

# On the Evolutionary Significance of Encephalization in Some Eutherian Mammals: Effects of Adaptive Radiation, Domestication, and Feralization

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## Key Words

Allometries · Mammals · Brain size · Encephalization · Phylogeny · Ontogeny · Adaptive radiation · Domestication · Feralization

## Abstract

Allometries of the brain to body size relationship in eutherian mammals are examined in this study as they can be used for comparative analyses concerning encephalization. In contrast with some modern presentations of this issue, an older concept is revived and expanded through this author's current study. Three allometries with clearly different slopes are valid and lead to reliable results: interspecific, intraspecific, and ontogenetic allometries. Interspecific allometries follow lines with slope values of 0.56 or 0.63 for larger and smaller species, respectively, and characterize different average encephalization plateaus with rodents and lagomorphs generally more strongly encephalized compared to basal insectivores. Artiodactyls, perissodactyls and carnivores as a whole are again on a higher but rather similar plateau. Several species of carnivores have reached different encephalization levels with respect to their average plateau indicating diverse radiations. A phylogenetic brain size increase from fossil to recent radiations is also evident. Intraspecific allometries have slope values of about 0.25. These are of help in comparing brain sizes

of ancestral species with their domesticated relatives. Domestication has generally led to a brain size decrease, but species on higher encephalization plateaus show this trend more strongly than species on a lower level of encephalization. Several brain parts and the sense organs also decrease in size during the domestication process, but vary arbitrarily and to different degrees. Ontogenetic growth allometries are species-specific, but are especially different between altricial and precocial mammals. A very steep 1st phase slope of highly encephalized species is particularly useful for understanding evolutionary and adaptive phenomena. Domesticated mammals that have become feral do not show an increase in brain size despite living many generations in wild habitats.

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## Introduction

As they mature, scientists sometimes recognize that old questions of biological phenomena which in principle have already been answered can be revived and discussed anew by younger generations of researchers. This is quite normal and through an increase in data, the application of new complex methods, and/or more sophisticated statistical treatments an increase in knowledge can result in fresh insights and a deeper understanding of natural phenome-

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na. However, in some cases despite the new methods, results and their interpretation are still questionable. This is particularly true when evolutionary research is conducted while lacking or even ignoring basic ideas on the methods applied and information on their history. To some extent it seems that much of the huge modern literature on brain evolution and associated behavior is an example of this, especially concerning a comparison of brain sizes, quantitative evaluations of the encephalization process and hypotheses regarding the evolution of mammalian brains and behavior. Therefore, some general remarks, criticisms, and results on this topic are presented here.

In conjunction with this, it is important to first recall the general concepts of evolutionary processes derived from paleontological, embryological and comparative anatomical research [Romer, 1966; Thenius, 1969; Starck, 1982, 1995; Carroll, 1988]. Since their emergence from synapsid reptilian-like ancestors, eutherian mammals have evolved and radiated at different times following a mosaic mode, and through divergence or convergence there derived a great number of extinct as well as extant species. The development and organization of body shapes and sizes have been, and in the case of recent species still are, adapted to diverse life-styles and ecological niches. Phylogenetic changes to the body and its diverse organs can be evaluated through interspecific (between species) comparisons. Following the generally accepted Darwinian idea that the origin of new species always occurs from ancestral species, it is clear that species differences actually derive from intraspecific (within species) variation. Additionally it is important to recognize that during this process the genetically determined structural changes are only manifested through different individual ontogenetic development that occurs within a species, as documented by species variation. Accordingly, interspecific comparison, intraspecific variability, and mode of ontogenetic development are all important for evaluating evolutionary processes in general and specific detail.

Following these ideas, structural changes must have always occurred prior to the subsequent testing of their adaptive worth by natural selection. All extinct and extant species had or have adaptive value, otherwise they would not have emerged and existed. Consequently, all recent species are examples of differently evolved and differently adapted survivors whether they are organized simply or advanced, and how specialized they are to a particular environment.

The above-mentioned ideas concerning evolutionary radiation are also valid for the brain of eutherian mammals. In general, the brains of this mammalian group show a common *grundbauplan*, a basal organization that is very different from reptiles, birds, or other vertebrate groups [Kappers et al., 1967; Kuhlenbeck, 1977, 1978; Butler and Hodos, 1996]. However, among mammalian species there are clear differences in the absolute and relative sizes of the whole brain, the proportion of brain parts, number and density of nerve cells, the degree of lamination pattern differentiation or nuclear organization, and the number and density of synapses. For neuroanatomists and zoologists all these parameters are structures that can be reliably measured and compared among species, among individuals within species, and during individual ontogenetic growth to quantitatively characterize evolutionary and developmental trends. Larger brains, brain subdivisions or numbers of nerve cells and synapses are considered characteristic of more highly evolved species, as are also more clearly differentiated and laminated structures. Yet special caution is mandatory concerning the comparative approach and interpretations of results.

Such quantitative comparisons of central nervous tissue only reveal reliable results when the species compared are equal in body size. For many centuries [Haller, 1762] it has been widely accepted that the brain size of any given mammalian species is somehow related to its body size. The problem of brain and body size relationships has been the subject of numerous investigations. Such studies led to the establishment of allometric methods to allow brain size comparisons in different sized mammals. These methods result in a reliable scaling from small to larger brains and indicate the encephalization level of diverse species independent of body size.

Although most scientists generally accept allometric methodologies for brain size comparisons, disagreements have occurred concerning the application of these methods. Consequently, the reliability and biological value of the results must then be questioned. As will be shown, the real question of such a comparative approach through allometry is not to demonstrate a relationship between brain and body size per se, but to determine of what kind the slope of allometric lines is and how this can be used in a comparative approach. Thus, it is not helpful to just analyze data on brain and body size of diverse species in the hopes of simply reaching statistical significance. It is often not acknowledged that three different allometries following three different rules must be distinguished in a study of brain to body size relationship. These three allometries are: interspecific, intraspecific, and ontoge-

netic. The differences should be distinguished in allometric analyses as they can serve very different research purposes in studying brain size comparisons and interpreting the results.

This review first presents a short historical overview of these three brain and body size allometries including some critical remarks. Subsequently, sample results are summarized with a discussion of the phylogeny and adaptive radiation of the brain during evolution. In this context domesticated mammals are included. This special group of eutherian mammals clearly differs in their origin and present a unique radiation. Wild species and domestic forms both show biological diversity, although their origins are quite different; wild species emerged through interspecific radiation and domesticated forms through intraspecific variability. In principle, phylogeny and domestication have characteristics in common. Although domestic species are the result of human intervention, they nevertheless demonstrate the potential for body structure changes, including the changeability of central nervous structures, over evolutionary time. As an 'artificial model' in a 'man-made experiment' they can increase our understanding of phylogenetic adaptive events in principle, especially on the species level. Finally, this review will discuss feralized mammals in the context of what happens to the brain when domesticated forms revert to life in the wild over several generations.

### **Classic Studies of Allometry and the Brain/Body Size Relationship**

#### *General Allometric Equation*

The relationship between brain and body size data is a double logplot and is best represented by the allometric equation:

$$\log y = a \log x + \log b$$

where  $x$  = body size;  $y$  = brain size;  $a$  = slope or power;  $b$  =  $y$ -intercept.

This line can be calculated as an axis through a distribution ellipse of several data points. However, uncertainties can occur concerning the calculation procedure. For a given data set this line can be obtained through least-square regression methods (regression on  $y$ ; regression on  $x$ ; reduced axis; main axis), or through canonical analyses [Rempe, 1962; Rempe and Weber, 1972]. Thus for an identical data set the different calculations can result in rather different slope values and consequently in the  $y$ -intercepts. This depends on the position of the distribu-

tion ellipse around the data, and the value of the slope is very important for comparative purposes. This is especially the case when relatively small sized mammals are compared with clearly larger ones. However, most scientists use the main axis or canonical analyses and therefore the results of these data analyses are quite comparable. Nevertheless, as shown below there are clear differences among the slopes of interspecific, intraspecific and ontogenetic brain to body size allometries.

#### *Interspecific Allometry*

Interspecific allometries are a useful approach to quantitatively estimate the encephalization values of different species because in such calculations the slope characterizes the dependency of body size on brain size, whereas the  $y$ -intercept indicates the encephalization level independent of body size. Consequently, encephalization indices or quotients can be calculated for diverse species. Such an index is the measurement of observed brain size relative to expected brain size derived from the interspecific allometric line.

However, encephalization indices or quotients calculated from allometric lines that vary significantly in slope are quite different. Thus, previous questions were primarily concerned with the 'true' or at least the 'most reliable' slope of interspecific allometries for a comparative approach. In other words, the question asked is: Is there a general slope in the relationship indicating a universal or similar brain/body dependency in mammals, or perhaps even other vertebrates?

Based mainly on a theoretically deduced prediction of Snell [1892], the creator of the allometric method, some authors such as Jerison [e.g., 1973, 1988] use a  $2/3$  power function for this comparison, whereas Dubois [1897, 1914] in the past, and numerous authors since, have empirically found slope values of 0.56 to 0.63 to be valid for interspecific comparisons after considering the special requirements for reliable allometric calculations. However, in sharp contrast to these researchers, other authors argue for the validity of a 0.73–0.75 encephalization slope value across all eutherian mammals, within orders or suborders, or they present very different slope values for other higher-order 'man-made' taxonomic units called taxon level effect [Martin, 1981; Armstrong, 1982, 1983, 1990; Hofman, 1982, 1983, 1989; Harvey and Bennett, 1983; Martin and Harvey, 1985; Gittleman, 1986; Harvey, 1988; Pagel and Harvey, 1988, 1989; Harvey and Krebs, 1990; and more recently Aboitiz, 1996 and Marino, 1998].

Most of these authors apply high standards of statistical analyses to their data of brain or brain case sizes and body weight estimates, but the biological relevance remains problematic. Some of these authors include a statement to the effect of: 'Until recently the interpretation of variation in relative brain size among mammals was dominated by a false fact – an incorrect value of the exponent scaling brain weight to body weight' [Harvey and Bennett, 1983]. These methodical treatments as well as the results and conclusions have been included in several current textbooks, monographs or treatises as 'common modern knowledge' [Martin, 1990; Van Dongen, 1998; Roth, 2000].

It must be emphasized that these sorts of calculations only repeat methodological misunderstandings and subsequent misinterpretations that have already been identified [Wirz, 1950]. They clearly must be corrected as they do not acknowledge some basic information and the special methodological needs for an interspecific allometric investigation of encephalization. They especially do not reflect the fact that extant species are simply a serendipitous sample of survivors having reached evolutionary plateaus at different levels of complexity. Consequently, less stringently applied general and taxonomically-specific calculations usually result in different slopes depending on the accidental distribution of high and low encephalization values of large- and small-sized mammals under investigation.

As an example, imagine that a sample taxonomic group of mammals is represented at one end by a species small in body size but relatively large in brain size, and at the other end by a species large in body but relatively small in brain size; then a small slope value will result. In another sample, a taxonomic group might accidentally be represented at one end by a small-sized form with a small brain and at the other end by a large species with an extremely large brain; then a steeper slope value will result. Such calculations in principle are reminiscent of those previously presented for eutherian mammals: from a shrew species to the blue whale; from mouse to elephant; or from monkeys to humans. Concerning brain size comparisons this must result in an equal encephalization value for both extreme forms of body size, as their data plots are situated on or near the calculated line. Thus, a shrew would then show a similar encephalization value as the blue whale, a mouse as the elephant and monkeys as humans. However, this cannot be valid either from a neuroanatomical or a biological point of view. Thus, this type of calculation is not valid for brain size comparisons and resulting encephalization scaling in eutherians, regardless of its statistical reliability.

In the 1950's and 1960's there were several discussions and scientific workshops (especially in Germany) addressing these problems and the value of the allometric method. The general result was that in an interspecific comparison brain size differences and thus encephalization levels can be established only with certainty when the influence of body size on brain size is rather similar for all mammals in the study. It must be remembered that the allometric line in a double log plot of body versus brain size values is one formula with two unknown quantities namely: slope (= body size dependency) and y-intercept (= encephalization level). To evaluate one value, the other must necessarily be known.

Another critical argument concerns the brain size dependency of body size excluding any degree of encephalization. In this respect it is easy to see that recent mammals have body structures that are differently evolved and adapted, which a priori implies differently evolved and adapted central nervous structures and circuits for somatic and visceral motor and sensory supply. For example, the five digit paws of carnivores or hands and feet of primates generally have greater numbers of individual muscles compared with the partially or totally reduced specialized autopodia of the cetaceans, ungulates or other groups. Undoubtedly, this is related to greater or lesser masses of white matter, numbers of nerve cells and more or less differentiated sensory and motor nuclei in the spinal cord (intumescentia cervicalis, intumescentia lumbalis) and connected portions of the brain. The same is true for other parts of the somatic and visceral musculature of the body, as well as the integumental and internal innervation and the sense organs. Evolutionary and adaptive peculiarities are always differently expressed and this seems as though it would doom the use of general allometric models. However, one of the main goals for the use of allometric method of investigations of overall brain size is to help identify specializations versus general trends. In many modern studies very often this is not addressed.

In an attempt to circumvent this problem the early studies of brain allometry first concentrated on the influence of body size on brain size. This can be accomplished only by a reliably a priori exclusion of the encephalization influence at all taxonomic levels. Consequently, calculations were performed first only on data of species similar in body plan but very different in body size, phylogenetically rather close to one another, and as closely related as possible in biology and behavior (a priori postulated similar encephalization). Thus within some families such as Cervidae, Felidae, or Canidae, several smaller and larger sized species can serve such demands.

This is not possible in all the recent mammalian orders or other taxonomic groups, as in many of them several species are not very different in body size (e.g., Proboscidea, Tubulidentata, Sirenia), whereas in other groups calculations do not make any sense. These include those groups that are known to be basally represented by both smaller sized species and by more highly evolved species with larger bodies (e.g., Primates). However, this approach was taken within several families of Insectivora [Stephan et al., 1991], Chiroptera [Baron et al., 1996], Lagomorpha [Kruska, 1980], Rodentia [Weidemann, 1970a; Kruska, 1980], Edentata [Röhrs, 1966], Artiodactyla [Oboussier and Schliemann, 1965; Kruska, 1970a, 1982a, b], Perissodactyla [Kruska, 1973] and Carnivora [Klatt, 1955; Röhrs, 1959a, b, 1966, 1985a, b, 1986a, b; Schumacher, 1963; Thiede, 1966, 1973; Kruska, 1980; Röhrs et al., 1989]. These numerous studies on highly diverse material resulted in a rather uniform pure body size influence on brain size as indicated by slope values of 0.56 or 0.63 for interspecific interrelationships. Additionally in a reevaluation of such 'somatic' brain-body scaling, Fox and Wilczynski [1986] obtained an exponent of  $a = 0.52$  for some laboratory rodent species. Marino [1998] more recently mentioned a slope value of this dimension ( $a = 0.53$ ) for some odontocete cetaceans of similar body plan, although it was not used for comparisons of encephalization indices. Altogether this indicates slope values clearly smaller than 0.72–0.75 and 0.66. Thus, the earlier assumptions of Dubois [1914] were in general verified.

Additionally, as argued by Count [1947], within those orders predominately composed of small sized recent species (Insectivora, Chiroptera, Rodentia) the higher value of 0.63 seems valid, whereas other orders show a 0.56 power. Most probably interspecific slope values of this magnitude are also valid for the brain to body size relationship of birds as tested in some European species of Corvidae with similar body plan and biology, including small sized jackdaws (*Corvus monedula*), some other medium sized species and the larger raven [*Corvus corax*; Kruska, unpubl. observations]. Anseriformes are another group of differently sized birds with species of generally similar body plan. Interspecific allometric calculations within this group led to a slope value of  $a = 0.567$  for the main axis [Iwaniuk and Nelson, 2001]. Furthermore, the use of such power value led to reliable results in an interspecific brain size comparison of different galeomorph and squalomorph shark species [Kruska, 1988a].

The interspecific allometric relationship of the spinal cord size to body size is also of interest, as this part of the

central nervous system best reflects the somatic and visceral part of nervous supply and therefore the dependency of the body on innervation. Unfortunately there is little information available on these parameters. Nevertheless, Klatt and Vorsteher [1923] present data for red fox (*Canis vulpes*), golden jackal (*Canis aureus*) and wolf (*Canis lupus*), three canid species similar in body plan but differing in size. Interspecific allometric calculations on this material revealed a slope value of  $a = 0.58$  [Röhrs and Ebinger, 1998], a value similar to that for the brain when small and large species of similar body plans are compared.

