

1-1-1993

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Recommended Citation

McFarlane, D.A., and R.D.E. MacPhee. "Amblyrhiza and the Vertebrate Paleontology of Anguillean Caves." *El Boletín de la Sociedad Venezolana Espeleología* 27 (1994): 33-38.

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AMBLYRHIZA AND THE VERTEBRATE PALEONTOLOGY OF ANGUILLEAN CAVES

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ABSTRACT

Recorded interest in the caves of Anguilla dates back to the second half of the nineteenth century. The earliest explorations were concerned with the locating phosphatic cave earths, and resulted in the mining of several sites. Incidental to this work, the bones of the largest island rodent ever discovered were collected from Anguillan caves. Whereas the phosphate mining operations were short-lived, the remains of the giant rodent *Amblyrhiza* have catalysed a continued interest in the caves of Anguilla. The most recent series of explorations have provided the first adequate documentation of *Amblyrhiza* fossil sites, and have started to yield radiometric dates.

RESUMEN

Documentación que denota interés en las cuevas de Anguilla data de la segunda mitad del

siglo 19. Las primeras exploraciones estuvieron motivadas en la prospección de cuevas por su contenido de tierras fosfáticas, resultando en su minería en varias localidades. Como algo incidental de estos trabajos, huesos del mayor roedor descubierto en las islas fueron colectados de cuevas de Anguilla. Aún cuando las operaciones mineras de fosfatos fueron de corta duración, los restos del roedor gigante *Amblyrhiza* han catalizado el continuo interés por las cuevas de esta isla. La más reciente serie de exploraciones ha permitido por primera vez, una adecuada documentación de las localidades de *Amblyrhiza* y ha empezado a producir edades radiométricas.

INTRODUCTION

Anguilla, St. Martin, St. Barthelemy, and a flock of smaller islets and cays comprise the subaerial parts of the Anguilla Bank in the far northeastern extremity of the Lesser Antilles. These landmasses (hereafter inclusively referred to as "Anguilla") have an aggregate area of about 250 km², and thus constitute one of the smallest archipelagos in the eastern Caribbean. Given their small size, it seems a little paradoxical that some of the islands of Anguilla once supported the largest rodent so far discovered in an insular context, the giant caviomorph *Amblyrhiza inundata* (COPE, 1869). In this contribution we survey the history of palaeontological exploration in the caves of Anguillae, with special reference to this remarkable rodent.

know, in Cuba). The outlier in this subfamily, morphologically as well as geographically, is *Amblyrhiza*.

How and when *Amblyrhiza* (or its ancestor) managed to reach Anguilla is not known; the islands of the Anguilla Bank are separated from the easternmost Virgin Islands by a water gap, the Anageda Trough, that is at least of Miocene age and may be considerably older. The trough appears to be a graben, or series of grabens, floored by a wedge of sedimentary strata which overlie Cretaceous to Eocene volcanic and sedimentary rocks similar to those exposed on the Virgin Islands and Puerto Rico (DONNELLY, 1964). The relationship of the Anegada Trough to the Puerto Rico Trough is unclear, and in any case, there are no fossils known from Puerto Rico or elsewhere that shed any light on the proximate origin of *Amblyrhiza*.

