A GEOMETRIC MORPHOMETRIC ANALYSIS OF CRANIAL AND MANDTBULAR SHAPE VARIATION OF DIDELPHTD MARSUPIALS

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ABSTRACT - The New World marsupial family Didelphidae is one of the oldest among mammals and is usually regarded as a morphologically conservative group. We analyzed cranial shape variation among six species of the six largest living genera of the family using two-dimensional landmark data. We captured and digitized video images of the skull and mandible for the following species: *Caluromys philander* (n = 65), *Chironectes minimus* (n = 30), *Didelphis aurita* (n = 70), *Lutreolina crassicaudata* (n = 37), *Metachirus nudicaudatus* (n = 77) and *Philander frenata* (n = 62). Fourteen landmarks were defined for the lateral, 25 for the ventral, 23 for the dorsal views of the skull, and nine on the mandibular lateral view. **Sex,** species, and interaction effects were analyzed with a two-way MANOVA on the matrices of coordinates aligned by general least squares. **All** four views had significant interactions. Canonical Variates Analysis was performed on sexes and species, and shape was regressed on the canonical variate scores for each species. *Caluromys philander* was clearly the **most** distinct species, with paedomorphic features that can be related to its arboreal habits. **A** conspicuous shortening of the rostrum distinguishes the highly carnivorous *Lutreolina crassicaudata. Didelphis aurita* and *Philander frenata* overlapped somewhat, reflecting shape similarities associated with their phylogenetic affinities, while the few differences observed are probably allometric consequences of size differences. *Philander frenata* and *Chironectes minimus* showed similar cranial shapes, while *Metachirus nudicaudatus* was distinctive with a broad and elongated rostrum. In spite of an overall similar shape, the geometric morphometric approach revealed several marked differences among species that can be related to their phylogenetic origin and their adaptive zone.

INTRODUCTION

The New World marsupial family Didelphidae has the longest fossil record (about 75 million years) of any known living family of Mammalia, and includes living species whose skull is very similar to extinct representatives from the Cretaceous. Thus, the living species' overall cranial shape is considered conservative, and their grouping within the family is based largely on retention of primitive characters (Reig *et al.*, 1987). Their masticatory apparatus is also classified as generalized, regarding both bone proportions and relative muscle importance (Turnbull, 1970).

All living Neotropical didelphids have an overall similarity in body and skull form, including species with body sizes ranging from 10g to more than 2000g. They also comprise a broad ecological radiation, with species showing locomotory habits as diverse as terrestrial (both cursorial and scan-

sorial), arboreal and semi-aquatic, and feeding habits ranging from highly frugivorous to almost strictly carnivorous. There are generalist species as well. This diversity in habits can be observed among the six large members of the Didelphidae studied here. The woolly opossum *Caluromys philander* is considered one of the most frugivorous species within the Didelphidae, with a diet including up to 75 % of fruits, and is also strictly arboreal (Charles-Dominique *et al.*, 1981, Julien-Laferrière and Atramentowicz, 1990, Leite *et al.*, 1996). The highly carnivorous water opossum *Chironectes minimus* is the only semi-aquatic didelphid (Hume, 1999, Marshall, 1978a). *Didelphis aur.itu*, the common opossum, is terrestrial with scansorial habits and omnivorous diet (Leite *et al.*, 1996, Santori *et al..* 1995). The thick-tailed opossum, *Lutreolina crassicaudata,* a terrestrial species with weasel-like body form, is the most carnivorous didelphid species, which is correlated with its cranial musculature (Delupi *et al.,* 1997, Hume, 1999, Marshall, 1978b). The brown four-eyed opossum *Metachir·us nudicaudatus* is terrestrial cursorial with a diet tending towards insectivory (Santori *et al.*, 1995). Finally, the gray four-eyed opossum, *Philander frenata* is a terrestrial species that occasionally climbs on trees, with a diet more carnivorous than *D. aurita*, yet less than C. *minimus* and *L. crassicaudata* (Santori *et al.*, 1997, Santori *et al.,* 1995b). The classification used here follows Gardner (1993), except for the specific status of *Philander frenata*, after Patton and da Silva (1997). However, the phylogenetic hypothesis for this group assumed here, based on morphological characters, DNA hybridization and mitochondrial DNA is: (**C.** *philander* (*M. nudicaudatus* (*C. minimus* (*L. crassicaudata* (*D. aurita - P. frenata*))))) (Kirsch and Palma, 1995, Kirsch *et al..* 1995, 1997, Patton *et al.,* 1996, Reig *et al..* 1987).

As are all marsupials, the young Didelphid is born after a short gestation period, when basic processes of craniofacial morphogenesis are still occurring. It must be immediately capable of breathing, suckling and holding on to the mother's teats to complete its development, although at this point important structures such as the premaxillae, maxillae, palatine and dentary bones are already in process of ossification (Clark and Smith, 1993, Maunz and German, 1996, Oliveira *et al.,* 1998). These reproductive and developmental characteristics have been suggested to be one of the reasons for this groups's conservative morphology, for they would impose a set of developmental constraints limiting the attainable final form. However, as Australasian marsupial forms present the same reproductive traits, and exhibit an amazing variety of forms, this should not be considered a reason for the morphologically conservative skull shape of the Didelphidae. The wide array of ecological specializations found in didelphids constrasted to their apparent conservative morphology, and the relatively well established relationships among the group makes them of particular interest to evaluate the level and possible origin of shape variation.

Here we use Geometric Morphometrics (Rohlf and Marcus, 1993) to compare the skulls and mandibles of representatives of six species of Didelphrd marsupials. We show the shape differences among species, and relate these to the diversity of ecological habits within the group.

METHODOLOGY

We selected adult specimens (*i.e.* individuals with fully erupted upper and lower P3 and M4) of *Caluromys philander*, *Chironectes minimus, Didelphis aurita, Lutreolina crassicaudata, Metachirus nudicaudatus* and *Philunder frenata*. The specimens arc listed in Appendix I.

