Bioenergetics, thermoregulation and urine analysis of squirrels of the genus *Xerus* from an arid environment

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A comparative thermoregulatory and bioenergetic study including urine analyses of two species of southern African ground squirrels from the genus *Xerus* was carried out. Both *X. princeps* (a rock dweller) and *X. inauris* (a burrow dweller) are well adapted to a hot and arid environment. Both species have low resting metabolic rates (RMR) and high conductances (C). In *X. princeps* RMR is lower and C is higher relative to *X. inauris*. Both species can increase their body temperature (T_b) in their thermoneutral zones and in ambient temperatures (T_a) above this. Salivation in both species was observed only at $T_a = 38°C$. At $T_a = 5°C$ *X. princeps* increase their oxygen consumption significantly *cf. X. inauris* ($p < 0,005$) and regulated their T_b at 36,1 ± 0,5°C while *X. inauris* maintained T_b at 34,8 ± 0,6°C. Nonshivering thermogenesis was measured as maximal $\dot{V}O_2$ and T_b of anaesthetized squirrels injected with noradrenaline (NA). *X. inauris* and *X. princeps* responded to NA by increasing $\dot{V}O_2$ and T_b. Both species show a low digestible dry matter intake as predicted for desert rodents. In both squirrels percentage moisture in faeces is low but significantly ($p < 0,05$) lower in *X. princeps* than in *X. inauris*. Urine analyses of hydrated squirrels showed that in *X. inauris* urea and Mg^{++} concentrations were significantly higher *cf. X. princeps* ($p < 0,05$; $p < 0,01$).

'n Vergelykende termoregulerings- en bioenergetikastudie wat ontleding van urine van twee spesies Suid-Afrikaanse grondeekhorings van die genus *Xerus* insluit, is uitgevoer. Beide *X. princeps* ('n klipbewoner) en *X. inauris* ('n gatbewoner) is goed aangepas by 'n warm en droë omgewing. Beide spesies het lae rustende metaboliese tempo's (RMT) en hoë geleidings (G). In *X. princeps* is RMT laer en G is hoër relatief tot *X. inauris*. Beide spesies kan hulle liggaamstemperatuur (T_b) in hul termoneutrale sones verhoog, en in omgewingstemperature (T_a) bokant dit. Produksie van speeksel in beide spesies is slegs by $T_a = 38°C$ waargeneem. By $T_a = 5°C$ verhoog *X. princeps* hul suurstofverbruik betekenisvol *cf. X. inauris* ($p < 0,005$) en reguleer hul T_b by 36,1 ± 0,5°C terwyl *X. inauris* T_b by 34,8 ± 0,6°C behou het. Nie-bewende termogenese is as maksimale $\dot{V}O_2$ en T_b van genarkotiseerde eekhorings wat met noradrenalien (NA) ingespuit is, gemeet. *X. inauris* en *X. princeps* het teenoor NA gereageer deur 'n toename in $\dot{V}O_2$ en T_b. Beide spesies vertoon 'n lae verteerbare inname van droë materiaal soos vir woestynknaagdiere voorspel word. In beide eekhorings is die persentasie vog in die faeces laag maar betekenisvol ($p < 0,05$) laer in *X. princeps* dan in *X. inauris*. Urienanalise van hidreerde eekhorings wys dat in *X. inauris*, urea- en Mg^{++}-konsentrasies betekenisvol laer was *cf. X. princeps* ($p < 0,05$; $p < 0,01$).

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Ground squirrels of the genus *Xerus* are represented in the Southern African subregion by two species: (i) The Cape ground squirrel *X. inauris* which is widely distributed in the subregion; in the Southern Savanna grasslands west of the Great Escarpment, and in the South West Arid biotic zone (De Graaff 1981; Smithers 1983), and (ii) the mountain ground squirrel *X. princeps* which occurs only in South West Africa/Namibia. This species is a typical representative of the South West Arid biotic zone and is distributed from Great Namaqualand in the south up into Angola in the north, through Damaraland and the Kaokoveld (De Graaff 1981; Smithers 1983). *Xerus princeps* and *X. inauris* are sympatric in South West Africa/Namibia throughout the areas in which *X. princeps* is distributed. *X. princeps* is a rock dweller and *X. inauris* a burrow dweller (Shortridge 1934). *X. princeps* is solitary or sometimes two individuals may dwell under the same boulder while *X. inauris* is social and up to 30 individuals can share the same burrow system (Herzig-Strachil 1978).

