



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA
BIOLOGÍA EVOLUTIVA

**EVOLUCIÓN DE LA PISCIVORÍA EN EL GÉNERO *Myotis* (CHIROPTERA:
VESPERTILIONIDAE)**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

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MÉXICO, D.F. MARZO, 2016.



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Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 9 de marzo de 2015, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **OSPINA GARCÉS SANDRA MILENA** con número de cuenta **508462391** con la tesis titulada: "Evolución de la piscivoría en el género *Myotis* (Chiroptera: Vespertilionidae)", realizada bajo la dirección del **DR. LUIS GERARDO HERRERA MONTALVO**:

Presidente: DR. JOSÉ JAIME ZÚNIGA VEGA
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Suplente: DR. RODRIGO ANTONIO MEDELLIN LEGORRETA

Sin otro particular, me es grato enviarle un cordial saludo.

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Cd. Universitaria, D.F. a 9 de febrero de 2016.

M. del Coro Arizmendi

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA



c.c.p. Expediente del (la) interesado (a).

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RESUMEN

El género *Myotis* es el más diverso taxonómicamente dentro de los murciélagos, además de ser cosmopolita y presentar diversas estrategias de forrajeo donde predominan las especies insectívoras aunque algunas pocas especies son piscívoras. Se estudiaron las conformaciones geométricas de cinco módulos craneales en 22 especies del género *Myotis* para examinar la relación entre la morfología externa del cráneo y la mandíbula, y la dieta. En particular, se usó la morfometría geométrica para analizar la variación morfológica del cráneo y la mandíbula en relación al cambio de una dieta insectívora a una dieta piscívora. Se compararon las cinco formas entre los grupos de dietas (piscívoros, piscívoros facultativos e insectívoros) mediante análisis multivariados y se evaluó la correlación de las cinco configuraciones con una variable funcional asociada al desempeño de los músculos masticatorios (factor de estiramiento).

Las configuraciones se usaron además para reconstruir las formas ancestrales y detectar el desplazamiento de los puntos anatómicos de referencia en las conformaciones de los descendientes para hacer inferencias sobre cambios asociados a la dieta. Las comparaciones se contrastaron con las especies insectívora y piscívora del género *Noctilio*, y el grupo hermano *Kerivoula palillosa* como grupos externos. Bajo un enfoque comparativo, las coordenadas de los dos módulos mandibulares se optimizaron sobre la filogenia obtenida a partir del análisis de una matriz combinada de configuraciones geométricas y fragmentos de los genes Cyt B y RAG 2 en el programa TNT. Bajo un enfoque filogenético, las coordenadas se analizaron mediante parsimonia para la construcción de la filogenia morfométrica. Las optimizaciones de las formas en ambos enfoques se calcularon implementando parsimonia cuadrada en el módulo Rethenor del programa Mesquite y parsimonia espacial con nuevos algoritmos para la reconstrucción de las formas ancestrales en el programa TNT.

Los análisis multivariados revelaron cambios en la región de los procesos masticatorios donde se insertan los músculos en las especies piscívoras respecto de las insectívoras. Se encontró una correlación alta y significativa entre la variación en la forma

de los procesos mandibulares y el factor de estiramiento del músculo masetero. Estos resultados sugieren diferencias en la morfología craneal y la función entre especies insectívoras y piscívoras. Dichos cambios podrán estar asociados a una mayor capacidad de apertura mandibular en las especies piscívoras. Estos cambios fueron optimizados en la filogenia como caracteres homoplásicos; tanto la forma de los procesos mandibulares como la dieta piscívora se originaron al menos dos veces en la historia del género *Myotis*. Así mismo, se encontraron tendencias de cambio diferentes en la forma de los procesos mandibulares entre las cinco especies piscívoras facultativas y la especie piscívora *M. vivesi*.

ABSTRACT

The genus *Myotis* is the most speciose in bats, presenting a cosmopolitan distribution and different foraging strategies where insectivorous species predominate and a few species have a piscivorous diet. I analyzed the geometric conformations of five cranial modules in 22 *Myotis* species to reconstruct the ancestral shapes and to make inferences about the morphological evolution of the structure. I analyzed the morphological variation of the cranium and the mandible in relation to dietary changes from insectivory to piscivory using geometric morphometrics. I compared five shapes among dietary groups (insectivores, facultative piscivores and piscivores) using multivariate analysis and I evaluated the correlation of five configurations with a functional variable related to the performance of masticatory muscles (stretching factors).

The reconstructions of shapes at nodes allowed detect displacement of landmarks in configurations of the descendants and make inferences about changes associated with diet. The comparisons were contrasted with the insectivorous and piscivorous species of genus *Noctilio*, and the sister group *Kerivoula palillosa* as outgroups. Under a comparative approach, the coordinates of the mandibular two modules were optimized on the phylogeny obtained from the analysis of a combination matrix of geometric configurations and DNA (Cyt B and RAG 2) in the program TNT. Under a phylogenetic approach, the coordinates were analyzed using parsimony for the optimization of the ancestral configurations. The optimizations of shapes in both approaches were calculated by implementing squared parsimony in module Rethenor of the Mesquite program, and spatial parsimony with new algorithms for the reconstruction of the ancestral forms in TNT.

The multivariate analyses revealed changes in the process of the masticatory muscle attachment in piscivorous species respect to insectivorous species. The mandibular process area and the stretching factor of the masseter muscle were highly correlated. These results suggest the existence of differences in cranial morphology and function between insectivorous and piscivorous species. Morphological and functional changes detected in piscivorous *Myotis* bats probably allow a wider gape capacity than other dietary groups.

These changes were optimized in the phylogeny as homoplasy; mandibular process shape and piscivorous diet evolved at least twice in the history of the genus *Myotis*. We also found different trends of mandibular morphology among the five facultatively piscivorous *Myotis* species and the piscivorous *M. vivesi*.

Evolución de la Piscivoría en el género *Myotis* (Chiroptera: Vespertilionidae)

Introducción

La relación recurrente entre un fenotipo y un ambiente particular en diferentes linajes ha sido comúnmente calificada como evidencia de adaptación, evidencia que es soportada por comparaciones en el desempeño de los fenotipos en tareas ecológicas específicas (Harvey y Pagel, 1991; Martins, 2000; Losos y Miles, 2002). La idea de probar el carácter adaptativo en un contexto evolutivo, donde una combinación particular de fenotipo y ambiente debe surgir independientemente durante la evolución de un linaje, ha llevado al desarrollo de métodos comparativos para poner a prueba estas hipótesis (Monteiro, 2013). Varios de estos estudios han evaluado la relación entre la forma del aparato masticatorio y la especialización dietaria, correlacionando variables funcionales (biomecánicas) y la dieta (Van Cakenberghe *et al.*, 2002; Dumont, 2004; Nogueira *et al.*, 2005; Clabaut *et al.*, 2007; Herrel *et al.*, 2008; Dumont *et al.*, 2009; Nogueira *et al.*, 2009; Monteiro y Nogueira, 2011).

La similitud morfológica entre las especies puede ser explicada por la historia evolutiva compartida o por la evolución paralela de formas equivalentes en condiciones ecológicas particulares. Tal es el caso de estructuras de relevancia biomecánica como lo es el aparato masticatorio. Especies con estrategias alimenticias similares que ocupan regiones discretas del morfoespacio evidencian que la variación morfológica está estrechamente relacionada a dieta más que a la filogenia (Clavaut *et al.*, 2007). Esta asociación entre morfología y estrategia alimenticia ha sido estudiada ampliamente en murciélagos, en los que se ha encontrado que una dieta concentrada en uno o pocos recursos alimenticios está relacionada a una morfología contrastante con respecto a especies que consumen más tipos de recursos y ocupan la mayor parte del morfoespacio (Freeman, 1984; Freeman 2000; Dumont *et al.*, 2009, Monteiro and Nogueira, 2009; Nogueira *et al.*, 2005; Nogueira *et al.*, 2009).

En murciélagos, la diversidad morfológica y ecológica, en términos de dieta y forrajeo, ha sido ampliamente documentada. En el caso de la familia Phyllostomidae se ha planteado la existencia de una radiación adaptativa sin comparación entre los mamíferos en términos de la diversidad ecológica y morfológica del grupo (Monteiro y Nogueira, 2011). Se ha demostrado que especies dentro de esta familia que presentan dietas

nectarívoras (e.g. *Erophylla sezekorni*, *Monophyllus redmani*, *Glossophaga soricina*) o dietas carnívoras (e.g. *Phyllostomus hastatus*, *Phyllostomus discolor*, *Cheiromeles torcuatus*, *Vampyrum spectrum*, y *Scotophilus gigas*) están bajo demandas funcionales que podrían explicar los cambios en la morfología craneal respecto de dietas omnívoras (Freeman, 1988; Dumont *et al.*, 2009; Nogueira *et al.*, 2009). Se ha demostrado que las dietas carnívora y piscívora evolucionan a partir de ancestros insectívoros y que la morfología craneal en estos grupos cambia en regiones de relevancia biomecánica para el consumo de presas de mayor dureza y tamaño (Freeman, 1988; Freeman 2000; Swartz *et al.*, 2003; Monteiro and Nogueira, 2009). Dichos cambios se presentan tanto en especies del mismo linaje como en especies que no comparten ancestros comunes inmediatos (Freeman, 2000; Monteiro and Nogueira, 2009), por lo cual las características craneales asociadas a la dieta aparecen como convergencias dentro de los murciélagos.

Las diferencias entre murciélagos insectívoros y especies de dietas menos frecuentes entre los murciélagos, como los carnívoros y piscívoros, se encuentran en la morfología craneal, asociadas al funcionamiento de los músculos masticatorios, y en la morfología externa de las alas y las garras, asociadas al forrageo. En especies en las que se alcanzan las mayores fuerzas de mordida se ha encontrado que una combinación de factores de forma y tamaño responden por estos valores (Dumont and Herrel, 2003; Nogueira *et al.*, 2009). Las diferencias en el sistema de palancas asociadas a los cambios en el tamaño corporal responden por diferencias en la fuerza de mordida (Anderson *et al.*, 2008), al igual que la forma del cráneo y la arquitectura de los músculos masticatorios (Herrel *et al.*, 2007; 2008). Por ejemplo algunas especies insectívoras de gran talla (*Cheiromeles torquatus*, *Scotophilus gigas*, y *Saccolaimus peli*) que consumen insectos duros poco comunes en la dieta de los murciélagos en general han convergido hacia rostros amplios y cortos, rasgos craneales relacionados al desempeño de los músculos ya que esta porción del cráneo transmite la fuerza de los músculos a la presa (Freeman 1981; Herrel *et al.*, 2008).

En el caso de la piscivoría, se presentan cambios relevantes para el desempeño en la dieta (Freeman, 1988). Por ejemplo, en la especie piscívora *Noctilio leporinus* el cambio en el músculo temporal a una posición más vertical, la alta razón origen/inserción del músculo, los bajos procesos coronoides y la fosa temporal verticalmente orientada sugieren una amplia mordida para desgarrar las presas (Emerson y Radinsky, 1980; Freeman, 1988; Van Cakenberghe, Herrel y Aguirre, 2002). Estas características podrían significar cambios en

la fuerza y la amplitud de la mordida, y podrían tener consecuencias en el desempeño alimentario de esta especie piscívora (Freeman, 1988). Además, se ha planteado que la presencia de garras grandes y lateralmente comprimidas está asociada a este tipo de dieta (Norberg y Rayner, 1987; Fenton y Bogdanowicz, 2002), características que también se han observado en algunas especies que incluyen peces en su dieta en el género *Myotis*.

El género *Myotis* representa un buen modelo para estudiar la relación entre morfología y dieta puesto que presenta una alta diversidad tanto en especies (~100 especies; Simmons, 2005), como en el forrajeo y las estrategias alimenticias (Ruedi and Mayer, 2001; Ruedi *et al.*, 2013). Aunque el género es reconocido por presentar una morfología generalista (Horáček *et al.*, 2000), estudios fenéticos han agrupado a las especies por su similitud morfológica y características ecológicas comunes (Findley, 1972; Fenton y Bogdanowicz, 2002), mencionando incluso equivalencias morfológicas entre especies de distintos clados (Ruedi and Mayer, 2001).

Dentro del género se reconocen tres ecomorfos, propuestos inicialmente como subgéneros, pero que actualmente representan paralelismos evolutivos y están definidos por las similitudes entre la morfología y el modo de forrajeo (Findley, 1972; Norberg y Rayner, 1987; Fenton y Bogdanowicz, 2002). El ecomorfo *Selysius* está constituido por especies pequeñas que capturan insectos con la boca, y que tienen alas cortas, amplias y redondeadas que favorecen la maniobrabilidad al permitir girar lentamente para forrajear sobre la vegetación (Norberg y Rayner, 1987). El ecomorfo *Myotis* reúne especies que cazan insectos al vuelo usando el uropatagio y se diferencian de las anteriores por tener una longitud alar media y un alto costo de energía en el vuelo (Norberg, 1994). Algunas especies de estos dos grupos pueden alternar ocasionalmente sus estrategias de caza entre capturar al vuelo y forrajear con la boca sobre el sustrato (Fenton y Bogdanowicz, 2002). El ecomorfo *Leuconoe* reúne especies que capturan insectos sobre la superficie del agua empleando el uropatagio, y presentan alas largas y punteadas que favorecen alta maniobrabilidad, con un vuelo sostenido y de bajo costo energético (Norberg y Rayner, 1987; Norberg, 1994).

Dentro de *Leuconoe* se presentan especies que emplean una técnica de caza denominada “trawling”, que consiste en capturar las presas arrastrando sus garras en la superficie del agua (Findley, 1972; Norberg y Rayner, 1987). Estas especies son de mayor talla, poseen garras grandes en proporción a la pata, y entre ellas se encuentran las que

consumen ocasionalmente peces, como *M. ricketti* (Aihartza *et al.*, 2008), *M. daubentonii*, *M. cappaccini* (Siemers *et al.*, 2001), *M. adversus* (Law y Urquhart, 2000), *M. macrotarsus* (Siemers *et al.*, 2001), *M. albescens* (Whitaker y Findley, 1980) y *M. stalkerii* (Flannery, 1995), y la especie piscívora *M. vivesi* (Blood y Clark, 1998). Esta última se diferencia del resto de las especies trawling por tener alas más largas y estrechas y baja carga alar, que le permite un vuelo lento y sostenido y de bajo costo energético para desplazarse más lejos y localizar presas en la superficie del agua (Norberg, 1994). Esta especie no comparte una historia común con las otras especies ocasionalmente piscívoras (Stadelmman *et al.*, 2004).

El análisis de estos ecomorfos requiere un muestreo taxonómico amplio así como incluir variables morfológicas y funcionales de las estructuras involucradas en la dieta y el modo de forrajeo, que están relacionados dentro de estos grupos. Previamente se realizó un análisis del aparato masticatorio en la especie piscívora *M. vivesi*, comparándola con algunas especies insectívoras, piscívoras facultativas y la especie piscívora *N. leporinus*. Se encontró una separación significativa en el espacio morfológico entre las especies insectívoras, la especie piscívora *M. vivesi* y la especie piscívora *N. leporinus*, así como tendencias de cambio común en la posición del músculo temporal y el proceso angular entre estas dos especies (Ospina-Garcés, 2010).

Dadas las similitudes morfológicas entre especies de la misma estrategia de forrajéo y los cambios en la morfología craneal de relevancia funcionales, se analizó la correlación entre la morfología y la función del cráneo con relación a la dieta en el género *Myotis*. Se realizó un muestreo taxonómico de los diferentes ecomorfos y clados y se describió la morfología craneal mediante el uso de la morfometría geométrica para detectar las similitudes y diferencias entre las especies y describir las tendencias evolutivas asociadas a la dieta en el género. Además, se implementaron análisis comparativos de datos ecológicos y morfométricos en un contexto filogenético para cuantificar el rol de la ecología y la filogenia en la evolución de la morfología craneal. Mi predicción en este estudio fue que si la piscivoría, sea facultativa o frecuente, aparece como un paralelismo en la historia evolutiva del género *Myotis*, debe haber tendencias de variación morfológica y funcional del cráneo compartidas por especies que incluyen peces en su dieta.

CAPÍTULO 1

“Cranial shape and diet variation in *Myotis* species (Chiroptera: Vespertilionidae): testing the relationship between form and function”

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Abstract:

The relationship between cranial morphology and diet has long been investigated in bats. Bats of the genus *Myotis* include insectivorous, facultatively piscivorous, and piscivorous species. We tested the hypothesis that facultatively piscivorous (five *Myotis* species) and piscivorous species (*M. vivesi*) present cranial morphological and functional changes with respect to insectivorous taxa (sixteen *Myotis* species). Cranial shapes in skull and mandible modules were described with four geometric landmark configurations in these dietary groups. Gape capacity was measured with the stretch factors for temporal and masseter muscles. Geometric configurations from two skull and two

mandible shapes were analyzed to detect differences in cranial morphology in relation to diet. Differences in cranial morphology were found between piscivorous and insectivorous species involving the mandibular process where masticatory muscles are attached. Linear regression analysis of Procrustes distances and gape capacity showed that the shape of the mandibular process region was highly correlated with the stretch factor of the masseter muscle in piscivorous and facultatively piscivorous species. These results suggest differences in cranial morphology and performance among diets but the hypothesis of gradual changes in cranial shape among diets was only accepted for the mandible and not for the skull. *Myotis vivesi* appears to improve mechanical advantage of masticatory muscles at lower gapes, presumably allowing more efficient chewing of slippery prey.

Keywords:

Myotis, piscivory, masticatory muscles, Geometric Morphometrics, stretch factor

INTRODUCTION

The relationship between cranial morphology and diet has long been investigated revealing that bat species with different diets occupy different regions of morphospace (Freeman, 1984; Freeman 2000; Dumont *et al.*, 2009, Monteiro and Nogueira, 2009; Nogueira *et al.*, 2005; 2009). Previous studies in bats have also found that large cranial changes related to different types of prey are located in anatomic regions of biomechanical relevance, such as the mandibles, the maxillae, and the processes of masticatory muscle insertion (Freeman, 2000; Dumont *et al.*, 2009; Nogueira *et al.*, 2005).

Diet diversification in bats is linked to extensive cranial shape divergence. For example, differences in cranial morphology and bite force among dietary groups are noticeable in Phyllostomidae, a family that includes insectivorous, frugivorous, nectarivorous, sanguinivorous, and carnivorous species (Freeman, 2000; Nogueira *et al.*, 2005; 2009; Monteiro and Nogueira, 2009; Dumont *et al.*, 2012). Even within dietary groups, cranial morphology varies in relation to food hardness; for example, insectivorous bats that feed on hard-shelled insects have short and thick-jawed skulls whereas those eating soft-shelled insects have long and delicate jaws (Freeman, 1981).

Changes in bat cranial morphology associated with vertebrate diets have been relatively less studied compared to other dietary transitions. Biomechanical data indicate that the skulls of carnivorous bats are larger and only modestly modified versions of soft-insect specialists (Freeman, 1979; Giannini and Kalko, 2005). Analyses of cranial morphology indicate that carnivorous and piscivorous species with wide faces and long canines have a strong bite, and they have extremely wide and high skulls that provide a greater attachment area for the jaw adductor muscles (Freeman, 1984; Van Cakenberghe *et al.*, 2002). The cusp shapes of molars are the most evident modifications in species with a carnivorous diet as compared to their insectivorous ancestors (Freeman, 1984; Dumont, 2004). However, the morphological changes in cranial morphology associated with the appearance of piscivory have not been thoroughly examined.

Piscivorous diets originated independently in the genera *Noctilio* and *Myotis* (Stadelman *et al.*, 2004). Piscivory involved small changes in cranial morphology from insectivorous ancestors, which might be related to a recent radiation from insectivory (Lewis-Orrit *et al.*, 2001). There is variation in morphological traits related to gape capacity in piscivorous bats. For example, *N. leporinus* has a vertically oriented temporal fossa, low coronoids, laterally-flaring angular processes, and a high temporal origin/insertion ratio which have been related to a wide gape (Freeman, 1984). Wide gapes can be advantageous if we consider that piscivorous bats capture prey with their claws and the interfemoral membrane, and immediately rotate the legs forward and the head downward to transfer the fish to the jaws (Schnitzler *et al.*, 1994). Changes related to a wide gape in piscivorous species thus underline the importance of cranial morphology in prey capture (Freeman, 1984).

Piscivory in *Myotis* appeared independently in the Old and New Worlds. Dietary diversity in the genus *Myotis* includes strict insectivory, facultative piscivory, and piscivory. In the Old World, several insectivorous species are known to occasionally include fish in their diet, including *M. ricketti* (Aihartza *et al.*, 2008), *M. daubentonii*, *M. cappaccini* (Siemers *et al.*, 2001), *M. adversus* (Law and Urquhart, 2000), *M. macrotarsus* (Siemers *et al.*, 2001) and *M. stalkerii* (Flannery, 1995). In the New World, *M. albescens* seems to supplement its insectivorous diet with fish (Whitaker and Findley, 1980) whereas *M. vivesi* feeds primarily on marine fish (Blood and Clark, 1998, Otálora-Ardila *et al.* 2013). These seven facultative and one fully piscivorous *Myotis* species were initially

classified in the ecomorph *Leuconoe* (Findley, 1972) because they share a larger body size than most insectivorous *Myotis* species, and laterally compressed, large claws (Norberg and Rayner, 1987; Fenton and Bogdanowicz, 2002). These characters have also been observed in the piscivorous species *N. leporinus* (Findley, 1972; Freeman, 1984; Norberg and Rayner, 1987) and have been interpreted as convergences in external morphology related to piscivory (Blood and Clark, 1998). Such ecological diversity and putative convergence within *Myotis* makes this genus a good model to study the relationship between cranial morphology and diet variation. Although modifications to the external morphology of the claws had been related to fish-eating bats (Norberg and Rayner, 1987; Fish *et al.*, 1991), knowledge of cranial morphological changes is limited. For example, changes in cranial structures related to gape capacity that can be relevant in capture and consumption of fish by *Myotis* bats have not been documented.

The study of shape variation and its covariation with other variables has greatly benefited from the “geometric revolution” in morphometric methodology (Adams *et al.*, 2004). Geometric morphometrics methods provide a more comprehensive quantification of biological shape as compared to alternative approaches (Adams and Otálora-Castillo, 2013). Modern geometric morphometrics offers the advantage of analyzing size and shape separately and is more sensitive in detecting differences between cryptic species than traditional methods (Adams *et al.*, 2004). The use of geometric morphometrics in studies of cranial shape variation in bats within ecological or evolutionary contexts has increased recently (Evin *et al.*, 2008; Monteiro and Nogueira, 2009; 2011; Nogueira *et al.*, 2009). This tool might be applied to study shape variation in relation to diet even when morphological differences are subtle, which might be the case of cranial shape variation among *Myotis* species with contrasting diets.

We used geometric morphometrics to examine whether *Myotis* species with different diets occupy different regions of cranial morphospace. We expected that differences would follow a gradual pattern in which cranial shape and functions were more contrasting between piscivorous and insectivorous species, with facultatively piscivorous species occupying an intermediate position. In particular, we expected morphological differences among dietary groups associated to fish-eating habits in the position of the masticatory process and the insertion area of the temporal muscle in the skull.

We focused on two skull and two mandibular shapes for the morphological comparison

among the three dietary groups. We evaluated differences in masticatory function among dietary groups using functional variables related to gape, such as the stretch factor of the masseter and temporal muscles. To interpret the findings of our comparisons of form and function, we tested the relationship between shapes and stretch factors.

MATERIALS AND METHODS

Geometric morphometric data

We studied variation in four skull and mandibular modules registered as landmark configurations in 22 *Myotis* species (Appendix I). Species were selected according to their diet and phylogenetic position within *Myotis* (Stadelman *et al.*, 2004). The sample contains the facultatively piscivorous and piscivorous *Myotis* species and their insectivorous sister species (Findley 1972; Ruedi and Mayer, 2001, Ruedi *et al.*, 2013). We chose only adult specimens based on cranial ossification criteria (Pacheco and Patterson, 1992). Specimen identifications were aided with descriptions and taxonomic revisions of the genus *Myotis* (La Val, 1973; López-González *et al.*, 2001; Dietz and Von Helversen, 2004; Larsen *et al.*, 2012), and the classification made by Simmons (2005). Digital photographs of skulls were directly obtained from specimens of *Myotis* (Appendix I) deposited in various collections: National Mammal Collection at the Universidad Nacional Autónoma de México (UNAM; Mexico City, Mexico), the Theriological Collection at the Universidad de Antioquia (Medellin, Colombia), the Doñana Biological Station (Seville, Spain), the National Museum of Natural History Mammal collection (Washington, DC, USA), and the American Museum of Natural History Mammal collection (New York, NY, USA). Lateral and ventral views of skulls, and lateral views of mandibles were taken with a digital SLR camera with a macro lens (Nikon D3100, DX Nikkor 18–55 mm lens, Japan). Skulls and mandibles from small specimens (distance corresponding to the greater length of the skull < 13 mm) were photographed with a Macroscope modular zoom system (Leica Z16 APOA, Germany) at the bioinformatics unit UNIBIO (Institute of Biology, UNAM).

Two-dimensional landmark configurations from images were obtained with the program TpsDig 2.16 (Rohlf, 2008a). Semilandmarks were registered with guides drawn with the program Make Fan (Sheets, 2014). The definition of landmarks and

semilandmarks in each configuration is in Appendix II. Four configurations were separately registered corresponding to cranial developmental modules in mammals that are also of biomechanical relevance when comparing different diets (Klingenberg *et al.*, 2003; Porto *et al.*, 2009). Lateral views of the skull (434 photographs) were divided into two modules based on results that demonstrated separate rostral and basicranial modules for all of Mammalia including Chiroptera (Marroig *et al.*, 2009; Porto *et al.*, 2009) (Fig. 1a, b). The first skull module comprised the parieto–occipital region and it was registered with a set of eight landmarks and 24 semilandmarks (Fig. 1a). The second skull module was the frontal–maxillary region and it was registered with a collection of 10 landmarks and 10 semilandmarks (Fig. 1b). Lateral views of the mandibles (446 photographs) were divided into two modules based on results that demonstrated separate mandibular processes and alveolar modules for all of Mammalia including Chiroptera (Klingenberg *et al.*, 2003). The first mandible module was the mandibular processes region, which was registered with four landmarks and 18 semilandmarks (Fig. 1c). The second mandible module was the dental row; it was registered with a configuration of 4 landmarks and 10 semilandmarks (Fig 1d).

Configurations were aligned, rotated and scaled under a generalized Procrustes analysis to obtain shape variables and centroid size (Rohlf, 1990). First, we used a Procrustes superimposition to align landmark coordinates with CoordGen 8 (Sheets, 2014) separately for each module. Second, semilandmarks were aligned with SemiLand 8 by sliding points along curves to minimize bending energy of deformation from the mean form. Shape modules were analyzed independently of size. Morphometric analyses were conducted with the IMP program series 8.0 (Sheets, 2014).

Modularity

Correlations between the two pairs of modules from the lateral view of skull and the lateral view of mandible (two comparisons) were tested with partial least squares (PLS) analyses. PLS analyses calculate pairs of orthogonal latent variables from the covariance matrices of each block, using the singular value decomposition. Correlation of singular vectors from two blocks, and the permutation tests to assign statistical significance of correlations were obtained in the program PLS version 8 (Sheets, 2014).

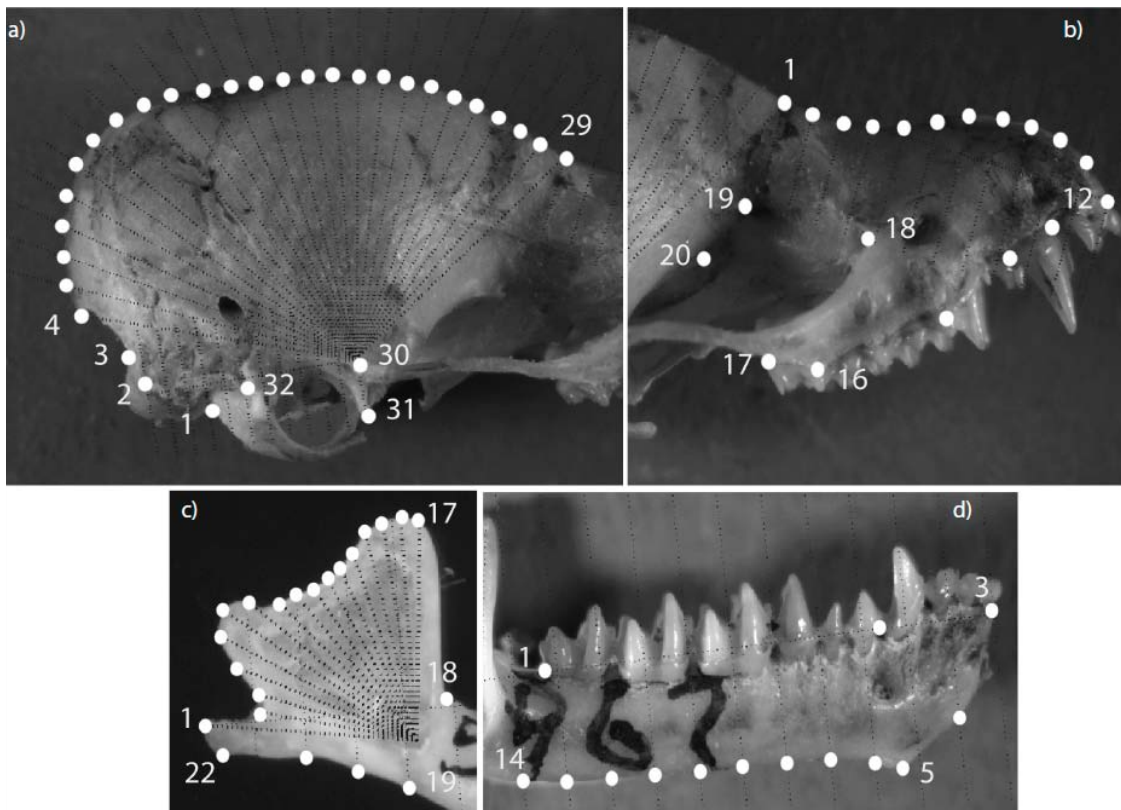


Fig. 1. Four configurations of points drew to register the shape of five cranial modules in 23 species. 1. parieto-occipital (module 1) region with 32 points, 1-32, lateral view. 2. Frontal-maxillary region (module 2) with 20 points, 1-20, lateral view. 3. Mandible process area (module 3) with 22 points, 1-18, 33-36, in lateral view. 4. Alveolar region (module 4) with 14 points, 19-32, lateral view.

