Brain Size in Vertebrates

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23.1
Introduction

Humanity and human intelligence are considered to be derived from the large human brain; therefore brain size is regarded as a relevant and interesting parameter. This chapter covers brain size in an evolutionary perspective. Such a starting point of course has an inherent limitation: attention is only paid to overall brain size, and not to the size of brain subsystems. Nevertheless, overall brain size is an interesting parameter.

23.1.1
Absolute and Relative Brain Sizes

Figure 23.1 shows the relationship between body weight and brain weight of 20 mammals in a double-logarithmic graph. The body weights range from 3 g to 150 metric tons: from the smallest shrew (*Suncus etruscus*) to the blue whale (*Balaenopterus musculus*). The smallest brain weight in an adult mammal (74 mg) is found in a bat (*Tylonycteris pachypus*, Stephan et al. 1981b), while brain weights of up to 10 kg have been described in sperm and killer whales (Kojima 1951). The mammalian brain weights differ by a factor of 130 000, while the body weights differ by a factor of 50 million. The human brain is large (about 1.4 kg), but still considerably smaller than the brains of elephants and some large whales (5–10 kg).

Figure 23.1 shows several elements we will often encounter in this chapter: a *regression line* and a *convex polygon*. A convex polygon is formed by straight lines enclosing all data points of a group; this polygon is convex, because all the inner angles are less than 180°.

We know intuitively that brain weight should be related to body weight, but our intuition fails us if we use a simple ratio, a percentage, to analyse this relationship. This is illustrated by Fig. 23.2, which shows the data for the same 20 mammals as relative brain weights (brain weight as a percentage of body weight). The brains of some small rodents comprise about 10 % of their body weight (Mace et al. 1981). In man this figure is about 2 %, in the pig less than 0.1 % and in the blue whale less than 0.01 %. Evidently, small animals have relatively large brains (Cuvier 1805; Weber 1896; Dubois 1897). When a selected body parameter does not scale proportionally with another body parameter, this phenomenon is called allometry. Such allometry is essential to evaluate the brain size of a given species. We need to compare its actual brain size with the brain size expected for an animal of this size. This is defined as the encephalisation quotient (*EQ*):
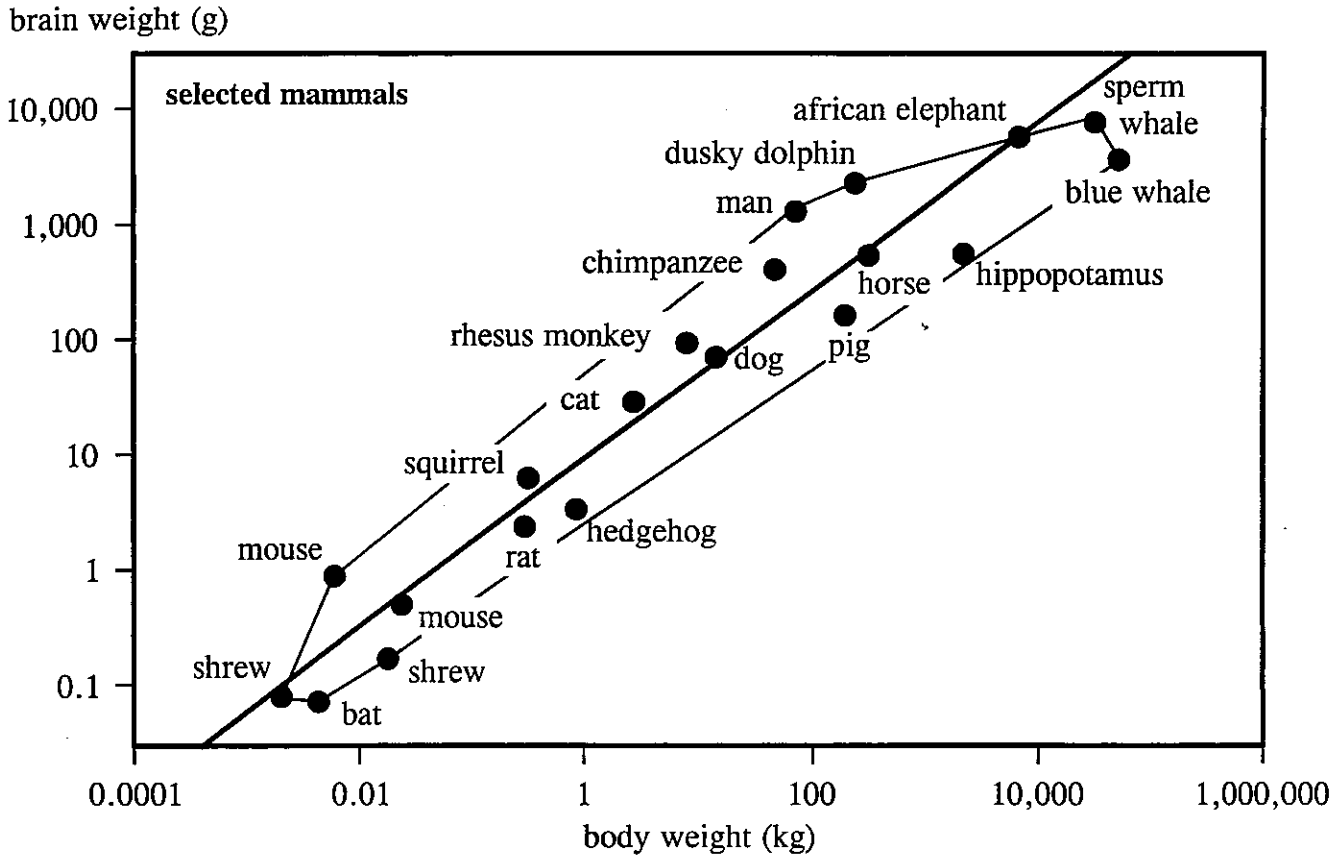
brain weight (g)

Fig. 23.1. Relationship between body weight and brain weight of 20 mammals, including those with the largest and smallest body and brain weights (double-logarithmic graph). Large mammals have larger brains. In a double-logarithmic graph like this one, the variation in brain weight between mammals of the same body weight seems rather small, but it can actually amount to a factor of 10. (See Table 23.2 for the sources of the data)

$EQ = E_a/E_e$

where E_a=actual brain weight and E_e=expected brain weight.

The key question is: what brain weight do we expect for a given species?

23.1.2
Experimental and Theoretical Body-Brain Relationships

The expected brain weight may be calculated by one of two strategies, either from regression analysis or theoretically (Harvey and Krebs 1990).

23.1.2.1
Regression Analysis

In 1891, Snell noted that the data points of brain versus body weight more or less follow a straight line on a double-logarithmic graph (Fig. 23.1). The equation for such a straight line is:

$\log(E) = \alpha.\log(S) + \log(k)$

where E=brain weight, S=body weight, α=slope of the line and k=intercept.

If this straight line is a correct description for these data points, then the relationship between brain weight and body weight is:

$E = k.S^\alpha$

A few authors (Count 1947; Bauchot et al. 1989b) claim that the data points are better fitted by a second-order function:

$\log(E) = \beta(\log(S))^2 + \alpha.\log(S) + \log(k)$

The great majority of investigators, however, regard a straight line in a double-logarithmic graph as the adequate description of the relationship between brain weight and body weight.

23.1.2.2
Theoretical Relationships

Another approach is fundamentally different: one starts with a theory about the relationship between brain and body size. Snell (1891) assumed that brain size would be proportional to the size of the body surface. Using this theory, the slope of the the-
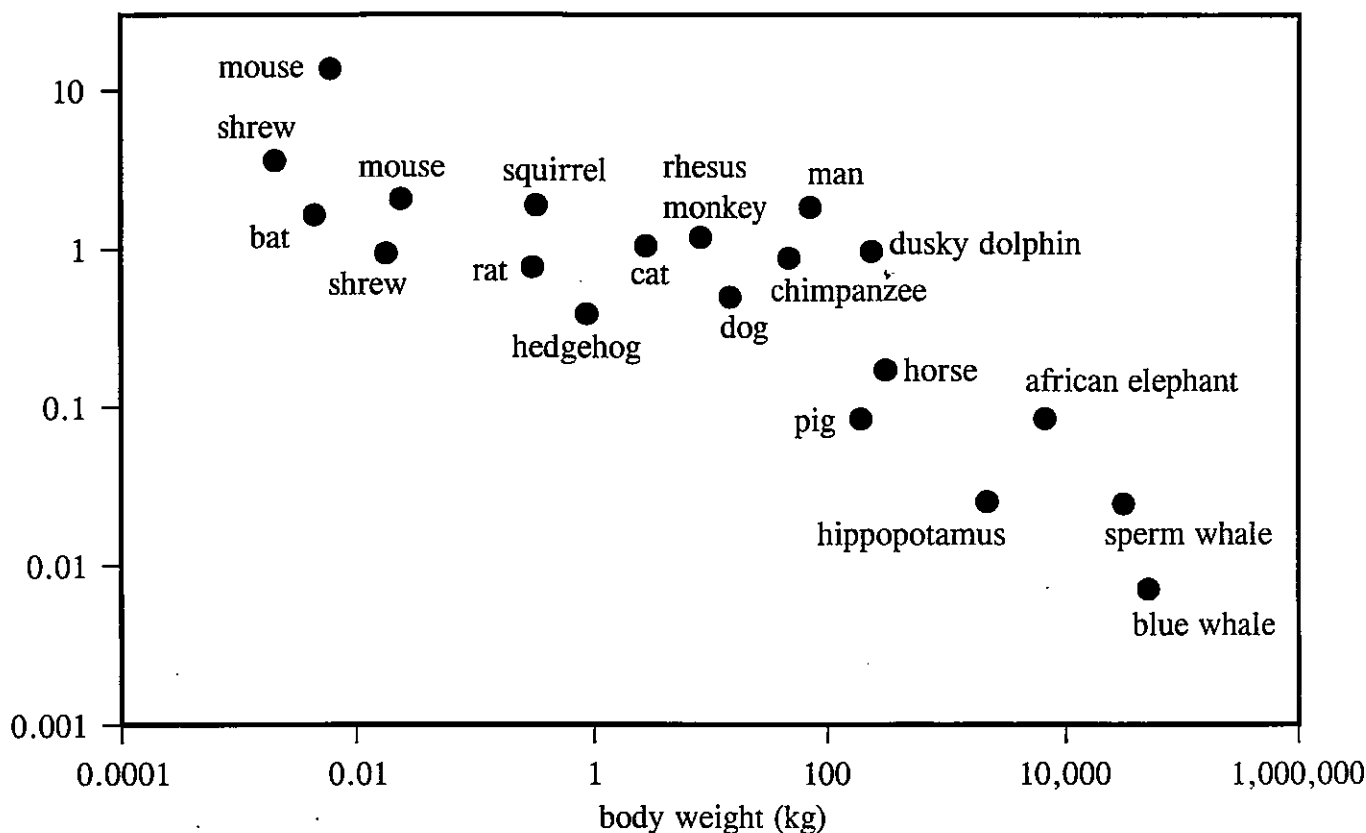
relative brain weight (percentage of body weight)

Fig. 23.2. Brain weight as a percentage of body weight for the same 20 mammals as in Fig. 23.1 (double-logarithmic graph). Small animals have large relative brain weights. (See Table 23.2 for the sources of the data)

oretical line between body weight and brain weight would be:

$$\alpha = 2/3$$

For 47 warm-blooded animals (22 mammals and 25 birds), Snell (1891) actually found a slope of 0.68, which he considered supported his theory. Jerison (1973) adopted this theory, implying that the true slope is 2/3. When larger samples of mammals were studied, however, the actual slope of the regression line was closer to 0.75 rather than 0.67. In a modification of the theory, Jerison (1988, 1994) argued

that in mammals the body surface is mapped to the neocortex, and that the neocortex is thicker in larger species. Maintaining the theory that body surface is mapped to cortical volume, and, after a correction for cortical thickness, Jerison concluded that the expected slope of a regression line for mammals would be about 0.78.

Table 23.1 shows the values of α for seven main groups of vertebrates. Most values range from 0.53 to 0.64, with a lower extreme of 0.21 (cyclostomes) and an upper extreme of 0.739 (mammals). Given this variation in the values of α, I am not really

Table 23.1. Allometric parameters for brain size of some main vertebrate groups. The values have been calculated with the linear regression function of EXCEL 5.0, based on the logarithmic values of body and brain weight (both in grams)

	Number of species	α (±SEM)	k	r^2	Variation in EQ (SD/average)
Cyclostomes	5	0.21 (±0.17)	0.0127	0.35	39%
Chondrichthyes	61	0.56 (±0.04)	0.0519	0.74	68%
Osteichthyes	878	0.639 (±0.009)	0.0104	0.85	52%
Amphibians	118	0.55 (±0.02)	0.0116	0.81	37%
Reptiles	74	0.53 (±0.02)	0.0179	0.91	43%
Birds	221	0.59 (±0.01)	0.1169	0.89	46%
Mammals	1174	0.739 (±0.005)	0.0626	0.96	55%

Table 23.2. Sources of the data used

Brain and body weight	
Vertebrates	Crile and Quiring 1940
Cyclostomes	Platel and Delfini 1981, 1986; Ebinger et al. 1983; Platel and Vesselkin 1989
Chondrichthyes	Bauchot et al. 1976; Myagkov 1991
Osteichthyes	Platel et al. 1977; Platel, personal communication
Teleosts	Ridet 1982; Bauchot et al. 1989a–c; Ridet and Beauchot 1990a
Amphibians	Thireau 1975; Bauchot et al. 1983; Taylor et al. 1995; Roth et al. 1995
Reptiles	Platel 1976, 1989
Birds	Lapicque and Girard 1905; Portmann 1947; Armstrong and Bergeron 1985; Rehkämper et al. 1991a,b
Mammals	Mangold-Wirz 1966
Monotremates	Pirlot and Nelson 1978
Marsupials	Elias and Schwartz 1969; Möller 1973; Eisenberg and Wilson 1981; Pirlot 1981
Cingulata	Röhrs 1966; Pohlenz-Kleffner 1969; Pirlot 1980; Pirlot and Kamiya 1983
Pilosa	Röhrs 1966; Pohlenz-Kleffner 1969; Pirlot 1980
Pholidota	Weber 1891; Elliot Smith 1898
Macroscelidea	Stephan et al. 1981
Lagomorpha	Mace et al. 1981
Rodents	Brummelkamp 1939; Pilleri 1959a–c; 1960a–c; Kretschmann 1966; Zepelin and Rechtschaffen 1974; Mace et al. 1981; Pirlot and Kamiya 1982; Meddis 1983; Hafner and Hafner 1984
Carnivores	Thiede 1966; Bronson 1979; Sheppey and Bernard 1984; Gittleman 1986; Kruska 1988
Pinnipedia	Worthy and Hickie 1986; Robin 1973
Tenrecomorpha	Bauchot and Stephan 1966; Stephan et al. 1981, 1990
Insectivores	Bauchot and Stephan 1966; Mace et al. 1981; Stephan et al. 1981, 1990
Scandentia	Stephan et al. 1981
Dermoptera	Pirlot and Kamiya 1982
Bats	Pirlot and Stephan 1970; Eisenberg and Wilson 1978; Stephan et al. 1974, 1981; Jürgens and Prothero 1987; Bhatnagar et al. 1990; Eisenberg, personal communication
Primates	Von Bonin 1937; Bauchot and Stephan 1966; Stephan et al. 1977, 1981; Hofman 1983; Armstrong 1985; Harvey and Clutton-Brock 1985
Tubulidentata	Pirlot and Kamiya 1983
Artiodactyles	Oboussier 1966; 1972; Haarmann and Oboussier 1972; Ronnefeld 1970; Kruska 1973; Haarmann 1975
Whales	Worthy and Hickie 1986; Gihr and Pilleri 1969; Kraus and Pilleri 1969; Pilleri and Gihr 1970
Perissodactyles	Kruska 1973
Hyracoidea	Meddis 1983
Elephants	Jerison 1973
Sirens	Worthy and Hickie 1986; Pirlot and Kamiya 1985; Reep et al. 1989; Reep and O'Shea 1990
Fossil vertebrates	Jerison 1969; 1973; Russell 1972; Radinsky 1981; Kruska 1982
Fossil hominids	Holloway 1983; Leigh 1992
Metabolic rates	McNab 1969, 1988; Eisenberg 1981; Bartels 1982; Hayssen and Lacy 1985;
Longevity	Crandall 1964; Jones 1979; Eisenberg 1981; Jürgens and Prothero 1987;
Ecology and diet	
Fishes	Bauchot et al. 1989a–c
Birds	Portmann 1947; Bennett and Harvey 1985a,b
Mammals	Eisenberg and Wilson 1978; Clutton-Brock and Harvey 1980; Mace et al. 1981; Stephan et al. 1981; Smuts et al. 1987

inclined to adhere to (or to develop) a general theory on the relationship between body weight and brain weight.

23.1.3
Inherent Problems with Allometric Analyses

For this chapter, a database of 1174 mammalian species has been constructed, but the various orders have different absolute and relative contributions to the database: for the Proboscidea (elephants) and Tubulidentata (aardvark), 100 % of the species are represented, for the primates 65 %, and for the rodents only 10 %. Even if we had a database for all the mammalian species for regression analysis, some fundamental – and insoluble – problems would remain.

First, from a statistical point of view, data points from species cannot be treated as independent (Harvey and Krebs 1990); neither can genera or families be regarded as independent. In my database of 1174 mammalian species, the rodents are represented by 267 species, the bats by 315 species, but for the orders Pholidota (pangolins), Dermoptera (flying lemur) and Tubulidentata (aardvark) there is only 1 species. Rodents and bats therefore contribute disproportionately to the slope and intercept of the mammalian regression line.

A second, insoluble, problem is the choice of reference group. The steepness of the regression line depends on the taxonomic level (Bennett and Harvey 1985). Suppose we are interested in the brain weights of wolves and races of dogs. Which regression line is the 'correct' reference line: that of mammals, carnivores, Canidae or races of dogs? The slopes of these regression lines differ considerably; so the choice of reference line has great influence on the EQ values.

23.1.3.1
Allometry in This Chapter

We must conclude that allometric analyses do not give straightforward evaluations of brain sizes of species with different body sizes. I do not want to enter into a discussion here on allometry of brain size. Therefore, allometric analyses will receive little mention. For the various groups, as far as possible the original body weight and brain weight data will be shown. Only when the relevance of various ecological factors has been evaluated will a combination of allometric and correlation analyses be used (see 'Appendix'); in these cases, the allometric analyses of brain weight and ecological factors will be performed on the same group of species, all of which contribute to the brain and ecological data.

23.1.4
r- and K-Selection: Body and Brain Size

Two general strategies in evolutionary biology may be relevant for the evolution of brain size. What is the optimum strategy for an animal to increase its inclusive reproductive success (a combination of inclusive fitness and reproductive success): investment primarily in the production of many offspring, or investment primarily in the increased fitness of a smaller number of offspring? The optimum strategy depends on the circumstances (MacArthur and Wilson 1967; Wilson 1975). When a region has a population density far below its carrying capacity, then an animal producing more offspring than its competitors will probably have a higher inclusive reproductive success. For a population in an unpredictable environment, producing large numbers of offspring is usually an effective strategy. For a population in a fairly stable region at a density close to the region's carrying capacity, investing in a small number of descendants to increase their fitness is often a better strategy than producing many descendants, and investing less in them after birth or after hatching.

Selection favouring investment in a large number of offspring is called 'r-selection' (derived from the parameter r, denoting the intrinsic rate of natural increase). Selection where investment in a small number of descendants to increase their fitness is more effective is called 'K-selection' (K denotes the carrying capacity). r- and K-selection are relevant for brain evolution, because they favour different traits. K-selection favours slower development, larger body size, longer life, more reproductive episodes, smaller litter size, lifetime production of fewer descendants and greater investment in individual descendants (Pianka 1970; Eisenberg 1981). Prolonged K-selection promotes greater longevity, slower development and a longer period for adult-offspring interactions; this provides the opportunity for a longer learning period. A prolonged history of r-selection leads to reduced longevity, rapid development, rapid sexual maturity and fewer reproductive episodes. There is, therefore, less time for learning, and consequently the necessity for genetic programming of several behavioural programs.

