Rev. Biol. Trop., 20(1): 5-27, 1972

Comparative post-natal growth in five species of the genus Sigmodon. II. Cranial character relationships*

by

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(Received for publication May 28, 1970)

ABSTRACT

At birth, the cotton rat skull is oval and the braincase continues to expand during the first 20 days to near the adult size. Subsequently with the development of the dorsal area and the extension of the bones at the base of the braincase, the rounded form is transformed into the typical long-snouted appearance of the adult. Skull measurements demonstrate the initial rapid expansion of the braincase and the subsequent extension of the rostrum. Adult skull size is attained within the first 100 days of life.

Normally, during the first days after birth, height of the braincase is greater than the length of the post-palatal area. However, at 20 to 30 days growth in the latter is greatest and its dimensions surpass those of the former. In three species, *Sigmodon hispidus, Sigmodon alleni* and *Sigmodon ochrognathus,* the rostral length exceeds the height of the braincase only after the animals are over 100 days old.

At 40 days palatal and maxillary tooth-row lengths are near the maximum adult size, while the diastema is 50 to 67 percent (depending on the species). At birth the zygomatic arches are small but rapidly expand laterally in comparison with the slower-growing braincase. This process, together with the lengthening of the rostral region is related to weaning and the development of the masticatory and facial muscles. The change of growth from an accelerated phase (1 to 40 days) to a much slower rate seems correlated with attainment of sexual maturity.

The age of the animals studied is often an important variable in taxonomic work, differential growth reflecting as it does on mophological details on to adulthood.

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* Part of a dissertation presented to the Graduate School of Michigan State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Detailed knowledge of the comparative cranial growth of the smaller mammals is not yet available; the present study is intended as a contribution to this need, and to describe the changes occurring with age in the dimensions of the skull of cotton rats *(Sigmodon)* kept under laboratory conditions.

MATERIAL AND METHODS

All rats in this study were kept under virtually identical conditions. Skeletal material was obtained from rats which had been bred in the laboratory of the Michigan State University Museum. Specimens were killed at several ages (1, 10, 20, 30, 40, 50, 100 and 200-400 days). Skulls were cleaned by the dermestid method.

Thirteen measurements were taken from each skull with vernier calipers to an accuracy of 0.1 mm as follows (Table 1): *greatest length,* from the tip of the nasals to the posterior bulge of the braincase; *height,* perpendicular distance between the greatest convexity of the parietal bones at the median, and a junction line formed by a glass slide placed horizontally to the basioccipital and basisphenoid bones (on the ventral surface), less the the width of the glass slide; *condylo-basal length,* distance along the midline of the skull from a line connecting the anteriormost portions of the premaxillae to a line connecting the posteriormost margin of the occipital condyles; *palatal length,* distance from the anterior part of the premaxillary bones to the anteriormost point on the posterior border of the palatine bones; *post-palatal length,* least distance from the indentation at the posterior end of the palatine bones to the anteriormost border of the foramen magnum; *length of the rostrum,* distance connecting the posterior margin of the anterior orbital bridge of the maxillary bone with the tip of the nasal bone on the same side; *least interorbital breadth,* width of the most constricted part of the interorbital space; *interparietal breadth,* greatest width across the interparietal bones; *breadth of the braincase,* breadth of the skull across the mastoid processes; *zygomatic breadth,* greatest distance between the lateral borders of the zygomata; *alveolar length of the maxillary tooth-row,* length of the alveoli of the three upper molariform teeth; *length of the diastema,* distance from the posterior margin of the alveolus of the upper incisor to the anterior margin of the alveolus of the first cheek tooth; *length of the incisive (anterior palatine) foramina,* greatest length of these foramina; *length of the nasals,* greatest length of the nasal bone.

Body weight was not taken into consideration because this value is particularly variable under laboratory conditions and depends largely on feeding (GEBCZYNSKA, 5); weight is not a uniform variable of age and therefore should not be used for analysis of age structure in populations of small mammals (DUNAWAY and KAYE, 3).

The skull measurements obtained were used to: a.) determine the comparative rate of increase (and percent increase) with age of the three principal regions of the skull; b.) analyze the growth of the palatal region by comparing the changes of the alveolar length of the maxillary tooth-row, the diastema and

palatal lengths; c.) determine the comparative increase in rostral length using the ratio: length of the incisive foramen/length of the diastema; d.) determine the comparative increase in the skull breadth in the five species of cotton rats by relating the growth of the zygomatic breadth and the breadth of the braincase; e.) analyze comparatively the interparietal space and the interorbital area, expressed as ratios of breadth of the braincase; f.) derive an aging formula by the multiple linear regression method (Gaus-Doolitle method) to help determine the approximate age of a cotton rat on the basis of skull and body dimensions.

RESULTS AND CONCLUSIONS

COMPARATIVE GROWTH OF SKULL: Skull growth in cotton rats is the result of an early rapid expansion in the dorsal and lateral dimensions of the braincase and a slower growth of longer duration resulting in the elongation of the base of the braincase and the forward projection of the rostrum.

During the first 20 days after birth, rapid growth of the dorsal part of the braincase is the major factor determining cranial shape. After this early expansion, however, the slower but steady lengthening of the base of the braincase and rostrum result in a reduction in the rounded dorsal profile, correlated with the flattening and decrease in the relative height of the cranium, and with the posterior elevation of the occiput and fronto-nasal area (BAER, 1).

The growth relationships between different parts of the skull are shown in Figures 1 and 2. The rostrum is characterized by the length of the nasal bones. The dimensions of the braincase are obtained by measuring the length of the braincase (greatest length of the skull less the length of the nasals), the height of the braincase and the postpalatal length.

The skull (as shown by the condylo-basal length) increases in length throughout the life of the cotton rat. This is further demonstrated by measurements of the length of the rostrum and three aspects of the braincase (Table 2, Fig. 2).

The lengthening of the rostrum with age was found to be directly correlated with the increase in condylo-basal length; however, other cranial dimensions grow progressively slower as age increases (Fig. 2). In *Sigmodon hispidus* the rostral length increases only 9.9 percent of the condylo-basal length in the first 200 days of life, whereas it increases to a maximum of 13.2 percent in *S. alleni.*

At one day old, *S. alleni* has proportionally the longest braincase (90.0 percent of the condylo-basal length) in relation to skull length; *S. hispidus* has the smallest (75.8 percent). However, at 200 to 400 days *Sigmodon leucotis* has the longest braincase (67.1 percent) while *S. alleni* has the shortest (62.4 percent). The braincase grows slowly from 13.0 percent of the condylo-basal length in *S. hispidus* to 27.6 percent in *S. alleni* during the first 200 days.

Lengthening of the basal part of the braincase in the first 200 days of life (as shown by the postpalatal length) is even slower (2.9 perecent of the condylo-basal length in *Sigmodon ochrognathus* to a maximum of 10.4 in *S.*

TABLE 1.

