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## Comparative Volumetric Analysis of the Principal Brain Subdivisions in Saurian Reptiles

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with 8 Figures and 8 tables)

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## Summary

[Translated in original paper.]

## Introduction

After Snell (1892), it was determined that the weight of the encephalon (Pe) can be expressed as a function of body weight (Ps) by means of the formula:

$Pe = k \cdot Ps^{\alpha}$ . Over the years, a major effort has been made to determine the parameters  $\alpha$  and  $k$  that pertain to each order of vertebrates from data obtained through a rigorous protocol and treated by statistical calculation. A series of previous works (Platel, 1972, 1974, 1975a) address this question for the order of saurians (and to lesser degree, for that of snakes). Thirty two species of lizards were studied and the calculation of the encephalization index for each of them enable realize a primary classifications (see Bauchot and Stephan, 1964 and 1969 for the definition and means of calculation for these data).

Globally, the index of encephalization expresses the encephalic characteristics of each species (evolutionary level and/or level of adaptation); the discussion of a recent article (Platel, 1975) showed these limits and provided the rationale for a more exhaustive analysis that we will take for the first time to the level of the volume of the principal units forming the brain: telencephalon, diencephalon, brain stem, mesencephalic roof, tegmentum and medulla oblongata, cerebellum etc... For each species studied, these volumes consist of data that can be utilized in several ways:

1. The use *relative volumes* (or the expression of the volume of the portion of the brain reserved as percentage the entire brain volume) and their comparison between species is the simplest and most commonly used method of study; it will reveal along the way that it is accompanied by a systemic error that considerably reduces its reliability.

Consequently, these results ought to be viewed as being of limited interest.

2. It is preferable to use *gross volumes* and to relate each of them to the body weight of the species being considered. This procedure is an extension to the constituents of the brain of what had been previously obtained for the entire brain. Snell's formula remains the basic relationship of such a study, nevertheless replacing brain volume (Pe) by that of the structure being analyzed (Str.) or:  $Str = k \cdot Ps^{\alpha}$  which is better to use following logarithmic transformation:

$$\log Str. = \alpha \log Ps + \log k.$$

For each brain unit and with the help of samples from 32 species of saurians (mentioned in the articles already cited), such a relation leads to two categories of results:

- a) Calculation of the value of  $\alpha$  and its comparison to that of the brain-body allometric coefficient of the thirty-two saurians (0.669) (PLATEL, 1975a) permits detecting parts of the brain that are the most "dynamic" (that is, those having a "phylogenetic" growth rate higher than that of the entire brain), those who are "stable" on the other hand (allometry close to that of the entire brain), and finally those that are "regressive" (whose "phylogenetic" growth rate is slower than that of the entire brain) (BAUCHOT, 1963 and 1966).

- b) For each species one can similarly calculate an appropriate *index* for each part of the brain; this index is obtained the same way as the encephalization index by taking the value derived from six lacertids as a reference. The choice of this method of calculation, which includes these "Reference Lizards" (PLATEL, 1975a), will be justified in the discussion.

Comparison of the indices is calculated as that for the encephalization indices; it is considered as a function of adaptive or evolutionary characteristics; one could thus hope to localize the part of the brain that supports it.

Nevertheless even to this level, it is frequent that some imprecisions remain; one

can only hope to eradicate them by a still more thorough analysis of nuclear groupings or even cytological components of the unit in question. It is this last aspect that we will attempt to explain finally by compensating for the areas of the telencephalon (PLATEL, in preparation).

Results and discussion refer essentially to saurians but the addition of several snakes gives ground for a tentative synthesis concerning the superorder Squamata. The study of three species of snakes also allows specifying, with a much greater acuity than that furnished by the encephalization index, that which unite and separates the saurians and snakes within the domain of brain organization.

## Material

The material for this study consists of thirty-two lizards and three snakes. The list of species and gross numerical data ( $P_e$ ,  $P_s$ ) are assembled in Table I. The lizards have already been presented (PLATEL, 1974 and 1975a) and are broken down into the main families; they provide a first approximation satisfying the diversity that reigns within the order of saurians. Only three snakes were retained: the results obtained concerning encephalization in snakes (PLATEL, 1975a) are still too partial to hope to analyze this group in a similar manner to that used for lizards; included are a boid: *Boa constrictor*, and two modern-type snakes (caenophidians), *Natrix natrix* and *Vipera aspis*; they allow for several comparisons with lizards but we reserve for the future more extensive studies of diverse families of snakes.

In many cases, because we only have a single specimen, the individual being studied has been submitted as an average adult for the species considered.

In other cases, one must use an animal whose brain and body weights differ from those of the reference animal. In fact, when a species sample has been studied using a significant sample, the coordinates for the average adult were obtained through calculation, and it is exceptional that they correspond to an individual from the sample. Therefore, we chose the example whose  $P_e$  and  $P_s$  are closest to the reference  $P_e$  and  $P_s$ , while giving priority to the most satisfactory  $P_e$  values. In spite

of these precautions, several species remain for which it seems imperative to establish a corrective term. The volume of each measured structure would then be multiplied by the ratio of brain weight between the animal being studied and the reference animal. However, this procedure deserves some explanation. In fact, to pass the brain weight of the studied individual to the brain weight of the reference by using a simple proportion, is equal to admitting that isometry exists between one individual and another when we are aware that the intraspecific allometric coefficient  $P_e/P_s$  of saurians has a value of 0.43 (and not 1.0) (PLATEL, 1974). To pass the volume of a brain structure of the studied individual to the volume of the corresponding structure in the reference animal by utilizing an allometric coefficient of 0.43, commits another error of the same kind: it has been shown (BAUCHOT and PLATEL, 1971) in *Scincus scincus* that the allometric coefficient varies from one structure to another (for example, 0.269 for the diencephalon to 0.659 for the dorsal striatum). These two observations are the origin of the reservations that will be made later regarding the use of relative volumes. However, the establishment of a rigorous corrective measure effected through calculation whose complexity does not measure up to the results desired: it will in principle require redoing a detailed intraspecific study for each species in question analogous to the one already conducted in *Scincus scincus*. Unquestionably, but the study based on the latter species provides instead the opportunity to assess the errors committed when using a simple corrective measure: it is negligible (2%) relative to other errors that will be evaluated later on. Table I indicates with a cross (x) the species whose measures were subjected to such a correction.

