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A SLIDE RULE FOR THE DETERMINATION OF INSTARS IN OSTRACOD SPECIES

BY
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CONTENTS

INTRODUCTION

An ostracod, like other crustaceans, grows by molting the old hard parts and secreting new and larger ones. The animal is enclosed in a bivalved carapace of chitin and calcite. Its body, which hangs down like a pouch from the dorsal part of the carapace, and the attached appendages are encased in chitin, with certain parts and the joints of the appendages coated with a thin flexible chitin which allows movement. Inasmuch as all soft tissues are covered by some kind of armor, the ostracod cannot add small increments to its body continuously and can reach a larger size only by breaking open and shedding all hard covering. Since increase in size occurs just during the brief interval before the new hard parts are secreted, the growth of ostracods is said to be discontinuous. Most of the animal's life is spent in fixed stages, called instars, and its ontogeny consists of a number of these stages. During each brief but crucial period of molting an individual not only increases in size but adds entire new appendages and organs, changes the form and function of the old appendages, and alters its shape. Consequently, in a species, the carapaces of the several instars will differ in size, shape, and details of structure.

Instars of fossil ostracods are more difficult to distinguish from one another than are those of living ostracods, because with rare exceptions, only carapaces or single valves are preserved and the rest of the anatomy is unknown. Recognition of immature instars and their assignment to species present serious problems to the micropaleontologist, so that dependable methods of solution need to be devised, before accurate work can be done in stratigraphy or before the evolution of the order can be understood. Specimens which differ in shape and ornamentation from any described ostracods and yet belong to a definite size group, sharply set off from any other group, may not constitute a new species but represent an immature instar of a species already established. Taxonomy would become confused indeed, if every instar were given a different trivial name. Care and discrimination are necessary to determine which differences are ontogenetic and which are specific. Kellett (1943, p. 616), writing on fossil ostracods, said that the "study of such early molts is as necessary to an understanding of ostracode classification and phylogeny as a knowledge of early chambers of the Foraminifera and ammonoids is to their classification."

Hiltermann and Kremp (1952, p. 708) discussed the problems encountered in their investigations of Upper Carboniferous ostracods and recommended procedures which apply excellently to all fossil ostracods. Among the procedures, they proposed statistical and graphical study of instars and wrote (1952, p. 708):

> Entsprechend den Ergebnissen *v. Keslings* erscheint es nötig, an einer grossen Anzahl von Individuen Länge, Höhe, Dicke und dgl. zu messen und graphisch darzustellen. Auf diese Weise lassen sich Einzelheiten über die sich ändernden Proportionen innerhalb der einzelnen Wachstumstadien (Instars) gewinnen. Grossenangaben von wenigen Exemplaren genügen nicht. (It appears necessary to measure and plot graphically the length, height, width, and other measurements of a great many individuals, corresponding to Kesling's results. In this way the characteristics of altered proportions can be determined within individual growth stages, or instars. Size details of only a few specimens are insufficient.)

Relatively few living ostracods have been thoroughly studied; hence, the immature instars of most species are still unknown. The first work on immature instars of live forms was done by Claus (1872, pp. 151–66), who investigated several species of fresh-water Cypridae. Molt stages of other fresh-water Cypridae were studied by Sars (1901, pp. 1–52), Müller-Calé (1913, pp. 113–70), Schreiber (1922, pp. 511–28), Scheerer-Ostermeyer (1940, pp. 349–70), and Kesling (1951*a*, pp. 94–114; 1951*b*, pp. 234–35). Scheerer-Ostermeyer (1940, p. 352) described the immature instars of *Limnocythere*, a fresh-water ostracod of the family Cytheridae, as well. Ontogenies of some marine ostracods have also been studied. Claus (1894, p. 5) reported immature instars of the Halocypridae; G. W. Müller (1893, p. 376) described those of the Halocypridae and (1894, pp. 176–78, 180–81, 183, 185) of the Cypridae, Cytheridae, Halocypridae, and Cypridinidae. Skogsberg (1920, pp. 132–44) studied instars of the Cyprinidae, Halocypridae, and Cytheridae; Elofson (1941, pp. 369–70) those of the Cypridinidae and Cytheridae.

