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COMPLETE ZYGOMATIC ARCHES IN THE LATE QUATERNARY SLOTH *NEOCNUS* FROM LA ALTAGRACIA PROVINCE, DOMINICAN REPUBLIC

Arcos cigomáticos completos en el perezoso *Neocnus* del cuaternario tardío de la provincia La Altagracia, República Dominicana

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ABSTRACT

Specimens of the extinct sloth genus *Neocnus* recovered from northwestern La Altagracia Province, Dominican Republic exhibit a unique zygomatic arch. The arch consists of the jugal anteriorly fused to the maxilla and the zygomatic arch ligament fully ossified between the jugal and the zygomatic process of the temporal bone. Evidence of the novel ossification is seen in adult and juvenile individuals. This occurrence is also unexpected as *Neocnus* individuals are 40 times smaller than the next sloth genus (e.g. *Nothrotheriops*) with a secondarily complete arch. No known species of *Neocnus* exhibits any of these jugal and zygomatic features and thus these specimens may represent a new species.

Keywords: *Neocnus*, paleontology, Hispaniola, morphology, jugal.

RESUMEN

Los especímenes del perezoso extinto del género *Neocnus* recolectados en el noroeste de la provincia La Altagracia, República Dominicana, exhiben un arco cigomático único. El arco tiene el yugal fusionado anterior al maxilar y el ligamento de arco cigomático completamente osificado entre el yugal y el proceso cigomático del hueso temporal. La evidencia de la nueva osificación se ve en individuos adultos y juveniles. Esta ocurrencia también es inesperada, ya que los individuos de *Neocnus* son 40 veces más pequeños que el siguiente género de perezosos (e.g. *Nothrotheriops*) con un arco secundario completo. Ninguna especie conocida de *Neocnus* exhibe ninguna de estas características yugulares y cigomáticas y, por lo tanto, estos especímenes pueden representar una nueva especie.

Palabras clave: *Neocnus*, paleontología, Hispaniola, morfología, yugal.

INTRODUCTION

Members of the Order Pilosa, which includes sloths and anteaters, are united by several shared skeletal features and molecular evidence, including a reduced jugal element and a lack of a bony zygomatic arch (Delsuc & Douzery, 2008; Wetzel, 1985). This characterization is especially pronounced in the anteater lineages but in sloths there exists additional complexity in the morphology.

In sloths the jugal (anterior zygomatic or malar) is typically separated from the zygomatic process of the temporal (posterior zygomatic), and with the jugal posteriorly developed into three processes: ascending (dorsal), middle (posterior), and descending (ventral). The morphologies of these processes differ across sloth taxa and are strongly influenced by feeding mechanics (Naples, 1982; Sicher, 1944). In the extant sloths, the arch is secondarily completed by a zygomatic arch ligament (ZAL; Naples, 1982) attaching between the anterior and posterior portions. A secondary completion by the ligament also occurs in the giant anteater (Naples, 1999). The zygomatic arch ligament in tree sloths also serves as an attachment site for masticatory muscles, and a similar condition is also predicted in the extinct sloths (Naples, 1987, 1989, 1990; Naples & McAfee, 2012, 2014). The strength of the arch connection and the fusion of the mandibular symphysis typically results in a weak maxillary-jugal connection to provide some level of cranial kinesis while chewing. The connection can be strengthened by age-related factors (i.e. fusion) but overall the suture joint remains weak to where absence or loss of the jugal is the standard condition in fossil sloth crania.

Individual size also plays a role in the morphology of sloth jugals and the zygomatic arch. In mid-to large-bodied sloths, those with an estimated body mass greater than 400 kg, the distance between the anterior and posterior arch elements decreases, and in the largest of sloths (e.g. *Eremotherium*, *Lestodon*) the squamosal process rests between and makes contact with the ascending and middle jugal processes. In some older individuals of *Megatherium*, the two arch bones will form a fused suture at the point of contact and thereby create a secondarily true bony arch (Bargo, 2001; De Iuliis, 1996). A completed zygomatic arch has also been noted for *Megalonyx* (McDonald, 1977).