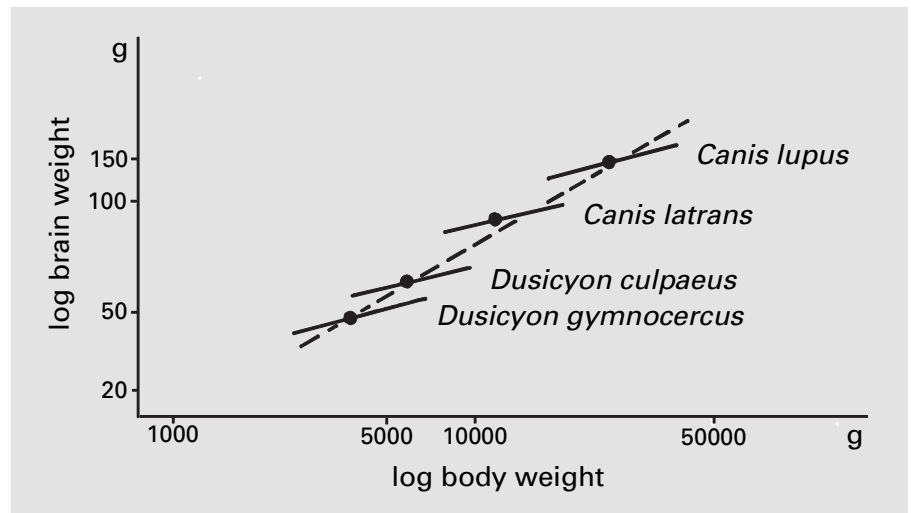
All these results support the assumption that a pure body size influence can be characterized that may or may not be common to all vertebrates, but at least seems to be specifically valid for mammals in interspecific comparisons of total brain sizes. Allometric slopes of 0.56 and 0.63 thus seem much more reliable than the theoretically predicted 0.66 power for negating the influence of body size in brain size comparisons and for quantitative investigations of the encephalization indices of species. In any case the 0.72–0.75 slope value of many modern studies clearly must be rejected as the basis for calculating different encephalizations. There is no general slope of this magnitude across the recent mammals that can be used for comparative brain purposes.

Therefore, it seems justified as a second step of allometrical analysis to use the slope values of 0.56 and 0.63 when calculating average encephalization levels of differently sized species within various taxonomic units. This can be done by calculating a general reference line with the above mentioned slope values either through recent basal forms of a taxonomic group [as did Stephan and co-workers with the line of so-called basal Insectivora; Stephan et al., 1991], or through mean brain size/body size values of several species within orders (as used in previous reports and here). Even estimated data from fossil forms can be included in such an analysis to arrive at a rough but reliable idea about the evolution of brain size and adaptive changes of this organ through geological time.

#### *Intraspecific Allometry*

Another kind of relationship pertinent to brain/body size comparisons involves intraspecific allometries (between adult individuals within a species). Earlier comprehensive investigations [Röhrs, 1959b] showed that these intraspecific allometries follow rules different from interspecific rules, but they both show certain principles of biological order and hierarchical arrangement.

**Fig. 1.** Transposed intraspecific allometries of the brain to body weight relationship for small and larger sized adult individuals of four different canid species ( $a = \text{ca. } 0.25$ ). The interspecific allometry (dotted line  $a = \text{ca. } 0.56$ ) indicates similar brain sizes and therefore similar encephalization level for all four species [redrawn from Röhrs, 1986].



Intraspecific allometries have not always been clearly established and therefore remained hidden or not reflected in reports since the time of Dubois [1897, 1914] and Lapique [1908]. This is especially true in the case of species where adult individuals do not differ very much in body size, which is a rather common circumstance. This is also the reason why intraspecific allometries were first described for humans and for domesticated mammals [Lapique, 1908; Dubois, 1914; Klatt, 1955].

Indeed, one of the most prominent characteristics of the domestication process is an enormous increase in body size variation within a species [Herre and Röhrs, 1990], which has resulted in dwarf and giant domestic races within several species (e.g., among canine breeds such as Chihuahua to Irish wolf or St. Bernhard; equine, caprine and porcine breeds also show huge size variation). Allometric calculations of the brain to body size relationships of adult individuals among such differently sized races resulted in slope values between  $a = 0.20$  and  $0.30$  (mostly  $0.25$ ) which is comparable to values from small to large sized adult humans. These intraspecific slopes are approximately half the size of interspecific values, but of course clearly reflect brain to body size relationships of similar body plans.

Intraspecific allometries of the same magnitude were later validated for wild species of mammals. The allometries are especially evident when individuals of a species have a wide distribution showing different sized individuals or populations according to Bergmann's rule [Röhrs, 1959b]. They are also found for species with a prominent sexual dimorphism in body size. In some exceptional cases slopes can reach rather steep values of  $0.40$  [Kruska,

1977, 1993]. Such intraspecific allometries can be used to study brain size differences independent of body size among individuals of a species, or among populations or races resulting from genetic peculiarities (e.g., breeding in captivity, domestication, feralization) or as a consequence of environmental effects (e.g., nutrition, enriched or impoverished habitats).

Very interestingly, intraspecific allometries show a special relationship to interspecific allometries. Intraspecific allometric lines of various different sized but equally encephalized species with similar body plans and close phylogenetic relationships run parallel to one another, but are transposed along the interspecific allometric line of this relation. Thus, in cases of similar encephalization, the mean values for brain and body sizes very clearly are adjusted to a major axis with an interspecific slope. An example is shown in figure 1 for four canid species.

In conclusion, intraspecific allometrical investigations can be used to show the variability and susceptibility of brain size to change within a species, which from individual to individual or population to population might be the result of different factors. Of course, all this occurs in individuals but is simultaneously demonstrated as a characteristic of encephalization at the level of the species.

Intraspecific allometries can also suggest mechanisms of brain size increase or decrease during adaptive radiation and the origin of species, especially when dwarf or giant species have evolved within taxonomic groups.

#### *Ontogenetic Allometry*

A further phenomenon concerns ontogeny. In most cases brain growth is investigated in relation to develop-

mental stages and thus the age of the individuals, just as studies are conducted concerning body growth [Kretschmann and Wingert, 1971]. Nevertheless, brain and body size data of differently aged individuals of a species can also serve to characterize ontogenetic allometries for the brain to body size relationship. These are growth allometries, whereas inter- and intraspecific allometries describe conditions in fully grown individuals. Similar to the previously examined allometries, ontogenetic allometries also show unique characteristics, in this case related to the intraspecific allometry of differently sized adult individuals. However, such ontogenetic allometries seem to be less uniform in eutherian mammals and are highly variable from species to species in slope.

Some further unique characteristics of ontogenetic allometries are evident. For example, clearly there are differences in the maturity of the brain at the neonate stage among various eutherian mammals. This was demonstrated through the so-called multiplication factor, which is the factor by which the neonate brain weight is to be multiplied to result in an adult brain weight [Portmann, 1952, 1957, 1962; Mangold-Wirz, 1966]. In eutherian mammals these factors generally are between 1–6 for precocial species and from 7–12 for altricial species. This has been demonstrated for many species of very different taxonomic groups and radiations.

There are some notable exceptions to these general principles in the group of arctoid carnivores. In some of these species, brains show an extremely limited degree of development at the time of birth and the appearance of neonatal brains in these species resembles that of embryonic stages in other mammals. Thus, to reach species-specific adult brain size and in general a high encephalization these extremely altricial carnivores show a remarkable postnatal increase in brain size resulting in higher multiplication factor values. For example, *Procyon cancrivorus* has a factor value of 14 [Kruska, 1975a], *Mustela vison* of 25 [Kruska, 1977] and Ursidae have values of 38–58 [Mangold-Wirz, 1966].

Another exception to the rule concerns human postnatal development and its factor of 4. This would place humans together with other primates in the group of precocial mammals, which clearly is at odds with behavioral and other biological phenomena pertaining to human postnatal ontogeny. For these reasons the human species is considered to represent a unique evolutionary phenomenon of a secondarily altricial mode of ontogeny [Starck, 1975].

The differences in brain to body size ontogenetic allometries are most clearly seen in the contrasting post-

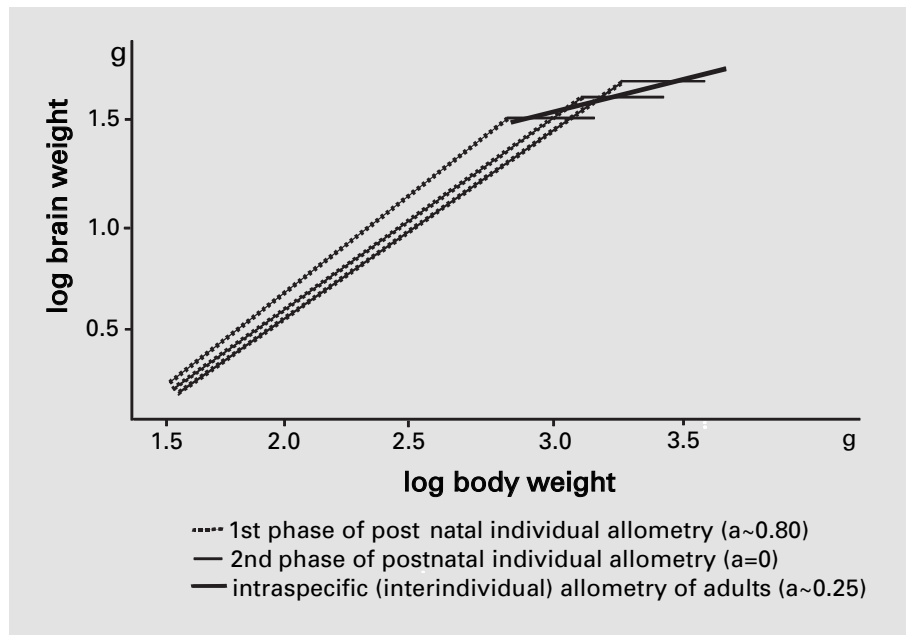
natal development schemes in altricial and precocial species of placental mammals. An analysis of data representing different stages of a postnatal ontogenetic sequence of the altricial carnivore *Procyon cancrivorus* [Kruska, 1975a] found that brain growth is asymptotic and can be described by two allometric lines describing the brain to body size relationship. During a 1st phase of development the data follow a steep growth line with a slope value of about 0.80 (in this special case), which indicates rather rapid brain growth in relation to the body. Furthermore, comparing graphs of brain as well as body size to age indicates that the final individual brain size is reached earlier than is body size, which continues to increase until full growth is attained. This same phenomenon was demonstrated earlier for human ontogeny [Kappers, 1936a, b]. It is additionally shown by the growth rate differences of spinal cord versus vertebral column, which in mammals leads to the cauda equina arrangement of lumbal and sacral spinal nerves. From this, it can be deduced that a 2nd phase allometric line with a slope of 0 is present in the ontogenetic brain to body size relationship of these species.

Additionally, individuals of a population or species might, for genetic or nutritive reasons, differ in prospective brain and body size. Then an individual fated to become small will follow a slightly steeper 1st phase line compared with an individual predisposed to become a larger individual. This means that some individual variability exists in the slope of the 1st phase line. Consequently, 2nd phase lines of differently sized individuals then must run parallel to each other but have different transposed values. The transposition then follows a particular arrangement where data for adults of a large sample are fitted to a distribution ellipse with a major axis slope for an intraspecific allometry. This is shown as a diagram for three differently sized individuals in figure 2.

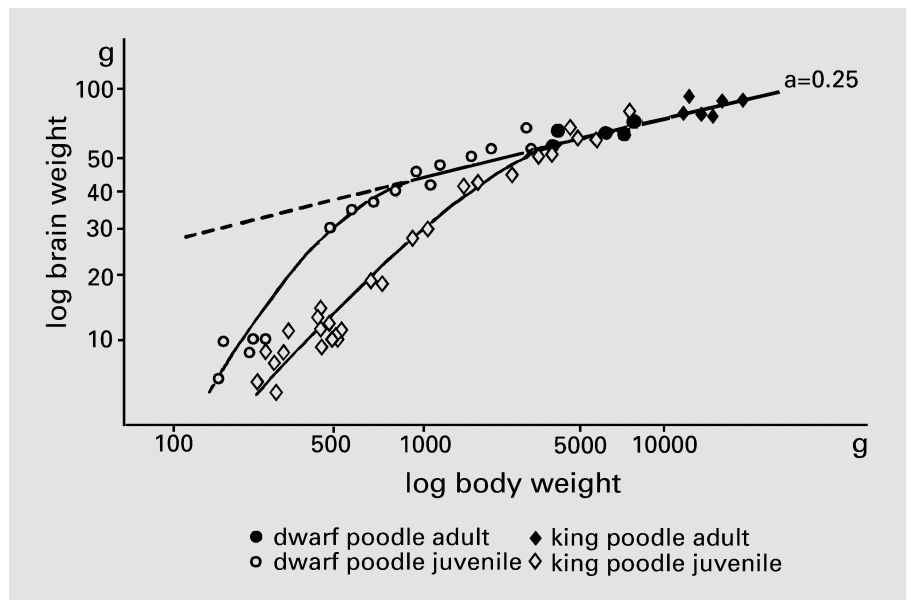
The fact that ontogenetic 1st phase lines within a species might differ in slope among individuals was previously shown for two differently sized domestic breeds of canine, namely dwarf and king poodles [Röhrs, 1959b]. Clearly in figure 3, steeper slope values are evident for dwarf poodles during the first postnatal phase compared to the larger king poodles. However, adult data plots are adjusted to a line with an intraspecific slope.

Although these ontogenetic allometries generally seem to be the rule for altricial mammals, there are exceptions such as some *Mustela* species. In these carnivores with an extreme altricial mode of ontogeny the brain size follows the 1st phase rules, increasing rapidly postnatally; but

**Fig. 2.** Postnatal ontogenetic allometries for three differently sized individuals of the altricial carnivore *Procyon cancrivorus*. Individual growth is characterized by 2 phases with allometric lines of different slope. Data for adult individuals are then described by a distribution ellipse with a major axis of intraspecific slope [redrawn from Kruska, 1975a].



**Fig. 3.** Postnatal growth allometries of two differently sized dog breeds, dwarf versus king poodle. 1st phase allometries follow different slopes in small and large sized breeds but the adult values are adjusted to an allometric line with an intraspecific ( $a = 0.25$ ) slope [redrawn from Röhrs, 1959b].

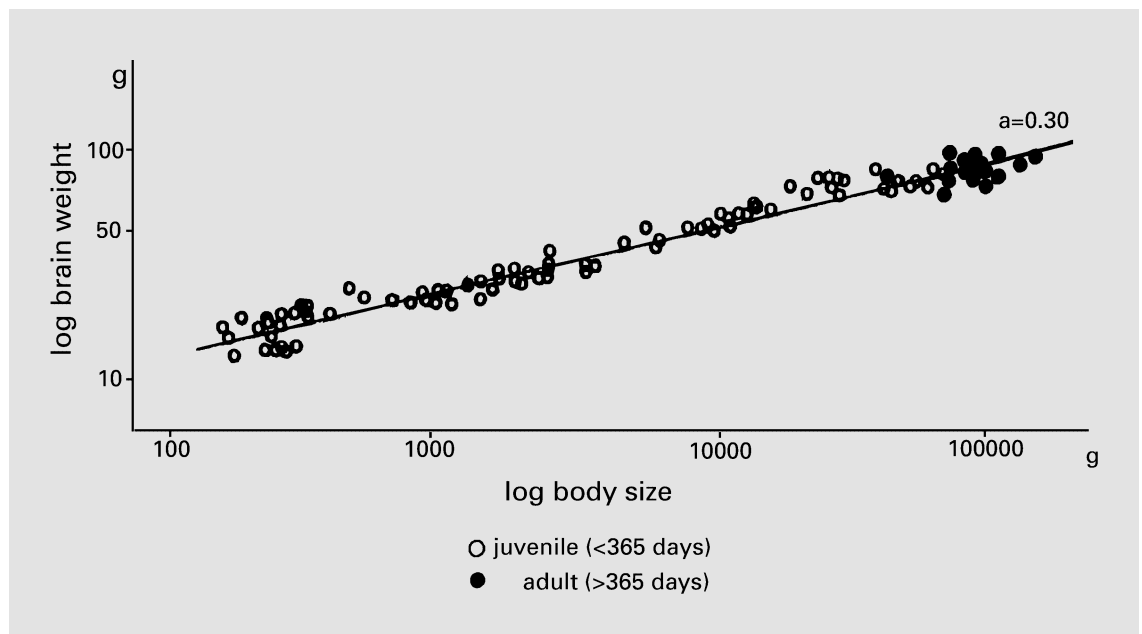


then brain, brain case and caudal skull height clearly decrease in absolute size during the early life span from a subadult (about 5 months old) to the adult state (7 months and older) before sexual maturity is reached [Kruska, 1977, 1979, 1993; Apfelbach and Kruska, 1979; Wiig, 1982, 1985; Schmidt, 1992]. In the mink (*Mustela vison*) the decrease of overall brain size during postnatal ontogeny amounts on average to about 16–18% the subadult brain size, whereas body size remains the same during this time. The isocortex, with a nearly 25% decrease, is espe-

cially noteworthy [Kruska, 1993]. Concomitantly, the bony brain case flattens but remains the same in breadth and length during this process, which is indicated histologically through the presence and activity of many osteoclasts on the outer surface of the cranial vault and newly built bony layers on the inner side [Kruska, unpubl. observations].