More articles, however, have been written on the growth forms of fossil species than on those of the living. Immature instars of fossil ostracods were first described by Verworn (1887, pp. 27–31), but most work is more recent. Kellett (1929, pp. 197–98) reported immature instars of the Hollinidae; Schmidt (1941, pp. 29, 43, 47; Pls. 2–3) mentioned and illustrated those of some Paleozoic species; and Cooper (1945, pp. 368–75) studied those of a species of Kirkbyidae and (1946, pp. 42, 67, 77, 90, 93, 95) listed immature instars of Bairdiidae, Cypridae, Cytherellidae, and Hollinidae. Le Roy (1945, pp. 81–86) described instars of the Cytheridae; Kesling (1951*b*, p. 235; 1952*a*, pp. 247–90; 1952*b*, p. 776) studied instars of the Hollinidae and (1953*a*, pp. 21–23; 1953*b*, pp. 223–25) Beyrichiidae; Spjeldnaes (1951, pp. 745–55) wrote on immature instars on the Beyrichiidae; and Levinson (1951, p. 555) recorded them for the Primitiidae. Hanai (1951, pp. 422–23) reported instars of fresh-water Cypridae. Scott (1951, pp. 321–26) studied instars of the Leperditiidae; Scott and Smith (1951, pp. 329–35), those of fresh-water Cypridae. Sohn (1950*a*, pp. 427–34) made a general study of ostracod growth rates and (1950*b*, pp. 33–39) described immature instars of the Kirkbyidae and Miltonellidae. Fossil carapaces and valves of immature instars are assigned to species on the basis of several criteria. The following ontogenetic relationships appear to be valid: (1) Change in shape[1] is progressive from youngest instar to adult. (2) Valves of the adult are thicker than those of the immature (immature valves in some species are very thin and easily broken). (3) Extent of ornamentation increases during ontogeny. (4) Adductor muscle scar shifts progressively forward. (5) Hinge structures become more complex. (6) Posterior part of valve becomes proportionately larger. (7) Volume of the carapace increases, from one instar to the next, by about twice its former value. This last relationship is the most difficult to evaluate and to apply to growth stages, because it involves several measurements for each specimens and mathematical comparison of such measurements.

The slide rule described in this paper is useful for quick comparison of volumes, areas, and linear measurements of ostracods. If the adult of the species is known, one setting of the device will solve the instar number of a particular specimen. The slide rule also serves to show which measurements are most significant in separation of instars. It offers a convenient method of testing the dictum of Przibram (1931, p. 26) that crustaceans double their volume during each molt stage.

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[1] "Shape" is used in this paper in the sense that it was used by Needham (1950*b*, p. 116) who formulated his concepts as:

"form = shape + size."

Shape is determined by relative proportions, whereas form is the summation of relative proportions and absolute values of dimensions.

GROWTH CONCEPTS OF BROOKS AND PRZIBRAM

Brooks (1886, pp. 5, 105) studied the growth of stomatopods and concluded that each instar differs from the preceding instar by an increase in length which is a fixed percentage, and that this percentage remains constant for all instars in the ontogeny of a species. Fowler (1909, p. 224) applied the concept to another group of crustaceans, the ostracods, and termed it Brooks' Law.

Skogsberg (1920, pp. 132–44), who used Brooks' formula, compared only lengths. He concluded (1920, p. 147):

> The final result of my investigations is thus that the growth-factor during the post-embryonal development of the Ostracods is presumably an inherited factor, but it is rather strongly influenced by external circumstances; in addition in a number of species it is not quite the same during the whole post-embryonal development.

