Ecomorphological analysis of the masticatory apparatus in the seed-eating bats, genus *Chiroderma* (Chiroptera: Phyllostomidae)

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Abstract

Recent data have shown that owing to their seed-predator capacity *Chiroderma doriae* and *Chiroderma villosum* trophically depart from all previously studied species within the canopy fruit-bat ensemble. In this paper, the hypothesis that morphological adaptations related to granivory have evolved in these bats is investigated and discussed. A canonical variate analysis was used to search for possible divergent trends between the masticatory apparatus of *Chiroderma* and other stenodermatines currently recognized in the same ensemble. A total of 142 specimens representative of eight species was included in the analysis. Species of *Chiroderma* can be discriminated from all other species in the sample based on the increased development of masseter-related variables (height of the anterior zygomatic arch, masseter moment arm, and masseter volume), which, in conjunction with other morphological characteristics (dentition and gape angle) discussed herein, corroborates the evolution of durophagy in this group. A complementary analysis based on a Mantel test revealed that the pattern of morphological differentiation that emerged from the canonical variate analysis does not agree with the one expected based solely on the phylogenetic relationships adopted for the canopy fruit-bats studied here. This result is consistent with the hypothesis that morphological adaptations related to granivory have evolved in *Chiroderma*.

Key words: Stenodermatinae, *Chiroderma doriae*, *Chiroderma villosum*, granivory, craniodental morphology, durophagy

INTRODUCTION

The relationships between diet and craniodental morphology in bats have long been investigated (e.g. Slaughter, 1970; Freeman, 1979, 1981, 1988, 1995, 1998, 2000; Strait, 1993; Dumont, 1997, 2003; Phillips, 2000; Van Cakenberghe, Herrel & Aguirre, 2002). Analyses based on biomechanical assumptions have indicated that, morphologically, species that use hard food items diverge in some features (e.g. mandible robustness) from those that use soft items (Freeman, 1979, 1981). Although only a few studies have focused on frugivorous species, strong morphological heterogeneity seems to exist within this group, probably reflecting diet particularities (Freeman, 1988; Dumont, 2003; Dumont & O'Neal, 2004). As demonstrated by Dumont (1999) and Aguirre *et al.* (2003), fruits used by bats vary greatly in their hardness. Figs, for example, are considered a relatively hard food item, while *Piper* fruits are soft and do not require great bite force or any specialized feeding behaviour during mastication (Dumont, 1999; Aguirre *et al.*, 2003). In a

recent study, Dumont (2003) applied an ordination method to craniometric variables and observed that canopy fruit-bats (fig-feeders) can be distinguished from ground-storey fruit-bats (e.g. *Carollia perspicillata*, a *Piper* specialist) by characters such as taller skulls, wider palates, and lower condyles and coronoid processes. These distinguishing characters suggest that, in the former group, the skull has more robust attachments for masticatory muscles. Considering dentition, which is the primary site of interaction with food, the morphological diversity within stenodermatines (a clade composed by strictly or predominantly frugivorous bats; Wetterer *et al.*, 2000) is expected to be higher than that observed within all other Microchiroptera combined (Freeman, 2000).

Variation in craniodental morphology among feeding specialists, however, may not be adaptive, but the result of common ancestry (phylogenetic effect; Felsenstein, 1985; Swartz, Freeman & Stockwell, 2003). Van Cakenberghe *et al.* (2002) were the first to study the correlation between cranial shape and diet in bats using an explicit phylogenetic framework. After controlling for the phylogenetic effect, only four of the five variables judged a priori to be important, based on their lack of phylogenetic signal, remained significantly different among trophic morphs. Contrary to the predictions of Van Cakenberghe *et al.*

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(2002), however, no divergent trend between soft and hard prey specialists was found in their analysis. Although behavioural adaptations for food processing may account for this lack of differences (Dumont, 1999), such a result may also derive from a low resolution in the composition of the groups under analysis (Van Cakenberghe *et al*., 2002). A significant amount of information on bat's diet has been accumulated in the past decades (Dumont, 2003; Jones & Rydell, 2003; Mickleburgh, Hutson & Racey, 1992; Patterson, Willig & Stevens, 2003; Von Helversen & Winter, 2003), but few species can be considered sufficiently well-known (e.g. Fleming, 1988; Handley, Gardner & Wilson, 1991). Bats are highly diversified in their feeding strategies and not only new food items (e.g. fruits and nectar from different plant species; Muchhala & Jarrín-V., 2002) but also new food categories (e.g. seeds; Nogueira & Peracchi, 2003) continue to be discovered.