Absolute brain size decreases of such dimensions during late postnatal ontogeny are surprising and were subsequently tested for possible behavioral implications. How-





**Fig. 4.** Postnatal growth allometry in the precocial Vietnamese potbellied pig. Brain and body weight relations follow an allometric line with intraspecific ( $a = 0.30$ ) slope over the whole developmental period [Kruska, unpubl. observations].

ever, after examining subadult and adult individuals no behavioral manifestations such as visual performance, learning ability or discrimination abilities accompanied the changes in absolute brain size [Steffen et al., 2001].

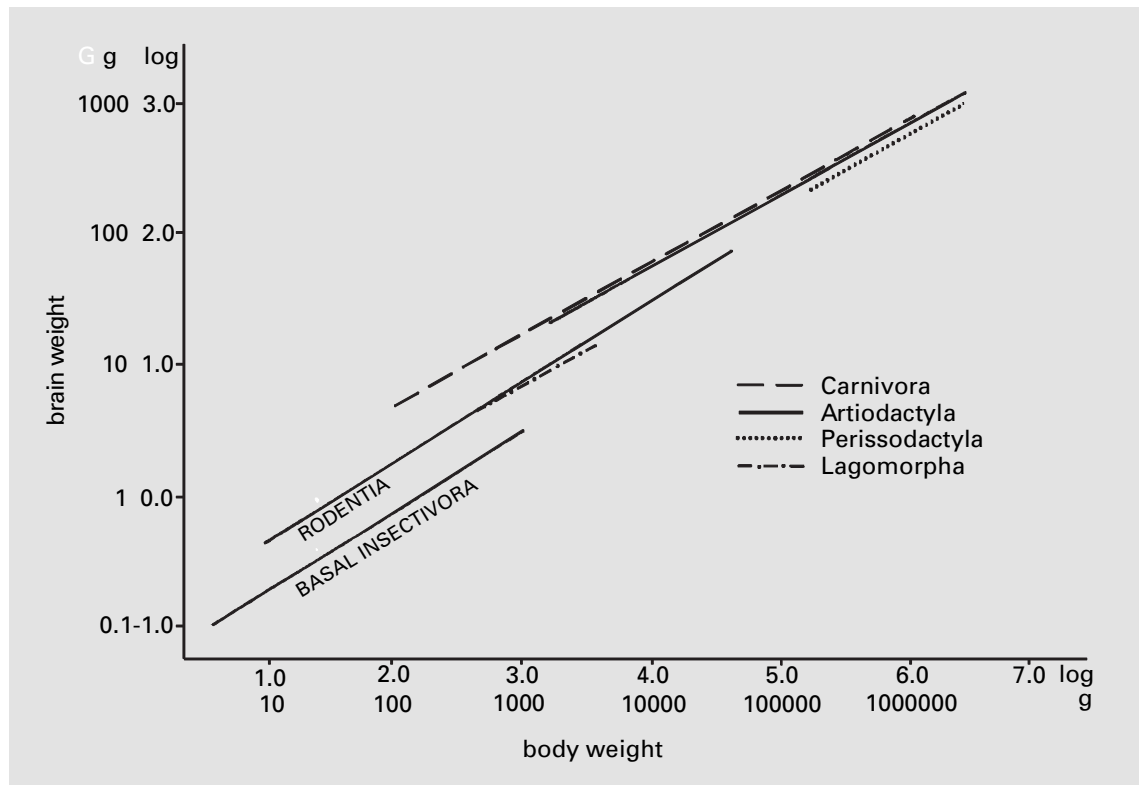
Most probably these size changes are comparable to the so-called Dehnel phenomenon described for some soricid species that show a winter depression of skull and brain size by a percentage comparable to the mustelids [Dehnel, 1949, 1950; Cabon, 1956; Bielack and Pucek, 1960]. However, as in the mustelid species, the soricid individuals' are arranged on a line with the typical intraspecific slope; but for subadults this line is in a higher position when compared to adults [Kruska, 1993]. Consequently, using data obtained from anonymous material to assess intra- or interspecific allometries and encephalizations can occasionally lead to misinterpretations when ontogenetic peculiarities are unknown. In such cases subadult individuals with their larger brains would be seen as more strongly encephalized compared with similarly sized adults, which at least seems doubtful, if not actually false.

Ontogenetic allometries of precocial mammals most probably follow the same rules as altricial mammals do normally, but with the exception that the 1st phase occurs prenatally. This is in agreement with the hypothesis that

precociality is a secondary effect that occurred in many radiations during mammalian evolution as a consequence of an elongated gestation period [Portmann, 1969; Starck, 1975]. Data on postnatal growth therefore present only values with a typical intraspecific slope ( $a = 0.30$ ) through juvenile, subadult, and adult individuals. This is shown for Vietnamese potbellied pigs as in figure 4 [Kruska, unpubl. observations].

In conclusion, ontogenetic allometries of brain to body size relationships can help in recognizing common or unique phenomena. As will be discussed later, the power of the 1st phase ontogenetic brain/body growth seems to be of especially great importance to understand the phenomenon of diverse encephalization levels that evolved and can be seen in eutherian mammals, regardless of whether this growth happens pre- or postnatally.

The following section presents the results of brain size comparisons based on the general concept of hierarchically arranged and transposed allometries calculated using a large database of species-specific information obtained from the author's institutional samples and reliable literature [Kruska, 1980].



**Fig. 5.** Average interspecific allometries of brain to body size relationship for different orders of recent eutherians in comparison to the most primitive Basal Insectivora (with slopes of  $a = 0.56$  and  $a = 0.63$ , respectively). These lines show different plateaus of stepwise evolutionary radiations with rodents and lagomorphs on one level and the ferrungulate groups on another [redrawn from Kruska, 1980].

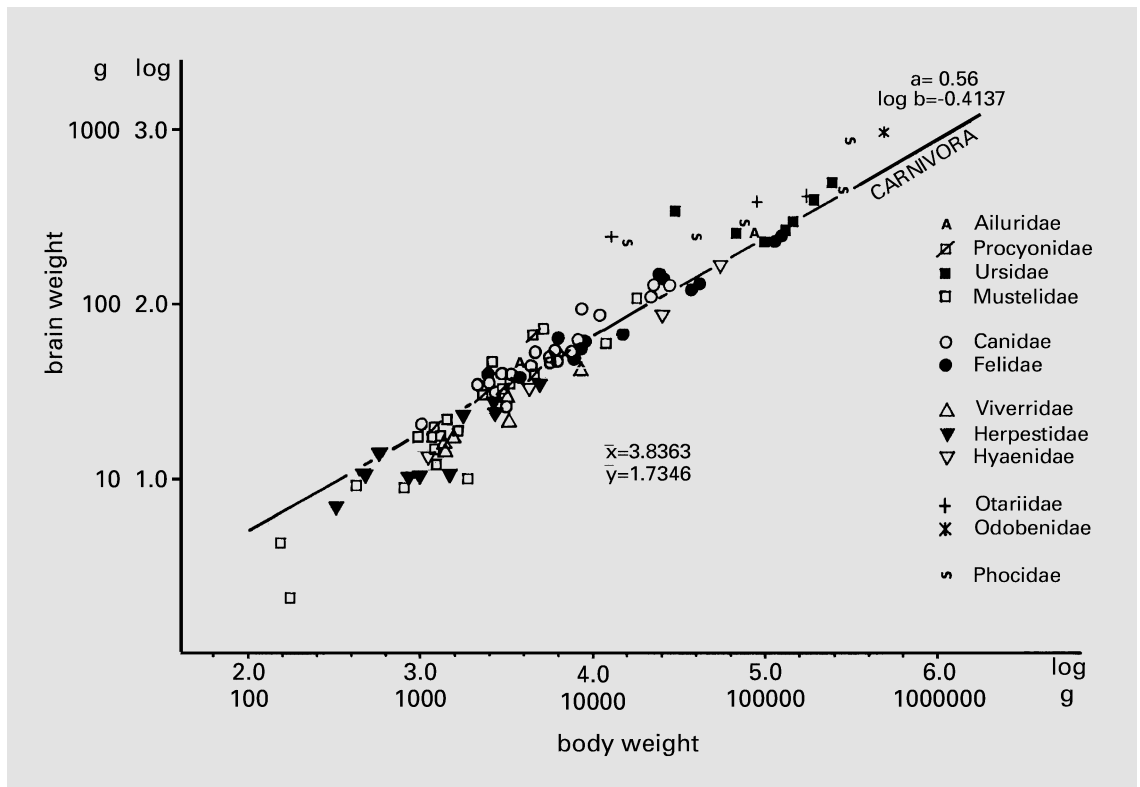
### Evolution and Radiation of Brain Size in Some Mammalian Orders

#### *Encephalization Levels of Some Extant and Extinct Species*

Reliable conclusions about the encephalization levels of diverse, differently sized eutherian mammals are possible using interspecific allometries only if the body size influence is known. As discussed above, this relationship was verified as an allometric line with slope values of  $a = 0.63$  (groups of mainly small sized species) or  $a = 0.56$  (groups of mainly larger sized species). Consequently, lines with these slopes can be drawn through the mean values of databases for different orders to compare average encephalization plateaus among mammalian orders. This is shown in figure 5 for the orders Rodentia (from a database of 65 species), Lagomorpha (5 species), Perissodactyla (7 species), Artiodactyla (74 species), and Carnivora (93 species). These orders are represented by differently positioned lines that are transposed compared to

each other and therefore, on average, indicate different encephalization plateaus independent of a reliable body size influence.

In this respect, Rodentia and Lagomorpha show a quite similar encephalization plateau with brains, independent of body size, about 2.5 times larger compared to recent eutherians with the smallest brains represented by the group of basal Insectivora. Artiodactyla and Carnivora have, on average, reached a similar and clearly higher encephalization plateau. These orders, representing general prey and predator species, have brain sizes also about 2.5 times larger than the plateau of the Rodentia/Lagomorpha. The Perissodactyla show a slightly lower plateau, but within this order the Equidae clearly are more encephalized than the Tapiridae and Rhinocerotidae. Species of these latter two families are reminiscent of ancestral forms in bodily appearance and biology. Independent of body size, for example, the diverse species of tapirs and rhinoceroses have brains only about 43% the weight of zebras. Conversely, zebras have brains that are about 2.3



**Fig. 6.** Interspecific allometric line of the order Carnivora and specific data plots for 93 diverse species within their taxonomic groups (families) showing variation around the average allometric line. Note: Pinnipedia (Otariidae, Odobenidae, Phocidae) generally have larger brains at comparable body weights than have Fissipedia [redrawn from Kruska, 1980].

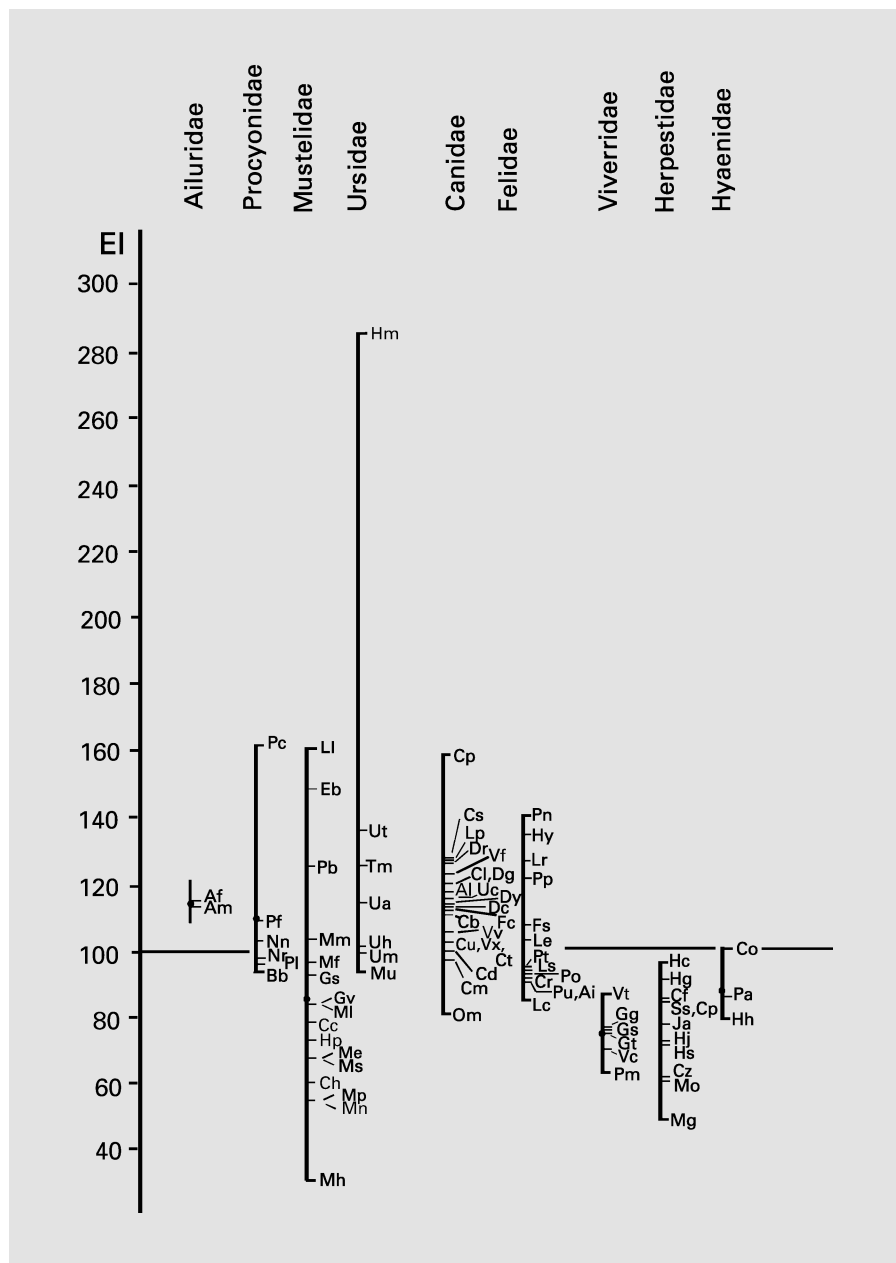
times larger than the tapirs or rhinoceroses independent of body size [Kruska, 1973].

Of course, there is also variation among diverse species within other orders, which was documented earlier for Rodentia, Artiodactyla and Carnivora [Kruska, 1980, 1988b] and is presented for the Carnivora in figure 6. From this data it is clear that the water-adapted Pinnipedia (Phocidae, Otariidae, and Odobenidae) generally have larger brains above the average values of the Fissipedia group. But the Fissipedia also show species-specific differences in brain sizes. These can be represented by encephalization indices (EI) calculated by measuring the distances of species mean values from the average line ( $EI = 100$ ) at the species characteristic body weight. A scaling of EI values for the diverse species in their families [Kruska, 1988b] is presented in figure 7.

In the following example results and conclusions can be obtained from the EI values. In general, species of the Herpestoidea group (Viverridae, Herpestidae, Hyaenidae) with EI values from 47 (Mg – *Mungos mungo* of the

Herpestidae) to 98 (Co – *Crocota crocuta* of the Hyaenidae) show a lower than average encephalization when contrasted with the Cynofeloidea (Canidae Felidae), with indices between 80 (Om – *Otocyon megalotis*) and 159 (Cp – *Cuon alpinus*), both of the Canidae family. Within the Arctoidea group the Ailuridae, Procyonidae and Ursidae are mainly encephalized between 92 (Mu – *Melursus ursinus*) and 135 (Ut – *Ursus torquatus*) with the exceptions of *Procyon cancrivorus* (Pc – 162) of the Procyonidae and *Helarctos malayanus* (Hm – 285) of the Ursidae, which are extremely highly encephalized. It seems noteworthy to mention that the giant panda (*Ailuropoda melanoleuca*), a monophagous and vegetarian carnivore, has a brain approximately the same size (Am – 112) as the lesser panda (*Ailurus fulgens* – Af – 114) and most of the omnivorous Ursidae (*Melursus ursinus* – Mu – 92 to *Ursus torquatus* – Ut – 135).

The Mustelidae again are represented with a very large EI range from very low (30 = Mh – *Mephitis mephitis*) to clearly higher relative brain sizes (160 = Ll – *Lutra lutra*).



**Fig. 7.** Scaling of encephalization indices (EI) of several fissiped Carnivora species within their families obtained as distances from the average line at species characteristic body weights. The line at EI = 100 characterizes the average level of the Carnivora encephalization [redrawn from Kruska, 1988].

It is especially noteworthy that again the water-adapted forms (*Lutra lutra* Ll – 160; *Pteronura brasiliensis* Pb – 124) are among the higher encephalized forms which is similar to the relationship of the aquatic Pinnipedia versus the Fissipedia as a whole. This relationship is also found within the order Insectivora, which represents the very basal encephalization plateau of eutherians, as some semiaquatic species show a higher encephalization level [Stephan et al., 1991]. Thus, adaptation to an aquatic life-

style in most cases is convergently correlated with larger brains. The same is commonly known for the Cetacea as a whole, but does not include the Sirenia (Dugongs, Manatees) which actually have rather small and primitive brains for their large bodies.