Przibram (1931, p. 26) calculated that crustaceans increase their weight to twice the former value during each molting, or ecdysis. From that, inasmuch as volume usually varies directly with weight, he concluded that the volume would also increase by a factor of 2 during each molting. From one instar to the next, that is, each linear dimension would become 1.25992 (the cube root of 2) times its former size. In computations Przibram used the factor 1.26. Kesling (1925*b*, p. 773) pointed out that the factor for growth of a single dimension would be exactly 1.25992 only if the shape of the animal remained the same from one instar to the next; that it would have a different value if the shape changed. Data on ostracod carapaces and valves indicate that the volume approximately doubles during each molt stage (Kesling, 1952*b*, pp. 773–77), so that Przibram's proposal that crustaceans double their size from one instar to another seems true for ostracods.

Needham (1950*a*) studied various reports of crustacean growth and compiled a bibliography of 81 references. He decided (1950*a*, p. 11) that in some crustaceans growth follows a constant geometric increment (which he called the "Przibram-factor") in size at each molt, but that in others the factor of increase "varies in almost every conceivable way."

In the graph shown in Figure 1 the length is plotted against the product of length, height, and width for carapaces of a beyrichiid ostracod from the Wanakah shale of western New York (Kesling, 1953*a*, pp. 19–24). Special double logarithm paper is used for the plotting in which the products of length, height, and width are ordinates on a logarithmic scale having cycles one-third the length of those for the abscissas. According to Przibram's concept, the lengths should fit into intervals of 1.25992 and the products into intervals of 2 on such paper; these dimensions are indicated in the figure by dotted lines. The × represents the length and the product of length, height, and width of an ideal specimen of that particular instar. Only one specimen failed to fit into the theoretical intervals of instars for both length and product. The instars of this species vary little in shape from the youngest to the adult, but separation into instars is distinct and the growth rate is remarkably close to that proposed by Przibram.

NUMBER OF INSTARS TO A SPECIES

The number of instars in the ontogeny of an ostracod appears to be constant for a genus. Insofar as is known, it is constant for certain families, but relatively few species have been studied and there may be exceptions. In fresh-water ostracods of the family Cypridae, Claus (1872, pp. 151–66) identified nine instars, of which only the final one was adult. His count has been substantiated by Müller-Calé (1913, pp. 113–70), Schreiber (1922, pp. 511–28), Sheerer-Ostermeyer (1940, pp. 349–50), and Kesling (1951*a*, pp. 94–114). Scheerer-Ostermeyer (1940, pp. 350–66) also reported nine in two families of fresh-water ostracods, Cytheridae and Darwinulidae.

Some marine ostracods have been reported as having fewer than nine instars. In specimens of *Philomedes globosus* (Lilljeborg) of the family Cypridinidae, collected during the Swedish Greenland Expedition, Skogsberg (1920, pp. 138–40) found seven free-living instars and, in addition, a very young instar in the brood space of the mother, which he presumed to be two instars younger than the smallest of the free-living. In specimens of *P. globosus* from the Gullmarfjord, however, Elofson (1941, p. 369) counted only six, of which the youngest was in the brood space of the mother; when he cultured the species in an aquarium, he concluded that only five immature instars existed in the material examined. Elofson (1941, p. 370) reported six instars in specimens of *Cypridina norvegica* Baird (family Cypridinidae), from the North Sea; Müller (1894, p. 185) six in *C. mediterranea* Costa, from the Mediterranean Sea; and Skogsberg (1920, p. 132) eight in *C. pectinata* Skogsberg, from the antarctic region.

In species of Halocypridae (= Conchoeciidae) Claus (1894, p. 5) and Müller (1894, p. 183) reported seven instars. Elofson (1941, p. 370) noted eight instars in three species of *Xestoleberis,* but there are nine in species of other genera of the family Cytheridae. He did observe, however, that young of species of *Xestoleberis* hatch from the egg with the same development of appendages as occurs in the second instar of other genera of the family. There is no published information on living marine ostracods of the families Asteropidae, Polycopidae, Bairdiidae (= Nesideidae), and Cytherellidae.

