COMPARATIVE MORPHOLOGY OF THE TONGUE AND PALATE IN NOCTILIONIDAE AND MORMOOPIDAE (CHIROPTERA: NOCTILIONOIDEA).

Eliana A. Gimenez
Departamento de Sistemática e Ecologia, CCEN, Universidade Federal da Paraíba, Cidade Universitária, 58059-900, João Pessoa-PB. gimenez_e@yahoo.com.br
Hebert Ferrarezzi
Laboratório de Herpetologia, Instituto Butantan, Av. Vital Brasil, 1500, São Paulo-SP. hferrarezzi@butantan.gov.br.
Alfredo Langguth
Departamento de Sistemática e Ecologia, CCEN,Universidade Federal da Paraíba, Cidade Universitária, 58059-900, João Pessoa-PB. alfredo@dse.ufpb.br

RESUMO

Morfologia comparada da língua e do palato em Noctilionidae e Mormoopidae (Chiroptera: Noctilionoidea). Descreve-se a anatomia macroscópica da superfície da língua e palato em representantes de Noctilionidae e Mormoopidae. A superfície do dorso e da região faringea da língua estão cobertas por papilas estruturalmente diferenciadas e agrupadas de acordo com sua função. As sinapomorfias de Noctilionidae são: papilas fungiformes restritas a séries longitudinais laterais; papilas cornificadas aumentadas formando um agrupamento volumoso; papilas medio-posteriores escamosas, em fileiras diagonais regulares; rugas palatais estreitas, número aumentado a 11-12; todas as rugas do palato não divididas. As sinapomorfias de Mormoopidae são: papilas cornificadas reduzidas formando um pequeno agrupamento na região apical da língua.

Palavras-chave: Noctilionidae, Mormoopidae, língua, palato, morfologia.

ABSTRACT

Comparative Morphology of the Tongue and Palate in Noctilionidae and Mormoopidae (Chiroptera: Noctilionoidea). The gross anatomy of the tongue's surface and palate in representatives of Noctilionidae and Mormoopidae are described. The surface of dorsum and pharyngeal region of the tongue are covered by a number of structurally differentiated papillae, grouped according to their function. Synapomorphies for Noctilionidae are: fungiform papillae restricted to a lateral longitudinal series; horny papillae enlarged, forming a large cluster; mid-posterior papillae scale-like, in regular

diagonal rows; increased number of narrow palatal ridges 11-12; all palatal ridges undivided. Synapomorphies for Mormoopidae are: Horny papillae reduced, forming a small cluster at the apical region of the tongue.

Key Words: Noctilionidae, Mormoopidae, tongue, palate, morphology

INTRODUCTION

The superfamily Noctilionoidea comprises the New World bat families Noctilionidae, Mormoopidae, Phyllostomidae, and the New Zealand Mystacinidae (VAN DEN BUSSCHE and HOOFER 2000; SIMMONS and CONWAY 2001). Noctilionidae has a single genus with two recent species and Mormoopidae consist of two genera with eight recent species, while the much more diverse Phyllostomidae groups about 49 genera and more than 140 species (KOOPMAN 1993; SIMMONS 1998; WETTERER *et al.* 2000). Noctilionoid bats share morphological (WALTON and WALTON 1968; SMITH 1972, 1976; HOOD and SMITH 1982), and karyological (PATTON and BAKER 1978), derived features, which strongly associate the three families as a monophyletic group, excluding the Mystacinidae (FERRAREZZI and GIMENEZ 1996; SIMMONS 1998).

On the other hand modern cladistic studies, based on morphological, molecular and total evidence approaches, have indicated a close association between Noctilionidae, Mormoopidae, Phyllostomidae and Mystacinidae (PIERSON *et al.* 1986; KIRSCH *et al.* 1998; KENNEDY *et al.* 1999; VAN DEN BUSSCHE and HOOFER 2000; SIMMONS and CONWAY 2001; VAN DEN BUSSCHE *et al.* 2002).

Anatomical characters of the tongue may be very useful to study phylogeny. However, the characters of the tongue in the order Chiroptera are not well known, studies are confined to some groups of Phyllostomidae and isolated descriptions in species belonging to a few other non-noctilionoid families. GREGORIN (2003) described and compared the tongue of the members of Molossidae, Mystacinidae and four Vespertilionidae, and observed that papillae present in *Mystacina robusta* remind more those of Phyllostomidae.

