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Investigating South American biogeographic history using patterns of skull shape variation on *Cerdocyon thous* (Mammalia: Canidae)

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Patterns of geographic variation of the canid *Cerdocyon thous* have historically been obscured by its remarkable intraspecific morphological variability. The observed distribution is highly associated with phytophysiognomy, a feature considered highly dynamic along geological time. In the present study, we tested whether vegetation distribution during the Holocene Glacial Maximum of South America (HGM) explains the patterns of morphological variation within *Cerdocyon thous*. The species was divided in groups according to paleohabitats that could support their presence during the HGM, and then tested for differences in skull morphometrics. The results obtained demonstrate that the climatic changes during the HGM influenced the population structure of this species, resulting in the establishment of geographical groups with different degrees of morphological cohesion. Higher morphological cohesion found in the Northern group might be explained by the marked discontinuity between its geographical range and the rest of the species'distribution. The Eastern and Southern morphological divergence is less striking and, although this could be related to past vegetation distribution, the disappearance of those barriers leads to a population structure that could be slowly breaking down. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **98**, 77–84.

ADDITIONAL KEYWORDS: geographical – intraspecific – morphometrics.

INTRODUCTION

The crab-eating fox *Cerdocyon thous* (Linnaeus, 1766) is a canid endemic to South America, generally recognized as a monospecific genus (Langguth, 1975; Berta, 1982; Tedford, Taylor & Wang, 1995; Prevosti, 2007). It occurs extensively throughout the South American continent: the northern limit of its distribution starts east of Panama on the open lowlands of northern Colombian coast. It largely bypasses the center–south-east equatorial forest of Colombia, as well as the western portion of the Andes. The distribution of *Cerdocyon* along the Andean slopes ranges as far south as the Equatorian border and as high as 3000 m. To the East, it ranges throughout the Venezuelan territory, except for the southern regions on the Amazon department. In the Guyanese region, its distribution is restricted to the south of Guyana. In the east of Pará state in Brazil, crab-eating foxes are recorded only at the Amazon River delta on both margins, including the Marajó Island. In north-eastern and central Brazil, the species is distributed throughout the open vegetation belt, also known as the dry diagonal corridor of South America. This open vegetation area crosses South America from north-eastern Brazil to south-eastern Bolivia and most of Paraguay, including the Caatinga, Cerrado, and Chaco domains. *Cerdocyon* extends its distribution to the area covered by the coastal Atlantic Forest, the seasonally flooded regions of the Pantanal, and the pampean regions of Brazil and Argentina. Five distinct subspecies have traditionally been recognized along its wide distribution: *Cerdocyon thous aquilus* described for savannas and forests in Colombia and

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Venezuela; *Cerdocyon thous azarae* described for coastal and central Brazil; *Cerdocyon thous entrerianus* described for the south of Brazil, north of Argentina, Paraguay and Uruguay; *Cerdocyon thous germanus* described for the high savannas of central Colombia; and *Cerdocyon thous thous* described for the Guianas and oriental Amazon (Cabrera, 1931, 1958; Tate, 1939; Berta, 1982). This taxonomic arrangement is not deprived of criticism because many of the original diagnostic characters were based on fur coloration, which exhibits remarkable intraspecific variability, thus potentially confounding the identification of within-species taxonomic units (Cabrera, 1931, 1958; Tate, 1939; Berta, 1982).

Although *C. thous* occurs on almost any vegetation type, it shows clear preference for open areas (Brady, 1979; Bisbal, 1989; Sunquist, Sunquist & Daneke, 1989; Macdonald & Courtenay, 1996; Beisiegel, 1999; Maffei & Taber, 2003; Trovati, Brito & Duarte, 2007), avoiding large areas of dense arboreal formations. Therefore, an ample area of predominantly dense forests is probably the only effective barrier to this species' distribution, which may explain the virtual absence of *Cerdocyon* from the Amazon basin (Berta, 1982; Bisbal, 1989; Voss, Lunde & Simmons, 2001; Courtenay & Maffei, 2004).

