

LACTATION, WEANING PERIOD, FOOD QUALITY, AND DIGESTIVE TRACT DIFFERENTIATIONS IN EUTHERIA

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Abstract.—Joint consideration of morphological studies, life-history data, and preferred food characteristics suggests that there may be optimal strategies for solid food supplementation during lactation for many mammals. This question was investigated by asking whether characteristics of food and morphological differentiation of the gastrointestinal tract as well as the specific differentiations of the weaning process in young eutherian mammals are related with each other and what such relationships might mean. Data on body mass, food quality, the differentiations of the digestive tract, and length of lactation and the weaning period represented the basis of the following discussion. A relatively long period when milk is supplemented by solid food is advantageous for the mother because she does not have to supply the total caloric needs of the young during lactation. On the other hand, an extended absolute length of the mixed-feeding period is advantageous for the offspring because energy is supplied by the solid food and supplemented by milk. Animals that eat high-quality food are characterized by a relatively short mixed-feeding or weaning period. In Eutheria that eat a food rich in plant cell wall material, the digestive tract shows high complexity and more than 40% of the lactation period is characterized by mixed feeding. The mother tries to reduce her energy expenditure as much as possible, while the offspring tends to obtain as much energy and building material for its developing body as possible. Both mother and young try to optimize their specific energy situation.

Key words.—Body weight, food classification, lactation, large intestine, mixed-feeding period, stomach, weaning period.

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According to Dettwyler (1999) the minimum age for a natural time of weaning in humans is 2.5 years, but the maximum age can be as high as seven years. Under normal conditions, breast milk alone satisfies the energy requirements of the average infant for the first six months of life. Before four months of age, infants are not ready to receive semisolid foods. When the infant is approximately six months old, however, it requires some complementary semisolid feeding, for which it is sufficiently developed functionally (Akré 1990). The process of functional differentiation seems to be influenced by the type of food eaten by the adult. For example, Pond (1977) indicates, rather unspecifically, that the adaptation of an Australian aboriginal infant to the coarse diet eaten by its parents is much more difficult than in the case of transition from milk to the type of food given to a white Australian child. However, it has to be kept in mind that *Homo sapiens* is not a good model for comparison with other mammals because humans can adapt to a wide range of highly seasonal and variable diets.

These examples dealing with human infant development show that there is remarkable variability in the length of lactation within one species. Of course, the variability between different eutherian species is also considerable. For example, lactation periods shorter than or equal to one month can be found in Macroscelidea (elephant shrews), Insectivora, Lagomorpha (hares, picas, and rabbits) and Muroidea (mice and their kin). Proboscidea (elephants), Odontoceti (toothed whales and dolphins), and Hominidae (apes) can lactate and nurse their young for a year and even longer. According to this compilation, body size influences the length of the lactation period, as has been discussed by Peters (1986), Reiss (1989), Clutton-Brock (1991), and Hayssen (1993).

Empirical and theoretical constraints on the evolution of lactation have been thoroughly discussed for mammals in

general in a study by Hayssen (1993). The length of lactation, time of intake of first solid food, and maternal body weight were taken into account. Pond (1977, p. 188) stated that lactation “provides the young with a buffer against hazards of fluctuations in quantity, quality and toxicity of the normal food supply.” Thus, energy is relatively easily obtained in an easily digestible form.

In both herbivores and carnivores nutritional independence is gained gradually as neonates shift from a milk diet to solid food (Derrickson 1992). In herbivorous mammals, the digestive tract has to be inoculated and colonized with microbes enabling fermentative digestion of a food rich in plant cell material (“alloenzymatic digestion,” Langer 1988); in the case of carnivores, the young animals finally have to gain the ability to capture their food.

The whole time of lactation can be subdivided into two sections. In the first period only milk is ingested, and in the second milk is taken together with solid food, known as the mixed-feeding or weaning period. Weaning is defined differently by various authors. As applied above, it can be considered as a process that does not occur abruptly (Eisenberg 1993). During this process of weaning the infant transfers from exclusive intake of milk to a semisolid and solid diet (Akré 1990). According to others, weaning can also be considered as the last day nursing was observed (Eisenberg 1993). An animal is weaned at the time of nutritional independence from the mother. Surprisingly, the period when a young animal adapts to the structure, taste, and chemical composition of adult food has not received much attention in studies of mammalian development.

The mixed-feeding or weaning period is pivotal in understanding the relation between life history, differentiation of the gastrointestinal tract, and the quality of food. The following five questions will be considered: (1) Are life-history

traits related to the anatomical differentiation of those regions that are necessary for alloenzymatic digestion? Such fermentation chambers can be differentiated in the large intestine and in the stomach (Langer 1988, 1991). (2) Are life-history traits related to the energetic load on the mother? (3) Are life-history traits related with nutritional aspects from the standpoint of the young? (4) Are life-history traits influenced by the quality of adult food? (5) Is the establishment of the microbial population that is necessary to enable fermentation related to life-history traits?

MATERIALS AND METHODS

Body Mass

Data on body mass (g) were compiled from the literature. Measurements published by Eisenberg (1981) and Silva and Downing (1995) represent the main databases, but compilations published by other authors were also consulted: Crile and Quiring (1940), Lechner (1978), Gehr et al. (1981), Garland (1983a,b), Scott (1983), Earle (1987), Nagy (1987), McNab and Eisenberg (1989), Weiner (1989), Korn (1992), and Lovegrove (2000). In this and the following sections references to 644 species are made (see Appendix). The data and characters discussed in this paper were not available for all species. The sexual dimorphism of body size when calculating means is only partly considered in this study because means for species, taking females and males together, were calculated.

Food Quality

Food quality in mammals varies widely. For domestic ruminants, pigs, horses, (Anonymous 1982, 1984a,b), and dogs and cats (Meyer and Heckötter 1986) many food items have been listed. This information was used to quantify food quality. Data were compiled and published previously (Langer 2002a). A modified version of this compilation can be found in Table 1. In the mammalogical literature feeding types are qualitatively characterized by different terms, which are compiled in Table 1a from publications by Eisenberg (1981) and Starck (1995). Feeds, as characterized in the abovementioned feeding value tables, can be grouped according to the list given in Table 1b. To quantify this information roughly, means of data on crude fiber per kilogram of dry matter, as presented in feeding value tables, are compiled as food classification. In studies of nutritional ecology the use of crude fiber is no longer recommended. It represents substances, such as cellulose, hemicelluloses, pectins, and lignin. The precise description of fiber in food is a complex problem (Wenk 1993). In studies by Van Soest (1982) classification according to crude fiber was replaced by acid detergent fiber (ADF, cellulose + lignin + ash) and neutral detergent fiber (NDF = hemicellulose + cellulose + lignin + ash) (Wenk 1993). However, these analytical procedures only approximate different fractions of nutritional fiber (Wenk 1993). Because of the wealth of the traditional qualitative data on feeding types, crude fiber was used in this study for the classification of food (Table 1c). Low values of food classification, (i.e., high food quality) represent foodstuffs with low amounts of plant cell wall substance. High values of food

TABLE 1. Sources of information from which food was classified. The feeding types were compiled from the literature, compared with foods as listed in feeding value tables, which also supply the contents in grams of crude fiber per kilogram of dry matter (DM). Means of these values are listed in the food classification column.

a	b	c
Feeding types ¹	Foods as listed in feeding value tables ²	Food classification (g crude fiber/kg DM)
Sanguivory, nectarivory, gumivory, sapovory	blood, milk, egg	0
Carnivory, ichthyophagy	fish, meat, offals of poultry and mammals	4
Insectivory, myrmecophagy, crustacivory	crustaceans	26
Granivory	grains and seeds	64
Frugivory, eaters of tubers and bulbs	tubers, roots, fruits	98
Herbivory, folivory	green fodder, leaves	207
Graminivory	grass, straw	343

¹ Most of the terms were taken from Eisenberg (1981) and Starck (1995).

² Raw data are from feeding value tables published for domestic mammals (Anonymous 1982, 1984a,b; Meyer and Heckötter 1986).

classification (i.e., low quality) are characterized by food rich in plant cell wall material. The following sources, presenting feeding types as listed in Table 1a, were used for this compilation: Burt and Grossenheider (1964), Van den Brink (1972), Dorst and Dandelot (1973), Niethammer and Krapp (1978, 1982, 1986, 1990, 1992, 1993a,b, 1994, 1995, 2001), Banfield (1981), Corbet and Ovenden (1982), Boitani et al. (1983), Smithers (1983), Strahan (1983), Schröpfer et al. (1984), Görner and Hackethal (1988), Eisenberg (1989), Redford and Eisenberg (1992), MacDonald and Barrett (1993), Lange et al. (1994), Hausser (1995), Qumsiyeh (1996), Kingdon (1997), Mills and Hes (1997), Eisenberg and Redford (1999), and Mitchell-Jones et al. (1999).

Postnatal Development and Definition of Terms for the Lactation Period and Its Subdivisions

Data on patterns of mammalian postnatal development, namely the duration of lactation and the postnatal day when first solid food is eaten (i.e., the length of the milk-only period) were extracted from Hayssen et al. (1993). Although the "age at first solid food is more precisely and uniformly defined than the age at weaning" (Hayssen 1993, p. 3214), the weaning period represents the difference between overall length of lactation and length of the milk-only period. It is the time of transition from complete milk dependency to consumption of adult food (Eisenberg 1993) and ends when the young animal is weaned. The mixed-feeding or weaning period is expressed in days and as percentage of the total lactation time:

$$\text{relative mixed-feeding period} = \frac{\text{mixed-feeding period}}{\text{lactation period}} \times 100.$$

Anatomy of the Digestive Tract and Morphotypes

I compiled table of 18 anatomical characters of the gastrointestinal tract (large intestine and stomach) of 644 eu-

TABLE 2. Calculation of specificity values for 18 morphological characters under consideration of the 644 eutherian species listed in the Appendix and of 124 morphotypes.

	a	b	c	d	e	f
	Number of species (total 644) with differentiation	Differentiation as percent of 644 eutherian species	Number of morphotypes (total 124) with differentiation	Differentiation as percent in 124 eutherian morphotypes	Means of percentages given in columns b and d (abundance, A) (%)	Specificity (100 - A) (%)
1 Caecum differentiated	419	65.1	84	67.7	66.40	33.60
2 Stomach glandular	457	71.0	70	56.5	63.75	36.25
3 Stomach composite	192	29.8	40	32.3	31.10	68.95
4 Stomach plurilocular	150	23.3	27	21.8	22.55	77.45
5 Caecum haustrated	101	15.7	31	25.0	20.35	79.65
6 Forestomach setoff	119	18.5	18	14.5	18.50	81.50
7 Colon haustrated	97	15.1	21	16.9	16.00	84.00
8 Stomach with set-off region	53	8.2	11	8.9	8.55	91.45
9 Reticulum cellular	74	11.5	6	4.8	8.15	91.85
10 Omasum differentiated	71	11.0	5	4.0	7.50	92.50
11 Forestomach part of esophagus	27	4.2	7	5.6	4.90	95.10
12 Stomach aglandular	27	4.2	4	3.2	3.70	96.30
13 Appendix vermiformis	18	2.8	4	3.2	3.00	97.00
14 Spiral fold	14	2.2	3	2.4	2.30	97.70
15 Reticulum sacculated	4	0.6	2	1.6	1.10	98.90
16 Paired caecum	2	0.3	2	1.6	0.95	99.05
17 Forestomach haustrated	5	0.8	1	0.8	0.80	99.20
18 Colon diverticulated	3	0.5	1	0.8	0.65	99.35

therian species belonging to a wide range of orders and families (Table 2). Raw data on the anatomy of the large intestine and the stomach are from and from Oppel (1896), Mitchell (1905, 1916), Jacobshagen (1937), Zietschmann et al. (1943), Hill (1954), Starck (1958, 1995), Vorontsov (1960, 1967), Camain et al. (1962), Oehmke (1963), Gorgas (1967), Nickel et al. (1967, 1973), Hebel (1969), Robert (1971), Yamasaki (1971), Yamasaki and Komatsu (1971), Garon and Piérard (1972), Carleton (1973), Langer (1973, 1974a,b, 1975, 1976, 1978, 1979, 1984a,b, 1985, 1987a,b,c, 1988, 1991, 1993, 1996, 2001), Peters and Gärtner (1973), Getty (1975), Snipes (1978, 1979a,b, 1981, 1982a,b, 1984), Chivers and Hladik (1980), Perrin and Curtis (1980), Snipes et al. (1982, 1988, 1990), Maddock and Perrin (1983), Perrin and Maddock (1985), Ludwig (1986), Perrin and Kokkin (1986), Bertone et al. (1987), Dyce et al. (1987), Perrin (1987), Amasaki et al. (1988), Bruerton and Perrin (1988), Naumova (1990), Koch and Berg (1990), Langer and Snipes (1991), and Caton (1999).

