

UNIVERSIDADE FEDERAL DE VIÇOSA

**Evolution and specialization of dental morphology in the Neotropical frugivore
bat subfamily Stenodermatinae (Chiroptera, Phyllostomidae)**

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Dissertation submitted to the Animal Biology Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: Guilherme S. Terra Garbino

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ABSTRACT

PAES, Juliano Alfenas Silva Valente, M.Sc., Universidade Federal de Viçosa, August, 2025. **Evolution and specialization of dental morphology in the Neotropical frugivore bat subfamily Stenodermatinae (Chiroptera, Phyllostomidae).** Adviser: Guilherme Siniciato Terra Garbino.

Bats exhibit a wide variety of diets that are associated with modifications in the cranium, masticatory muscles, and dental patterns. Teeth are durable structures with high morphological variability, closely related to feeding strategy and habits. The consumption of fruits led to the specialization of the dental structure in two bat groups: Pteropodidae in Afro-Eurasia and Stenodermatinae in the Americas. This frugivorous pattern in Stenodermatinae has prompted several studies on mechanical implications and dental development, but few have addressed the evolutionary transition from the ancestral insectivorous pattern. The present study investigates the evolution and specialization of dental morphology in this clade, aiming to reconstruct the evolutionary history of its characters and infer their functional implications in Stenodermatinae and its subgroups. For this purpose, this work analyzes 66 morphological characters using a standardized nomenclature for the upper and lower teeth in 11 of 19 genera of Stenodermatinae and five outgroup taxa, mapped onto a molecular phylogeny using the parsimony criterion. In addition to mapping synapomorphies, it assesses the consistency index (CI) and retention index (RI) of characters related to their general shape, presence of cusps, cristae, and cingula, as well as their overall arrangement in the dental arcade. The ancestral state reconstruction analysis maps the transformations of each character throughout the evolutionary history and reveals a high level of homoplasy ($CI = 0.423$), consistent with the evolutionary plasticity of the group, but also a strong phylogenetic signal ($RI = 0.800$), validating the use of these characters for clade diagnosis. The study details a series of key transformations associated with frugivory, such as the reduction in canine robustness, the specialization of the premolars, and the labial displacement of the molar cusps. Additionally, the work describes the emergence of accessory structures in Stenodermatinae, such as the mesoconule and its associated cristae, which increase the complexity and efficiency of the occlusal surface, and correlates cusp morphology with specific diets of hard (durophagy) or soft (juso-phagy) foods. The presence of cingula is interpreted as a biomechanical reinforcement structure, while diastemata and occlusal gaps are analyzed as adaptations for fruit handling and the ejection of its byproducts, such as fibers and seeds. This work

demonstrates that the dentition of Stenodermatinae evolved from an ancestral insectivorous pattern into a complex and highly derived set of characters, acting as a record of the group's adaptive history and being fundamental to understanding the macroevolutionary processes that led the Stenodermatinae to become one of the most diverse and successful groups of Neotropical bats.

Keywords: ancestral state reconstruction; cusps; mesoconule; synapomorphies

RESUMO

PAES, Juliano Alfenas Silva Valente, M.Sc., Universidade Federal de Viçosa, agosto de 2025. **Evolução e especialização de estruturas dentárias em morcegos frugívoros (Phyllostomidae: Stenodermatinae)**. Orientador: Guilherme Siniciato Terra Garbino.

Os morcegos possuem uma ampla variedade de dietas, que são associadas a modificações no crânio, nos músculos mastigatórios e no padrão dentário. Dentes são estruturas duráveis, com alta variabilidade em sua morfologia, que está intimamente relacionada a sua estratégia e hábito alimentar. O consumo de frutos levou a uma especialização da estrutura dentária de dois grupos de morcegos: Pteropodidae na Afro-Eurásia e Stenodermatinae nas Américas. Esse padrão frugívoro dos Stenodermatinae levou a diversos estudos sobre implicações mecânicas e desenvolvimento dentário, mas poucos sobre a transição evolutiva do padrão insetívoro ancestral. O presente estudo investiga a evolução e especialização da morfologia dentária neste clado, com o objetivo de reconstruir a história evolutiva dos caracteres e inferir suas implicações funcionais em Stenodermatinae e seus subgrupos. Para isso, este trabalho analisa 66 caracteres morfológicos com nomenclatura padronizada para os dentes superiores e inferiores em 11 de 19 gêneros de Stenodermatinae além de cinco táxons externos, considerando uma filogenia molecular e utilizando o critério de parcimônia. Além disso, o trabalho se propõe a mapear as sinapomorfias e avaliar o índice de consistência (IC) e de retenção (IR) dos caracteres quanto a sua forma geral, presença de cúspides, crista e cíngulos bem como sua disposição geral na arcada dentária. A análise de reconstrução de estado ancestral mapeia as transformações de cada caráter ao longo da evolução e revela um alto nível de homoplasia ($IC = 0,423$), consistente com a plasticidade evolutiva do grupo, mas também um forte sinal filogenético ($IR = 0,800$), validando o uso dos caracteres para a diagnose de clados. O estudo detalha uma série de transformações-chave associadas à frugivoria, como a redução da robustez dos caninos, a especialização dos pré-molares e o deslocamento labial das cúspides molares. Adicionalmente, o trabalho descreve o surgimento de estruturas acessórias em Stenodermatinae, como o mesocônule e suas cristas, que aumentam a complexidade e a eficiência da superfície oclusal, e correlaciona a morfologia das cúspides com dietas específicas de alimentos duros (durofagia) ou macios (jusofagia). A presença de cíngulos é interpretada como uma estrutura de reforço biomecânico, enquanto diastemas e aberturas oclusais são analisados como adaptações para o manuseio de frutas e seus dejetos, como fibras e

sementes. Este trabalho demonstra que a dentição dos Stenodermatinae evoluiu de um padrão ancestral insetívoro para um complexo e altamente derivado conjunto de caracteres, atuando como um registro da história adaptativa do grupo e sendo fundamental para compreender os processos macroevolutivos que levaram os Stenodermatinae a se tornarem um dos mais diversos e bem-sucedidos grupos de morcegos neotropicais.

Palavras-chave: reconstrução de estado ancestral; cúspides; mesocônule; sinapomorfias

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Evolution of the specialized dental morphology of the Neotropical frugivore bat subfamily Stenodermatinae (Phyllostomidae), with updated dental nomenclature

Abstract

Bats have a wide variety of diets associated with craniodental modifications. The consumption of fruits led to convergent dental specializations in Pteropodidae and Stenodermatinae. While the mechanics of frugivory in Stenodermatinae are well studied, the characters involved evolutionary transition from their insectivorous ancestors remains less explored. This study investigates the evolution of dental morphology in this clade, reconstructing the history of its characters, and inferring their functional implications. We also propose for the first time a standardized nomenclature for the dental structures in the group. We analyzed 66 dental characters in 11 of 19 genera of Stenodermatinae and 5 outgroup taxa, mapping them onto a molecular phylogeny using parsimony to assess synapomorphies, the consistency index (CI), and the retention index (RI). The analysis reveals high homoplasy ($CI = 0.423$), consistent with the group's adaptive plasticity, but also a strong phylogenetic signal ($RI = 0.800$), validating the use of these characters for clade diagnosis. We detail key transformations for frugivory, including reduced canine robustness, specialized premolars, and the labial displacement of molar cusps. The study also describes the emergence of accessory structures like the mesoconule and its cristae, which increase occlusal complexity, and correlates cusp morphology with durophagous (hard-item) and jusophagous (soft-item) diets. Cingula are interpreted as biomechanical reinforcements, while diastemata and occlusal gaps are analyzed as adaptations for fruit handling and the ejection of fibrous byproducts. This work demonstrates that the Stenodermatinae dentition evolved from an ancestral insectivorous pattern into a complex, derived toolkit. These teeth act as a record of the group's adaptive history, fundamental to understanding the macroevolutionary processes that made Stenodermatinae one of the most successful Neotropical bat radiations.

Keywords: Ancestral state reconstruction; cusps; mesoconule; synapomorphies

Introduction

Chiroptera is the second most diverse group of mammals in the world, with approximately 1470 living species (Mammal Diversity Database 2025). Such diversity, which reflects on the dietary habits of its members, may include insects, fish, small vertebrates, blood, nectar, and fruits (Gardner 1977; Ferrarezi and Gimenez 1996). This variety of feeding habits is associated with

modifications on the skull, masticatory muscle insertion and teeth morphology (Freeman 1988; Freeman 1998).

Teeth are the most durable structure in a mammal's body. Their variability of cusp patterns, size, and shape has an important role in studies of diet, feeding habits, as well as phylogenetic relationships between mammalian taxa, including Chiroptera (Bergqvist 2003; Fracasso et al. 2011). A molar tooth with more ridges and developed cusps, with a dilambdodont pattern, are present in most species of bat (Fracasso et al. 2011) and are associated with a hard-item alimentation, like insects and small vertebrates. On the other hand, those who eat nectar or fruit has a general different pattern, with highly modified teeth, mainly post-canines (Freeman 1998).

Obligate frugivory is a phylogenetically widespread habit in bats, having evolved at least twice – in family Pteropodidae and the Phyllostomidae clade comprising the subfamilies Carolliinae, Rhinophyllinae, and Stenodermatinae (Kalko et al. 1996; Rojas et al. 2011). Convergent evolution of frugivory in these two groups have led to different tooth morphologies. Pteropodidae bats have less discernible cusps in teeth, which usually have diastemata between them, while Phyllostomidae frugivores usually have styler shelves with conspicuous labially displaced paracone and metacone, as well as protoconid and hypoconid, resulting in a cookie-cutter mechanism (Freeman 1988).

Among Phyllostomidae frugivores, subfamily Stenodermatinae is the most diverse clade, with approximately 102 recognized species, divided in two major lineages, Sturnirini and Stenodermatini, occurring from Mexico to Argentina (Simmons and Cirranello 2025). They are characterized by having relatively short rostra, small ears, and a noseleaf. Several species of Stenodermatinae use foliage as a day roost, and all species lack a tail (Solari et al. 2019). Among stenodermatines, there are specialized frugivores, with some genera, such as *Sturnira* Gray, 1842, specializing in fruits of the genus *Solanum* (L.), and others, such as *Artibeus* Leach, 1821 and *Uroderma* Peters, 1865, specialized in wild figs (*Ficus* (L.)) (Estrada and Fleming, 1986; Kalko et al. 1996).

This distinct tooth pattern rendered many studies about the mechanical implications about the masticatory system in Stenodermatinae bats (Freeman 1988, 1998), as well as the development mechanism of teeth class in Chiroptera (Sadier et al. 2023). Stenodermatine bats are known to have highly divergent and variable dental morphology, which has been useful in estimating phylogenetic relationships among its members and within the family Phyllostomidae

(Owen 1987, Lim 1993; Tavares 2008). However, few studies have attempted to assess the evolutionary changes from the ancestral dilambdodont teeth in bats to those found in frugivorous bats. One of the obstacles for that absence of evolutionary studies could be the lack of a standardized dental nomenclature for bat taxa that lack the traditional dilambdodont tooth pattern. Fracasso et al. (2011), for example, did not include most of the Phyllostomidae taxa in their analysis, including Stenodermatinae, because of their highly modified teeth.

Because teeth are highly relevant in species delimitation, and to estimate phylogenetic relationships (e. g. Wetterer et al. 2000; Velazco 2005; Garbino et al. 2020), the two objectives of this study are: i) to provide an updated nomenclature of the Stenodermatine upper and lower post canine teeth; and ii) to reconstruct the tooth evolution in Stenodermatinae bats, based on cusp and cristae morphology, as well as differences in the general size and shape of the teeth.

Material and Methods

Examined specimens

We analyzed 229 specimens belonging to 29 species of Stenodermatinae, comprising 11 of the 19 extant genera (Appendix I). As outgroup taxa, we examined two species of insectivorous bats: *Pteronotus rubiginosus* (Wagner, 1843), *Micronycteris microtis* (Miller, 1898); one omnivore: *Phyllostomus hastatus* (Pallas, 1767); as well as the frugivores *Rhinophylla pumilio* (Peters, 1865), and *Carollia perspicillata* (Linnaeus, 1758). Specimens examined are deposited in the following collections: Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV), Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais (MCN-MQ), Coleção de Mamíferos da Universidade Federal de Lavras (CMUFLA), Museu de Zoologia, Universidade de São Paulo (MZUSP), and Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais (UFMG). The voucher number and current species identification of each specimen are available in Appendix I.

Tooth nomenclature

We follow Fracasso et al. (2011) to standardize the names of structures present in a generalized Stenodermatinae tooth, mainly in upper molariforms. For lower molars, there are no standardized names specifically for Chiroptera, but here we use Czaplewski and Baker (2022) nomenclature, which follows generalized mammalian names for cusplids, cristids, cingulids, and basin. We attribute the names to the structures based on primary homology, which consists of a topological and positional correspondence between the bat insectivorous-like molar and the frugivorous-like molar (Pinna 1991). We also consulted other references about tooth cusps

terminology (Miller 1907; Slaughter 1970), which are limited to superficial topography evaluations, not documenting other structures such as crista and cingula present in Stenodermatinae teeth.

