SEXUAL, GEOGRAPHICAL, AND INDIVIDUAL VARIATION IN THREE TEXAS POPULATIONS OF THE LIZARD *Uta stansburiana stejnegeri*

by

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INTRODUCTION

The lizard genus *Uta* in North America is composed of five species. One of these, *Uta stansburiana*, has been divided into the following subspecies: *Uta stansburiana stansburiana* of the Great Basin region, *Uta stansburiana hesperis* of the San Joaquin Valley of central California, southward to the coast in Los Angeles county, and *Uta stansburiana stejnegeri* of the southwestern United States, extending from southern Nevada and California to western Texas and northern Mexico (Smith, 1946).

All members of the genus are rather small in size (large adult male *Uta s. stejnegeri* may reach 60 mm. in snout-vent length). The dorsal color pattern is highly variable but generally consists of a brownish, striped or speckled appearance.

Flat desert is probably the preferred habitat for *Uta stansburiana*, but mountain slopes, canyons, and dry sandy stream beds may afford equally suitable habitat. In areas of optimum habitat within the range, this species is ubiquitous in nature and may be the dominant reptile. These lizards tend to occupy and abound near man-made alterations of their environment. Extensive debris areas, scattered about favorable habitats, support high density populations.

Uta are distinguished from other lizards within the range by their small size, distinct ear opening, divided frontal, and small, uniform, dorsal scales (Smith, op. cit.).

Differentiating the three races of *Uta stansburiana* is not easily accomplished. Close taxonomic discrimination of both quantitative and qualitative characters is required.

The genus *Uta* is replete with many interesting taxonomic problems, some of which are exceedingly complex. These exemplify the need for further study as the following authorities attest. Stebbins (1954) states: "*Uta* is a highly variable species in need of thorough study to determine validity of variants now recognized and presence or absence of other geographic trends." Smith (1946) suggests major taxonomic problems exist in each race of *Uta stansburiana*. Little is known of the distribution and areas of intergradation in several forms. Natural history data is scant for all species. Woodbury (1931) indicates the status of the subspecies has never been thoroughly worked out, with the range of each somewhat confused. Modern systematists lend support in still another way. Simpson (1960) states: "Probably the most active and certainly one of the most interesting fields of special study in systematics today is evolutionary investigation of variation within single species or subspecies." Mayr (1949) reiterates the need for studying trends of variation within a single subspecies, for it is in local populations comprising this category that micro-evolution is detected. The present study attempts to correlate morphological variation (genetic variation) with geographical and ecological differences as analysed in three local but geographically distinct populations of the same subspecies.

Although primarily a systematic problem, considerable data was obtained on periodicity, behavior, and aspects of the ecology of *Uta s. stejnegeri*.

OBJECTIVES

The ultimate goal of this investigation is to resolve or elucidate the following specific objectives:

1. To study variation in twelve selected morphological characters on a statistical basis in three populations and then compare the extents of variation from one population to the next.
2. To determine sexual, geographical, and individual variation within each population.
3. To define range and normal frequency of selected characters so deviations can be detected.
4. To determine if differences in the external environment are correlated with observed variation.
5. To detect and discuss ontogenetic changes if they occur.
6. To gain knowledge of extent of variation within one race of a wide-ranging species.
7. To evaluate the characters on which the races of Uta are based.
8. To integrate ecological data wherever possible.
9. To attempt a biological explanation of variational trends and discuss their importance.
10. To contribute to a better understanding of a little-known race.

HISTORICAL SKETCH

Uta stansburiana Baird and Girard

Uta stansburiana Baird and Girard, 1852, Stansbury's Expl. Surv. Valley of Great Salt Lake, p. 345, pl. 5, figs. 4-6. --Valley of Great Salt Lake.

Uta stansburiana stejnegeri Schmidt

Uta stansburiana stejnegeri Schmidt, 1921, Amer. Mus. Nov., 15.

TYPE.--A.M.N.H.No. 348; female; collected July 23, 1906 by A. G. Ruthven.

TYPE LOCALITY.--Mouth of Dry Canon, Alamogordo, Otero County, New Mexico.

In his revision of Uta stansburiana, Richardson (1915) applies the name elegans of Yarrow (1882) to the subspecies from Lower California. Few specimens were available for study at this time and several years lapsed before Schmidt (1921) proposed a new name for Uta stansburiana from Texas, New Mexico, and Arizona. Schmidt (op. cit.) distinguished the form U. s. elegans from those specimens in the southwestern United States, on the basis that Lower Californian specimens had a much greater hind leg length. He therefore restricted the name elegans of Yarrow and Richardson to this Mexican race, and proposed the new name stejnegeri for the form in Arizona, New Mexico, and western Texas.

Inasmuch as this species is very common throughout its range, one would suspect it has been intensively studied and the systematics of the group well understood. Such is not the case in either instance. The systematics of the genus *Uta* are still confused. There are several schools of thought concerning the status of this group. These views are far too numerous to consider here and interested persons are referred to Savage (1958). His study, through analysis of osteological material, presents a lucid account and possible solution to the problem. The status of the genera *Urosaurus* and *Uta* has been one of disagreement. No two authorities include the same species in either of these genera. Savage has shown both groups to be profoundly divergent. Differences in sternal anatomy, supported to some extent by external structures, provide the basis for his convictions. This author adheres to Savage's conclusions and prefers not to digress into this highly controversial subject.

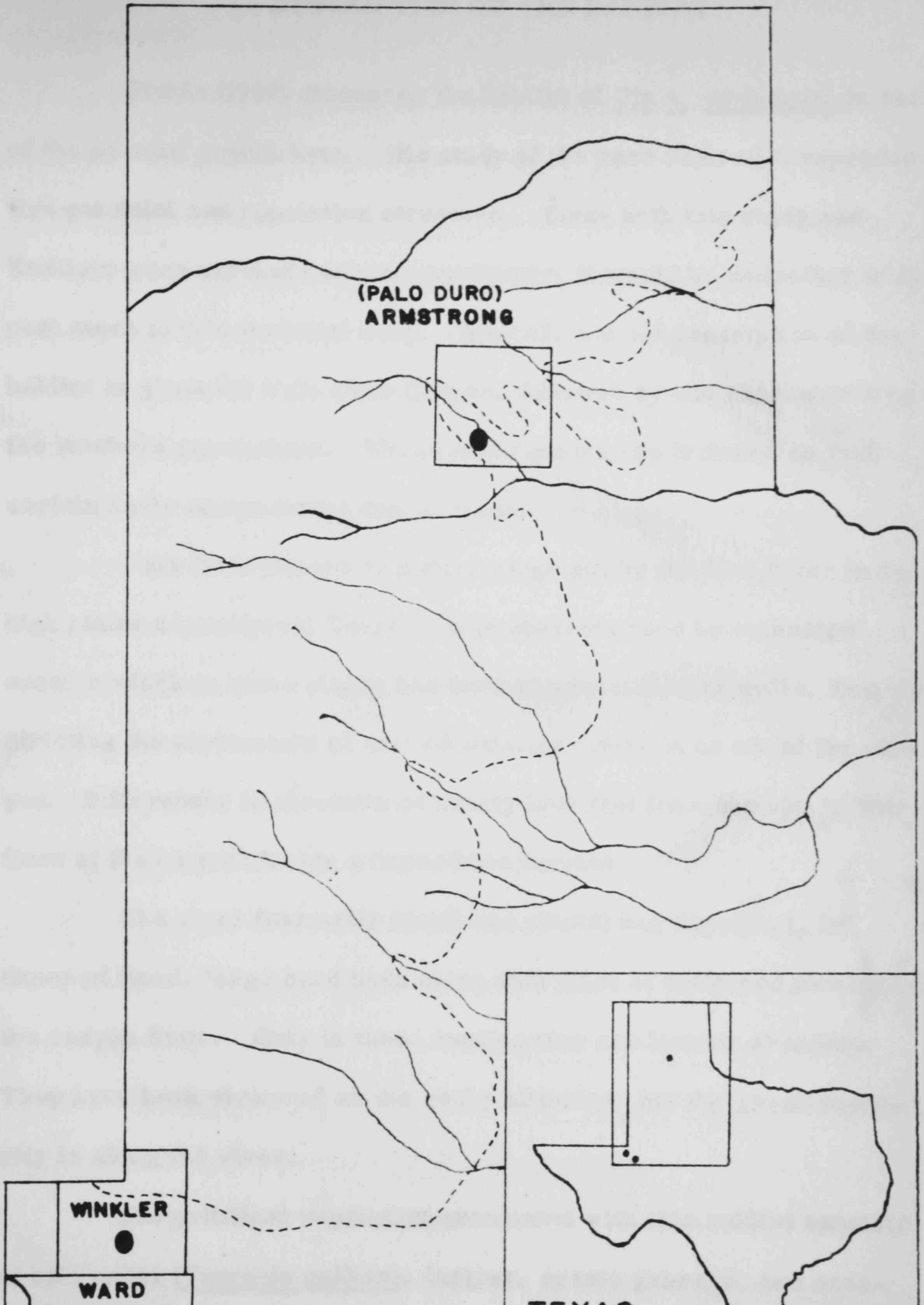
Recently completed studies have gained new knowledge of *Uta stansburiana*. Tinkle (1960) has investigated the home range, population structure, reproductive potential, and phases of the ecology and habitat in the race *Uta s. stejnegeri*.

LOCATION OF POPULATIONS

The three populations of Uta s. stejnegeri chosen for study are located in western Texas. Two of these, located near Kermit and Monahans, are 160 and 188 miles southwest of Lubbock respectively. These are termed the southern populations in contrast to the third or northern population located in Palo Duro Canyon of northwestern Texas. The latter area is 115 miles north of Lubbock and lies at the northern extreme of the range of this lizard in Texas. Nearly 250 airline miles separates the northern study area from those to the south. The southern populations are located as follows: One of the areas is 6 miles south of Kermit, Winkler County; the other 11.5 miles south of Monahans, Ward County. A distance of 23 airline miles separates these populations. Two sampling stations were selected in Palo Duro Canyon. Both are situated in Armstrong County; one area is 17 miles east southeast of Canyon, Texas, and the other is 36 miles north northeast of Tulia, Texas. The need for two stations developed after a series of flash floods almost destroyed the lizard population in Palo Duro Canyon.

Much of the region between the northern and southern study areas is under intensive cultivation and provides little suitable habitat. This has partially isolated the two southern populations from the one in Palo Duro Canyon by reducing gene flow between them. Scattered populations of Uta occur along the Caprock (Fig. 1) but in no place are they abundant. On many occasions collecting even a small sample in these areas has proven an arduous task. Several gaps in the distribution are evident along the Caprock, but their significance relies on further study. One thing is certain; any gene exchange between the northern and southern populations must depend on these intermediate groups along the Caprock. If gaps indicated above are found to be extensive, gene flow in the future may be further reduced. Certain statistical differences are already noted in this study. With the passage of time and continuance of present ecological conditions, lizards in Palo Duro may become taxonomically distinct entities.

Fig. 1. Map of northwestern Texas showing the county and location of each study population. The dotted line represents the position of the Caprock separating the mesquite plains to the east from the high plains to the west and northwest. Scale 1 inch = 42 miles.


(PALO DURO)
ARMSTRONG
WINKLER
WARD
TEXAS

DESCRIPTION OF THE HABITAT

Tinkle (1960) discusses the habitat of *Uta s. stejnegeri* in each of the present populations. His study of the race dealt with reproductive potential and population structure. Since both this study and Tinkle's were carried out concommitantly, it would be redundant to repeat much of this material here. Instead, a brief description of the habitat is given for Palo Duro Canyon, followed by one characterizing the southern populations. These descriptions are included so that certain basic comparisons can be made.

Palo Duro Canyon is a deep gorge cut by the Red River in the high plains of northwest Texas. It is characterized by extensive erosion which in some places has formed perpendicular walls, thus restricting the movements of certain animals either in or out of the canyon. Differences in elevation of nearly 1000 feet from the rim to the floor of the canyon create a formidable barrier.

The river (normally small and placid) has deposited, in times of flood, large sand beds along with piles of driftwood throughout the canyon floor. Only in these sandy areas are lizards abundant. They have been observed on the rocky hillsides, but the greatest density is along the river.

The principal vegetation associated with this habitat consists of salt cedar (*Tamarix gallica*), juniper, sparse grasses, and occasional mesquite.

Other reptilian associates occuring in the same habitat are members of the lizard genera *Phrynosoma*, *Eumeces*, *Sceloporus*, *Crotaphytus*, and *Cnemidophorus*. The more common snakes include two species of the genus *Heterodon*, and one species each in the genera *Crotalus* and *Masticophis*. Hognose snakes (*Heterodon*) are abundant and may constitute an important predator of *Uta*.

The discussion of the southern populations is treated as a single unit, since the habitat is practically the same. Both areas are located in the "sandhill" region of southwestern Texas. Active sand dunes surround the periphery of each area but have not penetrated the study sites themselves. The habitat was formerly undisturbed but with the discovery of oil some alteration has occurred. No mass destruction of the habitat is evident, although many new roads penetrate even remote sections.