Ventral, dorsal, lateral and mandible video images were captured using a COHU Color camera with a Fujinon 16 mm lens, connected to a TARGA+ digitizing board (5I2 x 400

pixels images); or a Pixera camera with Sony lens (848 x 640 pixels images); or using 10 x 15 cm photographic enlargements scanned on a flatbed scanner (500 x 400 pixels images *approx.*).In all cases skull and mandible orientation was the same. **All** the images in-

cluded a ruler for scale. Twenty-five land-marks were defined for the ventral view of the skull, 23 for the dorsal view, 14 for the lateral view, and nine for the lateral view of the mandible (Fig. 1). They were digitized using TPSDig, ver. 1.08 (Rohlf, 1996).
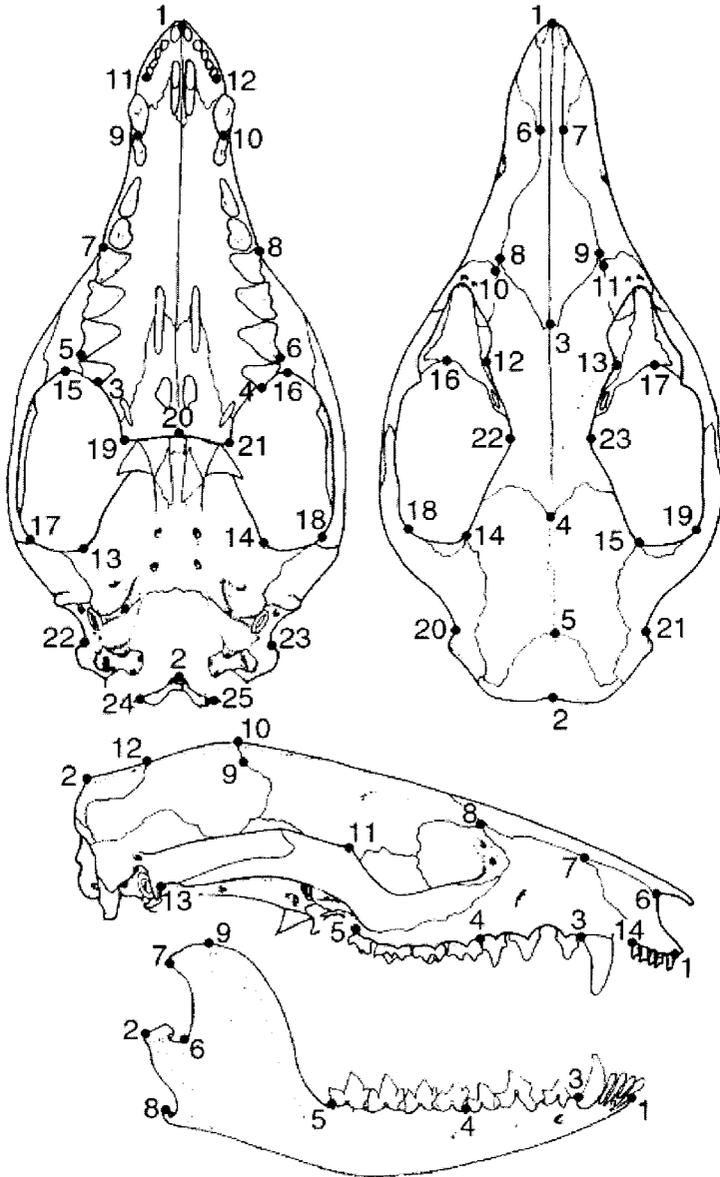

Figure 1. Location of the landmarks on the four views used. Skull of *Philander·*.

Landmarks used in this study were primarily chosen to describe major cranial and facial regions, and regions of particular morpho-functional or sensory interest. In ventral view, landmarks 1, 3-12 and 19-21 describe buccal shape, landmarks 13, 14 and 22-25 delineate braincase shape, while landmarks 13-18 represent shape of the zygomatic arches. In dorsal view, landmarks 1, 3 and 6-11 depict rostrum shape, landmarks 2, 4, 5, 12-15 and 20-23 describe braincase shape while landmarks 14-19 are the same as landmarks 13-18 of the ventral view. In lateral view, landmark 9 represents the root of the sagittal crest, at the union of the frontal and parietal bones, while in the lateral view of the mandible landmark 9 represents the tangent point of the farthest line parallel to the molar series. The use of landmarks present on two views allowed us to identify variations in specific regions in the skull as a whole. For the equipment and range of skull sizes used, a depth of field of 3 cm approximately was established as a trustworthy range in which deformations due to parallax were considered negligible, after testing for the size differences in pixels of a previously known length at different distances from the lens. Thus, all landmarks were determined to fall within this range.

The coordinates in millimeters were aligned with generalized least-squares Procrustes procedure **(GLS),** using the software TpsRelw, ver. 1.16 (Rohlf, 1997a), and the options unit scaling, orthogonal projections, $a = 0$ and include uniform. Sex and species effects were determined by a two-way Multivariate Analysis of Variance (MANOVA) using **SAS. A** Canonical Variates Analysis (CVA) was performed on the aligned coordinates, in order to find the axes of greatest variation among groups. Shape was then regressed on canonical variate scores using TpsRegr ver. 1.13 (Rohlf, 1997b).

The total number of images used for each species and sex is listed in Table 1.

Table 1. Number of images for each species used in the analysis, for each view. **M** = Males; F = Females.

Species	Ventral Total		Dorsal Total		Lateral Total		Mandible Total	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Caluromys philander	*63*		*64*		*65*		*64*	
	31	32	31	33	32	33	31	33
Chironectes minimus	*26*		*28*		*30*		*30*	
	15	11	17	11	18	12	19	11
Didelphis aurita	*67*		*70*		*67*		*66*	
	43	24	45	25	42	25	41	25
Lutreolina crassicaudata	*35*		*37*		*36*		*35*	
	22	13	24	13	23	13	22	13
Metachirus nudiraudatus	*76*		*77*		*74*		*71*	
	38	28	43	34	42	32	37	34
Philander jrenata	*60*		*62*		*62*		*58*	
	31	29	30	32	30	32	29	29

RESULTS

All four views had significant interactions at the 0.0001 level (Table 2), *i.e.* species present different degrees of sexual dimorphism. Therefore sexes and species were treated separately.

