

The Extinct Rodent *Clidomys* (Heptaxodontidae) From a Late Quaternary Cave Deposit in Jamaica

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Abstract.—We report a sample of over 20 fossils of the rare Jamaican rodent *Clidomys*, a genus of large body size belonging to the extinct West Indian family Heptaxodontidae. The fossils were collected from an indurated bone breccia of late Quaternary age in Slue's Cave, a small cave located near Lluidas Vale in the Worthy Park area of St. Catherine Parish in east-central Jamaica. The sample contains some of the most complete specimens known for *Clidomys*, including the first complete maxillary dentition, the first associated upper and lower dentitions, and two associated pairs of right and left dentaries. Teeth are intermediate in size between those of the larger *C. osborni* and the smaller *C. parvus*; the fossils are referred to the former, which appears to be the only valid species in this genus. The bones could not be radiocarbon dated because they lack collagen, suggesting an age older than 40 000 yrBP.

INTRODUCTION

Clidomys is a large extinct genus of rodent in the endemic Antillean family Heptaxodontidae. Woods (1989) placed *Clidomys* in the subfamily Clidomyinae, whereas the three other genera of heptaxodontids (*Amblyrhiza* from Anguilla and St. Martin in the northern Lesser Antilles, *Elasmodontomys* from Puerto Rico, and *Quemisia* from Hispaniola) are in the subfamily Heptaxodontinae. Anthony (1920) described *Clidomys* based on fossils from Wallingford Roadside Cave near Balaclava in St. Elizabeth Parish, west-central Jamaica. More than 25 Jamaican caves have produced Quaternary vertebrate fossils (MacPhee, 1984, 1997; Morgan, 1993), but *Clidomys* has been found in only six caves. In addition to Wallingford Roadside Cave, *Clidomys* is known from Sheep Pen Cave in Trelawny Parish and Molton Fissure in Manchester Parish, both within 20 km of Wallingford Roadside Cave. The other three sites with *Clidomys*, Worthy Park Cave 1 (McFarlane et al., 1998), Lluidas Vale Cave (MacPhee, 1984; Morgan, 1993), and our new site, Slue's Cave, are within a few kilometers of one another in the Worthy Park area of St.

Catherine Parish in east-central Jamaica. With the exception of Wallingford Roadside Cave and the fossils described in this paper, the other Jamaican records of *Clidomys* consist of small samples of isolated teeth, partial limbs, or both.

We report the second largest sample of *Clidomys* known from Jamaica. The fossils from Slue's Cave represent the most complete specimens of the dentary and maxilla known for this genus. The new sample more than triples the existing sample of *Clidomys* dentaries from two to seven, and includes the first complete maxillary dentition and the first associated upper and lower dentitions. We describe these specimens and compare them to other samples of *Clidomys*; we also provide information about Slue's Cave and the age of the fossils, which are deposited in the vertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville (UF). Other *Clidomys* specimens cited in the text are from the American Museum of Natural History, New York (AMNH). Upper teeth are designated by upper case letters and lower teeth by lower case letters (e.g., P4 is an upper 4th premolar, m1 is a lower 1st molar). All measurements of fossils are in mm.

LOCALITY AND AGE

Laurie Wilkins and Mikey Slue collected the fossils described herein in December 1989 from a small cave named Slue's Cave, in honor of the Slue family who are local residents. The cave is near the village of Lluidas Vale in the Worthy Park area of St. Catherine Parish. Lluidas Vale is a large interior valley surrounded by limestone bluffs and escarpments that reach almost 900 m in elevation. The elevation of Slue's Cave is about 380 m. In this region, deep, narrow valleys between limestone bluffs often become inundated by seasonal rains, about every four years, with water sometimes up to 25 m deep (Craton and Walvin, 1970). Erosion of the carbonate bedrock has produced extensive karst features in rocks of the White Limestone Group of Eocene to Miocene age. Concealed caves or sinkholes are occasionally exposed when limestone walls along the base of the cliffs fracture and collapse.

Slue's Cave formed by the collapse of a large section of exterior limestone wall exposing a small cave about 8 m wide, 3 m deep, and 4 m high (Fig. 1). Approximately

10 to 15 kg of indurated reddish-colored breccia was removed from the ceiling of the cave (Fig. 2). This sample contained more than 20 identifiable specimens of *Clidomys*; the only other vertebrate in the sample is the smaller capromyid rodent *Geocapromys brownii*, represented by two left dentaries and an upper incisor. Several species of large land snails are present in this breccia. Other cave breccia deposits from Jamaica, including Wallingford Roadside Cave (MacPhee, 1984) and Worthy Park 1 Cave (McFarlane et al., 1998), contain significant samples of aquatic vertebrates, primarily turtles and crocodiles, suggesting a freshwater aquatic depositional environment or perhaps deposition during floods. The small sample recovered from Slue's Cave consists entirely of terrestrial animals.