Cranial measurements of the five species of Sigmodon

Measurements taken	Age-Classes (in days) and Number of Specimens							
	1-7	10-6	20-6	30-4	40-8	50-6	100-6	Adult-27
Sigmodon hispidus major								
Greatest length skull	17.1 16.9-17.2	24.0 23.2-25	27.5 25.8-28.5	30.3 29.3-31.5	31.8 29.9-33.4	32.7 32-34	36.0 31.2-40.3	42.2 40.5-44.6
Height of braincase	8.5 8.1- 8.6	10.8 10.5-10.9	11.6 11-12.2	12.1 11.7-12.5	12.6 12.2-13	12.9 12.7-13.1	13.0 11.8-14.8	15.8 14.8-17.3
Condylo-basal length	16.1 15.9-16.3	21.7 20.9-22.8	25.1 23.5-26.2	28.4 27.2-29.6	30 28-32	31.3 30.3-32.3	34.6 29.9-38.8	40.9 39.1-42.5
Palatal length	8.4 8-8.6	10.8 10-12.2	14.0 12.9-14.6	16.0 15.2-16.7	17.0 15.6-18.2	17.7 17-18.4	19.6 16.3-22.5	23.5 21.7-24.9
Length of rostrum	5.1 5-5.3	7.8 7.3- 8.3	9.3 8.4- 9.7	10.9 10.3-11.5	11.6 10.7-12.3	11.9 11.1-12.7	13.6 11.9-15.6	16.6 15.6-17.8
Width of rostrum	4.4 4.3-4.5	5.1 4.9- 5.3	5.4 5.1- 5.6	5.8 5.3- 6.5	6.3 6.1- 6.6	6.7 6.4- 7.1	7.3 6.6- 8.2	8.9 8-9.9
Least interorbital breadth	4.6 4.5-4.7	4.6 4.5- 4.8	4.6 4.4- 4.8	4.8 4.5- 5.1	4.8 4.6- 5	4.8 4.6- 5	5.0 4.6- 5.4	5.6 5.2- 6.2
Interparietal breadth	8.0 7.8-8.4	9.4 8.7-10.2	10.4 10.2-10.8	10.3 9.9-11	10.4 9.8-10.5	10.9 10.5-11.2	11.3 10.8-11.5	12.1 11.2-13.3
Breadth braincase	10.6 10.3-10.8	12.5 12.4-12.7	13.4 13.1-13.7	13.7 13.2-14.4	14.6 14.3-15.2	14.8 14.5-15.2	15.0 14.8-15.5	16.4 15.5-17.6
Zygomatic breadth	10.0 9.8-10.2	13.5 13.3-13.8	15.4 14.3-16.1	17.2 16.1-18	18.1 17.3-19.3	18.8 18.3-19.2	20.5 18.2-22.9	23.7 22.1-25.4

Alveolar length of maxillary tooth-row	4.2 4-4.3	5.7 5.5- 5.8	5.9 5.6- 6.3	6.9 6.2- 7.1	6.9 6.6- 7.3	7.1 6.7- 7.5	7.1 6.2- 8	7.6 7.1- 8.2
Length of diastema	4.0 3.9-4.2	5.0 4.5- 5.2	6.4 5.6- 7	7.7 7.1- 8.4	8.1 7.3- 8.6	8.4 8-9	9.8 7.7-11.6	12.3 11.1-13.1
Length incisive foramen	2.4 2.2-2.5	4.3 4.1- 4.6	5.6 5.3- 5.9	6.4 5.9- 7	6.9 6.3- 7.5	7-1 6.8- 7.4	8.0 6.5- 9.4	9.9 9.5-10.5
Length of nasal	4.9 4.8-5.2	7.7 7.5- 8.2	9.3 8.3- 9.8	10.5 10-10.9	11.4 10.4-12.2	11.7 10.7-12.5	13.3 11.7-15.3	16.5 15.3-18
Sigmodon alleni								
Greatest length skull	17.9 17.8-18	23.2 22.3-24.6	26.6 26-27.8	28.6 27.5-29.1	29.0 28-30.7	30.9 29.7-32.1	33.3 32.1-34.4	36.0 33.4-37.8
Height of braincase	8.5 8.3- 8.6	9.6 9-10	10.6 10.3-11.4	11.3 10.5-12.2	11.5 11-12.1	11.5 11.1-12	12.3 11.9-12.9	13.2 12.2-13.9
Condylo-basal length	15.0 13.9-17.1	21.1 19.9-21.5	24.6 24.2-25.5	26.6 25.8-27.3	26.9 26.3-28.9	28.4 27.2-30.3	31.4 30.4-32-4	34.3 31.9-35.8
Palatal length	6.8 6.3- 8.4	11.4 10.8-11.9	13.4 12.8-14.1	14.8 14.5-15.1	14.9 14.4-15.7	15.7 15.3-16.4	17.6 17.3-18.1	19.1 17.4-19.9
Length of rostrum	5.5 5.2- 5.8	8.2 8-9	9.5 9.2- 9.9	10.2 9.8-10.7	10.7 10.5-11.7	11.5 10.5-12	12.8 12.2-13.7	14.1 12.1-15.2
Width of rostrum	4.5 4.4- 4.6	4.6 4.1- 4.9	5.4 5.2- 5.6	5.7 5.3- 6.2	5.8 5.4- 6.2	6.0 5.8- 6.4	6.7 6.- 7	7.5 6.6- 8.3
Least interorbital breadth	4.4 4.3- 4.7	4.5 4.3- 4.8	4.6 4.5- 4.9	4.6 4.3- 4.8	4.8 4.6- 5	4.9 4.8- 5.2	5.1 4.9- 5.5	5.4 4.9- 5.5
Interparietal breadth	8.5 8.4- 8.7	9.9 9.8-10.2	10.1 9.8-10.8	10.6 10.5-10.8	10.3 9.9-11.3	10.9 10.7-11.2	11.2 10.9-11.6	11.3 10.3-13.1

Table 1, Cont.	Age-Classes (in days) and Number of Specimens							
	1-7	10-6	20-6	30-4	40-8	50-6	100-6	Adult-27
Breadth braincase	10.5 10.3-10.8	12.1 11.9-12.4	12.4 11.9-13	12.5 12-13.2	12.9 12.8-13.5	13.0 12.7-13.6	13.2 12.9-13.7	14.2 13.2-14.9
Zygomatic breadth	9.7 9.1-10.6	12.9 12.6-13.2	14.7 14.2-15.1	15.6 14.8-16.4	16.2 15.7-17.2	16.9 15.9-18	18.1 17.6-19	20.0 18.1-20.7
Alveolar length of maxillary tooth row	3.8 3.5- 4.2	5.4 4.7- 5.5	5.7 5.4- 6.1	6.2 5.9- 6.4	6.2 5.9- 6.3	6.2 6.1- 6.3	6.3 6.1- 6.5	6.3 5-6.9
Length of diastema	3.9 3.5- 4.2	4.7 4.4- 5.1	5.7 5.2- 6.2	6.4 5.9- 6.9	6.7 6.6- 7.6	7.3 6.8- 8.1	8.6 8.2- 9.3	9.7 8.8-10.4
Length incisive foramen	1.9 1.4- 2.2	3.8 3.4- 4.3	4.6 4.3- 5.1	5.1 4.5- 5.6	5.4 4.9- 6.1	5.7 5.5- 6.3	6.5 6- 6.6	7.6 6.1- 8.4
Length of nasal	4.4 3.9- 5	7.6 6.9- 8.7	8.1 7.6-10.1	10.6 10.2-11.3	10.8 10.7-11.7	11.9 10.4-12.7	13.1 12.3-14.5	14.6 12.9-15.9
Sigmodon fulviventer								
Greatest length skull	17.9 16.3-19.8	23.4 22.2-26	26.4 26.6-28	29.7 27.6-31.6	30.5 28.8-33.1	31.4 27.7-32-7	32.6 29.4-36.9	36.6 32.2-40.1
Height of braincase	9.0 8.5- 9.8	10.7 9.7-11	11.3 11-12.7	12.2 11.8-13.4	12.5 11.9-13.3	12.8 11.6-13.7	13.3 12.3-14.4	14.6 13-15.8
Condylo-basal length	16.2 15.3-17.5	21.5 20-24.4	24.7 23-27.4	28.3 26-32.9	29.1 27.2-30.7	30.2 26.4-31.8	32.4 28.2-36.7	35.6 30.9-39.7
Palatal length	8.7 8.2- 9.6	11.9 11.1-13.6	13.8 13-14.9	15.7 14.9-17.8	16.4 14.5-17.3	17.1 14.6-18.2	18.3 16-20.2	20.3 17-22.2
Length of rostrum	5.3 4.6- 6.1	7.7 7.1- 9	9.2 8.5-10	10.7 9.5-14.3	11.6 10.5-11.8	11.6 9.8-12.3	12.7 11.8-13.7	14.3 12.7-15.7