Species in the neotropical genus *Chiroderma* have long been considered predominantly frugivorous and have been grouped with sympatric forms (e.g. *Artibeus* spp., *Platyrrhinus* spp., *Vampyressa* spp.) of the same subtribe (Ectophyllina, *sensu* Wetterer, Rockman & Simmons, 2000) in the canopy or fig-eaters ensemble (Bonaccorso, 1979; Kalko, Herre & Handley, 1996; Kalko & Handley, 2001; Giannini & Kalko, 2004). The recent discovery that at least two species of *Chiroderma* are habitual consumers of fig-seeds (Nogueira & Peracchi, 2003), however, raises the possibility that morphological adaptations specifically related to granivory have evolved in these bats. Behavioural observations have shown that *C. doriae* and *C. villosum* are highly specialized to feed on this potentially hard food item (Nogueira & Peracchi, 2003), and their strategy of crashing a large amount of fig-seeds in a relatively short period of time may have posed particular functional demands to their feeding apparatus (Strait, 1993; Swartz *et al*, 2003). In the present study, a search is made for possible divergent trends between the masticatory apparatus of *Chiroderma* and other stenodermatines currently recognized in the same ensemble (canopy fruit-bats). For most of these additional stenodermatine species (*Uroderma magnirostrum* and *Vampyrodes caraccioli* are exceptions), there is consistent evidence showing they are not fig-seed predators (Figueiredo & Perin, 1995; Figueiredo, 1999; pers. obs.). In addition to the exploratory analysis, the possible influence of the phylogeny in the observed pattern is also evaluated, variation in gape angle among the studied canopy fruit-bats is analysed, and some particularities of the dentition in *Chiroderma* are discussed.

MATERIALS AND METHODS

As emphasized by Dumont (2003), a well-established method to search for evidences of divergent morphological trends among frugivorous bats is the analysis of cranial and mandible shape based on important variables from a bio-mechanic approach (e.g. Freeman, 1988, 1995; Dumont, 1997; Van Cakenberghe *et al*., 2002). Nine variables that were potentially informative in respect to the mastication
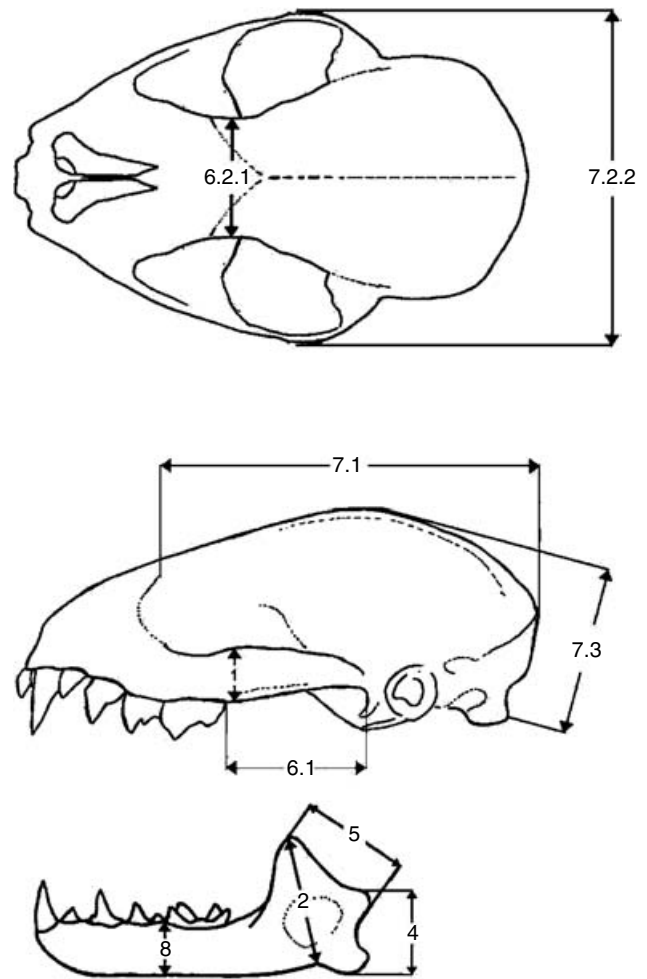
Fig. 1. Schematic representation of the skull and dentary of *Chiroderma doriae* (ALP7514) showing measurements used in this study. See text for definitions.

process were selected. A brief description of these variables (Fig. 1), most of which related to the action of the two main adductor muscles of the mandible – masseter and temporal (Maynard-Smith & Savage, 1959) – are:

(1) *anterior zygomatic arch* (AZA): greatest height of the zygomatic arch on its anterior portion, where the masseter originates;

(2) *coronoid height* (CH): from the indentation of ventral mandibular border to the tip of the coronoid;

(3) *angular process length* (APL): from mandibular foramen to the tip of the angular process;

(4) *masseter moment arm* (MMA): length from the middle of the mandibular condyle to the tip of the angular process;

(5) *temporal moment arm* (TMA): from the mandibular condyle to the anterior face of the coronoid process;

(6) *masseter volume* (MV): the product of masseter origin (length), depth, and height (masseter moment arm):

(6.1) *masseter origin* (MO): from the postglenoid process to the anteriormost extant of the muscle scar, in the area of junction of the zygoma with the maxilla.

(6.2) *masseter depth*: obtained from subtracting the width between the lingual mandibular foramina, at the base of the coronoids from the zygomatic breadth (greatest width across the zygomatic arches, 6.2.1):

(7) *temporal volume* (TV): product of temporal fossa length, width, and height:

(7.1) *temporal length*: greatest length from the anteriormost muscle scar (posterior to the eye) to the posteriormost edge of either lambdoidal or sagital crest.

(7.2) *temporal width*: derived subtracting the width at the postorbital constriction (least distance between the orbits – 7.2.1 – from the zygomatic breath.

(7.3) *temporal height*: least distance between the top of the braincase (including the sagital crest) and the line connecting the anteriormost point of the mesopterygoid fossa to the ventral median point of the foramen magno.

(8) *dentary height* (DH): height of the dentary obtained at the level of the anterior border of the second molar.