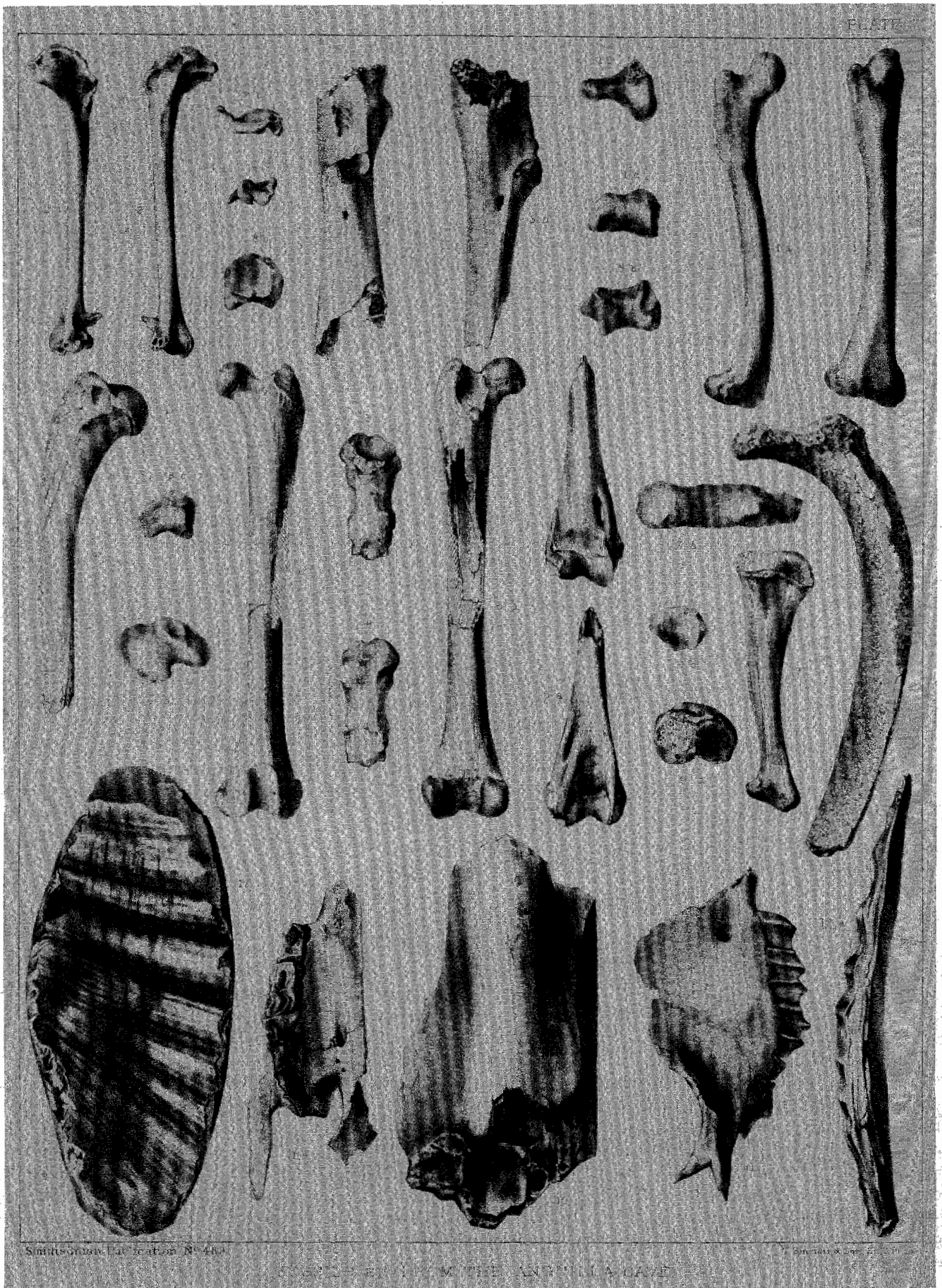
Amblyrhiza is noteworthy in at least two respects. Firstly, with an estimated body size of 80-120 kg (MacPHEE *et al.*, 1990; BIKNEVICIUS *et al.*, in prep.), it is by far the largest island rodent ever discovered. By contrast, the largest living rodent, the capybara or chigüire (*Hydrochaeris*) of northern South America, has an average body size of 50 - 60 kg (NOWAK & PARADISO, 1983), and individuals rarely attain weights in excess of 90 kg (OJASTI, 1973). The evolution of so large a rodent on comparatively small islands raises several interesting evolutionary and ecological questions. Secondly, on rather thin circumstantial evidence, it has long been believed that *Amblyrhiza* survived until the arrival of Amerindians in this part of the Caribbean, or even up to the European discovery of the New World (ANDERSON, 1984; NOVAK & PARADISO, 1983). If one or the other of these notions is correct, then *Amblyrhiza* is probably one more entry on the long list of insular terrestrial vertebrates brought to extinction as the result of human impact during the late Quaternary (MARTIN, 1984; BURNEY & MacPHEE, 1988).

