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Yucatán carnivorans shed light on the Great American Biotic Interchange

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The Great American Biotic Interchange is considered to be a punctuated process, primarily occurring during four major pulses that began approximately 2.5 Ma. Central America and southeastern Mexico have a poor fossil record of this dynamic faunal history due to tropical climates. Exploration of submerged caves in the Yucatán, particularly the natural trap Hoyo Negro, is exposing a rich and remarkably well-preserved late Pleistocene fauna. Radiometric dates on megafauna range from approximately 38 400–12 850 cal BP, and extinct species include the ursid *Arctotherium wingei* and canid *Protocyon troglodytes*. Both genera were previously thought to be indigenous to and confined to South America and appear to represent an instance of large placental mammals, descended from North American progenitors, migrating back north across the Panama Isthmus. This discovery expands the distribution of these carnivorans greater than 2000 km outside South America. Their presence along with a diverse sloth assemblage suggests a more complex history of these organisms in Middle America. We suggest that landscape and ecological changes caused by latest Pleistocene glaciation supported an interchange pulse that included *A. wingei*, *P. troglodytes* and *Homo sapiens*.

1. Introduction

North and South America were geographically separated for most of the Cenozoic, resulting in distinct vertebrate communities. Faunal interchange between the continents began in the late Cenozoic, and most dispersals occurred after the Panama Isthmus developed. This biogeographic phenomenon, known as the Great American Biotic Interchange (GABI), went in both directions [1–6] and enabled the expansion of placental mammals to South America, including the focus of this report, ursids and canids. Recently, researchers hypothesized the isthmus developed approximately 10 Myr earlier than previously thought, 13–15 Ma [7], well before the first large-scale faunal interchange around 2.5 Ma [5], suggesting a lag between continental connection and extensive migration [8].

2

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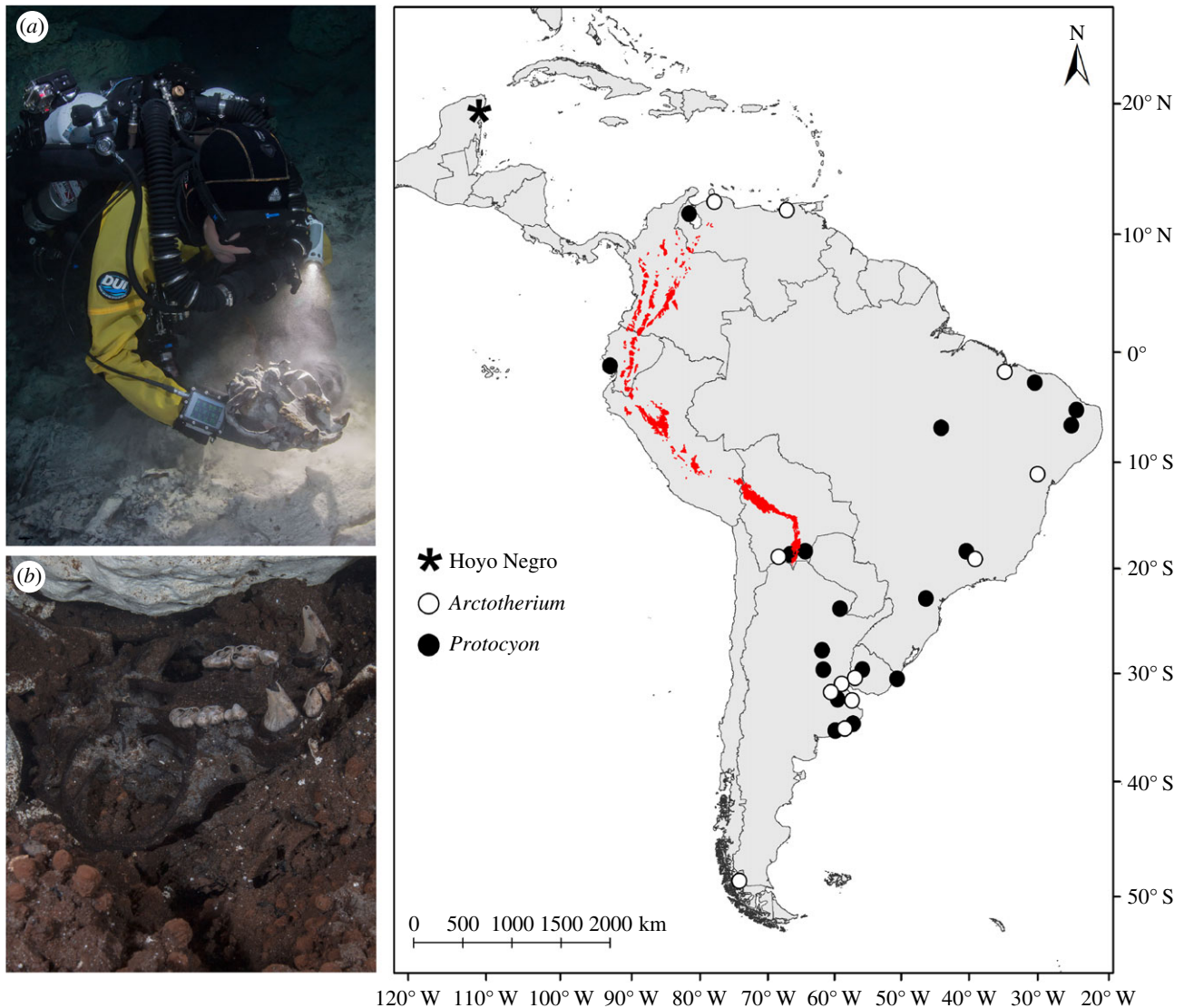
Figure 1. Specimen recovery in Hoyo Negro and map showing locations. (*a*) DP 5864 *Arctotherium wingei* cranium being recovered. (*b*) DP 5865 *A. wingei* cranium after overlying plant material was brushed away. *Tremarctos ornatus* distribution (in red) [22]. Photos by Roberto Chávez-Arce.