(9) *dentary width* (DW): width of the dentary obtained at the level of the anterior border of the second molar, in the middle portion of the dentary (in a sagittal plane).

All measurements were taken by a single person using a digital calliper precise to 0.01 mm. A total of 142 adult specimens (with phalangeal epiphyses and basisphenoid region completely ossified) of the following canopy fruit-bat species was included in the analysis (collection numbers in Appendix): *C. doriae* (10 males and 10 females), *C. villosum* (10/10), *Vampyressa pusilla* (15/4), *Uroderma magnirostrum* (8/3), *Platyrrhinus lineatus* (10/10), *Vampyrodes caraccioli* (6/5), *Artibeus lituratus* (10/10) and *A. obscurus* (10/10). Because a large size variation is noticeable among these species (from 8 g in *V. pusilla* to c. 80 in *A. lituratus*), raw data were transformed into ratios (Freeman, 1981), by using the variable 'size', proposed by Freeman (1988, 1995, 1998), as denominator. This variable corresponds to the sum of the natural logarithms of the following measurements: condylocanine length (from the anteriormost point of the canines to the posteriormost point of the occipital condyles), zygomatic breath, and temporal height. Except for *V. caraccioli*, all species were found sympatrically at the Botanical Garden of Rio de Janeiro, south-eastern Brazil, where the seed-predation behaviour of *Chiroderma* was observed (Nogueira & Peracchi, 2002, 2003). *Vampyrodes caraccioli* was included not only because it is a canopy fruit-bat (Bonaccorso, 1979), but also because its supposedly strong association with figs (Bonaccorso, 1979; Willis, Willig & Jones, 1990; Handley *et al.*, 1991). All specimens examined herein are deposited in the Adriano Lúcio Peracchi collection (ALP), at the Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, State of Rio de Janeiro.

Canonical variate analysis (CVA) was used to investigate potential variation in the shape of the masticatory apparatus of the canopy fruit-bats. With this multivariate technique, largely used in ecology and systematics as an exploratory ordination method (James & Mcculoch, 1990), groups are established a priori and the technique finds axes with major among groups variation, while maintaining within group variation constant (Monteiro & Reis, 1999). In the present study, these groups are formed by the 8 species included in the analysis. Because preliminary results showed a strong influence of the masseter in the discrimination of the species of *Chiroderma*, and a conspicuous trade-off has been reported between the action of this muscle and the capacity of increasing gape angle (Herring & Herring, 1974), an additional analysis was conducted to test if this pattern is corroborated. The gape as a variable has been frequently used in studies involving the ecomorphology of the masticatory apparatus in bats (Freeman, 1979; Jacobs, 1996; Barlow, Jones & Barratt, 1997) and corresponds to the ratio between the masseter origin (MO) and the moment arm of this muscle (MMA). Therefore, the larger the moment arm, the lower the maximum angle in which the bat is able to open its mouth. Average values of gape obtained for each species were visually compared, using confidence intervals of 95% calculated for each sample. Because a preliminary inspection of the results of this analysis revealed that a negative allometric relationship exists between gape and skull size, the residuals of the regression between them were used to eliminate the size effect on the original values of gape. Regression and canonical variate analysis were performed using the program STATISTICA 5.0 for Windows (StatSoft, 1995), and confidence intervals were obtained using SPSS 7.5 for Windows (SPSS, 1996).

Bat granivory has been documented only in *Chiroderma*, limiting the investigation of convergences related to this feeding strategy in distinct bat taxa. For morphological comparisons under an explicit phylogenetic context (e.g. Pérez-Barbería & Gordon, 1999; Van-Cakenberghe *et al.*, 2002), and in the absence of true evolutionary replicates (phylogenetically independent units with the same diet) that could be used in an analysis where species would be grouped in accordance to diet (e.g. frugivorous, frugivorous-granivorous), an alternative strategy was used to verify the possible influence of the phylogeny in the pattern of variation observed. Two symmetric matrices, one composed of phylogenetic distances and the other of morphological distances, were produced and then compared using the Mantel test. Phylogenetic distances were obtained from the sum of nodes present between each pair of species in the cladogram representing the phylogenetic relationships among the species studied here (Fig. 2). This cladogram is based on the total evidence (but primarily morphological) tree proposed by Wetterer *et al.* (2000) after a parsimony analysis and is also supported by the Bayesian analysis of the nuclear recombination activator gene-2 data presented by Baker *et al.* (2003). Additionally, the sister relationship between *Chiroderma* and *V. pusilla* that appears in our pruned tree is in agreement with the parsimony analysis of a mitochondrial DNA gene presented by Lim, Pedro & Passos (2003). Note, however, that the relationships within Ectophyllina (*sensu* Wetterer *et al.*, 2000) remain under
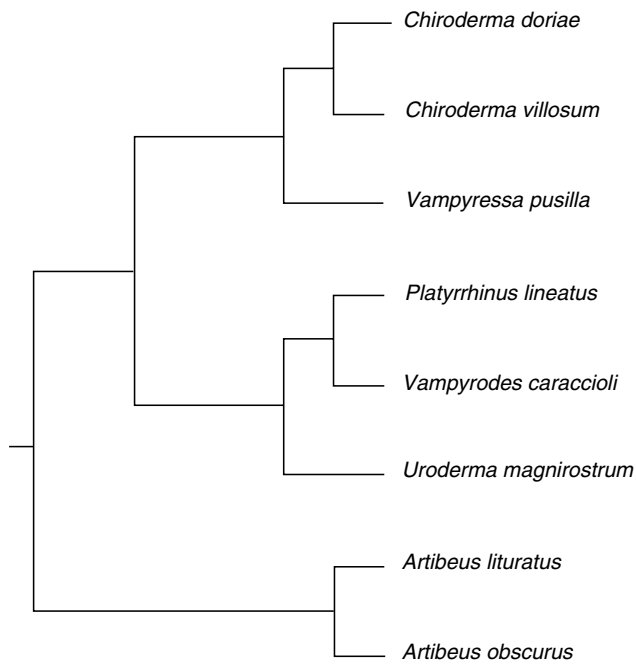
Fig. 2. Phylogenetic relationships among the canopy fruit-bat species analysed in this study. Topology based on the total evidence parsimony analysis of Wetterer *et al.* (2000), and also in agreement with the molecular (*Rag2* gene) Bayesian analysis of Baker *et al.* (2003).

