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QUANTITATIVE COMPARISONS OF BRAIN STRUCTURES FROM INSECTIVORES TO PRIMATES

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INTRODUCTION

The primary objective of this investigation is the quantitative study of the brain and its constituent parts in their phylogenetic development leading to man. There are two possible approaches for this purpose. One is that of paleoneurology, as employed by Tilly Edinger and others. This method deals with endocranial casts of extinct animals. The second is the approach of comparative neuroanatomy utilizing brains of living species. Living species, in contrast to the available fossils, may be further away from our phylogenetic line of interest. However, they permit a more detailed analysis of relationships among the internal brain structures. The primates, in addition to other orders of placental mammals, are thought to originate from primitive insectivores, and thus, the living representatives of the latter were used as a basal group of reference. This study extends from the primitive insectivores, through prosimians, to lower monkeys.

METHOD AND TECHNIQUE

Animals. The evolutionary levels were based upon the degree of development and differentiation of the neocortex (Fig. 7), since it is considered the most reliable measure presently available.

Fourteen species of insectivores, representing seven of the eight existing families; four species of prosimians, of three different families; and three monkeys from both families of new-world monkeys were used. In the tabulation which follows, their systematic position is shown as well as their English common names. For the analysis of the brain structures it was convenient to make use of four major groups as indicated by the entries in small capitals in the tabulation. The number which follows the species name shows how many specimens were used.

The group called basal forms includes terrestrial and non-specialized species of three families. They show the simplest cortical pattern and smallest cortical volume.

The "higher insectivores" include representatives of five families. These are specialized in respect to aquatic life, burrowing, or large eyes. For some of the comparisons, certain of them must be treated separately.

The tree shrew *Tupaia* is sometimes treated separately from the other prosimians since both its brain development and taxonomic position place it close to the insectivore-primate boundary.

Insectivora

SPECIES USED AS BASAL FORMS
Tenrecidae (tenrecs)
Tenrec ecaudatus 1 tenrec
Setifer (=Ericulus) setosus 2 hedge-

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hog tenrec
Erinaceidae (hedgehogs)
Erinaceus europaeus 2 European hedgehog
Soricidae (true shrews)
Crocidura occidentalis 2
Crocidura russula 2 house shrew
Sorex araneus 2 forest shrew
Sorex minutus 1 pigmy shrew

SPECIES REGARDED AS "HIGHER INSECTIVORES"
Soricidae
Neomys fodiens 2 old-world water shrew
Potamogalidae (otter shrews)
Potamogale velox 2
Chrysochloridae (golden moles)
Chlorotalpa stuhlmanni 2
Talpidae (moles)
Talpa europaea 1 common old-world mole
Galemys pyrenaicus 2 Pyrenean desman, almizilero
Macroscelididae (elephant shrews)
Elephantulus fuscipes 2
Rhynchocyon stuhlmanni 2

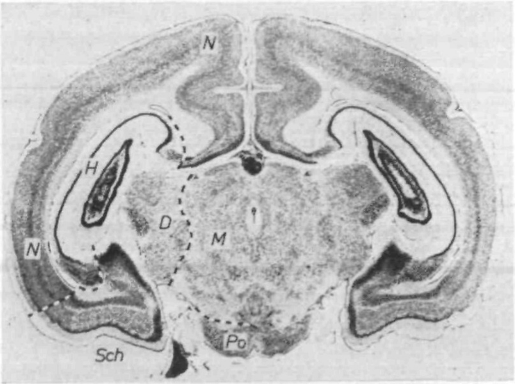
Primates

PROSIMII
Tupaiidae (tree shrews)
Tupaia glis 2 common tree shrew
Lorisidae (lorises)
Perodicticus potto 2 potto
Loris gracilis 1 slender loris
Galagidae (galagos)
Galago demidovii 2 bushbaby

ANTHROPOIDEA
Ceboidea (= Platyrrhina) new-world monkeys
Callithricidae
Callithrix (=Hapale) jacchus 1 marmoset
Leontocebus (=Oedipomidas) oedipus 1 tamarin
Cebidae
Aotes trivirgatus 1 douroucouli, owl monkey

The brain structures considered were: medulla oblongata, cerebellum, mesencephalon, diencephalon, and telencephalon. The telencephalon was further subdivided into neocortex, schizocortex, hippocampus, septum, paleocortex-amygdala complex, bulbus olfactorius, and striatum.

Histology and photography. The brains were perfused with Bouin's solution immediately after the animals were sacrificed. Serial paraffin sections, in the frontal plane, 10 to 20 μ thick, were stained with cresyl violet. All sections of the smaller brains and every tenth of the larger were stained. Fifty to sixty serial sections, taken at equal intervals in each brain, were pho-



ABBREVIATIONS FOR FIGS. 1, 2, and 3
C.a, Commissura anterior
D, Diencephalon
H, Hippocampus
M, Mesencephalon
N, Neocortex
P, Palaeocortex
Po, Pons
S, Septum
Sch, Schizocortex
St, Striatum

FIG. 1. *Galago demidovii*, brain A 87. Frontal section 596, ×4.5. Cresyl violet, 20 μ.

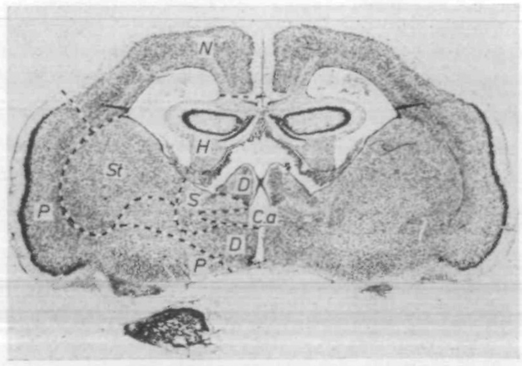


FIG. 2. *Tenrec ecaudatus*, brain 1015. Frontal section 889, ×5.5. Cresyl violet, 10 μ. (See Fig. 1 for abbreviations.)

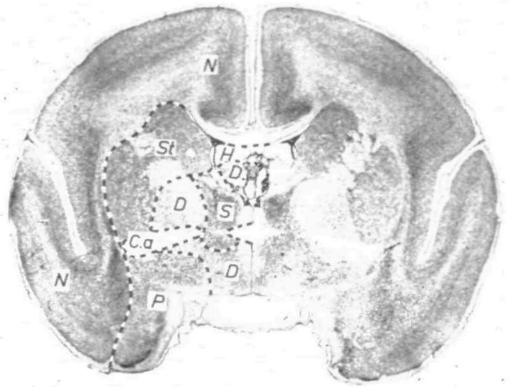


FIG. 3. *Leontocoebus oedipus*, brain 979. Frontal section 696, ×3.5. Cresyl violet, 15 μ. (See Fig. 1 for abbreviations.)

tographed with magnifications of 9 to 35 times. Photo-histologic details were enhanced by employing photographic paper of proper grain density for each brain series.

Volume determinations. The histological serial section method was used to determine the volumetric differences of various brain structures. The divisions were outlined on enlarged histological photographs (Figs. 1-3), cut out, and weighed. The photographic paper was measured and weighed to determine the number of square mm per gram. The volume of each structural division was then determined by obtaining the product of the interval distance between the sections and the mm equivalent of the weighed structures. This was then divided by the square of the linear magnification.

Evaluation of data. The volumetric changes of various brain structures were analyzed with two different systems of reference. (1) a: The five major subdivisions of the brain were evaluated in relation to total brain volumes, and b: the seven subdivisions of the telencephalon in relation to the total telencephalic volumes. (2) The five major divisions and the seven telencephalic subdivisions also were evaluated in relation to total body weight.

