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Gastrointestinal anatomy of the European badger *Meles meles* L.

A comparative study

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Abstract

The gastrointestinal tract of the European badger (*Meles meles* L.) consists of a simple elongated stomach, tortuous small intestine and simple smooth-walled colon. There is no caecum. Allometric comparison of the internal surface area of the main gut compartments with comparable data from a variety of mammal species shows that the badger has a marginally larger stomach, larger small intestine and smaller colon than expected for its body weight. Multivariate analysis based on the absorptive areas of the three main gut compartments, taking into account body size, places the badger close to other mustelids and within a cluster of species most of whose diets are faunivorous.

Introduction

KRUUK (1978a, b; KRUUK et al. 1979; KRUUK and PARISH 1981) has characterised the European badger as a specialist predator on earthworms, especially *Lumbricus terrestris*. Stomach contents and faeces of badgers from Osefordshire and Scotland reveal a high incidence of earthworm remains, while behavioural observations suggest not only that badgers spend most of their foraging time looking for and consuming worms, but also that wormhunting effort increases or decreases to compensate for changes in prey availability.

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In KRUUK's view worm availability is sufficiently crucial to the badger to determine both territory size and group size (see also MAC DONALD 1983 and VON SCHANTZ 1984a).

That worms are an important food for badgers is now beyond dispute (see NEAL 1977 and KRUUK 1978a, b, for a review of supporting evidence from a variety of geographical areas). However it is equally clear that badgers also eat many other foods, including plant as well as animal matter. Constituents of the diet include other invertebrates, expecially beetles and insect larvae (e.g. ANDERSEN 1955; CIAMPILINI and LOVARI 1985); small vertebrates such as amphibians, rodents and immature rabbits (e.g. ANDERSEN 1955; LIKHACHEV 1956; KRUUK and PARISH 1981); and a variety of vegetable matter including fruits, berries, nuts, tubers, garden vegetables and cereals (e.g. SKOOG 1970; BRADBURY 1974; NEAL 1977; KRUUK and DE KOCK 1981; KRUUK and PARISH 1981; HARRIS 1984; CIAMPILINI and LOVARI 1985).

The present study attempts to relate the gross anatomy of the badger gut to the species' taxonomic status and diet. It is suggested (CHIVERS and HLADIK 1980) that gut anatomy in mammals reflects dietary habits. Species that predominantly forage for fruits, seeds, flowers (generally termed as frugivores), possess a gut that is of a relatively unspecialised type in which simple stomach, small intestine, colon and caecum all are present. Those species, that eat leaves, grasses, stems, barks and gums (folivores) show enlargement of either stomach (in the case of "foregut fermenters") or of caecum and sometimes colon (in the case of "midgut fermenters") to form one or more chambers for the processing of the longchain carbohydrates. Species devouring animal matter including invertebrates (faunivores) exhibit a gut that tends overall to be short and to be dominated by small intestine rather than by stomach, colon or caecum. Given the badger's taxonomic status as a carnivore we expected it to exhibit a gut of the faunivore type. On the other hand since fruit, tubers and cereals do seem to be common constituents of the badger's diet the gut may have evolved partially towards frugivory.

The idea that gut anatomy reflects diet is not of course new: a pioneering attempt to relate the two was made by CUVIER (1805). In most cases, however, comparisons have been made on the basis of gut length in relation to body length (e.g. SKOOG 1970). There are two important problems with this type of comparison. First, digestive capacity is more closely related to the inner surface area of a particular gut compartment than to its length (e.g. MANGOLD 1950, cited in SKOOG 1970). Second, simple ratios such as intestine length to body length are misleading in that they are not "size-free"; they vary according to body size irrespective of any difference due to diet.

In this paper we present for the first time detailed quantitative anatomical data on gut morphology in the badger, including measurements of the inner surface area of different gut compartments. We also use an allometric method of analysis, developed by MARTIN et al. (1985) and MAC LARNON et al. (1986), to compare the badger's gut morphology with that of other mammal species for which comparable data are available.

Material and methods

Specimens

Anatomical data were obtained from 11 road-killed badgers; 8 males and 3 females (see Table 1). One male and one female were from East Sussex; the remainder were from East Anglia. All were found between late February and early April 1984, a season of the year when road mortality is high (DAVIES et al., in press).