AMBLYRHIZA AND THE TERRESTRIAL MAMMALS OF THE WEST INDIES

For oceanic islands, the West Indies - particularly the Greater Antilles - have, or recently had, a notably diverse terrestrial vertebrate fauna (WOODS, 1989). The mammalian component of this fauna includes the orders Chiroptera, Primates, Xenarthra, Lipotyphla, and Rodentia in its Quaternary record. The rodents, chiefly caviomorphs or "New World hystricognaths", were the dominant group of nonvolant mammals in the West Indies during Quaternary time. Although a residue of their former diversity continues to

survive into the present, a large number of West Indian rodents have become extinct (MORGAN & WOODS, 1986), as have all of the monkeys, sloths, and one of the two insectivore families.

Pre-eminent among the extinct rodents are the heptaxodontids, a probably paraphyletic group of large to gigantic species of quite uncertain relationship to other caviomorphs (eg. WOODS, 1989), most representatives of which lived in the Greater Antilles (in Jamaica, Hispaniola, and Puerto Rico, but not, as far as we now



CHRONICLE OF COLLECTING ACTIVITIES IN ANGUILLA, SAINT MARTIN, AND SOMBRERO

The history of recorded vertebrate fossil collection in Anguilla and Sombrero spans more than 120 years. In addition, we know that Anguillian fossils have been sporadically collected over the years by amateur collectors and others, because a few specimens have ended up as donations to museums (e.g., the 1937 Vlan collection in the American Museum of Natural History (AMNH)). Unfortunately, the ones that we know about are rarely documented as to exact provenance.

The history of vertebrate paleontology in the northeastern Caribbean began as an incidental result of phosphate operations in the middle years of the nineteenth century. In 1811, substantial deposits of phosphate minerals were discovered in limestone fissures on Sombrero, a small island off the Anguilla Bank located some 60 km NE of Anguilla itself. Significant exploitation of these deposits started in 1860, largely with Anguillian labor. Peak levels of ore retrieval were achieved by the late 1860s, when annual production of Sombrero phosphate reached 3000 tons a year and sold for \$34 a ton (Anon., 1978). Chelonian fossils were occasionally found by workers, and some of these were transmitted to specialists for description (JULIEN, 1867). By 1872, quarrying had extended below sea-level in some places, necessitating the use of divers and greatly increasing production costs. Faced with the foreseeable decline of the Sombrero operation, efforts were made to locate additional ore deposits on neighboring islands, including Anguilla and St. Martin. In 1868, a quantity of "cave earth, limestone fragments, and bone breccia" from Anguilla was shipped to the firm of Henry Waters and Brothers in Philadelphia to ascertain its potential value as fertilizer (COPE, 1883). The bones in breccia were in turn brought to the attention of Edward Drinker COPE, a leading American paleontologist who was then corresponding secretary of the Philadelphia Academy of Sciences. COPE immediately recognized the importance of the fossils, the majority of which were attributable to unknown rodents of unusually large size. In order to increase the sample available for description, he sought the assistance of Dr. Hendrik Eling Van RIJGERSMA, a physi-

cian and avid naturalist then resident in Sint Maarten, the Dutch portion of the island. The details of their collaboration are known only from references in COPE's publications and some documentary materials assembled by HOLTHIUS (1959). From these materials it appears that Van RIJGERSMA made the first of three collecting trips to Anguilla on COPE's behalf in mid-1868, and probably sent the fossils that he collected to Philadelphia sometime during the same year because in October of 1868 Van RIJGERSMA was elected a corresponding member of the Philadelphia Academy. Regardless, all trips had to have been undertaken prior to 1877, the year of Van RIJGERSMA's death. Between March 1869 and 1877 Van RIJGERSMA also recovered fossils from unspecified sites in the vicinity of Simson's Bay, Sint Maarten/St. Martin (HOLTHIUS, 1959). COPE's (1883) declaration that these latter specimens came from the "Virgin Island of St. Martins, W.I." is clearly a lapsus.