The CVA on sexes for each species indicated some overlap for all views and species, with the exception of *Chironectes minimus* in lateral view, *Didelphis aurita* in ventral view, *Lutreolina crassicaudata* in lateral view and *Philander frenata* in ventral view. Shape differences between sexes were very small in relation to those among species. Thus, only the results for one of the sexes will be shown here. Figures 2 to 5 show the mean configuration for males from each species, after scaling, rotating and translating. Mean configurations of females from of each species provided very similar shape patterns.

Results of the canonical variate analyses for the species are presented in Fig. **6** to 9, and the Mahalanobis D^2 between all species pairs for each view are given in Table **3**. Although CV1 is apparently mainly driven by the striking shape difference of the skull of C. *philander* (in fact, CV1 separates C. *philander* from the remaining species in all views and both sexes), the remaining CVs are able to distinguish all species in almost all cases. Thus, though some species overlap on the plots of the first two CVs, they separate in CV space. In Dorsal view, *P. frenata* and *D. aurita* separate on CV3, and C. *minimus* separates from all other species on CV4. For the Ventral view, CV3 distinguishes *M. nudicaudatus* from *L. crassicaudata*, while CV5 separates the latter from *P. frenata* (more striking in males than females). In Lateral view, CV3 distinguishes *L. crassicaudata* (males) from all other species, and for females *L. crassiraudata* is distinguished clearly from *D. aurita*, and *C. minimus*. *C. minimus* is clearly separeted from *P. frenata* along CV4 for both spxps and from all other species along CV5 for females. The values of Mahalnobis D^2 in Table *3* support this lack of overlap among the taxa.

Table 2. Results of the two-way MANOVA on aligned coordinates, for sex, species and sex*species interaction effects.

| View	Effect	Wilks' λ	d.f.	P
SKULL	Sex	0.70829167	42	0.0001
DORSAL	Species	0.00002040	210	0.0001
	Sex x Species	0.33247140	210	0.0001
SKULL	Sex	0.61764391	46	0.0001
VENTRAL	Species	0.00002590	230	0.0001
	Sex x Species	0.29281691	230	0.0001
SKULL	Sex	0.66689663	24	0.0001
LATERAL	Species	0.00003062	120	0.0001
	Sex x Species	0.44666074	120	0.0001
MANDIBLE	Sex	0.82113811	14	0.0001
LATERAL	Species	0.00369916	70	0.0001
	Sex x Species	0.56738864	70	0.0001
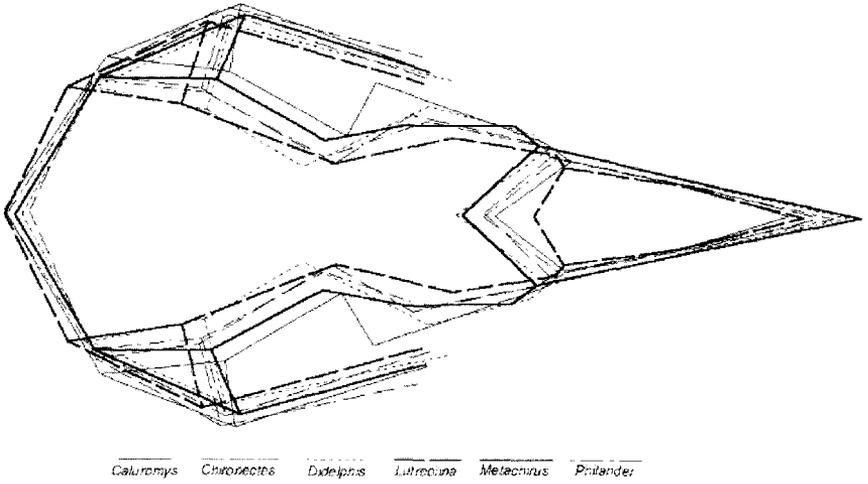
Figure 2. Means of the coordinates aligned by GLS for the **six** species for the dorsal view of the skull. Only males shown.

DISCUSSION

Despite their overall morphological similarities, it was possible to reveal differences of the skull and mandible shape of the six species studied here. For all of them. relations of the cranial and mandibular shape features to the species' ecological traits or phylogenetic position within the group may be proposed. Allometric relations or even possible heterochronic processes may also be involved, though additional data is needed to sustain such hypotheses.

In all four views, *C. philander* was clearly the most distinctive species, with a broader
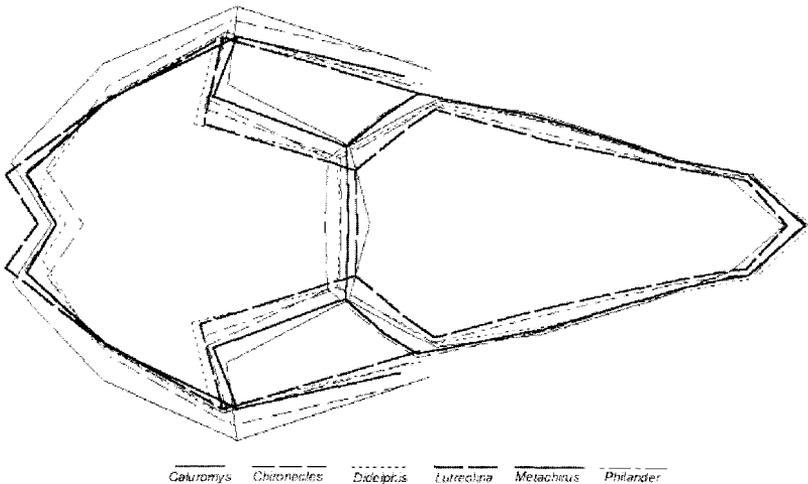