Seven anatomical characters refer to the large intestine and 11 to the stomach. The colon wall can be either haustrated or diverticulated. Haustrations are dilatations of the lumen that lie between muscular bands, the taeniae coli that run parallel to the longitudinal axis of the gut. Diverticulations represent blindsacs of the colonic lumen. They can be found in hyraxes (Hyracoidea). The caecum can either be absent or present in the Eutheria; it can have haustrations comparable to those in the colon. A vermiform appendix is differentiated in Primates and Lagomorpha and a complex spiral fold is found in Lagomorpha. Finally, the caecum can be doubled or paired, as in sea cows (manatees and dugongs). The morphology of the stomach is characterized according to the terminology recommended by Langer (1985, 1988). A composite stomach is lined with both nonglandular squamous epithelium and glandular epithelium. A glandular stomach

does not have a stratified squamous lining, and an aglandular stomach lacks secreting glandular epithelium (a rare situation found in a few murid rodents). Sections of the stomach can be set off from the shortest connection between cardia (entrance into) and pylorus (exit from the stomach). In some cases the stomach has more than one chamber, it is plurilocular. A forestomach is a section of the organ that is partly or totally lined with squamous epithelium, and it can have diverticulations. In Cetacea (whales) the forestomach is a section of the esophagus (Langer 1996, 2001). Similar to the situation in the large intestine, the gastric wall can possess haustra (in Colobinae) and in ruminants a reticulum and omasum are differentiated.

Quantification of Anatomical Structures in the Digestive Tract

To quantify morphological structures of the digestive tract, the frequency of their differentiation was determined in the range of 644 eutherian species for which anatomical information on the gastrointestinal tract is available (Table 2). It is possible that different species of a eutherian family have identical symplesiomorphic morphological characters. In the following account these characters will be called "morphotypes." For example, the primate families Galagidae (synonymous to Galagonidae according to Groves 1993; also Loriformes) and Cebidae (Platyrrhini) have similar types of gastrointestinal tracts but are considered here as separate morphotypes because they represent separate families. In addition, the colon of the galagos is characterized by a loop, the anso coli, which is not found in the Cebidae. To compensate for possibly biased data determined from species (Table 2, column b) and morphotypes (column d), the mean of the two values was computed (column e). A high mean percentage (A) means that a morphological character is highly

TABLE 3. In the original list of raw data (Appendix), information is incomplete in many species. When all considered characters were completely available, means of data were included in this table for 32 eutherian taxa. Means of body weight were calculated both from males and females, which means that sexual dimorphism was not taken into account. Only Microchiroptera were considered under Chiroptera.

No.	Taxon/morphotype	Number of species considered	Mean body mass (g)	Mean food (g CF/kg DM)	Mean lactation (days)	Mean first solid food (days)	Mean mixed feeding (days) ¹	Mean rel. mixed feeding	Mean sum large intestine	Mean sum of stomach	Sum of gastrointestinal tract
1	Sirenia	2	637500.00	207.00	545.65	88.25	457.40	83.83	99.05	226.75	325.80
2	Proboscidea	2	2748000.00	153.00	810.00	112.50	697.50	86.11	113.25	36.25	149.50
3	Hyracoidea	3	4000.00	230.00	90.00	2.30	87.70	97.44	212.60	68.90	281.50
4	Perissodactyla	3	1850000.00	297.67	464.60	25.33	439.27	94.55	197.25	68.90	266.15
5	Cetacea/Odontoceti	5	3976670.00	10.60	639.20	253.30	385.90	60.37	1.00	241.45	242.45
6	Artiodactyla/Hippopotamidae	2	774500.00	275.00	295.00	22.50	272.50	92.37	1.00	146.35	147.35
7	Artiodactyla/Suidae	5	75000.00	196.00	83.30	12.25	71.05	85.29	197.25	68.90	266.15
8	Artiodactyla/Tayassuidae	2	21570.00	126.00	49.00	7.00	42.00	85.71	197.25	227.85	425.10
9	Artiodactyla/Tylopoda	2	510000.00	275.00	457.50	32.00	425.50	93.01	33.60	326.75	360.35
10	Artiodactyla/Tragulidae	2	9500.00	180.00	90.00	14.00	76.00	84.44	33.60	319.70	353.30
11	Artiodactyla/Pecora/Giraffidae	2	621000.00	180.00	202.50	28.00	174.50	86.17	33.60	412.20	445.80
12	Artiodactyla/Pecora	14	163025.00	261.07	160.77	17.56	143.21	89.07	33.60	412.20	445.80
13	Macroscelidea	4	53.65	26.00	18.25	16.00	2.25	12.33	33.60	36.25	69.85
14	Insectivora	24	300.13	30.00	32.08	20.28	11.81	36.79	1.00	36.25	37.25
15	Carnivora	16	42481.38	32.94	160.77	51.05	109.72	68.25	25.45	36.25	61.70
16	Primates/Lemuriformes	10	3126.43	93.86	134.48	51.11	83.37	62.00	80.36	36.25	116.61
17	Primates/Lorisiformes	6	572.90	55.00	82.93	32.20	50.73	61.17	149.46	36.25	185.71
18	Primates/Platyrrhini	15	1651.47	69.43	161.92	68.25	93.67	57.85	117.60	36.25	153.85
19	Primates/Catarrhini	16	9051.81	115.00	209.88	55.13	154.75	73.73	197.25	36.25	233.50
20	Primates/Catarrhini/Colobinae	4	8024.33	189.00	265.00	53.00	212.00	80.00	197.25	294.40	491.65
21	Primates/Hylobatidae	1	6800.00	153.00	210.00	120.00	90.00	42.86	294.25	36.25	330.50
22	Primates/Hominidae	3	74166.67	134.33	742.20	173.92	568.28	76.57	294.25	36.25	330.50
23	Scandentia	1	200.00	110.00	42.00	35.00	7.00	16.67	33.60	36.25	69.85
24	Chiroptera	58	12.50	31.00	60.00	28.00	32.00	53.33	1.00	36.25	37.25
25	Lagomorpha	13	1360.80	239.00	23.50	14.00	9.50	40.43	312.30	36.25	348.55
26	Rodentia/Caviomorpha	10	6190.63	182.88	50.74	2.71	48.03	94.67	113.25	36.25	149.50
27	Rodentia/Hystricomorpha	2	1063.25	184.50	56.25	10.00	46.25	82.22	113.25	36.25	149.50
28	Rodentia/Muroidea	5	128.13	89.00	24.60	13.13	11.48	46.65	33.60	148.38	181.98
29	Rodentia/Glirimorpha	3	67.50	83.00	28.50	21.75	6.75	23.68	1.00	36.25	37.25
30	Pholidota	2	5150.00	26.00	105.00	60.00	45.00	42.86	1.00	160.35	161.35
31	Xenarthra/Pilosa	2	6275.00	180.00	93.15	17.75	75.40	80.94	1.00	227.85	228.85
32	Xenarthra/Myrmecophagidae	1	30500.00	26.00	165.00	84.00	81.00	49.09	1.00	68.90	69.90

¹ Calculated from means.

abundant. Character-specificity is expressed as $S = 100 - A$. For example, a spiral fold in the caecum (Table 2, line 14) is a rare differentiation and has a high specificity (97.70); on the other hand, differentiation of a caecum is a relatively abundant character with low specificity ($S = 33.60$). In Table 2 the morphological characters are arranged according to increasing specificity. Finally, it should be noted that new information for more species or more morphotypes would improve the quality of the scores on specificity.

Tabulation of Data on Food Quality, Life History, and Digestive Tract Anatomy

Comparisons of taxa were accomplished by calculating means from species and morphotypes (Table 3). The arithmetic means (see Blaxter 1989) of raw data from species that belong to 32 taxa or morphotypes were tabulated for body mass, food classification, and four life-history and three anatomical characters. The following aspects of life history were considered: lactation time (days), uptake of first solid food (days), absolute and relative mixed-feeding period (days and percent of total lactation). Specificity values for characters of large intestine and the stomach were summarized.

In addition, the total sums representing the gastrointestinal tract are also listed in Table 3. Taxonomic terminology for rodents follows Starck (1995); for primates reference is made to Storch et al. (2001).

Phylogenetic Tree

The degree of relatedness of taxa, or the taxonomic hierarchical level at which taxa are positioned, influences the quality of statistical correlations. To eliminate flaws created by taxonomic relationships, the tree for the abovementioned 32 taxa (Fig. 1) was used to calculate independent contrasts (differences) with the PDTREE program from the PDAP package, version 3.0 (Garland et al. 1996).

The phylogeny was displayed and printed with Treeview, version 1.6.6, drawing software supplied by Page (1996). It was drawn according to information from the following sources: Mammalia in general: de Jong and Goodman (1982), Wyss et al. (1987), Bollinger (1997); Eutheria: Eisenberg (1981), Shoshani et al. (1985), Miyamoto and Goodman (1986), Novacek et al. (1988), Honeycutt and Adkins (1993); Artiodactyla: Gentry and Hooker (1988), Janis and Scott (1988), Miyamoto et al. (1993), Scott and Janis (1994), Essop

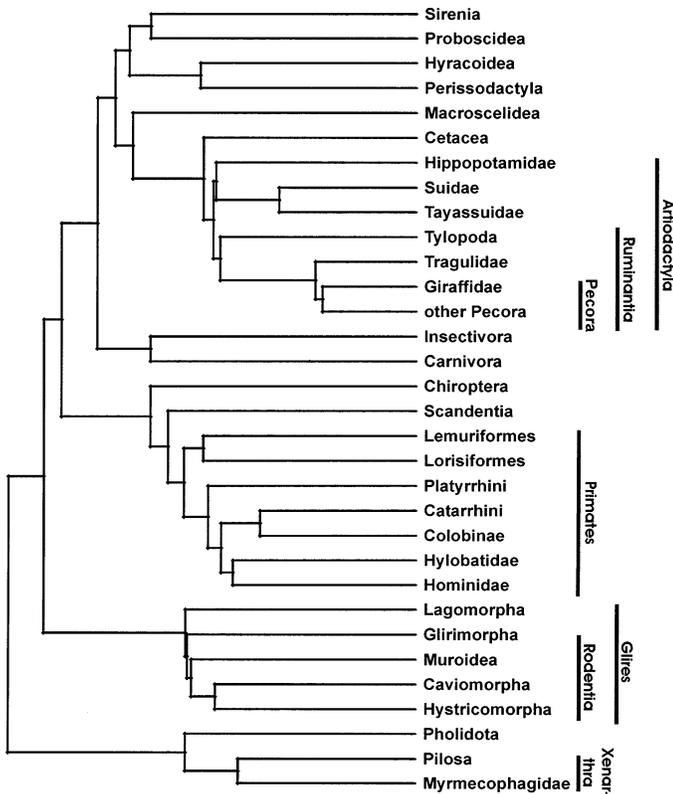


FIG. 1. Tree showing the relationships between the taxa considered in this study. The topology of the tree was drawn according to the literature cited in the text.

et al. (1997); Carnivora: Flynn et al. (1988), Wayne et al. (1989), Wozencraft (1989), Wyss and Flynn (1993), Dragoo and Honeycutt (1997); Cetacea: Arnason and Ledje (1993), Gatesy (1997), Hasegawa et al. (1997), Berta and Sumich (1999); Hippopotamidae: Gatesy (1998); Hyracoidea: Fischer and Tassy (1993), Shoshani (1993); Insectivora in general: Butler (1988); Insectivora (Lipotyphla): MacPhee and Novacek (1993); Lagomorpha: Yu et al. (1997); Macroscelidea: de Jong et al. (1993); Mesaxonia: Fischer and Tassy (1993); Perissodactyla: Hooker (1989); Pinnipedia: Arnason and Ledje (1993); Primates: Andrews (1988), Fleagle (1988); Proboscidea: Fischer and Tassy (1993); Rodentia: Bonhomme et al. (1985), Sarich (1985), Shoshani et al. (1985), Bonhomme and Thaler (1988), Jaeger (1988), Catzeflis et al. (1993, 1995); Sirenia: Fischer and Tassy (1993); Tethytheria: Tassy and Shoshani (1988); Ungulata: Prothero et al. (1988); Hasegawa et al. (1997).

