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A new bat record for the late Pleistocene of Jamaica: *Pteronotus trevorjacksoni* from the Red Hills Road Cave

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ABSTRACT. The Jamaican Red Hills Road Cave is known for its late Pleistocene bat fauna. Continued screening of the material has yielded fossil material of a species *Pteronotus* of similar size to *P. parnellii*, which currently inhabits the island. However, the dentition of the new finds is characterized by plump molars, quite unlike that of the recent representatives. Therefore, the Red Hills Road Cave material is considered to belong to a new species, *Pteronotus trevorjacksoni* sp. nov. The find of a fully unworn P4 suggests that *P. trevorjacksoni* may have roosted in the cave; *Pteronotus* species are still cave dwellers.

Keywords: biogeography, Chiroptera, Caribbean, Quaternary, dietary specialisations.

1. INTRODUCTION

The Recent bat fauna of Jamaica comprises 21 species (**Genoways et al., 2005**). Some of these species have also been found in the fossil record (**McFarlane et al., 2002; Ouwendijk et al., 2014**). Moreover, a number of fossil finds show species that either no longer live on the island or have become extinct altogether (**Table 1**). The most recent additions to the fossil record of Jamaican bats was the paper by **Ouwendijk et al.** (**2014**), who described material from the Red Hills Road Cave (RHRC), parish of St Andrew. Since then, the sorting of the sediment from the RHRC in Leiden has continued and more bat remains have come to light. Among these new finds was a mandible that preserved not only the p4 and all the molars, but also showed the alveoles of two additional premolars.

Based on the presence of three premolars in line, we initially identified the find as an unknown species of the mouse-eared bats, *Myotis*, and it appears as such in a recent conference abstract (**Van den Hoek Ostende et al., 2017**), as it did in our original manuscript. However, an anonymous reviewer pointed out that the morphology of the p4 did not match with an identification as *Myotis* and kindly suggested that the mandible could in fact belong to *Pteronotus*. As *Myotis*, *Pteronotus* has three lower premolars. The middle one, the p3, is small and only slightly offset in respect to the others. Alerted that our mandible could belong to *Pteronotus*, we had another look at the remainder of the newly found fossils. Indeed, a maxillary that we had previously not considered clearly belonged to a mormoopid bat and could also be identified as *Pteronotus*. In addition, we found an isolated P4 referable to that genus.

TABLE 1. The recent and fossil bat fauna of Jamaica, compiled from Genoways et al. (2005) and Ouwendijk et al. (2014). † indicates known from both fossils and recent, species marked †† are known from the fossil record only. The classification follows Simmons (2005).

Noctilionidae	
	Noctilio leporinus (Linnaeus)
Mormoopidae	
	Mormoops blainvilli Leach †
	Mormoops megalophylla Peters ††
	Pteronotus macleayii (Gray)
	Pteronotus parnellii (Gray) †
	Pteronotus quadridens (Gundlach)
	Pteronotus trevorjacksoni sp. nov. ††
Phyllostomidae	
	Macrotus waterhousii Gray †
	Monophyllus redmani Leach †
	Glossophaga soricina (Pallas)
	Erophylla sezekorni (Gundlach) †
	Phyllonycteris aphylla (Miller) †
	Artibeus jamaicensis Leach †
	Ariteus flavescens (Gray) †
	Tonatia saurophilia Koopman and Williams ††
	Brachyphylla nana pumila Miller ††
	Stenoderma rufum Desmarest ††
Natalidae	
	Chilonatalus micropus (Dobson)
	Natalus jamaicensis Goodwin †
Vespertilionidae	
	Eptesicus fuscus Beauvois †
	Lasiurus degelidus Miller
Molossidae	
	Tadarida brasiliensis I. Geoffroy St.-Hillaire †
	Eumops auripendulus (Shaw)
	Eumops glaucinus Wagner
	Molossus molossus (Pallas)

The neotropical genus *Pteronotus* traditionally encompasses six extant species and the recently extinct *P. pristinus* (**Simmons, 2005**). However, an integrative taxonomic approach recently suggested that many subspecies, particularly in the *P. parnellii* complex, should be raised to species level, raising the number of species to sixteen (**Pavan and Marroig, 2016**). But, despite deep genetic divergence, the morphology of the various *Pteronotus* species remains remarkable similar. Notably, the large *Pteronotus* from Jamaica is named *P. parnellii* in either classification, as Jamaica is the type locality of the species.

