

Morphological Re-examination of the Endemic Paraguayan Snake *Phalotris nigrilatus* Ferrarezzi, 1993 (Serpentes: Colubridae: Elapomorhini), with Notes on its Ecology and Conservation Status

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Abstract: The colubrid snake *Phalotris nigrilatus* is endemic to San Pedro Department (Paraguay) and is known from a very few historical specimens. We analyze morphological variation and geographic distribution of *P. nigrilatus* on the basis of currently available specimens, including long-overlooked museum material. Also, we briefly report for the first time its live coloration and behavior on the basis of a recently collected individual. Results of morphological and geographic analyses lead to a slight revision of diagnosis and an argument for a higher conservation priority for this species.

Key words: Distribution; Morphological variation; Rediscovery; San Pedro Department; Taxonomy

INTRODUCTION

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Phalotris Cope, 1862 is a genus of small to medium-sized, semi-fossorial, elapomorphine

snakes, distributed largely in open habitats in Brazil, Bolivia, Paraguay, and Argentina (Ferrarezzi, 1993). Grazziotin et al. (2012) recently showed *Phalotris* to be the most primitive genus of the Elapomorphini, but with a sister-group relationship to the derived *Elapomorphus/Apostolepis* clade, retrieving it as monophyletic only in analyses based on multi-alignment genes data. *Phalotris* is poorly represented in museum collections, but 15 species are currently recognised, forming three species groups (Ferrarezzi, 1993): six species in the *tricolor* group (Jansen and Köhler, 2008), four in the *bilineatus* group (Puorto and Ferrarezzi, 1993; Cabral and Cacciali, 2015), and five in the *nasutus* group (Moura et al., 2013). Seven species have been reported from Paraguay: two in the *tricolor* group, three in the *bilineatus* group, and a single species in the *nasutus* group, the endemic *P. nigrilatus* Ferrarezzi, 1993, (Cacciali et al., 2016; Atkinson et al., 2018). One additional species of the *bilineatus* group, the recently described *P. normanscotti* Cabral and Cacciali, 2015, is also considered to be endemic to Paraguay. Two synapomorphies distinguish the *nasutus* group: a pointed snout with a prominent rostral shield and fusion of the second and third series of temporal plates (sometimes present on only one side of the head) (Ferrarezzi, 1993; Moura et al., 2013). The five known species in this group all occur in the Cerrado region of central South America: *P. concolor* Ferrarezzi, 1993, *P. labiomaculatus* Lema, 2002, *P. lativittatus* Ferrarezzi, 1993, *P. nasutus* Gomes, 1915, and *P. nigrilatus* Ferrarezzi, 1993.

Phalotris nigrilatus was described from a single female specimen (FML 709) collected at “Carumbé,” San Pedro Department, Paraguay in July 1973 by R. Golbach. Cacciali et al. (2007) provided a redescription and the first description of hemipenes, based on two additional specimens (MNHN 89 and 91) that had been collected earlier, in 1957, at nearby “Primavera,” also San Pedro Department. More recently, a larger series of specimens of

P. nigrilatus from this same locality, collected between 1954 and 1959, came to light in the Natural History Museum, London (Cacciali et al., 2016). However, the morphological data associated with these specimens have not to date been published, and our knowledge of variation in this species is still derived entirely from the three original specimens.

Here, we compile the available data on the morphological variation of *P. nigrilatus*, following an examination of all known specimens. Additionally, we provide photographs, description of the appearance of the species in life, ecological observations, and a new geographic locality from a live individual encountered in San Pedro Department, 46 years after the last known specimen was collected.

MATERIALS AND METHODS

We examined and described the specimens housed in the Natural History Museum, London (NHM). Measurements were taken with dial callipers (to the nearest 0.01 mm), and lengths were measured with millimetre tape. Paired structures are presented as left/right. Ventral scale counts follow Dowling (1951), and dorsal scale counts and terminology follow Peters (1964), including measuring the reductions at one head distance after the neck and before the cloaca. For supralabial counts, scales in contact with the orbit are presented in parentheses. For infralabial counts, scales in contact with chinshields are presented in parentheses.

