INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313 761-4700 800 521-0600

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Order Number 9207090

Morphometric variability of the precaudal vertebrae of *Thamnophis sirtalis sirtalis* (Serpentes:Colubridae), and implications for interpretation of the fossil record

LaDuke, Thomas C., Ph.D.

City University of New York, 1991

Copyright ©1991 by LaDuke, Thomas C. All rights reserved.

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MORPHOMETRIC VARIABILITY OF THE PRECAUDAL VERTEBRAE OF THAMNOPHIS SIRTALIS SIRTALIS (SERPENTES: COLUBRIDAE), AND IMPLICATIONS FOR INTERPRETATION OF THE FOSSIL RECORD.

by

THOMAS C. LADUKE

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1991

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

© 1991

THOMAS C. LADUKE

All Rights Reserved

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

August 23, 1991
date

Chairman of Examining Committee
Prof. Max Hecht, Queens College

SEPT. 16, 1991
date

Executive Officer

Prof. Leslie Marcus, Queens College

Prof. John Wahlert, Baruch College

Prof. David Steadman, New York State Museum

Prof. Samuel McDowell, Rutgers University

Dr. Charles J. Cole, A.M.N.H.

Supervisory Committee

The City University of New York

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ABSTRACT

MORPHOMETRIC VARIABILITY OF THE PRECAUDAL VERTEBRAE OF THAMNOPHIS SIRTALIS SIRTALIS (SERPENTES: COLUBRIDAE), AND IMPLICATIONS FOR INTERPRETATION OF THE FOSSIL RECORD.

by

Thomas C. LaDuke

Adviser: Professor Max K. Hecht

Snake vertebrae are biologically interesting structures because of the important roles they play in the functional morphology, axial development, and paleontology of snakes. Yet, morphometric variability of these structures, both among and within taxa, is very poorly understood. This study lays a foundation for future comparative work by addressing several points about variability of shape of precaudal vertebrae of Thamnophis s. sirtalis: 1) Empirical studies of three different modes of comparison of vertebrae among snakes with different numbers of precaudal vertebrae demonstrate that axial positional identity is determined by the percentage position of a vertebra along the column [vertebra number/total vertebral count]. Sequential positions determined with respect to the cranial or caudal ends of the precaudal column are not comparable among columns with different precaudal counts. 2) Similar sized snakes with differing vertebral counts must pack their vertebrae into the same space. Graphic comparisons suggest that this is accomplished by a relative shortening of vertebrae in snakes with higher vertebral counts. An alternative model in which relative vertebral

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

length is unchanged, and snakes with higher vertebral counts are longer, is rejected. 3) Examination of vertebral growth trends in these snakes, suggests that growth in width and height dimensions is negatively allometric, but does not follow a geometrically simple trajectory. A change in the nature of vertebral growth appears to affect females as they grow beyond the size of reproductive maturity, such that length dimensions grow at a constant rate, relative to body length, but width and height dimensions grow at a lower rate above the size of reproductive maturity. 4) Sexual dimorphism in the vertebrae of similar sized Thamnophis s. sirtalis manifests itself in the relative size of the cotyle-condyle articular joint, which is larger in females.

It is concluded that vertebrae vary in a tightly controlled, regimented fashion that should be highly tractable, allowing shape to be modeled quantitatively. In some cases, precise statements as to the age and sex of fossil specimens should be possible. Although interspecific variability has not been addressed, it is hoped that similar precision will be available for discrimination of taxa.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Acknowledgements

It is with pleasure that I acknowledge the many people who have contributed to the completion of this dissertation. Many thanks are due to the following individuals and institutions.

Max K. Hecht, served as my advisor and mentor during the course of this study. A continual source of inspiration, he always challenged me to look at things from alternative perspectives. He also provided essential laboratory space and supplies. Leslie F. Marcus provided statistical counsel, thought provoking insights, encouragement and moral support. Samuel B. McDowell and Herndon Dowling have contributed ideas and information through various discussions.

Financial support was provided by the Graduate School of the City University of New York. A generous three-year fellowship was provided by Kenneth Smilen and the City University of New York. Queens College provided a teaching assistanceship, supplies, and work space.

Figure 8 was drawn by John Winsch. Peter Warney contributed specimens and information on the locations of potential study sites. Robert Cook assisted in obtaining field permits for working at the Floyd Bennett Field study site. Peter Warney, Robert Cook, Elaine Brown, Fred Petillo, Karen Karavanic, Patricia MacCabe-LaDuke, and Daniel LaDuke provided assistance in the field on one or more occassions. Barbara Kingsbury and the Ruffner family of Pike Co. PA provided access to their property for field work.

Finally, and above all, I am grateful to my wife, Patricia, to whom this work is dedicated, for her unfailing patience, indulgence, and support during the course of this project.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CONTENTS

Title page.....i
Copyright page.....ii
Approval page.....iii
Abstract.....iv
Acknowledgements.....vi
Table of Contents.....vii
List of figures.....ix
List of tables.....x

Chapter 1. INTRODUCTION.....1
1.A. Relationships of Thamnophis sirtalis.....2
1.B. Vertebral Shape.....5
1.C. Historical Overview of Analytical Methods Applied to Snake Vertebrae.....10
1.C.a. Fossil Snakes.....10
1.C.b. Recent Snakes.....17
1.D. Anatomy of the Axial Skeleton of Snakes.....23
1.D.a. Vertebral Anatomy.....23
1.D.b. Regions of the Vertebral Column.....26
1.D.c. Vertebral Number & Dermo-vertebral correlation...28

Chapter 2. INTRACOLUMNAR SIZE TRENDS.....31
2.A. Size Trends: Methods.....31
2.A.a. Skeletal Preparation.....31
2.A.b. Measurements.....33
2.A.c. Measurement Error.....35
2.A.d. Intracolumnar Patterns of Variation in Size.....35
2.A.e. Intracolumnar Rates of Change in size.....37
2.B. Size Trends: Results.....38
2.B.a. Measurement Error.....38
2.B.b. Intracolumnar Patterns of Variable Size.....39
2.B.c. Intracolumnar Rates of Change in Variable Size...41
2.C. Size Trends: Interpretation.....44

Chapter 3. Homology Analysis.....45
3.A. Homology Analysis: Methods.....46
3.A.a. Modes of Comparison.....46
3.A.b. Variance Comparisons.....49
3.A.c. Graphic Comparisons.....51
3.B. Homology Analysis: Results.....54
3.B.a. Variance Comparisons.....54
3.B.b. Graphic comparisons.....55
3.C. Homology Analysis: Interpretation.....56

Chapter 4. Growth.....58
4.A. Growth: Introduction.....58
4.B. Empirical Studies of Growth in Thamnophis.....61
4.C. Body Growth: Methods.....64
4.D. Snake Catching Techniques.....67
4.E. Description of Study Sites.....71
4.E.a. Ten Mile River.....71
4.E.b. Balsam Lake Mountain.....74

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

4.E.c. Floyd Bennett Field.....76
4.E.d. Barberry Knowe Kennels.....77
4.E.e. Miscellaneous Other Sites.....78
4.F. Body Growth: Results.....79
4.F.a. Size Differentiation among Sites.....80
4.F.b. Cohort Analysis of Growth Rates.....81
4.F.c. Recapture Analysis of Growth Rates.....84
4.G. Body Growth: Interpretation.....86
4.H. Vertebral Growth.....87
4.H.a. Vertebral Growth: Methods.....87
4.H.b. Vertebral Growth: Results.....88
4.H.c. Vertebral Growth: Interpretation.....90

Chapter 5. Sexual Dimorphism.....93
5.A. Sexual Dimorphism: Introduction.....93
5.B. Sexual Dimorphism: Methods.....93
5.C. Sexual Dimorphism: Results.....94
5.D. Sexual Dimorphism: Interpretation.....95

Chapter 6. Conclusion.....97
6.A. Summary of Results.....97
6.B. Implications for Fossil Identification.....99
6.C. Future Research.....103
Figures.....106
Tables.....167
Appendix I.....183
Appendix II.....184
Appendix III.....225
Bibliography.....226

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF FIGURES

1 Systematic arrangement of Dowling, 1988.....106
2 Systematic arrangement of McDowell, 1987.....107
3 Systematic arrangement of Reippel, 1988.....108
4 Systematic arrangement of Rage, 1987.....109
5 Alternative arrangements of Natricinae.....110
6 Diagram of factors influencing bone shape.....111
7 Shape factors examined in this study.....111
8 Vertebral anatomy.....112
9 Vertebral measurements.....113
10-13 Growth Series 114
14-22 Plots of size differences between neighboring vertebrae.....116
23 Different approaches to vertebral packing.....121
24 Demonstrations of counting modes.....122
25 Expected effects of positional variation on measurements in percentage mode.....123
26 Expected forward mode variation.....124
27 Expected reverse mode variation.....125
28 Zone in forward mode comparable to a position in percent mode.....126
29 Zone in percentage mode comparable to a forward mode position.....126
30 Expected trends for plots of variable*NOV.....127
31-35 Variance Plots for three comparative modes.....128
36-50 Examples of three dimensional plots of Variable*SVL *NOV, using CNT.....133
51 ANOVA of SVL primary study sites.....136
52-85 SVL histograms for major study sites, by month....137
86-88 Mean monthly growth rates, based on cohort data...143
89-90 Growth rate*mean size, based on recaptures.....144
91-110 Plots of Vertebral measurements vs. SVL.....145
111 Plot PC2*PC1, sexual dimorphism study.....165
112 Plot PC3*PC1, sexual dimorphism study.....166

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF TABLES

1 Frequency distribution of character size differences among neighboring vertebrae.....167
2 Average differences among ten consecutive vertebrae for five regions.....168
3 Vertebral positions (forward & percentage modes) measured for snakes with different vertebral numbers.....168
4 Specimens used in mode variance study.....170
5 Significance and direction of slope for trend plots..171
6 Head scutelation data.....172
7 Body scutelation data.....174
8 Summary of size differences among sites.....175
9 monthly mean cohort size.....176
10 Recapture results.....177
11 Estimated sizes at yearly intervals.....178
12 Eigenvalues and first two eigenvectors from principle components analysis of female growth data.....178
13 Eigenvalues and first two eigenvectors from principle components analysis of male growth data.....179
14 Data on specimens used in sexual dimorphism analysis.180
15 Eigenvalues from principle components analysis of sexual dimorphism data.....181
16 Eigenvectors of principle components analysis of sexual dimorphism data.....181
17 Data on specimens used to test discriminant analysis.181

APPENDICES

I. Data and data summaries on repeated measurements of one specimen, used to estimate measurement error.....182
II. Plots of measurement variables against vertebral position.....183
III. Map of study localities mentioned in text.....225

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter 1. INTRODUCTION

The morphometric variability of snake vertebrae is poorly known, considering the biological importance of these structures. The fossil history of snakes is primarily a history of vertebrae, because these are the only structures that fossilize readily and preserve well (Holman, 1981). Furthermore, lacking limbs, vertebrae are the most important locomotory structures in the snake skeleton, providing flexible structural support, and anchorage for many important muscles (Gasc, 1976; Pregill, 1977). Finally, several studies suggest that some aspects of vertebral morphology reflect phylogeny and may prove useful in snake systematics (Johnson, 1955).

One vertebral character, the presence or absence of posterior hypapophyses, has figured prominently in morphological classifications at the family and subfamily levels for over a century (Cope, 1886; Bogert, 1940; Hoffstetter, 1946; Underwood, 1967; McDowell, 1987). Thus, it is surprising that no study has attempted to quantify the nature of vertebral variability in a single population, species, or genus. Nor has any attention been paid to the effects of environmental or phenotypic variation on vertebral shape. One author laments: "Surprisingly, we still lack an adequate survey of vertebral morphology and variation for a single snake taxon (of either a lower or a higher category). This precludes a rigorous evaluation of the value of vertebral characters in reconstructing phylogenetic relationships among

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

snakes." (Cadle, 1987, p. 83). The present paper summarizes previous research on snake vertebral morphology, and provides data on vertebral variation in a series of populations of a single subspecies, Thamnophis sirtalis, the Eastern Garter Snake.

1.A. Relationships of Thamnophis sirtalis

Most recent studies on the classification of snakes above the genus level agree that the Colubridae, the family to which Thamnophis belongs, are among the most phylogenetically derived snakes (McDowell, 1987; Rage, 1987; Cadle, 1988; Dowling, 1988). Figures 1 - 4 show recent alternative views of snake systematics with the position of Thamnophis indicated by an asterisk. These contrast with the more classic notions of Bogert (1943), Romer (1966), and Smith et al., (1977), that colubrids comprise a basal, paraphyletic lineage from which viperids and elapids are derived.

Although most authors concur that snakes are directly derived from lizards, exactly which lizard taxon is the sister group of snakes is a topic of continuing controversy. Allegations range from the Platynota, including the Dolichosauria, an extinct group of aquatic varanoids (Nopcsa, 1923), and the bizarre Lanthanotus borneensis, the Bornean earless monitor (McDowell and Bogert, 1954); to the amphisbaenians (Rage, 1982), a fossorial group of squamates that are sometimes considered an infraorder of lizards (Camp, 1923), sometimes a separate suborder of the squamata (Rage,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1982). Some authors have even suggested that the Scincomorpha (Senn and Northcutt, 1973), which includes skinks, teiids, and lacertids, among others, may be the closest outgroup to the snakes. There has been little agreement among researchers, past or present, on the details of phylogenetic relationships within the order (or suborder) Serpentes or even within the Squamata. None of the recent arrangements presented in Figures 1-4 is entirely satisfactory. Since the precise arrangement of the higher level taxa of snakes has little impact on the present study, I have chosen not to adopt any of them as a working hypothesis. However, if the cladogram of Reippel (1988; Figure 3) were modified by removing the Acrochordoidea, and placing it in a more basal position, or even in incertae sedis, it would be the most satisfying, primarily because of its omission of details. Clearly, further work on higher snake systematics is needed to provide more universally convincing evidence of relationships.

Thamnophis belongs to the Natricinae, a well defined and nearly cosmopolitan subfamily (a family of Underwood, 1967; and Dowling, 1988) of the Colubridae, usually characterized by a combination of hemipenial characters and the presence of hypapophyses on all precaudal vertebrae (McDowell, 1987). Various lines of evidence have shown that all North American species of the Natricinae are more closely related to one another than they are to Old World natricines. They have therefore been accorded their own tribe, the Thamnophini (Rossman and Eberle, 1977). Figure 5 shows alterrative views

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the classification of modern natricine snakes.

The arrangement of Rossman and Eberle (1977) has become well established and is supported by a subsequent study (Chiasson and Lowe, 1989). The arrangement by Lawson (1987), suggesting that Thamnophis should be reduced to a subgenus of Nerodia, is not widely accepted, and is based entirely on a single character system, electrophoretic protein variability. Furthermore, only a single species of the genus Thamnophis was included in the analysis. I follow the arrangement of Rossman and Eberle (1977) because it is well corroborated by several lines of evidence, and because one phylogenetic arrangement of Lawson (1987: Figure 2) is compatible with it, provided Nerodia valida is transferred to Thamnophis, an arrangement suggested by studies on microdermatoglyphics (=scale surface microstructure), (Chiasson and Lowe, 1989).

Thamnophis sirtalis is a member of a diverse genus that includes 30 recognized species. Most of these inhabit moist or mesic habitat of varying types, and feed primarily on amphibians, fish, and annelids. Diets within the genus are rather variable with some species specializing on one or two prey types, while others are very catholic consumers.

Thamnophis sirtalis is among the most abundant of snake species in North America. Whether this was true before the settlement of the country by Europeans is not known, but it certainly thrives in habitats disturbed by humans (pers. obs). It also has one of the largest geographic ranges of any species of North American snake, stretching from the southern

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

edge of the Northwest Territories in the vicinity of Fort Smith, and central Quebec, south as far as the tip of Florida, and northern Mexico; and from the Atlantic Coast to the Pacific Coast (Fitch, 1980: range map). Within this range it is absent only from arid habitats. There are twelve recognized subspecies of T. sirtalis, but only three of these are geographically widespread: T. s. sirtalis in the East, T. s. parietalis in the Great Plains, and T. s. fitchi in the Rocky Mountains and West (Fitch, 1980).

1.B. Vertebral Shape

Figure 6 is a path diagram illustrating all of the known factors that could affect vertebral shape, either directly or indirectly. Proximate (direct effect) factors are closer to the parameter of interest (shape) in the diagram than are distal (ultimate) or general factors. As discussed below, the number of vertebrae in the vertebral column (NOV) and the position of the vertebra within the vertebral column are directly related factors that influence vertebral shape. The former is a question of vertebral packing, whereas the latter is a result of functional differences in different regions of the column. NOV, in turn, is directly affected by genetic components (Arnold, 1988), as well as sex and developmental temperature (Fox, 1948; Osgood, 1978), all of which modulate the process of vertebral column formation in development.

Body size, a function of age, genetics, and the stochastic factors that determine feeding and metabolic

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

opportunity, has obvious implications for shape. The vertebrae of immature snakes must be so constructed that they are functional at their current, smaller size, and are capable of growing into a functional adult form. Adult vertebrae must be able to withstand proportionately greater stresses than those of juveniles, and are expected to scale approximately in proportion to body weight (which is proportional to the cube of a linear dimension in an isometric system), because they are the only skeletal structures directly influenced by the muscular forces that act to propel the body (Prange and Christman, 1975). In rattlesnakes, vertebral width scales as length to the 1.3 power, while in tetrapod limb elements, width scales as length to the 1.5 power as predicted for the scaling allometry of weight bearing structures (Prange and Christman, 1975). Prange and Christman (1975) suggest an analogy between the compressive forces exerted by longitudinal muscles on snake vertebrae, and the stresses of weight on tetrapod limbs.

Sex also has an effect on body size in most snakes. In Thamnophis, females grow larger than males, suggesting the possibility of allometry leading to differences in shape between the two sexes. The two sexes also produce different numbers of precaudal vertebrae. This will be shown to influence vertebral shape (below). Behavioral or ecological differences may also result in sexual dimorphism in vertebral shape. The effects of sex might be more appropriately diagrammed between the genetic and developmental programs,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

since all sexual effects indicated are mediated by development. However, it is placed more proximally in order to directly show its effects on size and NOV.

It has been shown experimentally that the shape of a bone depends, in part, on its interactions with attached muscles (Gans, 1974). Muscle-bone interactions are mediated by developmental processes initially, and in the postnatal animal, by muscle use and exercise (Gans, 1974). The latter are functions of behavior, and ultimately, of ecology. Finally, there are undoubtedly genetic factors that affect vertebral shape through development, sex, behavior, body size and vertebral number. Indeed, most genetic effects on morphology are probably determined only through the developmental process. Whether there can be direct genetic effects on morphology, e.g. via bone remodeling or some other non-developmental regulatory mechanism, is not known.

Other, less direct influences include the long term historical effects of selective retention of alleles, genes, and gene patterns, portrayed in the diagram as phylogeny. This could have been lumped into the "genetics" category, but division of genetics into proximal and ultimate causes is more explicit. Behavior certainly has a strong genetic component in snakes, but is also influenced by ecological context. Ecology, on the other hand, is heavily influenced by behavioral parameters including habitat choice and prey choice, etc. Behavior and ecology may be affected by learning, and social evolution. An example of a learning

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

effect on behavior in a snake would be the reinforcement of secretive behaviors by encounters with predators in exposed situations. An example of the effects of learning and social evolution on ecology in snakes is the apparent learning by some neonatal snakes of the location of den sites by trailing conspecifics at the appropriate time of year (Brown & MacLean, 1983; Costanzo, 1986).

The effects illustrated in the diagram are tentative; some are known to occur, others may not exist or may be trivial. The magnitudes of the path coefficients for all of these interactions have yet to be determined. Other arrangements of the factors that affect shape could be supported on the basis of current theory. Those illustrated in Fig. 6 represent the factors that I find most intuitively satisfying.

Some of these effects will be examined in detail in the present study (Fig. 7). The others will require more involved experimental approaches and sophisticated experimental technology. The ultimate goal of this research program is to provide a data base and methodology for the discrimination of isolated snake vertebrae such as are often found in fossil deposits and raptor pellets. The results will also be applicable to questions of the functional morphology and systematics of snakes.

The study of variability of snake vertebrae is somewhat more complex than morphometric studies of other vertebrate skeletal elements. Most such studies involve considerations

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of geographic variation, sexual dimorphism, and individual (inter-individual) variability. Age class may also be of concern, particularly among ectotherms with indeterminate growth. Age class is usually not considered in studies of endotherms where growth normally stops abruptly with the onset of sexual maturity, and all normal adults are members of a single, more or less cohesive, size class (but, exceptions exist, including many rodents: see e.g. Voss et al., 1990). Snakes are among the vertebrates with indeterminate growth, notwithstanding Andrew's comment "there appears to be good evidence that individuals reach an asymptotic size after which growth is negligible" (1982, p.276). Most recapture studies (including this one) have documented growth in the largest individuals. Asymptotic change in growth rates would be difficult to distinguish from continuous, low growth rates in old adults. This question would probably be best addressed by studies of growth potential in captive animals. In either case, the span of sizes covered by mature snakes requires consideration of this variable in any morphometric study.

In addition to the above variables, snake vertebrae are subject to a considerable amount of intra-individual variation along the length of the vertebral column (LaDuke, 1991). There is a distinct pattern of size and shape change along the vertebral column that is presumably attributable to functional differences in the tasks performed by the various vertebral regions. Furthermore, there is intraspecific variation in the number of vertebrae present in a snake's vertebral column.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

This must contribute an additional component of variation, since snakes of the same size must pack different numbers of vertebrae into a unit of length. Thus, snake vertebrae offer a greater morphometric challenge than most other vertebrate structures because of the increased dimensionality of the sources of variability affecting their shape.

Another special problem in comparing vertebrae within a column is the correlation of characters among positions when samples of vertebrae are derived from a single collection of snakes. Special statistical techniques are required to handle these problems, such as repeated measures analysis. However, such techniques require large numbers of snakes.

1.C. Historical Overview of Analytical Methods Applied to Snake Vertebrae.

Following is a brief review of earlier approaches to the study of variability in snake vertebrae and a consideration of the factors that affect that variability. Most studies of snake vertebral shape have been associated with descriptions of fossil collections.

1.C.a. Fossil Snakes.

Early workers on fossil snakes primarily described the unusual and the colossal, with occasional reference to reputed ancestors of recent snakes. Only extinct taxa were deemed worthy of note. The rare complete or nearly complete skeleton also received attention. Techniques basically followed the principle that if a specimen was easily distinguished from

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

living snakes as a group, it deserved recognition as a species. Few attempts were made to compare fossils with comprehensive collections of representative living snakes (indeed, such osteological collections are rare even today). Paleontologists of the 19th century described forms such as Paleophis Owen 1841 and Pterosphenus Lucas 1899, giant marine snakes with unique vertebral processes (Gilmore, 1938). Simoleophis Sauvage 1880 is another unusual marine form with pachyostotic trunk vertebrae and ribs (Rage, 1984). Archaeophis Massalongo 1859 has an unusually large number of vertebrae, distinctive from those of modern forms, and a unique skull. Boavus Marsh 1871 and Paleopython Rochebrune 1880 are forms that were believed by their authors to be ancestral to modern boas and pythons, respectively. Coniophis Marsh 1892, Calamagras Cope 1873, and Ogmophis Cope 1884 are small forms, apparently related to living aniliids (Coniophis) and erycine boids (Gilmore, 1938), relictual remnants of once diverse and widespread groups. This descriptive trend continued with descriptions of giant representatives of the Aniliidae (Dinylisia Woodward 1901) and Boidae (Gigantophis Andrews 1901) near the turn of the century.

In 1938, the first comprehensive review of fossil snakes of a large geographic region appeared when C. W. Gilmore published "Fossil Snakes of North America." In addition to describing several new forms, particularly large primitive snakes of the family Boidae, Gilmore assigned many fossils from Pliocene and Pleistocene deposits to extant species on

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the basis of comparisons with a "...limited number of recent skeletons..." The practice of comparing fossil snakes of recent vintage with series of skeletons of extant species was uncommon prior to this.

Around the middle of this century, active collecting of large accumulations of disarticulated Neogene fossils by screening unconsolidated matrix began to produce large samples of small reptile remains including isolated snake vertebrae from many fossil localities in North America (Hibbard, 1949). These served as the basis of several inquiries into the evolutionary history of modern snake groups (Holman, 1958, 1959, 1962, 1963, 1964a, 1964b, 1965a, 1965b, 1966, 1967, 1968, 1970a, 1970b, 1971, 1972, 1973, 1975, 1976a, 1976b, 1977a, 1977b, 1977c, 1977d, 1977e, 1978; Brattstrom, 1967; Hill, 1971). The technique used to identify these fossils consisted primarily of a visual comparison of isolated vertebrae with disarticulated skeletons of living forms. Descriptions of the fossils were often limited, or were lacking altogether. The bases of identification were often subjective judgements of shape differences.

In 1963, W. Auffenberg revolutionized the study of fossil snakes in an article entitled "The Fossil Snakes of Florida." He introduced a quantitative approach by using ratios of measurements of vertebrae to distinguish among genera and species. This method, borrowed from R. G. Johnson (1955) who used it to differentiate vertebrae of higher taxonomic groups, was intended to allow the comparison of simple shape

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

differences while adjusting for size. The problem of size was considered to be a hinderance to simple comparative techniques because snakes grow continuously throughout life, unlike arthropods, birds, and most mammals, which usually reach characteristic adult sizes and then cease to grow. In these endothermic groups, size can often be used to discriminate among closely related species. Closely related snakes are not readily discriminated on the basis of size. The use of ratios as size-free discriminators has become standard in many studies of snake fossils, yet several investigators resist the use of ratios. The use of ratios depends, in part, on one's ability to determine position within the vertebral column in at least a vague way. Procedures for determining vertebral position have received little comment from most researchers, and only one author (Christman, 1975) has attempted to apply a quantitative method.

Christman (1975) studied vertebral variation in the rattlesnakes (Crotalus) to assess the status of an extinct species (Crotalus giganteus) whose primary distinction was its large size. It was found that the size of a rattlesnake can be estimated from a regression of midbody vertebral length against body size. In order to determine the region of the vertebral column that the fossil represented, a discriminant analysis was performed on samples of vertebrae representing five different precaudal regions of equal length. This analysis produced perfect discrimination of the five equal regions, and allowed Christman to assign the fossil vertebra

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to the middle of the column. Vertebrae from other regions could be multiplied by appropriate coefficients to estimate the size of their midtrunk vertebrae. It was also demonstrated that at least some ratios of linear measurements of rattlesnake vertebrae vary such that strongly curved lines are produced when the ratio is plotted against columnar position or total length. Christman is the only author to use quantitative techniques to synonymize a described fossil snake species with an extant species. He did this by showing that the fossils in question did not differ from vertebrae taken from very large individuals of the living species Crotalus adamanteus. Shape differences attributed to the fossil species were actually the result of allometric size increase. No attempt was made to discriminate among living taxa quantitatively.

M. J. Smith (1975), working with large Australian elapids, used frequency distributions of ratios of vertebral measurements to discriminate among taxa. She also used plots of various measurements against vertebral position using every fifth vertebra to determine the extent of intracolumnar variation within individuals. In both instances, quantitative data were used to support subjective conclusions that led her to allocate a homogeneous collection of fossil vertebrae to an extant genus (Pseudonaja) based on direct comparison with recent specimens.

P. Meylan (1982) used t-tests of univariate data and discriminant analysis (multivariate) to distinguish among

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

vertebrae of related, extant taxa, using ratios as raw data. He used the analyses to assign fossils to the extant taxa studied. He determined the appropriate taxa to consider in his analyses on the basis of visual comparison of with modern comparative specimens.

The use of ratios as data in statitistical analyses has been strongly criticised by Atchley et al. (1976). Meylan attempted to minimize the deleterious effects of ratio data by including only variables with approximately equal coefficients of variation. He states that test comparisons of ratio and non-ratio variables showed that the two performed comparably in two cases, while ratios provided marginally better discrimination in one case. In light of the theoretical and empirically demonstrated disadvantages associated with ratio data, Meylan's use of them on the basis of his own weakly favorable comparisons is highly questionable.

Other problems exist with the studies of Christman (1975), Smith (1975) and Meylan (1982). Relatively few specimens were used to represent each species studied. Sample size was increased by taking multiple vertebrae from each specimen. None of these authors considers sexual dimorphism. Although their results provide some useful discriminatory power, refined analyses with larger samples would probably increase that power.

A number of authors have used raw ratio data in the identification of fossil snake vertebrae, simply comparing ratios of the fossils with mean ratios and ranges of ratios

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

taken from extant forms (Van Devender and Mead, 1978; Mead et al., 1984; Van Devender et al., 1985; Fay, 1988; and Mead et al., 1989). Most of these authors allocate unknown vertebrae to some general group (e.g. "elongate colubrine" or "natricine with high neural spine") on the basis of gross morphology, and then proceed to compare ratios. Comparative data are often restricted to the geographical region of the fossil deposit. These authors generally state that they use mid-trunk vertebrae for their comparative material, but do not discuss intraspecific variability of ratios in any detail.

Some modern authors do not use any quantitative analysis for identification of fossil snakes (e.g. Brattstrom, 1967; Rogers, 1976; Hudson and Brattstrom, 1977; Holman, 1981; LaDuke, 1991). Presumably following the philosophy that the human eye and brain are capable of discerning much more subtle shape differences than are any instruments of measurement, these workers identify fossils by comparing them with skeletons of extant species, using whatever characters they can describe verbally to justify their dentifications. Unfortunately, many of the shape differences used are so subtle or complex, that adequate descriptions prove elusive. Furthermore, many characters must often be compared simultaneously, such that complete descriptions produce pages of dry, unpalatable text (LaDuke, 1991). This approach is not to be taken lightly, as many hours of comparative study of comprehensive skeletal collections of extant snakes are necessary to even begin comparing them to fossils. J. A.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Holman is perhaps the best known worker of this school. Holman has published many studies of fossil reptile faunas, including some that describe only the snakes present. Although Holman provides justifications for most of his taxonomic assignments, his terse descriptions belie the painstaking comparisons behind each identification, and the years of experience that have contributed to his expertise.

Perhaps the most thorough worker in this field is Z. Szyndlar (1984), who uses a combination of visual comparison and quantitative methods. Szyndlar differs from other workers in his careful documentation of intracolumnar, and ontogenetic differentiation in his comparative material. Unlike other workers, Szyndlar utilizes all parts of the skeleton in his determinations, and does not rely solely on mid-trunk vertebrae. He provides raw measurements as well as their ratios, and illustrations of both fossil and recent comparative material. He also plots intracolumnar variation of select measurements and their ratios for extant comparative material.

1.C.b. Recent Snakes

Several authors have discussed the morphological differences in vertebrae among and within recent snake groups. Many paleontologists provide brief descriptions of the differences among the snake species that they compare, but usually without extensive comment on populational or intracolumnar variation. Some systematists also provide drawings and brief descriptions of vertebrae (e.g. Dowling,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1958; Bogert, 1968; Cadle, 1989), but unless there is some salient neomorphic character, such as the interzygapophyseal shelf in Imantodes (Johnson, 1955) or the wing-like processes in Mehelya (Bogert, 1964), the descriptions lack sufficient detail to be useful in differentiating taxa.

R. Johnson (1955) made quantitative comparisons of taxonomic groups of living snakes and contrasted the results with ecologically convergent groups. He statistically compared ratios of measurements taken from X-rays, using only ratios that were biologically meaningful ("they...represent features that may be translated into functional requirements." Johnson, 1955, p. 370) and relatively constant within individuals. All measurements were taken from dorso-ventral projections. Values analyzed were averages of ten ratios from evenly spaced vertebrae throughout the precaudal column, beginning with V5. Johnson used non-parametric methods to compare populations because his ratio samples were not normally distributed and did not have comparable variances. The Kolmogorov-Smirnov statistic was used to determine whether two sample frequency distributions represented the same populations. When differences were found, the H-test of Kruskal and Wallis was used to ascertain the differences in central tendency between two populations. White's rank test was used when sample sizes were too small for the H-test.

Johnson's results showed that vertebral morphology is fairly conservative within taxonomic groups, but that very few ecological groupings have measurable morphological

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

consistency. Some ecological groups, such as arboreal or aquatic, do show extremes of adaptive form in a few species, but most other members of the same groups are more similar to their taxonomic relatives. In some cases, adaptive extremes apply to an entire taxon, e.g. the sea snakes were the only group tested that showed vertebral modification adapted to aquatic locomotion, and this adaptive form is found throughout the family.

In a similar study, Dessem and Younker (undated MS), applied Fourier Analysis to the digitized outline of photographs of snake vertebrae in lateral view. A single vertebra, that with the best developed hypapophysis, was selected from the skeletons of 31 snakes, each representing a different species. The snakes were classified according to "mode of life" and taxonomic family, as in Johnson's work. The harmonic amplitude coefficients of the fourier analysis were used as independent variables in a discriminant analysis to determine how well mode of life groups and families could be distinguished. Although several outliers were misclassified, the results were encouraging, as many of the mode of life groups and families clustered together. As in Johnson's work, the taxonomic groupings were more distinct than the mode of life groupings. Dessem and Younker's mode-of-life groups were found to be more distinct than Johnson's. In contrast to Johnson's results, they found the fossorial and aquatic groups to be more distinct from the general terrestrial forms than the arboreal species were. Johnson

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

indicated the reverse to be true. This is probably a reflection of the different vertebral views studied in the two cases (dorso-ventral in Johnson's, and lateral in Dessem and Younkers), and underscores the critically three dimensional nature of vertebral structure in snakes. Although the fourier approach appeared to be effective at the family level, its effectiveness at lower taxonomic levels remains untested. This method may merit further investigation.

Hoffstetter (1960) used plots of centrum length and hypapophysis length throughout the column to illustrate the extent of hypapophyseal development in several boid genera. Hoffstetter and Gayrard (1965) described the vertebral column of a single specimen of Acrochordus by plotting the logarithms of a series of measurements against vertebral position for each vertebra. The use of logarithms was supposed to facilitate comparisons among taxa, although such comparisons were not attempted. They described intracolumnar variation in detail, but made no morphometric analyses.

In a comprehensive study of the osteology of the Crotalidae, Brattstrom (1964) used ratio data from "midthoracic" vertebrae to characterize 19 species of American crotalids. He also suggested a unique approach to the identification of isolated vertebrae: graphs of ratios of vertebral measurements (various measurements / vertebral height) were constructed, plotting every tenth to twentieth vertebra for each representative specimen. The same ratios were calculated for an unknown vertebra and plotted on a card

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

with the same scale as the comparative graphs. The card was then compared to the graphs until a match was found. Although Brattstrom stated that interspecific differences in ratios are sufficiently distinct, he did not discuss intraspecific variation in ratios.

Thireau (1967a) compared the vertebral anatomy of three genera of West African vipers: Atheris, Atractaspis and Causus. Logarithms of measurements of ten variables were plotted against vertebral position for representatives of each genus. Caudal and cloacal vertebrae were plotted along with precaudal. Vertebrae from each of five separate vertebral regions were illustrated, showing five different views for each. Patterns produced by the measurements, and the features measured were described and compared qualitatively. The three genera were found to be quite distinctive in vertebral morphology, their differences attributed to adaptive radiation. In general, most features showed a decrease in size at the anterior and posterior ends of the vertebral column. He emphasized an abrupt change in morphology at the cloacal region, a transition between trunk and tail. Thireau (1967b) described the vertebral morphology of a single specimen of the sea snake Enhydrina schistosa in similar fashion. Again, graphical methods were used only to augment a qualitative description and a large series of illustrations.

Brummer (1980) devised a graphical method for comparing vertebral morphology among snake species. She compared intergeneric variation in vertebral morphology using a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

representative species of every genus of snake in North America, usually the type species. Brummer's data collecting techniques were thorough, including descriptions of qualitative features and measurements of 10 variables for each species. Her quantitative data consisted of ratios of measurements from "randomly selected" trunk vertebrae. Unfortunately, her study was hampered by small sample sizes, using only 5 specimens per species, and five vertebrae from each specimen. For this reason, the did not compare the samples statistically. Furthermore, many of her specimens lacked data on sex and locality, important sources of variability, while some of her samples included members of several distinct subspecies.

Brummer's study included attempts to investigate intracolumnar, ontogenetic, sexual, geographic, and intrageneric variation in the few taxa from which complete specimens (one of Elaphe guttata, one of Pituophis melanoleucus) or more than five individuals (Elaphe obsoleta) were available. Based on the fact that the means of ratios of measurements taken from every twentieth vertebra (excluding vertebra 20) from these two specimens fell within the range of variation of her "random samples" for their respective species, she concluded that intracolumnar variation can safely be ignored. She also ignored ontogenetic changes because the variables used to produce each ratio were highly intercorrelated. She did not provide correlation values, or any plots of the data. Furthermore, the single sample on

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

which this conclusion is based (eight specimens of Elaphe o. obsoleta) did not include any small juveniles. Her smallest specimen is 820 mm in length, whereas hatchlings are typically 290 to 368 mm (Fitch, 1963). Thus, the most interesting and radical changes in size and shape were not included in the study.

Brummer (1980) was unable to make a definitive statement on sexual dimorphism because most of her material was not identified to sex before skeletonization. In only two instances were both male and female specimens identified for a given species. She was able to confirm Keiser's (1970) observation of sexual differences in the hemapophyses of anterior caudal vertebrae, but did not notice any differences among trunk vertebrae.

Brummer's study does seem to suggest some interesting patterns of intraspecific and intrageneric variability, but her lack of rigorously controlled sampling methods merely beg the question of whether measureable interspecific differences exist. Perhaps the most useful product of this study is the graphical method of comparing "ratio profiles." If applied to larger samples of carefully selected individuals, it might produce a useful method of identifying isolated vertebrae.

1.D. Anatomy of the Axial Skeleton of Snakes.

1.D.a. Vertebral Anatomy.

Snake vertebrae are a modified form of the basic vertebrate ground plan (Figs. 8 and 9). The vertebral body is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

a procoelous centrum with a well developed, deep, anterior cotyle (Ct), and a rounded, knob-like, posterior condyle (Cn). The ventral face of the centrum bears a longitudinal process that may be nothing more than a ridge, the hemal keel (HK, Fig. 8), or it may be produced postero-ventrally as a blade or spine-like structure, the hypapophysis (HYD, Fig. 9). In most snakes, vascular foramina are located on the ventral face of the centrum lateral to the hemal keel, on the mid-lateral face, and on the anterior face just lateral to the cotyle.

The centrum is roofed over by a neural arch that is pierced by the neural canal (NC). The neural arch consists of two vertical plates of bone, the pedicels (NAP), that are fused, without trace of suture, to the dorsolateral edges of the centrum. These attach to dorsal plates of bone, the neural arch laminae (NAL), that may be flat or curved, and are usually inclined upward toward the middorsal line. Rising out of the union of these two plates, in alethinophidian snakes, is a dorsal neural spine (N), which is usually a flat, vertical plate of bone, but may be a nearly cylindrical spine in some forms.

The anterior dorsal edge of the neural arch is adorned by a tenon-like articular apparatus called the zygosphene (Z), that has flat, ventro-laterally directed articular facets (ZF). The posterior dorsal edge of the neural arch is excavated by a recess called the zygantrum (Zg), that has internal, dorso-medially directed facets that articulate with those of the zygosphene. The zygosphene - zygantrum articular

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

apparatus is often viewed as a specialization that has some unique significance for snakes, even though it is widely known that it occurs in diverse lizard groups, including such taxa as the iguanidae, Teiidae and Varanidae. Although the separation of the zygosphenal and zygapophyseal facets is greater in snakes than in lizards, it may be best to view the structure as a synapomorphy of the Squamata that is often lost independently in some lizard groups.

The postero-lateral corners of the neural arch are drawn out to end in flat, ventrolaterally directed articular facets, the postzygapophyseal facets (Po). In some taxa the neural arch lamina may bear a short, acute, posteriorly directed, epizygapophyseal spine (E) just above the postzygapophysis. Postzygapophyses articulate with the prezygapophyseal facets (Pr) of the following vertebra. These are flat, articular surfaces that face dorsally, and slightly medially, and are borne on strong, prezygapophyseal buttresses that project anterolaterally from the centrum, just beside the cotyle. Projecting anterolaterally from the buttresses, just below the prezygapophyseal facets are strong, spine-like structures called accessory processes (Acp, equivalent to the prezygapophyseal processes of some authors). Additional articular facets, the paradiapophyses, are borne laterally on the prezygapophyseal buttresses, for the attachment of the ribs. In the more derived lineages of snakes, these are divided into a dorsal, rounded, diapophysis (D) and a ventral, flattened, parapophysis (P), separated by a slight

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

constriction. Where hypapophyses are present in the vertebral column, the parapophyses bear antero-ventrally directed parapophyseal processes (Malnate, 1972). In the Scolecophidia and some other basal snake lineages, the rib articular surface is a single, rounded facet, or synapophysis.

The entire vertebral unit is a completely fused structure that lacks sutures or suture lines from the time of birth (hatching) onward. No epiphyses or intercalary cartilages are found associated with any portion of the vertebra. Growth apparently occurs entirely through resorption and remodeling of the bony surfaces (Enlow, 1969), with the possible exception of the articular facets, which may be constrained to grow by peripheral accretion.

1.D.b. Regions of the vertebral Column

In a review of the morphology of the vertebrae and ribs of reptiles, Hoffstetter and Gasc (1969) divide the vertebral column of snakes into four principle regions: 1) atlas and axis, 2) trunk, 3) cloacal, and 4) postcloacal. Hoffstetter and Gasc consider the trunk a morphologically homogeneous region in which no recognizable differentiation of subregions exists. They do note, however, that proportional changes occur along the length of the column. "Vertebral morphology does not vary along the trunk. However, the proportions change in a single individual..." (Hoffstetter and Gasc, 1969, p.290). They go on to contradict their earlier assertion, stating that an anterior region of the trunk, bearing hypapophyses in all snakes, is readily distinguishable even in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

forms which bear hypapophyses throughout the trunk. This region has elongate hypapophyses in the latter group, that abruptly decrease in length at the end of the region. Some authors recognize this as a distinct subregion of the trunk, the cervical (Holman, 1979, 1981; Szyndlar, 1984). The use of this term and others commonly used to describe mammalian vertebral column regions such as thoracic and lumbar, is to be avoided since there is no way to determine the homology of these regions between the two groups (LaDuke, 1991). I recognize the regions of Hoffstetter and Gasc (1969), but follow LaDuke (1991) in further dividing the trunk region into four subregions: anterior trunk vertebrae (ATV), midtrunk vertebrae (MTV), posterior trunk vertebrae (PTV) and precloacal vertebrae (PCV). These subregions do not change abruptly from one to the other, but merge gradually with more or less extensive areas of intermediacy.

The ATV bear hypapophyses in all Alethinophidia. In groups that have hypapophyses throughout the column, those of the ATV are more elongate than those of the other trunk vertebrae. This is a series of rapidly increasing size from anterior to posterior, with the rate of size increase decreasing as one approaches the MTV. ATV tend to be shortened cranio-caudally and have small zygapophyses. The neural canal is relatively large, with a broad zygosphene. Toward the caudal end of the ATV series, they converge on the shape of the anterior MTV.

MTV are the largest vertebrae in the column. They tend

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to have zygapophyses that are broadly divergent laterally from the centrum. Neural spines gradually decrease in height throughout this and the following region. Centrum lengths gradually increase relative to vertebral size from anterior to posterior. The neural canal becomes relatively smaller as vertebral size increases.

The PTV represent a series of decreasing overall size posteriorly, although the rate of decrease is less than the rate of increase in the ATV. PTV become relatively more elongate throughout the series, while their zygapophyses become less divergent. Neural spines in this region are often much lower than in MTV. The most distinctive feature of this region is the presence of subcentral lymphatic fossae, a feature described in detail by LaDuke (1991).

The PCV is a short series of three to five precaudal vertebrae that are distinctly smaller than any others. They resemble the cloacal vertebrae in proportions, but lack fused lymphapophyses, although the last one or two may have forked, articulating ribs. PCV are very short antero-posteriorly, with low, short (antero-posteriorly) neural spines. The neural arches are generally more vaulted than those of the PTV. PCV usually have very large lymphatic notches between the paradiapophyses and ventrolateral lip of the cotyle (LaDuke, 1991).

1.D.c. Vertebral Number and Dermovertebral Correlation

There is a direct one-to-one correspondence between vertebrae and ventral scutes in most advanced snakes

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Alexander and Gans, 1966). Morphological studies demonstrate that there is an intimate functional relationship between ventral scutes, vertebrae, and the intervening musculature and ribs in snake locomotion. The one-to-one correspondence rule is broken only in certain derived fossorial and aquatic groups (Alexander and Gans, 1966; List, 1966; Voris, 1975). Ventral scale counts have been used as taxonomic features since the first formal systematic investigations of snakes (Linnaeus, 1758). A lack of standardization in recognition of ventral scales by earlier workers prompted Dowling (1951) to propose a formal recognition criterion for counting ventral scales in snakes. Unfortunately, this approach involves the omission of several small ventral scales in the gular region that probably correspond to anterior vertebrae, hence, ventral counts thus standardized do not accurately reflect the number of vertebrae in snakes. However, these ventral counts should vary in parallel with the true number of vertebrae, and reflect the variability in vertebral numbers.

Sexual dimorphism in the number of ventrals and vertebrae in snakes is well known, males typically having fewer trunk vertebrae and more caudal vertebrae than females. Members of the genus Thamnophis are unusual in that males have more trunk and caudal vertebrae than females, a phenomenon also found in Imantodes (Myers, 1982). Geographic variation is also thoroughly documented in these characters, with most species showing distinct clines. In California, a trend of increasing vertebral numbers in warm continental localities, and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

decreasing vertebral numbers in cool coastal localities has been reported (Klauber, 1941). North to south clines have been found in some species, with vertebral numbers (based on ventral counts) decreasing northward (e.g. Christman, 1980; Grobman, 1984). Experimental studies show that developmental temperature influences the number of vertebrae in clutches brooded under controlled temperature regimes (Fox, 1948; Osgood, 1978), with lower temperatures producing lower vertebral numbers. Similar results have been found in studies of other vertebrate classes (Lindsey and Ali, 1965; Lindsey and Harrington, 1972; Lindsey et al., 1984), but the direction of response is not always the same. Arnold (1988) indicates that there is a "U" shaped response curve or "norm of reaction" in which the lowest vertebral counts are produced by temperatures that are near some optimum. As temperature deviates from this value, either higher or lower, vertebral counts, and the incidence of anomalous vertebral morphology both increase.

These factors all have an indirect influence on the shape of vertebrae through vertebral numbers. The effects of variation in vertebral numbers through vertebral packing are discussed below.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter 2. INTRACOLUMNAR SIZE TRENDS

2.A. Size Trends: Methods

2.A.a. Skeletal Preparation.

Individuals were selected from the study populations for skeletal analysis on the basis of size and sex. Although samples of all sizes and both sexes were made, large male specimens were collected preferentially because of the greater ecological importance of females for population stability, and because larger specimens are easier to handle and provide more reliable measurements.

Specimens were killed either by freezing, or etherization. Dead specimens were weighed on Pesola spring scales and measured for SVL and TAL to the nearest mm. Sex was determined by dissection of the tail base to examine scent glands and hemipenes. Gonads were also examined to determine reproductive status (mature or immature). The following scale counts were made: ventral scales (VE), following the methodology of Dowling (1951); subcaudals (SC); dorsal scale rows (DSR), made in three places: one head length behind the head, midbody, and one head-length before the vent; supralabials (SL); infralabials (IL); loreals (LO); preoculars (PR); postoculars (PO); temporals (TE); and the positions of supralabials entering the orbits (SLEE).

Snakes were skinned by making a mid-ventral incision from the vent to the gular region, and a second from the vent to near the tail tip. The entire skin was then peeled off, with every effort made to maintain the head skin intact. The skin

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the tail-tip was generally left on the carcass. Viscera were removed intact whenever possible, and remained attached to the skin at the mental scale and at the edges of the vent. The skin and viscera were then labeled and preserved in alcohol or formalin. The remaining carcass was labeled, dried, and cleaned by dermestid beetles. The smallest snakes (<250 mm SV) were preserved in formalin, and later cleared and stained according to the methods of Wassersug (1976).

Skulls and tail tips were carefully disarticulated from the cleaned carcasses. The remaining vertebral column was then strung on a monofilament nylon fishing line, leaving about 50% more line than the length of the carcass. A label was tied to the end of the line, identifying the specimen with a unique collection number (prefaced by TCL = author's initials). Strung carcasses were soaked in a solution of enzymatic laundry detergent to digest remaining ligaments (after the methodology of Ossian 1970). The cleaned, disarticulated vertebral columns and disassociated ribs were then rinsed under running tap water for about five minutes and soaked in 2 changes of tap water overnight. The final product was air-dried at room temperature. The vertebrae were counted such that the atlas was numbered 1, the axis 2, and so forth, to the end of the precaudal column. The first vertebra of the caudal series was identified by the presence of a fused lymphapophysis. The vertebra before this was considered the last precaudal. It was noted whether the first caudal vertebra bore one or two fused lymphapophyses. Every fifth

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

precaudal vertebra was marked with a spot of india ink on the right hand side of its neural arch. Larger specimens received special marks on vertebrae 25, 75, 125, (+); 50, 150 (++); and 100 (0).

2.A.b. Measurements.

Measurements were made on a Bausch & Lomb dissecting microscope fitted with a digital caliper (Fowler) whose jaws were fixed to a mechanical stage. Measurements were taken by aligning one end of a bone with a crosshair in an optical grid, taking a reading from the caliper, then moving the stage until the other end of the bone lined up with the same crosshair. The final reading was then subtracted from the original, and the difference stored as a length in a data file. The readings were exported directly to an IBM PC computer clone (Bentley 286) via a Fowler interface (Zubair Z-interface). The entire procedure was orchestrated by Lessoft Software. Data were analyzed using SAS PC Software, version 6.03 (SAS Inst., 1988).

The initial series of measurements was designed to include characters that were seen to vary along the vertebral column, as well as among taxa. Many of these measurements are similar to a set used by Auffenberg (1963), others are original (Fig. 9):

APL - Length of accessory process, measured parallel to its long axis, in dorsal view.

CNH - Condyle height, measured from top of condyle to lower lip of condyle, in posterior view.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CNT - Centrum length, measured in ventral view from the lower lip of the cotyle, to the furthest extent of the condyle.

CNW - Width of condyle, measured transversely from edge to edge, in posterior view.

COH - Height of cotyle, measured from outer edge of upper and lower lips of cotyle, in anterior view.

COW - Width of the cotyle, measured from outer edge of lateral lips, in anterior view.

HYD - Depth of hypapophysis, measured from ventral edge of condyle to lowermost edge of hypapophysis, perpendicular to long axis of centrum, in lateral view.

HYW - Width of hypapophysis, measured in ventral view.

NAH - Neural arch height, from the top of the anterior edge of zygosphene to the top edge of the cotyle, measured in anterior view.

NAW - Narrowest width of neural arch, measured between pre- and postzygapophyses in ventral view.

NSH - Neural spine height, measured from anterior edge of top of neural spine, to horizontal line tangent to top of anterior edge of zygosphene, in lateral view.

NSL - Length of neural spine, measured in dorsal view.

NSW - Width of neural spine, measured in dorsal view.

PCN - Paracotylar notch, measured from the level of the lower lip of the cotyle to the upper edge of the paracotylar notch, in anterior view.

PDD - Depth of paradiapophysis. Measured from top of diapophysis to ventral extremity of parapophysis, excluding

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

parapophyseal process, in lateral view.

POW - Greatest width across postzygapophyses, measured in ventral view.

PPL - Length of parapophyseal process. Measured from ventral extremity of diapophysis, to tip of parapophyseal process, parallel to long axis of process, in lateral view.

PrPo - Measured in ventral view, distance from anterior edge of right prezygapophysis to posterior edge of right postzygapophysis.

PRW - Width across prezygapophyses, measured in dorsal view.

PZH - Height of left postzygapophyseal body, measured from top of zygosphenal facet to level of lower, inner edge of postzygopophyseal facet, in posterior view.

PZL - Length of right postzygapophyseal facet measured in ventral view.

PZW - Width of right postzygapophysis, measured in ventral view.

ZYW - Width of zygosphene, measured in dorsal view.

2.A.c. Measurement Error.

A simple test was performed to evaluate the reliability of measurements. A single vertebra was measured for the 23 variables (above) ten times. Variability of the measurements was evaluated by comparison of the means, ranges, standard deviations, variances, and coefficients of variation.

2.A.d. Intracolumnar Patterns of Variable Size.

Whereas most paleontologists who work closely with snake vertebrae are able to recognize subtle variations in shape

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

among taxa, these variations have proven difficult to quantify. This is due to the gradational nature of shape changes within the column, providing each individual snake with almost as many morphological variations as vertebrae, and to the three-dimensional distribution of important shape variables within a vertebra.

To assess patterns of size variation within the vertebral column, an exploratory data set was established by measuring each precaudal vertebra in two specimens (TCL793 and TCL791) for a small series of characters (CNT, NAW, POW, NSH). A third specimen (TCL783) was measured for five variables (the four above plus HYD) on every other vertebra (odd numbered). In addition, one of the above specimens was measured for 23 variables on every fifth vertebra. Finally, three other specimens (TCL182, TCL449, and TCL469) were measured on every fifth vertebra for all 23 variables. These measurements were then plotted against vertebral numbers, as has been done by many authors (Hoffstetter, 1960; Bogert, 1964; Hoffstetter and Gayrard, 1965; Thireau, 1967a, 1967b; Brummer, 1980; Szyndlar, 1984), to examine patterns of intracolumnar variation. In contrast to most previous authors, the data were plotted on a direct, instead of a logarithmic scale, to portray regional differences proportionally.

The first three specimens (TCL783, TCL793, TCL791) constitute a series of males with increasing SVL and similar vertebral counts (149, 151, and 151 NOV respectively), all from the same locality. The latter three specimens include

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

two large females, greater than 500 mm in SVL, and a small female of 182 mm SVL, respectively. The plots were compared for differences in intracolumnar pattern among the sizes present and the two sexes.

2.A.e. Intracolumnar Rates of Change in Variable Size.

It has been suggested that vertebrae from consecutive positions within a column are visually indistinguishable (LaDuke, 1991). This leads to the question of whether consecutive positions are distinguishable within the limits of instrumentation. If not, how far apart must two vertebrae be before measurable differences are detectable? The answer to this question will indicate whether differentiation of neighboring vertebrae is sufficient to require an evaluation of the homology of vertebral positions among specimens with different numbers of precaudal vertebrae.

Several methods were applied to determine whether differences of sufficient magnitude exist among near neighbor vertebrae to affect comparisons among specimens with different NOV. First, the differences between consecutive vertebral positions were evaluated in a specimen (TCL791), for which every vertebra had been measured for four variables, by subtracting the measurement for a vertebra from that of the following vertebra. The differences were plotted against vertebral position. The measurements were then subtracted from those of vertebrae two positions higher, and finally, three positions higher. All were plotted against vertebral position to determine if any trends in these differences were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

apparent.

In a second approach, frequency distributions of differences between consecutive vertebrae were examined for position of the mode, to determine whether any values were particularly more abundant than others. The mode was compared with the means observed above.

Finally, the difference between consecutive vertebrae was averaged over ten consecutive positions in five different regions in a single specimen (TCL791) to estimate regional variation.

2.B. Size Trends: Results

2.B.a. Measurement Error.

Ten repeated measurements of all 23 variables on a single vertebra (VNO 65, TCL791) are presented in appendix 1. Most of the repeated measurements produce observed ranges that span only 0.02 to 0.05 mm, with a decided peak at 0.03 mm. The larger ranges are associated with features that are more difficult to measure due to irregular shape. The largest range, 0.08 mm, is associated with a feature (PRW) that was slightly damaged at one edge in this vertebra, interfering with accurate measurement. Interestingly, all ranges that were greater than 0.05 mm would actually have been smaller by at least 0.02 mm if not for a single outlier. Coefficients of variation of the repeated measurements are typically less than 4.0. The only exceptions are the smallest measurements (NSW: mean=0.13, CV=9.6; and PCN: mean=0.14, CV=7.5). Only two

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

other variables produced CV's greater than 3.0: HYW, also a small measurement (mean=0.23, CV=3.2), and PPL, a difficult measurement (mean=.67, CV=3.3). Measurement error may therefore be conservatively estimated to be about 0.025 mm on average, but, occasional outliers of up to 0.04 mm are to be expected.

2.B.b. Intracolumnar Patterns of Variable Size.

Patterns of size change within the column for the specimens listed above are illustrated in Appendix 2: Figs. 1 through 78. Several distinctive intracolumnar and ontogenetic patterns are apparent from these plots. These patterns reveal a number of important points that dictate the direction of the remainder of this study.

Most of the vertebral characters measured produced a characteristic arch-shaped curve when plotted against VNO with vertebrae from the middle regions of the column substantially larger than those from the extremities. However, there were some important exceptions. Four main patterns can be distinguished in specimen TCL793: 1) the arched curve is the most common, occurring in 17 of the 23 variables: CNH, CNT, CNW, COH, COW, NAW, NSH, NSL, PDD, POW, PPL, PRP, PRW, PZH, PZL, PZW and ZSW; 2) a pattern of continual size increase occurs in two variables: APL and PCN; 3) a continually decreasing pattern is found in two variables: NAH and HYD; and 4) a pattern of relatively constant size is found in two variables: HYW and NSW.

Most of the arched variables show a rapid increase in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

size in the anterior region of the column, peaking in size just anterior to the central vertebra, and then decreasing at a slower rate. In some instances the arch is interrupted by a break in the curve, such as in NSH, where there is a dip in the vicinity of 19% back from the anterior end. In NAW and ZSW, the lowest points in the arch are just caudal to the cranial end of the column, or cranial to the caudal end of the column, resulting in upwardly deflected extremities. In HYD there is a sudden drop in value at a point approximately 17% back from the anterior end of the column. These patterns are common to all specimens examined.

Different patterns also emerge among the variables that only increase or decrease along the length of the column. APL increases rapidly to nearly its maximum value in the anterior 25% of the column, remaining nearly constant thereafter. PCN increases steadily through most of the column, decreasing slightly near the caudal end. NAH decreases steadily through most of the column, increasing slightly near the caudal end. HYD is greatest anteriorly, decreases through the cranial 17% of the column, then drops suddenly, assuming a nearly constant value through the bulk of the column, decreasing again near the caudal end. The variables that appear constant throughout the column are very small measurements that vary widely within the limits of their size. Much of this variation is probably due to measurement error.

When a growth series is compared (figs. 10 - 13), we see that vertebral size is much more uniform throughout the column

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in young specimens for most characters. The arching of the variable plots is apparently due to more rapid growth of the vertebrae near the center of the column, since the distance between the extremities of the columns in the figures are less than the distance between the central portions. Furthermore, a slight craniad shift is apparent in the peaks of some arches with increasing size. Also, variables that produce flat plots, rising plots, or falling plots in smaller specimens produce slightly arched curves in large specimens (compare Appendix 2, Figs. 22, 45, and 68). No obvious differences between the sexes are apparent in these curves.

2.B.c. Intracolumnar Rates of Change in Variable Size.

Size differences between consecutive vertebrae in specimen TCL791 appear to be minimal. Plots of differences between consecutive vertebrae (figs 14, 17, and 20) show that through most of the column, there are almost as many negative differences as positive. Furthermore, two consecutive differences are almost as likely to be alike in sign as opposite. Definite trends toward positive or negative difference signs are apparent only at the distal extremities of the column. When measurements are subtracted from those of vertebrae two or three positions away, the trends in sign of the difference become much stronger, and the differences greater. Yet, over a large portion of the central region of the column, adjacent differences may be opposite in sign with little apparent pattern. It is not known whether this represents measurement error or an inherent instability in the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

system at this level of resolution. It is possible that the developmental system does not resolve vertebral shape as finely as the nearest 0.01 mm. Thus, measurement error may be compounded by a sort of developmental error. It is also possible that a pattern of periodically increasing and decreasing values may affect some variables, as is vaguely suggested in some plots of variable against position (see Sumida, 1987, for examples of such patterns in the neural spines of captorhinomorph reptiles), but that the patterns are beyond the resolution of the present measuring system.

Table 1 is a frequency distribution of the differences among neighboring vertebrae as determined above. For each of the three variables (CNT, NAW, POW), three distributions are compared: N-1, N-2, and N-3. Differences between increasingly distant vertebrae were examined in an attempt to average out the effects of measurement error that might influence differences among immediate neighbors. Many of these frequency distributions tend to be bimodal, with peaks centered around a difference of zero. Each difference is derived from actual differences in size between neighboring vertebrae, plus measurement error. Since measurement error should be relatively constant throughout, modal values in these distributions probably reflect average rates of change among neighboring vertebrae. This is supported by the fact that the modes tend to progress outward from zero, as the distance between compared vertebrae increases. Thus, differences among consecutive vertebrae are on the order of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

0.02 to 0.03 mm for larger variables over much of the column, and can be expected to be correspondingly less for smaller ones. At the extremities of the column, the differences will be larger. As the rate of change is comparable to measurement error over much of the column, one would not expect to be able to distinguish among consecutive vertebral positions. However, as the difference between the compared positions increases to three or four vertebrae apart, one would expect to be able to distinguish positions on the basis of size, assuming they represent the same snake, or one of equivalent body size, sex, and vertebral count.

Average differences between consecutive vertebrae over a 10 vertebra span in five different columnar regions are shown in Table 2 for three variables. The differences are obviously greater at the extremities of the column than in the center, and greater in the anterior region than in the posterior. In general, the progression from N-1 to N-2 in positions AA, MP, and PP results in an approximate doubling of the difference. Progression to N-3 results in approximate tripling of the N-1 value. These facts demonstrate that the values produced for these regions primarily represent actual differences in size; the effects of measurement error are secondary. The values produced in the AM and MM regions are mostly very small, and, while AM values increase continuously, MM values do not show any logical progression. These two regions are probably primarily influenced by measurement error, with change in size a secondary effect.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

2.C. Size Trends: Interpretations.

The results of section 2.A.d "Intracolumnar Patterns of Variation in Size" demonstrate that there is an appreciable amount of variation in the size of variables within a vertebral column, but that this variation follows a highly regulated pattern. The fact that different variables produce different intracolumnar patterns suggests that columnar position should be identifiable to some degree on the basis of shape differences.

In order to compare vertebrae among individuals, one must control for intracolumnar vertebral position. The tighter this variable is controlled, the more precisely one will be able to address the question of vertebral identity in questions involving vertebrae of unknown origin.

Finally, examination of the rate of change in size of consecutive vertebrae shows that average values of about 0.03 mm may be expected for large variables in the anterior or posterior regions of the vertebral column. As this is approximately the same as the amount of measurement error described in section 2.A.c (Measurement Error), one would not expect to be able to distinguish consecutive vertebral positions. However, vertebrae as little as 3 positions apart should be distinguishable in a single individual of known vertebral dimensions. Furthermore, comparisons among individuals will be affected if the number of precaudal vertebrae in the columns differs by as much as three.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter 3. Homology Analysis

Grouping vertebrae for statistical comparison is not as simple as it may first appear. The number of vertebrae in vertebral columns varies from individual to individual, raising the problem of how to determine the serial homology of vertebrae among individuals. Two approaches immediately suggest themselves: 1) Vertebrae may be compared on the basis of their numerical position, i.e. distance (in units of vertebrae) from the anterior end of the vertebral column. This is intuitively pleasing from the point of view of embryonic development, wherein the body's axis takes shape from front to back, but leaves the untidy problem of what to do with the excess vertebrae in specimens with higher counts. The last few vertebrae, those from the transition zone from body to tail, must be homologous among all individuals, since similar functional transformations are occurring. If these are allocated to the caudal region, then one could adopt the ad hoc explication that the vertebral column is an open ended system in which a variable number of similar vertebrae are appended to the terminus of the column. 2) The alternative is a column in which morphology depends on the proportional distance of a vertebra from the two ends of the column. In this instance, morphology is assumed to be determined by some positional factor other than the number of vertebrae preceding the one in question, such as a developmental gradient. This model solves the problem of excess vertebrae at the caudal end of the column, but requires an ad hoc explication for the lack

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of one-to-one ordinal correspondence between vertebrae that develop in an orderly front-to-back progression.

Intimately related to the homology question is the question of vertebral packing. A garter snake with 160 precaudal vertebrae must pack them into the same space as a specimen with 143 at a given snout-vent length. These represent the maximum and minimum number of vertebrae in males examined in this study. There are over ten percent more vertebrae in the higher count. This could be accomplished in one of two ways (Fig 23): 1) the snake with more vertebrae reaches the given snout-vent length at an earlier age with all vertebrae relatively smaller (i.e. its snout-vent length is proportionally greater, fig. 23b), or 2) its vertebrae are relatively shorter in antero-posterior dimensions, thus packing more vertebrae into the same snout-vent length, while other dimensions remain the same.

3.A. Homology Analysis: Methods

3.A.a. Modes of Comparison

Many theoretical models could be proposed to justify different modes of comparison of vertebrae. I have adopted an empirical approach wherein three straightforward modes of comparison are tested by comparing measurements of appropriately grouped samples. These can be compared *a posteriori* with appropriate theoretical models. The three modes of comparison are: 1) forward count comparison (Fig. 24B) - the 10th vertebra is compared with the 10th, the 100th

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

with the 100th, etc., regardless of the number present. 2) percentage position comparison (Fig. 24C) - vertebral position is determined as a percentage of the vertebral count, and vertebrae from like percentage positions are compared. 3) reverse count comparison (Fig. 24D) - vertebral count is determined by counting backward from the cloacal region with like counts compared e.g. the 140th vertebra from a specimen with 150 precaudal vertebrae is compared to the 141st vertebra from specimens with 151. The appropriate comparisons for five vertebral regions are presented in Table 3 for each of the various vertebral count categories encountered for male Thamnophis s. sirtalis in this study. Snakes with 151 precaudal vertebrae are used as a standard of comparison for all modes, so that all modes indicate the same positions at this vertebral count. As the number of vertebrae increases or decreases from this point, the positions compared diverge from those indicated by the standard. The percentage position (=VNO/NOV) is provided for each vertebra measured.

Theoretical models that might correspond to these three empirical approaches are as follows: 1) vertebral identity may be determined during embryogenesis by numerical sequence within the column, starting from the head region, and counting individual vertebrae toward the tail. In this model, the identity of a given vertebra is entirely dependent on the identity of the vertebra before it. This results in a consecutive chain of identity into a predetermined number of equivalent somites at some critical positions. 2) Vertebral

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

position may be determined by a homeobox-like mechanism, where the entire somatic field of the developing embryo is dividedstage of development. Identity is determined by the number of somites produced and by relative distance from both ends, or proportional position (VNO/NOV). This model requires that the number of segments, and the fate of a particular segment, be determined before segments are delimited in the underlying cellular medium. 3) Vertebral position could conceivably be determined by a process that is the reverse of the first model, i.e. positional identity is determined by the identity of the following vertebra, thus counting backward from the cloaca. In this instance positional identity would not be determined until the basic architecture of the embryo had already been laid out and the last precaudal somite produced.

Such theoretical constructs need not be restricted to the embryogenetic stages of development. Vertebral shape is undoubtedly heavily influenced by the stress and strain of muscular activity and compression by surrounding bones. Thus, positional shape may be in part determined by the nature of postnatal muscular development and excercise and the relative distribution of muscle fascicles to somites in individuals. These considerations lead to more complex models of vertebral shape differentiation that will be deferred to a later study. Clearly, the simple models sketched above could never fully account for the complexities involved in the shaping of living tissues. Nevertheless, by delineating a crude paradigm for

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

comparison with empirical data, we may be able to determine whether we are on the right track and merely need to refine one of these models, or need to start again with fresh ideas.

3.A.b. Variance comparisons.

To determine which mode of comparison is most effective, the three modes described above were analyzed in two ways. First, by computing the variance of measurements of five variables at each of five columnar positions (chosen to represent areas of rapid size change more heavily) determined by the three modes of comparison in a limited size series of male specimens. The five positions are: anterior (AA), approximately 12.5% of column length from the anterior end; midanterior (AM), approximately 25 % from anterior; middle (MM), approximately 50% from anterior; midposterior (MP), approximately 75% from anterior, and posterior (PP), approximately 87.5% from the anterior end. The variances produced were plotted against position within the column. Theoretically, the comparative mode that produces the lowest variance should be preferred since it is probably comparing more nearly homologous vertebral positions. The variance patterns are compared with null models that were produced by calculating the variances for each mode, of the positions specified by the two alternate modes. For example, the variances of the percentage values of the vertebrae specified by the forward and reverse modes produced patterns that one would expect to see produced by the actual forward and reverse

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

count measurement data if the percentage mode produced the best homology comparisons. These patterns are also affected by other factors, such as changes in overall size among positions that will tend to produce larger variances where there are larger measurements.

If the percentage position mode is the most appropriate, then variances produced by it should be consistently lower than those produced by the other two modes (Fig. 25). The forward count mode should be very close to the percentage count mode near the cranial end of the column, and progressively more divergent as the caudal region is approached. The opposite pattern should be produced by the reverse count mode. If the forward count mode is the most appropriate, then the forward count variances should be lowest. Reverse count variances should be consistently higher than forward count throughout the column, and percentage position variances should be similar to forward count variances cranially and diverge toward the reverse count values caudally (Fig. 26). If the reverse count mode of comparison is the most appropriate of the three, then the null model is the reverse of that produced by the forward count mode. That is, the reverse count mode provides consistently low variances, the forward count consistently high, and the percentage position variances should be similar to reverse count caudally, but diverging toward forward count values cranially (Fig. 27).

The specimens compared in this analysis and the following

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

one were all male, and were constrained to fit within a reasonably narrow size range (402 to 444 mm SVL). Table 4 lists the specimens used and their SVL and number of precaudal vertebrae present in each, as well as the vertebrae compared by each of the three modes at a single site (AM).

3.A.c. Graphic Comparisons.

The second analysis involves the direct comparison of patterns of variation within vertebral column positions among the three comparative modes. The same five positions are analyzed as above. Two factors should affect these patterns differentially: 1) As noted above, snakes with more vertebrae should have relatively smaller or shorter vertebrae to fit them into the same snout-vent length. The two alternatives may be discerned by comparison of length measurements with width and height measurements. 2) If a given mode of comparison is assumed to identify homologous positions within vertebral columns, then the other two modes will be comparing non-homologous vertebral zones, i.e. short, continuous series of vertebral positions (Figs. 28 and 29, Table 3). As vertebral size varies over any region of the vertebral column, such zones may be expected to reflect the nature of size trends in thatregion. For example, if the percentage mode produces homologous comparisons, then the forward mode would include higher vertebral positions than the percentage mode in columns with fewer vertebrae, whereas it would include lower vertebral positions in columns with high vertebral numbers (see Table 3). Thus, in the anterior

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

region, an inverse relationship is expected between variable magnitude and number of vertebrae in the column. Whereas in the posterior region, the reverse (a direct relationship) is expected.

If vertebral packing in snakes of similar SVL is the result of varying age in the sample, then snakes with more vertebrae will have smaller vertebrae in all dimensions, and both of the above factors (1 and 2) will apply for all variables. They will augment or counteract one another depending on the situation (Fig. 30). For example, in the graph in the upper left of Fig. 30, the effect of factor 2 (range effects) produces a positive slope with increasing NOV. But this effect will be counteracted to an unknown degree by the effects of factor 1 (packing effects) as indicated by the arrows. If vertebral packing is accomplished by decreasing vertebral lengths only, then both factors will only apply to length measurements. Width or height measurements will only be affected by trends in relative position. Figure 30 diagrams the expected direction and relative magnitude of the slope of the two inappropriate modes of comparison, assuming that the remaining mode (labeled on left) provides the best approximation to homology. In the anterior regions of the vertebral column, if the percentage mode provides the best approximation to homologous comparisons, then the forward mode is expected to produce a decreasing trend with rising vertebral counts, while the reverse mode is expected to produce an increasing trend. If the forward count provided

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the best comparisons, then both percentage and reverse modes would produce increasing size trends with increasing vertebral counts in the anterior half of the column, although the reverse mode would be expected to produce a steeper slope, due to augmentation by packing effects. If the reverse count mode were best, then the other two modes would produce decreasing trends in the anterior half of the column, with the forward count steeper. The middle of the column is posterior to the largest vertebrae. Although vertebrae are decreasing in size here, the rate of change is negligible. Any detectable trends would probably be similar to those in the posterior region.

In the posterior region, trends should run opposite to those described in the anterior region. If the percentage mode were the best approximation of homology, then the forward mode would produce an increasing trend, the reverse a decreasing trend with increasing vertebral counts. If the forward mode were the best, then the other two would produce decreasing trends. If the reverse mode were best, then the others would produce increasing trends. All trends should be most pronounced at the extremes of the column, and less pronounced as one approaches the middle, since the rate of change in vertebral size is greater at the extremes. In Fig. 30, the sloped lines indicate the effects of relative position variation alone. The effect of vertebral packing is to rotate the lines in a clockwise direction, accentuating negative slopes and decreasing positive. Multiple regression was used to determine the nature of trends in various morphometric

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

measurements while varying vertebral count and snout-vent length. Trivariate plots were produced to illustrate the effects and for comparison with the expected patterns in Fig. 30.

3.B. Homology Analysis: Results

3.B.a. Variance Comparisons

The variance comparisons did not produce unequivocal results, but some interesting patterns do emerge. Figs. 31 - 35 show the variances plotted against relative columnar position. First, in most of the plots, the variance patterns conform in gross outline to an inverted U shaped pattern. This is not surprising, since larger objects should produce larger variances. The only variables that do not conform to this pattern are those that are not largest in the center of the column (NAH and HYD), but these still follow the rule of larger variances for larger variables. Second, in the most cranial position, reverse count variances are always higher than those produced by the other two methods. In fact, in four of five cases, they are much higher than any other variance produced for that variable. This is strong evidence that the reverse count mode produces non-homologous comparisons. Third, the reverse count mode rarely produces the lowest variance for any columnar position except the second (four of five cases). With the exception of the second position, the reverse count mode is again rejected. Its low position in the second position is inexplicable in the light

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the proposed models. In the last columnar position, where the reverse count would be expected to produce as low a variance as any, it only does so once. Finally, the range of the variances produced by the three models is greatest in the first position, as suggested by the second point (above), but, it is lowest in the last position. This is also inexplicable with regard to the originally proposed models.

3.B.b. Graphic Comparisons.

Examples of the trivariate plots of vertebral count, snout-vent length, and morphometric variables, in all three modes, are shown for one of the six variables as Figs. 36 through 50. A fairly consistent positive relationship between snout-vent length and variable size, and a negative relationship between vertebral count and variable size were noted for all six variables. The significance and direction of the regressions are charted in Table 5 for comparison with Fig. 30. The positive relationship between SVL and each of the six variables is expected and is illustrated only to help clarify the relationship between NOV and each variable. Two important features of Table 5 are immediately apparent: 1) most of the slopes are negative throughout the table. The few positive slopes are fairly consistent in location on the table, being in the anterior regions of the reverse count mode, and in the posterior region of the forward count mode. 2) Most of the length characters have produced significant regressions, while width and height characters produced non-significant regressions.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

3.C. Homology Analysis: Interpretation.

The consistency of the negative direction of the regression slopes suggests that the effects of vertebral packing are much stronger than the range effects. Range effects are apparently overwhelmed by the effects of packing, particularly where range effects are expected to be weakest (i.e. in the center of the column). Positive slopes are found only where range effects are expected to be strongest, i.e. at the extremities of the column. They also occur in positions that support the percentage mode as the best approximation of homology, i.e. in the anterior region, they are produced by the reverse mode, but not the forward mode. in the posterior region, positive slopes are produced (in only two instances) only by the forward count mode, never by the reverse count mode. This pattern is consistent only with the hypothesis that the percent count mode produces comparisons of homologous columnar positions. Since the mode that produces homologous comparisons will be unaffected by range effects, it should only produce negative regressions due to the effects of packing. This is the case for the regressions produced by the percentage mode comparisons.

Both of the above studies provide empirical support for the use of the percentage mode of comparison over the other two. Therefore, this will be the mode used to group vertebrae for comparison through the remainder of the study. This should not be construed as implying, however, that vertebral identity is so simply determined in nature. In fact, the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

unusual order of variances found in the AM region in the variance study suggests that local perturbations may affect positional identity as much as distance from the termini of the column. For example, the AM region is close to the position of the heart. More detailed studies will be needed to resolve the exact nature of positional determination in snake vertebrae.

An alternative perspective deserves mention. Vertebral positions can never be exactly homologous since vertebrae are meristic features and positions can only be referred to in the whole, integer sense. Thus, it may be entirely inappropriate to compare vertebrae among specimens with different vertebral counts, since we have already established that this has a direct effect on vertebral shape. This would require that every possible vertebral count category be treated as a distinctive entity. Apart from the undesirable added complexity that this would impose, the massive sample sizes that would be needed to address the nature of vertebral shape would prohibit further study at this time.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CHAPTER 4. GROWTH

4.A. Introduction

Any study of growth in vertebral dimensions must logically be coordinated with a study of growth in general body dimensions. This permits the establishment of a clear relationship between the novel and the familiar, allowing the ages or sizes of snakes with vertebrae of given dimensions to be determined. Perhaps the most reliable single dimension for estimating overall size in snakes is snout-vent length (SVL). Although total lengths (TOL) were often used in older studies, tail lengths (TAL) have been found to be far more individually variable than SVL. Body weight is rarely used in studies of snake growth, but might show interesting results. It has the obvious drawbacks of dependency on feeding and reproductive status (the latter strongly affecting mature females), as well as seasonal fluctuations due to food and water availability. Weight will also be affected to some degree if an appreciable portion of the tail is missing, as is frequently the case for older snakes.

Considering their usual abundance and widespread occurrence, surprisingly few studies have been conducted on growth in garter snakes. Although many studies report sizes of individual snakes, or of samples of populations, few consider the actual progress of growth in populations. Some systematic treatments do not even report size (e.g. Ruthven, 1908; Fitch, 1941). Ruthven (1908), in a classic review of the genus Thamnophis, reports relative tail lengths as a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

proportion of total length. Thus, he must have amassed a large volume of data on sizes of garter snakes, but did not report them.

Reports of the sizes of snakes are widely scattered and often difficult to interpret. Many popular field guides and handbooks report size ranges without making it clear whether they refer to snout-vent length, or total length (Conant, 1975; Stebbins, 1985; Ernst and Barbour 1989). Most sources agree that the maximum size of Thamnophis sirtalis is about 4 feet (approximately 122 cm, presumably total length).

There are three general approaches to determining growth parameters in snakes (Andrews, 1982). One involves plotting the sizes of cohorts of similar aged individuals over seasons (Seibert & Hagen, 1947; Carpenter, 1952; Jackson & Franz, 1981). This method requires that birth (or hatching) be strongly seasonal, and that annual cohorts do not overlap strongly in size. A second method involves longitudinal data of the sort obtained by measuring the same individual repeatedly during its life, as by mark and recapture (Seibert and Hagen, 1947; Carpenter, 1952; Fitch, 1963, 1965; Plummer, 1985). Finally, growth parameters may be modeled by comparison with theoretical patterns determined by functional relationships, such as that between growth and metabolic rate (Andrews, 1982). Two models have been successfully employed in reptilian growth studies, the von Bertalanffy growth model, and the logistic model (Andrews, 1982). Both models produce growth curves that are asymptotic with a species-specific

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

maximum length. The logistic equation produces a sigmoidal curve in which maximum growth rates occur approximately half way through development. The von Bertalanffy model produces a curve in which growth rate is maximal at birth and decreases continuously thereafter.

The logistic growth model has been applied in studies of small, short-lived iguanid lizards such as Anolis, Sceloporus, and Uta (Andrews, 1982). Larger, long-lived reptiles appear to fit the von Bertalanffy model for growth in length (Andrews, 1982). Growth in snakes has apparently not been examined with regard to either of these models. In fact, although descriptive growth schedules are often reported for snakes, growth patterns are rarely analyzed quantitatively (Parker and Plummer, 1987). Many reported growth rates for given species are determined by conglomerating size data on scattered specimens from distinct populations to determine species-wide growth parameters (Parker and Plummer, 1987). Yet, growth rates in individual populations are likely to be strongly influenced by local conditions; thus, such studies should be restricted to the local population level.

