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Feeding biology of the dassie-rat *Petromus typicus* (Rodentia, Hystricognathi, Petromuridae) in captivity

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ABSTRACT. We examined the feeding biology of the poorly known dassie-rat *Petromus typicus*. External morphology indicates that the digging for soil-inhabiting invertebrates as food is unlikely. Animals in captivity refuse to eat insect larvae and data from field studies indicate that invertebrates play no major role with regard to the intake quantity. Observations on jaw movements and occlusion patterns of the cheek teeth indicate that *Petromus* is not restricted to high-fibre plant matter as food. This matches the catholic diet of *Petromus* in captivity and in the wild, where e.g. flowers and fruits are consumed when available. The rooted and moderately hypsodont cheek teeth suggest limited adaptation to abrasive plant material in comparison to other grass feeding hystricognaths. However, captive specimens consume high fibrous graminoid material during all activity phases, even when energetically more rewarding food is available. This suggests that fibre is an important food component. The stomach has no proventriculus or similar structure. Therefore, fermentation of plant matter in that region and/or rumination is unlikely. The caecum is large and haustrated, indicating the ability to process cellulose by micro-organisms. The morphology of the proximal colon indicates the presence of the so-called *colon separating mechanism* (CSM). It is therefore likely that the animals are able to produce vitamin and protein-rich faeces. This is confirmed by the occurrence of coprophagy by *Petromus*. The great variety of food sources hints at the ability of *Petromus* to cope with unstable environments, as is the case in xeric areas.

KEY WORDS : Rodentia, Hystricognathi, *Petromus*, feeding behaviour, nutrition, digestive system, coprophagy, rumination.

INTRODUCTION

African hystricognath rodents are well known as porcupines (Hystricidae), cane rats (Thryonomyidae), as well as by the group of subterranean species of mole rats (Bathyergidae). In contrast, the monotypic family Petromuridae (TULLBERG, 1899/1900; cf. MCKENNA & BELL, 1997; WILSON & REEDER, 1993) and its only member, the dassie-rat or noki *Petromus typicus* A. SMITH, 1831 (Fig. 1a), is less well known. *Petromus* is endemic to the Southern African Subregion, confined to the arid to semi-arid zone in the southernmost parts of Angola, in Namibia, and in the north-western part of the Cape Province in RSA (SKINNER & SMITHERS, 1990; COETZEE, 2002). It appears to be the geologically oldest rodent inhabitant of the Namib desert (MEESTER, 1965). It lives in rocky habitats, for instance in the crevices of the kopjes in the Namibian escarpment (SKINNER & SMITHER, 1990). Accordingly, *Petromus* possesses features regarded as adaptations for living in rock crevices, i.e. a flattened skull and flexible ribs (VAUGHAN et al., 2000; see also TULLBERG, 1899/1900; ELLERMAN, 1940; NOWAK, 1999).

Hystricognathi, including *Petromus*, differ conspicuously from other rodents : Derived characters (apomorphies) are associated with their reproduction which is characterised by a k-selective or precocial strategy (MESS et al., 2001). They are mainly herbivorous. Since *Petromus* is often suggested to have retained a large number of plesiomorphic conditions of Hystricognathi (cf. MESS, 1999a), this species is important for reconstructing the evolution of mammals in Africa. Particularly, according to the dassie-rats limited distribution and tolerance to xeric conditions, it could serve as a model for understanding how mammals use strategies to cope with the increasing aridity of the Southern African Subregion.