23.1.5
Selection for Large Bodies or Large Brains?

Body size is the single most important factor influencing brain size. Large animals have larger brains, but in general these larger brains do not contain larger neurons (for mammals see Haug 1987; for salamanders see Roth et al. 1995). As a consequence, large animals have more neurons, and – theoretically – a larger information-processing capacity, since information capacity is strictly coupled to the number of neurons. A theory on the evolution of brain size should be based on two more independent selection pressures: the selection pressure on body size and that on brain size (or number of neurons).

23.1.5.1
Selection Pressure in Favour of a Large Body

Selection pressure in favour of a large body is present when physical strength has a net positive influence on fitness. Also, for another reason, homeothermic animals with large bodies have an advantage: thanks to a smaller volume to surface ratio they lose proportionally less energy (although larger animals, of course, need a large absolute amount of food.) K-selection often promotes the increase in body size.
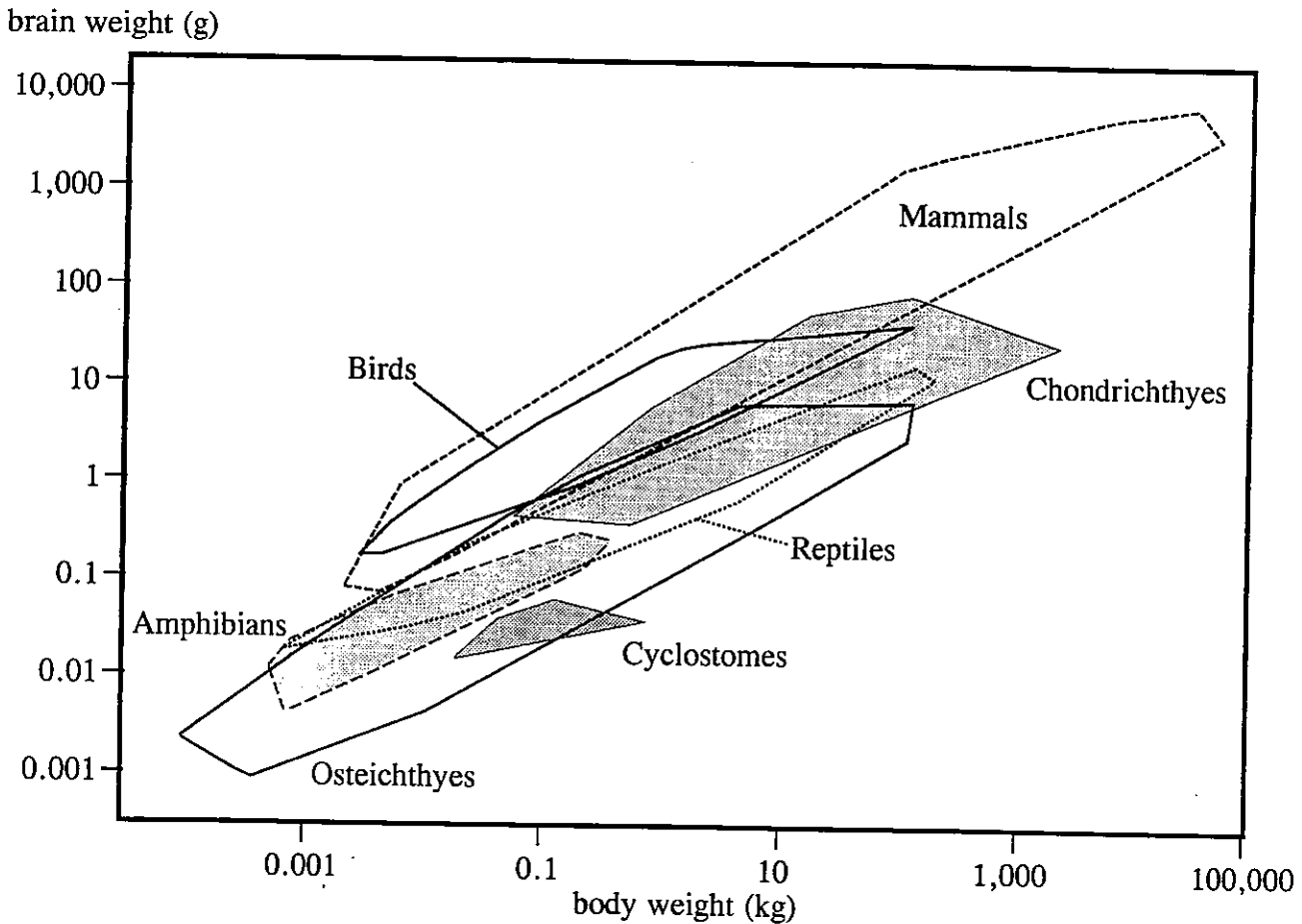
brain weight (g)

Fig. 23.3. Convex polygons for brain sizes of the main vertebrate groups

23.1.5.2
Selection Pressure in Favour of a Small Body

In general, r-selection is consistent with selection in favour of a small body size. Moreover, in flying, burrowing and arboreal vertebrates, selection pressure is active in keeping (or making) body weights low. Homeothermic vertebrates cannot become very small. Small homeothermic animals have a distinct problem. Their small bodies can contain only small energy stores (fat, glycogen), while they have a high metabolic rate (oxygen consumed per gram body weight); small mammals and birds are in constant danger of starvation if they cannot take food every few hours (Lindstedt and Boyce 1985). Small homeothermic animals consume much more energy per gram body weight than large ones. It has been suggested that the maximum attainable cellular metabolic rate for a homeothermic vertebrate is associated with a body weight of about 2 g (Dobson and Headrick 1995). The smallest adult birds and mammals weigh about 2 g. The smallest fishes, amphibians and reptiles are considerably smaller; the smallest fish (Pandaka) weighs about 0.1 g. During the process of minaturisation, strategies must

be used to preserve a sufficient neural information-processing capacity. In miniaturised salamanders, the strategies actually used are: obtaining larger EQs, obtaining more densely packed neurons and/ or obtaining smaller neurons (Roth et al. 1995).

23.1.5.3
Selection Pressure in Favour of a Large Brain

Theoretically, a brain containing more neurons has a larger information-processing capacity. It is often assumed that selection in favour of intelligence promotes an enlargement of the brain (Jerison 1973). Such a relationship between brain size and intelligence has not been demonstrated in a comparative study on animals, since no fair comparison of intelligence or learning capacity has been made between species. It is conceivable that such a comparison cannot be made fairly. In various groups, different parts of the brain have become enlarged (Barton et al. 1995; see also Chap. 22). Brain enlargement can be a consequence of selection pressures in favour of some sensory or motor systems, or in favour of intelligence
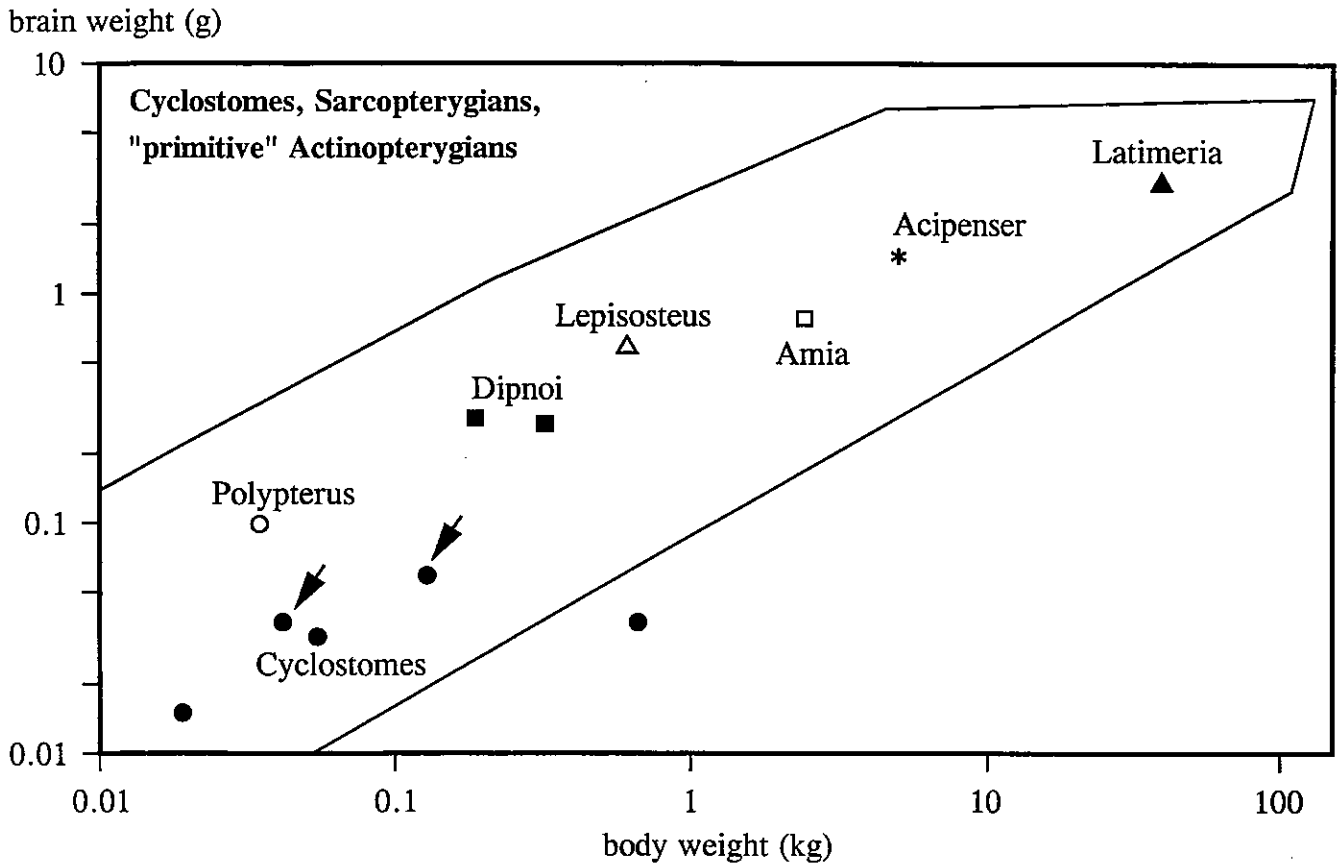
Fig. 23.4. Relationship between body weight and brain weight for cyclostomes (hagfishes marked by *arrows*), sarcopterygians and 'primitive' actinopterigians, in a double-logarithmic graph. Part of the convex polygon of the teleosts is also shown

23.1.5.4
Selection Pressure in Favour of a Small Brain

Few theories have been formulated for selection in favour of a proportionally small brain. (a) A strong selection pressure in favour of a small body mass in general might also reduce EQ (as suggested for insectivore bats, Eisenberg and Wilson 1978). (b) The brain is a rather energy-consuming organ; a strong selection pressure in favour of energy conservation would also keep (or make) brain mass small [as suggested for diving mammals (Robin 1973) and insect-eating bats, see below]. (c) r-Selection is suggested to reduce brain size. As far as I know, there are only two reliable examples of an actual reduction of the EQ: parasitic worms and domestic animals (Kruska 1988).

In many instances, the regression lines between body size and brain size for more related species are less steep than those for less related species. "One interpretation of this phenomenon is that body size responds more readily to selection over evolutionary time, and that changes in brain size lag somewhat behind" (Bennett and Harvey 1985a,b). As a consequence, selection in favour of a small body usually promotes the evolution of larger EQs, and vice versa.

23.2
Origin of the Chordate Brain

A characteristic feature of all chordates is the presence of a single dorsal nerve cord. The most 'primitive' chordates, the cephalochordates, have a rostral differentiation of their nerve cord, but very little or no brain enlargement (Chap. 9). Adult tunicates do not have a real brain, but a small brain is present in their larvae. Therefore it is assumed that the first rostral enlargement of the spinal cord (brain formation) occurred in the ancestors of the tunicates and vertebrates. In the most 'primitive' vertebrates, the cyclostomes (lampreys and hagfishes), a rather small, but well-differentiated brain is present. A survey of the brain weights in vertebrates is presented in Fig. 23.3, where the convex polygons of the main groups are shown in one figure.
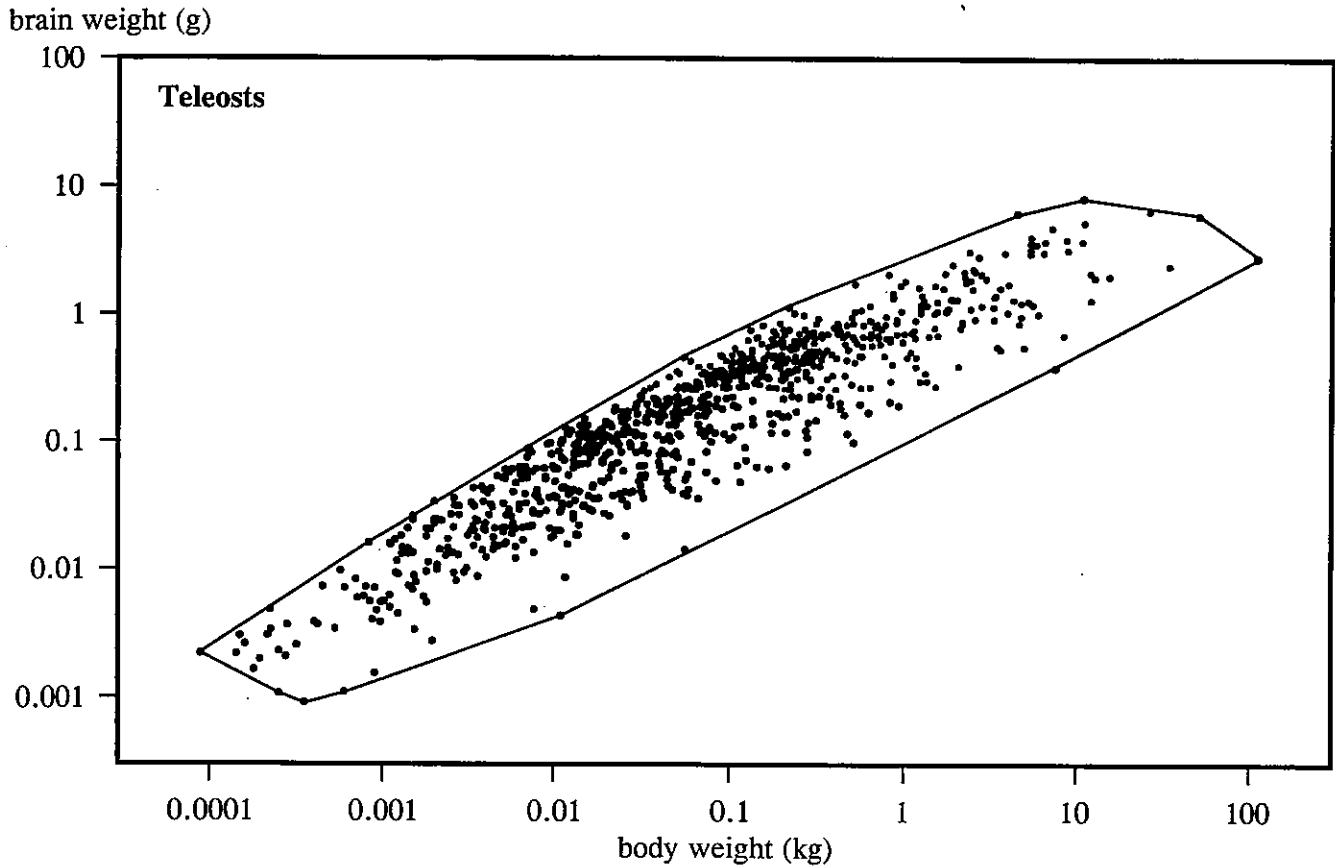
brain weight (g)

Fig. 23.5. Relationship between body weight and brain weight for teleosts, in a double-logarithmic graph. (This convex polygon for teleosts is preliminary, since data on the largest teleosts are not available.) (Based mainly on data by Ridet 1982 and Bauchot et al. 1989a-c)

23.3
Agnathans and Jawed Fishes

23.3.1
Cyclostomes

The brain of the cyclostomes is the most 'primitive' brain found in the vertebrates (see Chap. 10). Figure 23.4 surveys body and brain weights of the cyclostomes. To facilitate comparison, the convex polygon of the teleosts is also shown. The brains of adult cyclostomes range from 15 to 60 mg (Platel and Delfini 1981, 1986; Ebinger et al. 1983; Platel and Vesselkin 1989). The hagfishes (*Myxine*) have somewhat larger brains than the lampreys. The brains of the cyclostomes are small, but they are by no means the smallest chordate brains; these are only 1 mg in weight (about 1 mm^3 in a teleost fish, *Kraemeria*, Bauchot et al. 1989a,b). When cyclostome brains are compared with the brains of teleosts, the cyclostomes occupy the lower part of the teleosts' convex polygon (Fig. 23.4). This lower part of the convex polygon is occupied by only a few (eel-shaped) teleost species (cf. Fig. 23.5). Therefore the cyclostomes' brain is considerably smaller

(often by a factor of 6–10) than that of most bony fishes of their size. Lampreys and hagfishes have elongated bodies, and we will see below that animals with elongated bodies often have proportionally small brains.

23.3.2
Jawed Fishes

The two main groups of jawed fishes are the cartilaginous fishes (Chondrichthyes) with several hundreds of species, and the bony fishes (Osteichthyes) with over 30 000 species. The bony fishes again comprise two main groups: those with ray fins (the Actinopterygii, about 30 000 species), and those with lobe fins (Sarcopterygii, with 7 species). The group of Actinopterygii consists of some 'primitive' groups with a small number of species (see below) and a very large group of 'advanced' species, the Teleostei.
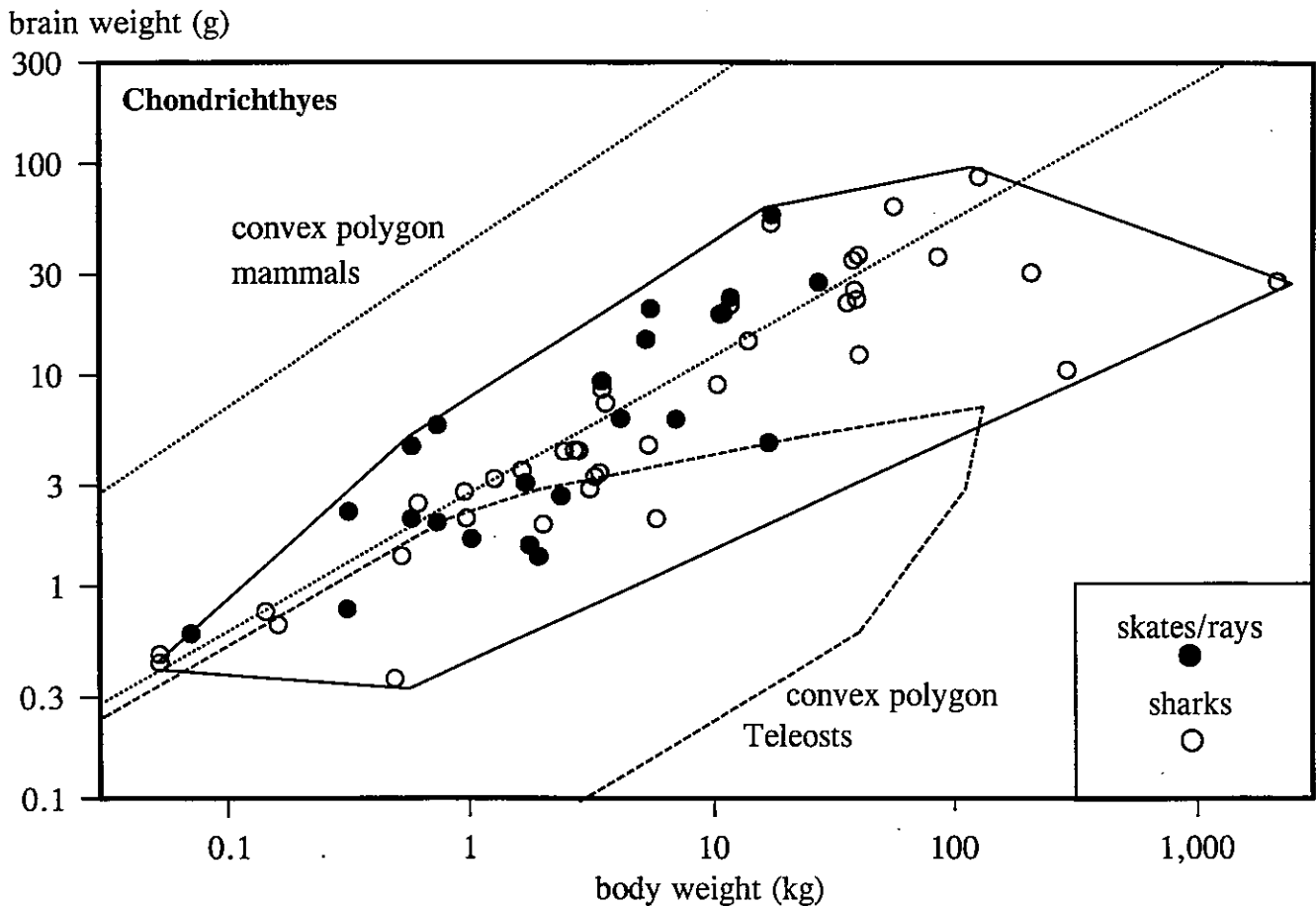
Fig. 23.6. Relationship between body weight and brain weight for Chondrichthyes, in a double-logarithmic graph. Note the large brains of the sharks and rays. (This convex polygon for Chondrichthyes is preliminary, since data on the largest Chondrichthyes not available.) For comparison the convex polygons for teleosts and mammals are also shown

23.3.2.1
Osteichthyes

23.3.2.1.1
'Primitive' Actinopterygii

Among the Actinopterygii, some groups are regarded as primitive: Polypterini (4 species), sturgeons (Acipenseroidei, 25 species) and Holostei (11 species, *Lepisosteus, Amia*). These 'primitive' bony fishes have brain weights within the range of the teleosts and above the values found in cyclostomes (Platel et al. 1977, Fig. 23.4). Therefore, it is assumed that the brain enlargement from cyclostomes to fish occurred early in fish evolution, i.e. around the Ordovician, some 450 million years ago.

