Apakará-tepui, around 2200 m in altitude. This species dominates the unique and characteristic "paramoid" shrublands of the Chimantá massif, to which it is endemic. Photograph by the author.

which one-third are endemic to Guayana and 10–20% are endemic to the highlands. The diversity of herpetofauna (frogs and reptiles) is about half that of birds, but the level of endemism is higher, reaching 60% in some tepuis. Mammals, most of them small, are also represented by even lower number of species, mainly of bats, rodents, and some marsupials (opossums). So far, felids, monkeys, and medium to large herbivores have not been observed atop the tepuis. Insects have not been studied systematically, but recently, a new genus of damselflies was described (*Tepuibasis*), with all its seven species being endemic to Pantepui.

The origin of such biotic features has been debated for long time. Based on floristic data, earlier researchers (up to about 1970) explained the uniqueness of the Pantepui biota as the result of evolution in isolation since the Cretaceous. According to this hypothesis, present species would be very old in origin. However, ecological and paleoecological evidence favoring genetic interchange among summit biotas is increasing. The proposed mechanism is related to the Quaternary (the last 2.6 million years) glaciations. Glacial cooling promoted downward migration and lowland spreading of summit taxa, whereas interglacial warming favored upward migration and colonization of new summits. Molecular phylogenetic studies on key taxa, such as *Stegolepis* and *Myoborus,* a genus of redstarts, agree with this view and favor a recent origin, probably Plio-Pleistocene (the last 5 million years), for their species. Such evolutionary processes would have promoted adaptative radiation, favored by the elevated habitat heterogeneity and ecological diversity of the tepui summits. A good example can be found in *Brocchinia* (Bromeliaceae), a genus of both lowlands and highlands with known morphological and functional adaptations. The issue of the origin of the Pantepui biota is a fascinating subject, which is still open to new ideas and further research efforts.

FIGURE 6 The insectivorous plant *Heliamphora minor* (Sarraceniaceae) from the summit of the Eruoda-tepui (Chimantá massif), at about 2600 m in altitude. Photograph by the author.

CONSERVATION

Pantepui is still virtually pristine. Indigenous people do not visit the tepui summits because they consider them the homeland of gods and therefore to be sacred places. Activities such as cultivation, lodging, burning, mining, tourism, and so forth are prevented by several protection efforts, including national parks, natural monuments, biosphere reserves, and a World Heritage Site. In addition, Pantepui has been considered by the WWF/IUCN as one of the neotropical plant diversity centers (SA-2), as well as a critical ecoregion (ER-45) of the Global 2000 Project. Therefore, the tepui summits seem to be well protected against direct human intervention. However, the potential consequences of the ongoing and predicted future global warming have not been fully realized until very recently. Increasing temperatures will cause an upward displacement of suitable environmental conditions for mountain species, such that a number of them may lose their habitat. In the tepuis' summits, this effect will be enhanced by the flat topography, which prevents further upward displacement. Preliminary estimations show that roughly 200–400 endemic vascular plant species (~30–50% of the total) of Pantepui are threatened with habitat loss because of the projected 2–4 °C warming for the end of this century. Owing to the singularity of the Pantepui biota, this would be a serious danger for Guayanan, as well as for global, biodiversity.

SEE ALSO THE FOLLOWING ARTICLES

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PAPUA NEW GUINEA

SEE NEW GUINEA

PEOPLING THE PACIFIC

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The islands of the Pacific Ocean were settled by humans in two major episodes. The earliest phase began in the Late Pleistocene, at least 40,000 years ago, and involved the movement of hunting-and-gathering populations into Near Oceania. The second major phase commenced about 4000 years ago and involved the diaspora of the Austronesian-language speakers into Remote Oceania, as well as into the Indian Ocean as far as Madagascar. The most isolated islands and archipelagoes of Remote Oceania, including Hawai'i, Easter Island (Rapa Nui), and New Zealand (Aotearoa), were settled by Polynesians between AD 800 and 1200.

GEOGRAPHIC BACKGROUND: NEAR AND REMOTE OCEANIA

The Pacific Islands, or Oceania, were classically subdivided into three main geographic regions, following the scheme of the French explorer Dumont d'Urville in the early nineteenth century: Melanesia, Micronesia, and Polynesia. Although these geographic terms continue to be widely used, except for "Polynesia," they have little cultural or historical basis. Only Polynesia stands out as a culturally and linguistically meaningful category. More recently, historical anthropologists and archaeologists stress the distinction between Near Oceania in the western Pacific (including New Guinea, the Bismarck Archipelago, and the Solomon Islands) and Remote Oceania (which includes all of island Melanesia southeast of the Solomons, along with Polynesia and Micronesia). Near Oceania, which was first settled by *Homo sapiens* in the late Pleistocene, is characterized by intervisible islands with a highly diverse biota, capable of supporting hunter-and-gatherer populations. The widely dispersed islands of Remote Oceania were discovered and settled only within the past 4000 years, by horticultural peoples who introduced food crops and domestic animals to these biotically more depauperate and resource-limited islands.

PLEISTOCENE SETTLEMENT OF NEAR OCEANIA

During periods of glaciation in the Late Pleistocene, lowered sea levels exposed the continental shelf joining New Guinea to Australia (and Tasmania to Australia in the south). This enlarged land mass is known to biogeographers as Sahul. Similarly, the Malaysian peninsula and much of Indonesia formed another exposed land mass called Sunda. The region between Sunda and Sahul, known as Wallacea, always had water gaps that acted as barriers to biotic dispersal. However, human entry into Sahul was facilitated when these water gaps were at their narrowest, and human expansion throughout Australasia occurred rapidly once people entered the region, at least 40,000 years ago. A number of occupation sites are now radiocarbon-dated to ~36,000 years ago, on the large island of New Guinea, and on New Britain and New Ireland in the adjacent Bismarck Archipelago. Late Pleistocene sites in the Admiralty Islands, New Ireland, and Buka (Solomons) all indicate the existence of open-ocean transport, thereby suggesting the presence of some form of early watercraft (possibly rafts, bark boats, or dugouts). There is no evidence, however, for human expansion beyond the eastern end of the main Solomon Islands chain until the Middle to Late Holocene.

The earliest human colonists in Near Oceania were hunters and gatherers, who exploited tropical rain forests but also made use of inshore marine resources. The presence of simple flake tools of obsidian (originating on the island of New Britain) at these sites provides evidence for long-distance communication and exchange between com-