Allometry

The size estimator “centroid size” corresponds to the square root of the sum of squared distances of each landmark to the centroid of each configuration (Bookstein, 1991). Since differences in size between sexes could hide differences between groups, we tested differences between diets and sexes with two-way analysis of variance (ANOVA) followed by Scheffe’s F post hoc comparisons. Values were normally distributed within dietary groups. These analyses were made in the program STATISTICA version 10 (Statsoft Inc., 2011). When sample sizes were very low ($n < 4$) for any of the sexes (Appendix III), species were not included in the analyses.

We tested the degree to which shape variation was explained by differences in centroid size, considering the entire sample. This allometric effect was determined by a multivariate regression of the partial warps (shape vectors) on the centroid size (size estimator). We obtained the percent of shape variance explained by size in each module. We used the multivariate statistic Wilk’s lambda on the partial warps to estimate the significance of the multivariate regression. Wilk’s values close to 0 represent a high effect of the independent variable. Additionally, we performed bivariate regressions between the centroid size and the shape as diagnosed by Procrustes distances from each specimen to the average of the five smaller individual configurations. We used the univariate statistic Z and the associated probability to evaluate the adjustment of points to the regression model between Procrustes distances and centroid size. Multivariate and univariate allometric analyses were made in Regress version 6 (Sheets, 2004).

We standardized size in modules with allometric effects using the residuals from the regression line between shape variables (partial warps) and centroid size (Zelditch *et al.*, 2004). The allometric standardization was performed with the tool standardize in the program Regress version 8 (Sheets, 2014). We used size corrected data for multivariate comparisons (Canonical Variates Analyses) in skull modules.

Shape variation among diet groups

We explored shape similarities among species with the same diet. We estimated the pairwise Procrustes distances between average shapes for each species with IMP CoordGen 8 software (Sheets, 2014). We performed a Cluster analysis of Procrustes distances separately for each module using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm in the program NTSYS versions 2.2 (Rohlf, 2008b).

We used Canonical Variates Analyses (CVA) with configurations of four shapes to evaluate differences among the three dietary groups. We calculated the variance of configurations in a multivariate space for each shape character and the significance of canonical axes using Bartlett's test, which determines the number of informative CVs. The test presents the Wilk's value, the corresponding χ^2 , the degrees of freedom and the probability for the hypothesis that there are differences among groups in a progressively smaller subset of the data. The first iteration using all of the CVs tests for differences among groups using all of the available data and the second interaction eliminates data discriminated by the CV 1; the analysis finishes when all discriminated groups are removed (Zelditch *et al.*, 2004).

We projected individuals on the canonical axis to infer the shape deformation relative to a consensus configuration (Bookstein, 1991). Changes in cranial shapes in each dietary group were graphically examined using deformation grids from a consensus shape in the canonical axes and the relative magnitude of changes were described by vectors on landmarks. As changes were small among diets, the deformations were exaggerated by a factor of 3 to better illustrate them. These procedures were made in CVAGen 8 (Sheets, 2014). We explored morphological differences among diets using a multivariate analysis of variance (CVA/MANOVA) on partial warp scores to calculate Mahalanobis distances (D^2) between centroids from each group. These analyses were made in STATISTICA version 10 (Statsoft Inc., 2011).

Variation in gape capacity among diet groups

Differences in masticatory function among the three dietary groups were evaluated using the stretch factors of the masseter and temporal muscles. The stretch factor model describes variation in the placement of the masticatory muscles relative to the

temporomandibular joint; changes in the location of muscle origin and insertion relative to the joint may permit wide gapes before the muscle is stretched (Herring and Herring, 1974). Stretch factors depend on the origin (distance 1) and insertion (distance 2) of the muscle and the angle between these two distances (Herring and Herring, 1974). Two distances and angles were calculated in photographs (213) of rearticulated skulls and mandibles (Fig. 2) using the model proposed by Herring and Herring (1974), and the methodology proposed by Dumont *et al.* (2009). The gape capacity is the extent to which the jaws can be opened before the muscle is stretched; it is described by the stretch factors of the masticatory muscles as the ratio between the length of the muscle when the mouth is closed and the length of the muscle when the jaw is rotated through the angle θ (Herring and Herring, 1974). In this case, θ is equal to 60° (Dumont *et al.*, 2009). We compared the stretch factors for the masseter and temporal muscle values among insectivorous, facultatively piscivorous, and piscivorous species. These values were not normally distributed within dietary groups and thus we used a Kruskal–Wallis analysis of variance followed by pairwise comparisons of dietary groups with post–hoc Mann–Whitney U tests. Stretch factor values were presented for each diet with median, interquartile 25–75%, and minimum–maximum value. Analyses of variation in gape capacity were performed in STATISTICA version 10 (Statsoft Inc., 2011).

Relationship between cranial shape and gape capacity

To explain differences in cranial morphology and function among diets, we tested the relationship between cranial shape and functional variables. We ran ordinary least squares regressions of the two stretch factors (masseter and temporal muscles) against the Procrustes distances between specific configurations and consensus shape. The associated Z statistic was used to test the explanatory power of the linear model to describe the relationship between cranial shape and masticatory function. These analyses were performed in the program Regress 6 (Sheets, 2004).

Considering that the insectivorous *Myotis* group is very diverse and its form and function could be affected by phylogeny, we evaluated the phylogenetic contribution on the variance of the functional and shape variables to support our interpretation of the regression results. We evaluated whether a given tree (topology and branch lengths) better fit a set of

tip data as compared with the fit obtained when data have been randomly permuted following Blomberg *et al.* (2003). To consider the phylogenetic

effect on the form–function correlations, we tested the significance of the phylogenetic signal, which was determined as the variance of contrasts for the real data compared with the values obtained after the data had been permuted randomly across the tips of the tree without considering phylogenetic relationships. We used the K statistic to quantify the proportion of variance explained by the candidate tree, where values <1 imply that relatives resembled each other less than expected under Brownian motion evolution along the candidate tree (Blomberg *et al.*, 2003). We obtained the twenty–two sequences of Cyt–b (1149 pb) and RAG2 (1054 pb) from Gen Bank (appendix II), and mapped them on the phylogenetic reconstruction of the genus *Myotis* from Ruedi *et al.* (2013) to calculate the branch lengths of the tree in the program TNT (Goloboff *et al.*, 2015). We calculated the phylogenetic effect on the correlated variables as the functional traits and Procrustes distances in the mandibular processes region using the R package “PICANTE” (Kembel *et al.*, 2010) in R statistical program version 3.2.2 (R Core Team, 2008).

RESULTS

Modularity

The correlations between two modules from the lateral view of skull and two modules from mandibles derived from the PLS analyses were lower than 0.5. Bootstrap analyses of the data (1000 replicates) revealed all correlations were significant ($P < 0.001$). The correlation between the frontal–maxillary region and the parieto–occipital region ($r = 0.36$) was higher than between mandibular processes region and alveolar region ($r = 0.31$).

Allometry

Results for sexual dimorphism analyses were presented only for modules with a significant size effect on morphological variation (Appendix III). We found significant differences in centroid size among diets but not between sexes (183 ♀ and 172 ♂). Post-hoc

comparisons indicated significant differences in centroid size among all diets ($P < 0.001$), except for skull module 2 between insectivores and facultative piscivores ($P = 0.93$).

The multivariate regression of partial warps on centroid size showed that the highest variance explained by size was for the parieto–occipital region (skull module 1, 13.92%), whereas size explained a low percentage of the variation in the frontal–maxillary region (skull module 2, 4.40%), the mandibular processes region (mandible module 1, 3.54%) and the alveolar region (mandible module 2, 1.73%). The F statistics associated with the multivariate regression were significant, but the Wilk’s lambda values were closer to one in the mandible modules indicating a lower effect of centroid size on shape variation than in skull modules (Table 1). The bivariate regressions between the centroid size and the Procrustes distances were significant only for skull shapes (Table 1).

Table 1. Results for regression analyses between shape variables and centroid size for 22 *Myotis* species. The first two columns describe the results of bivariate regression of Procrustes distances on centroid size. Fit of data to linear regression model was evaluated with the Z statistic. The last three columns present results of multivariate regression of the full set of partial warp scores on the centroid size.

	Bivariate regression (r)	Z (p)	Wilks Lambda	F (p)	df1, df2
Parieto-occipital region	0.37	7.87 (< 0.001)	0.32	12.33 (< 0.001)	58,337
Frontal-maxillary region	0.18	3.77 (< 0.001)	0.48	11.34 (< 0.001)	34, 359
Mandibular process region	*-0.01	-0.20(0.58)	*0.57	7.02 (< 0.001)	40, 379
Alveolar region	*-0.21	-4.4 (0.99)	*0.79	4.21(0.001)	24, 239

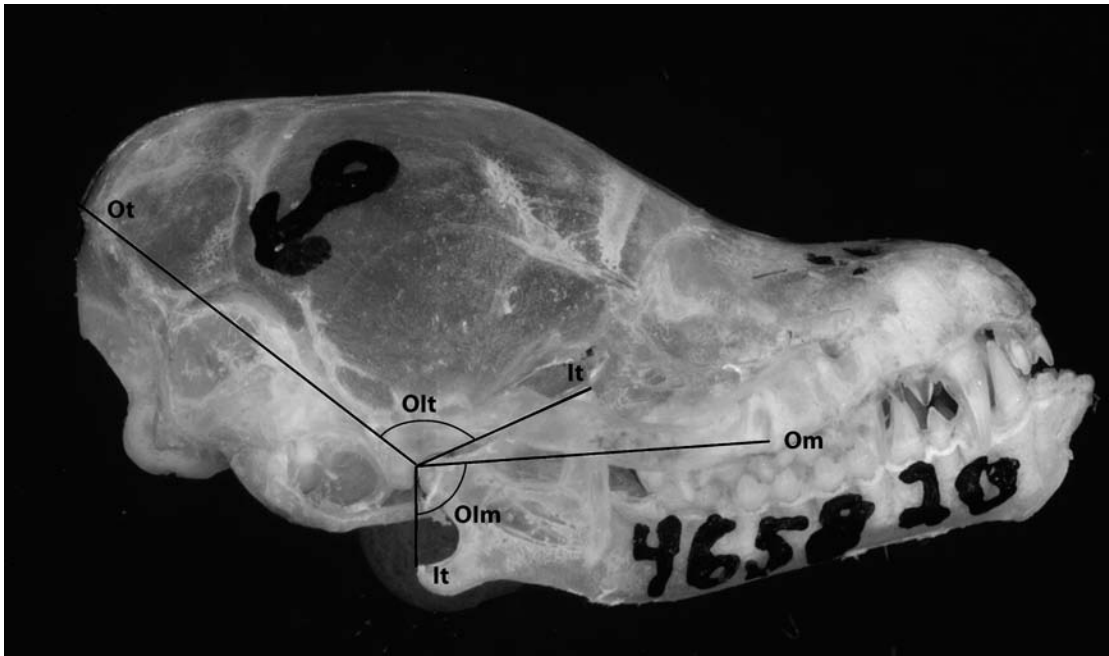


Figure 2. Image of an articulated skull and mandible used to measure the origin (Ot) and insertion (It) of the temporal muscle and the origin (Om) and insertion (Im) of the masseter muscle. The angles between origin and insertion distances for temporal (OIt) and masseter muscles (OIm) were drawn.

Shape variation among diets

Grouping by similarity based on Cluster analyses revealed differences among the four modules (Appendix IV). Facultatively piscivorous species were clustered into two groups in the mandibular processes region and they were more segregated in the rest of the modules. Additionally, morphological similarities did not reflect relatedness among species but the shortest distances among species were found in the alveolar region (Appendix IV). The CVAs showed differences in the amount of variation between skull and mandibular modules. The total variance in skull shapes was higher for the frontal–maxillary region (skull module 2, 0.0041), followed by the parieto–occipital region (skull module 1, 0.0021) (Fig. 3). Among mandibular modules, total variance was higher for the mandibular processes region (mandible module 1, 0.0049) followed by the alveolar region (mandible module 2, 0.0013). The alveolar region was the shape module with the lowest variance and had the highest overlap of data points in *Myotis* species (Fig. 4).

Skull shapes were significantly different among all dietary groups discriminated by canonical axis. The CVA of the parieto-occipital region revealed two significant canonical axes (CV 1: $\lambda = 0.232$, $\chi^2_{116} = 531.76$, $P < 0.001$; CV 2: $\lambda = 0.607$, $\chi^2_{57} = 181.73$ $P < 0.001$). Similarly, there were two significant canonical axes in the frontal–maxillary region (CV 1: $\lambda = 0.187$, $\chi^2_{72} = 626.21$, $P < 0.001$; CV 2: $\lambda = 0.462$, $\chi^2_{35} = 287.88$ $P < 0.001$).

Deformation grids in the skull shapes showed little changes based on landmark displacement vectors (Fig. 3). Changes in the cranial parieto-occipital region of *M. vivesi* with respect to the consensus shape were described by the first canonical axis with little displacements in the sagittal crest (landmarks 12-13, 18–21; Fig. 3a). The trend of variation described by the second canonical in the insectivorous species with respect to the consensus shape was a slight anterior displacement of the sagittal crest (landmarks 17-19, 25-27; Fig. 3a). The trend of variation in the frontal-maxillary region in facultative piscivores was described by the first canonical axis with an enlarging of the frontal bone (landmarks 4,6 8; Fig. 3b). Changes in the frontal-maxillary region in *M. vivesi* were described by the second canonical axis with respect to the consensus shape with a widening of the frontal (landmarks 4–7) and nasal regions (landmarks 10–11; Fig. 3b).

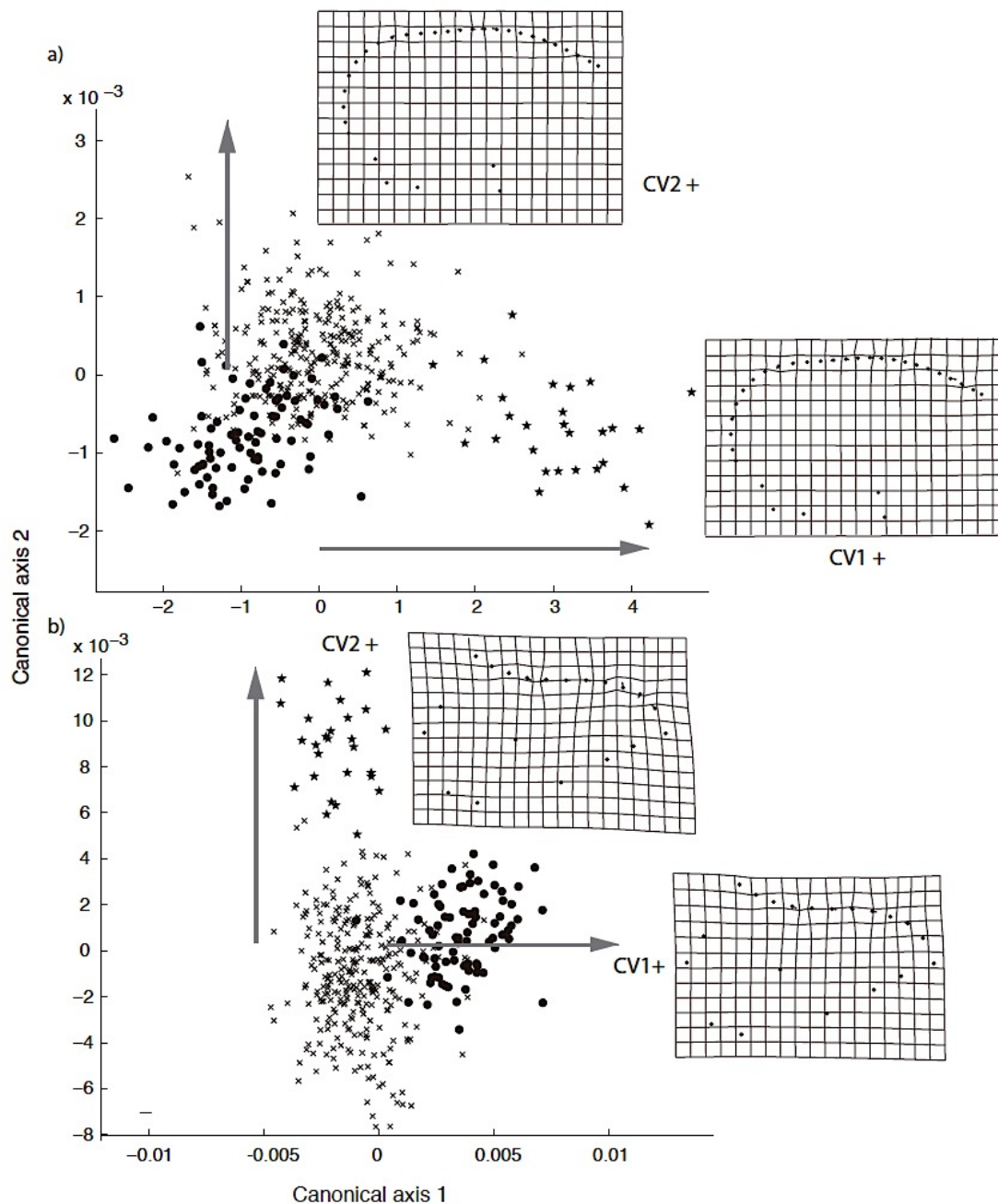


Fig. 3. Ordination plots of the first two canonical axes from skull modules among dietary groups. a) Plot of the first two canonical axes from parieto-occipital region (module 1) with deformation grids derived of each canonical axis. The horizontal arrow indicated the direction of change in *M. vivesi* with respect to the consensus shape. The vertical arrow indicated the directions of change in insectivores with respect to the consensus shape. b) Plot of the first two canonical axes from frontal-maxillary region (module 2) with deformation grids derived of each the canonical axis. The vertical arrow indicated the direction of change in *M. vivesi* with respect to the consensus shape. The horizontal arrow indicated the directions of change in facultative piscivores with respect to the

consensus shape. Three diets were compared: Insectivorous species (X), and facultative piscivorous species (●) and piscivorous species (★).

There were significant differences in skull shapes described by partial warps among dietary groups in all modules analyzed (parieto–occipital region: $F_{116, 672} = 7.22$, $P < 0.05$; frontal–maxillary region: $F_{72, 712} = 12.98$, $P < 0.05$). Post–hoc comparisons among all diets were significant ($P < 0.05$). The highest Mahalanobis distance was found between piscivores and facultative piscivores followed by the distances between piscivorous and insectivorous species (Table 2).

There were significant differences in shapes among dietary groups in all mandibular modules. The CVA of the shape of the mandibular processes region found two significant canonical axes (CV 1: $\lambda = 0.192$, $\chi^2_{80} = 654.67$, $P < 0.001$; CV 2: $\lambda = 0.557$, $\chi^2_{39} = 231.98$, $P < 0.001$). Also, there were two significant canonical axes in the alveolar region (CV 1: $\lambda = 0.103$, $\chi^2_{72} = 1003.97$, $P < 0.001$; CV 2: $\lambda = 0.47$, $\chi^2_{46} = 333.51$, $P < 0.001$).

Deformation grids of the mandibular shapes showed that the piscivorous species had the most divergent mandible region based on landmark displacement vectors. Changes in the mandible processes region were described by the first canonical axis with a reduction in the base of mandibles (landmark 19), the uplift in the angular process (landmark 21), and the contraction of condylar processes in mandibles of *M. vivesi* (landmarks 3–6; Fig 4a). Changes described by the second canonical axis were the extension of the contour between the condylar and the coronoid processes and the contraction of the angular processes in mandibles of facultative piscivores (landmarks 4–6, 7–13; Fig 4a). Changes in the alveolar region were described by the first canonical axis among all diets, with changes in the base of dentary of *M. vivesi* (landmarks 10–11; Fig. 4b). Changes in this module were unnoticeable in the other two dietary groups.

There were significant differences in mandibular shapes described by partial warps among dietary groups in the two modules analyzed (mandibular processes region: $F_{80, 756} = 12.08$, $P < 0.05$; alveolar region: $F_{48, 786} = 8.78$, $P < 0.051$). Post–hoc comparisons were significant ($P < 0.05$). The highest Mahalanobis distance in the mandibular processes region was registered between piscivorous and insectivorous species, followed by the distance between piscivorous and facultatively piscivorous species (Table 2).

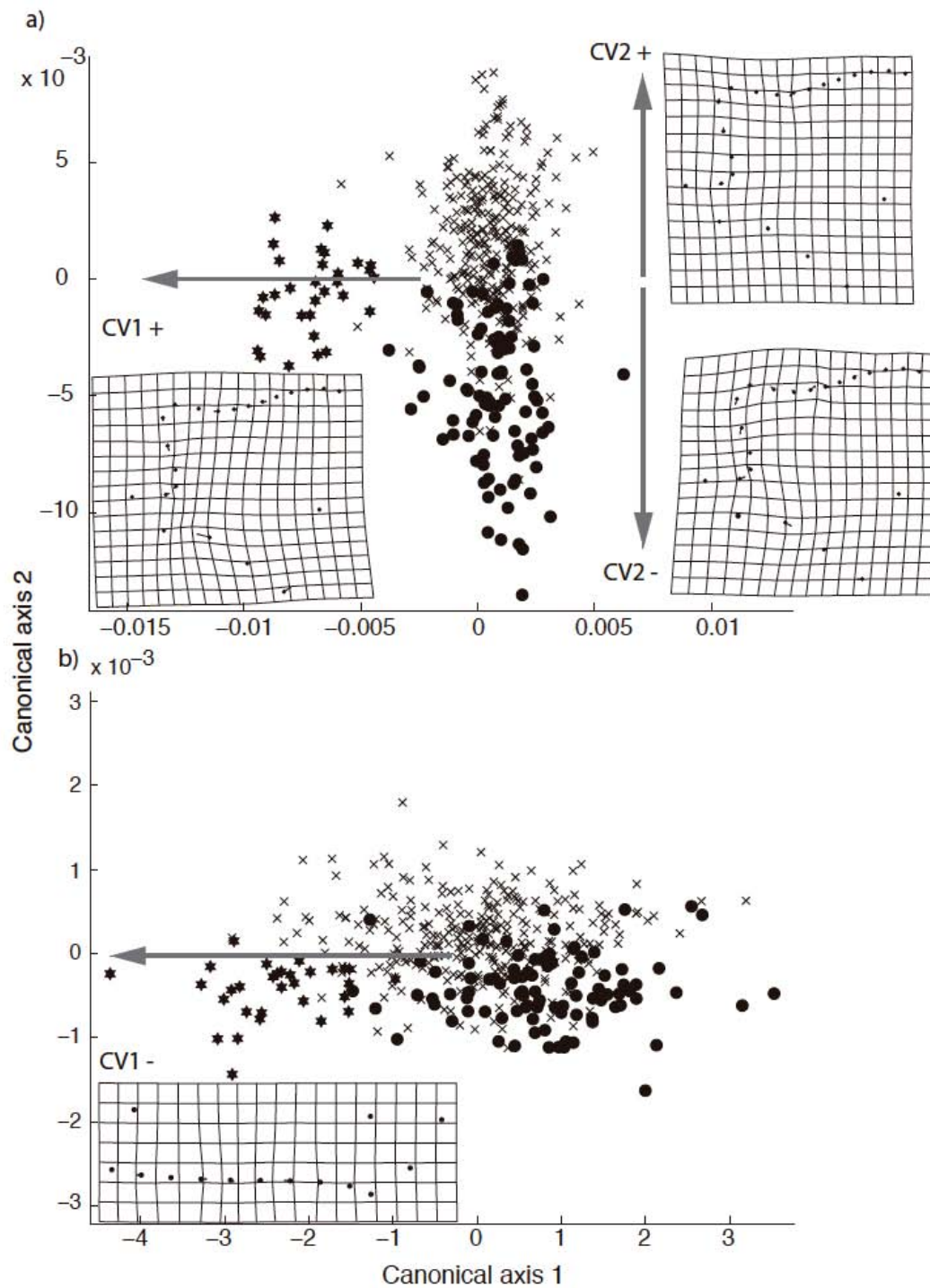


Fig. 4. Ordination plots of the first two canonical axes from two mandibular modules among dietary groups. a) Ordination plot of the first two canonical axes from mandibular process area with deformation grids derived of each the canonical axis. The direction of changes in *M. vivesi* with respect to the consensus shape was indicated for the horizontal arrow. The directions of change in facultative piscivorous and insectivorous species with

respect to the consensus shape were indicated for the vertical arrows. b) Ordination plot of the first two canonical axes from the alveolar region with deformation grids derived of each the canonical axis. The directions of change in *M. vivesi* and facultative piscivores with respect to the consensus shape were indicated for the double-headed arrow. Three dietary groups were compared: Insectivorous species (X), facultative piscivorous species (●), and piscivorous species (★).

Table 2. Squared Mahalanobis distances among *Myotis* dietary groups in skull and mandibular modules. All distances were significant ($P > 0.005$) after F tests. I = Insectivores, FP = Facultative piscivores, P = Piscivores.

Module	Shape	Distance between dietary groups		
		I-FP	I-P	FP-P
Skull	Parieto-occipital	4.88	21.48	31.07
	Frontal-maxillary	8.90	18.5	25.03
Mandible	Mandibular process	2.99	13.94	13.72
	Alveolar region	2.59	11.32	8.10

Stretch factors and diet

The analysis of variance showed significant differences among dietary groups in the stretch factors of the masseter ($K_{2, 212} = 38.44$, $P < 0.001$) and the temporal muscles ($K_{2, 212} = 64.95$, $P < 0.001$). Piscivorous species had the highest stretch values for the masseter muscle (1.27, 1.24–1.28, 1.22–1.31, $n = 17$), followed by facultatively piscivorous (1.22, 1.21–1.24, 1.16–1.29, $n = 49$), and insectivorous species (1.21, 1.20–1.24, 1.17–1.29, $n = 146$). The highest stretch values for the temporal muscle were found in *M. vivesi* (1.21, 1.20–1.22, 1.18–1.23, $n = 17$), followed by insectivorous (1.16, 1.14–1.17, 1.11–1.22, $n = 146$), and facultatively piscivorous species (1.14, 1.13–1.15, 1.08–1.22, $n = 49$, Fig. 5). All comparisons among dietary groups in the stretch factor of the masseter muscle ($P < 0.001$) and in the stretch factor of the temporal muscle ($P < 0.001$) were significant.

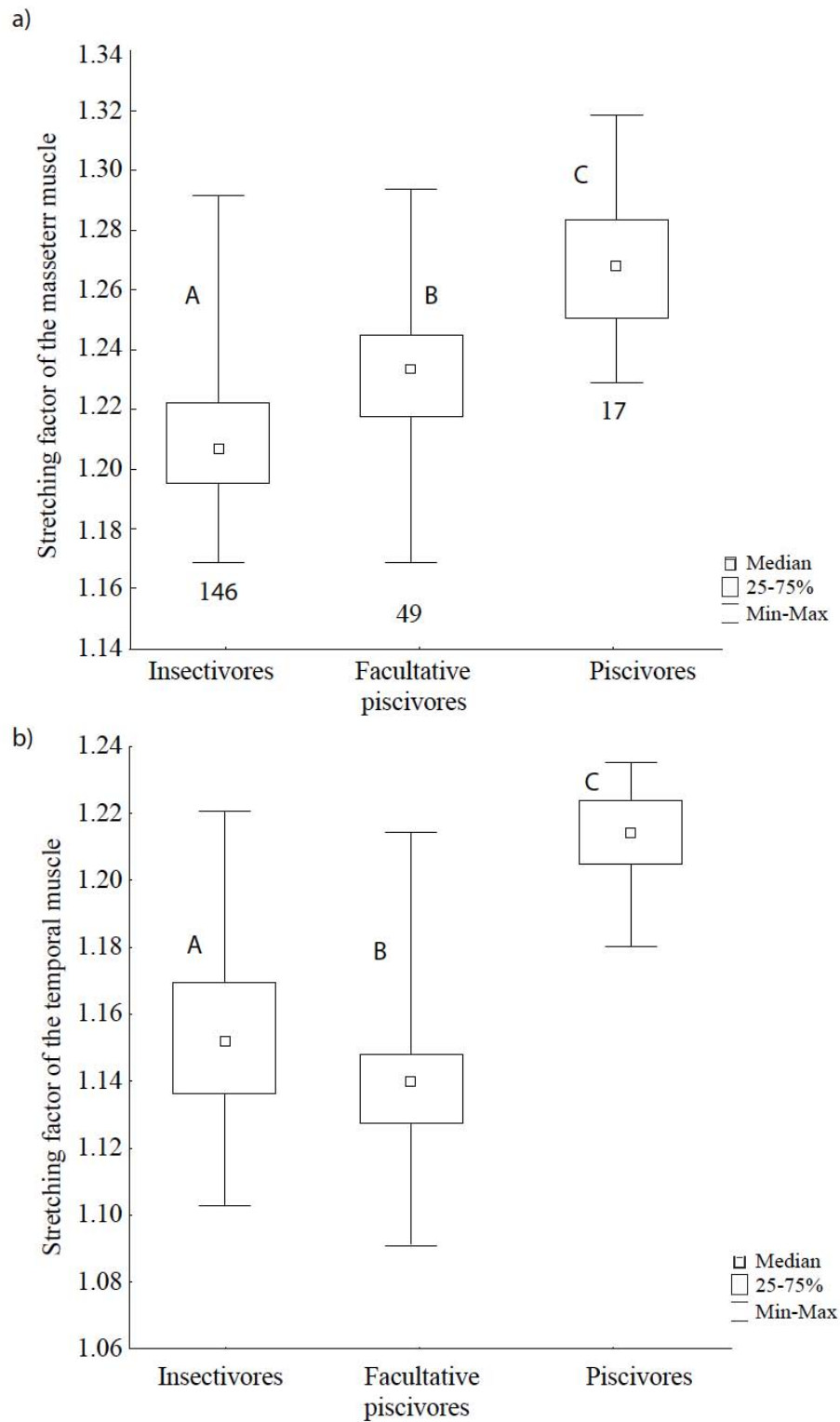


Fig. 5. Stretch factors of the masticatory muscles within genus *Myotis*. a) Stretch factors for the masseter muscle in each dietary group. b) Stretch factor for the temporal muscle in each dietary group. Data were presented with median, interquartile 25-75%, and minimum-

maximum value indicated in box plots. Sample sizes appear below each box plot. Letters indicate differences among groups.

