

Evolution of the brain and phylogenetic development of African Bovidae

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Evidence drawn from the study of 270 brains of 54 species and subspecies of African Bovidae makes it possible to base phylogenetic relationships on the similarities in the pattern of the cerebral sulci. Comparison of individual sulci of the cerebral cortex show that, despite individual variation, most genera can be characterized by distinctive patterns. A classification of the genera based on these patterns, after standardization, shows that they fall into seven discrete groups which, as a whole, agree with authorities such as Allen (1954) and Ansell (1971), who divide the family into 11 subfamilies. The surface area of the neocortex in the several genera is calculated revealing different levels of evolution in the subfamilies. This does not suffice as the only bases of comparison as the possibility of differences in the number of nerve cells remains. The neocortex development appears to be related to the social organization, feeding habits and the extent of similarity between the sexes.

S. Afr. J. Zool. 14: 119–124 (1979)

Gegronde op 'n studie van 270 breine van 54 spesies en subspecies van Afrika Bovidae, kan filogenetiese verwantskappe gebaseer word op ooreenkomste in die patrone van serebrale sulci. Vergelyking van individuele sulci van die serebrale korteks toon dat, ten spyte van individuele variasie, die meeste genera gekenmerk word deur eiesoortige patrone. 'n Klassifikasie van die genera gebaseer op hierdie patrone, na standaardisering, toon dat hulle in sewe herkenbare groepe val wat in die algemeen ooreenstem met dié van kenners soos Allen (1954) en Ansell (1971), wat die familie in 11 subfamilie indeel. Die oppervlakte area van die neokorteks in verskeie genera is bereken en dit dui op verskillende vlakke van evolusie in die subfamilie. Dit kan egter nie as die enigste maatstaf vir vergelyking gebruik word nie aangesien die moontlikheid van verskille in die aantal senuweeselle ook bestaan. Die ontwikkeling van die neokorteks hou blykbaar verband met die sosiale organisasie, voedingsgewoontes en die mate van ooreenkoms tussen die geslagte.

S.-Afr. Tydskr. Dierk. 14: 119–124 (1979)

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Accepted 15 January 1979

The study of the evolution of the mammalian brain, specifically of the neocortex of the telencephalon, provides significant information on the phylogeny of mammals. These relations are so obvious that the importance of brain size for any judgement of the phylogenetic position of large systematic units has been referred to again and again. The question is how to decide a reasonable standard brain size. Dubois (1898), Snell (1891) and Klatt (1921) emphasized the dependence of brain size on body size and proposed a brain exponent to measure it ($\text{brainweight} = b \times \text{body-weight}^a$, b = evolutionary factor, a = allometric exponent). Edinger (1948) analyzing brains of fossil Equidae, was the first to demonstrate the above mentioned relations for the different evolutionary levels of her material and to show that the evolution is also dependent on an encephalization factor. This factor relates, however, to the whole brain and therefore cannot be used satisfactorily to answer the more detailed questions arising within smaller systematic groups. Moreover, it can only be used efficiently for judging equally evolved types. The fossil brain, or endocast, which fills the mammalian skull, naturally yields only restricted information about those structures which have been significant in brain evolution. Only studies of recent species can reveal the missing details and these should be made before drawing further conclusions on phylogenetic questions. As has been pointed out repeatedly, for instance by Remane (1952) and Starck (1954), present-day living species cannot be regarded as direct descendants of other living species. Nevertheless comparative methods, if critically applied to the study of recent brain material, can yield significant results in phylogenetic deduction. It has been known for many years that primitive forms of certain lineages can remain alive throughout long geological periods, while more specialized relatives become extinct rather early.

It can also be seen within the Eutheria that the progressive development of the neopallium eventually suppresses the other parts of the pallium. Radinsky (1976a, b), comparing endocranial casts of different eutherian groups, established that the anterior part of the neopallium participates first in the increased size of the brain. This fact can also be confirmed by comparing living species of closely related systematic level but different brain size such as *Hyaena* and *Crocuta* or *Mustela* and *Martes*.

Attention can be drawn to the fact, however, that brain evolution in mammals took place in different ways. Within the basal group of the Insectivora Stephan (1961) found at least three different stages of neocortical evolution. Evolutionary change of the neocortex is indicated on its surface by the shift of the boundary sulcus (*Sulcus rhinalis*) between palaeocortex and neocortex (Fig. 1) towards the base of the brain, and can be confirmed by quantitative evaluation of the different brain parts.