## Method of Study

The measurement of brain volume is made by applying a method whose justification and modalities have already been demonstrated (BAUCHON and PLATEL, 1971). It is done by cutting at least 50 regularly spaced levels of the brain from front to back. As was seen in *Scincus scincus*, such slicing provides an approximation for the large brain subdivisions that is not improved by augmenting the number of levels. It is not the same for the smaller units which would have to be subjected to complementary

measurements; in effect it is estimated that the volume of a nuclear ensemble can only be known with accuracy if this structure is represented by at least 7 or 8 levels. The cerebellum of lizards frequently has the form of a transverse lamina; also the value for this brain unit is diminished by half which yields a number of levels that varies from 6 to 28 according to the species.

Some brains show long thin olfactory peduncles; in others, they are shorter and more massive; finally chameleons and snakes are devoid of them. In order that slicing is not affected by these varied aspects, calculation of the spacing is done by taking into account the slices that involve the olfactory bulbs and those things situated between the tip of the anterior olfactory nucleus (rostral part of the cerebral hemispheres) and the tip of the spinal cord (in principle up to the connection point of the first pair of cranial nerves). (Figure 1: in front of level AA on one hand, and from level BB to level CC on the other). Under these conditions the range varies from 140  $\mu\text{m}$  (*Hemidactylus mabouis*, *Psammodromus hispanicus*, *Anolis auratus*, *Chamaeleo lateralis*) to 440  $\mu\text{m}$  (*Zonosaurus maximus*) or 460  $\mu\text{m}$  (*Boa constrictor*).

Thus the following operations were performed on each series:

1. Each level was photographed and then printed on paper (with varying magnification from 35 to 50 according to the species); the photograms were accompanied by a micrometric scale photographed at the same time and printed under the same conditions as those above.

2. Then the limits of the architectural units were carried over to the photograms. The fragments that corresponded to each structure were cut and assembled. The parts were placed that represented the ventricles (a), optic fibers (b) as well as all the elements contributing to the initial brain weight but which would not be analyzed: meninges, choroid plexus, nerve roots, fragments of pineal gland and pituitary gland, peripheral blood vessels... (c). Lastly are made, from the use of the micrometric scale, 3 squares

with the corresponding scale unit (in other words, 1 mm multiplied by the magnification).

3. The weight of these 3 squares permits calculating an average weight of a unit of area. The ratio of the weight of the elements of the same structure to the weight of the area unit provides the total surface (in  $\text{mm}^2$ ); the product of this by the distance separating two photograms yields the volume of the slice (in  $\text{mm}^3$ ).

4. The sum of the volumes of different structures, ventricles (a), optic fibers (b) and various elements (c) leads to the volume of the sliced brain ( $E_c$ ). Comparing it with fresh brain weight ( $Pe_f$ ) permits calculation of the coefficient of transformation of the sliced volumes for the corresponding fresh weight:  $Pe_f = K \cdot E_c$ . This coefficient K is actually the product of the specific weight of the nerve tissue of the reptile by a coefficient  $K_0$  that expresses the volume modifications caused by the histological treatments (retraction by loss of water and lipids during several baths for fixation, dehydration, clarification, and paraffin). We cannot know precisely this specific weight, however it is known that in fishes it is:  $1.0414\text{g}/\text{cm}^3$  (CHEN, 1931) and in mammals it is  $1.036\text{g}/\text{cm}^3$ , in other words very close to 1. Consequently, it can be admitted that the error committed is negligible when using K instead of  $K_0$ .

Coefficient K varies from one species to another (Table II; column c. r.: coefficient of shrinkage) from 1.70 (*Psammodromus hispanicus*) to 2.43 (*Uromastix acanthinurus*): its average value is 1.99 for the 32 saurians (standard error 0.19), 2.00 for the 35 squamates (standard error 0.19). No significant error is made in considering that the brain of reptiles, like those of mammals and teleostean fishes (RIDET, DIAGNK, BAUCHOT and PLATEL, 1974), is subject to reduction by half following the cutting procedure. We have nonetheless utilized the K coefficient appropriate for each specimen to calculate fresh volume. In the end, it must be admitted that the different parts of the brain undergo shrinkage with equal intensity, which is plausible, but not yet fully demonstrated.

<p>Table 1. Presentation of studied material. List of species and abbreviations used. Columns 1 to 4: <math>Pe</math> (brain weight) (in mg), <math>\log Pe</math> (-1). <math>Ps</math> (body weight) (in g) and <math>\log Ps</math> of the average adult. In case there is no specimen matching these coordinates, an individual not very different should be chosen: 5. protocol number (cf. PLATEL, 1974 and 1975a); 6. <math>Pe</math> (mg); 7. <math>\log Pe</math> (-1); 8. eventual correction (x).</p>
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Fig. 1. Lizard brains, in lateral view. The vertical lines show the cross-sectional plane. The number of slices made to determine the interval of successive photograms did not take into account either portion AA-BB (olfactory peduncles) or the fragment of spinal cord situated behind segment CC. b. o.: olfactory bulbs; c: cerebellar lamina; h. c.: cerebral hemispheres; m. c.: spinal cord; n. o. a.: anterior olfactory nucleus; p. o.: olfactory peduncles; t. o.: optic tracts; T. O.: optic tectum.

## 2. Estimate of errors committed; search for a range of variation of gross values

The object of partial volume measurement is to compare the values obtained in two different species, or between two groups of species with contrasting morphological, ecological, or phylogenetic criteria. The results derived from such a comparison only have value if they take into account the errors committed when taking measurements. This is a difficult estimation because it is the product of varying imperfections. Concomitant with this error is the biological variability of the measured volumes; an attempt will be made to express these two types of disruption by means of a global value to which the name *range of variation* of gross values will be given.

a) The method for reconstituting and measuring brain volumes, whose principal stages were described above, was the object of an in-depth critical analysis (BAUCHOT, 1963). This author estimated that the delimitation of surfaces, weighing, and volume calculations are done with a global error of 5% (particularly if the nuclear structures have a roughly spherical form and if measuring their volume is done with the use of at least 4 levels). An estimate of the same order of magnitude (at least 4%) is obtained in measuring the incidence of the number of levels used for calculations of volumes in *Scincus scincus*: for the whole brain, taking 50 to 200 levels improves the results by reducing the total variation from 11.5% to 7.5% or 4% (BAUCHOT and PLATEL, 1971).

b) A second cause of error emanates from a complex ensemble that could be referred to by the

terms “studied species-observer” and which makes two factors intervene:

- the inconstancy (or indeterminacy) of the observer, in the setting of limits; this is a significant obstacle that does not appear solvable for the moment.

- the variability inherent to species.

The analysis conducted for *Scincus scincus* shows that in first approximation this double disruption represents a spread of about 7.5% for the measurement values.

