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THE HYOID IN NORTH AMERICAN SQUIRRELS, SCIURIDAE, WITH REMARKS ON ASSOCIATED MUSCULATURE

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RESUMEN

El aparato hioideo de las ardillas (Sciuridae) consiste de basihyal y thyrohyales, hypohyales (ausente en ocasiones), ceratohyales (comúnmente cada uno de dos partes) y stylohyales. Los tympanohyales están ausentes o persisten sólo como restos de cartilago. El basyhal se fusiona con los tyrohyales a edad temprana. Los ceratohyales son largos y comúnmente más largos que el basyhal. Los procesos hioideos están más desarrollados que en la mayoría de los roedores y la longitud de un hypohyal más un cerathyal más un stylohyal es igual a desde 4.4 a 8.3% (promedio = 6.4) de la longitud total del individuo. Las ardillas arboricolas carecen de hypohyales, sus tyrohyales son cortos y el basihyal es grueso, largo y triangular en vista transversal. Las ardillas voladoras tienen un músculo genioglossus conspicuo, un músculo digástrico anterior doble y un músculo styloglossus de dos elementos. Las ardillas terrestres tienen un basihyal circular en vista transversal, thyrohyales largos y los hypohyales están presentes excepto en *Eutamias.* Otros con hypohyales son *Tamias, Callospermophilus, Spermophilus, Ictidomys* y *Otospermophilus.* El mylohyoideo de *Ammnospermophilus* es una vaina doble. Los ceratohyales de *Tamias* son más delgados y rectos que en *Eutamias* y otras de sus diferencias se encuentran en las posiciones de los músculos geniohyoideo, hyoglossus y styloglossus. Los ceratohyales de los perritos de las praderas son menores de 5.0 mm y los de *Leucocrossuromys* mayores de esa talla.

Palabras clave: Hyoideo, ardillas, Sciuridae, músculos.

ABSTRACT

The hyoid apparatus of squirrels, Sciuridae, consists of a basihyal and paired thyrohyals, hypohyals (sometimes absent), ceratohyals (frequently each of two parts), and stylohyals. Tympanohyals are absent or persist only as short pieces of catilage. The basihyal fuses with the thyrohyals at an early age. Ceratohyals are long, usually longer than the basihyal. The hyoid cornua are better developed than in most other rodents, and the length of one hypohyal + one ceratohyal + one stylohyal equals 4.4 to 8.3 (average, 6.4) per cent of the length of the squirrel's body. Tree squirrels lack hypohyals, thyrohyals are short, and the basihyal is thick, triangular in cross-section, and long. Flying squirrels have a conspicuous genioglossus muscle, a double anterior digastric muscle, and a styloglossus muscle consisting of two elements. Terrestrial squirrels have a basihyal circular in cross-section, long thyrohyals, and the hypohyals present in all except *Eutamias.* Others with hypohyals are *Callospermophilus, Spermophilus, Otospermophilus,* and *Ictidomys. Ammospermophilus* has the mylohyoid as a double sheet. In the chipmunk *Tamias,* hypohyals are present, absent in *Eutamias;* in *Tamias,* ceratohyals are thinner and straighter than in *Eutamias;* other differences are found in the positions of the geniohyoid, hyoglossus, and styloglossus

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muscles. For prairie dogs, ceratohyals in *Cynomys* are shorter than 5.0 mm; in *Leucocrossuromys*, longer than 5.0 mm.

Key words: Hyoid, squirrels, Sciuridae, muscles.

INTRODUCTION

The hyoids and associated muscles of North American squirrels, family Sciuridae, previously have not been compared or described. The hyoids of 55 species of North America sciurids were examined and measured and the hyoid musculature was examined on 10 species. Some differences attributable to age and individual variation were analyzed.

MATERIALS AND METHODS

In the sections that follow, the generic name *Spermophilus* is used for all ground squirrels, including antelope and mantied ground squirrels. Thus within the genus *Spermophilus* the following subgenera are discussed: *Ictidomys, Ammospermophilus, Xerospermophilus, Otospermophilus, Spermophilus, Poliocitellus,* and *Callospermophilus.* Some of these subgenera are currently considered to be of generic rank. This does not invalidate our descriptions or discussions. Within *Cynomys,* the subgenera *Cynomys* and *Leucocrossuromys* are considered; within *Sciurus,* these subgenera: *Sciurus, Otosciurus, Parasciurus, Neosciurus,* and *Guerlinguetus.*

Various measurements of the hyoid as shown in Fig. 1 were taken with an ocular micrometer accurate to 0.01 mm. The basihyal remains a separate element only until about 2 months of age and then fuses with the thyrohyal in *Spermophilus tridecemlineatus.* However, in one specimen of *S. tridecemlineatus,* the basihyal-thyrohyal suture is not completely obliterated in a specimen more than a year old. When reference is made in the text to the basihyal, it is that portion of the basihyal-thyrohyal situated between the hypohyals. The fusion of these two elements, basihyal and thyrohyals, is illustrated in the age-changes in *S. tridecemlineatus,* Fig. 1. The length of the thyrohyal had to be approximated since the suture was obliterated so a measurement was taken from the center of the basihyal to the posterior end of the thyrohyal. Frequently in *S. tridecemlineatus,* two ceratohyals are present on each side and this may be evident more often in animals less than a year old. In the following accounts, specimens in which the bony hyoid was studied are listed first; those dissected for muscle examination, second.

Hyoids of as many specimens of as many genera, subgenera, and species were studied as available in the following collections: Museum of Natural History of the University of Illinois, Museum of Natural History of the University of Kansas, Museum of Zoology, University of Michigan, and American Museum of Natural History. Our thanks to the persons in charge of these collections for the opportunity to examine the specimens. We thank Alice Prickett for the drawings.

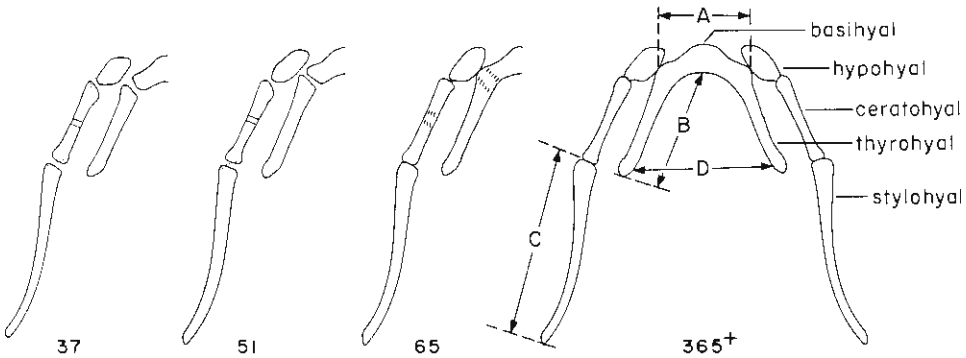

Fig. 1. Elements of the sciurud hyoid. Lettered parts indicate how measurements were taken: A, length of basihyal; B, length of thyrohyal; C, length of stylohyal; D, breadth of thyrohyal. Changes in age for the hyoid in *Spermophilus tridecemlineatus* are indicated at 37, 51, and 65 days, and over one year.

