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# Renal morphology, phylogenetic history and desert adaptation of South American hystricognath rodents

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**Summary**

**1.** To determine whether variation in kidney morphology is associated with environmental aridity in South American hystricognaths, we used conventional and phylogenetic analysis (independent contrasts) to correlate mass-independent renal variables (kidney size; relative medullar thickness, RMT; medulla/cortex ratio, MC; inner medulla/cortex ratio, MIC; relative medullar area, RMA) with environmental variables such as precipitation, temperature and a measure of primary productivity (NDVI).

**2.** Body mass and most renal indexes showed significant phylogenetic signal (the tendency of closely related species to resemble each other), as well as latitude, one index of minimum daily temperature ($T_{min}$) and NDVI, indicating that correcting for phylogenetic effects is necessary, hence results from independent contrasts are more reliable for these traits.

**3.** All renal indexes except RMA and MIC were significantly correlated with body mass. After correcting for size effects, inclusion of precipitation or NDVI improved significantly the regression model for kidney size and MIC regardless of the analyses employed, whereas $T_{min}$ was also a significant predictor of both indices according to independent contrasts. Precipitation was the best predictor of kidney size, with animals from dryer environments having larger kidneys. RMT was not correlated with any of the environmental indexes employed here.

**4.** Our results suggest that hystricognaths from environments with lower rainfall have evolved larger kidneys, probably to cope with aridity. Additional renal indices (RMT, MC and RMA) were not correlated with any environmental variable, and their relative importance as predictors of urine concentration ability for this group of rodents remains unclear.

*Key-words*: Comparative method, kidney, precipitation, temperature, water conservation

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## Introduction

Drylands were an important scenario in the evolution of the South American temperate mammalian biota (Reig 1986; Mares 1992; Ojeda, Blendinger & Brandl 2000). Aridity at medium latitudes became increasingly severe with the orogenic activity during the late Miocene (Solbrig 1977; Pascual 1996). South American hystricognaths rodents (e.g. caviomorphs) occupied the vacant herbivorous niche (Mares & Ojeda 1982), and some of its families (e.g. Octodontidae, Chinchillidae, Caviidae, Abrocomidae and Ctenomyidae) evolved during the period of increasing aridity (Mares 1975; Reig 1986). Because of their longer history in the arid regions of South America, it was suggested that the hystricognath rodents would have developed interesting desert specializations with respect to other lineages of desert rodents (i.e. murids) (Mares 1976).

If we assume the classical model of desert existence as that of the granivorous and bipedal Kangaroo Rat (Tracy & Walsberg 2002), no small mammal in South America would be desert adapted. This view has been adopted ever since the first studies of the South American mammal fauna (Mares 1976, 1980; Meserve 1978), although it was later revised (Mares 1993; Diaz & Ojeda 1999; Diaz, Dacar & Ojeda 2001; Diaz & Cortes 2003). It was only in the 1980s that the



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ecophysiological adaptations to arid environments, as regards water regulatory mechanisms, began to be studied more thoroughly in South American small mammals (Streilein 1982; Cortés 1985; Cortés, Zuleta & Rosenmann 1988). Most South American rodents are water dependent (Cortés, Rosenmann & Baez 1990; Diaz 2001), and among caviomorphs only *Chinchilla laniger* is water independent (Weisser *et al*. 1970; Kohl 1980). However, there are some species capable of producing highly concentrated urine, e.g. *Tympanoctomys barrerae* and *Octodon degus* (Diaz & Ojeda 1999; Bozinovic *et al*. 2003).

The mammalian kidney is unique in having all nephrons with loops of Henle, thus having the ability to concentrate urine more than blood plasma. The concentrating ability of the kidney is not a simple function of the length of the loop of Henle, medullary thickness or of any other single variable per se. The generation and maintenance of the osmotic gradient in the renal medulla will determine the final urine concentration (Bankir & De Rouffignac 1985). This gradient can produce a greater difference in concentration as the renal papilla grows longer, i.e. lengthened loops and collecting ducts (Bankir & De Rouffignac 1985). Hence, the length of the papilla has been considered the structural basis of the concentrating ability (Vimtrup & Schmidt-Nielsen 1952; Schmidt-Nielsen & O'Dell 1961; Beuchat 1990a) and different indices were used as estimators of renal performance (Sperber 1944; Brownfield & Wunder 1976; Geluso 1978). The relationship between the renal efficiency to conserve water in mammals and aridity and body mass has been demonstrated in the classical work of Sperber (1944) and later by Beuchat (1990a, 1996). Greater values of different renal indices are usually found in species of small body size living in arid environments.

A phylogenetic effect on renal morphology in mammals has been suggested by different authors, but only tested for the relative medullary thickness (RMT) and other indices in rodents and marsupials (Brooker & Withers 1994; Al-kahtani *et al*. 2004). Many authors choose to work with the same taxonomic group to minimize the confounding effects of body mass, dietary traits and phylogeny (e.g. bats, Geluso 1975; heteromyids, Lawler & Geluso 1986; sciurids, Blake 1977; Rickart 1989).

Our objectives were to estimate the relative importance of phylogenetic history on kidney morphology, testing statistically for the presence of phylogenetic signal (the tendency of closely related species in a phylogeny to resemble each other; Blomberg & Garland 2002; Blomberg, Garland & Ives 2003), to determine the relation between renal indices and environmental variables employing conventional and phylogenetic analysis, and to test the association of these indices and aridity. Because this group of rodents is entirely herbivorous we also study the relationship between the kidney and the Normalized Digital Vegetation Index (NDVI) as a measure of the primary productivity.

## Materials and methods

### RENAL MORPHOLOGY

Renal size and renal indexes (below) were estimated in a total of 16 species of hystricognath rodents (Appendix). Animals were collected with Sherman (www.shermantraps.com), Havahart, Museum Special and Victor traps. Only adult specimens were considered, and pregnant females were excluded. After capture, animals were brought to the laboratory and were killed humanely with ether (with Argentinean Government permit for scientific purposes, No. 461-1-04-03873), body mass was estimated, and both kidneys were removed and fixed in 10% formaldehyde. Animals were preserved as skins, skulls and skeletons and housed in the Mammal Collection of the Argentinean Institute for Arid Zone Research (IADIZA), Mendoza, Argentina.

In the laboratory, kidneys were weighed and their length, width and thickness were measured with a dial caliper to the nearest 0·1 mm. Kidney size ($mm^3$) was calculated as the product of these three variables. Analyses were performed only for renal size and not for renal mass, because of the differences observed between fresh and fixed tissues (renal mass values are reported for completeness, however; see Appendix). Sections along the frontal axis through the longest part of the renal papilla were obtained from the left kidney (if a complete sagital section could not be made, the right kidney was used). Thickness of the cortex (CT), outer zone of the medulla and inner zone of the medulla were distinguishable when viewed through a stereoscopic microscope (6× magnification); and the medulla thickness (MT) was calculated as the sum of the values for outer and inner medulla. The outline of the entire kidney, including the corticomedullar junction and the outer and inner boundaries of the medulla, were traced on paper using a camera lucida attached to a stereoscopic microscope M5 (Wild, Heerbrugg, Switzerland) (Geluso 1978). The thickness of each zone was measured with a ruler (±0·5 mm). The area of each zone was measured with a LI-COR 3000A portable area meter (LI-COR Inc., Lincoln, NE). Although relative medullar thickness (RMT) has been employed as a surrogate for urine concentration ability in mammals, considerable variation remains unexplained (about 41%, according to Beuchat 1990b), hence we employed additional renal indices potentially relevant (e.g. see Geluso 1978; Bankir & De Rouffignac 1985) to characterize the overall variation in kidney morphology observed within hystricognaths (see Appendix). The following indices were calculated: RMT (= 10 × medullar thickness/cubic root of the product of kidney length, width and thickness), medulla/cortex ratio (MC), inner medulla/cortex ratio (MIC) and relative medullar area (RMA = medullar area/cortical area) (Sperber 1944; Brownfield & Wunder 1976; Heisinger & Breitenbach 1969; Heisinger *et al*. 1973; Geluso 1978; Al-kahtani *et al*. 2004). Significant

associations between these indices and estimates of aridity would suggest that kidney morphology (and presumably urine concentration ability) have evolved as an adaptation to arid environments.

