DANIEL ALEXANDRE STÜPP DE SOUZA

ANÁLISE MORFOMÉTRICA DE *Molossus molossus* (CHIROPTERA, MOLOSSIDAE) AO LONGO DE UM GRADIENTE LATITUDINAL NO BRASIL

Dissertação apresentada ao Programa de Pós-graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

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Dissertação aprovada em ____/____/_____

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Orientadora

"Emancipate yourselves from mental slavery
none but ourselves can free our minds..."

BOB MARLEY

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SUMÁRIO

RESUMO

Os molossídeos são morcegos cujas características morfológicas externas mais marcantes são o pelo curto e aveludado e a cauda espessa e livre, sendo, por esta última característica popularmente conhecidos como morcegos-de-cauda-livre. Os membros da família são considerados os mais rápidos morcegos em voo. São insetívoros especializados e adaptados à natureza de sua dieta. Habitam regiões tropicais e temperadas da África, da América e da Europa e em apenas uma noite podem percorrer centenas de quilômetros em busca de alimento.

A espécie objeto deste estudo, *Molossus molossus*, está amplamente distribuída na Região Neotropical, sendo registrada desde o sul dos Estados Unidos até a Argentina. Dados sobre dimorfismo sexual e sobre variação geográfica da espécie usualmente são encontrados em trabalhos com um número pequeno de indivíduos analisados.

Nesse sentido, o objetivo deste trabalho é realizar uma análise morfométrica para avaliar o dimorfismo sexual na espécie e as diferenças de tamanho entre os indivíduos das diferentes regiões estudadas, além de ampliar o conhecimento sobre aspectos morfológicos da espécie.

Foram examinados neste estudo 446 indivíduos adultos de *M. molossus* provenientes de sete Estados do Brasil: Amazonas, Ceará, Mato Grosso do Sul, Rio de Janeiro, Rio Grande do Sul, Santa Catarina e São Paulo. Como ferramenta de detecção de variações foi utilizada a morfometria linear. Para tanto foram extraídas 19 medidas dos indivíduos, 14 do sincrânio e 5 de corpo.

Os resultados revelaram o maior tamanho dos machos em relação às fêmeas em todas as populações analisadas, bem como um gradiente de aumento de tamanho na espécie no sentido norte-sul.

Além do estudo morfométrico, foram analisadas as séries dentárias destes 446 indivíduos e de outros quatro, dois casais de dois Estados diferentes, Paraná e Piauí. Esta análise revelou a ocorrência de dentes extranumerários, incisivos inferiores e pré-molares superiores, em um número elevado de indivíduos.

Estes resultados colaboram com o aumento do conhecimento sobre a biologia da espécie, além de auxiliarem na correta identificação da mesma nas diferentes regiões do país.

CAPÍTULO INTRODUTÓRIO

I – INTRODUÇÃO

1. Molossidae

Os quirópteros são um grupo extremamente diversificado, ocorrendo em território nacional nove famílias, 64 gêneros e 167 espécies (PERACCHI *et al.* 2006). Os molossídeos são morcegos cujas características morfológicas externas mais marcantes são o pêlo curto e aveludado e a cauda espessa e livre (FABIÁN AND GREGORIN 2007), sendo, por esta última característica, denominados comumente morcegos-de-cauda-livre. Os morcegos desta família são considerados os mais rápidos dentre todas as espécies da ordem Chiroptera, e costumam voar acima do dossel das matas, portanto, fora do alcance humano. Em virtude destas duas últimas características existem dificuldades na coleta de algumas espécies de molossídeos. Por este motivo a família nem sempre se encontra bem representada em coleções científicas e o conhecimento taxonômico e ecológico ainda é escasso (FREEMAN 1981).

Os molossídeos são morcegos insetívoros especializados e adaptados à natureza de sua dieta (FREEMAN 1979). Habitam regiões tropicais e temperadas da África, da América, Ásia, Europa e Oceania (SIMMONS 2005). Em apenas uma noite, os membros desta família podem percorrer centenas de quilômetros em busca de seu alimento (MACDONALD 2001).

2. *Molossus molossus*

O gênero *Molossus* É. Geoffroy, 1805 apresenta oito espécies, das quais cinco têm registro para o território brasileiro. Distribui-se desde o sul dos Estados Unidos até o norte da Argentina e Uruguai (SIMMONS 2005). De acordo com GREGORIN AND TADDEI (2002) o gênero apresenta como características distintivas crânio com crista sagital anterior em geral desenvolvida, palato raso sem recurvamento em forma de domo e incisivos superiores triangulares, não caniniformes.

Há registros da presença de *Molossus molossus* (Pallas, 1766) no Estado da Flórida, sul dos Estados Unidos, porém FRANK (1997) considera que a presença da espécie neste Estado pode ser resultado do transporte de alguns indivíduos por humanos. Populações bem estabelecidas podem ser encontradas desde o norte do México, Caribe até a América do Sul, apresentando registros em diversos locais como Grandes e Pequenas Antilhas, Antilhas Holandesas, Trinidad e Tobago, Venezuela, Peru, Paraguai, norte da Argentina, Uruguai e Brasil (SIMMONS 2005) (Figura 1). No Brasil a espécie é encontrada nos cinco grandes biomas (MARINHO-FILHO AND SAZIMA 1998).

O complexo *M. molossus/M. pygmaeus* necessita de urgente revisão, uma vez que estes nomes são tidos como sinônimos (SIMMONS 2005), mas podem na verdade representar espécies distintas como sugerem LIM AND ENGSTROM (2001), principalmente em virtude do tamanho e da coloração dos espécimes coletados por estes autores.

Os padrões morfológicos descritos por FABIÁN AND GREGORIN (2007) caracterizam *M. molossus* com pelagem dorsal aveludada e coloração variável entre castanho escuro e negro, ocorrendo também indivíduos marrom-avermelhados. A pelagem ventral, em contraste com a dorsal, apresenta-se mais clara. Suas orelhas são arredondadas e unem-

se na linha média do crânio. Pode-se notar facilmente uma quilha localizada na região mediana da porção anterior do rosto. Existem pêlos rijos sobre o lábio superior, cuja função permanece sem investigação. A fórmula dentária da espécie é I1/1 C1/1 P1/2 M3/3 (GREGORIN AND TADDEI 2002).

M. molossus é exclusivamente insetívoro (FABIÁN AND GREGORIN 2007) e captura seu alimento em pleno vôo (MACDONALD 2001). A espécie encontra-se bem adaptada às áreas urbanas, freqüentemente utilizando construções humanas como abrigo. Já em áreas não-urbanizadas a mesma pode ser encontrada em ocos e frestas de árvores (BARQUEZ *et al.* 1999).

A despeito de sua ampla distribuição, não existem estudos morfométricos com ampla amostragem envolvendo *M. molossus*. Na literatura são apresentadas apenas poucas medidas, de um número bastante restrito de indivíduos de localidades específicas, obtidas para uma breve caracterização da população inventariada (PEDERSEN *et al.* 1996; GENOWAYS *et al.* 1998; PAZ AND MARTINEZ 1998; SIMMONS AND VOSS 1998; LIM AND ENGSTROM 2001; GENOWAYS *et al.* 2001; MUÑIZ-MARTÍNEZ *et al.* 2003; PEDERSEN *et al.* 2003; GENOWAYS *et al.* 2005; PEDERSEN *et al.* 2005; LARSEN *et al.* 2006; PEDERSEN *et al.* 2006; GENOWAYS *et al.* 2007a; GENOWAYS *et al.* 2007b; GENOWAYS *et al.* 2007c; PEDERSEN *et al.* 2007). Em sua maioria, essas medidas provêm de levantamentos realizados na América Central, principalmente em ilhas do Caribe. Dessa forma, pode-se afirmar que ainda são necessários estudos com grande número de indivíduos, de diferentes locais, para que seja avaliado corretamente o grau de variação entre as diferentes populações da espécie, e para a detecção de um possível padrão associado a esta variação.

Assim como há escassez de dados morfométricos, também é restrita a quantidade de informação disponível acerca de outros aspectos da biologia da espécie. FABIÁN AND MARQUES (1989) apresentam dados sobre a biologia reprodutiva da espécie, como tamanho testicular de machos ativos e inativos, região de implantação do blastocisto e período reprodutivo; a resposta a estímulos que controlam o ritmo circadiano em *M. molossus*, assim como os receptores fóticos ligados a esse mecanismo foi avaliada por ERKERT (2004); RAMÍREZ-CHAVES *et al.* (2008) apresentam dados pontuais sobre dieta, atividade e composição de uma colônia na Colômbia; MACÍAS *et al.* (2009) descrevem o córtex auditivo da espécie, importante região do cérebro ligada ao mecanismo de ecolocação. Estes dados são extremamente importantes, mas ainda são necessários mais estudos para aumentar o conhecimento sobre uma das espécies mais amplamente distribuídas em território brasileiro.

Figura 1: Mapa com a distribuição geográfica de *M. molossus*. Modificado de Barquez

et al. (2008).

3. Variação geográfica em Chiroptera

A variação geográfica vem sendo estudada e analisada desde a constatação de que populações de uma mesma espécie distribuídas em diferentes localidades poderiam apresentar variações em sua estrutura corporal. Desde DARWIN (1859) existe um grande interesse pela distribuição geográfica das espécies e os padrões associados a esta. Segundo FUTUYMA (2002), em virtude da dificuldade de se observar eventos evolutivos históricos diretamente, hipóteses e/ou tendências evolutivas podem ser constatadas em espécies atuais, e uma das formas mais simples de se perceber isto é através de estudos de variação geográfica.

A variação geográfica no tamanho dos quirópteros é um fenômeno bem documentado em estudos recentes para Pteropodidae (KITCHENER AND MAHARADATUNKAMSI 1996), Rhinolophidae (YOSHINO *et al.* 2006), Hipposideridae (ARMSTRONG 2002), Megadermatidae (HAND and YORK 1990), Emballonuridae (WILLIG *et al.* 1986), Mystacinidae (WORTHY *et al.* 1996), Phyllostomidae (MCLELLAN 1984), Noctilionidae (DAVIS 1976), Natalidae (TADDEI AND UIEDA 2001), Molossidae (RATRIMOMANARIVO *et al.* 2009) e Vespertilionidae (SOLICK AND BARCLAY 2006). Das 18 famílias de morcegos atualmente reconhecidas (SIMMONS 2005), 11 estão representadas na lista acima. Entre as famílias que não constam desta lista, a maioria é constituída de um número reduzido de espécies, estas muitas vezes endêmicas a regiões restritas. Entre estas famílias destaca-se o volume de informações referentes aos vespertilionídeos, fato que provavelmente se deve à sua ampla distribuição, pois espécies desta família podem ser encontradas em todos continentes (SIMMONS 2005). Como se trata de uma lista exemplificativa são citados apenas os trabalhos mais recentes, todavia há muitos estudos que reportam a variação geográfica nesta família.