We submitted two samples of *Clidomys* postcranial bones from Slue's Cave to Beta Analytic, Inc. in Miami, Florida for radiocarbon dating, but the fossils could not be dated because they lacked bone collagen (Chris Patrick, in litt., 16 September 1999). There are several explanations for the lack of datable organic material (i.e., collagen) in fossils, including leaching and an age



FIG. 1. Exterior view of Slue's Cave, Lluidas Vale, Jamaica.



FIG. 2. Interior view of Slue's Cave, Lluidas Vale, Jamaica. Mikey Slue with hammer. Fossil deposit located just above top of ladder at interface of vertical wall and ceiling.

greater than the limit of radiocarbon dating (approximately 40 000 years BP). We strongly suspect that the *Clidomys* fossils from Slue's Cave are older than 40 000 years BP.

Flowstone deposits associated with *Clidomys* fossils from two other caves in Jamaica were dated using different methods, and yielded pre-Wisconsinan dates older than 100 000 yrBP (MacPhee et al., 1989; McFarlane et al., 1998). A flowstone directly overlying a bone breccia containing a partial *Clidomys* femur from Worthy Park 1 Cave, located in the general vicinity of Slue's Cave, yielded a uranium-thorium disequilibrium date of 174 000 yrBP (McFarlane et al., 1998). This date is similar to a series of uranium series and electron spin resonance dates (between 100 000 and 200 000 yrBP) on flowstones from Wallingford Roadside Cave (MacPhee et al., 1989). The

only reliably-dated specimens of *Clidomys* are older than 100 000 yrBP. These dates, coupled with the absence of *Clidomys* from numerous late Pleistocene and Holocene cave deposits throughout Jamaica (Morgan and Woods, 1986; Morgan, 1993; MacPhee, 1997), suggest that this genus went extinct before the end of the Pleistocene.

SYSTEMATIC PALEONTOLOGY
CLASS MAMMALIA, ORDER RODENTIA
FAMILY HEPTAXODONTIDAE

Clidomys osborni Anthony, 1920

Referred Specimens: All fossils are from Slue's Cave, Lluidas Vale, St. Catherine Parish, Jamaica. UF 172946, associated maxilla and mandibles, including the left maxilla with P4-M3, right maxilla with P4-M2, left dentary with base of incisor and p4-m3, and right dentary with base of incisor and broken p4-m1 and m2 (Figs. 3A-F); UF 204854, fragment of left maxilla with M1; UF 204851, edentulous palate; UF 204853, left and right premaxilla with incisors; UF 204852, edentulous left and right premaxilla; UF 172945, associated right and left dentaries, left dentary with base of incisor and edentulous tooththrow and right dentary with p4-m3 (Figs. 4A-C); UF 204858, left dentary with m2-m3; UF 204855, 205856, two isolated teeth; UF 204857, three associated thoracic vertebrae; UF 204860; humerus; UF 204861, distal humerus; UF 204863, proximal radius; UF 204864, proximal ulna; UF 204866, distal femur. The collection contains many additional fragmentary limb bones of *Clidomys* not listed here.

Description and Comparisons: Anthony (1920) described two species of *Clidomys* from Wallingford Roadside Cave: a larger species *Clidomys osborni* based on a left dentary with p4-m3 (AMNH 17634) and a smaller species *C. parvus* based on a single p4 (AMNH 17637). Although Anthony stated that his fossil sample included much additional material of *Clidomys*, especially isolated teeth of *C. osborni*, he did not describe or measure these other fossils. MacPhee (1984) redescribed and measured the *Clidomys* sample from Wallingford Roadside Cave, including the type, another

dentary with i1, p4-m3 (AMNH 108543), many isolated teeth, and several postcranial elements.