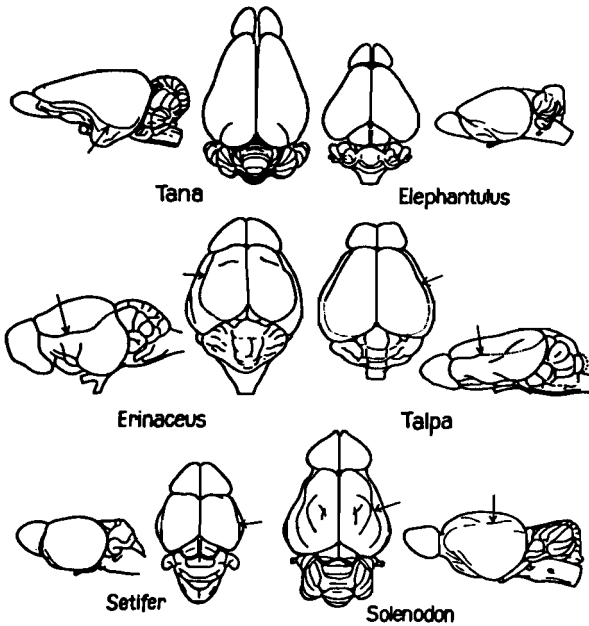


Fig. 1 Brains of primitive mammals (the arrow indicates the fissura rhinalis) (After Stephan 1959).

Nevertheless, morphological analysis shows that the different neocortical regions are not developing equally. The lineages of primates show a relative decline of the olfactory system, while the optical systems are enlarged. It is characteristic of the primates that the areas for associations in the frontal, temporal and parietal lobes are developed extraordinarily. The profound interest in human evolution — and man is the final stage of this trend — provides the motivation for the investigation of primate evolution and physiological studies have established connections between structure and function.

The analysis of the brain in order to corroborate supposed phylogenies in other mammalian orders has long been neglected. Though Krueg (1887) in his first studies on the development of cerebral sulci drew attention to their different shape in various mammalian orders, no information about smaller systematic groups existed. The investigations of Edinger (1948) verified that the patterns of cerebral sulci of recent equidae must have been established at about the Miocene period (Fig. 2) and Radinsky (1976a, b) came to the same conclusion regarding the Canidae and Felidae. This is, according to Thenius (1972), the period during which recent subfamilies originated and it should therefore be possible to base phylogenetic relations on the similarities of patterns in cerebral sulci. It should be understood that only richly grooved brains can serve as material for such analyses, as only they have sufficient complexity for differing trends to be distinguishable. In 1958 Anthony pointed out that the brain morphology of the artiodactyls differs significantly between the Bovidae and Suidae. Moreover, among the Bovidae the Cephalophinae show a charac-

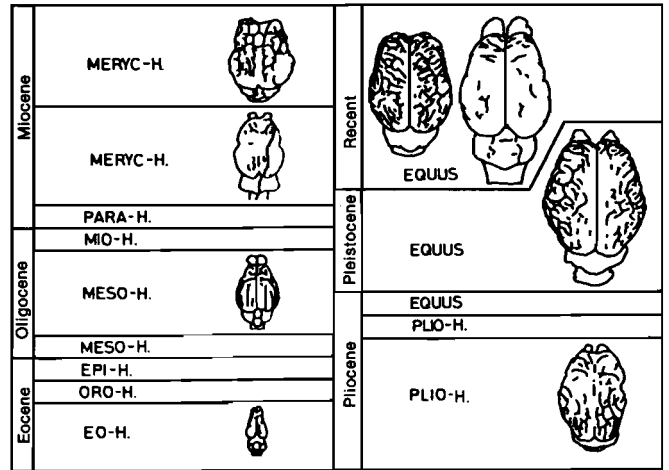


Fig. 2 Evolution of the horse brain (After Edinger 1948).

teristically small number of brain sulci. Further guidance on the possibility of using brain morphology for settling questions of phylogenetic correlations in the Bovidae was not given. In the course of several expeditions to Africa I have tried to obtain as representative a selection of material as possible, covering several genera and species, in order to study these continuing problems. As material coming from zoological gardens is only of limited use for brain investigations, I was fortunate to collect 270 brains of 54 species and subspecies, on which to base my studies. This means that nearly all African species could be taken into consideration. If the individual sulci of the cerebral cortex are compared, it can be shown that in spite of any individual variation most genera can be characterized by distinctive patterns.