The aims of the present study were to compare their bioenergetics, thermoregulation and urine composition, to establish if there are any differences between the two species, as well as to compare the results with those of ground squirrels from deserts of the new world, and tree squirrels from Africa.

Materials and Methods

Seven specimens of *X. inauris* (four males and three females) and seven specimens of *X. princeps* (three males and four females) were captured in the area of Usakos, South West Africa/Namibia, in August 1984. Most *X. inauris* were caught in the river bed while *X. princeps* were captured under boulders. All squirrels were trapped during daytime.

The squirrels were acclimated for at least three weeks to an ambient temperature (T_a) of 25°C with a photoperiod of 12L:12D. The animals were kept separately in cages and were fed Pronutro powder mixed with water *ad. lib.* Apples and carrots were added as a source of moisture. Shredded paper was provided for bedding.

Oxygen Consumption

Oxygen consumption ($\dot{V}O_2$) was measured for both species at different ambient temperatures between 5 – 38°C, using an open circuit system (Depocas & Hart 1957; Hill 1972). $\dot{V}O_2$ was monitored on a Beckman OM-14 Polarigraphic oxygen analyser. A flow of air, dried over silica gel, (uniLAB), at a rate of 1000 ml/min was used. $\dot{V}O_2$ was recorded for a period of 30 min after a 2 – 3 h stabilizing period at each temperature. The average resting metabolic rate RMR (oxygen consumption of the 30-min period) was calculated when readings did not differ by more than 0,02%. The oxygen analyser was calibrated before and after each measurement, as in Haim (1982). All results were corrected to standard conditions, (STPD).

Temperature

Body (rectal) temperatures (T_b) and ambient temperatures were measured using a chromel-alumel thermocouple connected to a Kane-May 2013 potentiometer. T_b was recorded

at the end of every $\dot{V}O_2$ measurement by inserting the thermocouple 3 cm into the rectum of the squirrel for a period of no longer than 1 min.

Overall thermal conductance

The overall thermal conductance (C) was calculated for both species at temperatures below their lower critical point (for *X. inauris* at T_a = 26°C and for *X. princeps* at T_a = 29°C) using the formula of Scholander, Hock, Waleters & Irving 1950 (in Hart 1971) (C = M/T_b − T_a; M — metabolism).

Nonshivering thermogenesis

Nonshivering thermogenesis (NST) was measured as the maximal $\dot{V}O_2$ of anaesthetized (Sagatal, Maybaker, S.A., 75 mg/kg *i.p.*) squirrels obtained, in response to noradrenaline (NA, Sigma, 1,5 mg/kg *S.C.*) injection according to Heldmaier (1971). Measurements were carried out at T_a = 28°C for *X. inauris* and at T_a = 31°C for *X. princeps*. $\dot{V}O_2$ and T_b were simultaneously measured and recordings of both parameters were made every 3 min during a period of 120 min after NA injection.

Urine analysis

Urine was collected over paraffin oil in metabolic cages, during a period of 24 h. During this period (as well as 24 h before) the squirrels were kept on a diet of freshly weighed carrots. The uneaten carrots were weighed after 24 h, and were replaced by another weighed portion of carrots. Urine volume was measured to the nearest 0,1 ml.

Sodium — Na^+, potassium — K^+, chloride — $Cl^−$, and urea were determined using iono-specific electrodes in an Astra-8 (Beckman) instrument, and in the case of urea, after a treatment with urease. Calcium — Ca^{++} and magnesium — Mg^{++} were determined by atomic absorption spectrometry using lithium nitrate dilution. Phosphate was determined by colour development according to the method of Taussky & Shorre (1953) and monitored on a fleacigen (ENI). Bicarbonate — $HCO_3^−$, was measured by titration as in Haim, Heth, Nevo, Gruner & Goldstein (1985).

Urine osmolarity was determined by using a 5130C vapor pressure osmometer (Wescor Inc.) and pH was measured by a Labotec pH meter.

The per cent moisture content in the faeces of both species was determined by collecting the faeces immediately after extrusion. The faeces were weighed and then dried to constant mass in an oven at 80°C.