There was a significant correlation between average Procrustes distances in the mandibular processes region and the stretch factors of the masseter muscle (Table 3, Fig. 6). The correlation between Procrustes distances of the parieto–occipital region and the stretch factor of the temporal muscle was significant but lower in magnitude than this correlation in the mandibular shapes (Table 3). All other correlations had correlation coefficients lower than 0.5 and were not significant, except for the frontal–maxillary region.

There was no phylogenetic signal in correlated variables. We found non-significant K values for the stretch factor of the masseter muscle ($K=0.55$, $p=0.75$) or the stretch factor of the temporal muscle ($K=0.79$, $p=0.20$). Procrustes distances of the mandibular processes region had the highest K value but it was not significant ($K=0.85$, $p=0.1$).

Table 3. Correlation values among the skull and mandible modules and the stretch factors for the masseter and temporal muscles in species of genus *Myotis* (Z values and probability associated).

Module	Stretching factor	
	Masseter muscle	Temporal muscle
Parieto-occipital region	-0.19 (-0.85, 0.8)	0.52 (2.55, 0.06)
Frontal-maxillary region	0.42 (1.93, 0.02)	0.48 (2.32, 0.009)
Mandibular processes area	0.6 (2.92, 0.001)	0.39 (1.79, 0.03)
Alveolar region	0.18 (0.20, 0.21)	0.25 (1.1, 0.13)

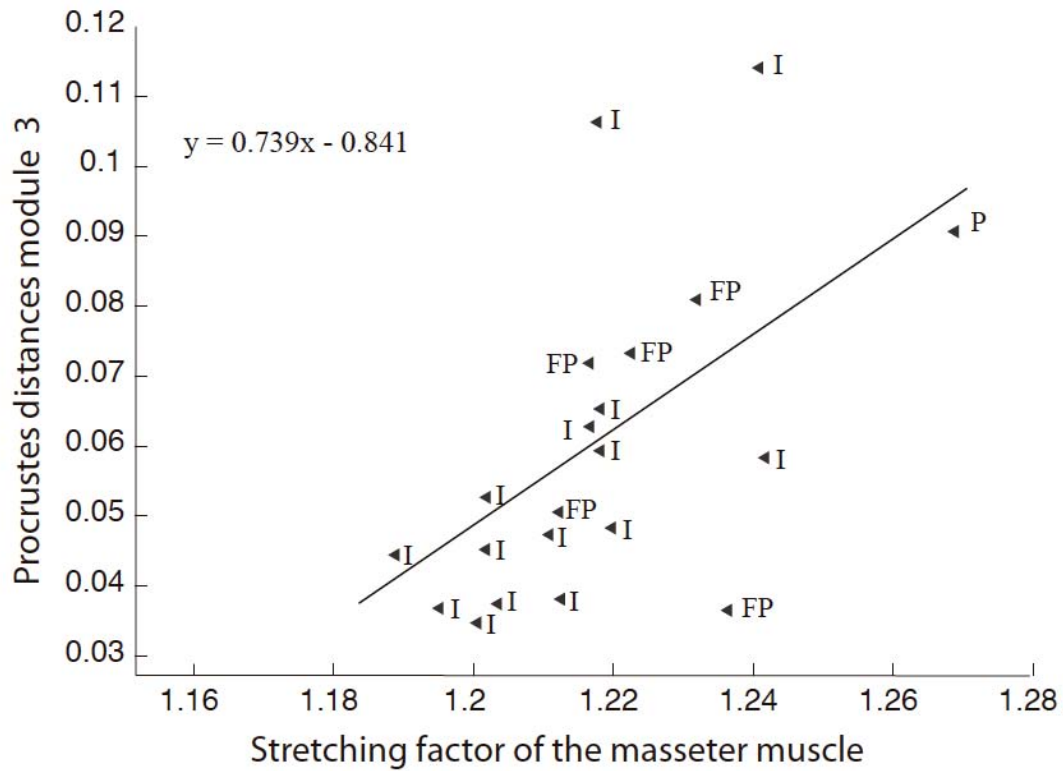


Fig. 6. Fitted regression line and data points for Procrustes distances between configurations of the mandibular process region and the stretch factor of the masseter muscle. FP: Facultative piscivorous species. P: piscivorous species. I: insectivorous species. The regression equation is presented.

DISCUSSION

Our findings support the idea of cranial morphological and functional differences in facultative piscivores and piscivores with respect to insectivores in the genus *Myotis*. Facultative piscivores and piscivores showed morphological and functional cranial differences relative to insectivores in the frontal–maxillary region, the mandibular processes region, and the stretch factor of the masseter muscle. Differences among diets suggest that shape changes occurred in the transition from insectivory to piscivory in *Myotis*. The largest differences in *M. vivesi* with respect to insectivores occurred in the position of the angular and condylar (masticatory) processes. These differences can affect the position of the masseter muscle, which displaces the lower jaws against the upper jaws and performs the sideward movement of the lower jaws (Turnbull, 1970). The relationship between shape and diet was evident for the mandibular processes region and the masseter muscle, and contrasted to a greater degree between piscivorous and insectivorous species, with facultatively piscivorous species occupying an intermediate position between these two diets.

However, the trends of skull variation indicated that facultatively piscivorous and piscivorous species are probably evolving in different directions from an ancestral insectivorous form. In the case of skull modules, the Mahalanobis distances between facultative piscivory and obligate piscivory are larger than between either forms of piscivory and insectivory for the skull (Table 2). This is even supported by the cluster analysis based on Procrustes distances, where the piscivorous taxon does not group with the facultatively piscivorous taxa, and the divergent trend of variation between piscivorous forms in the stretching factors of the temporalis muscle. These findings suggest that they evolved separately and not along a continuum.

Morphological variation among shape characters

Trends of morphological changes associated with diet can be more easily detected with the modularization of skull and mandibular structures. Our shape characters varied

among groups in different directions and by different magnitude. Although the covariation between skull and mandible modules was significant, the regression coefficient was lower than 0.4, as indicated by the PLS analysis, and the independent comparisons of modules revealed different trends. For example, the shape of the alveolar region in the mandible was relatively conserved in *Myotis*, in contrast to the mandibular processes region, which was the most variable shape.

Morphological variation among species with different diets can be interpreted in ecological terms after controlling for size effects in shape variation. Significant allometric effects were detected for morphological variation in two skull shapes (parieto–occipital and frontal–maxillary regions), whereas no effect was detected for the mandibular characters. Piscivorous and facultatively piscivorous species differed significantly in cranial morphology relative to insectivorous bats, but skull shapes changed slightly based on landmark displacement. The largest skull differences in *M. vivesi* occurred in the frontal–maxillary region, such as an expansion in the frontal and nasal regions (Fig 3b), whereas differences in facultative piscivorous with respect to insectivorous species followed a similar pattern in the rostrum but at a lower scale than in *M. vivesi* (Fig 3b). The differences in the parieto–occipital region in *M. vivesi* occurred in the sagittal crest, but changes were negligible. In addition, changes in facultatively piscivorous species were not observed and their shapes were closer to the general consensus shape in the CVA morphospace (Fig. 3a).

Our findings suggest that shape differences in skull modules in the genus *Myotis* could be better explained by differences in size among diets. Also, the high amount of variation within insectivorous *Myotis* observed from multivariate CVA space indicates that differences among species could be greater than differences among insectivorous and facultatively piscivorous groups. Differences in skull shape and size among insectivorous *Myotis* bats can probably be explained by adaptations for preying on insects with different sizes and exoskeleton hardness, as exemplified by the relatively wide braincase and short rostrum seen in small *Myotis* that consume big and hard prey items (Ghazali and Dzeverin, 2013).

Myotis vivesi differed from facultative piscivores and insectivores in the alveolar region of the mandible, the shape character with the lowest variance. Although we found significant differences among insectivores and facultative piscivores, shape changes were not detected in the deformations grids. The shortest distances among species from the

cluster analyses were found in the alveolar region, supporting the idea that shapes in this region are conservative characters in *Myotis*. The taxonomic relevance of this region can be seen in characters used to identify the genus *Myotis*, such as the number and size disparity of premolars (Gardner, 2008).

Differences in mandibular shapes among dietary groups could indicate an ecological effect of diet on the mandibular processes region (mandible module 1). The position of the angular and condylar processes, where the masseter muscle is inserted, differed in *M. vivesi* compared to other species. Differences in facultative piscivores with respect to insectivores also occurred in the mandibular processes region (Fig. 4a), where vectors of change were observed in the contour between the coronoid and the condylar processes and the angular process. This last change was similar to, but less pronounced than, those that occurred in *M. vivesi*.

The mandibular processes region is the anatomical region where the masseter muscle is inserted, and changes in the relative position of its processes have implications for muscle orientation and performance (Herring and Herring, 1974; Dumont and Herrel, 2003; Herrel *et al.*, 2008). Variation in mandible shape has been documented in Phyllostomidae where patterns of morphological integration in masticatory processes and the alveolar region vary among dietary groups (Monteiro and Nogueira, 2009). The shape of the mandibular processes region (mandible module 1) among *Myotis* species varied more among piscivorous species than among facultative piscivores relative to insectivorous species following a gradual pattern of change from insectivory to piscivory.

Functional shapes among diets

The stretch factor of the masticatory muscles has been used as a measure of performance in masticatory function in mammals because it describes gape capacity (Herring and Herring, 1974; Dumont *et al.*, 2009). Gape capacity is inversely related to stretch factor and it increases as the origin/insertion ratio increases above 1 (origin \neq insertion) and the origin-insertion angle becomes more obtuse; in contrast, the reduction of the origin/insertion ratio (value close to 1) and of the origin-insertion angle decreases gape capacity but increases the stretch factor and the moment arm for the muscle (Herring and

Herring, 1974). If gape capacity is limited, as could be the case for omnivorous mammals, selection could improve the mechanical advantage of the masticatory muscles, increasing the moment arm and decreasing the force required to stretch it (Herring and Herring, 1974). Also, more developed (massive) masticatory muscles could compensate for a limited gape capacity (Herrel *et al.*, 2008).

The comparison of gape capacity among dietary groups revealed that the mandibular processes region (mandible module 1) correlated most strongly with the stretch factor of the masseter muscle. Among *Myotis* diets, the origin/insertion ratio and angle decreased from insectivores to piscivores, while the stretch factor of the masseter muscle increased. For example, the origin-insertion angle in *M. vivesi* was slightly lower (average angle 82°) than in facultatively piscivorous species (average angle 91°) and insectivores (average angle 92°). In contrast, the highest stretch factors of the masseter muscle were found in *M. vivesi*, followed by facultatively piscivorous and insectivorous species. These findings could be explained by the contraction between the condylar and the angular processes found in piscivorous and facultatively piscivorous species, and suggest that the mandibular processes shape and the masseter muscle performance could be good predictors of diet in *Myotis*. The determinant role of the masseter muscle in bite force production and cranial shape variation among diets in bats has been previously hypothesized (Nogueira *et al.*, 2009) and seems to be confirmed in genus *Myotis*.

Previous studies have related the high values of masseter and temporal stretch factors to bite force production at low gape. For example, high stretch factors in frugivorous phyllostomids are explained by the gross anatomy of the masticatory system that favors high force production at low open gape angles in species that spend prolonged periods of time chewing fruits (Dumont *et al.*, 2009). Mammals that require high bite forces at low gapes, which seems to be the case for piscivorous bats, tend to have the largest moment at the temporomandibular joint axis generated by the masseter muscle (e.g. herbivores, Herring and Herring 1974; Santana *et al.*, 2010). These results could explain the high stretch factor of the masseter muscle found in *M. vivesi*, which feeds on preys with scales that are removed by chewing rapidly (S. M. Ospina-Garcés, personal observations). However our findings of high stretch factors in *M. vivesi* were not similar to cranial changes related to wide gape found in piscivorous *Noctilio* (Freeman, 1984).

There were differences in the stretch factor of the temporal muscle among dietary groups but changes followed a different pattern in comparison to the masseter muscle. *M. vivesi* had the highest stretch factor value followed by insectivores and facultative piscivores. The stretch factors of the temporal muscle calculated in frugivorous, nectarivorous and insectivorous phyllostomid bats fluctuate less among diets (e.g., 1.06 – 1.14) than the stretch factors for the masseter muscle (e.g., 1.22 – 1.46) (Dumont *et al.* 2009). Also, similarly to *Myotis* species, values of the stretch factors for the temporal muscle in phyllostomids are lower than values of the stretch factors for the masseter muscle (Dumont *et al.* 2009). Although it has been mentioned that the role of the temporalis in jaw moment dominates in bats with hard diets (Santana *et al.*, 2010), these results indicate that the mechanical advantage generated by the masseter muscle could be more determinant among diets in bats. The stretch factor of the temporal muscle found in *M. vivesi* was higher than values reported in other bats (Dumont *et al.* 2009), suggesting that the high mechanical advantage generated by masticatory muscles would favor chewing slippery prey (e.g., fish) that is captured with the claws on water surface and then transferred to the mouth (Schnitzler *et al.*, 1994).

The relationship between form and function

Morphological variation was related to functional variation in masticatory muscles as indicated by the correlation between the mandibular processes region and the stretch factor of the masseter muscle (Fig. 6). This relationship supports the idea of morphological variation in a dietary context considering that there was no phylogenetic signal in the stretch factors and shape distances from the mandibular processes region, probably because piscivory in *Myotis* has evolved convergently. Previous studies in bats have found large-scale cranial changes (cranial enlargement or shortening) and small-scale cranial changes (displacement of mandibular processes) (Aguirre *et al.*, 2002; Nogueira *et al.*, 2005), as in the case of *Myotis* species, among species from different dietary groups. In the case of cranial morphological changes from insectivory to piscivory in *Myotis*, small changes such as the displacement of the mandibular processes are enough to increase the moment arm of the muscle and probably the bite force production at lower gape angles, presumably

allowing the inclusion of fish in the diet. Our observations were similar to previous bat studies where variation in diet has been related to morphological variation in the dentition and the mandibular processes region (Dumont and Herrel, 2003; Monteiro and Nogueira, 2009).

Considering differences among diets in the stretch factor of the masseter muscle and its highest correlation with masticatory processes region, we can propose that the ecological effect on the mandibular processes region in *Myotis* species is more evident than in skull morphology. The facultatively piscivorous species were more similar to each other in the cluster groupings from this module, supporting the idea of ecological effect on the mandibular processes region. Additionally, the biggest deviations from insectivorous to piscivorous species occurred in the mandibular processes region. These results suggest a significant association between mandibular shape and diet in *Myotis* with a gradual pattern of change from insectivory to piscivory. However, this trend was not found in the skull suggesting that the cranial shape in both piscivorous forms from insectivorous ancestor evolved independently. The implementation of geometric morphometrics was a powerful tool to describe this variation in a morphologically conservative genus (Larsen *et al.*, 2012).

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Appendix I. Specimens examined (number of specimens) and access code to the sequences in GENBANK. Museum acronym are as follows: AMNH = American Museum of Natural History, New York; CNM= Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México, México; CTUA=Colección Teriológica Universidad de Antioquia, Medellín, Colombia; NMNH= National Museum of Natural History, Smithsonian Institute, Washington; EBD= Estación Biológica Doñana, Sevilla, Spain. Specimens are listed according to country and locality or province.

M. adversus (18)– NMNH: S. Makapan, Sumatra: 144266, 144286, 144295, 144296, 144292, 144294. Pulo mendanau, Indonesia: 124922, 124923, 125153, 112606. Siam, Thailand: 251719, 251721, 296508, 251720, 251717, 251716. Mankol, Borneo: 153937, 153938, 153936, 578490, 296770.

M. albescens (17)– CNM: Ocosingo, Chiapas, México: 9523, 19300, 19301, 22967, 22968, 23736, 23737, 23738, 23739, 23740, 24473, 24474, 24475, 24477, 24478, 24479, 41799. Sequence

M. bechsteinii (8)– AMNH: baden–wurttemberg, Germany: 245362, 217133. NMNH: Foret russy, France: 231169, 231170, 231171, 154080, 154081, 38016.

M. bocagii (16)– EBD: Nvuba river, Equatorial Guinea: 14164, 14915, 14916, 13943, 13944, 17639. NMNH: Kinshasa, Democratic Republic of the Congo: 19795, 197955, 260031. Bumba zone, Democratic Republic of the Congo: 38019, 465820, 537719, 537720, 537721, 547013, 547014.

M. capaccinii (24)– EBD: Valle Gruta del camello, Morocco: 15528, 15533, 15594, 15615. NMNH: Switzerland: 113906, 115276, 115277, 121193, 121195, 121196, 121197, 121198, 121199, 121200, 121201. Cagliari, Cerdeña: 38348, 38349, 38350. Oujda, Morocco: 476540, 476543, 476544, 476546, 540780, 86639.

M. dasycneme (5)– NMNH: Nr. Maesiricht, Holland: 154029, 153985, 153986, 153987, 153988.

M. daubentonii (22)– EBD: Malaga, Spain: 9661, 9663, 9779, 9780, 9781, 9782, 9784, 15973, 15575, 28793, 28794, NMNH: Lombardy, Italy: 86562, 86566, 86570, 86572, 86578, 16355, 152538.

M. dominicensis (6)–. NMNH: Clarke Hall, Dominica: 113547, 113555, 113563, 361911, 361912, 361913.

M. emarginatus (6)– NMNH: Bouches de rhônes, France: 85517, 105295, 105296, 319209, 476547, 476548, 540781.

M. evotis (25)– NMNH: Colorado, USA: 30305, 38680, 147660, 148161, 148163, 148164, 148165, 148166, 207988, 207989, 209037, 209218, 250566, 271166. New Mexico, USA: 349214, 349215, 349216, 349217, 349218, 506257, 554292, 554293, 554294, 552743, 570687.

M. horsfieldii (26)– NMNH: Borneo: 154646, 154647, 154648, 156560, 166561, 155798, 196561, 196562, 198933, 198936, 198937, 198939, 528299, 590138, 590139, 590140, 590141, 590142, 590143, 590145, 590434, 590698, 590699, 590700, 590701, 590702.

M. keaysi (25)– CNM: Tabasco, México: 6805, 7876, 7880, 7881, 7882, 7883, 7884, 7885, 7886, 7887, 7888. Yucatán, México: 16337, 16345, 18510, 18953, 18954, 20939, 20940, 20942, 20983, 32853, 32854, 404331, 40433, 40434.

M. leibii (23)– NMNH: Virginia, USA: 13194, 270086, 283778, 296798, 296799, 314985, 364631, 364632. Maryland, USA: 150274, 150275. New York, USA: 187406, 187497, 187408, West virginia, USA: 461879, 461880, 487616, 489615, 552741, 55845, 589246, 60949.

M. macrotarsus (13)– NMNH: Negros oriental, Phillippines: 254502, 254505, 254509, 254512, 254700, 256090, 256093, 458684, 458685, 458686, 478687, 498688, 498689.

M. myotis (20)– AMNH: bavaria–waldmünchen, Germany: 150109, 150106, 150111, 150112. NMNH: Germany: 37548, 86647, 86648, 86649, 152546. Uri, Switzerland: 113853, 113854, 113855, 113856, 113861, 121191, 145193, 145194. Czech republic: 347425, 347426, 540783.

M. muricola (29)– NMNH: Sabah, Malasya: 37355, 38352, 292392, 292393, 292394, 292395, 292396, 292401, 292403, 292404, 292405, 292406, 292448, . NW Pakistan: 353113, 353114, 353115, 353116, 353117, 353118, 353119, 353120, 353122, 3534433, 413505, 413506, 481081, 481082, 481083, 481085, 481086, 4810817, 481089.

M. nattereri (13)– AMNH: Holstein, Germany: 146358, 146359, 146360, 146364, 245371. NMNH: Thurgau, Switzerland: 113866, 113867, 113868. Mardebu, Germany: 152541, 152542, 152543. Valsesia, Italy: 38015. Central bohemia, czech republic: 540785.

M. nigricans (29)– CNM: Reserva del triunfo, Chiapas, México: 182, 6463, 20425, 20951, 20952, 20953, 20954, 20955, 20957, 20958, 22869, 22870, 22871. Veracruz, México: 14289, 8210, 8211, 8213, 8214, 8215, 8481. CTUA: Maceo, Antioquia, Colombia: 10061, 10228, 10447, 11173, 11206, 11290, 11292, 11293.

M. riparius (28)– AMNH: 208652 CTUA: Antioquia, Colombia: 10915, 10297, 10724, 11289, 11295, 11297, 20226, NMNH: Para, Belem, Brasil: 361782, 361786, 381788, 361790, 361791, 483949, 483950, 483951. Pichincha, Ecuador: 513482, 528567, 528568, 528570, 548342, 548344, 548345, 548347, 549518, 566455, 566456, 574564.

M. thysanodes (12)– CNM: N México: 2118, 5005, 5546, 18604, 12469. Querétaro, México: 20006, 20082. Ocampo, Guanajuato, México: 22472, 22473, 22474, 28886, 30922.

M. velifer (30)– CNM: Morelos, México: 473, 7156, 7902, 7903, 8241, 9069, 9450. Coahuila, México: 13817, 13818, 13819, 13820. Baja California, México: 15571, 15572. Puebla, México: 16857, 16867, 16809, 18523, Durango, México: 19996, 19997, 19998, 19999, 20000, 20001, 28883, 28884, 28856, 28858, 28859, 28860, 28861, 28863, 45807, 45808.

M. vivesi (31)– CNM: Isla Partida Norte, México: 15658, 15660, 15661, 15662, 15664, 15659, 16803, 16805, 16806, 16807, 23909, 23910, 23912, 23914, 23915, 39327, 45675, 45679, 45680, 45681, 45682, 41683, 45684, 45685, 45686, 45689, 45690, 45691, 45693, 45696, 45697.

GENBANK accessions codes Cyt b: JX130523, AY007528, AY007530, L19726, AJ504406, AJ504408, AF376843, AF376845, AF376846, AF376847, AF376848, AF376849, AF376852, AF376855, AF376861, AJ841957, AF376870, JX130552, JX130535, JX130588, GU372836, AJ841949.

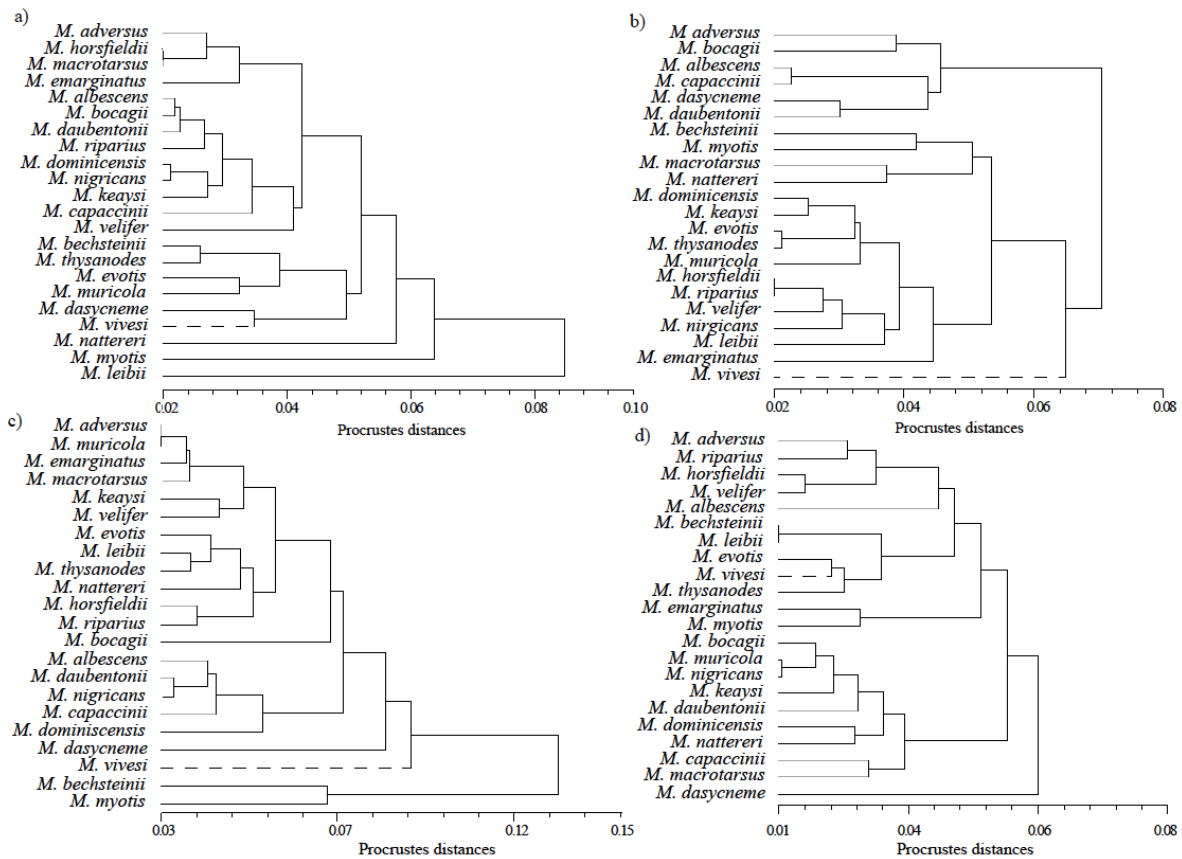
GENBANK accessions code RAG2: KF312536, AM265643, AM265646, KF312542, AM265652, AM265653, AM265656, AM265657, AM265666, AM265668, AM265671, AM265675, AM265679, AM265680, AM265681, AM265682, AM265687, AM265693, AM265695, AM265654, KF312553, AM265696.

Appendix II. Anatomical definition of landmarks and semilandmarks in cranial configurations (skull 1–2, and mandible 1–2), following the cranial nomenclature of Giannini *et al.* (2006).

Module	Number	Type	Anatomic description
Skull 1	29	Type I	End of the sutura coronalis
	30–31	Type I	Tip of the zygomatic arch, postglenoid process.
	32	Type I	Mastoid exposure of petrosal
	2	Type I	Paracondylar process
	1	Type II	The union of the condyle and the ectotympanic in lateral view
	3–4	Type II	Foramen magnum (vertices)
	5–28	Semi	Contour of the sagittal crest
Skull 2	1,12–17	Type I	End of the sutura coronalis, dental alveolus (tips)
	18–19	Type II	The bottom of the lacrimal foramen and the foramen for frontal diploic vein.
	20	Type II	The concavity of the orbitosphenoid and palatine suture.
	2–11	Semi	The external contour of the frontal and nasal bones
Mandible 1	1,22,17	Type II	Angular and coronoid process (tips)
	18	Type II	Concavity between the ramus and corpus of mandible
	2–16	Semi	Contour between angular and coronoid process
	19-21	Semi	Contour in the base of coronoid process
Mandible 2	1–2	Type I	Tips of the premolar-molar row on the dental alveolus
	3		Anterior tip of the dental alveolus (i3)
	5	Type II	Maximal curvatures on mental surface
	4,6–14	Semi	Inferior contour of the corpus

Appendix III. Statistical comparisons of centroid size among diets and sexes in 22 species of *Myotis*. F-statistics from the two-way ANOVA (p value) for the two factors are listed. Significant differences are indicated by an asterisk.

Species	Diet	Sex
	$F_{2, 351} (p)$	$F_{1, 351} (p)$
Parieto–occipital region (skull module 1)	*58.15 (<0.005)	0.041(0.83)
Frontal–maxillary region (skull module 2)	*89.30 (<0.005)	0.13 (0.71)



Appendix VI.

Dendrograms showing UPGMA clustering of species from Procrustes distances among configurations in four cranial modules. a) UPGMA clustering of species from Procrustes distances among configurations of the parieto-occipital region. b) UPGMA clustering of species from Procrustes distances among configurations of the frontal-maxillary region. c) UPGMA clustering of species from Procrustes distances among configurations of the mandibular process region. d) UPGMA clustering of species from Procrustes distances among configurations of the alveolar region. Facultatively piscivorous species are indicated by grey lines while piscivorous species are indicated by dotted lines.

CAPÍTULO 2

Evolution of cranial shape and diet in species of *Myotis* (Chiroptera: Vespertilionidae) as inferred with comparative and phylogenetic analyses of geometric morphometric data.