Ancestral state reconstruction

A total of 66 characters were selected to describe the morphological variation of upper (upper-case letter) and lower (lower-case letter) teeth (Appendix II), comprising 8 for incisors (I), 3 for canines (C), 24 for premolars (P), 30 for molars (M), and 1 for the general dental arch morphology. Characters were based on Owen (1987), Lim (1993), Wetterer et al. (2000), Velazco (2005), Tavares (2008), Garbino (2019), and our observations (6 of 66). Scored characters were binaries (87,9 %) or presented a maximum of three unordered states (12,1 %).

Especially for upper and lower premolar nomenclature, we follow Slaughter (1970), who numbered these teeth, for Stenodermatinae, as P3-P4 and p2-p4, respectively. Additionally, the characters were grouped into four sets: general tooth shape and proportion (TSP), presence and relative position of cusps (CSP), presence of cingula and cristae (CCP), and presence of diastemata and tooth position during occlusion (DTO). We calculated, for each character set, the level of homoplasy using the ensemble consistency and retention index (Kluge and Farris 1969; Farris, 1989).

For ancestral state reconstruction, characters were mapped based on the molecular phylogeny of Noctilionoidea (Rojas et al., 2016), pruned to include only Stenodermatinae and the outgroups (Figure 2), and with the addition of the recently described *Sturnira giannae* Velazco et al. 2019 as sister group of *Sturnira lilium* (Velazco et al. 2019). The tree topology was replicated in the software Mesquite 3.81 (Maddison and Maddison 2023), and ancestral states were estimated under the parsimony criterion (Fitch 1971). To map characters with relevant phylogenetic signal that could correspond to synapomorphies, we used the same character matrix in TNT software (Goloboff et al. 2008). See Appendix II for a list of characters and states, and Appendix III for the morphological matrix with scores for each taxon.

Results

Dental morphology and nomenclature compared to the ancestral pattern

Dental morphology of stenodermatine bats, when compared to the dilambdodont pattern of most Chiroptera, reveals notable differences in the arrangement of cusps and cristae. These include the absence or reduction of certain structures, such as the labiolingual contraction of

the styler shelf – along with the loss of the parastyle and metastyle – and a shallow protofossa in the upper molars, as well as the rearrangement of the protocristid in the lower molars, resulting in a deep central basin in the teeth (Figure 1).

In terms of nomenclature, every structure identified in the stenodermatine dentition could be traced to a homologue structure in the dilambdodont pattern. Therefore, it was possible to use the standardized nomenclature of the upper dentition proposed by Fracasso et al. (2011). For the lower teeth, we propose here for the first time a standardization (Figure 1).

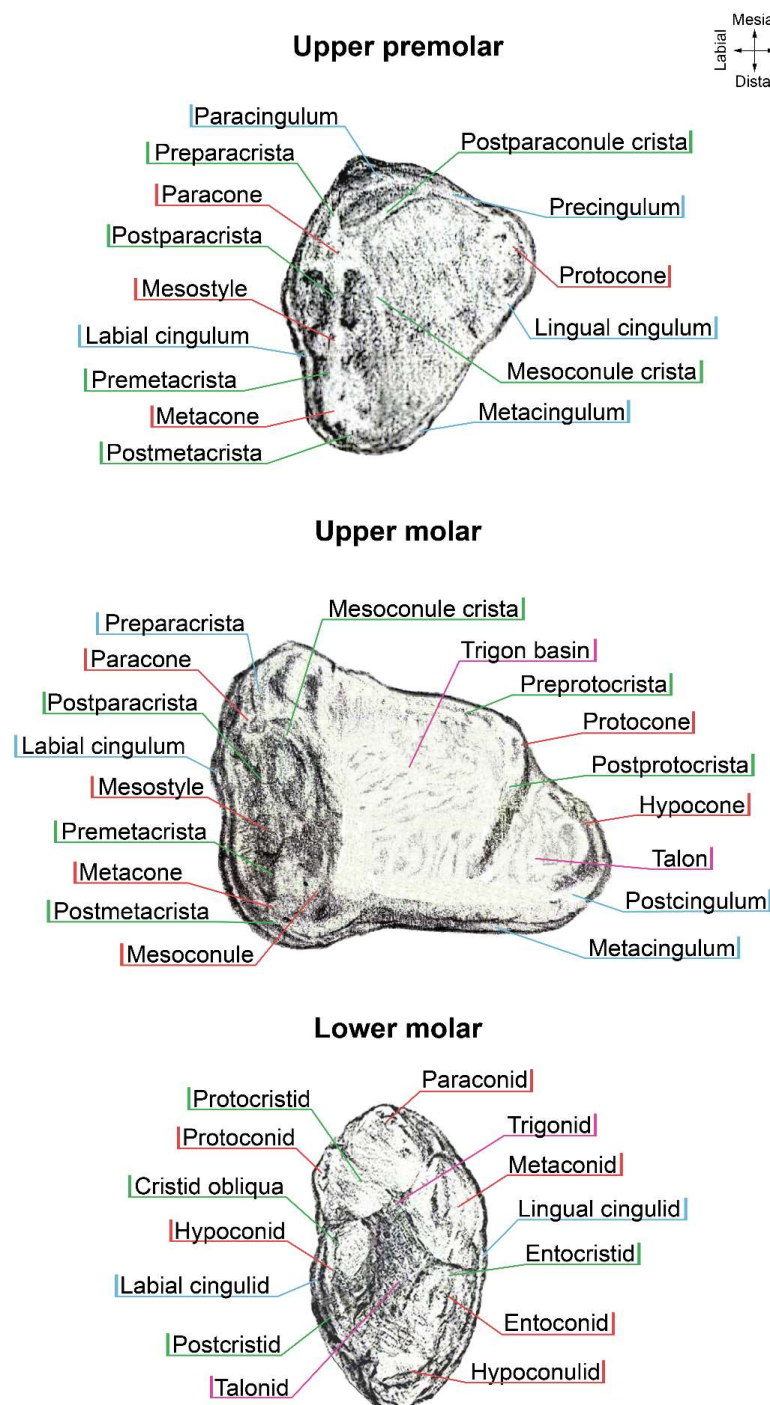


Figure 1. Generalized Stenodermatinae upper and lower postcanine teeth, illustrating the morphology of the cusps, cuspules and cuspulids (red), crista and cristid (green), cingula and cingulids (blue), and the talon(id) and trigon(id) basin (purple). The arrow diagram on the top right indicates the anatomical axes of a tooth. Illustration by Maxwell Douglas Crispim Borges.

Evolution of dental structures in Stenodermatinae

In obligate frugivorous phyllostomids, the total number of teeth ranges from 28 to 32, with all species analyzed without the P2 and p3. Also, some species do not have M3 and/or m3, and one of the analyzed species, *Vampyriscus bidens* (Dobson, 1878), lacks the second pair of lower incisors. Of the 66 characters analyzed, 43 (65%) are mapped as synapomorphies for at least one clade (Figure 2).

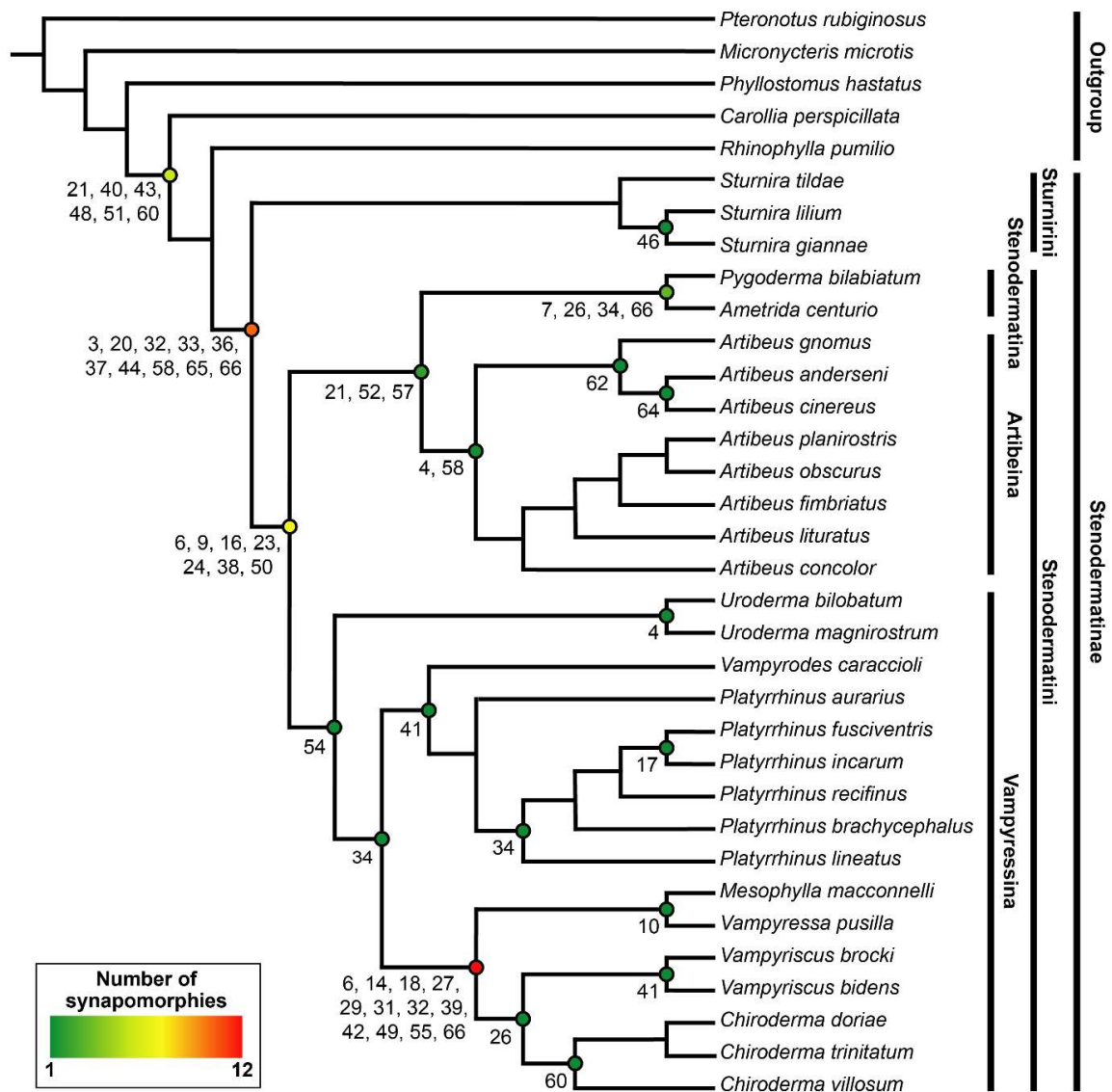


Figure 2. Dental characters that are synapomorphies of Stenodermatinae. Tree topology is based on the molecular phylogeny of Rojas et al (2016). Character names for the indicated number are available in Appendix II.

The ensemble consistency and retention indices showed slight variation across sets of characters (Table 1), with the TSP class having the highest CI and the CSP class having the highest RI. However, the DTO class showed the lowest results in both CI and RI. The CI for the entire dataset is below 0.5, although its RI is relatively high compared to that of other character classes.

Table 1. Ensemble Consistency and Retention indices for 66 dental characters on reconstruction of the ancestral state of Stenodermatinae. Character sets: General tooth shape and proportion (TSP); Presence and relative position of cusps (CSP); Presence of cingula and cristae (CCP); and Presence of diastemata and tooth position during occlusion (DTO).

Character sets	Total number of characters	Synapomorphic characters	Synapomorphic and homoplastic characters	Ensemble Consistency Index	Ensemble Retention Index
TSP	15	10	2	0.478	0.806
CSP	23	16	5	0.411	0.830
CCP	17	11	1	0.404	0.777
DTO	11	6	2	0.387	0.747
Total	66	43	10	0.423	0.800

In the (*Carollia perspicillata* (*Rhinophylla pumilio* + Stenodermatinae)) clade, we observed several simplifications regarding cusp presence and development (Figure 3) as follows: the absence of a protocone in P4, the absence of a hypocone in both M1 and M2 (though the talon is retained in some Stenodermatinae), and a reduction in the hypoconid of m2. Similarly, the mesio-distal length of m2 is reduced compared to m1, and the labial-lingual length of M3 is smaller than that of M2, in contrast to other outgroup taxa, such as *Phyllostomus hastatus*, *Micronycteris microtis*, and *Pteronotus rubiginosus*.

