

ORIGINAL ARTICLE

Taxonomical and distributional considerations for the *Artibeus* species (Chiroptera: Phyllostomidae) from the Tres Marias Islands, Mexico

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DOI: <https://doi.org/10.14709/BarbJ.16.1.2023.06>

Keywords: *Artibeus intermedius koopmani*, *Artibeus lituratus palmarum*, bats, colonization, cytochrome B, Pleistocene, wing morphometrics.

received: May, 25th 2023

accepted: December, 31st 2023

ABSTRACT

The controversial taxonomy of the *Artibeus lituratus-intermedius* complex and the lack of genetic studies in the *Artibeus* specimens reported in the Tres Marias Islands (TMI) have caused the taxonomic identity of these specimens to remain ambiguous. During an expedition carried out in May 2022, we captured four specimens of *Artibeus* in the Maria Madre and Maria Cleophas islands. The specimens were assigned by external morphological characters and traditional morphometrics, and were compared with the data available in the taxonomic descriptions of *A. lituratus* and *A. intermedius*. Additionally, we performed a phylogenetic analysis of cytochrome b sequences. Our genetic data suggest that the *Artibeus* populations are a lineage of the *Artibeus lituratus-intermedius* complex. In addition, the morphometric data suggest the presence of two morphotypes that, according to the literature, would correspond to *A. lituratus palmarum* and *A. intermedius koopmani*. With these results, we propose that both species of *Artibeus* are present and therefore the bat community of TMI is composed of ten species. However, future more detailed genetic studies are needed to elucidate the true taxonomic diversity of the archipelago.

INTRODUCTION

The archipelago of Tres Marias Islands (TMI) is a group of insular ecosystems located on the Pacific Ocean, 132 km from San Blas, Nayarit, in west Mexico. The archipelago is composed of four islands: San Juanito Island, Maria Madre Island, Maria Magdalena Island, and Maria Cleofas Island (Fig. 1). Geological evidence indicates that the archipelago separated from the mainland during the Eocene-Oligocene and eventually attained its present location in the Miocene epoch (23 to 5.3 my) (CONANP 2022). The archipelago has different kinds of vegetation: deciduous forest, medium deciduous forest, mangroves in Maria Magdalena, and secondary vegetation and temporal crops in Maria Madre (CONANP 2022). The TMI hosts a diverse range of vertebrate species and subspecies, including some that are endemic to the archipelago and are categorized as endangered according to both local laws and the IUCN Red List. (i.e., Yellow-headed Parrot, *Amazona oratrix* subsp. *tresmariae*) (SEMARNAT 2019).

The bat community of the TMI is composed of nine recognized species (Table 1). Most of them are considered

insectivorous and only two species, *Glossophaga mutica* and *Artibeus intermedius*, are considered nectarivores and frugivorous species, respectively. The certainty of the taxonomic identity of *Artibeus* populations from the archipelago has been controversial. The first mention of the genus *Artibeus* from the TMI was provided by Van Gelder (1959) as a part of the description of *Bauerus dubiaquercus*. However, Van Gelder (1959) did not refer to the specific identity of these bats and just mentioned “*Artibeus*” as those bats captured along with *Bauerus dubiaquercus*. Afterwards, Bogan (1978) mentioned *Artibeus lituratus* during his research work in which he described *Myotis findleyi* from TMI, pointing out the wide distribution of *A. lituratus* since it was collected on the three main islands of the archipelago. Subsequently, Davis (1984) analyzed the mainland populations of *A. lituratus* and reassigned the species status of *Artibeus intermedius*, previously described by Allen (1897). In this context, extensive work on the *Artibeus* of the three main islands of the TMI was carried out by Wilson (1991), and based on morphological differences, he described *A. intermedius koopmani* as a novel subspecies endemic from the TMI.