Data on *Petromus* is remarkably ”few” : Only some basic information on their natural habitat, nutrition and reproduction is available (e.g., WITHERS et al., 1980; DE GRAAFF; 1981; SKINNER & SMITHERS, 1990; COETZEE, 1983, 2002; NOWAK, 1999), including a few field studies (WITHERS, 1979, 1983; GEORGE, 1981; GEORGE & CROWTHER, 1981; COETZEE 2002; RATHBUN & RATHBUN, this volume). It had been assumed that *Petromus* is able to ruminate (COETZEE, 1983). According to GEORGE (1981) the diet is dominated by graminoids and the species is considered a herbivore (see also COETZEE, 1983). However, one report found that *Petromus* feeds to a significant degree on insects (WITHERS, 1979; apparently not known by GEORGE loc. cit.). Today a variety of food is reported to be taken (RATHBUN & RATHBUN, this volume) and

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rumination (including regurgitation and remastigation) would demand an elaborate gastro-intestinal apparatus, i.e. at least a proventriculus. The feeding capabilities of *Petromus* are still enigmatic. More information on these aspects, affecting the biology as well as the ecological significance of this species, is required. In the last couple of years, a breeding group of *Petromus* has been established and maintained successfully. Research so far deals with placentation and their evolutionary history (e.g., Mess, 1999b, 2001, 2003), external morphology (Ade, 1998, 1999; Ade et al., 2001) and general biology (e.g., Mess, 2002, 2005; Mess et al., 2000, 2002). Here, qualitative observations derived from the animals in captivity will be presented with special reference to nutrition, feeding behaviour and morphology of the digestive system. We will review scattered information about this poorly known species. Morphological data will help to integrate these data to a functional picture in the sense of ”whole organism biology” (Novacek, 1998).

Fig. 1. – Habits, environment and feeding conductance of *Petromus* from a breeding colony.
A : *Petromus* 43, a male individual that was given to the Tierpark Berlin.
B : Interior of the animal house at the Humboldt-University of Berlin.
C : *Petromus* 4, a male individual feeding on his daily food from the feeding dish.
D : *Petromus* 27, a female engaged with reingestation of faecal droppings.

MATERIAL AND METHODS

The breeding group, started in 1995, is based on 8 animals from the RSA. The group is now housed at the Humboldt-University, Berlin, and was formerly bred at the Universities of Tübingen and Göttingen. Currently, the animals are housed in primate cages : 1 x 0.7 x 0.8m for single individuals or pairs, and double this space for family groups (Fig. 1b). Inside, several resting places and a nest box are offered, as well as the possibility for sand bathing. The animal house is characterised by the following parameters : about 25°C air temperature, 50% humidity, 12 hour light with additional daylight spots provided 4 to 6 hours each day (Fig. 1b).

The animals are fed with hay, i.e. hard-pressed pellets containing dried graminoids with about 26% raw fibre material (Sniff ® Heucobs). Moreover, once a day standard food pellets for chinchillas (Sniff ® Chi, based on plant fibres with 14% raw fibre content) or a mixed food for guinea pigs (Sniff ® Ms Müsli) is given. These dry foods contain a considerable amount of vitamin C. This industrially produced food is supplemented by a mixture of fresh plant material. Most frequently used are carrots (roots as well as green parts), tomatoes, paprika, cucumbers, radishes, kohlrabi, broccoli, maize, and more rarely apples, pears, grapes and other fruits are given. (Fig. 1c)Occasionally dried bread, sunflower seeds or nuts are given in addition. Finally, mineral supply is provided by small pieces of standard pet limestone and salt stones.

This study is based on qualitative observations on various animals from the breeding group. Occasionally, a time lapse video camera using infrared spectrum was used to observe the behaviour during the dark phase. Behaviour in captivity is compared with data derived from field studies. The dassie-rats were conditioned to accept close observations by rewarding them with food and allogrooming by humans when approaching the animal keeper or student. This way it was possible to explore the direction of chewing movements by touching the working jaws.

Anatomical examination was conducted by gross morphological analysis using 60 fold magnification of the gastrointestinal tract of one female individual (*Petromus* Nr. 19 of the breeding colony) as well as of the morphology of the teeth and head region by using skulls and material from the wet collection that has been built up during the years. In particular, tooth structure is described on the basis of animals that have been born in the wild (*Petromus* SZ 7499, Zoologische Sammlung, University of Tübingen) as well as in captivity (*Petromus* Nr. 61 of the colony).