RESULTS

The Sciurid-type Hyoid

The hyoid of squirrels consists of nine elements: a single basihyal and paired thyrohyals, hypohyals, ceratohyals, and stylohyals. The basihyal is a medium-thick bone in comparison to the rest of the elements, usually round in cross-section, and crescent-shaped in its lengthwise perspective (Figs. 1 and 10). The basihyal fuses with the thyrohyals at an early age and the sutures soon completely disappear (see above under Methods). Thus, in all but young animals, one must estimate the limits of the basihyal or thyrohyals. The age changes in these elements in *Spermophilus tridecemlineatus* are shown in Fig. 1. Thyrohyals are short and straight, of about the same thickness as the basihyal, and may be round or flattened and blade-like in cross section. The thyrohyals attach to the dorsal surface of the thyroid cartilage. The structure formed by the basihyal and two thyrohyals, termed the posterior cornu, is markedly horseshoe-shaped.

The anterior or hyoid cornu consists of three paired elements hypohyals, ceratohyals, and stylohyals. Hypohyals are variably present in some species, absent in others, and always present in still others. The hypohyal actually may not be absent in any, but rather fused to the ceratohyal although this has not been ascertained. The hypohyals are joined to the basihyal at the "arch" and are curved (about 70°).

Ceratohyals are characterized by a nearly even diameter throughout the shaft of each bone, with slight "swellings" at their articulating surfaces.

Stylohyals are the longest elements of the hyoid apparatus. They are thin, often flattened, and curved in that portion that wraps around the auditory bulla. A thick cartilaginous ligament, the tympanostylohyal ligament, extends from the distal tip of the stylohyal to the point of attachment, just posterior to the external auditory meatus. The exact point of attachment is immediately ventral and posterior to the stylomastoid foramen.

The tympanohyal appears to be either completely lacking or to persist as a short cartilaginous connection between the stylohyal and the point of connection to the skull. In some other mammals, such as the Insectivora, the tympanohyal is represented by a small bone located close to the auditory bulla. The tympanohyal is attached distally to the stylohyal ligament, and proximally to the skull in the region of the stylomastoid foramen (Sprague, 1944). However, squirrels show no evidence of a tympanohyal, except possibly the presence of a tympanostylohyal ligament, or tympanostyloid synchondrosis (a term devised by Sivaram and Sharma, 1965). Sivaram and Sharma also found the tympanohyal to be lacking in the palm squirrel, *Funambulus*. In review, the hyoid apparatus of North American sciurids can be characterized by (a) basihyal and thyrohyals fusing early, (b) ceratohyal longer than the basihyal (sometimes two or three times longer) or if shorter, then only slightly so, (c) anterior and posterior bellies of the digastric muscle separated by a tendon, forming an arch (Sivaram and Sharma, 1965), and (d) length of the hyoid cornu (stylohyal, ceratohyal, and hypohyal, when present) 6.39 (S.D. 0.84) per cent of the body length, with a range of 4.4 to 8.3 per cent.

Terrestrial Squirrels

Terrestrial squirrels as a group are characterized as follows: (a) hypohyals usually present, (b) thyrohyals long, and (c) basihyal circular in cross section. Hypohyals are abset in *Eutamias, Poliocitellus, Xerospermophilus,* and *Ammospermophilus;* exceptions are noted in table 1. Although hypohyals are present in most specimens of *Otospermophilus,* they are absetn in the one specimen of *S. (O.) annulatus* and the three specimens of *S. (O.) adocetus* examined. These two species were placed in the subgenus *Notocitellus* by Howell (1938), although it is not recognized currently by most authors. In terrestrial squirrels the thyrohyals are longer than the basihyals (the opposite in tree squirrels). This is reflected in the ratio of the basihyal to the length of the thyrohyal being more than one in terrestrial squirrels (less than one in tree and flying squirrels), see table 1. The basihyal in terrestrial squirrels is short and this is reflected in the ratio of the basihyal to the hyoid cornua.

The chipmunks

Tamias. The hypohyal is present in all specimens, the ceratohyal is thin and straight, and overall size of the hyoglossum (hyoid) is small (see Fig. 6 [9]).

The geniohyoid, hyglossus, and styloglossus muscles are partly arranged in layers ventrodorsally, in the order named. The hyoglossus muscle runs anterolaterally and attaches some distance lateral to the symphysis (Fig. 2).

Specimens examined for bony hyoid, 9 *T. striatus;* for myology, 2 specimens.

Eutamias. The hypohyal is absent in all specimens (except in one subadult *E. minimus*) and the ceratohyal is of medium thickness and "telephone-shaped" (Fig. 10, B), all in marked contrast to the condition in *Tamias.* White (1953) previously pointed out these differences. The hyoglossum is small (Fig. 6 [10]).

The geniohyoid, hyoglossus, and styloglossus muscles all lie in about the same

TABLE 1
VARIATION IN ELEMENTS OF THE HYOIDS OF GENERA AND SUBGENERA (MARKED WITH*) OF SCIURIDAE.