A method for testing the assumption of phylogenetic independence of data of means was applied for the taxa and morphotypes presented in Table 3. Detailed explanation and information regarding the test for serial independence are supplied by Abouheif (1999). Technical information on the program Phylogenetic Independence, version 1.1, can be found in Reeve and Abouheif (1999).

Values of times when first solid food was eaten and percentages of the relative length of the mixed-feeding or weaning period, as well as the differentiations of large intestine and stomach, are grouped in Table 4. This information will

later be used to consider the evolutionary steps of life-history and morphological characters.

RESULTS

The test for phylogenetic independence (Abouheif 1999, Reeve and Abouheif 1999) was applied to logarithmic values of body mass; food classification; lactation time; day of intake of first solid food; absolute and relative length of mixed feeding period; and sum of differentiations of large intestine, stomach, and the total gastrointestinal tract. Body mass, length of mixed feeding time, the sum of differentiations of the large intestine and of the total digestive tract are dependent on their phylogeny and taxonomic relationships, that is, they are phylogenetically autocorrelated. This holds true for the original raw values from Table 3, as well as for the differences or contrasts. However, the contrasts of food classification, time of first intake of solid food (milk-only period), the relative length of mixed-feeding time, and the sum of differentiations of the stomach are not phylogenetically autocorrelated and therefore independent of their phylogenetic relationships. The original or raw values of the length of lactation are not phylogenetically autocorrelated but the contrasts are.

The PDTREE program from the PDAP package of Garland et al. (1996) calculated the correlation coefficients (Table 5) between original raw data as well as between contrasts based on the tree presented in Figure 1. For those cases where $P \leq 0.01$ slopes and intercepts of least-square regressions are listed in Table 6 and schematically depicted in Figure 2. Lactation is strongly correlated ($P < 0.001$) with body weight. Larger species have longer periods of lactation (Peters 1986; Clutton-Brock 1991; Hayssen 1993). The absolute and the relative lengths of the mixed-feeding period are also strongly correlated with body mass. Time of first intake of solid food and the sum of differentiations in the whole gastrointestinal tract are less strongly correlated ($P < 0.01$) with body mass, and the differentiations of the large intestine and the stomach, and food classification are not correlated with body mass.

The PDAP package also supplies the tabulation of residuals, which are differences between the observed values of the variables and those values that are predicted by the regression line on adult body mass (Harvey and Pagel 1995). These residuals (dependent on body mass) are correlated for the parameters depicted in Figure 2. The correlations between residuals are also listed in Table 5 and illustrated in Figure 3.

The time of first intake of solid food, the relative length of the mixed-feeding period, and differentiations of the stomach and large intestine are not correlated with each other (Fig. 2), thus allowing evolutionary steps of these four characters to be deciphered. The following classes of the four characters listed in Table 4 are considered as plesiomorphic conditions: (1) mean time of intake of first solid food between postnatal day 11 and 100; (2) mean relative time of the mixed-feeding period as compared to the time of the total lactation between 57% and 100%; (3) mean sum of differentiations of the large intestine between 1 and 10; and (4) mean sum of differentiations of the stomach between 32 and 100.

These four plesiomorphic characters are depicted with four

TABLE 4. For two life-history datasets and the differentiation of the large intestine and stomach, the distribution in 32 eutherian taxa is marked with an X (based on logarithmic mean values).

No.	Taxon/morphotype	Mean first solid food (days)			Mean relative mixed-feeding period (%)				Mean sum of large intestine			Mean sum of stomach		
		1-10	11-100	101-1000	10-17	18-31	32-56	57-100	1-10	11-100	101-1000	32-100	101-316	317-1000
1	Sirenia		X							X			X	
2	Proboscidea			X						X		X		
3	Hyracoidea	X								X		X		
4	Perissodactyla		X							X		X		
5	Cetacea/Odontoceti			X				X					X	
6	Artiodactyla/Hippopotamidae		X					X					X	
7	Artiodactyla/Suidae		X					X			X	X		
8	Artiodactyla/Tayassuidae	X						X			X		X	
9	Artiodactyla/Tylopoda		X					X		X				X
10	Artiodactyla/Tragulidae		X					X		X			X	
11	Artiodactyla/Pecora/Giraffidae		X					X		X				X
12	Artiodactyla/Pecora		X					X		X				X
13	Macroscelidea		X		X					X		X		
14	Insectivora		X			X		X				X		
15	Carnivora		X					X		X		X		
16	Primates/Lemuriformes		X					X		X		X		
17	Primates/Lorisiformes		X					X			X	X		
18	Primates/Platyrrhini		X					X			X	X		
19	Primates/Catarrhini		X					X			X	X		
20	Primates/Catarrhini/Colobinae		X					X			X		X	
21	Primates/Hylobatidae			X		X				X	X			
22	Primates/Hominidae			X			X			X	X			
23	Scandentia		X		X					X		X		
24	Chiroptera		X			X		X				X		
25	Lagomorpha		X			X				X		X		
26	Rodentia/Caviomorpha	X					X			X	X			
27	Rodentia/Hystricomorpha	X					X			X	X			
28	Rodentia/Muroidea		X			X				X			X	
29	Rodentia/Gliriformorpha		X		X			X				X		
30	Pholidota		X			X		X					X	
31	Xenarthra/Pilosa		X				X	X					X	
32	Xenarthra/Myrmecophagidae		X			X		X				X		

TABLE 5. With the help of the PDTREE program from the PDAP package of Garland et al. (1996), the correlations between raw data and contrasts (upper panel) and for residues and their contrasts (lower panel) were calculated. GIT, gastrointestinal tract.

		Correlations between contrasts of logarithmic raw data							
	Body weight	Food	Lactation	First	Mixed	Rel mixed	Large int	Stomach	GIT
Body weight	—	0.2487	0.8907**	0.5098*	0.8720**	0.5585**	0.1894	0.2153	0.4563*
Food	0.3122	—	0.1501	-0.3877	0.2918	0.4777*	0.5077*	0.2135	0.5420*
Lactation	0.8322**	0.179	—	0.6559**	0.9487**	0.5467*	0.0445	0.2072	0.3291
First	0.3365	-0.3786	0.6448**	—	0.4369	-0.1321	-0.2442	0.0152	-0.0511
Mixed	0.8558**	0.3189	0.9563**	0.4444	—	0.7834**	0.1517	0.2672	0.4464
Rel mixed	0.6487**	0.5156*	0.5787**	-0.1069	0.7920**	—	0.3143	0.3003	0.5353*
Large int	0.1267	0.5522*	0.1239	-0.1430	0.1900	0.2713	—	-0.0576	0.6480**
Stomach	0.4843*	0.2422	0.2904	-0.0261	0.3674	0.4182	-0.1762	—	0.5756**
GIT	0.5623**	0.6064**	0.4297	-0.0159	0.5370*	0.6004**	0.5677**	0.6038**	—

		Correlations between contrasts of residuals							
	Food	Lactation	First	Mixed	Rel mixed	Large int	Stomach	GIT	
Food	—	-0.1619	-0.6183**	0.1574	0.4215	0.4849*	0.1696	0.4975*	
Lactation	-0.1560	—	0.5164*	0.7731**	0.1307	-0.2784	0.0344	-0.1912	
First	-0.5344*	0.7095**	—	-0.0175	-0.5841**	-0.1619	-0.1134	-0.3710	
Mixed	0.1005	0.8529**	0.3376	—	0.7298**	-0.0279	0.1660	0.1112	
Rel mixed	0.4335	0.0838	-0.4510*	0.5918**	—	0.2568	0.2222	0.3796	
Large int	0.5409*	0.0440	-0.1560	0.1653	0.2477	—	-0.1013	0.6433**	
Stomach	0.1135	-0.2698	-0.2794	-0.1339	0.1608	-0.2799	—	0.5495*	
GIT	0.5487*	-0.0980	-0.2766	0.1178	0.3758	0.5951**	0.4638	—	

df = 30; * $P < 0.01$; ** $P < 0.001$.

TABLE 6. Least square regressions: in those cases of data comparison where $P \leq 0.01$, slopes and intercepts are listed for raw data and their contrasts. The latter are mapped back onto original data (intercept*), as supplied in the PDTREE program of Garland et al. (1996).

Paired characters		Raw data		Independent contrasts	
		Slope	Intercept	Slope	Intercept*
Body mass	Lactation	0.2635	1.0258	0.2941	0.9022
Body mass	First solid food	0.1707	1.0319	0.1739	0.8186
Body mass	Mixed feeding	0.3619	0.4132	0.3879	0.2888
Body mass	Relative mixed feeding	0.0984	1.3873	0.0938	1.3865
Body mass	GIT	0.1282	1.7329	0.1100	1.7324
Lactation	First solid food	0.6494	0.1091	0.6775	0.1128
Lactation	Mixed feeding	1.2772	-0.7951	1.2781	-0.8196
Lactation	Relative mixed feeding	0.2772	1.2048	0.2782	1.1803
Mixed feeding	Relative mixed feeding	0.2841	1.2522	0.2959	1.2230
Relative mixed feeding	GIT	0.9025	0.6393	0.7684	0.8084
Large intestine	GIT	0.2032	1.9460	0.2401	1.8631
Stomach	GIT	0.4976	1.2994	0.5154	1.1859
Food	Relative mixed feeding	0.2968	1.1841	0.2661	1.2273
Food	Large intestine	1.3352	-1.2055	1.0960	-0.9320
Food	GIT	0.5247	1.1900	0.4335	1.3135

symbols at the root of the tree in Figure 4, which is identical in topology to that in Figure 1. The size of the symbols differs from those representing plesiomorphic conditions to indicate apomorphic situations. To the right of the diagram the general character of the food eaten by the respective morphotypes is depicted.

To obtain a better understanding of the information Figure 4, the differentiation of the large intestine (colon and caecum) in Glires (Lagomorpha plus Rodentia) will be discussed in some detail. We can assume that all rodents evolved a well-differentiated large intestine as a synapomorphic character. Only in the Gliriforma (dormice and their kin) can the plesiomorph large intestine with limited differentiation be found. If, however, one assumes that the well-differentiated large intestine represents the plesiomorphic condition, the absence of a differentiated large intestine from the Gliriforma would represent the apomorphic situation. This is improbable because a higher degree of differentiation is more complex than a structure without differentiation.

Oftedal (1984) published data on peak lactation for some eutherian species. In Figure 5 means of these data are pre-

sented for different taxa together with data on the postnatal time of intake of first solid food (i.e., the length of the milk-only period).

A three-dimensional diagram (Fig. 6) is used to demonstrate those regions that can differentiate fermentation chambers in the total gastrointestinal tract. In the upper panel of Figure 7 the length of the lactation period is plotted against the length of the mixed-feeding period relative to total lactation. The lower panel of Figure 7 adds a third dimension by considering food quality, expressed as food classification.