Em relação a Molossidae, objeto deste estudo, há uma quantidade menor de informações e as análises restringem-se em sua maioria a faixas bastante estreitas da distribuição das espécies. WILLIG (1983), através de técnicas estatísticas rigorosas, comparou populações de *M. molossus* da Caatinga e do Cerrado e constatou claras diferenças de tamanho entre os indivíduos destes biomas, sendo os habitantes da Caatinga maiores. ASPETSBERGER *et al.* (2003) produziram dados morfométricos e através de comparações com dados da literatura verificaram que a população de *Chaerephon pumilus* (Cretzschmar, 1826) da Reserva Natural Amani, Tanzânia, possuía maiores proporções que outras populações da espécie estudadas por ALDRIDGE AND RAUTENBACH (1987) na África do Sul, MCWILLIAM (1988) em Gana e SKINNER AND SMITHERS (1990) em Botswana. TIMM AND GENOWAYS (2004) por sua vez verificaram diferenças tão pronunciadas entre populações de *Eumops glaucinus* (Wagner, 1843), que consideram a população da Flórida suficientemente diferente a ponto de tratarem-na como *E. floridanus* (G. M. Allen, 1932), antes tida como uma subespécie. O trabalho mais recente que reporta a variação geográfica em molossídeos é o de RATRIMOMANARIVO *et al.* (2009). Estes autores verificaram claras diferenças entre as populações de *Chaerephon leucogaster* (Grandidier, 1869) de Madagascar analisadas. Tais discrepâncias se deram entre ambientes distintos, o que demonstra que o ambiente pode moldar as características de uma espécie de maneira drástica.

É importante também reconhecer que assim como o tamanho, outras características podem variar entre diferentes regiões como, por exemplo, ecolocação (BARCLAY *et al.* 1999; ARMSTRONG AND COLES 2007; RUSSO *et al.* 2007), vocalização (DAVIDSON AND WILKINSON 2002), aspectos celulares (JUSTE *et al.* 1996), dieta (ASPETSBERGER *et al.* 2003) e até mesmo torpor (SOLICK AND BARCLAY 2007).

4. Dimorfismo sexual em Chiroptera

Estudos envolvendo elevado número de espécies já foram realizados abordando o dimorfismo sexual em morcegos. WILLIAMS AND FINDLEY (1979) estudaram as diferenças entre os sexos na família Vespertilionidae e observaram que as fêmeas eram, em média, maiores do que os machos em todas 18 espécies consideradas em seu estudo. Em 15 das 18 espécies houve diferenças significativas entre os sexos, e em nenhum caso os machos apresentaram superioridade de tamanho significativa. WILLIG AND HOLLANDER (1995) analisaram as diferenças morfométricas entre os sexos de 18 espécies de cinco famílias (Emballonuridae, Noctilionidae, Phyllostomidae, Vespertilionidae e Molossidae), constatando a presença de dimorfismo em 12 espécies: *Phyllostomus hastatus* (Pallas, 1767), *Phyllostomus discolor* Wagner, 1843, *Tonatia bidens* (Spix, 1823), *Artibeus jamaicensis* Leach, 1821, *Anoura geoffroyi* Gray, 1838, *Glossophaga soricina* (Pallas, 1766), *Lonchophylla mordax* Thomas, 1903, *Carollia perspicillata* (Linnaeus, 1758) (Phyllostomidae), *Peropteryx macrotis* (Wagner, 1843) (Emballonuridae), *Noctilio leporinus* (Linnaeus, 1758) (Noctilionidae), *Molossops mattogrossensis* Vieira, 1942 e *Molossus molossus* (Molossidae), todavia os autores explicam as diferenças de apenas três espécies: *A. planirostris* possui machos maiores em ambos biomas, os machos de *P. discolor* são maiores na Caatinga, porém no Cerrado as fêmeas são maiores ou mesmo indistinguíveis e em *M. molossus* os machos são consideravelmente maiores em ambos biomas.

Existem entre os mamíferos diversas espécies em que as fêmeas são maiores do que os machos (RALLS 1976), e este parece ser o padrão entre os quirópteros. Por exemplo, MANN AND AULAGNIER (1993) e DELPIETRO AND RUSSO (2002) observaram a presença de dimorfismo sexual em *Desmodus rotundus* (É. Geoffroy, 1810), com fêmeas maiores que os machos. Uma série de outros estudos realizados com espécies de diferentes

famílias corroboram esta observação (GANNON *et al.* 1992; KOFRON AND CHAPMAN 1994; BENDA 1994; JONES AND KOKUREWICZ 1994; LÓPEZ-GONZALEZ AND POLACO 1998; DIETZ *et al.* 2006).

Assim como existem diferenças de tamanho entre os sexos, também outras características morfológicas possuem acentuada variação entre machos e fêmeas, como as glândulas odoríferas de *Sturnira lilium* (É. Geoffroy, 1810) (GOODWIN AND GREENHALL 1961), o saco localizado na membrana antebraquial de *Saccopteryx bilineata* (Temminck, 1838) usado para *display* social (BRADBURY AND EMMONS 1974; BRADBURY AND VEHRENCAMP 1976) e a glândula gular de machos sexualmente maduros de *Tadarida brasiliensis* (I. Geoffroy, 1824) (GUTIERREZ AND AOKI 1973).

5. Justificativa do estudo

Apesar da ampla distribuição de *M. molossus* e de seu caráter relativamente comum, até o presente não haviam sido realizados trabalhos com indivíduos de diferentes locais ao longo do gradiente latitudinal no qual a espécie está estabelecida. Este fato, aliado à falta de revisões dos gêneros de Molossidae, pode acarretar possíveis erros taxonômicos. Consequentemente, a determinação do papel de cada espécie no ecossistema pode ser prejudicada pelo desconhecimento de suas características e particularidades. Este estudo, apesar de não apresentar um caráter taxonômico, contribuirá para o aumento do volume de informações sobre a família, e poderá auxiliar na devida identificação das espécies, especialmente porque a ampla distribuição da espécie abrange grande gradiente latitudinal e uma série de ambientes com variadas características de vegetação, pluviosidade e temperatura, que podem influenciar de maneira drástica nas características físicas dos indivíduos.

De acordo com PIERSON (1998), os esforços de conservação de quirópteros na América do Norte concentram-se principalmente em espécies raras ou ameaçadas, entretanto, em virtude do papel desempenhado por espécies abundantes no controle de insetos, pragas ou não, e distribuição de nutrientes pelo ambiente, espécies comuns de morcegos talvez apresentem maior importância econômica e ecológica. Assim como outras espécies amplamente distribuídas, que representam uma grande oportunidade de trabalho (AGOSTA 2002), *M. molossus* precisa ter mais aspectos de sua biologia investigados, pois como afirmado por FREEMAN (1981), ainda há uma grande lacuna no conhecimento sobre a biologia dos molossídeos em geral. Apesar de este trabalho ter 30 anos, continua sendo a principal referência sobre diversos aspectos da família. Suas observações e conclusões são ainda utilizadas e algumas das dificuldades estabelecidas pela autora continuam sem solução.

II – OBJETIVOS

O principal objetivo deste trabalho é apresentar uma análise morfológica comparativa de *M. molossus* entre indivíduos provenientes de diversas regiões do Brasil, de forma a verificar a existência ou não de dimorfismo sexual na espécie bem como avaliar as diferenças de tamanho dos indivíduos entre as diferentes regiões estudadas, permitindo, dessa forma, uma ampliação no conhecimento acerca de aspectos morfológicos da espécie.

III – CONSIDERAÇÕES METODOLÓGICAS

Estudar o dimorfismo sexual e a variação geográfica à luz da morfometria linear foi uma decisão baseada na falta de informações sobre características gerais de tamanho de *Molossus molossus*. Para tanto foram selecionadas coleções científicas acessíveis e com um volume de material suficiente para que fosse possível determinar estatisticamente as diferenças entre as populações representadas.

Os parâmetros das medidas realizadas basearam-se em FREEMAN (1981) e foram selecionados de modo a contemplar as três dimensões do sincrânio, além de medidas corporais que usualmente são usadas como referência para caracterização de espécies de morcegos. Resultados e conclusões desta análise encontram-se no Artigo I.

Como foi necessária a preparação da maioria dos sincrânios para a tomada de medidas, foram também analisadas as séries dentárias em busca de variações numéricas, de posição ou patologias. Os resultados destas observações estão no Artigo II.

IV – REFERÊNCIAS BIBLIOGRÁFICAS

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ARTIGO I

Morphometrics of *Molossus molossus* along a latitudinal gradient in Brazil: sexual dimorphism and geographic variation

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ABSTRACT

The Pallas' Mastiff Bat *Molossus molossus* (Chiroptera: Molossidae) is a common but little studied New World bat species that has a widespread distribution across the Neotropical region. We examined morphologic characters of the species in Brazil, including specimens from 7 states ranging from low (4°21' S) to high latitudes (33°32' S). Fourteen cranial and 5 body measurements revealed distinct patterns of sexual dimorphism between the states, but in all cases the males were larger than females. We also verified the pattern of geographic variation along the latitudinal gradient in Brazil, where specimens from populations from northern regions were smaller in general size than the southern ones. This southward increase in size is in agreement with Bergmann's rule and thus this study is another evidence of the rule's validity. Both sexual and geographic variability seem to be related to different environmental conditions found along the gradient where the species is distributed and thus these differences may be treated as adaptive.

Key words: Brazil, Chiroptera, geographic variation, *Molossus*, Molossidae, morphometrics, Neotropical, New World bat, sexual dimorphism

INTRODUCTION

Among the New World bats, Pallas' Mastiff Bat *Molossus molossus* (Pallas, 1766) (Chiroptera: Molossidae) has one of the widest distributions, ranging from

Mexico to the north of Argentina (SIMMONS 2005). The species has also been found in southern Florida; however, FRANK (1997) considers the Florida record a result of the transport of some individuals by humans. In Brazil, *M. molossus* can be found in the five larger biomes (MARINHO-FILHO AND SAZIMA 1998), being extremely adapted to urban areas and frequently using human buildings as roosts. These characteristics make it one of the most common bat species in Brazil.

Some populations of *M. molossus* are the subject of considerable controversy, such as those from French Guiana and Guyana surveyed by LIM AND ENGSTROM (2001), mainly because of observations on size and coloration of dorsal fur. These doubts still occur because some geographic areas are poorly represented in the major revision of the genus done by DOLAN (1989). From FREEMAN (1981) it is known that taxonomic and ecological knowledge of the species of *Molossus* are restricted. Unfortunately, information on its biology is still scarce and morphologic studies that subsidize other investigations are necessary.

