

BACULA OF *DIPodomys ordii compactus* AND *DIPodomys ELATOR*

Bacular variation in most species of *Dipodomys* was analyzed by Best and Schnell (1974), who had only two specimens of *D. ordii compactus* and four of *D. elator*. Both forms are of particular evolutionary interest. *D. elator* is a relict species whose range is confined to a few counties in Texas and Oklahoma (Martin and Matocha, 1972), and Wood (1935) considered *D. o. compactus* on the basis of tooth pattern to be the most primitive living form of *Dipodomys* that was available to him for study. This note presents additional data on the bacula of *D. elator* and *D. o. compactus*, and on age variation in the latter. It also points out anatomical differences in the bacula not previously described in the literature, and it discusses phylogenetic relationships of *D. clator*, a species for which the conclusions drawn by a numerical analysis of bacular data (Best and Schnell, 1974) and karyotypic data (Stock, 1974) are opposed.

TABLE 1.—Bacular measurements (in mm) and proportions from several species of *Dipodomys*.

Species groups and species	N	Length of baculum	Dorsoventral diameter at midshaft	Dorsoventral diameter of base	Lateral diameter of base	Roundness of base ^a	Index of robustness ^b
Ordii Group							
<i>D. ordii</i>	88 ^c	11.48		2.14	1.88	1.14	35.0
<i>D. ordii compactus</i>	2 ^d	9.75		1.90	1.40	1.36	33.8
<i>D. ordii compactus</i> field series	10 ^e	10.21 ± 0.18 (9.52–11.07)	0.87 ± 0.01 (0.80–0.94)	1.90 ± 0.04 (1.67–2.14)	1.61 ± 0.04 (1.43–1.78)	1.18 (1.05–1.34)	34.4 (29.0–37.5)
<i>D. ordii compactus</i> laboratory series	11 ^e	10.51 ± 0.10 (9.87–11.11)	0.88 ± 0.02 (0.76–1.02)	1.97 ± 0.05 (1.73–2.25)	1.65 ± 0.05 (1.44–2.00)	1.19 (1.02–1.42)	34.5 (30.9–40.6)
Phillipsii Group							
<i>D. elator</i>	4 ^d	13.08		1.70	1.73	0.98	26.2
<i>D. elator</i>	11 ^e	13.13 ± 0.19 (12.12–14.02)	0.69 ± 0.02 (0.61–0.76)	1.51 ± 0.04 (1.31–1.75)	1.47 ± 0.04 (1.31–1.74)	1.03 (0.88–1.12)	22.8 (20.0–25.0)
<i>D. phillipsii ornatus</i>	5 ^f	12.23	0.66	1.84	1.63	1.13	28.4
Merriami Group							
<i>D. merriami</i>	71 ^e	10.89		1.28	1.17	1.09	22.5
<i>D. nitratoides</i>	7 ^e	13.3		1.13	0.94	1.20	15.6
Spectabilis Group							
<i>D. spectabilis</i>	18 ^e	16.69		2.56	2.29	1.12	29.0
<i>D. nelsoni</i>	4 ^d	15.00		2.10	2.00	1.05	27.3

^a Dorsoventral/lateral diameter.^b (Dorsoventral diameter of base + lateral diameter of base) × 100/length of baculum.^c Burt (1960).^d Best and Schnell (1974).^e Present study.^f Lidicker (1960b).

Specimens of *D. o. compactus* were captured on Mustang Island and the northern end of Padre Island, Texas coastal islands which are sometimes connected as they were, for example, in 1938 (Baker and Lay, 1938). When I collected in 1969 they were separated. Specimens killed in the field are deposited in the collections of Tulane University (TU) and Cornell University, whereas specimens held in the laboratory for a year or more are in the collection (FJJ) of the author. Examples of *D. elator* were collected in Wichita Co., Texas, and are deposited in the Tulane University collection.

The phalli were removed from animals when they were killed and were preserved in 10 percent buffered formalin. They were later cleared in 3 percent KOH, stained with Alizarin Red S, and stored in glycerine. The glans was later dissected away. Length of the baculum was measured to the nearest .02 millimeter (mm) with an ocular micrometer, and the dorsoventral diameter of the proximal base, the lateral diameter of the base, and the dorsoventral diameter at the midshaft were measured to the nearest .01 mm. Length was measured along a line connecting the extreme distal and proximal tips of the baculum. Only bacula from adults were measured. An animal was categorized as an adult if it had fully erupted upper premolars worn to a peripheral band of enamel and a lake of dentine, substantially translucent auditory bullae, and ankylosed basioccipital suture (Desha, 1967).