Species assigned to the Caribbean sloth genus *Neocnus* represent one of the smallest sloth genera, of both living and extinct taxa. *Neocnus* species are known from the Late Pleistocene-Middle Holocene of Cuba and Hispaniola, with jugal elements associated to skulls recovered and that are identifiable to the genus level (McAfee, 2011; Silva Taboada et al., 2007). From the published cases, *Neocnus* represents another taxon where the zygomatic arch is incomplete as the jugals are separate from the squamosal processes. The condition of an incomplete arch was initially predicted for the Haitian species of *Neocnus* (MacPhee et al., 2000), in part due to the small contact area for the jugal with the maxilla, as well as the small size of the animals and the known relationship of zygomatic arches within sloths.

Recent expeditions of underwater caves in the La Altagracia Province by collaboration between the Museo Nacional de Historia Natural “Prof. Eugenio de Jesús Marcano” in Santo Domingo and the Dominican Republic Speleological Society (DRSS) have produced many new paleontological finds of Late Pleistocene-Early Holocene age. Of primary interest are several individuals of *Neocnus* that bear evidence of complete, bony zygomatic arches. These new specimens challenge the concept that such an arch is only possible in the largest of sloths, and we herein present the specimens and an overview of their novel morphology.

OBJECTIVES

-We report the finding of numerous specimens of the sloth *Neocnus* from a cave locality in the Dominican Republic who exhibit evidence of a complete zygomatic arch. Description of the unique morphology is given in comparison to that of other sloths, both Caribbean and continental.

MATERIALS AND METHODS

Expeditions to recover specimens from Cueva Macho have been conducted since 2018 and yielded numerous fossils of various taxonomic groups. All the specimens, including the sloths (*Acratocnus*, *Neocnus*, *Parocnus*), are housed at the Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano". The positively identified *Neocnus* specimens were studied in person, but also 3D surface scanned and printed to allow for additional study outside the Museo. The surface scans were made using an Artec Space Spider and the Artec Studio 15 software. 3D prints were produced from the scans with a Stratasys Object Prime 30 printer, using Vero Grey material. Morphological comparisons were made to specimens from housed in other institutions (see below) and to published reports in the literature.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; LACMHC, Los Angeles County Museum – La Brea, Los Angeles, USA; MNHNSD FOS, Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano", División de Geología y Paleontología, Santo Domingo, Dominican Republic; UF, University of Florida Museum of Natural History, Gainesville, USA.

RESULTS

Cueva Macho is an extensive underwater cave system with numerous chambers that have produced fossils of sloths, as well as bats, birds, crocodiles, lizards, monkeys, rodents, and turtles, which also indicates the caves were dry in the past. *Neocnus* remains in general have been sparse from Dominican Republic sites (5 individuals) and those recovered from Cueva Macho (18 individuals) far exceeds the combined total of all other cave sites to date. The *Neocnus* individuals with the completed arches or showing signs of ossification all come from the same chamber in the cave system and consist of various age classes, with a minimum number of individuals equaling 16, based on crania recovered. Another Cueva Macho chamber has produced two more individuals of *Neocnus* (1 adult, 1 juvenile), although only cranial remains currently exist for the adult that lacks jugals.

Skulls from nine individuals of various ages, but mostly adult, exhibit either complete zygomatic arch complexes or evidence that an arch was likely to exist, but the elements are broken or incompletely preserved. Three of the nine skulls are adults with associated mandibles that exhibit the complete zygomatic arch on both or one side (Table I). None of the specimen perfectly preserves the arch and jugal, although the left side of MNHNSD FOS 25.4430 is the most complete (Fig. 1A). Three additional adults present with roots of the jugals attached or the entire jugal (e.g. MNHNSD FOS 25.4279). In total there are six skulls where part of the jugal element is preserved, which allows for reconstruction of the complete and unique jugal morphology for specimens from this locality and enables comparison to jugals of other *Neocnus* specimens. The remaining three skulls belong to young adults or subadults and are included for their contributions to the posterior zygomatic arch element (Fig. 2). For the remaining seven individuals of the total 16, presence of jugal or arch elements were not discernable either due to preservation issues related either to damage or very young age.