Feaver (1977, in Parker and Plummer, 1987) described three basic species specific growth patterns in snakes, noting behavioral correlates. He characterized group I snakes as those in which males are larger than females, grow more rapidly than females, and engage in competitive combat for mates. These species are late maturing and have high adult survivorships. Group II snakes have larger females due to

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

more rapid female growth, and lack male combat. Maturity is early in these species and adult survivorship is low. A third group, type III, representing few species, combines some features of types I and II: females are larger and grow more rapidly than males, male combat is present, maturation is late, and adult survivorship high. Garter snakes belong to group II, and exhibit rapid growth rates in both sexes relative to other small to medium sized snakes.

4.B. Empirical studies of growth in Thamnophis.

Seibert and Hagen (1947) studied Thamnophis radix and Opheodrys vernalis in Chicago, Illinois. They reported a maximum size of 665.5 mm (total length) in their T. radix population. Growth rates in first year snakes ranged from 1.34 to 1.81 mm/da (mean=1.60 mm/da) in this species, based on cohort analysis. Individual recapture records indicated a growth rate of 1.63 mm/da. Among second year snakes, growth had slowed to an average of 1.34 mm/da on the basis of cohort analysis, while recapture records indicated a dichotomy between males (1.09 mm/da) and females (2.61 mm/da).

Carpenter (1952) studied growth in three species of Thamnophis living sympatrically at a single site in Michigan. He did not report specific sizes of specimens other than in graphic form. His largest T. sirtalis was a female of slightly over 700 mm SVL. His largest male is about 600 mm SVL. His largest female and male T. sauritus were between 650 and 700 mm, and 550 and 600 mm SVL, respectively, while in T.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

butleri, the largest female was between 450 and 500 mm, the largest male between 400 and 450.

Carpenter reports average growth rates by size class of 0.70 to 3.98 cm/mo (approximately 0.233 to 1.30 mm/da) in female T. sirtalis, and 0.41 to 3.69 cm/mo (0.137 to 1.23 mm/da) in males. Female T. sauritus grew at rates of 0.43 to 5.03 cm/mo (0.141 to 1.65 mm/da), while males grew at 0.47 to 2.43 cm/mo (0.154 to 0.797 mm/da). Female T. butleri grew at 0.20 to 1.24 cm/mo (0.066 to 0.407 mm/da) while males grew at 0.18 to 2.93 cm/mo (0.059 to 0.961 mm/da).

In all three species studied, growth was most rapid in neonates, and least rapid in the largest individuals. Carpenter's approach to comparison of growth rates was unusual in that he plotted rates as a percentage of size (length), producing a curved function when plotted against size, rather than the straight line produced by directly plotting rate against size in the von Bertalanffy model.

Fitch (1965) reported growth rates of Thamnophis sirtalis parietalis at two sites in Kansas prairie habitat. These snakes were somewhat larger than typical T. s. sirtalis, with maximum female size 950 mm SVL, and maximum male size 678 mm SVL. Fitch estimated growth rates from both cohort analysis and from recapture records. His estimates for growth rates in first year snakes ranged from about 0.7 mm/da to 2.7 mm/da, with females growing more rapidly than males. Females also grew to much larger sizes than males. Growth records from recapture data indicated a high degree of variability in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

growth rates among individuals, and a high degree of variability among years, apparently correlated with the quantity of rainfall, and temperature patterns during the activity season. Intersite differences in growth rate were also marked, with first year rates two to three times higher at a site with abundant moisture and high prey density (Harvey County Park) than at another, drier site (University of Kansas Natural History Reservation and Rockefeller Tract).

Other studies of growth in Thamnophis have not reported growth rates per se, but have reported average size at various points in the species' life history, such as birth, sexual maturity, maximum size, average adult size, etc. (Stewart, 1968, for Thamnophis sirtalis concinnus and T. ordinoides; Clark, 1974, for T. proximus).

Ontogenetic changes in size and shape of snake vertebrae have been largely neglected. Christman (1975) and Prange and Christman (1978) are the only authors to apply quantitative methods to such studies. They showed that centrum length in rattlesnakes scales as a function of body length (for mid-body vertebrae, centrum length=.006745[body length]$^{-0.674}$). Vertebral width, however, increases at a greater rate than vertebral length (width is proportional to $L^{1.30}$). Christman (1975) also demonstrated that ratios of vertebral measurements that have been used to distinguish taxa change rapidly during adult ontogeny. For example, the ratio of centrum length/centrum width in Crotalus decreases from approximately 0.95 in a one meter snake, to about 0.70 in a 1.8 meter snake.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

4.C. Body Growth: Methods.

Age and growth were estimated by mark and release studies at three collection localities, all in New York State. One of these was the natural area at Floyd Bennett Field in Brooklyn (hereafter designated FBF). The other two were small patches of old field habitat, one at Ten Mile River in Sullivan Co. (TMR), and the Balsam Mountain Trailhead in Ulster Co (BMT). Snakes were captured at these three locations at various times during the active season.

Captured snakes were weighed with Pesola spring scales (WT), measured for snout-vent (SVL) and tail (TAL) lengths to the nearest millimeter, sexed by probing their tail bases for hemipenes or palping for oviducal embryos, and marked with a hand-held surgical cautery tool by cauterizing a unique combination of scales from the first scale row on the right and left sides. This technique has not been reported before in the literature and bears commenting on. Cauterized scales usually did not grow back, but left a patch of bare skin in their place. If a scale was not completely cauterized, a tiny aberrant scale sometimes grew back in its place. Snakes caught as long as three years after marking had completely failed to produce any scale over the burn scar. The usual method of clipping a ventral scale with scissors has two disadvantages: 1) the open wound is larger, and exposed to the substrate. 2) scales tend to grow back after a period of years to some extent, such that the clipping marks may come to resemble marks caused by natural scale trauma that are often

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

observed following various types of infection or wounding.

Branding has been used to mark snakes by some previous workers using a variety of tools (Weary, 1969). The results of those studies were similar to those reported here, but the tools required electric current or large battery packs. The cautery tool described here is about the size of a small flashlight and runs on two "C" batteries. With a little practice, the fine wire tip allows even the smallest snakes to be marked accurately with no more injury than two small lateral burn wounds.

Probing was done by inserting a loop of fine gauge wire into the base of the tail and noting the depth of penetration. In males, the loop easily penetrated the hemipenial sack beyond the third subcaudal from the base of the tail, while in females the loop did not pass beyond the second subcaudal from the base. The rounded tip of the loop prevented it from puncturing the epithelium even in neonatal snakes.

Notes were also taken on color pattern, anomalous scales, and natural scars. Marked snakes were released at the site of capture, or within a few feet of it. Release was always within one to five hours of capture, or, occasionally, after being held overnight.

Growth rates for the three populations were estimated in two ways. One was by plotting the seasonal progression of age cohorts (less than 2 years old) through time. The other was by comparing the size of recaptured snakes with their size at first capture. The patterns were then compared to those

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

expected on the basis of the logistic and von Bertalanffy Growth models.

Individuals were selected from the study populations for skeletal analysis on the basis of size and sex. Although samples of all sizes and both sexes were made, large male specimens were collected preferentially because of the greater ecological importance of females for population stability, and because larger specimens are easier to handle and provide more reliable measurements.

The removed visceral tracts of skeletonized specimens were examined for signs of maturity. Males were judged to be sexually mature if their testes were enlarged or their ductuli deferenti were convoluted. The latter were often packed with spermatozoa, in which case reproductive state was obvious. When spermatozoa were absent, the ducts were examined microscopically for convolution. Females were judged to be reproductively mature when embryos or follicles were present in the oviducts. If the snakes were not gravid, they were judged as mature if the oviducts were enlarged as from stretching, or the ovaries had enlarged follicles.

Patterns of growth for individual variables were analyzed by plotting variables from a single columnar position against SVL over a growth series of males and a similar series of females. Linear patterns were analyzed by linear regression and multiple regression. The growth series was also subjected to eigenanalysis and principle components analysis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

4.D. Snake-catching techniques.

Previous studies have used a variety of methods for collecting large enough samples of specimens for analysis. This can be a serious problem for snakes, which are often inconspicuous, secretive animals that do not congregate in large numbers. In many areas they spend the bulk of their time sequestered individually in underground retreats, either natural or usurped from some other burrowing organism. Two systematized approaches have been taken in the past to collect large enough samples for ecological analyses:

1) Hibernaculum fencing. In this technique, a hibernaculum of snakes is located that has limited routes of ingress and egress. The entrance to the hibernaculum is fenced off so that snakes cannot enter under their own power. Snakes are then captured, either as they approach the hibernaculum to hibernate in the fall, or as they emerge from the hibernaculum in spring. After the appropriate data are gathered, the snakes are released on the opposite side of the fence. This system often has the advantage of providing access to a large portion of the snake population of a given area. Also, the population is concentrated in one place during a brief time interval. The drawbacks are that only one effective measurement of an individual can be taken per year (growth cannot occur during hibernation), and, young of the year are often underrepresented, because they appear to overwinter apart from the adults in some species.

2) Intensive trapping. In several studies, particularly those

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

conducted by Fitch (1960, 1963, 1965, 1975, etc.), snakes were trapped in wire funnel traps. Capture rates for funnel traps are relatively low because the traps cannot be effectively baited for snakes. They must be placed in sites where snakes are likely to be directed by natural contours of the environment, such as the base of a rock ledge, or along drift fences. Furthermore, mortality rates are high for snakes caught in traps due to losses to predators and heat exposure.

A third approach to catching snakes is general collecting. With a little knowledge of the general biology of a species, modest samples can be collected in appropriate habitat by simply looking in the right places at the right times. Unfortunately, this simple approach is ineffective for many overdispersed species, or for certain habitat types. For example, the eastern milk snake, Lampropeltis triangulum, was encountered occasionally in the field. This species appeared to be relatively abundant at the Ten Mile River site, but was very generally distributed throughout the region in low densities. This condition is referred to as overdispersed (Gregory et al., 1987). These species tend to be found one or two at a time, rarely under the same cover object. Other species in the area that appear to fit this pattern are Heterodon platyrhinos, Coluber constrictor, and Elaphe obsoleta.

Species with clumped distributions were found to fall into two categories in this study, those that are readily captured when encountered, and those that are not. The former

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

includes Thamnophis sirtalis, Storeria occipitomaculata, Storeria dekayi, and Diadophis punctatus. All of these species will sit tight under a cover object such as a rock or board when approached. They are usually easily caught by a quick grab after the cover object is lifted. Two clumped species that are not easily captured are Nerodia sipedon and Thamnophis sauritus. These species congregate in and around bodies of water. Although they may sometimes be captured from under surface objects, they are frequently active by day, and have the habit of basking watchfully from exposed areas such as hummocks of grass that are surrounded by water. When approached they slip into the water and swim off while at a safe distance.

It was noticed early in this study that large numbers of garter snakes could sometimes be found at certain localities, while none was found at the same localities at other times. These localities usually had large numbers of shed skins in the vicinity, indicating the presence of a sizable population of snakes. Other localities that were superficially similar to these only rarely had snakes, but never many. It was soon learned that the snakes follow a regular diel pattern of conduction basking that was altered by weather and season. Also, localities where snakes were abundant shared certain habitat features that were not found where snakes were less abundant.

In warm weather, snakes apparently conceal themselves deep underground or under massive surface objects at night, as

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

conditions are rarely warm enough for continued activity. They emerge in the morning a few at a time over a prolonged period to bask under surface objects that are exposed to the sun until warm enough to effectively conduct their daily activities. They then leave the basking site and apparently move about, or perhaps return to deep recesses. During the heat of midday, surface objects are much too warm for conduction basking, and snakes are never found under them. When evening approaches, and temperatures begin to drop, there is a massive and nearly synchronous return to surface cover objects, particularly by snakes that require higher body temperatures such as those that are incubating embryos, digesting a meal, or are about to shed their skins. A well timed sweep of the cover objects at an appropriate location can produce multiple snakes under almost every cover object, while only an hour before, none would be found in the same places. This behavior apparently represents an attempt on the part of the snakes to retain higher body temperatures for as long as possible into the night by huddling under rocks or other objects that retain heat for an appreciable time after sunset. A few snakes may be found under some of these objects for as long as two hours after sunset, but by the middle of the night, they have all been abandoned.

On days with intermittent sun and clouds, snakes may be found under surface objects throughout the day, but usually abandon them by sunset. In the early spring and mid to late fall, most conduction basking occurs during midday, as this is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

likely to be the only time when surface objects are warm enough to entice the snakes into basking. Snakes will also frequently bask exposed to direct sunlight at these times, an unusual activity at other times of year. Finally, basking behaviors may be modified when the weather is dry for prolonged periods. Snakes rarely bask under objects where the soil is completely dry to the touch. They will, on the other hand, bask under a rock whose depression has been completely inundated with water by rain, requiring them to poke their heads out from under the rock for air. Keeping all of these variables in mind, one can quickly amass large amounts of data with relatively few excursions to the field.

4.E. Description of the Study Sites (see Appendix III)

4.E.a. Ten Mile River, Sullivan County, New York

The most heavily studied site is a small old-field habitat located at the edge of the Ten Mile River Boy Scout Camp in the Catskill Mountains of Sullivan Co., NY. This site is on the northeast side of NY route 23 in the Town of Tusten, opposite the entrance to Davis Lake. Its elevation is approximately 372 m, and it lies approximately 9.05 km northeast from the Delaware River at its nearest point. The field has three old, collapsed stone building foundations in it from which rocks have been strewn in several places. Also present are two old well holes and a tiny temporary stream that travels across the edge of one building foundation. The surrounding forest is primarily oak-hickory, with scattered

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

white pine (Pinus strobus). This is the most common forest type in lowlands of the region. Garter snakes are unusually abundant in this locality. Ten to fifteen individuals can be caught here on an average collecting day, but sometimes as many as 25. Also abundant is the red-bellied snake, Storeria o. occipitomaculata. Ringnecked snakes (Diadophis punctatus edwardsi) and milk snakes (Lampropeltis t. triangulum) are found occasionally, and a single smooth green snake (Opheodrys v. vernalis) was caught.

This site is particularly attractive to garter snakes and appears to offer a number of resources that allow snakes to remain concentrated here throughout the activity seasons. Cover is abundant in the form of surface rocks that litter the ground, but are not deeply imbedded. In addition to simple shelter, these offer safe basking locations where snakes perform conduction basking while concealed beneath the sun-warmed rocks. These basking sites were heavily used by gravid female snakes, snakes that had recently fed, and those that were about to undergo ecdysis, as higher body temperatures are preferred by snakes in these conditions. Although surrounded by forest, most of the rocky areas in the field were insolated through much of the day.

The soil at this site is usually rather moist, and the center of the field often has a trickle of surface water in the spring months. Reeds and rushes grow in this portion of the field throughout the year. Earthworms are abundant, particularly in spring, and serve as the primary food source

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

for Thamnophis sirtalis. Newly captured garter snakes often regurgitated partially digested worms, and many were found in the stomachs of the snakes dissected prior to skeletonization. Pickerel frogs (Rana palustris) were also occasionally found in the field, and in the stomachs of garter snakes.

Finally, the site offers several potential hibernation sites, including the moist foundation rockpiles, and the old wells, which usually had standing water in them. Although I have no direct evidence that either of these sites were used as hibernation sites, several facts suggest that they would serve the purpose. It has long been known that garter snakes will hibernate in large numbers in subterranean cavities, but little is known of the factors that determine the suitability of a particular site. Recent studies by Costanzo (1985, 1986, 1989) reveal that moisture is critical, and Thamnophis sirtalis may often hibernate underwater. A study population in Wisconsin used an old abandoned well site, where the snakes remained submerged throughout the winter except when water levels dropped below the hibernation site of some individuals. Individuals so exposed were often subjected to predation by mice and shrews. The well was deep enough that the water surface did not freeze (Costanzo, 1986). Snakes at Ten Mile River were found in the field in the earliest spring and latest fall when weather conditions permitted activity, further suggesting that they wintered nearby.

Thus, the Ten Mile River site apparently offers all of the resources needed by these snakes. Gravid females remain

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in the area and deliver their young in the field, thus, all life history stages are available here. Sites such as these offer ideal conditions for studying the life histories of garter snakes, and do not appear to be uncommon in the mountainous regions of Eastern New York and Pennsylvania. It is odd, then, that the life history of Thamnophis sirtalis is best known from studies conducted in remote sites in central Canada, where the snakes are forced to hibernate and feed in localities separated by up to several miles. The latter pattern may, in fact, be a relatively uncommon one, imposed on these populations by the stringent ecological conditions near the periphery of the species' range.

The Ten Mile River Scout Camp has a variety of other habitats at other locations that were visited occasionally. Four other snake species were found in the vicinity on various occasions, and different localities had different proportions of the species listed above. Other species caught or seen within a three mile radius of the study site include Nerodia s. sipedon, the common watersnake; Heterodon platyrhinos, the eastern hognosed snake; Elaphe obsoleta, the black ratsnake, and Crotalus horridus, the timber rattlesnake.

4.E.b. Balsam Lake Mountain, Ulster County, New York

A second site where snakes were unusually abundant is also located in the Catskill Mountains, in Ulster County, NY, within the Catskills Preserve, Town of Hardenbergh on the side of Balsam Lake Mountain. This locality is in a high meadow (762 m) at the end of Beaver Kill Road, at a parking area for

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the Dry Brook Ridge Trail. The pitch of the slope is southeast, and the site is the coolest studied, as evidenced by the flora, and the timing of leaf and flower eclosure. This site is also a small old field, surrounded by secondary forest. The site is brushy with a variety of ericaceous shrubs, and includes several open grassy areas with exposed surface rocks. In the southern section of the field is a deep trash pit with a variety of refuse items that provide cover. A tiny temporary stream wells up from a spring near the center of the field. Again, the area supports reeds, rushes, and sphagnum, but no strictly aquatic vegetation. The surrounding forest is primarily beech-maple, with abundant hobblebush (Vibernum alnifolium), found primarily at high elevations in this region.

Three species of snakes are common at this site. Thamnophis s. sirtalis is the most abundant, but Storeria o. occipitomaculata and Opheodrys v. vernalis are also frequently seen. No other snake species were found. Garter snake food sources include abundant earthworms and frogs (Rana palustris). The eft stage of the red-spotted newt (Notophthalmus viridescens) is also abundant, but it is doubtful that it serves as a food source due to its poisonous skin secretions.

This site provides a high-altitude analogue to the Ten-mile River site described above. The snake species found here are characteristic of high latitudes, with none of the low latitude species found in the Ten Mile River vicinity. As in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the former locality, garter snakes were abundant throughout the activity season, weather permitting, and all life history stages were readily found. Garter snakes appear to attain somewhat larger sizes at this site than at the former, especially the females (see Table 8).

4.E.c. Floyd Bennett Field, Kings County, New York

The third heavily used site is Floyd Bennett Field of Brooklyn. This is a nearly abandoned military facility that has been largely converted into National Park. It is part of an artificially created island just off of Brooklyn in Jamaica Bay. On the west, it is bordered by Flatbush Ave. The ecological setting here is quite different from the previous sites, as is the climate. This is an insular site with typical coastal plain physiography. Its elevation is approximately one to three meters, and it is covered with patches of shrubby growth and Spartina grass.

Although several species of amphibians and reptiles that were once native to the Jamaica Bay area are currently being introduced here in an attempt to establish viable populations, there is a feral population of Thamnophis s. sirtalis that became naturalized long before the current recolonization program. Its place of origin is not known. However, several aspects of this population discussed below suggest that it is descended from a small propagule. Features of these snakes are similar to those from a vacant lot in Brooklyn, a few miles distant, on Flatbush Avenue.

These snakes are usually found under or near scattered

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

boards or trash items that lay strewn about the ground near abandoned buildings. Several small freshwater ponds and temporary pools are present at the site, but the garter snakes show no particular preference for them. The only other species that apparently occurs here naturally is Storeria dekayi.

4.E.d Barberry Knowe Kennels, Pike County, Pennsylvania

In Pike County, Pennsylvania, large numbers of Thamnophis sirtalis were obtained from the vicinity of Barberry Knowe Kennels (BKK), Greene Township, elevation approximately 520 m, on Route 390, about 3 miles north of the Pike/Monroe Co. Border. This site was not utilized until the summer of 1990. Snakes from this site were not marked or released, at the request of the property owners, until the summer of 1991.

Thamnophis sirtalis was very abundant here. Storeria occipitomaculata was also moderately common. A nearby pond had Nerodia sipedon, while Opheodrys vernalis and Diadophis punctatus were found in the immediate vicinity.

This site is a rural residence with a small open lot in mature secondary woodland. Cover objects are few and small in the immediate vicinity, and garter snakes are often found prowling through the lawn during the day. Storeria occipitomaculata and Diadophis punctatus use small rocks as cover. Nerodia sipedon is sometimes found basking on the shores of a nearby man-made pond.

The garter snakes from this site had many aberrant scale counts for this species were found. In spite of their well

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

known variability in color pattern, Thamnophis sirtalis is usually quite constant in the number of dorsal scale rows, and head scales, except labial counts, which vary within well defined limits (Ruthven, 1908). The normal number of scale rows is 19 in the anterior half of the body, reducing to 17 just posterior to mid-body. However, some snakes from Barberry Knowe Kennels and vicinity had 15 scale rows posteriorly, and a few had a maximum of 17 or 18. The number of ventral and subcaudal scute anomalies did not appear to be greater than normal. The snakes appear to be normal in all other respects.

4.E.e. Miscellaneous Other Sites

Garter snakes from a variety of other locations were also marked and released in an attempt to establish study sites. Most of these produced insufficient data for growth analysis, but skeletal specimens procured at these sites were used in some aspects of the study.

A small glade in a wooded section at the north end of Big Pond, in Delaware County, NY, often had juvenile garter snakes, as well as mature Storeria occipitomaculata and Diadophis punctatus. The lack of mature Thamnophis was probably due to a lack of appropriate sized cover objects.

A snowmobile trail on Campbell Mountain Road in Delaware County, NY, had abundant Thamnophis sirtalis, Storeria occipitomaculata, and Opheodrys vernalis. This site was of moderately high elevation and had snakes of all sizes, but was the furthest location from home and received correspondingly

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

less attention.

The Basherkill is a large, low lying marsh in a steep sided valley in Sullivan County, NY. Very few specimens of Thamnophis sirtalis were recovered here, but Nerodia s. sipedon and Thamnophis s. sauritus were abundant. Also found in this location were Heterodon platyrhinos and Coluber constrictor, species typical of low elevations in southeastern New York.

A powerline cut on Makamah Road in Suffolk County, Long Island, NY, produced a small number of specimens on two outings, but others were provided by an independent collector. Also known from this site is Storeria d. dekayi, a typical lowland species that is often found in heavily populated areas.

A vacant lot in Brooklyn, on Flatbush Avenue just a few miles distant from the FBF site produced several Thamnophis sirtalis, and abundant Storeria dekayi. The garter snakes from this site are similar in pattern to those of FBF.

4.F. Growth: Results

A total of 735 Thamnophis s. sirtalis were examined during the course of this study, of which 432 were marked and released at their original points of capture, while the remainder were skeletonized. General scutelational features of these specimens are summarized by location in Tables 6 and 7. Almost all of the specimens are from lower New York state and eastern Pennsylvania. The larger population samples

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

obviously differ in a number of respects, but most differences are a matter of shifting means in broadly overlapping character ranges. In addition to the quantitative differences shown, the three main study populations differed in color and pattern to such an extent that the origin of many specimens was evident on that basis alone.

4.F.a. Size Differentiation among Sites.

The three main study populations from New York and one from Pennsylvania are summarized independently (Table 8) for SVL of various groups. Differences in size are apparent, as determined by minimum size at maturity, average size, and maximum size among the large samples from the TMR, and BMT sites. Average adult sizes from the four localities were subjected to analysis of variance (General Linear Models procedure) by sex (Fig. 51). Garter snakes from TMR are significantly smaller than those from all other sites except BKK. Snakes from BKK are significantly smaller than those from FBF, but only the females are significantly smaller than those from BMT, while males are not distinguishable. There is no apparent relation between size and altitude, as the populations from the highest (BMT) and lowest (FBF) sites are not significantly different.

It is clear that the size differences among these populations are affected by the minimum size of mature adults, which determines the number of small individuals included in the analysis. In an attempt to eliminate this effect, the analysis was repeated with the same minimum adult size (300 mm

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SVL) applied to all populations. This increased sample sizes for the populations to varying degrees by adding individuals in the smaller size ranges. In this analysis, differences among populations are only affected by maximum size and the distribution of sizes within the populations. The results of this analysis were the same for females as in the previous approach. While the F value of the overall ANOVA was smaller (10.5, compared to 16.09 in previous analysis), the same populations proved to be significantly different from one another. Among males, the F value of the overall analysis dropped from 13.09 to 8.91, and the differences between populations from FBF and BKK were no longer significant. The importance of the size differences noted, and those of color pattern are difficult to determine with certainty, but some biological factors that may affect body size in these populations are discussed below.

4.F.b. Cohort Analysis of Growth Rates.

The cohort analysis shows that first year snakes are generally identifiable as such on the basis of size alone. Figures 52-85 illustrate the sizes of individual specimens plotted by month for each of the three main localities. Second year snakes, although they often produce a pulse in the histograms, are not distinctly separable from older specimens, and were not analyzed by this method. The sizes of the specimens in each cohort were averaged by month to arrive at a crude monthly mean size for each cohort (Table 9). The differences between these means were divided by the average

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

number of days separating the midpoints of two months (30.5) to arrive at an approximation of growth rate in millimeters per day.

The growing seasons at the three sites are different, such that the amount of annual growth expected at each site would be different even if growth rates were relatively constant among sites. Growth periods were determined for each site by comparing capture records with the number of field trips to the site in early spring and late fall. It is recognized that snakes will emerge from hibernation to bask for short periods on mild, sunny days during these seasons, but feeding, and probably growth, do not occur at these times. Growth periods were considered to begin when snakes were active in abundance on a regular basis, particularly noting if immature animals had food in their stomachs (adults may forego feeding during breeding seasons while the young are growing). Growth periods were calculated on the basis of the earliest and latest collecting trips to produce samples of active snakes, rounded to the nearest week. Thus, the growth period for Balsam Mountain snakes extends from mid-April to mid-September (about 151 days). TMR snakes grew from early April to late September (176 days). FBF snakes grew from the beginning of April to early October (about 206 days).

This approach is subject to several sources of error: 1) collecting dates were not controlled to fall at regular intervals, but were haphazard, occurring when opportunity allowed. 2) The number of specimens collected on a given date

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

was strongly influenced by weather conditions and the diel timing of collecting; thus, some monthly averages are heavily weighted by large samples near one end of the month, and small or no samples at the other end of the month. 3) Samples were pooled over years with varying annual weather cycles. Rapid growth during a month in one year may have been averaged with slow growth in that month the following year. 4) Snakes are more difficult to catch during some months of the activity season than others, providing small sample sizes. In spite of these disadvantages, estimates of growth rates obtained by this method agree fairly well with those obtained by repeated measures of recaptured snakes (see below).

The cohort growth summaries presented in table 9 start with the first month of life for which data are available. The differences in parturition date between TMR and BMT are real, and result from the later date of spring emergence at BMT, as well as slightly lower temperatures. Data for FBF are few and lacking for the months of July and August, respectively, so parturition date is not known.

Differences in growth rates are apparent both among sites and among months (Figs. 86-88) Growth is typically slow in the fall and early spring, but rapid in the late spring and summer months. Average growth rates are lowest at Ten Mile River, where the adult size is lowest. Average growth rate is highest at Balsam Mountain, where adult sizes are the largest, and where the growing season is shortest.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

4.F.c. Recapture Analysis of Growth Rates.

The results of the mark and recapture study are presented in Table 10. Thirty-six specimens were recaptured a total of 41 times at four separate localities. Twelve of the specimens were males, only one of which was recaptured twice. These males were recaptured at all of the three main mark and release sites plus two specimens from the immediate vicinity of the author's residence.

Twenty-four females were recaptured, four of them twice. Most are from the TMR and BMT sites, with only one recapture at FBF. Most of these data indicate growth rates that are lower than those found from cohort analysis; although, only five individuals were recaptured within the first year of growth. Of these five, two grew at >1.0 mm/day, and thus comparable to cohort rates. A third specimen grew at 0.90 mm/day, a little lower than cohort rates indicate, but this specimen was captured in late spring and recaptured in early summer, a little before the maximum rates are expected by cohort standards. The last two specimens representing first year recaptures grew at average rates of 0.313 and 0.342 mm/day, but, again, the original captures were in late summer, the recaptures in late spring. This period spans hibernation and the seasons of lowest growth rate.

Most of the recapture data are for older specimens and indicate lower growth rates. Recapture records that span less than 50 days are disregarded because they may include lulls or spurts in growth and because the amount of growth expected in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

these periods is little more than double the possible measurement error range in small snakes. Negative growth rates obtained for some individuals are obviously due to measurement error, and occur only for elapsed times of 21 days or less.

The average growth rate for seven males recaptured following the first year of growth was 0.515 mm/day. The largest specimens grew at lower rates than this, and the lowest rates were for snakes caught in late fall and recaptured in early spring. The average recapture growth rate for 21 females, larger than first year specimens, and whose recapture period was greater than 50 days was 0.359. This rate is lower than that shown for males, but includes several records for very large specimens, whereas all of the males were smaller than their estimated third year size. Interestingly, unusually low growth rates (less than 0.10 mm/day) are rare (only four instances documented), but one female that was recaptured twice grew at a rate less than 0.10 mm/day both times, suggesting that this individual may have ceased growing, but whether this condition was permanent or not is not known.

When plotted against average size of the paired capture records (Figs. 89 and 90), growth rates from the recapture data produce a nearly linear plot with a negative slope. Only two specimens to the extreme left fall far below the plot. Males produce a steeper slope than females, indicating a more rapid decline in growth rates.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Crude estimates of age are provided by comparing data from the first year cohort study above with growth rates of larger specimens obtained from the mark and recapture study. Thus, if males grow at about 0.45 mm/day during their second year (estimated from Table 10), the three populations will reach the sizes shown in Table 11, by the end of that year. The same figures were calculated for females on the basis of 0.55 mm/day (also estimated from Table 10). Older snakes appear to grow at an average rate of about 0.2 to 0.3 mm/day. Sizes of snakes at the end of their third year are based on these estimates.

4.G. Body Growth: Interpretation.

Of the two most commonly used growth models, the data presented in Table 9 and Fig. 86-88 would require use of the logistic model, because growth rates are clearly lower in the first month or two of active life than through most of the remainder of the first year. However, viewed from a coarser grained perspective, the von Bertalanffy model would be preferred, since growth is greatest in the first year and decreases steadily thereafter. Von Bertalanffy data typically plot as a linear function of age or size with negative slope, as suggested by Figs. 89 and 90. In reality, the data presented here do not fit either of these models well. Very few reptiles grow at anything like a steady rate, and models such as these are only useful in describing gross patterns.

Growth rates of the garter snakes varied over the course

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of a single growing season (Figs. 86-88) as well as over the course of a lifetime (Figs 89 and 90). Thus, while the von Bertalanffy and logistic growth models may be useful as crude models of average lifetime growth rates among years, a more detailed model would require oscillating annual growth parameters. Furthermore, individual variability in growth rate among specimens suggests that a model that takes increasing variability into account should also be used. Fitting a detailed model of growth to the present data has not been attempted here due to the low number of recaptures.

4.H. Vertebral Growth.

4.H.a. Vertebral Growth: Methods.

Vertebral measurements from a single columnar position were plotted against SVL for a growth series of garter snakes. Specimens from both sexes were plotted together in order to compare sex effects in older animals. Separate plots of each sex were also prepared to inspect for trends within sexes (not shown). All localities, (including several midwestern specimens) were used to provide larger samples for the upper portion of the size range. These data were then converted to logarithms and their covariance matrix subjected to principle components analysis by sex as suggested by Bookstein et al. (1985). The second and third eigenvectors were inspected for possible shape factors that might distinguish between large and small snakes in the absence of size.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

4.H.b. Vertebral Growth: Results.

Plots of each variable against SVL produce some very informative contrasts. Measurements of overall vertebral length (CNT and PRP) plot as linear functions of SVL (Figs. 91 and 92). This is logical, as the length of a snake is generally little more than the sum of the lengths of its component vertebrae. Furthermore, all variables show a strong positive relationship with SVL, as expected. However, very few of the plots of non-length variables that include data from large females produce convincingly linear plots.

With the exception of the two length measurements, all variables plot with a similar pattern (Figs 93-110). Growth of these variables appears to be separable into three distinct phases: 1) an early, juvenile phase, in which growth is regular and slow, 2) an early adult growth spurt, or robustification phase, in which non-length variables grow at a much more rapid pace for a short period, and 3) a later, slower, phase of elongation, comparable in rate to the juvenile phase. It should be borne in mind, when viewing these graphs, that SVL increases at a decreasing rate in older animals.

The differentiation of these phases is most pronounced in the following variables: APL, NAH, COH, COW, CNH, CNW, and HYD. Features of the cotyle-condyle articulation are prominent here, as are two muscle attachment processes. The neural arch, which encloses the spinal cord, would be expected to grow more slowly than the rest of the bone, since the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

nervous system usually grows more slowly than other body parts in adult development. The phase differentiation of the cotyle-condyle variable plots and muscle attachment processes are slightly exaggerated by a male-female difference in growth rates, but the phases are still distinct in plots showing only females. Males do not show the triphasic growth plan when plotted alone. This is because they usually do not grow large enough to express the third phase.

The first principle component of the analysis of the females accounts for more than 92% of the variability in the data (Table 12). This high value is expected when a large size range is covered, since most variables will increase during growth. All variable loadings on this component are positive (between 0.15 and 0.30). The second principle component has high negative loadings for APL, NSH and HYD, as one might expect on the basis of the bivariate plots, and PZL produces a high positive loading. Cotyle-condyle loadings and the NAH loading are not very high on any of the early eigenvectors. In fact, NAH does not produce a substantial loading until eigenvectors 9 - 13. The cotyle-condyle features (COW) produce one high loading on eigenvector 5.

The male data are more variable at any given SVL, and the first principle component accounts for 85% of the variability (Table 13). The loading patterns are very similar to those of the females on PC1 and PC2. The first eigenvector has positive loadings of moderate magnitude (between 0.13 and 0.32). The second eigenvector produces a contrast between PZL

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

with a high positive loading, and APL, HYD, and NSH, with high negative loadings, but males differ from females in that PZH also has a moderately high positive loading on the second principle component.

4.H.c. Vertebral Growth: Interpretation.

It is clear from the principle components analysis that young and old animals should be distinguishable on the basis of vertebral shape, irrespective of size. Important features that contribute to this difference are points of muscle attachment: NSH, HYD, and APL, and perhaps some articular surfaces such as the postzygapophysis. Judging from the bivariate plots, relative neural arch dimensions should also be helpful.

The tight, linear plots of CNT and PRP should allow reasonably accurate prediction of SVL from either or both of them in combination, given columnar position. Other variables will require a more sophisticated model before accurate prediction is possible. Nevertheless, several interesting features of snake vertebral development are apparent from comparisons among the bivariate plots of these variables and the principle components analysis. 1) early adulthood is apparently characterized by a robustification, or rapid growth of non-length features, of the vertebrae, at least in the central region of the vertebral column. 2) late adulthood (in females) is characterized by vertebral elongation, with most non-length variables following a negatively allometric trend.

Variables that appear to contribute the most to shape

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

differentiation along the juvenile - adult gradient are the muscular attachment processes (NSH, HYD, APL) and the neural arch. Articular facets also contribute to shape differentiation, but apparently to a lesser degree. Why NAH does not appear to contribute any significant loadings to the lower principle components is not known. Its contribution to the highest principle components is not informative, as these are generally considered to be uninterpretable.

The male and female data sets may be compared by determining the angles between their corresponding principle axes. These are calculated as the inner product of the compared vectors (Voss et al., 1991). Only the first two eigenvectors are compared in this case, as they are the only ones that are interpreted. The first principle axes of males and females differ in direction by only 3.928 degrees, while the second principle axes differ by 28.301 degrees. The similarity between the first principle axes of the two sexes suggests great similarity in the nature of the growth processes affecting both sexes. The greater difference between the second principle axes of the two sexes indicates that the shapes of the vertebrae differ between the sexes, in spite of their comparable growth patterns.

The differential growth parameters of the vertebrae of young and old adults suggest important changes in vertebral function during ontogeny. Several adaptive hypotheses may be offered by way of interpretation: 1) Vertebral elongation in old adult females may be a way of increasing the amount of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

space available for incubating embryos without producing excessive girth. 2) Elongate vertebrae are usually associated with cursorial snake species such as racers and whipsnakes. Vertebral elongation may therefore represent a change in behavior or microhabitat use by old/large adult females. If large animals tend to occupy exposed areas more, or if exposure during courtship and mating is critical, then perhaps a cursorial form would be more adaptive. Alternatively, elongation of vertebrae in large adults may be a non-adaptive (neutral) response: if external vertebral features such as zygapophyseal facets work as effectively at smaller adult sizes as larger, there may simply be no need for them to keep pace with overall vertebral size.

Several points of caution should be mentioned regarding the graphic plots of variables against SVL. Data are few in some critical areas of the graphs, rendering interpretations tenuous at best. The central region is most heavily sampled because usable data were available from other sections of this study. The extremes of the column are sparsely illustrated because appropriate material is less easily obtained. It is possible that the swollen central portion of each plot is only due to the increased variability derived from large samples in this region. The effects of pooling across geographic localities is also bound to have an effect. Clearly, more data and detailed analysis are needed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

5. Sexual Dimorphism

5.A. Sexual Dimorphism: Introduction

Sexual dimorphism in snake vertebrae has rarely been considered in the literature. This is undoubtedly because data on soft anatomy of skeletal specimens are rarely recorded when the specimens are skeletonized. Brummer (1980) measured vertebrae from 225 specimens representing 42 species of colubrid snakes. In only two of those species were both male and female specimens identified as such. She was thus unable to comment on sexual dimorphism extensively.

Keiser (1970) reported sexual dimorphism in the hemapophyses of caudal vertebrae of vine snakes (Oxybelis aeneus), but did not note any dimorphism in precaudal vertebrae. Bogert (1964) reported sexual dimorphism in the unusual precaudal vertebrae of Ninia sebae. The neural spine in this species is expanded laterally at the dorsal edge to form a platform. Bogert comments on two specimens, a male and a female, noting that although they are nearly the same size, the male had larger, more robust vertebrae, with more expanded neural spines and prezygapophyses. It is unfortunate that Bogert did not provide the snout-vent length measurements of these specimens, to allow a more informative comparison of the illustrations, since similar changes could be brought about ontogenetically.

5.B. Sexual Dimorphism: Methods

Comparisons among the sexes were made by assembling

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

samples of restricted SVL size range (396 to 451 mm SVL), and subjecting them to principle components analysis and discriminant analysis. Forty-five such specimens (Table 14) were measured at the 43 PCT position for 20 variables (the three smallest, HYW, NSW, and PCN, were excluded because of their high variability).

Principle components analysis was performed on these data in an attempt to determine if sex made any sizable contribution to intraspecific variation. If so, variable loadings on principle component axes that were influenced by sex might indicate which features differ among the sexes in similarly sized individuals. The analysis was performed on a covariance matrix of the log-transformed data as above.

The same data set was then subjected to a discriminant analysis to determine how effectively the two sexes may be distinguished in this size range. In this instance, the raw measurement data were analyzed.

5.C. Sexual Dimorphism: Results

An initial principle components analysis revealed a single outlier (TCL942, a male from FBF). Since this specimen plotted far down the male-female axis in the male direction, it was eliminated, and the data reanalyzed without it. Figure 111 is a plot of the specimens on the first two principle components of the reanalyzed data. Figure 112 shows the same data plotted on principle component axes two and three. The plots clearly show a relatively clean separation of males and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

females on component two, with very little overlap. Table 15 shows the eigenvalues and table 16 the first two eigenvectors resulting from the principle components analysis. These components account for nearly 83% of the variation in the data set. The second eigenvector reveals a strong contrast between features of the cotyle-condyle articular joint (COH, COW, CNH, CNW) and two apparently unrelated features, the depth of the hypapophysis (HYD) and height of the postzygapophysis. Only two other variables (NSL and APL) have loadings greater than 0.2. Both of these are protuberant processes of muscular attachment.

The discriminant analysis produced a very clean separation of the two sexes, with all individuals appropriately identified except one male that was assigned to the female category. Three vertebrae that were not included in the initial data set (two from specimens that were not included) were analyzed as a test data set, and all were correctly identified. These vertebrae were from slightly different columnar positions (table 17) than the original, learning set.

5.D. Sexual Dimorphism: Interpretation

The two sexes are clearly distinctive in morphology on the basis of the above analyses. It is interesting that the features that produce the strongest contrast between the sexes are related to the cotyle-condyle articulation. A retrospective examination of the morphology of this feature

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

revealed that the differences are clearly visible, although they had not previously been noticed. The question arises as to why these features should differ among the sexes. The most obvious possibility is the pronounced size difference between mature males and females. In snakes, large bony elements grow by a continual process of internal resorption and external deposition (Enlow, 1969). Perhaps bone cannot be resorbed from this critical articular surface because of potential impairment of vertebral function. If so, then this surface would be constrained to grow primarily by peripheral accretion. In this case, the functional joint in young snakes would have to be a functional model of the center portion of the adult joint. Since females will ultimately have larger vertebrae than males, the cotyles and condyles of younger females will have to be larger, and perhaps less curved, than in males of the same size. In this context, it is noteworthy that the male specimen that was classified as female by the discriminant analysis was collected in the vicinity of Erie, Pennsylvania. This represents a western population that presumably has larger maximum snout-vent lengths than most of the eastern populations that constitute the bulk of this study.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

6. CONCLUSIONS

6.A. Summary of Results.

The study of vertebral size and shape in snakes is still in its infancy. Detailed analyses of several additional factors will be required before a quantitative approach to vertebral identification can be perfected. The present study provides quantitative data on three sources of variability: number of vertebrae in the column, vertebral growth, and sexual dimorphism; and graphic descriptions of a fourth: intracolumnar variability. Detailed analyses of intracolumnar variability and geographic variation await more data collection. The following points are brought out by the foregoing analyses:

1) Vertebral position identity appears to depend on relative columnar position rather than absolute sequential distance from either end. The vertebral column may be most profitably visualized as a continuum of infinitesimal positional loci, each specifying a particular morphology. The morphology expressed is determined by the number of segments that ultimately make up the column. As segments are formed during ontogeny, their morphology is dictated by the locus nearest their center, and the distance between central loci. Local factors within the column, such as positions of internal organs, etc, may provide some secondary influences on positional identity.

2) Serial homology of vertebral positions is best determined among specimens with different numbers of precaudal

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

vertebrae on the basis of the percentage position of a vertebra within the column, determined by VNO/NOV.

3) The number of precaudal vertebrae in a column influences vertebral shape by causing a relative shortening of vertebrae as their number increases. This effect is referred to as vertebral packing, and is distinguished from general size effects which would cause smaller (younger) snakes to converge in snout-vent length on larger snakes with fewer vertebrae. The latter effect appears to be insignificant when compared to vertebral packing.

4) Overall body size is a biologically important, but too often overlooked aspect of snake morphology. In the present study, sexual dimorphism was pronounced, with females reaching sizes half again as large as males. Geographic variation in size parameters was also great, with significantly different average adult sizes among two pairs of populations. Oddly, the two populations with the largest individuals occur at opposite extremes of an altitudinal gradient (FBF and BMT).

5) Growth in Thamnophis s. sirtalis is in the form of a monotonically increasing function with annually varying rates, producing a step-like pattern when plotted against size. Taken from the broad perspective of mean annual growth, the pattern would probably be best modeled by the von Bertalanffy growth model, but, at a finer grain, viewed within years, growth would probably be best modeled by the logistic model. Large annual oscillations in growth rate in young snakes are damped as age progresses.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

6) Vertebral growth appears to proceed in several phases. Growth in general length dimensions proceeds at a regular linear pace. Other vertebral dimensions are characterized by a period of rapid development in young adults, referred to as robustification. Non-length features then slow in growth as the vertebra continues to lengthen. This phenomenon occurs primarily in females in the populations studied, as males rarely attain the sizes at which this transition takes place. Features that produce shape contrasts among small and large individuals include accessory process length, neural spine height, hypapophysis depth, and neural arch height. Cotyle and condyle dimensions and postzygapophyseal length may also play a lesser role.

7) Sexual dimorphism occurs in Thamnophis s. sirtalis vertebrae, particularly with respect to the relative size of the cotyle-condyle articular joint. Females tend to have larger cotyles and condyles than males of the same sizes (SVL). Discriminant analysis was able to differentiate among males and females with high consistency, and allocated all three test case specimens to the appropriate category.

6.B. Implications for fossil identification.

It is often claimed that vertebral variability is high in snakes and that the identification of isolated vertebrae is thus rendered difficult or impossible. However, when appropriate variables are controlled, it is seen that the myriad variations of vertebral shape seen in at least one

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

species, Thamnophis s. sirtalis, are rigorously patterned and highly systematized. If the empirical patterns seen here can be appropriately modeled, it seems reasonable to expect that precise identifications will be possible. The great majority of work that has been done on fossil snakes to date has been highly subjective in nature, depending on visual comparison of an overall gestalt impression of one species with another. Most such work is integrated into general studies of fossil snake assemblages or entire reptile faunas from a given locality. The primary goal of such studies is the enumeration of taxa present and general conclusions about habitat and climate of the site of deposition. Identifications of this nature are easily criticized, and difficult to defend. Given the rigorous nature of the patterns described herein, it seems reasonable to conclude that a worker who recognizes the appropriate sources of variability should be able to make effective allocations of isolated vertebrae to known taxa.

It is helpful to consider the situation in snake paleontology from a broader perspective. Most specialized fields of science can be divided into early exploratory - descriptive phases that are largely empirical in nature, and later analytical phases that are more theoretical in nature. Exploratory activity in a science should diminish as predictive theory becomes better developed. It is not unreasonable to expect the exploratory phase of a given field to be subjective in its interpretations. Furthermore, we

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

would expect perfectly reasonable hypotheses proposed in such an exploratory phase to be refuted or refined by subsequent analytical work. Paleontology is an unusual field in that it will always require intensive levels of exploratory/descriptive work regardless of the degree of progress in analytical aspects of the science. This is because new fossils will continue to become available as new strata are exposed, and what new fossils tell us cannot be predicted from theory.

Snake paleontology is a field that appears to be stalled in the exploratory - descriptive phase of faunal listing. In very few cases have snake taxa higher in rank than species and lower in rank than "all snakes" been revised with detailed consideration of their fossil representatives. Most taxonomic revisions of fossil forms consist of synonymizing or otherwise eliminating a fossil species, or the shifting of higher level taxa from one position to another on the basis of non-anatomical (e.g. temporal or ecological) reasoning.

The causes of this scholarly stalemate in snake paleontology appear to be largely sociological. Two contributing factors may be cited: 1) the complexity of the patterns of variability in snake vertebrae are forbidding to most students and require large investments of time for meager payoff in terms of results. 2) Criticisms of snake paleontology have been overly harsh and discouraging. Critics have suggested that the practice of naming fossil snakes on the basis of small samples of fossils should be abandoned

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(e.g. Brummer, 1980). This attitude is apparently due to a general lack of awareness of the tractability of patterns of intraspecific variability that occur in snake vertebrae. More constructive and perhaps valid criticisms would be that the field is not sufficiently analytical, that morphological variation in the vertebrae of modern snakes is too poorly known, and that very little synthetic work has taken place in fossil snake systematics. If anything, much more work is needed in this field.

The value of continuing general survey studies of fossil snake faunas should not be overlooked. An experienced and careful paleontologist can allocate specimens to taxa with a fair degree of accuracy. When published, these lists alert the scientific community to the presence and location of fossils that others may be interested in studying. Sufficiently unique fossils must be named, even if only a single representative is found, to alert others to the presence of, or unusual nature of a given fossil. Such a procedure is not to be taken lightly, however, and the proposal of a new name should be accompanied by detailed anatomical descriptions, figures, and accounts of comparisons with other taxa. Proliferation of names and descriptive text is objectionable to some, but in the end, it is probably better to have long synonymies in the literature, than museum cases full of undescribed species, whose presence is unsuspected by would-be workers.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

6.C. Future Research.

Two important sources of variability in vertebral shape have not been considered in detail in this paper: intracolumnar variability due to position, and geographic variability. The next step in this study will be to perform analyses of growth patterns and sexual dimorphism at several positions within the column, sampling more intensively where shape change is most rapid. Comparisons among positions can then be made. Geographic comparisons will be made controlling for sex, size, and position, to determine the nature and magnitude of variability among localities.

Ultimately, a quantitative approach to assigning unknown vertebrae to sex, position, and age (or at least, size) will be developed. Morphological variability of vertebrae will be modeled in terms of a series of interconnected multidimensional centroids within a framework of positional, age, and general magnitude axes. Probability contours will be used to produce a three dimensional morphoscape that is highly arched at one end, representing the adult condition, and slopes downward to a less arched, juvenile form at the other end. Unknowns would then be assigned to a position in this morphospace on the basis of their dimensions. Similar models will be developed for other species and genera to determine how readily they can be distinguished.

Studies of growth in captive populations from the same localities as studied here would help to define their inherent genetic growth potential. Captive growth patterns may be

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

compared to growth variability in free-living individuals to determine the influence of natural conditions on native growth rates.

Morphometric studies similar to those undertaken and suggested here will be performed on caudal vertebrae and skull elements. Ultimately, the morphology of modern taxa will be compared to Quaternary fossils that have been assigned to those taxa. Morphometric trends in fossil snakes will then be traceable through time. In addition to taxonomic conclusions that can be drawn, careful comparisons may enable more precise estimates of environmental parameters affecting fossil environments. For example, the shape of a precaudal vertebra is affected by the number of vertebrae in a column, and the number of precaudal vertebrae in a column is affected by average developmental temperature. Perhaps vertebral shape could be used to estimate the number of precaudal vertebrae present in a column, and, if a substantial population of specimens is present, the average number of precaudal vertebrae in their columns may provide a useful estimate of average paleotemperatures during development.

Finally, the phylogenetic implications of complex, three dimensional shapes that lack precise landmarks should be further explored. It is apparent that modern morphological systematics is reliant on a particular kind of character: those that can be easily divided into two, or a limited set of alternate states. Features that grade smoothly, or whose shapes can not be readily dichotomized due to complexity or

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

high variability may also provide significant information that has not been utilized.

In conclusion, the morphology of snake vertebrae is an untapped goldmine of useful information. The serial repetition of complex anatomical features along the vertebral column, each slightly different from its neighbors, has long been viewed as a deterrent to active study. I hope that this study will convince others that the opposite is true. Detailed studies of this unusual combination of features may provide insights into the nature of development, morphology, and evolutionary adaptation that are not available in other animals. Furthermore, these structures should ultimately provide finely resolved identifications of fossil specimens, particularly where the fossils are available in large enough samples to provide some insight into the variability present in the unknown taxon.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

+INFRAORDER CHOLOPHIDIA - Extinct Snakelike Vertebrates
  +Family Lapparentophiidae - Cretaceous "Terrestrial Snake"
  +Family Pachyophiidae - Cretaceous "Marine Snake"
  +Family Simoliophiidae - Cretaceous "Marine Snake"
 INFRAORDER HENOPHIDIA - Primitive Snakes
 +Superfamily PALAEOPHIOIDEA - Early Snakes
  +Family Dinilysiidae - Cretaceous "Snake"
  +Family Palaeophiidae - Early Cenozoic Sea-serpents
  +Family Archaeophiidae - Eocene Scaly Vertebrate
  Superfamily PYTHONOIDEA - Pythons & Allies
  +Family Madtsoiidae - Early Cenozoic Henophidian
   Family Pythonidae - Pythons
   Family Loxocemidae - Mexican Burrowing Python
   Family Xenopeltiidae - Sunbeam Python
   Family Calabariidae - African Burrowing Python
   Family Aniliidae - Coral Python
  Superfamily Booidea - Boas & Allies
   Family Boidae - Boas
   Family Erycidae - Sandboas
   Family Cylindrophiidae - Pipesnakes
  Superfamily TROPIDOPHIOIDEA -- Woodsnakes & Allies
   Family Tropidophiidae - Woodsnakes
   Family Bolyeriidae - Mauritius Snakes
INFRAORDER SCOLECOPHIDIA - Blindsnakes
  Superfamily UROPELTOIDEA - Slender Blindsnakes
   Family Uropeltidae - Shieldtail Snakes
   Family Leptotyphlopidae - Threadsnakes
  Superfamily TYPHLOPOIDEA - Typical Blindsnakes
   Family Anomalepididae - Primitive Blindsnakes
   Family Typhlopidae - Typical Blindsnakes
INFRAORDER CAENOPHIDIA - Advanced Snakes
  Superfamily Acrochordoidea - Ancient Watersnakes
  +Family Nigerophiidae - Early Watersnakes
   Family Xenodermatidae - Pebbled Swampsnakes
   Family Homalopsiidae - Rearfanged Watersnakes
   Family Acrochordidae - Asian Wartsnakes
  Superfamily LAMPROPHIOIDEA - Generalized Snakes
  +Family Anomalophiidae - Eocene Watersnake
  +Family Russelophiidae - Eocene Watersnake
   Family Lamprophiidae - Housesnakes & Allies
   Family Psammophiidae - Sandsnakes
   Family Xenodontidae - Neotropical Snakes
   Family Dipsadidae - Middle American Snakes
  Superfamily VIPEROIDEA - Vipers & Allies
   Family Viperidae - Vipers
   Family Crotalidae - Pitvipers
  Superfamily ELAPOIDEA - Front-fanged Snakes
   Family Elapidae - Cobras & Allies
   Family Hydrophiidae - Seasnakes
  Superfamily COLUBROIDEA - Harmless Snakes
   Family Colubridae - Racers & Allies
  *Family Natricidae - Modern Watersnakes

Figure 1. Snake classification, modified from Dowling (1988).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Infraorder Cholophidia +
  Family Simoliopheidae +
  Family Madtsoiidae +
  Family Dinilysiidae +
Infraorder Scolecophidia
  Family Anomalepididae
  Family Typhlopidae
  Family Leptotyphlopidae
Infraorder Alethinophidia
  Superfamily Acrochordoidea
    Family Nigeropheidae +
    Family Palaeopheidae +
    Family Anomalopheidae +
    Family Acrochordidae
  Superfamily Anilioidea
    Family Loxocemidae
    Family Xenopeltidae
    Family Aniliidae
    Family Uropeltidae
  Superfamily Tropidopheoidea
    Family Tropidopheidae
  Superfamily Bolyerioidea
    Family Bolyeriidae
  Superfamily Booidea
    Family Pythonidae
    Family Boidae
  Superfamily Colubroidea
    Series Proteroglypha
      Family Atractaspididae
      Family Elapidae
    Series Opisthoglypha
      *Family Colubridae
      Family Viperidae

Figure 2. Snake classification, modified from McDowell, 1987.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

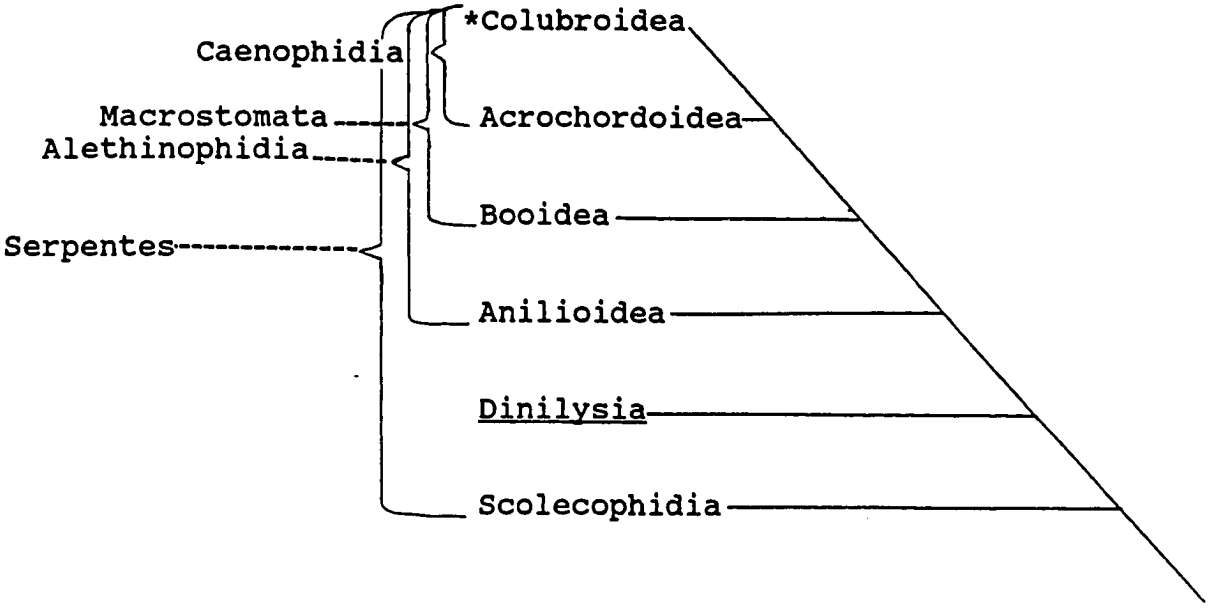


Figure 3. A cladogram of snake relationships, Modified from Reippel, 1988.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

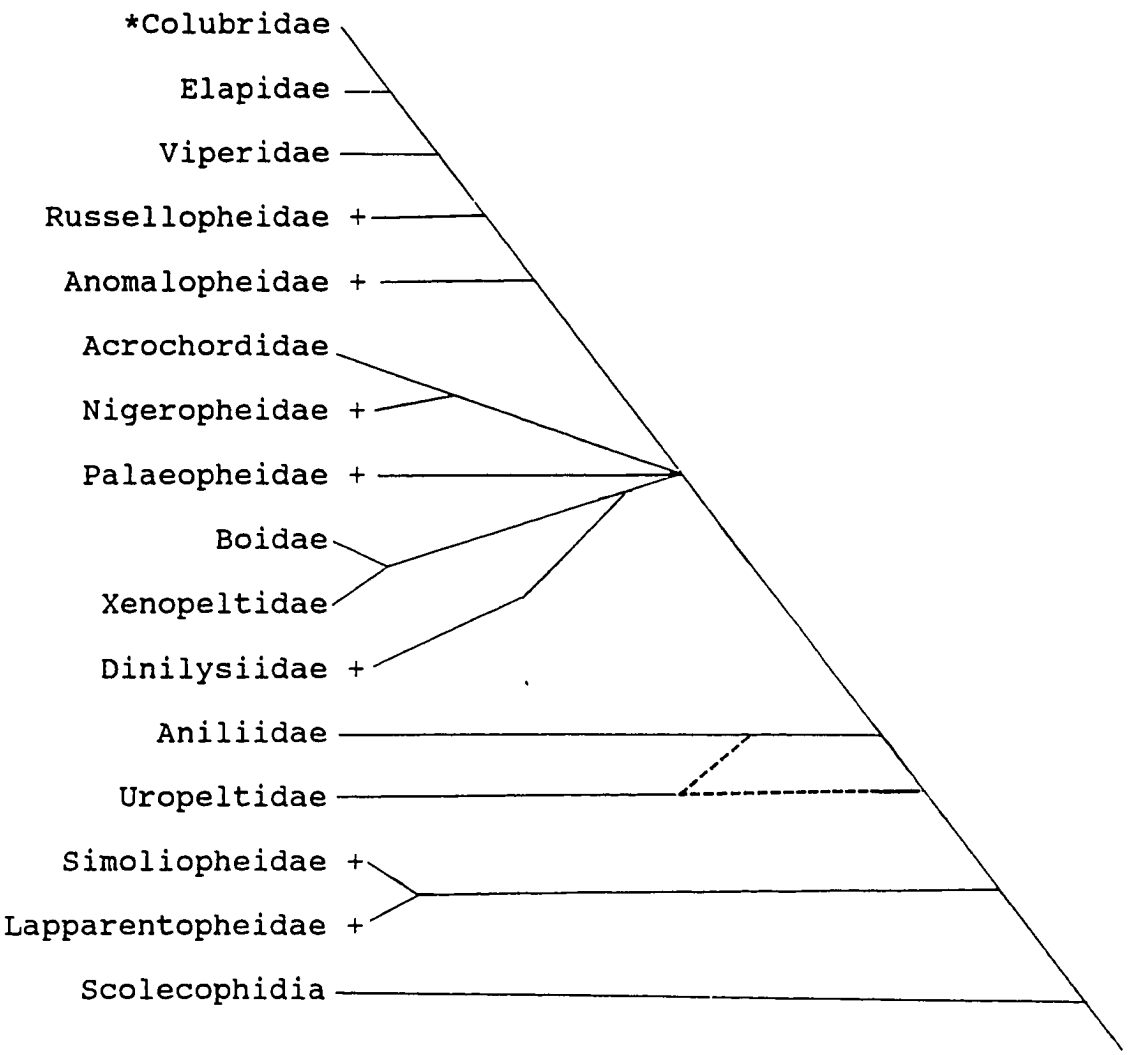


Figure 4. A cladogram of snake relationships, modified from Rage, 1987.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 5. Systematic arrangements of the Natricinae

Rossman & Eberle, 1977.	Lawson, 1987.
Subfamily Natricinae	
Tribe Natricini	
Afronatrix	
Natrix	
Sinonatrix	
& all other Old World genera	
Tribe Thamnophiini	Tribe Thamnophiini
Adelophis	Genus Nerodia
Clonophis	Subgenus Nerodia
Nerodia	taxispilota group
Regina	cyclopion group
Seminatrix	sipedon group
Storeria	Subgenus Thamnophis
Thamnophis	
Tropidoclonion	all other genera unchanged
Virginia	

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

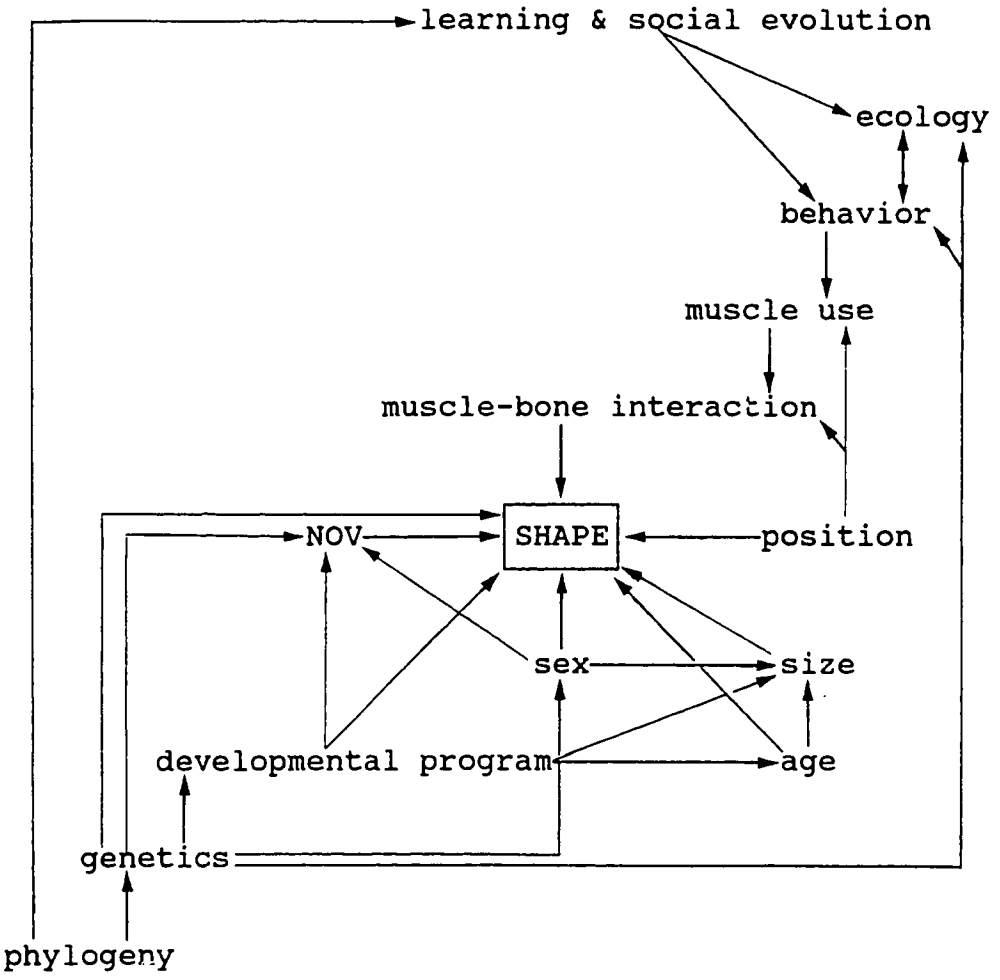


Figure 6. Path diagram of the factors that influence vertebral shape in snakes.

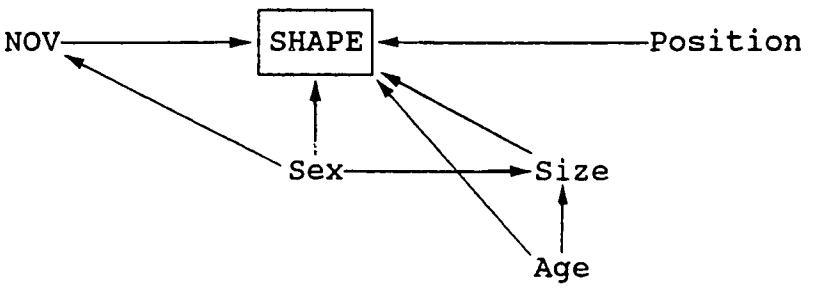


Figure 7. Factors influencing shape that are addressed in this paper.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

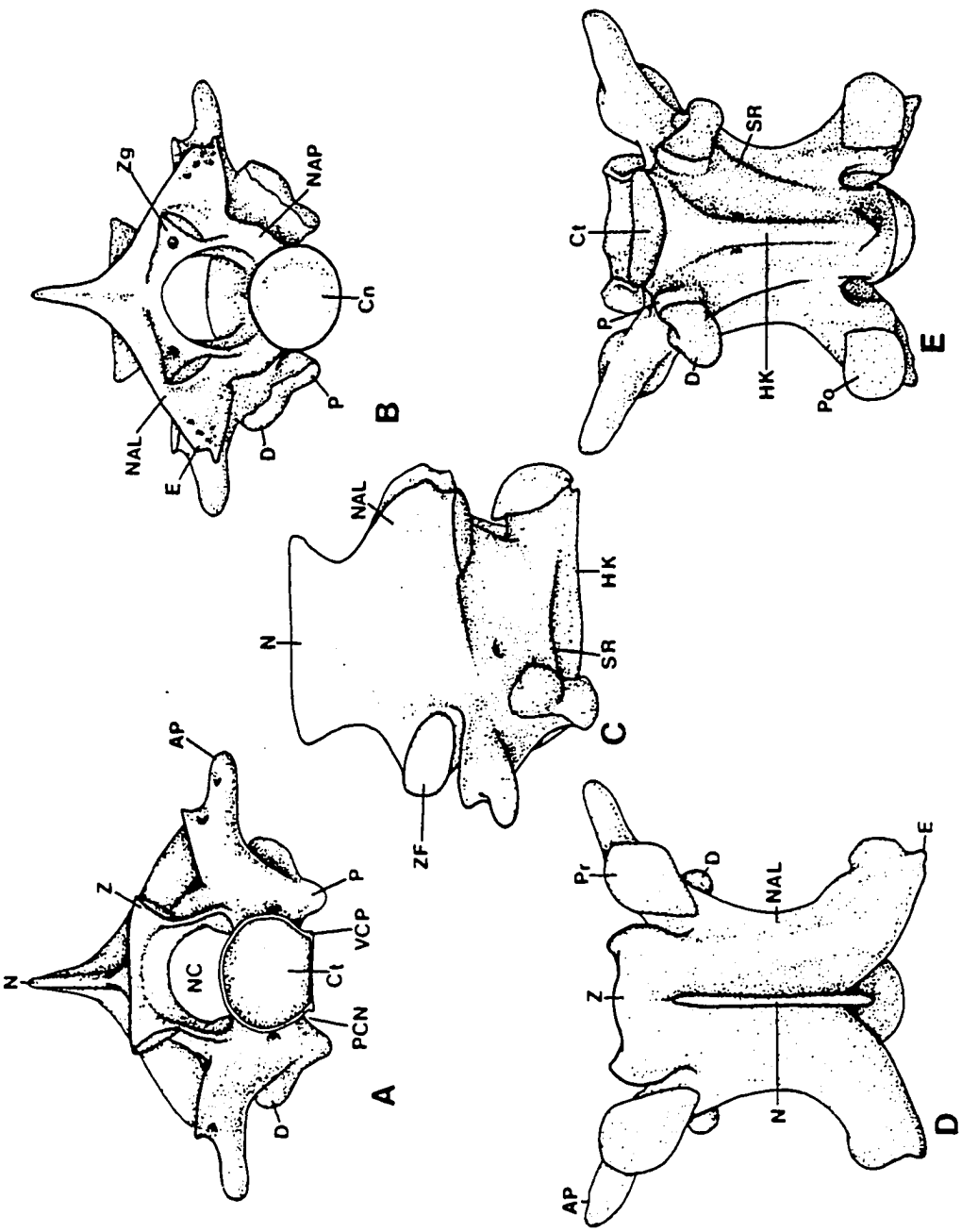


Figure 8. Five views of a vertebra of Coluber constrictor, showing the anhypapophyseal condition. A. anterior view, B. posterior view, C. lateral View, D. dorsal view, E. ventral view. AP=accessory process Cn=condyle, Ct=cotyle, D=diapophysis, E=epizygapophyseal spine, HK=hemal keel, N=neural spine, NAL=neural arch lamina, NAP=neural arch pedicel, NC=neural canal, P=parapophysis, PCN=paracotylar notch, Po= postzygapophyseal facet, Pr=prezygapophyseal facet, SR=subcentral ridge, VCP=ventrolateral cotylar process, Z=zygosphene, ZF=zygosphenal facet, Zg=zygosphene.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

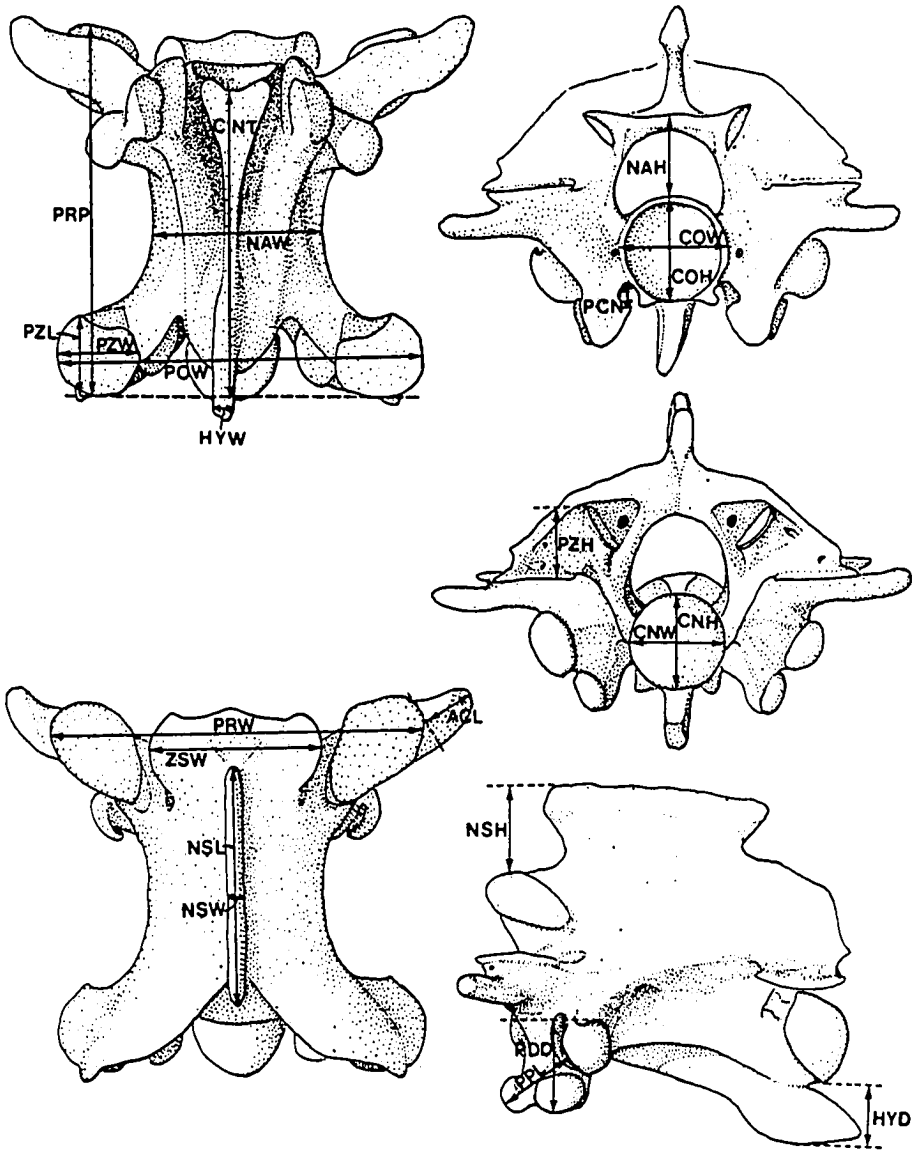


Fig. 9. Five views of a single vertebra from a female Thamnophis s. sirtalis, showing measurements taken for study. TCL 867, VNO 60, SVL=713. A. ventral view, B. anterior view, C. posterior view, D. dorsal view, E. lateral view. ACL=accessory process length, CNH=Condyle height, CNT=centrum length (from lower lip of cotyle to posterior extremity of condyle), CNW=condyle width, COH=cotyle height, COW=cotyle width, HYD=hypapophyseal depth, HYW=hypapophyseal width, NAH=neural arch height, NAW=neural arch width, NSH=neural spine height, NSL=neural spine length, NSW=neural spine width, PDD=depth of the paradiapophyses, POW=width across postzygapophyses, PPL=length of the parapophyseal process, PRP length from anterior edge of prezygapophyseal facet to posterior edge of postzygapophyseal facet, PRW=width across prezygapophyses, PZL=length of postzygapophyseal facet, PZW=width of postzygapophyseal facet, SCN=depth of subcentral notch, ZSW=zygosphene width.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

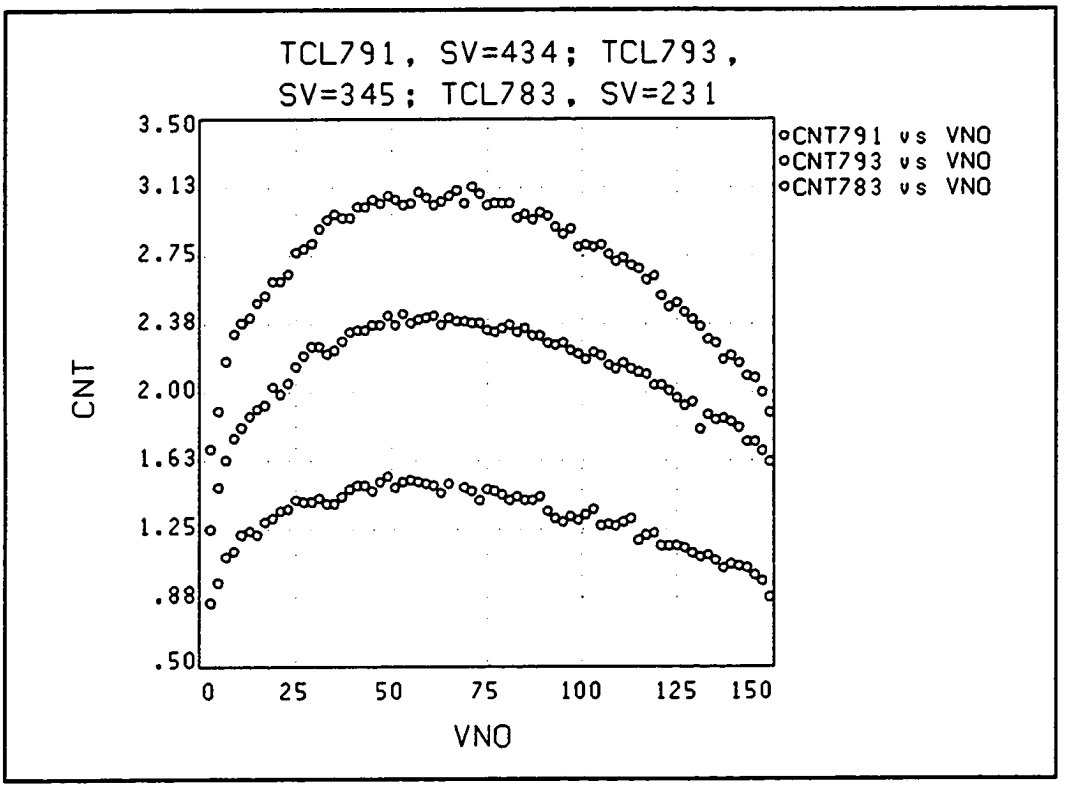


Fig. 10. Plots of CNT*VNO measured on every vertebra in three male specimens of different sizes.

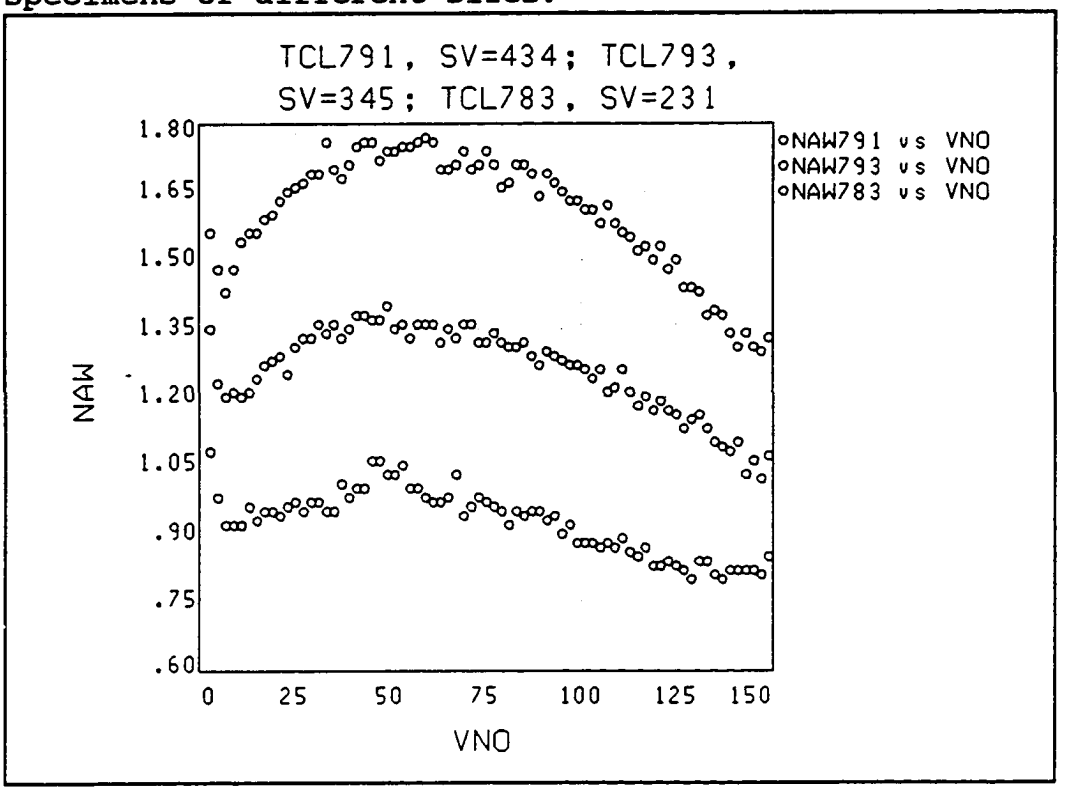


Fig. 11. Plots of NAW*VNO measured on every vertebra in three male specimens of different sizes.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

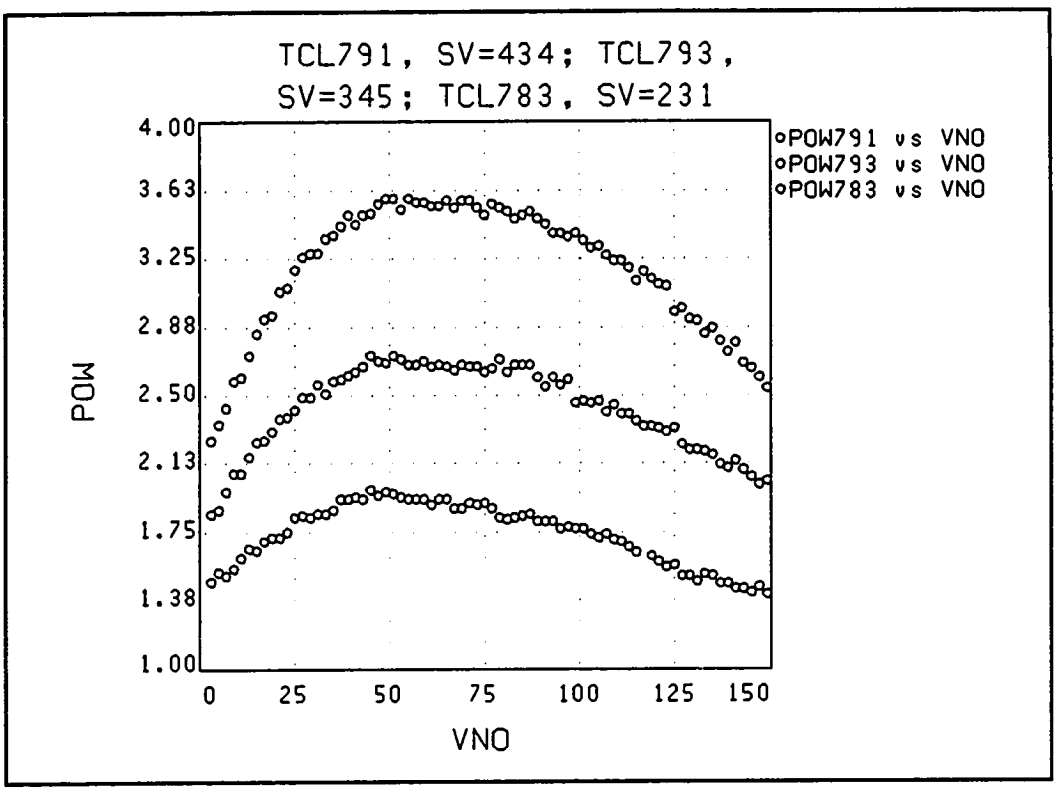


Fig. 12. Plots of POW*VNO measured on every vertebra in three male specimens of different sizes.