The teeth of *Clidomys* are high crowned, rootless, and evergrowing. With the exception of M3, each tooth is composed of three elliptical laminae of enamel enclosing den-

tine and separated from one another by a thin layer of cement (Figs. 3, 4). The mandibular teeth are emplaced at an oblique angle to the long axis of the toothrow, whereas the upper teeth are set in the maxilla at right angles to the long axis of the toothrow. MacPhee (1984) numbered the

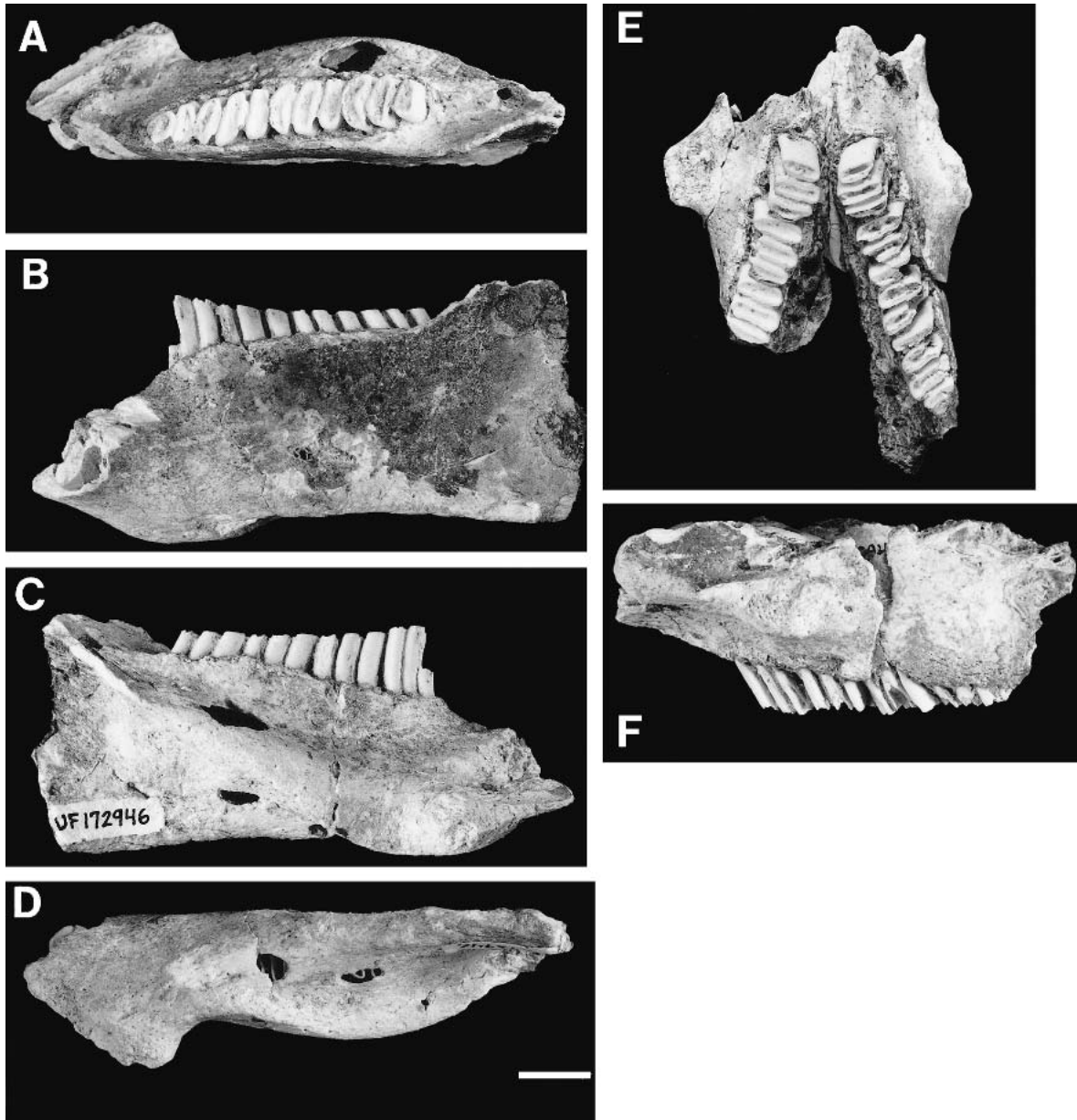


FIG. 3. *Clidomys osborni*, associated right and left maxillae and left dentary (UF 172946), from Slue's Cave, Lluidas Vale, Jamaica. A-D, left dentary, A. Occlusal view, B. Lateral view, C. Medial view, D. Ventral view, E. Occlusal view of right and left maxillae. F. Lateral view of left maxilla. Scale bar is 1 cm.