Table 1. Loadings (standardized coefficients) of nine skull and dentary variables of bats on the first two canonical variates (CV1 and CV2) obtained in a canonical variate analysis. Eigenvalues and the corresponding percentage of total variation explained by each CV are also provided. See Material and Methods for variable abbreviations

	CV1	CV2
AZA	0.1569	− 0.7946
CH	− 0.5327	0.7141
APL	− 0.0728	− 0.0086
MMA	− 0.0827	− 0.6740
TMA	− 0.0002	− 0.1018
DH	− 0.0835	0.2082
DW	− 0.0798	− 0.3339
MV	0.0843	− 0.5573
TV	− 0.7195	0.3480
Eigenvalue	53.47	11.36
% of explained variation	79	17

discussion. Molecular phylogenies alternative to those used here were provided by Baker *et al.* (2003) and Porter & Baker (2004), these latter reporting 2 conflicting topologies derived from parsimony and Bayesian analyses. The Mahalanobis distances (Mahalanobis' D^2), obtained from the canonical variate analysis, was used to compose the morphological matrix.

The Mantel test was used to estimate the degree of association among the 2 matrices, testing if the observed correlation was higher than could be expected by chance (Sokal & Rohlf, 1995). After calculating the matricial correlation coefficient (standardized Z of Mantel), which constitutes the statistic of the test, the significance test was performed by comparison with 10 000 independent random permutations of matrix elements. The null hypothesis under investigation here is that no association exists between the elements of each matrix. The acceptance of this null hypothesis could be taken as evidence that morphological divergences among species evolved independently of the phylogeny's topology. Its rejection (morphological variation following the topology of the phylogenetic tree), on the contrary, would reinforce the necessity of using a formal comparative method (e.g. Felsenstein, 1985; Garland, Midford & Ives, 1999) in further analyses. The Mantel test was performed in the program Mantel for Windows (Cavalcanti, 2001), available online at http://life.bio.sunysb.edu/morph. The program TREEVIEW (Page, 1996) was used to produce the phylogenetic tree presented here. A 5% significance level was adopted in all tests.

RESULTS

The canonical variate analysis resulted in two new variables (Fig. 3) that together accounted for 96% of the dispersion (variability) among groups (Wilks' lambda: 0.00021; F c. $_{63,715} = 39.539$, $P < 0.0001$). The first canonical axis described 79% of the total variation in the sample, showing a conspicuous divergence between *A. lituratus* and the other species. On the opposite side of this axis are *U. magnirostrum* and *V. pusilla*, with *A. obscurus*, *V. caraccioli*, and the two species of *Chiroderma* in an intermediate position. Variables that contributed most to discrimination were height of the coronoid and temporal volume (Table 1), both more developed in *A. lituratus*.

The second canonical axes explained almost all additional variability among species in the sample (17%) and was particularly informative, discriminating species of *Chiroderma* from all additional taxa (Fig. 3). Along this second axis, *V. caraccioli* appears as an intermediate form between *Chiroderma* and the other species in the sample. The standardized coefficients related to this second axis showed that species of *Chiroderma* can be discriminated based on the increased development of masseter-related variables (height of the anterior zygomatic arch, masseter moment arm, and masseter volume). The variable coronoid height also contributed to the discrimination of the species in the second axis, but here species of *Chiroderma* were allocated in a position corresponding to the lowest values of this variable.