The sum of the two variations, being 12.5% (5% + 7.5%) for the gross value of measured brain volumes, is set aside for later. This percentage is in fact the average value of a variation that sometimes differs appreciably from one structure to the other; in *Scincus*, for example, it can reach 17% for the dorsal portion of the striatum, but it is only 9% for the diencephalon. Lastly, it can be supposed that the different species of lizards studied would behave in this regard like *Scincus scincus*, which is reasonable but not yet demonstrated.

Preferably, comparisons are made with the help of indices rather than gross values; each index would be given with a range of variation of  $\pm 12.5\%$ . The comparison of the indices of two groups of species would be done by replacing the index of each of them by three values ( $i$ ,  $1.125 i$ , and  $0.875 i$ ), which allows for the introduction of measurement error and intraspecific variability in the comparison of average indices.

An identical estimation performed in regard to relative volumes shows that the range of variation is only 6% in this case. This result, which singularly minimizes the measurement variation, will be addressed later; it is an additional argument for not retaining relative volumes.

Table II. Fresh volumes (in  $\text{mm}^3$ ) of different brain subdivisions and shrinkage coefficient values (c. r.) (transformation of sliced volumes from fresh volumes). 1. Spinal cord; a. Ventricles; b. Optic fibers; c. Various; 2. Telencephalon; 3. Diencephalon; 4. Brain stem; 5. Mesencephalic roof; 6. Tegmentum + medulla oblongata; 7. Cerebellum; E2. Brain volume with ventricles (= 2 + 3 + 4 + 7 + a).

## Delineations and Retained Architectural Units

The description of the brain of *Scincus scincus* (PLATEL and BACHOT, 1970, BAUCHOT and PLATEL, 1971) provided the opportunity to sketch the major organizational traits of a saurian brain and specify the main constituent elements. Its characteristics are those of lizards belonging to the scincomorph group, in other words that in several differences of close detail, they apply as well to species of the genus *Lacerta* (which we have made Reference Lizards), as to *Cordylus*, zonosaur, and naturally other scincids. We have had the opportunity (PLATEL, 1974 and 1975) to show what might set it apart from the brain of iguanids, agamids, chamaeleonids, gekkonids, teiids, varanids, and anguids, but the main organizational lines of all these brains remain the same.

The delineation of slices for the main parts of the brain rests on definitions for which it became necessary to make a choice. In fact, after almost a century, each limit has been linked to a certain number of sometimes very removed points of view. The quantified results that we present will be useful in measurement where the retained limits for different structures are included, for the moment, by the majority of authors.

We have dedicated a number of descriptive works to the telencephalon of *Scincus scincus* (PLATEL, 1967, 1969, 1971); its detailed quantitative study is presently being conducted; for now the available choice is to analyze the principal constituents: the olfactory bulbs, the olfactory peduncles, and the pallium and basal areas within the cerebral hemispheres. The dorsal formations or *pallium* (or again episphaerium of EDINGER, 1896) comprise the anterior olfactory nucleus, pars dorsalis (PLATEL, 1967 and 1969), paleopallium, and archipallium (PLATEL, 1969). The ventral formations or basal areas (or again hyposphaerium of EDINGER, 1896) gather together the anterior olfactory nucleus, pars ventralis (PLATEL, 1967 and 1969), olfactory tubercle, strio-amygdala complex, and septum. The commissure level and the border with the rostral part of the diencephalon deserve several clarifications: the separation of the part belonging to the telencephalon (dorsally) from that representing the hypothalamus (ventrally) is made by a horizontal tract in the thickness of the anterior commissure. The lateral boundaries isolate the dorsal part of the interstitial core of the terminal

stria (which will be counted with the basal areas) from the ventral part which will be counted in with the hypothalamus.

Descriptions of the diencephalon group of squamates are not uncommon and address numerous species. The most recent and complete studies are those of SENN (1968): *Lacerta sicula*; BUTLER and NORTHCUTT (1973): *Iguana iguana*; CRUCE (1974): *Tupinambis nigropunctatus*; REPERANT (1973): *Vipera aspis*.

The diencephalon is subdivided into five units which were primitively recognized in reptiles by EDINGER (1899), HERRICK (1910), DE LANGE (1913), HUBER and CROSBY (1926), SHANKLIN (1930), KUHLENBECK (1931), PAPEZ (1935) and ARIANS KAPPERS, HUBER and CROSBY (1936–1960), to cite only the most in-depth studies among already established authors: epithalamus, dorsal thalamus, ventral thalamus, hypothalamus, and pretectum. It would not be a question of going beyond the measurement of volumes: the finest delineations are unusable due to the large interval imposed by slicing the entire brain into 50; a detailed study, along with more extensive slicing, will be provided at a later time (NIEUWENHUYIS and PLATEL, in preparation). Nonetheless, knowledge of the secondary components provides information that allows cutting through some contentious cases at present. On this subject we adopt the terminology and conclusions of BUTLER and NORTHCUTT (1973) to which we refer for everything concerning the historical and critical approach; their nomenclature tables indicate the correspondence of terms held by the main authors in the various species studied: eight figures illustrate their description of the diencephalon of the iguana (such that we were able to find the elements on our own series of slices of *Iguana iguana*); they are reproduced in Figure 2 by including there, in broad terms, the boundaries of groups in which the volume was measured.

The term *brain stem* was designated for the group of mesencephalic structures (mesencephalic tectum and tegmentum) to which the ventral part of the rhombencephalon was attached: the medulla oblongata. Because it is difficult to find the passage of the tegmentum to the medulla oblongata, we analyzed them together under the term tegmentum + medulla oblongata (Teg. + M. O.). It is possible to isolate the optic roof (optic tectum or midbrain) and posterior colliculi: the

group forms the roof of the mesencephalon (or mesencephalic tectum).

The cerebellum of lizards is shaped like a rather large lamina that is concave toward the front; it is reduced and lies flat on the choroid web of the fourth ventricle in snakes (LARSELL, 1926 and 1967, STEFANELLI, 1943, NIEUWENHUYS, 1967). In all cases its delineation is easy: the cerebellar lamina (which forms the main part of the cerebellum in squamates) is taken as well as the ventral cores (medial and lateral) that attach there. The most thorough analysis of the corpus cerebelli and auricular lobes could only be

considered later with the help of closer slices of this brain region.

The accepted notion is that the brain ends at the level of the first pair of cranial nerves (ANTHONY, 1970); this convention has not always been respected during sampling of the brain, and certain species show several photograms that include the spinal cord. These measurements allow appreciating the error committed, in this case, in the estimation of brain weight; we will dedicate a paragraph to expound on the results.