Table I. Age class estimate for Cueva Macho specimens of *Neocnus* exhibiting zygomatic arch structures

MNHNSD FOS Specimen	Age Class*	Notes
25.4276	3 – full adult	Both arches complete; associated with mandible 25.4299
25.4277	1 – immature	Both zygomatic arch ligaments ossified to squamosal processes
25.4278	3 – full adult	Jugals broken but roots fused to maxilla
25.4279	3 – full adult	Jugals damaged but fused to maxilla
25.4284	3 – full adult	Jugals broken but roots fused to maxilla
25.4286	1 – immature	Left zygomatic arch ligament ossified to squamosal process
25.4287	2 – young adult	Both zygomatic arch ligaments ossified to squamosal processes; associated with mandible 25.4296
25.4289	3 – full adult	Left arch complete; associated with mandible 25.4305
25.4430	3 – full adult	Both arches complete; associated with mandible 25.4431

*adapted from Anderson and Handley (2001)

Jugal Morphology. Aside from having a bony connection to the temporal bone to form a complete zygomatic arch, the jugals of the *Neocnus* specimens from Cueva Macho are quite different from those Haiti (McAfee, 2011; McAfee & Rimoli, 2019) and *N. gliriformis* in Cuba (Silva Taboada et al., 2007). The general form is the same with a distinct and slender ascending process and an inferior mass from which it is difficult to differentiate the middle and inferior processes. As the middle process in the Cueva Macho specimens is even less distinct than that of Haitian *Neocnus* and *N. gliriformis*, the overall jugal appears more akin to that of *Acratocnus* where the middle jugal process is fully absent. Another similarity to *Acratocnus* is the fusion of the malar root anteriorly to the maxilla, a feature seen in only a few ground sloths (e.g. *Megalonyx*) and very old individuals amongst the extant sloths (pers. obs.).

The fusion of jugal to maxilla also appears to be an adult character as the immature specimens do not retain the jugal element and exhibit the articular fossa just inferior to the lacrimal where the malar root would have articulated (Fig. 2B, D-F). Nevertheless, adults of equal age in the other *Neocnus* species do not demonstrate fusion of the jugal to the maxilla. The suture between the jugal and maxilla is also obliterated in all of the jugal bearing Cueva Macho specimens, except for MNHNSD FOS 25.4279 where the suture is somewhat visible on both sides (Fig. 1G, H). Additionally, the malar root is wider and thicker than in *Neocnus* from Haiti and *N. gliriformis*. Notable exceptions to the Haitian *Neocnus* jugal morphology are two specimens, UF 76807 from Trouing Marassa and UF 131990 from Trouing Jeremie 3, that possess broken jugals where the malar root is wide and fused to the maxilla like the specimens from Cueva Macho.

The ascending jugal processes are typically uniform and parallel in their width for Haitian *Neocnus* and *N. gliriformis*, with some variability in the morphology of the superiormost tip (McAfee, 2011; McAfee & Rimoli, 2019; Silva Taboada et al., 2007), but the same does not hold for the Cueva Macho specimens. Two specimens (MNHNSD FOS 25.4276, 25.4279) exhibit the middle portion of the ascending process to be widened with a posteriorly directed bulge that is part of the ascending process and not from the ossified ligament, as exhibited by the suture lines of MNHNSD FOS 25.4276 (Fig. 1E, F). A similar morphology is exhibited by an unattached jugal of *Megalonyx jeffersoni* (LACMHC 123453). The ascending jugal of MNHNSD FOS 25.4279 also bears an anterior bulge that is not present on any of the other specimens (Fig. 1H); it has the appearance of a healed bone break, but that status cannot be confirmed. The ascending process is not fully straight in the Cueva Macho specimens and bends posteriorly just prior to joining or right at the ossified zygomatic arch ligament. The dorsal half of the ascending process of MNHNSD FOS 25.4279 does remain straight as in the other *Neocnus* species, but that may be related to the potential healed break.