If Van RIJGERSMA supplied field notes with the specimens sent to COPE, these have not survived. Nor is there any useful documentation accompanying COPE's *Amblyrhiza* collection in the American Museum of Natural History, save for one handwritten note that bears the inscription "Anguilla. From out the Bat Cave. H. E. van RIJGERSMA." Unfortunately, "Bat Cave" is not a current toponym in Anguilla, and this epithet could readily be applied to any of several fossiliferous cave sites that now host bat colonies. Caves and fissures in which phosphate might accumulate occur only on Dutch Sint Maarten at Corner Hill, at the southeastern corner of Simson's Bay, and in the contiguous Terre Basse section of French St. Martin (HUMMELINCK, 1979). The only known phosphate works in Terre Basse occur behind Baie Rouge; these and the small caves and pits that dot the periphery of the bay, which have not been adequately reinvestigated, are threatened by encroaching development.

In cooperation with the Anguilla Archaeological and Historical Society, we have attempted to determine the location of Van RIJGERSMA's Anguillian sites, with limited success. Van RIJGERSMA noted

in a letter to COPE (26 March 1869; quoted in translation in HOLTHIUS, 1959) "Perhaps it will please you to learn that I have found some fossils in the phosphates of lime pit on Anguilla, and also from a cave there...". Two provenances are thus indicated, the second presumably being the same as the "Bat Cave" mentioned on the AMNH label. At present, we have information on only three significant underground phosphate works (McFARLANE & MacPHEE, 1989, 1991). The best known and most extensively worked of these is the well-known Cavannagh Cave, arguably one of Van RIJGERSMA's sites (CARTY, 1988, personal communication), although there appears to be no evidence to support this idea beyond the fact that Cavannagh appears to be the largest such phosphate working on the island. Exploration of this cave in 1989 failed to turn up any fossils, although it should be noted that Cavannagh was essentially worked out by phosphate miners. COPE published several small papers and notes on the vertebrate fossils from Anguilla (COPE, 1869a, 1869b, 1871a, 1871b), in addition to a long-delayed summary monograph that was issued in 1883. *Amblyrhiza* was not only big; it was also remarkably variable in body size (BIKNEVICIUS *et al.*, in prep.). This fact was only dimly appreciated by COPE, who interpreted size variation as an indication of the simultaneous presence of several species of giant rodents. In addition to naming *Amblyrhiza inundata*, COPE (1869b, 1871a, 1871b) went on to describe *Loxomylus longidens*, *L. latidens*, and *L. quadrans* - all of whom, one must infer, competed for the resources of islands that are corporately only a few hundred square kilometers in area. COPE (1883) later sunk *Loxomylus* into *Amblyrhiza*, but maintained that most of his species distinctions remained valid. Recent workers have generally preferred to sink all of the Anguilla / St. Martin giant rodents into *Amblyrhiza inundata* (SCHREUDER, 1933; WESTERMANN, 1957). COPE's finely illustrated monograph of 1883 (Plate 1, 2) attracted the attention of many subsequent workers, particularly with respect to a modified shell (*Strombus*) scraper of unquestionable Indian origin. Several of these workers chose to ignore COPE's caution: "Whether the extinct genus *Amblyrhiza* was contemporary with ... Man, is a question which must be left for future investigators." (COPE,

1883) and have presumed a contemporaneity between *Amblyrhiza* and humans. Only recently has this view been critically re-examined (WATTERS, 1989).

