Museum of Paleontology

PAPERS ON PALEONTOLOGY

Published with generous support of Edward Pulteney Wright Memorial Fund

No. 6 1973

By Robert V. Kesling, Sabeekah Abdul-Razzaq,
Cynthia Devore, & Robert Lattanzi :

Growth in Two Populations of the Crinoid *Eucalyptocrinites crassus*

By Jeanette M. Fini :

Observations on Evolution of Calycine Appendages in the Crinoid *Gilbertsocrinus*

By Robert V. Kesling :

A Cystoid Plate from the Lower Part of the Petoskey Formation

Return to: G. Newton, 1529 Museums

Growth in Two Populations of the Crinoid *Eucalyptocrinites crassus*

Robert V. Kesling, Sabeekah Abdul-Razzaq,
Cynthia Devore, & Robert Lattanzi

ABSTRACT.-- Two populations of *Eucalyptocrinites crassus* (Hall), one from Indiana and the other from Tennessee, show drastic differences in the way they grew. The Indiana crinoids without exception matured into adults with conical cups. The Tennessee crinoids, however, produced many adults with very large and flat cups, shaped more like pancakes than cones.

Proportions of any plate result from complex interactions with adjoining plates. Sometimes both plates become wider, or higher, but often one plate will become wider while the other becomes higher. Furthermore, the growth ratio of two parameters in young specimens is seldom the same as the growth ratio in mature specimens.

Although we are not absolutely certain why adult crinoids in Indiana maintained their conical shape while those in Tennessee flattened out, we suggest a logical possibility. Why one parameter suddenly speeds up or slows down its rate of growth relative to another parameter remains unexplained.

PART I: THE INDIANA POPULATION

Introduction

WHETHER we call it *ontogeny* or simply *growth*, the changes in an animal's size and shape during its lifetime provide a fascinating field for study. This is as true for fossil species as for the living. Not all such changes are as obvious as the introduction of new structures; some are very subtle alterations in geometry, little nuances in proportions, which may bear some relationship to the way the animal functioned in its environment.

Crinoids and other echinoderms have numerous discrete elements -- plates and ossicles in the fossil forms. It is always important to observe how these elements fit together in each specimen. Yet the study of single individuals may not be enough. We can sometimes learn more by measuring a series of individuals of different size.

Presumably, small crinoids were young when they died, and large crinoids were old; at least, in the absence of contrary evidence, we can proceed on this assumption. Our confidence increases if all the specimens of a species were preserved in one rock unit, for it would seem that they all lived at about the same time. So a series of fossils from small to large is a sampling of the original population -- individuals from young to adult. In this way, we have the chance to study changes that took place during the crinoid's lifetime: its ontogeny.

For living animals, ontogeny includes many features, such as strength, activity, glandular metababolism, and sexual development, as well as changes in proportions. Fossil animals are another matter. We can only look at the changes in shape of their preserved hard parts. Fortunately, crinoids have many plates and each plate has several sides, so that many parameters can be measured. The most important plates (and the largest) are those in the dorsal cup.

If all plates grew equally along all edges, the plates of the adult would be just the same shape as those of the baby crinoid. It is easy to see, even in a few specimens, that this is not so. With increase in size, some plates become longer and some become shorter; one side of a plate may stay about the same size and the others may extend greatly. Therefore, when we measure two parameters in a small crinoid and compare them with the measurements in a large crinoid, we may find that the ratio has changed -- the ratio may be smaller or larger, depending upon how it was set up. This is allometry in two growth stages.

Yet it is not enough to say simply that in allometry this parameter increases faster than that. We want to say how much faster it increases. Julian S. Huxley worked on this problem and published his results in 1924 and 1932. He mathematically reduced the rate of increase of one parameter relative to another to a number. He called it the "constant differential growth ratio"; we can refer to it just as CDGR. It is a useful synthesis of allometric growth.

Huxley's formula was very simple:

$$y = bx^k ,$$

where y is a parameter being compared in growth to the parameter x. The multiplier b, we see, does nothing more than show the relative sizes of x and y. The exponent k, on the other hand, is extremely important: it signifies how much faster or slower y is growing than is x. It is the CDGR. Usually, various parts are compared with the overall size; so for our own species, we might want to know how fast does our head or our leg grow in relation to our height.

Suppose we investigate two parameters in only two specimens, one small and the other large. Given enough time, we could come close to the value of k by trial and error. We could get the answer quicker and more accurately by using logarithm tables. But if we wanted to know the average CDGR for a hundred specimens, it would take hours of thumbing through the log tables. Nowadays, we could set up an appropriate program, punch the measured data into cards, and run them through a computer. A method every bit as easy was devised years ago by Kesling (1951). Data can be plotted on double-logarithm paper, a line drawn through the mean positions of the points, and the value of k read directly on a special protractor.

Using Huxley's formula for the CDGR, we can learn a great deal about how the plates grew in a crinoid species. We are able to detect small-scale changes in growth rate that would otherwise go unnoticed. We can learn how each parameter of each plate grew in relation to the size of the cup -- which grew faster, which grew slower -- and how much faster or slower. And if the shape of the cup itself has changed during the growing up process, we can with confidence point out the parameters responsible for such change.

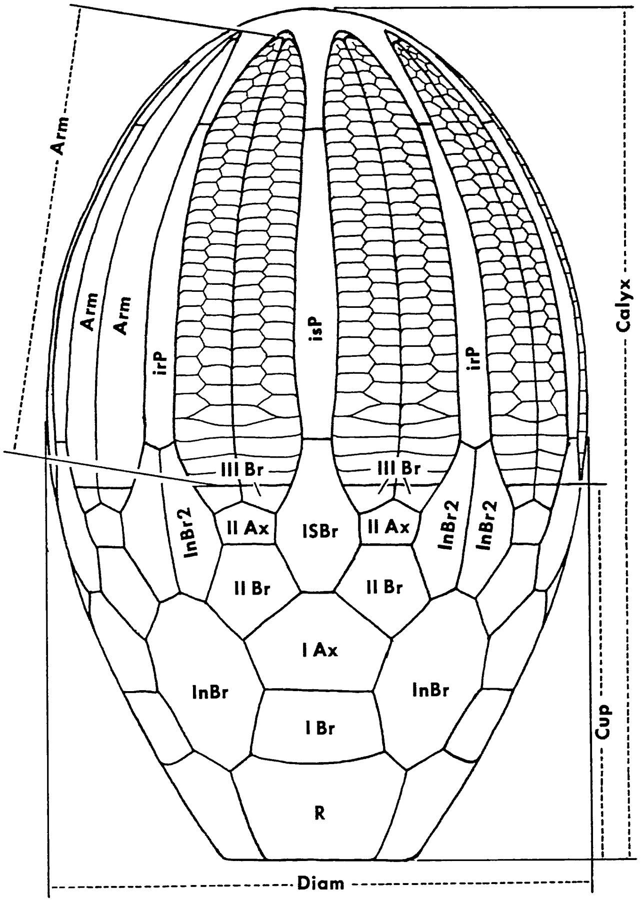
Eucalyptocrinites crassus is ideal for investigation. Its calyx is strongly constructed and resists distortion; its cup, tegmen, and arms are commonly preserved in association; and its plates are easily identified. The cup alone contains nine kinds of plates on its sides, and the tegmen has two kinds of elongate partition plates (to separate the arms). For each plate, its height, its width, and every one of its bounding edges can be measured. Hence, the species offers many parameters for ontogenetic study.

In his 1968 paper on "Ontogeny of the crinoid Eucalyptocrinites," Professor D. B. Macurda, Jr., included Eucalyptocrinites crassus (Hall). With his permission, we use some of his measurements in this study. Part I of our paper might be entitled, therefore, "Another look at the ontogeny of Eucalyptocrinites crassus from Indiana." Yet our investigation differs from that of Macurda in two important respects.

First, for each pair of parameters, he based his analysis on one computer-plotted regression line on double-arithmetic scale. We chose, instead, to plot measurements for each pair of compared parameters on double-logarithm scale and to note significant changes in allometry during ontogeny. Because growth develops in logarithmic progression, we think our approach is better. It is more discriminating, and it also shows up any change in growth rate from one interval of the crinoid's lifetime to the next. For many pairs of compared parameters, we discovered that the CDGR did indeed change during the ontogeny; and for some pairs, it changed several times!

A second difference from Macurda's study was the addition to the series of a very small but nearly perfect specimen of Eucalyptocrinites crassus. This tiny crinoid was found by Mr. and Mrs. E. Ray Lancaster, charter members of the Friends of the Museum of Paleontology at The University of Michigan, who generously presented it to the Museum. They discovered it at the same locality and in the same formation which yielded the specimens available to Macurda. In any study of ontogeny of fossil species, the very young specimens are almost invariably as scarce as they are important. We offer a special tribute to the Lancasters for being able to distinguish any fossil smaller than 8 mm long, for recognizing it as Eucalyptocrinites crassus, and for giving it to our museum. Their keen eyes and kind hearts have helped our collections on several occasions. The little crinoid, catalogued as UMMP 60781, is so well preserved that every parameter could be measured on more than one plate, and the average of two to four readings recorded.

Hopefully, studies in allometry will help us understand how the animal lived.



TEXT-FIG. 1 -- Sketch of Eucalyptocrinites crassus (Hall) with plates identified by abbreviations.

Many zoologists and paleontologists see a close connection between form and function. The zoologist can observe both form and function in his living subjects. The paleontologist is not so fortunate. In fossils, form can be examined but function must be inferred. Some doubt will always persist whatever the paleontologist suggests; but he can make his arguments acceptable and convincing by careful comparison with the living relatives of his fossils -- how they use their form to perform their functions. In the case of crinoids, we still have a lot to learn about the biology and behavior of the living species. So, we are not quite ready to fully interpret the meaning of our growth studies of such a crinoid as Eucalyptocrinites

TABLE 1 -- Measurements of Various Parameters in Eucalyptocrinites crassus From Indiana (in mm). "Total" refers to parameters which are proportional to the diameter of the cup at various levels: Total 1 = $IBr_5 + InBr_2$, Total 2 = $\frac{1}{2}$ $ISBR_2 + IIAx_2 + InBr2_1$, and Total 3 = $\frac{1}{2}$ $ISBr_2 + 2\ IIIBr_2 + InBr_2$. For explanation of plates and parameters, see text.

Specimen No.	Cup	Diam.	Calyx	Arm	R						IBr
					1	2	3	4	5	6	1
1. UMMP 60781	2.81	5.32	7.31	4.65	1.02	0.64	1.02	1.42	0.68	0.34	0.42
2. USNM 160553	3.5	8.2	12.5	8.3	1.5	1.3	1.6	2.7	0.9	0.86	1.0
3. USNM 160554	4.1	8.4	12.0	8.0	1.5	1.0	1.5	2.5	0.7	0.75	0.9
4. USNM S-5237	4.8	9.0	12.6	8.0	1.5	1.1	1.9	2.9	1.0	0.75	1.0
5. USNM 160555	4.9	9.8	15.0	10.0	2.0	1.8	1.8	3.0	1.0	0.85	1.0
6. USNM S-5238	5.0	9.5	13.4	9.1	1.5	1.0	2.2	2.9	1.0	0.95	0.9
7. USNM 160556	5.1	10.0	16.5	10.7	1.7	1.5	2.0	3.0	1.2	1.05	1.2
8. USNM S-5220	5.5	9.7	14.7	9.0	1.7	1.3	1.9	3.0	1.0	0.95	1.2
9. USNM S-5221	6.3	14.2	21.7	15.3	2.3	2.0	2.6	4.3	1.4	1.5	1.6
10. USNM S-5213	6.4	12.5	18.3	11.6	2.0	1.5	2.3	3.6	1.2	1.1	1.5
11. USNM S-5214	7.7	15.5	20.7	14.6	2.8	2.5	2.6	4.7	1.5	1.6	1.9
12. USNM S-5215	8.5	14.5	21.0	14.3	2.9	2.7	2.4	4.5	1.6	1.6	2.0
13. USNM S-5223	10.2	17.7	29.5	18.7	3.0	2.9	3.8	5.9	2.0	1.9	2.5
14. USNM S-5239	11.0	21.1	28.5	17.2	3.6	2.9	3.9	7.2	2.5	2.3	3.0
15. USNM S-5222	11.4	16.9	29.0	17.7	3.5	3.0	3.0	5.9	2.0	1.9	3.2
16. USNM S-5224	14.5	21.7	34.2	20.5	4.5	4.8	4.2	7.5	2.7	2.5	3.5
17. USNM S-5240	14.7	23.6	33.7	20.7	4.2	4.0	3.7	7.5	2.7	2.5	3.4
18. USNM S-5225	15.9	24.2	46.2	29.4	5.0	5.5	5.1	8.0	3.2	2.9	5.0
19. USNM S-5236	17.2	25.3	48.7	34.0	4.5	4.5	4.1	8.1	3.0	2.9	4.6
20. USNM 160557	17.5	22.4	50.3	28.7	5.7	5.4	3.9	8.4	3.3	2.9	4.5
21. USNM S-5228	18.1	28.0	52.2	34.3	5.4	5.9	6.5	8.7	3.3	3.0	4.9
22. USNM S-5226	21.0	24.7	51.1	30.0	6.3	6.3	4.4	8.6	3.3	3.1	6.0
23. USNM S-5229	21.0	29.5	58.0	35.6	7.0	6.6	5.9	10.0	3.4	3.3	6.0
24. USNM S-5230	21.2	32.7	63.6	40.0	6.4	7.1	4.8	11.0	4.3	4.0	6.8
25. USNM S-5228	21.9	25.0	52.3	29.4	6.0	6.2	4.9	8.4	3.0	2.9	5.1
26. USNM S-5232	27.7	30.1	74.6	45.0	8.2	8.5	6.1	11.2	4.0	3.9	8.3
27. USNM S-5233	29.6	36.6	78.0	49.3	8.5	8.2	6.5	12.0	4.4	3.9	7.9
28. USNM 160559	29.7	36.9	73.9	46.0	8.7	8.4	9.0	14.1	4.8	4.4	7.4
29. USNM S-5231	31.7	42.7	73.7	45.7	8.5	7.9	8.0	12.5	5.3	4.5	9.0
30. USNM 160558	33.8	39.3	78.0	50.0	8.7	9.1	8.2	13.4	4.3	4.4	8.5
31. USNM S-5234	35.9	39.1	80.0	50.0	11.3	11.9	9.8	14.7	5.8	5.6	11.0
32. USNM S-5235	41.8	46.6	93.3	51.0	12.2	11.9	8.9	16.1	6.3	5.7	11.0

crassus. At this stage we are simply collecting and processing some of the raw data that will some day be used in a better and firmer paleoecology.