Although the angular process length did not contribute to discrimination along the second axis, the greater development of this structure in *Chiroderma* and *Vampyrodes* is noteworthy (Fig. 4), and certainly contributes to the higher values of masseter moment arm in these bats. As predicted, these species exhibited, on average, lower gape values than those of other species in the analysis (Fig. 5). According to the confidence intervals, no significant difference exists between mean values of *C. doriae* and *V. caraccioli*; the mean value obtained for *V. caraccioli*
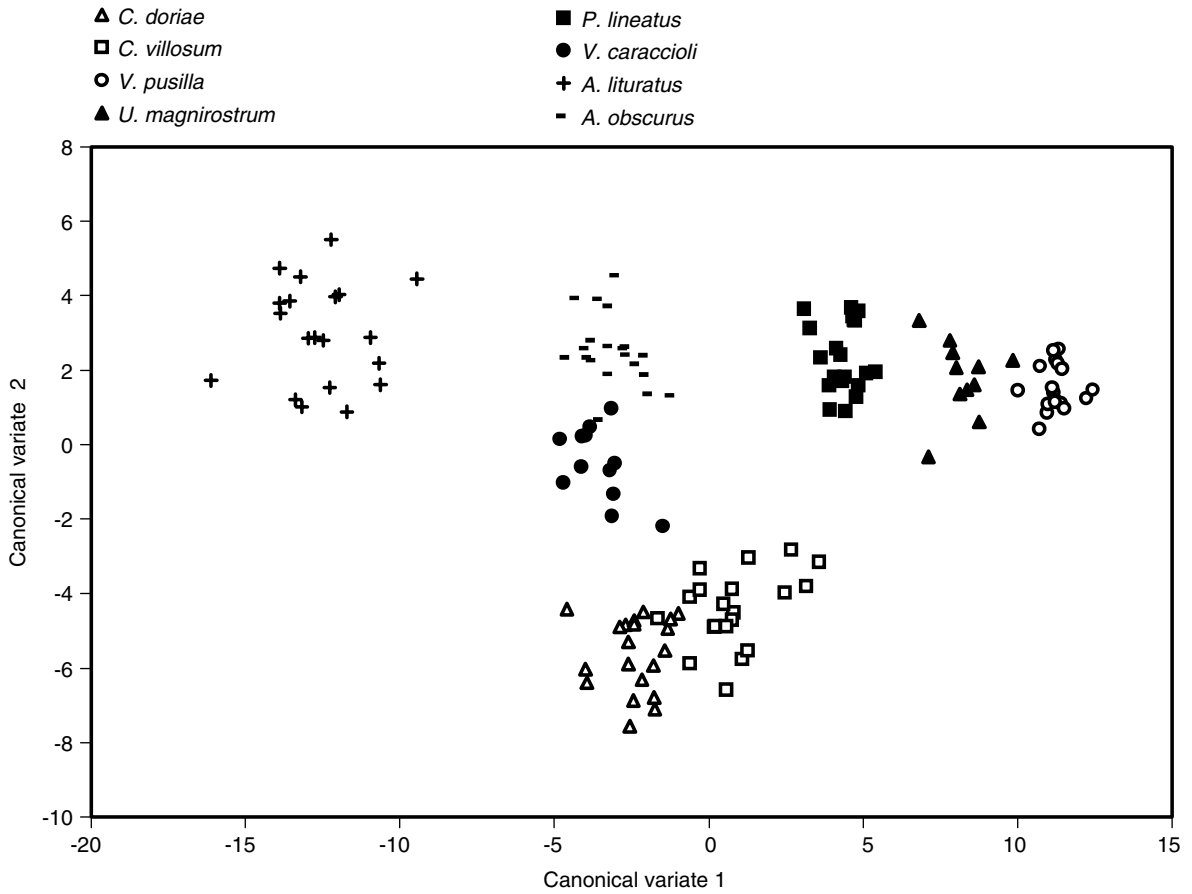
Fig. 3. Dispersion diagram of individuals from the eight species of canopy fruit-bats in the space defined by canonical variates 1 and 2.
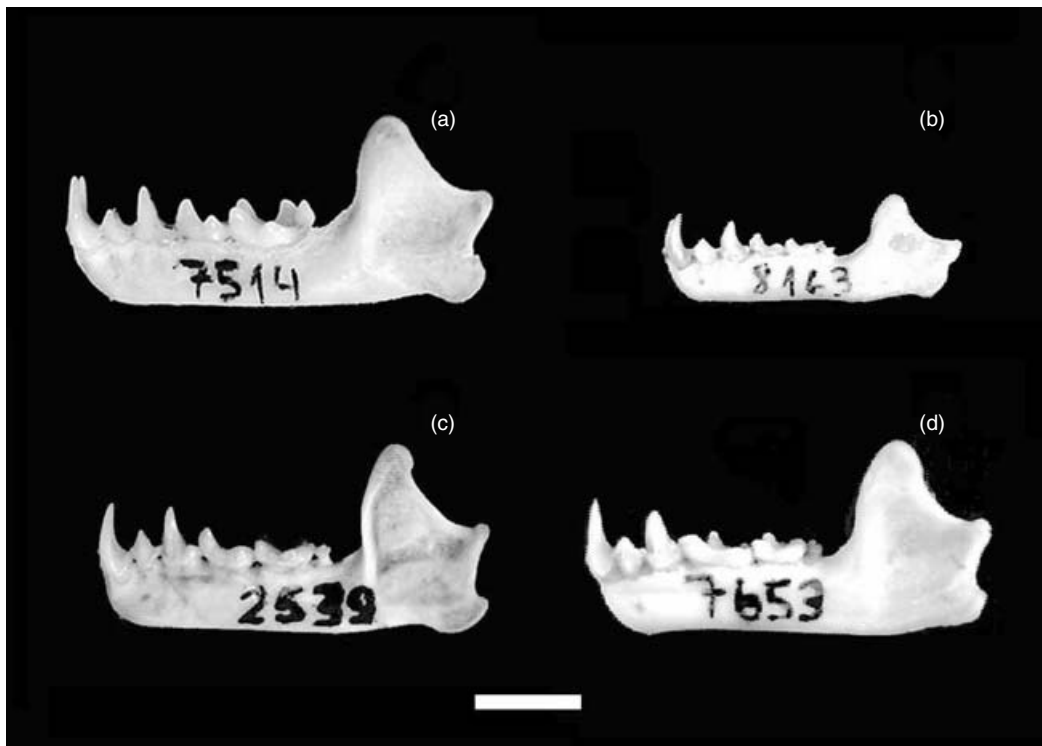
Fig. 4. Dentary of four canopy fruit-bat species used in this study: (a) *Chiroderma doriae*; (b) *Uroderma magnirostrum*; (c) *Vampyrodes caraccioli*; (d) *Artibeus obscurus*). Note the expansion of the angular process in (a) and (c). Scale bar = 5 mm.
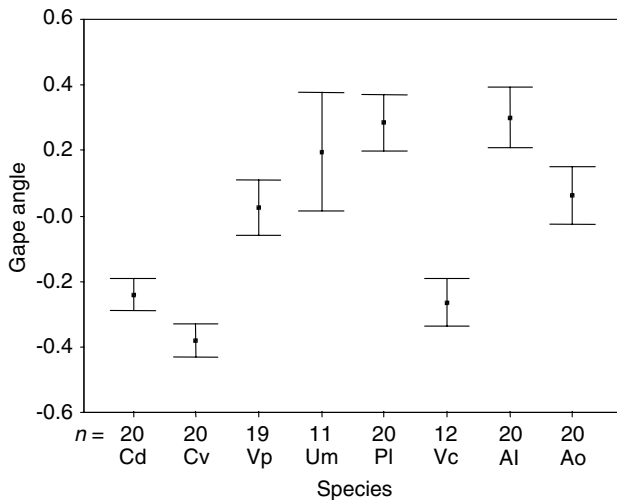
Fig. 5. Means and 95% confidence intervals for gape angle in the canopy fruit-bats analysed in this study. Vc, *Vampyrodes caraccioli*; see Table 1 for other abbreviations.