Fig. 2. *Iguana iguana* L. Main cytoarchitectural units of the diencephalon. The sketches of eight transverse levels are borrowed from BUTLER and NORTHCUTT (1973). We have delineated there (in broad terms) the five diencephalic subdivisions on which our volumetric analyses are based. Epithalamus (EPI), Dorsal thalamus (THD), Ventral thalamus (THV), Pretectum (PRT), and Hypothalamus (HYPO). The other brain stages present in the same sections belong to the telencephalon (TEL) or mesencephalon – Optic roof (T. O) or tegmentum (TEG). Other abbreviations are explained in BUTLER and NORTHCUTT (1973).

## Results and Discussions

### 1. Preliminary remarks

Addressing more in depth the idea already formulated by SENN (1970), NORTHCUTT (1972) proposed, taking a certain number of neuroanatomical characteristics as criteria for differentiation, to split lizards into two groups: the Type I Lizards (NORTHCUTT, 1972) or lacertomorphs (Lacertidae, Scincidae, Cordylidae, Gerrhosauridae, Gekkonidae, Xantusidae, and Anguidae) and the Type II Lizards (NORTHCUTT, 1972) or dracomorphs (Agamidae, Iguanidae, Chamaeleonidae, Teiidae and Varanidae).

The examination of encephalization indices (PLATEL, 1975a) shows that the average of these two groups varies in highly significant ways and brings a quantified initial justification to this subdivision. The

arguments maintained by NORTHCUTT (1972) (well-developed septum, voluminous preteectum, reduced medial cortex...) also involve assessments whose quantification is advisable. We chose to make this segregation of saurians into two groups into a working hypothesis. The numerical values are provided in the various tables not in the classic succession of families but respecting the regroupings recommended by NORTHCUTT. For each brain unit, after the comparison of species to species and within families, we devote a paragraph to the results from the comparison of lacertomorphs and dracomorphs. The values measured are compiled in Tables II and III. They deal with *fresh volumes* (slice volume multiplied by the shrinkage coefficient for each species) expressed in mm<sup>3</sup>.

Table III. Fresh volumes (in mm<sup>3</sup>) of various brain subdivisions. Detail of secondary subdivisions. 1. Telencephalon (reminder); 2. Olfactory bulbs; 3. Cerebral hemispheres; 4. Pallium; 5. Basal areas; 6. Diencephalon (reminder); 7. Epithalamus; 8. Dorsal thalamus; 9. Ventral thalamus; 10. Pretectum; 11. Hypothalamus; 12. Mesencephalic roof (reminder); 13. Optical roof; 14. Posterior colliculi.

Figs. 3 to 7. Brain Structures/Body Weight ratios. Graphic representation (in double logarithmic coordinates) of the Brain Structure/Ps ratio for the 32 saurians. Each species is represented by a dot whose identification is made using the landmarks of the abscissa axis (explanation of abbreviations can be found in Table I). The 19 lacertomorphs are represented by open circles, with a center point in the case of the six lacertids; the 13 black circles correspond to dracomorphs.

Two equilibrium lines have been added to each graphic; these are the reduced major axis that is appropriate for the group of 32 saurians (in dashes), and that relating only to the Reference Lizards; in Table V is found the value of the slope of these lines. The equilibrium lines corresponding to the Reference Lizards (in solid lines) is used to calculate indices. The points on the reference line have an index value of 100; there are included on both sides of the parallels in the presentation (in dotted lines) the 200 (above) and 50 (below) indices respectively, that is to say, where the volume being studied at constant Ps is double or half of the reference volume.

Among the brain units whose volume is known with a good degree of certainty are the telencephalon (32 levels on average), tegmentum + medulla oblongata group (20), cerebellum (12 levels but with an interval reduced by half), pallium (20 levels), basal areas (18), olfactory bulbs (12), hypothalamus (10); the others are less well represented: epithalamus (3), dorsal thalamus (4 to 5), ventral thalamus (5 to 6), pretectum (3), posterior colliculi (2 to 3); in these cases should be accorded more limited confidence in the results, which a comprehensive study with closer slices should verify later. The number of levels pertaining to a structure is a rough indication of its importance (rostrocaudal at least); hold it similar to an analysis of linear values, a process that should be able to highlight the interest in terms of quantitative neuroanatomy. For example, this approach is found in part of the work by ROSE (1957) (comparison of the lengths of different parts of the brain as a function of the total length of this organ or the snout-vent length among four species of *Lacerta* and *Anguis fragilis*, pages 445-449) and leads to hardly usable results.

Removal of the brain is usually accompanied by attachment of a spinal cord fragment whose volume represents 4.2% on average (standard error of 1.5%) of brain volume with extreme values such as 6.2% (*Varanus griseus*), 6.8% (*Lacerta viridis*), 7.0% (*Lacerta muralis* and *Chalcides mionecton*) and 0% for the chameleon. An average correction of 4.2% of Pe in the 32 species of lizards does

not modify (of course) the interspecific allometric coefficient Pe/Ps or the results (encephalization indices) to which it leads. It will become evident that it will be the same (or nearly so) when reserving the percentage of spinal cord for to each species.

## 2. Brain Structure/Ps allometric coefficients

These coefficients were calculated for the 32 saurians and six Reference Lizards, but also taking into account the Scincidae, Gekkonidae, Iguanidae, Agamidae, or finally regrouping the species into either Iguania and Scincomorpha or lacertomorphs and dracomorphs.

The analysis of structures was preceded by calculation of the allometric coefficient of every Pe/Ps, E1/Ps, E2/Ps, and Ventricles/Ps ratio (E1 = brain volume without ventricles – Table II: sum of columns 2 + 3 + 4 + 7; E2 = brain volume with ventricles – Table II: sum of columns  $\alpha$  + 2 + 3 + 4 + 7). The brain volume measured by slicing seems preferable to global brain weight (Pe); then only that which actually belongs to the central nervous system is taken into account. However, I should be noted that the results obtained from the unique ratio Pe/Ps are not called into question (in particular when replacing Pe by E2): the differences between coefficients are slight, from 0.003 (Gekkonidae) to 0.024 (Agamidae), with an average of 0.013 for the ten groups listed above.



The study of the ventricles led to allometric coefficients that are always elevated, from 0.778 (Agamidae) to 1.251 (Scincidae); the volume of the cavities therefore did not indifferently follow the increase of the brain; it has a greater importance among large species.

The comparison of allometric coefficients is a first stage that will be completed later by the analysis of indices of relation. But there are no elements that permit testing the significance of the differences that could turn up. We will therefore refer to the range of values provided by the E1/Ps and E2/Ps ratios, respectively; it suffices to *classify* structures with respect to the former, in particular by insisting on the extreme terms of this classification.