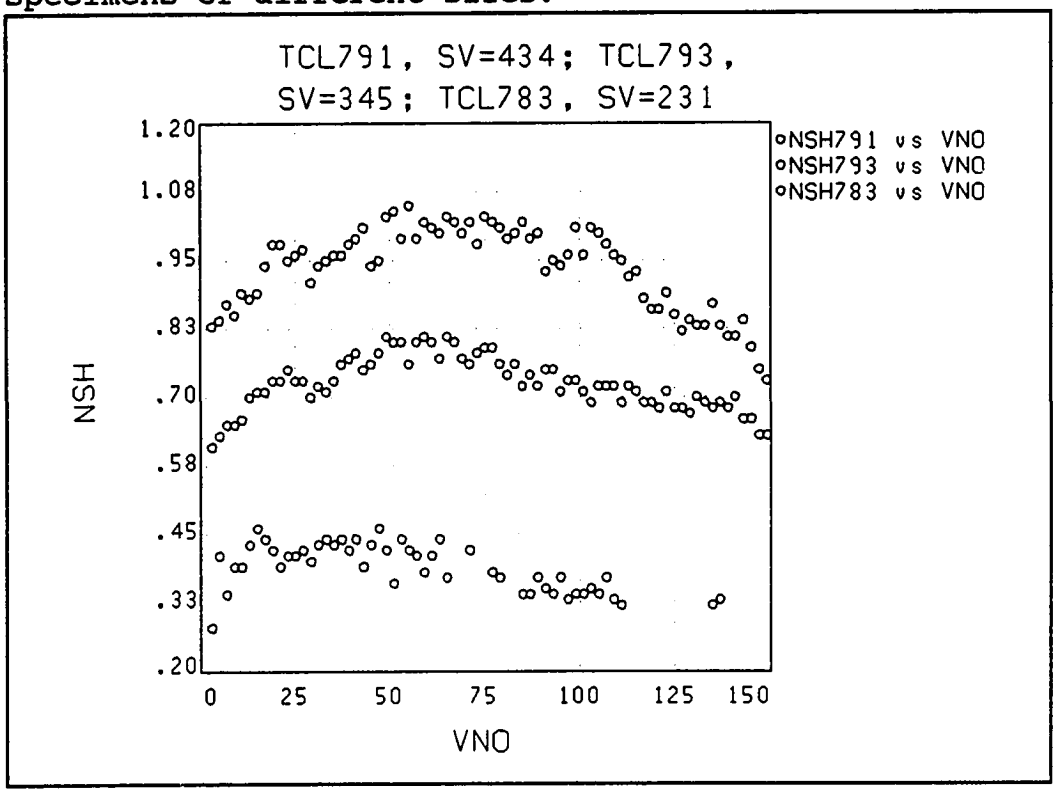


Fig. 13. Plots of NSH*VNO measured on every vertebra in three male specimens of different sizes.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

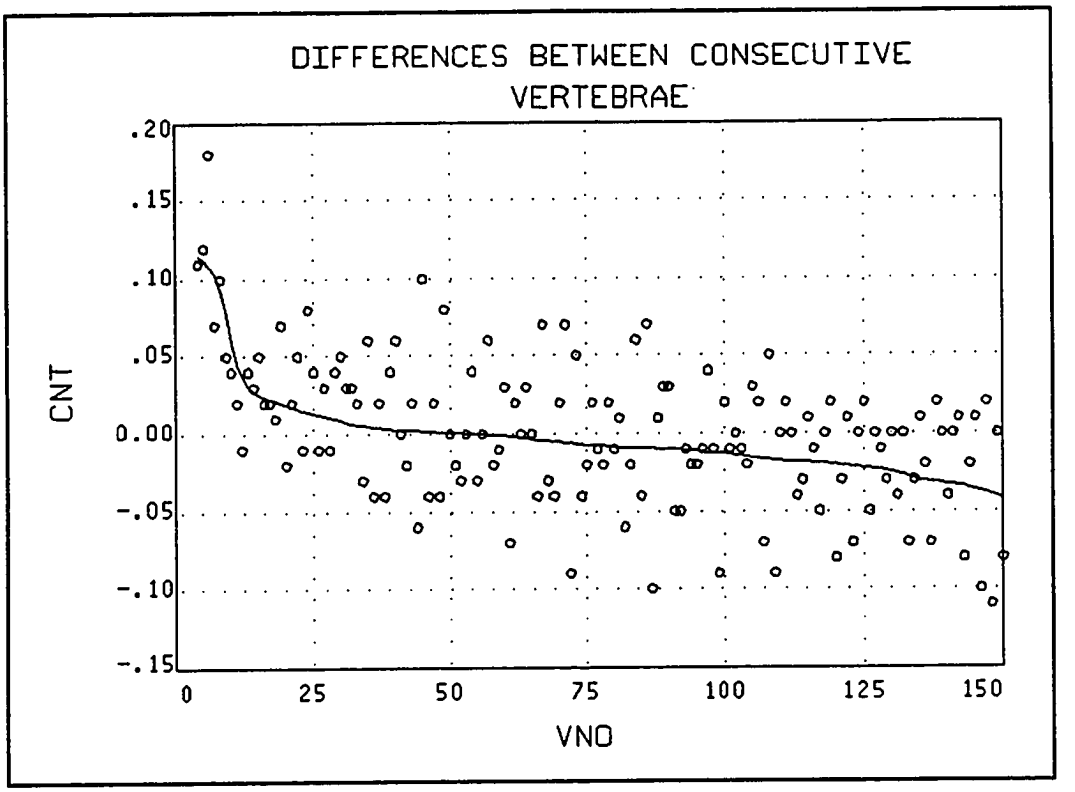


Fig. 14. Differences in CNT between consecutive vertebrae in TCL791, male, SVL=434. Line=median smooth (NCSS, 1990).

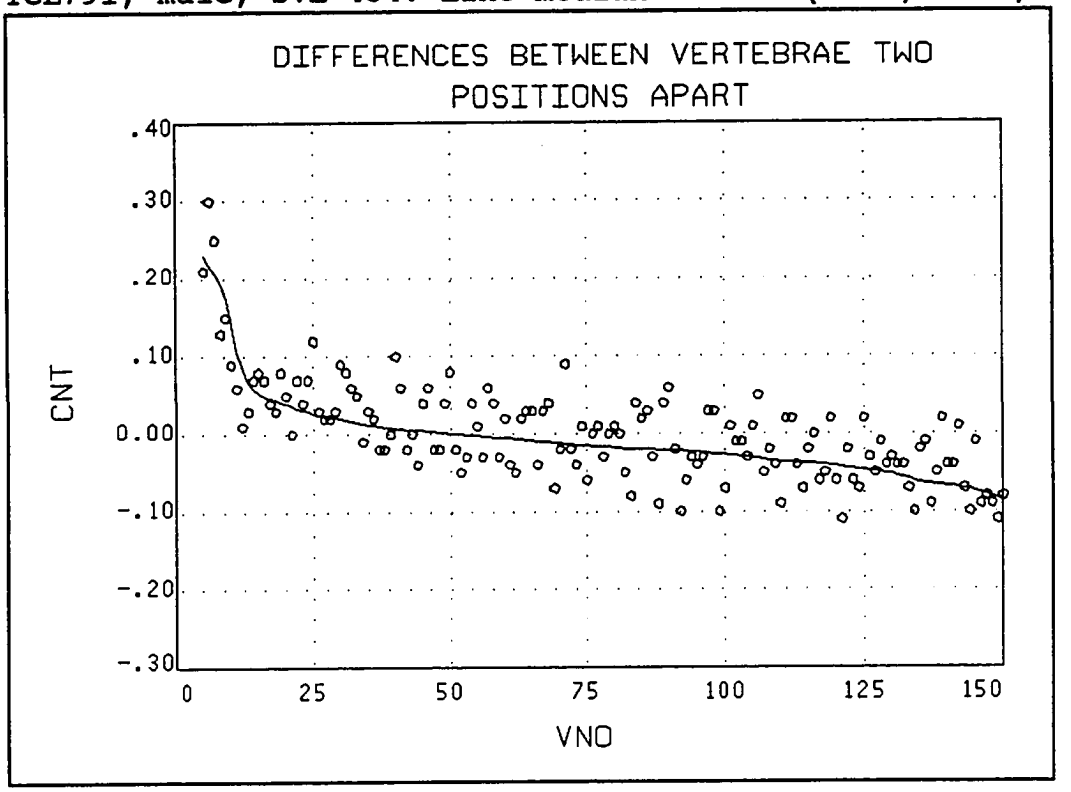


Fig. 15. Differences in CNT between vertebrae two positions apart in TCL791.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

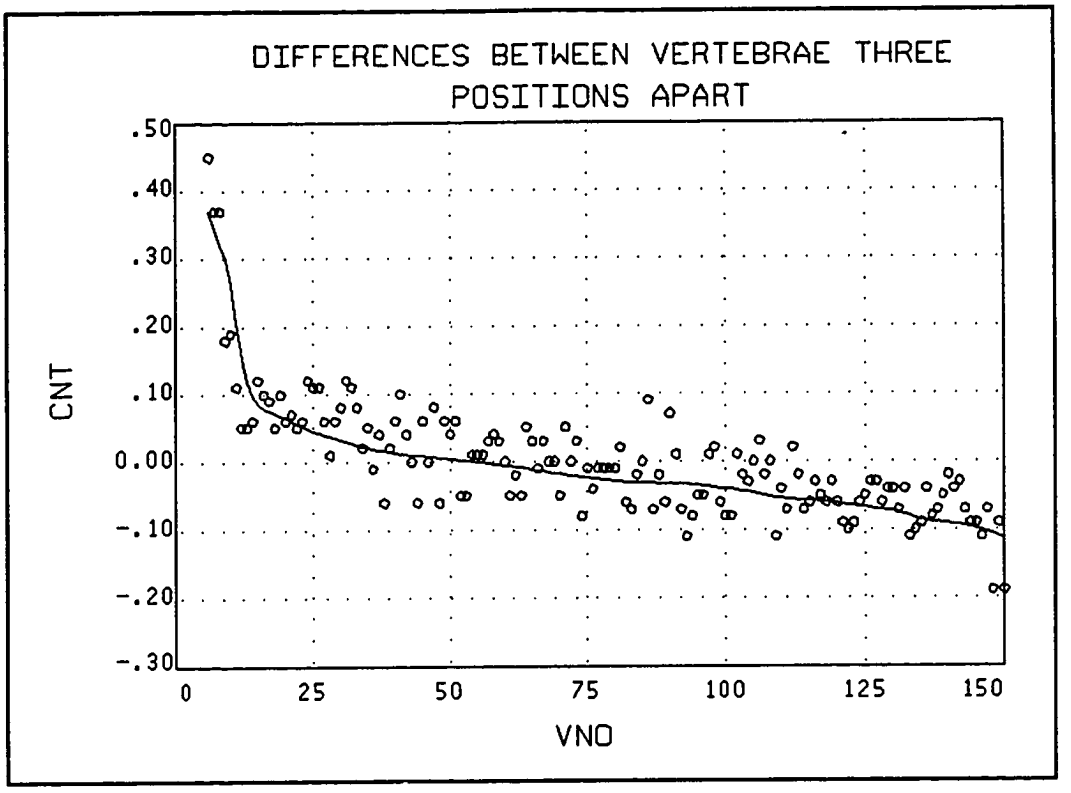


Fig. 16. Differences in CNT between vertebrae three positions apart in TCL791.

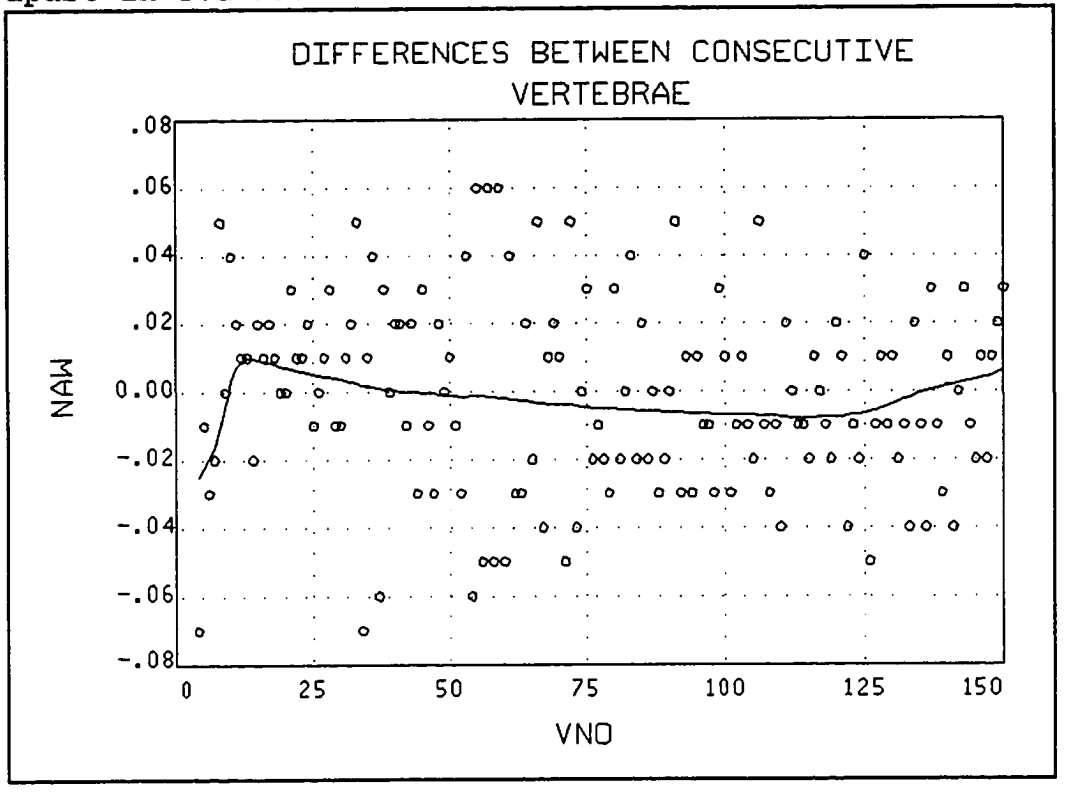


Fig. 17. Differences in NAW between consecutive vertebrae in TCL791.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

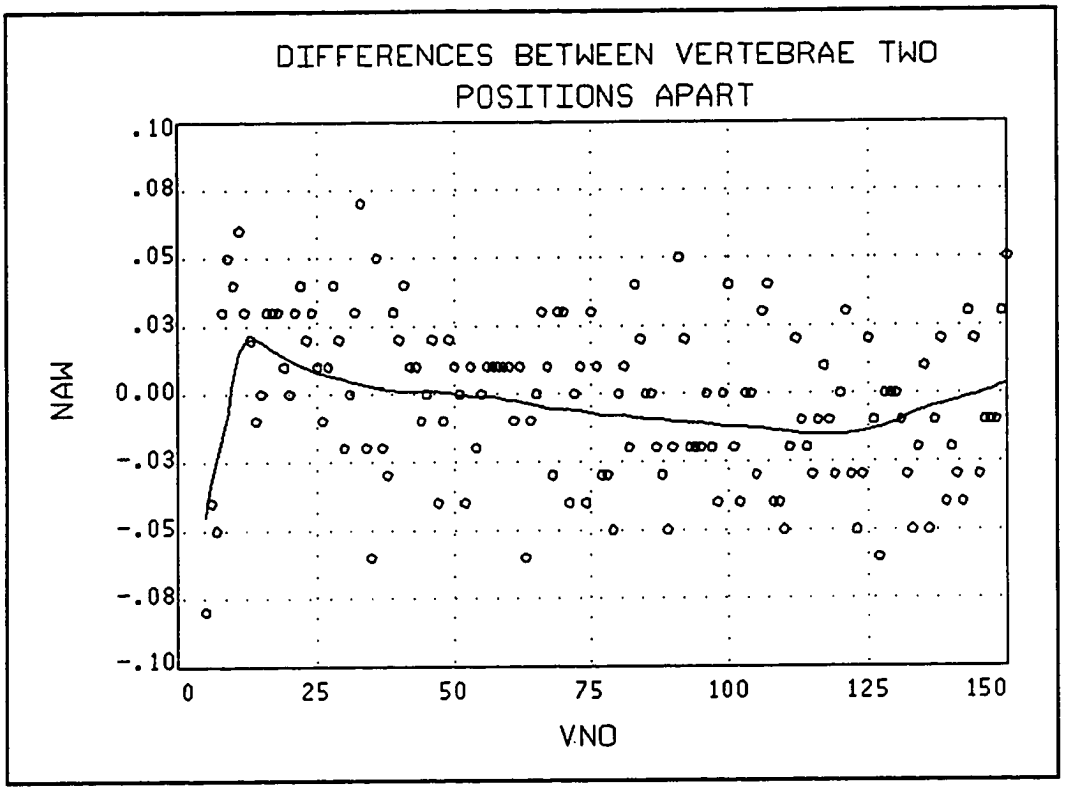


Fig. 18. Differences in NAW between vertebrae two positions apart in TCL791.

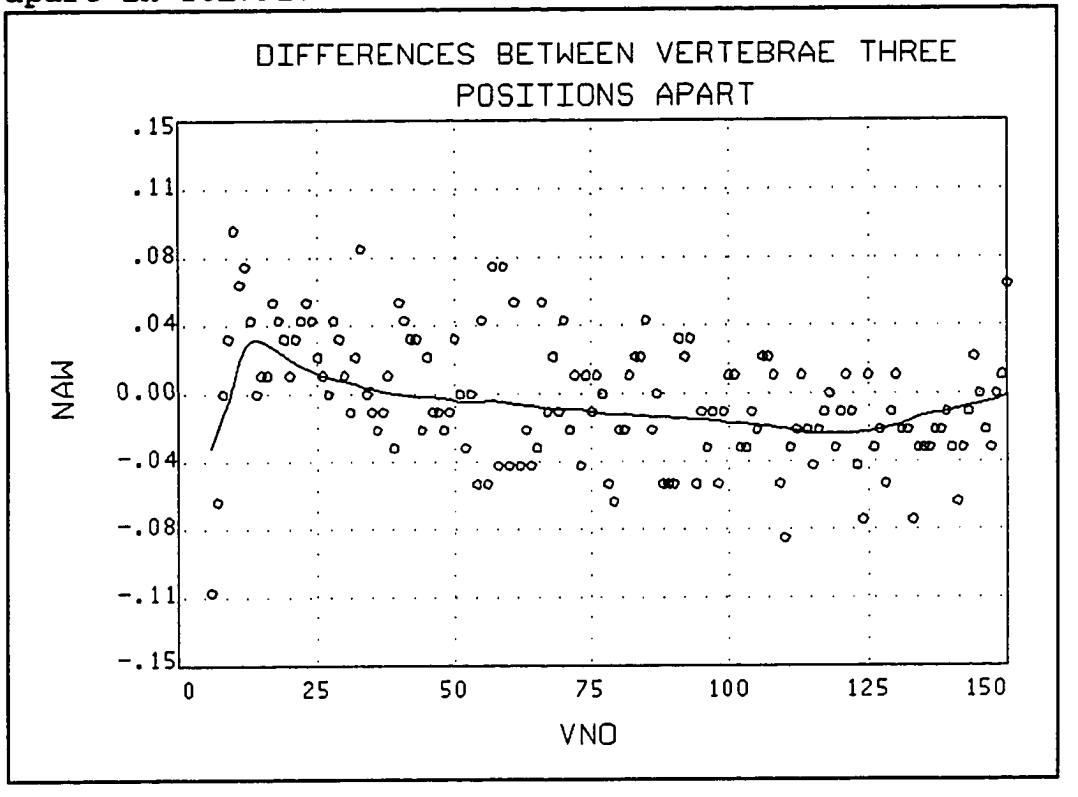


Fig. 19. Differences in NAW between vertebrae three positions apart in TCL791.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

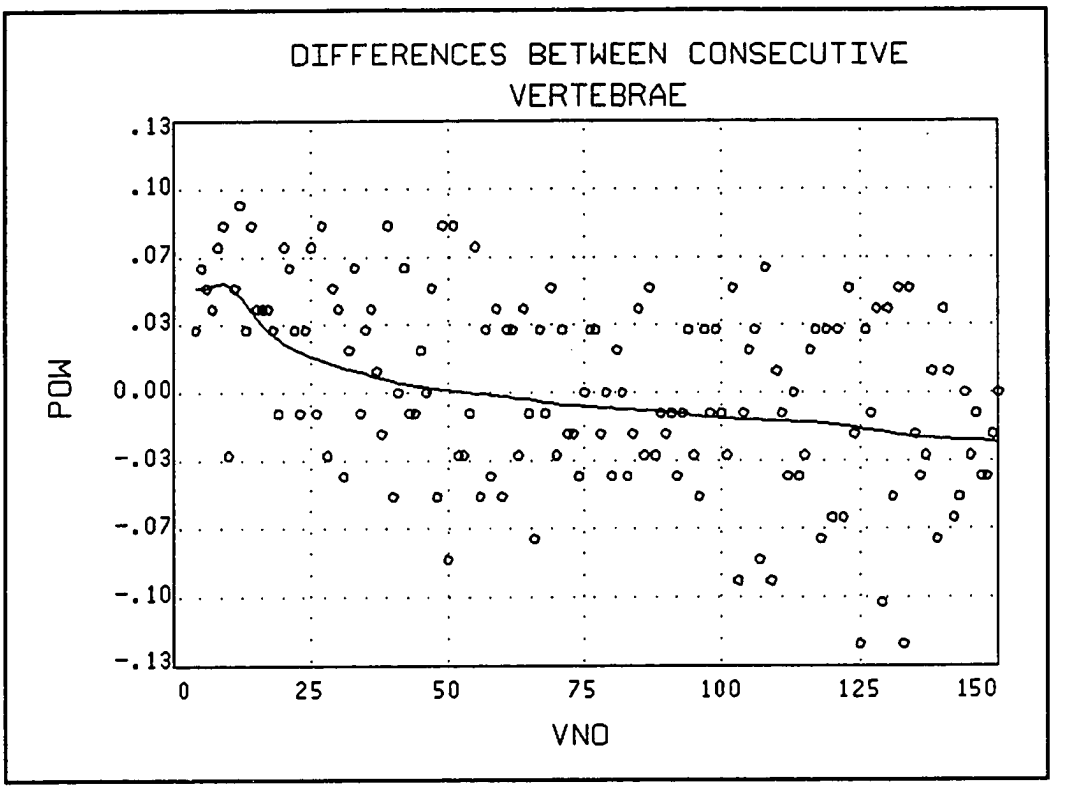


Fig. 20. Differences in POW between consecutive vertebrae in TCL791.

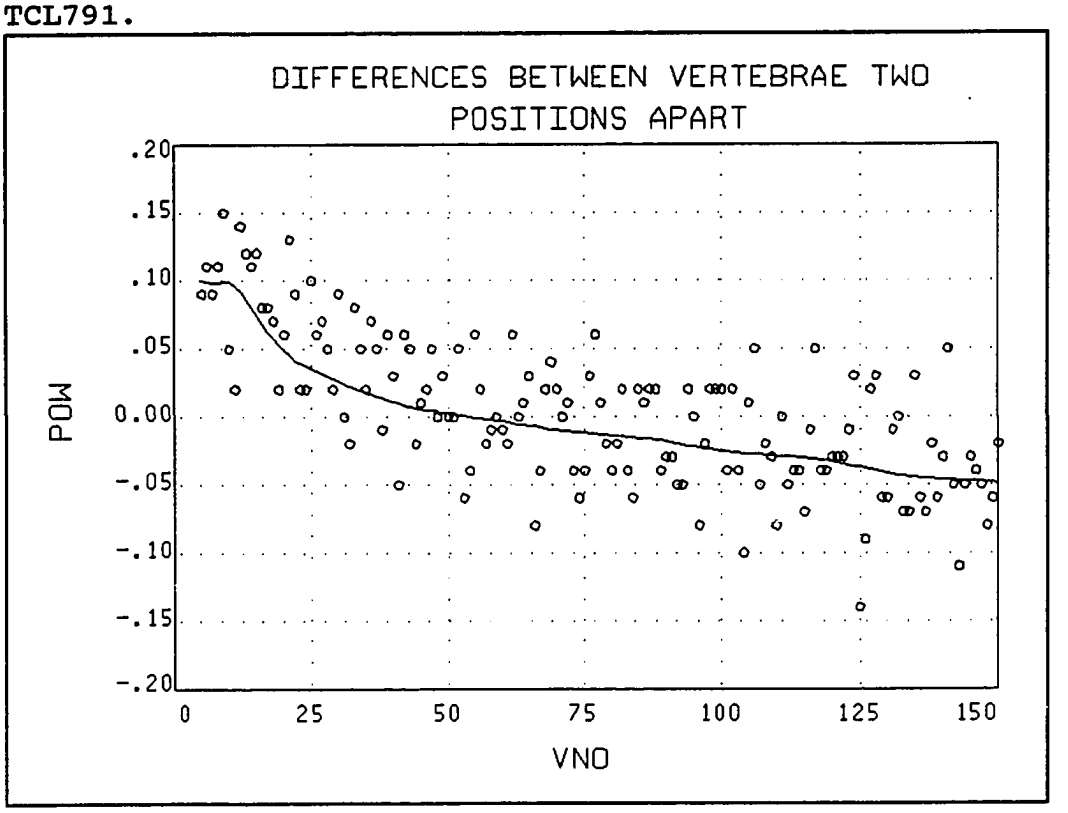


Fig. 21. Differences in POW between vertebrae two positions apart in TCL791.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

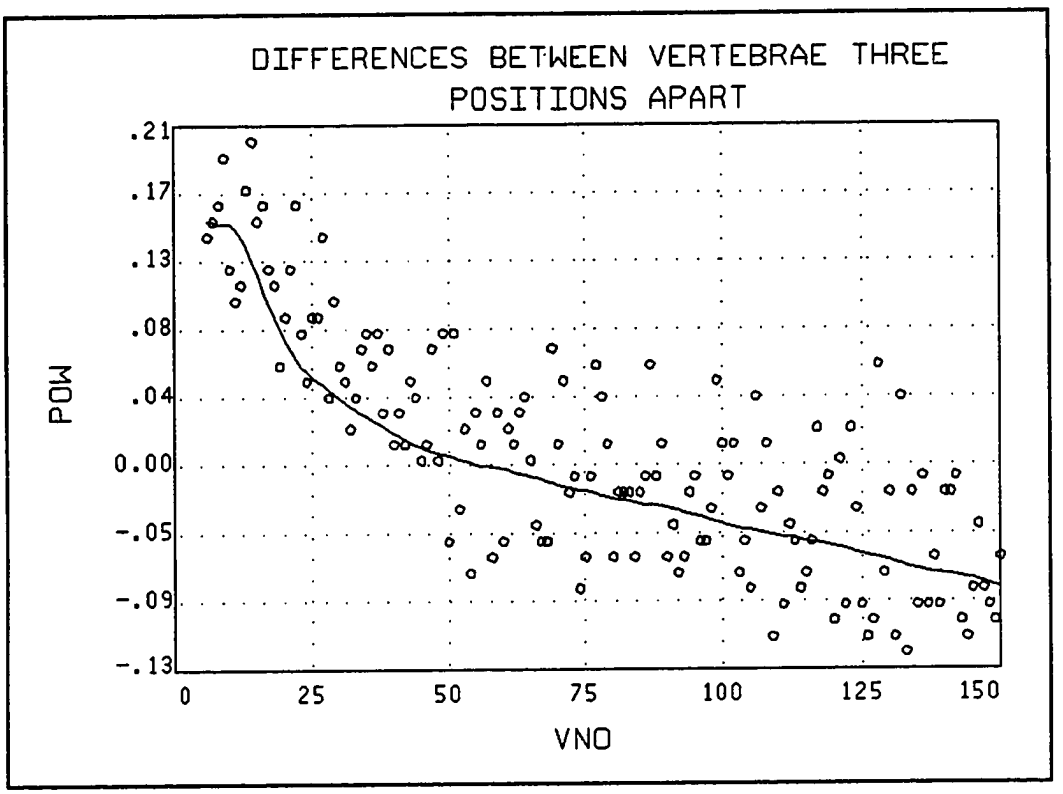


Fig. 22. Differences in POW between vertebrae three positions apart in TCL791.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

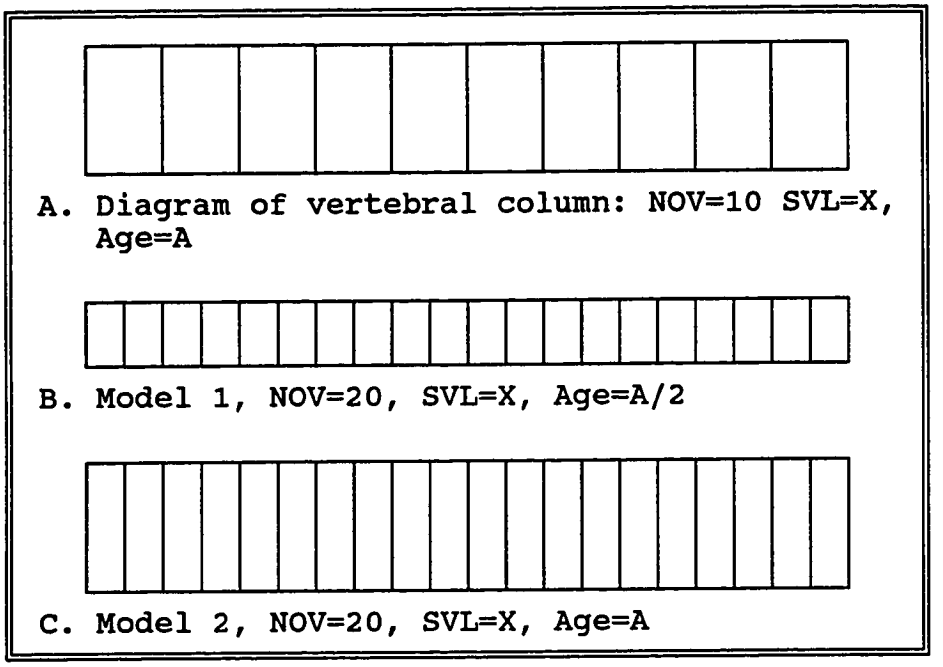


Figure 23. Two alternative models of vertebral packing. A. is a diagramatic sketch of a hypothetical vertebral column with 10 vertebrae. B. a similar column with twice as many vertebrae, similarly scaled and packed into the same snout-vent length, but at a younger age. C. as in B, but at the same age, vertebrae are packed in by shortening.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

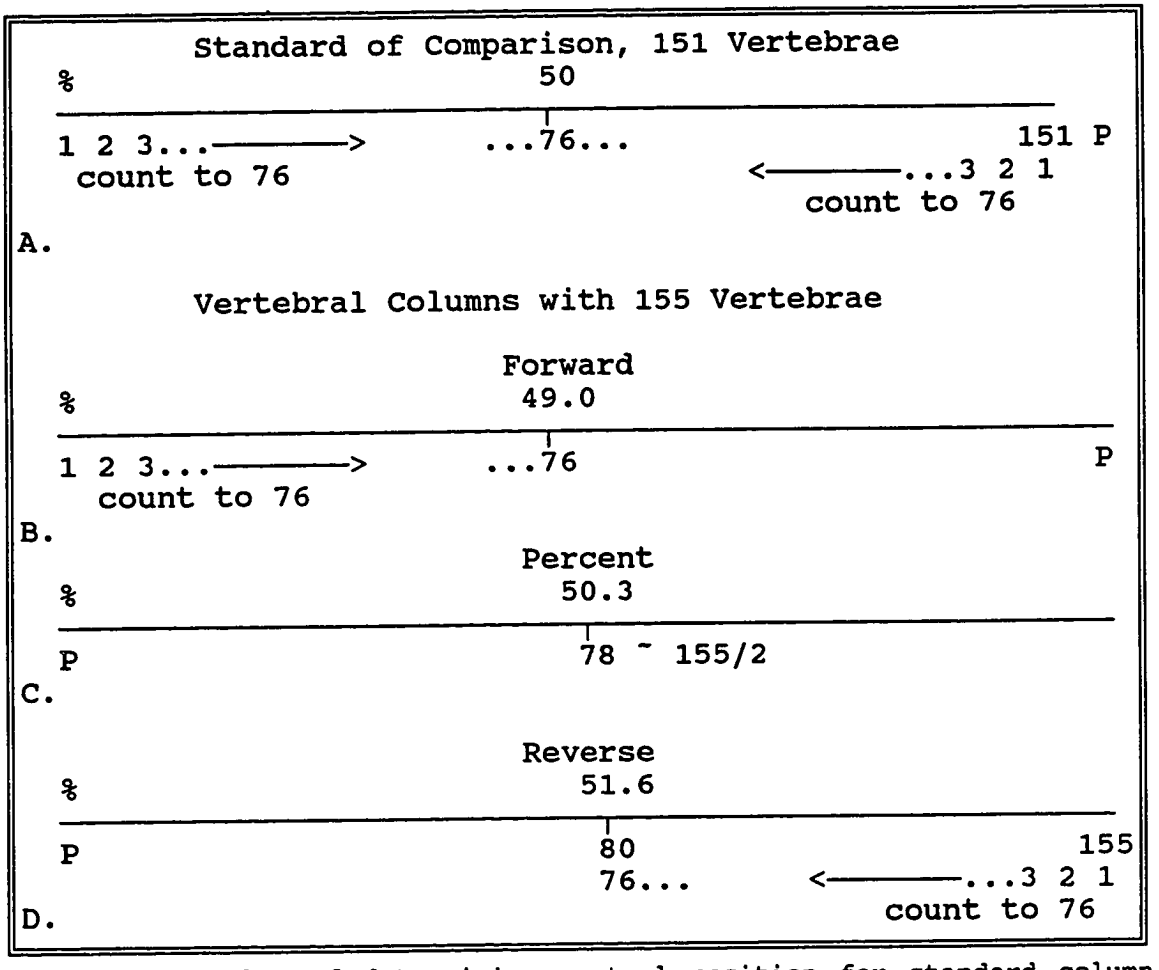


Fig. 24. Examples of determining central position for standard column length of 151 vertebrae (A), and for column of 155 vertebrae (lower 3). Percentage position (=%) given above line, numerical position (=P) given immediately below line, counting methods for forward and reverse modes indicated by arrows.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

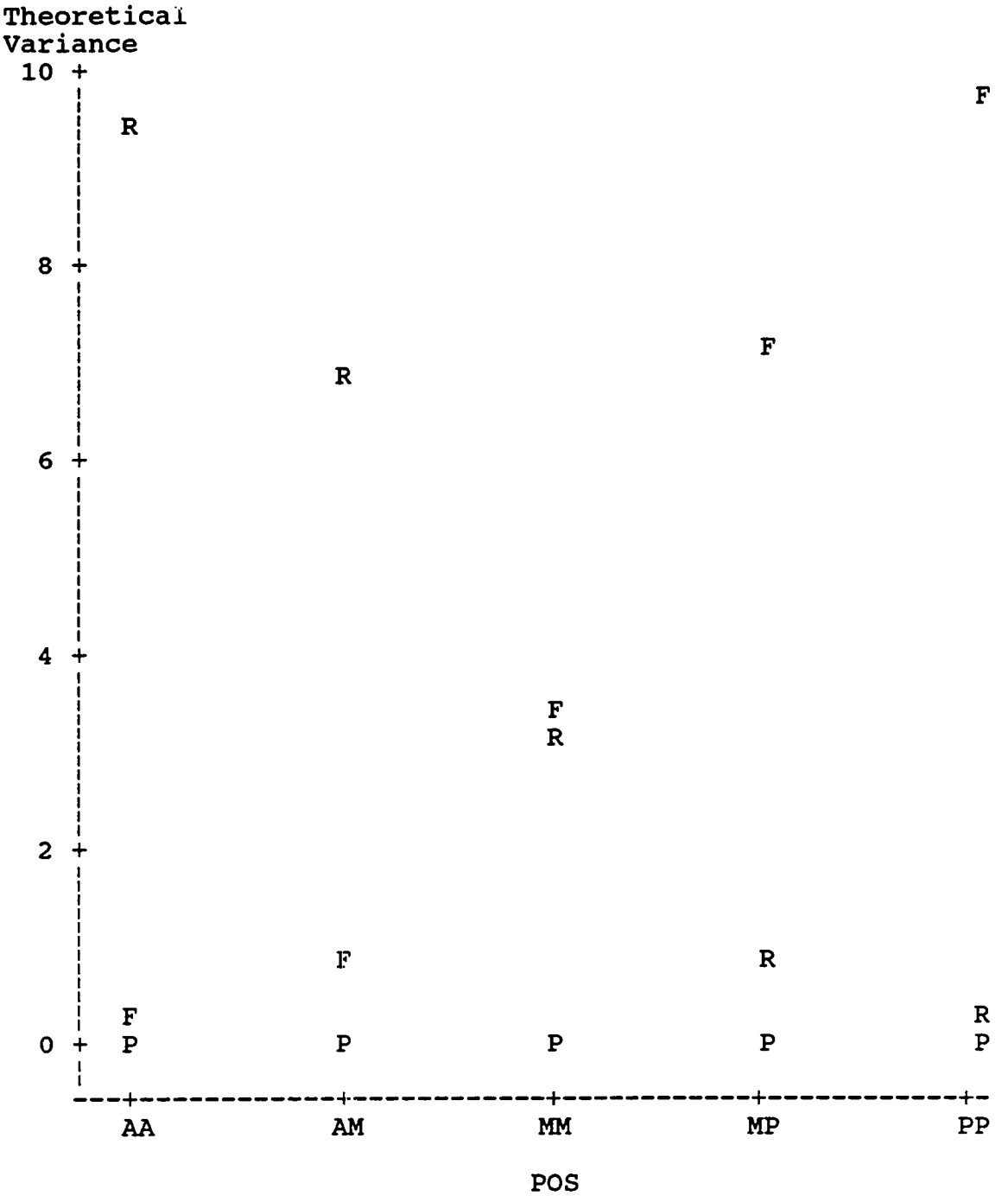


Figure 25. Model of predicted trends, assuming that the percentage mode produces the best approximation of homologous comparisons. Based on variance of positional information only. R=reverse mode variance, P=percentage mode variance, F=forward mode variance.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

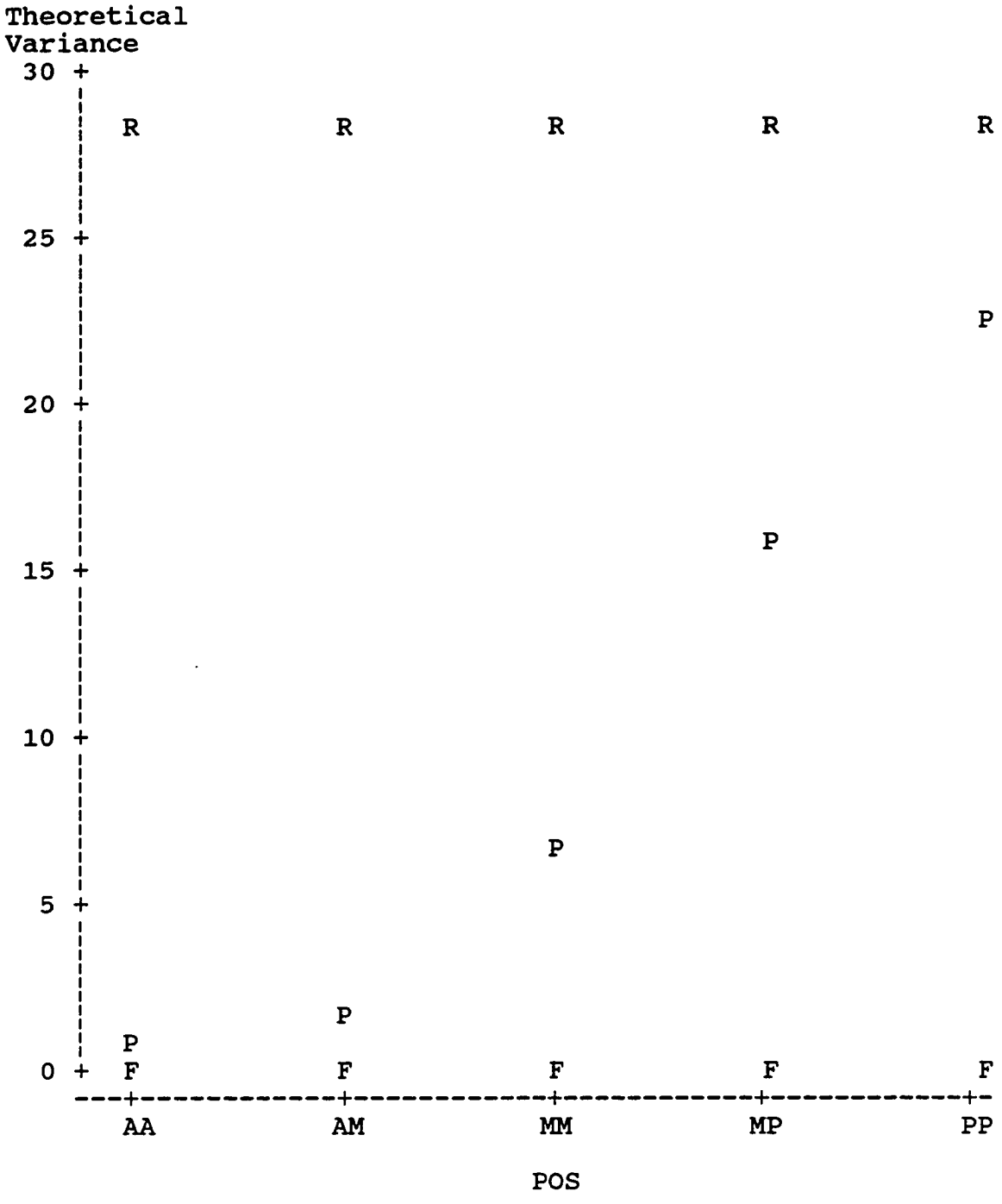


Figure 26. Model of predicted trends, assuming that the forward mode produces the best approximation of homologous comparisons. Based on variance of positional information only. R=reverse mode variance, P=percentage mode variance, F=forward mode variance.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

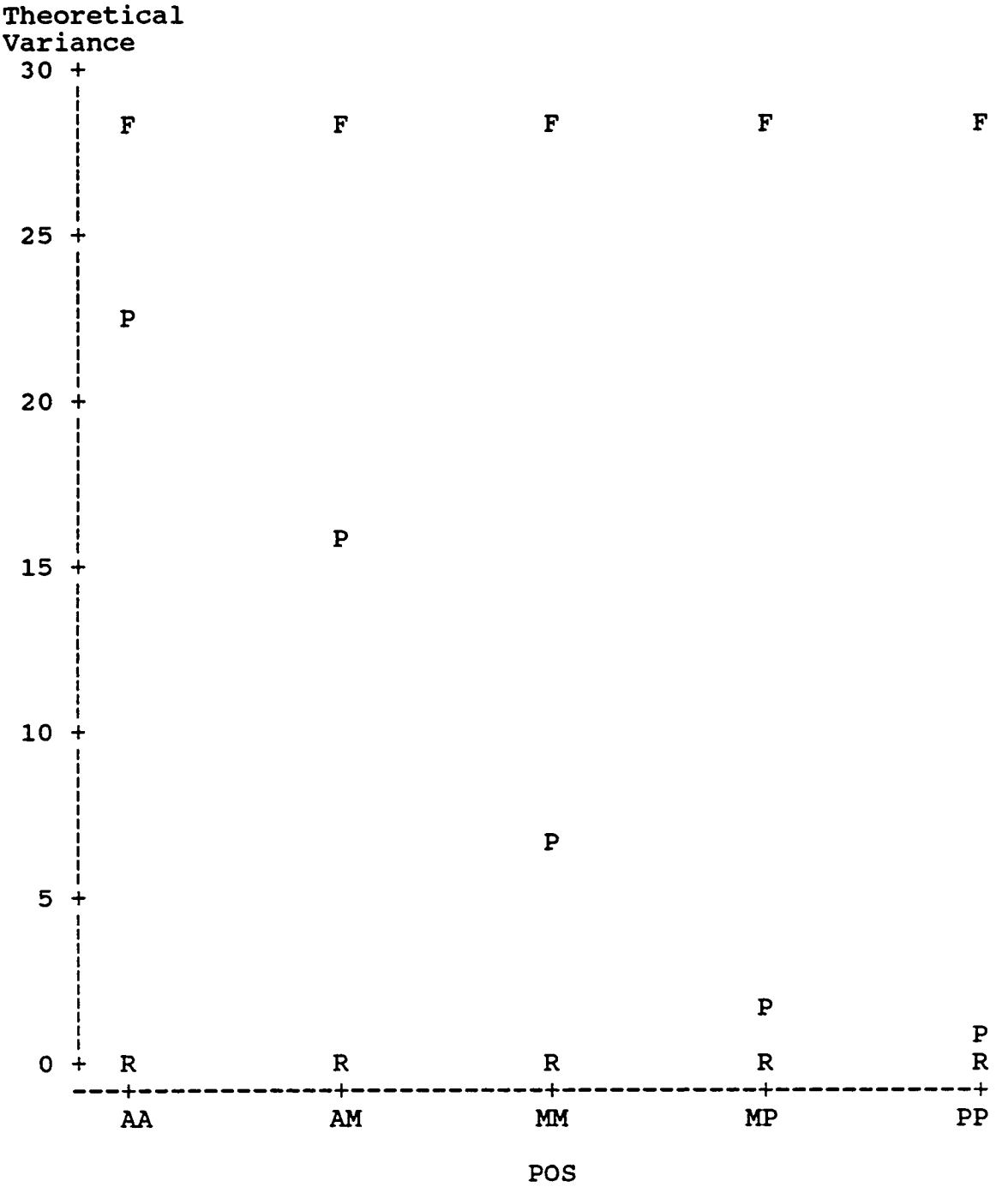


Figure 27. Model of predicted trends, assuming that the reverse mode produces the best approximation of homologous comparisons. Based on variance of positional information only. R=reverse mode variance, P=percentage mode variance, F=forward mode variance.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

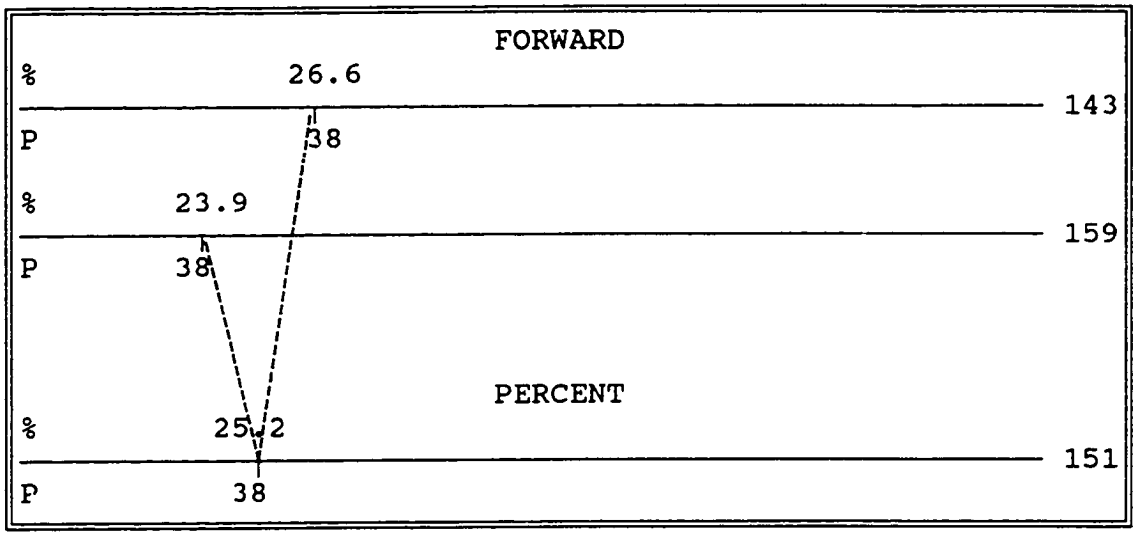


Figure 28. Example 1: demonstration of the equivalence of the AM position in percent mode (VNO 38 = 25.2%) on a column with standard vertebral count (151), to a range of percentage positions (23.8% to 26.6%) in forward mode on vertebral columns with 143 to 159 vertebrae. Column lengths standardized to demonstrate range. Not to scale.

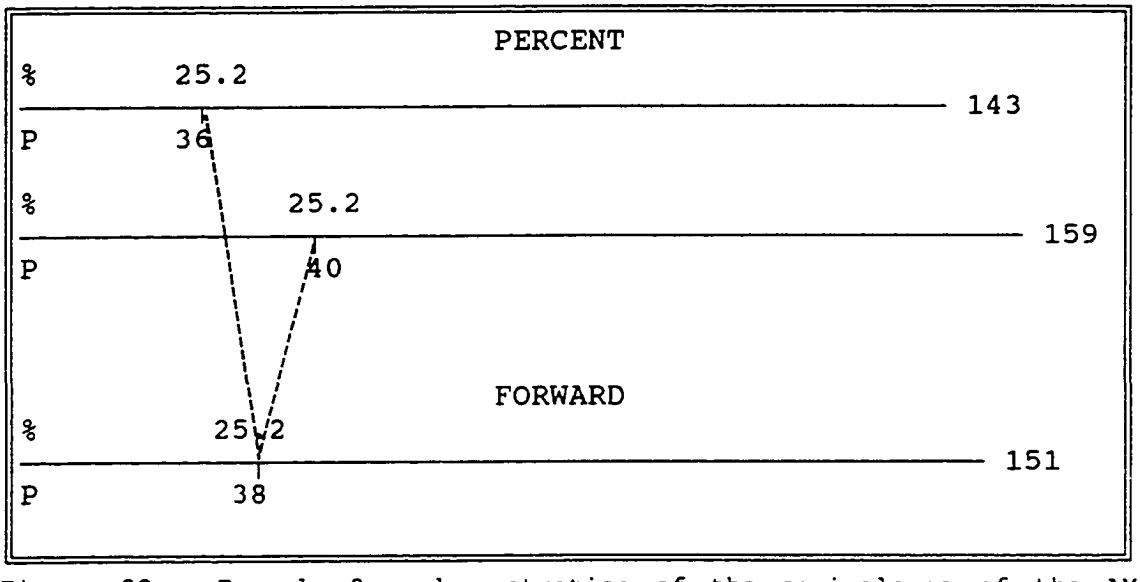


Figure 29. Example 2: demonstration of the equivalence of the AM position in forward mode (VNO 38 = 25.2%) on a column with standard vertebral count (151), to a range of forward mode positions (36 to 40) in percent mode on vertebral columns with 143 to 159 vertebrae. Column lengths vary to demonstrate range. Not to scale.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

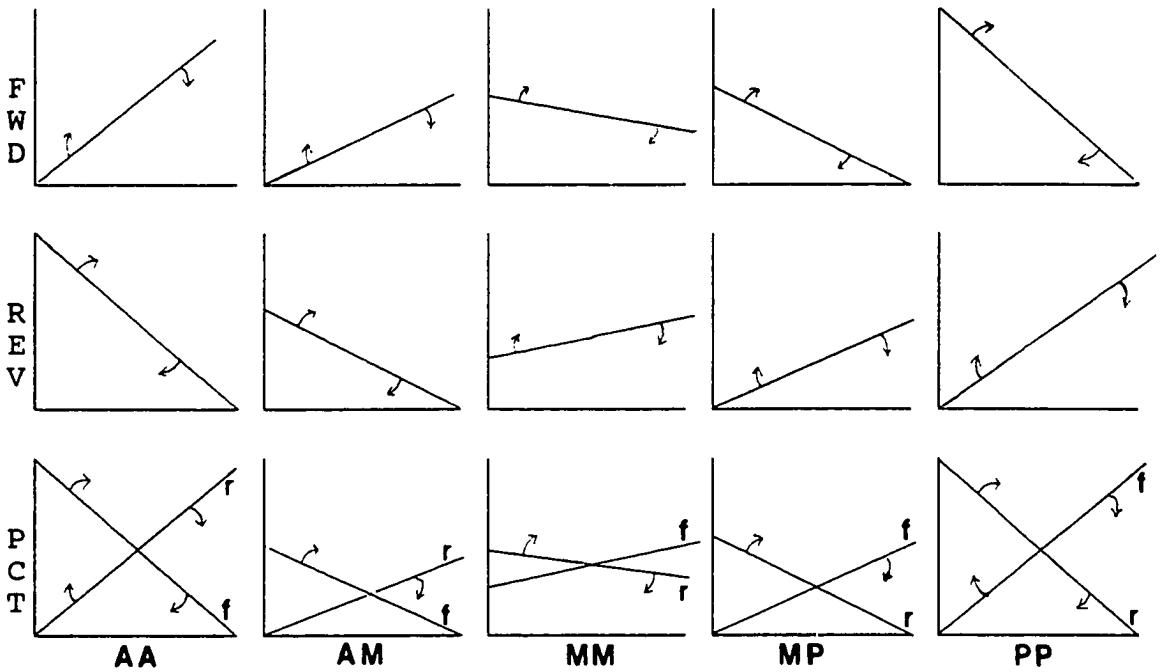


Figure 30. Predicted slopes of variables plotted against NOV with effects of size removed at each of the columnar positions examined. Upper row is forward count, middle row is reverse count, and lower row is percentage count.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

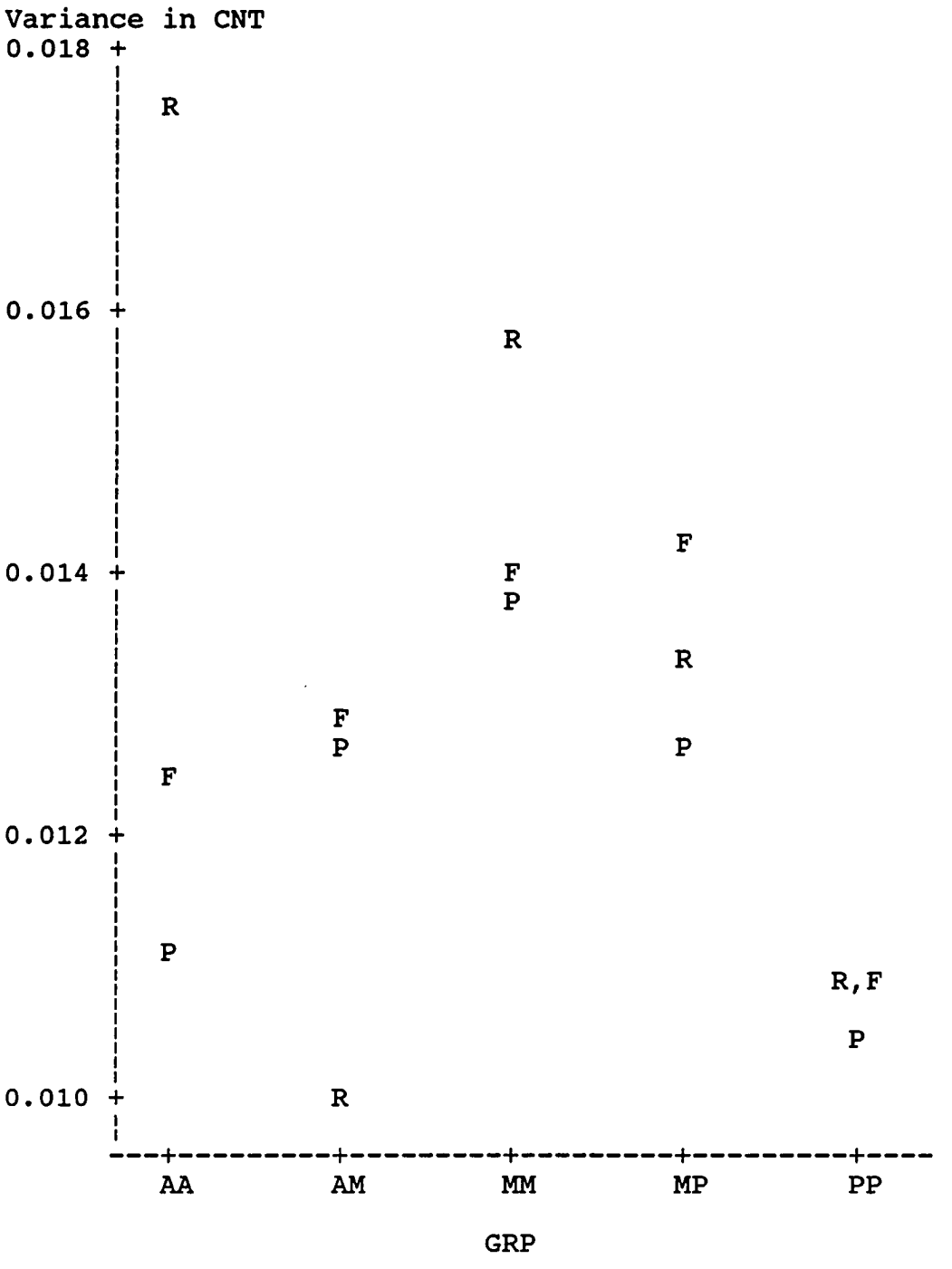


Figure 31. Variances produced by the three modes of comparison at each of five columnar positions. Variable is CNT. F=forward mode, P=percentage mode, and R=reverse mode.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

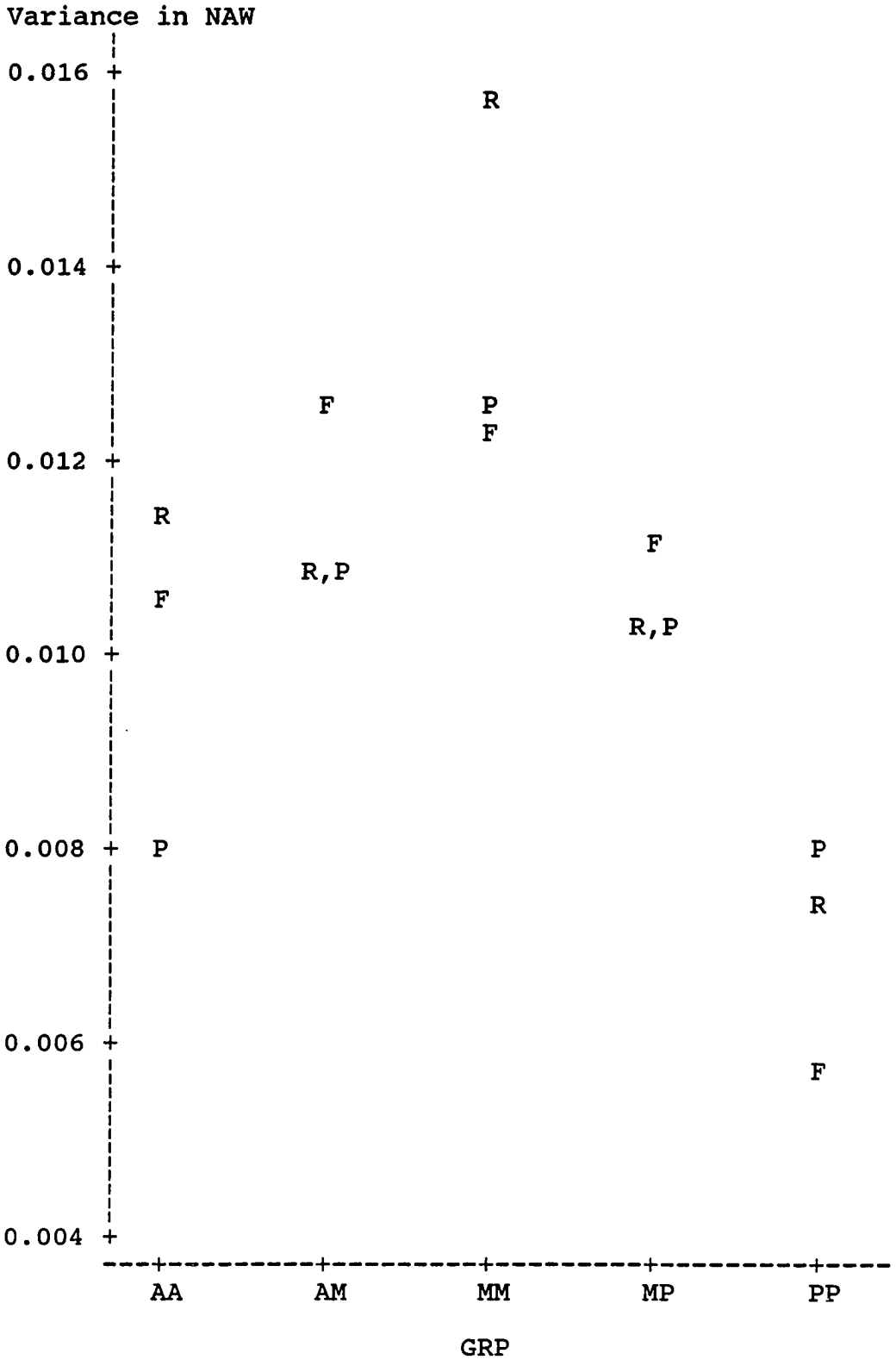


Figure 32. Variances produced by the three modes of comparison at each of five columnar positions. Variable is NAW. F=forward mode, P=percentage mode, and R=reverse mode.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

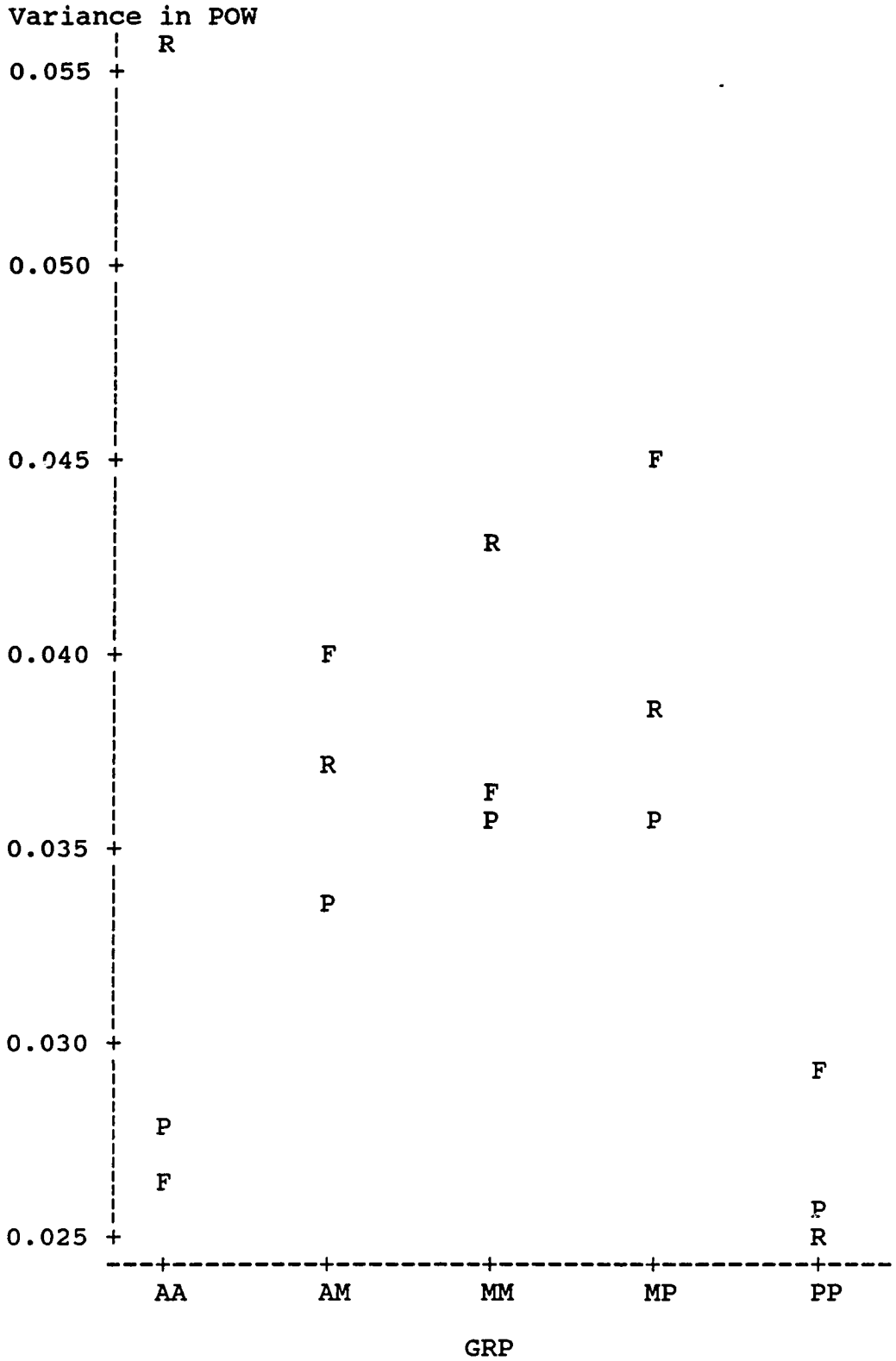


Figure 33. Variances produced by the three modes of comparison at each of five columnar positions. Variable is POW. F=forward mode, P=percentage mode, and R=reverse mode.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

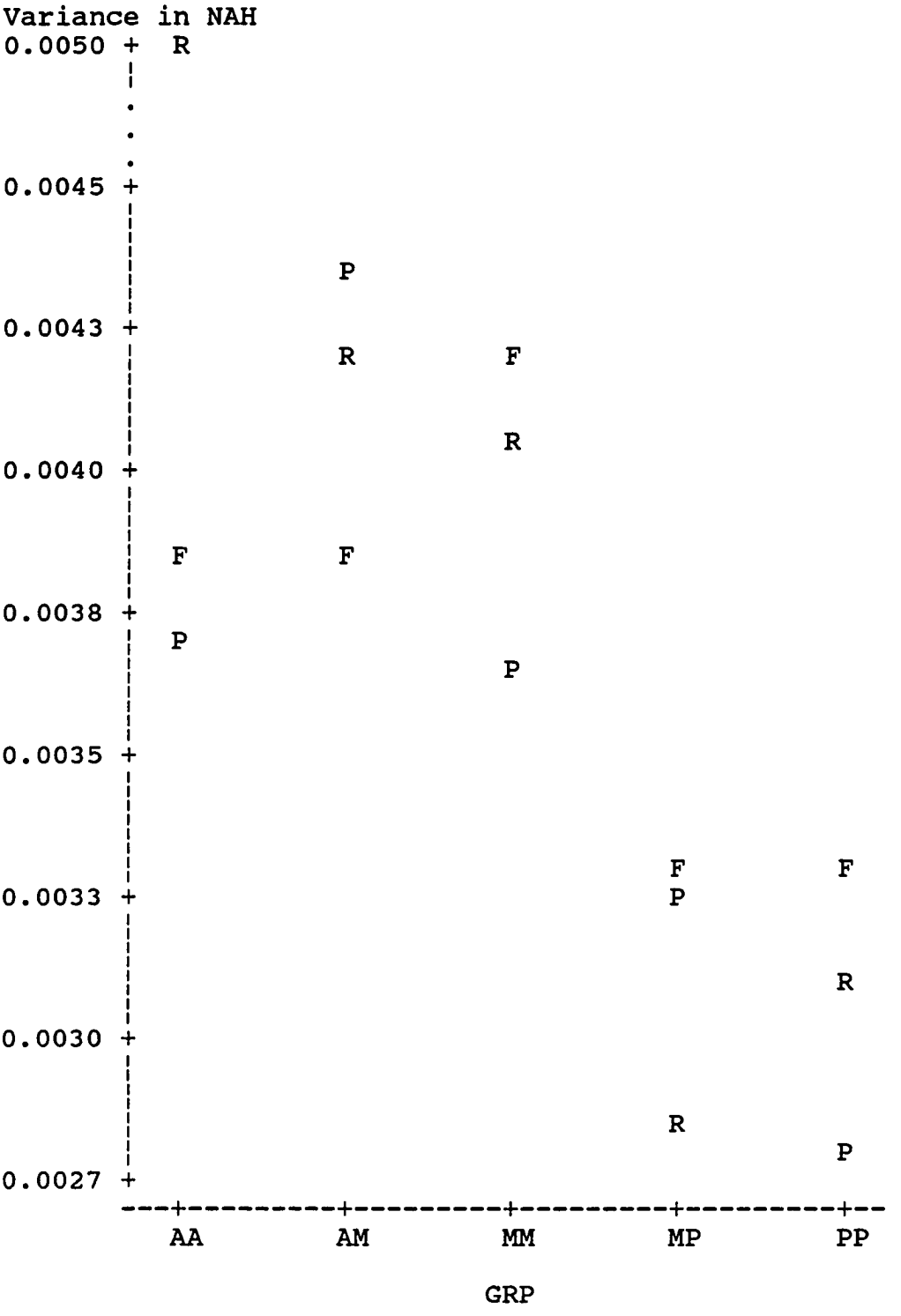


Figure 34. Variances produced by the three modes of comparison at each of five columnar positions. Variable is NAH. F=forward mode, P=percentage mode, and R=reverse mode.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

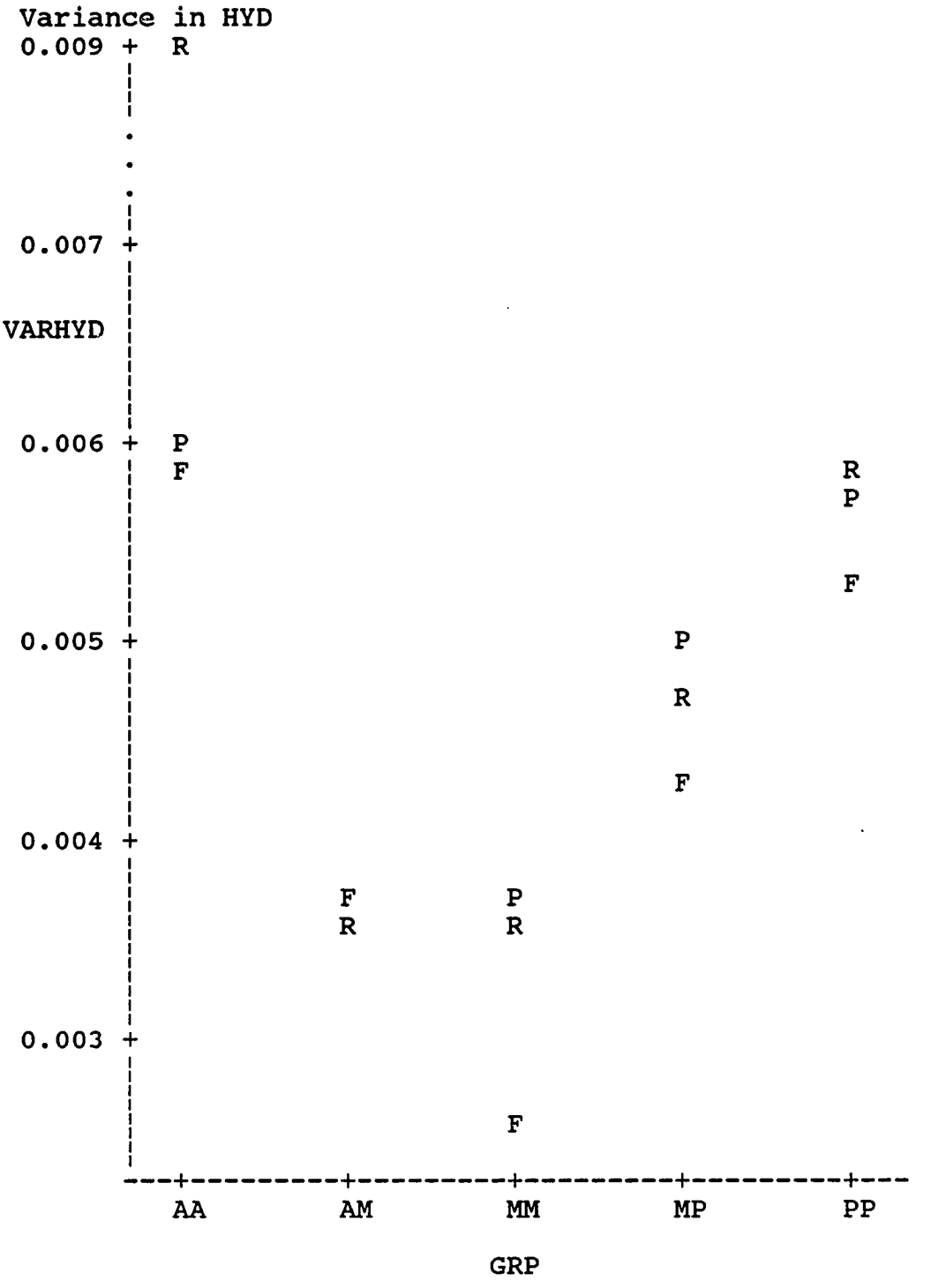


Figure 35. Variances produced by the three modes of comparison at each of five columnar positions. Variable is HYD. F=forward mode, P=percentage mode, and R=reverse mode.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

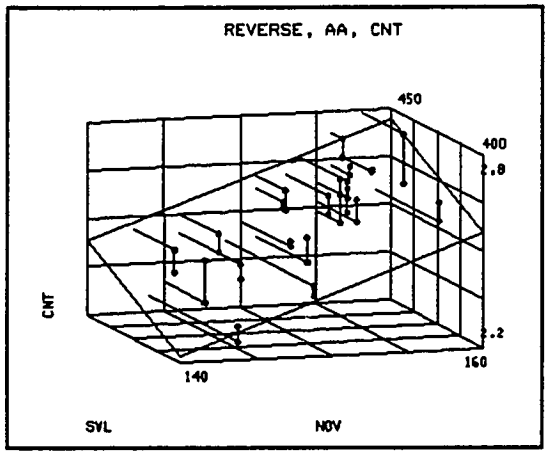


Figure 36.

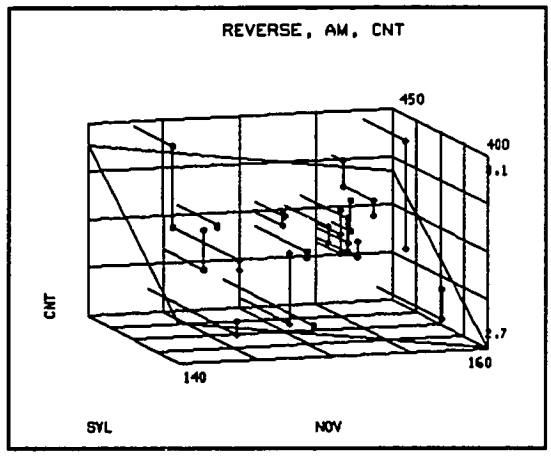


Figure 37.

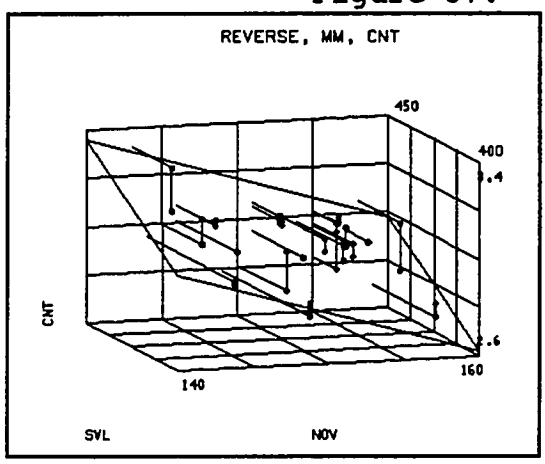


Figure 38.

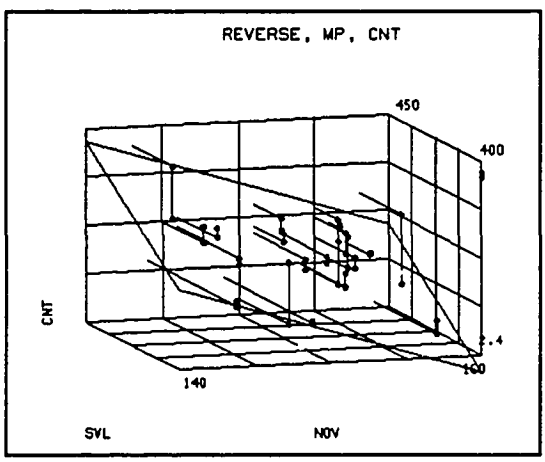


Figure 39.

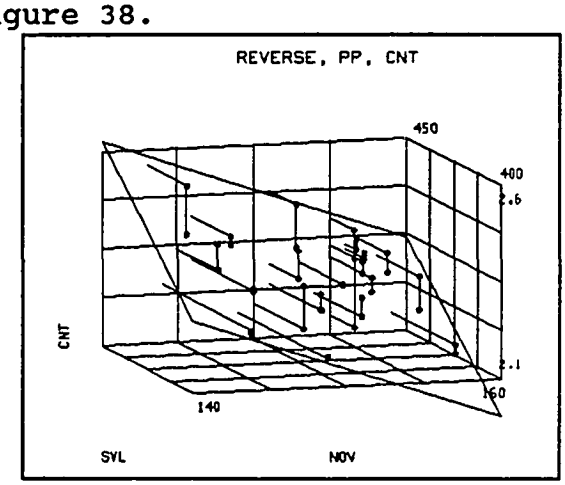


Figure 40.

Figures 36-40. Three dimensional plots of CNT against SVL and NOV. Data from reverse mode comparisons.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

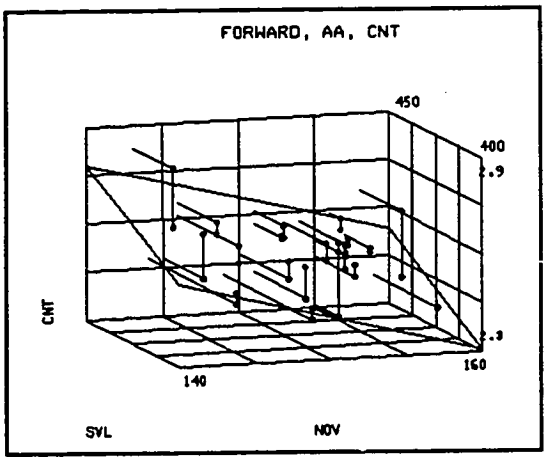


Figure 41.