Anatomical measurements

The anatomical techniques have been described in detail by CHIVERS and HLADIK (1980), and so will only be summarised here. Animals were first weighed intact, and body length was measured from bregma to ischial tuberosity. The complete gastrointestinal tract was then removed; the gut wall was opened out and flattened without stretching; and measurements were made of the length and breadth of stomach, small intestine and colon. The primary data of interest were the surface areas of stomach, small intestine and colon, and these were calculated from lengths and a series of breadths. In addition the three main gut compartments were weighed after removal of excess water. The nine East Anglian specimens were examined and measured in a fresh state as soon as possible after collection; the two East Sussex specimens were deep frozen for about a month prior to dissection.

Allometric analysis of data

For a cross-species comparison of quantitative gut anatomy it is necessary to take into account differences in body size. MARTIN et al. (1985) have shown that when the internal surface area of each of the gut compartments is plotted against body weight on logarithmic coordinates for a variety of mammals, a line of slope 0.75 can be fitted through the data points for each gut compartment. This is compatible with KLEIBER's law, whereby basal metabolic rate scales to body weight with an exponent of 0.75 (KLEIBER 1961). The line of fixed slope then gives the expected value of gut compartment surface area for a typical mammal of given body weight. If the data pont for a particular species falls above or below the line this indicates that the gut compartment in that species has a larger or smaller surface area than expected. Deviation from expectation is given by a quotient for each gut compartment.

In accordance with MAC LARNON et al. (1986) we have used log gut quotients (log observed surface area minus log expected surface area) rather than absolute quotients (observed/expected surface area) in our analysis. However when discussing individual quotients in the text we have cited the absolute quotient values, since these are more readily understood (the expected value of the absolute quotient for a typical mammal being unity).

In order to compare the overall pattern of quotient values for the four gut compartments across a spectrum of species, a multivariate technique is necessary. In studies by MARTIN et al. (1985) and MAC LARNON et al. (1986) the four gut quotient values from a variety of mammal species were used to generate a matrix of Euclidean distances between all pairs of species, and a multidimensional scaling technique was then applied to this matrix to provide a two-dimensional representation (a "multidimensional scaling plot") of these distances. On the multidimensional scaling plot species which have similar overall gut anatomy lie close together in space, so that the plot provides a pictorial representation of similarities and differences in gut morphology across a wide range of species. In the present study we present a multidimensional scaling plot for 79 mammal species previously described by MARTIN et al. (1985) and MAC LARNON et al. (1986), and we incorporate into this plot new data from the badger *Meles meles*. Since the badger was found to possess no caecum (see below), the present analysis was based on three quotient values for stomach, small intestine and caecum plus colon respectively.

Results

Anatomy of the gut

The gastrointestinal tract of *Meles meles* (see Fig. 1) consists of stomach, small intestine and colon: there is no caecum. A summary of anatomical data obtained from 11 road-killed animals is given in Table 1.

The stomach of *Meles meles* is simple but elongated. The small intestine is very long and tortuous (mean length 536 cm) and provides about 80 % of the surface area of the gastrointestinal tract. There is a very large Peyer's Patch (lymphoid), about 33 cm long, at the distal end. The colon is simple and fairly short (mean length 29 cm), with numerous lymphatic nodules in the last 10 cm. In the absence of a caecum the start of the colon can be identified by the abrupt transition from the villi of the ileum to the crypts of the colon. This corresponds with a colour change to the mucosa a few cm after the large Peyer's Patch, and with the ileocolic artery from the cranial mesenteric artery.

Inspection of the data in Table 1 suggests no sex difference in the absolute or relative size of the three gut compartments, but a larger sample of females is needed to confirm this statistically. In the single juvenile specimen (number 11 in Table 1) the surface area of stomach and colon and the length of the colon were within the range of values provided by the 10 adult animals; but the small intestine of the juvenile was shorter and smaller in surface area. In most specimens the stomach contained remains of earthworms together with grass and earth.