Morphometric analysis constitutes an important tool in the study of morphology, being used for detection of patterns or determination of anomalies and variations in size and form. Articles can easily be found in the scientific literature that investigate morphologic patterns in the most diverse taxa with the most diverse aims; however, two of the major objects of interest are sexual dimorphism and geographical variation.

Sexual dimorphism can be defined in many related ways that only differ by a few words. It can be characterized as the 'morphological differences between males and females' (RICKLEFS 2003). This phenomenon is reflected mainly in reproductive characteristics but it is important to recognize that other forms of dimorphism exist (see HILDEBRAND 1995). This same author recognizes that growth rates and the ultimate size of an adult's body are variable between the sexes and thus differences in body

configurations are normal. BADYAEV (2002) corroborated this statement and considers dimorphic body size to be the product of differences in growth patterns that result in unequal corporal proportions between males and females. According to RENSCH (1950) there is a macro-evolutionary trend that sexual size dimorphism increases with an increase of body size in species where males are larger than females. Therefore, it is normal that the New World bats do not present a very accentuated sexual size dimorphism because of their limited corporal size.

Geographic variation has been studied and analyzed far beyond the observation that populations of a species distributed at different locations could present variations in its corporal structure. Ever since the paper by DARWIN (1859), great interest exists in the geographical distribution of species and the patterns associated with this phenomenon. According to FUTUYMA (2002), due to the difficulty of observing historical evolutionary events directly, hypotheses and/or evolutionary trends can be verified in current species. Geographical variation in bats is not linked only to size or form of the body. Differences may also exist in echolocation calls (BARCLAY *et al.* 1999; ARMSTRONG AND COLES 2007; RUSSO *et al.* 2007), vocalization (DAVIDSON AND WILKINSON 2002), cellular aspects (JUSTE *et al.* 1996), diet (ASPETSBERGER *et al.* 2003) and even in use of torpor (SOLICK AND BARCLAY 2007).

Both phenomena, sexual dimorphism and geographic variation, are well documented among bats. Patterns of sexual dimorphism are deeply known especially in Vespertilionidae through studies by MYERS (1978) and WILLIAMS AND FINDLEY (1979). WILLIG AND HOLLANDER (1995) also made a great contribution, having studied 18 species of 5 families (Emballonuridae, Noctilionidae, Phyllostomidae, Vespertilionidae and Molossidae) and verifying the dimorphism in 12 of these. Patterns of geographic variation have also been described in the families Pteropodidae (KITCHENER AND

MAHARADATUNKAMSI 1996), Rhinolophidae (YOSHINO *et al.* 2006), Hipposideridae (ARMSTRONG 2002), Megadermatidae (HAND AND YORK 1990), Emballonuridae (WILLIG *et al.* 1986), Mystacinidae (WORTHY *et al.* 1996), Phyllostomidae (MCLELLAN 1984), Noctilionidae (DAVIS 1976), Natalidae (TADDEI AND UIEDA 2001), Molossidae (RATRIMOMANARIVO *et al.* 2009) and Vespertilionidae (SOLICK AND BARCLAY 2006). Among the 18 families of Chiroptera, only 7 lack any description of geographic variation and of these, 6 have between 1 and 4 described species (see SIMMONS 2005).

Due to its wide distribution and common status, *M. molossus* represents a great opportunity for the study of morphologic variation. Therefore our aim is to investigate the patterns of sexual dimorphism and geographic variation in the species through a latitudinal gradient in Brazil.

MATERIAL AND METHODS

We analyzed 446 specimens of *M. molossus*, 201 males (♂), 245 females (♀) from 7 states of Brazil (Fig. 1): Amazonas (n=34, ♂16, ♀18), Ceará (n=89, ♂43, ♀46), Mato Grosso do Sul (n=22, ♀22), Rio de Janeiro (n=44, ♂20, ♀23), Santa Catarina (n=118, ♂56, ♀62), São Paulo (n=10, ♂6, ♀4) and Rio Grande do Sul (n=130, ♂60, ♀70). This material was collected on a great latitudinal gradient ranging from low (4°21' S) to high latitudes (33°32' S) (Appendix I). All examined specimens present diagnostic characteristics of adults, such as completely fused epiphyses of forearms, metacarpals and phalanges, as well as prominent metacarpal-phalangeal articulations.
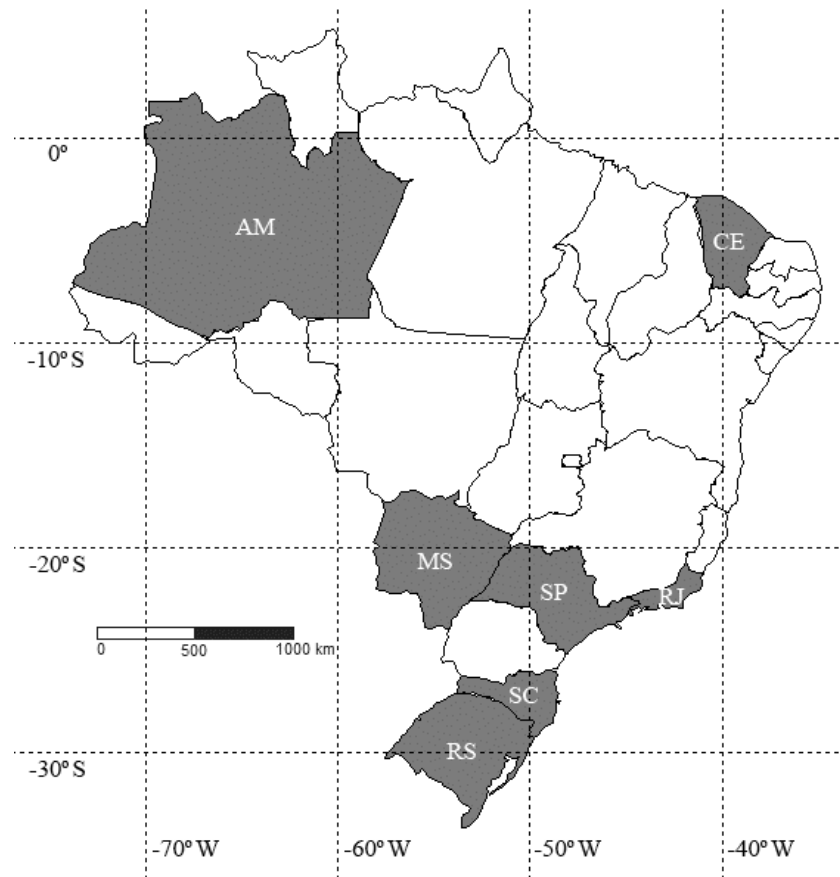
Figure 1: Map of Brazil showing, in gray, the states where the specimens used in this study were collected. Abbreviations: AM – Amazonas; CE – Ceará; MS – Mato Grosso do Sul; SP – São Paulo; RJ – Rio de Janeiro; SC – Santa Catarina; RS – Rio Grande do Sul.

From this material, we took 14 skull (Fig. 2) and 5 external measurements using a digital caliper with precision of 0.01 mm. The following parameters extracted from FREEMAN (1981) and GREGORIN AND TADDEI (2002) were used: greatest length of skull (GLS), length of maxillary toothrow (LMT), breadth of braincase (BB), breadth of rostrum (BR), interorbital constriction (IC), palatal breadth (PB), breadth across upper molars (BU), zygomatic breadth (ZB), mastoid breadth (MB), height of skull (HS), height of rostrum (HR), mandibular length (ML), length of mandibular toothrow (LmT),

mandibular height (MH), length of forearm (FA), length of metacarpals III, IV and V (MIII, MIV, MV), length of proximal phalanx of digit III (FIII).
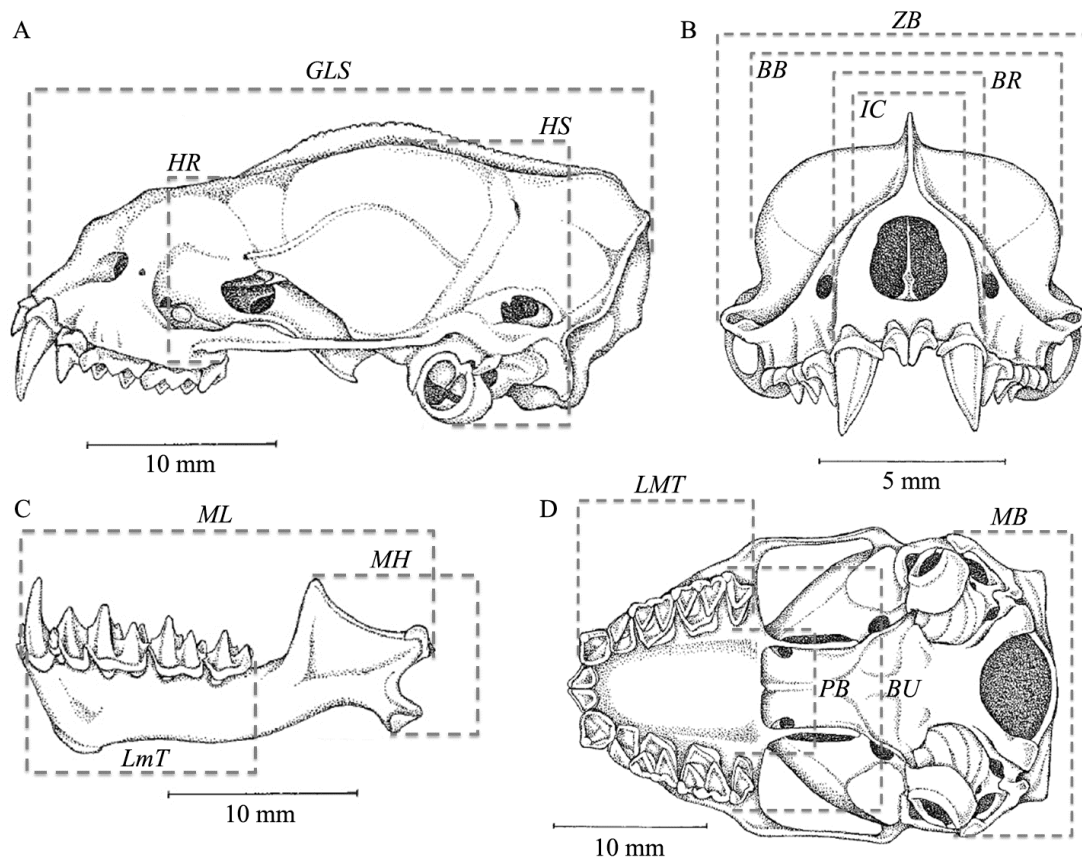

Figure 2: Limits of morphometric parameters taken from 446 skulls of *M. molossus*. A-lateral view of skull; B-rostral view of skull; C-lateral view of mandible; D-palatal view of skull. Image modified from SIMMONS AND VOSS (1998).

