1989

Sex-Related Morphological Differences in the Dentition of Anolis oculatus

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SEX-RELATED MORPHOLOGICAL DIFFERENCES IN THE DENTITION OF *ANOLIS OCULATUS* (SAURIA: IGUANIDAE)

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

Kevin W. Grierson

1989

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

Author

Approved, August 1989.

Garnett R. Brooks

Gustav W. Hall

Gregory M. Capelli

DEDICATION

This master's thesis is dedicated to the memory of

Laura Jean Grierson.

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ACKNOWLEDGEMENTS

The author wishes to express his appreciation to Professor Garnett Brooks, who supervised this thesis and provided many hours of guidance and criticism throughout. The author also wishes to thank Professor Gustav Hall for his careful reading and editing of the manuscript; Professor Russell Schenck, for his invaluable aid with the statistical work; and Professor Gregory Capelli, who kindly stepped in when another advisor was suddenly needed. Special thanks are due to Jewel Thomas for the use of the ultrasonic vibrator and aid with preparing slides, and Professor Joseph Scott for use of the ocular micrometer in the electron microscope prep room.

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ABSTRACT

Among Anolid lizards, only males use their jaws in both food procurement and aggressive behavior. Males might therefore have evolved different tooth morphology or number than females. To determine if male and female tooth size, number or type are different I studied the lower jaws of *Anolis oculatus*. Jaws were examined for number of teeth, number of triconodont teeth, length of jaw margin, height of jaw ridge, and height and width characters of individual teeth. Analysis revealed the following: (1) the number of both teeth and triconodont teeth at a given jaw length were greater for females than for males; (2) males tend to have higher jaw ridges than females at a given jaw length; and (3) that the width of the back teeth in males increased at a greater rate as jaw length increased than did those of females. No other across-sex comparisons were significant.

SEX-RELATED MORPHOLOGICAL DIFFERENCES IN THE DENTITION OF _ANOLIS OCULATUS_ (SAURIA: IGUANIDAE)

INTRODUCTION

Lizards of the genus *Anolis* (Sauria: Iguanidae) range from southeastern North America southward to northern South America, with numerous species present both on the mainland and on Caribbean Islands. Small, diurnal, easily caught, and occurring in large numbers, anoles have been the subject of many biological studies, especially in the fields of ecology and behavior.

Mating and territorial behavior have been studied extensively. Sex-related behavioral differences are fairly obvious--males usually play a much more aggressive role than females in courtship and defense of territory (but see Stamps, 1973, and Ruibal and Philibosian, 1974, for examples of territorial females). This aggressiveness often progresses beyond display and is then manifested in physical combat, which involves the locking of jaws. After jaw-locking, males attempt to dislodge each other from their perch. Often they release and re-lock their jaws, continuing the behavior until one male breaks off and retreats. Each episode of jaw-locking may last up to 45 minutes (Jenssen, 1970, and Brooks, pers. comm.). However, despite the sexual selection questions this behavior raises, little work has been done to investigate the presence of morphological differences directly related to such behavior, aside from the obvious (crests, dewlaps, coloration changes). Examples of characters affected by jaw-locking behavior in males would include head size, mandible size and strength, jaw musculature, and dentition. This study focuses on the dentition of the lower jaw.

Members of the genus _Anolis_ exhibit pleurodont dentition, the common form of tooth implantation in lizards and snakes (Edmund, 1969). The lingual wall is greatly reduced, and teeth are ankylosed to the labial wall of the jaw (see Figure 1). Lizard teeth are polyphyodont: they are replaced continuously throughout the life of the individual (Edmund, 1969). Previous work has dealt mainly with tooth replacement (Goin and Hester, 1961; Stephens and Presch, 1979; Kline, 1982; Kline and Cullum, 1984; Kline and Cullum, 1985), tooth number (Ray, 1965; Thorpe, 1983), and the relationship between dentition and diet (Hotton, 1955; Montanucci, 1968). Stephens (1977), working with _Anolis_ _sagrei_, found that a greater percentage of males than females (60 percent to 40 percent) showed significant tooth wear, as correlated with increasing tooth age. However, sex is most often ignored in dental analyses of reptiles and amphibians: Shaw (1984) uses only females in his study of tooth replacement in _Xenopus_; Hotton (1955), Goin and Hester (1961), Ray (1965), Thorpe (1983), Dessem (1984), and Kline and Cullum (1984, 1985) do not report the sexes of animals in their dentition studies.

Given the dearth of research in this area, this study is primarily exploratory in nature. The possible consequences of combat and jaw-locking behavior on the dentition of males are considered by across-sex comparisons of tooth and jaw characteristics.

The species _Anolis_ _oculatus_ was chosen for several reasons: it is an isolated species, with no congeners in its range to provide interspecific competition; a large number of specimens were available for study; and females have not been observed to enter into physical combat with conspecifics (Brooks, pers. comm.).

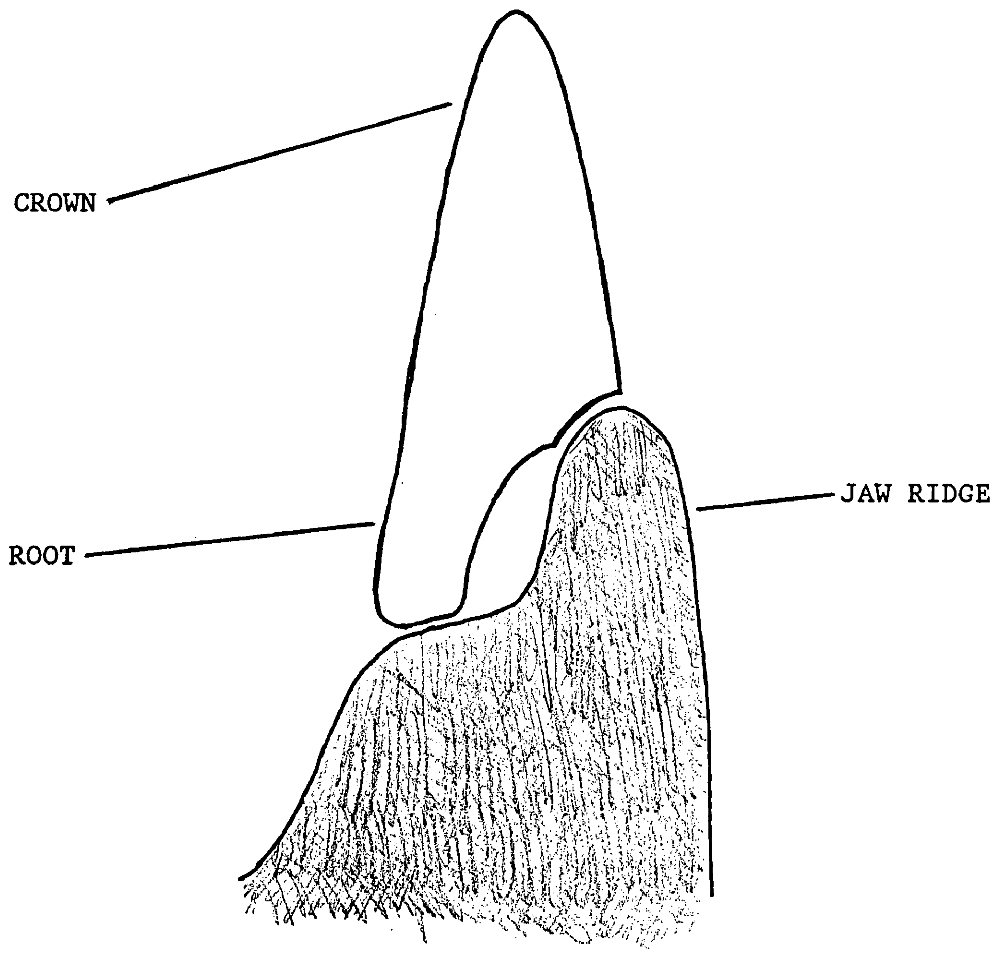
Anolis oculatus is a member of the *bimaculatus* group of Lesser Antillean anoles (Lazell and Williams, 1962). It is a medium sized anole restricted to the island of Dominica in the West Indies. *A. oculatus* is commonly found in banana and coconut groves; females and juveniles occur primarily in the ground litter, and males are found most frequently on the trunks of trees or other vertical supports (Brooks, 1968).

In *Anolis oculatus*, as in all anoles and most reptiles, there exists an allometric relationship between most morphological characters and overall body size. As the lizard grows, its individual characters undergo a similar increase in size (and number, in the case of teeth), although the rate of this increase may vary. Stephens and Presch (1979) noted that there were positive correlations between snout-vent length and number of teeth, and between snout-vent length and width of teeth.

My hypothesis is that the allometric relationship between body size and tooth characteristics will be different for males and females. Thus, the slopes of regression lines comparing a standard measurement of growth (jaw length or snout-vent length) to a specific character will have significantly different slopes or y-intercepts across sex.