It is entirely possible that a species may have a different number of instars in different environments, as was suggested by Elofson (1941, p. 371). He remarked that not the same number of instars was reported for specimens of *Philomedes globosus* collected near Greenland (Skogsberg, 1920, pp. 138–40) as for those collected from Gullmarfjord (Elofson, 1941, p. 369), and, furthermore, that a different number of instars was given for species of *Cypridina* from the antarctic region (Skogsberg, 1920, p. 132) as for those from the Mediterranean Sea (Müller, 1894, p. 185) or from the North Sea (Elofson, 1941, p. 370). For both *P. globosus* and the species of *Cypridina* a greater number of instars was reported among the specimens from cold waters than among those from temperate waters. The number of instars of some other crustaceans has been ascertained to vary with temperature, but not in this way. Balss (1927, p. 913) said that decapods in cold waters have fewer instars than those in warm waters.

Another unsolved problem in ostracod ontogeny is whether the adult animal molts or not. Old adult fresh-water ostracods are usually so encrusted with ciliate protozoans and algae that, obviously, they do not molt with the frequency of the immature, which are never encrusted. Müller (1894, p. 188) at first interpreted size differences in mature females of the genus *Asterope* to be the result of adult molting, but in two later publications (1912, p. 5; 1927, p. 422) he denied that adults molt. In 1912 (p. 5) he stated:

> Nach höchstens 8 Häutungen sind die Tiere geschlechtsreif und häuten sich dann nicht mehr. (After at most eight moltings the animals are sexually mature and then molt no more).

Alm (1916, p. 231) made the following statement but gave no evidence or observations to support it:

> Zwischen dem 8. Stadium und der reifen ausgebildeten Form finden sich indessen bisweilen eine oder mehrer Häutungen, denn bei einigen Arten sind die Tiere, obgleich in den Extremiteten und Geschlectsorganen vollständig ausgebildet, noch nicht zur völligen Grösse ausgewachsen, was am besten an den grossen *Eucypris*-Arten zu sehen ist. (Between the eighth instar and the mature there may occur one or many moltings, inasmuch as in certain species the animals are not yet grown to full size, although the appendages and sex organs are fully formed; this can best be seen in large species of *Eucypris*.)

Skogsberg (1920, p. 61), in discussing growth after maturity, wrote that "it is to be noted that in several Ostracod groups moults—characterized by small growth-factors and inconsiderable morphological alterations—occur after maturity is attained." In opposition to this is the view of Klie (1926, p. 16.47), who stated:

> Häutungen der geschlechtsreifen Tiere finden bei den Süsswasserostracoden nicht statt, auch bei der Mehrzahl der marinen Arten ist ein die Erreichung der Geschlechtsreife überdauerndes Wachstum wenig wahrscheinlich. (Molting of the sexually mature

animals does not occur in fresh-water ostracods, and in the majority of marine species growth beyond the attainment of maturity is little apparent).

Elofson (1941, pp. 398–402) agreed with Klie that adult ostracods do not molt. The question can only be settled by careful observation of many species under aquarium conditions.

Many ostracods of extinct families may have had more instars than existing forms, for Spjeldnaes (1951, p. 747) discovered eleven instars in *Beyrichia jonesi* Boll (family Beyrichiidae).

VARIATION IN FORM WITHIN AN INSTAR

In some species all members of an instar have nearly the same dimensions, whereas in others they may vary so much in size that the limits of the instar are difficult to determine. Why there should be such a difference in range of variation in living ostracods, in which presumably the specific assignment can not be questioned, is not fully understood. In fossil ostracods certain extremely variable instars may result from the inclusion of specimens of other closely related species in the study; particularly is this true in unornamented species that are very difficult to classify because they lack characteristics which can be compared. Some fossil ostracods now "species," according to the present classification, may only be form species, not true species.