Classification of the genera according to their similarity grade in sulcus patterns leads — after some standardization — to at least seven types (Fig. 3). As a whole these types reflect the same classification into 11 subfamilies which Allen (1954) established for the Bovidae and is in close agreement with Ansell (1971). Comparison with the aforementioned investigations of Edinger (1948) and

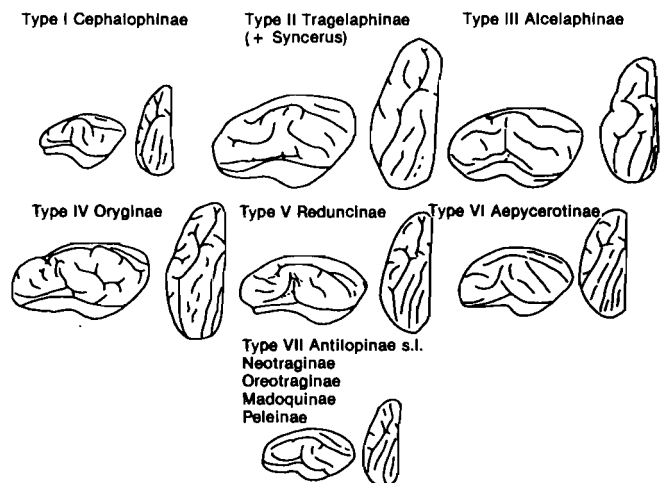


Fig. 3 Types of sulci patterns. Type I: *Cephalophinae*; Type II: *Tragelaphinae* (including *Syncerus*); Type III: *Alcelaphinae*; Type IV: *Oryginae*; Type V: *Reduncinae*; Type VI: *Aepycerotinae*; Type VII: *Antilopinae* s.l. (*Neotraginae*, *Oreotraginae*, *Madoquinae*, *Peleinae*).

Radinsky (1969) on fossil material suggests a classification of genera into at least seven subfamilies which have presumably existed since the Miocene period.

To find an answer to the question whether different evolutionary grades of encephalisation exist among the Bovidae, the brain weight of the species was plotted against the body weight. When the data are placed on a double logarithmic co-ordinate system, the arrangement of systematic groups along the regression line is noticeable (Fig. 4). Measurements of the same order have been combined. The arithmetic means of body weight and brain weight fit into a formula, which demonstrates interspecific relations between both parameters. According to Oboussier & Schliemann (1966) this formula reads:

$$\log \text{ brain weight} = 1,2258 + 0,56 \text{ body weight},$$

and the correlation coefficient is $r = 0,98$

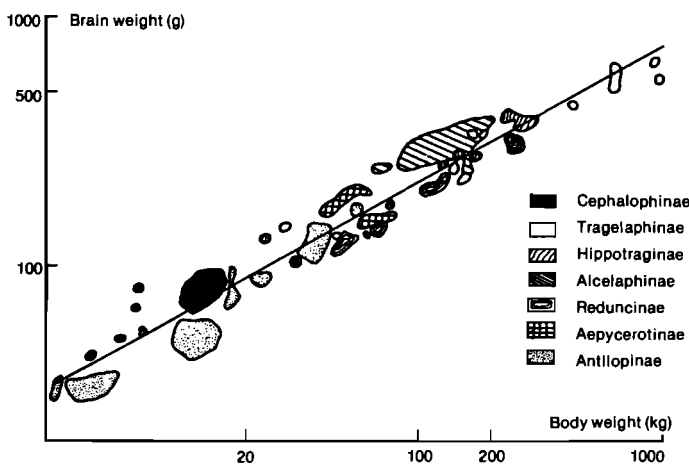


Fig. 4 Brain-body weight correlation of different sub-families compared to the general regression ratio.

By comparison of the difference in the brain weight after the effect of the body weight has been eliminated, it becomes evident that the encephalization grade in different groups is not uniform. If these lines are then compared with one another, it emerges that the Alcelaphinae and Cephalophinae are noticeably more encephalized than the Reduncinae and Tragelaphinae or Antilopinae (Fig. 5). An example will illustrate this point: individuals of the Cephalophinae, having a body weight of less than 20 kg, average 6,7 g of brain weight for every one kg of body weight. However, in Antilopinae this is only 4,6 g.

