A CONTRIBUTION TO LIFE AND DEATH ASSEMBLAGE STUDY

by

Robert Dennis Staton

SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

BACHELOR OF SCIENCE

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

1960

Signature of Author . . Signature redacted
School of Industrial Management

Certified by . Signature redacted
Faculty Advisor of the Thesis

Professor Philip Franklin
Secretary of the Faculty
Massachusetts Institute of Technology
Cambridge 39, Massachusetts

Dear Professor Franklin:

In accordance with the requirements for graduation, I herewith submit a thesis entitled "A Contribution to Life and Death Assemblage Study."

It is a pleasure to acknowledge the assistance and close supervision of Dr. Arthur J. Boucot of the Department of Geology and Geophysics.

Sincerely yours,

Robert Dennis Staton

A CONTRIBUTION TO LIFE AND DEATH ASSEMBLAGE STUDY

by ROBERT DENNIS STATON

Submitted to the School of Industrial Management on May 23, 1960 in partial fulfillment of the requirements for the degree of Bachelor of Science

In paleoecologic studies of fossil communities, differentiation between life and death assemblages is imperative before true mortality and survivorship rates can be determined. This differentiation has seldom been attempted and a true life assemblage has never been described. For marine invertebrates, one incomplete survivorship curve has been published, and no mortality rates have ever been described.

Criteria entailing the consideration of size frequency distributions, ratio of articulated to disarticulated shells, ratio of opposite valves, and population densities are applied to a collection of Wenlock age brachiopoda from the Mulde Marl of Gotland, revealing that the indigenous populations represent true life assemblages. The resulting positively skew mortality and survivorship rates are included.

Thesis Advisor: Arthur J. Boucot
Associate Professor of Geology

TABLE OF CONTENTS

LIST OF FIGURES, TABLES, AND DIAGRAMS

CHAPTER 1

INTRODUCTION

1-1. The Problem and Its Setting.

Paleoecology[1] is the study of the mutual relations between ancient organisms and their environments. Diverse fossil communities, entombed in the geologic column by sedimentary deposition, are the primary objects of study in this science. Investigations of fossil populations have long been handicapped by the difficulty of distinguishing between life and death assemblages. A death assemblage is the aggregated remains of organisms that have been brought together after death -- a miscellaneous assortment of organic debris transported from original habitat(s). A true life assemblage is the fossil remains of an ancient community that lived, died, and was buried within a particular area, having undergone no reworking or transportation. A modified life assemblage is the remnant of a true life assemblage that has suffered removal of specimens (largest and smallest)[2] to a variable degree. There has been no "in-flow" of fossil debris, however; this situation immediately causing some form of death assemblage.

Determination of the nature of the origin of ancient communities available for study enables the construction of mortality curves, survivorship rates, disarticulation ratios and rates, population densities, and source areas. Both Paleoecology and marine Biology would benefit greatly from increased data of this sort.

1 see Cloud (listed in Bibliography)
2 H.W. Menard and A.J. Boucot, Experiments on the Movement of Shells by Water,(cont)

Marine Biology is not directly concerned with fossil communities, but investigates the characteristics of biocoenoses and thanatocoenoses: Recent communities of life and death, respectively. However, mortality rates of ancient populations are useful for tracing the evolution and characteristics of living organisms.and their communities.

Criteria for distinguishing between life and death assemblages are based on statistical analyses of size-frequency distributions, ratios of articulated shells to disarticulated shells, ratios of opposite valves, and population densities. These criteria shall be applied in this thesis to a sample of Silurian brachiopoda from Gotland, Sweden.

The size-frequency distribution is perhaps the most important criterion. Width of brachiopods is a satisfactory character for measuring size, being easily determined and uniform for the opposite valves of any individual. The width-frequency data of a true life assemblage is expected to yield a positively skew (see section 1-2) curve.

A true life assemblage of a fossil marine invertebrate has never been described; very few modified life assemblages have been described, all within the last seven years. There is need of systematic testing and refinement of methodology in this area of research.

(Footnote continued from preceding page)
American Journal of Science, Volume 249, February 1951, pages 131-151

1-2. Purpose of the Study.

This study was suggested to the author by Dr. Arthur J. Boucot of the Department of Geology and Geophysics. His two papers[1], relating to the life and death assemblage problem, amount to virtually all[2] of the literature published in this area of study. Boucot's earlier paper (1953) represents the trial-and-error initial approach to a new branch of paleoecology. Its shortcomings and the subsequent refinements expressed in the 1958 paper are discussed in section 6-1.

The specific purpose of this project was to apply the as yet laboratory-unproven theories of life and death assemblage study to a sample having all the outward characteristics of a life assemblage. Deevey[3], speaking of survivorship curves of Recent populations, states that the Type III[4] positively skew survivorship curve showing "extremely heavy mortality beginning early in life," with "few individuals which survive to advanced ages.... has never been obtained with a laboratory population, though marine species with pelagic eggs and larvae, such as oysters, would doubtless fall here if complete data were available."[5]

It is the purpose of this study, then, to prepare data that will at once test the hypothesis that a Type III mortality curve is characteristic of marine invertebrate fossil life assemblages and yield the first laboratory-proven positively skew survivorship curve.

1 see Bibliography
2 In addition, F.M. Broadhurst (see Bibliography) has recently described a modified life assemblage of *Anthraconaia pulchella*, and J.J. Veevers (see Bibliography) has described two possible modified life assemblages of *Schizophoria stainbrooki*.

1-3. General Research Methodology.

The approach to the problem is straightforward. It entails the assemblage of a population by washing the sample free of sediment, sorting, and grouping the individuals by species. Each individual is then measured to obtain the required size-frequency data.

1-4. Major Conclusion.

The thesis sample proved to be a true life assemblage, characterized by very skew mortality curves for the two species analysed. The graphical results appear in Chapter 5, and the detailed conclusions in section 7-1.

(Footnotes continued from preceding page)

3 see Bibliography
4 Deevey, page 285
5 Author's note: E. Percival (see Bibliography) has described the structure of a living population of Terebratula inconspicua without mention of survivorship or mortality rates. This size-frequency distribution is a positively skew curve, and represents four age groups.

CHAPTER 2

THE SAMPLE

2-1. Size, Age, Source and Pertinent Geology.

The sample, filling a container 40 by 40 by 70 cm., was collected from the Mulde Marl (uppermost Wenlock in age) in the Mulde Tegelbruk (brickworks) south of the village of Mulde in Gotland, Sweden. It was taken from a single stratigraphic layer approximately 20 cm. thick, to insure uniform age and locality.

The location of the source area and local geology are diagramed on the sequential Figures 1, 2, and 3.

2-2. Faunal and Lithologic Characteristics.

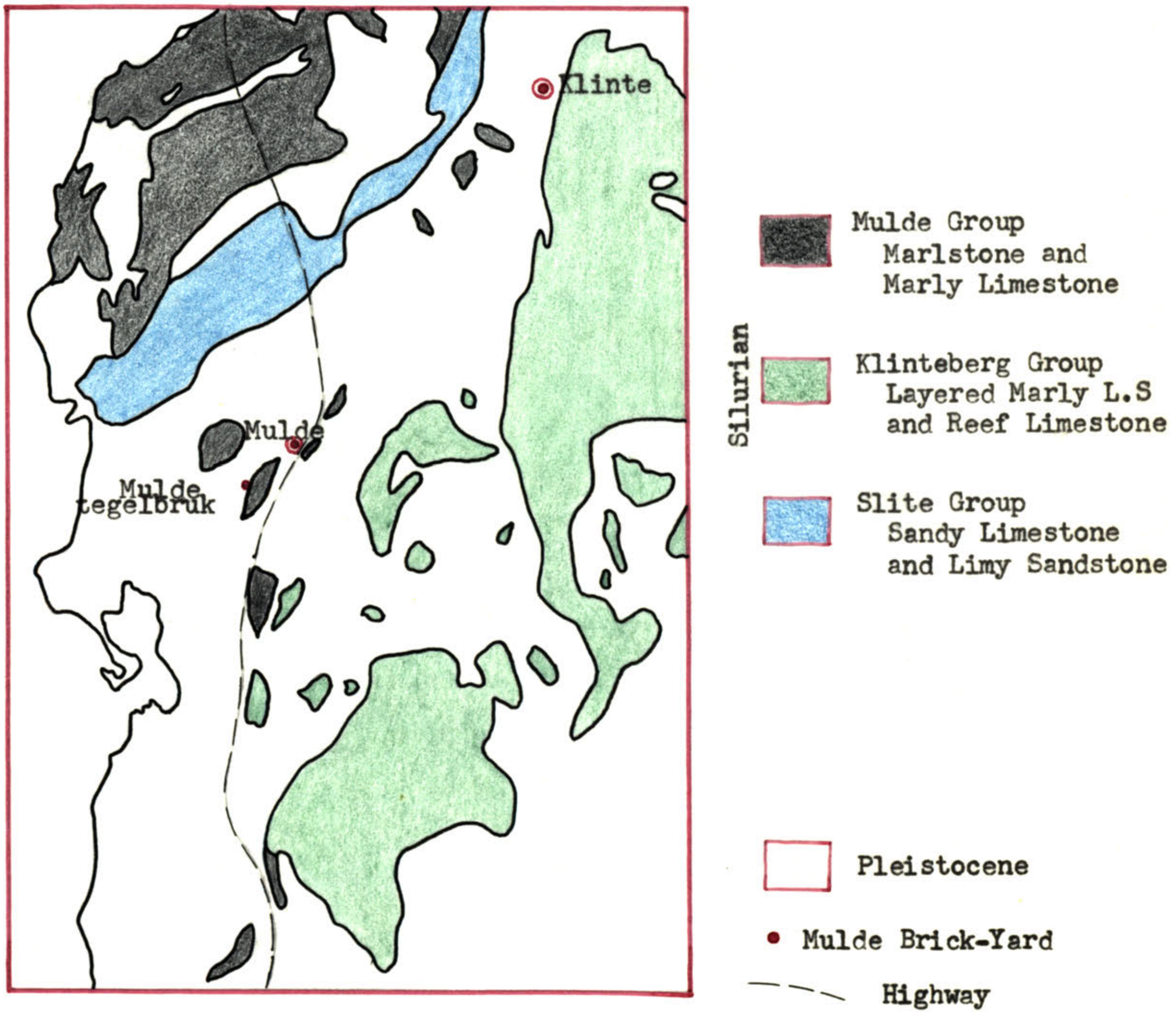
The Mulde Marl is characterized by the following species[1]:

Favosites Forbesi
Aulopora Roemeri
Cornulites scalariformis
    serpularius
Conchicolites Nicholsoni
    tuberculiferus
Spirorbis-arter
Ptilodictya lanceolata
Berenicea consimilis
Stromatopora minor
Cyclotrypa inflata
Pholidops implicata
Dalmanella crassa
    elegantula
Rhipidomella hybrida
Bilobites bilobus
Plectambonites segmentum
Leptaena laevigata
    rhomboidalis
Strophonella euglypha
    funiculata
Chonetes gotlandicus
Scenidium Lewisi
Rhynchotreta cuneata
Camarotoechia diodonta
    nucula
Wilsonia Wilsoni Davidsoni
Wilsonia sphaeroidalis
Atrypa reticularis
Glassia obovata
Spirifer crispus
    elevatus
    radiatus
Cyrtia trapezoidalis
Nucleospira pisum
Meristina tumida
Waldheimia bicarinata
Cornellites Damesi
    Sowerbyi
Modiolopsis Nilssoni
Ctenodonta sulcata
Nucula anglica
Cypricardinia crispula
Conocardium aequicostatus
Loxonema sinuosum
Tentaculites multiannulatus
    wenlockianus
Dawsonoceras annulatum
Beyrichia Jonesi
    spinigera
Primitia cristata
    mundula
    ornata

1 Munthe, Hede, and von Post (see Bibliography), page 21

Figure 1

GEOLOGIC SITUATION OF THE MULDE BRICK-YARD

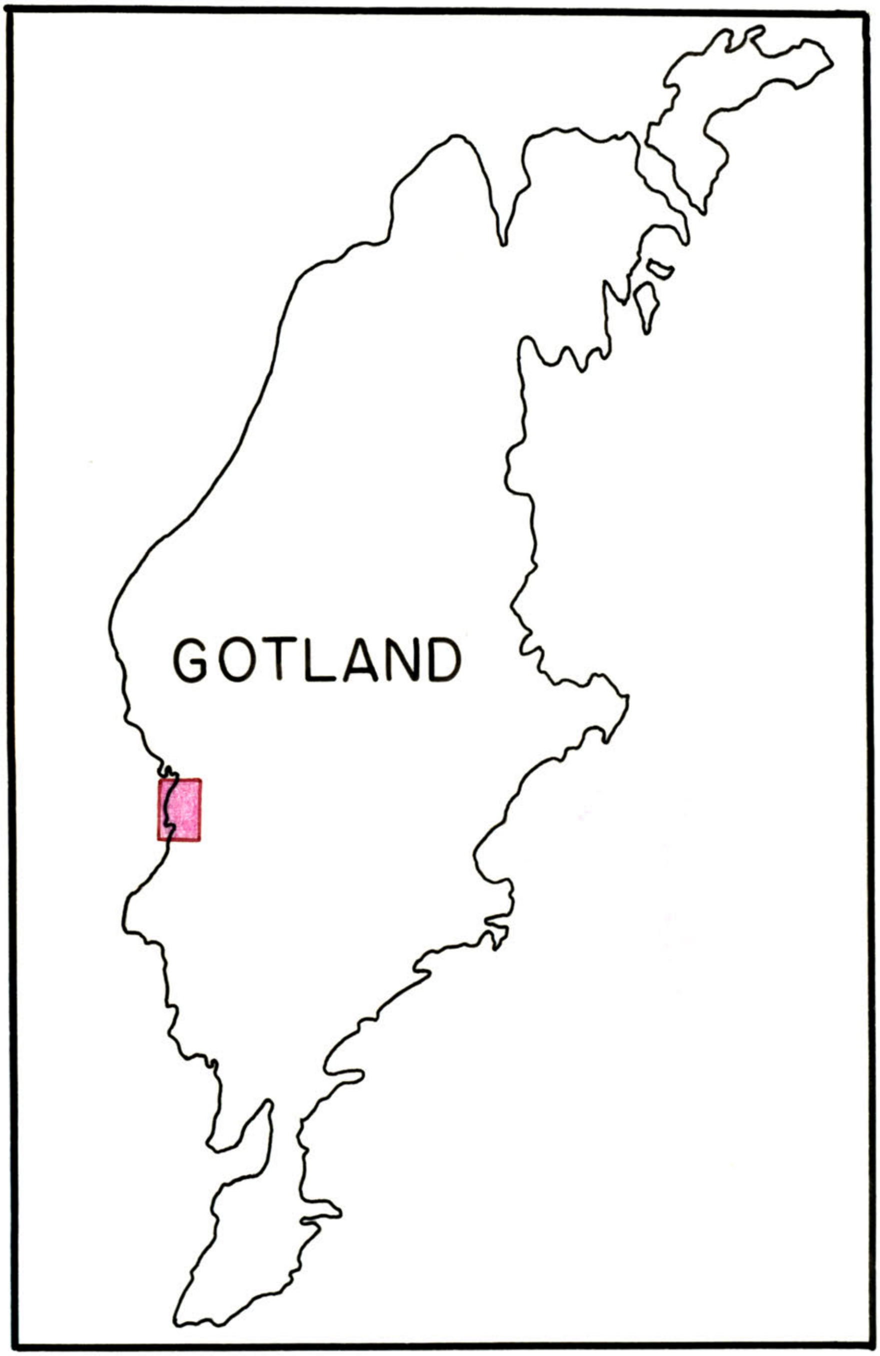


Scale 1:50,000

Source: Sveriges Geologiska Undersokning
Ser. Aa. No. 160

Figure 2

GOTLAND

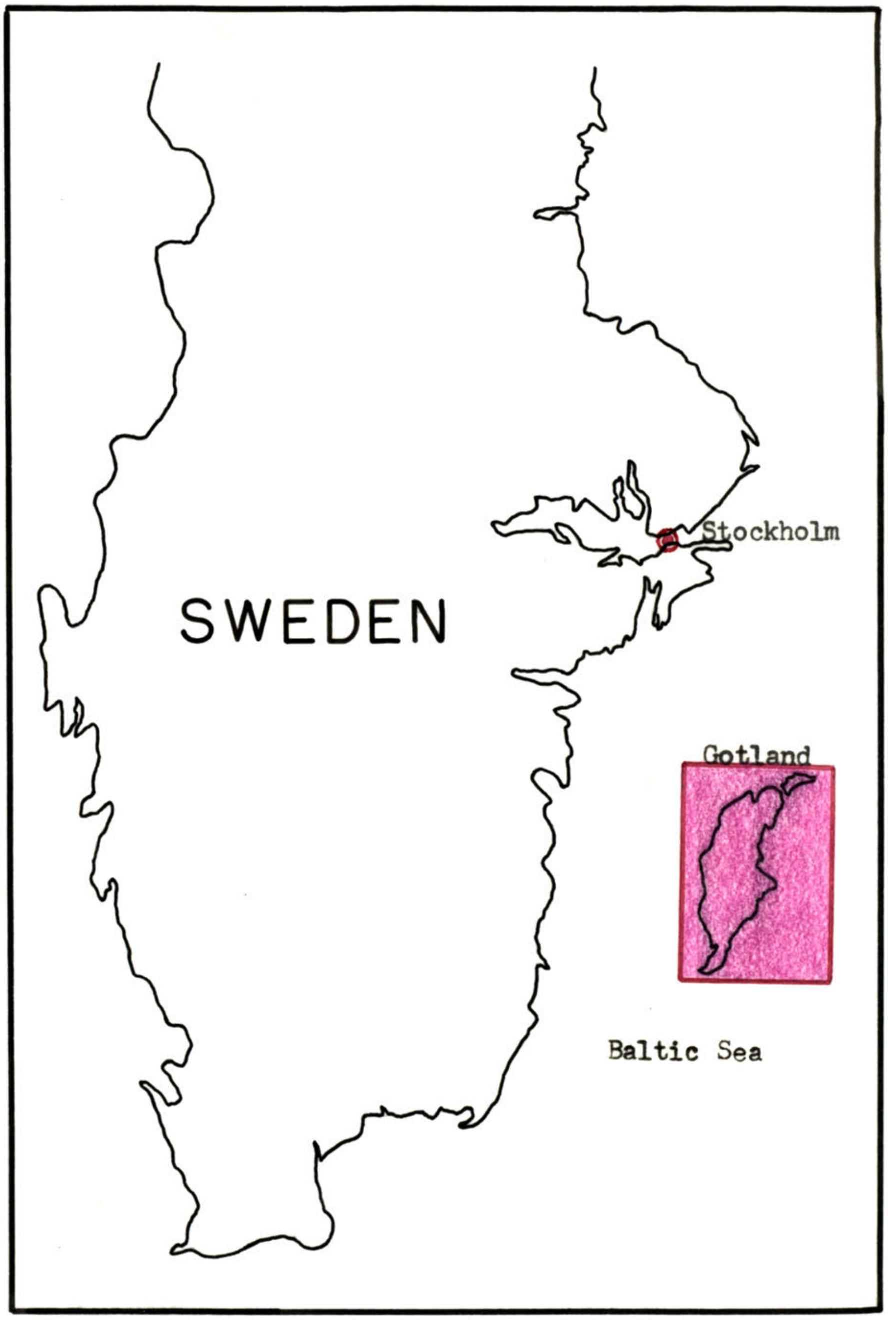


Scale: 1" = 18.2 km.