23.3.2.1.2
'Advanced' Bony Fishes

Teleosts comprise some 30 000 species. Investigators in Bauchot's group have performed systematic comparative studies on teleost brains (Ridet 1982;

Bauchot et al. 1989a,b,c). Figure 23.5 is based mainly on data from Bauchot's group. Some conclusions from the comparative studies on hundreds of teleost species by this group will be mentioned here. Within the group of teleosts, some orders are considered primitive (for instance eels and herrings) and others advanced (mackerels and flatfishes). However, brain size is hardly related to the degree of advancement as established by other criteria.

Elongated fishes (such as eels) have small brains for their body weight. This point will be commented on during the discussion on snakes below. Some fishes have a passive defence against predators, using thick scales or spines, protective colouring, burrowing into the ground, retreating into burrows, or skin toxins. Such fishes often have proportionally small brains. Fishes with more than one highly developed sensory system often have proportionally large brains.
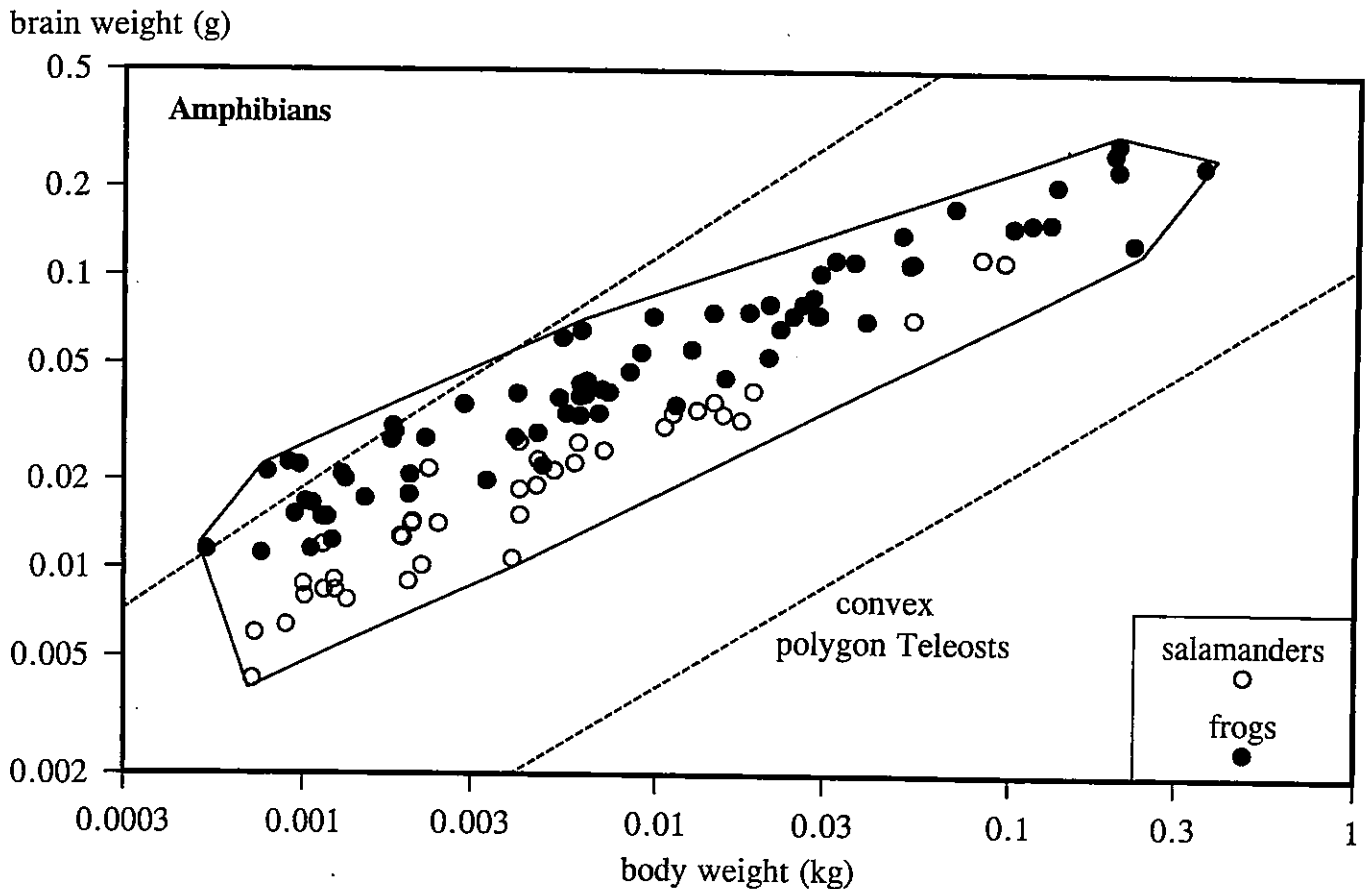
brain weight (g)

Fig. 23.7. Relationship between body weight and brain weight for amphibians, in a double-logarithmic graph. Salamanders have smaller brains than frogs. (This convex polygon for amphibians is preliminary, since data on the smallest and largest amphibians are not available.) For comparison the convex polygon for teleosts is also shown. (See Table 23.2 for the sources of the data)

23.3.2.1.3
Sarcopterygii

The Sarcopterygii deserve special interest, because they are related to the ancestors of the amphibians (and consequently of the reptiles, birds and mammals). Two orders are present: the Dipnoi (lung-fishes with six species) and the Crossopterygii (with one living species, the coelacanth, *Latimeria*). With respect to brain size, the Sarcopterygii fall within the range of the teleosts (Fig. 23.4).

23.3.2.2
Chondrichthyes

Chondrichthyes (sharks and rays) are conspicuous by their large brains (Bauchot et al. 1976; Northcutt 1989; Myagkov 1991). Most species have considerably larger brains than the bony fishes in their weight class: the difference is up to a factor of 10 (Fig. 23.6). The brain weights of several Chondrichthyes lie within the mammalian range. Sharks and rays have about the same brain size, with a rela-

tively large telencephalon (Chap. 23.12). In these respects, their brains are 'advanced'. What can sharks and rays do better thanks to their advanced brains? They have well-developed sensory systems, but so do several bony fishes. Extensive comparative behavioural studies in fishes and sharks have not yet been carried out. Compared to other fishes, the Chondrichthyes have a very small number of offspring; in this respect they are a clear example of *K*-selection.

23.4
Amphibians

Only a small number of studies have been devoted to the comparative study of brain size in amphibians (Thireau 1975; Bauchot et al. 1983; Roth et al. 1995; Taylor et al. 1995). The brain weights of the amphibians fall within the range of the teleost fishes (Fig. 23.7). Within the class of amphibians, frogs (*Anura*) have larger brains than the salamanders (*Urodela*); the average difference is almost a factor of 2. Within the frogs, the arboreal species
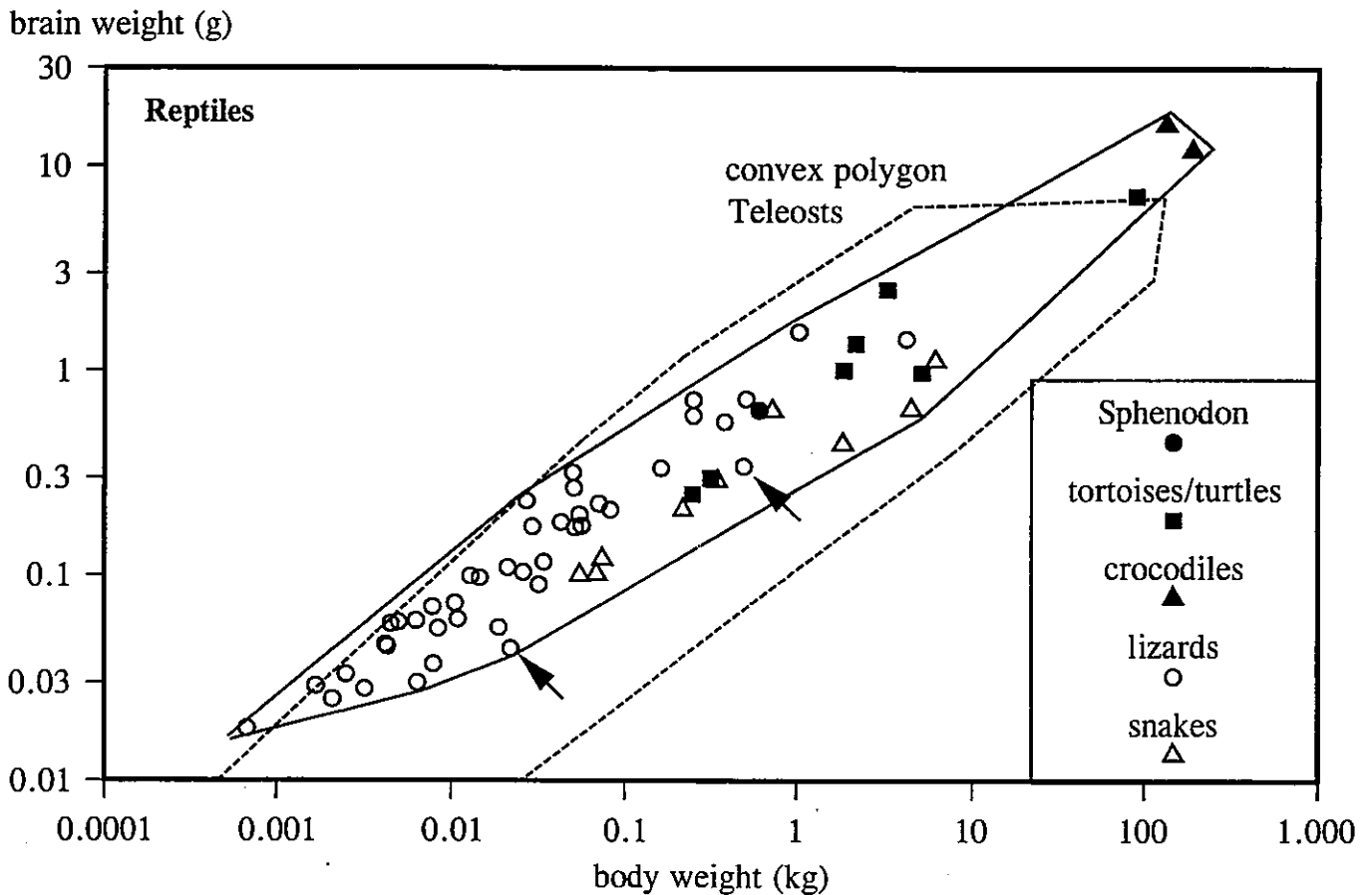
brain weight (g)

Fig. 23.8. Relationship between body weight and brain weight for living reptiles, in a double-logarithmic graph. Note the small brains of tortoises, turtles, snakes and slowworms (slowworms marked by *arrows*). For comparison the convex polygon for teleosts is also shown. (The convex polygon for reptiles is preliminary, since data on the largest reptiles are not available.) (See Table 23.2 for the sources of the data)

have larger brains than the terrestrial species (Bau-chot et al. 1983; Taylor et al. 1995). Arboreal frogs have slightly larger cerebella than frogs from other habitats. In fossorial frogs, olfactory and auditory structures are enlarged, while visual structures are diminished. Special attention has been paid to miniaturisation in a group of salamanders (pletho-dontid salamanders, Roth et al. 1995). During the process of body and brain miniaturisation, the most rigorous solution for preserving information capacity (and cell numbers) would be reduction of cell size. However, cell size depends strongly on genome size (Roth et al. 1995). Among the verte-brates, salamanders have large genomes. Genome size and cell size has been reduced in only a few species, but this has occurred in miniaturised and non-minaturised species (Roth et al. 1995). Why do salamanders have smaller brains than frogs? Most salamanders in Fig. 23.7 are aquatic species, but the aquatic salamanders have smaller brains than the aquatic frogs. So the small brains of salamanders cannot be explained by their habitat. Salamanders are elongated amphibians; in general, elongated

animals tend to have proportionally small brains. This probably applies too for salamanders.

23.5
Reptiles

23.5.1
Recent Reptiles

Reptiles have brain weights in the same range as teleost fishes (Fig. 23.8, Platel 1976, 1989). The low-est values for brain weights corrected for body weights are found in the Chelonia (tortoises and turtles) and the snakes; lizards of the same body weight have brain weights about twice as large. The small brains of the Chelonia are unremarkable, since these reptiles are regarded as 'primitive': the real Chelonia lived 220 million years ago. Chelonia have a simple locomotion, and a passive protection against predators, which often goes together with low brain weight. However, another 'primitive' reptile, *Sphenodon*, has a brain weight close to the average for reptiles. The low brain weights of snakes
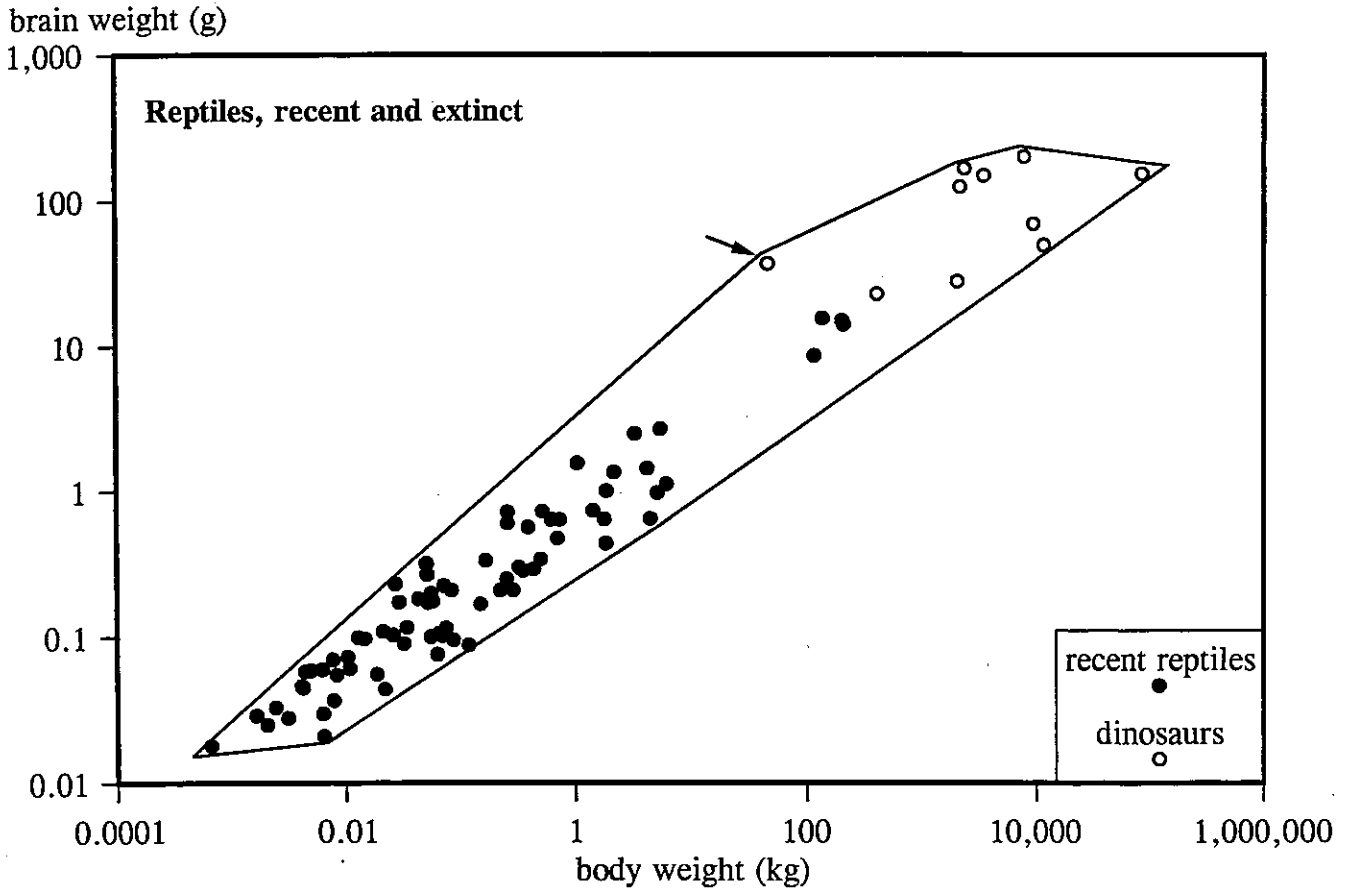
brain weight (g)

Fig. 23.9. Relationship between body weight and brain weight for living reptiles and dinosaurs, in a double-logarithmic graph, where the estimated brain volume is supposed to be half of the cranial capacity). *Arrow* points to *Stenonychosaurus*, an ostrich-like dinosaur with a large brain. (Data on dinosaurs from Jerison 1973)

are remarkable, because snakes are advanced animals with a sometimes complicated locomotion and specialised sensory systems. Snakes are characterised by an elongated body. The lizards with the smallest brain weights are the slowworms (Anguidae), elongated, legless lizards which the layman sometimes mixes up with snakes.

Apparently, it is a general trait that elongated animals (lampreys, eels, salamanders, snakes, slowworms) have small brain weights for their body weights. Do elongated animals have small brains or large bodies? Given their locomotion, selection pressure in favour of long bodies is plausible. Therefore: snakes, slowworms, salamanders, eels, lampreys and hagfishes have long (and consequently heavier) bodies rather than small brains.