The concept of an earlier isthmus and interchange lag has been challenged, citing insufficient evidence for a well-developed isthmus prior to 3 Ma [9–11].

Fossil evidence of GABI is well represented in the United States and parts of Mexico but sparse in southeastern Mexico and Central America, hereafter referred to as Middle America, where tropical conditions are unfavourable for preservation [4,12–15]. Thus, a significant geographical and temporal gap exists in understanding the fauna in the interchange region itself. New discoveries from submerged caves in the Yucatán are changing this, bringing to light an underworld of exquisitely preserved fossils from the late Pleistocene, when sea level and the water table were significantly lower during glaciations. Publications on these underwater discoveries have focused on early human skeletons [16,17], new mammalian genera (two ground sloths and a peccary) [18–20] and a new species interpreted to be a jaguar-like cat [21].

Hoyo Negro (HN), a submerged pit inside the Sac Actun cave system, is the focus of this paper. The site is located on the eastern Yucatán Peninsula, Quintana Roo, Mexico (figure 1). Hoyo Negro represents a collapse karst feature accessible from three submerged horizontal passages with floors that are approximately 12 m below sea level (mbsl). Flooding history of the cave has been reconstructed, indicating the base of

HN was flooded by 9850 cal BP, and upper passages leading to HN were submerged by 8100 cal BP [23]. Hoyo Negro drops from approximately 12 mbsl at the rim to at least 55 mbsl at the floor. The HN pit is bell shaped, approximately 62 m wide at the base, and served as a natural trap for animals moving through the cave in the late Pleistocene. Mammals discovered on the surface of the HN floor include multiple ground sloth species (including the newly named *Nohochichak xibalbah-kah*) [18], tapirs, sabertooth cats, cougars, gomphotheres, bears, canids and a relatively complete human skeleton that dates to terminal Pleistocene [16]. In addition, bones and trackways of extinct fauna are known from the upper passages.

Here we report two extinct carnivorans from HN, identified earlier as the bear *Tremarctos* and coyote *Canis latrans* [16]. Representative specimens have now been collected and we revise identifications to the ursid *Arctotherium wingei* and canid *Protocyon troglodytes*. Both genera and species were previously unknown outside South America.

2. Material and methods

Highly trained technical divers performed on-site photography, filming and collecting based on direction from researchers.

3

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Collecting focused on diagnostic specimens, particularly well-preserved skulls. Our emphasis here is systematic identifications; more-detailed skeletal descriptions are in progress. Identifications were made based on current literature. The abbreviation 'DP' is for Departamento de Prehistoria, the older name for the collection at the Instituto Nacional de Antropología e Historia (INAH), México. See supplementary material for details on photography, collecting, preparation and radiometric dating, as well as another figure of the crania (electronic supplementary material, figure S1).