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Short running title: Evolution of cranial shape and diet in *Myotis*

Abstract

Species in *Myotis* exhibit a pattern of variation in cranial morphology in association with insectivorous, facultatively piscivorous, and piscivorous diets. Our study is focused on examining changes in five cranial morphological traits related to the evolution of diets. Geometric configurations from two mandibular and three cranial modules in twenty-two species from *Myotis* were analyzed to infer evolution of shape. We included *Kerivoula papillosa*, an insectivorous species, and two species of genus *Noctilio* as outgroups, one piscivorous (*N. leporinus*) and one insectivorous species (*N. albiventris*). Our goals were the reconstruction of ancestral shapes to detect deformations, and to relate these with changes between diets. A reference phylogeny was estimated using TNT for the simultaneous analysis of previously available molecular sequences (Cyt-b, RAG2) and our five landmark data sets. Under a comparative approach, five configurations were mapped on this phylogeny, using squared-change parsimony as implemented in Rhetenor (Mesquite) and tpsTree. Under a phylogenetic approach, the same Procrustes landmark coordinates were mapped using linear parsimony in TNT. Both mapping methods reconstructed different ancestral landmark configurations. However, these differences are not related to branch lengths. Smaller shape change from ancestors to descendants was estimated with linear parsimony for some branches as well as with squared-change parsimony for other branches. These results hold whether the branch lengths are similar and even when branch lengths are asymmetrical. Our conclusion is that the incorporation of branch lengths had a minimal effect on ancestral reconstructions. Also, we estimated concerted changes to test the hypothesis that changes in shape are related to changes in diet. Optimizations of concerted changes in five morphometric modules and three diets imply that cranial morphology in piscivorous and facultatively piscivorous species changed at least in six branches from ancestral mandibular and cranial forms associated with an insectivorous diet.

Introduction

Inferences of morphological ancestral states and directionality of change are important in providing the phylogenetic pattern that can be further analyzed for the associated functional utility and performance advantage as required in hypotheses of adaptation (Grandcolas et al., 2004). Comparative methods reconstruct morphological change as a statistical estimation procedure, which attempts to remove statistical dependence created by phylogenetic relationships in independent contrasts (Felsenstein, 1985) and for estimation of ancestral states (Schluter et al., 1997). Assuming a model of Brownian motion, optimal morphological ancestral states and shifts can be calculated by mapping discrete states or continuous-valued data along a previously available phylogeny. As molecular data become easier to obtain, in comparison with morphological matrices, it is now customary that they provide the reference phylogeny for study of the evolution of morphological characters (Felsenstein, 2002). A review of conceptual issues, statistical methods, and some of the controversies was presented by Baker (2002). Inferences of geometric morphometric shape change under squared-change-parsimony optimize the ancestral configurations that minimize tree length as measured by the sum of the squared Procrustes distance between shapes; it is the shortest distance between shapes as points in the multivariate space defined by partial warps as shape variables (Rohlf, 2001; Felsenstein, 2002).

Under the alternative approach, phylogenetic methods reconstruct ancestral features as a non-statistical estimation procedure, sometimes referred to as the “lineage method” (Kluge, 2005). This parsimony estimation is based on a combined tree and thus the optimization of changes derives from the phylogenetic analysis of all available data including the morphological feature of interest (Luckow and Bruneau, 1997), and together with the out-groups in the taxon sampling (Grandcolas et al., 2004). Linear parsimony methods for mapping landmark configurations under a given tree and for building trees from geometric morphometric data were not implemented up until recently. First Catalano et al. (2010) described a method to analyze landmark data considering a given superposition. Later, Catalano and Goloboff (2012) described a method that superimposes and maps landmark data simultaneously. This is basically a phylogenetic superposition that removes differences among configurations by selecting optimal rotations and orientations that minimize linear (Euclidean) distances between each corresponding coordinate at a

landmark. The placement of terminals is swapped in a tree until the alignment of configurations of landmarks and the tree length are optimal in terms of the total cost over all landmarks and all branches of competing trees. This dynamic homology approach of Catalano and Goloboff (2012) can also be used to map landmark configurations under a given tree.

In the present paper, we test an ecological question in an evolutionary context using linear parsimony and squared-change parsimony methods for the optimization of continuous variation in landmark configurations. We ask how cranial shape and diets have changed in species of *Myotis* (Chiroptera: Vespertilionidae). This group of bats exhibits a pattern of variation in cranial morphology in association with three diets (insectivorous, facultative piscivorous, and piscivorous), which has not been documented before. Adaptations to different feeding habits have been in the core of the discussion of the subgeneric classification for *Myotis*. Although a number of scientists has shown that there is a considerable discordance between molecular and morphological divergence in genus *Myotis* (Ruedi and Mayer, 2001; Ruedi *et al*, 2013) there is no phylogenetic reconstructions with morphological data to test morphological convergences. Our research tests the hypothesis that skull traits in ecomorphs have evolved independently by mapping geometric morphometric shape characters on a combined molecular and morphometric phylogeny. Reconstructed ancestral landmark configurations were used to make inferences about the evolution of cranial shape in 22 bat species of the genus *Myotis* as exemplars of all subgeneric groups (Findley 1972, Ruedi *et al*. 2001) and three different ecomorphs and diets.

The genus *Myotis* is the most diverse genus of bats (Ruedi and Mayer, 2001; Stadelmann *et al*., 2004) with 95 species in the world covering diverse habitats and foraging strategies, including one species, *M. vivesi*, with a truly piscivorous diet (Blood and Clark, 1998). Piscivory in bats appeared in parallel also in *Noctilio leporinus* (Noctilionidae). We included *Kerivoula papillosa*, an insectivorous species, and two species of genus *Noctilio* as outgroups, one piscivorous (*N. leporinus*) and one insectivorous species (*N. albiventris*). Some species in genus *Myotis* (Vespertilionidae) are mainly insectivores but occasionally feed on fish (*M. ricketti*, *M. daubentonii*, *M. capaccinii*, *M. adversus*, *M. macrotarsus*, *M. albescens* and *M. stalkerii*), therefore these are considered facultatively piscivorous (Whitaker and Findley, 1980; Flannery, 1995; Law and Urquhart, 2000; Siemers *et al*.,

2001; Aihartza et al., 2008). These species were initially grouped in the same subgenus due to similar external characteristics associated with their common diet, for example the laterally compressed and large claws used to catch prey on the water surface (Findley, 1972; Norberg and Rayner, 1987; Lewis-Oritt et al., 2001). However, a phylogenetic analysis showed that the ecomorph of facultative piscivorous species was not monophyletic (Ruedi and Mayer, 2001; Stadelmann et al., 2004). Diet has been related to foraging strategy in *Myotis* species. For example, bats over gleaning for prey are more selective than aerial hawking species (Burles et al., 2008); likewise trawling species catch fishes on water (Stadelman et al, 2004). Members of the genus *Myotis* are thus an excellent model to examine changes in the morphological traits associated to the evolution of piscivory from insectivorous ancestors (Lewis-Oritt et al., 2001).

Our goals were the reconstruction of ancestral forms to detect shape deformations between species with different diets (piscivorous, facultatively piscivorous, and insectivorous). We addressed the following specific two questions: 1) are there changes in cranial morphology shared among species with the same diet? and 2) how has cranial morphology changed from insectivorous ancestors to piscivorous and facultative piscivorous species? We test the hypothesis that trends in cranial morphology would be similar between species with the same diet inferring morphological evolution of skulls and jaws under a phylogenetic approach using landmark configurations from mandibular and cranial modules. Although we focus on bats, our approach is of wider interest since it allows for evaluation of how shape variation and change in continuous character data derived from geometric morphometrics should be tested for homology and homoplasy in a phylogenetic analysis, as with any other type of data. This study uses a phylogenetic approach to analyze morphometric variation in our newly generated landmark data from five modules of cranial morphologies. We provide an empirical application of the method developed by Goloboff and Catalano (2011) to infer ancestral shape and change, using linear parsimony for optimizing shape data to a phylogeny, and also for directly estimating the phylogeny from combined molecular and landmark data. Furthermore, we compare how squared-change parsimony and linear parsimony influence on the phylogenetic pattern of reconstructed ancestral shapes and the hypothesis of association between cranial shape and diets in the diversification of *Myotis*.

Material and Methods

Molecular data

Twenty-five DNA sequences of two molecular markers were obtained from GenBank (Supplementary material 1: data matrix). We used 1140 pb of complete Cyt-b with ATG as a start codon and AGA as stop codon (Ruedi and Mayer, 2001; Stadelman et al., 2004). We also included a fragment of 1054 pb from a recombination activating protein gene (RAG2) from a recent phylogenetic study for *Myotis* (Ruedi et al., 2013). We aligned Cyt-b and RAG2 sequences with the multiple sequence alignment progressive method (FFT-NS-2) with the usual parameters (scoring matrix for nucleotide sequences 200PAM/K=2 and Gap opening penalty: 1.53) operating in the program MAFFT 7 (Katoh et al., 2002). These sequences in combination with landmark data were used to build a reference phylogeny for optimization of shape characters.

Morphometric data

Five different landmark configurations (shape characters) were defined in order to describe the cranial morphology in the same species included in the molecular study (Fig. 1) in the same twenty-five species (Supplementary material 1). These data came from a total of 421 specimens (Table 1) deposited in five mammal collections (Supplementary material 2: list of specimens). Specimen identifications on labels were corroborated in view of difficulties in the taxonomy of *Myotis* species (LaVal, 1973; López-González, 2001; Dietz and Von Helversen, 2004; Simmons, 2005; Larsen et al., 2012). We selected specimens from the same biogeographic region and we checked distributions following Simmons (2005). Digital photographs of lateral and ventral views of skulls, and lateral views of mandibles were acquired using a reflex camera Nikon D3100 with a DX Nikkor 18-55 mm lens. Small specimens were photographed with a Leica Z16 APOA “Macroscope” modular zoom system at the bioinformatics unit UNIBIO (Instituto de Biología, UNAM).

Two-dimensional landmark configurations from images were obtained with the program TpsDig 2.16 (Rohlf, 2008). Five configurations were registered separately which

correspond to cranial developmental modules in mammals, and are also of biomechanical relevance in diet differences (Porto et al., 2009). Lateral views of skulls (411 photographs) were divided into two modules (Fig. 1a, b). The first module comprises the parieto-occipital region and it was registered with a set of 8 landmarks and 24 semi-landmarks (Fig. 1a). The second module is the frontal-maxillary region; it was registered with collection of 10 landmarks and 10 semi-landmarks (Fig. 1b). The mandibles were divided into two modules in 421 photographs of lateral views. The third module is the process area, which was registered with 4 landmarks and 18 semi-landmarks (Fig. 1c). The fourth module is the dental row; it was registered with a configuration of 4 landmarks and 10 semi-landmarks (Fig. 1d). The fifth module corresponds to the ventral view of the skulls; we registered a set of 13 landmarks and 7 semi-landmarks on 407 photographs (Fig. 1e).

Statistical morphometric analyses were conducted with the IMP program series (Sheets, 2003). Procrustes coordinates were extracted from five alignments of configurations for the twenty-five species pooled together (Supplementary material 2). Separately for each module, we used a Procrustes superimposition to align landmark coordinates with CoordGen6h. Also semi-landmarks were aligned with SemiLand6 by sliding points along curves to minimize bending energy of deformation from the mean form. Instead of calculating partial warps as shape variables, we used the average Procrustes coordinates of each species in our simultaneous parsimony analyses to reconstruct a combined molecular-morphometric phylogeny, and for mapping five shapes on this resulting tree. Species averages of the five module configurations were prepared in the data matrix formats required by software we used for comparative and phylogenetic analyses. The combined data matrix with the two molecular markers and five characters in twenty-five terminals is presented as “Supplementary material 1”.

Phylogenetic analyses of molecular and geometric morphometric data

First, molecular phylogenetic analyses of twenty-five sequences of Cyt-b and RAG2 were executed in Winclada (Nixon, 2002) using Ratchet with 10% of characters sampled for reweighting, performing 200 iterations (Nixon, 1999). Support was calculated with Jackknife (1000 iterations, with 36% of character removal). The molecular tree from our subset of terminals was saved and compared with the previously published phylogeny by Ruedi et al., (2013), with 95 terminals (Supplementary material 3a).

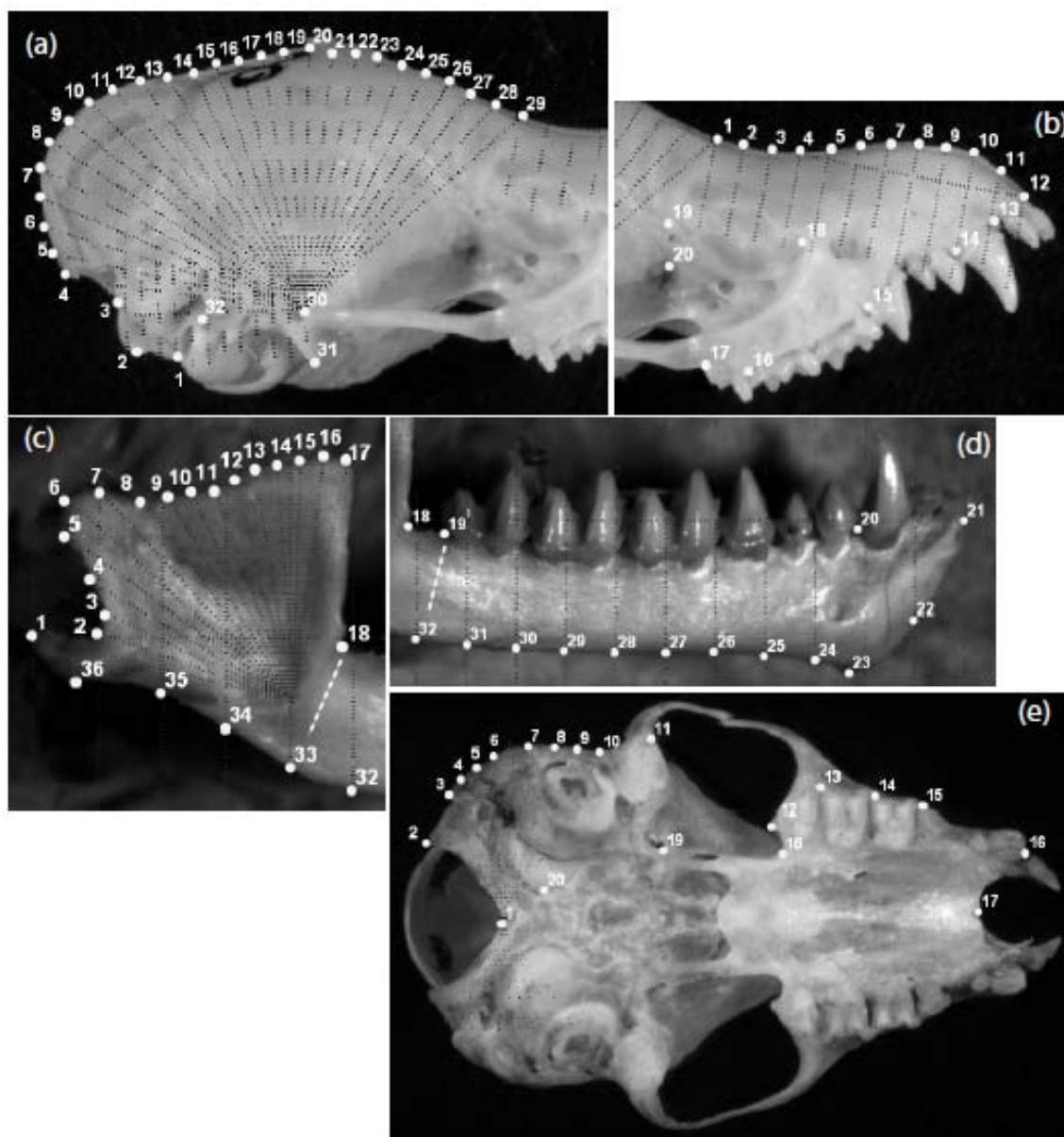


Fig. 1. Five configurations of points devised to register the shape of five cranial modules in *Myotis* (a-e). (a) Module 1, parieto-occipital region with 32 points, 1-32, lateral view; (b) module 2, frontal-maxillary region with 20 points, 1-20, lateral view; (c) module 3, mandible process area with 22 points, 1-18, 33-36, lateral view; (d) module 4, dental row with 14 points, 19-32, white dashed line connects initial and last points, lateral view; (e) module 5, skull with 20 points, 1-20, ventral view.

Next, morphometric phylogenetic analyses of landmark data alone were conducted with TNT (Goloboff et al., 2008). Five geometric morphometric characters, comprising two mandibular and three cranial modules (Fig. 1) were analyzed to test if the piscivorous and the five facultative piscivorous species in a landmark-only phylogenetic analysis group together. The aligned “x,y” Procrustes coordinates of the species mean shape for each module were analyzed without coding (Goloboff et al., 2006). Five landmark data blocks in 25 terminals were used for tree search with the new script “land_search.run” (written by Santiago Catalano). With this script, each landmark configuration, regardless of the number of “x, y” points, is weighted in such a way that the contribution to the total score of each configuration is similar to that of a single character. In this procedure for tree search, TNT simultaneously optimizes the total tree score and the landmark configurations at internal nodes by a dynamic superimposition solution (Catalano and Goloboff, 2012). The script was executed with 1st argument = 3 for “strength” (lm cell 6 nest 4 2), and 2nd argument = 1 (with realignment during TBR); we performed 100 replicates, each replicate starting from a Wagner tree, followed by TBR. The topology of the best tree from morphometric data alone was saved and compared with the molecular phylogenetic tree (Supplementary material 3b).

Third, the combined data matrix with aligned Cyt-b and RAG2 sequences and the five average configurations of aligned landmarks for twenty-five species were also analyzed in TNT to infer morphological evolution of skulls and jaws. We used the same script “land_search.run” running 100 replicates, under same argument values as with morphometric data alone. This script includes a series of instructions for running tree searches considering landmark data alone or in combination with other sources of evidence. Support for the combined tree was calculated with the new script “land_jakcs.run” (arguments 2 0). This new script (also written by Santiago Catalano) allows calculating Symmetric Resampling frequencies (Goloboff et al., 2003) from data matrices with landmark configurations alone or in combination with other data types. The topology of the best tree from our simultaneous parsimony analysis of molecular and morphometric data was saved and used as reference tree in our optimizations of shape change in *Myotis* (Figs. 2, 3).

Table 1. Number of specimens for the twenty-four species included in morphometric and phylogenetic analyses.

Species	Skull lateral view (modules 1 and 2)	Mandible (modules 3 and 4)	Skull ventral view (module 5)
<i>Myotis adversus</i>	17	18	18
<i>M. albescens</i>	16	17	17
<i>M. bechsteinii</i>	8	8	7
<i>M. bocagii</i>	10	16	14
<i>M. capaccinii</i>	20	24	24
<i>M. dasycneme</i>	5	5	5
<i>M. daubentonii</i>	17	14	18
<i>M. dominicensis</i>	6	6	5
<i>M. emarginatus</i>	7	7	5
<i>M. evotis</i>	25	24	24
<i>M. brandtii gracilis</i>	3	3	3
<i>M. horsfieldii</i>	25	26	26
<i>M. keaysi</i>	25	23	23
<i>M. leibii</i>	20	21	19
<i>M. macrotarsus</i>	13	13	14
<i>M. myotis</i>	20	20	18
<i>M. nattereri</i>	13	13	13
<i>M. nigricans</i>	28	28	28
<i>M. riparius</i>	28	25	26
<i>M. thysanodes</i>	12	12	11
<i>M. velifer</i>	30	30	33
<i>M. vivesi</i>	27	31	22
<i>Noctilio leporinus</i>	31	32	29
<i>N. albiventris</i>	3	3	3
<i>Kerivoula papillosa</i>	2	2	2
Total	411	421	407

Evolution of cranial shape

Within the “Procrustes paradigm” (Adams et al, 2013), the evolution of shape is regarded as a conventional statistical procedure to estimate deformations along tree branches drawn connecting ancestors and terminals plotted into a multivariate space determined by the major axes of variation among species (relative warps). This procedure was proposed by Rohlf (2002) and has been extended by Klingenberg and Gidaszewski (2010) to measure homology and homoplasy in shape; it is recommended as a particularly useful visualization to detect convergences among species in different branches (Monteiro, 2013). Instead, we prefer a phylogenetic procedure to study variability and change for geometric morphometric data. Shape variation in five modules of cranial morphologies was tested for homology and homoplasy directly over our reference tree, as with any other type of data (Nixon & Carpenter, 2011). For a simple measure of phylogenetic variability of landmark data along the tree we used the difference of the minimum parsimony score and the maximum parsimony score for each cranial configuration. Furthermore, we computed the retention index and the consistency index to estimate the amount of shape change that can be interpreted as synapomorphy, or as homoplasy. We are not using the two measures of the fit of morphometric data to the phylogeny offered by Klingenberg and Gidaszewski (2010), since these are based on Procrustes distances and squared-change parsimony as function of relative change. These chord distances in the multivariate shape space do not qualify as direct extensions of the consistency index and retention index in phylogenetics.

We estimated parsimony scores for each landmark configuration based on the sum of landmark displacements across alignments of configurations from node to node along a tree, as operated in linear parsimony for landmarks (Catalano et al., 2010). We computed parsimony scores with TNT separately for each landmark configuration (22 species, outgroups pruned) on the combined molecular and morphometric tree. We used the command “lmr Tree t cycles 5 level 2/c”, followed by “lmark lscore t/c”, where t= tree number, and c= character number. Each shape optimization was estimated approximating landmark positions with a 10x10 grid, nesting Sankoff 10 times, and using iterative-pass for landmark optimizations. These settings enable us to calculate the parsimony score with high precision (s) over our combined molecular and morphometric tree, the minimum possible steps (m) on the single character best tree, and the minimum steps on a bush tree (g) for each shape

character (modules 1-5). From these values we derived the character consistency (ci) and retention (ri) indices as usual ($ci = m / s$; $ri = g-s / g-m$). Results are presented in Table 2, and synapomorphies for *Myotis* are illustrated in Fig. 4.

Evaluating concerted change in shape and diet

The phylogenetic analysis of the combined molecular and landmark data would provide a reference tree to answer our question if changes in cranial morphology occur in different branches leading to one piscivorous and the five facultative piscivorous species. In order to evaluate within a phylogenetic framework if changes in shape are related to changes in diet (piscivorous, facultatively piscivorous, and insectivorous), both variables were optimized on the reference tree, and concerted changes in both characters were inspected. Since diet is related to foraging strategy, we also estimated if changes in foraging (aerial hawking, over gleaning, trawling) are related to changes in diet using pairwise comparisons module in Mesquite (Maddison, 2006). When characters are single variables (discrete or continuous) searching for a concerted pattern of change is pursued with implementations under a probabilistic framework (comparative methods, Pagel, 1994; Maddison, 2000). However, when a multivariate matrix represents a shape character, only a more “descriptive” approach is presented here for the optimization of diet type, foraging strategy (discrete variables) and five shape characters (modules 1-5, as five landmark coordinates sets) using TNT. We inspected optimizations to consider changes in diet or foraging in the branches leading to the piscivorous or facultative piscivorous species, and evaluating if the change in shape also occurs in those branches. Results are presented in Fig. 2 and Fig. 3.

Ancestral shapes under squared-change parsimony and linear parsimony

The reconstruction of ancestral shapes to detect changes among species with different diets was approached with two different mapping methods, squared-change parsimony (Maddison and Maddison 1990), and linear parsimony (Catalano et al. 2010). These two methods are used here to evaluate the effects of branch lengths and different parameterizations in cladistics parsimony and Brownian models to estimate cost of shape change in the interpretation of how two mandibular and three cranial modules changed from insectivorous ancestors to piscivorous and facultative piscivorous species. First, under

a squared-change parsimony approach, coordinates of five configurations were mapped onto the optimal tree from our combined matrix using Rhetenor (Dyreson and Maddison, 2005), from the software package Mesquite 2.75 (Maddison and Maddison, 2011). We also used the software tpsTree 1.21 (Rohlf, 2007). In both programs, “x,y” landmarks entered were already Procrustes aligned. Given a phylogenetic tree and observed shapes at terminals, Rhetenor and tpsTree calculate shapes at ancestral nodes using model based squared-change parsimony, which takes into account branch lengths. Since each shape is defined by a matrix of landmark points, the squared-change assumption is that the cost of a change from one reference shape (X) to another target shape (Y) is $[X-Y]$ squared-change, which for landmark data is the squared Procrustes distance along each branch on a traced tree across shape space. Rhetenor treats each landmark point as a different character, for which “Brownian default” is selected as probability model, in the “List & Manage Characters” window. The same model is the basis for reconstruction of ancestral shapes in tpsTree, but instead of landmarks, the partial warp scores are first computed for terminals and then operated for estimates of the partial warp scores for each internal node, following the squared-change parsimony procedure of McArdle and Rodrigo (1994). This distance along each branch in the tree connects points (observed and ancestral shapes) located in the multidimensional tangent space of partial warps. Landmark configurations of ancestral shapes are estimated in tpsTree with thin plate splines of the relative deformation on any node along the tree.

Under a linear parsimony approach, the five configurations of landmarks were mapped with TNT onto the optimal tree from our combined matrix. In this program, “x,y” landmarks of the terminals are operated to estimate shapes at ancestral nodes using linear or “spatial parsimony” as described the first time by Catalano et al. (2010). The cladistics parsimony change assumption is that the cost of change from one shape to another is not a Procrustes distance between shapes, but a landmark displacement computed adding the contribution of individual differences at each landmark point between configurations in a series of ancestor-descendant superpositions. The method proposed by Catalano and Goloboff (2012) is indifferent to any particular “static” superimposition (ordinary, or generalized). Such landmark displacements do not estimate shape deformation relative to the consensus landmark configuration, and are not estimates of the chord length between two points representing two shapes in tangent spaces of shape covariance, in which case

invariance to rotation would certainly matter (Bookstein, 2002; Rohlf, 2002). Classical methods of statistical superposition (such as Bookstein, SBR, Procrustes GLS, or RFTRA, sensu Zelditch et al., 2004, p 105) are not appropriate for inferring phylogenetic shape transformations and a new method to optimize translation, and rotation has to be developed. The method proposed by Catalano & Goloboff (2012) superimposes the configurations of ancestor-descendant nodes on a tree, and it is neither an ordinary nor a generalized superposition. The total landmark displacement for spatial parsimony is computed sequentially in a phylogenetically ordered superposition of shapes mapped from node to node along a given tree (Catalano et al., 2010).

Ancestral shapes were reconstructed to investigate how cranial morphology changed from insectivorous to facultative piscivorous and to piscivorous species in *Myotis*. At each ancestral tree node, we assessed two alternative “estimated shapes” (es1 & es2) produced by the two methods. Ancestral landmark “x,y” configurations reconstructed with squared-change parsimony were labeled “es1”, alternatively, we labeled “es2” ancestral shapes inferred with linear parsimony. Estimated shapes for internal nodes were retrieved as strings of hypothetical “x,y” landmarks, module by module. In tpsTree, we saved ancestral landmark configurations of HTUs. In TNT, we used the script “Export_tps” to save ancestral shapes. These two sets of alternative estimated shapes for each module were used to provide deformation grids for inferences of shape changes associated with changes in diet.

Identifying the effects of branch lengths in estimates of ancestors and shape changes.

The difference between ancestral shapes for a given node produced by squared-change parsimony (es1) and linear parsimony (es2) was examined with the comparison of deformation grids and with Procrustes distances. First, deformation grids showing the changes in landmark positions between configurations of ancestors and descendants were inspected for the direction and location of shape changes inferred in the six branches that subtend the piscivorous and facultatively piscivorous species. We present drawings of ancestral shapes from Mesquite and TNT (Fig. 5) for two modules, the parieto-occipital region (module 1) and the mandible process region (module 3). In this comparison, drawings of alternative hypothetical shapes (es1, es2) of the cranial parieto-occipital region (module 1, 32 points) were produced for tree node 40 with similar branch lengths (54, 55)

in our combined phylogeny. This node is the shared ancestor to a facultatively piscivorous species (*M. daubentonii*) and an insectivorous species (*M. beschteinii*). Similarly, we show the two hypothetical shapes (es1, es2) of the mandible process region (module 3, 22 points) produced for tree node 47 with asymmetrical branch lengths (45, 65) in our reference phylogeny. This node is the common ancestor to the facultatively piscivorous *M. macrotarsus* and the insectivorous *M. horsfieldii*.

Instead of providing all drawings of the pair of estimated shapes at a given node, we performed regression analyses to relate Procrustes distances between ancestral configurations at all internal nodes inferred by squared-change parsimony and linear parsimony methods, with branch lengths. We would expect a pattern of increasing differences between alternative shapes at those internal nodes subtending more asymmetrical branch lengths. The statistical evaluation of the relationship between differences in estimated shapes and branch lengths is used to test the presumed advantage of squared-change parsimony in modeling Brownian shape change weighted in proportion to branch lengths (Rohlf, 2001; Felsenstein, 2002). We used Procrustes distances (PD) to quantify the difference between ancestral shapes from each mapping method (es1, es2) at each of the twenty-three internal tree nodes in our reference tree. Differences in ancestral shapes for the five cranial modules were calculated with CoordGen6h (Sheets, 2003) from two comparisons: between alternative shapes at a node (PD A, Fig. 6) and between shapes of ancestors and descendants (PD B, Fig. 6). First, we examined the relation of "PD A" to branch length heterogeneity with a regression analysis for each shape character (Supplementary material 5). One shape character is presented in Fig. 7a because among the five we studied, the mandibular process area (module 3) is associated with diet and is the character with the highest homoplasy index (h, Table 2). We calculated branch length heterogeneity as the ratio between the largest and smallest length of branches descending from the same ancestor. The regression of the "PD A" between estimated shapes (es1 vs es2) and this ratio would test if such difference is related to branch lengths, which are accounted only in model based squared-change parsimony.