This paper is one of the products of our class in advanced invertebrate paleontology at The University of Michigan in the Winter term of 1973. We wanted to find out what sort of variations occur in proportions of an animal which had continuous-type

TABLE 1 -- (continued)

No.	IBr				Total			IAx					ISBr	
	2	3	4	5	1	2	3	1	2	3	4	5	1	2
1.	0.33	0.66	0.65	0.64	2.05	1.39	1.77	0.56	0.72	0.39	0.47	0.10	1.12	0.30
2.	0.9	1.7	1.7	1.5	3.4	2.6	3.1	1.3	1.5	0.6	1.2	0.1	2.0	0.8
3.	0.6	1.5	1.4	1.3	3.6	2.6	3.3	1.2	1.5	0.6	1.0	0.3	2.0	0.8
4.	0.8	1.5	1.5	1.4	3.8	2.6	3.6	1.2	1.6	0.7	1.0	0.6	2.3	1.0
5.	0.9	1.7	1.6	1.5	4.0	3.05	3.45	1.4	1.6	0.7	1.2	0.5	2.4	1.1
6.	0.8	1.8	1.8	1.5	3.8	2.9	3.4	1.5	1.7	0.6	1.1	0.4	2.5	1.2
7.	1.0	2.0	1.9	1.6	4.5	3.0	3.8	1.5	1.7	0.7	1.4	0.4	2.7	1.2
8.	0.9	1.8	1.8	1.6	4.1	3.2	4.2	1.5	1.8	0.7	1.3	0.1	2.5	1.2
9.	1.5	2.8	2.7	2.4	6.0	4.2	5.2	2.3	2.5	1.0	1.8	0.5	3.7	1.8
10.	1.4	2.1	2.1	2.0	5.2	3.7	4.8	1.9	2.1	0.8	1.7	0.5	3.0	1.6
11.	1.4	3.0	3.2	2.5	6.5	4.75	5.65	2.5	2.9	1.0	2.2	0.5	4.0	2.3
12.	1.5	3.0	3.0	2.5	6.0	3.95	5.15	2.1	2.5	1.0	2.0	0.5	2.9	1.5
13.	2.1	3.7	3.7	3.0	7.5	5.55	7.05	3.5	3.4	1.7	2.9	0.4	5.0	2.1
14.	2.4	4.5	4.7	4.0	9.4	6.4	8.0	4.1	3.9	1.7	3.5	0.5	6.3	3.0
15.	2.8	3.6	3.9	2.8	8.0	5.25	6.55	3.0	3.5	1.6	2.6	0.6	4.3	2.1
16.	3.0	4.8	4.9	4.0	10.0	6.7	8.0	4.3	4.2	1.7	3.7	0.1	5.9	3.0
17.	2.8	4.9	4.8	4.0	10.1	7.55	10.05	4.7	4.6	2.3	4.0	0.5	6.5	3.5
18.	4.4	5.6	5.5	4.4	10.7	7.1	8.9	4.6	4.6	2.3	3.7	0.5	7.0	3.2
19.	4.3	5.6	6.5	4.3	10.8	7.4	9.0	5.0	4.9	2.3	4.0	0.5	7.2	3.8
20.	4.2	5.7	5.2	4.2	10.7	6.7	8.5	4.7	4.9	2.2	3.9	0.4	6.9	3.0
21.	4.5	5.9	5.7	4.4	11.7	8.55	10.25	5.5	5.5	2.5	4.1	1.1	7.9	4.3
22.	5.4	5.9	5.7	4.3	11.9	7.25	8.35	5.7	5.4	3.0	4.1	0.5	7.2	3.7
23.	5.4	6.4	6.4	5.3	13.5	8.8	11.1	6.2	6.0	2.5	5.4	0.5	8.0	4.0
24.	6.1	7.8	7.5	5.8	14.3	10.2	11.4	7.1	7.0	3.5	5.7	1.0	11.0	4.6
25.	4.6	5.6	5.5	4.5	11.3	7.95	10.25	5.7	5.2	2.5	4.8	0.4	7.6	3.9
26.	7.5	7.5	7.1	5.0	14.0	9.1	9.9	7.2	6.7	3.9	6.2	0.5	9.3	4.2
27.	6.9	7.7	7.6	6.3	16.8	10.75	13.85	7.5	7.5	3.5	6.2	0.8	11.1	5.5
28.	6.5	8.7	9.0	7.3	18.1	11.0	13.6	7.5	7.5	3.0	6.4	1.1	10.9	5.4
29.	8.3	8.8	9.0	6.0	16.8	12.9	15.6	9.2	8.4	3.9	8.2	1.5	11.7	6.6
30.	7.3	8.5	8.1	7.1	18.0	11.25	14.05	9.2	9.1	3.8	7.5	0.7	11.4	5.5
31.	9.2	10.4	10.2	7.8	19.4	11.85	14.85	9.8	9.7	4.5	8.5	1.2	11.2	5.7
32.	10.2	11.3	10.6	8.5	21.9	13.95	15.55	10.9	9.5	3.7	9.2	1.0	13.6	6.7

growth. The research was still under way when the semester came to an end. By that time the plotting of parameters and the measuring of CDGRs were just starting to yield results, so our work continued for five weeks more. The extra effort was rewarding.

We enjoyed the valuable assistance of Mrs. Helen Mysyk in typing the final copy for offset. Mr. Karl Kutasi provided the very necessary photographic work in preparation of text-figures.

Methods

Parameters. -- In order to incorporate the data of Macurda, we used the same parameters as those he selected. Plates of *Eucalyptocrinites crassus* are identified in the diagrammatic sketch (text-fig. 1). The following are the parameters and the directions in which they were measured:

Calyx - height of the calyx.

Cup - height of dorsal cup measured parallel

TABLE 1 -- (continued)

No.	ISBr				IIBr						IIAx			
	3	4	5	6	1	2	3	4	5	6	1	2	3	4
1.	0.33	0.44	0.46	0.21	0.62	0.63	0.67	0.48	0.35	0.72	0.78	0.97	0.45	0.62
2.	0.6	0.6	0.9	0.4	1.1	1.0	1.3	0.8	0.6	1.0	0.7	1.5	0.7	0.7
3.	0.6	0.6	1.2	0.4	1.0	0.9	1.1	0.7	0.6	1.0	0.7	1.5	0.6	0.9
4.	0.6	0.6	1.2	0.5	1.2	1.0	1.2	1.0	0.6	1.0	0.8	1.4	0.8	0.8
5.	0.7	0.6	1.4	0.4	1.3	1.2	1.3	0.9	0.8	1.1	0.9	1.6	0.7	0.9
6.	0.8	0.6	1.2	0.5	1.3	1.2	1.6	1.0	0.6	1.2	0.9	1.5	0.7	0.8
7.	0.8	0.7	1.4	0.4	1.5	1.3	1.5	1.0	0.8	1.3	1.0	1.6	0.9	0.8
8.	0.9	0.6	1.3	0.5	1.5	1.5	1.7	1.1	0.9	1.2	0.8	1.6	0.7	0.8
9.	1.0	0.7	2.5	0.5	2.0	1.9	2.3	1.5	1.5	1.5	1.2	2.0	0.8	1.1
10.	1.0	0.6	1.8	0.5	1.6	1.5	2.0	1.1	1.2	1.4	1.0	1.7	0.7	1.0
11.	1.3	1.0	2.2	0.6	2.2	2.5	2.0	1.5	1.5	1.6	1.5	2.1	1.1	1.2
12.	1.0	0.7	1.8	0.5	2.0	1.9	2.5	1.5	1.1	1.7	1.0	2.0	1.0	1.0
13.	1.7	1.0	3.1	0.5	3.0	2.5	3.2	1.7	2.0	2.0	1.6	2.5	1.5	1.5
14.	1.8	1.0	3.6	0.7	3.5	3.4	3.9	2.6	2.0	2.5	2.1	3.0	1.5	1.8
15.	1.5	0.8	2.5	0.5	3.5	2.5	3.3	1.6	2.1	2.0	1.3	2.3	1.0	1.2
16.	2.0	1.2	3.4	1.1	3.7	3.4	4.3	2.6	2.4	2.5	2.1	3.1	1.5	1.5
17.	2.3	1.3	3.9	1.1	4.2	3.7	4.5	2.8	2.8	2.5	2.5	3.3	1.5	2.0
18.	2.2	1.0	4.4	0.8	4.0	3.5	4.4	2.8	2.5	2.6	2.1	3.2	1.4	2.0
19.	1.9	1.4	4.5	1.2	4.1	3.9	4.7	3.1	2.1	2.8	2.5	3.2	1.2	2.3
20.	2.2	1.2	4.2	0.7	4.0	3.4	4.4	2.5	2.5	2.6	2.0	3.0	1.5	1.8
21.	2.8	1.4	4.8	1.1	4.7	4.3	4.1	3.1	3.0	3.3	2.5	3.9	1.5	2.4
22.	2.5	1.2	4.3	1.0	4.9	4.1	5.0	3.2	3.2	2.8	2.3	3.1	1.5	2.0
23.	2.6	1.5	5.2	1.1	5.1	4.3	6.1	3.3	3.7	3.2	2.6	3.9	1.8	2.2
24.	3.2	2.8	6.8	1.2	6.0	5.4	6.3	4.5	3.7	3.8	3.5	4.4	2.0	2.5
25.	2.8	1.5	4.2	0.7	4.9	4.5	5.0	3.6	3.3	2.9	3.0	3.7	1.9	2.1
26.	3.0	1.2	5.4	1.6	6.0	5.5	6.8	3.5	4.5	3.7	3.1	4.0	1.7	2.5
27.	3.2	1.9	7.7	0.7	6.5	5.7	7.1	4.7	4.4	4.0	4.3	4.5	2.4	3.2
28.	3.0	1.5	7.0	1.7	6.5	6.0	7.3	5.0	4.6	4.1	4.0	4.4	1.5	3.2
29.	3.3	2.4	7.2	1.9	7.9	6.8	8.2	5.9	5.3	5.3	5.0	5.5	2.4	3.5
30.	3.4	1.9	7.5	1.0	7.5	7.0	8.5	6.0	5.3	4.2	4.5	5.0	2.6	3.5
31.	3.8	1.9	6.8	1.0	8.1	6.1	8.9	4.9	5.9	4.2	4.0	4.8	2.1	2.9
32.	4.3	3.3	7.2	1.3	10.0	8.6	10.6	8.0	6.6	5.6	5.7	6.2	3.8	3.5

to the axis of the calyx and including distance between base of the radial circlet and top of the first tertibrachials.

Diam - greatest diameter of the calyx measured perpendicular to its axis.

Radial

R_1 - height, measured through the middle of the plate.

R_2 - length of the R:R suture.

R_3 - width at base of plate.

R_4 - maximum width (between R:R:InBr junctions).

R_5 - length of R:InBr suture.

R_6 - distance from midpoint of R:IBr suture to R:IBr:InBr junction.

Primibrachial

IBr_1 - height, measured through middle of the plate.

IBr_2 - length of side (IBr:InBr suture).

IBr_3 - width across base, measured between R:IBr:InBr junctions.

IBr_4 - median width, measured between midpoints of IBr:InBr sutures.

IBr_5 - width across top of plate.

TABLE 1 -- (continued)

No.	IIIBr		InBr			InBr2					irP			
	1	2	1	2	3	1	2	3	4	5	1	2	3	isP
1.	0.53	0.67	1.11	1.41	1.23	0.42	0.38	0.86	0.15	0.31	4.16	0.26	0.29	4.22
2.	0.6	1.0	2.2	1.9	2.0	0.7	0.5	1.8	0.3	1.0	7.2	0.5	0.5	6.8
3.	0.6	1.1	2.1	2.3	2.1	0.7	0.7	2.0	0.3	1.1	6.9	0.5	0.5	6.5
4.	0.7	1.2	2.3	2.4	2.0	0.7	0.7	2.0	0.3	1.5	6.9	0.6	0.6	6.5
5.	0.6	1.0	2.5	2.5	2.4	0.9	0.7	2.4	0.3	1.4	8.5	0.4	0.5	8.3
6.	0.6	1.0	2.8	2.3	2.5	0.8	0.7	2.3	0.3	1.4	7.5	0.6	0.7	7.4
7.	0.7	1.2	3.1	2.9	2.8	0.8	0.5	2.5	0.3	1.5	8.9	0.5	0.6	8.6
8.	0.7	1.3	2.9	2.5	2.5	1.0	0.7	2.1	0.3	1.0	8.1	0.5	0.5	8.0
9.	1.0	1.5	4.0	3.7	3.4	1.3	0.8	3.6	0.4	2.4	11.3	0.8	1.1	11.0
10.	0.9	1.4	3.5	3.2	2.9	1.2	0.8	3.0	0.4	1.7	8.8	0.5	0.7	8.5
11.	1.1	1.5	4.5	4.0	3.9	1.5	0.6	3.6	0.5	2.3	11.6	1.0	1.2	11.5
12.	1.0	1.6	4.5	3.5	3.5	1.2	0.8	3.2	0.4	2.0	10.6	0.7	1.0	10.4
13.	1.1	2.0	5.7	4.5	4.4	2.0	1.0	5.3	0.5	2.0	14.3	0.8	1.0	14.0
14.	1.3	2.3	6.8	5.4	5.0	1.9	0.8	5.5	0.4	3.5	14.6	1.0	1.1	14.6
15.	1.0	1.8	6.3	5.2	4.5	1.9	1.1	5.0	0.5	3.0	14.7	0.9	1.3	14.1
16.	1.3	2.2	7.5	6.0	5.5	2.1	1.0	5.7	0.7	3.3	16.5	1.4	1.8	15.5
17.	1.4	2.9	8.0	6.1	5.7	2.5	0.8	7.0	0.8	3.7	16.3	1.5	1.5	15.6
18.	1.3	2.5	9.1	6.3	5.9	2.3	0.9	7.1	0.5	4.2	22.0	0.8	1.3	21.1
19.	1.5	2.4	9.2	6.5	6.4	2.3	1.3	6.7	0.8	2.8	24.5	1.3	1.7	24.4
20.	1.5	2.4	8.9	6.5	5.9	2.2	1.0	6.9	0.6	3.7	23.1	1.1	1.6	22.2
21.	1.5	2.8	9.6	7.3	6.1	2.5	0.7	7.8	0.8	4.5	25.3	1.2	2.5	26.5
22.	1.5	2.1	10.9	7.6	6.0	2.3	0.6	7.7	0.5	4.0	22.5	1.0	1.1	22.5
23.	1.6	3.1	10.9	8.2	7.0	2.9	0.9	8.0	0.6	4.4	27.5	2.0	2.3	26.8
24.	2.0	2.8	12.0	8.5	7.7	3.5	1.3	10.8	1.3	6.9	29.5	1.5	2.0	29.5
25.	1.5	3.0	10.5	6.8	6.0	2.3	0.8	7.5	0.6	3.5	23.3	1.2	1.5	22.8
26.	1.8	2.4	14.2	9.0	7.1	3.0	0.7	9.6	1.1	5.6	30.6	2.0	2.5	29.0
27.	2.1	3.8	14.9	10.5	8.5	3.5	1.4	13.8	0.5	7.9	32.3	0.9	2.4	31.6
28.	2.0	3.5	14.7	10.8	9.3	3.9	1.5	10.4	1.1	6.4	34.1	2.2	2.5	34.6
29.	2.6	4.1	16.4	10.8	10.4	4.1	1.5	11.5	1.2	6.8	37.5	2.5	3.0	36.0
30.	2.5	3.9	15.9	10.9	9.5	3.5	1.0	12.5	1.0	7.1	36.7	2.0	3.1	35.0
31.	2.1	3.9	17.5	11.6	9.3	4.2	0.9	12.1	1.5	6.7	36.0	2.7	4.4	35.5
32.	2.1	3.9	22.1	13.4	11.6	4.4	0.9	14.1	1.0	7.5	39.9	3.0	3.8	41.4

Primaxil

IAx$_1$ - height, measured through middle of plate.
IAx$_2$ - length of diagonal, measured from midpoint of IAx:InBr suture to midpoint of IAx:IIBr suture.
IAx$_3$ - length of IAx:InBr suture.
IAx$_4$ - length of IAx:IIBr suture.
IAx$_5$ - length of IAx:ISBr suture.
(Note: the base of IAx is measured as IBr$_5$.)

Secundibrachial

IIBr$_1$ - height, measured from lower apex to midpoint of IIBr:IIAx suture.
IIBr$_2$ - length of diagonal, measured from midpoint of IIBr:IAx suture to midpoint of IIBr:InBr2 suture.
IIBr$_3$ - length of diagonal, measured from midpoint of IIBr:InBr suture to midpoint of IIBr:ISBr suture.
IIBr$_4$ - length of IIBr:InBr suture.
IIBr$_5$ - length of IIBr:InBr2 suture.

TABLE 2 -- CDGRs of Other Parameters Compared to Height of the Cup.