Since significant differences are given when the patterns of the cerebral sulci are compared, it is better to base discussion concerning encephalization grades not on the entire brain weight but on development of the neocortex. In collaboration with Ronnefeld (1970) and Haarmann (1972), studies have been carried out, based on 123 individuals of 40 species following Elias, Haug, Lange, Schlenska and Schwarz (1969) calculating the neocortex surface after an analysis of rather thick sections through the brain material. Later new material was integrated but no significant differences were obtained.

The formula for this method is:

surface =

$$\frac{2 \times \text{line distance} \times \text{thickness of section} \times \text{number of intersection points}}{\text{number of countings}}$$

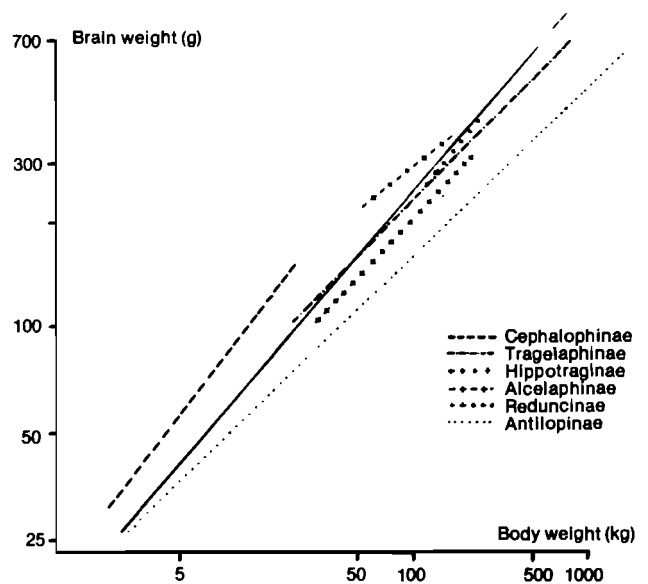


Fig. 5 Brain-body weight correlation, regression ratios of the subfamilies.

General regression ratio	$\log y = 1,2258 + 0,56 \log x$ ($r = 0,98$)
<i>Cephalophinae</i>	$\log y = 1,1178 + 0,72 \log x$ ($r = 0,99$)
<i>Tragelaphinae</i>	$\log y = 1,3726 + 0,48 \log x$ ($r = 0,96$)
<i>Hippotraginae</i>	
<i>Oryginae</i>	$\log y = 1,0800 + 0,62 \log x$ ($r = 0,88$)
<i>Alcelaphinae</i>	$\log y = 1,6716 + 0,38 \log x$ ($r = 0,76$)
<i>Reduncinae</i>	$\log y = 1,2355 + 0,52 \log x$ ($r = 0,93$)
<i>Antilopinae</i>	$\log y = 1,2514 + 0,46 \log x$ ($r = 0,98$)

Again straight lines of regression of neocortex size in relation to brain weight have been calculated and show the tendencies of the groups as such compared with the general straight line of regression based on average data (Fig. 6).

The differences in the cerebral sulcus patterns should be significant in this connection, but despite their small number

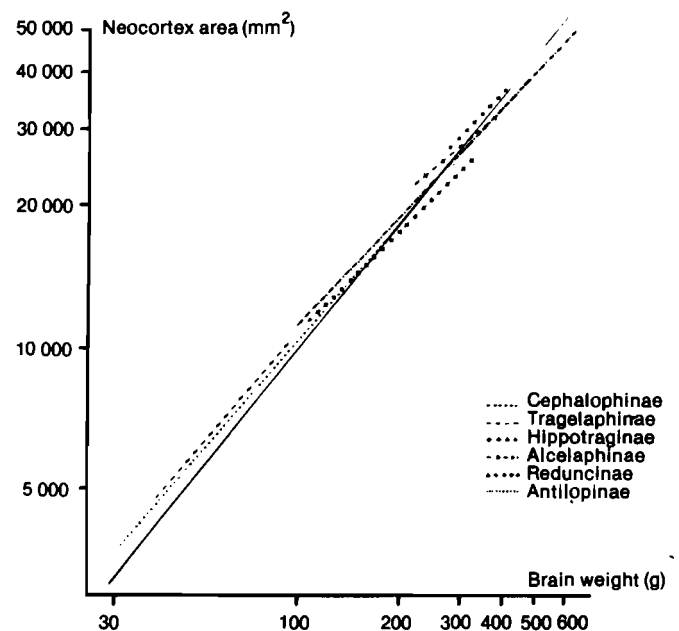


Fig. 6 Neocortex area-brain weight correlation of different subfamilies compared to the general regression ratio.