23.5.2
Dinosaurs

Several skulls of dinosaurs have been preserved so well that the cranial cavity is still intact or can be reconstructed. The volume of the cranial cavity (or of the endocast) is the maximum volume the brain

could have. *Tyrannosaurus* with a body weight of 7.7 metric tons had a cranial cavity of 400 cm³, and *Brachiosaurus* weighing 87 metric tons had a cranial cavity of about 300 cm³. This compares with brain weights between 5 and 10 kg for elephants and large whales. Consequently, dinosaurs have been thought of as extremely small-brained – 'stupid' – animals. The dinosaur brain size could even be smaller, since in several reptiles the brain occupies only a proportion of the cranial cavity (for references see Hopson 1979). For that reason, the brain volume cannot be directly deduced from the endocast. To deal with dinosaurs' brain size despite these limitations, the best Jerison (1969, 1973) could do was to assume that the brain volume was half of the cranial cavity. Another problem with the encephalisation of extinct animals is the estimation of their body size. In some instances, the body weight and brain weight were estimated from remains of different individuals, or even different species (Hopson 1979). Nevertheless, after a careful study of dinosaur endocasts, several conclusions could be drawn about dinosaur brain size and shape (Hopson 1979). Allometric analysis demon-
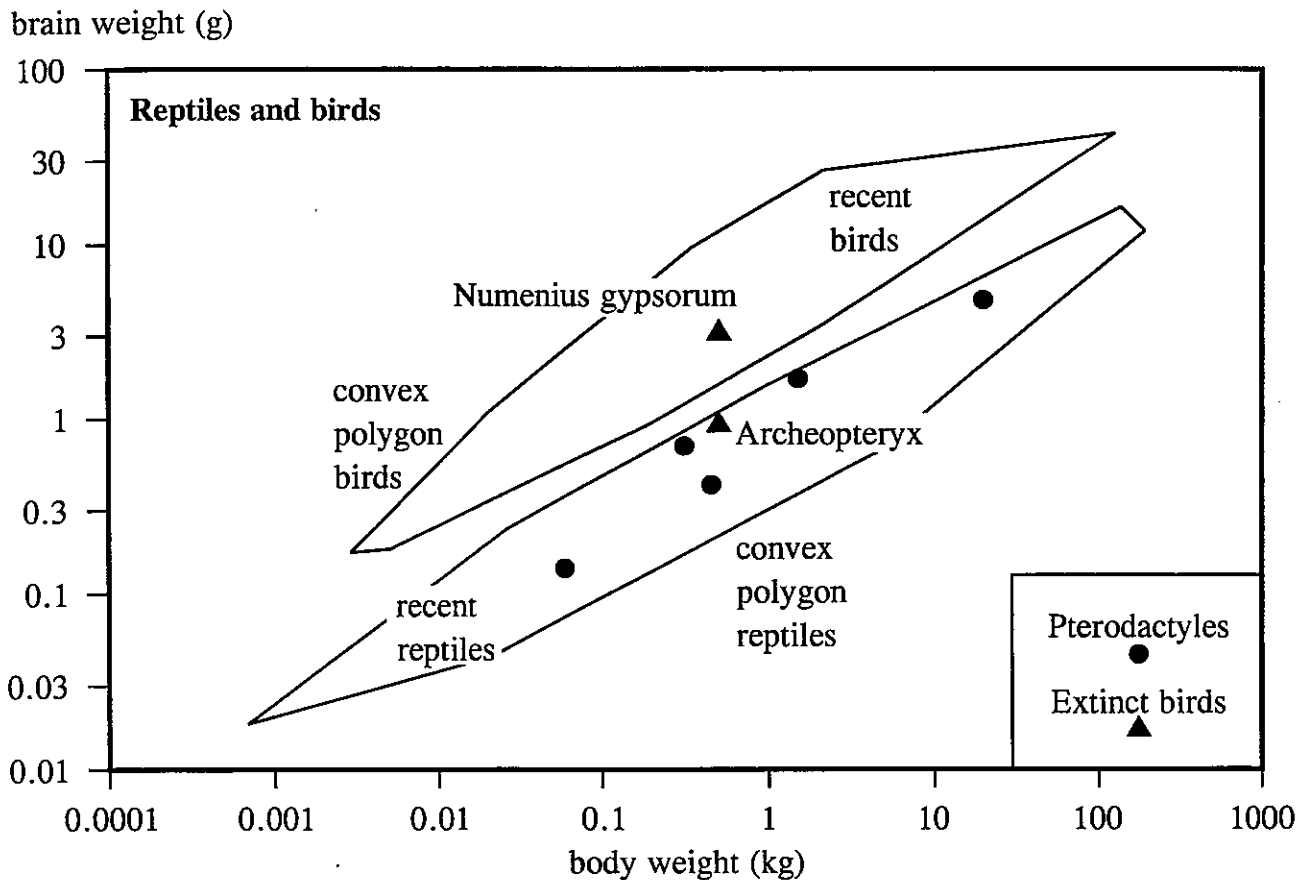
brain weight (g)

Fig. 23.10. Evolution of brain size in birds. For comparison the convex polygons of living reptiles and birds are shown, and some data points of pterodactyls and extinct birds. Birds have larger brains than reptiles. (See Table 23.2 for the sources of the data)

strated that most dinosaur brains are within the normal range – for reptilian brains (Fig. 23.9, Jerison 1973, Hopson 1979). Some small ostrich-like, carnivorous dinosaurs (*Stenonychosaurus* and *Dromiceiominus*) appeared to have remarkably large brains – for reptiles: their brains fall into the range of birds' brains (Russell 1972). Dinosaurs with body weights similar to those of the crocodiles have cranial capacities similar to those of the crocodiles. It has been suggested that carnivorous dinosaurs would have had larger brains than herbivorous ones, but this has been questioned (Hopson 1979).

23.6
Birds

23.6.1
Evolution of Brain Size in Birds

In general, birds have brain weights 6–10 times larger than reptiles of similar body weight (Fig. 23.10, Portmann 1947; Armstrong 1985; Rehkämper et al. 1991a,b). One might suppose that these larger brains are necessary for a well-coordinated flight. But the extinct flying reptiles, the

pterodactyls, have cranial capacities within the reptilian range (Fig. 23.10). Apparently a large brain is not absolutely necessary for flying (as flying insects have already demonstrated). The ancient fossil bird, *Archaeopteryx*, from the late Jurassic (some 150 million years ago), already had a brain weight in the lower range for birds (Fig. 23.10). A fossil bird from the upper Eocene (about 40 million years ago), *Numenius gypsorum*, had a larger brain within the range for birds (Jerison 1973). In the evolution of the birds, a strong degree of brain enlargement probably occurred before the late Eocene.

23.6.2
Brain Weights in Various Bird Orders

The relationship between body weight and brain weight for birds is shown in Fig. 23.11. The smallest hummingbirds have brains of only 0.17 g. The largest living bird, the ostrich, has the largest brain: 42 g. Within the class of birds, considerable variation in brain weight is found. Proportionally the smallest brains are found in the chicken-like birds (Galliformes) (Fig. 23.11b); this is not primarily due to domestication, since small brain weights are also

found in non-domesticated Galliformes. Also pigeons (Columbiformes) have small brains (Fig. 23.11a). Corrected for body weight, the largest brain weights in birds are found in the perching birds (Passeriformes), woodpeckers (Piciformes) and parrots (Psittaciformes, Fig. 23.11). The birds of prey (Falconidae) have rather large brains (Fig. 23.11b), but not as large as the perching birds. Owls (Strigiformes) have somewhat larger brains than the birds of prey (Fig. 23.11b). The ostrich has the largest absolute brain weight in the birds (Fig. 23.11a), but its brain weight lies considerably below the regression line for birds in general.

23.6.3
Brain Size and Ecology in Birds

In birds, brain size is associated with various ecological aspects (Bennett and Harvey 1985a). Three aspects were statistically significantly associated with overall brain size in two-way analyses of variance: neonatal development, mating system and mode of prey capture. However, some other aspects that were significant in a one-way analysis of variance will still be mentioned.

23.6.3.1
Neonatal Development

It has long been known that bird brain size is strongly associated with neonatal development (Portmann 1947, Fig. 23.12). Other studies have corroborated this finding (Bennett and Harvey 1985a,b). Immediately after hatching, some birds (for instance newborn chickens) have feathers, leave the nest, walk around and gather all their food themselves (precocial birds). At the other extreme, newborn perching birds are naked and absolutely helpless (altricial birds). Adults of altricial bird species have brain weights 1.5–2 times as large as those of adult precocial birds of the same body weight. This difference is found over various orders of birds. Can we explain this difference? *Precocial birds* are a product of *r*-selection. They invest a lot of energy in the eggs, i.e in their offspring before hatching. *Altricial birds* invest much in their offspring after hatching: in feeding and protecting them. They are a product of *K*-selection.

A clear difference in pre- and post-hatching brain growth is present between precocial and altricial birds. Precocial birds have a larger pre-hatching brain growth and development, while altricial birds have a larger post-hatching brain growth and development (Bennett and Harvey 1985a,b). There is reason to believe that the primitive situation was: precocial offspring with relatively less patental invest-

ment after hatching. Why did then altricial birds develop larger brains? It is difficult to identify cause and effect. Did an increase in parental investment promote inclusive reproductive success, and was a larger brain needed for better parental investment? Or did the increased parental investment enable a larger post-hatching brain growth and development? To my mind this is still an open question.

23.6.3.2
Mating System

Monogamous birds have larger brains than polygamous species (Bennett and Harvey 1985a). This association remained significant in the two-way analysis of variance, which implies that it is not due to other confounders (such as neonatal development). Almost all species with altricial offspring have a monogamous mating system, but the mating system still seems to be a relevant factor on its own.

23.6.3.3
Stratification and Habitat

Arboreal birds tend to have larger brains than terrestrial and water birds. Birds living in forest or woodland tend to have larger brains than those living in grassland, marshland or water (Bennett and Harvey 1985a).

23.6.3.4
Diet

Birds use a great variety of food: leaves, fruit, nectar, insects, fish, other birds, mammals or carrion. As regards brain size, two aspects are remarkable (Bennett and Harvey 1985a). Birds that feed on other birds or mammals have rather large brains. On the other hand, birds that feed on plants, without specialising on leaves or fruit, have rather small brains.

23.6.3.5
Migration

One would have expected that migratory birds would need rather large brains for orientation, but, remarkably, migration has not been associated with brain size (Bennett and Harvey 1985a). Pigeons, for instance, have rather small brains.
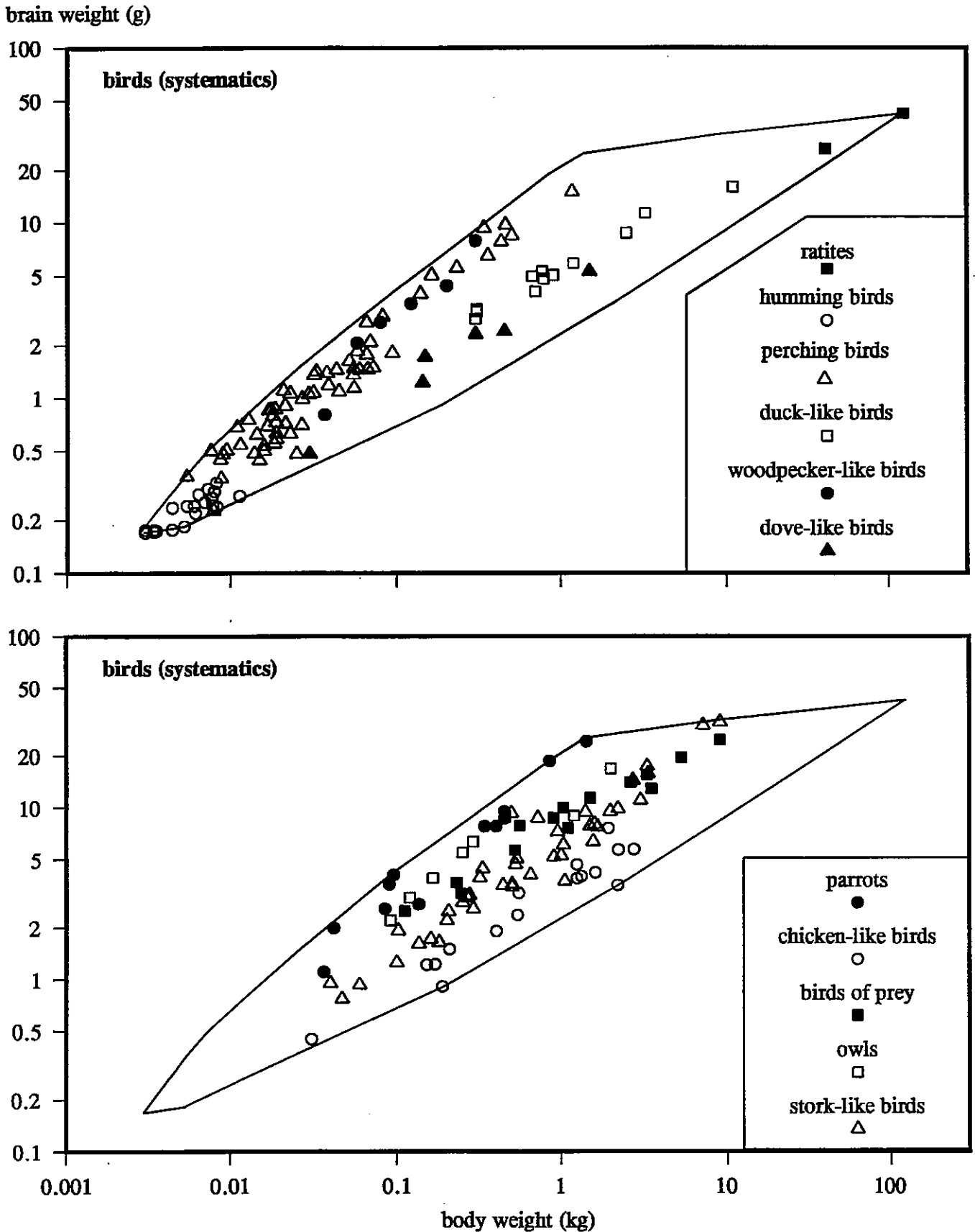
Fig. 23.11a,b. Relationship between body weight and brain weight for various orders of birds, in a double-logarithmic graph. Note the small brains of the gallinaceous birds and pigeons, and the large brains of the perching birds, parrots and woodpeckers. Note also the remarkable position of the ostrich. (See Table 23.2 for the sources of the data; for the classification of birds, the system of Sibley and Ahlquist 1990 is followed)

brain weight (g)

birds (precociality at birth)

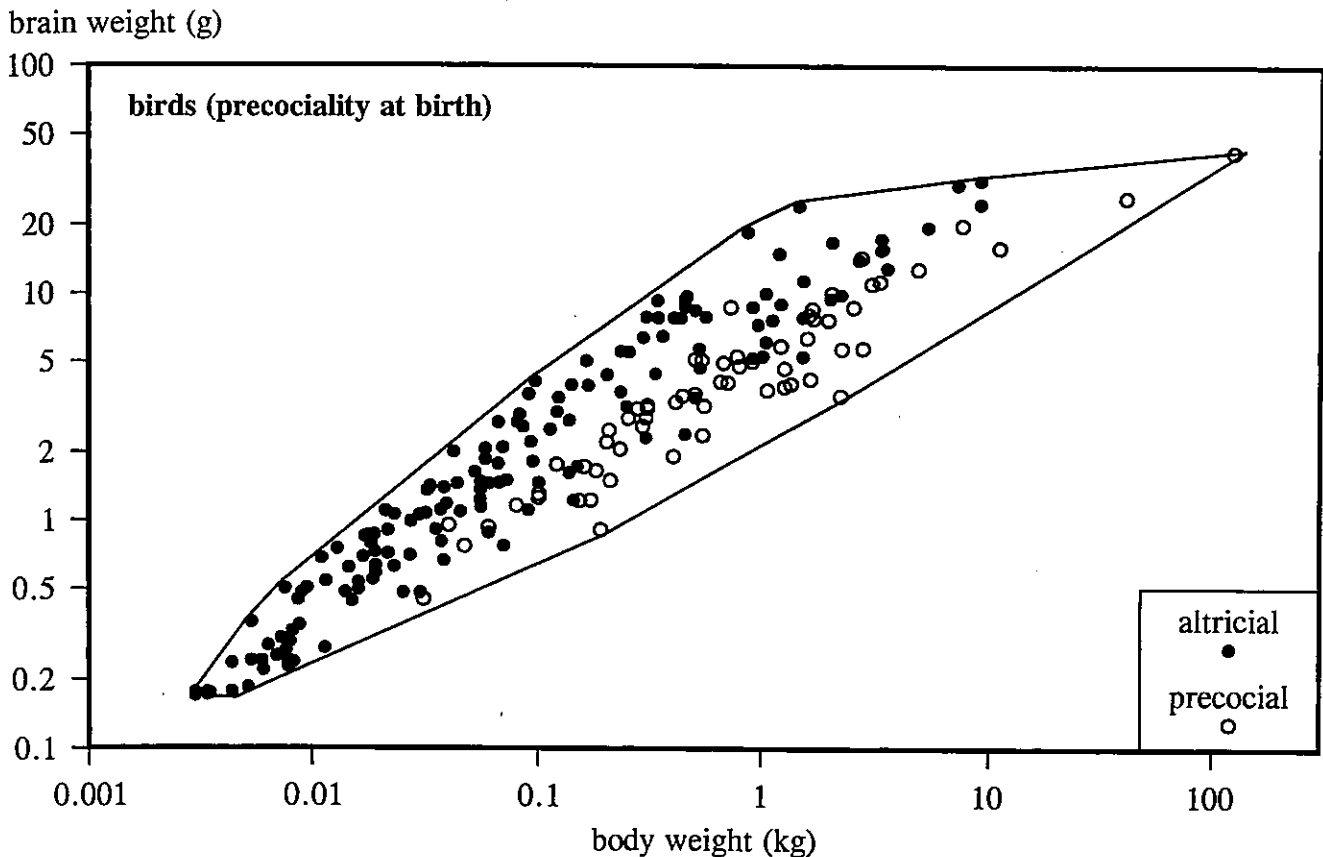altricial
●

precocial
○

body weight (kg)

Fig. 23.12. Relationship between body weight and brain weight for birds coded for their neonatal development, in a double-logarithmic graph. Note the small brains of the preco-
cial birds, and the large brains of the altricial birds. (See Table 23.2 for the sources of the data)

23.7
Mammals

Figure 23.13 is a cladogram of several orders of mammals, mainly based on the figure by Novacek (1992). The mammals comprise about 5000 species; they are divided into the following main groups:

1. The 'primitive', egg-laying monotremes with only six species
2. The more advanced, viviparous Theria, which comprise almost all mammals. The Theria are again subdivided into two main groups:
   a) The 'primitive' marsupials without placenta, with about 240 species
   b) The more advanced, placental Eutheria with over 4500 species