## PHYLOGENY AND ENVIRONMENTAL DATA

Renal indexes from a total of 31 species of South American hystricognaths belonging to nine different families were measured (above) or collected from the literature (Appendix). Our phylogenetic tree was a composite tree built based on previous molecular studies for this group (Fig. 1). The overall topology of the phylogenetic tree was built following Honeycutt, Rowe & Gallardo (2003). Five additional species belonging to the families Agoutidae and Caviidae were included in the tree following Rowe & Honeycutt (2002), and the position of Chinchillidae was determined according to Adkins *et al*. (2001). In addition, *Abrocoma uspallata* was added taxonomically as a politomy in the Abrocomidae family, and *Pipanacoctomys aureus* was placed in the tree as a sister species of *Tympanoctomys barrerae* (M. H. Gallardo, personal communication). Two populations of *Ctenomys* could not be identified at the species level (see Appendix; by providing the site of capture of these colonies and keeping these individuals in the IADIZA Mammal Collection, we expect that this species will be identified in the future). Nevertheless, these species – as well as the remaining *Ctenomys* in our database – were included as a politomy, given that the phylogenetic relationships within this group at the species level remain highly controversial (e.g. Mascheretti *et al*. 2000; Mirol, Mascheretti & Searle 2000).

Environmental variables used were latitude, altitude, annual precipitation, mean maximum and minimum temperature ($T_{max}$ and $T_{min}$; defined as the mean temperature of the hottest and the coldest month of the year, respectively). Data for environmental variables were collected from the nearest weather station available for each capture site (Fig. 2). When more than one station was available (i.e. at similar distances from the capture site), we chose the station that matched more closely the altitude of the capture site, given that altitude is the most influential variable affecting climatic conditions in a small geographical scale. With the exception of one station for *Abrocoma cinerea*, for which we found reliable data for only 2 years, all other climatic variables reflect the average value obtained after at least 6 years of data recording (see Appendix).

In addition, we estimated NDVI (Appendix) from Advanced Very High-Resolution Radiometer (AVHRR) data (Box, Holben & Kalb 1989; Ustin *et al*. 1991). NDVI is significantly correlated with vegetation parameters such as green-leaf biomass, green-leaf area and absorbed photosynthetically active radiation (Goward, Tucker & Dye 1985), and it has

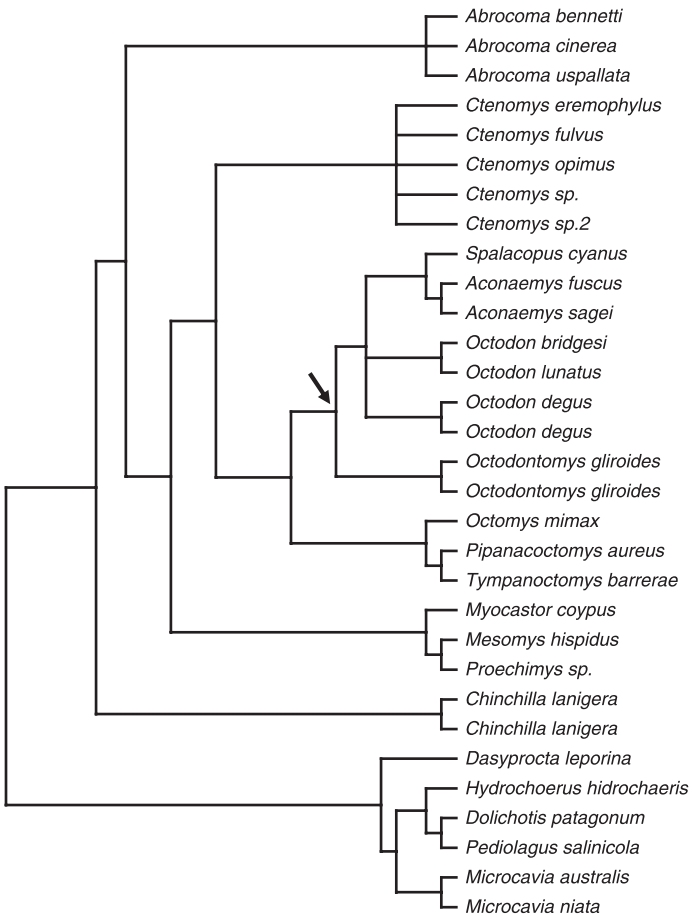


**Fig. 1.** Phylogenetic hypothesis for the 31 species of South American hystricognath rodents employed in the study, shown with arbitrary branch lengths. Different trees were employed depending on the trait, because indexes were not available for every species depicted on the phylogeny, by pruning this initial phylogeny (see *Methods*). The arrow depicts the node where estimated contrasts for precipitation or NDVI may be influential (Figs 3 and 4).

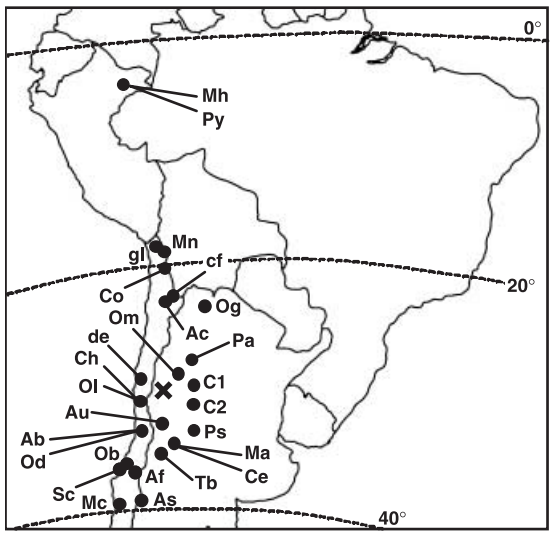


**Fig. 2.** Geographical distribution of species employed in this study (for codes and latitude and longitude values for each species, see Appendix). The cross represents the estimated latitude for the root node of the phylogeny (= 30°30′ S, with ±95% CI between 18°09′-S and 42°49′ S). Longitude for the root node was estimated by eye for illustrative purposes only.

recently been used as a good indicator of terrestrial primary productivity (Tognelli & Kelt 2004). Values of NDVI range from –1·0 to 1·0, with negative values indicating non-vegetated areas such as water, barren land, ice and snow, and positive values indicating increasing green vegetation (Tognelli & Kelt 2004). NDVI data were derived from data collected by the National Oceanic Atmospheric Administration (http://daac.gsfc.nasa.gov/data/dataset/AVHRR), at a resolution of approximately $8 \times 8$ km. The NDVI of each locality corresponds to year means calculated from monthly averages recorded for 18 years.