Allometric analysis

Figure 2 shows the surface areas of stomach, small intestine and colon plotted against body weight on logarithmic coordinates, for 80 mammals species including *Meles meles.* The data points for *Meles meles* represent the mean values from seven of the eleven animals included in Table 1: the remaining four animals were starved or damaged, and so were excluded from the analysis. Data for the 79 comparison species were provided by A. MacLarnon. The absolute gut quotient values for *Meles meles* are: stomach quotient, 1.1; small intestine quotient, 1.75; colon quotient, 0.40. Thus it can be concluded that the surface area of the stomach of the

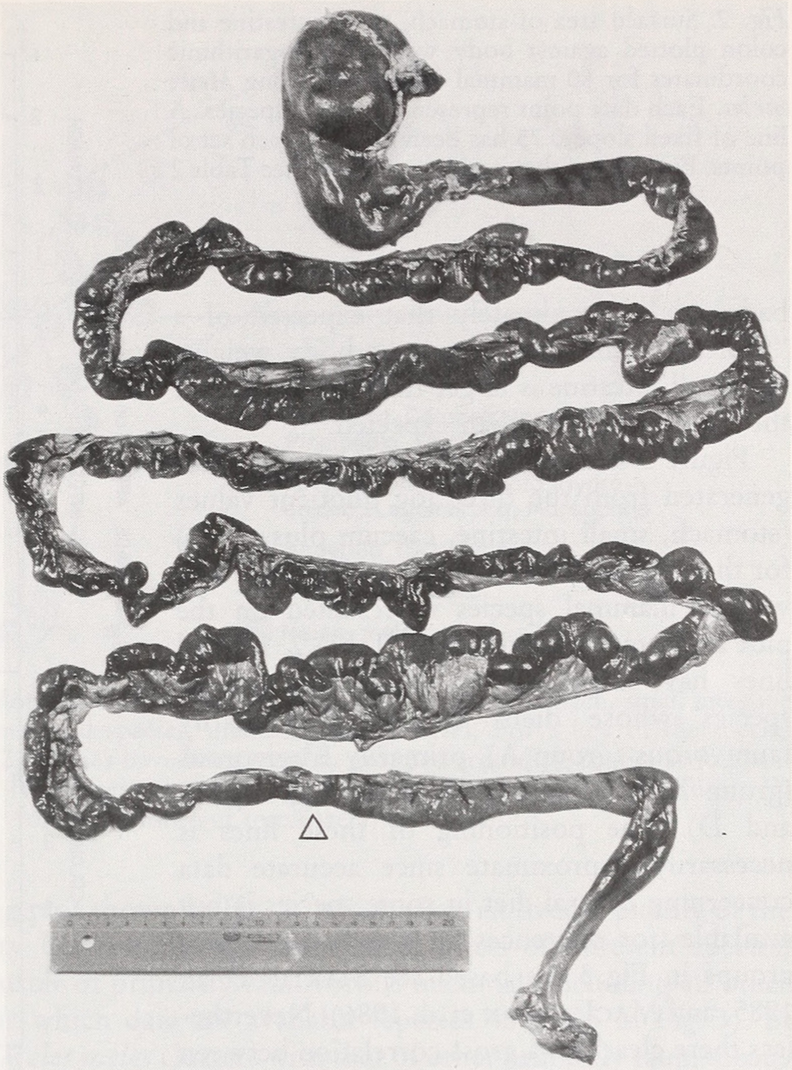


Fig. 1. Gut of a mature female badger weighing 8.5 kg, showing stomach, small intestine and colon. An arrow marks the beginning of the colon (the scale is 20 cm)