The first case to be examined will be that of the 32 saurians (Table IV). The allometric coefficients E1/Ps–E2/Ps are 0.647–0.657; only the mesencephalic roof (0.712) and cerebellum (0.846) show higher growth rates; the values for the telencephalon (0.635) and diencephalon (0.631) are on the other hand slightly lower, that of the tegmentum + medulla oblongata (0.654) takes place within the reference range.

After examining the results, it is tempting to conclude that the essence of the adaptive and evolutionary processes in saurians is manifested in the mesencephalic and metencephalic stages; it then seems highly unlikely that the phenomenon of telencephalization, so important among mammals, does not appear within an entire order of lower tetrapods. In fact, these values simultaneously express two very different processes, as each allometric coefficient translates: – on one hand, the allometric coefficients of various sub-groups (example: families) of saurians. Thus, the examination separating Lacertidae (Reference Saurians), Scincidae, Gekkonidae, Iguanidae, and Agamidae, shows that in the two last families the telencephalon has an elevated growth rate (which is explained by the evolution of the pallium); in lacertids, the telencephalon comes equally before the all of the brain (but

it appears partially caused by the development of the olfactory bulbs); in scincids is found the same sequence as in the 32 saurians (however with an inversion between the mesencephalic tectum and the tegmentum + medulla oblongata). Lastly, gekkonids are characterized by telencephalic growth that is the weakest of the entire brain; it is explained by reduced growth rates for the pallium and basal areas.

Other oppositions could be highlighted from one family to another, for the cerebellum or diencephalon, for example; they all contribute to isolating iguanids and agamids from that other extreme formed by gekkonids.

The differences are found with equal force whether contrasting Iguania and Scincomorpha or dracomorphs and lacertomorphs (Table V); the two subdivisions lead roughly to the same conclusions, which are perhaps even more clearly expressed in the second case. In lacertomorphs, the “dynamic” structures are the olfactory bulbs, cerebellum, optic roof, and in lesser measure the basal areas, the “regressive” structures being the diencephalon (more accurately, the dorsal thalamus) and pallium. On the other hand, in dracomorphs, with the exception of olfactory bulbs (allometric coefficient: 1.441), it is other structures that are “dynamic”: the pallium (and telencephalon), dorsal thalamus, and ventral thalamus; conversely, the basal areas, optic roof, and pretectum have clearly lower coefficients.

Therefore, opposition is very clearly manifest between the cerebellum, optic roof, and basal areas (lacertomorphs) on the one hand, and the pallium, dorsal thalamus, and ventral thalamus (dracomorphs) on the other. This result calls for two remarks:

– Pallium and basal areas intervening (concurrently) in the establishment of the allometric coefficients of the telencephalon, it is not surprising that the characteristics of each of the two groups escape the comprehensive review of the telencephalon.

– It is interesting to underline the parallel evolution of the pallium and dorsal thalamus in dracomorphs. This fact suggests an analogous characteristic evident in insectivores and lemurs (BAUCHOT, 1966) between the dorsal thalamic nuclei and neocortex. An effort is being made to explain which portion of the pallium is most closely associated with the dorsal thalamus. For the moment, this link between the pallium and dorsal thalamus of dracomorphs could be considered as an index of evolutionary progress of the latter relative to lacertomorphs. It is a hypothesis that cannot support any paleontological argument but which we will have to restate.

The analysis that has been conducted takes body weight Ps as an independent variable. A

comparable study could be carried out, this time taking the weight (or the volume) of the entire brain (Pe or E2) as reference. This choice is theoretically open to criticism; brain volume contains that of the structure being studied and it is not always negligible compared to that of the independent variable (the telencephalon represents close to 50% of brain volume!). The results that could be brought to light remain however in agreement with those being put forth: they underline the opposition between lacertomorphs and dracomorphs and on the dynamic plane (relative growth) confirm the combined importance of the pallium and thalamus in the latter.

Table IV. Brain Weight(Pe)/Body Weight and partial brain volume (large units and secondary subdivisions)/body weight ratios.  $\alpha$ : slope of allometric line (AMR); r: correlation coefficient; C. E.: equilibrium constant (logarithmic value); C. G.: center of gravity; abs: abscissa; ord.: ordinate (logarithmic value).

Table V. Partial Brain Volume/Body Weight ratios in lacertomorphs and dracomorphs.  $\alpha$ : slope of allometric line (AMR); r: correlation coefficient; C G. (x) and C. G. (y): center of gravity, abscissa and ordinate.

Table VI. Body ratio indices of various brain subdivisions. Lacertids provide the 100 reference. Each index is given with a range of variation of 12.5%. Pe: Brain weight; E1: Brain volume without ventricles; E2: Brain volume with ventricles (cf. Table II); A.: Telencephalon; B.: Diencephalon; C.: Brain stem; D.: Mesencephalic roof; E.: Tegmentum + medulla oblongata; 2. Olfactory bulbs; 3. Cerebral hemispheres; 4. Pallium; 5. Basal areas; 7. Epithalamus; 8. Dorsal thalamus; 9. Ventral thalamus; 10. Pretectum; 11. Hypothalamus. 13. Optic roof; 14. Posterior colliculi.

### 3. Comparison of body ratio indices

For each structure, beginning with the Brain Structure/Ps ratio, an index comparable to the encephalization indices can be calculated. The latter were calculated relative to the 100 reference of six lacertids from the sample (Reference Lizards). The structural indices, or body ratio indices were also calculated relative to the allometric line of the Reference Saurians: however, two alternatives became available:

– calculations can be made of the average value of slope (for the Reference Lizards) for

the various structures; this procedure, that furnishes a reference that could qualify as absolute, has the advantage of allowing comparisons of indices as well as one structure to another for a given animal, or one species to another for a given structure. However, the structures that are prone to vary significantly from one species to another show very high allometric coefficients, or conversely very low ones; an average value is inadequate to express this peculiarity so the index difference we seek to highlight is thus minimized.

– The Reference Lizards slope can be kept for each structure as needed; this reference, that could be qualified as relative, respects the individuality of each structure and has the advantage of possessing biological significance because it represents an average lacertilian state; on the other hand, it only validates the comparison of structures within species and not within a single brain.

The indices, calculated by adopting the second procedure, are known to be around 12.5%; the values shown in Table VI are core values; for comparison, each index is replaced by three data points:  $i$ ,  $0.875 i$ , and  $1.125 i$ , which allows including variation in the expression of different averages.

Comparisons are made between species or groups of species that combine one characteristic or another, between families or groups of families. However, it is hard to totally isolate a biological character but the hope is that certain traits are expressed in a *more marked* manner than others at the level of certain brain structures. It is within this perspective that we review the different indices while successively adhering to the form, locomotion, way of life, olfaction, and vision.