Geographic and morphological data used for comparisons with other species within the *nasutus* group were extracted from Ferrarezzi (1993) for *P. nasutus*; Ferrarezzi (1993) and Silveira Vasconcelos and Gomes dos Santos (2009) for *P. lativittatus*; Moura et al. (2013) for *P. concolor*; and Hamdan et al. (2013) for *P. labiomaculatus*. As available data for *P. labiomaculatus* were not provided for specific specimens, we used the pholidosis traits of this species only for a comparison of range values, and not for correlations. The morpho-

logical data were used to explore the variation in ventral and subcaudal scales among the species in the group. Statistical analyses (one-way ANOVA for several samples, box plots, and dispersion graphic with convex hulls) were made in PAST 3.14 (Hammer et al., 2001). For description of coloration in life we followed the terminology and codes by Köhler (2012).

Geographic information for high resolution elevation maps were obtained from the Consortium for Spatial Information (CGIAR-CSI), using SRTM30 (30 seconds resolution) datasets (Jarvis et al., 2008). Ecoregional maps were used based on Olson et al. (2001), available at http://maps.tnc.org/gis_data.html, and based on the national ecoregional proposal (Resolución SEAM N° 614/13).

A collection permit was issued by the Secretaría del Ambiente (Currently Ministerio del Ambiente) N° 116/2018. Museum acronyms are: FML (Fundación Miguel Lillo, Argentina), MNHN (Museo Nacional de Historia Natural, Uruguay), MNHNP (Museo Nacional de Historia Natural del Paraguay, Paraguay), and NHM (Natural History Museum, London, UK).

RESULTS

Pholidosis

A total of 15 specimens of *Phalotris nigrilatus* (including the holotype) were examined. There is little variation in scalation among the specimens of *P. nigrilatus* except for the rostral-prefrontal contact (present in ten specimens and absent in five specimens). Meristic and metric data are available in Appendix I. Photographs of specimens from the NHM are stored in figshare (<https://doi.org/10.6084/m9.figshare.c.4709231.v1>). The cephalic pholidosis is largely constant, with one preocular and two postoculars and the temporal formula consistent as 0+1. Supralabials are usually 6 (2nd–3rd) (with a few exceptions) and infralabials 8 (1st–5th) (with two specimens showing 8 (1st–4th) and the holotype with 7 (1st–4th)). Dorsal scale rows

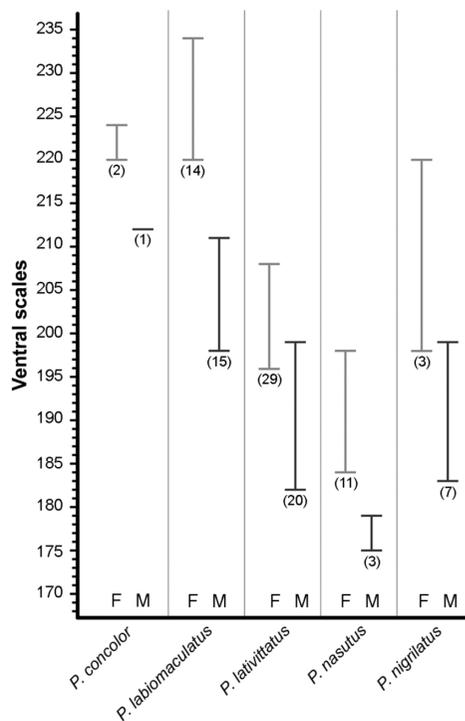


FIG. 1. Ventral scale ranges for females (F) and males (M) of the species of the *Phalotris nasutus* group. Numbers below (in parentheses) indicate sample size.

are typically 15-15-15, with the exception only of the holotype and the new specimen (MNHNP 12577), which present 17-15-15 (Appendix 1).