Dominant vegetation in both areas (Fig. 2) is low shrubby mesquite (*Prosopis glandulosa*) with large intervening areas of loose sand supporting clumps of broom weed (*Xanthocephalum sarothrae*), sand sage (*Artemesia filifolia*), allthorn (*Koberlinia spinosa*), huisache (*Mimosa* sp.), and beargrass (*Yucca angustifolia*).

Fewer reptilian associates occur in this habitat than in Palo Duro Canyon. The most abundant lizard genera are *Cnemidophorus*, *Phrynosoma*, and *Crotaphytus*. Snake genera include two species of

Crotalus, and one species each of *Arizona*, *Masticophis*, *Hypsiglena*, and *Pituophis*. Several of these snakes (*Hypsiglena* and *Arizona*) are noted predators of *Uta*.

FIG. 2

METHODS AND MATERIALS

Uta stansburiana stejnegeri, the desert side-blotched lizard is extremely abundant in western Texas; it is also more easily obtained in large numbers than most saurians. For these reasons it was chosen for sampling experiments. Both morphological variation and character stability were studied on a statistical basis in each population. The extent of variation observed in one population was compared to each of the other two. In this way, micro-variational differences were plotted for each population.

Whenever possible, a monthly sample was collected from each population. Samples from the southern populations were most difficult to obtain during the months of December and January; in Palo Duro Canyon adequate samples were always difficult to obtain, but particularly so during the winter. Prolonged cold spells in winter and periodic floods in summer contributed to this situation. Fewer lizards were collected in this northern area than in either southern population. At Kermit large samples were often obtained under debris; especially in cool wet weather. In all, 86 samples were collected, 33 from Palo Duro Canyon, 31 from Winkler County, and 22 from Ward County. Sampling began in early 1958 and extended through June of 1960. The number of specimens examined from each population are as follows: Palo Duro Canyon, 416

Winkler County, 875

Ward County, 616

This variational study is based on examination of 1907 preserved lizards. Of this number, probably half were collected by the author while the remainder were taken by Tinkle or fellow students. Lizards were collected by means of self manufactured "blowguns". This device is easily constructed and has proven highly satisfactory not only in collecting Uta, but other species as well (Tinkle, 1956).

Lizards were usually preserved shortly after capture (4-6 hours) and all data was obtained from this material. Measurements were taken with dividers to the nearest millimeter. Both measurements and meristic counts required the continual use of a dissecting microscope. All samples were rendered homogeneous as to sex and size groups before making statistical comparisons. Permanent museum numbers were assigned each sample and specimens therein. Beside aiding additional studies, this provided a means of rechecking suspicious data.

Sex in all lizards was determined by the following criteria: the presence of enlarged postanal scales; the dorsal color pattern; and, internal dissection.

Counts and descriptions of Uta stansburiana given by Smith (1946) were used in this analysis. With some exceptions, taxonomic characters commonly employed in lizard studies were used. A small sample of Uta s. stejnegeri from the type locality (Otero Co. N. M.) was used as comparative material but other than this served no further purpose.

Specimens examined in this study are deposited in the collection of Texas Technological College. Museum numbers are given for each sampling station. Each number generally includes a series rather than a single specimen.

Palo Duro

Numbers 233, 261, 265, 266, 268, 269, 270, 271, 565, 720, 793, 795, 803, 855, 857, 925, 940, 1007, 1028, 1033, 1041, 1100, 1158, 1197, 1210, 1382, 1393, 1403, 1620, 1733, 1808, and 1972.

Kermit

The numbers are as follows: 516, 762, 787, 794, 801, 805, 862, 897, 908, 966, 1029, 1042, 1113, 1220, 1226, 1233, 1237, 1383, 1384, 1397, 1482, 1705, 1720, 1737, 1738, 1739, 1740, 1979, 2001, 2126, and 2127.

Monahans

Museum numbers include the following: 510, 785, 802, 806, 881, 907, 950, 1030, 1114, 1219, 1227, 1234, 1235, 1238, 1385, 1396, 1483, 1980, 1985, 1987, and 2124.

Only external morphological features were selected. Also included but difficult to measure, are differences in ecology and behavior. These were used in conjunction with morphological variation to aid in ascertaining the population status. Several measurements listed below do not appear in this paper. These did not prove of use in determination of variation nor were the demarcations taxonomically sound. Characters typically diagnostic of the species were useful in showing statistically significant differences between populations (Figs. 4, 11). Besides these, a number of other characters listed below were employed. All characters are based on structures that do not grow or change in the adult lizard. Femoral pore and lamellae counts were made on juvenile lizards. Little difference was noted when the latter were compared with adults.

The following measurements (to the nearest millimeter) were made for each adult specimen: length of foreleg (from insertion at shoulder to tip of third toe), snout-vent length, hind leg length (from first femoral pore to tip of longest toe), length of femur (from first femoral pore to crease in hind leg), tip of snout to base of interparietal, width of head (measured over each ear), and length of tail (from anus to tip). These measurements (excluding tail, snout to interparietal, and snout to ear) were compared and developed into ratios. Use of ratio analysis was two-fold: first, it increased the number of characters available for study; second, it provided a means of comparing and expressing proportions.

Meristic characters were studied in both adult and jevenile lizards. These included circumorbitals (above right eye only), scales in gular fold, number of papillae (from lower eye lid only), gular scales (first scale behind mental to and including one in gular fold), dorsal scales (from first scale behind interparietal to point directly behind hind leg), scales between femoral pores (only those separating the first femoral pore on each femur), femoral pores (both sides), and number of lamellae on hind middle toe (from tip of claw to base of toe). Only the latter two characters proved useful in comparing juvenile lizards. Their small size and inconspicious features proved difficult to study.

Statistical treatment of data follows the methods outlined by Casier and Bacon (1949). The modified Tryon and Searle form (Casier and Bacon p. 364) was utilized in deriving the mean, standard deviation, and standard error for each character. Further modification of this form provided a means of plotting observed sample ranges and frequency distribution. Data thus obtained was plotted to a normal curve. Samples were recorded on separate data sheets, each bearing the collection date and locality. Each specimen in a given sample was entered separately, noting its museum number, age, sex, and size. The various measurements were then tabulated alongside every individual.

To minimize bias, locality labels were not observed until each sample had been examined. Samples from all populations were collected as randomly as possible both during the day and throughout the year. The series within each sample were rendered homogeneous. These homogeneous samples were then pooled for final statistical analysis. Pooled samples represent only those specimens from one sampling area. Determination of variation in all characters was dependent on pooled samples from each population. In several characters it does not appear that large samples were necessary. The observed range of variation did not increase proportionally after using a much smaller sample. When femoral pore and lamellae counts were compared between adult and juvenile lizards, the larger adult sample added little to the already statistically significant data shown by juvenile results. These examples do not apply with regard to all characters analysed.

Where the range of variation in a particular character was great, a larger sample was deemed essential to approximate the population extremes. Ratio proportions especially indicate that smaller samples could have been used with good results. Inasmuch as large samples were available, variational trends in the always unknown population were more accurately analysed. The advantages of this method far exceed statistical treatment of small samples, especially if the latter is not of necessity.

Graphic presentation of data follows the method of Hubbs and Hubbs (1953). The horizontal black line indicates range of variation. One-half of each black box plus the white box at each end outlines one standard deviation (indicates dispersion around the mean) on each side of the mean. The number of specimens, or N, is indicated on the right side of the mean. The black box represents two times the standard error (measure of reliability) of the mean, and the vertical line is the mean. The relative spread and position of standard deviation along the observed range of variation indicates its relation to the normal curve. With the aid of a ruler one can line up the means and standard error for each character. Comparisons can then be made by sex and between all three populations. Graphical analysis of the difference between means follows that method employed by Hubbs and Hubbs (op. cit.). Testing the significance of differences (t values) depends on varying lengths of standard error and the extent of separation or overlap between two samples. Visual indication of significance may be obtained by comparing different sample standard errors. If these meet, end to end, on the same horizontal, some degree of difference is indicated. Where they do not meet and a gap exists, significance of the difference is greater. Means were considered significantly different at the one percent level of confidence. Marginal significant difference is also indicated. In no case does the coefficient of difference (CD) approach the conventional subspecific level (1.28) in characters used in this study.

RESULTS

Characters showing sexual dimorphism, geographical, and individual variation are given separately for each population. The discussion and possible explanation of observed differences follows this section.

Sexual dimorphism

Palo Duro

The following characters show no sexual dimorphism: dorsal scales, gular scales, papillae on lower eye, neck scales, and ratio of snout-vent to foreleg (See Figs. 8, 9, 10, 11, 15).

Marginally significant differences are noted in the lamellae on hind middle toe, circumorbitals, scales between femoral pores, and in juvenile lizard femoral pore and lamellae counts (See Figs. 5, 6, 7, 16).

Those characters showing pronounced differences between the sexes are as follows: femoral pores, snout-vent length, ratio of snout-vent to hind leg, and ratio of hind leg to femur (See Figs. 4, 11, 13, 14). Finally, the dorsal color pattern is markedly distinct in each sex (Fig. 3).

Kermit

Sexual dimorphism does not exist in these characters: circumorbitals, dorsal scales, gular scales, papillae on lower eye, neck scales, and lamellae in juvenile lizards (See Figs. 6, 8, 9, 10, 12, 16b).

Only one character, ratio of snout-vent to hind leg, shows marginal difference (Fig. 13).

Significant differences are evident in a number of characters. These include: femoral pores, lamellae on hind middle toe, scales between femoral pores, snout-vent length, ratio of hind leg to femur, ratio of snout-vent to foreleg, and femoral pores in juvenile lizards (See Figs. 4, 5, 7, 11, 14, 15, 16a). Each sex retains the distinct dorsal color pattern (Fig. 3).

Monahans

Characters showing no sexual differences include: scales between femoral pores, papillae on lower eye, and lamellae in juvenile lizards (See Figs. 7, 10, 16b).

Statistical differences at the marginal level occur in lamellae on hind middle toe, circumorbitals, gular scales, neck scales, ratio of snout-vent to hind leg, ratio of hind leg to femur, and ratio of snout-vent to foreleg (See Figs. 5, 6, 9, 12, 13, 14, 15).

Pronounced differences exist in the characters which follow: femoral pores, dorsal scales, snout-vent length, and femoral pores in juvenile lizards (See Figs. 4, 8, 11, 16b). Color differences between the sexes remain distinct.

Geographical Variation

Palo Duro

In comparing the Palo Duro population with those to the south, some noticeable differences were observed. Fewer femoral pores are present in both sexes (Fig. 4), lamellae on hind toe are similarly reduced (Fig. 5), considerable reduction in snout-vent length is evident (Fig. 11), and both sexes possess more neck scales than either of the other two populations (Fig. 12). Reduced numbers of femoral pores and lamellae in juvenile lizards is noted (Fig. 16), and finally, several characters show greater differences in one or the other sex but not in both (See Figs. 5, 6, 10, 11).

There seems to be more affinity in some traits between Palo Duro and Monahans than between the former and Kermit (See Figs. 11, 13, 14, 15). Proportional differences especially indicate similarity between Palo Duro and Monahans.

The following characters show no geographical variation between Palo Duro and Kermit: scales between femoral pores, dorsal scales, gular scales, ratio of snout-vent to hind leg, and ratio of hind leg to femur (See Figs. 7, 8, 9, 13, 14).

Marginal significant differences include papillae in males only (Fig. 10), circumorbitals in males only (Fig. 6), and lamellae in juvenile male lizards (Fig. 16b). No character shows marginal significance in comparing females.

Characters exhibiting the greatest variation are femoral pores, lamellae on hind middle toe, circumorbitals in females only, snout-vent length, neck scales, ratio of snout-vent to foreleg, and both juvenile characters except lamellae in males (See Figs. 4, 5, 6, 11, 12, 15, 16).

Differences between Palo Duro and Monahans are not significant in number of circumorbitals, scales between femoral pores, dorsal scales, gular scales, or in any of the previous listed ratios (See Figs. 6, 7, 8, 12, 13, 14, 15).

Marginal characters include lamellae in females only (Fig. 5), snout-vent length in females only (Fig. 11), and papillae on lower eye in both sexes (Fig. 10).

Significant differences are noted in the number of femoral pores, lamellae on hind middle toe, snout-vent length, neck scales, and both characters analysed in juvenile lizards (See Figs. 4, 5, 11, 12, 16).

A striking indication of geographical variation in Palo Duro lizards is the distinct dorsal color pattern (Fig. 3). Although this is most pronounced in females, the males also show considerable variation. This character alone would suffice to separate with 90%+ efficiency any mixed sample containing lizards from the three populations. Occasional individuals have been collected at Kermit which show a similar pattern, but these are exceptions. Likewise, the Kermit phenotypic pattern has been noted in Palo Duro lizards, but again is exceptional. No attempt was made to analyse the intensity of these color differences; this does not negate their importance. Color variation coupled with other variational trends supports the view that Palo Duro lizards are diverging.