Data are presented in Table 1 with averages of measurements of previous authors for comparison.

Dipodomys ordii compactus.—The wide separation between *compactus* and other forms of *D. ordii* suggested by Best and Schnell (1974) was not explained by these workers with respect to the opinion that *compactus* is a subspecies of *D. ordii*, albeit a very distinct one (Davis, 1942; Setzer, 1949; Hall and Kelson, 1959; and Stock, 1974).

Numerous authors, including Burt (1936), Desha (1967), and Best and Schnell (1974), have found age variation in bacular measurements. Because comparisons are by necessity often made on the basis of very few specimens, care must be taken to use only full adults. To ascertain the effects of additional age on bacular measurements, I have compared the measurements from the field series ($N = 10$) with those from a laboratory series ($N = 11$) consisting of animals captured as adults with scrotal testes and held in the laboratory for one to two years. Because the bacula in the latter series could presumably only be equal to or larger than those of the bacula in the field series, a one-sided Student *t*-test was used. There were no significant differences in the four measurements, but length approached significance ($t = 1.495$, $.9 < P < .95$), and thus caution should be exercised in age class determination for any critical consideration of bacular measurements.

The baculum of *D. o. compactus* resembles that of *D. ordii* depicted by Burt (1960). In all specimens the distal end is strongly curved at a right angle to the shaft of the baculum, but the resulting hook is longer in some specimens than in others. There is less of a curve and hook depicted by Burt (1936) and Best and Schnell (1974), and virtually no curve depicted by Desha (1967). The baculum of *D. o. compactus*, and perhaps of the species as a whole, differs from the bacula of other species of the genus in the structure of the distal tip which flares out laterally in a plane perpendicular to the dorsoventral plane formed by the shaft and hook. The tip is essentially spatulate. This structure, if present on other species, should have been obvious on the ventral views of bacula published by previous workers. Among the field series of *D. o. compactus*, bacula of specimens TU 3626 and TU 3580 have the widest spatulate tips. At the distal end, after having curved, they have minimal lateral diameters of .35 mm and .26 mm, respectively, and then flare to overall widths of .53 mm and .45 mm, respectively. Of all specimens, FJJ 886 has the least expansion, from .26 mm to .32 mm. In general, the outer side of the tip is essentially flat, and the side toward the shaft and proximal end of the baculum is faintly divided by a furrow on some specimens.

Because Burt (1936, 1960), Desha (1967), and Best and Schnell (1974) did not describe distal expansion of the tip, I examined two specimens of *D. ordii* in the collection of the University of Wyoming to see if it was present on other *D. ordii*. Neither individual

appeared to be as old as those included in the *D. o. compactus* field series. Both had spatulate expansions of the tip. The baculum of UW 470 (a specimen from between Tipton and Table Rock, Sweetwater Co., Wyoming) narrowed to .31 mm near the tip and then flared to .48 mm; the baculum of UW 506 (a specimen from "White Valley" 60 mi. W Delta, Utah) narrowed to .27 mm near the tip and then flared to .42 mm.

Genoways (1973) found specific differences in the shape of the distal tip of the bacula of *Liomys* (Heteromyidae). A more careful study of the morphology of *Dipodomys* bacula is warranted to determine variation in the structure of the distal tip. Indeed, a detailed study of the bacula, including the possible presence of a cartilagenous tip, and of the glans itself, as undertaken profitably for other genera (see Hooper, 1958), is recommended. The baculum of *D. o. compactus* clearly resembles the bacula of *D. ordii* from the mainland, but a thorough systematic analysis of the insular form(s) and mainland forms should be undertaken to determine the taxonomic and evolutionary status of the insular form(s).

Dipodomys elator.—Grinnell (1921) placed *D. elator* in a *phillipsii* group with *D. phillipsii*, *D. perotensis*, and *D. ornatus*, all three of which have been synonymized (see Genoways and Jones, 1971). Dalquest and Collier (1964) discussed the similar external morphology of *D. elator* and *D. phillipsii ornatus*. However, Davis (1942) placed *D. elator* in a separate group and suggested affinity with *D. spectabilis*. Lidicker (1960a) placed *D. elator* in a *spectabilis* group, as did Stock (1974) on the basis of karyological data. Setzer (1949) placed both *D. phillipsii* and *D. elator* in a *merriami* group.