	HYPOHYAL			STYLOHYAL	BASIHYAL				
	+/—		S/L	Length min.—max.	Length min.—max.	Length min.—max.	Shape	Attachment of hyoid cornua	SM/P	Length of hyoid cornual basihyal
TERRESTRIAL SQUIRRELS										
1. *Tamias*	+		L	1.53–2.27	4.39–6.14	2.29–3.00	Box	anterior	SM	3.98
2. *Eutamias*	—	(1)		–	3.88–6.60	1.58–2.40	Box to angle	anterior	SM,P	4.56
3. Spermophilus*	+	(2)	L	1.53–2.46	5.81–9.18	2.65–5.61	Box to angle	anterior	SM,P	3.67
4. Ictidomys*	+	(3)	L	1.33–2.04	4.08–7.04	2.24–3.57	Arched box	anterior	SM	3.58
5. Poliocitellus*	—			—	—	3.26–4.18	Box	anterior	SM	3.31
6. Xerospermophilus*	—			—	—	2.67–3.88	Box	anterior	P	3.33
7. Otospermophilus*	+	(4)	S	1.94–2.65	—	3.77–6.22	Box to angle	anterior	P	4.11
8. Callospermophilus*	+		S	1.43–1.84	—	3.16–3.27	Box	anterior	SM	3.15
9. Ammospermophilus*	—	(5)		—	—	2.81–3.55	Box	anterior	SM	3.32
10. Cynomys*	+		S	2.50–3.47	—	4.18–4.79	Box	anterior	SM	3.79
11. Leucocrossuromys*	+	(6)	S	2.14–3.26	—	3.21–6.76	Box	anterior	SM,P	4.59
12. *Marmota*	+			2.04–3.98	—	3.57–6.73	Angle	anterior	SM	4.82
TREE SQUIRRELS										
13. Neosciurus*	—			—	—	4.90–7.55	Variable	Middle or posterior	variable	2.57
14. Otosciurus*	—			—	—	5.10–6.73	Box	anterior	P	2.68
15. Parasciurus*	—			—	—	5.36–7.65	Box to angle	variable	SM	2.54
16. Geurlinguetus*	—			—	—	5.78–6.32	—	—		2.21
17. Tamiasciurus*	—			—	—	4.13–5.20	Box to arch	anterior	SM	2.59
FLYING SQUIRRELS										
18. *Glaucomys*	—			—	—	2.55–3.77	Arch	middle	P	3.22

Table 1. Continued.

	THYROHYDAL					CERATOHYAL		
	Breadth min.—max.	Lenght min.—max.	Breadth thyrohyal Basihyal	Length of thyrohyal Basihyal	Length of Ceratohyal breadth of Thyrohyal	Length min.—max.	Thin Medium Thick	Shape: Regular Telephone
1.	3.26– 3.88	3.57– 4.52	1.45	1.62	0.76	2.14– 5.00	Thin	Regular
2.	2.04– 3.16	2.24– 3.67	1.31	1.48	1.38	2.96– 4.74	Medium	Telephone
3.	4.61– 7.24	4.28– 7.55	1.57	1.58	0.76	2.55– 5.47	Thin	Regular
4.	3.95– 5.22	3.98– 5.10	1.58	1.54	0.84	3.21– 5.10	Medium-Thick	Regular
5.	5.69– 6.53	5.81– 6.83	1.70	1.63	0.97	5.51– 5.81	Thin	Telephone
6.	4.10– 4.59	3.88– 4.69	1.37	1.27	1.04	4.08– 4.79	Medium	Regular
7.	5.20– 7.20	5.41– 6.83	1.71	1.76	0.73	3.88– 5.98	Thin-Medium	Regular
8.	3.77– 5.10	4.08– 5.51	1.28	1.32	0.84	2.86– 4.16	Thin	Regular
9.	3.98– 4.69	3.62– 4.69	1.43	1.36	0.86	3.16– 4.18	Thin-Medium	Regular
10.	5.20– 6.43	6.65– 8.47	1.25	1.58	0.82	4.28– 4.81	Medium	Regular
11.	5.71– 7.59	6.43– 9.22	1.54	1.82	0.82	4.49– 6.73	Thin	Regular
12.	8.47–13.98	8.36–13.87	2.32	2.33	0.79	6.12–11.73	Medium	Regular
13.	4.25– 7.80	3.88– 7.34	0.96	0.92	0.94	3.93– 6.53	Thin-Medium	Telephone
14.	4.69 6.53	3.06 5.71	0.96	0.83	1.04	4.18– 6.53	Medium	Telephone
15.	4.79– 6.83	5.30 7.14	0.94	0.95	1.02	5.10 7.24	Variable	Variable
16.	5.81– 6.63	4.69– 5.61	1.01	0.84	0.72	3.90 5.10	—	—
17.	4.08– 4.90	3.88– 5.30	0.92	0.92	0.97	3.62– 5.03	Thin	Telephone
18.	3.16– 4.54	2.81– 3.49	1.23	0.97	0.80	2.55– 3.57	Medium-Thick	Telephone

(1) = Present in one subadult *Eutamias minimus*. (2) = Absent in *Spermophilus beldingi* (1 specimen examined). (3) = Absent in *Spermophilus spilosoma*. (4) = Absent in *Spermophilus annulatus* (1 examined) and *adocetus*. (5) = Present in some *Spermophilus (Ammospermophilus) interpres*. (6) = Absent in *C. parvidens;* absent in some *leucurus* and *gunnisoni*. (7) = But short. + = Present. —3 = Absent. S = Short. L = Long. SM = Smooth. P = Pointed.

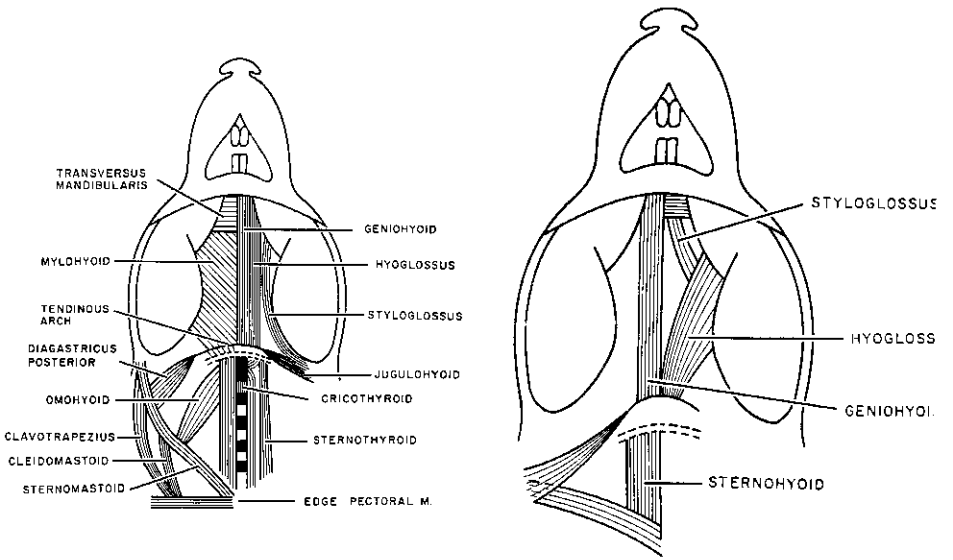

Fig. 2. Muscles associated with the hyoid in *Eutamias minimus* to left and *Tamias striatus* to right. For *Eutamias*, the more superficial muscle are shown on the left side. For *Tamias*, some of the muscle that differ from those in *Eutamias* are shown.

plane, all run parallel to one another (except where the styloglossus curves around the posterior end of the dentary bone), and the three muscles never cross.