Figure 3. Means of the coordinates aligned by GLS for the **six** species. ventral view of the skull. Only males shown.
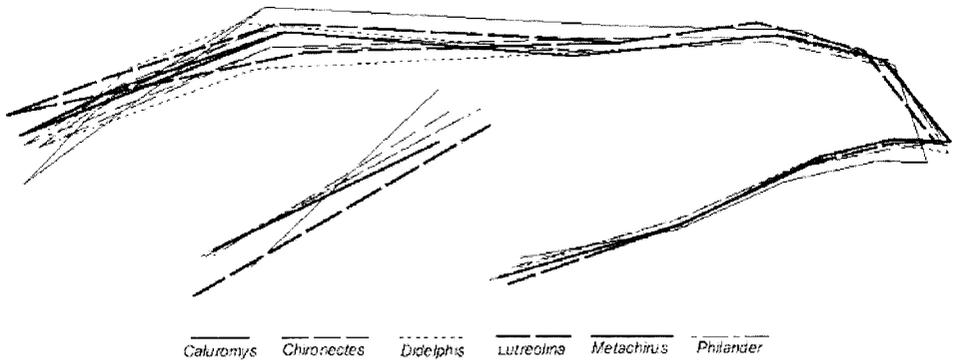
Caluromys   Chironectes   Didelphis   Lutreolina   Metachirus   Philander

Figure 4. Means of the coordinates aligned **by** GLS for the six species. Lateral view of the **skull.** Only males shown.

braincase, a shorter snout. and differences on the posterior region of the palate. The skull as a whole is compressed longitudinally (uniform component). This compression is mainly responsible for the overall appearance **of** the *Caluromys* skull in dorsal/ventral view, that is, the simultaneous broadening of the braincase and shortening of the snout, when compared to all the remaining species studied here. The mandible is dorsally sheared (top of the coronoid directed posteriorly), with an elevation at the back of the molar series and a depressed anterior mandible. It also presents the highest angular process of all species. The skull in lateral view is also ventrally arched when compared to all other species. *L. crassicaudata*, the second most distinctive species, shows a clearly shorter nasal and a narrow and posteriorly elongated braincase in dorsal view. Its coronoid process is broader and more perpendicular to the horizontal ramus
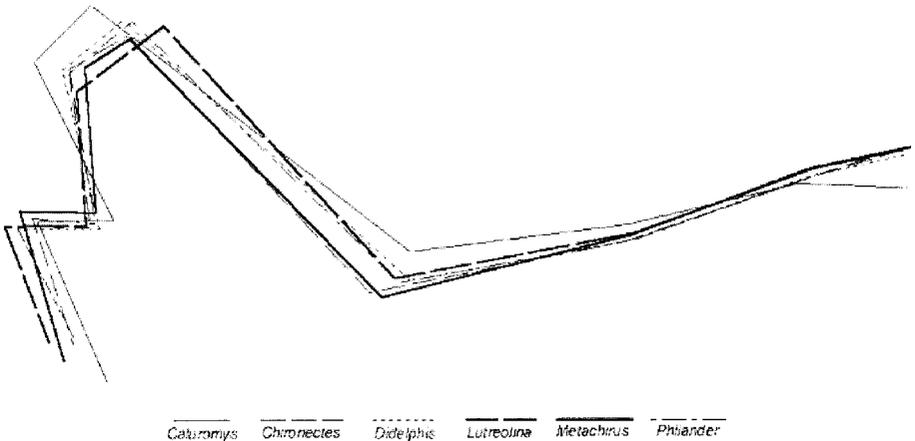

Caluromys   Chironectes   Didelphis   Lutreolina   Metachirus   Philander

Figure **5.** Means of the coordinates aligned by GLS for the six species. Lateral view of the mandible. Only males shown.
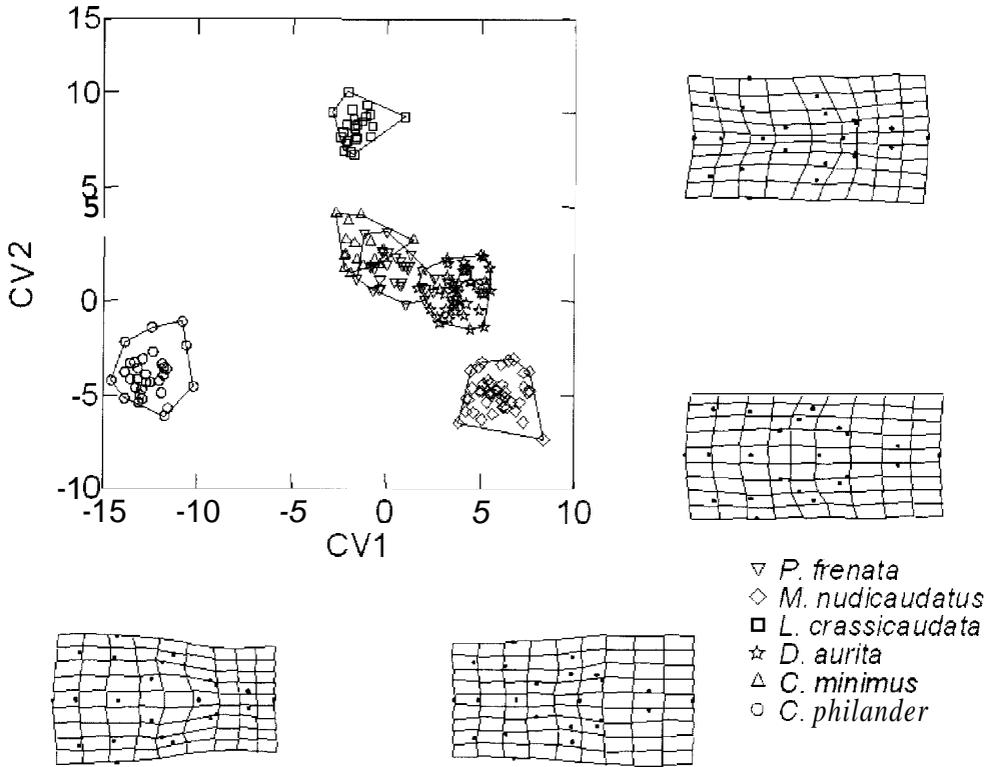
Figure 6. Canonical variates scores of first and second canonical variates based on the coordinates aligned by GLS. Dorsal view of the skull, males shown. Pattern is similar for females.