### STATISTICAL ANALYSES

Phylogenetic signal (*sensu* Blomberg & Garland 2002) for body mass, renal indexes and environmental variables was calculated employing the PHYSIG module developed by Blomberg *et al*. (2003). Assessing whether traits show significant signal is important because it allows the researcher to choose the most adequate statistical analyses for a given data set. We calculated the *K* statistic described in Blomberg *et al*. (2003), which indicates the amount of signal in a trait relative to what would be expected for the specified phylogenetic tree (topology and branch lengths) given a Brownian motion model of evolution. If $K = 1$, then that trait has exactly the amount of signal expected for that given phylogenetic tree, whereas values greater than one indicate more and value less than one indicate less signal than expected (see Blomberg *et al*. 2003). We calculated the amount of signal for both raw and mass-independent values. To compute mass-corrected values and estimate phylogenetic signal in these 'traits', we used the residuals values calculated by PDTREE (screen 9D; residuals were listed in column 5 of the RSD output of PDTREE). These residuals are calculated by mapping the regression slope obtained with independent contrasts back onto the original data space, and then vertical deviations are then calculated (see Garland & Ives 2000; for additional details on this procedure). Because the power to detect phylogenetic signal is highly dependent on the sample size used (e.g. the number of tip branches in the tree; Blomberg *et al*. 2003), we included for these trees all the species that had each renal index available in the data set (Appendix). Constant branch lengths were used to determine phylogenetic signal in each trait when adequate (see below), except for NDVI where we used trees with all branch lengths = 1 and with Nee's arbitrary branch lengths (Table 1).

The relationship between kidney indexes and environmental traits was assessed with multiple regressions with the raw data (e.g. conventional statistics) and also with phylogenetic-independent contrasts (Felsenstein 1985; Garland, Harvey & Ives 1992; Garland *et al*. 1993). Phylogenetic contrasts were calculated using the PDTREE program, developed and described in Garland *et al*. (1992). Because many traits correlate allometrically with body size, we $\log_{10}$-transformed body mass and all renal indexes prior to the calculation of the contrasts. Allometric equations for each renal index were calculated using linear regressions, and all species that had renal indexes measured were used in this context (this was not the case when we performed regressions between these indexes and environmental variables).

Given that some renal indexes were not available for every species, and because some of the renal values were estimated in individuals from zoos (i.e. renal indexes may not necessarily reflect 'real' values for these species in the wild; data from Sperber 1944), we

**Table 1.** Phylogenetic signal, diagnostic graphs, and *K* statistic for all traits (either raw or mass-corrected values; see Materials and methods). All branch lengths (b.l.) = 1, except for NDVI, where Nee's arbitrary branch lengths were used as diagnostic graphs were not significant in this case. Renal indexes and body mass were $\log_{10}$-transformed before analyses. Values highlighted in bold are statistically significant ($P < 0{\cdot}05$)

| | | Raw data | | | Mass-corrected data | | |
|---|---|---|---|---|---|---|---|
| | *N* | Diagnostic $r_p$ | *P* signal | *K* | Diagnostic $r_p$ | *P* signal | *K* |
| Body mass | 31 | 0. 1954 | **0·001** | 0·957 | | | |
| RMT | 30 | 0·1444 | **0·029** | 0·451 | –0. 1725 | **0·002** | 0·562 |
| Kidney size | 20 | –0·2255 | **0·002** | 0·670 | –0·1162 | **0·005** | 0·568 |
| RMA | 14 | –0·2611 | 0·516 | 0·335 | –0·2192 | 0·450 | 0·364 |
| MC | 27 | 0·1549 | **0·023** | 0·432 | –0·1108 | **< 0·001** | 0·855 |
| MIC | 16 | 0·0293 | 0·065 | 0·472 | 0·0711 | **< 0·001** | 1·174 |
| Precipitation | 27 | 0·3222 | **< 0·001** | 1·038 | | | |
| $T_{max}$ | 27 | –0·2163 | 0·505 | 0·261 | | | |
| $T_{min}$ | 27 | –0·0044 | **0·007** | 0·461 | | | |
| Latitude | 27 | –0.1935 | **0·014** | 0·419 | | | |
| Altitude | 27 | –0·3277 | 0·189 | 0·300 | | | |
| NDVI (b.l. = 1) | 27 | **–0·4762** | **0·030** | 0·357 | | | |
| NDVI (b.l. = Nee) | 27 | –0·2463 | **0·024** | 0·717 | | | |

Abbreviations: RMT = relative medullary thickness, RMA = relative medullar area, MC = medulla/cortex ratio, MIC = inner medulla/cortex ratio, $T_{max}$ and $T_{min}$ = mean maximum and minimum ambient temperature, respectively, NDVI = normalized digital vegetation index (see Methods).

built several different trees to analyse the data, in the following manner. First, we started with the original phylogenetic tree with 31 species (Fig. 1), and trimmed those branches for which there were no data available, and the resulting tree was rescaled to simplify analyses. For example, to perform a multiple regression between RMT and environmental variables, we deleted the tip branches leading to *Dasyprocta leporina*, *Dolichotis patagonum*, *Hydrochoerus hidrochaeris* and one population of *Chinchilla lanigera* (Sperber 1944), and *Mesomys hispidus* (given that RMT was not available in this species; Appendix). The resulting tree had therefore 26 species in total. After trimming these branches, the tree was rescaled arbitrarily according to Grafen (1989), Pagel (1992) and assuming a speciational model (all branch lengths = 1). Hence, variables such as precipitation, $T_{max}$ and $T_{min}$ were used repeated times in different trees, because these variables were regressed against many renal indexes for which values from different species were available. For simplicity, we included the number of species with results for each analysis (Tables 2–5).

Adequacy of branch lengths was then assessed by correlating absolute values of standardized phylogenetically independent contrasts (Felsenstein 1985) and their standard deviation (i.e. branch length; diagnostic graphs 1 and 2 in PDTREE), as suggested by Garland *et al.* (1992). Pagel's and Grafen's branch lengths were not adequate for our data set ($P < 0{\cdot}05$ for RMT, $T_{min}$ and $T_{max}$ in several trees), whereas trees with all branch lengths = 1 were adequate in all cases ($P > 0{\cdot}05$ in diagnostics of all traits, and all trees). In two cases, however, the diagnostic graphs for $T_{max}$ and latitude bordered significance ($P = 0{\cdot}061$ and 0·064, respectively; $T_{max}$ bordered significance in the tree to analyse MIC, and latitude in the tree for RMA; Table 4), and it was significant for NDVI ($P = 0{\cdot}014$). For these trees we analysed the data with both regular (branch lengths are the same for all traits) and mixed models (i.e. different branch lengths depending on the trait; in this case, we employed trees with all branch lengths = 1 for all variables, trees with Pagel's branch lengths for $T_{max}$ and latitude, and a tree with Nee's branch length for NDVI). However, given that results were qualitatively identical, we report results for models with all trees having all branch lengths = 1 for simplicity (Tables 4 and 5).