Due to possible selection favoring an increase in strength and /or size in jaw and tooth morphology, a male of a given size might exhibit the following traits, as compared to a female of the same size: longer jaws, wider teeth (which provides larger cross-sectional surface area and therefore greater resistance to breakage), greater tooth height, greater jaw ridge height, or more triconodont teeth (which should have greater grasping ability than one-cusp teeth).

FIGURE 1. PLEURODONT DENTITION



MATERIALS AND METHODS

Specimens used were collected on Dominica by G.R. Brooks, Robert Gatten, and Eugene Nicholls between December, 1965, and December, 1966. Specimens were fixed in formalin for 24 hours and then stored in a 70 percent ethanol solution. I removed the lower jaws from 131 specimens (71 male and 60 female) using a straight-edged scalpel. The flesh was removed by placing the jaws in specimen containers with enough 40 percent potassium hydroxide and 30 percent hydrogen peroxide (in a 2:1 ratio) to cover the jaw. The jaw was then placed in a Sonicor G580/PC-1 ultrasonic vibrator for approximately 2 hours at its highest setting, time of vibration depending on the size of the jaw.

Once the flesh was removed, jaws were cleaned in distilled water and stored in 70 percent ethanol again. Then, under a binocular dissecting scope, each tooth position on the right half of each jaw (numbered anterior-posterior) was marked on a chart in the following manner: 1 for a tooth with one cusp, 3 for a tooth with 3 cusps, and X for a position where the tooth was missing. The first triconodont (3-cusp) tooth was circled, as were any intermediate teeth. Since there are intergradations between 1 and 3-cusp teeth, the first triconodont tooth was determined as one in which the two secondary cusps formed ridges which were at least horizontal to the plane of the tooth shelf (see Figure 2). The number of teeth were totaled, as were the number of 1-cusp teeth and the number of 3-cusp teeth. Transitional teeth (teeth which did not meet the criteria for triconodont teeth but nevertheless showed development in that direction) were marked with a 1, which was circled.

Occasionally, a tooth was missing at the juncture between the 1 and 3-cusp teeth. Determinations for the total number of 1 and 3-cusp teeth required a determination of the status of the missing tooth. Since preliminary data indicated that there were usually 2 intermediate teeth, but only occasionally 1 or 3, decisions for each tooth were made as follows: if there were none or one transitional teeth before the missing tooth, it was considered to have one cusp; if 2 or more transitional teeth were present before the missing tooth, it was considered to have 3 cusps.

After these measurements were taken, jaws were again placed under a dissecting scope. This scope contained an ocular micrometer, which was used to measure the length of the portion of the jaw containing teeth, the height of the jaw ridge, and the height and width of 3 triconodont teeth (Figure 3). Teeth were selected for measurement by dividing the area containing triconodont teeth into thirds (front, middle, and back), and measuring the largest tooth in each third. This division was necessary because the height and width of triconodont teeth generally increase from anterior to posterior of the jaw. Measurements were taken without snout-vent length and tooth number data present to avoid bias. Once data were collected, 10 data sets (for males with jaw lengths larger than 11.0 mm) were excluded so that no males larger than the largest female were included.

Once all measurements were completed the following statistical tests were performed:

1. Individual regressions (male and female data separated) for:

   a) snout-vent length vs. jaw length,

   b) jaw length vs. number of teeth,

   c) jaw length vs. number of triconodont teeth,

   d) jaw length vs. jaw ridge height,

   e) jaw length vs. average tooth height,

   f) jaw length vs. average tooth width,

   g) Jaw length vs. height of each measured tooth,

   h) Jaw length vs. width of each measured tooth.

2. In cases where traits were found to be expressed allometrically (as a function of increasing size of the independent variable) the male and female regression equations were compared in an analysis of covariance to determine:

   a) Whether or not the slopes of the lines were equal, and

   b) _if_ the slopes were equal, whether or not the adjusted means of the slopes were equal.

FIGURE 2 AND FIGURE 3.

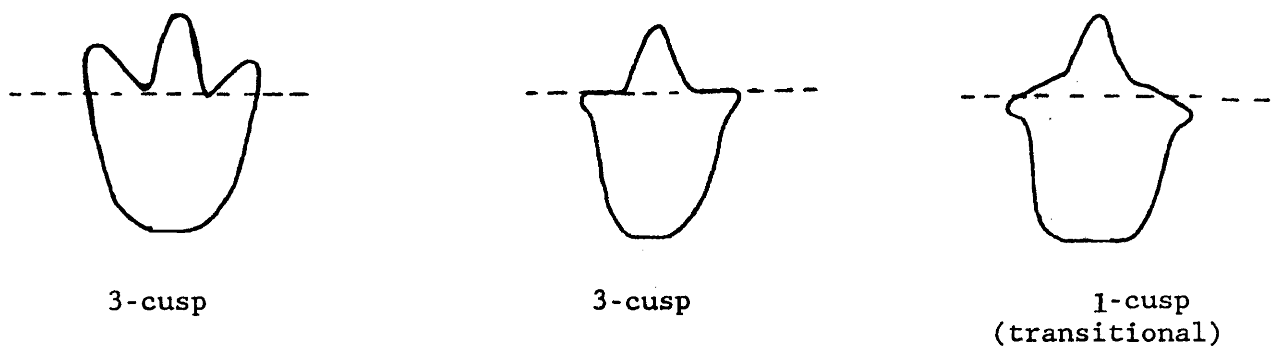


Figure 2. Determination of Triconodont Teeth.

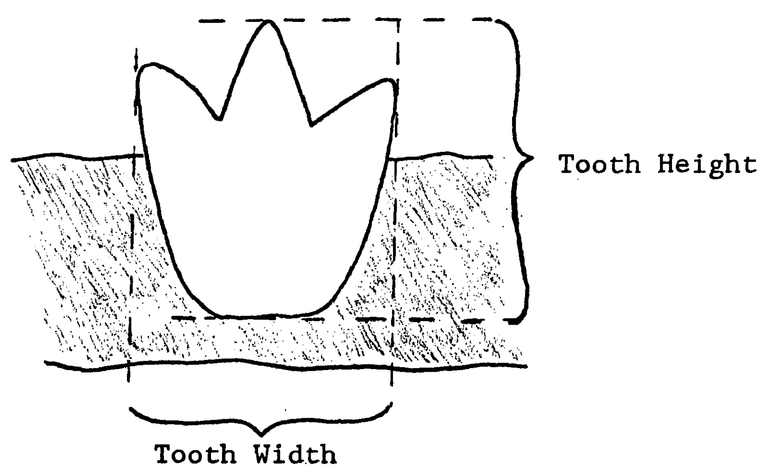


Figure 3. Measuring Tooth Height and Width.

RESULTS

Regression analyses comparing jaw length to all variables were performed, and analyses of covariance were performed on all significant regressions. The length of the jaw in millimeters (which correlated with snout-vent length strongly: see Table 1a, Figure 4) was used as a standard covariate rather than snout-vent length because the allometric relationship between jaw length and the variables tested was more direct.

Correlations. Length of jaw was positively correlated with the following characteristics:

1) number of teeth (Table 1b, Figure 5),
2) number of triconodont teeth (Table 1c, Figure 6),
3) height of the jaw ridge (Table 1d, Figure 7),
4) average tooth height (Table 1e, Figure 8),
5) average tooth width (Table 1f, Figure 9),
6) individual tooth measurements of height and width of front, middle, and back teeth (Table 1g-1l, Figures 10-15).

Covariance statistics. The assumption of homogeneity of slopes (H0: slope1 = slope2) was rejected in one case. Width of the back tooth increased with jaw length at a significantly faster rate for males than for females (p=.034: see Table 2l, Figure 15). Test for homogeneity of means (H0: mean1 = mean2) was rejected in three cases:

1) jaw length vs. number of teeth,

2) jaw length vs. number of triconodont teeth, and

3) jaw length vs. height of jaw ridge.

Females had significantly more teeth for all sizes than males ($p<.01$: see Table 1b, Figure 5: but note that while male y-intercept is greater than female y-intercept, values of the regression lines are higher for females over the range of jaw lengths studied). Measurements of number of triconodont teeth were similarly larger for females across sizes ($p=.025$: see Table 1c, Figure 6). Males had significantly higher jaw ridges across size than females (see Table 1d, Figure 7). Values for numbers of triconodont teeth, and values for tooth height and width, both individual and averaged, were converted to log values because variance tended to increase as jaw length increased. Means of males and females could not be compared for back tooth width because the assumption of equal slopes was not met. Comparisons across sex of average tooth height and width, and all valid comparisons of grouped height and width were not significant ($p>.05$).

DISCUSSION

Males and females of _Anolis oculatus_ show clear sex-related differences in a number of dentition characteristics. The difference in jaw ridge height (Table 2d) across sexes has the strongest implications: since there is no significant difference in tooth height between males and females, the jaw shelf must cover a larger percentage of each tooth in males. Since a greater percentage of each tooth would be ankylosed to the mandible for males than for females, male teeth would probably be more resistant to shearing forces (forces applied to the labial or lingual surfaces of the teeth).