RESULTS

DESCRIPTION OF FEATURES ASSOCIATED WITH NUTRITIONAL BIOLOGY

1. Morphology of the digestive system and associated structures

Oral head region

The oral cavity, as in all rodents, is bipartite. A gnawing compartment and a chewing compartment are present. The compartments are produced by inwardly projecting ”lips” (inflexa pellita) provided with micro vibrissae, separating the front or gnawing teeth, respectively, from the cheek teeth (Fig. 2a). These oral rim projections meet nearly at the median plane, separated by a well developed, longitudinally extending papilla palatina. The gnawing teeth are easily exposed by an upper lip cleft (Fig. 2a). The rhinarium of *Petromus* is strongly reduced; not even small narial pads are present (Fig. 2b). Instead, there are only small, reduced, inconspicuous cushions at the entrance of the nares (Fig. 2b). The chewing compartment proximal of the diastema (”filled” with the inflexa) consists of 4 cheek teeth (dP4, M1-3). The teeth possess deep transverse infolding of the enamel, referred to as bilophodont condition with an anterior protoloph and a posterior metaloph (sensu THENIUS, 1989, see Fig. 2c.) The borders of the lophs below (buccal side) and above (lingual side) form distinct cusps (Fig. 2c). As judged from the occlusion pattern, the grinding and shearing actions are not produced in the horizontal plane as in mainly grass-consuming hystricognaths (THENIUS, 1989). Instead, there is a more strongly developed vertical tooth relief. The relief indicates a ”mortar- and- pestle” action (see LUCAS, 1979) as in dilambdodont teeth (e.g. *Tupaia*, THENIUS, 1989). This means that there is a marked transverse component of action during chewing. Reflecting this transverse component, the upper tooth row is markedly abraised at the buccal side (Fig. 2c), whereas, correspondingly, the lower interacting gnawing teeth show abrasion on the lingual side. The morphology of the jaw joint indicates that propalineal (back- and forth) movements are likewise possible, as in all rodents (see BUTLER, 1985; THENIUS, 1989).

The gastro-intestinal tract

The stomach is large. Moreover it is markedly curved, almost U-shaped (Fig. 2d). It has no transversely-running folds or septa producing proventriculus-like structures without glands as, e.g. in murids (Fig. 2d). There is a continuous layer of glands present as judged from gross morphological analysis. The caecum is large in diameter and strongly subdivided or haustrated (Fig. 2e). The transition area from the caecum towards the colon is inflated (Fig. 2e). The proximal part of the colon is moderately large in diameter. Dissection of the proximal colon region reveals that longitudinally-running ridges are present (Fig. 2f). Two prominent ridges run distally. Proximally, they are associated with some low oblique ridges in the transition zone between the caecum and the colon. The longitudinal ridges possess a transversely ridged surface structure. The two main ridges are closely apposed to each other, enclosing a distinct groove (Fig. 2f).

2. Behaviour associated with feeding

Feeding

The hands are used to hold the food during gnawing action (Fig. 1c). This is a remarkable process by which *Petromus* adjusts the position of the food item to the gnawing tooth (Fig, 1c; see also LANDRY, 1970). The food pieces lay between a groove formed by the reduced thumbs and the proximal and distal pads (for terminology of hand morphology see ADE & ZIEKUR, 1999). It appears that *Petromus* eats repeatedly during the whole day, especially on hay which is provided without restriction. In between feeding activities, extended resting phases take place, using the warm day-light spots. The animals are active every few hours during the night or dark phase, which is usually linked with feeding on hay or other available food. Both during day and night, the hay pellets are eaten either at the place where they have been deposited by the animal keepers or they are transported to where the dassie-rats prefer to sit down and rest. Fresh food and food pellets are more often eaten directly from the feeding dishes without transporting them (Fig. 1c). Within pairs or family groups, a female has first access to the feeding dish, especially when she is pregnant or lactating. Typically, conflicts at the feeding dish are settled by vocal dispute between the individuals and not by physical attacks. If such attacks occur they are usually not violent (our animals have been carefully accustomed to each other before putting them together).