Stock (1974) also commented that the baculum of *D. elator* was similar to that of *D. spectabilis*, but Blair (1954) examined a single baculum of *D. elator* and stated that it was very similar to the baculum of *D. merriami* and quite unlike that of *D. spectabilis*. The analysis of Best and Schnell (1974) indicated close similarity between the bacula of *D. elator* and *D. p. ornatus*, but the authors tentatively placed *D. p. phillipsii* in a different cluster with *D. merriami*. They concluded that their numerical analysis produced inter-specific groups similar to those obtained from karyological data (Stock, 1974), but they made no attempt to explain the discrepancy about *D. elator*.

In general form the baculum of *D. elator* resembles that of *D. p. ornatus*, described by Lidicker (1960b), more closely than the baculum of any other species of the genus. Both are about the same size; however, the baculum of *D. elator* is slightly longer and has a slightly smaller base. The base of each is essentially round in cross section; that of *D. elator* is perhaps rounder than any previously described. Both bacula have similar values for Lidicker's (1960b) index of robustness which incorporates the size of the base and the length of the entire baculum. At midshaft, the dorsoventral diameter of the baculum of *D. elator* is .69 mm and that of *D. p. ornatus* is .66 mm. The curvature at the distal end of the baculum of *D. elator* is only slightly more pronounced than that of the baculum of *D. p. ornatus*. The bacula of both species tend to slope gradually from base onto shaft but there is more variation in the ventral aspect of the specimens from *D. elator* than was depicted for *D. p. ornatus* (Lidicker, 1960b). Of the 13 specimens from adult *D. elator* I examined, one shows a distinct concave slope in the profile of the ventral aspect, eight slope gently, and four have a distinct flat appearance that extends far proximally. The proximal base shows variation in shape and has irregularities similar to those depicted for *D. p. ornatus*. Rugosity associated with attachment of the corpora cavernosa is more prominent on the dorsal surface and extends farther distally on the dorsum than on the venter. The shaft of the baculum is compressed laterally and on some specimens a slight keel reaches the proximal base.

The tips of three or four bacula in the series taper to an essentially square end as viewed from the base of the baculum. The remaining specimens have various degrees of lateral expansion as seen on the bacula of *D. o. compactus*, but the most expansive, that on the baculum of TU 3646, flares from .21 mm to only .27 mm.

In certain details the bacula of *D. elator* and *D. p. ornatus* show similarities to the bacula of species in several other groups. They are somewhat intermediate between the

baculum of *D. spectabilis* and those of the *merriami* group species (see Table 1). They more closely resemble the latter in measurements. A recalculation of the index of roundness of the base of the *D. merriami* baculum using the averages for 71 specimens from Burt (1960) and Best and Schnell (1974) indicates that the bacular base of this species is as round as that of *D. p. ornatus*. The index of robustness for *D. spectabilis* is only slightly greater than that for *D. p. ornatus*, but the shaft of the *D. spectabilis* baculum is thick (Burt, 1960) whereas that of the bacula of the other species, including *D. merriami*, is thin, a factor not incorporated into the index. The proximal flattened ventral aspect of some of the *D. elator* bacula resembles that of *D. merriami* and *D. nitratoideus* outlined by Burt (1936).

As Lidicker (1960b) pointed out, the baculum of *D. p. ornatus* resembles the bacula of *heermanni* group species in robustness. However, their bacula are shorter than those of *D. p. ornatus* and *D. elator* and perhaps have thicker shafts and more pronounced distal curves (see Burt, 1936, 1960; Best and Schnell, 1974).

Dipodomys elator and *D. phillipsii* (*sensu lato*) should remain in a *phillipsii* group on the basis of similar body (Dalquest and Collier, 1964) and bacular morphology. Karyotypic data for *D. p. ornatus* (Stock, 1974) also supports this placement if one considers the hypothesis that these species are phylogenetically very old. As such they might differ from each other more than do species within other species groups. Johnson and Selander (1971) concluded that *D. elator* is not closely similar genically to any other species which they examined (which did not include *D. phillipsii*). This distinctiveness, details of the bacula showing likenesses to details of bacula of species in several other groups (particularly *merriami*), and the presumed ancestral diploid number of the species (Stock, 1974) support the hypothesis that *D. elator* is an early offshoot in the evolution of the genus and not merely a specialized form to be fitted into a *merriami* or *spectabilis* group. This alternate hypothesis to Stock's placement of *D. elator* in a *spectabilis* group is consistent with his own conclusion that *D. merriami* has evolved separately from the other kangaroo rats for a considerable length of time.

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FREDERICK J. JANNETT, JR., New York Cooperative Wildlife Research Unit, Cornell University, Ithaca, New York 14853. Submitted 6 June 1974. Accepted 31 October 1975.