Width of rostrum	3.8	4.9	5.4	6.0	6.2	6.3	6.6	7.3
	3.2- 4.7	4.4- 5.3	5-6.1	5.2- 7.4	5.8- 7	5.3- 6.9	5.6- 7.7	6.1- 8.6
Least interorbital breadth	3.9	4.4	4.4	4.6	4.6	4.6	4.8	5.2
	3.5- 4.7	4.1- 5	4.2- 5	4.2- 5	4.2- 4.9	4.1- 5	4.3- 5.4	4.5- 6
Interparietal breadth	8.5	10.0	10.5	11.0	11.2	11.5	11.5	12.7
	7.7- 9.4	9-11.3	9.8-11.3	10.3-11.9	10.5-11.8	10.9-12.4	10.5-12.5	11.6-14.6
Breadth braincase	10.2	11.4	13.1	13.7	14.1	14.2	14.5	15.7
	9.7-10.8	10.8-12.9	12.6-13.5	13.1-14.3	13.5-15.1	12.8-15.8	13.6-15.2	14.4-17.5
Zygomatic breadth	10.4	13.5	15.5	17.7	18.2	18.5	19.5	20.9
	9.6-11.1	12.7-15.1	15.1-16.3	16.8-19.6	17.2-19.1	16.4-20	17.3--20.9	17.9-23.4
Alveolar length of maxillary tooth-row	4.3	5.6	6.0	6.5	6.5	6.6	6.7	6.7
	3.5- 5	5.2- 6.4	5.5- 6.7	6-6.9	6.1- 7	5.7- 6.9	6.3- 7.5	6.2- 7.3
Length of diastema	3.7	5.2	6.2	7.5	8.0	8.4	9.2	10.7
	3.3- 4.2	4.4- 6.9	5.8- 6.9	6.7- 9	7-8.8	7.2- 9	7.9-10.8	9-12.2
Length incisive foramen	2.5	4.4	5.6	6.5	6.9	7.1	7.7	8.7
	2-3.2	3.5- 5.5	4.8- 6.1	5.8- 8	5.7- 8.1	6.5- 7.8	5.7- 9.4	7-10.3
Length of nasal	4.6	7.1	8.8	9.9	10.8	11.3	12.2	13.9
	3.9- 4.9	6.6- 8.8	8.2- 9.8	9.1-14.3	9.6-11.3	9.4-12.1	10.6-13.9	12-15.7
Sigmodon leucotis								
Greatest length skull	18.7	22.9	24.7	—	28.0	—	31.2	35.4
	17.4-19.8	22-23.1	24.2-25.2	—	25.9-30.1	—	30-31.3	33.4-37
Height of braincase	9.4	10.5	10.9	—	11.9	—	13.3	14.1
	9.3- 9.8	10.2-10.7	10.8-11	—	11.2-12.6	—	13.1-13.5	13.6-14.6
Condylo-basal length	16.9	21.0	23.1	—	26.3	—	30.2	33.7
	15.8-17.9	20.1-21.4	22.5-23.7	—	24.3-28.3	—	30-30.5	32.4-35.4

Table 1, Cont.	Age-Classes (in days) and Number of Specimens							
	1-7	10-6	20-6	30-4	40-8	50-6	100-6	Adult-27
Palatal length	8.2	11.3	12.9	—	14.8	—	16.3	19.1
	8.2	10.8-11.7	12.5-13.3	—	13.6-16	—	15.6-17.8	18.2-20.1
Length of rostrum	5.2	7.1	8.1	—	9.6	—	10.8	13.8
	4.9- 5.7	6.7- 7.5	8-8.2	—	8.8-10.4	—	10.6-10.9	12.8-14.7
Width of rostrum	4.3	4.7	5.0	—	5.7	—	6.7	7.7
	4.2- 4.5	4.4- 4.9	4.9- 5.1	—	5.3- 6.1	—	6.5- 7	6.9- 8.3
Least interorbital breadth	4.5	4.5	4.6	—	4.6	—	5.0	5.1
	4.4- 4.6	4.4- 4.7	4.6	—	4.5- 4.7	—	4.9- 5.2	4.9- 5.4
Interparietal breadth	8.3	9.3	10.8	—	10.5	—	11.8	12.2
	8.1- 8.4	9.2- 9.5	10.8	—	9.8-11.2	—	11.7-11.9	11.5-12.9
Breadth braincase	10.5	12.3	13.0	—	14.0	—	14.6	15.3
	10.2-11.1	12.2-12.5	12.9-13.1	—	13.3-14.7	—	14.6	14.8-16
Zygomatic breadth	10.6	13.0	14.6	—	16.5	—	18.3	19.8
	10.4-11	12.6-13.4	14.3-14.9	—	15.1-17.9	—	18.1-18.5	19.3-20.8
Alveolar length of maxillary tooth-row	4.2	5.3	5.5	—	6.3	—	6.3	6.6
	3.7- 4.4	5-5.6	5.3- 5.7	—	6-6.6	—	6.1- 6.5	6-7.2
Length of diastema	4.2	5.4	6.0	—	7.1	—	8.8	9.8
	4.1- 4.6	5.1- 5.7	5.7- 6.3	—	6.5- 7.7	—	8.4- 9.5	9.4-10.5
Length incisive foramen	2.8	4.3	4.6	—	5.7	—	7.0	7.4
	2.4- 3.3	4-4.6	4.4- 4.8	—	5.- 6.2	—	6.6- 7.4	7-8.5
Length of nasal	4.6	6.5	7.9	—	9.1	—	11.2	12.8
	4.2- 5.3	5.9- 6.8	7.7- 8	—	8.6- 9.6	—	10.3-12.5	12.8-13.4
Sigmodon ochrognathus								
Greatest length skull	17.2	23.1	24.5	—	29.2	29.9	32.0	33.8
	16.6-17.5	21.5-27	23.2-25.5	—	28.1-30	28.3-30.1	30.8-36	32.6-34.9