In addition, the more strongly arboreal species within the Mustelidae (*Eira barbara* Eb – 147; *Martes martes* Mm – 102; *Martes foina* Mf – 95) also have greater encephalization indices than the ground dwellers such as the

*Mustela* species (*M. nivalis* Mn – 55; *Mustela putorius* Mp – 55; *M. erminea* Me – 66; *M. nigripes* Ms – 66). This again is in accordance with information regarding the order Rodentia, in which the arboreal Sciuridae are compared to ground dwellers. A similar relationship is also seen in the Primates. Thus, the encephalization indices of recent species suggest evolutionary changes in brain size following adaptive radiations that resulted in different encephalization levels characteristic of each species and higher taxonomic group. Despite some exceptions, several consistent relationships of life styles with smaller or larger relative brain size can also be seen.

Cautiously and with some restrictions, encephalization indices can also be investigated when fossil material is included in the analysis. In fossil and recent Camelidae the brain size of extant forms consistently remained at a low encephalization level, from the earliest record in the Eocene until the middle Oligocene (about 40–30 million years B.P.). Then from the Miocene to Holocene the encephalization index increased at a greater rate until the highest level was reached with recent species [Kruska, 1987]. This can also be shown for carnivores. In Carnivora two groups representing different radiations of terrestrial forms can be documented from Eocene to Pleistocene: the Creodonta, which disappeared, and the true Carnivora, which evolved into the current extant species. Taxonomically both groups clearly differ in their carnassial teeth. Although somewhat variable, the Creodonta have carnassials M1–2/M2–3, whereas the true fossil Carnivora and modern species show carnassials P4/M1. The Hyaenodontidae is one family within the Creodonta, and endocast volumes and estimated body weights are available for some species in this group. This is also true for some extinct true carnivores from different time periods [Jerison, 1973; Radinsky, 1977]. Encephalization indices derived from these approximations fall on the allometric scale as predicted (fig. 8).

Such estimates can lead to a general assumption that all these fossil forms were already encephalized at about the basal level of modern species, but actually most were below the average (EI = 100). Furthermore, the documented species of Hyaenodontidae show an increase in brain size from an Eocene radiation to Oligocene/Miocene forms. Such a time-dependent, stepwise increase of brain size might also have occurred in the Carnivora, although some species with small brains were still extant during the Oligocene. Altogether, during the Oligocene and Miocene species of Hyaenodontidae and true Carnivora showed approximately the same level of encephalization. However, a second step of general brain size increase

can be inferred as occurring during the further radiation of true Carnivora after the extinction of Hyaenodontidae. This might have occurred during the Pliocene and Pleistocene, with some radiations showing a further acceleration in encephalization during the Holocene with the origin of modern species. Thus, a body size independent increase of brain size during phylogeny is also valid for the Carnivora.

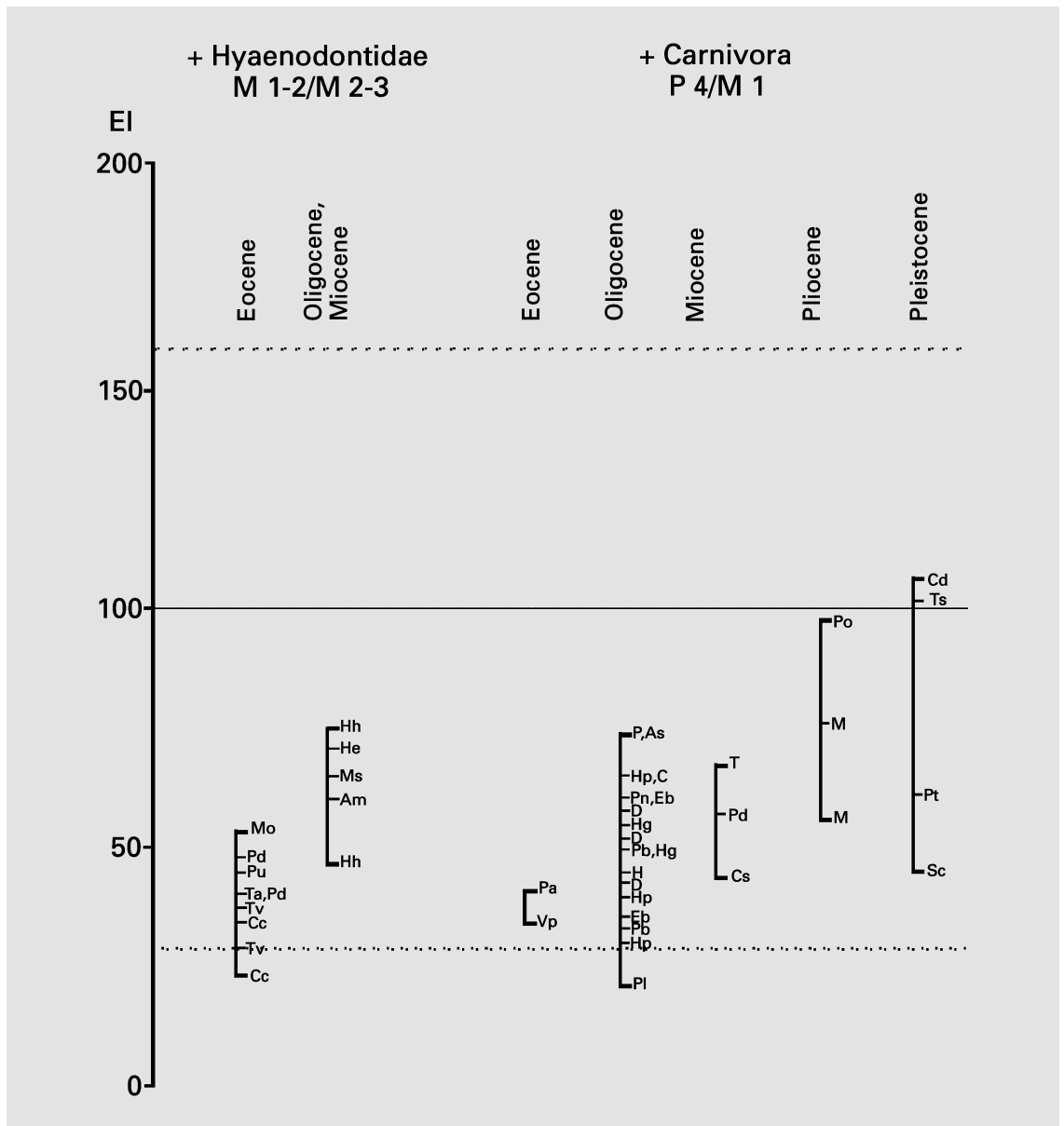
It can be concluded that the use of slope values 0.56 and 0.63 best excludes the influence of body size on brain size in an interspecific comparison of eutherian mammals. The results of this allometric approach show encephalization plateaus for orders and indices for species within these orders that are in good agreement with general comparative anatomy, embryology and paleontology [Romer, 1966; Thenius, 1969; Carroll, 1988; Starck, 1995].

During the evolution of diverse mammalian groups, brain size increased independently of body size and arrived at different plateaus of encephalization. Radiative adaptation to aquatic or arboreal life-styles often is related to larger sized brains, and this occurs convergently in different encephalization plateaus to very different degrees. However, the general increase of brain size during mammalian phylogeny is an evolutionary trend of this organ in this taxonomic group.

#### *Evolution of Brain Parts Responsible for Encephalization*

The evolutionary trend of brain size increase in mammals and the radiation of progressive encephalization is mainly caused by an increase of the telencephalon (telencephalization). The iso-(= neo-)cortex shows an especially large increase in size. In its six-cell-layered arrangement this most prominent structure of the hemispheres is characteristic only for mammals. Accordingly, isocorticalization is the main and principal source of evolutionary or adaptive brain size increase in mammals, although of course enlargement of the isocortex always implies a related increase of correlated tissue in other brain parts (thalamus, pyramidal tract, etc.).

Such different degrees of isocorticalization can be visualized rather simply without using allometries when contrasting two species similar in body weight but clearly on different encephalization plateaus. For example, a basal rodent, the Norwegian rat (*Rattus norvegicus*) with an average body size of 214 g has a brain weight of 2.1 g [Kruska, 1975b], whereas a basal carnivore species, the stoat (*Mustela erminea*) has a slightly smaller body size of 185 g but a clearly greater brain weight of 4.5 g [Schu-

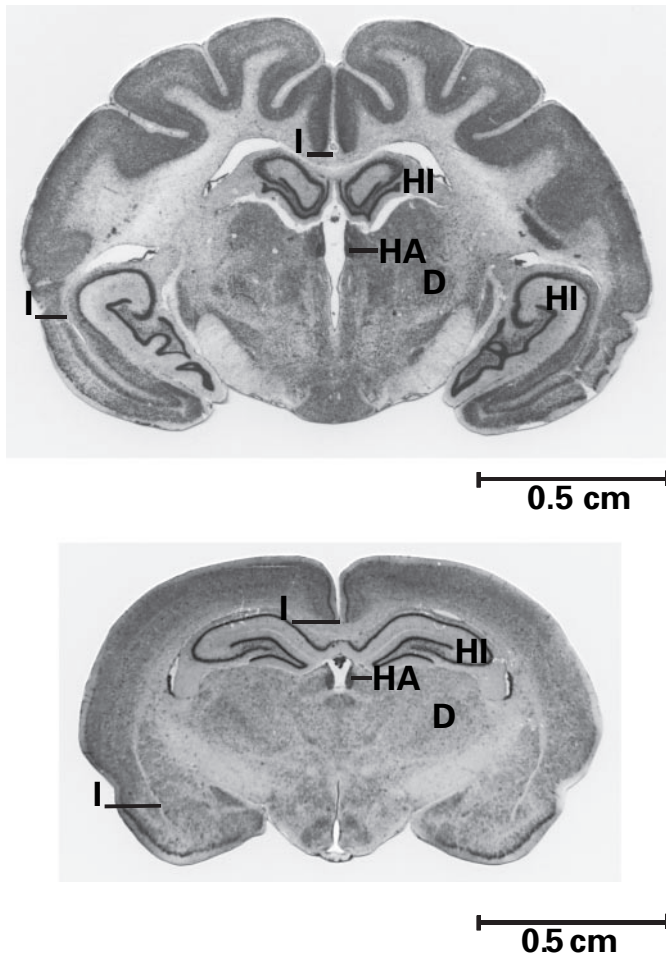


**Fig. 8.** Scaling of encephalization indices (EI) of several extant Hyaenodontidae (order Creodonta) and of extant true Carnivora as a function of their existence at different geological times. The line at EI = 100 characterizes the average level of the extant Carnivora; dotted lines demarcate the variation from lowest to highest encephalization of recent species [after brain and body size estimations of Jerison, 1973 and Radinsky, 1977].

macher, 1963]. Differences between these brains become clear from comparisons of the relative values. In the rat the telencephalon accounts for only 56% and the isocortex for 30% of total brain size, whereas in the stoat the corresponding values are 68% and 45%, respectively.

Sections through the telencephalon at a comparable region (habenular complex of the diencephalon) addition-

ally support this fact as shown in figure 9. Here, the larger brain of the stoat is characterized by a clearly enlarged surface of the isocortex with a complex gyrification and fissuration and a more prominent lamination pattern of grey matter. Additionally the isocortical white matter is relatively larger, which again points to a greater number of neurons in the grey part that are connected with basal



**Fig. 9.** Transverse sections through the forebrain of a stoat, *Mustela erminea* (above) and a Norwegian rat, *Rattus norvegicus* (below) at comparable regions of the diencephalic habenular complex (HA) to show impressive size differences of the brain in general and the isocortex (I) especially in mammals of nearly similar body size. The lamination of the isocortex is also more strongly differentiated in the bigger brain. D = thalamus of the diencephalon; HI = hippocampus formation of the telencephalon [modified from Kruska, 1988].

brain regions. The isocortex of the rat, on the contrary, is not only smaller and lissencephalic but also less differentiated in its lamination; and the white matter is less pronounced.

The accuracy of the isocorticalization phenomenon in very diverse radiations was especially well quantified by Stephan and co-workers for a large variety and number of species of the orders Insectivora, Chiroptera, and Primates [Stephan, 1972; Stephan et al., 1981, 1988, 1991; Baron et al., 1996]. As an example, high levels of isocorticalization, although different, were reached through an

increase in the mass of this brain part by several primate species in diverse radiations. Humans are especially noteworthy in having a greatly enlarged isocortex which is associated with special so-called 'higher central nervous system abilities'. Compared with the most basal recent eutherians the isocortex of humans is 156 times larger at a comparable body size [Stephan, 1972].

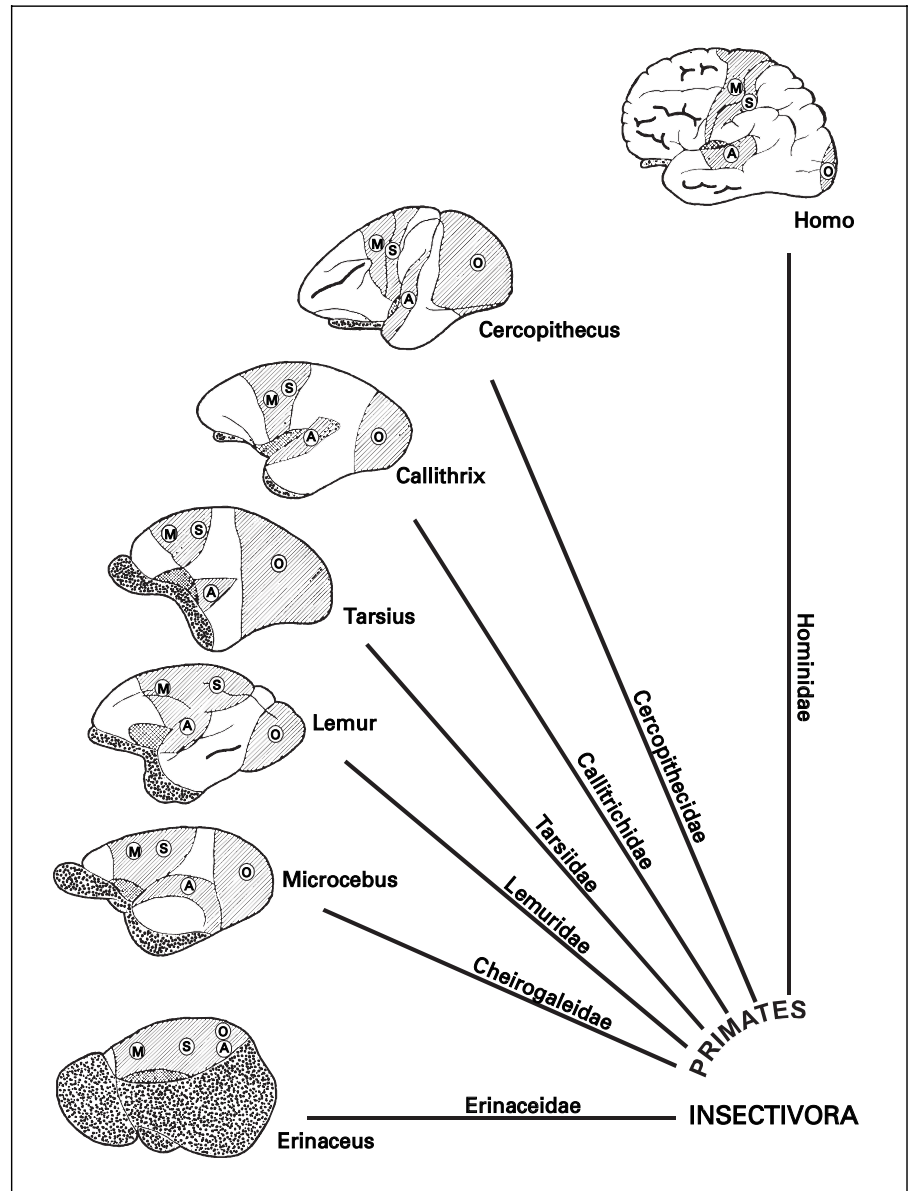
Although the isocortex shows a six-layered basic pattern and laminar organization and therefore can be histologically distinguished from the allocortex [which includes several diverse other cortical regions at the lateral, basal and medial wall of the endbrain; Stephan, 1975], this structure is not homogeneous over its entire surface. Differences in relative thickness, neuron size, cell density and other criteria have been recognized and used since the initial investigations of Brodmann [1909] to divide the isocortex into cytoarchitectonic areas and fields. As confirmed by later neurophysiological studies, this structural differentiation is paralleled by functional differentiations.

In this sense primary cortical areas can be contrasted with secondary cortical areas. The primary fields either receive afferent projections via the thalamus directly from various special senses, or control motor activity through efferents via the pyramidal tract. These primary areas thus perform as a general somatosensory area receiving impulses from sense organs and other receptors of the skin, muscles and joints, as a visual area, and as an auditory area, as well as a motor control area. The secondary cortical areas, by contrast, are mainly involved in inter-cortical connective functions such as association, coordination and integration.