General regression ratio	$\log y = 2,1035 + 0,94 \log x$ ($r = 0,98$)
<i>Cephalophinae</i> and <i>Antilopinae</i>	$\log y = 2,5344 + 0,68 \log x$ ($r = 0,96$)
<i>Tragelaphinae</i>	$\log y = 2,4416 + 0,80 \log x$ ($r = 0,98$)
<i>Oryginae</i>	$\log y = 2,5300 + 0,78 \log x$ ($r = 0,99$)
<i>Alcelaphinae</i>	$\log y = 2,8763 + 0,63 \log x$ ($r = 0,58$)
<i>Reduncinae</i>	$\log y = 1,5265 + 0,75 \log x$ ($r = 0,92$)

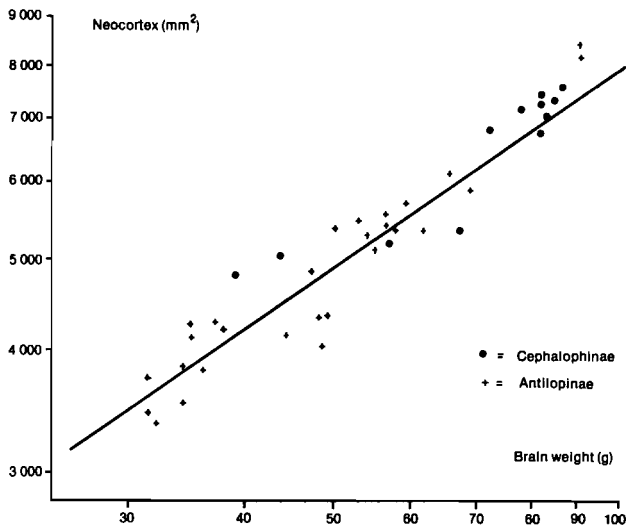


Fig. 7 Neocortex area-brain weight correlation of *Cephalophinae* and *Antilopinae* single figures in correlation to the regression ratio. (log y = 2,5344 + 0,68 log x (r = 0,96).

of sulci, the *Cephalophinae* show, in relation to brain weight, the same development of the neocortical surface as the *Antilopinae* which are richly endowed with sulci of shallower depth than the former (Fig. 7). In other species the differences show no change. This is even more striking if, in spite of the numbers of individuals on which it is based, the formulae for each group are considered separately as shown for example for the *Hippotraginae* or *Tragelaphinae* (Figs. 8 & 9). Thus, if the results gained so far on the relation of brain weight to body weight are summed with the results gained for the relation between neocortical development and brain weight, in order to find out the relation between neocortical surface to body weight (Fig. 10), the differences are not eliminated. It must be presumed that different directions of evolution in the *Bovidae* have been followed, viz. the enlargement of the cerebrum; and development of sulci; the latter showing a small number of rather deep sulci, (e.g. *Cephalophinae*) or rich endowment with superficial sulci, (e.g. *Antilopinae*).

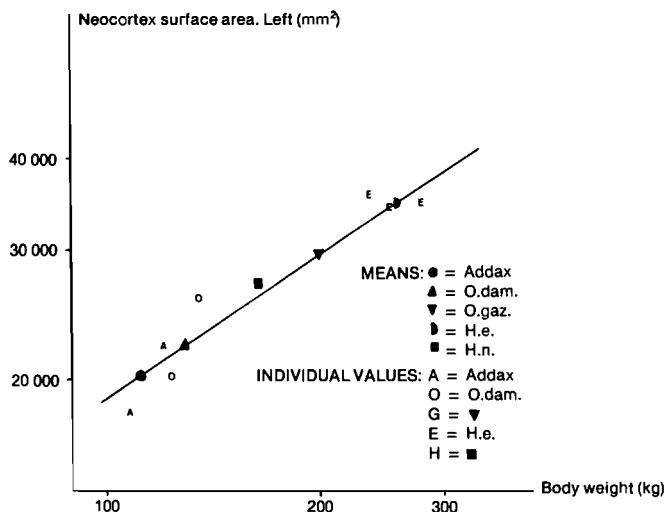


Fig. 8 Neocortex area-body weight correlation in *Hippotraginae*. Regression ratio: log y = 2,94 + 0,66 log x (r = 0,99) (After Oboussier 1974).

