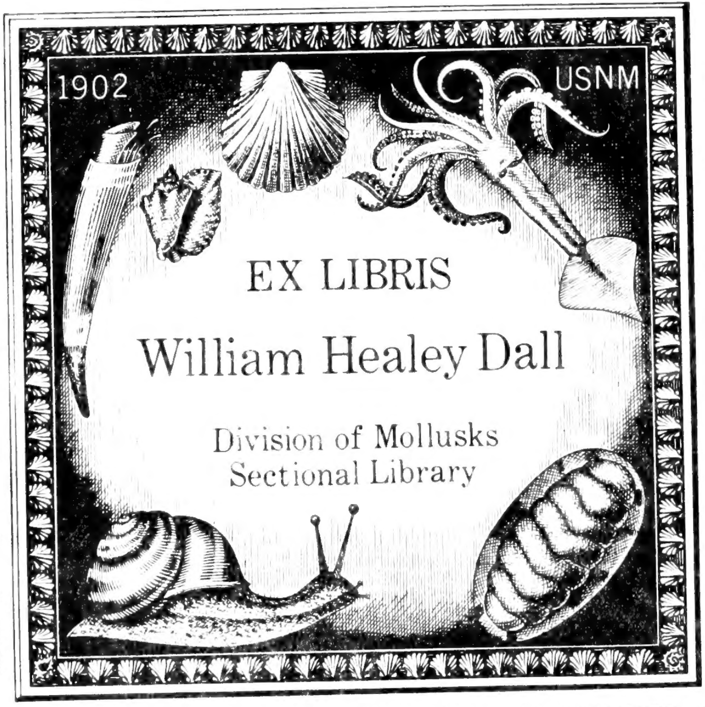

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THE VARIATIONS AND ECOLOGICAL DISTRIBUTION OF THE SNAILS OF THE GENUS IO.

BY

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CONTENTS.

CAUSES AND CONDITIONS.

"The law of causation, the recognition of which is the main pillar of inductive science, is but the familiar truth, that invariability of succession is found by observation to obtain between every fact in nature and some other fact which has preceded it. * * * The invariable antecedent is termed the cause; the invariable consequent, the effect. * * * It is seldom, if ever, between a consequent and a single antecedent, that this invariable sequence subsists. It is usually between a consequent and the sum of several antecedents; the concurrence of all of them being requisite to produce, that is, to be certain of being followed by, the consequent. In such cases it is very common to single out one only of the antecedents under the denomination of cause, calling the others merely conditions. * * * The real cause, is the whole of these antecedents; and we have, philosophically speaking, no right to give the name of cause to one of them, exclusively of the others. * * * All the conditions are equally indispensable to the production of the consequent; and the statement of the cause is incomplete, unless in some shape or other we introduce them all."

John Stuart Mill.

THE VARIATIONS AND ECOLOGICAL DISTRIBUTION OF THE SNAILS OF THE GENUS IO.

INTRODUCTION.

In this paper are presented the results of a study of the variations and ecological distribution of the river snails of the genus *Io*. The great amount of variation in these shells is as striking as that found in the famous Slavonian Paludinas, studied by Neumayr ('75), or the Planorbes of Steinheim, studied by Hilgendorf ('66, '01) and Hyatt ('80), and while these fossils are found in different strata, and probably therefore are of diverse ages, *Io* is found living to-day in a single river system, that of the Tennessee.

Since this investigation began the point of view of naturalists has undergone several important changes. The older conception of the species as the unit for study has been constantly undergoing disintegration, as the significance of local races, varieties, colonies, pure strains, characters, factors, and environmental influences has been enlarged as the result of the recent investigations of variation, heredity, and more recently with the important advances made in ecology. As the study of *Io* advanced it progressively became less and less a study of variation and taxonomy in the older sense, and more and more of a study of the relation of *Io*, to its complete organic and inorganic environment; or, in other words, it became more ecological.

In spite of its limitations I hope the present study will help to make concrete an idea so well expressed by Brooks ('06, pp. 75–76):

> Inheritance and variation are not two things, but two imperfect views of a single process, for the difference between them is neither in living beings nor in any external standard of extermination, but in the reciprocal interaction between each living being and its competitors and enemies and the sources of food and the other conditions of life. * * * You will note that it is as great an error to locate species in the external world as it is to locate it in germ cells or in chromatin. It neither exists in the organisms nor in the environment, because it is in the reciprocal interaction between the two.

In harmony with this ecological point of view an effort has been made to study these shells in such a manner as to show the reciprocal responses of the changing environment and the changing shells, because until both variables are studied and related little symmetrical progress can be made. Our problem is more and broader than the origin of the differentiations found, for it is concerned as well with the conditions of their survival and perpetuation where they now live. For this reason the development of the environment is considered an essential part of this study, a phase which the students of variation and heredity seldom consider very fully. This study has been devoted mainly to the interpretation of the conditions found in nature rather than from the standpoint of the student interested mainly in the immediate control of nature.

This group was chosen for study because of the large size of the shells, their great variability, and their relatively limited geographic range. They are confined solely to the Tennessee River system, and mainly to that part which lies upstream from Chattanooga. With such a limited distribution it seemed possible to cover entirely the geographic range, and thus secure a certain completeness which it is very difficult or impossible to secure in many wide ranging kinds. An examination of the material in some of our largest museums revealed at once the necessity of gathering fresh material for this study, because of the lack of adequate data with the collections previously made. To make these collections it was necessary to go on expeditions for them for three consecutive years during the late summer and fall, when the streams are at low water. In this way the territory from the Muscle Shoals in northern Alabama to the upper limit of *Io* in each tributary of the Tennessee was sampled. Collectors were also secured and instructed in the methods of collecting and preserving the shells, and thus valuable materials were obtained. In the examination of the rivers all available methods were used, rowboats, steamboats, journeys on foot, by horse, mule, and railways, and thus many hundreds of miles of the rivers were traversed, and in all over 1,200 miles of the river system was sampled, and between 6,000 or 7,000 shells were secured with accurate data. Plans were made for breeding experiments, but were necessarily abandoned after a start had been made for the lack of adequate facilities.

In attempting to interpret the results of the present study the feeling has developed that had some of the elaborate studies of heredity been built upon preliminary studies similar to the present one the experimental results would have been of much wider application to the conditions found in nature. The primroses *Oenothera* might be mentioned as such an example. Certain groups of animals, particularly the song sparrows (*Melospiza*), the horned larks (*Otocoris*), and among the mammals the red squirrels (*Sciurus*), the white-footed mice (*Peromyscus*), and our native rabbits (*Sylvilagus*, *Lepus*) are groups which would richly reward a student of them, and also would do much to help give to modern taxonomy a somewhat different outlook.

In general, in the earlier descriptive parts of the present paper no attempt has been made to emphasize the interpretative aspect, because that phase is discussed more fully in later chapters.

When we consider the rapid rate at which our native plants and animals are being destroyed by the encroachment of civilization, it will be realized that in a few generations a fairly full account of many of our native species will be forever lost. I hope that the present record will be a contribution to the preservation of such "vanishing data," and that the photographic record and the collection will preserve a reliable sample of one of nature's vast experiments.

THE HABITS AND LIFE HISTORY OF IO.

HABITS.

Very little detailed knowledge is recorded of the habits of *Io*. It is an aquatic, gill-bearing, operculate gasteropod which frequents only certain rivers of southwestern Virginia, eastern Tennessee, and northern Alabama. Only a few references to its habits have been made in the literature, and during my field work this phase of study was almost entirely neglected on account of limited time at my disposal and the large area to be covered in the field work. The best accounts of the habits are those by Lewis ('76) and by Wetherby ('76).

The most characteristic habit is that of frequenting the moderately rapid, probably well oxygenated and shallow water of the shoals and rapids of rivers. In such situations the water is generally only a few inches deep, as is usually the case in the smaller or headwater streams, or even only a few feet deep in the large rivers. In general all the river tributaries of the Tennessee inhabited by these shells may be considered as producing much of the shallow rapid-water habitat; and it is on such shoals that these shells occur in the greatest abundance and occupy the greatest area of habitat. The shells do not occur in creeks nor in rivers whose drainage area is primarily from nonlime-bearing rocks. The deepest water in which these shells occur in abundance is in the upper Tennessee from about Knoxville to Loudon, Tenn. These conditions are also approximated in the lower part of the French Broad and possibly in the lower Holston. As a rule, the animals live in shallow water, but one shell (lot 156, No. 72) was taken by a collector in about 6 feet of water in the French Broad. Below Loudon the abundance of live specimens decreases with suddenness. This apparently is due to several causes: The greater depth of the water on the shoals, the limited number of shoals, their limited area, and possibly also to navigation improvements. Lot 151 from Dayton, Tenn., was taken in water which was generally from knee to waist deep upon the shoals. Collecting is difficult under such circumstances, as the scattered individuals must be found largely by feeling for them barefooted or with the hands.

An animal as characteristic of such definite environmental conditions may be expected to show equally marked characteristics which permit it to live in them. This is conspicuously shown in the great muscular strength of the foot. Many years ago Miss Annie E. Law, of Concord, Tenn., observed that (Lewis, '71, p. 223), "The muscular power of *Io* is astonishing. I frequently find one adhering to a rock half as large as my head, and when I take up the shell it brings the rock with it, and requires much force to separate it." These observations were in all probability made in the Tennessee River between Little River Shoals, below Knoxville, and the Chota Shoals, about 20 miles below. (Lewis, l. c., p. 216). This strength, therefore, applies to the large individuals of *loudonensis* or *turrita,* and not to the smaller forms, although they are also well able to maintain a hold in swiftly flowing water. An orienting response to the swift current might be expected, but this subject has not been carefully investigated. Wetherby ('76, p. 5) remarks that in the Powell River at Kraushorns Ferry: "The *Ios* lay thick, clinging to the rocks, generally across the current." My own observations were neither detailed nor definite enough to recognize a rheotropic response.

The food of *Io* consists of the slimy algal coating and entangled organic débris on the rocks, bowlders, and gravel upon which they creep. Wetherby ('76, p. 3) speaks of the food habits of the family as follows:

> The *Strepomatidae* feed upon the *confervae* growing upon the rocks and stones in the river, through which the tortuous path they eat in their meal takings may easily be seen. Now, every flood of a mountain stream, with its rasping sand and gravel, has a tendency to scour off this growth, and to subject the animals that feed upon it to a greater or less privation in regard to food.

A series of *Io fluvialis* from Clinch River (lot 53) which I kept in a glass-sided aquarium were seen to feed upon the algæ growing upon the well-lighted side of the vessel. This may explain, in part, their apparent preference for the sides rather than the bottom of the vessel.

The large quantities of lime used in the formation of the shell must thus be secured from this algal slime. A study of the conditions which determine the growth of these algæ will undoubtedly throw much light upon the occurrence of these shells. The absence of *Io* from certain streams may be due in part to the dependence of certain algæ upon lime, which is largely lacking. It is well known (Davis, '01, p. 495) that certain algæ secrete and concentrate lime from fresh waters as well as that some perforate the living shells of mollusks. (Cf. Collins, Erythea, vol. 5, p. 95, 1897.) Upon the shoals in the smaller rivers *Io* was very commonly associated with *Anculosa,* so that it is probable that the two are competitors for food. Mr. Hinkley found a single specimen of *Io turrita* on the Muscle Shoals of Alabama associated with *Angitrema* and *Anculosa.*

The reproductive habits of *Io* have an important bearing upon the interpretation of the peculiarities of this group but little attention has been given to this subject. In this family Stimpson ('64, p. 45) has shown that the sexes are distinct and that there is an absence of a copulatory organ in the male. The external character, by means of which the sexes may be distinguished, is by the presence, in females containing ova, of a "conspicuous slit or sinus in the right side of the foot, about midway between the tentacle and operculigerous lobe" and the absence of this sinus in the males. Stimpson (p. 46) further remarks:

> In view of these remarkable characters of the sexual system, the Melanians, the American species, at least, must be separated from the ordinary Ctenobranchiate Gasteropods as a group of far more than family importance; for by the entire absence of an intromittant organ in the male, which must be connected with a very peculiar, and as yet unknown, method of impregnation, they diverge greatly from other families of the group, and approach the Cyclobianchiata. * * * There is no difficulty in conceiving that the impregnation may take place in the way which is known to occur in the Lamellibrianchiata, the spermatic particles reaching the ovary of the female through the medium of the water, into which they are discharged by the male. In our freely-moving Melanians, however, such a mode of impregnation is quite unnecessary; it is far more probable that some direct connection takes place between the sexes; and it is highly desirable that this subject should be carefully investigated, at the proper season, by those who have the opportunity of doing so.

Haldeman ('41, p. 22) states that this family is oviparous, a fact confirmed by Stimpson ('64, p. 46).

ENEMIES.

At present the most important enemy of *Io* is man. The contamination of streams by factory waste, as at Saltville, Va., or in the Clinch by mine drainage and waste, are of a character which is destined to increase for some time to come. The influence of sewage, from the few large cities located along the stream, has not been determined. The deforestation of the mountain and the floods formed by these conditions are very injurious, as in the case of lot 112, from Peltier, on the South Fork of the Holston, where hundreds of *Io* had been killed by the floods. Further injury is caused by the action of sand and gravel, etc., upon the shoals which destroys the algal food, and also changes the channels of the streams by the deposits of great quantities of material eroded from the bare steep mountain slopes. Still another unfavorable factor, is conditioned by *Io* living upon shoals. These shoals tend to be the favorite fording places in a country which builds relatively few bridges. In the past, of course, there were even a smaller number of bridges. The tramping of horses, mules, and the wheels of vehicles injure, and must kill a large number of these shells. I have observed many shells, showing repair after injury, which were found upon such shoals. I have in mind such localities as Chissolms Ford and Kyle Ford, on the Holston. This form of injury is mainly in the smaller rivers, because farther down stream the water is so deep that ferries are much more common.

THE RACES AND FORMS OF IO.

It is necessary to have some general idea of the degrees of diversity in this genus before their variations can be intelligently discussed. This chapter is mainly intended to give a concise idea of the most distinctly defined forms. The detailed evidence upon which these distinctions are made will be discussed in later chapters. As I do not know the relative rank of the different elements in the genus, I have called all of them forms. There are so many variations and degrees of intergradation, and in so many directions, that it is very difficult to distinguish them; and probably few persons would agree as to where the lines of demarcation should be drawn. As a rule, I have tried to distinguish only those forms which are fairly abundant and well defined. No effort has been made to discuss fully the quantitative data, and only such results are used in describing the forms which appear to be from fairly homogeneous series of shells. It will be observed that the basis for the distinctions drawn have been primarily based upon the character of the development of the shell and its spinosity, and that the quantitative data have been used as a means of relatively concise description of the average dimensions of these characteristics.

It will be observed that only a selection of individuals are included in the forms described. The shells from the lower Powell, groups 4 and 5, from the Clinch, groups 9 and 11, from the Holston, groups 15, 16, 17, from the French Broad, group 21, and from the Tennessee, group 22, are not considered. The same is true of many supplementary lots of specimens. These series are not sufficiently large or homogeneous, but mixed lots of several forms, or they include individuals in large numbers whose position is uncertain. This uncertainty may be due to the erosion of the apical whorls, which leaves doubt as to whether the shell was smooth, undulate, or spinose when young, or it may be due to the intermediate position or admixture of characters in the individual. The significance of some of these individuals will be discussed elsewhere.

Particular attention should be called to the fact that, as shown by the plattings of the quantitative data, none of these forms are distinctly isolated from allied forms by the absence of all intergradations. The best marked discontinuity is shown between the smooth and the spinose forms, as between *fluvialis* and *turrita;* this is the most fundamental division within the genus, and yet it is not complete.

I do not have access to the literature which is necessary to bring the nomenclature up to the latest standard, nor have I examined the type specimens, but I have attempted to utilize the information given in Tryon's ('73) monograph and have aimed to utilize as many of the old names as possible. I have indicated which forms I have considered typical and all the new forms are figured. The types and the representative specimens are shown on plate 1.

In most cases the type localities of the older authors are too inaccurate or too indefinitely known to be of much value. Usually the "Holston River" or "Tennessee" represents the degree of definiteness, and in a genus varying so much within a short segment of the river such indefinite information is of very limited value.

The average relations of the various forms to one another are shown in the following table:

Table of average dimensions of the forms of Io.

[Maxima above or below the mode are indicated by the class at which the maxima occurs, or when there is only a decided asymmetry of the curve this is indicated by a +.]

Group.	Form No.	Name.	Shell dimensions.						Spinosity.								
			Diameter, mm.			Globosity, per cent.			Height, mm.			Distance between spines, mm.			Index $\frac{w}{d}$ per cent.		
			–	Mode.	+	–	Mode.	+	–	Mode.	+	–	Mode.	+	–	Mode.	+
1	1	Powellensis	–	15.5	–	–	77	–	–	0.3	–	–	0.5	–	–	12	+
6	2	Clinchensis	–	18.5	21.5	+	85	–	–	.3	–	–	.5	–	–	–	–
12	3	Fluvialis	–	18.5	–	–	75	+	–	.3	–	–	.5	–	–	12	–
13	4	Verrucosa	–	18.5	+	–	73	+	–	.8	–	.5	6.5	–	–	12	+
3	5	Lyttonensis	–	17.5													
				18.5	–	–	77	+	+	1.8	–	+	8.5	–	–	17	+
8	6	Paulensis	+	14.5	16.5	–	73	+	0.3	1.5	–	–	6.5				
												–	7.5	–	–	17	–
14	7	Recta	+	20.5	–	+	71	–	–	1.8	2.3	10.5	11.5	–	–	17	–
10	8	Brevis	–	17.5	–	–	73	–	+	1.8	–	–	9.5	–	–	17	–
18	9	Spinosa	–	14.5	18.5	–	67	71	–	1.8	2.3	–	9.5	–	–	22	–
19	10	Unakensis	–	15.5	18.5	–	–	–	–	1.8	–	–	7.5	+	–	17	+
20	11	Nolichuckyensis	–	11.5	19.5	+	73	–	–	1.8	+	–	7.5	12.5	–	22	+
21	12	Angitremoides															
24	13	Loudonensis	–	17.5	21.5	–	73	–	–	3.3	–	+	13.5	–	–	27	–
27	14	Turrita	+	22.5	–	–	–	–	–	2.8	–	–	11.5	–	–	27	–

1. *Powellensis* C. C. Adams. 1914. New. These are the smooth or slightly undulated or carinated shells, group 1, lot 47, from the headwaters of the Powell River at Olinger, Va. Type specimen, plate 28, figure 17. Shell width modal at 15.5 mm., plate 6. These are the dwarfs or smallest forms in the genus. The large number of young in this group have also influenced the curves, as of width, plate 6. The globosity of the shell is modal at 77 per cent, plate 10. The relative thinness of this form is noticeable, a trait also of young shells generally. All young shells are smooth, plate 3, figures 1 and 2.

2. *Clinchensis* C. C. Adams. 1914. New. These are the smooth or slightly undulated shells, group 6, lot 56, from the headwaters of the Clinch River, Cleveland, Va. Type specimen, plate 34, figure 13. Width of shell with a maximum ranging from 18.5 to 21.5 mm., plate 7, with mode at 18.5 mm. The globosity of the aperture is modal at 83 per cent, plate 11, and shows considerable variation toward a lower maximum. This shows the greatest degree of globosity in the genus. Shells very thick and heavy, plate 34. Young shells are very probably smooth, judging from the apices of adult shells.

3. *Fluvialis* Say. 1825. These are smooth or slightly undulated shells, group 12, lot 79, from the headwaters of the North Fork of the Holston River, at Saltville, Va. This is probably the type locality, and plate 40, figure 24, shows a representative specimen. The shells vary from smooth to those of moderate undulations, as shown in plate 40. Modal width of shell, 18.5 mm., plate 8. The young shells are smooth or undulated, as shown by the apices. The aperture shows a high degree of globosity, with a mode at 75 per cent, plate 12, but this is less than in the headwater groups in the Clinch River (groups 6 and 7), which have maxima ranging from 77 to 83 per cent (plates 11 and 12), while those in the Powell have a mode at 77 per cent (group 1, plate 10).

The three preceding relatively smooth forms differ so much in general appearance that they can readily be distinguished by inspection. I know of no way to distinguish which of these is the simplest, least specialized, or nearest the ancestral form or forms. There is considerable individual variation in each form, and no locality is free from incipient carina, undulations, or spines, at least on some of the mature shells.

4. *Verrucosa* Reeve. 1860. This includes the nodulate and undulate shells, group 13, lots 94 and 116, from the North and South Forks of the Holston River in Virginia and Tennessee. They are represented by group 13, from the South Fork of the Holston, at Bluff City, Tenn. The type, figured by Tryon (1873, p. 6, fig. 31), is near enough to the predominant form at Bluff City and in the lower part of the North Fork, lot 91, to warrant the use of this name for this form. The specimen on plate 41, figure 9, is considered a typical one. Width of shell modal at 18.5 mm. and with many individuals at 19.5 and 20.5 mm., plate 8. The globosity of the aperture is modal at 73 per cent and has a maximum extending to 77 per cent, plate 12.

The mode for spine height is at 0.8 mm., plate 16. This is the only group with a maximum of this dimension. The young shells, and the apical whorls of the older, are smooth or corrugated, plate 4, figures 1 to 13, and plate 41. The average height of spines is modal at 12 per cent of the average distance between the spines, plate 24. The young shells are undulated.

These shells are relatively large and heavy. They form the most distinctly uniform series of the intergradations between the smooth and spinose series of shells.

5. *Lyttonensis* C. C. Adams. 1914. New. This peculiar spinose shell, group 2, lot 39, is from the upper Powell River, near Pennington Gap, Va. They are distinctly spinose rather than corrugated, as in *verrucosa*. The type is shown on plate 29, figure 15. The maximum for shell width stands at 17.5 mm., plate 6. This is a relatively wide shell. The globosity of the aperture is modal at 75 per cent, which is a high degree, plate 10. Height of spines is modal at 0.3 mm., and with many shells at 0.8 mm., plate 14. The distance between the spines reaches a maximum at 7.5 mm., plate 18. The average height of spines is modal at 12 per cent of the average distance between them, plate 22. The young shells are smooth or corrugated and develop spines at about the class 2 stage.

6. *Paulensis* C. C. Adams. 1914. New. This shell is generally spinose on the last whorl only. The type specimen from group 7, St. Paul, Va., lot 11, is figured on plate 35, figure 3. This shell represents the transitional stage between smooth and spinose shells in the Clinch. The dimensions of the shells for this form are taken from group 8, as this group is a more homogeneous series than group 7 of this kind of shell. The maximum for shell width is very narrow, at 14.5 and 16.5 mm., plate 7. This is the narrowest series in the Clinch, while the corresponding shell in the Powell, *lyttonensis*, is wider. The globosity of the shell is modal at 73 per cent, plate 11. Spine height is modal at 1.5 mm., plate 15. The distance between the spines reaches a maximum at 6.5 and 7.5 mm., plate 19. The average height of spines is modal at 17 per cent of the distance between them, plate 23. The young shells are relatively smooth or undulated and develop spinosity as a rule at about the beginning of the class 4 stage. Consult plate 36 for the general appearance of this form.

7. *Recta* Reeve. 1860. This is a large, rather heavy form, with spines rather than nodules. Represented abundantly by group 14, lot 178, from Kingsport, Tenn., near the confluence of the North and South Forks of the Holston River. The shell on plate 42, figure 12, is considered a typical specimen. Shells very wide, with the mode at 20.5 mm., plate 8. The globosity of the shell has a maximum at 71 per cent, plate 12. This is a significant reduction in globosity from that of *verrucosa*. Spine height has a maximum at 1.3 and 1.8 mm., plate 16. The apices of older shells indicate spinose young, plate 42. The average spine height is modal at 17 per cent of the distance between the spines, plate 24.

It is remarkable that this spinose form is isolated and surrounded so completely by less spinose ones. Thus *verrucosa* bounds it upstream in both Forks of the Holston, and downstream, in group 15, there are both spinose and relatively smooth shells. This is a unique condition.

8. *Brevis* Anthony. 1860. This is a short, rather thick shelled form with low, blunt spines. It is represented by group 10, lot 17, from Kyle Ford, Clinch River, Tenn. The typical form is shown in plate 38, figure 12. Group 10 is from a restricted locality, and is fairly homogeneous, and the dimensions may be considered representative. The modal condition for shell width is 17.5 mm., plate 7. The degree of globosity of the shell is 73 per cent, plate 11. The height of the spine reaches a maximum at 1.8 mm., plate 15. This means very low spines. The undulate form, *verrucosa*, has lower spines but these are very low for a distinctly spinose

shell. This form must also be considered somewhat transitional between the smooth and spinose forms, and it does not belong to a community of mixed spinose or undulate shells, as do some other transitional series. There is a long distance between spines, the mode is at 9.5 mm., plate 19. This appears to be the most stable condition in the Clinch River. The average height of spines is modal at 17 per cent of the average distance between them, plate 23.

The young shells are imperfectly known. Few immature shells were found, and the apices of old shells are generally eroded. Two immature individuals, lot 17, Kyle Ford, are shown on plate 3, figures 43 and 44. These indicate that the young are relatively smooth or corrugated, and that spines develop at an early age.

9. *Spinosa* Lea. 1837. I have restricted the use of this term to shells which are very spinose throughout life, from near Morristown, Tenn., in the Holston River. A typical specimen, from group 18, lot 96, is shown on plate 46, figure 7. As this series is fairly homogeneous, its dimensions will be used in describing this form. The diameter of the shells is small and variable, with a mode at 14.5 mm., plate 8. The globosity of the shells is relatively low and variable, with a maximum ranging from 67 to 71 per cent, plate 12. The height of the spines reaches a maximum from 1.8 to 2.3 mm., plate 16. This indicates very spiny shells, a degree closely corresponding to that of *recta* (group 14) from Kingsport, farther upstream. The distance between the spines is relatively very long, variable, and with a mode at 9.5 mm., plate 20. The average height of spines is modal at 22 per cent of the average distance between them, plate 24. The young shells appear to be undulate or spinose, as is indicated by the apices of the older shells.

The type locality given by Lea was the "Holston River, Washington County, Va." This locality, for the kind of shell figured by Tryon (1873, p. 7) must be erroneous, because in this county, on the South Fork of the Holston, I found only shells of the general type of group 13, *verrucosa,* and in the North Fork the shells are of the similar nodular type. The Rotherwood shells, group 11, *recta,* are the spinose shells which are the nearest geographically to the locality given by Lea. Evidently the specimen of Lea must have come from farther downstream.

10. *Unakensis* C. C. Adams. 1914. New. This form is spinose throughout life, and is confined solely to the headwaters of the Nolichucky River, group 19, lot 118, from Conkling, Tenn. The type is shown in plate 47, figure 4. Only dead shells are known and these were found about the site of old Indian camps. On account of the injured apertures, globosity could not be determined accurately, and therefore only the diameter of the shell was measured. The shell was found to be very variable and relatively narrow, the mode at 15.5 mm. and a secondary maximum at 18.5 mm., plate 9. This is a degree of narrowness quite comparable to that found in the headwaters of the Powell River. The spines are relatively low, with the mode at 1.8 mm., plate 17, also recalling the degree of spinosity found in the upper Powell. The space between the spines is variable and has a maximum ranging from 7.5 to 9.5 mm., plate 21. The average height of spines has its maximum from 17 to 22 per cent of the average distance between them, plate 25. The young shells are spinose.

11. *Nolichuckyensis* C. C. Adams. 1914. New. This is the characteristic form of shell in the lower part of the Nolichucky River. The shells are spinose throughout life, as shown by the young and by the apical whorls. The small spines on young shells are *sharp pointed* and not corrugated or nodulate, as are the relatively spinose shells in the headwaters of the Powell, Clinch, and Holston Rivers. This form is represented by group 20, lot 104, from White Pine, Tenn. The type is figured on plate 48, figure 13. The shell is very narrow and very variable, with a mode at 11.5 mm., plate 9. In general terms, these are the narrowest shells of the genus. The degree of globosity of the shell is modal at 73 per cent, plate 13. Spine height is modal at 1.8 mm., plate 17. The space between the spines is variable, with a maximum at 7.5 and 8.5 mm., plate 21, which is a relatively narrow space between the spines. This narrowness is probably influenced, as are also the other dimensions, by the large number of young shells present in the group, plate 48. The average height of spines has its maximum at 22 per cent of the average distance between them, plate 25.

12. *Angitremoides* C. C. Adams. 1914. New. This anomalous form is found in the lower part of the French Broad River at Dandridge, Tenn., and in the upper part of the Tennessee River. The type is shown on plate 1, figure 12, Looneys Island, near Knoxville, Tenn., from group 21, lot 124. The shells are as a rule spinose throughout life, judging from the apices. These shells have the general appearance of young shells of the smaller specimens of *turrita*, such as those of group 22, from the Lyon Shoals, below Knoxville, but instead of being thin, as is the rule for young shells, these are thick, and the spines are relatively short, recalling those of *unakensis*.

This form has been found only in rather small numbers, and were it not for the mature appearance of the shells, their short spines, combined with their relative small size, and their occurrence in a large stream where large mature shells are to be expected, this form would hardly justify recognition.

In addition to the type specimen, others are figured as follows: From lot 136, plate 5, figures 28–30; Looneys Island, below Knoxville, lot 124, plate 5, figures 44–48 and lot 136 on plate 49, figures 26, 28, 29, 31, and 32, and lot 137, figures 27 and 30. Possibly some individuals grade into *turrita*, as in lot 152, from Loudon, Tenn.

Two individuals of *angitremoides*, from lot 124, below Knoxville on Looneys Shoal, are shown on plate 5, figures 45 and 47, which appear to have been smooth when at the class 2 stage. As a rule this shell appears to be spinose at the class 1 stage. This lot is composed solely of one kind of shell, of which there are 34 specimens in addition to those figured.

There is a remarkable superficial similarity between this form and mature specimens of *Angitrema armigera* Say, and hence the name of this form. *Angitrema* is a genus allied to *Io*.

13. *Loudonensis* C. C. Adams. 1914. New. This is a large spinose kind of shell whose young are without spines, corrugations, or nodules, but as the mature whorls are developed the longest spines found in the genus are formed. Group 24, lot 152, from Loudon, Tenn., and group 26, from between Dayton and Chattanooga, Tenn., exemplify this form. These shells have been found most abundantly at Loudon, Tenn., and on account of the large homogeneous series which forms group 24, the type specimen has been selected from the series. This is shown on plate 52, figure 12. The individuals of group 26 are more extreme in the development of their spinosity, plate 54. In this form the young shell reaches considerable size before the spines develop, as is clearly shown on the apical whorls on plate 52, and plate 5, figures 49–53.

As shown by group 24, the width of shell is modal at 17.5 mm., plate 9. The globosity of the shell is modal at 73 per cent, plate 13. The length of spines is modal at 3.3 mm., plate 17, and the space between the spines reaches its maximum at 12.5 and 13.5 mm., plate 21. Group 26 has a maximum for distance between spines at 15.5 to 16.5 mm.

The average height of spines, in groups 24 and 26, is modal at 27 per cent of the average distance between them, plate 25.

Undoubtedly this form has been confused, in collections, with *spinosa* and *turrita*.

14. *Turrita* Anthony. 1860. This is a very elongate form with numerous close-set spines and is spinose (probably) throughout life. A typical form is shown from group 27, lot 187, on plate 55, figure 13, from Bellefonte, Ala. It is a dead shell from the site of an ancient Indian camp. The mode for shell width is at 22.5 mm., plate 9. The degree of globosity was not determined for these old shells. Spine height is modal at 2.8 mm., plate 17, and the distance between the apices of the spines is modal at 11.5 mm., plate 21. The average height of spine is 27 per cent of the average distance between the spines, plate 25.

The narrowness of the space between the spines allows a greater number per whorl than if the space was larger as in *loudonensis*.

THE GEOGRAPHIC RELATIONS OF THE SHELLS EXAMINED.

As the shells were collected a special effort was made to secure an exact record of the location, particularly with regard to such landmarks as might enable others to closely approximate the location. Such records are an essential part of a study of this character because, at times, there is a great diversity among the shells within even a limited segment of a stream, and further great changes are made in the streams with increasing population. In order to preserve a record of such local diversity, the shells from the same shoals or the same portion of the stream (except, in general, when only scattered individuals were found) were given the same "lot" number. Later, after the shells had been studied, these lots were combined into "groups" for purposes of statistical comparison. Care was necessary in this grouping in order not to obscure the significant details, and yet to avoid too many units for convenient comparisons. It is here impossible to avoid the personal equation. Numerous supplementary lots, not used statistically but in other ways, are also included in this series.

In general the "groups" are numbered consecutively, beginning with the headwaters and passing downstream, the rivers being taken up in the following order: Powell, Clinch, North Fork of Holston, South Fork of Holston, Holston proper, Nolichucky, French Broad, and the Tennessee. The relative positions of these streams and the positions of the groups are shown on the map, plate 61.

Unless otherwise indicated the shells were collected by the writer during the seasons of 1899, 1900, and 1901. The distances given are taken from the topographic sheets of the United States Geological Survey or are from the maps or data of the United States Army Engineers. For geographic details the topographic maps should be consulted.

1. POWELL RIVER.

GROUP 1. *Lot 45*. Olinger, Va. Found living in abundance below the mill dam, where the shoal contained numerous large bowlders and furnished a representative habitat for this kind of snail. September 5, 1899. Although the shoals were carefully searched, only one specimen, lot 49, was found above the mill dam, and this was about 2 miles upstream. At Big Stone Gap the North and South Forks of the Powell were examined, but no *Io* were found, although other Pleurocerids were abundant. The water of the Powell is quite clear and the bowlders are iron stained. Most of the drainage area above this point is not limestone but "freestone," as the natives call it. The rocks are carboniferous sandstones, conglomerates, and shales. Consult Estillville Folio, United States Geological Survey.

These shells are the relatively smooth *powellensis*. Undulated and keeled shells are abundant, but spinose shells are quite the exception. A large series consisting of several hundred specimens.

Supl. Lot 42. From about 3 miles below Olinger, Va. A small series, six specimens of *powellensis*.

Lot 41. Dryden, Va. About 2 miles up stream from the town. About 4 miles downstream from lot 45, September 3, 1899. Water fairly rapid, a rocky shoal with a slight coating of algal slime. Most of the shells found in fairly rapid water, about ankle deep or a little more. A large number of small shells were found here, the largest series of young shells found in any locality. The series consists of several hundreds of specimens of *powellensis*. These shells are shown in plate 28.

GROUP 2. *Supl. Lot 40*. From about a mile above Lyttons Mill, near Pennington Gap, Va. September 1, 1899. Four specimens, of which three are *lyttonensis* and one is relatively smooth.

Lot 39. Mile below Lyttons Mill, near Pennington Gap, Va. September 1, 1899. On a bowldery shoal. About 10 miles below lot 41. These shells are shown in plate 29. They are the form *lyttonensis* with a few smooth shells. If these smooth shells are *powellensis*, then the spinose shells of lots 45 and 41 should be considered *lyttonensis*.

GROUP 3. *Lot 106*. Pleasant Grove Shoal, 5 or 6 miles south of Rose Hill, Va. August 5, 1901. About 24 miles downstream from lot 39, near the Virginia-Tennessee line.

Lot 180. Holiday Shoals, about 10 miles from Rose Hill, Va. Collected September 4 and November 18, 1901, by John W. Pace, of Harvest, Va. *Lyttonensis*, with a very few examples of relatively smooth shells. Many shells were slightly injured during shipment so that the series is about three times larger than is indicated by the number used in the quantitative study.

GROUP 4. *Lot 38.* From McHenrys Ford to Bussels Ford, about 3 miles south of Shawanee, Tenn. August 31, 1899. Rocky bottom. About 69 miles from lot 45, the headwater shells.

This series is from the vicinity of Cumberland Gap, and is from about the same region where the Powell River is thought by Campbell ('94) to have turned northward and flowed through Cumberland Gap as a tributary to the Cumberland River in Kentucky. Shells smooth, intergrading and spinose.

Lot 37. Powell River Station, Tenn. On the Knoxville and Middlesboro branch of the Southern Railroad, above Island Ford. August 30, 1899. Cf. Maynardville sheet, U. S. G. S. These shells were taken from Bryant Shoals, above the mouth of Gap Creek, on downstream to Powell Station. Gap Creek heads near Cumberland Gap. The proximity of these shells to Cumberland Gap is also to be noted. Gap Creek does not contain these shells, as it is too small a stream.

The shells of lots 37 and 38 are shown in plate 31. The series does not appear homogeneous. Their relations are doubtful. The shells which are at first smooth and become spinose are thus related to *lyttonensis.*

GROUP 5. *Lot 29.* Greens Ford, extreme southwestern corner of Claiborne County, Tenn. The river bottom was rocky. August 23–24, 1899. About 34 miles from lot 38. Spinose shells with a few of *powellensis.*

Lot 28. Powell River P. O., Campbell County, Tenn. About 4½ miles below Greens Ford. Rocky bottom. August 23, 1899.

Lot 31. Craigs Ford, mouth of Cedar Creek, about 3½ miles above the mouth of Powell River at Agec, Tenn. Gravel bottom. August 22, 1899.

Lot 30. Mouth of Powell River, Agec, Tenn. August 22, 1899. The distance covered by this group is about 15 miles, and the fall of the river is about 3 feet per mile for this distance. From Big Stone Gap to the mouth of Powell River is 117 miles.

The affinities of the shells of group 5 are similar to those of group 4, and are of similar uncertain relationship.

2. CLINCH RIVER.

In southwestern Virginia, along the Norfolk & Western Railway, Clinch River drainage is reached at Tip Top (Pocahontas sheet). But on account of the small size of the stream it was not examined until Kelly or North Tazewell was reached (Tazewell sheet). Here the stream was found dammed, and I was told that it had been so for many years. No trace of *Io* could be found, not even weathered shells, either below the dam or upstream above its influence. At Cedar Bluff sand and gravel bars were carefully examined but with only negative results. At Cleveland, Va., however, about a mile above the town, I found the first live specimens of *Io.* Three dead shells were also found at Cleveland, lot 193.

GROUP 6. *Supl. lot 194.* Finney Siding, Va. Below the mouth of Big Cedar Creek, on a sandbar. August, 1899. Two fragments of shells, one smooth and the other with incipient nodules. As these shells are worn, the living shells are probably still farther upstream. These furnish the known upstream limit in the Clinch.

Supl. lot 198. Cleveland, Va., and upstream to near the mouth of Big Cedar Creek. August 3, 1899. Thirteen specimens of dead shells were found along the river, *clinchensis.*

Lot 56. Cleveland, Va. Found on a shoal, about 1 mile upstream. Collected by J. L. Litton from a bar near his home, about the middle of November, 1899. This is the series of shells figured in part on plate 34. These are the form *clinchensis.* A good series.

Supl. lot 193. Cleveland, Va. August 1, 1899. A series of four specimens, three of which were dead, and the first live specimen taken. One of the dead shells is nodulose on most of the body whorl.

Supl. lots 197 and 217. Cleveland, Va. August, 1899. Two series of dead shells taken from the river. These are of the same kind as the living ones. Such collections of dead shells from gravel bars show how reliable such collections are as samples of the local *Io* population. It required hours of work to find the dead shells in this part of the river.

GROUP 7. *Lot 11.* St. Paul, Va., on a rocky shoal about a mile and a half below the town. August 5, 1899. About 23 miles downstream from lot 56. The type specimen of *paulensis* is from this lot.

Lots 14, 16, and 52. St. Paul, Va., as above. August, 1899.

Lot 53. Wheelers Ford. St. Paul, Va. October, 1899. Collected by N. F. Blevins, and sent alive to me at Chicago. These snails were received October 28 and kept alive for several months in an aquarium. From St. Paul it is about 53 miles downstream to the Virginia State line.

Supl. lot 12. St. Paul, Va. Dead shells found at sites of old Indian camps. August, 1899. The series contains immature and adult shells and is a fair sample of those found living in the river.

Supl. lot 6. Between St. Paul and Dungannon, Va., near the mouth of Bull Run Creek. August, 1899. A small series.

Supl. lot 50. Dungannon, Va. August, 1899.

GROUP 8. *Lot 170.* Grears Ford, about 1 mile below Dungannon, Va. Bristol sheet. Collected by T. W. Stratton, of Clinchport, Va., during July, 1901. Thirty-six shells.

Lot 166. About one-fourth of a mile above Wood P. O., Va., Estillville sheet. Collector, T. W. Stratton, July, 1901. Thirty-seven shells.

Lot 168. Just below the mouth of Stony Creek, Fort Blackmore, Va. T. W. Stratton, July, 1901. Thirty-five shells.

Lot 51. About the third shoal below the mouth of Stony Creek, near Fort Blackmore, Va., August 12, 1899.

Lot 164. Pendleton Islands, 2 miles below the mouth of Stony Creek, Fort Blackmore, Va. T. W. Stratton, July, 1901. About 13 miles above Clinchport, Va. Twenty shells, much like lot 55, from Clinchport.

Lot 167. Just above the "Suck," about 4 miles below Fort Blackmore, Va. T. W. Stratton, July, 1901. Thirty-nine shells.

Lot 165. Sallings Ford, about 4 miles below Fort Blackmore and above Crafts Ferry, Va. T. W. Stratton, July, 1901. Twenty-seven shells.

Lot 169. Stanus Bend, 2 miles above Crafts Ferry, Va. T. W. Stratton, July, 1901. Sixteen shells.

Supl. lot 161. From a bend in the river one-half mile below Crafts Ferry, Va. T. W. Stratton, July, 1901. Fifteen strongly spinose shells.

Group 8 consists of many small lots of shells, and extends over about 14 miles of the river. The shells are just beyond the transitional stage from the smooth to the strongly spinose forms, and are the form *paulensis*.

GROUP 9. *Supl. lot 160.* Near Fort Blackmore, Va. Just below Crafts' milldam, below the mouth of Stony Creek. Collected by T. W. Stratton, July, 1901. Fifteen shells.

Supl. lot 162. Stanton Shoals, Va., about 1 mile below Crafts Mill. Collected by T. W. Stratton, July, 1901. Fifteen shells.

Supl. lot 174. Carters Ferry, 3 miles above Clinchport, Va. T. W. Stratton, July, 1899. Twenty-nine shells.

Supl. lot 171. Clinchport, Va. Just below the mouth of Stock Creek. T. W. Stratton, July, 1901. Eighteen shells.

Lot 55. Clinchport, Va. Indian Shoals, near McDonald's sawmill. Collected in the latter part of September, 1899, by T. W. Stratton. Estillville sheet, U. S. G. S. Consult plate 37.

Supl. lot 172. Indian Shoals, about 100 yards below McDonald's sawmill, Clinchport, Va. T. W. Stratton, July, 1901. Thirty-two shells.

Supl. lot 173. Clinchport, Va. Thomas Shoals, 1 mile below the town. T. W. Stratton, July, 1901. Twenty-three shells.

Supl. lot 163. From below Venables mill dam at Speers Ferry. T. W. Stratton, July, 1901. Seventeen shells.

Group 10. *Lot 17.* About 4 miles above Kyle Ford, above Sneedville, Tenn. August 15, 1899.

This lot came from a very limited area, a rocky bar across the river, and in the relatively shallow and moderately swift water. These shells were very abundant. About 20 miles downstream from Clinchport. They are the form *brevis.*

Supl. lot 196. Four dead shells taken from a sandbar below the milldam, near Kyle Ford, Tenn. These are of the same character as lot 17.

Group 11. *Lot 18.* Between Kyle Ford P. O. and Sneedville, Tenn., extending over about 12 miles of the river. August 16, 1899. Jonesville sheet.

Lot 21. Upper part of Thirtymile Shoals, between Cloud Ford (southwest of Xenophon, Morristown sheet) and the mouth of Big Sycamore Creek, Tenn. August 18, 1899.

Supl. lot 24. Also from the Thirtymile Shoals, which end at about Sheltons Ford. August, 1899. Maynardville sheet.

Lot 20. Needhams Ford, Little Barren, Tenn. August 19, 1899. Maynardville sheet.

Lot 32. Agec to Offut, Tenn. August 25, 1899. The Powell River unites with the Clinch at Agec, about 89 miles above the mouth of the Clinch.

Lot 34. Offut to Clinton, Tenn. August, 1899. Covering about 10 miles of the river. Four shells only.

Supl. lot 216. Clinton, Tenn. August, 1899. Three very spinose shells.

Supl. lot 188. Hickory Creek Shoals, Knox County, Tenn., north of Loudon. Collected in spring of 1904 by W. L. Julian. Loudon sheet. These are fragments of three dead shells, much worn and evidently derived from farther upstream. About 29 miles above the mouth of the river at Kingston and 30 miles below Clinton.

Supl. lot 154. Two spinose fragments of dead shells were taken in the Clinch at Kurry's Island north of Loudon, Tenn., in October, 1901, by W. L. Julian. This is the downstream limit observed for these shells in this river.

Distance from Artrip, Va., the upper limit of *Io* in the Clinch to the mouth at Kingston, about 290 miles.

3. HOLSTON RIVER DRAINAGE SYSTEM.

a. North Fork of Holston.

Group 12. *Lot 79.* Saltville, Va. From above the "alkali works" upstream for 2 or 3 miles. August 20, 1900. Abingdon sheet.

This is probably the type locality for *Io fluvialis* Say. The shells of lot 79 were collected most abundantly from large flat rocks in moderately swift water, which was generally less than knee-deep. Many large bowlders occurred in the river at this place. The river was examined for several miles farther upstream, but no more shells were found. As far as my observations go this lot represents the headwater limits of these shells. It is probable, however, that the upper limit reaches a few miles farther upstream.

At and below the alkali works the refuse flowing into the river has covered all the rocks and the bed of the stream with a whitish coating. Natives reported that fish had been killed in great quantities by this refuse. Had this factory been located a few miles farther upstream, *Io* would have become extinct in all this portion of the stream. Such influences show the importance of studying the animals of our streams before such pollution.

At about 25 miles below this factory, at Holston, Va. (Bristol sheet), the North Fork was again examined on August 13, 1901. Below the mill, the river apparently afforded an excellent habitat for *Io*. The water was shallow, about a foot deep, with an abundance of large rocks covered with a slimy algal growth, and varied in current from eddy to that of moderate swiftness. The water was clear, and yet no shells were found. I then examined the river for about a mile upstream, above the ford. Here favorable looking situations were found on the flat and angular rocky bed of the stream, and farther upstream a fine shoal was found. Although the water was very clear, so that the bottom could be very carefully examined, no *Io* were found, except an old weathered shell. I was told by a resident that occasionally the "alkali" refuse came down in such a quantity as to give the river a milky color. In this we probably have an adequate explanation for the scarcity of the shells. Unionidæ were present, however, as shown by the bivalves on the banks where they had been opened by raccoons or muskrats.

Supl. lot 191. Mendota, Washington County, Va. October 13, 1900. Northwest of Bristol. Bristol sheet. This locality is downstream from Holston about 17 miles and 42 from Saltville. This is the county from which the type of *spinosa* Lea is said to have come, but evidently this is an error.

About a half dozen shoals were examined while ascending the river for 3 or 4 miles. The conditions seemed favorable, but no live *Io* were found, although three dead and worn shells were obtained; one was a smooth shell, the others are undulated. These shells are apparently nearer the Saltville shells than to *verrucosa.*

Supl. lot 116. Holston Bridge, Va., 2½ miles east of Big Moccasin Gap, Va. August, 1901. Estillville sheet. This series consisted of 3 live specimens and 19 dead shells. The individuals are all rather nodulose and similar to those found at Bluff City on the South Fork, lot 94. They are thus strictly transitional between *fluvialis* from Saltville, lot 79, and the spinose shells farther downstream.

Supl. lot 111. Holston Bridge, Va., 2½ miles east of Big Moccasin Gap, Va. August 11, 1901. Ten fresh shells. Estillville sheet. This is about 25 miles downstream from Mendota. There is a marked change in the character of the *Io* shells; they approach those of the South Fork (*verrucosa*) rather than those of Saltville. It is unfortunate that the details of the transition in the North Fork are so little known. A reëxamination of the river should be made upstream from this point. Compare with lot 178, from near the mouth of the North Fork.

Another feature of interest is the proximity of this portion of the river to Big Moccasin Gap, plate 59, and hence its bearing upon changes in drainage.

About 15 miles below this locality the North and South Forks of the Holston are confluent at Rotherwood, Tenn., and form the Holston trunk stream. It is about 80 miles from Saltville to Rotherwood.

b. Middle and South Forks of the Holston.

The conditions for examination of the Middle Fork of the Holston were unfavorable on account of the recent rains and the vast quantities of yellow clay which discolored the water. A search was made, however, at Seven Mile Ford, also south of Glade Springs, Va. The South Fork apparently does not drain as much of a limestone area as the Middle Fork, because its waters were clearer. At Holston Mill and near Friendship, Va., the waters were clear, the shoals apparently favorable, but no *Io* were found. The probabilities are that *Io* does not occur in the Middle Fork, nor in the South Fork, above the junctions of the two streams near Barron, Va. I examined the streams at this place (and the South Fork upstream as far as Damascus, Va.) with considerable care, but found no evidence of them upon the rocky shoals which abound in the Middle Fork near its mouth or on the sandbar below the junction where the railroad crosses the South Fork. Cf. Abingdon sheet.

GROUP 13. *Supl. lot 115.* Fishdam, Tenn. This locality is downstream from the confluence of the Middle Fork of the Holston about 15 miles. It may be reached from Bristol, Tenn., by a narrow-gauge lumber railroad, the Holston Valley Railroad. At Fishdam there is a large shoal with many bowlders. The river was a little high, so that only dead shells of *verrucosa* were found here August 31, 1901. This lot gives the known upstream limit in the South Fork of the Holston. Abingdon sheet.

Supl. lot 120. Fishdam, Tenn. One live *Io verrucosa* was found here September 7, 1901. A number of dead shells were also found, thus establishing the type for the locality. The water was very clear and the bottom could be clearly seen in water knee-deep. Shoals, islands, and sluices were examined for about 3 miles upstream. Several apparently very favorable places were seen, but the only results were those stated above.

Supl. lot 157. Fishdam, Tenn. While in this series perfect and fresh shells are too limited for detailed statistical study, yet this large series gives a good sample of the *verrucosa* population. Collected by John A. Offield, October, 1901. A few shells (10) were in excellent and fresh condition.

Supl. lot 121. Grant, Tenn. About 5 miles downstream from Fishdam, September 7, 1901. About 1½ miles southeast of Ruthten, Tenn. Bristol sheet. This is a series of dead and weathered shells found upon a sand bar near the railway bridge.

Lot 94. Bluff City, Tenn. About 16 miles downstream from Fishdam, October 12, 1900. These shells were taken from a strip of the river reaching from the mill above the town downstream and past it for about one-half mile. The shells were widely scattered and could not have been found without clear water. The water of this stream when clear is a beautiful blue-green, quite in contrast with the "freestone" areas, where the iron stains the bowlders and river bed and thus gives a dark background for the water. Roan Mountain sheet.

A previous examination had been made of the river at this point on August 23, 1900, but rains had so roiled the water that only dead shells were found upon the sand bars, lot 192. This fact is of interest for its bearing upon the reliability of such sand-bar samples as an index to the presence of the shells in a given locality. Elsewhere such a criterion became of much value. This is the form *verrucosa,* plate 41.

Supl. lot 158. Bluff City, Tenn. Collected by W. M. Madison, November 18–23, 1901.

Supl. lot 192. Bluff City, Tenn. Sand-bar collection of dead shells. August, 1900.

The Watauga River was examined at Carter, Tenn., where the Southern Railroad crosses it; and also at Elizabethtown, Tenn., but no *Io* were found at either place. The headwaters of the Watauga are largely from "freestone." This stream joins the South Fork of the Holston about 11 miles below Bluff City and about 18 miles above Rotherwood.

GROUP 14. *Supl. lot 112.* Peltier, Tenn., now called Lovedale. This locality on the South Fork is about 2 miles above the confluence of the North and South Forks of the Holston. There is a large island in the river at this point; and at its head, among the gravel, were found large numbers of dead but no fresh *Io* shells. August 11, 1901. These shells appear intermediate between *recta* and *verrucosa,* but this is due to the fact that the sharp points of the spines have been worn off during transportation. Evidently *recta* reaches upstream above Peltier. This is a large series of several hundreds of specimens.

Lot 175. Kingsport, Tenn. Collected by May Netherland, October 11, 1902. Estillville sheet. These are the form *recta.* A large series.

Lot 178. Jourdans Dam, above Rotherwood, Tenn. Near the junction of the two forks of the Holston. November 2, 1902. Collected by May Netherland. This lot is really in the North Fork of the Holston, but it is here included because of its intimate relation to the South Fork shells, which are also *recta.* A large series of shells.

Supl. lot 176. Kingsport, Tenn. Horse Ford, November 2, 1902. Collector, May Netherland. Forty-two shells in this lot.

Supl. lot 177. Kingsport, Tenn. Lynns Ford, one-half mile east of town, November 2, 1902. Collector, May Netherland. Ninety-one shells in this lot.

Supl. lot 179. Kingsport, Tenn. May 18, 1901. Collector, May Netherland. A large collection of several hundred shells, of the form *recta.*

It should be recalled that much of the South Fork drainage comes from a mountain district. In the vicinity of the junction of the Middle and South Forks (Barron, Va.) it rained every day for about three weeks (August and September, 1901), and many of these rains were such downpours that the river became a raging torrent. The Watauga drains even more mountainous country, and these conditions easily account for the destruction of these shells noted in lot 112. (Cf. Ayers and Ashe, 1905, p. 91.)

c. Holston River (proper), Rotherwood to mouth.

GROUP 15. *Supl. lot 86.* Curry Ford, Tenn., southeast of Church Hill. September 26, 1900. Estillville sheet. A series of about 10 shells.

Supl. lot 85. Hord Ford, New Canton, Tenn. September 26, 1900. Estillville sheet. Two shells, one resembling *recta* and the other undulate and relatively smooth on part of the body whorl.

Lot 97. Chissolms Ford, Burem, Hawkins County, Tenn. Collected by David Hayes during the latter part of September, 1900. Greenville sheet. This and lot 98 are remarkable for containing smooth, spinose, and shells which are both smooth and spinose.

Lot 98. Same locality as above and about the same date, collected by David Hayes. About 23 miles below Rotherwood.

Group 16. *Lot 87.* Rogersville, Tenn. About 2 miles south of town, from a shoal below the Southern Railway bridge. September 26 and 27, 1900. This is a bowldery shoal with rock bottom. The shells were much more abundant upon the bowlders than upon the rock bottom. Both smooth and spinose shells occur here on the same shoal. Rather young shells were also found here. Morristown sheet.

Lot 88. Rogersville, Tenn. From the shoals above the Southern Railway bridge, near the mill. Not so abundant on the flat rock surfaces as below the bridge, lot 87. September 28, 1900. About 39 miles from Rotherwood.

A very remarkable feature of the Rogersville shells is the abundance of the smooth *fluvialis* (?) type of shells, after their scarcity or absence between this group and the intervening river up to lot 111, Holston Bridge, Va., about 48 miles upstream. A few smooth shells are also found in lot 90. The abundance of these shells, elsewhere found in *headwaters only,* is certainly remarkable, as is also the character of the intergrading forms.

Group 17. *Lot 90.* Cobb Ford, Tenn., between Three Springs and Mooresburg. September 28, 1900. Morristown sheet. On the ford, where the water was about ankle deep, the younger shells largely occured. A little farther upstream, where the water was about knee-deep, the current was swifter and large shells were found under the edges of the large bowlders. This is a series of about 400 shells.

These shells are remarkable for the large number of moderately small individuals and the very small number of smooth, *fluvialis* shells. This locality is about 14 miles below Rogersville, yet the character of the shells has greatly changed toward the *spinosa* type. This locality is 53 miles below Rotherwood.

Group 18. *Lot 96.* Holston Station, Tenn., 4 miles north of Morristown. From Long Ferry to about one-fourth of a mile below the railroad bridge. Abundant. September 10 and 11, 1900. In moderately quiet water. About 13 miles below lot 90. There was much algal growth on the boulders. Most of the *Io* were taken on the quiet, shallow, and inner sides of the bend of the river, about 66 miles from Rotherwood. The original number of shells in this lot was 343. The individuality of this lot, particularly with regard to height of spines, was such as to warrant its separate grouping. There was one smooth shell in this lot. These shells are the form *spinosa.*

Supl. lot 91. Strawberry Plains, Tenn., Galt Island, about 3½ miles upstream from the station to the town, including the shoal at a fish trap and a small island above town. September 29, 1900. About 25 miles above Knoxville and about 121 miles from Rotherwood. A series of 13 shells, apparently *spinosa* and *loudonensis.*

At McBees Ford, northeast of Strawberry Plains, several shoals were examined, particularly those west of McBees Island, but no shells were found. About 35 miles above Knoxville and about 110 miles from Rotherwood.

Supl. lot 123. Dopes Bar, 15½ miles above Knoxville in the Holston River. Collectors, Sam George and Henderson. September 25, 1901. About 130 miles below Rotherwood, and about 10 miles below lot 91. These shells appear to be *loudonensis.*

Supl. lot 203. Boyds Shoal, Holston River, about 5½ miles above Knoxville, Tenn. November 16, 1900. Collector, Sam George. This is near the mouth of the Holston.

From the confluence of the North and South Forks of the Holston at Rotherwood to the mouth of the Holston it is about 141 miles.

4. NOLICHUCKY, LOWER FRENCH BROAD, AND TENNESSEE RIVERS.

a. Nolichucky.

The Nolichucky is formed by the confluence of the Caney and North Toe Rivers in the mountains of North Carolina, a short distance southwest of Roan Mountain. (Cf. Roan Mountain sheet.) This mountain stream at the time of heavy rains becomes a raging torrent. When this stream was examined late in the summer of 1901, destruction by floods was very evident. Islands which I had seen the year before as good farms or covered with dense forest, were now bare bowlder beds in the river, or only the wrecked remains of islands with trees uprooted and soil swept away. In places the driftwood, fence rails, household wreckage, and furniture covered the ground several feet deep. In other places what had been fertile bottom land was buried by abandoned sand bars; in still other places "scours" were formed where the rapidly flowing current had cut deep into the black soil. In some places where nearly a foot of soil had been washed from the fields, old Indian camp sites were exposed, as was shown by the burnt soil, the cracked bowlders, and fragments of pottery and camp refuse.

All these demonstrations of the destructive power of the floods have an important bearing upon the nature of the rapid water or shoal habitat of *Io*, because such influences are often particularly vigorous upon shoals where the fall of the stream is marked. The destruction of the forests upon these mountains, and the consequent increase in destructive floods is certainly a condition unfavorable to the perpetuation of *Io* in these streams.

The Nolichucky River was examined in 1900 to within about 15 miles of its headwaters. This was in East Tennessee at Love, a small station about 3 miles up the river from Erwin. The river in this vicinity contained many large bowlders. Large sand bars were also examined but no traces of *Io* were found. A number of apparently favorable localities between here and Embreville were examined but with the same results. The soil of this region was sandy, the bedrock "freestone," the vegetation composed of pines, cedars, holly, ivy, and laurel. All of these conditions show that this is not a limestone region.

About 2 miles below Embreville (Roan Mountain sheet), at Deadericks Island, is a fine shoal with large bowlders, shallow water, and apparently ideal condition for *Io*. These shoals were carefully searched both in 1900 and 1901 but no traces of the shells were found, although the water was perfectly clear. During October, 1900, the shoal at the mouth of Cherokee Creek was examined but no *Io* were found. The water was very clear and the bowlders in swift and eddy waters, furnished apparently an ideal habitat for them.

For many years the Deadericks had maintained a sawmill on their island, and an active logging business was carried on. The battering of the shoals by the logs would be a condition decidedly unfavorable for *Io* shells.

The only information which I have been able to find of the occurrence of *Io* shells in this particular part of the river is from Mr. H. M. Deaderick, an intelligent resident who had in his collection of Indian relics two *Io* shells, lot 182. These he thought came from the Nolichucky at this point. These were the only shells in the collection. Both of these are of the smooth *Io* shell type and have the appearance of Rogersville shells from the Holston River.

Particular attention should also be called to the fact that the eastern boundary of the limestones on the Nolichucky is at about this locality, and that this is probably the limiting factor in this stream.

GROUP 19. *Lot 119.* Conkling, Tenn. Dead shells from an Indian camp between Graham's house and the wagon bridge. September 5, 1901.

This lot of shells is the farthest upstream record for the Nolichucky River. Greenville sheet. About 75 miles above the mouth of the river. These are the form *unakensis;* a large series of specimens.

Lot 118. Broylesville, Tenn. Indian camp on the river bank. Dead shells. September 3, 1901. Also *unakensis;* 53 specimens. About 8 miles downstream from Conkling. There is an island in the river at this point and the gravels about it were carefully examined, but no *Io* shells were found.

It might well be questioned if such dead shells really came from the Nolichucky; and might be contended that they are not a fair index of shells from the vicinity. On the other hand the shells from the headwaters of the Nolichucky River can readily be told from those found in any other stream and are perfectly characteristic. This is an example of the general rule, that the shells found at the old Indian camps are a fair index of the local *Io* fauna.

Supl. lot 219. A dead shell with an abnormal canal was found in the river at Fullen (Chuckey City), Tenn., above Earnest Bridge.

Supl. lot 182. Deadericks Island (?); 3 miles below Embreville, Tenn. Presented by H. M. Deaderick. Two smooth shells.

Supl. lot 117. Limestone, Tenn. Dead shells (42) from an Indian camp, 2½ miles below Limestone, Tenn. About 13 miles below Conkling. These are *unakensis.* In one shell a high keel replaced the normal spines.

Group 20. *Supl. lot 81.* From near Springvale, Tenn. Morristown sheet. These are *nolichuckyensis.*

Supl. lot 80. Near the Joseph Thompson farm, Springvale, Tenn. September 5, 1900. About 60 miles from Conkling.

Supl. lot 220. From the Joseph Thompson farm, Springvale, Tenn. On the bottoms of the Nolichucky.

Lot 83. East of White Pine, Tenn. A shoal with large bowlders, September 7, 1900. About 10 miles below lot 80.

Lot 104. White Pine, Tenn. Collected by J. J. Thompson, October, 1900. Morristown sheet. Near the mouth of the Nolichucky. These are the form *nolichuckyensis.*

b. French Broad River.

Above the mouth of the Nolichucky the French Broad was examined at Asheville, Hot Springs, and Paint Rock, N. C., and at Bridgeport, Tenn., where a fine shoal was found but no trace of *Io.* Upstream from this point the area drained by the French Broad is out of the limestone area so that these shells could hardly be expected, and search confirmed this. The Big Pigeon River was examined at Newport, Tenn., where fine shoals were found, but there was no evidence of the shells. It thus seems fair to conclude that *Io* does not extend its range far above the mouth of the Nolichucky. The upper limit of *Io* in the French Broad is given by the single shell found below the mouth of the Nolichucky (lot 82) on Hills Shoals.

Group 21. *Supl. lot 82.* Below the mouth of the Nolichucky, in the French Broad River, on Hills Shoals, Tenn., September 6, 1900. A single immature shell of *nolichuckyensis.*

Lot 136. Byrnes Shoals, 2 miles below Dandridge, Tenn. Collector, Sam George, October, 1901. About 27 miles below the mouth of the Nolichucky River. Morristown and Mount Guyot sheets. Most of these are the form *loudonensis*, and a smaller number are *angitremoides.* A series of 72 shells.

Lot 137. Hanging Rock Shoals, Boyd Creek, Tenn. Collector, Sam George, October, 1901. About 46 miles below the mouth of the Nolichucky River. About 25 miles above the mouth of the French Broad. Knoxville sheet. Shells similar to those of the preceding lot; 42 shells.

Supl. lot 156. Seven Islands Shoals, northeast of Gap Creek, Tenn. Collector, Sam George, November, 1901. About 57 miles from the mouth of the Nolichucky and 15 miles from the mouth of the French Broad. Knoxville sheet. Almost exclusively *loudonensis,* one shell of *turrita* (No. 55). A plate was once planned of these shells, but as they were so much like the shells on plate 49, figures 1 to 16, the plate was not used.

Supl. lot 195. Seven Islands, Gap Creek, Tenn. Dead shells (22) from an old Indian camp on an island opposite the mill. All are *turrita,* some are very large and heavy shells

The Little Pigeon River was examined about Catlettsburg, Tenn., and also about its mouth, but no *Io* were found.

c. Tennessee River.

The Tennessee River is formed by the confluence of the French Broad and the Holston Rivers, about 4½ miles above Knoxville, Tenn. Consult Robert, 1893, pp. 33–35, for table of distances.

Group 22. *Supl. lot 47.* Dickinsons Island, Knoxville, Tenn. This island is about a mile below the confluence of the Holston and French Broad Rivers. Shells presented by Charles T. Simpson. A small series of immature *loudonensis* shells.

Supl. lot 124. Knoxville, Tenn. Looneys Island, about 9 miles below Knoxville. Collected by Sam George and Henderson. September 26, 1901. These are the form *angitremoides.*

Lot 100. Lyons Shoals, about 12 miles below Knoxville, Tenn. Collectors, Sam George and C. C. Adams. October 7, 1900. A few individuals of *loudonensis,* but shells with spinose apices *turrita,* are predominant in this large series.

Supl. lot 101. Lyons Shoals, about 12 miles below Knoxville, Tenn. October, 1900. Collector, Sam George. This is a series of completely spinose shells. There is a chance that I have transposed the data of lots 100 and 101, but the localities are in close proximity.

Supl. lot 102. Williams Shoals, 14 miles below Knoxville, Tenn. October 11, 1900. Collector, Sam George. This lot is composed almost exclusively of spinose *turrita* shells and a very few of *loudonensis.*

GROUP 23. *Lot 105.* Little River Shoals, at the mouth of Little River, 16½ miles below Knoxville, Tenn. A series loaned by the late Mrs. George Andrews, of Knoxville, Tenn. A very large series, of several hundred, composed of *loudonensis* and *turrita.*

Supl. lot 103. Little River Shoals, 16½ miles below Knoxville, Tenn. Collectors, Sam George and Henderson. October 11, 1900. Eighty-two shells not mature, a few of *loudonensis,* but the great majority are *turrita.*

GROUP 24. *Lot 152.* Loudon, Tenn. About Sams Island and downstream to Huffs Ferry. Collected in fall of 1901 by W. L. Julian. This is a very large series of several hundred specimens, only a part of which has been used for statistical study. About 48 miles downstream from lot 105; from the headwaters about 65 miles. Mainly of the form *loudonensis,* a very few individuals of *turrita.*

Supl. lot 126. Loudon, Tenn. September 30, 1901. Collectors, W. L. Julian and C. C. Adams. *Loudonensis* and a very few of *turrita.*

Supl. lot 134. Loudon, Tenn. Collected by W. L. Julian, fall of 1901. *Loudonensis,* with a very few of *turrita.*

Supl. lot 130. Loudon, Tenn. Collected by W. L. Julian. Late in September, 1901. Fourteen specimens, *loudonensis* and *turrita.*

Supl. lot 189. Loudon, Tenn. Sams Island and Huffs Ferry. Collected by W. L. Julian in the spring of 1904.

This group is one of the finest series of *Io* shells secured from any locality, and much credit falls to W. L. Julian for his faithful work in collecting them.

The Little Tennessee River empties into the Tennessee River opposite Lenoir, Tenn. This is about 15 miles upstream from Loudon. On October 1, 1901, I examined the Little Tennessee at Coytee, where there is a shoal. Several small islands were also examined, but although the condition of the water looked favorable no *Io* shells were found. A little later in the season W. L. Julian repeated the examination at Coytee Shoals and also examined the stream at Carpenters Island. Although the river was very low, he found no shells. This stream largely drains a nonlimestone area.

The Clinch River joins the Tennessee at Kingston, 104 miles above Chattanooga and about 84 miles from the headwaters of the Tennessee.

GROUP 25. *Lot 155.* Rockwood Landing, King Creek, Tenn. Dead shells from an Indian shell heap near the ferry landing, on the east bank of the river. This locality is about 15 miles below the mouth of the Clinch River at Kingston, Tenn., and 38 miles below Loudon; about 99 miles from the headwaters. Kingston sheet. A series of large individuals of *turrita* and *loudonensis.* Consult plate 53.

GROUP 26. *Lot 183.* Rockwood Landing, King Creek, Tenn. From Crabtree Landing, above the ferry. October 10, 1901. South of Rockwood, Tenn. Three shells of *loudonensis.*

Supl. lot 185. North Dayton, Tenn. October, 1901. One dead shell of *turrita.*

Lot 150. East of Dayton, Tenn., at Cotton Port, Tenn. One large shell of *loudonensis.* October, 1901. Cleveland sheet.

Supl. lot 149. Near Rathburn, Tenn, Dead shells from the island at the mouth of Soddy Creek. November 14, 1901. Chattanooga sheet. One fragment of *turrita* and 3 of *loudonensis.*

Lot 184. Moon Bar, above Bells Landing, above the mouth of Hiwassee River, east of Dayton, Tenn. October 8, 1901. Four shells of *loudonensis.*

Lot 151. Head of Hiwassee Island, at the mouth of the Hiwassee River. East of Dayton, Tenn. October 13, 1901. Shells in deep water, knee to waist deep. About 150 miles from the headwaters. A series of 30 specimens, mostly large individuals of *loudonensis.*

Supl. lot 203. Chattanooga, Tenn. Taken from the Tennessee River just above the Cincinnati Southern Railway bridge. October 5, 1904. Collector, J. Jones.

Lot 201. Chattanooga, Tenn. Just above the Cincinnati Southern Railway bridge in the Tennessee River at the Balon Bar. Collected in 1903 by Charles Pollard. Three shells of *loudonensis.*

Lot 202. Chattanooga, Tenn. Just above the Cincinnati Southern Railway bridge in the Tennessee River. October 5, 1904. Collected by J. Jones. About 181 miles from the headwaters. Fourteen specimens of *loudonensis.*

Supl. lot 199. Chattanooga, Tenn. Taken above the Cincinnati Southern Railway bridge, above the city at Walkers Island. Collector, Charles Pollard. A fresh specimen of *loudonensis* and a dead one of *turrita.*

Supl. lot 200. Chattanooga, Tenn. Large dead shells taken from an Indian mound on the Hunter farm 15 miles northeast of city, by G. D. Barnes, of Chattanooga. Two large specimens of *turrita.*

This group of shells covers a long stretch of the river, about 90 miles, but this has been necessary on account of the very rapid reduction in the number of specimens below Loudon, Tenn. Chattanooga is 188 miles from the headwaters of the Tennessee River and 104 miles from the mouth of Clinch River.

The Hiwassee River was examined October 9, 1901, but the conditions were not favorable on account of high water. An island about a mile above the new Kincannon Ferry was examined but no shells were found. This stream is too well graded for *Io.* It is depositing, as is clearly evidenced by the extensive mud banks which line the stream, and there were no shoals. These are conditions unfavorable for *Io.* The stream was again examined on October 16, at Charleston, Tenn. (Cleveland sheet), but here again the river was up. A local river man did not know the shell, nor were any found in the old Indian camps, although other molluscan shells were found in such places. The mud banks here were much like those at the mouth of the river.

South Chickamauga Creek was examined on October 21, 1901, at Ringgold, Ga. I had been told that the shells were here, but no evidence of them was found. Some places looked favorable, except that the stream appeared to be much too small.

Below Chattanooga the Tennessee River enters the "mountain section" where it traverses the mountain for about 40 miles and is then joined by the Sequatchie River. This small river was examined October 29, 1901, at Dunlap, Tenn., about 32 miles above the mouth. Where the stream was not dammed, it was about 75 or 100 feet wide. At the time the examination was made the water was quite clear and several miles of stream were thus carefully examined but no specimens of *Io* were found. A local fisherman who had fished much of the stream had not noticed this kind of shell.

A few miles below the mouth of the Sequatchie, at Bridgeport, Ala., several bars and other favorable looking habitats were examined without finding even dead shells. So that below Chattanooga I found only one live *Io,* all the others were deal shells, and all of these were found at the sites of old Indian camps on the banks of the river.

GROUP 27. *Supl. lot 186.* Bridgeport, Ala. On the Widows Bar, 4 or 5 miles above the town. I was told that the Government officials had blasted out this bar about three years previously. A single live specimen and the last live shell that I found was taken October 26, 1901. It gives the downstream limit of live *Io* in my collecting. About 50 miles below Chattanooga, and 237 miles from the headwaters, the junction of the Holston and French Broad, above Knoxville. This is an immature specimen of *loudonensis.*

Lot 143. Bridgeport, Ala. Dead shells from old Indian camp above the town near the Widows Bar. November 1, 1901. Stevenson sheet. About 50 shells of *turrita,* including some very large individuals.

Lot 146. Bellefonte, Ala. Dead shells from old Indian camps at head of Bellefonte Island, at mouth of Mud Creek, November 10, 1901. Three shells of *turrita.*

Lot 187. Bellefonte, Ala. Dead shells from old Indian camps just above Sublet Ferry (west bank). November 10, 1901. Over 25 specimens of *turrita.*

Lot 148. South of Dodsonville, Ala. Two or three miles above Pine Island. Dead shells of *turrita* from a shell heap or Indian camp, in McCamy's field. November 11, 1901. There was quite a little shoal water in the region. This is about 15 miles above Guntersville, which is 292 miles from the headwaters and 105 miles from Chattanooga, and forms the extreme southern limit. This was the downstream limit for the genus *Io* in my collecting. The shells appeared to be more scarce in this region than they were at Bellefonte and Bridgeport. Scottsboro sheet.

Below Cowley Landing search was made in the region of Guntersville, Ala. (Gadsden sheet). About 2 miles above the mouth of Town Creek were large shell heaps, at an old Indian camp. This and two other small sites were carefully examined but no *Io* were found. A similar search was made at Manchester and Fort Deposit below Guntersville where there were large shell mounds, particularly at Manchester. In all, about half a dozen of these heaps were examined, and although they contain many other molluscan shells, the desired kind was lacking.

Farther downstream at Hobbs Island, near Whitesburg, Ala., an intelligent fisherman did not know *Io.* At Whitesburg there is a very large shell heap on the river bank. This is sectioned and exposed by the cutting of the river so that it could be seen to extend along the bank for about one-fourth of a mile, and had a height of from 1 to 2 feet. This immense shell heap was composed largely of Unionid shells. The undercutting had strewn shells along the river margin in large numbers. Even with these exceptional opportunities for examination no *Io* were found.

In the vicinity of the Muscle Shoals, above Florence, Ala., there is a vast area of what appears to be a favorable habitat for *Io.* The river here spreads out over an extensive rock bottom. This region was examined (November 4, 1901) and large shell heaps were found. At the Elk River Shoals, near Miltons Bluff (354 miles from the headwaters), one heap was found at the south bank, about one-fourth of a mile upstream from the bluff. Here Unionids, Strepomatids, and Viviparids were present in immense quantities. On the following day a large shell heap, "Penniewinkle Mound," was examined. This is on the north bank of the river near the head of the canal. This remarkable heap is about 300 feet long, and about 25 feet high, and is composed largely of Viviparid shells. If *Io* was present in this part of the stream, it seems that such a collection could hardly be made without accidentally including some specimens of *Io.* Furthermore, local fishermen, familiar with Viviparids, did not know *Io.*

It may appear that the search of the lower part of the river below Guntersville was unnecessary, but it seemed the safest course to follow, particularly as there appeared to be a possibility of an isolated colony on the Muscle Shoals. The apparent absence of these shells in the lower reaches of the river examined seem to indicate that the shells are not indefinitely rolled or washed downstream but tend to be relatively local; an inference further supported by other data. It is probable that the shells become eroded and corroded at a rate which prevents their extensive downstream transference through the long reaches of eddy water.