Table 2. Phylogenetic distances (inferior part of the matrix) and morphological distances (Mahalanobis' D^2) for the canopy fruit-bat species analysed in the present study. Vc, *Vampyrodes caraccioli*; see Table 1 for other abbreviations

	Cd	Cv	Vp	Um	Pl	Vc	Al	Ao
Cd	0	21	246	123	116	28	189	79
Cv	1	0	153	73	66	33	252	71
Vp	2	2	0	12	53	174	582	228
Um	4	4	3	0	14	88	318	99
Pl	5	5	4	2	0	60	305	66
Vc	5	5	4	2	1	0	79	15
Al	5	5	4	4	5	5	0	103
Ao	5	5	4	4	5	5	1	0

is inside the 95% confidence interval which includes the mean value for the population of *C. doriae*. *Chiroderma villosum* presented an even lower gape potential than these two species.

Results of the Mantel test ($r = 0.107$; $P = 0.2621$) revealed that the pattern of morphological differentiation that emerged from the canonical variate analysis based on cranial and mandibular features associated to mastication did not agree with the one that could be expected based solely on the phylogenetic relationships proposed for the group. Therefore, the null hypothesis is accepted that no association exists between the elements in the phylogenetic distance matrix and those in the morphological matrix (Table 2), and that morphological similarity is not dependent on phylogenetic descent for this group of species.

DISCUSSION

The results presented here are consistent with the prediction that the inclusion of seeds (a potentially hard food item) in the presumably frugivorous ancient diet of

Chiroderma (Wetterer *et al.*, 2000) may have selected structural modifications of the masticatory apparatus, finally adapting the bats for the new demand. The greater development of the masseter, a muscle primarily associated with mastication in herbivores (Maynard-Smith & Savage, 1959), constitutes a typical feature of durophagy in bats (Freeman, 1988, 1995, 2000). Although the angular process presented only a slight contribution to the discrimination between *Chiroderma* and the other taxa, which may be because of an inadequate selection of landmarks, it is probable that this structure plays an important role in the biomechanics of the masticatory apparatus of these bats. Radinsky (1985) observed that in ungulates the expansion of the angular process occurred independently at least 12 times, and that an expected expansion of the masseter (and also of the intern pterygoid), determined by this modification, could represent an adaptation to enhance the control of grinding action during mastication. In accordance with Radinsky (1985), such adaptation, absent among Carnivora, is justified not only by the diversity of plant material, representing different consistencies, eaten by ungulates, but also because these herbivores chew their food more thoroughly than do carnivores. The same need of a 'fine control over the magnitude and direction of the forces between opposing teeth during mastication' (Radinsky, 1985: 313), which seems to have influenced the evolution of the masticatory apparatus in ungulates, may also be associated to the modifications observed in *Chiroderma*.