DISCUSSION

Data on the anatomy of the gastrointestinal tract, its function, and the ontogeny are now available for a wide range of eutherian species. In the present paper these data are used to compare different eutherian orders. The diverse types of gastrointestinal tracts of mammals are products of evolutionary differentiation. They represent adaptations to different functional needs related to digestion of different types of food. The question arises whether a relationship exists between

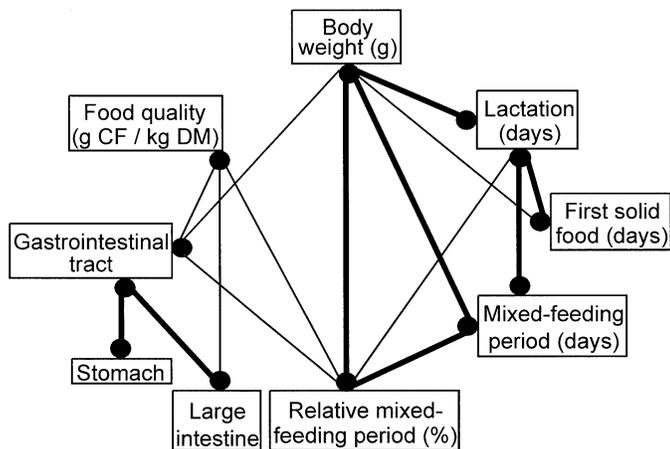


FIG. 2. Relationships between differences or contrasts of nine characters. Bold lines represent strongly related characters ($P < 0.001$); thin lines represent relationships with $P < 0.01$.

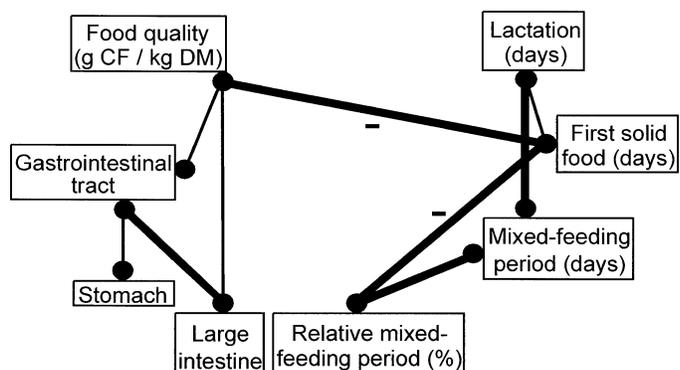


FIG. 3. To eliminate the influence of body weight, relationships between residuals were calculated with the help of relationships between the considered parameters and body weight. Bold lines represent strongly related characters ($P < 0.001$); thin lines represent relationships with $P < 0.01$.

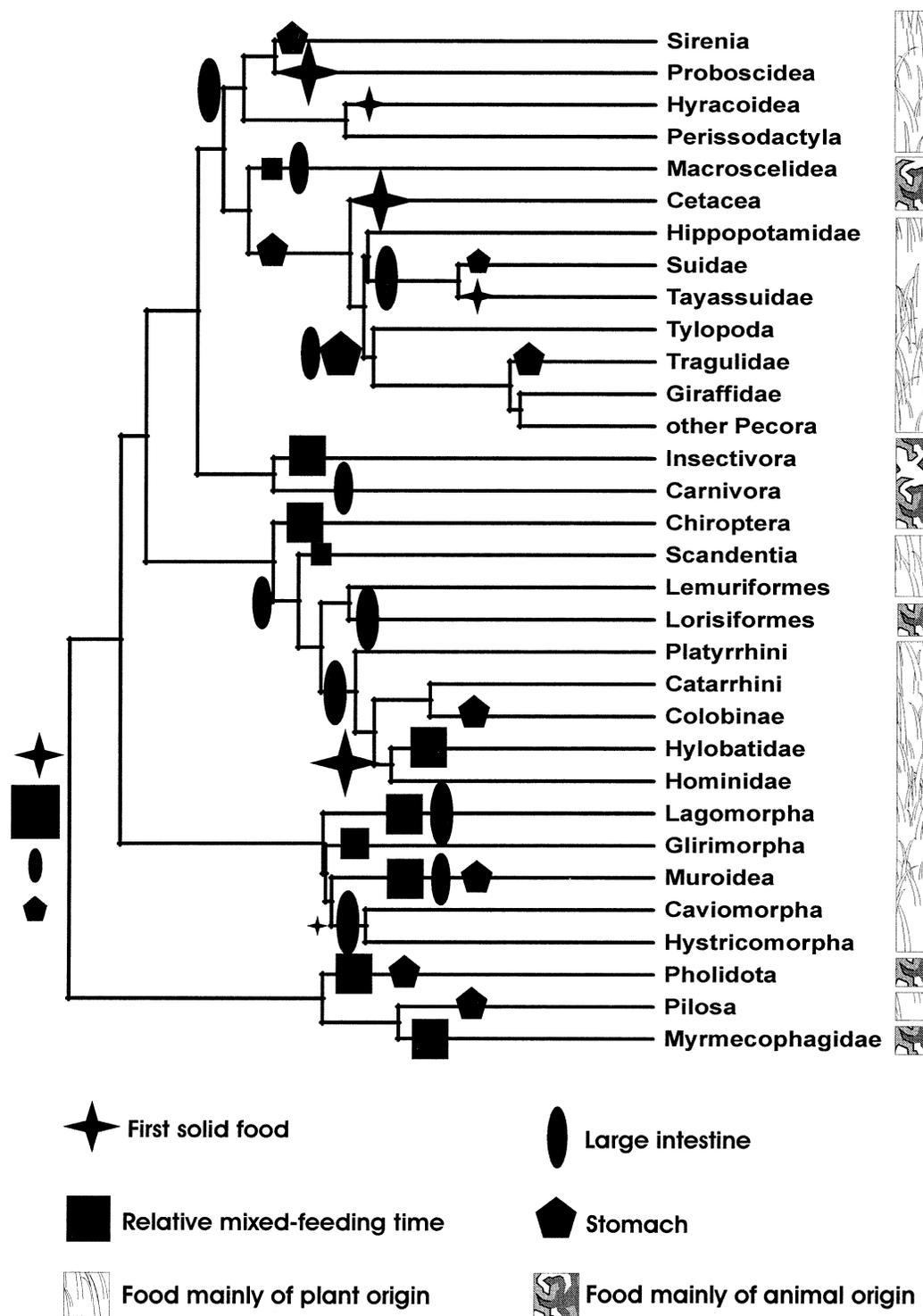


FIG. 4. Tree demonstrating the phylogeny of four characters, based on the tree shown in Figure 1. The size of the four symbols for the time of intake of first solid food (star), relative length of the mixed-feeding or weaning time (square), the differentiation of the large intestine (oval), and the stomach (pentagon) is variable. Large symbols represent strong, small symbols weak differentiations of characters. The types of food are marked to the right of the illustration.

adaptations to plant food and an anatomically complex tract, which is able to digest such food effectively.

To obtain an idea of the differentiation of the gastrointestinal tract, the present paper considers those sections of the

tract that can serve as fermentation chambers for alloenzymatic digestion, that is, digestion with the help of microbial symbionts (Langer 1988). In mammals that digest their food with their own set of enzymes (i.e., autoenzymatically), the

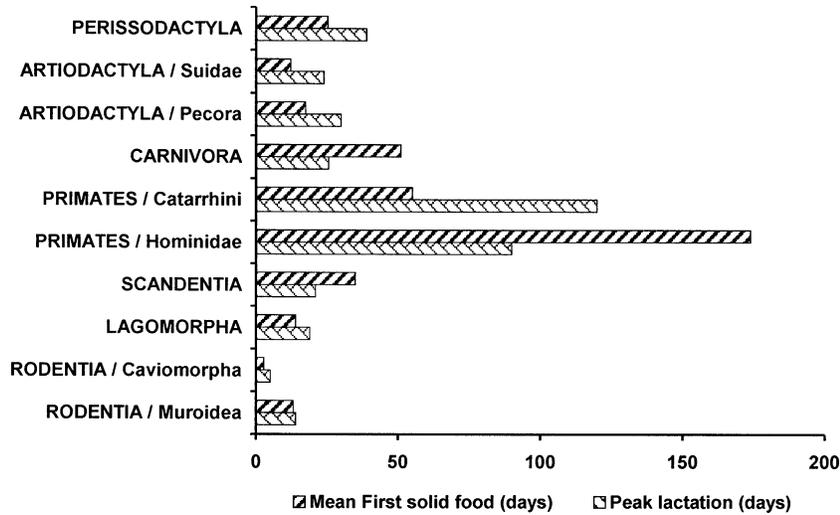


FIG. 5. Compilation of the day when first solid food is ingested (i.e., length of the milk-only period) and time of peak lactation according to data published by Oftedal (1984).

components of the digestive system that are mainly responsible for the digestion and absorption of food are the stomach, small intestine, pancreas, and liver (Cranwell 1995). The small intestine and a stomach lined with secreting epithelium (glandular stomach) are sites where digestion with the mammal's own set of enzymes takes place. In many eutherian groups, those sections of the digestive tract characterized by an extended volume are the sites where alloenzymatic digestion takes place.

During the weaning period the gastrointestinal tract has to adapt to a diet of different physical and chemical composition. In the laboratory rat (*Rattus norvegicus*) the set of di-

gestive enzymes produced by the small intestine changes and differentiates considerably during ontogeny (Kennedy 1967; Deren 1968; Henning 1981; Klein 1989a,b). This mammalian species is certainly not a strict herbivore or a graminivore (for terms, see Table 1), but the quality of food certainly changes considerably during the weaning period. Cranwell (1995) discusses the changes during the weaning process in the domestic pig: The milk of the sow provides the piglet with a source of highly digestible nutrient with immunological and nonimmunological protection agents and supplies stimulatory and regulatory factors that may be important for the development of the digestive tract and its regulatory sys-

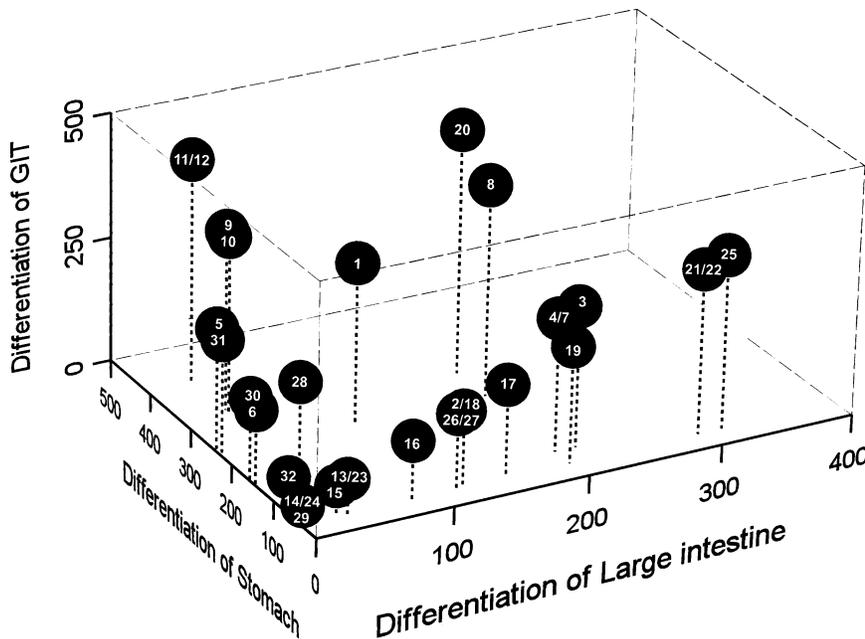


FIG. 6. Three dimensional diagram showing relationships between differentiation of the large intestine and stomach, as well as the gastrointestinal tract as a whole, according to data listed in Table 3. The numbers in the black dots are identical with those in the first column of that table. Differentiation of the total gastrointestinal tract is plotted to give a direct impression of this differentiation.