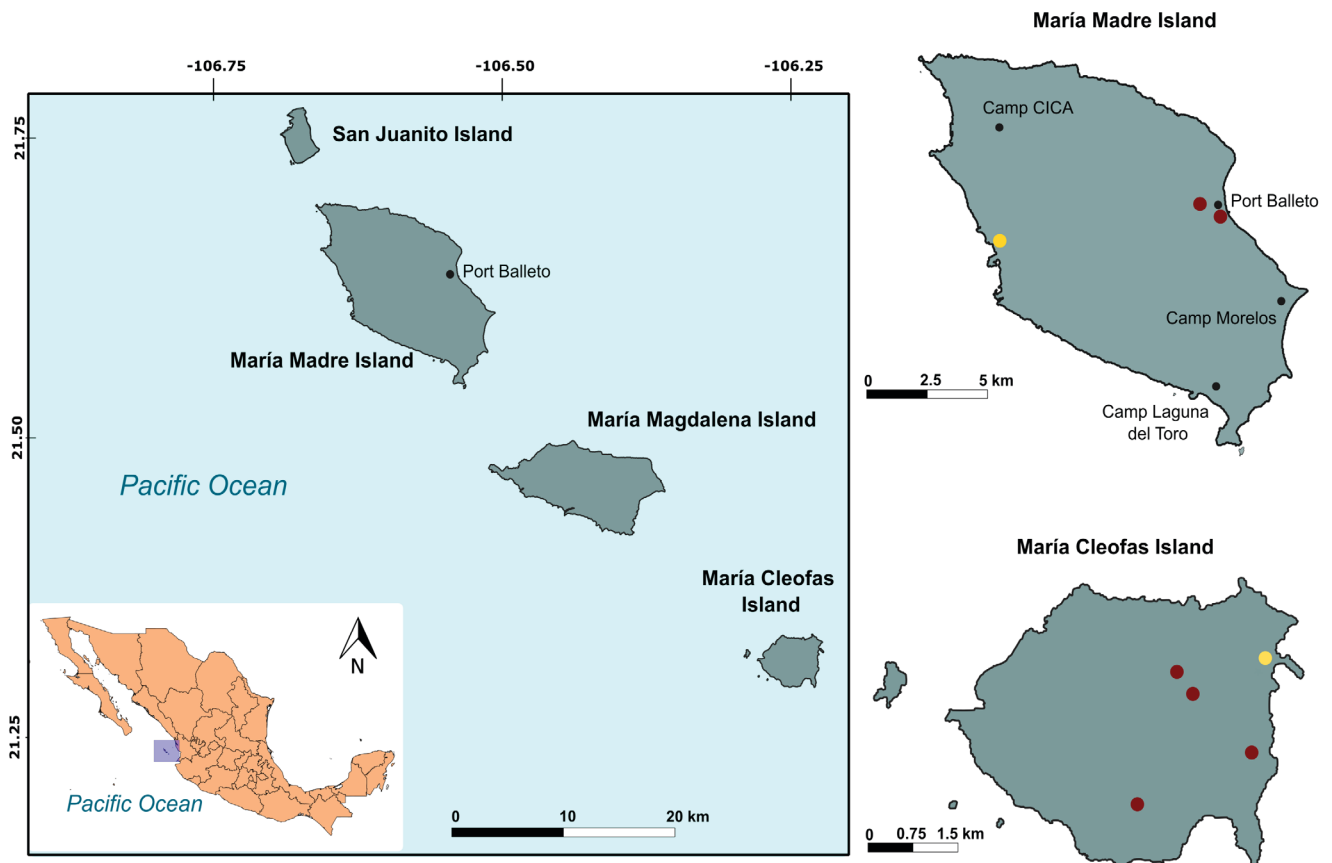


Fig. 1 - Map of the archipelago of the Tres Marias Islands with historical records of *Artibeus* specimens on María Madre and Cleofas Islands (right). Red dots indicate historical records and yellow dots correspond to records reported in this study. Human settlements are indicated by black dots.

Table 1 - Bat species reported in the archipelago Tres Marias Islands.

Species	Reference
<i>Artibeus intermedius koopmani</i>	Wilson, 1991
<i>Macrotus waterhousii bulleri</i>	Nelson, 1899
<i>Glossophaga mutica mutica</i>	Nelson, 1899
<i>Myotis findleyi</i>	Bogan, 1978
<i>Lasiurus frantzi teliotis</i>	Nelson, 1899
<i>Rhogeessa parvula parvula</i>	Nelson, 1899
<i>Bauerus dubiaquercus dubiaquercus</i>	Van Gelder, (1959)
<i>Natalus mexicanus</i>	Wilson, 1991
<i>Balantiopteryx plicata plicata</i>	Nelson, 1899
<i>Artibeus lituratus palmarum</i> *	This study

In the following years, the taxonomic status of *A. intermedius* fell into disuse mainly due to the overlapping diagnostic characteristics between this species and *A. lituratus*, and it was formally positioned as a subspecies of *A. lituratus* (e.g., Jones & Carter 1976). Therefore, the *Artibeus* species from TMI was recognized as *A. lituratus koopmani* (Larsen et al. 2010). Recently, with the rise of different molecular markers, several authors were able to corroborate the taxonomic validity of *A. intermedius* differently from *A. lituratus*, but without a molecular review of the *Artibeus*

specimens from the TMI to date (Clare et al. 2011, Larsen et al. 2013).