#### a) Form, locomotion, way of life

The orvet and scincids provide examples of animals where leg reduction effectively leads to leglessness (*Anguis fragilis*, *Chalcides chalcides*). The encephalization index is particularly low among such species, and this fact has already been linked to leg reduction (PLATEL, 1975a). Is this process, expressed by low values indicative of a privileged brain stage? In fact, *all* of the brain subdivisions studied are subject to regression as shown by the comparison, structure by structure, of the orvet-scincid group (6 species) with the Reference Lizards. The averages are significantly different with a high threshold of probability (0.1: Student's  $t = 3.17$  with 10 degrees of freedom): epithalamus ( $t = 5.94$ ), cerebellum ( $t = 4.86$ ), hypothalamus ( $t = 4.76$ ), optic roof ( $t = 4.39$ ), mesencephalic

roof ( $t = -4.23$ ), diencephalon ( $t = 3.79$ ) and brain stem ( $t = 3.42$ ); the other structures show averages that differ with less elevated threshold of significance (0.05), with the exception of basal areas and posterior colliculi for which there is no noticeable difference. If the structures involved in body mobility and stasis are retained in this list, it is shown that the cerebellum shows the greatest range of variation (from 16 for *Anguis fragilis* to 76 for *Scincus scincus*); the variances of the indices and the average indices are important for the other structures: tegmentum + medulla oblongata, ventral thalamus, basal areas. It is true that these structures already show indices close to those of the Reference Lizards in *Eumeces schneideri* and, in lesser measure, in *Scincus scincus*. For the moment, at the level of brain stages, therefore the cerebellum would be retained as a criterion of the growing importance of leglessness in certain saurians. It would be interesting to see whether this criterion remains viable in arboreal species or those with highly specialized mobility. Among the sampled lizards the following would be retained: (*Chalarodon madagascariensis*, *Anolis auratus*, *Oplurus sebae*, *Iguana iguana*, *Agama inermis*, *Agama agama*, *Calotes versicolor*, *Chamaeleo lateralis*, *Ameiva* species, *Callopiastes trimaculatus*, and *Varanus griseus*). For these eleven species, the index average for the cerebellum is 225.3, which differs significantly from that of the Reference Lizards (100.8). Living at ground level, with the possibility of rapid locomotion in biped posture (*Chalarodon madagascariensis* and the sampled teiids), or arboreality, are accompanied by an important development of the cerebellum; the other structures show highly varying indices (for example, in chameleons and the oplure), as glimpsed from the diversity of encephalization indices. Lastly, the other species from the sample are terrestrial species moving quickly or slowly on or near the ground (cerebellar indices from 80 to 130). These results express in a quantified form certain functional-anatomical conclusions of STEFANELLI (1943).

### b) Olfaction

From the initial examination, the brain shows pronounced differences in size of the olfactory bulbs from one species to another; the indices are also highly varied: from 5 (*Anolis auratus* and *Chamaeleo lateralis*) to 201 (*Ameiva* species). The other olfactory centers show more modest differentiation because they are more often included here within the most important groups that contribute to varied functions (pallium, basal areas, hypothalamus...). One is limited therefore to the primary olfactory center (olfactory bulbs) in order to appreciate the importance of this function. In this regard, certain families show a great homogeneity (iguanids, for example); others show instead a certain variability (*Phelsuma cepediana* among the gekkonids). In relation to the lacertids (Reference Lizards), scincids have the least-developed olfactory bulbs (Table VII, 2nd column); it seems reasonable to relate this reduction to the mode of life of the latter in desert regions (dry), because indices of the same order (or even inferior) are found in lizards of other families having a sabulicolous, xerophilic, or

even rupicolous mode of life: *Cordylus cordylus* (39), *Chalarodon madagascariensis* (25), *Liolaemus chiliensis* (26), *Agama inermis* (10), *Uromastix acanthinurus* (17) *Varanus griseus* (59)...The weakest values are found in *Calotes versicolor* (11), *Anolis auratus* (5), and *Chamaeleo lateralis* (5), all three of which are arboreal lizards. BAUCHOT and STEPHAN (1966 and 1969) have already underscored the existence of a similar relationship in Primates (arboreal and microsmatic). Distinguishing between microsmatic and macrosmatic lizards only by examining the size of the olfactory bulbs (during dissection of the brain) should be verified by calculating the index ratios of the bulbs. Provided that lacertids are considered microsmatic lizards (average index 100), the average state should fall between indices 80 and 90, which is the case in geckos (with the exception of *Phelsuma cepediana*). The other species are microsmatic to different degrees, from the monitor (in spite of appearances) to *Chamaeleo* and *Anolis*. As far as the ameiva, it provides on the other hand an example of strong macrosmaty (comparable to that of *Phelsuma*).

Table VII. Comparison of body ratio indices of the various brain structures studied while grouping species by family or groups defined in the text. LR: Reference Lizards; Ge: Gekkonids; Ig: Iguanids; Ag: Agamids; IG: Iguania; SC: Scincomorpha; DR: Dracomorphs; LA: Lacertomorphs. For each comparison it is specified whether the index averages are significantly or not significantly (NS) different, the value of Student's *t* and the significance threshold (0.05 or 0.01). When the difference can be retained, it is specified which of the two groups shows the highest average. The number of degrees of freedom (d. l.) is obtained by the formula ( $n + n' - 2$ ); the two last lines give the limits (0.05 and 0.01) of the corresponding *t*.

### c) Vision

Structures linked to vision are split within the first three stages of the brain: at the level of the optic tectum; in the diencephalon, at the level of the thalamus (dorsal thalamus primarily, and in lesser measure the ventral thalamus with the lateral geniculate nucleus, pars ventralis) and the pretectum; finally, in the telencephalon, it is possible that the visual fibers project into a portion of the dorsal cortex; a detailed review has already been offered on this subject (BECKERS, PLATEL and

NIEUWENHUY, 1972; PLATEL, BECKERS and NIEUWENHUY, 1973).

The chameleon has an improved visual organization that hints at considerable modifications at the level of these structures. In fact, among relatively low indices (most often below 100), relatively strong values are noted in the dorsal thalamus, pretectum, and optic tectum: 109, 118, and 107. In the Reference Lizards these same structures have indices of 100.3, 103.6, and 102.5, respectively; it should be noted that the differences with the chameleon are slight and of limited

significance. On the other hand, in other species with reduced olfaction the visual sense is developed: this is the case with *Chalarodon madagascariensis*, *Anolis auratus*, *Oplurus sebae*, *Iguana iguana*, *Agama inermis*, *Calotes versicolor*, *Agama agama*, *Varanus griseus*. At a significance threshold of 0.05, the averages for the optic roof (142.2), dorsal thalamus (132.2), and pretectum (138.7) differ from those of the Reference Lizards. Lastly, two species merit particular attention: the orvet and the ameiva. The orvet, under-equipped in the olfactory domain, is similarly affected in vision. The ameiva, on the other hand, already introduced as a strongly microsmatic lizard, should be considered as macroptic; this characteristic is sufficiently rare to be emphasized: in mammals, for example, it is not found except in proboscideans.