Despite this fact, the species has stable and viable local populations in all habitats where it occurs (Courtenay & Maffei, 2004), mainly because of its plastic habitat choice, tolerating even high levels of anthropic pressure (Juarez & Marinho-Filho, 2002; Michalski & Peres, 2005; Pedó *et al.*, 2006), but also because of its opportunistic and omnivorous feeding behavior. Although analyses of *C. thous* feeding ecology are abundant (Montgomery & Lubin, 1978; Brady, 1979; Bisbal & Ojasti, 1980; Sunquist *et al.*, 1989; Olmos, 1993; Motta-Junior, Lombardi & Talamoni, 1994; Macdonald & Courtenay, 1996; Juarez & Marinho-Filho, 2002; Jácomo, Silveira & Diniz-Filho, 2004; Gatti *et al.*, 2006; Pedó *et al.*, 2006), there are apparently no obvious differences between animals in different areas that cannot be attributed to local food availability. An integrative study, however, is still lacking.

Originally, the biogeographic patterns of South American mammals have been investigated to emphasize general species distribution, mainly with the identification of zoogeographical zones (Hershkovitz, 1972). Recently, however, there is a tendency to the establishment of complex scenarios for speciation and extinction of species (Bush, 1994); Marroig & Cerqueira (1997) presented a review of many geological and environmental changes, mainly in the Amazon Basin, that could have influenced species richness in South America; Costa (2003) showed how the formation and disappearance of forest belts could be associated with Atlantic Forest's small mammal (e.g. rodents and marsupials) diversity and phylogenetic patterns; Vivo & Carmignotto (2004) proposed that the megafaunal extinction was associated with the dynamics of vegetation cover in the continent.

The wide distribution of *C. thous* and its generalist habits suggest that any wide-range population structure is based on vegetation density. If this idea holds, any pattern of geographic variation can be related to past and present vegetation dynamics. In the present study, we explicitly test the model proposed by Vivo & Carmignotto (2004) for vegetation distribution during the Holocene Glacial Maximum (HGM) and its possible effect on extant population structure.

Accordingly, we investigated cranial shape variation of *C. thous* in light of the species' distribution. Skull shape is a very reliable source of information for taxonomic investigation in mammals and has not been explored in a wide geographical range for this species so far.

MATERIAL AND METHODS

Sample

We examined material from the following collections: Brazil: Museu de Zoologia da Universidade de São Paulo, Museu Nacional do Rio de Janeiro, Museu de Zoologia da Universidade Federal de Viçosa, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Coleção de Mamíferos do Departamento de Zoologia da Universidade Federal de Minas Gerais, Museu Paraense 'Emílio Goeldi' and Instituto Nacional de Pesquisas da Amazônia; Argentina: Museo Argentino de Ciências Naturales 'Bernardino Rivadavia' and Museo de Ciencias Naturales de La Plata; USA: Museum of Vertebrate Zoology of the University of California in Berkeley, American Museum of Natural History and National Museum of Natural History Smithsonian Institution; France: Muséum national d'Histoire naturelle. We also examined three specimens from a private collection (see Acknowledgements). Specimens were identified to species level based on discrete morphological characters *sensu* Berta (1982, 1988), Tedford *et al.* (1995) and Stains (1975), totalling 398 specimens (both skin and/or skull). On the basis of overall skull size, state of skull sutures, tooth eruption, and toothwear, we selected 355 adult skulls from both sexes, belonging to 286 distinct sampling locations.

A priori groups were assigned based on the model for the phytophysiognomy for the HGM for South America (Fig. 1). A Northern group is associated with the small patches of dense savanna found in the region today corresponding to the 'llanos' and tropical and subtropical lowland forests of Colombia and Ven-

