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one biosphere reserve (Alto Orinoco-Casiquiare), and there are also five Ramsar Sites (Archipiélago Los Roques, Ciénaga de Los Olivitos, Cuare, Laguna de la Restinga, Laguna de Tacarigua) and three UNESCO World Heritage Sites, one of which is a natural site: Canaima National Park, featuring the “tepuí” table mountains (Rull, this volume).

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# A SHORT HISTORY OF THE STUDY OF VENEZUELAN VERTEBRATE FOSSILS

# 2

Marcelo R. Sánchez-Villagra

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Paleontological and stratigraphical studies of South America have a long history, dating back to the prominent contributions of D'Orbigny (1835) and Darwin (1846). Detailed studies of this kind in Venezuela started later and with less known works, although early mentions of fossils are known. The most prominent explorer in Venezuela was undoubtedly Alexander von Humboldt, who visited the Andes of Trujillo and Mérida, the Serranía del Interior of eastern Venezuela including the Cueva del Guácharo, and the Orinoco River, reaching the Casiquiare region in the south. Humboldt reportedly found Pleistocene megafauna (e.g., mastodons) during his trip, in particular from an area near Cumanacoa, Estado Sucre (cf. Carillo-Briceño, Alfonso, and Chávez 2008).

The German naturalist Hermann Karsten (1817–1908) noted in several publications (1851, 1862) the presence of *Megatherium* or related taxa at different localities in western and eastern Venezuela. He also mentioned for two localities in central Venezuela the presence of footprints of “*Chirotherium*,” an unconfirmed report of an ichnotaxon of uncertain significance (Odreman and Medina 1984).

Adolf Ernst (1874) reported the presence of numerous extinct Pleistocene mammals remains of large size. Ernst (1832–99) was born in what is currently Pryemków, Poland, and arrived in Venezuela in 1861. For the rest of his life Ernst studied different aspects of natural history in that country. He was one of the founding members of the Museo Nacional and founder of the Sociedad de Ciencias Físicas y Naturales of Venezuela.

José María Vargas (1786–1854), who became rector of the Universidad Central de Venezuela and president of the country, started the first collection of fossil vertebrates in Venezuela, according to Von der Osten (1947). This collection was deposited in the Museo de Ciencias Naturales de Caracas, the same collection in which A. Ernst deposited fossils in 1874 (ibid.).

Single and brief reports of Pleistocene vertebrates from several areas, including Zulia State, were presented in the geological synthesis of Venezuela by Liddle (1928).

In the 1930s a few descriptions of Venezuelan fossil vertebrates were published. Collins (1934) described the megatherid *Prepootherium venezuelanum* from the Río Tucupido, near Guanare, Portuguesa state (see

Sánchez-Villagra et al. this volume for a discussion of the stratigraphic provenance and age of this fossil). Schaub (1935) noted the presence of the toxodont genus *Nesodon* in Miocene sediments near San Pedro, Falcón state. He also described a new species of *Megatherium*, *M. rusconii*, from Pleistocene rocks of the Barquisimeto area, a species which, if valid, is most likely part of the genus *Eremotherium*.

The priest Nectario Maria (1937, 1941, 1944) from the Colegio La Salle in Barquisimeto conducted the first paleontological investigation initiated in Venezuela, resulting in reports on Quaternary localities in the Barquisimeto area, Lara state.

The well-known North American paleontologist G. G. Simpson had a short but productive research activity in Venezuela. In 1938 and 1939, Simpson went to Venezuela on a fossil-collecting expedition at the invitation of the government of Venezuela (Simpson 1939). One of his trips took place soon after his marriage to Anne Roe (1904–91), who accompanied him. Some of the various mammals collected by Simpson are in the collections of the American Museum of Natural History (Laporte 2000). As a result of his expeditions to Venezuela, Simpson described a new turtle species "*Podocnemis*" *geologorum* (Simpson 1943) (Sánchez-Villagra and Scheyer this volume) and a new glyptodont, *Asterostemma venezolensis* (Simpson 1947), recently included in the new genus *Boreostemma* by Carlini et al. (2008). These two are still the most significant vertebrate finds from eastern Venezuela and were collected from sites that no longer exist.

Simpson worked jointly with Nectario María in the area of Barquisimeto for several months. The toxodont materials found by Simpson in his expedition, in the area of San Miguel near Barquisimeto, were described by R. Van Frank (1957) from the Museum of Comparative Zoology in Harvard as the new species *Mixotoxodon larensis* (Bond and Gelfo, this volume). The paper was intended to be part of a series of two, but a second paper describing other large mammals was never published.