The first mention of additional *Amblyrhiza* fossils from Anguilla subsequent to Van RIJGERSMA's collecting appears in J.W. SPENCER's (1901) short paper on the island's geology. He described a visit to a number of eroded sea caves and fissures in the cliffs between what is now Benzie's Bay and Katouche Bay. However, SPENCER's description is enigmatic on the question of whether these localities were the same as the ones at which Van RIJGERSMA collected, or were merely of a similar nature: "In Anguilla, Mr. Wager RAY found a number of mammalian remains when digging for phosphate. I was fortunate in finding him on the island, and he kindly took me to the locality where he had obtained them—perhaps a mile north-east of the present landing, east of Road Bay.... In such a fissure the bones were obtained, among which Cope discovered remains of three species of *Amblyrhiza*—a rodent as large as a Virginia deer".

SPENCER noted the presence of a mammalian radius in deposits in one of these fissures, but did not collect it. The final disposition of RAY's "mammalian remains" is not known. The next expedition to collect *Amblyrhiza* fossils was organized by Harold E. ANTHONY of the Department of Mammalogy of the American Museum of Natural History. Although primarily a student of living mammals, ANTHONY spent a significant portion of his early career collecting Quaternary fossils in various parts of the West Indies. Among his many notable achievements was the discovery of many new taxa, including the insectivore *Nesophontes* (a member of an endemic family that lived in Cuba, Hispaniola, and Puerto Rico), the heptaxodontids *Elasmodontomys* and *Clidomys* (from Puerto Rico and Jamaica, respectively), and the jaw that later became the first unassailable evidence for the presence of primates in the West Indies (the Jamaican monkey *Xenothrix*, described by WILLIAMS & KOOPMAN [1952]). His expedition of 1926 in the eastern Caribbean included a short stopover in Saint Martin, where a few, mostly fragmentary fossils of *Amblyrhiza* were collected: "The first cave we explored, called the Devil's Hole, had been exploited some for

phosphate....[A]fter a while I discovered the characteristic teeth of *Amblyrhiza*.... Judging from the incisor teeth found, there are two rodents on St. Martins, one much smaller than *Amblyrhiza*." (ANTHONY, ms, p. 46). Later on the same day (March 27), "George [Goodwin] dug out a tooth of what appears to be an undescribed genus of rodents, about the size of *Elasmodontomys*. This was in breccia cemented to the wall about 12 ft or so from the rim of the hole. Fragments of *Amblyrhiza* were in the same deposit" (ANTHONY, ms, p. 49-50).

The considerable size range in *Amblyrhiza*, referred to earlier, seems to us to be a sufficient explanation for width differences in incisors found by ANTHONY. GOODWIN's specimen (AMNH 55035) is distinctive, but RAY (1964) has argued that it is best interpreted as a milk premolar of *Amblyrhiza*. Other localities on Simson's Bay that ANTHONY's team inspected include Cuckoo Hole, Office Quarry, and several unnamed caves, none of which have been adequately documented. Little success was had at these sites, and ANTHONY decided to leave for St. Thomas via Statia on March 31. However, not wishing to give up on making a good collection of *Amblyrhiza*, he sent GOODWIN on the sloop "Speed" to Anguilla to continue the hunt.

GOODWIN spent the period March 31-April 9 in Anguilla, mostly engaged in cave exploration for fossils and bats. He visited Cavannagh Cave (which he calls Katouche Cave—a common error even today), 6 small unnamed caves on the North Side Estate and Flat Cap Point, and Jackass Cave, an eroded sea cave below Flat Cap. A few *Amblyrhiza* fragments were found in the un-named cave at Flat Cap. After visiting Jackass Cave, the party climbed up to the top of the cliff that overlooks Little Bay, and "passing along the the high ridge we came to a deep cavern going through to the face of the cliff. Descending into this hole some thirty feet deep and close to the bottom I found...parts of the skull of *Amblyrhiza*. This material was embedded in very hard rock, a red breccia which was very much harder than the bones".