The knowledge on structural and functional morphology of the tongue within the Noctilionoidea has been addressed mainly to the nectarivorous (PARK and HALL 1951; GLASS 1970; GREENBAUM and PHILLIPS 1974; HOWELL and HODGKIN 1976; GRIFFITHS and CRILEY 1989; GIMENEZ *et al.* 1996) and sanguivorous (MANN 1950; VILLA, 1957; UIEDA 1986) phyllostomids. PARK and HALL (1951) compared the tongue, palate and the

gastric tract among seven species of Phyllostomidae, making some correlations with the different feeding habits of each one. GRIFFITHS (1982) compared the superficial morphology and histology of the tongue and hyoid apparatus among the glossophagine- phyllonicterine genera and a few other Phyllostomidae, defining many systematic characters. E. A. Gimenez, in an unpublished dissertation of 1993, described general features of the tongue for several bat families and made an extensive comparative study of its morphology in representatives of the three noctilionoid families. This comparative data, is partially published here for the first time,

Another structure functionally related to the tongue, and in the same way important to the manipulation of the alimentary bolus, is the soft palate. PARK and HALL (1951) observed in some insectivorous and nectarivorous Microchiroptera, that the width of the median groove of the palate seems to depend on the feeding habits of the bats. EISENTRAUT (1976) studied the morphology of the palate in several orders of mammals, including bats, recognizing two basic structural patterns of palatal ridges: the primary or simple type present in most groups, including the order Chiroptera, is formed of transverse ridges, usually slightly convex forward, crossing the entire palate (EISENTRAUT, 1976); the second pattern where the ridges are more numerous and very close, is present in some orders as Cetacea, Lagomorpha, Perissodactyla, Artiodactyla, Tubulidentada, and Hyracoidea. According to EISENTRAUT (1976) it is difficult to determine the relationship of the pattern of ridges of the palate with the feeding habits.

In this paper we conduct a comparative study of the gross morphology of tongue and palate in representatives of the families Noctilionidae and Mormoopidae, with references to the related Phyllostomidae. Our goal is to find new diagnostic characters of the taxa, trace structural homologies, and attempt to find a pattern of taxonomic distribution of structures, in order to better understand their phylogenetic meaning.

MATERIAL AND METHODS

We have studied the tongue and soft palate gross morphology of species of Noctilionidae, *Noctilio leporinus, N. albiventris* and species representing all genera and subgenera of Mormoopidae, *Mormoops megalophylla; Pteronotus (Pteronotus) davyi, P. (Pteronotus) gymnonotus, P. (Chilonycteris) personatus, P. (Phyllodia) parnelli*. In addition, we have examined at least four tongues of representatives of all subfamilies and most genera of the related Phyllostomidae (see Appendix for origin and number of specimens

examined).

The tongues were removed from ethanol preserved, formalin fixed specimens, by incision at the level of the glottis and along the mandibles, and then have been kept individually in small vials containing glycerinated 70% ethanol. Structures were observed and photographed under a stereomicroscope. The terminology for lingual structures used herein follows that of SONNTAG (1920, 1925); PARK and HALL (1951); GREENBAUM and PHILLIPS (1974); GRIFFITHS (1982); and GIMENEZ *et al.* (1996), with some adjustments for proper designation of specific features (see below).

RESULTS

General morphology of Chiropteran tongue

On the dorsal surface of the tongue we may distinguish two main regions limited by the imaginary line that cross the vallate or circumvallate papillae. They are a) the surface of the basal or pharyngeal portion and b) the dorsum or dorsal surface of the lingual body (*corpus linguae*) including the tip or apex. In turn, the dorsum may be divided in an anterior (mid-anterior region), and a posterior (mid-posterior region). The last has been called “posterior middle region” by PARK and HALL (1951) or “medial-posterior region” by GIMENEZ *et al.* (1996); and WETTERER *et al.* (2000). We consider also the lateral surface of the body on both sides.

The Form of the Tongue. In Noctilionidae and Mormoopidae the tongue is, usually, not much elongated, with the pharyngeal portion wider and the narrower body something elongated and flattened dorsally. The dorsal and lateral surfaces are covered by structurally and functionally differentiated papillae, distributed in specific areas. The ventral surface of the free portion of the tongue is, as in other mammals, smooth, lacking any kind of papillae.

The Gustative Papillae. There are two basic types of gustative papillae, without mechanical function, which present gustative buttons, carrying out the function of taste. a) The **circumvallate papillae** (Fig. 1, 3A), located between the pharyngeal region of the tongue and the *dorsum*. They are usually large, and of circular to elliptical shape, consisting of a well developed internal pair, named medial vallate papillae, and an external pair, often not so much developed, named lateral vallate papillae. These papillae are usually large, something salient, and surrounded by a deep circular or oval sulcus denominated “vallum”. b) The **fungiform papillae**, that are moderate to small sized, variable in number and location, being often irregularly distributed, mainly

on the mid-posterior region of the dorsum and lateral surface of the tongue, surrounded by mechanical papillae. They have a fleshy globose aspect, with lighter coloration, and are often quite salient on the lingual surface, emerging amongst the scale-like or fleshy, filiform mechanical papillae (Fig. 2C, 3D).