The *Artibeus lituratus* complex is currently composed of two recognized species (Simmons & Cirranello 2022): *A. intermedius* distributed from western Mexico to Central America (Gardner 2008) with the subspecies *Artibeus intermedius koopmani* endemic from de TMI, and *A. lituratus* with two subspecies, *Artibeus lituratus lituratus* which distribution ranging from the south of the Orinoco basin to the north of Argentina, and *Artibeus lituratus palmarum* which occurs from the north of the Orinoco basin, to Mexico including Lesser Antilles (Gardner 2008). Both species occur in sympatry in Mexico and Central America, and they can be easily recognized by the large morpo exhibited in *A. l. palmarum* and the small morpo present in *A. intermedius* (Davis 1984, Marchán-Rivadeneira et al. 2012).

Another issue pending for *Artibeus* populations from TMI is their phylogenetic affinity. The evolution of the genus *Artibeus* includes colonization events from South America to Central America and, in the case of species present in the Antilles, island colonization by multiple ways and species (Larsen et al. 2013). In this sense, phylogenetic analysis using molecular data could clarify if *Artibeus* populations from TMI are grouped within the *Artibeus lituratus* complex or another *Artibeus* species, considering *Artibeus jamaicensis* and *Artibeus hirsutus* are other *Artibeus* species with distribution in the west coast of mainland Mexico (Medellín et al. 2008).

In this work, we report the presence of two morphos of *Artibeus* in the TMI, and based on external morphological traits and genetic distance we propose the presence of two *Artibeus* species in the archipelago. We also brought a first approximation of the phylogenetic affinity of *Artibeus* populations with respect to the whole genus using mitochondrial data. Finally, we updated the taxonomic list of bats from TMI.

MATERIAL AND METHODS

In May 2022, we carried out a field trip to the Tres Marias Islands to collect tissues from all bat species of the archipelago. For six nights, we placed mist nets of 6, 9, and 12 meters along bodies of water on the three main islands. We handled animals following the guideline approved by The American Society of Mammalogists (Sikes et al. 2016). Collecting permits were provided by the Ministry of Environment and Natural Resources of Mexico (Permits SGPA/DGVS/07992/20 – SGPA/DGVS/10357/21 – SGPA/DGVS/08926/21). During this period, we captured four *Artibeus* individuals and other bats from different species. All bats, including *Artibeus* specimens, were identified through the use of specialized field guides (Medellín et al. 2008, Reid 2009). Six external measurements were collected from individuals captured using a digital caliper with an accuracy of ± 0.1 mm (Mitutoyo CD-6'' Mitutoyo U.S.A): 1. Total length (TL), 2. Foot length (FL), 3. Ear length (EL), 4. Tibial length (TiL), 5. Tragus length (TrL), and 6. Forearm (FA). Body weight was measured using a Pesola spring-scale ($100\text{ g} \pm 0.5$). Additionally, we measured metacarpals of 2nd, 3rd, 4th, and 5th digits, and the first phalanx of 3rd, 4th and 5th digits from right-wing photographs. We compared the average and standard deviation (mean \pm standard deviation) of external measurements of sampled *Artibeus* with respect to morphological information available for *Artibeus* species from the mainland.