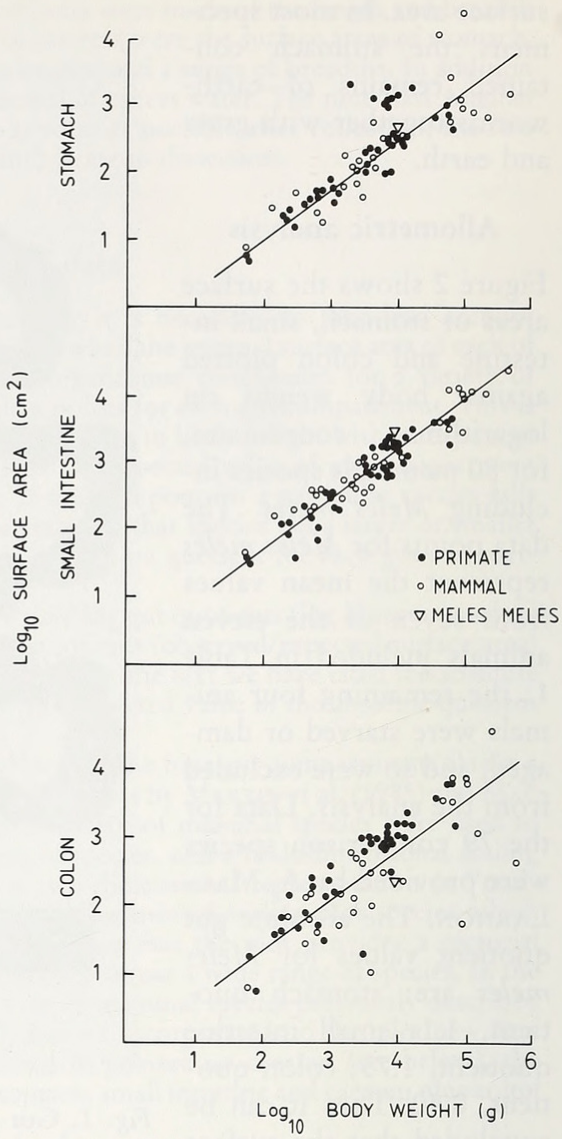
Table 1

Anatomical data from 11 road killed animals

Ident. No	Origin[1]	Sex	Body length (cm)[4]	Body wt (kg)	Surface area (cm)[2] Stom.	S.I.	Colon	Weight (qm) Stom.	S.I.	Colon	Length (cm) S.I.	Colon
1	EA	M[3]	58	9.8	228	1603	139	30	74	13	473	25
2	EA	M	59	9.3	540	2782	212	65	139	18	587	29
3	EA	M	63	9.1	546	3007	190	72	184	30	575	27
4	EA	M	63	9.5	437	2851	217	57	178	24	559	31
5	EA	M[3]	62	9.1	316	2021	210	42	110	27	470	30
6	EA	M	62	10.4	460	2910	208	77	170	26	594	32
7	EA	M	60	12.0	303	1767	151	80	132	21	437	28
8	ES	M[3]	54	7.3	460	2892	266	72	135	25	553	30
9	EA	F	55	7.8	435	2168	194	66	103	19	542	27
10	ES	F	54	8.0	366	2626	180	83	150	28	574	29
11	EA	F[2]	57	4.6	441	2006	226	34	82	14	458	29
Mean			59	9.2	409	2663	197	64	138	23	536	29

[1] EA = E. Anglia; ES = E. Sussex. – [2] Immature animal, data not included in mean. – [3] Data not included in allometric analysis. – [4] Measured from bregma to ischial tuberosity.

Fig. 2. Surface area of stomach, small intestine and colon plotted against body weight on logarithmic coordinates for 80 mammal species including *Meles meles*. Each data point represents a single species. A line of fixed slope 0.75 has been fitted to each set of points. For a list of the species in question see Table 2



badger is approximately that expected of a "typical" mammal of the same body weight; the small intestine is larger than expected; and the colon is smaller than expected.

Figure 3 is a multidimensional scaling plot generated from the three log quotient values (stomach, small intestine, caecum plus colon) for the same spectrum of mammal species. The various mammal species represented on the plot are listed numerically in Table 2. Dotted lines have been drawn around groups of species whose diets are either primarily faunivorous (group A), primarily frugivorous (group B) or primarily folivorous (groups C and D). The positioning of these lines is necessarily approximate since accurate data concerning natural diet in some species is not available (for references on which the dietary groups in Fig. 3 are based see MARTIN et al. 1985, and MACLARNON et al. 1986). Nevertheless there clearly is a gross correlation between the diet of a species and the position that it occupies, by virtue of its gut anatomy, in the multidimensional scaling plot. In general faunivorous mammals fall into the upper right-hand quadrant of the plot; frugivorous mammals form a cluster to the left of centre; and folivores form two clusters at the bottom and left-hand extremities of the plot, according to whether they possess enlarged fore-gut or enlarged mid-gut respectively. Within the faunivorous group, species whose diet is mainly insectivorous tend to fall to the left of cluster A. *Meles meles* (species numer 80) can be seen to fall within the faunivorous cluster.