Source: On the Correlation of the Silurian
of Gotland, by J. Ernhold Hede
Lunds Geologiska Faltklubb
N:o 101, 1942

Figure 3

SWEDEN



Scale: 1" = 72 miles

Source: New World Atlas
C. S. Hammand & Co., Inc.
New York

Primitia reticristata
 valida
Primitiopsis planifrons
Thlipsura V-scripta discreta
Macrocypris siliquoides
 Vinei
Cytherella Smithi
Aechmina bovina
 bovina punctata
Bythocypris Holli
 phaseolus
 symmetrica

Calymene tuberculata
 tuberculosa
Cyphaspis elegantula
Proëtus concinnus
 Stokesi
Encrinurus punctatus
Acidaspis crenata
Dalmanites vulgaris

Gothograptus nassa[1]
Monograptus dubius

The species collected by hand from the Mulde Marl are listed in section 2-4; the species present in the thesis sample are listed in section 3-6. The brachiopods are the only species to be analysed in this study and consequently exact identification of species of other phyla has not been attempted.

Lithologically, the sample is an extremely loosely-compacted, clayey marl, moderately fossiliferous[2], with no secondary replacement.

2-3. Previous Publications on the Source Area Pertinent to this Study.

Ontogeny of Beyrichia jonesi Boll by Nils Spjeldnaes[3] is the only work of specific interest, although there are numerous descriptions of the regional geology and paleontology available[4].

Spjeldnaes is not aware of or concerned with the life and death assemblage problem, and his paper is useful (for this study) only insofar as he includes size-frequency data for a natural population of Beyrichia jonesi, and discusses, in general terms (for ostracods), the requisites of a population suitable for

1 from Hede, On the Correlation of the Silurian of Gotland (see Bibl.)
2 population density data appears in section 7-1.
3 see Bibliography
4 see bibliographies included in Hede, and in Munthe, Hede, and von Post references in the Bibliography

laboratory analysis of growth rates:[1]

"The growth rate and final size of individuals depends on ecologic factors, such as temperature and food supply.... A species, therefore, has no absolutely fixed growth rate and this may be expected to vary within certain limits with sex and between different populations....

In order to obtain reliable information.... it is necessary that all the specimens studied be from as nearly the same population as possible. The number of specimens must be sufficiently great to minimize errors that are likely to occur in connection with statistical treatment. The population should be unaccompanied by related species with similar young specimens. No important ecologic changes must have taken place during the interval represented by the fossiliferous layer. This last is very difficult to prove, but fossils which may have been redeposited should be avoided. If these precautions are observed, fossil material has one distinct advantage over living specimens. Among the fossils one may expect to find the remains of all stages of development and there is opportunity to compare the relative number of young and adult valves....

The Mulde population of Beyrichia jonesi seems to have been extremely stable and completely preserved.... Migration of individuals into or out of this population seems to be unimportant..., no evidence of redeposition...."

Table 1 contains size-frequency information incorporated from Spjeldnaes, and Figure 4 graphically shows these results.

2-4. Hand Collected Sample.

At the same time that the thesis sample was collected (summer 1956), a random sample of various brachiopod species was gathered at the same locality. This sample was collected from different stratigraphic horizons, however, encompassing the entire brick-yard. The species collected include:

Resserella (Dalmanella elegantula)
Rhipidomella hybrida
Chonetes gotlandicus
Meristina tumida
Atrypa reticularis
Eospirifer
Howellella
Plectodonta
Leptaena rhomboidalis
Amphistrophia
Mesopholidostrophia
Rhynchonellids (unidentified)

1 Spjeldnaes, pages 746, 751 and 752 (see Bibliography)

Table 1

Size-Frequency Data

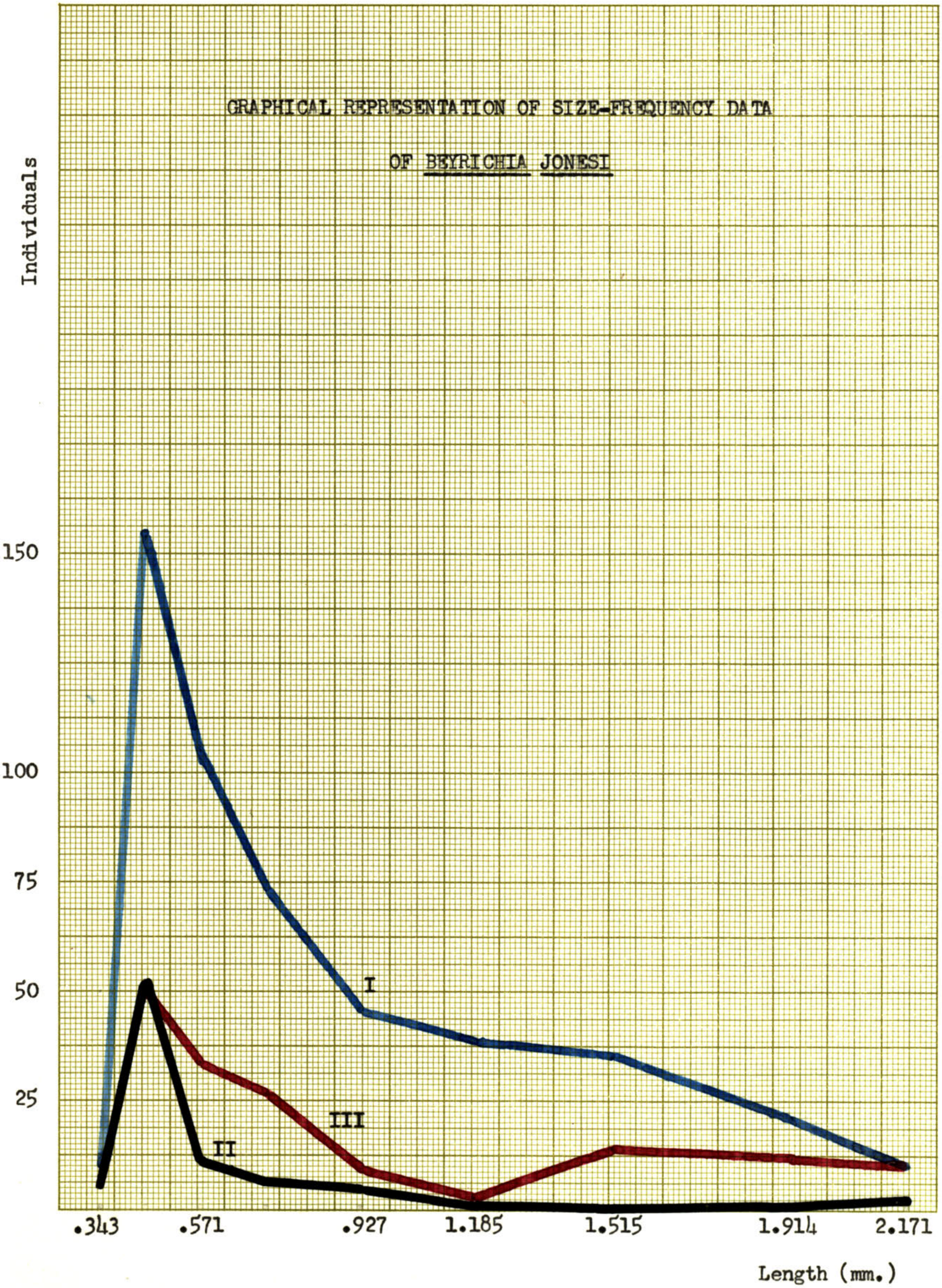
of Beyrichia Jonesi

(Spjeldnaes, page 747)

(mm.) Length	I Total Specimens and Moults, i.e. Total Valves / 2 (Complete Specimens = 2 Valves)	II Complete Specimens	III Specimens Representing "Loss" at Next Stage
0.343	9	5	-
0.443	155	53	50
0.571	105	10	33
0.728	73	6	27
0.927	46	4	9
1.185	38	1	3
1.515	35	0	14
1.914	21	1	12
2.171	10	2	10

In Figure 4, column I (blue), column II (black) and column III (red) do not graphically represent true size-frequency rates, but should be taken as "trend" curves because of the nature of the data (length data not continuous, but given in terms of growth stage means). Column III approximates the mortality rate.

Figure 4


GRAPHICAL REPRESENTATION OF SIZE-FREQUENCY DATA
OF BEYRICHIA JONESI
Individuals
150
100
75
50
25
I
II
III
.343
.571
.927
1.185
1.515
1.914
2.171
Length (mm.)

It is planned to contrast the size-frequency curves of a typical hand collected sample (presumably normally distributed) with the results of the laboratory analysed sample at a later date. The significance of this comparison will be the proof that a typical hand collected sample is unrepresentative of the actual fauna present. This is of general interest since most ecologic discussions are based on bias samples of this sort. On the other hand, the laboratory sample by itself may also prove somewhat limited in scope.

CHAPTER 3

SAMPLE PREPARATION

3-1. Initial Preparation.

The sample volume was computed to be 0.112 cubic meters. The sample was not weighed since population densities, in terms of weight of sample tested, were not within the scope of this project.

The sample was divided by eye into two approximately equal sub-samples which were then treated independently of each other throughout the analysis.

3-2. Purpose of Preparing Two Samples.

The two methods described below (3-3, elutriation, and 3-4, sifting) are alternative methods available for cleaning the sample in preparation for isolation of the various populations within. Insofar as no data was available as to which method might yield more accurate results, it was decided that both methods should be employed, and a "best procedure" conclusion included in the thesis.

3-3. Elutiation.

Elutriation is the introduction of water of controlled turbulence and the decantation of the sediment by allowing the turbid water to flow out of the container before its sediment load has had time to settle; the supposition being that the larger brachiopod fossils are less likely to be thrown into suspension than the fine grained marl particles. To offset the possibility that the smallest fossil specimens might be carried away in suspension the turbulence of the water flow was minimized. In addition, the final stages (where increased turbulence would be required) were completed by sifting.

This method, like the following, was only possible because of the loose, uncompact nature of the sample. The resultant mixture of fossils, fossil fragments, Recent plant debris (roots[1]), and pebble-size rock fragments was then sorted (section 3-5).

3-4. Sifting.

This portion of the sample was placed in a water bath, breaking the sediment into a plastic clay solution, which was then sifted with running water through a sequence of sieves. The smallest sieve (on the bottom) was underlain by a container to retain the sediment for later study. Excess water was allowed to overflow the container providing slight elutriation.

The problem inherent with this method is possible abrasion, fragmentation, or disarticulation of the fossils (making accurate size determination difficult or impossible) during passage through the sieve meshes; some being forced through sieves where free passage is not possible. These occurences were minimized by allowing slowly running water to circulate and promote passage, avoiding any stronger physical forces.

The size differentiation of the resultant fossiliferous residue was retained as an anticipated aid in sorting (section 3-5).

1 During collection of the sample, an effort was made to avoid inclusion of Recent plant matter by stripping 12 to 18 inches of overburden before collection. This evidently was not completely effective.

3-5. Sorting.

The purpose of sorting is to obtain the maximum number of individuals of each specific population present whose original size can be measured without likelihood of duplication. This means that all whole tests or valves, or fragments greater than half their original size were removed from the cleaning residue. This was done systematically by naked eye with the larger sizes and binocular microscope with the smaller sizes. Care was taken to keep the elutriated and sifted batches separate. Only brachiopods were removed from the sample since they were the most abundant faunal element and were of primary interest to the author.

Because of the large size of the total sample and the time constraint imposed on this project it was decided to restrict analysis to those individuals greater than 0.5 mm. in smallest dimension. The anticipated effect of this diminutive element being simply accentuation of an already sufficiently skew curve.

Subsequently the brachiopods, all greater than 0.5 mm. in width, were sorted into individual species in final preparation for measuring.

3-6. Results.

The brachiopod species found in the laboratory sample are:

Elutriated	Sifted
Resserella elegantula	Resserella elegantula
Chonetes gotlandicus	Chonetes gotlandicus
Pholidops implicata	Pholidops implicata
Protozeuga bicarinata	Protozeuga bicarinata
Eospirifer	Eospirifer
Rhynchonellids (unidentified)	Rhynchonellids (unidentified)
Mesopholidostrophia	--

The *Resserella* were the most abundant, with a large representation of *Pholidops* and *Chonetes*. *Protozeuga bicarinata* was present to a lesser degree, with *Eospirifer*, *Rhynchonellids*, and *Mesopholidostrophia* in small numbers.

Other faunal elements were not identified with any detail, but it is noted that numerous ostracods (including *Beyrichia* and *Aechmina*) and occasional trilobite fragments were present.

It should be noted that the elutriated sample was consistently 50% larger than the sifted batch, indicating that the two sub-samples were probably not originally equal, and should have been split by weight. In general, the elutriated fossils were cleaner than the sifted, as might be expected.

CHAPTER 4

MEASUREMENTS

4-1. General Considerations.

For the reasons listed in section 3-5, the measurements were restricted to the two most abundant species: The articulate Resserella and the inarticulate Pholidops. With the exception of the Chonetids, none of the other species has sufficient representation to be as statistically significant.

The purpose of measuring the fossils is to relate frequency with size, which is largely a function of age. Graphical presentation of this data yields a mortality curve, since each size represents size (age) at death.

The measurement of one dimension is sufficient. With the Resserella the commonly accepted width (maximum width parallel to the hinge line -- see diagram) was used. Since Pholidops is rare, and there is no commonly accepted measurement standard, it was arbitrarily decided that that dimension should be measured which would best offset the breakage factor; thereby producing the optimum size sample. The "width" as shown in Diagram 2 was chosen to be most satisfactory.