Stage	Cup h (mm)	Diam	Calyx	Arm	R						IBr		
					1	2	3	4	5	6	1	2	3
I	2.81-4	0.965	0.925	0.89	0.895	1.21	0.76	1.61	0.94	1.36	2.00	1.23	2.33
II	4-7.2	0.965	0.925	0.89	0.895	1.21	0.76	0.875	0.94	1.36	1.18	1.23	0.96
III	7.2-12	0.655	0.925	0.89	0.895	0.99	0.76	0.875	0.94	0.78	1.18	1.23	0.96
IV	12-16	0.655	0.925	0.89	0.895	0.99	0.76	0.70	0.75	0.78	1.18	1.23	0.76
V	16-41.8	0.655	0.925	0.89	0.895	0.99	0.76	0.70	0.75	0.78	1.03	1.02	0.76

Stage	IBr		IAx					ISBr					
	4	5	1	2	3	4	5	1	2	3	4	5	6
I	2.12	1.87	2.00	1.72	0.985	2.02	0.505	0.945	2.83	1.02	0.605	2.18	1.75
II	1.21	1.09	1.15	1.06	0.985	1.17	0.505	0.945	1.35	1.02	0.605	1.25	0.585
III	0.775	0.72	0.92	0.81	0.985	0.905	0.505	0.945	0.745	0.875	0.605	0.90	0.585
IV	0.775	0.72	0.92	0.81	0.985	0.905	0.505	0.735	0.745	0.875	0.605	0.90	0.585
V	0.775	0.72	0.92	0.81	0.75	0.905	0.505	0.735	0.745	0.645	0.605	0.70	0.585

Stage	IIBr						IIAx				IIIBr	
	1	2	3	4	5	6	1	2	3	4	1	2
I	1.08	1.20	1.11	2.45	1.49	0.725	-0.36	0.595	0.605	0.695	0.59	0.605
II	1.08	1.20	0.88	0.915	1.49	0.725	0.86	0.595	0.605	0.695	0.59	0.605
III	1.08	0.80	0.88	0.915	0.90	0.725	0.86	0.595	0.605	0.695	0.59	0.605
IV	0.775	0.80	0.88	0.915	0.90	0.725	0.86	0.595	0.605	0.695	0.59	0.605
V	0.775	0.80	0.88	0.915	0.90	0.725	0.86	0.595	0.605	0.695	0.59	0.605

Stage	InBr			InBr2					irP			isP
	1	2	3	1	2	3	4	5	1	2	3	
I	1.20	0.97	1.00	1.20	0.29	2.30	0.625	3.60	0.82	0.72	0.825	0.81
II	1.20	0.97	1.00	1.20	0.29	0.965	0.625	1.12	0.82	0.72	0.825	0.81
III	0.915	0.735	0.64	0.85	0.29	0.965	0.625	0.765	0.82	0.72	0.825	0.81
IV	0.915	0.735	0.64	0.595	0.29	0.795	0.625	0.765	0.82	0.72	0.825	0.81
V	0.915	0.735	0.64	0.595	0.29	0.795	0.625	0.765	0.82	0.72	0.825	0.81

IIBr$_6$ - length of IIBr:IIAx suture.
(Note: two sides of IIBr are measured as IAx$_4$ and ISBr$_3$.)

Secundaxil

IIAx$_1$ - height, measured from midpoint of IIAx:IIBr suture to upper apex of plate.
IIAx$_2$ - maximum width of plate.
IIAx$_3$ - length of IIAx:InBr2 suture.
IIAx$_4$ - length of IIAx:IIIBr suture.
(Note: two sides of IIAx are measured as IIBr$_6$ and ISBr$_4$.)

First tertibrachial

IIIBr$_1$ - height of plate.
IIIBr$_2$ - width of plate.
(Note: outer side and IIIBr:IIIBr suture not measured.)

Intersecundibrachial

ISBr$_1$ - height, measured through middle of plate.
ISBr$_2$ - width, measured between midpoints of ISBr:IIAx sutures (not necessarily the maximum width).
ISBr$_3$ - length of ISBr:IIBr suture.
ISBr$_4$ - length of ISBr:IIAx suture.
ISBr$_5$ - distance from ISBr:IIAx:IIIBr junction to upper corner of plate.

First interbrachial

InBr$_1$ - height, measured through middle of plate from apex to apex.
InBr$_2$ - width, measured between InBr:IBr:IAx junctions.
InBr$_3$ - width, measured between InBr:IAx:IIBr junctions.

TABLE 3 -- CDGRs of Parameter-Pairs Showing Some Changes in Plate Size.

Stage	Approx. Cup h	IBr_4: R_4	IAx_2: R_4	$ISBr_2$: R_4	$InBr_2$: R_4	$IIIBr_2$: R_4	$InBr_1$: R_1
I	2.81-5.0	1.28	1.80	2.30	0.985	0.775	1.18
II	5.0-7.2	1.28	1.07	1.04	0.985	0.775	1.18
III	7.2-12	1.03	1.07	1.04	0.985	0.775	1.18
IV-V	12 -41.8	1.03	1.07	1.04	0.985	0.775	1.00

(Note: sides of InBr are measured as R_5, IBr_2, IAx_3, $IIBr_4$, and $InBr2_2$.)

Second interbrachial

- $InBr2_1$ - width, measured horizontally from midpoint of InBr2:IIAx suture.
- $InBr2_2$ - length of InBr2:InBr suture.
- $InBr2_3$ - length of InBr2:InBr2 suture (vertical).
- $InBr2_4$ - length of InBr2:irP suture.
- $InBr2_5$ - distance from InBr2:IIAx:IIIBr junction to upper corner of plate.

Intersecundibrachial partition plate

- isP - height, measured through middle of plate.

Interradial partition plate

- irP_1 - height, measured through middle of plate.
- irP_2 - width, measured at base of plate.
- irP_3 - maximum width.

Arm - length of arm, measured from base of second tertibrachial to tip of arm plates.

Measurements are summarized in table 1.

Constant differential growth ratios. -- For comparison of growth, each pair of parameters was plotted on double-logarithm paper (about $7\frac{1}{2}$ inches/cycle). The mean line was located by averaging pairs of adjacent measurements, then groups of four consecutive measurements (from table 1). With the special protractor devised by Kesling (1951), the value of the CDGR could be read directly from the slope of the mean line in any interval of plotted data.

To establish one particular parameter against which each of the others could be compared, we studied the apparent accuracy with which each could be measured. Our selection was the height of the cup. Text-figures 2-7 show the results of plotting each of the other parameters against Cup. Table 2 summarizes the CDGRs for these parameter-pairs.

It was soon apparent that growth of each parameter did not continue at the same rate throughout ontogeny. From the smallest cup (2.81 mm) to the largest (41.8 mm), significant changes in the rates of growth occur when the cup height reaches 4, 7.2, 12, and 16 mm. This divides the ontogeny into five stages, which might be termed infantile, early juvenile, late juvenile, pre-adult, and adult. It is perhaps better to designate the stages by Roman numerals -- I to V -- as we did in tables 2-5. Because stage I is based on only two specimens, the control must be regarded as weak. For that reason, we did not feel justified in shifting the bottom part of the mean line for each little departure (brought on by the measurements of our one tiny specimen); instead, we adjusted the mean line only when the projected value of the parameter was off from the observed value by more than 25 per cent. The only way we could improve this part of the ontogenetic record would be to find more little specimens. But, working with the crinoids available (as indeed we must), we call attention to the fact that it is definitely possible that more CDGRs change at the 4-mm level of cup height.

To emphasize changes in plate size,

TABLE 4 -- CDGRs of Parameter-Pairs Showing Some Changes in Plate Proportions.

Stage	Approx. Cup h	R_4: R_1	IBr_4: IBr_1	IAx_2: IAx_1	$ISBr_2$: $ISBr_1$	Calyx: Diam
I	2.81-4.0	1.08	0.875	1.49	1.46	1.11
II-III	4.0 -12.0	1.08	0.875	0.88	1.46	1.11
IV-V	12.0-41.8	0.72	0.655	0.88	0.915	1.43

TABLE 5 -- CDGRs of Parameter-Pairs Showing Changes in the Shape of the Cup and Calyx. Parameters serving as indices of the cup diameter at higher levels are compared to the width of the base of R (R_3).

Stage	Approx. Cup h	R_4: R_3	Total 1: R_3	Total 2: R_3	Total 3: R_3	Total 3: Total 1	Total 3: Total 2
I-III	2.81-12.0	1.20	1.16	1.04	1.09	0.905	0.965
IV-V	12.0-41.8	0.91	0.865	0.875	0.795	0.905	0.965

plate proportions, and shape of the cup and calyx, we plotted other parameter-pairs. The double-log plots are shown in text-figures 8 to 10, and the CDGRs are listed in tables 3 to 5.

Just a glance at the plotted data will show that all parameter-pairs do not have the same significance. For instance, points are so scattered in Cup:IAx_5 (text-fig. 4), Cup:$ISBr_6$ and Cup:irP_2 (text-fig. 6), and Cup:$InBr2_4$ (text-fig. 7) that the CDGRs are obviously insignificant -- even though the mean lines show definite "trends." On the other hand, such plots as IBr_4 :R_4 (text-fig. 8) and Total 3:Total 2 (text-fig. 10) have points so close to the mean lines that the growth ratios are highly significant.

Models

We pointed out that CDGRs change when the cup reaches 4, 7.2, 12, and 16 mm high. Many of the mean lines show kinks at one or more of these levels. Since each of the other parameters is compared against Cup (text-figs. 2 to 7), we can select the measurements of an idealized specimen -- or model -- at cup height of 2.8 mm (smallest specimen), 42 mm (largest specimen), and two significant sizes in between. Data for these models are presented in table 6 as computed "measurements." For handy comparison of changes from one model to another, these data are expressed as percentages of cup height in table 7.

Using the percentages from table 7 as dimensions, we sketched plate diagrams for the four models. The cup heights selected were 2.8, 7.2, 12, and 42 mm. The diagrams (text-fig. 11) show dramatically how each plate of the cup changes in relative size and proportions during ontogeny. For example, IBr increases in size (relative to total size of the cup) and then in relative height; IAx expands slightly and then contracts; ISBr widens and then diminishes in relative size; InBr gradually shrinks as a cup element, becoming much more elongate in the process; and IIIBr decreases from a plate as large as IAx to one less than one-sixth the size. If the absolute size were unknown, most paleontologists would assign the models to different species.

One of the unusual features of *Eucalyptocrinites crassus* revealed in the newly discovered tiny specimen -- and strongly emphasized in the models (text-fig. 11) -- is

TABLE 6 -- Parameters of Models Computed at Six Significant Heights of the Cup. Based on mean lines of double-logarithm plots of parameters compared with cup height (text-figs. 2-7), except smallest model based on measurements of actual specimen (table 1).

Cup	Diam	Calyx	Arm	R						IBr
				1	2	3	4	5	6	1
2.8	5.3	7.3	4.6	1.02	.64	1.02	1.42	.68	.34	.42
4.0	8.0	11.5	7.7	1.42	1.04	1.58	2.45	.82	.65	.85
7.2	14.1	19.8	12.8	2.40	2.15	2.45	4.11	1.42	1.45	1.73
12.0	19.8	31.7	20.5	3.81	3.55	3.60	6.54	2.30	2.15	3.10
16.0	23.7	41.1	26.2	4.90	4.70	4.48	7.95	2.82	2.65	4.31
42.0	44.7	100.0	62.5	11.60	12.30	9.20	15.70	5.95	5.7	11.70

Cup	IBr				IAx					ISBr	
	2	3	4	5	1	2	3	4	5	1	2
2.8	.33	.66	.65	.64	.56	.72	.39	.47	.10	1.12	.30
4.0	.68	1.48	1.36	1.25	1.15	1.32	.57	.97	.30	1.96	.83
7.2	1.40	2.60	2.75	2.36	2.22	2.48	1.02	1.94	.41	3.39	1.80
12.0	2.63	4.25	4.08	3.40	3.60	3.76	1.67	3.05	.53	5.50	2.62
16.0	3.80	5.28	5.10	4.17	4.65	4.76	2.20	3.92	.61	6.80	3.24
42.0	10.06	10.98	10.70	8.30	11.25	10.35	4.62	9.40	.98	10.39	6.71

Cup	ISBr				IIBr						IIAx			
	3	4	5	6	1	2	3	4	5	6	1	2	3	4
2.8	.33	.44	.46	.21	.62	.63	.67	.48	.35	.72	.78	.97	.45	.62
4.0	.59	.54	1.00	.38	1.05	.96	1.15	.79	.56	.96	.71	1.38	.64	.73
7.2	1.07	.77	2.05	.55	1.96	1.98	2.20	1.35	1.34	1.47	1.16	1.95	.92	1.09
12.0	1.67	1.05	3.22	.74	3.40	2.95	3.41	2.15	2.10	2.13	1.82	2.65	1.25	1.55
16.0	2.17	1.25	4.20	.88	4.25	3.70	4.40	2.80	2.68	2.64	2.31	3.17	1.50	1.91
42.0	3.97	2.21	8.35	1.53	9.05	8.00	10.20	6.68	6.35	5.30	5.28	5.65	2.70	3.71

Cup	IIIBr		InBr			InBr2					irP			isP
	1	2	1	2	3	1	2	3	4	5	1	2	3	
2.8	.53	.67	1.1	1.4	1.2	0.42	0.38	0.9	.15	.31	4.2	.26	.29	4.2
4.0	.62	1.03	2.1	2.1	1.9	0.65	0.61	1.9	.27	1.08	6.6	.45	.52	6.3
7.2	.87	1.47	4.1	3.6	3.4	1.30	0.72	3.3	.39	2.08	10.5	.68	.85	10.2
12.0	1.18	2.01	6.6	5.3	4.7	2.01	0.83	5.4	.54	3.03	15.9	.99	1.28	15.4
16.0	1.40	2.37	8.5	6.5	5.7	2.36	0.90	6.8	.64	3.81	20.1	1.21	1.62	19.5
42.0	2.48	4.27	21.7	13.1	10.6	4.20	1.18	14.6	1.16	7.90	43.8	2.46	3.61	42.7

that some plates change their junctions during ontogeny. For example, the tiny specimen has such large IIIBr plates that they reach well beyond the ends of the ISBr and InBr2 plates, with their distal parts in contact with the isP and irP plates. Their drastic reduction in size in the very early stages of growth bring the IIIBr plates to lie in contact only with the ISBr and InBr2 plates; the IIIBr:isP and IIIBr:irP sutures are eliminated before the cup reaches 4 mm in height (compare IIIBr$_1$, ISBr$_5$, and InBr2$_5$ in table 7), we suspect even before the cup attains $3\frac{1}{2}$ mm.

With slight modification, the plate diagrams of the smallest and largest models can be made into continuous rolled-out plate diagrams (text-fig. 12). These diagrams stress

TABLE 7 -- Parameters of Models Expressed as Percentages of the Height of Cup. Computed from data in table 6. Plate diagrams of four models based on this table shown in text-figure 11.

Cup (mm)	Diam	Calyx	Arm	R						IBr		
				1	2	3	4	5	6	1	2	3
2.8	189	260	165	36	23	36	51	24	12	15	12	24
4.0	200	288	193	36	26	40	61	21	16	21	17	37
7.2	196	275	178	33	30	34	57	20	20	24	19	36
12.0	165	264	171	32	30	30	55	19	18	26	22	35
16.0	148	257	164	31	29	28	50	18	17	27	24	33
42.0	107	238	149	28	29	22	37	14	14	28	24	26

Cup (mm)	IBr		IAx					ISBr					
	4	5	1	2	3	4	5	1	2	3	4	5	6
2.8	23	23	20	16	14	17	4	40	11	12	16	16	7
4.0	34	31	29	33	14	24	8	49	21	15	14	25	10
7.2	38	33	31	34	14	27	6	47	25	15	11	29	8
12.0	34	28	30	31	14	25	4	46	22	14	9	27	6
16.0	32	26	29	30	14	25	4	43	20	14	8	26	6
42.0	25	20	27	25	11	22	2	25	16	9	5	20	4

Cup (mm)	IIBr						IIAx				IIIBr	
	1	2	3	4	5	6	1	2	3	4	1	2
2.8	34	35	37	27	19	40	28	35	16	22	29	37
4.0	26	24	29	20	14	24	18	35	16	18	16	26
7.2	27	28	31	19	19	20	16	27	13	15	12	20
12.0	28	25	28	18	18	18	15	22	10	13	10	17
16.0	27	23	28	18	17	17	14	20	9	12	9	15
42.0	22	19	24	16	15	13	13	13	6	10	6	10

Cup (mm)	InBr			InBr2					irP			isP
	1	2	3	1	2	3	4	5	1	2	3	
2.8	40	50	44	15	14	31	5	11	148	9	10	150
4.0	52	53	48	16	15	48	7	27	165	11	13	158
7.2	57	50	47	18	10	46	5	29	146	9	12	142
12.0	55	44	39	17	7	45	5	25	132	8	11	128
16.0	53	41	36	15	6	43	4	24	126	8	10	122
42.0	52	31	25	10	3	35	3	19	104	6	9	102

the changing relationships of IIIBr and the bordering plates during growth.