From comparative studies of different primate brains, and in contrast to a basal organization represented by some insectivores, it can be seen that different levels of isocorticalization were reached in different species during phylogenetic radiation mainly by enlargements of the secondary cortical areas while the primary fields became increasingly smaller relative to the former. This is illustrated in figure 10. Although insectivores generally have no, or almost no, association cortex at all, primates and especially *Homo* have these cortical regions to a much greater extent. Here, the especially prominent enlargement of secondary cortical areas is assumed to be responsible for the unique cognitive abilities of the human brain.

However, an expansion of the isocortex can also be the result of an extreme enlargement and progressive lamination pattern of one or several primary cortical areas. As an example, this is shown in figure 10 for the brain of *Tar-*

**Fig. 10.** Different levels of isocorticalization in the radiation of primates compared with an insectivore species. The stepwise increasing expansion of the association cortex (white) is indicated in relation to the primary sensory and motor areas (lineated). A = auditory area; S = somatosensory area; O = visual area; M = motor area; cross lined = insular region; dotted = allocortex [redrawn and newly arranged after Starck, 1982].



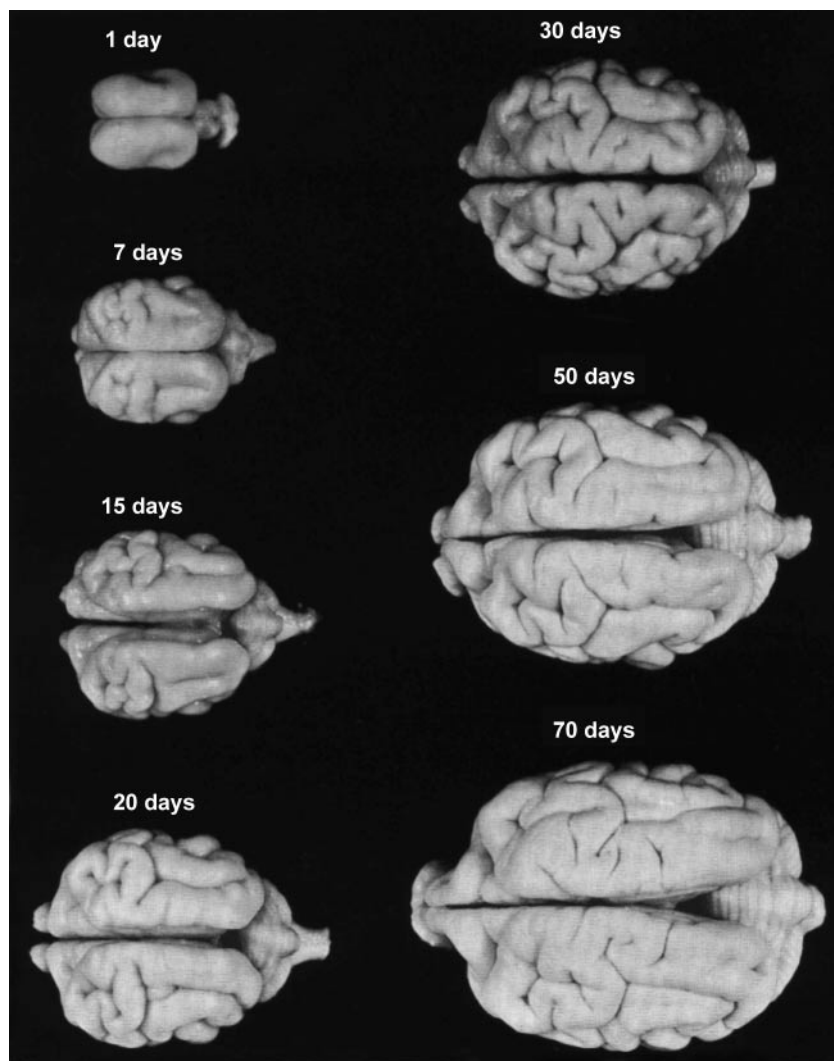
*sius*, which has an impressively large visual cortex. This species is known for its sensory specialization of the optic system with eyes that are so large that their weight is greater than the total brain weight. In other examples specializations of the visual sense is documented by stepwise progressive differentiation and structural organization of the striate area [Northcutt and Kaas, 1995].

A similar effect of sensory specialization was shown by Welker and co-workers [Welker, 1990] for the somatosensory cortex area representing the touch sense of the forepaw in raccoons. The cortical region corresponding to the

forepaw is very much enlarged, more strongly convoluted and especially fissurated in the raccoon *Procyon lotor* compared with other species of the family. In this case it is also notable that in the *Procyon* genus frontal regions of the isocortex including this special area are accelerated in development relative to other isocortex parts during post-natal growth [Kruska, 1975a]. This finding comes from a comparison of differently aged growth stages for *Procyon cancrivorus* as documented in figure 11. Here, these parts are relatively large, convoluted and fissurated earlier in development (7, 15, and 20 days after birth) than is the



**Fig. 11.** Brains of individuals of different ages of the altricial *Procyon cancrivorus* in a dorsal view to show ontogenetic dynamics during development of the hemispheres. The nearly embryonic appearance and hardly developed state of an extremely altricial mammal at day 1 after birth is evident. Subsequently the brain is broader and gyrification and fissuration are clearly accelerated in the frontal hemispheres in contrast to caudal parts (days 7, 15, 20). The form and fissuration pattern of adults is reached later (days 30, 50, 70). This documents the mosaic mode of development and the slope of ontogenetic allometry with an acceleration of the special somato-sensory systemogenesis characteristic for the genus [Kruska, 1975 a].



rest of the isocortex. The normal evenly configured and fissurated form of the hemispheres is reached only later (50, 70 days after birth). This again indicates that the slope of the ontogenetic allometry of specific parts of the brain and functional subsystems can vary, reflecting accelerated or retarded growth rates [Kretschmann and Wingert, 1971]. Therefore, the so-called systemogenesis was evaluated as the general regulator of brain development [Anokhin, 1964]. Very interestingly this is paralleled with the ontogenesis and maturation of special behaviors [Löhmer, 1976]. Consequently, a general isocorticalization per se is not only correlated with an enlargement of secondary cortical areas; in some cases a certain degree of isocorticalization can also result from the enlargement of special primary areas which indicates certain specializations that occurred during evolutionary radiation.

In conclusion, isocorticalization differences are the main contributor to the evolution of specialized mammalian brains. Enlargements of isocortex size or an increase of specific brain parts imply evolutionary changes and specializations that occur in a complicated mosaic mode of ontogenesis and subsequent phylogenesis within the diverse radiations of extinct and extant eutherian mammals.

### **Domestication and Brain Size in Some Mammalian Species**

#### *Some General Remarks on Domestication*

The domestication process must, in general, be evaluated as a notable and important event during the cultural history of the human species, as no advanced civilization

has existed without domesticated animals and plants. However, the domestication of animals is also a special zoological phenomenon, as the diverse domesticated forms of eutherian mammals show a very impressive variability in outer appearance, anatomy, physiology, behavior and other biological characteristics. Domesticated animals clearly differ from their wild ancestors and present a unique radiation since their appearance in human culture.

The physical and behavioral alterations from a wild to a domesticated animal are the consequences of human breeding for diverse purposes. In general, domestication still is the most significant experiment in the genetic influence of animals in terms of the length of time over which it has occurred, the number of individuals and species involved and the stated purposes of the manipulations. The heritability and malleability of an organism's characteristics are illustrated by domesticated animals that can show extreme examples of genetically determined traits in a way not seen in nature. It is especially notable that this variability must be found in the genetic makeup of the original wild organism's gene pool. It can be assumed in principle that this is similar to natural events during phylogeny. In this view the phenotypic variability of the organism is the most basic phenomenon no matter what selective forces are in power: those of natural selection during evolution or those determined by humans during domestication. Darwin [1868] recognized this fact in pre-Mendelian times and used the diversity of domesticated races as a model to argue his ideas concerning general mechanisms of phylogeny, evolutionary radiations and the origin of species.

Indeed, some breeds of domesticated species are so different in appearance (e.g., Chihuahua versus Irish wolfhound) that if they had been found in the wild they would have been described taxonomically as separate species or even genus. Very remarkably, however, it is also evident that no new species has ever originated through domestication. Domesticated animals still can and in some cases they also frequently do interbreed with their wild relatives of common ancestry and produce fertile offspring [Herre and Röhrs, 1990]. Changes in appearance or behavior resulting in domesticated types therefore are intraspecific in nature. This is in contrast to phylogenetic changes among species, which document the emergence of species in interspecific radiations, although the cumulative changes that result in speciation must have originated intraspecifically.

The domestication of mammals is restricted to a few, diverse species of Rodentia, Lagomorpha, Artiodactyla, Perissodactyla, and Carnivora. In terms of brain size this

means that domestication has occurred in species representing very different evolutionary plateaus of encephalization. Domestication of different species also started at very different times during human history. The oldest archaeological remains of domestic species from the Near East were dated to approximately 10,000 or 12,000 years ago [Zeuner, 1963; Mason, 1984]; other species were domesticated later in history and some species are still involved in this artificial selection process. Consequently, the periods of time during which domestication has occurred are considerably short compared to phylogenetic events, but the notable physical and behavioral changes in the species are even more impressive as a result.

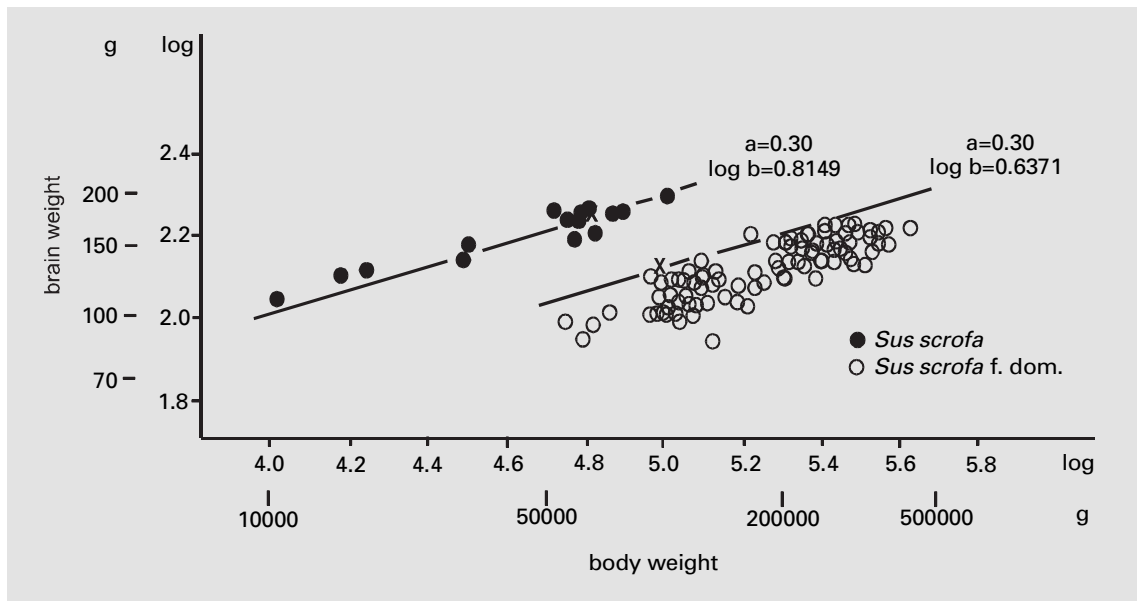
Furthermore, during the domestication process animals were selected to serve very different human demands (e.g., for production of meat, fat, milk, fur, etc.; for labor; for research; as pets, etc.). Such differences occur not only between species, but within species as well. Thus, selective breeding goals are numerous and can change over time even within species as human needs or demands change. Here again it must be emphasized that humans select the breeding program from the organism's already existing genetic variability as evaluated through phenotypic appearance. Nevertheless, despite differences in purpose, time frame and species, all domesticated breeds seem to share some common characteristics that are very different from those of their counterparts in the wild; for instance, domestic breeds are generally adapted to the special 'ecological niche' of domestication, no matter how diverse this might be. Because of obvious physical and behavioral differences between domestic breeds and their wild ancestors, it is of great interest to compare the brains of these related forms to learn what changes have occurred in the brains of animals due to domestication.

#### *Domestication and Overall Brain Size*

In order to determine the effects of domestication on brain size, intraspecific allometric calculations were performed to compare the brain to body size relationship of wild ancestral types with domestic relatives. These studies have produced similar results for several species as follows:

1. The slopes of intraspecific allometric lines are less steep than those for interspecific comparisons. They are nearly identical for several species with values between  $a = 0.20$  and  $a = 0.30$ , only occasionally  $a = 0.40$ .

2. The data for the wild individuals of the stem species are associated with one allometric line, those for the domesticated relatives with a significantly different one. Both these lines have identical slopes and run parallel to one



**Fig. 12.** Intraspecific relation of brain to body weight in European boars and different pig races with average allometric lines. To make body sizes comparable the line for pigs is displaced to the left because of fat [redrawn from Kruska, 1970].

another. Consequently domestication has not affected the dependency of the brain on the body size but has changed the brain size.

3. Domesticated forms often show a greater variability of brain size at any given body size compared with the corresponding wild forms. Their data are reflected in clearly wider distribution ellipses. Therefore, the selection pressure in domestication must be less strong compared to natural events.

4. On average, domesticated mammals have smaller brains than their wild ancestral relatives.

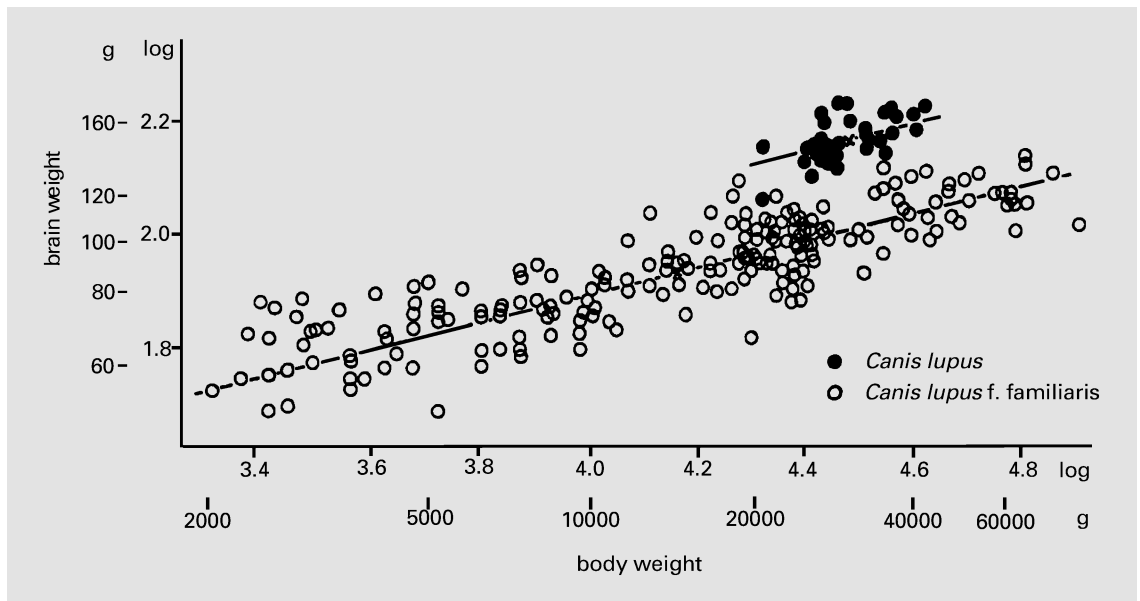
This is shown for two examples in figure 12 (European boars versus pigs) and figure 13 (wolves versus dogs). Furthermore, allometric calculations of spinal cord to body size for wolves and dogs resulted in no difference between these forms in slope and intercept [Röhrs and Ebinger, 1998]. Undoubtedly this means that the wild and domestic types are similar in body plan and central neural distribution. Consequently, domestication has in general led to a decrease in overall brain size. Most probably this indicates a concomitant reduction of the functional capacity and performance of this part of the central nervous system, which is discussed later.

It is of further interest to learn how strongly the domestication process has affected brain size. Therefore, differences were calculated from the log b values of the two par-

allel average lines arriving at species-specific decrease values for the domestic compared to the wild types (= 100%). Such body size independent average decrease values (DV) are listed in table 1 for diverse species. As shown, the dimensions of average quantitative decrease vary considerably from species to species. Altogether they cover a range from 0% (laboratory mouse) to 34% (pig).

In this respect, however, a certain implication of the species' evolutionary state and thus encephalization level is striking, which might indicate a relation between phylogeny and domestication. Evidently, brains of the generally less encephalized species of Rodentia and Lagomorpha only show a minor decrease in value from the wild to the domesticated form in the range from 0% (mouse) to 15% (laboratory gerbil). In contrast, the brains of the more strongly encephalized Carnivora, Artiodactyla, and Perissodactyla clearly show a greater decrease in value of between 16% (horse, donkey) and 34% (pig). Consequently a special rule could be proposed to the effect that species which have larger brains through natural phylogeny and evolutionary radiation abandon more brain tissue during the domestication process than do those species with smaller brains.