Kermit

Results obtained in comparing this population with Palo Duro have previously been discussed. A number of significant geographical differences are evident. As would be expected, extent of variation between Kermit and Monahans is much less significant than between these and the northern area. When Kermit and Monahans were compared, however, some interesting differences were detected.

Variation in the following characters was not significant: dorsal scales in females only (Fig. 8), femoral pores in males only (Fig. 4), ratio of snout-vent to foreleg in males only (Fig. 15), and ratio of snout-vent to hind leg in females only (Fig. 13).

Marginal significant characters include: dorsal scales in males (Fig. 8), femoral pores in females (Fig. 4), lamellae on hind toe in both sexes (Fig. 5), ratio of snout-vent to foreleg in females (Fig. 15), and ratio of snout-vent to hind leg in males (Fig. 13).

Sexual geographical variation is evident from the greater number of lamellae in Monahans males (Fig. 5), presence of more circumorbitals in Monahans females (Fig. 6), and proportional differ-

Fig. 3. View of dorsal color pattern in *Uta s. stejnegeri*. Upper photos from left to right are Palo Duro male and female; below from left to right are Kermit male and female.

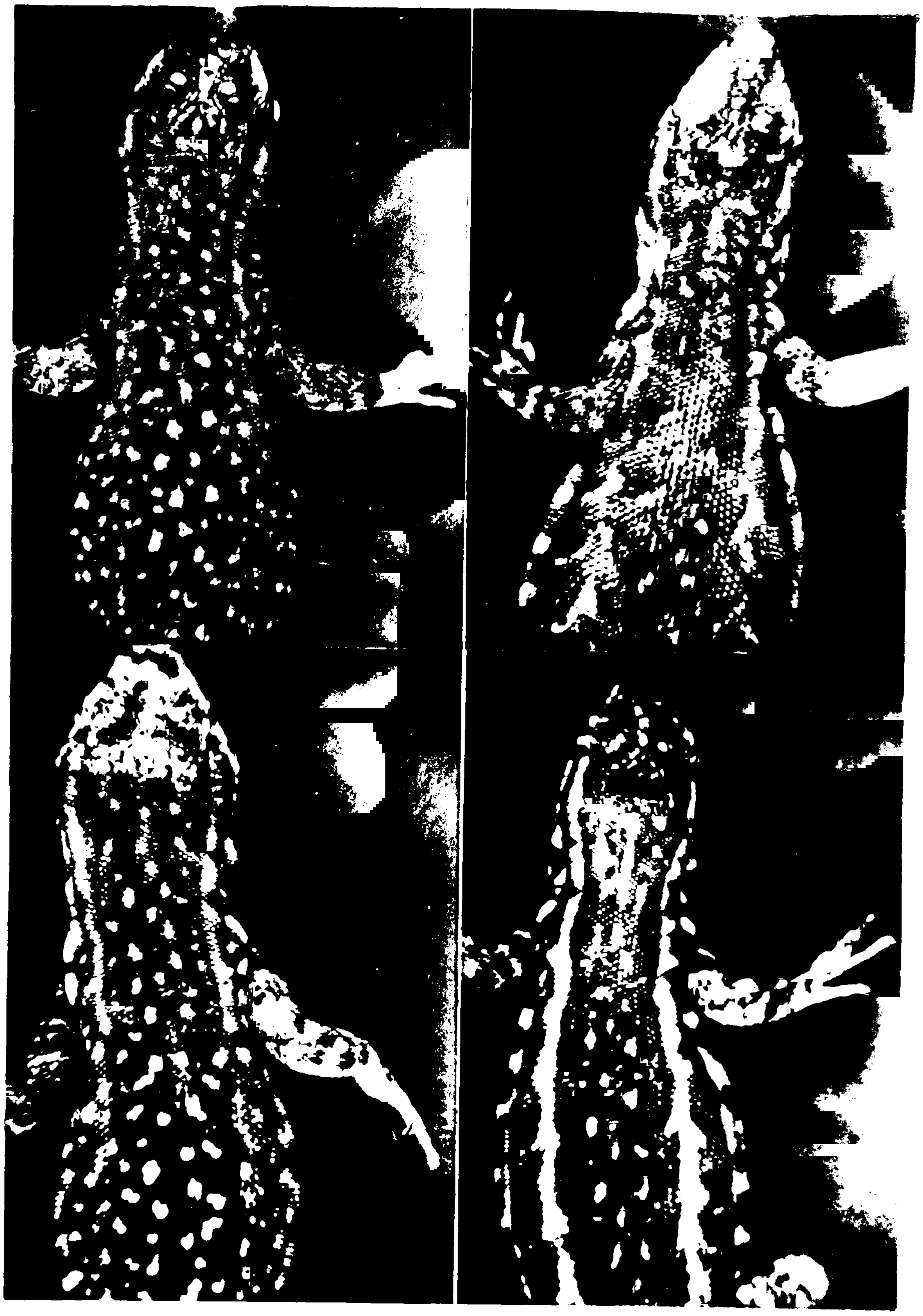


FIG. 3

ences in females represented by ratio of snout-vent to foreleg (Fig. 15). In both sexes, the snout-vent length is considerably less than comparable Kermit lizards (Fig. 11).

Monahans

From results obtained, the extent of variation in most characters compared between this and the Kermit population, suggests similar but slightly intergrading gene frequencies.

That certain affinities prevail in some characters between Monahans and Palo Duro, but fail to exist between the latter and Kermit has been established (See Figs. 11, 12, 13, 14). Discussion of these and other trends suggestive of geographical variation are included in the section following results.

The phenotypic Palo Duro like color pattern has not been observed in the Monahans population. It seems probable, however, that some individuals show this northern pattern. As previously indicated, it is evident but not common in Kermit lizards. A distance of 28 miles should not prevent expression in some Monahans lizards.

Individual Variation

Graphic material (Figs. 4-6) must be used in conjunction with these results. These graphs have definite patterns which may be similar but not identical in two samples. Each character exhibits a given range of variation, frequency distribution, and mean. From these values patterns which approximate the normal curve of probability can be established. Other differences may result from frequency distributions that are skewed. When this condition exists, numerous theoretical possibilities must be postulated.

Individual variation was studied only in the pooled sample. Although the series in each sample were examined individually, subsample comparisons showed little variation. For this reason all samples from a given population were pooled. Where populations are compared, extent of individual variation must be considered an indicator of geographical difference.

Palo Duro

Characters displaying greatest range of variation include lamellae, circumorbitals, scales between femoral pores, dorsal scales, gular scales, papillae on eye, snout-vent length, neck scales, and ratio of hind leg to femur. (See Figs. 5, 6, 7, 8, 9, 10, 11, 12, 14). All characters show some individual variation.

Kermit

Range of variation is greatest in dorsal scales and snout-vent length (Figs. 8, 11). Both characters show similar variable qualities in Monahans and Palo Duro lizards. Some degree of variation is evident in all characters; these differences may be obtained from Figs. 4-16.

Monahans

A wide range of variation is present in snout-vent length, gular scales, dorsal scales, lamellae, circumorbitals, and ratio of hind leg to femur. (Figs. 5, 6, 8, 9, 11, 14). Only the most variable characters are listed above. Other traits may be compared in Figs. 4-16.

DISCUSSION

Many aspects of this study are difficult to explain and interpret. Multiple evolutionary factors (mutability, natural selection, isolation, species gene pool, and population size) are not only involved but must be considered and applied in the interpretation of results. Where variation may result from interacting factors, the merits of each is discussed. This multiple-speculative approach provides the basis for my views.

Population genetics in reptiles is poorly known; even less is known of micro-variation in reptilian populations. Few studies have been conducted below the sub-specific level in one race of a wide ranging reptilian species. Consequently, very little comparative material was available.

Of the characters analysed, most approximate the normal curve of probability. When individuals comprising the local population take any of a considerable number of values for a given character, the pattern of this frequency distribution most often resembles a bell-shaped curve. Less common genotypes lie on either side of the bell, but the average or most common genotype is clustered at the middle. Statistical analysis of variation within and between populations has given an approximate indication of hereditary variation; extent of environmentally induced variation is more complex and difficult to detect. Currently, little is known of the micro-habitat of Uta s. stejnegeri. Minute differences probably prevail in all three populations but their detection requires further study. Although too numerous to list in detail, possible differences may include edaphic and climatic factors, population density, etc.

In some characters (Figs. 4, 5, 7, 10) frequency distribution is "skewed" from the normal curve. Here the average individual no longer is clustered at the center of the range but rather on either side. The overabundance of individuals in the above figures is negatively skewed towards the smaller values. Skewed curves are noted only between sexes and within one population. In no character was skewedness evident in all three populations.

The gradient of skew in these characters is only slight to moderate. Several possible explanations for these skewed curves is suggested. First, due to some unknown factor, slightly heterogeneous samples may have been included. Second, selection pressure for a given character may be operating only in one sex or on one population. Third, skewed curves in the Palo Duro and Monahans populations may result from the reduced body size in both sexes and consequent reduction in expression of quantitative variation. Fourth, since all characters studied are probably polygenic (and pleotropic), the population size (gene pool) regulates phenotypic variability. The Palo Duro population exemplifies very well this latter condition. This group is subject to periodic destruction of the habitat (by floods) and consequent reduction of population size. Both conditions prevent stability and genetic equilibrium, with the population in a continual state of flux.

Characters exhibiting sexual dimorphism do not appear stable in any population. Where sexual variation is pronounced (size, femoral pores, lamellae, etc.), it should not result entirely from genetic and hormonal sex differences. If this were true, then sexual variation between populations would be relatively uniform and stable. However, this is not the case; secondary sex characters exhibit differential variation in each population. Certain of these differences must represent selective adaptations to the local environment. Furthermore, selection appears to favor one sex or the other but not both. These differences may be correlated with some allometric growth factor; or, differential selection may favor longer survical in one or the other sex. Rather than place emphasis on either of the foregoing possibilities, perhaps it is best to assume multiple factors are involved.

Timofeeff-Ressovsky (1941a) suggests geographical variation may be characterized by three types of characters and character-combinations: neutral characters, adaptive ones, and harmonious character-combinations which acting together have an adaptive relation to the local environment. Although several characters (Figs. 8, 9) may appear neutral, since significant difference does not exist, the range of variation in each is quite different. Thus, they do not conform to the neutral definition. Certain character affinities are noted between Palo Duro and Monahans, while Kermit appears strikingly different. Possibly selective pressure does favor some neutral character common to both Palo Duro and Monahans. In the strict sense of being neutral, however, no character studied complies with this definition.

Clearly adaptive characters undoubtedly prevail in all three populations. To what extent a character is adapted is not easily determined. This depends on multiple environmental factors, many of which are present only in one micro-habitat. From here a gradient of adaptations to the specific local environment occurs; differences between the sexes and interspecific variation have been established in this study.

The southern populations are characterized by greater stability and lack of catastrophic reduction in population size. The components of genetic equilibrium (population size, mutation, and random reproduction) acting in conjunction, have established relatively stable gene frequencies. The extent of variation between Kermit and Monahans is far less than between these and the northern population.

Characters showing significant differences between Kermit and Monahans (Figs. 5, 6, 11, 15) are probably the result of selective forces. The selective value of a given character may be correlated with some phase of the environment as yet undetermined. In general, there are slight differences in all characters studied, but extent of variation appears less at Monahans.

Greater population size at Kermit, in contrast to Monahans, appears to inhibit to some extent gene flow between these areas. A larger and more variable gene pool is indicative of Kermit. Any scattering of this variability depends on intermediate sub-populations located in the 28 miles that separate Kermit from Monahans.

Gene flow between the southern populations and Palo Duro can only occur via the intermediate Uta populations located along the Caprock (Fig. 1). Since these groups are small and geographically scattered, Palo Duro must be effectively isolated. The extent and magnitude of variation is indicative of a diverging species. If isolation is not yet complete, then differences probably represent uninterrupted intraspecific evolutionary trends which have not resulted in biological differentiation.

There exists the remote possibility that Uta may occur in the Canadian River Valley, allowing gene flow between Palo Duro and populations in eastern New Mexico. However, absolutely no evidence of this is indicated; extensive collecting in these areas has failed to reveal Uta.

CONCLUSIONS

1. Three major levels of population differentiation (variation) are presented. Sexual, geographical, and individual variation has been determined in three populations of *Uta stansburiana* belonging to to the same subspecies *stejnegeri*.
2. Each population differs to some degree from each of the other two. Differences are most accentuated in the more isolated Palo Duro population.
3. Both southern populations show more genetic similarity than do either of these and the northern population. Variation in most characters is less significant between Kermit and Monahans and probably represents continuous variation with only slightly different gene frequencies.
4. The Kermit population is characterized by a larger and more variable gene pool. Gene flow between Kermit and Monahans occurs via sub-populations of *Uta* located between these areas. Any restriction of this exchange probably results from reduced population size at Monahans.
5. Where significant statistical differences exist between Kermit and Monahans, some as yet undetermined selective factor may be responsible. Body size at Kermit is significantly greater in both sexes, yet Monahans lizards exhibit greater number of lamellae

on the hind middle toe.