The first method of analysis only indicates changes which are relative to volumes of other brain structures. In order to obtain a better measure of the phylogenetic changes, it is necessary to compare a structure with an independent reference point (Stephan, 1960). Body weight was used

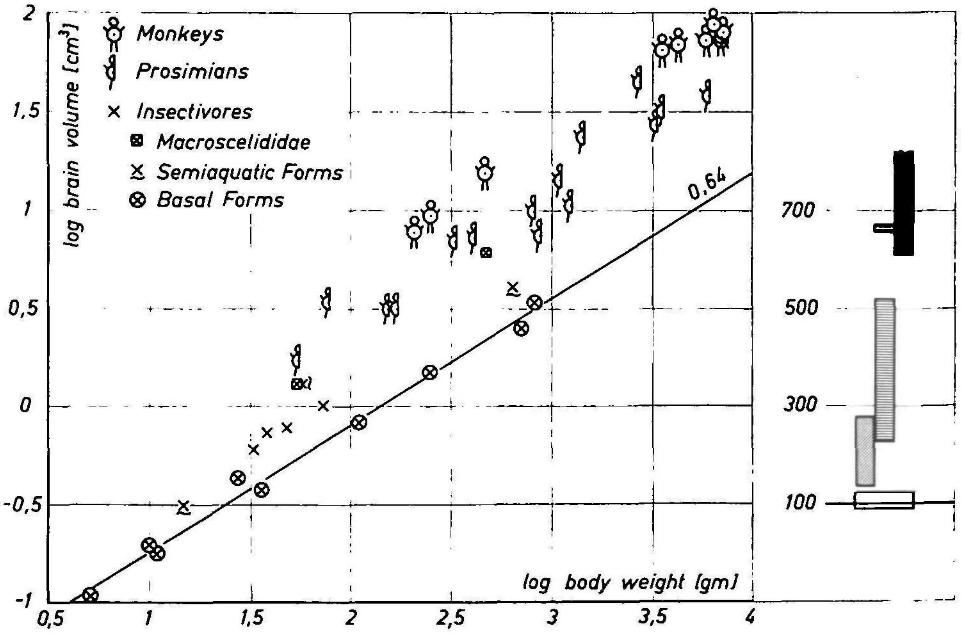


FIG. 4. Total brain volumes plotted against body weight. Regression lines in this and other figures were constructed from insectivores identified by encircled crosses (basal insectivores).

for this purpose, in accord with the allometric method developed by Snell (1892) and Dubois (1897). The relationship between body weight and brain volume, within a group of closely related species, is characterized by the allometric formula $h \sim k^r$; that is, the brain volume is proportional to the body weight raised to the power r (< 1). In the system of double logarithmic coordinates, which must be used to save space, this parabola becomes a straight line ($\log h \sim r \cdot \log k$) the slope of which corresponds to the tangent of the exponent r (Fig. 4).

Base line of reference for phylogenetic changes. This method was applied to determine the relation between the volumes of various brain structures and body

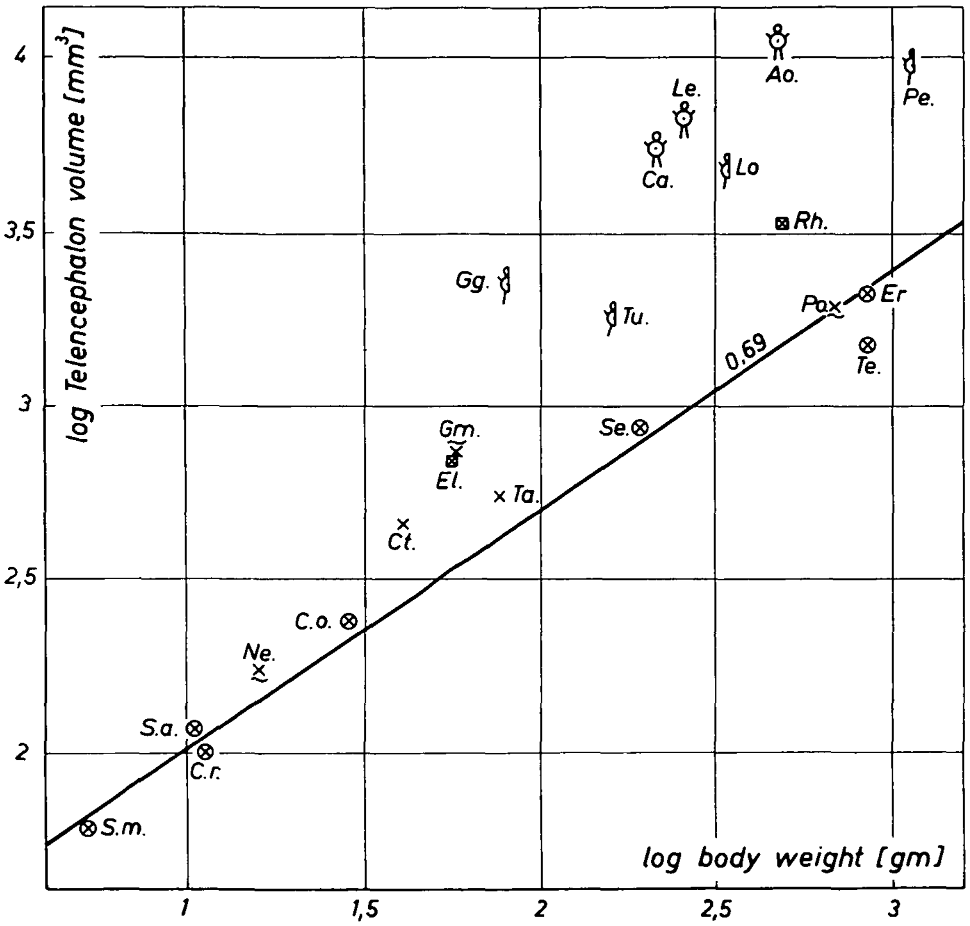


FIG. 5. Telencephalon volumes plotted against body weight.

ABBREVIATIONS FOR FIGS. 5-10

Ao., *Aotes trivirgatus*
Ca., *Callithrix jacchus*
C.o., *Crocidura occidentalis*
C.r., *Crocidura russula*
Ct., *Chlorotalpa stuhlmanni*
El., *Elephantulus fuscipes*
Er., *Erinaceus europaeus*
Gg., *Galago demidovii*
Gm., *Galemys pyrenaicus*
Le., *Leontocoebus oedipus*
Lo., *Loris gracilis*
Ne., *Neomys fodiens*
Pe., *Perodicticus potto*
Po., *Potamogale velox*
Rh., *Rhynchocyon stuhlmanni*
S.a, *Sorex araneus*
Se., *Setifer setosus*
S.m., *Sorex minutus*
Ta., *Talpa europaea*
Te., *Tenrec ecaudatus*
Tu., *Tupaia glis*

weights in the basal insectivores (terrestrial forms of the Soricidae, Tenrecidae, and Erinaceidae). The values obtained for each "brain-structure/body-weight" relationship was then used as a baseline of reference for phylogenetic changes among the higher forms, i.e., higher insectivores, prosimians, and monkeys (Figs. 5-10).