The results being presented (locomotion, way of life, olfaction, and vision) stress the coincidence between macropty, microsmaty, and arboreality in a certain number of species. This is the case for the chameleon, anole, oplure, iguana, and garden lizard. This connection brings to mind a comparable situation evident in mammals, in the group Primates.

#### d) Analysis of indices by family or other groupings

Comparisons were made between families represented by at least four species: lacertids, gekkonids, scincids, iguanids, and agamids (Table VII). Only the family Gekkonidae shows a clear heterogeneity due to *Phelsuma cepediana*, whose characteristics have already been mentioned. The results differ radically from one family to another; they can be summarized as follows:

– with regard to lacertids, gekkonids show greater development of the cerebral hemispheres (essentially because of the importance of the pallium) (Table VII, column 1).

– scincids with lower indices to those of Reference Lizards for the majority of structures (Table VII, column 2).

– lastly, agamids and iguanids (which do not really differ that much from one another), show significant cerebellar development and (most certainly correlative) some expansion of the basal areas. Conversely, the olfactory bulbs are reduced as well as the epithalamus (habenula), at least in iguanids (Table VII, columns 3 and 4).

Iguanids and agamids showing such character concordance, their grouping in the *Iguania*, the chameleon inclusive, results in a relatively homogenous group. Contrasting these *Iguania* with the *Gekkota*, limited only to Gekkonidae, and the *Scincomorpha* which resemble the other species from the sample (with the exception of the orvet and monitor, which belong to the *Anguimorpha*, but are not included because of the insufficient number of species). Table VII, column 5 shows that the *Scincomorpha* and *Gekkota* do not differ greatly except by a limited number of structures: the cerebral hemispheres and pallium (more developed in the *Gekkota*). By contrast, the *Iguania* differ from the *Scincomorpha* in the importance of the mesencephalic roof, optic roof, cerebellum, and basal areas (Table VII, column 7).

One last comparison of species is possible by regrouping them into lacertomorphs and dracomorphs (Table VII, column 8). As a general rule, the index averages in the dracomorphs are higher – at a threshold of 0.1 for the cerebellum, brain stem, mesencephalic roof, tegmentum + medulla oblongata, basal areas, dorsal thalamus, pretectum, and optic roof – at a threshold of 0.5 for the diencephalon, cerebral hemispheres, ventral thalamus, with the same averages in the lacertomorphs. These differences are visible, in the absence of any calculation, on certain graphs (Figures 3 to 7). The only exception is at the level of olfactory bulbs, which have a higher average index in the lacertomorphs.

Thus a pattern was found that matches the defining elements proposed by NORTH CUTT: the dracomorphs have a highly developed striatum (basal areas pro parte) (153.7), a voluminous pretectal region (137.7), reduced

olfactory bulbs (in the Iguania). Quantified confirmation is observed at all levels regarding qualitative neuroanatomical, functional, and phylogenetic arguments presented by their inventors (SENN, 1970 and 1974, NORTHCUTT, 1972).

For each structure, from the above-mentioned Brain Structure/Pe (or E2) ratio, an index comparable to the body ratio index can be calculated; it is given the name *brain ratio index*. The study of these indices leads to results that differ little from those presented above.

#### 4. Expression of different brain volumes as percentages of global brain volume (E2)

Gross values can be used in a final way by expressing the volume of each of these structures as a function of global brain volume (in percent of E2). Two possibilities are offered – either to introduce the Brain Structure/Ps (or Brain Structure/E2) allometry, – or to resort to relative volumes.

##### a) *Isoponderous percentages*

For each species, we retain the origin of the line passing through the representative point of the species (log Brain Structure, log Ps) and parallel to the allometric line for the Reference Lizards for each structure; in other words, it is the logarithm of the volume of structure when the body weight of the species is equal to 1 gram (log  $k_i$ ). The values of different structures corresponding to these logarithms ( $K_1, K_2, K_3, \dots, K_n$ ) represent, added up, what we have named E2 which brings the value to 100; the *isoponderous body percentages* are then calculated (Table VIII; figure 8). The principle and results remain the same (or close) when using the Brain Structure/E2 ratio; the *isoponderous brain percentages* are drawn from that. The intervention of either of the allometric ratios in the calculation of the percentages provides immunity to further critiques against relative volumes. But the calculation of various  $K_i$  is based on the choice of lacertids as the reference group and,

as we already mentioned, why this approach is more restrictive but more reliable and natural than the use of an average slope.

We will address the results brought by 17 of the 32 species from the sample, as well as the Reference Lizards taken as a whole. For each brain unit, the average of the percentages (for the Reference Lizards and the other 17 species) was calculated, as well as the concomitant standard error (as seen before, an index of variability of data around the average taken to the value of 100) (see the last two columns in Table VIII). The large units exhibit a lesser variability than the constituent subdivisions, which again verifies that the sum varies less than the constituent elements. The diencephalon holds the greatest stability (standard error = 8.9%), followed by the brain stem (11.4%), tegmentum + medulla oblongata (13.7%), and hypothalamus (14.0%); by contrast, the standard errors calculated for the olfactory bulbs (78.8%), cerebellum (39.6%), optic roof (24.8%), mesencephalic roof (24.2%), and pallium (24.0%) indicate great variability. It should be noted that the average percentage calculated for the diencephalon (9.9%) differs little from that known in mammals, for example in bats (STEPHAN and PIRLOT, 1970).