6. Large population size characterizes Kermit and Monahans. Gene frequencies have reached more equilibrium in these populations than has the Palo Duro population.

7. The status of the Palo Duro population appears one of divergence. Not only is this group more genetically isolated, than are the southern populations, but is subject to extreme fluctuation in population size (by floods). Both conditions favor possible genetic drift.

8. Marginal or significant statistical differences have been established between Palo Duro and the populations to the south. These differences prevail in the majority of the 13 morphological characters analysed. One character, the dorsal color pattern, appears strikingly different in Palo Duro lizards.

9. The large series of specimens analysed, has greatly increased the chance that major variants in the natural population have been examined.

10. Character analysis has revealed which traits appear most stable, those that are taxonomically sound, and those showing greatest variation.

11. Statistical methods have aided in proving the significance and reliability of observed differences in all the populations.

12. The taxonomic status of the race stejnegeri will and should depend on population comparisons from other parts of the vast range.

SIGNIFICANCE OF THE STUDY

Results of this study provide the foundation for the following biological problems.

Future genetic studies are now possible. Determination of range of variation, frequency distribution, and mean, have been established for 13 morphological characters.

Additional populations of Uta s. stejnegeri may now be compared. Whether from Arizona or northern Mexico, the status of this subspecies depends on these comparisons.

SUMMARY

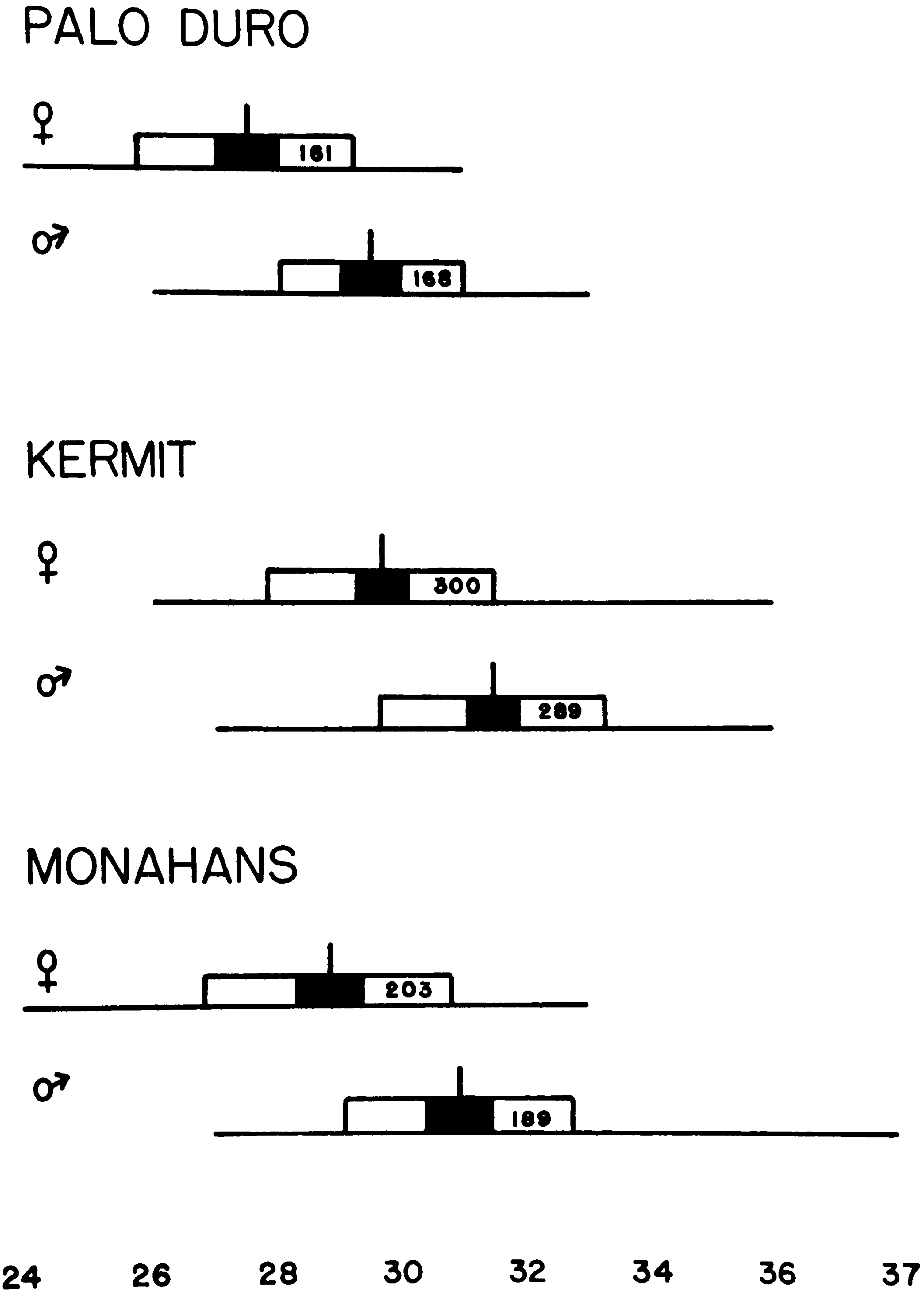
Three populations of Uta stansburiana belonging to the same subspecies (stejnegeri), located in western Texas, were chosen for study. Being abundant and easily collected, this species provided excellent study material. A taxonomic analysis to determine extents of sexual, geographical, and individual variation both within and between populations was the primary purpose of this work. Random sampling of study areas began in early 1958 and continued until June of 1960. Large samples were thus obtained, with subsequent examination of over 1900 lizards. Where pertinent, ecological observations have been included and discussed.

Twelve morphological characters were selected for taxonomic analysis. Nine of these were meristic and four were quantitative characters. Samples were rendered homogeneous as to sex and size groups for statistical comparisons. All data was treated statistically and significance tests applied to observed differences. This data for each population is tabulated in the Appendix. For results of population comparisons, reference is made to Appendix D. Graphic presentation of data (Figs. 4-16) illustrates concisely the facts and relationships involved. The significance of these data can best be analysed by comparing the illustrations.

Of the three populations studied, the one in Palo Duro Canyon, which is separated by a distance of 250 miles from either of the other two, is the most divergent (See Figs. 4, 5, 11, 12). Multiple factors are involved not only in explaining Palo Duro differences, but in interpreting many other aspects of this study. The complexity of population genetics still requires speculative biological reasoning. Certain complex conditions have prompted such an approach in this investigation.

Although significant statistical differences have been established in a number of different characters, taxonomically, all data falls below the conventional level necessary for subspecific recognition (90% rule).

Fig. 4. Variation in femoral pore counts. Horizontal black lines indicate range of variation. One-half of each black box plus the white box at each end outlines one standard deviation on each side of the mean. The dark box represents two times the standard error of the mean on each side of the mean, and the vertical line is the mean. Number of specimens represented by the figure to the right of each mean.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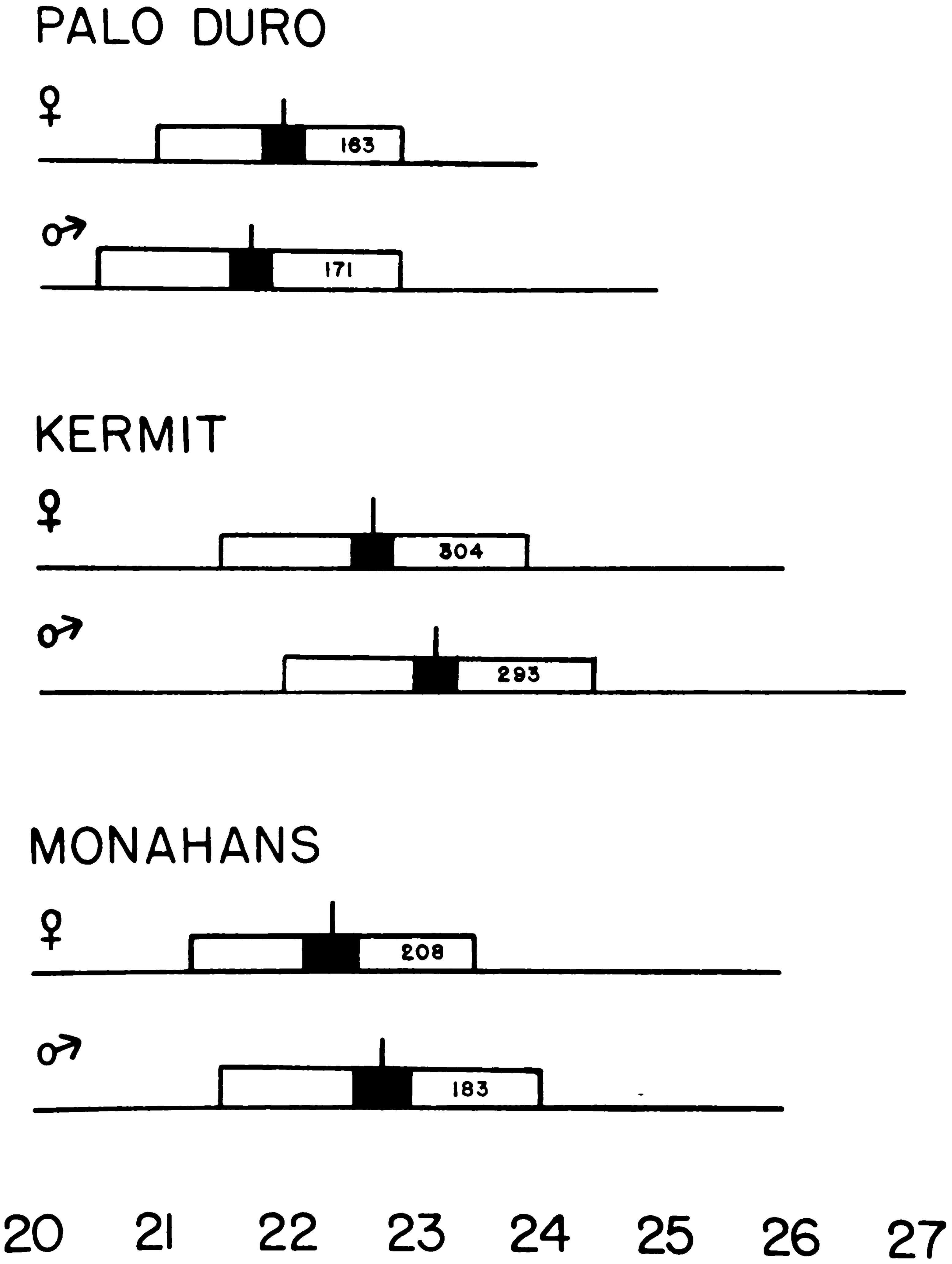
♀
161
♂
168
KERMIT
♀
300
♂
289
MONAHANS
♀
203
♂
189
24
26
28
30
32
34
36
37

Fig. 5. Variation in lamellae counts on hind middle toe. Symbols as in Fig. 1.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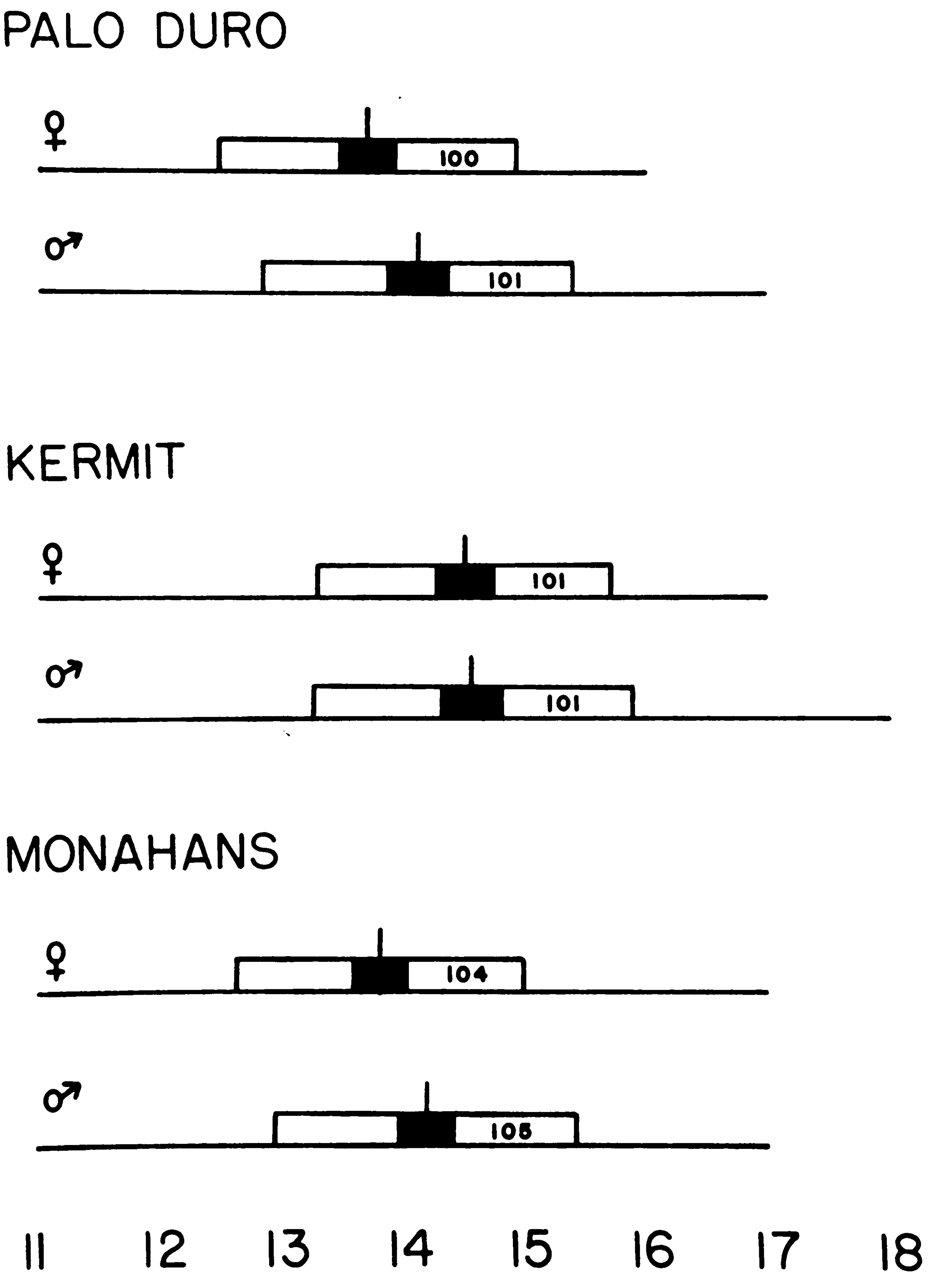
163
♂
171
KERMIT
♀
304
♂
293
MONAHANS
♀
208
♂
183
20
21
22
23
24
25
26
27