Statistical analyses were performed with SPSS 17 (Lead Technologies Inc., Chicago) and STATISTICA 8.0 (Stat Soft Inc., Tulsa). Analysis of Variance (ANOVA) was used to verify the sexual dimorphism of the species. The *t*-test gave standard statistics for each sample and statistical significance of differences in group means. We made these comparisons to assess patterns of sexual dimorphism within states, thus the samples were analyzed separately. Multiple Analysis of Variance (MANOVA) was used to verify the differences among the political states. Principal Components Analysis

(PCA) with no transformed data was used to further differentiate populations between the analyzed political states. Additionally, we conducted a Multiple Regression Analysis to verify the relationship between latitude and body size. The latitude used refers to the place where the specimen was collected.

RESULTS

Sexual dimorphism

Our results confirm the previously described sexual dimorphism in this species. ANOVA tests show that the differences between males and females are highly significant ($F = 13.27$, $d.f. = 19$, $P < 0.01$). The t-test confirmed this observation, demonstrating that males are statistically larger ($P \leq 0.01$) for 18 measurements. The only parameter that did not differ statistically is MV ($F = 5.819$, $d.f. = 430$, $P \geq 0.05$). Within the samples different patterns of sexual dimorphism are registered. However, one measurement, at least, presents significant differences between males and females. Males from Amazonas are statistically larger in 9 of the 19 measurements. The parameters that did not differ were LMT ($F = 0.175$, $d.f. = 31$, $P = 0.062$), BB ($F = 0.099$, $d.f. = 31$, $P = 0.346$), IC ($F = 0.367$, $d.f. = 31$, $P = 0.269$), PB ($F = 8.990$, $d.f. = 31$, $P = 0.559$), HS ($F = 0.150$, $d.f. = 31$, $P = 0.697$), FA ($F = 0.139$, $d.f. = 31$, $P = 0.344$), MIII ($F = 0.438$, $d.f. = 31$, $P = 0.839$), MIV ($F = 0.156$, $d.f. = 31$, $P = 0.783$), MV ($F = 0.193$, $d.f. = 31$, $P = 0.351$) and FIII ($F = 0.219$, $d.f. = 31$, $P = 0.923$). Males are significantly larger in 16 of the 19 analyzed measurements in the sample from Ceará. The only three measurements that did not differ statistically are MIII ($F = 0.763$, $d.f. = 82$, $P = 0.084$), MIV ($F = 1.752$, $d.f. = 82$, $P = 0.109$) and MV ($F = 1.261$, $d.f. = 82$, $P = 0.775$). The sample from São Paulo shows the lowest number of specimens. We were able to take body measurements of only 1 male and 1 female, thus it was

impossible to compare the differences between the external parameters. The skulls are not statistically different in 12 measurements, LMT ($F = 1.452$, $d.f. = 8$, $P = 0.159$), BB ($F = 0.832$, $d.f. = 8$, $P = 0.460$), IC ($F = 0.311$, $d.f. = 8$, $P = 0.756$), BU ($F = 2.033$, $d.f. = 8$, $P = 0.138$), MB ($F = 0.699$, $d.f. = 8$, $P = 0.194$), BR ($F = 0.594$, $d.f. = 8$, $P = 0.398$), ZB ($F = 1.486$, $d.f. = 7$, $P = 0.282$), HS ($F = 0.266$, $d.f. = 4$, $P = 0.797$), HR ($F = 1.004$, $d.f. = 8$, $P = 0.446$), MH ($F = 1.871$, $d.f. = 7$, $P = 0.344$), ML ($F = 0.190$, $d.f. = 8$, $P = 0.078$) and LmT ($F = 0.061$, $d.f. = 8$, $P = 0.127$). In the sample from Rio de Janeiro, 5 measurements did not differ between the sexes: HS ($F = 0.263$, $d.f. = 39$, $P = 0.062$), FA ($F = 0.648$, $d.f. = 42$, $P = 0.155$), MIII ($F = 0.039$, $d.f. = 42$, $P = 0.353$), MIV ($F = 0.667$, $d.f. = 42$, $P = 0.682$) and MV ($F = 1.516$, $d.f. = 42$, $P = 0.873$). The sample from Santa Catarina showed males that are statistically larger than females in all measurements except MV ($F = 0.840$, $d.f. = 116$, $P = 0.101$). In the sample from Rio Grande do Sul the measurements that did not present statistical differences were the same as for the sample of Rio de Janeiro, except for HS: FA ($F = 0.981$, $d.f. = 121$, $P = 0.099$), MIII ($F = 0.000$, $d.f. = 121$, $P = 0.061$), MIV ($F = 0.098$, $d.f. = 121$, $P = 0.215$) and MV ($F = 0.026$, $d.f. = 121$, $P = 0.633$).

Despite the almost complete differences observed in the sample from Santa Catarina, sexual dimorphism is related to the size of the skull and not to the size of the body. Because males are larger than females, in subsequent analyses the sexes are treated separately.

Geographic variation

Results of MANOVA tests demonstrate that males are significantly different between the analyzed political states ($F = 12.43$, $d.f. = 95$, $P < 0.01$) as also are females ($F = 16.76$, $d.f. = 114$, $P < 0.01$).

The PCA showed that the first 2 principal components were the only two that possess *eigenvalues* greater than 1 and thus are considered the most important in our analysis. Table I presents the loadings of PC1 and PC2 for males and females. In males PC1 presented positive values for all loadings, and PC2 had negative values for all measurements except LMT, ML, FA, MIII, MIV, MV and FIII. In females PC1 had positive values, but PC2 had negative values for LMT, ML, FA, MIII, MIV, MV and FIII, while the other measurements possessed positive values. Despite this counterpoint, PC1 is clearly related to the overall size while PC2 is more related to the shape of the specimens. Projections of principal components of males (Fig. 3A) and females (Fig. 3B) shows partial overlap but even thus it is possible to separate the analyzed populations. The first 2 combined components express 76.310% of the observed variation (PC1 59.976%; PC2 16.334%) in males. In females, the first 2 components represent 81.187% of the observed variation (PC1 67.490%; PC2 13.698%).
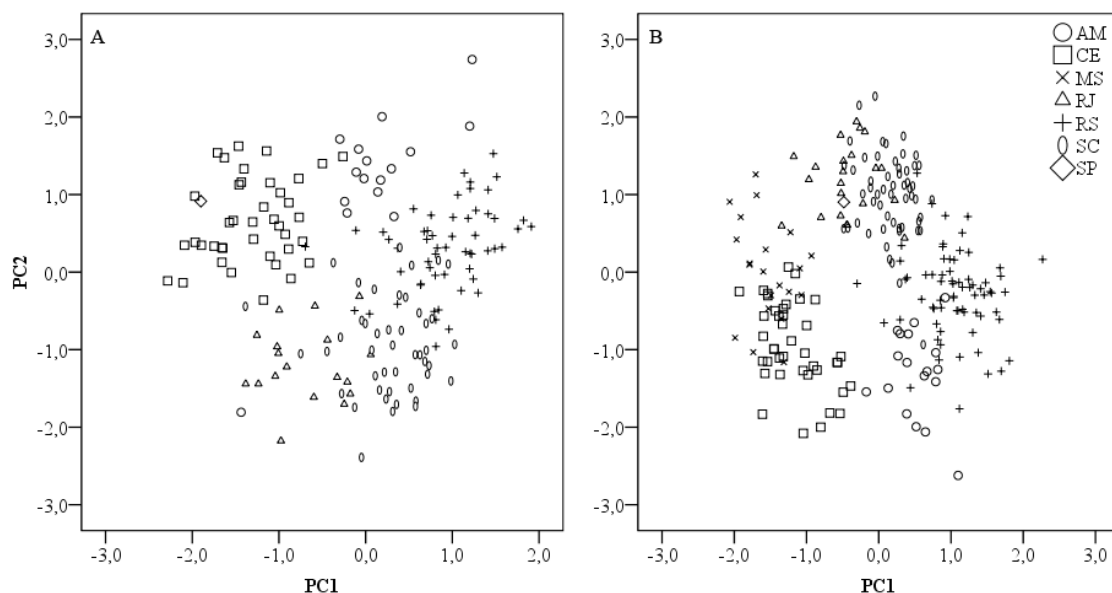

Figure 3: Projection of principal component 1 (PC1) and principal component 2 (PC2) for skull and body measurements of *M. molossus* from the different analyzed states. A: males; B: females.

Table 1: Factor loadings of principal component analyses of skull and body measurements of male and female *M. molossus* from the analyzed states in Brazil.

Measurement	Males		Females	
	PC1	PC2	PC1	PC2
GLS	0.947	-0.018	0.955	0.035
LMT	0.893	0.110	0.915	-0.111
BB	0.649	-0.619	0.748	0.531
IC	0.816	-0.398	0.819	0.388
BU	0.836	-0.231	0.890	0.169
MB	0.820	-0.409	0.871	0.325
PB	0.713	-0.070	0.822	0.034
BR	0.619	-0.499	0.621	0.535
ZB	0.881	-0.239	0.939	0.240
HS	0.629	-0.440	0.668	0.387
HR	0.803	-0.249	0.869	0.255
MH	0.684	-0.039	0.789	0.114
ML	0.917	0.167	0.939	-0.104
LmT	0.869	0.106	0.858	-0.167
FA	0.682	0.617	0.752	-0.546
MIII	0.685	0.688	0.760	-0.596
MIV	0.688	0.673	0.755	-0.603
MV	0.744	0.553	0.788	-0.518
FIII	0.715	0.329	0.758	-0.354
Eigenvalue	11.396	3.103	12.823	2.603
% total variance explained	59.976	16.334	67.490	13.698

Regression analysis (Table 2) revealed that the overall size of *M. molossus* is highly correlated with the latitude. In males all measurements shows statistically significant correlation with the latitudinal gradient analyzed. In females this relation was

obtained for all skull measurements and only for 2 body parameters (MV and FIII). Even with some of the body measurements of females not related to latitude, these results demonstrate that specimens from higher latitudes have larger size than those from lower latitudes. This finding corroborates the hypothesis of a latitudinal gradient in which an increase in size follows an increase in latitude. The most important variable of PCA, greatest length of skull, was selected to demonstrate such relationship (Fig. 4).