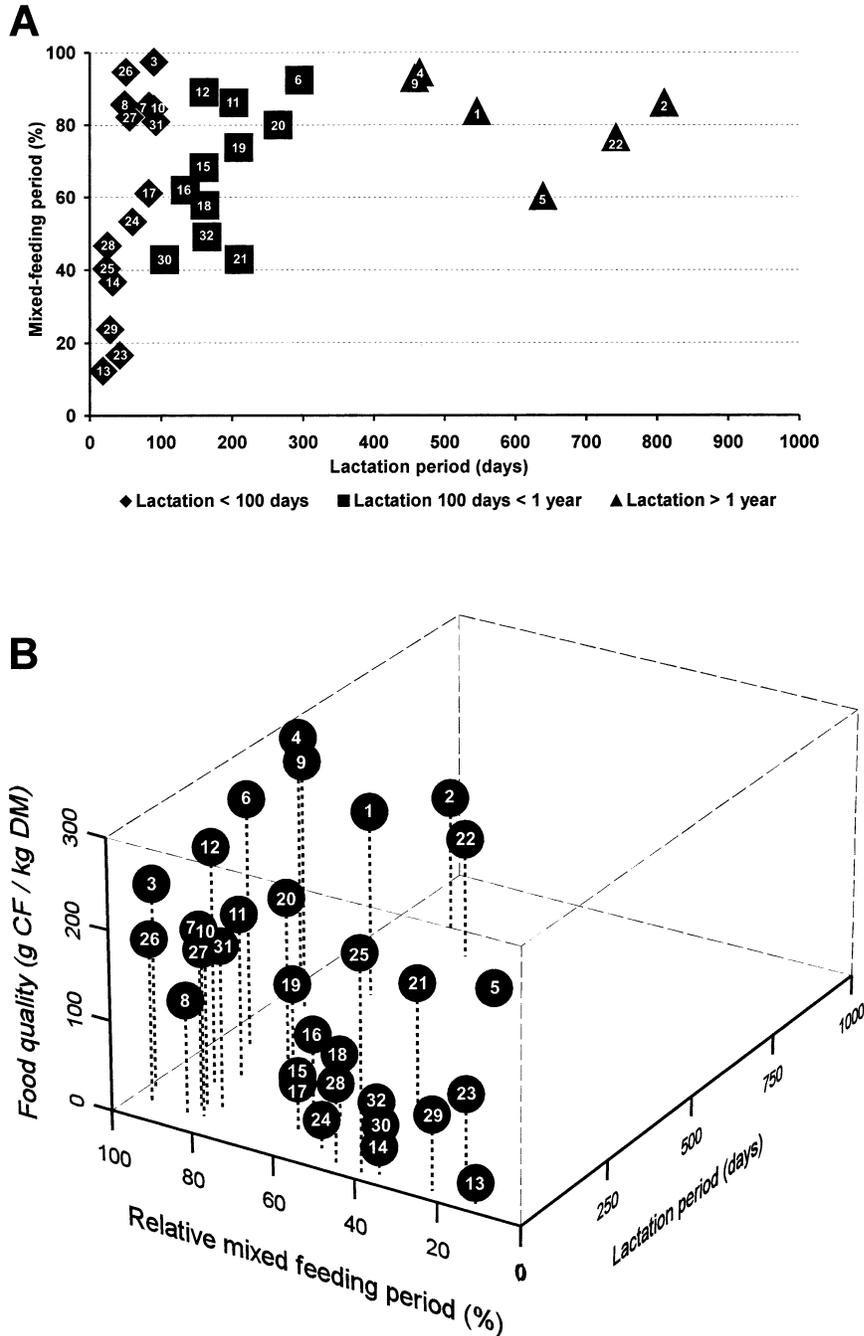


FIG. 7. (A) Diagram depicting relationship between length of lactation period in days and relative mixed-feeding period in percent. The numbers in the black symbols are identical with those in the first column of Table 3. (B) Data on food quality are presented on the vertical axis as gram crude fiber per kilogram dry matter. The numbers in the black dots are identical with those in the first column of Table 3.

tems. The postweaning diet, on the other hand, is usually less digestible than the mother's milk and it is supplied more irregularly.

Exposure of different segments of the digestive tract to symbiotic microbes changes the physiological and chemical environment in the digestive tract, and these changes coincide with anatomical changes. Four phases of microbial incubation of the digestive tract by microbes have been differentiated for human infants by Perman (1989) and Beckmann and R f-

fer (2000): Phase I occurs during the first 2 weeks of life. During birth and afterward the newborn is inoculated with microbes from its environment, mainly with aerobic bacteria. These organisms create an environment favorable for the subsequent appearance of anaerobes. This first aerobic population can be considered a preparatory state of inoculation (Sonnenborn and Greinwald 1991). In phase II, the first balanced microbial flora is established approximately two weeks after birth in the period prior to the introduction of solids. An-

aerobes of the genera *Lactobacillus* and *Bifidobacterium* dominate this microbial population (Beckmann and Ruffer 2000). In phase III, the addition of solid foods has a major impact on the microbial ecosystem in the digestive tract. A strictly anaerobic flora can be found. In phase IV, an adult-type microbial flora appears at the time when weaning is complete, although shifts within the anaerobic flora might occur during the first two years of life.

The inoculation of fermentation chambers, in ruminants, for example, happens in a process similar to the situation just described for humans. First, aerobic and facultatively anaerobic bacteria initiate inoculation of the ruminoreticulum, followed by a phase when *Lactobacillus* plays an important role. In calves, reduction in the total number of aerobic microbes begins in the period between the third and sixth week after birth (Giesecke 1973). In mammals with a unilocular stomach (i.e., those that do not have a forestomach) the most numerous population of strict anaerobes can be found in the caecum and colon (Raibaud et al. 1982). In these postgastric sections of the digestive tract, as well as in forestomachs (when differentiated), a substantial portion of the daily energy requirement of the mammalian host is derived from absorption of volatile (VFA) or short-chained fatty acids (SCFA) through the wall of the forestomach, caecum, or large intestine. For humans, the importance in the total energy metabolism of VFA that are absorbed from the caecum and colon is uncertain (Perman 1989) because the data are ambiguous. However, Parra (1978) made clear that fermentation in the large intestine can play a very important role. In humans, the ambient intestinal bacteria are beneficial by synthesizing B vitamins (Postgate 1992).

Functional differentiation during ontogeny is connected with a morphological differentiation. In those mammals possessing a unilocular stomach that are not strictly herbivorous (e.g., *Homo sapiens* and *Sus scrofa*) it is the functional differentiation of stomach, small intestine, and the digestive glands that enables the change from milk to adult food possible (for discussion of this and related problems, see Leberthal 1989; Cranwell 1995). There is continued growth of all sections of the digestive tract, but dramatic changes of proportions of the different compartments cannot be observed. In those eutherians that ingest considerable amounts of food rich in structural carbohydrates of plant origin however, the establishment of a balanced microbial population coincides with the increase in volume of fermentation chambers. For example, in *Babyrusa babyrussa*, *Hippopotamus amphibius*, *Hexaprotodon (Choeropsis) liberiensis*, and in different species of ruminants, the forestomach volume increases considerably from birth to weaning and further to adulthood (Langer 1988). The same tendency could also be demonstrated in the stomach of toothed whales, which eat food of animal origin (Langer 1996).

Fermentation in the large intestine salvages calories that have escaped absorption in the small intestine (Perman 1989), but fermentation products of the large intestine are partly lost with the feces. In this study the differentiations of pre- and postgastric fermentation chambers, namely forestomach, caecum, and colon, are considered.

Large Intestine and Stomach

As can be seen in Figure 6, differentiation of the large intestine is often (in 13 groups) accompanied by very little differentiation of the stomach: Proboscidea, Hyracoidea, Perissodactyla (2, 3, 4 in Table 3), Suidae (7), Primates (16, 17, 18, 19, 21, 22), Lagomorpha (25), and South American rodents, namely Caviomorpha and Hystricomorpha (26, 27). However, nine groups of Eutheria with a complex stomach generally show little differentiation of the large intestine (odontocete whales, 5; Artiodactyla, 6, 9, 10, 11, 12; muroid rodents, 28; Pholidota, 30; Pilosa, 31). Seven groups show low differentiation in the stomach as well as in the large intestine (Macroscelidea, 13; Insectivora, 14; Carnivora, 15; Scandentia, 23; Chiroptera, 24; glirimorph rodents, 29; Myrmecophagidae, 32), and there are only three groups where the stomach together with the large intestine are intermediately differentiated, namely, Sirenia (sea cows, 1), Tayassuidae (peccaries, 8) and Colobinae (leaf monkeys, 20).

The mixed-feeding period is neither correlated with the differentiation of fermentation vats in the digestive tract, nor with the differentiation of a voluminous large intestine or stomach. This holds true when contrasts of raw data (Fig. 2) or residuals (Fig. 3) were correlated. However, the relative mixed-feeding period shows a correlation ($P < 0.01$) with the formation of fermentation vats in the total gastrointestinal tract (Fig. 2), but not between stomach or large intestine and relative mixed-feeding time.

Food quality in the sense applied here is correlated ($P < 0.01$) with differentiations of the total gastrointestinal tract and differentiations of the large intestine, but not with those of the stomach (Figs. 2, 3). A highly differentiated stomach is not necessarily an adaptation to microbial fermentation. A stomach with an extensive storing volume, where microbial fermentation is not of great importance, can be found in Muroida (mice and their kin) and Pholidota (pangolins or scaly anteaters). The forestomachs can be thick-walled muscular structures that press and squeeze the content in a fashion comparable to the activity of the crop in birds. The esophageal pouch (Langer 2001) of odontocete whales, is such a structure that churns and mills fish, squid, and other types of materials originating from prey animals.

Milk-Only Period

The length of the milk-only period, ending by the first intake of solid food between 11 and 100 days, is a plesiomorphic character widely found in the Eutheria (Table 4, Fig. 4). Shorter or longer milk-only periods are apomorphic characters. Hyracoidea, Tayassuidae, Caviomorpha, and Hystricomorpha ingest milk only for less than 10 days. Long milk-only periods are found in Proboscidea, Cetacea, Hylobatidae, and Hominidae, that is, in very large Eutheria and in Primate families where the mother-young relationship is lengthened. The Ruminantia, a highly derived group in relation to their stomach and large intestinal morphology, eat their first solid food from 11 to 100 days after birth.

The milk-only period before the first intake of solid food is correlated ($P < 0.001$) with the quality of food when influences of adult body mass are eliminated, that is, when residuals are correlated (Fig. 3): When food quality is low

(food classification high), the milk-only period is short. This means that the young animal, which later has to rely on a food of low quality, starts to eat this material after a short interval of exclusive ingestion of milk.

Mixed-Feeding Period in Relation to Total Lactation Period

A mixed-feeding or weaning period (Table 4) that comprises from about 60% to 100% of the total lactation time is widely found in Eutheria and represents a plesiomorphic character, found in 22 of the 32 groups considered here. A relatively long mixed-feeding time ($\geq 57\%$ of the length of lactation) can be found in the "PSHM-group" (sensu Fischer and Tassy 1993), which consists of Proboscidea, Sirenia, Hyracoidea and Mesaxonia, and in the Artiodactyla. The weaning period is also very long in Carnivora, many Primates, including Hominidae, in caviomorph and hystricomorph rodents, and in sloths (*Pilosa*). A decrease in the relative length of the mixed-feeding time, which means that pure milk without additional solid food is eaten during a relatively longer portion of lactation, can be found in Glires (*Lagomorpha* and *Rodentia*), *Pholidota*, *Xenarthra*, insectivores, chiropterans, and *Scandentia* (tree shrews).

Considering contrasts calculated from raw data, why is it that the contents in crude fiber in the food and the differentiation of the morphology of the gastrointestinal tract are closely related with the relative length of the mixed-feeding or weaning period (in percent of the length of total lactation), but not with the absolute length in days? It should be kept in mind that there is no correlation between the residuals of length of the mixed-feeding period (absolute and relative) and food quality, when influence of adult body weight is eliminated.