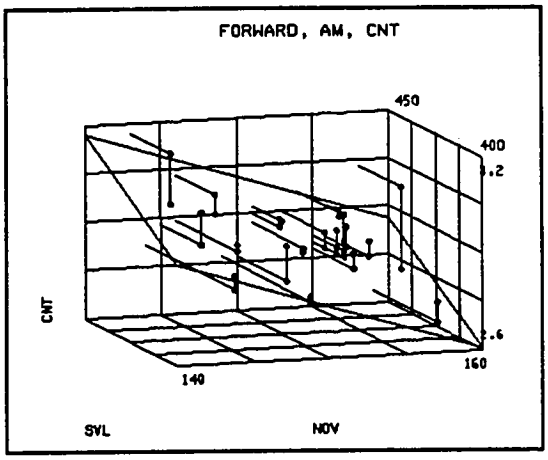


Figure 42.

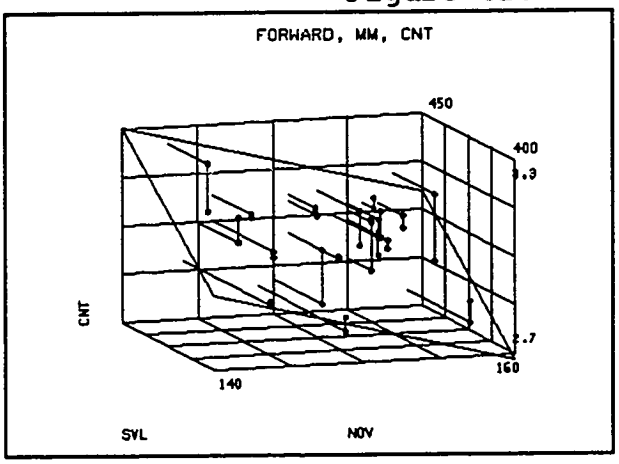


Figure 43.

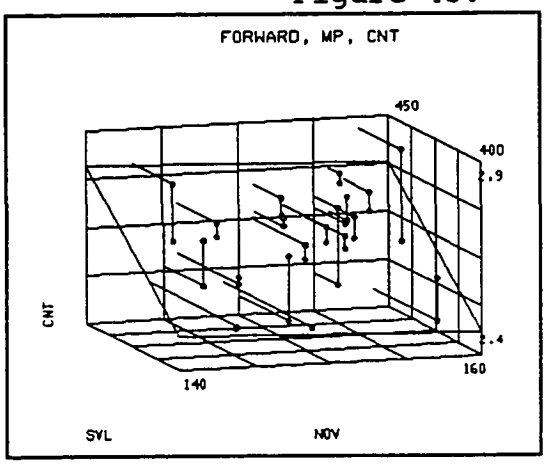


Figure 44.

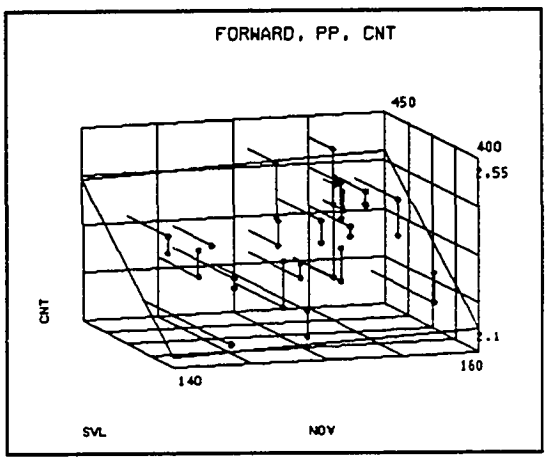


Figure 45.

Figures 41-45. Three dimensional plots of CNT against SVL and NOV. Data from forward mode comparisons.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

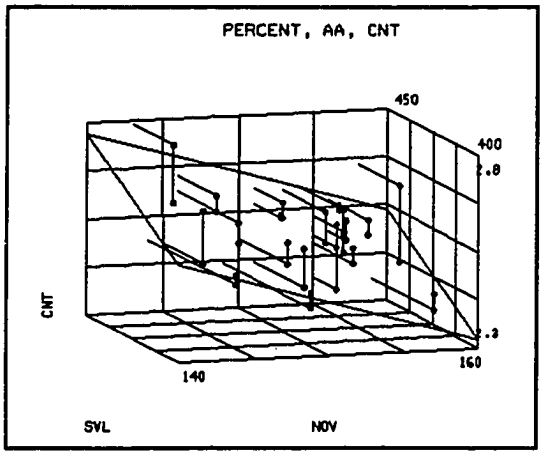


Figure 46.

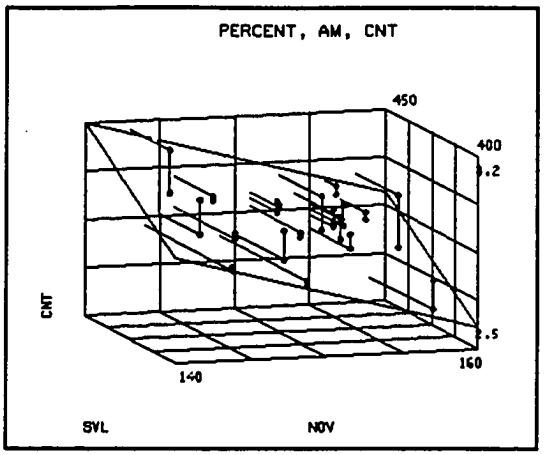


Figure 47.

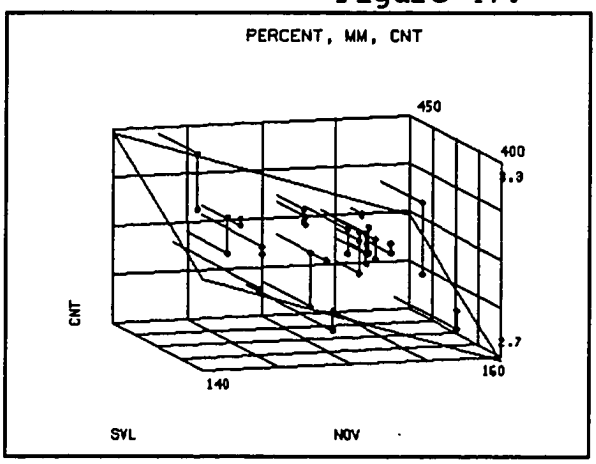


Figure 48.

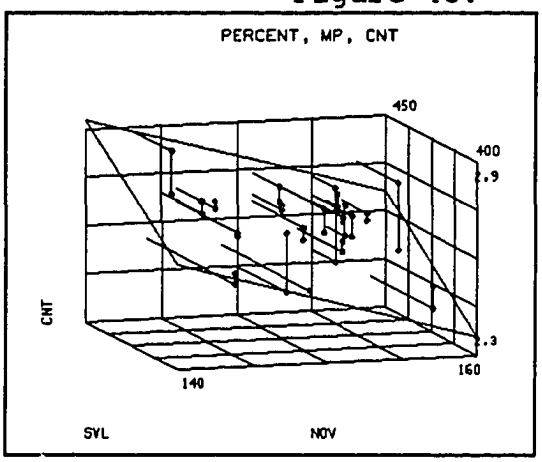


Figure 49.

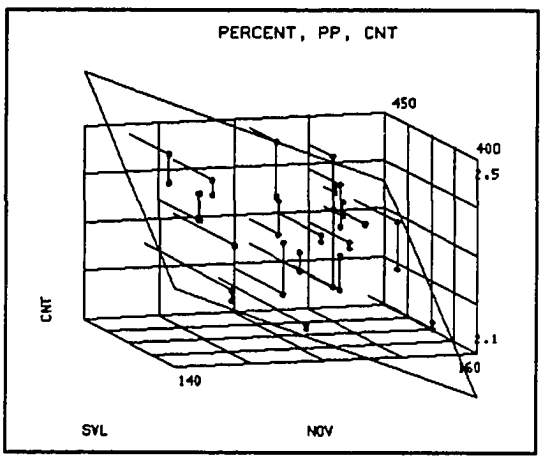


Figure 50.

Figures 46-50. Three dimensional plots of CNT against SVL and NOV. Data from percent mode comparisons.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Fig. 51. Analysis of variance of average adult SVL of four main study populations (BKK, BMT, FBF, TMR) by sex.

----------FEMALES----------

Source	DF	Mean Square	F Value	Pr > F
Model	3	53988.0259	16.09	0.00
Error	170	3356.1721		
Cor Tot	173			

Number obs.	R-Square	C.V.	SVL Mean
174	0.2211	12.701	456.098

Duncan's Multiple Range Test for variable: SVL
Alpha= 0.05 df= 170 MSE= 3356.172

Means with the same letter are not significantly different:

Duncan Grouping	Mean	N	LOC
A	493.74	47	BMT
A			
A	480.91	33	FBF
B	433.33	60	TMR
B			
B	420.15	34	BKK

----------MALES----------

Source	DF	Mean Square	F Value	Pr > F
Model	3	20041.34418	13.09	0.00
Error	124	1530.51530		
Cor Tot	127			

Number Obs.	R-Square	C.V.	SVL Mean
128	0.2405	10.070	388.477

Duncan's Multiple Range Test for variable: SVL
Alpha= 0.05 df= 124 MSE= 1530.515

Means with the same letter are not significantly different:

Duncan Grouping	Mean	N	LOC
A	418.39	36	FBF
A			
B A	399.77	13	BMT
B			
B C	389.50	20	BKK
C			
C	367.39	59	TMR

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

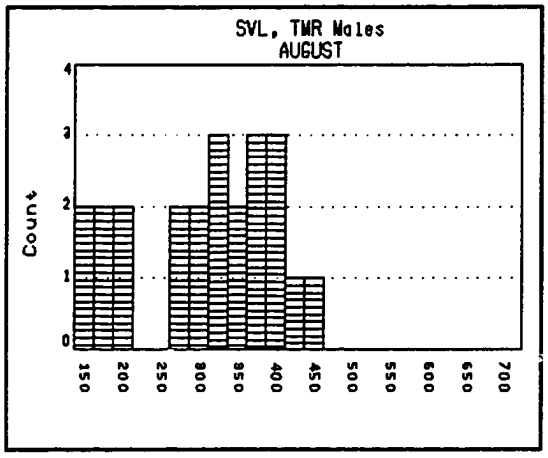


Figure 52.

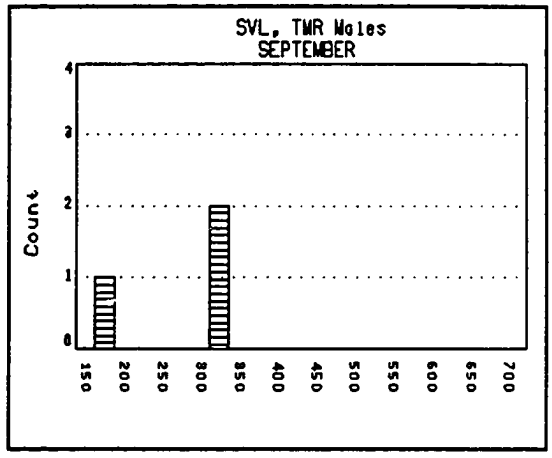


Figure 53.

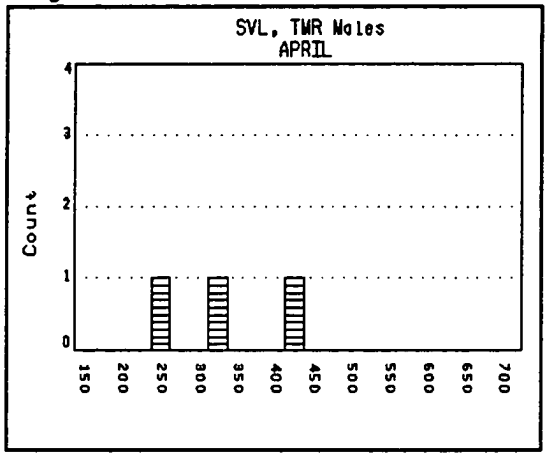


Figure 54.

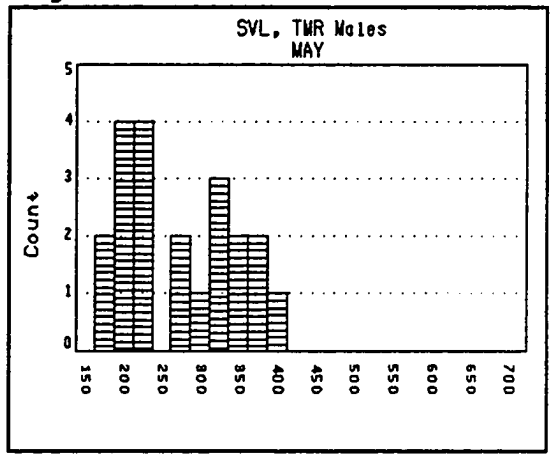


Figure 55.

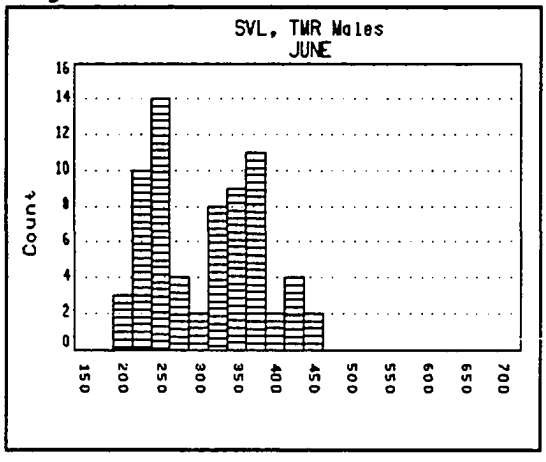


Figure 56.

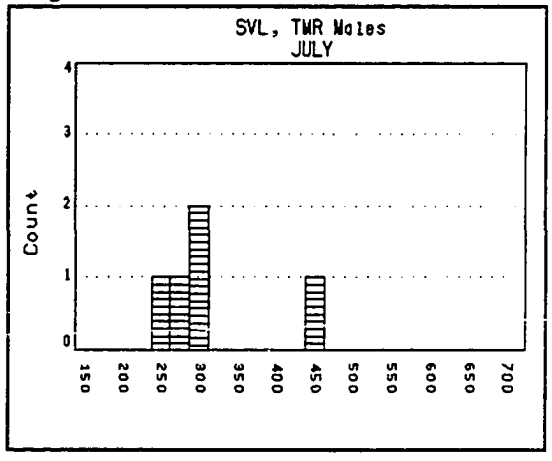


Figure 57.

Figures 52-57. Frequency distributions of SVL of all male Thamnophis s. sirtalis from TMR, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

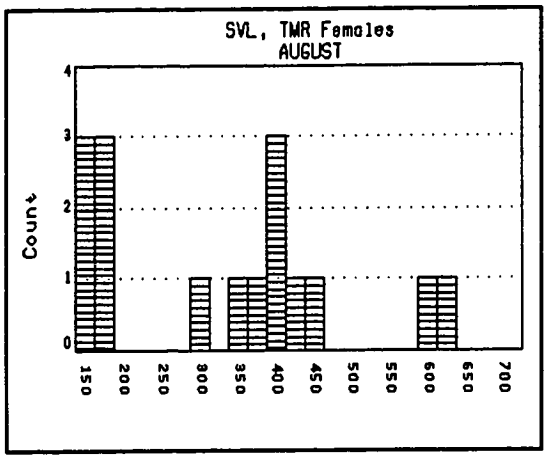


Figure 58.

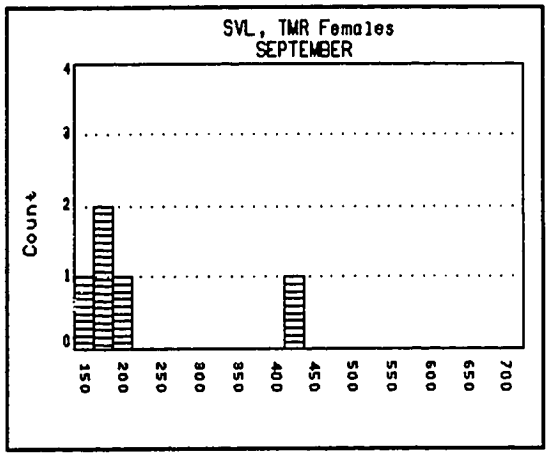


Figure 59.

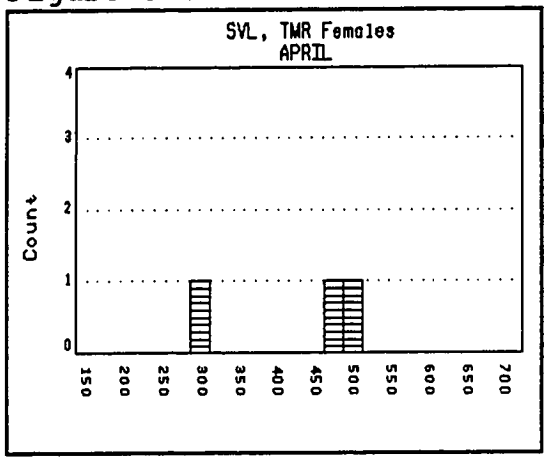


Figure 60.

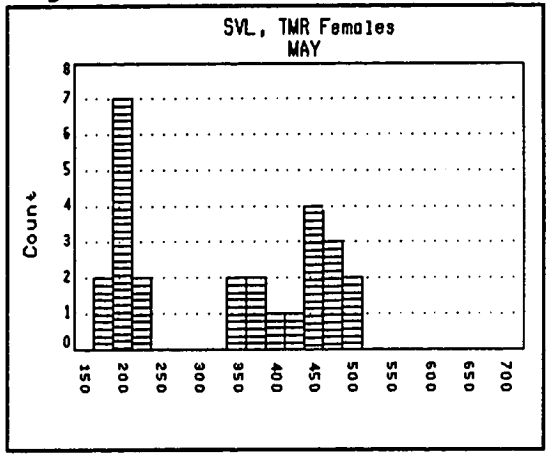


Figure 61.

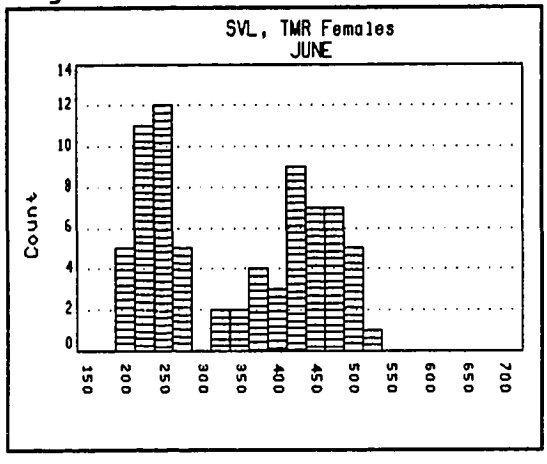


Figure 62.

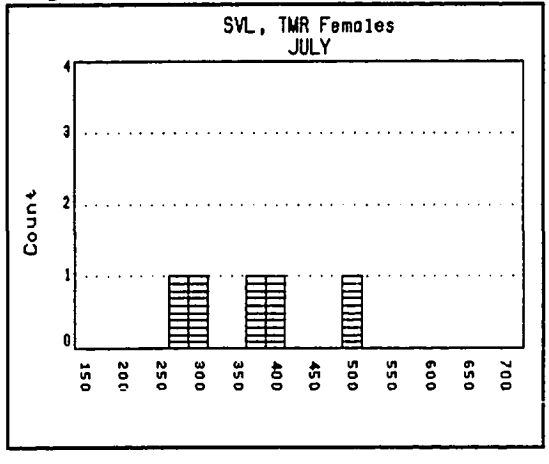


Figure 63.

Figures 58-63. Frequency distributions of SVL of all female Thamnophis s. sirtalis from TMR, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

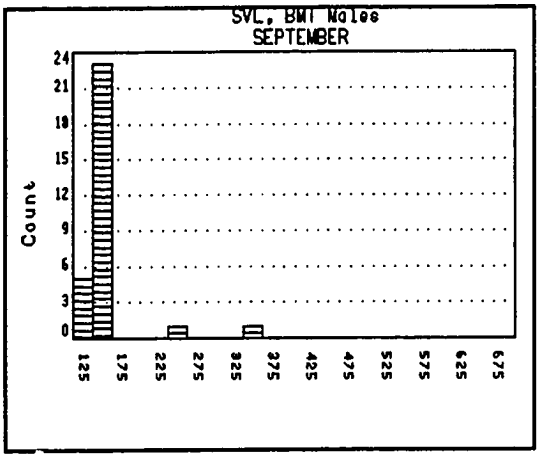


Figure 64.

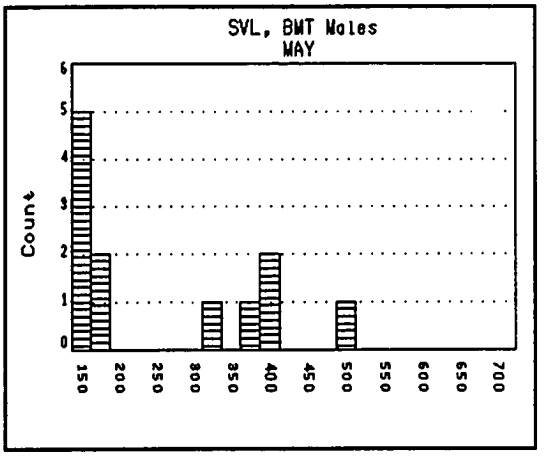


Figure 65.

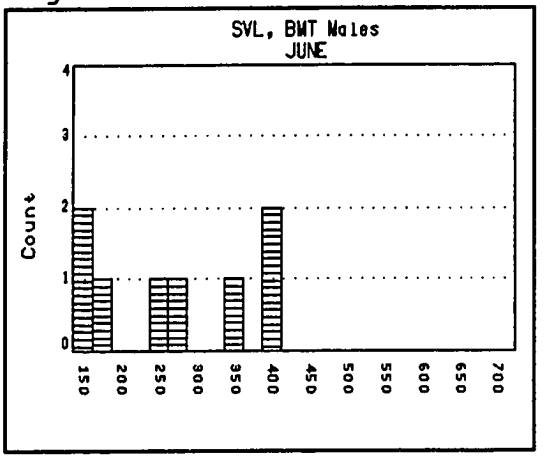


Figure 66.

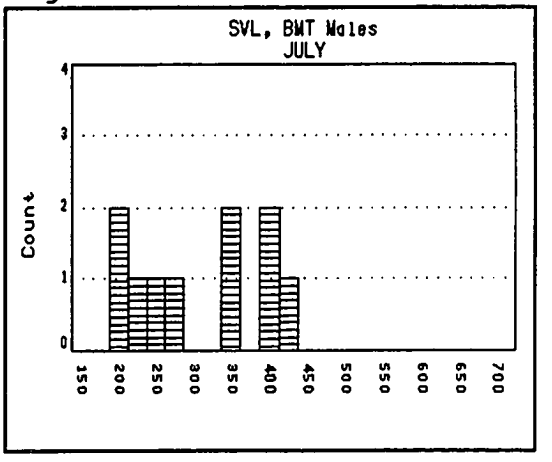


Figure 67.

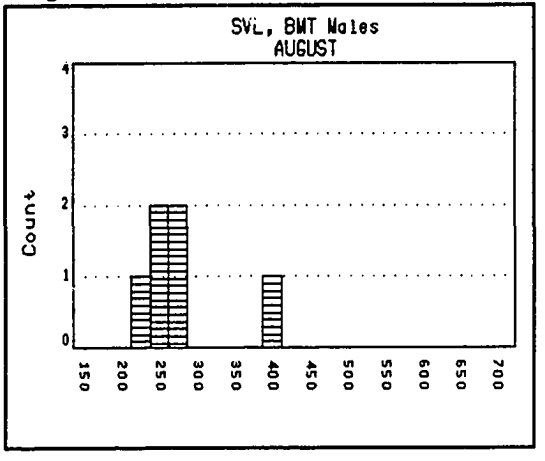


Figure 68.

Figures 64-68. Frequency distributions of SVL of all male Thamnophis s. sirtalis from BMT, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

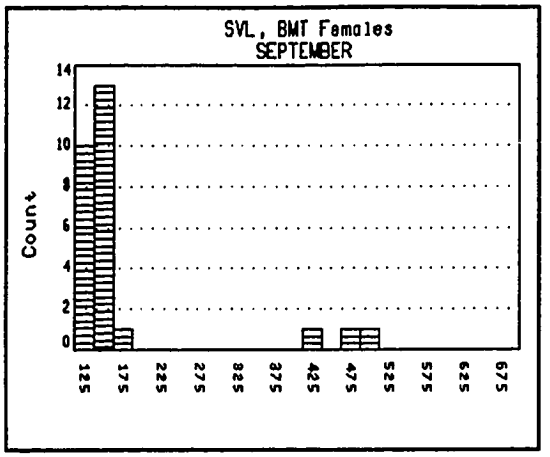


Figure 69.

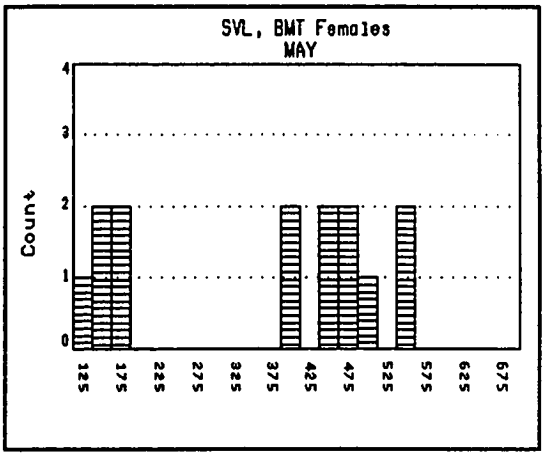


Figure 70.

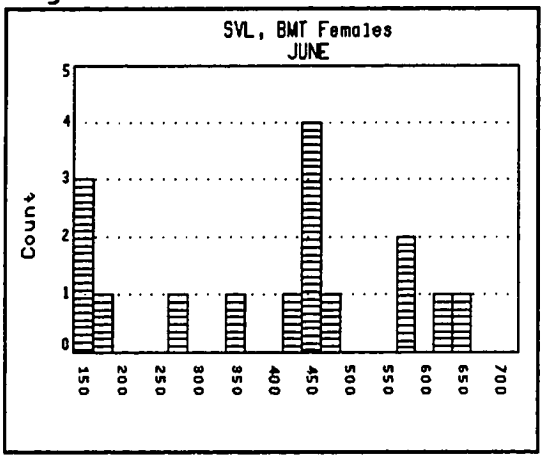


Figure 71.

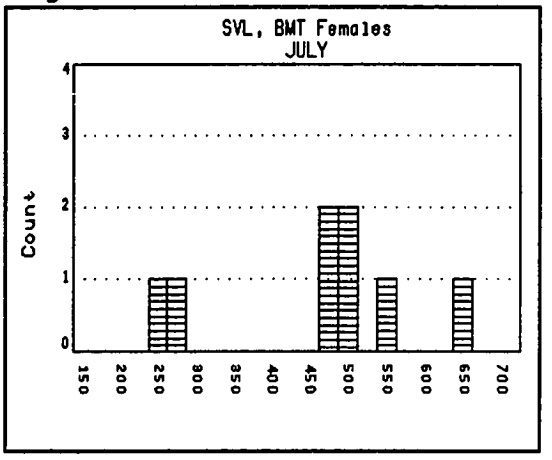


Figure 72.

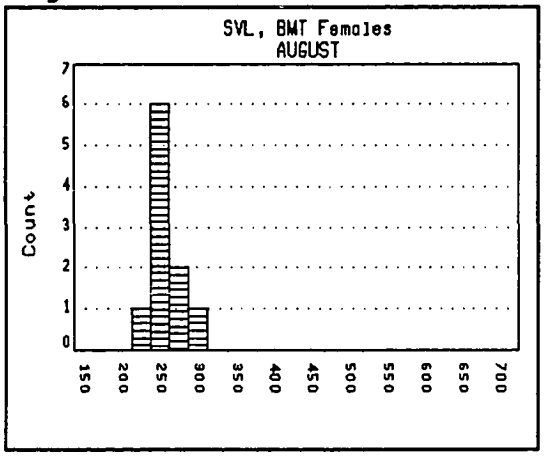


Figure 73.

Figures 69-73. Frequency distributions of SVL of all female Thamnophis s. sirtalis from BMT, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

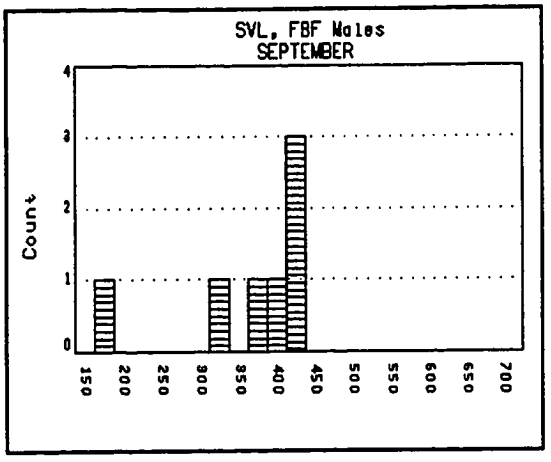


Figure 74.

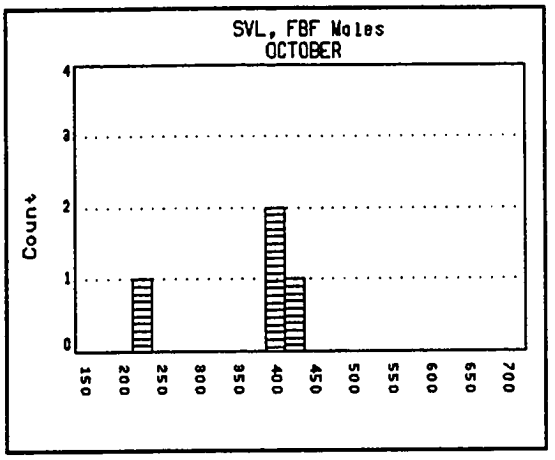


Figure 75.

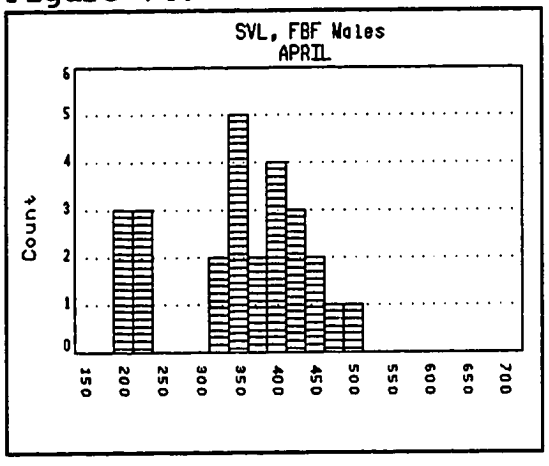


Figure 76.

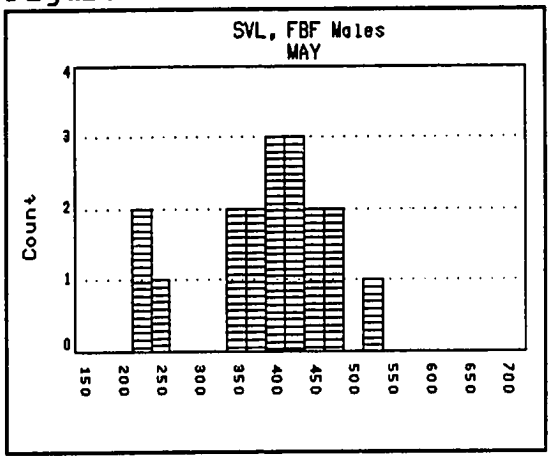


Figure 77.

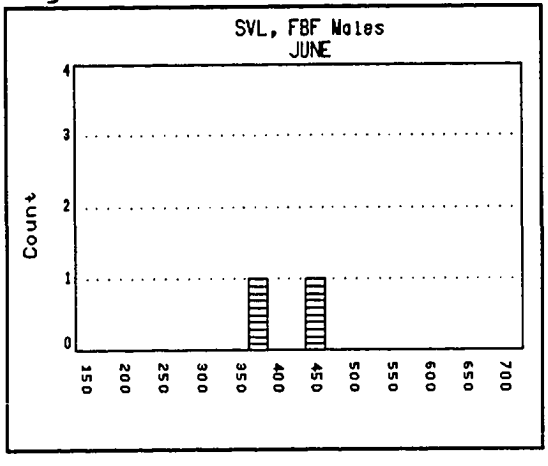


Figure 78.

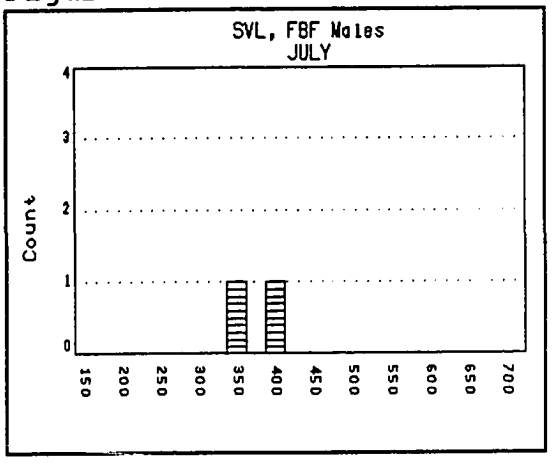


Figure 79.

Figures 74-79. Frequency distributions of SVL of all male Thamnophis s. sirtalis from FBF, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

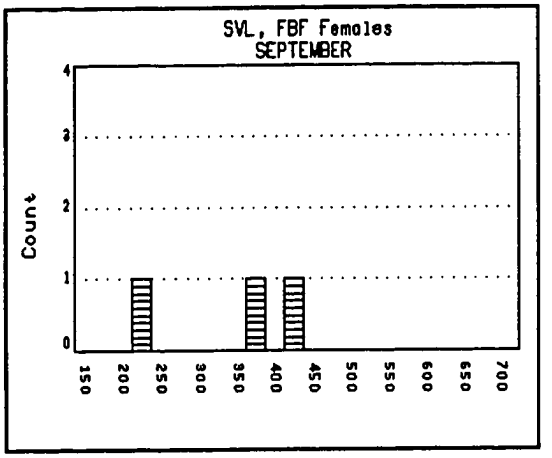


Figure 80.

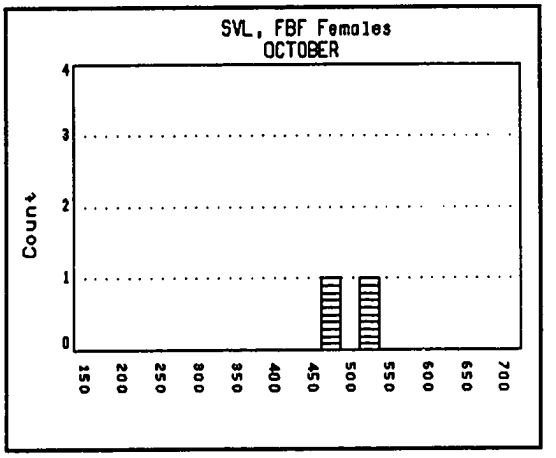


Figure 81.

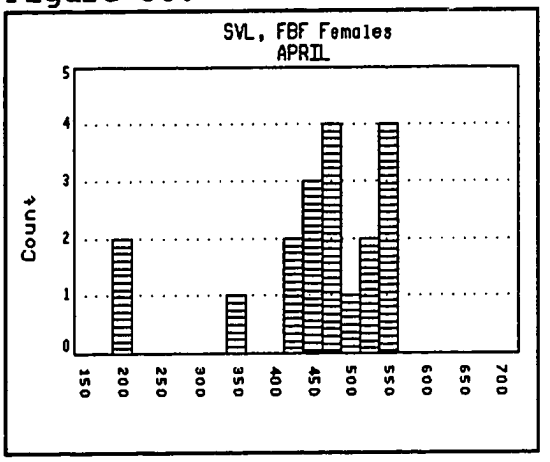


Figure 82.

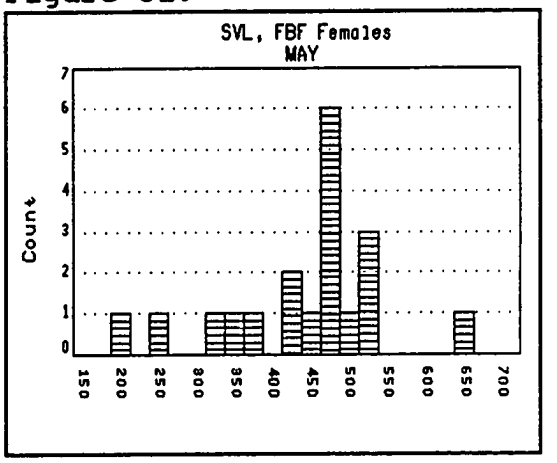


Figure 83.

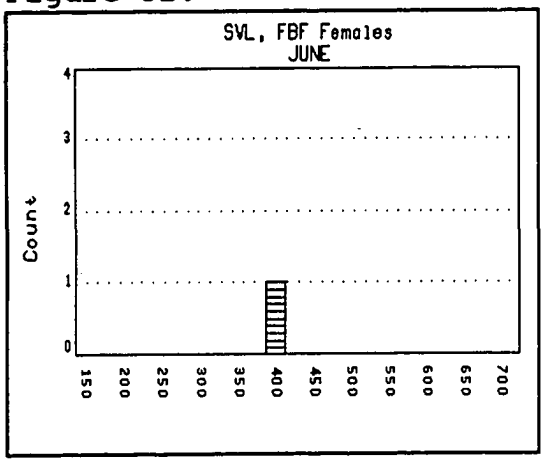


Figure 84.

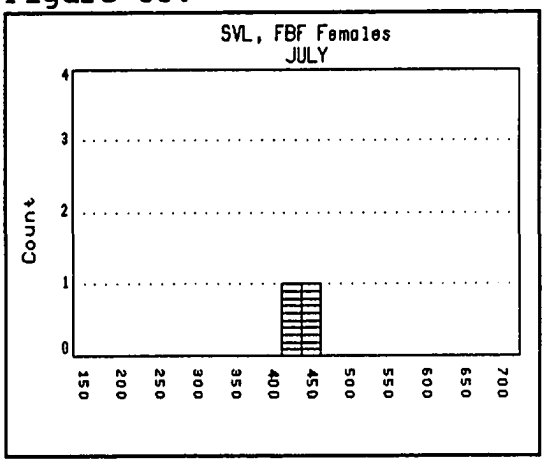


Figure 85.

Figures 80-85. Frequency distributions of SVL of all female Thamnophis s. sirtalis from FBF, by month.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

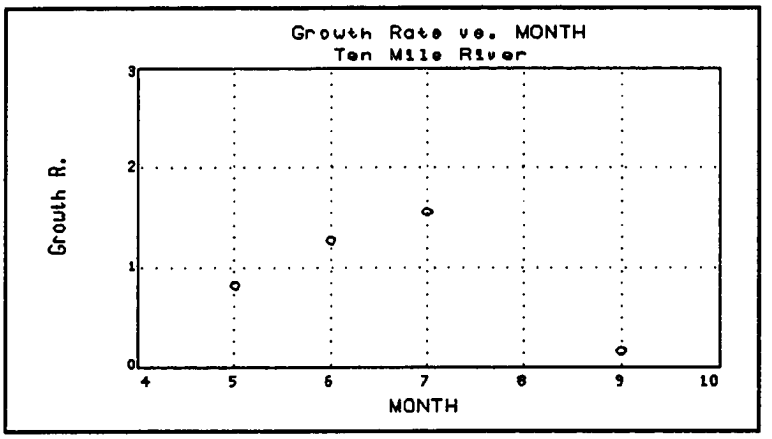


Fig. 86. Growth rates of first year snakes at Ten Mile River locality, by month, based on cohor data.

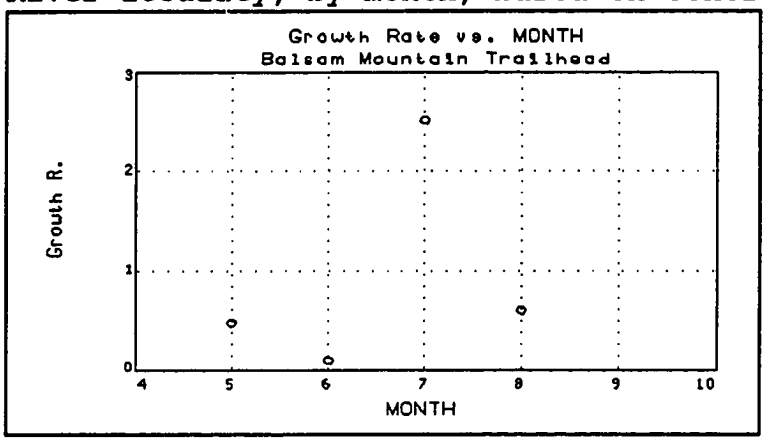


Fig. 87. Growth rates of first year snakes at Balsam Mountain Trailhead locality, by month, based on cohort data.

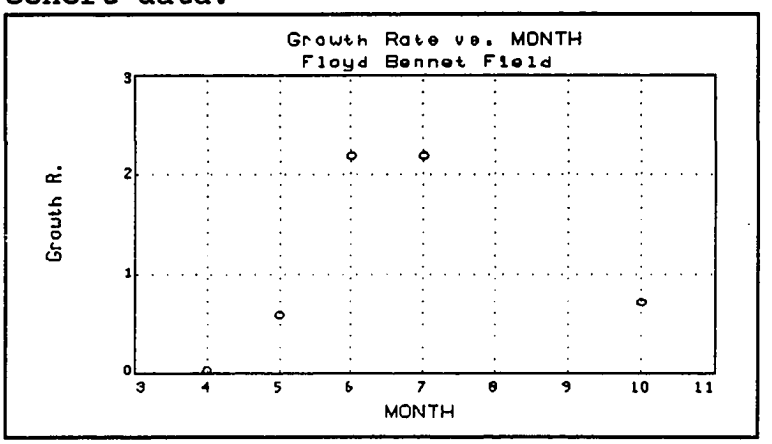


Fig. 88. Growth rates of first year snakes at Floyd Bennett Field locality, by month, based on cohort data.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

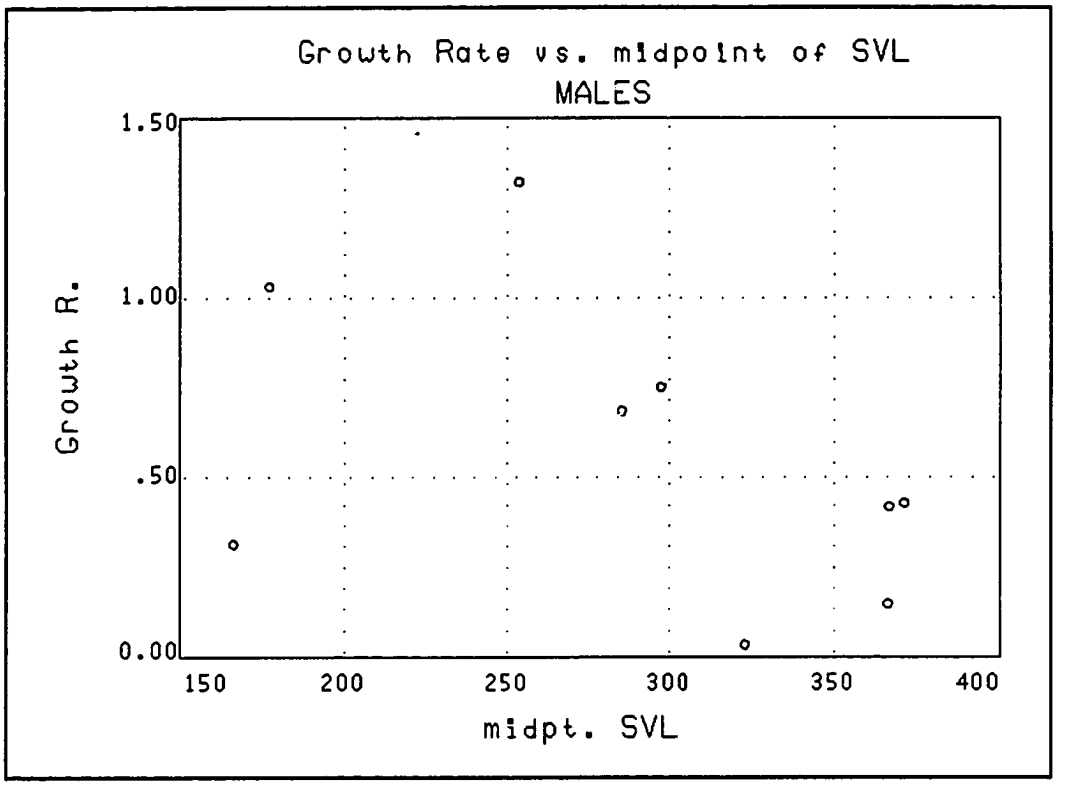


Fig. 89. Growth rates of male Thamnophis s. sirtalis from three main study localities, based on recapture data.

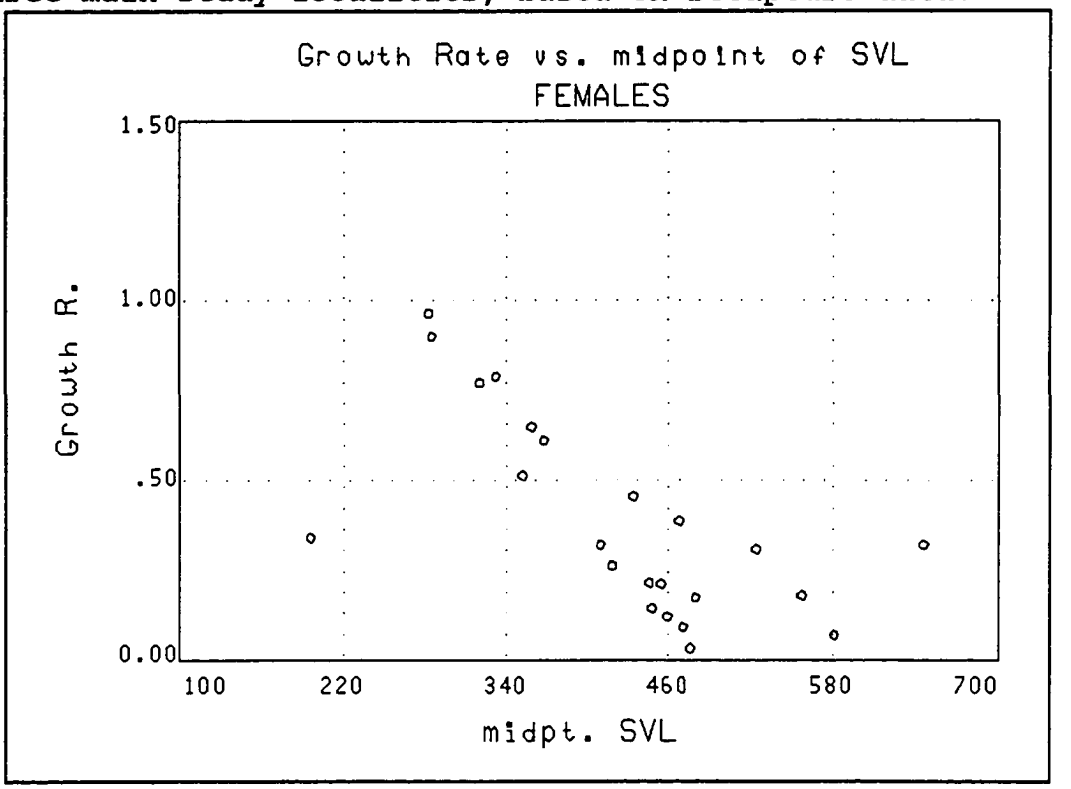


Fig. 90. Growth rates of male Thamnophis s. sirtalis from three main study localities, based on recapture data.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