In comparison with other species, according to the data available to us, females of *Phalotris labiomaculatus* have the highest number of ventral scales, followed by *P. concolor*, whilst the lowest values are found in males of *P. nasutus* (Fig. 1). The range of ventral scale variation in males of *P. lativittatus* and *P. nigrilatus* almost completely overlaps, but there is a significant difference ($P=0.0024$, $df=29$, $F=7.6$, excluding *P. concolor* and *P. labiomaculatus* for lack of enough data) in the result for females (Fig. 1). The new specimen of *P. nigrilatus* (MNHNP 12577) presents the lowest number of ventral scales for females within the species (Appen-

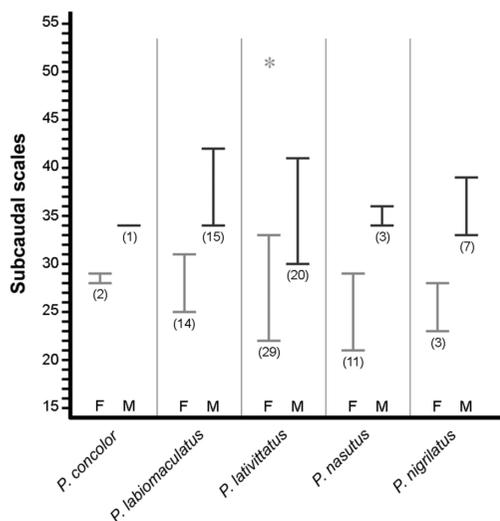


FIG. 2. Subcaudal scale ranges for females (F) and males (M) of the species of *Phalotris nasutus* group. Asterisk indicates an outlier. Numbers below (in parentheses) indicate sample size.

dix 1), falling within the range of variation of the males (Fig. 1).

Males of *P. labiomaculatus* have marginally the highest number of subcaudal scales, closely followed by *P. lativittatus*, whereas females of *P. nasutus* and *P. lativittatus* have the lower numbers (Fig. 2). In each sex, however, there is considerable overlap in the subcaudal counts of all five species, even when bearing in mind the limited number of available specimens.

The dispersion graphic (ventral scales vs subcaudal scales) shows a clear discrimination between males and females, but a high degree of overlap between males of *P. lativittatus* and *P. nigrilatus*, as well as females of these two species (and *P. nasutus* to a lesser degree) (Fig. 3).

Coloration

The coloration of the preserved specimens is rather constant and is consistent with the previously described color pattern of the species. Coloration in life based on the new specimen (MNHNP 12577; Fig. 4) is as

follows: Head sepia (286) all around. Body with a fuscous (283) vertebral stripe (one scale in width), followed laterally by wider robin rufous (29) paravertebral stripes (one on each side, two and a half scales in width). Body sides fuscous (283) reaching the ventrals. Ventral scales with fuscous (283) suffusions on lateral edges (contacting the dorsals) on a Pratt's rufous (72) background restricted to the midventral region. Preloacal plates strongly suffused with fuscous (283) on a Pratt's rufous (72) background. Tail follows the same pattern and color of the body, with the vertebral line extending over the first third of the tail.

Habitat and distribution

Limited information is available on the distribution and ecology of most species of *Phalotris* because of their fossorial behavior and the rarity with which they are encountered. *Phalotris nigrilatus* is one of the least known of all species, as to date all known specimens have been from historical collections, and only vague collection data accompany them (detailed in Appendix 2).

Little can be inferred about the habitat where the specimens were found from the existing data (Appendix 2). The lack of coordinates also makes it difficult to identify a specific collection locality in this heterogeneous environment. The original landscape matrix was a transitional zone between grassy marshes and savannas, typical of the Humid Chaco, with patches of sub-humid Alto Paraná Atlantic Forest. Estancia Carumbé (type locality for *P. nigrilatus*) shows similar environmental characteristics to Colonia Primavera, but with a predominance of savanna-like vegetation. Historically Estancia Carumbé was larger than it is today, and recently it has been split into several farms.