3. Results and discussion

(a) Age and chronology

An accelerator mass spectrometer (AMS) radiocarbon analysis on extracted protein from *Arctotherium* dentine (from DP 5865) resulted in an age of 11 298 ± 138 rcy BP (D-AMS 1 176 911). When calibrated using Calib 7.1 [24] with intCal13 calibration dataset [25], the two-sigma age range is 12 850–13 430 cal BP. This date represents the only protein-based radiocarbon date from the site and first absolute date for *Arctotherium wingei*. While no dates on *Protocyon* have been successful, systematic dating attempts on this taxon and others from HN continue. Currently, the inclusive age range of HN large mammals is approximately 38 400–12 850 cal BP, with the oldest date on gomphothere [16].

(b) Arctotherium

With multiple individuals identified, the bear is the most abundant large mammal from HN. Individuals range in age from subadult to adult and represent the South American short-faced bear, *Arctotherium* (figure 1 and figure 2). The following combined characters diagnose the genus: notch absent on dorsal margin of the foramen magnum, the distance between C1 and P4 less than mesio-distal length of P4, P1–P3 compressed and arranged in a triangle, M1 metastyle reduced or absent [26]. Portions of two individuals are reported here, DP-5864 and DP-5865.

Arctotherium is part of Tremarctinae, an endemic American subfamily. Besides *Arctotherium*, this group includes *Plionarctos*, *Tremarctos* and *Arctodus*. *Plionarctos* is recorded from the late Miocene to early Pliocene and is only known from the United States [27]. *Tremarctos* appeared in the Pliocene of North America and now occurs only in South America [22,28]. *Arctodus* appeared in the late Pliocene, and by the late Pleistocene it occurred across the United States, much of Canada and portions of Mexico [29,30]. *Arctodus* and *Tremarctos* went extinct in North America near the end of the Pleistocene [31].

The oldest record of Ursidae in South America is early Pleistocene, with the appearance of *Arctotherium* at 0.98–1.76 Ma [32]. Ursids are considered to be part of GABI 2, a dispersal pulse that occurred around 1.8 Ma [5]. Five species of *Arctotherium* are recognized, *A. angustidens* (early–middle Pleistocene), *A. vetustum* (middle Pleistocene) and three middle–late Pleistocene species, *A. bonariense*, *A. tarijense* and *A. wingei* [26,32]. *Arctotherium angustidens* was particularly large [33], but over time this genus is represented by smaller forms, culminating in *A. wingei*, the smallest [32,34].

Disagreements have occurred over the evolutionary relationship of *Arctotherium*, *Tremarctos* and *Arctodus*, with earlier morphological interpretations placing *Arctotherium* and *Arctodus* as sister taxa [26]. Recent genetic analyses indicate

Arctotherium is more closely related to *Tremarctos*, and therefore *Arctotherium* and *Arctodus* share morphologies that may relate to their large size and/or dietary behaviour [35]. Based on our understanding of the group, *Arctotherium* arose from *Tremarctos*, or a common ancestor that excluded *Arctodus*.

The HN bear is identified as *A. wingei*, the only *Arctotherium* species known from northern South America, with occurrences in Bolivia, Brazil and Venezuela (figure 1) [32,36,37]. While partial *A. wingei* skulls and isolated teeth are reported from South America, the material is poorly represented. The remains from HN represent the best-preserved and most-extensive record of *Arctotherium* from any locality and they exhibit a high degree of intraspecific morphological variation. These specimens are assigned to *A. wingei* using a suite of characters: separate openings for foramen rotundum and alisphenoid canal on cranium, tympanic bulla inflated, greatest mesio-distal length of M1 slightly larger than greatest labio-lingual length, shape of M1 lingual border convex, p1–p3 arranged in a triangle, m2 entoconid with two apices [26].

In addition to HN fossils, other submerged caves of the Yucatán are producing photographic records of *Arctotherium*, and one specimen is known from a dry cave in Belize [38]. Further, a fragmentary distal humerus from another submerged Yucatán cave was recently described as a new species of cat, *Panthera balamoides* [21]. However, published images in that paper are morphologically similar to *Arctotherium*, and we feel this identification should be reassessed.

Arctotherium is the only known bear from the Yucatán Peninsula. In terms of diet, *A. wingei* has been interpreted as a herbivorous omnivore like *Tremarctos ornatus* [39,40]. Although *T. ornatus* occurs in the Andean region of western South America today, it is not known from that continent until the early Holocene [41–43]. While *Tremarctos* is known from North America until the Pleistocene/Holocene transition [44], there is only one fossil occurrence in Middle America [45]. Identification of this specimen is tenuous because the skeleton is in a Belizean cave. Based on the current record, we propose that competition with *Arctotherium* in Middle America may have limited the southern distribution of *Tremarctos* until the former became extinct in the latest Pleistocene or early Holocene.