When a lactating and nursing mother is forced to eat only low-quality food with a high content in crude fiber and low availability of protein and fat, she can experience nutritional problems. Are life-history traits related to the energetic load put on the mother? Millar (1977) states that late lactation is energetically the most critical period of the whole breeding cycle. This is because it is an energy burden for the mother to replace the nutrients she exports into milk (Hammond and Diamond 1992). This load increases the daily energy requirements considerably (Farmer 2000). However, the composition of milk varies not only among species of mammals, but also with the course of lactation, and to some extent with the composition of the diet (Jenness and Sloan 1970). It was shown by Oftedal (1985) and Oftedal and Gittleman (1989) that milk contains very low dry matter and the energy content is low at the time when intake of solid food begins (i.e., at the end of the milk-only period). During normal lactation "milk yield rises to a peak and then declines over a period of time that may be long or short, according to species" (Oftedal 1984, p. 68). In the latter study Oftedal presented data on the time of peak lactation (in days). When his data are combined with a compilation of days of intake of first solid food (Fig. 5), it becomes obvious that peak lactation and the time of first intake of solid food lie generally close together. Exceptions occur only in primates: In the *Catarrhini* (represented in Oftedal's publication by the baboon) peak lactation lies considerably later to the intake of first solid

food; in the *Hominidae* (represented by man) peak lactation takes place well within the milk-only period.

When a eutherian mammal is adapted to a relatively extended mixed-feeding period, the digestive tract should be able to handle material that can only be digested alloenzymatically (i.e., with the help of microbes). In fact, the correlation between differentiation of the digestive tract and *relative* length of the mixed-feeding period, is a consequence of the correlation between food and relative mixed-feeding period (Fig. 2). Residuals of food classification and those of the intake of first solid food, as well as this latter parameter and the relative length of the mixed-feeding period, are negatively correlated with each other, so that low food quality (high values in food classification) are related with a short milk-only period (early first intake of solid food), and this short milk-only period is related with a relatively long mixed-feeding period.

According to Hayssen (1993), energetic demands on mothers are largest directly before weaning. In precocial young, as found in guinea pigs (*Cavia porcellus*), where pups begin to nibble solid food very soon after birth, energy acquisition of the mother is highest during the first half of the lactation period (Künkele and Trillmich 1997). When the offspring starts to eat solid food relatively early during lactation, the nutritional stress on the mother can be reduced because she can use a greater percentage of the food she ingested for herself while still supplementing the young animal nutritionally.

I now examine whether life-history traits are related with nutritional aspects from the standpoint of the young. According to Pond (1977, p. 191), "from the point of view of the juveniles, suckling is energetically very inexpensive compared to regular food gathering processes, so they are able to devote a high proportion of the calories they obtain from milk to growth, and relatively little to maintenance." An extended *absolute* length of the mixed-feeding period is positive for the offspring, "when the age at first solid food occurs long before weaning, lactation may have significant functions beyond nutrition or energy" (Hayssen 1993, p. 3227). For example, sufficient time to train food acquisition and to exercise avoidance of predators would be available during an extended mixed-feeding time. The weaning period would be extended. During this period antibodies enabling passive immunity and immunoglobulins can be transferred through milk by the mother, thereby increasing the immune competence of the young.

Lactation Period, Mixed-Feeding Period, and Food Quality

Are life-history traits influenced by the quality of adult food? In Figure 7A the relative length of the mixed-feeding or weaning period (percent) is plotted against the total length of the lactation period. The longer the lactation period, the higher the contribution of the mixed-feeding period during lactation. When lactation extends over 100 days or more, at least 40% of this time is a period when milk and solid food are ingested, and about 60% is taken up by a mixed-feeding period. Only short time spans of lactation that are, at most, 100 days long can be characterized by extremely short (< 40%) mixed-feeding periods, which means that for most of

the lactation time the young animals depend totally on milk and on the mother.

Comparison of Figures 2 and 3 makes clear that body weight may contribute to the relationship between length of lactation and relative length of the mixed-feeding period. When influence of body mass is eliminated (Fig. 3), there is no relationship between the abovementioned two parameters.

In Figure 7B the quality of food is introduced as a third dimension. The following generalizations can be made. Animals ingesting a food with a low content of crude fiber (i.e., high food quality), are characterized by a short lactation with a relatively short ($\leq 40\%$) mixed-feeding period. Foods containing very high amounts of crude fiber are ingested by eutherians with a lactation period of less than 500 days, at least 40% of which are characterized by solid food in addition to milk, including Perissodactyla, hippos, ruminating Artiodactyla, and colobine monkeys that eat high amounts of leaves supplemented by seeds and unripe fruit. In the toothed whales, the lactation period is long (> 600 days), and during about 60% of this period the young animal supplements its milk supply with additional solid food. There is practically no crude fiber from plant cell wall material in their food. In animals with an extremely long lactation period, during which young animals ingest a mixture of milk and solid food (e.g., Sirenia, Proboscidea, and Hominidae), the content of adult food of crude fiber is intermediate. When the maternal effort is smaller, that is, when the length of the lactation period is shortened, but when solid food is eaten in addition to milk, the crude fiber content of adult food can be extremely high. A digestive tract inoculated with a cellulolytic microbial flora and adapted to food rich in plant cell wall material is no longer adapted to a food rich in protein and fat, as can be found in milk (Henning 1981). If, however, a food of higher quality is eaten by the adult, the change in digestive enzymes is not as drastic as in herbivorous mammals and the parallel ingestion of milk and solid food can be shortened.

Food rich in plant cell wall material can only be digested alloenzymatically. As noted by Mackie 2002 (p. 319), "The processes involved in the establishment of microbial populations are complex, involving succession of microorganisms and many microbial and host interactions eventually resulting in dense, stable populations inhabiting characteristic regions of the gut." Is the establishment of the microbial population related with the length of the mixed-feeding period?

The present study does not supply information about whether the inoculation process per se is related to any of the life-history traits. However, the information to be obtained from consideration of absolute and relative length of the mixed-feeding or weaning period can now be clearly compared. The absolute length of the mixed-feeding period depends on the needs of the young animal (Langer 2002b). The longer the mixed-feeding period, the more time is available for ontogenetic developments, for example, learning how to obtain food, avoidance of predators, and establishment of immune competence. The length of the mixed-feeding period relative to total lactation represents the period when energetic loads on the mother are reduced because the young itself obtains additional energy sources.

Evolutionary Differentiation of Subdivisions of Lactation and of the Fermentation Chambers

Returning to Figure 4 and Table 4, we follow the evolutionary differentiation of the milk-only (first solid food, in days) and the relative mixed-feeding or weaning period (percent) as well as the differentiations of the large intestine and the stomach. The food of the adult animal is differentiated according to plant or animal material.

The number of taxa with an extended length of the milk-only period is small and the distribution of eutherians with a late time of ingestion of first solid food (101–1000 days) is disjunct. This is the case in the Proboscidea, toothed Cetacea (Odontoceti), Hylobatidae, and Hominidae. In Hyracoidea, Tayassuidae, and South American rodents (Caviomorpha, Hystricomorpha), and Pilosa (sloths) first solid food is eaten very early (1–10 days after birth).

A mixed-feeding period that lies below 18% of the total length of lactation (very small quadrangle in Fig. 4) can be found in two nonrelated taxa, the Scandentia and Macroscelidea. Only in Gliriforma does the weaning period contribute 18–31% of lactation. A relative length of the mixed-feeding period between 32% and 56% is also distributed rather haphazardly in the Eutheria: Insectivora, Chiroptera, Hylobatidae, Lagomorpha, Muroidea, Pholidota, and Myrmecophagidae (Xenarthra). The uneven distribution of the relative length of mixed-feeding period indicates that the length of this period represents an adaptation to functional needs and is not a character representing relationship. However, the ungulates (sensu Prothero 1993) are characterized by a very long relative mixed-feeding time that represents more than 57% of the entire lactation.

Differentiation of the large intestine differs among groups. The plesiomorphic situation with no considerable differentiation of the large bowel, such as formation of a caecum, can be found in the branch leading to Pholidota and Xenarthra, the latter consisting of Pilosa and Myrmecophagidae. However, ungulates show considerable differentiation in the large intestine; a caecum is not differentiated in the Hippopotamidae and odontocete whales (Mysticeti, baleen whales, have a caecum; Langer 2001). Insectivora, Chiroptera, and Gliriforma do not have a highly differentiated large intestine.

In relation to gastric differentiation, the situation is ambiguous. Artiodactyla have a highly complex stomach (large pentagon in Fig. 4), and there seems to be a regression in complexity only in the Suidae (very small pentagon). Complex stomachs can also be found in the Cetacea, Colobinae, Muroidea (mice and their kin), and Pholidota and Pilosa (sloths), which have a forestomach (Langer 1988). Large forestomachs (i.e., higher gastric complexity), can be found in faunivores, such as Odontoceti (toothed whales), as well as in plant-eaters, such as many Artiodactyla and Colobinae. It is therefore not surprising that food quality and stomach differentiation are not correlated with each other (Fig. 2). The differentiation of just four characters already produces a remarkable complexity within eutherian mammals.

Concluding Remarks

Alloenzymatic digestion can take place in the foregut (fermentation chambers of the stomach) and in the hindgut (fer-

mentation chambers in the large intestine; Parra 1978). The present study shows that the quality of food and the differentiation of the large intestine (colon and caecum combined) are clearly correlated ($P < 0.01$), even when influence of body mass is eliminated by use of residuals. However, there is no significant correlation between the differentiation of the stomach and food quality. This means that the differentiation of the stomach is not necessarily adapted to microbial fermentation, but can serve many other purposes, for which the organ has to be adapted and differentiated. One such purpose could be simple increase of storing volume without synchronous fermentation. Pholidota (pangolins or scaly anteaters) ingest considerable quantities of soil and debris (Smithers 1983). The ingested grit may assist in the process of food grinding (Smithers 1983). In the opesophageal pouch, a part of the forestomach of Cetacea (whales), the ingested food (e.g., fish, squids) are churned or milled (Langer 1996).

An extended absolute length of the mixed-feeding period depends mainly on the needs of the offspring. During this period, it still obtains energy from the mother, although it already partly relies on solid food. This extended period can be used to train the juvenile to acquire food and avoid predators, as well as social rules that dominate life in a group. This means that aspects other than just nutritional ones can influence the ontogenetic development of the young mammal considerably.

For the mother the energetic load is reduced when the juvenile begins to consume solid food in addition to milk. It is in the interest of the mother that the juvenile enter the mixed-feeding period as early as possible.

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APPENDIX

The 644 eutherian species considered in this paper. *Homo sapiens* is also considered in the text, but not listed below.