Discussion

In its gross anatomy the badger's gastrointestinal tract follows the typical faunivore pattern: there is a simple stomach, tortuous small intestine and simple smooth-walled colon, none of which is elaborated in any obvious way. In common with a number of other faunivores the badger lacks a caecum. This condition is shared, for example, by the mustelids *Mustela nivalis* and *M. erminea,* by the cetaceans *Phocaena phocaena* and *Tursiops truncata,* and by some tropical insectivorous mammals such as *Manis tricuspis* and *Potomogale velox* (see CHIVERS and HLADIK 1980, Table 8). However a few non-faunivorous mammals also lack a caecum, e.g. *Nandinia binotata,* which is primarily frugivorous (CHARLES-DOMINIQUE 1978).

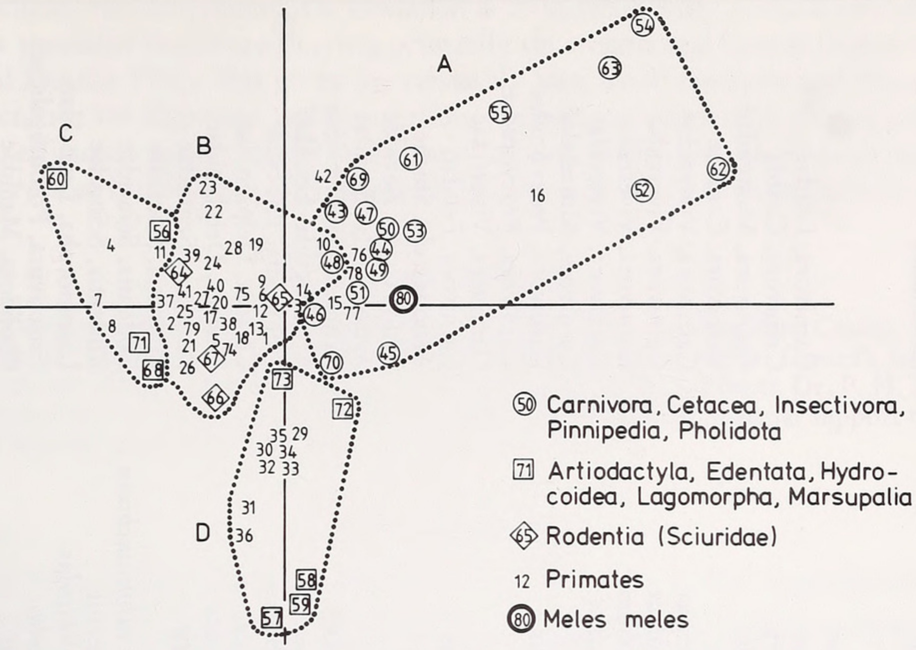


Fig. 3. Multidimensional scaling plot based on three log gut quotient values (stomach, small intestine and colon plus caecum) for 80 mammal species, including *Meles meles*. For a key to the species represented in the plot see Table 2. Species have been roughly grouped according to diet as follows: cluster A: faunivores; cluster B: frugivores; cluster C: folivores (mid-gut fermenters); cluster D: folivores (fore-gut fermenters)

The multidimensonal scaling plot shown in Fig. 3, which gives an overall picture of the degree of anatomical similarity between the gastrointestinal tracts of different species, places *Meles meles* within a cluster of primarily faunivorous mammals including all other members of the Carnivora for which data are available (species 43 to 55 in Fig. 3). In particular, the gut anatomy of *Meles meles* clusters with that of other primarily faunivorous mustelids (*Mustela nivalis*, 45; *Mustela sp.*, 51) A particularly interesting comparison is with the fox, *Vulpes vulpes*, which like the badger eats a wide range of foods including small vertebrates, worms and other invertebrates, fruits, berries, tubers, carrion and scavenged items (e.g. ENGLUND 1965; MACDONALD 1980; HARRIS 1981; CIAMPILINI and LOVARI 1985). *Vulpes vulpes* (46) lies further towards the inner end of the faunivorous cluster in Fig. 3 than does *Meles meles*, suggesting a degree of morphological adaptation to frugivory.