Measurements were taken for the following groupings of faunal elements:

Elutriated Resserella	Sifted Resserella	Elutriated Pholidops	Sifted Pholidops
Whole Tests	Whole Tests	Whole Tests	Whole Tests
Pedicle Valves	Pedicle Valves	Pedicle Valves	Pedicle Valves
Brachial Valves	Brachial Valves	Brachial Valves	Brachial Valves

Diagram 1

<u>Resserella</u> <u>elegantula</u>

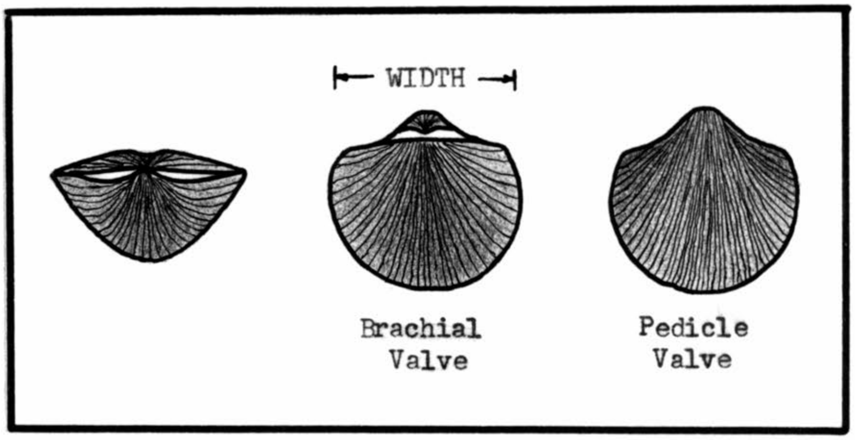
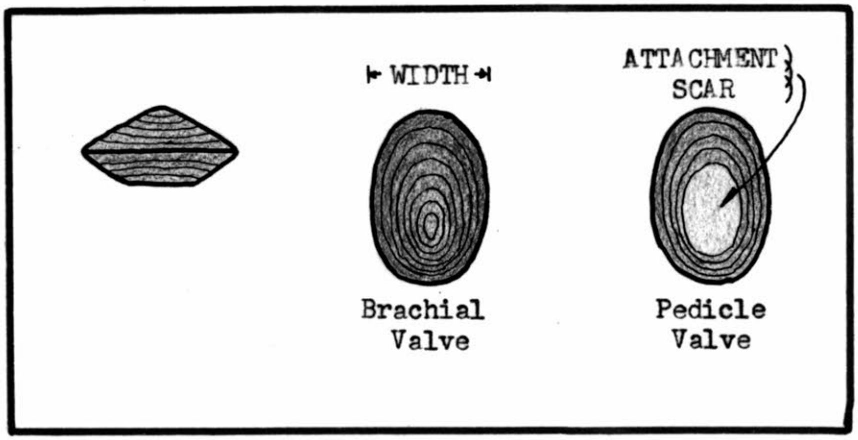


Diagram 2

<u>Pholidops</u> <u>implicata</u>



By combination of pedicles and brachials of the same size and taking an average of the two, a size-frequency distribution of disarticulated tests is obtained. In this manner the number of original whole specimens can be accurately determined.

Paleontologists[1], working with a few poorly preserved specimens, have been unable to ascertain which valve of Pholidops is pedicle and which is brachial. All have consistently denied the existence of an attachment scar on either valve. Since approximately half of the numerous, excellently preserved specimens of this sample exhibit an attachment scar (see Diagram 2), it was decided to use this criterion for brachial-pedicle differentiation, designating as pedicles those valves possessing attachment scars. This conclusion was further substantiated by internal differences consistent with the attachment scar criteria.

4-2. Equipment and Accuracy.

Since there were over 4,000 individuals to be measured as accurately as feasible, the author followed the helpful suggestion of Dr. Murray Copeland and made use of a camera-lucida--binocular microscope measuring apparatus. This combination superimposed an image of the object being measured on a piece of millimeter graph paper, from which measurements were taken directly. The magnification was determined to be 22X by use of a millimeter standard calibrated to one-hundredths. Since objects could be measured to the nearest one-half millimeter (measured units) from the graph paper, data accuracy is 1/44 mm. The accuracy requirements are much less, perhaps on the order of 1/10 mm.

1 Hall and Clark, 1892 (see bibliography)

4-3. Results, Considerations for Presentation of Data.

It was observed that measurements to the nearest whole measured unit were more common than half units. For example:

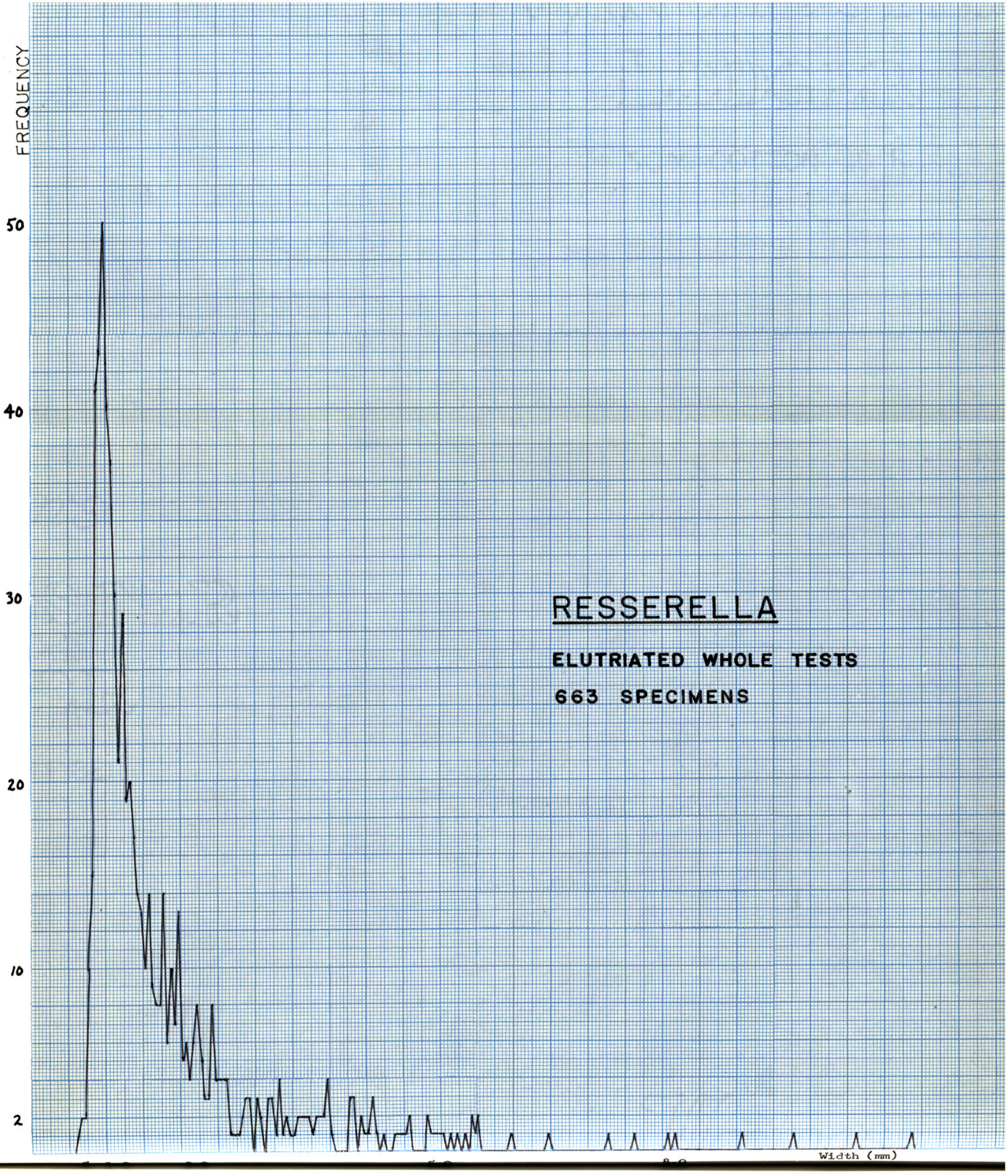
Millimeter Equivalents	Measured Units (22X)	Sifted Complete Tests	Elutri-ated Complete Tests	Sifted Pedicle Valves	Elutri-ated Pedicle Valves	Sifted Brach-ial Valves	Elutri-ated Brach-ial Valves	Total Resserella Specimens
1.14	25.0	12	16	3	9	8	5	40
1.16	25.5	5	4	4	2	2	1	13
1.18	26.0	7	15	5	8	9	9	38
1.20	26.5	5	5	3	4	3	4	17

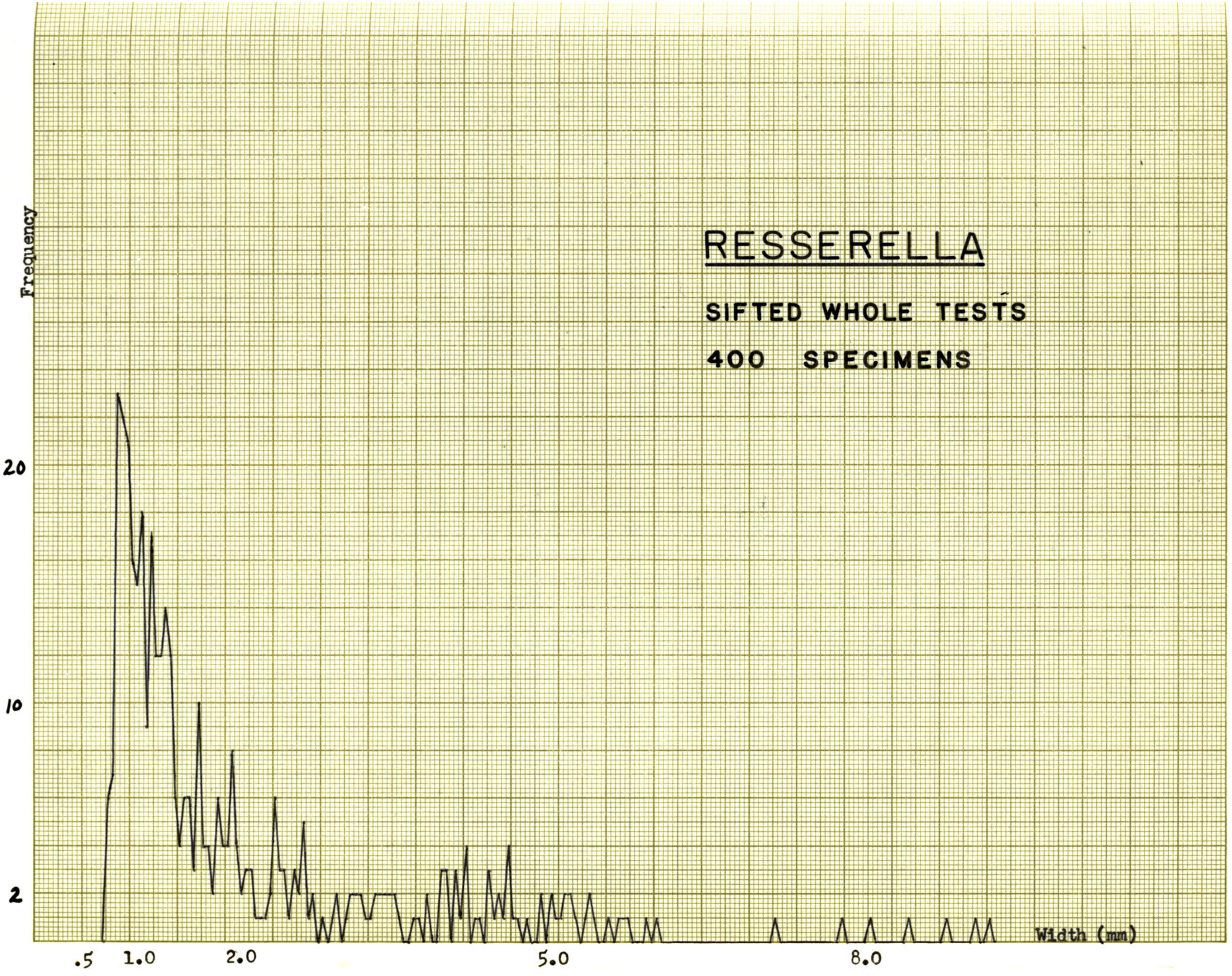
The rows for 25.0 and 26.0 are unnaturally larger than 25.5 and 26.5. This is interpreted as evidence that the "in-between" sizes (not clearly 25.0 or 25.5) were more often rounded to the nearest integer, whereas only those values very close to the one-half point were taken thusly. This observation of "human error" indicates that the accuracy in reality is not 1/44 mm., but somewhat less. For graphical presentation this situation was circumvented by using 1/22 mm. size ranges, so that 25.5 would be rounded to 26.0 and the sum plotted as 1.18 mm.

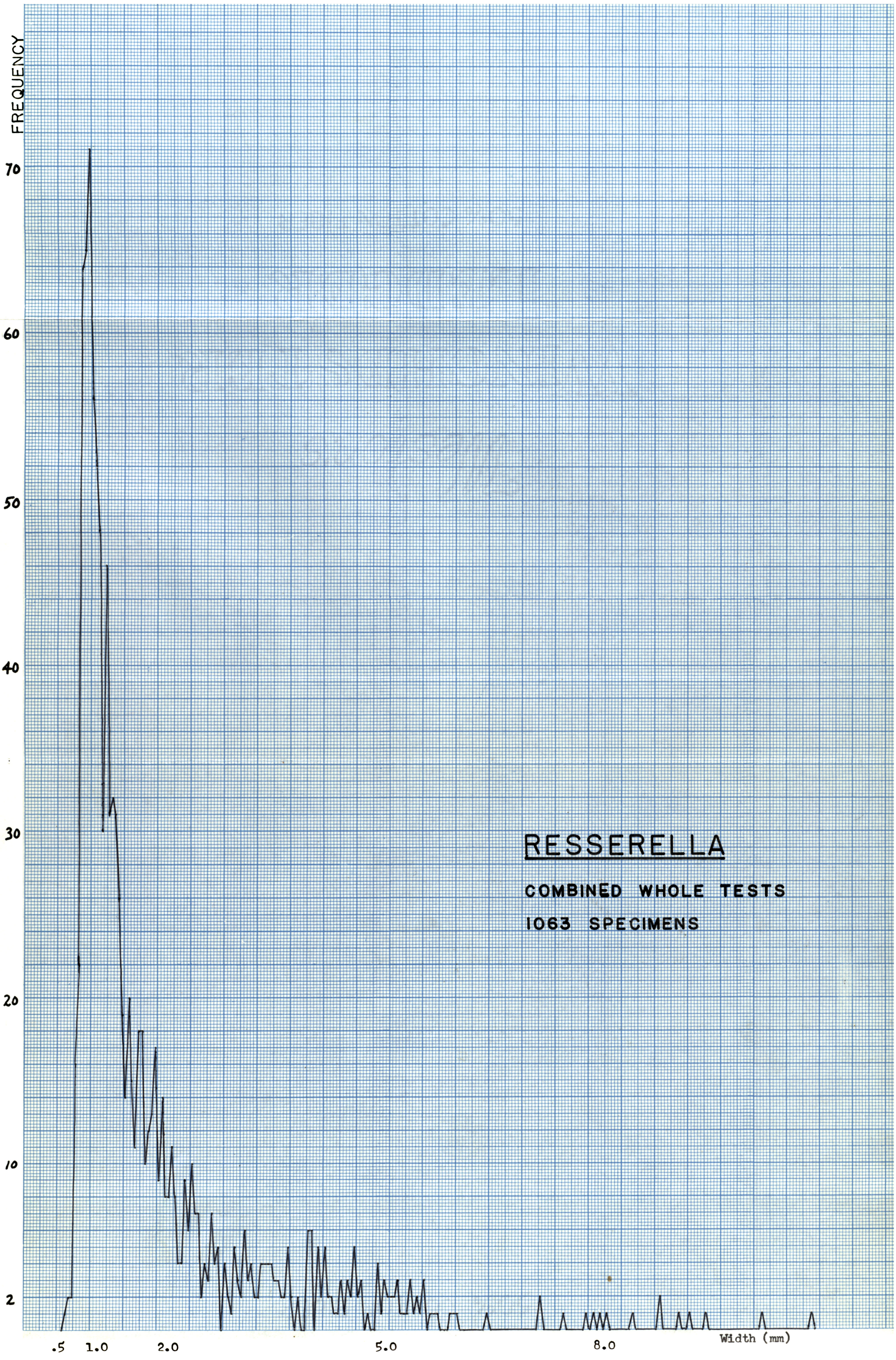
As will be seen in Chapter 5, various combinations of measured data were graphed in an effort to make the results as comprehensive as possible.