Artiodactyla	<i>Cervus nippon</i>	<i>Ovis ammon</i>	<i>Arctocephalus pusillus</i>
<i>Aepyceros melampus</i>	<i>Cervus unicolor</i>	<i>Ovis canadensis</i>	<i>Arctonyx collaris</i>
<i>Alcelaphus buselaphus</i>	<i>Choeropsis liberiensis</i>	<i>Ovis dalli</i>	<i>Atilax paludinosus</i>
<i>Alces alces</i>	<i>Connochaetes gnou</i>	<i>Ovis musimon</i>	<i>Bassaricyon gabbii</i>
<i>Ammotragus lervia</i>	<i>Connochaetes taurinus</i>	<i>Phacochoerus aethiopicus</i>	<i>Bassariscus astutus</i>
<i>Antidorcas marsupialis</i>	<i>Damaliscus dorcas</i>	<i>Potamochoerus porcus</i>	<i>Callorhinus ursinus</i>
<i>Antilocapra americana</i>	<i>Elaphurus davidianus</i>	<i>Procapra gutturosa</i>	<i>Canis adustus</i>
<i>Antilope cervicapra</i>	<i>Gazella dorcas</i>	<i>Pudu pudu</i>	<i>Canis aureus</i>
<i>Babyrousa babyrussa</i>	<i>Gazella subgutturosa</i>	<i>Rangifer tarandus</i>	<i>Canis latrans</i>
<i>Bison bison</i>	<i>Gazella thomsoni</i>	<i>Raphicerus campestris</i>	<i>Canis lupus</i>
<i>Bison bonasus</i>	<i>Giraffa camelopardalis</i>	<i>Rupicapra rupicapra</i>	<i>Canis mesomelas</i>
<i>Blastoceros dichotomus</i>	<i>Hippopotamus amphibius</i>	<i>Saiga tatarica</i>	<i>Chrysocyon brachyurus</i>
<i>Bos frontalis</i>	<i>Hippotragus equinus</i>	<i>Sus scrofa</i>	<i>Civettictis civetta</i>
<i>Bos grunniens</i>	<i>Hippotragus niger</i>	<i>Syncerus caffer</i>	<i>Crocuta crocuta</i>
<i>Bos taurus</i>	<i>Hyemoschus aquaticus</i>	<i>Taurotragus oryx</i>	<i>Crossarchus obscurus</i>
<i>Boselaphus tragocamelus</i>	<i>Hylochoerus meinertzhageni</i>	<i>Tayassu pecari</i>	<i>Cryptoprocta ferox</i>
<i>Bubalus bubalis</i>	<i>Kobus ellipsiprymnus</i>	<i>Tayassu tajacu</i>	<i>Cuon alpinus</i>
<i>Budorcas taxicolor</i>	<i>Kobus kob</i>	<i>Tragelaphus angasi</i>	<i>Cystophora cristata</i>
<i>Camelus bactrianus</i>	<i>Kobus leche</i>	<i>Tragelaphus euryceros</i>	<i>Dusicyon australis</i>
<i>Camelus dromedarius</i>	<i>Lama glama</i>	<i>Tragelaphus oryx</i>	<i>Eira barbara</i>
<i>Capra caucasica</i>	<i>Lama vicugna</i>	<i>Tragelaphus strepsiceros</i>	<i>Enhydra lutris</i>
<i>Capra falconeri</i>	<i>Madoqua kirki</i>	<i>Tragelaphus scriptus</i>	<i>Erignathus barbatus</i>
<i>Capra hircus</i>	<i>Madoqua saltiana</i>	<i>Tragulid napu</i>	<i>Eumetopias jubatus</i>
<i>Capra ibex</i>	<i>Mazama americana</i>	Carnivora	<i>Eupleres goudotii</i>
<i>Capreolus capreolus</i>	<i>Nemorhaedus goral</i>	<i>Acinonyx jubatus</i>	<i>Felis bengalensis</i>
<i>Cephalophus monticola</i>	<i>Odocoileus hemionus</i>	<i>Ailuropoda melanoleuca</i>	<i>Felis chaus</i>
<i>Cephalophus sylvicultor</i>	<i>Odocoileus virginianus</i>	<i>Ailurus fulgens</i>	<i>Felis concolor</i>
<i>Cephalophus zebra</i>	<i>Okapia johnstoni</i>	<i>Alopex lagopus</i>	<i>Felis nigripes</i>
<i>Cervus axis</i>	<i>Oreamnos americanus</i>	<i>Arctictis binturong</i>	<i>Felis pardalis</i>
<i>Cervus dama</i>	<i>Oreotragus oreotragus</i>	<i>Arctocepalus australis</i>	<i>Felis serval</i>
<i>Cervus duvauceli</i>	<i>Ourebia ourebi</i>	<i>Arctocephalus forsteri</i>	<i>Felis silvestris</i>
<i>Cervus elaphus</i>	<i>Ovibos moschatus</i>		<i>Felis tigrina</i>

APPENDIX
Continued.

<i>Felis viverrina</i>	<i>Pteronura brasiliensis</i>	<i>Micropteropus pusillus</i>	<i>Suncus murinus</i>
<i>Felis wiedii</i>	<i>Speothos venaticus</i>	<i>Miniopterus schreibersi</i>	<i>Talpa europaea</i>
<i>Fossa fossa</i>	<i>Spilogale putorius</i>	<i>Molossus molossus</i>	<i>Tenrec ecaudatus</i>
<i>Galictis cuja</i>	<i>Suricata suricatta</i>	<i>Myotis albescens</i>	Lagomorpha
<i>Galidia elegans</i>	<i>Taxidea taxus</i>	<i>Myotis lucifugus</i>	<i>Lepus americanus</i>
<i>Genetta genetta</i>	<i>Tramarcos ornatus</i>	<i>Myotis myotis</i>	<i>Lepus californicus</i>
<i>Genetta tigrina</i>	<i>Urocyon cinereoargenteus</i>	<i>Myotis nattereri</i>	<i>Lepus capensis</i>
<i>Gulo gulo</i>	<i>Ursus americanus</i>	<i>Myotis nigricans</i>	<i>Lepus europaeus</i>
<i>Halichoerus grypus</i>	<i>Ursus arctos</i>	<i>Myotis sodalis</i>	<i>Lepus timidus</i>
<i>Helarctus melayanus</i>	<i>Ursus maritimus</i>	<i>Myotis tricolor</i>	<i>Ochotona pallasii</i>
<i>Helogale parvula</i>	<i>Ursus thibetanus</i>	<i>Myotis velifer</i>	<i>Ochotona princeps</i>
<i>Herpestes ichneumon</i>	<i>Vulpes rueppelli</i>	<i>Noctilio albiventris</i>	<i>Oryctolagus cuniculus</i>
<i>Herpestes sanguineus</i>	<i>Vulpes velox</i>	<i>Nyctalus noctula</i>	<i>Romerolagus diazi</i>
<i>Hyaena brunnea</i>	<i>Vulpes vulpes</i>	<i>Nycteris macrootis</i>	<i>Sylvilagus audubonii</i>
<i>Hyaena hyaena</i>	<i>Vulpes zerda</i>	<i>Nycteris nana</i>	<i>Sylvilagus brasiliensis</i>
<i>Hydrurga leptonyx</i>	<i>Zalophus californianus</i>	<i>Nycteris thebaica</i>	<i>Sylvilagus floridanus</i>
<i>Ictonyx striatus</i>	Cetacea	<i>Nycticeius humeralis</i>	<i>Sylvilagus transitionalis</i>
<i>Leptonyxotes wedelli</i>	<i>Balaena mysticetus</i>	<i>Nyctophilus gouldi</i>	Macroscelidea
<i>Lobodon carcinophagus</i>	<i>Balaenoptera acutorostrata</i>	<i>Pipistrellus ceylonicus</i>	<i>Elephantulus intufi</i>
<i>Lutra canadensis</i>	<i>Balaenoptera borealis</i>	<i>Pipistrellus kuhlii</i>	<i>Elephantulus rufescens</i>
<i>Lutra lutra</i>	<i>Balaenoptera borealis</i>	<i>Pipistrellus natusii</i>	<i>Macroscelides proboscideus</i>
<i>Lycaon pictus</i>	<i>Balaenoptera edini</i>	<i>Pipistrellus pipistrellus</i>	<i>Rhynchocyon chrysopygus</i>
<i>Lynx canadensis</i>	<i>Balaenoptera musculus</i>	<i>Pipistrellus subflavus</i>	Perissodactyla
<i>Lynx caracal</i>	<i>Balaenoptera physalus</i>	<i>Plecotus townsendii</i>	<i>Ceratotherium simum</i>
<i>Lynx lynx</i>	<i>Cephalorhynchus hectori</i>	<i>Pteropus geddeiri</i>	<i>Diceros bicornis</i>
<i>Lynx rufus</i>	<i>Delphinapterus leucas</i>	<i>Pteropus giganteus</i>	<i>Equus asinus</i>
<i>Martes americana</i>	<i>Delphinus delphis</i>	<i>Rhinolophus euryale</i>	<i>Equus burchelli</i>
<i>Martes foina</i>	<i>Eschrichtius robustus</i>	<i>Rhinolophus ferrumequinum</i>	<i>Equus grevyi</i>
<i>Martes martes</i>	<i>Globicephala macrorhynchus</i>	<i>Rhinolophus hipposideros</i>	<i>Equus przewalskii</i>
<i>Martes pennanti</i>	<i>Globicephala melaena</i>	<i>Rhinolophus landeri</i>	<i>Equus zebra</i>
<i>Martes zibellina</i>	<i>Hyperoodon ampullatus</i>	<i>Rhinolophus megaphyllus</i>	<i>Rhinoceros unicornis</i>
<i>Meles meles</i>	<i>Kogia breviceps</i>	<i>Rhinopoma hardwickei</i>	<i>Tapirus indicus</i>
<i>Mellivora capensis</i>	<i>Lagenorhynchus acutus</i>	<i>Rhynchonycteris naso</i>	<i>Tapirus terrestris</i>
<i>Melursus ursinus</i>	<i>Megaptera novaeangliae</i>	<i>Rousettus aegyptiacus</i>	Pholidota
<i>Mephitis mephitis</i>	<i>Mesoplodon bidens</i>	<i>Saccopteryx bilineata</i>	<i>Manis temminckii</i>
<i>Mirounga angustirostris</i>	<i>Monodon monoceros</i>	<i>Saccopteryx leptura</i>	<i>Manis tricuspis</i>
<i>Mirounga leonina</i>	<i>Neophocaena phocaenoides</i>	<i>Tadarida aegyptiaca</i>	Primates
<i>Monachus monachus</i>	<i>Orcinus orca</i>	<i>Vespertilio murinus</i>	<i>Allenopithecus nigroviridis</i>
<i>Monachus schauinslandi</i>	<i>Phocoena phocoena</i>	Hyracoidea	<i>Alouatta caraya</i>
<i>Mungos mungo</i>	<i>Phocoenoides dalli</i>	<i>Dendrohyrax arboreus</i>	<i>Alouatta palliata</i>
<i>Mungotictis decemlineata</i>	<i>Physeter macrocephalus</i>	<i>Heterohyrax brucei</i>	<i>Alouatta seniculus</i>
<i>Mustela erminea</i>	<i>Pseudorca crassidens</i>	<i>Procavia capensis</i>	<i>Aotes azarai</i>
<i>Mustela eversmanni</i>	<i>Sousa chinensis</i>	Insectivora	<i>Aotes trivirgatus</i>
<i>Mustela frenata</i>	<i>Stenella attenuata</i>	<i>Blarina brevicauda</i>	<i>Ateles belzebuth</i>
<i>Mustela lutreola</i>	<i>Stenella coerulealba</i>	<i>Chrysochloris stuhlmanni</i>	<i>Ateles fucipes</i>
<i>Mustela nivalis</i>	<i>Stenella longirostris</i>	<i>Crociodura bicolor</i>	<i>Ateles geoffroyi</i>
<i>Mustela putorius</i>	<i>Tursiops truncatus</i>	<i>Crociodura hirta</i>	<i>Ateles paniscus</i>
<i>Mustela vison</i>	Chiroptera	<i>Crociodura leucodon</i>	<i>Callimicio goeldii</i>
<i>Nandinia binotata</i>	<i>Antrozous pallidus</i>	<i>Crociodura russula</i>	<i>Callithrix jacchus</i>
<i>Nasua nasua</i>	<i>Chaerephon pumila</i>	<i>Cryptotis parva</i>	<i>Cebus apella</i>
<i>Neofelis nebulosa</i>	<i>Cynopterus sphinx</i>	<i>Echinops telfairi</i>	<i>Cebus capucinus</i>
<i>Neophoca cinerea</i>	<i>Desmodus rotundus</i>	<i>Erinaceus albiventris</i>	<i>Cercocebus albigena</i>
<i>Nyctereutes procyonides</i>	<i>Eidolon helvum</i>	<i>Erinaceus europaeus</i>	<i>Cercopithecus aethiops</i>
<i>Odobenus rosmarus</i>	<i>Epomophorus crypturus</i>	<i>Hemicentetes semispinosus</i>	<i>Cercopithecus ascanius</i>
<i>Otaria byronia</i>	<i>Epomophorus gambianus</i>	<i>Microgale dobsoni</i>	<i>Cercopithecus diana</i>
<i>Octocyon megalotis</i>	<i>Eptesicus fuscus</i>	<i>Microgale talazaci</i>	<i>Cercopithecus mitis</i>
<i>Panthera leo</i>	<i>Eptesiscus regulus</i>	<i>Myosorex varius</i>	<i>Cercopithecus mona</i>
<i>Panthera onca</i>	<i>Glossophaga soricina</i>	<i>Neomys anomalus</i>	<i>Cercopithecus neglectus</i>
<i>Panthera pardus</i>	<i>Hipposideros ater</i>	<i>Neomys fodiens</i>	<i>Cercopithecus nictitans</i>
<i>Panthera tigris</i>	<i>Hipposideros caffer</i>	<i>Setifer setosus</i>	<i>Cercopithecus talapoin</i>
<i>Panthera uncia</i>	<i>Hipposideros commersoni</i>	<i>Solenodon paradoxus</i>	<i>Cheirogaleus major</i>
<i>Phoca groenlandica</i>	<i>Lasionycteris noctivagans</i>	<i>Sorex araneus</i>	<i>Cheirogaleus medius</i>
<i>Phoca hispida</i>	<i>Lasiurus borealis</i>	<i>Sorex cinereus</i>	<i>Colobus polykomus</i>
<i>Phoca vitulina</i>	<i>Lasiurus cinereus</i>	<i>Sorex minutus</i>	<i>Daubentonia madagascarensis</i>
<i>Poecilogale albinucha</i>	<i>Lavia frons</i>	<i>Sorex monticulus</i>	<i>Erythrocebus patas</i>
<i>Potous flavus</i>	<i>Leptonyxetrus sanborni</i>	<i>Sorex vagrans</i>	
<i>Procyon lotor</i>	<i>Megaderma lyra</i>	<i>Suncus etruscus</i>	
<i>Proteles cristatus</i>	<i>Megaderma spasma</i>		

APPENDIX
Continued.