The causes of variation within an instar in a living ostracod species include: (1) sex, (2) individual variation, (3) diet, (4) parasitism, and (5) temperature. The categories are considered below.

1. Males and females in some species differ in form. Although the difference is best exhibited in the adult instar, in some marine species the oldest immature instar shows sexual dimorphism by very slight differences in shape. Dimorphism cannot be recognized in very young ostracods.

2. In ostracods which are raised in the same environment, the range of variation within instars of a species may be a specific character. Why many species show strong degrees of variation, has yet to be explained by any factor other than individual variation.

3. Diet modifies the shape of carapaces in some species and produces changes in at least some of the dimensions. The known effects of diet have been listed by Kesling (1951*a*, pp. 72–73, 78; 1952*a*, pp. 267–68).

4. Parasites of ostracods include cestodes, acanthocephalans, nematodes, copepods, and isopods, and also small ciliate protozoans which may be considered ectoparasites. Rome (1947, pp. 3–4) found that a parasitic cestode produced a hypertrophy in the adult ostracod. Other parasites may alter the proportions and dimensions of the host if the infestation takes place before the last molting.

5. Temperature has been suggested by Elofson (1941, p. 399) as a cause for variations in size. He reported that specimens of ***Philomedes globosus*** from the North Sea and the Skagerak were smaller than those from near Greenland (see Table I). Skogsberg (1920, p. 147) had already noted this and stated: "Thus the specimens of ***Philomedes globosus*** measured by me were only 2.4–2.6 mm. at Skager Rack while the same species attained a length of 2.9–3.1 mm. at Greenland." From the measurements obtained for this species it appears that a species attains a larger size in colder waters. Elofson (1941, p. 400) noted that specimens of *Cytherura nigrescens* (Baird) from one locality were larger in each instar in winter than in summer (see Table II). If substantiated by data for other species, this discovery would prove useful in determining temperature variations which existed during the lifetime of fossil ostracods, provided the size differences caused by temperature can be differentiated from those caused by other factors.

TABLE I

LENGTHS OF VALVES OF *Philomedes globosus* (LILLJEBORG)[1]

All measurements are in millimeters.

Locality	Instar						
	Adult Females	5 Females	5 Males	4	3	2	1
Greenland	2.90–3.10	2.40	2.40	1.90	1.50	1.20	1.00
Öresund	2.50–2.63	2.01–2.20	2.05–2.16	1.52–1.61	1.21–1.29	1.07	0.80–0.89
Skagerak	2.40–2.61	1.90–2.32	1.98–2.30	1.55–1.87	1.21–1.40	....	0.81–0.87
Gullmarfjord	2.22–2.59	1.98–2.20	1.87–2.10	1.45–1.72	1.24–1.32	0.98–1.09	0.75–0.87

[1] Data from Skogsberg (1920, p. 138) and Elofson (1941, p. 399).

TABLE II

LENGTHS OF VALVES OF *Cytherura nigrescens* (BAIRD)[1]

All measurements are in millimeters.

Season	Instar			
	8	7	6	5
Summer	.354	.270	.229	.195
Winter	.372	.300	.244	.205

[1] Data from Elofson (1941, p. 400).

SLIDE RULE FOR DETERMINATION OF INSTARS

A circular slide rule with special divisions has proved to be a useful device for statistical comparison of specimens of a species and for their assignment to a particular instar. This rule, illustrated in Figure 2, consists of an outer part marked off in a logarithmic cycle and an inner turntable marked off in a logarithmic cycle and also into intervals which represent theoretical increases in one dimension, in area, and in volume. For convenient use, cut the figure into two parts, along the circle separating the opposing logarithmic cycles, and mount each part on a disc of heavy cardboard. Then, attach the turntable by a pivot through its center so that it rotates upon the outer part.