Three species of *Pteronotus* inhabit Jamaica today. Two of these, *P. macleayi* and *P. quadridens*, form a clade that seems to have reached the Greater Antilles during the late Miocene. The third species, *P. parnellii*, presumably reached the islands at the beginning of the Quaternary (**Pavan and Marroig, 2016**). Hitherto, it was the only species of the genus that has also been found on the island as fossils (**Williams, 1952**). These finds from the Portland Cave and Dairy Cave are considered to come from the late Quaternary, without pursuing greater accuracy as to the age. Unfortunately, as the fossils were neither figured nor described in detail, we cannot compare the Red Hills Road Cave *Pteronotus* with these finds.

2. Locality and Age

[Abridged from **Donovan et al., 2013**.] The RHRC was discovered in 1988 by two students, Mss Anita Godwin (now Dr Anita Warrington) of the University of Liverpool and Marlene Britton of the University of the West Indies, Mona. The cave was first visited by the Geological Society of Jamaica in February 1989 (**Donovan and Gordon, 1989**). This and other excursions led to new specimens being collected. In the mid-1990s a large bulk sample was deposited in the Geology Museum of the University of the West Indies, Mona (**Donovan, 1997**). An aliquot of this sample has been the subject of research at Naturalis, Leiden, since 2009.

The site is on the south side of the Red Hills Road (**Donovan et al., 2013**, fig. 2; Jamaica 1:50,000 new series, NGR 13/643 572), in the parish of St. Andrew, Jamaica, about 3.3 km west from the lookout between mileposts 9 and 10. The cave is flask-shaped and exposed in vertical section, with a narrow opening at the apex (**Donovan et al., 2013**, fig. 3). The cave was dissolved into well-lithified limestones of the Walderston Formation (mid-Cenozoic White Limestone Group), and is partially infilled with dripstones, fallen limestone boulders and siliciclastic sediment. The last is largely derived from the *terra rossa* soils that are prevalent in this area, hence the name Red Hills. Where lithified, the sediment is cemented by calcite. Much unconsolidated sediment is deduced to have been washed out of the cave following exposure, which may have been near-completely filled before excavation. It is unknown how far the infilled cave extends below road level. The site is Late Pleistocene, about 40,000-25,000 years old (**MacPhee et al., 1989**; **McFarlane and Blake, 2005**, pp. 402-403; **Paul and Donovan, 2006**, p. 110).

3. Systematic Palaeontology

Mammalia Linnaeus, 1758
Chiroptera Blumenbach, 1779
Vespertilionidae Gray, 1821
Pteronotus Gray, 1838

***Pteronotus trevorjacksoni* sp. nov.**
Fig. 1.

2017 *Myotis* sp. nov.; Van den Hoek Ostende et al., pp. 19-20.
2018 *Myotis* sp. nov.; Van den Hoek Ostende et al., pp. 142-143.

Etymology. In honour and memory of Professor Trevor A. Jackson.

Type material. Holotype: Left mandible preserving p4 - m3 and four alveoles (RGM 1285849; **Figure 1**). Paratypes: Fragment left maxillary with P4-M2 (RGM 1309345); one isolated left P4 (RGM 1309346).

Locality and age. Red Hills Road Cave, parish of St Andrew, Jamaica; late Pleistocene (see above).

Diagnosis. A large species of *Pteronotus* (lm1-m3 = 6.1 mm), characterized by its relatively heavy-built dentition with sturdy cusps. The p4 is shortened with reduced anterior and posterior flanges. The mandible is stout.

Description. Upper dentition: The last upper premolar is longer than wide. The labial part is occupied by the large and high paracone, which bears a slightly curved posterocrista. The anterocrista is weakly developed. It is connected to the parastyle and tapers out at half the height of the paracone. There is a thick cingulum on the anterolingual side of the P4, which is part of a ridge connecting parastyle and protocone. The latter is not discernable as a separate cusp, but is incorporated in the lingual ridge. This ridge continues to the posterior end of the posterocrista of the paracone, encircling a rather deep posterolingual basin.