The principle of utilizing primitive insectivores as the base for comparisons was also used by Wirz (1950). However, she employed rather rough macromorphologic criteria for determining structural boundaries, whereas we used histological ones. She also used the brain-stem/body-weight relationship as the single point of reference for all brain structures. In addition, two of the three insectivores that she used for the base line (*Neomys, Talpa*) do not represent true basic forms, since they have specialized habits. For this reason we did not include those two among the basal forms in the present study.

Illustrations of results. Graphic presentations of the results were made by constructing individual regression lines for each brain-structure/body-weight value found in the basic forms (Figs. 5-10), and plotting the corresponding brain-structure/body-weight value of higher forms on the same graphs. In addition, the percentage deviation of a given structure from the base line (or regression line) was illustrated on a vertical graph in which the value of the basic forms was considered 100% and represents the reference point. The points of reference for the various structures are represented by the 100% horizontal bar (Figs. 13, 14). A similar method was previously employed in a

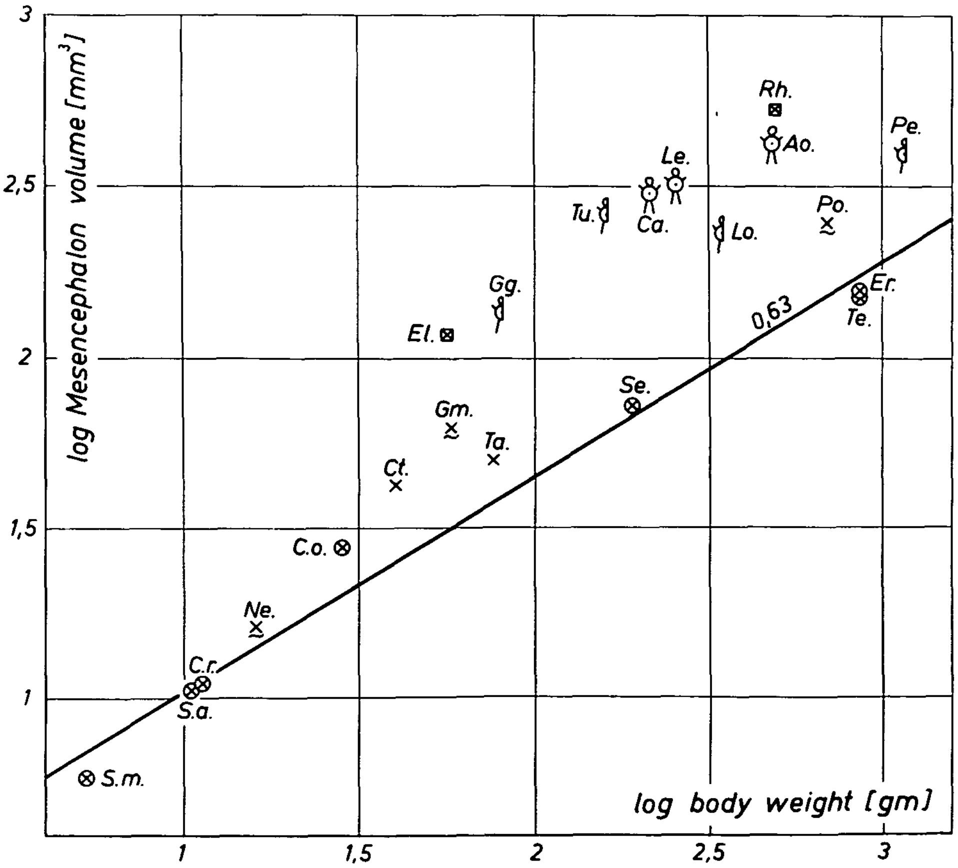


FIG. 6. Mesencephalon volumes plotted against body weight. (See Fig. 5 for abbreviations.)

quantitative study of the phylogenetic development of the septum in insectivores and lower primates (Stephan and Andy, 1962).

RESULTS

Major brain divisions in relation to total brain volume (Fig. 11). The average brain in the basal insectivores was composed of 13% medulla, 12% cerebellum, 6% mesencephalon, 8% diencephalon, and 61% telencephalon. In monkeys, the telencephalon made up 74% of the total brain weight. With this method of comparison, percentages of other subdivisions were, of course, reduced. The greatest reduction was evident in the medulla from 13% in basal insectivores to 4% in monkeys. The mesencephalon underwent a reduction of 6% to 3%, whereas no significant changes were noted in the cerebellum and diencephalon.

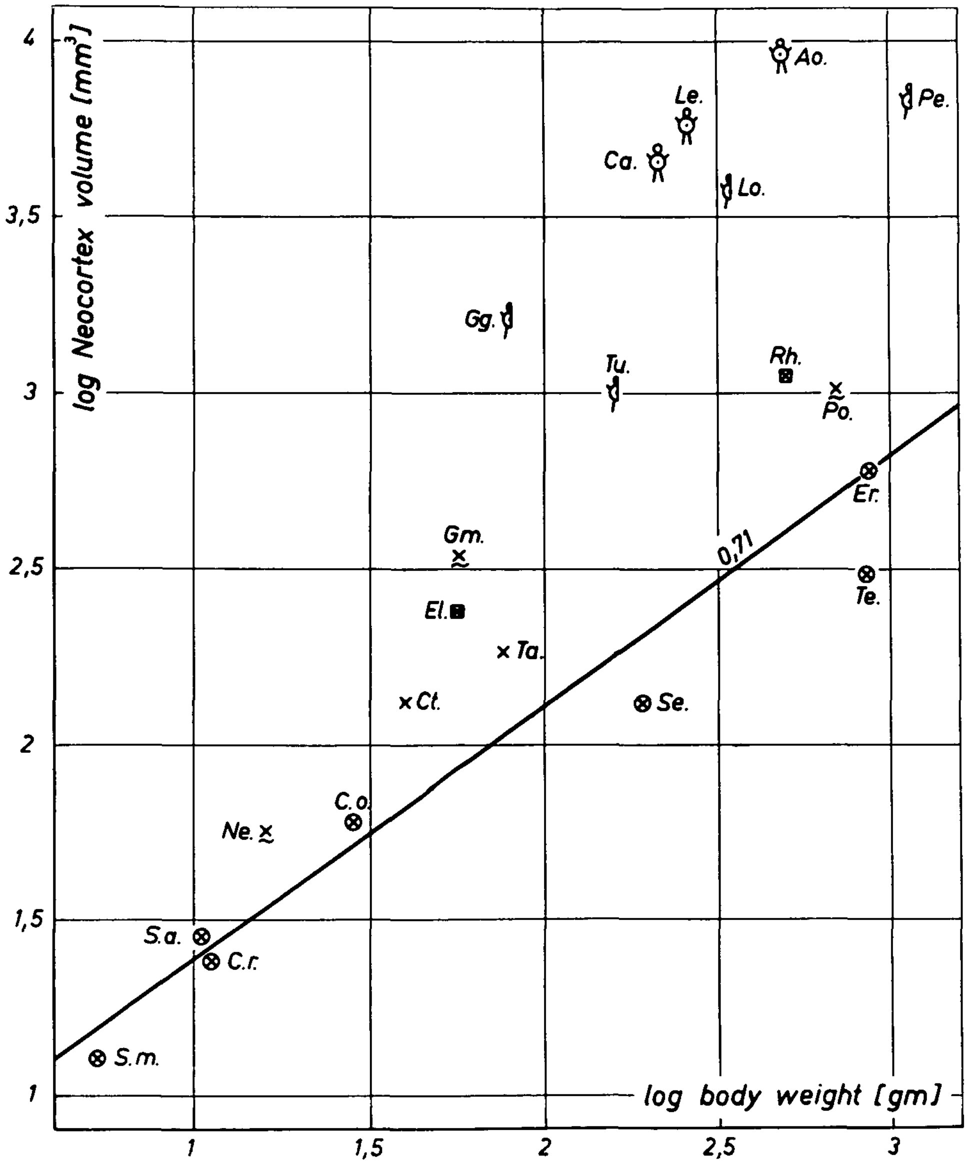


FIG. 7. Neocortex volumes plotted against body weight. (See Fig. 5 for abbreviations.)