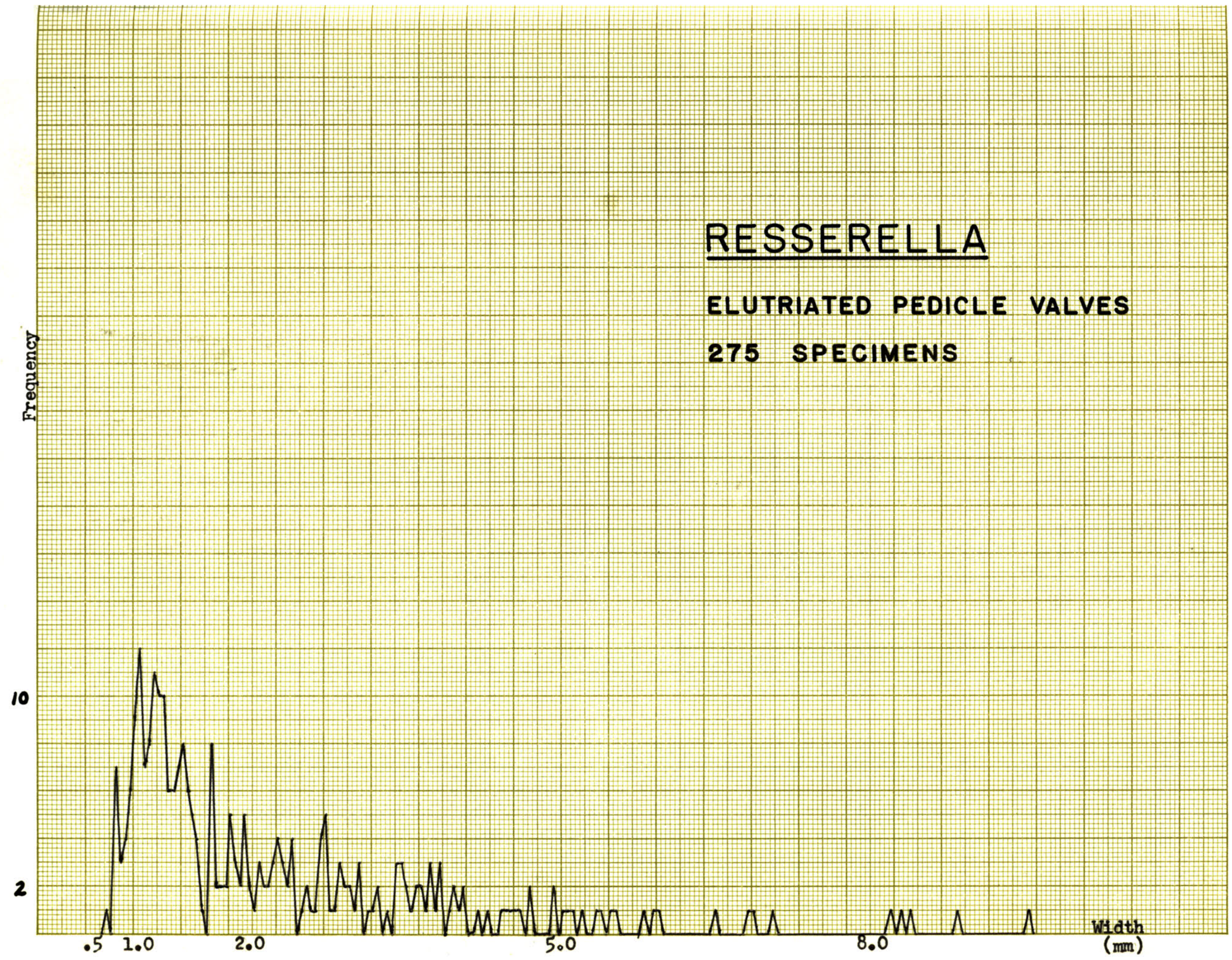
CHAPTER 5

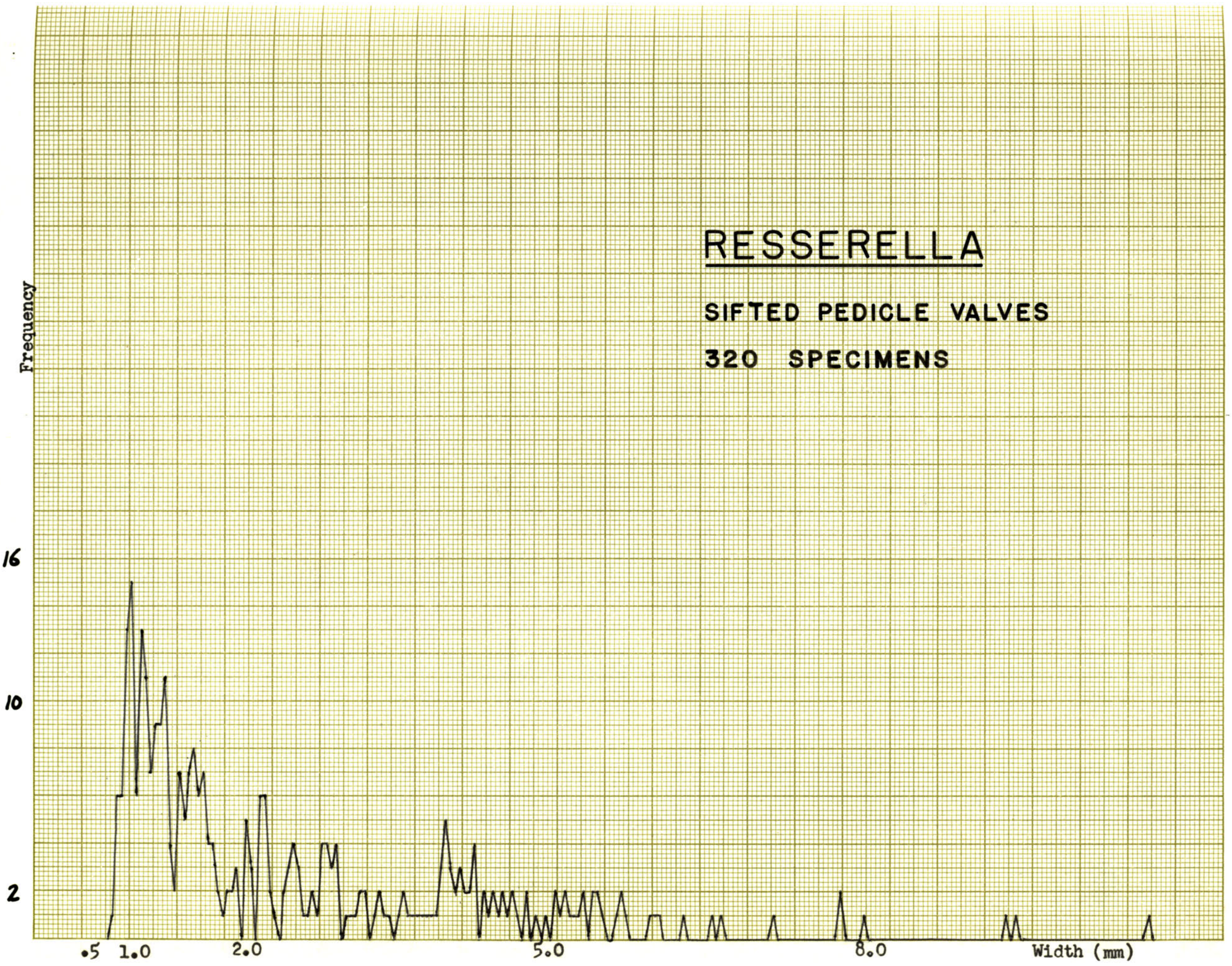
GRAPHICAL PRESENTATION OF DATA

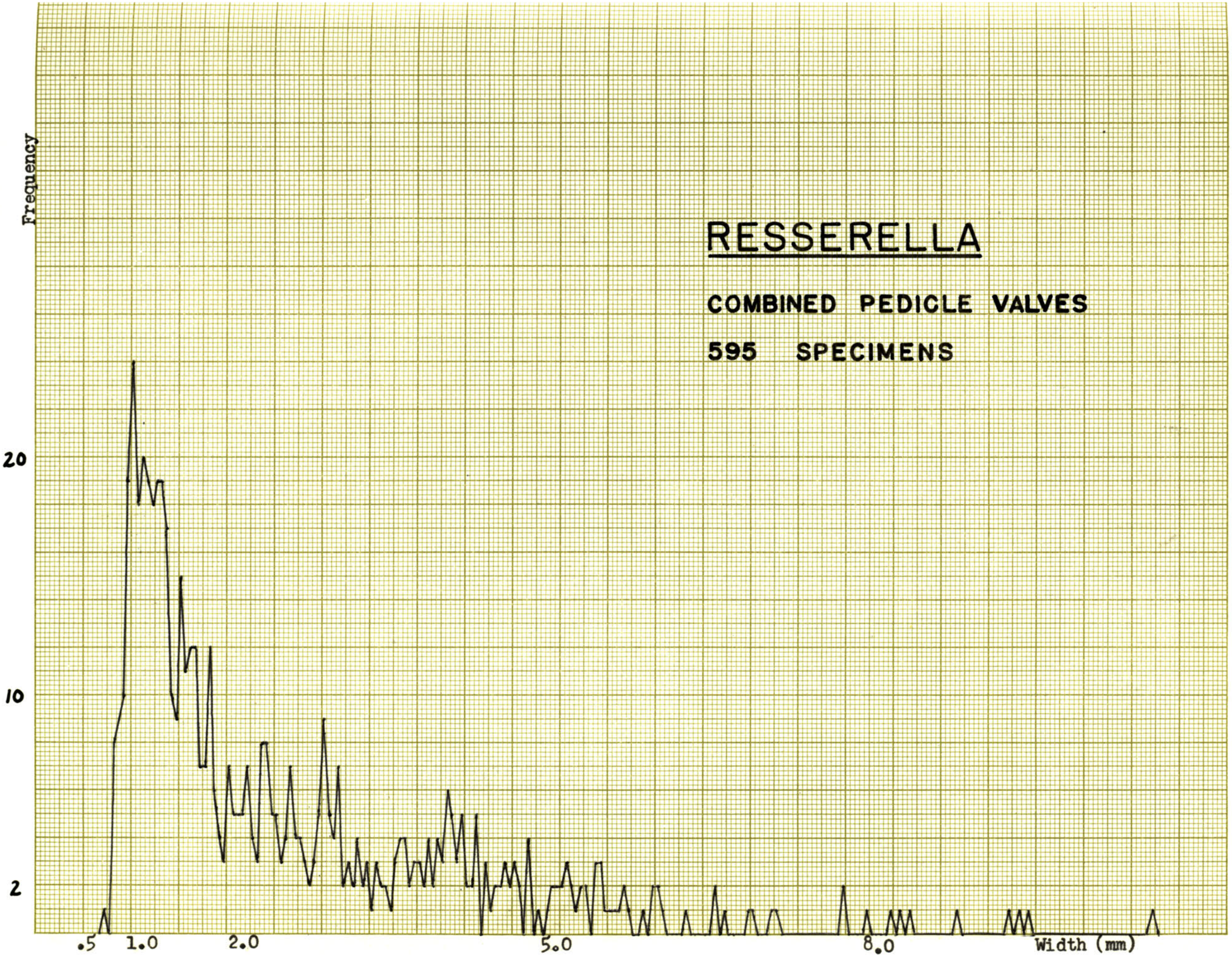

FREQUENCY
50
40
30
20
10
2
RESSERELLA
ELUTRIATED WHOLE TESTS
663 SPECIMENS
Width (mm)

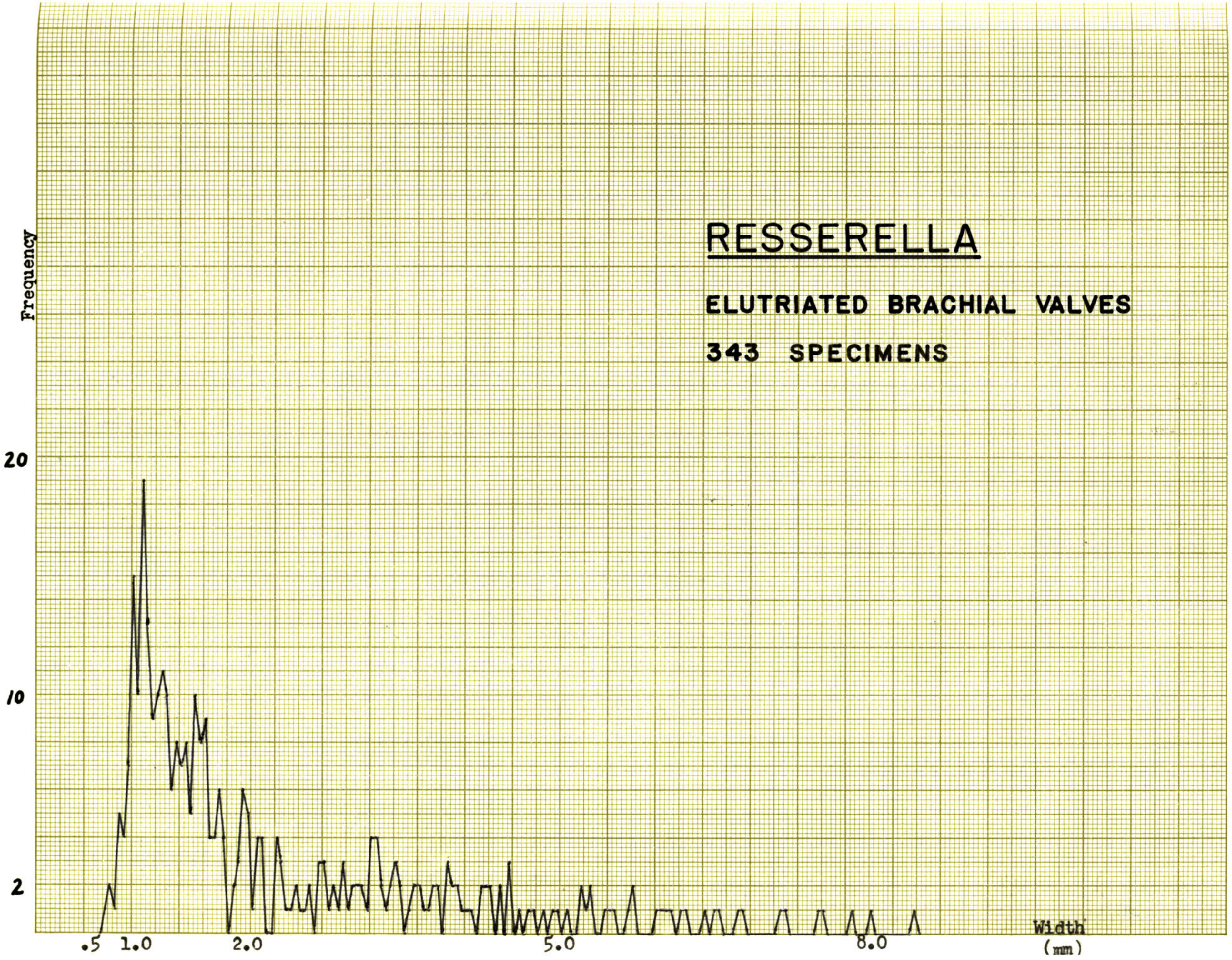

RESSERELLA
SIFTED WHOLE TESTS
400 SPECIMENS
Frequency
20
10
2
.5
1.0
2.0
5.0
8.0
Width (mm)

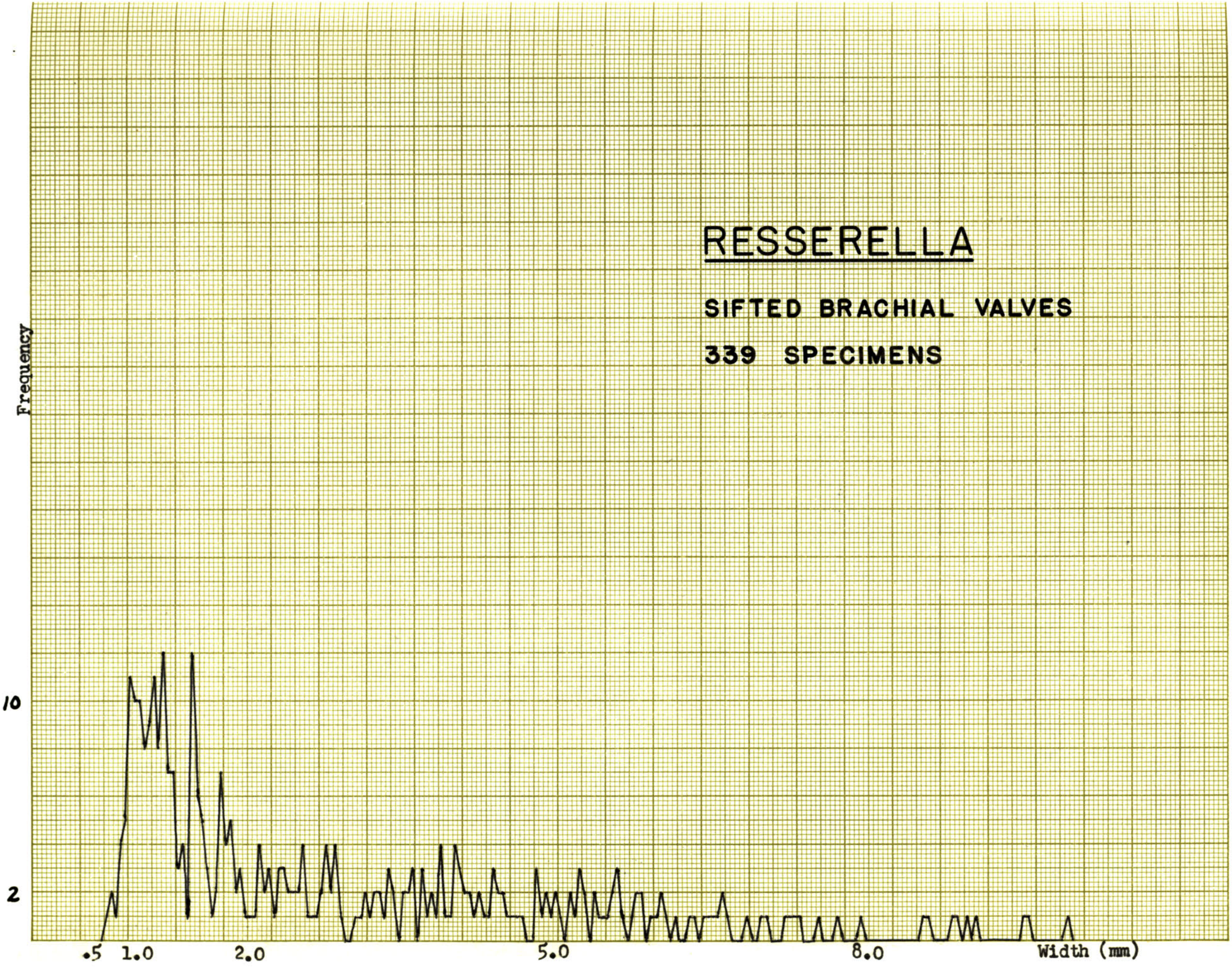

FREQUENCY
70
60
50
40
30
20
10
2
RESSERELLA
COMBINED WHOLE TESTS
1063 SPECIMENS
.5
1.0
2.0
5.0
8.0
Width (mm)