Specimens examined for hyoid, 4 *E. umbrinus adsitus,* 6 *E. d. dorsalis,* 5 *E. c.* cinereicollis, 4 *E. townsendii siskiyou,* 3 *E. amoenus luteiventris,* 4 *E. quadrivittatus hopiensis,* 2 *E. minimus consobrinus;* for myology, 2 specimens of *E. minimus neglectus.*

The ground squirrels

Ictidomys. *Ictidomys* has unusually long ceratohyals (Table 1). The hypohyal is absent in *S. spilosoma* but present in *S. tridecemlineatus* and *S. mexicanus* (see Fig. 5). *Ictidomys* has a double mylohyoid muscle with anterior and posterior slips and a slight muscular connection (part of mylohyoid?) between the hyoglossus and styloglossus muscles. The rest of the muscles follow the general pattern of sciurid throat musculature (Fig. 3).

Specimens examined for hyoid included 9 *S. spilosoma,* 7 *S. mexicanus,* 24 *S. tridecemlineatus:* for myology, one each of preceding.

Ammospermophilus. There was nothing unique in the hyoid of *Ammospermophilus.* The hypohyal was absent in all but 2 specimens of *S. interpres.* This subgenus has the same "double" mylohyoid muscle as *Ictidomys* Nadler (1969:301) pointed out that there is a close similarity between the chromosomes of *Ammospermophilus* and *Ictidomys* and *Spermophilus* (subgenus). There is nothing sufficiently unique about the hyoid of *Ammospermophilus* to warrant generic rank as suggested by Bryant (1945) and Black (1963).

Specimens examined for hyoid: 7 specimens of *S. leucurus,* 5 *S. harrisii,* 5 *S.*

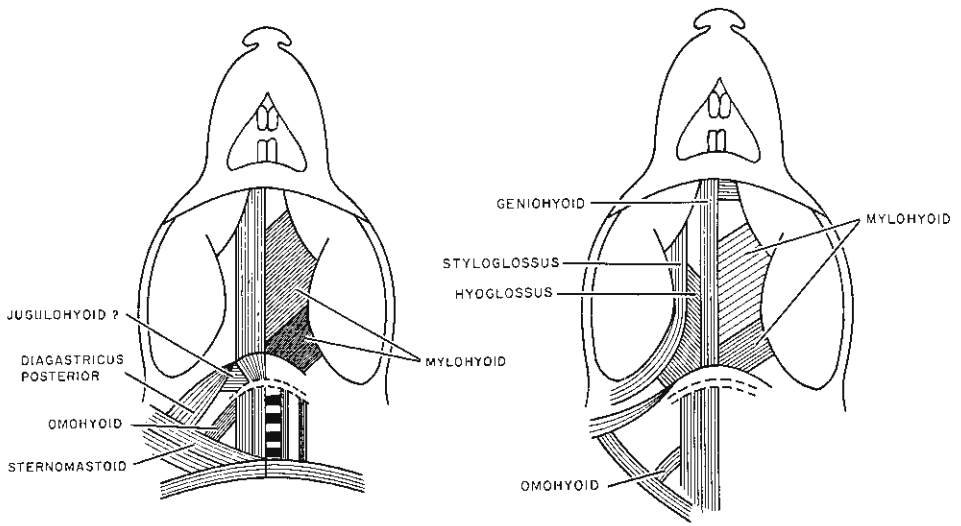

Fig. 3. Hyoid musculature in two ground squirrels of the subgenus *Ictodomys;* to left, *spilosoma,* right, *tridecemlineatus.* Note the similirity of muscles in the two species.

interpres, 3 *S. nelsoni;* for myology, one specimen of *S. harrisii.*

Xerospermophilus. This subgenus lacks unique characteristics; the posterior end of the posterior cornua is flared, rather than straight, resembling *Poliocitellus* and *Callospermophilus.* The hyoglossus, geniohyoid, and styloglossus are distinctive muscles.

Specimens examined for hyoid: 8 specimens of *S. tereticaudus neglectus;* for myology, one specimen of this species.

Otospermophilus. The hyoids of this subgenus are the largest of the genus *Spermophilus.* In *S. variegatus,* length of the stylohyal averaged 9.0 mm, the thyrohyal, 6.5 mm. Unique features in musculature are as follows: mylohyoid muscle extends only about three-fourths the length of the jaw (in other ground squirrels it extends the full length of the jaw) and a muscle not present in other ground squirrels was found in *variegatus.* It is located in the hyoglossus-geniohyoid-styloglossus region. This muscle originates on the anterior edge of the ceratohyal and inserts on the medial side of the dentary bone about half-way along its length. It may be a part of the geniohyoid muscle that has attached along the length of the dentary (Fig. 4).

Specimens examined for hyoid: 8 specimens of *S. variegatus,* 1 *S. annulatus,* 4 *S. beecheyi,* and 3 *S. adocetus;* for myology, 2 specimens of *S. variegatus.*

Spermophilus. There is nothing distinctive or unique regarding the hyoid of *Spermophilus.*

Specimens examined for hyoid: 5 specimens of *S. richardsonii,* 3 *S. parryii,* 1 *S. beldingi,* 1 *S. undulatus,* 7 *S. armatus,* 3 *S. columbianus,* 3 *S. townsendii;* no study of muscles.

Poliocitellus. The only thing distinctive is the large size of the hyoid, though not

quite as large as in *Otospermophilus.*

Specimens examined for hyoid: 6 specimens of *S. franklinii;* no study of muscles.

Callospermophilus. There is nothing distinctive regarding the hyoid of this subgenus; it is most similar to that of *Poliocitellus.*

Specimens examined for hyoid: 11 specimens *S. lateralis; no study of muscles.*

Prairie dogs

Cynomys. The basihyal is generally smooth, the ceratohyal of medium thickness and short, less than 5.0 mm. Hypohyal is present.

Specimens examined for hyoid: 7 specimens of *C. ludovicianus;* no study of muscles.

Leucocrossuromys. The basihyal is slightly humped anteriorly (Fig. 10,A), the ceratohyal thin and relatively long, over 5.0 mm in all but three (which were subadults). Hypohyal is present (Fig. 6[13]).

Specimens examined for hyoid: one specimen of *C. parvidens,* 4 *C. leucurus,* 9 *C. gunnisoni;* no study muscles.