Next, we compared the amount of shape change from ancestors to descendants. For a given internode, we computed two Procrustes distances (PD B1, B2, Fig. 6) for the shape change as minimized by squared-change parsimony in tpsTree or linear parsimony in TNT. The amount of shape change along each of the 44 branches (PD distances B1 and B2) was

analyzed in relation to branch lengths, as measured by the parsimony scores (Fig. 7b). Moreover, since the most asymmetrical branch lengths were the exterior branches, we inspected separately the amount of change between the shape of most recent ancestors (es1, es2), and each the 22 observed shapes in *Myotis*. The general pattern of Procrustes distances from ancestors to all observed shapes in descendants provided a measure to compare, whether the inferred ancestors (es1, es2) are intermediate shapes, as expected under squared-change parsimony (weighted average between descendants, Madisson, 1991), or the ancestral shapes are more similar to one of the observed shapes in the terminals, as expected with linear parsimony. These results are presented in Fig. 8 only for the cranial parieto-occipital region (module 1) and the mandible process region (module 3). We then compared the amount of shape change in relation to changes in diet. We estimated a T test, using STATISTICA 10 (Statsoft, 2010) to ask if the average change in 16 insectivorous species was different from the average change in six facultative and truly piscivorous species.

Results

Phylogenetic analyses

Parsimony analysis of Cyt-b and RAG2 sequences in 25 terminals resulted in a single optimal tree, 4497 steps (Supplementary material. 3a). In this molecular tree, all the species belonging to the New World formed a clade. The Asian species *M.brandtii gracilis* appear inside nearctic clade species. Our molecular tree also recovers the African clade with the two species we sampled. Relevant to our question of the evolution of shape, the truly piscivorous species *M. vivesi* is sister to an insectivorous species *M. keaysi* (Supplementary material. 3a).

The topology of the single best tree from geometric morphometric data describing variation in three cranial and two mandibular modules has a total score of 14.6501 (Supplementary material. 3b). Relationships among species of *Myotis* in the morphometric tree recover clades not found in the analyses of molecular data alone (Supplementary material 3) or in the combined analysis (Fig. 2). In the phylogenetic morphometric tree (supplementary material 3b) the truly piscivorous *M. vivesi* is sister to a group of two insectivorous species *M. evotis* and *M. leibii*. The five facultative piscivorous species are not grouped in phylogenetic analyses of morphometric shape characters.

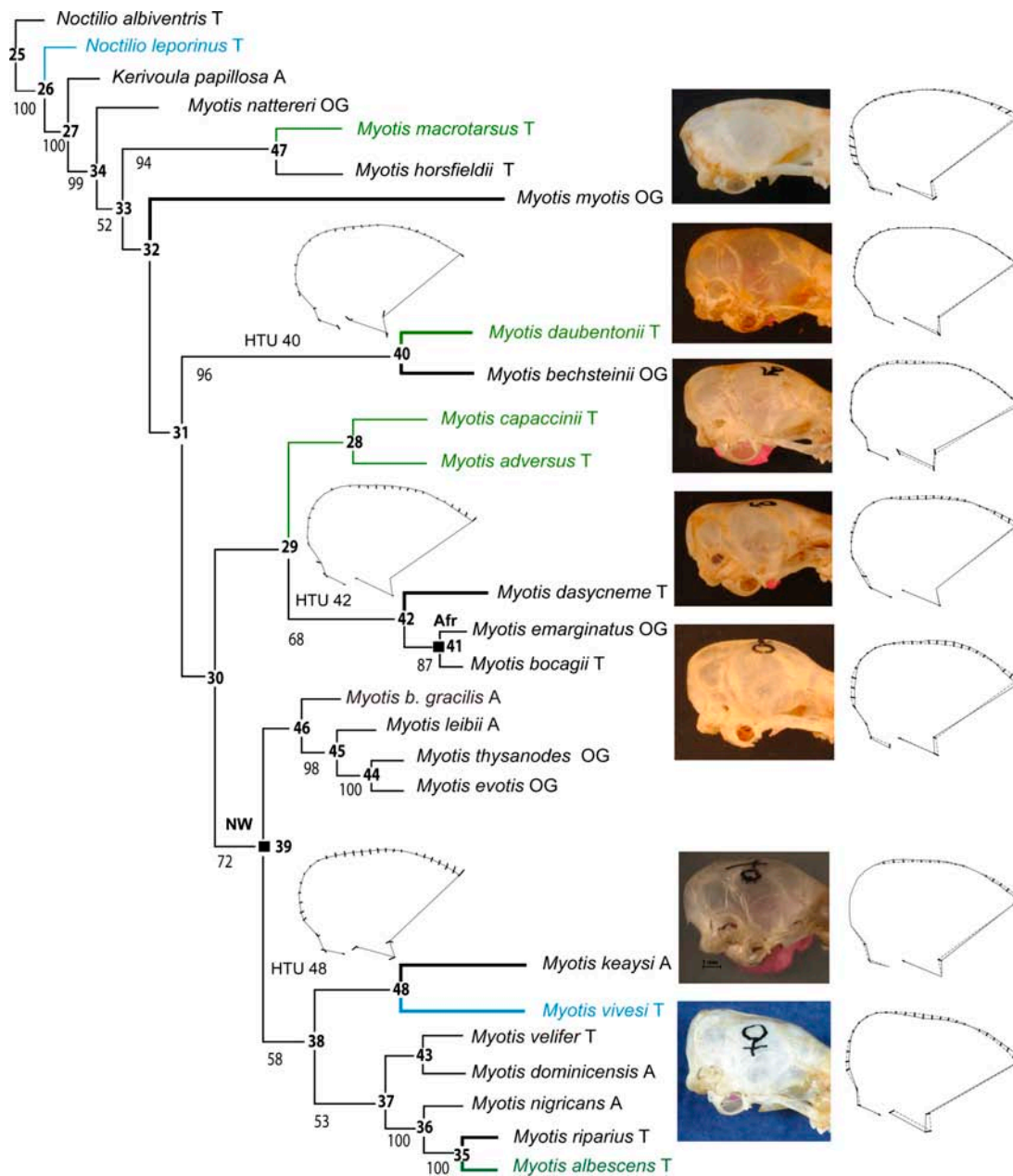


Fig.

2. Phylogeny of *Myotis* obtained from the parsimony analysis of combined molecular (Cyt-b, 1140 pb, RAG2, 1054 pb) and landmark data of five cranial modules in TNT. Single optimal tree, with internal nodes numbered in bold for reference in the optimizations of diets, foraging strategy, and landmark shape data. Numbers below branches are Jackknife values. Branch lengths are not proportional to changes. Colors of branches and taxon names indicate similar diets; facultative piscivorous are marked in green, piscivores in blue, insectivores species in black. The foraging strategy is indicated with a label after taxon name, A = Aerial-Hawking, T = Trawling, and OG = Over-gleaning. Synapomorphies for geometric morphometric data are shown only at four branches. At node 40, 42 and 48 there are three ancestral configurations to illustrate changes in the cranial parieto-occipital region. In all landmark configurations, deformation vectors at each point indicate displacements relative to the ancestral shape, as optimized with spatial parsimony with TNT.

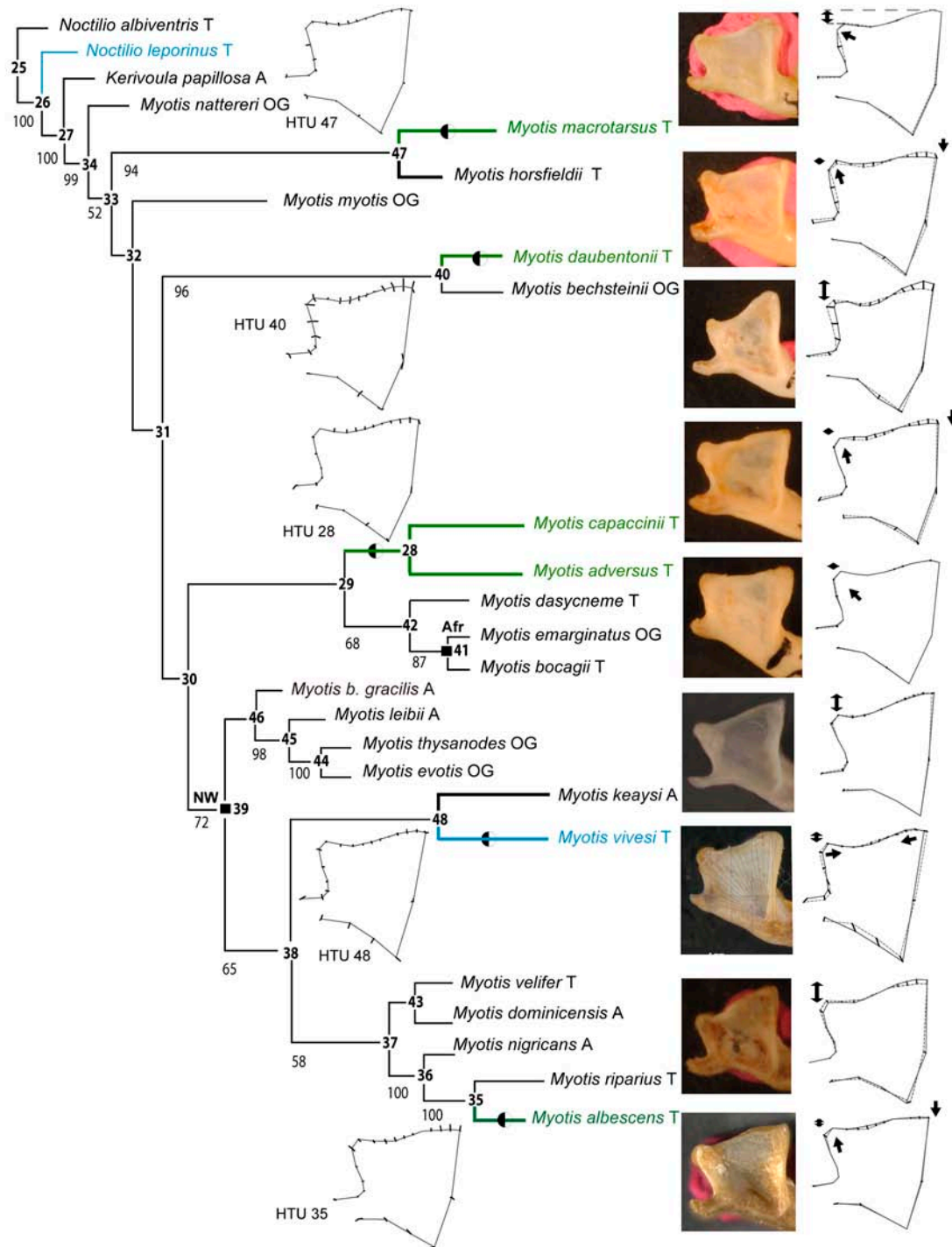


Fig. 3. Concerted change in shape, diet and trawling in the combined phylogeny of *Myotis* (as in Fig. 2). Colors of branches and taxon names indicate similar diets; facultative piscivorous are marked in green, piscivores in blue, insectivores in black. The foraging strategy is indicated with a label after taxon name, A = Aerial-Hawking, T = Trawling, and OG = Over-gleaning. At nodes 47, 40, 28, 48 and 35, the landmark configuration is the estimated ancestral shape of the process area. Double headed arrows show tendency of change. Arrows point to landmark displacements in module 3 interpreted as homoplasy in

facultatively piscivorous species. Concerted changes between shape and diet are marked with five half filled circles on branches. In all landmark configurations, deformation vectors at each point indicate displacements relative to the ancestral shape, as optimized with spatial parsimony with TNT.

The parsimony analysis of the combined geometric morphometric and molecular data found one most parsimonious tree (score = 2373.25; Fig. 2). Relationships among species of *Myotis* in this combined tree recover the Neotropical and African clades, also found in the analyses of molecular data alone (supplementary material 3a). The combined tree also places separately three facultatively piscivorous species (*M. albescens*, *M. daubentonii*, *M. macrotarsus*) each one sister to a different insectivorous species. The truly piscivorous *M. vivesi* is sister to a clade of insectivorous species. This combined tree is used as reference to optimize shape and diet changes (Fig. 2 and 3).

Shape synapomorphy and homoplasy

Our analyses of the evolution of five cranial shapes reveal changes in landmark configurations consisting of synapomorphy and homoplasy (Table 2). The parieto-occipital region changes as a synapomorphy for *Myotis* (module 1, Fig. 4a), although later major changes are optimized as autoapomorphies in *M. myotis*, *M. bechsteinii*, *M. dasycneme*, *M. emarginatus* and also in *M. vivesi* (Fig. 2). This is the shape character with the second highest homoplasy index (ci= 0.81, Table 2). The frontal-maxillary region (module 2) shows most of the change at node 32 (Fig. 4b), and there are only small changes in *M. bechsteinii*, *M. myotis*, and *M. vivesi*. This is the shape character with the highest consistency index (ci= 0.75). The shape of mandible process area (module 3) also changes as a synapomorphy for *Myotis* (Fig. 4c); later multiple independent changes are in the facultatively piscivorous species *M. capaccinii*, *M. daubentonii*, *M. macrotarsus*, *M. albescens*, and in the piscivorous *M. vivesi*. This is the shape character with the highest homoplasy, the lowest consistency index, and the lowest phylogenetic variability (h= 0.91, ci= 0.70, g-m= 2.37, Table 2). In contrast, the shape of the mandible dental row (module 4) changes as a synapomorphy for *Myotis* (Fig. 4d), and then there is practically no change in the rest of the tree. This is the shape character with the lowest homoplasy, highest phylogenetic variability, and highest retention index (h= 0.33, g-m= 4.26, ri= 0.92, Table 2). Shape changes in the ventral view of skull (module 5) are also a synapomorphy for *Myotis*

(Fig. 4e), later there is some shape change in the psicivorous *M. vivesi*. This shape character has low homoplasy ($h = 0.51$).

Table 2. Estimates of variability in five shape characters among species of *Myotis*. Parsimony scores were estimated from Manhattan distances in TNT with the following metrics: “s”= actual steps of a character on the combined tree; “m” = minimum possible steps for the character alone; “g” = minimum steps on a bush; “g-m” phylogenetic variability; homoplasy index for a character, “h” = $s - m$; character consistency index, “ci” = m / s ; retention index, “ri” = $g-s / g-m$.

Module	s	m	g	g-m	h	ci	ri
1. Cranial parieto-occipital	2.77	1.96	4.52	2.49	0.81	0.71	0.68
2. Frontal-maxillary region	2.47	1.85	5.31	3.47	0.62	0.75	0.82
3. Mandibular process area	2.99	2.08	4.45	2.37	0.91	0.70	0.62
4. Mandible dental row	1.15	0.82	5.08	4.26	0.33	0.71	0.92
5. Ventral view of skull	1.82	1.31	4.95	3.64	0.51	0.72	0.86

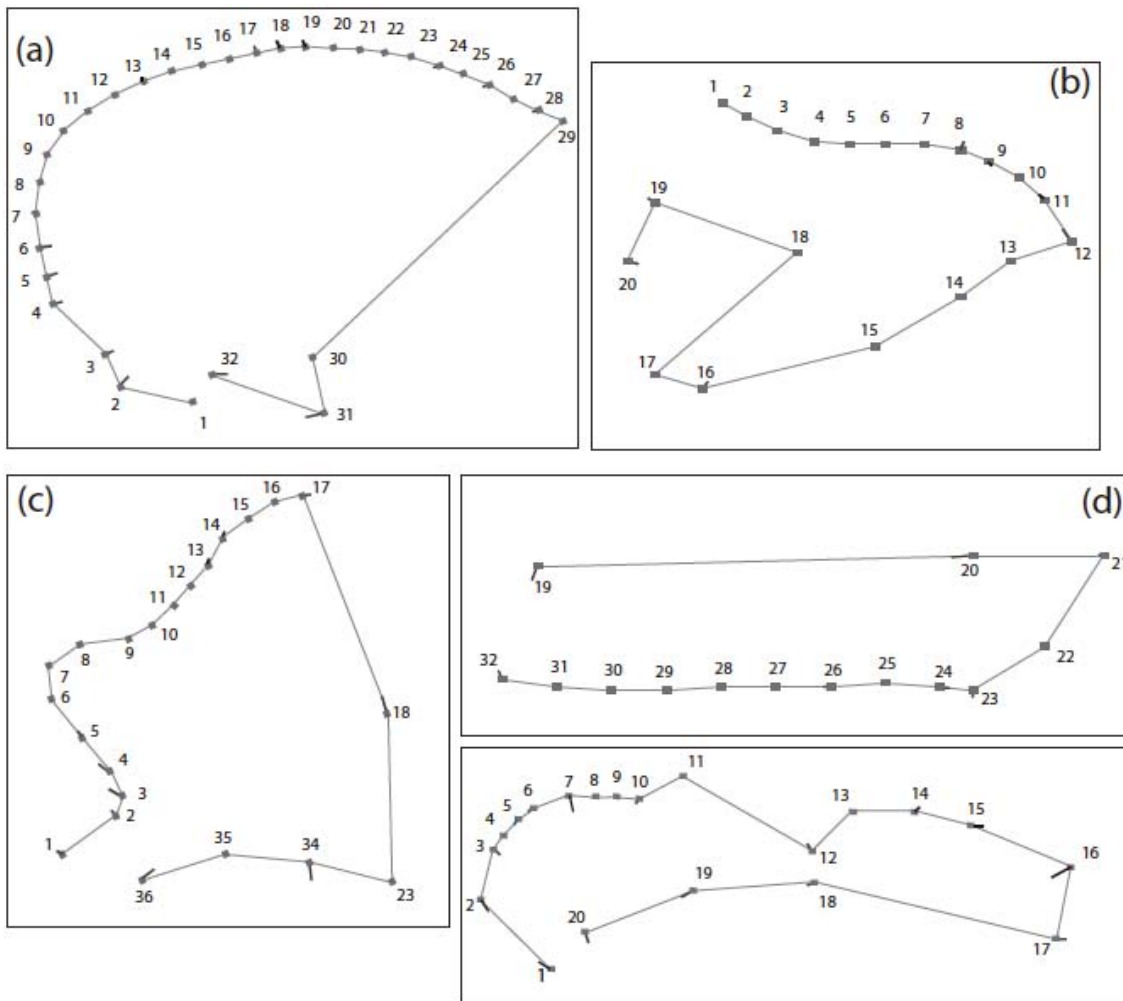


Fig. 4. Five geometric morphometric synapomorphies for *Myotis* (a-e). Landmark points in each shape character correspond to those in Fig 1. The lines depict multivariate vectors of landmark displacements from the reference ancestral shapes at tree node 34 in Fig. 2, as optimized with spatial parsimony in TNT. These vectors are not comparable between drawings of modules a-e. (a). Shape change in the landmark configuration for the parieto-occipital region (module 1); (b) shape deformation in the frontal-maxillary region (module 2); (c) change in the process area (module 3); (d) landmark displacements in the configuration of the dental row (module 4); (e) displacements in the ventral view of skull (module 5).

Concerted change in shape, diet and trawling

Optimizations with TNT uncover five changes of shapes and diets (half filled circles, Fig. 3). Three pairs consist of a shape change associated with a change in diet from an insectivorous ancestor to a facultatively piscivorous descendant (nodes 40, 35 and 47, Fig. 3) and one pair consist of a shape change associated with an facultatively piscivorous ancestor (node 28, Fig. 3). Optimizations of shape at these nodes reveal changes in the mandibular process region, and in the height of two processes (double headed arrows in Fig. 3). One additional concerted change is identified at node 48 from an insectivorous ancestor to a piscivorous species (Fig. 3). Results of pairwise comparisons in Mesquite show no pairs of concerted changes between foraging strategy and diet (Supplementary material 4).

There is no general trend in the changes of cranial shape from insectivorous ancestors to facultative or truly piscivorous species (Fig. 2, and 3). Four shapes (modules 1, 2, 4, 5) show minor changes only in three of the six branches from insectivorous ancestors to piscivorous and facultative piscivorous species. The parieto-occipital region (module 1) with the second highest homoplasy (0.81), changes mostly at the sagittal crest, only in the piscivorous species *M. vivesi*. There are small changes in the position of the glenoid fossa (landmarks 30 – 31, Fig. 2) only in *M. daubentonii*. This module has no change in the other four facultatively piscivorous species *M. albescens*, *M. capaccinii*, *M. macrotarsus*, and *M. adversus*. The frontal maxillary region (module 2, homoplasy index 0.62) presents autoapomorphic changes at the nasal region (landmarks 1 – 12) in the piscivorous species *M. vivesi* and one facultatively piscivorous *M. daubentonii* (not illustrated). This module does not change in the other four facultatively piscivorous species. The dental row (module 4) shows practically no change from insectivorous ancestors to the piscivorous species *M. vivesi* and the five facultatively piscivorous species. The ventral view of the skull (module 5) has only small changes at the maxillary region (landmarks 12-18). In the piscivorous *M. vivesi* the skull is extended, but in one facultatively piscivorous, *M. daubentonii*, the skull is shortened (not illustrated). This module does not change in the other four facultative piscivorous species.

Among the five modules, only the mandible (module 3, homoplasy index 0.91) shows major changes in the five transitions from insectivorous ancestors. Landmark displacements are located in the area of the two mandibular process; these changes are

illustrated for all facultatively piscivorous and piscivorous species (arrows, Fig. 3). There are three different patterns of shape change associated with changes in diet. First, in three species, shape change consists in a reduction of the height between the condylar process and the coronoid process (double headed arrows, Fig. 3). The outline between the condylar process and coronoid process goes from a soft sigmoid curve, as in the insectivorous *M. bechsteinii*, to an almost straight line in the facultatively piscivorous *M. capaccinii*, *M. daubentonii* and *M. albescens*. This deformation is interpreted as an extension of the condylar process (module 3, landmarks 4 -8) together with a contraction of the coronoid process (module 3, landmarks 13 -17, arrows, Fig. 3). However, in the other two facultative piscivorous species (nodes 28, 47, Fig. 3), shape change in the mandible only involves the condylar process, without change in the position of the coronoid process. The condylar process expands the mandible in *M. macrotarsus*, in *M. adversus* change is subtly in this direction. The third pattern of shape change is observed in the mandible of the truly piscivorous *M. vivesi*. The condylar process and the coronoid process move toward each other, which results in a unique contraction of the area between these two processes.

Comparison of ancestral shapes under squared-change parsimony and linear parsimony

Configurations of ancestral shapes reconstructed by both methods are not similar at all internal and external nodes considering the five modules. Moreover, in the case of the most external nodes, comparisons of drawings reveal that ancestral configurations (es1, es2) are not intermediate between the two observed shapes. For example (Fig. 5a), the ancestral shape (es1) of the parieto-occipital region (module 1) at tree node 40 is more similar (Procrustes distance, PD = 0.019) to the facultative piscivorous *M. daubentonii* than to the observed shape in the insectivorous *M. bechsteinii* (PD = 0.024). Also the ancestral shape (es2) of the parieto-occipital region (module 1) at tree node 40 is more similar (Procrustes distance, PD = 0.021) to the facultative piscivorous *M. daubentonii* than to the observed shape in the insectivorous *M. bechsteinii* (PD = 0.033).

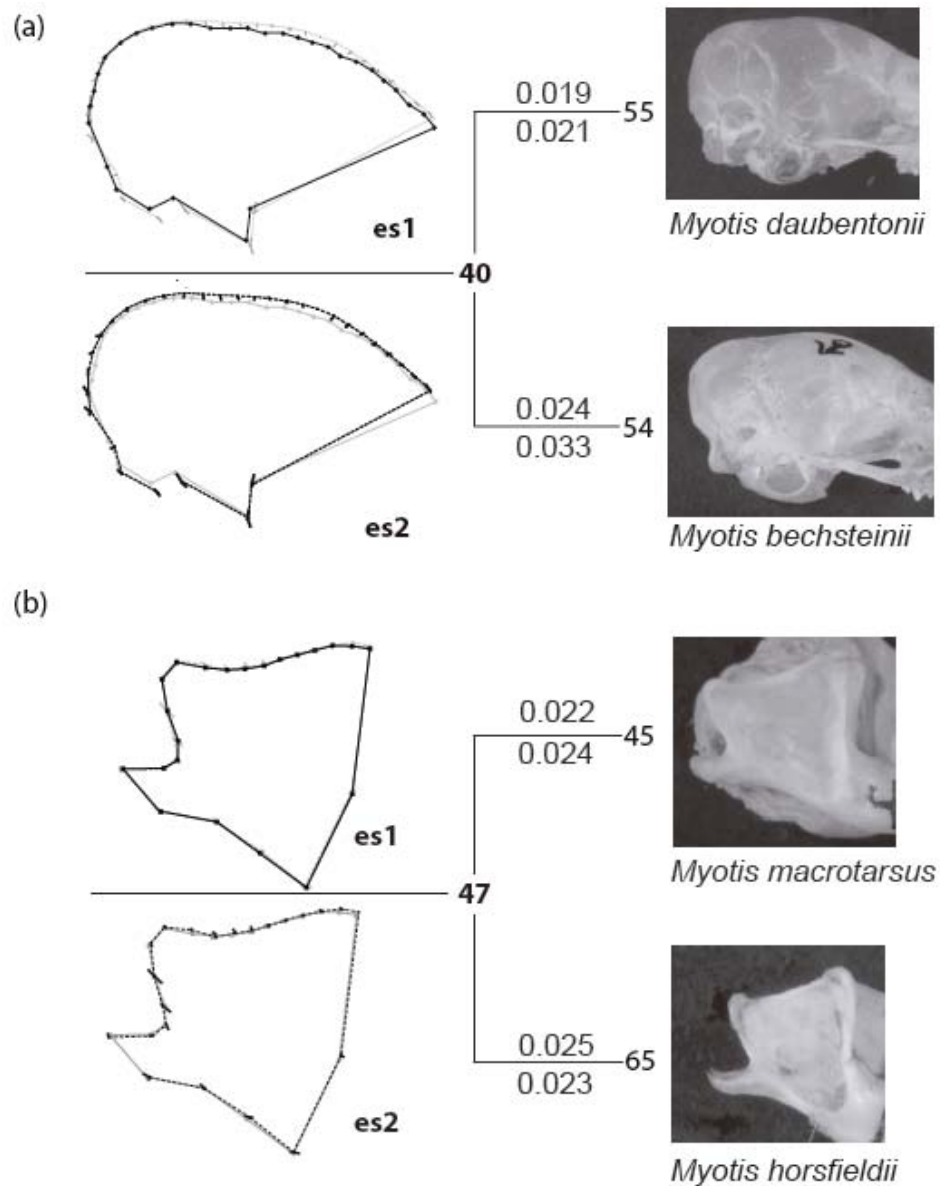


Fig. 5. Comparison of ancestral shapes obtained from mapping shape data onto a phylogeny using squared parsimony and spatial parsimony methods to illustrate the effect of branch lengths (four numbers at the tip of branches). In both figures, the estimated shape 1 (es1) was optimized using model-based squared parsimony with Rhetenor; the estimated shape 2 (es2) was optimized under spatial parsimony with TNT; for easy of comparison the alternative shape is drawn with gray lines. Numbers above and below branches are the Procrustes distances (PD) between one of the estimated shapes (es1, above branches; es2, below branches) and the corresponding species at each node. (a) The two hypothetical shapes of the cranial parieto-occipital region (module 1, 32 points) produced by each method for tree node 40, with almost same branch lengths (55 and 54). The ancestral shapes

reconstructed by both methods are closer (PD = 0.019 or 0.021) to the shape *M. daubentonii* (facultatively piscivorous). (b) The two

hypothetical shapes of the mandible process region (module 3, 22 points) produced by each method for tree node 47, with asymmetrical branch lengths (45 and 65). The ancestral shape reconstructed by squared parsimony (es1) is closer (PD = 0.022) to the shape of *M. macrotarsus* (facultatively piscivorous). The ancestral shape reconstructed by spatial parsimony (es2) is closer (0.023) to the shape of *M. horsfieldii*.

The squared-change parsimony (es1) and spatial parsimony (es2) reconstruction of the ancestral shapes of the mandible process area (module 3) at node 47 (Fig. 5b) are closer. The ancestral shape (es1) of the mandibular process area (module 3) is more similar (PD = 0.023) to the piscivorous *M. macrotarsus* than to the insectivorous *M. horsfieldii* (PD = 0.025). However, the spatial parsimony reconstruction of the ancestral shape (es2) of the mandible process area (module 3) at node 47 is more similar (PD = 0.023) to the facultatively piscivorous *M. horsfieldii* than to the insectivorous *M. macrotarsus* (PD = 0.024, Fig. 5b). In case of node 40, the two branch lengths are very similar (54, and 55, Fig. 5a), but at node 47, the two branch lengths are very different (45, and 65, Fig. 5b). The closer similarities between ancestral shapes and one of the observed shapes in the terminals are reconstructed both with squared-change parsimony and linear parsimony, regardless of whether branch lengths are slightly different or very asymmetrical.

No effects of branch lengths

The Procrustes distances between alternative ancestral configurations (PD A, in Fig. 6) at most internal nodes range from 0.009 to 0.055 (Fig. 7a). However, results of four regression analyses document that these differences in ancestral shapes are not proportional to branch lengths (Supplementary material 5). For example, low values of Procrustes distances (around 0.012, Fig 7a) are obtained between es1 and es2 at any given node, in a range of cases with small or large differences in branch lengths. Also, the amount of shape change estimated from ancestors to descendants at a single branch with linear parsimony (PD B2, in Fig. 6), or with squared-change parsimony (PD B1, in Fig. 6) is independent from branch lengths. The regression of the two alternative Procrustes distances of shape change along the 44 branches (PD B1, PD B2, in Fig. 6) reveals no relationship with branch lengths (Fig. 7b). The separate analysis of the Procrustes distances of shape change along

the 22 exterior branches reveals that the most recent ancestral shapes are more similar to one of the two observed shapes in the species of *Myotis* (Fig. 8). The amount of shape change is bigger when the optimization method is spatial parsimony. For example, for the parieto-occipital region (module 1, Fig. 8a) most of the Procrustes distances are larger (18 cases) when change is inferred with linear parsimony than when it is inferred with squared-change parsimony (4 cases). The same pattern is present for the mandibular process area (module 3, Fig. 8b); most of the Procrustes distances for change under linear parsimony (17 cases) are larger than Procrustes distances of change inferred under squared-change parsimony (5 cases).