Height of braincase	8.7	10.2	10.5	—	11.5	11.6	12.4	12.8
	8.3- 9	9.7-11.2	10.2-10.8	—	11.3-11.8	11.3-11.7	11.9-14	12-13.9
Condylo-basal length	15.3	21.2	22.5	—	26.3	27.8	32.1	31-33.4
	15.1-15.7	19.1-25.7	21.1-23.7	—	25.3-27.8	26.4-27.6	28.6-34.9	30.2
Palatal length	8.1	11.3	12.2	—	15.1	15.0	16.9	17.9
	7.8- 8.5	10.2-14.6	11.4-13	—	14.8-15.2	14.5-15.5	16.1-19.6	17-18.7
Length of rostrum	4.8	7.6	8.5	—	10.8	10.9	12.3	13.1
	4.7- 5.1	6.7- 9.9	7.8- 9	—	10-11.3	10.6-11.7	11.4-14	12.3-13.9
Width of rostrum	4.1	4.9	5.1	—	6.1	6.3	6.7	7.1
	3.9- 4.3	4.5- 5.7	4.7- 5.4	—	5.7- 6.3	6-6.7	6.2- 7.5	6.5- 8.1
Least interorbital breadth	4.2	4.4	4.3	—	4.7	4.6	4.9	5.0
	4-4.3	4.3- 4.5	4.2- 4.5	—	4.6- 4.8	4.5- 4.8	4.7- 5.1	4.6- 5.3
Interparietal breadth	7.7	9.7	9.6	—	10.4	10.7	10.2	11.7
	7.5- 8	9.3-11	9.2-10.1	—	10.2-10.9	10.2-10.9	9.6-11.4	11-12.6
Breadth braincase	9.8	12.0	12.6	—	13.4	13.5	13.9	14.8
	9.6-10.2	11.4-13.1	12.1-13.2	—	13.2-13.7	13.3-13.8	13.5-14.9	14-15.9
Zygomatic breadth	9.9	10.6	14.5	—	17.0	16.9	18.6	19.3
	9.6-10.3	10.3-12.3	13.4-15.5	—	16.5-17.5	16.3-17.6	17.7-21.2	18.4-20.5
Alveolar length of maxillary tooth-row	3.7	5.2	5.3	—	6.2	6.3	6.3	6.3
	3.4- 3.9	4.8- 6	5.2- 5.6	—	6-6.3	6.2- 6.4	6.1- 7.3	5.7- 6.5
Length of diastema	3.8	4.8	5.5	—	6.9	6.9	8.3	9.1
	3.4- 4.1	3.9- 6.7	5.1- 6.1	—	6.8- 7	6.7- 7.1	7.5-10	8.2- 9.7
Length incisive foramen	2.5	3.9	4.3	—	5.6	5.7	6.8	7.1
	2.3- 2.8	3.5- 5	4.1- 4.6	—	5.1- 5.8	5.4- 5.9	6.2- 8.6	6.6- 7.6
Length of nasal	4.4	7.3	8.3	—	9.1	10.2	12.2	13.0
	4.1- 4.6	6.2-10.1	7.8- 9	—	8.5-11.2	9.9-10.8	11.1-13.8	11.9-13.9

TABLE 2.

Development with age of the rostrum and the braincase (expressed in percentages) in relation to skull length (expressed in terms of the condylo-basal length) in Sigmodon

Age (days)	Condylo-basal length	Length of rostrum (%)	Length of braincase (%)	Postpalatal length (%)	Height of braincase (%)
Sigmodon hispidus					
1	16.1	30.4	75.8	47.8	52.8
10	21.7	35.5	75.1	45.6	49.8
20	25.1	37.2	72.8	44.4	46.4
30	28.4	37.0	69.7	43.7	42.6
40	30.0	38.0	68.0	43.3	42.0
50	31.3	37.4	67.1	43.5	41.2
100	34.6	38.6	65.8	43.5	37.7
adult	40.9	40.3	62.8	42.5	38.6
Sigmodon alleni					
1	15.0	29.3	90.0	54.7	56.7
10	21.1	36.0	73.9	46.0	45.5
20	24.6	32.9	67.1	45.5	43.1
30	26.6	39.8	63.9	44.4	42.5
40	26.9.	40.1	66.2	44.6	42.8
50	28.4	41.9	66.9	44.7	40.9
100	31.4	41.7	64.3	43.9	39.2
adult	34.3	42.6	62.4	44.3	38.5
Sigmodon fulviventer					
1	16.2	28.4	82.1	46.3	55.6
10	21.5	32.9	75.5	44.4	49.4
20	24.7	35.6	71.3	44.1	45.7
30	28.3	35.0	69.6	44.5	43.1
40	29.1	37.1	67.7	43.6	43.0
50	30.2	37.4	66.6	43.4	42.4
100	32.4	37.7	65.4	43.5	41.0
adult	35.6	39.0	63.8	43.0	41.0
Sigmodon leucotis					
1	16.9	27.2	83.4	51.5	55.6
10	21.0	31.0	78.1	46.2	50.0
20	23.1	34.2	78.1	46.2	50.0
30	—	—	—	—	—
40	26.3	34.6	71.9	43.7	45.2
50	—	—	—	—	—
100	30.2	37.1	66.2	46.0	44.0
adult	33.7	38.0	67.1	43.3	41.8
Sigmodon ochrognathus					
1	15.3	28.8	83.7	47.1	56.9
10	21.2	34.4	74.5	46.7	48.1
20	22.5	36.9	72.0	45.8	46.7
30	—	—	—	—	—
40	26.3	34.6	68.4	42.6	43.7
50	27.8	36.7	67.3	46.0	41.7
100	30.2	40.4	65.6	44.0	41.1
adult	32.1	40.5	64.8	44.2	39.9

alleni). Likewise, the heightening of the braincase is proportionately slower in relation to the lengthening of the skull. In this period the smallest growth is in *S. leucotis* (13.8 percent of the condylo-basal length), the greatest in *S. alleni* (18.2 percent).

The changes in the cotton rat skull from a short, rounded structure at one day of age to an elongated, flattened condition at 200 days is demonstrated by the histogram in Fig. 2. The height of the braincase at birth is great in proportion to the other skull dimensions (e.g. rostral and postpalatal lengths), but the subsequent rate of elongation far exceeds that of heightening. In fact, the measurements of postpalatal length surpass those of the height of the skull by the time cotton rats are between 20 to 30 days old. The rostral length in the 200 day old cotton rat exceeds the cranial height in all species except *Sigmodon fulviventer* and *S. leucotis.*

Comparison of the growth of the height and length of the braincase using the ratios length/height and postpalatal length/height of the braincase (Table 3) shows that the antero-posterior dimensions of the braincase and post-palatal length increase more rapidly than does the height.

TABLE 3.