After obtaining phylogenetically independent contrasts for all traits, regular correlations and multiple regressions (through the origin when working with contrasts; Garland *et al.* 1992) were performed with SPSS for Windows. Regression models (always performed through the origin for analyses of contrasts; Felsenstein 1985) were compared employing

**Table 2.** Pearson product–moment correlations between pairs of environmental variables employed in this study. Values in bold indicate a two-tailed *P*-value <0·05 (not corrected for multiple comparisons). $N = 27$ species. Correlations were estimated through the origin for contrasts (26 contrasts, all branch lengths = 1 except for NDVI; see Table 1). Abbreviations are shown Table 1

| | $T_{max}$ | $T_{min}$ | Latitude | Altitude | NDVI |
|---|---|---|---|---|---|
| **Conventional** | | | | | |
| Precipitation | 0·229 | **0·676** | **−0·455** | **−0·404** | **0·638** |
| $T_{max}$ | | **0·632** | 0·014 | **−0·686** | 0·380 |
| $T_{min}$ | | | **−0·539** | **−0·547** | **0·412** |
| Latitude | | | | −0·349 | 0·242 |
| Altitude | | | | | **−0·810** |
| **Independent contrasts** | | | | | |
| Precipitation | 0·142 | 0·341 | −0·175 | −0·267 | **0·539** |
| $T_{max}$ | | **0·671** | 0·257 | **−0·811** | **0·534** |
| $T_{min}$ | | | −0·348 | **−0·490** | 0·227 |
| Latitude | | | | **−0·576** | **0·509** |
| Altitude | | | | | **−0·794** |

**Table 3.** Allometric equations for all variables (body mass expressed in g), obtained with conventional regressions and phylogenetically independent contrasts (all branch lengths = 1). All values were $\log_{10}$-transformed before regressions, and the lower and upper limit for the 95% confidence intervals are indicated between parentheses. Abbreviations are shown in Table 1

| | | Conventional statistics | | Independent contrasts | |
|---|---|---|---|---|---|
| | *N* | Slope | Intercept | Slope | Intercept |
| RMT | 30 | −0·158 (−0·222, −0·094) | 1·197 (1·036, 1·358) | −0·216 (−0·290, −0·142) | 1·378 (1·122, 1·635) |
| Kidney size | 20 | 0·793 (0·648, 0·938) | 1·428 (1·043, 1·813) | 0·833 (0·667, 0·999) | 1·249 (0·682, 1·816) |
| RMA | 14 | −0·0307 (−0·391, 0·329) | 0·054 (−0·739, 0·847) | −0·088 (−0·583, 0·408) | 0·233 (−1·070, 1·535) |
| MC[a] | 27 | −0·185 (−0·303, −0·067) | 1·022 (0·720, 1·323) | −0·304 (−0·421, −0·187) | 1·399 (1·000, 1·798) |
| MIC | 16 | 0·043 (−0·286, 0·199) | 0·562 (−0·015, 1·139) | −0·175 (−0·486, 0·136) | 0·982 (0·103, 1·861) |

[a]Slopes and intercepts differ significantly following the criterion that the mean value obtained with independent contrasts does not fall within the 95% confidence interval from conventional statistics (T. Garland and A. Ives, personal communication). The opposite is not true, however.

**Table 4.** Results from multiple regressions between renal indexes, body mass and environmental variables, employing conventional and phylogenetically correct statistics (all branch lengths = 1). Only those models for which at least one environmental variable remained significant ($P < 0{\cdot}05$, in bold) are shown (mass effects were reported for all renal indexes). Regressions were performed including mass plus one additional environmental variable at a time (precipitation, $T_{max}$, $T_{min}$, latitude and altitude). Renal indexes were $\log_{10}$-transformed before multiple regressions. Values from Sperber (1944) were not included in these analyses (see Methods). Abbreviations are shown in Table 1

| Dependent variable | *N* | Model | Partial regression coefficient sign | Multiple $R^2$ | Standard error | *F* change | 2-tailed *P* for *F* change |
|---|---|---|---|---|---|---|---|
| **Conventional** | | | | | | | |
| RMT | 26 | Body mass (*M*) | – | 0·263 | 0·1054 | 8·555 | **0·007** |
| | | *M* + precipitation | – | 0·433 | 0·0944 | 6·885 | **0·015** |
| Kidney size | 16 | Body mass | + | 0·695 | 0·2682 | 31·865 | **< 0·001** |
| | | *M* + precipitation | – | 0·824 | 0·2112 | 9·570 | **0·009** |
| | | *M* + altitude | + | 0·798 | 0·2259 | 6·732 | **0·022** |
| | | *M* + NDVI | – | 0·880 | 0.1743 | 20·136 | **0·001** |
| RMA | 14 | Body mass | + | 0·003 | 0·2101 | 0·034 | 0·856 |
| MC | 24 | Body mass | – | 0·185 | 0·2078 | 4·978 | **0·036** |
| | | *M* + precipitation | – | 0·369 | 0.1871 | 6·143 | **0·022** |
| | | *M* + NDVI | – | 0·323 | 0.1938 | 4·290 | 0·051 |
| MIC | 14 | Body mass | – | 0·009 | 0·2524 | 0·111 | 0·745 |
| | | *M* + precipitation | – | 0·486 | 0.1898 | 10·226 | **0·008** |
| | | *M* + NDVI | – | 0·493 | 0.1885 | 10·511 | **0·008** |
| **Independent contrasts** | | | | | | | |
| RMT | 26 | Body mass (*M*) | – | 0·343 | 0·0637 | 12·537 | **0·002** |
| Kidney size | 16 | Body mass | + | 0·794 | 0·1603 | 54·069 | **< 0·001** |
| | | *M* + precipitation | – | 0·870 | 0·1324 | 7·540 | **0·017** |
| | | *M* + $T_{min}$ | – | 0·858 | 0·1381 | 5·873 | **0·031** |
| | | *M* + NDVI | – | 0·875 | 0·1297 | 8·404 | **0·012** |
| RMA | 14 | Body mass | – | 0·012 | 0.1706 | 0·149 | 0·706 |
| MC | 24 | Body mass | – | 0·351 | 0·1111 | 11·909 | **0·002** |
| MIC | 14 | Body mass | – | 0·070 | 0·1623 | 0·907 | 0·360 |
| | | *M* + precipitation | – | 0·497 | 0·1247 | 9·330 | **0·011** |
| | | *M* + $T_{min}$ | – | 0·492 | 0·1253 | 9·138 | **0·012** |
| | | M + NDVI | – | 0·442 | 0·1313 | 7·319 | **0·020** |

cross-validation (Roff 2006): we set a portion of the data (three contrasts) aside and ran the alternative models with the remainder data *n* times, calculating residual sums of squares (RSS) between predicted values and values set aside as if they were new observations in each iteration. We estimate mean RSS for each model over *n* iterations, and then compare adequacy between models with a paired *t*-test (df = $n - 1$ iterations). Cross-validation was performed with S-PLUS 6·2 for Windows.