Of course the ability of an animal to digest particular types of food depends on factors other than gross gastro-intestinal anatomy: for example enzyme secretion and dentition are obviously important. In addition, it should be noted that all our road-killed specimens were collected in the spring, and it is possible that the gut may undergo minor morphological adjustment in the autumn in response to a more frugivorous diet (see CHIVERS and HLADIK 1980). Nothing seems to be known of enzyme activity in the badger gut, and detailed analysis of badger faeces is required to determine what if anything is digested out of the various fruits and cereals that are known to be eaten. As regards dentition, NEAL (1977) comments that the last premolar and molars are enlarged and flattened for crushing and grinding, and hence are indicative of an omnivorous diet (see also SKOOG 1970; BORN-MUELLER 1974). However the unusual jaw articulation of the badger, in which the squamosal is folded almost completely over the condyle to form a transverse hinge, restricts sideways movement of the lower jaw relative to the upper and so permits very little grinding action (MAYNARD SMITH and SAVAGE 1959; POLYAKOVA 1974); and inspection of badger faeces suggests that most seeds and berries are subjected only to repliminary crushing (STARK 1984).

Table 2

List of 80 mammal species included in the data on which Figs. 2 and 3 are based

PRIMATES		39. *Pongo pygmaeus*	Pongidae
1. *Arctocebus calabarensis*	Lorisidae	40. *Pan troglodytes*	Pongidae
2. *Avahi laniger*	Indriidae	41. *Gorilla gorilla*	Pongidae
3. *Cheirogaleus major*	Lemuridae	42. *Homo sapiens*	Hominidae
4. *Euoticus elegantulus*	Lorisidae		
5. *Galago alleni*	Lorisidae		
6. *Galago demidovii*	Lorisidae	NON-PRIMATES	
7. *Lepilemur mustelinus*	Lemuridae	43. *Felis domestica*	Carnivora, Felidae
8. *Lepilemur leucopus*	Lemuridae	44. *Canis familiaris*	Carnivora, Canida
9. *Loris tardigradus*	Lorisidae	45. *Mustela nivalis*	Carnivora, Mustelidae
10. *Microcebus murinus*	Lemuridae	46. *Vulpes vulpes*	Carnivora, Canidae
11. *Perodicticus potto*	Lorisidae	47. *Atilax paludinosus*	Carnivora, Viverridae
12. *Saguinus geoffroyi*	Callitrichidae	48. *Nandinia binotata*	Carnivora, Viverridae
13. *Aotus trivirgatus*	Cebidae	49. *Poiana richardsoni*	Carnivora, Viverridae
14. *Ateles belzebuth*	Cebidae	50. *Genetta servaliba*	Carnivora, Viverridae
15. *Saimiri oerstedii*	Cebidae	51. *Mustela sp.*	Carnivora, Mustelidae
16. *Cebus capucinus*	Cebidae	52. *Ailurus fulgens*	Carnivora, Procyonidae
17. *Alouatta palliata*	Cebidae	53. *Nasua narica*	Carnivora, Procyonidae
18. *Lagothrix lagothricha*	Cebidae	54. *Genetta sp.*	Carnivora, Viverridae
19. *Miopithecus talapoin*	Cercopithecidae	55. *Panthera tigris*	Carnivora, Felidae
20. *Cercopithecus cephus*	Cercopithecidae	56. *Sus scrofa*	Artiodactyla, Suidae
21. *Cercopithecus neglectus*	Cercopithecidae	57. *Capra hircus*	Artiodactyla, Bovidae
22. *Cercopithecus nictitans*	Cercopithecidae	58. *Ovis aries*	Artiodactyla, Bovidae
23. *Cercocebus albigena*	Cercopithecidae	59. *Cervus elaphus*	Artiodactyla, Cervidae
24. *Macaca sylvanus*	Cercopithecidae	60. *Equus caballus*	Artiodactyla, Equidae
25. *Macaca sinica*	Cercopithecidae	61. *Halichoerus grypus*	Pinnipedia, Phocidae
26. *Macaca fascicularis*	Cercopithecidae	62. *Phocoena phocaena*	Cetacea, Delphinidae
27. *Papio sphinx*	Cercopithecidae	63. *Tursiops truncata*	Cetacea, Delphinidae
28. *Erythrocebus patas*	Cercopithecidae	64. *Sciurus vulgaris*	Rodentia, Sciuridae
29. *Colobus polykomos*	Cercopithecidae	65. *Epixerus ebii*	Rodentia, Sciuridae
30. *Presbytis entellus*	Cercopithecidae	66. *Heliosciurpus rufobranchium*	Rodentia, Sciuridae
31. *Presbytis cristata*	Cercopithecidae	67. *Sciurus carolinensis*	Rodentia, Sciuridae
32. *Presbytis obscura*	Cercopithecidae	68. *Oryctolagus cuniculus*	Lagomorpha, Leporidae
33. *Presbytis melalophos*	Cercopithecidae	69. *Potomogale velox*	Insectivora, Potomogalidae
34. *Presbytis rubicunda*	Cercopithecidae	70. *Manis tricuspis*	Pholidota, Manidae
35. *Nasalis larvatus*	Cercopithecidae	71. *Dendrohyrax dorsalis*	Hyracoidea, Procaviidae
36. *Pygathrix nemaeus*	Cercopithecidae	72. *Bradypus tridactylus*	Edentata, Bradypodidae
37. *Hylobates pileatus*	Hylobatidae	73. *Macropus rufus*	Marsupialia, Macropodidae
38. *Hylobates (Symphalangus) syndactylus*	Hylobatidae	80. *Meles meles*	Carnivora, Mustelidae