Since my examination of the Tennessee River, through the kindness of the veteran collector, Mr. A. A. Hinkley, of Dubois, Ill., I have examined the *Io* shell which he collected on November 10, 1904. It was collected by him alive, and the remains of the dried animal and the operculum now remain with the shell. Mr. Hinkley's label is as follows: "*Io spinosa* Lea. Tennessee River at the foot of Muscle Shoals, south shore, with *Angitrema* and *Anculosa,* which were very numerous. This specimen was the only *Io* found." The apical portion of the shell is badly eroded, so that the character of the apical whorls is unknown, but I am inclined to consider this *turrita.*

This shell forms the extreme downstream known limit of *Io,* and at the same time its extreme western limit.

QUANTITATIVE VARIATION OF IO.

1. VARIATION IN SHELL DIAMETER.

The quantitative study of variation is a subject which has received very little attention from the students of fresh-water mollusca, and even qualitative studies of variation in these animals have rarely been considered from a geographic and environmental point of view. The character of the variation in *Io* is of such a nature that some quantitative method seemed essential for comparative studies. It was found difficult to secure adequate series for this purpose, not only on account of the large number of individuals needed, but also on account of the difficulty of securing perfect specimens. On account of the thin edge of the peristome it is quite liable to injury, especially during shipment. In several localities dead weathered shells from the sites of Indian camps had to be utilized, and such shells are very frequently injured. Often a small number of individuals is found toward the limit of range, and the smallness of such series tends to introduce errors in quantitative studies. Perhaps the greatest source of error is due to the fact that it is practically impossible to sort the shells into *homogeneous* series, on account of the imperfection of the specimens, their graduated age, the intergradations from one extreme form into another, and to irregularities of development.

The dimensions of the shell were measured upon the last whorl. The diameter of the shell was determined by spreading the caliper from near the upper angle of the aperture to the opposite side of the shell. The length of the aperture was measured from the upper angle to the end of the canal. All measurements were made in millimeters, and tenths were estimated.

The entire series of shells will be discussed by groups and rivers in the following order: Powell, Clinch, Holston, Nolichucky, French Broad, and Tennessee; and in general from the headwaters progressively downstream. It should be borne in mind that we are dealing with averages, modes or the prevailing class of the same dimension, or other maxima, and for brevity this is assumed in the discussion.

a. Powell River.

Group 1. This is composed of a very large series from the headwaters and contains numerous young, and small-sized shells, which are largely smooth or with low spines, plate 28.

By reference to the platted curve, plate 6, group No. 1, it is seen that the mode occurs at 15.5 mm. A diameter of 15.5 mm. may be taken to indicate the normal size of adult shells. The numerous young clearly explain the skewness of the lower side of the curve, and its uniform lower slope is an expression due in part to the completeness in the series from young to adults.

Group 2. These shells are from about 10 miles farther downstream than the preceding group. Young shells are not abundant among this series, plate 29.

The curve, plate 6, No. 2, shows by its narrowness and single mode at 17.5 mm. that the shells have a greater average diameter or are larger by 2 mm. than in the preceding group. The skewness on the lower left side is in harmony with that of the preceding group.

Group 3. This series is from about 25 to 30 miles below the preceding group. It is a series of fairly mature shells, plate 30.

The curve, plate 6, No. 3, shows a large proportion of relatively large shells with a maxima at 17.5 and 18.5 mm., making them, as a group, the largest shells in the Powell River. The occurrence of these large shells, not the farthest downstream, but in the vicinity of Cumberland Gap, is a point of interest.

Group 4. Roughly estimated, this group was found about 30 miles below the preceding and in the vicinity of Cumberland Gap, plate 31.

As shown in plate 6, No. 4, the curve is broadly truncated with a broad apex ranging from 16.5 to 18.5 mm., and thus includes within its range the modes of groups 2 and 3. The skewness on the lower left side is marked. This is quite a variable group, as is shown by the breadth of the curve and the broad apex.

Group 5. Roughly estimated, this series is from about 30 miles downstream from the preceding group and about 100 miles from group 1. They are from the region of the lower course of the Powell, plates 32 and 33.

This curve, plate 6, No. 5, is remarkable in that its mode is at 15.5 mm., and therefore the same as in the headwater shells of group 1, while its skewness is on the opposite or upper side of the curve, distinctly leaning toward group 4. The variability, as indicated by the breadth of the curve, is similar to that of group 1.

The Powell as a whole.—In considering the diameter of the Powell River shells as a unit, they are remarkable for their definite relations. This is a rather variable headwater group, with a mode at 15.5 mm. This indicates a small shell, and progressively downstream the diameter increases (in groups 2 and 3) with modes at 17.5 and 18.5 mm., respectively, and finally through a variable transitional series (group 4) returns, as the lower course is reached, to a mode (group 5) at 15.5 mm., the same as in the headwaters, but with a skewness on the upper side toward the transitional group 4.

The range of variation of the extreme groups shows a remarkable similarity, one with a left and the other with a right handed skewness. There is thus a general progressive downstream increase in the diameter or size of the shell, and some reduction in variability, except in the extreme lower course, where there is a reduction in size and an increase of variability closely paralleling the headwater shells. It should be recalled that the headwater shells are mainly smooth and those downstream are spinose and that the most variable group (4) is a mixed series of some relatively smooth and many spinose shells.

b. Clinch River.

Group 6. These shells are from the headwaters of the Clinch and are quite mature and large shells and are smooth, plate 34.

The curve, plate 7, No. 6, shows that the shells are of large size, with the mode at 18.5 mm., and with a minor maximum at 21.5 mm. Young shells were relatively few in this group, and this in part explains the steepness of the lower side of the curve. The skewness of the upper slope, with the minor mode at 21.5 mm., shows that the shells are quite variable. These are the largest shells found in the Clinch, and not the smallest as might be anticipated.

Group 7. From about 23 miles farther downstream than the preceding group, plate 35.

The curve, plate 7, No. 7, shows that these shells are smaller, with a single well-defined maximum at 17.5 mm. The narrowness of the curve shows relative stability, as contrasted with the variability of the preceding group, and yet these shells show great variation in spinosity from a smooth to a spinose shell.

Group 8. This group of shells is from a long segment of the river which begins about 16 miles below the preceding group and extends over about 14 miles of the river, plate 36.

The curve, plate 7, No. 8, shows that the shells are narrower or smaller than those of the two preceding groups, much more variable, as shown by the breadth of the curve and the maxima at 16.5 and 14.5 mm. The number of immature shells in this group is a factor which has perhaps influenced the lower portion of the curve.

Group 9. This is a series of mature shells from a limited section of the river at Clinchport, Va., plate 37.

The curve, plate 7, No. 9, shows that the shells have increased in diameter, are much more stable than the preceding group, and have a mode at 17.5 mm.

Group 10. This series is from a very restricted locality, and might be expected to be fairly homogeneous. The curve, plate 7, No. 10, shows the mode at 17.5 mm., the prevailing modal condition for this river, plate 38.

Group 11. This group came from that part of the river into which the Powell empties, and includes the Thirtymile Shoals. The Powell enters the Clinch about 89 miles above the mouth of the Clinch, plate 39.

The curve, plate 7, No. 11, shows the mode at 17.5 mm. with groups 7, 9, and 10, but with greater variability, as shown by the breadth of the curve. The skewness of the lower side of the curve with a maximum at 14.5 mm., approaches that of group 5, from the lower Powell with its mode at 15.5 mm.

The Clinch as a whole.—In considering the shells of the river as a whole, it is seen that the headwater shells have the greatest diameter, 18.5 and 21.5 mm., are relatively variable, and progressively downstream they become narrower (groups 6, 7, and 8). Farther down the diameter again increases to 17.5 mm. (groups 9, 10, and 11), but the variability is limited in groups 9 and 10, and increases much in group 11. Groups 8 and 11 are the most variable and the narrowest shells. Group 6 is smooth; group 7 is a mixture of smooth and spinose; while the shells of the remaining groups are largely spinose.

c. Holston River System.

Group 12. These smooth shells, from the type locality of *Io fluvialis,* are from near the headwaters of the North Fork of the Holston, and are mature shells, plate 40.

The curve, plate 8, No. 12, shows relative stability and a mode at 18.5 mm. The relative absence of young shells is undoubtedly a cause of the steep slope of the lower side of the curve.

Group 13. These are nodulose shells from the South Fork of the Holston at Bluff City, and are largely mature shells, plate 41.

The curve, plate 8, No. 13, shows a relatively variable series with a mode at 18.5 mm. Many shells reach 20.5 mm., and are thus relatively large shells, and recall group 6 from the headwaters of the Clinch.

Group 14. This series is from about 20 miles downstream from the preceding group, and from near the confluence of the North and South Forks of the Holston, plate 42.

The curve, plate 8, No. 14, shows the shells to be larger than those of the preceding group and with a mode at 20.5 mm., which is the greatest modal diameter of any group yet considered. The skewness of the upper side of the curve at group 13 is in harmony with that of the lower side of this group. In general, the group is intermediate between groups 12 and 14.

Group 15. This series is from the headwaters of the Holston River proper, about 25 miles downstream from the preceding group. This group is composed of both smooth and spinose shells, plate 43.

The curve, plate 8, No. 15, shows a reduction from the maximum diameter of 20.5 mm., reached by the mode of the preceding group, to 19.5 mm., and with two important secondary maxima at 16.5 and 14.5 mm. The extreme variation indicated by these maxima is due in part to immature shells, and primarily to the transitional character of the shells from smooth to spinose. Even a superficial inspection of this group makes evident its remarkable complexity and uniqueness.

Group 16. This series is also composed of both smooth and spinose shells, and is about 16 miles downstream from the preceding group. From the vicinity of Rogersville, Tenn., plate 44.

The curve, plate 8, No. 16, is about as remarkable as the preceding, and continues the transitional character initiated by it. The mode is at 16.5 and 15.5 mm., with a secondary maxima, at 13.5 mm., and the skewness of the upper side of this curve corresponds roughly with the same tendency, though to a less degree, shown on the lower side of group 15.

Group 17. A series from about 14 miles downstream from the previous group. It is a spinose series containing a large number of young shells, plate 45.

The curve, plate 8, No. 17, shows a mode at 12.5 mm. This extremely small diameter is remarkable. It may be due, in part, to the large number of young and spinose shells, but immaturity can hardly be the sole factor because of the definite tendency toward smaller diameter already shown in the preceding upstream, groups 16, 15, and 14, and its harmony with the next following downstream, group 18. The influence of the young shells may have shifted the mode 1 or 2 mm. smaller, but it is an undeniable fact that there has been a very marked change in the character of the shells below Rogersville in this river. This group contains (with the one exception of group 20) the lowest mode (12.5 mm.) for the genus, even smaller than those of the Powell River.

Group 18. This series is from about 13 miles below the preceding one, and is spinose. From the lower course of the Holston, near Morristown, Tenn., plate 46.

The curve, plate 8, No. 18, shows the tendency for the downstream shells of the Holston to become narrower, but not to the extreme degree shown in the preceding group. The mode is at 14.5 mm., with a skewness toward increased diameter.

Holston system as a whole.—When we consider the Holston system as a unit, it is seen that the headwater shells have a relatively large diameter, as the modes are at 18.5 mm. (groups 12 and 13). The mode for the largest shells is 20.5 mm. (group 14). Below this point in the river the diameter rapidly decreases and becomes quite variable, the maxima ranging from 19.5 to 13.5 mm. (in groups 15 and 16); but in group 17 it again becomes relatively stable and low, with a mode at 12.5 mm. The extreme downstream group increases some in diameter and has a mode at 14.5 mm. (group 18). Groups 15 and 16 are thus transitional in shell diameter, between the headwater and downstream groups, a result of the mixture of both kinds in these localities. This has been done by a mingling of the smooth and spinose kinds of shells.

The superimposed curves show that group 14 stands with a mode at the extreme of shells with great diameter, 20.5 mm., and group 17 stands at the other extreme with its mode at 12.5 mm.; but between these maxima occur at several intermediate points.

d. Nolichucky, French Broad, and Tennessee Drainage.

Group 19. This series is composed of dead shells from the site of an Indian camp near Conckling, Tenn., on the Nolichucky River. They should be considered headwater shells. About 75 miles above the mouth of the river, plate 47.

The curve, plate 9, No. 19, shows that the mode occurs at 15.5 mm., and also that a secondary maximum occurs at 18.5 mm. This means a considerable relative variability for these headwater shells.

Group 20. This series is from near the mouth of the Nolichucky, plate 48.

The curve, plate 9, No. 20, shows a mode which indicates the least diameter of shells from any locality, and therefore for the genus, at 11.5 mm., and yet some individuals have very wide shells. The extremely small diameter is undoubtedly due to the large proportion of young shells which the group contains. The skewness of the upper side of the curve is in harmony, not only with the preceding group, but also with the following one, and is therefore of significance. Had it not been for the large number of young, the mode would probably have been at about 13.5 mm.

Group 21. This group is composed of shells from three localities in the French Broad, near Dandridge, about 25 miles below the mouth of the Nolichucky, plate 49.

The curve, plate 9, No. 21, shows a mode at 16.5 mm., indicating a wider shell and greater variability than in that of group 19. A secondary maximum occurs at 20.5 mm., and indicates much variation. Inspection of the plate shows that the series is not homogeneous.

Group 22. This series represents the headwater shells of the Tennessee River proper. They are from Lyon Shoals below Knoxville, plate 50.

The curve, plate 9, No. 22, shows a surprisingly small diameter, with a maximum at 12.5 to 14.5 mm. Here the youth of the shells is probably a factor in giving such a low maximum to the group, because the shells are largely the narrow form *turrita*. In shell diameter this group stands intermediate between the two Nolichucky groups, 19 and 20.

Group 23. This series is from the Little River Shoals, about 12 miles below Knoxville, Tenn. The shells are largely mature individuals, plate 51.

The curve, plate 9, No. 23, shows the mode to occur at 18.5 mm., and its limited range suggests relative stability. Curiously this series is not homogeneous but is composed of two forms, *loudonensis* and *turrita*, a fact to be remembered throughout this discussion.

Group 24. From Loudon, Tenn., about 40 miles below the preceding group. Large spinose shells, plate 52.

The curve, plate 9, No. 24, shows the mode to be at 17.5 mm., and a similar limited variability as in the preceding group; but the upper side of the curve shows a skewness which becomes more pronounced in the succeeding groups, and thus merits notice.

Group 25. From about 40 miles below Loudon, below the mouth of the Clinch River. Dead shells from Indian shell heap, plate 53.

The curve, plate 9, No. 25, shows a wide range of variation and the large size of the shells. The maximum range from 18.5 to 21.5 mm. The secondary maximum at 15.5 mm. is significant as shown by the plate, for it indicates the *turrita* type; the widest shells are *loudonensis*.

Group 26. These fresh shells are of value, as they tend to corroborate the worth of the preceding group of dead shells. This series extends over the river from the preceding group to Chattanooga, a distance of about 90 miles, plate 54.

The curve, plate 9, No. 26, shows much the same range as the preceding group, and has maxima at 15.5, 17.5, and 22.5 mm. But as their number is rather limited, little emphasis can be placed upon them. But if both groups 25 and 26 are considered, they confirm the fact of the increased diameter of the shells in this course of the river. These shells are *loudonensis.*

Group 27. This group includes only dead shells found at old Indian camp sites, from the vicinity of Bridgeport to Dodsonville, Ala., plate 55.

The curve, plate 9, No. 27, shows a well-defined mode at 22.5 mm., and suggests relative stability, although numbers of individuals are rather limited. These shells are the large individuals of *turrita.*

Nolichucky, French Broad, and Tennessee drainage as a whole.--Taking this drainage as a whole, it is seen that the modal dimensions run the entire scale from 11.5 to 22.5 mm. The Nolichucky contains the smallest shells with modes at 11.5 and 15.5 mm. for groups 19 and 20. The single group from the French Broad shows an increase in diameter, with 16.5 mm. as the mode. The secondary maximum at 20.5 mm. is probably due in the main to specimens of *loudonensis.* The Tennessee shells show a maximum ranging from 14.5 to 12.5 mm. in group 22 (the immature *turrita*); and a marked increase to 18.5 mm. in group 23 (adult shells). The mode drops to 17.5 mm. at Loudon in group 24, while the groups 23, 25, 26, and 27 all show some increase in the diameter of the shell in both *loudonensis* and *turrita.* Group 27, from the extreme lower range of the genus, exclusively *turrita,* appears to show greater stability than that in groups 25 and 26. This series, then, shows the greatest amount of variability, a fact which is not remarkable, in a way, because of the extensive area covered by it and the variety of forms composing it.

2. VARIATION IN GLOBOSITY OR SHELL INDEX.

In addition to the diameter of the shell, the length of the aperture was measured from its upper angle to the extreme tip of the canal. The diameter of the shell also gave absolute dimensions, which were desirable for comparative purposes. At the same time it was desirable to have some index which would give relative values. This has been secured by dividing the length of the aperture by the diameter of the shell: $\frac{\text{length of aperture}}{\text{diameter of shell}} = \text{shell index}$. This gives a measure of the aperture in terms of the shell diameter and may be considered a measure of globosity. It should be recalled that 100 per cent means that the diameter of the shell and the length of the aperture are of the same magnitude.

a. Powell River.

Group 1. By reference to the curve, plate 10, No. 1, it is seen that the mode occurs at 77 per cent globosity and that the normal form of the curve indicates relative stability.

Group 2. The mode occurs at 75 per cent and lies almost entirely within that of group 1.

Group 3 modes at 77 per cent and closely parallels group 1.

Group 4 has its mode at 71 and 73 per cent, but its irregularities suggest greater variability.

Group 5 falls even lower in its mode, this occurring at 69 per cent, and it is also variable.

Taking the stream as a whole, it is seen that the groups fall into two distinct classes:

(1) The first includes groups 1, 2, and 3, which have high indices and have a high degree of globosity, 75 or 77 per cent, are relatively stable, and are headwater groups.

(2) The second includes groups 4 and 5, which have relatively low indices, 69, 71, and 73 per cent, are relatively variable, as shown by the broad curves, and are downstream groups.

b. Clinch River.

Group 6. The curve, plate 11, No. 6, shows a very high index, with the mode at 83 per cent.

Group 7 has a lower modal index, at 77 per cent, and with a secondary maximum at 81 per cent, thus clearly showing a skewness related to the preceding group.

Group 8 continues the progressive modal decline to 73 per cent and has a similar significant skewness.

Group 9 drops modally to 71 per cent, while *Group 10* stands intermediately between groups 8 and 9.

Group 11 has the same mode as group 9, at 71 per cent.

Taken as a whole, the almost uniform decline in globosity from the headwaters downstream, from a mode at 83 to 71 per cent, is very remarkable for its uniformity. The position of group 10 is intermediate between groups 8 and 9 and is the only irregularity. This group is related to the shells of the lower Powell in globosity. The headwater groups 6 and 7 show an individuality, higher index, and greater variability than those from farther downstream, which also show a similar individuality, a low index, and relative stability.

c. Holston River System.

Group 12. The curve, plate 11, No. 12, shows a moderately high index at 75 per cent, with a skewness which recalls the curve of group 7 in the Clinch.

Group 13 declines modally to 73 per cent and also shows a skewness toward a higher index.

Group 14 continues the progressive modal decline to 71 per cent.

Group 15 checks the modal decline and returns to 73 per cent and closely approximates group 13 in the character of its curve.

Group 16 also has the mode at 73 per cent, with a marked secondary maximum at 69 per cent.

Group 17 has its maximum from 71 to 73 per cent, and thus carries the decline beyond 73 per cent.

Group 18 continues the decline by a double-peaked maximum at 71 per cent and at 67 per cent, and gives the lowest mode for the Holston.

Considering the Holston as a whole, there is seen to be a somewhat wavering yet progressive and definite decline in the degree of globosity from the headwaters downstream, the headwater group and the extreme downstream group representing the extremes in this respect. Group 12 has a mode at 75 per cent; group 13 declines to 73 per cent; group 14 even to 71 per cent; group 15 increased it to 73 per cent. Group 16 remained at 73 per cent, but had a secondary maximum at 69 per cent; group 17 continued the decline to 71 per cent, and group 18 carried it from 71 per cent down to 67 per cent. The distinctness of the curves for groups 12 and 18 is so marked as to be worthy of special mention. The groups as a whole appear relatively variable.

d. Nolichucky, French Broad, and Tennessee Systems.

Groups 19, 25, and 27 are composed of dead shells which on account of injury could not be used for shell index.

Group 20, plate 13, No. 20, has a relatively low mode at 73 per cent, with a lower skewness.

Group 21 has the highest index for this system, with a mode at 77 per cent and a secondary maximum at 73 per cent.

Group 22 declines to the opposite extreme, with a mode at 69 per cent; but, as in the preceding group, there is a skewness toward a higher per cent, and thus these extremes meet.

Group 23 has its mode at 75 per cent; *Group 24* at 73 per cent, and *Group 26* at 75 per cent, with a secondary maximum at 69 per cent.

Taking the series as a whole, at first glance there seems to be much chaos. Group 21 has its mode at 77 per cent and is at one extreme, while group 22, at 69 per cent, is at the other modal extreme. Between these at 73 per cent groups 20 and 24 are located and at 75 per cent groups 23 and 26. The central position of group 20, between the extremes and at the point of the secondary maxima, is of interest. The shells from the Tennessee River proper, groups 23, 24, and 26, reach their maxima at 73 or 75 per cent.

If all groups are considered, it is clearly evident that the headwater group in the Powell, Clinch, and Holston tend to be relatively globular, while the downstream groups are relatively narrow or elongated. In the remainder of the groups examined, the upper part of the

Tennessee and French Broad are relatively globular on account of the presence of the shells of *loudonensis*, while the relatively elongate shells, which abound in the Nolichucky and the Tennessee, are the form *turrita* and its allies.

3. VARIATION IN SPINOSITY.

The variation in this genus, from the smooth shells to the most spiny kinds, is perhaps their most striking feature and one of their most variable characteristics. It should be recalled that nodules and spines, of the character found in this genus, are of rare occurrence in the family Pleuroceridae, but sculptured surfaces, produced by carina, nodules, and low spines are of frequent occurrence. The two genera which show the greatest sculptural tendencies are *Io* and its nearly related genus *Angitrema*. The smooth shells of *Io* show little resemblance to *Angitrema*, but the spinose shells, particularly the form *angitremoides* from the Tennessee and the Nolichucky Rivers show much superficial similarity to *Angitrema armigera* Say.

The tendency to form spines is thus seen not to be solely confined to this genus, although it receives its greatest development in it. In order to study the variation in this trait, quantitative estimates have been made of it. The last two or three spines formed on the last whorl have been measured. It must be recalled that this whorl may be smooth or show all gradations to strong spines. These spines are the latest formed and are thus less liable to be injured, and are most likely to give the adult condition. They are also, in general, the largest spines. A serious difficulty, for comparative purposes, is the difference in size of the shells which is due to age; but we have not been able to see how to overcome this difficulty, without at the same time running the risk of an equal or greater error due to the personal equation. At any rate, the curves show the condition of the population at a given place, even if it is occasionally influenced by the inequality due to age. But in general the definiteness of the results gives confidence to their general reliability. No effort has been made to carry the statistical method to its full extent. There are several reasons why this has not been done. Only to one familiar with the material can the chances for errors in handling such a collection be realized. The spines were in many cases eroded or slightly injured; how much, no one can tell. To cast out all such material would soon present serious difficulties of even greater importance than a slight error in spine height, because of the limited number of specimens that would remain. Then again, erosion or injury of the spines is not uniformly distributed among the shells. And lastly, the incipient stages of spinosity could not be measured with much accuracy, as, for example, when only one spine was present, or some irregularity of the shell could not be distinguished from a spine, or the spines or nodules were too far apart, etc. In localities where the relatively smooth shells are present many individuals may be spinose and become less so or even smooth on the body whorl. As the spines were measured on this whorl such "inverted" spinose individuals must count as smooth shells. In groups where the smooth and spinose are mixed the smooth shells were counted and placed in the lowest class. I cite such cases to emphasize that caution is necessary in drawing conclusions from such material.

I have tried to draw conclusions only within relatively safe limits. Undoubtedly the greatest source of error is due to the heterogeneous character of the groups, but as mentioned, I have found no practicable way of avoiding this.

All measurements have been made in mm., the tenths having been estimated. These determinations have been made by the use of an instrument designed by Dr. C. B. Davenport, which measured the depth of the valley between the spines and the distance between the apices of the spines. The spine index is derived by dividing the average height of the spines by the average of the distance between them.

a. Height of Spine.

A. POWELL RIVER.

Group 1. This series of shells were smooth or with low spines, as indicated by the curve, plate 14, No. 1, with its mode at 0.3 mm.

Group 2 also shows its mode at 0.3 mm., but with a decided skewness toward 1.3 mm.

Group 3 has a mode at 1.8 mm.—a modal condition not surpassed in the Powell.

Group 4 unexpectedly drops in spine height to a mode at 1.3 mm. It also shows by the maximum at 0.3 mm. the influence of the nodular or smooth shells. This is the most distinctly transitional group in the Powell, as its mode is intermediate between the modal extremes.

Group 5 represents the extreme degree in spine height found in the Powell, with its mode at 1.8 mm.

Taking the stream as a whole, the groups fall into two distinct series: Those which are composed primarily of smooth and low spines, not exceeding 0.8 mm. (groups 1 and 2), and those which are spinose and have a mode at 1.8 mm. spine height. Group 4 is intermediate modally at 1.3 mm. In general there is a progressive increase in spine height from the headwaters downstream, with the lagging increase of group 4.

B. CLINCH RIVER.

Group 6. The curve for this series has a mode at 0.3 mm., plate 15, No. 6. The shells were practically smooth with traces of nodules.

Group 7 also shows a mode, plate 15, No. 7, at 0.3 mm., but with a tendency toward increasing spinosity.

Group 8 has two maxima, one at 1.3 mm. and a similar one at 0.3 mm.

Group 9 has greatly increased in spine height to a mode at 2.3 mm., although it almost equaled the mode at 1.8 mm., and shows a progressive increase.

Group 10 drops back to a lower mode at 1.8 mm., and a skewness toward 1.3 mm.

Group 11 again advances to a mode very similar to that of group 9.

As in the case of shell index, spine height shows a similar and rather uniform progressive change from headwaters downstream. The headwater groups 6 and 7 are relatively spineless; group 8 is a mixed series of smooth and spinose, but the spines are low, with a mode at 1.3 mm.; group 10 lags with its maxima at 1.3 and 1.8 mm.; while groups 9 and 11 advance to extreme spine length at 2.3 mm.

C. HOLSTON RIVER SYSTEM.

Group 12. This series, as shown by the curve, plate 16, No. 12, has its mode at 0.3 mm., and are practically smooth shells.

Group 13 increases in spinosity and has a mode at 0.8 mm. This is a unique condition.

Group 14 has greatly increased and has its maxima at 1.8 and 2.3 mm.

Group 15 shows an anomalous curve with its mode at 0.3 mm., with a sprawling range to 1.8 mm.

Group 16 shows great similarity to the preceding group and has its maxima in harmony with it at 1.3 and 1.8 mm. Both of these groups have remarkable relative variability.

Group 17 has a mode at 1.8 mm. and is intermediate between groups 13 and 14, on account of its numbers at 1.3 mm.

Group 18 is like group 14, with its maxima at 1.8 and 2.3 mm.

In general terms, in spite of the irregularities, there is an increase in height of spines from the headwaters downstream. The most marked exception, and really a remarkable one, is in the case of groups 15 and 16. They are not only anomalous for the Holston but are not equaled elsewhere in their mixed character. The progressive change is shown, in group 12, with a mode at 0.3 mm.; group 13, with a mode at 0.8 mm., and groups 14 and 18 with modes at 1.8 mm. and almost reached a mode at 2.3 mm. While group 17 has its mode also at 1.8 mm., it has a large frequency at 1.3 mm.

D. NOLICHUCKY, FRENCH BROAD, AND TENNESSEE SYSTEMS.

Group 19. In marked contrast with the previous streams, there are no smooth headwater shells. Even those farthest upstream, plate 17, No. 19, show a mode at 1.8 mm., and are thus comparable with the most spiny shells from the Powell.

Group 20. This also has the same mode as the preceding, at 1.8 mm., but the tendency toward higher spines is greatly developed.

Group 21, with its mode at 2.8 mm., shows a marked increase in length, and the low sprawling curve indicates considerable variability.

Group 22 declines to a mode at 2.3 mm. and appears relatively stable. This is a curve similar to what we might expect from the lower Nolichucky in a series of adult shells.

Group 23 carries the mode again forward to 2.8 mm.

Group 24 advances the mode on to 3.3 mm.

Group 25 has a mode at 2.8 mm. This is due to the large individuals of the form *turrita*, and the form *loudonensis*. This group is based on a small series.

Group 26 is based also upon few specimens, the mode is at 4.3 mm., but a secondary maximum is at 3.3 mm., which is clearly due to the young shells.

Group 27 shows a very great decline in spine height from that of the preceding group to a mode at 2.8 mm. These shells are all of the elongated form *turrita*. This decline is probably due to the absence of *loudonensis*.

Taking these series as a whole there appears to be much confusion, but if the shells are sorted into two main series, one containing chiefly shells which are spinose throughout post embryonic development—such as *turrita* and its allies, and the other composed of shells which are at first smooth and which become spinose later—such as *loudonensis*, much more regularity is found. We will first consider the *turrita* series. Beginning with groups 19 and 20 it will be seen that the modes, and maxima, increase from 1.8 mm. to 2.3 mm. in group 22, and on to 2.8 mm., in group 27, which is composed solely of *turrita*. There is thus a progressive downstream increase in spine height in this series. Let us now consider the *loudonensis* series. These shells are absent in the Nolichucky and group 21 is a mixed series (some of the *turrita* allies are present), but it is primarily a *loudonensis* population. Here the mode is at 2.8 mm. In group 24 the mode has increased to 3.3 mm., and in group 26 the mode is at 4.3 mm. Thus there is a progressive downstream increase in the length of the spines, not only in *loudonensis* but also in *turrita* and its allies, just as there was a similar change in the Powell, Clinch, and Holston Rivers.

b. Distance between Spines.

A. POWELL RIVER.

Group 1. These shells were almost entirely smooth or with low spines with a short distance between them, as is seen by the curve, plate 18, No. 12, No. 1, with a mode at the 0.5 mm.

Group 2 also has its mode at the 0.5 mm. class, which includes the smooth shells, and has the mode for the spinose shells at 7.5 mm. There is thus a very marked discontinuity.

Group 3 contains only a few individuals in the smooth class, but reaches a very distinct mode at 8.5 mm., which shows that the distance between the spine crests is progressively increasing and has reached the maximal distance for the Powell as a whole.

Group 4 shows an unexpected increase in the smooth class, with a well defined maximum at 0.5 mm.; and the mode for the spinose shells is at 7.5 mm., and thus coincides with group 2.

Group 5 again carries forward the mode to 8.5 mm., and thus has as great a distance between the spines as group 3.

Taking the Powell as a whole, there is of course the greatest discontinuity which exists between smooth and spinose shells. The mode of the smooth shells falls in the 0.5 mm. class and of the spinose shells at 7.5 mm. and 8.5 mm. This shows that the distance between the spines does not vary more than 1 mm. in the position of the modes. Groups 2 and 4 are the most intermediate groups, as was the case in spine height. The same groups are also the most variable. Group 3 is relatively the most stable, with a mode showing a distance of 8.5 mm. between the spines.

B. CLINCH RIVER.

Group 6 is composed of spineless shells, plate 19, No. 6.

Group 7 has its mode with the spineless or 0.5 mm. class of shells, and has a mode for spinosity at 6.5 mm. for distance between spines.

Group 8 also has its mode with the spineless shells and a mode similar to the preceding group for distance between spines at 6.5 and 7.5 mm. Both of these curves show considerable relative variation in the spinose shells.

Group 9 shows a great increase in the distance between spines, with its mode at 9.5 mm.

Group 10 is very similar to the preceding and with the same mode.

Group 11 largely coincides with the two preceding groups, but shows greater relative variability.

Considering the stream as a whole, there is the marked discontinuity between the smooth and spinose shells, with group 8 as the transitional one. Groups 7 and 8 are relatively variable, and groups 9, 10, and 11 relatively stable. The shells with short spines have also a short distance between them. From the headwaters downstream there is a general increase in the distance between the spines, from spineless shells to those having modes at 6.5 mm., 6.5 to 7.5 mm., and on to 9.5 mm.

C. HOLSTON RIVER SYSTEM.

Group 12. As shown by the curve, plate 20, No. 12, these shells are practically spineless.

Group 13 shows marked discontinuity and with two maxima, one for the relatively smooth shells at 0.5 mm., and the other, the mode for spinose shells, is at 6.5 mm.

Group 14 shows a very wide distance between the spines, with a maximum from 10.5 mm. to 11.5 mm., and thus the greatest distance yet found between the spines.

Group 15 shows a remarkably variable group with the mode at 8.5 mm. and a spinose maximum at 8.5 mm. For this group reservations must be made with regard to spinosity, because of the apparent exaggeration of smoothness through the *dropping of spines on the last whorl,* while the previous ones were spinose.

Group 16 is similar to the preceding, but the mode has declined to 7.5 mm. It is also relatively variable.

Group 17. This series very closely approximates the spinose shells of group 13 and has a mode showing a distance between spines at 7.5 mm., both of which show relative stability.

Group 18 stands somewhat transitional between the maxima at 7.5 mm. and that at 10.5 mm. It has a mode at 9.5 mm. and is a variable group.

Taking the shells of this system as a whole, considerable variability is shown. The discontinuity between the spineless and the spinose continues, as in the preceding rivers. Another marked feature is shown by the narrow distance between the groups with small spines (groups 13 and 17) and the greater distance between those (groups 14 and 18) with the larger spines. The relatively wide distance and relative variability of groups 15 and 16 are unique.

D. NOLICHUCKY, FRENCH BROAD, AND TENNESSEE SYSTEMS.

Group 19. There are no spineless shells in the headwaters of this stream, the Nolichucky. The modal class for distance between spines is at 7.5 mm., plate 21, No. 19, but the broad maximum extends to 9.5 mm. This is a relatively variable group, as is indicated by the truncation of the curve.

Group 20 has a mode at the same class as the preceding, 7.5 mm., and its lower range is due to its young shells. There is a minor maximum at 12.5 mm. This is also a relatively variable group.

Group 21 shows the tendency for a marked increase in the distance between spines. This is due to the presence of the form *loudonensis.* The mode has advanced to 10.5 mm. and has a broad apex at 12.5 mm. and is relatively a very variable series.

Group 22 retains the mode reached by the last group, at 10.5 mm., and is composed of young shells of *turrita.*

Group 23 again carries forward spine distance to a mode at 11.5 mm. and a further tendency toward increase, as shown by the maximum at 13.5 mm.

Group 24 maintains the advance, with a mode at 13.5 mm.

Group 25 is from the Indian shell heap and is another mixed series composed of *turrita* and *loudonensis.* The mode, evidently for the *turrita* type of shell, is at 10.5 mm., and for *loudonensis* is at 14.5, 15.5, and distinctly at 17.5 mm. This series is excessively variable, but the numbers are too small to make the modes of much significance. The great distance between the spines and the range is very remarkable.

Group 26 also shows great variability and great distance between the spines, as is shown by the maxima at 15.5 mm. and 16.5 mm. This is the maximum modal condition of significance, and this, as a group, contains the spines with the greatest distance between them from any locality. They are of the *loudonensis* type of shell.

Group 27 is of the *turrita* type, and, as might be expected, has a much narrower distance between the spines. The mode is at 11.5 mm., and the curve is remarkably symmetrical, excepting for the skewness on the upper side at 14.5 mm. These shells, from Indian camps, should be compared with the same kind in group 25 from an Indian shell heap on account of the similarity in their range of variation. In both cases the number of individuals is limited.

Taking this series as a whole, it is noticeable that on account of the lack of smooth shells, there is, of course, no discontinuity between smooth and spinose shells, as in the case of the other streams. Contrasting the headwater shells, of *turrita* affinities (group 20), with those below Chattanooga (group 27) there is seen to be a marked difference, a break which is completely bridged by an intergrading mode (group 22). Groups 21, 24, and 26 show corresponding changes in the *loudonensis* shells.

c. Spine Index.

A. POWELL RIVER.

Group 1. The spine index is the average of $\frac{\text{height of spines,}}{\text{distance between spines,}}$ and gives a percentage ratio in terms of spine height. In group 1 this index is modal at 12 per cent, plate 22, No. 1.

Group 2 has the same mode.

Group 3 shows a progressive increase to a mode at 17 per cent, in harmony with a tendency also shown in groups 1 and 2.

Group 4 shows even greater advance with a mode at 22 per cent and with a decided skewness toward the preceding groups.

Group 5 is modal at 22 per cent. Considering the river as a unit there is a downstream progressive increase of index from 12 to 22 per cent. The gradual character of the change from one extreme to another is quite remarkable.

B. CLINCH RIVER.

Group 6. Smooth shells. *Group 7* is modal as groups 1 and 2 of the Powell, at 12 per cent, plate 23, No. 7. *Group 8* has progressed to 17 per cent, *Group 9* to 22 per cent, the extreme for this river. *Group 10* has declined to 17 per cent, and *Group 11* advances to 22 per cent.

The stream, as a whole, shows greater irregularity than the Powell. If group 10 is excepted, there is a progressive downstream increase from 12 to 22 per cent, as in the Powell.

C. HOLSTON RIVER SYSTEM.

Group 12 is modal at 12 per cent, plate 24, No. 12, as is also *Group 13,* but the latter inclines toward a higher degree. *Groups 14, 15,* and *16* are all modal at 17 per cent. *Groups 17* and *18* continue to a higher mode at 22 per cent. Group 17 is transitional between the lower modes and group 18. This gradual progressive downstream increase in shell index from 12 to 22 per cent recalls that of the Powell and indicates a considerable local degree of stability.

D. NOLICHUCKY, FRENCH BROAD, AND TENNESSEE SYSTEMS.

Group 19 is modal at 17 per cent, plate 25, No. 19, a higher mode than in other headwater groups. *Groups 20, 21, 22, 23,* and *25* are clustered at 22 per cent, and *Groups 24, 26,* and *27* are at 27 per cent. If the *turrita* types are assembled, groups 19, 20, 22, and 27, their respective modes are at 17, 22, 22, and 27 per cent, a progressive series. By a similar arrangement of groups 21, 24, and 26 the modes—22, 27, and 27 per cent—are also progressive. Thus the approximately homogeneous series of shells show a progressive downstream increase in spine index.

Spine index is dependent upon two variables, the height of spines and the distance between them. If progressively downstream both varied directly, or inversely, at the same rate, the index would not change, and if spine height increased more slowly than the distance between them, the spine index would decrease downstream, but as there is an increasing index downstream it shows that the height of the spines increases more rapidly than the distance between the spines. This law, in general terms, is true for all of the upper Tennessee system.

d. Summary of the Laws of Quantitative Variation.

The Powell River shells are relatively narrow in the headwaters and become progressively wider in groups 2, 3, and 4, and near the mouth again return to the narrow modal condition. The shells of the headwater groups 1, 2, and 3 have a high degree of globosity, with modes at 75 or 77 per cent. Groups 4 and 5 show a progressive decline. Therefore globosity of the shell progressively declines downstream. Spinosity shows a general progressive downstream change. The headwater shells are relatively smooth but the change in spine height is not uniformly progressive because group 4, instead of group 3, as might be anticipated, is the transitional series from the relatively smooth to the strongly spinose kinds. The distance between the spines is less in the headwaters (groups 2 and 4) than downstream (as in groups 3 and 5). This is a progressive change toward increase in distance between them, except in the case of group 3, which was also exceptional with regard to spine height. Spine index shows a rather uniform progressive change from a low index in the headwaters to a higher index downstream.

In general, then, there is a progressive change from the headwaters downstream, as follows: From a greater diameter of the shell to less; from a high degree of globosity to one of a less degree; from a spineless to relatively long spines; from a narrow space between the spines to a wider space; and from a relatively low spine index to one of a higher degree. The change from the smooth to the spinose shell is relatively abrupt, as shown by the modes, but there is a perfect series of individual intergradations.

The Clinch shells are relatively wide in the headwaters and soon become relatively narrow and remarkably stable in all the downstream series. Group 8 is exceptional and is even narrower than the narrow headwater and downstream (groups 1 and 5) series from the Powell. The degree of globosity of the shell shows a progressive decline from the headwaters downstream. This change is nearly uniform, except that groups 8 and 10 have the same modal condition. The height of spines shows the same degree of progressive increase from smooth shells to strongly spinose ones, group 10 also again lagging in its modal condition. The distance between spines shows a rather uniform progressive change toward a downstream increase in the distance between spines, and groups 7 and 8 are the transitional steps between the extremes. The spine index shows a progressive change from a lower to a higher index, except the lagging of group 10.

In general, then, there is a progressive change from the headwaters downstream of the same general character as in the Powell. In the Clinch, group 10 is a downstream group with the characters usually found farther upstream.

As in the Powell, the transition from the smooth to the spinose shells is relatively abrupt, as shown by the modes, but all degrees of individual intergradations are found between these two kinds.

The Holston shells do not change so regularly downstream as those of the Powell and Clinch, and consequently it is much more difficult to summarize their general relations. There is a much greater diversity in the shells. This is clearly due to the distracting influence of the South Fork of the Holston, as shown by group 14, and by the unique occurrence of smooth shells far from the headwaters, as in groups 15 and 16, from near Rogersville. In general, the relations are about as follows: The comparatively wide and globular shells from the headwaters (group 12) are relatively smooth and change downstream to (group 13) a relatively wide and globular shell, with low close set spines, a relatively higher spine index, and thus grade into group 14, which has the greatest shell width for the Holston, a moderate (71 per cent) degree of globosity of the shell, very long spines, very wide apart (the widest for the Holston and wider than those of the Powell and Clinch), and a moderate (17 per cent) spine index. Continuing downstream group 15 shows a transitional stage to group 16 in width of the shell, an increase in globosity of the shell (due to the reappearance of smooth shells), a reduction in spine height and the presence of smooth shells, a reduction of the space between the spines, and an unchanged spine index. Group 16 continues the decline of shell width, the globosity of the shell (maximum at 69 per cent), smooth shells, and the low spines remain about stationary, but the distance between the spines is reduced, and the spine index remains stationary. Group 17 shows extreme reduction in shell width, about a stationary condition in the globosity of the shell, an increase in spine height, a relatively stationary condition with regard to the distance between spines, and an increase of spine index. Group 18 is only excelled in shell width by group 17, in globosity of aperture it is not excelled, it is equal to group 14, in distance between spines it is only excelled by group 14, and forms the extreme limit in its high spine index.

In general, then, the smooth headwater shells grade, group 12, into group 14, and from this group downstream they again grade down to some smooth shells and rise again into the very spinose shells of groups 17 and 18. The transition from relatively smooth to spinose shells is made twice in this drainage, but the character of the transition is very differently shown in group 13 and in groups 15 and 16. In group 13 there is true blending, while in group 15 and 16 it is an imperfect and confused mixture, and in marked contrast with that found in the Powell and Clinch.

The Nolichucky, French Broad, and Tennessee Rivers, considered as a whole, also show considerable complexity in their shells. To simplify these relations the shells will be considered in two series, one containing shells which are spinose throughout postembryonic development, as *turrita* and its allies (groups 19, 20, 22, and 27), and the others which are at first smooth and later become spinose, as *loudonensis* (in groups 21, 24, and 26).

The allies of *turrita*, in the headwaters of the Nolichucky (group 19), are taken as the standard, and downstream, in group 20 there is a marked narrowing of the shell (due largely to young shells), the character of globosity of the shell is not known, but group 20 has a mode at 73 per cent; there is an increase in spine height; the distance between spines makes no significant change; and the spine index shows an increase. In group 22 the width of the shells stands intermediate between groups 19 and 20, and is an increase over that of group 20; the globosity of the shell shows a marked decline; both the height of spines and distance between them shows a distinct increase; and the spine index is little changed, and possibly indicates a slight decline. In group 27, composed of the form *turrita*, the shells are very wide, they are real giants; globosity of the shell was not determined; spine height has greatly increased, and there is an increase in the distance between the spines and in the spine index. We find, then, that from the headwaters downstream there is a progressive increase in size of shell and in its spinosity.

Turning now to the series of *loudonensis*, as shown in group 21, the width of the shell is modal at 16.5 mm., and with a maxima at 20.5 mm.; globosity of the shell is modal at 77 per cent; spine height at 2.6 mm.; distance between spines has a maxima from 9.5 to 12.5 mm.; and spine index is modal at 22 per cent. From this standard, group 24 shows an increase in shell width; in globosity of the shell there is a marked decline, which is in harmony with a secondary maxima present in group 21; the spines have elongated considerably, as has also the distance between spines, and there has been an increase in spine index. In group 26 the width of the shell has greatly increased; the globosity of the shell has increased, height of spines has greatly increased, as has also the distance between them; and the spine index possibly shows a slight tendency toward an increase. Thus we find that from the lower French Broad downstream in the Tennessee there is also a progressive increase in size and decrease in the globosity of the shell and in the length of spines and the distance between them. Thus the general character of the progressive changes downstream which characterize the Powell, Clinch, and Holston also applies to the remainder of the upper Tennessee drainage. Therefore in all streams the quantitative data show that there is a general increase in the degree of spinosity, and the length of the spines increases more rapidly than the increase in the distance between them. Therefore the quantitative data show graphically and rather precisely that in all the streams there is a general progressive increase in the spinosity of the shells, in their size, and a reduction in their globosity downstream. The extreme forms are very far apart, but in the intervening localities the intergrading forms are found. The degree of intergradation between the smooth and spinose is most completely shown in the upper parts of the Holston system.

THE EVOLUTION OF THE GROSS ENVIRONMENT.

> To study life we must consider three things: First, the orderly sequence of external nature; second, the living organism and the changes which take place in it; and, third, that continuous adjustment between the two sets of phenomena which constitutes life.—W. K. BROOKS, 1899.

1. INTRODUCTORY.

The preceding part of this paper has been devoted to a detailed consideration of the facts of the variation and distribution of the forms of *Io*, considered mainly from the standpoint of masses or as populations. A sifting process has been carried on in order to secure fairly homogeneous units and populations which represent the average status of *Io* in the various parts of its geographic range. These quantitative studies aid in giving a fairly precise and uniform method of describing the local differences found. Attention has been given primarily to this descriptive aspect, theoretical considerations and interpretations having been left in the background because of the greater opportunity for the correlation of their general relationships in the topical treatment which will follow.

We wish now to turn to another series of facts, fundamental to our problem, but whose intimate relation may not be apparent at first glance, the development or genesis of the environment in which *Io* has developed. The intimate character of this relation is frequently neglected or even ignored in zoological studies, and yet it is an essential part of such a problem as is here under consideration. This relation has been very clearly expressed by Brooks ('99, p. 54), as follows:

> The physical sciences deal with the external world, and in the laboratory we study the structure and activities of organisms by very similar methods; but if we stop here, neglecting the relation of the living being to its environment, our study is not biology or the science of life.

In this discussion we will consider the "orderly sequence of external nature," or, in other words, the orderly sequence followed in the development of the gross environment, so that we may see how this factor has been able to influence *Io*.

To make this point of view as concrete as possible has been one of the principal aims of this section. To be sure the results of such attempts to harmonize the "internal" and "environmental" relations of *Io* are not entirely satisfactory in many respects; and yet no real advance can be made without squarely facing the problems and attempting to analyze and formulate them. It is considered that a knowledge of the development and structure of the environment is as essential in our problem as is the development and structure of the animals themselves. Attention is therefore given to those conditions and forces which appear to be the dominant environmental factors, so that we may see how the general principles involved are relatively few and orderly rather than chaotic and innumerable, as they may appear upon superficial examination.

Considered in detail, the complexity of the problem is so great that it is comparatively easy to overlook the general principles. It is mainly for this reason that much emphasis must be placed upon these dominant environmental features and their sequential relations.

The evolution of the Southern Appalachian province, and particularly the region of the upper Tennessee drainage, in which *Io* has evolved, includes three classes of variables: First, those geologic influences or processes which have caused the uplifting and depression of the land surface relative to sea level; second, those processes of degradation of the land which tend to reduce it again to sea level; and third, the composition and structure of the rocks. The complexity of the evolution of the drainage of this region is due to the interrelations of these three classes of influences. Since the region now occupied by the Appalachian Valley became dry land, at the close of the Carboniferous, its history, in harmony with the above classes of variables—crustal movements, degradation, and rock structure—has probably been, in brief, as follows: According to Hayes and Campbell, it was elevated, folded, and truncated by erosion to a final peneplain at the close of the Cretaceous; then was again uplifted and again partly reduced by erosion during the Tertiary, and still again uplifted to form the present cycle; or, according to Keith ('96, p. 524), there have been four periods of "approximate reduction" to a peneplain.

Fortunately for our purpose the general physical history of the Southern Appalachian province has been carefully worked out by McGee, Davis, Hayes and Campbell, Hayes, Campbell, Willis, Keith, and others. Their methods of study, as applied to this region, are relatively new, but have become classical. In spite of the large amount of work already done, much remains to be accomplished on the detailed history of the drainage, and there is no better field in eastern North America for such studies than the area south of the Ohio and east of the Mississippi rivers.

a. Present geographic relations.—In tracing the evolution of the present geography and topography, only the major features need be borne in mind, as the details are of such late origin that they have little bearing on the early history. It should be understood that the general Southern Appalachian province includes the area roughly bounded on the north by the New-Kanawha and Ohio River divide, and elsewhere it is bounded by the Coastal Plain of the Atlantic coast and the Mississippi embayment. Within these lowlands lie plateau belts, the Piedmont Plateau on the east and the Cumberland Plateau on the west; while between these plateaus are included two belts, extending northeast and southwest, the Southern Appalachian mountains on the east, and on the west a lowland interrupted by low narrow axial ridges, the Appalachian or Great Valley, plate 2. The highest parts of the Appalachian Mountains lie in east Tennessee and western North Carolina. These mountains, on account of their relation to moisture-bearing winds and their altitude, have an abundance of rainfall and are the sources of many large rivers. The *Io* shells occupy a part of the drainage of the Great Valley above Chattanooga, and to a very limited extent the Tennessee River below Chattanooga to the Muscle Shoals in northern Alabama.

b. Processes involved.—On account of the great complexity of the detailed physical history of the Southern Appalachian region, it is desirable to introduce the problem by an outline of the general principles involved, and by a brief statement of their methods of working. But before considering these factors by groups, let us recall that in nature these influences do not act separately but influence one another, and that generally several or all are acting at any given time, although there are periods when certain factors are dominant. We may think of the interaction of these forces as follows: The crustal movements of the earth, which relatively elevate or depress it with reference to sea level, may be considered as producing a condition of unstable equilibrium or a condition of tension. This is because, when once above the sea level, the sea, the atmosphere, and running water, or various combinations of these, at once begin to influence the land. Runnning water tends to seek its equilibrium, which is ultimately at sea level, and tends to carry with it the products of weathering and erosion of the land. Such a state of tension will continue as long as the land surface is above sea level and possesses a slope down which the water can flow, or, in other words, as long as any land remains above sea level. A land surface cut down in this manner to near sea level, a peneplain, reduces to a corresponding degree this state of tension and acquires to a corresponding degree an equilibrium or adjustment of the existing forces acting upon it. There are thus given to the environment definite and determinate tendencies, whose activities show an orderly successional relation and resultant topographic forms and drainage features. It is therefore possible to see that the inland physical habitats of animals dependent upon the topography, although of great diversity in a humid region, are determined by relatively few fundamental laws.

Any interruption of such a condition of equilibrium will cause another condition of tension and initiate a new cycle of changes, which in turn will tend to restore a new equilibrium. The topographic forms and all other physical features of the region are thus the by-products of the interaction of certain forces and agents acting under certain conditions.

c. Crustal movements of the earth.—In the Southern Appalachian region the crustal movements of the earth have been one of the dominant factors in the history of the environment. While certain upward crustal movements appear to have been of exceedingly long duration, yet in general the movements have been periodic. The records of certain of such periods are well preserved, particularly at the close of the Carboniferous, during which period the

Appalachians were first formed by a great uplift and foldings. The slopes of the surface thus formed were in a condition of unstable equilibrium, for the rains which fell upon them and the resultant streams developed gulleys, ravines, and valleys, which cut down the land and formed, by the close of the Cretaceous, an extensive surface of low relief near sea level, a peneplain. Upon this peneplain there remained certain unreduced mountains (monadnocks and unakas) which perpetuated the slopes and continued the unstable equilibrium as an inherited condition until the renewed uplift of the Tertiary and later periods. It is thus seen that uplift or slope has been accumulating from the Cretaceous monadnocks, from the Tertiary uplift, the unreduced tracts upon the Tertiary peneplain, and finally by the later uplifts. It is therefore evident that there has been a cumulative elevation and a lag of degradation, thus showing that upward crustal movements have been a dominant environmental factor.

This cumulative uplift has had a dominant influence upon the development of the drainage lines. The residuals and axes of uplifts being in a condition of unstable equilibrium, have thus continuously changed, as the drainage lines have developed upon the surface, except where (relatively) continuous uplift has maintained the old divides. The persistence of the uplifts in certain areas, as the south slope of the New Kanawha divide and in the large residuals, as the higher Southern Appalachians, has given certain divides and streams remarkable relative stability. Campbell ('96, p. 580) has shown that divides tend to migrate up slopes toward the axis of uplift. Such relations show the intimate dependence existing between the development of drainage lines and the axes of uplifts. Depressions due to local crustal movements are difficult to recognize in a region in which uplift is prominent, because of their liability to obliteration by later uplifts.

d. Baseleveling processes.—As previously mentioned, uplifts which raise a land surface relative to the sea and bring it into contact with the atmosphere and running water, produce upon it a condition of tension which will continue as long as it possesses a slope down which the rainfall may run with the burden of surface waste produced by weathering and erosion. The Southern Appalachian province is an area which, as is testified by the character of the baseleveling which it has undergone in the past, and its proximity to the warm sea, has had a relatively abundant rainfall. The height of the mountains has no doubt been an important factor in influencing the amount of this supply, which continues in abundance to the present day. The composition and structure of the rock is still another fundamental factor in the history of these conditions. The present mountain area consists largely of metamorphic rocks, the folded Appalachian Valley of limestone, shales, and sandstones, and the Cumberland Plateau of sandstones. It is thus evident why the Valley area is more responsive to erosion.

e. Some principles of drainage development.—The drainage development resulting from the unstable equilibrium initiated by the crustal uplifts of a peneplain of relatively homogeneous surface rocks, and the erosion of the land surface, presents a succession of conditions to be expected somewhat as follows:

1. Upon the peneplain, which is relatively a stage of equilibrium, the drainage acquires a corresponding condition of equilibrium, and the streams become relatively uniformly adjusted and symmetrical on account of the nearly equal chances for each one afforded by relatively uniform or homogeneous conditions. On such a surface of low relief the similar minor streams flow down the slopes of the peneplain, from the low divides or the monadnocks, at right angles to the axes of slope, and tend to have separate mouths, as on a coastal plain near the sea. But any inequality that will give advantage to some stream will tend to favor its capturing others and thus ultimately to concentrate the drainage into an axial stream in a depression, at right angles to the minor streams (Campbell, '06, pp. 657, 665) and parallel with the divide.

2. Uplift such a peneplain, the slope is increased, the velocity and erosive power of the streams are increased, and they entrench themselves on the surface. The heads of streams will become extended up the slope, and the lateral tributaries will encroach upon their minor divides, erode and completely remove them, and thus capture adjacent drainage. This etching process will continue until the level interstream areas are worn away and a period of maximum rough-

ness in relief is produced, similar to that of West Virginia. With continued erosion the divides tend to become lowered and less in number, and the drainage more concentrated and adjusted to a condition of relative equilibrium. In this manner a peneplained surface is again acquired, and a cycle of erosion is completed or developed.

3. Let us now consider the influence of a large uplift and folding of the strata parallel to the axis of the former main divide and intermediate between this divide and the coast, or the major axial stream.

If we assume that such an uplift is gradual, it will tend to retard or pond the minor streams above it and form a divide along the axial line of the uplift. The small stream will flow down such a slope and its head will tend to migrate up the slope toward the crest of the uplift. A trunk or axial stream will tend to form in the depression (Campbell, '96, p. 658) and parallel to the axial divide. Major through-flowing streams crossing such an uplift on account of their erosive power and volume may drain the streams in the axes of the depressions. These same processes and conditions will be repeated as frequently as there are distinct folds or trough valleys in the uplifted and folded belt.

It is also possible to think of the various degrees or transitional stages between this condition and one of a sudden uplift, when drainage is ponded and turned into axial depressions formed by the uplift and its foldings.

If, however, the upturned rocks are composed of beds of relatively soft and hard rocks, erosion upon them will be correspondingly varied and complex in its details. Although all the surface rock may be rather uniform and resistant, yet the uplift will hasten erosion and enable it to penetrate to the softer rocks which, once exposed, will erode with relative rapidity and become reduced as previously outlined, so that such an uplifted area will be peneplained somewhat similar to that before the uplift.

f. The faunal criterion of drainage changes.—The value of faunal evidence in studying stream development presents a problem over which there has been some confusion and discussion. Johnson ('05b) has considered this criterion and concludes that faunal evidence can only be suggestive or secondary and is not positive proof of drainage changes. It is well that this distinction has been emphasized, as the position seems a valid one. The faunal argument must not be too general or it loses the influence of the local environment, and, further, it must harmonize with the ecology of the particular animals involved rather than with the group in general. In other words, each case must be tested on its own merits and harmonize with the local conditions and the special ecology of the animals. Of course there are degrees of value in this secondary or suggestive evidence of stream changes, and it is particularly to this subject that most attention should be directed in the future. Throughout the present study of *Io* the suggestive value has been recognized and a special effort has been made to utilize the physical history of the streams. The general faunal evidence has not been considered. In the past there has been a tendency toward placing too much emphasis upon "accidental dispersal" (White, '83, p. 482), and this idea has retarded a just valuation of the real importance of a knowledge of stream histories which may be developed by the convergence of all lines of evidence.

The facts of distribution of *Io* can not be a positive proof of drainage changes, because these snails were apparently used as food by the Indians; at least these shells are abundant about the sites of old Indian camps and mounds, to which they had been carried. Shells thus transported by the Indians might be carried from one drainage line to another, and yet even such dispersal would not seem to have been very general, because of the amount of individuality now shown in the shells of different streams. Of course at the confluence of streams there could easily be such an interchange of shells by the Indians; and yet this would only be hastening a process which would in all probability take place, though at a much slower rate, by the activities of the snails themselves. Portages would possibly seem to offer the most favorable situations for transportation and mingling of these shells, but drainage modifications may also be involved in such localities. I have not been able to recognize the influence of this factor.

The following outline indicates the general conditions and the processes which have brought about base-leveling in the southern Appalachians: Slopes have been reenforced by uplift and crumpling; an abundant rainfall; a great diversity in rock structure, including resistant metamorphic rocks and sandstones and less resistant limestones and shales; vast periods of time; and periods of tension followed by those of adjustment and of relative equilibrium.

At no time has the region been completely reduced to base level, so that there has persisted the condition of unstable equilibrium or tension which conditioned the persistent denudation of the land surface. The nearest approach to an equilibrium for which there is abundant evidence is the extensive development of the Cretaceous peneplain.

2. FROM THE ORIGIN OF THE APPALACHIAN LAND HABITAT TO THE FORMATION OF THE CRETACEOUS PENEPLAIN.

As *Io* is a river snail, and therefore dependent upon a land area, as contrasted with the sea, most of the early marine history of the southern Appalachian province may be ignored. It is likely, however, that this family of shells descended from marine ancestors, but at what time or place this occurred is not definitely known. There is the possibility that this evolution may have occurred in this general region, as an ancient land area or continent, Appalachia, lay to the eastward of the present Appalachian Valley. The products of erosion and other débris from this ancient continent encroached to the westward upon the sea and deposited littoral beds of limestone, shales, and sandstones (Willis, '95, p. 196), which at the close of the Carboniferous or during the Permian period were elevated and crumpled to form the first installment of the Appalachian Mountains; and thus was produced a large land habitat with lime-bearing surface rocks. "The streams," says Hayes ('95, p. 329), "flowing from the old land into the interior sea before the emergence [of the Appalachian Valley belt] doubtless continued in the same direction, extending their lower courses across the newly added land as successive belts emerged. Since the process of folding was exceedingly slow, they may have held their original courses for a long time in spite of the folds rising across their path. These folds, however, although not directly able to turn the rivers aside, brought bands of soft rocks above base level, and so were able to indirectly accomplish that result. Streams flowing southward parallel with the folds were located entirely upon soft rocks, and so were able to deepen their channels more rapidly than those flowing westward across many hard beds; hence the streams parallel with the folds encroached upon the territory of the transverse streams and successively captured them and led them by southward courses directly to the Gulf.[1] When once fairly started the conquest proceeded rapidly toward the northeast, but before it had reached New River the latter had been able to sink its own channel so deeply that the Holston could not cut through its banks and divert it. New River therefore continued northward from its source in the Blue Ridge, across the mountain belt, the great valley, and the Cumberland Plateau. It is the only stream in the entire Appalachian province which retains throughout its entire length approximately its original position."

An alternative view, that the Appalachian uplift of the Permian may have ponded some of the transverse streams and turned them northward toward the headwaters of the New River or southward toward the headwater of the axial line from Asheville to the Chattahoochie River, seems plausible. This appears to have been an axis of depression in the following Triassic period (Campbell, '96, p. 676) and the later movement may have obscured the earlier depression.

The hypothetical drainage of the Permian is shown in plate 57, A. This is an effort to restore an intermediate stage in the development of the Tennessee system of drainage. It is assumed that the northwestern slope of the Cumberland Plateau drained into the interior sea and was mainly traversed by through-flowing streams from the abundantly supplied rainfall upon the mountains to the eastward. The transverse drainage of the Appalachian Valley is thus a characteristic feature at this stage of development, part of which, the New River and the projected heads of other northwestward draining streams, have persisted through the Cretaceous and Tertiary to the present time.

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[1] A questionable interpretation, to be discussed later. C. C. A.

The rate and characteristic details of the erosive processes during the Triassic and Jurassic periods is not now recognized, because, as expressed by Chamberlin and Salisbury ('06, III, p. 60):

> Since the uplifted and deformed Triassic system, along with the Appalachain Mountain Region, was essentially baseleveled before the Cretaceous period was far advanced, the intervening Jurassic period must have been a time of great erosion, so far as the Appalachian belt and the Piedmont Plateau to the east were concerned.

It is therefore probable that most of the topographic features developed during these periods were effaced during the prolonged erosion which resulted in the most perfect peneplain ever developed in this province, the Cretaceous peneplain.

A characteristic feature of a well-matured peneplain near sea level is the truncation and reduction of both the hard and the soft rocks to nearly the same plane. Such a tendency is unfavorable to the preservation or development of distinct surface relief. It is probable that at this time the Appalachian Valley had not been eroded, or if so, was only a slight topographic feature. South of New River, to Chattanooga, a marked characteristic of this valley has been its basin-like character, which has been drained only to the westward by transversely flowing streams over a rim of resistant sandstone; and this has effectually prevented the reduction of the valley at a rate greater than the lowering of the outlets. The relative perfection of the Cretaceous peneplain, as shown by the truncation of both hard and soft rocks, suggests that the balanced character of the drainage toward the embayment was quite probable. The alignment of the drainage from the bases of the mountain favors outlets via Cumberland Gap, Emory River, and Chattanooga. These important relations make it possible to estimate the origin of this valley, and the recent investigations of Johnson ('05, p. 218) show that the Tennessee has persisted in its present course across Walden Ridge at Chattanooga since Cretaceous times. These relations seem to indicate clearly the post-Cretaceous erosion or development of this valley. These interpretations are introduced at this point to emphasize the very strong probability of the transverse drainage across this valley throughout the Cretaceous—a view in harmony with the opinion expressed by White ('04, p. 38). This view favors the interpretation that the development of axial streams was moderate or slight, and that the critical period of transitional development from the transverse to the axial drainage was post-Cretaceous, and was brought about by the destruction of the Cretaceous equilibrium initiated by the Tertiary uplift. As expressed by Campbell ('96, p. 665):

> If streams are in their old age, the surface of the land will constitute a peneplain, and if in extreme old age, this peneplain will approach very closely to baselevel. At such times the drainage basins are delicately balanced against each other; not alone are the systems so balanced, but each individual stream is pitted against its neighbors in a balance so delicate that the least outside influence may turn the scale, and the favored stream conquer the ground now occupied by its neighbors. It is at such times that crustal movements are accompanied by the most profound results; consequently we find that a large majority of the changes in the alignment of the drainage systems of the Appalachian region have occurred after a period of extensive baseleveling; they were caused by the first movement which terminated the quiet of the long period of uninterrupted erosion.

These general drainage relations are indicated in plate 57, B, which summarizes the conditions at the close of the Cretaceous.

The general topographic relations of the Cretaceous peneplain were somewhat as follows: The unreduced areas upon this peneplain, which are now preserved, lie scattered throughout the present Appalachian Valley, generally as small areas, plate 56 (Hayes and Campbell, '94, pl. 5), but in the southern part of the mountains there was, as to-day, an extensive unreduced area, where the mountains stood at a height of from 3,000 to 3,600 feet (Hayes and Campbell, 1894, p. 78); these were deeply eroded or dissected by numerous valleys. The height of these mountains, their relatively abundant rainfall, and drainage to the northwest suggest transverse streams across the Appalachian Valley and northwest or west over Kentucky, as indicated. That all the drainage was not down the valley, as an axial stream, is an opinion expressed by Campbell ('94, p. 29) as follows:

> In Cretaceous time Powell River was the sole surviving member of the Cumberland River system within the Appalachian Valley.

And Hayes and Campbell ('94, p. 103) state that:

> In the central portion of the province the Cumberland River probably drained a portion of the Appalachian Valley in Southwestern Virginia, holding its antecedent course through Cumberland Gap and flowing into the extreme end of the Mississippi embayment.

It should be stated that at this time Campbell was of the opinion, previously expressed by Hayes and Campbell ('94, p. 103), that most of the valley drained to the southward as an axial stream the Appalachian River. But, as previously mentioned, Johnson's ('05) recent investigations do not support the southward course of this stream to the Coosa River, but indicate a westward flow, as in the case of the present course of the Tennessee. The denudation of this valley is thus probably very much slower than that assumed by Hayes and Campbell, and this view further favors the conception that the area of Cumberland drainage in the upper part of the valley was greater than has been previously assumed.

Let us consider some of these hypothetical drainage features in greater detail. At this time the Hiwassee may have been the main stream working upon the Tennessee outlet to the west. The main drainage from the mountains farther north was by the Emory River route—Loudonensis River—and may have formed the trunk line of the lower Cumberland drainage, a rather direct route. The remainder of the valley drainage was perhaps through Cumberland Gap—Fluvialis River, although an apportionment of the drainage between the Emory and Cumberland Gap is very difficult to make. The location of transverse sections of the streams, the general stream courses, gaps and such relicts, are the main clues to such an interpretation. In addition to the Powell, which was tributary to Cumberland drainage, other streams to the east may have belonged to this same system. Davis ('91, p. 577) cites the anomalous course of the Clinch across Lone Mountain (Maynardville, Tenn., sheet) as due to its location on the Cretaceous peneplain. The Clinch may have turned north at this point and joined the Powell and Cumberland Rivers, as indicated in Plate 57 B. It is probable that most of the course of the river has been determined by other later conditions. East of Clinch River lies the remarkable baseleveled crest of Clinch Mountain, which marks the present level of this remnant of the Cretaceous peneplain. This resistant sandstone mountain is notched in several places, but particularly at Big Moccasin Gap (Estillville sheet), where a fault occurs. This is a water gap, plate 59, which as Campbell remarks, is:

> The only water gap in Clinch Mountain in a distance of 150 miles.

This gap is in alignment with the Watauga and the South Fork of the Holston, and shows how the upper Holston drainage might have been tributary to the Clinch at Clinchport, as indicated in Plate 57 C. The alignment of the Nolichucky also suggests that it may, at this time, have been tributary to the Clinch-Cumberland.

The French Broad, Little Pigeon, and Little Tennessee, and possibly parts of the lower courses of the Clinch and Holston, may have all combined to flow to the westward from Kingston, as the alignment of most of these is in harmony with such a direction.

In this connection it is well to mention again that the tendency toward relatively adjusted drainage is a characteristic feature of a peneplain; and further, that great changes are likely to follow any marked disturbance of such an equilibrium (Cf. Campbell, '96, p. 665), as when a region is uplifted.

3. THE TERTIARY PENEPLAIN AND ITS DRAINAGE DEVELOPMENTS.

The prolonged relative stability of the land surface which made possible the formation of the Cretaceous peneplain, was checked and its destruction initiated by crustal uplifts in the early Tertiary, before the Columbia depression. This upward movement, however, was not uniform, according to Hayes and Campbell ('94, pp. 79, 88), but one which varied so that these authors have been able to recognize, in addition to the general uplift of the region, more or less distinct axes of elevation and depression. Two of these are transverse; the northern uplift, the Cincinnati-Hatteras axis, lies at about the course of the New-Kanawha River, plate 56, and the other at the southern limit. The Memphis-Charleston axis of uplift and depression is roughly parallel to the westward-flowing portions of the Tennessee River in northern Alabama, A B. There are also more or less longitudinal axes of uplifts, also indicated on plate 56. The axis O P extends in a north and south direction; E F and G H are longitudinal with the Appalachians. Still another longitudinal axis crosses the Kanawha, and is indicated C D. The evidence for these axes is determined by the present altitudes of the deformed and tilted remnants of the Cretaceous peneplain, and clearly indicate that the greatest elevation of the peneplain is toward New River. As stated by Hayes and Campbell ('94, p. 93):

> This is in northern Virginia and West Virginia and * * * exhibits an aggregate uplift since the completion of the Cretaceous peneplain of 4, 000 feet. During the Tertiary base-leveling this region was necessarily free from movement, but at no other time does there seem to have been a complete cessation of the uplift. The axes along which it culminated in pre-Tertiary time are C D and E F. [Cf. pl. 56.]

While thus the highest parts of the Appalachians are in the south, this is mainly because of the unreduced Cretaceous areas upon that peneplain rather than the post-Cretaceous uplift of this peneplain. Thus two slopes were produced, one from the southern mountains and the other a southwestward tilting from New River. Such a tendency to uplift the divides must have favored large axial streams in the intervening region. The position of the Memphis-Charleston axis crossing the lower Appalachian Valley was probably the factor which has prevented the formation of a large Appalachian Valley axial stream. (Pl. 56.) Keith ('96), on the other hand, is inclined to consider that the influence of local axes has been overestimated in the study of this region. He is inclined (pp. 521–522) to attribute the present variation in the altitudes of the different fragments of ancient peneplains more to the local conditions under which they were formed than to differential uplifts. Thus distance from the sea and character of stream débris will influence the formation of more or less local base-levels of erosion. He says:

> It is to be expected, therefore, that widely dissimilar basins will have peneplains formed at the same time, but at somewhat different altitudes. Such expectation is amply borne out by the facts of the field, and is in fact exceeded. The least inspection of peneplains shows differences of altitude amounting to 3,000 feet. Two explanations can be made of such great differences, either that one or two peneplains have been warped out of their original plane, or that many peneplains are represented which were produced at different periods and successively elevated with little warping.

The conditions in the early Tertiary therefore appear to have been: An uplifted, deformed Cretaceous peneplain, with transverse Appalachian Valley drainage; drainage slopes from New River to the southwest and from the higher mountains; uplift along both transversely bounding axes and more or less longitudinal ones, the greatest uplift being to the north, or there may have been an uplift with little warping. With these conditions and an abundant rainfall and diverse rock structure the present topographic features and drainage of the Southern Appalachians have been developed. With the exception of the highest parts of the Southern Appalachians and other Cretaceous relicts these general conditions are duplicated in part in the mountains of Pennsylvania; as expressed by Davis ('91, p. 583):

> They are essentially the products of Tertiary erosion on an uplifted Cretaceous peneplain of moderate relief. The pre-Cretaceous forms are in nearly all parts lost; the post-Tertiary work is in nearly all places insignificant. Our topography is, for the most part, a Tertiary product.

And this would also be true, in a measure, even to-day, of the drainage and the major habitats and environments, which are dependent upon the topography in the Southern Appalachian region, had it not been for a later baselevel which was first clearly recognized by Keith. This plane will be considered later.

The Tertiary period was one of tension, for as the uplift advanced erosion progressed; but as soon as the uplift ceased, a period of partial equilibrium was initiated as erosion developed the peneplain. But that the duration of this period of stability was not as long as that during which the Cretaceous peneplain was formed is clearly shown by the fact that only the less resistant rocks were reduced, and the harder ones have remained as unakas and monadnocks and have formed large interstream areas, as shown in plate 58. The softer rocks of the Appalachian Valley eroded rapidly and the valley continued to develop and to become a more and more marked topographic feature of the region. The differences, due to rock structure and differential erosion, which were relatively latent upon the peneplain, now became more and more prominent. The general parallel or axial courses of the strata within the valley favored the development of a corrugated topography, and the streams located upon soft rocks eroded deeply and rapidly and tended to migrate from the harder to the softer and lower rock surfaces. This lateral movement was supplemented by the southwestward slope of the general land surface, which favored longitudinal movement; and migration was possibly even further favored by the location of the various local axes. The erosion of land surface and the growth of the newly forming peneplain thus spread from the softer rocks up the slopes toward the axes and the old reinforced divides; and the general southwestward slope of the surface favored the encroachment and extension of the peneplain toward the northeast, in the general direction of the present Appalachian Valley, and of course erosion was relatively more rapid near the larger streams. Such relations, in outline, indicate the general dynamic tendencies of this newly forming peneplain and also indicate in what general direction drainage development was likely to take place.

At this critical period in the history of the Tennessee drainage, the period of transition from the Cretaceous to the Tertiary peneplains, detailed studies are unfortunately very few in number. For this reason, probable, provisional, and suggestive relations must form a prominent feature in the discussion which follows.

Early in the Tertiary an uplift occurred along the axis O P, plate 57, C, according to Hayes and Campbell ('94, p. 92), reaching its maximum at Chattanooga and declining gradually to the north. This axis may be expected to have had a fundamental influence upon the embayment streams and the transverse drainage in general, particularly the Cumberland system. Considering the resistant sandstones over which the transverse drainage flowed to the west, even a moderate uplift along this axis would increase the unfavorable conditions for such streams. This uplift in itself may have destroyed the lower Cumberland-Emory River water gap, and possibly the distance of Cumberland Gap from it permitted its existence for a longer time. The diversion of water from these gaps to the lower Tennessee system would help make it possible for the Tennessee to maintain its course across Walden Ridge. Not only would this axis favor early diversion of the Cumberland drainage, but the general slope of the land surface and the development of the axial streams upon softer rocks would tend to begin at the southwestern margin and migrate up the Great Valley slope. Furthermore, it is probable that even if the uplift was general and not localized, the relatively softer rocks of the Appalachian Valley tract would erode faster than the bordering areas of more resistant rocks. All of these conditions combine to favor the idea of an early southward diversion of the Emory drainage; and because of the great volume of the former stream enough erosion had perhaps been done to be a determining factor in the location of the present Emory River.

This southward diversion was accomplished by the northward migration of a stream north of the mouth of the Hiwassee River. The Little Tennessee was thus diverted to the southward, and with the continued migraton of streams progressively to the northeast the drainage of the region west of Clinch Mountain was diverted by the Lower Clinch below Lone Mountain (at about Walkers Ford).

At this time it is probable that the upper Holston, flowing through Big Moccasin Gap (plate 59) was a tributary of the Clinch and aided that stream in maintaining a part of its ancient course on the Cretaceous peneplain, as it was elevated and was able to cut through Lone Mountain, which arose in its path. As Clinch Valley was degraded, a tributary of Clinch River was able to capture and divert the upper Powell River and thus make the last important capture from the Cumberland system.