**Table 5.** Urine concentration values available for South American hystricognaths. Maximum values obtained under different conditions: in the field (*), in captivity without water stress (**) and in captivity with water stress (***)

| | Urine concentration (mOsm/kg) | Source |
|---|---|---|
| *Cavia porcellus* | 1045** | Bellamy & Weir (1972) |
| *Chinchilla lanigera* | 1808** | Bellamy & Weir (1972) |
| *Ctenomys eremophylus* | 1253* | Diaz (2001) |
| *Galea musteloides* | 1061** | Bellamy & Weir (1972) |
| *Lagostomus maximus* | 1650** | Bellamy & Weir (1972) |
| *Microcavia australis* | 2891* | Diaz (2001) |
| *Octodon degus* | 4338*** | Cortés *et al.* (1990) |
| *Octomys mimax* | 2071* | Diaz & Ojeda (1999) |
| *Pediolagus salinicola* | 1627* | Diaz (2001) |
| *Spalacopus cyanus* | 3272*** | Cortés *et al.* (1990) |
| *Tympanoctomys barrerae* | 7080* | Diaz & Ojeda (1999) |

## Results

### PHYLOGENETIC SIGNAL AND CORRELATION BETWEEN VARIABLES

Most traits showed significant phylogenetic signal (Table 1). Among the physiological variables, only RMA did not show significant signal. In addition, all physiological variables except mass-corrected MIC showed less signal than expected (i.e. $K < 1$) assuming a Brownian motion mode of evolution. Environmental variables also showed significant signal in most cases (that was not the case for $T_{max}$ and altitude; Table 1), and precipitation exhibited precisely the amount of signal expected for the tree we employed (all branch lengths = 1).

As expected, many environmental traits were significantly correlated, either using conventional statistics or independent contrasts (Table 3), although multicollinearity did not appear to be a problem ($T_{max}$ and altitude were highly correlated using contrasts, though

they were not included together in any model). On the other hand, kidney indexes were highly correlated, according to conventional Pearson's product–moment correlations (RMT with MC and MIC, $N = 26$, $r = 0{\cdot}866$ and $N = 15$, $r = 0{\cdot}767$, respectively; $P < 0{\cdot}001$ in all cases). Hence, we analysed one index at a time, using models including both mass and one environmental variable in the multiple regressions (see Table 4).

## ALLOMETRIC RELATIONSHIPS

Allometric equations obtained with conventional regressions and with independent contrasts are shown in Table 3. Intercepts and 95% confidence limits for the independent contrasts regressions were calculated by plotting the slope obtained through the origin back onto the original data space in PDTREE, following Garland & Ives (2000). In most cases, there was no significant difference between equations, although slope and intercept values changed slightly (Table 3). However, the mean slope obtained with contrasts for MC was outside the 95% confidence interval obtained for the slope with conventional statistics, but the opposite was not true (Table 3). Hence, the allometric relationship for MC seems to change 'significantly' depending on which statistical method is used. Given that both raw MC and mass-corrected MC showed significant phylogenetic signal (Table 1), the allometric equation obtained with independent contrasts would be more appropriate in this case.

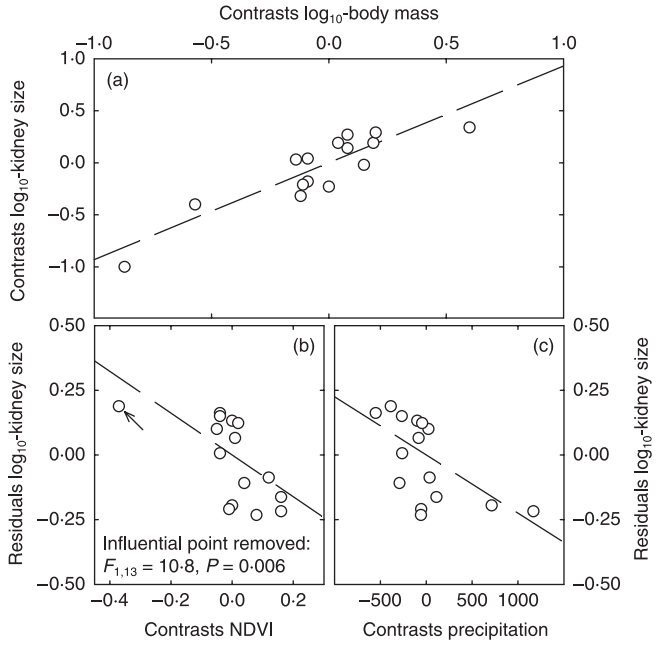


**Fig. 3.** Relationship between independent contrasts of kidney size *vs* body mass (panel a) and mass-corrected contrasts of kidney size plotted *vs* contrasts of NDVI and precipitation (panels b and c, respectively). Dashed lines represent linear regressions through the origin for the entire data set (the allometry for 20 species is shown in Table 3, results for models including environmental variables are listed in Table 4). The arrow in panel (b) highlights a potentially influential contrast shown in Fig. 1. Results were identical regardless of whether this contrast was removed from the analysis or not (compare results from Table 4 with those after removing influential point in panel b).

## KIDNEY INDEXES AND ENVIRONMENTAL VARIABLES

Body mass was not significantly correlated with $T_{min}$, $T_{max}$, altitude and NDVI, regardless of whether phylogeny was controlled or not ($N = 26$ species; $F_{1,24} < 2{\cdot}27$, $P > 0{\cdot}145$ in all cases). The relationship between body mass and precipitation was positive and approached significance according to conventional regression ($F_{1,24} = 4{\cdot}17$, $P = 0{\cdot}052$), although this relationship was not significant with phylogenetic analyses ($F_{1,24} = 0{\cdot}93$, $P = 0{\cdot}763$). Discrepancies between analyses were because values for *Proechimys* and *Myocastor* (i.e. sister species in this analysis because *Mesomys* was not included; Fig. 1) had higher body mass and precipitation values than the average (Appendix), and were influential points for conventional regressions but not for contrasts. Conversely, there was no correlation between body mass and latitude according to conventional analysis ($F_{1,24} = 0{\cdot}049$, $P = 0{\cdot}826$), whereas for phylogenetic analyses latitude and mass were positively but not significantly correlated ($P = 0{\cdot}069$) because the contrast calculated from the same two species was an influential point (notice the difference in geographical location between these species; Fig. 2). After removing this value, no significant relationship between body mass and latitude was observed ($F_{1,23} = 1{\cdot}062$, $P = 0{\cdot}313$).

Although conventional multiple regressions suggest that, after correcting for size differences, RMT, kidney size, MC and MIC are significantly negatively correlated with precipitation, this remained true only for kidney size and MIC when analyses were performed with independent contrasts (Table 4, Figs 3 and 4). Moreover, these two renal indexes were also negatively correlated with $T_{min}$. Accordingly, $T_{min}$, precipitation and NDVI were significantly correlated according to conventional statistics, and NDVI remained correlated with precipitation after controlling for phylogenetic history (Table 2). In models including more than one environmental variable, NDVI was close to significance after controlling for precipitation effects ($F_{1,12} = 3{\cdot}49$, two-tailed $P = 0{\cdot}086$) or significant in models accounting for $T_{min}$ ($F_{1,12} = 6{\cdot}42$, $P = 0{\cdot}026$), whereas precipitation was never significant in models controlling for $T_{min}$ ($F_{1,12} = 1{\cdot}76$, $P_{rainfall} = 0{\cdot}209$) and vice versa ($F_{1,12} = 0{\cdot}65$, $P_{Tmin} = 0{\cdot}437$). Employing cross-validation on the contrasts of kidney size ($N = 15$ contrasts, subsets of 12 contrasts were randomly picked 1000 times; body mass was always included), precipitation was a significantly better predictor of kidney size than $T_{min}$ (paired $t_{999} = 4{\cdot}93$, $P < 0{\cdot}001$) and NDVI ($t_{999} = 14{\cdot}93$, $P < 0{\cdot}0001$; mean RSS = 0·056 for precipitation, 0·062 for $T_{min}$ and 0·090 for NDVI). Inclusion of NDVI or $T_{min}$