To conclude, the morphological evidence is consistent with a characterisation of the badger as a specialist faunivore preying primarily on worms and insects (Kruuk 1978a, b; Kruuk and Parish 1981). But given the relatively long small intestine and the consequent large surface area for digestion and absorption, the badger is probably able to process with reasonable efficiency small fleshy fruits and tubers containing shortchain sugars. The alimentary system is not, however, morphologically well suited to mastication or digestion of cereals.

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Zusammenfassung

Der Gastrointestinaltrakt des europäischen Dachses Meles meles L. Eine vergleichende Studie

Der Gastrointestinaltrakt des europäischen Dachses (*Meles meles* L.) setzt sich zusammen aus einem einfachen, ungegliederten Magen, einem in Schlingen gelegten Dünndarm und einem einfachen, leicht gewellten Dickdarm. Der Dachs besitzt keinen Blinddarm. Ein allometrischer Vergleich der inneren Oberflächen von Magen, Dünn- und Dickdarm zwischen verschiedenen Säugetierarten ergibt, daß der Dachs einen nur wenig vergrößerten Magen hat. Die Innenfläche des Dünndarms ist größer, die des Dickdarms kleiner als man für das Körpergewicht des Dachses erwarten würde. Eine Varianzanalyse der Gastrointestinaltrakte, die die unterschiedlichen Körpergewichte der untersuchten Säugetierarten berücksichtigt, zeigt, daß der Dachs zusammen mit anderen Musteliden und weiteren Vertretern der Carnivora eine Gruppe bildet, die gekennzeichnet ist durch faunivore Ernährung.

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Die Analbeutel von *Civettictis civetta* (Schreber, 1776) (Mammalia, Viverridae)

Über ihren Bau, die chemische Zusammensetzung ihrer Sekrete und ihre biologische Bedeutung[1]

Von Alice von Saldern, H. Schliemann, F. I. B. Kayanja und J. Jacob

Eingang des Ms. 14. 5. 1986

Abstract

The anal sacs of Civettictis civetta (Schreber, 1776) (Mammalia, Viverridae). Morphology, chemical composition of the secretions and functional significance

The anal sacs of *Civettictis civetta* lying on both sides of the anal canal consist of an epithelium lining the central lumen of these organs, a lamina propria rich in free cells, connective tissue and smooth muscle fibers, and a thick layer of skeletal musculature being derived from the M. sphincter ani ext. The lamina propria contains about 10 complexes of sebaceous glands each of which is associated with apocrine glands. Histology and ultrastructure of the epithelium and the glands are analysed emphasizing the conspicuous development of the smooth endoplasmatic reticulum of lipogenic cells. No highly

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