All results are given as mean and standard deviations. Student's *t* test was used to test significant differences.

Results

The relationships between $\dot{V}O_2$ and T_b at different ambient temperatures are illustrated in Figure 1 for *X. inauris* and in Figure 2 for *X. princeps*. The thermoneutral zone TNZ for *X. inauris* lay between T_a = 29−35°C and for *X. princeps* between 32−35°C. $\dot{V}O_2$ in TNZ was 0,602 ± 0,08 ml O_2/g h with T_b between 36,8−39,1°C for *X. inauris* and 0,565 ± 0,10 ml O_2/g h for *X. princeps*, with T_b between 37,6−38,7°C. In TNZ and above it, both species became hyperthermic. T_b in both species always exceeded T_a. Salivation in both species was observed only at T_a = 38°C. A significant difference in thermoregulation between these two species was observed at T_a = 5°C. *X. princeps* showed higher $\dot{V}O_2$ values (2,00 ± 0,22 ml O_2/g h) and maintained its T_b at 36,1 ± 0,5°C, while *X. inauris* had a significantly ($p < 0,005$) lower oxygen consumption (1,65 ± 0,29 ml O_2/g h) and body

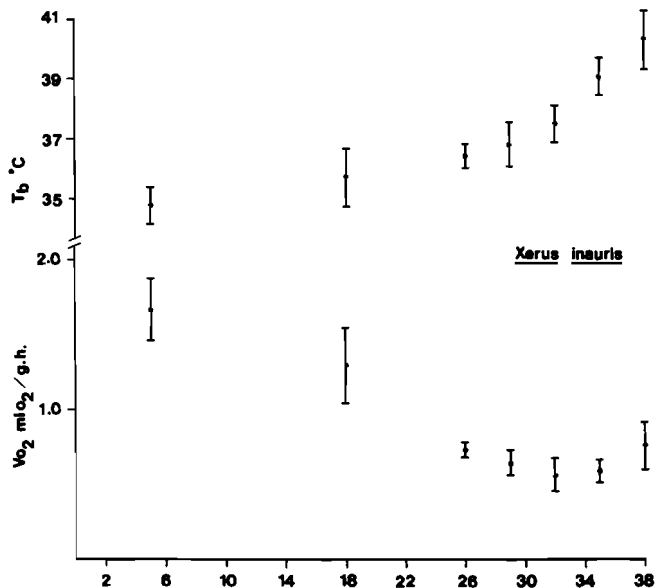**Figure 1** Oxygen consumption ($\dot{V}O_2$; ml O_2/g h) and body temperature (T_b; °C) of *X. princeps* at different ambient temperatures (T_a; °C). Squirrels acclimated to T_a = 25°C, with a photoperiod of 12L:12D. All results are given as mean ± *S.D.* of six individuals.

Figure 2 Oxygen consumption ($\dot{V}O_2$; ml O_2g h) and body temperature (T_b; °C) of *X. inauris* at different ambient temperatures (T_a; °C). Squirrels acclimated to T_a = 25°C, with a photoperiod of 12L:12D. All results are given as mean ± *S.D.* of six individuals.
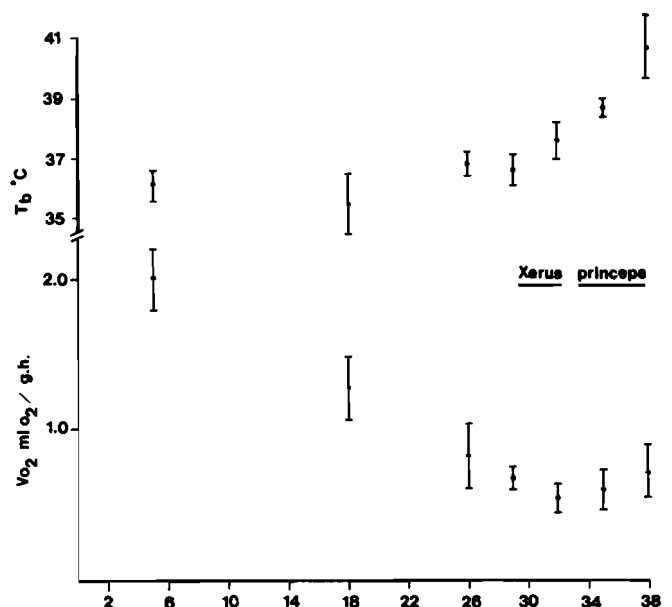
temperature declined to 34,8 ± 0,6°C.