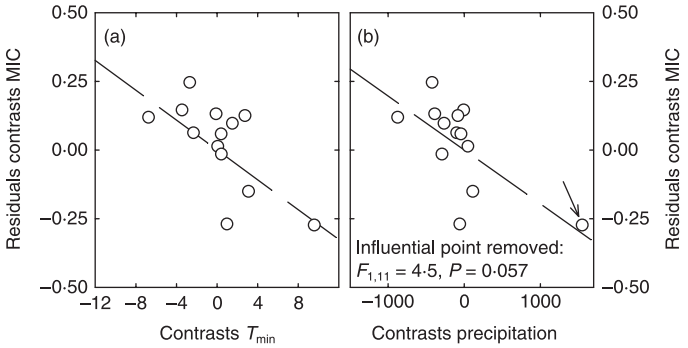


**Fig. 4.** Relationship between residual (mass-corrected) contrasts of MIC plotted *vs* contrasts of $T_{min}$ and precipitation (panels a and b, respectively). Dashed lines represent linear regressions through the origin for the entire data set (results for the two models are listed in Table 4). The arrow in panel (b) indicates a potentially influential contrast (see Fig. 1), but the relation remains negative and borders significance after the removal of this point (see Table 4 for results without removing this point).

did not improve significantly the model containing precipitation (mean RSS [precipitation + $T_{min}$] = 0·073, mean RSS [precipitation + NDVI] = 0·071).

For MIC, precipitation and $T_{min}$ remained close to significance in models controlling for NDVI ($F_{1,10}$ = 3·43, $P$ = 0·094 and $F_{1,10}$ = 4·19, $P$ = 0·068, respectively), but the opposite was not true ($P_{NDVI}$ > 0·119 in both cases). After controlling for precipitation, $T_{min}$ effects were not significant ($F_{1,10}$ = 0·77, $P$ = 0·402) and vice versa ($F_{1,10}$ = 0·89, $P$ = 0·373). According to cross-validation (subsets of 10 of 13 contrasts), the regression model with $T_{min}$ (mean RSS = 0·057) was significantly better than models with precipitation (mean RSS = 0·062; $t_{999}$ = −4·38, $P$ < 0·0001) and NDVI (RSS = 0·108; $t_{999}$ = −16·91, $P$ < 0·0001). Adding either precipitation or NDVI did not improve the fitness of the model with $T_{min}$ (mean RSS = 0·072 and 0·063 for these models, respectively).

## Discussion

### PHYLOGENETIC SIGNAL

Most environmental traits showed significant phylogenetic signal, i.e. closely related species were statistically more similar than expected at random, except for $T_{max}$ and altitude. Patterns of vicariance might account for the presence of significant phylogenetic signal in traits such as latitude, which has been repeatedly the case (Freckleton, Harvey & Pagel 2002; Blomberg *et al*. 2003; Rezende, Bozinovic & Garland 2004), but not for altitude (Rezende *et al*. 2004). These results suggest that altitude has not been an obstacle for geographical radiation within the hystricognaths rodents (i.e. the phylogenetic signal may have been obscured by more recent events of dispersal and/or migration). Conversely, significant signal in latitude could indicate that latitudinal trends might still reflect ancient patterns of speciation and vicariance within these groups. In our study $K$ was 0·419 for latitude, being lower than 1 for this hierarchical tree (all body length = 1) and in accordance with $K$-values reported for most ecological or environmental traits (between 0·2 and 0·5; Blomberg *et al*. 2003; Al-kahtani *et al*. 2004; see also Garland, Bennett & Rezende 2005), except for latitude among different rodent species across South and North America, Europe and Australia ($K$ = 1·048, Rezende *et al*. 2004).

Body mass and most kidney indices exhibited significant phylogenetic signal as previously reported (Freckleton *et al*. 2002; Blomberg *et al*. 2003; Al-kahtani *et al*. 2004; Rezende *et al*. 2004), particularly for kidney mass, RMT and urine concentration (Al-kahtani *et al*. 2004). The only exception was RMA and mass-corrected RMA, which showed no significant signal (MIC bordered significance, $P$ = 0·065; Table 1). Although RMA could be more 'labile' than the other kidney indexes (hence evolving faster and obscuring signal; Blomberg *et al*. 2003), we believe this pattern was probably due to the reduced statistical power to detect signal as sample size decreases, being 0·6 or lower for trees with 14 species (Fig. 2 in Blomberg *et al*. 2003).

Estimates of $K$ for body mass, RMT and mass-corrected RMT (Table 1) were consistently higher than values reported for 141 species of rodents (0·678, 0·302 and 0·192, respectively, using $\log_{10}$-transformed data; Al-kahtani *et al*. 2004). It is not clear whether this pattern is a real biological phenomenon resulting from phenotypic divergence in contrasting time scales, or whether it reflects differences on the quality of the phylogenies and data employed by each study. Phylogenetic effects could be more important in our study owing to the more recent evolutionary history of hystricognaths (compared with rodents in general), which would result in lower divergence times for phenotypic evolution everything else being the same (for comparisons of $K$ indexes across several trees, see Blomberg *et al*. 2003).

The use of an accurate phylogeny to describe the evolutionary history of a lineage is critical to estimate the presence and magnitude of signal on a trait, and discrepant $K$-values could result from different sources of errors on the topology and lengths of branches adopted in each study. The existence of phylogenetic signal in most ecological and physiological traits studied here highlights the necessity of considering the phylogenetic history of this lineage in the analyses (Blomberg *et al*. 2003; Al-kahtani *et al*. 2004; Rezende *et al*. 2004; Garland *et al*. 2005).

### RENAL FUNCTION AND ENVIRONMENTAL VARIABLES

The main factors involved in shaping renal morphology in mammals are body mass, diet and habitat (Lawler & Geluso 1986; Beuchat 1990a, 1996; Brooker & Withers 1994; Schondube, Herrera and Martinez del Rio 2001). In this study we separated the effects of phylogeny,

body mass and climate (although dietary habits might be associated with some of the phenotypic variation observed in our sample, most hystricognaths are strictly herbivorous, hence diet effects were probably small). After accounting for phylogenetic effects, results from multiple regressions show that body mass is the main factor determining the renal gross size and morphology. Regarding the allometry of kidney indexes, caviomorph rodents show the general pattern expected for mammals and rodents (see Beuchat 1996; Al-kahtani *et al*. 2004): smaller species possess significantly higher RMT and MC (Table 4). Allometric slopes and intercepts for RMT in our study were similar to those reported for 141 species of rodents by Al-kahtani *et al*. (2004) for both conventional (RMT $= 5{\cdot}28 \times \text{mass}^{-0{\cdot}16}$ *vs* $4{\cdot}09 \times \text{mass}^{-0{\cdot}15}$, respectively; mass in kg) and phylogenetically corrected regressions ($5{\cdot}37 \times \text{mass}^{-0{\cdot}22}$ *vs* $5{\cdot}00 \times \text{mass}^{-0{\cdot}13}$; mass in kg), with 95% CI overlapping in all cases. Similarly, allometric slopes for kidney size in this study (Table 3) and kidney mass reported for rodents in general (Al-kahtani *et al*. 2004) did not differ significantly according to 95% CI.