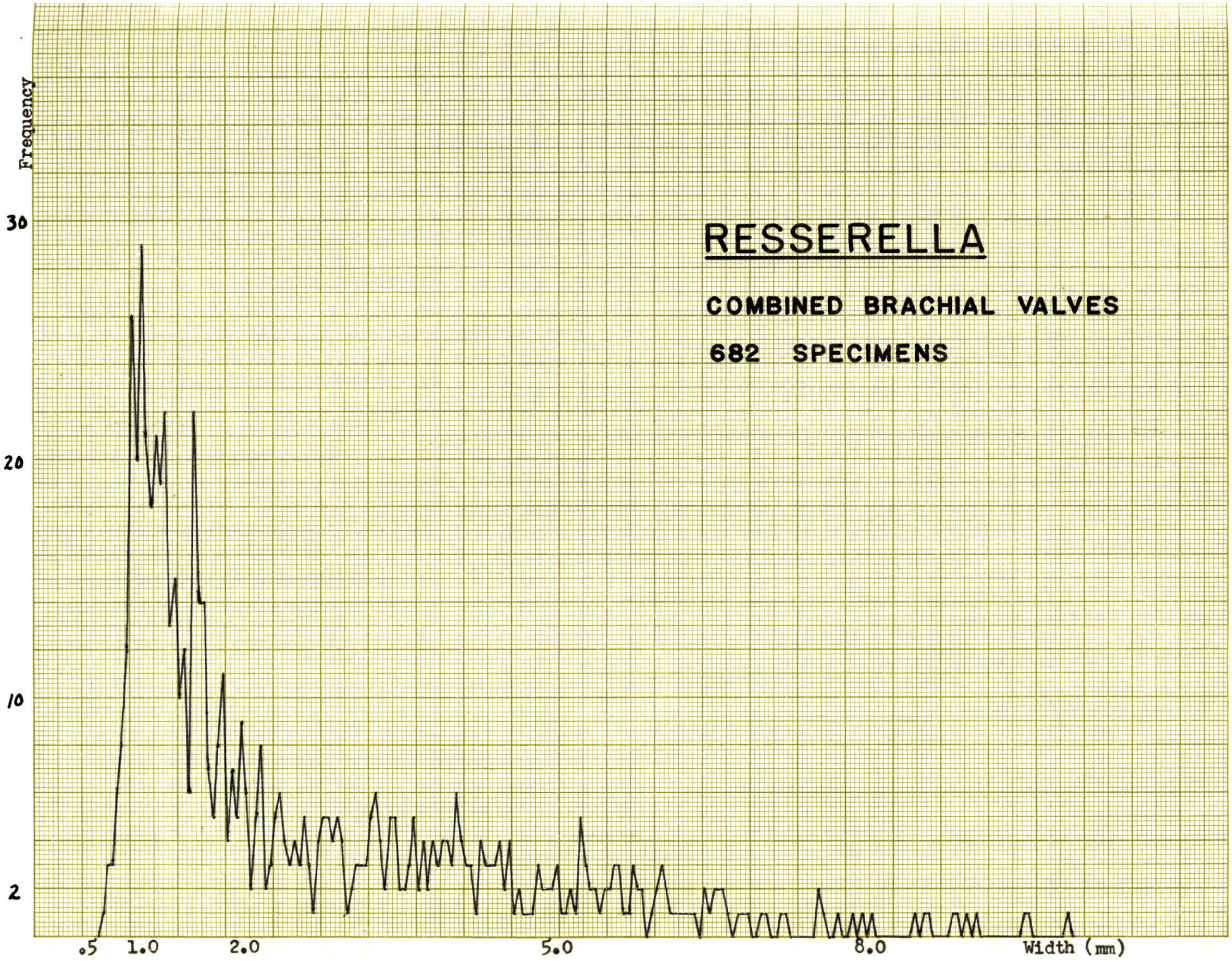

RESSERELLA
ELUTRIATED PEDICLE VALVES
275 SPECIMENS
Frequency
10
2
.5
1.0
2.0
5.0
8.0
Width
(mm)

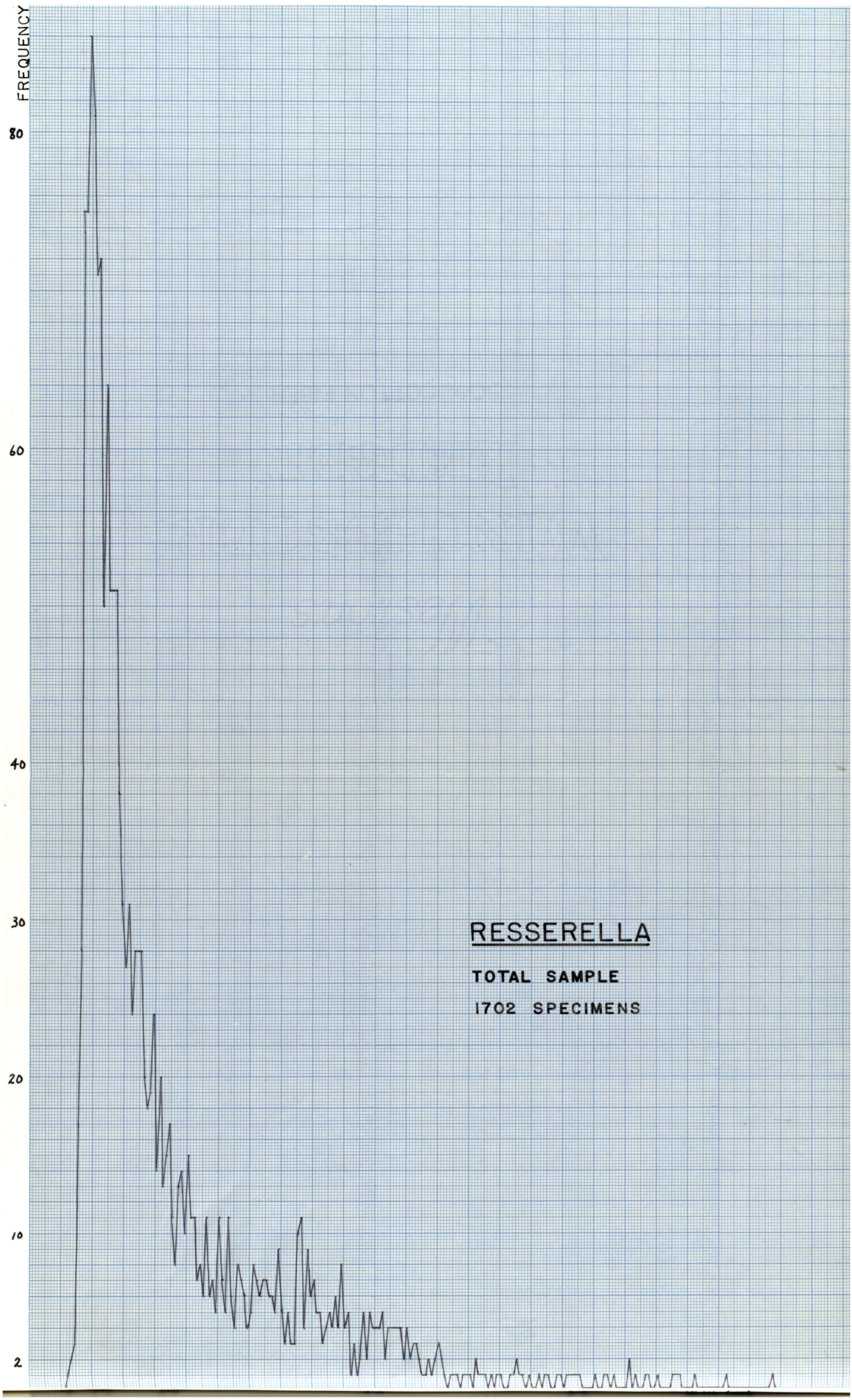

RESSERELLA
SIFTED PEDICLE VALVES
320 SPECIMENS
Frequency
16
10
2
.5
1.0
2.0
5.0
8.0
Width (mm)


RESSERELLA
COMBINED PEDICLE VALVES
595 SPECIMENS
Frequency
20
10
2
.5
1.0
2.0
5.0
8.0
Width (mm)

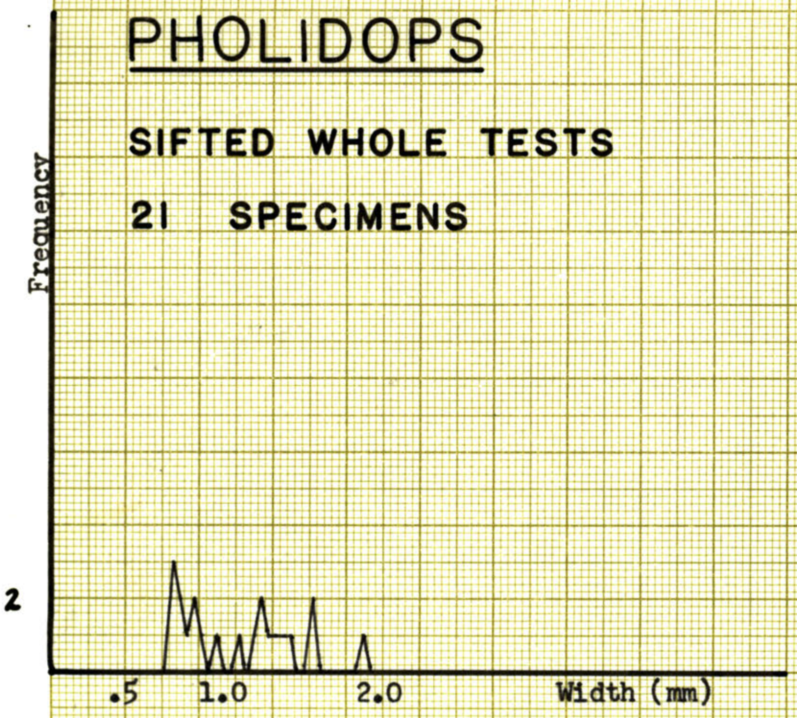

RESSERELLA
ELUTRIATED BRACHIAL VALVES
343 SPECIMENS
Frequency
20
10
2
.5
1.0
2.0
5.0
8.0
Width
(mm)

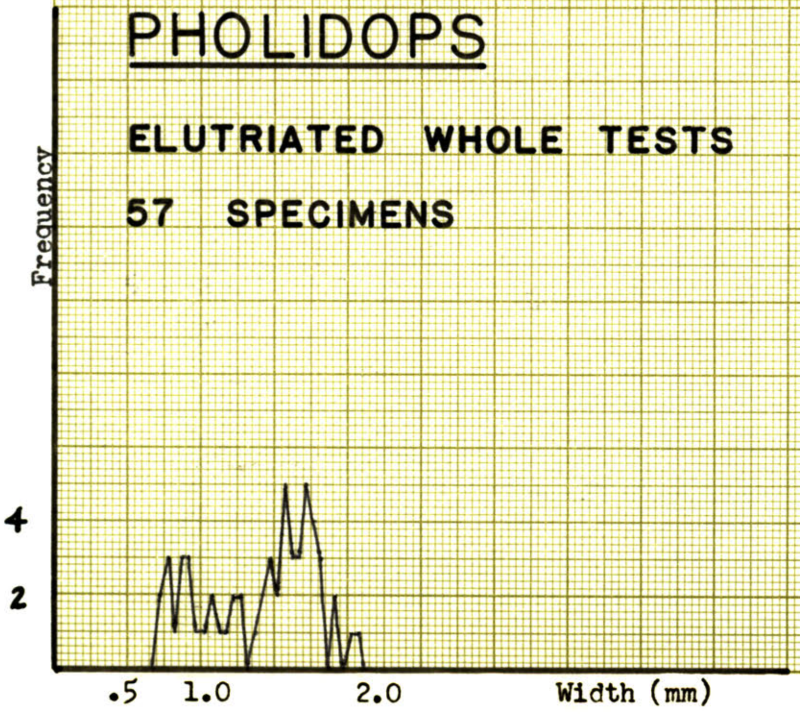

RESSERELLA
SIFTED BRACHIAL VALVES
339 SPECIMENS
Frequency
10
2
.5
1.0
2.0
5.0
8.0
Width (mm)

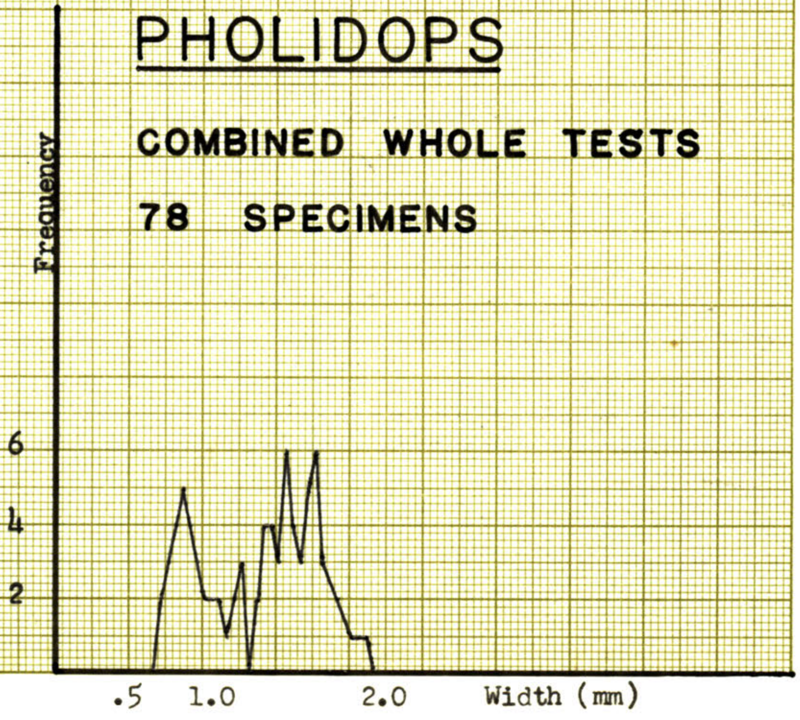

RESSERELLA
COMBINED BRACHIAL VALVES
682 SPECIMENS
Frequency
30
20
10
2
.5
1.0
2.0
5.0
8.0
Width (mm)