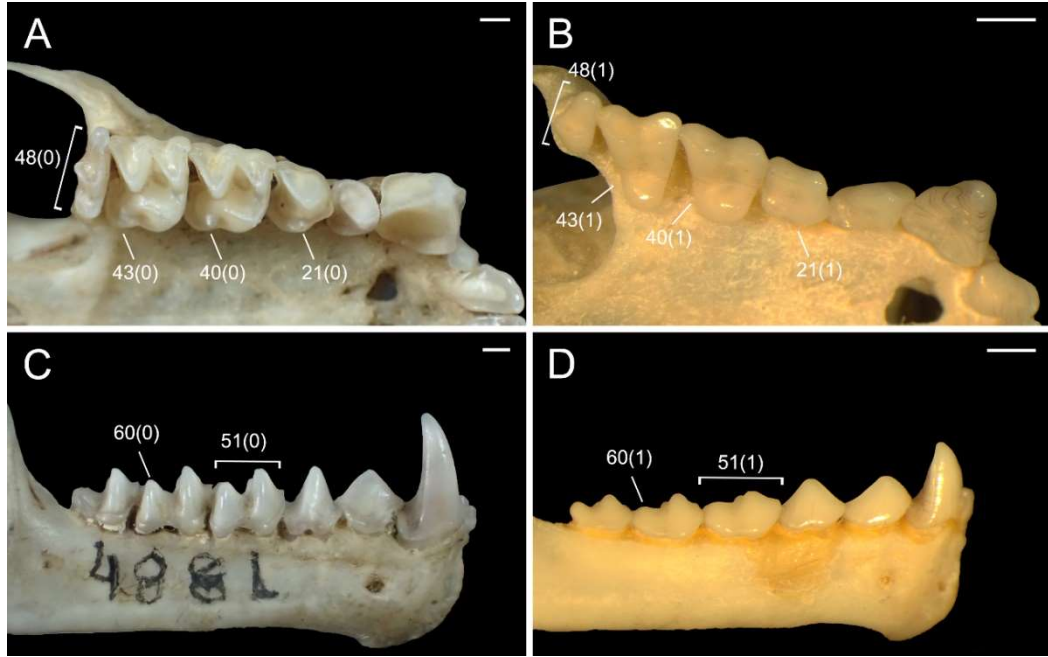


Figure 3. Synapomorphic dental characters of the (*Carollia perspicillata* (*Rhinophylla pumilio* + *Stenodermatinae*)) clade in occlusal view of the skull (A and B) and lateral view of the mandible (C and D). A, C: *Phyllostomus hastatus* (MZUFV 4881); B, D: *Carollia perspicillata* (MZUFV 1759). Characters and states: 21 – Protocone of P4: (0) present, (1) absent; 40 – Hypocone of M1: (0) present, (1) absent; 43 – Hypocone of M2: (0) present, (1) absent; 48 – Labial-lingual length of M3 relative to M2: (0) Subequal, (1) Less than 2/3; 51 – Mesiodistal length of m1 relative to m2: (0) Subequal, (1) Larger; 60 – Development of hypoconid of m2: (0) well developed, (1) less developed. Scale bar: 1 mm.

In *Stenodermatinae*, a notable synapomorphy is the displacement of labial cusps in the upper molar to the labial edge of the tooth, resulting in a decrease in the crista of the styler shelf, and forming a surface between the lingual and labial cusps. Furthermore, the upper incisors become less proodont, with the slope between the mesial face of the incisors and the rostrum becoming more obtuse. There is a development of the posterior labial cusp of the upper and lower second premolars (P4 and p4), metacone and hypoconid respectively, besides an increase in the proportions of p4, where the height is greater than the mesiodistal length. M1 and M2 features a crista on the lingual face of the labial cusps, termed the mesoconule crista. The paraconid of m2 becomes absent, and, when present, m3 is much smaller than m2. (Figure 4). The general shape of the dental arch is more sub-square than sub-triangular, as observed in outgroup taxa (Figure 5).

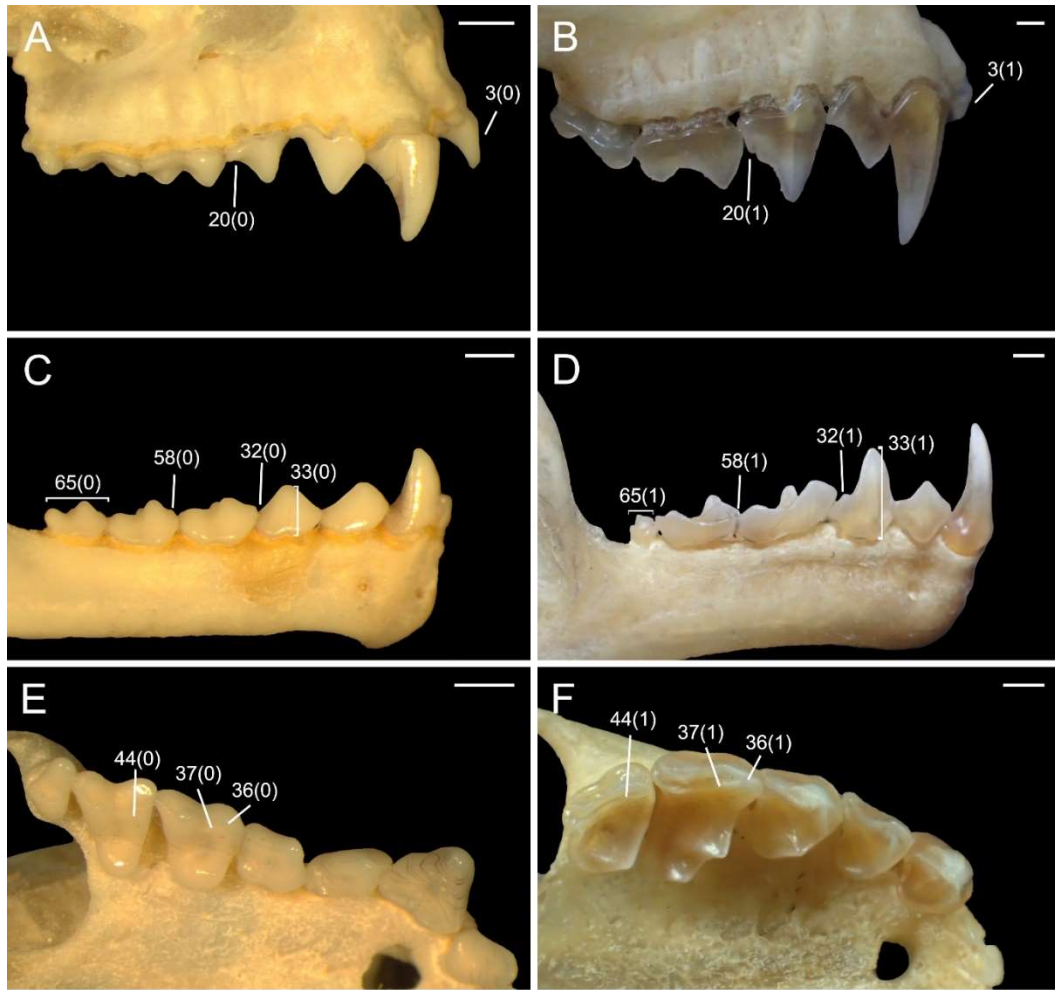


Figure 4. Synapomorphic dental characters of Stenodermatinae in lateral (A and B) and occlusal view (E and F) of the skull, and lateral view of the mandible (C and D). A, C, and E: *Carollia perspicillata* (MZUFV 1759); B, D, and F: *Artibeus lituratus* (MZUFV 1511). Characters and states: 3 – Inclination of I1: (0) proodont, (1) orthodont; 20 – Metacone of P4: (0) absent, (1) present; 32 – Hypoconid of p4: (0) absent, (1) present; 33 – Height relative to mesial-distal width of p4: (0) subequal, (1) larger; 36 – Position of the paracone and metacone of the molars: (0) centered on the mesial-distal axis, (1) labially displaced; 37 – Mesoconule crista of M1: (0) absent, (1) present; 44 – Mesoconule crista of M2: (0) absent, (1) present; 58 – Paraconid on m2: (0) present, (1) absent; 65 – Mesial-distal axis of m3 relative to m2: (0) more than 1/4, (1) less than 1/4. Scale bar: 1 mm.

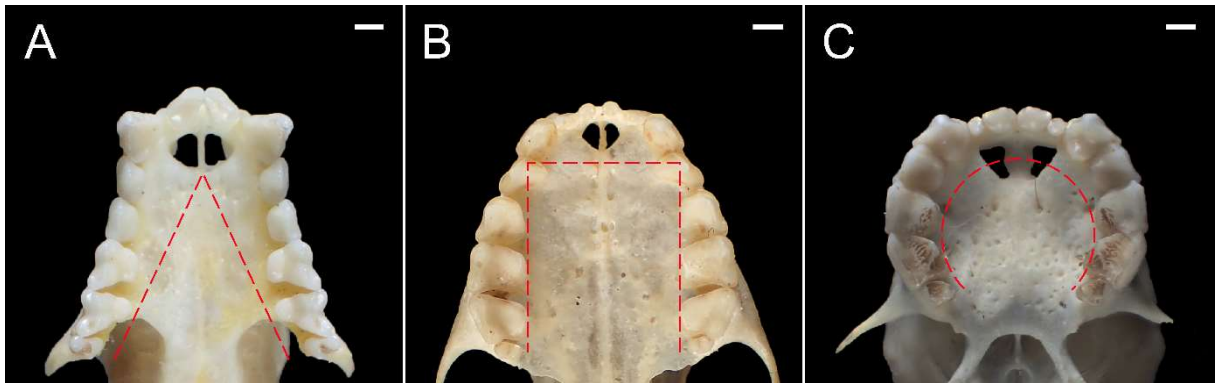


Figure 5. General shape of the dental arch of frugivorous bats (Character 66): (A) sub-triangular; (B) sub square; (C) Sub-circular. A: *Carollia perspicillata* (MCN-MQ 407); B: *Uroderma magnirostrum* (MZUSP 30258); C: *Pygoderma bilabiatum* (CMUFLA 1627). Scale bar: 1 mm.

In Stenodermatini, the upper and lower incisors form a frontal opening when it is in occlusion. The upper canine becomes less robust with the mesiodistal length subequal to or smaller than P4. The upper premolars have some modifications on the appearance of some crista, such as the postparaconule crista (present in P3 and P4) and mesoconule crista in P4. A secondary cusp emerges on the distal edge of M1, the mesoconule, at the base of the metacone. The height of m1 relative to p4 is smaller when compared to the outgroup and Sturnirini (Figure 6). Although no synapomorphies were mapped for Sturnirini, some characters have unique states for this tribe, such as the trilobed tips of the lower incisors and a p2 height greater than that of p4. (*Sturnira lilium* + *S. giannae*) has a single synapomorphy: the presence of a labial cingulum on M2.

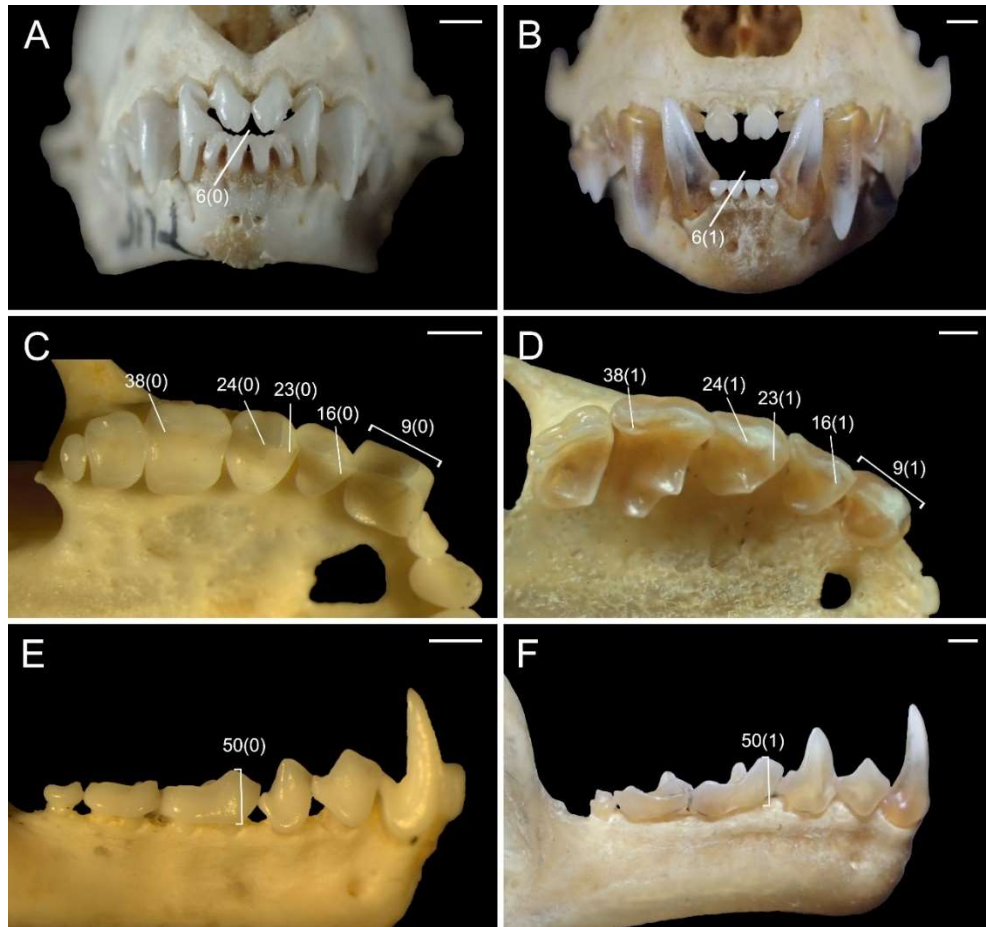


Figure 6. Synapomorphic dental characters of Stenodermatini in frontal (A and B) and occlusal view (C and D) of the skull and lateral view of the mandible (E and F). A, C, and E: *Sturnira lilium* (MCN-MQ 417); B, D, and F: *Artibeus lituratus* (MZUFV 1511). Characters and states: 6 – Front opening between the upper and lower incisors: (0) absent, (1) present; 9 – Mesial-distal length of C relative to P4: (0) larger, (1) subequal; 16 – Postparaconule crista of P3: (0) absent, (1) present; 23 – Postparaconule crista of P4: (0) absent, (1) present; 24 – Mesoconule crista of P4: (0) absent, (1) present; 38 – Mesoconule of M1: (0) absent, (1) present; 50 – Height of m1 relative of p4: (0) more than $2/3$, (1) less than $2/3$. Scale bar: 1 mm.