23.7.1
The Brain in Extinct Mammals

Overall, mammals have brain weights a factor of 10 higher than reptiles of similar body weights (Fig. 23.14). For many extinct mammals belonging to various orders, data are available on brain size,

so we can trace more or less the evolution of mammalian brain size. Most mammal-like reptiles (Permian and Triassic, 290–210 million years ago) had brain weights within the reptilian range, so the increase in brain size in the mammalian evolution started later. The mammals from the Cretaceous, Paleocene and Eocene had brains larger than the reptiles, but smaller than those of most existing mammals (Fig. 23.14). With one notable exception: the Paleocean and Eocean primates already had rather large brains. From the Eocene (38 million years ago) to the Miocene/Pliocene (5 million years ago), the brains in several mammalian groups gradually enlarged (Jerison 1973). It has been argued that the increases in brain size in carnivores and ungulates were mutually dependent (Jerison 1973). The carnivores were suggested to have somewhat larger brains than the ungulates; the larger carnivores' brain was suggested to be a selection pressure for brain increase in ungulates, which urged the carnivores to develop still larger brains. It has been suggested that, in South America, the hoofed mammals and their predators (carnivorous marsupials) had a different evolutionary development. According to Jerison (1973), the brains of preys and
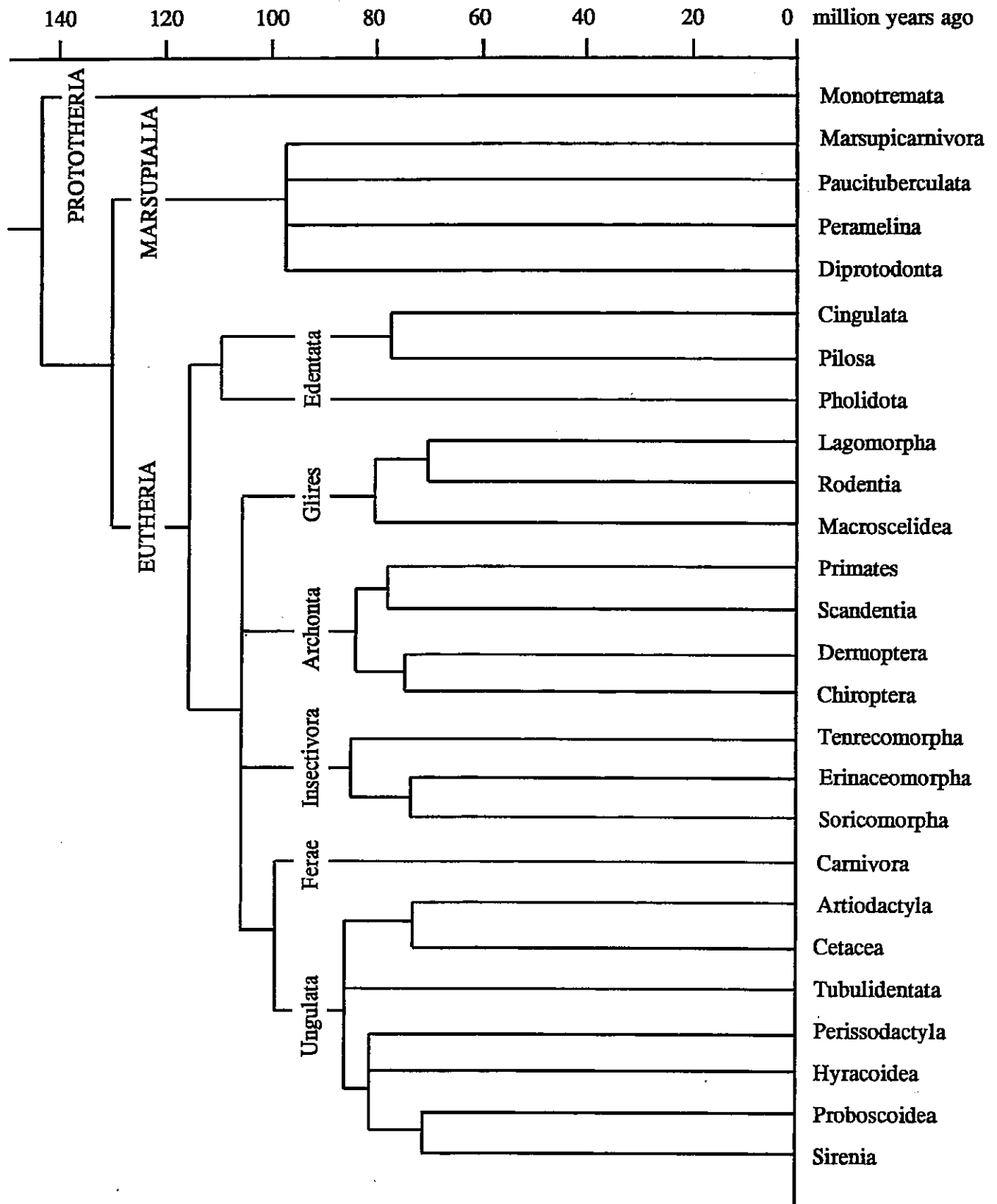
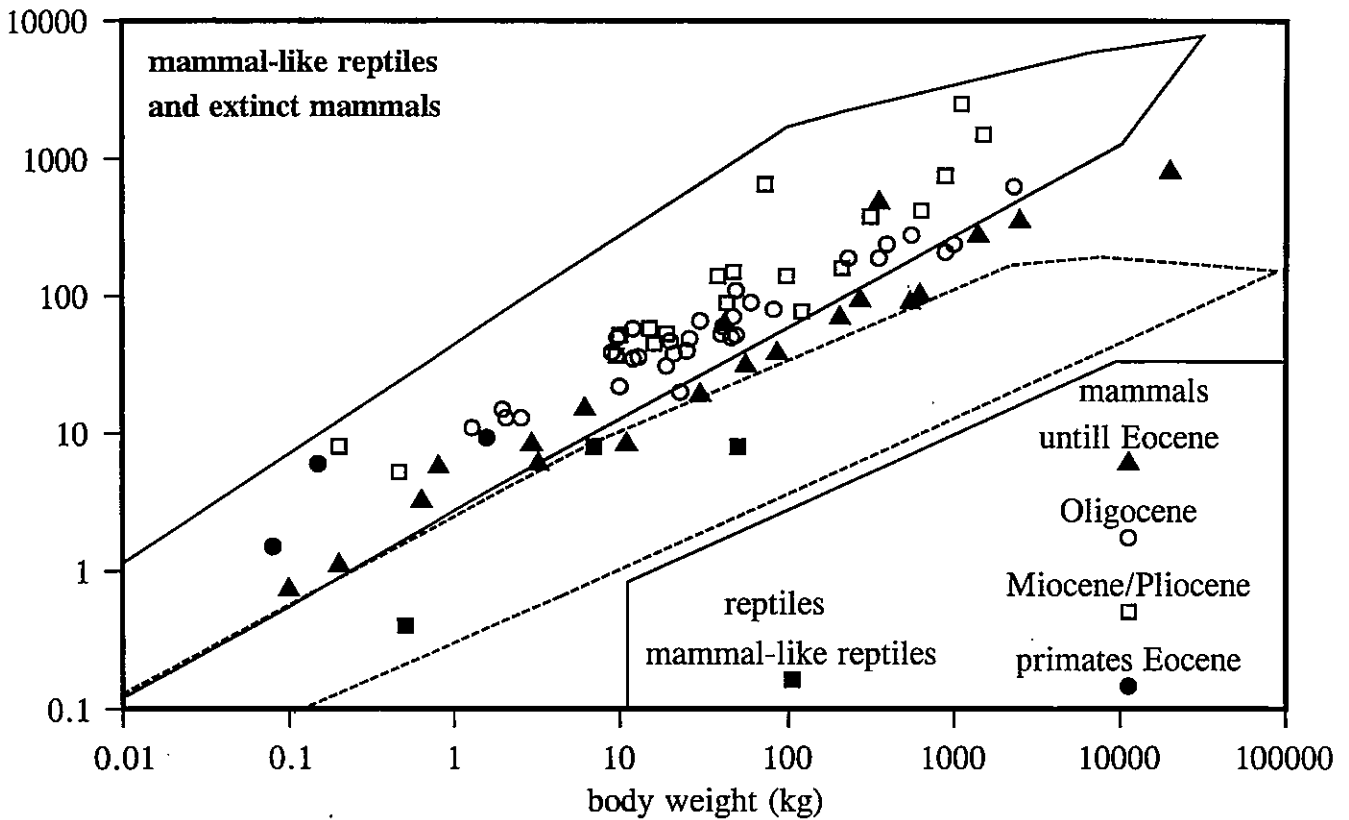Fig. 23.13. Cladogram of mammalian orders. (Based mainly on Novacek 1992)

brain weight (g)

Fig. 23.14. Evolution of brain size in mammals. For comparison the convex polygons of living reptiles and mammals are shown. Most mammal-like reptiles have reptile-sized brains.

During mammalian evolution, brain size has gradually increased. By the Eocene, the primates already had large brains for their body size. (Based on data from Jerison 1973)

predators in South America did not grow progressively: these groups seemed not to stimulate one another to develop larger brains (Jerison 1973). According to Radinsky (1981), however, the South American hoofed mammals had larger EQs than was originally presumed.

23.7.2
Ecology, Ethology and Brain Size in Mammals

In the literature of the past decades, various ecological and ethological features have been related to brain size. In the following sections these and other features will be discussed for some selected mammalian orders.

23.7.2.1
Metabolic Rate

It has been suggested that brain size is related to the basal metabolic rate (Martin 1981; Armstrong 1983; Hofman 1983a). The basal metabolic rate is the metabolism during a behaviourally inactive state (often sleep). Like brain size, the basal metabolism is an allometrically scaled parameter. From the lit-

erature, I have collected data on 264 mammalian species where body weight and brain weight as well as basal metabolic rate are known. The regression lines (based on the same species) have the same slopes: brain weight 0.71 (SEM 0.01) and metabolism 0.72 (SEM 0.01). Since these slopes are similar, it has been suggested that brain weight in some way is causally related to the basal metabolic rate (Martin 1981). The crucial question is: do mammals with large brains (for their body weight) also have large metabolic rates (for their body weight)? By a method described in the 'Appendix', the correlation coefficient between brain weight corrected for body weight (EQ) and basal metabolic rate corrected for body weight (MEQ) has been calculated for these 264 mammals: the correlation coefficient was 0.08 (Table 23.3). So for mammals in general, the EQ is not associated with the MEQ. However, in some selected groups (bats, primates), stronger correlations between MEQ and EQ have been found (see below).

Table 23.3. Correlation coefficients between the EQ and various ecological parameters. Longevity, home range, group size and metabolic rate have been corrected for body weight by a method explained in the text. For the feeding pattern such a correction did not apply (primate diet data from Smuts et al. 1987)

	Mammals		Primates	
	Number	r	Number	r
Longevity	389	0.37**	80	0.70**
Home range	114	0.33**	62	0.45**
Group size	Only primate data		89	0.46**
Basal metabolic rate	264	0.08	22	0.40*
Feeding pattern				
% Fruit in diet	Only primate data		25	0.35*
% Herbs in diet	Only primate data		25	−0.55**

* $P < 0.05$
** $P < 0.01$

23.7.2.2
Longevity

Like metabolism, longevity has been related to encephalisation (Hofman 1983a, 1993). Longevity is an interesting feature, because it is part of the life history strategy. Prolonged K-selection tends to increase longevity. Moreover, K-selection is expected to increase body and brain size. Longevity is related to body size: large animals tend to live longer. Again the question becomes: do mammals with large brains (for their body weight) also have long life expectancies (for their body weight)? For mammals in general, the EQ is associated with the 'longevity quotient' (LOQ): $r=0.37$ (Table 23.3, $n=389$, $P < 0.01$). In primates, this correlation is stronger (see below).
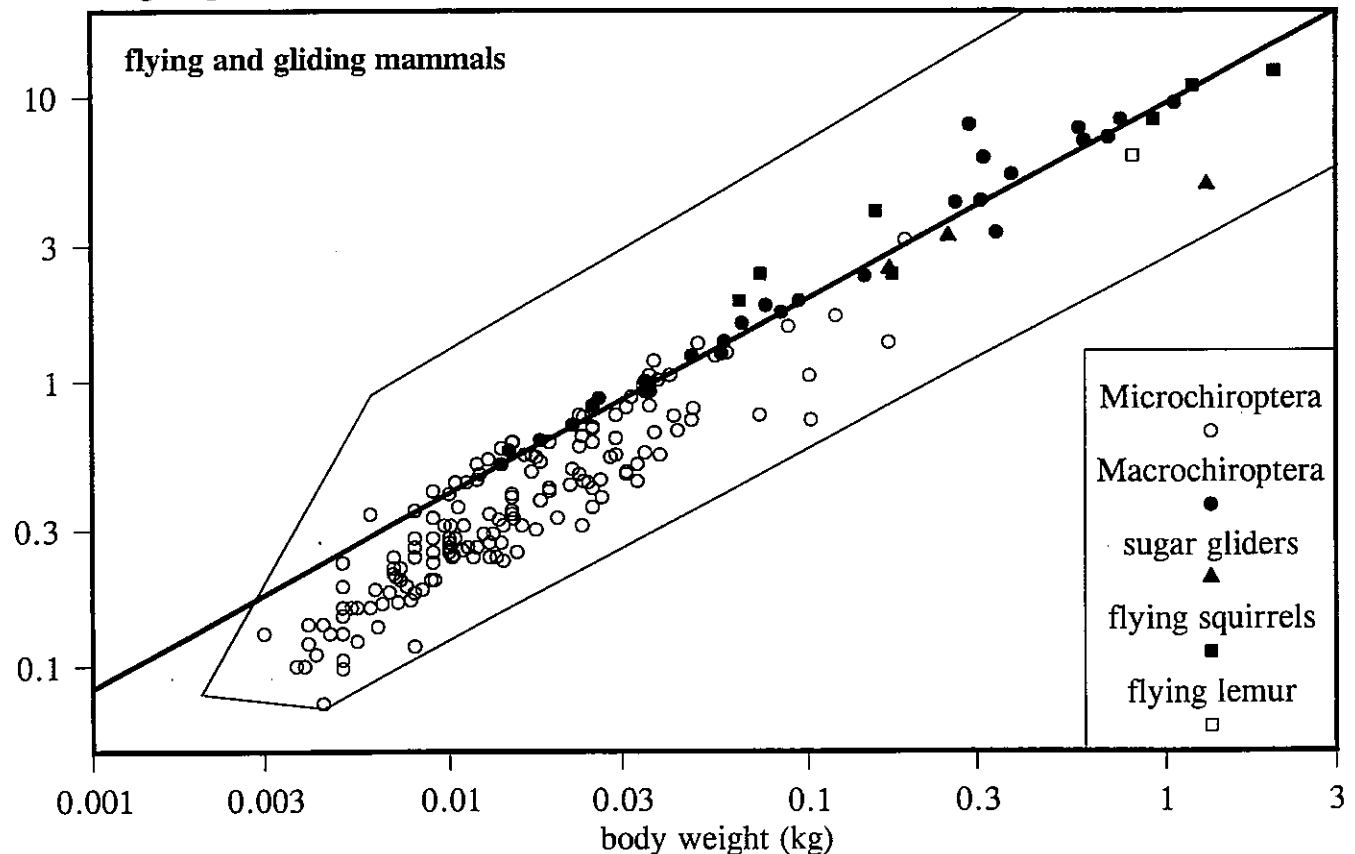

Fig. 23.15. Brain size in flying and gliding mammals. Flying foxes (Macrochiroptera) have brain sizes in the upper range of the other bats (Microchiroptera). For comparison the convex polygon of mammals is also shown: Microchiroptera occupy the lower part of this convex polygon
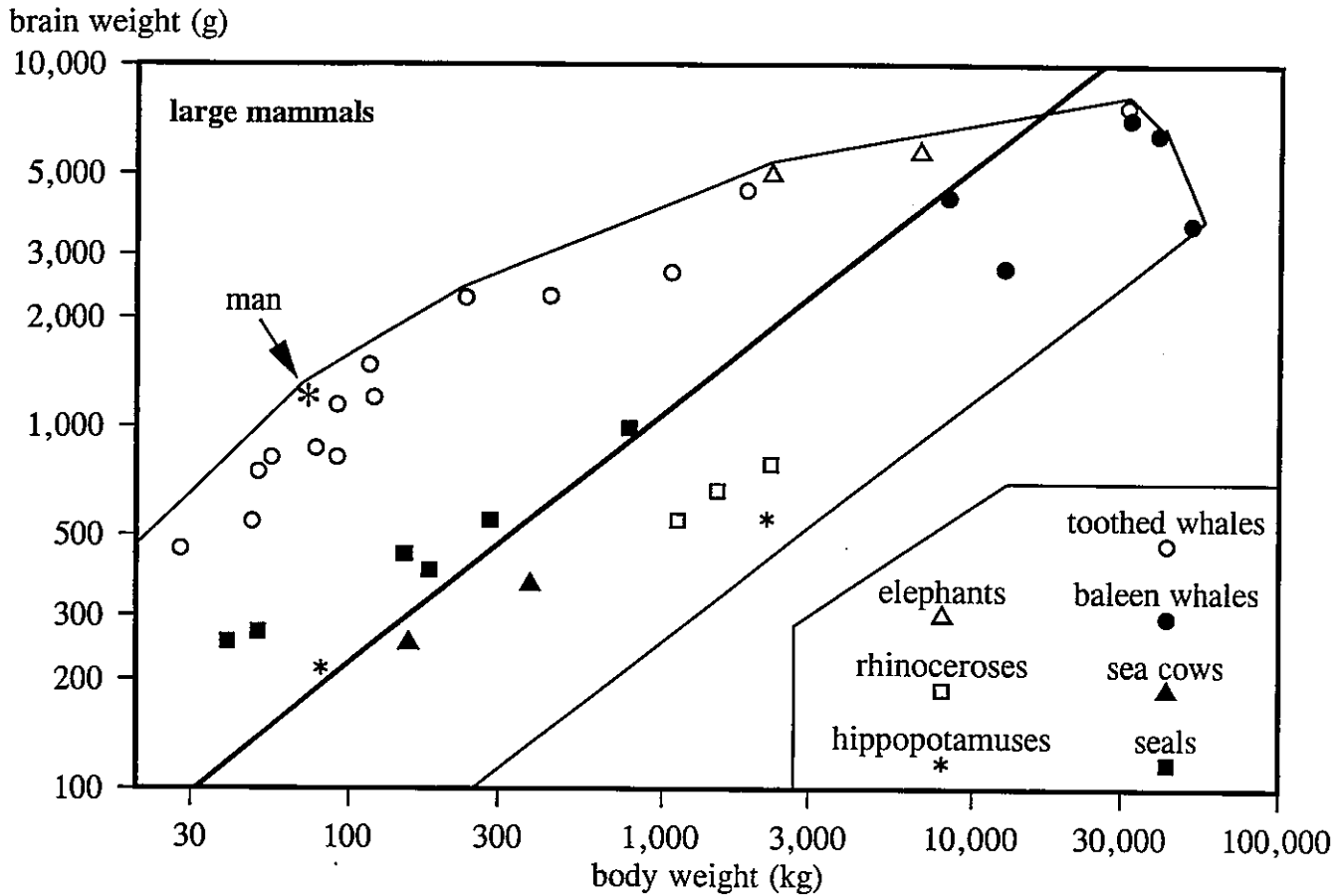
Fig. 23.16. Brain size in whales, sea cows, seals, elephants and a few large ungulates, in a double-logarithmic graph. Most toothed whales (especially dolphins) have very large brains. Sea cows, rhinoceroses and hippopotamusses have rather small brains. For comparison the convex polygon of mammals is also shown. (See Table 23.2 for the source of the data)

23.7.2.3
Neonatal Development

Unlike the situation in birds (see above), brain weight of mammals is not associated with precociality at birth (Eisenberg 1981, p. 325; Bennett and Harvey 1985b).

23.7.2.4
Flying and Gliding Mammals

Bats are the only mammals that can really fly. Among the bats, the Microchiroptera have small brains for their body size, while the Macrochiroptera have brain sizes around average for mammals (Fig. 23.15). In three other orders, species have evolved that can bridge considerable distances by gliding through the air. These are found in the marsupials (sugar glider, *Petaurus*), Dermoptera (flying lemur, *Cynocephalus*) and rodents (several flying squirrels). The brains of these gliding mammals are about average for mammals of their body size (Fig. 23.15, Pirlot and Kamiya 1982).

23.7.2.5
Aquatic Mammals

An aquatic life has other demands and opportunities for mammals than a terrestrial life. The larger an animal is, the larger the ratio of its volume to surface area, which is better for heat conservation (in homeothermic animals). Since mammals are likely to lose more energy under water than on the earth, an additional selection pressure is present to increase the body size of aquatic mammals. Moreover, in terrestrial animals, a rapid increase in body size during evolution is restricted, because bones and muscles must grow disproportionally large to carry a larger body. But in aquatic animals, this constraint is not present, so body size can increase rapidly. As a consequence, all sea mammals (whales, seals, sea cows) are large. It has been suggested that a small brain would be advantageous for aquatic mammals, since it would enable longer diving times because of the smaller oxygen demand (Robin 1973). However, in aquatic mammals, no correlation was found between diving time and EQ (Worthy and Hickie 1986). The brain sizes of
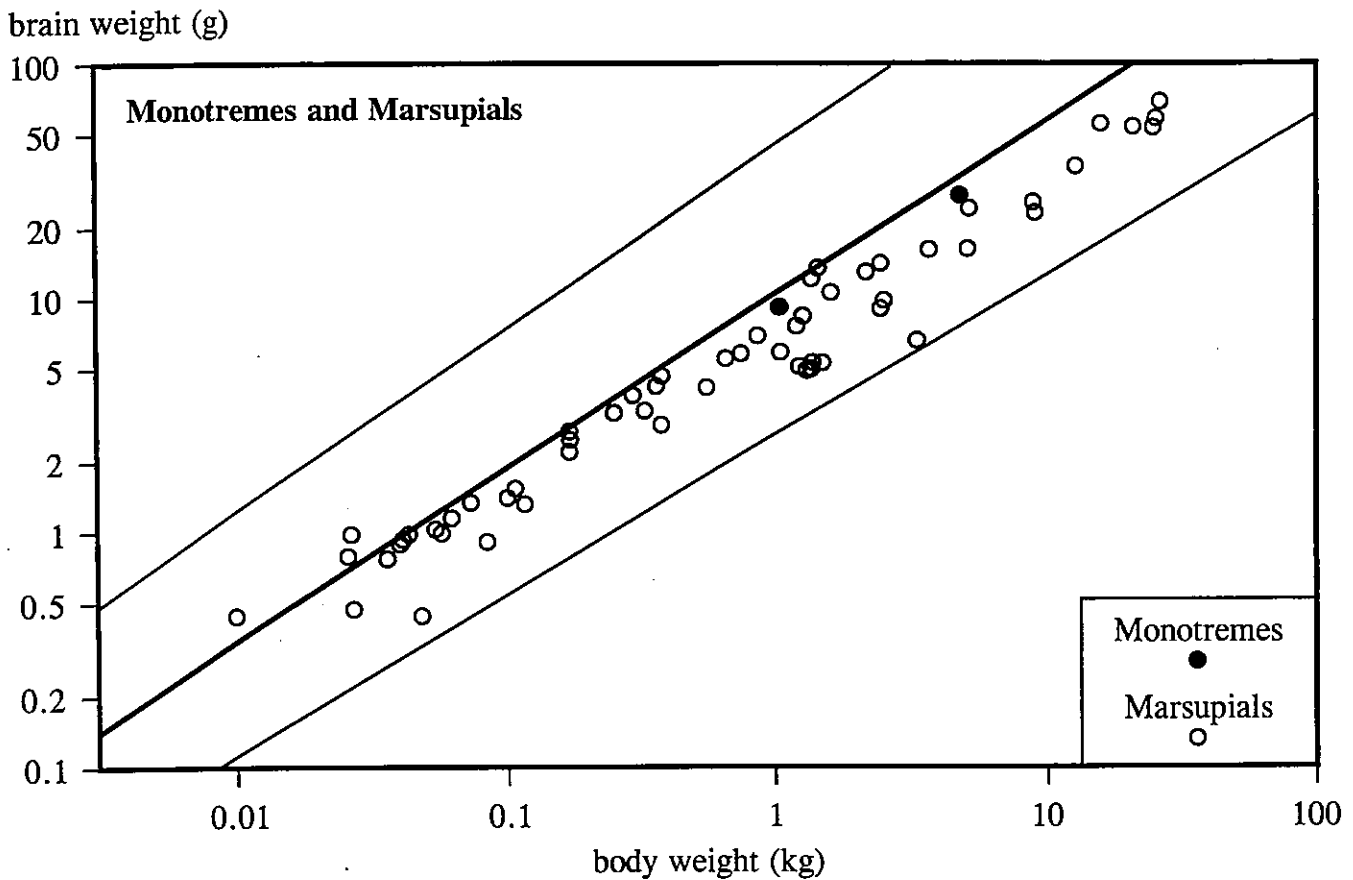
brain weight (g)

Fig. 23.17. Relationship between body weight and brain weight for monotremes and marsupials, in a double-logarithmic graph. For a comparison the convex polygon of mammals is shown. (See Table 23.2 for the sources of the data)

aquatic mammals differ greatly (Fig. 23.16): whales have large brains, seals slightly above average for mammals and sea cows slightly below average.