Focusing on the external internodes with changes in diet from insectivorous ancestors to the piscivorous and facultatively piscivorous species, the Procrustes distances (PD) of the amount of shape change in the six branches in most of cases (4 from 12 cases) is lower when it is inferred from ancestral shapes reconstructed with squared-change parsimony (es1) than linear parsimony in TNT (es2). This pattern is only illustrated for two shapes (Fig. 8), the parieto-occipital region (module 1), and the shape of mandible process area (module 3), but it is also present in the other three configurations studied. All T-tests of the average PD from ancestors to insectivorous (n=16) and the average PD from ancestors to piscivorous species (n=6) reveal no difference in the amount of shape change estimated with squared-change parsimony or linear parsimony in the change of diet. The comparison between insectivorous and piscivorous reveals very similar amounts of shape change estimated by spatial parsimony for the parieto-occipital region (module 1, mean insectivorous PD =0.031, mean piscivorous PD= 0.028), the mandibular process area (module 3, mean insectivorous PD =0.043, mean piscivorous PD= 0.038), the dental row (module 4, mean insectivorous PD =0.028, mean piscivorous PD= 0.021), the skull ventral view (module 5, mean insectivorous PD =0.026, mean piscivorous PD= 0.029). The estimated amount of shape change in the frontal–maxillary region is slightly different (module 2, mean insectivorous PD =0.023, mean piscivorous PD= 0.032) but not significant. Similar values of Procrustes distances between ancestors and descendants indicate the same shape change is optimized along internodes with the two mapping methods, even when branch lengths are asymmetrical.

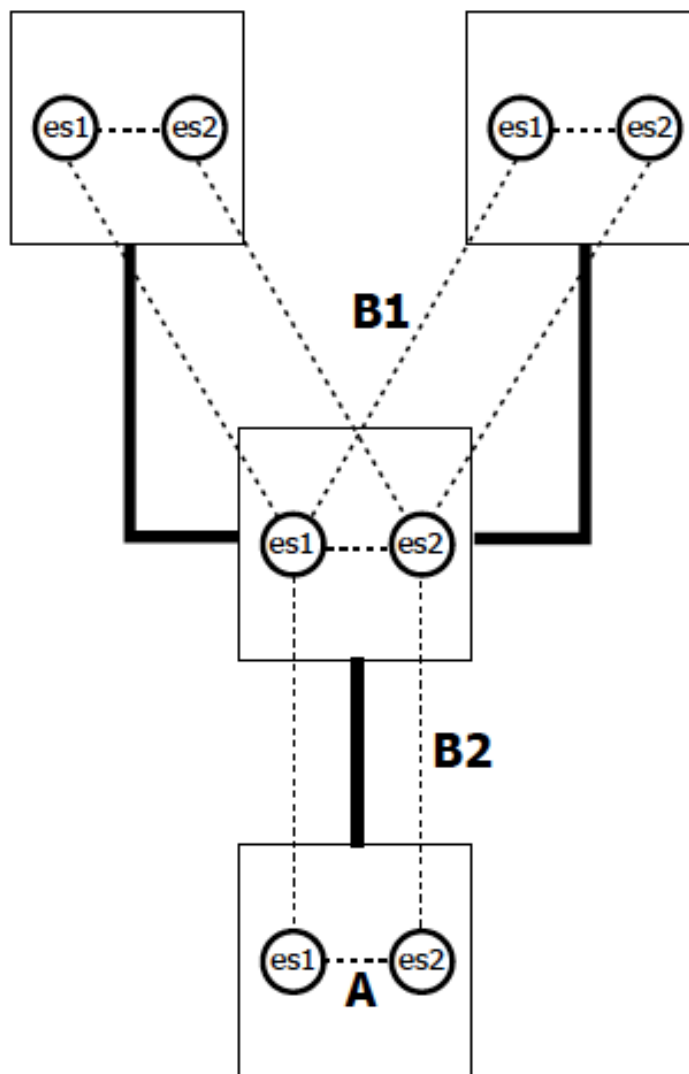


Fig 6. Diagram illustrating the two Procrustes distances calculated between estimated shapes. Distance A is the Procrustes distance between alternative ancestral shapes at a given node from tpsTree and TNT (es1–es2). DistanceB1 is the Procrustes distance between ancestral and descendant shapes es1-es1) estimated with squared parsimony at every internode. DistanceB2 is the Procrustes distance between ancestral and descendant shapes (es2-es2 as reconstructed with linear parsimony).

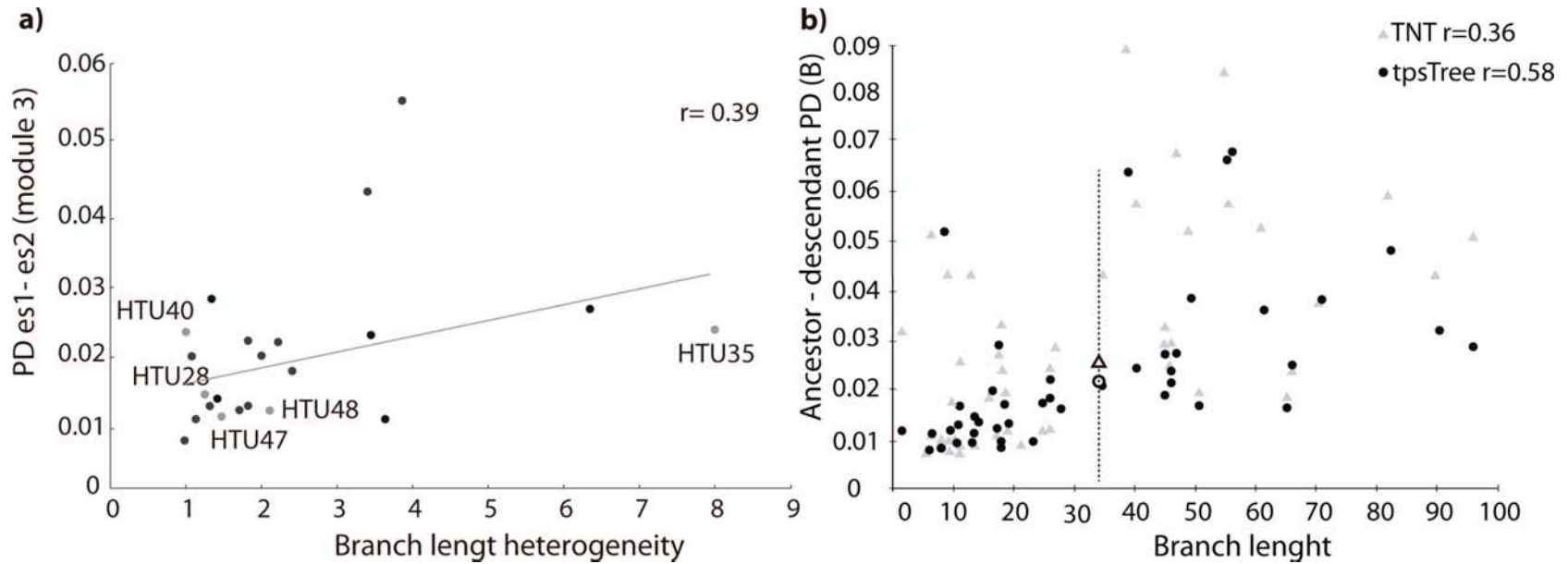


Fig. 7. Evaluation of the effect of branch length differences in estimations of ancestral shapes and changes between ancestors and descendants, as inferred with squared parsimony and spatial parsimony methods. Linear regressions Procrustes distances calculated to quantify shape change between ancestral and descendant configurations of the mandibular process area (module 3) and of branch heterogeneity. (a) Linear regression of Procrustes distances between estimated shapes at ancestral nodes (PD A= es1-es2) and branch length heterogeneity; six labeled HTUS are the most recent ancestors of the six transitions to facultative or truly piscivorous species (b) linear regression of Procrustes distances of shape change from ancestors to descendants (PD B, in Fig. 6) as estimated by squared change parsimony (circles) or linear parsimony (triangles) with branch lengths; the dotted line indicates the average branch length in our reference tree, the empty circle is the average amount of change as estimated with squared parsimony (tpsTree), the empty triangle indicates the average shape change as estimated with linear parsimony (TNT).

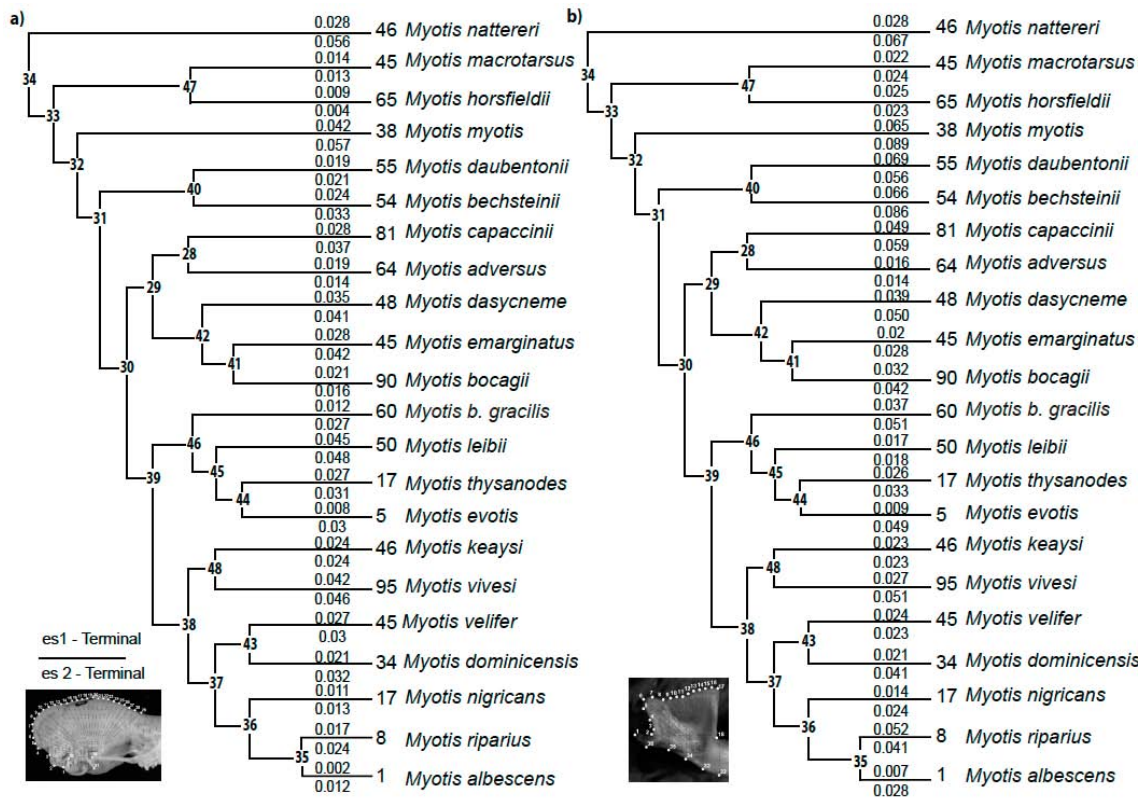


Fig. 8. Comparisons of differences in shape changes between reconstructed ancestors and observed shapes, as inferred with squared parsimony and spatial parsimony methods. These comparisons illustrate the effect of branch lengths (numbers at the tip of branches) in the estimation of shape change. Numbers above branches are the amount of change (Procrustes distances) between most recent common ancestors (es1) and species in *Myotis*, as estimated by squared parsimony. Numbers below branches are the amount of change from ancestral shapes as estimated with linear parsimony (es2). The reference tree and node numbers are the same as in Fig. 3, but with out-groups pruned. (a) Procrustes distances from ancestral estimated shapes to terminals for the cranial parieto-occipital region (module 1); (b) Procrustes distances from ancestral estimated shapes to terminals for the mandibular process area (module 3).

Discussion

Phylogenetic analyses of molecular and geometric morphometric data in *Myotis*

Our parsimony analysis of twenty-five DNA sequences of *Myotis* basically recovered the same relationships as in the larger likelihood analysis of 95 terminals by Ruedi et al (2013). In contrast, the morphometric phylogeny based on the five shape characters (Supplementary material 3b) did not recover relationships congruent with the molecular tree (Supplementary material 3a). The Neotropical and the African clades were not present in the morphometric tree, either in the combined (Supplementary material 3b) analyses of shape characters. The combination of five geometric morphometric characters with molecular data support similar species relationships recovered with the molecular data alone, in our analyses or in previous studies. The similarity of the topology of the combined analysis (fig. 2) with the topology of the molecular characters (Supplementary material 3a) just reveals the minimal effect of adding five morphometric characters. Although our study only sampled a subset of 22 out of 95 species of *Myotis* worldwide, the same broad inferences survive from previous studies. For example, the 10 morphologically diverse species we included were grouped within the New World clade (Node 39, Fig. 2), this clade includes all species from New World plus the palearctic species *M. brandtii gracilis*, as in previously published phylogeny New World clade that includes palaeartic species (*M. brandtii*). In agreement with Ruedi and Mayer (2001), a general pattern in our combined phylogenetic hypothesis of *Myotis* is that the biogeographic distribution of the species appears to be a much better predictor of their phylogenetic position than their cranial and mandibular morphology.

Geometric morphometric data in five modules produced hierarchically structured relationships, although such nested sets of species found in parsimony analyses did not agree with clades in the molecular tree for *Myotis* (Fig. 2). Still, any of the combined and separate parsimony analyses of the five shapes (Supplementary material 3) did not group the facultatively piscivorous species with presumably similar shapes. The optimization of configurations on our reference tree revealed localized changes in the mandibular process area (arrows, Fig. 3), which are indications of homoplasious similarity in cranial

morphology among species with the same diet in the five facultatively piscivorous species. The same results of the optimizations of shape and diet on our combined phylogeny (Fig. 3) imply that facultatively piscivorous and piscivorous diets originated independently from trawling insectivorous ancestors in the diversification of *Myotis*.

Synapomorphy and homoplasy in the evolution of cranial shape characters

A generalization from our results of phylogenetic analyses of variation (Table 2) is that some changes in each of the five cranial shapes can be interpreted as hypothesis of homology, and some are best interpreted as homoplasy. The most evident synapomorphies in our geometric morphometric data are in the frontal-maxillary region (module 2, Fig. 4b), the mandibular dental row (module 4, Fig. 4d) and the ventral view of skull (module 5, Fig. 4e) with lowest homoplasy. Our underlying assumption is that character parsimony scores (homoplasy index, consistency index, and the retention index) for each module provide evidence to interpret phylogenetically informative changes in landmark configurations (Table 2). These parsimony scores are indicators of the levels of character synapomorphy and homoplasy (Wenzel 2002), and we suggest to routinely using these as measures of character state transformations and the agreement of character changes in geometric morphometric data on a particular cladogram, just as it is standard for other character systems (Goloboff, 1991a; Schuh, 2000).

Concerted change of shape, diet and trawling

Optimizations of five morphometric modules and three diets resulted in five branches with concerted changes in shape and diet (half filled circles, Fig. 3). Some of these homoplasious changes in cranial morphology seem associated to changes in piscivorous and facultatively piscivorous species. Among the five modules, the mandible (module 3) of facultatively piscivorous species shows two patterns of change from insectivorous ancestors. Shape deformations in mandibular regions are interpretable in terms of the functional implications for the associated changes in the position of muscles and gape of skulls (increase of insertion area), the position of processes and crest in skulls, all of which are related to the capacity to chew hard items (Freeman, 1981; Dumont and Herrel, 2003; Herrel et al., 2008). Changes detected in cranial morphology should lead to additional research and discover functional relationships among the cranial modules

correlated with the putative switch in diet from insects to fishes or other marine resources. Adaptations have already been explored in linking cranial morphologies in bats to a sequence of dietary transitions from insectivores through omnivores to feeding on nectar, and fruit feeding (Wetterer et al. 2000; Monteiro and Nogueira, 2009) or carnivores (Freeman, 1984). In particular, wide faces and the height of the condylar process above the tooth row have been associated with greater attachment area for the masticatory muscles (Freeman, 1984). Our results on the inferred phylogenetic pattern of change in the mandible process area (arrows, Fig. 3) suggest that this is one of the main structures with biomechanical relevance in relation to diet, as Monteiro and Nogueira (2009) already found for Phyllostomidae, and it should be further analyzed in *Myotis* to evaluate if there is an associated functional utility and performance advantage as a hypotheses of adaptation.

Our findings document that piscivory does not imply a particular morphotype, as previously known only in *Noctilio* (Freeman, 1984). The two patterns of mandibular shape in facultative piscivorous *Myotis* and the different morphotype in the truly piscivorous *M. vivesi* suggest additional modifications in external morphology, likely related to foraging strategies. Among other species of *Myotis* there are three ecomorphs, “Selysius” characterized by aerial hawking foraging strategy, “Myotis” with over gleaning, and “Leuconoe” with trawling (Findley, 1972; Norberg and Rayner, 1987; Ruedi and Mayer, 2001). The five facultative piscivorous species and the truly piscivorous species capture prey by trawling, using their claws and the uropatagium to capture prey and move it towards a wide opened mouth. The positions of condylar and coronoid process in these six species indicate a vertically oriented temporal muscle, different from the insectivorous species. These morphological characters may be related to how wide a bat could open its jaws, following a model of muscle stretching proposed by Herring and Herring (1974). Greater muscle stretch depends on longer temporalis fibers, which is probably a feature of a greater gape to capture preys (Emerson & Radinsky, 1980; Freeman, 1984). If position of coronoid process and temporal muscle are involved in gape capacity in the piscivorous species of *Myotis*, our results suggest performance experiments to test the importance of the mandibular process area in how bats capture preys to include fishes in their diet.

Comparison of methods to map shape changes

This study documents that optimizations of five ancestral shapes and shape change (Fig. 2 and 3) are not very affected by the particular method chosen to map shape along a given tree. Ancestral shapes reconstructed under squared-change parsimony and spatial parsimony methods (es1, es2) differ in various degrees as shown in comparisons of deformation grids of ancestral shapes (Fig. 5) and the estimated Procrustes distances between them (PD A, Fig. 7a). But small or large differences in reconstructions of shape (for example, the mandibular process area) are produced whether branch lengths are similar (branch length heterogeneity lower than 3, Fig. 7a) or even when branch lengths are asymmetrical (branch length heterogeneity larger than 4). If large differences between reconstructed shapes are not related to branch lengths, there are a few cases, which may give a clue to a still unexplored factor. The average Procrustes distance between the observed shapes in three pairs of insectivorous and facultatively piscivorous sister species (nodes 35, 40, 47) is larger than the average Procrustes distance between three pairs of insectivorous species (nodes 41, 44, 43). This suggests that the morphological difference between the adjacent terminals is having a synergistic effect with branch length, being more evident in spatial parsimony. For example, large differences between es1-es2 are produced in four out of five shapes at the most recent common ancestor (node 35) of *M. albescens* (facultatively piscivorous) and *M. riparius* (insectivorous). The Procrustes distance between these two species is the third highest for the mandibular process area (module 3, PD=0.060), and the difference in the ancestral shapes for node 35 is the fourth largest (PD A = 0.023), together with extreme branch length asymmetry (8:1) and with biggest shape changes optimized by spatial parsimony.

Also, the results from comparisons of the Procrustes distances along short or long internodes (Fig. 8) indicate that there is no effect of branch lengths on estimations of the amount of shape change to descendants. This could be due to the fact that there is no relationship, considering that branch length are calculated from molecular data, or it could be due to a small sample on phylogeny. Also the cranial shape in *Myotis* could not be enough variable to detect the effect of branch length in the ancestral reconstructions method, the inclusion of more landmark configurations from different structures not only could improve the results in terms of congruence with alternative source of evidence, as

Catalano *et al* (2014) have mentioned, it could clear the patter of optimizations of the ancestral shapes with spatial parsimony.

The estimated shape change in general terms are biggest in spatial parsimony reconstructions but differences between the two alternative Procrustes distances (B1/B2) are not explained by branch length effect. The highest ratio between the two alternative Procrustes distances (B1/B2 = 6) of the change in the parieto-occipital region (module 1) is in the branch leading the to *M. albescens* (branch length =1, Fig. 8a). This comparison shows that large differences between alternative amounts of shape change (B1/B2 > 2, 14 cases for the five shapes) are reconstructed along short branches. But also, large differences are produced in branches of average length, as is the case of the ratio between the two alternative Procrustes distances (B2/B1 = 2.5) of the change in the mandibular process area (module 3) in the branch leading the to *M. nattereri* (branch length =46, Fig. 8b).

Our study case suggests that ancestral reconstructions of shape by mapping the same landmark data onto the same combined tree are robust to distinct parameterizations of models of shape change in spatial parsimony (Catalano et al., 2010; Catalano and Goloboff, 2012) and in current Brownian models for squared-change parsimony (Rohlf, 2001; Felsenstein, 2002). In general, the optimizations of the five cranial shapes we examined do not show the presumed advantage of squared-change parsimony in modeling Brownian shape change weighted in proportion to branch lengths (Rohlf, 2001; Felsenstein, 2002). This is a single case study; but if this were a general phenomenon, it would have empirical consequences, particularly when it is difficult to estimate branch lengths.

Conclusions

A phylogenetic approach to analyze morphometric variation in landmark data allowed the hierarchical partitioning of total shape change. Some shape deformation in each of the five modules of skull morphologies are best interpreted as synapomorphies for *Myotis*. However, most of shape changes in cranial and mandibular morphology are interpreted as homoplasy; these are not shared among the five species of *Myotis* with the same facultative piscivorous diet; there are three different morphologies associated with the change in diet. Concerted changes of shapes and diets in six branches showed that cranial morphology changed independently from insectivorous ancestors to piscivorous and

facultative piscivorous species. Common independent shifts in shape seem to be related to a common functional utility of specific morphologies in facultatively piscivorous, for example the process area in the mandible (module 3).

In the context of comparative and phylogenetic studies, geometric morphometric data should be scrutinized as any other type of data, as if potentially containing homology and homoplasy. We treated shape as a single multivariate character for deriving homology and homoplasy hypotheses in cranial structures associated with diets in *Myotis*. We subdivided the complex cranial morphology into modules to reflect named structures accepted in bat comparative morphology. As suggested by MacLeod (2002) for the analysis of relative warps, we used substructures (our modules 1-5) and carried out separate morphometric analyses on these substructures to describe patterns of variation. Instead of relative deformation variables (such as relative warps), we used Procrustes coordinates without coding to search for hierarchical patterns of variation, and finally, estimated a parsimony-based phylogeny using dynamic landmark homology methods developed by Catalano et al., (2010). Under the general principle that all data should be allowed to participate in the inference of phylogeny (Kluge, 1989; Nixon and Carpenter, 1996; Wheeler, 2012), the use of geometric morphometric data for estimates of phylogenetic relationships should be promoted. The qualification of homology and homoplasy in morphometric data should be investigated shape by shape in more empirical studies using parsimony methods for dynamic optimization of landmark configurations and trees (Catalano and Goloboff, 2012). Our phylogenetic analysis of landmark and molecular data illustrates the analytical procedure to test optimizations of geometric morphometric data onto a combined phylogeny. A complete integration of systematics, morphometrics, and comparative biology is achievable when phylogenetic trees are generated with all available evidence at hand, including geometric morphometric data. This protocol provides a rigorous analysis of the optimizations of shape changes and robust interpretations on the pattern of morphological character evolution needed for further evaluations of the adaptive nature, selective regimen (Baum and Larson, 1991; Losos and Miles, 2002), and macroevolutionary patterns of shape change (Grandcolas and D'Haese, 2003).

This particular study revealed little influence of branch lengths on the phylogenetic pattern of reconstructed ancestral shapes and estimates of shape change along internodes. Interpretations of ancestral shapes and shape change associated with changes in diet from

insectivorous to five facultative piscivorous and one truly piscivorous species do not depend on the incorporation of branch lengths. It remains to be explored with more empirical cases if branch lengths are not so critical importance. The practical implication of this study is that linear parsimony and squared-change parsimony should be applied for optimizing ancestral shapes from landmark data provided that both a total evidence tree is used and branch heterogeneity are within moderate ranges, though the exact bounds of this branch asymmetry also remains to be explored. Investigators should consider always performing a comparison of ancestral shape reconstructions with both squared-change parsimony and linear parsimony.

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Supplementary material 1. Data matrix.

xread

2199 25

&[landmark 2d]

N_albiventris -0.0537502,-0.2012387 -0.1225850,-0.1679097 -0.1217583,-0.1508023 -0.1576833,-0.1049420 -
0.1640570,-0.0805621 -0.1678253,-0.0533132 -0.1781403,-0.0274116 -0.1904460,-0.0022600 -
0.1806980,0.0278733 -0.1582487,0.0463460 -0.1345213,0.0584278 -0.1100133,0.0683087 -
0.0838864,0.0759572 -0.0601504,0.0847563 -0.0360350,0.089744067 -0.0124086,0.092523367
0.01041381,0.093354067 0.032947067,0.092888533 0.055077167,0.092524 0.077056367,0.0912437
0.098866267,0.087882267 0.120361,0.083450633 0.141789333,0.078064933 0.163228333,0.072316967
0.184162,0.065255567 0.204475667,0.056138467 0.224621333,0.0443908 0.246155333,0.032994033
0.253551333,0.027791767 0.073318,-0.213258667 0.0523341,-0.253135333 -0.006150123,-0.207399
N_leporinus -0.0537830,-0.2006965 -0.1253822,-0.1583424 -0.1247470,-0.1531478 -0.1502095,-0.1166901 -
0.1563816,-0.0834830 -0.1623604,-0.0557872 -0.1714975,-0.0292157 -0.1827225,-0.0067894 -
0.1766512,0.0196367 -0.1570375,0.0398388 -0.1339013,0.0521926 -0.1102770,0.0630859 -
0.0856630,0.0726720 -0.0614543,0.0811292 -0.0375303,0.087946823 -0.013879481,0.093210645
0.009318221,0.096243239 0.032124413,0.098569819 0.055184529,0.099528045 0.077980103,0.098389387
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M_myotis -0.20614695,0.1461893 -0.15261445,0.12795035 -0.1071185,0.1140603 -0.06012162,0.102884885 -
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M_nattereri -0.171581692,0.140541231 -0.146540462,0.125767154 -0.102254085,0.107666854 -
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M_nigricans -0.209692241,0.149973897 -0.155079103,0.122030966 -0.108874345,0.106260517 -
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M_riparius -0.194909464,0.145609357 -0.1524445,0.1220175 -0.107470429,0.104527996 -0.059275625,0.092757596 -
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M_thysanodes -0.198895917,0.137034667 -0.155949167,0.114097667 -0.10938525,0.098079567 -
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M_velifer -0.202124567,0.1386035 -0.155321567,0.116681867 -0.108722047,0.101616243 -0.0600295,0.092162733 -
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M_vivesi -0.19551037,0.131271704 -0.152716778,0.115744296 -0.106270778,0.101723596 -
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N_albiventris -0.178580333,-0.112141833 -0.164634333,-0.1029398 -0.145837667,-0.0778682 -0.145675333,-
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0.071307033,-0.247499 -0.1054342,-0.214460667

N_leporinus -0.186120781,-0.099738897 -0.166753688,-0.088664394 -0.14915625,-0.070997697 -0.139303813,-
0.0396475 -0.157660469,0.017328015 -0.189325438,0.086580706 -0.1584505,0.151815406 -
0.074992334,0.145804688 -0.029053494,0.112313 0.00223021,0.100582781 0.036127544,0.090548181
0.077313988,0.088676231 0.120648031,0.101474903 0.157595063,0.122670741 0.187022125,0.146148469
0.217662688,0.163735031 0.220051031,0.161528531 0.240578594,-0.086469563 0.127018813,-0.331978813
0.026418031,-0.304602125 -0.074785956,-0.245267031 -0.087063547,-0.221840875

K_papillosa -0.231184,-0.1133345 -0.1586795,-0.0958396 -0.1448195,-0.07570695 -0.140283,-0.0414927 -
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0.110218,0.1356155 0.1466355,0.1435725 0.1822885,0.1600855 0.2231035,0.161756 0.2530965,0.153252
0.22162,-0.1401175 0.143205,-0.3528025 0.0372777,-0.2808745 -0.0428463,-0.204691 -0.133784,-0.1772785

M_adversus -0.232936444,-0.112106222 -0.157315444,-0.104166211 -0.130874,-0.082306994 -0.135055444,-
0.041951639 -0.159205667,0.014138975 -0.172235389,0.083033289 -0.139857389,0.115448706 -
0.082994278,0.104057567 -0.032681622,0.099363156 0.006282575,0.105095794 0.041126694,0.112390444
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0.221030444,0.159134611 0.256078111,0.151625111 0.226453556,-0.141990056 0.133770333,-0.337356889
0.044485156,-0.274999333 -0.046329194,-0.213995889 -0.148975,-0.192844222