Comparison of growth of height and length of braincase

Age (days)	*S. hispidus*		*S. alleni*		*S. fulviventer*		*S. leucotis*		*S. ochrognathus*	
	*	**	*	**	*	**	*	**	*	**
1	1.43	0.90	1.58	0.96	1.47	0.83	1.50	0.92	1.47	0.82
10	1.50	0.91	1.62	1.01	1.52	0.89	1.56	0.92	1.54	0.97
20	1.56	0.95	1.55	1.05	1.55	0.96	1.61	0.93	1.54	0.98
30	1.59	0.97	1.50	1.04	1.61	1.03	—	—	—	—
40	1.61	1.03	1.54	1.04	1.57	1.01	1.58	0.96	1.56	0.97
50	1.62	1.05	1.65	1.10	1.57	1.02	—	—	1.61	1.10
100	1.74	1.15	1.64	1.12	1.59	1.06	1.50	1.04	1.59	1.07
adult	1.62	1.10	1.62	1.15	1.55	1.04	1.60	1.03	1.62	1.10

* — Length/height of braincase

** — Postpalatal length/height of braincase.

The length of the skull can be expressed in terms of the condylo-basal length which may be divided into the palatal and postpalatal lengths. The ratios of the palatal and postpalatal lengths to the condylo-basal length are inversely related in all species of *Sigmodon* and for all age-groups studied. When the skull lengthens the rostrum maintains the same pattern of growth, while the braincase shows a progressive reduction in relative size (Table 4).

TABLE 4.

Comparative lengthening (expressed in percentage of condylo-basal length) of the rostrum and braincase

	One day old		Adult stage	
	Palatal	Postpalatal	Palatal	Postpalatal
S. hispidus	52.2	47.8	57.5	42.5
S. alleni	45.3	54.7	55.7	44.3
S. fulviventer	53.7	46.3	57.0	43.0
S. leucotis	48.5	51.5	56.7	43.3
S. ochrognathus	52.9	47.1	55.8	44.2

The ratios of the least interorbital breadth and the interparietal breadth to the breadth of the braincase in the various species of *Sigmodon* are shown in Table 5. Measurements of the breadth of the braincase at birth vary between 64.5 percent to 73.9 percent of the adult breadth in the five species of cotton rats studied. At the same age, the dimensions of the least interorbital breadth are from 75.0 precent to 88.4 percent those of the adult. The interparietal breadth at birth is from 65.8 to 75.2 percent as broad as the same region in the adult stage.

Table 4 shows that the interorbital area and the interparietal space increase more slowly in breadth from birth to adulthood (except in *S. leucotis* and *S. ochrognathus*) in relation to the broadening of the braincase.

Three measurements of the palatal region of *Sigmodon* were used to relate growth in this area during the first 100 days of life (Table 6).

The palatal length in *S. hispidus* and *S. alleni* as shown in Table 6 more than doubles (102 and 104 percent, respectively) in the first 40 days of life, while in the other three species this increase is less, between 65 and 86 percent. The species seem in better accord when comparing growth in alveolar length with an increase between 50 and 67 percent in the first 40 days and almost no growth thereafter. However, the increase in length of the diastema (Table 7) shows a marked variation between species, from 71 to 116 percent in the first 40 days. As shown by all three measurements, the palatal region of the skull has virtually completed its growth by the time the cotton rats are 40 days old.

The growth rate of the lateral expansion of the skull was determined through measurements of the breadth of the braincase and the zygomata (Table 8).

At birth, the breadth of the braincase is smaller than the zygomatic breadth in all species except *S. hispidus* and *S. alleni*. However, in all species the zygomata broaden faster than the braincase. From one day to adulthood the zygomatic breadth increases most in *S. hispidus* (13.7 mm) and least in *S. leucotis* (9.2 mm). The greatest growth of the breadth of the braincase is in *S. hispidus* (5.8 mm) and the least in *S. alleni* (3.7 mm).

The incisive foramina vary considerably in shape (both intra- and inter-specific) from oval to sharply pointed, and the posterior ends vary as to position

TABLE 5.

Comparative broadening (expressed as ratios of the width of the braincase) of the interorbital area and interparietal space

Species	Age (days)	Breadth of braincase (1)	Least inter-orbital breadth (2)	Ratio (2)/(1)	Inter-parietal breadth (3)	Ratio (3)/(1)
S. hispidus	1	10.6	4.6	0.43	8.0	0.75
	10	12.5	4.6	0.36	9.4	0.75
	20	13.4	4.6	0.34	10.4	0.77
	30	13.7	4.8	0.35	10.3	0.75
	40	14.6	4.8	0.32	10.4	0.71
	50	14.8	4.8	0.32	10.9	0.73
	100	15.0	5.0	0.33	11.3	0.75
	adult	16.4	5.6	0.34	12.1	0.73
S. alleni	1	10.5	4.4	0.41	8.5	0.80
	10	12.1	4.5	0.37	9.9	0.81
	20	12.4	4.6	0.37	10.1	0.81
	30	12.5	4.6	0.36	10.6	0.84
	40	12.9	4.8	0.37	10.3	0.79
	50	13.0	4.9	0.37	10.9	0.83
	100	13.2	5.1	0.38	11.2	0.84
	adult	14.2	5.4	0.38	11.3	0.79
S. fulviventer	1	10.2	3.9	0.38	8.5	0.83
	10	11.4	4.4	0.38	10.0	0.87
	20	13.1	4.4	0.33	10.5	0.80
	30	13.7	4.6	0.33	11.0	0.80
	40	14.1	4.6	0.32	11.2	0.79
	50	14.2	4.6	0.32	11.5	0.80
	100	14.5	4.8	0.33	11.5	0.79
	adult	15.7	5.2	0.33	12.7	0.80
S. leucotis	1	10.5	4.5	0.42	8.3	0.79
	10	12.3	4.5	0.36	9.3	0.75
	20	13.0	4.6	0.35	10.8	0.83
	30	—	—	—	—	—
	40	14.0	4.6	0.32	10.5	0.75
	50	—	—	—	—	—
	100	14.6	5.0	0.34	11.8	0.80
	adult	15.3	5.1	0.33	12.2	0.79
S. ochrognathus	1	9.8	4.2	0.42	7.7	0.78
	10	12.0	4.4	0.36	9.7	0.80
	20	12.6	4.3	0.34	9.6	0.76
	30	—	—	—	—	—
	40	13.4	4.7	0.35	10.4	0.77
	50	13.5	4.6	0.34	10.7	0.79
	100	13.9	4.9	0.35	10.2	0.73
	adult	14.8	5.0	0.33	11.7	0.79

TABLE 6.

Increase in length (in mm) of three characteristics of the maxillary bone

	S. hispidus	*S. alleni*	*S. fulviventer*	*S. leucotis*	*S. ochrognathus*
Alveolar space for the maxillary tooth-row					
1 day increase at	4.2	3.8	4.3	4.2	3.7
40 days increase at	2.7	2.4	2.2	2.1	2.5
100 days length at	0.2	0.1	0.2	0.0	0.1
100 days	7.1	6.3	6.7	6.3	6.3
Diastema					
1 day increase at	4.0	3.9	3.7	4.2	3.8
40 days increase at	4.1	2.8	4.3	4.6	3.1
100 days length at	0 7	1.9	1.2	0.0	1.4
100 days	8.8	8.6	9.2	8.8	8.3
Palate					
1 day increase at	8.4	6.8	8.7	8.7	8.1
40 days increase at	8.6	7.1	5.7	6.1	7.0
100 days length at	2.6	3.7	3.9	1.5	1.8
100 days	19.6	17.6	18.3	16.3	16.9

TABLE 7.