- Addax = *Addax nasomaculatus*
- O. dam. = *Oryx dammah*
- O. gaz. = *Oryx gazella*
- H. e. = *Hippotragus equinus*
- H. n. = *Hippotragus niger*

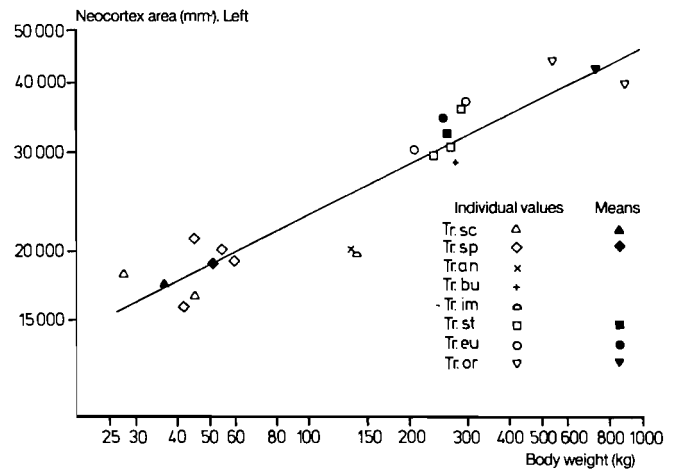


Fig. 9 Neocortex area-body weight correlation in *Tragelaphinae*. Regression ratio: log y = 3,76 + 0,30 log x (r = 0,92).

- Tr. = *Tragelaphus*
- sc = *scriptus*
- sp = *spekei*
- an = *angasi*
- bu = *buxtoni*
- im = *imberbis*
- st = *strepsiceros*
- eu = *euryceros*
- or = *oryx*

The differences in the encephalization grades between the subfamilies of the *Bovidae* are confirmed with regard to the development of the neocortex. It remains to be tested whether the anatomy of the neocortex in both mentioned subfamilies is the same, or whether there are differences in the number of nerve cells. If so, the extension of the neo-

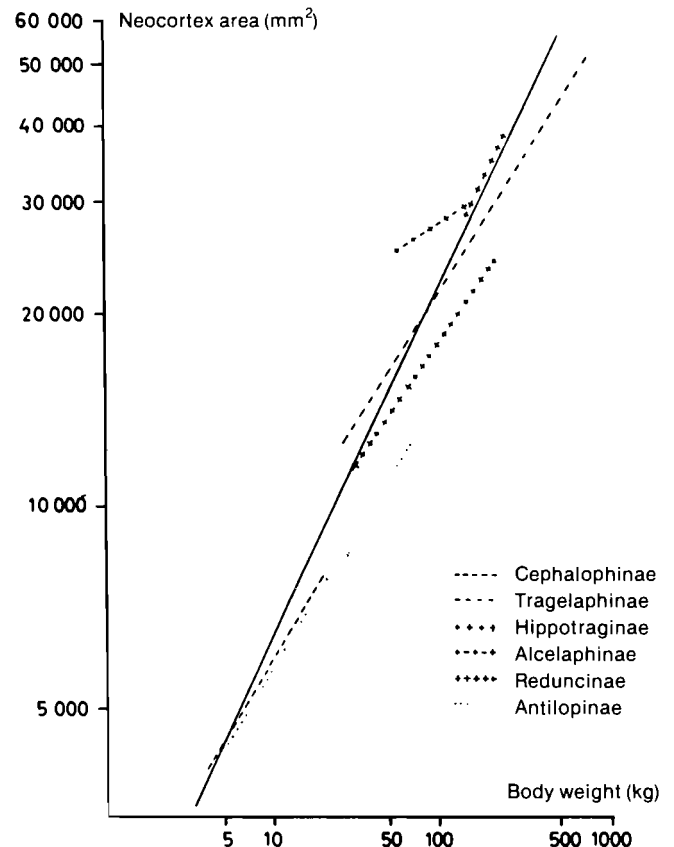


Fig. 10 Neocortex area-body weight correlation. General regression ratio Log y = 3,2860 + 0,51 log x

- Cephalophinae* and *Antilopinae* log y = 3,3659 + 0,39 log x
- Tragelaphinae* log y = 3,5246 + 0,39 log x
- Oryginae* log y = 4,0975 + 0,52 log x
- Alcelaphinae* log y = 3,2900 + 0,16 log x
- Reduncinae* log y = 3,5100 + 0,36 log x

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cortical surface could not be made the only basis of comparison, as experienced from the well-known examples of the dolphin and man.