In a similar manner the upper French Broad was probably diverted at an early date by the upper part of the Tennessee proper and by the lower French Broad. The Nolichucky was probably not tributary to the French Broad at this time, but was a part of the lower Holston. Several terraces found by Glenn ('11, p. 44) at Allens Bridge on the lower Nolichucky "on the general country levels," 220 feet above the present flood plain, shows that this part of the stream has long flowed in its present channel. The progressive northeastward migration of this plane of degradation moved up the Great Valley to the vicinity of Big Moccasin Gap. At the forks of the Holston, a few miles farther downstream, this peneplain is clearly recognized by

Keith ('96, p. 522). Its fragments are here preserved at an altitude of from 1,600 to 1,800 feet. This is the best preserved ancient peneplain in the upper part of the Great Valley—along the Powell, Clinch, Holston, and Nolichucky—and into which the present streams are trenched. This peneplain was perhaps formed during the late Eocene or Miocene.

It was probably late in the formation of this peneplain, or possibly early in the following cycle, that the upper Holston was diverted to the southwest, the North Fork by the upper Holston proper, and the South Fork above the confluence of the Watauga by the lower part of the South Fork. The affinities of some of the spinose *Io* shells also suggests the possibility that the South Fork and the upper Nolichucky have communicated, and if so, it was probably ended at about this time.

The southward diversion of the Cumberland-Emory drainage or Loudonensis River thus included the great volume of the westward drainage from the high Appalachians and enables one to see how the course of the lower Tennessee could be maintained through Walden Ridge. At this point Johnson's ('05) paper should be consulted for the detailed evidence favoring the post-Cretaceous persistence of the Tennessee (rather than only a Tertiary cutting) and the formation of the Chattanooga gorge. The character of the meanders across Walden Ridge, and the absence of Tertiary gravels on the Tennessee-Coosa divide, are easily seen to have much weight. At Chattanooga, the Tennessee has been able to lower its channel about 250 feet below the level of the Tertiary peneplain (Hayes and Campbell, '94, p. 91).

4. THE POST-PLIOCENE AND RECENT CYCLES OF DRAINAGE CHANGES.

The Lafayette depression along the axis AB, plate 58, must have reduced the rate of erosion to some degree; but following this, in the late Tertiary, or Pliocene, was an uplift along the axis KL, Hayes and Campbell ('94, p. 94). This uplift was greater to the north and initiated the present cycle of erosion. As expressed by Chamberlin and Salisbury ('06, III, p. 316):

> On the whole, the close of the Pliocene must be looked upon as a time of great crustal movement, a critical period in the history of North America. * * * The Ozarkian epoch, the transition from the Tertiary to the Pleistocene, was, so far as North America is concerned, an epoch of great erosion.

Toward the close of the formation of the Tertiary peneplain, Cumberland River, according to Hayes and Campbell)'94, p. 108)—

> had cut deeply into the old Cretaceous peneplain and again base-leveled its valley in the soft limestones of the plateau region. It also probably base-leveled a small area of folded rocks in the Appalachian Valley—the present basin of Powell River which then flowed westward through Cumberland Gap.

Elsewhere Campbell ('94, p. 26) states that the axis KL had warped the previously formed Tertiary peneplain and diverted the Powell River from the Cumberland drainage. This would place the final diversion of the Powell in the Pliocene or the Ozarkian uplift. These authors do not seem to consider the Clinch and Holston as tributary to the Powell and thus belonging to the Cumberland drainage.

Another uplift, about the axis AB, tilted the land surface toward the north (Hayes and Campbell, '94, p. 119). This tended to reinforce in part the axis KL, previously mentioned. Early in the present cycle of erosion there was an uplift along the axis MN. This had a tendency to increase the canyon of the French Broad and to hasten the waters of other mountain sections of the Tennessee system. The latest movement, according to Hayes and Campbell ('94, p. 95) has been along both the axes KL and a reinforcement of OP.

Whether this uplift was general or local, it hastened the processes of erosion already in operation, caused this plane to begin in the southwest and to migrate progressively to the northeast, and to destroy the preceding peneplain upon which it was developing. According to Keith ('96, p. 522) this peneplain progressed up the Great Valley and is now a prominent topographic feature near the union of the Nolichucky, Holston, and French Broad Rivers. Here broad bottoms and terraces exist at an altitude between 1,000 and 1,100 feet above the sea. Attenuated portions of this plane appear to reach up the Holston River to Rogersville, Tenn., and the date of capture of the upper Holston may have taken place at this time, through the piracy of a stream which flowed to the Clinch through Big Moccasin Gap. To the west of Clinch Mountain this plane probably moved up the Clinch to about the mouth of Powell River. It is also probable that it was upon this plane that the latest adjustments have been made in the lower courses of the tributaries of the upper Tennessee. The Holston, Nolichucky, and lower French Broad have probably undergone important changes. The affinities of the *Io* shells in the lower Nolichucky and those of the lower Holston (near Morristown) are apparently closer than those existing between the French Broad and the Nolichucky, and therefore suggest that the lower Nolichucky may have once flowed to the northwest and joined the Holston, and that later it was captured and diverted by a tributary of the French Broad. This peneplain may provisionally be considered as having been formed during the Pleistocene.

The present cycle of erosion.—The youngest plane in this region, according to Keith ('96, pp. 522–523), is only in its initial stages, and is shown by terraces and bottoms which are formed at an elevation of from 600 to 700 feet in the lower part of the Great Valley. This plane has probably not yet been influential in causing any very important drainage changes. The uplift initiating this latest cycle of erosion will of course hasten erosion in all the streams.

By way of summary, the position of Keith ('96, p. 523) is well shown in the following quotation:

> Thus in the Tennessee Valley are seen four distinct groups of peneplains and associated features, marking four periods of stable land and long degradation. The greatest of these is the first, because it extended to the headwaters of the main rivers, and only the most obdurate and remote masses escaped reduction. Each successive period was less important than the preceding as measured by the results accomplished. The forms of any minor period would have been obliterated, however, by a greater subsequent one, so that the record can only be expected to preserve those which were in descending order of magnitude. At the present day the most conspicuous are the 1,600 to 1,800 and the 1,000 to 1,100 foot peneplains, which occupy much of the Great Valley. * * * Areas occur in which peneplains are indubitably warped, but they are readily recognized on the ground and are distinctly the exception. In short, erosion has produced in this basin at least four peneplains, each approximately level and each swinging around the heads of the lower plains in successive steps.

5. GENERAL SUMMARY.

Let us sum up the history of the Upper Tennessee region and its drainage from the standpoint of *Io*. The region is a very old land mass, which has, in an orderly manner, been elevated, degraded, or base-leveled several times. The process of elevation, although it has not been continuous, has been persistent and cumulative and has perpetuated a condition of unstable equilibrium to the rain which fell upon its surface, so that the degradative processes of running water have been continuously active. Furthermore, the variable durability of the rocks, the presence of lime-bearing rocks, the mild climate, abundant rainfall, and the large streams are physical features which combine to produce the rapid water environment and vital optimum demanded by *Io* if it persists in a region.

As the Appalachian Valley belt was elevated and folded in the Permian, the streams flowing westward from Appalachia continued to flow across this belt as it emerged from the sea.[1]

It is probable that the Permian drainage over this coastal zone was mainly to the west and northwest, plate 57, A, and the New River, even to this day, has persisted, in the main, in this ancient course across the Appalachian Mountains as they arose, showing clearly that its course is older than the mountains themselves. The New River has thus had not only a very remarkable history, but it has for a correspondingly long period bounded the upper Tennessee drainage area on the northeast and has repeatedly been pirated by the Tennessee system.

The topography and drainage produced during the Triassic and Jurassic were etched away during the prolonged erosion which developed the Cretaceous peneplain. This relatively perfect peneplain resulted in a relatively balanced condition between the stream which drained from the eastern uplands into the western embayment, and it is probable that at this stage the Appalachian Valley was not differentiated. The three main drainage lines at this stage are indicated in plate 57, B.

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[1] These conditions may give us some idea of how the marine ancestors of these shells might have invaded fresh water. These animals, inhabiting a wave-washed, rocky shore, and living in conditions approximating the agitated waters of rapid rivers, might thus have been afforded a favorable opportunity to make a change of habitat. As the zone of rapidly flowing fresh-water migrated inland, on the rising coast with progressive degradation, and as the sea migrated to the west with the progress of the uplift, such animals in time would be led far inland.

With the renewed uplift at the beginning of the Tertiary, profound changes were made in adjustment to the new condition. The greatest uplift was to the northeast and the greatest slope was from that direction, and consequently the drainage was destined to migrate up this slope toward the New River divide. Therefore the southwestward flowing streams had increased slopes and eroded faster than the inherited northwesterly flowing ones, which were progressively diverted to the southwest. In general this process of diversion took place more rapidly where the slopes were greater and at a slower rate where they were less.

The western drainage into the embayment by the Upper and Lower Cumberland was probably early diverted to the south with the development of the Tertiary peneplain, the Lower Cumberland-Emory Tennessee drainage axis was diverted by a tributary north of the Hiwassee River. The Appalachian or Great Valley now developed rapidly. The lower part of the Clinch developed and captured the Upper Clinch below Lone Mountain, and thus diverted it from the Cumberland Gap route; by a similar method a tributary of the Lower Clinch captured the Upper Powell. The Upper Holston up to this time was probably tributary to the Clinch, through Big Moccasin Gap in Clinch Mountain, but finally the Lower Holston captured the upper part and led it southward by a more direct route. This was probably one of the latest developments upon the Tertiary peneplain or soon after its uplift. Fragments of this old peneplain are preserved at an elevation of from 1,500 to 1,600 feet. In a similar manner the Lower Nolichucky, as tributary of the Lower Holston, captured the Upper Nolichucky and diverted it to the southwest. In general then these diversions took place most rapidly from the southwest toward the northeast, skirting the inner or concave margin of the uplift indicated by Hayes and Campbell as O L, plate 57, C. Those streams were the last to be diverted which were farther from this axis and to the northeast. The main diversions are the result of Tertiary erosion.

Following the Tertiary base-level, another peneplain began to the south and migrated to the northeast, where at an elevation of from 1,000 to 1,100 feet it is well preserved along the Upper Tennessee, the Lower Holston, French Broad, and Lower Nolichucky. The development of this plain resulted in the latest adjustments of the streams just mentioned to one another, particularly in the relation of the lower courses of the streams tributary to the Tennessee.

As there are reasons for believing that *Io* has developed solely within this region, and mainly in the Tennessee system above Chattanooga, where these important drainage changes took place during the Tertiary and Pleistocene, it seems that such changes must have had much influence upon this group of shells.

THE GEOGRAPHIC ORIGIN OF THE FAMILY.

Io is confined solely to the Tennessee River system, so that its place of origin seems to be a relatively simple problem. No fossil remains are known; therefore other lines of evidence must be utilized in any attempt to solve this problem. The living members of this family, the Pleuroceridæ, are exclusively American. The oldest known fossils are from the upper Cretaceous (Laramie). It is because these are the oldest known remains that it is generally assumed that these animals originated in the region in which the Laramie strata are found, in Colorado, Wyoming, Montana, Alberta, and Saskatchewan; and further that their surviving descendents have migrated to the Mississippi Valley and southeastern United States, where they now live in great abundance and diversity. But the Pleuroceridæ are not the only family which was abundantly represented in the Laramie and which is now flourishing in southeastern United States. To this group also belongs the Viviparidæ and the Unionidæ.

White, who was our leading authority on the Laramie mollusca, states ('83) that this fauna migrated from the West eastward. Thus, he says (pp. 483–485):

> The great lakes which existed in western North America in the Tertiary and Laramie periods successively became obliterated, but we may reasonably conclude that at least a part of the river channels of today have existed as such from earlier geological times; that the greater part of them were established in epochs anterior to our own, and that those of some of the tributaries of the present Mississippi River system are identical, at least in part, with former outlets or inlets, or both, of the great ancient lakes which have just been referred to. Consequently we may reasonably conclude also that the molluscan fauna of the Mississippi River system is lineally descended from the faunae of those ancient

> lakes, and the river systems of which they constituted lacustrine portions. The Ohio and Upper Mississippi, the two most ancient portions of the present great system, were once separate rivers, emptying into a northern extension of the Great Gulf; and it is practically certain that neither of them received that portion of the molluscan fauna, which now so strongly characterizes them, until after the confluence with them of the western portions of the present great river system which brought that fauna from its ancient home in the western part of the continent.

He further remarks that this last statement applies particularly to the Unionidæ, but is also applicable to the gill-bearing mollusca and some fishes. Later White ('05) reiterated this opinion regarding the origin of the Unionidæ. Simpson ('96, p. 336) accepts this view also. I know of no dissenting opinion from this position.

On the other hand, something may be said in favor of the view that they originated in southeastern United States, and that their spread was westward, in a manner similar to the post-Glacial migrations of life into the glaciated region. The following facts and inferences are favorable to this alternative hypothesis:

Southeastern United States (exclusive of the Costal Plain) has been a land area sufficiently long, since the close of the Palaeozoic, to have been the original home of the Laramie types of molluscs. The southeast was being base-leveled while the Laramie strata were being formed. At this time the southeastern streams were well developed, particularly certain ancient streams or drainage lines, such as the New-Kanawha, upper Tennessee, and Cumberland drainage, Coosa-Alabama and the upper French Broad. It seems very improbable that these streams, so favorably located with regard to lime-bearing rocks, favorable temperature, abundant and suitable food, clear and rapid water, and abundant rainfall, should have remained unpopulated by shells showing a preference for rapid water from the close of the Palaeozoic, and had therefore developed no endemic element which can now be recognized. If such a fauna was present, some fragments of it at least are to be expected mixed with the derived western element. Such an element has not been recognized or even been suggested. Of course if this region was wholly stocked from the West this native element would not be expected. Had the southeastern streams been fully stocked their population might have retarded or prevented the arrival of further invaders. The southeastern streams have been favorable for a stream fauna so long that it seems almost gratuitous to assume that the mollusca have come from elsewhere, rather than that they have had a continuous development where they now flourish. The diversity we now find in these animals is such as might be expected in a group long resident in a region.

The present endemic element in the southeastern streams is so large, there being hundreds of species peculiar to the region, and a large number are confined solely to certain streams or systems. This has the appearance of vicarious endemism rather than relict endemism, because in so many cases the intergradations between the forms now exist in very large numbers, and these would probably be lacking in the case of relict endemism.

The lack of fossils in the Southeast may be urged against this view. This old land mass has been one mainly occupied by streams rather than lakes and other water bodies, and stream deposits are very rarely preserved, particularly in a region subjected to prolonged erosion and repeated base-leveling. The paucity of streams deposits is recognized in the following manner by White ('85, p. 484):

> The discovery of so few traces of fluviatile deposits as have been made among the strata of the earth is probably due to the persistent adherence of rivers to their ancient channels. * * * If the land continued to rise, as has been so generally the case in the gradual production of the North American continent, the earlier river deposits were swept away in later times by their waters, as their valleys were broadened and deepened. It is therefore, as a rule, only in deposits of the lacustrine portions of ancient river systems that their faunae have been preserved.

Although the Pleurocerid genus *Goniobasis* was abundant in the Laramie, White ('85, p. 465) knew of none found in deposits later than the Eocene, although the genus has lived here continuously and abounds today in the Southeast. This lack of fossils in the presence of the evidence of the surviving animals shows how little weight the lack of fossils carries in the present case.

Thus in spite of the older fossil remains in the West, the physical and biotic history of the southern Appalachian region and the present apparent vicarious endemism in the family point strongly to the probability that this fauna is native and developed in place with the evolution of this part of the continent and its drainage. Such considerations, combined with others derived from the distribution of *Io* in the different parts of the Tennessee system, are favorable to the view that *Io* has always been solely confined to the drainage now included in the Tennessee system. *Io* literally "grew up with the country."

DEVELOPMENT OF THE SHELL AND ITS SCULPTURE.

1. INTRODUCTORY.

The development of the environment and the geographic origin of the family Pleuroceridæ have been discussed. We turn now to the development or "orderly sequence" of the changes in the shell and its sculpture. This, in contrast with the quantitative descriptive data, is a descriptive historical study of the development of the shell. This is based upon the comparative study of immature shells, the adult stages of which are, of course, unknown, and also upon the study of the older whorls of adult shells, where the intermediate stages are generally fairly well preserved, but whose older apical whorls are frequently destroyed. These records are often fragmentary, but this defect is overcome in part by the large number of individuals studied, and by a knowledge of the probable lines of development, which comes with a knowledge of the general relations within the genus as a whole. Thus, for example, all of the immature shells found in the Nolichuchy are spinose and, therefore, it is considered very probable that all are, even though the apical whorls of some may be eroded and the spines destroyed upon these whorls.

It is remarkable that, in spite of the extensive collections made, relatively so few very young shells were found, although particular attention was given to them; and further, that large numbers of immature shells were found in relatively few localities. This suggests that there may be a lack of uniformity in the breeding season, as it hardly seems possible that the young were overlooked in so many localities. These animals must be relatively sedentary, and it seems probable that the young frequent the same habitat as the adults.

In order to secure a just basis for comparison, it has been necessary to devise some estimate of the age of individuals. Size is perhaps the most reliable criterion; but after the first season's growth, erosion of the apex may be so marked that measurements of the total length of the shell are useless for determining age. Then again, size is greatly influenced by the dimensions of the stream in which the shells occur; small shells occur in small streams and large shells in large streams. For this reason, there is no absolute test of size which can be applied. Its value is, therefore, relative.

The number of whorls is a valuable index in the case of young and perfect shells; but the frequent destruction of the older whorls by erosion limits the general application of such a test. The diameter of the shell, as measured on the last whorl, is one of the most reliable tests of age, but this is also limited by the fact that some shells, which are below the normal in size for a given locality, show distinct signs of old age. The relative thinness of the shell is characteristic of immaturity, and this is shown by the thin or sharp-edged peristome and the feeble development or lack of a varix or scar which marks the position where growth is resumed after a period of rest. This resting period, in general, we may assume to cover the winter season, although it is probable that several kinds of stimuli may produce the same result.

Maturity and old age may thus generally be recognized by the large size, or large whorls (when the apex is defective), the thickness or heaviness of the shell, a thick peristome, and the distinct varix, which marks the position of a period of arrested growth. Old age may further be indicated by the worn apex or truncated eroded apex and the extreme heaviness or thickness of the shell. The increased number of varices upon a single whorl also appears to be an index of advancing age, showing that the rate of growth has diminished with age.

It is thus seen that there are several lines of evidence by means of which age may be estimated, and in practice it is seldom desirable to depend upon any single test.

In order to have some basis for comparisons, the shells have been roughly sorted into five classes, as follows:

Class 1. This includes the youngest shells found. These have been considered shells of the first season's growth, as they were collected in the fall. There is considerable variation in size even among these shells. This suggests a breeding season not closely limited in time, or variation in the rate of growth. These shells have seven whorls. The embryonic whorls form the apex of the shell at this stage.

Class 2. Includes shells that are considered to be the second season's growth.

Class 3. Includes, usually, shells which appear to closely approach maturity in the smaller rivers.

Class 4. Includes the largest and oldest individuals which characterize the smaller rivers tributary to the Tennessee.

Class 5. This class seems necessary for the very large shells from the large rivers, as the Lower French Broad and the Tennessee Rivers.

It is difficult to group these shells because of the lack of distinctly defined stages. The addition of a third or one-half of a whorl makes quite a difference in the size and appearance of a shell, particularly of the larger specimens. Such a method of growth, by whorls, makes it particularly difficult to sort specimens into classes. In many cases allowance must be made for defective whorls. On the other hand, this form of growth and the preservation of the earlier stages on the older whorls, is a distinct advantage in the study of ontogeny.

The importance of all records throwing light upon the ontogeny of these shells is so great that all data concerning the occurrence of immature shells will be given in some detail, by streams. The shell will be considered from two standpoints; first, the normal development of the shell and its sculpture, and second, from the standpoint of its inverse development and abbreviation.

2. THE NORMAL DEVELOPMENT OF THE SHELL AND ITS SCULPTURE.

a. Powell River.—The two smallest shells from the headwaters of the Powell, Dryden, Va., lot 41, measure in height, from the apex of the spire to the end of the canal 11 mm. and 12.5 mm., respectively; and in width 6.5 mm. and 7.6 mm. They have seven whorls; both show faint carination but are otherwise smooth. (Pl. 3, figs. 1 and 2.) These shells were collected September 3, so that there is the possibility of a long period of growth preceding. This size includes shells of class 1, which are taken to approximate the growth of the first season. Upon older shells this portion may often be recognized by its limiting varix and by a change in the color of the shell, the fresher portion being less stained, eroded, or encrusted.

After what is considered the first season's growth, comprising class 1, erosion is often so marked and the apex so truncated that measurements of the length of the shell are useless. For this reason the width of the shell or the dimensions of the aperture are better for estimates of age. The estimated second season of growth includes shells of about 11 mm. in diameter, plate 3, figures 3–5. Such shells appear to grow about one complete whorl in a season. These comprise class 2. Very rarely carination may develop at this stage. The third season, or class 3, also appears to average about one whorl and gives a dimension of about 15 mm., plate 3, figures 7–9. This size is the most abundant of the younger, or at least the smaller sized shells. The shells from this area (lots 41, 45) which develop carination, undulations, nodulations, or spines do so as a rule, at this stage. It is difficult to make an accurate statement because the smooth shells (*powellensis*) grade into the spinose shells (*lyttonensis*). The first distinctly defined varix is formed at the close of this period of growth. Carination may or may not precede undulations and spines, and may follow nodules or spines.

The fourth size of shell, class 4, includes those of a diameter of about 17 mm. and over. These include the mass of the adult shell population, and the largest shells. But in all probability, this class includes animals of the most diverse ages, from those which have just reached mature size to very old individuals. As a rule, the rate of growth upon the last whorl appears to be slower than in the previous ones, because from one to four varices, indicating periods of rest or lack of growth, are found upon this whorl. In one case the entire last whorl was the product of uninterrupted growth, but this rate is exceptional.

Old age is indicated by the thickening of the peristome, the heaviness of the shells, and also generally by the truncation of the apex by erosion and acids. The shells are frequently pitted where the epidermis has been broken and allowed the acids and bombardment of sand particles to wear away the shell, even occasionally to the extent of causing perforation. It is also possible that algæ are a factor in the destruction of the apex (cf. Collins: Erythea, vol. 5, p. 95, 1897). The slow rate of growth, with approaching old age, probably accounts for the large number of varices found upon the last whorl. If each of these periods indicates a season's growth, the shells possibly reach the limit of growth in seven or eight years. In some mature shells the spines appear to be worn, and a part of the shell is even polished where the shell has been pulled over the substratum upon which the animal crawled.

In these lots, carination and undulations, nodules, or spines are almost, at least generally, confined to the class 4 stage in *powellensis*, although they are much less frequent upon the preceding whorl of the class 3 stage, particularly in shells approaching *lyttonensis*. An exceptional feature of this upper portion of the Powell River is the abundance of the immature shells.

Passing progressively downstream, the next immature shells were found in lots 37 and 38 (group 4), collected between McHenrys Ford and extending downstream to Powell River station. These shells were represented by two specimens, class 2 in size, lot 38. One is of the almost smooth kind, plate 3, figure 10, and the other is distinctly spinose at an early age, figure 11. There are thus degrees of spinosity in this lot, and these young are entirely different from those found farther upstream in the Powell. These shells have become slightly spinose late in the class 2 stage, as in figure 10, or distinctly spinose early in class 2 stage, as in figure 11. Two shells in lot 37 show similar differences, except that in one the shell was carinate before the spines developed. Upstream when spines are developed, it is, as a rule, late in the class 3 stage or even late in class 4 stage. Class 3 is, however, abundantly represented in these lots, and they show practically all transitional degrees of intergradation between the smooth and spinose types of shells; a condition also shown in the adult shells. Both relatively smooth and spinose adults occur in these same lots, plate 31. Some, apparently adults, or nearly so, have remained smooth until the last whorl was formed and then became quite spinose, as figures 30 and 40.

Lots 28, 29, and 30 (group 5), from the lower Powell, contain only a small number of immature shells, and they closely approximate the two kinds found in lots 37 and 38. A few shells belong to class 2, but the majority to class 3, plate 3, figures 12–16. No representatives of the absolutely smooth shells are found among them, although figure 15 is relatively so (and comparable with No. 10). A very few relatively smooth adults were found in group 5, plates 32 and 33.

A shell of the class 3 stage in lot 28 (No. 28) is distinctly undulate at the class 1 stage. These are incipient spines for they are progressively larger in the later whorls. In lot 29, from Greens Ford, two young shells have the purple pigment, which characterized *Io lurida* Reeve. In some of the young shells there is shown a considerable variation in the degree of overlapping which the last whorl makes upon its predecessor, and this exposes the spines to a variable degree. In lot 28 the spines are well exposed, as is shown on plate 3, figure 13, and a similar exposure of a keeled shell is found in lot 29 (No. 202).

A series of shells from the lower Powell, in Union County, Tenn., in the collection of the late Mrs. George Andrews, of Knoxville, contains numerous immature shells. There are spinose young in the class 2 stage. At the class 1 stage some of these shells were apparently smooth, and became undulated and spinose at the class 2 stage. These parts of the shell are frequently eroded and give many shells the appearance of being altogether spinose. A few individuals in this series are smooth at the class 2 stage, and possibly a part of the class 3 stage, before developing the strong spines.

b. Clinch River.—Immature shells were not found as abundantly in the Upper Clinch River as in the Upper Powell. No young of classes 1 and 2 were found at Cleveland or St. Paul, Va. The young of the Cleveland shells are probably smooth or undulate. Lots 11 and 14, from St. Paul, contained a few individuals belonging to class 3. Some of the large shells have sharp peristomes, indicating that growth was still in progress early in August. The season's growth on some of these thin shells was only a small segment of a whorl. On the apex of some shells, corresponding to class 1 of the young, undulations are found which are not continued, and the remainder of the shell is smooth. In one case (lot 11, No. 93) the shell was undulate at the class 3 stage, then became undulate and spinose; but after the varix was formed, the spines were almost completely dropped and a smooth, thin shell growth was formed, plate 3, figure 19. Undulations and spines develop at the class 3 stage of some individuals, and others remain smooth. The adult spinose shells, as a rule, were smooth at the class 2 and much of the class 3 stage, so that for some individuals spines indicate approaching or achieved maturity, plate 35.

From the vicinity of Fort Blackmore, Va., an excellent series of very young shells of class 1 was secured (lot 51) on August 12, plate 3, figures 24–42. This was the best series of very young found in the Clinch, and was superior to any found in the Powell for the very early stages. As other members of this family are oviparous, it seems probable that this is true for this genus also, but no observations have been made upon this phase of their life history. Like the adults, these young were also found in the rapid water upon shoals. It therefore seems necessary that there be some method of anchoring the eggs, or of depositing them under stones, etc. The smallest individual is 4 mm. in diameter and 5 mm. in height; and the larger individuals reach 6.5 mm. in diameter and 11 mm. in height. These shells have seven whorls. There can be but little doubt but that these are the young of the season. The conical spire and carination of the smaller shells gives them a certain resemblance to the young of the genus *Pleurocera,* and this is perhaps of phylogenetic significance. The variation among this class of young is of considerable interest, and shows that caution is quite necessary in any attempt to determine the primitive form within too narrow limits, because there may also have been diversity in the ancestral forms just as there is diversity to-day. The young are horn colored, but one very dark individual, due to the deep purple pigment, was found. This is of interest because this same tendency occurs sporadically in several localities. The carination of the whorls, except the minute apical ones, is a feature which is quite characteristic, yet is variable in distinctness. Perhaps an even more important and variable feature is the tendency to form faint transverse undulations, mainly upon whorls six and seven, but also upon five. A perfectly smooth shell, without irregularities of the surface or undulations, is quite rare. It should be mentioned that these shells come from a region where the adults are primarily spinose, plate 36.

The nearly adult or adult shells of lot 51 contain many individuals which possess a sharp peristome, thus showing that the growing season continues at least until about the middle of August in the Upper Clinch. These sharp-edged shells further show that their last period of growth was a short one, involving only a fraction of a whorl, even about a centimeter in linear growth, as in plate 3, figure 19.

In lot 169, from near Crafts Ferry, there are two shells, one of class 2, plate 3, figure 21, and the second of class 3, figure 22. The class 2 shell is distinctly spinose on the last half of the body whorl, while the other has low nodules. In addition, there is a shell smooth at the class 2 stage and spinose at the class 3 stage (No. 5).

A few young shells were found in group 8 from the vicinity of Fort Blackmore, Va., in lots 165, 166, 167, 168, and 170, most of which belong to class 3, and possibly also to class 2 in a few cases. These shells include not only smooth individuals which were smooth at the class 2 stage, and also those which showed their spinose tendency at the class 2 stage, but on the last whorl (class 3) became spinose. Lot 165 (No. 1) contained a small, smooth shell, class 2, which has faint transverse undulations upon the two whorls preceding the last one, plate 3, figure 23. One shell from the lot was irregularly smooth during the class 2 stage, and became feebly undulate and developed two low but distinct spines, and then grew about one half of a whorl with an imperfect keel and low nodules. The possible significance of such shells will be discussed later. The apical whorls of some specimens from Clinchport, Va., were secured from shells which had been purposely broken. An examination of these fragments showed that in the revolving growth of a whorl, the upper edge of the aperture varies in its line of contact or fusion with the preceding whorl. In very young shells this line may be just below (away from the apex) the carina and thus leave it exposed; in case of overlapping on the carina there may be the apparent lack of it. In older shells this same process may leave undulations and spines either covered or exposed. In case low spines and undulations are hidden, it gives the shell the appearance of having smooth apical whorls. For this reason it is evident that real and apparent smoothness must be borne in mind when referring to the spinosity or smoothness of the apical whorls. It is apparent that in some cases it will be impossible by inspection alone to determine the true character of the shell, but this may be learned by breaking away the overlying whorls. And in case no young shells are found, it is at least sometimes possible to thus restore the lacking youthful stages.

The apices show that adult spinose shells may be smooth or corrugated in a late stage in class 1; and an examination of adult shells in group 9, from Clinchport, also agrees with the broken shells, and shows two kinds of apices at the class 2 stage—one smooth, plate 37, figures 23, 28, 29, 31, and 32, and the other corrugated, as in figures 1, 15, 19, and 20. One relatively smooth shell, figure 33, shows spines and by its spines suggests contamination or inversion.

Below Clinchport, in the Clinch, very few immature shells were found, and some belonging to class 3 were found in lot 17. These show, plate 3, figures 43–44, an undulate tendency on the upper whorls at the class 2 stage, and the last whorl is strongly spinose. A shell in lot 18 (No. 48) is in the class 2 stage, and it was spinose from the class 1 stage onward. Two other individuals have evidently had the same history (Nos. 47, 49). Two shells in the class 3 stage from lot 21 have relatively smooth apical whorls, but are undulate. One continued faint undulations after the class 1 stage, while the second passed the class 2 as a smooth shell. Both are spinose on the remainder of the shell. Lot 20 contains two shells of the class 3 stage, with apices and spines on the last and the whole or a part of the preceding whorl. Lot 32 contains one shell in the class 2 stage. It was minutely spinose from the class 1 stage, and remained spinose. The other shell is in the class 3 stage, and has two whorls with spines.

c. Holston River System.—Very young shells are rarely found in the upper Holston. The apices of the shells in group 12, from Saltville, at the class 2 stage, were smooth or possibly corrugated, plate 40. The few immature shells are mainly of class 3. The two individuals of class 2 are smooth, but at the class 1 stage both (Nos. 166, 167) had undulations. As class 3 stage develops, all degrees up to a distinctly undulate condition are produced. Even among the adult shells perfectly smooth individuals are the exception. In lot 111, from Holston Bridge, near Big Moccasin Gap, there are two shells in the class 3 stage. The apex of one at the class 1 stage was smooth, but showed minute undulations; after this stage it became undulate. The other shell was strongly undulate or truly spinose from the start. From the South Fork at Bluff City, lot 94, classes 2 and 3 are represented among these by a few individuals, plate 4, figures 1–6, 8–9. These shells are smooth or show irregular transverse undulations or corrugations, as is also clearly shown on the apical whorls of some of the older shells, plate 41. A very few individuals remain smooth through the class 3 stage, plate 4, figure 10, and others to maturity. In a few of the adults the body whorls are practically smooth, even though some of the younger whorls are undulate, plate 41, figure 1. In several old individuals the latest growth, only about one-fourth of a whorl, is free from undulations or nearly so. The early development of undulations on these shells is characteristic of the South Fork shells. The undulations on the apical whorls recall somewhat similar ones found upon class 1 shells in lot 51 from Clinch River, plate 3, figures 35 and 36, but the Clinch River and Bluff City shells develop with age very different kinds of undulations or spines.

Four specimens of about class 2 and class 3 stage were found at Curry Ford, lot 86. All are spinose on the body whorl, as shown in plate 3, figures 45–48. In lot 85, from Hord Ford, there are two smooth shells of class 2, plate 3, figures 49–50. The shells from Chissolms Ford, lots 97 and 98 (group 15), are quite remarkable for immature shells, plate 3, figures 51–67, also plate 43. No individuals were found belonging to classes 1 and 2, but class 3 is represented by small and large individuals, the large ones more abundantly. In some of these shells the upper edge of the whorls tend to overlap to such a degree as to obscure the spinosity of the earlier whorls. At the class 2 stage some individuals show a marked tendency to be spinose; and later, as the shells mature, to reduce or eliminate these spines, as shown on the plate. There is a great variation in the degree of completeness of this loss of spines. In no other locality is this tendency so well marked and complete. Class 3 at this locality contains both smooth and spinose shells. The occurrence of such large smooth (*fluvialis* ?) shells so far from the headwaters is particularly remarkable.

The young shells of group 16, lots 87 and 88, plate 4, figures 21–34, from near Rogersville, are similar to those from Chissolms Ford, but include a smaller proportion of shells which are spiny at the class 2 or class 3 stage and become smooth later. Young shells at the class 2 or 3 stage are quite variable on the last whorl; smooth, transversely undulate, carinate, and nodulose. Many of the class 3 shells are smooth or approximately so at the class 2 stage. At the class 1 stage some of these shells were smooth, as figure 22, while others, as figure 23, were spinose. The class 1 shells of lot 88, plate 4, figures 14–20, are smooth, carinated, and with traces of spines.

A good series of shells from Rogersville, belonging to the Mrs. George Andrews' collection, contains a number of immature shells. The youngest are in the class 2 group, and smooth with indications of corrugations and carination. The young of the class 3 stage are of two kinds. One kind would be considered smooth, but it shows faint and irregular undulations on the apices and even nodules or spines on the latest formed part of the whorl. The other kind has similar apices, but at the class 2 and almost the class 3 stage it becomes very spinose. Inversion is frequent in this series, and there is a considerable amount of overlapping of the whorls upon the spines.

In lot 90, from Cobb Ford, plate 4, figures 35–47; plate 5, figures 1–5; and plate 45, immature shells are particularly abundant. A few belong to class 2, but class 3 is very abundant. The apical whorls of the class 3 shells, corresponding to class 2, are either smooth, plate 4, figure 43, or spinose, as on plate 5, figure 2. Some individuals in class 2 are nodulose, as plate 4, figure 35, while others reach class 3 before nodules or spines are developed, as figure 44. The variations in classes 2 and 3 are well shown on the plates. Among these shells are three which are nearly smooth, figures 42–44, but these when older might have developed large spines, as did one individual of this lot, plate 5, figure 4.

From about 13 miles farther downstream, at Holston Station, north of Morristown, lot 96 (group 18) is found to contain shells which are much more mature and larger than those in lot 90. The immature shells, except one individual of class 1, plate 5, figure 12, belong to classes 2 and 3. Only a few belong to class 2. The class 1 individual has seven whorls. The five apical, evidently embryonic, whorls appear nearly smooth, and no carina can be recognized. The undulations on the last two whorls are distinct and numerous but not strongly carinated as are the young of lot 104 from the Nolichucky, to be discussed later. This shell is 10 mm. long and 6 mm. in diameter, and has an aperture of 6.8 mm. in length. The spinose class 2 individuals are distinctly corrugated at the class 1 stage, and the corrugations develop directly into distinct spines. The smooth individual of this class was corrugate at the class 1 stage, then became smooth, and on the last formed part of the shell made two incipient nodules.

In lot 91, from Strawberry Plains, Tenn., the few shells of class 3 show apical whorls smooth at the class 2 stage, but with distinct spines on the body whorl as in plate 5, figures 6–8. This is one type of young which is also very characteristic of the Tennessee River, as will be shown later. Other individuals show the transition to the distinctly spinose young at about the class 2 stage, plate 5, figures 9–10, and spinose at class 1 stage, figure 11. Lot 123, from Dopes Bar, plate 5, figures 13–14, contains two young shells which are smooth at practically the class 2 stage, but contain large spines on the body whorls; others remained smooth through the class 3 stage, and then became spinose. Another shell, lot 203, from near the mouth of the Holston, is in class 3 and is also smooth on all but the body whorl, plate 5, figure 15. The shells of the lower Holston, as in the lower Powell and Clinch, show both smooth and spinose young shells.

d. Nolichucky and French Broad Rivers.—From the upper waters of the Nolichucky no live shells were secured; and the few dead shells were found on the sites of ancient Indian camps. These shells are of importance because they show clearly that the young shells are spiny, like the adults. Small shells of about classes 2 and 3 occurred in lot 119 from Conkling, Tenn., plate 47, figures 14–16; in lot 118 from Broylesville, Tenn., a few individuals of class 2 and a few of class 3, and some also in lot 117 from Limestone, Tenn. These observations on the young hells corroborate the evidence preserved upon the apical portions of older shells, and show clearly that they are very spiny and that only shells which are spinose when young occur in the

Nolichucky. This is the only stream which is uniform in this respect and contains only one kind of young shells.

Immature live shells were found in the Nolichucky at only one locality, and that was near the mouth of the river, lot 104. This series is fortunately very complete, containing specimens from those of class 1 on to the fully mature, plate 48. They were collected in October. This is the only series of very young *Io* which is comparable with lot 51 from Clinch River, in the extent of the series of very young shells. In these shells, all the whorls are carinated, with the exception of the minute apical embryonic one. The second, third, and fourth, and in some cases the fifth whorl, do not possess spines or undulations. There are 7 whorls in the youngest shells, and they average slightly larger than those in lot 51 from the Clinch. The first six whorls at least are probably embryonic. The spines themselves are variable, distinctly carinated, corrugated, and green in color, and are variable in carination, plate 5, figures 16–25. These young shells stand in marked contrast with those of lot 51; they agree in the carination of the whorls, and lack of spines on the extreme apical or embryonic whorls, but beyond this stage there are radical differences. It should be recalled that the young of lot 51, in all probability, contains young of both the smooth and spinose shells of the Clinch River, the younger stages of which are both smooth or faintly undulated, in marked contrast with those of lot 104, which are strongly spinose.

A young shell, lot 182, was found near the mouth of the Nolichucky in the French Broad. This was in the class 3 stage, and clearly of the Nolichucky type. Young shells from the lower French Broad are exceedingly limited in number. One shell, class 3, lot 136, plate 5, figure 26, from Dandridge, Tenn., was smooth until class 3 was reached, and then spines were developed, not like those of the Nolichucky, but more like those of the shells in the upper parts of the Tennessee River proper and in the lower Holston. A second specimen, figure 27, developed traces of spines at class 2 stage. Other shells, somewhat smaller but of the same type (i. e., smooth at apex and spiny later), were found at Hanging Rock Shoal, lot 137, plate 5, figure 31, and at the Seven Islands Shoals, lot 156, plate 5, figures 32–36. It is important to note the contrast in the character of these young shells and those found in the Nolichucky. Among the shells from Dandridge, lot 136, there are a few individuals of about class 3 stage which appear to be mature on account of the heaviness of the shells, plate 5, figures 28–30. They are different in appearance from other mature shells, and are the form *angitremoides*. The apical whorls of this form appear spiny. These shells are evidently more closely related to the spinose Nolichucky shells than to those with smooth apices during the classes 1 and 2 stage. Others from lot 124, from near Knoxville, plate 5, figures 44–48, are also of this form.

Tennessee River.—A series of young shells from Dickinsons Island, lot 47, from near the headwaters of the Tennessee River proper, contain shells of classes 2 and 3, with smooth apices, but the last whorl may be smooth or spinose, plate 5, figures 37–43. Almost all of the shells in the class 2 stage possess some carina, traces of nodules, or spines. These are the young of *loudonensis*.

The shells from Looneys Island, lot 124, *angitremoides*, appear to be a dwarfed variety, plate 5, figures 44–48. This lot contains only a very few which, from their smaller size, appear immature; these belong perhaps to class 3. As very young shells are lacking, and the apical whorls are eroded, the proportion of shells having smooth or spiny apices can not be definitely determined. But judging from the pits formed by erosion, which generally mark the position of a spine, it appears that a great majority of the shells are spinose, nearly to the apex. One individual was found which reached the class 2 stage as a smooth (?) shell, and then became spinose, plate 5, figure 45. There is considerable overlapping of whorls and this tends to obscure the degree of spinosity.

Lot 101, from Lyon Shoal, contains only a few of the very immature individuals. These are all very spiny and are thin shelled, when contrasted with those of the *angitremoides* form of lot 124. They occur only about 2 miles farther upstream. A larger series from the above locality, lot 100, contains young belonging to or approaching class 2. These young vary much; at the class 1 stage some were spiny and others were smooth, developing spines only as class 3 was approached and thus corresponding with those of lot 47. The apical whorls of other shells, plate 50, confirm these differences. Lot 102, from Williams Shoals, contains a few immature shells of class 3, and show both types of young. In lot 103, from Little River Shoals, there are a few small individuals of class 3, the spiny ones predominating. The apical whorls of class 3 and older shells clearly show the predominance of the spiny kind, but the number of those with smooth apices is greater than in previous lots from the Tennessee, excepting lot 47. Lot 105, also from Little River Shoals (group 23) is composed mostly of very large and mature or old individuals, whose apices are much eroded, plate 51. The youngest shells of lot 105 are about the size of class 2 of lot 45, from the headwaters of the Powell River. One of these shells is entirely smooth, and two others are carinated and with undulations. Such young are clearly the dominant kind; they are *loudonensis*. Other immature shells (*turrita*) show indications of spines at the class 1 stage and continued spinose, while others pass the class 3 stages as practically smooth shells before developing spines. This group is a mixture of *loudonensis* and *turrita*.

A very large series of shells was secured from Loudon, Tenn. These included lots 126, 130, 134, 152, and 189, and contained very few immature shells. In the scale of five sizes the immature shells belong mainly to class 3, with a few in class 4. Shells with smooth apical whorls (*loudonensis*), plate 5, figures 49–53, far outnumber the very few with spiny apices. As a rule, also, the spiny *angitremoides* shells are of smaller size than the large shells with smooth apices, *loudonensis*, and belong mainly to class 4. Below Loudon, Tenn., no young live shells of *angitremoides* were found, although the adults of *turrita* range far downstream in the Tennessee.

A few young with smooth apical whorls are in lots 199, 202, and 203, from Chattanooga. Those in lot 199 reached the size of shells in classes 2 and 3 from the headwaters of the Powell before undulations or spines were formed, plate 5, figures 54–55. The apical whorls of lot 202, plate 5, figures 56–58, and lot 203, figure 59, show the same kind of young as lot 199. A similar shell was found at Bridgeport, Ala., lot 186. This was the farthest downstream that I secured living *Io*. These apically smooth shells are the form *loudonensis*. No young of those with spinose apices were found below Loudon, Tenn.

3. ABBREVIATION AND INVERSE DEVELOPMENT OF SPINOSITY.

In what may be considered the normal development of spinosity or undulations the sculpture begins to develop upon a smooth shell and progressively, with age, becomes more spinose or undulate, or spines or undulations may be present throughout the post-embryonic development. There is still another sequence of development, in which a shell begins normally and after forming spines or undulations, becomes less so, or ceases altogether to form them. This form of development will be called the inverse development of sculpture.

Previously, brief mention has been made of cases where a shell inversely changed its sculpture with age, as in group 16, from the Holston River. These shells were spinose and later became less spinose or smooth. This kind of change may possibly be the result of crossing. It is desirable, therefore, to investigate the occurrence of such shells, among the mixed series, in order to see how general this tendency is. Of course if the mixing of forms has taken place this would be more likely to occur where both forms are found in the same locality. Relatively isolated examples of one form, occurring in a region where others predominate, would be expected to be favorable to mixing because of the few chances for them to mate with their own kind.

Do such isolated individuals show in their development variations from those individuals found in homogeneous communities? For example, do smooth shells develop the same in a smooth shell community as they do in a spinose colony? Answers to such questions should aid in an understanding of the significance of some of the peculiarities of development found in the mixed communities of shells.

In the headwaters of the Powell, group 1, in a primarily smooth-shell colony, a few shells develop spines only as they approach maturity or very late in life. In such shells, of course, there is little chance to show inversion, or the cessation of spine formation, and I have not found it in them, unless we consider the formation of sporadic undulations on an otherwise smooth shell as an example of this. In group 2, in a community of smooth and spinose shells, many primarily smooth individuals, as shown in plate 29, figures 22, 23, 24, 25, 32, 37, and 39, developed spines before maturity, and later became less spinose or entirely smooth and thus show inversion. The expression of inversion is thus conditioned in part by the early acquirement of spinosity, or we may say spinosity has been crowded back in ontogeny, and permitted time enough to again suppress it. In group 3 the erosion of the shells is so great that it is more difficult to draw safe conclusions on this point. This group, as a whole, is more spinose. Those that most nearly approach the smooth shells, as on plate 30 (mainly on the lower half of the plate) do not show so clearly that they may have been spinose, and later on lost some of this character. One individual in the group, however, clearly showed inversion. In group 4, the approximately smooth shells are more in evidence, plate 31, and most of them have nodular spines. Clearly, then, the relatively smooth shells are becoming spinose at about the class 3 stage, and therefore before maturity. A few shells in this group are entirely smooth, as in figure 39, and one became spinose very late in life, figure 30, and others appear to have been spinose onward from the class 2 stage. One individual in lot 180 (No. 52) shows inversion.

In group 5, from the lower Powell, plates 32 and 33, the presence of smooth shells is still evident. A perceptible degree of loss of spinosity is indicated on plate 32, figures 36 and 39, and in several specimens in lots 28 (Nos. 2, 5) and lot 29, which are not figured. The well-preserved condition of the apices shows that spinosity is developed very early in some shells, as on plate 33, figures 2, 5, 13, 21, and 24, and much later in others, figures 3, 11, and 35. Inversion is clearly shown in a few individuals in lots 37 (No. 33) and 38 (Nos. 2, 6).

In the Clinch, in group 7, from St. Paul, Va., although the shells are both smooth and spinose, spinosity is mainly developed only on the last or adult whorl. There is a suggestion that occasionally incipient nodules and spines are present on the whorl preceding the last, as in plate 35, figures 4, 26, and 29. In several smooth shells, after they had developed nodules, they ceased to do so (in lots 11 and 14), as is shown in plate 3, figure 19. Spinosity has been "crowded back" in these shells.

In group 8 the shells are mainly spinose, and frequently develop spines before maturity, plate 36. The smoother shells seldom change from greater sculpturing to less, but two shells, plate 36, figures 52 and 55, were undulate or smooth, then became distinctly undulate, and later practically smooth. In lot 164 (No. 5) a very spiny shell changed from spines to a long, strong keel which culminated in a spine, and after a varix had been formed it was continued as an undulating keel. In lot 168 (No. 8) a shell was smooth, then became undulate and nodulate, and finally nearly smooth; in lot 165 a corrugated and nodulate shell developed an undulating keel.

In group 9, from the vicinity of Clinchport, lot 55, a few individuals show some degree of inversion. The spinose condition changes to a very strong keel and traces of nodules on the last half of the body whorl (Nos. 6, 106); and in others (Nos. 52, 83, 161) inversion is shown in different degrees. One example of this is figured on plate 37, figure 33.

In group 10, from Kyle Ford, a few shells show some reduction in the spines on the body whorl, and a tendency to form keeled spines, or nodules.

In general, then, the changes in the Clinch are similar to those in the Powell, the down-stream shells show an earlier development of spines than in the headwaters and they also show some inverted development, but not to such a marked degree.

In the Holston, in group 12, from Saltville, Va., young shells are few in number, and on these as also upon the apices of the older shells nodules may develop very early, at the class 1 or 2 stage, plate 40, figure 18. Well-defined nodules are present on some individuals at the class 3 stage, as, for example, in figures 11, 16, 17, and 18, and this nodulation is less developed on the last whorl in many cases, as in figures 13, 17, 18, 23, 26, 29, and 33, and in several clearly defined examples which are not figured. Nodulation is sometimes irregular, and not definitely limited to the last whorl, as in the Powell, and in this respect they show affinity to the shells of the Upper Clinch. In lot 111, from Holston Bridge, inversion was observed in one shell.

In group 13, well defined undulations are even present at the class 1 stage, plate 41, figure 9, and are frequent at the class 2 stage, and are the prevailing type in class 3. Some individuals remain roughly and irregularly corrugated, but essentially a smooth shell up to the class 3 stage, and then become nodulose, as in plate 41, figure 10. In some cases the nodules are present up to the class 3 stage, and then are possibly less developed or practically absent at maturity, as in figures 2, 8, and 10. Numerous individuals in lot 94 show all degrees from normal development to almost perfect inversion. This is shown on the body whorl by the presence of lower nodules, a smaller number on a whorl, so that only a part of a whorl possesses them. There are only a few of the relatively smooth shells in this series, and yet the different degrees of inversion are abundant. In lot 157, from Fishdam, Tenn., there are also inverted individuals. Compared with group 12 the nodulations of group 13 is more uniform and it generally develops at an earlier age.

In group 14, inverse development of spines was observed in lot 112, in which two individuals were found which were nodulose or spinose at the class 3 stage, and became less so or smooth on the last whorl. Similar examples are also found in lot 175 (Nos. 3, 27, and 79). Inversion is shown on plate 42, figures 16, 21, and 29. Several of such shells are found in lot 178, in a very spinose population.

In group 15, from Chissolms Ford, in a mixed population of intergrading spinose and relatively smooth shells, inversion has run riot in both degrees and numbers, and is itself "crowded back" in development from the nearly adult or adult stage to the class 2 or 3 stage. Thus, shells which were spinose at the class 1 and 2 stage become at class 2 and 3 less spinose or perfectly smooth. The degree of inversion here reaches the most perfect development found in any locality. Some of these changes are shown on plate 3, figures 51, 60–67, and on plate 43, figure 31. Carination is often well defined in these shells of inverted development.

In group 16, from the vicinity of Rogersville, much the same conditions are found as in the preceding group, but the relative number of the smoother shells is much larger. A large number of the relatively smooth shells show traces of nodules or spines, suggesting that they have been contaminated by association with the spinose kind. Some of the relatively smooth shells began to develop as smooth, then become spinose, and again smooth, as is shown in plate 44, figure 25. This same kind of change in ontogeny was found in the Powell River in group 2, plate 29, figure 32. Of the distinctly spinose shells some begin as smooth, plate 44, figures 12 and 14, while others are spinose and remain so, as shown in plate 44, figure 2. Inversion is also shown in figures 21, 22, 24–27.

No case of inversion was observed in group 17, where the adult shells are all spinose. Three shells are smooth or with only incipient nodules in the class 3 stage (lot 90). These would probably have become spinose, as other individuals are smooth on the apical parts at a corresponding age.

Inversion does not normally occur in localities where all the shells are spinose; nor have I observed it in such a shell as *loudonensis* (which is smooth in the early stages and later becomes spinose) except in the case of one shell (lot 126). This shell apparently begins smooth, developed nodules irregularly, again becomes smooth for about one-half of a whorl, and then developed a keeled spine and continued as a very spinose shell. This shell is thus somewhat transitional between *loudonensis* and *turrita.* Inversion is characteristic of localities where the shells are mainly smooth or undulate, or, in other words, where the smooth and sculptured shells have a chance of crossing.

The following table has been prepared to show the development of the sculpture in the recognized forms of the genus. The smooth kinds are placed at the upper part of the table and the spinose forms at the lower part. Two inverted examples are also included.

An examination of the following table will show that as a rule the smooth shells, as *powellensis,* develop spinosity and allied sculpture only late in life. In passing on to the spinose forms, as *spinosa,* there is a progressively earlier development of the spines from the class 4 to the class 1 stage. The embryonic whorls are probably smooth, or keeled in all forms. The position of *loudonensis* and its allied variations is remarkable. *Loudonensis* has a continuous range in the lower French Broad, Lower Holston, Tennessee, and allied variations of similar development are found extending up the Powell to group 2, and up the Clinch to group 7, thus far into the headwaters.

Table showing the ontogeny of shell sculpture in Io.

Name.	Embryonic whorls.	Class 1.	Class 2.	Class 3.	Class 4.	Class 5.
1. *powellensis*	Pl. 3, figs. 1, 2	Smooth	Smooth	Smooth	Smooth, or shoulder, keel, nodules, late in this stage.	
2. *clinchensis*	Unknown, probably smooth.	Unknown, probably smooth.	do	do	Smooth, or shoulder, keel, nodules, late in this stage.	
3. *fluvialis*	do	Smooth or undulate.	Smooth or corrugated.	Smooth or corrugated.	Smooth or corrugated.	
4. *lyttonensis*	do	Smooth	Keel smooth	Small spines	Small spines	
5. *paulensis*	Probably smooth	do	Smooth or undulate.	Smooth or undulate, rarely spinose.	Spinose	
6. *loudonensis*	Unknown, probably smooth.	Pl. 52, smooth	Smooth	Smooth, or nodulose on younger part.	Large, spinose	Very spinose.
7. *verrucosa*	do	Pl. 4, fig. 7, smooth (?) or corrugated.	Corrugated	Corrugated or nodulose.	Nodulose	
8. *brevis*	do	Pl. 3, figs. 43, 44, smooth or corrugated.	Smooth or corrugated.	Spinose	Spinose, some spines keeled.	
9. *recta*	do	Pl. 42, spinose	Smooth (?) or spinose.	do	Spinose.	
10. *unakensis*	do	Pl. 47, figs. 14–16, spinose.	do	do	Do.	
11. *nolichuckyensis*	Pl. 5, figs. 16–25, smooth.	Pl. 48, spinose	do	do	Spinose, some spines keeled.	Spinose.
12. *spinosa*	Pl. 5, fig. 12, smooth	Spinose	Spinose	do	Spinose	Do.
13. *angitremoides*	Unknown, probably smooth.	Unknown, probably spinose.	Rarely smooth, spinous.	do	do	
14. *turrita*	do	Probably spinose	Spinose	do	do	Do.
Chissolms Ford, lots 97, 98.	Pl. 3, figs. 60, 61, 65, smooth.	do	do	do	Smooth	Inverse development.
Pennington Gap, lot 39.	Pl. 29, figs. 32, 37, 39, unknown, probably smooth.	Probably smooth	Smooth	do	do	

Discussions and general summary.—The smoothest young shells are found in the headwaters of the Powell, group 1, and as a rule they do not become carinate or spinose. These are the form *powellensis*. Some individuals, however, as they approach maturity, or are mature, do develop a carina, nodules, or spines, and they thus grade into the form *lyttonensis* which is represented by a few individuals even in the headwaters. *Lyttonensis* develops spines at the class 3 stage, so that one can not tell into which kind of an adult a very young smooth shell will develop, because both kinds of young are intermingled in this region. This is in a population of shells which is primarily smooth.

The shells of group 2 are smooth, or until they reach the class 3 stage, when a sculpture may be developed and continue, or this sculpture may be lost, and thus show inversion. The shell population is mainly spinose and of the form *lyttonensis*, but mingled with them are forms which intergrade, in sculpture, into the smooth form *powellensis*. Thus there is a condition which is the reverse of that found in group 1. Inversion is relatively abundant in these shells and the sculpture develops earlier than in *powellensis*.

In the lower Powell, the young shells at the class 1 and 2 stages, and the apices of older shells, may be smooth or spinose, and the adults show similar differences. Relatively smooth shells are few in number, and they often show indications of spines, which suggest contamination by the spinose shells. The population is not homogeneous, but is much mixed. Spinosity develops much earlier than in the headwaters, and inverse development is generally of relatively rare occurrence in the Powell.

In the Clinch immature shells were not found in group 6, but it is highly probable that the young are smooth or undulated. Nodules develop irregularly on adult shells with approaching maturity. In group 7, at the class 2 stage, the shell may be smooth or develop corrugations, and these corrugations may or may not develop later into spines. Nodules or spines rarely develop on a shell in the class 3 stage, but are found abundantly upon mature shells, and many mature shells remain without spines. In group 8 the transition has been made from the predominance of smooth to the spinose shells. The shells tend to become spinose before maturity even at the class 2 stage, and some degree of inversion may be shown. The relatively smooth shells are evidently contaminated by the spinose ones. Relatively smooth mature shells are almost absent from the lower Clinch, and occasionally inversion is found.

Group 2 in the Powell may be compared with group 8 in the Clinch, and they show similarities in their transitional stages from the smooth to the spinose shells. Relatively smooth shells reach to the mouth of the Powell, but in the Clinch the corresponding point is at about Clinchport.

In the Holston the headwater shells, group 12, are smooth or undulate when mature, and they show the undulate tendency more than the corresponding shells in the Powell and Clinch. Furthermore, undulations become well pronounced before maturity, at the class 3 stage, in many individuals, while others remain smooth. A few show inversion. Downstream, group 13, the undulations become more pronounced, and at the class 1 stage are smooth or corrugated, and a few remain almost smooth, but as a rule they progressively develop the corrugations. These corrugations have been crowded back so that they are well defined at the class 2 stage, and a few individuals show inversion. This is a transitional group between the smooth and spinose shells, and yet the transition is very different from that in the Powell or Clinch.

In group 14 the shells are distinctly spinose, rather than undulate. At the class 1 stage the apices show that the shells were undulate or spinose, or smooth. A shell may even reach the class 3 stage smooth, and then develop the normal degree of spinosity for the group. These shells also show inversion. Groups 15 and 16 form quite a unique series of shells. They are a mixed series with almost every possible intergradation between smooth and very spiny shells, and even mixtures of smooth and spinose whorls on the same shell. The young are correspondingly variable. Inversion has here reached its extreme development. In the Holston there are thus two transitional series of shells between the smooth and spinose, and the transition has been made in a different way in each case. Downstream from this point the character of the young shells and their development is greatly changed. In group 17, from Cobb Ford, at the class 2 stage, the young are smooth or spinose, and these at the class 3 stage are all spinose. These two types of young extend down the Holston to its mouth, in the Lower French Broad, and in all of the Tennessee proper. From these two kinds of young, spinose adults develop, the one with the smooth shell become *loudonensis* and the other *spinosa* and its allies. Inversion has not been recognized in these shells.

The shells of the Nolichucky are spinose throughout their postembryonic development, and do not show inversion. Inversion therefore appears to be confined to those localities in which relatively smooth shells are present with the spinose. A common form of development among the transitional shells is for a young smooth shell to develop spines at the class 2 or 3 stage, and to continue spines to maturity. Similar shells are found in abundance in group 2 in the Powell and group 7 in the Clinch. In the Lower Holston and French Broad, and in the Tennessee, this kind of development is found in the form *loudonensis*, which is smooth up to the class 3 stage, and then develops the longest spines in the genus.

The development of the shells in different streams and localities is thus seen to differ as much as the adult shells do, and further the transitional stages of intergradation, instead of being uniform, show a similar amount of individuality.

A tabulation of the different forms of development of sculpture shows that in advancing from the smooth to the spinose shells there is a progressively earlier development of the sculpture from approaching maturity backward to an earlier and earlier stage so that in the extreme spinose shells the entire post-embryonic stages are spinose. The spinose shells thus show an abbreviated development.

Judging from ontogeny, particularly the smooth character of the embryonic whorls, the normal development of the spines and other sculptural features, and the dominance of the relatively smooth shells over the undulate and spinose in inverse development, the smooth shells are the nearest living approximation to the ancestral form from which all the forms have probably been derived.

Turrita represents the extreme degree of specialization, or departure from the ancestral form, in its elongate shell, small aperture, degree of spinosity, and early age at which spines are developed. It has, as it were, abbreviated its ontogenetic development of spines so much that spines develop very early in life, and not relatively late, as in its associated form *loudonensis*. It is remarkable that we can find living to-day what appear to be several stages or kinds of development from the smooth to the sculptured shells, not only in a single stream but also duplicated in other streams. This naturally raises the question as to which transition most nearly approaches the ancestral one: Were the ancestral ones duplicated also or have all of them been formed by combinations of relatively independent characters and are lacking of much phylogenetic significance? If ontogenies are modified by combinations, a decision must be made as to the relative values of each one.

The perfection of the transition seen in *verrucosa,* and the attenuation of undulations with departure from the Upper Holston, and its inverse development suggests its independent character. A similar independence of development is seen in *loudonensis,* but each seems lacking in both *lyttonensis* and *paulensis,* and these may represent new or later combinations. In view of the probability that spinosity developed farther south, *loudonensis* may give us the best idea of the transition from smooth to spinose shells, and *verrucosa* the best idea of transition from smooth to undulate, on the one hand, and from undulate to spinose.

GENERAL DISCUSSION AND SUMMARY.

1. INHERITANCE IN MOLLUSKS.

Early in my studies of these shells I had planned for hybridization experiments which were to be conducted after some perspective had been acquired by a preliminary study of the shells from many localities. Live specimens were secured in 1900 and kept alive for some months, but proper aquaria were not available, so that this important phase had to be abandoned. Some one with the facilities of a trout hatchery in southwestern Virginia or eastern Tennessee ought to be able to secure valuable results from this kind of experimentation, as this family of shells is one of the most plastic and characteristic groups of North American animals. Bartsch ('06, p. 465) has proposed a series of transplantation breeding experiments upon a member of this family belonging to the genus *Goniobasis.* It should be added that pedigreed material, or pure strains from nature, should if possible be used in such an experiment.

Very little is known in general of inheritance in gasteropods. A few references have been found in the literature, in which the parent and young of viviparous species have been compared, although it is probable that many of such cases are scattered about in conchological literature. Mayer ('02, p. 121) observed in the hermaphroditic and viviparous land snail *Partula,* from Tahiti, that:

> The young of dextral or sinistral snails are usually dextral or sinistral respectively, but this is not invariably the case. * * * All of the young developed within any given adult are either dextral or sinistral, never some of them dextral and others sinistral.

The significance of this form of inheritance is shown in a further statement that—

> All the snails of Tipærui Valley are dextral, while all of the same species in Pirae Valley are sinistral. In the two intermediate valleys of Hamuta and Fautaua some individuals are dextral and some sinistral.

Bartsch ('07, p. 146) has observed the inheritance of shell sculpture in the variable fresh water snail *Vivipara lanaonis* Bartsch. He says:

> It is an interesting fact that in all the gravid specimens examined, the nepionic shells taken from the parent always had the sculpture of the parent.

Coutagne (1894, 1896) has studied inheritance in *Helix,* but his work is not accessible to me.

The most important and prolonged studies in inheritance in molluscs have been made by Lang (1904, 1906, 1906a, 1908). I have only had access to a part of Lang's papers, and abstracts of the others (Darbishire, 1905). The following observations pertain to the present problem;

Morgan (Experimental Zoology, 1907, p. 166) states that Lang bred together left-handed individuals of the right-handed species *Helix pomatia*, and only right-handed young were produced, even when they were inbred. (Cf. Lang, 1906a, p. 495.)

Lang (1906, 1908) for many years studied heredity in *Helix nemoralis* and *Helix hortensis*. These shells show great variation in shell color, banding, size, and form of the umbilicus. To a large degree, similar variations take place in both species. The different colonies of these shells show considerable individuality in the kind of variations found in them. Thus some colonies are composed solely of five-banded shells, and these are relatively common; others are composed of the bandless individuals, which are rare; some colonies may stand anywhere between these two extremes, and still others are composed of both the banded and the bandless shells, both sharply defined and with no intermediate forms.

Inbred snails from the pure five-banded colonies were found to produce only the five-banded shells; they bred true. Pure bandless colonies were much more difficult to find but were also found to breed true.

When pure strains or races of the banded and bandless were crossed the young of the first generation (F_1) were all bandless. The bandless were dominant (d) and the banded were recessive (r). When these hybrids of the first generation (F_1) were bred together in pairs, their progeny, the hybrids of the second generation (F_2), were found to split up into the bandless and banded kinds, in the proportion of three bandless (dominants) to one banded (recessive). This splitting up in the second generation of the hybrids (F_2) into the two grand-parental strains is typical Mendelian inheritance. When the progeny of the second generation (F_2) of hybrids are bred together in pairs, it is found that the progeny of the banded shells give rise only to banded shells, a pure race of banded shells, the extracted recessives. These are a pure race extracted from the hybrid mixture. The bandless shells are found to be of two kinds, those which breed true bandless shells, the extracted dominants, which form a pure strain of bandless shells, and finally those (dominant-recessives) which produce bandless and banded shells in the proportion of the three bandless to one banded. The entire population of this F_3 generation is composed of bandless and banded individuals in the ratio of three bandless to one banded.

These relations may be made more graphic by reference to figure 60, in which *Io* shells have been arranged as if they showed Mendelian inheritance in the same way in which Lang found that it takes place in *Helix*. In this case the smooth shells (s) are considered dominant (d) and the spinose shells (t) are considered as recessive (r). The results of such a cross are, in the first generation (F_1) all are smooth or dominant (d) and the spinose character is hidden or latent, or it is said to be recessive (r). Pairing individuals of this generation, their young, hybrids of the second (F_2) generation, split into two kinds, both spinose and smooth, like the grandparents, but the smooth are three times as numerous as the spinose. If these shells are bred in pairs, it is found that the progeny of the spinose shells give rise only to spinose young (F_3), a pure race of spinose shells, the extracted recessives. The smooth shells are in this way found to be of two kinds because they give rise to different kinds of progeny. One produces smooth shells only (F_3), the extracted dominants, a pure race of smooth shells extracted or split off from the hybrid mixture, and the other (dominant-recessives) produce young (F_3) smooth and banded in the proportion of three smooth to one spinose. The entire F_3 population is composed of smooth and spinose shells which occur in the ratio of three smooth to one spinose shell.

This splitting up of hybrids into the parental strains is considered the essential feature of Mendelian inheritance, according to Bateson (1909, p. 50), who considers dominance as subordinate and incidental. Lang (1908, p. 53) found that this splitting or segregation occurred in the second (F_2) generation. Mendelian inheritance was found to apply to the following characters: (1) Banding of the shell, (2) ground color of the shell, (3) size of the shell, (4) form of the umbilicus. He also showed (1906, p. 233) that in hybridization the varietal characters Mendelized or split, as did also crosses between the species, in the same general way. Crosses between varieties are generally fertile, while crosses between species are only so very rarely.

In these hermaphroditic, but not self-fertilizing land shells, Lang (1908, p. 40) proved that after copulation potent sperm may remain in the receptaculum seminis for years. Also that if a snail has already copulated with one of its own species, and later copulates with an individual of another species, it is only the older sperm of its own species which fertilizes the eggs.

Certain banded varieties were found to be characteristic of *hortensis* and *nemoralis* (1906, p. 253).

Lang's (1906, 1908) observations on dominance are of much value. He has found that bandlessness is dominant over banded, and red ground color over yellow (1906, p. 334), and probably the less banded condition over the more banded condition. He also observed (1908, pp. 54, 59, 77) that when a yellowish shell is crossed with a red or brown one, the young shell is at first yellow and later, as growth progressed, the red or brown color became fully dominant. This change of dominance with age has been observed in widely different organisms.

If two varieties are crossed, each having different dominant characters, the hybrid offspring will contain both dominant features in distinctness. There is a mixing but not a blending. Thus if (1906, p. 234) a yellow bandless variety of *nemoralis* is crossed with a red banded one, the young will be red and bandless. The dominant red is derived from one parent and the dominant bandlessness from the other. "They are indeed not intermediate forms, but mixed forms," says Lang.

The same kind of characters which go to make up individual variations Lang (1906, pp. 248–250) found to be inherited. Here is seen the basis for such differences as are found in colonies and in many geographic variations. Some colonies contain widely distinct types while in others all intergradations exist between these.

On account of the inheritability of large and slight variations, Lang considers that heritability of a character rather than its abruptness and distinctness is the better criterion of a mutation. He (1906, p. 253) thus holds that there is in reality no fundamental distinction between variations and mutations. Holmes (1909, p. 283) has expressed a similar opinion about mutations:

> About the only criterion by which they may be recognized is their stability, and even that gives some evidence of being a matter of degree. No limit has been discovered to the minuteness of the stable modifications that will occur, and it may happen that further study will reveal the comparatively frequent appearance of very slight variations of this kind.

Lang's studies of *Helix* are epoch making in their bearing upon the problems of differentiation in snails. They show, as never before, the need of further pedigree experiments, the value of detailed studies of snail colonies, local and geographic races, and the need of a careful analysis of the conditions which determine and influence the conditions of breeding.

The manner of inheritance, of shell color and banding, in *Helix hortensis* and *memoralis* at once raises the question as to whether or not this same kind of inheritance does not apply to the Acitinellidæ of the Hawaian Islands. According to Gulick (1905, pp. 37–43) the island of Oahu is 40 miles long, and alone possesses from 200 to 300 species, and over 1,000 varieties of these shells. Great numbers of them occupy areas of only a few miles in extent, or are limited to single valleys. They show a great amount of intergradation. One of the latest studies of these shells is by Borcherding (1906), but it has been conducted along the older purely taxonomic lines with no attempt to relate his results to the general conclusions of Gulick's work or to Lang's earlier work (1904). Hyatt (1898), and Hyatt and Pilsbry (1911) have discussed their migrations and zoogeographic relations, but also without regard to Lang's studies.

The probabilities appear to be that Mendelian inheritance holds for these shells, much as in *Helix*. It also appears probable that the same conditions will be found to apply to the genus *Partula*, investigated by Mayer (1902) and Crampton (1907, 1909). Crampton and Mayer agree with Gulick that the environment can not be the determining factor in producing the varietal and specific differences. Both Crampton and Mayer favor "mutation," evidently in the De Vriesian sense, as contrasted with that of Lang. In the light of Lang's experiments, and his idea of the inheritance of all degrees of variation and mutation, his use of the term mutation seems much more applicable.

Color differences form a conspicuous feature in the variation of the Achitinellidæ, as in the Helices studied by Lang. *Io* also possesses color bands which are very variable in their number and distinctness. They vary also from partial to complete fusion so that the entire whorl is of a nearly uniform deep purple color. Such purple shells are very rare (=*lurida* Reeve). These color variations have not been the subject of special investigation, but they are mentioned because of the possibility of their also showing Mendelian inheritance.

2. ONTOGENY AND PHYLOGENY.

As has been pointed out, Lang's experiments with inheritance in *Helix* are our main guide in a knowledge of heredity in mollusks. He has shown that the same kinds of variation which appear as individual may be inherited so that between fluctuating variations and marked variations or "mutations" there is only a distinction of degree; the colonies or strains are found in nature, which by experiment have been shown to breed true; that many characters show Mendelian inheritance in its typical form, and that in others the splitting takes place in the first generation of hybrids (F_1). Bandlessness is dominant over the banded, red shell color over yellow, and this dominance has been observed to change with age, as when yellow and red shelled individuals are crossed with brown, the young were first yellow and later became fully brown. On the other hand, dextrality is not inherited in Mendelian fashion. But as we have races of both dextral and sinistral mollusks, it is evident that such traits are inherited and possess individuality. Lang further showed that the same general forms of inheritance existed between races of species as between species.

In the absence of experimental evidence of the manner of inheritance in *Io*, let us consider the observations recorded on other animals and see what light these results throw upon our subject. That spinosity is inherited is evident from the spinosity of the young shells from the Nolichucky, and that different degrees of it may be inherited is indicated by the local races, which vary in this character. The mixed character of the inheritance or expression, seen in the Hoston shells from the vicinity of Rogersville (lots 87 and 88), suggests Mendelian inheritance with a change of dominance with age. When yellow and brown shelled *Helix* were crossed, yellow was first dominant and later brown. In the supposed crosses between smooth and spinose *Io*, it looks as if the spinose trait was first dominant and later the smooth became dominant. As a descriptive term this form of development was called "inverse." This change of dominance or expression with age has been observed in many localities where relatively smooth and spinose shells are found together. This change of expression, or change of dominance with age, appears to be a hybrid characteristic and has been observed in many organisms. It has been observed in hybrid oaks by MacDougal (1907, p. 48). Standfuss (1896, pp. 66–115) has shown that in some hybrid moths, the larvæ first resemble the maternal species and with age approach the paternal. Davenport (1910, p. 131) has shown that when white and black leghorn chickens are crossed, the white is dominant, but it is so imperfect in the females that they may be blue, and it is only in the later moults that they become nearly pure white. Guyer (1909, p. 725) reports that in guinea-chicken hybrids the young at first resemble the guinea, but with age become intermediate and still later, at the age of 5 years, even more nearly approach the chicken parent (a male). Tower (1910, p. 298) found that in the cross produced by two species of potato beetles the larvæ were all of the female type, while the adult beetles which developed from these larvæ were intermediate between both parents. Giard (1903) reports similar observations for moths and birds. Thomson (1908, p. 114) states that a boy or girl may change with age from resembling one parent to the other; and Newman (1908) has shown that in fish hybrids the dominance [or expression] of either parent may fluctuate and change more or less with the age of the hybrid. Tower's (1910) experiments on hybrid beetles further show that dominance may be changed by environmental influences. Some plants growing under unfavorable conditions (Shull, 1908, p. 446) do not show or express all of their inherited characteristics, but do show more under favorable conditions. It is thus evident that the change of dominance with age is frequent in hybrids and is also found in other organisms, and must be considered in connection with the degree of expression of inherited characters. When we consider that inverse development in *Io* is confined to localities where the smooth and spinose shells are not only found together, but is best shown in those localities where all degrees of intergradations are found, we are thus further impressed with the importance of the phenomena of inverse development. This is probably due to the crossing of the smooth and spinose forms of *Io*. The degrees of expression of inversion are numerous, and the differences are nearly as great as the differences observed between the different typical forms in the genus.

Mendelian inheritance applies to some of the characters which show this change of dominance with age, and this suggests the possibility that such a change may be used as a criterion for the recognition of some hybrids in nature, and further as indicative of their form of inheritance. It would greatly extend the application and utility of pedigree experiments if such a criterion could be established.

The possibility of the spreading of dominance in Mendelian inheritance is one that deserves mention here. Shull ('07), Hardy ('08), and Johnson ('08) have discussed phases of this question. Shull and Hardy claim that in the absence of selection dominance does not tend to crowd out the recessive character, but that their ratio remains constant. Hardy states that under conditions of random mating "there is not the slightest foundation for the idea that a dominant character should show a tendency to spread over a whole population, or that a recessive should tend to die out" (p. 49).

On the other hand, with selection or associative mating we should expect to find a change in ratios, especially in those cases where dominance is influenced, or at least in its expression, by favorable or unfavorable conditions. The opportunities for random selection are quite different in colonies of different composition, even if we assume that fertility exists. Thus a smooth shell in a primarily spinose population, or a spinose shell in a primarily smooth population, has very different chances to get a mate of its own kind, even if they make a random choice, the selection may be equally random but it is from different materials. In *Io* the smooth and spinose shells so overlap in their geographic range that their chances of mating vary much and this is probably a reason why the results are so variable in different localities. Inverse development is most pronounced in the localities where spinosity is well developed and both relatively smooth and spinose shells are relatively abundant.

Tower ('10, pp. 307–323) records that when two species of beetles, *Leptinotarsa undecimlineata* and *L. signaticollis*, are allowed to freely interbreed for several generations, there was a progressive decline of *undecimlineata* until all had in the seventh generation become *signaticollis* and the other species had apparently been obliterated. Progeny of this fusion were found to breed true and did not tend to split up. Three species were similarly combined but did not do so as perfectly. The details of this process of fusion are not given, but such observations suggest to us how the dominance of a species over another may expand and ultimately change the entire population, even though Mendelian splitting is present, as when the female of *undecimlineata* is crossed with the male of *signaticollis* (Tower, '10, pp. 297–299). In this manner apparently pure strains may be formed by hybridization or fusion, or the result may be due to the extermination of one member of the cross. If prolonged crossing will lead to a blend and pairs of such individuals, as well as extracted dominants or recessives should be isolated, they might be capable of founding new colonies and new local races, as seems to have been the case in *Helix*.