M_albescens -0.235540588,-0.122458706 -0.152837412,-0.113099188 -0.128614412,-0.084685329 -0.136158,-
 0.043896271 -0.160000176,0.01318551 -0.184777588,0.084242371 -0.141041176,0.118962471 -
 0.082315812,0.111277235 -0.034036753,0.112578059 0.003968627,0.118755059 0.039255053,0.124473647
 0.07344,0.132819529 0.109131824,0.139135235 0.145594118,0.140990882 0.182517941,0.139692706
 0.221232412,0.138009529 0.265713,0.137644059 0.216413412,-0.129117882 0.133380941,-0.335067824
 0.051602082,-0.268863765 -0.044691794,-0.214440235 -0.142235706,-0.200137
M_bechsteinii -0.2488285,-0.112494275 -0.16134225,-0.097996338 -0.130721625,-0.08878165 -0.11560775,-
 0.048482163 -0.124752575,0.017138345 -0.137042125,0.08231105 -0.13340975,0.099419838 -
 0.0858299,0.106714613 -0.035812288,0.090140063 0.005819881,0.088686863 0.0417414,0.1005209
 0.072239475,0.117244125 0.101846975,0.137031375 0.133564375,0.158717 0.172729875,0.173051375
 0.222282125,0.18838675 0.26289375,0.17759525 0.2155745,-0.173863 0.12007875,-0.331913125
 0.037123038,-0.283830125 -0.04512585,-0.20658825 -0.16742125,-0.193009
M_bocagii -0.239655188,-0.1161211 -0.14964575,-0.113279075 -0.129160188,-0.079740463 -0.147362625,-
 0.046310556 -0.175172125,0.016690456 -0.16887725,0.087031594 -0.136238063,0.1027588 -
 0.079960125,0.092821338 -0.029064475,0.094116344 0.010545807,0.100324919 0.045786219,0.109229588
 0.078308019,0.123233188 0.111371063,0.138192438 0.146546125,0.149042188 0.185161813,0.15510675
 0.224222563,0.158674125 0.2639635,0.151275875 0.224864125,-0.128497819 0.127658313,-0.328114688
 0.051508363,-0.262431813 -0.0450932,-0.208722563 -0.169707,-0.195280063
M_capaccinii -0.249851958,-0.127496833 -0.1535585,-0.112029304 -0.13440525,-0.082500496 -0.136166125,-
 0.044039838 -0.154289458,0.014633942 -0.167341917,0.080705154 -0.140206583,0.116683917 -
 0.082631425,0.115961363 -0.032985917,0.110740404 0.003887228,0.118133667 0.040080467,0.122163625
 0.073818992,0.129640625 0.10909075,0.136325917 0.145190083,0.138401333 0.182943292,0.139634625
 0.221475875,0.141768042 0.261979833,0.136346958 0.227612042,-0.119025383 0.129541125,-0.329536542
 0.054150825,-0.264714292 -0.044600313,-0.214385833 -0.15373325,-0.207410792
M_dasycneme -0.2462498,-0.10341162 -0.1523794,-0.1105574 -0.1221202,-0.08227584 -0.1326878,-0.03884326 -
 0.1528998,0.01823168 -0.1638552,0.0837678 -0.1349952,0.09995118 -0.0809262,0.08550388 -
 0.0280356,0.09011654 0.009210674,0.10302054 0.0409693,0.1171822 0.0701151,0.1333546
 0.10268134,0.1527406 0.1444992,0.1649414 0.185435,0.16258 0.2230678,0.158115 0.2563748,0.1500162
 0.2203988,-0.15204 0.1224388,-0.3269962 0.03821278,-0.2789714 -0.05252124,-0.2234256 -0.1467338,-
 0.2030006
M_daubentonii -0.235662765,-0.128169588 -0.150696353,-0.113778576 -0.135908647,-0.082730671 -0.146482647,-
 0.046326394 -0.163539824,0.013395811 -0.174001588,0.083975376 -0.143031,0.124674706 -
 0.081371053,0.111772529 -0.032167859,0.111142624 0.006530146,0.114849582 0.041746647,0.117789294
 0.075375029,0.127010235 0.110018059,0.135853941 0.146106235,0.139743471 0.182936882,0.139462412
 0.221220647,0.138860353 0.263552,0.135309471 0.217344765,-0.114353753 0.138768,-0.337067
 0.055046553,-0.265570235 -0.041512065,-0.210240353 -0.154271094,-0.195602706
M_dominicensis -0.234572833,-0.112920867 -0.150586,-0.1118565 -0.132369667,-0.081617333 -0.14439,-
 0.048306333 -0.1690185,0.014567133 -0.168785167,0.084579667 -0.140924,0.1171345 -
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 0.074380367,0.128891833 0.109269833,0.136633333 0.145259333,0.145705167 0.183357167,0.149344167
 0.220459167,0.1473505 0.257229167,0.139814 0.221493833,-0.1353165 0.141592167,-0.339636667
 0.053844733,-0.265183833 -0.042681467,-0.209870167 -0.157573667,-0.191982
M_emarginatus -0.2326785,-0.111213483 -0.155483667,-0.105895 -0.127078,-0.0828726 -0.139166167,-0.042133083 -
 0.163031333,0.014926167 -0.171130167,0.08375115 -0.1378765,0.111731683 -0.083120267,0.0966938 -
 0.031950983,0.092413767 0.00844099,0.09791475 0.04386805,0.10704705 0.07712985,0.117868667
 0.1100315,0.1327355 0.143114833,0.1490555 0.1807485,0.1630815 0.222219,0.162341833
 0.256104,0.157586667 0.229212167,-0.139420167 0.137152667,-0.3435705 0.043188867,-0.274121167 -
 0.043861533,-0.205579333 -0.1658325,-0.182343
M_evotis -0.23128288,-0.11547296 -0.15891608,-0.103122648 -0.1306496,-0.085473172 -0.12828128,-0.043162732 -
 0.14973996,0.015605872 -0.16343724,0.080625484 -0.13998904,0.112349068 -0.083944492,0.104777564 -
 0.033794616,0.093443884 0.00603653,0.100048476 0.040573348,0.10974632 0.07371666,0.12160748
 0.10652654,0.13646808 0.14123484,0.15104932 0.17860352,0.1649066 0.22171508,0.16949152
 0.26399376,0.16012328 0.2045674,-0.1585804 0.13699724,-0.3459364 0.04261834,-0.27867452 -
 0.042239872,-0.20252812 -0.15430804,-0.18729188
M_gracilis -0.233537333,-0.106927667 -0.152943,-0.103651433 -0.133505,-0.0806946 -0.130674667,-0.041462767 -
 0.160311333,0.012820233 -0.175270333,0.083865333 -0.136916,0.110372 -0.082389033,0.097991067 -
 0.031401467,0.094185533 0.008873663,0.100806633 0.042306133,0.113701 0.073128833,0.128852333
 0.109044667,0.140643667 0.145856333,0.150561 0.182876333,0.153832 0.219039667,0.148334667
 0.249132333,0.141791 0.231193333,-0.128980667 0.147738667,-0.346503 0.0518523,-0.268523 -
 0.043848467,-0.216361667 -0.180244667,-0.184647333
M_horsfieldii -0.245941846,-0.114171038 -0.156745577,-0.1076822 -0.124176808,-0.089724073 -0.125418335,-
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 0.083304485,0.109134646 -0.034333985,0.104051065 0.003544938,0.110080877 0.038889738,0.116392615
 0.073001996,0.123129192 0.107361038,0.132710423 0.142976423,0.143529 0.180424846,0.151972808

0.219562577,0.156447769 0.261191423,0.152988538 0.227054846,-0.137546692 0.130275269,-
0.336067769 0.046112162,-0.273388346 -0.044979092,-0.209431846 -0.161503154,-0.198970731
M_keaysi -0.244608696,-0.11448 -0.152187391,-0.114657739 -0.128852522,-0.082978013 -0.134027217,-0.042375735
-0.155787478,0.015581257 -0.17481313,0.0839705 -0.139082435,0.116690452 -0.082602043,0.097271304 -
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0.266718304,0.150668 0.208486739,-0.112116713 0.138963087,-0.34483087 0.048851343,-0.270062043 -
0.0438936,-0.208424696 -0.163512217,-0.197905652
M_leibii -0.239285522,-0.112242709 -0.158125,-0.102749448 -0.132741913,-0.083666809 -0.130429039,-
0.044567661 -0.149478826,0.015154304 -0.166267739,0.081782017 -0.140464565,0.113525639 -
0.08370997,0.10212517 -0.033537357,0.095794648 0.005822635,0.101940748 0.041443852,0.107200826
0.075829296,0.115498609 0.110561348,0.127334478 0.14433713,0.14282313 0.17843813,0.159574174
0.220097217,0.170669174 0.265276478,0.164131043 0.217170391,-0.144516087 0.134258043,-0.338306609
0.048865052,-0.271152652 -0.043578539,-0.20939513 -0.164481348,-0.190956826
M_macrotarsus -0.244033769,-0.106185462 -0.153304769,-0.106288654 -0.127393769,-0.0835266 -0.135396846,-
0.043233023 -0.164541077,0.014095487 -0.165656462,0.082147123 -0.137957923,0.107279869 -
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0.050009792,-0.266590462 -0.044861846,-0.211075692 -0.169966,-0.184388692
M_myotis -0.23057475,-0.093656035 -0.1587616,-0.100138705 -0.12618995,-0.08821791 -0.118857025,-0.04183825 -
0.13931805,0.017987545 -0.14066535,0.078738875 -0.132506,0.09646901 -0.084221405,0.09900153 -
0.03531775,0.082478385 0.008630147,0.08676398 0.0432184,0.10153832 0.07230907,0.1194608
0.10026925,0.14006495 0.132567,0.1599183 0.1710885,0.17786715 0.22607025,0.18963655
0.2559995,0.183072 0.21543515,-0.1741998 0.12597295,-0.3401035 0.023449345,-0.296637 -0.048098315,-
0.20970085 -0.1604994,-0.18850555
M_nattereri -0.239064308,-0.114116462 -0.155133462,-0.109310092 -0.129149,-0.086135454 -0.127840538,-
0.045021308 -0.142216923,0.015442562 -0.155466769,0.080735862 -0.139517154,0.111198077 -
0.082497177,0.114380315 -0.034836023,0.094994662 0.005855606,0.096647308 0.040841346,0.108784369
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0.219519462,0.164246462 0.254406308,0.156038154 0.217951,-0.165003615 0.137014308,-0.340501692
0.047814185,-0.272925231 -0.041473438,-0.207078154 -0.170250462,-0.184780385
M_nigricans -0.243133571,-0.120078714 -0.1530635,-0.110504282 -0.131826214,-0.082916061 -0.140020393,-
0.044704232 -0.159877143,0.014053264 -0.174511821,0.083488589 -0.141131929,0.120378089 -
0.081733411,0.109567218 -0.032399207,0.105386796 0.005799965,0.111242146 0.040875143,0.11817425
0.074530961,0.127672357 0.109594393,0.136420714 0.146031857,0.141387714 0.183297071,0.142704071
0.2208825,0.143428393 0.263187571,0.13707275 0.219354429,-0.117275468 0.138127964,-0.340006821
0.055361,-0.263514536 -0.043274057,-0.209271857 -0.156071643,-0.202704357
M_riparius -0.24262444,-0.119117528 -0.15588128,-0.110017196 -0.12690712,-0.084955948 -0.13158152,-0.04209 -
0.15655376,0.0154463 -0.16349852,0.08226704 -0.138808,0.11081118 -0.082991224,0.103740232 -
0.032660124,0.096082216 0.006280249,0.103958424 0.040550228,0.11424588 0.073579856,0.12557544
0.10766162,0.13776128 0.144363,0.14769896 0.18267584,0.15417324 0.22116512,0.1579766
0.26690372,0.15148936 0.22660052,-0.14043012 0.1243324,-0.32888316 0.050787832,-0.26492332 -
0.044169392,-0.20357488 -0.16922448,-0.2072338
M_thysanodes -0.242240833,-0.114465842 -0.1567095,-0.108848117 -0.131024333,-0.08462025 -0.135378083,-
0.04394425 -0.151536,0.015583608 -0.163522,0.082629258 -0.139436,0.11087715 -0.08383795,0.108270567 -
0.03348025,0.093995058 0.007252289,0.09785995 0.042424692,0.106876733 0.074210225,0.121523
0.108792667,0.132424333 0.143183167,0.147064083 0.181114833,0.158376833 0.2208815,0.163818167
0.267818,0.159997167 0.214862833,-0.136163667 0.132335667,-0.341305583 0.044626333,-0.274723667 -
0.0412828,-0.19795925 -0.1590545,-0.197265833
M_velifer -0.239733933,-0.112016613 -0.1556421,-0.107314637 -0.129500833,-0.082333787 -0.135104933,-
0.041591787 -0.1591847,0.016214897 -0.169282567,0.08401463 -0.1376338,0.111696423 -
0.083519717,0.095007997 -0.03110518,0.092383483 0.008429736,0.100865567 0.042674257,0.1119914
0.07551518,0.123967333 0.1091687,0.1370865 0.145275167,0.147978667 0.183126967,0.158204933
0.2228655,0.1621809 0.2660446,0.154485467 0.217955567,-0.131293733 0.127655367,-0.334394767
0.043964173,-0.273696167 -0.046298103,-0.2093552 -0.155669433,-0.204081367
M_vivesi -0.223249548,-0.103319845 -0.157564677,-0.09600341 -0.140111323,-0.080351158 -0.139316097,-
0.044407819 -0.147181871,0.014835153 -0.158176129,0.079760597 -0.139103065,0.112676806 -
0.082765739,0.104717068 -0.033150326,0.096502597 0.00654539,0.100854655 0.042200297,0.108444194
0.075768848,0.119503548 0.108732323,0.134240613 0.143245774,0.148353065 0.180590613,0.161548484
0.220862677,0.163661613 0.252702968,0.156013742 0.19976129,-0.123281548 0.156604097,-0.360590194
0.040099965,-0.285928871 -0.051278765,-0.228146097 -0.155216452,-0.17908329

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N_albiventris -0.278391333,0.198979667 0.311143333,0.160745 0.391663,0.129467333 0.308329667,0.032223367
0.212668667,-0.051220633 0.188390667,-0.053556933 0.114957333,-0.064355733 0.039814633,-0.0583343 -
0.0323464,-0.0552035 -0.104938,-0.057130733 -0.178540667,-0.056187967 -0.252170667,-0.0544344 -
0.328226333,-0.048928867 -0.392354333,-0.022062667

N_leporinus -0.28529625,0.186396281 0.309300656,0.160376313 0.394394188,0.134624625
0.313774563,0.028047896 0.204129094,-0.062711938 0.190665625,-0.054657416 0.116000781,-0.059410194
0.041630563,-0.056407994 -0.031472872,-0.054150072 -0.104441,-0.052392009 -0.177598281,-0.050846184 -
0.251113438,-0.050082881 -0.3264605,-0.046304625 -0.393513094,-0.022481775

K_papillosa -0.3349675,0.1345185 0.2729435,0.1297925 0.4064295,0.114131 0.3379925,-0.00217744 0.2445385,-
0.0640077 0.1855125,-0.03648505 0.115657,-0.03288925 0.0426064,-0.0347759 -0.03020065,-0.0365633 -
0.1028475,-0.03768865 -0.17554,-0.04052205 -0.248437,-0.0379917 -0.321442,-0.0348955 -0.392246,-
0.02044545

M_adversus -0.323422722,0.135788783 0.238819667,0.129306833 0.416036722,0.123020222
0.339176944,0.001881966 0.253048333,-0.070888106 0.189992389,-0.045545483 0.117700778,-0.038175522
0.044294344,-0.036608689 -0.02913725,-0.0374399 -0.102291494,-0.037928611 -0.175580778,-0.037594678 -
0.249020667,-0.036216639 -0.322299667,-0.0310958 -0.397316278,-0.018504422

M_albescens -0.341178882,0.134802353 0.227317294,0.132827824 0.419997588,0.128690824
0.343393941,0.00233119 0.238971765,-0.072970653 0.195698941,-0.059735988 0.120370118,-0.043710106
0.047440294,-0.039888035 -0.025835694,-0.036971729 -0.099011429,-0.035366435 -0.172260353,-
0.032680459 -0.245604235,-0.0307923 -0.318731059,-0.027308447 -0.390568706,-0.019228129

M_bechsteinii -0.337638875,0.133222375 0.247828375,0.119886875 0.41714675,0.11910725
0.34020475,0.004697532 0.240853125,-0.059473063 0.19170125,-0.046669325 0.119709625,-0.037022263
0.046069888,-0.037727163 -0.027535763,-0.037567988 -0.10080045,-0.038813163 -0.17414075,-0.036813388
-0.24764475,-0.035151225 -0.320728,-0.028672513 -0.39502525,-0.0190037

M_bocagii -0.336008063,0.132113188 0.244206813,0.128433313 0.414356813,0.1190665 0.341223938,0.00010983
0.247586188,-0.065923544 0.190597313,-0.046411919 0.118513813,-0.03886495 0.045240556,-0.036485613 -
0.028039731,-0.036049006 -0.101090125,-0.036524306 -0.174244813,-0.035894181 -0.247454938,-
0.033924206 -0.320689625,-0.030755619 -0.394198625,-0.018889669

M_capaccinii -0.327140333,0.116631417 0.241124875,0.1316975 0.4162525,0.113256042 0.345497167,-0.006911669
0.252223583,-0.061851508 0.189404333,-0.042894333 0.117988333,-0.034369029 0.044168596,-0.033392908
-0.029371304,-0.034347813 -0.102573154,-0.035392542 -0.175843,-0.035460538 -0.249096375,-0.032320396
-0.32214425,-0.026333525 -0.400491125,-0.018310688

M_dasycneme -0.3147812,0.1304558 0.2452134,0.1375546 0.4176322,0.1268914 0.3431912,-0.00385281 0.2398716,-
0.0690987 0.1890828,-0.04487632 0.117758,-0.03739546 0.04396134,-0.03672556 -0.02941256,-0.040584 -
0.1027714,-0.04243138 -0.1761972,-0.0390746 -0.2495336,-0.03563462 -0.3225738,-0.02814746 -0.4014404,-
0.01708052

M_daubentonii -0.339511176,0.119291806 0.229832941,0.135504647 0.416697,0.112046747 0.344395412,-
0.002904016 0.255214941,-0.069285276 0.191120706,-0.0441991 0.119538118,-0.036895106 0.045949465,-
0.036567941 -0.027493865,-0.036623659 -0.100785259,-0.036704118 -0.173930471,-0.0342639 -
0.247059235,-0.030796006 -0.319671353,-0.021211871 -0.394297,-0.017392218

M_dominicensis -0.343927167,0.118411667 0.229543667,0.125701167 0.412267167,0.118114167 0.346533,-
0.009678655 0.262253,-0.072953633 0.190464167,-0.045783317 0.118666667,-0.032311383 0.044982617,-
0.028986233 -0.028275183,-0.031974367 -0.100970583,-0.033774083 -0.1738605,-0.033359533 -
0.246736333,-0.0309178 -0.319557167,-0.0257955 -0.391382667,-0.016692617

M_emarginatus -0.336077167,0.1419585 0.253911333,0.125126833 0.41392,0.126421667 0.339595667,0.001953157
0.237137333,-0.063323533 0.190170833,-0.044960733 0.118386333,-0.03820185 0.04531955,-0.040537417 -
0.0279041,-0.041884167 -0.1009775,-0.042186883 -0.174247833,-0.040494033 -0.247368,-0.035696667 -
0.320299667,-0.029891883 -0.391566667,-0.018283083

M_evotis -0.35554808,0.13628312 0.24500864,0.11699624 0.41793824,0.12454368 0.34095552,0.003760081
0.23363968,-0.063492168 0.19372036,-0.050664724 0.12065736,-0.039006624 0.047501452,-0.037103784 -
0.025756832,-0.037496008 -0.098796384,-0.037928792 -0.17183444,-0.036607304 -0.24496,-0.034272256 -
0.3176352,-0.027303592 -0.38489032,-0.017707796

M_gracilis -0.340469333,0.123976333 0.231089333,0.118543667 0.41931,0.112697333 0.343712667,-0.000437977
0.254611667,-0.062232933 0.192033,-0.0430263 0.119412667,-0.0333223 0.0462749,-0.031378667 -
0.027603567,-0.0348217 -0.100746667,-0.037502967 -0.174151,-0.036036767 -0.247669667,-0.032354167 -
0.320897333,-0.026819267 -0.394907333,-0.0172847

M_horsfieldii -0.338413538,0.1409855 0.2402465,0.129601962 0.414779462,0.12219865 0.337141846,0.008356337
0.245693577,-0.073964435 0.1930555,-0.051708869 0.119636692,-0.041295531 0.046418854,-0.039265238 -
0.026926369,-0.036894046 -0.100085812,-0.036022185 -0.173349269,-0.035232 -0.246634615,-0.034773754 -
0.320014962,-0.032418654 -0.391547808,-0.019567823

M_keaysi -0.348938522,0.128478739 0.237326478,0.126831087 0.412816696,0.117971478 0.343684261,-
0.003671883 0.252481739,-0.072682391 0.19076587,-0.045009487 0.119319565,-0.035938787 0.04604003,-
0.034367578 -0.027046165,-0.034422626 -0.099810878,-0.03421043 -0.172709043,-0.03280437 -
0.245673348,-0.032257726 -0.318428478,-0.028552239 -0.389828391,-0.019363796

M_leibii -0.341095565,0.126931087 0.246002739,0.116605861 0.421401826,0.119851004
 0.338941391,0.008075787 0.237727652,-0.060334561 0.192998957,-0.048163574 0.120304174,-0.039077322
 0.046682357,-0.037565617 -0.026882226,-0.037861209 -0.100239426,-0.036754348 -0.173638391,-
 0.03475973 -0.247112783,-0.031732565 -0.320376565,-0.026652865 -0.394714043,-0.018561987
 M_macrotarsus -0.329847769,0.124944923 0.236008923,0.129025385 0.419951077,0.111555108
 0.341310692,0.000951229 0.252258308,-0.075177585 0.190299077,-0.039899908 0.119090308,-0.030390008
 0.044970831,-0.030990162 -0.028704638,-0.032154854 -0.101867115,-0.035436608 -0.175152538,-
 0.036216431 -0.248675154,-0.037266077 -0.322022692,-0.030490669 -0.397619231,-0.018454469
 M_myotis -0.33971555,0.14917665 0.26582095,0.1157332 0.40975165,0.13185105 0.33682545,0.005258379
 0.2318223,-0.0549469 0.19002685,-0.046288865 0.1183376,-0.04416898 0.04529701,-0.042720535 -
 0.027766055,-0.043096475 -0.10067902,-0.042322695 -0.17375175,-0.041246325 -0.24680215,-0.03760296 -
 0.3195488,-0.03056301 -0.38961845,-0.019062725
 M_nattereri -0.339941231,0.122687692 0.234468846,0.128840308 0.416398692,0.107343692 0.343550846,-
 0.005705272 0.260889385,-0.065128115 0.188943538,-0.036498308 0.117877923,-0.031242708
 0.044348315,-0.033406123 -0.028756808,-0.035062662 -0.101687815,-0.037169162 -0.174781615,-
 0.037101808 -0.247841385,-0.033614031 -0.320584462,-0.026755315 -0.392884385,-0.017188215
 M_nigricans -0.345525704,0.122206037 0.238110259,0.125100333 0.415662259,0.11290507 0.345326,-0.004228377
 0.24986663,-0.063818952 0.191120963,-0.044554111 0.119728259,-0.034802922 0.046095574,-0.033276644 -
 0.027271589,-0.034186048 -0.100307333,-0.033854641 -0.173431481,-0.03358893 -0.246513333,-
 0.031118948 -0.319559,-0.027586441 -0.393301296,-0.019195478
 M_riparius -0.33191116,0.13932984 0.24134972,0.12728512 0.41073372,0.13234244 0.34150932,-0.001290941
 0.2503512,-0.069397288 0.19043504,-0.050266052 0.11785036,-0.043931496 0.044853756,-0.040799472 -
 0.02837072,-0.039078532 -0.1012543,-0.03720328 -0.17424768,-0.034605124 -0.24732024,-0.032901004 -
 0.32038712,-0.02997354 -0.39359216,-0.019510864
 M_thysanodes -0.34545575,0.139806583 0.24030475,0.125149667 0.417234917,0.120402667
 0.339966333,0.006144471 0.2394,-0.059017375 0.19398025,-0.052789217 0.120369917,-0.041932267
 0.047273108,-0.040561867 -0.02614165,-0.040739142 -0.099339492,-0.040281317 -0.172603833,-
 0.037541617 -0.245740917,-0.0331836 -0.318693833,-0.026473083 -0.39055375,-0.0189839
 M_velifer -0.3361893,0.1388505 0.2455582,0.125369167 0.415708833,0.128828567 0.339717267,0.003866676
 0.238827633,-0.067010473 0.192501233,-0.05286151 0.119044667,-0.041584433 0.045922657,-0.039236573 -
 0.027355953,-0.038693507 -0.100470437,-0.037752153 -0.173656,-0.036147447 -0.24692,-0.034368987 -
 0.320033833,-0.030120183 -0.392654733,-0.019139647
 M_vivesi -0.355197161,0.134922903 0.23827671,0.121093581 0.423747161,0.111569577 0.342016032,0.002994698
 0.23596729,-0.059003819 0.192596387,-0.046074306 0.121084226,-0.034843848 0.047479132,-0.034867713 -
 0.025790387,-0.036479761 -0.09879931,-0.038651719 -0.171914065,-0.037397961 -0.245117323,-
 0.035312548 -0.318076065,-0.029486726 -0.386272548,-0.018462368

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N_albiventris -0.15957300,-0.14537100 -0.23018300,-0.05549320 -0.22066400,0.00940388 -0.21597100,0.02884790 -
 0.20253600,0.04535535 -0.18652450,0.06369155 -0.13897500,0.10911900 -0.11471750,0.08840910 -
 0.09067045,0.06541045 -0.08636295,0.06308210 -0.01335190,0.09022875 0.11889600,-0.00434923
 0.17178750,0.03859335 0.25227650,0.02617440 0.32517150,0.00461767 0.39793600,-0.06695905
 0.43474300,-0.13320250 0.11868400,-0.06427555 -0.03430350,-0.06104095 -0.12566050,-0.10224200
 N_leporinus -0.15691900,-0.13909779 -0.23152869,-0.05808036 -0.22659479,0.01277794 -0.21825890,0.03122349 -
 0.20532866,0.04950073 -0.18697166,0.08038978 -0.15767224,0.10230204 -0.11452710,0.06613017 -
 0.08930366,0.05728156 -0.07183429,0.05558218 -0.01087349,0.07801753 0.12655272,0.00910436
 0.18222821,0.04203615 0.26124121,0.02734068 0.33313366,0.00375714 0.38757531,-0.07381486
 0.42342324,-0.13151938 0.12197317,-0.04541406 -0.03694581,-0.06542708 -0.12936931,-0.10209020
 K_papillosa -0.17519100,-0.12326900 -0.24397900,-0.03726790 -0.23160450,0.01670330 -0.22083350,0.02873060 -
 0.20048300,0.03948595 -0.18384500,0.05423660 -0.14441000,0.07370595 -0.11458300,0.06828145 -
 0.09032750,0.06204985 -0.07138405,0.06063005 -0.01240420,0.09133415 0.12034750,-0.02195650
 0.16407500,0.02571425 0.23637100,0.02088905 0.31250950,0.00094141 0.46449750,-0.05058490
 0.39437600,-0.12571500 0.14570700,-0.05049015 -0.01444045,-0.04995725 -0.13439900,-0.08346190
 M_adversus -0.17273112,-0.13744571 -0.26172265,-0.04291112 -0.24266088,0.01693492 -0.22452888,0.03286775 -
 0.20533476,0.04627102 -0.18493335,0.05777281 -0.14801965,0.07338110 -0.11499424,0.07127184 -
 0.08928701,0.06813130 -0.06117936,0.06562596 -0.00862735,0.07781430 0.13616582,-0.01743090
 0.18858694,0.02661348 0.25416882,0.02111767 0.31869776,0.00799310 0.42383982,-0.04871782
 0.38044753,-0.12914224 0.13977335,-0.04714849 0.00301795,-0.04772557 -0.13067835,-0.09527351
 M_albescens -0.17939059,-0.13530524 -0.26648271,-0.04200398 -0.24183471,0.01129885 -0.22517406,0.03390031 -
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 0.18555124,0.02341414 0.24510124,0.01841938 0.30843800,0.00606992 0.42318665,-0.04786618
 0.39175929,-0.12505865 0.14882553,-0.04753946 0.00721497,-0.04993106 -0.13364041,-0.09221934
 M_becksteinii -0.18020314,-0.12292157 -0.25693286,-0.03208430 -0.23815471,0.01284746 -0.22217771,0.03064291 -
 0.20319143,0.04280144 -0.18373914,0.05269439 -0.14537057,0.06202531 -0.11392729,0.06391811 -