Additionally, males have significantly fewer teeth and fewer triconodont teeth at a given jaw length than do females (see Tables 2b and 2c), while the jaw lengths of males and females of the same snout-vent length are not significantly different (Table 2a). This is explained, in part, by the fact that the width of the back triconodont tooth increases much more rapidly as jaw length increases for males than for females. Having fewer (but wider) teeth in the back of the jaw may increase the total cross-sectional area of the teeth (by eliminating tooth gaps), which would contribute to an increase in overall resistance to breakage.

What function could these sex-related dentitional differences serve? Teeth in anoles serve the primary function of capturing, killing, and manipulating prey, and the secondary function of aggression. Differences in dentition between sexes, where significant, should involve one or both of these functions.

The capture and eating of prey are obviously activities common to both males and females. Differences in diet could account for some differences in dentition. However, evidence in this area is conflicting: Schoener (1967) and Roehrig (1987) found that the size and species composition of the prey of Anolis was dependent on the sex of the predator, not size, but work by Brooks indicates that size is the predominant factor. Floyd and Jenssen (1984) found no differences in prey intake by size or sex. No work of this type has been done with A. oculatus. However, the function of teeth is much the same regardless of the size of the food item: prey is simply seized with the teeth and swallowed whole. It has not been determined at present, but it would seem that little shearing force is applied to the teeth in this activity by either sex.

The other major function of anole teeth is in physical aggression. Here, the roles of males and females are clearly different: Males fight for favorable territory (by engaging in jaw-locking behavior), females do not. The twisting motions involved in jaw-locking exert considerable side-to-side force on the teeth and jaws of males. The two major differences found in this study--increased jaw ridge height and increased back tooth width in males--could directly affect the structures most affected by this force.

It might be asked why this reinforcement is not present in females, needed or not. In many reptiles, especially turtles and crocodiles, sex is environmentally determined (Head, May and Pendleton, 1987). This would mean that there is no distinctive genotype for males and females, since genotype does not determine sex. However, anoles and most lizards employ (in the evolutionary sense) genotypic sex determination, which would allow for genotypic determination of the traits studied here.

For a species in which members of one sex compete for mates and territory, one logically expects that natural selection will favor individuals possessing traits which enable them to compete successfully with conspecifics, and that these traits (provided the traits are sufficiently heritable) will be passed on to the offspring of those successful individuals. These traits need not appear in members of the sex which has no "use" for it: witness the reduction or complete absence of horns in many species of antelope and deer (Vaughan, 1978). Horns, frills, elaborate coloration--examples abound in the animal world of traits possessed by males which are absent in females.

The above data indicate that there are sex-related morphological differences for characteristics which may affect, and be affected by, aggressive behavior in male Anolis oculatus. Although these behavioral differences may not be the direct cause of such morphological variations across sex, they are certainly conducive to them. Results of this study suggest other possible sex-related differences due to this behavior: tooth replacement rates might be higher in males (since the teeth are used more strenously), and jaw musculature may also differ across sexes (to facilitate jaw-locking by males). Further study should reveal more exactly the nature of these combat-related differences across sexes. In any event, researchers cannot afford to ignore sex in dentition studies of Anolid lizards, since several sex-related differences apparently do exist.

TABLE 1. CORRELATIONS AND REGRESSION EQUATIONS

a. Snout-vent length (SV) vs. Jaw length (jaw)

	male	female
Correlations	.911 ($p<.001$)	.918 ($p<.001$)

male jaw = 1.53 x SV + .458
female jaw = 1.69 x SV + .424

b. Jaw length vs. Number of teeth (teeth)

	male	female
Correlations	.712 ($p<.001$)	.766 ($p<.001$)

male teeth = 1.183 x jaw + 16.837
female teeth = 1.387 x jaw + 16.062

c. Jaw length vs. Log of Number of triconodont teeth (3-cusp)

	male	female
Correlations	.604 ($p<.001$)	.343 ($p=.004$)

male 3-cusp = 0.025 x jaw + .919
female 3-cusp = 0.017 x jaw + 1.000

d. Jaw length vs. Height of Jaw ridge (jawhi)

	male	female
Correlations	.750 ($p<.001$)	.710 ($p<.001$)

male jawhi = .183 x jaw - .011
female jawhi = .147 x jaw + .179

e. Jaw length vs. Log of Average tooth height (AH)

	male	female
Correlations	.879 (p<.001)	.866 (p<.001)

male AH = .047 x jaw - .069
female AH = .045 x jaw - .043

f. Jaw length vs. Log of Average tooth width (AW)

	male	female
Correlations	.908 (p<.001)	.838 (p<.001)

male AW = .047 x jaw - .592
female AW = .039 x jaw - .532

g. Jaw length vs. Log of Height of front triconodont tooth (HF)

	male	female
Correlations	.854 (p<.001)	.853 (p<.001)

male HF = .049 x jaw -.118
female HF = .045 x jaw -.080

h. Jaw length vs. Log of Height of middle triconodont tooth (HM)

	male	female
Correlations	.787 (p<.001)	.823 (p<.001)

male HM = .045 x jaw - .050
female HM = .043 x jaw - .030

i. Jaw length vs. Log of Height of Back triconodont tooth (HB)

	male	female
Correlations	.878 (p<.001)	.856 (p<.001)

male HB = .048 x jaw - .043
female HB = .044 x jaw - .022

j. Jaw length vs. Log of Width of front triconodont tooth (WF)

	male	female
Correlations	.806 (p<.001)	.749 (p<.001)

male WF = .042 x jaw - .643
female WF = .037 x jaw - .591

k. Jaw length vs. Log of Width of middle triconodont tooth (WM)

	male	female
Correlations	.818 ($p<.001$)	.786 ($p<.001$)

male WM = .043 x jaw - .574
female WM = .040 x jaw - .545

l. Jaw length vs. Log of Width of back triconodont tooth (WB)

	male	female
Correlations	.873 ($p<.001$)	.750 ($p<.001$)

male WB = .052 x jaw - .553
female WB = .039 x jaw - .471

TABLE 2. ANALYSES OF COVARIANCE FOR REGRESSION EQUATIONS

Comparison	Assumption	Source	d.f.	S.S.	F	P
a. S-V vs.	slopes	residual	117	32.344		
jaw length	equal	jaw x sex	1	0.396	1.433	.234
	means	residual	118	32.740		
	equal	jaw	1	0.074	.267	.607
b. Jaw vs.	slopes	residual	117	266.520		
# teeth	equal	jaw x sex	1	1.975	.867	.354
	means	residual	118	268.495		
	equal	jaw	1	25.337	11.135	**.001**
c. Jaw vs.	slopes	residual	117	0.307		
# 3-cusp teeth	equal	jaw x sex	1	0.003	.957	.330
	means	residual	118	0.309		
	equal	jaw	1	0.013	5.144	**.025**
d. Jaw vs.	slopes	residual	117	4.725		
height of jaw ridge	equal	jaw x sex	1	0.063	1.599	.214
	means	residual	118	4.788		
	equal	jaw	1	0.380	9.736	**.003**
e. Jaw vs.	slopes	residual	117	0.129		
Log of Avg. Tooth height	equal	jaw x sex	1	0.000	.319	.574
	means	residual	118	0.129		
	equal	jaw	1	0.000	.395	.531

Comparison	Assumption	Source	d.f.	S.S.	F	P
f. Jaw vs.	slopes	residual	117	0.106		
Log of Avg.	equal	jaw x sex	1	0.003	3.352	.070
Tooth Width						
	means	residual	118	0.109		
	equal	jaw	1	0.001	1.225	.271
g. Jaw vs.	slopes	residual	117	0.165		
Log of	equal	jaw x sex	1	0.001	.445	.506
Front tooth						
height	means	residual	118	0.165		
	equal	jaw	1	0.002	1.383	.242
h. Jaw vs.	slopes	residual	117	0.220		
Log of	equal	jaw x sex	1	0.000	.050	.824
Middle tooth						
height	means	residual	118	0.220		
	equal	jaw	1	0.002	1.924	.258
i. Jaw vs.	slopes	residual	117	0.135		
Log of	equal	jaw x sex	1	0.000	.414	.521
Back tooth						
height	means	residual	118	0.136		
	equal	jaw	1	0.001	.569	.452
j. Jaw vs.	slopes	residual	117	0.194		
Log of	equal	jaw x sex	1	0.001	.669	.415
Front tooth						
Width	means	residual	118	0.195		
	equal	jaw	1	0.004	2.664	.107
k. Jaw vs.	slopes	residual	117	0.187		
Log of	equal	jaw x sex	1	0.001	.353	.553
Middle tooth						
Width	means	residual	118	0.188		
	equal	jaw	1	0.000	.020	.889
l. Jaw vs.	slopes	residual	117	0.196		
Log of	equal	jaw x sex	1	0.008	4.626	.034
Back tooth						
Width	means	residual	118	0.204		
	equal	jaw	1	0.018	10.264	.002