of the mandible than that of any other species. *D. aurita* has a wider anterior palate, a narrow but shorter braincase, and the most prominent sagittal crest. *C. minimus* has an intermediate braincase, as does *M. nudicuudatus.*

Cranial shape in *Caluromys philander* appears to be related to its arboreal habits. Arboreal mammals are known to have a relatively larger brain than their terrestrial counterparts (Eisenberg and Wilson, 1981, Pirlot, 1981). *Caluromys* presents the highest encephalization quotient among the Didelphidae, having a broader braincase to accommodate a greater encephalic volume. The increased orbital processes that can be identified in the splines (Fig. *6*) may be providing enhanced support to the muscles involved in

eye movement. These are more frontally oriented in *C. philander* than in the other species studied, a trait also related to arboreal habits. The ventral arching of the skull in lateral view, with the occipital condyle slightly more ventrally located, allows a better positioning of the skull when the body is in an upwards position (*e.g.* when climbing) than a skull with a more posteriorly located condyle. The mandibular shearing and increased angle between the mandible and the coronoid process are probably related to this arching of the skull, adjusting for the gape reduction imposed by the decrease of the angle between the presphenoid, basisphenoid and basioccipital bones. In fact, as the skull bends ventrally, the coronoid would approach the anterior end of the masseteric fos-
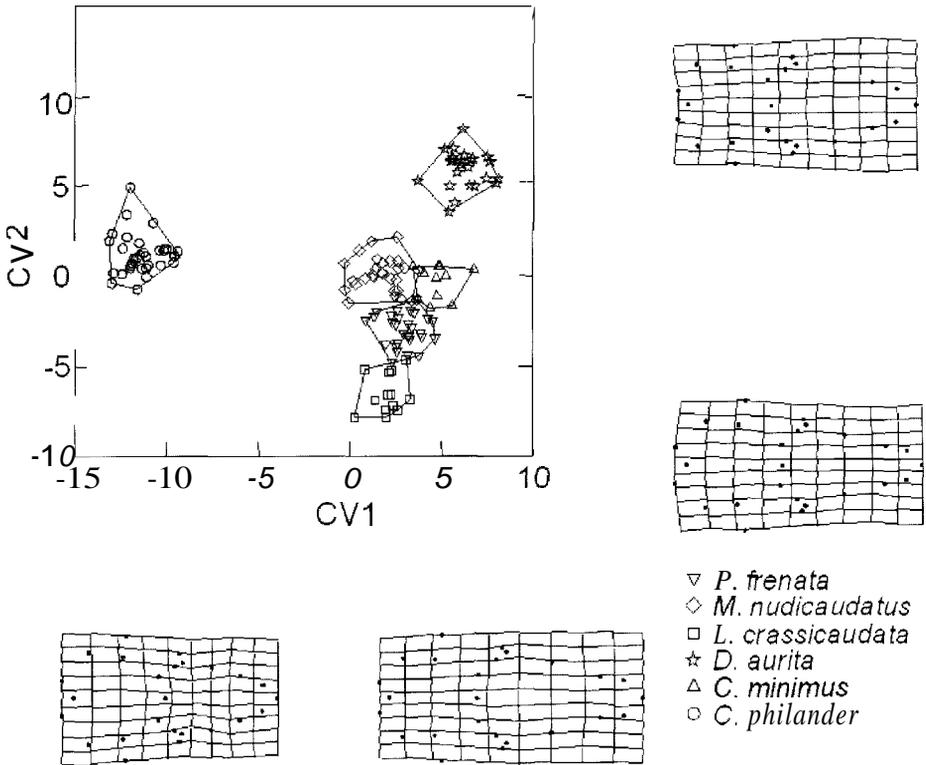
Figure **7.** Canonical variates scores of first and second canonical variates based on the coordinates aligned **by GLS.** Ventral view of the skull, females shown. Pattern is similar for males, except for males C. *minimus*, which have an intermediate position between *D. aurita* and *P. frenata*, *M. nudicaudautus* **and** *L. crassicaudata* on CV2.

sa more quickly when mouth opens. By inclining the coronoid dorsally through shearing, an increase in gape is attained. This shearing, however, is more evident in a Relative Warp Analysis than in the CVA presented here (Astúa de Moraes, 1998). The apparent greater development of the angular process in C. *philander* is a visual artifact due to the incomplete medial inflection of this structure, while all other genera studied here show the medial inflection typical of marsupials (Sánchez-Villagra and Smith, 1997). Therefore, in the lateral view of the mandible, landmark 8 appears to be closer to landmark 2 in all species but C. *philander*. Nevertheless, in the traditional two-dimen-

sional mechanical analysis of mastication (*e.g.* Maynard-Smith and Savage, 1957), this could also mean an increased lever arm for the masseter, which is usually more developed in herbivorous and frugivorous mammals than in carnivores, and *Caluromys* is the most frugivorous genus of all living didelphids. It is interesting to note that the skull features separating C. *philander* from the other five species are typical of young mammals, characterizing its cranial shape as paedomorphic in relation to the others. Heterochronic changes in ontogeny oriented by environmental pressures or random modifications in a developmental program may lead to paedomorphosis (Gould, 1977).