FIG. 4. *Clidomys osborni*, right and left dentaries (UF 172945), from Slue's Cave, Lluidas Vale, Jamaica. A. Occlusal view, B. Ventral view, C. Lateral view. Scale bar is 1 cm.

laminae from 1 to 3 on each tooth, except M3, which has four laminae. In the dentary, m1 through m3 are similar in size and morphology (Figs. 3, 4, Table 1). In the two dentaries from Slue's Cave, p4 is a smaller triangular-shaped tooth in which the laminae increase in size from anterior to posterior, with lamina 1 very small and elliptical. Measurements of the width of laminae on p4 of UF 172945 and 172946, respectively are: lamina 1, 3.7, 3.4; lamina 2, 5.7, 4.9; lamina 3, 7.0, 5.5. The morphology of the p4

matches the description of the smaller species *C. parvus* (Anthony, 1920; MacPhee, 1984) in which the p4 is small and the anterior two laminae are reduced compared to lamina 3. In the type dentary of the larger *C. osborni*, the p4 is more molariform, the first lamina is concave on its posterior surface, and the second lamina is almost as wide as the first. The shape of the laminae vary somewhat on m1-m3, particularly the anteriormost or first lamina. MacPhee (1984) noted that the first laminae on the

TABLE 1. Measurements (in mm) of the lower teeth and dentaries of *Clidomys osborni* from Slue's Cave, Luidas Vale, Jamaica and the type specimens of *C. osborni* and *C. parvus* from Wallingford Roadside Cave, Jamaica (from Anthony, 1920). Dashes represent measurements not taken because the fossils are incomplete.

Specimen	p4			m1			m2			m3			Alveolar length of mandibular tooththrow (p4-m3)	Occlusal length of mandibular tooththrow (p4-m3)	Length of mandibular symphysis	Length of i1-p4 diastema
	L	W	L	L	W	L	L	W	L	L	W	L				
<i>C. osborni</i>																
Slue's Cave																
UF 172945	8.6	7.0	11.2	7.4	11.6	7.6	11.8	7.7	46.3	45.2	51.1	35.9				
UF 172946	7.9	5.6	10.1	7.2	10.0	7.2	10.3	7.8	40.6	39.6	—	—				
<i>C. osborni</i> (holotype)																
AMNH 17634	9.8	7.0	11.1	9.5	11.4	9.1	12.2	8.8	—	46.2	—	—				
<i>C. parvus</i> (holotype)																
AMNH 17637	6.1	4.4	—	—	—	—	—	—	—	—	—	—				

molars were characterized by a "boomerang" shape (convex surface anterior), with the inflection of the boomerang increasing from m1 to m3.

The horizontal ramus of the dentary in *Clidomys* is very deep to accommodate the high-crowned cheek teeth (Figs. 3B, 3C, 4C). The right and left dentaries in UF 172945 and UF 172946 are strongly fused at the mandibular symphysis, with no hint of a suture separating the two dentaries (Figs. 3A, 3D, 4A, 4B). The symphysis is long extending posteriorly to the level of m1, and the incisors project at a low angle. The symphyseal region of the dentary in *Clidomys* is similar in shape to that of the even larger heptaxodontid *Amblyrhiza inundata* Cope from the northern Lesser Antilles (Cope, 1883; Biknevičius et al., 1993). Both genera have an elongated symphyseal region in which the two dentaries are fused.

The upper tooththrows of *Clidomys* converge anteriorly (Fig. 3E), with only about 3 mm separating the alveoli of the right and left P4s. The first three maxillary teeth, P4-M2, are very similar in size and shape (Fig. 3E, Table 2). Anthony (1920) and MacPhee (1984) suggested that the isolated teeth in the Wallingford sample with four laminae were M3, but neither of them had a complete maxillary dentition with M3 in place. The left maxilla of UF 172946 from Slue's Cave (Figs. 3E, 3F) is the only known specimen of *Clidomys* with a complete maxillary dentition (P4-M3), and as Anthony and MacPhee suggested, the in-place M3 in this specimen has four laminae. The anterior two laminae are about equal in breadth (lamina 1, 7.0; lamina 2, 7.4), whereas the third laminae is about 75 % the width (5.8) of the two anterior laminae; the fourth lamina is less than half as wide (3.2) as laminae 1 and 2. The morphology of M3, in which the laminae become progressively smaller from anterior to posterior, is essentially the opposite of p4 in which the laminae become larger from anterior to posterior.

Tables 1 and 2 compare measurements of the upper and lower teeth and dentary of the specimens from Slue's Cave, the type dentary of *C. osborni*, and the type p4 of *C. parvus* from Wallingford Roadside Cave

TABLE 2. Measurements (in mm) of the upper teeth of *Clidomys osborni* from Slue's Cave, Lluidas Vale, Jamaica.