Even if Mendelian inheritance of spinosity should be present in some of these shells the spinose shells of the Nolichucky show no recognizable tendency to split, and the same is true of the dextrality of the shell. I do not recall ever having seen a sinistral individual in the thousands of shells examined.

Mendelian inheritance may also apply to the smaller degrees of spinosity, but this might be much more difficult to recognize in a mixed population. But if very spiny and the very smooth individuals were crossed at first the Mendelian inheritance might be so distinct and the change of dominance with age so marked that it could easily be distinguished. After prolonged interbreeding the characteristics of the two forms might become so finely divided as to appear as a blend. Bean ('09, p. 943) has suggested that composite types or races of men "when crossed with opposite types follow the laws of Mendel for not many generations, then begin to blend. * * * At present all mixed races are probably in condition of spurious Mendelism or no Mendelism."

This seems to be the most accurate description of what appears to be the condition in *Io,* where the population is much mixed, assuming that inverse development of the degrees of dominance may be taken as a rough estimate of the character of inheritance. Inversion has its maximum development in the vicinity of Rogersville in the Holston, and a lesser degree of development in the Upper Clinch and Powell. We might look upon these as different stages or degrees in the process of fusion, a process which in all probability has been in progress for thousands of years.

Because the embryonic whorls of all the forms are smooth, carinate, or undulated, but not spinose, we infer that the spinosity is a later degree of development and that the relatively smooth shell represents approximately the ancestral form. Upon the bases of his very extensive experimental studies upon moths, Standfuss ('96, pp. 110–117; '00–'01) claims that in crosses the phylogenetically older "enforces its biological, morphological, and physiological characters on its hybrid offspring to a greater degree than the younger." The supposed hybrid *Io* with inverse development of spinosity may then be looked upon as the reassertion of dominance of the phylogenetically older smooth shell upon the phylogenetically younger and spinose kind. Thus inversion might be considered as a case of reversion to the ancestral form.

Except in the case of specialized shells which are spinose throughout their postembryonic development, spinosity develops at a variable age, from a very early age onward to very late in life. In such shells as *lyttenensis, paulensis,* and *loudonensis* the shell is fairly large (class two or three) before spines develop. Spinosity in such shells is clearly a later development and would generally be considered of later phylogenetic development. Davenport ('08, pp. 60–61) claims that:

> A progressive variation, one which means a further stage in ontogeny will dominate over a condition due to an abbreviation of the ontogenetic process, or a condition less highly developed than the first. The more developed condition dominates over the less developed.

From this standpoint the spinose shells would be expected to be dominant over the smooth, but this is contrary to what we find in the case of the shells showing inverse development. Thus inverse development agrees with Standfuss's law of the dominance of the phylogenetically older over the younger. It may be possible that Standfuss's law applies to the earlier stages of crossing and that later Davenport's law applies, because there are reasons (to be considered later) which suggest that the greater degree of inversion seen in the Holston shells may be due to the relatively recent date at which the smooth and spinous shells were thrown together by a change of drainage. As has been previously shown, in passing from the headwaters downstream there is a progressively earlier acquirement of spinosity; spinosity may be said to be "crowded back" or acquired earlier and earlier until it occupies the entire postembryonic development of the shell as in *spinosa* and its allies. We may even go further and note that the old-fashioned, smooth shells have taken to the hills, to the headwaters, where isolated, they have survived, while farther downstream on the lower lands the ascendant spinose forms are abundant and have an extensive range; a story often paralleled in the history of the human races.

It has long been known to palæontologists that the earliest known forms of animals are often small, without spines, or other forms of "ornamentation." This law has been formulated by Beecher ('01, p. 99) as follows:

> The first species [of a group of animals] are small and unornamented. They increase in size, complexity, and diversity, until the culmination, when most of the spinose forms begin to appear. During the decline extravagant types are apt to develop, and if the end is not yet reached, the group is continued in the small and unspecialized species which did not partake of the general tendency to spinose growth.

In the family Pleuroceridæ spinosity reaches its extreme development in *Io,* but none equal or surpass that of the large individuals of *loudonensis* and *turrita.* These shells, both in size and sculpture, thus harmonize with Beecher's law. In this connection, however, mention should be made of the fact that the size of the shell influences the size of the spines and that large shells have large spines, and live in the large rivers.

3. AGENCIES AND MEANS OF DISPERSAL.

The present geographic relations of *Io,* as have been indicated in the chapter on the history of the Upper Tennessee drainage, can not be understood without considering the present condition as a product of changes which have taken place in the past. In addition to the historical influences there are those of the present time which make possible the presence of the animal under existing conditions, such as rapidly flowing water, certain algæ, a firm substratum and a supply of lime. The persistence of this kind of animal in this region, for perhaps millions of years, implies that in all probability very similar conditions are of equal duration. It therefore seems very evident that where the time element is concerned there has been an abundance of it. It is frequently stated that the antiquity of the fresh-water fauna is an important element in its extensive range, but in this case we have an ancient group which is of relatively limited range, and most of the different forms are also of very limited range, in spite of the fact that they frequent a habitat which would be expected to give wading and water birds many chances to disperse them to other drainage areas. Personally I have felt that undue confidence in the influence of the ''accidental means'' of dispersal, particularly of macroscopic aquatic animals by birds, has favored the negligence of other more normal or usual methods of dispersal. Thus a whole volume has been devoted to the dispersal of mollusks (as Kew, The Dispersal of Shells. 1893) and with such little consideration, that it amounts to neglect, of the influence of the movements of the animals themselves or to the migration of their environment. But before turning to what might be considered the normal methods of dispersal of *Io* mention should be made of the fact that these shells were transported by the aboriginal Indians. I have found hundreds of these shells upon the sites of ancient Indian camps, particularly upon the Clinch, Nolichucky, and along the Tennessee proper. Also the two shells of *turrita* which form lot 200, were taken from an Indian mound near Chattanooga. There can therefore be no question that the shells were transported, at least short distances. These shells found about the camps are of the same kind as those living in the near-by rivers, or when the living snails were not found the dead ones possessed enough individuality to make it certain that they had not been carried from some other stream, or were contradictory to the natural probabilities of their occurrence. That the snails could survive such transportation seems likely because *Io* will live for several hours, or even a few days out of water, as I have received live specimens at Chicago sent through the mail from Clinchport, Va.

The localities where transportation was most likely to occur are at the important portages, and perhaps one of the most important of these was at Big Moccasin Gap, through Clinch Mountain, at Gate City, Va., plate 59. This might make possible a transference between the upper Clinch and Holston. There were probably other portages, but if their influence was large it seems that these shells should also have been established in some streams outside of the Tennessee. In view of these observations and inferences I conclude that the Indians were not an important factor in the inter-stream dispersal of these shells.

There are very few observations made or recorded which bear directly upon the means of dispersal of *Io.* Its habit of living on shoals isolates it and retards or prevents extensive excursions. Near the headwaters of rivers, where *Io* flourishes, the riffles are relatively close together but vary much, depending upon local conditions; in places these are probably two or three to a mile of the river, while farther downstream they are often a mile apart, and in the lower reaches, where the stream has more nearly cut its bed to grade, the shoals or bars are then often several miles apart, and the water on the shoals is relatively deep.

There is a constant tendency for the rapidly flowing stream to wash loose the animals and carry them into the pools below the shoals. This in the case of headwater streams is probably of no serious disadvantage because of the shallow waters along whose margins and bottoms the snail may be able to crawl back to the rapid water and upstream. But farther downstream where the pools are deeper, muddier, and the distances to other shoals are greater, dislodgment is much more serious and tends to isolate more completely the different colonies of snails. The greater velocity of headwater streams must also increase the chances of carrying shells from farther upstream downward, much more so than in the lower courses of the streams.

But on the other hand the habits of the animal help to resist this persistent tendency to wash the shells downstream. Besides the muscular power which enables the snails to hold fast to the substratum, it probably has a positive rheotropic response which leads it into rapid water and consequently at times upstream. That there is a tendency to migrate upstream is also suggested by the fact that what seems to be the most ancient forms, the smooth shells, are mainly confined to the headwaters. The presence of these ancient kinds of shells in the headwaters is also due in part to the slow migration of the habitat itself. It is a well-known physiographic principle that as drainage lines are perfected or developed the obstacles in their paths (falls, rapids, shoals, or riffles) are removed and the areas of rapid water tend to migrate upstream toward the divides (Adams, '01) and take their animals with them. The river profiles of the upper Tennessee system (Kingman, '00c; Kingman and others, '00, '00a) show clearly that the course of these streams forms a succession of pools, progressively elevated one above another toward the divides. These pools overflow at their rim and as their waters fall to the lower basin the rapid water habitat is formed. In general these obstacles, the rims between the basins, are removed first in the lower parts of the streams and progressively upstream quiet waters advance and the rapids recede. This migration of the habitat is only a part of the general problem of changes in drainage to which reference will be made later.

4. LONGITUDINAL DISTRIBUTION IN STREAMS.

Io is a river snail. It does not live in creeks or brooks, and for this reason it does not occupy the extreme headwaters of streams. However, other members of this family of shells, as some *Pleurocera* do inhabit such situations exclusively and shun the very conditions in which *Io* flourishes. After a stream reaches a certain degree of topographic development and in other favorable conditions, as at Dryden on the Powell, Artrip on the Clinch, Saltville and Fishdam on the Holston, and Conkling on the Nolichucky, *Io* makes its appearance and persists in the downstream reaches of this drainage to the Muscle Shoals in northern Alabama. In no case does the kind of *Io* found farthest upstream extend downstream to the other limit. In the Powell, Clinch, and Holston a relatively smooth shell occurs in the headwaters for a variable distance, only to be replaced sooner or later downstream by a very spinose kind. Even in the Nolichucky, which has a spinose shell in the headwaters, the shell, while it remains spinose, becomes more so downstream. There is then in all the streams a replacement in the kinds of shells and in the degrees of spinosity progressively downstream. Somewhat similar conditions are found in some elongated lakes. In Lake Tanganyika of central Africa, Moore ('03, pp. 149–150, 261) found and figures a Viviparid shell, *Neothauma tanganyicense,* which varies in its habitats in the lake. A strongly ribbed or keeled shell lives "exclusively at the south end of the lake, swarming in the broad and more or less sheltered reaches into which the southern end of Tanganyika expands. In the narrow, surf-swept, and turbulent portion of the lake which stretches between the north of Cameron Bay and Tembwi, *Neothauma* is only found in the little bays and sheltered places occurring along both shores, and here the character of the form changes, the double-keeled shell of the former variety being replaced by the elongated type." * * * [A shell with larger body whorl and aperture which is smooth and lacks the keel.] "Northward the lake terminates again in more or less sheltered expanses like the Gulf of Ubuari, the deep bays near Ujiji, and the extreme northern extremity of Tanganyika. In these the form of the genus again changes, the two more southern varieties being generally replaced by the curious rounded form." This is a less elevated shell similar to the one from the central part of the lake. It should be noted that the shells living in the quiet waters at each end of the lake are quite different, but the one from the exposed shores is much like the one from quiet waters at the north end of the lake. This appears to be a replacement of races comparable to the downstream change in the Tennessee system.

This law of replacement is not confined to this family or genus of shells, but has long ago been observed in many other kinds of animals. Thus Möllendorff (1873, pp. 59–60) has shown that in the Bosnia River, a tributary of the Upper Danube, in Bosnia, the snail *Melania holandri* Fer. (Family Melaniidæ) varies greatly in passing from the headwaters downstream. In the upper and more rapid parts of the stream the shells are thicker and smooth; farther down they are thinner and smooth; and still farther downstream they have well-developed spines and a thin shell. This longitudinal replacement of forms is a condition frequently observed in streams.

Voigt (1904, 1907) has shown that some planarian worms in the mountain streams of Germany are found in an orderly arrangement. In the extreme headwaters of certain brooks *Planaria alpina* is found, farther downstream pioneers of *Polycelis cornuta* are found with it, still farther down *P. cornuta* is alone. Still farther down pioneers of *Planaria gonocephala* are associated with *cornuta*, and still farther downstream *gonocephala* occurs alone. A similar condition is found among the crawfishes, as has been shown by Williamson (1901, p. 11), who says: "A collector starting at the headwaters of Squaw River (in western Pennsylvania) would find *bartonii;* following the stream he would soon notice *robustus* among his captures; then an occasional *propinquus* (=*obscurus*), till finally *bartonii* would become rare and disappear, then *robustus* would disappear, and near the mouth of the creek he would find only the species *propinquus* (=*obscurus*)."

Nor is this condition limited to invertebrates because it was long ago pointed out by Agassiz in 1850 and 1854, as applying to stream fishes, and has since been studied by Cope in 1868 and Jordan in 1878, in the southern Appalachians; and very recently in small streams by Shelford in 1911.

In view of these facts, how do the various kinds of animals reach their respective segments in a stream where they find favorable conditions of life? The answer to this question must vary with the history and ecology of the animals considered. There are evidently many causes which produce this result. Transportation will apply to some animals, others have reached these conditions in the past, under other climatic conditions (Voigt), as in the case of the planarians in the alpine streams. Some, as in the case of animals possessing good powers of locomotion, by their own movements alone, and still others by changes in the topography and drainage (Cf. Adams, 1901). In the case of *Io* it seems probable that the main factors which have influenced the longitudinal arrangement have been the movements of the animals themselves, in combination with the migration of the habitat, as the shoals have been changed with crustal movements and the processes of baseleveling. What are considered to be the most ancient forms, the smooth shells, are in the headwaters, in those drainage lines which have encroached upon the very ancient New River divide. This view favors the idea that in normal stream development the older relatively sedentary forms will occur upstream the farthest, because they were the first invaders and have migrated with the stream, and that later the stream was successively invaded by the forms which differentiated later. The most spinose shells occur downstream farthest from the headwaters, and they show in their early ontogenetic development of spines that they are more highly specialized.

It thus appears highly probable that the order of arrangement in some ancient streams of normal development is indicative to some degree of the antiquity and degree of specialization of the group. If the stream has had a very complex history, with considerable deviations from the normal or ideal development, this arrangement may be greatly obscured. It will be best shown in those parts of the stream which have the most normal development. In the Tennessee system I believe this applies best to their upper courses, and it is in these that we find the shells showing parallel lines of development, as in the Powell and Clinch, but in the upper Hoiston system, the complex piracy in its upper course appears to have caused the peculiar inverted arrangement with some smooth shells far from the headwaters. It is possible that where these smooth shells now live (near Rogersville) was once the headwaters of a northward flowing stream, which was captured, its current reversed, and the snails thus given their anomalous location. In my field work I had anticipated that ancient types of shells might be found in the extreme headwaters, and for this reason a special effort was made to determine the kind of shell and the upper limit of these shells in each stream, and this idea may prove useful to others in similar studies.

It was with considerable interest that after I have worked on this assumption for two years I learned that Wetherby ('76, pp. 6–7) had long ago expressed a similar opinion as follows:

> Now on this hypothesis of origin if any ancestral types of the *Strepomatidæ* remain at all, we shall find them among the species inhabiting the upper part of the drainage or that part least affected by changes of level. * * * What the headwaters of the Clinch may produce is yet unknown; and if the suggestion of Dr. Lewis be a just one, that shells are propagated *downstream*, a part of the key to the solution of this problem lies in the mountain source explorations of Clinch, Holston, and Powells.

The persistence of these lime-requiring snails near the New River divide, rather than in the correspondingly rapid waters from the Unaka Mountains and the Blue Ridge is at once explained in part if we recall that lime-bearing rocks abound in the north while they are conspicuously lacking in the higher mountains to the south.

The longitudinal changes or variations in *Io*, progressively downstream, appear to be very similar to what have been called *morphologic-geographic chains*, which have been described in certain land snails by the Sarasins ('99, '01, '01a), Plate ('08), and Davenport ('10a). These differences or series appear to be very similar to many geographic variations long ago pointed out by Allen (Cf. Smithsonian Rep. for 1905, pp. 375–402, 1907, for mammals). Unfortunately I do not have access to the work of the Sarasins and can not fairly discuss the bearing which their studies may have upon the present subject. Plate, however, claims that the Cerions of the island of New Providence, Bahama Islands, vary from west to east with increasing rainfall and show an increasing number of ribs which give sculpture to the shell; at the same time there is a decrease in size and the shells become progressively thinner. These differences he attributes to the climate and to a responsiveness of the animal. Davenport, however, revises somewhat Plate's observations on their occurrence and considers that the facts may be explained if we assume an invasion of New Providence from the eastern end, accompanied by migrations and diverse crossings, because he finds that Plate's "western" and "eastern" types are more or less intermingled.

5. CAUSES OF VARIATION.

Since beginning the study of *Io* the most frequent question has been concerning the use and cause of spines. Is it an advantage for the headwater shells to be smooth and to lack spines? is a representative question. But all of the headwater shells are not smooth, as in the South Fork of the Holston, where they are mainly undulate, and in the upper Nolichucky, where they are spinose. It has been suggested that the spines favor entanglement with objects floating downstream and it might be an advantage not to possess them. I have not been impressed by the force of this suggestion and I know of no advantage derived from the lack of spines, nor have I been able to see any advantage derived from the possession of them.

Physiologists have asked about the composition of the water and of its possible influence, assuming that spines might be a response to its composition. That there are chemical differences in the different parts of the rivers is well known, and further that these influences affect these snails is also known. First of all it should be stated that we have no chemical survey of any large river system in North America in sufficient detail to be of much use in such a study, certainly not of the Tennessee and its tributaries. That the shells do not abound in waters other than those draining lime-bearing rocks clearly shows that lime is a limiting factor in their range. Industrial refuse in the stream has already exterminated the shells from a part of the North Fork of the Holston and doubtless sewage and mining products will continue this kind of work in other localities. The relatively light weight of the shells in the upper Powell, when compared with those of the upper Clinch and Holston, shows that when the drainage is largely from nonlime-bearing rocks the shells are not as heavy as in the streams from lime rocks. Originally a small salt stream flowed into the Holston near the locality from which Say's type specimens were taken, but we have no record of its influence upon *Io*. The erosion of the shells shows that there are considerable differences in the different streams. This is shown in part by the plates of the shells. The shells of the upper Powell are iron stained, much eroded, and relatively free from encrustation. The Clinch shells are much like those of the lower

Powell. The Saltville shells are iron stained; the South Fork shells are large, heavy, with moderate erosion, and suggest an abundance of lime. The lower Nolichucky shells show considerable erosion on old shells and they are not encrusted. The shells from near the mouth of Little River are stained and eroded as in waters containing little lime. The shells from the Upper Tennessee proper are in general not iron stained or encrusted, while farther downstream (lot 151) they are eroded and with filamentous algæ growing on them. While not much weight can be attached to these observations, they are clearly indicative of variable local chemical conditions. From the standpoint of the chemical composition of the water the presence of mixed communities of shells as near Rogersville, with great extremes from smooth to spinose shell on the same shoal, is particularly confusing, because we can not believe that in such a situation the agitated waters can show a corresponding chemical diversification.

Another characteristic closely associated with smooth shells, but not confined solely to them (in group 3), is the relative degree of globosity of the aperture in terms of the diameter of the shell, the shell index. The relatively globular shells are headwater shells in the Powell, Clinch, and Holston. It is possible that this feature is influenced by the size of the foot, because we may infer that a larger foot is an advantage over a smaller one to an animal living in rapidly flowing water. Cooke ('95, pp. 89–90) has shown that in the marine shell, *Purpurea lapillus*, the exposed shells were stunted with a short spire and have a large mouth or aperture, while the shells from sheltered places were larger, often had a spire and a smaller aperture. Russell ('08) found that the limpet, *Patella vulgata*, upon an exposed shore was dwarfed somewhat, the shells were thick and heavy and thus in contrast with shells from sheltered situations. Walker ('09, p. 289, fig. 63) has shown that the large pond snail *Lymnaea stagnalis* produces local or habitat variations. In exposed situations a smaller low-spired shell with a large body whorl aperture is produced (variety B), while in quieter waters the shells are larger, have a higher spire, and when the aperture is very large the shell is thinner. Semper ('81, p. 440) states that *Nerita mortoniana* lives in salt, brackish, and fresh water. The salt-water form is smooth, but the brackish and fresh-water forms often develop spines, and a related subgenus *Cliton*, which is spinose, is characteristic of streams.

In *turrita* and its allies the shells tend to elongate and the aperture remains small, but *loudonensis* has a shorter spire and a larger aperture and lives in the same situations as *turrita*.

The variations of the size of the shell (small *Io* in small streams, and large in large streams) appear to be a general rule, although there are some exceptions. Thus the headwater shells (group 6) of the Clinch are large shells, and the *angitremoides* from the French Broad and upper Tennessee are relatively small shells which live in a large stream. The size of the shells is probably influenced to some degree by the abundance of lime available.

The climatic differences between the conditions where the headwater shells live and those farther downstream deserve mention as a possible cause of variations. The differences in the size of the shells from headwaters downstream may not be due solely to the size of the stream but to the combined influence of the size of the stream and to the climatic difference, because the streams become larger southward. To the south there is not only the higher average temperature but there is also the longer growing season. A comparison of the mean annual temperatures (Bull. Q, U. S. Weather Bureau, 1906) of Big Stone Gap, Va., and Wytheville, Va., which may be taken to approximate the climate of the headwater shells is 54° and 53° F., respectively, while in Knoxville and Chattanooga it is 57° and 60° F., respectively. The temperature of the air thus averages a few degrees higher. If the average latest date of killing frost (for vegetation) in the spring and average latest dates of killing frost in the fall are used as rough estimates of the warm growing season for snails, the southern localities have a spring about a month longer, and a fall about two weeks longer, thus in all a growing season from six to eight weeks longer than have the headwater shells. It thus seems reasonable to expect that the difference in climate is to some degree responsible for the larger shells to the south.

From the preceding discussion it will be seen that the causes for the differences observed in these shells may be due to several factors. The ones just mentioned appear to be due primarily to the character of the medium in which the animal lives. Another set of influences conditions or permits the different kinds of shells to intermingle, cross, and thus diffuse through the *Io* population certain germinal characteristics; or even to isolate or segregate them, because the segregation of characteristics, as in individuals, may preserve differentiation. Long ago Wetherby ('76, p. 4) suggested that in this family hybridization "may account largely for variation in form." If we ignore the history which permits these germinal conditions and their effects and study effects only comparatively we are particularly liable to attribute to a single cause the results which are due to the influence of several causes. It is therefore only by the history of each case that we may hope to make each conclusion stand upon its own merits. There is thus the same need for considering the history of results produced in the past as there is now for giving the history or method of procedure in a contemporary experiment. It is from this standpoint that one of the main values of the history of the Tennessee River system is derived. The changes in the drainage may be looked upon as just so many opportunities for the diffusion or expansion of the hereditary characteristics of these snails as a means of reaching new environments and as a means of remaining with or in the same environment. In this manner is seen the biological justification of such facts and inferences.

The development of the conditions which have permitted and caused the present diversity and geographic range in *Io* show clearly that some of these influences are due to the responses to the physical environment, while others are due to responses which different kinds of germinal substances produce when isolated, or produce in response to one another.

6. GEOGRAPHIC RANGE AND VARIATION OF EACH FORM.

The different forms of *Io* not only show much local variation, but they also do in different parts of the same stream and in different streams. To understand these it is necessary to recall the races of forms which were indicated in an earlier chapter. The degrees of intergradations which exist between these different forms make it very difficult or impossible to give their precise range. Some of the variations in the development of the shell, have been discussed in the chapter on ontogeny of the shell, and others were when discussing the quantitative data. Here we wish to consider the geographic range of each of the 14 forms recognized, and to observe the variations of the shell which change with locality, and to indicate the affinities suggested by such relations. Cf. Plate 1.

Powellensis.—This shell is found almost solely in the headwaters of the Powell River. Downstream below Pennington Gap it can not be recognized in abundance. Smooth shells are found in lot 37, from Powell River station, and in lot 29, from Greens Ford. I have considered all the smooth shells in the Powell as *powellensis.* The optimum development of this shell is seen in groups 1 and 2. A few smooth, or relatively smooth, shells with low spines or nodules, reach to near the mouth of the river. It appears that these shells with incipient spines are due to crossing with the spinose population in which they occur. That these have not been recently transported to these lower waters by floods and similar agencies, is suggested by the fact that such shells tend to develop spinosity at an earlier age than those in the headwaters, and can thus be distinguished from them in some cases.

The small size and relative thinness of these shells is probably due in part, to the small size of the stream and to the relatively small part of the headwaters which drains a limestone region. The shells in groups 1, 2, and 3 are strongly stained brown with iron, derived from the sandstones, while the remaining groups of shells are not so stained, but are encrusted with clay and algæ.

Lyttonensis.—This is a transitional form between the smooth and spinose kinds of shells in the Powell. It occurs in the headwaters in small numbers, evidently pioneers which have become established upstream in advance of the main body which predominate farther downstream, where their numbers increase until in group 2, at Lyttons Mill they are the most abundant shell. In group 3 they appear to be almost the only form present, and below this point its recognition is obscured. This form of shell appears to grade, in the lower Powell, very gradually into the shells which are spinose throughout their post-embryonic development, or which become spinose at the class 2 stage. These shells have been exceedingly puzzling and I have been inclined to consider them as the extreme geographic representatives of the forms *loudonensis* and *spinosa*. It looks somewhat as if *lyttonensis, loudonensis,* and *spinosa* all intergrade in this region. If this is not the case their ontogeny possesses a degree of variability not known elsewhere in these shells.

Clinchensis.—Confined to the headwaters of the Clinch, group 6, and still abundant at St. Paul, group 7, but below this locality even relatively smooth shells become spinose earlier than upstream, so that by the time Clinchport is reached the influence of all relatively smooth shells (*clinchensis* and *paulensis*) is practically gone. At St. Paul *clinchensis* has made rapid progress in intergrading into *paulensis*. Fort Blackmore (lots 167, 168) is about the downstream limit of *clinchensis,* and the change to the spinose is relatively abrupt.

Paulensis.—This form ranges from St. Paul to about Clinchport. It is transitional between the smooth and spinose shells in the Clinch. This form appears to grade into the Clinchport shells much as *lyttonensis* does into the mixed population of the lower Powell.

Brevis.—This shell, with rather blunt spines, is typically developed in the lower Clinch, group 10, lot 17, near Kyle Ford, Tenn. Individuals, at least closely resembling them, are found upstream in the vicinity of Fort Blackmore, Va., lot 164, in lot 55, from Clinchport, and downstream in the Clinch below Kyle Ford in lots 18 and 21, above the mouth of the Powell. Some of the shells in the Powell near its mouth, as in lot 28, suggest this form also. With departure from the vicinity of Kyle Ford this form becomes more and more obscure and difficult to recognize, so that it is practically impossible to determine its limits. In general it is bounded both up and down stream by more spinose shells.

Fluvialis.—Mainly confined to the headwaters of the North Fork of the Holston. Progressively downstream the undulations and nodules become more pronounced until in lot 191, Mendota, Va., it grades very gradually into the form *verrucosa,* near the mouth of the North Fork, as in lots 111 and 116, from Holston Bridge, Va. This is a very gradual transition into the downstream forms, while in the Powell and Clinch the smooth shell is rather sharply segregated because the transition is more abrupt. It is interesting to observe that *fluvialis* is not the predominant headwater form in the South Fork, but its near relative *verrucosa* has this range In a large series of *verrucosa,* as in lot 94, from the South Fork, at Bluff City, there are a few individuals which can not be distinguished from *fluvialis,* plate 41, figures 27–31, and a few similar individuals are found in the different lots from farther upstream at Fishdam.

In the headwaters of the Holston proper smooth and relatively smooth shells again reappear in large numbers in groups 15 and 16; but these smooth shells are not associated with nodulose or undulate shells like *verrucosa,* as upstream in the North Fork, but with very spinose individuals. The intermediate individuals are in part not only spinose toward maturity, as the usual transitional individuals in groups 2 and 7 in the Powell and Clinch Rivers, but in addition there is a great amount of inverse development. Therefore in the upper Holston proper the gradation from the smooth shells into the spinose is very abrupt on the downstream side into group 17 and upstream into group 14 it is possibly a few degrees less so. In this case strong spinosity bounds the smooth shells up and down stream, a condition not found in any other locality. Clearly the history of the shells in this portion of the river shows some unique influence in its development.

The smooth, or relatively smooth, *fluvialis* are thus found not continuously in the upper Holston drainage, as in the Powell and Clinch, but they are interrupted near the forks of the Holston by the spinose shell *recta*. *Fluvialis* also outcrops throughout the range of *verrucosa* into which it grades imperceptibly. In the Holston the downstream limit of *fluvialis* is in the vicinity of Rogersville, group 16, where they end quite suddenly.

Verrucosa.—This undulate and nodulose shell is found only in the lower part of the North Fork of the Holston, from about Mendota onward to near its mouth, to the vicinity of lot 178, above Rotherwood where *recta* abounds, and in the South Fork above Kingsport, upstream to Fishdam, Tenn., where it is the predominant headwater form of shell. This is the only case in the genus where a form, intermediate between the smooth and spinose kinds of shells, is the dominant form in the extreme headwaters. Near the mouths of both the North and South Forks *verrucosa* grades into *recta* (lots 175, 178). There is thus a double series of intergradations between these two forms, one in each fork of the Holston. This form is relatively limited in range and local differentiations have not been recognized.

Loudonensis.—To understand this kind of shell it is necessary to recall that shells having a similar manner of development are found in the Powell and Clinch under the respective names of *lyttonensis* and *paulensis.* These three forms have the first postembryonic whorls smooth, and as they grow they become spinose and normally remain so. Clearly they are related and the differences appear to be those of degree. In the Holston, from Cobb Ford, lot 90, downstream, *loudonensis* can be clearly recognized. It is here associated with *spinosa.* In the French Broad it continues from Dandridge, lot 136, downstream to its mouth, and from the headwaters of the Tennessee proper, lot 47, downstream to Bridgeport, Ala., lot 186. It is, however, far from uniform throughout this extensive range; the size of the shell and spinosity increases greatly as the stream becomes larger.

Recta.—This spinose shell is found near the confluence of the North and South Forks of the Holston, group 14. It is probable that it ranges upstream in the South Fork, but how far is not known. In the part of the Watauga which I examined no *Io* were found; possibly this shell is found in its lower parts. It is also found in the upper part of the Holston proper at Hords Ford, lot 85, and at Currys Ford, lot 86. Certain spinose shells in lots 97 and 98 from Chissolms Ford appear to be of this form, but they are not the most spinose individuals in the lots, for such are apparently *spinosa.* Somewhat similar conditions are also found in lots 87, 88, from near Rogersville.

This form is clearly related to *spinosa,* but they only come in contact with it in a community where *fluvialis, spinosa,* and *recta* are intermingled and intergrade to a remarkable degree.

Spinosa.—In the headwaters of the Holston proper *recta* and *spinosa* are so closely related that no sharp boundaries can be drawn. I am inclined to place the upstream limit of *spinosa* at about Chissolms Ford, lots 97 and 98. Passing farther downstream by the time Cobb Ford is reached (lot 90) *spinosa* is sufficiently free from *recta, fluvialis,* and intergrades, that it is the predominant form of shell. By the time the vicinity of Morristown is reached *spinosa* reaches what I have considered its typical form, lot 96. At Cobb Ford *spinosa* is associated with young shells which are at first smooth and later are spinose. These I consider *loudonensis,* a form with which it continues to associate to the mouth of the Holston. I have not been able to recognize with certainty *spinosa* in the French Broad, and this seems very remarkable when we consider that *spinosa* is very clearly related to the spinose Nolichucky shells, particularly *nolichuckyensis,* and yet these forms are not in contact. If *spinosa* and *nolichuckyensis* were intermingled or in close proximity in the same stream, it might seem trivial to separate them. *Spinosa* is also closely related to the kind of *turrita* which occurs in the French Broad and Upper Tennessee proper. It even appears that *spinosa* and *loudonensis* in the lower Holston and French Broad converge, because there is a variable age at which spines are developed in *loudonensis.* This is a condition which recalls the relation between *lyttonensis* and the spinose shells of the lower Powell and *paulensis* and the spinose shells in the vicinity of Clinchport in the Clinch. The shells of group 22 from near Knoxville show how closely *spinosa* is related to *turrita* in the upper Tennessee.

Unakensis. This spinose shell is confined solely to the upper parts of the Nolichucky River. It was found between Conkling and Limestone, Tenn. Although shells are unknown from the intermediate reaches of the river downstream, yet there is no reason to think that they do not grade completely into the form *nolichuckyensis* from near its mouth. This is the most spinose shell found in the headwaters of the Tennessee drainage. The spinosity of *unakensis* is less than in the shells from farther downstream. There is a resemblance between this shell and *recta* which is worthy of notice.

Nolichuckyensis and *turrita. Nolichuckyensis* clearly appears to be a larger downstream variation of *unakensis.* It is found only in the lower part of the Nolichucky and in the French Broad at the mouth of the Nolichucky; below the mouth of the Nolichucky it grades perfectly into *turrita.* The highest upstream that *turrita* was found alive in the French Broad was at Seven Island Shoals (lot 156, No. 55). In the same vicinity, lot 195, I found a good series of dead shells, the small individuals of which can not be distinguished, by inspection, from *nolichuckyensis,* but the largest individuals are much larger and heavier than the largest shells from the Nolichucky, as was to be expected from the larger size of the stream. These large dead shells resemble so much the very large *turrita* found much farther downstream (lot 187, Bellefonte, Ala.) that had not the living shell been found in the same vicinity I would have considered it most likely that these shells had been transported by man. It is very surprising that the *turrita* shells just mentioned are the only ones found in the French Broad. In the Tennessee proper, however, *turrita* is a relatively abundant shell, as is shown by its presence in large numbers in lots 100, 101, 102, and 103, from near Knoxville. In these lots *turrita* grades into the form *angitremoides* and into *spinosa* and some individuals are practically indistinguishable from *nolichuckyensis.* Of course these lots are composed of relatively immature shells, but to a corresponding degree they are well preserved and show that the apices are spinose. *Turrita* is abundant on the Little River Shoals, at the mouth of Little River. Below Little River the largest number of live *turrita* came from (lot 130) Loudon, and with farther advance downstream these shells become very large. *Turrita* extends downstream the farthest of any member of the genus and finds its extreme limit on the Muscel Shoals of Alabama, and thus it has the most extensive range of any form in the genus.

Angitremoides. This rather anomalous shell is recognized only in the lower French Broad where it occurs in lots 136, from Dandridge, lot 137, and from Hanging Rock Shoals; and in the upper Tennessee, lot 124, from Loneys Island, and in lot 152, from Loudon. The largest series of this kind found in any single locality came in lot 124, in which 35 out of 36 shells were of this form. Were it not for such a series this form might be considered as composed only of extreme individual variations. It is significant that *angitremoides* is most abundant in the same vicinity from which lots 100, 101, 102, and 103 came, as these are the series of *turrita* shells, to which they are most closely related. This form is clearly related to the Nolichucky shells and to *turrita.*

The general geographic relations of these shells is summarized on plate 1. The approximate range of each form is shown on the upper part of the plate, and on the lower part is given a figure of the kinds of shells, as represented by the type specimen or representative specimens.

7. THE MIGRATIONS OF THE ENVIRONMENT AND THE MIGRATIONS AND RELATIONS OF IO.

In the earlier chapter on the evolution of the gross environment the main facts in the history of the physical environment were outlined, but the relation of the changes to *Io* were not elaborated. I wish now to summarize these facts and inferences and indicate their relation to the migrations, history, and interrelations of these shells. Such a discussion must be provisional and will require revision with advances in our knowledge of the interpretation of the environment and with similar advances in our interpretation of the snails, because relative values are constantly changing. This discussion is built upon several assumptions, and first of these is that the responses of the animals to the present conditions give us the most important clues to their responses in the past. To-day these shells inhabit small rivers, rapidly flowing well oxygenated waters on shoals, are larger in larger streams, show greater spinosity downstream, inhabit streams draining lime-bearing rocks and show local differentiation. It is not necessary to assume that the original form of shell was invariable because it may have been smooth and undulate, as the Saltville shells of to-day. I infer that incipient spines, apparently a different character than undulations, developed in the downstream portions of a transversely flowing stream, and have migrated upstream and to the northeast. Spinosity apparently developed in the vicinity of the western part of the South Fork of Fluvialis River, or in Loudonensis River. With the development of longitudinal streams there has been a migration of the streams to the northeast, and the smooth shells of the present headwaters probably originated farther to the south. While the habitat of *Io* has migrated upstream it has at the same time tended to become extinct farther downstream, primarily because the various base-levels since the Cretaceous, have made their start and had their greatest development in that region, and hence the limited progress which these shells have made south of Fluvialis River.

To what degree transportation has been a factor in the history of *Io* can not now be determined, and therefore this discussion assumes that the primary influences have been the activities of the animals themselves in combination with the changes of drainage and the migration of their habitats. With this preliminary understanding we may now turn to the discussion.

Up to the close of the Cretaceous the drainage of the Upper Tennessee area was probably transverse from the mountains to the northwest into the Gulf embayment. At this time there appears to have been two drainage systems in the upper part of the Great Valley, one which may be called the Fluvialis River, draining through Cumberland Gap, plate 57, B, and the other Loudonensis River, draining the area of the Upper Tennessee proper through the Emory River route. The northernmost system or its North Fork probably contained relatively smooth forms of *Io*, while the South Fork or the other system contained relatively spinose shells. The relatively smooth primitive shells show considerable diversification in the upper parts of the Great Valley, while the spinose, more specialized shells show a similar degree of diversification in the area bordering this on the south. It is also probable that the smooth shells were in the headwaters of the Fluvialis system, as to-day they are headwater shells, and that undulations and less globular shells developed mainly lower downstream. Spinosity also declined upstream in the spinose shells, and in both systems the smaller shells were found in the smaller streams and the larger shells in larger streams. At the close of the Cretaceous the major differentiation within the genus had taken place and centered in two different forks of one river or in two river systems. With the perfection of the Cretaceous baselevel these shells, which must live in rapidly flowing water, must have occupied the upper reaches of the rivers mainly, and this probably tended to isolate the lower parts of each system as much as if they emptied as separate streams into salt water.

The uplift which inaugurated the Tertiary began the destruction of the relatively balanced condition of the drainage which developed on the Cretaceous peneplain and led to the drainage changes which resulted in the diversion of the northwestward flowing streams to the southwest. As the Appalachian Valley developed and migrated to the northeast it progressively captured and diverted to the southwest the northwestward flowing streams. Thus Loudonensis River was early diverted south and it is not unlikely that this system at an early date made two important captures, one by the lower Clinch which pirated the upper Clinch, and the other when the Nolichucky system was diverted to the southwest and its headwaters were invaded by spinose shells from the South Fork of Fluvialis River, or from Loudonensis River. Along the Clinch spinose shells were taken upstream and as the Clinch lowered its channel one of its tributaries, the lower Powell, captured the upper Powell and introduced spinose shells into its upper course. At this time also the forks of the Holston were probably tributary to the Clinch through Big Moccasin Gap, plate 59. It was probably by means of the Lower Holston that the Nolichucky system was diverted to the Loudonensis system from the Fluvialis. The absence of smooth shells from the Nolichucky suggests that the main South Fork of Fluvialis River was not invaded by the smooth forms of *Io*. The peneplain and drainage adjustments which produced it were probably completed late in the Eocene or Miocene. It may have been late in this stage or in the Pleistocene that the Lower Holston captured the forks of the Holston from Clinch River and conducted the spinose shells into the upper course of the Holston, if they had not already invaded these waters from the Clinch, and if so there has been a double invasion of these shells.

With the diversion of the Upper Holston was completed the metamorphosis of the drainage from transverse to longitudinal, from northwest to southwest, and at the same time the smooth and spinose kinds of shells were intermingled and a commingling and fusion began on a large scale in each stream. The blending or intermingling appears to be most perfect where it has been in progress the longest, as in the Clinch and Powell, and is most imperfect where we have reason to think that it is of relatively late origin, as in the Upper Holston near Rogersville, where inversion runs riot and crossing has been possible on a large scale.

The uplift at the beginning of the Pleistocene continued the active migration of the rapid-water habitat. The drainage responses to the new conditions again began in the southwest and migrated to the northeast, but mainly on account of the relatively short time which has elapsed since the initiation of this cycle the peneplain has only progressed, in a well-developed condition, up the Great Valley to the vicinity of the headwaters of the Tennessee proper. It is also probable that at this time the lower parts of the Holston, French Broad, and Nolichucky developed their present relations to the Tennessee proper. The French Broad probably captured the Nolichucky from the Lower Holston, and some tributary of the Nolichucky may even have been captured by the South Fork of the Holston, and thus introduced the spinose *recta* if it is not the result of transportation.

But beyond the broad plain there developed by erosion, near the head of the Tennessee proper, extended valley tongues for some distance up the other rivers and up the Holston possibly to the vicinity of Rogersville, Tenn., and this suggests that it was probably at this relatively late date that the forks of the Holston were diverted to the southward. Of course during all this time the headwaters of all the tributaries of the Tennessee were advancing toward the divides, and in this way the shells have had their range extended where lime-bearing rocks have permitted it. By this method of elongation of the habitat its extent has increased and the animals at the extremities of their range have been more and more isolated by separation. A few of the shells have spread far downstream, even to the Muscle Shoals in northern Alabama, but in general with the perfecting of the drainage the habitat of *Io* in the Tennessee tends to become extinct. To-day below the mouth of the Clinch in the Tennessee these shells do not appear to flourish as they do above this point.

The general relations of these shells to one another and their hypothetical migrations are indicated in the following diagram. (Fig. 1, text figure map.) This should be compared with plate 1, on which is shown a diagram of the present distribution of the different forms.

To understand the evolution of the spinose shells from the smooth or undulate it is desirable to form some idea of the relations between the different characters which differentiate these forms. If we look upon the smooth shells as those which lack the character of undulations and of spines, those with undulations (as *verrucosa*) as having an additional character, and spines as of still another character, we may gain some suggestions of value in attempting to understand the relations of these shells to one another. The smooth shells live in such large numbers as to make it clear that they must form at least one race which breeds true. Undulations are also found among the relatively smooth Powell shells, but not to a marked degree, and their presence suggests some degree of mixture of undulate individuals. However, undulations are more conspicuously developed in the Upper Clinch, but to a less degree at the upper limit of *Io*. In the North Fork of the Holston, undulations are well developed in some individuals at Saltville, farther downstream, and in the South Fork the conditions are completely reversed. Here the undulate shells make up the mass of the population and appear to be a race which breeds true, and the smooth shells are the exception. That undulations are thus able to form a local race suggests that we are dealing with a character of some individuality, whose presence in the smooth shells may be looked upon as so much contamination from another strain with which they are fertile when crossed. Undulations progressively decline with departure from the South Fork of the Holston. The relations of these forms seem relatively simple. On the other hand, spinosity presents a much more complex problem, because it not only varies in degree, but also in the time of its appearance in the life of the animal. It may develop only late in life, or it may do so from its earliest postembryonic development; and at least several of these different degrees of spinosity are represented by local races. Some of the degrees of spinosity are dependent on the size of the stream, because in general large shells live in large streams, and large shells have large spines; but the time of life at which spinosity develops appears to be more of a racial character. For this reason the time of life at which spines develop will be given

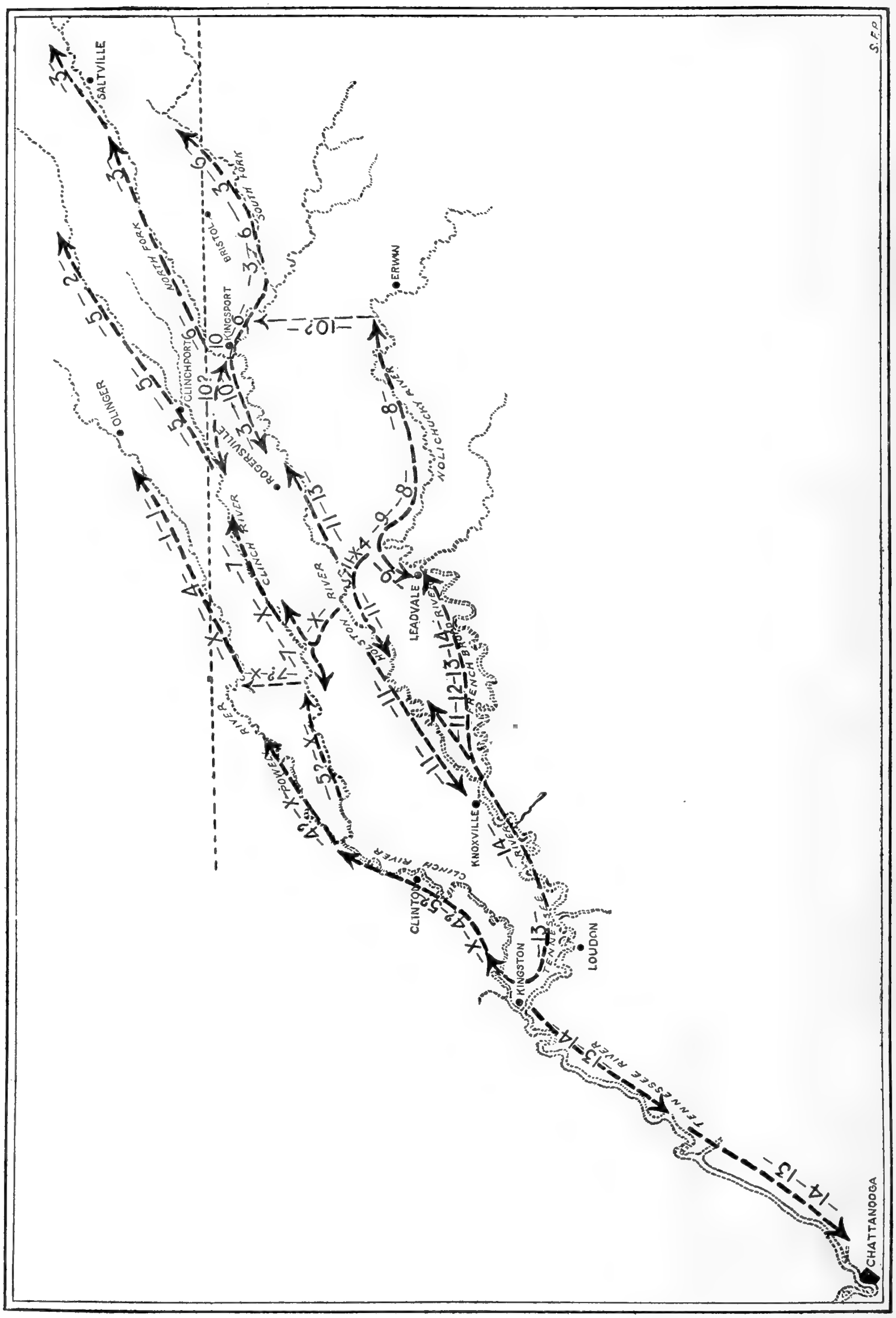

Fig. 1.—Diagram of the upper Tennessee drainage showing by arrows the hypothetical migrations of the forms of *Io*. The numbers refer to the forms as given on Plate 1.

more weight in estimating the genetic relations than the degree of spinosity, although it must be borne in mind that the time of life at which spines develop may be only an expression of the degree of intensity of the spinose character, a lesser degree of spinosity may be said to be dominant over a greater degree, because relatively smooth shells appear to be dominant in inversion.

Turning now to the evolution of the different forms, it seems that on account of the lack of spines, few undulations, and their occurrence in the headwaters, the smooth shells are the most primitive. On examination of the forms of shells which appear to stand more or less intermediate between the relatively smooth and those of the *turrita* type, as *paulensis, lyttonensis, loudonensis,* and possibly *verrucosa,* it is readily seen that they are not a homogeneous series of transitional forms. All are geographically located between smooth and spinose shells, with which they intergrade more or less, except *loudonensis. Verrucosa* intergrades perfectly upstream with *fluvialis* and downstream with *recta.* Undulations are also present in the Upper Clinch, in *clinchensis,* and particularly in *paulensis,* which develops spines late in life. *Paulensis* might be described as a combination of a smooth and undulate shell contaminated by spines late in its development. Such a combination has the appearance of a product of relatively local conditions which has permitted these three characters to be combined. *Lyttonensis* also appears to be a combination of smooth shells and those with small spines, and the amount (relatively large) of inversion associated with it suggests that different degrees of spinosity may be expressed in such a combination, and it does not follow that all which is inherited is shown. *Loudonensis* appears to be a shell very similar to *lyttonensis,* and to a less degree to *paulensis,* in the ontogeny of its spines, but in these the spines are of course much smaller, as they are from much smaller streams than the Tennessee. *Loudonensis* is a very spinose shell which develops from a smooth young shell. The similarity of development raises the question as to whether or not *lyttonensis* and *paulensis* are not simply geographic or habitat variations of the same form, which with the diversion of the drainage early migrated far up each of these rivers, or on the other hand, were they independently, or convergently, formed by the combination of the spinose shells invading the streams and crossing with them in approximately the places where they now live? The history of the streams seems favorable to either view. The lack of inversion in *loudonensis* might be interpreted to mean that it is not a combination, as in the other forms, but that it has the characteristic to develop spines at a certain age.

Verrucosa is not intermediate between the smooth and spinose kind of shells, except in the North Fork of the Holston. It is not found intermediate between the smooth and spinose shells in either the Clinch and the Powell, where as a distinct type it is completely lacking. In the Holston it forms a perfect transition between the smooth *fluvialis* and the spinose *recta. Verrucosa* has invaded the headwaters of the South Fork as *fluvialis* has the North Fork, and develops with such distinctness as to indicate its independent character. With departure from the forks of the Holston undulations rapidly diminish. They are shown only to a small degree in the upper Clinch, and to a much less degree in the Powell, and what is even more remarkable they are absent from that part of the upper Holston proper where the smooth and spinose shells are so confusedly intermingled (near Rogersville). In view of these relations it appears that these apparently intermediate forms of shells are not a homogeneous series, because their homogeneous character is much more apparent than real. They appear to have been formed by combinations of several different degrees of intergradation rather than as a single series between the smooth and spinose shells. The presence of inversion in *verrucosa* is significant and suggests that undulations as well as spines are capable of suppression by the dominant smooth shells.

Among the shells which are spinose throughout post-embryonic development there is little that can be used to measure values. As these shells are spinose from the start and the degree of spinosity varies so much with the size of the shell and the stream the characters useful in the other shells are not applicable here. There is remarkable unity and continuity in this series: *unakensis, angitremoides, nolichuckyensis, spinosa,* and *turrita. Brevis* and *recta* are the odd members of the series. The *turrita* series seem to converge toward the headwaters of the Tennessee proper, as here *turrita* and *spinosa* converge, *unakensis* and *angitremoides* are closely related, although their range is discontinuous. These two bear much the relation to one another that *nolichuckyensis* and *spinosa* do to each other.

Turrita in the French Broad (lot 195) grades into *nolichuckyensis*. As *recta* approaches both *spinosa* and *unakensis* it appears that it may have been derived from the region to the south of its present location where the other spinose shells flourish. *Brevis*, on the other hand, appears to be most closely related to the complex mixtures of spinose shells of the lower Powell and Clinch, and is not directly related to the other spinose shells. It may be a relic or representative of the ancient form and a degree of spinosity developed as a local race in a transverse stream. The development of the *turrita* series in the Nolichucky and Tennessee Rivers is strong evidence favoring the view that they have originated in this vicinity, and that spinosity has spread elsewhere from here.

Among the spinose shells the amount of differentiation in the forms indicates that not only are some different degrees of spinosity inherited, but also the size and thickness of the shell (*angitremoides*), degree of elongation of the shell, size of aperture, relative number of spines on a whorl (*turrita*), and possibly other characteristics.

The mixed shell populations not considered in the preceding discussion must now be considered. The shells of the Powell River below *lyttonensis* appear to be a very mixed and variable population, due to the intermingling of different degrees of relatively smooth and spinose shells. The relatively smooth shells are possibly relics of an ancient colony antedating the invasion of the spinose shells, which lagged behind while the other migrated farther upstream. In the Clinch the degree of spinosity in the Clinchport shells is puzzling, particularly when we consider that they are bounded upstream by *paulensis* and downstream by the small, low-spined *brevis*. One wonders if some of the relatives of *recta* had not at one time, when the Holston was tributary to the Clinch, had a colony of these shells which have since been absorbed. Below *brevis* (lot 17) in the Clinch the population is again a mixed one, comparable to that of the lower Powell. In the Holston confusion begun in the vicinity of Rogersville, with the mixed population of smooth (*fluvialis*) and spinose shells of the *loudonensis*, *spinosa*, and *recta* types, and a series which also includes the shells of inverse development. It may seem strange that the dominance of the smooth shell does not spread over the *Io* population so that smooth and not the spinose shells could be the most abundant kind. A similar condition is found in cattle, in which the hornless condition is dominant when crossed with the horned, and yet horned cattle and not the hornless are the predominant kinds.

It may be possible to interpret the variations of these cross-fertilized snails in terms of pure strains, which are the nearest approach to the pure lines of the self-fertilized plants studied by Johannsen, and Lang's experiments on *Helix* appear to harmonize with this view. There may be pure strains of the smooth shells, of the undulated shells, of shells developing spines, not only in different degrees but also at progressively earlier ages until the entire postembryonic life is spinose. Obviously it would be a large undertaking to prove this. Yet the individuality of the 14 recognized forms readily lends itself to such an interpretation, particularly if we assume, and with considerable reason, that almost any degree of a character may be inherited. This gives this view wonderful adaptability and it gives another standpoint from which to view the intergradations. The idea of pure strains harmonizes well with the form of inheritance, Mendelian, which is so characteristic of snails and which probably applies to *Io*. The variation which we see in dominance with age (inverse development) suggests the dominance of smooth shells over undulations, and some degrees of spinosity. The different degrees of inversion may be considered as due to the different amounts of the characters present in the strains crossed, combined with normal fluctuations. In the Rogersville shells, which show the greatest amount of inversion, the smooth shells appear to be crossed with shells of greater spinosity than in the other localities, and it looks as if the crosses are in a greater degree of instability than when less contrasted forms are crossed.

This change of dominance with age calls to mind the condition which we see in these animals which have marked secondary sexual characters. Often in such animals the young male resembles the female, but with maturity it develops the secondary sexual characters of the male.

This may be compared with the change of dominance with age, but in the case of secondary sexual characters castration may be able to change or prevent the development or expression of the adult characters. Furthermore females occasionally develop male characters and thus both sexes may show latent or unexpressed characters which vary with age. The castration which may influence the dominance of one sex may be compared with the influences of the dominant smooth shell in the cross which leads to inversion. It is of further interest that such sex characters, and even sex itself, appears to be inherited in some animals in Mendelian fashion (cf. Morgan. Amer. Nat., vol. 45, 1911, pp. 65–78). In *Io* undulations, low and long spines, show inverse development in many degrees, apparently depending on the degree of amount or intensity of the character. The vast amount of diversity and variation in these shells, from this point of view, may be looked upon as due to the numerous strains and their combinations in different degrees of intensity, made possible by the environment, and supplemented by the fluctuations which are due to the influence of the local environments, not only upon the body but also possibly upon the germ. This is a condition similar in many respects to the complex mixtures or strains seen in those domestic animals which are of multiple origin from diverse races (cf. Ewart. The Principles of Breeding and the Origin of Domesticated Breeds of Animals. Twenty-seventh Ann. Rep. Bureau of Animal Industry, U. S. Dept. Agric. (1910), pp. 125–186, 1912).

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Note.—This paper was completed April, 1912, and since then Ortmann's valuable paper: "The Alleghenian Divide, and its Influence upon the Freshwater Fauna" (Proc. Amer. Phil. Soc., vol. 52, pp. 287–390, 1913), has appeared, but it has not been possible to incorporate his results in this paper. Attention should also be called to the discussion of local variations and allied problems in Bateson's "Problems of Genetics," 1913; and to comments on the crosses of snails in Przibram's "Experimentale-Zoologie. 3. Phylogenese." 1910, pp. 63–68.

BIBLIOGRAPHY.

1. THE ORGANISM AND ITS RESPONSES.

Adams, Chas. C.
1900. Variation in *Io*. Proc. Amer. Assoc. Adv. Sci., vol. 49, pp. 208–225.
Bartsch, P.
1906. Variation in the shell of *Goniobasis virginica,* with an outline for breeding experiments. Science, n. s., vol. 23, pp. 465–466.
1907. The Philippine pond snails of the genus Vivipara. Proc. U. S. Nat. Mus., vol. 32, pp. 135–150.
Bateson, W.
1909. Mendel's principles of heredity. Cambridge.
Bean, R. B.
1909. A scheme to represent type heredity in man. Science, n. s., vol. 29, pp. 942–944.
Beecher, C. E.
1901. The origin and significance of spines. A study in evolution. Studies in evolution. pp. 1–105, Yale Bicentennial Publications. New York.
Borcherding, Fr.
1906. Achatinellen-Fauna der Sandwich-Insel Molokai, nebst einem Verzeichnis der übrigen daselbst vorkommenden Land- und Süsswassermollusken. Zoologica. (C. Chun.) Heft 48, pp. 1–195.
Brooks, W. K.
1899. The foundations of zoology. New York.
1906. Heredity and variation; logical and biological. Proc. Amer. Phil. Soc., vol. 45, pp. 70–76.
Cooke, A. H.
1895. Molluscs. Cambridge Natural History. Vol. III. N. Y.
Coutagne, G.
1894–96. Recherches sur le polymorphisme des mollusques de France. Ann. Soc. Agric. Soc. Nat. et Arts Utiles Lyon. 7 series, vol. 2, 1894, pp. 397–460; vol. 3, 1896, pp. 291–450.
Crampton, H. E.
1907. A study in variation, geographical distribution and mutation in snails of the genus Partula from Tahiti. Science, n. s., vol. 25, p. 729.
1909. The Partulæ of the Society Islands, and the problems of distribution and isolation. Science, n. s., vol. 29, p. 434.
Davenport, C. B.
1908. Determination of dominance in Mendelian inheritance. Proc. Amer. Phil. Soc., vol. 47, pp. 59–63.
1910. The interpretation of dominance and some of its consequences. Amer. Nat., vol. 44, pp. 129–135.
1910. Variability of land snails (Cerion) in the Bahama Islands with its bearing on the theory of geographical form chains. Science, n. s., vol. 31, p. 600.
Davis, C. A.
1901. A second contribution to the natural history of Marl. Journ. Geol., vol. 9, pp. 491–506.
Darbishire, A. D.
1905. Professor Lang's breeding experiments with *Helix hortensis* and *H. nemoralis;* an abstract and review. Journ. Conch., vol. 11, pp. 193–200.

Giard, A.

1903. Caracteres dominants transitoires chez certains hybrides. C. R. Seances et Mem. Soc. de Biol. année 1903, vol. 55, pp. 410–413.

Guyer, M. F.

1909. Atavism in guinea-chicken hybrids. Journ. Exper. Zool., vol. 7, pp. 723–745.

Gulick, J. T.

1905. Evolution, racial and habitudinal. Publ. No. 25, Carnegie Inst. Washington.

Haldeman, S. S.

1841. Observations on the Melanians of Lamarck. Amer. Journ. Sci. Arts., vol. 41, pp. 21–23.

Hardy, G. H.

1908. Mendelian proportions in a mixed population. Science, n. s., vol. 28, pp. 49–50.

Hilgendorf, H.

1866. Planorbis multiformis im Steinheimer Süsswasserkalk. Monatsber. Kön. Preuss. Akad. Wiss. Berlin. pp. 474–504.

1901. Der Übergang von Planorbis multiformis trochiformis zum Pl. mul. oxystomus. Arch. Nat. 1901, 67 Jahrg. Suppl., pp. 331–346.

Holmes, S. J.

1909. The categories of variation. Amer. Nat., vol. 43, pp. 257–285.

Hyatt, A.

1880. The genesis of the tertiary species of Planorbis at Steinheim. Mem. Boston Soc. Nat. Hist. Fiftieth Anniversary, pp. 1–114.

1898. Evolution and migration of Hawaiian land shells. Science, n. s., vol. 8, p. 395.

Johnson, R. H.

1908. Determinate evolution in the color pattern of the Lady Beetles. Publ. No. 122. Carnegie Inst. Washington.

Lang, A.

1904. Über Vorversuche zu Untersuchungen über die Varietätenbildung von *Helix hortensis* Müller and *Helix nemoralis* L. Festschrift zum siebzigsten Geburtstage von Ernst Haeckel. Jena.

1906. Über die Mendelschen Gesetze, Art und Varietätenbildung, Mutation und Variation, insbesondere bei unseren Hain- und Gartenschnecken. Verh. Schweizerischen Naturforch. Gesell. Luzern. 88 Jahresversm., pp. 209–254.

1896. Kleine biologische Beobachtungen über die Weinbergschnecke (Helix pomatia L.). Vierteljahrsschr. Naturforcsh. Gesell. Zürich. 41 Jahrg. Teil 2, pp. 488–495.

1908. Über die Bastarde von Helix hortensis Müller und Helix nemoralis L., Jena, pp. 120.

Lewis, James.

1871. On the shells of the Holston River. Amer. Journ. Conch., vol. 6, pp. 216–226.

1876. Io and its habits. Amer. Nat., vol. 10, pp. 321–335.

MacDougal, D. T.

1907. Hybridization of wild plants. Bot. Gaz., vol. 43, pp. 45–58.

Mayer, A. G.

1902. Some species of Partula from Tahiti. A study in variation. Mem. Mus. Comp. Zoöl., vol. 26, no. 2, pp. 117–135.

Mollendorff, O. von.

1873. Beiträge zur Fauna Bosniens. Görlitz, H. Tzschaschel, pp. 73.

Moore, J. S. E.

1903. The Tanganyika problem. London, pp. 371.

Newman, H. H.

1908. The process of heredity as exhibited by the development of Fundulus Hybrids. Journ. Exper. Zool., vol. 5, pp. 503–561.

Neumayr, M. und Paul.
1875. Die Congerien- und Paludinenschichten Westslavoniens. Abh. K. K. geolog. Reichsanstalt, Wien, Bd. 7.

Pilsbry, Henry A. and Hyatt, Alpheus.
1911. Achatinellidae. Manual of Conchology. Structural and systematic. Second series. Pulmonata. Philadelphia. vol. 21.

Plate, L.
1908. Variabilität und Artbildung nach dem Prinzip geographischer Formenketten bei den Cerion-Landschnecken der Bahama-Inseln. Archiv für Rassen- und Gesellschafts-Biologie, 4. Jahrgang, pp. 1–71.

Russell, E. S.
1908. Environmental studies on the limpet. Proc. Zool. Soc., London. 1907. pp. 856–870.

Sarasin, F. and P.
1899. Die Landmollusken von Celebes. Wiesbaden.
1901. Ueber die geologische Geschichte der Insel Celebes auf Grund der Thierverbreitung. Materialien zur Naturgesch. der Insel Celebes. Dritter Band.
1901. Entwurf einer geographisch-geologischen Beschreibung der Insel Celebes. Wiesbaden.

Semper, K.
1881. Animal life as affected by the natural conditions of existence. New York.

Shull, G. H.
1907. Elementary species and hybrids of Bursa. Science, n. s., vol. 25, pp. 590–591.
1908. A new Mendelian ratio and several types of latency. Amer. Nat., vol. 42, pp. 433–451.

Simpson, C. T.
1896. The classification and geographical distribution of the pearly fresh-water mussels. Proc. U. S. Nat. Mus., vol. 18, pp. 295–343.

Standfuss, M.
1896. Handbuch der paläarktischen Grossschmetterlinge. 2. Aufl., Jena.
1900–1901. Synopsis of experiments in hybridization and temperature made with Lepidoptera up to the end of 1898. Trans. E. M. Dadd. Reprinted from "Entomologist." Pls. I–IV.

Stimpson, W.
1864. On the structural characters of the so-called Melanians of North America. Amer. Journ. Sci. Arts, ser. 2, vol. 38, pp. 41–53.

Thomson, J. A.
1908. Heredity. Progressive Science Series, London.

Tower, W. L.
1910. The determination of dominance and the modification of behavior in alternative (Mendelian) inheritance, by conditions surrounding or incident upon the germ cells at fertilization. Biol. Bull., vol. 18, pp. 285–352.

Tryon, G. W.
1873. Land and fresh-water shells of North America. Pt. IV. Strepomatidæ. Smithsonian Misc. Coll., vol. 16, pp. 490.

Voigt, W.
1904. Über die Wanderungen der Strudelwürmer in unseren Gebirgsbächen. Verh. Naturhis. Ver. Preuss. Rheinlande, Westfalens und des Regierungsbezirks Osnabrück. 61. Jahrg., pp. 103–178.
1907. Wann sind die Strudelwürmarten *Planaria alpina, Polycelis cornuta,* und *Planaria gonocephala* in die Quellbäche un den Vulkanen der Eifel eingewandert? Ber. über die Versammlungen des Bot. u. Zool. Vereins f. Rheinl.-Westf., 64. Jahrg., pp. 67–75.

Walker, B.

1909. Annotated list of the mollusca of Isle Royale, Michigan. Ann. Rep. Mich. Geol. Surv. for 1908, pp. 281–298.

Wetherby, A. G.

1876. Remarks on the variation in form of the family Strepomatidæ, with descriptions of new species. Proc. Cincinnati Soc. Nat. Hist., no. 1, pp. 1–12.

1881. On the geographical distribution of certain fresh-water molluscs of North America, and the probable causes of their variation. Journ. Cincinnati Soc. Nat. Hist., vol. 3, pp. 317–324; vol. 4, pp. 156–166.

White, C. A.

1883. A review of the non-marine fossil mollusca of North America. 3rd Ann. Rep. U. S. Geol. Surv., 1881–82. pp. 403–550.

1905. The ancestral origin of the North American Unionidæ, or fresh-water mussels. Smithsonian Misc. Coll., vol. 48, pp. 75–88.

Williamson, E. B.

1901. The crayfish of Allegheny County, Pennsylvania. Ann. Carnegie Mus., vol. 1, pp. 8–13.

2. THE ENVIRONMENT, ITS DESCRIPTION AND EVOLUTION.

Adams, Charles C.

1901. Base-leveling and its faunal significance, with illustrations from southeastern United States. Amer. Nat., vol. 35, pp. 839–851.

Ayers, H. B., and Ashe, W. W.

1905. The southern Appalachian Forests. Prof. Paper, no. 37, U. S. Geol. Surv.

Campbell, M. R.

1893. Geology of the Big Stone Gap Coal Field of Virginia and Kentucky. Bull. 111, U. S. Geol. Surv.

1894. Tertiary changes in the drainage of southwestern Virginia. Amer. Journ. Sci., vol. 48, pp. 21–29.

1894. Estillville folio. U. S. Geol. Surv.

1896. Drainage modifications and their interpretation. Journ. Geol., vol. 4, pp. 567–581; 657–678.

Campbell, M. R., and W. C. Mendenhall.

1896. Geologic section along the New and Kanawha Rivers in West Virginia. 17th Ann. Rep. U. S. Geol. Surv. 1895–96. Pt. 11, pp. 1–39.

Chamberlin, T. C., and R. D. Salisbury.

1906. Geology. New York.

Davis, W. M.

1891. The geological dates of origin of certain topographic forms on the Atlantic Slope of the United States. Bull. Geol. Soc. Amer., vol. 2, pp. 545–586.

Glenn, L. C.

1911. Denudation and erosion in the southern Appalachian Region and the Monongahela Basin. Prof. Paper, no. 72, U. S. Geol. Surv.

Harris, J. A.

1903. An ecological catalogue of the crayfishes belonging to the genus Cambarus. Kans. Univ. Sci. Bull., vol. 2, pp. 170–180. Includes many references to descriptions of streams, and particularly valuable to the student of river faunas.

Hayes, C. W.

1895. The southern Appalachians. Nat. Geogr. Monographs, vol. 1, pp. 305–336.

1899. Physiography of the Chattanooga District in Tennessee, Georgia, and Alabama. 19th Ann. Rep. U. S. Geol. Surv., 1897–98, pt. 2, pp. 1–58.

Hayes, C. W., and M. R. Cambell.

1894. Geomorphology of the southern Appalachians. Nat. Geog. Mag., vol. 6, pp. 63–126.

1900. The relation of biology to physiography. Science, n. s., vol. 12, pp. 131–133.

Johnson, D. W.

1905. The tertiary history of the Tennessee River. Jour. Geol., vol. 13, pp. 194–231.

1905. The distribution of fresh-water faunas as an evidence of drainage modifications. Science, n. s., vol. 21, pp. 588–592.

Keith, A.

1896. Some stages of Appalachian Erosion. Bull. Geol. Soc. Amer., vol. 7, pp. 519–525.

King, W. R., and others.

1881. Holston and Clinch Rivers. House Ex. Doc. No. 77, 46th Cong., 3rd session. vol. 28, pp. 1–27, No. 1978. Useful table of shoals, fall, distances, etc.

Kingman, D. C.

1899. Examination of Powell River, Virginia and Tennessee. House Ex. Doc. No. 58, 56 Cong., 1st sess., vol. 57, pp. 1–8. Cf. also House Ex. Doc. No. 52, 46 Cong., 3rd sess., 1881.

1900. Survey of Tennessee River at the "Suck," or Mountain Section, below Chattanooga, Tenn. House Ex. Doc. No. 461. 56th Cong., 1st sess., vol. 91, pp. 1–49. Maps.

1900. Examination and survey of Hiawassee River. House Ex. Doc. No. 593, 56th Cong., 1st sess., pp. 1–9, List of shoals on the Hiawassee.

1900. Annual report upon the improvements of Tennessee River and its tributaries. Ann. Rep. Chief of Engineers, U. S. Army for 1900. App. FF. pp. 2907–3084. Contains useful references to the Tennessee drainage system.

1900. Final report on survey of Holston River, Tennessee. House Ex. Doc. No. 218. 56 Cong., 2nd sess., vol. 74, pp. 1–24, No. 4148. Maps. Contains very useful maps and a profile of the river.

Kingman, D. C., and others.

1900. Survey of French Broad River, Tennessee. House Ex. Doc. No. 616, 56th Cong., 1st sess., vol. 100, pp. 1–14. Maps and profile. Valuable detailed maps of shoals from the mouth of the Nolichucky to the Holston River. Cf. also House Ex. Doc. 141, 44th Cong., 1st sess., 1876, pp. 5–11.

1900. Final report on Survey of Clinch River, Tennessee. House Ex. Doc. No. 75, 56th Cong., 2nd sess., vol. 60, pp. 1–56, No. 4134. Maps. Detailed maps and profile of shoals from the mouth of Sycamore Creek to the mouth of the river. The best for the field.

Lesley, J. P.

1873. The geological structure of Tazewell, Russell, and Wise Counties, in Virginia. Proc. Amer. Phil. Soc., vol. 12, pp. 489–513. Map.

Long, S. H.

1846. Report on survey in relation to the improvement for navigation of the Holston and Tennessee Rivers. House Ex. Doc. No. 167, 29th Cong., 1st sess., vol. 6, pp. 41–91. General descriptions of the rivers and the character of the shoals. No maps.

1875. Holston and Tennessee Rivers. House Ex. Doc. No. 167, 43rd Cong., 2nd sess., pp. 1–51. Maps 25. Detailed outline maps of many shoals. The best maps for use in the field. A reprint of the above with maps. Cf. also Rep. Sec. War, 1876–'77, vol. 2, pt. 1, p. 710; and maps of shoals above Chattanooga, 1872–73, vol. 2, p. 488.

Morgan, J. T., Carmack, E. W., and Overman, L. S.

1906. Navigation of Tennessee River. Senate Doc. No. 83, 59th Cong., 1st sess., vol. 3, pp. 1–72.

Packard, A. S.

1898. A half century of evolution, with special reference to the effects of geological changes on animal life. Amer. Nat., vol. 32, pp. 623–674.

Pressey, H. A.

1902. Hydrography of the southern Appalachian Mountain Region. Water Supply and Irrigation Papers. U. S. Geol. Surv. no. 62, pt. 1; and No. 63, pt. 2.

Robert, H. M.

1893. Survey of the Tennessee River. House Ex. Doc. No. 252, 52 Cong., 2 sess., vol. 32, pp. 1–47. The best description of the river based upon an accurate survey. The detailed maps are not published. Reprinted (without maps) Rep. Sec. War. House Ex. Doc. No. 1, pt. 2, 53 Cong., 2 sess., vol. 5, pp. 2333–2375, No. 3201.

Roosevelt, T., and others.

1902. Message of the President of the United States transmitting a report of the Secretary of Agriculture in relation to the forests, rivers, and mountains of the southern Appalachian Region. Washington.

Sanborn, W. G., and Tallinger, E. C.

1881. Holston and Clinch Rivers. House Ex. Doc. No. 77, 46th Cong., 3d sess., vol. 28, pp. 1–27. Lists of shoals, distances, and falls on upper courses of Clinch and Holston Rivers. Cf. also Ann. Rep. Chief of Engineers for 1881, pp. 1878–1886.

Simpson, C. T.

1900. On the evidence of the Unionidæ regarding the former courses of the Tennessee and other southern rivers. Science, n. s., vol. 12, pp. 133–136.

Tight, W. G.

1903. Drainage modifications in southeastern Ohio and adjacent parts of West Virginia and Kentucky. Prof. Paper, no. 13, U. S. Geol. Surv.

Vanderford, C. F.

1897. The soils of Tennessee. Bull. Tenn. Agric. Exper. Stat., vol 10, pp. 1–139. Contains relief and geological map of Tennessee.

White, C. H.

1904. The Appalachian River versus a tertiary Trans-Appalachian River in eastern Tennessee. Journ. Geol., vol. 12, pp. 34–39.

Willis, B.

1887. Topography and structure in the Bays Mountains, Tennessee. School of Mines Quarterly, vol. 8, pp. 242–252.

1895. The Northern Appalachians. Nat. Geogr. Monographs, vol. 1, no. 6, pp. 169–202.

Woodworth, J. B.