The two logarithmic cycles can be used alone as a circular slide rule for multiplication. The three sets of special divisions on the turntable labeled "One dimension," "Area," and "Volume" correspond to the amounts by which successive instars differ, according to Przibram's concept, in these measurements.

TABLE III

Relative Values of One Dimension, Area, and Volume in Instars of a Species of Ostracod

Instar	One Dimension	Area	Volume
1	L_1	A_1	V_1
2	1.25992 L_1	1.5874 A_1	2 V_1
3	1.58740 L_1	2.5198 A_1	4 V_1
4	2.00000 L_1	4.0000 A_1	8 V_1
5	2.51984 L_1	6.3496 A_1	16 V_1
6	3.17480 L_1	10.0794 A_1	32 V_1
7	4.00000 L_1	16.0000 A_1	64 V_1
8	5.03968 L_1	25.3984 A_1	128 V_1
9	6.34960 L_1	40.3174 A_1	256 V_1
10	8.00000 L_1	64.0000 A_1	512 V_1
11	10.07937 L_1	101.5937 A_1	1024 V_1
12	12.69920 L_1	161.2698 A_1	2048 V_1
13	16.00000 L_1	256.0000 A_1	4096 V_1

In all of the species which have been studied in detail, each specimen could be assigned to an instar by its dimensions and each instar was distinct from every other instar of the species. For species which show progressive changes in proportions from one instar to the next, volume increases have to be compared rather than single dimensions, such as length. For most species, the products of length, height, and width will be sufficiently accurate for comparing volume increases. But if the shape, in lateral or dorsal view, changes drastically from one instar to another, more accurate measurements of volume should be made (see Kesling, 1952*b*, p. 778). The theoretical increases in volume from the youngest instar to the adult are listed in Table III. Volumes of instars of a particular species can be quickly compared by rotating the turntable so that the instar number in the "Volume" set of divisions is aligned with the numerical value for that instar on the outer part of the slide rule. For example, if the fifth instar of the species whose dimensions are shown (Fig. 1) is known to consist of specimens having an average product of length, height, and width equal to .1207 cu. mm., then a specimen which has a product equal to .0300 cu. mm. would be in the third instar, inasmuch as its product is close to the theoretical value of .0302 for that instar, and a specimen which has a product of 1.0400 cu. mm. would be in the eighth instar, because its product is closer to the theoretical value of .9656 than to any other.

If the width increases progressively by a factor of 1.26 from one instar to the next, then the product of length and height will increase as shown in Table III for area. If the shape in dorsal view does not vary from one instar to another in a species, the "Area" set of divisions on the turntable can be used to compare areas in lateral view or the products of length and height. For example, if a specimen in the eighth instar has length and height of .60 mm. and .45 mm. respectively, a specimen which has dimensions of .23 mm. and .18 mm. would be in the fourth instar, because its product of .0414 sq. mm. is near the theoretical value of .0425 for that instar. For another example, if the adult of a species having nine instars has length and height of 1.80 and 1.32 mm., a specimen which has dimensions of .43 and .35 mm. would be in the third instar, because its product of .1505 sq. mm. is closer to the theoretical value of .1485 than to any other shown on the slide rule.

If specimens in all instars have approximately the same shape, the instar can be determined from only one dimension. Length is the largest dimension and can be measured most accurately. Each dimension will increase as shown in Table III. The "One dimension" set of divisions on the turntable can be used to compare lengths of instars of a species. In *Philomedes globosus* from near Greenland (Table I) the specimens in the fifth instar average 2.40 mm. long; a specimen 1.20 mm. long, therefore, would be in the second instar, since it is exactly the theoretical value of that instar, and a specimen 1.00 mm. long would be in the first instar, since it is closer to the theoretical value of .952 than to any other given.