Overall thermal conductance — C calculated for *X. inauris* (M_b = 542,3 ± 52,1 g) at T_a = 26°C was 0,071 ± 0,003 ml O_2/g h 1°C while for *X. princeps* (M_b = 602,3 ± 98,1 g), the calculated C at T_a = 29°C was 0,084 ± 0,005 ml O_2/g h 1°C. In *X. princeps* values were 15,9% greater than in *X. inauris*.

The values of NST for both species are given in Table 1. Both species showed a high response to NA injection by increasing $\dot{V}O_2$ which was accompanied by an increase in T_b.

The urine analyses for both species are summarized in Table 2. Urea and magnesium concentrations were significantly higher in the urine of *X. inauris* when compared with *X. princeps* ($p < 0,05$; $p < 0,01$). All the other values were

Table 1 Nonshivering thermogenesis (NST) measured as the maximal oxygen consumption ($\dot{V}O_2$max) obtained as a response to a noradrenaline (NA — 1,5 mg/kg S.C.) injection into an anaesthetized squirrel. T_b max — maximal body temperature measured as a response to NA. $\dot{V}O_2$min and $T_b$min — minimal values measured in anaesthetized squirrels. $\dot{V}O_2$max/$\dot{V}O_2$min — NST capacity, ΔT_b — the rate of increase in T_b from $T_b$min to $T_b$max, M_b — body mass. The figures are mean ($\pm$ *S.D.*) of six individuals

	X. inauris	X. princeps
M_b (g)	515,3 $\pm$ 63,3	627,0 $\pm$ 91,5
$\dot{V}O_2$max ml O_2/g h	1,99 $\pm$ 0,28	1,66 $\pm$ 0,46
$\dot{V}O_2$min ml O_2/g h	0,43 $\pm$ 0,06	0,37 $\pm$ 0,05
$T_b$max °C	39,3 $\pm$ 1,8	37,3 $\pm$ 1,6
$T_b$min °C	32,8 $\pm$ 0,8	33,2 $\pm$ 1,8
$\dot{V}O_2$max/$\dot{V}O_2$min	4,8 $\pm$ 1,2	4,6 $\pm$ 1,4
ΔT_b °C	6,5 $\pm$ 1,1	4,1 $\pm$ 0,6

Table 2 Comparison of several variables in the urine of two ground squirrel species from the genus *Xerus*. 24 h water intake, when kept on a diet of carrots was 69,04 $\pm$ 26,22 ml/1000 g for *X. inauris* and 57,83 $\pm$ 24,42 ml/1000 g for *X. princeps*. All figures are mean ($\pm$ *S.D.*) of seven individuals ([a]$p < 0,05$; [b]$p < 0,01$)

	X. inauris	X. princeps
Body mass (g)	523,8 $\pm$ 50,7	612,4 $\pm$ 94,8
Urine volume ml/1000 g W_b	71,4 $\pm$ 16,6	66,4 $\pm$ 10,2
pH	6,70 $\pm$ 0,15	7,04 $\pm$ 0,75
Osmolality mmol/liter	431,6 $\pm$ 80,4	403,4 $\pm$ 43,0
Urea mmol/liter	231,0 $\pm$ 58,9[a]	152,7 $\pm$ 52,9
HCO_3^- mEg/liter	16,6 $\pm$ 6,4	18,9 $\pm$ 11,1
Cl^- mEg/liter	33,7 $\pm$ 20,5	22,3 $\pm$ 9,7
Phosphate mmol/liter	2,57 $\pm$ 1,30	2,57 $\pm$ 0,62
K^+ mmol/liter	78,1 $\pm$ 19,9	99,0 $\pm$ 36,3
Na^+ mmol/liter	32,4 $\pm$ 23,4	17,1 $\pm$ 8,9
Ca^{++} mmol/liter	0,91 $\pm$ 0,40	0,84 $\pm$ 0,20
Mg^{++} mmol/liter	3,01 $\pm$ 0,50[b]	2,08 $\pm$ 0,50

statistically indistinguishable. Dry matter intake (carrots) was 8,266 $\pm$ 3,43 g/1000 g day for *X. inauris* and 6,696 $\pm$ 3,42 g/1000 g day for *X. princeps* which did not differ significantly from one another.