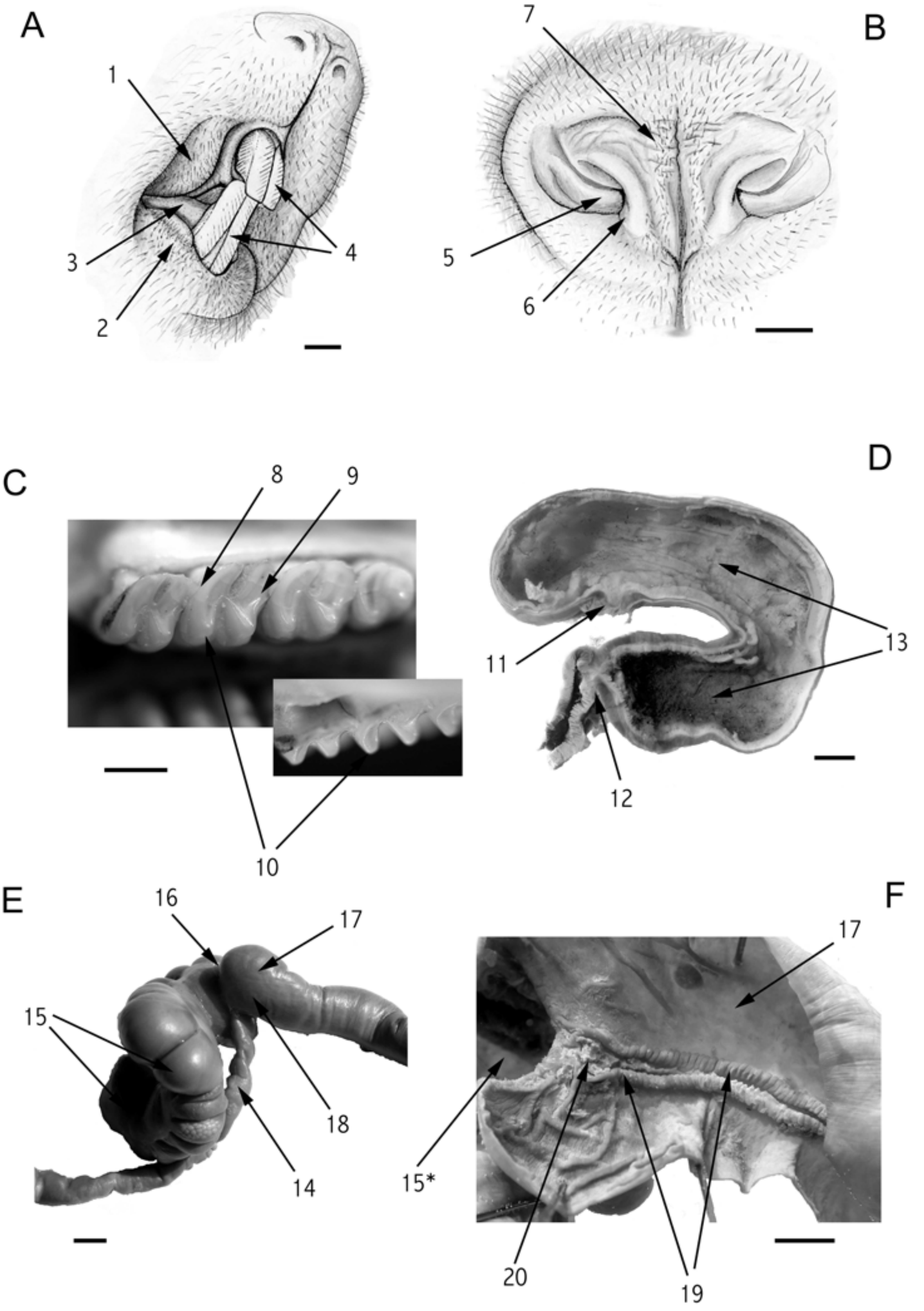

Fig. 2. – Morphology of oral head and gastro-intestinal tract in *Petromus typicus*.
A : The mouth cavity and gnawing teeth. Scale bar = 0.2 cm. (ADE, 1998).
B : The rhinaric region in a subadult individual. Scale bar = 0.1 cm. (ADE, 1998).
C : The left upper cheek teeth row (dP4, M1-3) of *Petromus* SZ 7499 from above (full-size photo) and from the buccal side (inlet) to demonstrate the distinct cusps. Accordingly, mesial is on the left hand side and buccal on top. Scale bar = 0.2 cm.
D : The stomach of *Petromus* 19 after macroscopic preparation. Scale bar = 0.5 cm.
E : Transition from the haustrated caecum into the proximal colon. Scale bar = 0.5 cm.
F : The proximal colon after preparation with longitudinal folds. Scale bar = 0.5 cm.

Abbreviations in Fig. 2 :

1 : upper inflexa pellita
2 : lower inflexa pellita
3 : the tongue
4 : upper and lower gnawing teeth (dI2)
5 : external opening of the nares
6 : inconspicuous rudiments of narial pads
7 : hairy parts in the rhinaric region
8 : protoloph of M1
9 : metaloph of M1
10 : cusp of M1, present at the lingual side
11 : opening of the oesophagus into the stomach
12 : pylorus, i.e. transition from stomach into proximal gut
13 : internal region of the stomach
14 : duodenum
15/15* : the caecum : external view and lumen of caecum
16 : transition zone between caecum and colon
17 : the proximal colon
18 : area of the colon possessing longitudinal folds inside
19 : longitudinal ridges inside the proximal colon
20 : groove between the ridges

Coprophagy

The animals are able to produce two different kinds of faecal droppings, dark brown ones which are considerably dry and a second type that is more greenish in colour and wet. It was never observed that a specimen consumes the brown pellets, but the greener ones were eaten frequently (Fig. 1d). It appears that a transitional production from brown to greenish faecal pellets occur. The two different sorts of pellets are easily recognised by the animals : When the droppings are changing their colour towards greenish, *Petromus* pick