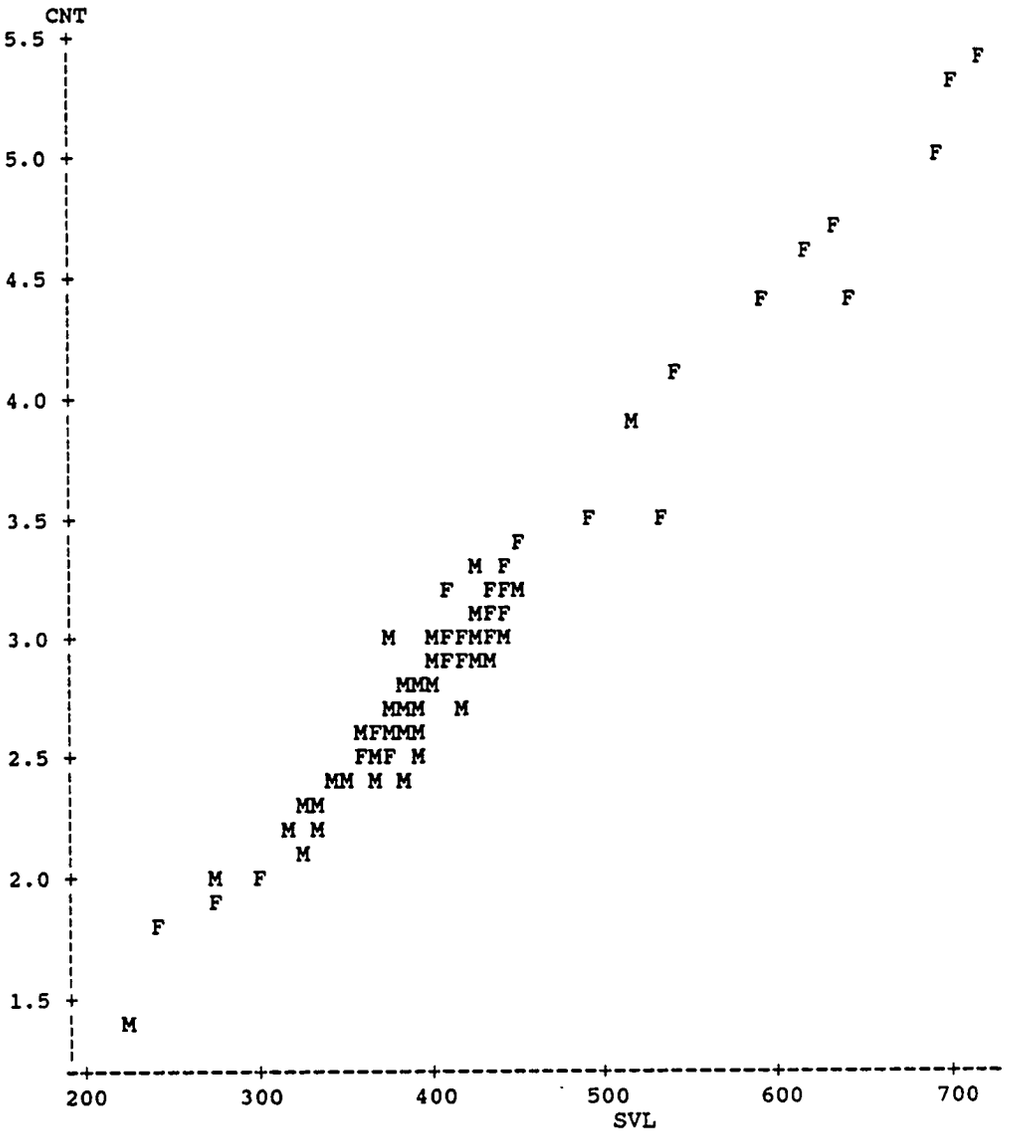


Figure 91. Plot of CNT vs SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

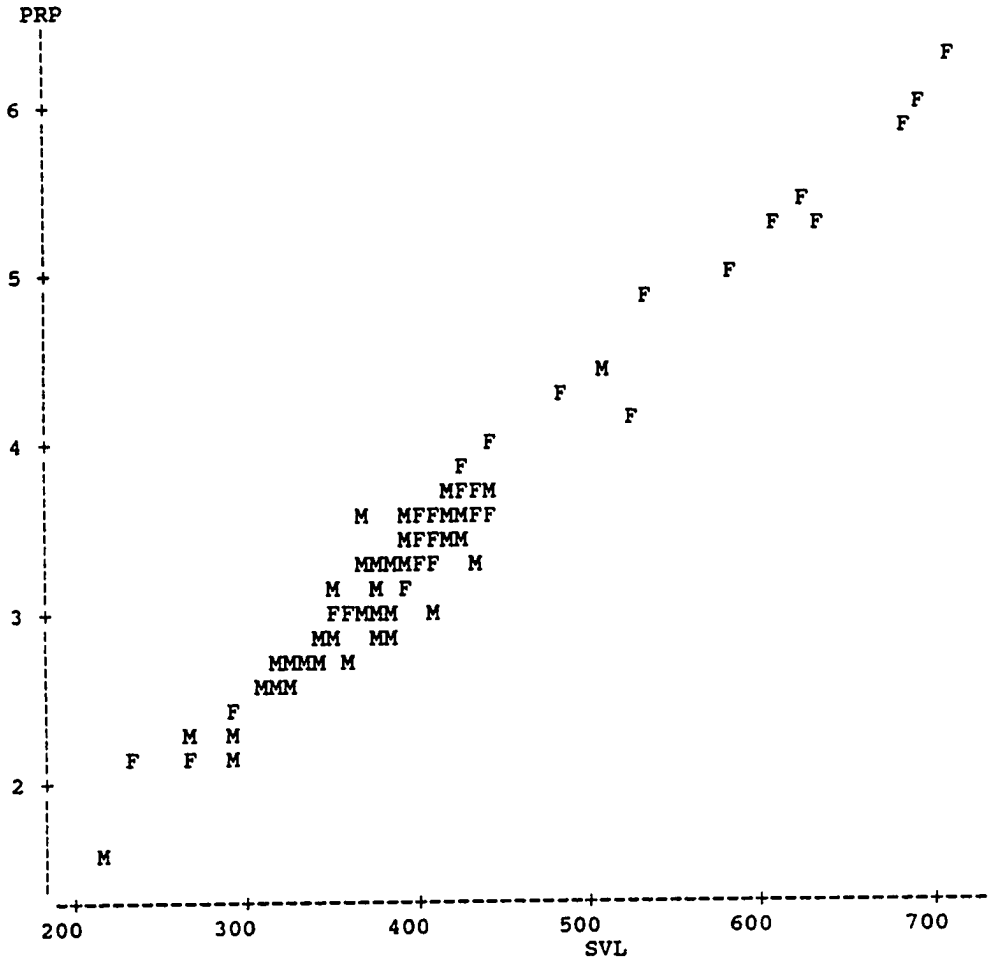


Figure 92. Plot of PRP vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

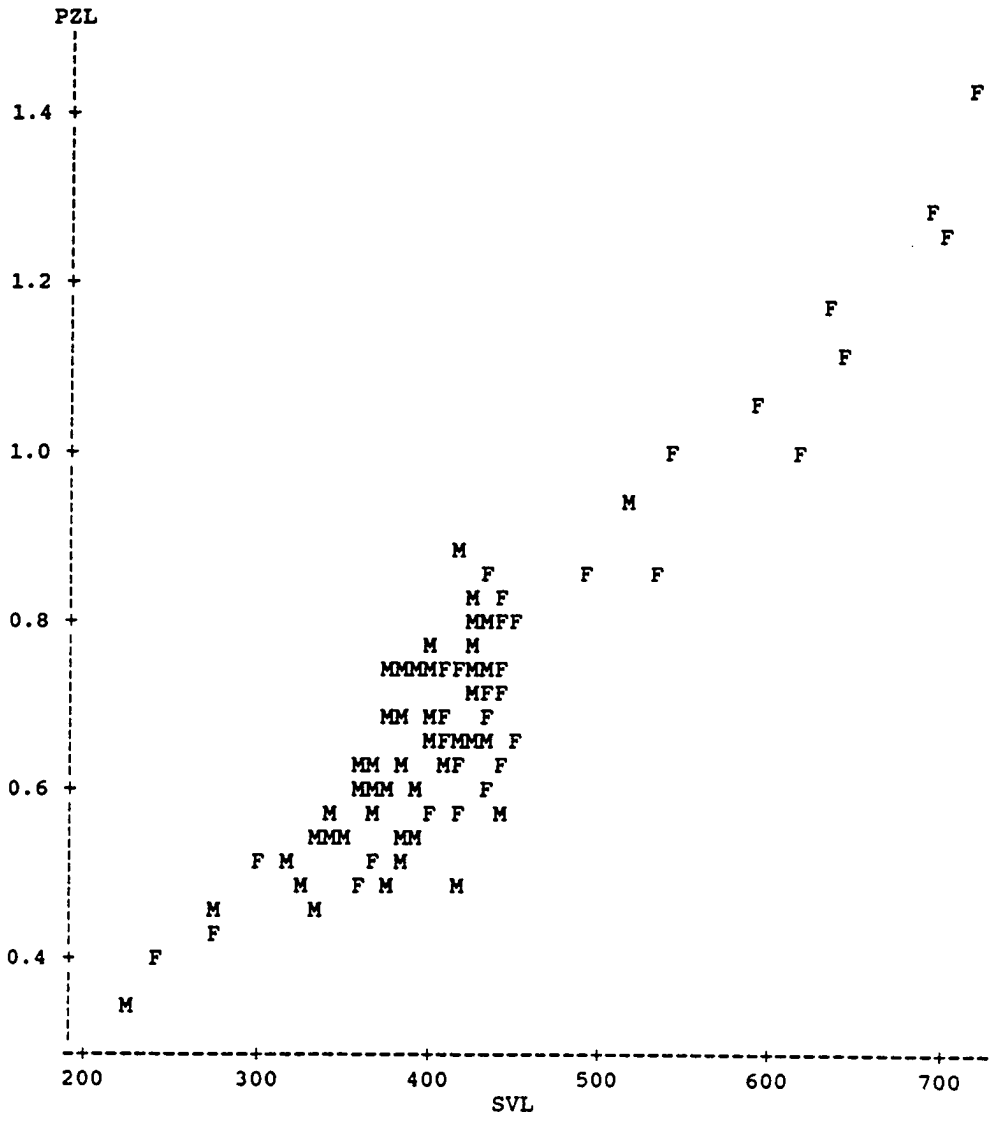


Figure 93. Plot of PZL vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

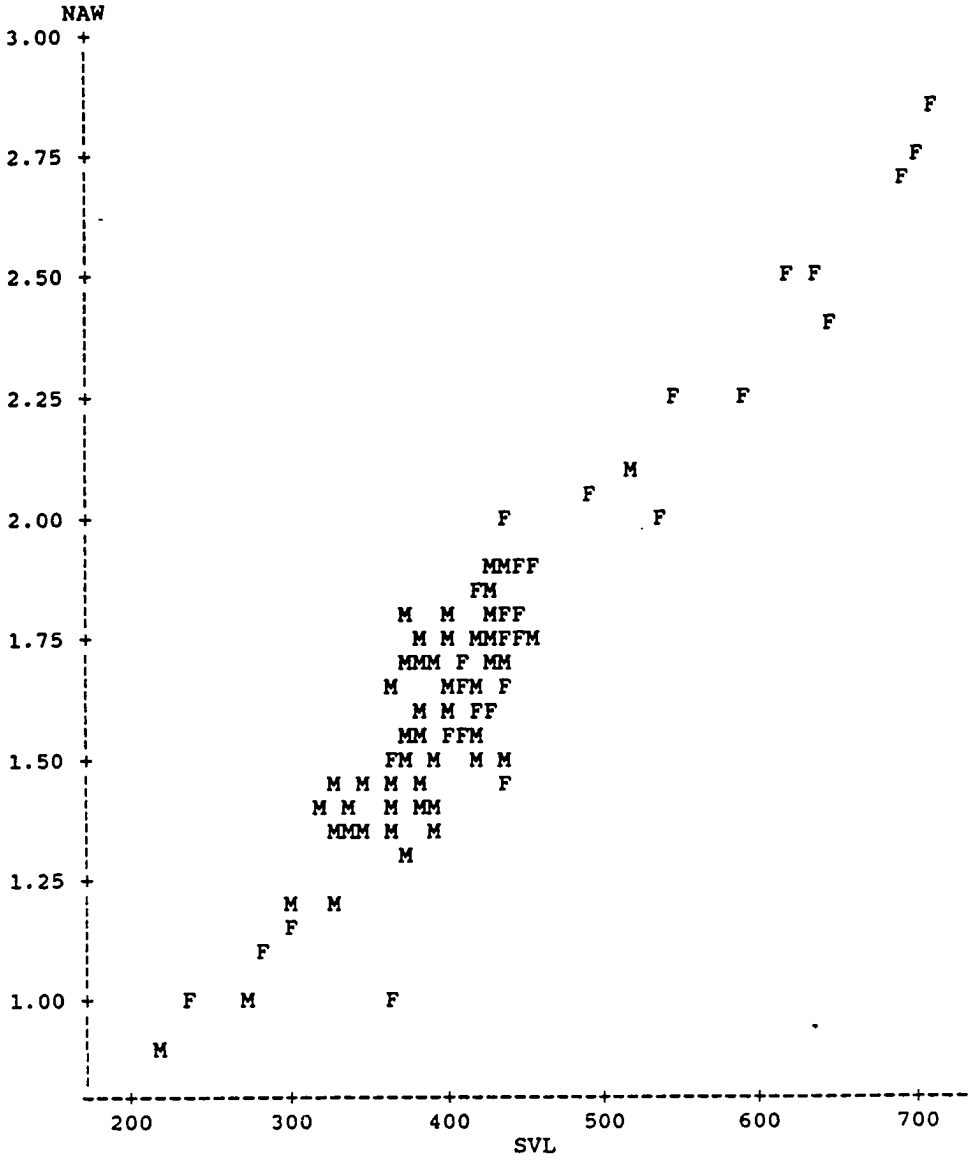


Figure 94. Plot of Naw vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

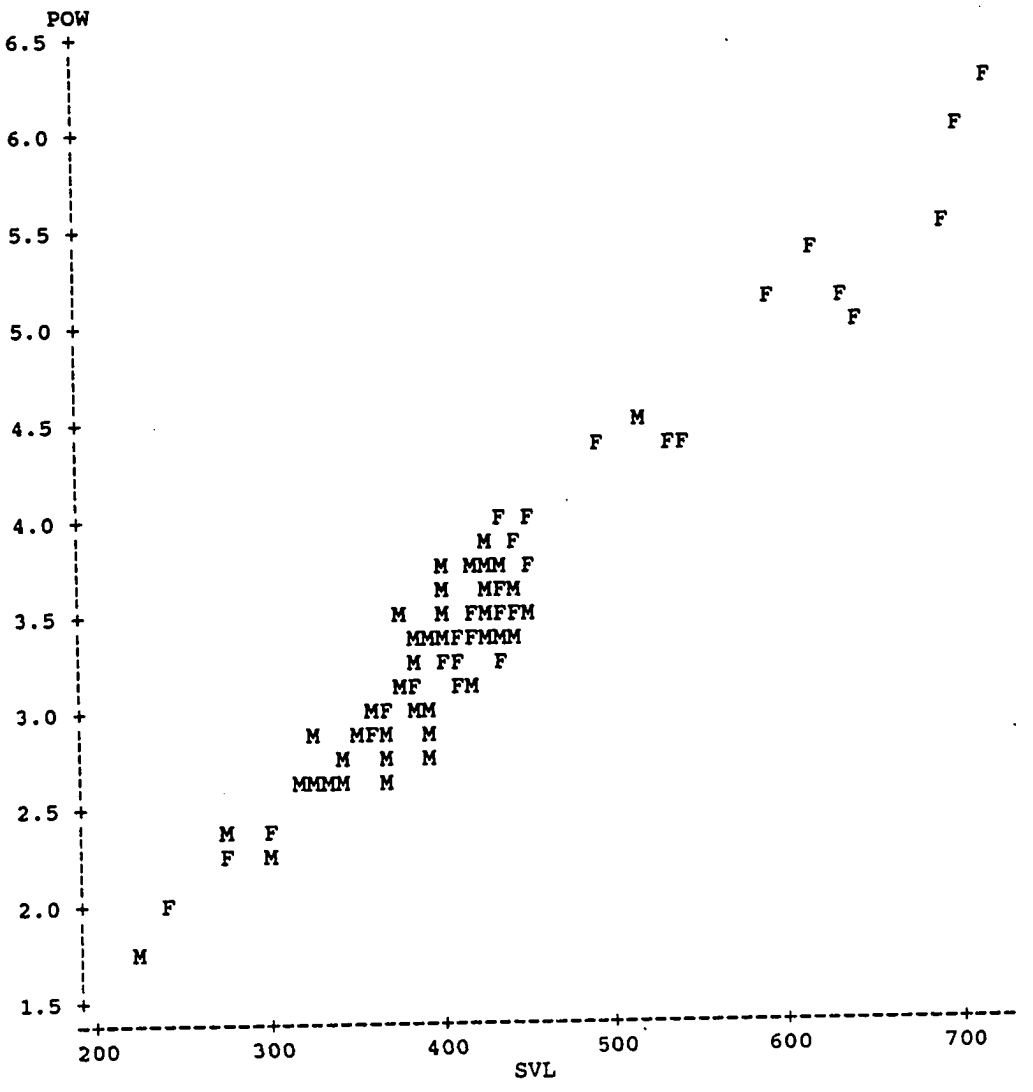


Figure 95. Plot of POW vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

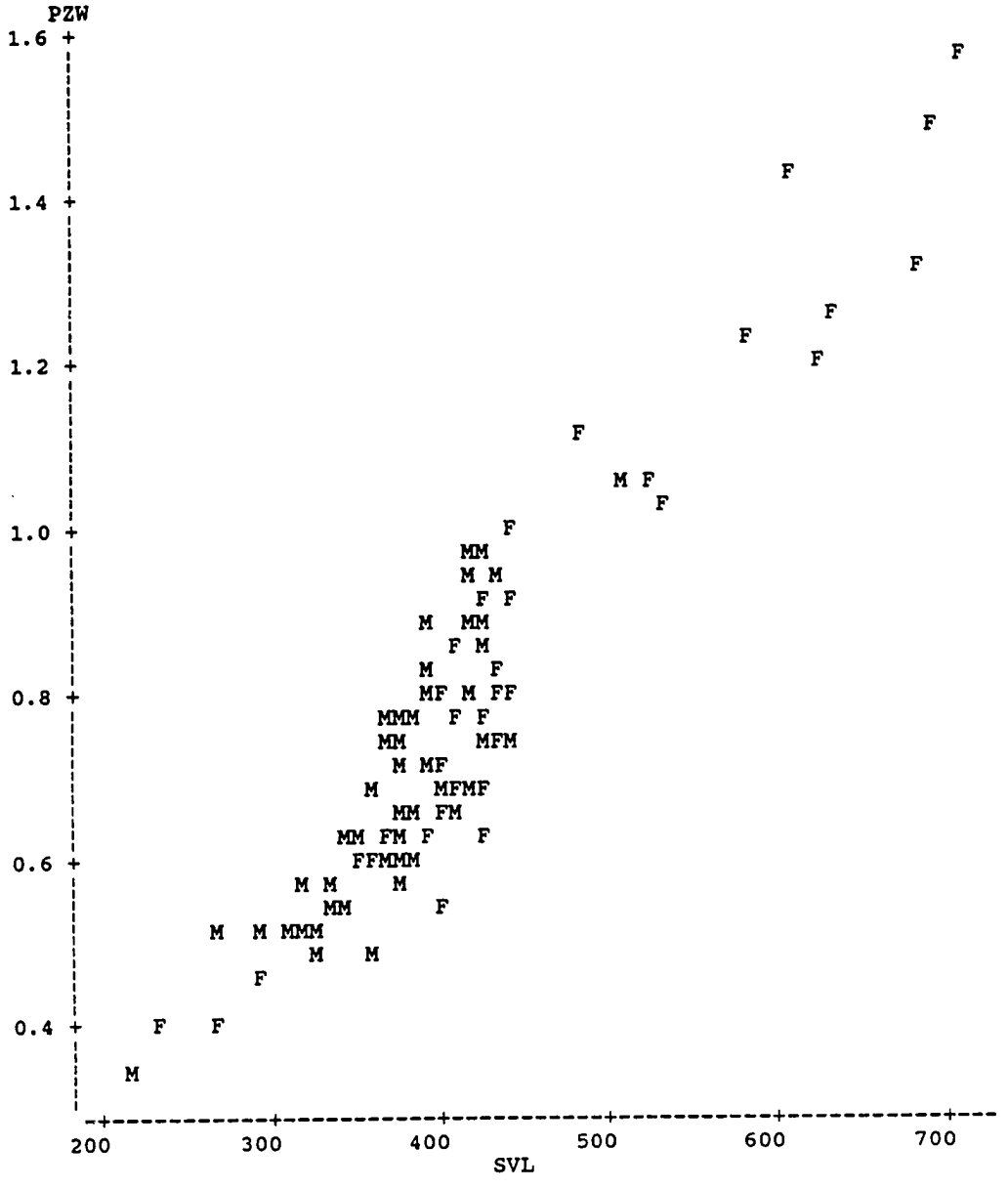


Figure 96. Plot of PZW vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

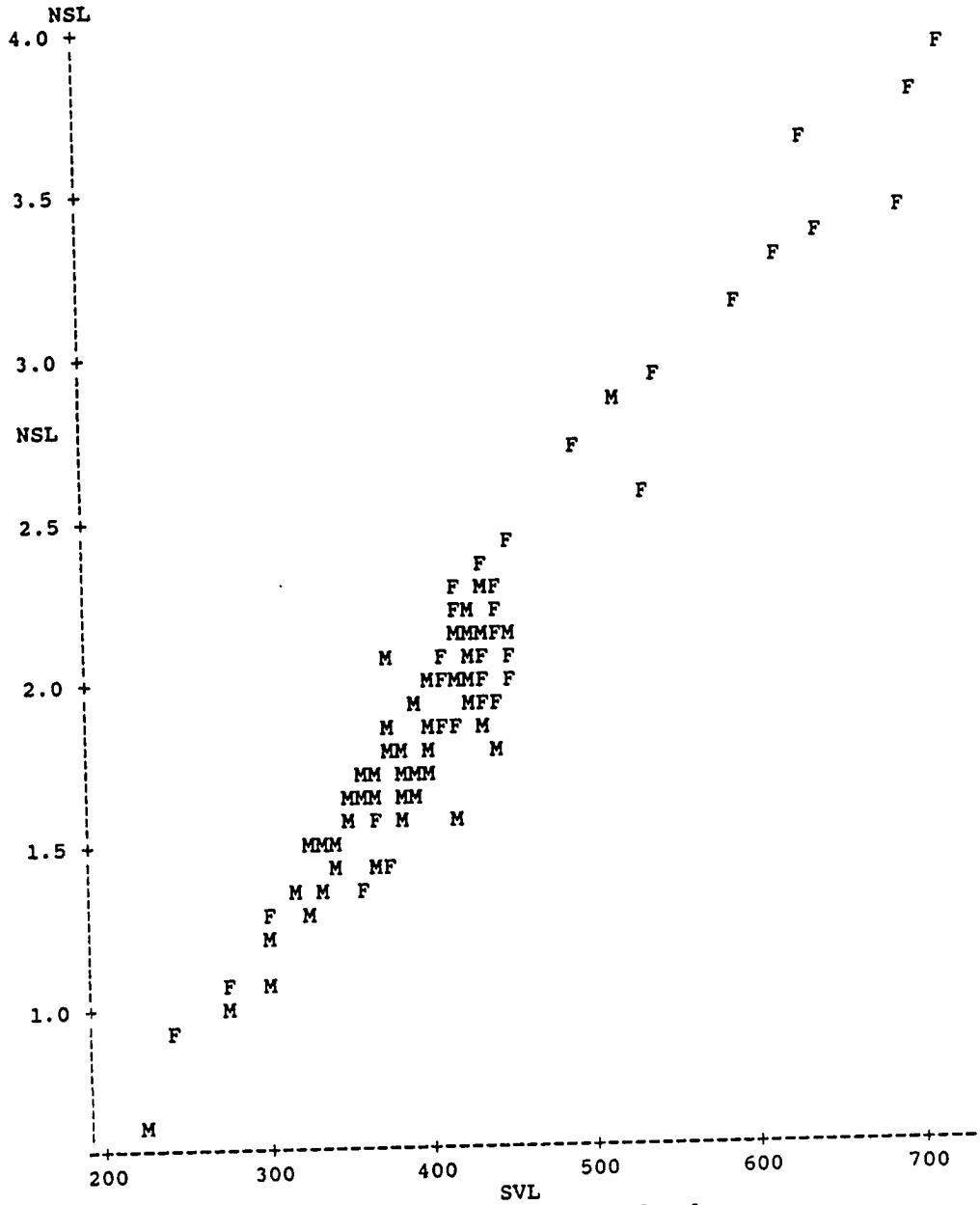


Figure 97. Plot of NSL vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

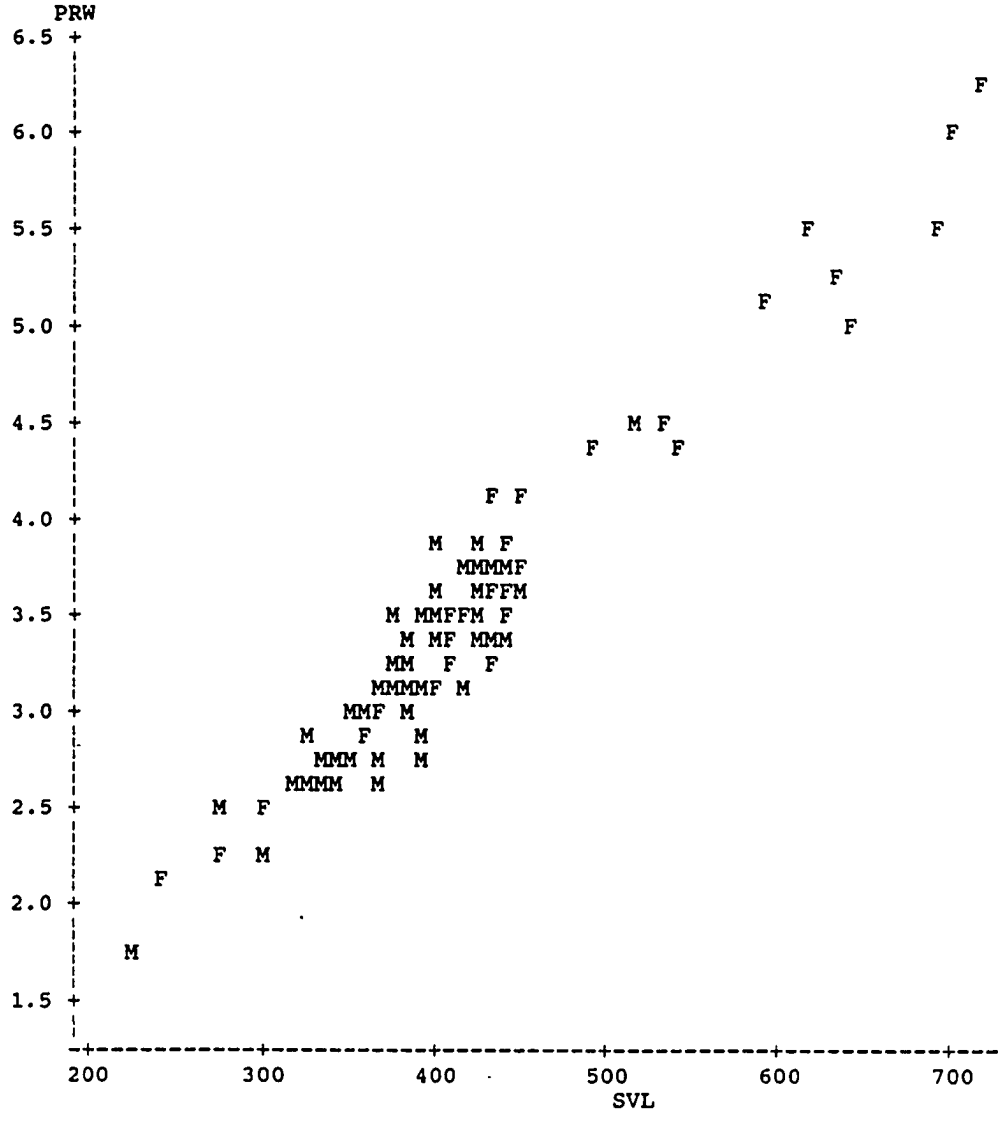


Figure 98. Plot of PRW vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

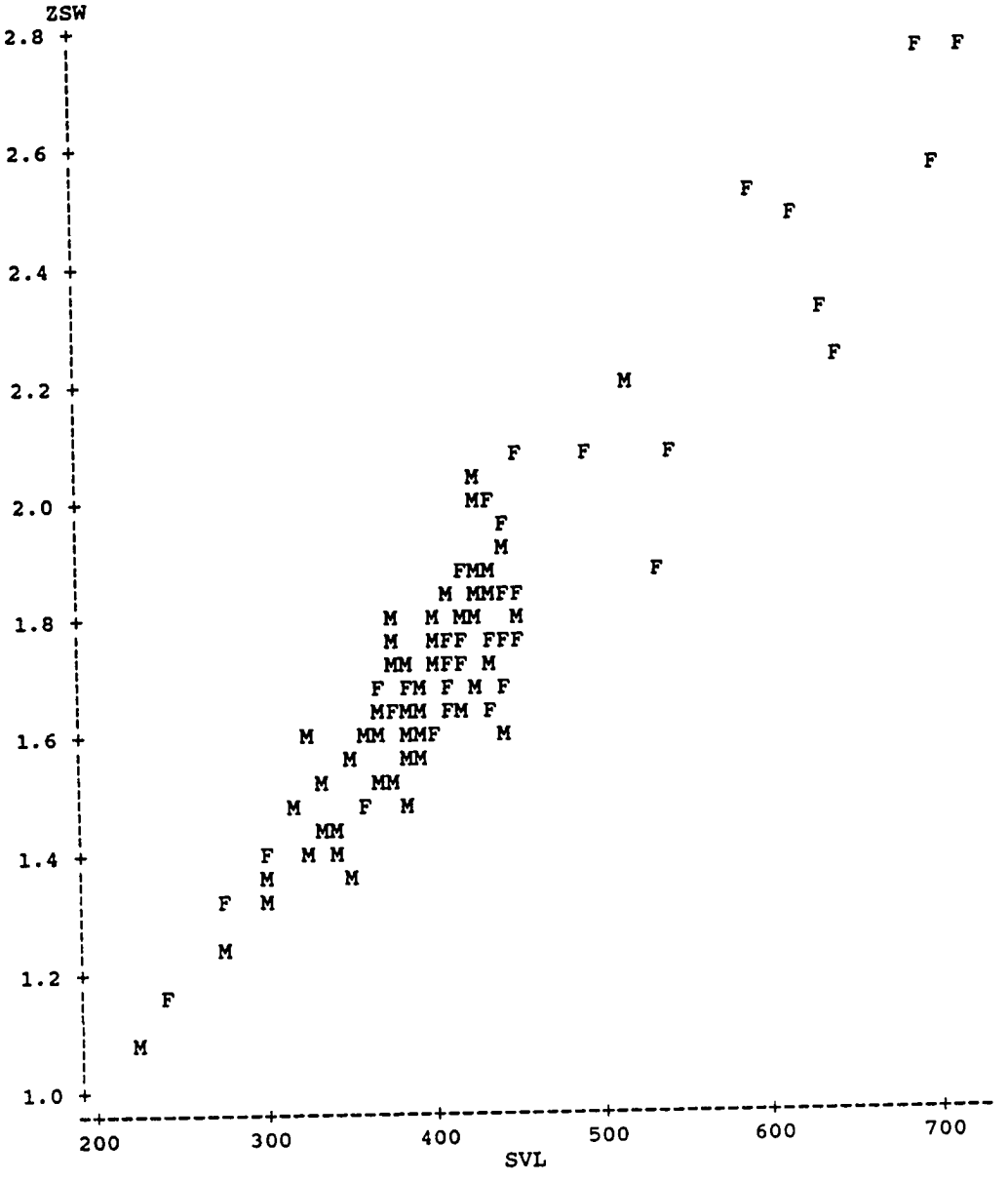


Figure 99. Plot of ZSW vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

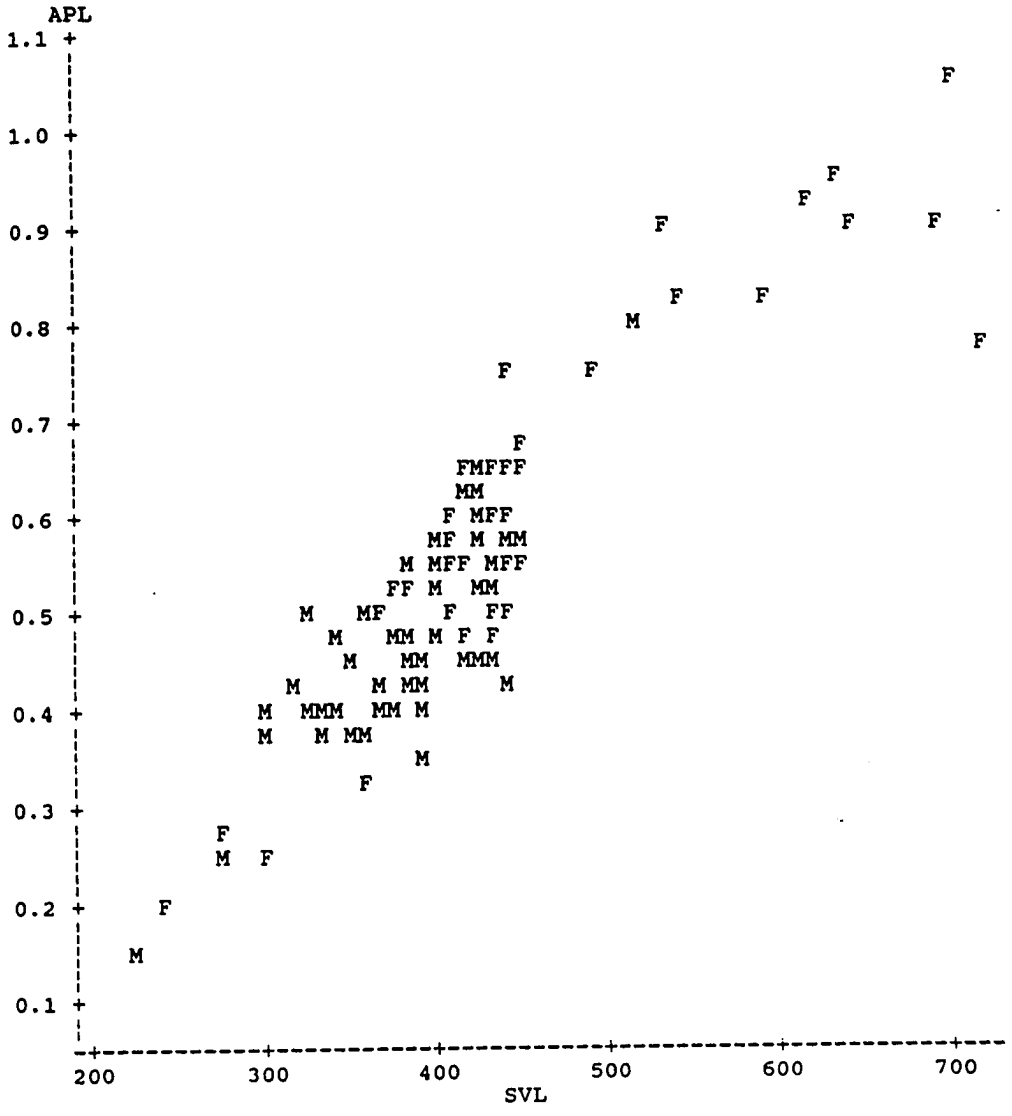


Figure 100. Plot of APL vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

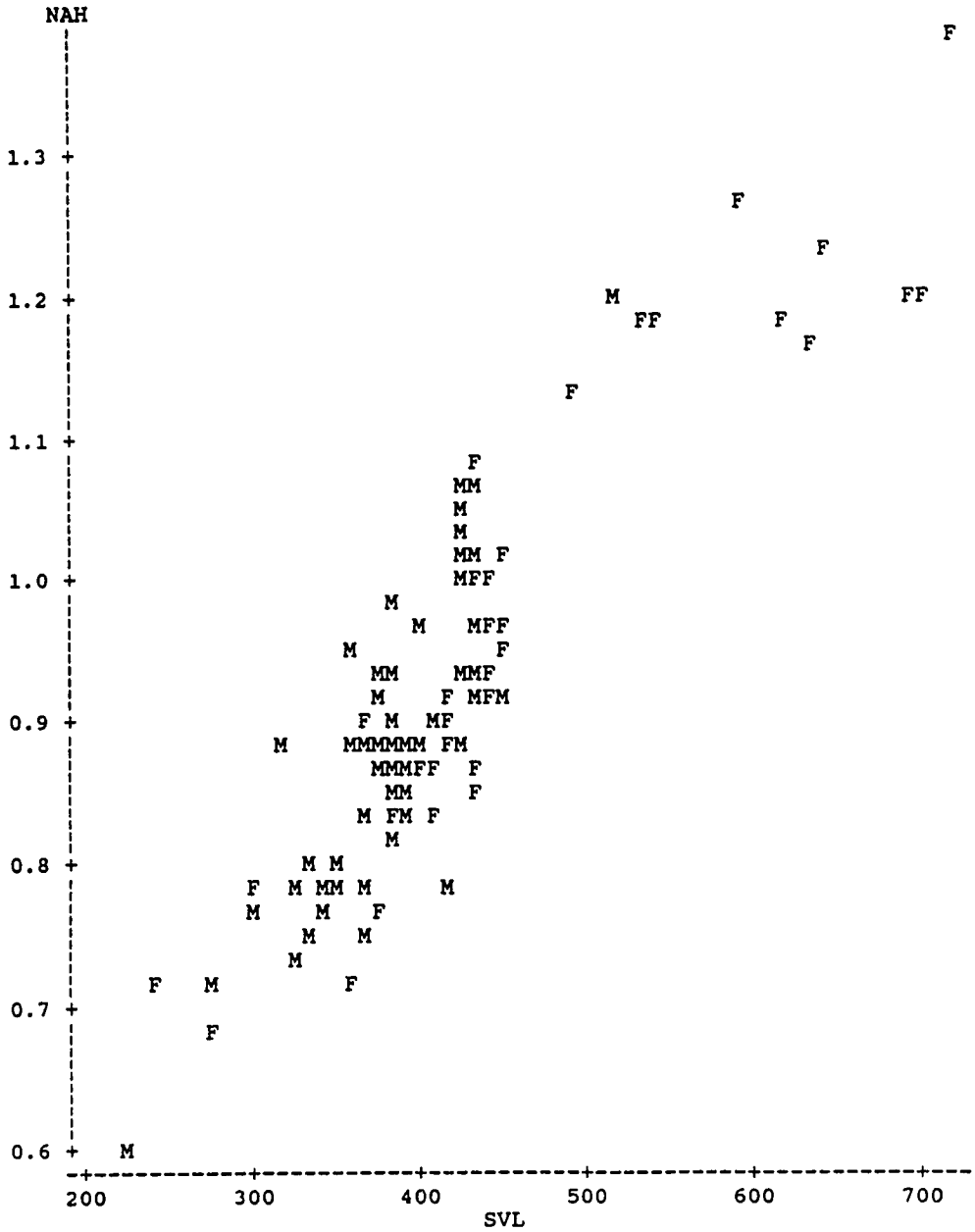


Figure 101. Plot of NAH vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

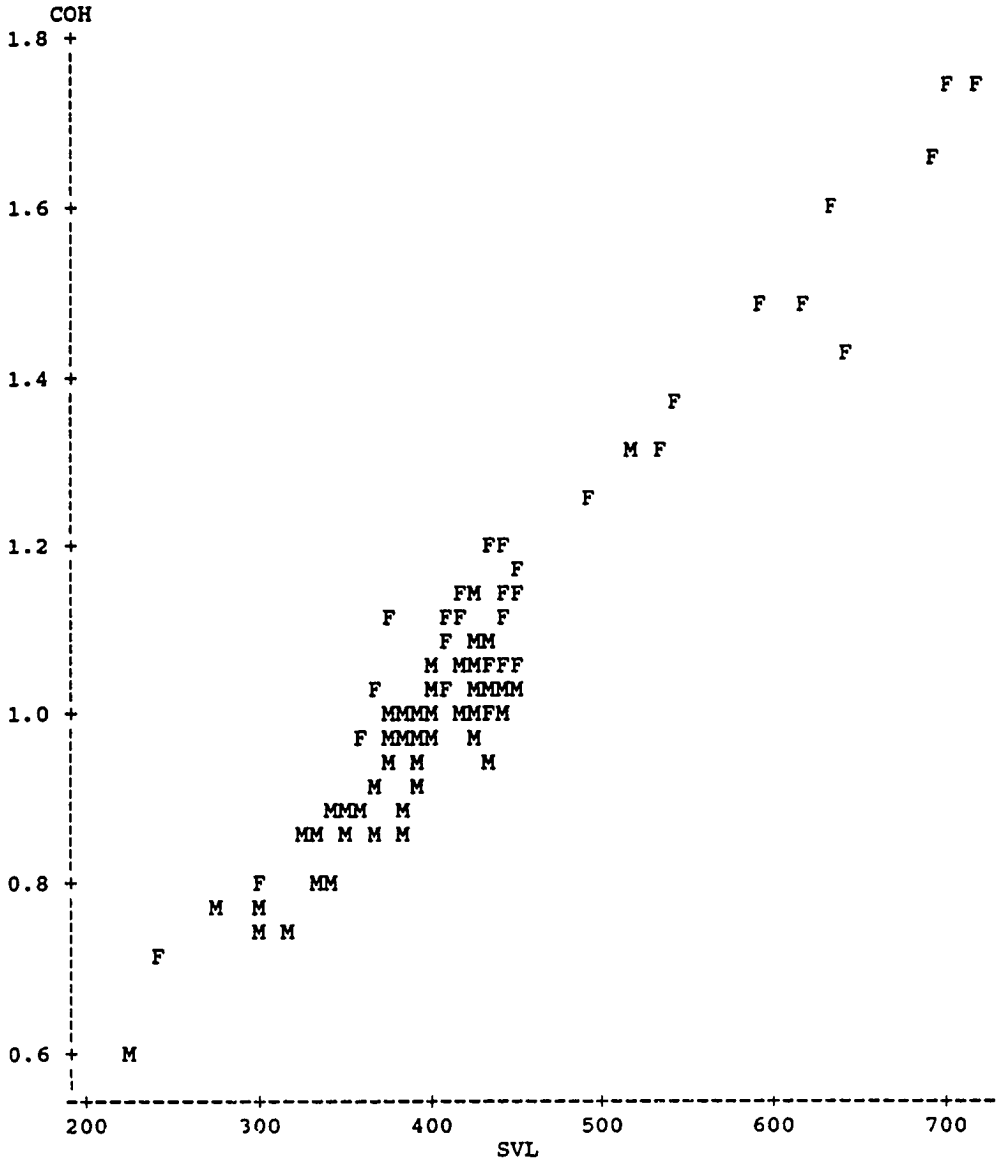


Figure 102. Plot of COH vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

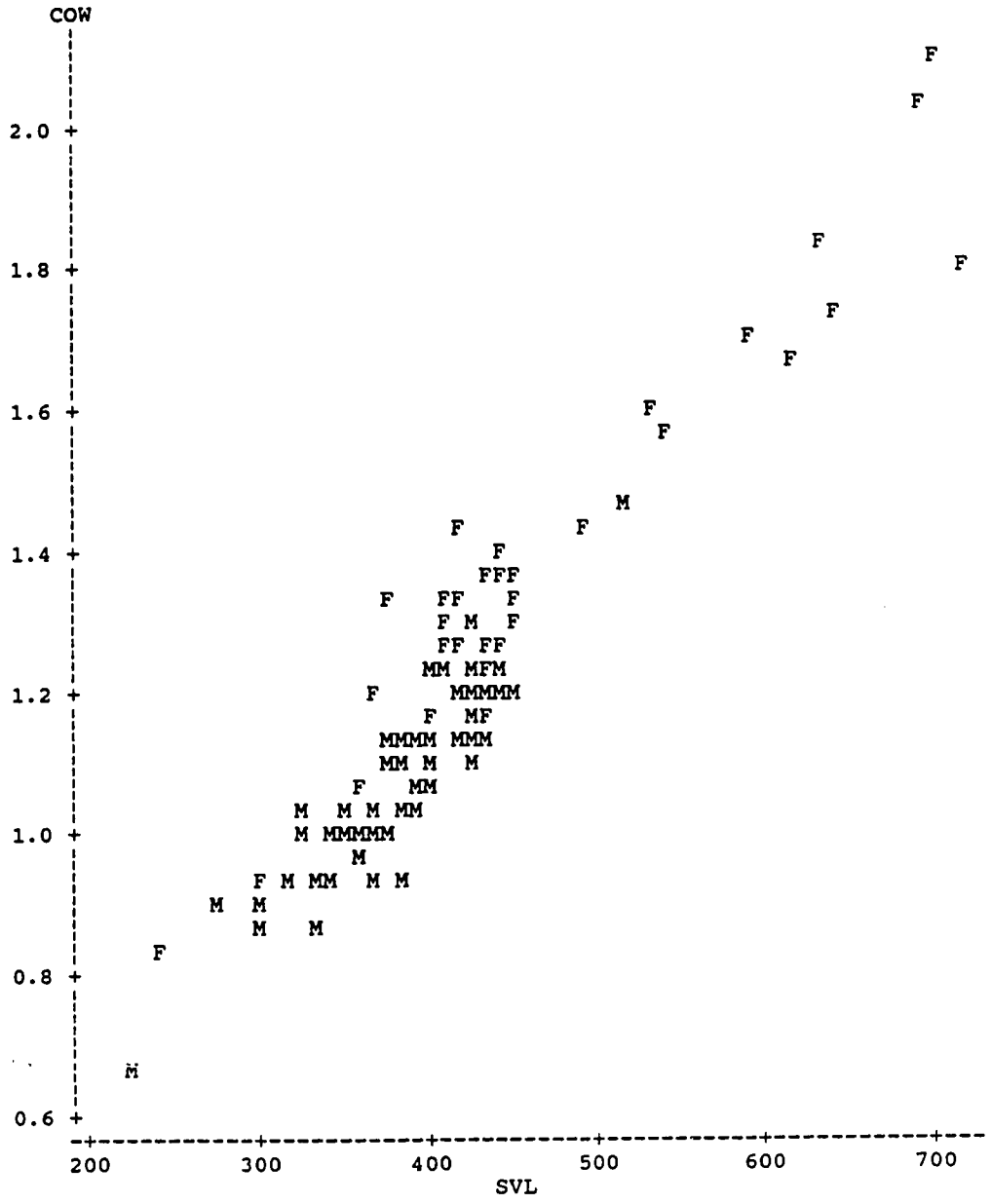


Figure 103. Plot of COW vs SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

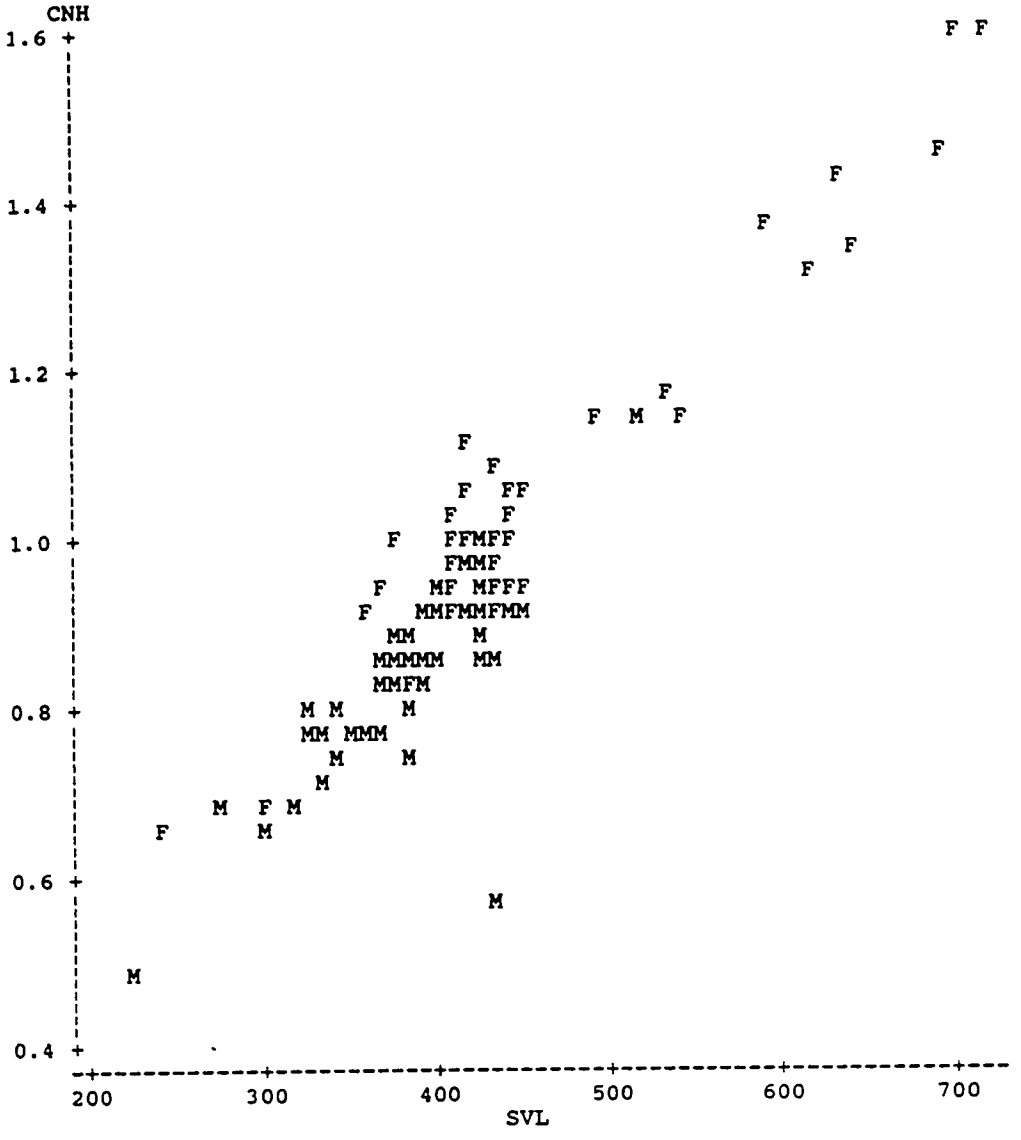


Figure 104. Plot of COH vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

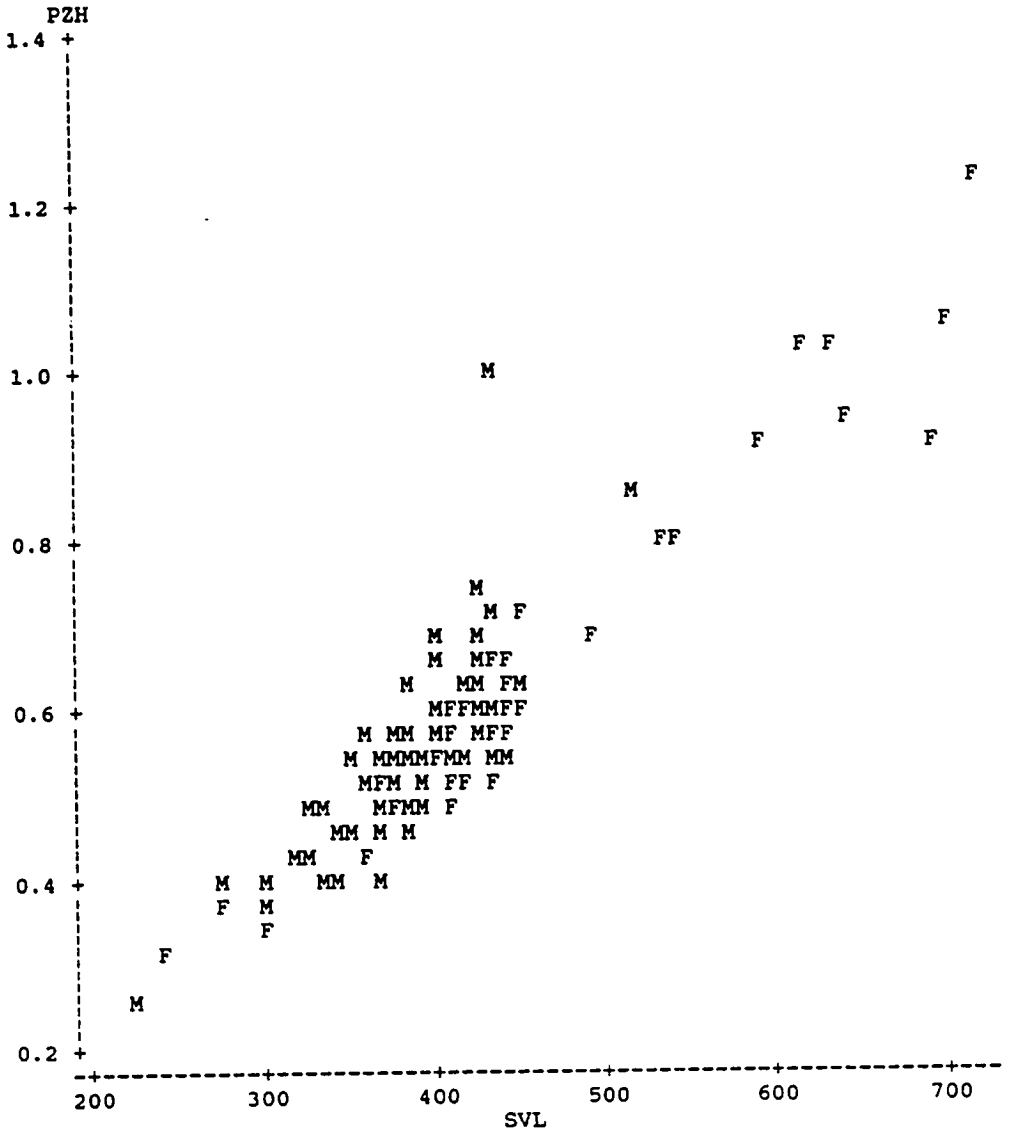


Figure 105. Plot of PZH vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

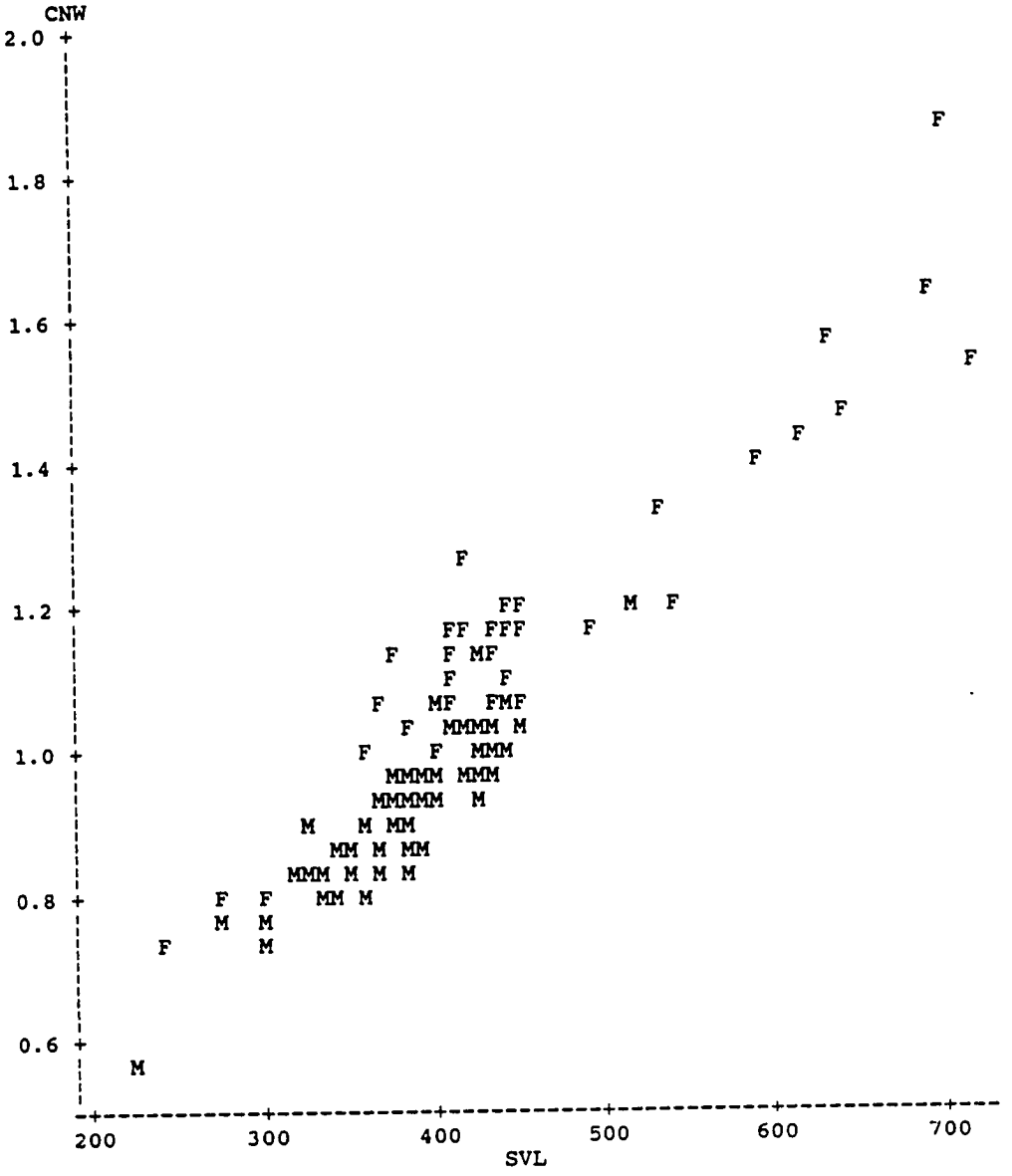


Figure 106. Plot of CNW vs SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

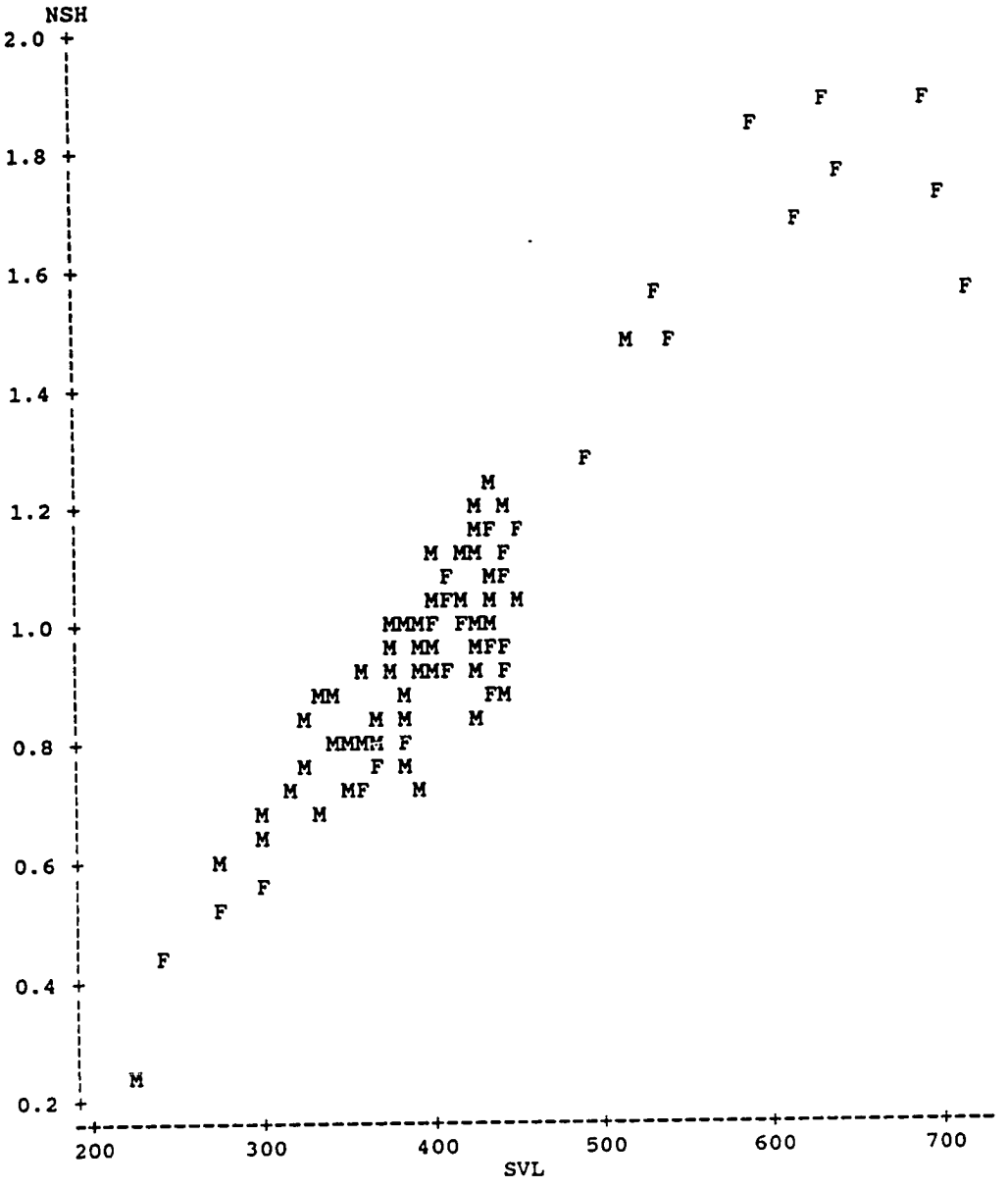


Figure 107. Plot of NSH vs SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

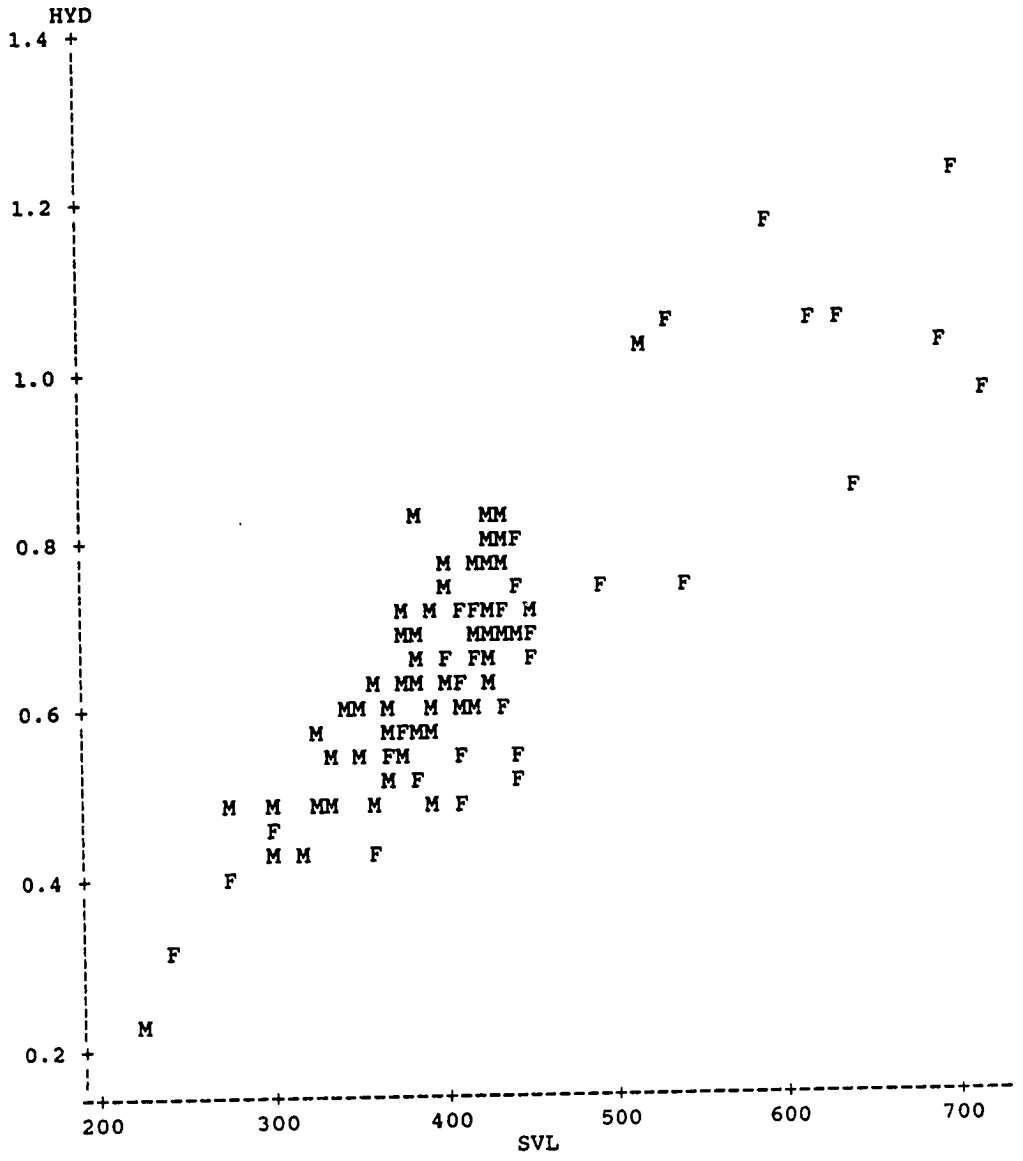


Figure 108. Plot of HYD vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

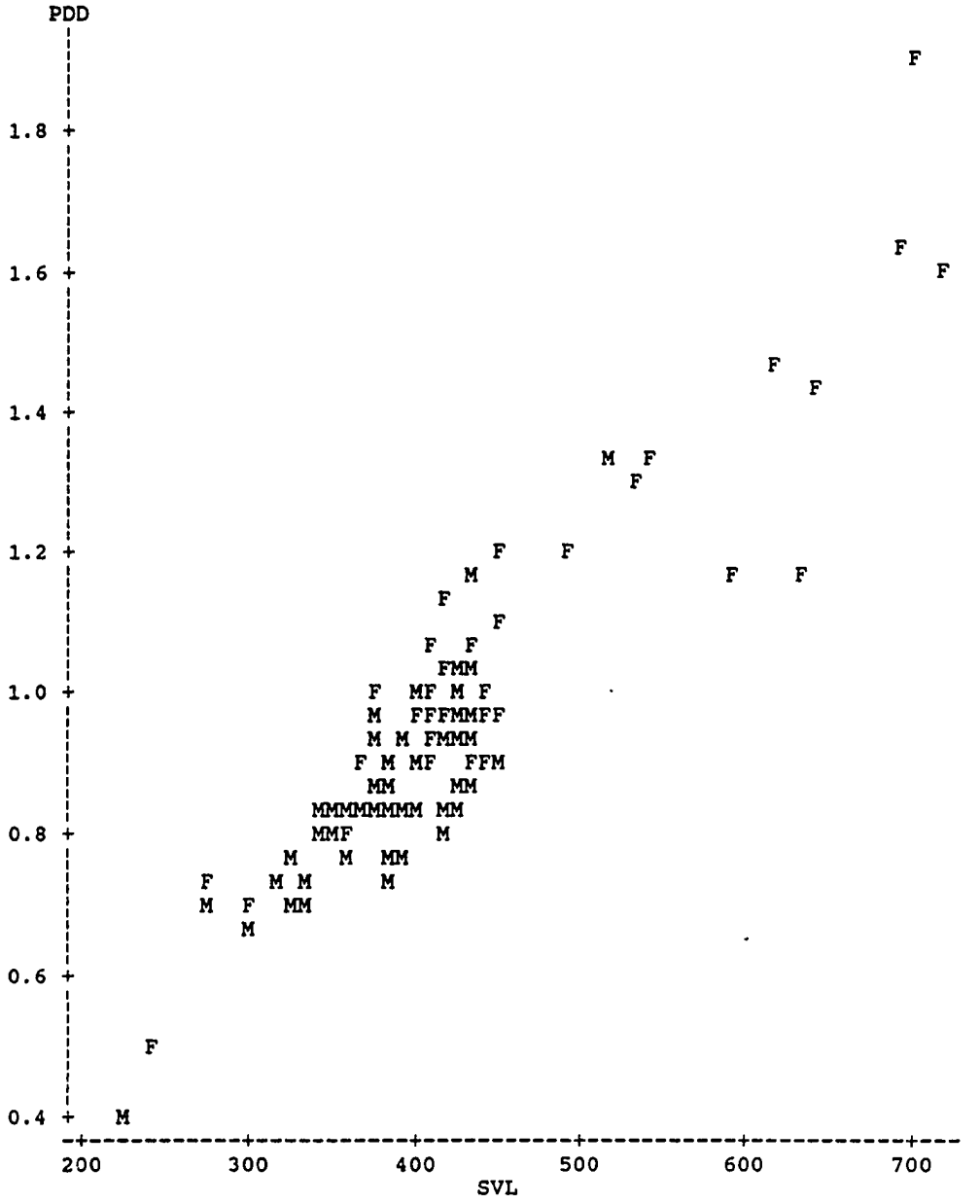


Figure 109. Plot of PDD vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

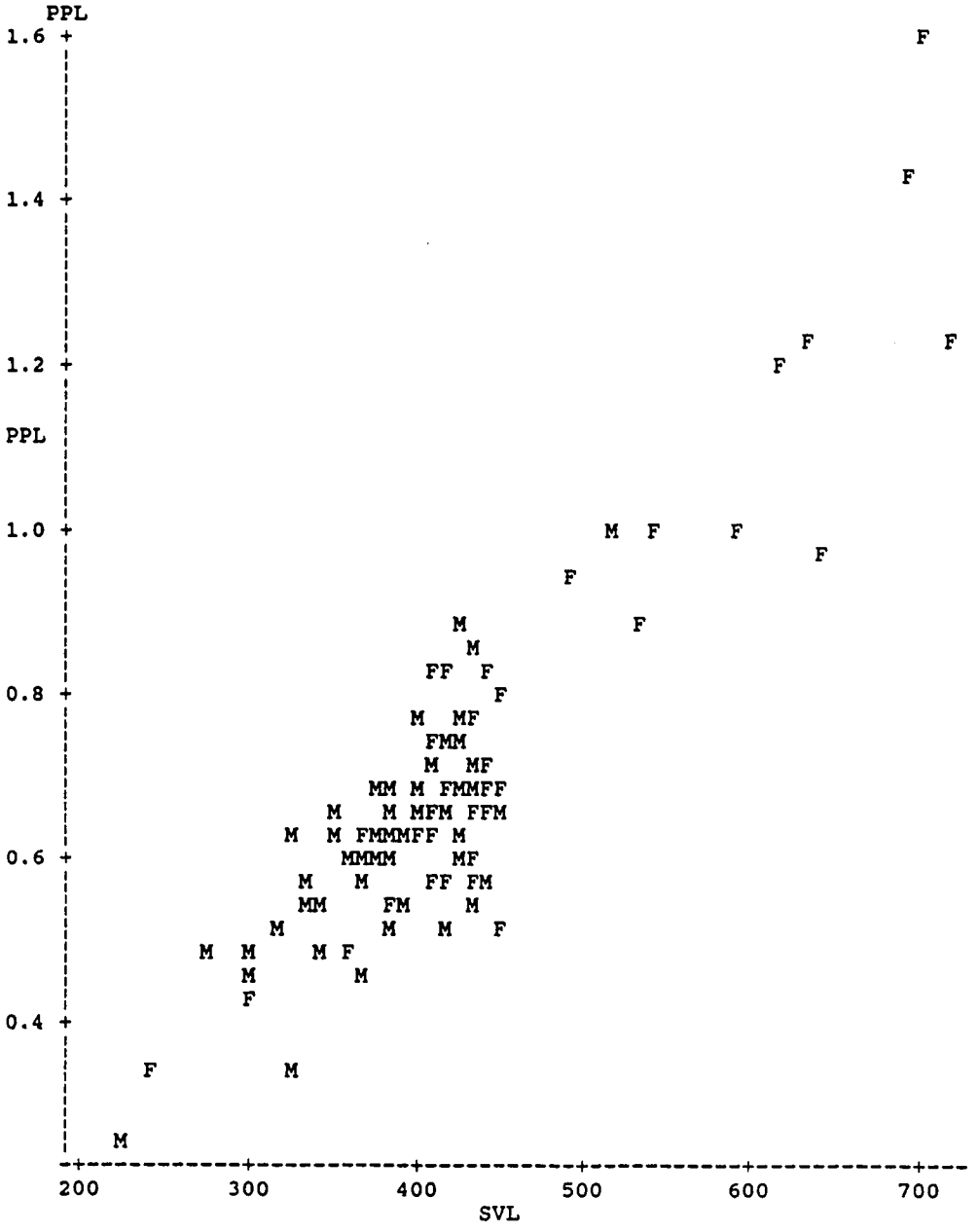


Figure 110. Plot of PPL vs. SVL. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

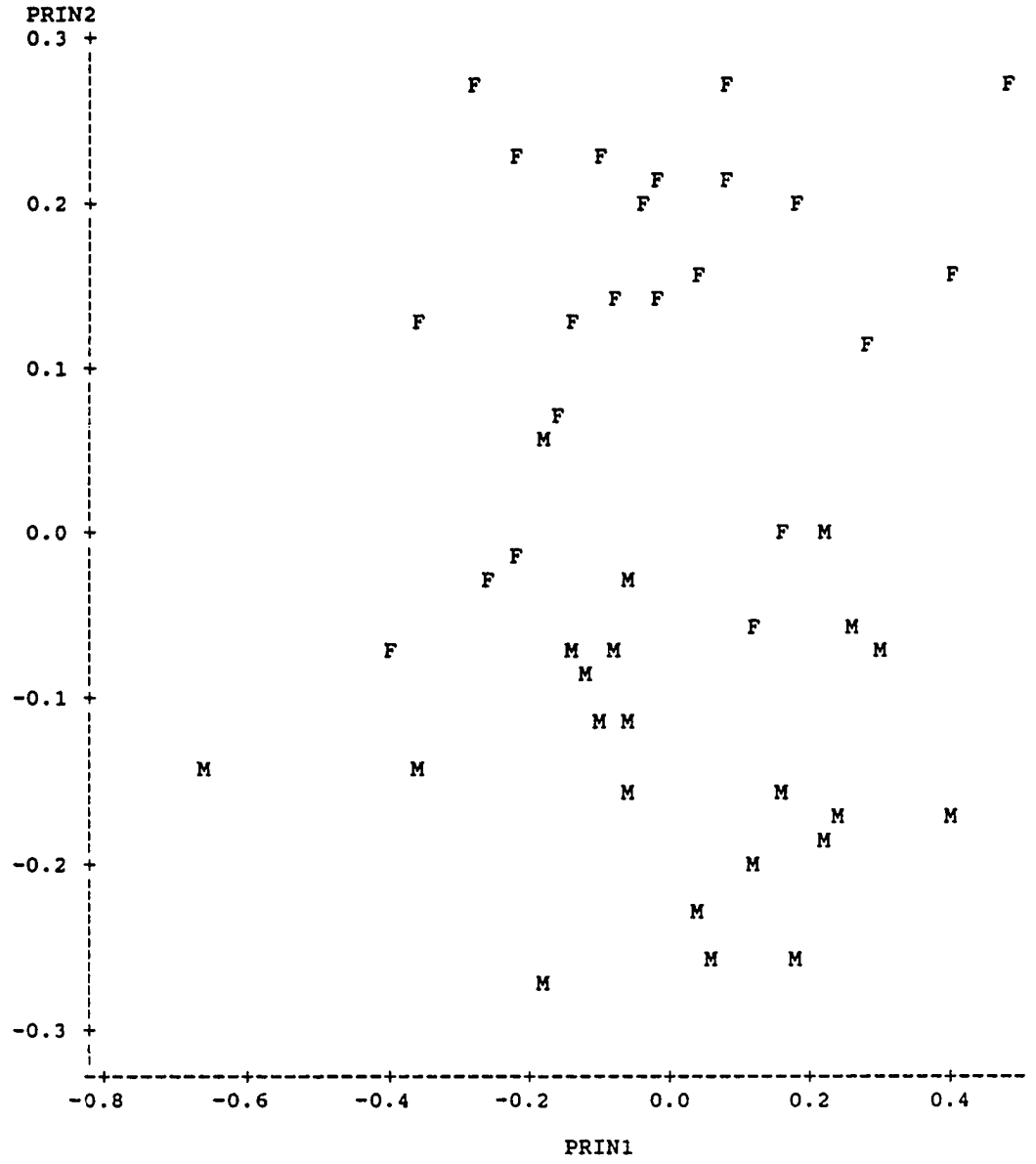


Figure 111. Comparison of sexes. Plot of Principle Axis 2 vs. Principle axis 1. Specimens constrained by size: 400<SVL<445. M=male, F=female.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

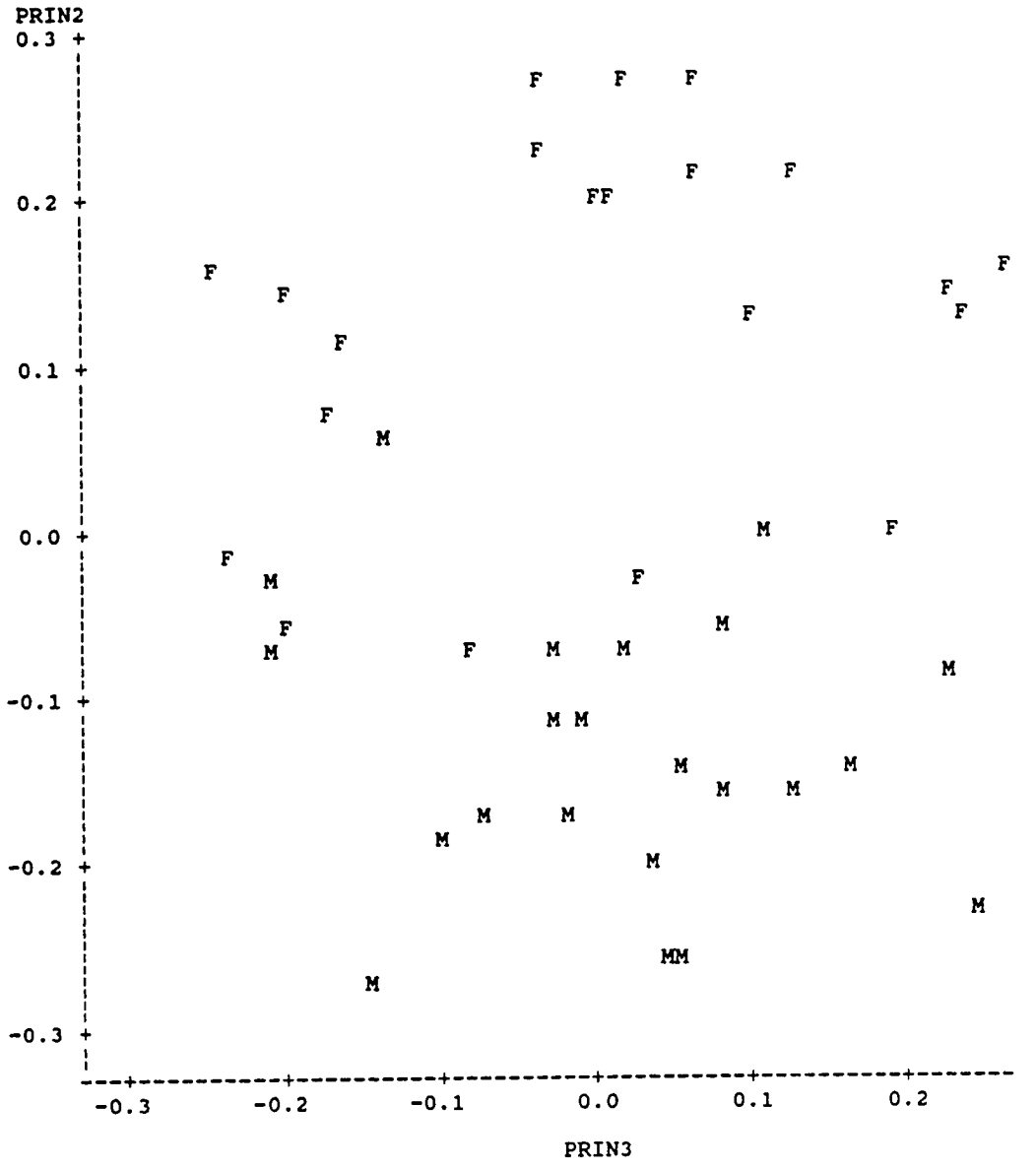


Figure 112. Comparison of sexes. Plot of Principle Axis 2 vs. Principle axis 3. Specimens constrained by size: 400<SVL<445. M=male,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1. Frequency distributions of differences between neighboring vertebrae for three variables. N-(X) represents the distance between positions, N=the reference position, and X=the distance of compared position from N.

	FREQ, CNT			FREQ, NAW			FREQ, POW		
DIF	N-1	N-2	N-3	N-1	N-2	N-3	N-1	N-2	N-3
-0.31			1						
-0.30			1						
-0.22		2	1						
-0.19			2						
-0.17		1						1	1
-0.14	1							1	
-0.12							2		1
-0.11	1	2	4			1		1	4
-0.10	2	4	2				2	1	4
-0.09	4	5	6				2	1	7
-0.08	4	3	5		1	1	2	4	5
-0.07	5	6	9	3		2	4	5	6
-0.06	2	5	11	2	3	3	3	8	8
-0.05	4	7	10	5	7	10	7	8	9
-0.04	11	12	7	7	12	7	11	14	4
-0.03	8	10	6	14	13	15	13	8	4
-0.02	12	13	7	16	16	18	9	10	13
-0.01	14	6	7	24	15	19	18	6	9
0	17	7	9	13	19	11	9	11	4
0.01	8	8	7	23	19	19	4	6	11
0.02	19	11	5	16	12	10	5	20	5
0.03	9	11	6	11	17	9	21	7	5
0.04	7	9	4	6	7	9	12	1	7
0.05	6	3	7	7	4	5	10	10	6
0.06	4	6	9	3	1	2	5	7	6
0.07	5	4	2		1	3	4	3	4
0.08	2	4	3		2	1	6	3	5
0.09		3	2			1	1	4	3
0.10	2	1	3			1		1	2
0.11	1		4			1		3	2
0.12	1	1	3					2	3
0.13			1					1	
0.14								1	2
0.15			1					1	2
0.16									3
0.17									1
0.18	1								
0.19			1						1
0.20									1
0.21		1							
0.22			1						
0.25		1							
0.30		1							
0.35			1						
0.37			1						
0.45			1						

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2. Average difference between vertebra and neighbor P distant. AA is V10-V19, AM is V35-V44, MM is V70-V79 MP is V106-115, PP is V131-V140.

P	VAR	AA	AM	MM	MP	PP
N-1	CNT	0.029	0.004	0	-0.013	-0.024
N-2	CNT	0.053	0.016	-0.019	-0.027	-0.039
N-3	CNT	0.092	0.018	-0.013	-0.034	-0.067
N-1	NAW	0.012	0.004	-0.006	-0.008	-0.010
N-2	NAW	0.018	0.007	-0.008	-0.011	-0.015
N-3	NAW	0.040	0.007	-0.011	-0.018	-0.028
N-1	POW	0.036	0.013	-0.004	-0.018	-0.019
N-2	POW	0.078	0.021	-0.010	-0.032	-0.037
N-3	POW	0.130	0.046	-0.001	-0.044	-0.057

Table 3. Record of vertebral positions measured for homology study. Positions examined: .125, .25, .5, .75, and .875. Each VNO followed by its percentage position (VNO=PCT).

NOV	MODE	AA	AM	MM	MP	PP
143	%	18=12.6	36=25.2	72=50.0	108=75.5	126=88.1
143	->	19=13.3	38=26.6	76=53.1	114=79.7	133=93.0
143	<-	11=07.7	30=21.0	68=47.6	106=74.1	125=87.4
144	%	18=12.5	36=25.0	72=50.0	108=75.0	126=87.5
144	->	19=13.2	38=26.4	76=52.8	114=79.2	133=92.4
144	<-	12=08.3	31=21.5	69=47.9	107=74.3	126=87.5
145	%	19=13.1	37=25.5	73=50.3	109=75.2	127=87.6
145	->	19=12.6	38=26.2	76=52.4	114=78.6	133=91.7
145	<-	13=09.0	32=22.1	70=48.3	108=74.5	127=87.6
146	%	19=13.0	37=25.3	73=50.0	110=75.3	128=87.7
146	->	19=13.0	38=26.0	76=52.1	114=78.1	133=91.1
146	<-	14=09.6	33=22.6	71=48.6	109=74.7	128=87.7
147	%	19=12.9	37=25.2	74=50.3	111=75.5	129=87.8
147	->	19=12.9	38=25.9	76=51.7	114=77.6	133=90.5
147	<-	15=10.2	34=23.1	72=49.0	110=74.8	129=87.8
148	%	19=12.8	37=25.0	74=50.0	111=75.0	130=87.8
148	->	19=12.8	38=25.7	76=51.4	114=77.0	133=89.9
148	<-	16=10.8	35=23.6	73=49.3	111=75.0	130=87.8
149	%	19=12.8	38=25.5	75=50.3	112=75.2	131=87.9
149	->	19=12.8	38=25.5	76=51.0	114=76.5	133=89.3
149	<-	17=11.4	36=24.2	74=49.7	112=75.2	131=87.9

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 3 continud.

NOV	MODE	AA	AM	MM	MP	PP
150	%	19=12.7	38=25.3	75=50.0	113=75.3	132=88.0
150	->	19=12.7	38=25.3	76=50.7	114=76.0	133=88.7
150	<-	18=12.0	37=24.7	75=50.0	113=75.3	132=88.0
151	%	19=12.6	38=25.2	76=50.3	114=75.5	133=88.1
151	->	19=12.6	38=25.2	76=50.3	114=75.5	133=88.1
151	<-	19=12.6	38=25.2	76=50.3	114=75.5	133=88.1
152	%	19=12.5	38=25.0	76=50.0	114=75.0	133=87.5
152	->	19=12.5	38=25.0	76=50.0	114=75.0	133=87.5
152	<-	20=13.2	39=25.7	77=50.7	115=75.7	134=88.2
153	%	20=13.1	39=25.5	77=50.3	115=75.2	134=87.6
153	->	19=12.4	38=24.8	76=49.7	114=74.5	133=86.9
153	<-	21=13.7	40=26.1	78=51.0	116=75.8	135=88.2
154	%	20=13.0	39=25.3	77=50.0	116=75.3	135=87.7
154	->	19=12.3	38=24.7	76=49.4	114=74.0	133=86.4
154	<-	22=14.3	41=26.6	79=51.3	117=76.0	136=88.3
155	%	20=12.9	39=25.2	78=50.3	117=75.5	136=87.7
155	->	19=12.3	38=24.5	76=49.0	114=73.5	133=85.8
155	<-	23=14.8	42=27.1	80=51.6	118=76.1	137=88.4
156	%	20=12.8	39=25.0	78=50.0	117=75.0	137=87.8
156	->	19=12.2	38=24.4	76=48.7	114=73.1	133=85.3
156	<-	24=15.4	43=27.6	81=51.9	119=76.3	138=88.5
157	%	20=12.7	40=25.5	79=50.3	118=75.2	138=87.9
157	->	19=12.1	38=24.2	76=48.4	114=72.6	133=84.7
157	<-	25=15.9	44=28.0	82=52.2	120=76.4	139=88.5
158	%	20=12.7	40=25.3	79=50.0	119=75.3	139=88.0
158	->	19=12.0	38=24.1	76=48.1	114=72.2	133=84.2
158	<-	26=16.5	45=28.5	83=52.5	121=76.6	140=88.6
159	%	20=12.6	40=25.2	80=50.3	120=75.5	140=88.1
159	->	19=11.9	38=23.9	76=47.8	114=71.7	133=83.6
159	<-	27=17.0	46=28.9	84=52.8	122=76.7	141=88.7
160	%	20=12.5	40=25.0	80=50.0	120=75.0	140=87.5
160	->	19=11.9	38=23.8	76=47.5	114=71.3	133=83.1
160	<-	28=17.5	47=29.4	85=53.1	123=76.9	142=88.8

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 4. Data on specimens compared and a contrast of the numerical and percentage positiona specified by the three modes of comparison.

CAT	SVL	NOV	REVERSE		FORWARD		PERCENT	
TCL1103	428	143	30	0.210	38	0.266	36	0.252
TCL1070	402	144	31	0.215	38	0.264	36	0.250
TCL727	428	145	32	0.221	38	0.262	37	0.255
TCL759	429	146	33	0.226	38	0.260	37	0.253
TCL1053	417	146	33	0.226	38	0.260	37	0.253
TCL1071	402	149	36	0.242	38	0.255	38	0.255
TCL782	423	150	37	0.247	38	0.253	38	0.253
TCL624	422	151	38	0.252	38	0.252	38	0.252
TCL791	434	151	38	0.252	38	0.252	38	0.252
TCL1102	435	151	38	0.252	38	0.252	38	0.252
TCL940	427	153	40	0.261	38	0.248	39	0.255
TCL686	425	154	41	0.266	38	0.247	39	0.253
TCL942	433	155	42	0.271	38	0.245	39	0.252
TCL943	437	155	42	0.271	38	0.245	39	0.252
TCL797	437	155	42	0.271	38	0.245	39	0.252
TCL730	428	155	42	0.271	38	0.245	39	0.252
TCL760	440	156	43	0.276	38	0.244	39	0.250
TCL989	444	156	43	0.276	38	0.244	39	0.250
TCL918	436	157	44	0.280	38	0.242	40	0.255
TCL682	427	158	45	0.285	38	0.241	40	0.253
TCL888	416	159	46	0.289	38	0.239	40	0.252

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 5. Tests of mode of determination of homology slope sign and significance for plots of variable against SVL and NOV. Significance of slope on NOV only considered.

CNT

	AA	AM	MM	MP	PP
FWD	S -	S -	S -	NS -	NS +
REV	S +	S -	S -	S -	S -
PCT	S -	S -	S -	S -	NS -

PRP

	AA	AM	MM	MP	PP
FWD	S -	S -	S -	NS -	NS -
REV	S +	S -	S -	S -	S -
PCT	S -	S -	S -	S -	S -

NAW

	AA	AM	MM	MP	PP
FWD	NS -	NS -	NS -	NS -	NS -
REV	NS +	NS -	NS -	NS -	NS -
PCT	NS -	NS -	NS -	NS -	NS -

POW

	AA	AM	MM	MP	PP
FWD	NS -	NS -	NS -	NS -	NS +
REV	S +	NS +	NS -	NS -	NS -
PCT	NS -	NS -	NS -	NS -	NS -

NAH

	AA	AM	MM	MP	PP
FWD	NS -	NS -	NS -	NS -	NS -
REV	NS -	NS -	NS -	NS -	NS -
PCT	NS -	NS -	NS -	NS -	NS -

HYD

	AA	AM	MM	MP	PP
FWD	NS -	NS -	NS -	NS -	NS -
REV	S -	*NS +	NS -	NS -	NS -
PCT	NS -	NS -	NS -	NS -	NS -

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 6. Scutelational variability, by locality. SL=supralabials, IL=infralabials, LO=loreals, PRE=preoculars, POC=postoculars, SR1=scale rows around body, about one head length behind head, SR2=scale rows at midbody, SR3=scale rows one head length before vent, A=condition of anal plate: 0=entire, 1=divided. Bilateral characters summed.

Varbl.	Min	Max	Mean	CV
BMT, Ulster Co. NY				n=20
SL	14	16	14.4	5.5
IL	20	21	20.1	1.9
LO	2	4	2.3	33.1
PRE	2	2	2.0	0
POC	6	7	6.1	6.2
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	16	19	17.1	3.0
A	0	0	0	.
FBF, Kings Co. NY				n=23
SL	13	16	14.1	5.5
IL	13	21	18.7	12.6
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	5	7	6.0	8.3
SR1	19	19	19.0	0
SR2	18	19	19.0	1.1
SR3	16	18	17.0	1.8
A	0	0	0	.
Makamah Suffolk Co. NY				n=6
SL	14	16	14.3	5.7
IL	20	20	20.0	0
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	6	6	6.0	0
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	17	17	17.0	0
A	0	0	0	.
Misc. sites, mostly NY,				n=48
SL	11	16	14.1	7.2
IL	17	21	19.6	4.7
LO	2	4	2.1	22.3
PRE	2	2	2.0	0
POC	6	7	6.1	3.9
SR1	17	19	18.9	1.7
SR2	17	19	19.0	1.5
SR3	16	17	17.0	0.9
A	0	0	0	.

Varbl.	Min	Max	Mean	CV
Campbl. Mt. Delw. Co. NY				n=4
SL	14	15	14.3	4.0
IL	19	20	19.3	3.0
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	6	6	6.0	0
SR1	19	19	19.0	0
SR2	17	19	18.5	5.4
SR3	17	17	17.0	0
A	0	1.0	0.3	200.0
Flatbush Av Kings Co. NY				n=5
SL	14	16	14.5	6.9
IL	18	22	20.0	8.2
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	6	6	6.0	0
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	16	17	16.8	2.7
A	0	0	0	.
TMR, Sullivan Co. NY				n=80
SL	14	15	14.1	2.2
IL	18	20	19.6	3.7
LO	2	3	2.0	7.8
PRE	2	3	2.0	7.8
POC	4	7	5.9	7.1
SR1	17	19	19.0	1.3
SR2	17	19	19.0	2.0
SR3	15	17	17.0	2.3
A	0	1	0.0	200

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 6, continued.

Varbl.	Min	Max	Mean	CV
BKK, Pike Co. PA				n=47
SL	14	16	14.3	4.0
IL	17	21	19.5	5.0
LO	2	2	2.0	0
PRE	2	4	2.1	16.9
POC	6	7	6.0	2.9
SR1	17	19	18.9	2.4
SR2	16	21	18.9	3.7
SR3	15	17	16.0	1.9
A	0	0	0	.
Erie Co. PA				n=6
SL	14	14	14.0	0
IL	19	20	19.7	2.9
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	6	7	6.7	8.7
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	17	17	17.0	0
A	0	0	0	.

Varbl.	Min	Max	Mean	CV
Canadensis, Monroe Co. PA				n=5
SL	14	14	14.0	0
IL	17	20	19.0	9.1
LO	2	2	2.0	0
PRE	2	2	2.0	0
POC	6	7	6.3	9.1
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	17	17	17.0	0
A	0	0	0	.
SGL 221, Monroe Co. PA				n=5
SL	14	16	14.4	6.2
IL	19	21	20.0	3.5
LO	2	2	2.0	0
PRE	2	3	2.2	20.3
POC	5	6	5.8	7.7
SR1	19	19	19.0	0
SR2	19	19	19.0	0
SR3	15	17	16.6	5.4
A	0	0	0	.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 7. Variability in ventrals and subcaudals.
V=Ventrals, SC=subcaudals

n	Sex	Varbl	Min.	Max.	Mean	CV
BMT, Ulster Co. NY						
9	F	V	137	147	140.8	2.2
		SC	53	63	59.9	5.3
11	M	V	141	151	145.9	2.2
		SC	65	74	68.6	3.8
FBF, Kings Co. NY						
5	F	V	143	146	144.8	0.9
		SC	63	70	66.0	5.0
18	M	V	145	157	150.9	2.1
		SC	66	81	74.0	5.8
Flatbush Ave, Vacant lot, Kings Co. NY						
4	F	V	140	142	141.5	0.7
		SC	58	63	61.0	3.5
1	M	V	149	149	149.0	.
		SC	74	74	74.0	.
TMR, Sullivan Co. NY						
19	F	V	137	147	142.0	2.5
		SC	51	66	60.9	5.4
53	M	V	114	153	146.2	3.6
		SC	57	77	70.8	4.4
Miscellaneous localities, mostly NY						
26	F	V	134	147	142.3	2.2
		SC	51	65	60.6	5.4
22	M	V	124	156	147.4	5.2
		SC	63	79	72.8	5.2
BKK, Pike Co. PA						
23	F	V	135	146	139.8	1.8
		SC	56	68	61.9	5.6
17	M	V	140	151	145.9	2.0
		SC	61	79	71.6	6.2
Canadensis, Monroe Co. PA						
5	M	V	141	147	143.6	1.7
		SC	71	74	72.3	1.7
SGL 221, Monroe Co. PA SEX=F						
1	F	V	133	133	133.0	.
		SC	59	59	59.0	.
4	M	V	143	148	144.8	1.6
		SC	67	71	68.3	3.4

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 8. Size parameters of the four primary study populations. Max F = maximum female size, Min F = minimum male size, Min Mat F = minimum size of mature females, Mn Mat F = mean size of mature females (size of sample of mature females in parentheses). Identical categories for males (M) follow. Based on pooled field released and skeletonized specimens.

	TMR	BMT	FBF	BKK
Max F	621	713	645	502
Min F	153	124	198	170
Min Mat F	316	411	427	350
Mn Mat F (subsample)	433.3 (60)	493.7 (47)	480.9 (33)	420.1 (34)
Total Sample Size	116	97	43	37
Max M	454	492	535	480
Min M	141	127	165	174
Min Mat M	313	353	365	333
Mn Mat M (subsample)	367.4 (59)	399.8 (13)	418.4 (36)	389.5 (20)
Total Sample Size	122	63	57	24

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 9. Monthly progression of average size of presumed first year Thamnophis sirtalis sirtalis and estimated growth rates (in mm/day) at three main study sites in New York. All months set to 30.5 days.

Loc.	N	Month	Ave. SVL	SE	Est. Growth Rate	Annual Average
TMR	12	August	170.083	5.556		.9515
	5	September	175.000	6.301	0.161	
	21	May	199.904	2.881	0.817	
	66	June	238.621	2.960	1.269	
	6	July	286.167	8.304	1.559	
BMT	51	September	142.431	1.302		1.671
	12	May	156.917	4.162	0.475	
	7	June	159.857	3.863	0.096	
	7	July	236.571	10.578	2.515	
	22	August	254.773	9.989	0.597	
FBF	2	September	190.000	25.000		1.144
	1	October	212.000	-	0.721	
	8	April	212.875	4.549	0.029	
	5	May	230.800	7.896	0.588	
	2	June	406.500*	33.500	2.192	
	2	July	364.500	23.500	2.192	

* Small sample size and unusually large size difference suggest that this value is an overestimate. June & July rate values at FBF calculated on basis of July size values averaged over two months.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 10. Recapture data. Date1=date of first capture, Date2=date of recapture, SV1=snout-vent length at first capture, SV2=snout-vent length at second capture, elap=total number of days elapsed between captures, elap-W=elapsed days minus estimated winter dormancy days, SVdif=SV2-SV1, Grorate=SVdif/elap-W.

Field No.	Loc	Date1	SV1	Date2	SV2	elap	elap-wint.	SVdif	Grorate
				MALES					
164	TMR	5/27/88	192	8/28/88	315	93	93	123	1.322
360	TMR	5/20/89	217	6/13/90	354	389	200	137	0.685
055	TMR	8/05/87	358	6/05/90	375	305	116	17	0.147
240	BMT	7/27/88	263	5/29/89	332	306	92	69	0.750
240	BMT		263	6/14/90	402	381	167	70	0.419
533	BMT	9/09/89	156	6/14/90	176	278	64	20	0.313
546	FBF	9/20/89	322	4/24/90	324	216	57	2	0.035
331	FBF	5/12/89	353	5/19/89	355	7	7	2	0.286
309	FBF	4/28/89	355	7/14/89	388	77	77	33	0.429
553	FBF	4/16/90	419	5/14/90	421	28	28	2	0.071
323	FBF	4/28/89	420	5/19/89	416	21	21	-4	-0.190
609	CVC	5/30/90	146	7/29/90	208	60	60	62	1.033
659	CVC	6/21/90	356	7/02/90	360	11	11	4	0.364
				FEMALES					
272	TMR	8/28/88	183	5/20/89	209	265	76	26	0.342
370	TMR	5/20/89	195	6/13/89	375	389	200	180	0.900
202	TMR	6/05/88	203	5/25/89	362	354	165	159	0.964
221	TMR	7/17/88	270	6/13/90	433	696	318	163	0.513
188	TMR	6/05/88	352	6/13/90	516	738	360	164	0.456
162	TMR	5/27/88	390	6/05/88	383	9	9	-7	-0.778
598	TMR	5/12/90	427	6/13/90	431	32	32	4	0.125
193	TMR	6/05/88	436	5/25/89	460	354	165	24	0.145
430	TMR	6/25/89	437	6/13/90	472	353	164	35	0.213
358	TMR	5/20/89	438	4/26/90	497	341	152	59	0.388
054	TMR	8/05/87	452	6/05/88	466	305	116	14	0.121
054	TMR		452	5/20/89	494	349	160	28	0.175
066	BMT	8/13/87	233	5/29/89	408	655	227	175	0.771
066	BMT		233	8/20/89	430	83	83	22	0.265
228	BMT	7/27/88	274	6/14/90	442	687	259	168	0.649
072	BMT	8/13/87	298	5/29/89	437	655	227	139	0.612
072	BMT		298	8/20/89	455	83	83	18	0.217
491	BMT	8/20/89	397	6/14/90	424	298	84	27	0.321
178	BMT	6/04/88	468	7/27/88	473	53	53	5	0.094
178	BMT		468	8/20/89	479	389	175	6	0.034
071	BMT	8/13/87	476	8/20/89	572	738	310	96	0.310
341	BMT	5/20/89	478	5/29/89	485	9	9	7	0.778
381	BMT	5/29/89	550	8/20/89	565	83	83	15	0.181
180	BMT	6/04/88	573	8/20/89	589	442	228	16	0.070
179	BMT	6/04/88	638	7/27/88	655	53	53	17	0.321
483	BMT	8/20/89	435	9/09/89	433	20	20	-2	-0.100
481	BMT	8/20/89	504	9/09/89	497	20	20	-7	-0.350
344	FBF	5/19/89	253	5/14/90	412	360	201	159	0.791

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 11. Estimated sizes of garter snakes at given ages for three localities, based on growth rates from cohort and recapture data.

	1 yr old	Sex	2 yr old	3 yr old
TMR	286.2	F	382.8	418.0
		M	365.8	401.0
BMT	254.8	F	337.9	368.1
		M	322.8	353.0
FBF	364.5	F	477.8	519.0
		M	457.2	498.4

Table 12. Principal component analysis results for females. 39 Observations, 20 Variables, Total Variance = 1.4165735 Covariance matrix analysed. First two eigenvectors shown.

	Eigenvalue	Cumulative Proportion		Eigenvectors PRIN1	PRIN2
PRIN1	1.30710	0.92272	LCNT	0.213805	0.104623
PRIN2	0.02868	0.94296	LPRP	0.215445	0.149521
PRIN3	0.01807	0.95572	LPZL	0.242446	0.392509
PRIN4	0.01336	0.96515	LNAW	0.209957	0.131406
PRIN5	0.01120	0.97306	LPOW	0.213146	0.111580
PRIN6	0.00871	0.97920	LPZW	0.280143	0.128556
PRIN7	0.00698	0.98413	LNSL	0.277865	0.138621
PRIN8	0.00509	0.98772	LPRW	0.211726	0.122643
PRIN9	0.00391	0.99048	LZSW	0.157786	0.129873
PRIN10	0.00328	0.99280	LAPL	0.291065	-.667709
PRIN11	0.00292	0.99486	LNAH	0.138613	0.117770
PRIN12	0.00218	0.99640	LCOH	0.172549	0.077081
PRIN13	0.00200	0.99781	LCOW	0.167850	0.008378
PRIN14	0.00109	0.99858	LCNH	0.171275	0.075688
PRIN15	0.00093	0.99923	LPZH	0.257671	0.172711
PRIN16	0.00057	0.99964	LCNW	0.152449	-.001209
PRIN17	0.00024	0.99981	LNSH	0.287179	-.236272
PRIN18	0.00015	0.99991	LHYD	0.244479	-.339371
PRIN19	0.00009	0.99997	LPDD	0.199084	-.062218
PRIN20	0.00004	1.00000	LPPL	0.267281	-.197793

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 13. Principle components analysis results for males. 61 Observations, 20 Variables, Total Variance = 0.6416632 Covariance matrix analysed. First two eigenvectors shown.

	Eigenvalue	Cumulative Proportion		Eigenvectors PRIN1	PRIN2
PRIN1	0.543422	0.84690	LCNT	0.205716	0.038753
PRIN2	0.021951	0.88111	LPRP	0.211318	0.087148
PRIN3	0.017370	0.90818	LPZL	0.226104	0.386788
PRIN4	0.013187	0.92873	LNAW	0.199882	0.141140
PRIN5	0.009920	0.94419	LPOW	0.214829	0.128875
PRIN6	0.006856	0.95487	LPZW	0.278487	0.392091
PRIN7	0.006226	0.96458	LNSL	0.296599	-.076979
PRIN8	0.005475	0.97311	LPRW	0.212250	0.126775
PRIN9	0.004223	0.97969	LZSW	0.156649	0.008617
PRIN10	0.003922	0.98580	LAPL	0.300907	-.552790
PRIN11	0.002262	0.98933	LNAH	0.136003	0.102434
PRIN12	0.001985	0.99242	LCOH	0.158302	0.036669
PRIN13	0.001431	0.99465	LCOW	0.150817	0.067338
PRIN14	0.001140	0.99643	LCNH	0.146979	-.083351
PRIN15	0.000766	0.99762	LPZH	0.271663	0.262403
PRIN16	0.000591	0.99854	LCNW	0.138631	0.032906
PRIN17	0.000398	0.99916	LNSH	0.319643	-.386372
PRIN18	0.000322	0.99966	LHYD	0.266064	-.271776
PRIN19	0.000149	0.99990	LPDD	0.197963	0.018920
PRIN20	0.000066	1.00000	LPPL	0.238879	-.081391

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 14. Specimens used in analyses of sexual dimorphism.

CAT	SEX	SVL	NOV	VNO	CAT	SEX	SVL	NOV	VNO
TCL1089	F	396	144	62	TCL1070	M	402	144	62
TCL890	F	405	146	63	TCL1071	M	402	149	65
TCL1039	F	406	144	62	TCL860	M	402	145	63
TCL467	F	409	142	62	TCL933	M	411	151	65
TCL1052	F	412	144	62	TCL1063	M	416	151	65
TCL689	F	412	149	65	TCL888	M	416	159	69
TCL758	F	413	145	63	TCL1053	M	417	146	63
TCL678	F	420	149	65	TCL624	M	422	151	65
TCL886	F	420	150	65	TCL782	M	423	150	65
TCL883	F	431	149	65	TCL682	M	427	158	68
TCL683	F	433	150	65	TCL940	M	427	153	66
TCL865	F	434	146	63	TCL1103	M	428	143	62
TCL657	F	435	143	62	TCL727	M	428	145	63
TCL798	F	435	150	65	TCL730	M	428	155	67
TCL574	F	440	148	64	TCL759	M	429	146	63
TCL956	F	442	146	63	*TCL942	M	433	155	67
TCL1040	F	443	143	62	TCL791	M	434	151	65
TCL627	F	443	143	62	TCL1102	M	435	151	65
TCL586	F	445	148	64	TCL918	M	436	157	68
TCL1080	F	446	143	62	TCL797	M	437	155	67
TCL415	F	448	143	62	TCL943	M	437	155	67
TCL1092	F	451	145	63	TCL760	M	440	156	68
					TCL989	M	444	156	68

*Aberant specimen omitted from final analysis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 15. Eigenvalues of the principle components analysis of sexual dimorphism, and the cumulative percent of the variance that they account for.

	Eigenvalue	Cumulative Percent
PRIN1	0.055276	0.35336
PRIN2	0.027891	0.53166
PRIN3	0.019409	0.65573
PRIN4	0.012650	0.73660
PRIN5	0.009160	0.79516
PRIN6	0.007268	0.84162
PRIN7	0.005561	0.87717
PRIN8	0.004388	0.90522
PRIN9	0.003807	0.92955
PRIN10	0.002664	0.94659
PRIN11	0.002601	0.96321
PRIN12	0.001836	0.97495
PRIN13	0.001208	0.98267
PRIN14	0.001035	0.98929
PRIN15	0.000635	0.99335
PRIN16	0.000478	0.99641
PRIN17	0.000241	0.99795
PRIN18	0.000179	0.99909
PRIN19	0.000102	0.99974
PRIN20	0.000040	1.00000

Table 16. Eigenvectors of the first two principle components used in sexual dimorphism analysis.

Varbl	PRIN1	PRIN2
LCNT	0.141507	0.089216
LPRP	0.169086	0.084091
LPZL	0.328679	-.004079
LNAW	0.230348	0.038656
LPOW	0.250838	-.006193
LPZW	0.440477	-.099848
LNSL	0.250076	0.178674
LPRW	0.245706	0.004294
LZSW	0.210977	0.054051
LAPL	0.278428	0.154306
LNAH	0.212922	-.046046
LCOH	0.097376	0.260139
LCOW	0.016952	0.349076
LCNH	0.081035	0.322496
LPZH	0.269429	-.249428
LCNW	0.009596	0.464286
LNSH	0.212361	-.101954
LHYD	0.225733	-.493968
LPDD	0.143915	0.277104
LPPL	0.193111	0.100823

Table 17. Test specimens used in discrim analysis

CAT	SEX	SVL	NOV	VNO
TCL580	M	399	146	71
TCL624	M	422	151	75
TL475	M	317	149	74

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX 1.

Repeated measurements of the same vertebra: VNO 65 from TCL791. A male, 434 mm SVL, NOV=151.

CNT	PRP	PZL	NAW	POW	PZW	HYW	NSL	NSW	PRW	ZSW
3.07	3.53	0.70	1.68	3.52	0.76	0.23	2.10	0.14	3.52	1.71
3.07	3.53	0.68	1.69	3.52	0.70	0.23	2.10	0.10	3.54	1.73
3.08	3.53	0.70	1.68	3.52	0.74	0.24	2.11	0.14	3.57	1.74
3.08	3.55	0.70	1.69	3.54	0.76	0.23	2.09	0.12	3.56	1.73
3.08	3.52	0.68	1.68	3.53	0.73	0.22	2.10	0.14	3.55	1.73
3.08	3.52	0.68	1.70	3.52	0.75	0.23	2.12	0.13	3.60	1.73
3.07	3.55	0.71	1.71	3.51	0.74	0.23	2.10	0.14	3.56	1.71
3.08	3.52	0.68	1.68	3.53	0.74	0.24	2.11	0.13	3.56	1.73
3.07	3.54	0.69	1.69	3.51	0.73	0.24	2.10	0.13	3.54	1.74
3.06	3.54	0.69	1.68	3.52	0.73	0.22	2.11	0.13	3.55	1.72

ACL	NAH	COH	SCN	COW	CNH	PZH	CNW	NSH	HYD	PDH	PPL
0.45	0.99	0.96	0.14	1.13	0.86	0.68	0.99	0.98	0.71	0.93	0.68
0.46	1.03	0.95	0.15	1.13	0.88	0.65	1.00	1.03	0.71	0.98	0.64
0.45	1.03	0.95	0.16	1.12	0.87	0.65	1.00	0.98	0.71	0.93	0.64
0.48	1.01	0.96	0.14	1.17	0.86	0.66	0.98	0.99	0.70	0.97	0.66
0.47	1.03	0.94	0.13	1.14	0.85	0.65	0.99	1.00	0.71	0.98	0.65
0.46	1.02	0.95	0.14	1.15	0.86	0.65	0.99	0.98	0.70	0.95	0.71
0.47	1.01	0.95	0.14	1.14	0.87	0.63	0.99	1.01	0.72	0.96	0.68
0.48	1.03	0.95	0.14	1.11	0.88	0.66	0.99	0.98	0.71	0.96	0.67
0.49	1.02	0.96	0.12	1.11	0.86	0.65	1.00	1.00	0.73	0.94	0.67
0.47	1.03	0.94	0.14	1.14	0.89	0.66	0.98	1.00	0.72	0.95	0.69

Vbl	Min	Max	Max-Min	Mean	Variance	Std Dev	CV
CNT	3.06	3.08	.02	3.07	0.000049	0.006992	0.227458
PRP	3.52	3.55	.03	3.53	0.000134	0.011595	0.328192
PZL	0.68	0.71	.03	0.69	0.000121	0.011005	1.592627
NAW	1.68	1.71	.03	1.68	0.000107	0.010328	0.611846
POW	3.51	3.54	.03	3.52	0.000084	0.009189	0.260913
PZW	0.70	0.76	.06	0.73	0.000307	0.017512	2.372886
HYW	0.22	0.24	.02	0.23	0.000054	0.007379	3.194220
NSL	2.09	2.12	.03	2.10	0.000071	0.008433	0.400796
NSW	0.10	0.14	.04	0.13	0.000156	0.012472	9.593993
PRW	3.52	3.60	.08	3.55	0.000450	0.021213	0.596715
ZSW	1.71	1.74	.03	1.72	0.000112	0.010594	0.613405
ACL	0.45	0.49	.05	0.46	0.000173	0.013166	2.813165
NAH	0.99	1.03	.04	1.02	0.000178	0.013333	1.307190
COH	0.94	0.96	.02	0.95	0.000054	0.007379	0.775883
SCN	0.12	0.16	.04	0.14	0.000111	0.010541	7.529233
COW	1.11	1.17	.06	1.13	0.000338	0.018379	1.620699
CNH	0.85	0.89	.04	0.86	0.000151	0.012293	1.416213
PZH	0.63	0.68	.05	0.65	0.000160	0.012649	1.934115
CNW	0.98	1.00	.02	0.99	0.000054	0.007379	0.744566
NSH	0.98	1.03	.05	0.99	0.000272	0.016499	1.658207
HYD	0.70	0.73	.03	0.71	0.000084	0.009189	1.290641
PDH	0.93	0.98	.05	0.95	0.000339	0.018409	1.927637
PPL	0.64	0.71	.07	0.66	0.000499	0.022336	3.338688

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX 2.