Specimen	P4		M1		M2		M3		Alveolar length of maxillary tooththrow (P4-M3)	Occlusal length of maxillary tooththrow (P4-M3)
	L	W	L	W	L	W	L	W		
UF 172946	8.1	6.8	9.3	7.4	9.4	7.6	10.4	7.5	42.9	38.2

(from Anthony, 1920). Our measurements, like Anthony's, were taken on the occlusal surface of the teeth. Because all the teeth in our sample are firmly emplaced in either dentaries or maxillaries, we could not take the dental measurements described by MacPhee (1984, fig. 6), which were designed to be taken on isolated teeth.

The sample of *Clidomys* from Slue's Cave consists of maxillary and premaxillary fragments, mandibles, and limb bones, representing a minimum of three individuals based on the presence of three left maxillae and three left dentaries. Several sizes and ontogenetic ages of individuals are present in the sample, and there is some association of skeletal elements. A right and left maxillary were collected in occlusion with a pair of dentaries (UF 172946) and there are three articulated thoracic vertebrae (UF 204857) from a subadult in which the epiphyses of the vertebral centra are not fused.

DISCUSSION

Anthony (1920) described four new genera and five new species of large heptaxodontid rodents from Wallingford Roadside Cave in Jamaica based primarily on differences in the shape of the elliptical enamel laminae that compose their teeth: *Clidomys osborni*, *C. parvus*, *Spirodontomys jamaicensis*, *Speoxenus cundalli*, and *Alterodon major*. Although the laminae usually consist of enamel ellipses separated by cement, in certain specimens the laminae coalesce or fuse to form unusual shapes, explaining the profusion of generic names proposed by Anthony. MacPhee et al. (1983) and MacPhee (1984) documented considerable variation in the enamel pattern of teeth referred to *Clidomys* and syn-

onymized *Alterodon*, *Speoxenus*, and *Spirodontomys* with *Clidomys*.

On the basis of the disparity in size between certain specimens of *Clidomys*, MacPhee (1984) followed Anthony (1920) in recognizing two valid species in the genus, the larger *C. osborni* and the smaller *C. parvus*. MacPhee (1984) noted the large coefficients of variation observed in measurements of the Jamaican *Clidomys* teeth. Measurements of the *Clidomys* teeth from Slue's Cave, particularly the p4, are intermediate between the measurements of the holotypes of *C. osborni* and *C. parvus* (Table 1). The p4s in the new specimens of *Clidomys* are smaller than the p4 in the type of *C. osborni* (7.8, 8.6, and 9.8, respectively) and larger than the type p4 of *C. parvus* (6.1). The molars in the larger of the two new *Clidomys* dentaries are very similar in length to the molars of the *C. osborni* type, but are considerably narrower (Table 1). The teeth from Slue's Cave are closest in size to *C. osborni*.

The variation in size exhibited by the new sample of *Clidomys* from Slue's Cave (Tables 1, 2) is comparable to the substantial size variation in this genus noted by MacPhee (1984) and questions the validity of *C. parvus*. Biknevicius et al. (1993) observed a significant size range in measurements of the humerus and femur in *Amblyrhiza inundata*, which they interpreted as individual variation within a single species. Most of the teeth in our sample are intermediate in size between the smallest individuals referred to *C. parvus* and larger individuals referred to *C. osborni* (Anthony, 1920; MacPhee, 1984). Furthermore, juveniles are often difficult to recognize in rodents such as *Clidomys* that possess high-crowned, ever-growing teeth. We found no morphological differences in the teeth and mandibles that reliably distinguish these

two species. Thus, it seems very likely that *C. osborni* is the only valid species of *Clidomys* present in Jamaica.

Acknowledgments.—We thank Mikey Slue for his valuable assistance in removing the fossil-bearing breccia from Slue's Cave. He, his father Owen, and the entire Slue family made L. Wilkins welcome during this and many other visits to Luidas Vale while in search of living *Geocapromys*. L. Wilkins visited Jamaica thanks to the friendship and support of Pam and James Williams, hosts for the *Geocapromys* Reintroduction and Survey Project funded by Jersey Wildlife Preservation Trust. We are grateful to Drs. Ross D. E. MacPhee and Donald A. McFarlane for their helpful comments on the manuscript. Russell McCarty of the Florida Museum of Natural History skillfully prepared many of the fossils. Shannon Montgomery, a summer intern from Eckerd College, prepared some of the material and provided insight. Patrick Payne, Office of Instructional Resources, University of Florida, photographed the fossils.

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