The descending jugal process is only completely retained in MNHNSD FOS 25.4430 and is indistinguishable from the assumed middle process in the region where they would meet (Fig. 1A). The lack of a distinct middle process is common amongst Caribbean sloth jugals, with exceptions being a jugal attributed to *Acratocnus odontrigonus* from Puerto Rico (see Anthony, 1926: AMNH 17711) and an associated skull and jugal of *Parocnus torrei* from Cuba (Fischer, 1971). The inferior jugal process is more blade like than other *Neocnus* species and does not have the two distinct prongs noted by McAfee (2011) for Haitian *Neocnus* specimens. Although there are some small tubercles on the posterior surface of the descending process and inferiormost tip that would correlate with the various slips of the masseter musculature. The overall morphology of the descending jugal process is more akin to that of *Acratocnus ye*, including the presentation of the small tubercles.

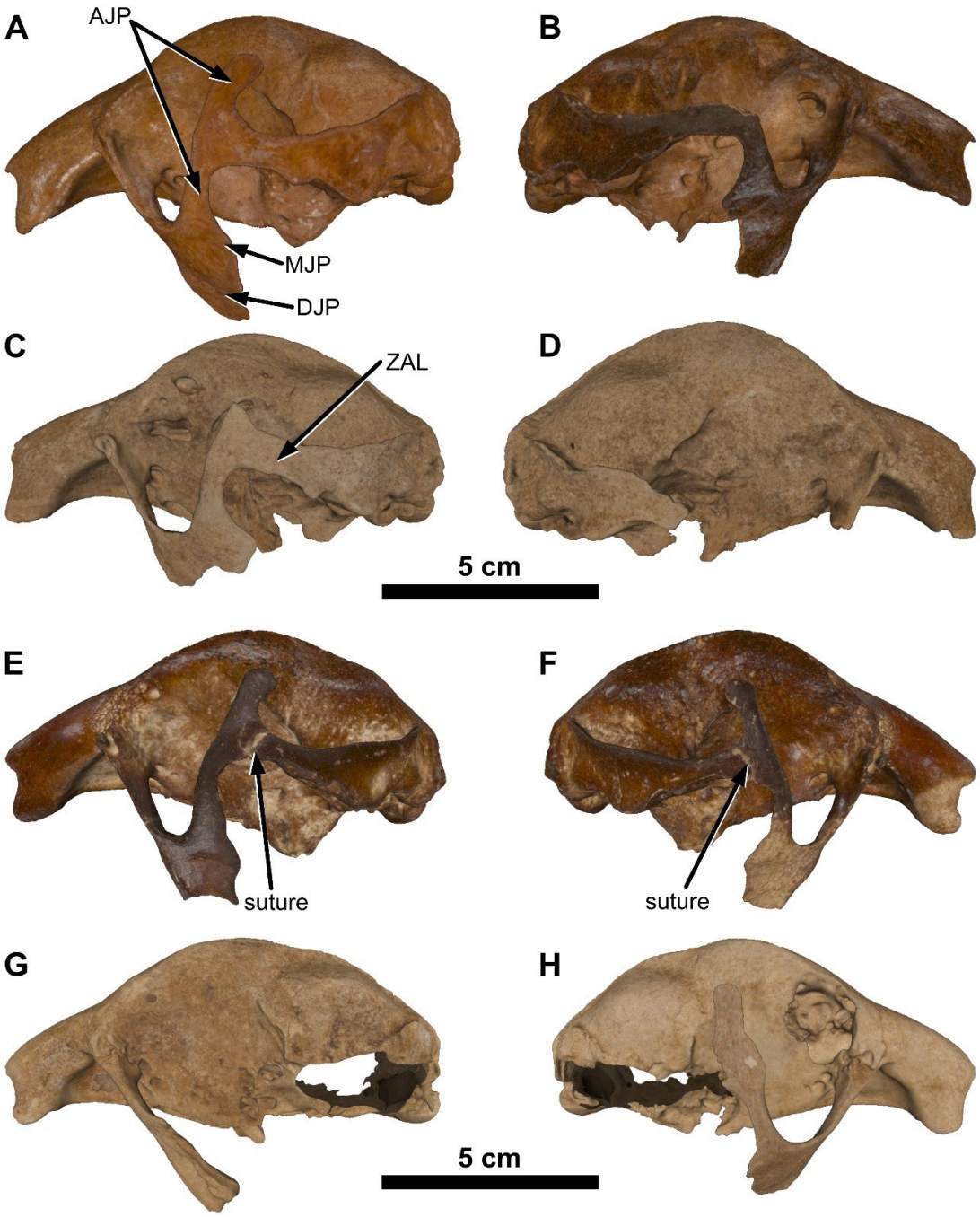

Figure 1. Lateral views of adult *Neocnus* crania from Cueva Macho exhibiting zygomatic arch complexes. All specimen numbers preceded by MNHNSD FOS. **A**, **B)** Left and right view of 25.4430; **C**, **D)** left and right views of 25.4289; **E**, **F)** left and right views of 25.4276; **G**, **H)** left and right views of 25.4279. **AJP**, ascending jugal process; **DJP**, descending jugal process; **MJP**, middle jugal process; **ZAL**, zygomatic arch ligament. Scale bar is equal to 5 cm.

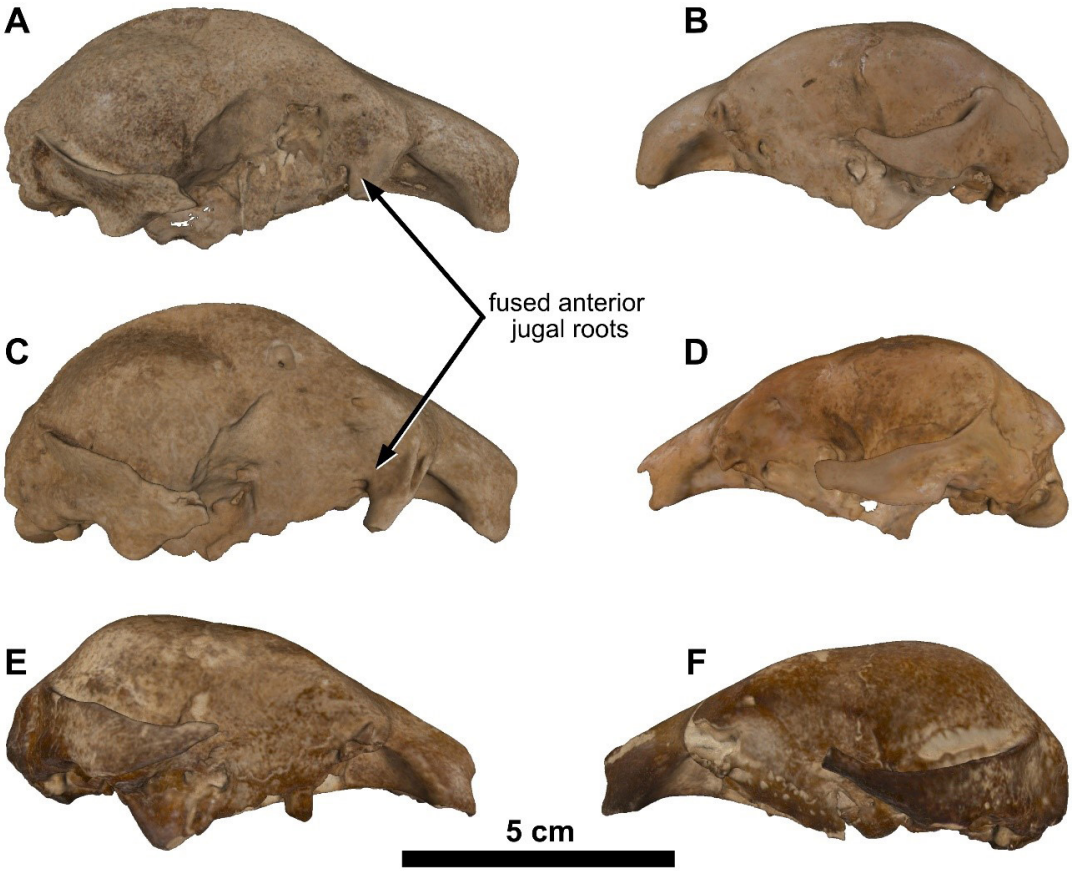

Figure 2. Lateral views of subadult and juvenile *Neocnus* crania from Cueva Macho exhibiting fused jugal roots or ossified zygomatic arch ligament remnants. All specimen numbers preceded by MNHNSD FOS. **A)** Right view of 25.4278; **B)** left view of 25.4386; **C)** right view of 25.4284; **D)** left view of 25.4277; **E-F)** right and left views of 25.4287. Scale bars equal to 5 cm.