Some of the fossil localities studied by Simpson were in an area occupied by native Americans known as "Kamarakotos," and he wrote a highly praised monograph on this tribe, including topics such as linguistics and artifacts (Simpson 1940).

José Royo y Gómez (1895–1961) was a pioneering student of vertebrate fossils in Colombia and Venezuela. He was involved in the beginning of exploration of the La Venta fauna while working in Colombia (Madden, Savage, and Fields 1997). In 1951 Royo y Gómez moved to Caracas and became professor of Geology at the Universidad Central de Venezuela (UCV). He was a charismatic and inspiring figure for many geologists working on the sedimentary basins of Venezuela (Charlton de Rivero 1962). Royo y Gómez published among the first contributions about the fossil vertebrates from Falcón, having started work in the localities of Urumaco and at important Pleistocene sites, as described below. Royo y Gómez organized a collection of fossil vertebrates at the UCV that still exists.

In 1993 new legislation was made official that regulates paleontological work in Venezuela (Aguilera 2004). Fossils are considered part of Venezuela's national patrimony, and the Instituto del Patrimonio Cultural regulates and approves work conducted in Venezuela.

The American geologist John M. Moody (born 1952) made several discoveries alone and with colleagues from outside Venezuela of several groups of fossil vertebrates from the Andean and Sierra de Perijá regions (e.g., Moody and Maisey 1994). He established a significant paleontological collection at the Universidad del Zulia in Maracaibo during his *ad honorem* work there from 1990 until 2001. His studies included those of numerous fossils from previously unstudied areas in Zulia, and he developed a productive research program with international collaborations on different groups of organisms (e.g., Berry, Casas, and Moody 1993; Carvalho and Moody 2000). Moody also started work on the Pleistocene Inciarte Mene site in 1997, which has successfully continued under Ascanio D. Rincón (see Sánchez-Villagra et al., this volume). With his work on the rodents of the Mene de Inciarte, Rincón (2005) completed the first Ph.D. thesis on fossil mammals from Venezuela.

In the last decade, my own efforts in collaboration with several colleagues has resulted in several publications (e.g., Johnson, Sánchez-Villagra, and Aguilera 2009) and in three edited journal issues including mostly descriptive papers (Sánchez-Villagra and Clack 2004; Sánchez-Villagra 2006; Sánchez-Villagra and Aguilera 2008). The collaborative work has been coordinated mostly with Orangel Aguilera and most recently also with Fredy Carlini. Several institutions have supported or been represented in the projects, principally the University of Tübingen, the Natural History Museum in London, the Smithsonian Tropical Research Institute, the Museo de La Plata, and most recently the University of Zürich.

The early history of work in Urumaco is related to oil exploration. Many geologists and paleontologists have been attracted to the productive oil fields of Falcón for more than seven decades. Oil companies were operating in the 1930s near Urumaco. An important center of operation was the oil camp of El Mamón, located in one of the richest paleontological areas. This camp generated about 400,000 barrels until 1930, when oil exploitation in the area ended (Aguilera 2004).

The first reports of fossil vertebrates were made in the 1950s during exploration by the Texas Petroleum Company, which donated the first fossil vertebrate to the Universidad Central de Venezuela (Aguilera 2004). Inspired by these first discoveries, Royo y Gómez conducted the first two expeditions in 1958 and 1959, in collaboration with his students and with a teacher from the school in Coro, the Liceo Cecilio Acosta. Among the specimens they collected are fish skulls and teeth, turtle shells, crocodile scutes and vertebrae, and a mammalian skull and vertebrae (Royo y

## Vertebrate Paleontological Exploration and Investigations in Urumaco

Gómez 1960a, b). Since the pioneering studies of Royo y Gómez, several teams of investigators or individuals have worked in Urumaco.

During a short visit to Caracas, the Argentinean paleontologist Rosendo Pascual from the Museo de La Plata collaborated with the Venezuelan geologist María Lourdes Díaz de Gamero in the report of the rodent *Eumegamys* from Urumaco (Pascual and Díaz de Gamero 1969), and in 1970 the American W. Sill described the new gharial *Ikanogavialis gameroi* from Urumaco.

In 1972 Bryan Patterson from the Museum of Comparative Zoology at Harvard University led an expedition to Urumaco. The crew included R. Wood, D. Fisher, A. Lewis, R. Reppening, and M. Stanford. Their discoveries led to the first series of publications on specific aspects of the Urumaco fauna, including the description of the world's largest turtle (Wood 1976) as well as other new turtles and crocodiles (Sánchez-Villagra and Scheyer this volume; Scheyer and Moreno-Bernal this volume).