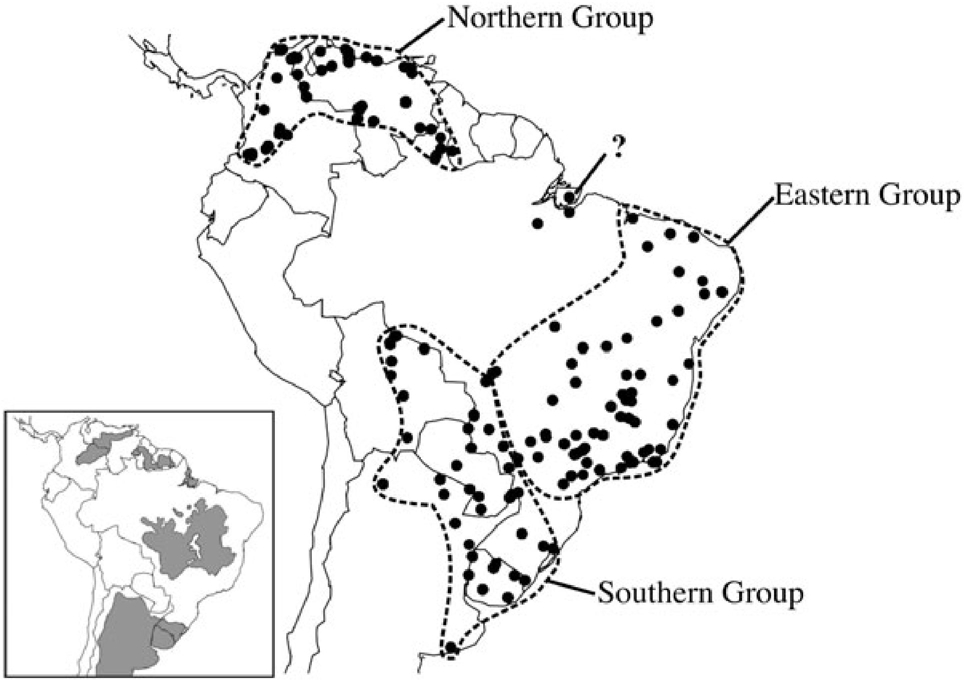

Figure 1. Distribution of *Cerdocyon thous* and the delimitation of the geographical groups based on the model for the Holocene Glacial Maximum phytophysiognomy distribution proposed by Vivo & Carmignotto (2004). The open areas capable of sustaining *C. thous* during this period are shown in the lower left corner in grey. The population of the east of the Brazilian state of Pará, indicated by '?', was not classified as a result of the small sample size.

ezuela, including higher elevations of the Andean slopes. An Eastern group occurs in the larger central dense savanna region that corresponds to the extant Brazilian Cerrado. This group also includes individuals found in the regions associated with the Atlantic Forest, and the Northeast Caatinga because these are adjacent to the main hypothesized open area. The last group, a Southern one, corresponds to the temperate formations associated today with the grasslands (Pampas region) and steppes of Brazil, Uruguay, and Argentina, including some regions assigned to the Chaco formation of Argentina. We also included some individuals from the Chacos of Paraguay and Bolivia based on phytophysiognomy similarities. Individuals from the east of the Brazilian state of Pará were kept out of the analysis as a result of the small sample size, despite it being a possible site for holocenic *C. thous* distribution (Vivo & Carmignotto, 2004).

IMAGE ACQUISITION AND ANATOMICAL LANDMARKS

The 355 specimens selected had their skulls photographed with a digital camera in dorsal view and two-dimensional landmarks were digitized over the images using the software tpsDIG, version 1.40 (Rohlf, 2004) (Fig. 2). The anatomical landmarks were defined as follows: 1, tip of premaxillae; 2, tip of nasals; 3, left premaxilla-nasal-maxillar suture; 4, nasal-frontal suture; 5, frontal-parietal suture at the midline; 6, parietal-occipital suture; 7, inion; 8, lateral point of maximum curvature on the left occipital crest; 9, end of occipital crest; 10, most lateral external point on the zygomatic arch; 11, tip of the frontal process; 12, curve corresponding to contact between P4 and M1; 13, curve corresponding to posterior end of canine alveolus; 14, lateral tip of nasal; 15, anterior point of orbital border; 16, interorbital constriction; 17, tip of post-orbital process; 18, post-orbital constriction; 19, frontal-parietal suture over lyriform temporal ridge. We inspected landmark repeatability through assessing the intraclass correlation coefficient sensu Falconer & Mackay (1996) for Procrustes residuals for ten randomly selected specimens digitized six times.

MORPHOMETRICS

Landmark configurations were Procrustes superimposed (Dryden & Mardia, 1998) and shape variables were extracted using the thin-plate splines interpolation technique (Bookstein, 1989) and the complementary subspace method (Rohlf & Bookstein, 2003).