Fig. 6. Variation in circumorbital counts. Symbols as in Fig. 1.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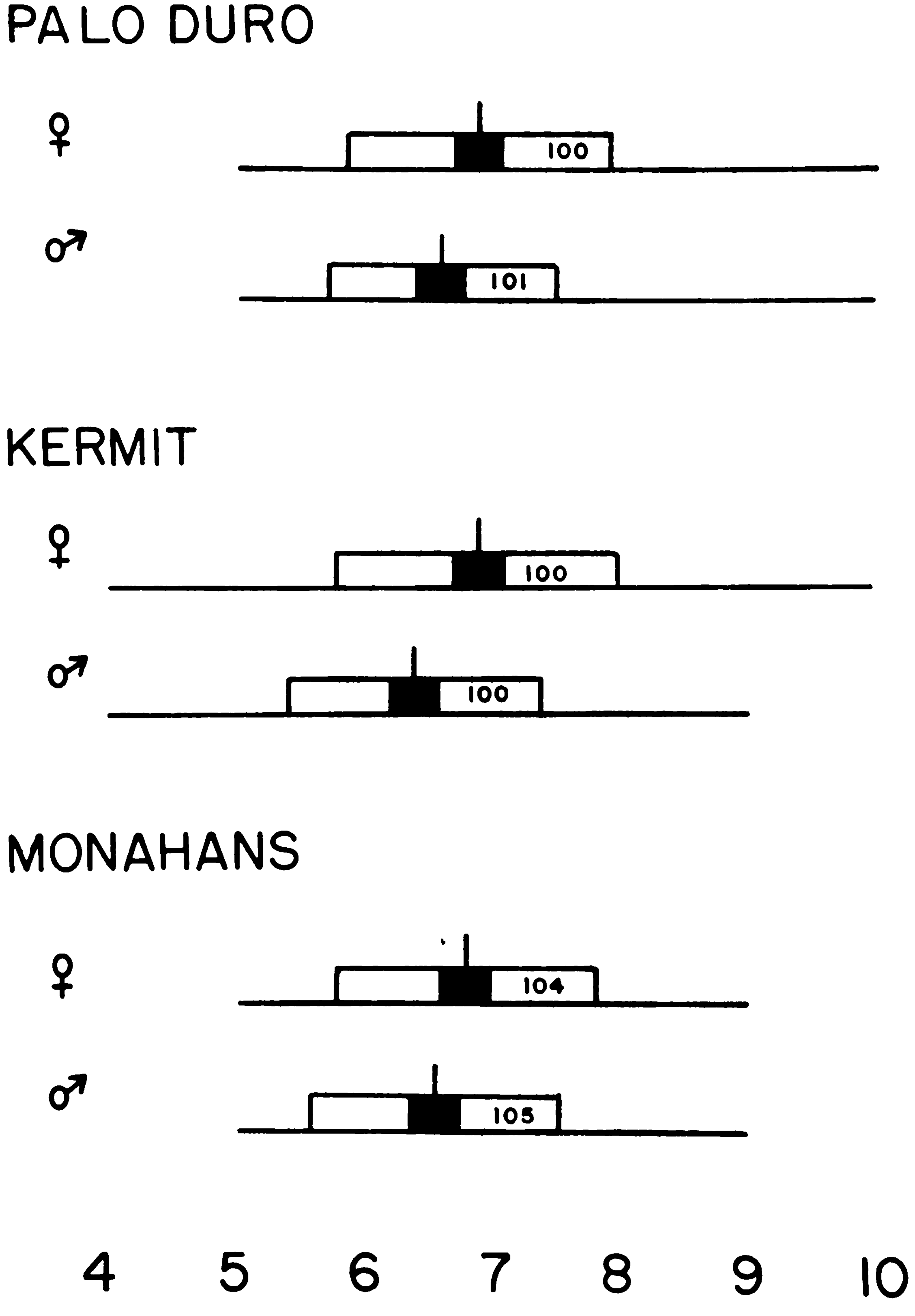
100
♂
101
KERMIT
♀
101
♂
101
MONAHANS
♀
104
♂
108
11
12
13
14
15
16
17
18

Fig. 7. Variation in scales between femoral pores. Symbols as in Fig. 4.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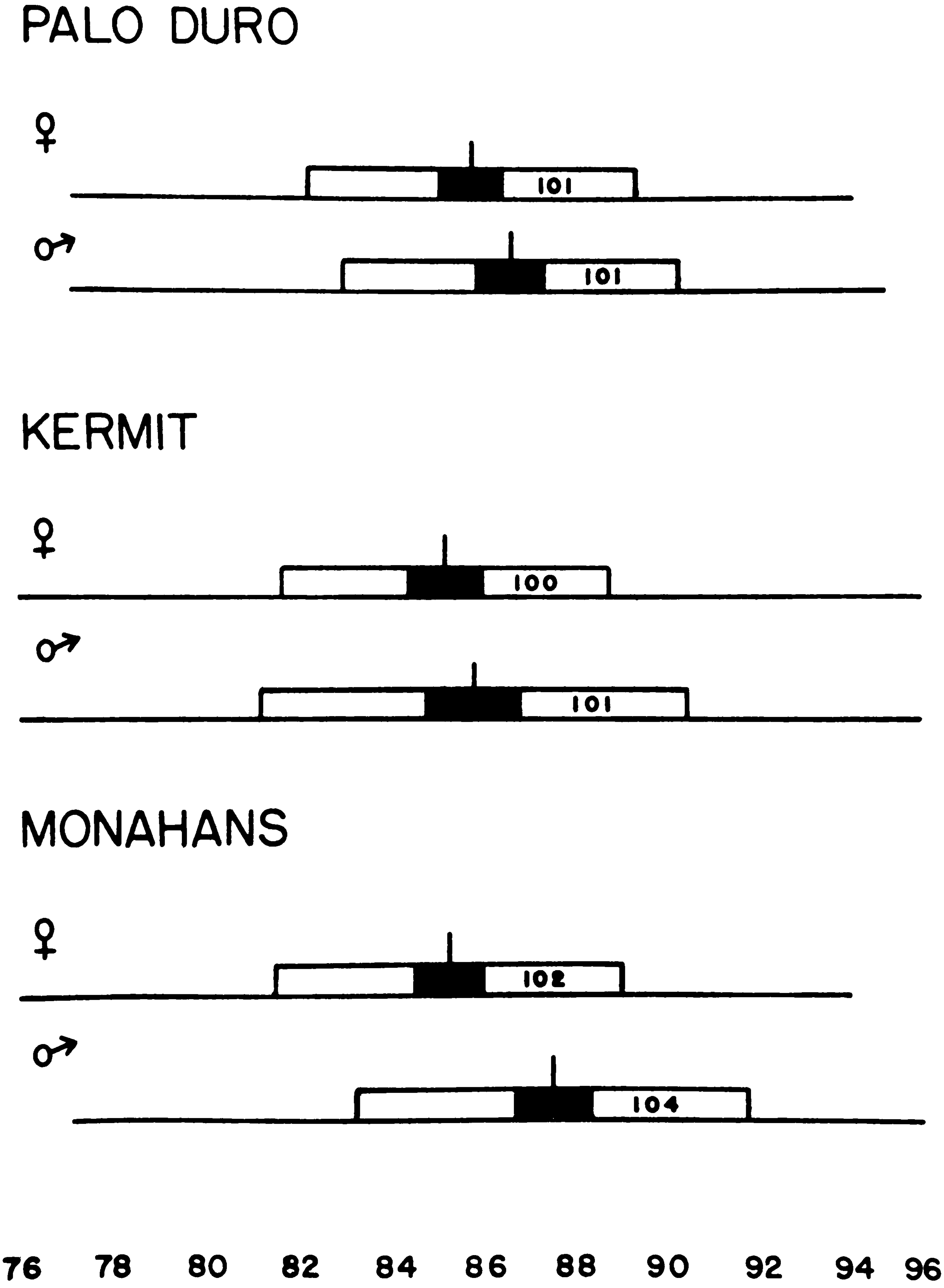
100
♂
101
KERMIT
♀
100
♂
100
MONAHANS
♀
104
♂
105
4
5
6
7
8
9
10

Fig. 8. Variation in dorsal scale counts. Symbols as in Fig. 4.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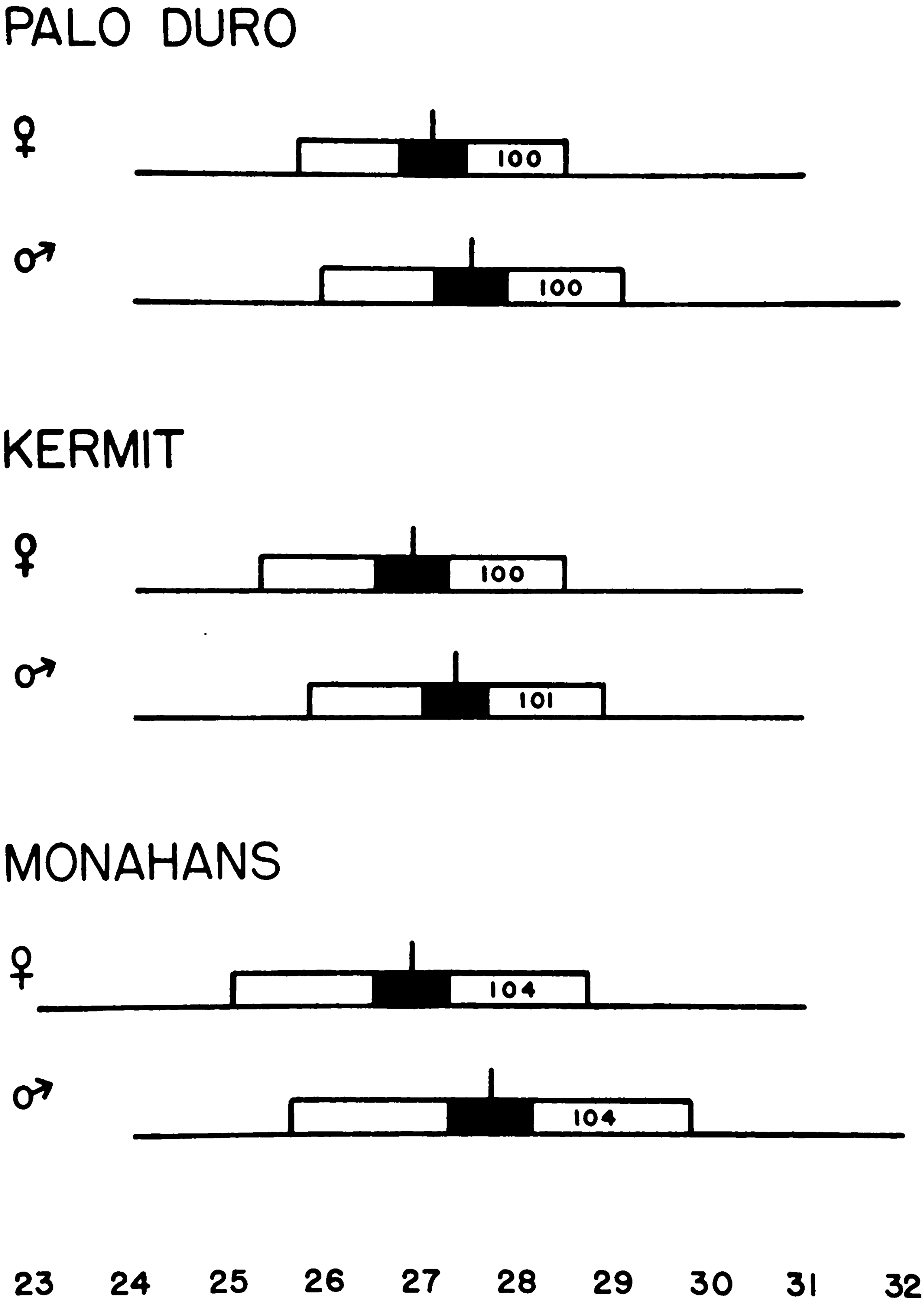
♀
101
♂
101
KERMIT
♀
100
♂
101
MONAHANS
♀
102
♂
104
76 78 80 82 84 86 88 90 92 94 96