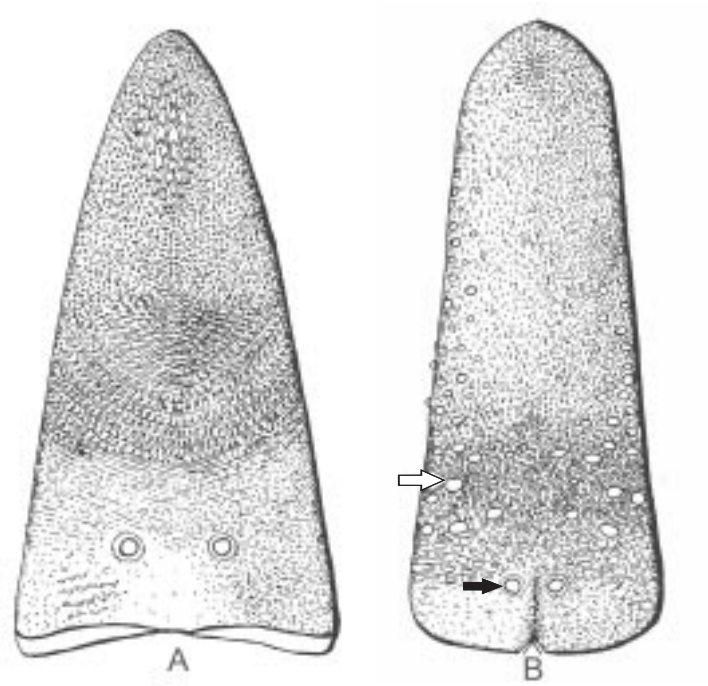

Figure 1 - Dorsal view of the tongue. A= *Noctilio leporinus* (DZUNESP 32), B= *Pteronotus (Phyllodia) parnellii* (DZUNESP 12318). Solid arrow = medial circumvallate papilla, open arrow = fungiform papilla.

The Mechanical Papillae. These papillae exhibit a large morphological diversity, being differentiated according to the position that they occupy in the surface of the tongue and having different functions. In the pharyngeal region of the tongue, behind the circumvallate papillae, there are fleshy filiform mechanical papillae. They are variable in form, directed posteriorly or without defined orientation. This kind of papillae has not been described nor properly named in former studies on lingual morphology of Chiroptera. The fleshy mechanical papillae of the pharyngeal portion of the tongue are here denominated the **basal papillae**. They exhibit different character states, from rudimentary and poorly distinct to plentiful developed, but generally arranged as a pair of clusters placed dorso-laterally, just behind the circumvallate papillae,

leaving the medial area bare (Fig. 1A). The papillae of the mid-posterior region of the *dorsum* of the tongue are generally differentiated, fleshier and larger than the scale-like mechanical papillae (see below) of the mid-anterior region. They form numerous and distinct groupings in front of the circumvallate papillae and for about half of the *dorsum*. In order to distinguish them from the other mechanical papillae, they are here denominated **mid-posterior fleshy papillae** (Fig. 1, 2E). They show varied form and direction, having fringed borders, bifid or smooth single point, with or without a dorsal depression, according to the taxon. Certain species, however, do not show differentiation between the mid-posterior fleshy papillae and the scale-like mechanical papillae.

The **scale-like mechanical papillae** cover the mid-anterior part of the

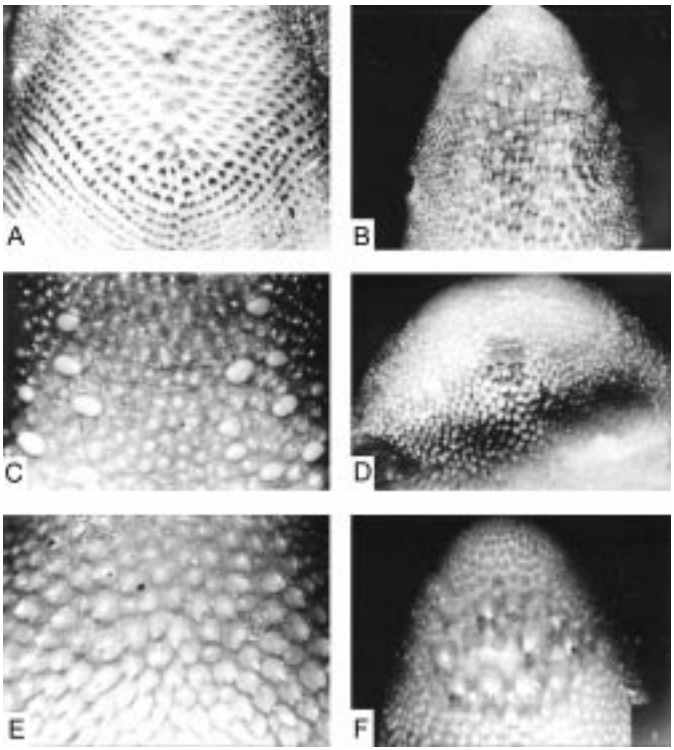

Figure 2 - Mid-posterior region and apex of tongue. A= *Noctilio leporinus*, scale-like mechanical papillae; B= *Noctilio leporinus*, developed horny papillae cluster; C= *Pteronotus (Phyllodia) parnellii* fungiform papillae among mechanical papillae; D= *Pteronotus (Phyllodia) parnellii*, reduced horny papillae; E= *Tonatia bidens* mid-posterior fleshy papillae with dorsal depression; F= *Tonatia bidens* moderate horny papillae.

dorsum of the tongue, being smaller and more numerous. They are keratinized, elongated and flattened dorso-ventrally, fringed, single pointed or bifid, always directed backwards. The **horny papillae** represent a differentiated large mechanical papillae, extremely hard (keratinized), wide, dorso-ventrally flattened, generally bilobed, and forming a group located close to the tip or apex of the tongue (Fig. 2B, 2F). The horny papillae are always directed backwards, as the scale-like mechanical papillae that surround them.