Until recently the appearance of this species in life was unknown. However, a new specimen (MNHNP 12577) was found at Reserva Natural del Tapiracuay (24°40'07.8"S, 56°43'38.0"W), Colonia Friesland, San Pedro Department (Fig. 5), on 22

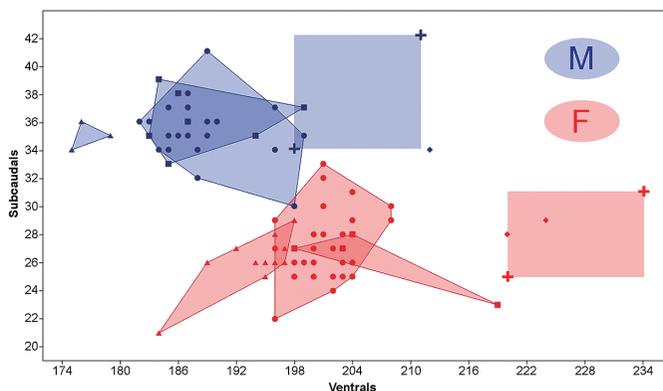


FIG. 3. Dispersion graphic indicating both subcaudal and ventral scalation of *Phalotris concolor* (diamonds), *P. lativittatus* (dots), *P. nasutus* (triangles), and *P. nigrilatus* (squares). For species with three or more specimens, the convex hull is shaded, representing the variation area. The outlier for *P. lativittatus* (see Fig. 2) was excluded. In the case of *P. labiomaculatus* (pluses) only minimum and maximum values were available, which were used as lower and higher vertices representing a shaded rectangle as a hypothetical variation area. Values are presented for females (F) and males (M).



FIG. 4. Live female of *Phalotris nigrilatus* (MNHNP 12577), collected in Reserva Natural del Tapiracuay Colonia Friesland, San Pedro Department, Paraguay on 22 March 2019. Photograph by Anthony Plettenberg Laing.

March 2019 at ca. 20:00 h. This location is 33 km south of Colonia Primavera, extending the range slightly. However, the entire known range of *P. nigrilatus* is included within a 78 km long north to south transect.

Habits and behavior

Like other members of the genus, *P. nigrilatus* is a fossorial snake, and most of the specimens with available data were collected diurnally. Specimens have been collected in

February to May, July, August, and November (see Appendix 1). However caution should be exercised when associating these dates with above ground activity as some specimens were dug out of the ground and a majority of specimens do not have any accompanying temporal data. The only specimens specifically referring to above ground activity are NHM 1960.1.3.6 (April), NHM 1960.1.3.8 (August), and the latest specimen, MNHNP 12577 (March).

No climatic data are available for the NHM specimens, but the weather conditions for the collection of the latest specimen (MNHNP 12577) were relatively cold (less than 20°C), humid, and a little windy. It was found lying on leaf litter on a slight embankment at the edge of a footpath. When manipulated for photography, this specimen coiled and lifted its tail, and waved it gently, while the head was on the ground or hidden under the body.

DISCUSSION

With a significant sample of *P. nigrilatus* specimens now available, it is possible to confirm that it is a valid and morphologically distinguishable species. The morphology of *P.*