Because we identified two morphos within *Artibeus* specimens (see Results section), we decided to carry out molecular analyses from these morphos. A tissue sample from both wings was taken from each collected specimen, these were placed in an Eppendorf tube with 96% alcohol and stored in a nitrogen liquid container for later transport to the laboratory. Genomic DNA from tissue samples was extracted according to the universal and rapid salt-extraction protocol (Aljanabi & Martínez 1997). The quality of DNA was quantified by electrophoresis on 1% agarose gels and assessed with molecular weight standards. We used two universal primers (MVZ05 and H15915 – Irwin et al. 1991, Smith & Patton 1999) to amplify a fragment of ≈ 1140 base pairs (bp) of the mitochondrial cytochrome-b (Cyt-b). We performed a PCR reaction in a total volume of 25 μL with 0.2 μL Taq DNA polymerase (InvitrogenTM), 2.5 μL 10x RXN buffer, 2.5 μL of dNTP's, 2 μL of each primer 10 mM, 1.5 μL of 50 mM MgCl₂, 5 μL of DNA, and 9.3 μL of bidistilled water. We followed the standard protocol for the PCR reaction: 3-min denaturation at 94°C, followed by 30 cycles of 94°C for 30 s, 46°C for 30 s, and 72°C for 30 s; with a final 6-min elongation step at 72°C. All positive products were confirmed using an agarose gel (1.5%) stained with SYBRGreen (InvitrogenTM); we included a 100 bp ladder and

negative control in our electrophoresis. All PCR reactions were sent to the MACROGEN® facility in Korea for their posterior sequencing. The resulting Cyt-b sequences were aligned and edited using SEQUENCHER® and subsequently aligned in the MEGA X software (Kumar et al. 2018) using the ClustalW algorithm.

In order to corroborate the species identity that we previously assigned to individuals; we calculated the K2P genetic distance (Kimura 1980) with respect to *Artibeus* species in the MEGA X software (Kumar et al. 2018). We used 73 sequences of the whole Cyt-b gen (~ 1140 bp) of 13 *Artibeus* species (SM Table 1). We also used sequences of *Dermanura cinerea* as outgroup. All sequences were obtained from GenBank. For *A. intermedius* we only used sequences from the same individuals used by Larsen et al. (2013). A phylogenetic analysis was performed using Bayesian inference with the BEAST v2.6.4 program (Bouckaert et al. 2019). The nucleotide substitution models used were HYK+G4 empirical base frequency for Cyt-b. The values of the parameters of the new models were calculated automatically by BEAST v2.6.4 program. The Markov Monte Carlo Chain (MCMC) algorithm was used as a simulation method for generating the posterior probability distribution (Drummond et al. 2002). Four independent chains were carried out with 100,000,000 iterations with samples every 1000 and a burn-in of 10%. The convergence of the parameters was checked visually, as well as the effective sample size (ESS > 200) in the Tracer 1.7.2 program (Rambaut et al. 2018). The .log files and the trees of each chain were concatenated in the LogCombiner v2.6.4 program with a burn-in of 10%. The clade tree with the highest credibility was estimated in the TreeAnnotator v2.6.4 program and visualized with the FigTree v1.4.4 program.

RESULTS

A total of four individuals of *Artibeus* were sampled in TMI, one was captured on Cleophas Island (21° 19' 24.09'' N; 106° 13' 42.06'' W) and the rest on Maria Madre Island (21° 37' 26.22'' N; 106° 37' 45.2'' W). We identified two morphotypes clearly differentiated by size and external appearance. One individual per morph was collected and deposited in the mammal collection of the "Alfonso L. Herrera" Museum of Zoology, Faculty of Sciences, UNAM. The small morphotype had dark brownish dorsal fur with no prominent white facial stripes, including the cheek stripe. This morphotype resembled *Artibeus intermedius koopmani* (MZFC-M16777) and corresponded to three specimens with similar size and appearance captured in Maria Madre and Cleophas Islands (Fig. 2A). Moreover, the large morpho was represented by one individual captured on Maria Madre Island. This individual showed external morphological measurements that resembled *A. l. palmarum* (MZFC-M16778) such as paled dorsal fur and prominent white facial stripes, including the cheek stripe (Fig. 2B). This individual was also greater in size than the rest in most of the external measurements, except for the total length and ear length (Table 2). Similarly, wing size was greater in this individual than in the rest of the sampled individuals. Body weight was similar between individuals, but smaller specimens were slightly heavier than the large one (Table 2).