them up with the mouth and bite into it. If they are not appropriate – usually when the colour is still brownish – the droppings are immediately thrown away, and the next droppings that appear at the anus are tested again. Pellets of distinctly greenish colour are eaten, often chewing them a while before swallowing. The activity related to reingestation mostly occurs during the extensive resting periods.

Rumination, ”jack knife behaviour” and ”tail stand”

Although hundreds of hours have been spent observing different individuals of *Petromus*, it was not possible to find any indication for the occurrence of rumination as suggested in literature. Neither after the animals had eaten their daily amount of vegetables and food pellets, nor after feeding on hay at other times has an indication of rumination been found (Our *Petromus* have been accommodated to close sight contact by the observer). Rumination-related ”jack-knife behaviour” as described by COETZEE (1983), i.e. bending down of the head toward the abdomen, seems to be restricted to male individuals, and associated with the cleaning of the genitals. During the bending down action the penis is elongated to about double its normal length. Afterwards the penis is taken into the mouth and cleaned by moving the mouth up and down. Finally, after interrupting the close contact between mouth and penis, the individual jerks up upright, often chewing or smacking with its lip region. Such cleaning activities in males occur frequently, distributed throughout the day, indicating that the jack-knife action is a comforting behaviour. The newly described ”tail stand behavioural pattern”, which means that an animal stand on its front feet while propping up the hind feet and drumming them against the abdomen for several seconds has been suspected to be important for digestive efficiency (see Fig. 3 in RATHBUN & RATHBUN, this volume). This behaviour has been observed from time to time in captive animals from the breeding group too. It is more rare than, for instance, coprophagy or the jack-knife movements.