The hyoid in the genus *Cynomys* can be distinguished from that in the genus Marmota by the following: the hyoid of Marmota is larger; *Cynomys* has a box-shaped posterior cornua, whereas that of *Marmota* is Λ-shaped (Fig. 10, A2).

Marmots, woodchucks

Marmota. The hyoid is of very large size; otherwise, nothing unique noted. Hypohyals are present (Fig. 6 [14]).

Specimens examined for hyoid: 2 specimens of *M. caligata,* 4 *M. monax,* 10 *M. flaviventer;* no study of muscles.

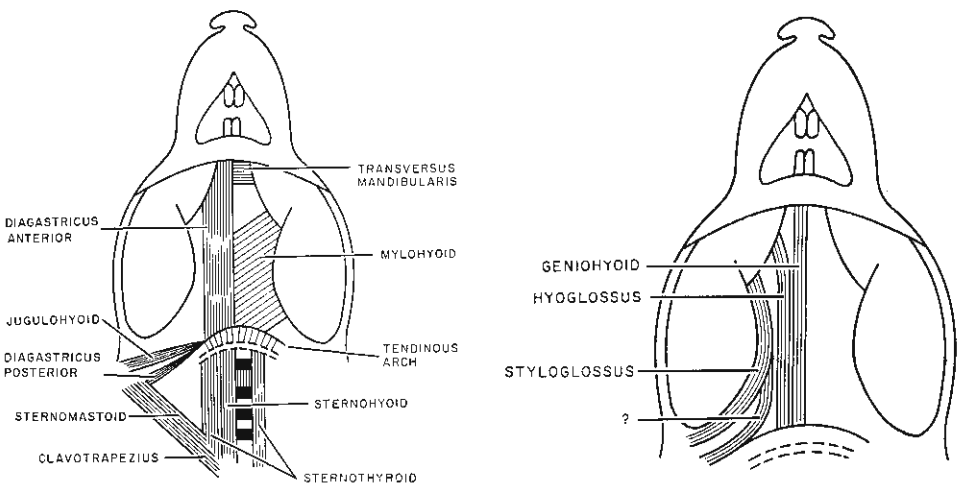

Fig. 4. Part. of the hyoid musculature in the ground squirrel subgenus *Otospermophilus (variegatus).* In drawing to right the mylohyoid, digastric posterior, and jugulohyoid muscles have been removed.

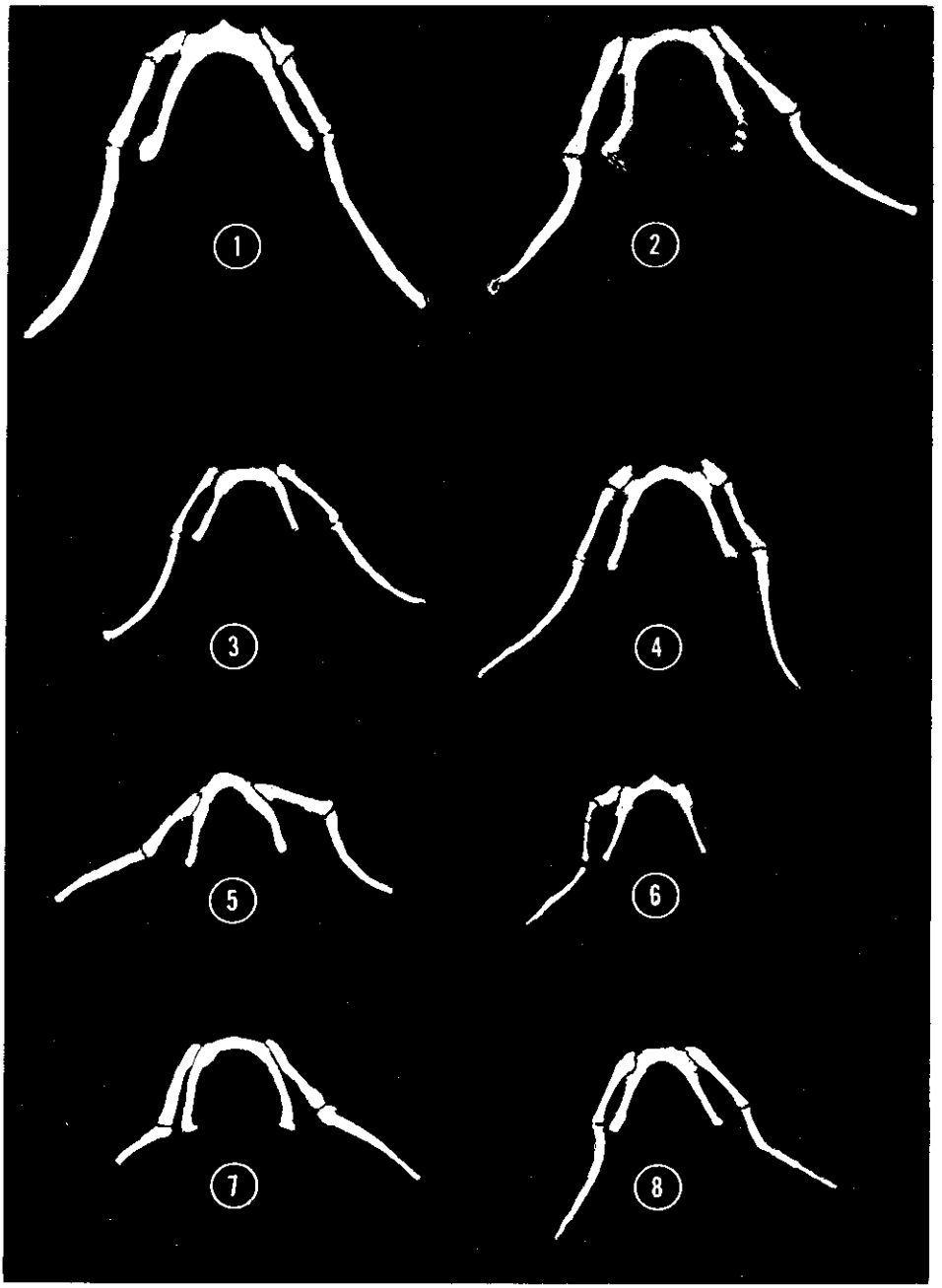

Fig. 5. Photographs (retouched) of hyoids of various ground squirrels (subgeneric names are employed), all enlarged about x 2.5 1. *Otospermophilus (variegatus).* 2. *Poliocitellus (franklini).* 3. *Ammospermophilus (interpres).* 4. *Callospermophilus (lateralis).* 5. *Ictidomys (spilosoma).* 6. *Ictidomys (tridecemlineatus).* 7. *Xerospermophilus (tereticaudus).* 8. *Ammospermophilus (leucurus).*