Zygomatic Arch Complex. Unlike most of the larger bodied sloth taxa, the zygomatic process of the temporal bone is not aligned with the notch between the ascending and middle jugal processes but is superiorly positioned such that the ossified extension contacts the middle portion of the ascending jugal process (Fig. 1). This condition was also suggested for *N. gliriformis* by Silva Taboada et al. (2007), whereas McAfee (2011) reconstructed that of *Neocnus* from Haiti to align more with the middle jugal process. The later assumed the zygomatic arch ligament was more likely to connect there from the temporal process and that the position would better align the superior part of the ascending jugal process with the postorbital process, which may be erroneous as proximity of the two is not necessary to complete the orbital ring with the postorbital ligament (Naples, 1982). A similar orientation is also seen in some specimens of the Miocene aged sloth *Hapalops*, which is on the low end of sloth body masses (~40 kg sensu Croft, 2016) but not nearly as small as *Neocnus* (6–11 kg, based on formulas for femur length from Farina et al., 1998). In those sloths without a contacting or complete arch, the anterior end of the zygomatic process of the temporal tapers to a blunt point.

The ossification and completion of the zygomatic arch was not confined just to the adults. While the jugals are unfused and lacking for those younger age classes (i.e. 1 and 2, Table I), there is evidence for ossification of the posterior arch. On various specimens, extensions from

the zygomatic processes of the temporals are present (Fig. 2B, E-F). The extensions are not as dorsoventally broad as the zygomatic processes and are anterodorsally inclined in the same manner as the posterior arch portions in the adult specimens. Given the visible suture lines in the adult MNHNSD FOS 25.4276, it is possible the zygomatic processes in the younger specimens were still in the process of making contact to form the suture and the extensions in the subadult MNHNSD FOS 25.4287 do extent anterior to near the point where they would have contacted the jugals (Fig. 2E, F).

CONCLUSIONS

The presence of a complete zygomatic arch complex in multiple specimens of *Neocnus* from Cueva Macho is a unique discovery amongst sloths. With an estimated body mass of ~10 kg, these sloths are 40 times smaller than the next closest sloth taxon (*Nothrotheriops shastensis*) to possess an arch where the posterior and anterior components consistently come into contact. The morphology exhibited is also different from that of most *Neocnus* specimens recovered from other regions of Hispaniola (e.g. Haiti).

Neocnus remains are currently rare in the Dominican Republic, making it difficult to currently determine if there is something unique about the preservation at Cueva Macho versus other localities. However, the lack of ossified ligamentous structures on any of the other skeletal elements suggests that it is not special preservation resulting in the mineralization of the zygomatic arch ligament but that the ligament was already ossified during the life of the sloths. The ossification also does not seem to be fully dependent on age of the individual given the evidence presented by younger age classed specimens, though age does play a role with the anterior attachment of the jugal.

Although there is some jugal morphology variation amongst the individuals from Cueva Macho, it is far less when compared to the various species of *Neocnus* from elsewhere in Hispaniola and Cuba. A locality near to Cueva Macho (Oleg's Bat Cave) has produced a jugal attributed to *N. cf dousman* that is morphologically more akin to *Neocnus* from Haiti than to the Cueva Macho individuals. The overall implications of the differential jugal morphologies suggest that the Cueva Macho specimens may represent a new species, but further investigation of the post-cranial elements is required.

Additional work also needs to be applied to the chewing mechanics of *Neocnus*. A revision is likely necessary for Haitian *Neocnus* given the potential misalignment of the jugal mentioned earlier, but the fused zygomatic arch for the Cueva Macho individuals would likely require changes to the masticatory patterns given the loss of cranial kinesis that sloths without fused arches are able to employ. Comparison against *Acratocnus* and *Megalonyx* is also of interest as those genera have anteriorly fused jugals and similar morphologies, which may further indicate that the jugal form is correlated to their functional ability or restraints.

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