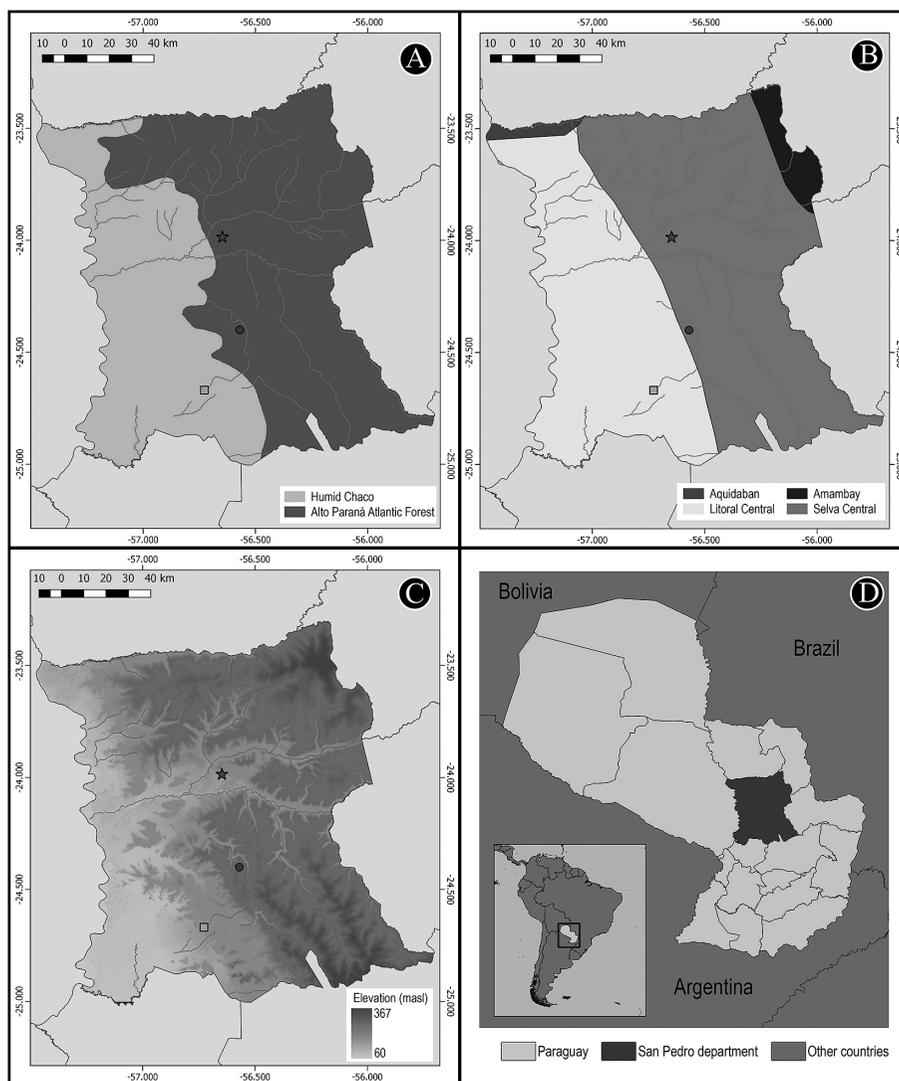


FIG. 5. Known distribution of *Phalotris nigrilatus*, showing the type locality in Estancia Carumbé (star), Colonia Primavera (circle) where most specimens were collected, and the new record (square) at Reserva Natural del Tapiracuy Colonia Friesland. A: Ecoregional map based on Olson et al. (2001). B: National classification of ecoregions (Resolución SEAM N° 614/13). C: Elevation map of the San Pedro Department. D: Location of San Pedro in the geographic context of Paraguay.

nigrilatus is perhaps suggestive of a close phylogenetic relationship with *P. lativittatus* (Fig. 2), however more data are required to confirm this. It is important to note that the contact between the rostral and prefrontal scales, recognized as a diagnostic character by Ferrarezzi (1993) and Cacciali et al. (2007),

shows variation and thus cannot be considered diagnostic. The remaining diagnostic characters are both consistent and reliable.

The observed defensive behavior of coiling whilst hiding the head and lifting and offering the tail is a display often observed in coral snakes (*Micrurus*, Elapidae) and their mimics

(Sazima and Abe, 1991; Fiorillo et al., 2018). There is little published information about defensive behavior in *Phalotris* (Atkinson et al., 2018), although this strategy has also been observed in *P. tricolor* (Marques et al., 2005).

The recent rediscovery of the species, 46 years after the last specimen was collected, confirms that it still survives in an extremely restricted range at the transitional zone of Humid Chaco/Atlantic Forest habitats, within a single Paraguayan department. With the rediscovery of the endangered *P. multipunctatus* at nearby Rancho Laguna Blanca, 36 years after the last specimens of that species were collected (Atkinson et al., 2018), it seems that San Pedro department in Paraguay may be of global importance for the conservation of this poorly known genus.