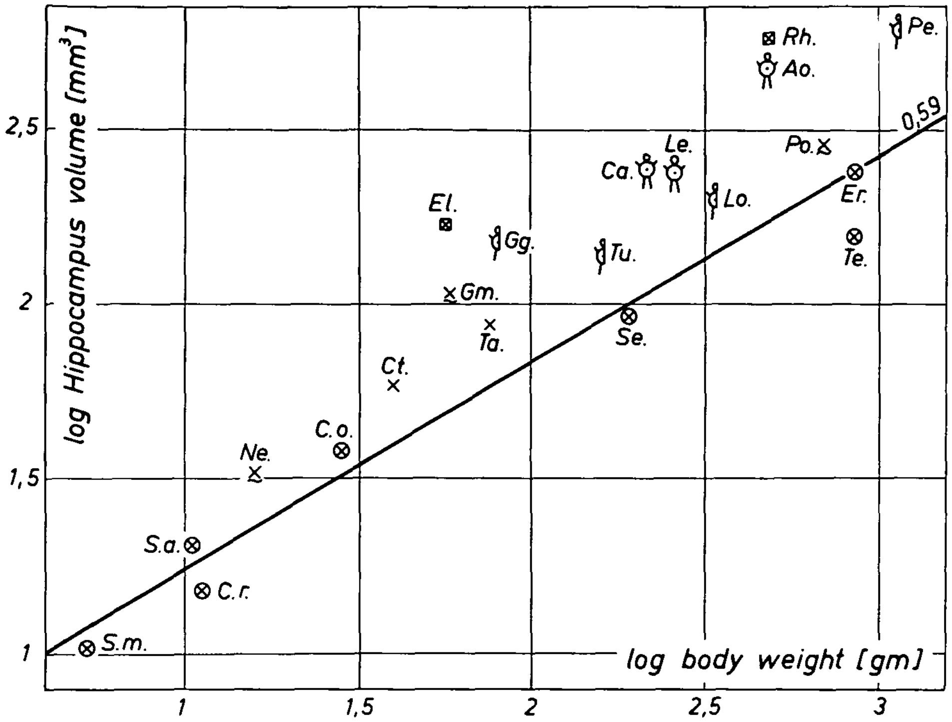


FIG. 8. Hippocampus volumes plotted against body weight. (See Fig. 5 for abbreviations.)

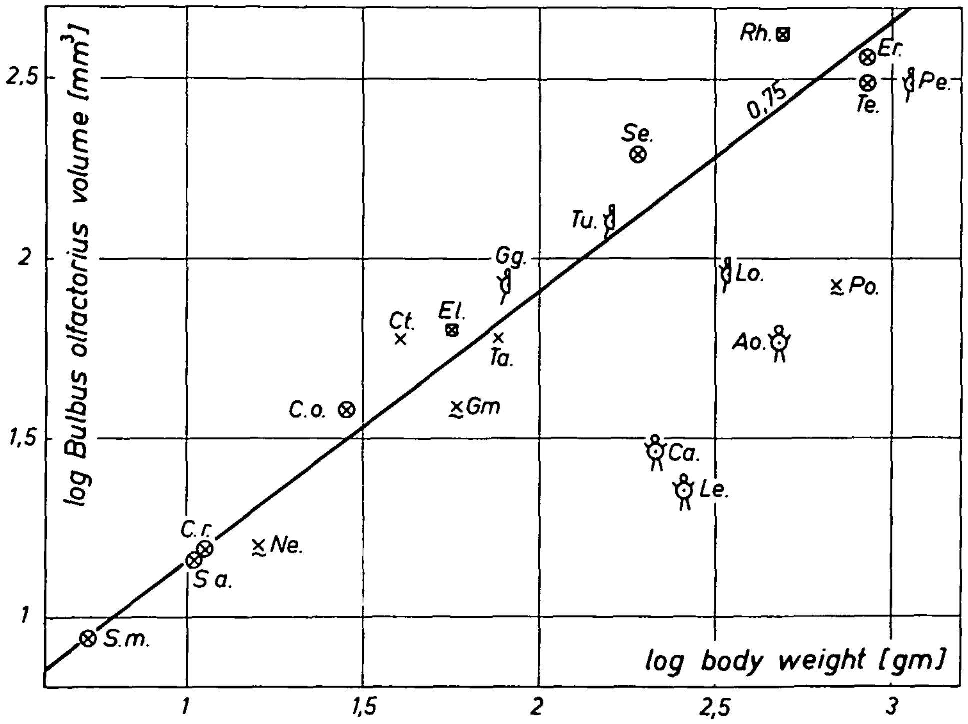


FIG. 9. Bulbus olfactorius volumes plotted against body weight. (See Fig. 5 for abbreviations.)

Subdivisions of the telencephalon in relation to total telencephalon volume (Fig. 12). Analyses of subdivisions of the telencephalon revealed a very marked increase of the neocortex, from 22% in basal insectivores to 83% in monkeys. Other telencephalic structures underwent a relative reduction, the greatest were in the olfactory bulb (17% to 0.4%) and paleocortex-amygdaloid complex (31% to 4%). The least reduction was in the striate body (8% to 6%). Small reductions were also present in the schizocortex, hippocampus, and septum.

The question arises as to whether or not these decreases are a result of true phylogenetic reduction or whether they are primarily due to the marked growth of the neocortex. The following method, utilizing body-weight as a reference system, is applied to the data in order to answer the question.

Major brain divisions in relation to body-weight (Fig. 13). Among the five major divisions of the brain, the *telencephalon* (Fig. 5) undergoes the greatest phylogenetic development. In monkeys it reaches a size 6.5 to 7.5 times the size in the basal insectivores (x BI). It is next highest in prosimians, and lowest in the insectivores. In *Tupaia,* as would be expected, the enlargement is between that of insectivores and prosimians. Among the Macroscelididae the telencephalon is larger than in the other insectivores. However, a semiaquatic form, *Galemys,* has an enlargement equal to that of the Macroscelididae.