The first two upper molars are very similar in size and morphology. They are squarish with

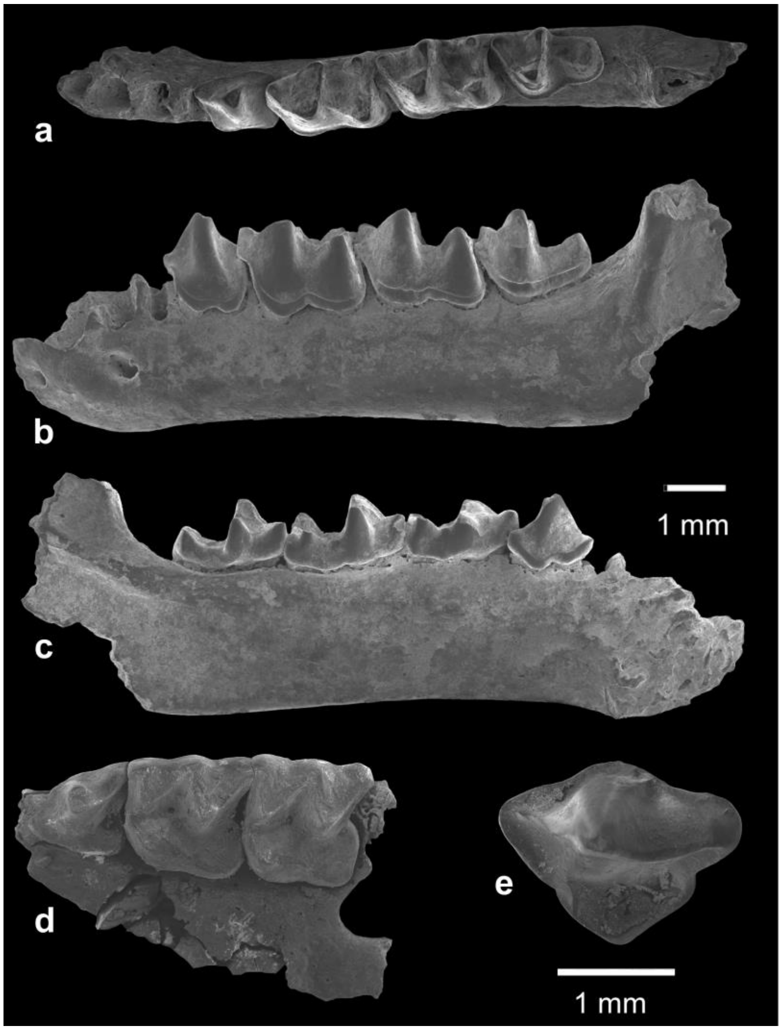

Figure 1. ***Pteronotus trevorjacksoni*** **sp. nov. from Red Hills Road Cave, parish of St Andrew, Jamaica. 1a-c, RGM 1285849, holotype, left mandible with p4 - m3; a. occlusal view, b. labial view; c. lingual view; 1d , RGM 1309345, paratype, left maxillary with P4-M2, occlusal view; 1e, RGM 1309346, paratype, left P4, occlusal view. Scalebar = 1 mm.**

relatively sturdy cusps. The labial cusps reach to halfway on the occlusal surface. In the M1 the paracone is clearly smaller than the metacone; in the M2, this difference is far less pronounced. The protocone is large. Its wear surface is directed posterolingually. A low ridge continues from the back of the protocone, bordering the posterolingual and posterior sides. The hypocone is not discernable as a separate cusp in this ridge. The hypoconal flange is moderately developed and hardly protrudes lingually. The posterior emargination in weak.

Lower dentition: The dentary preserves the p4 and all of the molars. It is broken behind the m3, with only a small part of the ramus ascendens preserved. The latter seems to stand at almost a right angle to the ramus horizontalis. In front of the p4, four alveoles are preserved. The foremost of these is tiny and evidently belongs to an incisor. It contains part of the root. The alveole behind this is large. It has a sub-elliptical shape with the length axis in the direction of the mandible. This is considered to be the alveole of the canine. The last two alveoles are smaller, with the front one being larger than the other, but still clearly smaller than the canine alveole. The alveoles stand in line and are interpreted as the alveoles of the p2 and a relatively small p3.

The p4 has a sub-trapezoidal occlusal outline. The premolar consists for the most part of a large, trifaced cusp, which extends to the posterolingual corner of the p4. The back face of the main cusp is convex. There is a small anterolingual bulge. The molars are brachyodont. The m1 and m2 are of similar size; the m3 is only somewhat smaller. The paraconid is somewhat displaced labially, particularly in the m1, resulting in rather open trigonid basins. The oblique cristid ends halfway against the trigonid wall in the m1 and m2, near the metaconid in the m3. The hypolophid runs behind the entoconid without leaving a valley between the arm and the cusp. On the reduced talonid of the m3, the hypolophid forms a continuous ridge with the oblique cristid, encircling a small talonid basin. There is a well-developed cingulid on the anterior, labial and posterior sides. In the m1, the cingulid is strongly undulating, sloping up below the re-entrant valley. This pattern is somewhat more weakly developed in the m2; in the m3 the labial cingulid is straight. Labially, the cingulid is very weak.