Fig. 9. Variation in gular scale counts. Symbols as in Fig. 4.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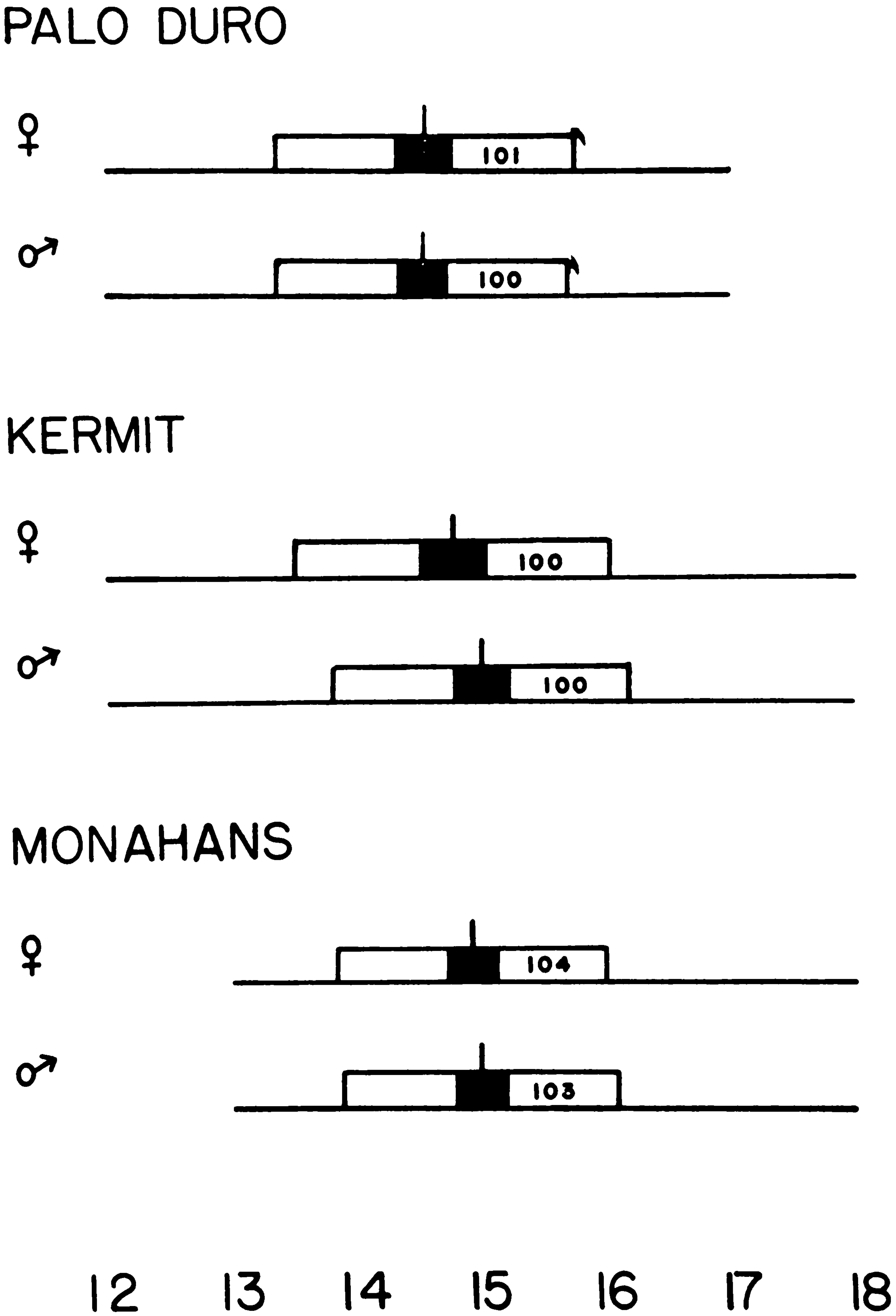
♀
100
♂
100
KERMIT
♀
100
♂
101
MONAHANS
♀
104
♂
104
23
24
25
26
27
28
29
30
31
32

Fig. 1. Variation in papillae on lower eye lid. Symbols as in Fig. 4.



PALO DURO
♀
101
♂
100
KERMIT
♀
100
♂
100
MONAHANS
♀
104
♂
103
12
13
14
15
16
17
18

Fig. 11. Variation in snout-vent length. Symbols as in Fig. 4.

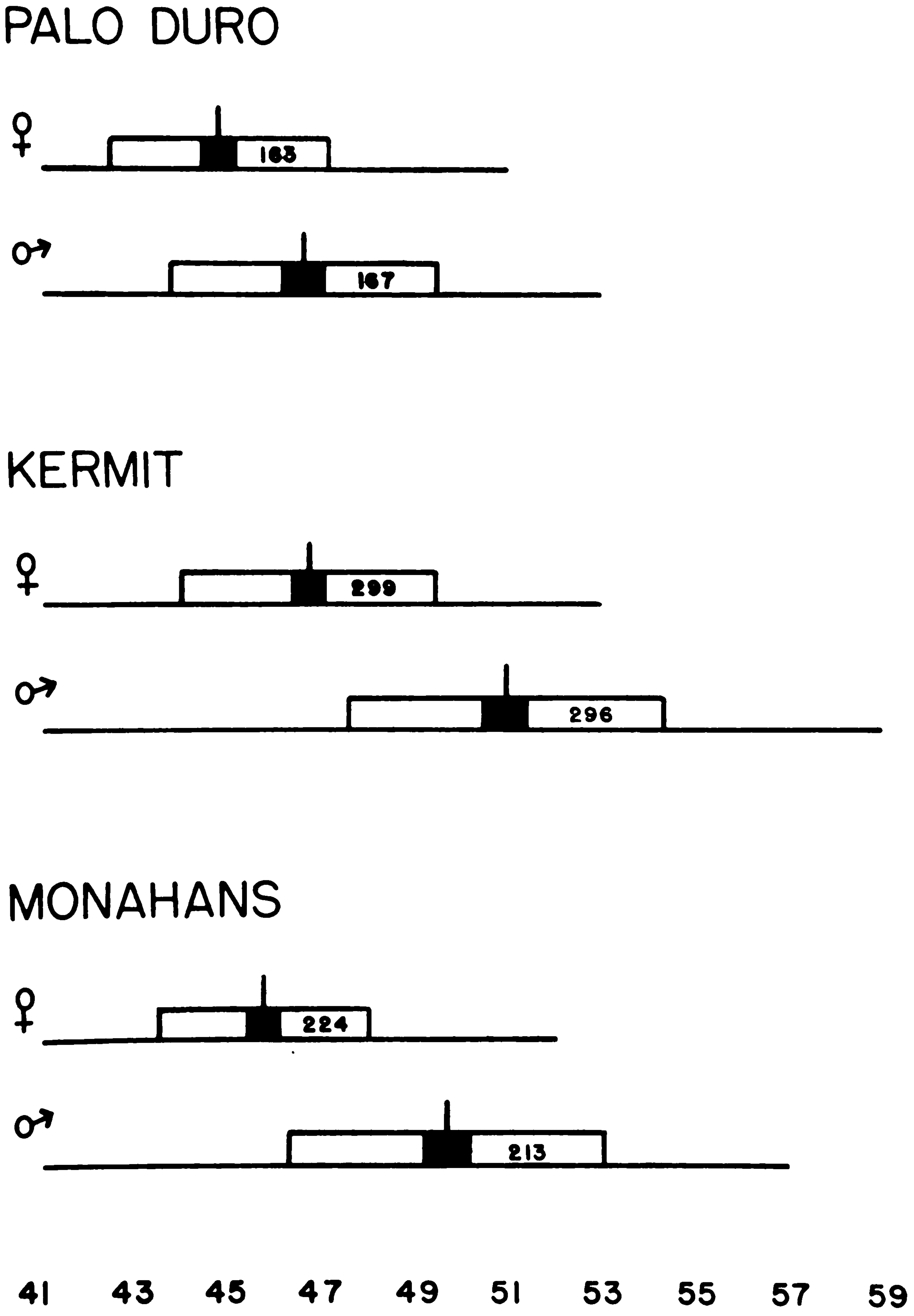
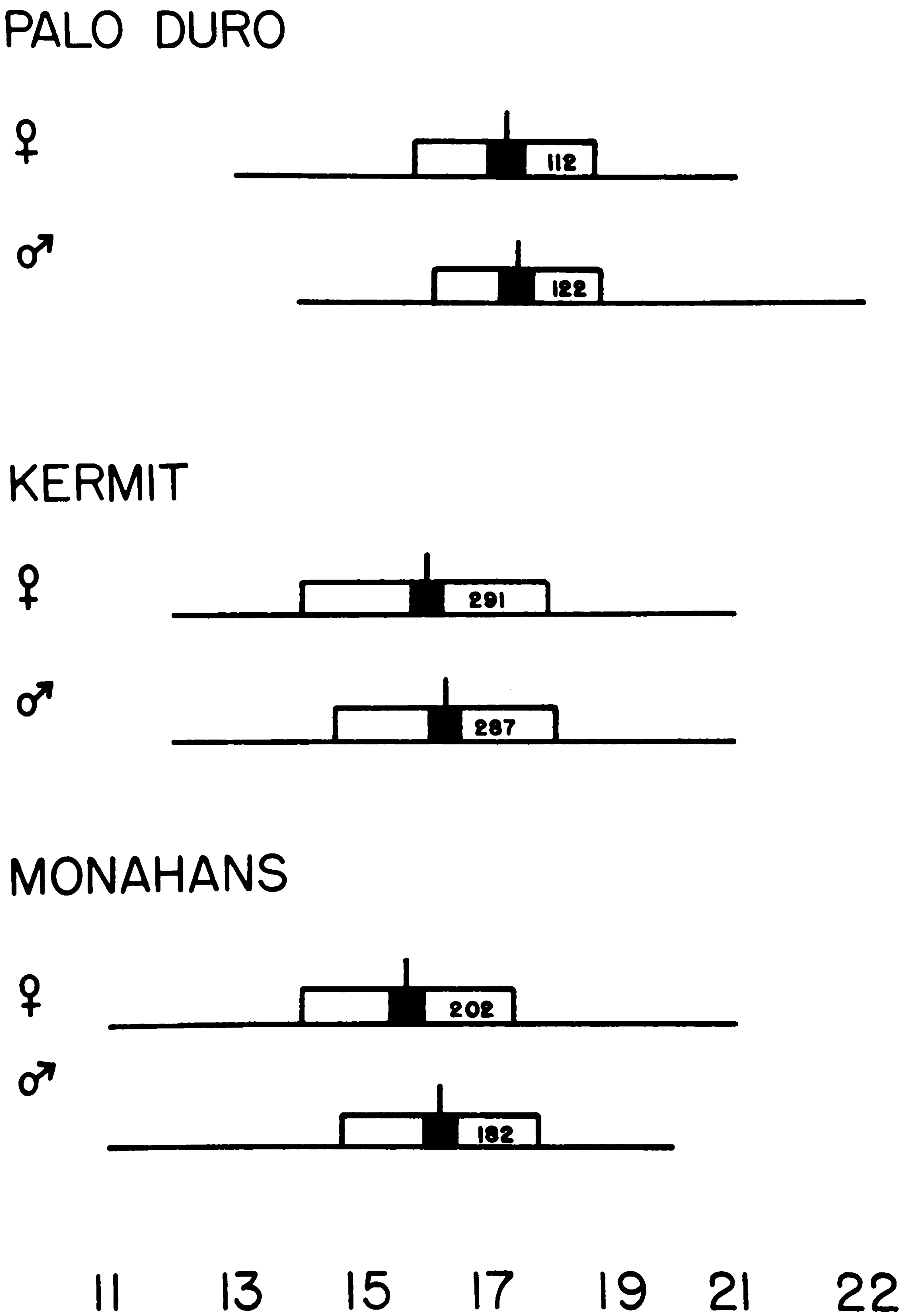

PALO DURO
♀
163
♂
167
KERMIT
♀
299
♂
296
MONAHANS
♀
224
♂
213
41
43
45
47
49
51
53
55
57
59

Fig. 12. Variation in neck scale counts. Symbols as in Fig. [illegible].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♀
112
♂
122
KERMIT
♀
291
♂
287
MONAHANS
♀
202
♂
182
11
13
15
17
19
21
22

Fig. 13. Ratio snout-vent to hind leg. Symbols as in Fig. 4.