This locality is almost certainly Little Bay Phosphate Cave (McFARLANE & MacPHEE, in press), a site that also bears evidence of extensive phosphate mining. GOODWIN does not specifically state that his discovery was made in a former phos-

phate mine, but comments that "Blasting close by this find had probably shattered the bone but not loosened the rock any"

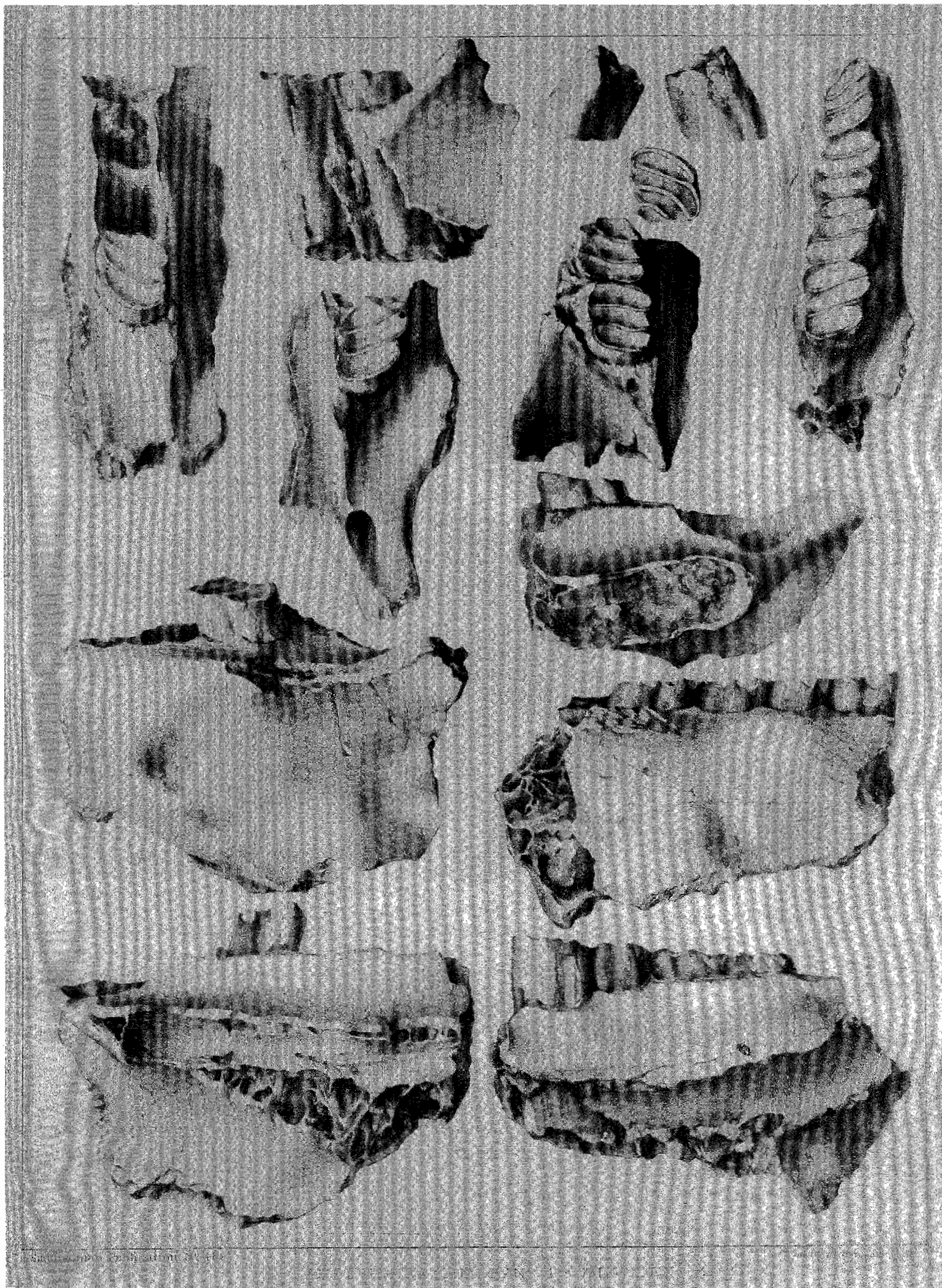
Since intensive phosphate mining on Anguilla seems to have been a short-lived enterprise, it is likely that Little Bay Phosphate Cave was worked in the late 1860's or early 1870's. GOODWIN also states that: "[COPE's fossils] were found in a cave at Flat Cap, where phosphate was being worked at the time" (GOODWIN, ms, 1926).