CDGRs and Their Interpretation

Areas of plates. -- Even though the same dimension (height or width) can be compared in any two plates (either as absolute size at a particular growth level, as in table 6, or as relative growth during an interval, as in table 3), it is helpful to study the areas at particular sizes of the calyx. As a standard for comparison of plate sizes, we selected the cross section area of the calyx. Roughly, this is nearly the area of an ellipse having axes of Calyx and Diam; actually, the area is slightly more because of the expansion of the lower (dorsal) end of the calyx to

TABLE 8 -- Computed Standard Area (Cross Section of Calyx) and Computed Areas of Cup Plates (in mm^2). See text for methods of computing areas.

Cup (mm)	Standard Area	R	IBr	IAx	ISBr	IIBr	IIAx	IIIBr	InBr	InBr2
2.8	122	1.63	.25	.31	.29	.41	.29	.53	1.19	.44
4.0	289	3.67	1.02	1.21	1.19	.98	.62	.80	3.19	1.09
7.2	877	10.20	3.87	4.29	4.17	3.23	1.16	1.81	10.94	3.51
12.0	1972	25.34	10.28	10.31	8.99	8.52	2.01	3.74	26.78	7.22
16.0	3060	39.40	17.64	16.63	14.00	13.21	2.68	5.64	43.61	10.19
42.0	14050	181.82	95.54	84.31	53.01	57.83	7.29	22.07	217.71	32.58

TABLE 9 -- Computed Areas of Cup Plates Expressed as Percentages of Standard Area. Based on areas in table 8.

Cup (mm)	R	IBr	IAx	ISBr	IIBr	IIAx	IIIBr	InBr	InBr2
2.8	13.36	2.06	2.50	2.35	3.38	4.32	2.41	9.76	3.59
4.0	12.70	3.53	4.17	4.10	3.39	2.76	2.13	11.04	3.77
7.2	11.65	4.42	4.90	4.77	3.68	2.06	1.32	12.48	4.00
12.0	12.84	5.20	5.23	4.55	4.41	1.90	1.02	13.57	3.66
16.0	12.89	5.77	5.43	4.58	4.32	1.85	0.88	14.26	3.33
42.0	12.94	6.80	6.00	3.78	4.12	1.57	0.52	15.49	2.32

form the radial circlet. Hence, the standard for comparing plate areas is π x Calyx x Diam.

From the geometry of each plate, a formula can be devised that will approximate the area. The following formulas were tested upon camera lucida sketches of plates and found to give reasonably good results:

Radial: $R_1/2\,(R_3 + R_4) + 2/5\,R_4R_5$

Primibrachial: $\mathrm{IBr}_2\,\mathrm{IBr}_5 + 2/3\,\mathrm{IBr}_3\,(\mathrm{IBr}_1 - \mathrm{IBr}_2)$

Primaxil: $\mathrm{IAx}_1/4\,(\mathrm{IBr}_5 + 2\,\mathrm{IAx}_2 + \mathrm{IAx}_5)$

Intersecundibrachial: $\mathrm{ISBr}_3/2\,(\mathrm{IAx}_5 + \mathrm{ISBr}_2) + \mathrm{ISBr}_2\,\mathrm{ISBr}_4 + \mathrm{ISBr}_5/3\,(\mathrm{ISBr}_2 + \mathrm{ISBr}_6)$

Secundibrachial: $(\mathrm{IIBr}_6 + \mathrm{IIBr}_5/2)\,(\mathrm{IIBr}_1 - \mathrm{IIBr}_4/3)$

Secundaxil: $\mathrm{IIAx}_3/2\,(\mathrm{IIBr}_6 + \mathrm{IIAx}_2) + \mathrm{IIAx}_2/2\,(\mathrm{IIAx}_1 - \mathrm{IIAx}_3)$

First tertibrachial: $\mathrm{IIIBr}_2\,(\mathrm{IIIBr}_1 + \mathrm{IIAx}_3 - \mathrm{IIAx}_1) + \mathrm{IIAx}_2/2\,(\mathrm{IIAx}_1 - \mathrm{IIAx}_3)$

First interbrachial: $\mathrm{IBr}_2/2\,(\mathrm{InBr}_2 + 2\,R_5) + \mathrm{IAx}_3/2\,(\mathrm{InBr}_2 + \mathrm{InBr}_3) + \mathrm{InBr}_3/2\,(\mathrm{InBr}_1 - \mathrm{IBr}_2 - \mathrm{IAx}_3)$

Second interbrachial: $\mathrm{InBr2}_1\,\mathrm{IIAx}_3 + \mathrm{IIBr}_5/2\,(\mathrm{InBr2}_1 + \mathrm{InBr2}_2) + (\mathrm{InBr2}_1 + \mathrm{InBr2}_4)\,(\mathrm{InBr}_3 - \mathrm{IIAx}_3 - \mathrm{IIBr}_5)/2.$

The results are listed in table 8 for the models (the dimensions of which are given in table 6).

The comparative areas of the plates in different models can be seen in table 9. Here, each area is expressed as a percentage of the standard area, which is that of the ellipse fitting the height and width of the calyx.

Obviously, the area of each kind of plate changes during ontogeny, some becoming proportionally larger and some proportionally smaller. It would, of course, be inaccurate to say that one plate grows "at the expense" of another, for the differential in relative size is the product of growth proceeding more rapidly in one plate than in the other. Table 9 attests that the radial and second interbrachial plates are remarkably stable elements of the calyx, filling about the same area throughout ontogeny. The secundibrachial and first interbrachial are fairly consistent, both increasing slightly. In contrast, great changes occur in the primibrachial, primaxil, secundaxil, and first tertibrachial. As elements of the calyx, the first two expand and the last two diminish during growth. The contrast is most marked between the primibrachial and the first tertibrachial, as shown in the following excerpt from table 9:

Cup (mm)	IBr	IIIBr
2.8	2.06	2.41
4.0	3.53	2.13
7.2	4.42	1.32
12.0	5.20	1.02
16.0	5.77	0.88
42.0	6.80	0.52

Although the first tertibrachial is slightly larger than the primibrachial in the very young Eucalyptocrinites crassus, it is less than 1/13th the size of the primibrachial by the time the crinoid reaches old age. This relationship is qualitatively indicated in text-figure 11.

Shape of cup. -- To study the modification of the shape of the cup during ontogeny, we selected parameters which could serve as indices of the cup diameter at four levels. First, at the base of the cup the diameter is proportional to the base of the radial (R_3). Second, near the top of the radial plates, the cup diameter is proportional to the R-IBr junction (R_4). Third, at the top of the primibrachials the cup diameter is proportional to the sum of the IBr-IAx junction (IBr_5) and the greatest width of the first interbrachial ($InBr_2$); this sum is entered in table 1 as "Total 1." Still higher, a little below the top of the cup, the diameter is approximately proportional to the sum of three parameters: half the median width of the intersecundibrachial ($ISBr_2$), the width of the secundaxil ($IIAx_2$), and the median width of the second interbrachial ($InBr2_1$); this sum is entered in table 1 as "Total 2." At the top of the cup, the diameter is approximately proportional to the sum of three parameters: half the median width of the intersecundibrachial ($ISBr_2$), twice the width of the tertibrachial (IIIBr), and the median width of the second interbrachial ($InBr2_1$); this sum is entered in table 1 as "Total 3."

For comparison, R_4, Total 1, Total 2, and Total 3 were each plotted against R_3. Then Total 3 was plotted against Total 1 and against Total 2 to show the behavior of the upper part of the cup apart from the general changes in convexity. The determined CDGRs are shown in table 5.

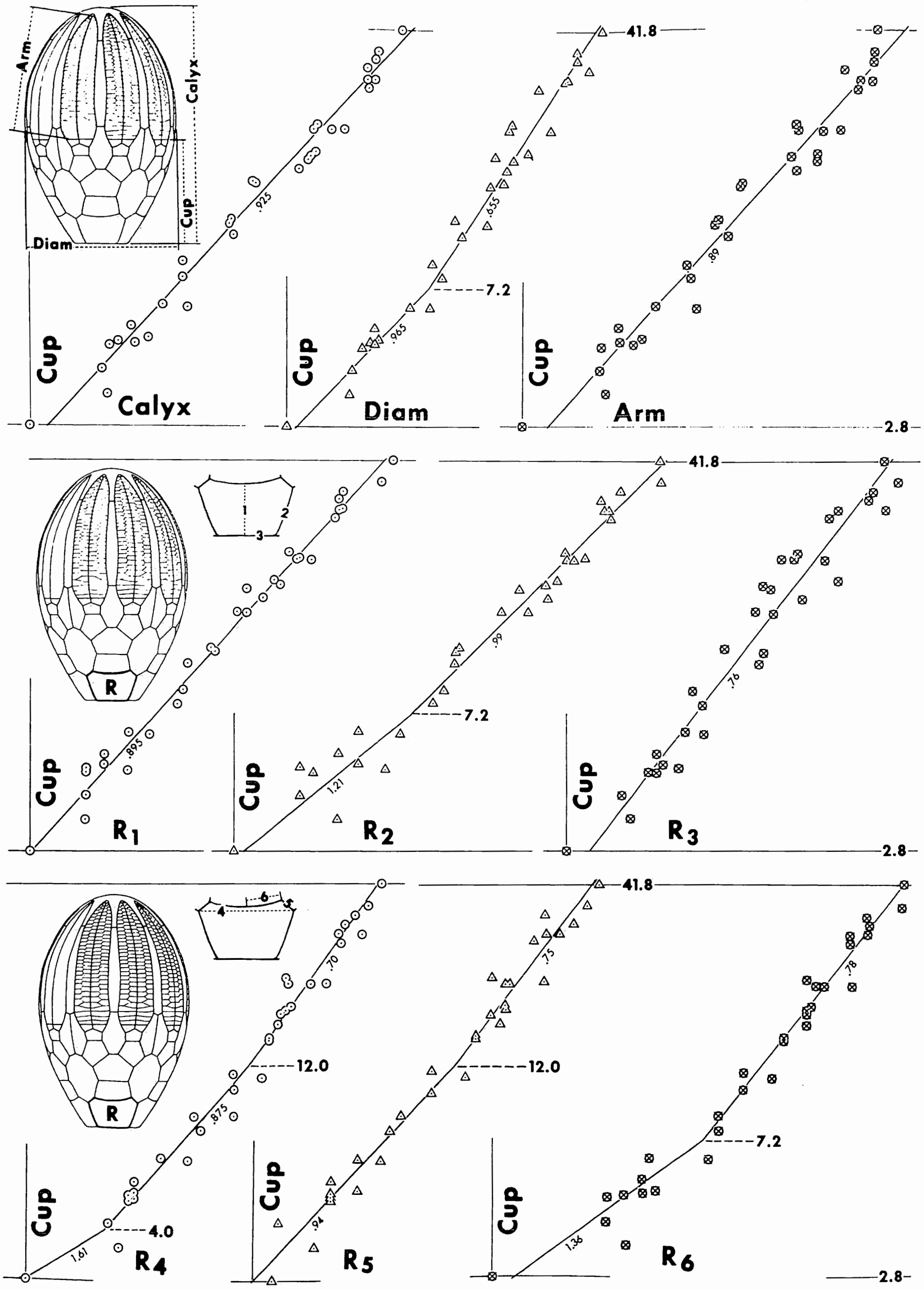
To our surprise, the cup does not change in the same way throughout its ontogeny. During stages I through III, the cup expands at upper levels relative to the base, with the greatest expansion at the level of the primibrachial-primaxil contact (Total 1:R_3 = 1.22). Hence during the young stages the cup becomes more convex in the middle and expands even to the top. During stages IV and V, however, the cup contracts at upper levels relative to the base, with the greatest contraction at the top (Total 3:R_3 = 0.795). The upper part of the cup contracts slightly and evenly during ontogeny relative to the middle (Total 3:Total 1 = 0.905; Total 3:Total 2 = 0.965). To state the change simply, the middle of the cup continues to bow outward until the cup is 12 mm high, and thereafter progressively and slowly contracts. The overall change in cup proportions has already been shown in table 2; Diam:Cup (height) declines from 0.965 in stages I and II to a steady 0.655 during the remainder of growth. This may be interpreted as follows: along with the changes in lateral convexity, the cup keeps about the same height/width ratio until it reaches 7.2 mm high, then rather rapidly increases in height. As the cup stretches upward in the adult stages, it loses some of the convexity it acquired during youthful stages.

A very intriguing aspect of the growth of the cup in stage V (16 to 41.8 mm high) concerns the source of the increase in height. Heights of the various plates comprising the cup are compared to the height of the cup in table 2. In stage V (the adult stage) the following CDGRs of height are listed: R_1 = 0.895, IBr_1 = 1.03, IAx_1 = 0.92, $IIBr_1$ = 0.775, $IIAx_1$ = 0.86, and $IIIBr_1$ = 0.59; hence, of the plates contributing to the cup height, only the primibrachial increases in height faster than the cup (and does so by only a few insignificant percentage points). How then does the cup increase its height in the adult stage, if the individual plates do not add their share? The solution, as we see it, lies in the way the heights of the plates are measured. Height of each plate is measured in a plane tangent to the middle of the plate; were it not for the convexity of each plate, the measurement would be made in the plane of the plate. On the other hand, the height of the cup is measured between a plane passing through the bases of the radials and a plane passing through the tops of the first tertibrachials. The heights of the plates will always, therefore, add up to more than the height of the cup, since they are measured more or less along the sides of the cup. The reason for the increase in height of the cup during stage V must be the straightening of the sides of the cup -- elimination of some of the middle convexity and steepening the angle of the sides. This confirms what we arrived at above by comparing the increases in cup diameter at five successive levels and indicated by the CDGRs listed in table 5. It is somewhat reassuring when two lines of investigation lead to the same conclusion.

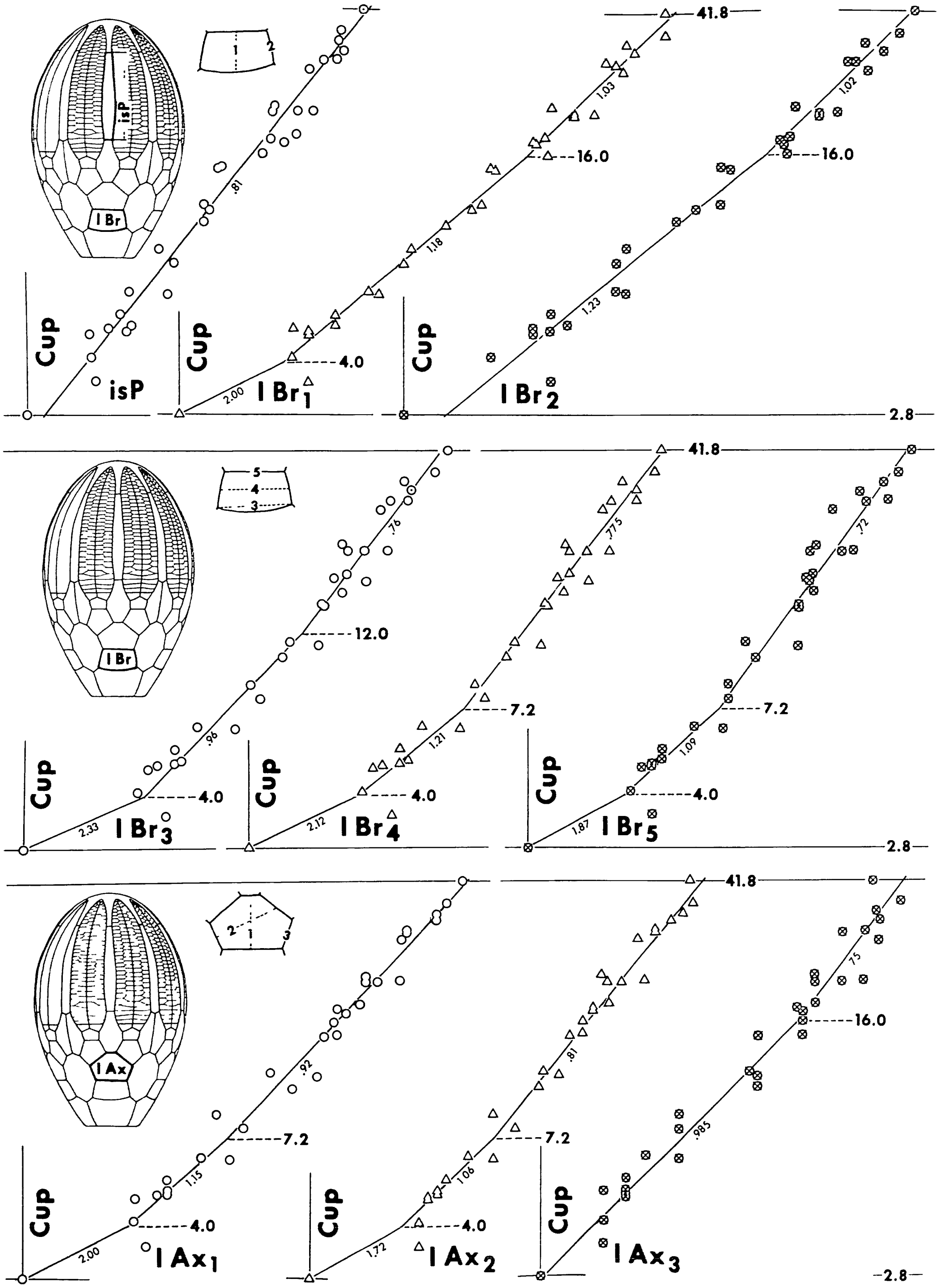
Shape of calyx. -- The height of the calyx is compared to its maximum width in table 4 (Calyx:Diam) and plotted in text-figure 9. The scatter in the plotted values is very small, marking this as a reliable constant differential growth ratio. The calyx becomes progressive but slowly more elongate (Calyx:Diam CDGR = 1.11) until the end of stage III, then much more elongate through the adult stages (Calyx:Diam CDGR = 1.43). Accordingly, we may generalize that the smallest specimen is the most rotund and the largest is the most elongate. Even though some plates may show exceptions, the majority of plates must increase more in height than width in order to produce the elongation observed in the calyx.