1894. The relation between baseleveling and organic evolution. Amer. Geol., vol. 14, pp. 209–235.

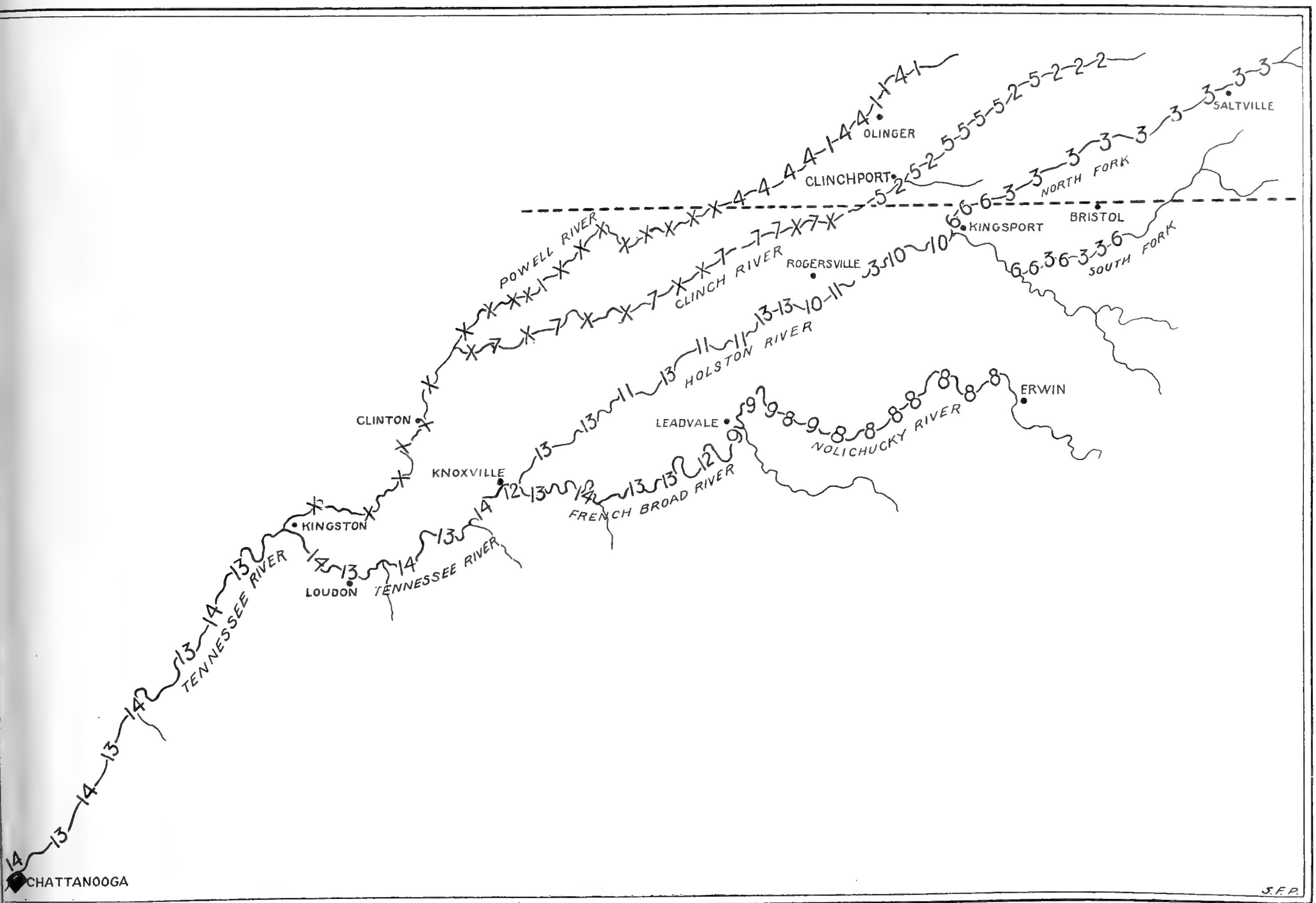
PLATES.

EXPLANATION TO PLATE 1.

Representative individuals of the forms of the genus *Io*, showing types, typical specimens, and a diagram of the upper Tennessee River to show the general range of each form in the system. The numbers under each kind of shell correspond with the numbers and range of the shell as shown on the map above. The shells in the upper row probably begin development smooth; those in the lower row as undulate or spinose.

1. *powellensis.*
2. *clinchensis.*
3. *fluvialis.*
4. *lyttonensis.*
5. *paulensis.*
6. *verrucosa.*
7. *brevis.*
8. *unakensis.*
9. *nolichuckyensis.*
10. *recta.*
11. *spinosa.*
12. *angitremoides.*
13. *loudonensis* (ranges downstream to Bridgeport, Ala.).
14. *turrita* (ranges downstream to the Muscle Shoals, Ala.).

x = spinose undetermined shells. Natural size.


OLINGER
CLINCHPORT
SALTVILLE
KINGSPORT
BRISTOL
ROGERSVILLE
NORTH FORK
SOUTH FORK
POWELL RIVER
CLINCH RIVER
HOLSTON RIVER
ERWIN
LEADVALE
NOLICHUCKY RIVER
FRENCH BROAD RIVER
CLINTON
KNOXVILLE
KINGSTON
LOUDON
TENNESSEE RIVER
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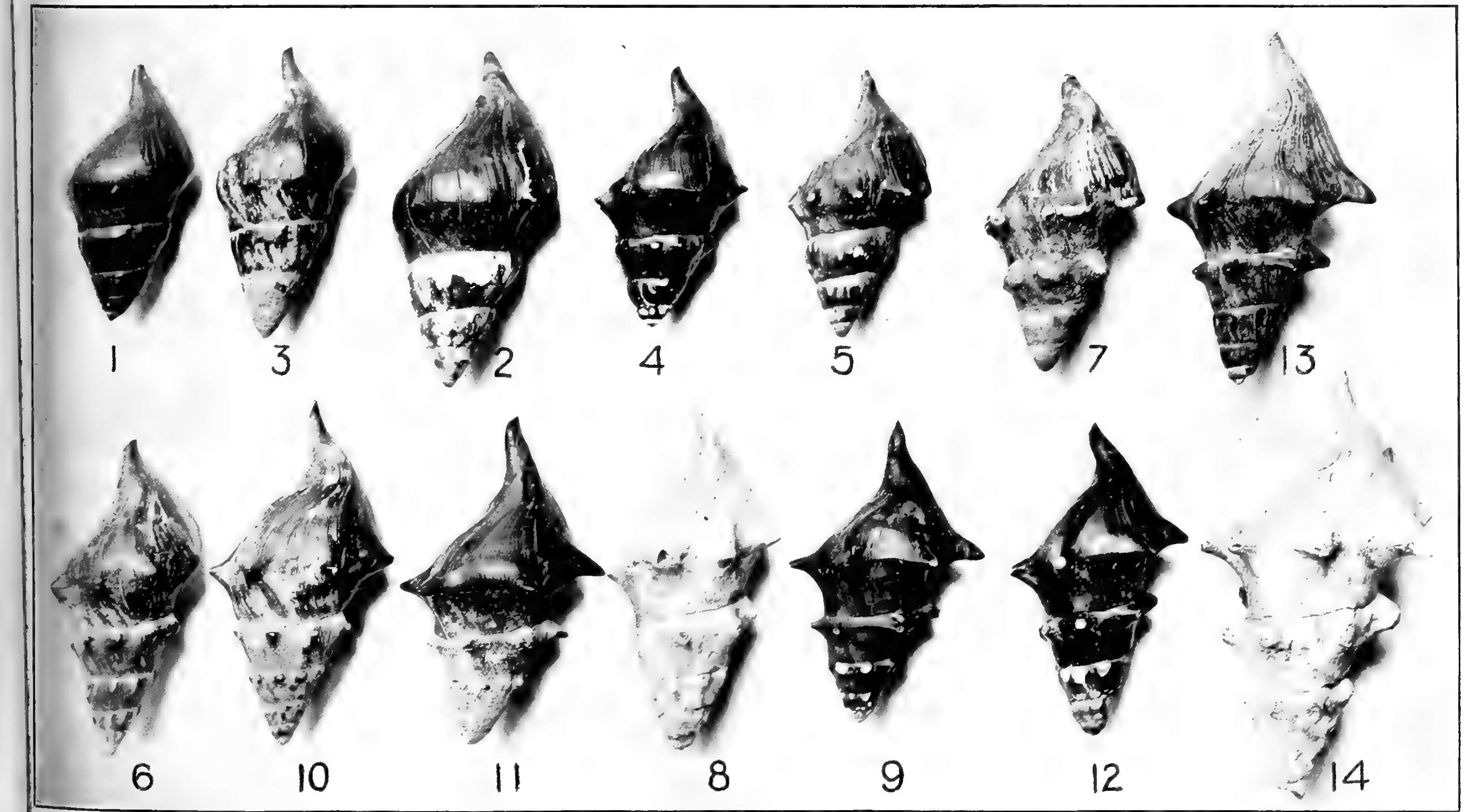
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EXPLANATION TO PLATE 2.

Relief map of the southern Appalachian Region, showing the topography and drainage of the Tennessee River system above Chattanooga. From the United States Geological Survey.

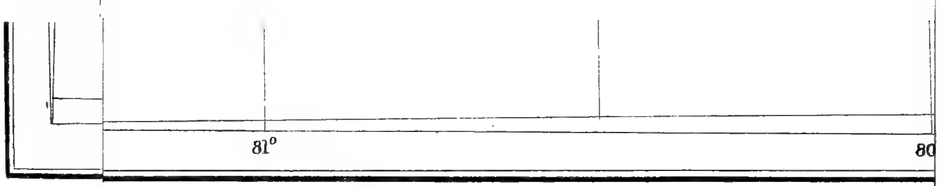
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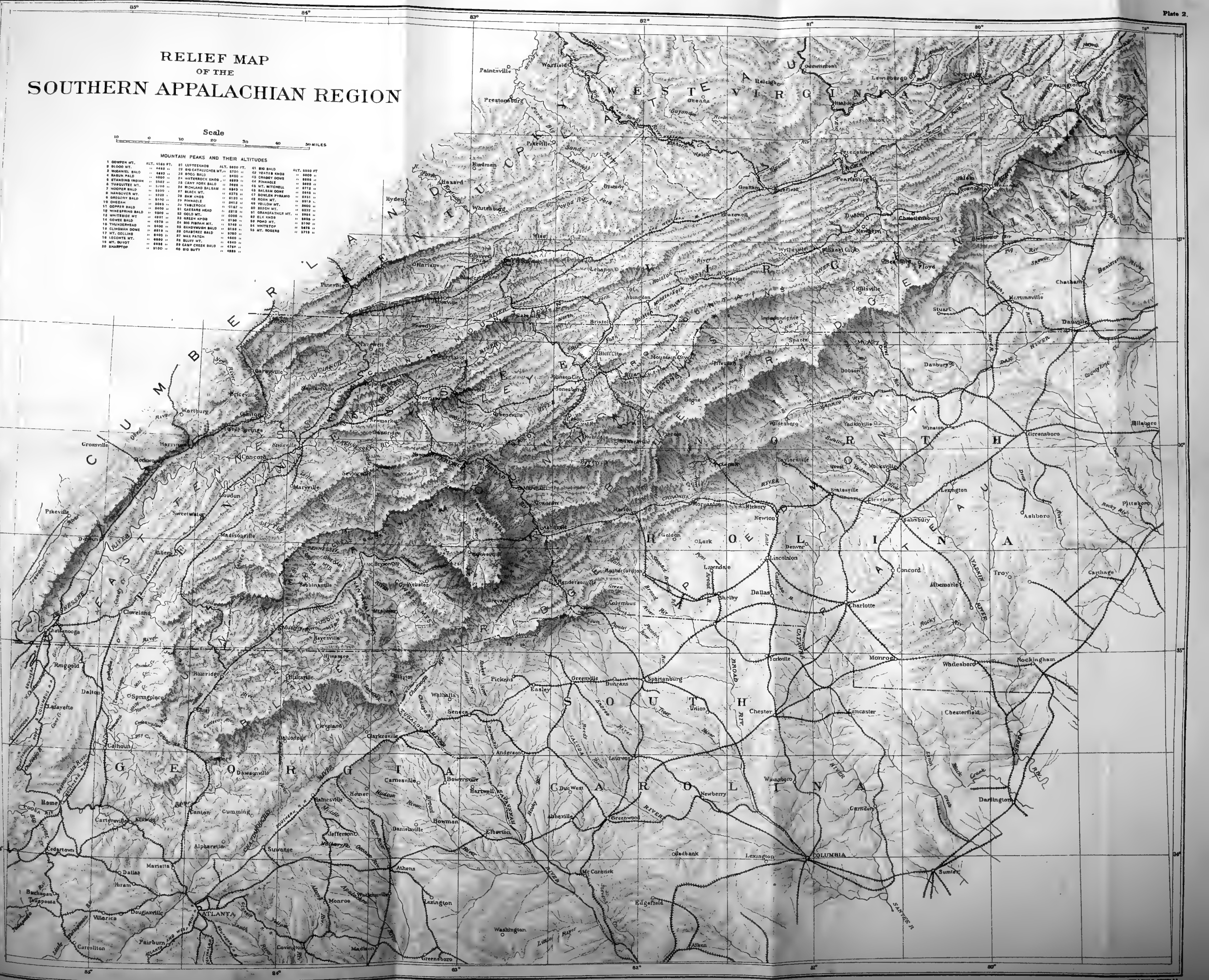
Plate 2.


RELIEF MAP
OF THE
SOUTHERN APPALACHIAN REGION
Scale
10 0 10 20 30 40 50 MILES
MOUNTAIN PEAKS AND THEIR ALTITUDES
1 COWPEN MT. ALT. 4166 FT.
2 BLOOD MT. " 4468 "
3 McDANIEL BALD " 4682 "
4 RABUN BALD " 4800 "
5 STANDING INDIAN " 5562 "
6 TUSQUITEE MT. " 5700 "
7 HOOPER BALD " 5500 "
8 HANGOVER MT. " 5320 "
9 GREGORY BALD " 5100 "
10 CHEOAH " 5065 "
11 COPPER BALD " 5400 "
12 WINESPRING BALD " 5500 "
13 WHITESIDE MT " 4931 "
14 COWEE BALD " 4976 "
15 THUNDERHEAD " 5400 "
16 CLINGMAN DOME " 6619 "
17 MT. COLLINS " 6400 "
18 LECONTE MT. " 6680 "
19 MT. GUYOT " 6636 "
20 SHARPTOP " 5100 "
21 LUFTEEKNOB ALT. 6200 FT.
22 BIG CATALUCHEE MT. " 5700 "
23 SOCO BALD " 5400 "
24 WATERROCK KNOB " 6292 "
25 CANY FORK BALD " 5926 "
26 RICHLAND BALSAM " 6540 "
27 BLACK MT. " 6370 "
28 SAM KNOB " 6120 "
29 PINNACLE " 6412 "
30 TABLEROCK " 3167 "
31 CAESARS HEAD " 3218 "
32 COLD MT. " 6000 "
33 GREEN KNOB " 6150 "
34 BIG PISGAH MT. " 5749 "
35 SANDYMUSH BALD " 5150 "
36 CRABTREE BALD " 5280 "
37 MAX PATCH " 4660 "
38 BLUFF MT. " 4840 "
39 CAMP CREEK BALD " 4760 "
40 BIG BUTT " 4888 "
41 BIG BALD ALT. 5550 FT
42 YEATES KNOB " 6000 "
43 CRAGGY DOME " 6095 "
44 PINNACLE " 5665 "
45 MT. MITCHELL " 6712 "
46 BALSAM CONE " 6645 "
47 BOWLEN PYRAMID " 6351 "
48 ROAN MT. " 6313 "
49 YELLOW MT. " 5600 "
50 BEECH MT. " 5532 "
51 GRANDFATHER MT. " 5964 "
52 ELK KNOB " 5555 "
53 POND MT. " 5100 "
54 WHITETOP " 5678 "
55 MT. ROGERS " 5719 "

EXPLANATION TO PLATE 3.

(Showing the development of the shell and its spinosity.)

POWELL RIVER.

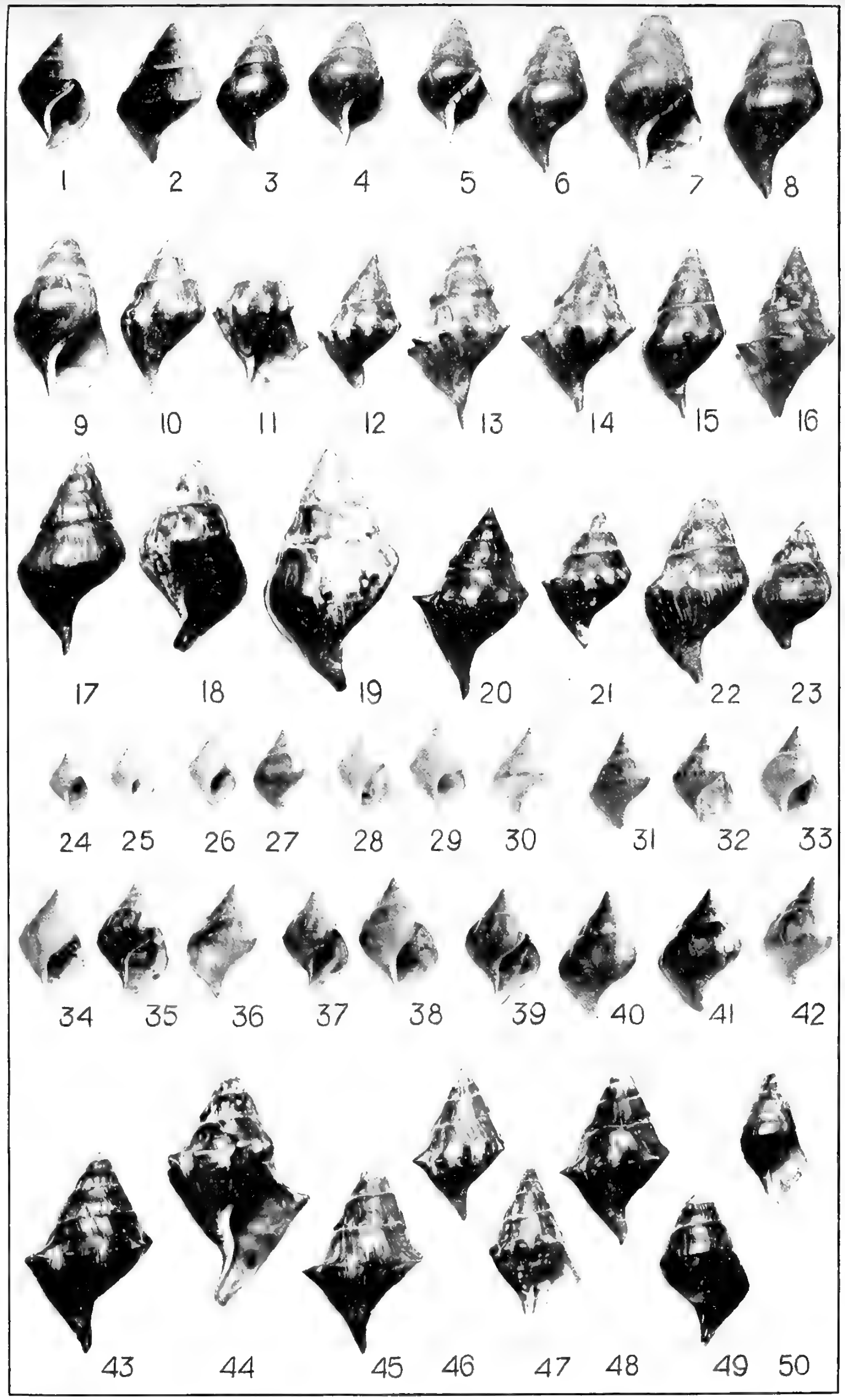
Figs. 1–2. Lot 41. Group 1. Dryden, Va. Enlarged 1/2.
Fig. 3. Lot 45. Group 1. Olinger, Va. Natural size.
Figs. 4–5. Lot 41. Group 1. Dryden, Va. Natural size.
Figs. 6–9. Lot 45. Group 1. Olinger, Va. Natural size.
Figs. 10–11. Lot 38. Group 4. Shawanee, Tenn. Natural size.
Figs. 12–14. Lot 28. Group 5. Powell River P. O., Tenn. Natural size.
Fig. 15. Lot 29. Group 5. Greens Ford, Tenn. Natural size.
Fig. 16. Lot 30. Group 5. Agee, Tenn. Natural size.

CLINCH RIVER

Figs. 17–18. Lot 11. Group 7. St. Paul, Va. Natural size.
Fig. 19. Lot 11. Shell No. 93. St. Paul, Va. Natural size.
Fig. 20. Lot 51. Shell No. 33. Group 8. Fort Blackmore, Va. Natural size.
Figs. 21–22. Lot 169. Group 8. Crafts Ferry, Va. Natural size.
Fig. 23. Lot 165. Group 8. Crafts Ferry, Va. Natural size.
Figs. 24–42. Lot 51. Group 8. Fort Blackmore, Va. Enlarged 1/2.
Figs. 43–44. Lot 17. Group 10. Kyle Ford, Tenn. Natural size.

HOLSTON RIVER SYSTEM.

Figs. 45–48. Lot 86. Group 15. Curry Ford, Tenn. Natural size.
Figs. 49–50. Lot 85. Group 15. Hord Ford, Tenn. Natural size.
Figs. 51–67. Lots 97 and 98. Group 15. Chissolms Ford, Tenn. Figs. 51–56, enlarged 1/8. Figs. 57–62, enlarged 1/16; and Figs. 63–67, natural size.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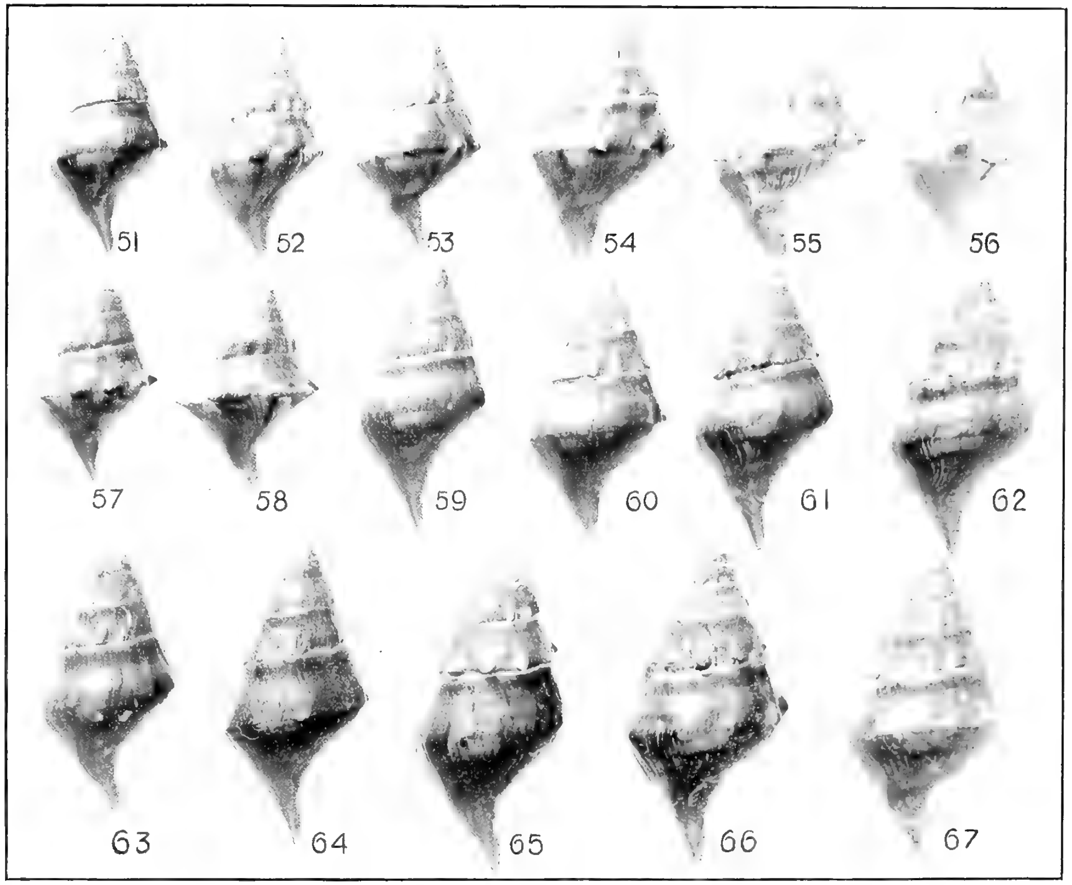
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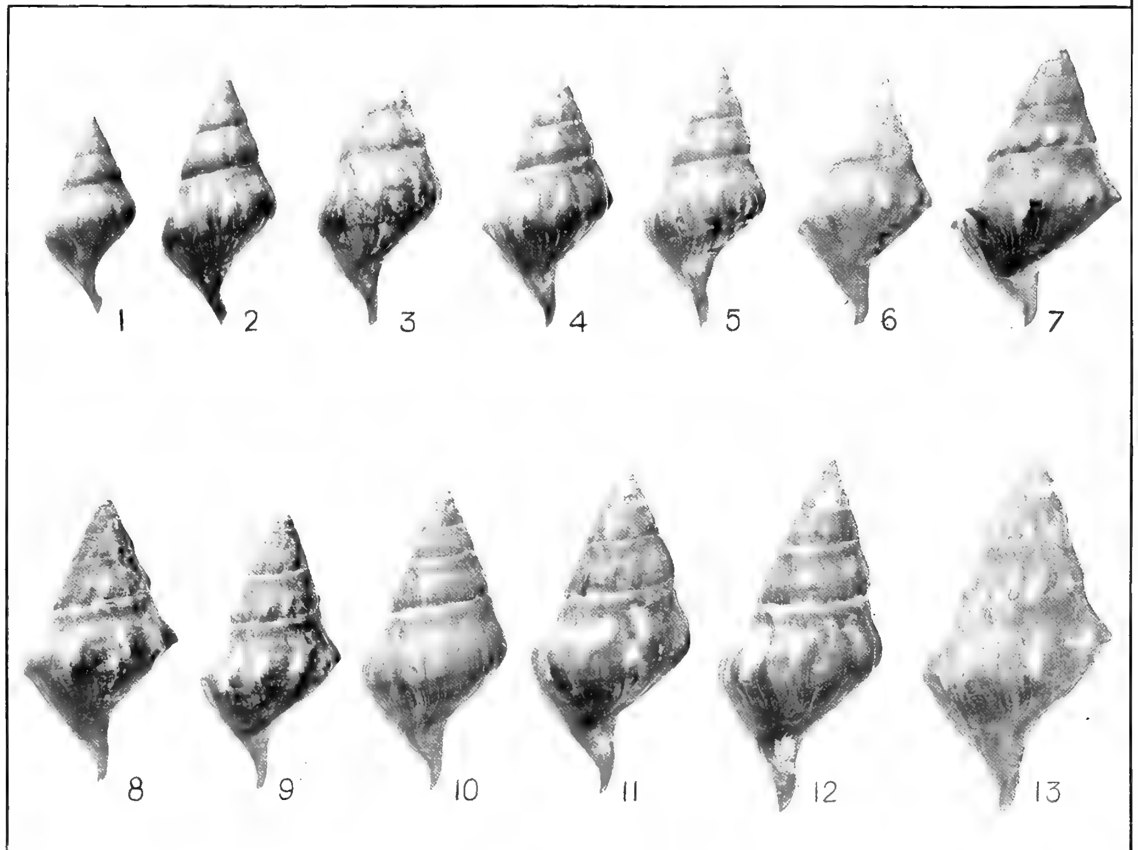
EXPLANATION TO PLATE 4.

(Showing the development of the shell and its spinosity.)

HOLSTON RIVER SYSTEM—continued.

Figs. 1–13. Lot 94. Group 13. Bluff City, Tenn. Enlarged 1/6.
Figs. 14–20. Lot 88. Group 16. Rogersville, Tenn. Enlarged 2/5.
Figs. 21–34. Lots 87 and 88. Group 16. Rogersville, Tenn. Natural size.
Figs. 35–47. Lot 90. Group 17. Cobb Ford, Tenn. Natural size.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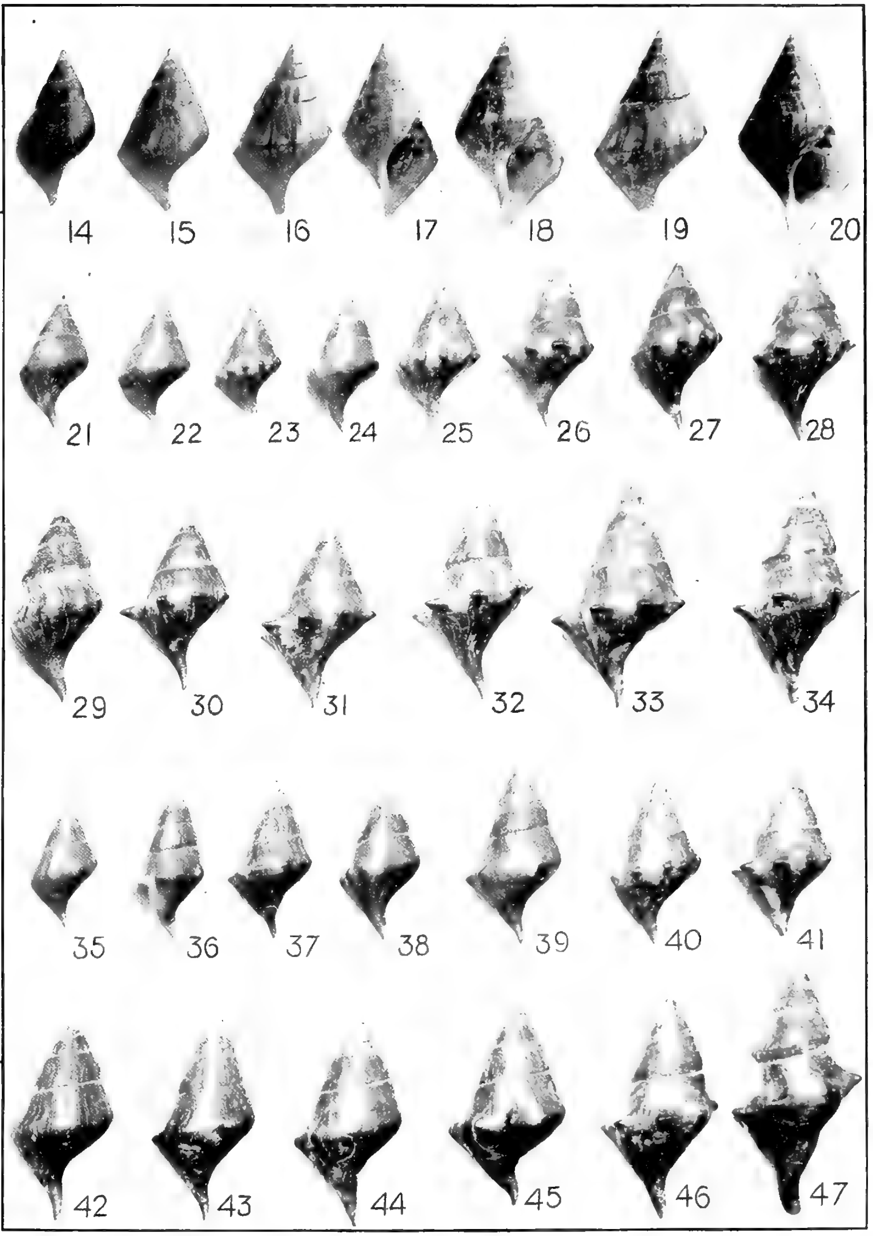
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EXPLANATION TO PLATE 5.

(Showing the development of the shell and its spinosity.)

HOLSTON RIVER SYSTEM—continued.

Figs. 1–5. Lot 90. Group 17. Cobb Ford, Tenn. Natural size.
Figs. 6–11. Lot 91. Group 18. Strawberry Plains, Tenn. Natural size.
Fig. 12. Lot 96. Group 18. Morristown, Tenn. Enlarged 2/5.
Figs. 13–14. Lot 123. Group 18. Dopes Bar, Tenn. Natural size.
Fig. 15. Lot 203. Group 18. Boyd Shoal, Tenn. Natural size.

NOLICHUCKY RIVER.

Figs. 16–22. Lot 104. Group 20. White Pine, Tenn. Enlarged 2/5.
Figs. 23–25. Lot 104. Group 20. White Pine, Tenn. Natural size.

FRENCH BROAD RIVER.

Figs. 26–30. Lot 136. Group 21. Dandridge, Tenn. Natural size.
Figs. 31. Lot 137. Group 21. Hanging Rock Shoal, Tenn. Natural size.
Figs. 32–36. Lot 156. Group 21. Seven Islands Shoals, Tenn. Natural size.

TENNESSEE RIVER.

Figs. 37–43. Lot 47. Group 22. Dickinsons Island, Tenn. Natural size.
Figs. 44–48. Lot 124. Group 22. Knoxville, Tenn. Natural size.
Figs. 49–53. Lot 152. Group 24. Loudon, Tenn. Reduced 1/18.
Figs. 54–55. Lot 199. Group 26. Chattanooga, Tenn. Reduced 1/10.
Figs. 56–59. Lot 202. Group 26. Chattanooga, Tenn. Reduced 1/10.


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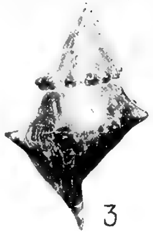
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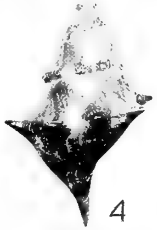
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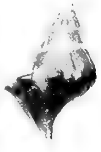
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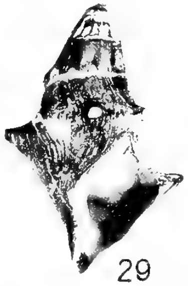
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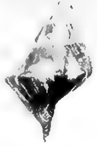
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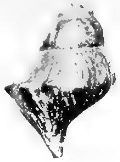
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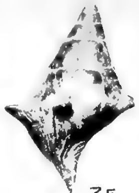
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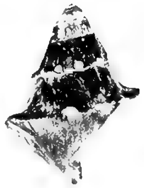
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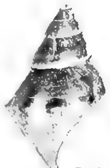
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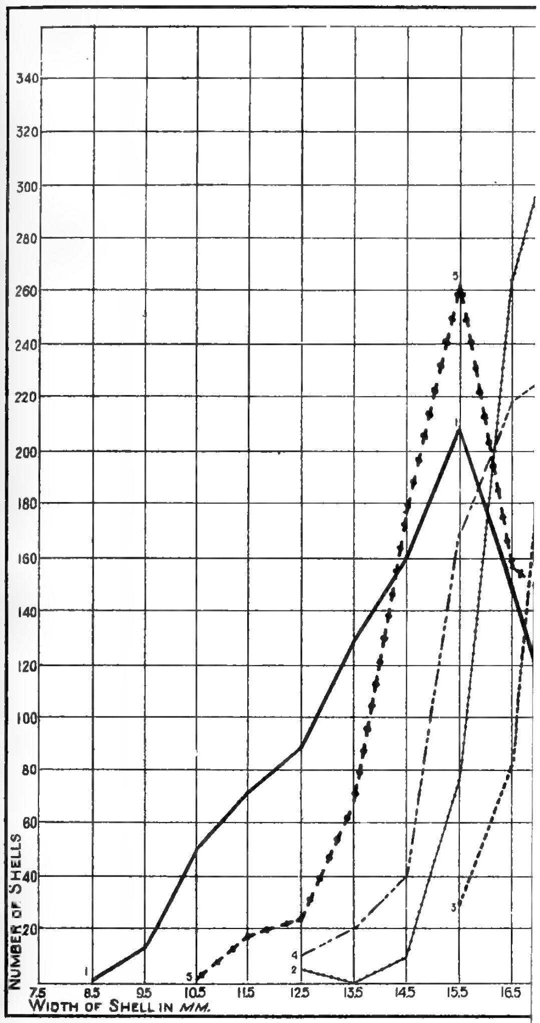
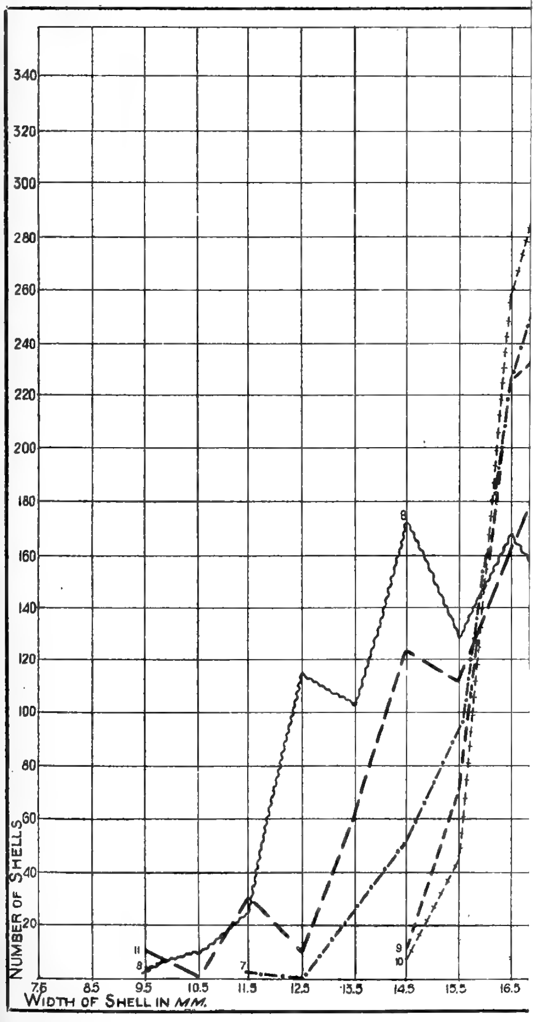
EXPLANATION TO PLATES 6–9.

(Width of shell.)

Plattings of quantitative data to show the average width of the shell, by groups, throughout the Tennessee River system.





THE NORRIS PETERS CO., WASHINGTON, D. C.

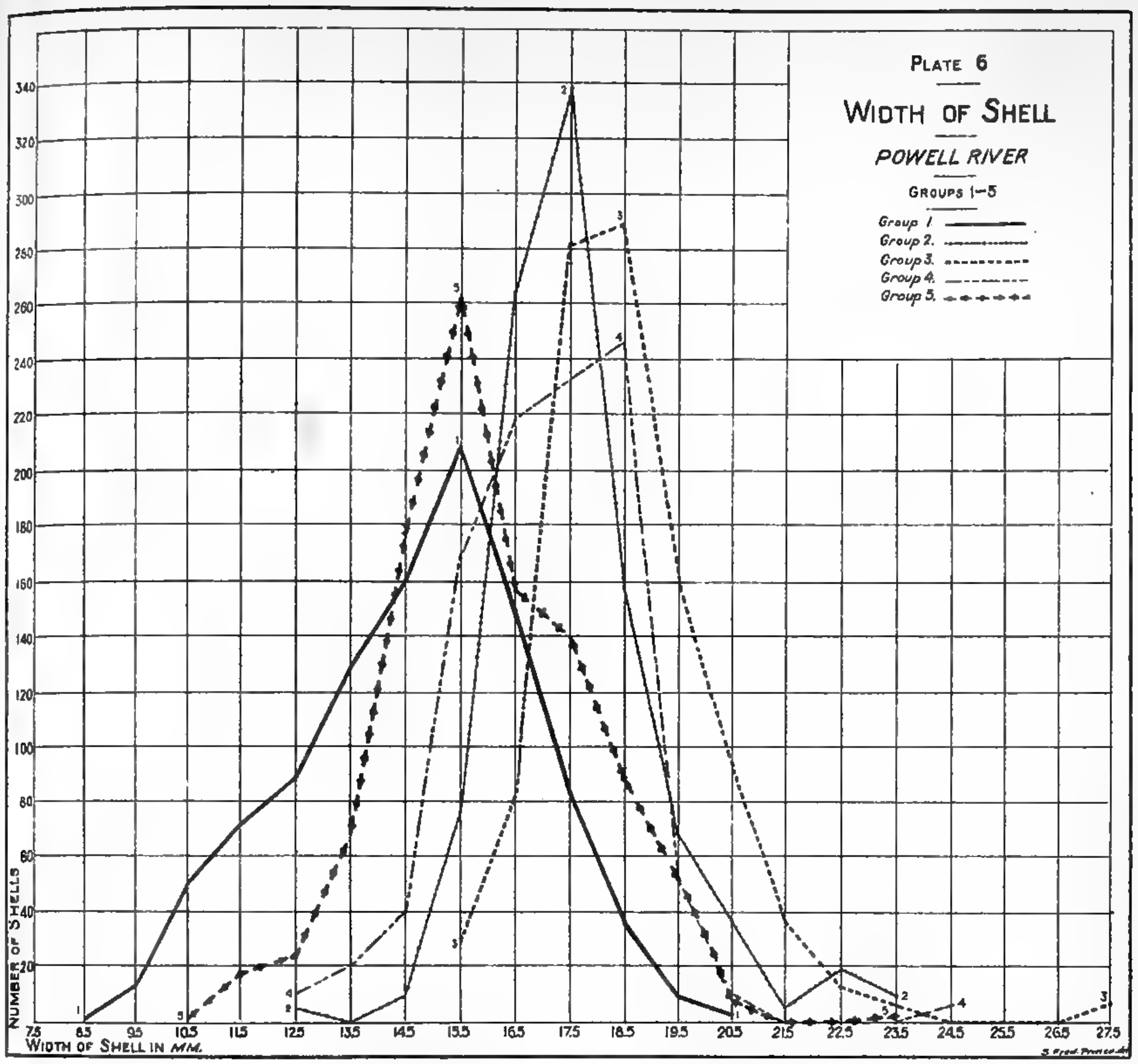


PLATE 6

WIDTH OF SHELL

POWELL RIVER

GROUPS 1–5

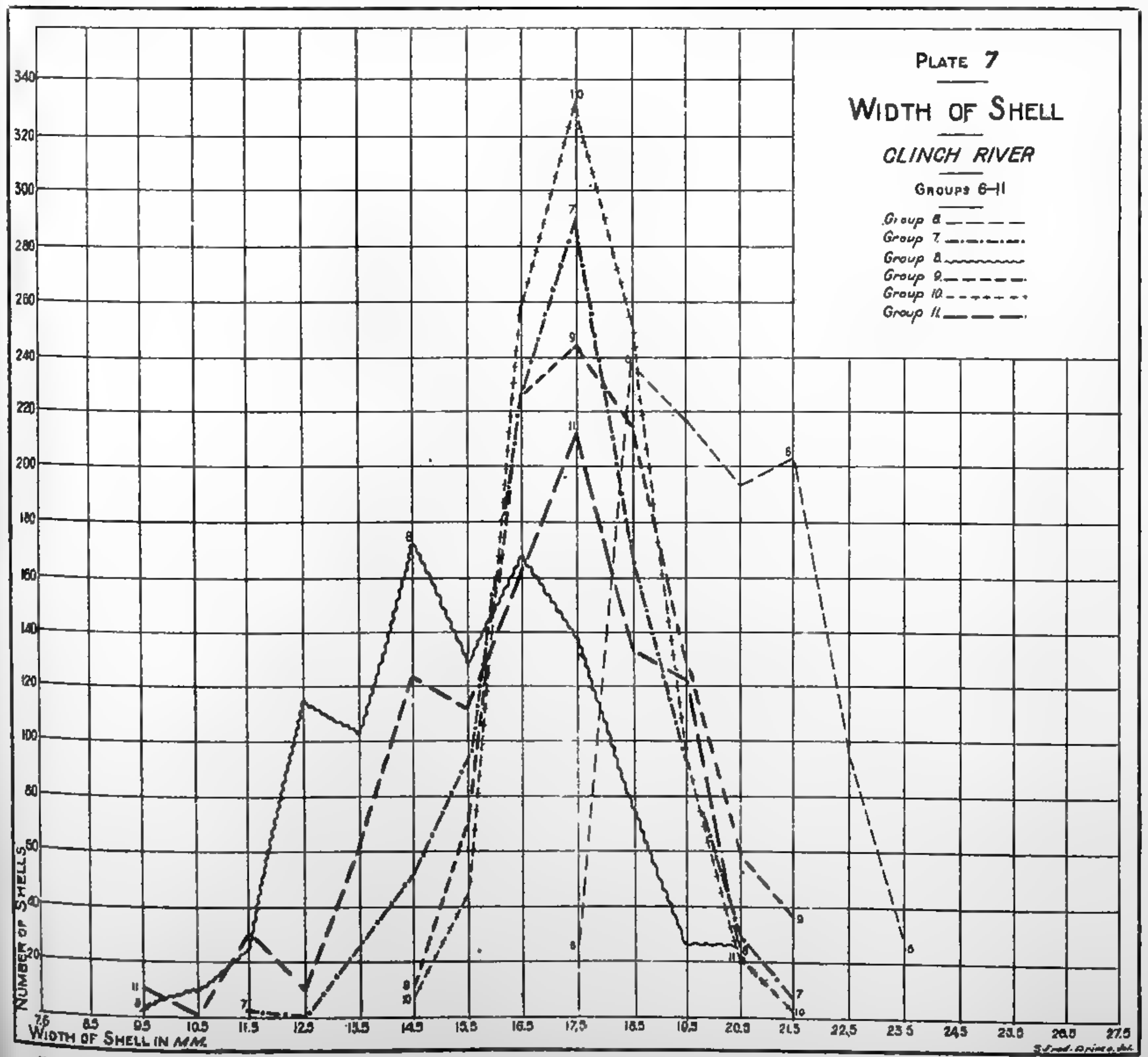


PLATE 7

WIDTH OF SHELL

CLINCH RIVER

GROUPS 6–11

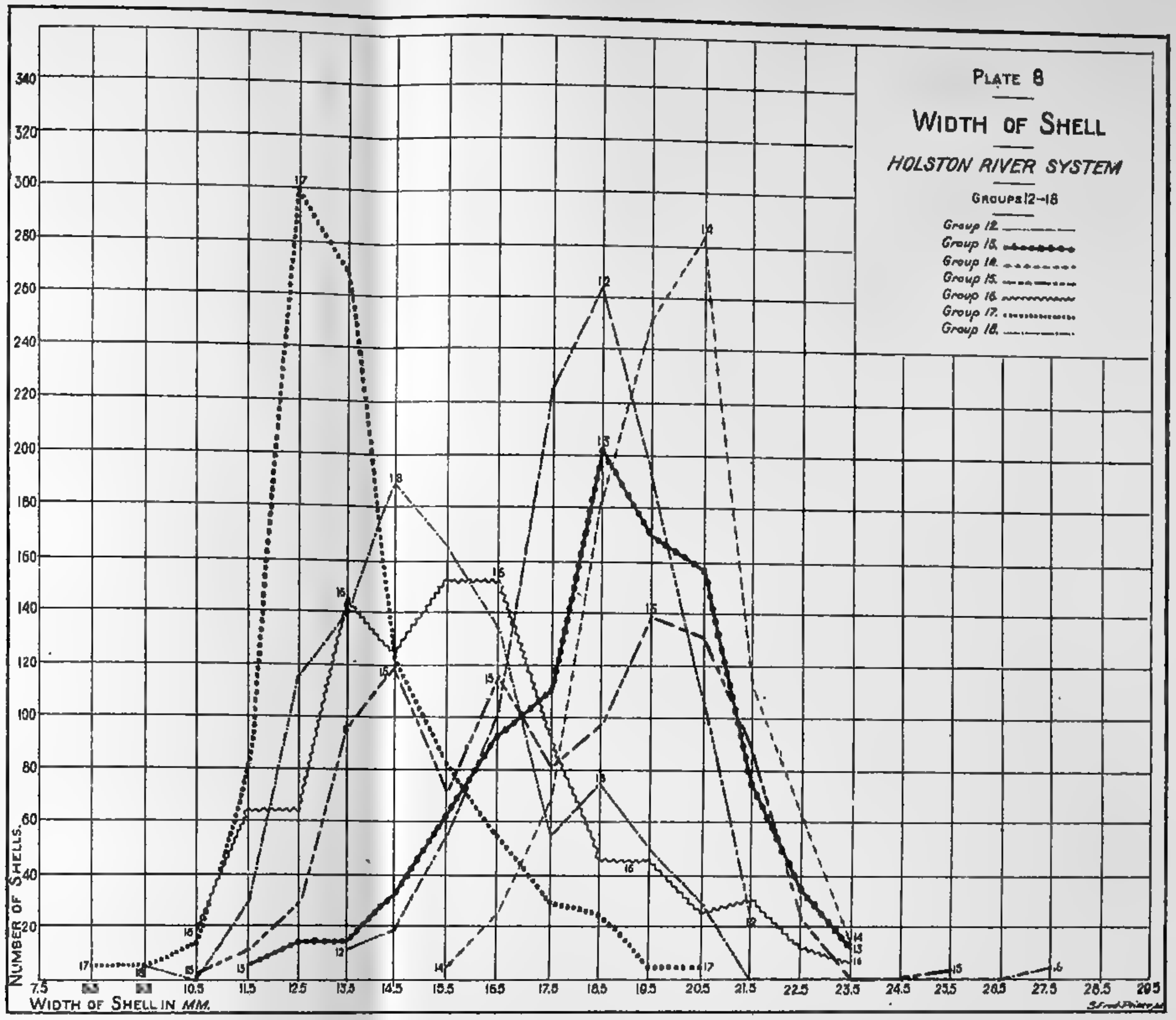


PLATE 8

WIDTH OF SHELL

HOLSTON RIVER SYSTEM

GROUPS 12–18

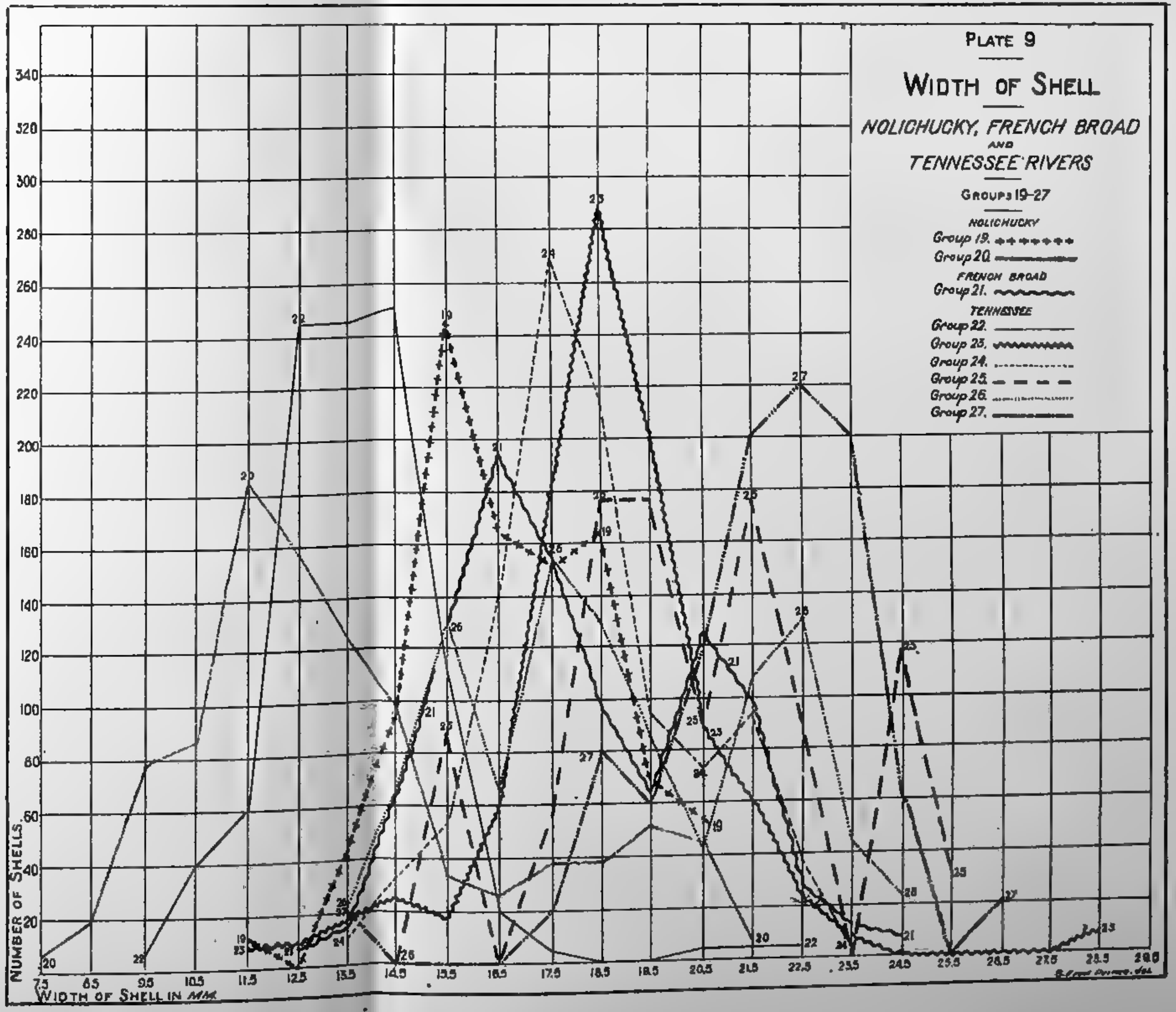


PLATE 9

WIDTH OF SHELL

NOLICHUCKY, FRENCH BROAD AND TENNESSEE RIVERS

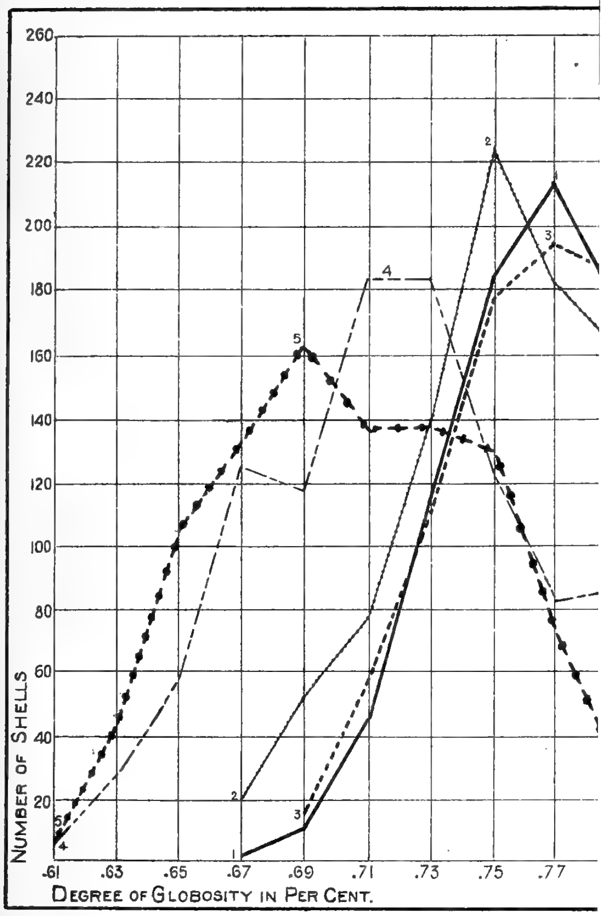
GROUPS 19–27

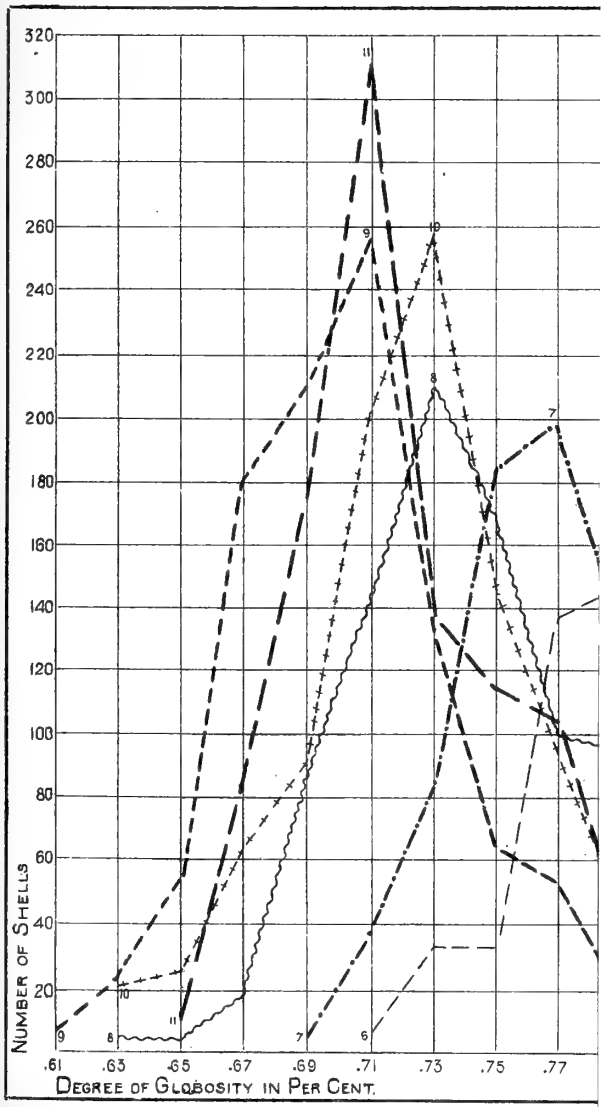
THE NORRIS PETERS CO., WASHINGTON, D. C.

EXPLANATION TO PLATES 10–13.

(Shell Index.)

Plattings of quantitative data to show the average degree of globosity of the aperture of the shell in terms of the diameter of the shell, the shell index, by groups, throughout the Tennessee system.





THE NORRIS PETERS CO., WASHINGTON, D. C.

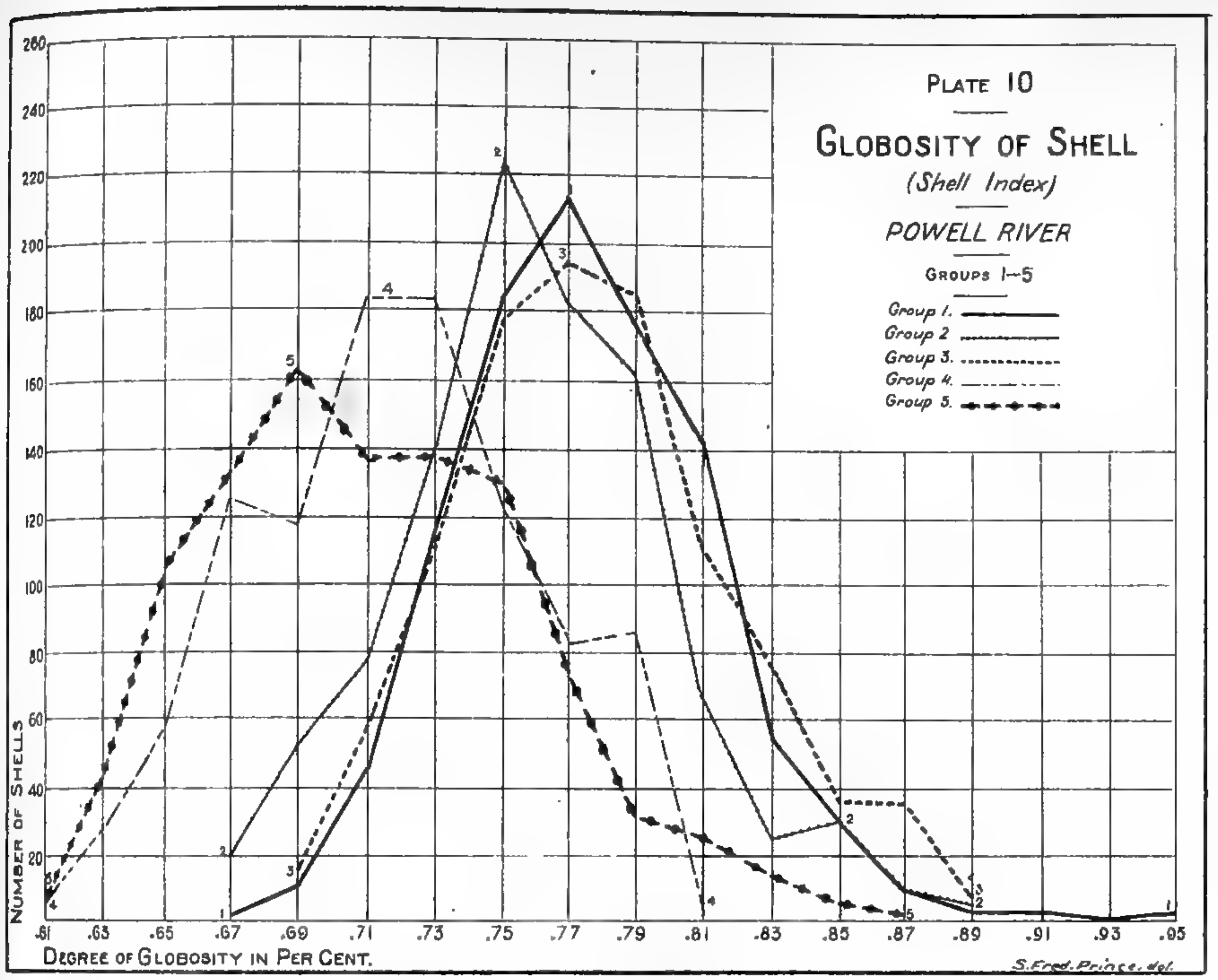


Plate 10

Globosity of Shell

(Shell Index)

Powell River

Groups 1–5

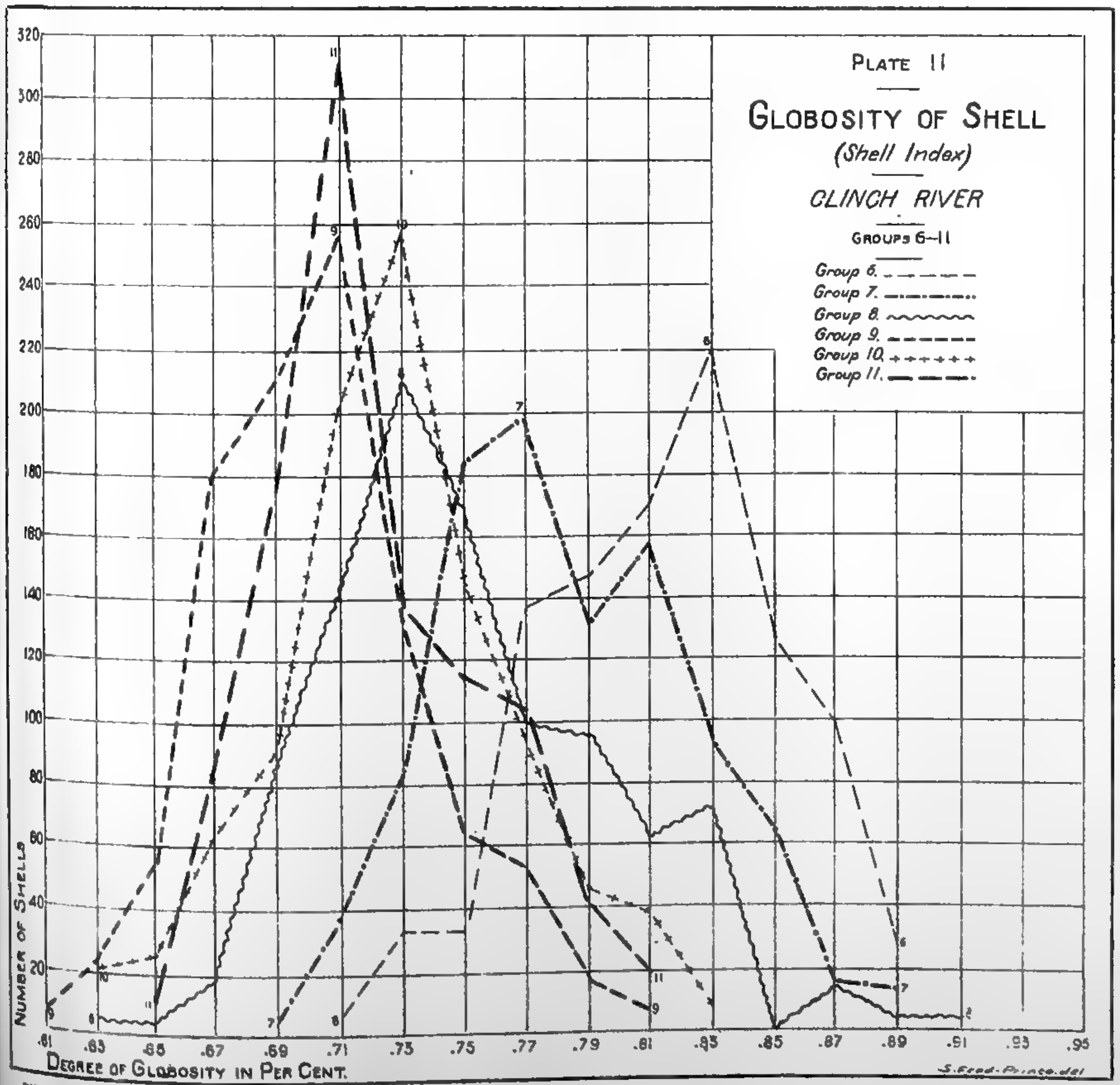


Plate 11

Globosity of Shell

(Shell Index)

Clinch River

Groups 6–11

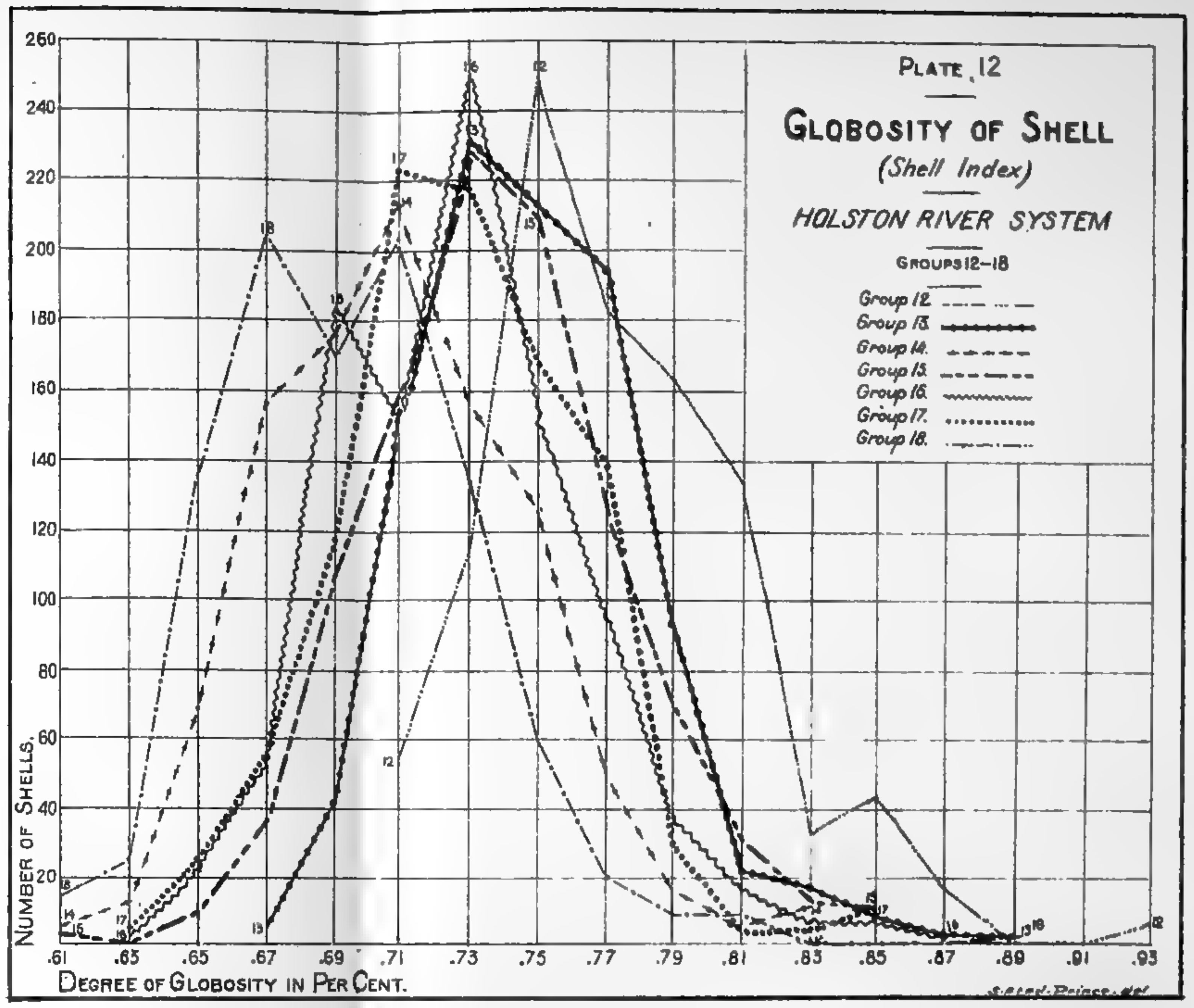


Plate 12

Globosity of Shell

(Shell Index)

Holston River System

Groups 12–18

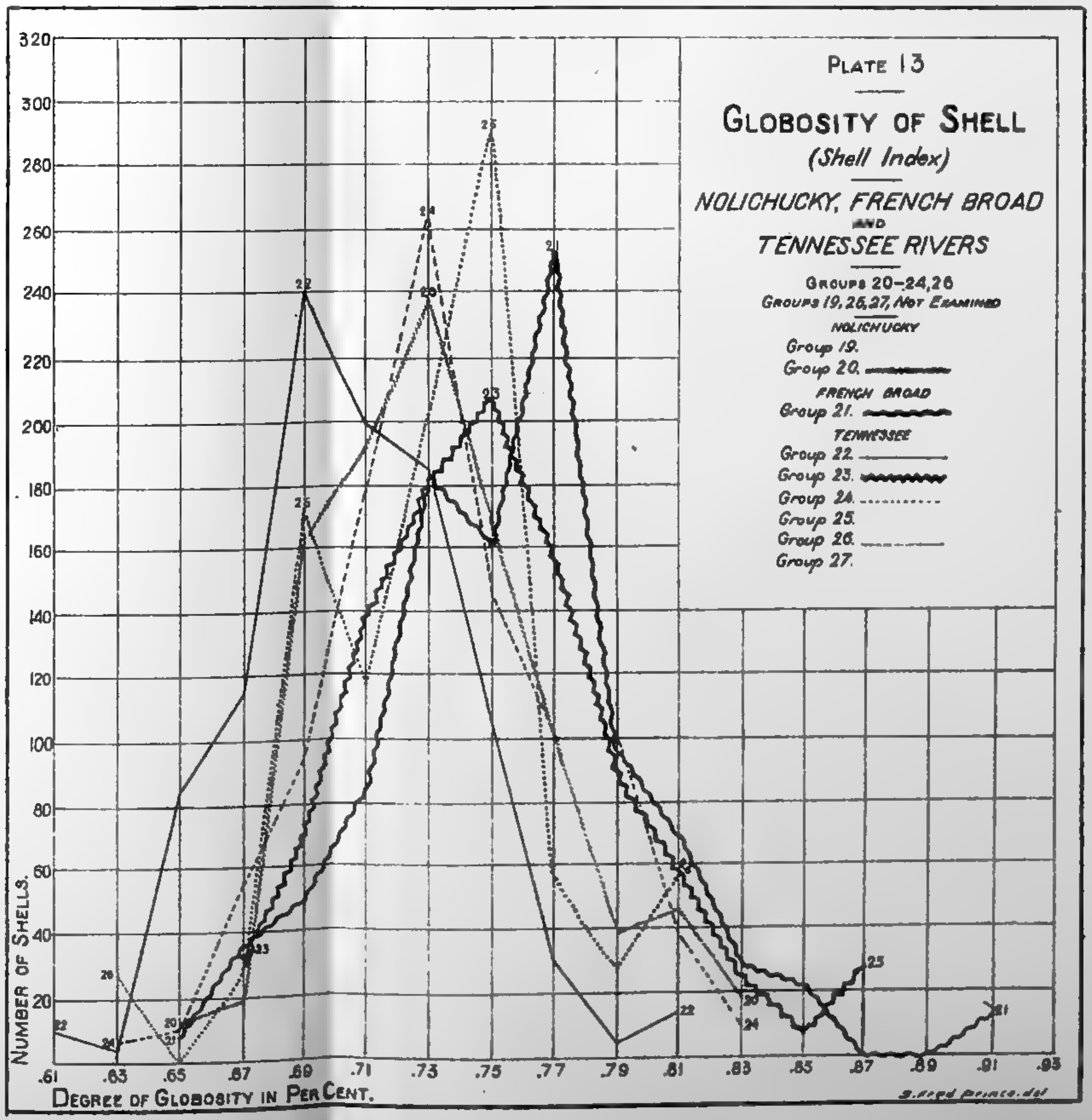


Plate 13

Globosity of Shell

(Shell Index)

Nolichucky, French Broad and Tennessee Rivers

Groups 20–24, 26

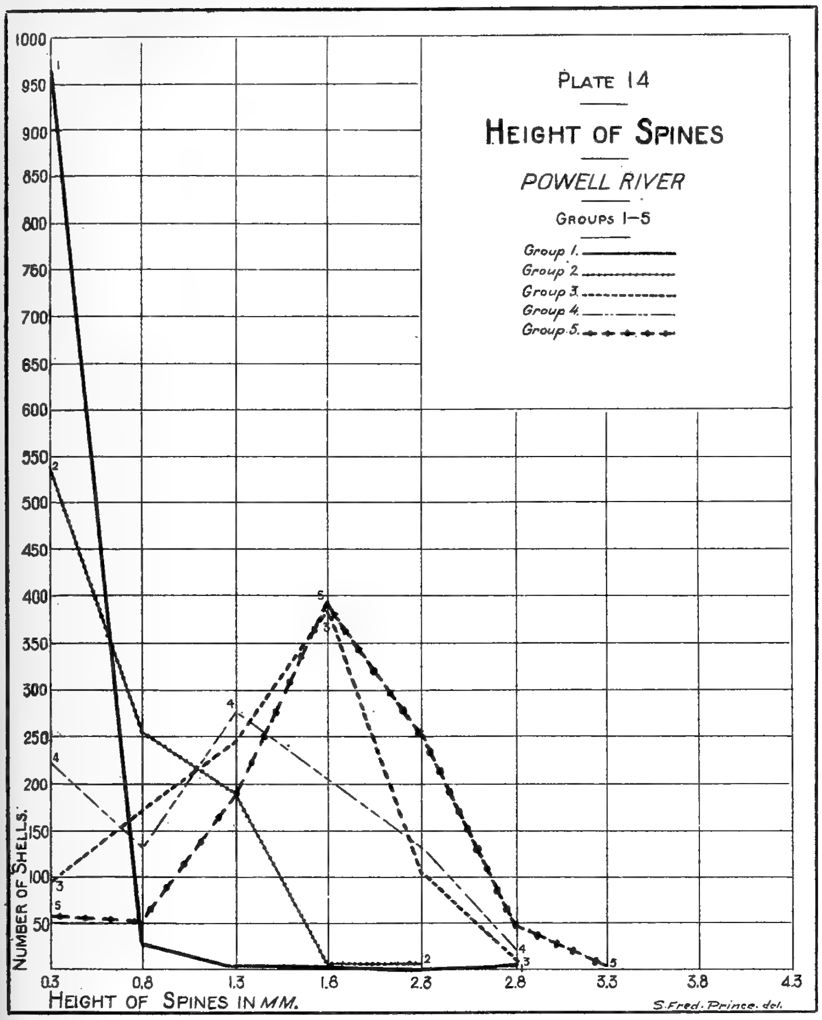
Groups 19, 25, 27, Not Examined

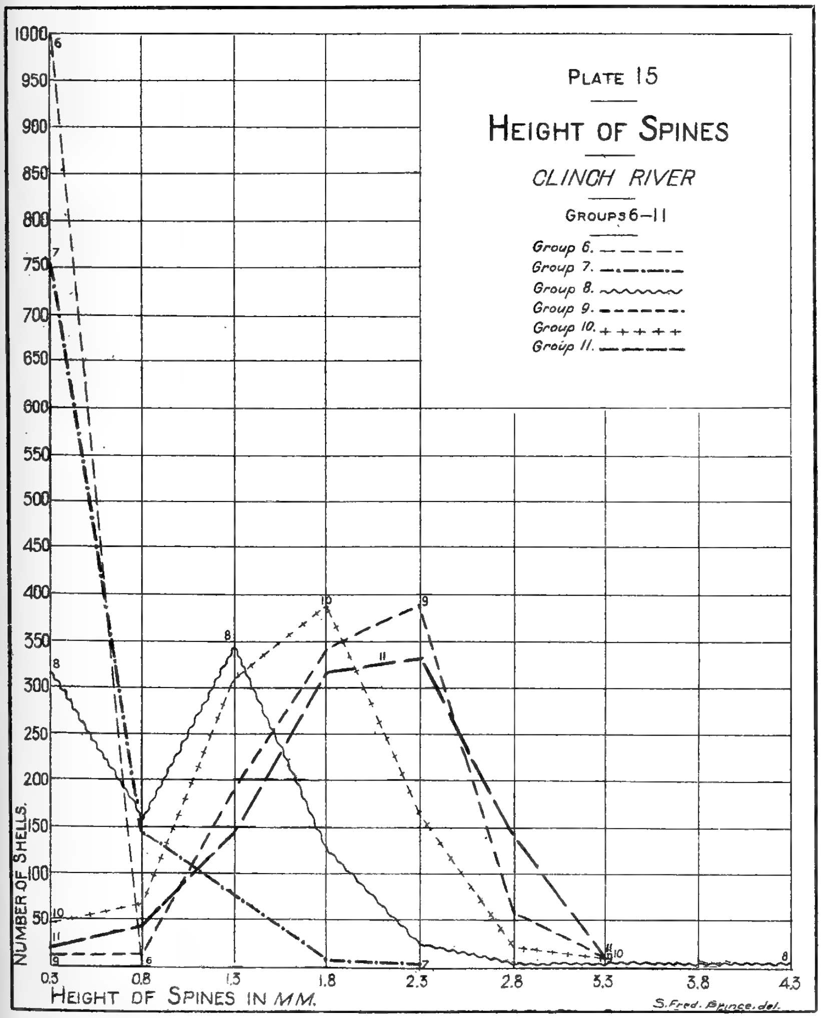
The Norris Peters Co., Washington, D. C.