Most studies consider aridity as a categorical variable (e.g. Sperber 1944; Beuchat 1996; Al-kahtani *et al*. 2004), which can be vague because aridity is the result of several interacting factors such as precipitation, ambient temperature and primary productivity. Therefore, it is not possible to address which selective pressures these lineages may have faced during their evolutionary history, or to understand how organisms may adapt to arid habitats with different environmental characteristics (e.g. cold *vs* hot deserts). According to our analyses employing continuous variables as surrogates of environmental aridity, in hystricognaths both kidney size and MIC were negatively correlated with $T_{min}$, precipitation and NDVI (Table 4). Moreover, although these environmental variables are not orthogonal to one another (Table 2), results from models controlling for more than one environmental variable at a time suggest that NDVI effects are somewhat independent of precipitation and $T_{min}$.

Nevertheless, it is difficult to discriminate which of these variables may be more relevant in determining kidney size or MIC based solely on our results. Multiple regressions including more than one variable at a time suggest that NDVI is a better descriptor of residual (i.e. mass-independent) variation in kidney size. Although NDVI has been employed as an index of primary productivity, which suggests that this factor might affect kidney size and function to some extent independently of precipitation, it is not clear whether other factors associated with NDVI might be involved on the correlations observed between this index and kidney size.

In addition, both precipitation and $T_{min}$ were significantly correlated with kidney size and MIC, and it was not possible to separate these effects despite the medium to low degree of collinearity between these variables (Table 2).

Conversely, cross-validation analysis suggests that precipitation is a significantly better predictor of kidney size than NDVI, whereas $T_{min}$ explained significantly better the residual variation of MIC than the other two environmental variables (see Results). Discrepancies between results may be due to influential contrasts present in the regression with the full data set (Fig. 3), which would suggest that results from cross-validation are more reliable. We emphasize that cross-validation employing contrasts should be performed with caution, because the subsets are not necessarily independent owing to the hierarchical nature of contrasts calculations (i.e. contrasts from nodes deep in the phylogeny are calculated based on values for higher nodes; see Felsenstein 1985; Garland *et al*. 2005). Nevertheless, the cross-validation employed in this study may be useful to address effects of potential influential contrasts on alternative regression models (e.g. Figs 3b and 4b), and support that South American hystricognaths have evolved larger kidneys in response to increased aridity (measured as precipitation or NDVI; Fig. 3).

The significant negative correlation between kidney size and MIC with $T_{min}$ (Table 4), and $T_{min}$ being a significantly better predictor of MIC than precipitation were unexpected results. In addition, $T_{max}$ was not correlated with kidney size or MIC. Interestingly, in dasyurid marsupials MIC was positively correlated with $T_{max}$ (Brooker & Withers 1994), whereas in our study we obtained a significant negative correlation between $T_{min}$ and residual MIC (Table 4). However, $T_{max}$ for their set were in average 6·5 °C higher than ours, being statistically significant according to a *t*-test ($t_{66} < 0{\cdot}0001$), which suggests that species from our study encounter colder environments than those marsupials. One possibility is that selective pressures associated with temperature differ at different ranges of temperature, hence the relation between kidney indices and temperature may not be linear. However, it is not functionally clear how increased inner medulla could be advantageous at colder temperatures, whereas the negative correlation between kidney size and $T_{min}$ could suggest that kidney size and thermoregulatory requirements are somehow related (see Greenwald & Stetson 1988). Nevertheless, whether the association between $T_{min}$ and kidney size or MIC is a general pattern across more distant groups or a characteristic of hystricognaths in particular remains unclear.

## Conclusion

Although our working hypothesis is that kidney function and water retention mechanisms were under selection during the evolution of hystricognaths, it remains to be determined which renal index is a better predictor of the concentrating ability in this group. Most urine concentration values for hystricognaths (Table 5) possibly do not reflect the maximum urine concentrating ability (G. B. Diaz and R. A. Ojeda,

unpublished data). Kidney size and/or MIC may be associated with maximum urine concentrating ability in this group, although this issue remains to be tested. Moreover, other factors involved in water balance such as dietary water and salt content may influence kidney morphology and function. We found that precipitation is correlated with kidney size and MIC, but not with RMT. The later index was traditionally used as a good predictor of the maximum urine concentrating ability in mammals (see Al-kahtani *et al*. 2004 and references therein), whereas in our study none of the environmental indexes was significantly correlated with residual RMT.

How can we account for these discrepant results? On one hand, our approach might have some limitations. For instance, variables included in this study may not reflect accurately those selective pressures imposed by arid environments (nevertheless, some kidney indexes were significantly correlated with those environmental variables). We employed long-term averages for temperature and precipitation in our analyses, but deviations around these mean values may be more evolutionarily relevant and we did not control for seasonality (specimens were collected at different seasons, and kidney size can be plastic; e.g. Hammond, Szewczak & Krol 2001; Bacigalupe *et al*. 2004) or environmental unpredictability (e.g. either food or water availability). In addition, phylogeny may have been a confounding factor at least in some studies (but see Brooker & Withers 1994; Al-kahtani *et al*. 2004). In our study, we obtained a significant negative correlation between residual RMT and precipitation employing only conventional analyses, although the presence of signal in body mass, RMT and precipitation suggest that results with independent contrasts should be more accurate.

On the other hand, these results may be biologically realistic, and other renal traits (i.e. nephron heterogeneity, the presence of extensions of the renal pelvis into the medulla, degree of confluence of the collecting ducts in the inner medulla, among others; Dantzler & Braun 1980; Bankir & De Rouffignac 1985; Dantzler 2005) may be better predictors of the maximum urine concentrating ability (Brownfield & Wunder 1976). For example, how the organization of tubules and vascular bundles inside the renal medulla, especially within the inner stripe of the outer medulla (i.e. simple *vs* complex medullary organization; Kriz 1981), affects urine concentration ability has not been properly assessed. Interspecific variation at this level might account for differences in urine concentration independently of RMT (which does not take into account the architectural organization of tubules and blood vessels inside the medulla). Little information in this context is available for hystricognaths: whereas a complex medulla has been described for *Octodon degus* (Barrett & Majack 1977), a simple medullary organization has been described for the chinchilla (Bankir & De Rouffignac 1985). Additional studies regarding the evolution of medullary organization in this group might provide important insights on how complex medullae may have evolved as a response to environmental aridity.

Our results support that hystricognaths have evolved larger kidneys in response to increased aridity, which could lead to higher medullary thickness with no significant changes in RMT (which is standardized by kidney size, not body size; see Beuchat 1990b). It is possible that selective factors independent of aridity per se may account for this pattern; perhaps the strategy of having larger kidneys instead of higher RMT has resulted from selective pressures on higher metabolic rates (e.g. see Greenwald & Stetson 1988). Although this hypothesis is supported by the significant correlations observed with $T_{min}$, further studies are necessary to elucidate the mechanisms underlying the association between renal function and thermoregulatory abilities.