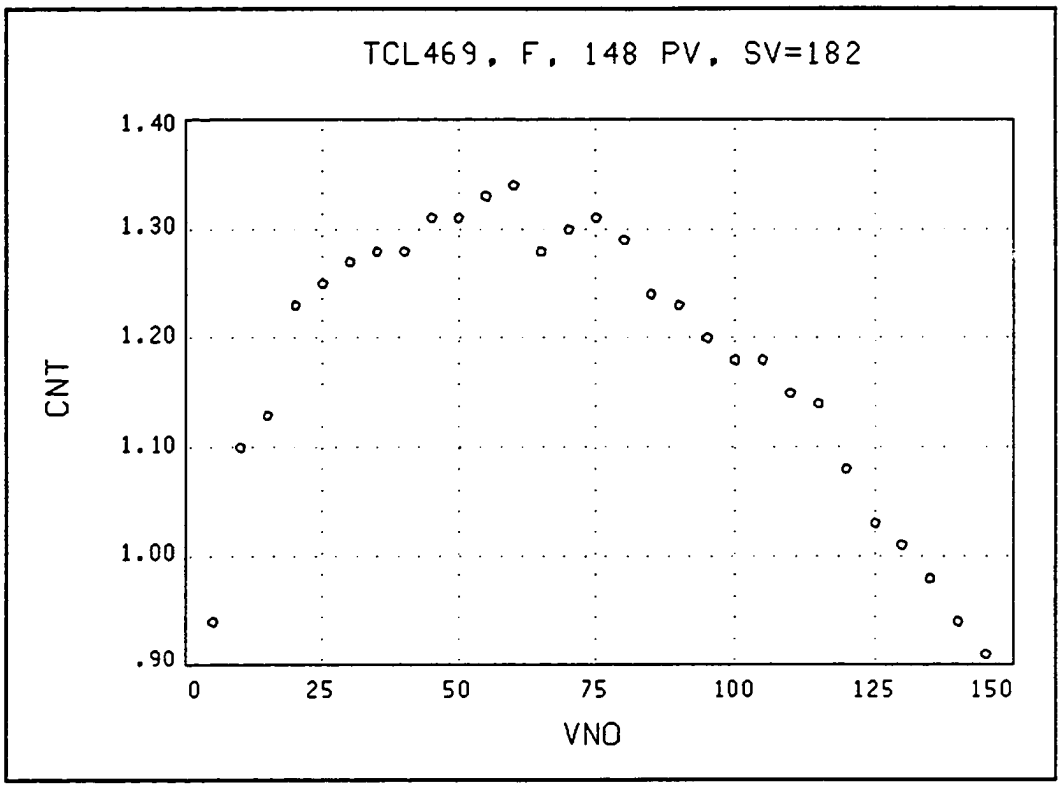
Plots of variable*vertebral number for five specimens:

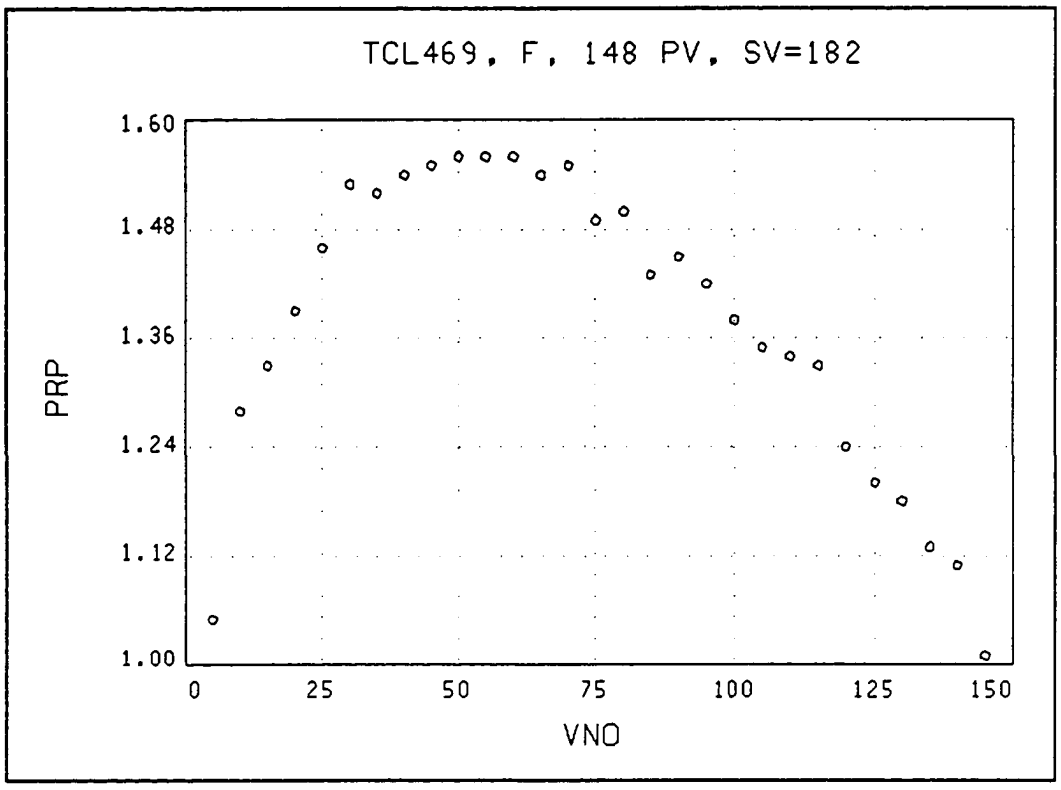
Every vertebra measured for 5 variables:
TCL 791, male, 151 precaudal vertebrae, SVL = 434.
TCL 793, male, 151 precaudal vertebrae, SVL = 345.
TCL 783, male, 149 precaudal vertebrae, SVL = 231

Every fifth vertebra measured for 23 variables:
TCL 449, female, 150 precaudal vertebrae, SV = 597.
TCL 469, female, 148 precaudal vertebrae, SV = 182.

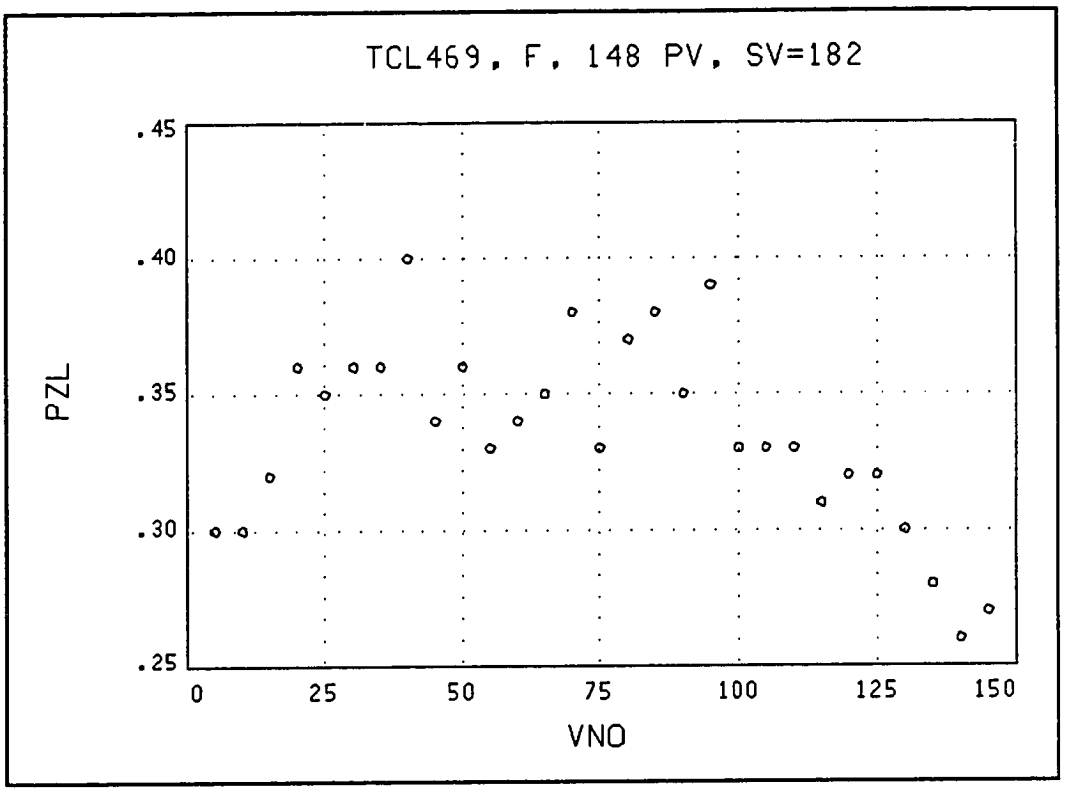
Characters measured:
APL - accessory process length
CNT - centrum length measured along venter
CNH - condyle height
CNW - condyle width
COH - cotyle height
COW - cotyle width
HYD - hypapophysis depth
HYW - hypapophysis width
NAH - neural arch height
NAW - least width of neural arch
NSH - neural spine height
NSL - neural spine length
NSW - neural spine width
PCN - depth of paracotylar notch
PDD - depth of paradiapophysis
POW - width across postzygapophyses
PPL - length of parapophyseal process
PRP - length from anterior edge of prezygapophysis to posterior edge of postzygapophysis
PRW - width across prezygapophyses
PZH - height of postzygapophyseal process
PZL - length of postzygapophyseal facet
PZW - width of postzygapophyseal facet
ZSW - width of zygosphene

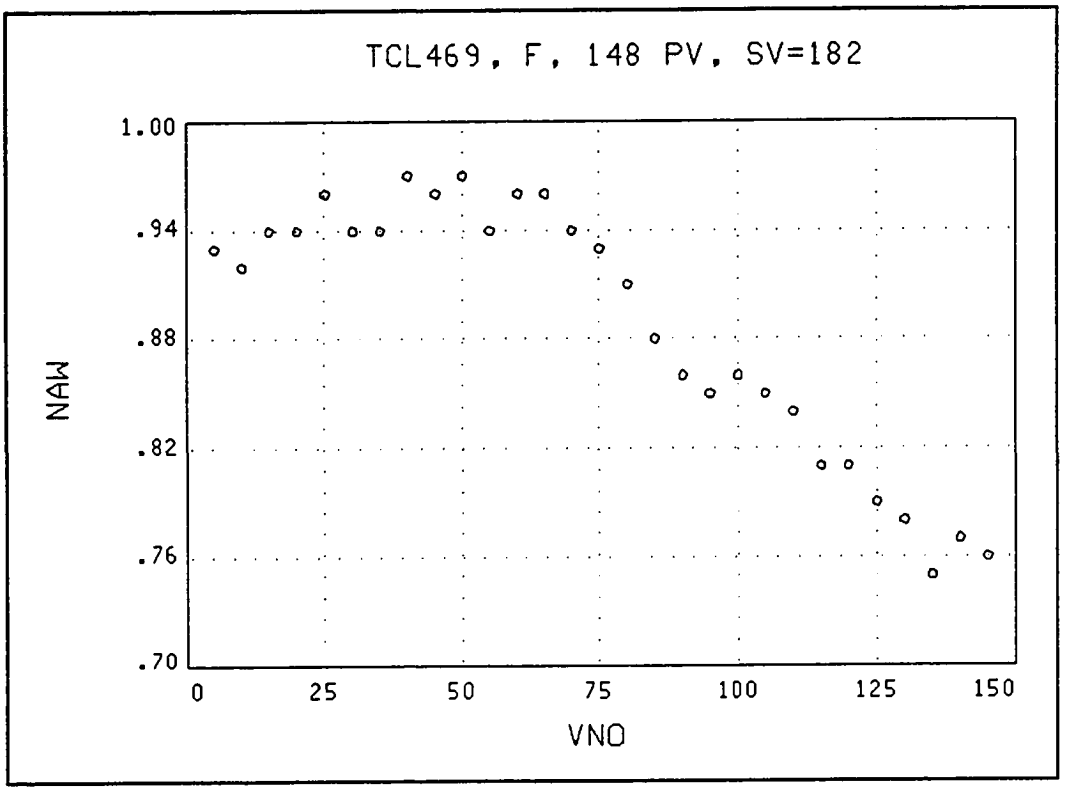
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



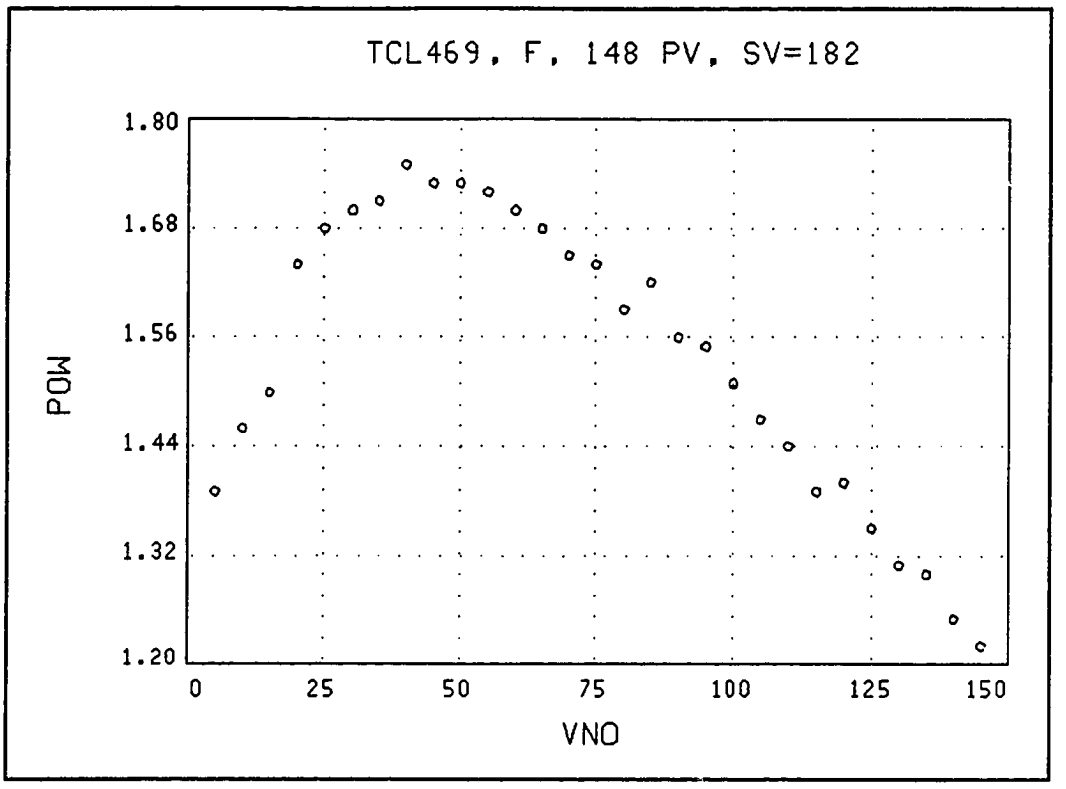


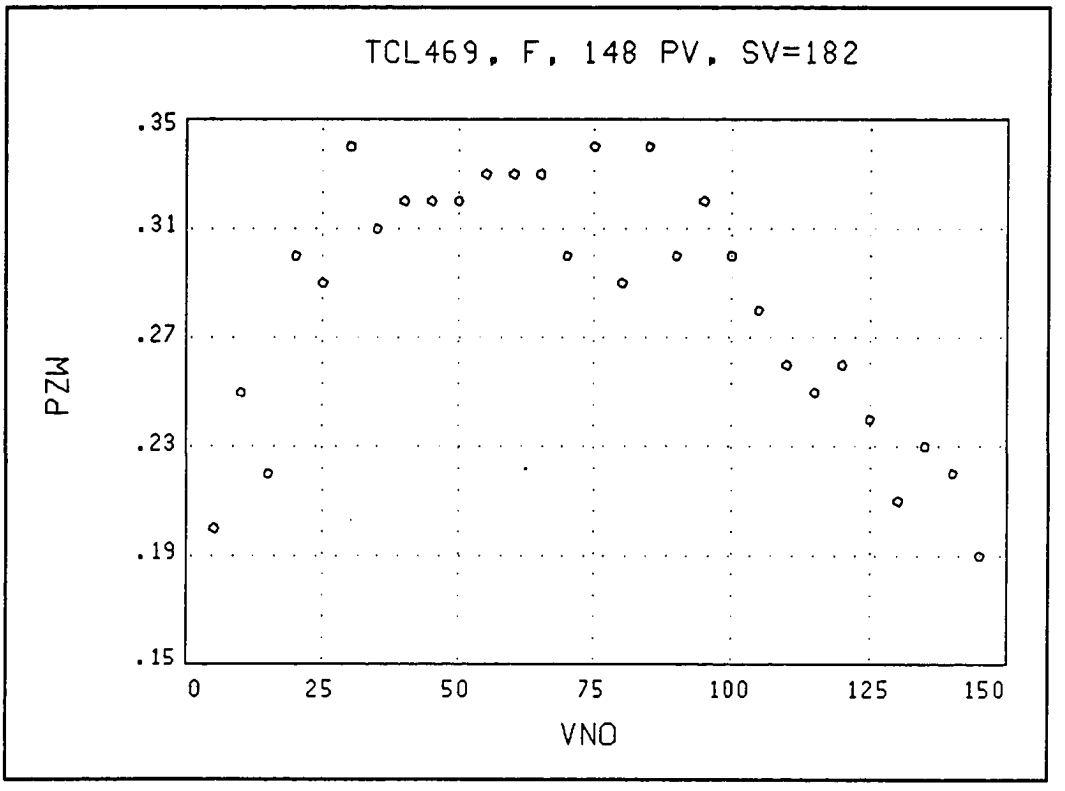
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



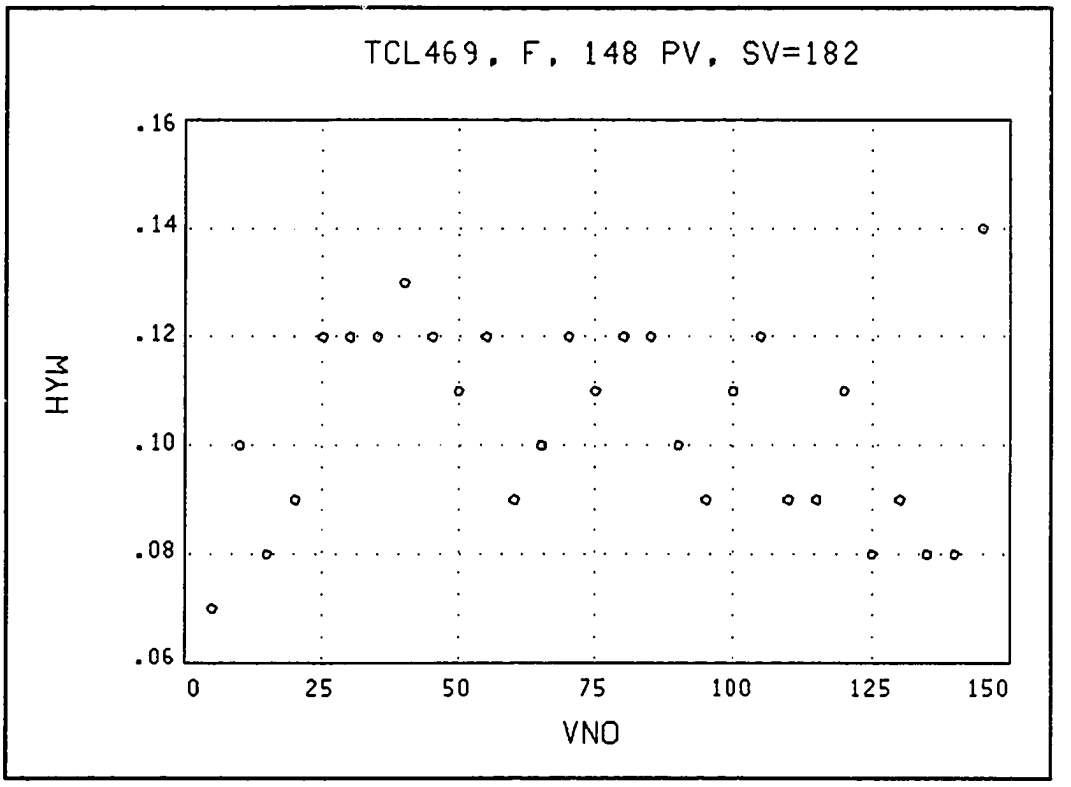


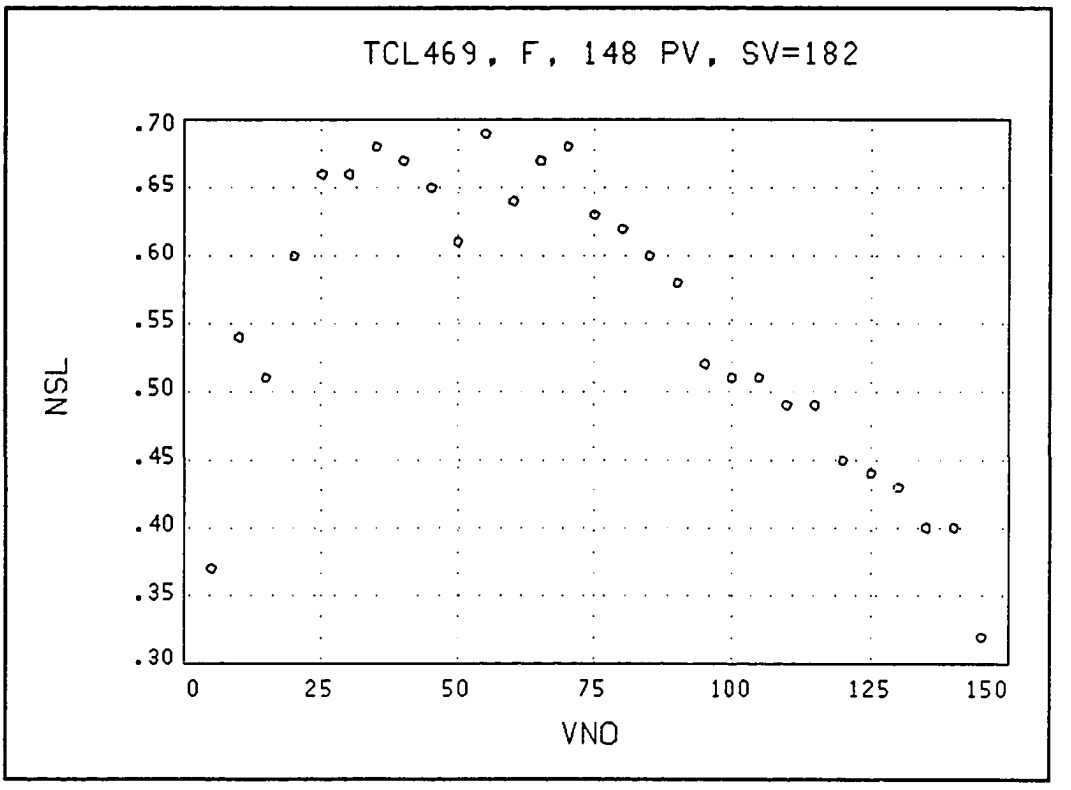
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



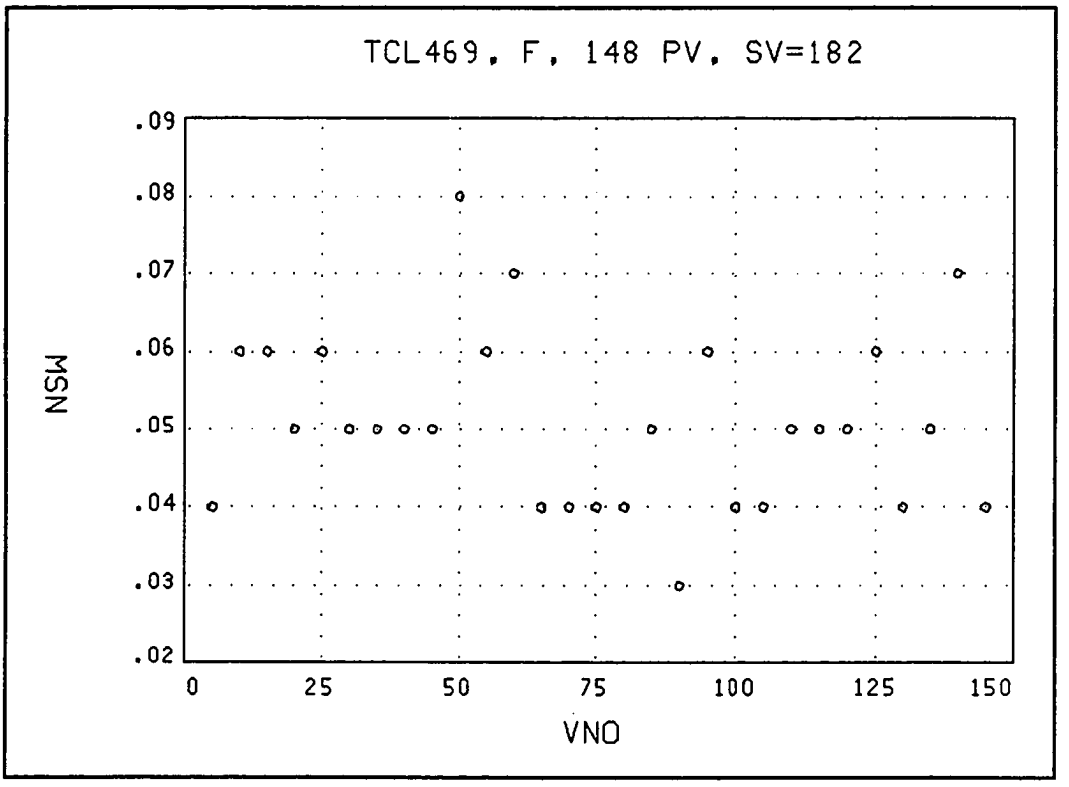


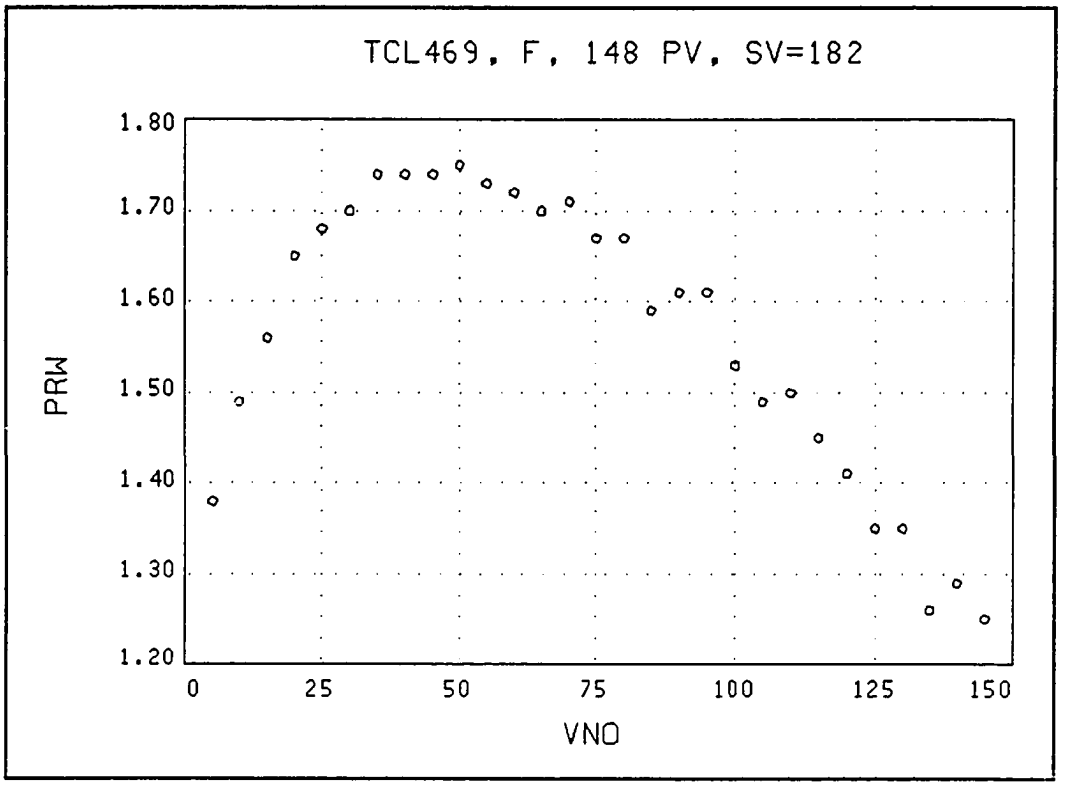
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



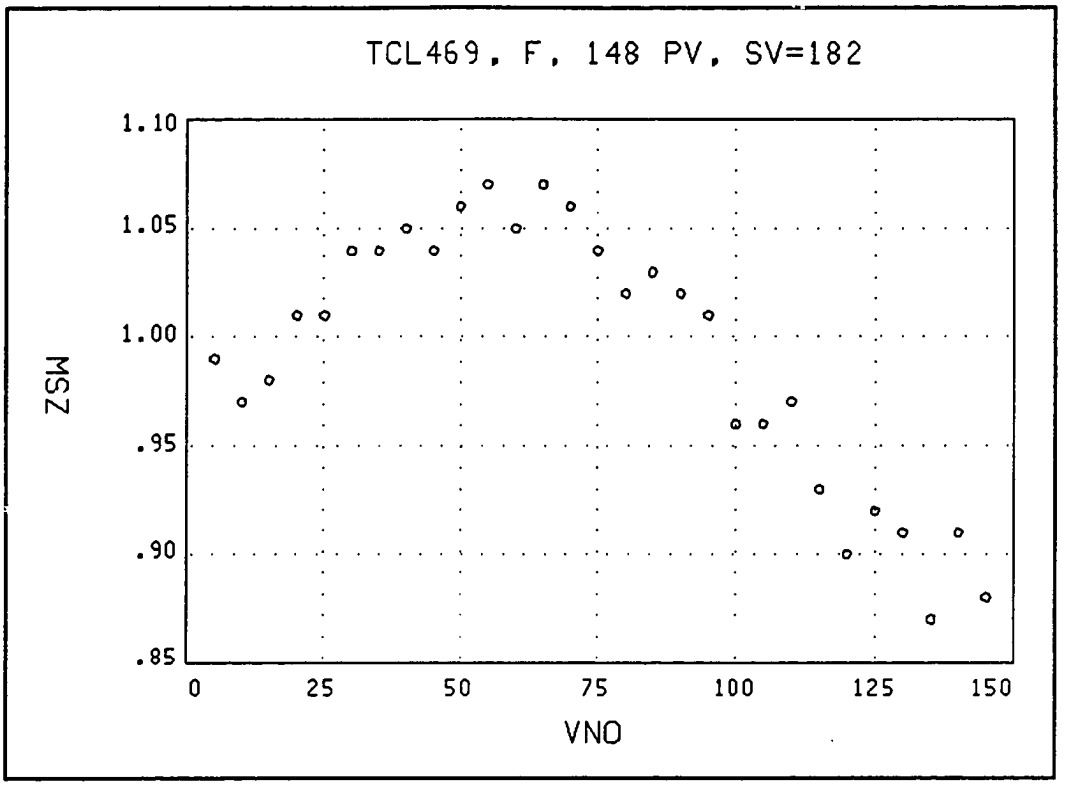


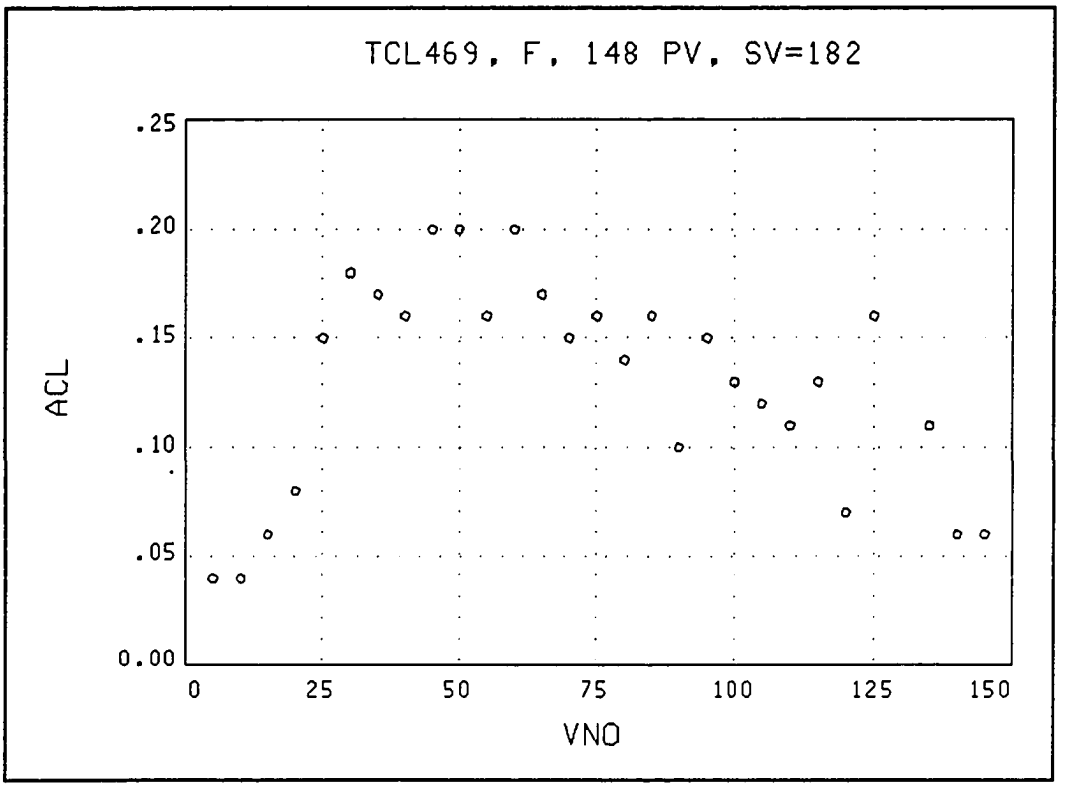
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



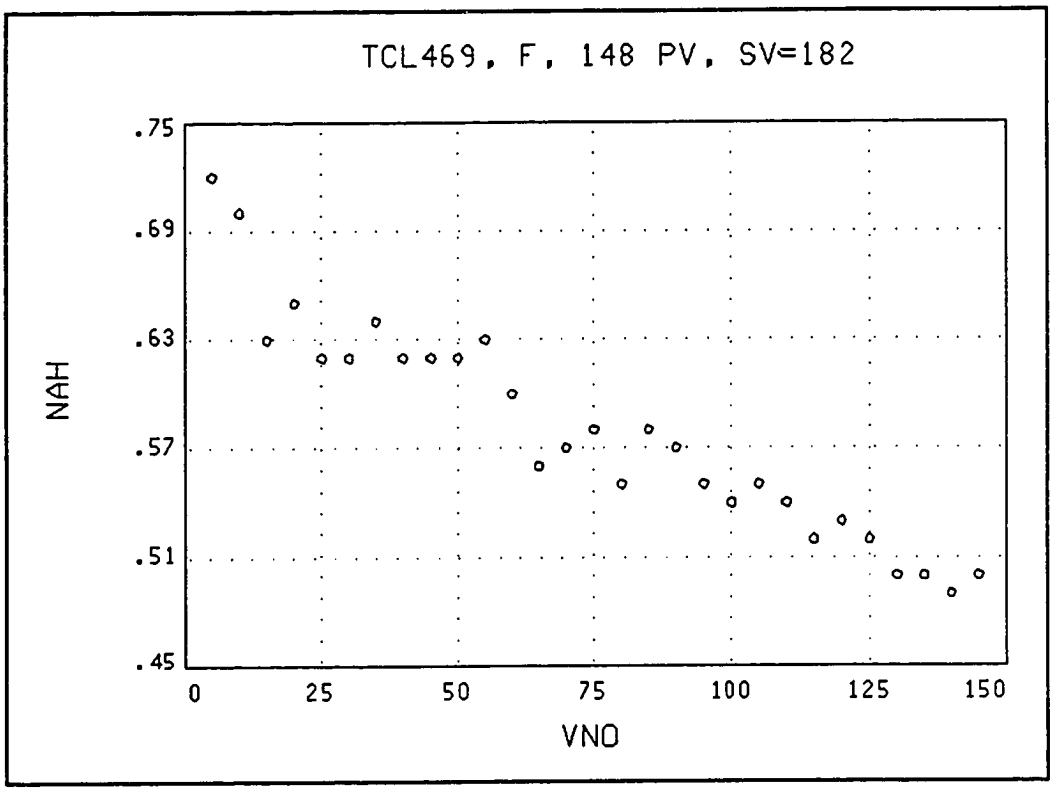


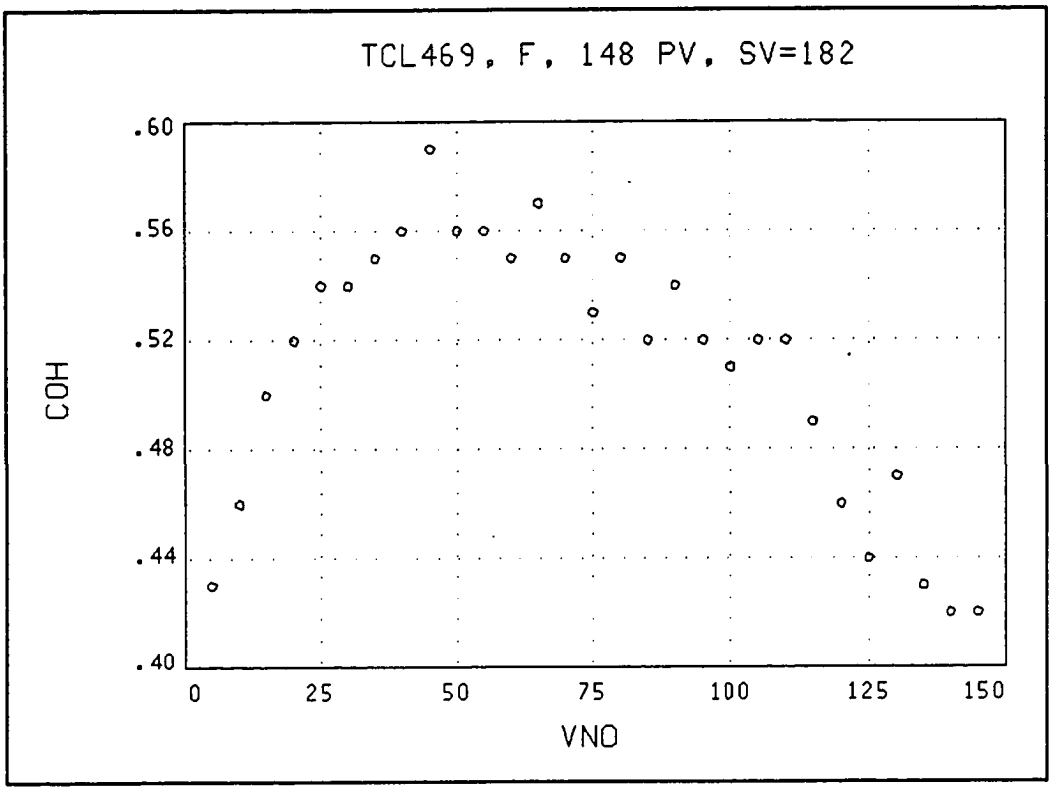
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



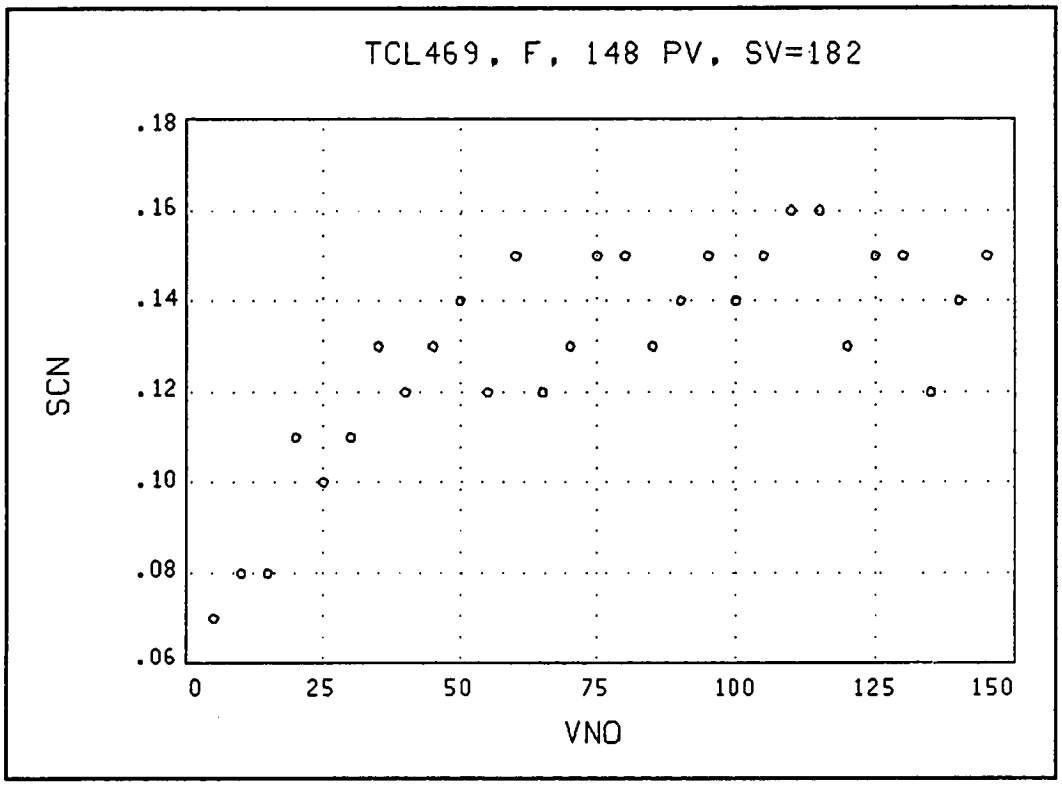


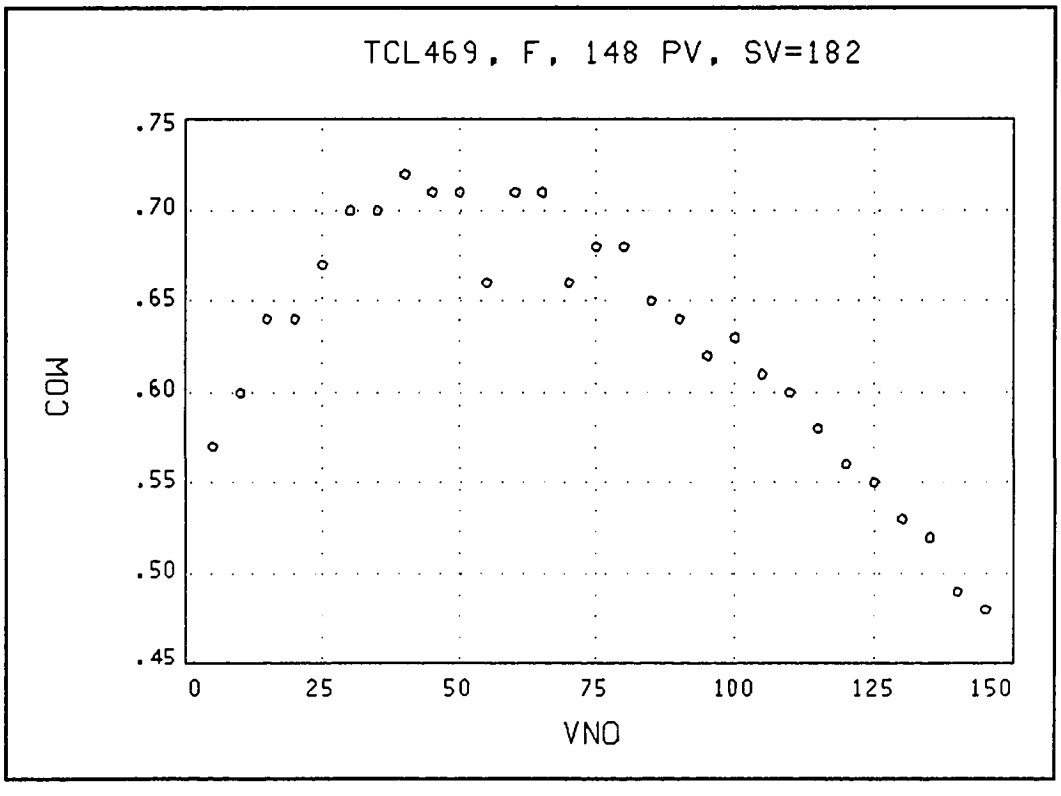
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



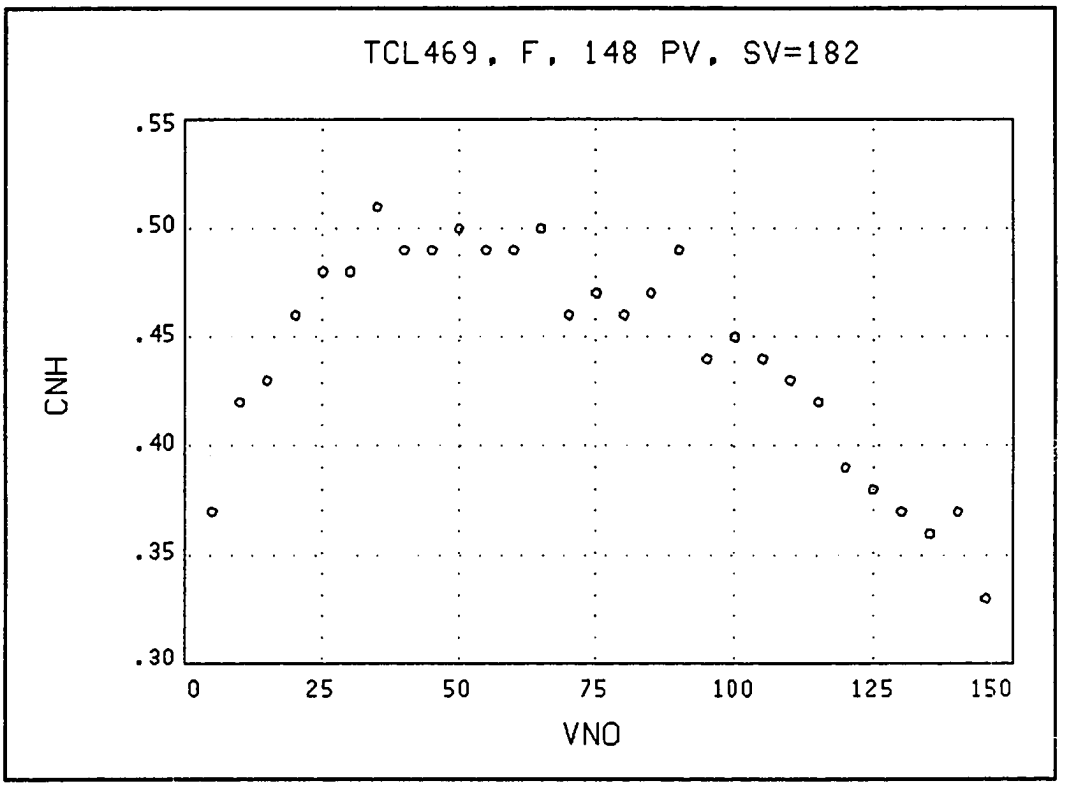


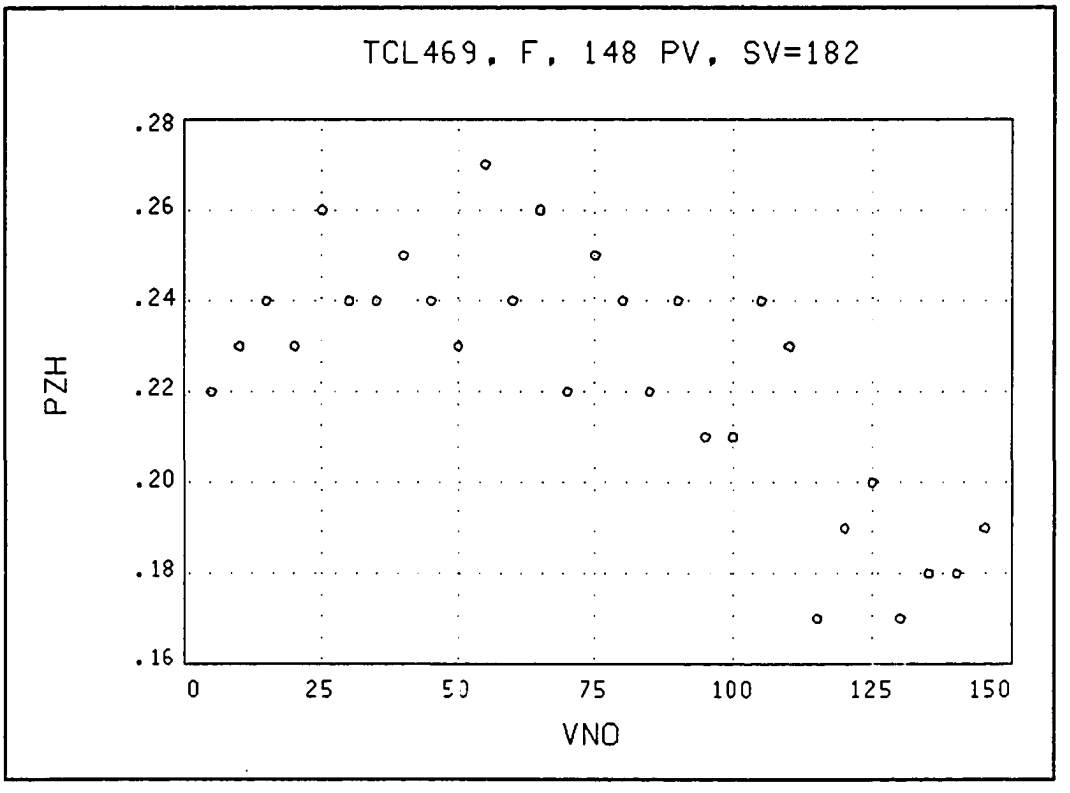
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



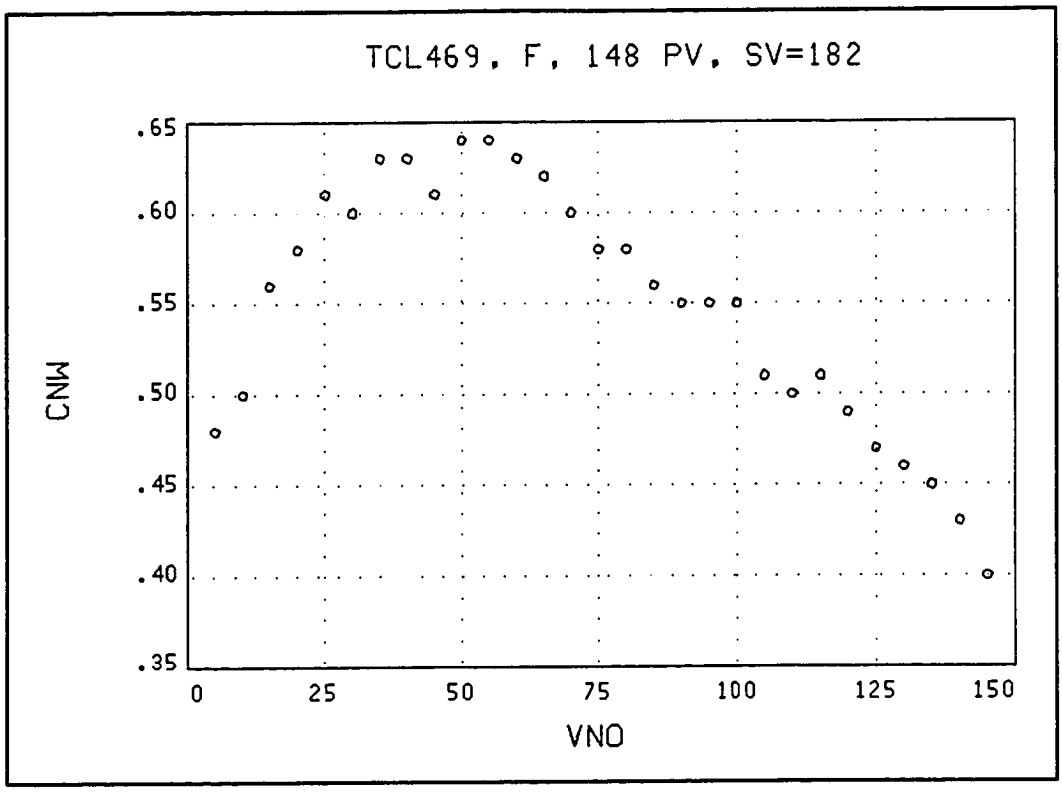


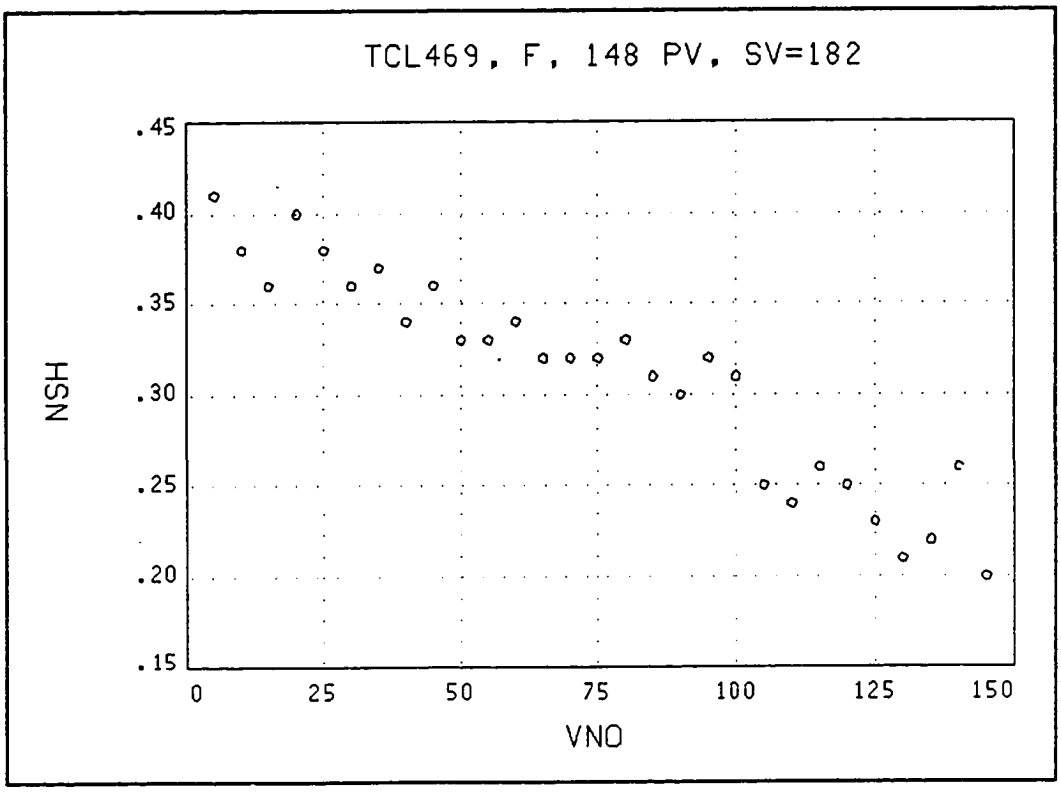
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



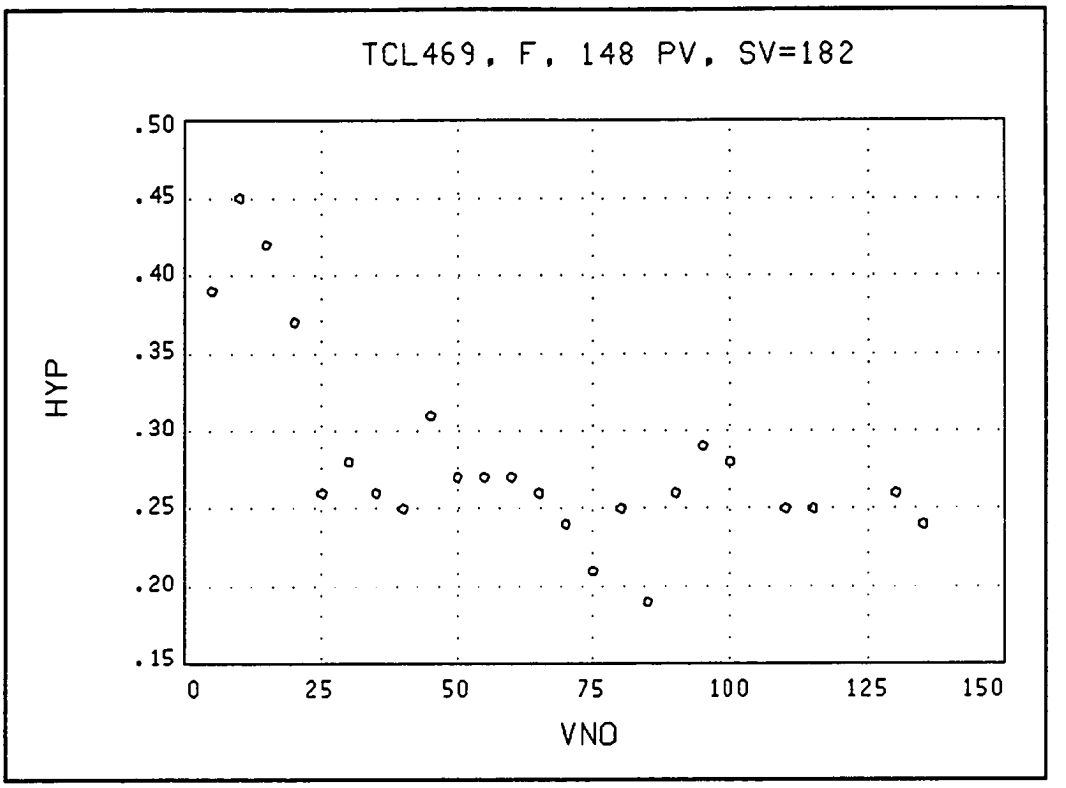


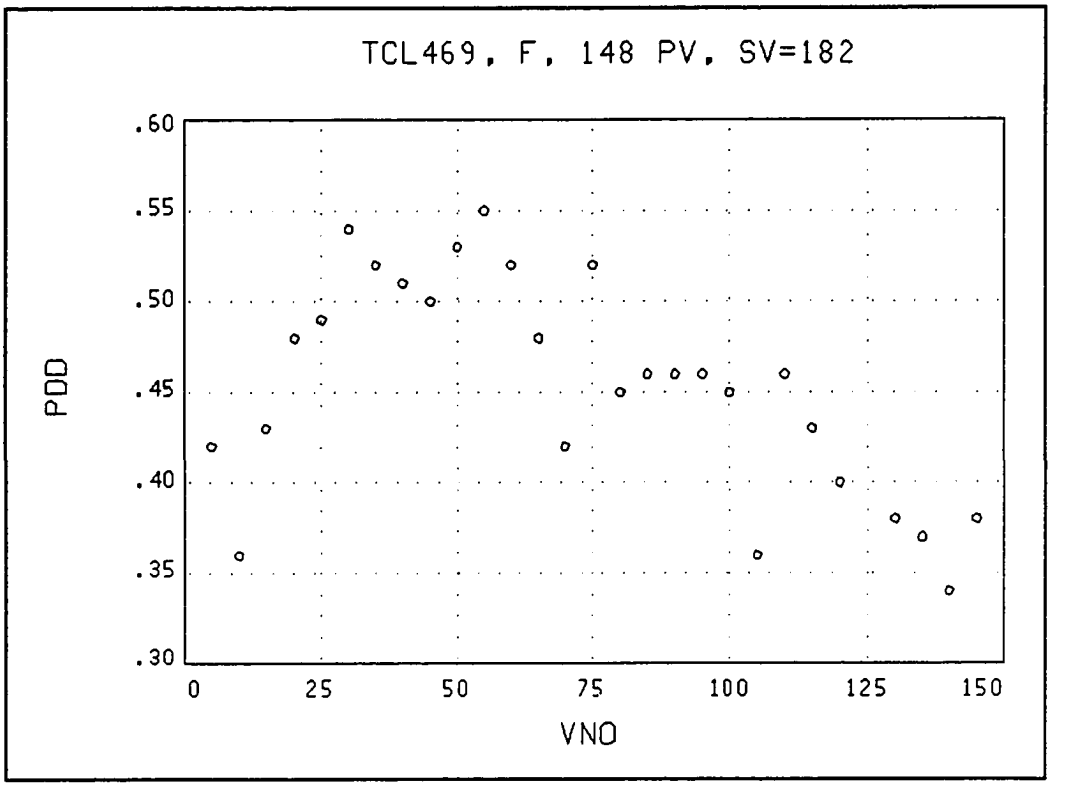
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



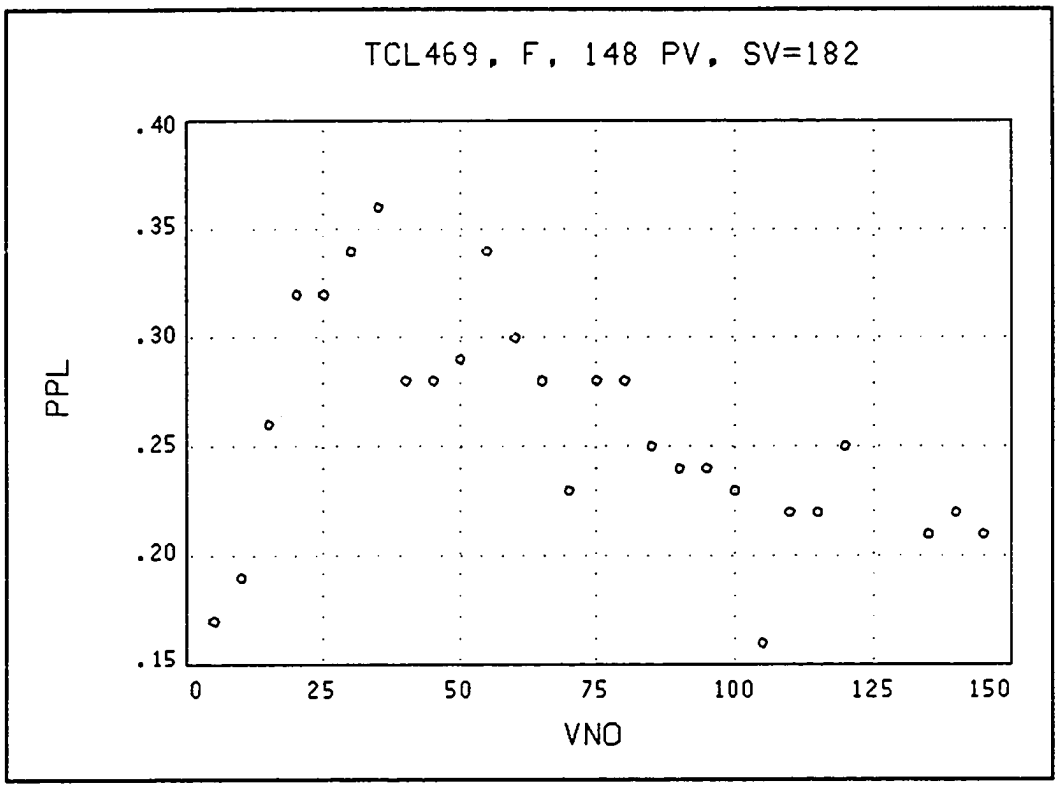


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

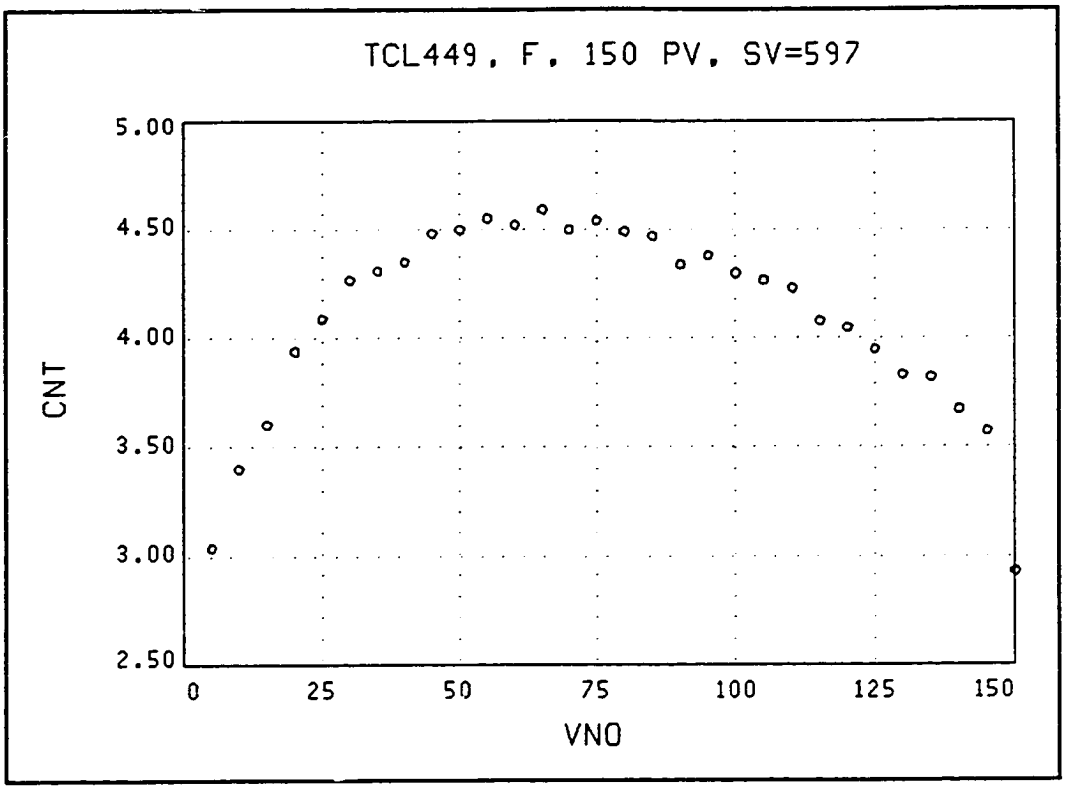


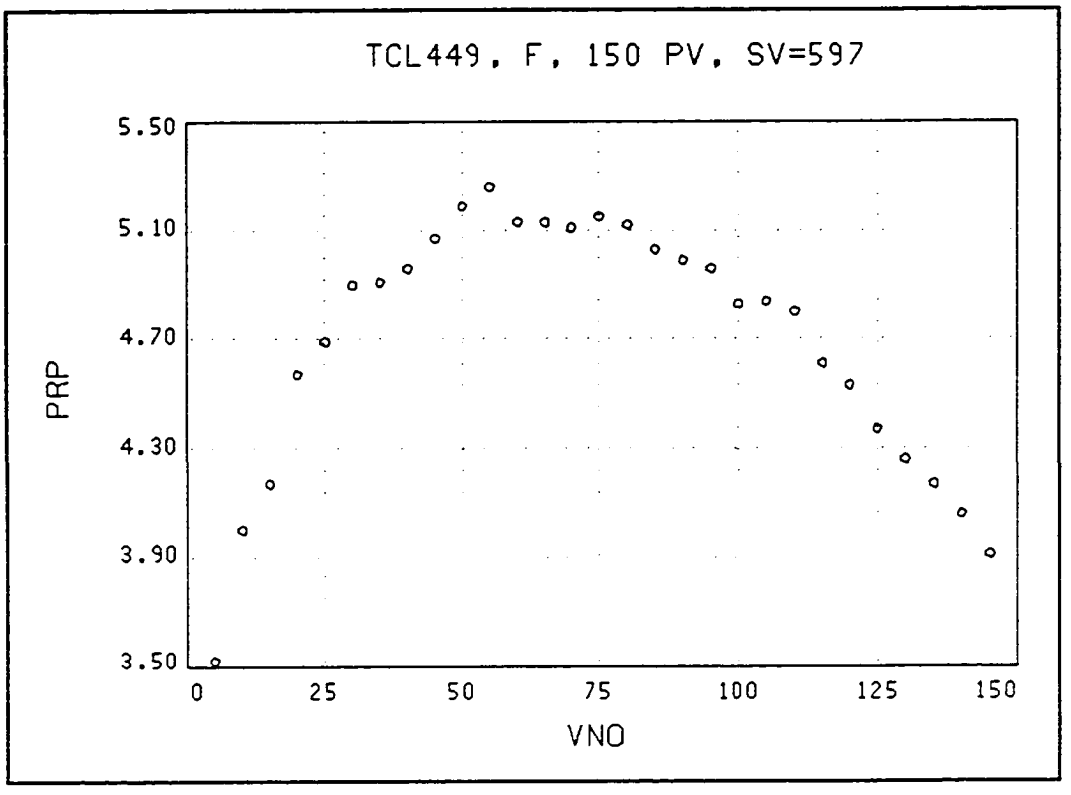


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

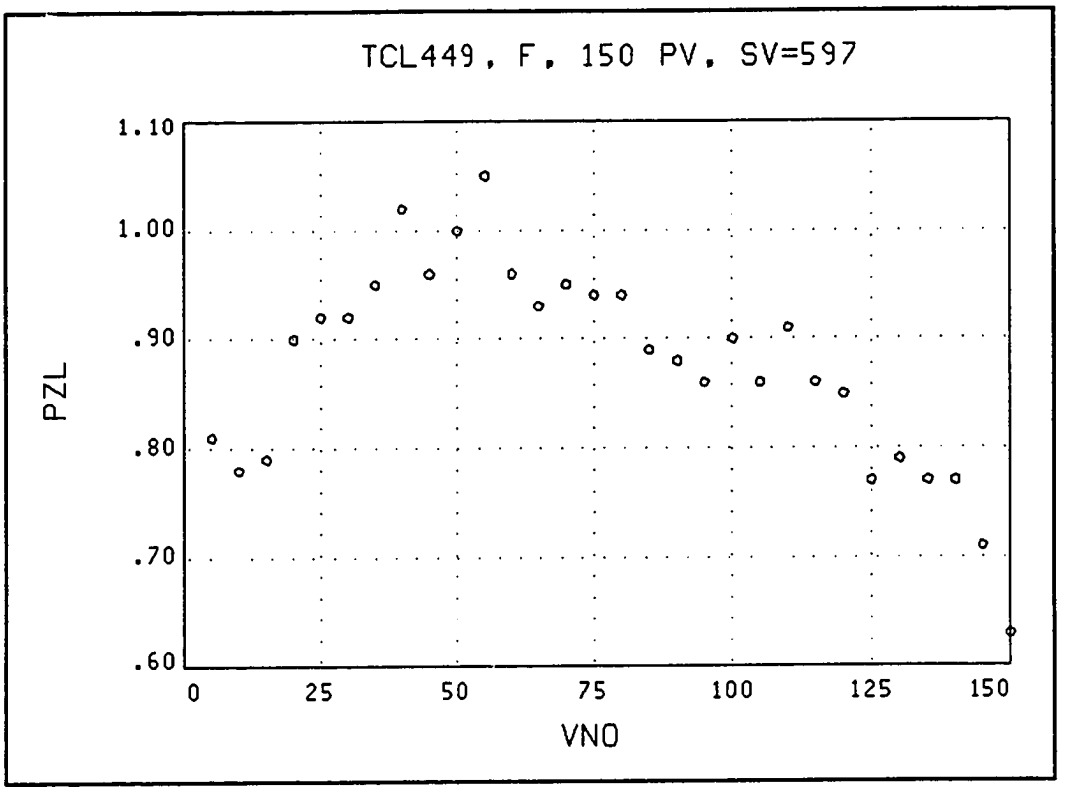


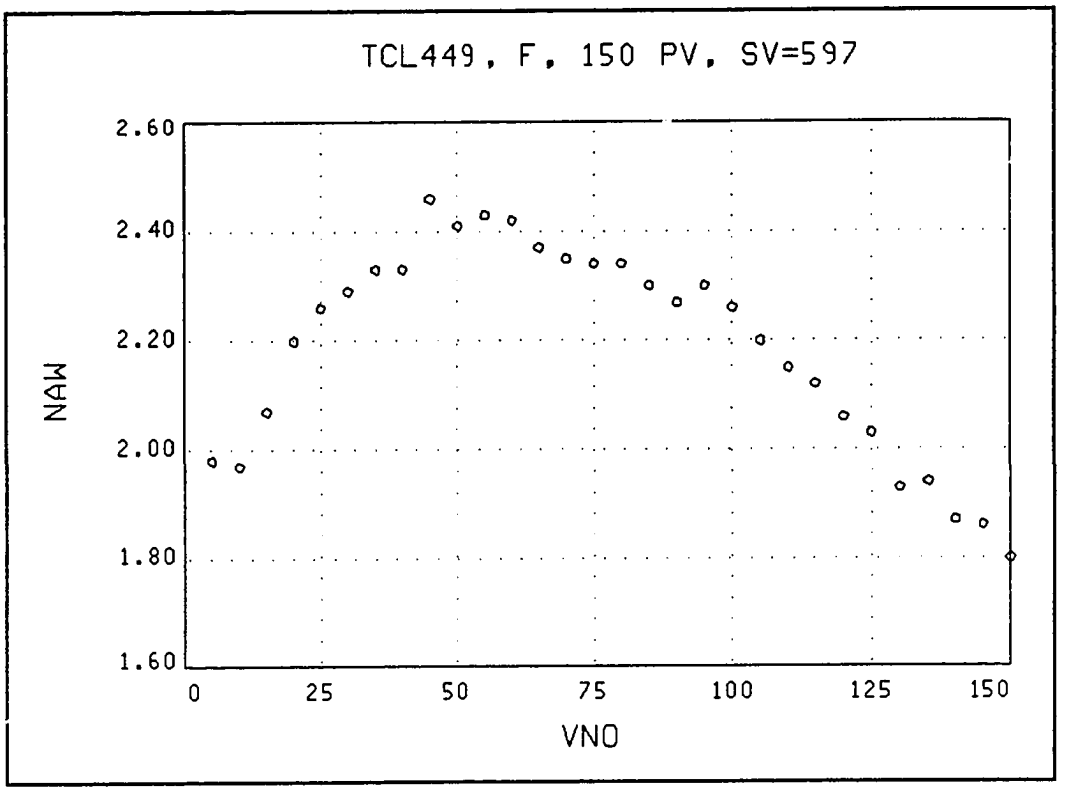
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



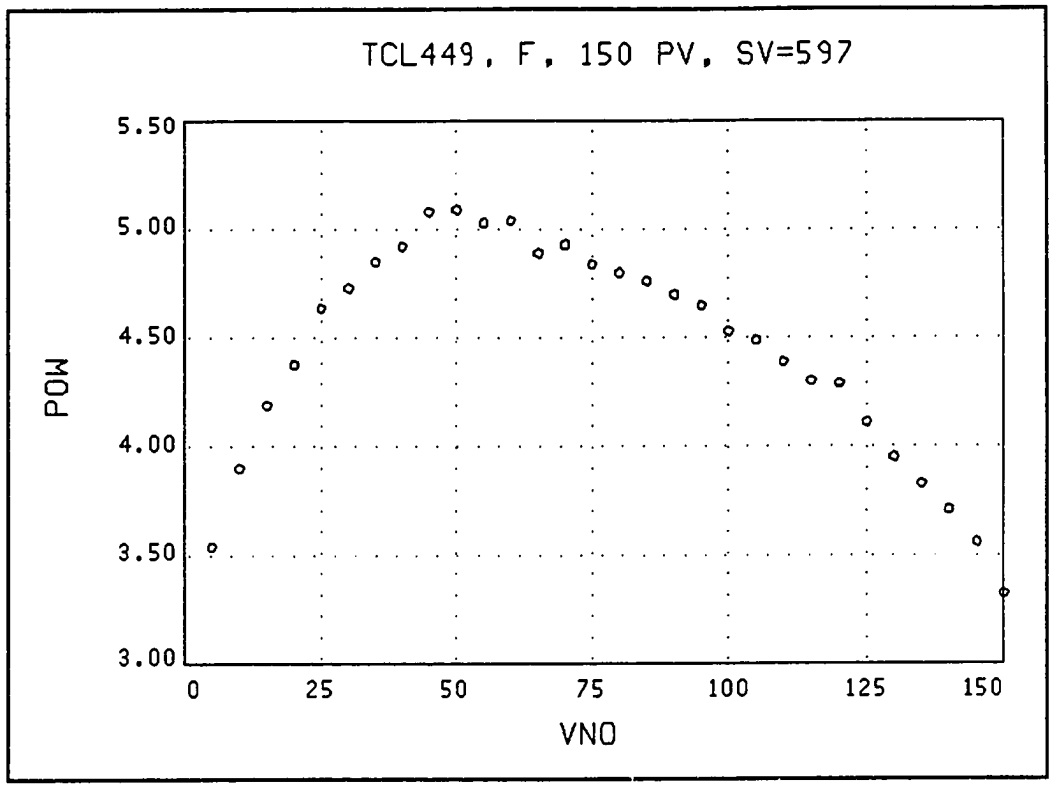


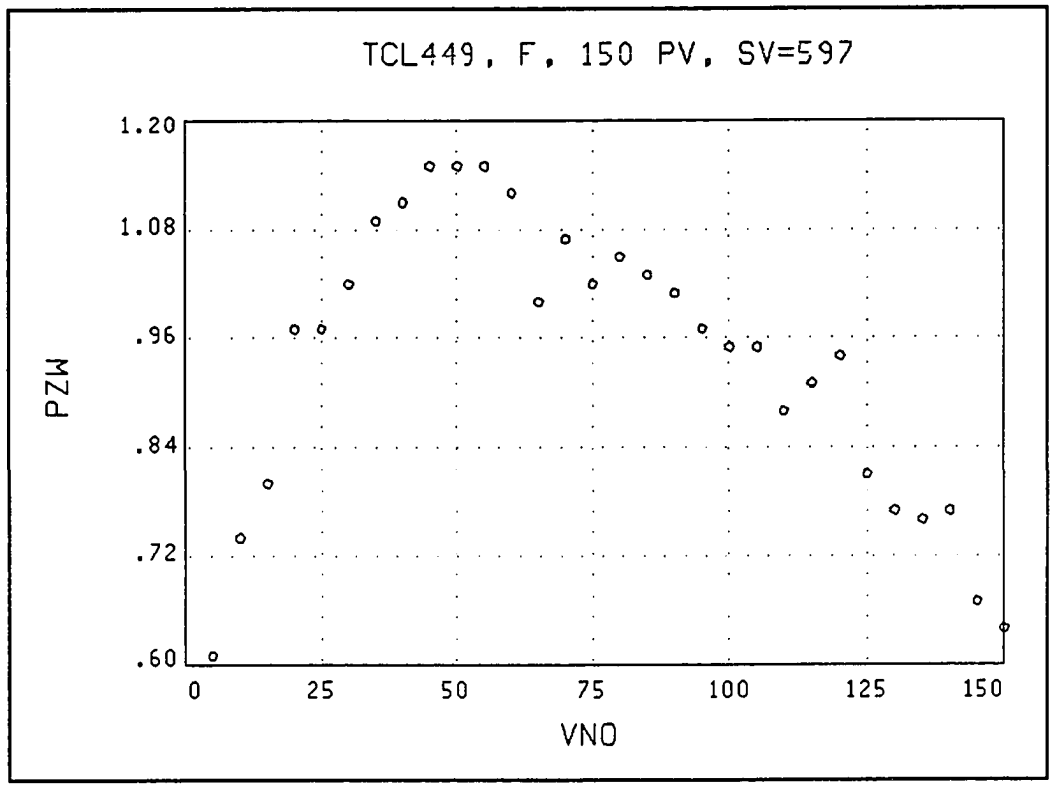
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