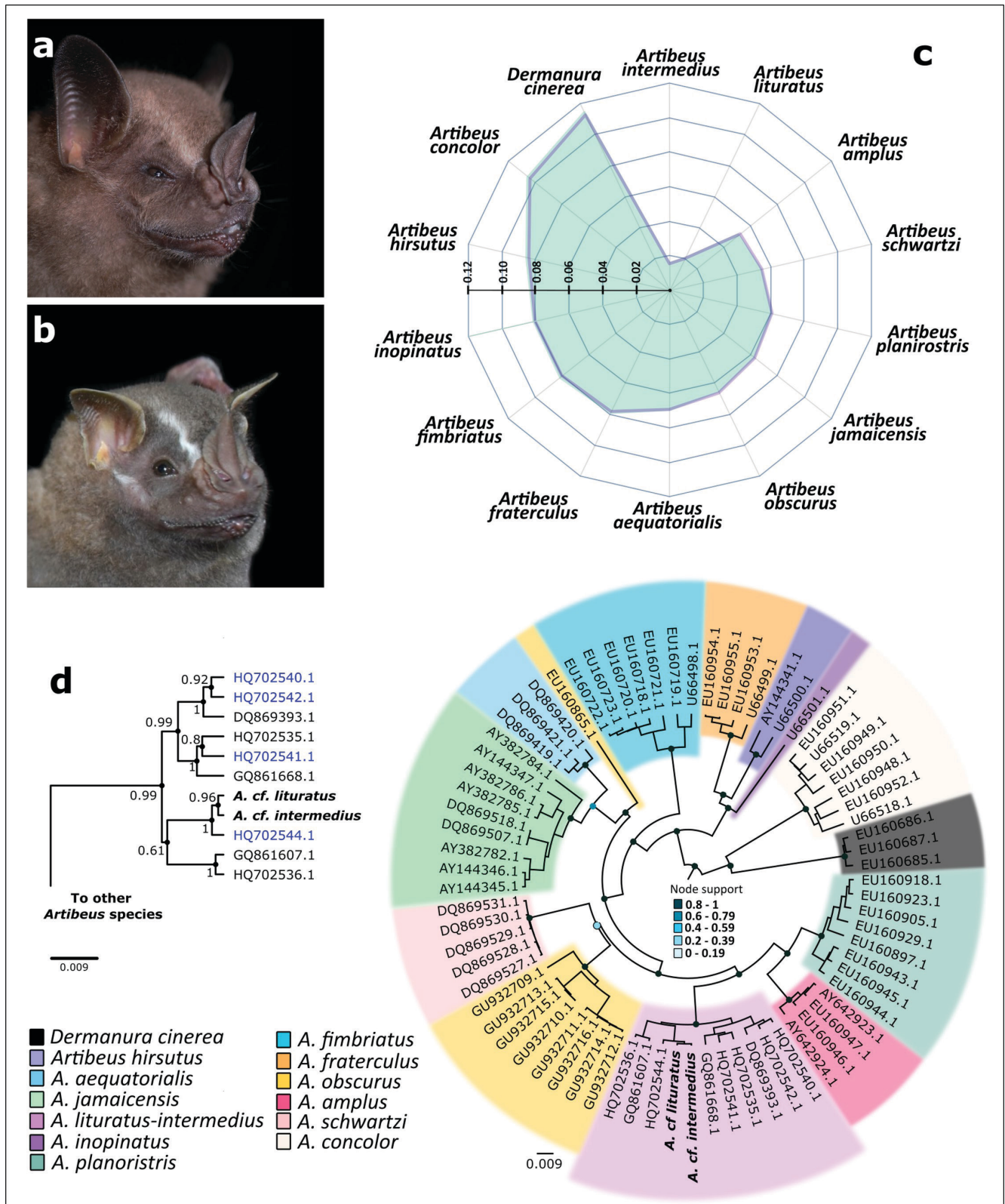


Fig. 2 - Morphological external evidence of differences among collected individuals of *A. cf. lituratus* (A) and *A. cf. intermedius* (B). K2P genetic distance among *A. cf. lituratus* (blue line) and *A. cf. intermedius* (green area) from Tres Marias Islands and the rest of the genus *Artibeus* (C). The radial Bayesian phylogenetic tree is based on 1140 bp of Cytochrome B from thirteen species of the *Artibeus* genus according to Simmons & Cirranello (2022) and *Dermanura cinerea* as an outgroup (D). Specimens from Tres Marias Islands are shown in bold. The colour of nodes indicates Bayesian posterior probabilities. Details of the clade *Artibeus lituratus-intermedius* are shown in the upper-left part of panel D. Individuals of *A. intermedius* s. str. (Larsen et al. 2013) are shown in blue letters. Tip's names in both trees indicated the Genbank accession numbers of sequences used in the analysis.