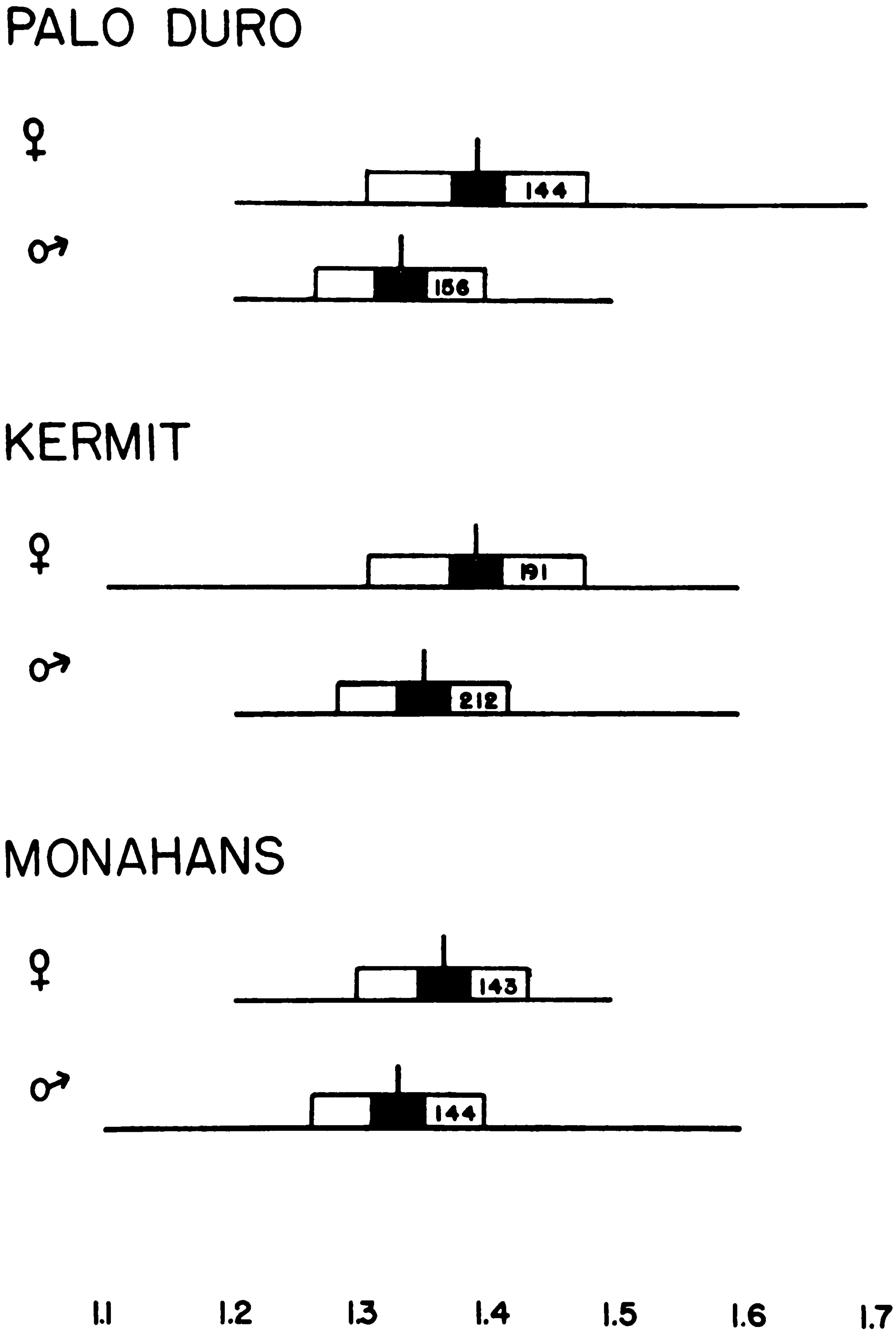

PALO DURO
♀
144
♂
156
KERMIT
♀
191
♂
212
MONAHANS
♀
143
♂
144
1.1
1.2
1.3
1.4
1.5
1.6
1.7

Fig. 14. Ratio of hind leg to length of femur. Symbols as in Fig. 4.

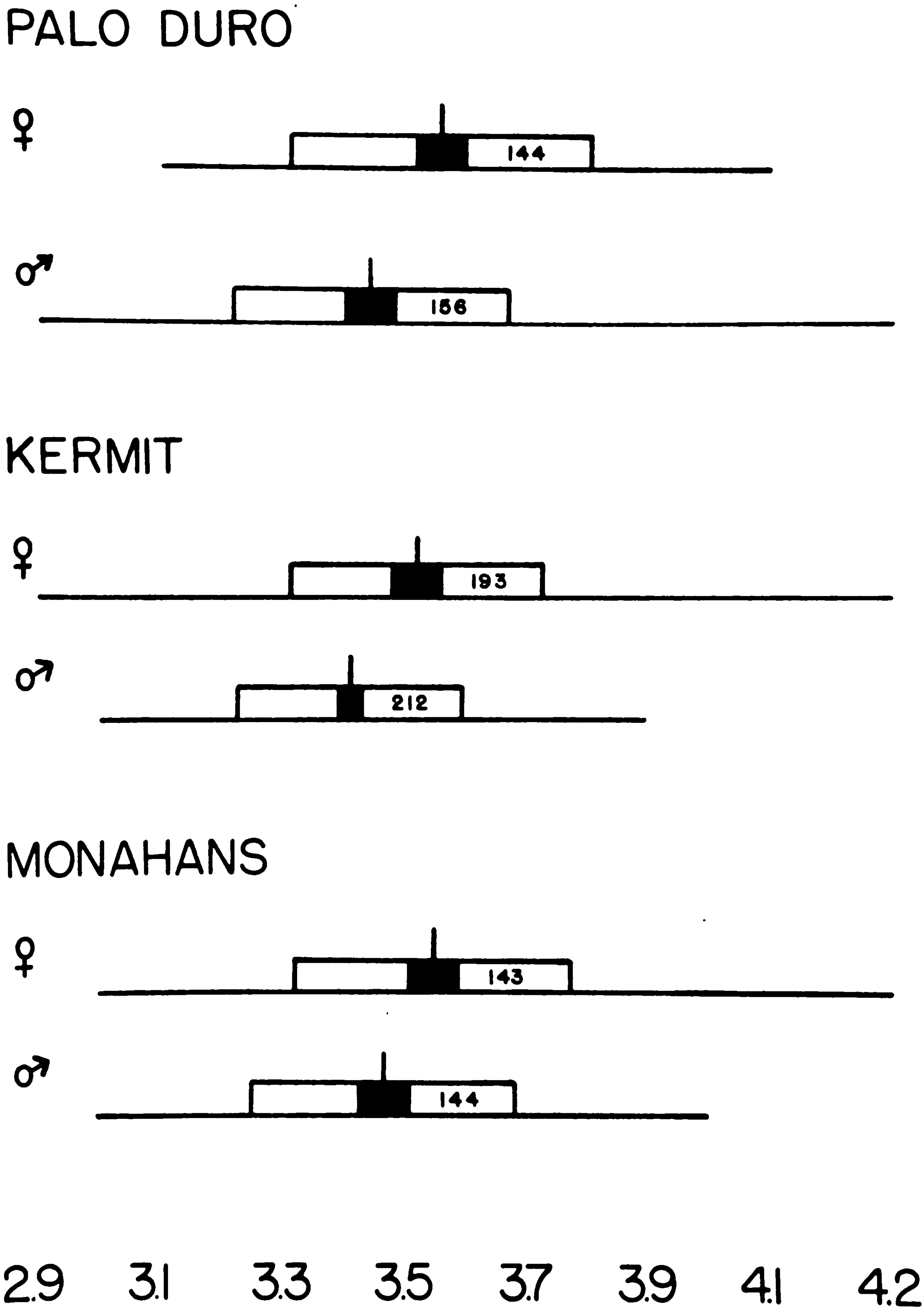
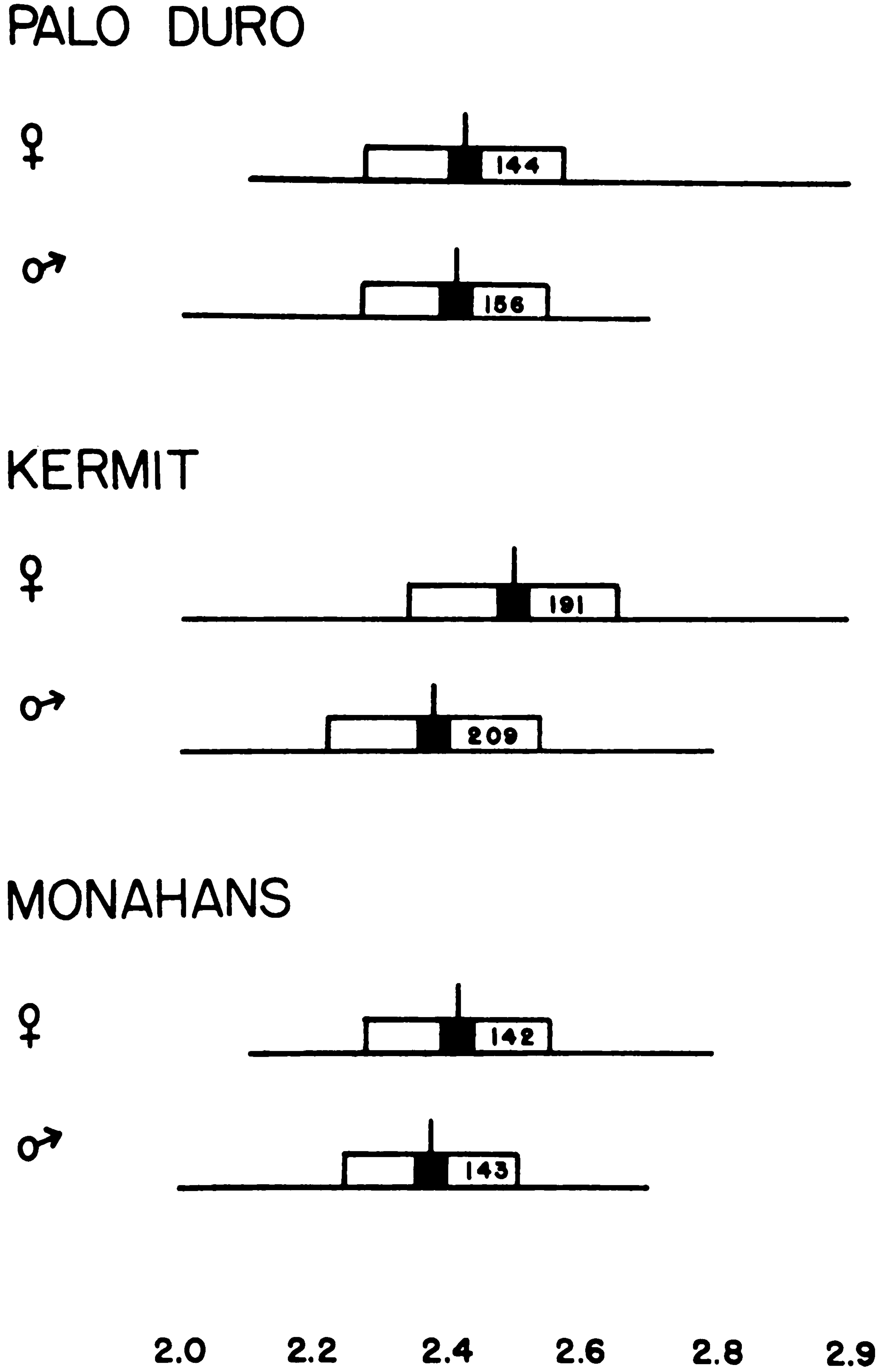