23.7.3
Monotremes

Although the monotremes are regarded as the most 'primitive' group of mammals, their brains have about the average size for a mammal of their body size (Fig. 23.17).

23.7.4
Marsupials

The marsupials show a large morphological and ecological variation. In this group we find small bandicoots with a body weight of 10 g, and a brain weight of 0.5 g; but also kangaroos of 30 kg with brain weights of 60 g. Overall, marsupials have small brains, compared to other mammals (Fig. 23.17).

23.7.5
Eutheria

The Eutheria are discussed in this chapter under five groups, which are suggested to be monophyletic (Novacek 1992):

1. The Insectivora, which are often subdivided into three orders: tenrecs, hedgehogs and shrews (including moles)
2. The Edentata
3. The rodents and their presumed relatives, the elephant shrews and the rabbits
4. The Archonta, which comprise the tree shrews, flying lemurs, bats and primates
5. The Ferungulata, which comprise among others the carnivores, ungulates, whales, elephants and sea cows

23.7.5.1
Insectivores

The insectivores show considerable variation in brain weight. Some insectivores have remarkably small brains for their body size: tenrecs, shrews and
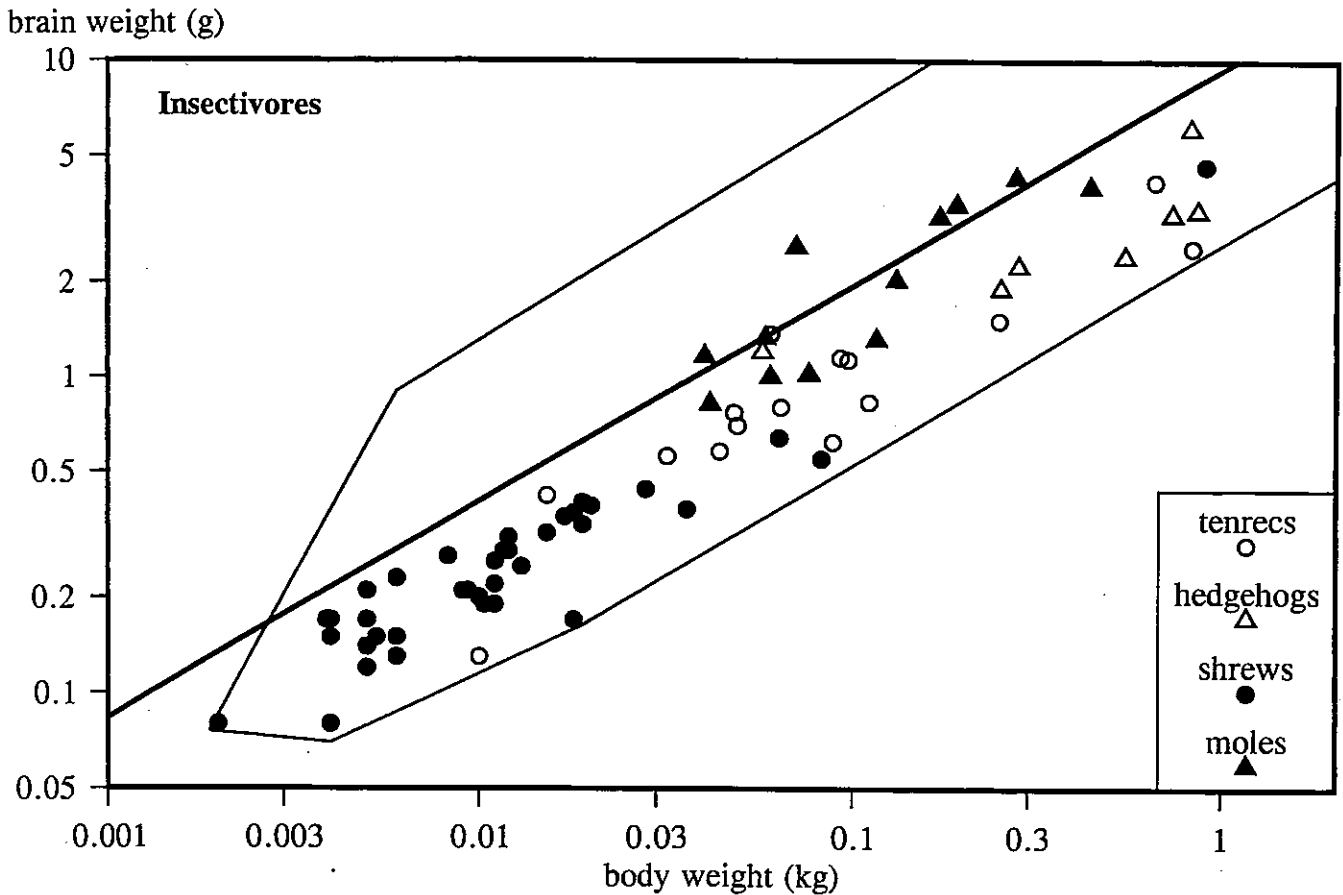
brain weight (g)

Fig. 23.18. Relationship between body weight and brain weight for various groups of insectivores, in a double-logarithmic graph; note the relatively large brains of moles.

For comparison the convex polygon of mammals is shown. (See Table 23.2 for the sources of the data)

hedgehogs (Fig. 23.18); these are sometimes included together as 'basal insectivores' (Bauchot and Stephan 1966). The moles are conspicuous by their large brains – at least for insectivores of their body sizes, but it is not clear why they evolved large brains. At the moment, no clear relationship has been found for insectivores between their brain weight and their ecology or ethology. Semi-aquatic insectivores have advanced brains, but this is expressed in internal brain structure rather than in brain weight (Stephan et al. 1990).

23.7.5.2
Edentates

Edentates have smaller brains than the average mammal of their body size (Fig. 23.19). The Cingulata (armadillos) and Pilosa (sloths and anteaters) have similar brain sizes. Among the edentates, the pangolins (*Manis*) have the smallest brain.

23.7.5.3
Rodents and Their Presumed Relatives

The taxonomic position of rodents, rabbits and elephant shrews is not at all clear, but some authors regard these groups as related. It is even not clear whether the rodents form a monophyletic group. Arguments have been presented that the guinea-pig-like rodents might not be monophyletic with the other rodents (Graur et al. 1992). Macroscelidea (elephant shrews) used to be included in the group of the insectivores, but now they are regarded as a separate order, possibly a sister group of the Lagomorpha. The brain sizes of elephant shrews are only average for a mammal of their body size. So they have considerably larger brains than the real shrews. The brains of the Lagomorpha (hares, rabbits and piping hares) are somewhat smaller than those of the average mammal of their body size.

Three main groups of rodents are distinguished: squirrel-like (sciuromorphs), mouse-like (myomorphs) and guinea-pig-like (caviomorphs). Small myomorphs have remarkably large brains for mammals of their size: up to a factor of 10 larger than
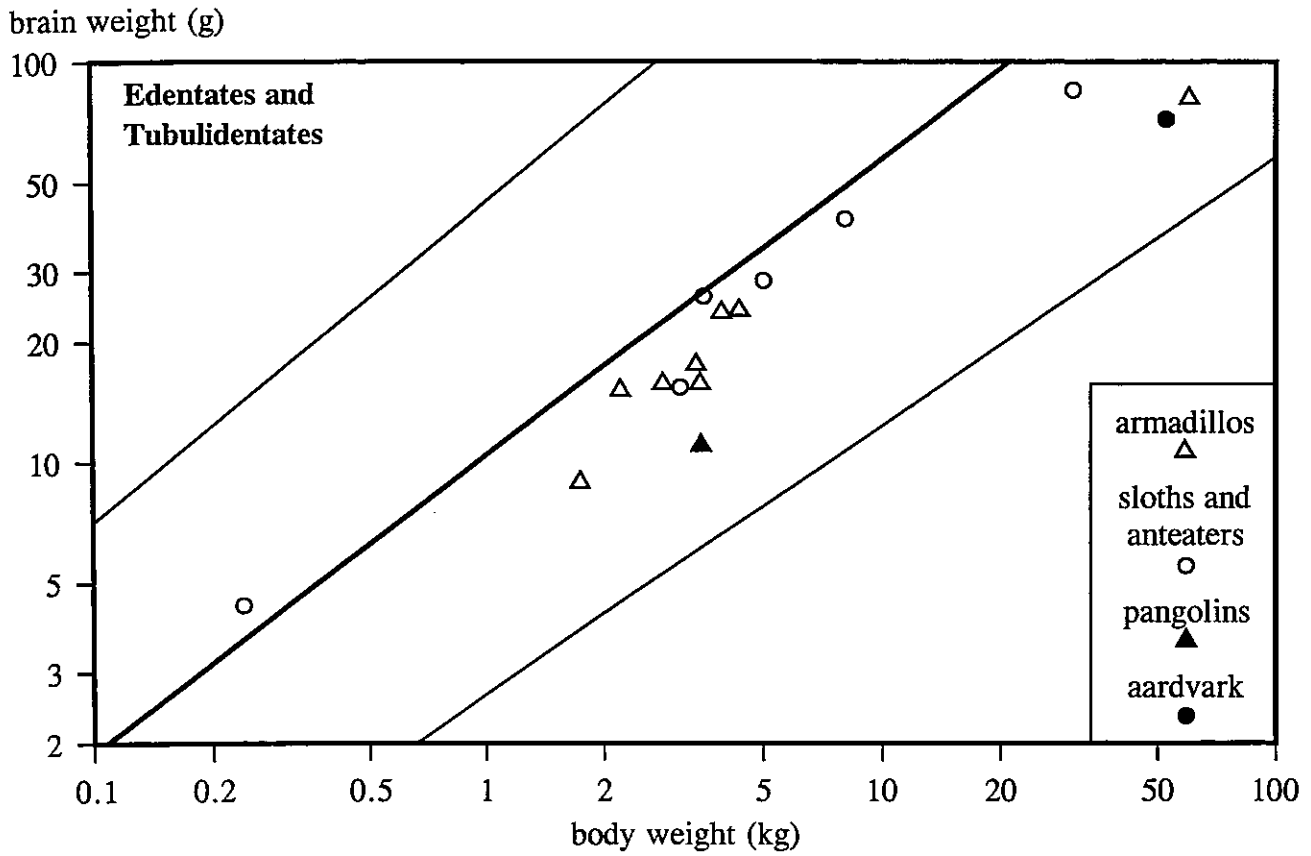
brain weight (g)

Fig. 23.19. Relationship between body weight and brain weight for edentates and tubulidentates, in a double-logarithmic graph. For comparison the convex polygon of mammals is shown. (See Table 23.2 for the sources of the data)
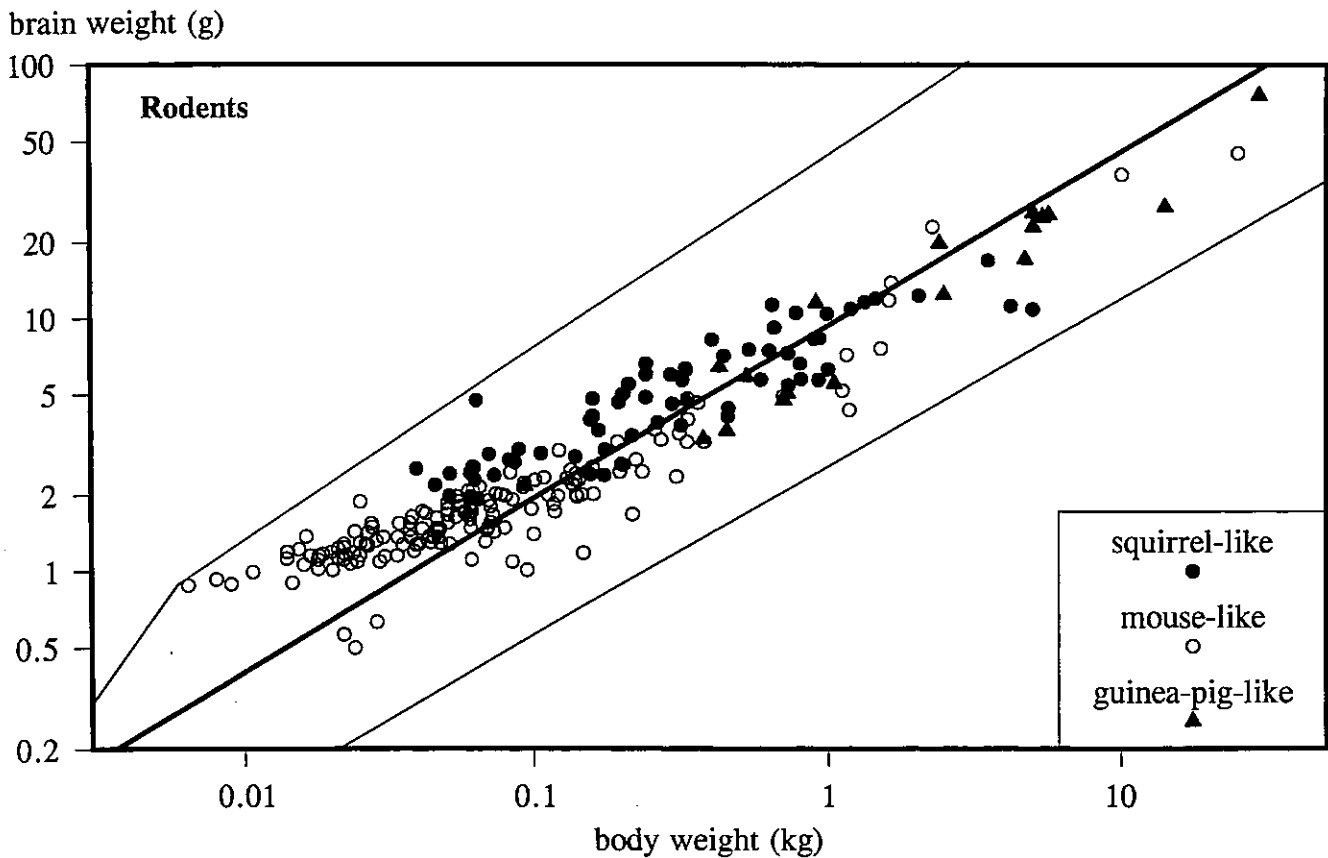
brain weight (g)

Fig. 23.20. Relationship between body weight and brain weight for rodents, in a double-logarithmic graph. For comparison the convex polygon of mammals is also shown. (See Table 23.1 for the sources of the data)
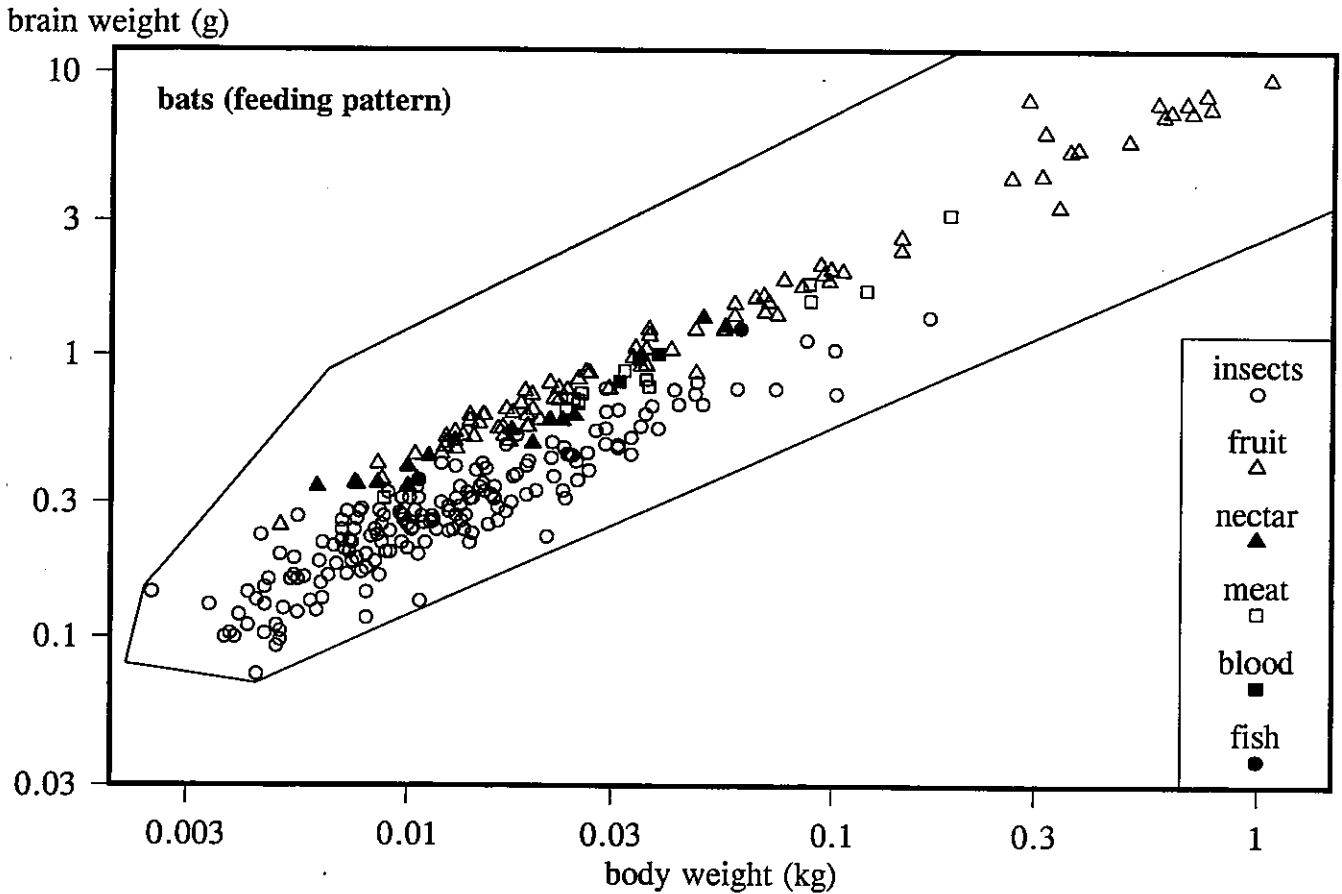
brain weight (g)

Fig. 23.21. Brain size in bats in a double-logarithmic graph. Insect-eating bats have proportionally small brains. For comparison the convex polygon of mammals is also shown. (See Table 23.2 for the sources of the data)

insectivores or bats (Fig. 23.20). The squirrels are conspicious by their proportionally large brains. This applies for the ground and the tree squirrels; the large squirrel brain cannot therefore simply be explained by their arboreal way of life. The brains of the caviomorphs are somewhat below average for mammals of their body size.