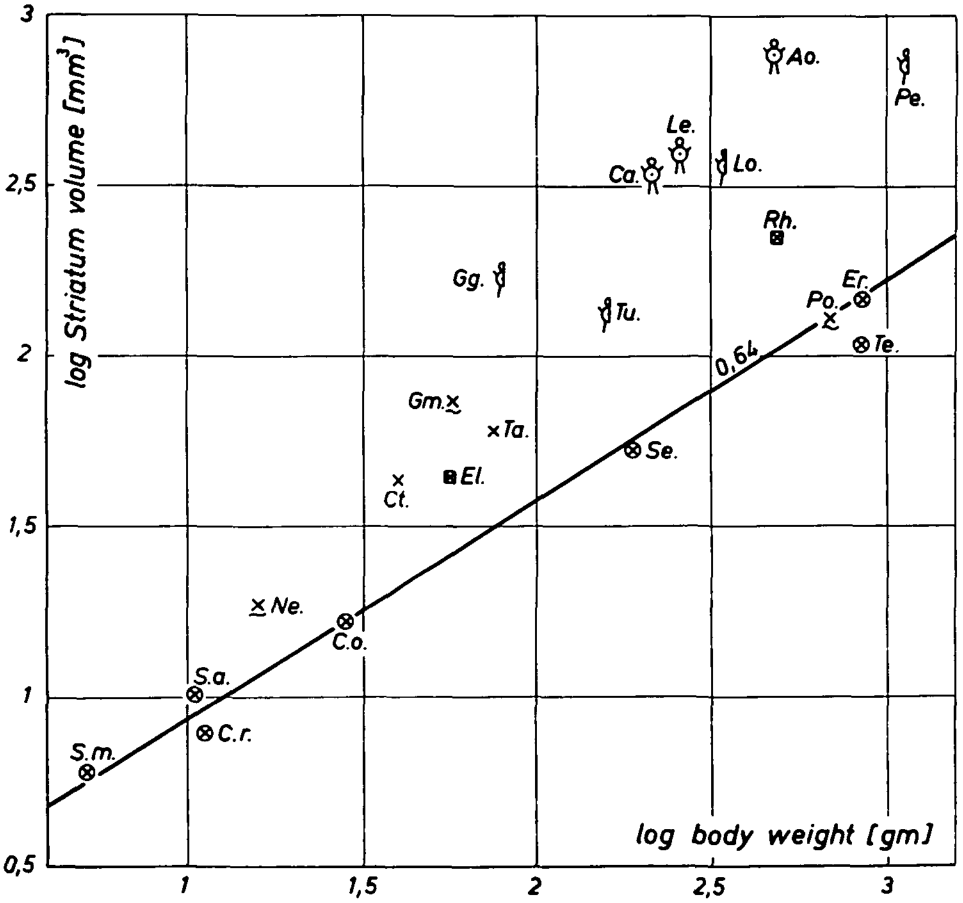


FIG. 10. Striatum volumes plotted against body weight. (See Fig. 5 for abbreviations.)

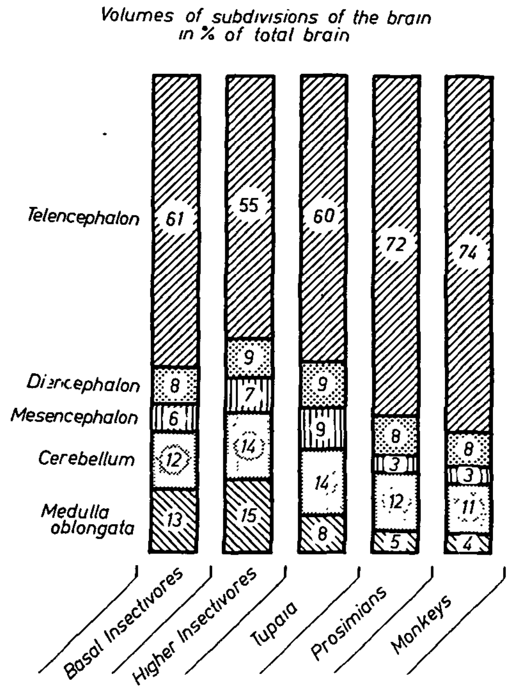

Volumes of subdivisions of the brain in % of total brain

FIG. 11. Volumes of subdivisions of the brain in % of total brain.

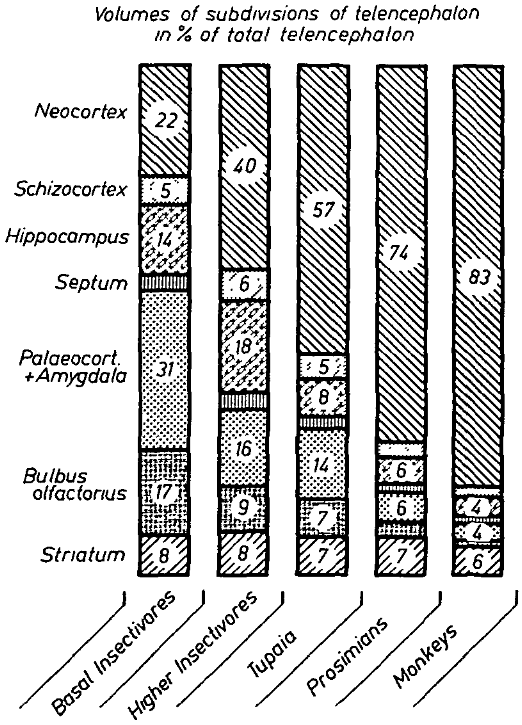

Volumes of subdivisions of telencephalon in % of total telencephalon

FIG. 12. Volumes of subdivisions of telencephalon in % of total telencephalon.

The structure displaying the next largest degree of development is the *diencephalon.* It is greatest in the monkeys and closely followed by the prosimians and the Macroscelididae. *Galemys* and the Macroscelididae possess enlargements almost equal to that of the prosimians. The rest of the insectivores do not display any marked growth.

The evolutionary growth of the *cerebellum* (including pons) is almost similar to that of the diencephalon.

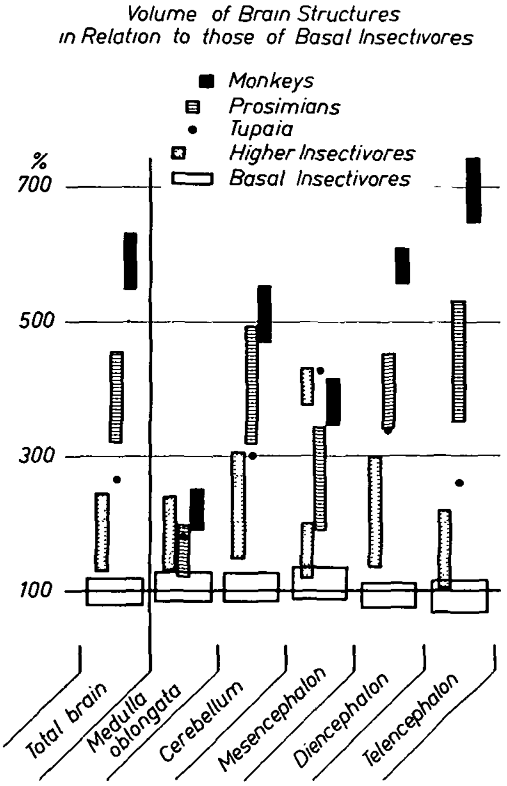

Volume of Brain Structures in Relation to those of Basal Insectivores

FIG. 13. Volumes of the 5 major brain divisions in relation to those of basal insectivores.