Table 2: Regression analysis summary statistics for all measurements tested as dependent variables against the latitude. *ns* = not significant

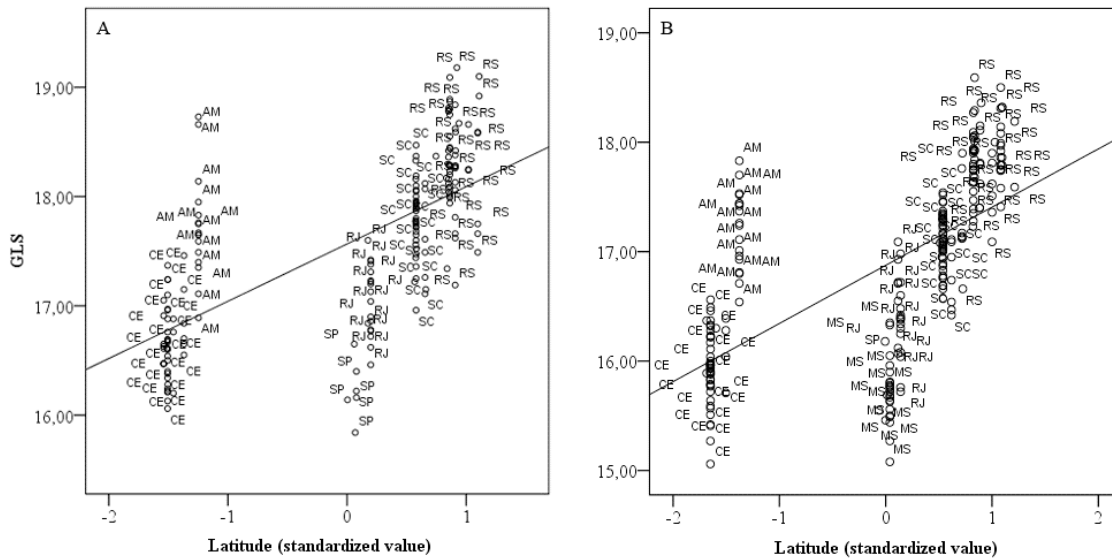| Measurement	Males			Females	
	F	*P*		*F*	*P*
GLS	172.08	< 0.0001		157.57	< 0.0001
LMT	136.65	< 0.0001		110.51	< 0.0001
BB	201.17	< 0.0001		208.37	< 0.0001
IC	364.80	< 0.0001		427.76	< 0.0001
BU	137.91	< 0.0001		157.70	< 0.0001
MB	210.83	< 0.0001		231.06	< 0.0001
PB	84.95	< 0.0001		100.79	< 0.0001
BR	83.52	< 0.0001		84.18	< 0.0001
ZB	262.42	< 0.0001		254.37	< 0.0001
HS	127.69	< 0.0001		101.69	< 0.0001
HR	105.46	< 0.0001		157.21	< 0.0001
MH	32.91	< 0.0001		57.24	< 0.0001
ML	107.24	< 0.0001		95.56	< 0.0001
LmT	96.29	< 0.0001		64.21	< 0.0001
FA	4.47	< 0.05		2.91	> 0.05 [ns]
MIII	5.12	< 0.05		2.41	> 0.05 [ns]
MIV	4.30	< 0.05		2.32	> 0.05 [ns]
MV	21.59	< 0.0001		11.86	< 0.001
FIII	26.26	< 0.0001		20.17	< 0.0001

Figure 4: Projection of linear regression of the greatest length of skull (GLS) against the latitude for *M. molossus* from the analyzed states. A: males ($r^2 = 0.457$, $F = 155.888$, $P < 0.001$); B: females ($r^2 = 0.400$, $F = 157.571$, $P < 0.001$). Abbreviations used: AM – Amazonas; CE – Ceará; MS – Mato Grosso do Sul; SP – São Paulo; RJ – Rio de Janeiro; SC – Santa Catarina; RS – Rio Grande do Sul.

DISCUSSION

Sexual dimorphism

Our results confirm the existence of sexual dimorphism in *M. molossus,* but differences are sometimes very slight. Previous authors already mentioned the dimorphism in this species without presenting much analysis of the phenomenon. DICKERMAN *et al.* (1981) mentioned the clear dimorphism in a sample from Guatemala. TAMSITT AND VALDIVIESO (1966) found few differences between the sexes in Colombia; in their sample males were slightly larger than females, but only body measurements were made. In contrast, MYERS AND WETZEL (1983) verified a clear

dimorphism with males approximately 5% larger than the females in almost all analyzed dimensions in *M. molossus* from Paraguay.

On the other hand, several authors presented morphometric data for the species by which it was possible to verify the larger size of the males (PEDERSEN *et al*. 1996; GENOWAYS *et al.* 1998; PAZ AND MARTINEZ 1998; SIMMONS AND VOSS 1998; LIM AND ENGSTROM 2001; MUÑIZ-MARTÍNEZ *et al.* 2003; PEDERSEN *et al.* 2003; PEDERSEN *et al.* 2005; LARSEN *et al.* 2006; PEDERSEN *et al.* 2006; GENOWAYS *et al.* 2007a; GENOWAYS *et al.* 2007b; PEDERSEN *et al.* 2007). However, these workers used the measurements only to characterize the size of the collected individuals on the surveyed area. In spite of lacking detailed analysis, these data contribute to the recognition of the sexual dimorphism in *M. molossus*.

Better evaluations of differences between males and females in the species were also conducted. WILLIG (1983), WILLIG *et al.* (1986) and WILLIG AND HOLLANDER (1995) diagnosed a clear dimorphism in *M. molossus* in populations from the Caatinga and Cerrado of Brazil, with males larger than females in both bioregions. In a study conducted in Dominica, GENOWAYS *et al.* (2001) noticed that the males were significantly larger in all skull measurements analyzed; however, the forearm means of males were not statistically significantly larger. GENOWAYS *et al.* (2005) noted in Jamaica that males were significantly larger than females in all measurements, including the forearm. In Saba, Netherlands Antilles, GENOWAYS *et al.* (2007c) found statistical differences in 3 skull measurements, while in 4 other measurements the averages of the males were larger but not significant and in one case the values of both sexes were the same. The absence of a consistent pattern within samples is similar to our results in which each state presented a different degree of sexual dimorphism. Such differences possibly are related to the different environments and to the resources available in each

one of them. Differences in structure of these populations may also influence this phenomenon.

The sexual dimorphism favoring males indicates competition for females once the larger size represents an advantage, making it possible that larger males can mate with more females and generate more offspring (RALLS 1976). For *M. molossus* this is just a hypothesis; the reproductive behavior of this species remains unstudied. Among Molossidae apparently there is not a clearly established pattern of sexual behavior. The Little Free-tailed Bat *Chaerephon pumilus* is a species in which harems are formed (MCWILLIAM 1988), but in the Brazilian Free-tailed Bat *Tadarida brasiliensis* males do not defend a territory or even females (KEELEY AND KEELEY 2004). Despite this lack of a pattern among species of the family, harems may occur in *M. molossus* because in colonies it is usual to find a larger number of females than males.

In Chiroptera it is common that the weight of a baby is high relative to the mother's weight (Ralls 1976). In Vespertilionidae, for instance, the offspring weight after birth can vary between 20-30% of the mother's weight (MYERS 1978). DAVIS *et al.* (1962) observed in *T. brasiliensis* that females are capable of carrying the young, although this is an uncommon behavior. Maybe this is a determining factor of size among bats, because when there is sexual dimorphism favoring larger males, the females are not much smaller. It is possible that females of *M. molossus* are also capable of transporting their nursing young, but even if they do not, it is still necessary that they support the extra weight of pregnancy during flight. The absence of significant differences between sexes in some body measurements of the analyzed populations supports this theory, and may indicate that the species needs a great load capacity.

In the vast majority of studies on sexual dimorphism in bats, the results reveal sexual dimorphism favoring larger females (WILLIAMS AND FINDLEY 1979; GANNON *et*

al. 1992; MANN AND AULAGNIER 1993; JONES AND KOKUREWICZ 1994; DELPIETRO AND RUSSO 2002). In contrast, males are larger in *M. molossus*. Therefore there probably exist different selective processes acting in the determination of size in males and females. These processes act distinctively in skull and body proportions, producing significantly larger skulls in males and wings with approximately equal sizes in both sexes.

The phenotypic variation between populations is the raw material on which natural selection acts. However, only the portion of variation that is under the control of genetic mechanisms can be affected. The statistical analysis is an important tool, but small inter-population differences can result from several factors, and the chances of those variations being detected increases as the samples size is increased (WILLIG 1983). The same can happen in relation to intra-specific differences as in sexual dimorphism, and therefore for a correct establishment of patterns it is necessary to use a great number of specimens in the analysis. The impossibility of increasing the size of the Amazonas and São Paulo samples may be decisive for the nondetection of a larger sexual dimorphism in those populations.

Geographic variation

Outstanding morphologic differences exist among the analyzed populations with samples from low latitudes having smaller size than the ones from higher latitudes. Bergmann's rule (BERGMANN 1847) predicts that a homoeothermic endothermic individuals' body size increases with latitude, thus in colder environments the animals would possess a smaller surface area/volume ratio that avoids the excessive loss of body heat. ASHTON *et al.* (2000) tested this hypothesis and found enough evidence to consider it as a general tendency for mammals. The pattern of geographic variation in

M. molossus is in agreement with this proposition, which was clearly demonstrated by our regression results.

Geographic variation was previously verified in this species; however, the analyzed populations were geographically close to one another. WILLIG (1983) studied populations of *M. molossus* in the Caatinga and Cerrado of Brazil and noted that the specimens from the former averaged larger in approximately half of the analyzed characters, and of this group, nine measurements were significantly different. MYERS AND WETZEL (1983) verified that there is variation among proximate populations in the same environment. These authors observed that specimens located in northern portions of the Chaco Boreal in Paraguay were 3-4% larger than those in southern portions. These data reinforce the occurrence of geographical variation in the species and they help to corroborate the results of our study; geographic variation is frequent in the species, even when analyzed among individuals from nearby places. In this study samples from various locations were included, allowing a general vision of the species as it varies from northern to southern Brazil.

Our hypothesis is that the pattern of geographic variation observed in *M. molossus* is due to a series of merged environmental conditions. Factors such as temperature, moisture and volume of resources may be related to this, because the wide distribution of this species includes a series of different environments along a great latitudinal gradient. ALLEN (1877) wrote about the role of physical conditions in speciation. In his paper, he discussed various environmental conditions that act upon the process of speciation. In a second paper on the same theme, ALLEN (1905) listed some groups of organisms that are very susceptible to what he called 'differentiation without isolation', and among these are the bats. In the same work ALLEN (1905) presented evidence of species that vary according to Bergmann's rule.