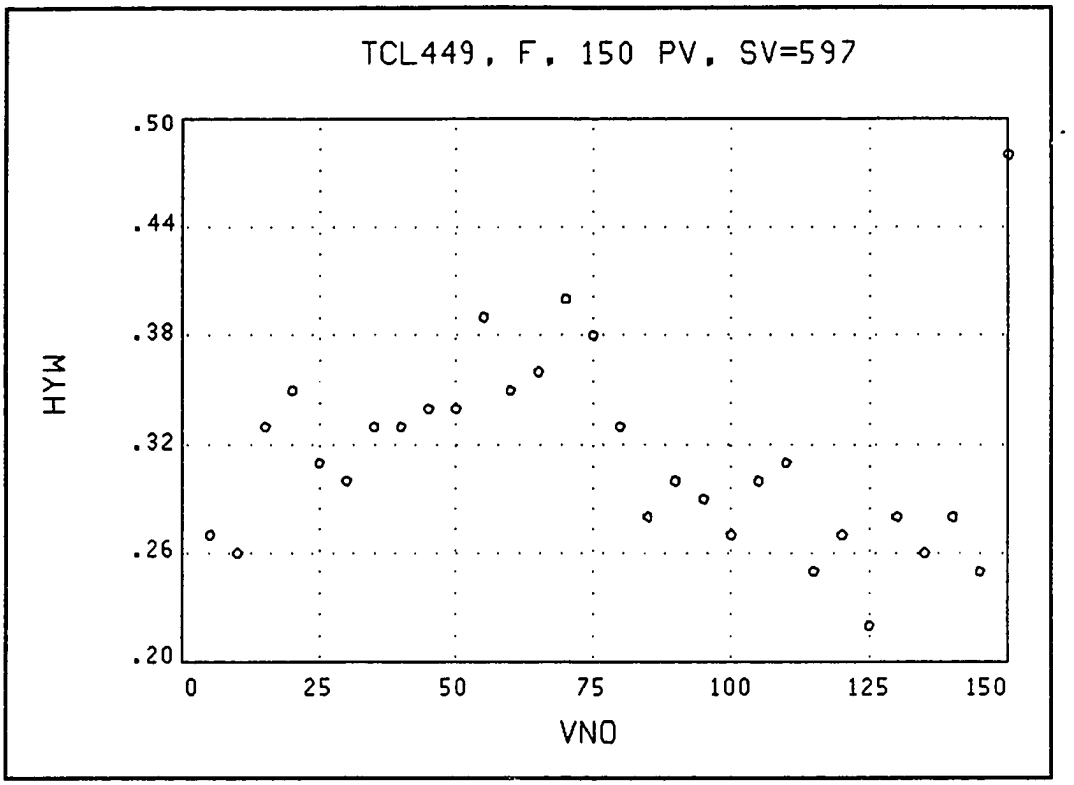


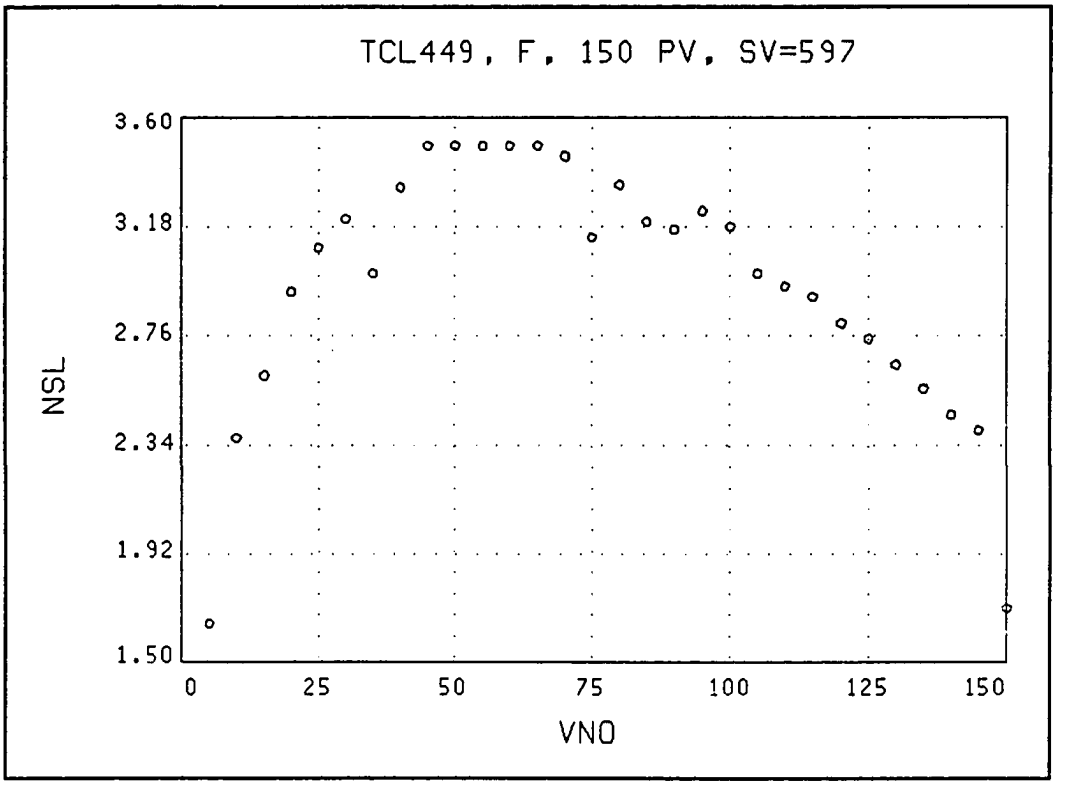
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



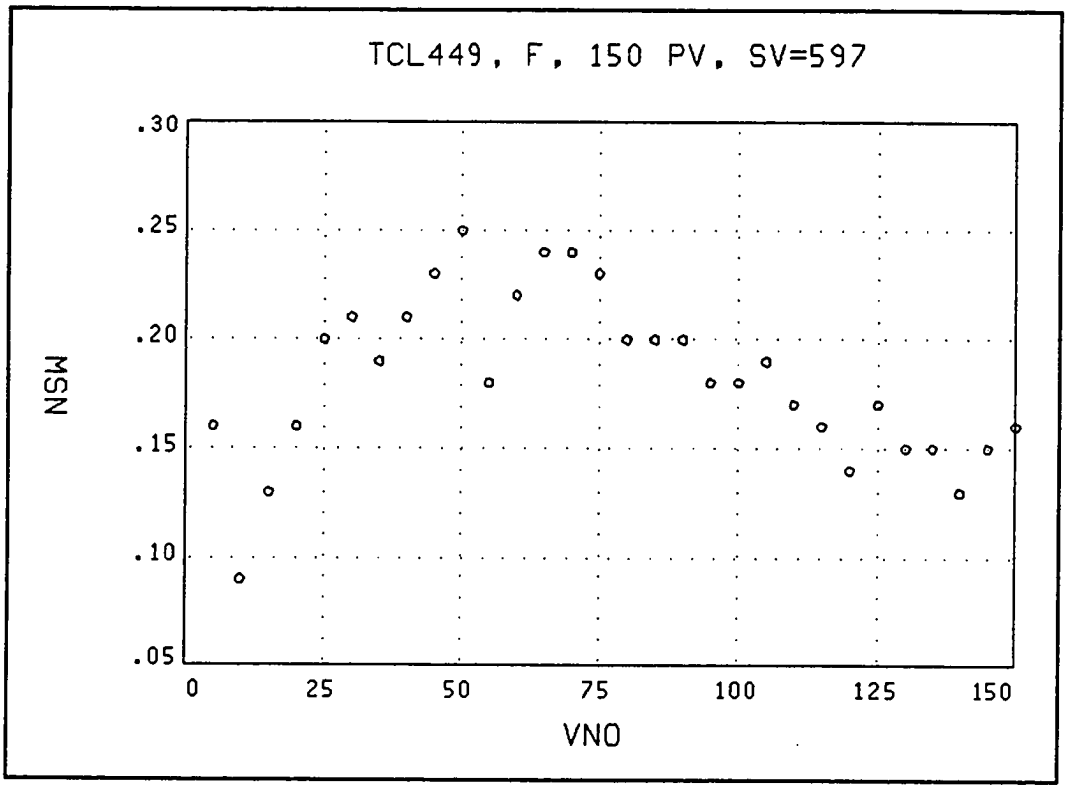


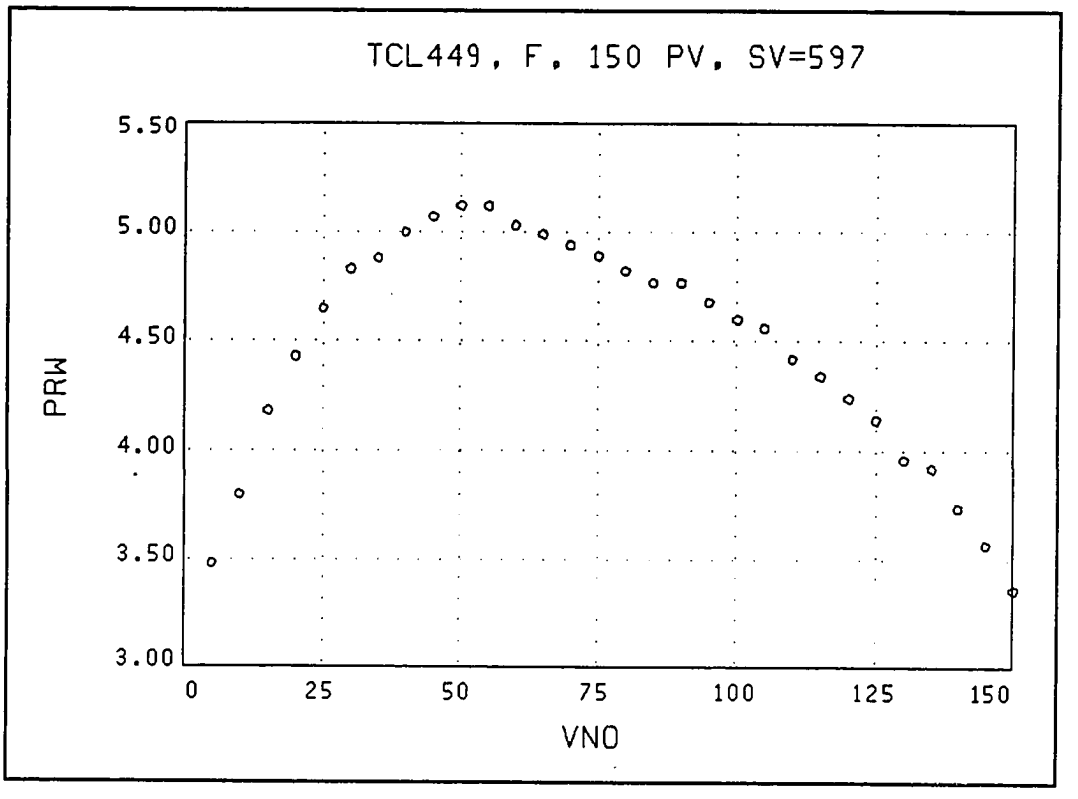
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



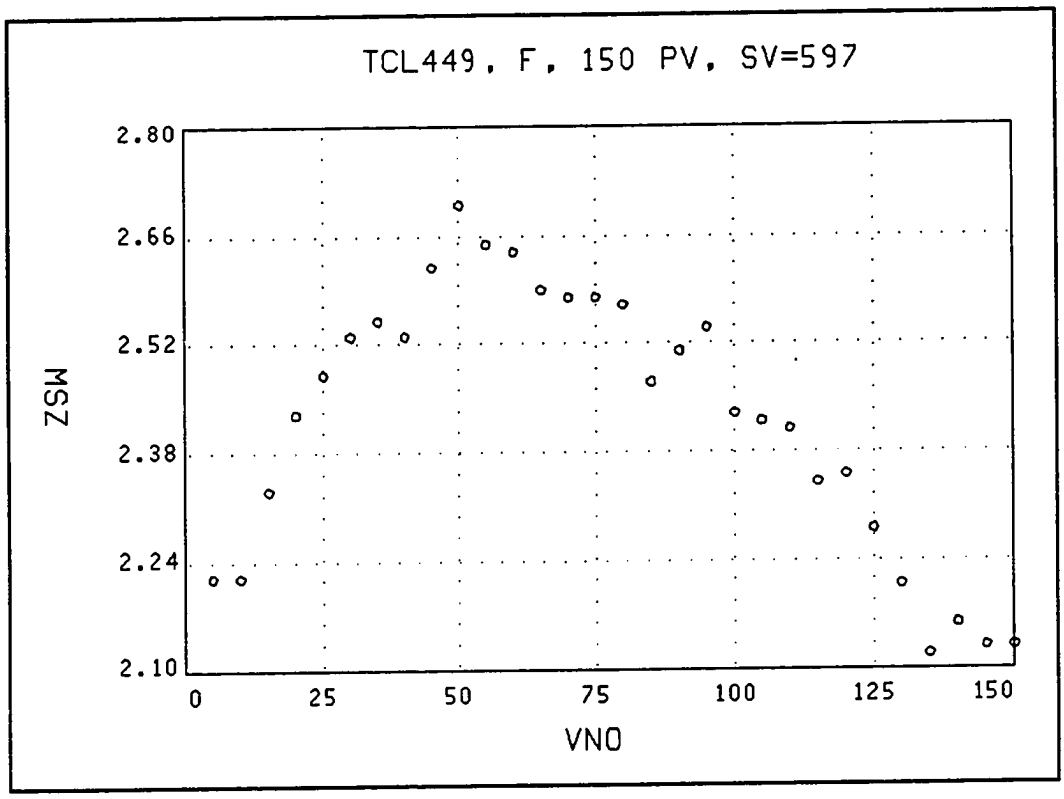


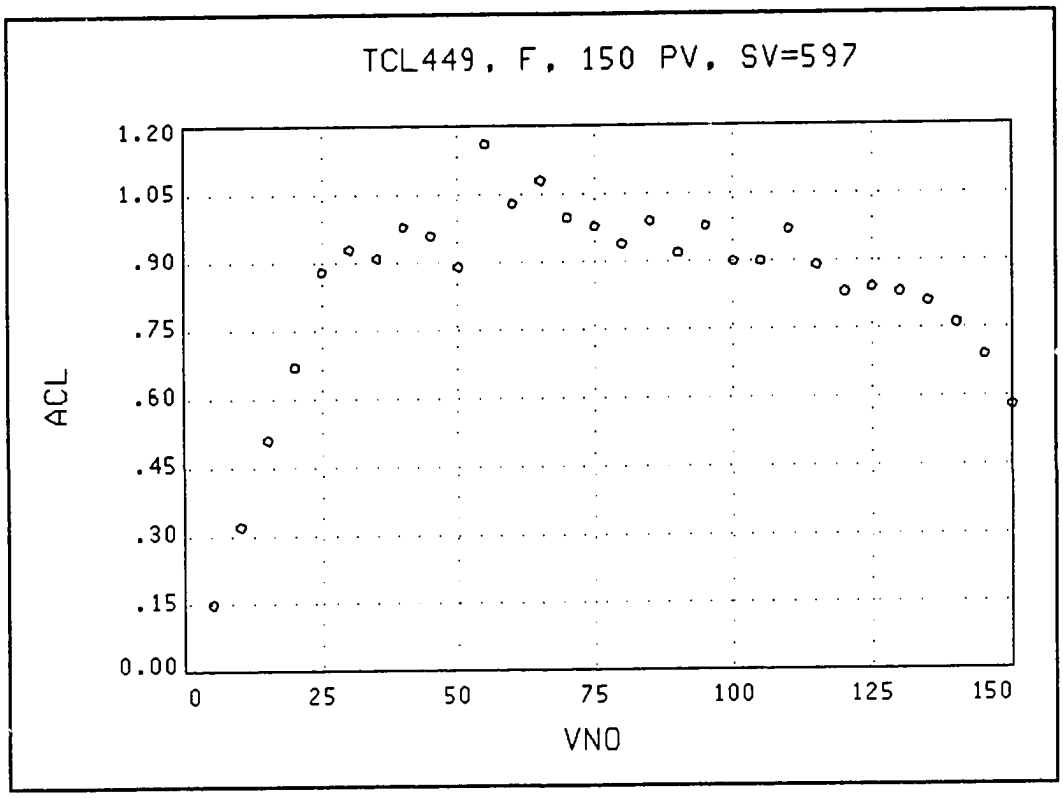
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



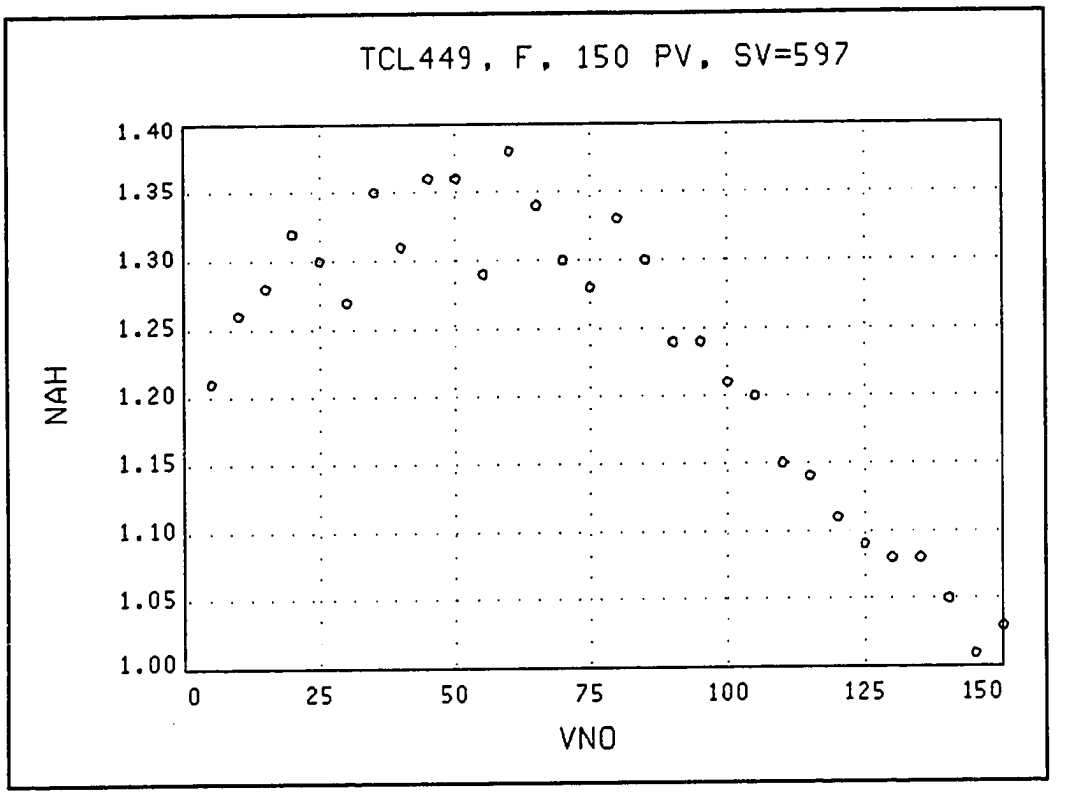


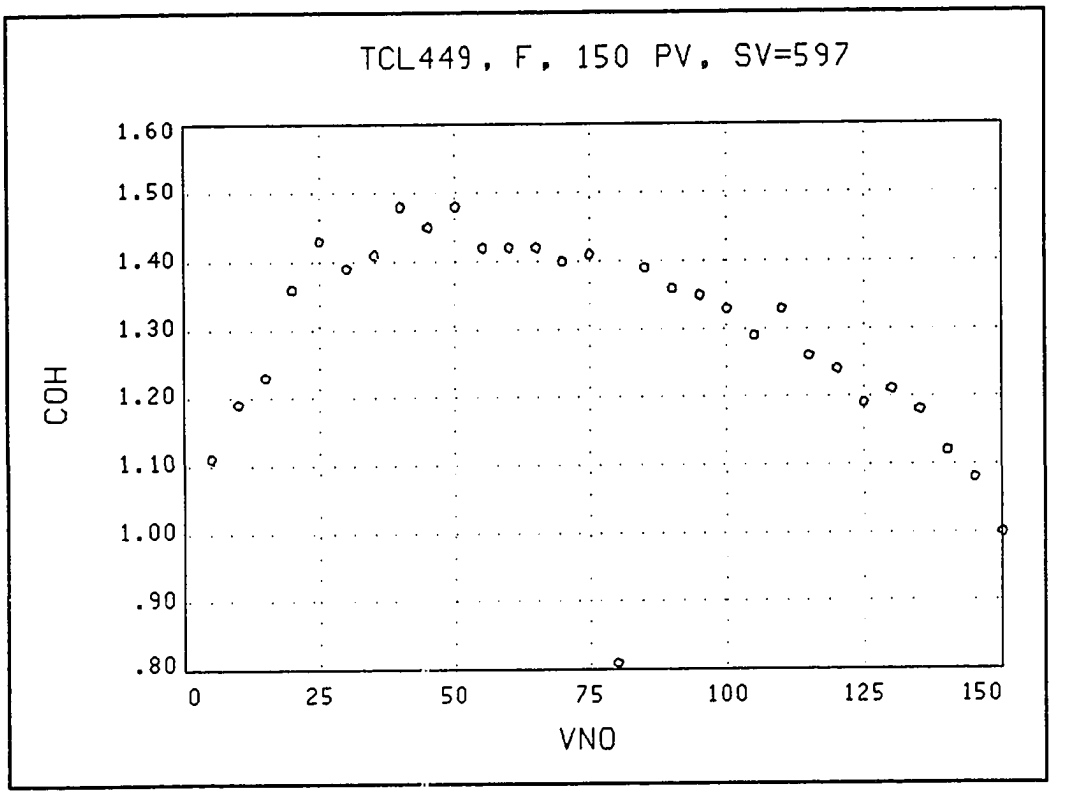
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



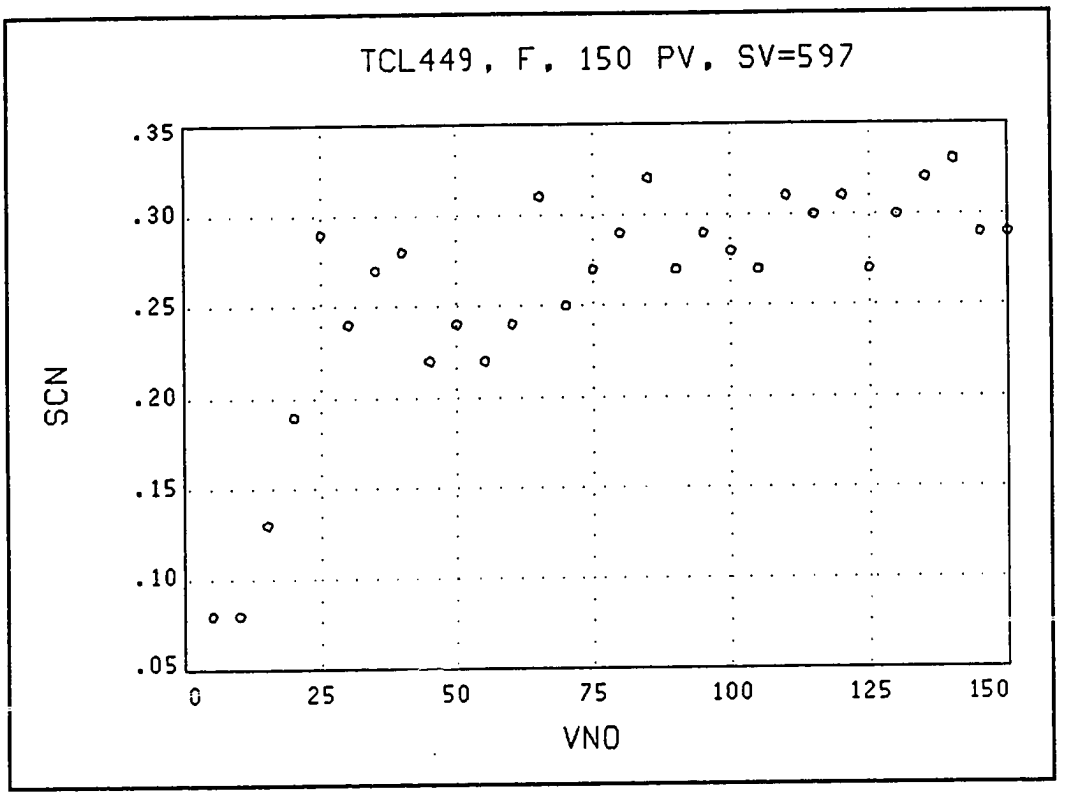


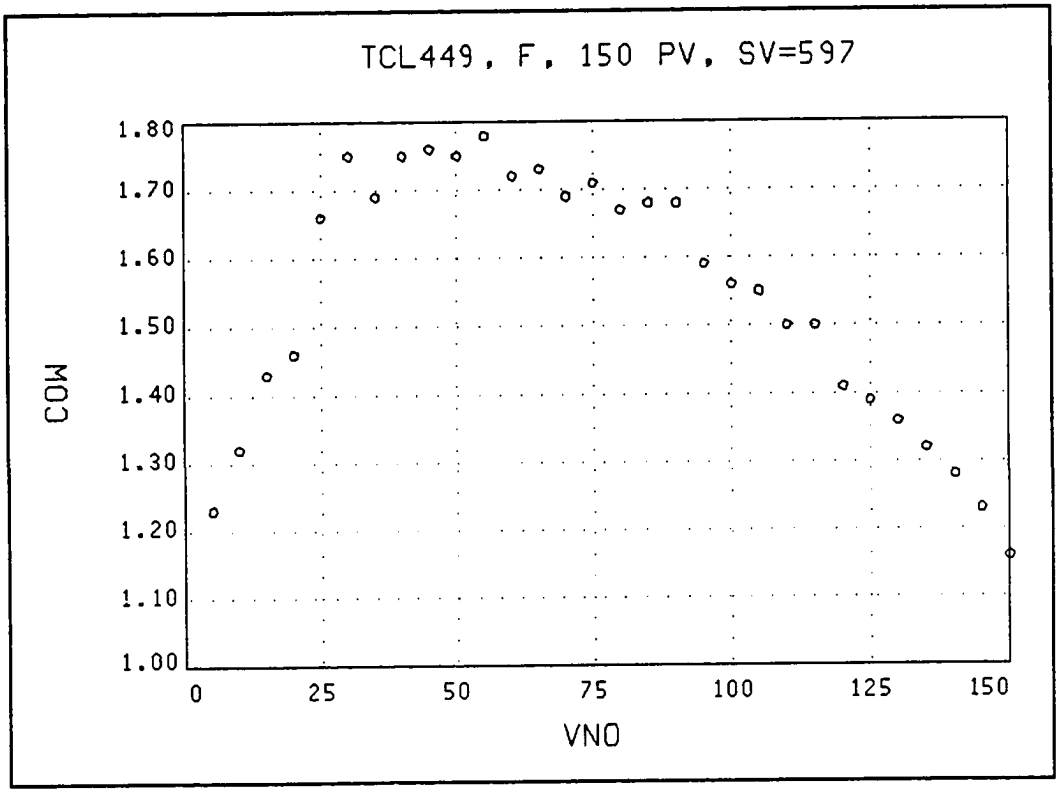
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



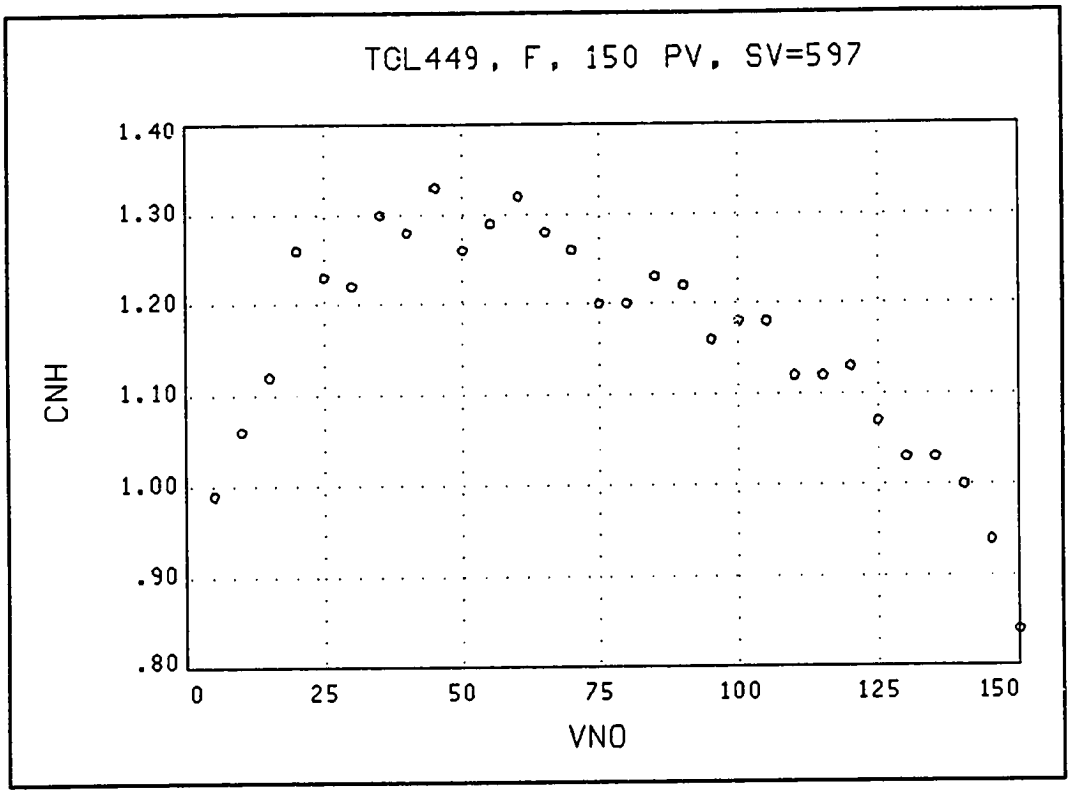


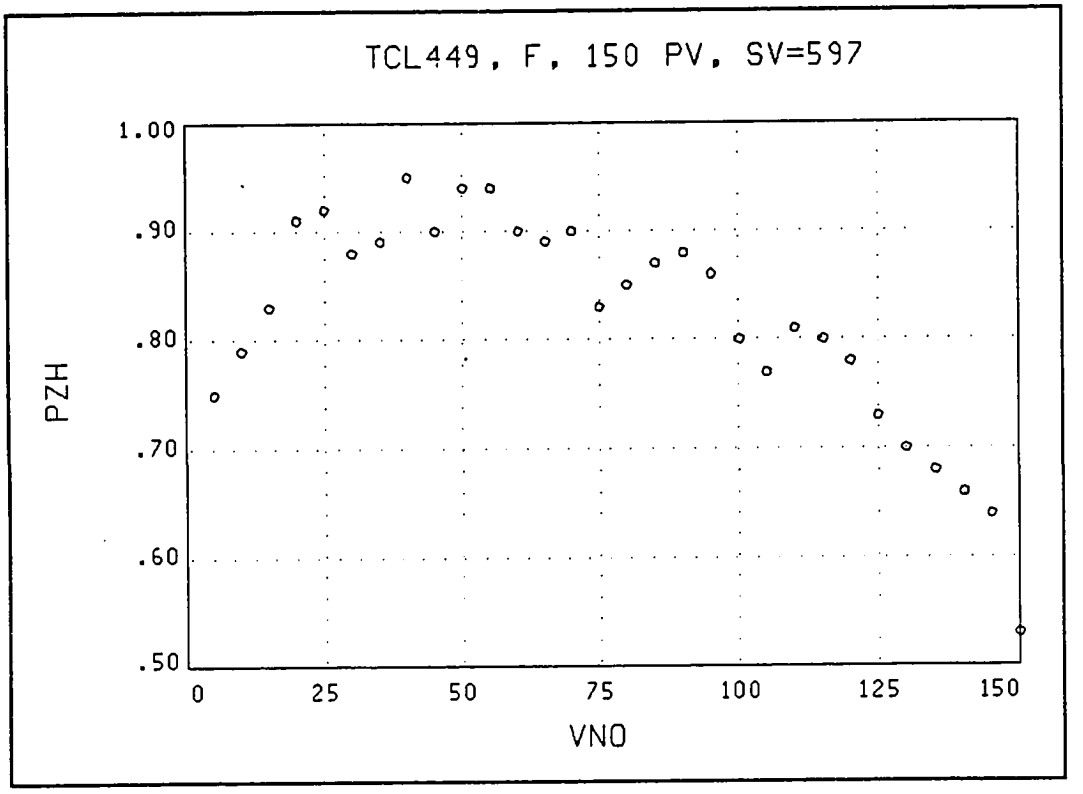
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



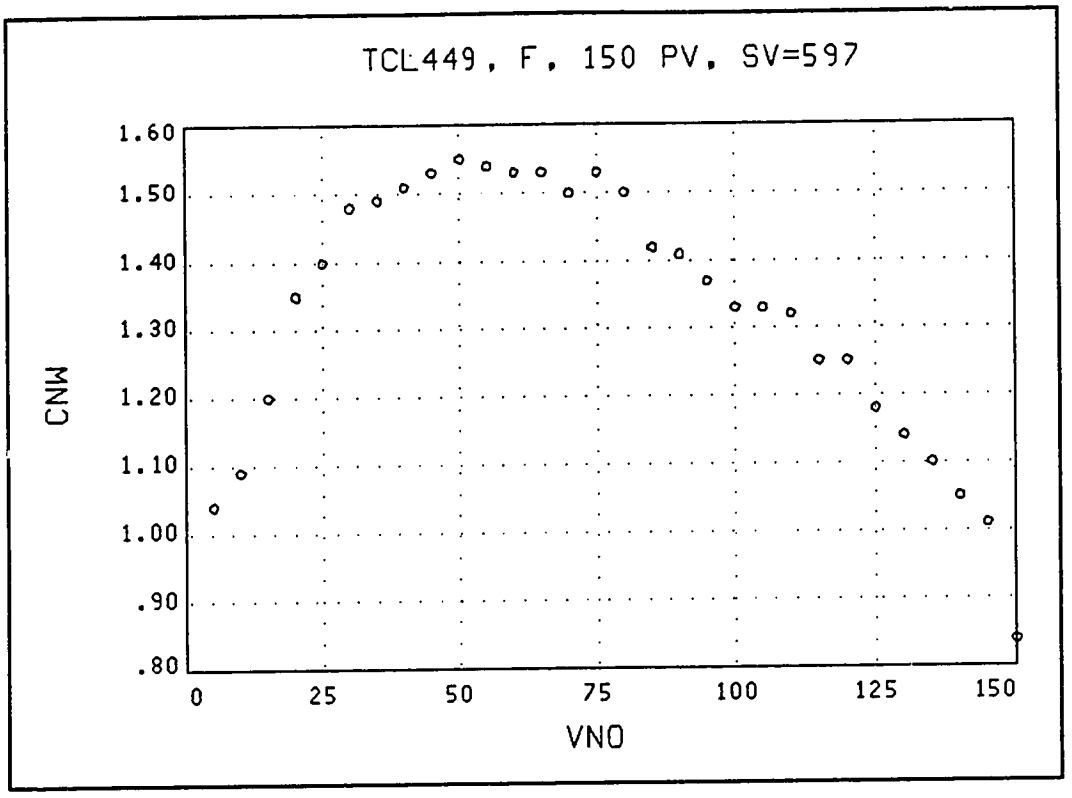


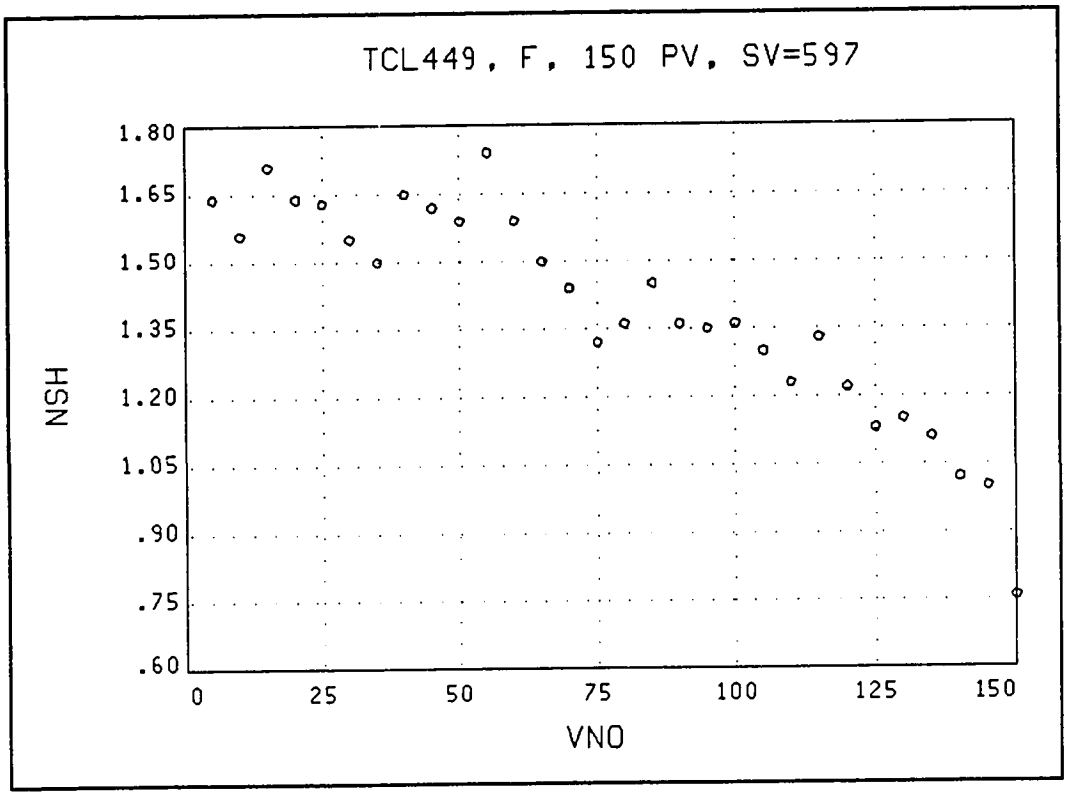
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



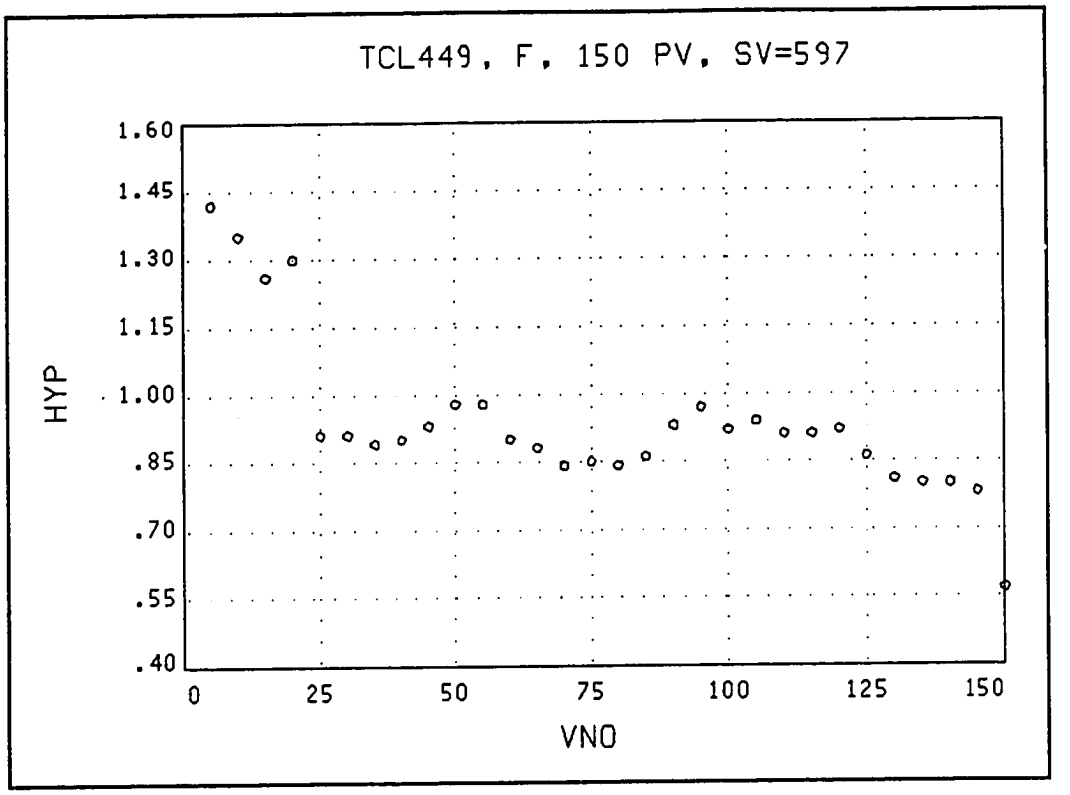


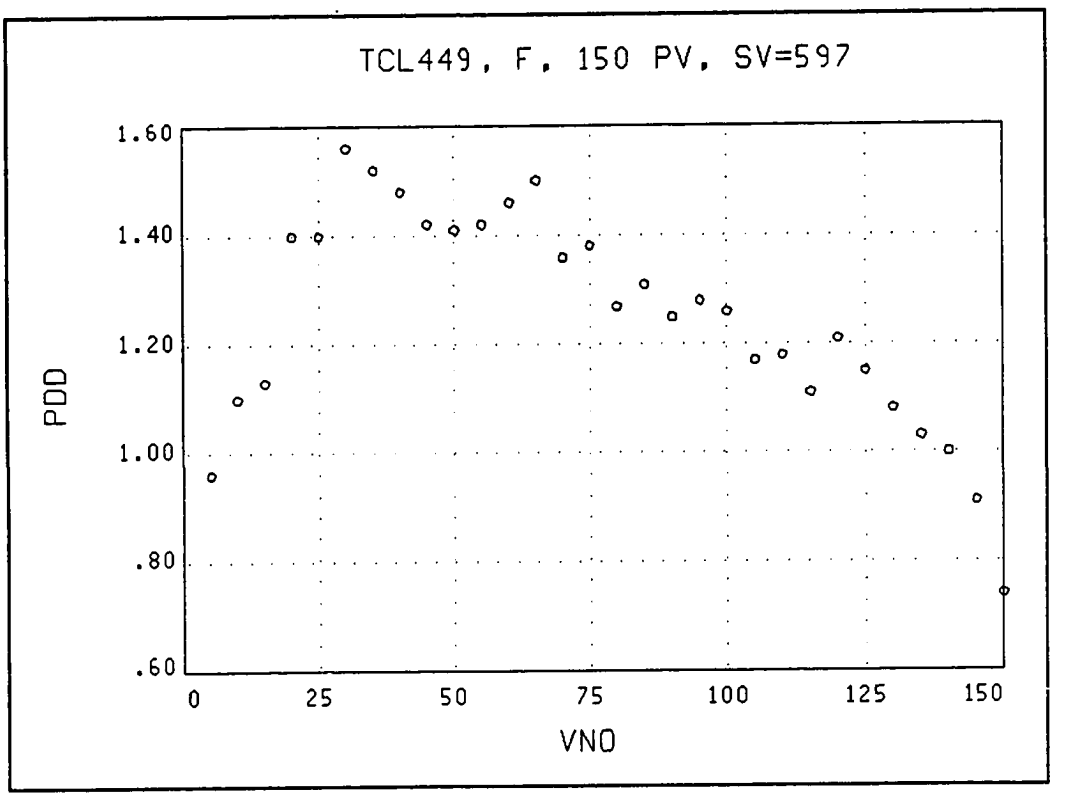
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



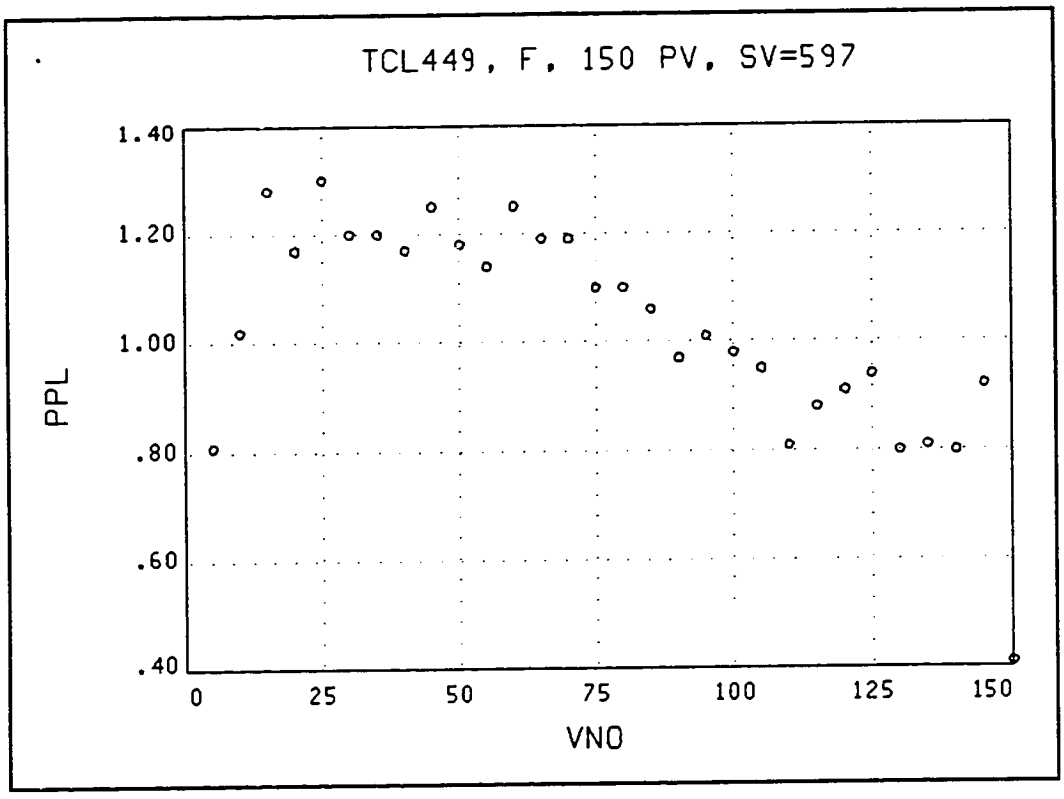


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

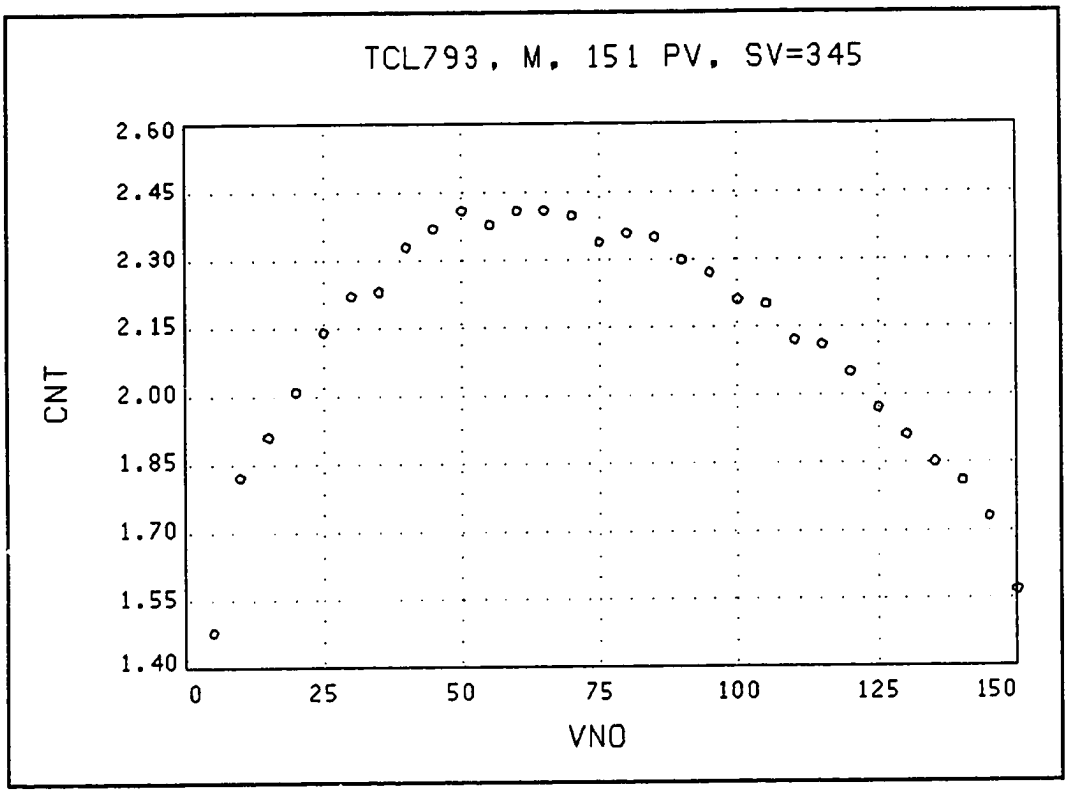


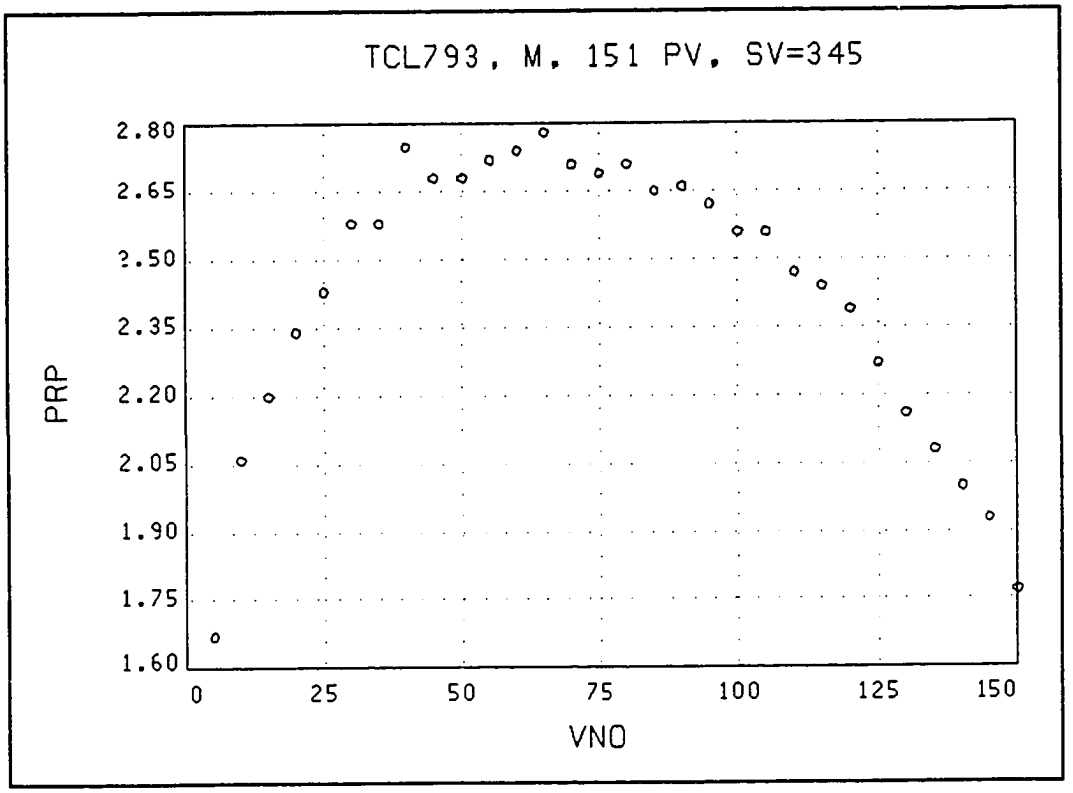


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

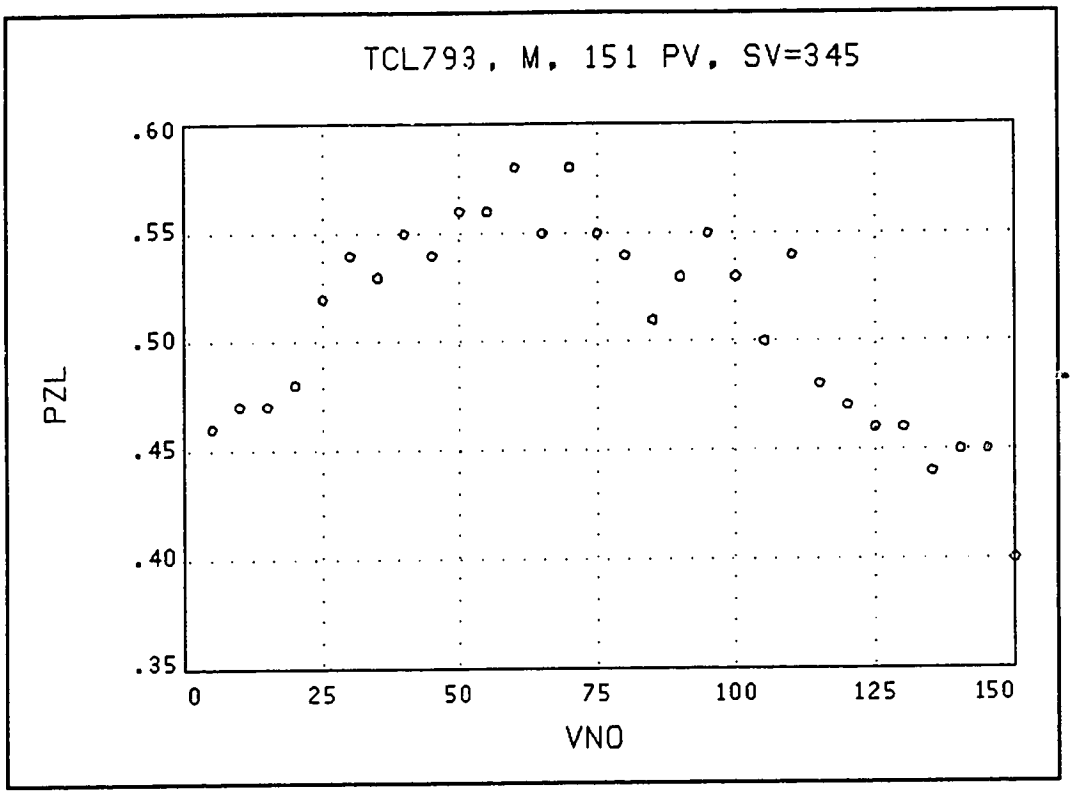


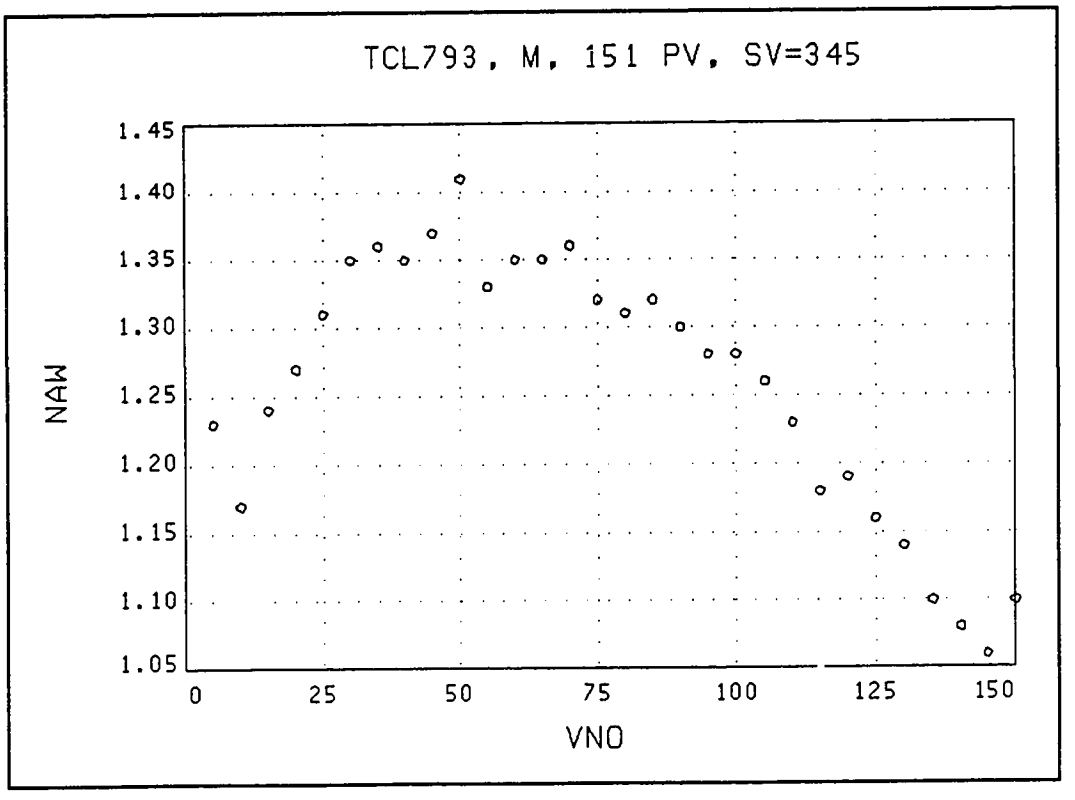
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



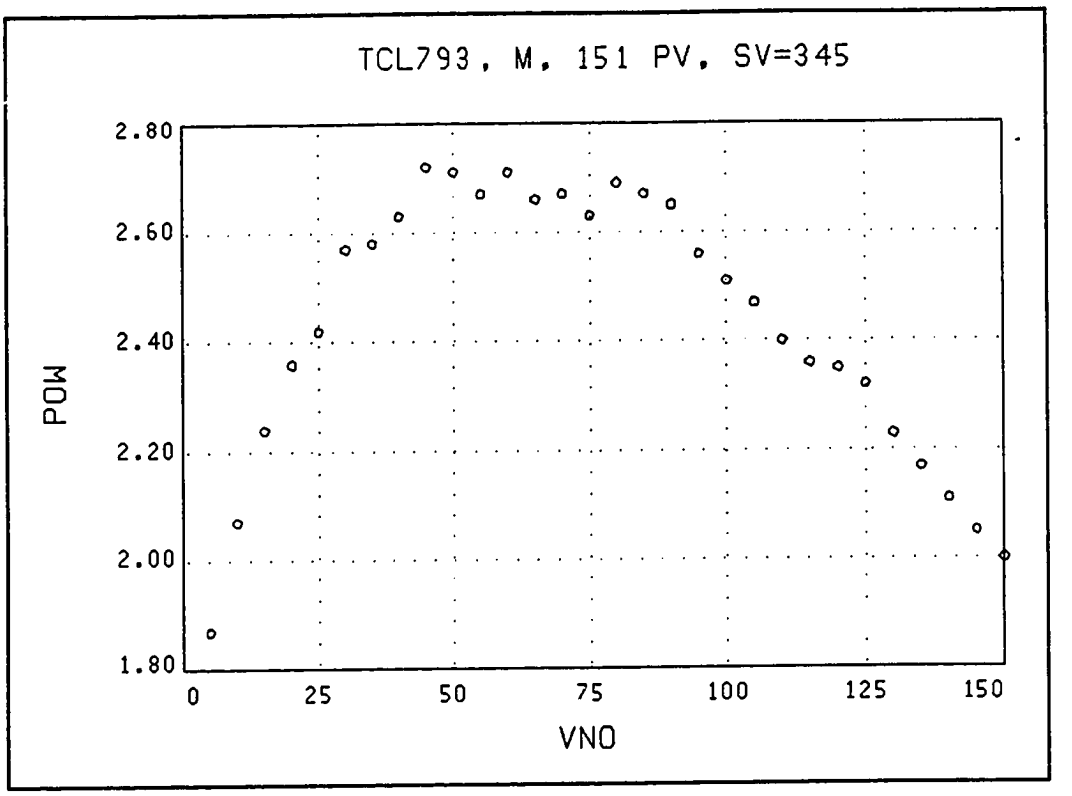


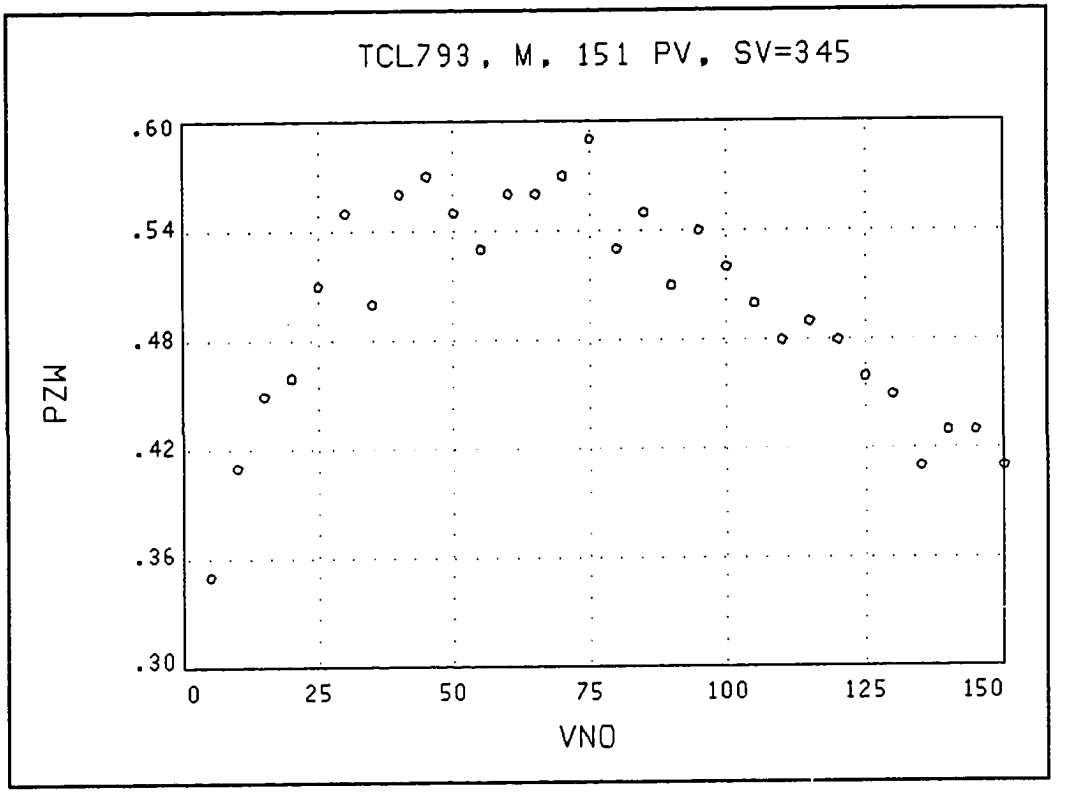
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



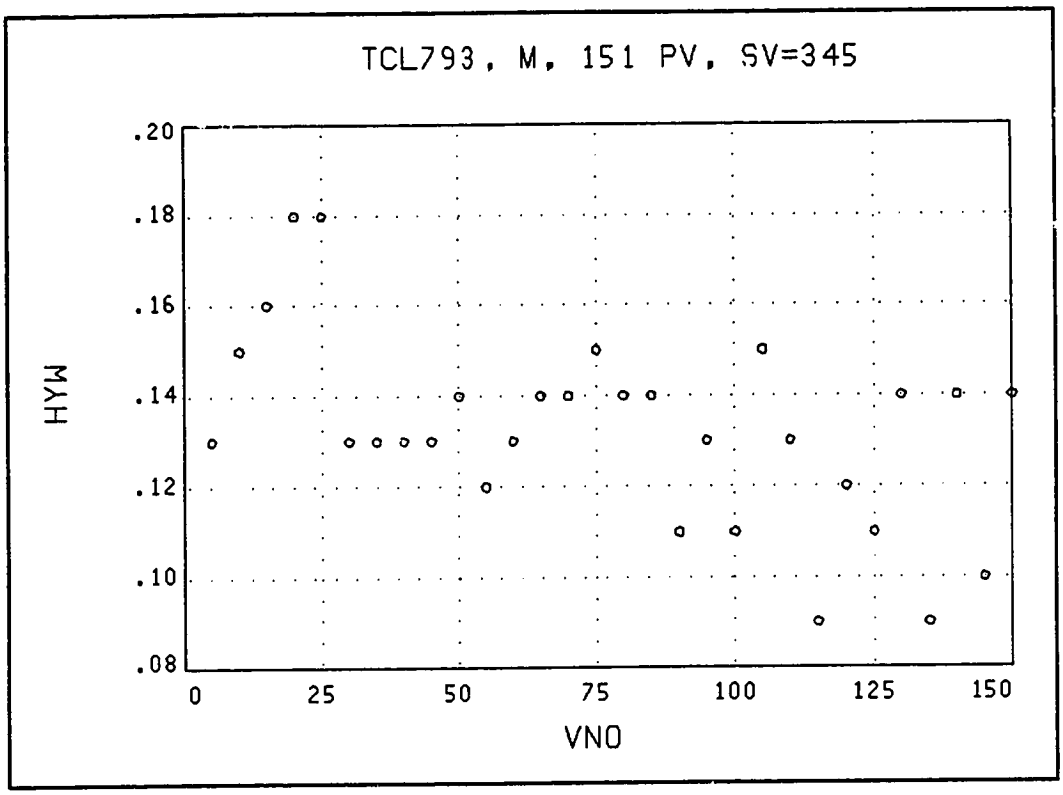


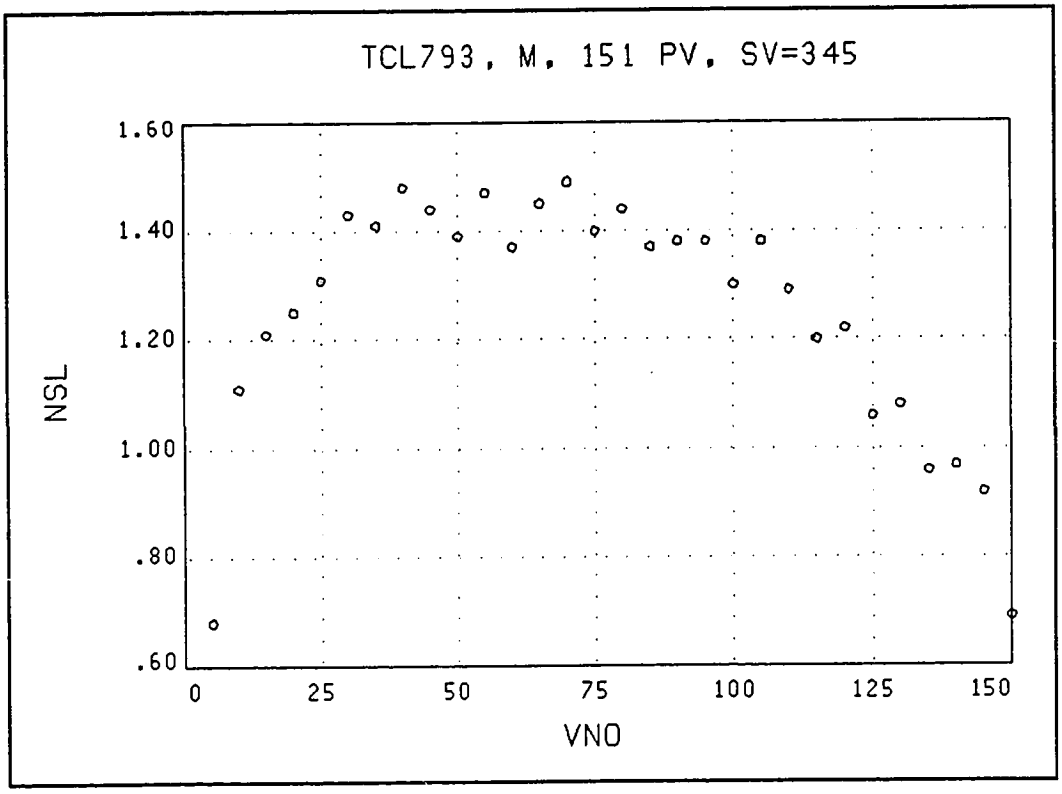
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



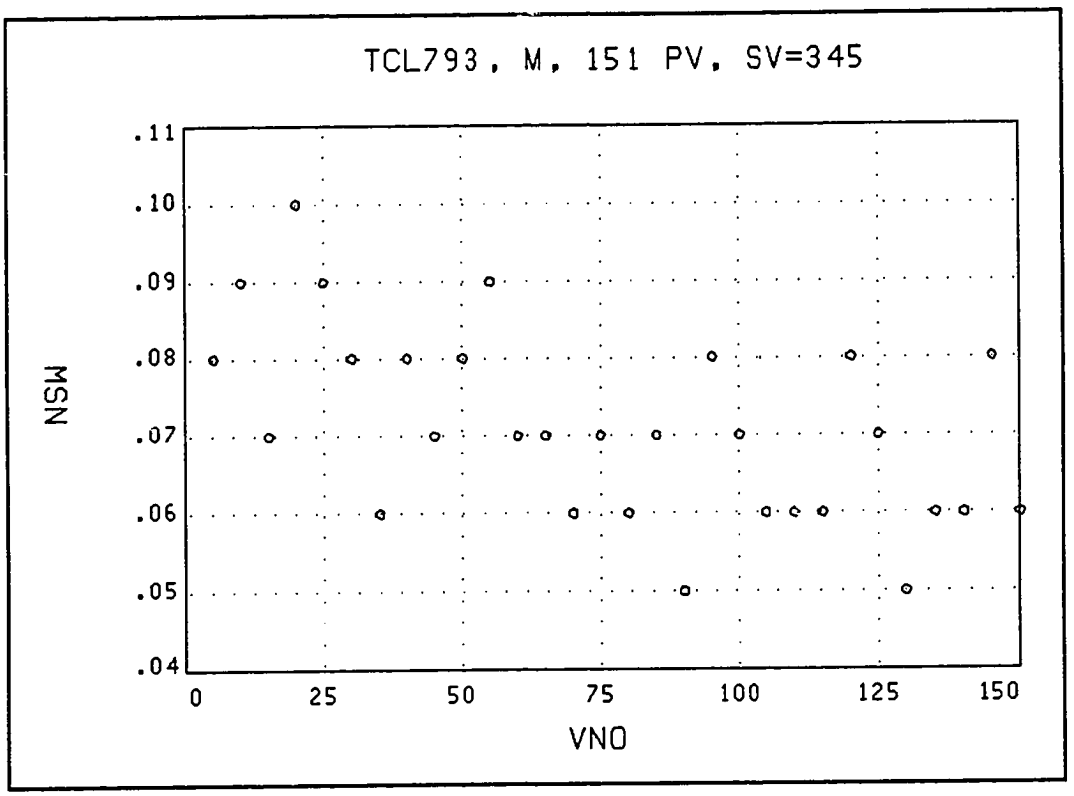


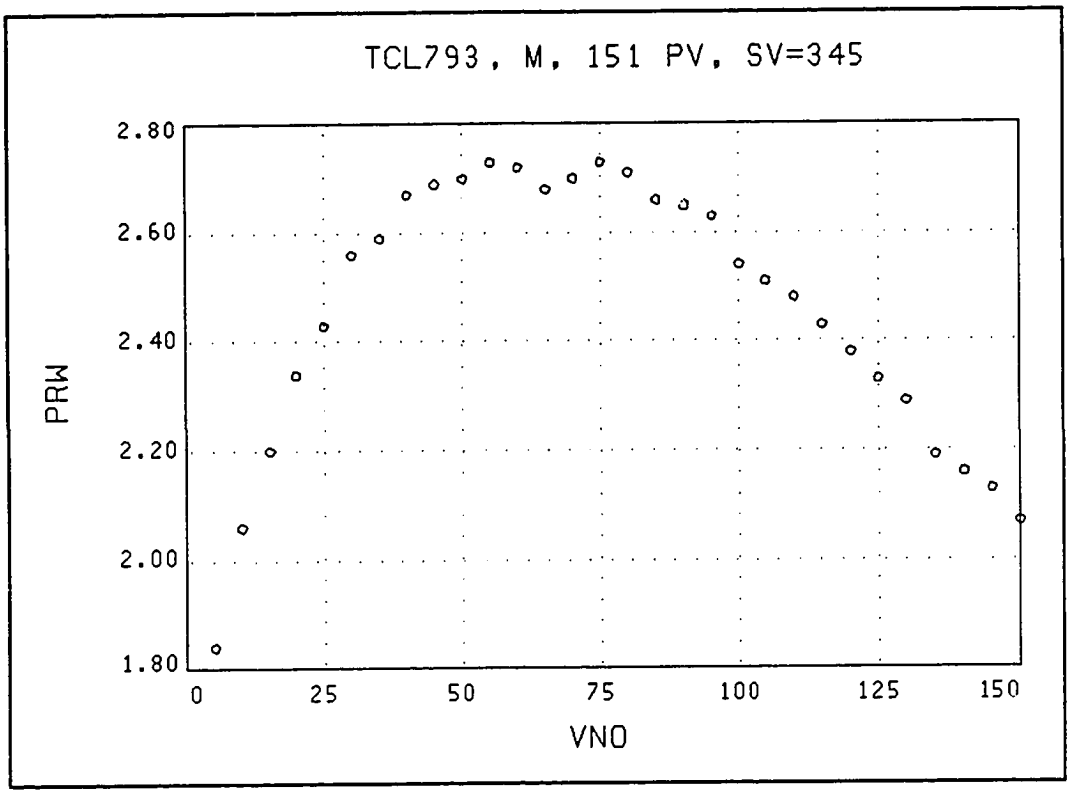
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



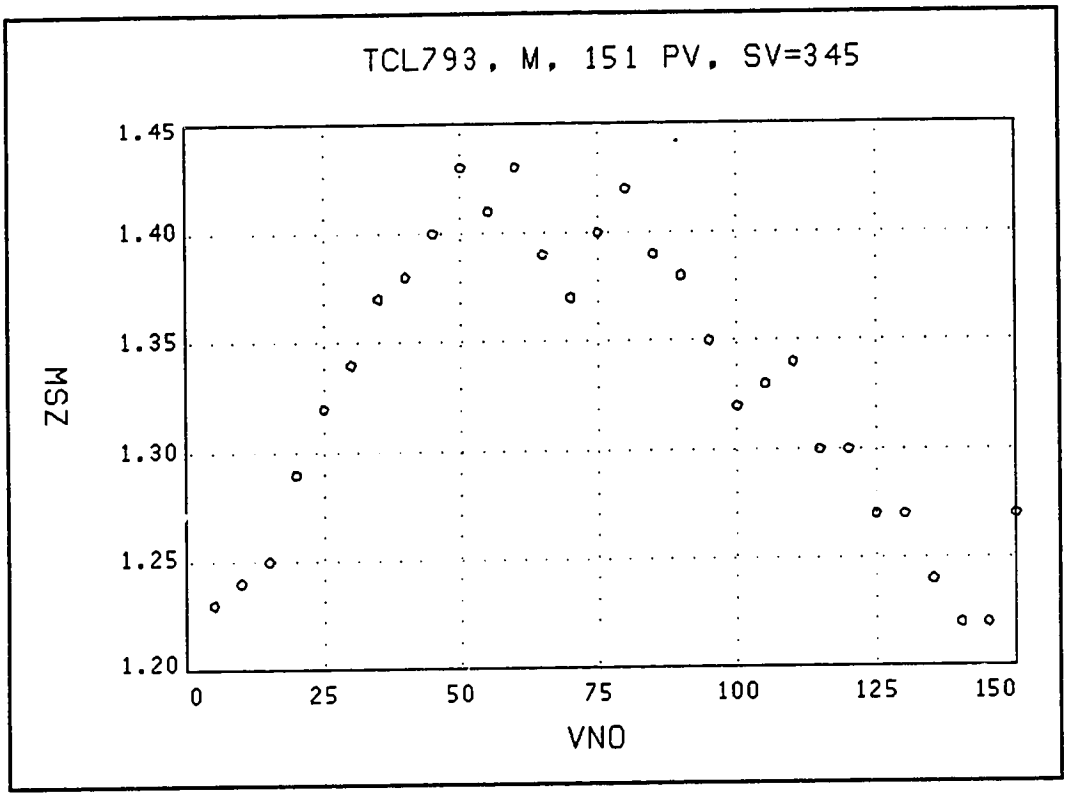


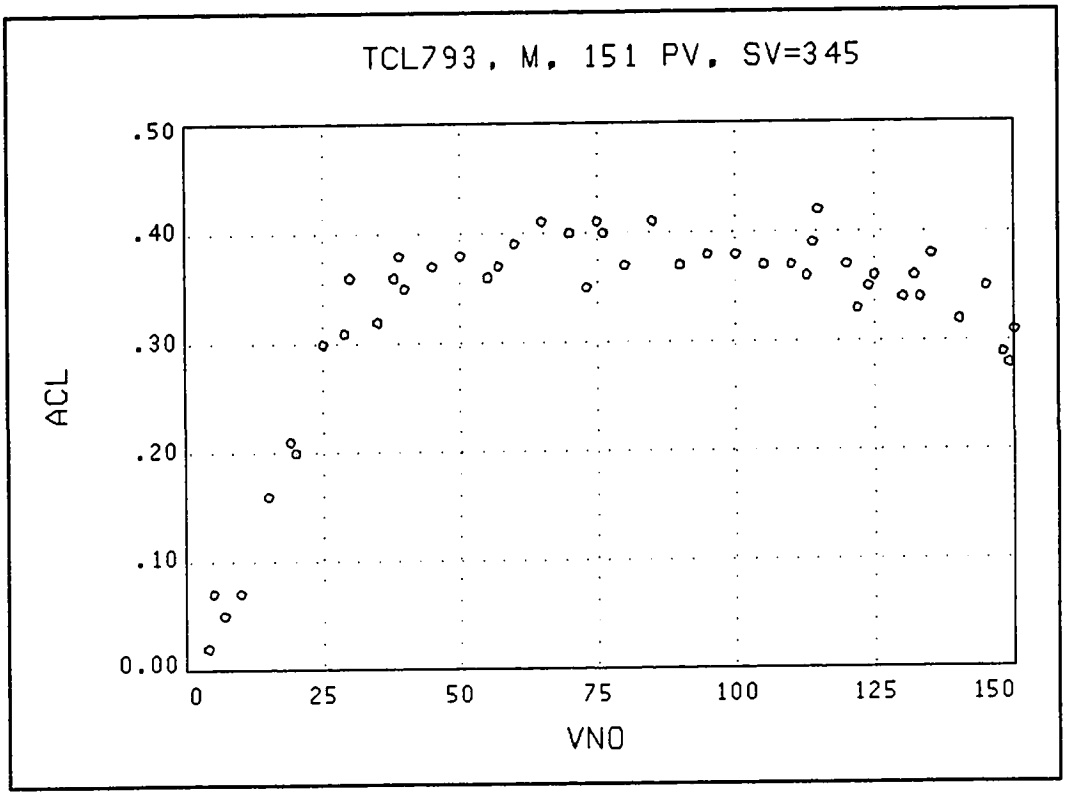
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