Food preferences

Petromus has been frequently observed to drink water, using the outlets of the water bottles. The tongue is used during water uptake. Hay is given ad lib. and the animals feed on the pellets repeatedly during the day. Standard pet limestones as well as salt stones are used sporadically. According to the consumption of fresh plant material, *Petromus* accepts a variety of various vegetables and fruits (see Material & Methods). It appears that *Petromus* have individual preferences with regard to the food offered. When extra food is given, it appears that the animals show a clear preference for seeds and nuts, but do not feed exclusively on them. Instead they switched between the extra food and hay pellets. Thus far, *Petromus* has never been observed to eat insects or other animals offered. Feeding trials have been conducted by using meal-worms or crickets. Even during pregnancy or lactation, the animals refused such food. Moreover, trials to feed them with pellets for hamsters and mice were not successful. Cheese or small amounts of meat products were not accepted.

DISCUSSION AND CONCLUSION

Petromus possesses characteristics of the naso-labial and oral region linked with a flexible diet. The bipartite organisation of the oral mouth cavity allows the gnawing teeth to be easily exposed and used for exploration, e.g. of food consistency or texture (ADE, 1998; LUCAS, 1979), while the inner part of the mouth is protected. In terms of evolution, the exploratively used gnawing teeth have replaced functions of the rhinarium, i.e. the originally tactile region of the head in rodents (ADE, 1998). According to the almost complete reduction of the rhinarium in *Petromus* and the fact that the animal projects the dorsum nasi rostrally and not the rhinaric region when exploring its surroundings, it can be concluded that the rhinaric region is not extensively used for specific exploration of the environment as i.e. in insectivorous terrestrial mammals. This is supported by behavioural observations comparing *Rattus norvegicus*, *Petromus typicus*, *Cavia porcellus and Octodon degus* (see observations of MESS & ADE described in ADE, 1998). Thus, extensive rummaging in the soil for insects is very unlikely. However, morphology does not preclude consumption of non-soil insects, i.e. insects from higher strata of the vegetation or surface running forms. *Petromus* has not been observed to feed on insects when we offered them to our captive animals. On the basis of observations on feeding behaviour, COETZEE (1983) came to the conclusion that *Petromus* is mainly herbivorous in the field. DE GRAAFF (1981), referring also to stomach contents, classifies the species as strictly feeding on plant matter (leaves, berries, seeds, flowers of compitae). GEORGE (1981) and COETZEE (1983) claim a preference for grasses. RATHBUN & RATHBUN (this volume) did not observe dassie-rats searching for, or eating, invertebrates. However, WITHERS (1979) has found a significant contribution of insects in stomach contents. The latter reference has not been cited in any paper except for RATHBUN & RATHBUN (loc. cit.).

The puncture-crushing mode with high and sharp cusps of the teeth, enabling similar sized mammals to use invertebrates as food (LUCAS, 1979; PFRETSCHMER, 1997), is not present in *Petromus*. The cusps of the cheek teeth of *Petromus* are blunt. During the mortar- and- pestle action, compressive forces should prevail. Referring to LUCAS (1979), our tentative conclusion is that the cheek teeth are more adapted to fracture plant material than invertebrate material. However, it cannot be excluded that the *gnawing teeth* may serve to puncture and crush exoskeletons, especially when bearing in mind the sophisticated ability to use the hands during the gnawing process. The cheek teeth may then also serve as crushing devices. In fact, crushing is the presumed major function of these kind of teeth with blunt cusps (see THENIUS, 1989). Constraints on the amount of microfaunivory may come from the need to preserve a sufficiently dense population of cellulose processing micro-organisms in the intestinal tract (see below), i.e. a sufficient amount of cellulose has to be ingested to enable the animal to live solely from plant matter. This may be crucial when facing the dryness of the habitat, which is negatively correlated to the amount of invertebrates (SCHULTZ, 2000). Thus, we suspect that physiological regulation might suppress the consumption of invertebrates. Even WITHERS (1979) points out that *Petromus* is predominantly herbivorous, despite the fact that he notes a high proportion of insects in the stomachs of some specimens. The point is that it uses cellulose rich material.