FIGURE 4. SNOUT-VENT LENGTH VS. JAW LENGTH

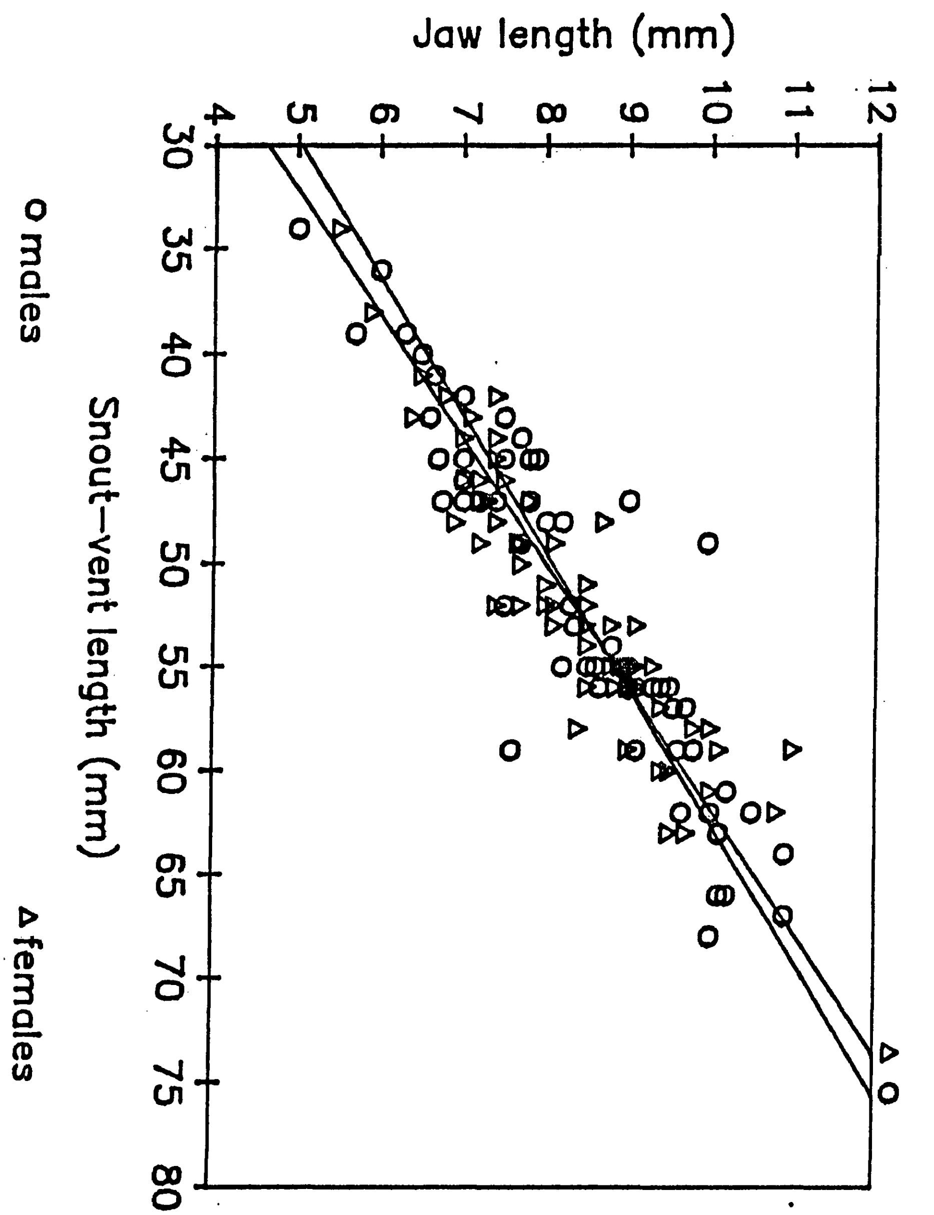


FIGURE 5. JAW LENGTH VS. NUMBER OF TEETH

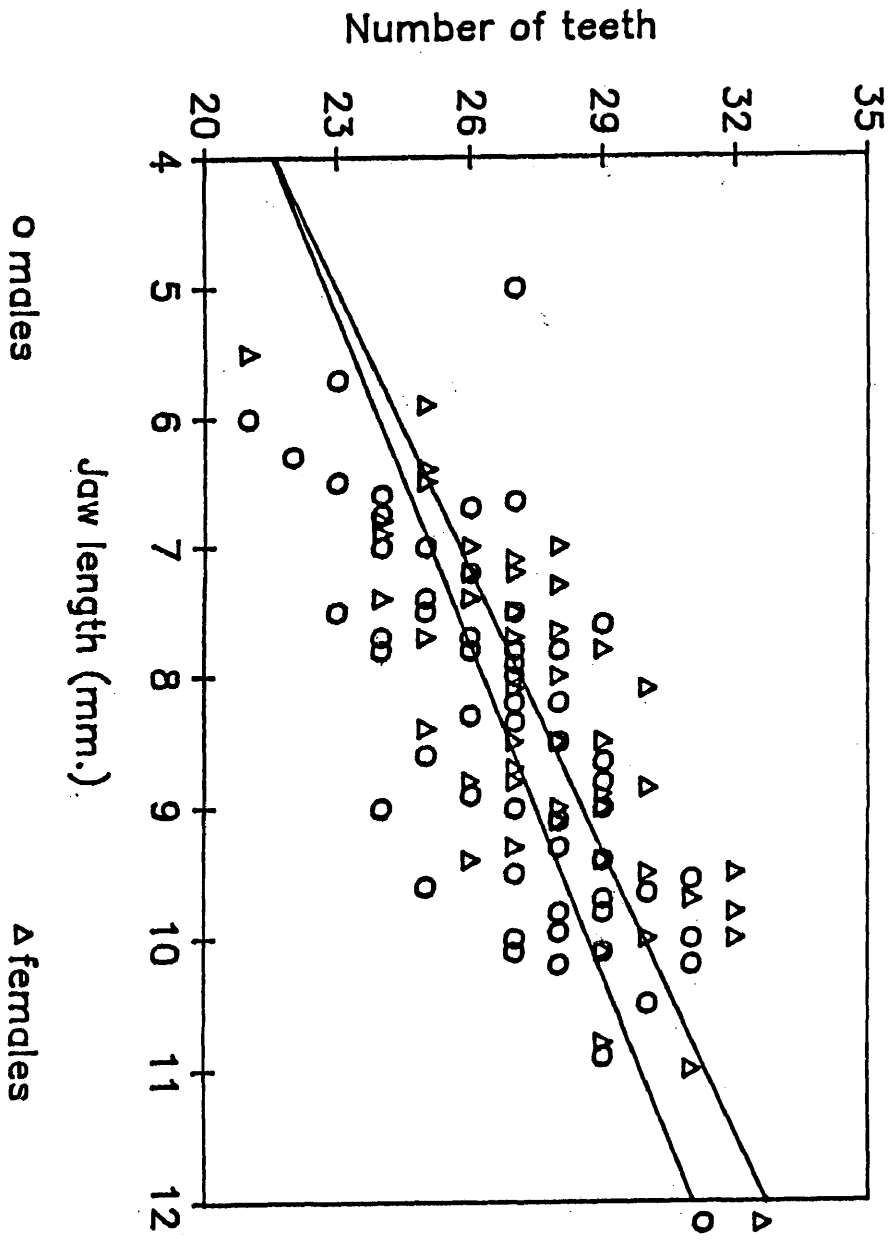


FIGURE 6. JAW LENGTH VS. LOG OF NUMBER OF 3-CUSP TEETH