Although GOODWIN does not indicate how he came about this information, if it is accurate it suggests Little Bay Phosphate Cave is a leading candidate for the locality of at least one of van RIJGERSMA's, and therefore COPE's, original specimens.

The American Museum collections include a few *Amblyrhiza* fragments, without useful documentation, donated by a Mr. VLAN in 1937, but the next documented work in the area is attributable to Walter AUFFENBURG of the Florida State Museum. AUFFENBURG visited the neighbouring island of Sombbrero in April of 1966 and collected new specimens of the extinct giant tortoise *Geochelone sombreroensis*, the extant lizard *Ameiva*, and unidentified birds from phosphatic fissure fills and mined caves on the island (AUFFENBURG, 1966). It is not clear whether he investigated any Anguillian sites.

In 1982 a palaeontological expedition mounted jointly by the San Diego Natural History Museum and the United States National Museum visited Anguilla and investigated some 14 cave sites (McFARLANE & MacPHEE, in press). No *Amblyrhiza* remains were found, but evidence of an extinct rice rat, *Oryzomys*, was recovered (PREGILL, 1988, pers. comm.)

The present authors began fieldwork on Anguilla in 1988 in close collaboration with the AAHS, with the specific aim of locating new cave sites from which datable remains of *Amblyrhiza* might be recovered. The 1988 fieldwork resulted in the discovery of an undisturbed site, Pitchapple Hole, which yielded remains of at least four adult *Amblyrhiza* (McFARLANE & MacPHEE, 1989). A specimen from this collection submitted for radiocarbon dating contained too little organic material for a reliable date, but it was not certain at the time whether this was because the bone was too old or because it had been too severely affected by



poor conditions of preservation within the cave. It now appears that the first explanation may be the correct one, because two bone-calcite associations from Pitchapple collected in the subsequent 1989 expedition yielded uranium-series dates of slightly more than 100,000 yr (MacPHEE *et al.*, 1990; Table 1.).

Cave investigations during the 1989 expedition resulted in the discovery of a second new locality, now known as Tanglewood Cave. This cave has yielded remains of at least two adult and one juvenile *Amblyrhiza*. Continued work in the summer of 1990 produced the first documented *Amblyrhiza* fossils from Katouche Cave, with good stratigraphy and calcite associations. The bones from these sites are currently under study or in laboratory preparation for dating. Work in 1991 provided two further sites, named Anonymous Hole and Cave No Cave (McFARLANE & MacPHEE, in press), although of minor significance.

International interest in the life and extinction of Anguilla's giant rodent, *Amblyrhiza*, has stimulated more than 120 years of intermittent explorations in the caves of the Anguilla Bank - the reliquaries in which these remains are uniquely preserved. The recent discoveries of new material accompanied by detailed descriptions of site and stratigraphy are now yielding new insights into the morphology and natural history of *Amblyrhiza* (MacPHEE *et al.*, 1990; BIKNEVICUS *et al.*, in prep) and may permit a critical re-evaluation of the supposed human role in *Amblyrhiza*'s extinction. Furthermore, the compilation of the first systematic catalogue of Anguillan caves (McFARLANE & MacPHEE, in press) provides a foundation for the organization of future speleological research and conservation on the island.

ACKNOWLEDGEMENTS

None of the fieldwork undertaken by the authors since 1988 would have taken place without the constant support and encouragement of the Anguilla Archaeological and Historical Society. We are especially indebted to David Carty, Bob Conrich, Nik Douglas, Don Mitchell, and François Petit for their efforts above and below ground in support of this work. We are also grateful to the Government of Anguilla for their cooperation in arranging permission to excavate a portion of Anguilla's subterranean heritage.

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