23.7.5.4
Archonta

The tree shrews, flying lemurs, bats and primates are usually regarded as one monophyletic group, the Archonta (Novacek 1992).

23.7.5.4.1
Scandentia (Tree Shrews)

The taxonomic position of the tree shrews has been a matter of dispute for some time. For a long time, they were included in the insectivores; thereafter they were regarded as primates, and now they are usually considered as a separate order. The tree shrews have brain weights just above average for mammals.

23.7.5.4.2
Dermoptera (Flying Lemurs)

The brain weight of the flying lemur is slightly below the average for a mammal of the same body weight (Fig. 23.15).

23.7.5.4.3
Bats

Bats are the only mammals that can really fly. They are distinguished in the (small) Microchiroptera and the (larger) Macrochiroptera (the flying foxes). Figure 23.15 shows that the Macrochiroptera have brain weights in the upper range of the bats. The Macrochiroptera have large visual and olfactory brain centres, while most Microchiroptera have a large auditory system, and small olfactory centres (Baron and Jolicoeur 1980). Also within the Microchiroptera, brain weights vary considerably. In bats, brain weight is related to diet rather than to taxonomic grouping. The insect-eating bats have the lowest brain weights: only 60%–70% of those of the nectar- or fruit-eating bats, which is in the same range as the basal insectivores. Proportionally the
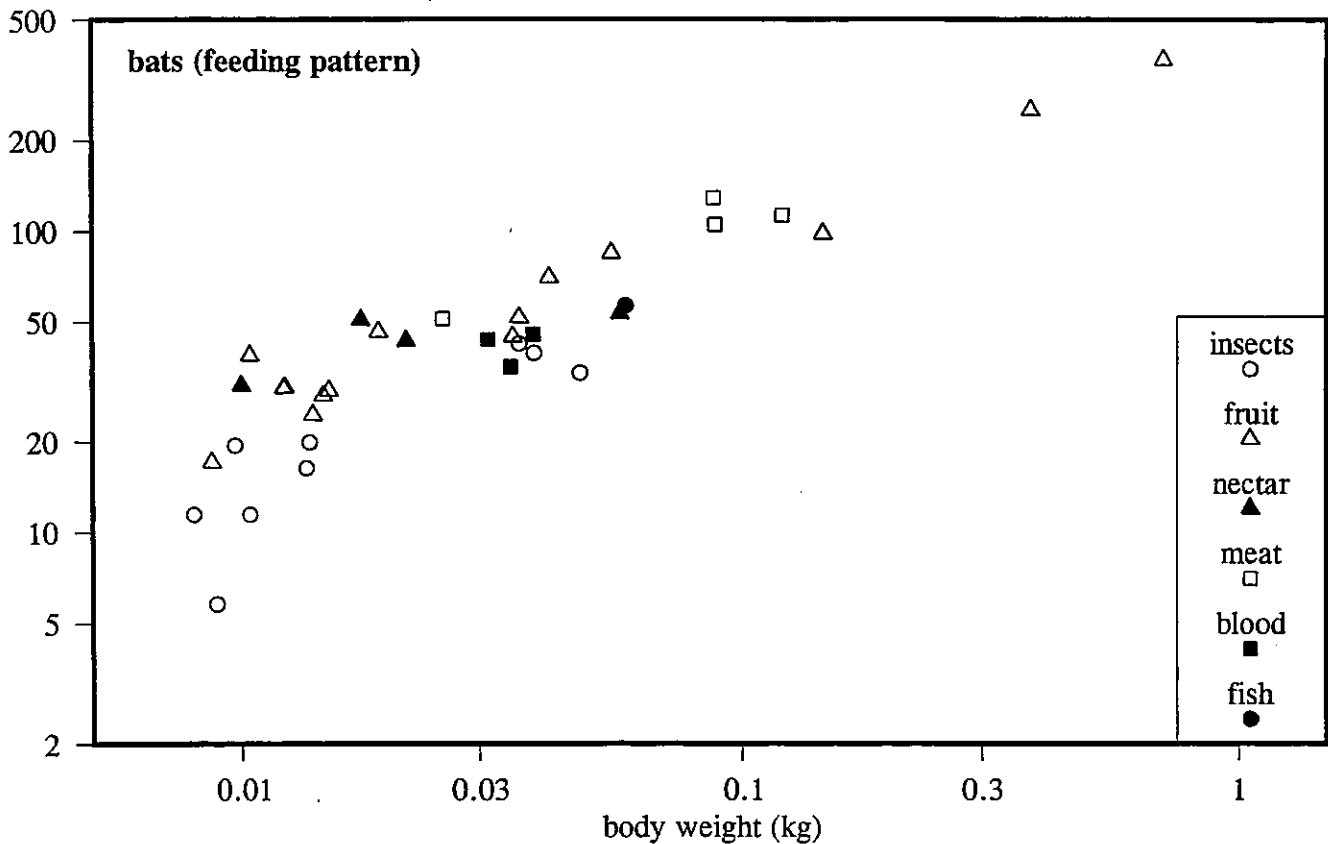
basal metabolism ($cm^3 O_2$ per hour)

Fig. 23.22. Basal metabolism in bats. Insect-eating bats have the lowest basal metabolism. (Based on data by McNab 1969)

highest brain weights were found in the fruit-, nectar- and blood-eating bats (Fig. 23.21, Pirlot and Stephan 1970; Eisenberg and Wilson 1978; Stephan et al. 1981). The carnivorous bats occupy an intermediate position. Although many bats use echolocation, it seems to be a special quality in insect-eating bats, for they must quickly detect small moving targets by their sonar mechanism, and they must make quick, precisely timed manoeuvres in three dimensions guided by their sonar mechanism to catch their prey (Simmons and Stein 1980). Therefore, it is surprising that insect-eating bats have such small brains.

A similar trend is found with the basal metabolic rate. In bats, the EQ is rather strongly associated with the MEQ ($r=0.58$, $n=36$, $P<0.01$). Figure 23.22 shows the metabolic rate for various bats coded for their diet. Again the insect-eating bats occupy the lower part of the figure (McNab 1969). Among the bats, the insect-eating bats are most economical with energy. It is hypothesised that the small brain size and the small metabolic rate are the product of the same selection pressure. During the night, insect-eating bats can only catch a limited amount of insects, since they must remain light

enough for flight and quick manoeuvring. It is impossible for them to store supplies of insects. Therefore, a strong selection pressure to conserve energy is suggested for insect-eating bats. This energy conservation is also evident from another trait: insect-eating bats easily enter torpor, an energy-sparing state of hypothermia (McNab 1988). Since the brain is an energy-consuming organ, a selection pressure to conserve energy would also reduce the size of the brain. Energy conservation might explain both the low metabolic rate and the proportionally small brain weight in insect-eating bats.

23.7.5.4.4
Primates

A simplified phylogenetic tree of primates is shown in Fig. 23.23. For the classification of the Hominoidea (gibbons, apes and man), the terminology of Goodman et al. (1990) is followed. This figure reflects the recent opinion of several authors that the chimpanzee is more closely related to man than to the gorilla or other apes.
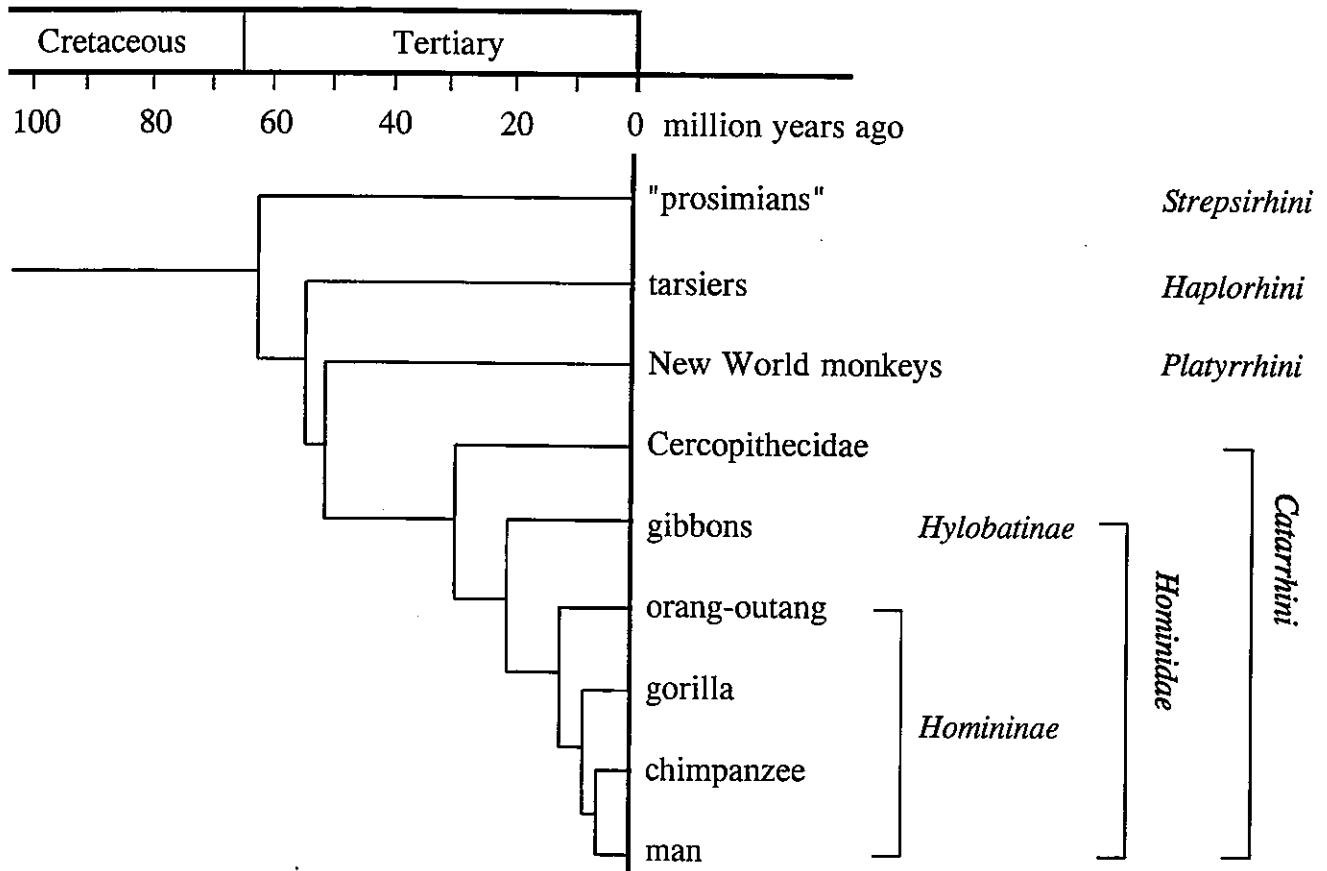
Fig. 23.23. Cladogram of the primates

Brain Size and Taxonomic Relationships. Figure 23.24 gives a double-logarithmic survey of the body and brain weights of 118 living primates. Some differences are more evident in the linear graph of Fig. 23.25a, which shows data on primates with body weights between 1 and 12 kg. The following facts are notable:

1. Primates have large brains for mammals of their body weight.
2. Within the primates, the 'prosimians' (Strepsirhini and Haplorhini) have the smallest brain weight, but most prosimians still have larger brains than the average mammal of their body size. We have seen in Sect. 23.7.1 that the prosimians of the Paleocene and Eocene already had proportionally large brains. These extinct prosimians had overlapping binocular fields and grasping forepaws; they probably had an arboreal (squirrel-like) way of life, and this could explain their large brains.
3. Since man is a member of the Old World monkeys (Catarrhini), we are inclined to regard the Catarrhini as being 'higher' than the New World monkeys (Platyrrhini). Yet some New World monkeys have larger brains than Old World monkeys.

4. Gibbons (Hylobatinae) have large brains for their body size.
5. Within the Homininae, man has an exceptionally large brain, while the brain weights of the other Homininae (the apes) are a continuation of the monkey brain weights.

Brain Size and Ecology. Brain size in primates has been related to various ecological factors: longevity (Sacher 1975; Allman et al. 1993; Hofman 1993), group size (Dunbar 1992), home range (Dunbar 1992), basal metabolic rate (Armstrong 1985) and feeding patterns (Clutton-Brock and Harvey 1980). The problem with primate brain size is that it is associated with all these parameters (Table 23.3).

1. Longevity: Large primates tend to live longer. When the longevity of primates is corrected for body size (by a method described in the 'Appendix'), it is still strongly associated with the EQ. In fact, of the parameters investigated, EQ is most strongly associated with longevity ($r=0.70$, Table 23.3). With a longer life span, the period for learning increases. A plausible interpretation is that some groups of primates have passed through a period of K-selection, promoting a longer life span and a larger brain.
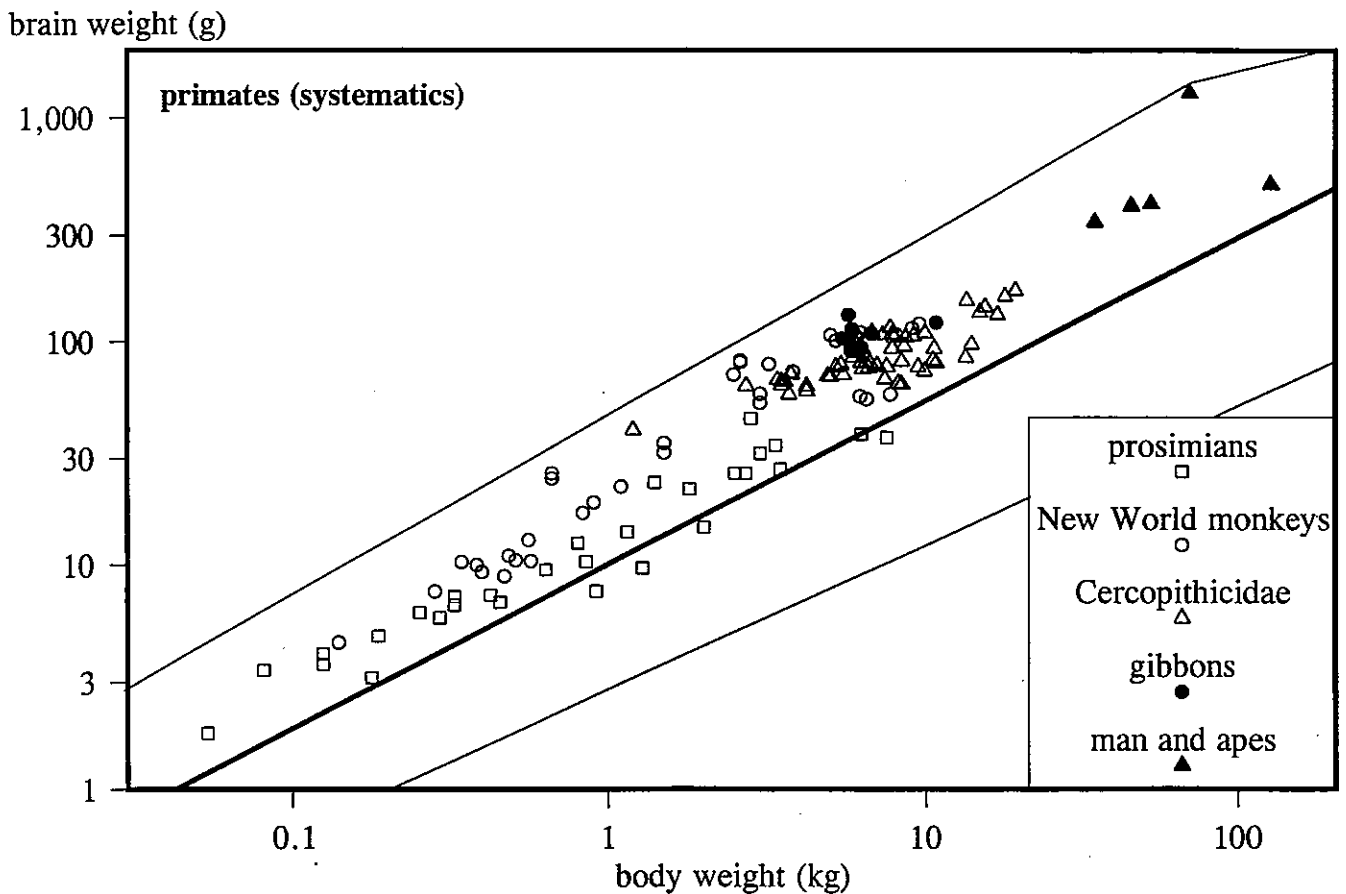
brain weight (g)

Fig. 23.24. Relationship between body weight and brain weight in primates in a double-logarithmic graph. For comparison the convex polygon and regression line (based on

$\alpha=0.739$ and $k=0.0626$) for the mammals are shown. Most primates have larger brains than the average mammal of their body size. (See Table 23.2 for the source of the data)

2. Diet: Herbivore primates have proportionally smaller brains than frugivore and insectivore primates (Fig. 23.25b, Table 23.3). In some frugivore species, the brains are twice as large as in herbivore species with the same body weight. In the Old and the New World monkeys, brain size is related to diet rather than to taxonomy. In Fig. 23.25a, puzzling data have been presented on the brain weights of Old and New World monkeys. Herbivore monkeys of both groups have rather small brains. Fruit-eating monkeys in the Old and the New World developed larger brains independently of each other. Living on a fruit diet is more difficult than living on herbs. The various types of fruit are only available during separate seasons, and they are to be found over a much wider region. Fruit-eating primates benefit from their better colour vision for the detection of ripe fruits. These factors might explain the larger brains of fruit-eating primates.

3. Group size: Large primates tend to live in large groups. The group size of primates, corrected for body size, is associated with the EQ ($r=0.46$, Table 23.3). It is easy to imagine that a monkey living in a larger group needs more social intel-

ligence to know how to deal with its group members. Primates living in large groups benefit from improved vision for the recognition of group members at a large distance. Moreover, a larger group needs a larger home range to collect enough food (see below).