Many new taxa from Urumaco were described by Jean Bocquentin Villanueva and collaborators (e.g., Bocquentin Villanueva and Buffetaut 1981). Between 1982 and 1986 he made the first large collection of vertebrates, deposited at the Centro de Investigaciones Antropológicas, Arqueológicas, y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda in Coro. Bocquentin Villanueva conducted at the time the study and description of fossils from Pleistocene sites led by J. M. Cruxent (Bocquentin Villanueva 1979, 1982a, 1982b).

The Venezuelan Research Council (at the time known as CONICIT) funded paleontological work in Urumaco done by María Lourdes Díaz de Gamero and Omar J. Linares between 1984 and 1989. A reference work on the geology of Urumaco, with new lists of fossil vertebrates, resulted from this research (Díaz de Gamero and Linares 1989). A few papers and abstracts were published on vertebrate fossils collected during this project (Lundberg et al. 1988; Linares 1990; Sánchez-Villagra, Linares, and Paolillo 1995). The vertebrate collections resulting from this project are deposited at the Universidad Simón Bolívar, and include some of the best previously undescribed fossils from Urumaco, including a sirenian, a small cetacean, among others (Sánchez-Villagra et al. this volume). O. J. Linares funded an electronic journal published irregularly by his own lab, in which results of the studies of the editor on the Urumaco sequence fauna have been more recently described (Linares 2004a, b). In 1989 the first television documentary on Venezuelan fossils, organized by O. J. Linares, was made in Urumaco, as part of a prominent series on local TV (*Expedición*, CORAVEN-RCTV). This documentary raised general awareness in Venezuela about Urumaco and paleontology.

Orangel A. Aguilera and collaborators have been involved in active fieldwork and study of collections of Urumaco vertebrates since the early 1990s. Many diverse clades of vertebrates and invertebrates have been collected and studied, but emphasis has been on fish, an area where active

research has produced numerous publications (Aguilera and Lundberg this volume). In 2004 Aguilera published the first book on Urumaco, in Spanish, followed by a similar book on the Quaternary of Falcón state in 2006.

Collections of vertebrates from the Urumaco region are deposited at the Universidad Nacional Experimental Francisco de Miranda (UN-EFM), Alcaldía del Municipio Urumaco (AMU-CURS), Universidad Simón Bolívar (USB) and Universidad Central de Venezuela (UCV).

The German naturalist Hermann Karsten published in 1886 the first fossil from Falcón state, the femur of a mastodont from the locality of La Ciénega, in the Paraguaná Península. Half a century later, in 1936 the Swiss paleontologist Samuel Schaub discovered in the Quebrada Ocando de Guaibacoa remains of a megathere, which was assigned to a species he had previously (1935) described as *Eremotherium rusconi* (= *E. laurillardi*) based on materials from El Totumo in Lara state.

A starting point for local studies of Quaternary vertebrates in Falcón state was when Francisco Gutiérrez, a teacher at a school in Coro, discovered in 1952 several fossil vertebrates in Muaco. Several years later paleontological and archaeological studies described the fauna from that locality (Royo y Gómez 1960a, b; Cruxent 1961; Ochsenius 1980), as well as from Cucuruchú (Cruxent 1970), and from TaimaTaima (Cruxent 1967; Bryan et al. 1978; Ochsenius and Gruhn 1979; Ochsenius 1980; Gruhn and Bryan 1984).

Much of the work on Quaternary fossil vertebrates from Falcón has been tied to archaeological research, and has concentrated on the search for human interactions with the extinct fauna (e. g., Bryan et al. 1978). The site of "El Jobo" purportedly preserves interactions of humans with a mastodont going back 13,000 yr BP. Due to a fire on 29 August 1978 at the Departamento de Antropología del Instituto Venezolano de Investigaciones Científicas (Altos de Pipe, Caracas), most of the archaeological and paleontological samples on which these studies were based were lost. The fossils from TaimaTaima and Cucuruchú described by Casamiquela (1979) have also been lost, as was the complete carapace of a glyptodont illustrated by Ochsenius (1979) and mentioned by Gruhn (1979).

After a collaboration between the Universidad Nacional Experimental Francisco de Miranda and the Instituto del Patrimonio Cultural de la República Bolivariana de Venezuela, a museum at the site of TaimaTaima was created and the excavations were continued, without any archaeological and with only a few paleontological finds (Aguilera 2006).