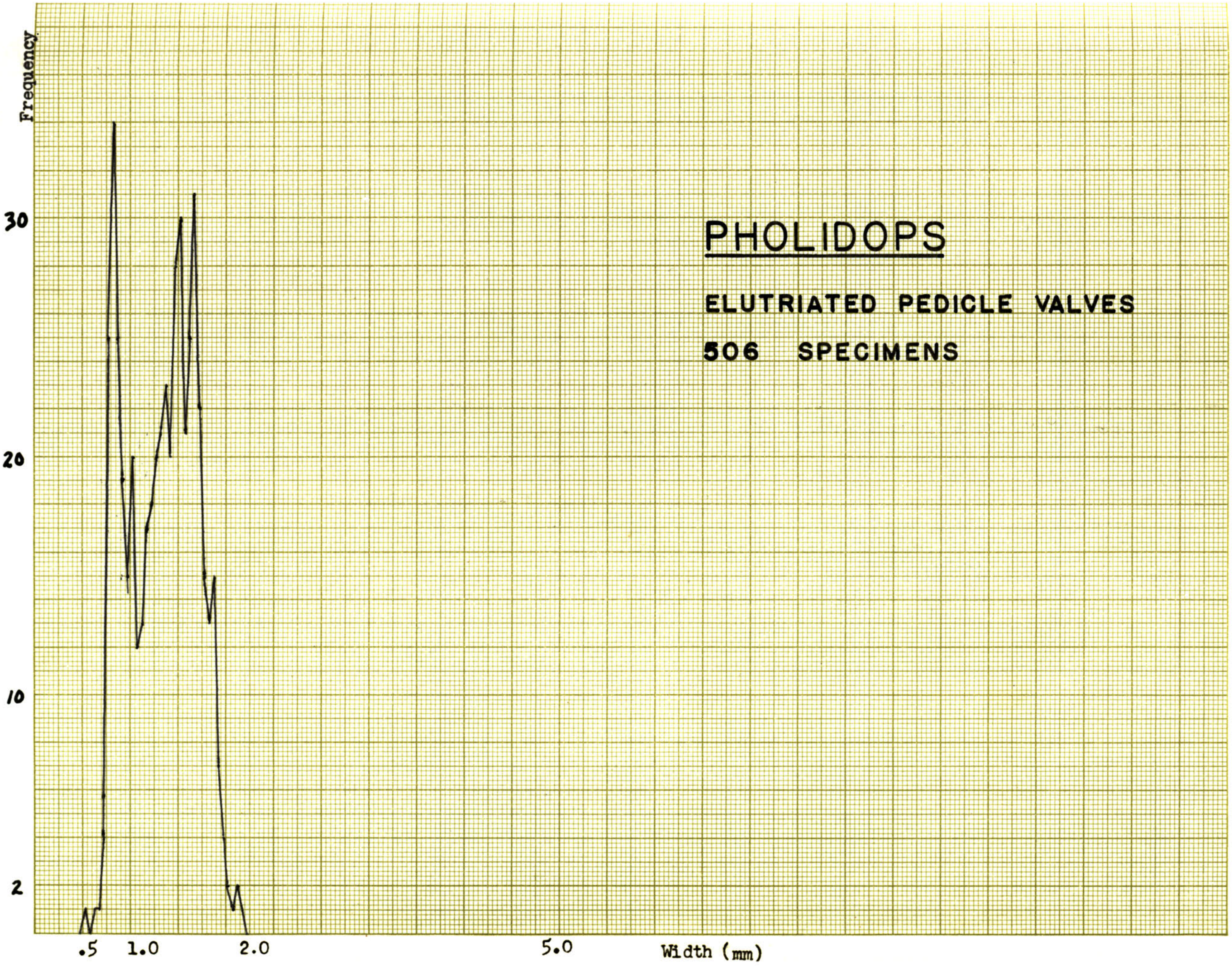


FREQUENCY
80
60
40
30
20
10
2
RESSERELLA
TOTAL SAMPLE
1702 SPECIMENS

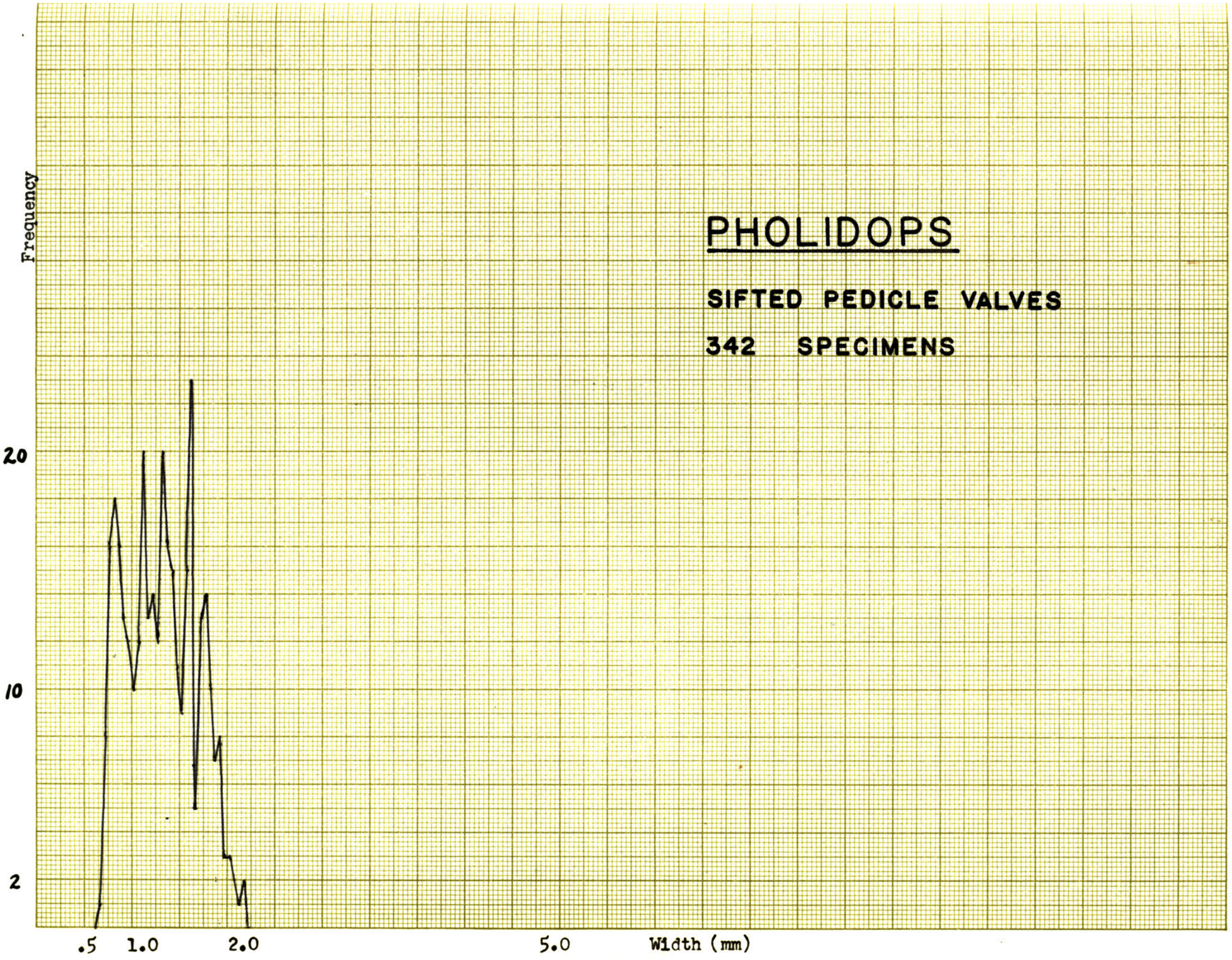

PHOLIDOPS
SIFTED WHOLE TESTS
21 SPECIMENS
Frequency
2
.5
1.0
2.0
Width (mm)

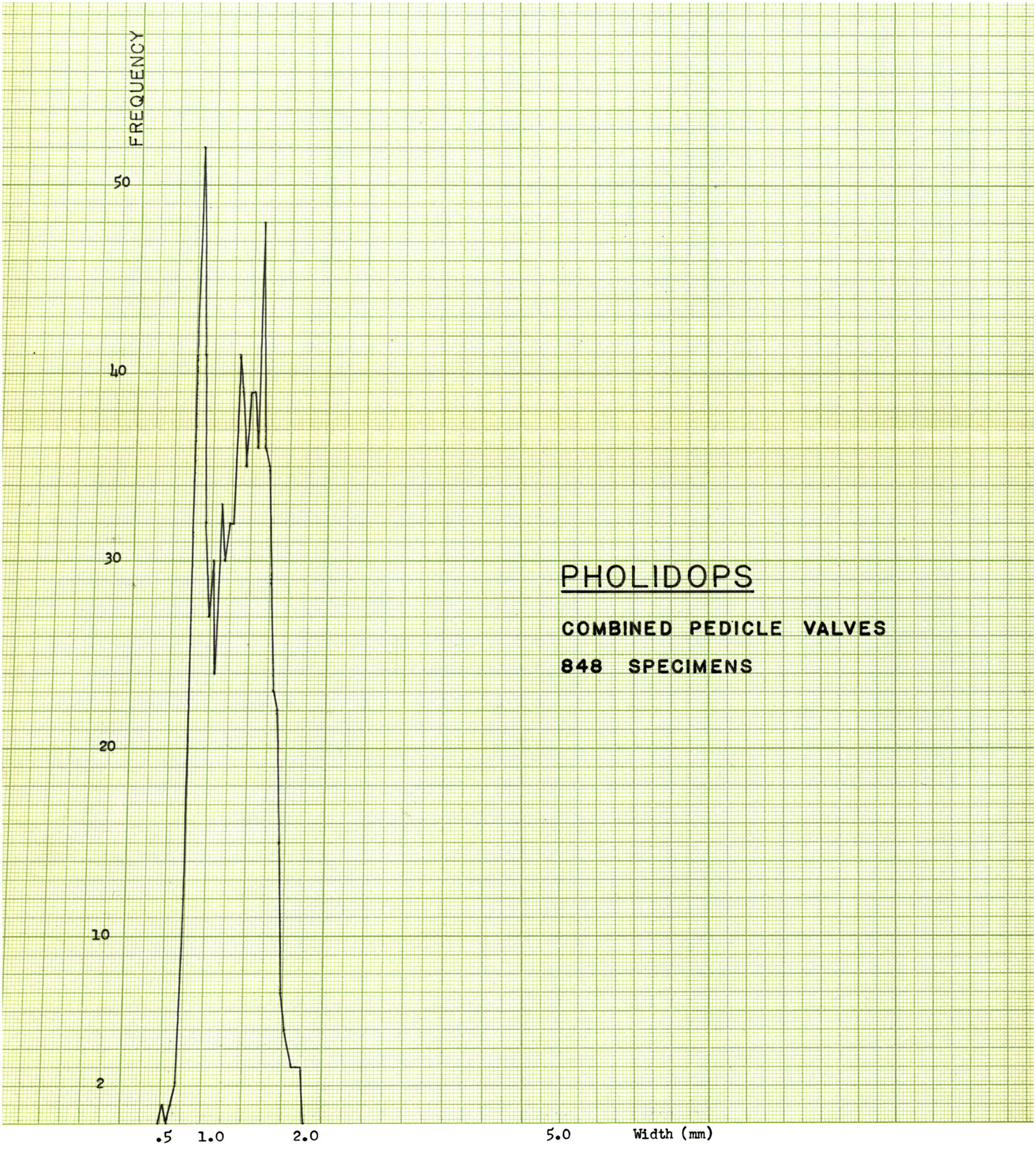

PHOLIDOPS
ELUTRIATED WHOLE TESTS
57 SPECIMENS
Frequency
4
2
.5
1.0
2.0
Width (mm)

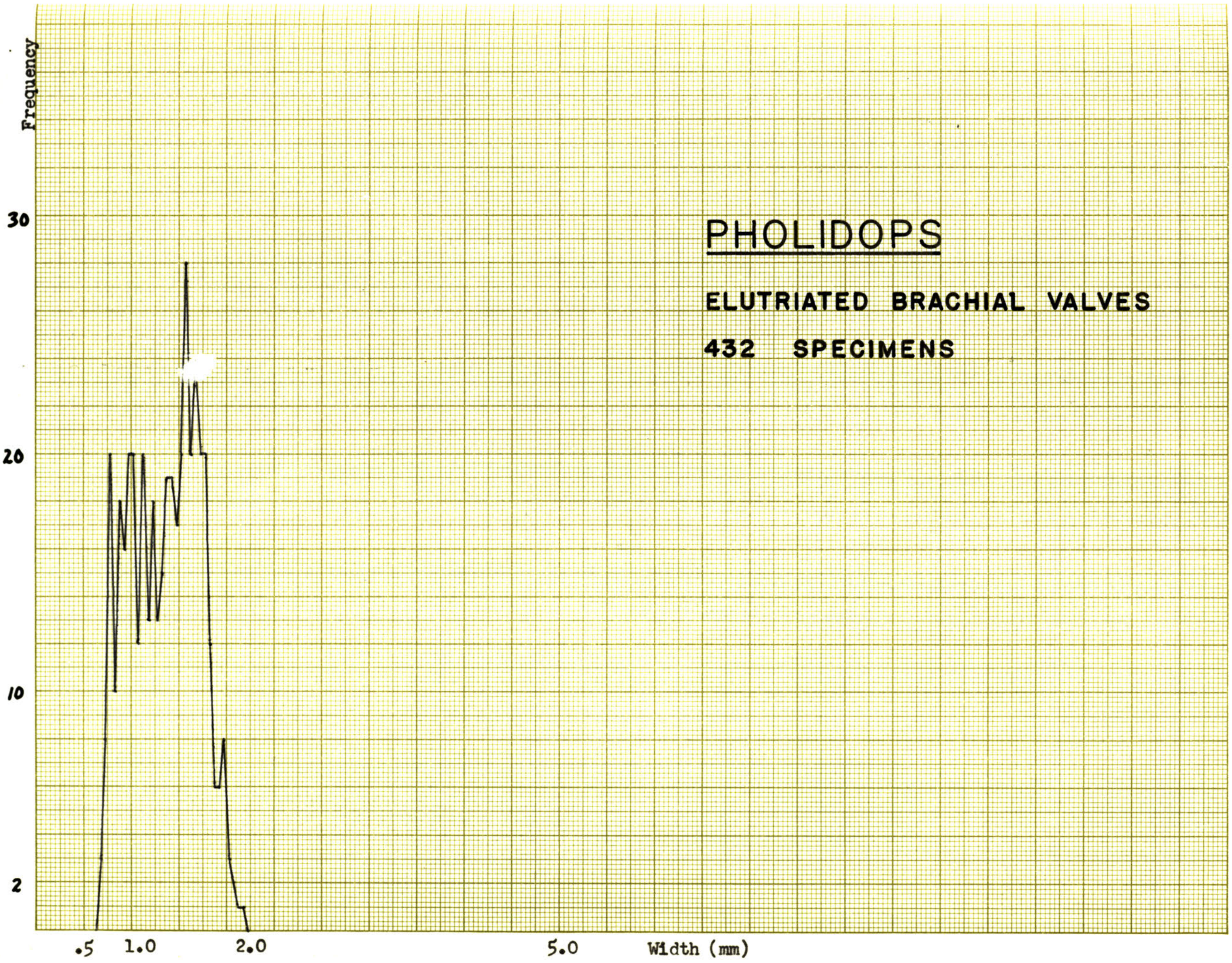

PHOLIDOPS
COMBINED WHOLE TESTS
78 SPECIMENS
Frequency
6
4
2
.5
1.0
2.0
Width (mm)