4. Home range: Large primates tend to have large home ranges. A confounding factor is present: often one cannot speak about the home range of an individual monkey, but only of its group. Here an analysis is made for the home range of the social unit of primates, irrespective of the group size. The home range of primates, corrected for body size, is associated with the EQ ($r=0.45$, Table 23.3). For obvious reasons, home range and group size are correlated: it takes a larger group to defend a large territory, and it takes a larger home range to feed a large group. Primates with a large home range also need greater geographical insight. Fruit-eating primates need a larger home range to find a good supply of fruit throughout the year. Diet, home range, group size and brain size are probably causally related through these factors.
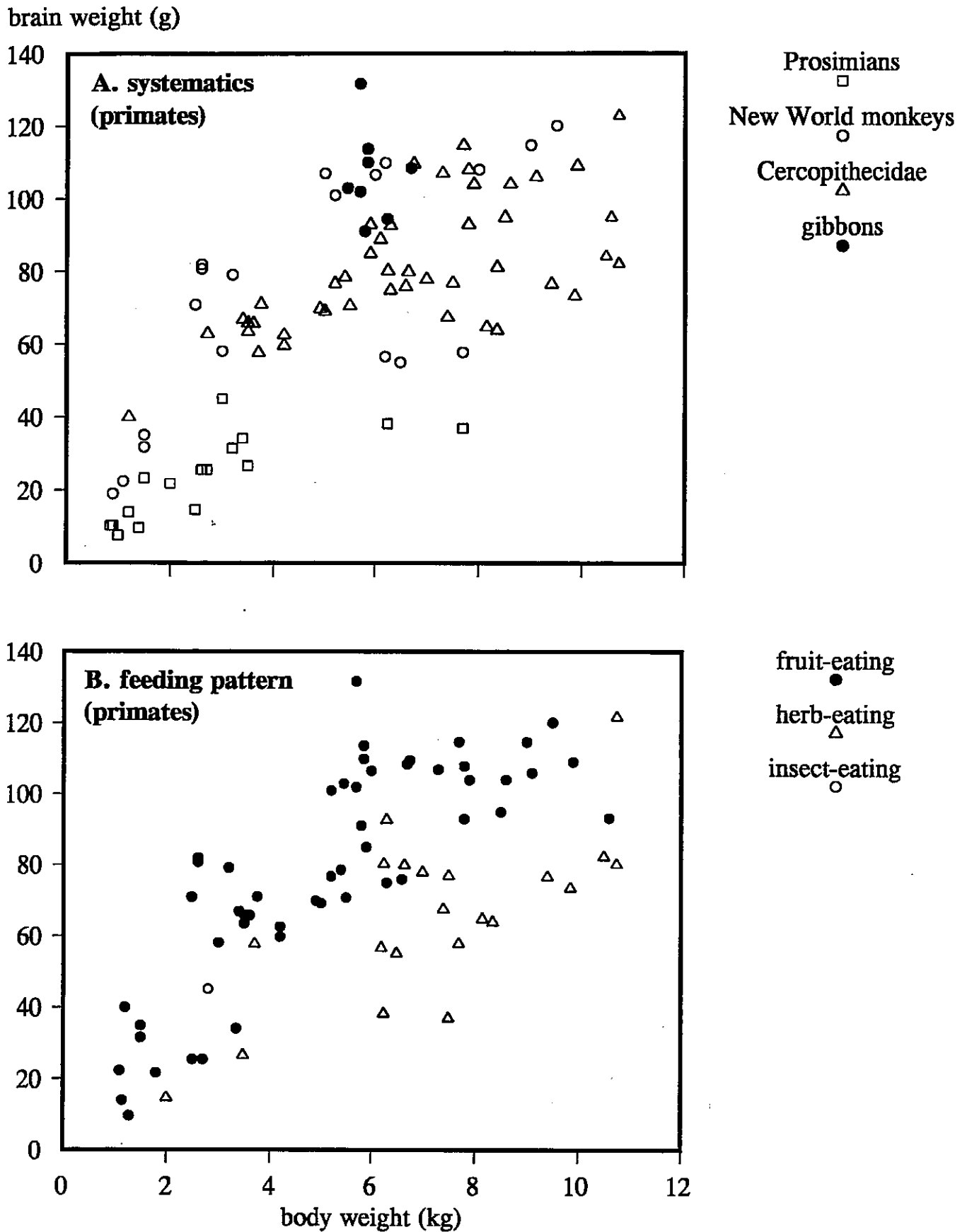
brain weight (g)

Fig. 23.25. a Linear graph showing the relationship between body weight and brain weight of primates with a body weight between 1 and 12 kg. The actual differences are clearly visible in this linear graph. For primates, prosimians have small brains. Some New World monkeys have rather small brains, others large. The same applies to Old World monkeys. Gibbons have large brains. b Linear graph showing the relationship between body weight and brain weight of the same primates. Herb-eating primates have rather small brains, while fruit-eating primates have large brains

5. Basal metabolic rate: For mammals in general, the *EQ* is not associated with the *MEQ*, but for primates a positive association between *EQ* and *MEQ* is present ($r=0.40$, Table 23.3). This positive relationship has been noted by Armstrong (1985), but the relevance of this finding is hard to interpret. The basal metabolic rate in primates might be related to feeding pattern. [A positive association between *EQ* and *MEQ* has been found in bats (see above), but the hypothetical explanation for that association does not hold for primates.]

6. Conclusion: I hoped to be able to propose a plausible scenario for primate brain evolution after these analyses. However, too many factors seem to be associated with brain size in primates. Independently of each other, in some groups of New and Old World monkeys, *K*-selection has been active, leading to an increase in longevity, the use of higher quality food (fruit) and an increase in group size and home range. However, which factors prevailed for the increase in brain size, and in which order, is still unclear.

Increase in the Hominid Brain Size. The evolution of the brain of man will be discussed somewhat more extensively. Figure 23.26b shows the brain weights of fossil hominids and man. The brain of *Australopithecus afarensis* is only slightly larger than that of the chimpanzee; therefore it is generally assumed that the common ancestor of man and chimpanzee, who lived some 7 million years ago, probably had a brain of about 350 g. About 3.5 million years ago, *Australopithecus afarensis*, a probable ancestor of man, still had a similar brain weight. However, the pattern of cortical sulci in *Australopithecus afarensis* deviates in some respects from the ape-like pattern (Holloway 1983). In the evolution from *Australopithecus afarensis* to the recent *Homo sapiens*, brain size increased to the present value of about 1400 g, an increase by a factor of 3–4 (Fig. 23.26b). The semi-logarithmic graph of Fig. 23.26b shows that the data points follow a straight line; this implies that the average percentage increase per unit of time was constant over this period of time (but no clear indications are present for or against gradualism or punctuated equilibria, cf. Hofman 1983b; Holloway 1983). Over the last 3.5 million years, the increase in brain weight has been 43% per million years [or 0.43 darwin (d), Haldane 1949]. Over that time, body weight has increased by 26% per million years (0.26 d, Fig. 23.26a). An increase by 0.43 d over a period of 3.5 million years is rather slow (Gingerich 1983). Although the chimpanzee has a much smaller brain than man, the proportion of its neo-

cortex is about the same (72% in the chimpanzee vs. 76% in man). So contrary to popular belief, it was not primarily the neocortex that increased during hominid evolution, but rather a similar increase in brain stem, cerebellum and neocortex took place. Which selection pressures caused this increase or these increases in brain size?

Selection Pressures and the Hominid Brain. Several selection pressures have been suggested as the main cause of the increase (or the increases) in brain size during hominid evolution (e.g. Gibson and Ingold 1993). Most of these are plausible, but at the moment it is not really possible to test these suggestions critically.

1. Motor skills: With respect to motor skills, various differences are present between the chimpanzee and man. (a) Anatomically and behaviourally, man is much better equipped for a *bipedal* life than the chimpanzee. Convincing evidence has been presented that the small-brained *Australopithecus afarensis* walked on two legs (Hay and Leakey 1982; Lovejoy 1988). Apparently, hominids do not need a large brain to walk on two legs. (b) The chimpanzee is far superior to man for a life in the trees, including *arboreal acrobatics*, and consequently in the sensorimotor skills required for it. (c) Kortlandt (1972) suggested that a main selection pressure contributing to hominid brain enlargement was improvement of *throwing accuracy*, which is probably important for a hunter. In the hominid evolution to *Homo sapiens*, some motor skills were lost and others gained. It is unclear why precision throwing (which was gained) would require more brain than arboreal acrobatics (which was lost). Therefore, it is unlikely that changes in motor skills have contributed considerably to the increase in brain size in hominid evolution.

2. Intelligence: Our intelligence is due to our large brain. No one doubts this when man and chimpanzee are compared, but there is no fair way to measure and compare human and chimpanzee intelligence. Human intelligence is usually measured with IQ tests. In older studies on head size and IQ, the correlation coefficients between head size and IQ were small – usually between 0.1 and 0.2 (Van Valen 1974; Passingham 1979). But in recent studies, magnetic resonance imaging has been used to measure brain size directly in vivo: larger correlation coefficients between brain size and IQ have now been found (0.3–0.5, Willerman et al. 1991). Great scientists (such as Einstein or von Helmholtz) stand out by their brain

A. body weight (kg)
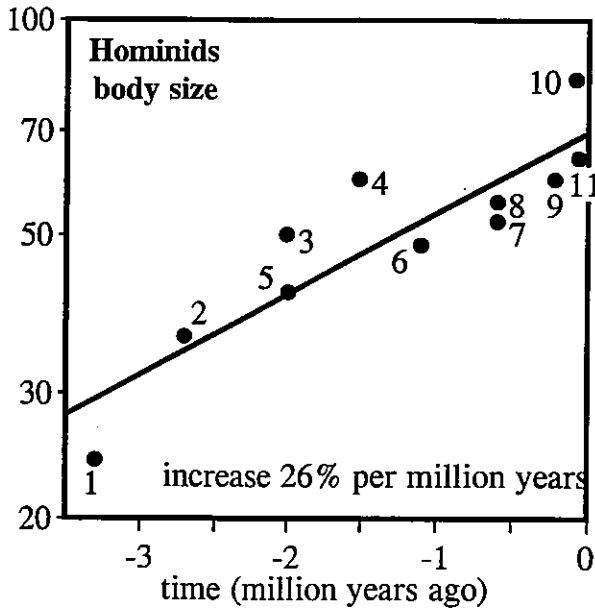
B. brain weight (g)
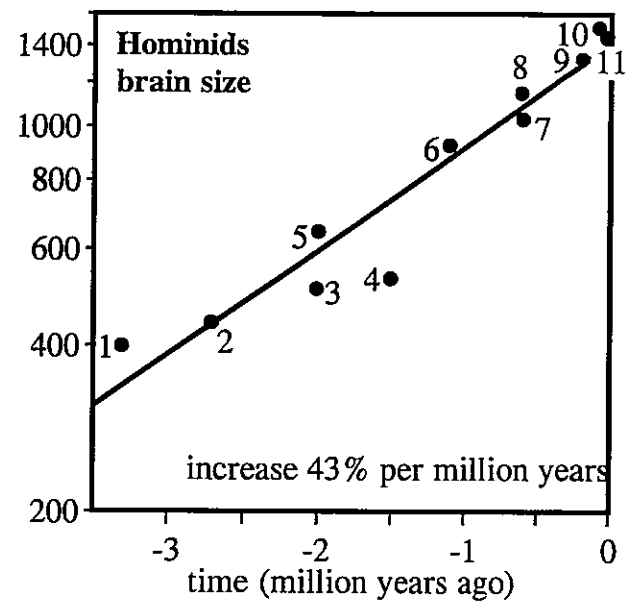
1. Australopithecus afarensis
2. Australopithecus africanus
3. Australopithecus robustus
4. Australopithecus boisei

5. Homo habilis
6. Homo erectus (Java)
7. Homo erectus (Peking)
8. Homo erectus (Solo)

9. Homo sapiens archaicus
10. Homo sapiens neanderthalensis
11. Homo sapiens sapiens

Fig. 23.26a,b. Evolution of body and brain size in the hominids. a Over the past 3.5 million years, hominid body size has increased by a factor of 2.5, or 26 % per million years. b Over the past 3.5 million years, hominid brain size has increased by a factor of 3.5, or 43 % per million years. (Based on data from Hofman 1983b)

function, but not by their brain size (Hansemann 1899; Cobb 1965; Diamond et al. 1985).

3. Language: The greatest achievement of the human brain is probably speech/language. In the human brain, asymmetries are present between the left and right hemispheres, which are related to speech. Some of these asymmetries have also been found in the brains of apes (Holloway and De la Coste-Lareymondie 1982). However, a vivid discussion is going on about the linguistic capacities of the apes (Terrace et al. 1979; Savage-Rumbaugh et al. 1983; Gardner and Gardner 1989). Nevertheless, a selective pressure in favour of linguistic capacities probably contributed to the emergence of the large human brain.

4. Social learning and culture: Social learning is the basis of culture. Two aspects of social learning are distinguished: learning by imitation and intentional teaching. Learning by imitation has been seen in monkeys, but only anecdotal evidence is offered for intentional teaching by chimpanzees (of offspring by the mother, McGrew 1992). Whether a consequence of social learning or not, regional differences in chimpanzees'

behaviour are found, for instance in the use of stone hammers to break open nuts, and ways of grooming (McGrew 1992). When such regional differences are found in human societies, they are invariably called a product of culture. However, culture in human societies is infinitely more elaborate than in chimpanzees. An example of culture which leaves behind archeological traces is tool making. Apes are capable of making simple tools to solve an actual problem (for instance ripping off leafs from a twig to obtain termites), whereas humans sometimes spend much effort to make a tool for future use. Examples of such tools are the durable stone tools. The oldest reliably identified, manufactured stone tools were associated with Homo habilis. Probably it is no coincidence that tools are associated with the larger-brained Homo habilis. From that time on, brain size increased, as did the quality of the tools. The making of tools should not be discussed in isolation. The production of stone tools in present cultures living 'in the Stone Age' is characterised by (a) the emergence of a group of specialised tool makers (labour specialisation), (b) a tutor system to transmit these skills

and (c) a language enabling the transfer of knowledge (Toth et al. 1992). Remarkably, the brain sizes of the Neanderthalers and of modern man (*Homo sapiens sapiens*) do not differ. Yet, the Neanderthaler artefacts (Mousterièn) are stable and characterise a relatively conservative culture. Modern man, on the other hand, is continuously improving his tools from stones to computers. Modern man is really the Great Innovator.

On the basis of the material available, it is not possible to critically test the various hypotheses which selection pressure mainly contributed to the emergence of the large human brain. I would expect solutions to come from a different field of investigation. When the genes have been identified that distinguish human from chimpanzee brains, the products of these genes can be specified: molecular products, as well as their effects on brain size and structure. Such a scientific program is not simple, but its development is now in progress. It will take many years before we have some idea about how natural selection could eventually produce the brains of Kant, Einstein, Mozart, Michelangelo, Confucius or Buddha.   .

23.7.5.5
Ferungulata

The carnivores and ungulates are often considered sister groups. The basic pattern of cortical folding in these groups is similar (see also Chap. 22).

23.7.5.5.1
Carnivores

Most carnivores have brain weights above average for mammals of their body size.

1. Taxonomic relationships: Among the carnivores, the bears and canines have the largest brains, while the civets (Viverridae) and hyenas have proportionally the smallest brain weights (Gittleman 1986). However, these differences are rather small: the brain weights of civets and hyenas are about 70% of those of canines of comparable body weight. These differences in brain weight are hard to appreciate, since the behaviour of canines and hyenas does not seem to be too different.

2. Ecological relationships: Contrary to what their name suggests, several carnivores are not primarily meat eating. The bears are mainly fruit and leaf eating, and in various families of carnivores species eating mainly insects are found. A relationship between brain size and feeding pattern in carnivores is less clear than in bats, whales and primates, but it is present. Insect-eating carnivores have somewhat smaller brains than meat-, fruit/leaf-eating or omnivore carnivores (Gittleman 1986). Catching insects is more easy than catching mammalian prey; this could explain the smaller brains in insect-eating carnivores. In bats as well as carnivores, the insect-eating species are small brained, but in bats this is explained by a selection pressure to preserve food energy.

3. Parental care: In some carnivores, the offspring is raised by the mother alone (for instance the domestic cat), in others by both parents (for instance foxes) and in others by a larger social community (for instance wolves). Female carnivores that raise their offspring alone have somewhat larger brains than females that share parental care with their partner or other co-specifics (Gittleman 1994). Remarkably, this small difference is only present in females; carnivore male brain size does not depend on the system of parental care.

23.7.5.5.2
Tubulidentata

For a long time, the aardvark (*Orycteropus*) was considered an edentate. Elliot Smith (1898) noted large differences between the aardvark's brain and those of the edentates. The aardvark is now placed in a separate order (Tubulidentata), related to the ungulates. The aardvark has a small brain (Fig. 23.19).

23.7.5.5.3
Artiodactyla

The artiodactyles have brain weights close to average for mammals of their body weight. Corrected for body weight, small brains are found in pigs (Suidae) and the hippopotamus (but not in the pygmy hippopotamus, Fig. 23.16). Proportionally large brains are found in deer (Cervidae).

23.7.5.5.4
Cetaceans: Dolphins and Whales

The whales are now considered to be closely related to a group of artiodactyles, the Bovidae. Two main groups of whales are distinguished. The *baleen whales* are very large animals with body weights above 5 metric tons. They feed on plankton. Most *toothed whales* are smaller, with body weights between 50 and 2000 kg; only the adult sperm whale

is larger than 30 metric tons. Most toothed whales eat fish or sea mammals.

Toothed whales (except the sperm whale) have brain weights a factor of 2–5 above those of average mammals of their body size (Fig. 23.16). Their brains are three to five times heavier than those of seals and sea cows with similar body weights, so the large brains of whales are not simply due to their aquatic habitat. The brain weights of baleen whales on the other hand lie below the regression line for mammals. Must we then regard their brains with weights between 2 and 10 kg as small brains? I am not really inclined to do so.

Dolphins are the only animals with body as well as brain weights in the range of man (Fig. 23.16). The 91-kg white-beaked dolphin (*Lagenorhynchus albirostris*) has an average brain weight of 1.15 kg, and the 234-kg Risso's dolphin (*Grampus griseus*) a brain weight of 2.27 kg (Pilleri and Gihr 1970). As early as 15–20 million years ago (Miocene), toothed whales existed with large brains; the dolphin-like *Argyrocetus* of about 72 kg with a brain of 650 g, and the sperm-whale-like *Aulophyseter* with a presumed body weight of 1100 kg and a brain of about 2.5 kg (Jerison 1973). So for 15 million years, the whales were the mammals with the largest *EQ*s, and they still have the largest brains ever during the history of life. At the moment, we can only guess what selection pressures gave the Miocenic whales such large brains.

Toothed and baleen whales are often regarded as intelligent animals. Both groups use echolocation. But we have already seen in bats that excellent echolocation can be achieved by a very small brain. Whales make large migrations, which requires an elaborate guiding system. However, the homing specialists among birds, the pigeons, have small brains, and also migratory birds can accomplish long journeys with a small brain. The social organisation of groups of whales can be rather complex: conspecific helping and formation of alliances have been described (Caldwell and Caldwell 1966; Connor et al. 1992).

Aquatic mammals tend to develop large bodies (Sect. 23.7.2.5). Most fresh waters are not large enough for really big animals, but the oceans are. In toothed whales several selection pressures work together in favour of a large body, but they cannot become too big, since they must be able to make quick manoeuvres to catch their prey. This constraint does not apply to plankton-eating baleen whales. (This applies generally: also in sharks and rays, the plankton-eating species are huge: the whale shark and the manta ray). Therefore, it is suggested that especially in the evolution of baleen whales a strong net selection pressure is working in

favour of a large body. Probably, no selection pressure was then working to further increase their large brains. Baleen whales have large bodies rather than small brains.

23.7.5.5.5
Perissodactyla

Many good fossils are available of the ancestors of horses. During horse evolution, the sizes of body and brain gradually increased to their present size. The brain of the Eocean ancestor of horses, *Hyracotherium (Eohippus)*, had a size in the lowest range for a mammal of its body size. The present horses are much larger and have brains slightly smaller than the average mammal of their body size: not only the body and brain size has increased, but also the *EQ* of the horses. Other members of the Perissodactyla, the rhinoceroses and tapirs, have small brains: about half of the weight of that of the average mammal (Fig. 23.16).

23.7.5.5.6
Hyracoidea

The hyraxes have brain weights around the average for mammals of their body size.

23.7.5.5.7
Elephants

Elephants have large brains: the Indian elephant about 5 kg and the African elephant about 5.7 kg. The elephants' brains are in the same order of magnitude of those of whales with similar body sizes, but they are six to ten times larger than those of other large terrestrial mammals, the hippopotamus or rhinoceroses (Fig. 23.16).

23.7.5.5.8
Sirenia

Sea cows have rather small brains (Fig. 23.16), somewhat below the mammalian average, and about a tenth of the size of the brains of dolphins with similar body weights.

23.8
Concluding Remarks

A comparison of brain size in various groups of vertebrates does not lead to a general summarising conclusion, except that brain size in various groups is the product of different selection pressures. We are only beginning to understand why some animals have comparatively large brains. Writing and

understanding a detailed history of the evolution of brain size and ecology will still take many years. This chapter presents many facts about brain size and ecology that need to be explained in future analyses.

Appendix

In most discussions on brain size, allometric regression lines play a central role. But for instance in the discussion of the *EQ* of dogs (Sect. 23.1.3), the question was raised whether the dog data should be related to the regression line of dogs or of mammals. In my opinion, this problem is insoluble. In some instances, however, the problems of choosing the 'right' regression line are not relevant. Suppose one wants to investigate the relationship in mammals between brain size and the basal metabolic rate. Brain size and basal metabolic rate are allometrically scaled with body weight. Do then mammals with a large brain for their body weight also have a large metabolic rate for their body size? A solution then is to construct a database of species with data on body weight and brain weight as well as basal metabolic rate. The regression line between body weight and brain weight can be calculated. For each species in this database, the encephalisation quotient (*EQ*) is then calculated in the conventional way. Similarly, the regression line between body weight and metabolic rate is calculated. A new statistical parameter is calculated, the 'metabolic quotient' (*MEQ*), by exactly the same arithmetic as for the *EQ*. *MEQ* and *EQ* are calculated based on the regression lines for the same mammals (thereby escaping the problem of the choice of the correct regression line). The correlation coefficient between *EQs* and *MEQs* measures the strength of the association between brain weight (corrected for the body weight) and metabolic rate (corrected for the body weight). This applies not only for the basal metabolic rate, but also for other parameters that depend on body weight, such as longevity, home range and group size. The results of such calculations are presented in Table 23.3 and are mentioned in the text.

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