(c) Protocyon

Canid material from HN represents the South American genus *Protocyon* (DP 5867, figure 2). The following combined characters distinguish the genus: robust skull, wide zygomatic arches and palate, short rostrum, paraoccipital process directed posteriorly, P4 large with small protocone, M1–M2 with reduced or absent hypocone, M2 reduced, lower premolars with acute and weak principal cusps, m1 without metaconid and entoconid [46–53].

Protocyon is part of Caninae, a large canid subfamily that originated in North America and dispersed into the Old World and South America. The subfamily occurs in South America by 2.5 Ma [43,52] and was part of GABI 1 [5]. By the early Pleistocene, South American Caninae were diverse, with multiple *Lycalopex* species, and the emergence of two genera thought to be endemic, *Theriodictis* and *Protocyon* [43,47,49,50,52,54]. *Protocyon* is considered to be closely related to *Theriodictis* [52,55,56], which was questionably reported from the late Pliocene or early Pleistocene of Florida as *Theriodictis? floridanus* [57]. No solid records of *Theriodictis* are known outside South America. Three *Protocyon* species
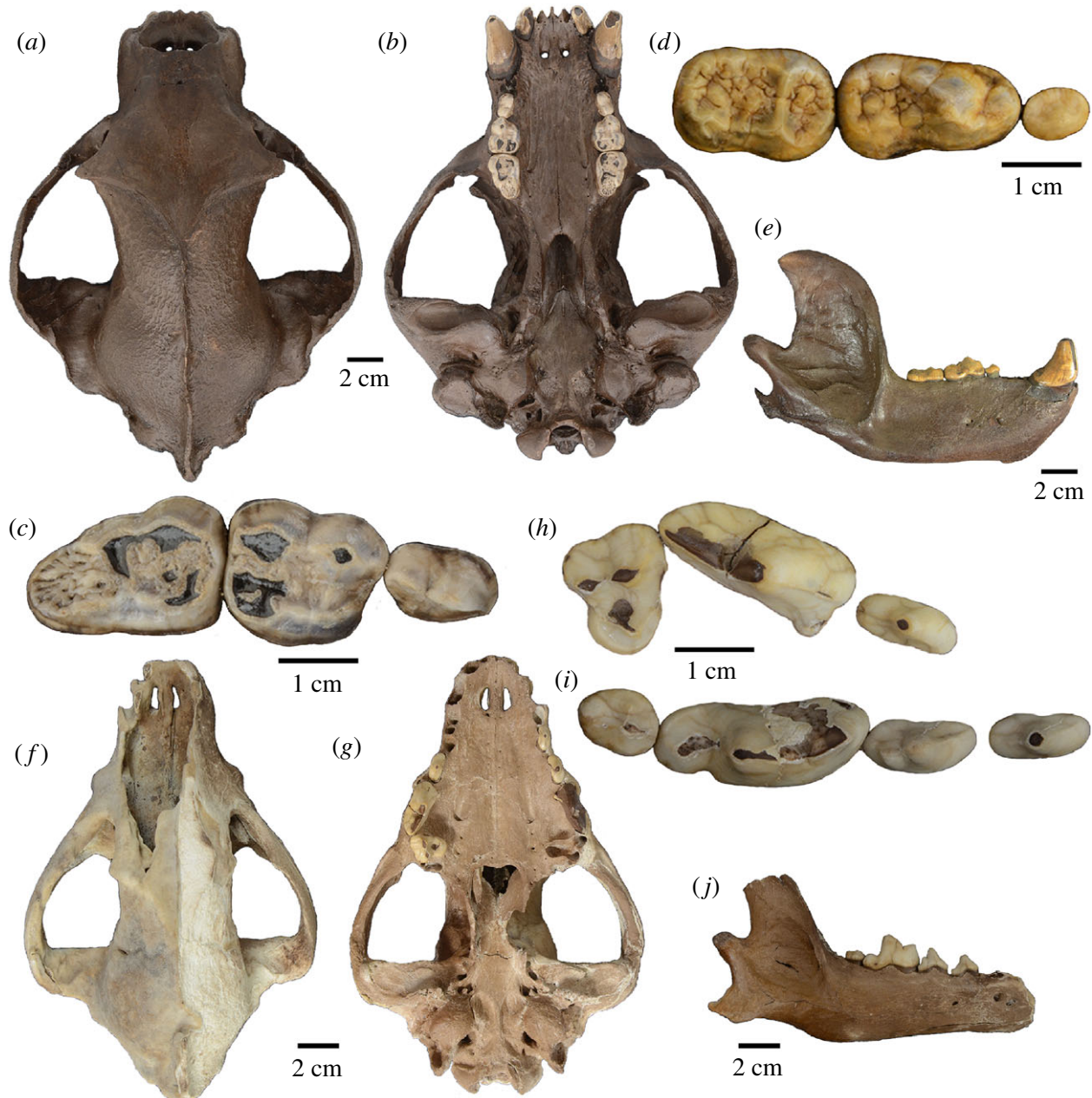
Figure 2. *Arctotherium wingei* and *Protocyon troglodytes* from Hoyo Negro. DP 5865 *A. wingei*, (*a*) dorsal and (*b*) ventral view of the cranium, and (*c*) occlusal view of right P4–M2. DP 5864 *A. wingei*, (*d*) occlusal view of right p4–m2 and (*e*) lateral view of right dentary; m3 broken and missing. DP 5867 *P. troglodytes* (*f*) dorsal and (*g*) ventral view of cranium, (*h*) occlusal view of right P3–M2, (*i*) occlusal view of right p3–m2 and (*j*) lateral view of the right dentary. (Online version in colour.)