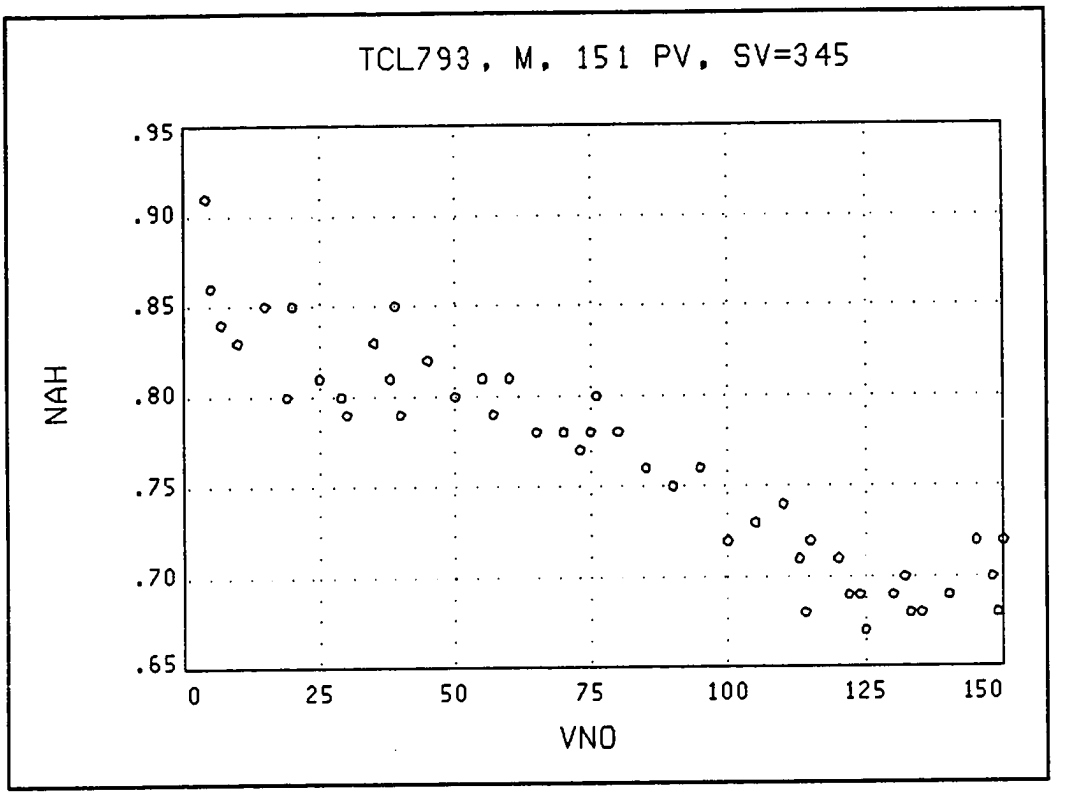


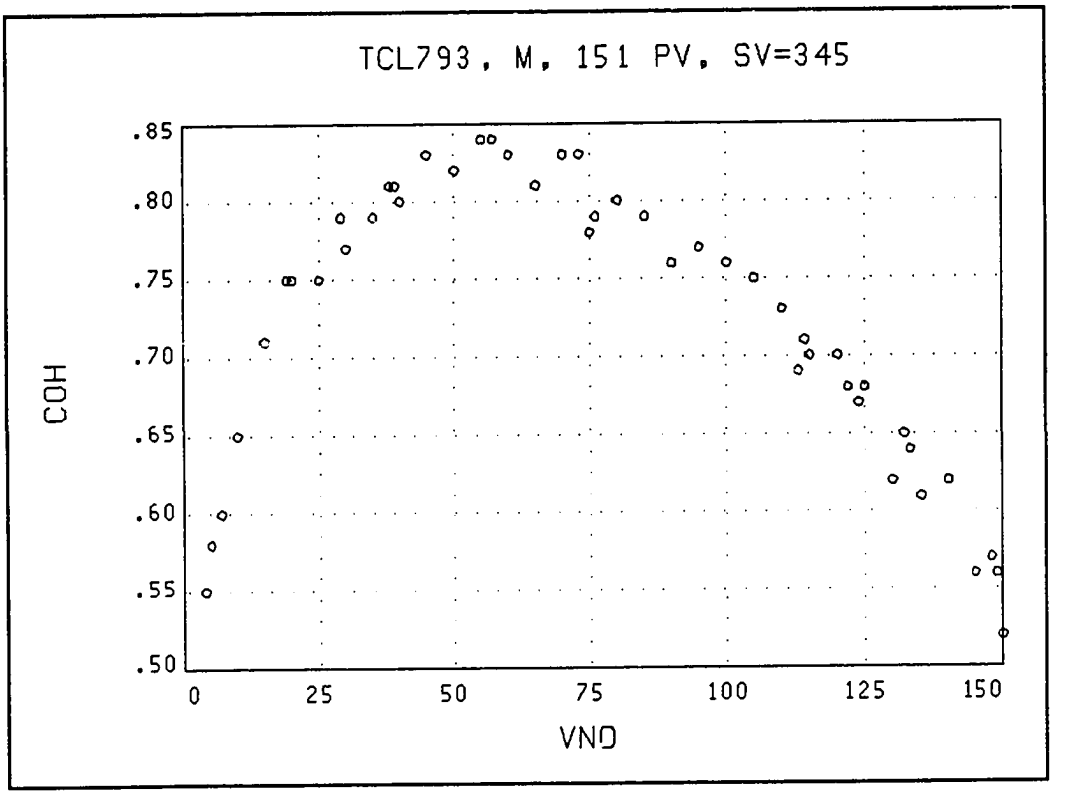
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



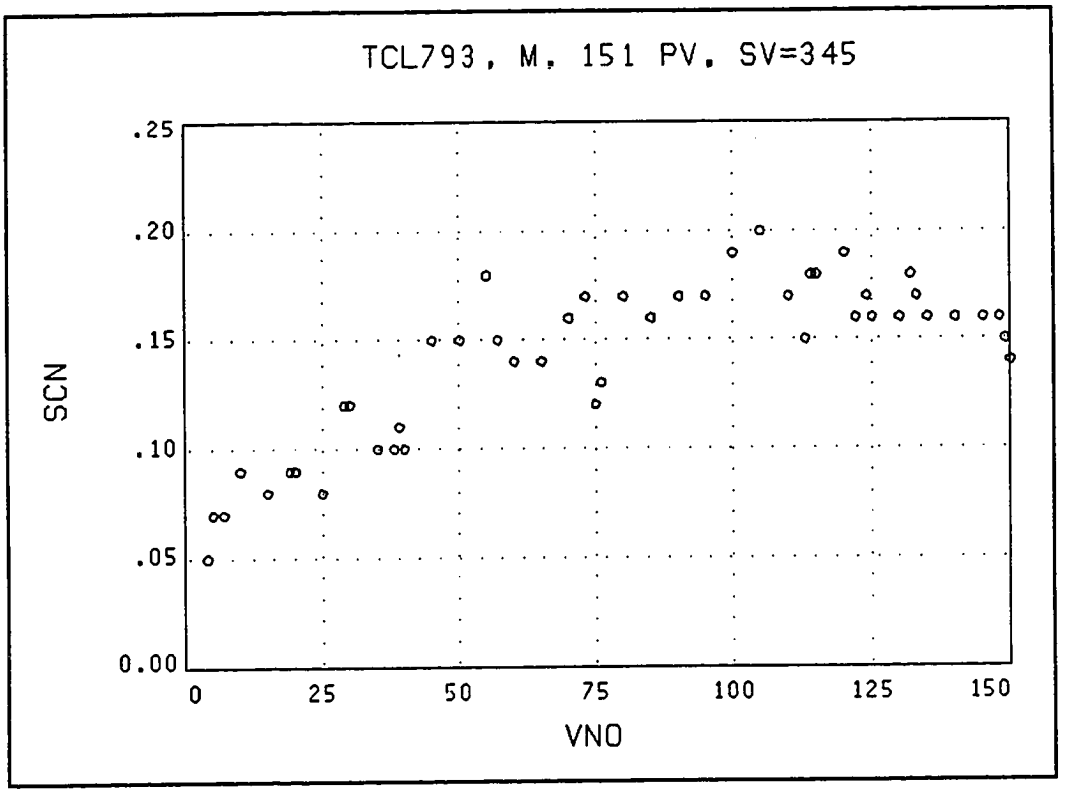


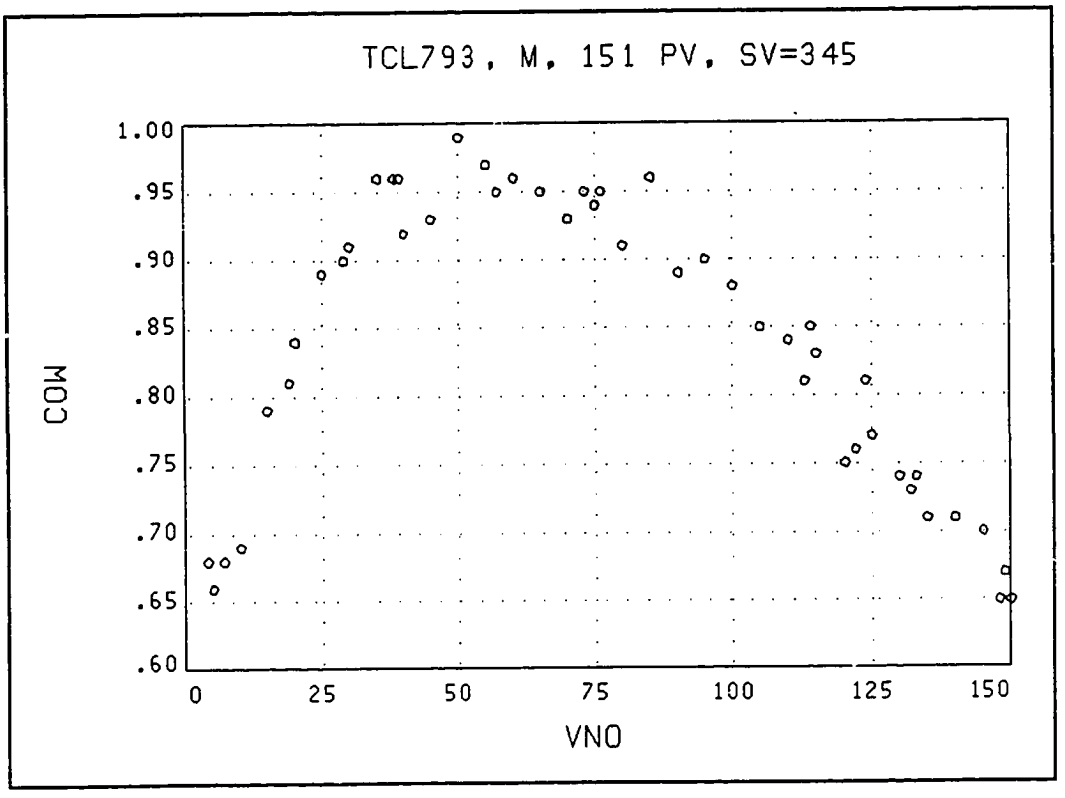
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



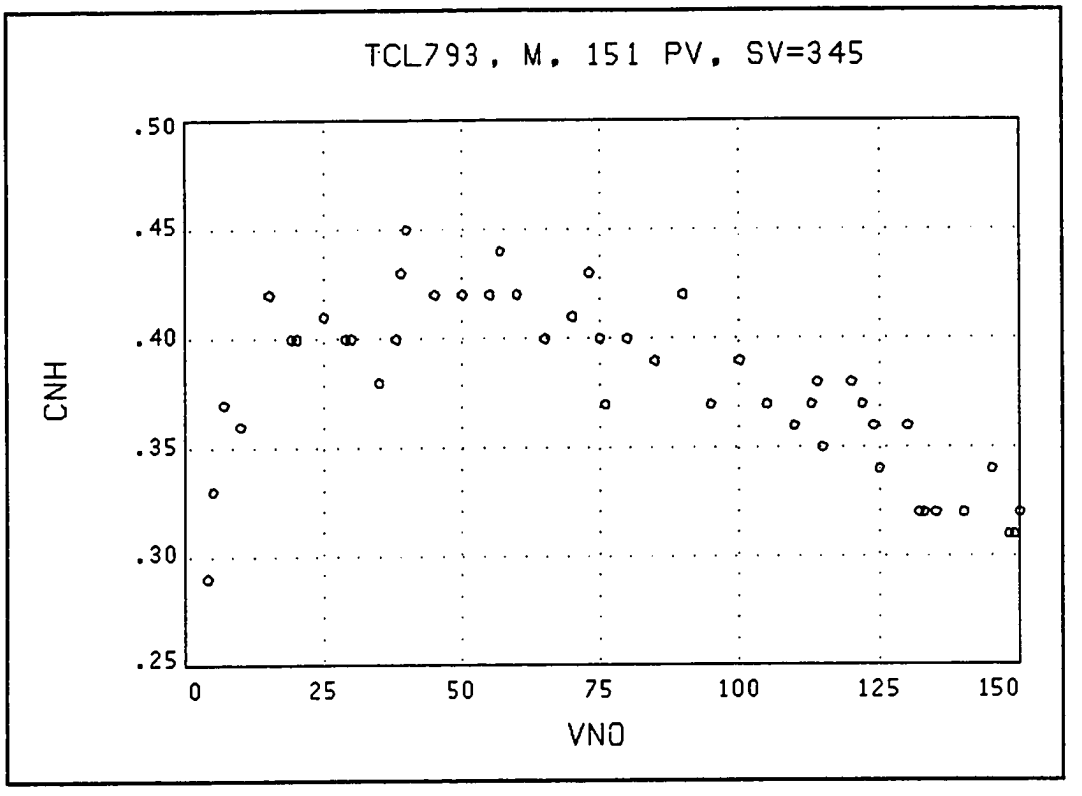


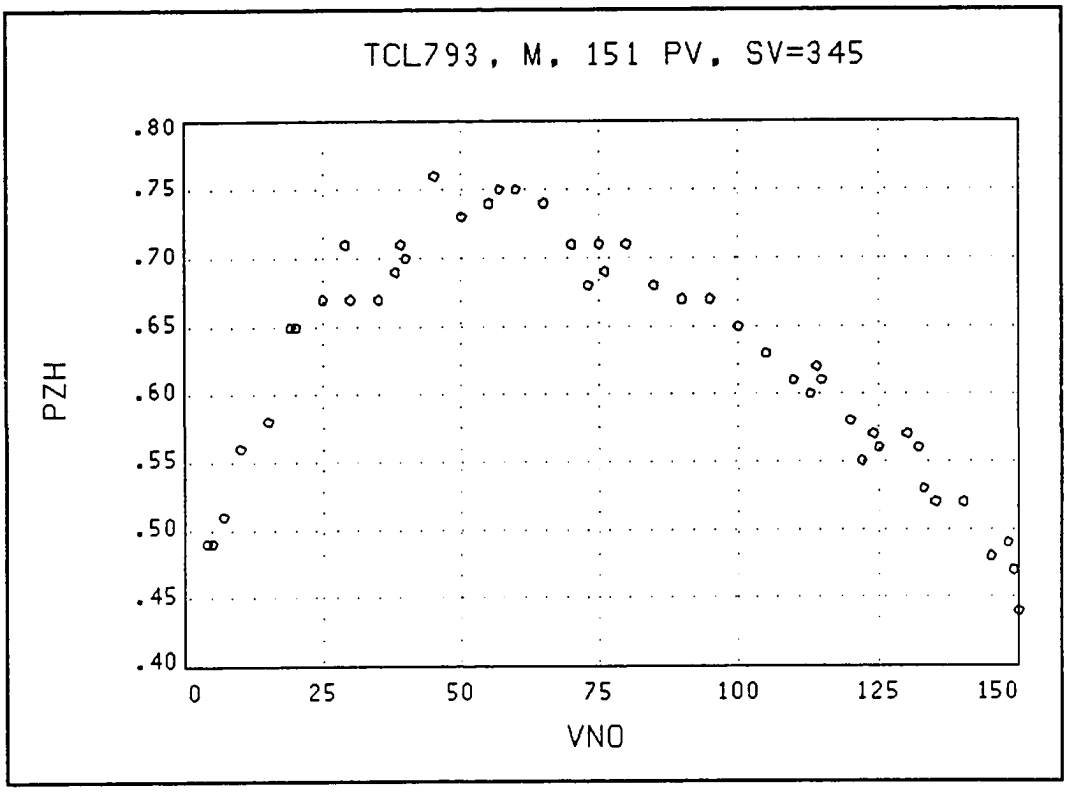
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



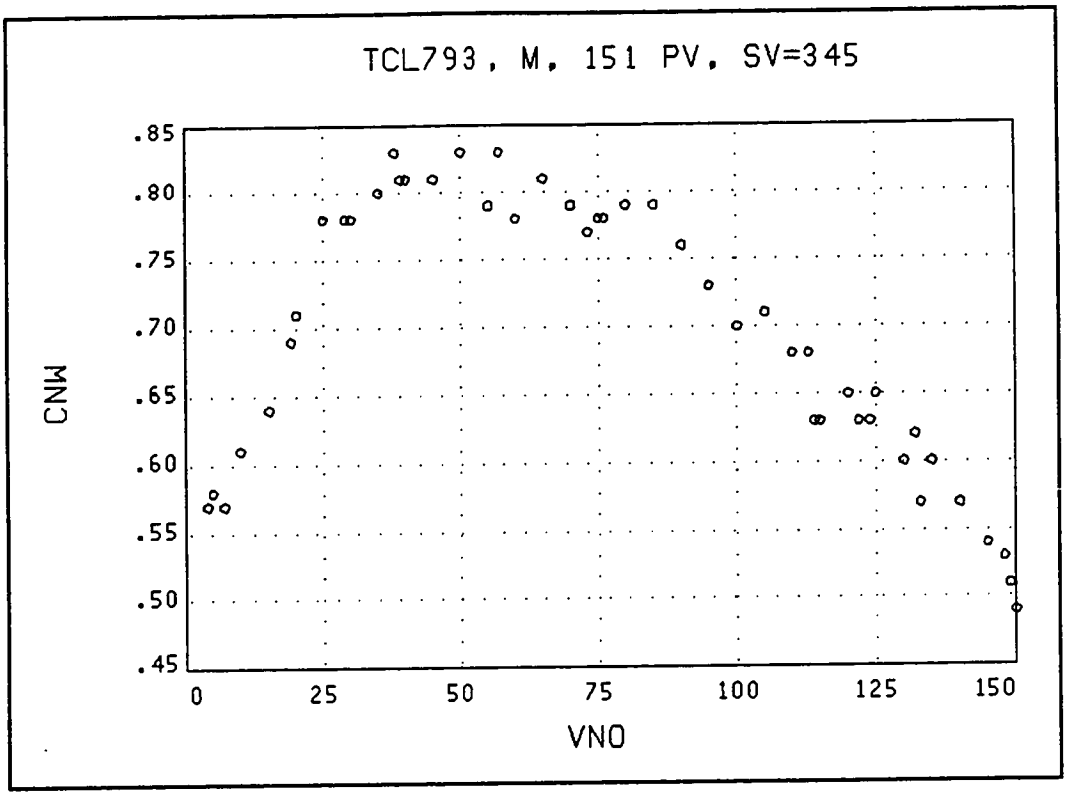


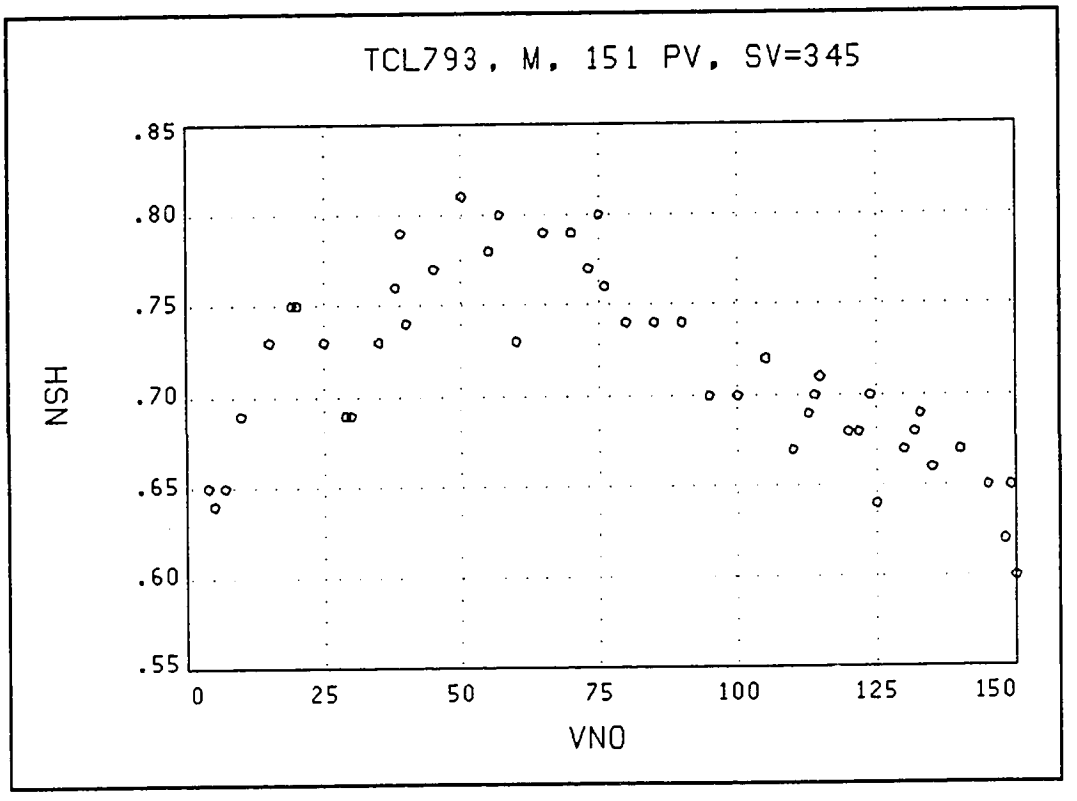
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



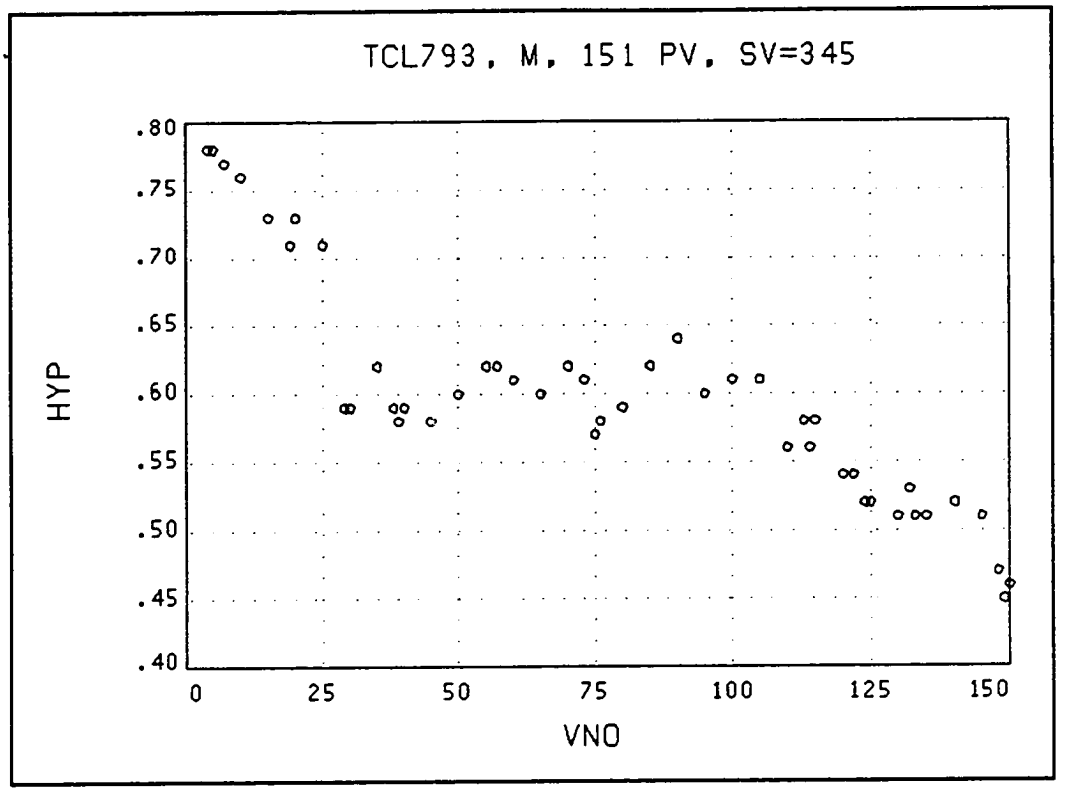


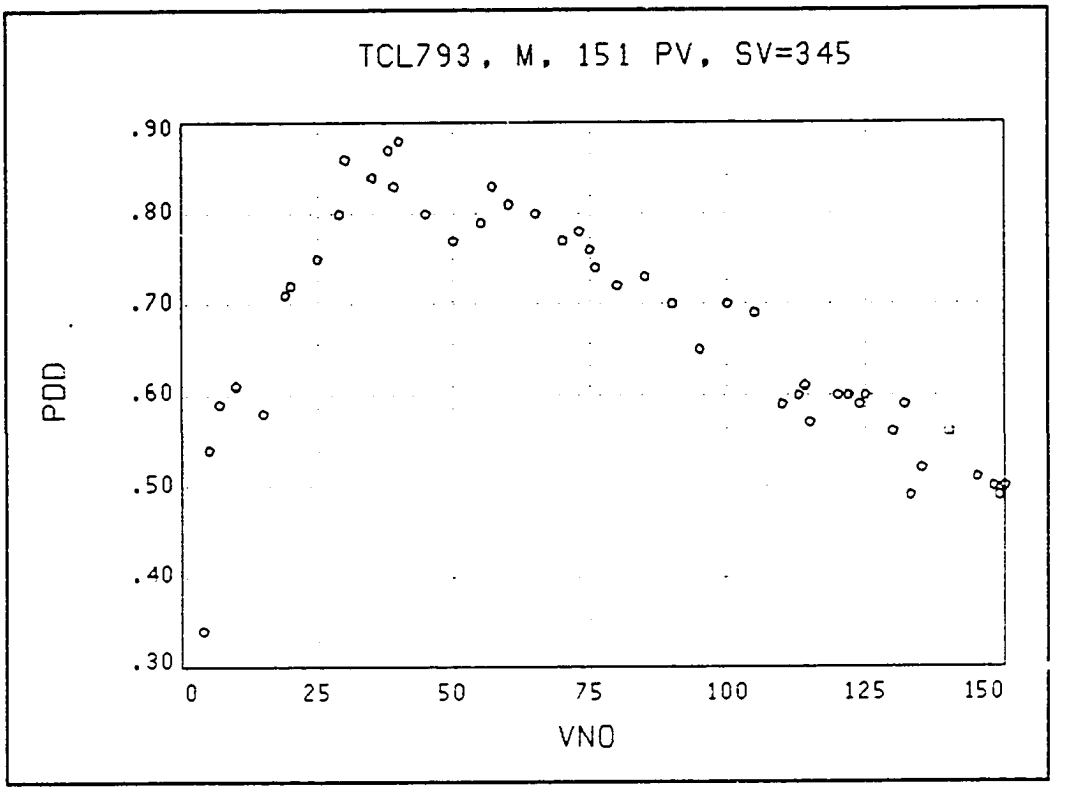
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



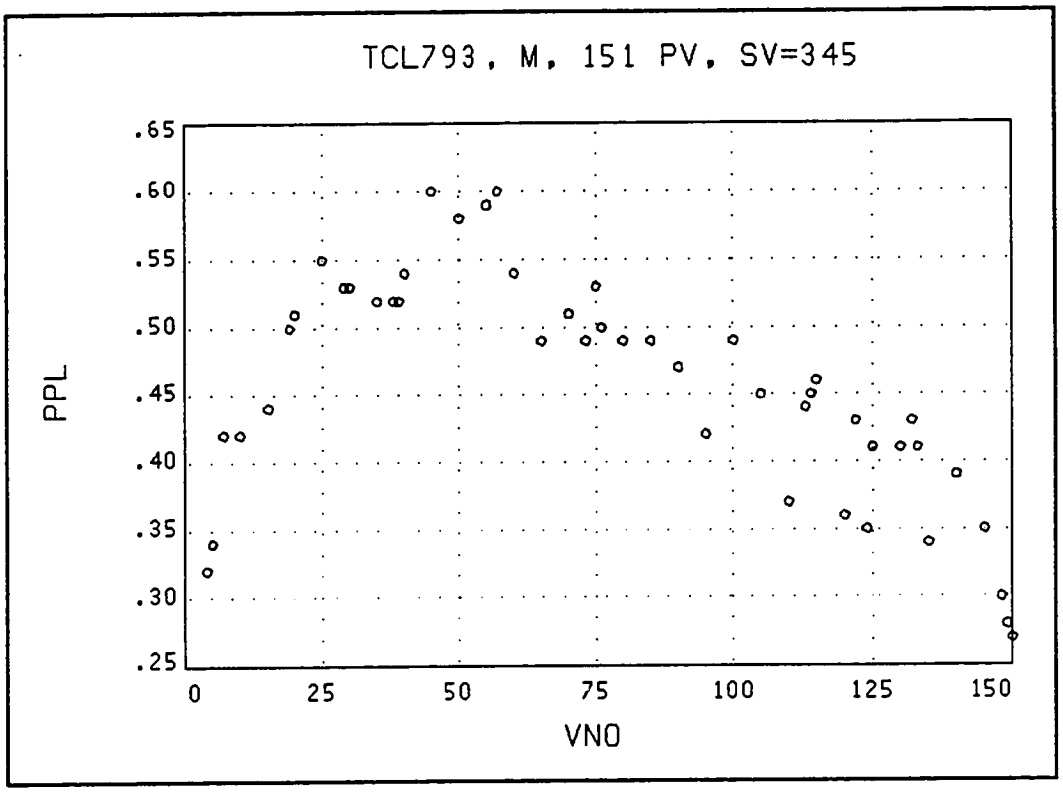


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

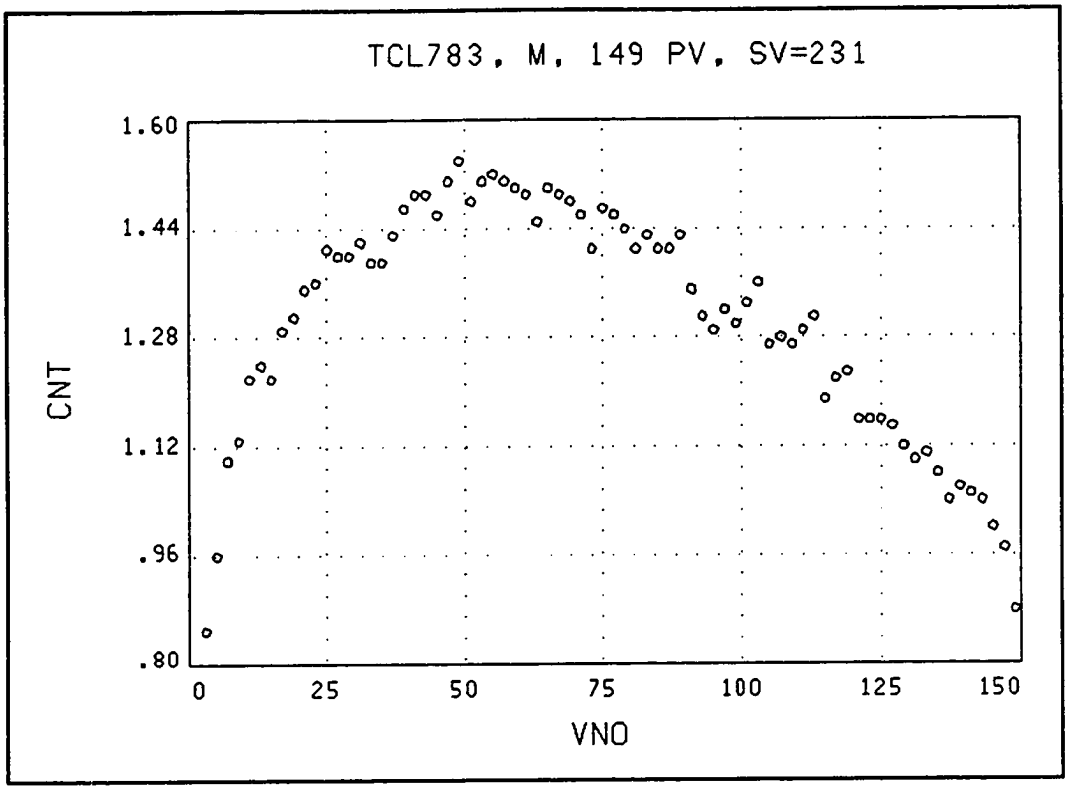


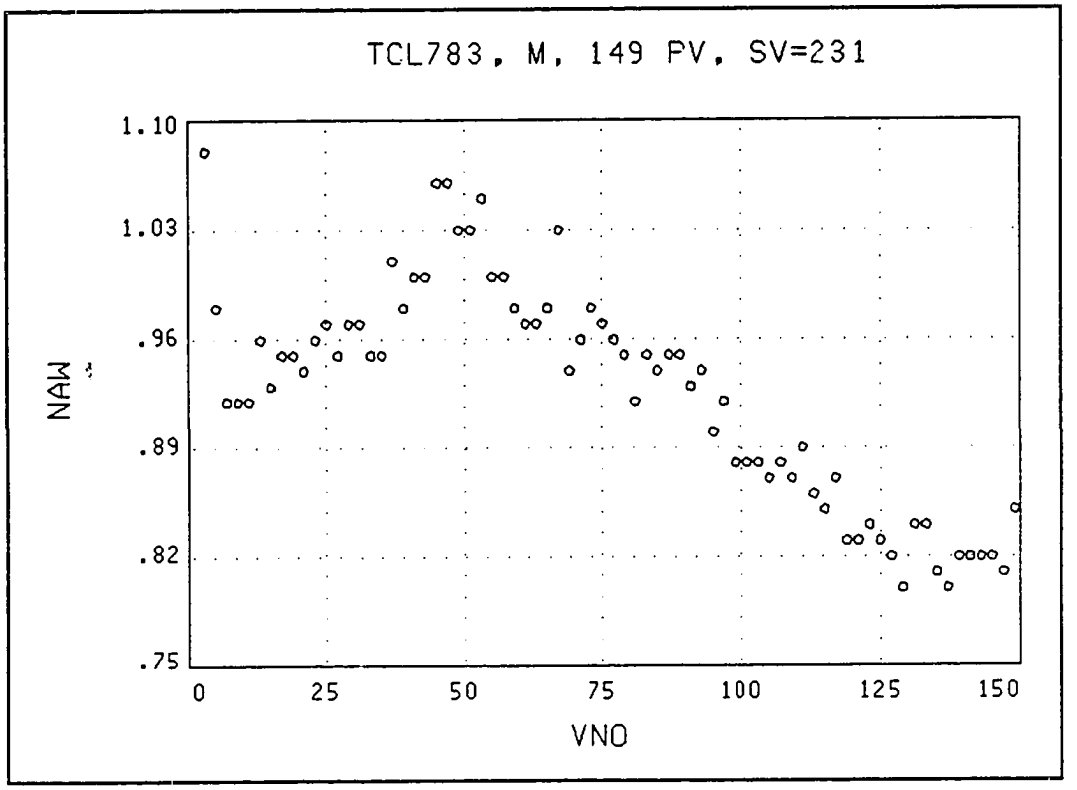


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

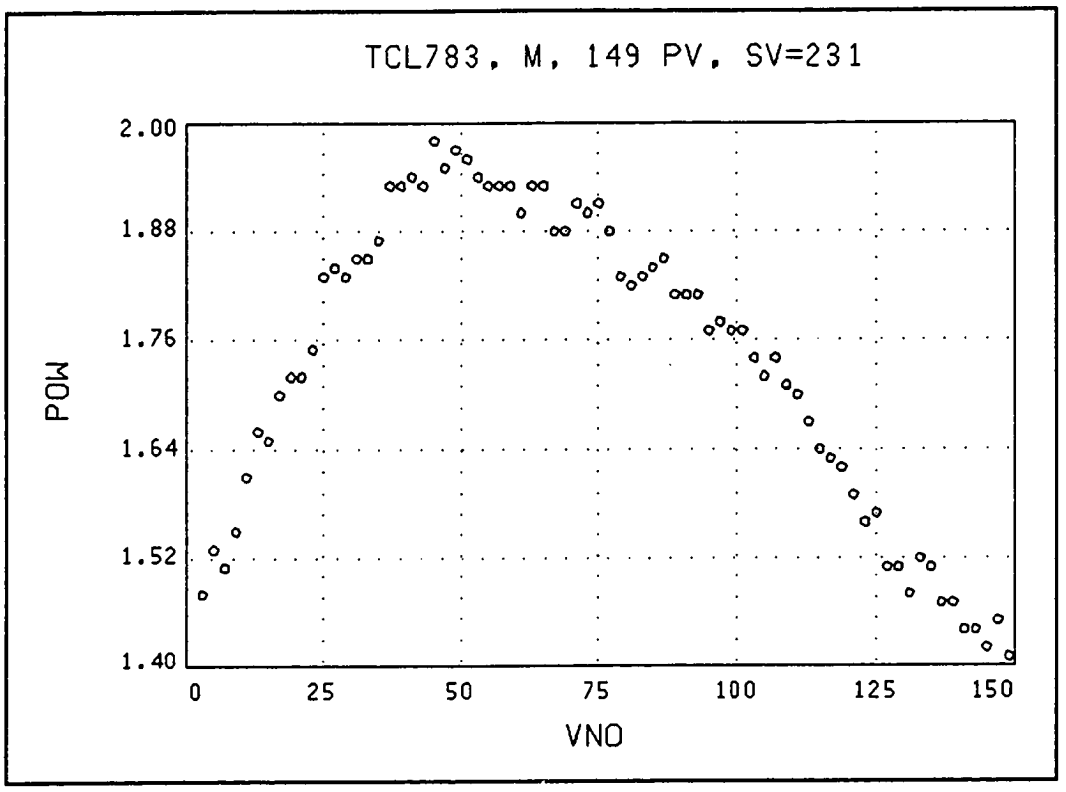


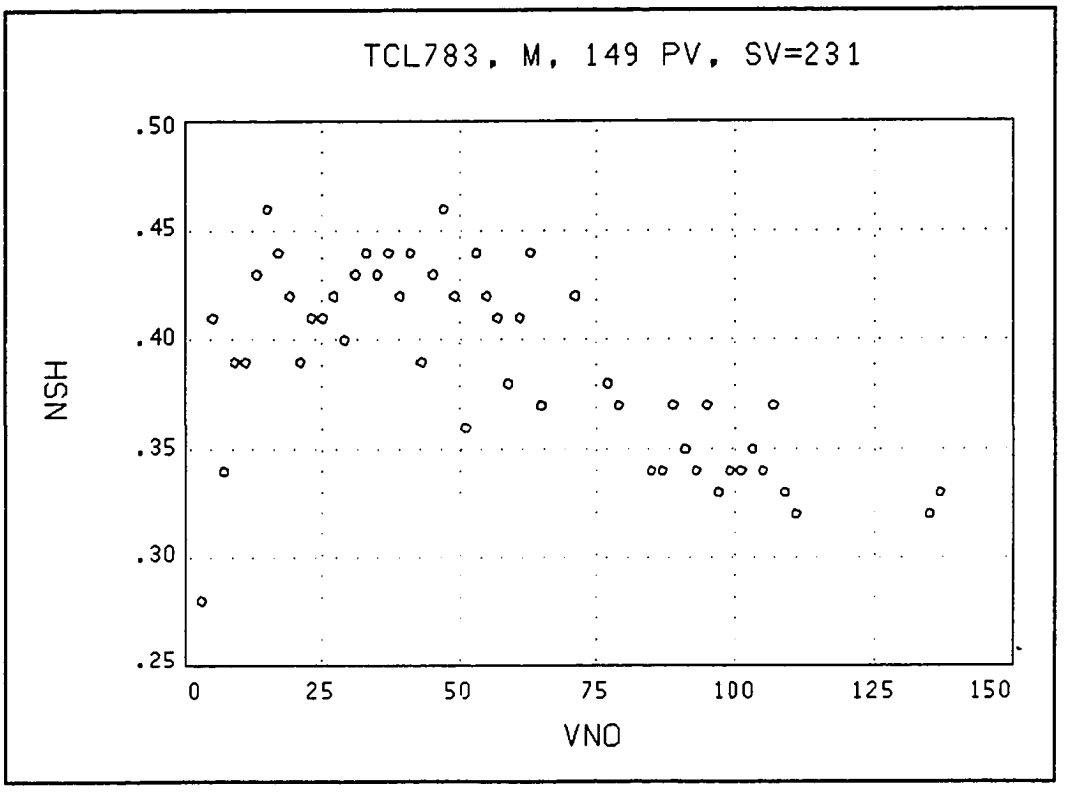
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



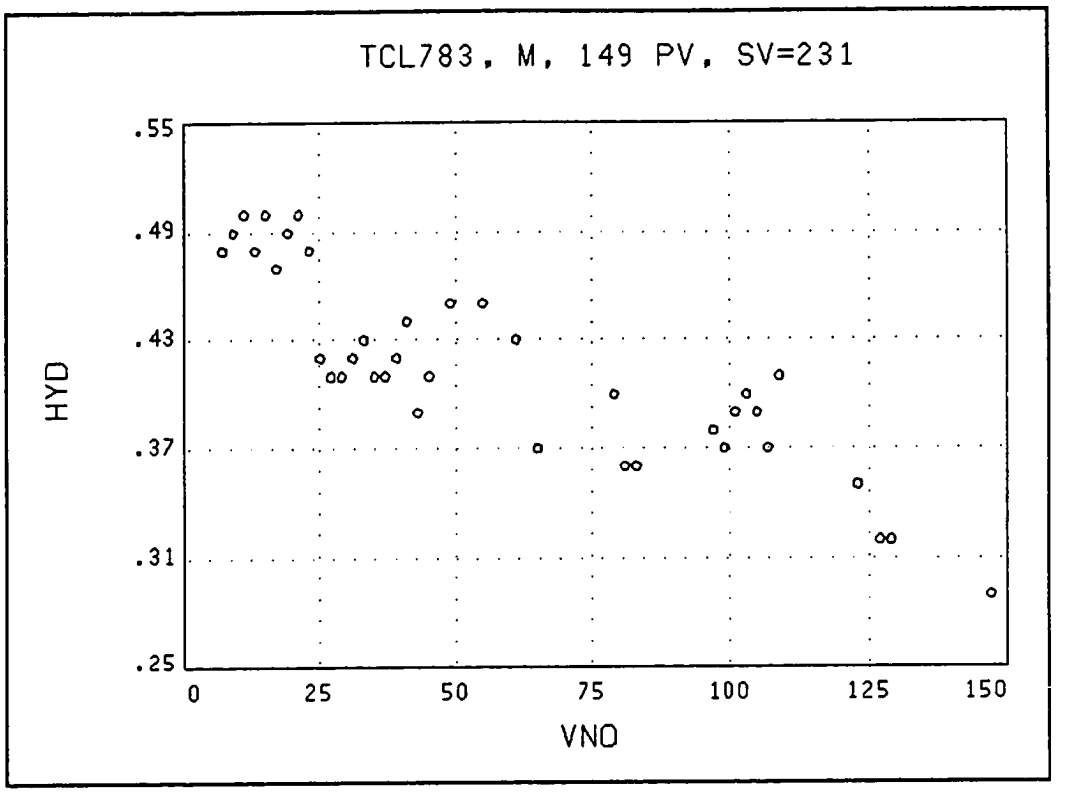


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

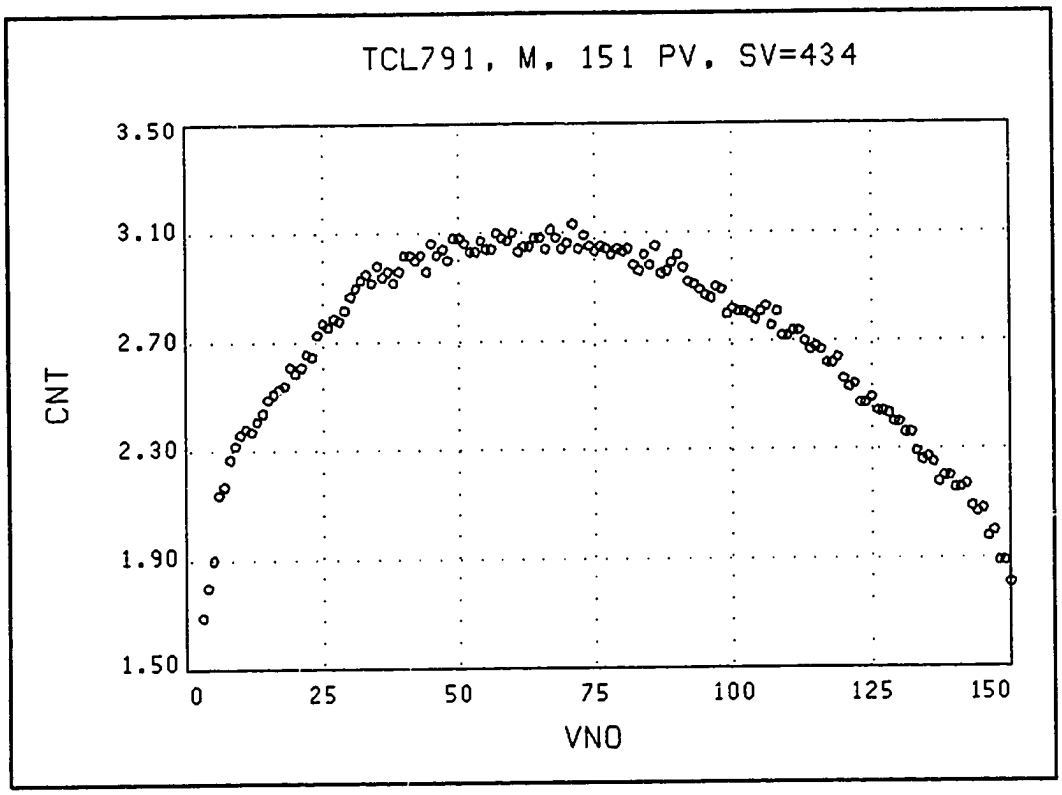


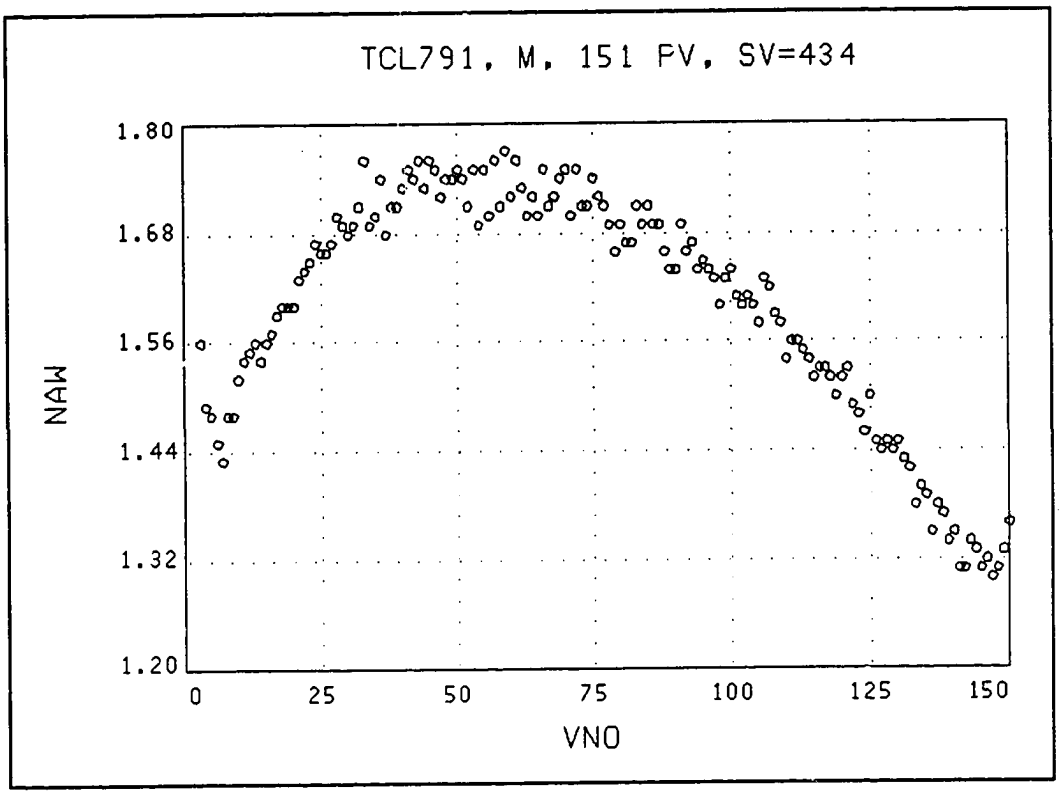


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

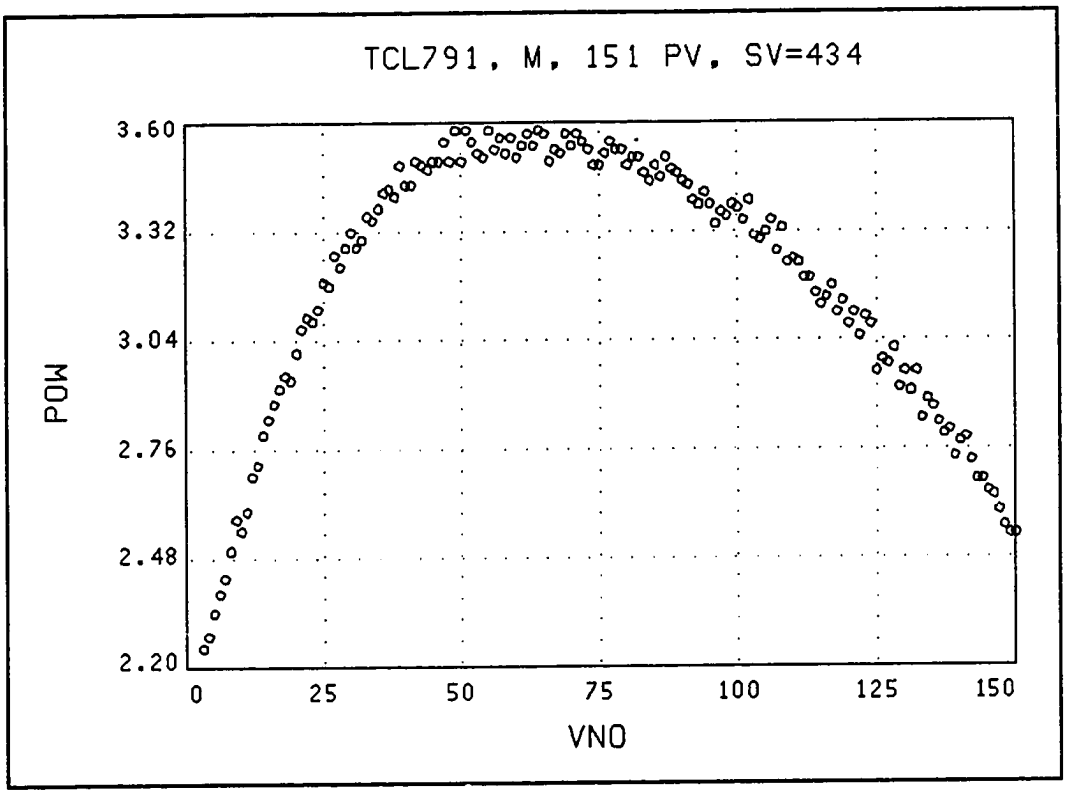


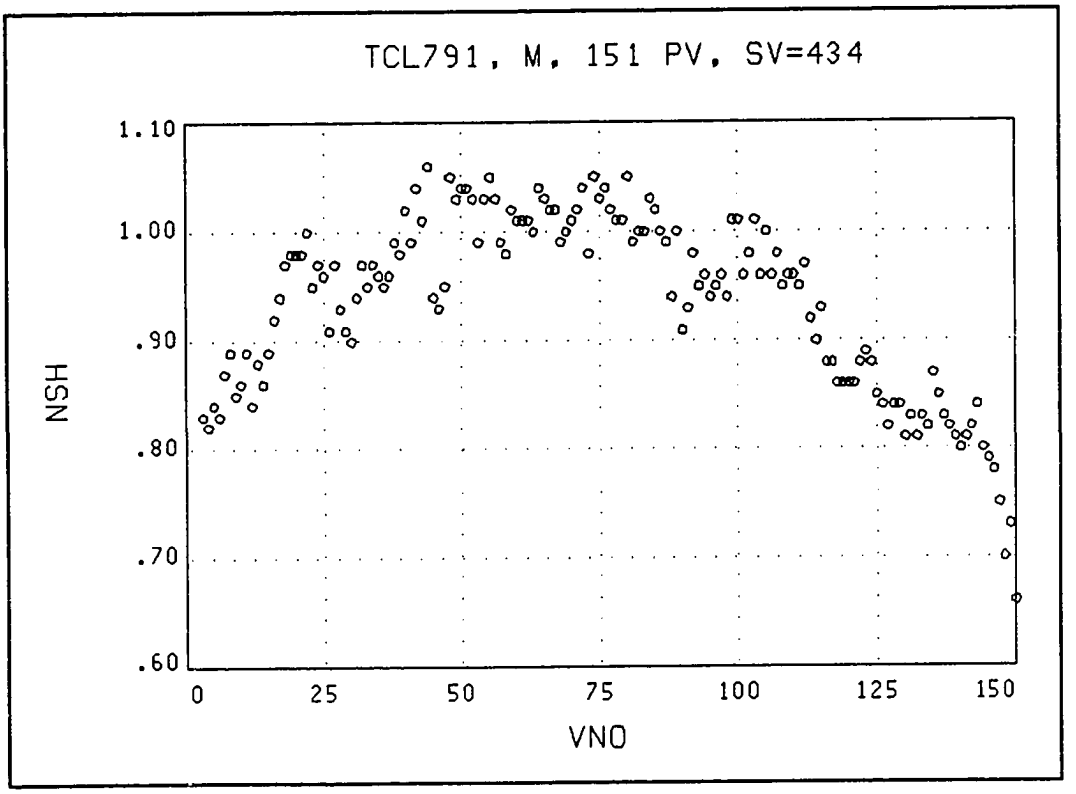
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.





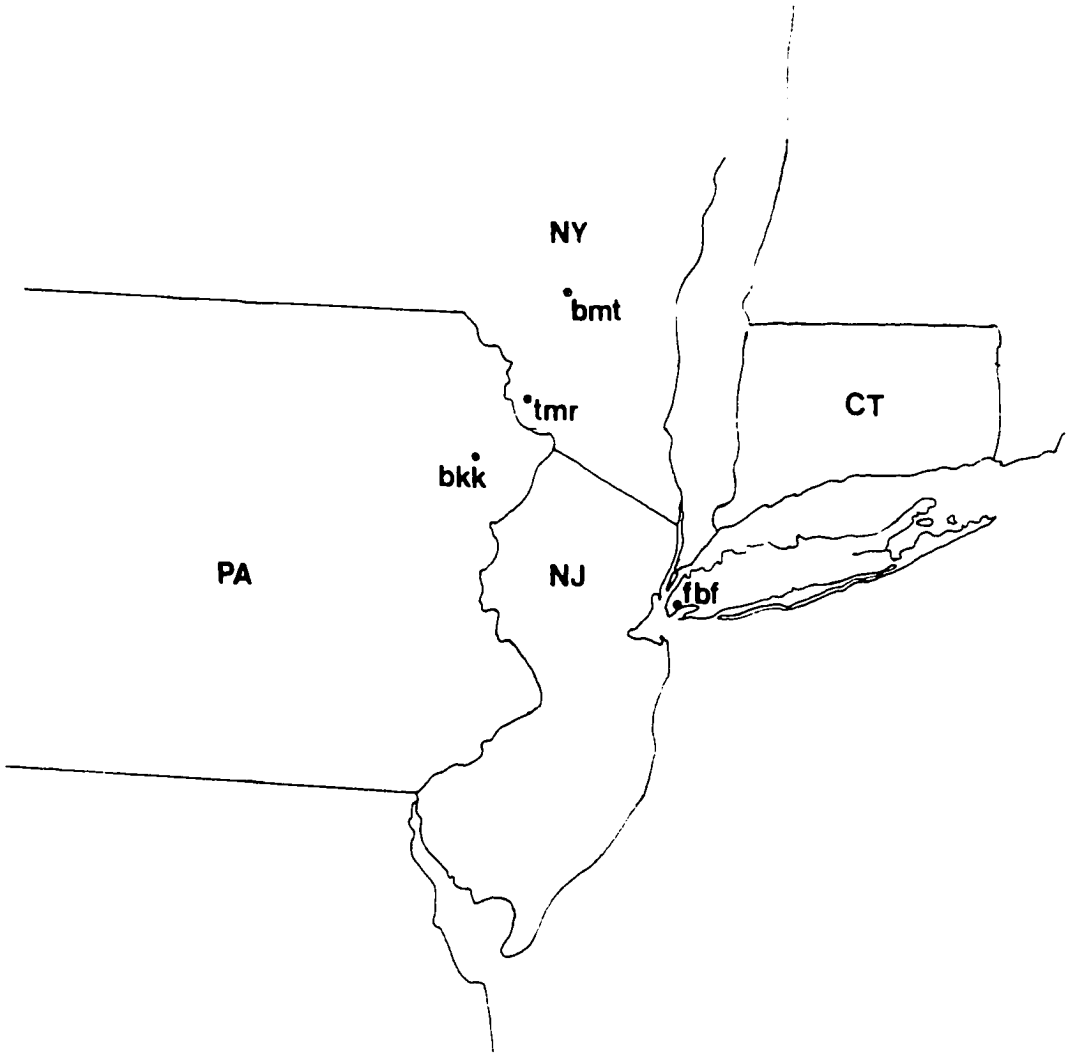
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.





Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX III



Map of major study localities mentioned in text.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Literature Cited

Alexander, A. Allan, and Carl Gans. 1966. The Pattern of Dermal-Vertebral Correlation in Snakes and Amphisbaenians. Zoologische Mededelingen, 41(11):171-190.

Andrews, Robin M., 1982. Patterns of Growth in Reptiles. Chapter 6, Pp. 273-320 in: Biology of the Reptilia, Vol 13, C. Gans and F. H. Pough eds. Academic Press, NY.

Arnold, Stevan J. 1988. Quantitative Genetics and Selection in Natural Populations: Microevolution of Vertebral Numbers in the Garter Snake Thamnophis elegans. Proc. Second Internat. Conf. on Quantitative Genetics. pp. 619-638.

Auffenberg, Walter. 1963. The Fossil Snakes of Florida. Tulane Stud. Zool. 10(3):131-216.

Bogert, Charles M. 1940. Herpetological Results of the Vernay Angola Expedition. Bul Amer. Mus. Nat. Hist. 77(1):1-107.

Bogert, Charles M. 1943. Dentitional Phenomena in Cobras and Other Elapids with Notes on Adaptive Modifications of Fangs. Bul. Amer. Mus. Nat. Hist., 81(3):285-360.

Bogert, Charles M. 1964. Snakes of the Genera Diaphorolepis and Synophis and the Colubrid Subfamily Xenoderminae (Reptilia, Colubridae). Senckenbergiana Biologica 45(3/5):509-531.

Bogert, Charles M. 1968. A New Genus and Species of Dwarf Boa from Southern Mexico. AMNH Novitates 2354:1-38.

Bogert, Charles M. 1968. The Variations and Affinities of the Dwarf Boas of the Genus Ungaliophis. AMNH Novitates 2340. 26 pp.

Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss. 1985. Morphometrics in Evolutionary Biology. Special Pub. 15. Acad. Nat. Sci. Philadelphia. 277 pp.

Brattstrom, Bayard H. 1964. Evolution of the Pit Vipers. Trans. San Diego Soc. Nat. Hist. 13(11):185-268.

Brattstrom, Bayard H. 1967. A Succession of Pliocene and Pleistocene Snake Faunas from the High Plains of the United States. Copeia, 1967(1):188-202.

Brown, William S. and Frances M. MacLean. 1983. Conspecific Scent-trailing by Newborn Timber Rattlesnakes, Crotalus horridus. Herpetologica 39(4):430-436.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Brummer, Barbara. 1980. The Taxonomic Significance of Vertebrae from Recent Colubrid Snake Genera of North America (North of Mexico). Unpub. Ph.D. Dissertation, New York Univ.

Cadle, John E. 1987. Geographic Distribution:Problems in Phylogeny and Zoogeography. In: Seigel, Collins and Novak eds. Snakes: Ecology and Evolutionary Biology, Chapter 3, pp. 77-105. MacMillan, Toronto and London.

Cadle, John E. 1988. Phylogenetic Relationships Among Advanced Snakes: A Molecular Perspective. Univ. Cal. Pub. Zol. 119:1-77.

Cadle, John E. 1989. A New Species of Coniophanes (Serpentes: Colubridae) from Northwestern Peru. Herpetologica 45(4):411-424.

Camp, Charles L. 1923. Classification of the Lizards. Bul. Amer. Mus. Nat. Hist. 48(11):289-481.

Carpenter, Charles C. 1952. Growth and Maturity of the Three Species of Thamnophis in Michigan. Copeia 1952(4):237-243.

Chiasson, Robert B., and Charles H. Lowe. 1989. Ultrastructural Scale Patterns in Nerodia and Thamnophis. J. Herp. 23(2):109-118.

Christman, Steven P. 1975. The Status of the Extinct Rattlesnake, Crotalus giganteus. Copeia 75(1):43-47.

Christman, Steven P. 1980 Patterns of Geographic Variation in Florida Snakes. Bul. Fla. St. Mus. Biol. Sci. 25(3):157-256.

Clark, D. R. Jr. 1974. The Western Ribbon Snake (Thamnophis proximus): Ecology of a Texas Population. Herpetologica 30(4):372-379.

Conant, Roger. 1975. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. The Peterson Field Guide Series. Houghton Mifflin Co., Boston. 429 pp.

Cope, E. D. 1886. An Analytical Table of the Genera of Snakes. Proc. Amer. Philos. Soc. pp.479-499.

Costanzo, Jon P. 1985. The Bioenergetics of Hibernation in the Eastern Garter Snake, Thamnophis sirtalis sirtalis. Physiol. Zool. 58(6):682-692.

Costanzo, Jon P. 1986. Influences of Hibernaculum Microenvironment on the Winter Life History of the Garter Snake (Thamnophis sirtalis). Ohio J. Sci. 86(5):199-204.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Costanzo, Jon P. 1989. Effects of Humidity, Temperature, and Submergence Behavior on Survivorship and Energy Use in Hibernating Garter Snakes, Thamnophis sirtalis. Can. J. Zool. 67:2486-2492.

Dessem, D. A., and J. L. Younker. Analysis of Snake Vertebral Shape by Fourier Analysis. undated M.S. 16 pp. + 5 figures.

Dowling, Herndon G. 1951. A Proposed Standard System of Counting Ventrals in Snakes. Brit. J. Herpetol. 1:97-99.

Dowling, Herndon G. 1958. A Taxonomic Study of the Ratsnakes VI. Validation of the Genera Gonyosoma Wagler and Elaphe Fitzinger. Copeia 1958(1):29-40.

Dowling, Herndon G. 1988. Prodromus of a New Classification of the Serpentes. MS.

Enlow, Donald H. 1969. The Bone of Reptiles. Ch. 2, pp. 45-80, in: Biology of the Reptilia, Vol. 1. C. Gans, A. d'A. Bellairs, and T. S. Parsons eds., Academic Press Inc., London.

Ernst, Carl H. and Roger W. Barbour. 1989. Snakes of Eastern North America. George Mason University Press. Fairfax, Virginia. 282 pp.

Fay, Leslie P. 1988. Late Wisconsinan Appalachian Herpetofaunas: Relative Stability in the Midst of Change. Annals of Carnegie Museum 57(9):189-220.

Fitch, Henry S. 1941. Geographic Variation in Garter Snakes of the Species Thamnophis sirtalis in the Pacific Coast Region of North America. Amer. Midland Nat. 26(3):570-592.

Fitch, Henry S. 1960. Autecology of the Copperhead. Univ. Kansas Publ. Mus. Nat. Hist. 13(4):85-288.

Fitch, Henry S. 1963. Natural History of the Black Rat Snake (Elaphe o. obsoleta) in Kansas. Copeia 1963(4):649-658.

Fitch, Henry S. 1965. An Ecological Study of the Garter Snake, Thamnophis sirtalis. Univ. Kansas Publ. Mus. Nat. Hist. 15(10):493-564.

Fitch, Henry S. 1975. A Demographic Study of the Ringneck Snake (Diadophis punctatus) in Kansas. Univ. Kansas Mus. Nat. Hist. Publ. 62. 53 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Fitch, Henry S. 1980. Thamnophis sirtalis (Linnaeus). Common Garter Snake. Cat. Amer. Amph. Rept. 270:1-4.

Fox, Wade. 1948. Effect of Temperature on Development of Scutellation in the Garter Snake, Thamnophis elegans atratus. Copeia 1948(4):252-262.

Gans, Carl. 1974. Biomechanics. Ann Arbor. Univ. Michigan Press. 261 pp.

Gasc, Jean-Pierre. 1976. Snake Vertebrae - A Mechanism or Merely a Taxonomists Toy? pp. 177-190, in: Morphology and Biology of the Reptiles. Linnean Soc. Symp. Series #3. Academic Press.

Gilmore, Charles W. 1938. Fossil Snakes of North America. Geol. Soc. North America. Spec. Papers 9. 96 pp.

Gregory, Patrick T., Malcolm J. Macartney, and Karl W. Larsen. 1987. Spatial Patterns and Movements. Ch. 12, pp. 366-395, in: Snakes, Ecology and Evolutionary Biology. R. A. Seigel, J. T. Collins, and S. S. Novak eds. MacMillan Publishing, New York.

Grobman, Arnold B. 1984. Scutellation Variation in Opheodrys aestivus. Bul. Fla. St. Mus. Biol. Sci. 29(3):153-176.

Hibbard, Claude W. 1949. Techniques of Collecting Microvertebrate Fossils. Contrib. Mus. Paleont. Univ. Mich. 8:7-19.

Hill, William H. 1971. Pleistocene Snakes from a Cave in Kendall County, Texas. Texas J. Sci. 22(2 and 3):209-216.

Hoffstetter, Robert. 1946. Remarques sur la Classification des Ophidiens et particulierement des Boidae des Mascareignes (Bolyerinae Subfam. Nov.). Bul. du Mus Nat d'Hist. Nat. 2nd ser. 18(1):132-135.

Hoffstetter, Robert. 1960. Sur la Classification Des Boides de Madagascar et des Mascareignes. Bul. Mus. Nat. D'Histoire Nat., 2 437e:131-138.

Hoffstetter, Robert, and Jean-Pierre Gasc. 1969. Vertebrae and Ribs of Modern Reptiles. Ch. 5, pp. 201-310, in: Biology of the Reptilia, Vol. 1. C. Gans, A. d'A. Bellairs, and T. S. Parsons, eds., Academic Press Inc., London.

Hoffstetter, Robert, and Yvette Gayrard. 1965. Observations sur l'Osteologie et la Classification des Acrochordidae (Serpentes). Bul. Mus. Nat. D'Histoire Nat., 2e Ser. T36 N5:677-696.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Holman, J. Alan. 1958. The Pleistocene Herpetofauna of Saber-tooth Cave, Citrus Co. Florida. Copeia 1958(4):276-280.

Holman, J. Alan. 1959. Amphibians and Reptiles from the Pleistocene (Illinoian) of Williston, Florida. Copeia 1959(2):96-102.

Holman, J. Alan. 1962. A Texas Pleistocene Herpetofauna. Copeia 1962(2):255-261.

Holman, J. Alan. 1963. Late Pleisticene Amphibians and Reptiles of the Clear Creek and Ben Franklin Local Faunas of Texas. J. Grad. Research Ctr. 31(3):152-167.

Holman, J. Alan. 1964a. Pleisticene Amphibians and Reptiles from Texas. Herpetologica 20(2):73-83.

Holman, J. Alan. 1964b. Fossil Snakes from the Valentine Formation of Nebraska. Copeia 1964(4):631-637.

Holman, J. Alan. 1965. Pleisticene Snakes from the Seymore Formation of Texas. Copeia 1965(1):102-104.

Holman, J. Alan. 1965. A Late Pleistocene Herpetofauna from Missouri. Trans. Illinois Acad. Sci. 58(3):190-194.

Holman, J. Alan. 1966. The Pleistocene Herpetofauna of Miller's Cave, Texas. Texas J. Sci. 18(4):372-377.

Holman, J. Alan. 1967. A Pleistocene Herpetofauna from Ladd's, Georgia. Bul. Georgia Acad. Sci. 25(3):154-166.

Holman, J. Alan. 1968. Upper Pliocene Snakes from Idaho. Copeia, 1968(1):152-158.

Holman, J. Alan. 1970a. Herpetofauna of the Wood Mountain Formation (Upper Miocene) of Saskatchewan. Canadian J. Earth Sci. 7(5):1317-1325.

Holman, J. Alan. 1970b. A Pleistocene Herpetofauna from Eddy County, New Mexico. Texas J. Sci. 22(1):29-39.

Holman, J. Alan. 1971. Herpetofauna of the Sandahl Local Fauna (Pleistocene: Illinoian) of Kansas. Contrib. Museum Paleo., Univ. Michigan 23(22):349-355.

Holman, J. Alan. 1972. Herpetofauna of the Calf Creek Local Fauna (Lower Oligocene: Cypress Hills Formation) of Saskatchewan. Canadian J. Earth Sci. 9(12):1612-1631.

Holman, J. Alan. 1973. A New Pliocene Snake, Genus Elaphe, from Oklahoma. Copeia 1973(3):574-580.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Holman, J. Alan. 1975. Herpetofauna of the Wakeeney Local Fauna (Lower Pliocene: Clarendonian) of Trego County, Kansas. Pp. 49-66 in: Studies on Cenozoic Paleontology and Stratigraphy. Claude W. Hibbard Memorial Volume 3. Papers on Paleontology No. 12. Museum of Paleontology, Univ. Michigan, Ann Arbor.

Holman, J. Alan. 1976a. Snakes from the Rosebud Formation (Middle Miocene) of South Dakota. Herpetologica 32(1):41-48.

Holman, J. Alan. 1976b. Snakes of the Gering Formation (Lower Miocene) of Nebraska. Herpetologica 32(1):88-94.

Holman, J. Alan. 1977a. Additional Snakes from the Miocene of Western Nebraska. Herpetologica 33(4):443-446.

Holman, J. Alan. 1977b. Amphibians and Reptiles from the Gulf Coast Miocene of Texas. Herpetologica 33(4):391-403.

Holman, J. Alan. 1977c. Upper Miocene Snakes (Reptilia, Serpentes) from Southeastern Nebraska. J. Herpetol. 11(3):323-335.

Holman, J. Alan. 1977d. Snakes of the Monroe Creek Formation (Lower Miocene: Arikareean) of Wyoming. Copeia, 1977(1):193-194.

Holman, J. Alan. 1977e. Upper Eocene Snakes (Reptilia, Serpentes) from Georgia. J. Herpetol. 11(2):141-145.

Holman, J. Alan. 1978. Herpetofauna of the Bijou Hills Local Fauna (Late Miocene: Barstovian) of South Dakota. Herpetologica 34(3):253-257.

Holman, J. Alan. 1979. A Review of North American Tertiary Snakes. Pub. Mus. Mich. St. Univ. Paleo. Ser. 1(6):203-260.

Holman, J. Alan. 1981. A Review of North American Pleistocene Snakes. Pub. Mus. Mich. St. Univ. Paleo. Ser. 1(7):263-306.

Hudson, Dennis M., and Bayard H. Brattstrom. 1977. A Small Herpetofauna from the Late Pleistocene of Newport Beach Mesa, Orange County, California. Bul. So. California Acad. Sci. 76(1):16-20.

Jackson, Dale R. and Richard Franz. 1981. Ecology of the Eastern Coral Snake (Micrurus fulvius) in Northern Peninsular Florida. Herpetologica 37(4):213-228.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Johnson, Ralph Gordon. 1955. The Adaptive and Phylogenetic Significance of Vertebral Form in Snakes. Evolution, 9(4):367-388.

Keiser, Edmund D. Jr. 1970. Sexual Dimorphism and Ontogenetic Variation in the Haemapophyses of Ophidian Postcloacal Vertebrae. Herpetologica 26(3):331-333.

Klauber, Lawrence M. 1941. The Correlation Between Scalation and Life Zones in San Diego County Snakes. Bul. Zol. Soc. San Diego 17(III):73-79.

LaDuke, Thomas C. 1991. The Fossil Snakes of Pit 91, Rancho La Brea, California. Contr. Sci. 424:1-28.

Lawson, Robin. 1987. Molecular Studies of Thamnophiine Snakes: 1. The Phylogeny of the Genus Nerodia. J. Herp. 21(2):140-157.

Lindsey, C. C., and M. Y. Ali. 1965. The Effect of Alternating Temperature on Vertebral Count in the Medaka (Oryzias latipes). Canadian J. Zol. 43:99-104.

Lindsey, C. C., A. M. Brett, D. P. Swain, and A. N. Arnason. 1984. Responses of Vertebral Numbers in Rainbow Trout to Temperature Changes During Development. Canadian J. Zol. 62:391-396.

Lindsey, C. C., and Harrington, Robert W. Jr. 1972. Extreme Vertebral Variation Induced by Temperature in a Homozygous Clone of the Self-fertilizing Cyprinodontid Fish Rivulus marmoratus. Canadian J. Zol. 50:733-744.

Linnaeus, C. 1758. Systema Naturae. 10th ed. Vol. 1. Stockholm. 824 pp.

List, James Carl. 1966. Comparative Osteology of the Snake Families Typhlopidae and Leptotyphlopidae. Illinois Biological Monogr. 36. 112 pp. The University of Illinois Press. Urbana.

Malnate, Edmond V. 1972. Observations on the Vertebral Hypapophyses and Associated Musculature in Some Snakes, with Special Reference to the Colubridae. Zool. Meded. 47(18):225-239.

McDowell, Samuel B. 1987. Systematics. In: Seigel, Collins and Novak eds. Snakes: Ecology and Evolutionary Biology, Chapter 1, pp. 3-50. MacMillan, Toronto and London.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

McDowell, Samuel B., and Charles M. Bogert, 1954. The Systematic Position of Lanthanotus and the Affinities of the Anguinomorphan Lizards. Bul. Amer. Mus. Nat. Hist. 105:1-142.

Mead, Jim I., Edward L. Roth, Thomas R. Van Devender, and David W. Steadman. 1984. The Late Wisconsinan Vertebrate Fauna from Deadman Cave, Southern Arizona. Trans. San Diego Soc. Nat. Hist. 20(14):247-276.

Mead, Jim I., Timothy H. Heaton, and Emilee M. Mead. 1989. Late Quaternary Reptiles from Two Caves in the East-Central Great Basin. J. Herp. 23(2):186-189.

Meylan, Peter A. 1982. The Squamate Reptiles of the Inglis IA Fauna (Irvingtonian:Citrus County, Florida). Bul. Florida State Mus. Biol. Sci. 27(3):1-85.

Myers, Charles W. 1982. Blunt-Headed Vine Snakes (Imantodes) in Panama, Including a New Species and Other Revisionary Notes.Amer. Mus. Nat. Hist. Novitates 2738:1-50.

Nopcsa, F. 1923. Eidolosaurus und Pachyophis. Zwei neue NeocomReptilien. Paleontographica 65:97-154.

Osgood, David W. 1978. Effects of Temperature on the Development of Meristic Characters in Natrix fasciata. Copeia 1978(1):33-47.

Ossian, Clair R. 1970. Preparation of Disarticulated Skeletons Using Enzyme-based Laundry. "Presoakers." Copeia 1970(1):199-200.

Parker, William S., and Michael V. Plummer. 1987. Population Ecology. Ch. 9, pp 253-301, in: Snakes: Ecology and Evolutionary Biology. R. A. Seigel J. T. Collins, and S. S. Novak eds. MacMillan Publishing Co., NY.

Prange, Henry D., and Steven P. Christman. 1976. The Allometrics of Rattlesnake Skeletons. Copeia 1976(3):542-545.

Pregill, Gregory K. 1977. Axial Myology of the Racer Coluber constrictor with Emphasis on the Neck Region. Trans. San Diego Soc. Nat. Hist. 18(11):185-206.

Rage, J. C. 1982. La Phylogenie des Lepidosauriens (Reptilia): Une approche Cladistique, C. R. Acad. Sci. Paris 294:563-566.

Rage, J. C. 1984. Serpentes. Handbuch der Palaoherpetologie, Teil Gustav Fischer, Stuttgart. 11. 80 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Rage, Jean-Claude. 1987. Fossil History. Chapter 2, pp. 51-76 in: Snakes: Ecology and Evolutionary Biology., R. A. Seigel, J. T. Collins, and S. S. Novak eds. MacMillan Publishing Co., New Yo

Rogers, Karel Louise. 1976. Herpetofauna of the Beck Ranch Local Fauna (Upper Pliocene: Blancan) of Texas. Pub. Museum, Michigan State Univ., Paleontological Series 1(5):167-200.

Romer, Alfred Sherwood. 1966. Vertebrate Paleontology. The University of Chicago Press. Chicago. 468 pp.

Rossman, Douglas A., and W. Gary Eberle. 1977. Partition of the Genus Natrix, with Preliminary Observations on Evolutionary Trends in Natricine Snakes. Herpetologica 33(1):34-43.

Ruthven, Alexander G. 1908. Variations and Genetic Relationships of the Garter-snakes. Smithsonian Inst. US Nat. Mus. Bul. 61:1-201.

SAS Institute, Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC: SAS Institute Inc., 1028 pp.

Seibert, Henri C., and Charles W. Hagen Jr. 1947. Studies on a Population of Snakes in Illinois. Copeia, 1947(1):6-22.

Senn, D. G., and R. G. Northcutt. 1973. The Forebrain and Midbrain of some Squamates and their Bearing on the Origin of Snakes. J. Morphol. 140:135-152.

Smith, Hobart M., Rozella B. Smith, B. Sawin, and H. Lewis. 1977. A Summary of Snake Classification (Reptilia, Serpentes). J. Herp. 11(2):115-121.

Smith, Meredith J. 1975. The Vertebrae of Four Australian Elapid Snakes (Squamata:Elapidae). Trans. R. Soc. S. Aust. 99(2):71-84.

Stebbins, Robert C. 1985. A Field Guide to Western Reptiles and Amphibians. Second Ed. 429 pp.

Stewart, Glenn R. 1968. Some Observations on the Natural History of Two Oregon Garter Snakes (Genus Thamnophis). J. Herp. 2(3-4):71-86.

Sumida, Stuart S. 1987. Two Different Vertebral Forms in the Axial Column of Labidosaurus (Captorhinomorpha: Captorhinidae). J. Paleo. 61(1):155-167.

Szyndlar, Zbigniew. 1981. Early Pleistocene Reptile Fauna from Kozi Grzbiet in the Holy Cross Mountains. Acta Geol. Polonica 31(1-2):81-100.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Szyndlar, Zbigniew. 1984. Fossil Snakes from Poland. Acta Zool. Cracov. 28(1):1-156.

Szyndlar, Zbigniew. 1985. Ophidian Fauna (Reptilia, Serpentes) from the Uppermost Miocene of Algora (Spain). Estudios Geol. 41:447-465.

Szyndlar, Zbigniew. 1987. Snakes from the Lower Miocene Locality of Dolnice (Czechoslovakia). J. Vert. Paleo. 7(1):55-71.

Thireau, Michel. 1967a. Contribution a L'etude de la Morphologie Caudale, de L'Anatomie Vertebrale et Costale des Genres Atheris, Atractaspis et Causus (Viperides de L'ouest Africain). Bul. Mus. Nat. Hist. Nat. (Paris) 2nd Ser., 39:454-470.

Thireau, Michel. 1967b. Analyse Descriptive et biometrique de la Colonne Vertebrale du Serpent Marin Enhydrina schistosa Daudin (Hydrophiines). Caracteres Vertebraux des Hydrophiides. Bul. Mus. Nat. Hist. Nat. (Paris) 2nd Ser., 39:1044-1056.

Underwood, Garth. 1967. A Contribution to the Classification of Snakes. British Mus. Nat. Hist. London.

Van Devender, Thomas R. and Jim I. Mead. 1978. Early Holocene and Late Pleistocene Amphibians and Reptiles in Sonoran Desert Packrat Middens. Copeia, 1978(3):464-475.

Van Devender, Thomas R., Amadeo M. Rea, and Michael L. Smith. 1985. The Sangamon Interglacial Vertebrate Fauna from Rancho La Brisca, Sonora, Mexico. Trans. San Diego Soc. Nat. Hist. 21(2):23-55.

Voris, Harold K. 1975. Dermal Scale-Vertebra Relationships in Sea Snakes (Hydrophiidae). Copeia 1975(4):746-757.

Voss, Robert S., Leslie F. Marcus, and Patricia P. Escalante. 1990. Morphological Evolution in Muroid Rodents I. Conservative Patterns of Craniometric Covariance & Their Ontogenetic Basis in the Neotropical Genus Zygodontomys. Evolution, 44(6):1568-1587.

Wassersug, Richard J. 1976. A Procedure for Differential Staining of Cartilage and Bone in Whole Formalin-fixed Vertebrates. Stain Technology 51(2):131-134.

Weary, G. C. 1969. An Improved Method of Marking Snakes. Copeia, 1969(4):854-855.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.