Although this holds true in general among orders, it is not the case for differently encephalized species within orders. It is clear from order-specific encephalization

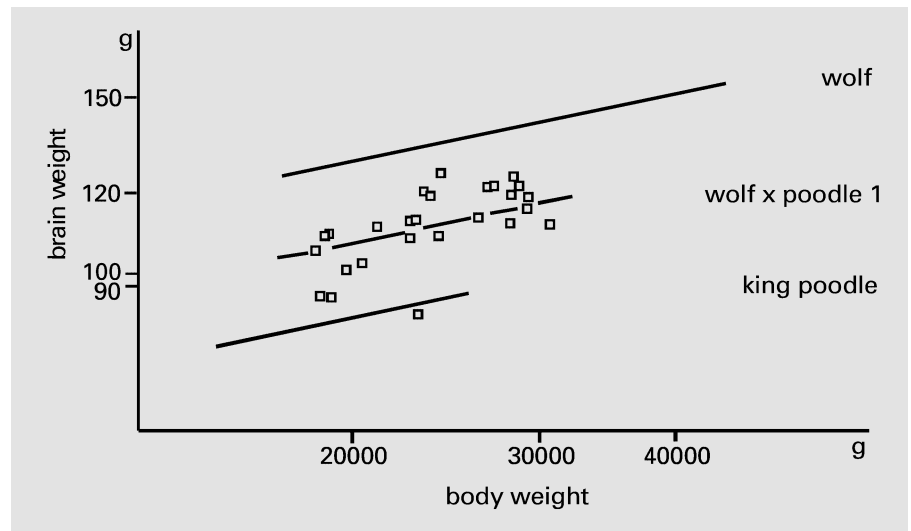


**Fig. 13.** Intraspecific relation of brain to body weight in wolves and diverse dog races with average allometric lines [redrawn from Schultz, 1969]. Note the greater variability of brain size at any given body size in the domesticated forms.

**Table 1.** Species-specific encephalization indices (EI) of wild stem species within their orders resulting from interspecific allometries contrasted with species-specific values for brain size decrease (DV) resulting from intraspecific allometries of wild type versus domesticated forms

	EI	DV, %	
<b>Rodentia</b>			
<i>Rattus norvegicus</i>	62		
(Wistar albino)		-8	Kruska [1975b]
(DA pigmented)		-12	Kruska [unpubl.]
<i>Mus musculus</i>	66	-0	Frick and Nord [1963]
<i>Meriones unguiculatus</i>	88	-15	Leybold [2000]
<i>Cavia aperea</i>	90	-13	Ebinger et al. [1984]
<b>Lagomorpha</b>			
<i>Oryctolagus cuniculus</i>		-13	Fischer [1973]
<b>Carnivora</b>			
<i>Mustela vison</i>	55	-20	Kruska [1996]
<i>Mustela putorius</i>	55	-29	Espenkötter [1982]
<i>Felis silvestris</i>	104	-28	Röhrs and Ebinger [1978]
			Bronson [1979]
<i>Canis lupus</i>	119	-29	Röhrs and Ebinger [1978]
<b>Artiodactyla</b>			
<i>Sus scrofa</i>	97	-34	Kruska [1970 b]
<i>Ovis ammon</i>	117	-24	Ebinger [1974]
<i>Llama guanacöe</i>	127	-18	Kruska [1980]
<b>Perissodactyla</b>			
<i>Equus (Equus) przewalskii</i>		ca. -16	Kruska [1973]
<i>Equus (Asinus) africanus</i>		ca. -16	Kruska [1973]

**Fig. 14.** Average intraspecific allometries of the brain to body size relation for wolves and king poodles as well as data plots and average line for wolf x king poodle first generation hybrids. Note: All allometric lines follow an intraspecific slope of  $a = 0.25$  with the hybrid line intermediate [redrawn from Weidemann, 1970b].



indices (EI) that the Rodentia species show a stepwise increasing encephalization from *Rattus* to *Cavia*, but the decrease values (DV) due to domestication are not in accord with this trend (table 1). Likewise within the Carnivora, ferrets and dogs have identical decrease values, but wolf brains are about double the size of polecats independent of body size. Additionally, the two sister species of *Mustela* with identical encephalization show different degrees of brain size decrease compared to ferrets or to ranch minks, respectively. In contrast, the three Artiodactyla species show increasing DV with decreasing EI values.

It is very important to realize that these changes of brain size from wild ancestors to the domesticated types are genetically determined. This was demonstrated through interbreeding experiments of wolves with poodles [Weidemann, 1970b]. In that experiment, the brain to body size relationship in the first generation offspring was intermediate between wolves and poodles (fig. 14). Further interbreeding of these hybrids led to second generation individuals with more variable brain sizes, including some individuals with brains the size of wolves and others of poodles. This is consistent with Mendelian genetic rules to some extent, although most probably brain size is not homozygotic in the parental generation. Brain sizes of mules, which result from artificial interspecific breeding between horses and donkeys also seem to reflect this [Kruska, 1973].

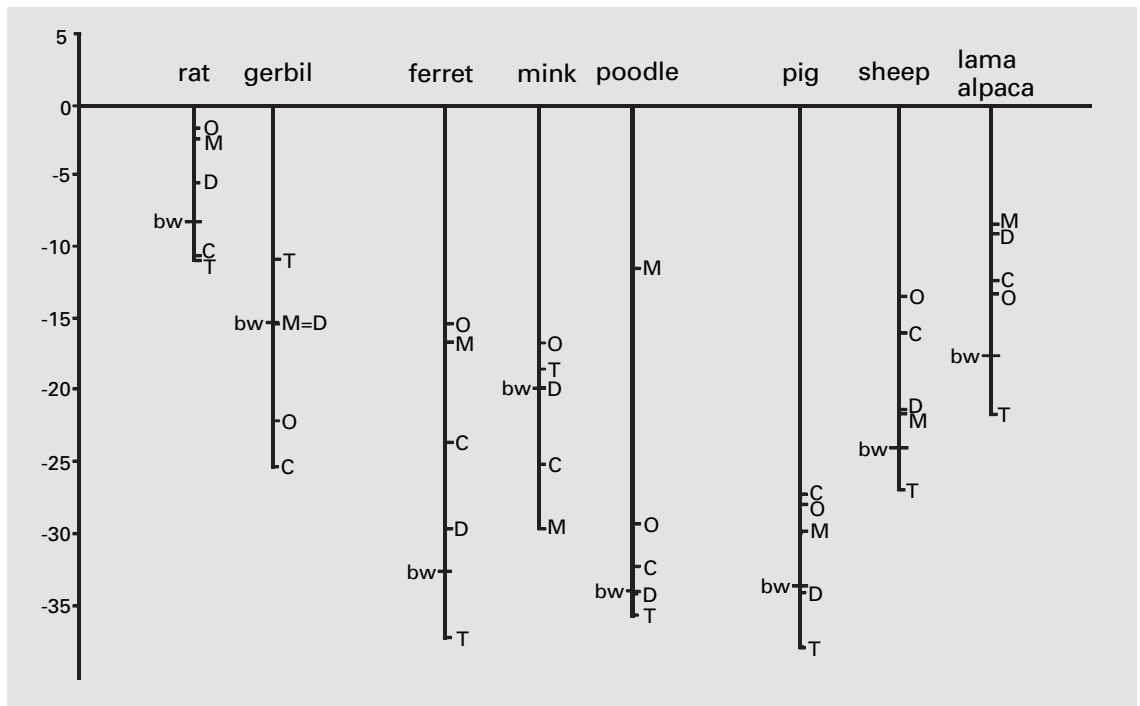
In conclusion, in contrast to the evolutionary radiation of eutherian mammals through phylogeny, domestication is in general an intraspecific phenomenon correlated with

a genetically determined decrease of overall brain size. No brain size increase ever occurred due to domestication. It might be of further interest to characterize these changes in more detail and in contrast to evolutionary trends.

#### *Domestication and Brain Subdivisions*

Several studies compared the volume of different brain parts in wild and domesticated forms by use of the serial sections method and intraspecific allometries [Stephan, 1960; Kruska, 1970b; Kruska and Stephan, 1973]. These include wild rats versus laboratory rats of the Wistar strain [Kruska, 1975b, c; Kruska and Schott, 1977]; wild gerbil versus laboratory gerbil [Leybold, 2000]; polecat versus ferret [Schumacher, 1963]; wild mink versus ranch mink [Kruska, 1996]; wolf versus poodle [Schleifenbaum, 1973]; European boar versus pig [Kruska, 1970b, 1972, 1973; Kruska and Stephan, 1973; Plogmann and Kruska, 1990]; mouflon versus sheep [Ebinger, 1974, 1975a, b]; guanaco versus llama and alpaca [Kruska, 1980].

Allometric comparisons of the five fundamental brain parts, namely telencephalon, diencephalon, mesencephalon, cerebellum and medulla oblongata [Kruska and Stephan, 1973], resulted in a large range of different decrease values. These are scaled comparatively in figure 15. Little conformity is evident between the different species concerning the arrangement of these brain parts from highest to lowest decrease. However, with the exception of gerbil and mink (two species domesticated relatively recently) all the other forms consistently show the telencephalon as having decreased to the greatest extent of all the brain



**Fig. 15.** Scaling size decrease values of total brain and the fundamental brain parts for several species from the wild to the domesticated form. bw = brain weight; T = telencephalon; D = diencephalon; M = mesencephalon; C = cerebellum; O = medulla oblongata. Note: With the exceptions of gerbil and mink the telencephalon is always the most decreased brain part.

subdivisions even though the investigated ancestral wild type forms are encephalized differently. Additionally, in these species the isocortex is always especially involved and more prominently decreased than overall brain size (fig. 16).

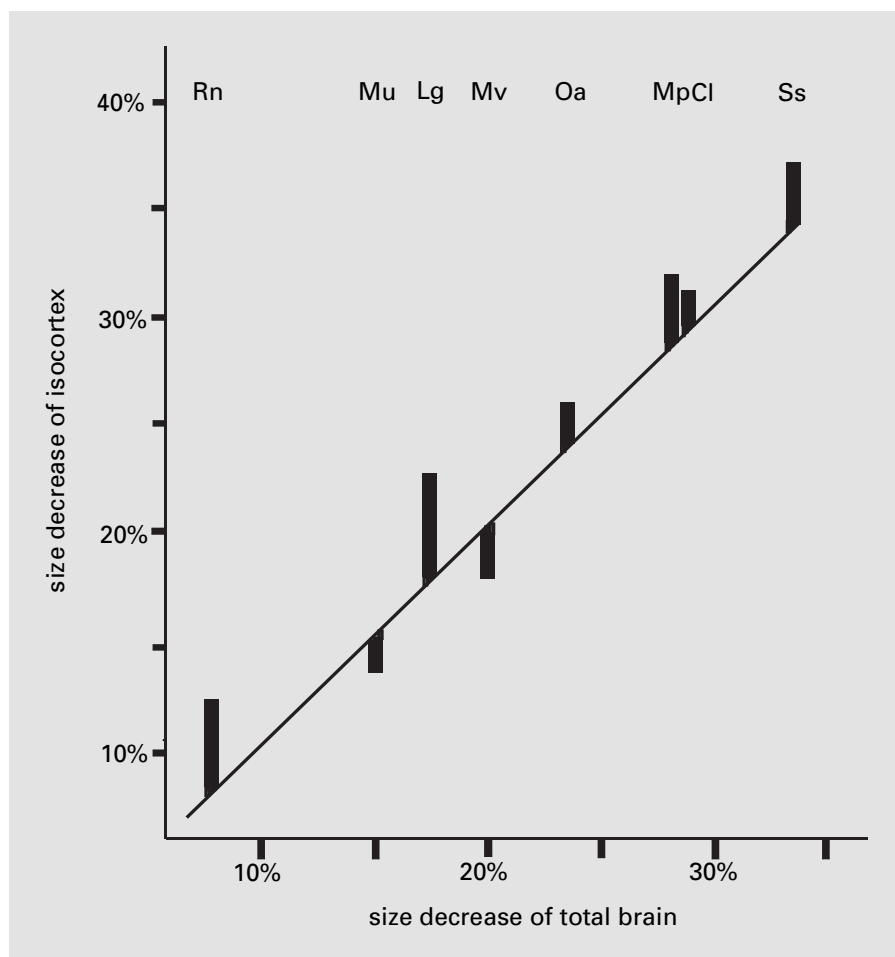
These results again point to the phenomenon that those special brain parts with higher processing functions are especially affected through the domestication process. This intraspecific phenomenon is clearly in opposition to interspecific events that are characterized by an increase of these same brain parts in diverse evolutionary radiations. For these reasons domestication events might be considered as special evolutionary phenomena with regressive trends.

Quantitative investigations were also performed for several structures that serve in different functional systems, e.g., sensory systems for olfaction, vision, and hearing; motor structures of pyramidal or extrapyramidal quality; limbic structures. Species-specific decrease values for these are listed in table 2.

Altogether these values point to the fact that diverse interior structures have also decreased from wild to domesticated forms with only one exception. This exception is the optic tract of rats, which is larger in the investigated laboratory strain when compared with wild rats; even though associated grey matters of the lateral geniculate body and superior colliculus are smaller. Here it is notable that individuals of the albino Wistar strain were investigated and that albinism is known to be associated with quantitative and qualitative disorders of the visual projections in several mammalian species [see Kruska and Schott, 1977 for further details].

However, all the other data in table 2 show an inconclusive mosaic picture regarding the decrease intensity not only among species, but also from one functional system to another and within the systems as well. Nevertheless, with the exception of Wistar rat vision as already mentioned, some conformity in the sensory systems of the other investigated species can be seen. Within these different sensory systems those neural structures with primarily a basal stimulus-spreading function are often less

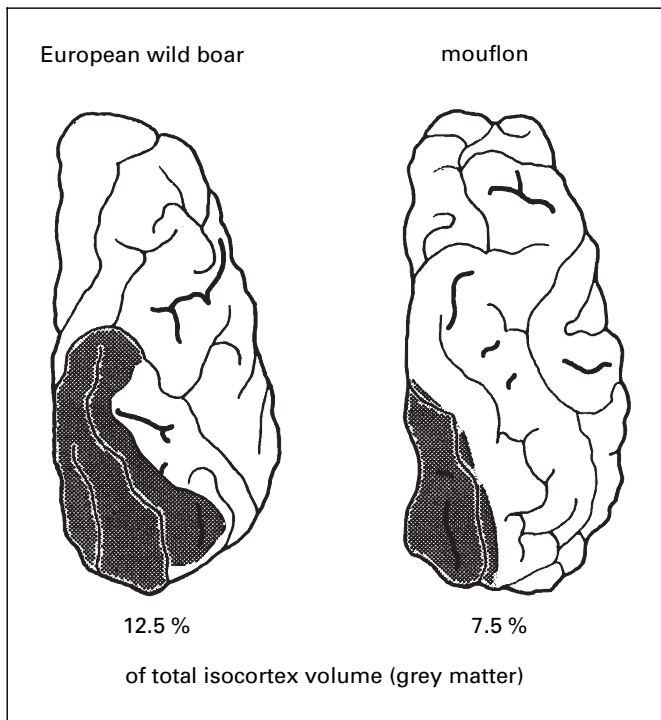
**Fig. 16.** Relation between size decrease intensity of isocortex and total brain due to domestication in several species. The line serves as an orientation assuming isocortex has decreased to same extent as has total brain. Consequently, bars above the line indicate greater, whereas those below lesser, decrease intensity for the isocortex. Rn = *Rattus norvegicus*; Mu = *Meriones unguiculatus*; Lg = *Llama glama*; Mv = *Mustela vison*; Oa = *Ovis ammon*; Mp = *Mustela putorius*; Cl = *Canis lupus*; Ss = *Sus scrofa*.



decreased in size compared with those that act with higher stimulus-processing functions in the ascending pathways; a phenomenon that can also be seen in the larger brain part comparisons.

This holds true for the values of the lateral geniculate body versus the striate area in the visual systems of mink, pig, and sheep, although these regions are tonotopically organized and one would have expected a similar relative decrease for both. In the olfactory system the olfactory bulb is less decreased in gerbil [Leybold, 2000], mink [Kruska, 1996], pig [Kruska and Stephan, 1973], and sheep [Ebinger, 1974] compared with the secondary olfactory regions of the allocortex, but this is not so in the microsmatic llama [Kruska, 1980]. Similarly, within the auditory system of pigs the cochlear nucleus and the medial geniculate body are less decreased than are the other structures, especially the auditory cortex [Plogmann and Kruska, 1990].