Relative size of plates. -- In his study of Eucalyptocrinites, Macurda (1968, p. 108) concluded that "the relative contribution of a plate to the height or width of the calyx also remains constant throughout growth." Our models of four significant sizes of cup (text-fig. 11) and our comparison of various parameters to cup height (text-figs. 2-7) and their CDGRs (table 2) all strongly suggest that this interpretation should be modified, and that the relative contribution of a plate to the height or width of the calyx does not remain constant through any appreciable interval of the entire ontogeny.

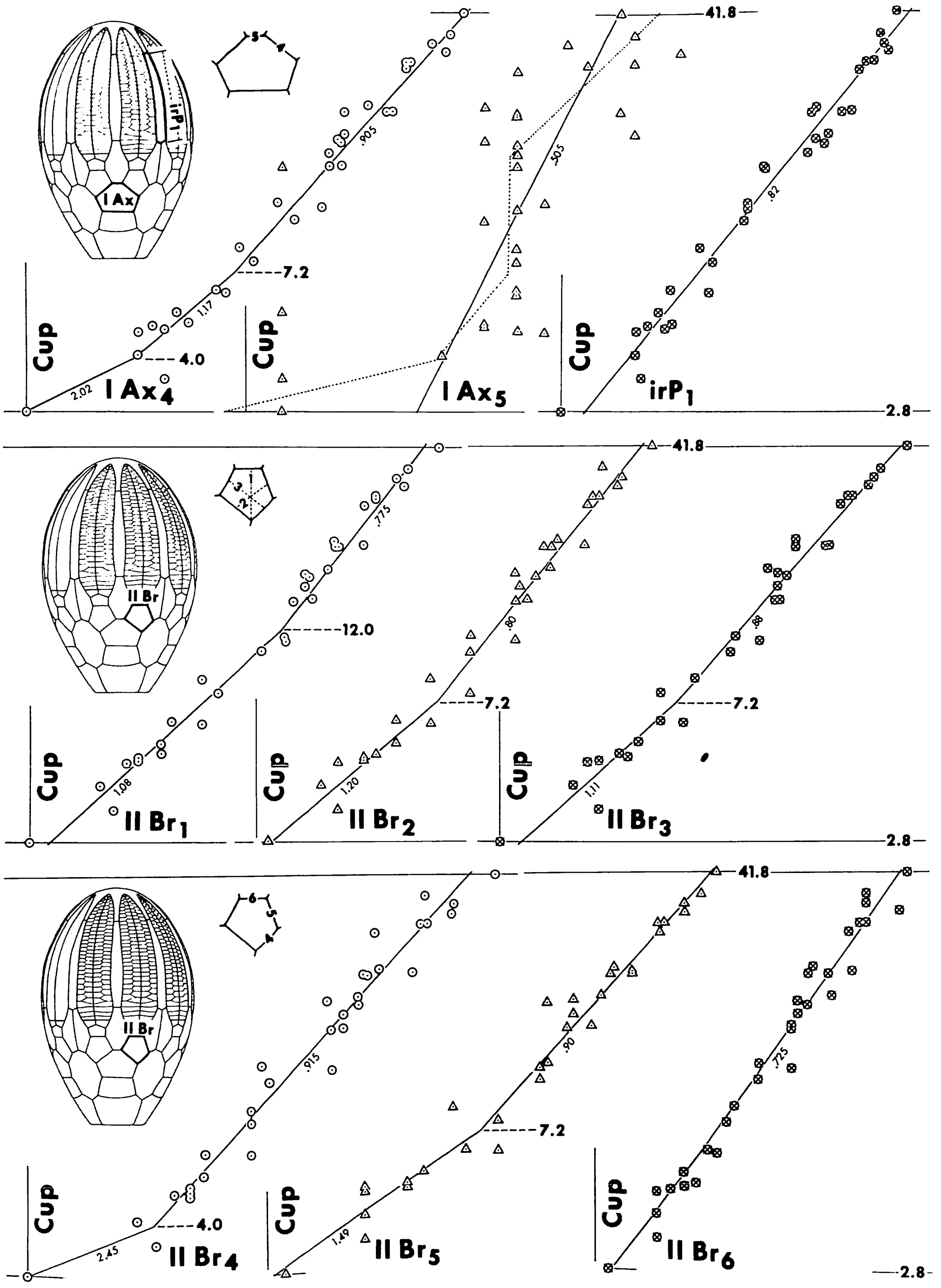
The width of the radial (R_4) can be used as a standard for comparison of the widths of other plates (text-fig. 8, table 3). Not all plate widths were plotted against R_4, although the data is available in table 1. Before comparing any of the other plates against the radial, however, it is well to note that the width of the radial (R_4) does not itself increase uniformly or in accord with the height of the cup; as seen in table 2, R_4 has a CDGR of 1.61 in stage I, 0.875 in stages II and III, and 0.70 in stages IV and V, as compared with growth of the cup. Compared with the width of the radial (R_4), the median width of the primibrachial (IBr_4) grows much faster in stages I and II (CDGR = 1.28), then slows down to about the same rate (CDGR = 1.03). Similarly, the diagonal width of the primaxil IAx_2) and the median width of the intersecundibrachial ($ISBr_2$) both grow nearly twice as rapidly as the width of the radial in stage I, thereafter slowing down to about the same rate (table 3). Of the cup plates, the width of



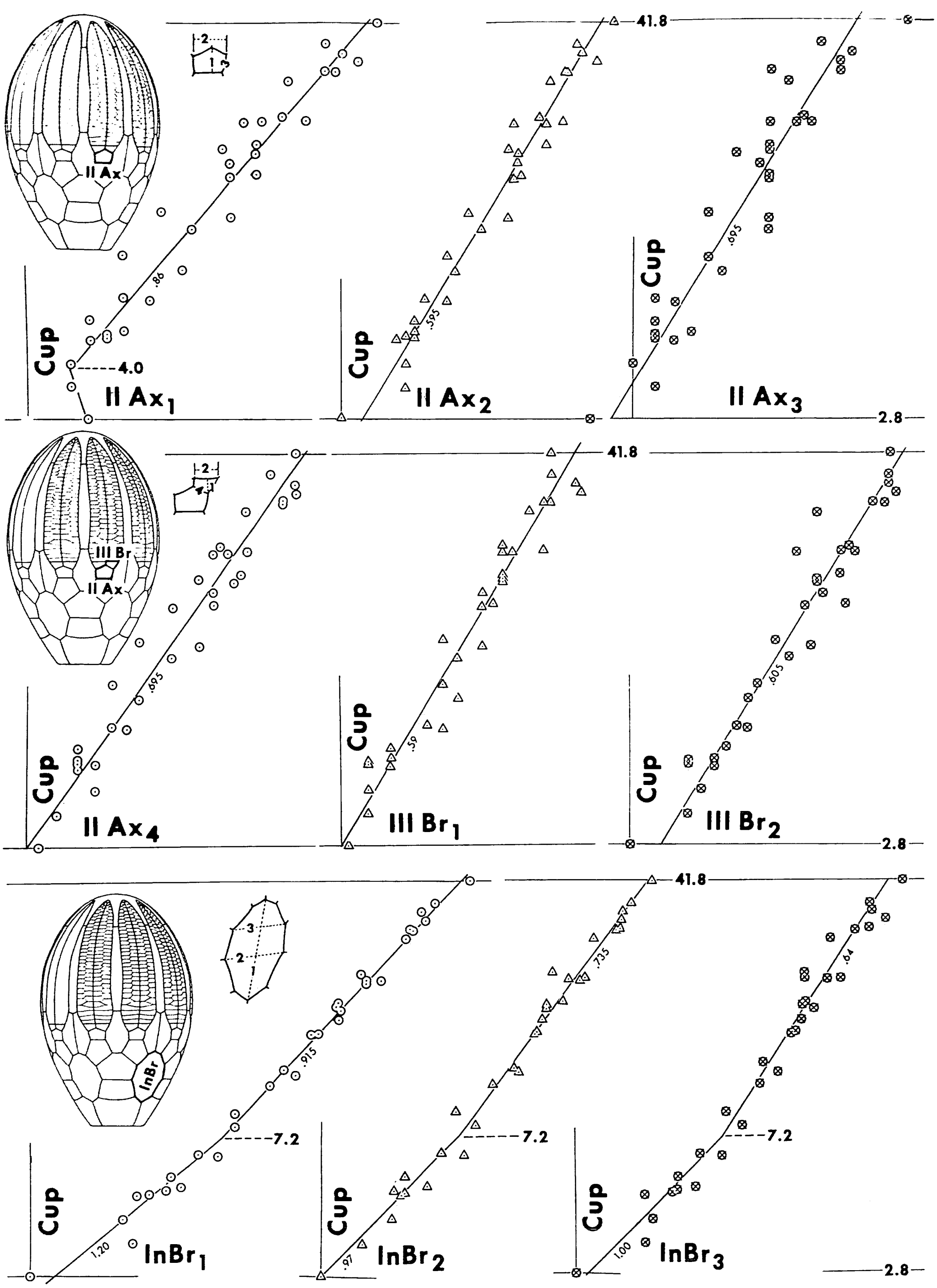
TEXT-FIG. 2 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.



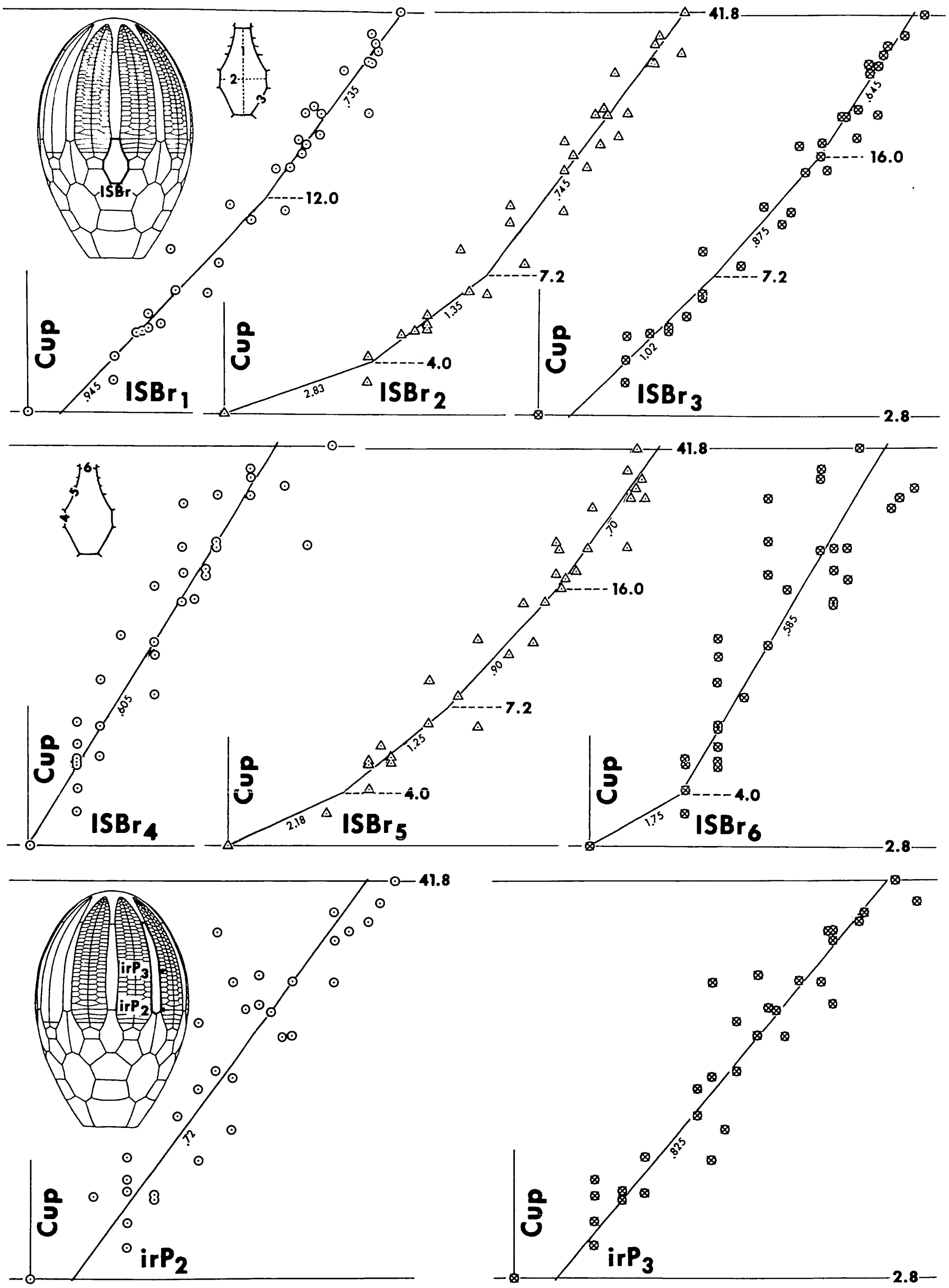
TEXT-FIG. 3 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.



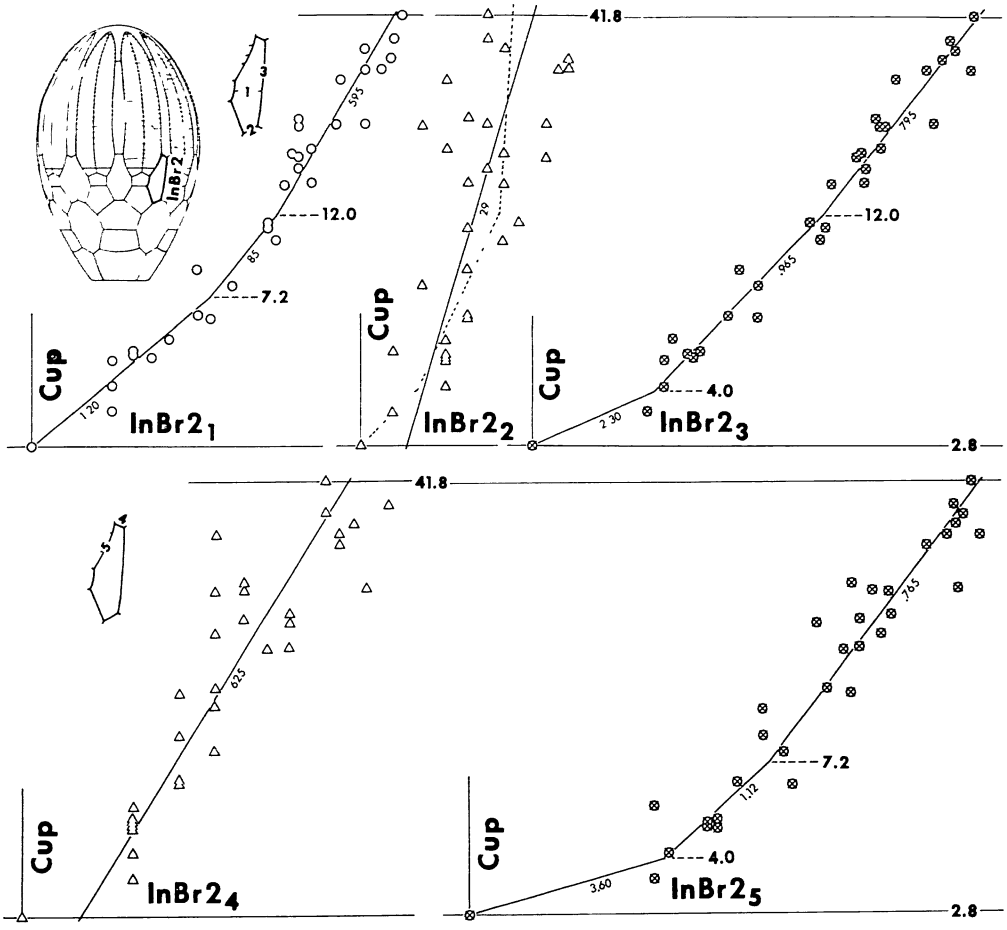
TEXT-FIG. 4 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.