To test whether we should use pooled sexes on the analyses, we employed a two-way multivariate analysis of variance (MANOVA) over the shape variables using the *a priori* groups and sex as factors.

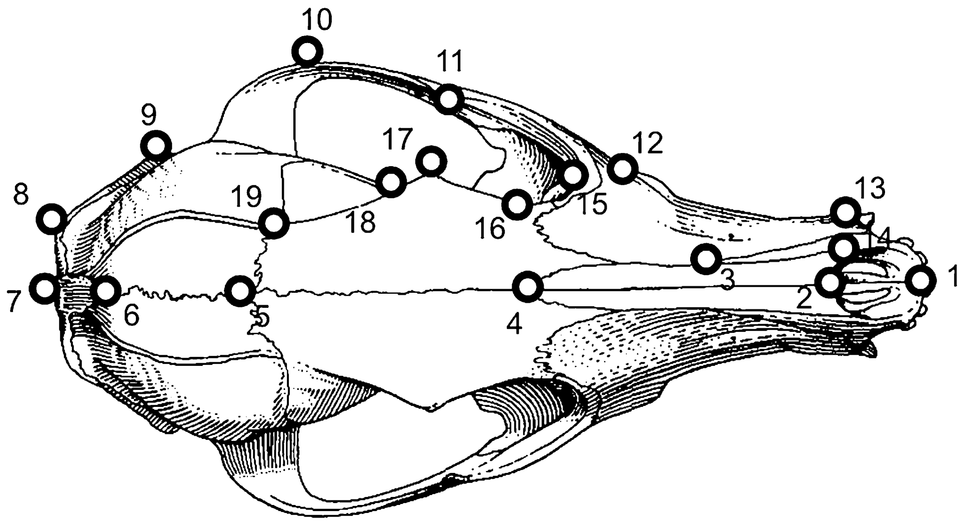

Figure 2. Nineteen two-dimensional anatomical landmarks placed over images of the dorsal view of *Cerdocyon thous* skull. For definitions, see text. Image modified from Berta (1982).

Table 1. Results for the multivariate analysis of variance performed over the W matrix for the fixed effects of a priori groups, sex, and the interaction between them, on *Cerdocyon thous* specimens

	d.f.	Hotelling–Lawley	Approximate F	d.f. (numerator)	d.f. (denominator)	P_r ($>F$)
Sex	1	0.3175	1.9610	34	210	0.002247
Group	2	2.9609	9.1005	68	418	$< 2.2 \times 10^{-16}$
Sex × Group	2	0.3448	1.0598	68	418	0.359390

Both the differences between a priori groups and sexes were significant at the $\alpha = 0.05$ level, but not their interaction. d.f., degrees of freedom.

To test our biogeographical hypothesis, we employed a shape linear discriminant analysis (LDA) over the a priori groups (Northern, Eastern, and Southern), computing the percentage of correctly classified specimens. Because LDA classifies the specimen based on the largest group-membership probability, to access consistency of the results, we also computed the mean posterior probabilities of members of each group belonging to its own group and to other groups. These statistics were also computed using a leave-one-out cross-validation procedure. All analyses were performed on R, version 2.8.1 (R Development Core Team, 2008).

Table 2. Percentages of correctly classified individuals by the linear discriminant analysis of shape variables of the skull of *Cerdocyon thous*

	Correct classifications
Northern	0.8636 (0.8273)
Eastern	0.8487 (0.7731)
Southern	0.7745 (0.7157)
Total	0.8308 (0.7734)

Numbers in parentheses indicate the percentage for the leave-one-out cross-validation.

RESULTS

Repeatability of digitalization was significant for all landmarks chosen, with resampling indexes in the range 0.7–0.9. The results of the two-way MANOVA for group × sex effects are depicted in Table 1. Both groups and sexes were shown to be statistically different. The interaction between factors, however, was not significant, therefore allowing the use of males, females, and individuals of unknown sex in subsequent analysis.