In a study of morphological adaptations to diet in primates, Anapol & Lee (1994) observed that in strictly phytophagous species, the masseter moment arm tended to be more developed than the temporal moment arm, while in omnivorous species the opposite trend was observed. In addition to the expansion of the angular process, which implies a larger attachment area for the masseter, two other characteristics found in *Chiroderma* are among those cited by Anapol & Lee (1994) as indicative of preferential use of the masseter. First, a greater development of the zygomatic arch (also emphasized by Vaughan, 1972), can be refined if the majority of the masseter is considered as attached to the anterior portion of the arch, where more conspicuous modifications could be expected (Hylander & Johnson, 1997). Monteiro, Duarte & Reis (2003) verified that populations of the punaré rat *Thrichomys apereoides* from drier areas (caatinga) present a jugal bone (anterior zygoma) relatively longer than those observed in samples from more humid areas (cerrado), which may be related to the harder seeds they feed on. Bouvier & Hylander (1981) found that monkeys fed on a diet based on hard food items exhibited more extensive evidence of secondary Harvesian remodelling in their mandibles, and that the mandibles were also deeper than those from individuals fed on soft items. They interpreted these characteristics as adaptive answers to higher stress levels associated with durophagy, emphasizing that remodelling is a way of removing and replacing fatigued mandibular bone. The anterior zygomatic arch in *Chiroderma* is not only higher and, apparently, more robust than those observed in other
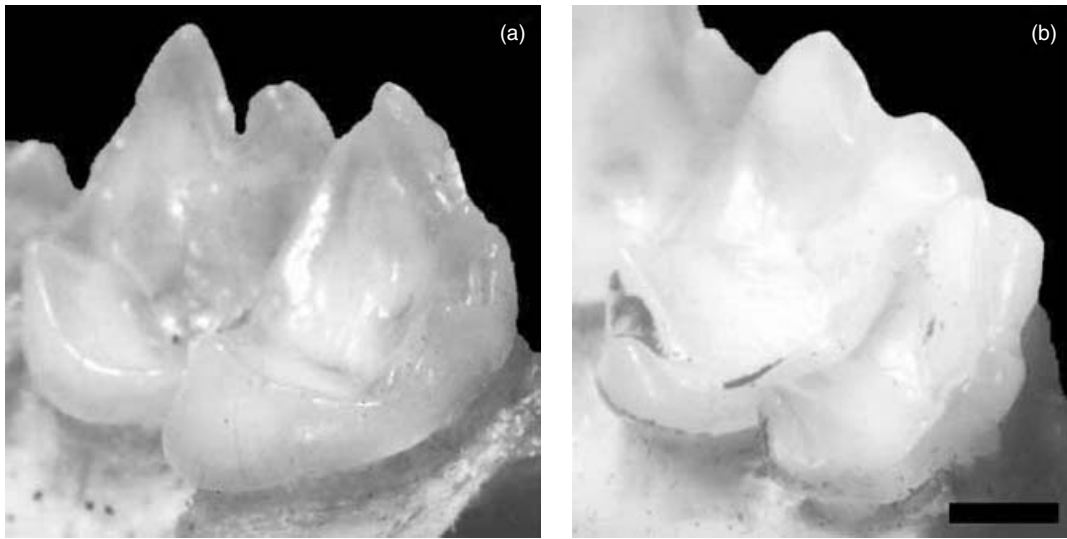
Fig. 6. Posterior view of the upper molars in: (a) *Chiroderma doriae* (ALP7514); (b) *Artibeus lituratus* (ALP7696). Note the elevated internal border of the second upper molar in *C. doriae*. Scale bar = 1 mm.

species analysed in the present study, but also presents the scar of the origin of the masseter that extends beyond the ventral surface of the arch, advancing through the lateral surface (Fig. 1). Although the functional importance of this expansion, apparently absent in the other canopy fruit-bats studied here, needs to be further investigated, its occurrence in *Chiroderma* seems to constitute additional evidence of the preponderant action of the masseter in the mastication of this group.

The second feature associated by Anapol & Lee (1994) to the higher participation of the masseter during food processing is related to the low ratio values between measures of the origin and insertion of the masseter (gape variable). Herring & Herring (1974) argued that in mammals in which higher gape angles become relatively unimportant (e.g. herbivores), natural selection probably acts improving mechanical advantage of the masseter. Although it is apparently easier to evaluate relative importance of higher gape angles when distinct groups such as herbivores and carnivores are compared, it is possible that the feeding specialization of *Chiroderma* on figs (Nogueira & Peracchi, 2002, 2003) has made the consumption of larger fruits unimportant, opening space for the evolution of a more efficient masticatory apparatus to process seeds. This morphological improvement may imply, therefore, a limitation in the spectrum of resources that *Chiroderma* is able to explore, which would characterize a trade-off (Bolnick *et al.*, 2003). Additional data, however, is necessary to evaluate whether the difference in gape angles observed, for example, between *C. doriae* and *A. obscurus*, has a significant impact on the potential of these species to explore the feeding resources available in their habitats.

Another morphological aspect of the masticatory apparatus of *Chiroderma* that apparently corroborates the evolution of durophagy in this group is dentition. In agreement with the pattern already known for bats (Freeman, 2000) and carnivores (Biknevicius & Ruff,