Description of the tongue of Noctilionidae, Mormoopidae and some Phyllostomidae

The **pharyngeal region** of the tongue is short, wider than long in *Pteronotus and Mormoops*. The papillae are here absent along the lateral borders, the few basal papillae observed are fleshy and low, organized in several transverse rows behind the medial circumvallate papillae and giving a bare appearance to the region (Fig. 1, 3A, 3B). This bare mid-dorsal area of the base of the tongue extends slightly in front of the medial circumvallate papillae. In Noctilionidae and *Mystacina tuberculata* (Mystacinidae) (SIMMONS and CONWAY 2001) the pharyngeal region of the tongue is bare only in the medial portion (Fig. 1, 3A). The basal papillae are scarce and short, without defined direction, and organized in a few dorso-lateral rows. In Phyllostomidae the pharyngeal region is variable in length, may be completely covered with papillae, with papillae only in the lateral surface , or without papillae (Fig. 3C).

In the Noctilionoidea (including Noctilionidae, Mormoopidae and Phyllostomidae), there are two globose medial **vallate papillae** of relatively large size (Fig. 1). In *Mormoops* and *Pteronotus* there are also two lateral vallate papillae, moderately large, of elliptical form, and located on the lateral surface of the tongue, but in *Noctilio* they are absent (Fig. 1, 3A). Most members of Phyllostomidae (GIMENEZ *et al.* 1996; WETTERER *et al.* 2000) as well as *Mystacina tuberculata* (SIMMONS and CONWAY 2001) share these lateral vallate papillae.

In *Mormoops* and *Pteronotus* the **fungiform papillae** are distributed over the dorsum of the tongue, they are globose (Figs. 1B, 2C), large and numerous. In the species of Noctilionidae the fungiform papillae are scarce in number and reduced on the dorsal surface, but there is an array of longitudinally arranged fungiform papillae on the lateral region of the tongue(Fig. 3D). This characteristic is an apomorphy of the family (Fig. 5). In the phyllostomids the number and size of these papillae is variable.

In **the mid-posterior region** of the dorsum of the tongue we find mechanical papillae which are caudally arranged in rows or ridges (Figs. 1A,

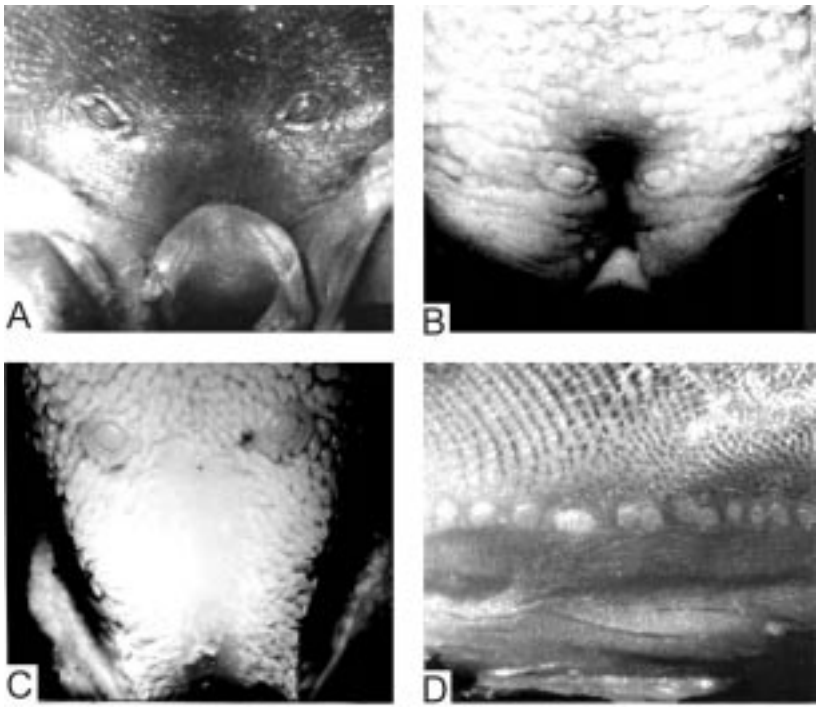

Figure 3 - Basal region of the tongue. A= *Noctilio leporinus*, short pharyngeal region and medial circumvallate papillae; B= *Pteronotus (Phyllodia) parnellii* short pharyngeal region and reduced basal papillae; C= *Tonatia bidens* long pharyngeal region with numerous basal papillae; D= *Noctilio leporinus* lateral fungiform papillae.