The LDA results are summarized in Table 2 and Table 3. The Northern group showed very high correct classification rates for both original count and cross-validation (86.36% and 82.73%, respectively). The Eastern group showed an intermediate correct

Table 3. Mean posterior probabilities of group membership associated with the a priori groups found by the linear discriminant analysis of shape variables of the skull of *Cerdocyon thous*

	Group mean posterior probabilities		
	Northern	Eastern	Southern
Northern	0.8267 (0.7849)	0.0750 (0.0960)	0.0984 (0.1191)
Eastern	0.0515 (0.0711)	0.7813 (0.7231)	0.1672 (0.2058)
Southern	0.1124 (0.1434)	0.1717 (0.2117)	0.7159 (0.6450)

Numbers in parenthesis indicate the percentage for the leave-one-out cross-validation.

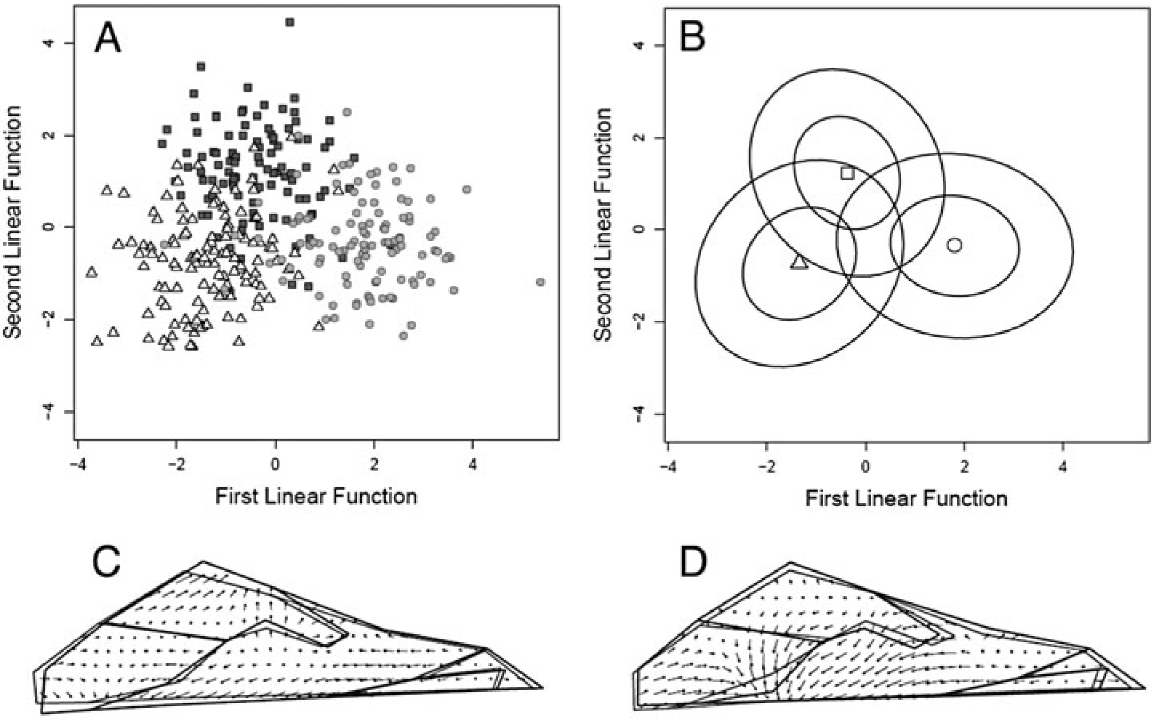

Figure 3. A, individual scores based on geometric morphometric variables related to skull shape of *Cerdocyon thous*, projected onto the linear functions axes. B, representation of 90% and 95% confidence intervals ellipses of the three geographical groups. The circles represents the Northern group, the triangles represents the Eastern group and the squares represents the Southern group. C, D, Generalized Procrustes analysis superimposed configurations of landmarks of extremes shapes along the first and the second discriminant function axis (respectively). Shape deformations are represented as field vectors through TPS interpolation. The lowest score is shown in grey and the greatest in black.