1992), species of *Chiroderma* are characterized by presenting fewer but larger teeth. Regarding the reduction in number of molar teeth in the lower jaw, *Chiroderma* is similar to *Vampyressa*, its closest relative (Wetterer *et al.*, 2000; Lim *et al.*, 2003), in having only two molars on each side (Koopman, 1994). The second molar of *Chiroderma*, however, is unusually large and with postero-lingual cusps relatively well developed (Fig. 4; Dobson, 1878; Miller, 1907; Taddei, 1979). *Vampyressa pusilla* also presents the entoconid of the second lower molar well developed (Peterson, 1968; Barquez, Mares & Braun, 1999), but does not exhibit the alternative cusp found in *Chiroderma* (Dobson, 1878; Miller, 1907). At the moment of occlusion with the second upper molar, the entoconid and the alternative cusp present in *Chiroderma* enclose the postero-internal corner of this tooth, possibly to prevent the escape of the slippery fig-seeds. Also conspicuous in *Chiroderma* is the elevated internal border of the second upper molar (Fig. 6), leaving the lingual basin on a plane inclined toward the raised rim formed by external cusps (the cutting edge characteristic of frugivorous bats; Freeman, 1998). This arrangement also seems favourable to the contention of the seeds and sharply contrasts with the condition found in *Artibeus* spp., *P. lineatus* and *U. magnirostrum*. In these latter taxa, the lingual basin of the second upper molar is inclined toward the posterior palate, possibly to facilitate the escape of the juice of the fruit during mastication (Fig. 6).

Regarding the additional species analysed here, *V. caraccioli* presents an inclination outline in the internal border of the second upper molar that is more similar to the pattern that seems to characterize classical jusophagous species (e.g. *A. lituratus*), while *V. pusilla* is, again (considering the unusual development of the entoconid), similar to *Chiroderma*. A point that seems relevant, however, is that in *Chiroderma*, only the second upper molars have the particular configuration that, in conjunction with the elevated internal cusps in the second

lower molars, seems to form a kind of 'seed-trap' (Lucas & Luke, 1979). The first upper molars in these bats follow a toward-palate pattern of internal inclination. Conversely, in *V. pusilla* both first and second upper molars follow a similar outline, suggesting no particular specialization in a more favourable site (e.g. a point closer to the fulcrum). The functional importance of concentrating the masticatory action in a more posterior point of the mandible was discussed by Dumont (1999, 2003) and is associated to the mechanical efficiency of reducing the resistance moment arm (Dumont & Herrel, 2003).

While analysing folivory by leaf fractionation in bats, Kunz & Ingalls (1994) suggested that this feeding habit is an extension of frugivory and that specializations in teeth and intestines, associated respectively to extraction and digestion of an essentially liquid diet (fruit juice), would have worked as pre-adaptations to the use of leaves. Regarding seeds, however, the structural differences, particularly hardness level, provide support to the contention that the morphological features reported here for *Chiroderma* may be indeed adaptations to granivory. Data presented here showing no correlation between morphology and phylogeny can be viewed as favourable evidence for this adaptationist hypothesis. To advance on this investigation, however, it will be necessary not only to consistently resolve the phylogenetic relationships among Ectophyllina bats, but also to demonstrate that the same features observed in *Chiroderma* have also evolved in other groups of frugivorous/granivorous bats. As emphasized by Swartz *et al.* (2003), morphological similarity owing to shared ancestry alone needs to be distinguished from those owing to similar selective pressures. Current knowledge about the diet of *V. caraccioli*, a species that apparently converged to a masticatory apparatus similar to that of *Chiroderma*, is still scarce but also reveals a strong association with *Ficus* (Bonaccorso, 1979; Handley *et al.*, 1991), which needs to be further investigated.

The morphological features discussed here for species of *Chiroderma* provide additional support to the inclusion of these bats in a sub-group, within the canopy fruit-bats, with specializations that go beyond diet and behaviour (Nogueira & Peracchi, 2002, 2003). This subdivision of broad categories into finer, more informative units is important not only to our understanding of niche partitioning (Strait, 1993), but also to the composition of a more reliable database on which evolutionary pathways of trophic diversification can be traced (Simmons & Conway, 2003). It is emphasized, however, that a formal functional approach (e.g. De Gueldre & De Vree, 1988, 1990; Aguirre *et al.*, 2002; Dumont & Herrel, 2003) testing the differences raised here between granivorous (fig-seed eaters) and non-granivorous canopy fruit-bats has yet to be done.

Acknowledgements

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APPENDIX

Specimens examined (taxa in alphabetic order): *Artibeus lituratus*, ALP6862, 6864, 6868, 7445–7446, 7452–7457, 7459, 7669–7670, 7696–7697, 7700–7701, 7715, 7719; *Artibeus obscurus*, 7469, 7472–7473, 7476–7477, 7480, 7553, 7556–7557, 7559–7561, 7563, 7572, 7642, 7646, 7650, 7653, 7790, 7794; *Chiroderma doriae*, ALP5684, 5693, 5714, 5761, 5784, 7508–7510, 7513–7515, 7517, 7519, 7520, 8059, 8062, 8077, 8079–8081; *Chiroderma villosum*, ALP2714, 2806, 3327, 3408, 4560, 5578–5579, 7018, 7022, 7050, 7419, 7421, 7423, 7424, 7426–7429, 7431, SN; *Platyrrhinus lineatus*, ALP7432, 7481–7482, 7490, 7920–7921, 7931, 8023–8025, 8027–8032, 8035–8037, 8043; *Uroderma magnirostrum*, ALP1648, 2807, 3012, 3942, 6029, 6033, 6831, 6834–6835, 7179, 8163; *Vampyressa pusilla*, ALP3159, 3312, 3334, 3336–3337, 5716–5717, 5731, 8125–8133, 8135, 8138; *Vampyrodes caraccioli*, ALP2021–2026, 2539, 2612, 2704, 7089, 7094, 7102.