Increase (expressed in percent) in the length of three dimensions of the palatal region, from 1-40 days (accelerating phase) and from 41-100 days (decelerating phase)

	Palatal length		Alveolar length of maxillary tooth-row		Length of diastema	
	1-40	41-100	1-40	41-100	1.40	41-100
S. hispidus	102	0.02	64	0.03	102	0.01
S. alleni	104	0.03	63	0.02	71	0.03
S. fulviventer	65	0.03	51	0.03	116	0.02
S. leucotis	70	0.01	50	0.00	109	0.00
S. ochrognathus	86	0.01	67	0.02	81	0.02

TABLE 8.

Measurements (in mm) of the zygomatic breadth (a) and breadth of the braincase (b)

Age (days)	*S. hispidus* (a)	(b)	*S. alleni* (a)	(b)	*S. fulviventer* (a)	(b)	*S. leucotis* (a)	(b)	*S. ochrognathus* (a)	(b)
1	10.0	10.6	9.7	10.5	10.4	10.2	10.6	10.5	9.9	9.8
10	13.5	12.5	12.9	12.1	13.5	11.4	13.0	12.3	10.6	12.0
20	15.4	13.4	14.7	12.4	15.5	13.1	14.6	13.0	14.5	12.6
30	17.2	13.7	15.6	12.5	17.7	13.7	——	——	——	——
40	18.1	14.8	16.2	12.9	18.2	14.1	16.5	14.0	17.0	13.4
50	18.8	14.6	16.9	13.0	18.5	14.2	——	——	17.8	13.5
100	20.5	15.0	18.1	13.2	19.5	14.5	18.3	14.6	18.6	13.9
200-400	23.7	16.4	20.0	14.2	21.7	15.7	19.8	15.3	19.4	14.8

in relation to the maxillary tooth-row in the adult. In *S. ochrognathus* and *S. alleni* they do not reach a line drawn between the anterior margins of the alveoli of these tooth-rows; in *S. leucotis* the incisive foramina reach but do not extend beyond this line, whereas in *S. hispidus* and *S. fulviventer* they extend posteriorly beyond it. Table 9, Fig. 3 show the relationship between the length of the incisive foramina and the diastema. Those species with the foramina extending anteriorly between the tooth-rows have the highest ratios.

TABLE 9.

Ratio between length of the incisive foramina and the diastema

Age (days)	*S. hispidus*	*S. alleni*	*S. fulviventer*	*S. leucotis*	*S. ochrognathus*
1	0.60	0.48	0.67	0.66	0.65
10	0.86	0.80	0.84	0.79	0.81
20	0.87	0.80	0.90	0.76	0.78
30	0.83	0.79	0.86	——	——
40	0.85	0.80	0.86	0.80	0.81
50	0.84	0.78	0.84	——	0.82
100	0.81	0.75	0.83	0.79	0.81
200	0.80	0.78	0.81	0.75	0.78

Interspecific relationships are demonstrated by the ratio between the length of the incisive foramina and the diastema (Fig. 3) for all species of rats of the genus *Sigmodon.* The curves indicate that the incisive foramina lengthen rapidly up to 20 days of age, although maximum length is not reached until 40 days of age in *S. leucotis* and 50 days in *S. ochrognathus.* After 20 days of age this growth rate is greatly reduced. The ratio as shown in Fig. 3 also declines because of the rapid increase in the length of the diastema after 20 days.

FORMULA FOR CALCULATING AGE OF COTTON RATS: The availability of specimens of known-age of the five species of cotton rats makes application of an aging formula possible. The multiple linear regression method (Gaus-Doolitle method) was applied with 9 variables selected from measurements for all age-groups of each species.

Assuming linear relationships between the unknown Y (age) and X (selected parameter), the following formula was applied:

$$Y = a + b_1X_1 + b_2X_2 + \ldots + b_9X_9$$

with

a: constant (intercept of the line) = 0
b: constant value obtained from Table 10, specific for appropriate measurements in each species
X_1: length of body
X_2: length of tail
X_3: length of hind foot
X_4: greatest length of skull
X_5: height of braincase
X_6: condylo-basal length
X_7: palatal length
X_8: length of rostrum
X_9: length of nasal bone
Y: age of the specimen as determined in Table 11.

TABLE 10.

Constant values (b values) for each of the 9 measurements for the five species of Sigmodon

Species	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
S. hispidus	0.78	−0.003	1.54	− 0.18	− 0.19	5.10	−13.22	−1.43	− 1.59
S. alleni	−0.20	0.25	−0.24	− 0.27	− 0.23	−0.58	− 0.02	1.64	− 1.67
S. fulviventer	0.26	−0.16	0.02	−11.06	13.79	1.15	0.01	−1.81	12.46
S. leucotis	−0.26	−0.03	−0.49	− 0.20	− 0.05	−0.01	0.96	−2.20	0.84
S. ochrognathus	−0.07	−0.03	0.08	− 0.03	5.41	2.47	40.10	−0.22	5.98

TABLE 11.

Specific numbers associated with each age-group of cotton rats, when the aging formula is applied.

Species	1 day	10 d	20 d	30 d	40 d	50 d	100 d
S. hispidus	18.80	28.54	37.42	43.97	49.19	52.23	62.06
S. alleni	−20.55	−25.83	−31.42	−34.10	−34.10	−35.70	−40.41
S. fulviventer	1.61	2.02	2.10	2.76	3.64	4.50	4.55
S. leucotis	−11.51	−15.67	−19.52	−21.11	−22.79	−23.37	−26.60
S. ochrognathus	286.97	403.39	434.42	501.81	538.14	556.64	584.34

The formula was tested with four known-age cotton rats belonging to each of the five species studied. In 90 percent of the tests the formula gave the correct age. Consequently, this age-calculating formula seems useful as another method to add to those now in use (external measurements, wearing of molar teeth, development of the skull ridges and condition of pelage).

DISCUSSION

With increase in age, the cotton rat skull becomes steadily more slender in its proportions. The braincase becomes progressively deeper but not wider, giving the appearance of increased arching in cross section (FINDLEY and JONES, 4). The skull has a pattern of growth at variance with that shown by external measurements. Growth is divided into two well-defined phases: from birth to 100 days and from 100 to the maximum adult size. Most skull dimensions reach at least minimum adult stage during the first phase of cranial growth. Changes in length are due to the increase in nasal length, in the length of the braincase, or in both dimensions. This was also emphasized by HALL (6) who pointed out that most post-natal development of the skull is concerned with muscular development, since much of the formation of the brain (and its case) occurs in the prenatal period. As shown in Table 1 the nasal and condylo-basal lengths increase progressively during the first 100 days but the breadth of the braincase increases faster than either during the first 20 days of life, at which time its size closely approximates that of the adult. The rostral region is small in the newborn, while the braincase is relatively large. With increase in age, the extension of the nasal bones gives the skull its typical long-snouted appearance. The larger the skull, the narrower it is in a relative sense (4), with the greatest percent of increase in the breadth being in the mastoid region associated with increase in growth of the zygomata (Table 8). The flattened appearance of the adult skull of *Sigmodon* is emphasized by the progressive development of crests or ridges (CHIPMAN, 2). At 20 to 30 days of life, the frontal bones first show ridging in all species except in *S. ochrognathus* where the ridges do not appear until 30 to 40 days of age.