2A). In the lateral side of the tongue, the rows are bent backwards (Fig. 3D). In noctilionids, approximately 1/3 of the mid-posterior region of dorsum occupied with mid-posterior mechanical papillae is ridged. In the medial region the papillae become more pointed. Here the mechanical papillae are directed backwards, sharply and single pointed, (some bifid), flat, horny (not fleshy), in form of scales and arranged in several and distinct diagonal rows. The posteriormost rows are directed forward, while the anterior and the middle rows in the mid-posterior part of dorsum are directed to the center of the area (Figs. 1A, 2A). In *Mormoops* and *Pteronotus* the mid-posterior mechanical papillae are fleshy at the base with a deep dorsal circular depression, crater like, with the borders slightly fringed. The fringes have no defined direction in *Pteronotus* (Fig. 2D) but are directed toward the pharyngeal region in *Mormoops*. In Phyllostomidae the mechanical papillae of this part of the tongue are variable

in size and form: they may have a deep dorsal circular depression or may be single pointed, bifid and smooth.

As in Phyllostomidae, **the mid-anterior region** of the dorsum in Noctilionidae and Mormoopidae (Fig. 1) is densely covered by small scale-like mechanical papillae, which are elongated and tapered, single pointed or bifid being shorter and broader around the horny papillae. In *Mormoops megalophylla* these papillae are reduced in size.

In **the apical region** of the tongue of both species of *Noctilio* there is a very large elliptic cluster of enlarged, and slightly bifid horny papillae (Fig. 2B). In the two genera of Mormoopidae, horny papillae are present in this area, but are not so differentiated from surrounding scale-like papillae, and form just a small circular cluster. In the two species of *Mormoops* they are of different size. In *Pteronotus* the horny papillae are small (Fig. 2D) and in some Phyllostomidae they may be of moderate size (Fig. 2F). The large group of horny papillae present in *Noctilio* is unique among Noctilionoidea, shared only with (Fig. 5), *Vampyrum spectrum*.

Description of the soft palate in Noctilionidae, Mormoopidae, and some Phyllostomidae

The mucous membrane covering the hard palate is firm and has an stratified squamous epithelium, which adheres to the bone, lacking a submucosa. It possesses transverse palatine ridges (rugae palatinae), whose epithelium can be cornified. The number and width of the rugae vary from species to species, and according to the characteristics of the food (TULLBERG, 1899). They may be missing (Cetacea) or reduced in number (man).

PARK and HALL (1951) observed in some species of insectivorous and nectarivorous Microchiroptera that the posterior ridges of the palate, are divided, limiting a median groove that may be broad or narrow and that its width seems to depend on the food habits of the bat. According to these authors, bats with insectivorous and frugivorous habits have a narrow and shallow groove, while in nectarivorous bats it is wide and deep.

The palate of *Noctilio leporinus* has 11 to 12 narrow transverse ridges, not very convex. The first ridge is located near the canine tooth and is arch shaped. The ridges are complete, not divided. The 10th and 11th ridges form short arches, not reaching the dental series, but in one of the specimens the 11th ridge becomes divided by a narrow groove. *Noctilio albiventris* presents a pattern similar to that of *N. leporinus*, confirming the observation of

EISENTRAUT (1976) (Fig. 4A).

Mormoops megalophylla showed eight broad ridges. The less convex first ridge, is located in the same level as the canine teeth. The second and third ridges are covered by low papillae. The five remaining rugae are divided in two arms by a median, very narrow, groove and the arms are quite strongly arched as observed by EISENTRAUT (1976) (Fig. 4B).

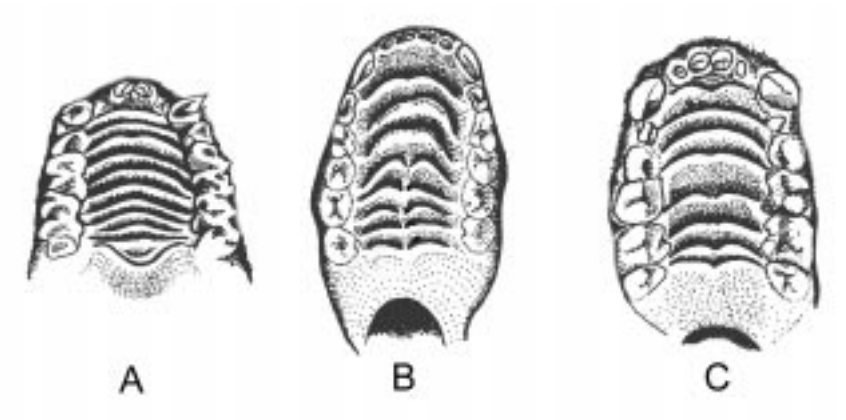

Figure 4 - Soft palate. A= *Noctilio albiventris* (UFPB 3897), B= *Mormoops megalophylla* (AMNH 144998), C= *Pteronotus (Phyllodia) parnellii* (UFPB 3786).

In *Pteronotus [Phyllodia] parnellii* eight thick palatal ridges were observed. The first 4 are complete, while the last four are divided by a shallow median groove (Fig. 4C). In *Pteronotus [Pteronotus] davyi* we found seven protuberant and complete palatal ridges. The first is located at the level of the canines. The fifth is less convex, and the sixth ridge bends backwards in the middle, and this area becomes very deep. The seventh ridge is narrow.