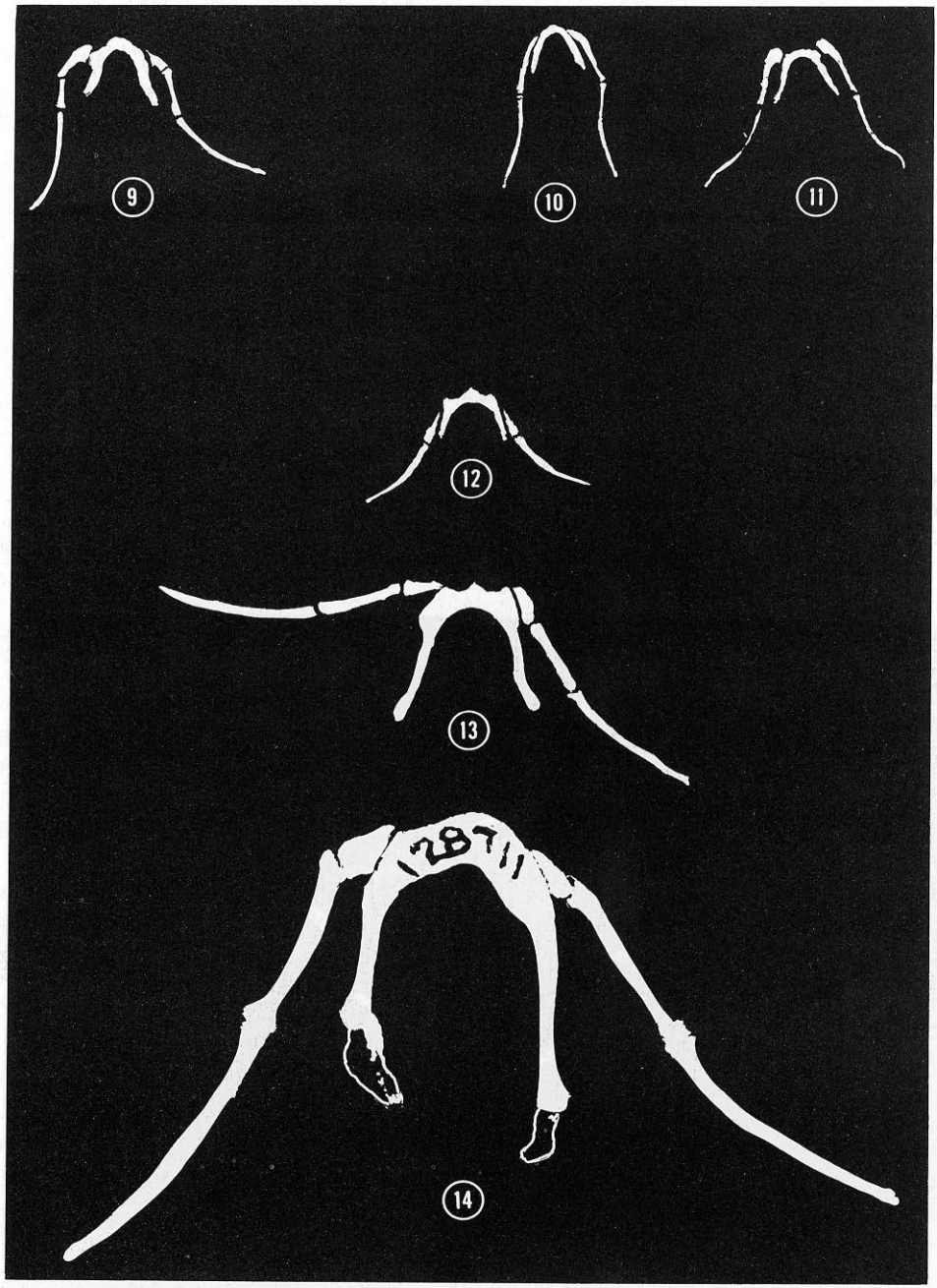

Fig. 6. Photographs (retouched) of hyoids of various squirrels, enlarged about × 2.2. 9. *Tamias striatus.* 10. *Eutamias cinereicollis.* 11. *Eutamias dorsalis.* 12. *Glaucomys volans.* 13. *Cynomys gunnisoni.* 14. Marmota caligata.

Tree Squirrels

Hyoids of tree squirrels are characterized as follows: (a) hypohyal absent, (b) thyrohyals short (and shorter than basihyal), (c) basihyal thick and triangular, not circular, in cross-section, and (d) the basihyal sweeps far posteriorly. The basihyal is long and this is reflected in the ratio (lower than in ground squirrels) of the basihyal to the anterior cornua. The absence of the hypohyals is compensated for by the lengthening of the ceratoyals and stylohyals.

Otosciurus. Unique to this subgenus are the anterior projection from the basihyal and the greatly shortened, inwardly curved thyrohyals (Fig. 7 [18]). Also characteristic of *Otosciurus* is the relatively far posterior attachment of the ceratohyals (Fig. 10, C1).

Specimens examined for hyoid: 10 specimens of *S. aberti;* no study of muscles.

Parasciurus. Nothing unique to this subgenus except as indicated under *Neosciurus.*

Specimens examined for hyoid: 5 specimens of *S. alleni,* 5 *S. arizonensis,* 8 *S. niger,* 3 *S. nayaritensis* (including *S. chiricahuae*), and 3 *S. oculatus;* for myology, one speciemen of *S. niger.*

Neosciurus. In both this subgenus and in *Parasciurus* a great deal of individual