As was mentioned previously, the one day old rat has a small rostrum, a short postpalatal length and a conspicuous dorsally-expanded braincase (6). In subsequent growth, the height of the braincase grows relatively little compared to the lengthening of the rostrum and the postpalatal area. In other words, the basal part of the braincase elongates more rapidly than does the dorsal part. Whereas the dimension of the postpalatal length exceeds that of the height of the braincase in adults of all species (Fig. 2), that of the adult rostrum exceeds that of the height of the braincase only in *S. hispidus, S. alleni* and *S. ochrognathus*. The growth of the rostrum seems also to be correlated with time of weaning. This event takes place between 10 and 25 days (HOFFMEISTER, 7; MEYER, 8; SVIHLA, 9). As shown in Figure 2 the growth of the rostrum accelerates between 20 and 100 days of age. This rapid increase in size appears to be directly correlated with dietary change.

RESUMEN

El cráneo de las ratas algodoneras, al nacer, muestra una forma oval debido a la gran expansión de la caja craneal y al poco crecimiento del rostro del animal. En todas las especies estudiadas, la caja craneal se expande continuamente durante los primeros 20 días de vida, alcanzando en este período casi el tamaño máximo típico de la especie. Al mismo tiempo el cráneo comienza a alargarse rápidamente debido al crecimiento de la región rostral, y a la expansión lateral de los huesos de la base del cráneo. Durante los primeros 100 días de vida extrauterina, este crecimiento transforma al cráneo, de una figura redondeada al nacer a la forma típica del animal adulto.

Las medidas craneales muestran la correlación entre la rápida expansión inicial de la caja craneal y el subsecuente crecimiento del rostro y la base del cráneo. El ancho y la altura de la caja craneal reflejan el desarrollo de esta estructura. La longitud postpalatal y la del rostro reflejan alargamiento del cráneo.

Normalmente, la altura de la caja craneal es mayor que la longitud postpalatal en el primer día de vida del animal. Sin embargo, de los 20 a los 30 días, el crecimiento de la región postpalatal aumenta hasta sobrepasar la altura de la caja craneal. En tres especies, *S. hispidus, S. alleni* y *S. ochrognathus,* la longitud rostral no excede en tamaño a la altura de la caja craneal sino después de los 100 días de vida extrauterino.

A la edad de 40 días, la longitud palatal y la longitud de los molares del maxilar superior alcanzan el tamaño adulto, mientras que la diastema es de 50 a 67 por ciento (dependiendo de la especie) del tamaño adulto. Al nacer, el arco zigomático del cráneo es muy reducido, pero éste se expande en dirección lateral muy rápidamente en comparación con el desarrollo de la caja craneal. Este desarrollo, junto con el alargamiento del rostro, tiene una gran relación con el destete y con el desarrollo de los músculos masticatorios y faciales del animal. También, el cambio de un crecimiento acelerado (1-40 días) a uno más reducido (40-100 días) parece estar relacionado con la madurez sexual.

Fig. 1. Graphs of the curves of 4 cranial measurements in relation to the condylo-basal length.

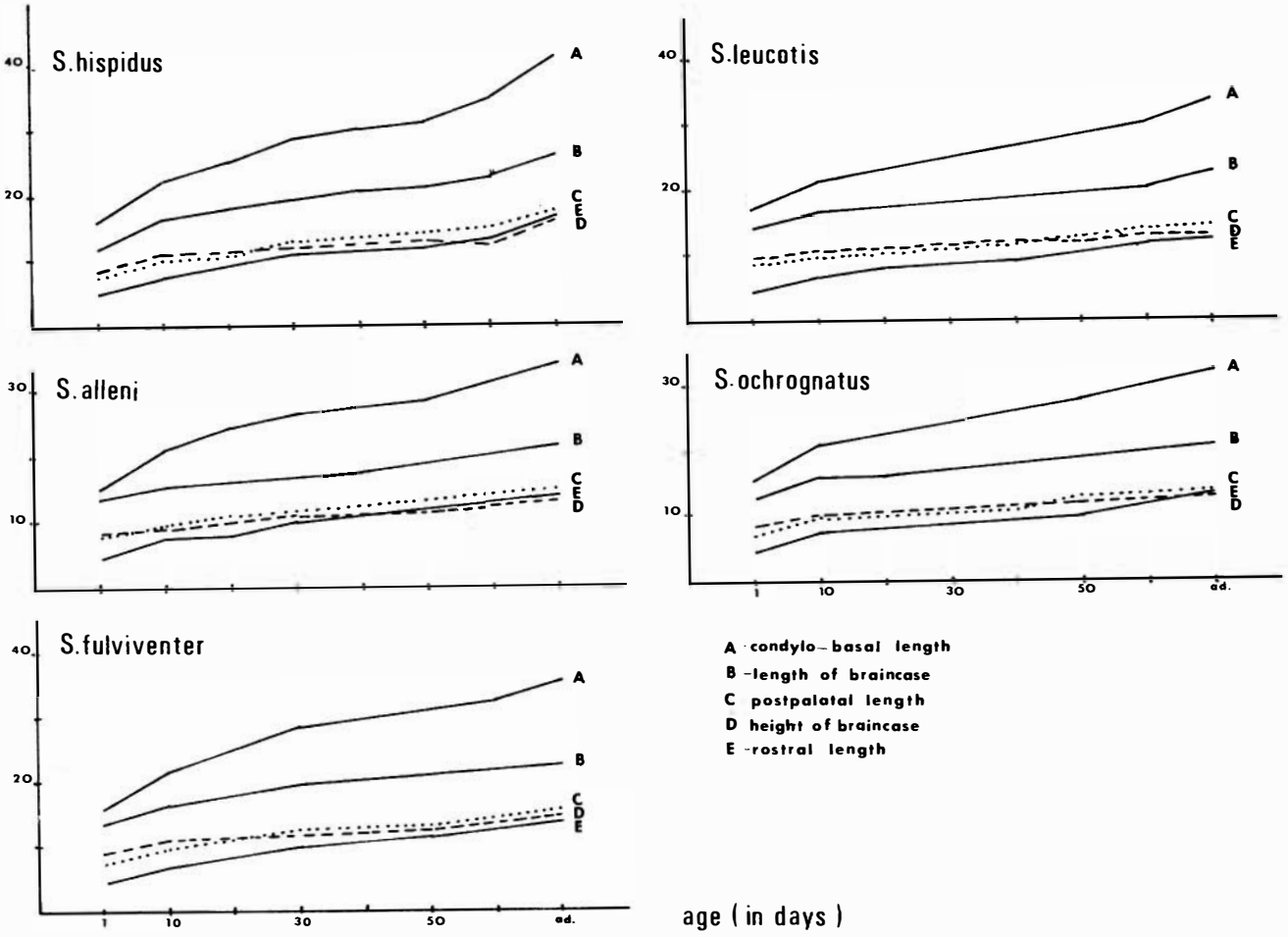
S.hispidus
S.leucotis
S.alleni
S.ochrognatus
S.fulviventer
A
B
C
D
E
40
20
30
10
1
10
30
50
ad.
A condylo-basal length
B -length of braincase
C postpalatal length
D height of braincase
E -rostral length
age (in days)

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Fig. 2. Histogram of the relationships of growth between the rostral length, the length of the braincase, the height of the braincase, the postpalatal length, with the condylo-basal length.