However, as *C. philander* is phylogenetical-ly distant from the other species studied here, the adaptive processes determining on-togenetic changes resulting in the final shape can only be fully understood if related to its phylogenetic position, in a morphometric analysis including all the extant species of the family. The proper identification of the relation between this paedomorphic cranial shape and its advantages for arboreal loco-motion (when compared to the remaining species analyzed, all more terrestrial) should thus include an analysis of murine opossums (which are all aiborealj, not examined in this study. Likewise, identification of the precise heterochronic process involved requires da-ta on ontogenetic processes and rates, as pure allometric differences *per se* do not necessarily reflect heterochronic phenomena (McKinney, 1988). Therefore, a comparison

of change rates of both cranial shape and size in terrestrial and arboreal didelphid species is needed to ellucidate this question. On the other hand. *L. crassicaudata* presents a distinct cranial shape with specific func-tional implications. For this species, a short-er rostrum is accompanied by a very narrow braincase. In this case, as the shortening of the rostrum (reflected by a shorter nasal bone) **is** not accompanied by the broad and globulous braincase shape seen in *Caluromys*, but by a slender and elongated one (more characteristic of the Didelphinae), it may have a different explanation. In fact, for this species, the skull and mandibular shape seems to be related to its feeding habits. *L. crassicaudata* is one of the most carnivorous species of the Didelphidae (Astua de Moraes, 1998, Marshall, 1978b). Shortening of the rostrum reduces torsion
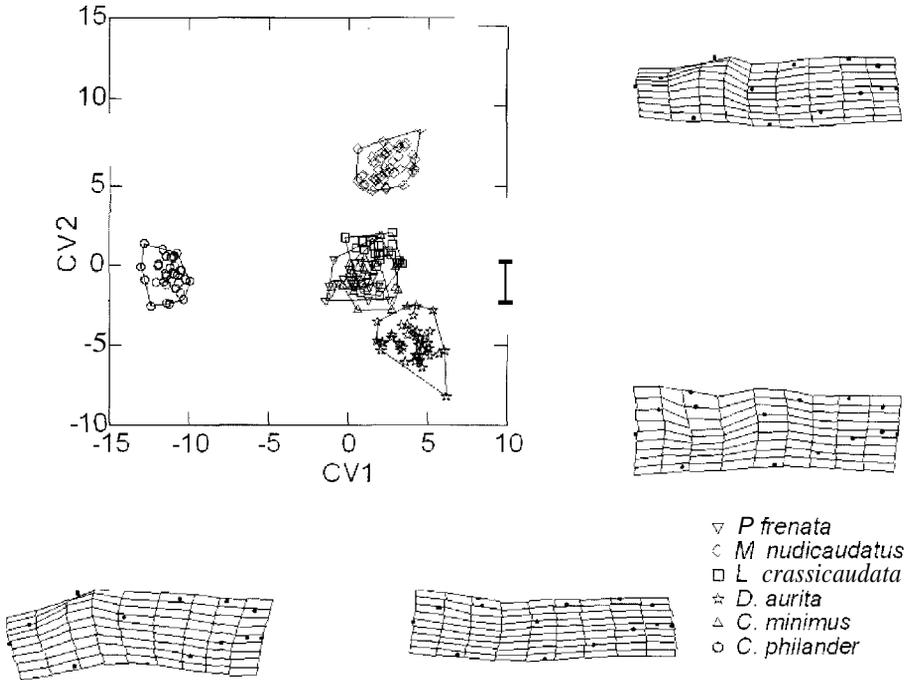

Figure 8. Canonical variates scores of first and second canonical variates based on the coordinates aligned by GLS. Lateral view of the **skull,** males shown. Pattern **is** similar for females, except that *Chironectes minimus* and *Lutreolina crassicaudata* females do not overlap with *Philander frenata*, but with *Didelphis aurita* instead, in the lower end of CV2.

Table 3 Mahalanobis D^2 between taxa for aligned landmarks - females above the diagonal, males below

Ventral View

Taxon	Caluromys	Chironectes	Didelphis	Lutreolina	Metachirus	Philander
Caluromys	0.00	17.47	18.31	15.98	14.41	15.14
Chironectes	20.36	0.00	9.83	11.01	11.36	7.85
Didelphis	19.82	10.71	0.00	13.48	9.78	10.00
Lutreolina	17.99	13.75	13.02	0.00	9.47	6.96
Metachirus	15.97	11.86	11.13	10.39	0.00	7.69
Philander	15.14	7.85	10.00	6.96	7.69	0.00

Dorsal View

Taxon	Caluromys	Chironectes	Didelphis	Lutreolina	Metachirus	Philander
Caluromys	0.00	14.77	16.58	15.46	16.77	12.76
Chironectes	20.36	0.00	8.36	13.49	11.74	8.43
Didelphis	17.92	9.27	0.00	13.98	9.89	8.31
Lutreolinu	17.78	11.56	14.12	0.00	16.58	10.13
Metachirus	18.97	13.41	10.92	16.11	0.00	9.18
Philander	14.62	8.30	8.42	9.32	9.41	0.00

Lateral View

Taxon	Caluromys	Chironectes	Didelphis	Lutreolina	Metachirus	Philander
Caluromys	0.00	15.58	18.48	16.81	16.22	13.56
Chironectes	13.55	0.00	7.53	9.24	10.87	9.25
Didelphis	15.99	7.34	0.00	10.42	10.26	9.09
Lutreolina	15.64	9.97	11.12	0.00	12.52	10.42
Metachirus	15.34	8.80	11.19	11.21	0.00	7.74
Philander	12.45	7.08	6.96	9.91	8.30	0.00

Mandible

Taxon	Caluromys	Chironectes	Didelphis	Lutreolina	Metachir-us	Philander
Caluromys	0.00	11.37	10.39	11.92	12.30	9.56
Chironectes	9.74	0.00	4.96	7.87	4.78	4.90
Didelphis	8.36	4.71	0.00	5.52	5.79	2.63
Lutreolina	10.80	5.94	5.57	0.00	7.67	5.60
Metachirus	9.94	4.37	5.87	5.75	0.00	5.70
Philander	8.58	4.58	2.10	5.34	5.78	0.00

forces imposed by asymmetrical pressures on canine biting, and is repeatedly found in carnivoran species (Covey and Greaves, 1994). Thus, the shorter rostrum is probably an adaptation for increased carnivory. This hypothesis is also supported by the presence of a broader coronoid process, which provides a larger insertion area for its particu-

larly well developed temporal muscle (Delupi *et al.,* 1997).