Taking these possibilities into account, Haarmann (1972) measured the thickness of the cortex in Tragulidae as well as in Cephalophinae and Antilopinae. The cortex was 1,3 mm thick in Tragulidae, 1,8 mm thick in Cephalophinae and 1,6 mm thick in Antilopinae. He compared the number of pyramid cells in corresponding neocortical areas of these groups. The primitive Tragulidae have approximately 10^8 pyramid cells in the neocortex of one hemisphere while the Bovidae have nearly double this figure namely $1,6 \times 10^8$. The Cephalophinae have more space between the pyramid cells. Therefore it can be presumed that they have more connecting cells. The Antilopinae split in three different groups: Antilopini, Neotragini and Oreotragini (Fig. 11). The brain of the latter has a thinner cortex

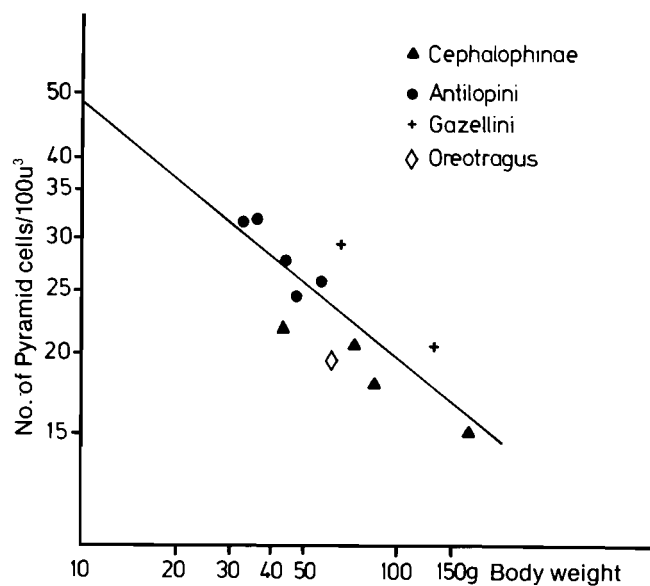


Fig. 11 Correlation between number of pyramid cells and brain weight in *Cephalophinae* and *Antilopinae*. (After Haarmann 1972).

and has nearly the same proximity of pyramid cells as in *Cephalophinae*. This species must be less evolved with reference to the brain as the total surface is smaller. The brains of the Antilopini are richly endowed with sulci and the surface area of the neocortex is of the same order as that in the *Cephalophinae*, but the volume is less as the cortex is thinner, and the pyramid cells are a little closer. The index is lower than in the *Cephalophinae* but higher than in the *Neotraginae*, the brains of which are less endowed than in *Antilopinae*. Taking these results into account, it is apparent that the *Cephalophinae* are not primitive and that the structure of the brain of the *Antilopinae* suggests that this subfamily is composed of three different groups: Antilopini, Neotragini and Oreotragini.

At present, the close relationship between the other subfamilies seems to allow the presumption that the results obtained might be regarded as a hint of the phylogenetic subdivision of the family Bovidae. However, more individual sampling of material could result in a further revision and might lead to a clearcut separation of *Syncerus* from the *Tragelaphinae* or other splitting.

Comparing the results of the investigations on neocortex development in Bovidae with other findings on antelopes, it

is apparent that a higher degree of development of the neocortex is linked with a trend to a more social organization (Leuthold 1977) and a change from browser to grazer. This results at the same time in a higher degree of specialization in the structure of the stomach related to changes in the digestive tract (Hofmann 1973) as well as the structure of the lower jaw (Stöckmann 1975). Higher brain evolution is apparently also linked with greater similarity between the sexes as in the upper groups *Alcelaphinae* and *Hippotraginae* in which both sexes are of approximately the same size with similar horns. Some of these trends may even be apparent in a single subfamily such as the *Tragelaphinae* (Oboussier 1978; Oboussier & Ernst 1977).

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