The northernmost and southernmost localities for *P. nigrilatus* are separated by just 78 km, representing an extremely restricted global range with a specific, restricted and transitional habitat association. The species is currently classified as nationally (and thus also presumably globally) Vulnerable (B1a) according to the IUCN criteria (Motte et al., 2009). This classification pertains to species with an estimated occurrence of less than 20,000 km² and with a severely fragmented range, known to exist at less than 10 localities. Given that the known range of the species is extremely restricted (516 km² according to our estimate), and most of the area in which it is known to occur is an agricultural matrix undergoing constant alteration, we suggest that this designation may be overly optimistic for this Paraguayan endemic species. A designation of Endangered (B1a, biii) better fits the available data, this classification pertaining to species with an estimated occurrence of less than 5000 km² and with a severely fragmented range and known to exist at less than 5 localities, with continuing decline inferred from the extent and quality of the habitat. We suggest that urgent measures are required to conserve this globally restricted Paraguayan endemic from extinction.

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APPENDIX 1

Metric and metric data for *Phalotris nigrilatus*, showing presence (+) or absence (-) of rostral-prefrontal contact (Ro-PFr), white collar (Collar), ventral spotting (Vspotting), and vertebral line (Vert Line). Scapulation codes are: preocular (PrO), postocular (PoO), supralabials (SL), infralabials (IL), temporals (Temp), dorsal scale rows (DSR), ventrals (Vent), and subcaudals (SC). Incomplete tails are indicated with "+". "D" indicates damaged characters. Measurements are provided for snout-vent length (SVL) and tail length (TL). Fragmented specimens were not measured, and are indicated by "-". In the Sex column, we identify males (M), females (F), and juveniles (J). Specimens with doubtful sex determination are indicated by "?". For museum acronyms and scapulation specifications, see text.

Specimen	Ro-PFr	Collar	Vspotting	VertLine	PrO	PoO	SL	IL	Temp	DSR	Vent	SC	SVL	TL	Sex
FML 0709	+	-	+	+	1/1	2/2	6(2-4)/6(2-4)	7(1-4)/7(1-4)	0+1/0+1	17-15-15	203	27	692	59	F
MNHN 00089	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-4)/8(1-4)	0+1/0+1	15-15-15	183	35	809	182	M
MNHN 00091	+	-	+	+	1/1	2/2	6(2-3)/7(3-4)	8(1-4)/8(1-4)	0+1/0+1	15-15-15	185	33	727	171	M
NHM 1955.1.5.99	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	180	39	260	36	?
NHM 1955.1.6.2	+	-	+	+	1/1	2/D	6(2-3)/D	8(1-5)/D	0+1/D	15-15-15	194	35	-	-	M
NHM 1955.1.6.3	-	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	D	36	-	-	J (?)
NHM 1956.1.3.48	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	187	36	474	71	M
NHM 1956.1.16.39	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	184	39	305	39	M
NHM 1956.1.16.40	-	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	186	36	215	29	J (?)
NHM 1958.1.2.30	-	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	186	38	518	77	M
NHM 1960.1.3.5	-	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	189	17+	-	-	M
NHM 1960.1.3.6	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	199	37	388	52	M
NHM 1960.1.3.7	-	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	219	23	360	28	F
NHM 1960.1.3.8	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	15-15-15	204	28	349	31	F
MNHNP 12577	+	-	+	+	1/1	2/2	6(2-3)/6(2-3)	8(1-5)/8(1-5)	0+1/0+1	17-15-15	198	27	361	31	F

APPENDIX 2

Data for examined specimens in the NHM. Information was taken from the original labels.

Specimen	Field No.	Date of collection	Observation
NHM 1955.1.6.2	R 41	29 Feb 1954	Found damaged (maybe by [unreadable]) on patch in woods
NHM 1960.1.3.5	R 160	12 May 1958	Found in hole in earth. Low camp. Daytime
NHM 1960.1.3.6	R 150	15 Apr 1959	Found dead on land road apparently run over by car at night
NHM 1960.1.3.7	R 169	23 May 1959	Dug out of ground. 6 deep
NHM 1960.1.3.8	R 181	21 Aug 1959	On path, daytime, low camp

No data were available for NHM 1955.1.5.99, NHM 1955.1.6.3, NHM 1956.1.3.48, NHM 1956.1.16.39, NHM 1956.1.16.40, and NHM 1958.1.2.30