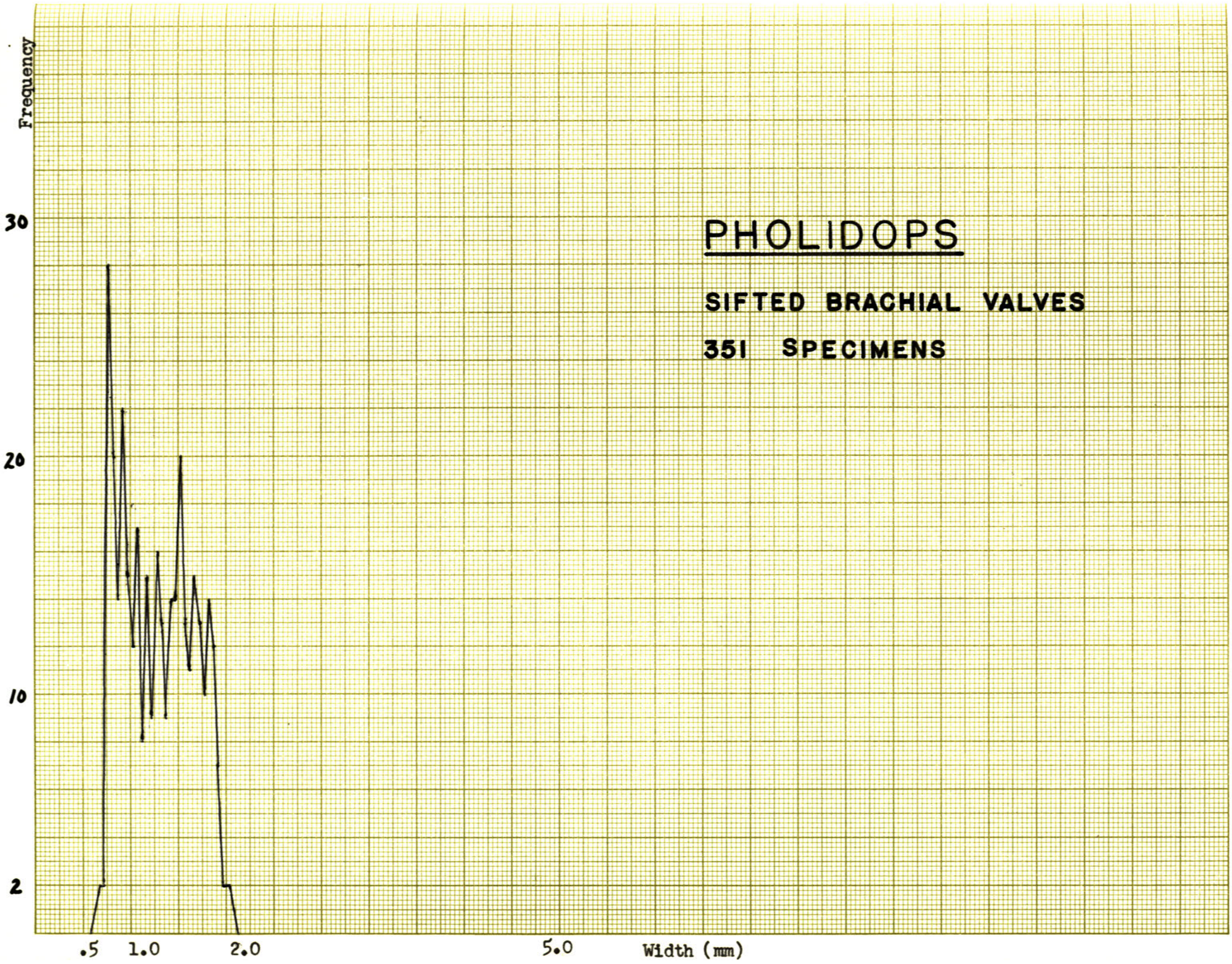


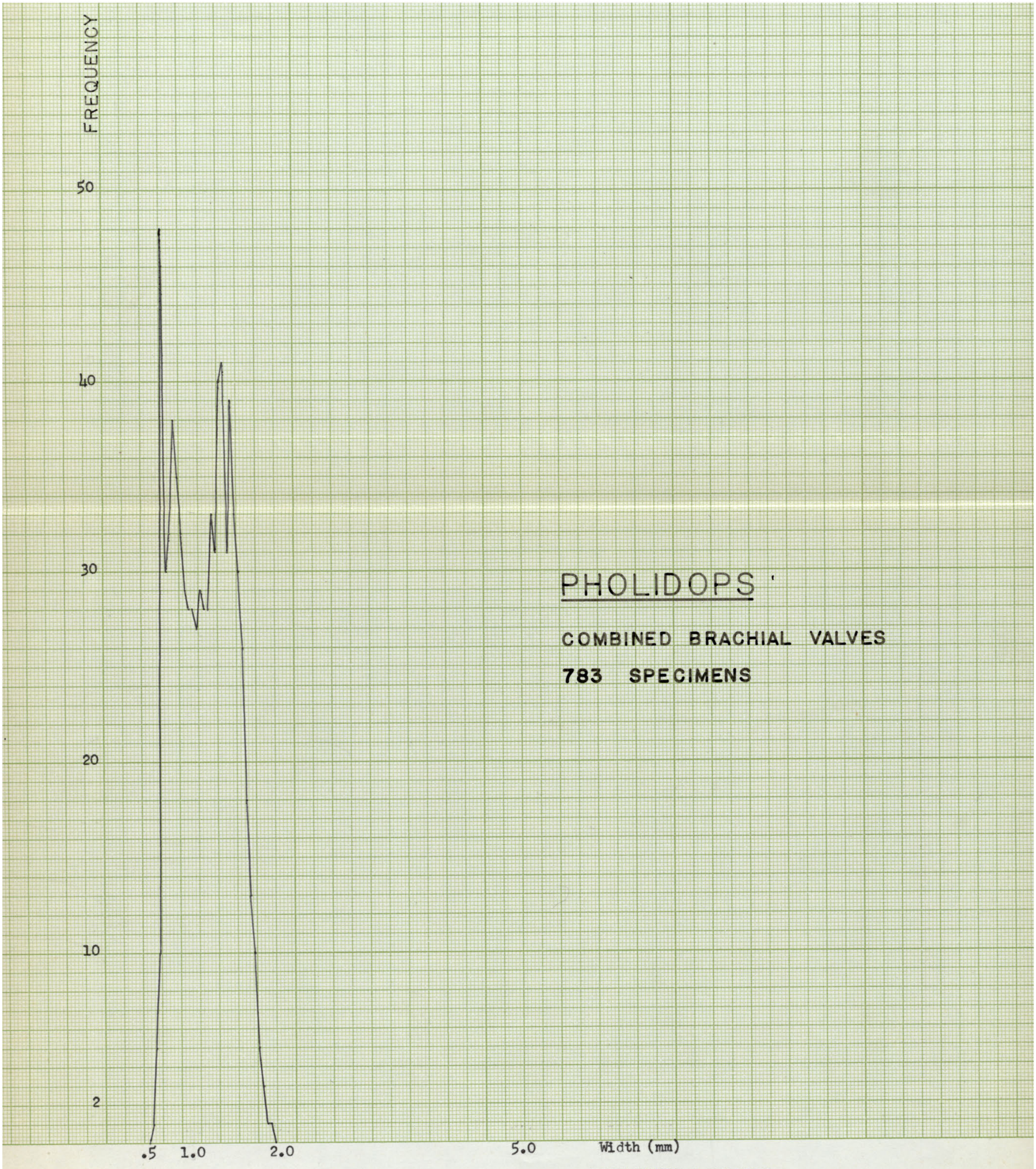
PHOLIDOPS
ELUTRIATED PEDICLE VALVES
506 SPECIMENS
Frequency
30
20
10
2
.5
1.0
2.0
5.0
Width (mm)


PHOLIDOPS
SIFTED PEDICLE VALVES
342 SPECIMENS
Frequency
20
10
2
.5
1.0
2.0
5.0
Width (mm)

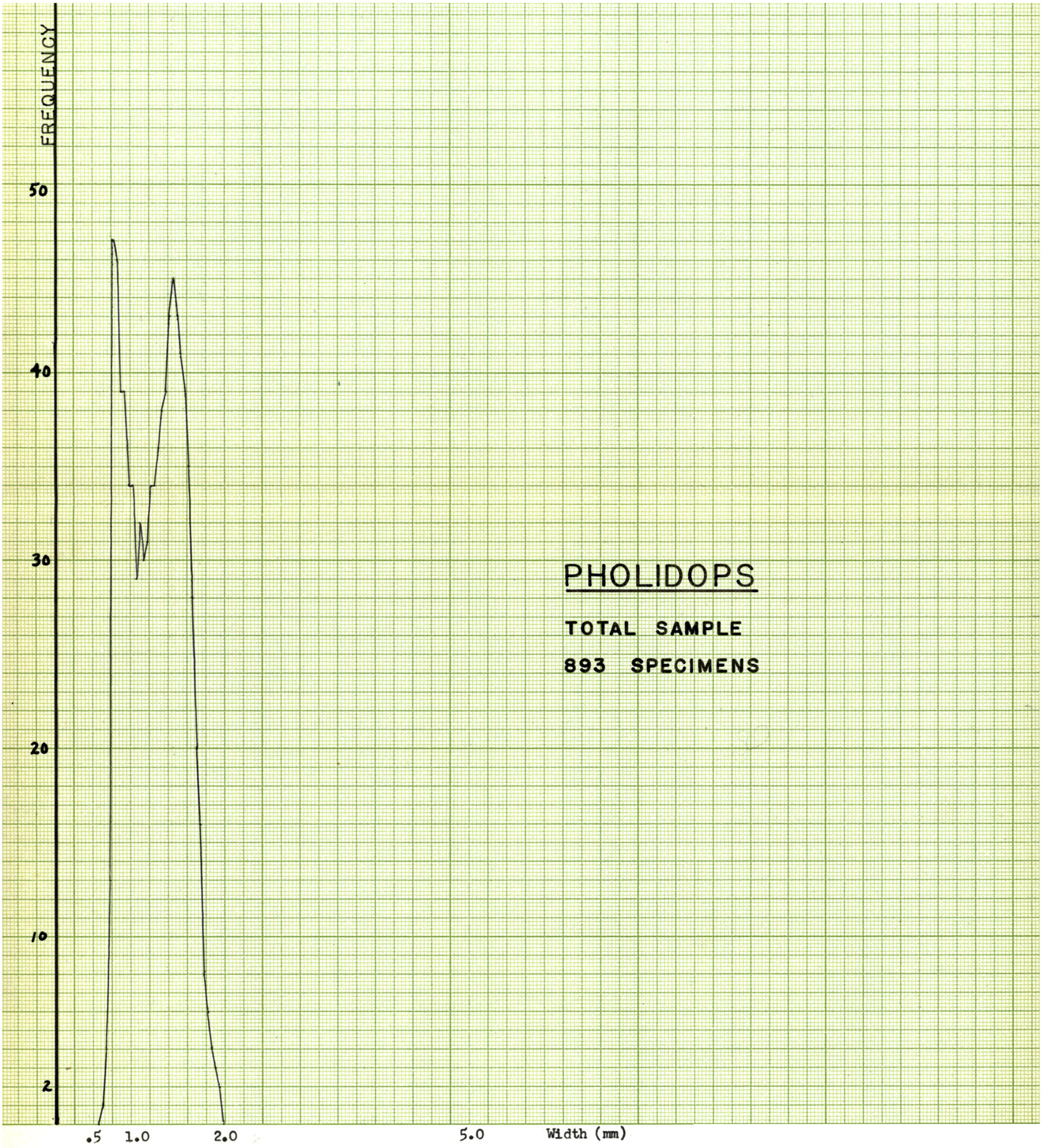

FREQUENCY
50
40
30
20
10
2
.5
1.0
2.0
5.0
Width (mm)
PHOLIDOPS
COMBINED PEDICLE VALVES
848 SPECIMENS


PHOLIDOPS
ELUTRIATED BRACHIAL VALVES
432 SPECIMENS
Frequency
30
20
10
2
.5
1.0
2.0
5.0
Width (mm)


Frequency
30
20
10
2
.5
1.0
2.0
5.0
Width (mm)
PHOLIDOPS
SIFTED BRACHIAL VALVES
351 SPECIMENS



K+E STANDARD CROSS SECTION MILLIMETER


FREQUENCY
50
40
30
20
10
2
.5
1.0
2.0
5.0
Width (mm)
PHOLIDOPS
TOTAL SAMPLE
893 SPECIMENS

CHAPTER 6

PREVIOUS WORK

6-1. Arthur J. Boucot.

As discussed in section 1-2, the theoretical considerations and criteria and many of the laboratory techniques employed in this study are the result of Dr. Boucot's early experimentation in this field. The interested reader should refer to his publications on this subject[1] for more detailed analyses of the subject matter. The respective abstracts are included herein.

Life and Death Assemblages Among Fossils (1953)

Abstract. Discrimination of fossil bivalve life assemblages and death assemblages comparable to Recent biocoenoses and thanatocoenoses is difficult. Size-frequency distributions have been analysed in terms of the biocoenosis of the following: wave action, solution and abrasion, lower survivorship curve, in addition to the biological and physical forces tending to modify the initial distribution. The ratio of articulated shells to disarticulated shells is considered to be a function of time and to be related to the ease with which the shell may be disarticulated by biological and physical agencies. The departure from unity of the ratio of matching opposite valves is is thought to be caused by the disruptive effects on the biocoenosis of the following: wave action, solution and abrasion, lower limit of observation, selective action of predators, scavengers and boring or triturating organisms. Comparison of the population densities observed among living forms may aid in differentiating between life and death assemblages among fossils. Aplication of some of these criteria to assemblages obtained from the Lower Devonian of northern Maine suggests the presence of five death assemblages plus one life assemblage.

It should be noted that the "life assemblage" reported above is not a true (or complete) one, but has been modified by the removal of most of the specimens less than 3.0 mm. in size. This distinction is an important one.

1 see Bibliography

Distribution of Brachiopod and Pelecypod Shells by Currents (1958)

Abstract. A statistical method of discrimination between life and death assemblages of brachiopods in fossil shell beds is demonstrated. The method utilizes the relative numbers of pedicle and brachial or right and left valves present in a sample of shell bed as well as the relative numbers of large and small shells and the relative numbers of articulated and disarticulated specimens.

Application of this method to a brachiopod-rich sample of a shell bed from strata of Early Devonian age in northern Maine shows that two of the contained species are indigenous whereas a third is not. The relationship between the number of articulated and disarticulated valves reveals that one of the two indigenous species has a unit disarticulation rate about eight times greater than the other. The extreme rarity of certain species in any one area is illustrated by the fact that in a sample of almost 5,000 specimens, one species is represented by only one specimen.

Theoretical considerations of the transportation of articulated and disarticulated shells suggest that by contouring the amount of disarticulation of a species from a region it should be possible to locate the source area from which the shells came. It should also be possible to locate the source area by contouring the ratio of the disarticulated opposite valves of a species from one region.

The two indigenous species reported above exhibit normally distributed size-frequency curves and should be considered modified life assemblages. Neither species has appreciable specimens smaller than 5.0 mm.

CHAPTER 7

CONCLUSION

7-1. Specific Conclusions.

The total Resserella population is a true life assemblage, exhibiting an extremely skew mortality curve. The resultant survivorship curve[0] has ideal Type III positively skew properties. The population either represents one set[1], or several sets having uniform mortality rates.

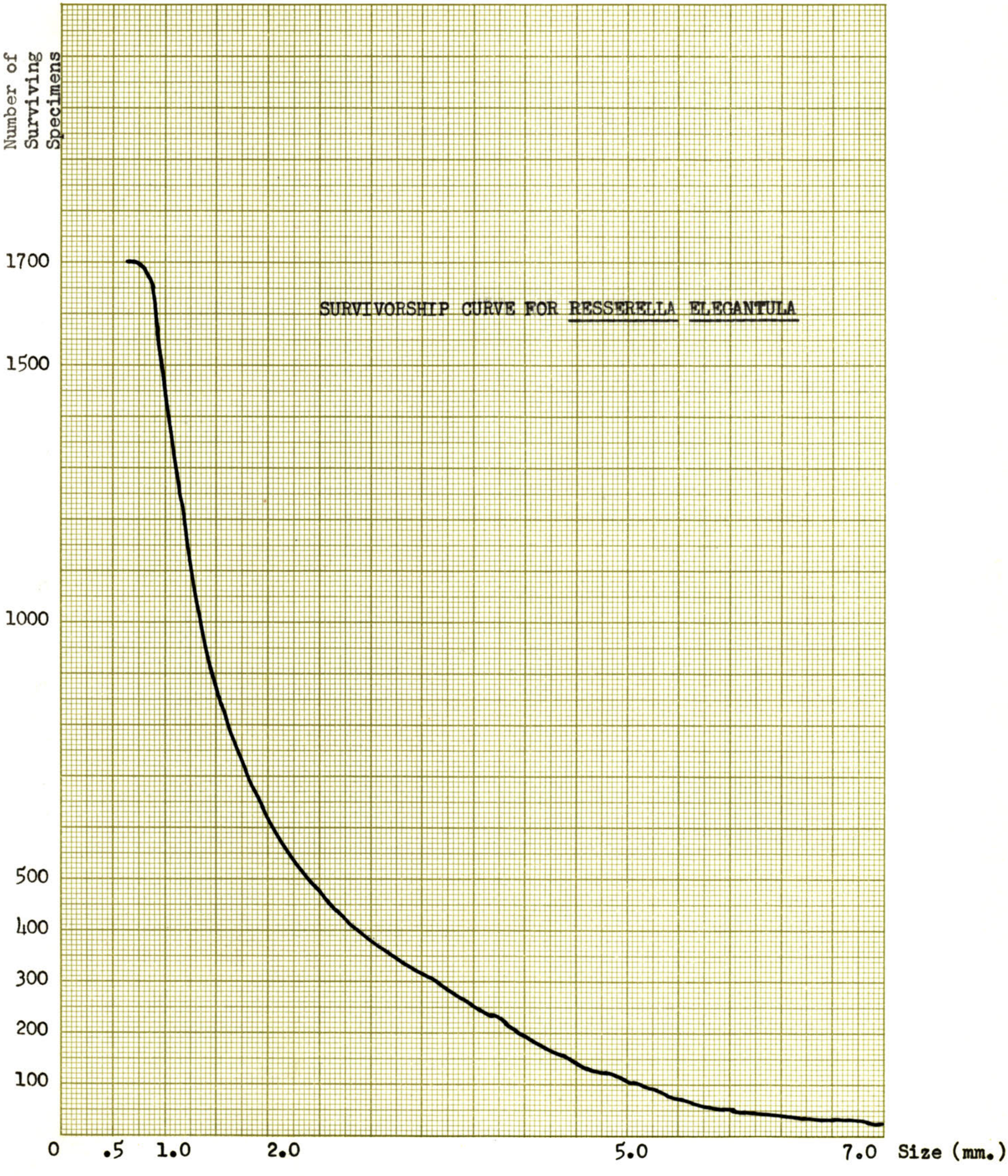
The disarticulated brachial and pedicle valves vary by 12.8%, considerably more variation than the 1.6 and 2.3 per cents reported by Boucot (1958) for Leptocoelia and Platyorthis. However, the opportunity for breakage and loss during collection, transportation, and laboratory preparation is much greater with a loosely compact sample of this sort. In lieu of this, and the fact that the previously mentioned samples contained negligible small specimens (less than 5.0 mm.), this percentage variation is reasonable. The largest variation is with the elutriated sub-sample in the smallest size group, indicating possible elutriation loss. It is also possible that some specimens passed through the sieve into the unsorted smaller (less than 0.5 mm.) size group and will be recovered later.

The Resserella disarticulation ratio[2] is 0.625. The population density of the Resserella life assemblage (Silurian, Mulde Marl) is 3280 specimens per cubic foot.

0 Figure 5
1 Boucot (1953): "The term 'set' as used by the marine biologist

(cont.)

Figure 5


Number of Surviving Specimens
1700
1500
1000
500
400
300
200
100
0
.5
1.0
2.0
5.0
7.0
Size (mm.)
SURVIVORSHIP CURVE FOR RESSERELLA ELEGANTULA

The Pholidops also represent a true life assemblage with a very skew mortality curve. However, this population contains at least two sets having slightly different mortality rates. This is evidenced by the bimodal skew distribution[3].

The disarticulated brachial and pedicle valves vary by 7.7%. The disarticulation ratio is 0.087 and the population density (for the specific age and locality) is 1720 specimens per cubic foot.

(Footnotes continued from preceding page)

refers to the larvae, of one species, that settle down on a particular portion of the bottom after they have passed through a planktonic stage. The larvae spawned at any one time and place may be the source of the set at a number of localities, their distribution being dependent upon the transporting currents. Set is not synonymous with rate of reproduction."