In the (Artibeina + Stenodermatina) clade, the protocone of P4 becomes present again, and the m1 develops a cingulid at the base, and has its protoconid displaced mesially (Figure 7). In Stenodermatina, a rostral contraction results in the alignment of the upper incisors in the same plane, giving the dental arch a rounded appearance (Figure 5). Furthermore, members of this subtribe have a p2 crown height greater than its mesiodistal length, and the protoconid of p4 is also displaced mesially (Figure 8). In Artibeina, the upper incisors are deeply bilobed, and the paraconid of m2 is present. Additionally, in the clade of subgenus *Artibeus* (*Dermanura*)

analyzed, the labial cingulid of m2 is absent, and the m3 is absent in the (*A. anderseni* + *A. cinereus*) clade (Figure 9).

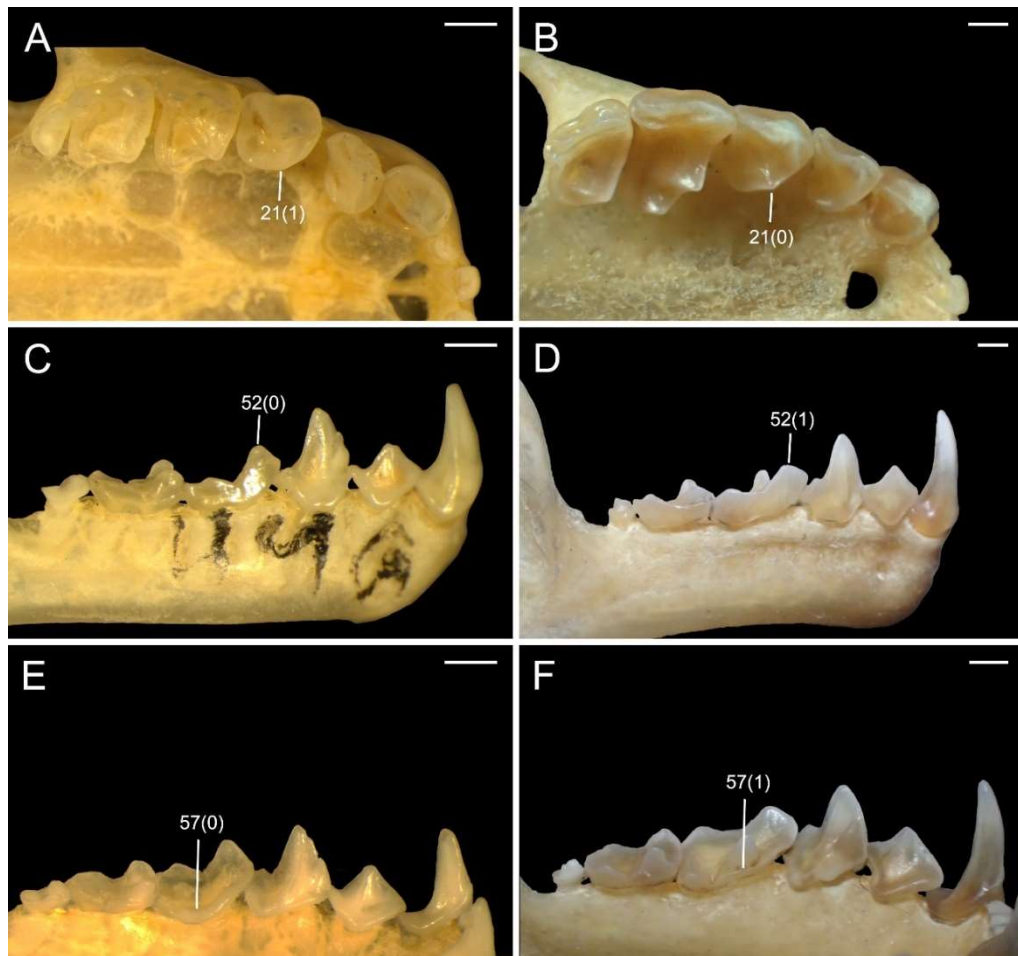


Figure 7. Synapomorphic dental characters of the (Artibeina + Stenodermatina) clade in occlusal (A and B) and lateral (C and D) views of the skull, and dorsolateral oblique view of the mandible (E and F). A, C, and E: *Uroderma bilobatum* (MCN-MQ 446); B, D, and F: *Artibeus lituratus* (MZUFV 1511). Characters and states: 21 – Protocone of P4: (0) present, (1) absent; 52 – Displacement of the protoconid of m1: (0) not displaced, (1) mesially displaced; 57 – Lingual cingulid of m1: (0) absent, (1) present. Scale bar: 1 mm.

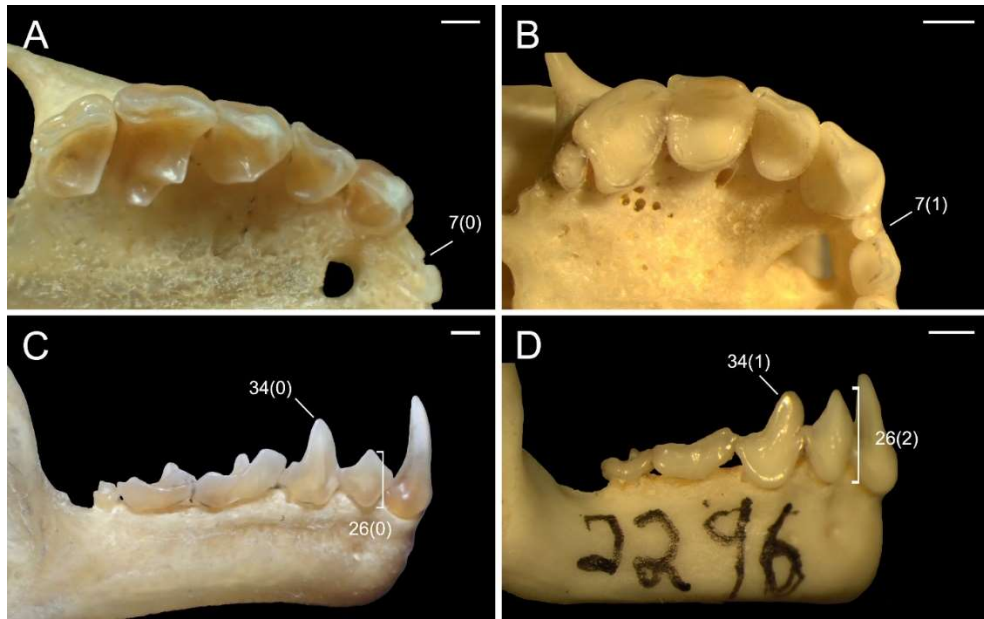


Figure 8. Synapomorphic dental characters of Stenodermatina in occlusal view (A and B) of the skull and lateral view (C and D) of the mandible. A and C: *Artibeus lituratus* (MZUFV 1511); B and D: *Pygoderma bilabiatum* (CMUFLA 2296). Characters and states: 7 – Alignment of the upper incisors in occlusal view: (0) in an arch, (1) in a straight line; 26 – Height relative to mesial-distal width of p2: (0) subequal, (2) Larger; 34 – Position of the protoconid of p4 in lateral view: (0) aligned on the central axis of p2, (1) mesially displaced. Scale bar: 1 mm.

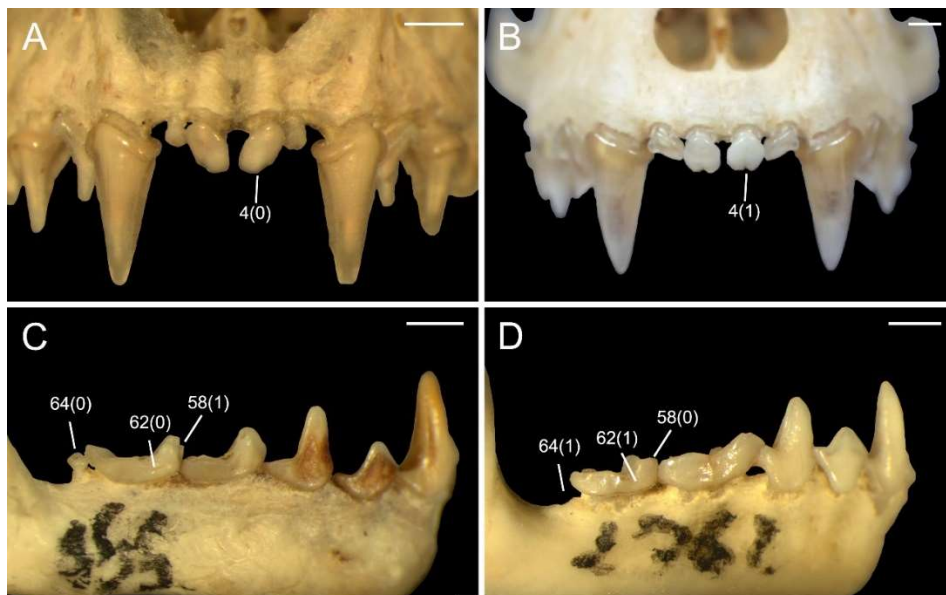


Figure 9. Synapomorphic dental characters of Artibeina and subclades in frontal view (A and B) of the skull and lateral view (C and D) of the mandible. A: *Platyrrhinus incarum* (MZUFV 5177); B: *Artibeus lituratus* (MZUFV 1511); C: *Vampyriscus bidens* (MCN-MQ 55); D:

Artibeus (Dermanura) cinereus (CMUFLA 1762). Characters and states: 4 – Tip of I1: (0) simple or slightly bilobed, (1) deeply bilobed; 58 – Paraconid of m2: (0) present, (1) absent; 62 – Labial cingulid on m2: (0) present, (1) absent; 64 – m3: (0) present, (1) absent. Scale bar: 1 mm.

In Vampyressina, the only morphological change shared by all groups is the absence of the m1 metaconid (Figure 10). Several subgroups exhibit one additional synapomorphy each. In the clade ((*Vampyrodes* + *Platyrrhinus*) + ((*Vampyressa* + *Mesophylla*) + (*Vampyriscus* + *Chiroderma*))), the protoconid of p4 is mesially displaced (Figure 11). However, in the small *Platyrrhinus* clade, this condition is reversed, and the protoconid becomes realigned with the central axis of the tooth. The clade (*Vampyrodes* + *Platyrrhinus*) is characterized by a labial cingulum on M1 (Figure 11). The clade (*Platyrrhinus fusciventris* + *P. incarum*) is distinguished by a diastema between P3 and P4 (Figure 11). Finally, *Uroderma* has a single derived modification: deeply bilobed upper incisors (Figure 10).