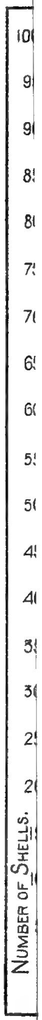
EXPLANATION TO PLATES 14–17.

(Height of Spines.)

Plattings of quantitative data to show the average height of spines, by groups, throughout the Tennessee River system.







THE NORRIS PETERS CO., WASHINGTON, D. C.

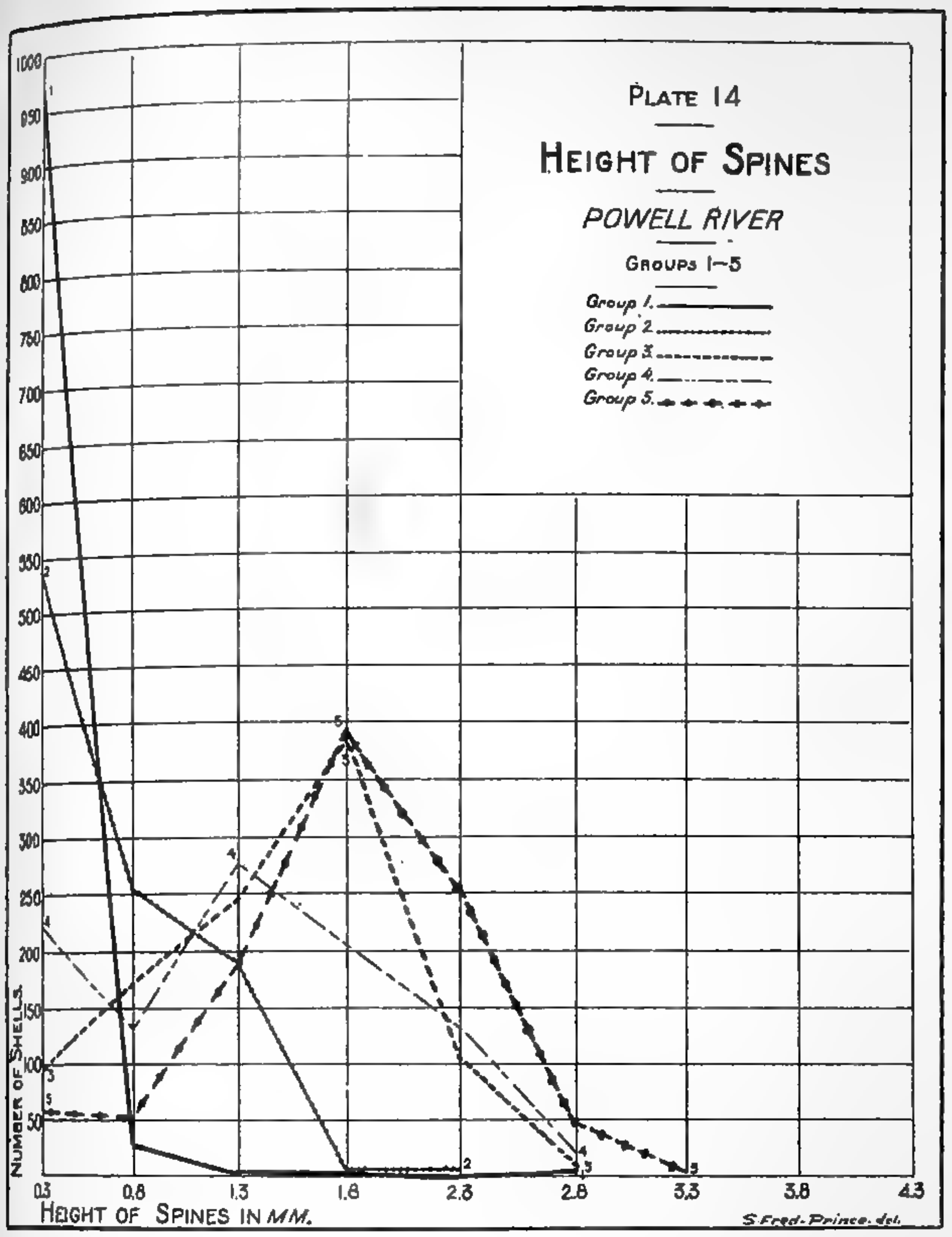


PLATE 14

HEIGHT OF SPINES

POWELL RIVER

GROUPS 1–5

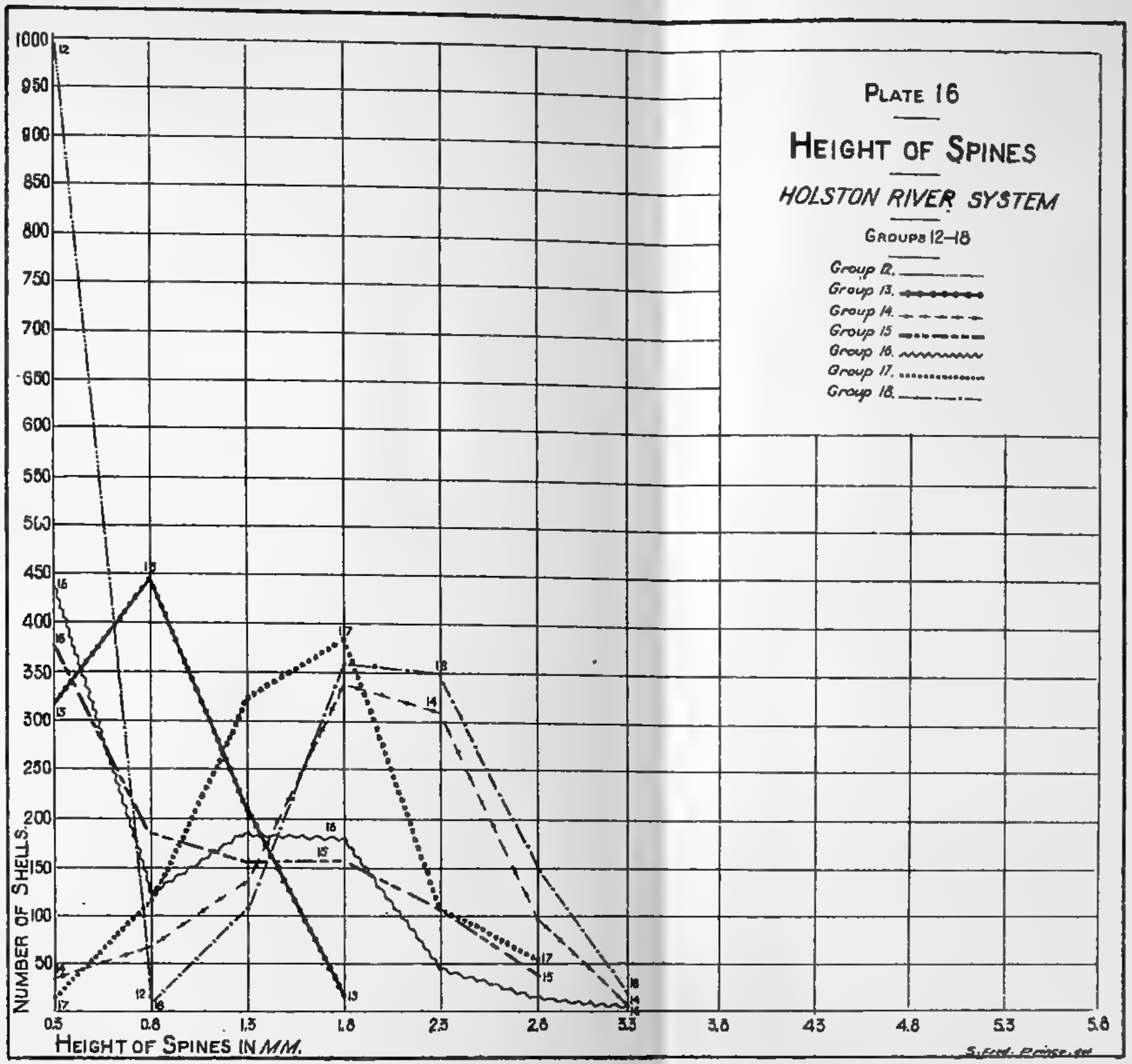


PLATE 16

HEIGHT OF SPINES

HOLSTON RIVER SYSTEM

GROUPS 12–18

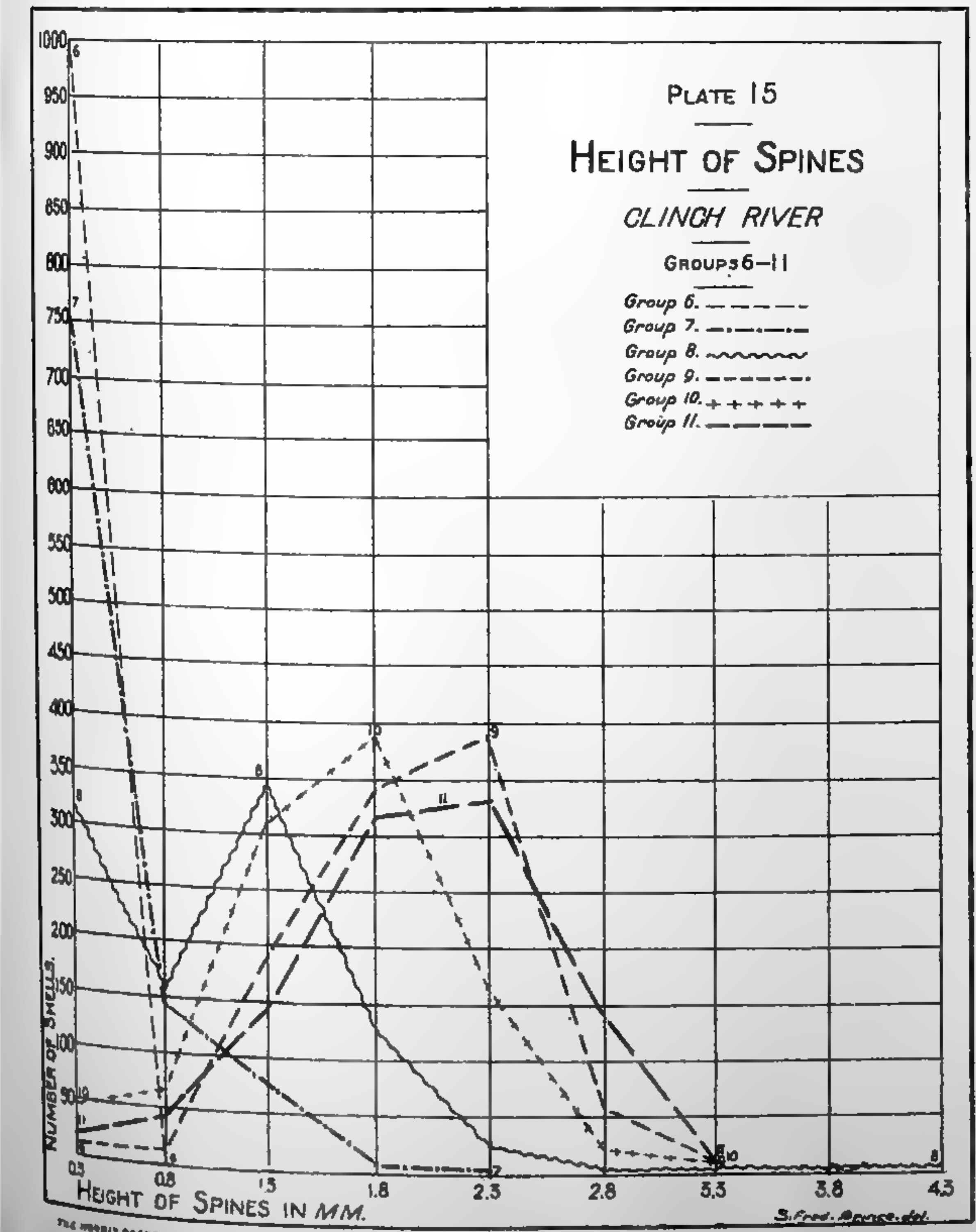


PLATE 15

HEIGHT OF SPINES

CLINCH RIVER

GROUPS 6–11

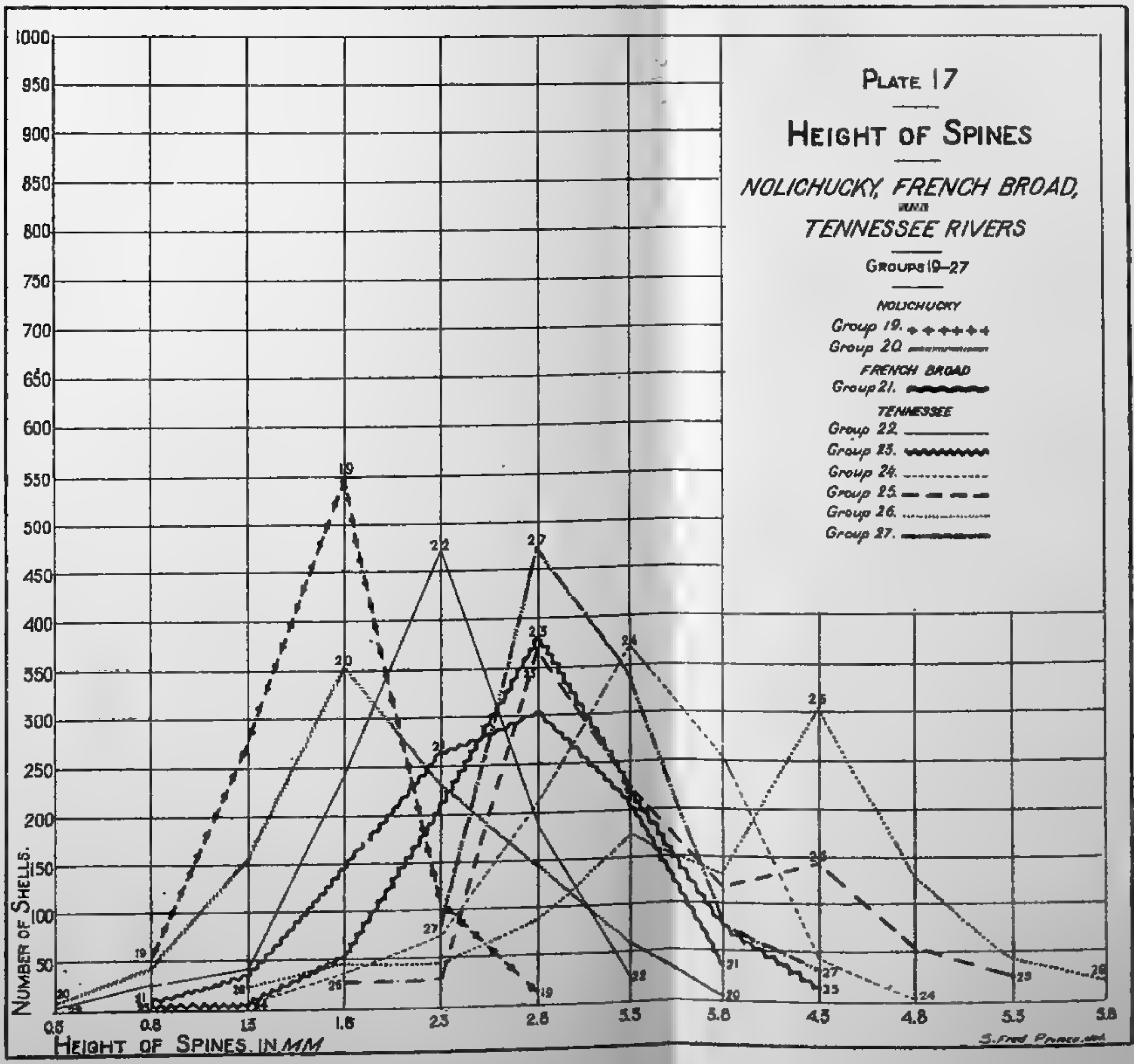


PLATE 17

HEIGHT OF SPINES

NOLICHUCKY, FRENCH BROAD,
AND
TENNESSEE RIVERS

GROUPS 19–27

THE NORRIS PETERS CO., WASHINGTON, D. C.

EXPLANATION TO PLATES 18–21.

(Distance between spines.)

Plattings of quantitative data to show the average distance between the spines, by groups, throughout the Tennessee system.

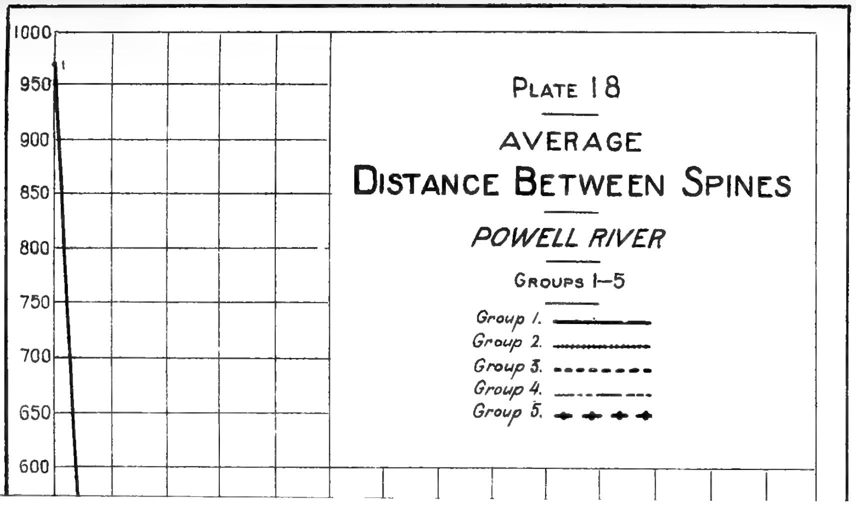


PLATE 18

AVERAGE

DISTANCE BETWEEN SPINES

POWELL RIVER

GROUPS 1–5

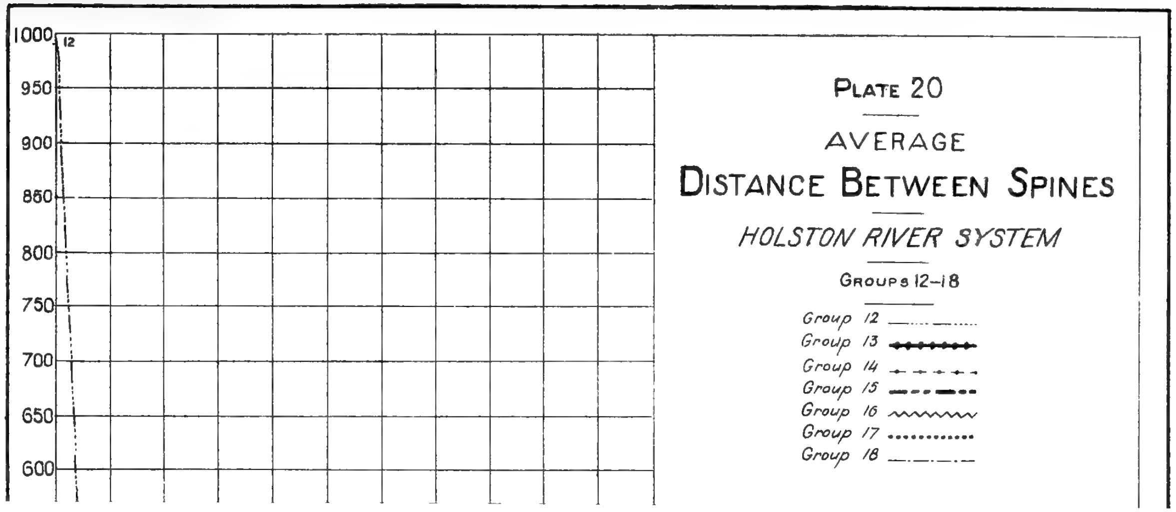


PLATE 20

AVERAGE

DISTANCE BETWEEN SPINES

HOLSTON RIVER SYSTEM

GROUPS 12–18

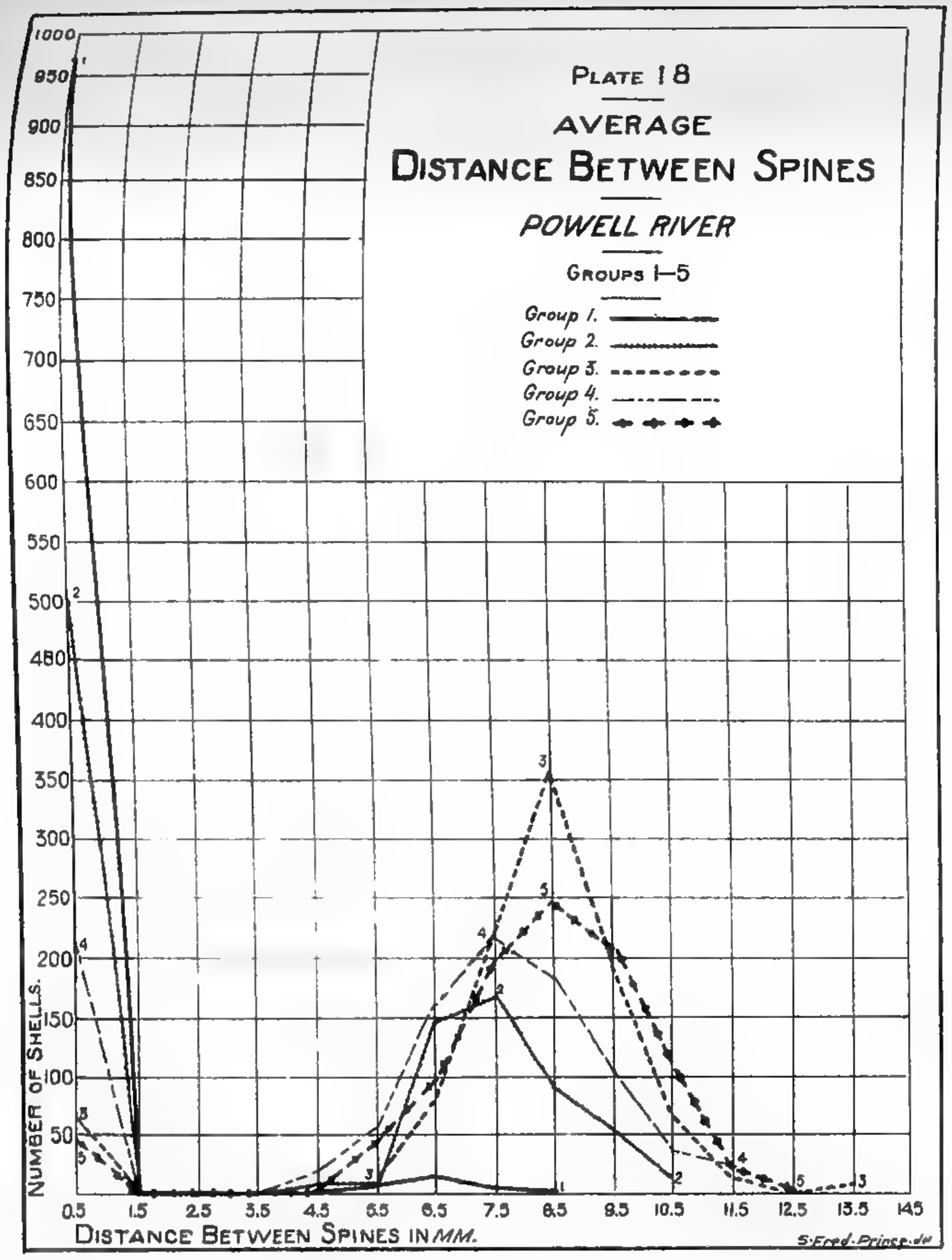


PLATE 18

AVERAGE

DISTANCE BETWEEN SPINES

POWELL RIVER

GROUPS 1–5

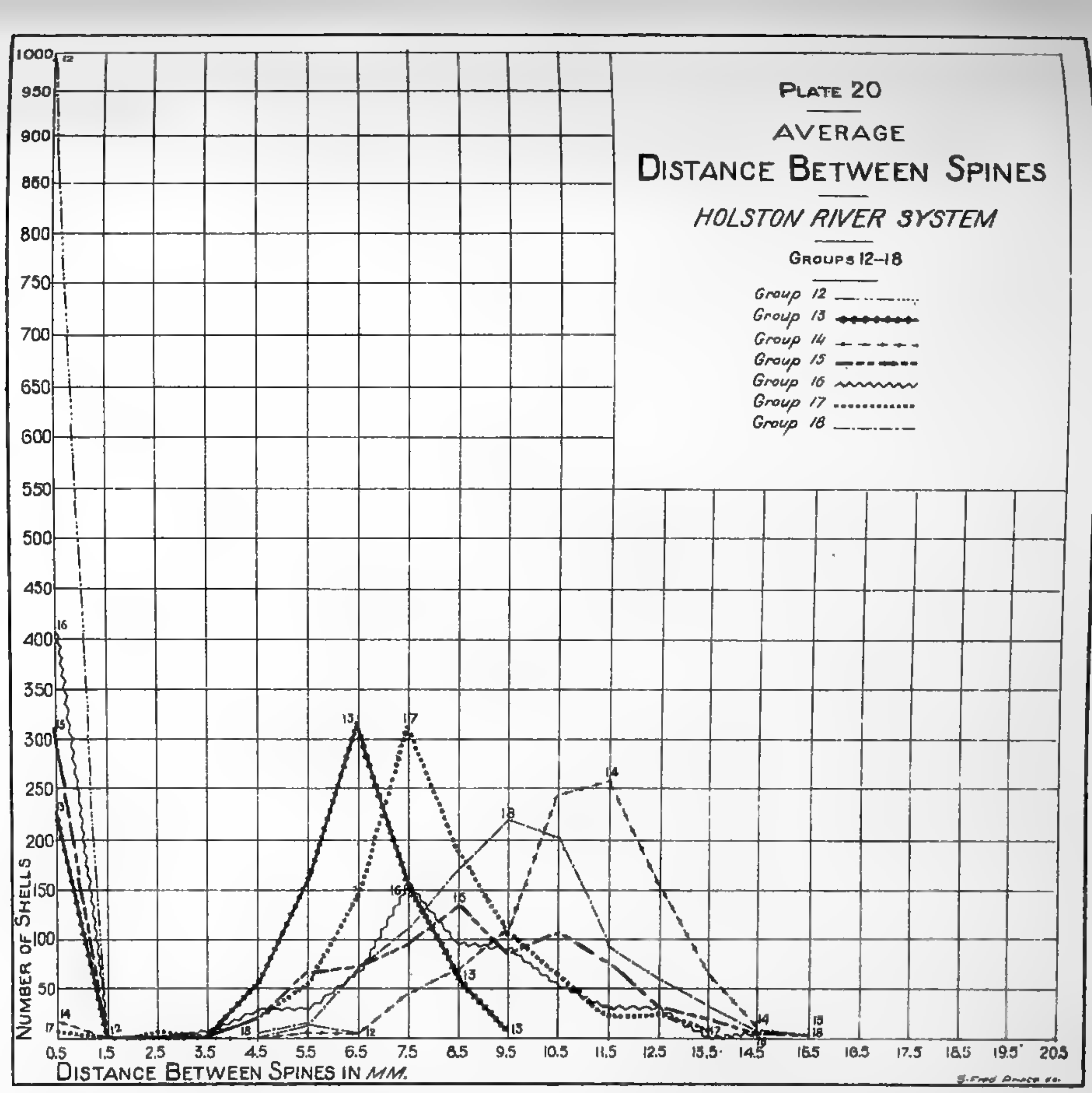


PLATE 20

AVERAGE

DISTANCE BETWEEN SPINES

HOLSTON RIVER SYSTEM

GROUPS 12–18

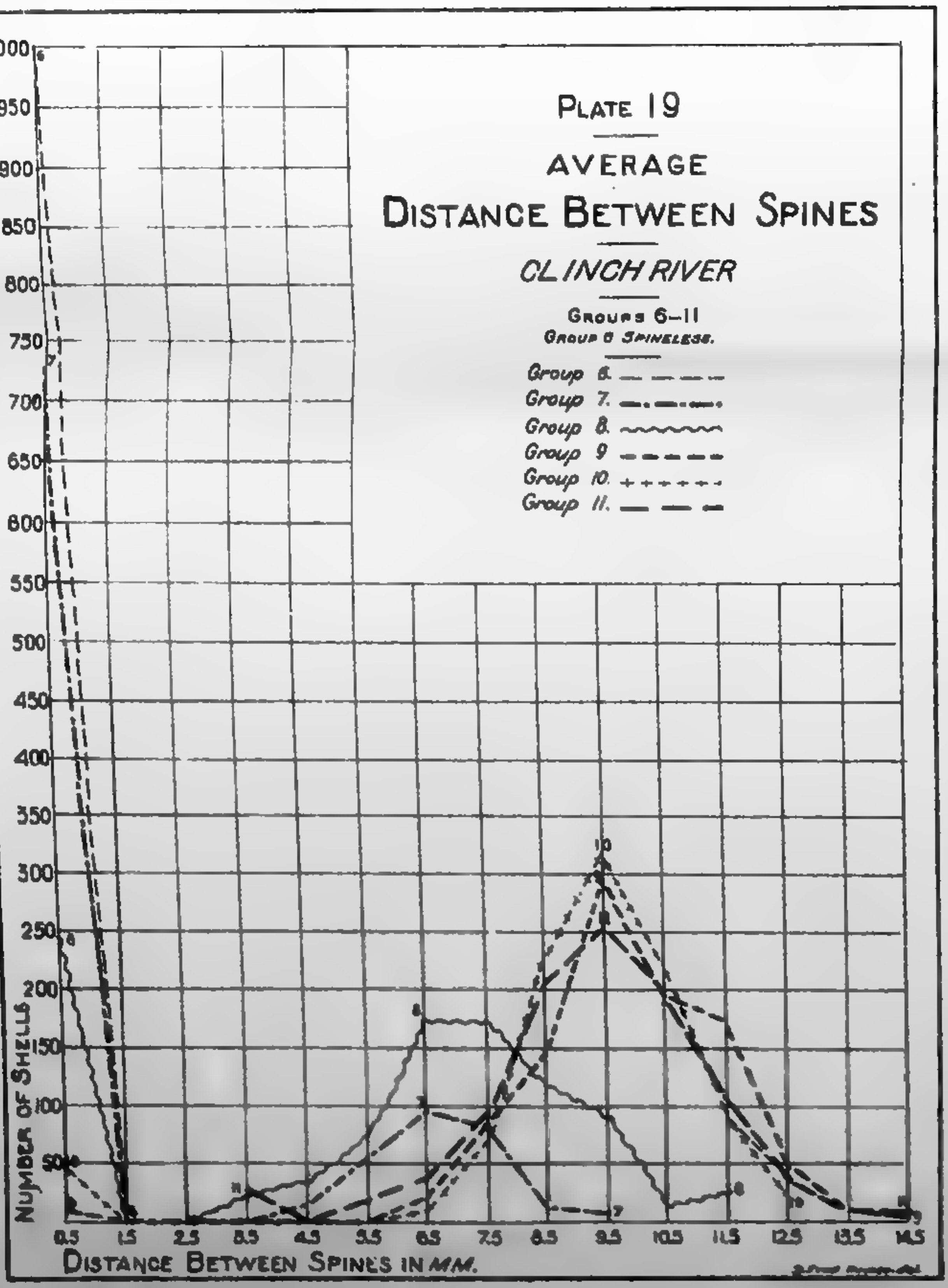


PLATE 19

AVERAGE

DISTANCE BETWEEN SPINES

CLINCH RIVER

GROUPS 6–11

GROUP 8 SPINELESS.

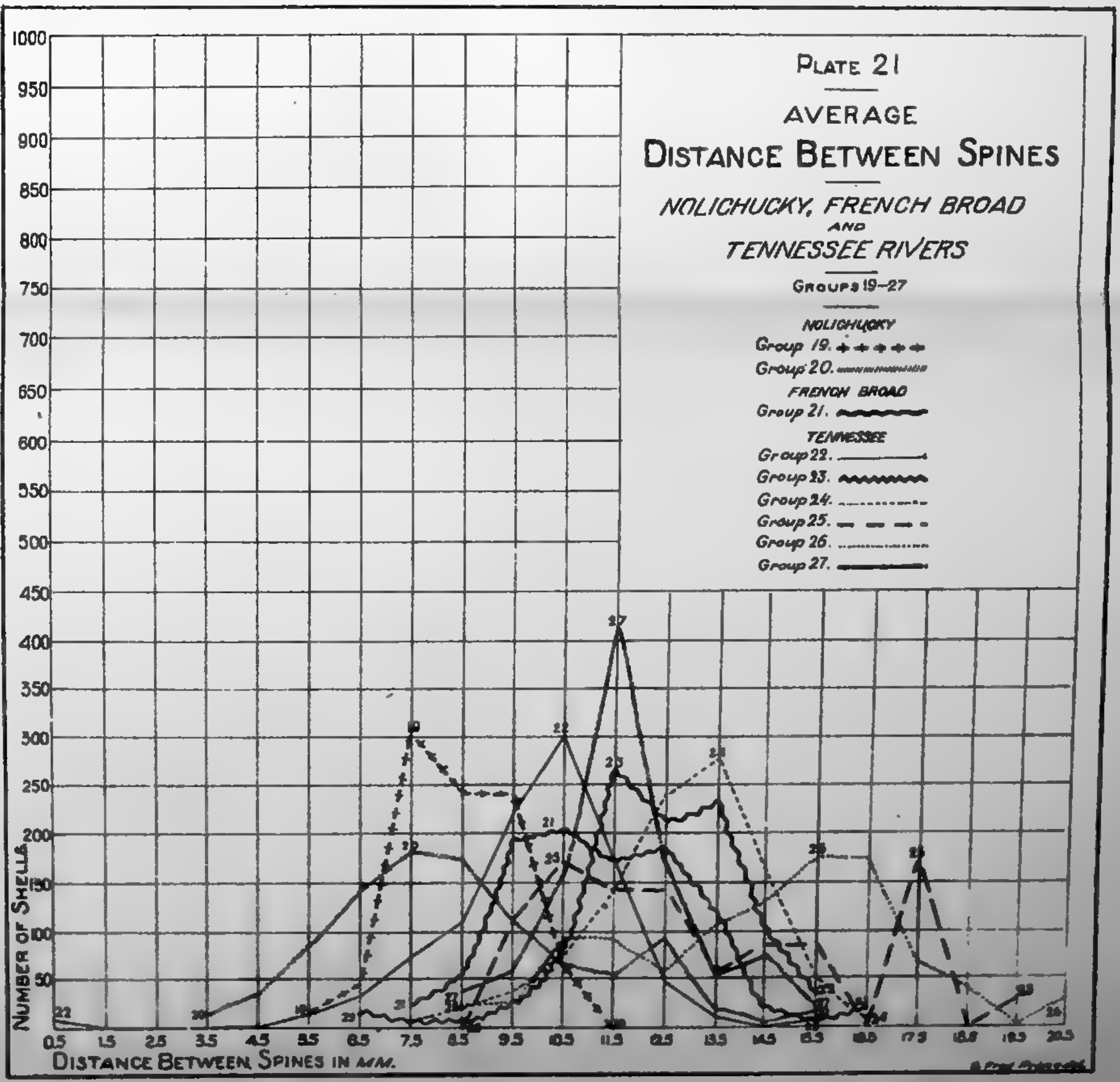


PLATE 21

AVERAGE

DISTANCE BETWEEN SPINES

NOLICHUCKY, FRENCH BROAD AND TENNESSEE RIVERS

GROUPS 19–27

THE NORRIS PETERS CO., WASHINGTON, D. C.

EXPLANATION TO PLATES 22–25.

(Spine index.)

Plattings of the quantitative data to show the average distance between spines in terms of the height of the spines, the spine index, by groups, throughout the Tennessee system.

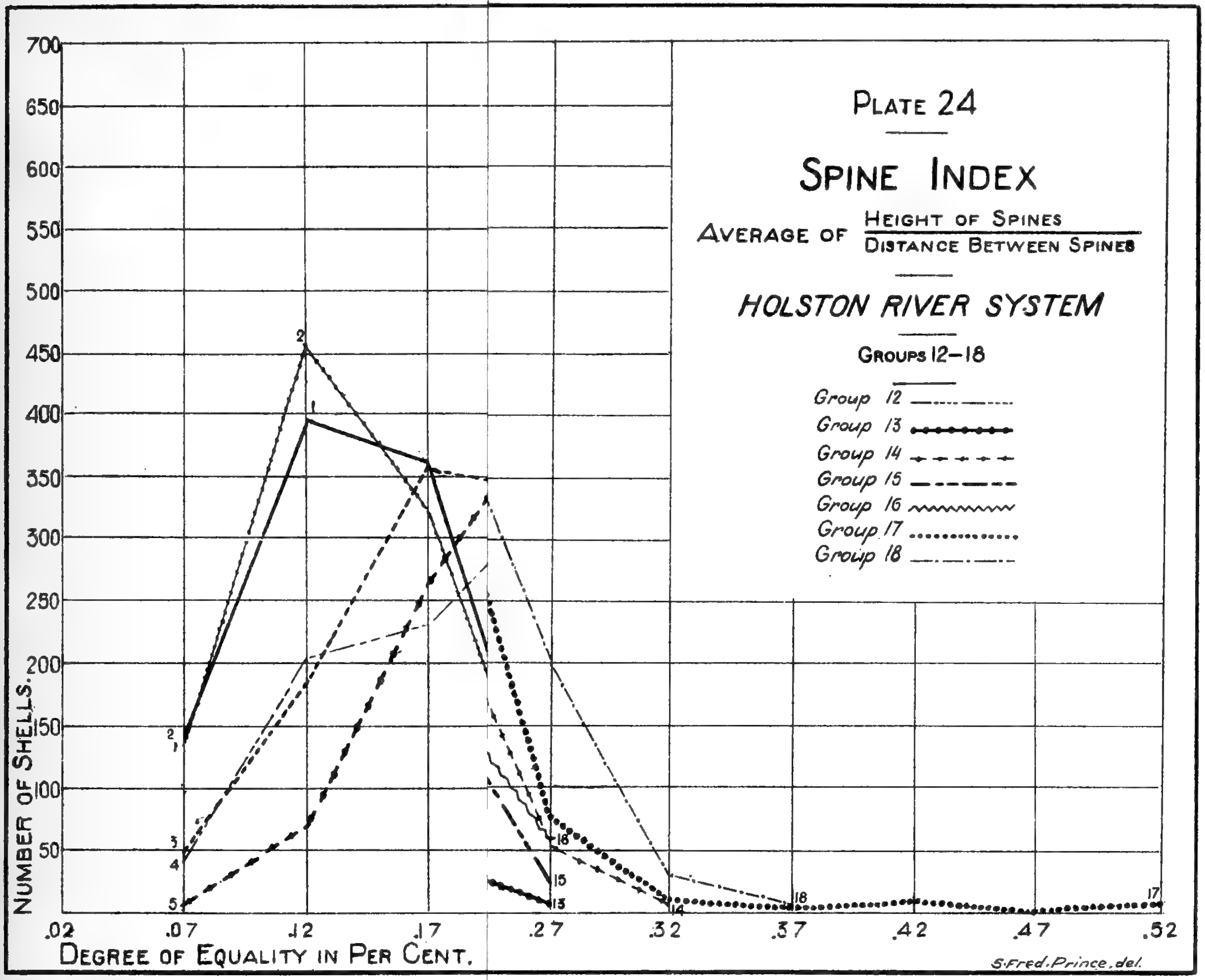


PLATE 24

SPINE INDEX

Average of $\frac{\text{Height of Spines}}{\text{Distance Between Spines}}$

HOLSTON RIVER SYSTEM

GROUPS 12–18

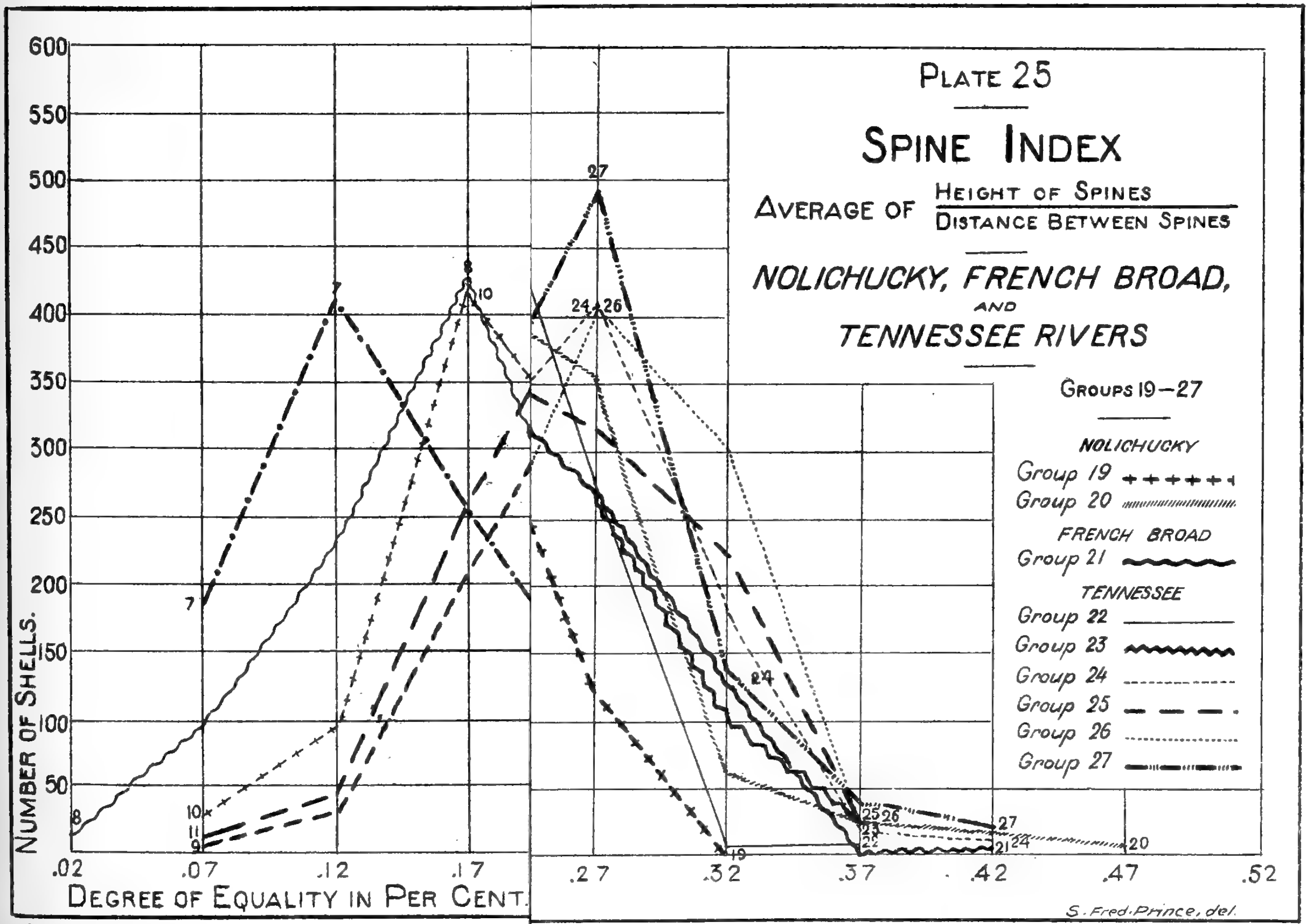


PLATE 25

SPINE INDEX

Average of $\frac{\text{Height of Spines}}{\text{Distance Between Spines}}$

NOLICHUCKY, FRENCH BROAD, AND TENNESSEE RIVERS

GROUPS 19–27

THE NORRIS PETERS CO., WASHINGTON, D. C.

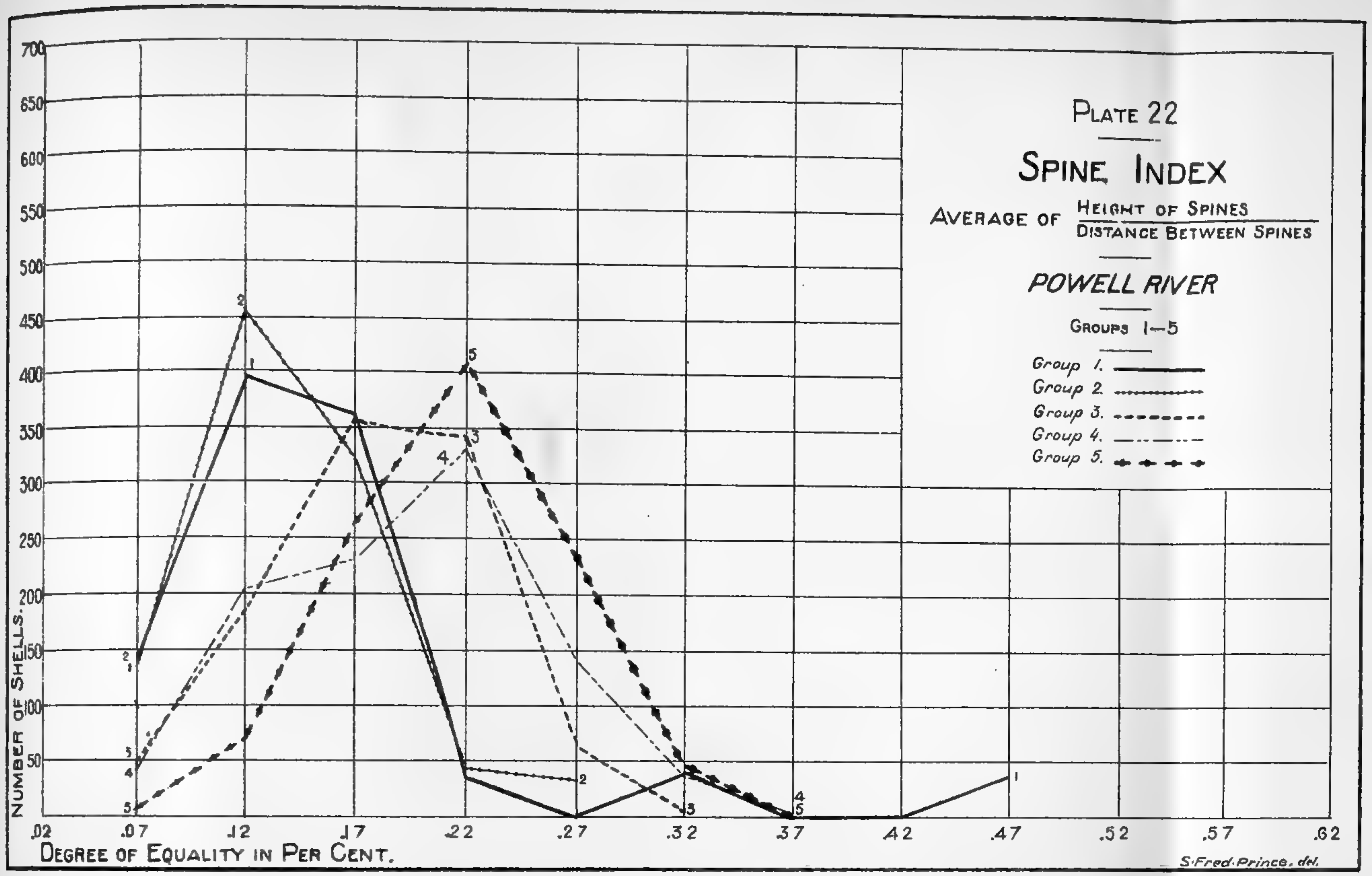


PLATE 22

SPINE INDEX

AVERAGE OF $\frac{\text{HEIGHT OF SPINES}}{\text{DISTANCE BETWEEN SPINES}}$

POWELL RIVER

GROUPS 1—5

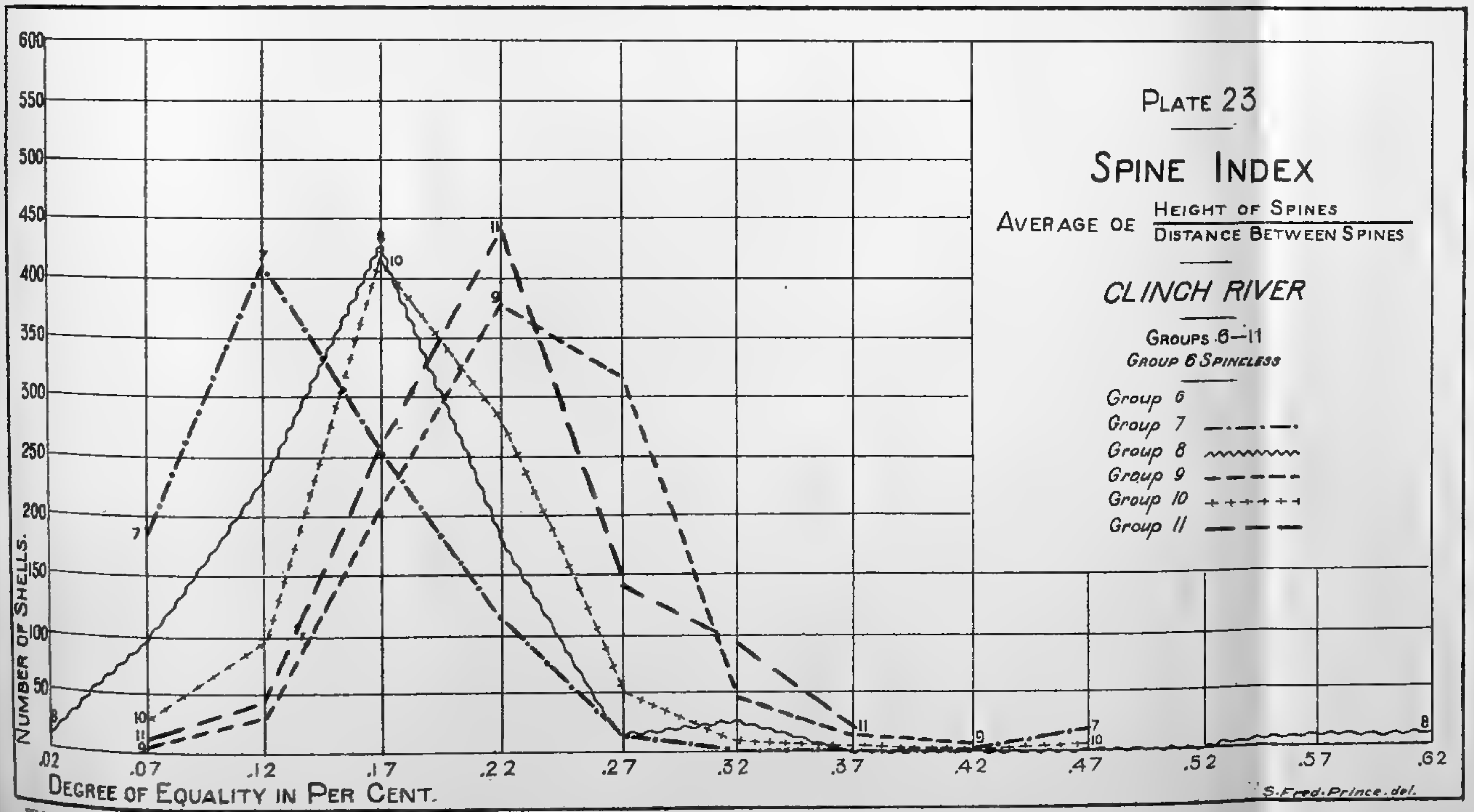


PLATE 23

SPINE INDEX

AVERAGE OF $\frac{\text{HEIGHT OF SPINES}}{\text{DISTANCE BETWEEN SPINES}}$

CLINCH RIVER

GROUPS 6—11

GROUP 6 SPINELESS

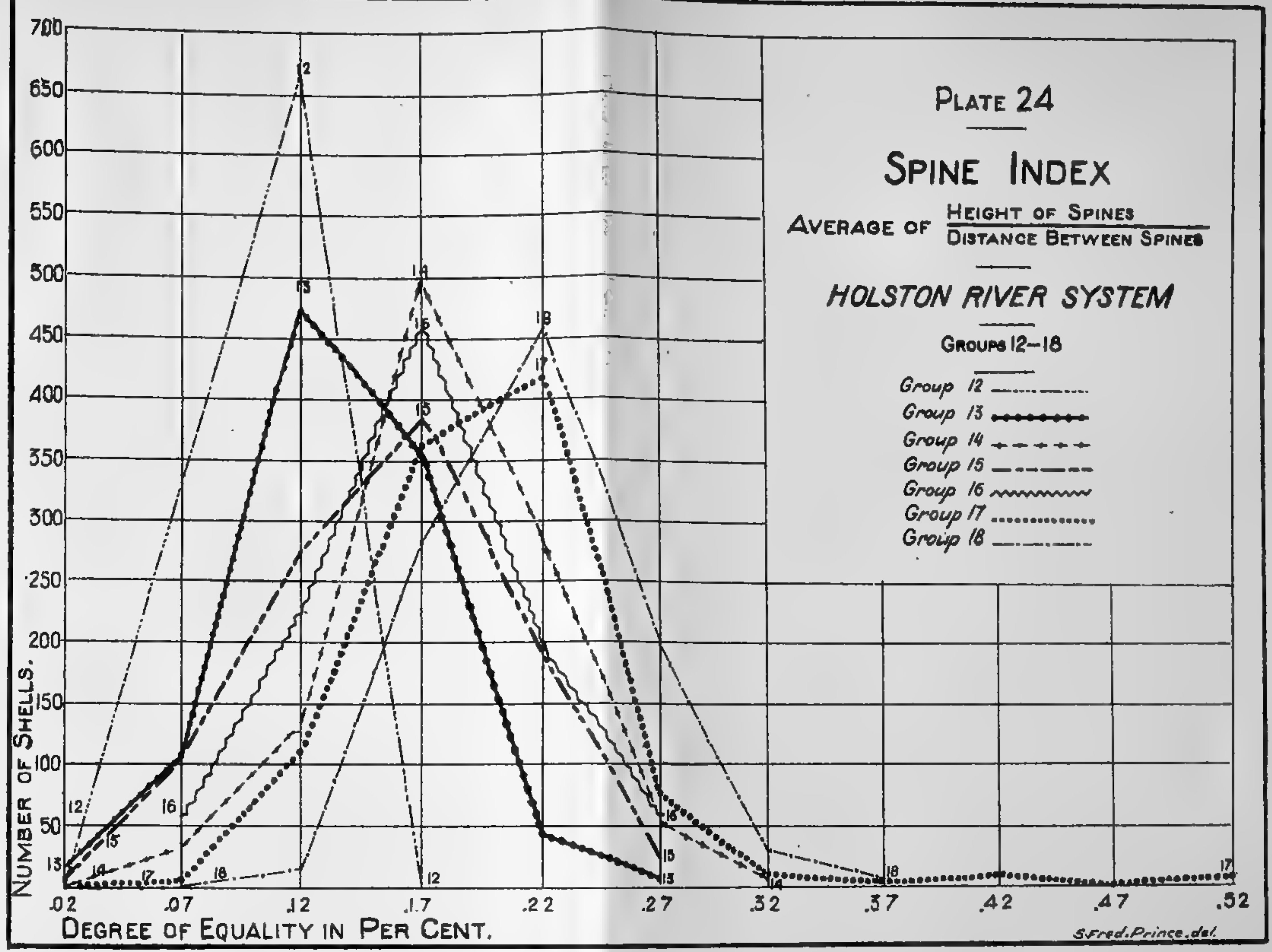


PLATE 24

SPINE INDEX

AVERAGE OF $\frac{\text{HEIGHT OF SPINES}}{\text{DISTANCE BETWEEN SPINES}}$

HOLSTON RIVER SYSTEM

GROUPS 12—18

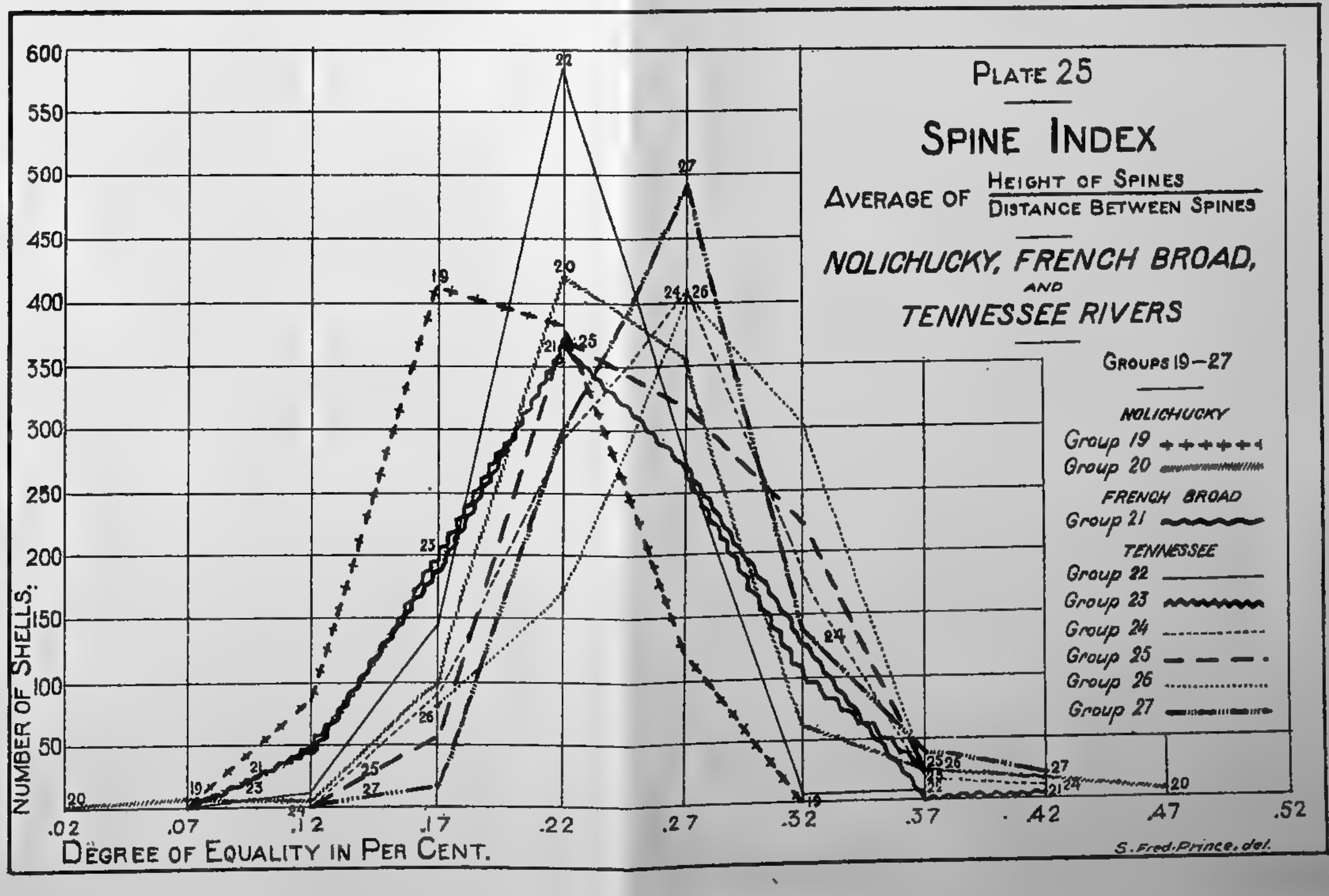


PLATE 25

SPINE INDEX

AVERAGE OF $\frac{\text{HEIGHT OF SPINES}}{\text{DISTANCE BETWEEN SPINES}}$

NOLICHUCKY, FRENCH BROAD, AND TENNESSEE RIVERS

GROUPS 19—27

THE NORRIS PETERS CO., WASHINGTON, D. C.

EXPLANATION TO PLATE 26.

(Dimensions of the shell.)

Table showing the diameter of shell, and shell index, by groups, throughout the Tennessee River system.

Classes	7.5	8.5	9.5	10.5	11.5	87	0.89	0.91	0.93	0.95	Number of shells used. Index.	Number of shells used. Diameter of shell.	Constants for reduction of totals to 1,000. Index.	Constants for reduction of totals to 1,000. Diameter.	Classes.
1. Table of frequencies reduced to thousands.															**1. Table of frequencies reduced to thousands.**
Powell River:															Powell River:
Group 1		1.5	13.5	51	72	.5	3	3		1.5					1 Group.
Group 2						.4	5.2								2 Group.
Group 3							7.4								3 Group.
Group 4															4 Group.
Group 5				2.3	18.4	.5									5 Group.
Total		.6	5.4	21	33.6		1.8	1.8		.6					Total.
Clinch River:															Clinch River:
Group 6							27.5								6 Group.
Group 7					4.4	.6	13.2								7 Group.
Group 8			4.8	9.6	24	.4	4.8	4.8							8 Group.
Group 9															9 Group.
Group 10															10 Group.
Group 11			10.2		30.6										11 Group.
Total			1.6	1.6	7.2	.5	8.1	.9							Total.
Holston River:															Holston River:
Group 12						.3			6.1						12 Group.
Group 13					6.2	.1	3.1								13 Group.
Group 14															14 Group.
Group 15				3.4	13.6										15 Group.
Group 16				17.2	64.5	.3									16 Group.
Group 17		5.1	5.1	15.3	81.6										17 Group.
Group 18			5		30		5								18 Group.
Total		.6	1.2	4.8	25.8		1.2		.6						Total.
Nolichucky River:															Nolichucky River:
Group 19					13.7										19 Group.
Group 20	6.6	19.8	79.2	85.8	181.8										20 Group.
Total	4.4	13.2	52.8	57.2	127.6										Total.
French Broad River:															French Broad River:
Group 21								14							21 Group.
Tennessee River:															Tennessee River:
Group 22			5	40	60										22 Group.
Group 23					8.7	.1									23 Group.
Group 24															24 Group.
Group 25															25 Group.
Group 26															26 Group.
Group 27															27 Group.
Total			1.6	12.8	20.8	.7									Total.
2. Table of absolute frequencies, by groups and rivers.															**2. Table of absolute frequencies by groups and rivers.**
Powell River:															Powell River:
Group 1			9	34	48		2	2		1	661	668	1.5	1.5	1 Group.
Group 2								1			192	203	5.2	4.9	2 Group.
Group 3							1				136	136	7.4	7.4	3 Group.
Group 4											185	196	5.4	5.1	4 Group.
Group 5				1	8						402	435	2.5	2.3	5 Group.
Total		1	9	35	56		3	3		1	1,576	1,638	.6	.6	Total.
Clinch River:															Clinch River:
Group 6							5				182	197	5.5	5.1	6 Group.
Group 7					1		3				225	226	4.4	4.4	7 Group.
Group 8			1	2	5		1	1			207	207	4.8	4.8	8 Group.
Group 9											167	184	6	5.4	9 Group.
Group 10											276	288	3.6	3.5	10 Group.
Group 11			1		3						96	98	10.4	10.2	11 Group.
Total			2	2	9		9	1			1,153	1,200	.9	.8	Total.
Holston River:															Holston River:
Group 12									1		165	160	6.1	6.3	12 Group.
Group 13					2		1				320	320	3.1	3.1	13 Group.
Group 14											160	160	6.3	6.3	14 Group.
Group 15				1	4						298	298	3.4	3.4	15 Group.
Group 16				4	15						230	230	4.3	4.3	16 Group.
Group 17		1	1	3	16						197	197	5.1	5.1	17 Group.
Group 18			1		6		1				199	199	5.0	5	18 Group.
Total		1	2	8	43		2		1		1,569	1,564	.6	.6	Total.
Nolichucky River:															Nolichucky River:
Group 19					1							73		13.7	19 Group.
Group 20	1	3	12	13	28						152	152	6.6	6.6	20 Group.
Total	1	3	12	13	29						152	225	6.6	20.3	Total.
French Broad River:															French Broad River:
Group 21								2			143	143	7	7	21 Group.
Tennessee River:															Tennessee River:
Group 22			1	8	12						199	199	5	5	22 Group.
Group 23					1	3					115	115	8.7	8.7	23 Group.
Group 24											180	180	5.6	5.6	24 Group.
Group 25												34		29.4	25 Group.
Group 26											34	46	29	21.7	26 Group.
Group 27												50		20	27 Group.
Total			1	8	13	3					528	624	1.9	1.6	Total.
Total shells used											5,121	5,394			Total shells used.

DIMENSIONS OF THE SHELL.

	Diameter of shell (in millimeters).																					
Classes	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.5
1. Table of frequencies reduced to thousands.																						
Powell River:																						
Group 1		1.5	13.5	51	72	88.5	129	160.5	208.5	117	82.5	37.5	9	3								
Group 2						4.9		9.8	78.4	261.6	338.1	156.8	68.6	39.2	4.9	19.6	9.8					
Group 3									29.6	81.4	281.2	288.6	162.8	96.2	37	11.8	7.4				7.4	
Group 4						10.2	20.4	40.8	168.3	219.3	229.5	244.8	51	10.2				5.1				
Group 5				2.3	18.4	23	66.7	177.1	262.2	158.7	140.3	87.4	52.9	9.2			2.3					
Total		.6	5.4	21	33.6	43.2	71.4	116.4	183.6	165	160.8	108.6	45	17.4	3.6	3.6	2.4	.6			.6	
Clinch River:																						
Group 6											25.5	239.7	219.3	193.8	204	96.9	25.5					
Group 7					4.4		26.4	52.8	96.8	224.4	290.4	167.2	92.4	30.8	8.8							
Group 8			4.8	9.6	24	115.2	105.6	172.8	129.6	168	139.2	76.8	24	24								
Group 9								10.8	70.2	226.8	243	216	129.6	59.4	37.8							
Group 10								7	45.5	259	332.5	252	87.5	21	3.5							
Group 11			10.2		30.6	10.2	61.2	122.4	112.2	163.2	214.2	132.6	122.4	20.4								
Total			1.6	1.6	7.2	20	27.2	51.2	68.8	171.1	208.8	180.8	104	55.2	40	15.2	4					
Holston River:																						
Group 12							12.6	18.9	56.7	100.8	226.8	264.6	195.3	107.1	25.2							
Group 13					6.2	15.5	15.5	31	62	96.1	111.6	201.6	170.5	158.1	74.4	34.1	12.4					
Group 14									6.3	25.2	69.3	182.7	252	283.5	113.4	63	12.6					
Group 15				3.4	13.6	27.2	98.6	119	71.4	115.6	81.6	98.6	139.4	132.6	85	23.8			3.4			
Group 16				17.2	64.5	64.5	146.2	124.7	154.8	154.8	90.3	47.3	47.3	25.8	30.1	12.9	8.6					
Group 17		5.1	5.1	15.3	81.6	300.9	270.3	122.4	81.6	56.1	30.6	25.5	5.1	5.1								
Group 18			5		30	115	140	190	165	135	55	75	50	30							5	
Total		.6	1.2	4.8	25.8	66	90.6	83.4	81.6	95.4	87	118.2	113.4	99	46.8	18.6	4.8		.6		.6	
Nolichucky River:																						
Group 19					13.7		41.1	95.9	246.6	164.4	150.7	164.4	68.5	54.8								
Group 20	6.6	19.8	79.2	85.8	181.8	158.4	125.4	99	33	26.4	39.6	39.6	52.8	46.2	6.6							
Total	4.4	13.2	52.8	57.2	127.6	105.6	96.8	96.8	101.2	70.4	74.8	79.2	57.2	48.4	4.4							
French Broad River:																						
Group 21						7	14	63	133	196	154	98	63	126	98	28	14	7				
Tennessee River:																						
Group 22			5	40	60	245	245	250	110	20	5			5	5	5						
Group 23					8.7	8.7	17.4	26.1	17.4	60.9	182.7	287.1	200.1	87	60.9	26.1	8.7					8.7
Group 24							11.2	28	56	140	268.8	196	95.2	72.8	95.2	39.2	5.6					
Group 25									88.2		58.8	176.4	176.4	88.2	176.4	88.2		117.6	29.4			
Group 26							21.7	65.1	130.2	65.1	151.9	130.2	86.8	43.4	108.5	130.2	43.4	21.7				
Group 27							20				20	80	60	120	200	220	200	60		20		
Total			1.6	12.8	20.8	80	88	97.6	68.8	62.4	128	134.4	84.8	56	73.6	49.6	22.4	12.8	1.6	1.6		1.6
2. Table of absolute frequencies, by groups and rivers.																						
Powell River:																						
Group 1			9	34	48	59	86	107	139	98	55	24	6	2								
Group 2						1		2	16	54	69	32	14	8	1	4	2					
Group 3									4	11	38	39	22	13	5	2	1				1	
Group 4						2	4	8	33	43	45	48	10	2				1				
Group 5				1	8	10	29	77	114	69	61	38	23	4			1					
Total		1	9	35	56	72	110	194	306	275	268	181	75	29	6	6	4	1			1	
Clinch River:																						
Group 6											5	47	43	38	40	19	5					
Group 7					1		6	12	22	51	66	38	21	7	2							
Group 8			1	2	5	24	22	36	27	35	29	16	5	5								
Group 9								2	13	42	45	40	24	11	7							
Group 10								2	13	74	95	72	25	6	1							
Group 11			1		3	1	6	12	11	16	21	13	12	2								
Total			2	2	9	25	34	64	86	218	261	226	130	69	50	19	5					
Holston River:																						
Group 12							2	3	9	16	36	42	31	17	4							
Group 13					2	5	5	10	20	31	36	66	55	51	24	11	4					
Group 14									1	4	11	29	40	45	18	10	2					
Group 15				1	4	8	29	35	21	34	24	29	41	39	25	7			1			
Group 16				4	15	15	31	29	36	36	21	11	11	6	7	3	2					
Group 17		1	1	3	16	59	53	24	16	11	6	5	1	1								
Group 18			1		6	23	28	38	33	27	11	15	10	6							1	
Total		1	2	8	43	110	151	139	136	159	145	197	189	165	78	31	8		1		1	
Nolichucky River:																						
Group 19					1		3	7	18	12	11	12	5	4								
Group 20	1	3	12	13	28	24	10	15	5	4	6	6	8	7	1							
Total	1	3	12	13	29	24	22	22	23	16	17	18	13	11	1							
French Broad River:																						
Group 21						1	2	9	19	28	22	14	9	18	14	4	2	1				
Tennessee River:																						
Group 22			1	8	12	49	49	50	22	4	1			1	1	1						
Group 23					1	1	2	3	2	7	21	33	23	10	7	3	1					1
Group 24							2	5	10	25	48	35	17	13	17	7	1					
Group 25									3		2	6	6	3	6	3		4	1			
Group 26							1	3	6	3	7	6	4	2	5	6	2	1				
Group 27							1				1	4	3	6	10	11	10	3		1		
Total			1	8	13	50	55	61	43	39	80	84	53	35	46	31	14	8	1	1		1
Total shells used																						

	Shell index.																		Number of shells used.		Constants for reduction of totals to 1,000.		
Classes	0.61	0.63	0.65	0.67	0.69	0.71	0.73	0.75	0.77	0.79	0.81	0.83	0.85	0.87	0.89	0.91	0.93	0.95	Index.	Diameter of shell.	Index.	Diameter.	Classes.
1. Table of frequencies reduced to thousands.																							
Powell River:																							Powell River:
Group 1				3	10.5	46.5	115.5	183	213	177	141	51	30	10.5	3	3		1.5					1 Group.
Group 2				20.8	52	78	140.4	223.6	182	161.2	67.6	26	31.2	10.4	5.2								2 Group.
Group 3					14.8	59.2	118.4	177.6	192.4	185	111	66.6	37	37	7.4								3 Group.
Group 4	5.4	27	59.4	124.2	118.8	183.6	183.6	124.2	81	86.4	5.4												4 Group.
Group 5	5	42.5	105	132.5	102.5	137.5	137.5	130	75	30	25	15	5	2.5									5 Group.
Total	1.8	13.2	31.8	49.2	63.6	85.8	125.4	158.4	148.8	121.2	79.8	33.6	19.8	9	1.8	1.8		.6					Total.
Clinch River:																							Clinch River:
Group 6						5.5	33	23	137.5	148.5	170.5	220	126.5	99	27.5								6 Group.
Group 7					4.4	39.6	83.6	184.8	198	132	158.4	92.4	66	17.6	13.2								7 Group.
Group 8		4.8	4.8	19.2	86.4	144	211.2	168	100.8	96	62.4	72		14.4	4.8	4.8							8 Group.
Group 9	6	24	54	180	210	258	126	66	54	18	6												9 Group.
Group 10		21.6	25.2	64.8	90	201.6	259.2	144	93.6	46.8	39.6	7.2											10 Group.
Group 11			10.4	83.2	176.8	312	135.2	114.4	104	41.6	20.8												11 Group.
Total	.9	9.9	16.2	54	86.4	152.1	157.5	130.5	122.4	87.3	84.6	70.2	34.2	22.5	8.1	.9							Total.
Holston River:																							Holston River:
Group 12						54.9	115.9	250.1	183	164.7	134.2	36.6	42.7	18.3			6.1						12 Group.
Group 13				6.2	43.4	158.1	232.5	210.8	192.2	93	21.7	18.6	9.3	3.1	3.1								13 Group.
Group 14	6.3	12.6	69.3	157.5	176.4	214.2	157.5	126	50.4	18.9	6.3	12.6											14 Group.
Group 15	3.4		10.2	37.4	108.8	159.8	231.2	210.8	125.8	71.4	30.6	13.6	10.2										15 Group.
Group 16		4.3	21.5	55.9	184.9	150.5	249.4	150.5	94.6	38.7	17.2	8.6	8.6	4.3									16 Group.
Group 17		5.1	25.5	56.1	117.3	224.4	219.3	168.3	137.7	30.6	5.1	5.1	10.2										17 Group.
Group 18	15	25	135	205	170	205	135	60	20	10	10				5								18 Group.
Total	3	5.4	30.6	61.8	104.4	156.6	189	172.6	114	58.8	27.6	12.6	10.2	3	1.2		.6						Total.
Nolichucky River:																							Nolichucky River:
Group 19																							19 Group.
Group 20			13.2	19.8	165	191.4	237.6	171.6	99	39.6	46.2	19.8											20 Group.
Total			13.2	19.8	165	191.4	237.6	171.6	99	39.6	46.2	19.8											Total.
French Broad River:																							French Broad River:
Group 21			7	35	49	84	182	161	252	98	70	28	21			14							21 Group.
Tennessee River:																							Tennessee River:
Group 22	10	5	85	115	240	200	185	105	30	5	15												22 Group.
Group 23				34.8	69.6	139.2	182.7	208.8	156.6	87	60.9	26.1	8.7	26.1									23 Group.
Group 24		5.6	11.2	56	95.2	179.2	263.2	145.6	100.8	100.8	39.2	11.2											24 Group.
Group 25																							25 Group.
Group 26		29		29	174	116	203	290	58	29	58												26 Group.
Group 27																							27 Group.
Total	3.8	5.7	30.1	72.2	150.1	174.8	212.8	153.9	83.6	57	36.1	9.5	1.9	5.7									Total.
2. Table of absolute frequencies, by groups and rivers.																							
Powell River:																							Powell River:
Group 1				2	7	31	77	122	142	118	94	36	20	7	2	2		1	661	668	1.5	1.5	1 Group.
Group 2				4	10	15	27	43	35	31	13	5	6	2		1			192	203	5.2	4.9	2 Group.
Group 3					2	8	16	24	26	25	15	9	5	5	1				136	136	7.4	7.4	3 Group.
Group 4	1	5	11	23	22	34	34	23	15	16	1								185	196	5.4	5.1	4 Group.
Group 5	2	17	42	53	65	55	55	52	30	12	10	6	2	1					402	435	2.5	2.3	5 Group.
Total	3	22	53	82	106	143	209	204	248	202	133	56	33	15	3	3		1	1,576	1,638	.6	.6	Total.
Clinch River:																							Clinch River:
Group 6						1	6	6	25	27	31	40	23	18	5				182	197	5.5	5.1	6 Group.
Group 7					1	9	19	42	45	30	36	21	15	4	3				225	226	4.4	4.4	7 Group.
Group 8		1	1	4	18	30	44	35	21	20	13	15		3	1	1			207	207	4.8	4.8	8 Group.
Group 9	1	4	9	30	35	43	21	11	9	3	1								167	184	6	5.4	9 Group.
Group 10		6	7	18	25	56	72	40	26	13	11	2							276	288	3.6	3.5	10 Group.
Group 11			1	8	17	30	13	11	10	4	2								96	98	10.4	10.2	11 Group.
Total	1	11	18	60	96	169	175	145	136	97	94	78	38	25	9	1			1,153	1,200	.9	.8	Total.
Holston River:																							Holston River:
Group 12						9	19	41	30	27	22	6	7	3			1		165	160	6.1	6.3	12 Group.
Group 13				2	14	51	75	68	62	30	7	6	3	1	1				320	320	3.1	3.1	13 Group.
Group 14	1	2	11	25	28	34	25	20	8	3	1	2							160	160	6.3	6.3	14 Group.
Group 15	1		3	11	32	47	68	62	37	21	9	4	3						298	298	3.4	3.4	15 Group.
Group 16		1	5	13	43	35	58	35	22	9	4	2	2	1					230	230	4.3	4.3	16 Group.
Group 17		1	5	11	23	41	43	33	27	6	1	1	2						197	197	5.1	5.1	17 Group.
Group 18	3	5	27	41	34	41	27	12	4	2	2				1				199	199	5.0	5	18 Group.
Total	5	9	51	103	174	261	315	271	190	98	46	21	17	5	2		1		1,569	1,564	.6	.6	Total.
Nolichucky River:																							Nolichucky River:
Group 19																				73		13.7	19 Group.
Group 20			2	3	25	29	36	26	15	6	7	3							152	152	6.6	6.6	20 Group.
Total			2	3	25	29	36	26	15	6	7	3							152	225	6.6	20.3	Total.
French Broad River:																							French Broad River:
Group 21			1	5	7	12	26	23	36	14	10	4	3			2			143	143	7	7	21 Group.
Tennessee River:																							Tennessee River:
Group 22	2	1	17	23	48	40	37	21	6	1	3								199	199	5	5	22 Group.
Group 23				4	8	16	21	24	18	10	7	3	1	3					115	115	8.7	8.7	23 Group.
Group 24		1	2	10	17	32	47	26	18	18	7	2							180	180	5.6	5.6	24 Group.
Group 25																				34		29.4	25 Group.
Group 26		1		1	6	4	7	10	2	1	2								34	46	29	21.7	26 Group.
Group 27																				50		20	27 Group.
Total	2	3	19	38	79	92	112	81	44	30	19	5	1	3					528	624	1.9	1.6	Total.
Total shells used																			5,121	5,394			Total shells used.