Being the most basal among the five species in the Subfamily Didelphinae, *M. nudicaudatus* is also quite distinctive, with a broad and elongated rostrum and lacking a sagittal crest. *D. aurita* overlaps with *P. frenata* in dorsal (CV2) and ventral views (CV1) of the

skull as well as in the lateral view of the mandible (CV1 and CV2). They also partially overlap in lateral view, though *D. aurita* shows a markedly developed sagittal crest. Similarities between these species are probably related to their phylogenetic relations as sister groups. The development of the sagittal crest may be reflecting effects of the size difference between these species. as they present similar allometric coefficients (Lemos *er al.,* 1996). Finally, C. *minimus* has some overlap with *P. frenata.* Such similarity in skull shape, body sizes, and to some degree, of carnivory, could imply in potential ecological niche overlap. However competition is avoided by simple marked different habitat use, as C. *minimus* is restricted to water courses, while *P. frenata* uses a much broader range of habitats.

The phylogeny proposed by Reig et al. (1987) is based on morphological characters. Subsequent molecular phylogenies (Kirsh and Palma, 1995; Kirsh et al., 1995, 1997; Patton et al., 1996) have displayed similar relationships among the six taxa studied here. Thus. the shape differences described in this study can reliably be related to a stable phylogeny.

It is reasonable to relate the cranial shape features of *L. crassicauda* to function and to ecology, as the shape represents adaptations occurring separately within the Didelphinae. C. *minimus* and the *Didelphis-Philander* group are more similar in their cranial and mandibular shape than any of them is to *L. crassicauda.* Though the cranial shape of C. *philander* can be related in some ways to ecology, it is not clear whether such cranial
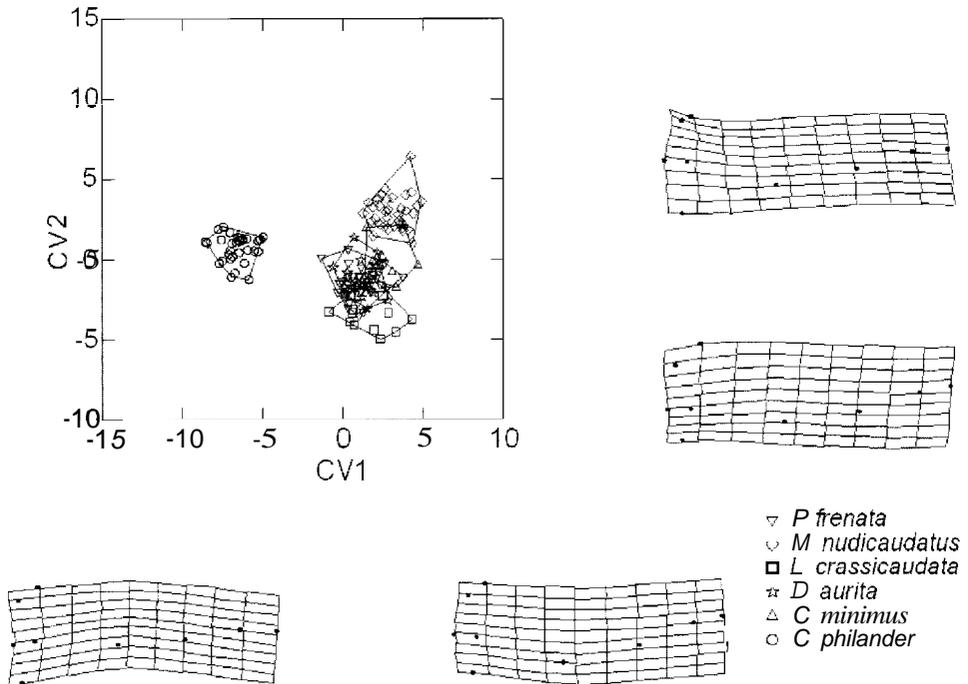

Figure 9. Canonical variates scores of first and second canonical variates based on the coordinates aligned by GLS. Lateral view of the mandible. Females shown. Pattern is similar for males.

features appeared as adaptive responses to ecological pressures, or are merely the result of the long time since the separation of the Caluromynae group (Kirsh et al., 1977). Furthermore, as all members of this group (*Caluromys, Caluromysiops* and *Glironia)* are arboreal species, the conjectured relation of their cranial features to arboreal life cannot be tested within it, and depends again on the analysis of the cranial shape of the arboreal murine opossums.

CONCLUSIONS

Landmark geometric morphometrics provides a fundamental tool that shows marked shape differences among members of a group usually considered morphologically conservative. The Canonical Variates extracted from the matrix of aligned coordinates were sufficient to separate almost all species. This approach yielded preliminary identification of shape features that can be related to ecology or phylogeny. The methodology used here, when coupled with additional detailed anatomical and morphological analysis of these species as well as the inclusion of representatives of the other species belonging to the family Didelphidae will help clarifying evolutionary, ecological and functional aspects of the biology of this family.

Appendix I. List of specimens examined. Museum numbers as follows: MN: Museu Nacional (Rio de Janeiro), MZUSP: Museu de Zoologia / Universidade de São Paulo (São Paulo), AMNH: American Museum of Natural History (New York). Sex of the specimen is indicated in parenthesis.

Caluromys philander
MN 1225 (M), 1227 (F), 1230 (F), 1233 (F), 5591 (M), 5970 **(F).** 5971 (F), 6100 (M). 10432 (F), 10434 (F), 10436 (M), 10437 (M), 10438 (M). 10440 (M), 10442 (M), 10444 (F), 10450 (F). 11722 (M), 11723 (F), 11724 (M), 16113 (M), 16114 (F), 16121 (F), 16123 (F), 16124 (M), 16126 (M), 20000 (F), 20001 (F), 20588 (F), 20772 (F), 20773 (M), 20776 (M), 20781 (F), 20782 (F), 20783 (F), 20784 (F), 20787 (M), 20964 (M), 20965 (M), 20966 (F), 20968 (M), 20970 (M), 24518 (M), 24520 (M), 27828 (M), 27829 (F), 28897 (M), 30562 (M), 33432 (M) - **MZUSP** 3173 (F). 4163 (F), 4518 (M), 4521 (M), 4663 (M), 4751 (F), 4752 (F), 10030 (F). 10107 **(M),** 11576 (F), 11.577 (F), 11599 (M), 11603 (F), 11607 (F), 11608 (M), 11612 (F), 21283 (F).