Measurements (in mm). Dentary: Lm1-m3: 6.1 mm; p4 = 1.61 x 1.11 mm; m1 = 2.25 x 1.40 mm; m2 = 2.18 x 1.45 mm; m3 = 2.02 x 1.36 mm. Total length preserved 12.3 mm. Height ramus horizontalis ~ 2.1 mm

Maxillary: P4 = 2.09 x 1.53 mm; M1 = 2.10 x 2.29 mm; M2 = 2.12 x 2.31 mm.

Isolated P4: P4 = 2.14 x 1.70 mm.

Discussion. Based on their size, the RHRC fossils clearly do not belong to the smaller *Pteronotus* species in the Jamaican extant fauna, *P. macleayi* and *P. quadridens*. Rather, the new species is more comparable in size to *P. parnellii*. We compared the fossils to a Recent *Pteronotus* skull and mandible from an owl pellet in the Naturalis collections, collected at the Green Park Resort, parish of Trelaway, Jamaica (ZMA.MAM.31705). Also based on its size, this Recent skull can only be assigned to *P. parnellii*. This comparison showed remarkable morphological differences. The Recent species has very sharp cusps on its molars, whereas in the fossil material the cusps are rather blunt and heavily built. The clearest difference lies in the p4, which in *P. parnellii* consists of a pointed cusp with clear flattening in the front and at the back. The p4 of *P. trevorjacksoni* is less elongated. The main cusp reaches the anterior and posterior borders on the lingual side, and the flattenings, limited to the labial side, are much reduced. In addition, the mandible of *P. trevorjacksoni* is stouter than in the recent form. Subsequent comparison of photographs of *P. parnellii* in literature (**Clare et al., 2013**, fig. 1; **Velazco et al., 2013**, figs 3C and 5C) confirmed these differences.

The description of *Pteronotus trevorjacksoni* brings the number of *Pteronotus* species present on Jamaica in the late Pleistocene up to four. Actually, this mirrors the situation on Cuba, which also has three recent *Pteronotus* species and one that has recently become extinct (**Silva-Taboada, 1974**). This appears not to be a big problem; sympatric insectivorous bats are well adapted to partitioning the resources (**Emrich et al., 2014**). Being similarly-sized as *P. parnellii*, this bat seems to have been the most direct competitor to *P. trevorjacksoni*. *Pteronotus parnellii* seems to have a preference for Lepidoptera. Although a general feeder, a large part of it diet consists of moths (**Silva-Taboada, 1979**; **Emrich et al., 2014**). The plumb dentition and stout mandible suggest that *P. trevorjacksoni* had a more durophagous diet and may have had its diet consisting primarily of Coleoptera. **Ghazali and Dzeverin** (**2013**) pointed out that, within *Myotis*, the species most adapted to a diet consisting of Coleoptera, namely *M. myotis*, had shortened its premolar row which enhanced the effectiveness of the jaw movement. This is in line with the shorter p4 found in *P. trevorjacksoni*. In any case, the differences in dentition that warrant the description of a separate species also indicate the niche differentiation between *P. parnellii* and the extinct species.

Pteronotus roosts in warm and humid caves. Given the high number of bat species recovered from the Red Hills Road Cave, in contrast to very few fossils of other mammals, it seems logical to assume that at least some of these species had roosts in the cavern. This was probably the case for *P. trevorjacksoni*. The single P4 found (RGM 1309346) is virtually unworn and presumably belonged to a very young individual that may have lived and died in the cavern without ever leaving it. It is unfortunate that there are no descriptions of the *P. parnellii* material from the Portland Cave and Dairy Cave (**Williams, 1952**). The discovery of a fourth species of *Pteronotus* makes it possible that this material could also belong to *P. trevorjacksoni*, which is, after all, of similar size. It will indeed be interesting to scour younger cave deposits on the island, in order to get a better impression of the timing and possible causes of the extinction of this fossil bat.

4. Conclusion

The discovery of a new species of *Pteronotus*, *P. trevorjacksoni*, in the Red Hills Road Cave, parish of St Andrew, Jamaica, shows that the diversity within that genus was larger in the past. The sturdy dentition suggests that *P. trevorjacksoni* had its own dietary specialisation, presumably having a more durophagous diet than the similarly sized *P. parnellii*. The discovery of an extinct species of bat provides another glimpse in the diversity changes in the bat fauna the geological past, in line with previous studies. This could also be a harbinger for future discoveries, as the highly fossiliferous infill of the RHRC has yet to reveal all of its secrets.

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