The *mid brain* (Fig. 6) also becomes relatively large although irregular in its phylogenetic picture. In the monkeys the increase nearly equals that of the cerebellum. It should be noted, however, that in some more advanced insectivores the mid brain is equal to, or larger than in the primates. This is especially true in specialized species. For example, in the family Macroscelididae the mesencephalon

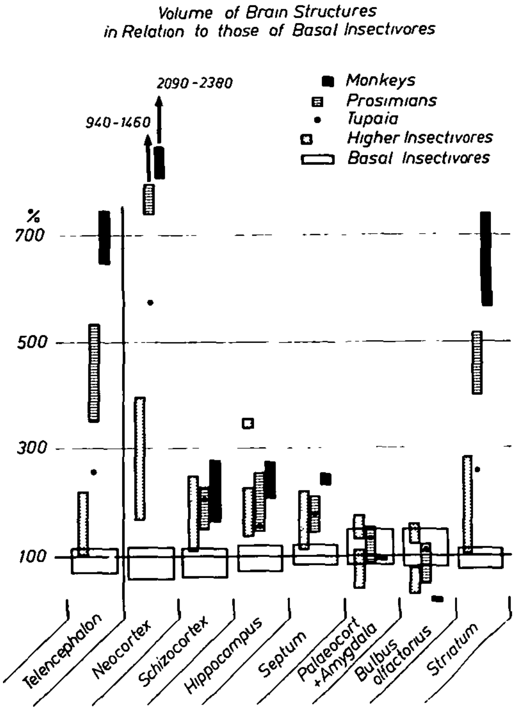


FIG. 14. Volumes of the 7 subdivisions of the telencephalon in relation to those of basal insectivores.

is larger than in the prosimians (except *Tupaia*) and equal to that of some monkeys. This group of animals has a relatively primitive but very large visual apparatus with large superior colliculi (Fig. 18) and poor cortical representation. In contrast, the mid brain in two of the three prosimians was small, being within the range of some insectivores. It is of interest that these two animals, *Loris* and *Perodicticus,* possess slow body movements in contrast to the remaining prosimian, *Galago demidovii,* which is fast moving.

The *medulla* does not display a marked increase from basal insectivores to monkeys (1.8 to 2.5 x BI). The size is almost in the same range for higher insectivores, prosimians, and monkeys, irrespective of their different levels of phylogeny. For example, the medullas of *Potamogale,* a specialized insectivore, and *Aotes trivirgatus,* a monkey, are almost equal. The development of the medulla in one prosimian, *Loris,* does not go beyond that found in the basal insectivores.

Subdivisions of the telencephalon in relation to body-weight (Fig. 14). In contrast to other telencephalic structures, the *neocortex* (Fig. 7) in monkeys undergoes a tremendous evolutionary growth (21 to 24 x BI). Its size is: *Aotes* 24 x BI, *Leontocebus* 23 x BI, and *Callithrix* 21 x BI. The prosimians display roughly half this growth (9 to 15 x BI). *Galago* is 15 x BI, *Loris* 12 x BI, and *Perodicticus* 9 x BI. Among insectivores, *Galemys* and the Macroscelididae have the greatest cortical growth (2.8 to 4.0 x BI). The rest of the insectivores possess little neocortical development in relation to the basal forms. Among basal forms, *Tenrec* and *Setifer* possess the smallest neocortical volume and therefore are considered the most primitive. It is significant that *Tupaia,* which is a true transitional form from insectivores to primates, has a cortical size between that of the lower primates and highest insectivores (6 x BI).

It should be stressed that a subcortical structure, the *striatum,* rather than a cortical one, possesses the next greatest development (Fig. 10). It is largest in the monkeys (5.5 to 7.5 x BI) and somewhat less developed in the prosimians (4.0 to 5 x BI). The striatum is approximately equal in *Tupaia* and *Galemys.* The latter possesses the largest striatum within the higher insectivores.

The *schizocortex,* although largest in *Aotes,* is poor in both monkeys and prosimians. The Macroscelididae and *Galemys* have a larger schizocortex than most of the primates. Two of the monkeys (*Callithrix* and *Leontocoebus*) and one prosimian (*Loris*) have values only slightly above the basal forms.

The *hippocampus* (Fig. 8) is definitely larger in the specialized insectivores, Macroscelididae (3.5 x BI), than in the monkeys (2.0 to 2.8 x BI) and two of the prosimians (2.0 to 2.4 x BI). However, in *Tupaia* and *Loris,* it is close to the basal forms (1.5 x BI). In *Galemys* it is as large as in some monkeys and prosimians (2.2 x BI).

The *septum* displays definite evolutionary growth, although small in monkeys (2.3 to 2.5 x BI) and in prosimians (1.4 to 2.1 x BI). In Macroscelididae and two of the aquatic insectivores, *Galemys* and *Neomys*, the septum equals that of the prosimians.

The only structure undergoing a reduction in size during evolution of higher primates is the *olfactory bulb* (Fig. 9). It is markedly reduced in all monkeys (0.14 to 0.22 x BI) but not in all prosimians. There are prosimians such as *Galago demidovii* in which the size of the olfactory bulb is similar to that in basal insectivores. In contra-distinction, there also are insectivores, such as the semiaquatic *Potamogale,* which possess a reduced olfactory system (0.25 x BI).

The *paleocortex-amygdala* complex reveals no volumetric change in phylogenetic development. This may be due to its containing representative parts of the olfactory system, which were previously shown to undergo reduction in phylogeny, and parts of the limbic system, which have displayed progressive enlargements in evolution. The increase of one component probably cancels the decrease of the other. Future investigations are planned to differentiate these two components.

DISCUSSION

Absolute and relative values in brain development.

(1) The greatest rate of development among the five major brain divisions is in the telencephalon. Diencephalon and cerebellum possess the next largest growth rates. It is significant that these structures, especially the telencephalon and cerebellum, are usually associated with higher level central nervous system activity, such as mentation and intricate motor activity. Among these three structures, the diencephalon may be considered as passively responding, in part, to the growth of the other two. It may be more dependent upon the telencephalon, since the relative rank of each animal from the prosimians through primates is exactly similar for both diencephalic and telencephalic growth rates, whereas relative ranks representing cerebellar growth are somewhat different. Among the prosimians, for example, *Galago* possesses a larger cerebellum than either of the monkeys, *Callithrix* and *Leontocoebus.* This, in part, may be correlated with *Galago*'s marked agility. In contrast, the other two prosimians, *Loris* and *Perodicticus,* move about slowly and possess a definitely smaller cerebellum. Among the phylogenetically older brain stem structures, the mesencephalon reveals a greater evolutionary growth rate than the medulla.

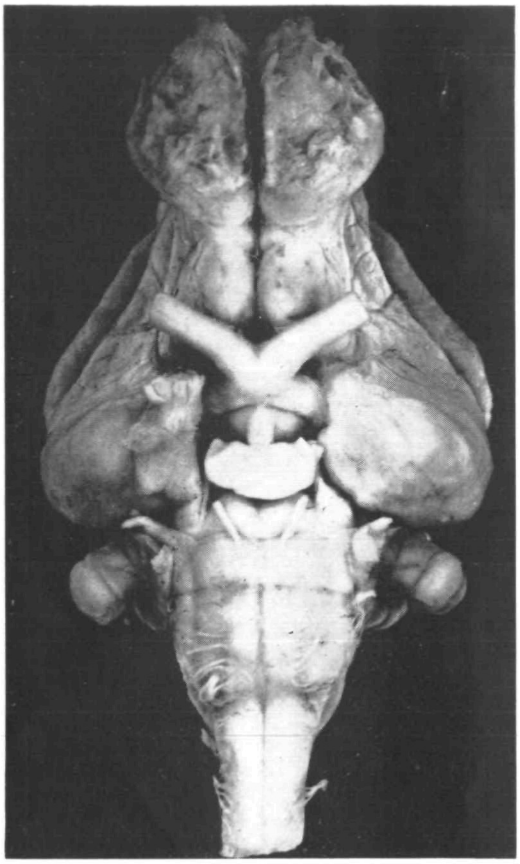


FIG. 15. Brain of *Rhynchocyon stuhlmanni* A 257, ventral view.