It should be emphasized again: The degree of size decrease is always associated with the evolutionary plateau of the ancestral wild type, its unique radiation and ecological niche adaptations. For example, the less encephalized wild boar is mainly macrosmatic with its visual sense of less importance. Accordingly, the lateral geniculate body is not very prominently laminated [Kruska, 1972]. In contrast, the higher encephalized mouflon is mainly visually guided with olfaction of secondary importance [Ebinger, 1975a]. From comparisons of hemispheric size (fig. 17) it can be seen that the expansion of the striate area is relatively greater in boars (12.5% of isocortex grey matter) compared with mouflons (7.5%) although the latter is more strongly specialized for vision. These discrepancies can only be explained by gradual differences in isocorticalization. From the fissuration pattern and convolutions of gyri on the mouflon endbrain it can be deduced that other cortex regions (most probably parts of the association cortex) are expanded to a greater extent.



In comparison, there does not seem to be very much surface area left for these sensory regions in the more primitive boar.

Within species size decreases of sensory brain structures have been interpreted as evidence of a concomitant functional decrease, which in general might be debatable. Comparing results of nerve cell counts might validate such a relationship. Unfortunately until now such investigations have been performed only in the medial superior olivary complex of boars and pigs [Plogman and Kruska, 1990]. There were only 9% fewer neurons in the domesticated form, but as this nucleus was more strongly decreased in total size ( 29.0%) the neuron density must have actually increased.

**Fig. 17.** The expansion of the striate area on the hemispheres of wild boar and mouflon is different relative to the isocortex. Although mouflon is a more visually guided species its visual cortex has a smaller relative value; see figure 10 for comparison [redrawn after Kruska, 1972, and Ebinger, 1975a].

**Table 2.** Percentage decrease values (–) of brain structures from the wild ancestral type to domesticated forms (except one single + value of increase) that serve in different functional systems compiled from literature cited in the text. (values in brackets are preliminary data not yet published)

	Rat	Gerbil	Mink	Poodle	Pig	Sheep	Llama
Olfactory structures	–6	–9	–25	–33	–31	–22	–4
Visual structures	–4		(–27)		–41	–26	
Optic tract	+24		(–28)		–49	–21	
Lateral geniculate body	–16		(–22)		–39	–25	
Superior colliculi	–3		(–26)		–32	–12	
Striate area (grey matter)	–12		(–28)		–41	–30	
Auditory structures					–30		
Cochlear nucleus					–15		
Superior olive					–28		
Lateral lemniscus					–33		
Inferior colliculi					–28		
Medial geniculate body					–20		
Auditory cortex (grey matter)					–32		
‘Motor’ structures							
Cerebellum	–10	–25	–25	–32	–27	–16	–12
Corpus striatum	–11	–8	–16	–27	–29	–21	–9
Area gigantopyramidales (4 a.Br.)			(–26)			–30	
Area frontalis agranularis (6 a.Br.)			(–25)				
Limbic structures	–10	–4	–17	–34	–41	–35	–6
Hippocampus	–12	–1	–17	–42	–44	–41	–3



Some quantitative data are also available for motor structures, although these are less numerous (table 2). To compare motor structure and function, cerebellum size might serve as a special parameter indicative of total motor ability and performance as this brain part is generally responsible for initiation, regulation, and coordination of movements and body posture. The cerebellum integrates, associates, and modulates manifold sensory inputs with the two prominent telencephalic motor systems. Of these, the corpus striatum might be representative of the more automatically acting extrapyramidal motor system, as opposed to the pyramidal system represented by the two isocortex regions: Area gigantopyramidalis (Brodmann Area 4) and Area frontalis agranularis (Brodmann Area 6). These brain parts are also smaller in domesticated breeds compared with their ancestors, but do reflect some species-specificity. In most cases the domestic cerebellum is more strongly decreased than is the corpus striatum and, as far as can be judged, the motor isocortex also shows a high decrease value.

Changes in limbic structures with the domestication process seem of special interest. According to Stephan [1975] the allocortex is a special part of the mammalian telencephalon cytoarchitectonically formed by several lateral, basal, and medial regions. These structures mainly serve in two functional systems: the olfactory and the limbic. Although the former is directly sense-dependent, the latter is not or at least mostly independent of one special sense. Both these systems evolved progressively or regressively but differently and independently of one another during the evolution of the diverse mammalian radiations. For example, whales are anosmatic mammals; they have no olfactory bulbs at all, but limbic structures are rather large. Similarly, microsmatic humans have small olfactory but very large limbic centers. The limbic structures of the mammalian allocortex are represented mainly by the hippocampus, but additionally by the septum, the schizocortex (entorhinal region, pre- and parasubiculum), and some medial nuclei of the amygdala. These endbrain structures are highly interconnected with the anterior nuclei of the thalamus, the habenula complex and most prominently the hypothalamus. Consequently they are in a position to directly influence neuroendocrine, autonomic and special behavioral mechanisms associated with these parts of the diencephalon. For these reasons the limbic system was functionally evaluated as the 'visceral brain' by Mac Lean [1949, 1952, 1954].

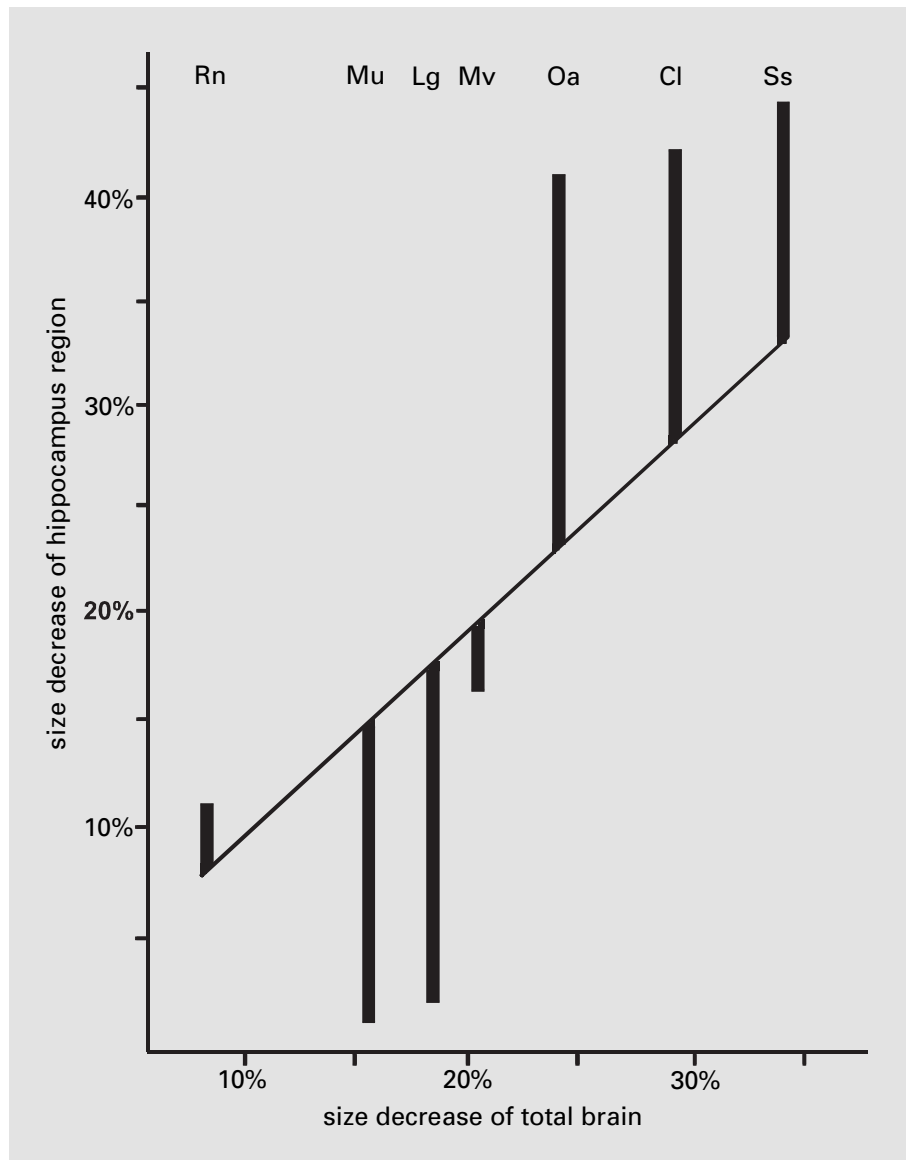
However, the limbic system is a very complicated functional circuit and even today many questions remain unanswered with respect to the detailed anatomy of its

parts and their related functions. Nevertheless it is still generally accepted that the hippocampus is the main center of this system and, although it is influenced by other brain regions (including the isocortex), it mostly acts endogenously. Accordingly, this nuclear formation not only plays an important functional role in several behavioral complexes, such as emotionally guided behavior and individual self-protection [MacLean, 1992; Nieuwenhuys, 1998], but also in learning and memory. Emotional reactions, aggression and other affective functions, attention as well as motivational and activating functions seem to be guided, controlled and regulated by this limbic center [Hassler, 1964; Stephan, 1975].

The various regions of the limbic system are also smaller in the domesticated forms compared with their wild type counterparts. This is documented in table 2 by the decrease values for the sum of some telencephalic limbic structures and the hippocampus formation. But also here the picture is not the same for all of the species as in the gerbil and llama these brain parts are only minutely changed from wild progenitor to domestic breeds, whereas very high values for sheep, poodle, and pig are seen. In these so-called highly domesticated forms the hippocampus size is decreased by over 40% which is a most remarkable degree compared with their wild ancestors. These are very impressive reduction values that exceed even the decrease values for total brain (fig. 18) and isocortex size.

These size changes in limbic structure might be indicative of a very special functional effect of domestication. Attenuation of aggressive behavior, general attention, and diminution of endogenously produced drive or temptation are fundamental attributes of the domestication process. Such quantitative functional or behavioral changes enable humans to keep and handle large mammals without danger and related problems. Consciously or unconsciously humans must have sought these changes, especially during the initial phases of domestication. Undoubtedly they were an important selective advantage for domesticated mammals. Roughly evaluated, a wolf for example will always remain an 'aggressive' carnivore and will never behave like a 'docile' dog, not even after taming or habituation. Of course, not all dogs are 'docile' but they normally act upon human instructions and wolves do not [Hare et al., 2002; Miklosi et al., 2003].

Long term experiments on ranched silver foxes over several generations demonstrate the importance of such adaptive and selective breeding in domestication when seeking certain behavioral patterns [Belyaev, 1969, 1979, 1980]. Destabilizing the effects of domestication led to



**Fig. 18.** Relation between size decrease intensity of hippocampus and total brain due to domestication in several species. The line serves as an orientation assuming hippocampus has decreased to the same extent as has total brain. Consequently, bars above the line indicate greater, bars below lesser decrease intensities for the hippocampus (see figure 16 for abbreviations).

the existence of aggressive individuals, but resulted also in silver foxes with almost dog-like behavior. These individuals showed other morphological and physiological attributes characteristic of many domesticated mammals, although brain sizes were not studied comparatively.

#### *Domestication and Sense Organs*

It seems valuable to mention comparative results for the sense organs along with the central nervous system. Sense organs have only been sporadically studied but decreases in the number of receptor cells in the olfactory epithelium [Güntherschulze, 1979] and the retina of eyes

[Wigger, 1939] in the domestication process from boar to pig were comparable to the amount of change in associated sensory brain nuclei. Structures of the ear are also decreased in wild versus laboratory rats [Burda, 1985]. In the domesticated form decreases were found in the volume of the tympanic cavity, size of auditory ossicles, bony cochlea, spiral length of cochlear duct, basilar membrane and total number of cochlear hair cells in the organ of Corti; but the density of inner as well as outer hair cells was slightly increased in the domestic breeds.

Eye weights were also compared within several species [Herre and Röhrs, 1990] with a general decrease seen in

the domestic breeds. Only albino Wistar rats have heavier eyes [Ebinger, 1972], but for pigmented DA rats this is not valid [Kruska, unpubl. observations]. Although this has been known for a long time, there are no further investigations focusing on specific parts of the eyes in these forms. Most probably the retina itself is not enlarged in Wistar rats as the visual parts in the brain are smaller in size compared with the wild form [Kruska and Schott, 1977].

The morphology and topography of ganglion cells in the retinas of wolves and dogs were examined in more detail by Peichl [1992a, b]. A pronounced visual streak of high ganglion cell density in the horizontal direction from nasal to temporal is characteristic for the wolf retina. This was not recognized for dogs or at least only present in some individuals, but even when present it is clearly less pronounced. Furthermore, a total number of about 200,000 ganglion cells in wolves is in sharp contrast to only 115,000 in dogs, which translates into a 42.5% decrease in number. Nevertheless, this relatively high value seems doubtful especially as the investigated dogs were small sized breeds, about half the size of wolves, and body size differences were not taken into account.

The very accurate quantitative investigations of Steffen [2000] on wild and ranch mink eyes are of special value because allometries were used. The ranch mink eyes are 17% smaller in weight independent of body size and they have retinas 22% smaller in surface compared to wild mink; the relationship of eye to retina size remains the same in both types. The topography of ganglion cells and their densities are highly diverse in ranch mink. A scanty visual streak only occurs in the wild species, never in the ranch mink retina; the total number of ganglion cells is 15% fewer in the domesticated form, but these are differently arranged in several rings around the central area. Receptor cells were also compared in quality, number, distribution and relationship. In general, rods and cones are present in ratios from 26:1 to 39:1 depending on topographic location with an average of only 2.5% cones. This means that, as in other mammals, the scotopic visual system is prominent over the photopic portion. Investigations of cones revealed that 83,600 short-wave length receptor cones were present in the wild species, but only 68,100 in the ranch mink retina, a decrease of 18.5%. Long-wave length cones decreased only by 9.2% due to domestication (835,700 versus 758,600), but the relative numbers of short- to long-wave length cones remained the same with around 8.5% to 91.5%. All these data on sense organs are in good quantitative agreement with the results on the sensory processing neural systems in the brain.

#### *Domestication and Behavioral Implications*

Comparisons of general behavior and special behavioral patterns between wild and domesticated relatives were also performed in Norwegian rats versus laboratory rats [Richter, 1949, 1954; Boice, 1970, 1972; Price, 1973, 1984; Price and Huck, 1976; Price et al., 1976; Price and Belanger, 1977], wild cavy versus guinea pig [Stahnke, 1987], wolf versus poodle [Zimen, 1971], and European boar versus pig [Hafez et al., 1962; Gundlach, 1968; Reicher, 1969; Briedermann 1971]. Except for the fact that the domesticated forms can be trained to follow human orders and commands, these investigations showed that in general no new behavioral patterns have developed due to domestication. However, qualitative and quantitative diminutions were found in many behavioral traits and sensory abilities. Very often elements of fixed action patterns characteristic for the ancestral wild type are dissociated in the domesticated relative [Lorenz, 1959]. Decreases in brain size and changes in the proportion of brain areas due to domestication might in some way be connected with these behavioral peculiarities.

It must also be stressed, though, that not only hypotrophied but also hypertrophied behavioral elements were found in domesticated forms which is interesting as no brain region is larger in comparison with the wild-type counterparts. Such hypertrophies occur in sexuality. The results of some experimental studies on rats and cats [Schreiner and Kling, 1956; Green et al., 1957] might be of help to explain the obvious contradiction between quantitative decreases in neuroanatomical structure and ethologically related behavioral increases. These studies have highlighted the inhibitory character of some allocortical structures, such as the piriform cortex and parts of the amygdaloid complex. Experimental removal and destruction of these brain regions clearly results in hypersexual behavior of the lesioned animals. It seems then that the gradual size decrease of these nuclear masses due to domestication might be responsible for a disinhibition effect and consequently a behavioral increase.

Similarly, domesticated mammals might show a somewhat greater learning ability and memory capacity in specific behavioral tests and experiments. This was established in laboratory rats as compared to wild rats by Boice [1970, 1972]. At first, these behavioral hypertrophies also seem surprising in light of the brain area decreases, but there might be an explanation for this effect as well. It is commonly known that using tamed or habituated wild animals in experimental settings often results in some general problems. These animals are constantly attentive and aware of the environment, very probably as a conse-

quence of their larger sensory and limbic brain structures. Because of that, they may not 'concentrate' on the particular tasks of the 'human-initiated' test procedures, and as a result, these animals show decreased performance. In contrast, domesticated animals might act rather relaxed in similar tests, most probably as a consequence of their smaller and altered brains and the resultant higher sensory and attentive thresholds. One of the characteristics that has resulted from domestication is the ability of breeds to live in close human proximity and to follow human instructions.

#### *Conclusions on the Domestication Effect*

The domestication of mammals has led to species-specific, gradually different decreases of brain size and alterations of various cortical nuclei. As brain size and brain construction are mainly genetically determined these changes from the wild ancestral type to domesticated relatives are clearly the result of artificial selective breeding. Nevertheless, domesticated mammals generally provide proof for the intraspecific variability and the evolutionary malleability of the brain.

However, the size and structure of the brain itself cannot be the actual characteristic that is subject to selective breeding, but only indirectly evaluated through its functional outcome as expressed by behavioral peculiarities. Therefore, very probably the selection goals of humans always were consciously or unconsciously evaluated through behavioral traits expressed by individuals chosen for breeding. Although there is only a little evidence it seems reasonable to suppose that the domestication of animals started with only a small number of individuals of a wild-type population. With respect to brain and behavior these might already, within the normal variability of the species, have been gradually preadapted to the special conditions of domestication.