Collections of Pleistocene vertebrates from Falcón are housed at the Universidad Nacional Experimental Francisco de Miranda, the Museo de Ciencias Naturales de Caracas, the Instituto Venezolano de Investigaciones Científicas, and the Universidad Central de Venezuela.

## Paleontological and Archeological Studies in the Quaternary of the Falcón Basin

The sedimentary basins of Venezuela contain large volumes of oil, and this has led to a great interest in Venezuelan geology for a long time (Tankard, Suarez, and Welsink 1995). Perhaps the most prominent early works of a synthetic and comprehensive nature were Hermann Karsten's (1886) *Géologie de l'ancienne Colombie Bolivarienne, Vénézuéla, Nouvelle Grenade, et Ecuador* and Alfredo Jahn's (1921) *Esbozo de formaciones geológicas de Venezuela*. A later classic historical reference for the geology of Venezuela was R. A. Liddle's (1928) *The Geology of Venezuela and Trinidad*, with a second edition in 1946. A later comprehensive compilation of geological information was published by González de Juana, professor of geology at the Universidad Central de Venezuela, and collaborators (1980). More recently the most prominent reference for synthetic and nomenclatural purposes has been the "Léxico estratigráfico de Venezuela," with the first printed edition of 1956 superseded by the second of 1970 and the latest of 1997 (Ministerio de Energía y Minas 1997), which is being updated in an Internet-accessible version. An important synthetic reference because of the several contributions treating different topics and regions, concerning mostly plate interactions in Venezuela, is the edited volume by Avé Lallemant and Sisson (2005).

Although they are not the subject of this brief review, it is worth pointing out the contributions of some personalities in the paleontological community of Venezuela who had a big impact on the knowledge of sedimentary basins and biostratigraphy in that country.

The Cuban geologist Pedro Joaquín Bermúdez (1905–1979), worked mostly on Venezuelan foraminifera at the Ministerio de Minas e Hidrocarburos in Caracas and as professor of micropaleontology at the Universidad Central de Venezuela. His research concerned mostly the Neogene, as did that of the Swiss geologist Hans Bolli (1917–2007).

Hollis Hedberg (1903–88), soon after obtaining a master's degree at Cornell University at twenty-three years of age, started in the 1920s to work for an oil company, where he carried out influential stratigraphic research in both western and eastern Venezuela, with field investigations expanding until the 1930s (Hedberg 1988). Many famous and infamous American and European geologists worked in Venezuela around this time for the oil industry, among them John Scopes of "monkey trial" fame, as related by Hedberg (1988) in his autobiographical essay about this period.

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## THE FOSSIL VERTEBRATE RECORD OF VENEZUELA OF THE LAST 65 MILLION YEARS

# 3

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In his 1940 “Review of the mammal-bearing Tertiary of South America,” G. G. Simpson summarized the scanty record of Venezuela (703–704): “Few as discoveries are, they are important because they show unquestionable affinities with fossil mammals of Argentina and none with those of North America. In view of the fact that no South American mammals had reached North America in the Miocene or earliest Pliocene, even this small budget of evidence is enough to prove that South America was then a unified continent with its northern and southern parts united by land and that the northern part, as well as the southern, was then separated from North America by a marine barrier.” What little was known about northern neotropical vertebrate paleontology in 1940 was already important in addressing some large issues about biogeography and the past history of the American continent. Vertebrate paleontology in Venezuela is still in a descriptive phase, but the number of discoveries has increased exponentially in the last few years, and contributions in this volume exemplify how some of them are being used to address fundamental issues about evolution in the tropics and major events in vertebrate evolution, such as the Great American Biotic Interchange in both terrestrial and marine habitats.

Here we present a chronological review of Venezuelan formations and sites with reported fossil vertebrates. Many of the sites and their fossils are also discussed specifically in different chapters of this book.

Paleogene vertebrates from Venezuela are almost unknown. Several aspects on paleoenvironments and palynology of the Paleocene and Eocene of Venezuela were discussed by Rull (2000). There are several Neogene fossil sites, but most are poorly known localities with only one or a few taxa or remains reported. By far the most important section with vertebrates in the Cenozoic of Venezuela is that of the Urumaco sequence, the geology of which is treated in a separate chapter (Quiroz and Jaramillo this volume). Most vertebrate faunas from the Neogene show very low diversity, with the sole exception of the Urumaco sequence and the Cerro La Cruz site. Faunas with vertebrates are found in the Guárico sub-basin, Barinas basin, and Falcón basin. Pleistocene and Holocene deposits are becoming better known, and as discussed below the recently