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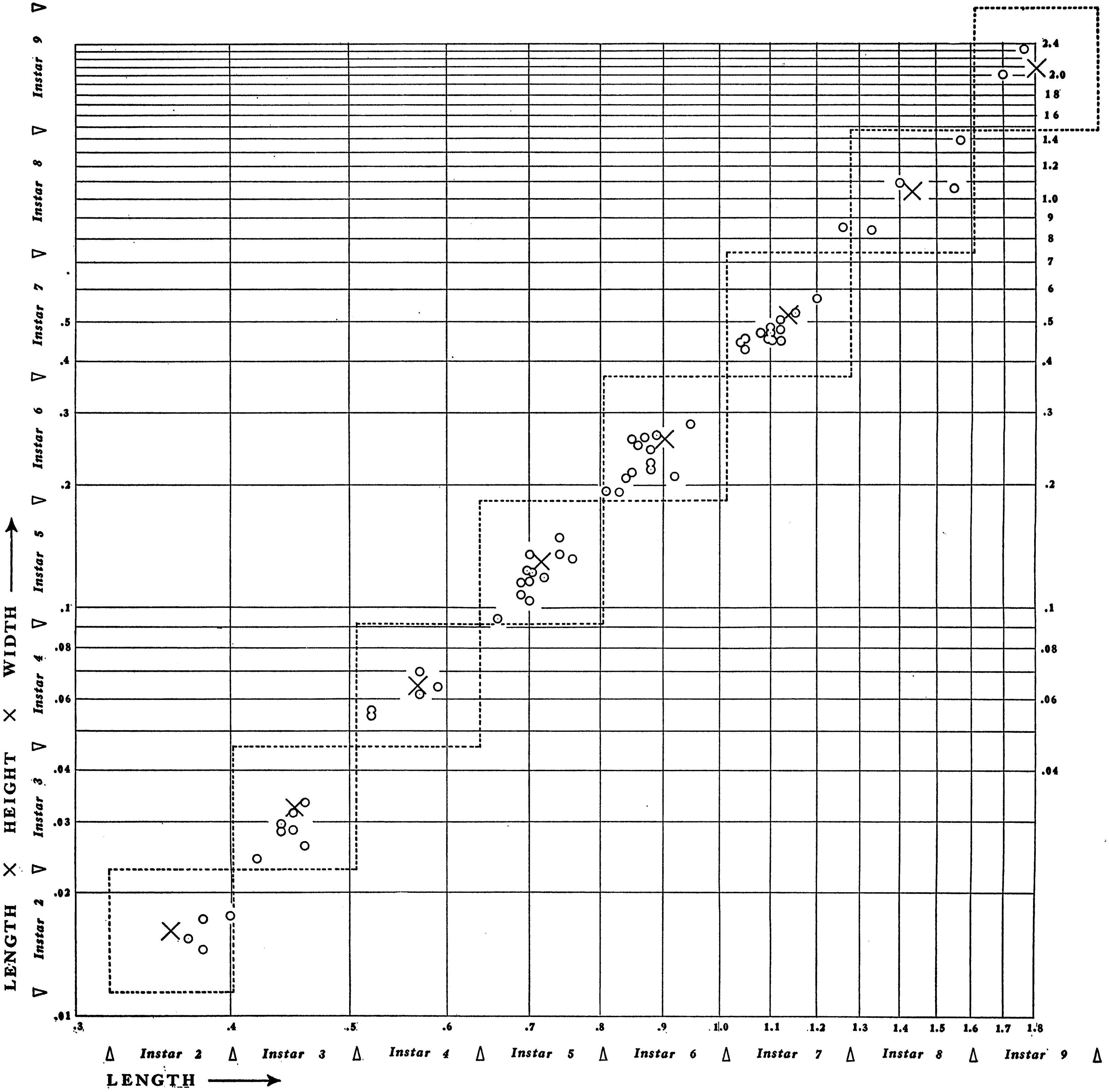
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FIG. 1