0.08984366,0.06164217 -0.06016679,0.06246739 -0.00645994,0.08207626 0.13105557,-0.00871411
 0.17610814,0.03164670 0.24463300,0.02209350 0.30824571,-0.00082337 0.44498100,-0.05526230
 0.39955543,-0.12625629 0.13530043,-0.04220769 -0.00419244,-0.04960213 -0.13551914,-0.08698374
 M_bocagii -0.18124243,-0.12899707 -0.26771186,-0.04099011 -0.23920036,0.01278913 -0.22168929,0.02936288 -
 0.20281343,0.04272352 -0.18444736,0.05604036 -0.14696671,0.07109741 -0.11489271,0.07092804 -
 0.08944699,0.06904399 -0.06182355,0.06612554 -0.01173979,0.08469221 0.13536429,-0.01458741
 0.18746321,0.02296776 0.25152450,0.01683861 0.31390529,0.00151841 0.42873129,-0.04381572
 0.38419379,-0.12578979 0.14301936,-0.05075849 0.00671756,-0.04731191 -0.12894500,-0.09187758
 M_capaccinii -0.17929971,-0.13519250 -0.26668838,-0.04265342 -0.23862529,0.01345042 -0.22477083,0.03446095 -
 0.20562492,0.04889140 -0.18451075,0.05996145 -0.13873017,0.07050745 -0.11367958,0.06951309 -
 0.08874506,0.06847629 -0.05762299,0.06585163 -0.00871553,0.07763749 0.13524108,-0.01746177
 0.18807421,0.02261238 0.25034179,0.01686510 0.31002458,0.00729895 0.42451725,-0.04523661
 0.39338042,-0.12506500 0.13851846,-0.04701156 -0.00020774,-0.04769347 -0.13287692,-0.09521233
 M_dasyne -0.17914240,-0.13725280 -0.26735240,-0.04717818 -0.23872660,0.01211063 -0.22293920,0.03232826 -
 0.20481560,0.04693426 -0.18401460,0.05720816 -0.14197560,0.07313096 -0.11435560,0.07254122 -
 0.08861404,0.06956608 -0.05951222,0.06652852 -0.01116382,0.07756794 0.14057360,-0.01420788
 0.19333600,0.02598112 0.25899360,0.02035760 0.31926000,0.01059579 0.42209360,-0.04773254
 0.37548400,-0.12885700 0.13762180,-0.04784386 -0.00328681,-0.04899772 -0.13146320,-0.09278026
 M_daubentonii -0.17667642,-0.14019737 -0.26602437,-0.04342247 -0.24353316,0.01694601 -0.22648700,0.03665155
 -0.20611305,0.04958220 -0.18460974,0.05992587 -0.14101837,0.06862550 -0.11370837,0.06767950 -
 0.08893493,0.06814004 -0.05718855,0.06407111 -0.00487619,0.07530559 0.14048195,-0.01705311
 0.19175495,0.02190069 0.25237500,0.01700596 0.31287063,0.00553253 0.42097047,-0.04617199
 0.38452832,-0.12121216 0.14509842,-0.04324703 -0.00392124,-0.04664251 -0.13498821,-0.09341982
 M_dominicensis -0.17758800,-0.13135820 -0.25957140,-0.04011024 -0.24038600,0.01399940 -
 0.22723000,0.03687424 -0.20730100,0.05197090 -0.18464980,0.06375834 -0.14276700,0.07100812 -
 0.11328280,0.06748922 -0.08883734,0.06310822 -0.05516252,0.06073354 -0.00966844,0.07337668
 0.13476000,-0.01942802 0.18403600,0.02142312 0.24882480,0.01703994 0.31013140,0.00505334
 0.42411720,-0.04875920 0.40339120,-0.11855680 0.13538500,-0.04619786 -0.00012862,-0.04435618 -
 0.13407140,-0.09706882
 M_emarginatus -0.17363800,-0.12707820 -0.25182860,-0.03913720 -0.23579740,0.01409272 -0.22333040,0.03150816
 -0.20492300,0.04542786 -0.18513760,0.05740062 -0.14727180,0.06982492 -0.11480660,0.06980684 -
 0.09018152,0.06370338 -0.06676826,0.06214442 -0.00875270,0.08428784 0.13351520,-0.01303957
 0.18029940,0.02464444 0.24331600,0.01846972 0.30664980,0.00310682 0.44154500,-0.05178948
 0.40003160,-0.12531940 0.13873240,-0.04998288 -0.00857176,-0.05089486 -0.13308160,-0.08717616
 M_evotis -0.17905675,-0.12268179 -0.25824058,-0.03970925 -0.24088075,0.01174393 -0.22347083,0.03262343 -
 0.20449096,0.04620671 -0.18374679,0.05550617 -0.14865429,0.06738362 -0.11376579,0.06656339 -
 0.08922804,0.06318090 -0.04953182,0.06129073 -0.00585374,0.07917507 0.13224529,-0.01745574
 0.17839125,0.02543868 0.24402354,0.02203154 0.30903571,0.00491729 0.43271679,-0.05551423
 0.40555317,-0.12081692 0.13761429,-0.04619700 -0.00278937,-0.04637778 -0.13987008,-0.08730876
 M_gracilis -0.17230835,-0.12822419 -0.25897523,-0.03849736 -0.23987492,0.01568144 -0.22332796,0.03182950 -
 0.20473892,0.04591478 -0.18405838,0.05494015 -0.14784919,0.07161090 -0.11438585,0.06831773 -
 0.08957723,0.06504002 -0.06214560,0.06120620 -0.00835570,0.08139582 0.13223027,-0.01703279
 0.18404073,0.02704923 0.24733319,0.01945640 0.31114554,0.00534231 0.42901485,-0.04755417
 0.40019792,-0.12831404 0.13709715,-0.05139227 0.00044001,-0.04842456 -0.13590250,-0.08834506
 M_horsfieldii -0.17656796,-0.13233752 -0.26054074,-0.04121810 -0.24006939,0.01430922 -0.22360791,0.03377385 -
 0.20570357,0.04982305 -0.18401030,0.06113380 -0.14402378,0.07301225 -0.11316591,0.07045109 -
 0.08808545,0.06649137 -0.05372285,0.05921889 -0.01127569,0.07672223 0.13264835,-0.01917104
 0.18142409,0.02560386 0.24633483,0.01844580 0.31047709,0.00413187 0.42732552,-0.04702189
 0.39911396,-0.12189417 0.14387939,-0.04967065 -0.00157368,-0.04834111 -0.13885617,-0.09346278
 M_keaysi -0.17942426,-0.12951237 -0.25821032,-0.04086617 -0.24041605,0.01484296 -0.22434716,0.03409614 -
 0.20506979,0.04814783 -0.18411968,0.05757264 -0.14875542,0.06965634 -0.11363658,0.06747532 -
 0.08897514,0.06456236 -0.05383137,0.06279222 -0.00597440,0.07754723 0.13656616,-0.01930906
 0.18339458,0.02009584 0.24514468,0.01645293 0.30932147,0.00359281 0.42370253,-0.04715218
 0.40338632,-0.11925947 0.14552626,-0.04704584 -0.00201862,-0.04398932 -0.14226311,-0.08970022
 M_leibii -0.17298521,-0.13108729 -0.25465000,-0.04331839 -0.23718707,0.01582424 -0.22233421,0.02993826 -
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M_bocagii

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M_dominicensis

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M_vivesi

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Supplementary material 2. List of 421 specimens examined.

Museum acronyms are as follows: AMNH = American Museum of Natural History, New York; CNM= Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México, México; IEX= Colección de vertebrados INECOL; CTUA=Colección Teriológica Universidad de Antioquia, Medellín, Colombia; NMNH= National Museum of Natural History, Smithsonian Institute, Washington; EBD= Estación Biológica Doñana, Sevilla, Spain; IEX=Instituto de Ecología, Xalapa, México.

M. adversus- NMNH: S. Makapan, Sumatra: 144266, 144286, 144295, 144296, 144292, 144294. Pulo mendanau, Indonesia: 124922, 124923, 125153, 112606. Siam, Thailand: 251719, 251721, 296508, 251720, 251717, 251716. Mankol, Borneo: 153937, 153938, 153936, 578490, 296770.

M. albescens- CNM: Ocosingo, Chiapas, México: 9523, 19300, 19301, 22967, 22968, 23736, 23737, 23738, 23739, 23740, 24473, 24474, 24475, 24477, 24478, 24479, 41799.

M. bechsteinii- AMNH: baden-wuerttemberg, Germany: 245362, 217133. NMNH: Foret russy, France: 231169, 231170, 231171, 154080, 154081, 38016.

- M. bocagii*- EBD: Nvuba river, Equatorial Guinea: 14164, 14915, 14916, 13943, 13944, 17639. NMNH: Kinshasa, Democratic Republic of the Congo: 19795, 197955, 260031. Bumba zone, Democratic Republic of the Congo: 38019, 465820, 537719, 537720, 537721, 547013, 547014.
- M. capaccinii*- EBD: Valle Gruta del camello, Morocco: 15528, 15533, 15594, 15615. NMNH: Switzerland: 113906, 115276, 115277, 121193, 121195, 121196, 121197, 121198, 121199, 121200, 121201. Cagliari, Cerdeña: 38348, 38349, 38350. Oujda, Morocco: 476540, 476543, 476544, 476546, 540780, 86639.
- M. dasyncneme*- NMNH: Nr. Maesiricht, Holland: 154029, 153985, 153986, 153987, 153988.
- M. daubentonii*- EBD: Malaga, Spain: 9661, 9663, 9779, 9780, 9781, 9782, 9784, 15973, 15575, 28793, 28794, NMNH: Lombardy, Italy: 86562, 86566, 86570, 86572, 86578, 16355, 152538.
- M. dominicensis*- NMNH: Clarke Hall, Dominica: 113547, 113555, 113563, 361911, 361912, 361913.
- M. emarginatus*- NMNH: Bouches de rhônes, France: 85517, 105295, 105296, 319209, 476547, 476548, 540781.
- M. evotis*: NMNH: Colorado, USA: 30305, 38680, 147660, 148161, 148163, 148164, 148165, 148166, 207988, 207989, 209037, 209218, 250566, 271166. New Mexico, USA: 349214, 349215, 349216, 349217, 349218, 506257, 554292, 554293, 554294, 552743, 570687.
- M. mystacinus (brandtii) gracilis*: NMNH: Seul, Korea: 298015, 298017, 298018.
- M. horsfieldii*- NMNH: Borneo: 154646, 154647, 154648, 156560, 166561, 155798, 196561, 196562, 198933, 198936, 198937, 198939, 528299, 590138, 590139, 590140, 590141, 590142, 590143, 590145, 590434, 590698, 590699, 590700, 590701, 590702.
- M. keaysi*- CNM: Tabasco, México: 6805, 7876, 7880, 7881, 7882, 7883, 7884, 7885, 7886, 7887, 7888. Yucatán, México: 16337, 16345, 18510, 18953, 18954, 20939, 20940, 20942, 20983, 32853, 32854, 404331, 40433, 40434.
- M. leibii*- NMNH: Virginia, USA: 13194, 270086, 283778, 296798, 296799, 314985, 364631, 364632. Maryland, USA: 150274, 150275. New York, USA: 187406, 187497, 187408, West virginia, USA: 461879, 461880, 487616, 489615, 552741, 55845, 589246, 60949.
- M. macrotarsus*- NMNH: Negros oriental, Phillipines: 113460, 254502, 254505, 254509, 254512, 254700, 256090, 256093, 458684, 458685, 458686, 478687, 498688, 498689.
- M. myotis*- AMNH: bavaria-waldmünchen, Germany: 150109, 150106, 150111, 150112. NMNH: Germany: 37548, 86647, 86648, 86649, 152546. Uri, Switzerland: 113853, 113854, 113855, 113856, 113861, 121191, 145193, 145194. Czech republic: 347425, 347426, 540783.
- M. nattereri*- AMNH: Holstein, Germany: 146358, 146359, 146360, 146364, 245371. NMNH: Thurgau, Switzerland: 113866, 113867, 113868. Mardebu, Germany: 152541, 152542, 152543. Valsesia, Italy: 38015. Central bohemia, czech republic: 540785.
- M. nigricans*- CNM: Reserva del triunfo, Chiapas, México: 182, 6463, 20425, 20951, 20952, 20953, 20954, 20955, 20957, 20958, 22869, 22870, 22871. Veracruz, México: 14289, 8210, 8211, 8213, 8214, 8215, 8481. CTUA: Maceo, Antioquia, Colombia: 10061, 10228, 10447, 11173, 11206, 11290, 11292, 11293.
- M. riparius*- AMNH: 208652 CTUA: Antioquia, Colombia: 10915, 10297, 10724, 11289, 11295, 11297, 20226, NMNH: Para, Belem, Brasil: 361782, 361786, 381788, 361790, 361791, 483949, 483950, 483951.

Pichincha, Ecuador: 513482, 528567, 528568, 528570, 548342, 548344, 548345, 548347, 549518, 566455, 566456, 574564.

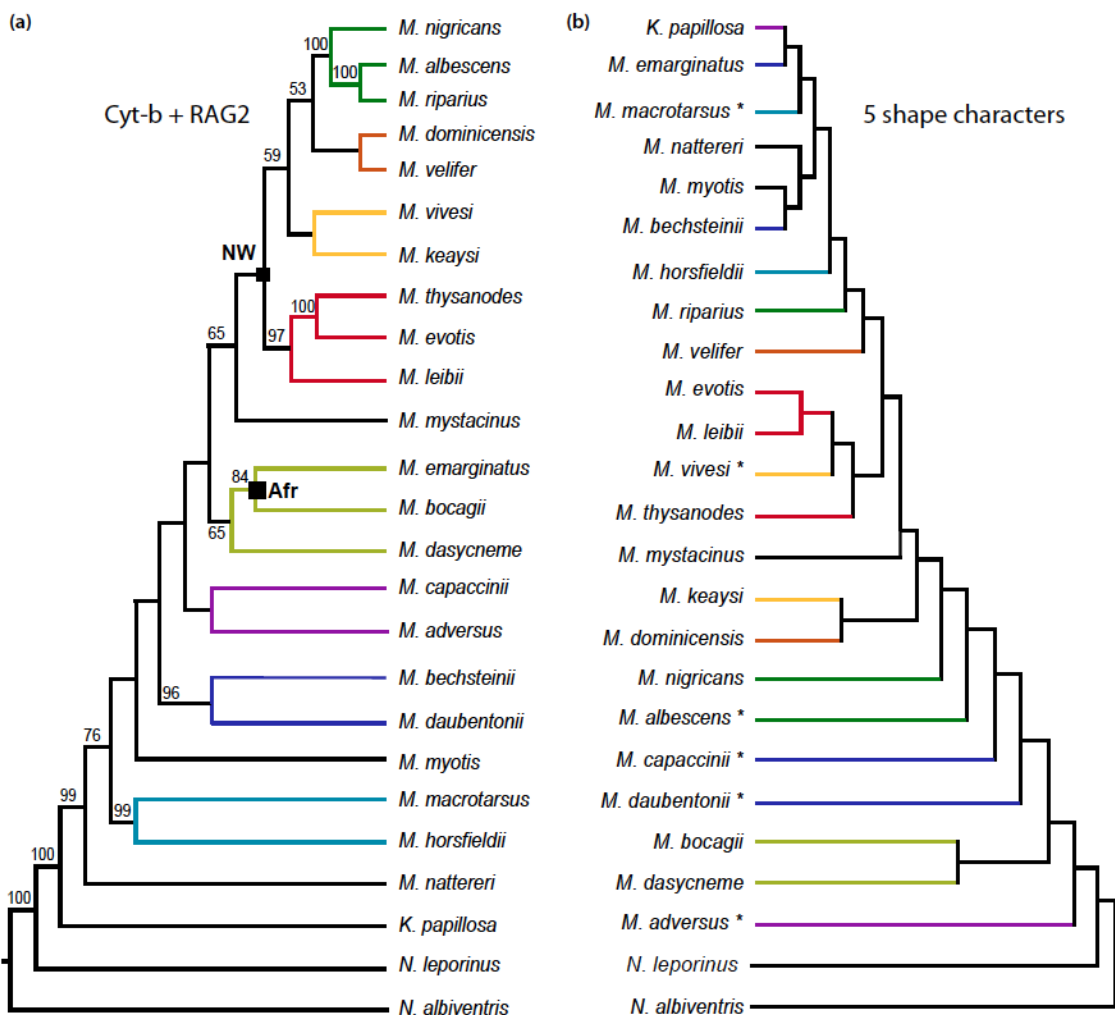
M. thysanodes- CNM: N México: 2118, 5005, 5546, 18604, 12469. Querétaro, México: 20006, 20082.

Ocampo, Guanajuato, México: 22472, 22473, 22474, 28886, 30922.

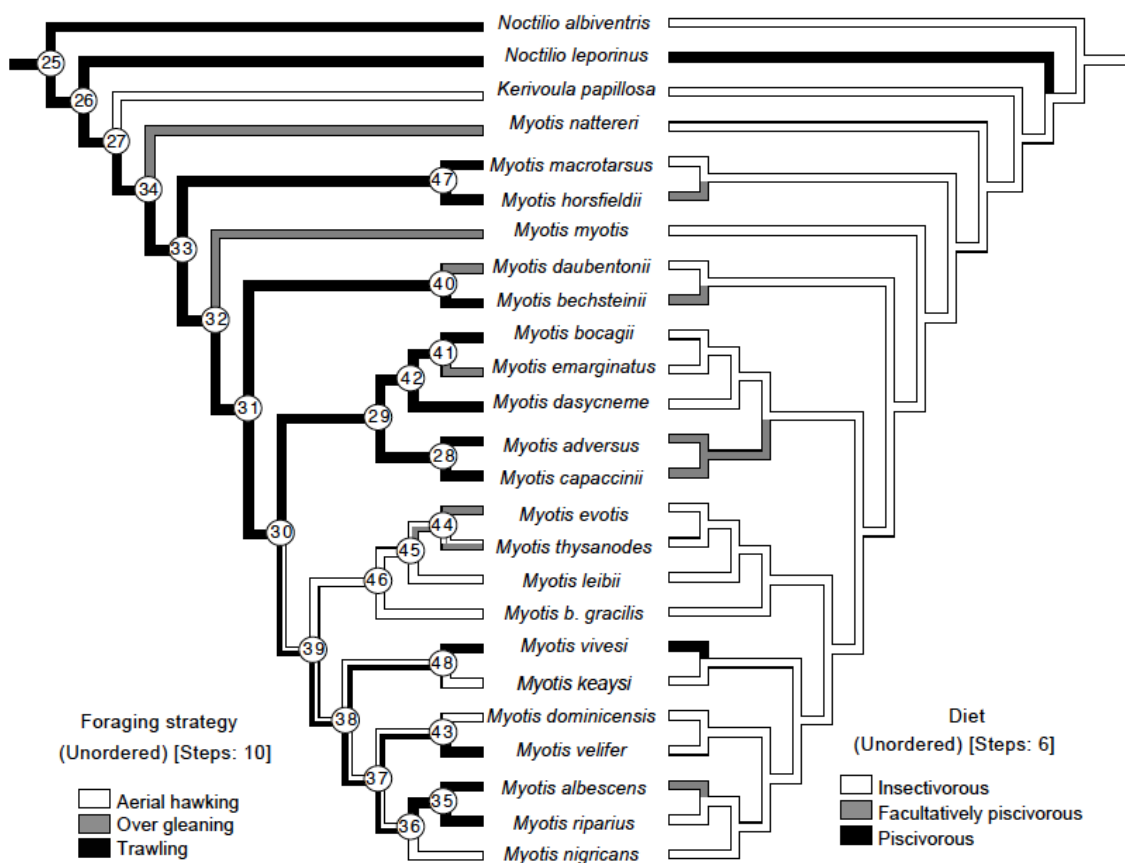
M. velifer- CNM: Morelos, México: 473, 7156, 7902, 7903, 8241, 9069, 9450. Coahuila, México: 13817, 13818, 13819, 13820. Baja California, México: 15571, 15572. Puebla, México: 16857, 16867, 18609, 18523, Durango, México: 19996, 19997, 19998, 19999, 20000, 20001, 28883, 28884, 28856, 28858, 28859, 28860, 28861, 28863, 45807, 45808.

M. vivesi- CNM: Isla Partida Norte, México: 15658, 15660, 15661, 15662, 15664, 15659, 16803, 16805, 16806, 16807, 23909, 23910, 23912, 23914, 23915, 39327, 45675, 45679, 45680, 45681, 45682, 41683, 45684, 45685, 45686, 45689, 45690, 45691, 45693, 45696, 45697.

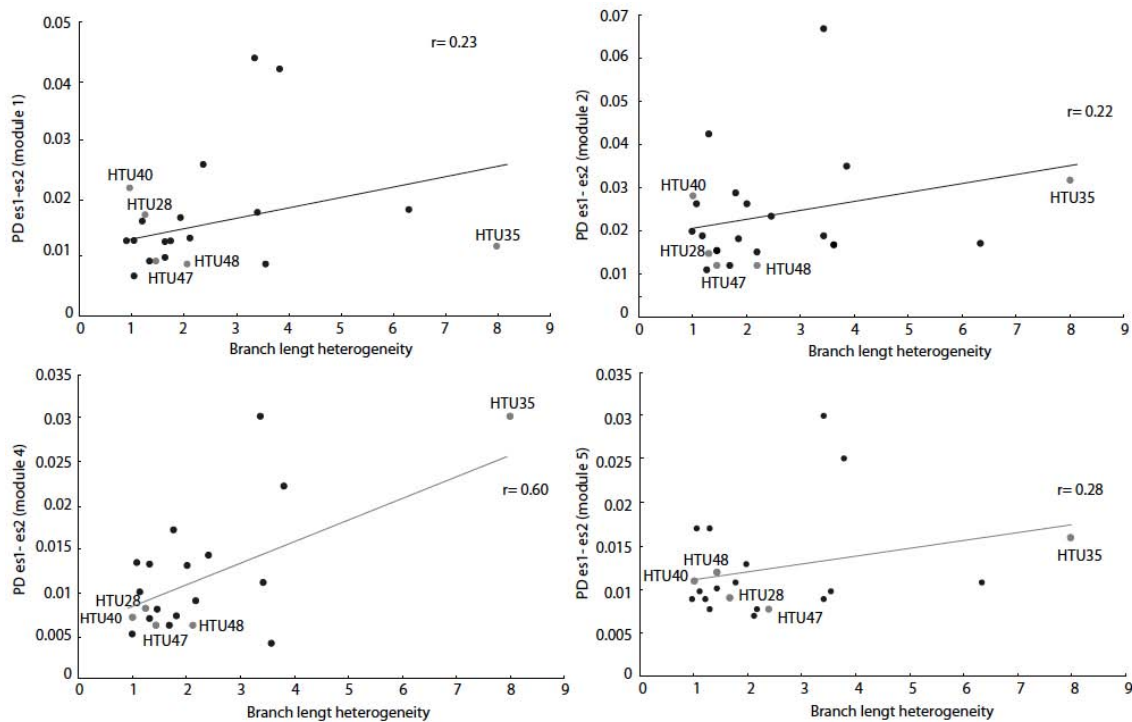
N. albiventris- CNM: Bolivar, Colombia: 32136, 32137, 32138. *N. leporinus*- CNM: Tonalá, Chiapas, México: 5921, 6208, 6209, 6210, 6211, 6212, 6213, 6214, 6215, 6216, 6217, 6218, 6219, 6220, 6221, 6222, 6490, 6623, 6931. Rio popoyuta, Michoacán, México: 17133, 17135, 18118, 19117, 19116, 19119, 19120. Guerrero, México: 34400, 34401, 23701, 27886, 34402, 34403. *K. papillosa*- IEX: Krabi, Thailand: M0114, M0113



Supplementary material 3. Phylogeny of *Myotis* obtained from separate analyses of molecular and geometric morphometric data. (a) Single optimal tree from our parsimony analysis of Cytb and RAG 2 sequences with NONA, numbers above branches are Jackknife values, branch colors indicate species in the same clade, and squares represent African (Afr) and New World (NW); (b) single optimal tree found in the parsimony analysis of landmark data from five morphometric shape characters (modules 1-5) with TNT. Taxa labeled with an * are facultatively piscivorous species.



Supplementary material 4. Evaluation of concerted change in diet and foraging strategy. Mirror tree from Mesquite with optimizations of foraging strategy and diet on our reference phylogeny numbers of nodes indicated at left side or mirror tree. Foraging strategy and diet were optimized as discrete characters with three unordered states. Left tree: optimization of three foraging strategies (aerial hawking, over gleaning, and trawling). Right tree: optimization of three diets (Insectivorous, facultatively piscivorous, and piscivorous).



Supplementary material 5. Linear regressions of Procrustes distances between estimated shapes from the same node (A) and branch length heterogeneity in four modules. (a) Linear regression of Procrustes distances between estimated shapes (es1-es2) from a node and branch length heterogeneity in module 1 (parieto-occipital region). (b) Linear regression of Procrustes distances between estimated shapes (es1-es2) and branch length heterogeneity in module 2 (frontal-maxillary region). (c) Linear regression of Procrustes distances between estimated shapes (es1-es2) and branch length heterogeneity in module 4 (alveolar region). (d) Linear regression of Procrustes distances between estimated shapes (es1-es2) and branch length heterogeneity in module 5 (ventral view of skull). Ancestral shapes for piscivorous species (node 28,35,40, 47,48) were marked on grey.

CAPÍTULO 3

DISCUSIÓN GENERAL Y CONCLUSIONES

La variación en la forma del cráneo bajo una perspectiva ecológica y evolutiva

La evolución de la piscivoría en el género *Myotis* puede ser explicada por la interacción de factores históricos y ecológicos. El componente histórico fue mayor en alguno módulos, estos representan sinapomorfías que corroboran la idea del género como un grupo monofilético (Ruedi y Mayer, 2001; Stadelman *et al.*, 2004; Gardner, 2008). La base del cráneo (módulo 5) y la región frontal-nasal (módulo 2) fueron las más conservadas dentro del género. La region alveolar presenta pocos cambios dentro del género en especies de difentes clados, en general las especies que concentran más cambios fueron *M. myotis* y *M. bechsteinii* en la misma dirección pero no explicados por ancestría común y *M. leibii* y *M. evotis*, especies cercanamente emparentadas.

Las marcadas diferencias en el tamaño entre las especies del género resultan un factor importante en la variación para uno de los cinco módulos, la caja craneana, el resto de las estructuras varían en función de otros factores históricos o ecológicos. La mandíbula es la estructura que presenta el menor efecto del tamaño y el mayor efecto ecológico, dada su relevancia en la función masticatoria (Herring y Herring, 1974; Dumont y Herrel, 2003; Dumont *et al.*, 2009). La morfología del cráneo presenta mayor efecto histórico y pocos cambios en algunas especies, algunos de ellos explicados por las diferencias en el tamaño. La base del cráneo y la región frontal nasal presentan menores cambios en la filogenia de *Myotis* y mayores cambios respecto de los grupos externos. Estos caracteres representan sinapomorfías para el género dado que mostraron además los índices de homoplasia más bajos.

La morfología generalista en el género, que se considera ancestral entre los murciélagos (Gardner, 2008), es la clave para entender las tendencias de variación morfológica en el género (Tate, 1942; Findley, 1972; Koopman, 1994). La baja discriminación entre algunas especies del género muestra equivalencias morfológicas entre

especies que podrían compartir condiciones ecológicas similares (Findley, 1972; Ruedy y Mayer, 2001). Los módulos donde se encontró el menor porcentaje fueron los módulos mandibulares, el área de los procesos mandibulares (módulo 3) seguido de la región alveolar (módulo 4), es probable que las similitudes en esta región, la más generalizada entre las especies, este asociada al oportunismo en la captura de presas y la alternancia en las estrategias de forrajeo en el caso de las especies insectívoras (Fenton y Bogdanowicz, 2002; Bogdanowicz *et al.*, 2002).

Aunque la mandíbula presenta similitud entre las especies insectívoras es el módulo que revela mayor información sobre la dieta. En el caso de los procesos mandibulares la separación fue mayor para especies que forrajean sobre el agua. Las especies que mostraron mayor diferenciación fueron los piscívoros facultativos y la especie piscívora *M. vivesi*. Las deformaciones en el primer eje canónico mostraron cambios en la posición del proceso condilar respecto al coronoide. La piscivoría facultativa aparece en el género como una convergencia entre especies con una estrategia de forrajeo similar (trawling), en estas especies además de los cambios morfológicos anteriormente mencionados se presentan características externas asociados a la captura de presas sobre el agua (Ruedi and Mayer, 2001; Kawai *et al.*, 2003; Lewis-Oritt *et al.* 2001).

El área de los procesos mandibulares presenta además la mayor correlación con el factor de estiramiento del músculo masetero, en este modulo la relación forma – function se hace evidente. Las especies piscívoras presentaron los factores de estiramiento más altos y los piscivoros facultativos presentaron valores intermedios. Considerando el modelo del factor de estiramiento del músculo masetero (Herring y Herring, 1974) altos valores en esta variable implican cambios en la posición de los procesos mandibulares y aumento del ángulo origen/insersión, que se traducen en una alta capacidad de apertura mandibular (Herring y Herring, 1974; Herrel *et al.*, 2008). Bajo este escenario se espera una ventaja en la captura y consumo de presas para las especies piscivoros y piscivoros facultativos respecto de las especies insectivoros.

Estos resultados muestran que tanto la historia común como la ecología juegan un importante papel en la diversificación morfológica en el género *Myotis*. La optimización de los cambios en la reconstrucción filogenética permitió detectar las convergencias en la mandíbula en diferentes clados y el componente histórico en los módulos del cráneo. La ocupación del morfoespacio por las especies del género es diferentes según el módulo, cada

uno de ellos presenta un efecto ecológico o histórico distinto, sin embargo la clave de la morfología craneal y mandibular en el género es el oportunismo y la inclusión de nuevos ítems en la dieta puede lograrse con pequeños cambios.

Conclusiones

- La variación en la morfología craneal debe ser descrita considerando la modularidad en el cráneo y la mandíbula ya que la respuesta de cada uno de los módulos a diferentes presiones ecológicas como la dieta es diferente, además existe un mayor efecto histórico en algunas estructuras que han evolucionado y se han mantenido constante a lo largo de distintos clados, o con poca variación, dentro del género.
- La piscivoría en el género ha evolucionado de manera paralela a partir de una morfología insectívora con pocos cambios en los descendientes respecto de los ancestros, estos cambios están localizados fundamentalmente en la region de los procesos mandíbulares y representan desempeño diferencial en el estiramiento del músculo masetero.
- La mayoría de las especies del género *Myotis* presentan una morfología generalista, con pocos cambios en la region frontal maxilar y base del cráneo, mayores cambios en la caja craneana asociados a las diferencias en el tamaño entre las especies y en la region de los procesos mandíbulares asociados al funcionamiento de los músculos masticatorios.
- El oportunismo en la dieta y las diferentes estrategias de forrajeo en el género estan asociadas a una morfología conservativa, que con pocos cambios de relevancia funcional ha permitido la inclusion de una dieta piscívora en el género.

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