2 see Boucot (1958), page 328

3 see Boucot (1953), page 29

7-2. Significance.

The results are most significant insofar as they represent the first laboratory description of a true life assemblage -- and the corresponding first laboratory proof of a Type III survivorship curve. These results are of interest to two scientific groups, Paleoecology and Marine Biology, as discussed in sections 6-1 and 6-2.

7-3. Plans for Future Study.

Future plans entail completion of the analysis of this sample, followed by analysis of a second sample, and comparison of the two.

Regarding the Gotland sample, completion includes: sorting and measurement of the specimens of Resserella and Pholidops smaller than 0.5 mm. and inclusion with the thesis data; analysis of the remaining species, and computation of mathematical expressions for the mortality and suvivorship curves.

The second sample, taken from the Buildwas beds (Wenlock group) of Great Britain, contains the outward characteristics of a life assemblage, as did the Gotland sample, and is approximately three times as large. This sample shall be completely analysed, making use of insight gained from the first experiment. The results of the two samples will then be correlated, including comparison of mortality rates and survivorship curves, since both samples are approximately the same age.

The resultant study shall then be prepared for publication.

APPENDIX

Size-Frequency Data for

Resserella elegantula

and *Pholidops implicata*

Section A-1. Resserella elegantula.

Millimeter equivalents	Measured Units*	400 Sifted Complete Tests	663 Elutri-ated Complete Tests	320 Sifted Pedicle Valves	275 Elutri-ated Pedicle Valves	339 Sifted Brach-ial Valves	343 Elutri-ated Brach-ial Valves	1702 Total Resserella Specimens
.50	11.0							
.52	11.5							
.55	12.0							
.57	12.5							
.59	13.0		1					1
.61	13.5							
.64	14.0		2					2
.66	14.5							
.68	15.0		2		1		1	3
.70	15.5	1	2					3
.73	16.0	5	8			1	2	14
.75	16.5	2	2		2		1	6
.77	17.0	5	13	1	5	2		22
.80	17.5	6	7	1		1	3	17
.82	18.0	17	34	5	3		2	58
.84	18.5	8	9	1	1			18
.86	19.0	14	34	5	3	4	4	57
.89	19.5	6	14	3	2	2	3	25

.91	20.0	15	36	10	4	3	4	61
.93	20.5	8	14	4	3	4	3	29
.95	21.0	8	26	11	6	7	12	52
.98	21.5	7	11		3	2	3	22
1.00	22.0	8	26	6	9	8	7	49
1.02	22.5	7	11	5	1	3	5	25
1.05	23.0	11	19	8	6	7	14	47
1.07	23.5	3	7	1	2	2	4	14
1.09	24.0	6	14	10	6	6	9	36
1.11	24.5	5	13	4	2	1	4	24
1.14	25.0	12	16	3	9	8	5	40
1.16	25.5	5	4	4	2	2	1	13
1.18	26.0	7	15	5	8	9	9	38
1.20	26.5	5	5	3	4	3	4	17
1.23	27.0	7	15	6	6	5	7	34
1.25	27.5	7	8	3	2	3	5	21
1.27	28.0	7	9	8	4	9	5	30
1.30	28.5	2	4	1	2	4	2	11
1.32	29.0	10	10	3	4	3	4	27
1.34	29.5	2	3	1	1	1	4	9
1.36	30.0	4	10	1	6	6	4	22
1.39	30.5	1	2	3	3	1	1	7
1.41	31.0	3	8	4	5	2	6	20
1.43	31.5	1	8		2	2	1	11
1.45	32.0	5	6	5	4	2	7	20
1.48	32.5	3	2	3	3	1	2	10
1.50	33.0	3	7	4	2		3	14

	33.5		3	3	1	2	2	7
	34.0	3	5	5	3	10	8	21
	34.5	3	3	2		3	1	9
	35.0	7	5	4	1	3	7	19
1.61	35.5	1	2	3		1	2	6
1.64	36.0	3	12	4		4	7	22
	36.5	2	4	4	2	2		11
	37.0	2	2		6	1	4	9
	37.5	1	5	2	1		2	8
	38.0	1	5	2	1	1	2	10
	38.5	3	4	2	1		4	10
	39.0	3	3		1	2	2	9
	39.5	1	5			3	2	8
1.82	40.0	3	8	1	2	4	2	16
1.84	40.5	3	3		4	1	3	8
	41.0	1	2	2	1	3		6
	41.5	3	3	1		4		9
	42.0	5	3	1	3	1	2	11
	42.5		4	1	1			5
	43.0	4		2	1	2	3	8
	43.5		4		1		1	5
2.00	44.0	2	2		4	3	5	10
	44.5	2	4	1		1	2	8
2.05	45.0	1	4	4	2		3	9
2.07	45.5	2	3	1				6
	46.0	1	2	2	1	1	1	5
	46.5		1		2	1	1	3
	47.0	1	2		1		3	5

	47.5	1	1	1		1	1	4
	48.0		2	5	2	3	3	9
	48.5		2	3		1		4
	49.0	1	6	3	2	1		10
	49.5			1		1		1
2.27	50.0	2	4	1	3	2		9
2.30	50.5	1	2	1	2			5
	51.0	5	2		2	1	4	10
	51.5	1	2		1	1	1	4
	52.0	2	2		2	2	2	7
	52.5	1	3	2	1	2	1	7
	53.0	2	1		1	1		4
	53.5	1	1	1	1		1	4
	54.0			2	3	2		3
	54.5	2		2				3
	55.0	1	1	2		2	2	5
	55.5	1		1				1
	56.0	1	1	2	1	2	1	5
2.57	56.5	2	1	1		3		5
2.59	57.0	3	1		2	1	1	6
	57.5		1					1
	58.0	1	2	1	1	1	2	5
	58.5		1					1
	59.0	2	2	2	1	1		6
	59.5				1			1
	60.0			1	3	1	3	4
	60.5		1	2	2			3
	61.0	1	2	2	3	2	3	8

	61.5		2	2		1		4
	62.0			2	1	3	1	3
	62.5	1		1	1	1		3
2.86	63.0			2		1	2	2
2.89	63.5			3	2	2		4
	64.0	2	3	1	1	2	1	7
	64.5		1		1	1		2
	65.0		2		1		3	4
	65.5		2		1		3	1
3.00	66.0	1	1	1	1		1	3
	66.5	1	1	1				3
	67.0	1	3		1		2	5
	67.5	1			2	1		3
	68.0	1	1	1	1		2	4
	68.5	1		1				1
	69.0	1	2	1		1	2	5
	69.5		1	1				1
	70.0	1		1	1	2	1	3
	70.5						2	1
3.23	71.0	1	1		1	1	2	4
3.25	71.5	1	1		1			2
	72.0	1	1	1	1	2	4	6
	72.5		1	1		1	2	3
	73.0	2	1	1		1		4
	74.0	2	2	1	1	1		5
	74.5	1		1		1		2
	75.0	1	2			2	2	5
	75.5	1	1	1	1		1	3

	76.0	1			3	2	1	4
	76.5		1		2		1	3
	77.0	1	1	1	1		1	3
	77.5			1		1		2
	78.0		2	1	2	1		4
	78.5				1	1		1
	79.0		2	1		1	1	4
3.61	79.5	1	1	1		1	1	4
3.64	80.0		3		2	2	1	5
	80.5			1		1	1	1
	81.0	1	1		2		1	4
	81.5					2		1
	82.0			1	1	1	1	2
	82.5	1		1		1		2
	83.0	1			3		1	3
	83.5					1		1
	84.0			1	1	1	2	2
	84.5			1	1	1	1	2
	85.0				2		1	1
	85.5	1	2	2				4
	86.0	2	1	1		4		6
	86.5	1		2				2
	87.0	2	3	3	1	1	3	9
	87.5			1			1	1
	88.0			2	2	1	1	3
4.00	88.5		1	2		2	1	3
	89.0	3	1		1	2	1	6
4.07	89.5		1	1		1		2

4.09	90.0	1		2	2	2	1	4
	90.5	1	1	2		1		3
	91.0	3				1	1	4
	91.5			1				1
	92.0		2	1		2	1	4
	92.5			2		1		2
	93.0	1	1	2	1			3
	93.5					1	1	1
	94.0	1				1	1	2
	94.5			2			1	2
	95.0		1		1	1	1	2
	95.5	1						1
	96.0	2		1		1	2	4
	96.5			1		1		1
	97.0	1		1		2		3
	97.5				1	2		2
	98.0	2	1	1			2	4
	98.5	1	1	1	1	1		3
	99.0			1		1		1
	99.5	2						2
4.55	100.0	2	1	1	1	1	3	6
4.57	100.5			1	1	1		2
4.59	101.0	1	1	1				2
	101.5		2					2
	102.0	1		1	1	1	1	3
	102.5							
	103.0					1		1
	103.5	1			1			1

	104.0			2	1		1	2
	104.5							
	105.0						1	1
	105.5			1		2		1
	106.0					1		1
	106.5	1	1					2
	107.0	1	1			1	1	3
	107.5							
	108.0		1	1		2		2
	108.5				1	1		1
	109.0	2	1		1		1	4
	109.5	1		2				2
5.00	110.0		1			2	1	2
	110.5	1						1
	111.0	1						1
	111.5	1						1
	112.0	1		2	1		1	3
	112.5		1	1	1	1		3
5.14	113.0	2				1		2
5.16	113.5	1				1		1
	114.0			1				1
	114.5					1	1	1
	115.0		1	1	1	2	1	3
	115.5					1		1
	116.0	1		2		1	1	3
	116.5							
	117.0	2	1				2	4
	117.5	1				1		2

	118.0			2	1	1		2
	118.5		1					1
	119.0		1	2	1	1		3
	119.5		1					1
	120.0			1		1	1	1
	120.5		1		1	1	1	2
	121.0	1	1					2
	121.5					1	1	1
	122.0				1	1		1
	122.5					1		1
	123.0	1		1		2		2
	123.5	1						1
	124.0			2		1		2
	124.5	1						1
	125.0			1			1	1
	125.5							
	126.0					1	2	1
	126.5							
5.77	127.0					2		1
	127.5				1			1
	128.0					2		1
	128.5	1						
	129.0							
	129.5							
	130.0		1	1	1	1		2
	130.5							
	131.0	1		1	1	1	1	3
	131.5					1	1	1

6.00	132.0		1		1		1
	132.5					1	
	133.0				1		1
	133.5						
	134.0					1	
	134.5						1
	135.0				1		
	135.5						
	136.0					1	1
	136.5		1				1
	137.0					1	
	137.5						
	138.0				1		
	138.5						1
	139.0				1		
	139.5	1					1
	140.0						
	140.5						
	141.0				1	1	1
	141.5						
	142.0				1		
	142.5			1		1	1
	143.0		1		1		1
	143.5						
	144.0				1	1	1
	144.5						
	145.0		1		2		1
	145.5				1		1

	146.0							
	146.5							
	147.0							
	147.5						1	
	148.0							1
	148.5						1	
	149.0							
	149.5							
	150.0				1	1		1
	150.5							
	151.0				1			1
	151.5							
	152.0							
	152.5							
	153.0					1		
	153.5							1
7.00	154.0					1		
	154.5							
	155.0				1			1
	155.5							
	156.0	1	1	1				2
	156.5							
	157.0						1	1
	157.5						1	
	158.0					1		1
	158.5					1		
	159.0							
7.25	159.5					1		

160.0						1
160.5						
161.0				1		
161.5						
162.0						
162.5						
163.0		1				1
163.5						
164.0						
164.5					1	
165.0				1		1
165.5						
166.0					1	1
166.5						
167.0						
167.5						
168.0						
168.5						
169.0			1	1		1
169.5			1			
170.0	1		1			1
170.5						
171.0						
171.5					1	
172.0		1				1
172.5						
173.0						1
173.5						
174.0		1		1		1

	174.5						
	175.0		1				1
	175.5						
8.00	176.0	1				1	1
	176.5						
	177.0						
	177.5						
	178.0						
8.11	178.5						
	179.0						
	179.5						
	180.0			1			
	180.5						1
	181.0						
	181.5			1			
	182.0						
	182.5						
	183.0						
	183.5						
	184.0	1		1			1
	184.5						1
	185.0						
	185.5						
	186.0						
	186.5						
	187.0				1		1
	187.5				1		
	188.0						
	188.5						

	189.0							
	189.5							
	190.0							
	190.5							
	191.0							
	191.5							
	192.0	1	1					2
	192.5					1		
	193.0							
	193.5							
	194.0				1	1		1
	194.5							
	195.0							
	195.5							
	196.0					1		
	196.5							
	197.0							1
	197.5							
9.00	198.0	1				1		1
	198.5							
	199.0							
	199.5							
	200.0							
9.11	200.5							
	201.0	1						1
	201.5							
	202.0							
	202.5							

203.0						
203.5						
204.0						
204.5						
205.0		1				
205.5						
206.0	1					1
206.5						1
207.0		1				
207.5						
208.0				1		1
208.5			1			
209.0				1		
209.5						
210.0						
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211.0						
211.5						
212.0						
212.5						
213.0						1
213.5						
214.0						
214.5						
215.0						
215.5						
216.0						
216.5						

	217.0		1	
	217.5			
	218.0			
	218.5			
	219.0			
	219.5			
10.0	220.0			
	220.5			
	221.0			
	221.5			
	222.0			
	222.5	1		1
	223.0			
	223.5			
	224.0			
	224.5			
	225.0			
	225.5			
	226.0			
	226.5			
	227.0			
	227.5			
	228.0			
	228.5			
	229.0			
	229.5			
	230.0			
	230.5			
	231.0			

	231.5			
	232.0			
	232.5			
	233.0			
	233.5			
	234.0			
	234.5			
	235.0		1	
	235.5			
	236.0			
	236.5			
	237.0			
	237.5			
	238.0	1		1
	238.5			
	239.0			
	239.5			
	240.0			
	240.5			
	241.0			
	241.5			
11.0	242.0			
	242.5			
	243.0			
	243.5			
	244.0			
	244.5			
	245.0			

Section A-2. Pholidops implicata

Millimeter equivalents	Measured units*	21 Sifted Complete Tests	57 Elutri-ated Complete Tests	342 Sifted Pedicle Valves	506 Elutri-ated Pedicle Valves	351 Sifted Brach-ial Valves	432 Elutri-ated Brach-ial Valves	893 Total Pholidops Specimens
.50	11.0				1			
.52	11.5							
.55	12.0							
.57	12.5							
.59	13.0				1	1		1
.61	13.5					1		1
.64	14.0			1	1	1	3	3
.66	14.5			1			1	1
.68	15.0		2	7	4	2	7	12
.70	15.5			2	3	8	5	9
.73	16.0		3	14	22	20	15	38
.75	16.5	1		3	8	6	1	10
.77	17.0	2	1	15	26	14	9	36
.80	17.5		2	5	8	1	3	10
.82	18.0	2	1	11	17	13	15	29
.84	18.5			2	4	8	1	8
.86	19.0	1	3	11	15	14	15	31
.89	19.5			2	4	3	3	6
.91	20.0	2	1	10	11	12	17	28
.93	20.5			6	8	2	7	13
.95	21.0	1	1	4	12	10	13	21
.98	21.5		1	4	4	4	4	9
1.00	22.0		1	8	8	13	8	20

1.02	22.5	1		3	3		2	5
1.05	23.0		1	17	10	8	18	27
1.07	23.5		1	2	4	6	8	10
1.09	24.0			11	13	9	5	20
1.11	24.5		1	2	6		4	7
1.14	25.0		1	12	12	9	14	24
1.16	25.5	1		3	6	5	3	10
1.18	26.0		2	9	14	11	10	24
1.20	26.5			3	5	4	6	9
1.23	27.0			17	16	9	9	25
1.25	27.5			4	5	1	5	8
1.27	28.0	1	1	12	18	8	14	28
1.30	28.5			7	8	3	6	12
1.32	29.0	2	2	8	12	11	13	26
1.34	29.5			1	8	3	3	8
1.36	30.0	1	3	10	20	11	14	31
1.39	30.5		1	3	7	4	5	11
1.41	31.0	1	1	6	23	16	15	32
1.43	31.5	1	2	4	3	2	8	12
1.45	32.0		3	11	18	11	20	33
1.48	32.5		1	7	7	3	3	11
1.50	33.0	1	2	16	18	8	17	32
	33.5		3		6	5	6	12
	34.0			5	25	10	18	29
	34.5		3	7	6	2	5	13
	35.0		2	6	16	11	15	26
1.61	35.5		2	6	4	5	8	13
1.64	36.0	2	2	8	11	5	12	22
	36.5		1	3	6	4	4	10

	37.0		2	7	7	10	8	18
	37.5			2	9	3	2	8
	38.0			5	6	9	4	12
	38.5			2	3	1	2	4
	39.0		2	6	4	6	4	12
	39.5			1		2	4	3
1.82	40.0			2	4		4	5
1.84	40.5			1			2	2
	41.0		1	2	2	2	1	4
	41.5			1			1	1
	42.0		1	1	1	1	1	3
	42.5							
	43.0	1		1	2		1	3
	43.5			2	1		1	2
2.00	44.0							

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