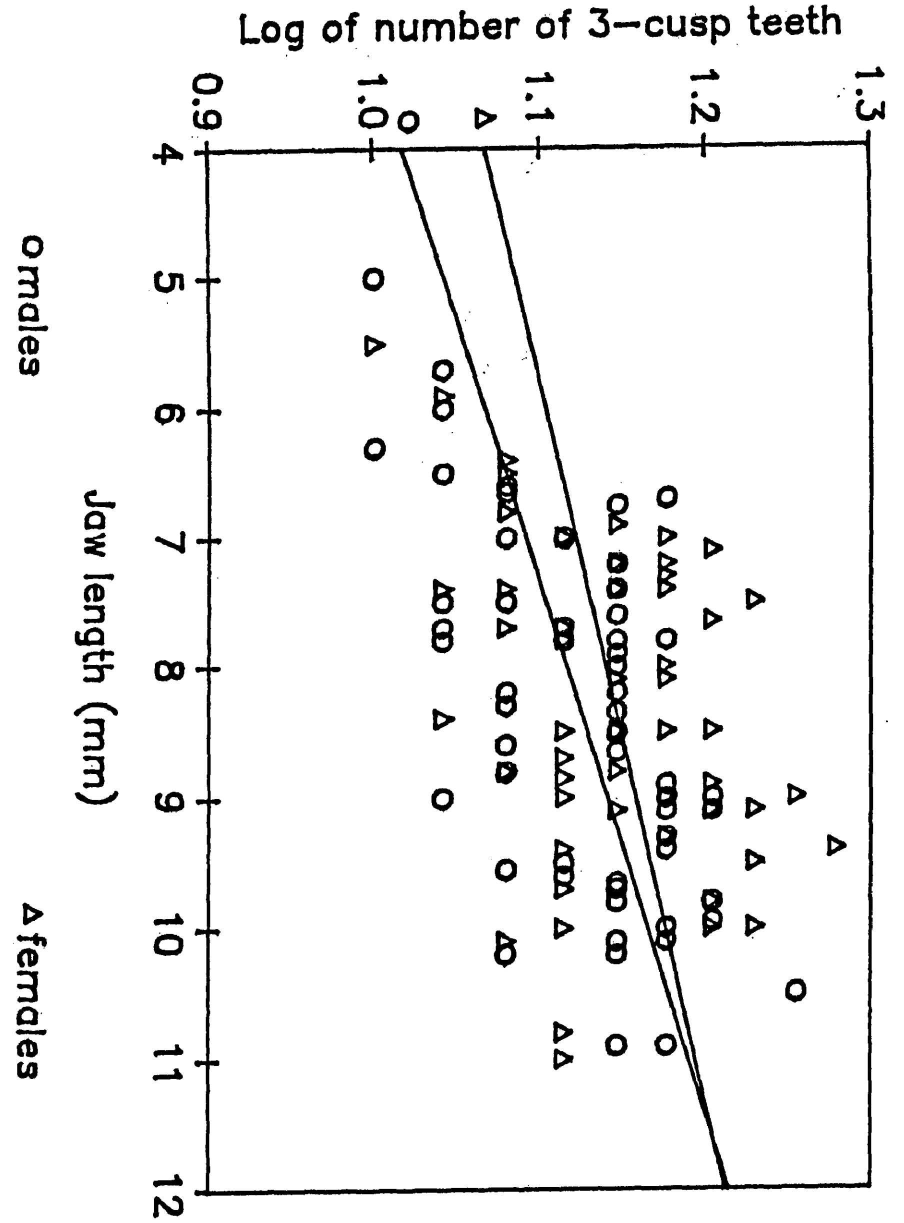


FIGURE 7. JAW LENGTH VS. JAW RIDGE HEIGHT

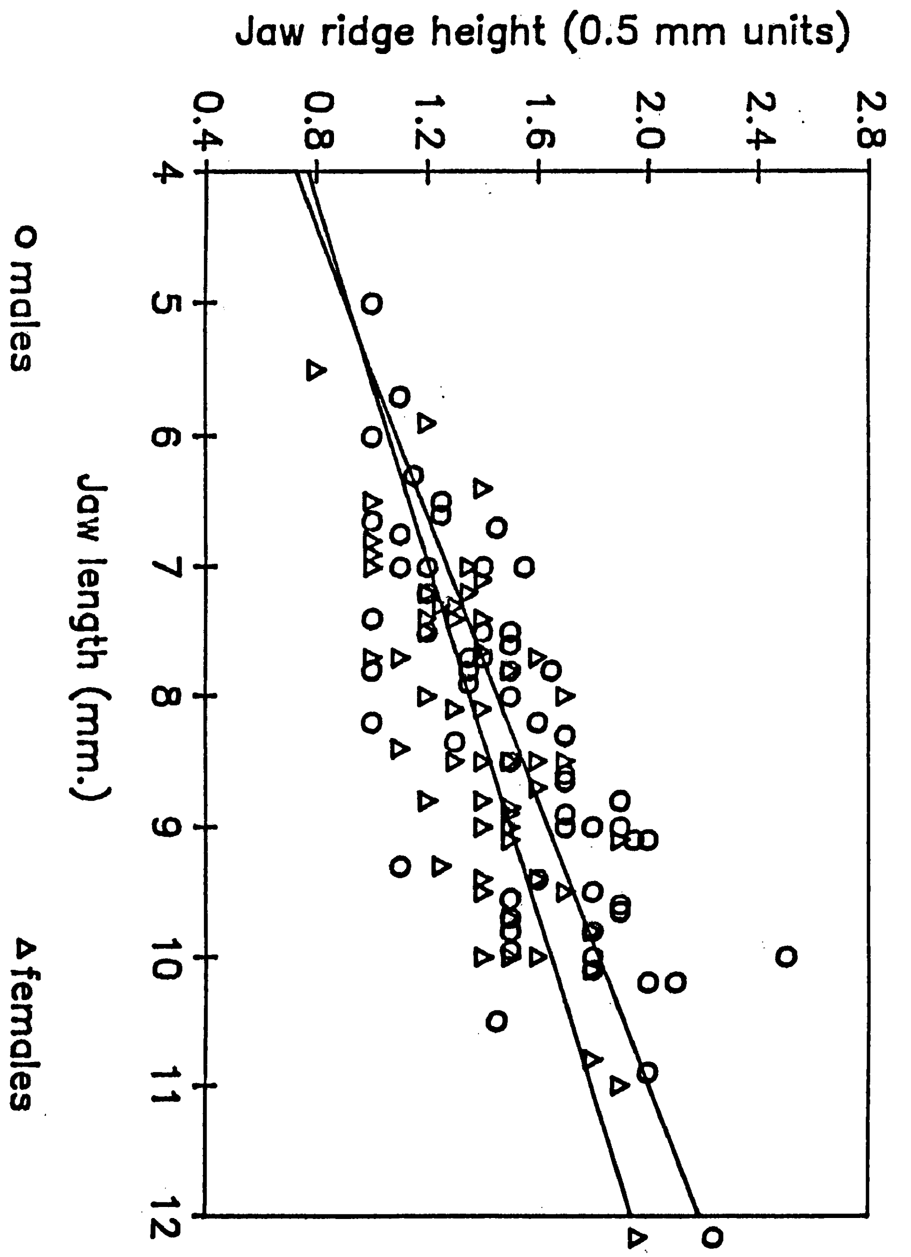


FIGURE 8. JAW LENGTH VS. LOG OF AVERAGE TOOTH HEIGHT

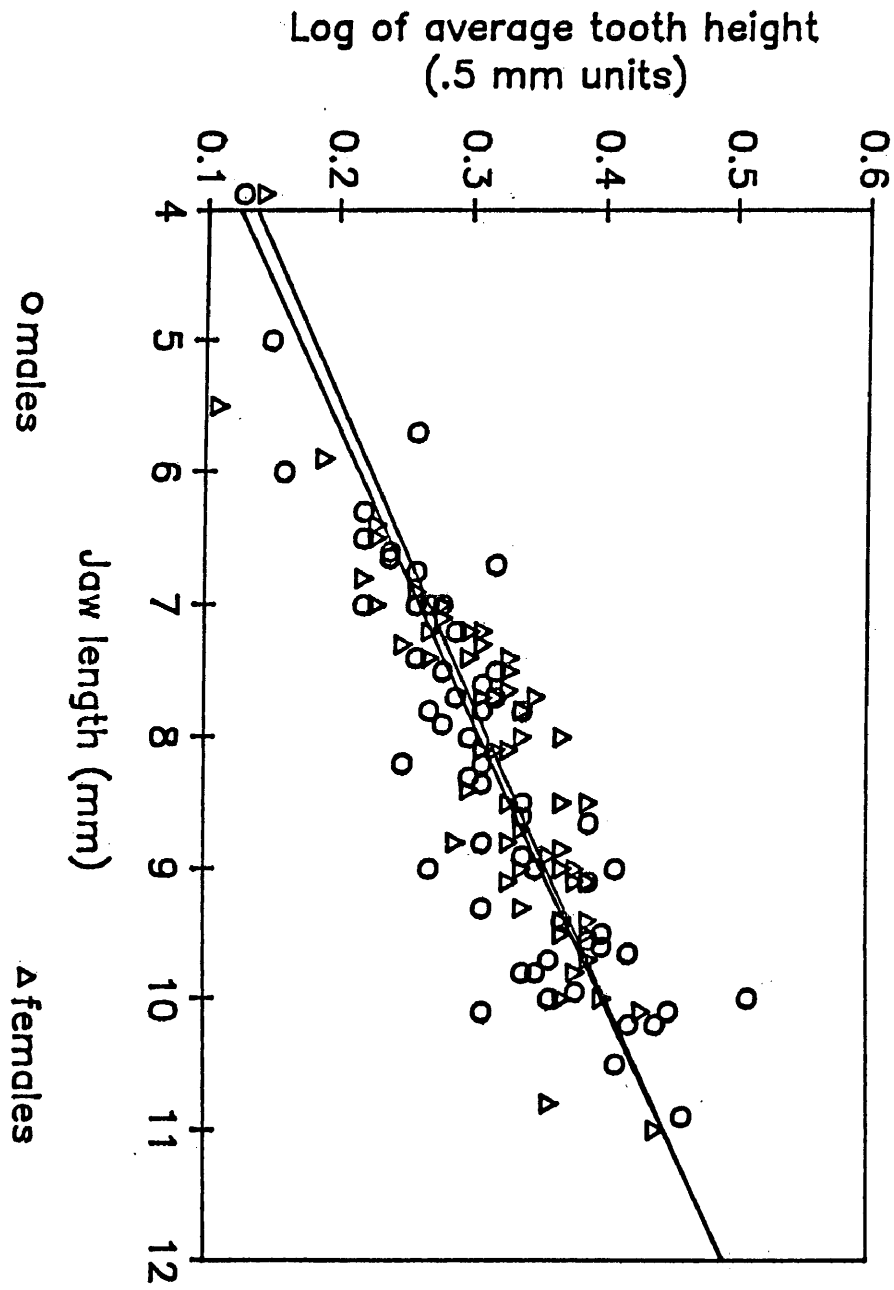


FIGURE 9. JAW LENGTH VS. LOG OF AVERAGE TOOTH WIDTH