Meteorological data from INMET (Brazilian National Institute of Meteorology) show the diversity of conditions in the studied states and corroborate the relationship between latitude and size for *M. molossus*, because the seasons are not as marked in low latitudes as in the higher latitudes. In high latitudes the biological productivity is smaller and therefore may reflect a resource shortage during a period of the year (GEIST 1987). LINDSTEDT AND BOYCE (1985) proposed that a larger body size confers greater resistance to starvation, which according to BLACKBURN *et al.* (1999) could represent an advantage in environments where resources are seasonally scarce. In strongly seasonal environments, high mortality increases the volume of resources available to the survivors, leading to a larger body size. Besides, those extreme environments can be exploited by a reduced number of species, which allows them to acquire more resources due to lessened competition on an ecological niche, and therefore they grow to a larger body size (ZEVELOFF AND BOYCE 1988).

All these factors are possibly linked to one other while acting upon *M. molossus* and leading to the observed variation. Conditions that lead to differences in the quality and volume of resources generate environments with favorable characteristics promoting a greater growth of the species. These environments are not necessarily better than those of low latitudes, but indirect physical factors act on populations and then the individuals become proportionally larger. This explains the latitudinal variation in size observed in *M. molossus* and allows us to conclude that the species possesses resistance to starvation and that possibly there is a process of natural selection excluding smaller individuals of those populations.

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APPENDIX I

Localities, geographic coordinates and material used in this study. The examined material are deposited in 5 collections from Fundação Universidade Regional de Blumenau (SLA), Fundação Zoobotânica do Rio Grande do Sul (MCN), Universidade Estadual Paulista (DZSJRP), Universidade Federal de Pelotas (AMR, RP, SV, MB), Universidade Federal do Rio Grande do Sul (MAM), Universidade Federal Rural do Rio de Janeiro (ALP).

AMAZONAS—Humaitá 7°30'22.20"S, 63°01'37.82"W (DZSJRP 12781 ♂, DZSJRP 12783 ♂, DZSJRP 12786 ♀, DZSJRP 12787 ♀, DZSJRP 12788 ♂, DZSJRP 12911 ♂, DZSJRP 12912 ♀, DZSJRP 12914 ♀, DZSJRP 12915 ♀, DZSJRP 12919 ♀, DZSJRP 12920 ♀, DZSJRP 12921 ♀, DZSJRP 13175 ♂, DZSJRP 13176 ♂, DZSJRP 13177 ♂, DZSJRP 13178 ♀, DZSJRP 13187 ♀, DZSJRP 13188 ♀, DZSJRP 13189 ♀, DZSJRP 13190 ♀, DZSJRP 13191 ♀, DZSJRP 13192 ♀, DZSJRP 13193 ♀, DZSJRP 13194 ♀, DZSJRP 13195 ♀, DZSJRP 13268 ♂, DZSJRP 13270 ♂, DZSJRP 13271 ♂, DZSJRP 13273 ♂, DZSJRP 13275 ♂, DZSJRP 13278 ♂, DZSJRP 13305 ♂, DZSJRP 13306 ♂).

CEARÁ—Canindé 4°21'28.62"S, 39°18'07.06"W (MCN 1159 ♂, MCN 1161 ♀, MCN 1166 ♂, MCN 1167 ♂, MCN 1280 ♂, MCN 1281 ♀, MCN 1286 ♂, MCN 1385 ♂, MCN 1386 ♂, MCN 1448 ♂), Jaguaruana 4°49'51.33"S, 37°46'53.79"W (MCN 1277 ♂), Limoeiro do Norte 5°08'56.00"S, 38°05'51.57"W (MCN 1185 ♂, MCN 1190 ♀, MCN 1192 ♂, MCN 1198 ♂), Pereiro 6°02'43.92"S, 38°27'35.86"W (MCN 1172 ♂, MCN 1173 ♀, MCN 1394 ♂, MCN 1396 ♂, MCN 1399 ♂, MCN 1400 ♂, MCN 1401 ♀, MCN 1451 ♀, MCN 1452 ♂, MCN 1453 ♀), Quixadá 4°58'41.28"S, 39°01'07.68"W (MCN 1370 ♀, MCN 1374 ♂, MCN 1420 ♀, MCN 1421 ♀, MCN 1422 ♂, MCN 1423 ♀, MCN 1425 ♀, MCN 1426 ♂, MCN 1429 ♀, MCN 1432 ♂, MCN 1440 ♀, MCN 1441 ♀, MCN 1442 ♀, MCN 1443 ♂, MCN 1444 ♀, MCN 1454 ♀, MCN 1455 ♂,

MCN 1456 ♀, MCN 1457 ♀, MCN 1458 ♀, MCN 1459 ♀, MCN 1460 ♀, MCN 1461 ♂, MCN 1462 ♂), Russas 4°56'21.50"S, 37°58'43.03"W (MCN 1118 ♂, MCN 1119 ♀, MCN 1120 ♂, MCN 1122 ♂, MCN 1125 ♀, MCN 1126 ♂, MCN 1129 ♂, MCN 1131 ♂, MCN 1132 ♀, MCN 1200 ♂, MCN 1202 ♂, MCN 1204 ♀, MCN 1205 ♀, MCN 1206 ♂, MCN 1207 ♀, MCN 1210 ♂, MCN 1211 ♀, MCN 1213 ♀, MCN 1215 ♂, MCN 1246 ♂, MCN 1247 ♀, MCN 1249 ♂, MCN 1251 ♂, MCN 1252 ♂, MCN 1253 ♀, MCN 1254 ♀, MCN 1256 ♀, MCN 1261 ♀, MCN 1262 ♀, MCN 1263 ♀, MCN 1266 ♀, MCN 1268 ♀, MCN 1269 ♂, MCN 1270 ♀, MCN 1271 ♀, MCN 1272 ♀, MCN 1388 ♀, MCN 1389 ♂, MCN 1449 ♀, MCN 1450 ♀).

MATO GROSSO DO SUL—Água Clara 21°53'09.53"S, 54°09'21.17"W (DZSJRP 11891 ♀, DZSJRP 11892 ♀, DZSJRP 11893 ♀, DZSJRP 11894 ♀, DZSJRP 11895 ♀, DZSJRP 11896 ♀, DZSJRP 11897 ♀, DZSJRP 11898 ♀, DZSJRP 11899 ♀, DZSJRP 11900 ♀, DZSJRP 11901 ♀, DZSJRP 11902 ♀, DZSJRP 11903 ♀, DZSJRP 11904 ♀, DZSJRP 11905 ♀, DZSJRP 11906 ♀, DZSJRP 11907 ♀, DZSJRP 11910 ♀, DZSJRP 11912 ♀, DZSJRP 11914 ♀, DZSJRP 11915 ♀, DZSJRP 11916 ♀).

RIO DE JANEIRO—Niterói 22°52'50.76"S, 43°06'15.61"W (ALP 440 ♂), Petrópolis 22°30'16.70"S, 43°10'56.38"W (ALP 169 ♀, ALP 271 ♀, ALP 295 ♀, ALP 296 ♀, ALP 297 ♀, ALP 298 ♀, ALP 299 ♀, ALP 461 ♂, ALP 568 ♂), Rio de Janeiro 22°54'12.74"S, 43°12'34.51"W (ALP 10 ♀, ALP 13 ♀, ALP 59 ♀, ALP 76 ♀, ALP 80 ♀, ALP 172 ♀, ALP 186 ♂, ALP 187 ♂, ALP 214 ♀, ALP 215 ♀, ALP 216 ♂, ALP 226 ♂, ALP 227 ♀, ALP 228 ♂, ALP 233 ♀, ALP 294 ♀, ALP 308 ♂, ALP 369 ♂, ALP 370 ♀, ALP 371 ♀, ALP 372 ♂, ALP 373 ♂, ALP 374 ♂, ALP 375 ♀, ALP 376 ♀, ALP 377 ♂, ALP 378 ♂, ALP 379 ♀, ALP 380 ♂, ALP 381 ♂, ALP 439 ♂, ALP 552 ♂, ALP 583 ♂).

SANTA CATARINA—Águas Frias 26°52'47.55"S, 52°51'43.29"W (SLA 2310 ♂, SLA 2312 ♂, SLA 2313 ♀, SLA 2314 ♂), Blumenau 26°55'07.47"S, 49°03'57.73"W (SLA 1132 ♂, SLA 1202 ♂, SLA 1211 ♂, SLA 1306 ♂, SLA 1317 ♂, SLA 1319 ♀, SLA 1401 ♀, SLA 1402 ♀, SLA 1403 ♂, SLA 1419 ♀, SLA 1420 ♀, SLA 1421 ♀, SLA 1422 ♀, SLA 1424 ♀, SLA 1426 ♀, SLA 1428 ♀, SLA 1429 ♀, SLA 1431 ♀, SLA 1432 ♀, SLA 1433 ♀, SLA 1437 ♀, SLA 1438 ♀, SLA 1439 ♀, SLA 1440 ♀, SLA 1441 ♀, SLA 1442 ♂, SLA 1444 ♀, SLA 1476 ♂, SLA 1483 ♀, SLA 1484 ♀, SLA 1485 ♂, SLA 1486 ♀, SLA 1557 ♂, SLA 1562 ♂, SLA 1572 ♂, SLA 1665 ♂, SLA 1669 ♂, SLA 1671 ♂, SLA 1691 ♂, SLA 1731 ♂, SLA 1787 ♂, SLA 1795 ♂, SLA 1796 ♂, SLA 1809 ♂, SLA 1827 ♂, SLA 1926 ♂, SLA 2105 ♂, SLA 2341 ♂), Florianópolis 27°35'48.85"S, 48°32'58.03"W (SLA 0432 ♀, SLA 0436 ♂, SLA 0437 ♀, SLA 0438 ♂, SLA 0443 ♀, SLA 0444 ♀, SLA 0603 ♂, SLA 0607 ♂, SLA 0608 ♀, SLA 0626 ♀, SLA 0627 ♂, SLA 0629 ♀, SLA 0630 ♀, SLA 0631 ♀, SLA 0633 ♂, SLA 0636 ♀, SLA 0637 ♂, SLA 0638 ♂), Gaspar 26°55'54.30"S, 48°57'33.76"W (SLA 0365 ♂, SLA 0537 ♂, SLA 0538 ♂, SLA 0717 ♀, SLA 0719 ♀, SLA 0720 ♂, SLA 0721 ♀, SLA 0724 ♀, SLA 0726 ♀, SLA 0729 ♀, SLA 0731 ♀, SLA 0732 ♀, SLA 1019 ♂, SLA 1140 ♂, SLA 1157 ♂, SLA 1158 ♂, SLA 1160 ♂, SLA 1391 ♀, SLA 1392 ♀, SLA 1467 ♂, SLA 1468 ♀, SLA 1507 ♀, SLA 1508 ♀, SLA 1700 ♂, SLA 1703 ♂), Indaial 26°53'51.14"S, 49°13'54.15"W (SLA 1169 ♀, SLA 1170 ♀, SLA 1171 ♀, SLA 1449 ♀, SLA 1450 ♀, SLA 1452 ♀, SLA 1453 ♀, SLA 1455 ♂, SLA 1456 ♀, SLA 1466 ♂, SLA 1806 ♂), Jaraguá do Sul 26°29'07.16"S, 49°04'01.92"W (SLA 1462 ♀), Nova Veneza 28°38'13.20"S, 49°29'53.94"W (SLA 0894 ♀, SLA 0896 ♂), Penha 26°46'11.40"S, 48°38'46.09"W (SLA 1463 ♀), Quilombo 26°43'44.97"S, 52°43'09.14"W (SLA 2259 ♂), Santo Amaro da Imperatriz 27°41'18.31"S, 48°46'44.81"W (SLA 1124 ♂), São José 27°35'18.08"S, 48°36'45.90"W (SLA 0584 ♂),

Siderópolis 28°35'56.01"S, 49°25'31.47"W (MAM 1019 ♀, MAM 1020 ♀, MAM 1021 ♀, MAM 1022 ♀), Urussanga 28°31'21.63"S, 49°19'03.38"W (MAM 1074 ♂).