TEXT-FIG. 5 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.



TEXT-FIG. 6 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.



TEXT-FIG. 7 -- Double-logarithm plots of various parameters compared with the height of the cup. Data from table 1. Mean lines are labeled with CDGR values. Inset sketches show location of the parameters.

only the interbrachial ($InBr_2$) grows at the same rate as the radial. The width of the first tertibrachial ($IIIBr_2$) is uniformly and strikingly slower in growth than the width of the radial (CDGR = 0.775).

The same inconsistency of plate size appears when other dimensions are compared. For example, compared with the height of the radial (R_1), the height of the first interbrachial ($InBr_1$) increases more rapidly through the first three stages of growth (CDGR = 1.18).

Relative growth in heights of plates can be approximated from the CDGRs in table 2. For example, in stage I the height of the radial (R_1) has a CDGR of 0.895 and the height of the primibrachial (IBr_1) has a CDGR of 2.00; we may compute that, compared with R_1, IBr_1 has a CDGR of about 2.24. In the same way, we can determine that the IBr_1:R_1 CDGR will continue to be greater than 1 throughout ontogeny; simply stated, with respect to the radial the primibrachial becomes higher as the crinoid grows, rapidly at first and then somewhat more slowly. During growth, the height of the intersecundibrachial ($ISBr_1$) shows an odd relationship to the height of the radial (R_1); as seen in table 2, in the first three stages the ISBr increases in height more rapidly than does the R, but after the cup reaches 12 mm high the R increases in height more rapidly than the

ISBr -- yet in no stage of growth does either plate increase in height as rapidly as the dorsal cup!

Other parameters can be compared for growth in any stage from the CDGRs listed in table 2.

Proportions of plates. -- Just as heights or widths of various plates could be compared during growth by their growth ratios in relation to height of the cup, as explained above, so can various parameters of the same plate be compared by their CDGRs listed in table 2. For example, in the primibrachial the height (IBr$_1$) increases at about the same rate as the median width (IBr$_4$) in stages I and II (CDGR = 2.00 and 1.18 as compared with CDGR = 2.12 and 1.21); however, in all later stages the height increases faster than the median width. This analysis is based on the supposition that all values of IBr$_1$ and IBr$_4$ bear a close relationship to height of the cup. Inspection of the plotted values (text-fig. 3) shows that all points do not not fall exactly on the median line for either IBr$_1$ or for IBr$_4$. A more precise picture of the change in proportions of the primibrachial can be obtained by plotting IBr$_1$ directly against IBr$_4$, as in text-figure 9. The resultant CDGRs (table 4) demonstrate that width increases less than height throughout ontogeny. Hence, although the CDGRs of different parameters plotted against a standard give an indication of their relative rates of growth -- particularly in the middle and large size ranges, where specimens are more plentiful -- the best results come from direct comparison. In the case of the primibrachial, the results are well illustrated in the plate diagrams of models (text-fig. 11).

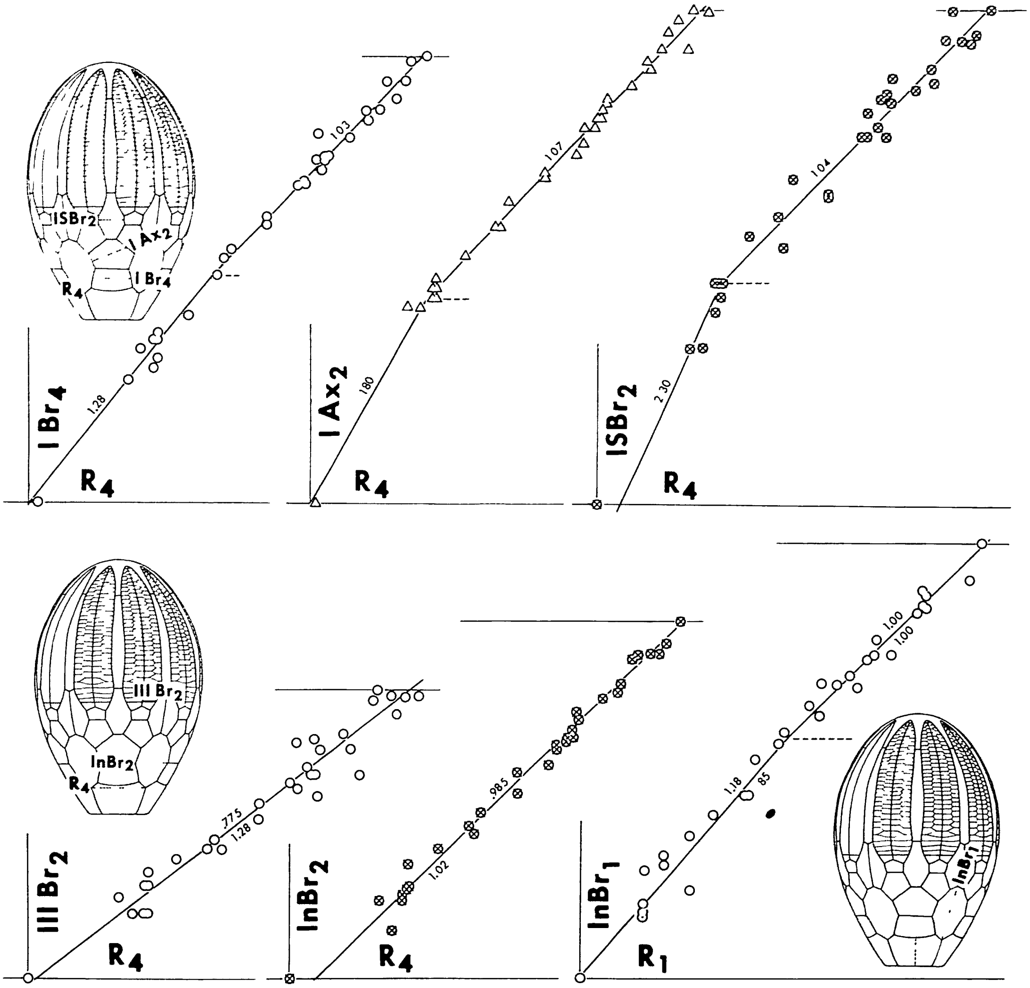
When any two parameters are considered by their CDGRs to a third parameter (as is the case in table 2, where each other parameter is compared with the cup height) the ratio of their CDGRs may not be exactly the same as the CDGR derived by plotting the two parameters against each other. In other words, second-hand allometry may differ slightly from first-hand allometry. In stage I of the population used here, control is particularly weak, since only two specimens are in it; and, for another good reason not to trust CDGR ratios from table 2 in this interval, many parameters have a different CDGR in stage I from that in the next stage, some drastically different. On the other hand, in stages III through V the control is good, and the estimates based on CDGRs in table 2 show reasonable agreement with values derived by direct plotting (table 4).

To test this, let us examine the proportions of the primaxil. In stages III-V, the diagonal width (IAx$_2$) has a CDGR = 0.81 and the height (IAx$_1$) has a CDGR = 0.92 (table 2); the predicted CDGR of IAx$_2$:IAx$_1$ for this growth interval is 0.81/0.92 = 0.88. Actually, when IAx$_2$ is plotted against IAx$_1$ on double-logarithm paper (text-fig. 9), the CDGR is found to be exactly 0.88 (table 4). Such agreement is exceptional.

The other proportions of plates with CDGR values computed in table 4 show that for the radial, primibrachial, primaxil, and intersecundibrachial the relative growth of width:height decelerates in the adult stages. In brief, these major plates all grow much more in height than width from the time the cup reaches 12 mm high until the crinoid dies.

The general pattern for other plates -- how they change in proportions -- can be learned from table 2. Width and height increase can be compared in each plate: IIBr$_2$ and IIBr$_1$ (generally more in width), IIAx$_2$ and IIAx$_1$ (consistently more in height), IIIBr$_2$ and IIIBr$_1$ (scarcely any difference), InBr$_2$ and InBr$_1$ (much more in height), and InBr2$_1$ and InBr2$_3$ (at first more in width, later more in height).

Other changes in proportions, perhaps better termed changes in plate shape, can be detected in table 2. Let us look at the intersecundibrachial, as an example. After stage I, the lower edge (IAx$_5$), the sides (IAx$_4$), and the top edge (ISBr$_6$) grow very slowly. In the first two stages, most growth is concentrated in the plate width (ISBr$_2$) and the upper sides (ISBr$_5$) abutting against the tertibrachials. In stages IV and V, the growth of the entire plate is slow in relation



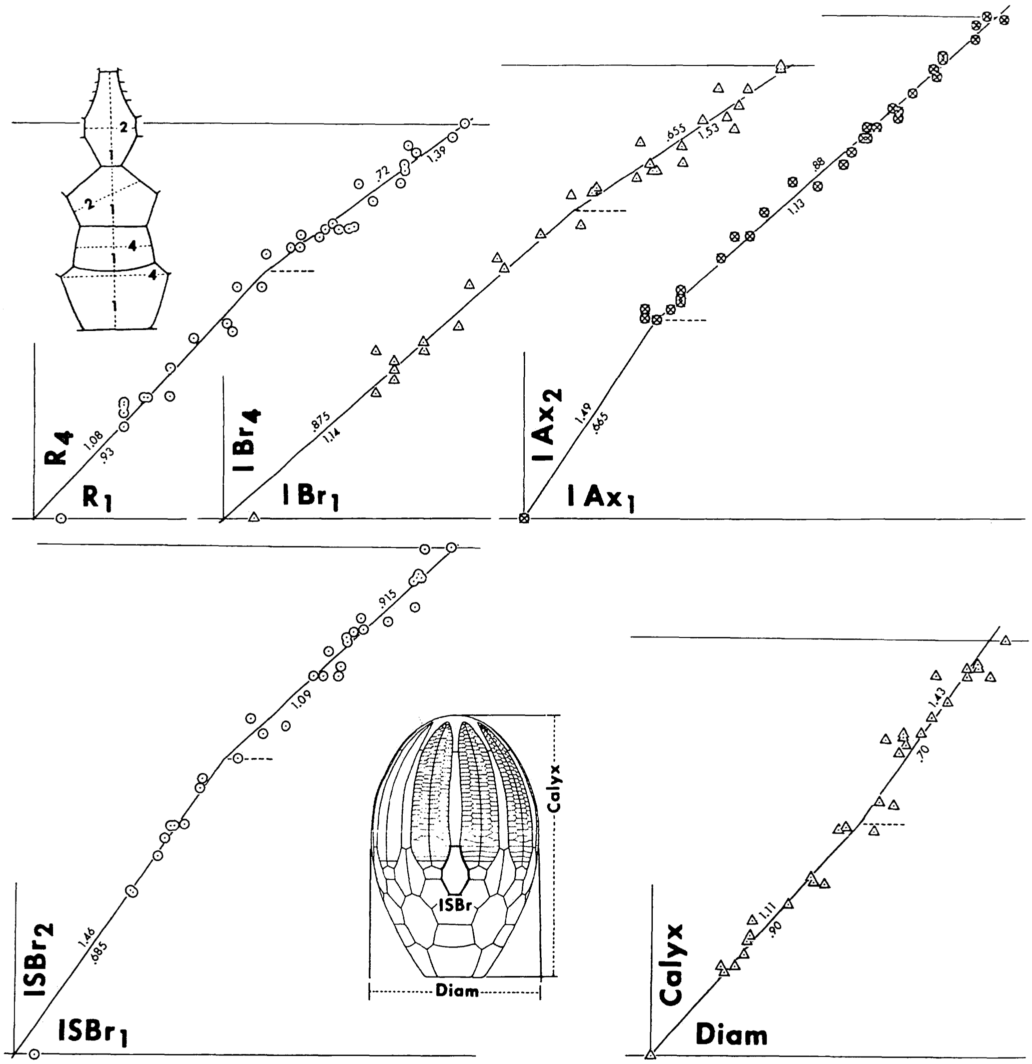
TEXT-FIG. 8 -- Double-logarithm plots of comparable parameters of various plates, showing the changes in relative size of the plates during growth. Data from table 1. Mean lines labeled with CDGR values. Inset sketches show location of the parameters. Summary in table 3.

to most other plates of the cup; nevertheless, within the secundibrachial, most growth in this interval occurs in height ($ISBr_1$), median width ($ISBr_2$), and the upper sides ($ISBr_5$).

The use of CDGRs leads to rather accurate pinpointing of just where growth is concentrated or diminished in any interval of growth. Insofar as we know, this is the only way. Macurda said (1968, p. 103):

> The exposed length of the interradial suture (R_2) is isometric with the widths (R_3 and R_4) of the radial plate...; thus, the same shape is maintained throughout development.

Exceptions to this generalization can be found. As shown in table 2, the basal width (R_3) and the maximum width (R_4) do not themselves grow at the same rate; furthermore, for all specimens larger than 4 mm in cup height, both widths increase at rates appreciably less than the length of the R:R suture (R_2). Thus, the suture grows faster than the widths. The best evidence of this is

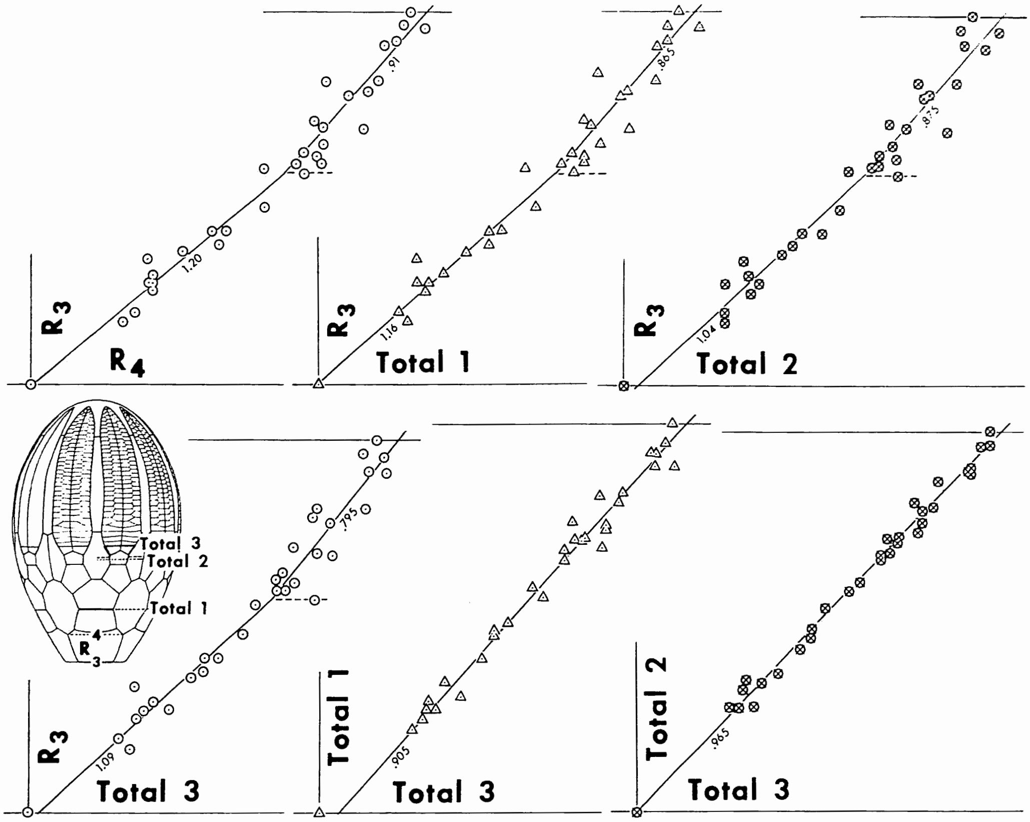


TEXT-FIG. 9 -- Double-logarithm plots of pairs of parameters in particular plates, showing changes in proportions; and plot of calyx:diam, showing overall change in shape of the crinoid. Data from table 1. Summary in table 4.

the R_3/R_2 ratios of the models (table 6): at cup height of 4 mm, this ratio is 1.58/1.04 = 1.52; but at cup height of 42 mm, the ratio has become 9.20/12.30 = 0.75. The same conclusion can be reached from the actual measurements (table 1), which records that R_3 is greater than R_2 in the smallest 12 specimens, but R_3 is less than R_2 in the largest 12 specimens (with 2 exceptions).