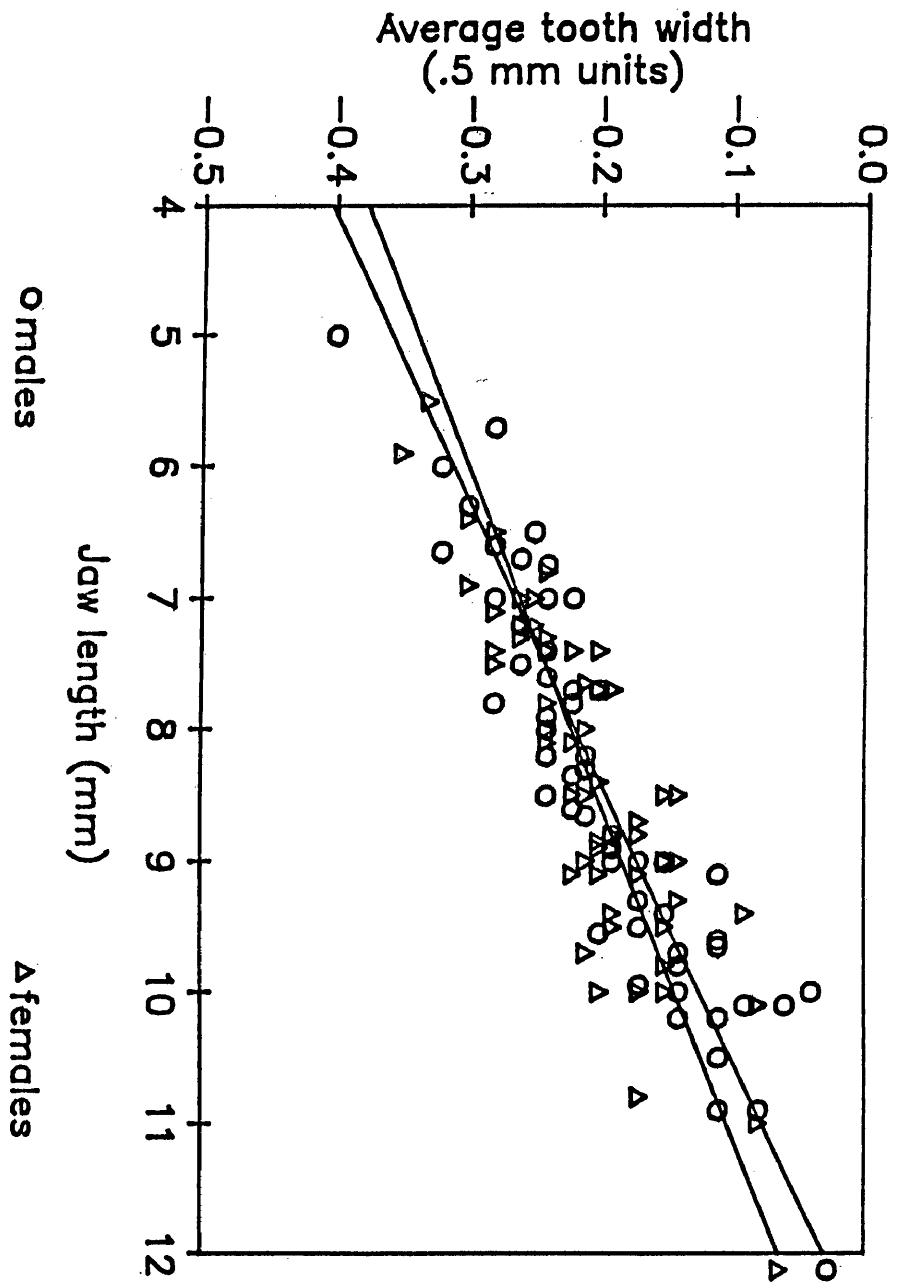


FIGURE 10. JAW LENGTH VS. LOG OF HEIGHT OF FRONT 3-CUSP TOOTH

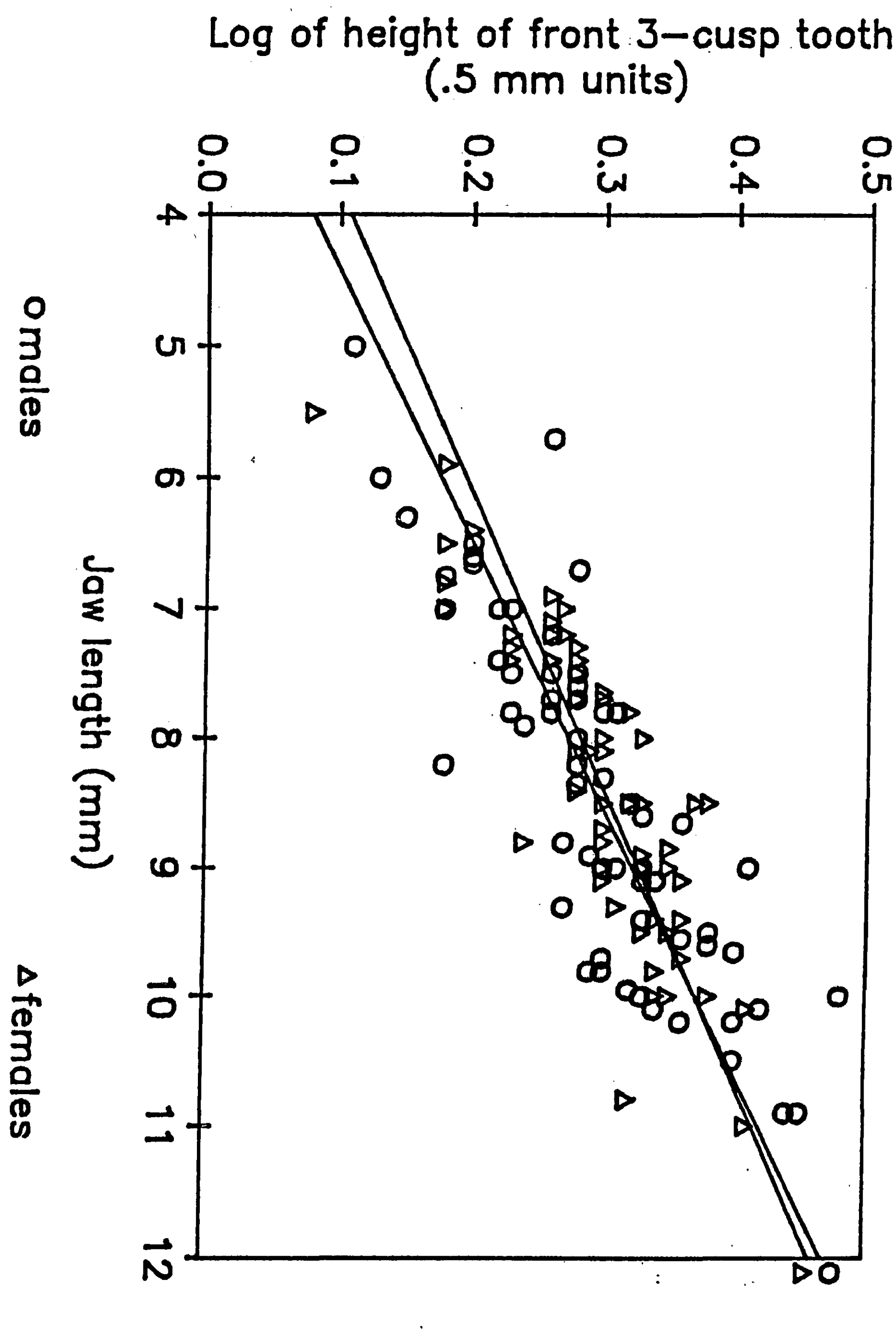


FIGURE 11. JAW LENGTH VS. LOG OF HEIGHT OF MIDDLE 3-CUSP TOOTH

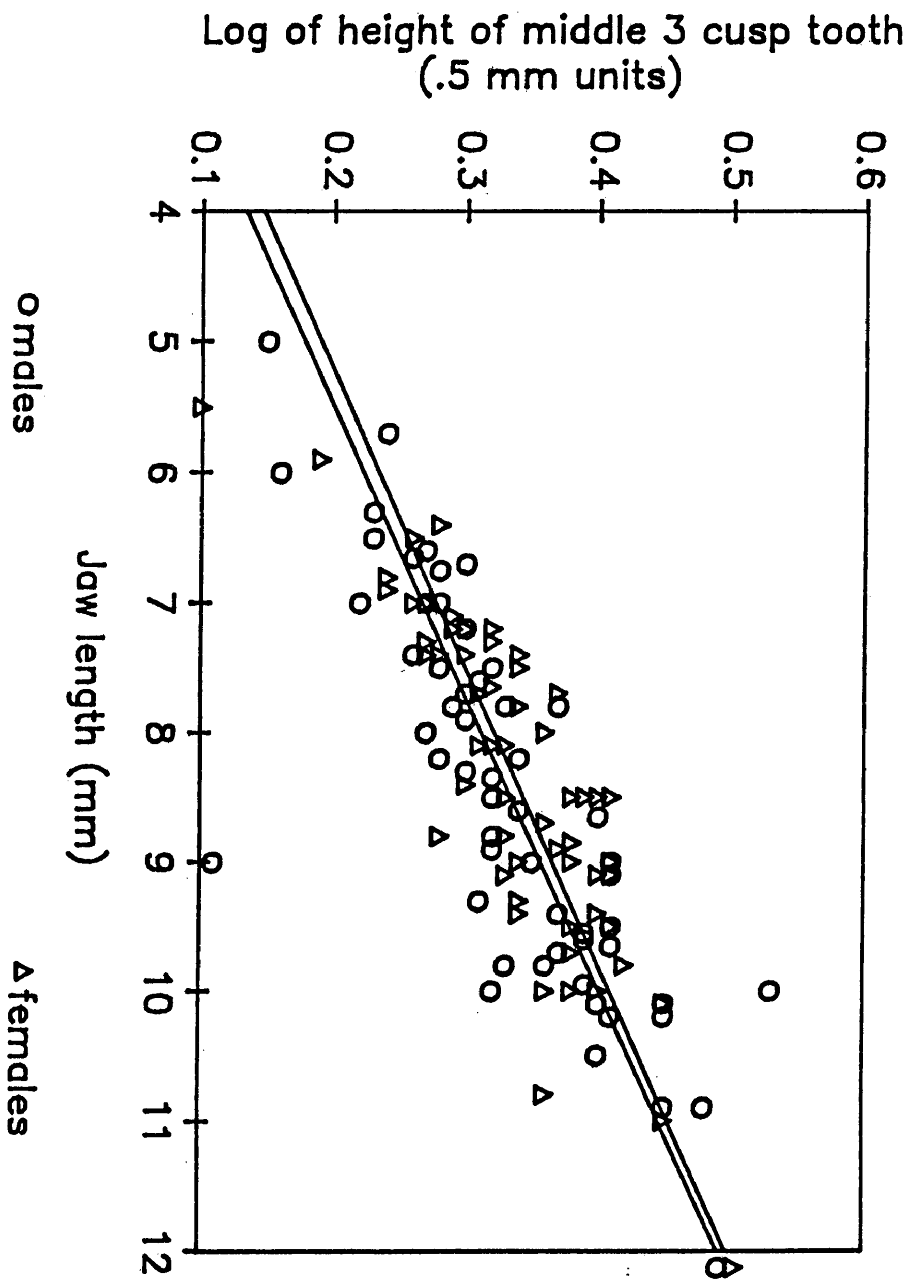