SÃO PAULO—Avanhandava 21°27'49.53"S, 49°56'57.78"W (DZSJRP 2632 ♀, DZSJRP 2633 ♂, DZSJRP 2634 ♂, DZSJRP 2635 ♂), Catanduva 21°08'17.73"S, 48°58'25.54"W (DZSJRP 16456 ♂, DZSJRP 16457 ♀), Irapuã 21°17'01.71"S, 49°24'23.04"W (DZSJRP 3092 ♂), São José do Rio Preto 20°49'12.65"S, 49°22'46.85"W (DZSJRP 2715 ♀, DZSJRP 16654 ♂), Urupês 21°12'01.79"S, 49°17'26.34"W (DZSJRP 3091 ♀).

RIO GRANDE DO SUL—Arroio Grande 32°14'19.45"S, 53°05'26.47"W (RP 40 ♂, RP 43 ♀, RP 44 ♀, RP 45 ♀, RP 46 ♀, RP 47 ♂), Bagé 31°19'42.61"S, 54°06'26.17"W (MCN 2340 ♂, MCN 2341 ♀, MCN 2342 ♀, MCN 2343 ♂, MCN 2344 ♀, MCN 2345 ♂, MCN 2346 ♀, MCN 2347 ♀, MCN 2348 ♀), Bossoroca 28°42'37.05"S, 54°52'42.25"W (MCN 224 ♀), Cruzeiro do Sul 29°30'47.21"S, 51°59'07.03"W (MAM 903 ♂), Dom Pedro de Alcântara 29°23'45.92"S, 49°50'47.92"W (MAM 204 ♂), Guaíba 30°06'50.82"S, 51°19'41.22"W (MCN 2317 ♀, MCN 2318 ♀), Maquiné 29°42'15.81"S, 50°11'46.13"W (AMR 620 ♀, AMR 623 ♀, AMR 627 ♀, AMR 634 ♀, AMR 641 ♀, AMR 643 ♂, AMR 644 ♂, AMR 645 ♀, AMR 646 ♀, AMR 647 ♂, AMR 648 ♀, AMR 649 ♀, AMR 652 ♂, AMR 653 ♀, AMR 654 ♀, AMR 655 ♀, AMR 656 ♂, AMR 667 ♂, AMR 680 ♀, AMR 704 ♂, AMR 789 ♂, AMR 790 ♂, MAM 423 ♀, MAM 424 ♀, MAM 425 ♀, MAM 426 ♀, MAM 427 ♀, MAM 428 ♀, MAM 429 ♀, MAM 430 ♀, MAM 431 ♀), Osório 29°54'01.25"S, 50°16'25.58"W (AMR 794 ♂, AMR 795 ♀, AMR 796 ♂, AMR 804 ♂, AMR 805 ♀, AMR 811 ♀, AMR 822 ♂, AMR 826 ♂, AMR 845 ♀, AMR 853 ♀, AMR 902 ♂, AMR 903 ♂, AMR 904 ♂, AMR 905 ♂, AMR 906 ♀, AMR 915 ♂, AMR 916 ♂, AMR 917 ♂, AMR 918 ♂, AMR 919 ♂, AMR 920 ♂, AMR 921 ♂, AMR 922 ♂, AMR 923 ♂, SLA

0955 ♂), Palmares do Sul 30°16'17.46"S, 50°28'35.53"W (MB 83 ♀, MB 84 ♂), Pelotas 31°46'33.72"S, 52°21'33.72"W (MAM 761 ♀), Porto Alegre 30°01'39.73"S, 51°13'43.45"W (MAM 437 ♀, MAM 652 ♀, MAM 790 ♂, MAM 971 ♂, MAM 998 ♂, MCN 560 ♂, MCN 1652 ♂, MCN 1771 ♂, MCN 2122 ♂, MCN 2339 ♂, MCN 2360 ♂, MCN 2388 ♂, MCN 2404 ♀), Rio Grande 32°01'59.51"S, 52°05'55.01"W (DZSJRP 14565 ♀, DZSJRP 14566 ♂, DZSJRP 14568 ♂, DZSJRP 14569 ♂, DZSJRP 14570 ♀, MCN 1658 ♀, MCN 1659 ♂, MCN 1660 ♀, MCN 1661 ♀, MCN 1662 ♀, MCN 1663 ♀, MCN 1664 ♀, MCN 1665 ♂, MCN 1666 ♂, MCN 1667 ♂, MCN 1668 ♀, MCN 1669 ♀, MCN 1670 ♀, MCN 1671 ♀, MCN 1680 ♀, MCN 1681 ♀, MCN 1684 ♀), Santa Vitória do Palmar 33°32'01.77"S, 53°20'58.44"W (SV 01 ♀, SV 02 ♀), São Leopoldo 29°45'38.80"S, 51°09'07.80"W (AMR 925 ♂), Sentinela do Sul 30°35'29.85"S, 51°33'48.72"W (MAM 792 ♂), Taquara 29°38'32.02"S, 50°47'44.07"W (MCN 813 ♀), Viamão 30°05'18.09"S, 51°05'25.64"W (MAM 411 ♂, MAM 707 ♀, MAM 708 ♀, MAM 728 ♂, MAM 860 ♂, MAM 862 ♂, MCN 757 ♂, MCN 2754 ♀), Victor Graeff 28°33'16.08"S, 52°44'09.64"W (MCN 2291 ♀).

ARTIGO II

Supernumerary teeth in *Molossus molossus* from Brazil and its possible taxonomic implications

Daniel Alexandre Stüpp de Souza, César Jaeger Drehmer, Ana Maria Rui, Marta Elena Fabián

ABSTRACT

Dental anomalies in many mammals groups have been taking the attention of researchers during the course of the past years. Although there is a considerable information volume about it, little is known on its occurrence among bats. We present the register of 30 anomalies in 24 individuals from a sample of 450 specimens of *Molossus molossus.* The observed anomalies resemble teeth of normal presence in a phylogenetically related species, so the abnormal teeth are considered atavistic structures in which the appearance is possibly controlled by some genetic mechanism. The record of dental anomalies among New World bats represents an alert to researches to be careful in the species identification because anomalous structures may lead to taxonomic mistakes once the dental formula is used as a diagnostic character.

Key words: Chiroptera, *Molossus molossus*, atavism, dental anomalies, extra teeth

The knowledge on dental abnormalities in mammals, especially those with genetic basis, is very important. The recognition of supernumerary teeth can be of major importance for taxonomic studies (PHILLIPS AND KNOX-JONES 1968). Dental anomalies are reported in almost every mammalian order (WOLSAN 1984). Recent researches with regard to the occurrence of numerical alterations in the dental formula can be found in Artiodactyla (KIERDORF AND KIERDORF 2002), Carnivora (GOMERČIĆ *et al.* 2009),

Chiroptera (GHAZALI 2008), Perissodactyla (YASUI 2009), Pinnipedia (LOCH *et al.* 2010) and Soricomorpha (KAWADA *et al.* 2006).

Despite the importance of dental anomalies in studies of comparative osteology in mammals (LOCH *et al.* 2010), there are few data concerning its occurrence and implications in bats, especially in Molossidae. Reports on numerical anomalies in bats of this family are found for *Chaerephon chapini* (J.A. Allen, 1917) (FENTON AND EGER 2002), *Eumops maurus* (Thomas, 1901) (EGER 1977; EISENBERG 1989; MARES *et al.* 1989) and *Tadarida brasiliensis* (I. Geoffroy, 1824) (HALL 1981). The dental formula of Molossidae is I1/1-3 C1/1 P1-2/1-2 M3/3, varying from 24 to 32 teeth. Due to this variation, phylogenetically related species may show numerical differences usually in form of small and reduced teeth. Our aim is to report and discuss the supernumerary teeth observed in the dental formula of *Molossus molossus* (Pallas, 1766) as also as present an hypothesis to explain its occurrence.

M. molossus (Chiroptera, Molossidae) is a widespread insectivore bat distributed from Florida to Argentina (SIMMONS 2005), inhabiting tree holes or human buildings (BARQUEZ *et al.* 1999) and is very specialized and well adapted to the nature of its food (FREEMAN 1979). Its dental formula is I1/1 C1/1 P1/2 M3/3 (GREGORIN AND TADDEI 2002). We examined the syncrania of 450 individuals, 203 males and 247 females, from 9 states of Brazil: Amazonas (n=34, ♂16, ♀18), Ceará (n=89, ♂43, ♀46), Mato Grosso do Sul (n=22, ♀22), Rio de Janeiro (n=44, ♂20, ♀23), Paraná (n=2, ♂1, ♀1), Piauí (n=2, ♂1, ♀1), Santa Catarina (n=118, ♂56, ♀62), São Paulo (n=10, ♂6, ♀4) and Rio Grande do Sul (n=130, ♂60, ♀70). The reviewed material are deposited in 5 collections from Fundação Universidade Regional de Blumenau (SLA), Fundação Zoobotânica do Rio Grande do Sul (FZB), Universidade Estadual Paulista (DZSJRP), Universidade Federal de Pelotas (AMR), Universidade Federal do Rio Grande do Sul (MAM),

Universidade Federal Rural do Rio de Janeiro (ALP). All individuals present diagnostic adult characteristics, such as complete fusion of epiphyses on forearms, metacarpals and phalanges, besides prominent metacarpal-phalanges articulations. We follow PAULA COUTO (1979) and MENU *et al.* (2002) to designate superior or inferior teeth.