Table 2 - External measurements taken from *Artibeus* specimens sampled. Average \pm standard deviation measurements to *A. cf. intermedius* are presented. External measurements of *A. lituratus palmarum* and *A. intermedius* are taken from Allen & Chapman (1897) and Allen (1897) respectively. TL: Total length, FL: Foot length, EL: Ear length, Ti: Tibial length, TrL: Tragus length, FA: Forearm, BW: Body weight. Distance measurements and weight are given in mm and g, respectively.

Measurement	<i>A. cf. lituratus</i> (large morpho) n=1	<i>A. cf. intermedius</i> (small morpho) n=3	<i>A. lituratus palmarum</i>	<i>A. intermedius</i>
TL	76.9	78.39 \pm 0.64	91	-
FL	16.42	12.05 \pm 1.8	14	-
EL	13.98	18.09 \pm 2.5	13.5	17
TiL	26.39	22.78 \pm 1.48	26	22
TrL	5.59	5.03 \pm 1.04	-	-
FA	67.9	62.09 \pm 0.8	68	65
BW	43.5	44 \pm 3	-	-
2nd digit: metacarpal	45.01	45.03 \pm 0.42	-	-
3rd digit: metacarpal	59.97	56.57 \pm 0.7	64	57
4th digit: metacarpal	58.58	56.17 \pm 1.99	-	-
5th digit: metacarpal	61.82	59.55 \pm 1.81	-	-
3rd digit: phalanx I	22.92	21.75 \pm 0.28	23	20
4th digit: phalanx I	18.71	17.19 \pm 0.57	-	-
5th digit: phalanx I	14.58	13.22 \pm 0.91	-	-
3rd digit: phalanx II	32.65	31.46 \pm 0.64	38	31

On the other hand, the K2P genetic distance (K2P-distance) calculated within *Artibeus* species suggested both morphotypes of *Artibeus* (#Genbank: OP271664 for small morpho and OP271665 for large morpho) from TMI were more similar to *A. intermedius* and *A. lituratus* (K2P-distance < 2%), than other *Artibeus* species, including *A. jamaicensis* (K2P-distance \sim 6.2 %) and *A. hirsutus* (K2P-distance \sim 8.4 %) which distributions also occur in the west coast of the mainland of Mexico (Fig. 2C). For phylogenetic reconstruction, the matrix of sequences was composed of 73 sequences with 1095 bp of length after excluding alignment gaps, 335 polymorphic sites, and 274 parsimony informative sites. The topology of phylogenetic tree also recovered a closer relationship among *Artibeus* specimens from TMI and *Artibeus lituratus-intermedius* from the mainland. However, despite our phylogenetic reconstruction recovered a topology where most clades correspond to recognized *Artibeus* species, the relationship between the species *A. intermedius* and *A. lituratus* was not resolved (Fig. 2D), and it was not possible to assign a specific identity to both *Artibeus* morphotypes present in TMI using only cytochrome b data.

DISCUSSION

The work presented here is the first report of two morphs that resemble two different species of *Artibeus* present in the Tres Mariás Islands (TMI), as well as the first attempt to clarify the phylogenetic affinity of the populations of *Artibeus* from TMI. Our work happened in a context where morphological, ecological and molecular data support the split of *A. intermedius* and *A. lituratus* (Larsen et al. 2013).

However, although both species have been widely studied and there is a large amount of morphometric data available, we did not compare our data with those available in the literature, because during the time when *A. intermedius* was synonymized under the name of *A. lituratus*, morphological data of both species were usually reported as belonging to a single species. For this reason, we present a comparison of our data with respect to original descriptions of *A. intermedius* (Allen 1897) and *A. lituratus palmarum* (Allen & Chapman 1897). According to these works, both morphotypes of *Artibeus* sampled in TMI correspond in more than one measurement to *A. intermedius* and *A. l. palmarum* (Table 2). With these results, we propose that the large morphotype captured in Maria Madre Island corresponds to *A. lituratus palmarum* and the small morphotype captured in Maria Madre and Cleophas Islands corresponds to *A. intermedius*. Our proposal finds partial support in Davis' work (1984), where the author differentiated between *A. intermedius* and *A. lituratus* in Middle America, primarily based on forearm length and other external morphological traits. According to Davis, the small morphotype of *Artibeus* (*A. intermedius*) exhibits a forearm length ranging from 62.2 to 68.2 mm, while the large morphotype (*A. lituratus*) has a forearm length between 66.5 to 75 mm. The forearm length of the *A. cf. lituratus* individual captured on Maria Madre Island falls within the extreme upper values of *A. intermedius* or the lower values of *A. lituratus*. Nevertheless, the presence of external features such as paled dorsal fur and prominent white facial stripes, including the cheek stripe, suggests a closer resemblance to *A. lituratus* rather than *A. intermedius*.