The occlusion pattern of the cheek teeth, resembling omnivorous types of teeth (see THENIUS, 1989), indicates a less specialised mode of chewing compared to other Hystricognathi. This fits into the picture that *Petromus* utilises a variety of (plant) material ranging from stems, leaves to fruits and even insects. Strict herbivory, e.g. using high fibrous plant material is related to enamel ridges working in a more or less common horizontal grinding plane (BUTLER, 1985; PFRETSCHMER 1997). This is not the case in *Petromus*. Moreover, the cheek teeth are hypsodont but not continuously-growing, i.e. protection of the teeth from rapid abrasion by silicate containing material such as grasses is not well developed.

The stomach is large and curved, but internally undivided. This uniform cavity indicates that the stomach content will be exposed to an acid and enzymatic milieu. This implies two important consequences. 1) The milieu for the stomach content has a low pH preventing the effective establishment of micro-organism populations that could serve as fermenters and protein donors (proventriculus-function possibly in rodents (STARCK, 1995) and ruminants). 2) The chymus is itself acidic and contains enzymes. Both could strongly affect the mucosa. This means that rumination would be detrimental if there is no extensive buffering by mucus in the oesophagus and oral cavity. The latter is unlikely, and completely unknown, for mammals. Furthermore, the data derived from the laboratory group suggest that the so-called ”jack-knife behaviour” described by COETZEE (1983) can not be confirmed to be associated with rumination. A similar behaviour occurs restricted to male individuals when cleaning the penis. The animals regularly show chewing movements afterwards without any indication of food matter inside the mouth. Thus, it appears likely that this behaviour belongs to comfort behaviour (including masturbation which might explain the chewing and smacking afterwards, G. RATHBUN, pers. comm.). The ingested plant material is most likely fermented by micro-organisms in the intestinal tract. The caecum is large and haustrated in comparison to hystricognaths with marked herbivorous and high fibrous diet, such as the chinchilla (TULLBERG, 1899/1900). Large caecae are typical for herbivorous rodents (HESSE & DOFLEIN, 1935; WITHERS, 1979). Longitudinal folds in the proximal colon reveal that a colon separating mechanism (CSM) as the structural prerequisite of coprophagy is present. This is supported by the production of special feacal droppings and their ingestion (also WITHERS, 1979). The CSM creates a selected reflux of chymus into the caecum as the basis for the production of specialised pellets which contain a significantly higher amount of vitamins and protein (BJÖRNHAG & SNIPES, 1999; HOLTMAIER, 2002). Thus, the ability to use high fibre matter for energy and protein production has to be assumed for *Petromus*. The fact that captive specimens consume high fibrous graminoid material all day long, even if energetically more rewarding food is available suggests that there is conspicuous dependency on this kind of food.

The newly described ”tail-stand behaviour” (RATHBUN & RATHBUN, this volume) is seen from time to time in the caged animals. It is suspected by RATHBUN & RATHBUN that this behaviour is related to digestive efficiency by mechanical stimulation and support of peristaltic movements of the intestine.

Judged from the data on morphology and behaviour, *Petromus* is 1) a hindgut fermenter of cellulose with a special mechanism to utilise micro-organisms as a source of protein and vitamin supply, 2) depending mainly on plant matter, but the variety of food in this regard is large, 3) not confined to high fibrous plant material, but able to use this kind of material successfully in various combinations, and 4) not micro-faunivorous to a large degree. The CSM enables the animals to produce foreign protein within themselves which hints that they are potentially independent from animal protein. In summary, a great variety of food is used. This hints at the ability of *Petromus* to cope with unstable environments as is the case in xeric areas, such as in the Southern African Subregion.

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