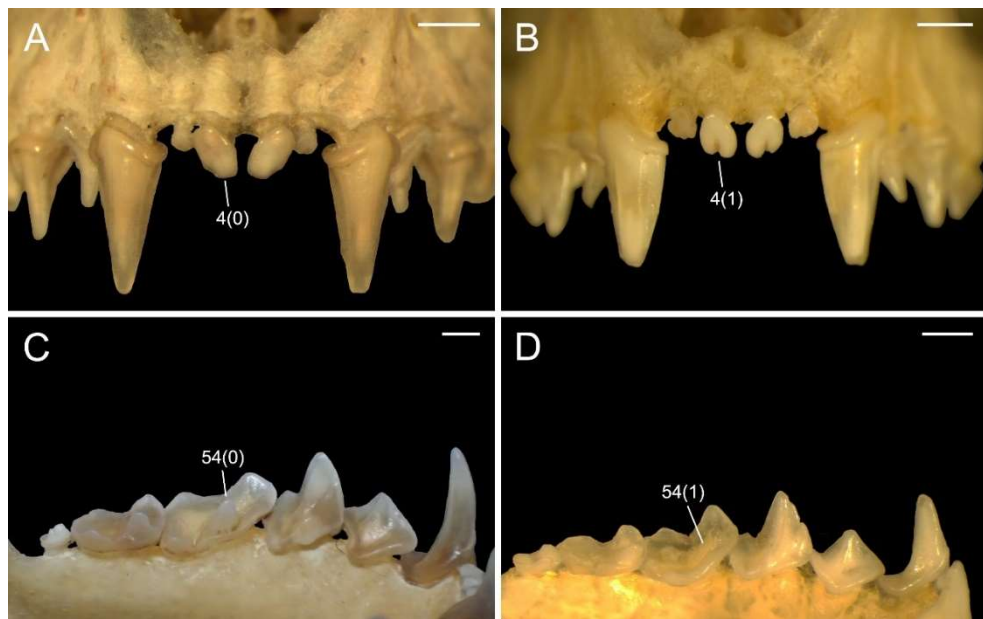


Figure 10. Synapomorphic dental characters of the Vampyressina clade and the genus *Uroderma* in frontal view (A and B) of the skull and dorsolateral oblique view (C and D) of the mandible. A: *Platyrrhinus incarum* (MZUFV 5177); B and D: *Uroderma bilobatum* (MCN-MQ 446); C: *Artibeus lituratus* (MZUFV 1511). Characters and states: 4 – Tip of I1: (0) simple or slightly bilobed, (1) deeply bilobed; 54 – Metaconid of m1: (0) present, (1) absent. Scale bar: 1 mm.

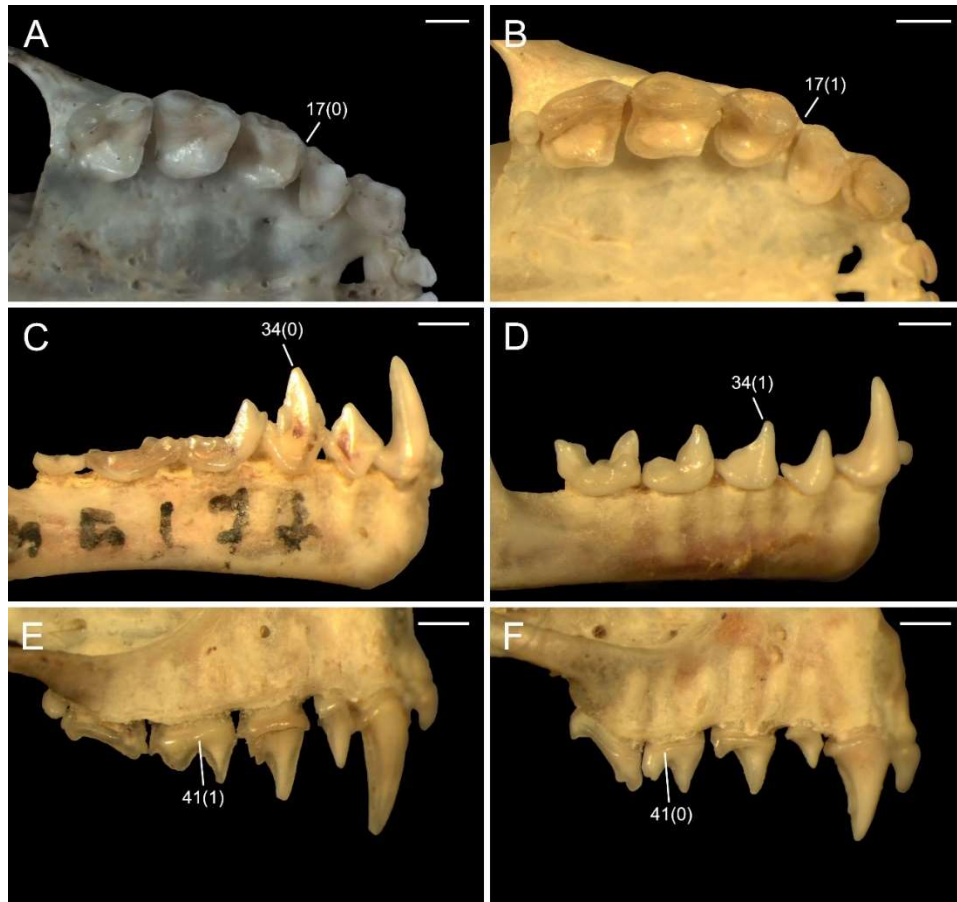


Figure 11. Synapomorphic dental characters of the ((*Vampyrodes* + *Platyrrhinus*) + ((*Vampyressa* + *Mesophylla*) + (*Vampyriscus* + *Chiroderma*))) clade, the (*Vampyrodes* + *Platyrrhinus*) clade, and the small *Platyrrhinus* clade in occlusal (A and B) and lateral (E and F) views of the skull and lateral view (C and D) of the mandible. A: *Platyrrhinus lineatus* (MZUFV 3455); B, C, and E: *Platyrrhinus incarum* (MZUFV 5177); D and F: *Vampyressa pusilla* (CMUFLA 2132). Characters and states: 17 – Diastema between P3 and P4: (0) absent, (1) present; 34 – Position of the protoconid of p2 in lateral view: (0) aligned on the central axis of p2, (1) mesially displaced; 41 – Labial cingulum on M1: (0) absent, (1) present. Scale bar: 1 mm.

However, the ((*Vampyressa* + *Mesophylla*) + (*Vampyriscus* + *Chiroderma*)) clade exhibits 12 synapomorphies, the highest number among the analyzed groups (Figure 12). The height of P3 is reduced relative to P4, with less than 2/3 of the latter. The p2 has a mesially displaced protoconid and is also reduced, with the mesiodistal length smaller than that of p4, which lacks the hypoconid. Furthermore, a diastema is present between these two premolars. The upper molars, which are more triangular, have lost the talon. The m1 is subequal in

mesiodistal length to p4, and the m1 lacks an entoconid. Regarding occlusion, the dental arch is subtriangular (Figure 5), with no frontal gap, but with a lateral gap present.

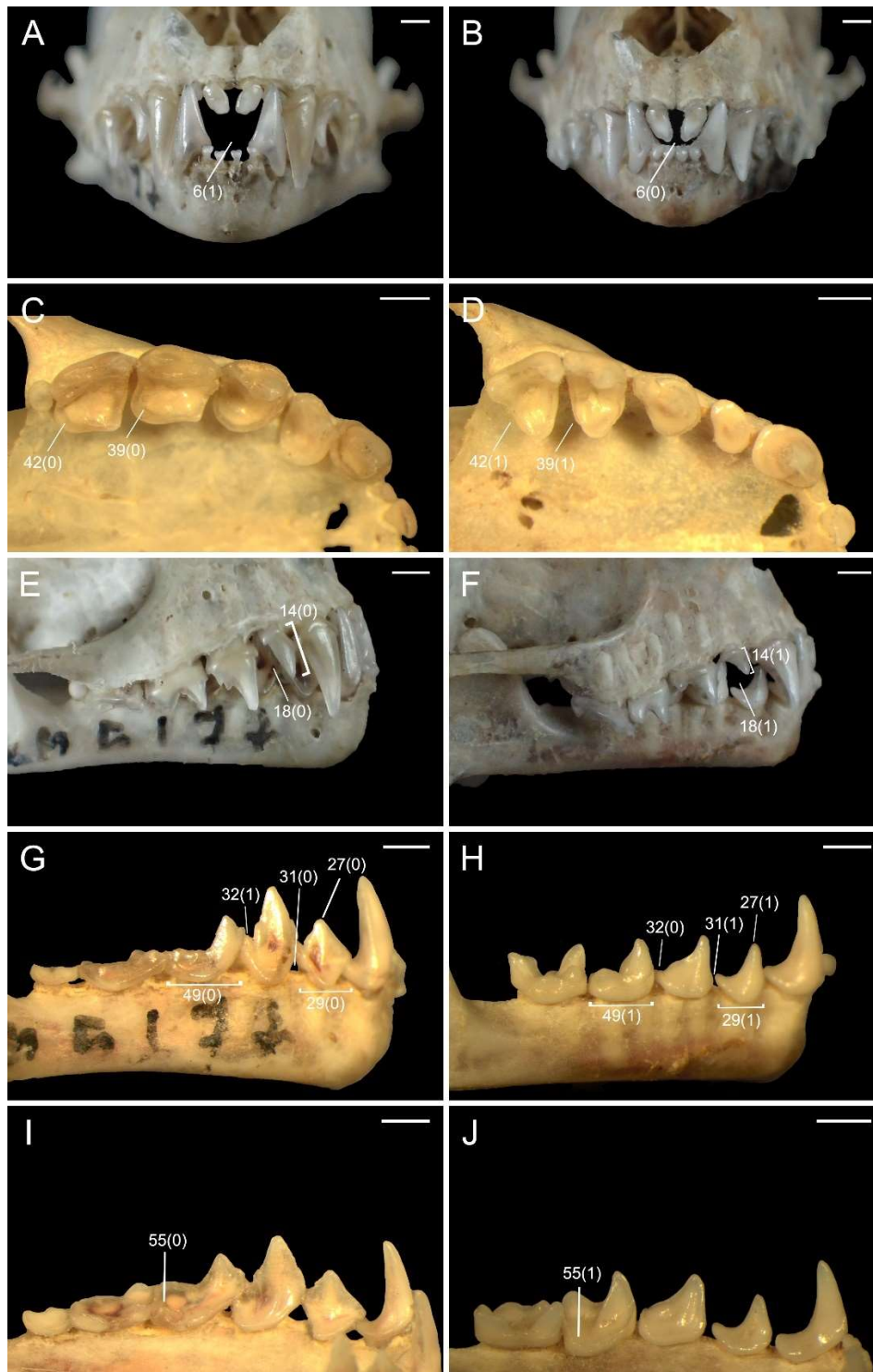


Figure 12. Synapomorphic dental characters of the ((*Vampyressa* + *Mesophylla*) + (*Vampyriscus* + *Chiroderma*)) clade in frontal (A and B), occlusal (C and D), and lateral (E and F) views of the skull, and lateral (G and H) and dorsolateral oblique (I and J) views of the mandible. A, C, E, G, and I: *Platyrrhinus incarum* (MZUFV 5177); B, D, F, H and J:

Vampyressa pusilla (CMUFLA 2132). Characters and states: 6 – Front opening between the upper and lower incisors: (0) absent, (1) present; 14 – Height of P3 relative to P4: (0) more than 2/3, (1) less than 2/3; 18 – Lateral gap between upper and lower premolars: (0) absent, (1) present; 27 – Position of the protoconid of p2 in lateral view: (0) aligned on the central axis, (1) mesially displaced; 29 – Mesiodistal length of p2 relative to p4: (0) subequal or larger, (1) smaller; 31 – Diastema between p2 and p4: (0) absent, (1) present; 32 – Hypoconid of p4: (0) absent, (1) present; 39 – Talon of M1: (0) present, (1) absent; 42 – Talon of M2: (0) present, (1) absent; 49 – Mesiodistal length of m1 relative to p4: larger (0), subequal (1); 55 – Entoconid of m1: (0) present, (1) absent. Scale bar: 1 mm.

For the subclades (*Vampyressa* + *Mesophylla*) and (*Vampyriscus* + *Chiroderma*), only one synapomorphy was found for each: a diastema between C and P3 and a change in the proportions of p2, with the length being larger than the height, respectively. Similarly, for the genus *Vampyriscus* and *Chiroderma*, a single synapomorphy was also mapped for each: the presence of a labial cingulum on M1 and the well-developed m2 hypoconid, respectively (Figure 13).