The encephalization index (calculated from the E2/Ps ratio) was brought under the representation of each species (Figure 8), and in some cases it is possible to discern the brain stages that intervene predominantly within the low or high values for this index. The gecko (Ge. g) differs little from the Reference Lizards (L. R.), similarly from the chalcid seps (Ch. c), girdled lizard (Co. c), and zonosaur (Zo. m). The forced limb reduction in the seps is accompanied by particularly low indices (58) and seems to be echoed over all parts of the brain; in fact, the proportions remain the same as those of the Reference Lizards or scincomorphs, nevertheless with the exception of the cerebellum and mesencephalic roof which are slightly less developed in the seps. The iguanids and agamids (Figure 8, middle) show slightly different types of organization from one

species to another without such differences becoming significantly worthy of being retained. Paradoxically, the chameleon shows similar proportions in the principal stages to those of the Reference Lizards; this is likewise the case in the ameiva (Am. s.): for this species, the high index (185) originates in the growth of all parts of the brain, while maintaining the proportions of a green lizard for example; in this respect, it could be considered as the opposite of the chalcid seps. In orvets (An. f.) the absence of legs has an effect on the cerebellum; the mesencephalic roof is also less important but an increase in relative volume of the telencephalon is observed (especially the olfactory bulbs). The monitor (Va. g.) demonstrates that its high index is due to exceptional growth in the

cerebellum and brain stem, to the detriment of the telencephalon, which leads to proportions far removed from those found so far: it is those of *Agama agama*, *Calotes versicolor*, and *Chalarodon madagascariensis* that are the most closely associated. One last point deserves some explanation: it concerns the comparison of percentages linked to the pallium and basal areas; the values are conspicuously equal in lacertomorphs whereas dracomorphs have a considerably less developed pallium (it represents less than half the percentage of the basal areas in *Anolis auratus* and *Calotes versicolor*). In this peculiarity is found new confirmation of two new types of organization, without being able to tell which of the two correspond to the most primitive arrangement.

Table VIII. Volume of various brain units expressed as a percentage of global brain volume (E2). The values are derived from the Brain Structure/Ps ratios, in each case taking the six lacertids as reference (L.R.: Reference Lizards). Only 23 lizards were analyzed, the average of six lacertids and several representative species from each family, and 2 snakes (a boid and a modern-type snake).

Fig. 8. Proportions of the main brain units among the different saurian species being studied. These were regrouped by family and under each is figured the index of encephalization (E2/Ps). The meaning of the abbreviations is provided in Table I; the numerical values of the isoponderous percentages are compiled in Table VIII.

1a.: Olfactory bulbs; 1b.: Pallium; 1c.: Basal areas; 2.: Diencephalon; 3a.: mesencephalic tectum; 3b.: Tegmentum + medulla oblongata; 4.: Cerebellum; 5.: Ventricles.

#### b) Relative volumes

These are obtained directly from weighing photogram elements, and many neuroanatomists think they have the right to use them for comparative studies. The analyses conducted in *Scincus scincus* (BAUCHOT and PLATEL, 1971), later generalized to squamates (PLATEL, 1975b) and two other orders of reptiles (PLATEL, 1976), show that for a given species, the representative points for "adults" are spread around an allometric line  $Pe/Ps$  that is not isometric. This allometry (negative) is relatively strong and lies in the neighborhood of 0.43 for squamates. In addition, it has been shown in *Scincus scincus* that the allometric coefficient varies greatly from one structure to

another (but it is not likely the same for the other species of lizards). It follows that calculation of a corrective term (evoked at the time of choosing our material) or the use of relative volumes for comparisons within the same species leads to unavoidably faulty results; in effect, suppose that in both cases the allometric coefficient is equal to unity. It can be accommodated when it is a matter of the corrective term; regarding relative volumes, the study done in *Scincus scincus* shows that error incurred is rarely greater than 5%. The interspecific study conducted on another allometric coefficient (0.669 for saurians) that equally differs from isometry implies use of relative volumes; in addition, this value is the result of allometric coefficients of different structures composing

the brain, and Tables IV and V show that these vary considerably from one structure to another and from one group of species to another. But this mostly a second argument that leads us to proscribe the usage of relative volumes in our interspecific comparisons: it is a matter of estimating the range of variation which is minimized by half (as demonstrated for *Scincus scincus*) and carried over to an average value of 6%; such an error (more than 100%) is incompatible with the interspecific analyses that we want to undertake. In the present case, the differences in the isoponderous percentages oscillate between 2.2 (ventricles) and -1.7 (brain stem), but for relative values, the differences are much more impressive: +88% (ventricles) , +73% (olfactory bulbs), -13.6% (hypothalamus) or even -15.2% (diencephalon).

### 5. The case of snakes

Three species of snakes were studied following the same protocol as the saurians; these are the *Boa constrictor* (henophidian), *Natrix natrix* and *Vipera aspis* (caenophidians). It will stand on examination of percentages (Table VIII and Figure 8) which highlight the following characteristics:

a) If snakes are compared among themselves, it is evident that there is no fundamental difference between *Natrix natrix* and *Vipera aspis*. Figure 8 shows that modern-type snakes (represented by *Natrix natrix*) have a relatively more elevated development of the mesencephalic roof than the boid *Boa constrictor*; the diencephalon is conversely less important.

b) If the organization of the two snakes in Figure 8 (*Boa constrictor* and *Natrix natrix*) is compared to that of lizards with greatly reduced limbs (*Chalcides chalcides*) or to legless forms (*Anguis fragilis*), only the reduced size of the cerebellum and mesencephalic roof stand out as characteristics common to the four species which are additionally very different in terms

of other structures. This result also sets apart the boid from the grass snake or the orvet from the chalcid seps as well as lizards from snakes; it confirms the fact that in the two percentages retained, one has the reflection of a form and mode of locomotion (cerebellum) and perhaps of different modalities in the organization of vision.

c) When comparing our snakes with the Reference Lizards, it could be concluded that boids and caenophidians are differentiated by a relatively more voluminous telencephalon and tegmentum + medulla oblongata and a smaller mesencephalic roof (in particular the optic roof) and cerebellum. Within the telencephalon, the olfactory bulbs and pallium are primarily responsible for the volume increase, the basal areas being less significant in contrast.

These several elements of comparison show that diversity in lizards is opposite to a certain homogeneity in snakes, among which nevertheless it is necessary to expect finding two types of organization, the most evolved seems to be set apart by a more pronounced process of telencephalization than that of boids and numerous lizards.

### Conclusion

The allometric analysis of the volume of different parts of the brain (and the establishment of indices and isoponderous percentages) allows connecting certain biological characteristics of species (or families or still larger groups) to the development of a stage or a great brain subdivision. But one cannot hope to isolate a functionally (or phylogenetically) homogeneous group. A more in-depth study of their constitutive elements is advisable, but slicing the entire brain into fifty levels is not compatible with the volumetric estimation of such components. Consequently, it is important to redo the analysis of each brain stage with the help of a number of photograms that permit making such



measurements. The present work allowed establishing the modalities for further analysis in practical terms by the estimation of volumes, calculation of the shrinkage coefficient inherent in slicing, access to fresh volumes; on the methodological plan, the regression analysis was completed by the definition and calculation of indices and isoponderous percentages (which are preferable to relative volumes). It is important to acknowledge the essential intermediate step that extends the examination of brain indices and prepares for a quantified investigation of nuclear masses.

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### **Bibliography**

[not included]