As a matter of fact, the changes in convexity of the cup (already discussed under "Shape of the cup") imply that the shape of the radial must also change. As shown in table 4, the R_4:R_1 CDGR decreases during ontogeny from 1.08 to 0.72. The spurt in height occurs in stages IV and V. The models illustrated in text-figure 11 bear out the overall changes in proportions of the radial.

The various parameters of models (expressed as percentages of the height of the cup in table 7) demonstrate that each parameter reaches its maximum relative

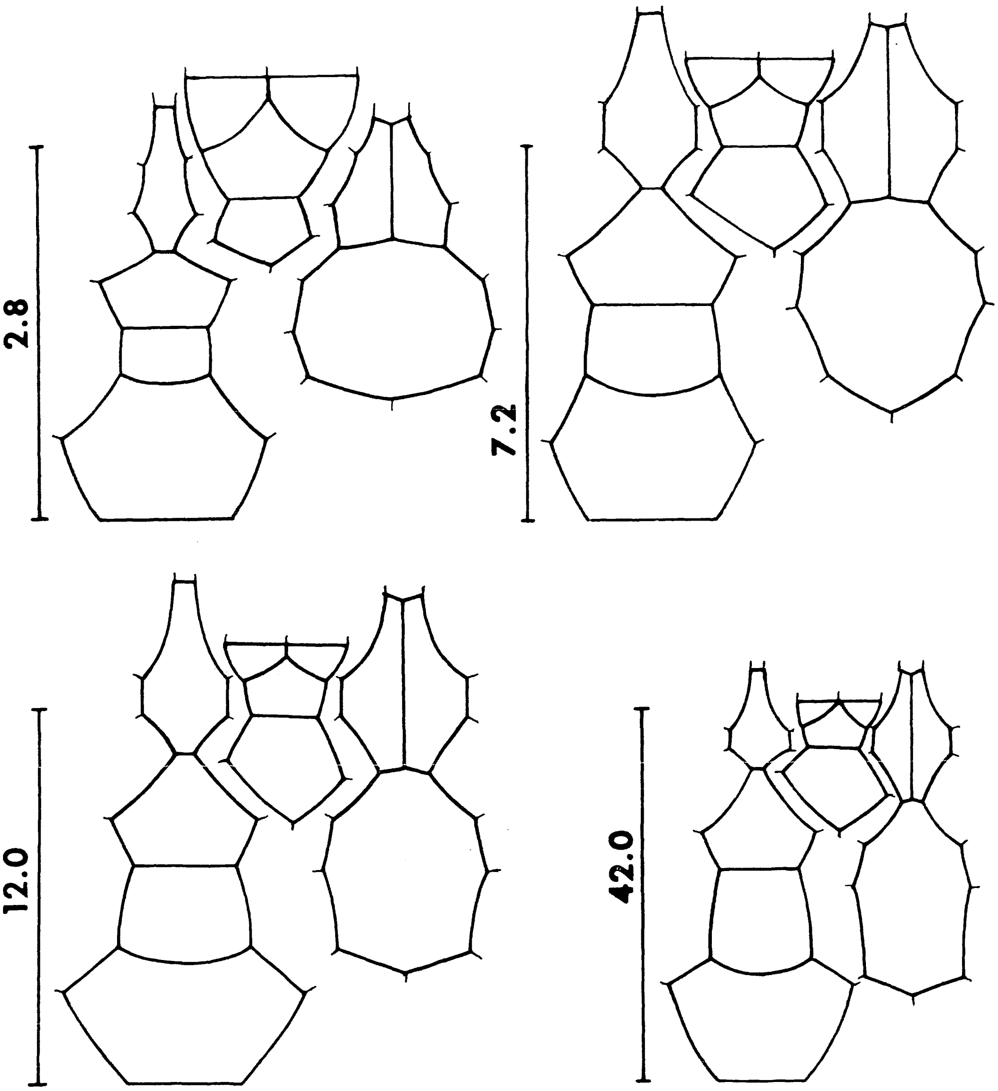


TEXT-FIG. 10 -- Double-logarithm plots of various parameters indicative of cup diameter at several levels. From base upward these parameters are R_3, R_4, Total 1, Total 2, and Total 3. Data from table 1. Summary in table 5.

size at a particular time in ontogeny -- a time that is characteristic for that parameter and not necessarily for others of the same plate. Consider the primibrachial. The height (IBr_1) and the sides (IBr_2) attain their maximum relative size in the largest specimen (with cup 42 mm high), the basal width (IBr_3) reaches its maximum when the cup is only 4 mm high, and the median width (IBr_4) and the upper edge (IBr_5) reach their maxima when the cup is about 7.2 mm high.

As Macurda strongly emphasized (1968, p. 108), "The development of any plate in the cup is directly influenced by neighboring plates as there are no free bounding edges... The ontogenetic development of Eucalyptocrinites is highly coordinated in all parts of the animal..." We should keep this in mind when considering the length of the plate sutures as well as the plate proportions.

For instance, the first interbrachial becomes proportionally narrower during growth. The magnitude of the narrowing is visually apparent in the plate diagrams of the models (text-figs. 11 and 12) and indicated by their widths ($InBr_2$) and heights ($InBr_1$) expressed as percentage of the cup height (table 7). For the models, based on mean dimensions at particular heights of the cup (table 7), $InBr_2$ declines from 50 to 31%, whereas $InBr_1$ rises from 40 to 52%. As the interbrachial narrows, it also increases as an element of the calyx, its area increasing from 9.8 to 15.5% of the vertical cross section of the calyx (table 9). In this narrowing and general enlargement of InBr, the neighboring R, IBr, IAx, IIBr, and



TEXT-FIG. 11 -- Plate diagrams of models representing four growth stages. Radial series at left, interradial series at right, and intervening plates in the middle. Line at left represents height of cup at the stage.

InBr2 plates are affected in (1) lengths of their sutures, (2) slope and position of these sutures, and (3) relative size or area. The parameter herein called Total 1 is the sum of the first interbrachial width ($InBr_2$) and the length of the IBr:IAx suture (IBr_5); relative to the basal diameter of the cup, this parameter itself shows ontogenetic change (table 5), but the following data from table 6 reveals that most of the adjustment in size is accomplished in the very early stages of development:

Cup (mm)	IBr_5	$InBr_2$	$IBr_5/InBr_2$
2.8	0.64 mm	1.4 mm	.46
4.0	1.25	2.1	.60
7.2	2.36	3.6	.66
12.0	3.40	5.3	.64
16.0	4.17	6.5	.64
42.0	8.30	13.1	.63

The same conclusion could be reached from the growth ratios in table 2:

Cup (mm)	IBr_5	$InBr_2$	$IBr_5/InBr_2$
2.81-4.0	1.87	.97	1.93
4.0 -7.2	1.09	.97	1.12
7.2-12.0	.72	.735	.98
12.0-16.0	.72	.735	.98
16.0-41.8	.72	.735	.98

Thus, the IBr:IAx suture increases faster than the width of the InBr plate only in the very early stages of growth. In this case, changes in proportions do not last long. For the continued changes in proportions of the IBr beyond stage II (table 4), therefore, we must look for other relationships than those involving InBr.

Let us turn to some pairs of adjacent plates which have comparable changes in area (table 9). For example, IBr and IAx increase from 2.06 and 2.50% of the calyx to 6.80 and 6.00%, respectively. As seen in table 2, in stages III through V the IBr:IAx suture (IBr_5) decreases relative to the cup height, with a CDGR = 0.72. The increase in size of both plates must be connected to other parameters. If we examine the median widths and heights of these plates, we find that in the primibrachial the width (IBr_4) grows at a rate comparable to that of the suture, but the height (IBr_1) grows much faster, whereas in the primaxil both width (IAx_2) and height (IAx_1) grow faster than the suture:

Stage	IBr_4	IBr_1	IBr_5	IAx_2	IAx_1
III-IV	.775	1.18	.72	.81	.92
V	.775	1.03	.72	.81	.92

In this pair of adjacent plates, relative expansion is accomplished by different means.

Let us turn to a pair of adjacent plates which decrease as calyx elements, IIAx and IIIBr. Respectively, they decrease from 4.32 and 2.41% of the calyx in the smallest specimen to 1.57 and 0.52% of the calyx in the largest (table 9). The suture between them ($IIAx_4$) grows consistently much slower than the cup height (table 2, CDGR = 0.695). Nevertheless, the proportions of IIIBr do not change appreciably, its CDGRs of width ($IIIBr_2$) and height ($IIIBr_1$) remaining about the same; but the proportions of IIAx do change continuously, with considerably more growth in height ($IIAx_1$) than in width ($IIAx_2$), as shown in excerpts from table 2:

Stage	$IIAx_1$	$IIAx_2$	$IIAx_4$	$IIIBr_1$	$IIIBr_2$
II-V	.86	.60	.70	.59	.61

In this case, the suture has a growth rate intermediate between the growth rates of height in the two plates involved, not closely attuned to the growth rate of width in either.

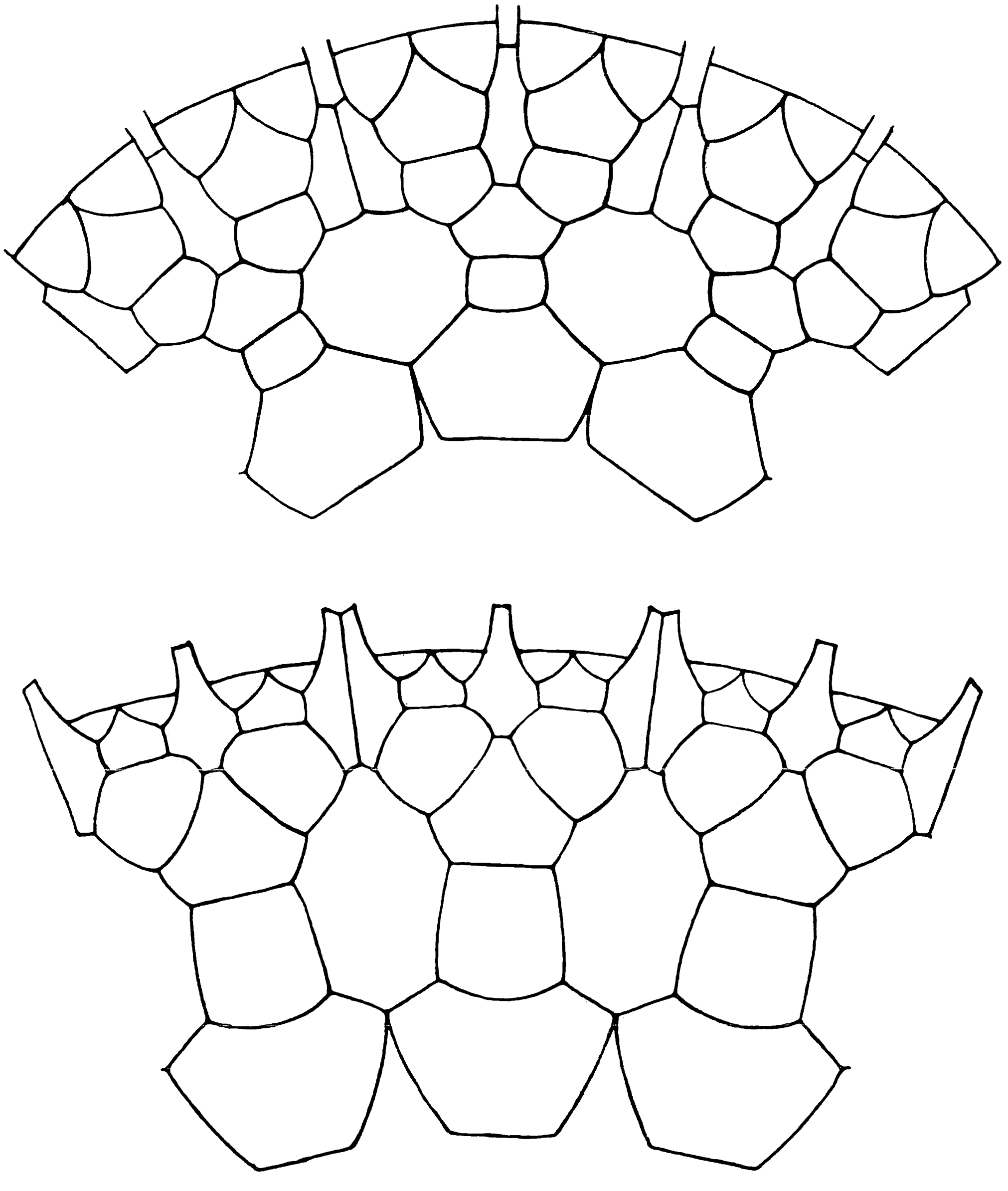
We can only deduce that growth changes in the suture between two plates does not necessarily affect each plate in the same manner, and that proportions of any plate are the end product of a very complex set of growth interactions.

Summary of Part I

Let us review what we have learned about the Indiana population of Eucalyptocrinites crassus, keeping in mind that we have only examined the dorsal cup, two plates of the tegmen, and the overall shape of the calyx.

1. Adults vary no more than the young crinoids in any parameter.

2. As growth progresses, some plates come to occupy less relative area of the calyx whereas others come to occupy more. Only a few, such as IIBr and InBr, remain at a consistent percentage of the calyx area. Relative to the calyx area, IBr and IAx expand during ontogeny; IIAx and IIIBr contract. In the smallest specimen, IIIBr is 20% larger than IBr; by the time the crinoid has reached the size of the largest specimen, however, IIIBr is more than 92% smaller than IBr.



TEXT-FIG. 12 -- Plate diagrams of models representing the smallest and largest specimens used in the study. Plate outlines slightly adjusted to fit into a continuous, or roll-out, pattern. Three radial and interradial sectors shown.

3. The cup changes shape as it grows. During young stages, it becomes more convex; but during late stages it loses some of the acquired convexity. At the same time, the cup becomes higher.

4. Neither in width nor in height do plates grow uniformly, many changing their relationship one or more times during ontogeny. Compared to the width of R, the widths of IBr, IAx, and ISBr at first grow more rapidly, and then slow down to about the same rate. In width, IIIBr grows exceptionally slower than any other plate. Compared to the height of R, the heights of IBr and InBr grow faster. Relationships

may reverse during ontogeny: in young stages ISBr increases faster in height than does R, but in the adult stage it is R that grows the faster.

5. Parameters of the same plate may also vary in their rate of growth. For examples, proportions of R stay nearly constant until late stages of ontogeny, at which time height increases much faster than width. In IBr, much the same pattern prevails, although width always grows slower than height. From the time the cup reaches 12 mm high until the crinoid expires, the relative growth of width-height slows up -- as in R, IBr, IAx, and ISBr. As a result, the cup (which, after all, is made up of all these plates) becomes more elongate.

6. Even adjacent plates which are growing at about the same rate may not keep the same shapes. Also, the suture between adjacent plates may follow a growth pattern very different from other parameters in either plate.

7. The concentration or diminution of growth shifts many times in the cup of Eucalyptocrinites crassus. In very young crinoids, the concentration of growth lies in IBr, IAx, and ISBr; later, it is in only the first two plates. During ontogeny, InBr slowly and consistently increases as an element of the cup, but IIAx and IIIBr strongly decrease. ISBr and InBr reach their greatest relative extent in middle-sized cups. Shifts also occur within plates. For example, in IBr growth is initially concentrated in the width across the base, then in the length of the side, and finally in the height of the plate. And in InBr2 growth is at first greatest along the edge next to IIIBr, later along the edge next to the paired InBr2.