Chironectes minimus
AMNH 33027 (F), 37482 (M), 37483 (F), 47190 (M), 62365 (M). 72020 (M), 96759 (M). 96760 (M). 97319 (M), 123288 (M), 129704 (F), 141918 (M), 148720 (F), 264572 (M), 266477 (M) - **MN** 1281 (F). 23752 (M), 25738 (M). 30373 (F) - **MZUSP** 4644 (F), 4654 (M), 4658 (M), 4659 (F), 4669 (F), 4673 (F), 4755 (F), 4762 (F), 4837 (M), 6701 (M), 7793 (M). 16544 (M), 17081 (F).

Didelphis aurita
MN 1179 (F), 3850 (M), 3851 (M), 3853 (F), 3854 (M), 3855 (M), 3856 (M), 3858 (F), 3859 (M), 3860 (M). 3862 (M). 3863 (M), 3865 **(M).** 5614 (M), 5615 (F), 5616 (M), 5641 (M). 5688 (M), 5700 (F), 5718 (F), 5720 (M), 5732 (M), 5739 (M), 5744 (M). 5793 **(F),** 5795 (F), 5811 (M), 5862 **(M).**

71.52 (M), 7153 (M), 7157 (F), 7160 (M),7166 (F), 7721 (F), 7722 (F), 8297 (F),10485 (M), 10486 (F), 10493 (M). 11323 (M), 11324 (F). 11424 (M), 11426 (F), 11437 (M), 11438 (M), 11445 (M), 11446 (M), 11448 (F), 11450 (M), 11671 (M), 20938 (F), 20939 (Mj, 20940 (F), 20941 (M), 20943 (F). 20946 (M), 20948 (M), 20950 (**F),** 23721 (M), 23732 (F), 23748 (M), 23758 (M), 24443 (F), 25677 (M), 28896 (M), 30276 (M), 33425 (M), 43753 (F), 43966 (F), 46503 (M), 46509 (F), 46910 (F).

Lutreolina crassicaudata
AMNH 133249 (M). 133250 (F), 139825 (F), 210420 (M), 254512 (M), 254513 (F) - **MN** 1292 (F), 1294 (M), 24162 (F), 24163 (F), 24447 (M), 24448 (F),24449 (M), 24450 (M). 24451 (F), 24452 (M), 24453 (Mj, 24454 (M), 24455 (F), 24457 (F), 24458 (F), 43797 (F) - **MZUSP** 14 (M), 233 (F), 325 (M), 343 (M), 1006 (M), 3674 (M), 6469 (M), 7098 (Mj, 7146 (Mj, 7147 **(M).** 7387 (M), 12744 (M), 12748 (Mj, 20188 (M).

Metachirus nudic audautus
MN 3982 (F), 3983 (M), 5223 (M), 5578 (M), 5580 (F), 5581 (M), 5590 (F). 5603 (F), 5805 (M), 5806 (F), 10245 (M). 10246 (F), 10247 (M), 10248 (M), 10254 (F), 10269 (M), 10271 (**F).** 10272 (M), 10274 (M), 10279 (M), 10283 (M), 10285 (F), 10287 (M), 10400 (M), 10401 (**F),** 10403 (F), 10416 (F), 10420 (F), 10421 (M), 10422 (F), 10423 (F), 10424 (F), 10426 (M), 10964 (M), 11290 (F), 11339 (F), 11350 (M), 11354 (M), 11360 (M), 11361 (F). 11365 (M), 11369 (M), 11375 (F), 11376 (M), 11380 (M), 11384 (M). 11387 (M). 11388 (F). 11401 (F), 17182 (M), 17196 (M), 20142 (F), 20203 (F), 20204 (F). 20206 (M). MN 20207 (F), 20208 (F),20228 (M), 20229 (F), 20230 (M), 20231 (F), 25304 (Fj, 25991 (F), 26612 (M). 26889 (M). 26890 (M), 26891 (F), 26926 (M), 28811 (M). 28937 (F), 28958 (M), 29951 (F), 30571 (F), 30572 (M). 30573 (F), 31405 (Mj. 31425 (M), 31454 (M), 42774 (M), 42817 (M), 46562 (M), 46904 (F)

Philander frenata
MN 1202 (M), 5587 (F), 5596 (F), 5605 (M), 5698 (M), 5750 (F), 5753 **(M),** 5802 **(F),** 5807 (F), 6219 (F), 6242 (M), 6420 (M). 6421 (M), 6836 (M), 6850 (M), 7183 (F), 7187 (M), 7204 **(M).** 7212 (F), 7215 (M), 7291 **(F).** 7320 (F). 8221 (M). 8224 (M), 8226 (F), 8228 (F), 10374 (M), 10376 (M), 10382 (F), 30383 (F). 13450 (M), 13493 (M). 13499 (F), 13500 (F), 26620 (F), 26624 (M). 26629 (F), 26630 (M), 26778 (M), 26781 (F), 28803 (F), 29731 (F), 29810 (Mj, 29934 (F). 29938 (F), 29950 (M), 30410 (F), 42777 (F), 42779 (F), 42782 (M), 42783 (F), 42785 (F), 42786 (F). 42788 (F), 43751 (M), 43760 (M), 43960 (F), 43961 (M), 43962 (F), 46908 (F), 46915 (M), 46916 (M) - **MZUSP** 6206 (M), 7425 (M), 8883 (M), 10416 (M), 17034 (F), 17599 (F).

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