<i>Galago demidovii</i>	<i>Clethrionomys glareolus</i>	<i>Microtus agrestis</i>	<i>Pseudomys nanus</i>
<i>Galago senegalensis</i>	<i>Coendu prehensilis</i>	<i>Microtus arvalis</i>	<i>Pseudomys novaehollandiae</i>
<i>Galagoides zanzibaricus</i>	<i>Conilurus penicillatus</i>	<i>Microtus californicus</i>	<i>Pseudomys praeconis</i>
<i>Gorilla gorilla</i>	<i>Cricetomys gambianus</i>	<i>Microtus guentheri</i>	<i>Rattus fuscipes</i>
<i>Hylobates lar</i>	<i>Cricetulus migratorius</i>	<i>Microtus montanus</i>	<i>Rattus lutreolus</i>
<i>Indri indri</i>	<i>Cricetus cricetus</i>	<i>Microtus nivalis</i>	<i>Rattus norvegicus</i>
<i>Lagothrix lagotricha</i>	<i>Cryptomys hottentotus</i>	<i>Microtus oeconomus</i>	<i>Rattus rattus</i>
<i>Lemur catta</i>	<i>Ctenomys talarum</i>	<i>Microtus oregoni</i>	<i>Reithrodontomys humulis</i>
<i>Lemur fulvus</i>	<i>Cynomys ludovicianus</i>	<i>Microtus pennsylvanicus</i>	<i>Reithrodontomys megalotis</i>
<i>Lemur macaco</i>	<i>Dasymys incomptus</i>	<i>Microtus xanthognathus</i>	<i>Reithrodontomys montanus</i>
<i>Leotopithecus rosalia</i>	<i>Dasyprocta leporina</i>	<i>Mus musculus</i>	<i>Saccostomys campestris</i>
<i>Lepilemur mustelinus</i>	<i>Dasyprocta punctata</i>	<i>Mus triton</i>	<i>Sciurus aberti</i>
<i>Loris tardigradus</i>	<i>Desmodillus auricularis</i>	<i>Muscardinus avellanarius</i>	<i>Sciurus carolinensis</i>
<i>Macaca fascicularis</i>	<i>Dicrostonyx groenlandicus</i>	<i>Myocastor coypus</i>	<i>Sciurus niger</i>
<i>Macaca fuscata</i>	<i>Dinomys branickii</i>	<i>Myoprocta acouchy</i>	<i>Sciurus vulgaris</i>
<i>Macaca mulatta</i>	<i>Dipodomys deserti</i>	<i>Myoxus glis</i>	<i>Scotinomys teguina</i>
<i>Macaca silenus</i>	<i>Dipodomys heermanni</i>	<i>Mystromys albicaudatus</i>	<i>Scotinomys xerampelinus</i>
<i>Microcebus murinus</i>	<i>Dipodomys merriami</i>	<i>Napaeozapus insignis</i>	<i>Sicista betulina</i>
<i>Nasalis larvatus</i>	<i>Dipodomys microps</i>	<i>Neotoma albigula</i>	<i>Sigmodon hispidus</i>
<i>Nycticebus coucang</i>	<i>Dipodomys nitratoides</i>	<i>Neotoma cinerea</i>	<i>Sigmodon ochrognathus</i>
<i>Otolemur crassicaudatus</i>	<i>Dipodomys panaminticus</i>	<i>Neotoma floridana</i>	<i>Spermophilus beecheyi</i>
<i>Pan troglodytes</i>	<i>Dipodomys stephensi</i>	<i>Neotoma fuscipes</i>	<i>Spermophilus citellus</i>
<i>Papio hamadryas</i>	<i>Dolichotis patagonum</i>	<i>Neotoma lepida</i>	<i>Spermophilus columbianus</i>
<i>Papio leucophaeus</i>	<i>Eliomys quercinus</i>	<i>Notomys alexis</i>	<i>Spermophilus franklini</i>
<i>Papio sphinx</i>	<i>Erethizon dorsatum</i>	<i>Notomys cervinus</i>	<i>Spermophilus pygmaeus</i>
<i>Perodicticus potto</i>	<i>Funisciurus congicus</i>	<i>Notomys fuscus</i>	<i>Spermophilus saturatus</i>
<i>Pithecia pithecia</i>	<i>Galea musteloides</i>	<i>Notomys mitchellii</i>	<i>Spermophilus suslicus</i>
<i>Pongo pygmaeus</i>	<i>Geocapromys ingrehami</i>	<i>Ochrotomys nutalli</i>	<i>Spermophilus tridecemlineatus</i>
<i>Presbytes entellus</i>	<i>Gerbillus nanus</i>	<i>Octodon degus</i>	<i>Synaptomys cooperi</i>
<i>Presbytis obscura</i>	<i>Gerbillus pyramidum</i>	<i>Ondatra zibethicus</i>	<i>Tamias amoenus</i>
<i>Propithecus verreauxi</i>	<i>Glaucomyus sabrinus</i>	<i>Onychomys leucogaster</i>	<i>Tamias cinereicollis</i>
<i>Pygathrix nemaus</i>	<i>Glaucomyus volans</i>	<i>Oryzomys nigripes</i>	<i>Tamias ochrovittatus</i>
<i>Saguineus oedipus</i>	<i>Grammomys dolichurus</i>	<i>Oryzomys palustris</i>	<i>Tamias sibiricus</i>
<i>Saguinus bicolor</i>	<i>Graphyurus murinus</i>	<i>Otomys irrotatus</i>	<i>Tamiasciurus hudsonicus</i>
<i>Saguinus imperator</i>	<i>Heterocephalus glaber</i>	<i>Otomys slogetti</i>	<i>Tatera brantsii</i>
<i>Saguinus labiatus</i>	<i>Hydrochaeris hydrochaeris</i>	<i>Oxymycterus rutilans</i>	<i>Tatera inclusa</i>
<i>Saguinus tamarin</i>	<i>Hydromys chrysogaster</i>	<i>Pachyuromys duprasi</i>	<i>Tatera indica</i>
<i>Saimiri scinereus</i>	<i>Hystrix africaeaustralis</i>	<i>Paraxerus cepapi</i>	<i>Tatera leucogaster</i>
<i>Symphalangus syndactylus</i>	<i>Hystrix cristata</i>	<i>Pedetes capensis</i>	<i>Thrynomys swinderianus</i>
<i>Tarsius spectrum</i>	<i>Hystrix indica</i>	<i>Perognathus californicus</i>	<i>Tylomys nudicaudus</i>
<i>Theropithecus gelada</i>	<i>Jaculus jaculus</i>	<i>Perognathus longimembris</i>	<i>Uromys caudimaculatus</i>
Proboscidea	<i>Kerodon rupestris</i>	<i>Perognathus parvus</i>	<i>Zapus hudsonius</i>
<i>Elephas maximus</i>	<i>Laggadina lakedownensis</i>	<i>Peromyscus californicus</i>	<i>Zapus princeps</i>
<i>Loxodonta africana</i>	<i>Lagidium peruanum</i>	<i>Peromyscus crinitus</i>	<i>Zygodontomys brevicauda</i>
Rodentia	<i>Lagostomus maximus</i>	<i>Peromyscus difficilis</i>	<i>Zygomys argurus</i>
<i>Acomys cahirinus</i>	<i>Lagurus crutatus</i>	<i>Peromyscus eremicus</i>	<i>Zygomys woodwardi</i>
<i>Aethomys chrysophilus</i>	<i>Leggadina forresti</i>	<i>Peromyscus leucopus</i>	Scandentia
<i>Aethomys kaiseri</i>	<i>Lemmus lemmus</i>	<i>Peromyscus maniculatus</i>	<i>Tupaia glis</i>
<i>Aethomys namaquensis</i>	<i>Lemmus schisticolor</i>	<i>Peromyscus megalops</i>	Sirenia
<i>Agouti paca</i>	<i>Lemniscomys striatus</i>	<i>Peromyscus polionotus</i>	<i>Dugong dugon</i>
<i>Akodon azarae</i>	<i>Leporillus conditor</i>	<i>Peromyscus truei</i>	<i>Trichechus manatus</i>
<i>Akodon molinae</i>	<i>Liomys pictus</i>	<i>Peromyscus intermedius</i>	Tubulidentata
<i>Aplodontia rufa</i>	<i>Lophuromys sikapusi</i>	<i>Phodopus sungorus</i>	<i>Orycteropus afer</i>
<i>Apodemus sylvaticus</i>	<i>Malacothrix typica</i>	<i>Pitymys pinetorum</i>	Xenarthra
<i>Arvicanthis niloticus</i>	<i>Marmota bobak</i>	<i>Pitymys ochrogaster</i>	<i>Bradypus tridactylus</i>
<i>Arvicola terrestris</i>	<i>Marmota marmota</i>	<i>Pitymys subterraneus</i>	<i>Bradypus variegatus</i>
<i>Atherurus africanus</i>	<i>Marmota monax</i>	<i>Praomys morio</i>	<i>Chaetophractus villosus</i>
<i>Beamys hindei</i>	<i>Mastacomys fuscus</i>	<i>Praomys natalensis</i>	<i>Choloepus didactylus</i>
<i>Callosciurus prevostii</i>	<i>Melomys cervinipes</i>	<i>Proechimys guairae</i>	<i>Choloepus hoffmanni</i>
<i>Cannomys badius</i>	<i>Meriones crassus</i>	<i>Psammomys obesus</i>	<i>Dasytus novemcinctus</i>
<i>Capromys piloridea</i>	<i>Meriones lybicus</i>	<i>Pseudomys hermannsburgensis</i>	<i>Euphractus sexcinctus</i>
<i>Castor canadensis</i>	<i>Meriones persicus</i>	<i>Pseudomys albocinereus</i>	<i>Myrmecophaga tridactyla</i>
<i>Castor fiber</i>	<i>Meriones shawi</i>	<i>Pseudomys apodemoides</i>	<i>Tamandua tetradactyla</i>
<i>Cavia aperea</i>	<i>Meriones unguiculatus</i>	<i>Pseudomys australis</i>	<i>Tolypeutes matacus</i>
<i>Cavia porcellus</i>	<i>Mesembriomys gouldi</i>	<i>Pseudomys delicatulus</i>	
<i>Chinchilla lanigera</i>	<i>Mesocricetus auratus</i>	<i>Pseudomys desertor</i>	
<i>Clethrionomys gapperi</i>	<i>Mesocricetus brandti</i>	<i>Pseudomys gracilicaudatus</i>	
	<i>Micromys minutus</i>	<i>Pseudomys higginsi</i>	