FIGURE 12. JAW LENGTH VS. LOG OF HEIGHT OF BACK 3-CUSP TOOTH

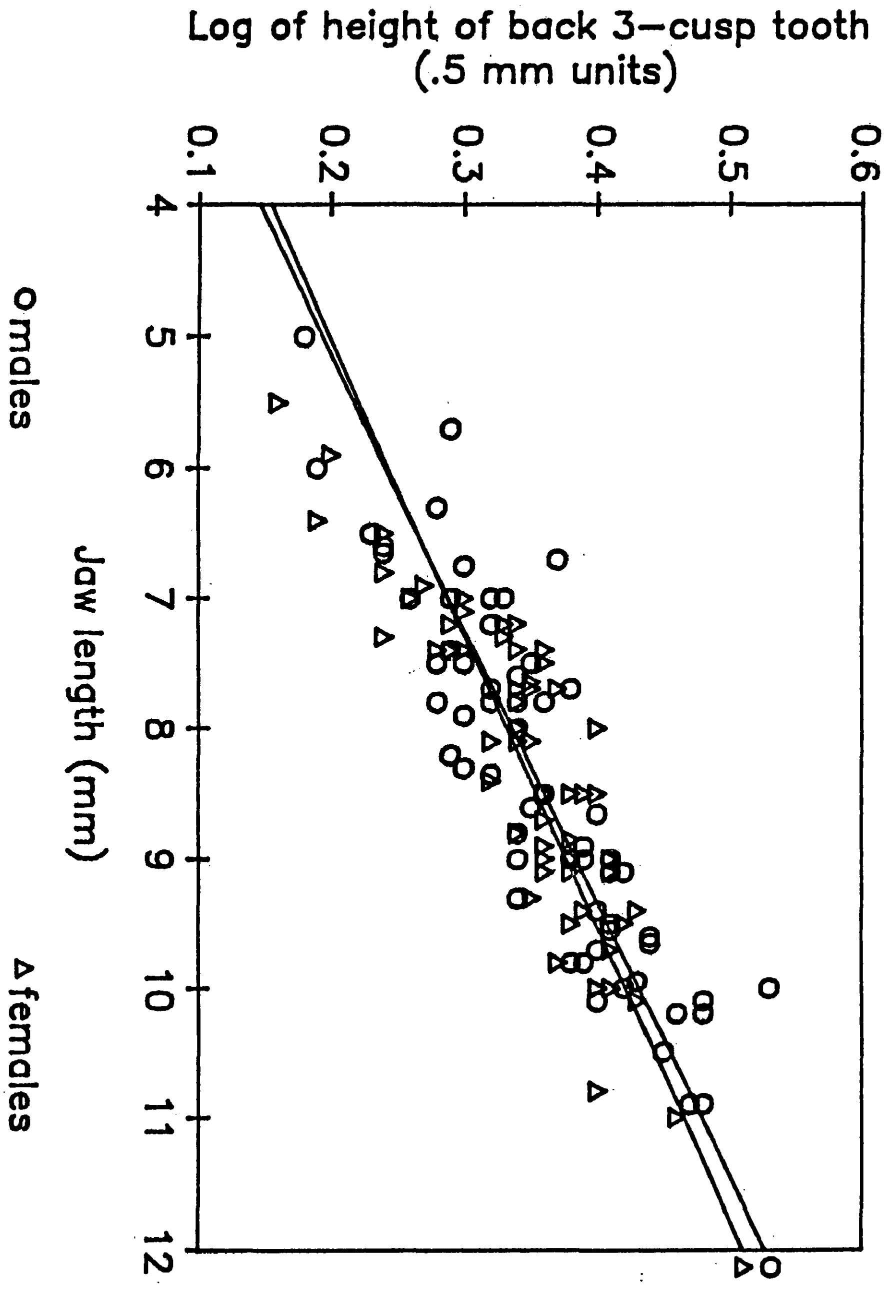


FIGURE 13. JAW LENGTH VS. LOG OF WIDTH OF FRONT 3-CUSP TOOTH

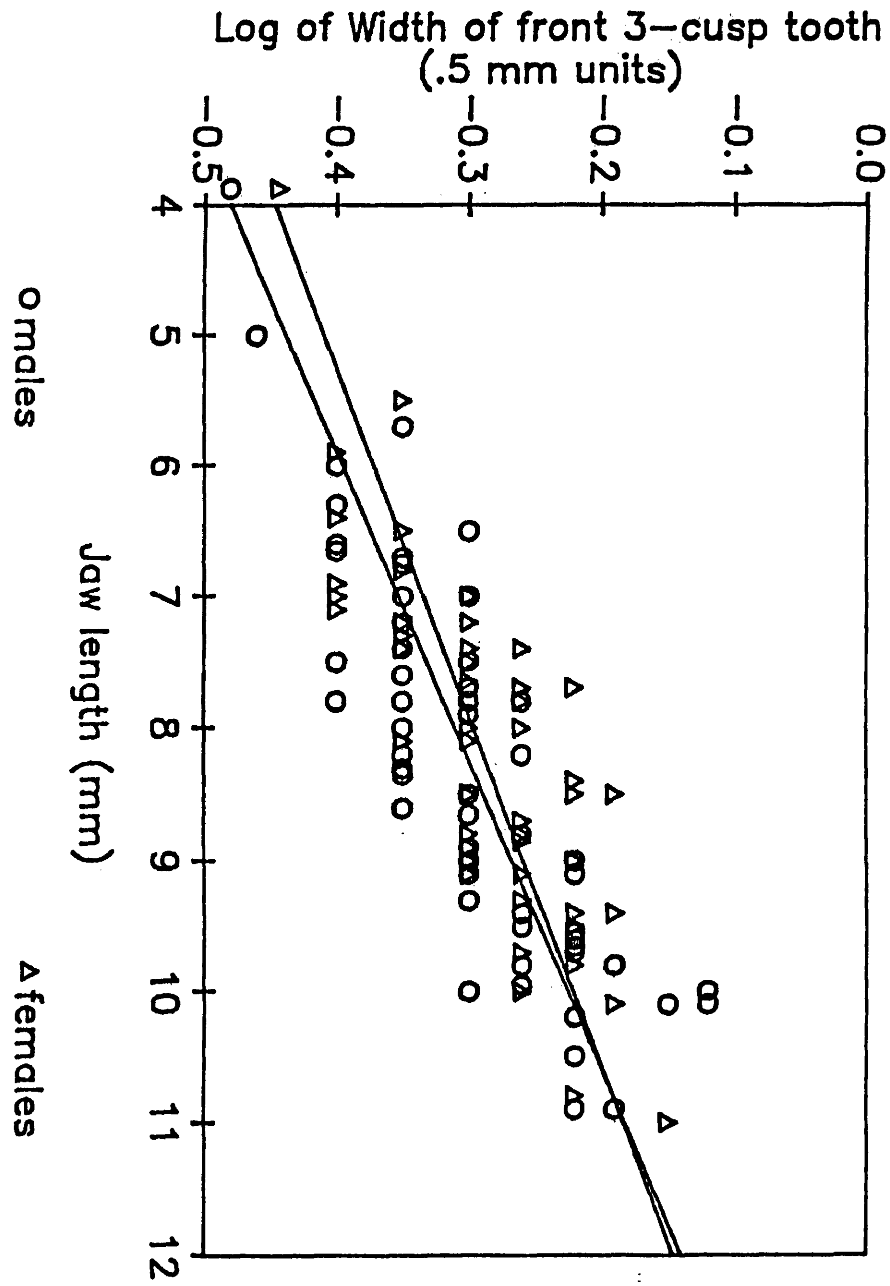