PALO DURO
♀
144
♂
156
KERMIT
♀
193
♂
212
MONAHANS
♀
143
♂
144
2.9
3.1
3.3
3.5
3.7
3.9
4.1
4.2

Fig. 15. Ratio of snout-vent to foreleg. Symbols as in Fig. 4.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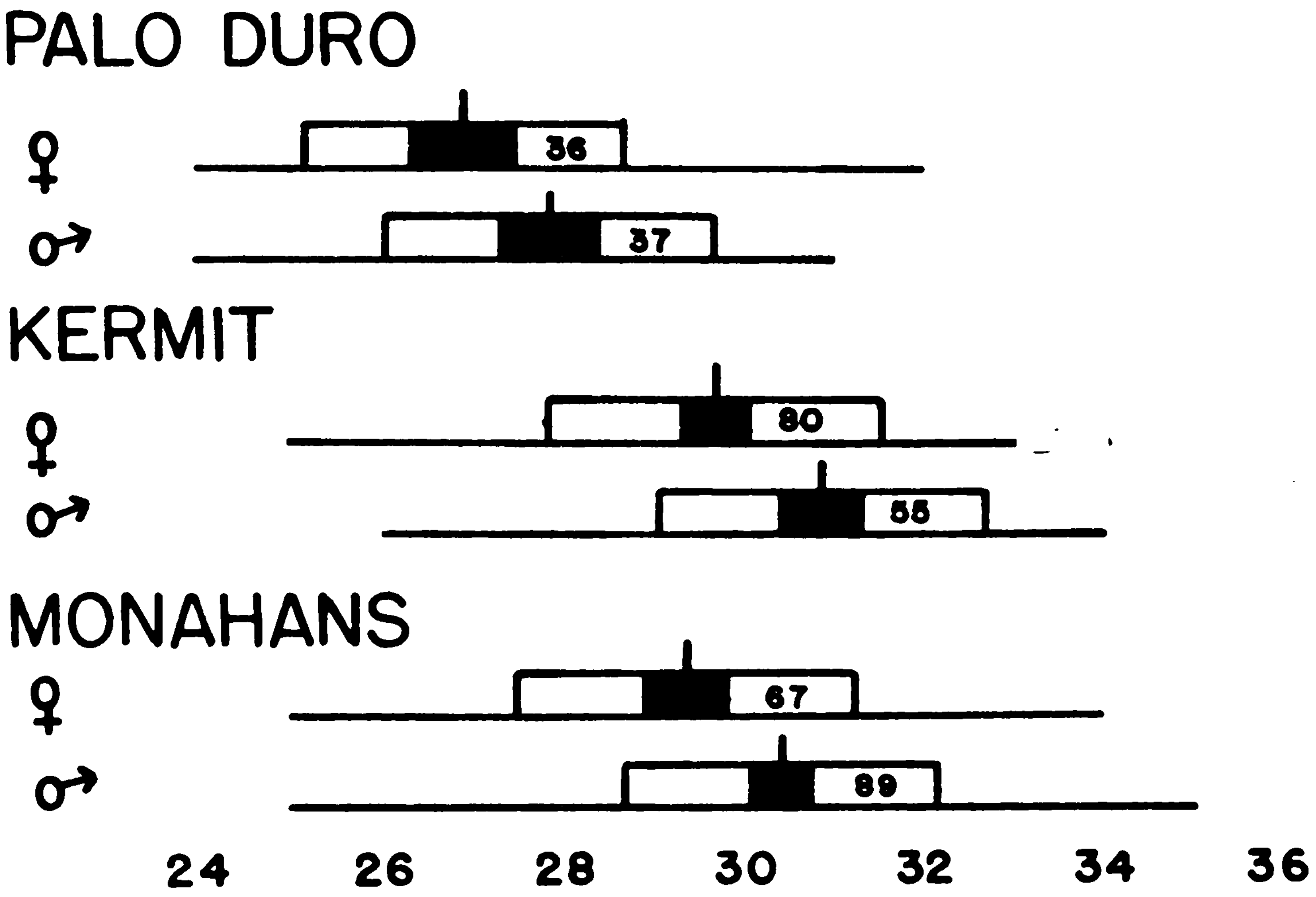
♀
144
♂
156
KERMIT
♀
191
♂
209
MONAHANS
♀
142
♂
143
2.0
2.2
2.4
2.6
2.8
2.9

Fig. 16. Variation in juvenile lizards. Top, variation in femoral pore counts. Bottom, lamellae counts. Symbols as in Fig. 4.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♀
36
♂
37
KERMIT
♀
80
♂
55
MONAHANS
♀
67
♂
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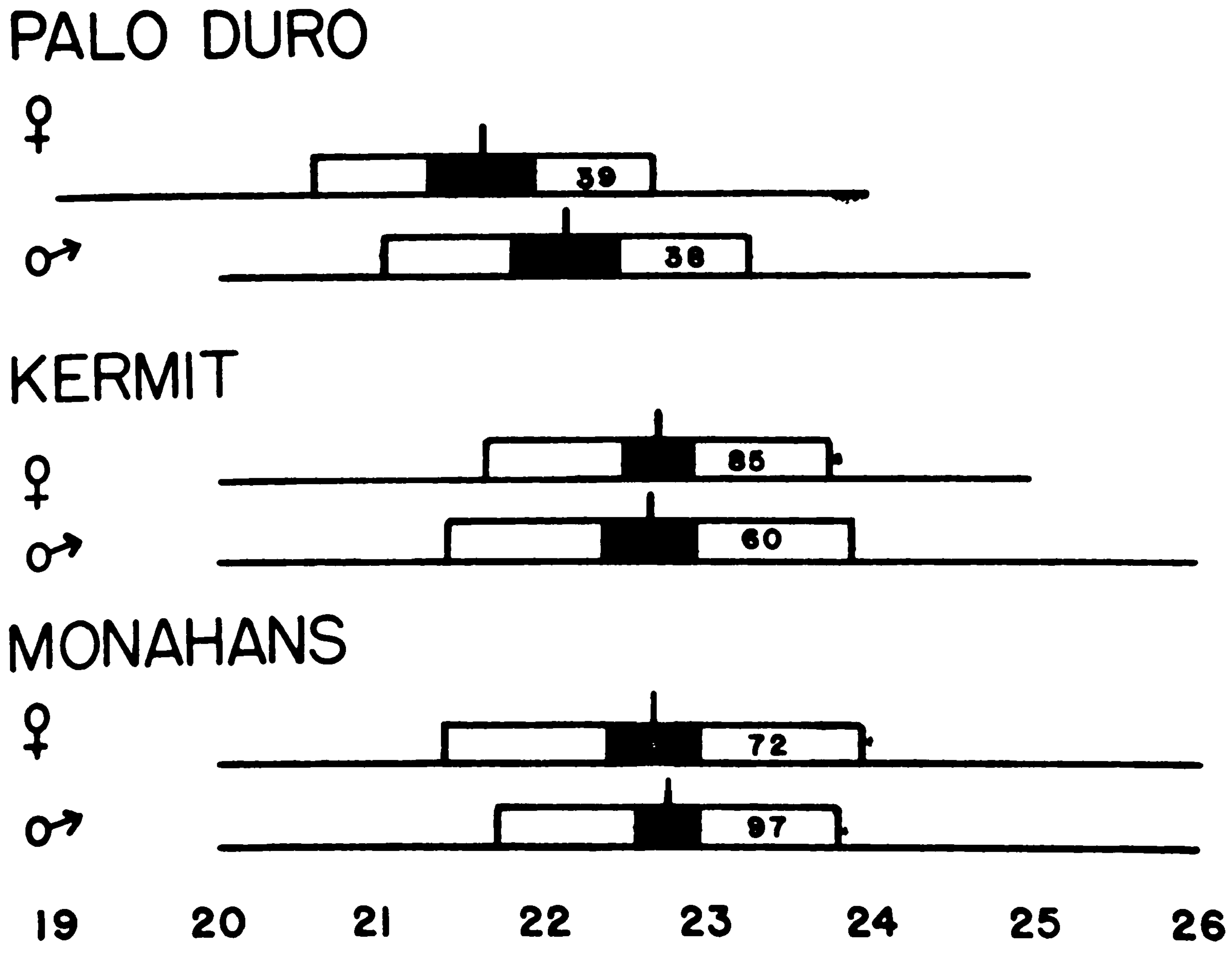
24
26
28
30
32
34
36


PALO DURO
♀
39
♂
38
KERMIT
♀
85
♂
60
MONAHANS
♀
72
♂
97
19
20
21
22
23
24
25
26

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Appendix A. Palo Duro Statistical Data. Abbreviated letters across the top represent number of specimens, mean, standard deviation, standard error, and significance of difference (t values). Variation between the sexes is compared. Means are significantly different at the one percent level of confidence. Marginally significant differences (between the one and five percent level) are indicated by M in the tv column. The letters NS signify the difference was not significant at or above the 5% level.

APPENDIX A

Palo Duro Population

	Females				Males				
Fig.	N	M	SD	SE	N	M	SD	SE	tv
4.	161	27.6	1.71	.13	168	29.5	1.60	.12	6.0
5.	163	21.9	1.02	.08	171	21.7	1.10	.08	M
6.	100	13.7	1.23	.12	101	14.1	1.30	.13	M
7.	100	6.9	1.00	.10	101	6.6	.90	.09	M
8.	101	85.6	3.66	.37	101	86.5	3.79	.38	NS
9.	100	27.2	1.52	.15	100	27.6	1.60	.16	NS
10.	101	14.6	1.20	.12	100	14.6	1.11	.11	NS
11.	163	44.9	2.35	.18	167	46.7	2.61	.20	5.9
12.	112	17.3	1.50	.14	122	17.5	1.40	.13	NS
13.	144	1.39	.08	.01	156	1.33	.07	.01	3.5
14.	144	3.56	.25	.02	156	3.44	.23	.02	3.8
15.	144	2.42	.15	.01	156	2.41	.14	.01	NS
16.a	36	26.9	1.81	.30	37	27.9	1.76	.29	M
b	39	21.6	1.12	.18	38	22.2	1.14	.19	M

Appendix F. Kermit Statistical Data. Method and symbols as in Appendix A.

APPENDIX B

Kermit Population

Fig.	Females N	Females M	Females SD	Females SE	Males N	Males M	Males SD	Males SE	tv
4.	300	29.7	1.85	.11	289	31.5	1.86	.11	5.5
5.	304	22.7	1.24	.07	293	23.2	1.30	.08	4.3
6.	101	14.5	1.22	.12	101	14.6	1.30	.13	NS
7.	100	6.9	1.09	.11	100	6.4	1.02	.10	3.5
8.	100	85.2	4.21	.42	101	85.8	4.60	.46	NS
9.	100	26.9	1.64	.16	101	27.4	1.54	.15	NS
10.	100	14.8	1.30	.13	100	15.0	1.20	.12	NS
11.	299	46.8	2.63	.15	296	51.0	3.54	.21	8.0+
12.	291	16.1	1.89	.11	287	16.3	1.82	.11	NS
13.	191	1.39	.08	.01	212	1.35	.07	.01	M
14.	193	3.52	.21	.02	212	3.41	.19	.01	4.5
15.	191	2.44	.16	.01	209	2.38	.16	.01	6.5
16.a	80	29.7	1.85	.21	55	30.9	1.80	.24	3.7
b	85	22.7	1.11	.12	60	22.7	1.22	.16	NS

Appendix C. Monahans Statistical Data. Method and symbols the same as Appendix A.

APPENDIX C

Monahans Population

	Females				Males				
Fig.	N	M	SD	SE	N	M	SD	SE	tv
4.	203	28.8	2.01	.14	181	30.9	1.86	.14	5.5
5.	208	22.4	1.24	.09	183	22.8	1.34	.10	M
6.	104	13.8	1.21	.12	105	14.2	1.25	.12	M
7.	104	6.8	.98	.10	103	6.6	.92	.09	NS
8.	102	85.2	3.84	.38	104	87.4	4.29	.42	4.0
9.	104	26.9	1.81	.18	104	27.8	2.00	.20	M
10.	104	15.9	1.11	.11	103	15.0	1.13	.11	NS
11.	224	45.7	2.33	.16	213	49.6	3.50	.24	8.0 +
12.	202	15.7	1.76	.12	182	16.1	1.68	.12	M
13.	143	1.37	.07	.01	144	1.33	.07	.01	M
14.	143	3.55	.23	.02	144	3.47	.22	.02	M
15.	142	2.42	.14	.01	143	2.38	.13	.01	M
16.a	67	29.4	1.85	.23	89	30.6	1.71	.19	3.6
b	72	22.7	1.31	.16	97	22.8	1.05	.11	NS

Appendix D. Comparison of Populations. Palo Duro females were compared to Kermit females then to Monahans. Kermit females were likewise compared to Monahans. Results are tabulated under Palo Duro females, Palo Duro females, and Kermit females respectively. Males follow the same sequence as for females. Only means significantly different at the one to five percent level of confidence are listed. All comparisons correspond to figures listed on the left margin. Other symbols as in Appendix A.

APPENDIX D

	PALO DURO-KERMIT		PALO DURO-MONAHANS		KERMIT-MONAHANS	
	Females	Males	Females	Males	Females	Males
Fig.	tv	tv	tv	tv	tv	tv
4.	5.1	5.6	4.0	3.7	M	NS
5.	5.6	8.0 +	2.8	5.3	M	2.7
6.	4.5	M	NS	NS	4.0	NS
7.	NS	NS	NS	NS	NS	NS
8.	NS	NS	NS	NS	NS	M
9.	NS	NS	NS	NS	NS	NS
10.	NS	2.6	2.6	3.1	NS	NS
11.	6.7	8.0 +	3.7	8.0 +	3.3	3.4
12.	5.9	5.4	7.6	5.6	NS	NS
13.	NS	NS	NS	NS	NS	NS
14.	NS	NS	NS	NS	NS	NS
15.	4.3	NS	NS	NS	4.3	NS
16.a	8.0 +	8.0 +	6.8	8.0 +	NS	NS
b	6.3	M	4.5	3.5	NS	NS