Comparison of the palate between members of the Noctilionidae and Mormoopidae reveals a number of differences. In Noctilionidae there is a higher number (11 - 12) of narrower, complete or undivided palatal ridges. In Mormoopidae, ridges vary from seven to eight, and they are divided and thicker, especially in *Mormoops megalophylla* (Fig. 4B).

The numbers and form of palate rugae in the Phyllostomidae is variable among species. *Lonchorhina aurita* bears eight thick ridges, the first three are smooth, and complete, the second is shorter. The fourth ridge is slightly concave and the remaining four are divided by a narrow groove. *Chrotopterus auritus* has eight rugae smooth and thick. The first seven are convex forward and divided and the last ridge is undivided. *Phyllostomus hastatus* has, according

to EISENTRAUT (1976), seven rugae, the first three are complete and narrow, while the last four are rather thick and convex forward, but are not divided by a groove. We examined the palate of *P. discolor* and observed that the third, fourth and fifth ridges are divided. In *Carollia perspicillata* there are six thick ridges forming a hump. The first and second are complete and undivided and the remaining four are divided. The last four ridges have the borders covered with a row of wartlike papillae as observed also by PARK and HALL (1951) and EISENTRAUT (1976). In *Artibeus jamaicensis* the first ridge projects forward and the second is bent backwards, both are complete. The three remaining ridges are divided. In the posterior region of the palate there is an area with irregular ridges also observed by PARK and HALL (1951) and EISENTRAUT (1976). In *Glossophaga soricina* there are eight broad and thick ridges, the first four are complete and the remaining four are divided. *Lichonycteris obscura* has seven thick and protuberant ridges. The first three are complete, the remaining four are divided by a deep median groove. One specimen of *Macrophyllum macrophyllum* observed by us showed six ridges, the first is complete and the others are broad and divided.

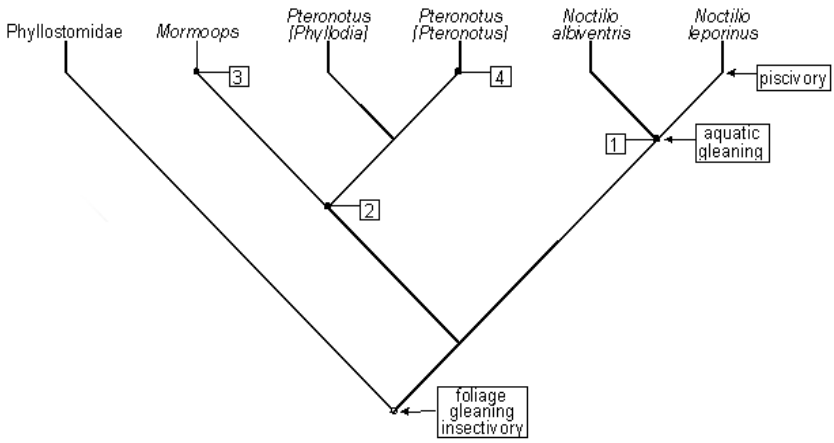

Figure 5. Cladogram showing the phylogenetic relationships among members of Noctilionidae and Mormoopidae (tree topology according to SIMMONS 1998). Numbers in nodes and terminals refers to character state transformations observed in tongue and palate morphology. See text for explanations. Major evolutionary changes in feeding habits are labeled at right.

DISCUSSION

The observation and comparison of the lingual and palatal structures between the species of Noctilionidae and Mormoopidae revealed the existence of variations both at the genus and the family levels. We included the inferred synapomorphies and autapomorphies in an available cladogram of Noctilionidae and Mormoopidae (SIMMONS 1998) and the results are shown in Fig. 5. Even so, the comparison with other families is necessary for a better understanding of the structural homology and evolutionary divergence of the transformation series.

The following character state transformations observed in tongue and palate are suggested. Numbers refers to nodes and terminals in cladogram of Fig. 5

0.- (Ancestral) Fungiform papillae spread out dorsally; Horny papillae developed, moderate cluster; Mid-posterior fleshy papillae fringed, crater/ basket-like, not placed in diagonal rows; Palatal ridges 6-8, moderately broad, and in part (or mostly) divided.

1.- Fungiform papillae restricted to a lateral longitudinal series; Horny papillae enlarged, forming an outsized cluster; Mid-posterior papillae scale-like, in regular diagonal rows; (Noctilionidae). Increased number of narrow palatal ridges 11-12; All palatal ridges undivided. (Noctilionidae).

2.- Horny papillae reduced, forming a small cluster. (Mormoopidae).

3.- Anterior scale-like papillae reduced in size (Mormoopidae). Palatal ridges broader. (Mormoops).

4.- Palatal ridges reduced to 6; All palatal ridges undivided.

From the present study we can conclude that, within a clade consisting of the Noctilionidae and Mormoopidae, the evolutionary divergence of lingual and palatal gross morphology follows a pattern of distribution better consistent with their phylogenetic relationships, rather than with the differentiation of feeding habits, that is also consistent with the phylogenetic pattern, but at another level of universality. See FERRAREZZI and GIMENEZ (1996) for a detailed analysis of the diversity and evolution of feeding habits within the Phyllostomidae.