EXPLANATION TO PLATE 27.

(Spinosity of the shell.)

Table showing the height of spines, distance between them, and spine index, by groups, throughout the Tennessee River system.

Classes	Spine index.									Number of shells used.			Constants for reduction to 1,000.		Classes.
Classes	22	0. 27	0. 32	0. 37	0. 42	0. 47	0. 52	0. 57	0. 62	Total.	Smooth shells (0.5) class.	Distance between spines and spine index.	Spine index.	Height of spines, and distance between spines.	Classes.
1. Table of frequencies reduced to thousands.															1. Table of frequencies reduced to thousands.
Powell River:															Powell River:
Group 1			36			36									1 Group.
Group 2	. 4	31. 8													2 Group.
Group 3	. 2	62. 4	7. 8												3 Group.
Group 4	. 5	140. 8	38. 4	6. 4											4 Group.
Group 5	7. 5	235	42. 5	2. 5											5 Group.
Total	5. 6	152. 4	30	2. 4		1. 2									Total.
Clinch River:															Clinch River:
Group 6															6 Group.
Group 7	. 8	16. 4				16. 4									7 Group.
Group 8	. 2	12. 8	25. 6					6. 4	6. 4						8 Group.
Group 9	. 5	319	44	11	5. 5										9 Group.
Group 10	. 8	50. 4	10. 8	3. 6		3. 6									10 Group.
Group 11	. 6	142. 8	91. 8	20. 4											11 Group.
Total	2. 5	115. 7	31. 2	6. 5	1. 3	2. 6		1. 3	1. 3						Total.
Holston River:															Holston River:
Group 12															12 Group.
Group 13	5. 1	8. 2													13 Group.
Group 14	. 6	51. 2	6. 4												14 Group.
Group 15	2	28. 8													15 Group.
Group 16	. 8	59. 2													16 Group.
Group 17	. 2	71. 4	10. 2	5. 1	10. 2		5. 1								17 Group.
Group 18	0	200	30	5											18 Group.
Total	6. 4	70. 2	8. 1	1. 8	1. 8		9								Total.
Nolichucky River															Nolichucky River:
Group 19	3. 6	123. 3													19 Group.
Group 20	2. 4	356. 4	66	26. 4	13. 2	6. 6									20 Group.
Total	4. 8	277. 2	44	17. 6	8. 8	4. 4									Total.
French Broad Riv															French Broad River:
Group 21	4	273	126		7										21 Group.
Tennessee River:															Tennessee River:
Group 22	1. 4	265. 2	5. 1	5. 1											22 Group.
Group 23	5. 4	269. 7	104. 4	26. 1											23 Group.
Group 24	6. 8	414. 4	184. 8	11. 2	5. 6										24 Group.
Group 25	1. 8	314. 6	228. 8	28. 6											25 Group.
Group 26	3. 6	412. 3	303. 8	21. 7											26 Group.
Group 27	4	490	137. 2	39. 2	19. 6										27 Group.
Total	2	339. 2	120	16	3. 2										Total.
2. Table of absolute frequencies by groups and rivers.															2. Table of absolute frequencies by groups and rivers.
Powell River:															Powell River:
Group 1	1		1			1				669	641	28	36	1. 5	1 Group.
Group 2	4	3								192	98	94	10. 6	5. 2	2 Group.
Group 3	4	8	1							136	8	128	7. 8	7. 4	3 Group.
Group 4	1	22	6	1						196	41	155	6. 4	5. 1	4 Group.
Group 5	3	94	17	1						444	34	410	2. 5	2. 3	5 Group.
Total	3	127	25	2		1				1, 637	822	815	1. 2	. 6	Total.
Clinch River:															Clinch River:
Group 6										182	182			5. 5	6 Group.
Group 7	7	1				1				226	165	61	16. 4	4. 4	7 Group.
Group 8	8	2	4					1	1	208	52	156	6. 4	4. 8	8 Group.
Group 9	9	58	8	2	1					184	2	182	5. 5	5. 4	9 Group.
Group 10	8	14	3	1		1				288	14	274	3. 6	3. 5	10 Group.
Group 11	3	14	9	2						98		98	10. 2	10. 2	11 Group.
Total	5	89	24	5	1	2		1	1	1, 186	415	771	1. 3	. 8	Total.
Holston River:															Holston River:
Group 12										165	162	3	333. 3	6. 1	12 Group.
Group 13	1	2								320	75	245	4. 1	3. 1	13 Group.
Group 14	4	8	1							160	3	157	6. 4	6. 2	14 Group.
Group 15	0	6								298	91	207	4. 8	3. 4	15 Group.
Group 16	7	8								230	94	136	7. 4	4. 3	16 Group.
Group 17	2	14	2	1	2		1			197	1	196	5. 1	5. 1	17 Group.
Group 18	2	40	6	1						199		199	5	5	18 Group.
Total	6	78	9	2	2		1			1, 569	426	1, 143	. 9	. 6	Total.
Nolichucky River															Nolichucky River:
Group 19	8	9								73		73	13. 7	13. 7	19 Group.
Group 20	4	54	10	4	2	1				152		152	6. 6	6. 6	20 Group.
Total	2	63	10	4	2	1				225		225	4. 4	4. 4	Total.
French Broad Ri															French Broad River:
Group 21	2	39	18		1					143		143	7	7	21 Group.
Tennessee River:															Tennessee River:
Group 22	4	52	1	1						199	1	198	5. 1	5	22 Group.
Group 23	12	31	12	3						115		115	8. 7	8. 7	23 Group.
Group 24	3	74	33	2	1					180		180	5. 6	5. 6	24 Group.
Group 25	13	11	8	1						35		35	28. 6	28. 6	25 Group.
Group 26	8	19	14	1						46		46	21. 7	21. 7	26 Group.
Group 27	15	25	7	2	1					51		51	19. 6	19. 6	27 Group.
Total	45	212	75	10	2					626		625	1. 6	1. 6	Total.
Total in all										5, 386	1, 664	3, 722			Total in all rivers.

SPINOSITY OF THE SHELL.

1. Table of frequencies reduced to thousands.

	Height of spines (in millimeters).											
Classes.	0.3	0.8	1.3	1.8	2.3	2.8	3.3	3.8	4.3	4.8	5.3	5.8
Powell River:												
Group 1.	967.5	28.5	3	3		1.5						
Group 2.	540.8	254.8	192.4	5.2	5.2							
Group 3.	96.2	170.2	244.2	384.8	103.6	7.4						
Group 4.	224.4	132.6	275.4	209.1	137.7	20.4						
Group 5.	57.5	50.6	186.3	395.6	255.3	48.3	4.6					
Total.	504.6	83.4	124.2	160.8	91.8	16.2	1.2					
Clinch River:												
Group 6.	1,000											
Group 7.	756.8	149.6	74.8	8.8	4.4							
Group 8.	316.8	158.4	345.6	129.6	28.8	4.8	4.8	4.8	4.8			
Group 9.	10.8	10.8	189	340.2	383.4	54	5.4					
Group 10.	49	66.5	308	388.5	164.5	21	10.5					
Group 11.	20.4	40.8	142.8	316.2	326.4	142.8	10.2					
Total.	350.4	73.6	180.8	187.2	125.6	24.8	4.8	.8	.8			
Holston River:												
Group 12.	994.3	12.2										
Group 13.	316.2	449.5	213.9	12.4								
Group 14.	37.2	68.2	136.4	334.8	310	99.2	6.2					
Group 15.	374	183.6	153	156.4	108.8	37.4						
Group 16.	438.6	120.4	184.9	180.6	47.3	12.9	4.3					
Group 17.	15.3	117.3	321.3	382.5	107.1	61.2						
Group 18.		10	105	360	350	150	20					
Total.	291.6	159	157.8	175.8	110.4	43.2	3.6					
Nolichucky River:												
Group 19.		54.8	274	548	109.6	13.7						
Group 20.	6.6	39.6	158.4	356.4	231	145.2	59.4	6.6				
Total.	4.4	44	193.6	413.6	189.2	101.2	39.6	4.4				
French Broad River:												
Group 21.		7	35	147	266	301	210	35				
Tennessee River:												
Group 22.	5	25	40	245	470	185	25					
Group 23.		8.7	8.7	52.2	226.2	382.8	226.2	78.3	17.4			
Group 24.			5.6	39.2	72.8	212.8	369.6	257.6	44.8	5.6		
Group 25.				28.6	28.6	371.8	228.8	114.4	143	57.2	28.6	
Group 26.			21.7	43.4	43.4	86.8	173.6	130.2	303.8	130.2	43.4	21.7
Group 27.					78.4	470.4	333.2	78.4	39.2			
Total.	1.6	6	17.6	104	224	256	208	110.4	49.6	14.4	4.8	1.6

	Distance between spines (in millimeters).																				
Classes.	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5
Powell River:																					
Group 1.	961.5				3	10.5	16.5	9	3												
Group 2.	509.6				10.4	10.4	145.6	166.4	88.4	57.2	10.4										
Group 3.	59.2				7.4	14.8	74	214.6	355.2	192.4	66.6	14.8		7.4							
Group 4.	209.1				20.4	56.1	158.1	209.1	183.6	102	35.7	25.5									
Group 5.	43.7			2.3	9.2	48.3	98.9	193.2	248.4	207	112.7	20.7	2.3								
Total.	493.2			.6	7.8	25.8	73.8	115.2	126.6	88.2	40.2	9.6	.6	.6							
Clinch River:																					
Group 6.	1,000																				
Group 7.	726				13.2	52.8	96.8	83.6	13.2	8.8											
Group 8.	249.6			24	33.6	76.8	177.6	177.6	124.8	91.2	11.4	28.8									
Group 9.	10.8						21.6	81	145.8	297	199.8	172.8	48.6	10.8	5.4						
Group 10.	49						10.5	73.5	224	318.5	220.5	87.5	24.5								
Group 11.				30.6		20.4	40.8	91.8	201	255	193.8	102	40.8	10.2	10.2						
Total.	332			6.4	8	24	56	80.8	112	153.6	97.6	58.4	16	2.4	1.6						
Holston River:																					
Group 12.	988.2					12.2	6.1														
Group 13.	232.5			6.2	52.7	158.1	316.2	158.1	62	6.2											
Group 14.	18.6					6.2	6.2	49.6	68.2	111.6	248	251.2	155	62	12.2						
Group 15.	309.4				27.2	64.2	68	88.4	132.6	81.6	105.4	78.2	30.6	20.4	3.4	3.4					
Group 16.	404.2			4.3	25.8	25.8	64.5	154.8	98.9	90.3	55.9	30.1	30.1		4.3						
Group 17.	5.1		5.1		20.4	51	193.8	311.1	188.7	102	66.3	25.5	25.5	10.2							
Group 18.					5	15	70	110	170	220	205	90	60	35	10	5					
Total.	255.6		.6	1.8	21.6	55.2	114.6	122.4	98.4	77.4	82.8	56.4	34.8	15	3.6	1.2					
Nolichucky River:																					
Group 19.						13.7	41.1	301.4	287.7	287.7	68.5										
Group 20.				13.2	33	85.8	145.2	184.8	171.6	112.2	63	59.4	92.4	19.8	6.6	13.2					
Total.				8.8	22	61.6	110	220	205.8	167.2	63	39.6	61.6	13.2	4.4	8.8					
French Broad River:																					
Group 21.								21	56	196	203	175	189	119	21	7	14				
Tennessee River:																					
Group 22.	5					15	35	75	110	220	300	170	45	15		5					
Group 23.							17.4	8.7	8.7	26.1	78.3	269.7	217.5	234.9	104.4	34.8					
Group 24.								5.6	11.2	39.2	72.8	145.6	240.8	274.4	162.4	50.4	5.6				
Group 25.										114.4	171.6	143	143	57.2	85.8	85.8		171.6		28.6	
Group 26.									21.7	21.7	86.8	86.8	65.1	108.5	130.2	173.6	173.6	65.1	43.4		21.7
Group 27.									39.2	58.8	156.8	411.6	176.4	58.8	78.4	19.6					
Total.	1.6					4.8	14.4	27.2	44.8	99.2	160	193.6	150.4	142.4	86.4	41.6	4.4	14.4	3.2	1.6	3.2

	Spine index.													Number of shells used.			Constants for reduction to 1,000.		
Classes.	0.02	0.07	0.12	0.17	0.22	0.27	0.32	0.37	0.42	0.47	0.52	0.57	0.62	Total.	Smooth shells (0.5) class.	Distance between spines and spine index.	Spine index.	Height of spines, and distance between spines.	Classes.
Powell River:																			Powell River:
Group 1.		144	396	360	36		36			36									1 Group.
Group 2.		137.8	455.8	328.6	42.4	31.8													2 Group.
Group 3.		46.8	179.4	358.8	343.2	62.4	7.8												3 Group.
Group 4.		44.8	204.8	230.4	331.5	140.8	38.4	6.4											4 Group.
Group 5.		5	65	267.5	407.5	235	42.5	2.5											5 Group.
Total.		38.4	162	276	315.6	152.4	30	2.4		1.2									Total.
Clinch River:																			Clinch River:
Group 6.																			6 Group.
Group 7.		180.4	410	262.4	114.8	16.4				16.4									7 Group.
Group 8.	12.8	96	230.4	428.8	179.2	12.8	25.6					6.4	6.4						8 Group.
Group 9.		5.5	27.5	209	379.5	319	44	11	5.5										9 Group.
Group 10.		25.2	198	414	280.8	50.4	10.8	3.6		3.6									10 Group.
Group 11.		10.2	40.8	255	438.6	142.8	91.8	20.4											11 Group.
Total.	2.6	45.5	162.5	339.3	292.5	115.7	31.2	6.5	1.3	2.6		1.3	1.3						Total.
Holston River:																			Holston River:
Group 12.		333.3	666.6																12 Group.
Group 13.	12.3	110.7	475.6	352.6	45.1	8.2													13 Group.
Group 14.		38.4	134.4	492.8	281.6	51.2	6.4												14 Group.
Group 15.	4.8	110.4	273.6	384	192	28.8													15 Group.
Group 16.		59.2	220.4	458.8	199.8	59.2													16 Group.
Group 17.		5.1	112.2	362.1	418.2	71.4	10.2	5.1	10.2		5.1								17 Group.
Group 18.			15	285	460	200	30	5											18 Group.
Total.	3.6	59.4	226.8	389.7	266.4	70.2	8.1	1.8	1.8		9								Total.
Nolichucky River:																			Nolichucky River:
Group 19.			82.2	411	383.6	123.3													19 Group.
Group 20.		6.6	6.6	99	422.4	356.4	66	26.4	13.2	6.6									20 Group.
Total.		4.4	30.8	198	404.8	277.2	44	17.6	8.8	4.4									Total.
French Broad River:																			French Broad River:
Group 21.			49	182	364	273	126		7										21 Group.
Tennessee River:																			Tennessee River:
Group 22.			10.2	142.8	581.4	265.2	5.1	5.1											22 Group.
Group 23.			43.5	191.4	365.4	269.7	104.4	26.1											23 Group.
Group 24.			5.6	89.6	296.8	414.4	184.8	11.2	5.6										24 Group.
Group 25.				57.2	371.8	314.6	228.8	28.6											25 Group.
Group 26.				86.8	173.6	412.3	303.8	21.7											26 Group.
Group 27.				19.6	294	490	137.2	39.2	19.6										27 Group.
Total.			12.8	116.8	392	339.2	120	16	3.2										Total.

2. Table of absolute frequencies by groups and rivers.

	Height of spines (in millimeters).											
Classes.	0.3	0.8	1.3	1.8	2.3	2.8	3.3	3.8	4.3	4.8	5.3	5.8
Powell River:												
Group 1.	645	19	2	2		1						
Group 2.	104	49	37	1	1							
Group 3.	13	23	33	52	14	1						
Group 4.	44	26	54	41	27	4						
Group 5.	35	22	81	172	111	21	2					
Total.	841	139	207	268	153	27	2					
Clinch River:												
Group 6.	182											
Group 7.	172	34	17	2	1							
Group 8.	66	33	72	27	6	1	1	1	1			
Group 9.	2	2	35	63	71	10	1					
Group 10.	14	19	88	111	47	6	3					
Group 11.	2	4	14	31	32	14	1					
Total.	438	92	226	234	157	31	6	1	1			
Holston River:												
Group 12.	163	2										
Group 13.	102	145	69	4								
Group 14.	6	11	22	54	50	16	1					
Group 15.	110	54	45	46	32	11						
Group 16.	102	28	43	42	11	3	1					
Group 17.	3	23	63	75	21	12						
Group 18.		2	21	72	70	30	4					
Total.	486	265	263	293	184	72	6					
Nolichucky River:												
Group 19.		4	20	40	8	1						
Group 20.	1	6	24	54	35	22	9	1				
Total.	1	10	44	94	43	23	9	1				
French Broad River:												
Group 21.		1	5	21	38	43	30	5				
Tennessee River:												
Group 22.	1	5	8	49	94	37	5					
Group 23.		1	1	6	26	44	26	9	2			
Group 24.			1	7	13	38	66	46	8	1		
Group 25.				1	1	13	8	4	5	2	1	
Group 26.			1	2	2	4	8	6	14	6	2	1
Group 27.					4	24	17	4	2			
Total.	1	6	11	65	140	160	130	69	31	9	3	1
Total in all rivers.												

	Distance between spines (in millimeters).																				
Classes.	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5
Powell River:																					
Group 1.	641				2	7	11	6	2												
Group 2.	98				2	2	28	32	17	11	2										
Group 3.	8				1	2	10	29	48	26	9	2		1							
Group 4.	41				4	11	31	41	36	20	7	5									
Group 5.	34			1	4	21	43	84	108	90	49	9	1								
Total.	822			1	13	43	123	192	211	147	67	16	1	1							
Clinch River:																					
Group 6.	182																				
Group 7.	165				3	12	22	19	3	2											
Group 8.	52			5	7	16	37	37	26	19	3	6									
Group 9.	2						4	15	27	55	37	32	9	2	1						
Group 10.	14						3	21	64	91	63	25	7								
Group 11.				3		2	4	9	20	25	19	10	4	1	1						
Total.	415			8	10	30	70	101	140	192	122	73	20	3	2						
Holston River:																					
Group 12.	162					2	1														
Group 13.	75			2	17	51	102	51	20	2											
Group 14.	3					1	1	8	11	18	40	41	25	10	2						
Group 15.	91				8	19	20	26	39	24	31	23	9	6	1	1					
Group 16.	94			1	6	6	15	36	23	21	13	7	7		1						
Group 17.	1		1		4	10	38	61	37	20	13	5	5	2							
Group 18.					1	3	14	22	34	44	41	18	12	7	2	1					
Total.	426		1	3	36	92	191	204	164	129	138	94	58	25	6	2					
Nolichucky River:																					
Group 19.						1	3	22	21	21	5										
Group 20.				2	5	13	22	28	26	17	10	9	14	3	1	2					
Total.				2	5	14	25	50	47	38	15	9	14	3	1	2					
French Broad River:																					
Group 21.								3	8	28	29	25	27	17	3	1	2				
Tennessee River:																					
Group 22.	1					3	7	15	22	44	60	34	9	3		1					
Group 23.							2	1	1	3	9	31	25	27	12	4					
Group 24.								1	2	7	13	26	43	49	29	9	1				
Group 25.										4	6	5	5	2	3	3		6		1	
Group 26.									1	1	4	4	3	5	6	8	8	3	2		1
Group 27.									2	3	8	21	9	3	4	1					
Total.	1					3	9	17	28	62	100	121	94	89	54	26	9	9	2	1	1
Total in all rivers.																					

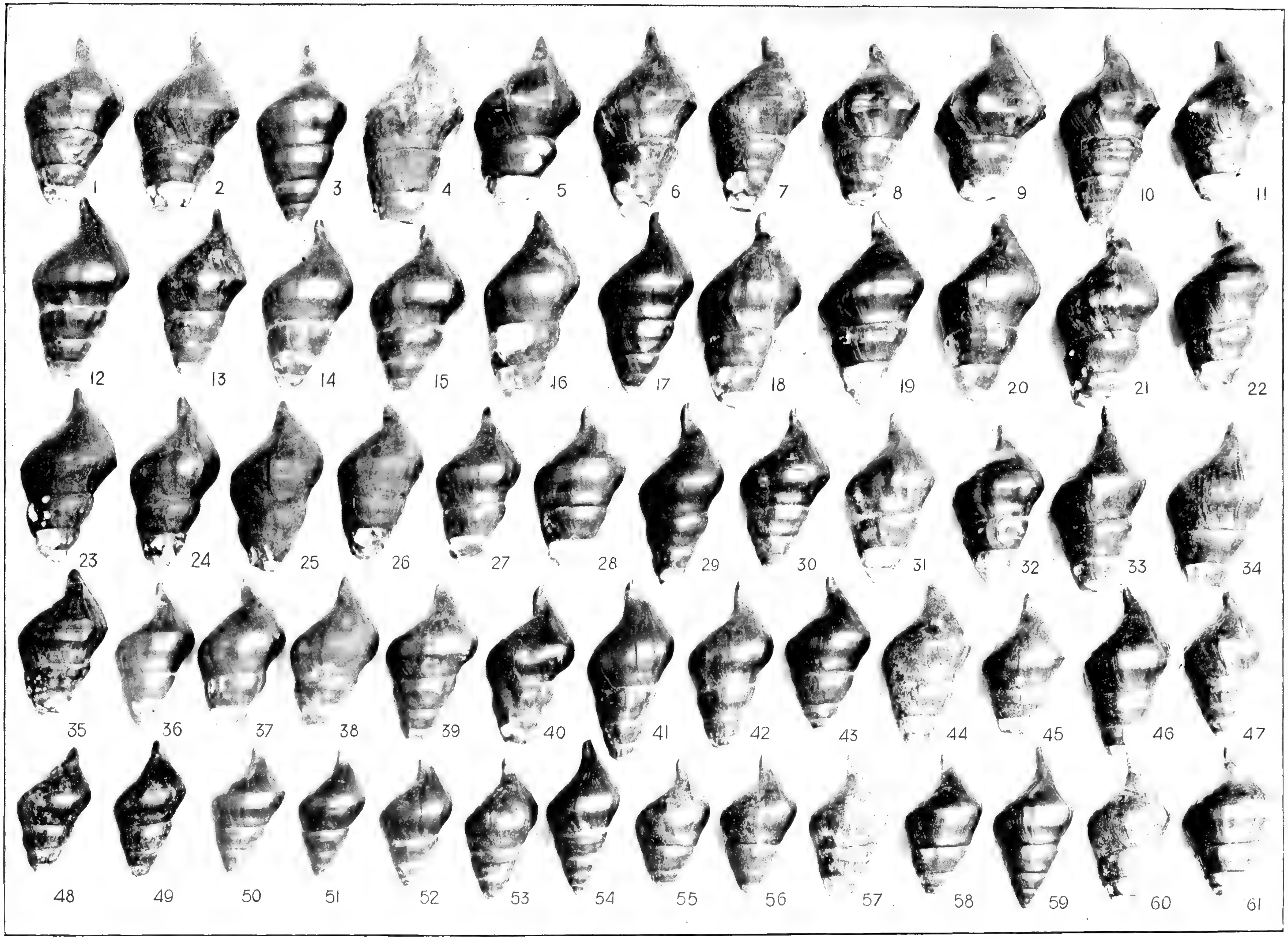
	Spine index.													Number of shells used.			Constants for reduction to 1,000.		
Classes.	0.02	0.07	0.12	0.17	0.22	0.27	0.32	0.37	0.42	0.47	0.52	0.57	0.62	Total.	Smooth shells (0.5) class.	Distance between spines and spine index.	Spine index.	Height of spines, and distance between spines.	Classes.
Powell River:																			Powell River:
Group 1.		4	11	10	1		1			1				669	641	28	36	1.5	1 Group.
Group 2.		13	43	31	4	3								102	98	94	10.6	5.2	2 Group.
Group 3.		6	23	46	44	8	1							136	8	128	7.8	7.4	3 Group.
Group 4.		7	32	36	51	22	6	1						196	41	155	6.4	5.1	4 Group.
Group 5.		2	26	107	163	94	17	1						444	34	410	2.5	2.3	5 Group.
Total.		32	135	230	263	127	25	2		1				1,637	822	815	1.2	.6	Total.
Clinch River:																			Clinch River:
Group 6.														182	182			5.5	6 Group.
Group 7.		11	25	16	7	1				1				226	165	61	16.4	4.4	7 Group.
Group 8.	2	15	36	67	28	2	4					1	1	208	52	156	6.4	4.8	8 Group.
Group 9.		1	5	38	69	58	8	2	1					184	2	182	5.5	5.4	9 Group.
Group 10.		7	55	115	78	14	3	1		1				288	14	274	3.6	3.5	10 Group.
Group 11.		1	4	25	43	14	9	2						98		98	10.2	10.2	11 Group.
Total.	2	35	125	261	225	89	24	5	1	2		1	1	1,186	415	771	1.3	.8	Total.
Holston River:																			Holston River:
Group 12.		1	2											165	162	3	333.3	6.1	12 Group.
Group 13.	3	27	116	86	11	2								320	75	245	4.1	3.1	13 Group.
Group 14.		6	21	77	44	8	1							160	3	157	6.4	6.2	14 Group.
Group 15.	1	23	57	80	40	6								298	91	207	4.8	3.4	15 Group.
Group 16.		8	31	62	27	8								230	94	136	7.4	4.3	16 Group.
Group 17.		1	22	71	82	14	2	1	2		1			197	1	196	5.1	5.1	17 Group.
Group 18.			3	57	92	40	6	1						199		199	5	5	18 Group.
Total.	4	66	252	433	296	78	9	2	2		1			1,569	426	1,143	.9	.6	Total.
Nolichucky River:																			Nolichucky River:
Group 19.			6	30	28	9								73		73	13.7	13.7	19 Group.
Group 20.		1	1	15	64	54	10	4	2	1				152		152	6.6	6.6	20 Group.
Total.		1	7	45	92	63	10	4	2	1				225		225	4.4	4.4	Total.
French Broad River:																			French Broad River:
Group 21.			7	26	52	39	18		1					143		143	7	7	21 Group.
Tennessee River:																			Tennessee River:
Group 22.			2	28	114	52	1	1						199	1	198	5.1	5	22 Group.
Group 23.			5	22	42	31	12	3						115		115	8.7	8.7	23 Group.
Group 24.			1	16	53	74	33	2	1					180		180	5.6	5.6	24 Group.
Group 25.				2	13	11	8	1						35		35	28.6	28.6	25 Group.
Group 26.				4	8	19	14	1						46		46	21.7	21.7	26 Group.
Group 27.				1	15	25	7	2	1					51		51	19.6	19.6	27 Group.
Total.			8	73	245	212	75	10	2					626	1	625	1.6	1.6	Total.
Total in all rivers.														5,386	1,664	3,722			Total in all rivers.

EXPLANATION TO PLATE 28.

NOTE.—The shells shown on plates 28–55, except when stated to the contrary, are random samples of the shells used in the quantitative studies. These are considered fairly representative of the shell population of the various groups and of the corresponding parts of the streams. A comparison of these plates with the location of the groups, as shown on plate 61, will enable one to get a concrete idea of the changes of these shells throughout their range. In general the relatively smooth shells are upon the lower parts of the plates. The scale varies, and is indicated on each plate.

POWELL RIVER.

Group 1. Lot 41. Dryden, Va. This sample is from lot 41 only and does not include lot 45, which inspection shows to be practically of the same character. These are mainly the form *powellensis*. Natural size.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EXPLANATION TO PLATE 29.

POWELL RIVER.

Group 2. Lots 39 and 40. Pennington Gap, Va. The spinose shells are *lyttonensis* Natural size.


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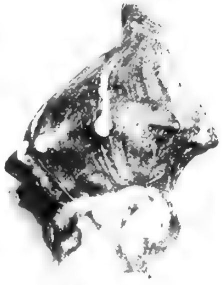
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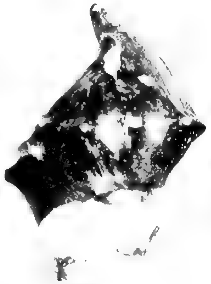
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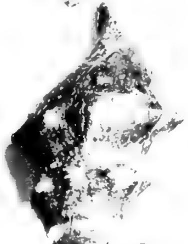
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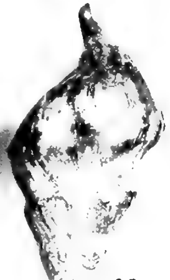
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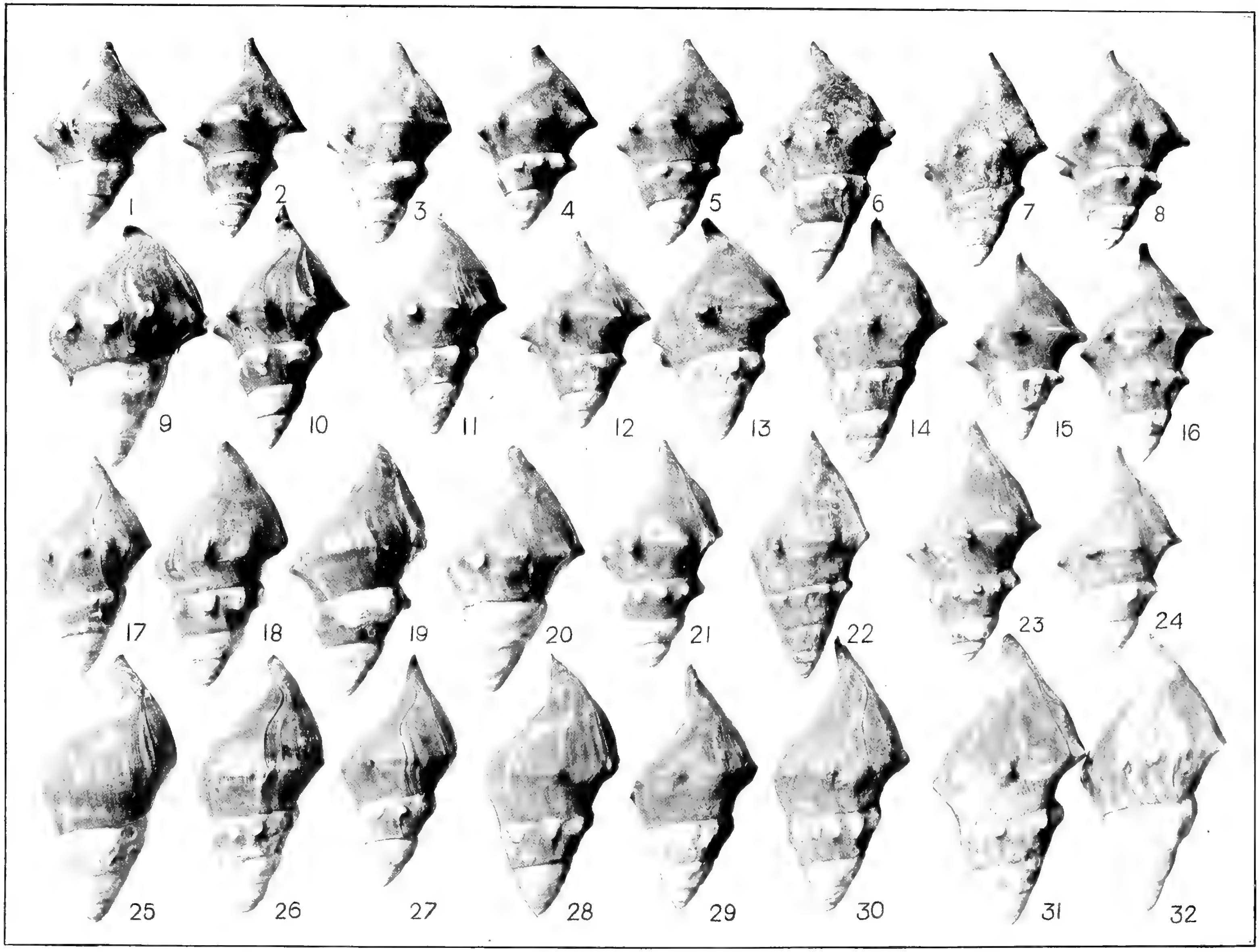
EXPLANATION TO PLATE 30.

POWELL RIVER.

Group 3. Lots 106 and 180. Rose Hill, Va. The form *lyttonensis*. Slightly reduced.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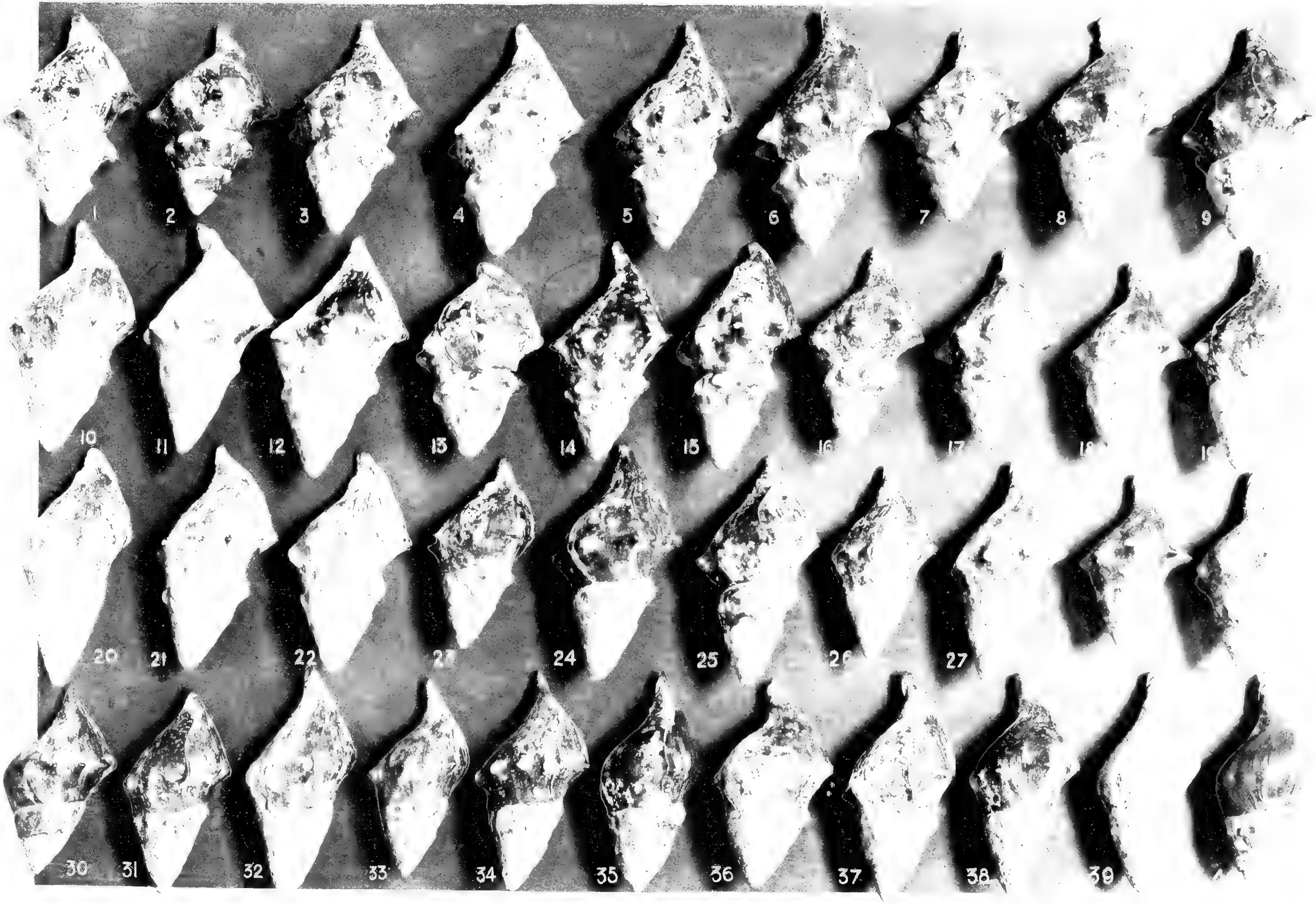
EXPLANATION TO PLATE 31.

POWELL RIVER.

Group 4. Lots 38 and 37. From McHenrys Ford to Powell River station, near Cumberland Gap, Tenn. Natural size.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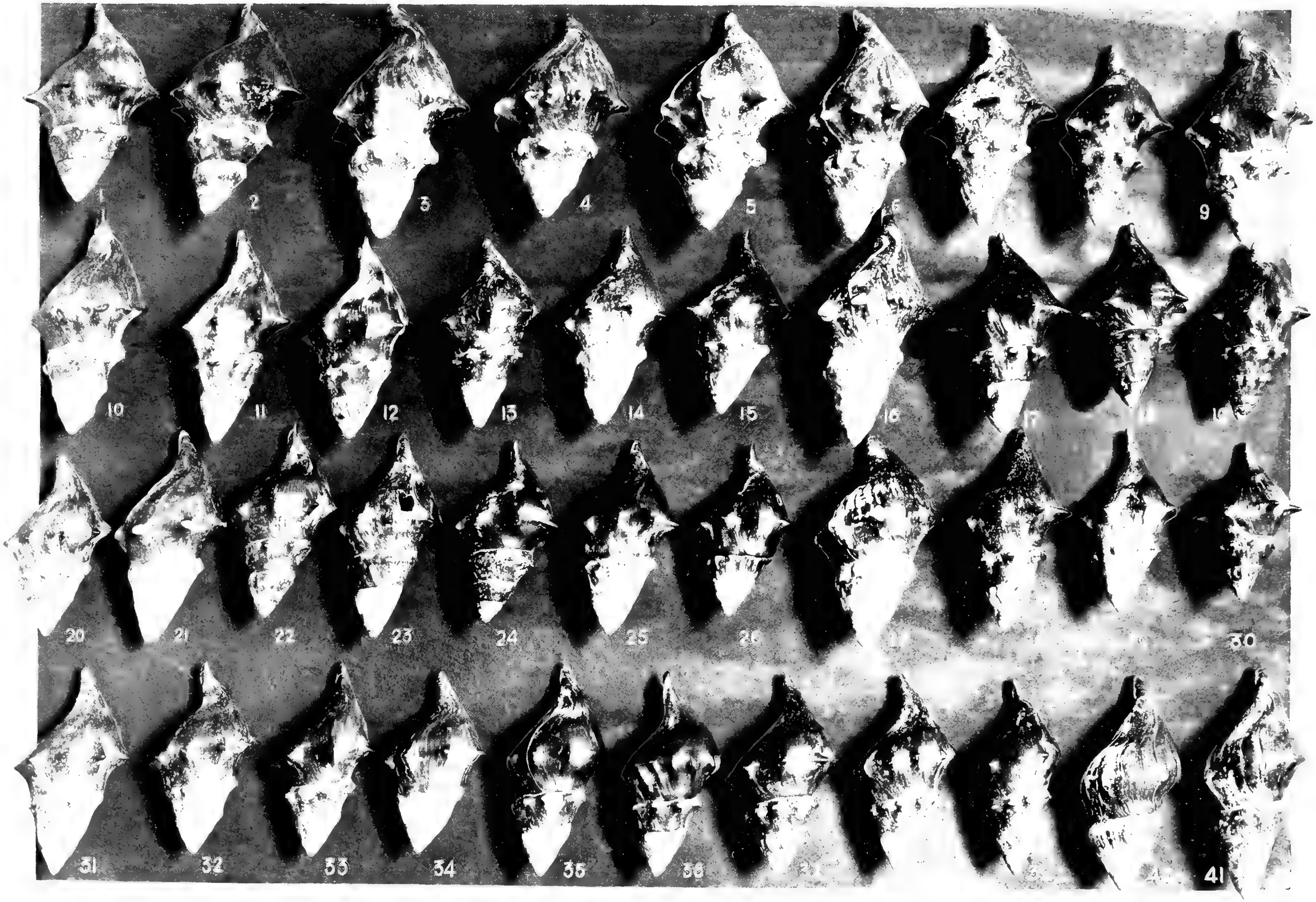
EXPLANATION TO PLATE 32.

POWELL RIVER.

Group 5 (in part). This group is shown by two plates. Lot 29, from Greens Ford, is shown by plate 32, and the other by the following plate. Natural size.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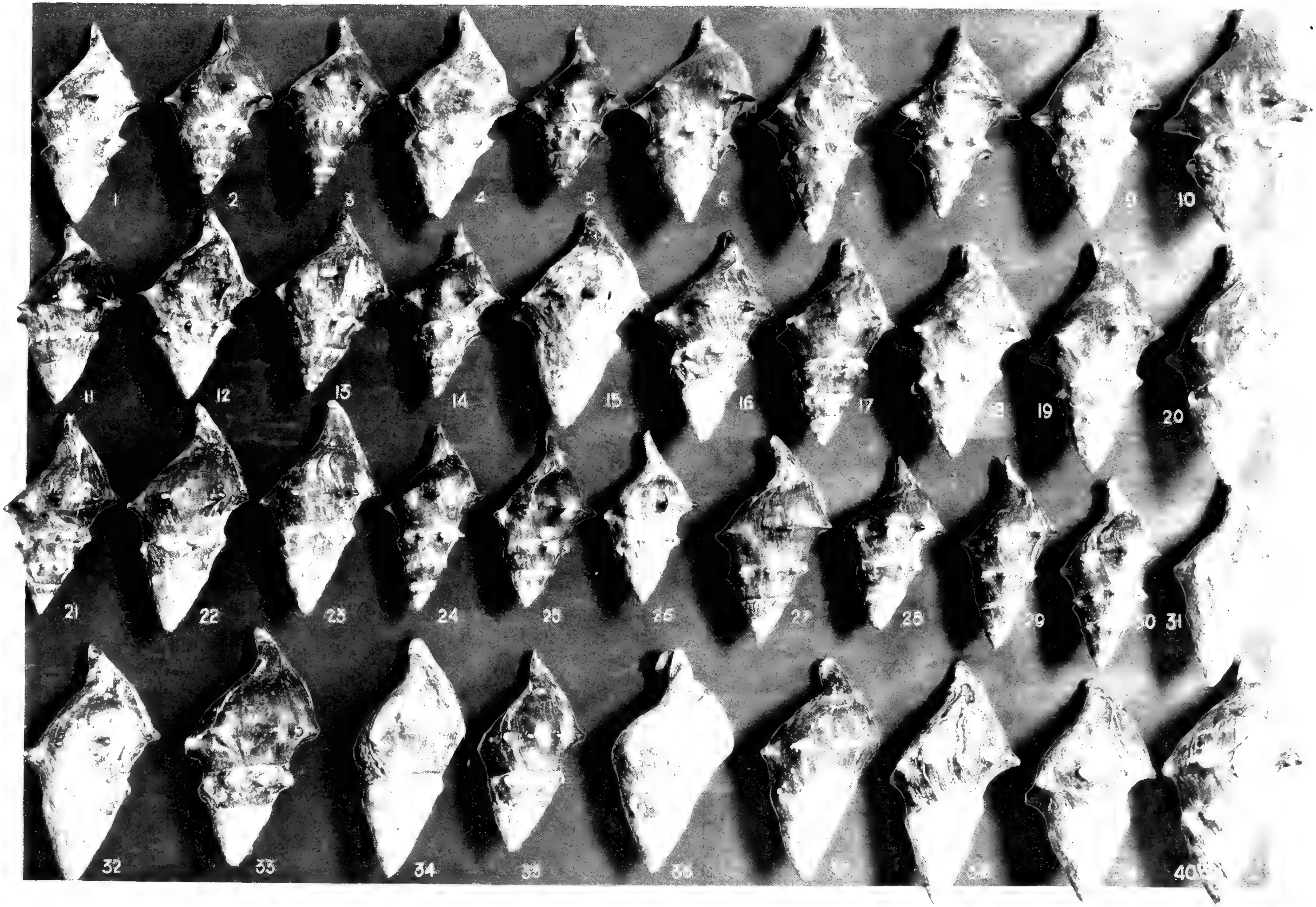
EXPLANATION TO PLATE 33.

POWELL RIVER.

Group 5 (continued). Lots 28, 31, and 30, from near the mouth of the Powell River, Tenn. Natural size.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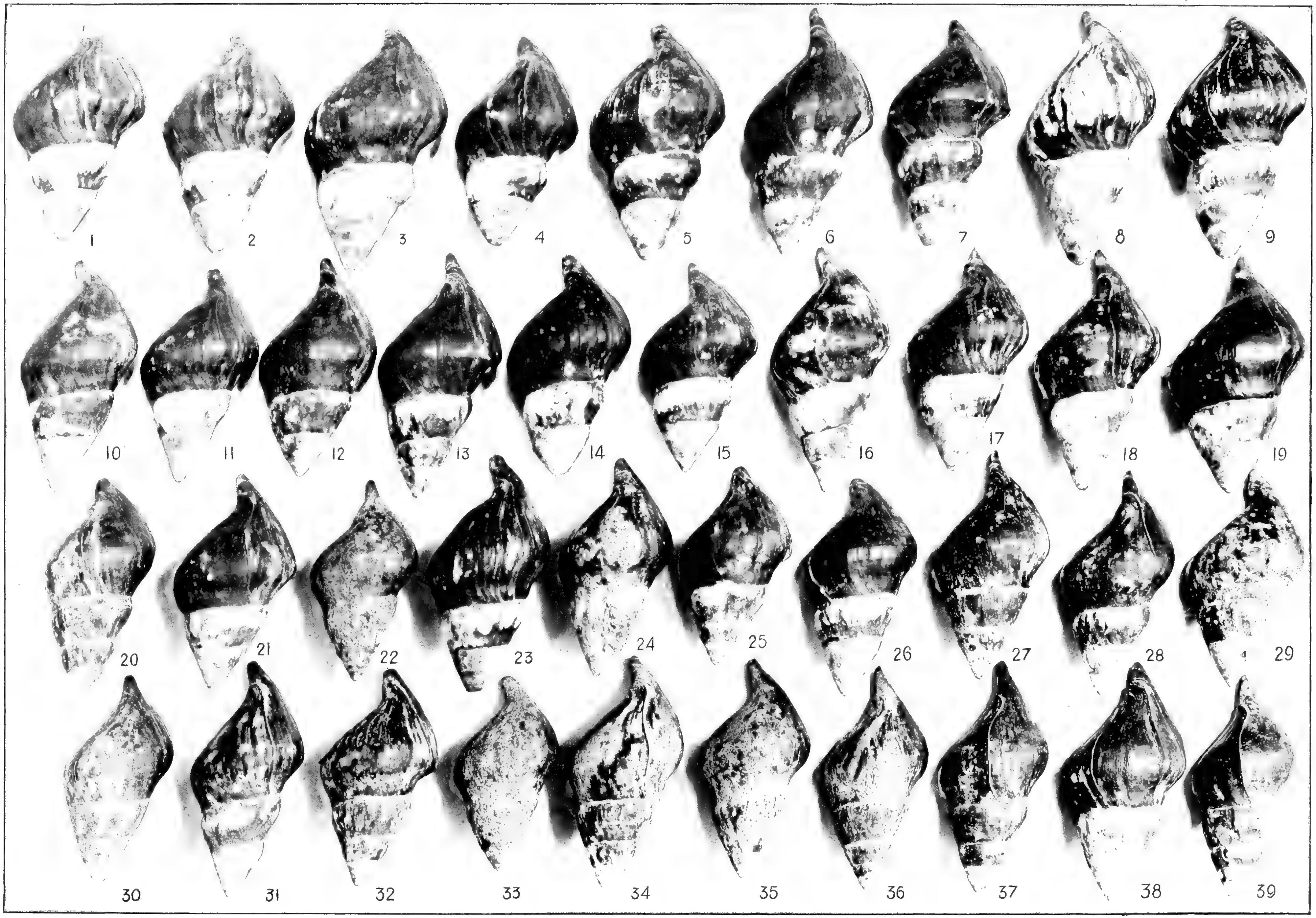
EXPLANATION TO PLATE 34.

CLINCH RIVER.

Group 6. Lot 56, Cleveland, Va. These are headwater shells in the Clinch, and are the form *clinchensis.* Slightly enlarged.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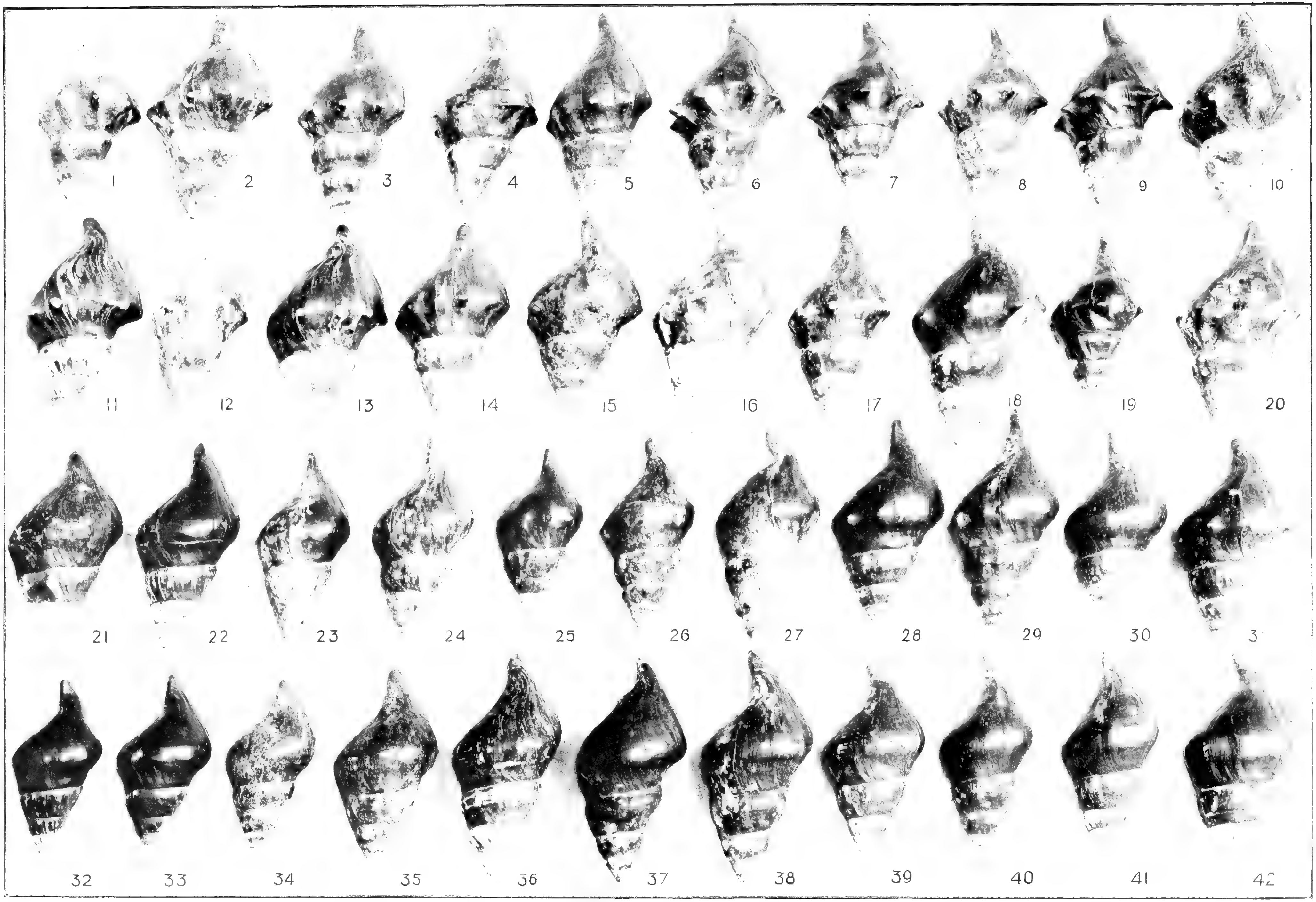
EXPLANATION TO PLATE 35.

CLINCH RIVER.

Group 7. Lots 11, 14, 16, 52, 53, 50, 6, and 51. This plate is a sample from several small lots, extending from St. Paul, Va., to the mouth of Stony Creek. This plate is not strictly representative of the quantitative data of this group, as individuals of lots 6 and 51 (group 8) were in the series from which the sample was taken. They are, however, mainly from St. Paul and are fairly representative. About natural size.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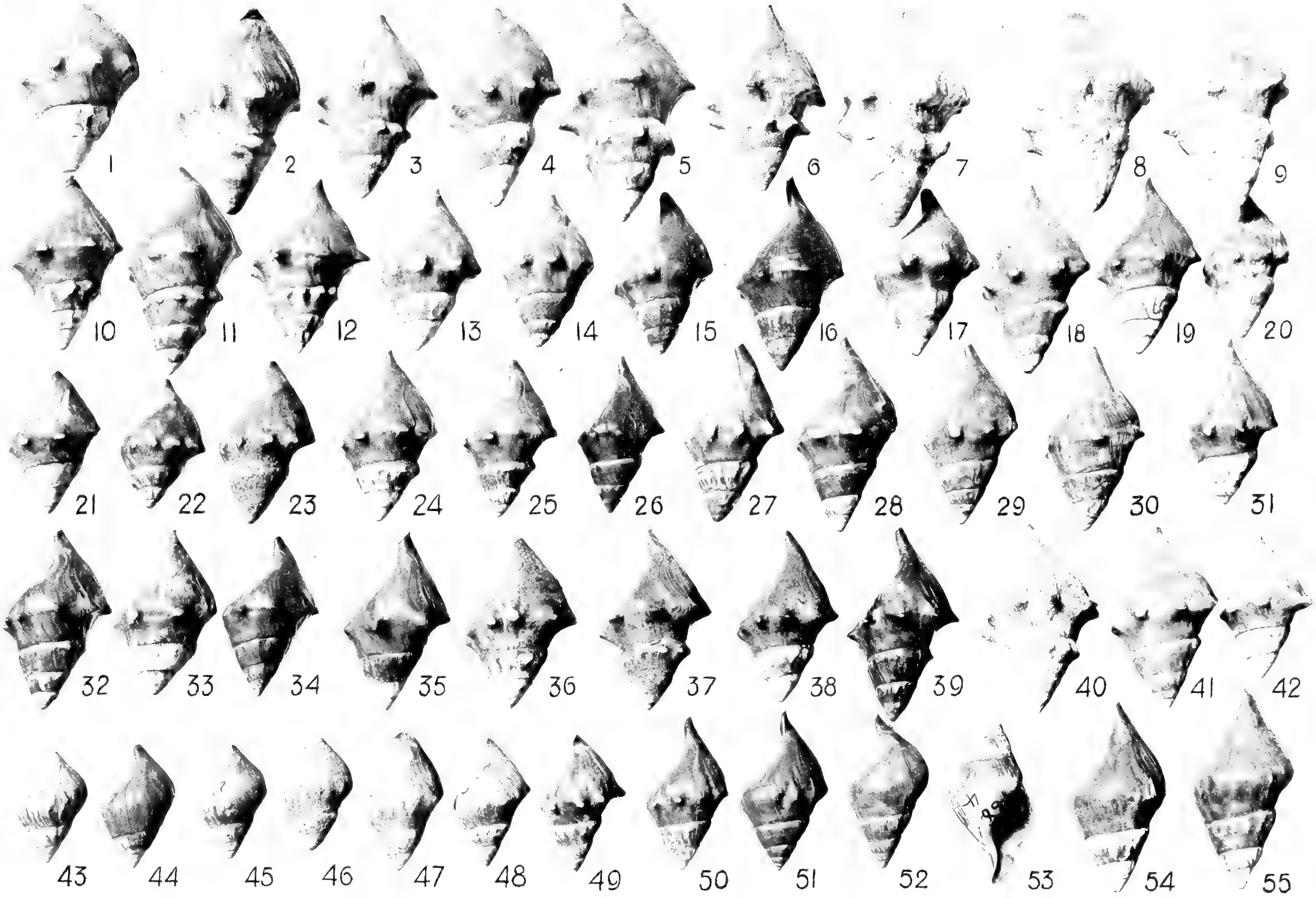
EXPLANATION TO PLATE 36.

CLINCH CIVER.

Group 8. Lots 170, 166, 168, 51, 164, 167, 165, and 169. This series is composed of several small lots, extending from Dungannon to Crafts Ferry, Va. This is the transitional series in the Clinch from the smooth to the spinose shells, and is the form *paulensis*. About natural size.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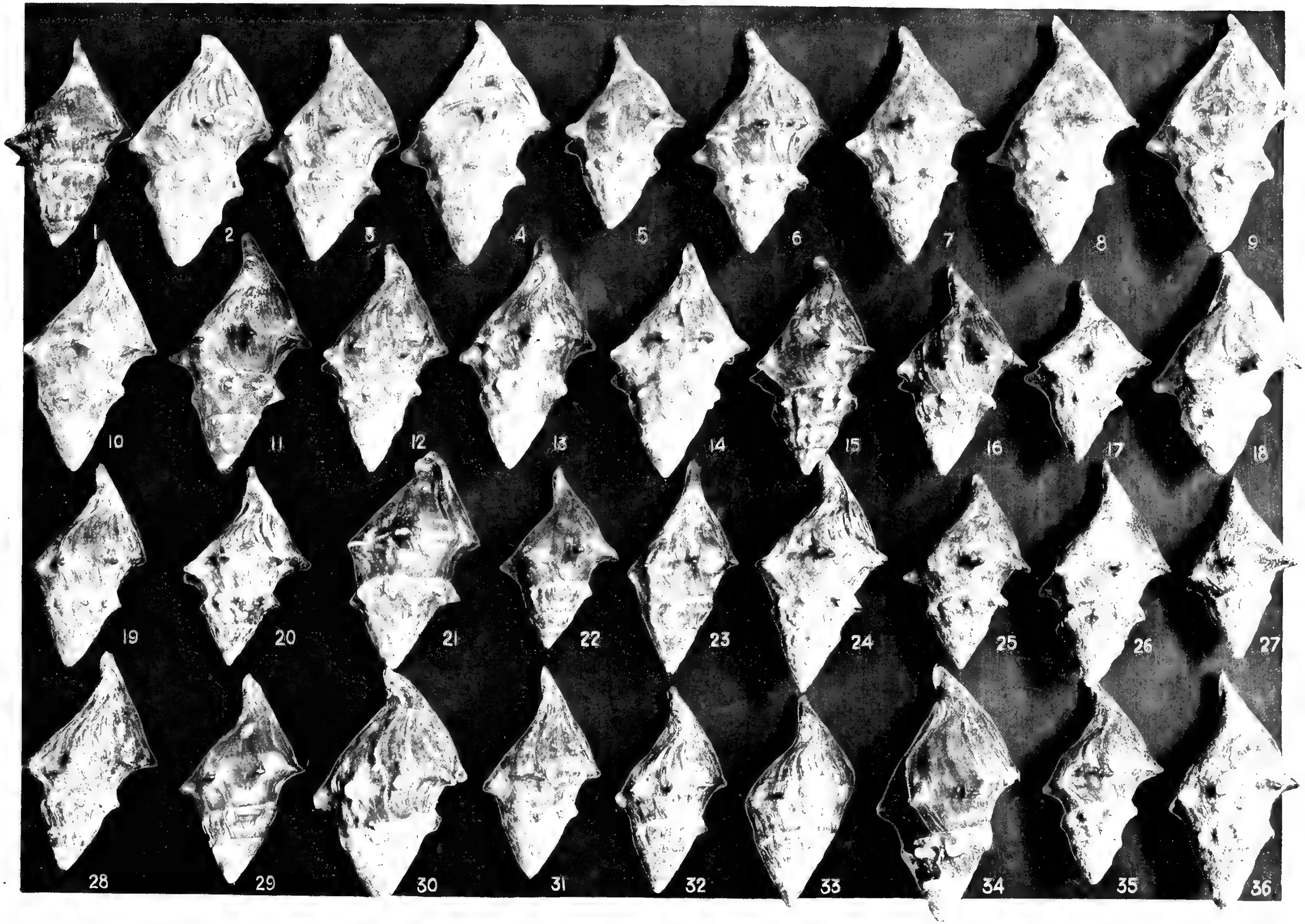
EXPLANATION TO PLATE 37.

CLINCH RIVER.

Group 9. Lot 55. Clinchport, Va. Very spinose shells. Natural size.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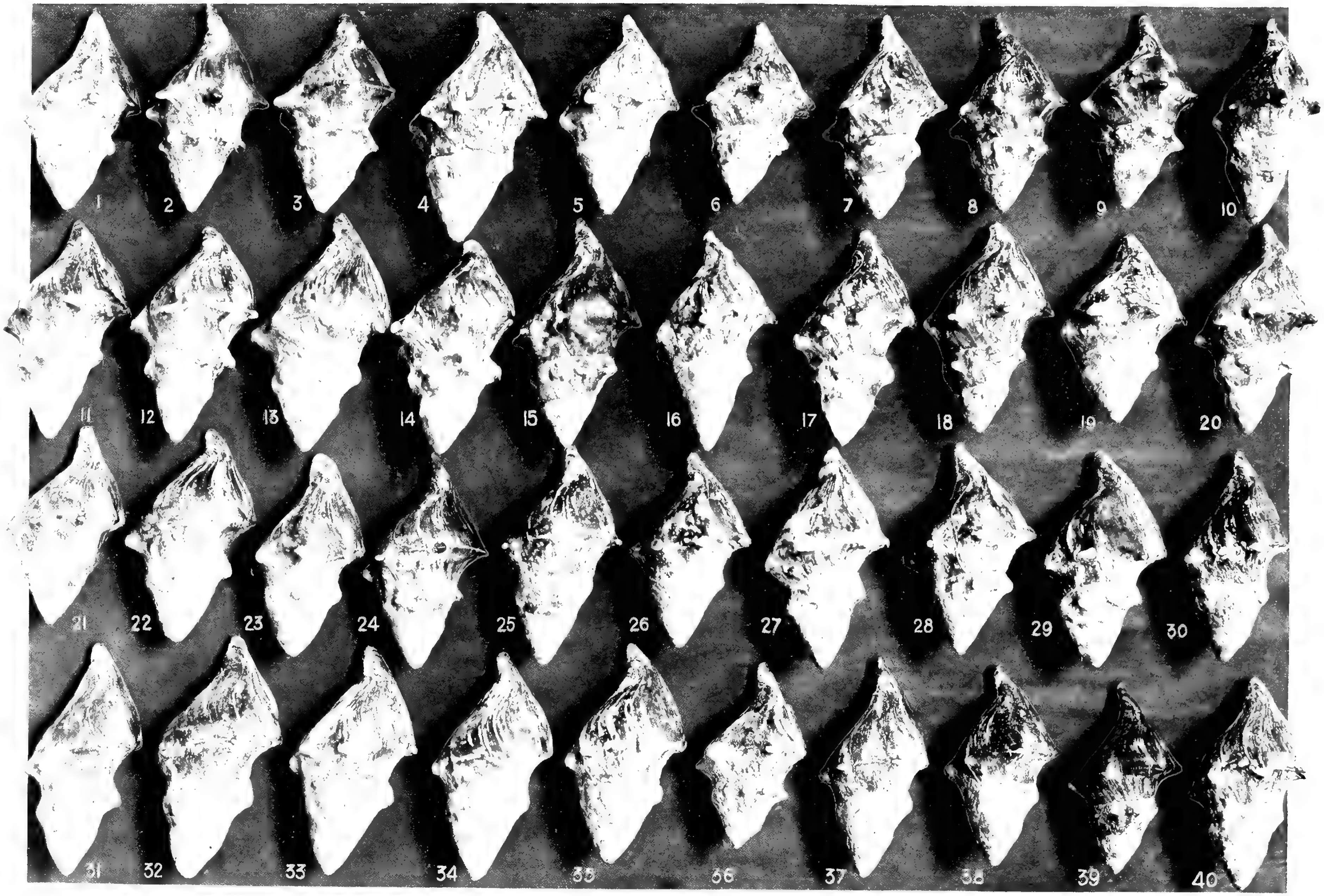
EXPLANATION TO PLATE 38.

CLINCH RIVER.

Group 10. Lot 17, near Kyle Ford, Tenn. This is the form *brevis*. Natural size.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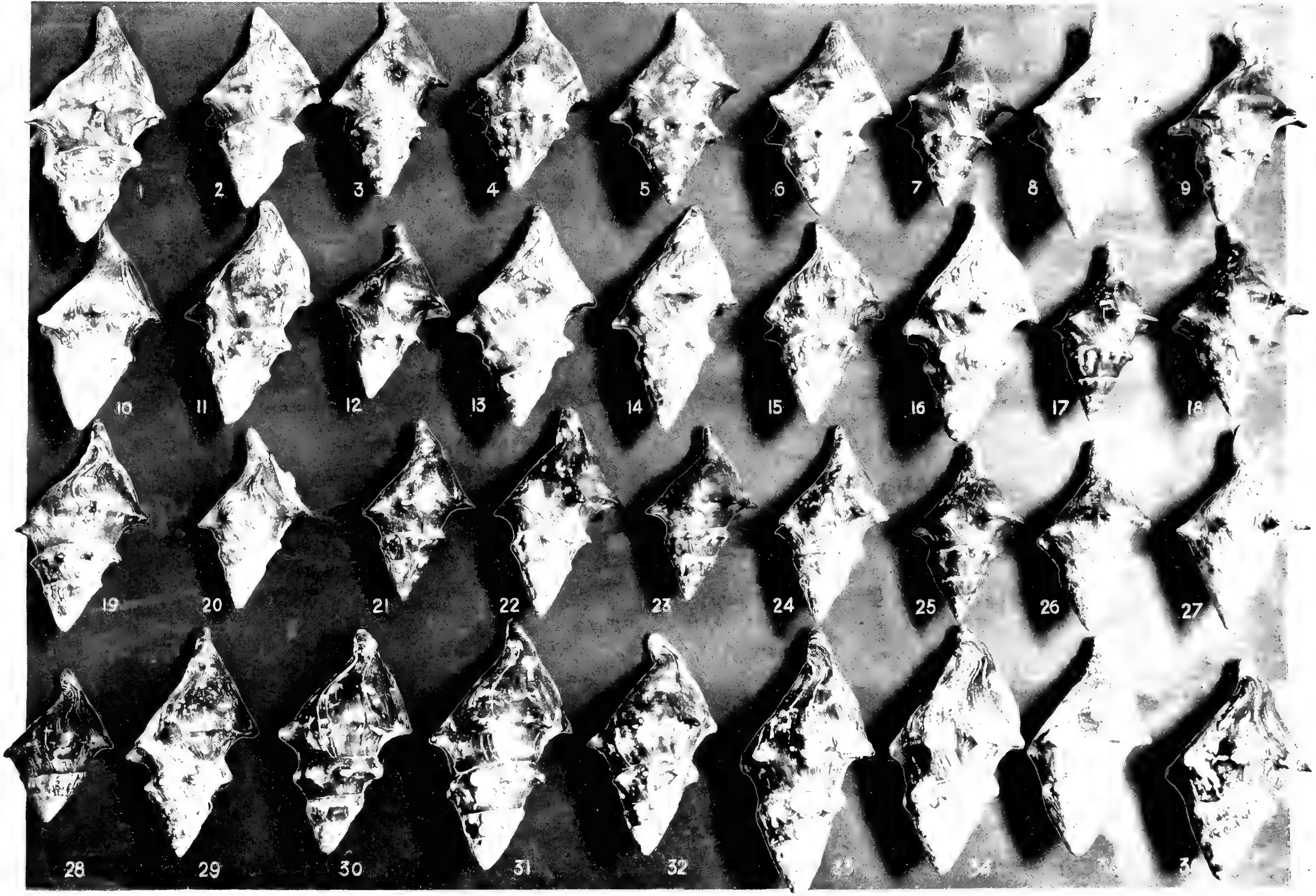
EXPLANATION TO PLATE 39.

CLINCH RIVER.

Group 11. Lots 18, 21, 20, 32, and 34. Small lots from below Kyle Ford to Clinton, Tenn. Natural size.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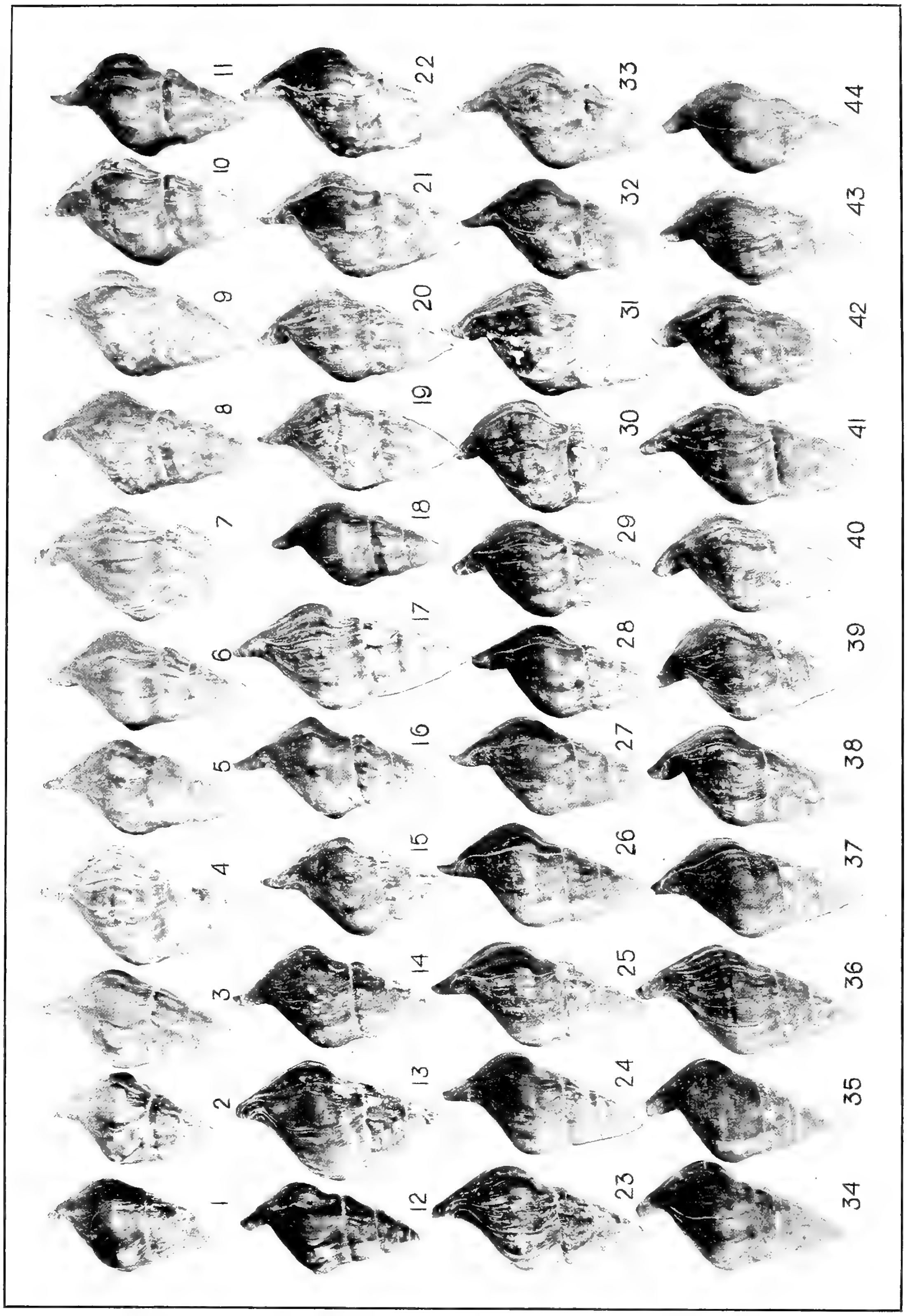
EXPLANATION TO PLATE 40.

HOLSTON RIVER SYSTEM.