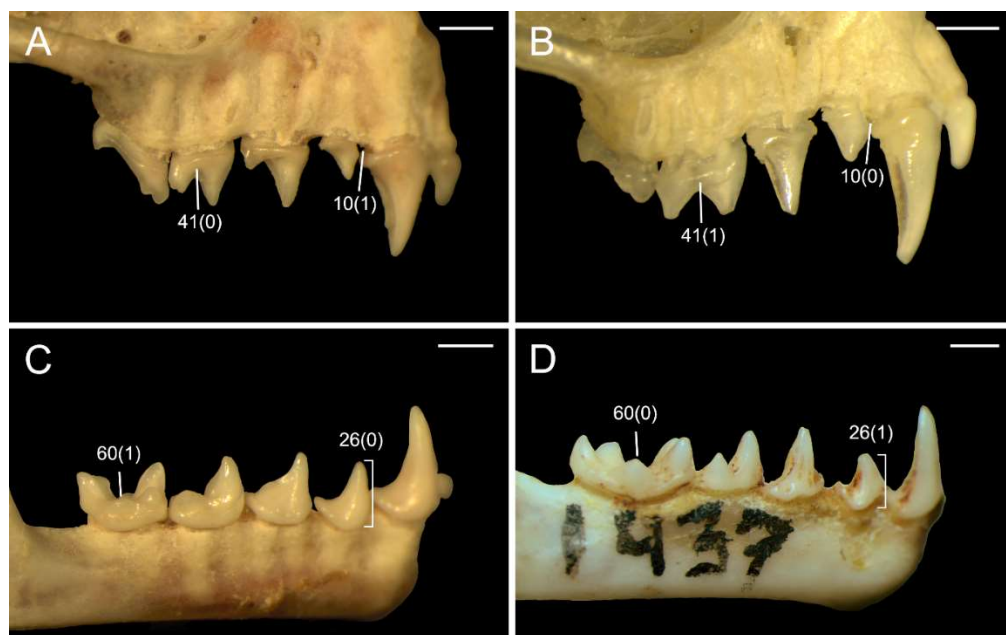


Figure 13. Synapomorphic dental characters of the clades ((*Vampyressa* + *Mesophylla*) clade and (*Vampyriscus* + *Chiroderma*), and for the genus *Vampyriscus* and *Chiroderma* in lateral view of the skull (A and B) and lateral view of the mandible (C and D). A, C: *Vampyressa pusilla* (CMUFLA 2132); B: *Vampyriscus brocki* (MCN-MQ 443); D: *Chiroderma trinitatum* (UFMG 10642). Characters and states: 10 – Diastema between C and P3: (0) absent, (1) present; 26 – Height relative to mesial-distal width of p2: (0) subequal, (1) smaller; 41 – Labial cingulum

on M1: (0) absent, (1) present; 60 – Development of hypoconid of m2: (0) well developed, (1) less developed. Scale bar: 1 mm.

Discussion

The present study reconstructed the evolution of dental characters in obligate frugivorous bats, particularly Stenodermatinae and its subclades. It revealed a series of gradual transformations in the rearrangement and specialization of the general tooth morphology based on 66 characters, encompassing variations in shape, proportions, and the presence of structures such as cusps and cristae, as well as the overall arrangement of teeth in the dental arcade. The high level of homoplasy observed suggested that different lineages within the subfamily converged on similar morphological solutions to exploit a variety of plant resources, in contrast to the ancestral insectivorous/omnivorous pattern.

The ensemble consistency index (CI) for the dental character matrix was 0.429, while the ensemble retention index (RI) was 0.803. The low CI value indicates a high degree of homoplasy among the studied taxa, which can be explained by convergences and reversals driven by similar selective pressures for frugivory (Wake et al. 2011). A similar pattern has been reported for Phyllostomidae regarding morphological characters of the cranium and dentition (CI = 0.555; RI = 0.832) (Wetterer et al. 2000). This pattern contrasts with that of Mormoopidae (CI = 0.653; RI = 0.750), a family that, while related to Phyllostomidae, exhibits less homoplasy, probably due to being much less diverse morphologically and in feeding habits, as all species are insectivorous (Simmons and Conway 2001). Despite the high level of homoplasy in dental characters of Stenodermatinae, the relatively high RI suggests that the characters carry a relevant phylogenetic signal, making them useful for diagnosing monophyletic groups (Farris 1989) and justifying their use in chiropteran phylogeny due to their richness of phylogenetic information (Fracasso et al. 2011).

The general dental shape and proportions exhibit major alterations within the group, with 10 out of 15 characters being synapomorphic for at least one clade. Changes in canine size and robustness in the tribe Stenodermatini [9(1)] (Figure 5) indicate a shift in food-handling strategy; since many species carry fruits to feed elsewhere and there is no need to subdue the "prey" (fruit), less canine robustness is required (Freeman 1998). Similarly, premolars, especially p4, in the subfamily Stenodermatinae [33(1)], become more developed (Figure 4), forming a pestle-like structure that fits into the basin of the upper premolar. This upper premolar may, in turn, possess an accessory cusp for this mortar-and-pestle function, such as the

protocone of P4 [21(0)] in the (Artibeina + Stenodermatina) clade (Figure 6). Furthermore, canines and premolars have an integrated relationship, forming a continuous blade that aids in cutting the skin of fruits, making the primary processing of food more efficient in the anterior dentition (Freeman 1988).

Of the 23 characters related to the presence and position of cusps, 17 are synapomorphic for at least one group. Among these, the labial displacement of cusps in Stenodermatinae [36(1)] is noteworthy (Figure 4). This feature, together with the modified premolars and canines, gives the dental arcade a "cookie-cutter" appearance (Freeman 1988). This alteration, combined with the lower relative height and rugose surface of the molars, leads to the formation of a complex and sharp maceration basin that increases tooth-fruit contact, enhancing the processing of fruit pulp (López-Aguirre et al. 2022). Additionally, in Stenodermatinae, a postero-labial cusp emerges on the last upper [20(1)] and lower [32(1)] premolar (Figure 4), here named metacone and hypoconid, respectively, providing a new cutting/piercing surface that facilitates access to the food. Another cusp present in the molars of Stenodermatini is the mesoconule [38(1) and 45(1), the latter not as a synapomorphy], located postero-labially on the lingual face of the metacone (Figure 5). This structure is referred to as a metaconule in other works (e.g., Slaughter 1970; Freeman 2000); however, it can connect to a crista extending from the paracone, named the mesoconule crista, whereas a metaconule is a small expansion typically associated with the postprotocrista (Fracasso et al. 2011).

The presence or absence of cusps is intimately related to the nature of the consumed fruit. Durophagous bats, which feed on hard fruits and seeds, possess robust cusps, such as the well-developed mesoconule of M2 [45(1)] and the hypoconid [60(0)] and hypoconulid [61(1)] of m2 in the clade ((*Vampyressa* + *Mesophylla*) + (*Chiroderma* + *Vampyriscus*)) (Figure 12), especially in the genus *Chiroderma* (Nogueira et al. 2005; Nogueira et al. 2009). Conversely, flatter teeth with more open basins are more efficient for consuming fruits with softer pulp, a strategy termed jusophagy (Freeman 1998).

Of the characters related to the presence of cristae and cingula, 11 out of 17 are considered synapomorphies for at least one clade. The cristae associated with the labial cusps (pre- and postparacrista; pre- and postmetacrista) are present and give a blade-like appearance to the labial edge of the tooth. Additionally, other cristae are present in Stenodermatini, such as the postparaconule crista of P3 [16(1)] and P4 [23(1)] (Figure 5), and the mesoconule crista on P4 [24(1)]. In Stenodermatinae, the mesoconule crista is also present on M1 [37(1)] and M2 [44(1)] (Figure 4). Cristae and cristids are important superficial structures for increasing

shearing efficiency; when arranged in series, they enhance the propagation of the initial fracture in the outer layer of the food (Evans and Sanson 2003). This form and function are analogous to the carnassiform notches of insectivorous bats (Czaplewski and Baker 2022). In the (*Vampyroides* + *Platyrrhinus*) and (*Artibeina* + *Stenodermatina*) clades, cingula and cingulids are present, respectively, on the first upper [41(1)] and lower [57(0)] molars (Figure 10). Cingula and cingulids play an important role in protecting the gingiva from insect exoskeleton fragments in insectivorous bats (Freeman 1998). Similarly, the cingula also protect the gingiva of frugivorous bats during the feeding on large and hard fruits. Beyond this, they also serve as a crucial structure for dissipating forces, thereby preventing tooth fracture and wear (Anderson et al. 2011)

Diastemata and tooth occlusion include 8 out of 11 synapomorphic characters. The presence of diastemata (i.e., gaps between teeth) is often related to nectar and pollen feeding (Freeman 1998), however, several lineages of frugivorous bats in the clade ((*Vampyressa* + *Mesophylla*) + (*Chiroderma* + *Vampyriscus*)) possess diastemata between the premolars [31(1)] (Figure 11) or between the premolar and the canine [10(1)] (Figure 12). In addition to inter-tooth diastemata, the Stenodermatini have a frontal opening when the teeth are in occlusion [6(1)] (Figure 5), whereas in the clade ((*Vampyressa* + *Mesophylla*) + (*Chiroderma* + *Vampyriscus*)), this frontal occlusion is closed, and instead a lateral opening exists between the upper and lower premolars [18(1)] (Figure 11). This opening may be related to carrying more voluminous fruits and handling food (Dumont 2007), as well as functioning as a channel for ejecting seeds and fibers from the mouth after mastication (Morrison 1980). The absence of the upper and lower third molars is variable within Stenodermatinae, and is probably related to brachycephaly and the shortening of the mandible in the group (Sadier et al. 2023). Furthermore, the extreme shortening of the rostrum in Stenodermatina, commonly known as “short-faced bats”, leads to a rounding of the dental arcade [66(2)] and the alignment of the incisors in these bats [7(1)] (Figure 7).

Conclusion

The evolutionary history of the Stenodermatinae dentition, as well as its extensive diversification, is intimately linked to its specialized diet of fruits and the allocation into new, specialized, trophic niches within frugivory (Dumont et al. 2012). From an insectivorous ancestor with a typical dilambdodont pattern, this group of bats underwent a series of transformations resulting in a highly derived and complex dentition featuring labial cutting blades, maceration basins, and accessory cristae and cusps.

Our study, despite not including key taxa such as *Ectophylla alba* Allen, 1892, *Enchisthenes hartii* (Thomas, 1892), and other genera of Stenodermatinae (e.g., *Ardops*, *Centurio*, *Sphaeronycteris*, *Stenoderma*), covers the majority of Stenodermatinae genera and demonstrates that dental morphology, although marked by homoplasy, retains strong phylogenetic potential. When integrated with molecular data into a total-evidence framework, it contributes to testing the robustness of clades and clarifying relationships among subgroups (Dávalos et al. 2012).

The specialized dentition acts as a record of the Stenodermatinae adaptive history, proving to be fundamental for understanding the evolutionary pathways that led the group to become one of the most species-rich and successful groups of Neotropical bats.

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Appendix I

List of 229 examined specimens deposited in the following collections: Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV), Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais (MCN-M), Coleção de Mamíferos da Universidade Federal de Lavras (CMUFLA), Museu de Zoologia, Universidade de São Paulo (MZUSP), and Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais (UFMG).

Ametrida centurio (n: 2): BRAZIL: Amazonas, R. Japurá, Limoeiro (MZUSP 14209). Pará, Marabá, Vila União (MCN-MQ 383)

Artibeus (Dermanura) anderseni (n: 6): BRAZIL: Ceará, Fortaleza, UTE Setentrional-Pecém (MCN-MQ 71). Maranhão, São Luís, Ponta da Madeira (MCN-MQ 110, 114, 259). Minas Gerais, Cabeceira Grande, UHE Queimado (MCN-MQ 205). Pará, UTE Barcarena (MCN-MQ 265).

Artibeus (Dermanura) cinereus (n: 7): BRAZIL: Ceará, Fortaleza, UTE Setentrional-Pecém (MCN-MQ 70). Goiás, Itumbiara, (MCN-MQ 147). Maranhão, São Luís, Ponta da Madeira (MCN-MQ 116). Minas Gerais, Conceição do Mato Dentro (UFLA 1760, 1762). Pará, Ourilândia do Norte (MCN-MQ 448). Rio Grande do Norte, Natal, Parque das Dunas (MCN-MQ 429).

Artibeus (Dermanura) gnomus (n: 1): BRAZIL: Pará, Ourilândia do Norte, (MCN-MQ 466).

Artibeus (Koopmania) concolor (n: 5): BRAZIL: Pará, Canaã dos Carajás, FLONA Carajás (UFMG 10155, 10750), Ourilândia do Norte (MCN-MQ 463), Parauapebas, Mina do Alemão (UFMG 10253, 10254).

Artibeus fimbriatus (n: 10): BRAZIL: Minas Gerais, Caeté, Morro Vermelho, Mina Apolo (UFLA 338, 362, 373), Viçosa, EPTEA Mata do Paraíso (MZUFV 2543, 2548, 2600, 2672, 2683, 5147, 5148)

Artibeus lituratus (n: 10): BRAZIL: Minas Gerais, Belo Horizonte (MCN-MQ 334), Betim (MCN-MQ 18, 21), Caeté, Morro Vermelho, Mina Apolo (UFLA 361), Itabira (MCN-MQ 532, 535), Viçosa, EPTEA Mata do Paraíso (MZUFV 1494, 1511, 1516, 1517).