The structural modifications of the tongue and palate observed in Noctilionidae, should be taken as synapomorphies at the level of genus and / or family and, therefore, they precede the origin of the piscivory. This feeding habit is an autapomorphy of *Noctilio leporinus* while its lingual morphology is shared with *N. albiventris*, which has maintained an insectivorous diet. Alternatively this could be better interpreted as an adaptation to aquatic surface gleaning habits, which is also synapomorphic at this level.

We hope that the report of such diversity of lingual surface and palate

structures encourage further studies on the much needed functional morphology of the tongue-palate complex in noctilionoid bats.

ACKNOWLEDGEMENTS

The first two authors are indebted to the late Valdir A. Taddei, from Universidade Estadual Paulista (UNESP), for introducing both of them to bat Systematics and by kindly allowing the use of his laboratory and valuable bat collection. They also thank the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) for support. The last author is indebted to the Conselho Nacional de Desenvolvimento Cientifíco e Tecnológico (CNPq) for a research fellowship. We thank Nancy Simmons (American Museum of Natural History) and Mario De Vivo (Museu de Zoologia da Universidade de São Paulo) for specimens loan and/or permission to examine material from the collections under their care. Alexandre R. Percequillo and Eulampio da Silva Neto kindly read the manuscript and made valuable suggestions.

REFERENCES

EISENTRAUT, M. 1976 - Das Gaumenfaltenmuster der Säugetiere und seine Bedeutung fur stammesgeschichtliche und taxonomische Untersuchungen. *Bonn. Zool. Monogr.* 8: 50-214.

FERRAREZZI H. and GIMENEZ, E.A. 1996 - Systematic patterns and evolution of feeding habits in Chiroptera (Archonta: Mammalia). *J. Comp. Biol.* 1(3/4): 75-94.

GIMENEZ, E.A., FERRAREZZI, H. and TADDEI, V.A. 1996 - Lingual morphology and cladistic analysis of the New World nectar-feeding bats (Chiroptera: Phyllostomidae). *J. Comp. Biol.* 1: 41-64.

GLASS, B.P. 1970 - Feeding mechanisms of bats; pp 84-92 *In:* Slaughter, B.H. and D.W. Walton (Eds.). **About Bats**. Southern Methodist Univ., Dallas.

GREENBAUM, I.F. and PHILLIPS, C.J. 1974 - Comparative anatomy and general histology of tongues of long-nosed bats (*Leptonycteris sanborni* and *L. nivalis*), with reference to infestation of oral mites. *J. Mamm.* 55(3): 489-504.

GREGORIN, R. 2003 - Comparative morphology of the tongue in free-tailed bats (Chiroptera, Molossidae). *Iheringia.* 93(2): 1-9.

GRIFFITHS, T. A. 1982 - Systematics of the New World nectar-feeding bats (Mammalia, Phyllostomidae), based on the morphology of the hyoid and lingual regions. *Amer. Mus. Novitates.* 2742: 1-45.

GRIFFITHS, T.A. and CRILEY, B.B. 1989 - Comparative lingual anatomy of the bats *Desmodus rotundus* and *Lonchophylla robusta* (Chiroptera:Phyllostomidae).

J. Mamm. 70(3): 608-613.

HOOD, C.S. and SMITH, J.D. 1982 - Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. *Syst. Zool.* 31(3):241-251.

HOWELL, D.J. and HODGKIN N. 1976 - Feeding adaptations in the hairs and tongues of nectar-feeding bats. *J. Morph.* 148: 329-336.

KENNEDY, M., PATTERSON, A.M., MORALES, J.C., PARSONS, S., WINNINGTON, A. P. and SPENCER, H.G. 1999 - The long and short of it: branch lengths and the problem of placing the New Zealand short-tailed bat, *Mystacina. Mol. Phylogenet. Evol.* 13: 405-416.

KIRSCH, J.A.W., HUTCHEON, J.M. BYRNES, D.G.P and LLOYD, B.D. 1998 - Affinities and historical zoogeography of the New Zealand short-tailed bat, *Mystacina tuberculata* Gray 1843, inferred from DNA-hybridization comparisons. *Jour. Mamm. Evol.* 5: 33-64.

KOOPMAN, K.F. 1993 - Order Chiroptera; pp. 137-241. *In*: D.E. WILSON and D.M. REEDER (Eds.). **Mammal species of the world, a taxonomic and geographic reference**. Smithsonian Inst., Washington, D.C.

MANN, G. 1950 - Succión de sangre por *Desmodus*. *Invest. Zool. Chilenas*. 1: 7-8.

PARK, H. and HALL. E.R. 1951 - The gross anatomy of tongues and stomachs of eight New World bats. *Trans. Kans. Acad. Sci.* 54: 64-72.

PATTON, J.C. and BAKER R.J. 1978 - Chromosomal homology and evolution of phyllostomoid bats. *Syst. Zool.* 27: 449-462.

PIERSON, E.D., SARICH, V.M., LOWENSTEIN, J.M., DANIEL M.J. and RAINEY W.E. 1986 - A molecular link between the bats of New Zealand and South America. *Nature*. 323: 60-63.