(2) Among the seven subdivisions of the telencephalic structures, the neocortex was primarily responsible for the tremendous evolutionary growth (21 to 24 x BI in

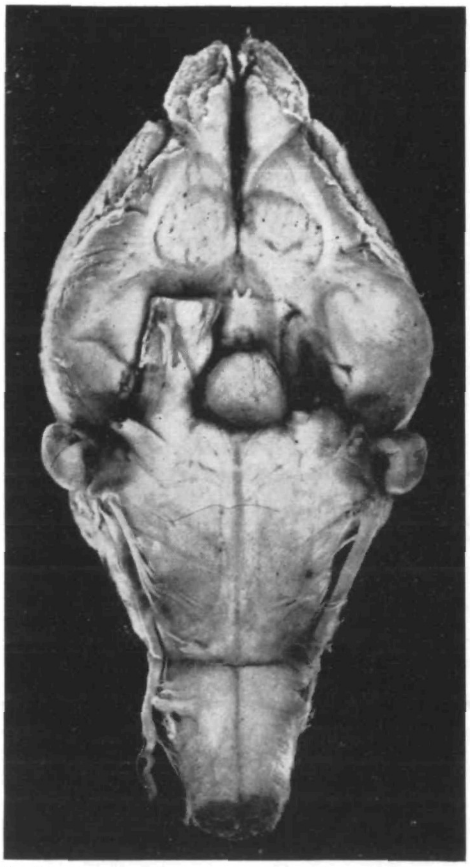


FIG. 16. Brain of *Potamogale velox* A 367, ventral view.

monkeys). It was three times greater than the next largest contributing structure, the striatum. This extraordinary growth (Figs. 2, 3, 17, 19), which is out of proportion to other brain divisions, supports the thesis that the neocortex acquired an increased number of elements independent of other brain structures. These intracortical elements may be "associational" and very likely may be one of several factors which provide the substrata for progressively increased cerebration in phylogenetically higher forms. The degree of neocortical growth in the various mammals corresponds with the developmental group level reached during evolution. Thus, the neocortex development serves as a very good criterion for evaluating the evolutionary levels.

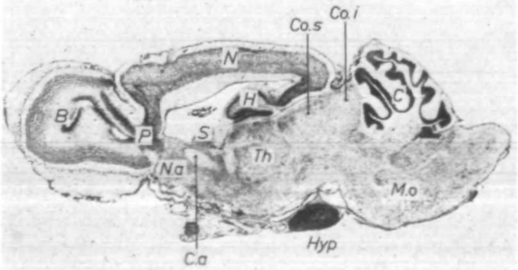


FIG. 17. *Erinaceus europaeus,* brain 518. Sagittal section 604, ×3. Cresyl violet, 20 μ.

ABBREVIATIONS FOR FIGS. 17-21

B, Bulbus olfactorius
C, Cerebellum
C.a, Commissura anterior
Co.s, Colliculus superior
Co.i, Colliculus inferior
D, Diencephalon
H, Hippocampus
Hyp, Hypophysis
M, Mesencephalon
M.o, Medulla oblongata
N, Neocortex
N.a, Nucleus accumbens
N.c, Nucleus caudatus
N.II, Nervus opticus
P, Palaeocortex
S, Septum
Sch, Schizocortex
Th, Thalamus
T.II, Tractus opticus

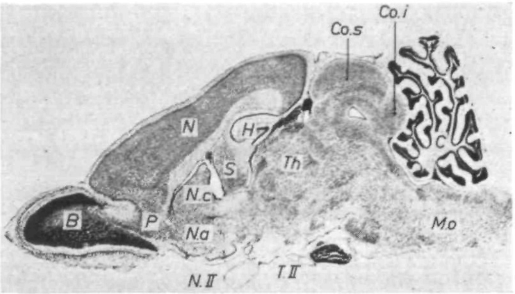


FIG. 18. *Rhynchocyon stuhlmanni,* brain A 282. Sagittal section 1010, × 2. Cresyl violet, 10 μ. (See Fig. 17 for abbreviations.)

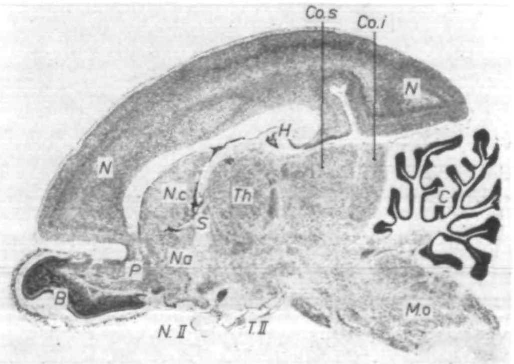


FIG. 19. *Galago demidovii,* brain A 41. Sagittal section 430, × 4. Cresyl violet, 10 μ. (See Fig. 17 for abbreviations.)

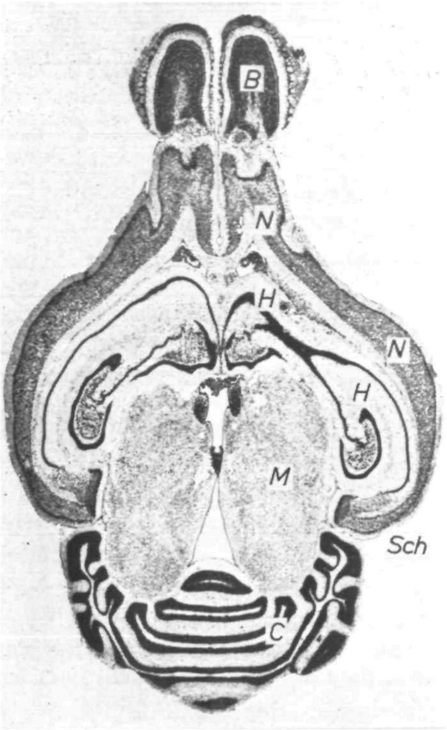


FIG. 20. *Elephantulus fuscipes,* brain A 300. Horizontal section 292, × 5. Cresyl violet, 10 μ. (See Fig. 17 for abbreviations.)

The other telencephalic srtuctures show varying degrees of development; striatum is 7 x BI in monkeys and all other structures are below 3 x BI (Fig. 14). It was rather surprising to find that although the schizocortex, hippocampus, and septum became larger, their rate of growth was much smaller than that of the striatum.

Animals in the prosimian and monkey groups display a similar relative position when ranked according to either neocortical or striatum growth rates. It is thus suggested that striatum development is, in part, dependent upon the neocortex. It should be noted that the internal capsule lying between the caudate nucleus and putamen was incorporated in the measurements and thus may have influenced the results. However, the contribution by the internal capsule is undoubtedly small, since it is only a small part of the striatum in monkeys (*Aotes* 13.1%, *Callithrix* 13.0%, and *Leontocoebus* 13.6%).

It is obvious that the neocortex and limbic system structures are to a great extent independent of one another in their evolutionary development. The septum, schizocortex, and hippocampus undergo definite growth in evolution, but their rate is much slower (2 to 3 x BI) than that of the neocortex. The palaeocortex-amygdala combination, however, does not reveal any size alteration. Since previous data on surface measurements (Stephan, 1961) revealed a decreased paleocortex in phylogeny, its present lack of accord with a decreasing olfactory bulb may be due to the inclusion of the subcortical non-olfactory components of the amygdala.