classification rate for original count (84.87%) and performed relatively good on the cross-validation (77.31%). The Southern group showed the lowest correct classification rates for both original count (77.45%) and cross-validation (71.57%). The mean posterior probability of belonging to the correct group showed a similar trend (Table 3) with the Northern, Eastern, and Southern groups having means of 82,67% (78.49% on the cross-validation), 78.13% (72.30% on the cross-validation), and 71.59% (64.50% on the cross-validation), respectively. It is worth noting that most misclassifications are tied to the Southern group because most incorrect mean posterior probabilities in both other groups were biased towards it on both original analysis and cross-validation. Both linear discriminant functions explain 17.088% of the total variance and, although the scores of the specimens belonging to different groups appear to be dispersed (Fig. 3A), there is a clear pattern shown by the ellipses representing 90% of the observations (Fig. 3B). The first linear discriminant axis separates the Eastern from the Northern Group, with the Southern group in an intermediate position, explaining 71.62% of the intergroup variance. The second axis discriminates the Southern group from the other two, and explains 28.38% of the intergroup variance. The shape variation depicted by both axes is shown in Figure 3C and D.

DISCUSSION

The results obtained in the present study demonstrate the existence of three distinct and fairly uniform geographic groups of crab-eating foxes showing a certain degree of shape cohesion. The first discriminant function axis separates the Eastern group (with lower scores) from the Northern group (with higher scores). It shows that the difference resides in the relatively wider braincase, wider zygomatic arch and smaller rostrum (but with a relatively large nasal) in the Northern population. Although the southern group presents intermediate scores in this first axis, it is discriminated in the second axis, presenting high scores. This second axis also expresses a deformation relative to the widening of zygomatic arch, but it is less noticeable and detached from the brain case, which is actually relatively smaller in the Southern population. These deformations appear to be related to functional parameters because animals with shorter rostrum and wider zygomatic arches can have stronger bite force (Christiansen & Adolfssen, 2005). This could be a morphological specialization of the Northern animals for preying on crabs because most of the observations of this behavior originate from this region (Sunquist *et al.*, 1989). Analogously, Southern animals with more constricted lyriform crest could have a more developed masseteric muscle, also influencing bite force. However, the shape differences depicted by these groups are small, and the question of whether or not they are functionally favorable or detrimental should be put to test if selective explanations are to be proposed.

Nevertheless, the discrimination of the groups is indicative that our previous hypothesis is correct, and that HGM vegetation distribution indeed comprises a good explanation for the extant distribution of *C. thous*. As noted previously, the only readily identifiable extant barrier for the distribution of this species is the presence of dense, continuous forested areas in the Amazon Basin. This fact can indeed be related to the existence of the Northern group, but no extant biomes could account for the distinction between the Eastern and the Southern groups.

In a recent molecular study, Tchaicka *et al.* (2007) identified a north–south division of female crab-eating foxes within the eastern population of Brazil, in a pattern that they considered similar to the one found for small vertebrates of the Atlantic Forest. Subsequently, the same processes that allowed multiple invasions of other taxa in the Atlantic Forest might also have an effect on larger open area mammals, acting as a barrier, rather than promoting, gene flow. The process that most likely explains these multiple invasions is the formation of forest belts, and the co-occurrence of these invasions shows that repeated processes have allowed the formations of these belts on Southeastern Brazil as far as the Plio-Pleistocene boundary (Costa, 2003). If this assumption holds, this region could be a preferable site of forest formation during more humid periods.

Tchaicka *et al.* (2007) also estimated the divergence of these groups at approximately 400 000–600 000 years ago, which puts the group formation and its geographical structure at variance. This does not necessarily pose a paradox because it might be considered that the successive cycles of forest dynamics have affected this species throughout the ages in different ways. Although the establishment of the groups happened long before the HGM, it was this harsh environmental alteration that shaped the extant distribution or maybe even maintained a distribution already in place: the past increase in South American forested areas could have affected the populations of *C. thous* not only by the formation of the forest belts itself, but also by increasing the forest areas over previously open area matrices (Vivo & Carmignotto, 2004). This could have driven crab-eating foxes to open southern areas, leading to the origin to the Southern group. An older group, now occupying the eastern region of the continent, could also have persisted in open areas that currently comprise the Cerrado and Caatinga (Tchaicka *et al.*, 2007). Differences in habitat and resource availability could then have altered population dynamics, changing gene flow and, in the presence of some degree of isolation, determining local variants. The disappearance of the barrier, however, could have restored contact between the Eastern and Southern populations, thus slowly breaking down their divergence through male-mediated gene flow (Tchaicka *et al.*, 2007).

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