The only type of abnormality registered was the poliodonty, observed in superior premolars and inferior incisors. Each extra tooth is treated as a single abnormality because it may occur alone or combined with another one. Despite the number of observed extra teeth, morphologic characteristics of these are very similar. Due to this similarity, we grouped the descriptions below according to the position and the type of registered extra tooth:

- Maxillary supernumerary premolar: observed on the right side in 5 individuals (ALP 216♂; ALP 380♂; SLA 636♀; SLA 1124♂; SLA 1453♀; 1.11% of the sample) (Fig. 1A) and on the left side in 8 individuals (ALP 369♂; ALP 373♂; AMR 655♀; AMR 920♂; SLA 438♂; SLA 637♂; SLA 1806♂; DZSJRP 13270♂; 1.78% of the sample) (Fig. 1B). These teeth are much smaller than the normal premolars registered in the dental formula of this species. Its crown is low and variable in size (Figs. 1A and 1B), but is always simplified, no cusps, clearly distinct from the root and it is usually inserted in the conjunctive tissue. They are vertically oriented between C^1 and P^1 on the labial face of toothrow.

- Mandibular supernumerary incisor: recorded on the right side in 4 individuals (ALP 59♀; AMR 845♀; AMR 925♂; SLA 1317♂; 0.89% of the sample) (Fig. 1C) and on the left side in 3 individuals (AMR 919♂; MAM 426♀; MCN 1670♀; 0.67% of the sample) (Fig. 1D). They have small, no lobed and few distinct crows. In some cases the top of the extra teeth can be positioned above the crown of the current incisors of this species. In all observed material the

supernumerary teeth are located laterally to the normal incisors and below the cingulum of C_1.

- Maxillary supernumerary bilateral premolars (ALP 271♀; DZSJRP 16456♂; MCN 2754♀; 0.67% of the sample): these extra teeth present the same morphology and are positioned in the same way described above. The size of supernumerary premolars is the same in both sides of dental row.

- Maxillary supernumerary bilateral premolars and mandibular bilateral incisors (MCN 1318♂; 0.22% of the sample): these teeth were registered with the same size, morphology and at the same position of the cases described above. Bilateral extra incisors are shown in Figure 1E.

The presence of dental anomalies as a whole is independent of sex (χ^2=2.40, $d.f.$=1, P<0.05) as well as the occurrence of extra P^1 (χ^2=3.624, $d.f.$=1, P<0.05) or extra I_2 (χ^2=0,006, $d.f.$=1, P<0.05). Males and females showed supernumerary teeth in 7.39% (n=15) and 3.64% (n=9) of the sample, respectively. Extra P^1 occurred in 5.91% of males (n=12) and in 2.03% of females (n=5). Males showed extra I_2 in 1.97% (n=4) and females in 1.62% of the sample (n=4). The presence of supernumerary teeth is still independent of the side of dental series (χ^2=0.115, $d.f.$=1, P<0.05) and confirming our previous observations, the occurrence of extra upper premolars is also independent of the presence of extra inferior incisors (χ^2=2.693 $d.f.$=1, P<0.05).
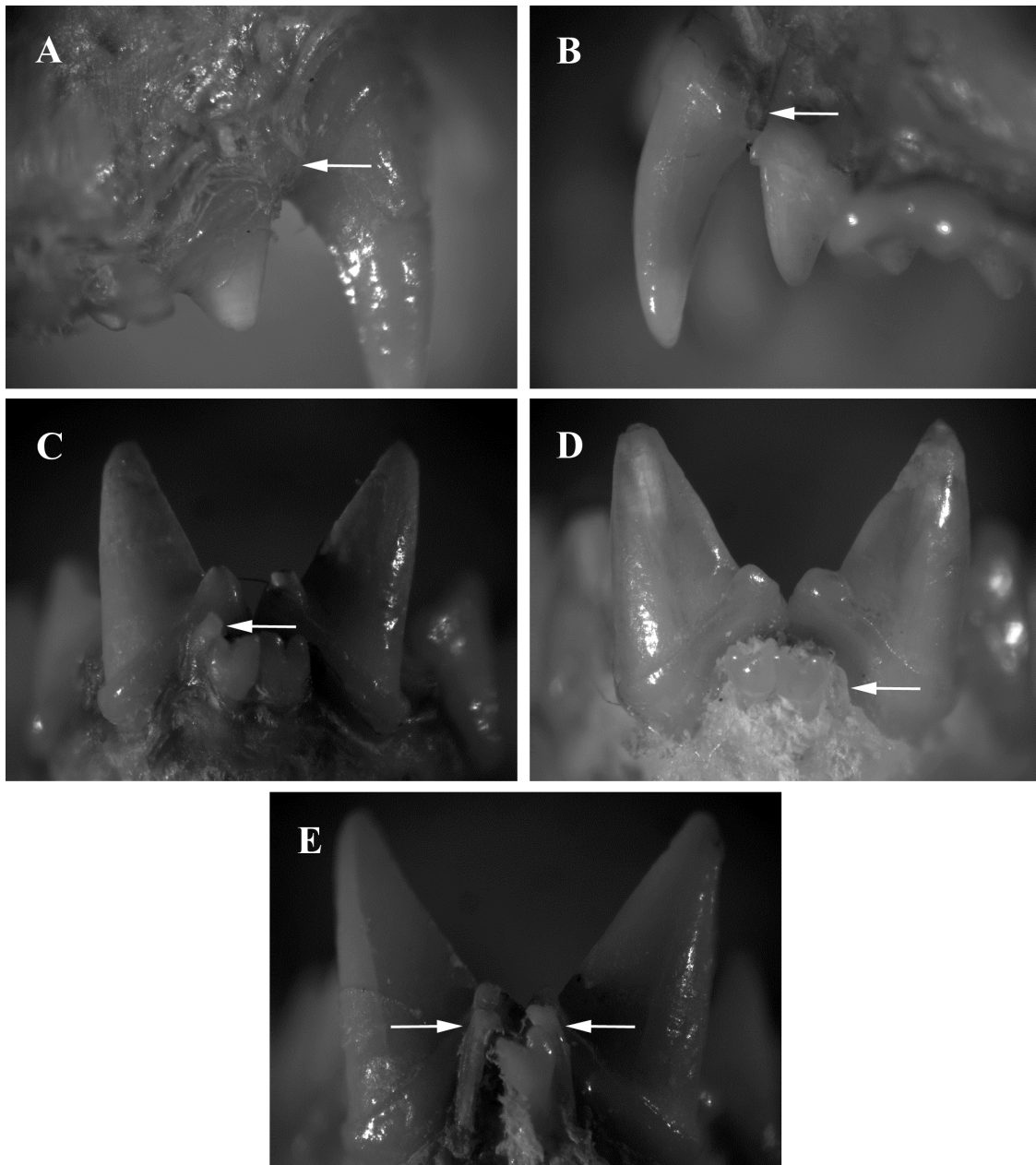
Figure 1: Supernumerary teeth – arrows – in *Molossus molossus.* A – right maxillary premolar; B – right maxillary premolar; C – right mandibular incisor; D – left mandibular incisor; E – bilateral mandibular incisors.

Slightly biological variations can be treated as normal between individuals of the same species but when deviations are more uncommon they are named as anomalies (MILES AND GRIGSON 1990). The dental formula of mammals species are strongly conserved (NOVACEK 1986) and usually are used as diagnostic characters in systematic

and taxonomic studies (WOLSAN 1984). Alterations in its structure may indicate evolutionary trends (WOLSAN *et al.* 1985) thus the deviations here reported are of special interest. As LOCH *et al.* (2010) we consider these deviations as 'typical cases of dental anomalies'.

According to HOFF AND HOFF (1996), dental anomalies may be numerical, morphological, structural and of eruption, position or occlusion. The causes of numerical anomalies registered are difficult to establish and proof, however we believe that these can be considered cases of atavisms. Atavism refers to the reappearance of a common feature of a remote ancestor in an individual that shouldn't have it. Usually this character appears in one or few individuals in a population (STIASSNY 1992). HALL (1984) defined four basic criteria for the recognition of a characteristic as an atavism: I - persistence in adult life; II - absence in parents or recent ancestors; III - occurrence in one or few individuals in a population; IV - similarity with a characteristic presented by all members of an ancestral population. Both extra P^1 and I_2 here reported are teeth of normal occurrence in *Promops nasutus* (Spix, 1823), a species in which the dental formula is I1/2 C1/1 P2/2 M3/3 (BARQUEZ *et al.* 1999).

Considering the proposed phylogeny for Molossidae, *Promops* and *Molossus* are two sister genera (JONES *et al.* 2002). In the genus *Promops* the dental formula shows incisors I1/2 and premolars P2/2 and in *Molossus* the incisors are I1/1 and premolars P1/2 (GREGORIN AND TADDEI 2002). The P^1 of *P. nasutus* is reduced, sometimes lost during skull preparation and difficult to see without magnification and I_2 is always smaller than I_1 (BARQUEZ *et al.* 1999). In our observations we identified clearly this morphological similarity, what reinforces the hypothesis that these are atavistic structures, lost in the course of the evolution, and reappeared in sporadic individuals. RUI AND DREHMER (2004) already registered the occurrence of atavistic teeth in bats,

but in the genus *Artibeus* Leach, 1821. These authors also use the characteristics of atavic structures described by HALL (1984) to confirm their observations.

The reappearance of these teeth suggests that some changes may be occurring in genetic mechanisms that regulates morphogenesis, which seems to be related to macroevolutionary events in mammals and consequently to their diversification (LINE 2003). This proposition seems to be very plausible, once the atavisms have been related to macroevolutionary events (RIEDL 1977). In this sense, we believe that some gene may be being expressed in few individuals leading to the appearance of the observed supranumerary teeth, which may indicate a recent phylogenetic divergence between *Molossus* and *Promops*.

The extreme case of the individual MCN 1318 called us attention for presenting a total dental formula, including the supernumeraries, identical to *P. nasutus*. Despite the low frequency observed (0.22% of the sample, n=1 in 450 individuals), this case is very important to systematics. The dental formula is used to separate the very similar bats *M. molossus* from *P. nasutus* in identification keys (GREGORIN AND TADDEI 2002). When other populations are examined, the researchers need to be careful to correctly identify the species, avoiding taxonomic mistakes due to anomalies in some individuals as the reported here, even if they are slight and difficult to determine.

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