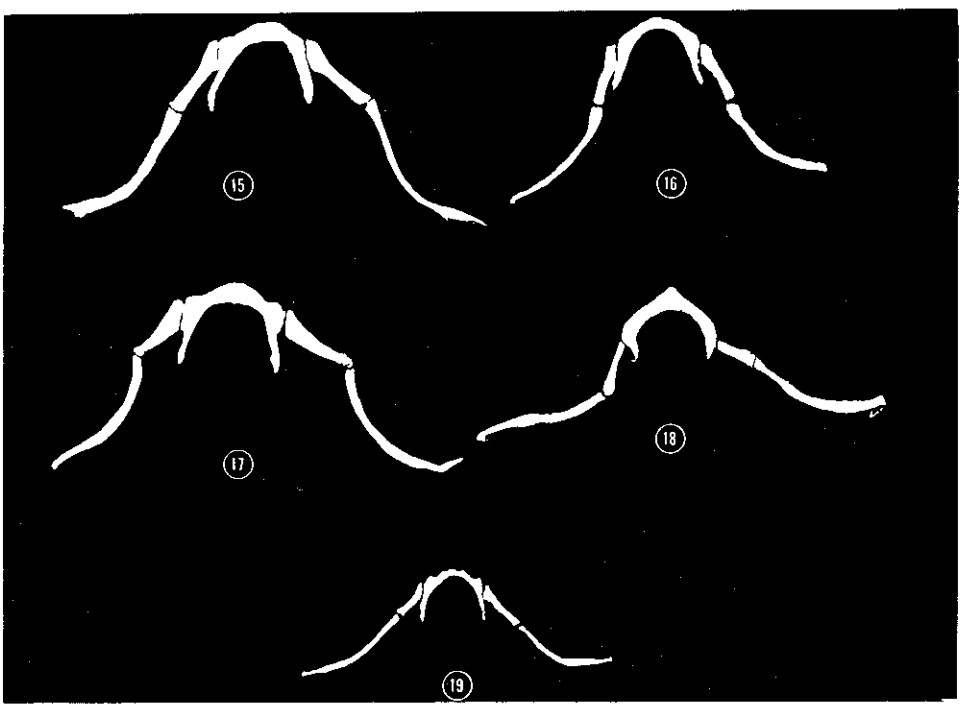

Fig. 7. Photographs (retouched) of hyoids of various tree squirrels (subgeneric names for *Sciurus* are included), enlarged about ×2.5. 15. *Sciurus (Parasciurus) nayaritensis chiricahuae.* 16. *S. (Neosciurus carolinensis* 17. *S. (Parasciurus) niger.* 18. *S. (Otosciurus aberti.* 19. *Tamasciurus hudsonicus.*

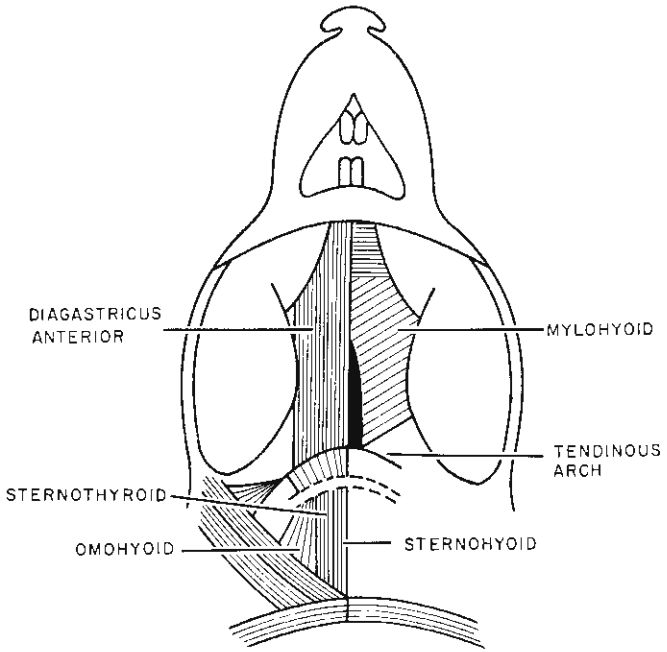

Fig. 8. Hyoid musculature in the red squirrel *Tamasciurus (T. douglasii albolimbatus).* Left view shows the more superficial muscles.

variation is found. A distinguishing feature between the two subgenera is the length of the thyrohyal: in *S. niger (Parasciurus)* the thyrohyal is always about 7.0 mm, whereas in *Neosciurus* the length varies from 4.0 mm to 6.0 mm in *S. aureogaster, S. carolinensis,* and *S. socialis* (18 specimens).

The styloglossus muscle in *Neosciurus* is reduced in size. The geniohyoid muscle is smaller than the hyoglossus muscle; the fibers of the hyoglossus run at about a 45° angle (to the geniohyoid) anteriolaterally to posteromedially. Other than these differences, this subgenus follows the same general plan as other squirrels.

Specimens examined for hyoid; 5 specimens of *S. colliaei,* 3 *S. yucatanensis,* 2 *S. griseoflavus,* 5 *S. socialis,* 2 *S. poliopus,* 3 *S. nelsoni,* 6 *S. carolinensis,* 7 *S. aureogaster,* 6 *S. deppei,* 3 *S. variegatoides;* for myology, one specimen of *S. carolinensis.*

Guerlinguetus. There is nothing distinctive in the hyoid morphology of this subgenus.

Specimens examined for hyoid: 3 specimens of *S. granatensis;* no study of muscles.

Tamiasciurus. The hyoid is similar to that of *Sciurus* in the following features: absence of hypohyal, general shape of basihyal, tickness and shape of ceratohyal, and relative length and form of thyrohyal. *Tamiasciurus* differs from *Sciurus* in the following: hyoid bone of *Tamiasciurus* thinner and finer in structure, the stylohyal less flat and broad, and the ceratohyal of *Tamiasciurus* never exceeds 5.0 mm

whereas that of *Sciurus* (52 specimens) is always longer than 5.0 mm (Fig. 7[15-19]).

The geniohyoid and hyoglossus muscles are of equal size and the fibers of each run parallel in an anteroposterior direction. The styloglossus muscle is reduced in size (Fig. 8).

Specimens examined for hyoid: 11 specimens of *T. hudsonicus;* for myology, 2 specimens of the same.

Flying Squirrels

Flying squirrels are characterized as follows: (a) double anterior digastric muscle, with anastomosing fibers (Fig. 9), (b) genioglossus muscle relatively well developed, (c) styloglossus muscle consists of two elements (rather than one), (d) hypohyals absent and (e) the basihyal is pointed.

Glaucomys. There is nothing unique about the hyoid in this genus. Thyrohyals are relatively shorter than those of *Sciurus* and resemble those of *Tamiasciurus,* except much smaller (Fig. 6[12] and Fig. 7[19]). The hyoid of *G. sabrinus* is larger than that of *G. volans;* the ceratohyals of *G. sabrinus* are longer (more than 3.2 mm rather than less than 2.9 mm).

The musculature of *Glaucomys* differs from that of the other genera. The digastricus anterior (one on either side of the midline) is double, with the fibers of the medial portion anastomosing with those on the other side (of the midline). However, the mylohyoid and transversus mandibularis muscles are typical. The genioglossus muscle is relatively large, and situated dorsal to the mylohyoid, and running anteroposteriorly midway between the two dentary bones. The geniohyoid and hyoglossus muscles run somewhat laterally in an anterolateral to posteromedial sequence, rather than extending anteroposteriorly as in the other squirrels. Also, unlike other squirrels, the styloglossus muscle consists of two components, one of which runs dorsal, the other ventral, to the geniohyoid and the hyoglossus (Fig. 9).