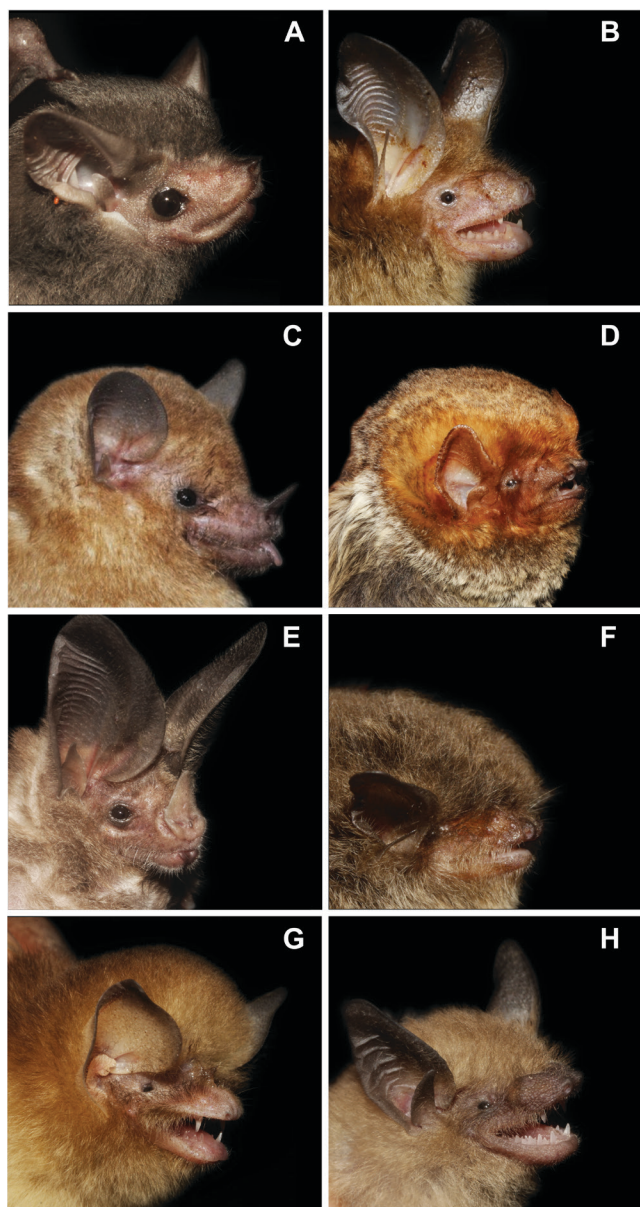


Fig. 3 - Non-*Artibeus* bat species from Tres Marias Islands. (A) *Balantiopteryx plicata plicata*; (B) *Bauerus dubiaquercus dubiaquercus*; (C) *Glossophaga mutica mutica*; (D) *Lasiurus frantzi telioti*; (E) *Macrotus waterhousii bulleri*; (F) *Myotis findleyi*; (G) *Natalus mexicanus* and (H) *Rhogeessa parvula parvula*. Photos by Juan Cruzado.

On the other hand, we did not compare our data with the original description of *A. intermedius koopmani* since when Wilson (1991) described it, the mainland populations of *A. lituratus* in Mexico had been assigned to *A. intermedius*. Hence, it is likely that the sample in Wilson's study contains a combination of individuals from both species. The noteworthy variation in morphological measurements observed in both *A. intermedius koopmani* from TMI and the "*A. intermedius*" from the mainland implies that Wilson's study might encompass specimens from both species in both sample sets. In this sense, we highlight the need to review the morphological variation between *A. intermedius* populations from mainland and TMI to clarify the validity of *A. intermedius koopmani*.