The percentage moisture content in faeces of *X. princeps* (14,21 $\pm$ 4,2%) was significantly ($p < 0,05$; $n = 6$) lower when compared to *X. inauris* (21,97 $\pm$ 4,61%).

Discussion

The two species of the genus *Xerus* were captured during daytime around Usakos. The strictly diurnal activity of *X. inauris* was noted by Herzig-Strachil (1978). Individuals of *X. princeps* were captured in rocky areas under rocks as well as along river beds (gravel). In one case an individual of *X. princeps* was captured in an opening of a burrow and 200 m away in another burrow *X. inauris* was captured. From our studied individuals *X. inauris* was never captured under a rock. Roberts (1951) states that *X. princeps* can inhabit plains as well as rocky areas and our capture data support this idea.

Rodents from desert habitats usually display low values of $\dot{V}O_2$ (Hudson & Wang 1969; MacMillan & Lee 1970; Hudson,

Deavers & Bradley 1972; Hart 1971; Borut & Shkolnik 1974). Low metabolic rates are an indication of water and food conservation which is an important adaptation to an arid habitat (Haim & Fourie 1980; Haim & Borut 1981; Haim 1984).

Both species of ground squirrels showed a low $\dot{V}O_2$ in relation to their body mass, according to Kleiber's (1961) equation. *X. princeps* and *X. inauris* had $\dot{V}O_2$ values which were 20% and 21% less than predicted for rodents of 608 g and 528 g body mass respectively. A low basal metabolism was recorded from desert and semi-desert species of new world ground squirrels and this was shown to be an adaptation to tolerance of high temperatures (Hudson & Deavers 1973).

In a recent study (Viljoen 1985) on thermoregulation of Southern African tree squirrels, all four species had RMR values below those predicted from Brody's (1945) equation ($\dot{V}O_2 = 3,8W^{0,75}$, W — body mass). These low values were interpreted as an adaptation to a warm climate. Furthermore, the two xeric species, *Paraxerus cepapi* from woodland savanna in Central Southern Africa, and *Funiscurus congicus* from arid savanna habitats in north-western Namibia, were further below the predicted values (Brody-Proctor equation) for their body mass (34% and 26% respectively).

In both species of *Xerus*, the thermoneutral zone is high, yet the lower critical point for *X. princeps* ($T_a = 32°C$) is higher than for *X. inauris* ($T_a = 29°C$). High values for lower critical points are recorded from several rodent species from extreme arid areas: *Acomys russatus* (Haim & Borut 1981), *Gerbillus nanus* (Haim 1984), *Sekeetamys calcurus* (Haim & Borut 1986). The difference in the lower critical point between the two species may indicate that the rock-dwelling *X. princeps* is better adapted to high temperatures than the burrow-dwelling *X. inauris*. Both species at $T_a = 35°C$ become hyperthermic, $T_b = 38,7 \pm 0,3°C$ for *X. princeps* and $T_b = 39,1 \pm 0,6$ for *X. inauris*.

It was assumed by Goyal, Ghosh & Prakash (1982) that a relatively high T_b may help to reduce evaporative water loss. In a comparative study of ground squirrel thermoregulation, Hudson *et al.* (1972) discovered that the most tolerant species to high ambient temperatures was *Citellus tereticandus* which inhabits hot deserts and can withstand ambient temperatures up to 46°C with a T_b of only 41,2°C. They also noted that the appearance of thermal distress varied in conformity with the habitat of the species.

In the southern African tree squirrels from arid habitats, *F. congicus* and *P. cepapi*, a resistance to high ambient temperatures was noted and at $T_a = 38°C$; T_b was only 39,8 $\pm$ 0,3 and 39,7 $\pm$ 0,35 respectively (Viljoen 1985).

Marsh, Louw & Berry (1978) noted that *X. inauris* is well adapted to hot and arid areas and can withstand high ambient temperatures. They also mention that the tail is used as a parasol to reduce heat load by creating shade for the squirrel. Bennett, Huey, John-Adler & Nagy (1984) however, claim that despite the behavioural and morphological adjustments of the parasol tail in *X. inauris* it can not replace the thermoregulatory difficulties in their hot and arid habitat.