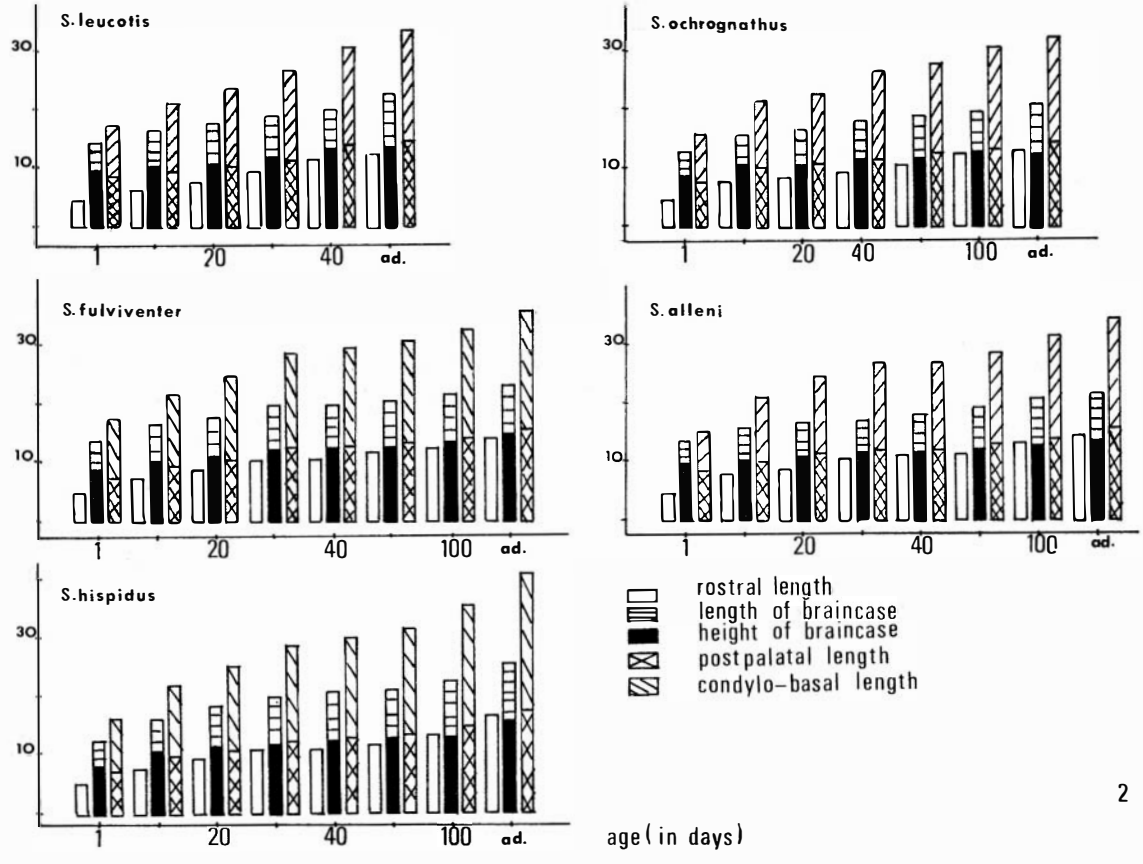
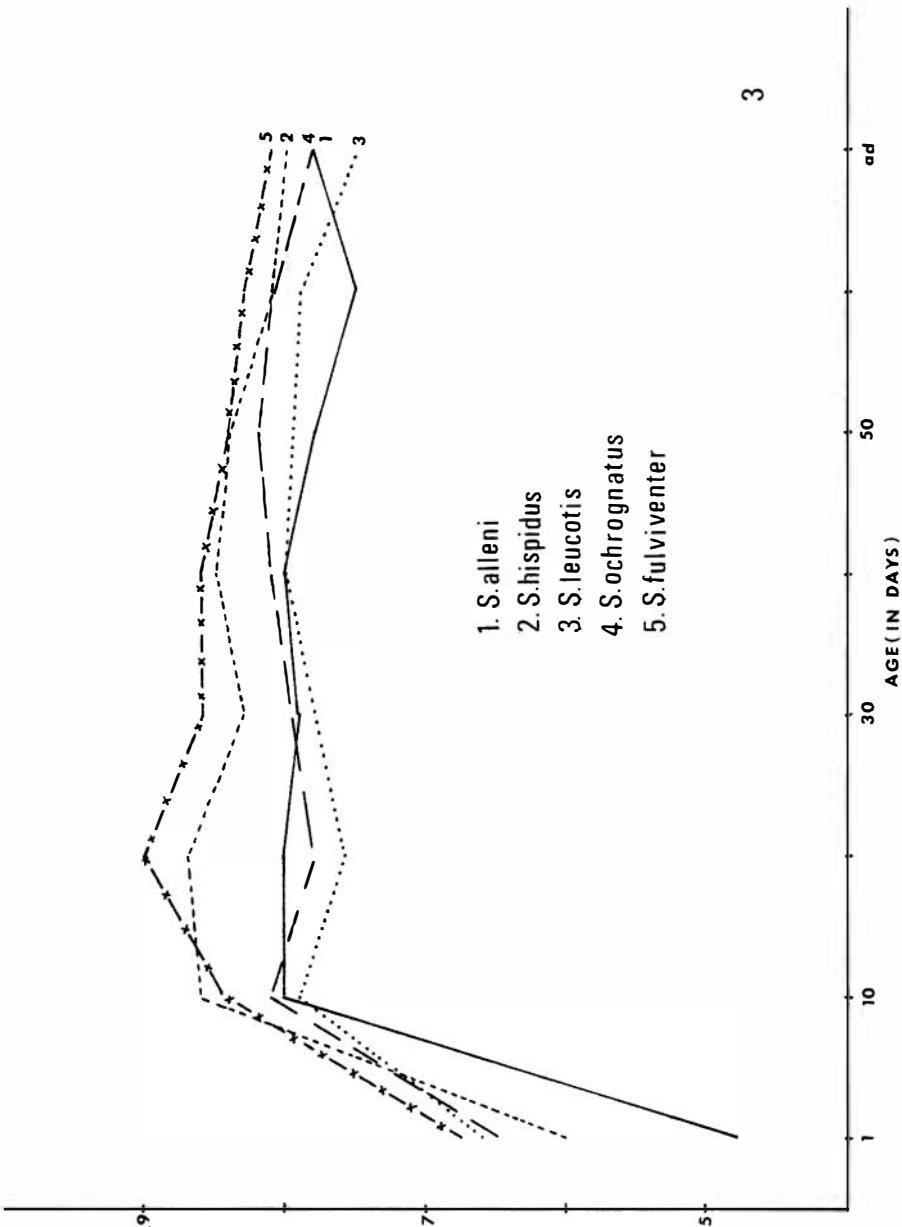

S. leucotis
S. ochrognathus
S. fulviventer
S. alleni
S. hispidus
30
10
1
20
40
100
ad.
rostral length
length of braincase
height of braincase
postpalatal length
condylo-basal length
age (in days)

Fig. 3. Graph of the curves of the ratio: length of the incisive foramen/length of the diastema for all the species of cotton rats.


RATIO : LENGTH OF INCISIVE FORAMEN / LENGTH OF DIASTEMA
0.9
0.7
0.5
1
10
30
50
AGE(IN DAYS)
1. S.alleni
2. S.hispidus
3. S.leucotis
4. S.ochrognatus
5. S.fulviventer
3