With respect to molecular data, the genetic distance also corroborated that both morphotypes present in TMI

are genetically more similar to the *A. lituratus* and *A. intermedius*. In fact, this high similitude brings into question the hypothesis that *Artibeus* populations from TMI have been isolated a long time ago, during the rise of the TMI in the Miocene. Ortiz-Ramirez et al. (2018) proposed that passerine birds colonized TMI in recent times when the marine regression occurred, during the late Pleistocene and early Holocene, occasioning the islands to be closer (~25km) to the mainland than they currently are (~112 km). This actual distance is less than the maximum flight distance reported to *A. lituratus* (113 km, Arnone et al. 2016), therefore a similar colonization process probably occurred with the ancestral populations from TMI. This recent colonization has caused that at the genetic level, these species are not much different from continental populations, and the morphological differences observed may be caused by adaptation to the environmental conditions of islands.

On the other hand, the phylogenetic tree topology produced a taxonomical reconstruction with high resolution, shaping clades composed of recognized *Artibeus* species (Simmons & Cirranello 2022). Moreover, the *Cyt-b* sequences indicated that *Artibeus* population from TMI belongs to *A. lituratus-intermedius* clade and discarded the chance that correspond to isolated lineages of *A. jamaicensis* or *A. hirsutus*, the other two mainland *Artibeus* species that inhabit west Mexico (Medellín et al. 2008). However, despite molecular data defining the phylogenetic affinity of the *Artibeus* from TMI, the molecular dataset failed to elucidate at molecular level if the *Artibeus* specimens are grouped to *A. intermedius* or *A. lituratus s. str.* This is because our phylogeny failed to resolve the *A. lituratus-intermedius* complex such as previous mitochondrial-based phylogenies have failed too (Hooper et al. 2008, Larsen et al. 2013). Further studies may implement nuclear data (such as AFLP markers; Larsen et al. 2013) or genomic tools to enhance our understanding of the specific affinity of *Artibeus* from the TMI.

Bats from the Tres Marias Islands: opportunities of research and conservation

The bats of the TMI have been studied from different scientific and naturalist expeditions, which have resulted in a taxonomic list for the group of nine species (Jiménez-Guzman & Niño-Ramírez 1994, López-Wilchis et al. 2020). However, according to the molecular and morphometric data of our records, we propose that the bat assemblage in the Tres Marias Islands is composed of ten species (Table 1, Fig. 2A and 3). But we highlight the potential of change in the number and composition of species in the future, especially when the age of the archipelago combined with the geographical distance between the islands and the mainland becomes the native populations into candidates to be novel species. With the exception of *Bauerus dubiaquercus* (Van Gelder, 1959) and *Myotis findleyi* (Bogan, 1978), which were described from individuals captured in the archipelago, the taxonomy and systematic of the rest of the bat species is scarcely understood, offering a field of opportunities for bat research.

On the other hand, bats inhabiting island ecosystems are one of the most susceptible to extinction (Frick et al. 2020).

In this context, Wilson (1991) mentioned that *Artibeus* from TMI were common in the three main islands and even collected several individuals for his work. However, in six days of fieldwork we only captured four individuals. This low number of captures could also be related to a limited availability of food resources during the dry season, when we carried out the fieldwork, however, we also saw many threats to bats in TMI. During our expedition, we saw exotic fauna such as domestic cats (*Felis silvestris catus*) and black rats (*Rattus rattus*), both species have been reported as predators of bats (Fellers 2000, Ancillotto et al. 2013). We also observed several goats (*Capra aegagrus hircus*), cows (*Bos taurus*), and horses (*Equus ferus caballus*) that could be affecting the plant community, including food resources for *Artibeus*. The Tres Marias Islands represent a threatened hotspot of biodiversity that is poorly known. We expect that our work will enhance our understanding of the fauna of TMI and contribute to conservation efforts.

ACKNOWLEDGMENTS

We appreciate the support provided by all CONANP (Comisión Nacional de Áreas Naturales Protegidas) staff assigned to the Marias Islands, with special emphasis to H. Montesinos by his efficient field assistance. This work was funded by Consejo Nacional de Ciencia y Tecnología (CONACyT - Proyectos Fronteras de la Ciencia 2019) under Grant Agreement # 15307. MCMG received financial support from Centro de Investigaciones Tropicales, Universidad Veracruzana. ILLC received a supportive MSc scholarship provided by Consejo Nacional de Ciencia y Tecnología (CONACyT – CVU 1018336. SMOG received a postdoctoral fellowship by Consejo Nacional de Ciencia y Tecnología (CONACyT). We greatly appreciate the field work provided by Martín Aguilar, Edgar Gutiérrez, Mercedes Morelos, and Carlos Barrera.

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