The marked difference in response to cold between *X. inauris* and *X. princeps* is illustrated in Figures 1 and 2. *X. inauris* increased $\dot{V}O_2$ above RMR only 2,8 times while *X. princeps* increased $\dot{V}O_2$ 3,7 times above RMR at $T_a = 5°C$. This difference in $\dot{V}O_2$ between the two species is significant ($p < 0,005$). In conformity with $\dot{V}O_2$, a significant difference ($p < 0,005$) was recorded in T_b. This difference could have resulted from different rates of conductivity or differences in heat production. Conductance in both species is high yet in

X. princeps it is higher than in *X. inauris*, which may be important for a rock dweller in hot and arid areas. High conductance is a great advantage in heat dissipation and water conservation (Haim & Fourie 1980; Haim & Borut 1981; Haim 1984). On the other hand, when exposed to low ambient temperatures a rapid increase in heat production is of great importance for the squirrel to compensate for heat loss.

Webster (1974) emphasized the advantage of heat production by means of NST for small mammals. In this process a great amount of heat is generated in a short period without the involvement of muscle contraction. Cold acclimated rodents depend on NST for heat production when exposed to lower ambient temperatures (Jansky 1973). This mechanism is body mass dependent (Heldmaier 1971, 1972). Results from the present study show that both species when anaesthetized responded to NA injection by increasing $\dot{V}O_2$ and T_b (Table 1) although they were not cold acclimated. In *X. inauris* $\dot{V}O_2$max (maximal $\dot{V}O_2$ owing to NA injection) is 20% higher when compared to *X. princeps* whose body mass is 21% higher than that of *X. inauris*. Yet at $T_a = 5°C$ *X. princeps* increased heat production significantly ($p < 0,005$) more than *X. inauris*. This difference may be due to shivering thermogenesis and this parameter was not measured.

Under conditions of water shortage, reduction of faecal water loss is advantageous to an animal. Katz (1973) showed that in desert rodents water content of faeces is less than in the white rat *Rattus norvegicus* when given water *ad libitum* but faecal water content is even lower when they are deprived of water. Ward & Armitage (1981) compared the water budgets of mesic and xeric populations of the yellow-bellied marmot (*Marmota flaviventris*). They report a 40 – 55% faecal water content in the two populations when water is given *ad libitum*. They also note that when water was limited, faecal water loss further decreased by 72% for the mesic population and 65% for the xeric population to reduce water content to about 15%. In the present study, where the squirrels were kept on a diet of Pronutro powder mixed with water, fresh apples and carrots *ad lib.*, a low faecal water content was nevertheless recorded for both species. The value of 14,21 ± 4,2% recorded for *X. princeps* is significantly ($p < 0,05$) lower than 21,97 ± 4,6% recorded for *X. inauris*. Both species occur sympatrically in an arid area and the difference may be due to *X. princeps* being a rock dweller while *X. inauris* inhabits burrows.

Aspects of renal physiology in *X. inauris* were studied by Marsh *et al.* (1978). In their study they compared the urine collected from the urine bladder of squirrels shot in the dry season with that collected from squirrels shot in the wet season. The results from our study fall within their range for squirrels shot in the wet season.

There is a significant difference ($p < 0,05$) in the urinary urea concentration between the two species, values being higher for *X. inauris* (Table 2). In desert rodents urinary urea concentration is much higher than in rodents from mesic habitats, and urea has a pronounced effect on the urine-concentrating capacity of rodents Pfeiffer (1970). A parallel increase in urinary urea and urine osmolarity was reported in *Mus musculus* following water restriction (Haines, Ciskowski & Harms 1973). In the present study the interpretation of the difference in urine concentration is complicated as the squirrels had enough water in their diet and the difference in urine osmolarity is not significant. Differences in Mg^{++} concentration may emerge from a difference in absorption of Mg^{++} in the intestine. A similar phenomenon was found in the rabbit and rat by Cheeke & Amberg (1973). They explained the difference in urine Mg^{++} concentration by a differential intestinal absorption of Mg^{++}.

Acknowledgements

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