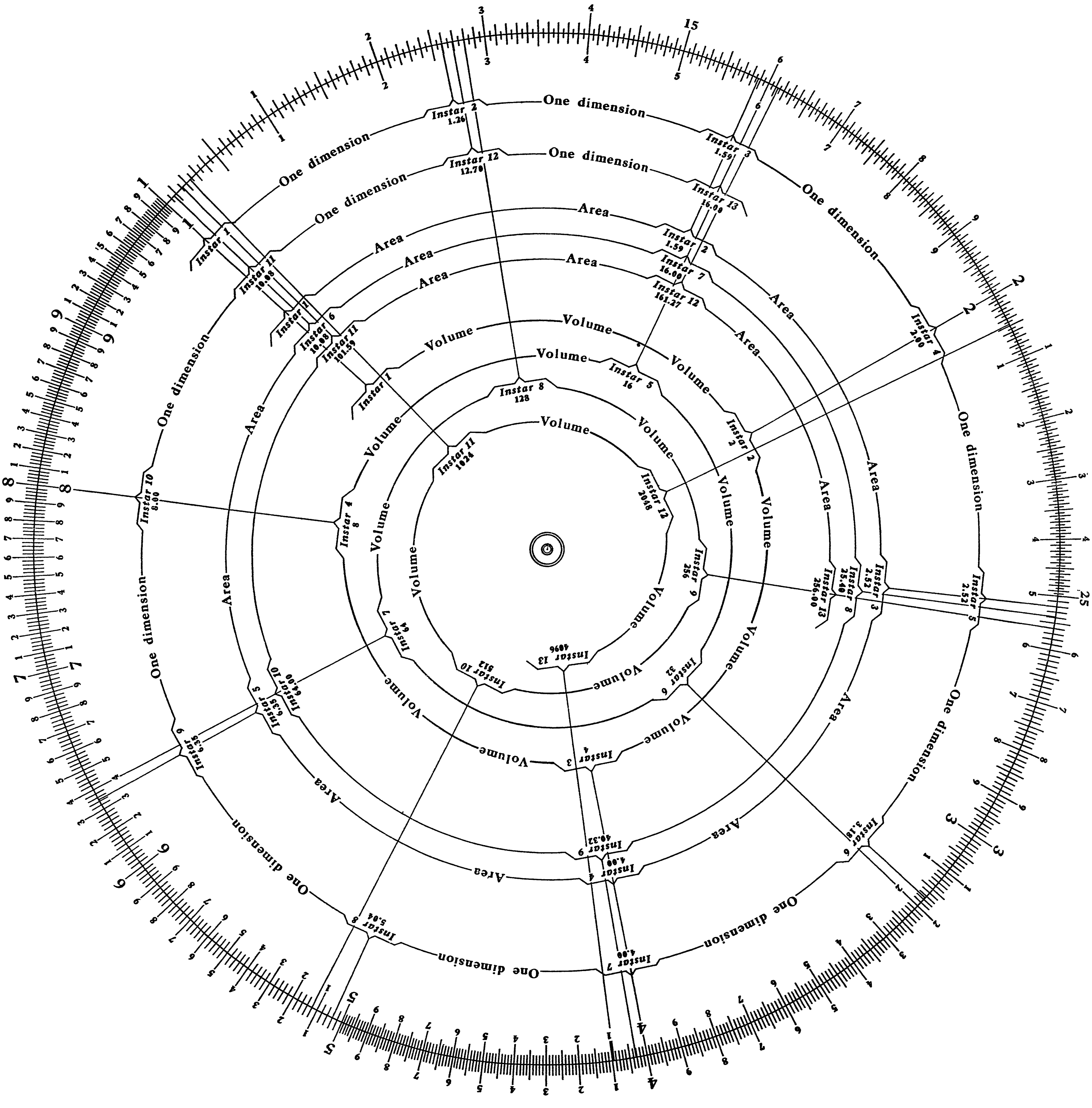
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FIG. 2

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