Artibeus obscurus (n: 12): BRAZIL: Maranhão, São Luís, Ponta da Madeira (MCN-MQ 111). Minas Gerais, Belo Horizonte (MCN-MQ 333), Caeté, Morro Vermelho, Mina Apolo

(UFLA 337), Conceição do Mato Dentro (UFLA 1757), Viçosa, EPTEA Mata do Paraíso (MZUFV 4927, 4928, 5077, 5142, 5144-5146). *Rondonia*, Porto Velho (MCN-MQ 231).

Artibeus planirostris (n: 8): BRAZIL: *Ceará*, Fortaleza, UTE Setentrional-Pecém (MCN-MQ 72, 81). *Maranhão*, São Luís (MCN-MQ 263), São Luís, Ponta da Madeira (MCN-MQ 261). *Minas Gerais*, Leme do Prado, Posses, UHE Irapé (MCN-MQ 53), Pompéu UHE Retiro Baixo (MCN-MQ 130), São José da Lapa (MCN-MQ 422). *Pará*, Ourilândia do Norte (MCN-MQ 474).

Carollia perspicillata (n: 10): BRAZIL: *Bahia*, Porto Seguro (MZUFV 379). *Minas Gerais*, Betim (MCN-MQ 20, 22), Itabira (MCN-MQ 533, 534), Parque Estadual do Rio Doce (MZUFV 3-968), Parque Estadual Serra do Brigadeiro, Fazenda Brigadeiro (MZUFV 2166), São José da Lapa (MCN-MQ 407), Serro (MCN-MQ 472), Uberaba, UHE Volta Grande (MZUFV 1759).

Chiroderma doriae (n: 8): BRAZIL: *Goiás*, Itumbiara (MCN-MQ 145). *Minas Gerais*, Itambé do Mato Dentro, Serra do Cipó (MZUFV 4162), Pompéu (MCN-MQ 253), Rio Piracicaba (MCN-MQ 513). *São Paulo*, Ilha Anchieta (MZUSP 29456), Iporanga, Parque Estadual Turístico do Alto do Ribeira, Caverna Morro Preto (MZUSP 34012), Parelheiros, Parque Cratera (MZUFV 5801), Ubatuba, Parque Estadual Ilha Anchieta (MZUSP 31852).

Chiroderma trinitatum (n: 3): BRAZIL: *Pará*, Parauapebas, Fazenda Bocaina (UFMG 10642), Rio Xingu (MZUSP 35033). *Rondonia*, Monte Negro/Cacaulândia, Rio Janari (MZUSP 35026).

Chiroderma villosum (n: 7): BRAZIL: *Espírito Santo*, Aracruz, Restinga Aracruz Celulose (MZUSP 35032), Linhares, Fazenda Santa Teresinha (MZUSP 35030, 35031). *Minas Gerais*, Caratinga, PCH Areia Branca (MZUFV 3119), Pompéu, UHE Retiro Baixo (MCN-MQ 128). *Piauí*, Serra das Confusões, Acampamento 2 (MZUSP 33502). *Tocantins*, São Salvador, UHE São Salvador (MZUSP 35097).

Mesophylla macconelli (n: 3): BRAZIL: *Mato Grosso*, Aripuanã (UFMG 6749). *Rondonia*, Pedra Branca (MZUSP 22903). *Roraima*, BR-174, Marco de Fronteira BV-8 (MZUSP 22332).

Micronycteris microtis (n: 5): BRAZIL: *Minas Gerais*, Barão de Cocais (MCN-MQ 489, 490), Belo Horizonte (MCN-MQ 323), Viçosa (MZUFV 373).

Phyllostomus hastatus (n: 10): BRAZIL: *Ceará*, Ubajara, Gruta Araticon (UFMG 5278, 5304). *Maranhão*, São Luís, Parque Estadual Bacanga (UFMG 3593, 3598). *Minas Gerais*, Conceição do Mato Dentro (MCN-MQ 269), Formoso, Bela Lorena (UFMG 3435), Sabará, Roça Grande, Fazenda Experimental Agroecológica Izabela Hendrix (UFMG 3533), São Gonçalo do Rio Abaixo, Estação de Pesquisa e Desenvolvimento Ambiental de PETI (UFMG 4884), São Gotardo (UFMG 4681), Viçosa, Universidade Federal de Viçosa, Pomar do Fundão (MZUFV 4881).

Platyrrhinus aurarius (n: 1): BRAZIL: *Amazonas*, Barcelos, Missão Marari, Rio Katana (UFMG 3534).

Platyrrhinus brachycephalus (n: 1): BRAZIL: *Amazonas*, Boca do Canumã (MZUSP 14125).

Platyrrhinus fusciventris (n: 9): BRAZIL: *Amazonas*, Iranduba, Reserva de Desenvolvimento Sustentável Rio Negro (MZUSP 36401, 36402). *Goiás*, São Simão (UFMG 5061, 5315), Paranaiguara (UFMG 5450). *Minas Gerais*, Felixlândia (UFMG 5968). *Pará*, Canaã dos Carajás, FLONA Carajás (UFMG 5842), Ourilândia do Norte (MCN-MQ 456), Parauapebas, Mina do Alemão (UFMG 10239).

Platyrrhinus incarum (n: 9): BRAZIL: *Amazonas*, Iranduba, Reserva de Desenvolvimento Sustentável Rio Negro (MZUSP 36403). *Minas Gerais*, Conceição do Mato Dentro (UFLA 2138). *Mato Grosso*, Poconé, Pousada Jofre Velho (MZUFV 5177, 5178). *Pará*, Marabá, Vila União (MCN-MQ 395), Ourilândia do Norte (MCN-MQ 449, 476). *Rondônia*, Porto Velho (MCN-MQ 222, 234).

Platyrrhinus lineatus (n: 10): BRAZIL: *Espírito Santo*, Linhares (MZUFV 1673). *Minas Gerais*, Arinos, Fazenda Rui Lage, Ribeirão Areia (MZUFV 3444, 3446, 3455), Belo Horizonte (MCN-MQ 345), Caeté, Morro Vermelho, Mina Apolo (UFLA 385), Januária, APA Pandeiros (MZUFV 2482), Viçosa (MZUFV 1671, 1679, 1708).

Platyrrhinus recifinus (n: 10): BRAZIL: *Minas Gerais*, Araponga, Parque Estadual Serra do Brigadeiro (MZUFV 1857), Caeté, Morro Vermelho, Mina Apolo (UFLA 384), Ervália, Careço (MZUFV 4875), Itabira, Fazenda Maquiné (UFLA 549), Mariana, Fazenda Lavoura (MZUFV 4882), Viçosa, EPTEA Mata do Paraíso (MZUFV 2530, 2592, 2673, 4321), Viçosa, Mata do Seu Nico (MZUFV 4038).

Pteronotus rubiginosus (n: 10): BRAZIL: *Pará*, Canaã dos Carajás / Curionópolis, Fazenda Senhor Veloso (UFMG 10197), Canaã dos Carajás, FLONA Carajás, Serra Sul (UFMG 10067, 10097, 10110, 10112, 10114, 10128, 10261), Parauapebas, Fazenda do Mauro (UFMG 10059) Parauapebas, Portaria Alvo 118 (UFMG 10056).

Pygoderma bilabiatum (n: 10): BRAZIL: *Minas Gerais*, Caeté, Morro Vermelho, Mina Apolo (UFLA 2296, 2297), Conceição do Mato Dentro (UFLA 1627, 1758), Viçosa, Universidade Federal de Viçosa (MZUFV 5032). *Paraná*, indet. (MZUSP 5863). *São Paulo*, Iguapé, (MZUSP 22193), Itapetininga (MZUSP 16428), Ubatuba, Parque Estadual Ilha Anchieta (MZUSP 31855), Ilha Anchieta (MZUSP 29437).

Rhinophylla pumilio (n: 7): BRAZIL: *Bahia*, Macarani, Reserva Mata do Passarinho (UFMG 7514). *Espírito Santo*, Domingos Martins (UFMG 7657). *Mato Grosso*, Aripuanã (UFMG 6746). *Pará*, Parauapebas, Fazenda do Mauro (UFMG 10060, 10085), Parauapebas, Mina do Alemão (UFMG 10229). *Rondônia*, Porto Velho (MCN-MQ 243).

Sturnira giannae (n: 2): BRAZIL: *Pará*, Parauapebas, Portaria Alvo 118 (UFMG 10055), Santana do Araguaia, Fazenda Fartura (MZUSP 36547).

Sturnira lilium (n: 10): BRAZIL: *Minas Gerais*, Betim (MCN-MQ 16, 23, 24), Caratinga, PCH Areia Branca (MZUFV 3112), Ervália, Careço (MZUFV 4876), Itabira (MCN-MQ 480), São José da Lapa (MCN-MQ 417, 419), Viçosa, Universidade Federal de Viçosa, Pomar do Fundão (MZUFV 4889). *São Paulo*, São Lourenço da Serra, Sítio Piraquara (MZUSP 36477).

Sturnira tildae (n: 3): BRAZIL: *Mato Grosso*, Aripuanã (UFMG 3387). *Rondônia*, Porto Velho (MCN-MQ 242). *São Paulo*, Iporanga, Parque Estadual Turístico Alto do Ribeira (MZUSP 33980).

Uroderma bilobatum (n: 5): BRAZIL: *Mato Grosso*, Porto Estrela, Estação Ecológica da Serra das Araras (MZUSP 35989, 35990). *Pará*, Barcarena, UTE Barcarena (MCN-MQ 58), Ourilândia do Norte (MCN-MQ 444, 446).

Uroderma magnirostrum (n: 6): BRAZIL: *Minas Gerais*, Belo Horizonte (MCN-MQ 339, 341). *Mato Grosso*, Vila Rica, Fazenda Ipê (MZUSP 29086). *Pará*, Marabá, Vila União (MCN-MQ 389), Ourilândia do Norte (MCN-MQ 450). *Piauí*, Bom Jesus, Estação Ecológica de Uruçuí (MZUSP 30258).

Vampyressa pusilla (n: 10): BRAZIL: *Minas Gerais*, Belo Horizonte (MCN-MQ 331), Conceição do Mato Dentro (UFLA 1755, 1756, 2132), Ervália, Careço (MZUFV 5063, 5064), Grão Mogol (MCN-MQ 267), Laranjal / Recreio, UHE Barra do Braúna (MZUFV 3024), Santa Cruz do Escalvado / Rio Doce, Fazenda Floresta (MZUFV 4480), Viçosa (MZUFV 1710).

Vampyriscus bidens (n: 9): BRAZIL: *Mato Grosso*, Alta Floresta, Rio Teles Pires (MZUSP 28237). *Pará*, Barcarena, UHE Barcarena (MCN-MQ 55), Itaituba (MZUSP 12285). *Rondônia*, Cacaulândia (MZUSP 36528), Cachoeira de Nazaré, Rio Ji-paraná (MZUSP 20246 – 20249), Porto Velho (MCN-MQ 230).

Vampyriscus brocki (n: 8): BRAZIL: *Amazonas*, Iranduba, Reserva de Desenvolvimento Sustentável Rio Negro (MZUSP 36412), Manaus, Museu da Amazônia (MZUSP 36413). *Pará*, Canaã dos Carajás, FLONA Carajás, Serra do Tarzan (UFMG 10184, 10657, 10687), Marabá, Vila União (MCN-MQ 393), Ourilândia do Norte (MCN-MQ 443), Parauapebas, FLONA Carajás, Serra Norte (UFMG 10688).

Vampyrodes caraccioli (n: 2): BRAZIL: *Pará*, Ourilândia do Norte, Área Indígena Kaiapó (MZUSP 29149), Parauapebas, Mina do Alemão (UFMG 10215).