Group 12. Lot 79. Saltville, Va. Type locality of the form *fluvialis.* Reduced 1/5.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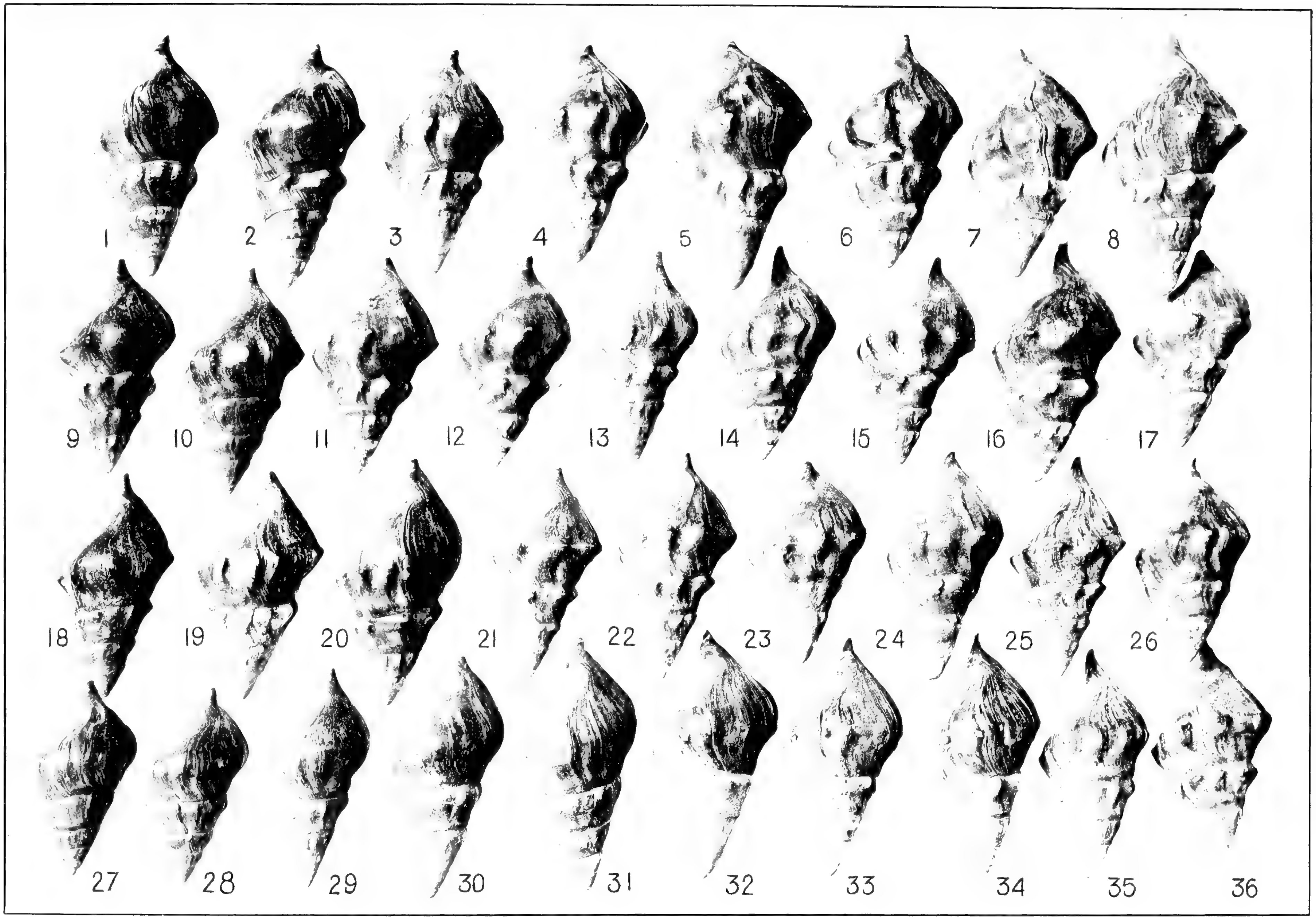
EXPLANATION TO PLATE 41.

HOLSTON RIVER SYSTEM.

Group 13. Lot 94. Bluff City, Tenn. This is the form *verrucosa*. Enlarged about 1/4.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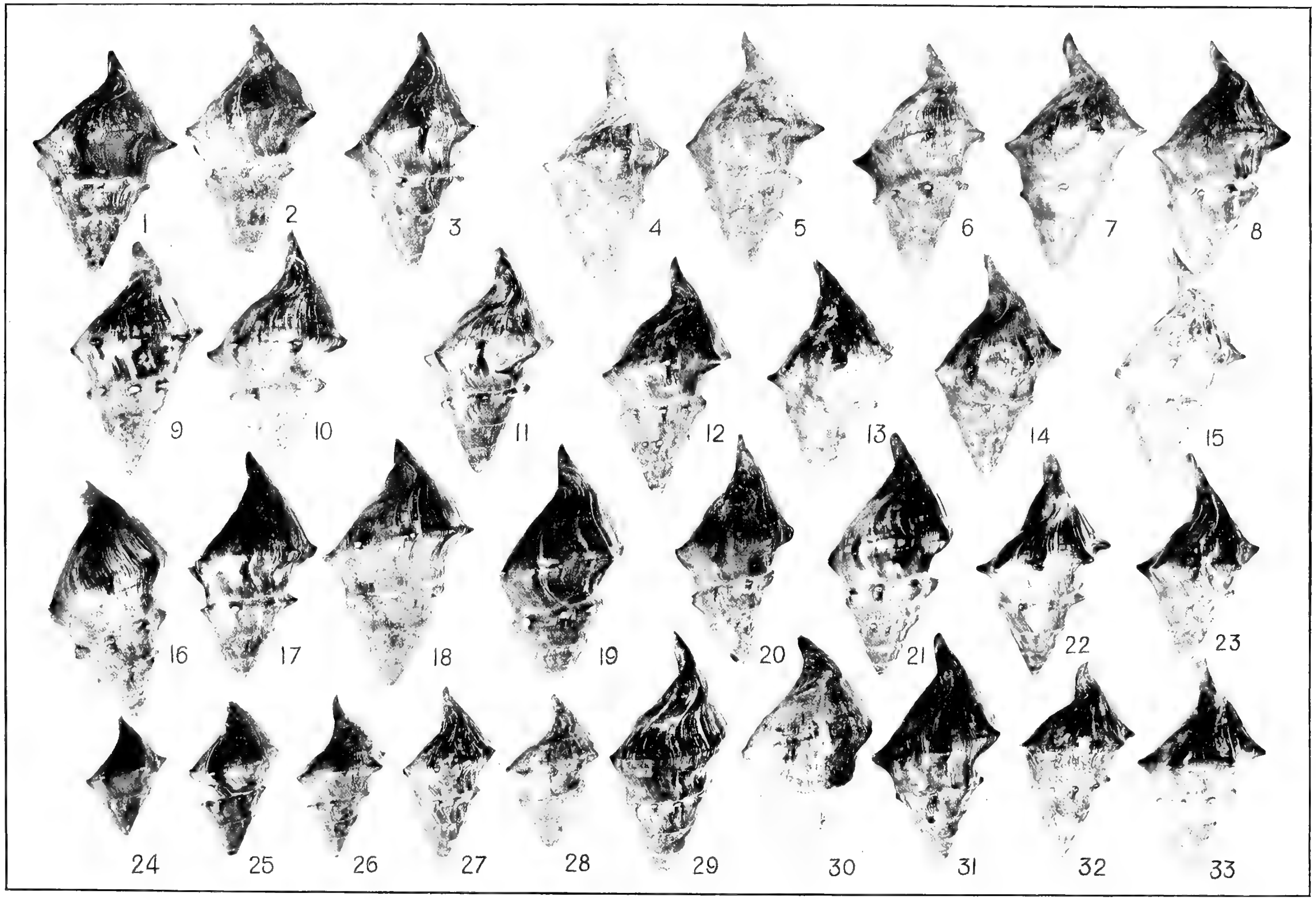
EXPLANATION TO PLATE 42.

HOLSTON RIVER SYSTEM.

Group 14. Lots 175 and 178. Near the confluence of the North and South Forks of Holston, near Rotherwood. Reduced 1/4.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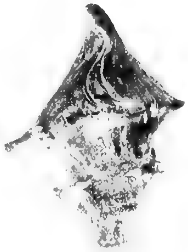
EXPLANATION TO PLATE 43.

HOLSTON RIVER.

Group 15. Lots 97 and 98. Chissolms Ford, Tenn. The mixed community of smooth, spinose, and shells of inverse development. Reduced about 1/4.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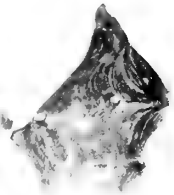
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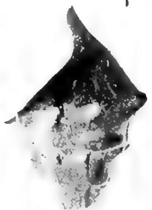
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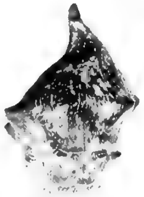
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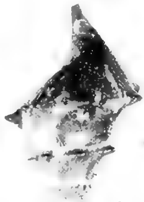
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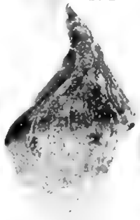
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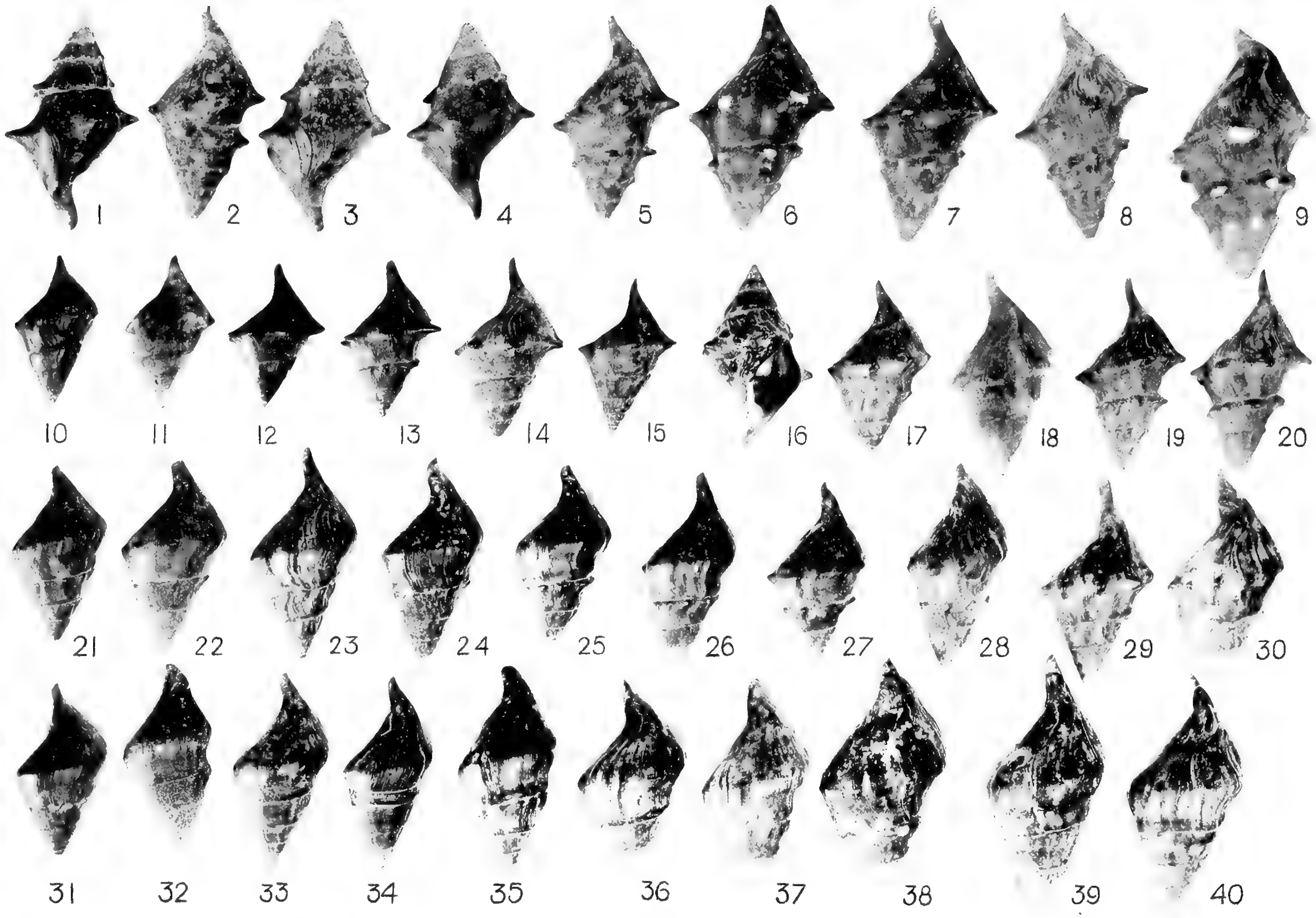
EXPLANATION TO PLATE 44.

HOLSTON RIVER.

Group 16. Lots 87 and 88. Rogersville, Tenn. Shells similar to those of group 15. Reduced 1/5.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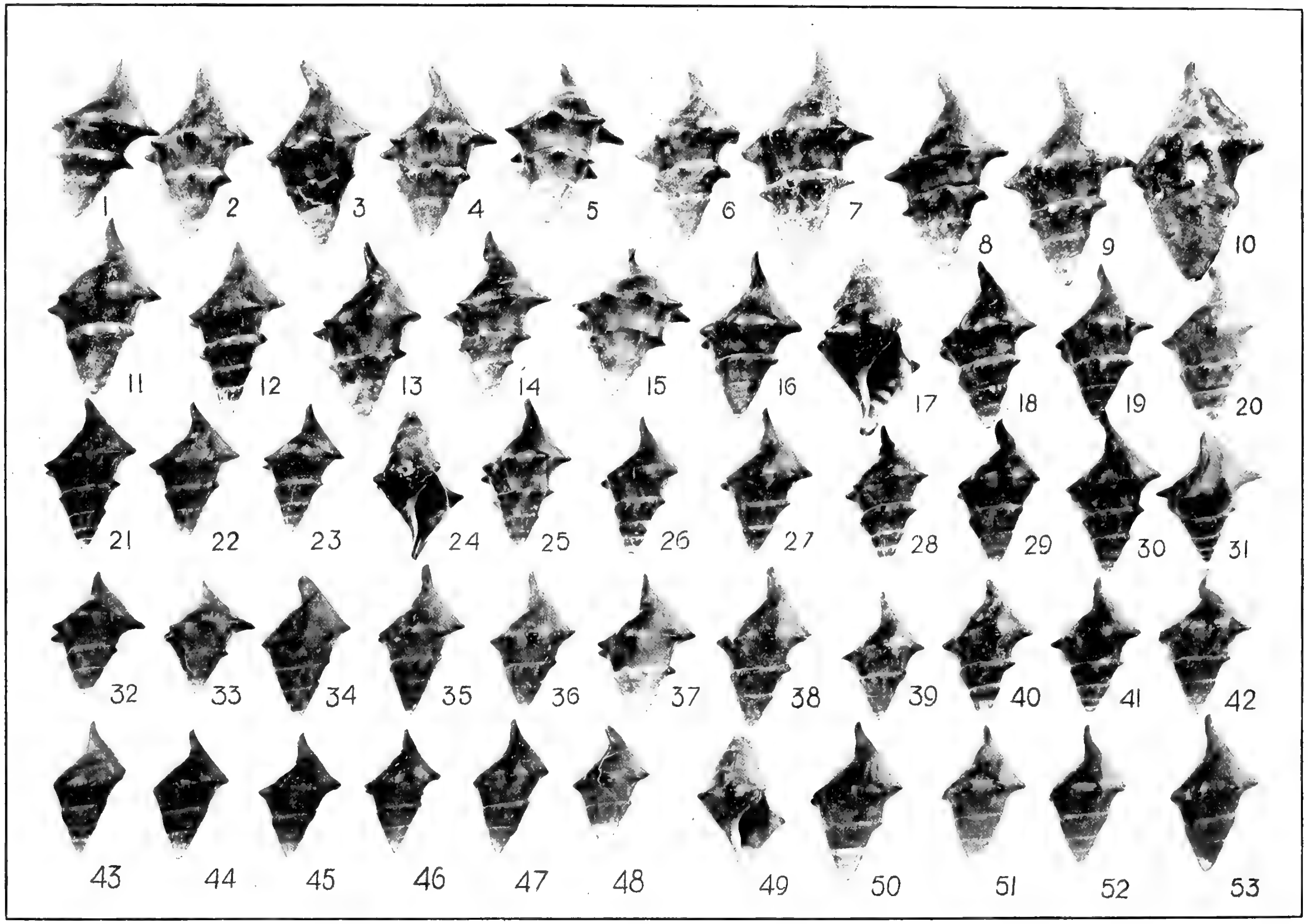
EXPLANATION TO PLATE 45.

HOLSTON RIVER.

Group 17. Lot 90. Cobb Ford, Tenn. Upper rows reduced 1/3, lower rows 1/4.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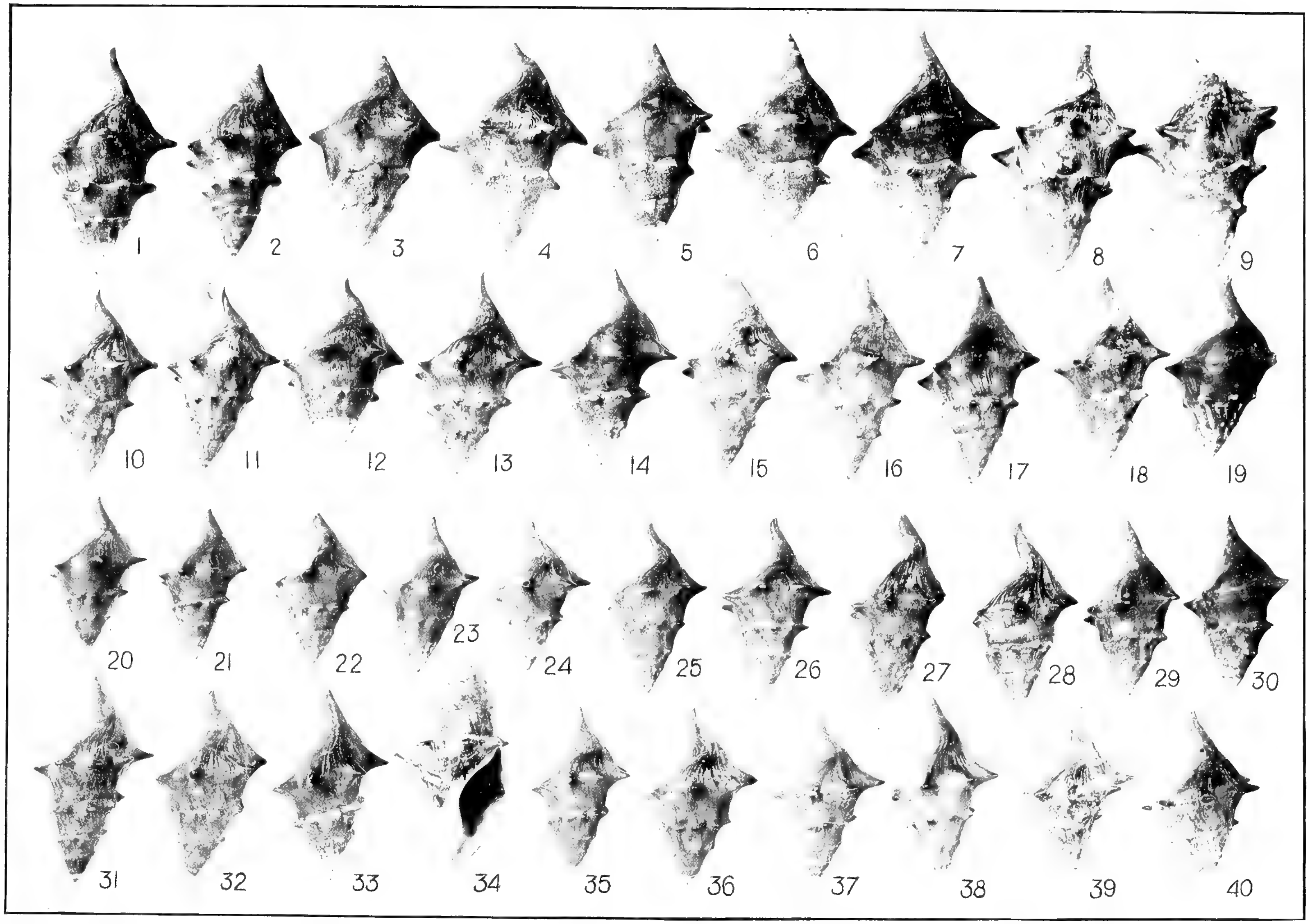
EXPLANATION TO PLATE 46.

HOLSTON RIVER.

Group 18. Lot 96. Near Morristown, Tenn. These are the form *spinosa.* Upper rows reduced 1/3, lower rows 1/7.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EXPLANATION TO PLATE 47.

NOLICHUCKY RIVER.

Group 19. Lots 119 and 118. Conkling and Broylesville, Tenn. From the headwaters of the Nolichucky, the form *unakensis*. About natural size.


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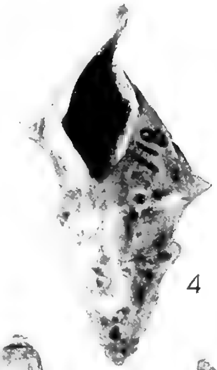
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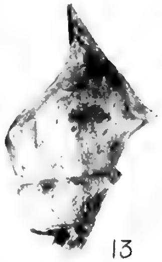
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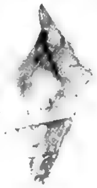
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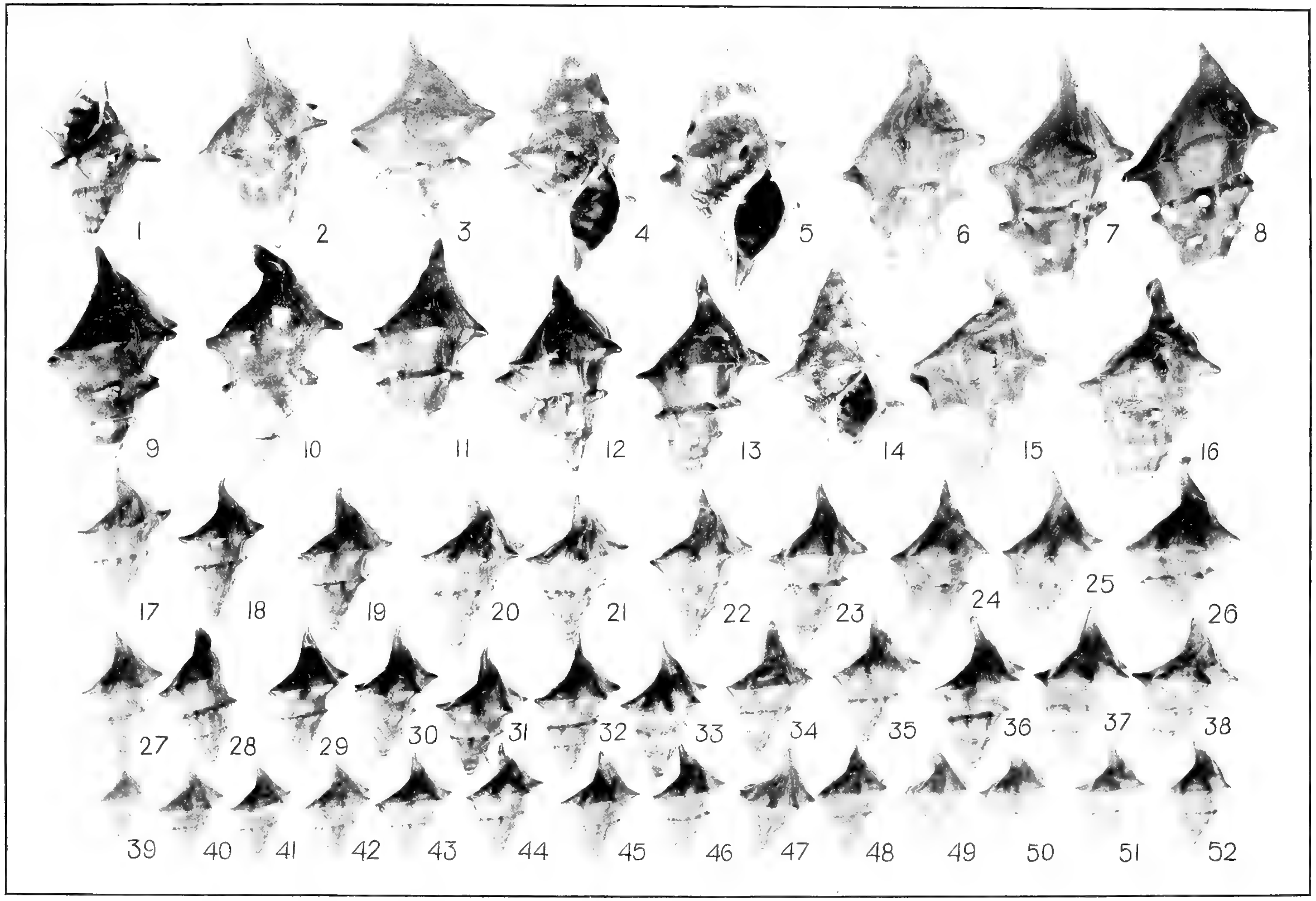
EXPLANATION TO PLATE 48.

NOLICHUCKY RIVER.

Group 20. Lot 104 and 83. White Pine, Tenn. This is the form *nolichuckyensis.* Reduced 1/3.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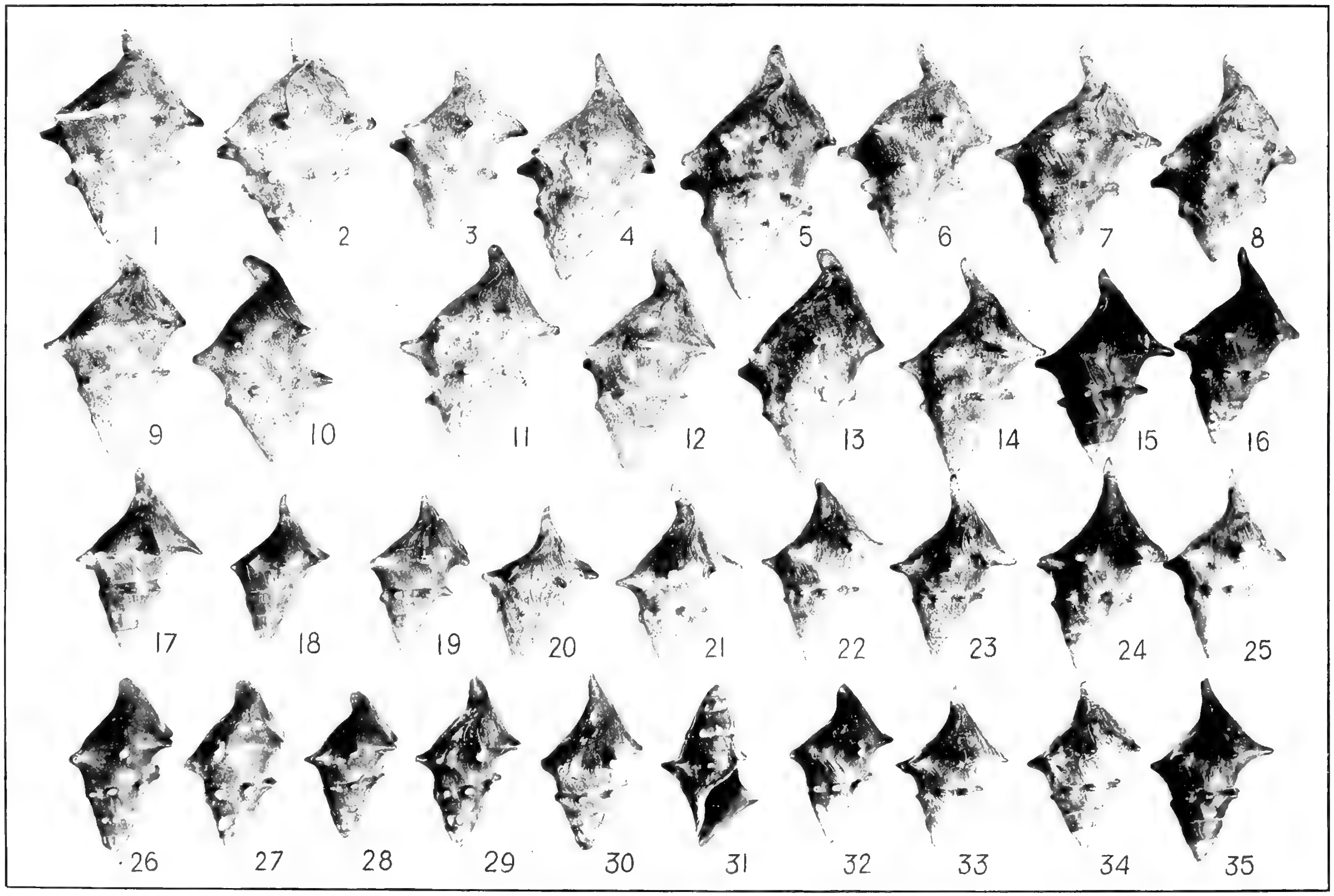
EXPLANATION TO PLATE 49.

FRENCH BROAD RIVER.

Group 21. Lot 136 from Byrnes Shoals, and lot 137 from Hanging Rock Shoals, Tenn. Reduced 1/4.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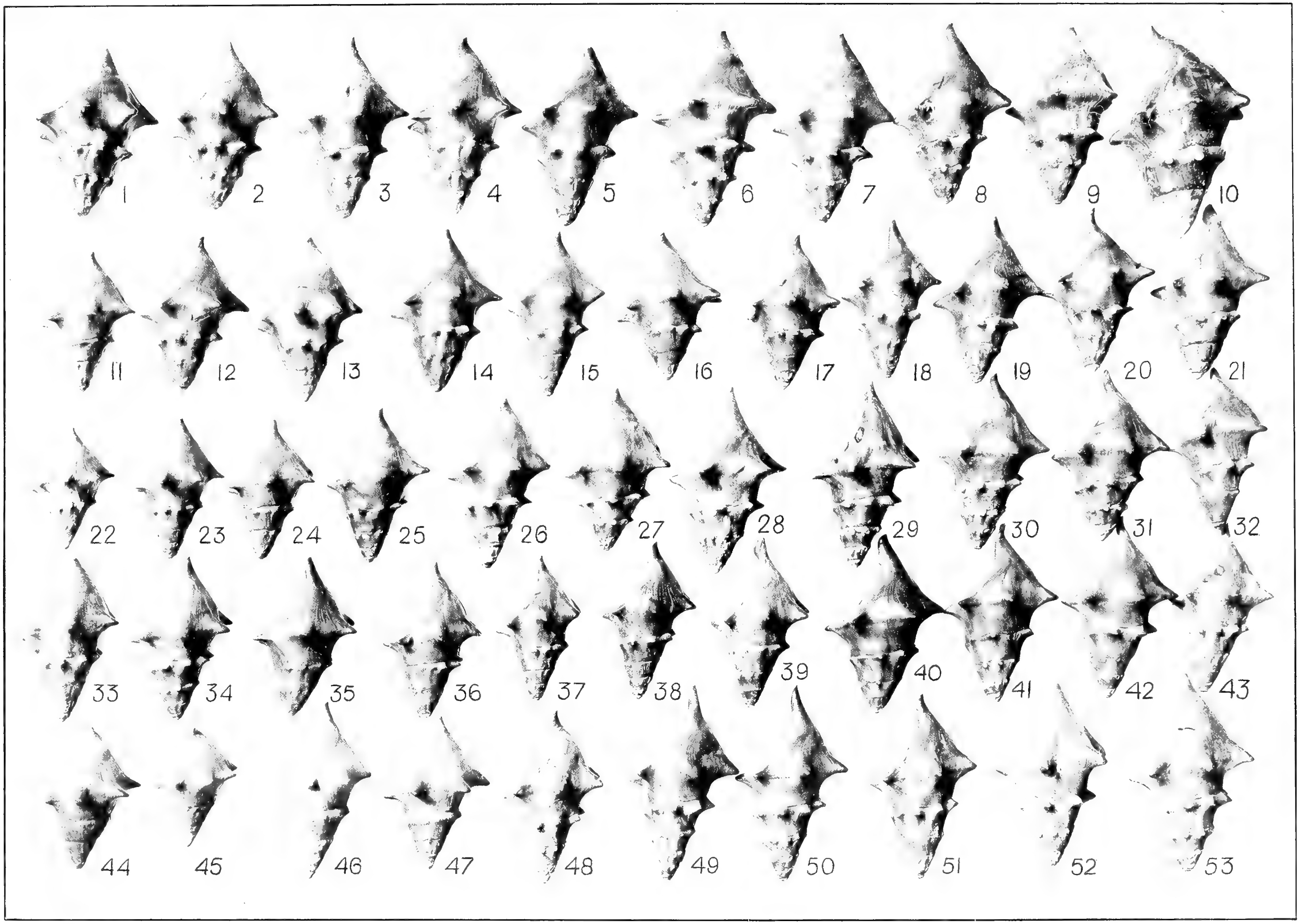
EXPLANATION TO PLATE 50.

TENNESSEE RIVER.

Group 22. Lot 100. Lyon Shoals, below Knoxville, Tenn. These are the immature of the form *turrita*. Natural size.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EXPLANATION TO PLATE 51.

TENNESSEE RIVER.

Group 23. Lot 105. Little River Shoals, below Knoxville, Tenn. A series of *turrita* and *loudonensis.* Slightly reduced.


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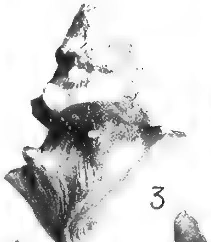
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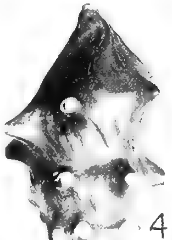
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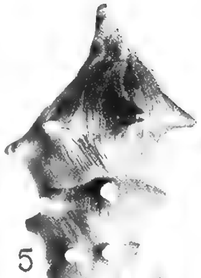
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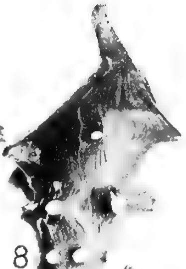
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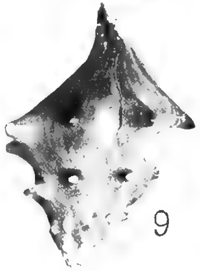
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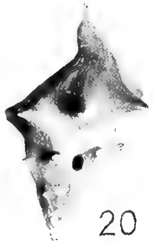
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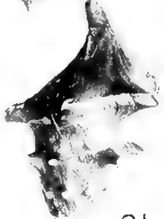
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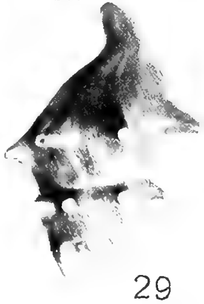
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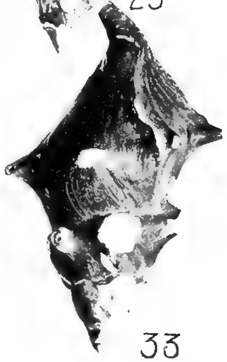
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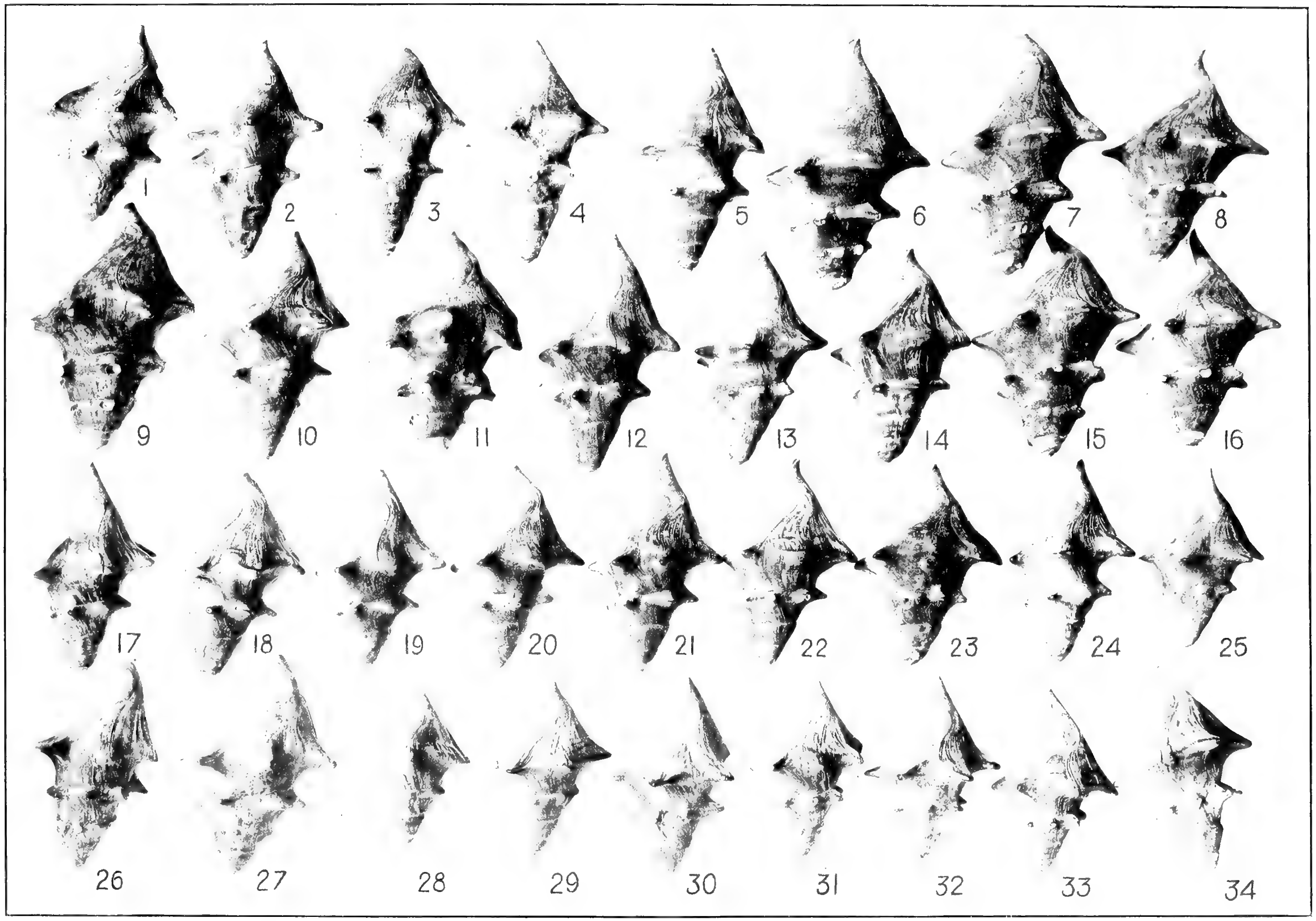
EXPLANATION TO PLATE 52.

TENNESSEE RIVER.

Group 24. Lot 152. Loudon, Tenn. A series largely of *loudonensis*. Slightly reduced.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EXPLANATION TO PLATE 53.

TENNESSEE RIVER.

Group 25. Lot 155. Rockwood Landing, Tenn. Shells from an Indian shell heap. Upper row reduced 1/4, lower row reduced 1/5.


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EXPLANATION TO PLATE 54.

TENNESSEE RIVER.

Group 26 (in part). Lot 151. Hiwassee Island, Tenn. This plate of shells is composed solely of individuals from lot 151 and is not a sample of the group as a whole. They show the great degree of spinosity developed in *loudonensis*. Natural size.


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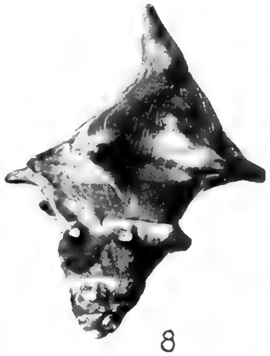
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EXPLANATION TO PLATE 55.

TENNESSEE RIVER.

Group 27 (in part). Lots 143, 146, 187, and 148, extending from Bridgeport to near Dodsonville, Ala. These are *turrita*.

Figs. 1–4, 9–12, 17–20, from lot 143.
Figs. 5–6, from lot 146.
Figs. 7–8, 13–14, from lot 187.
Figs. 15–16, 21–24, from lot 148.

Upper row reduced 1/4, lower row reduced 1/5.


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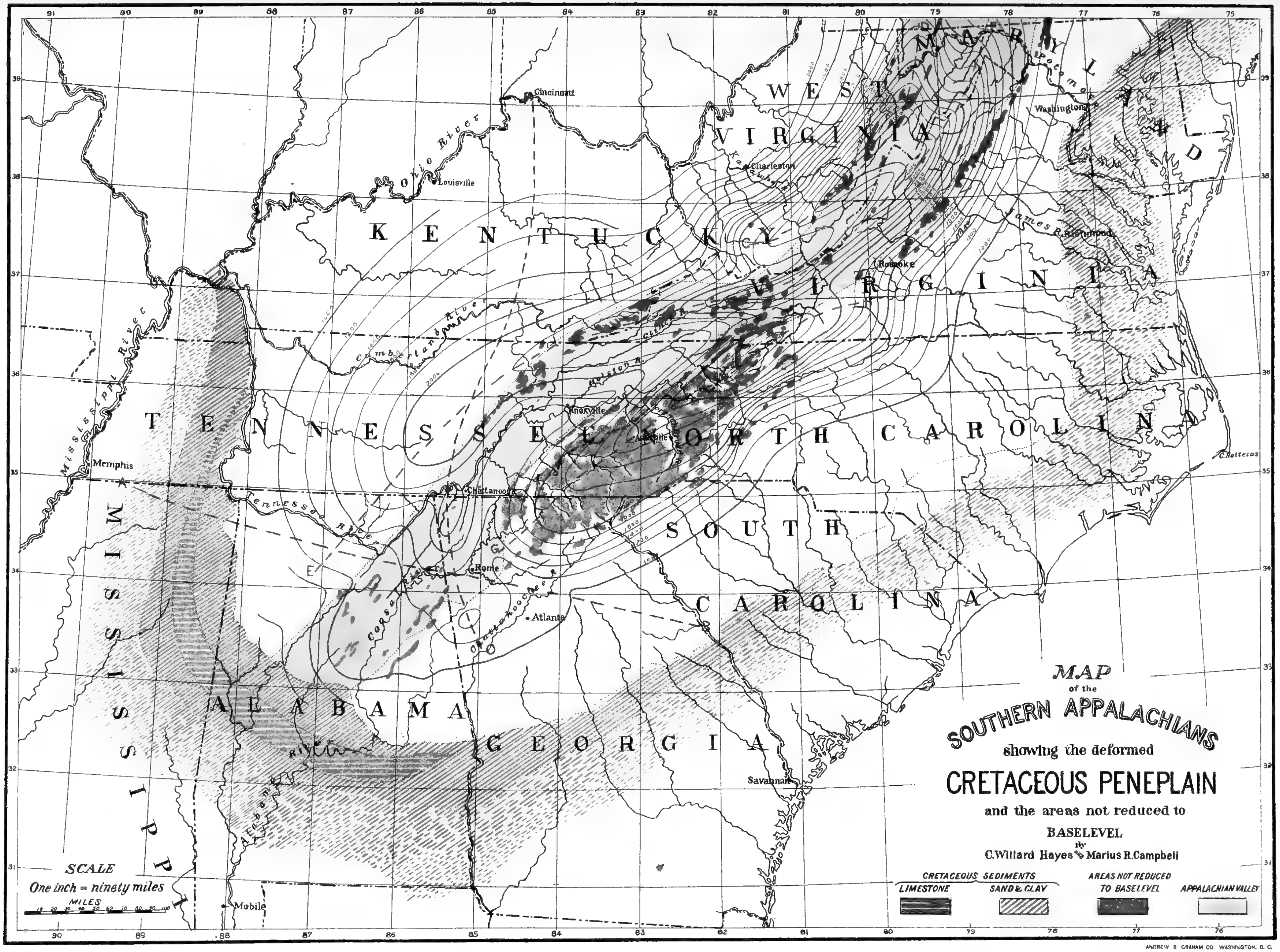
EXPLANATION TO PLATE 56.

Map of the Cretaceous Peneplain in the Southern Appalachian Mountain region. After Hayes and Campbell.



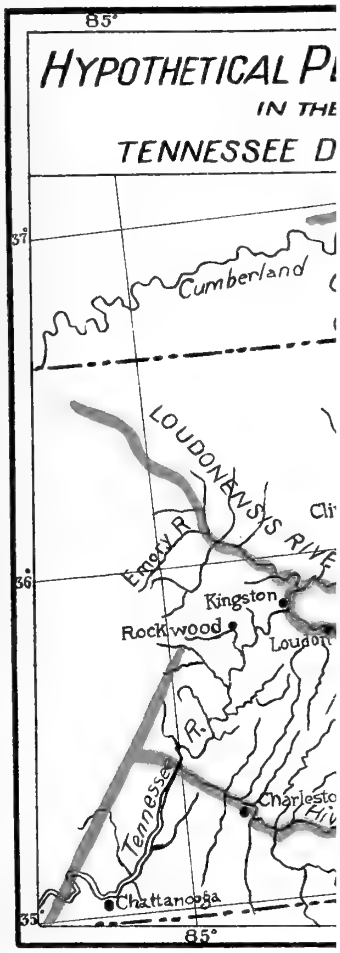
MAP of the SOUTHERN APPALACHIANS showing the deformed CRETACEOUS PENEPLAIN and the areas not reduced to BASELEVEL by C. Willard Hayes and Marius R. Campbell

ANDREW B. GRAHAM CO. WASHINGTON, D. C.

EXPLANATION TO PLATE 57.

Hypothetical drainage of the Tennessee system above Chattanooga.

A. Permian drainage.	C. Tertiary drainage.
B. Cretaceous drainage.	D. Present drainage.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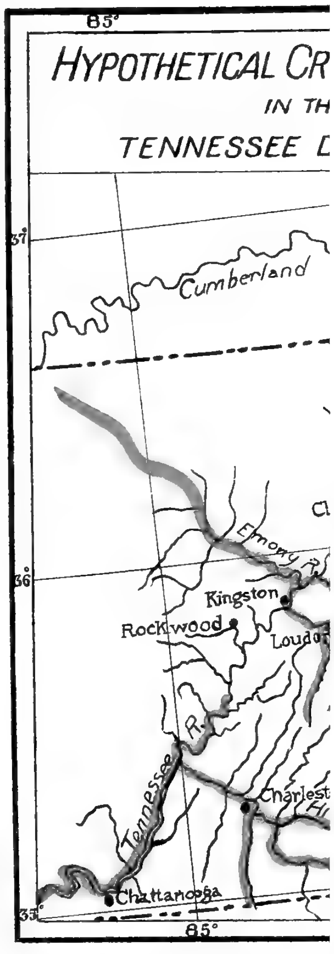
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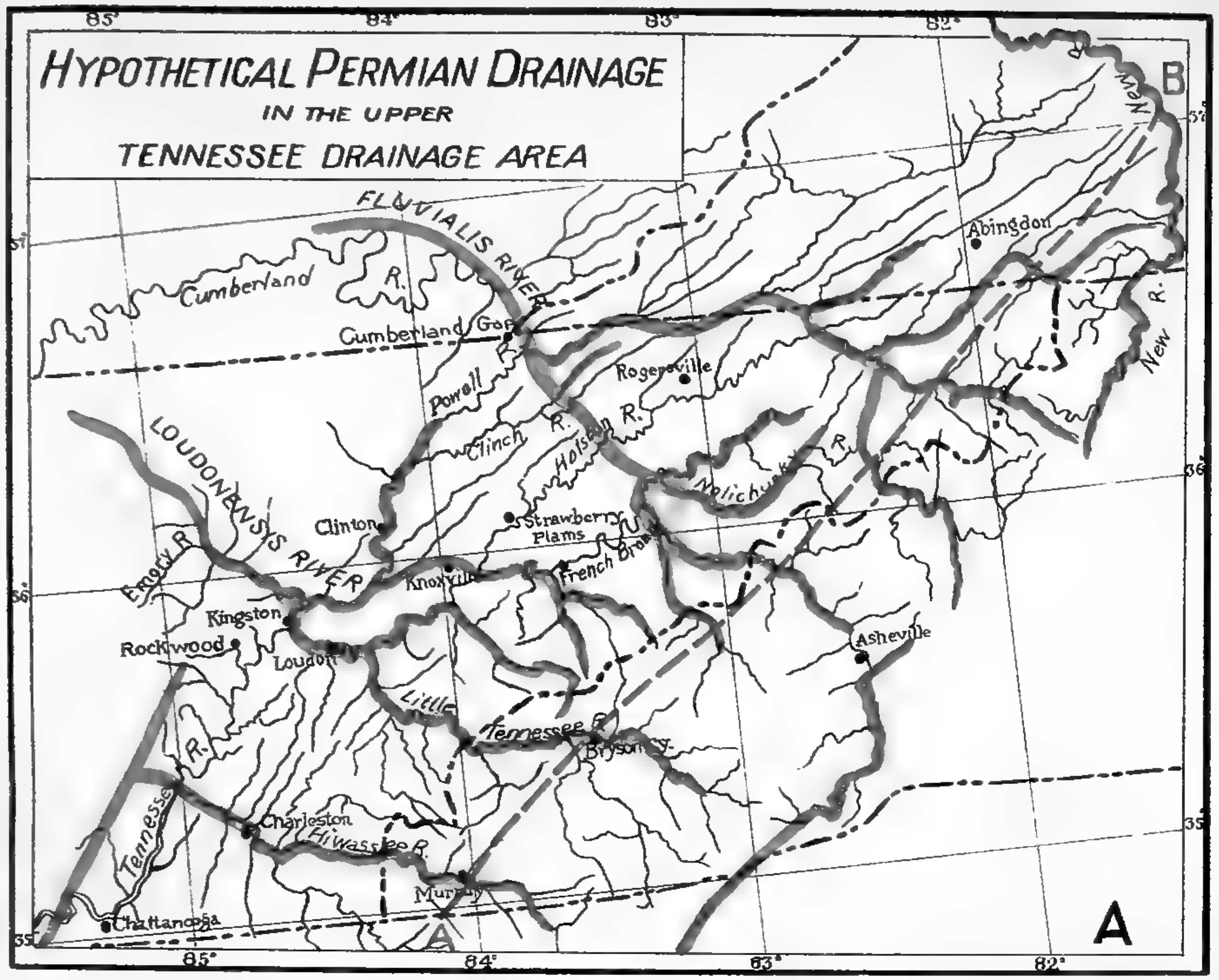
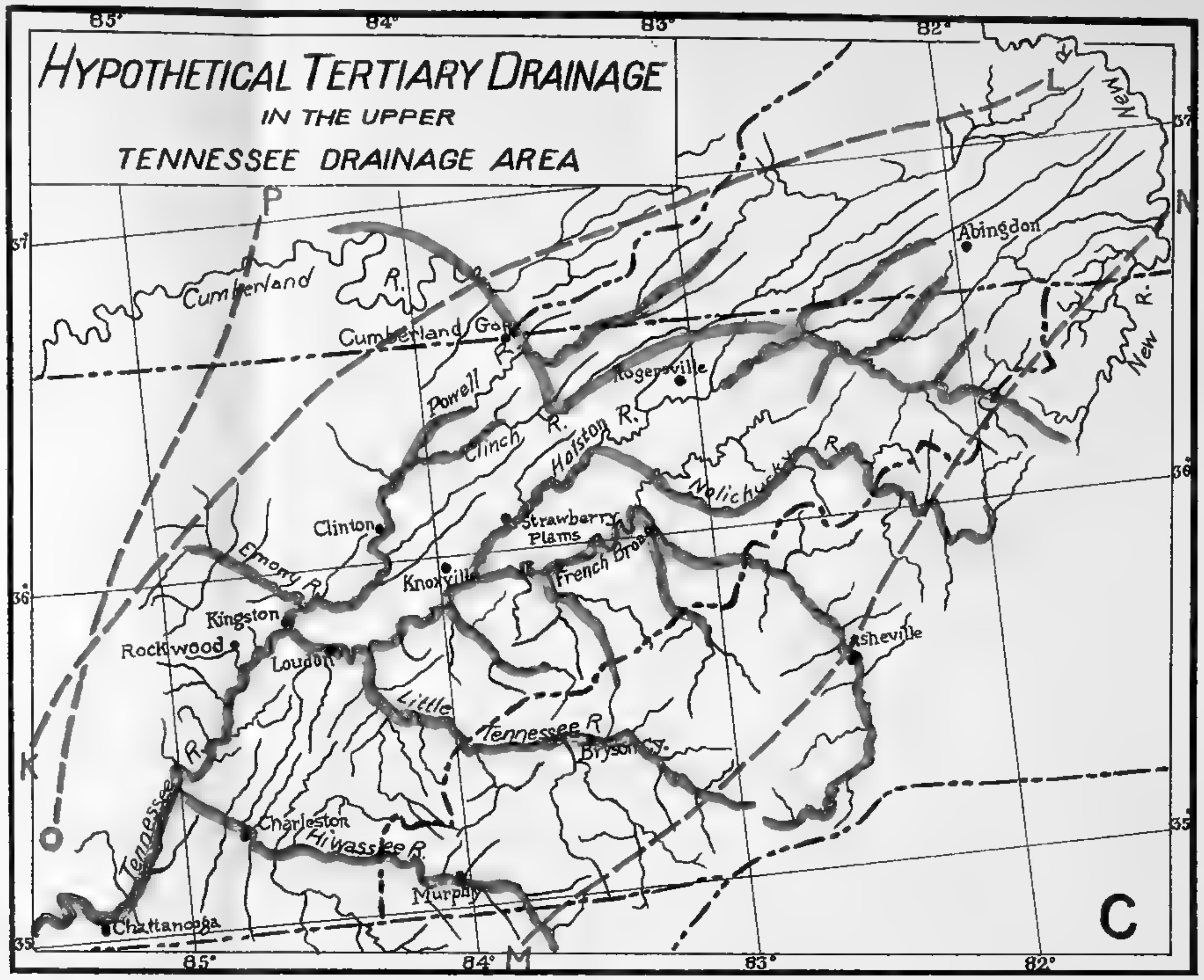
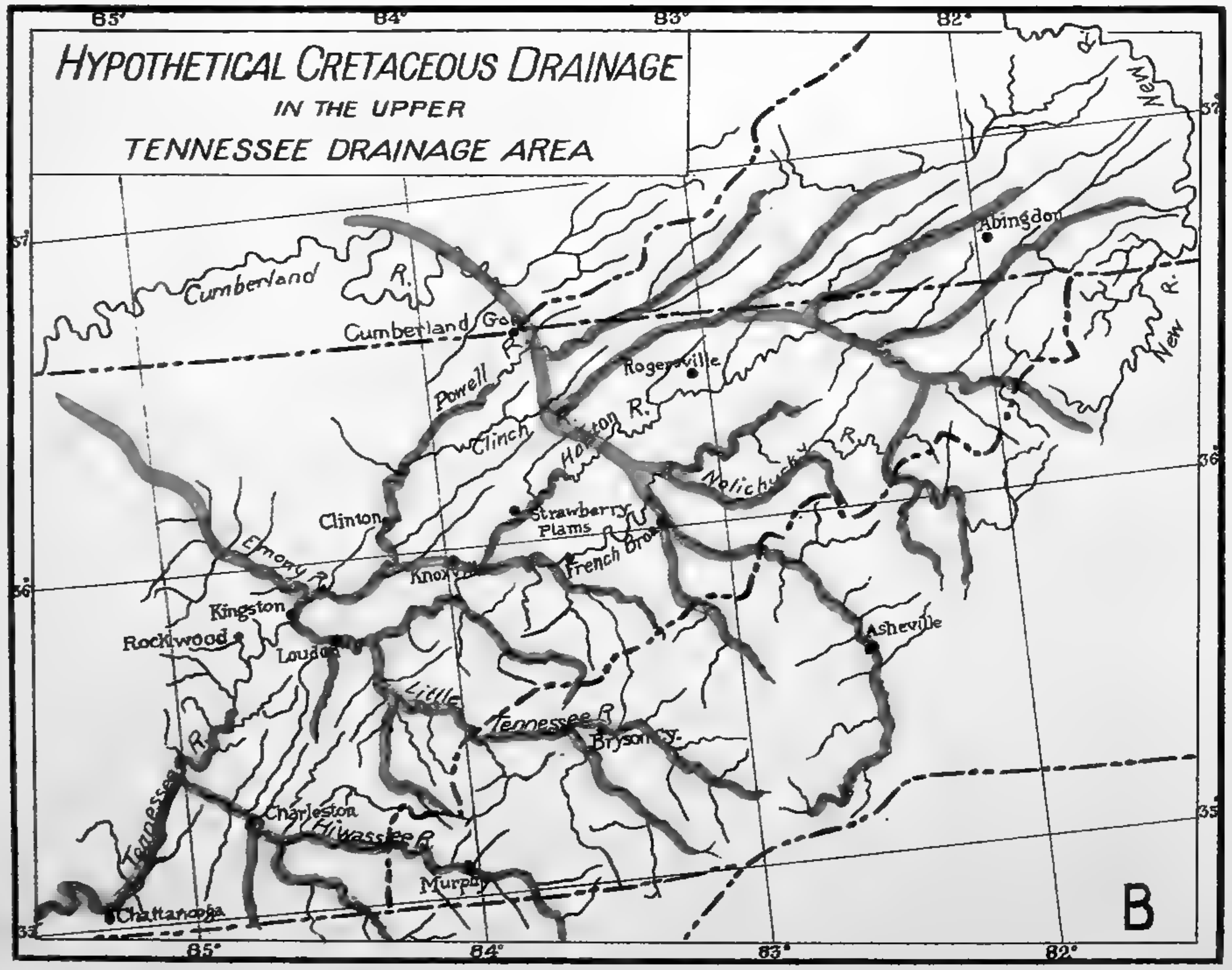


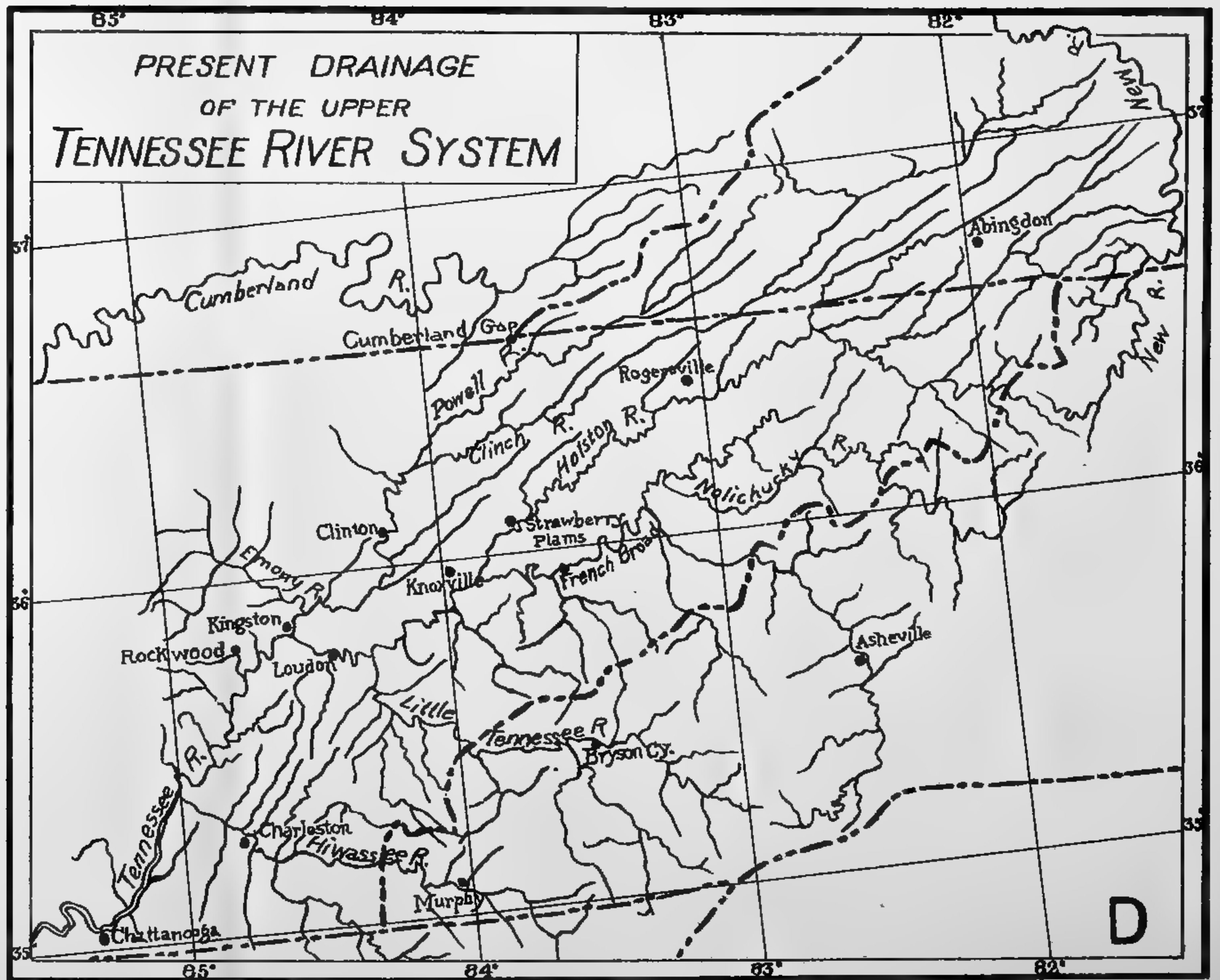
HYPOTHETICAL PERMIAN DRAINAGE
IN THE UPPER
TENNESSEE DRAINAGE AREA



HYPOTHETICAL TERTIARY DRAINAGE
IN THE UPPER
TENNESSEE DRAINAGE AREA



HYPOTHETICAL CRETACEOUS DRAINAGE
IN THE UPPER
TENNESSEE DRAINAGE AREA



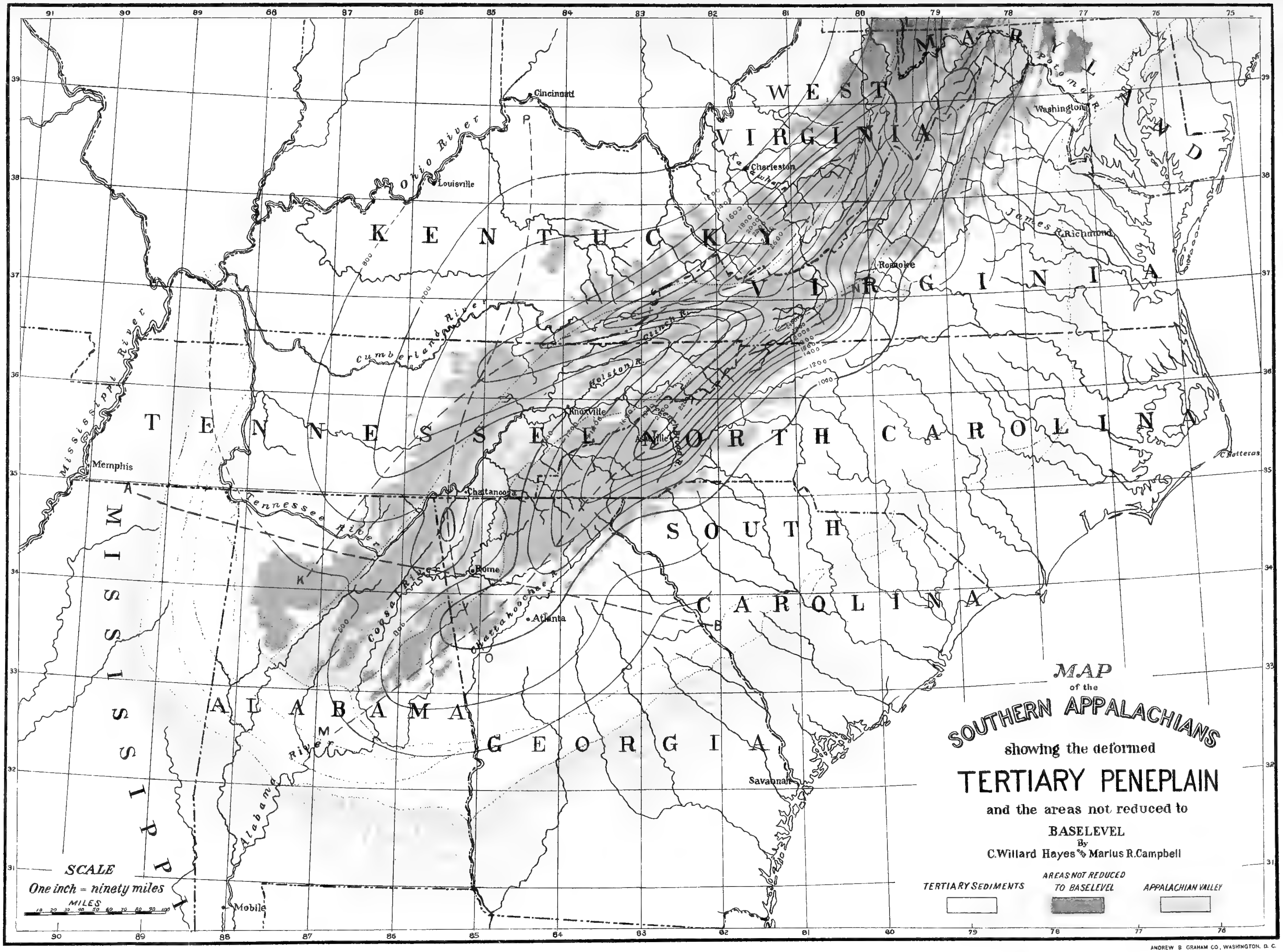
PRESENT DRAINAGE
OF THE UPPER
TENNESSEE RIVER SYSTEM

ANDREW B. GRAHAM CO., WASHINGTON, D. C.

EXPLANATION TO PLATE 58.

Map of the Tertiary Peneplain in the Southern Appalachian Mountain region. After Hayes and Campbell.

Plate 58

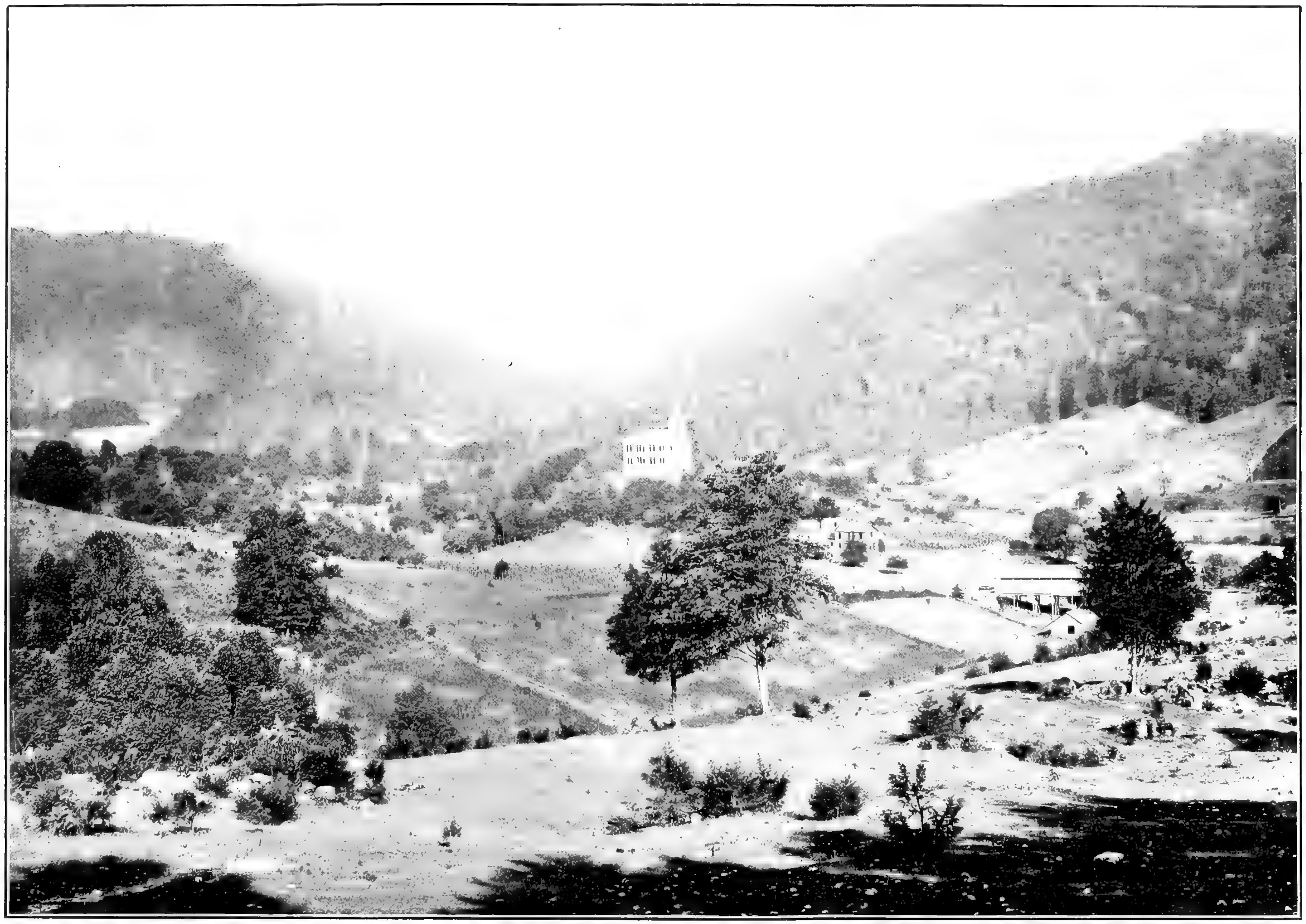


MAP
of the
SOUTHERN APPALACHIANS
showing the deformed
TERTIARY PENEPLAIN
and the areas not reduced to
BASELEVEL
By
C. Willard Hayes and Marius R. Campbell

ANDREW B. GRAHAM CO., WASHINGTON, D. C.

EXPLANATION TO PLATE 59.

Big Moccasin Gap, in Clinch Mountain, Gate City, Va. The crest of the Clinch Mountain represents the present level of the remnant of the Cretaceous peneplain. During Tertiary or Pleistocene times this gap was probably formed by the drainage of the Upper Holston system which was then tributary to the Upper Clinch River.



EXPLANATION TO PLATE 60.

Diagram with smooth and spinose *Io* shells to illustrate Mendelian inheritance. Smooth shells from lot 41, Powell River; spinose from lot 100, Tennessee River.

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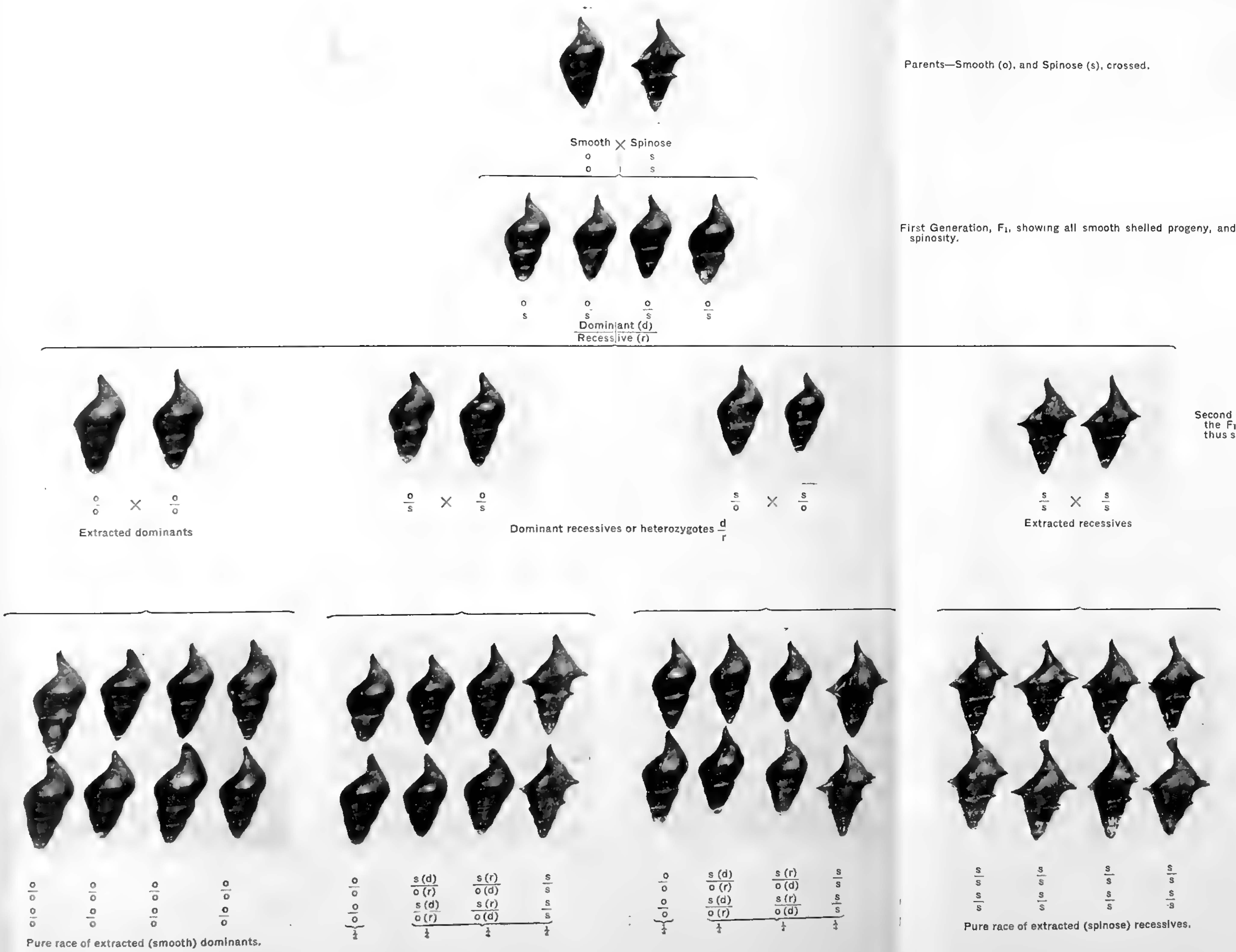
Pure race of extracte

DIAGRAM SHOWING MENDELIAN INHERITANCE IN THE GENUS Io. (HYPOTHETICAL.)



Parents—Smooth (o), and Spinose (s), crossed.

First Generation, F_1, showing all smooth shelled progeny, and the dominance of smoothness over spinosity.

Second Generation, F_2, showing results of crossing in pairs, the F_1 generation; ¼ are spinose and ¾ are smooth, and thus show the Mendelian ratio.

Third Generation, F_3, showing the proportion of dominant (¼) and recessives (¼), and the Mendelian ratio in the progeny of the dominant recessives.

EXPLANATION TO PLATE 61.

Map of the Tennessee River to show the location of the groups of shells used in the quantitative studies. The numbers from 1 to 27 show the location of the groups. By comparison with appropriate plates, plates 28–55, one may at a glance get an idea of the shell population in representative parts of the rivers.

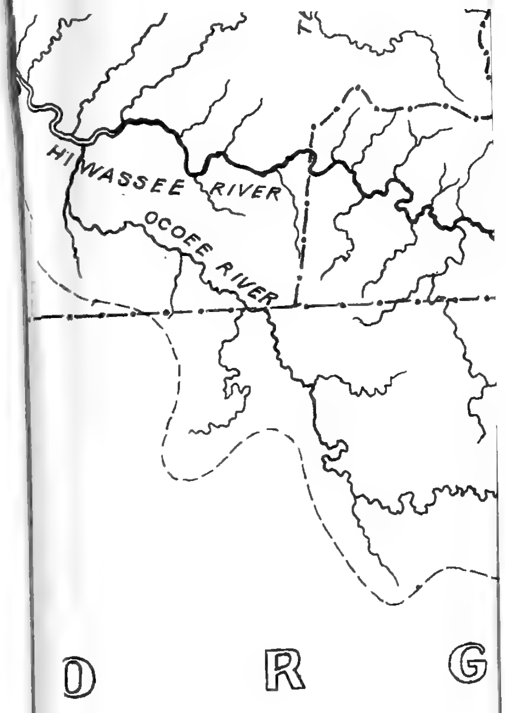

HIWASSEE RIVER
OCOEE RIVER
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PLATE 61.

MAP OF THE

TENNESSEE RIVER

Showing Distribution of Snails of the Genus IO

BY

CHARLES C. ADAMS.

1912

(Adapted from an old Government Map.)

The Large Numbers, 1 to 27, Indicate the Approximate Location of the Different Groups of Shells Which Furnish the Basis for the Plates and the Quantitative Studies of the Genus.

S. Fred Prince, del.

THE MORRIS PETERS CO., WASHINGTON, D. C.