FIGURE 14. JAW LENGTH VS. LOG OF WIDTH OF MIDDLE 3-CUSP TOOTH

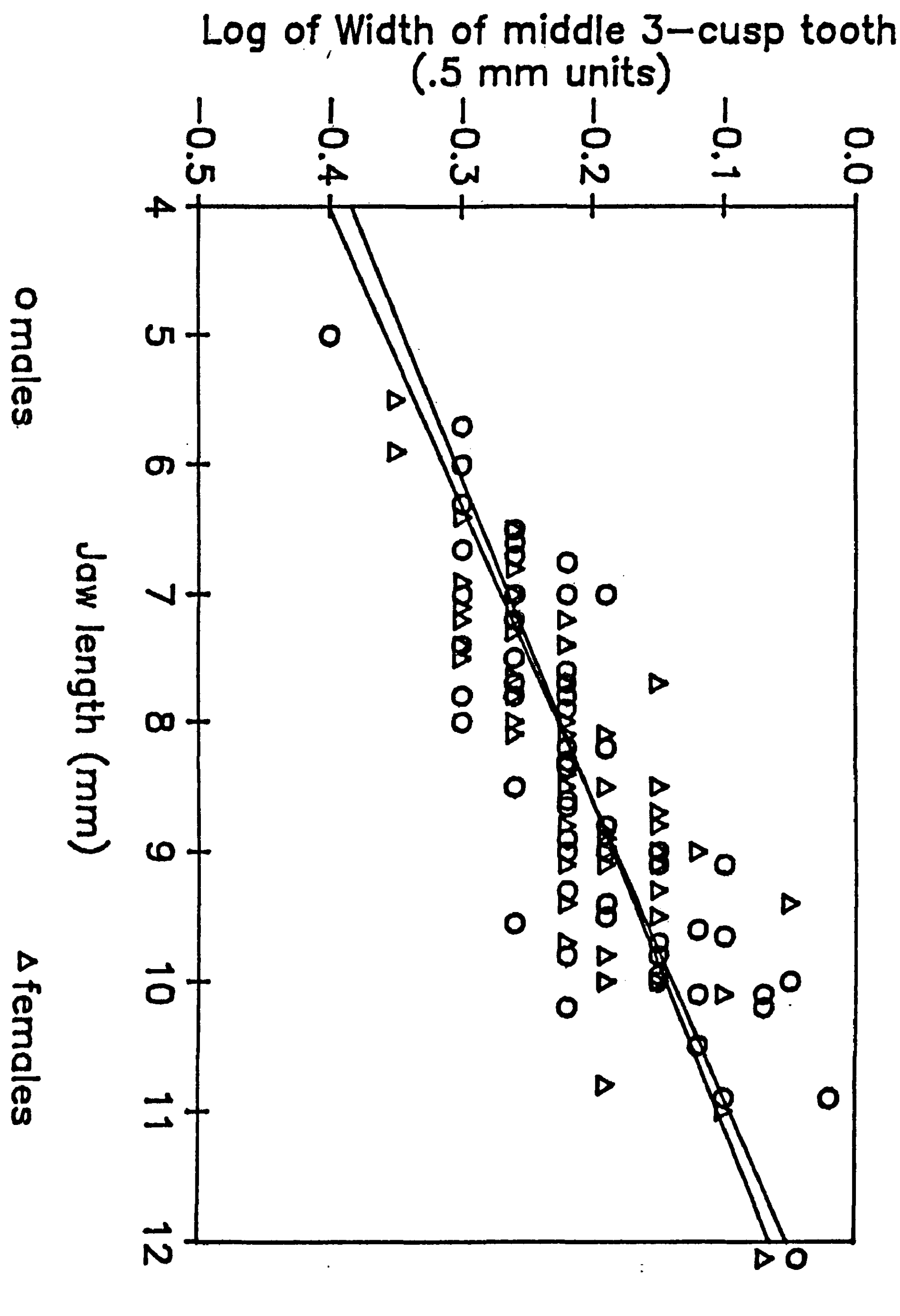
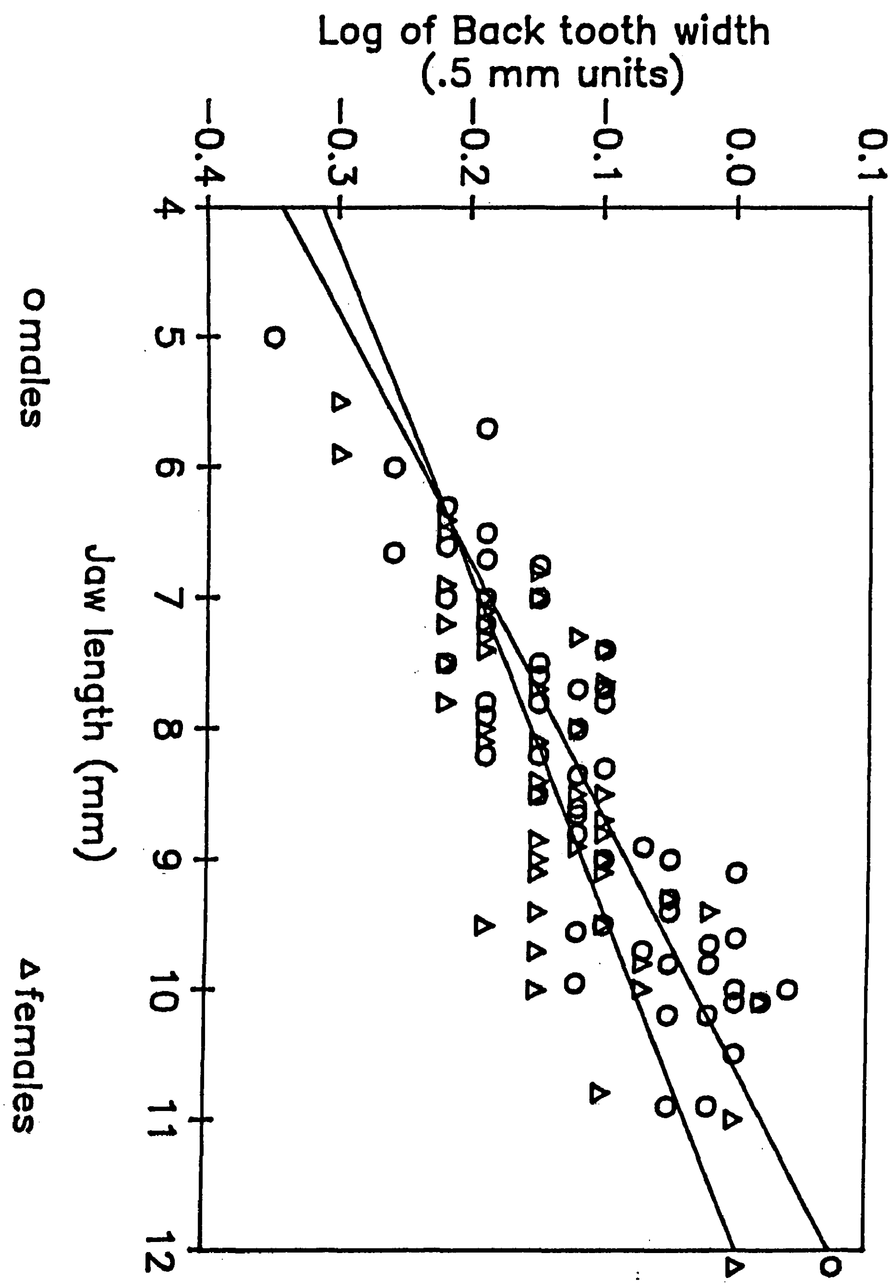


FIGURE 15. JAW LENGTH VS. LOG OF WIDTH OF BACK 3-CUSP TOOTH



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