8	Tip of the lower incisors	Simple or slightly bilobed	Trilobed		CSP	Tavares 2008 (184)
UPPER CANINE						
9	Mesial-distal width of C relative to P4	Larger	Subequal or smaller		TSP	This study
10	Diastema between C and P3	Absent	Present		DTO	Lim 1993 (11)
LOWER CANINE						
11	Diastema between c and p2	Absent	Present		DTO	Tavares 2008 (255)
UPPER PREMOLARS						
12	Height relative to mesial-distal width of P3	Larger	Subequal	Smaller	TSP	Tavares 2008 (198)
13	Labial-lingual axis relative to mesial-distal axis of P3	Subequal	Larger	Smaller	TSP	Garbino 2019 (35)
14	Height of P3 relative to P4	More than 2/3	Less than 2/3	P3 larger than P4	TSP	Velazco 2005 (27)
15	Labial cingulum on P3	Present	Absent		CCP	This study
16	Postparaconule crista on P3	Absent	Present		CCP	This study
17	Diastema between P3 and P4	Absent	Present		DTO	Wetterer et al. 2000 (71)
18	Lateral opening between upper and lower premolars	Absent	Present		DTO	Tavares 2008 (261)
19	Labial cingulum on P4	Present	Absent		CCP	Tavares 2008 (203)
20	Metacone of P4	Absent	Present		CSP	Lim 1993 (6)
21	Protocone of P4	Present	Absent		CSP	Fracasso et al. 2011 (27)

22	Mesostyle of P4	Absent	Present		CSP	Tavares 2008 (204)
23	Postparaconule crista on P4	Absent	Present		CCP	Velazco 2005 (30)
24	Mesoconule crista on P4	Absent	Present		CCP	Velazco 2005 (29)
25	Diastema between P4 and M1	Absent	Present		DTO	Lim 1993 (11)
LOWER PREMOLARS						
26	Height relative to mesial-distal width of p2	Subequal	Smaller	Larger	TSP	Tavares 2008 (208)
27	Position of the protoconid of p2 in lateral view	Aligned on the central axis	Mesially displaced		CSP	Garbino 2019 (59)
28	Labial cingulid on p2	Present	Absent		CCP	Garbino 2019 (52)
29	Mesiodistal length of p2 relative to p4	Subequal or larger	Smaller		TSP	Garbino 2019 (54)
30	Height of p2 relative to p4	Approximately equal	Larger	Smaller	TSP	Garbino 2019 (55)
31	Diastema between p2 and p4	Absent	Present		DTO	Lim 1993 (11)
32	Hypoconid of p4	Absent	Present		CSP	Garbino 2019 (61)
33	Height relative to mesial-distal width of p4	Subequal	Larger		TSP	This study
34	Position of the protoconid of p4 in lateral view	Aligned on the central axis	Mesially displaced		CSP	Garbino 2019 (60)
35	Labial cingulid on p4	Present	Absent		CCP	Velazco 2005 (49)

UPPER MOLARS						
36	Position of the paracone and metacone of the molars	Centered on mesial-distal axis	Labially displaced		CSP	Wetterer et al. 2000 (60)
37	Mesoconule crista on M1	Absent	Present		CCP	Velazco 2005 (35)
38	Mesoconule on M1	Absent	Present		CSP	Velazco 2005 (36)
39	Talon of M1	Present	Absent		CCP	Tavares 2008 (218)
40	Hypocone on M1	Present	Absent		CSP	Owen 1987 (14)
41	Labial cingulum on M1	Absent	Present		CCP	Tavares 2008 (215)
42	Talon of M2	Present	Absent		CCP	Tavares 2008 (223)
43	Hypocone on M2	Present	Absent		CSP	Fracasso et al. (2011)
44	Mesoconule crista on M2	Absent	Present		CCP	Tavares 2008 (226)
45	Mesoconule on M2	Absent	Present		CSP	Velazco 2005 (44)
46	Labial cingulum on M2	Absent	Present		CCP	This study
47	M3	Present	Absent		DTO	Owen 1987 (15)
48	Labial-lingual length of M3 relative to M2	Subequal	Less than 2/3		TSP	Tavares 2008 (229)
LOWER MOLARS						
49	Mesiodistal length of m1 relative to p4	Larger	Subequal		TSP	Garbino 2019 (63)
50	Height of m1 relative to p4	More than 2/3	Less than 2/3		TSP	Garbino 2019 (64)

51	Mesiodistal length of m1 relative to m2	Subequal	Larger	Smaller	TSP	Garbino 2019 (62)
52	Displacement of the protoconid of m1	Not displaced	Mesially displaced		CSP	Tavares 2008 (234)
53	Paraconid on m1	Present	Absent		CSP	Lim 1993 (9)
54	Metaconid on m1	Present	Absent		CSP	Lim 1993 (9)
55	Entoconid on m1	Present	Absent		CSP	Lim 1993 (9)
56	Labial cingulid on m1	Present	Absent		CCP	Velazco 2005 (69)
57	Lingual cingulid on m1	Absent	Present		CCP	Velazco 2005 (53)
58	Paraconid on m2	Present	Absent		CSP	Garbino 2019 (53)
59	Entoconid on m2	Present	Absent		CSP	Tavares 2008 (240)
60	Development of the hypoconid on m2	Well developed	Less developed		CSP	Velazco 2005 (69)
61	Hypoconulid on m2	Absent	Present		CSP	Tavares 2008 (242)
62	Labial cingulid on m2	Present	Absent		CCP	Velazco 2005 (58)
63	Lingual cingulid on m2	Absent	Present		CCP	Velazco 2005 (58)
64	m3	Present	Absent		DTO	Owen 1987 (22)
65	Mesial-distal axis of m3 relative to m2	More than 1/4	Less than 1/4		TSP	Tavares 2008 (244)
GENERAL FORM						
66	Shape of the dental arch	Subtriangular	Sub square	Subcircular	DTO	This study

<i>Micronycteris microtis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phyllostomus hastatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carollia perspicillata</i>	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1
<i>Rhinophylla pumilio</i>	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1
<i>Sturnira tildae</i>	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1
<i>Sturnira lilium</i>	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1
<i>Sturnira giannae</i>	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	1
<i>Artibeus concolor</i>	0	0	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus lituratus</i>	0	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus fimbriatus</i>	0	0	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus obscurus</i>	0	0	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus planirostris</i>	0	0	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus cinereus</i>	0	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus anderseni</i>	0	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Artibeus gnomus</i>	0	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Ametrida centurio</i>	0	0	1	1	0	2	0	0	0	0	0	1	1	1	0	1	1	1	0	0
<i>Pygoderma bilabiatum</i>	0	1	1	1	0	2	0	0	0	0	0	1	1	1	0	1	1	1	0	0
<i>Uroderma bilobatum</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Uroderma magnirostrum</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0
<i>Vampyrodes caraccioli</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	1	0	1	1	1	0	1
<i>Platyrrhinus aurarius</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	1	0	1	1	1	0	1

<i>Platyrrhinus lineatus</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	1
<i>Platyrrhinus brachycephalus</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	1
<i>Platyrrhinus recifinus</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	1
<i>Platyrrhinus incarum</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	1
<i>Platyrrhinus fusciventris</i>	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	1	1	0	1
<i>Mesophylla macconnelli</i>	1	0	1	1	1	0	1	0	1	2	1	0	0	1	0	1	1	1	1	1
<i>Vampyressa pusilla</i>	1	0	1	1	1	0	1	0	1	2	1	0	0	1	0	1	1	1	1	1
<i>Vampyriscus brocki</i>	1	0	1	1	1	1	1	0	1	2	1	0	0	1	0	1	1	1	1	1
<i>Vampyriscus bidens</i>	1	1	1	1	1	1	1	0	1	2	0/1	0	0	1	0	1	1	1	1	1
<i>Chiroderma doriae</i>	1	1	1	1	0	1	1	0	1	2	1	0	1	1	0	1	1	1	1	1
<i>Chiroderma trinitatum</i>	1	1	1	1	0	1	1	0	1	2	1	0	1	1	0	1	1	1	1	1
<i>Chiroderma villosum</i>	1	0	1	1	0	1	1	0	1	2	1	0	1	1	0	1	1	1	1	1

Taxon/Character	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Pteronotus rubiginosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Micronycteris microtis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phyllostomus hastatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carollia perspicillata</i>	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Rhinophylla pumilio</i>	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	1	1
<i>Sturnira tildae</i>	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1

<i>Sturnira lilium</i>	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0	1	0	1
<i>Sturnira giannae</i>	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0	1	0	1
<i>Artibeus concolor</i>	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	1	1	0	0	1
<i>Artibeus lituratus</i>	0	0	0	1	1	0/1	1	-	0	1	1	1	1	0	0	1	1	0/1	0	1
<i>Artibeus fimbriatus</i>	0	0	0	1	1	0/1	1	-	0	1	1	1	1	0	0	1	1	0/1	0	1
<i>Artibeus obscurus</i>	0	0	0	1	1	0/1	0/1	1	0	1	1	1	1	0	0	1	1	0	0	1
<i>Artibeus planirostris</i>	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	1	1	0/1	0	1
<i>Artibeus cinereus</i>	0	0	0	1	1	0	1	-	0	1	1	1	1	0	0	1	1	0/1	0	1
<i>Artibeus anderseni</i>	0	0	0	1	1	0	1	-	0	1	1	1	1	0	0	1	1	0/1	0	1
<i>Artibeus gnomus</i>	0	0	0	1	1	0	1	-	0	1	1	1	1	0	0	1	1	0	0	1
<i>Ametrida centurio</i>	0	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1
<i>Pygoderma bilabiatum</i>	0	0	0	1	1	0	0/1	1	0	1	1	1	0	0	0	0	1	1	0	1
<i>Uroderma bilobatum</i>	0	0	0	1	1	0	0	1	0	1	1	0	1	1	0	0	0	1	0	1
<i>Uroderma magnirostrum</i>	0	0	0	1	1	0	0	1	0	1	1	0	1	1	0	1	0	1	0	1
<i>Vampyrodes caraccioli</i>	1	0	1	1	1	1	1	-	0	1	2	0	0/1	0/1	0	0	0	0	0	1
<i>Platyrrhinus aurarius</i>	1	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1
<i>Platyrrhinus lineatus</i>	1	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0	0	1	0	1
<i>Platyrrhinus brachycephalus</i>	1	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1
<i>Platyrrhinus recifinus</i>	1	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1
<i>Platyrrhinus incarum</i>	1	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1
<i>Platyrrhinus fusciventris</i>	1	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1

<i>Mesophylla macconnelli</i>	0	1	1	0	1	0	1	-	1	1	2	0	1	1	1	1	0	1	0	1
<i>Vampyressa pusilla</i>	0	1	1	1	1	0	1	-	1	0	2	0	1	1	1	0	0	1	0	1
<i>Vampyriscus brocki</i>	1	1	1	1	1	1	1	-	1	1	2	0	1	1	1	0	0	1	0	1
<i>Vampyriscus bidens</i>	1	1	1	1	1	1	1	-	1	1	2	0	1	1	1	0	0	0/1	0	1
<i>Chiroderma doriae</i>	0	1	1	1	1	1	1	-	1	1	2	0	1	1	1	1	0	1	0	0
<i>Chiroderma trinitatum</i>	0	1	1	1	1	1	1	-	1	0	2	0	1	1	1	1	0	1	0	0
<i>Chiroderma villosum</i>	0	1	1	1	1	1	1	-	1	1	2	0	1	1	1	1	0	1	0	0

Taxon/Character	61	62	63	64	65	66
<i>Pteronotus rubiginosus</i>	0	0	0	0	0	0
<i>Micronycteris microtis</i>	0	0	0	0	0	0
<i>Phyllostomus hastatus</i>	0	0	0	0	0	0
<i>Carollia perspicillata</i>	0	0	0	0	0	0
<i>Rhinophylla pumilio</i>	0	1	0	0	0	0
<i>Sturnira tildae</i>	0	1	0	0	1	1
<i>Sturnira lilium</i>	0	1	0	0	1	1
<i>Sturnira giannae</i>	0	1	0	0	1	1
<i>Artibeus concolor</i>	0	0	1	0	1	1
<i>Artibeus lituratus</i>	0	0	1	0	1	1
<i>Artibeus fimbriatus</i>	0	0	1	0	1	1

<i>Artibeus obscurus</i>	0	0	1	0	1	1
<i>Artibeus planirostris</i>	0	0	1	0	1	1
<i>Artibeus cinereus</i>	0	1	1	1	-	1
<i>Artibeus anderseni</i>	0	1	1	1	-	1
<i>Artibeus gnomus</i>	0	1	1	0	1	1
<i>Ametrida centurio</i>	0	0	0	0	1	2
<i>Pygoderma bilabiatum</i>	0	0	0	0/1	1	2
<i>Uroderma bilobatum</i>	0	0	1	0	1	1
<i>Uroderma magnirostrum</i>	0	0	1	0	1	1
<i>Vampyrodes caraccioli</i>	0	0	1	0	1	1
<i>Platyrrhinus aurarius</i>	0	0	1	0	1	1
<i>Platyrrhinus lineatus</i>	0	0	1	0	1	1
<i>Platyrrhinus brachycephalus</i>	0	0	1	0	1	1
<i>Platyrrhinus recifinus</i>	0	0	1	0	1	1
<i>Platyrrhinus incarum</i>	0	0	1	0	1	1
<i>Platyrrhinus fusciventris</i>	0	0	1	0	1	1
<i>Mesophylla macconnelli</i>	0	0	1	0	1	0
<i>Vampyressa pusilla</i>	1	0	1	1	-	0
<i>Vampyriscus brocki</i>	1	0	1	1	-	0
<i>Vampyriscus bidens</i>	1	0	1	0	1	0
<i>Chiroderma doriae</i>	1	0	1	1	-	0

<i>Chiroderma trinitatum</i>	1	0	1	1	-	0
<i>Chiroderma villosum</i>	1	0	1	1	-	0