The olfactory bulb is the only telencephalic structure which undergoes obvious regression in evolution. The reduction first takes place during the prosimian stage. Among the prosimians there are representatives with relatively small olfactory bulbs (*Perodicticus* and *Loris*). In other pro-

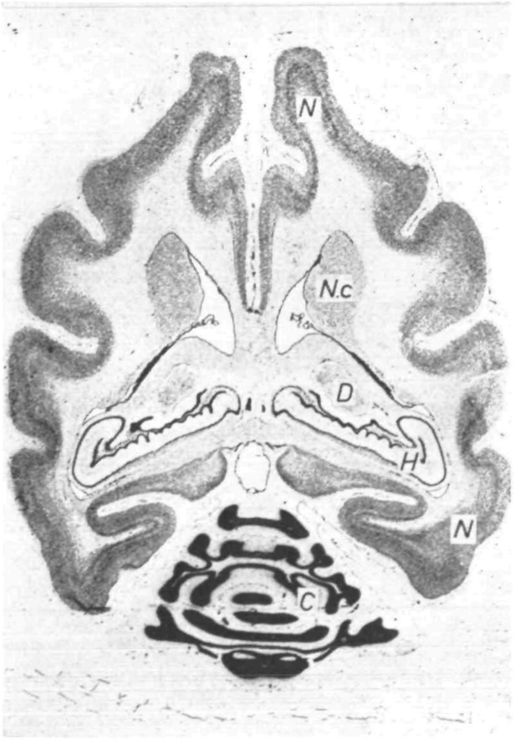


FIG. 21. *Perodicticus potto,* brain A 173. Horizontal section 475, × 2.5. Cresyl violet, 15 μ. (See Fig. 17 for abbreviations.)

simians, such as *Galago demidovii* and *Tupaia,* the olfactory bulb remained relatively large, as it does in primitive insectivores. The behavioral correlates and significance of this difference are not immediately apparent.

As previously found (Stephan and Andy, 1962), it is evident that there is no correlation between the development of the olfactory bulb and the septum. Thus these volumetric studies tend to contradict the impression that the septum is dependent upon olfaction (Smith, 1895). These observations also hold true for the other limbic structures; thus olfaction and the limbic system are also independent of one another. In general, highly specialized specific sensory functions (such as vision, olfaction, etc.) appear to bear little influence upon the growth of the septum, hippocampus, schizocortex, and other structures.

(3) These studies make it obvious that varied growth rates account for the distorted phylogenetic picture obtained by merely comparing brain structure volumes with total brain or telencephalic volumes. For example, the marked neocortical growth went from 22% in basal forms to 83% in primates. This enlargement is so great that other brain structures appear as if they regressed in evolution, unless compared to an indifferent reference such as body weight.

Specialization and brain development.

(1) It should be emphasized that the evolutionary levels of the three groups, insectivores, prosimians, and monkeys are not always clearly separated. There are animals among the lower forms which possess brain structures that approach, and in some cases surpass, the development of corresponding structures in higher forms. Furthermore, among the higher forms there are animals which possess primitive brain structures that have remained large and unchanged. This overlapping may be due to two factors: (a) in general, a low structural growth rate of various brain components (medulla, mid brain, limbic, and olfactory structures), and (b) specialization of individual animal groups accompanied by growth increases or decrease of specific brain structures such as in the medulla of *Potamogale. Potamogale* possesses a larger medulla than some prosimians. Its medullary enlargement undoubtedly resulted from its unusually well developed trigeminal system (Fig. 16). This system innervates the vibrissae which are most likely vibration receptors, adapted for detecting crustaceans under water. Another example is found in the Macroscelididae, which possess a very large mesencephalon (Fig. 18), approaching that of lower primates. The enlargement is undoubtedly due to its extraordinarily large superior colliculus. The presence of very large eyes and the large superior colliculus suggests the existence of a specialization of the visual system which is much more advanced than in other insectivores (Fig. 15). In the same animals, the hippocampus is extremely large (3.5 x BI) (Fig. 20), even larger than in primates (2.5 x BI) (Fig. 21), whereas in other insectivores it does not surpass the primates in its development.

(2) These studies show that the size of the brain and its various divisions are influenced by two major factors: first, the various changes inherent in the process of evolution and second, specialization such as represented by vision, olfaction, etc. The technique of comparative volumetric brain changes makes the differences obvious and thus provides a greater insight into a correlation of function and development of various brain structures. It must be emphasized, however, that volumetric studies which reveal parallel growth rate between two structures, do not necessarily imply a functional interdependence between them.

SUMMARY

(1) The quantitative phylogenetic development of various brain structures was determined in 14 insectivores, 3 prosimians, 3 monkeys, and *Tupaia glis,* a mam-

mal which is thought to be a link between the insectivores and lower primates.

(2) All major brain divisions undergo enlargement during evolution. The greatest development is in the telencephalon, followed by diencephalon, cerebellum, mesencephalon, and medulla, in that order.

(3) Among the telencephalic structures the neocortex has the greatest growth.

(4) The striate body undergoes moderate development.

(5) The schizocortex, hippocampus, and septum possess a significant but slight enlargement in comparison to the neocortex. It is even smaller than in the striatum.

(6) The olfactory bulb and its associated structures are the only ones to undergo an absolute size reduction in phylogeny.

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DISCUSSION

DR. H. H. HOFFMAN (Department of Anatomy, University of Alabama Medical Center, Birmingham, Alabama. See Editor's note at the beginning of the paper.)—

This paper by Dr. Stephan and Dr. Andy shows the importance of the development and differentiation of the neocortex as an index of the relative position of mammals in the evolutionary scale. It points out the necessity for a comparison of the absolute values obtained by measuring the various brain areas against some value which does not represent brain measurements and which can be used as a reference quantity. For this, the body weight was used. This is a generally acceptable method, termed the allometric method. It would be interesting to know how the body weight constant was established in these animals. There is evident variation in body weight depending on age and general body condition (that is, the animal may be fat or lean) so that some comment concerning the method of selection may be warranted.

Furthermore, when the brains of prosimians were compared with those of monkeys, the telencephalon showed the most extensive evolutionary growth but there was also evident proportional increase in the cerebellum and the diencephalon. The conclusions presented are most interesting and I would like to ask these additional questions:

With reference to the increased size of the cerebellum: Is this increase in the cerebellum particularly associated with an increase in the cortico-ponto-cerebellar system with the largest increase in the cerebellar hemispheres and systems through the superior cerebellar peduncles?

With reference to the midbrain: Is there in the monkey, as compared to the prosimian, an increase in the basal part of the midbrain due to the larger corticopontine and corticospinal tract? Is this associated with a proportional decrease in the tectal areas (with greater cephalization of the optic system)? Is there also a decrease in the magnocellular part of the red nucleus? If so, a proportionately smaller tectal and tegmental area, as balanced against an increased basis pedunculi, would give a midbrain showing relatively less increase in monkeys compared with the prosimians than do other brain regions.

With regard to hippocampal areas, I should be interested in knowing whether you have compared the relative size of the dentate gyri in the monkey and prosimian, since the prosimian has a proportionately large olfactory system.

Considering the better development of epithalamic centers in prosimians as compared with monkeys, would not the figures tend to minimize rather than accent the differences in proportional development of the dorsal thalamic areas in the monkeys as compared with prosimians?

AUTHORS' REPLY — Wild animals obtained from their natural habitat and utilized in the study reveal relatively small variability in comparison to domesticated animals or animals from zoological gardens. Among the animals utilized, the weight is thought to be characteristic for the species or subspecies living in the region where they were collected. This investigation serves as a framework upon which more detailed comparative analysis of the brain structures can be made. The answers to the additional and more detailed questions posed by Dr. Hoffman will thus be answered by future investigations.