It is commonly known from many species and experiences in zoological gardens that not all wild caught animals are willing to breed in captivity or under human care, which means they are necessarily not preadapted to the conditions necessary as a first step toward future domestication. Animals in zoological gardens are also not intended to become behaviorally changed or domesticated. Nevertheless they are exposed to human influence which might exert certain selective effects on brain size and behavior in the sense of an unintended domestication. Sporadic investigations, however, have found no significant evidence for a brain size decrease in wild mammals kept in zoos or under human care over several generations when compared with individuals in the wild living

in natural environments [Kruska, 1987, 1989]. Thus captivity itself does not necessarily affect brain size. Therefore, concerning any future domestication process, an immense selection pressure on behavior with consequent changes in brain size must be applied.

This selection pressure seems to act especially strongly during the first generations of the domestication process. As documented in the ranch mink for example, behavior and brain size in this species very clearly changed due to domestication over the first (approximately) 80 generations [Kruska and Sidorovich, 2003]. On the other hand, it also seems valid that a final brain size decrease is reached rather rapidly and subsequently remains stable. This can be assumed for ranch mink [Kruska and Sidorovich, 2003], but is very impressively evident for dogs as well. That is, prehistoric dogs from about 1000 to 2000 B.P. found in some places of northern Germany already had brain case sizes smaller than wolves and roughly identical with those of modern dog breeds [Reichstein, 1985].

The domestication effects on brain size and brain proportioning document an enormous variability of these parameters within a species and they also demonstrate genetically determined intraspecific changes regressive in character. They clearly occur within shorter time intervals and are of minor distinction compared with interspecific events as a consequence of phylogenetic radiation. However, phylogenetic features and species characteristics are still seen in the domesticated individuals, as in most cases neural structures with basal functions are affected by domestication to a lesser extent than brain regions serving in more complicated, highly species-specific capacities. Thus, brain size changes due to domestication must zoologically be evaluated as special adaptations occurring on a species level and being directed to the special 'ecological niche' of domestication even though this description might be considered very broad.

### **Feralization and Brain Size in Some Mammalian Species**

#### *Some General Remarks on Feralization*

Concomitantly with the expansion of some human cultures on earth and as a consequence of human activities many mammalian species have been translocated to places of the world to which they were not indigenous. This happened and still happens now not only with diverse wild-type individuals but also with domestic breeds. In many cases these animals adapted to the new habitat and established large populations over long peri-

ods of time in a process described as introduction or naturalization. Similarly, domesticated individuals have accidentally escaped in small numbers from husbandry at all times during history and returned to living in a wild state. In some cases domesticated mammals were released by humans for special purposes. This has led sometimes to stable populations in a process described as feralization [Lever, 1985]. Such adaptations to wildlife conditions secondarily occurring from a domesticated state can be evaluated as a special zoological experiment; feralization implies an environmental enrichment for the individuals involved. After escape or release these animals encounter biological situations not existent or at least of minor importance in domestication. The feralization process can be considered the opposite of domestication in cases where such feralized species have existed for a long time and over several generations in greater populations independent of human influence and at places where the ancestral wild type is not distributed (exclusive of wild introgression). Therefore, it is also of interest to ask: What happens to the brain under conditions of feralization?

#### *Feralization and Overall Brain Size*

Diverse domesticated mammals have been feralized primarily in Australia and the Americas, but also at several places in Eurasia; however, there is only sparse information concerning their brain sizes. For instance, goats and pigs were released on the Galapagos Islands about 100–150 B.P. to serve as a meat reserve for seafarers at that time. They have thrived there since and, although they are not preyed upon by carnivores, they are heavily hunted by humans and must live on their own. The brains of these mammals have been investigated in small numbers. In an intraspecific allometry of brain to body size it was determined that these feralized goats and pigs have brain sizes within the normal distribution of domesticated forms but not of the ancestral wild type [Kruska and Röhrs, 1974; Herre and Röhrs, 1990]. Further quantitative cytoarchitectonic investigations of Galapagos pig brains revealed a composition of brain parts only slightly different from modern European domesticated races [Kruska and Röhrs, 1974].

In addition, feralized cats were investigated from the Kerguelen archipelago, where they thrive on their own in the absence of any original wild type or human impact. After about 20 years of feralization these animals still had brain case sizes similar to domesticated but not wild individuals [Derenne, 1972].

Another example is the American mink. Domestication of this species started about 1866 in Canada [Shackelford, 1949; Enders, 1952] with increasing, stepwise changes leading to current very diverse color strains [Nes et al., 1988]. Early ranch mink were imported to several European countries around 1920 where numerous farms were established. In the course of ongoing and flourishing European mink ranching, occasional individuals have accidentally escaped from captivity, at an especially high rate during World War II. This led to stable populations that are still increasing in distribution and causing severe problems for autochthonic wildlife communities in all northern European countries [Lever, 1985]. Additionally, ranch mink were deliberately released at different sites in European and Asiatic regions of the former Soviet Union since 1933 to enrich wildlife and fur trapping [Heptner and Naumov, 1974]. Certain mink populations from different river systems of Belarus can be traced back to an establishment around 1950 [Ulevicius et al., 2001]. Allometric skull morphometrics of such feralized Belarus individuals obtained around 1990 were compared with wild mink of Canadian origin. No brains were analyzed directly but from the relation of brain case size to body size as well as to skull length it turned out that the feralized mink had significantly smaller brain cases. Moreover, the size differences between these two types were identical to the size decrease from wild Canadian to domesticated individuals obtained from farms [Kruska and Sidorovich, 2003]. From this it must first be concluded that, as in other cases, no increase of brain size resulted from feralization after about 40 generations under wild-life conditions. Secondly, it must be concluded that at the times of the release, which means after about 80 generations of domestication, the decrease of brain case size due to domestication had already reached the dimensions of modern strains and consequently has remained stable ever since. Thus, the effects of domestication on brain size obviously occur rather rapidly and subsequently remain stable.

Nevertheless, the most remarkable example of feralization effects concern canids, as feral dogs are distributed virtually worldwide. A special case is the dingo of Australia and the so-called Hallstrom or singing dog from Papua, New Guinea. Both these wild canids undoubtedly derived from early domesticated dogs [Leonard et al., 2002; Pennisi, 2002; Savoleinen et al., 2002] and were introduced to these regions by Aboriginal voyagers from Southeast Asia [Lever, 1985]. Presumably this happened about 3,000–8,600 B.P. as indicated by excavation and dating of ancient dingo remains from several sites in Australia

[MacIntosh, 1975]. Thus, they existed as feralized forms for extremely long times and many generations. Yet dingos as well as singing dogs at comparable body size have brain sizes clearly within the distribution of domestic dogs not of wolves [Schultz, 1969]. Even after such a long time under wild natural conditions the brain size did not change concomitantly. This example also indicates that most probably the brain size decrease from wolf to dog was already present at the time of the dingo's origin, which means before the feralization of these canids started.

#### *Conclusions on the Feralization Effect*

Although the investigations of feralization effects on brain size are few in number they nevertheless reveal similar results in different species. From these data it must be concluded that no actual return to the brain size of the former wild ancestor has occurred. Therefore it seems to be true that 'once domesticated – always domesticated'. In this sense the intraspecific domestication effect on brain size is just as irreversible as the interspecific evolutionary radiation according to the rule of Dollo [Marshall et al., 1994]. Zoologically it is obvious that species-specific modes of adaptation to a wild lifestyle and ecological niche are not necessarily connected with the evolution of a larger brain. Despite a loss of 20–33% of the wild-type brain mass (as in Carnivora, Artiodactyla) a 'domesticated brain' can still enable an individual to survive after feralization and its more enriched environment. This finding might contribute to future discussions regarding the meaning, importance, or consequence of the evolution and adaptation of brain size.

Nevertheless, some additional remarks can be added concerning the consequences of an enriched environment on the brain size of mammals as some earlier results seem to contradict the effects of the feralization process. Several past experimental studies on rats and other rodents raised in captivity under conditions of enriched environments resulted in a gradual increase of brain size, isocortical thickness, neuron number, and other neuroanatomical parameters compared to individuals raised under impoverished conditions [Rosenzweig et al., 1962, 1968; Diamond et al., 1964; Diamond, 1967; Rosenzweig, 1971; Rosenzweig and Bennett, 1972]. Unfortunately changes in the skull, especially the massive, bony part of the brain case necessary to accommodate the brain size increase, were not studied. However, as reviewed by Bedi and Bhide [1988], all the corresponding results obtained from such studies indicate that environmental influences on brain structures, if they do occur at all, rarely exceed 4–

5%. These are dimensions clearly within the normal distribution of genetically determined brain size variance within both wild species and domesticated derivatives.

It must be mentioned that these probable consequences of environmental influences have nothing in common with the effects of domestication or feralization. In contrast, they must be evaluated as modifying changes probably of importance for the life of the individual, but by no means comparable to the genetically determined effects described here.

#### **Brain Size and Intelligence**

Another issue concerns discussions on brain size and structure related to general and special behaviors, but especially to certain higher central nervous functions such as learning and memory, problem solving and cognitive abilities, mind and global intelligence. Many publications and several meetings and workshops among neuroanatomists, psychologists, ethologists and other researchers have dealt with these problems in general or in detail [e.g., Jerison, 1973, 1991; Macphail, 1982; Weiskrantz, 1985; Jerison and Jerison, 1988; Pirlot, 1989; Powers and Day, 2003]. Total brain size is sometimes used in a comparative approach as the morphological substrate of, and a general measure to evaluate what is called the 'global intelligence' of mammals. Consequently the encephalization degree of a species and the evolution of brain size is equated with the evolution of intelligence [Jerison, 1973].

Such ideas are not commonly accepted and remain controversial. They are discussed mainly in terms of a general definition of intelligence from neuroanatomical versus psychological viewpoints, focusing on the complexity of brain structure and its very diverse functions [Hodos, 1988]. Neuroanatomically evaluated total brain size seems to be only a very rough parameter and minimally suited for use as an indicator of such higher functions. There is very little evidence of any brain structure or circuit responsible for intelligence, except perhaps some secondary areas of the human isocortex.

However, such reflections are still open for discussion and shall not be dealt with here in more detail, but some of the contradictory results of this review might stimulate a rethinking. That is, if one assumes brain size indicates intelligence, then domesticated mammals with their smaller brains should be less intelligent or even stupid compared with their wildlife counterparts, as commonly believed. But from psychological tests on rats [Boice,

1970, 1972] and dogs [Hare et al., 2002] they seem more intelligent, at least concerning learning, memory and social-cognitive abilities. It therefore seems more correct to consider the changes from a wild to a domesticated brain as special adaptations to the ecological niche of domestication. This may be correlated with special behaviors as a result of selection. In any case, domesticated animals show that intelligence is not necessarily related to or dependent on larger brains.

Likewise, the brains of juvenile and subadult soricids and *Mustela* species clearly decrease in size as the individual ages to the adult state. In mink this decrease starts at times when the young leave the natal burrow and search for their own future home range and solitary life. One would assume that at this time of their life they would need a bigger brain for future competition as an adult than the smaller one they actually have. Again, are these individuals then more intelligent during their youth than as adults? In any case they were not when given tasks of visual performance, learning or discrimination ability [Steffen et al., 2001]. Thus there are several peculiarities that do not support the brain size-intelligence ideas.

Another argument concerns the worth and use of a bigger brain. Sometimes it is argued that an evolutionary brain size increase happened because there is a 'need' for a bigger brain for certain life style adaptations. These ideas also must be questioned, although several convergent effects of brain enlargements can be listed connected with life style peculiarities. The question is: Are they really 'needed'? In this respect the feralization results are of interest. Feralized mammals with their smaller domesticated brains are obviously able to survive in a wild environment far richer than captivity from a sensory, motor and cognitive problem-solving perspective. One might argue that in this special case the time span of feralization is not great enough for recognizing probable reversion effects to larger wild-type brains. However, feralized mammals have existed for a long time and because populations are still flourishing they indicate that survival is possible. Thus, there seems to be no necessary 'need' for the larger ancestral brain in identical environments. The paradox is: A more or less larger brained, 'intelligent' wild species is able to survive in captivity without a loss of brain mass, and conversely more or less smaller brained, 'stupid' domesticated mammals are able to survive in natural environments without a gain of brain substance. Consequently there is empirical evidence that might revitalize the discussions of brain size, animal intelligence and the relatedness of these characteristics during evolutionary radiation and niche adaptation.

## Conclusions

Using the most reliable, rather common, relationship of brain to body size in an interspecific allometric approach clearly reveals that different average plateaus of encephalization are characteristic for some orders of recent eutherian mammals. It is also evident that within orders the diverse species have different brain sizes at comparable body weights. On these different plateaus, species adapted to semi aquatic, aquatic or arboreal lifestyles in most cases have larger brains compared to terrestrial surface dwellers of even close phylogenetic relatedness. This shows that certain adaptations for specific habitats show several convergent effects. Furthermore, including data for fossil forms revealed some convergent steps of independent body and brain size increases at different geological times with a last step of increase to most, although not all, recent species.

Consequently the evolution of brain size is generally connected with an enlargement of the brain. The telencephalon and the isocortex are always especially involved. However, this evolutionary trend happened rather differently and arbitrarily in diverse radiations, leading to different plateaus and species-specific encephalizations. From ontogenetic investigations on some particularly specialized species it also becomes evident that those central nervous structures responsible for some special functional circuits develop much faster compared to others. This also reveals the evolutionary trend of increase in a mosaic mode. Thus, the slope of ontogenic allometry seems most important for understanding any evolutionary increase.

On the other hand, intraspecific allometric analyses of wild ancestral types with their domesticated descendants revealed a general brain size decrease on a species level due to the special selection process of domestication. Species more strongly encephalized are more heavily impacted in this process compared to species on a lower encephalization plateau. In most cases the telencephalon and isocortex are especially decreased, but other central nervous structures are also prominently reduced in size. These changes due to domestication also follow a mosaic mode with structural decreases that characterize phylogenetic factors as well as certain adaptations to demands of the special ecological niche of domestication. These brain size changes from a wild to a domesticated mammal remain stable following feralization and re-establishment of wild populations. Even after long periods of time and many generations under wild conditions no secondary evolutionary trend of brain size increase has occurred.

Contrasting the phylogenetic effects of encephalization due to evolution and adaptive radiation with the consequences of domestication highlight very complex phenomena. Domestication effects do not seem very useful for explaining the increase of brain size through evolutionary processes in general, as the opposite always is the case for domestic forms. Possibly regressive trends of phylogeny (reduction of the visual sense, olfaction, etc.) during niche adaptation can be specifically examined in these comparisons. However, the domestication effects especially illuminate the variability of brain size and proportioning, and the plasticity, changeability, heritability and susceptibility of this organ to change through selection.

Some general conclusions might arise concerning the different slopes of intra- and interspecific allometries of the brain to body size relationship. New species are generally assumed to have originated from intraspecific variation of ancestral forms. Excluding any progressive encephalization during the emergence of a new species, a diminution or an enlargement of only the body size resulting in a new dwarf or new giant species would a priori follow the allometric relation of the ancestor with its smaller intraspecific slope. Consequently, after species establishment this would result in a small-sized species more strongly encephalized than the ancestor on a steeper interspecific line. Dwarfism would thus always be associated with an evolutionary interspecific increase of brain size in terms of the encephalization indices. On the other hand, the newly originated larger sized species would then turn out to be less interspecifically encephalized compared to the intermediate sized ancestor. Consequently, without any evolutionary brain size increase phylogenetic gigantism would be connected with lower encephalization.

However, in general this does not hold true because many small and larger sized species of close phylogenetic relatedness are similarly encephalized, and many large sized mammals are known to be extraordinary highly encephalized (elephants, whales, primates). There are at least some examples to support this argument. Within the Hippopotamidae the giant species *Hippopotamus amphibius* is phylogenetically derived from a smaller sized ancestor approximately the size of the recent pigmy hippo *Choeropsis liberiensis*. The same is true for the giant forest hog *Hylochoerus meinertzhageni*, in contrast to other recent species of the Suidae family [Thenius, 1969]. Both these giant forms are clearly less encephalized in an interspecific allometric analysis compared to their smaller sized relatives [Kruska, 1970a]. Strangely enough, allometries calculated from the smaller sized to the giant recent species clearly show slopes more similar to an intra- than

an interspecific relationship. Thus, some exceptional phenomena seem explainable. The general phenomenon of evolutionary progressive encephalization is best understood by an immense acceleration of brain size in relation to body size during ontogeny, which means very high slope values during the 1st phase of development as described previously.

It should be concluded from this review that despite the classic nature of brain/body investigations, many exciting questions remain open concerning the evolution of the mammalian brain, its ontogeny, the effects of domestication, feralization and especially an understanding of brain structure and function in relation to behavior. Scientists, including young members of the field, should be encouraged to occasionally review and question accepted general tenets of biology in the hopes of clarifying, extending and sometimes correcting prevailing assumptions.

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