Some small and delicate muscles could not be identified. Of these, one was probably the jugulohyoid and another lay anterior and lateral to the omohyoid.

Specimens examined for hyoid: 7 specimens of *G. volans,* 6 *G. sabrinus;* for myology, 2 specimens of *G. volans.*

DISCUSSION

The sciurid hyoid bone consists of nine elements but thyrohyals fuse with the basihyal at an early age (as early as two months in *Spermophilus tridecemlineatus*). There are no distinctive tympanohyals. Ceratohyals are relatively long. An arch-like tendon separates the anterior and posterior bellies of the digastric muscle.

The hyoids of terrestrial squirrels can be distinguished from those of tree and flying squirrels by a thyrohyal that is longer than the basihyal, rather than the opposite, by the frequent occurence of hypohyals, and the circular cross section of the basihyal. The hyoids of genera and subgenera of terrestrial squirrels seem not to

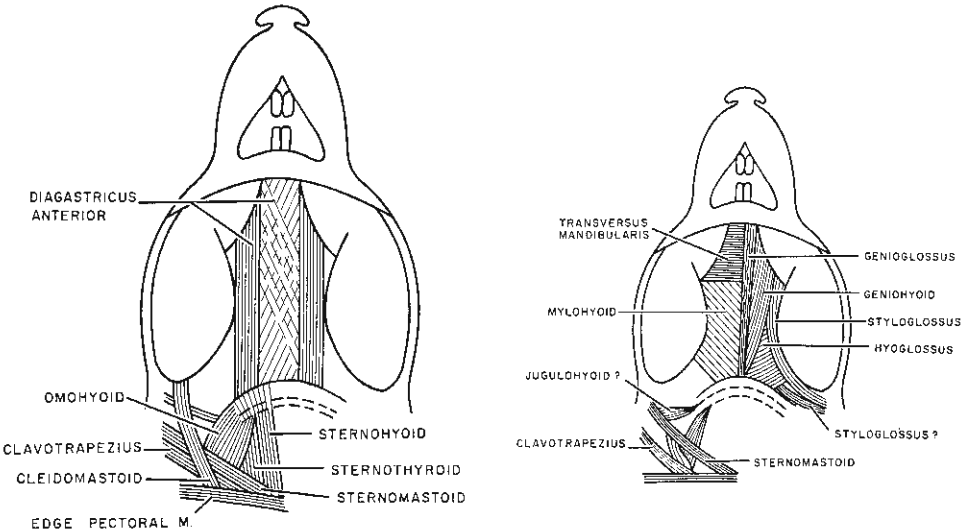

Fig. 9 Hyoid musculature in the flying squirrel *Glaucomys (G. volans).* In drawing to right, the more superficial muscles have been removed. Note the double anterior digastric with anastomosing fibers, presence of *M. genioglossus,* and two elements of *M. styloglossus.*

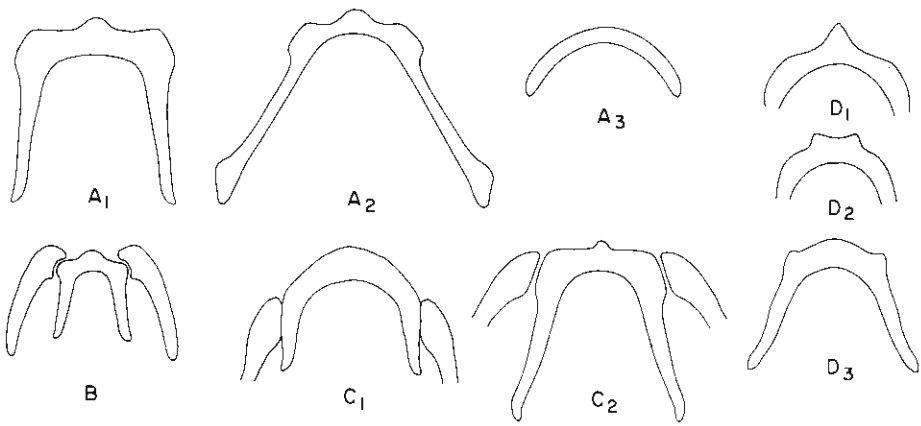

Fig. 10. Variations in the shape of the sciurud hyoid to illustrate some of the terminology used in the text and the Table 1. A, shape of the basihyal; A_1, box, A_2, A shaped; A_3, arched. B, "telephone-shaped" ceratohyal. C, attachment of the cornu: C_1, posteriorly; C_2, far anteriorly. D, shape of the anterior edge of the basihyal: D_1, ponited; D_2 two-pointed; D_3, smooth.

be well differentiated. The hypohyal probably is not an important taxonomic character. This element may be present or absent in the subgenera *Ictidomys, Ammospermophilus, Spermophilus,* and *Otospermophilus.* Species of the once recognized subgenus *Notocitellus* lack hypohyals. *Tamias* and *Eutamias* differ in the presence of the hypoyal and shape of the ceratohyal, but these are not necessarily generic

differences. Of those subgenera examined for muscles, only *Ictidomys* and *Ammospermophilus* han a double mylohyoid. *Otospermophilus* has a mylohyoid that is only about three-fourths the length of the jaw. If more specimens had been examined, these conditions might have been found in other subgenera.

Our study of the hyoid apparatus in *Marmota* adds no information as to whether or not it should be given the status of a subtribe as indicated by Moore (1959) or that the chipmunks be given tribal rank as suggested by Black (1963). There is no evidence from this study that the ground squirrels *Ammospermophilus, Callospermophilus,* and *Otospermophilus* are so interrelated as to be distinctive from other ground squirrels, as suggested by Bryant (1945).

Tree squirrels are distinguishable from terrestrial squirrels particularly in the posterior cornua. Those of tree squirrels are more of a single unit, ie., the thyrohyals are short and attached to the basihyal by completely fused sutures, and the basihyal is thick, never rounded in crossection, and sweeps quite far posteriorly. *Tamiasciurus* is distinguishable from *Sciurus* on the hyoid musculature and the shortness of the ceratohyal. Differences in the hyoid distinguish *Otosciurus* from *Neosciurus* and *Parasciurus.*

The genus *Glaucomys* is very distinctive in musculature. However, the hyoid bone does not reflect these differences. This genus is most closely related to *Sciurus* among all the squirrels, but, in light of its unique musculature, it must have separated from *Sciurus* quite early in its evolutionary history.

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