SIMMONS, N.B. 1998 - A reappraisal of interfamilial relationships of bats; pp. 3-26. *In:* T.H. Kunz and P.A. Racey. (Eds.) **Bats: biology and conservation**. Smithsonian Inst., Washington D.C.

SIMMONS, N.B. and CONWAY, T.M. 2001 - Phylogenetic relationships of mormoopid bats (Chiroptera: Mormoopidae) based on morphological data. *Bull. Amer. Mus. Nat. Hist.* 258: 1-97.

SMITH, J.D. 1972 - Systematics of the Chiropteran family Mormoopidae. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas*. 56: 1-132.

SMITH, J.D. 1976 - Chiropteran evolution. *Spec. Publ. Mus. Texas Tech Univ*. 10: 49-69.

SONNTAG, C.F. 1920 - The comparative anatomy of the tongues of the Mammalia. I. General description of the tongue. *Proc. Zool. Soc. London.* 1920: 115-129.

SONNTAG, C.F. 1925 - The comparative anatomy of the tongues of the Mammalia. XII. Summary, classification and phylogeny. *Proc. Zool. Soc. London.* 1925: 701-762.

TULLBERG, T. 1899 - Über das System der Nagethiere eine phylogenetische Studie. *Nova Acta regiae Societatis Scientiarum Upsaliensis*. Sér. 3, 18: 1-514.

UIEDA, W. 1986 - Aspectos da morfología lingual das três espécies de morcegos Hematófagos (Chiroptera, Phyllostomidae). *Rev. Brasil. Biol.* 46(3): 581-587.

VILLA, R.B. 1957 - El acto de tomar la sangre en los murciélagos hematofagos (family Desmodontinae). *An. Inst. Biol. Univ. Mex.* 28: 339-343.

VAN DEN BUSSCHE, R.A. and HOOFER, S.R. 2000 - Further evidence for inclusion of the New Zealand short-tailed bat (*Mystacina tuberculata*) within Noctilionoidea. *J. Mamm.* 81: 262-271.

VAN DEN BUSSCHE, R.A. HOOFER, S.R. and SIMMONS, N.B. 2002 - Phylogenetic relationships of mormoopid bat using mitochondrial gene sequences and morphology *J. Mamm.* 83: 40-48.

WALTON, D.W.; and WALTON, G.W. 1968 - Comparative osteology of the pelvic and pectoral girdles of the Phyllostomatidae (Chiroptera:Mammalia) *J. Grad. Res. Center Southern Methodist Univ.* 37: 1-35.

WETTERER, A. L., ROCKMAN, M.V. and SIMMONS, N.B. 2000 - Phylogeny of phyllostomid bats (Mammalia: Chiroptera) Data from diverse morphological systems, sex chromosomes, and restriction sites. *Bull. Amer. Mus. Nat. Hist.* 248: 1-200.

APPENDIX: Specimens Examined

The specimens examined belong to the following collections: Laboratório de Quiropterologia, Departamento de Zoologia da Universidade Estadual Paulista (UNESP), Campus de São José do Rio Preto-SP = **DZUNESP**. Museu de Zoologia da Universidade de São Paulo. São Paulo = **MZUSP**. Departamento de Sistemática e Ecologia da Universidade Federal da Paraíba João Pessoa = **UFPB**. Department of Mammalogy, American Museum of Natural History, New York = **AMNH**. Eliana do Amaral Gimenez field catalogue number = **EAG**.

NOCTILIONIDAE: ***Noctilio albiventris*** DZUNESP 15443, 15450, 15454, 15455, 15457, 15545, UFPB 3897, 3898; ***Noctilio leporinus*** DZUNESP 30, 32, 33, 10332, 10612, 12130, UFPB 4095, 4336, 4337.

MORMOOPIDAE: ***Mormoops megalophylla*** AMNH 144998; ***Pteronotus davyi*** DZUNESP 10155, MZUSP 13870, UFPB 3891; ***Pteronotus gymnonotus*** MZUSP 13870; ***Pteronotus parnellii*** DZUNESP 11500, 12288, 12296, 12317, 12318, 12320, 12321, 12322, 12323, UFPB 3786, 3899, 4335.

PHYLLOSTOMIDAE: ***Lonchorhina aurita*** DZUNESP 11547, 11550, 11552, EAG 20; ***Macrophyllum macrophyllum*** DZUNESP 12740, 12741, 12742, UFPB 3892; ***Chrotopterus auritus*** DZUNESP 4788, 10534, 11172; EAG 58; ***Tonatia bidens***

DZUNESP 10057, 10058, 10059; ***Phyllostomus hastatus*** DZUNESP 10883, 10887, 11154; UFPB 4718; ***Carollia perspicillata*** DZUNESP 14252, 14244, 14245; ***Artibeus jamaicensis*** DZUNESP 3697, 3719, 3720; ***Glossophaga soricina*** DZUNESP 02745, 03047, 02757; ***Lichonycteris obscura*** UFPB 4202; 4350; ***Diphylla ecaudata*** DZUNESP 11543, 11544, 11546.

Specimens listed above have been studied for tongue, for palate or for both.