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## Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

**Appendix S1.** Body mass and renal, geographical (latitude, longitude and altitude) and environmental variables employed in this study

**Sources of environmental data**

**Appendix S1.** Body mass and renal, geographical (latitude, longitude and altitude) and environmental variables employed in this study.

| Species | Tip code | Body mass (g) | Renal size ($mm^3$) | Renal mass (g) | RMT | MC | MIC | RMA | Annual rainfall (mm) | Lat. South | Long. West | Alt. (m) | Tmin (°C) | Tmax (°C) | NDVI | Ref |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| N = | | 31 | 20 | 23 | 30 | 27 | 16 | 14 | 27 | 27 | 27 | 27 | 27 | | | |
| *Abrocoma bennetti* | Ab | 245 | 2311 | 1.19 | 6.93 | 2.75 | 1.79 | 0.63 | 481.5 | 33°09' | 71°32' | 360 | 9.40 | 17.10 | 0.6907 | 1 |
| *Abrocoma cinerea* | Ac | 85 | | 0.71 | 6.9 | 3.41 | | | 1.3 | 23°35' | 67°53' | 3350 | 7.30 | 13.40 | 0.1593 | 2,3 |
| *Abrocoma uspallata* | Au | 149.9 | 2490 | 1.42 | 6.85 | 4.08 | 3.25 | | 324.0 | 32°35' | 68°58' | 1783 | 5.00 | 17.10 | 0.4660 | 4 |
| *Dasyprocta leporina* | Da | 2600 | 12167 | 7.69 | 3.9 | 1.8 | | | | | | | | | | 5 |
| *Dolichotis patagonum* | Dp | 8030 | 42875 | | 5.7 | 4 | 2.6 | | | | | | | | | 5 |
| *Microcavia australis* | Ma | 222.9 | 2582 | 1.74 | 9.76 | 7.99 | 5.72 | 1.74 | 310.0 | 34°02' | 67°58' | 572 | 6.40 | 25.00 | 0.5367 | 1 |
| *Microcavia niata* | Mn | 181 | | 0.93 | 8.1 | 7.6 | | | 316.0 | 20°03' | 68°50' | 3990 | 0.20 | 8.20 | 0.1507 | 2,3 |
| *Pediolagus salinicola* | Ps | 1440 | 9459 | 4.4 | 7.02 | 4.5 | 3.12 | 1.26 | 450.0 | 33°16' | 66°21' | 713 | 9.67 | 24.84 | 0.5353 | 1 |
| *Chinchilla lanigera* | cl | 312 | | 1.01 | 6.7 | 5.6 | | | 175.0 | 31°38' | 71°11' | 290 | 11.20 | 20.20 | 0.5013 | 2,3 |
| *Chinchilla lanigera* | Ch | 475 | 2197 | | 9.6 | | 2.8 | | | | | | | | | 5 |
| *Ctenomys eremophylus* | Ce | 112.1 | 1253 | 0.8 | 9.22 | 5.46 | 4.28 | 0.89 | 310.0 | 34°02' | 67°58' | 572 | 6.40 | 25.00 | 0.5367 | 1,6 |
| *Ctenomys fulvus* | cf | 185 | | 0.94 | 6.9 | 6.23 | | | 25.4 | 23°11' | 68°05' | 2430 | 8.30 | 19.40 | 0.1187 | 2 |
| *Ctenomys opimus* | Co | 370 | | 1.29 | 6.3 | 2.45 | | | 179.3 | 21°57' | 68°31' | 3318 | 8.00 | 12.10 | 0.1327 | 2 |
| *Ctenomys* sp. 1 | C1 | 78 | 948.5 | | 8.14 | 3.85 | 2.88 | 1.17 | 320.0 | 30°22' | 66°17' | 461 | 11.27 | 26.42 | 0.6073 | 1 |
| *Ctenomys* sp. 2 | C2 | 52 | 329.8 | | 12.12 | 8.33 | | 1.43 | 242.9 | 31°20' | 66°36' | 658 | 10.16 | 26.68 | 0.5887 | 1 |
| *Mesomys hispidus* | Mh | 210 | | | | 2.2 | 1 | 0.53 | 2878.3 | 03°45' | 73°15' | 126 | 24.86 | 25.97 | 0.7753 | 1 |
| *Proechimys* sp. | Py | 263.3 | 785.1 | | 4.6 | 2.3 | | 0.63 | 2878.3 | 03°45' | 73°15' | 126 | 24.86 | 25.97 | 0.7753 | 1 |
| *Hydrochoerus hidrochaeris* | Hh | 53000 | 148877 | | 2.1 | 1.22 | | | | | | | | | | 5 |
| *Myocastor coypus* | Mc | 4455 | 20368 | 14.5 | 3.5 | 1.37 | | | 1871.0 | 39°38' | 73°05' | 19 | 6.76 | 15.73 | 0.7807 | 1 |
| *Aconaemys fuscus* | Af | 123.3 | 703.4 | 0.44 | 4.88 | 2.31 | 1.7 | 1.75 | 1107.0 | 36°52' | 71°38' | 710 | 6.70 | 17.60 | 0.7220 | 1 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aconaemys sagei* | As | 106 | | 0.34 | 5.9 | | | | 1157.4 | 39°16' | 71°58' | 215 | 7.70 | 17.30 | 0.9133 | 3 |
| *Octodon bridgesi* | Ob | 163 | | 0.46 | 5.4 | | | | 690.0 | 35°26' | 71°38' | 110 | 8.00 | 21.00 | 0.6833 | 3 |
| *Octodon degus* | de | 160 | | 0.70 | 6.7 | 2.66 | | | 81.8 | 29°55' | 71°12' | 146 | 10.63 | 17.02 | 0.4400 | 2,3 |
| *Octodon degus* | Od | 118.6 | 981 | 0.46 | 7.08 | 3.6 | 2.38 | 0.85 | 481.5 | 33°09' | 71°32' | 360 | 9.40 | 17.10 | 0.6907 | 1 |
| *Octodon lunatus* | Ol | 171 | | 0.67 | 5.3 | | | | 175.0 | 31°38' | 71°11' | 290 | 11.20 | 20.20 | 0.5013 | 3 |
| *Octodontomys gliroides* | gl | 187 | | 0.86 | 8.5 | 3.26 | | | 316.0 | 18°12' | 69°16' | 4392 | -1.20 | 6.20 | 0.2973 | 2,3 |
| *Octodontomys gliroides* | Og | 153 | 2009 | | 5.35 | 3.73 | 3.19 | 1.03 | 25.4 | 23°11' | 68°05' | 2430 | 8.30 | 19.40 | 0.1187 | 1 |
| *Octomys mimax* | Om | 94.6 | 1164 | 0.52 | 6.11 | 3.59 | 2.52 | 0.83 | 150.0 | 30°15' | 68°45' | 1165 | 9.70 | 24.95 | 0.4287 | 1 |
| *Pipanacoctomys aureus* | Pa | 107 | 3381 | 1.74 | 10.52 | 10.47 | 8.03 | | 183.0 | 28°04' | 67°34' | 1201 | 10.10 | 24.90 | 0.3093 | 1 |
| *Spalacopus cyanus* | Sc | 85.6 | 352.2 | 0.23 | 5.92 | 2.66 | 1.75 | 0.42 | 695.0 | 36°15' | 71°32' | 380 | 7.30 | 19.50 | 0.7780 | 1 |
| *Tympanoctomys barrerae* | Tb | 81.5 | 2124 | 1.27 | 9.62 | 7.99 | 5.66 | 1.8 | 300.0 | 35°02' | 68°40' | 1258 | 6.20 | 19.80 | 0.2920 | 1 |

References: 1. Diaz (2001); 2. Diaz & Cortés (2003); 3. Al-kahtani *et al.* (2004); 4. G.B. Diaz, unp. data; 5. Sperber (1944); 6. Diaz & Ojeda (1999).

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