are recognized, *P. scagliarum* (early–middle Pleistocene), *P. troglodytes* (middle?–late Pleistocene) and *P. orcesi* (late Pleistocene) [49,53,54].

The HN *Protocyon* is assigned to *P. troglodytes*, known from Argentina, Brazil, Bolivia, Ecuador, Uruguay and Venezuela [53] (figure 1). Northern records of *P. troglodytes* led researchers to speculate the possibility of their occurrence in Central America as well [51]. Other *Protocyon* species have only been recovered from their type localities, *P. scagliarum* in Argentina and *P. orcesi* from Ecuador. *Protocyon troglodytes* is distinguished from *P. scagliarum* based on the absence of an anterior cusplet on p4, and *P. orcesi* based on the presence of m3 [47,50,52]. Intraspecific variation may account for the difference between *P. troglodytes* and *P. orcesi* [49,50,53].

As part of the late Pleistocene Yucatán fauna, *Protocyon* would have been a hypercarnivorous large canid [53]. *Canis*

dirus, *C. lupus* and *C. latrans* are reported from Loltun Cave in northeast Yucatán, but *Protocyon* was not recovered [58,59]. Thus, the degree of geographical, temporal and ecological overlap of *Protocyon* and these canids is unclear.

(d) Interchange, biogeography and evolution

This report presents the first published records of *Arctotherium* and *Protocyon* outside South America, expanding their distributions over 2000 km out of South America. *Arctotherium* and *Protocyon* are considered to be endemic South American taxa that developed on that continent after their ursid and canid ancestors crossed the Panama Isthmus from Middle America [32,43,60]. While this scenario is supported by the occurrence of these carnivorans in South America, and lack of their fossil remains in Middle America, the record is biased by a relative

lack of fossil sites from the latter region. Thus, we cannot discount the possibility that *Arctotherium* or *Protocyon* occurred in Middle America at various times during the late Cenozoic. Further, it is also possible that Middle America played a role in the evolution of these genera, either through ongoing gene flow with South American populations or origination in Middle America.

These carnivorans, recent discoveries of new ground sloth genera from the Yucatán, and controversy about age estimates on the development of the Panama Isthmus 'bridge', all indicate we still have a lot to learn about GABI. Interpretations of the fossil record suggest four main pulses of interchange, GABI 1–4, at around 2.5 Ma, 1.8 Ma, 0.8 Ma and 0.125 Ma, respectively [5,6]. These pulses overlap with glacial episodes, sea-level lowering, widening of the isthmus and more-open habitats that would have created opportunities for dispersal of large mammals adapted to open habitats [5,13].

If the existing fossil record is an accurate representation of *Arctotherium* and *Protocyon* through time, and these genera developed strictly in South America, the Yucatán material represents a reversed dispersal of these families across the isthmus. Further, if this migration occurred during the latest Pleistocene, in line with existing radiometric dates, one possibility is they moved north during or since the last full glacial, between approximately 35 000 and 12 000 years ago. Because

this glacial pulse would have caused similar landscape changes and migration opportunities as GABI 1–4, this additional interchange could be referred to as GABI 5. Unlike earlier interchanges, 'GABI 5' involved humans and culminated with the mass extinction of most American megafauna, including *Arctotherium* and *Protocyon*.

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