PART II: THE TENNESSEE POPULATION

Introduction

A POPULATION of Eucalyptocrinites crassus from Tennessee gives us the opportunity to compare these crinoids with the population from Indiana. Geographic variation within a species deserves all the study we can give it. It is all too easy to make a new species when crinoids from a new locality do not match exactly with those we already know. But this is not good paleontology. Our science has taken a refreshing turn -- from species-making to trying to understand what makes a species grow up differently in two places. One approach to this investigation of geographic variation is through the ontogenetic growth patterns of populations in the two places.

In this case, the two places are 245 miles apart. The Indiana specimens come from the Waldron Shale at the type locality. The Tennessee specimens were collected in the summer of 1966 from the same formation at Newsome, Tennessee, by Dr. D. B. Macurda, Jr., of our museum and Dr. Alan H. Horowitz of Indiana University.

We started this study because we were intrigued by the differences in the adult crinoids from the two places. The Indiana crinoids keep the conical shape of their cups (with minor changes in proportions), but many of the Tennessee crinoids change to a very flattened adult cup. We hoped that our growth studies might reveal the cause of such drastic differences in adult form.

There were plenty of crinoids to work with. Of the 315 fairly complete cups in the collection, we sorted out 37 of the best to represent the growth series. In contrast with the Indiana specimens, which are buried in soft shale and weather out as excellently preserved calyces, those from Tennessee are embedded in limy strata that yield only cups. Even these are in many cases partly encrusted and partly hidden in the limy matrix. Cleaning them is tedious but necessary.

TABLE 10 -- Measurements of Various Parameters in *Eucalyptocrinites crassus* from Tennessee (in cm). For explanation of plates and parameters, see text.

For the location of plates, see text-figure 1 (p. 3); for the method of measuring parameters, see discussion on pages 5 through 9. The locations of parameters in this population are also shown in sketches in text-figures 14 (p. 38), 15 (p. 39), 16 (p. 40), 17 (p. 41), 18 (p. 42), and 19 (p. 43).

Specimen	Diam	R						IBr				
		1	2	3	4	5	6	1	2	3	4	5
60793	2.66	.28	.26	.43	.63	.23	.22	.28	.30	.45	.48	.4
60794	1.74	.30	.27	.31	.55	.19	.20	.29	.23	.39	.39	.32
60795	3.16	.50	.53	.41	.92	.25	.36	.58	.5	.68	.68	.50
60796	2.10	.24	.21	.22	.45	.16	.15	.21	.15	.30	.32	.27
60797	2.30	.17	.14	.15	.53	.45	.18	.27	.26	.36	.37	.33
60798	1.50	.18	.10	.24	.42	.10	.15	.18	.16	.26	.27	.23
60799	2.7	.52	.50	.40	.80	.20	.27	.55	.50	.54	.55	.46
60800	2.43	.28	.25	.61	.74	.16	.27	.39	.32	.51	.50	.41
60801	3.00	.26	-	.61	.98	.25	.34	.60	.41	.67	.60	.45
60802	3.35	.45	.38	-	.90	.31	.30	.60	1.51	.60	.65	.52
60803	4.10	.60	.62	.80	1.17	.30	.45	.75	.66	.80	.81	.70
60804	3.40	.43	.40	.55	.91	.22	.34	.59	.41	.59	.59	.49
60805	3.30	.58	.57	.49	1.00	.24	.34	.65	.59	.72	.72	.6
60806	2.83	.40	.36	.40	.68	.20	.29	.40	.38	.43	.49	.41
60807	3.70	.50	.40	.80	1.00	.22	.31	.78	.49	.70	.70	.55
60808	2.80	.45	.41	.50	.81	.19	.30	.40	.35	.54	.56	.46
60809	3.10	.43	.40	.42	.80	.23	.28	.43	.37	.54	.58	.50
60810	4.00	.50	.46	.50	1.08	.30	.39	.62	.58	.75	.80	.70
60811	4.50	.51	.45	.60	1.40	.34	.40	.60	.52	.76	.83	.75
60812	4.50	.78	.80	.89	1.31	.30	.50	.97	.85	.99	.85	.70
60813	3.70	.63	.61	.96	1.38	.39	.48	.72	.60	.90	.95	.70
60814	3.90	.61	.55	.63	1.18	.36	.40	.78	.65	.80	.80	.66
60815	4.30	.78	.75	.64	.86	.33	.47	.86	.74	.88	.96	.80
60816	5.00	.68	.57	.82	1.41	.40	.50	.91	.79	1.00	1.06	.91
60817	5.70	.78	.78	.92	1.34	.31	.54	1.00	.87	1.00	1.01	.88
60818	7.10	.70	.71	.82	1.43	.32	.54	.80	.70	1.08	1.10	1.00
60819	5.70	.61	.59	.64	1.17	.30	.40	.75	.60	.80	.93	.70
60820	6.10	.76	.70	.64	1.41	.37	.54	.95	.81	1.05	1.06	.94
60821	5.60	.49	.50	.76	1.20	.30	.42	.82	.68	.90	.98	.79
60822	6.90	.90	1.01	.89	1.63	.27	.60	1.10	.96	1.18	1.27	1.05
60823	7.20	.76	.82	.74	1.68	.33	.65	1.12	.96	1.24	1.28	1.04
60824	2.72	.36	.35	.47	.75	.17	.29	.49	.45	.57	.55	.46
60825	5.42	.90	.91	.81	1.56	.30	.61	1.10	1.02	1.19	1.15	.90
60826	2.30	.47	.42	.39	.71	.18	.28	.40	.35	.48	.50	.39
60827	3.95	.55	.54	.83	1.30	.34	.47	.71	.64	.92	.89	.67
60828	2.62	.40	.35	.45	.85	.25	.29	.49	.44	.52	.52	.42
60829	2.00	.40	.39	.35	.69	.19	.28	.48	.40	.45	.48	.35

For this part of the paper we are indebted to Dr. Macurda and to Dr. Horowitz for their perseverance in collecting, as well as to Mrs. Mysyk for typing and Mr. Kutasi for photography.

Methods

Parameters. -- Parameters used in this part of the study are the same as those used in Part I -- with one notable exception. This involves the "standard" parameter, against which all others could be compared.

TABLE 10 -- (continued)

Specimen	IAx					ISBr					
	1	2	3	4	5	1	2	3	4	5	6
60793	.46	.47	.19	.40	.07	.61	.40	.20	.18	.39	.10
60794	.32	.35	.12	.29	.09	.37	.29	.13	.10	.19	.08
60795	.60	.58	.22	.54	.10	.75	.45	.30	.18	.50	.12
60796	.34	.32	.12	.30	.08	.50	.30	.19	.13	.31	.12
60797	.41	.38	.15	.34	.05	.53	.28	.18	.12	.30	.06
60798	.22	.25	.11	.19	.04	.37	.26	.10	.09	.19	.05
60799	.52	.49	.25	.46	.04	.72	.36	.25	.13	.44	.10
60800	.49	.45	.19	.40	.08	.59	.36	.22	.13	.32	.09
60801	.60	.52	.24	.49	.15	.84	.45	.21	.19	.55	.09
60802	.65	.62	.29	.51	.24	.90	.75	-	-	-	-
60803	.80	.80	.31	.69	.20	.90	.60	.32	.20	.50	.21
60804	.62	.60	.30	.49	.17	.7	.50	.30	.19	.43	.19
60805	.7	.70	.30	.60	.10	.75	.50	.32	.13	.43	.16
60806	.50	.48	.18	.40	.10	.62	.40	.24	.16	.37	.14
60807	.71	.70	.31	.62	.12	.86	.53	.31	.17	.50	.17
60808	.47	.56	.28	.44	.0	.50	.41	.25	.18	.28	.17
60809	.56	.58	.22	.49	.18	.73	.52	.29	.20	.42	.18
60810	.78	.79	.24	.69	.22	.87	.61	.28	.20	.52	.28
60811	.86	.89	.30	.65	.26	.98	.68	.38	.19	.60	.28
60812	.80	.76	.36	.70	.20	1.00	.66	.36	.20	.59	.30
60813	.89	.85	.40	.62	.26	1.09	.62	.39	.20	.60	.30
60814	.80	.79	.30	.71	.15	.90	.56	.30	.21	.56	.20
60815	.91	.89	.36	.86	.15	1.07	.65	.37	.20	.68	.14
60816	.80	.99	.31	.79	.31	1.00	.76	.39	.11	.63	.25
60817	1.00	1.00	.36	.88	.30	1.18	.90	.40	.26	.71	.35
60818	1.10	1.09	.36	1.00	.32	1.40	.92	.40	.34	.90	.45
60819	.91	.90	.34	.81	.19	1.28	.84	.49	.27	.70	.39
60820	1.18	1.05	.40	1.08	.20	1.37	.85	.47	.31	.80	.32
60821	1.09	1.00	.41	.90	.14	1.30	.82	.50	.16	.80	.32
60822	1.24	1.22	.41	1.05	.29	1.63	1.00	.50	.32	1.01	.31
60823	1.38	1.25	.44	1.18	.20	1.59	.92	.48	.41	.89	.50
60824	.50	.49	.21	.40	.10	.75	.40	.24	.12	.50	.09
60825	1.07	1.00	.40	.90	.21	1.12	.79	.49	.20	.68	.30
60826	.42	.43	.18	.34	.10	.55	.35	.22	.11	.32	.11
60827	.89	.82	.39	.70	.13	1.00	.62	.37	.23	.60	.23
60828	.52	.48	.21	.45	.05	.69	.41	.29	.14	.40	.42
60829	.49	.46	.20	.38	.07	.68	.35	.20	.17	.40	.05

It is fairly obvious that a vertical measurement of cup height does not mean much for a group of crinoids that includes an appreciable number that are strongly flattened. Furthermore, the base of the cup is seldom well preserved, more often than not worn, encrusted, and/or chipped. We settled on a different "standard" parameter, one which seems relative to the plate parameters in this population. It is the sum of the heights of IBr, IAx, and ISBr -- roughly the direct distance from the middle of the R:IBr suture to the tip of the ISBr. We call it H.

Measurements of the 37 selected specimens are listed in table 10. Some of the variation in form is suggested by the camera lucida sketches and plate diagrams in text-fig. 13.

TABLE 10 -- (continued)

Specimen	IIBr						IIAx				IIIBr	
	1	2	3	4	5	6	1	2	3	4	1	2
60793	.43	.35	.49	.28	.3	.29	.29	.33	.15	.20	.15	.25
60794	.3	.28	.34	.2	.19	.2	.2	.26	.12	.13	.10	.2
60795	.5	.46	.6	.38	.31	.37	.38	.41	.19	.28	.20	.38
60796	.31	.28	.34	.21	.20	.21	.24	.29	.15	.19	.14	-
60797	.37	.35	.39	.28	.21	.25	.21	.31	.13	.18	.12	.23
60798	.23	.21	.25	.18	.17	.14	.13	.17	.09	.11	.07	.15
60799	.46	.43	.52	.34	.29	.29	.27	.36	.15	.22	.16	.30
60800	.39	.34	.48	.28	.26	.29	.26	.31	.15	.19	.15	.20
60801	.50	.50	.60	.40	.30	.44	.34	.48	.12	.26	.26	.29
60802	.60	.51	.61	.40	.50	.36	.35	.46	.19	.29	.19	.30
60803	.70	.61	.78	.50	.50	.49	.41	.56	.20	.31	.23	.43
60804	.51	.42	.58	.35	.38	.36	.34	.40	.20	.29	.19	.38
60805	.65	.57	.72	.49	.48	.40	.39	.45	.20	.30	.20	.35
60806	.46	.40	.50	.29	.29	.31	.25	.34	.15	.26	.20	.26
60807	.60	.51	.55	.48	.39	.40	.31	.20	.50	.31	.22	.40
60808	.45	.54	.51	.31	.31	.25	.26	.36	.17	.20	.10	.26
60809	.55	.45	.54	.31	.39	.30	.31	.40	.20	.26	.19	.33
60810	.66	.59	.79	.48	.46	.49	.40	.51	.20	.33	.26	.40
60811	.75	.68	.90	.52	.60	.50	.50	.59	.24	.40	.28	.45
60812	.69	.60	.82	.70	.38	.45	.41	.53	.15	.36	.24	.40
60813	.80	.61	.82	.60	.52	.50	.41	.50	.19	.32	.20	.40
60814	.70	.60	.80	.53	.51	.49	.49	.54	.28	.38	.25	.41
60815	.84	.73	.98	.60	.60	.53	.45	.50	.20	.36	.22	.37
60816	.85	.71	.91	.61	.51	.59	.49	.64	.21	.35	.25	.45
60817	.92	.78	1.09	.65	.62	.69	.58	.79	.30	.49	.30	.60
60818	1.10	.90	1.21	1.13	.28	.70	.70	.81	.30	.60	.40	.53
60819	.87	.80	.94	.60	.62	.60	.53	.71	.25	.45	.28	.50
60820	1.00	.90	1.22	.73	.72	.69	.72	.80	.30	.60	.32	.40
60821	.92	.90	1.08	.70	.60	.62	.65	.70	.30	.50	.35	.49
60822	1.10	1.06	1.21	.93	.73	.72	.74	.83	.37	.55	.35	.51
60823	1.26	1.10	1.41	.92	.85	.82	.78	.86	.36	.57	.37	.66
60824	.45	.49	.41	.42	.23	.30	.28	.33	.18	.20	.15	.22
60825	.85	.71	1.02	.55	.60	.60	.50	.70	.20	.45	.30	.50
60826	.35	.33	.38	.25	.26	.26	.21	.30	.11	.18	.14	.20
60827	.74	.66	.82	.55	.49	.48	.45	.55	.24	.33	.21	.39
60828	.46	.42	.53	.32	.30	.31	.30	.35	.17	.21	.15	.28
60829	.40	.39	.52	.28	.29	.27	.30	.31	.15	.21	.15	.25

Constant differential growth ratios. -- CDGRs were determined in the same way as those in Part I. Other parameters are plotted against H in text-figures 14 to 17. The CDGRs are summarized in table 11.

We plotted up all the other parameters against H. Some did not turn out too well: the points were widely scattered on the double-log paper. These were left out in the text-figures. Maybe we made a mistake in leaving them out, for the great variation itself must be a characteristic of the parameter-pair in the growth series.

Other approaches. -- For these crinoids, so strongly altered as they grew, we tried several ways to find a synthesis of their "flattening." For one thing, we compared the area in lateral view against the area in basal view, using a camera lucida to sketch the outlines and a polar planimeter to measure the

TABLE 10 -- (continued)

Speci-men	InBr			InBr2					H	Total 1	Total 2
	1	2	3	1	2	3	4	5			
60793	.76	.61	.61	.30	.12	.60	.09	.50	1.35	1.01	.83
60794	.57	.50	.45	.20	.10	.37	.08	.30	.98	.82	.61
60795	1.08	.80	.80	.38	.20	.75	.12	.60	1.93	1.30	1.02
60796	.52	.41	.48	.24	.11	.48	.10	.30	1.05	.68	.68
60797	.71	.54	.54	.21	.09	.51	.09	.24	1.21	.87	.66
60798	.44	.39	.36	.15	.08	.35	.05	.20	.77	.62	.45
60799	.96	.70	.62	.28	.11	.75	.10	.45	1.79	1.16	.82
60800	.77	.65	.63	.27	.13	.60	.09	.31	1.47	1.06	.76
60801	.90	.79	.73	.41	.19	.75	.19	.49	2.04	1.24	1.12
60802	1.17	.91	.82	.32	.24	.90	.11	.51	2.15	1.43	1.16
60803	1.41	1.05	.95	.49	.15	.84	.21	.52	2.45	1.75	1.35
60804	1.05	.79	.69	.32	.17	.80	.15	.60	1.91	1.28	.97
60805	1.13	.97	.90	.40	.16	.91	.17	.69	2.1	1.03	1.14
60806	.70	.61	.60	.29	.18	.62	.11	.40	1.52	1.02	.63
60807	1.10	.90	.82	.40	.20	.89	.12	.70	2.35	1.45	.87
60808	.90	.65	.66	.22	.13	.70	.09	.33	1.37	1.11	.79
60809	.92	.74	.71	.38	.18	.76	.19	.60	1.72	1.24	1.04
60810	1.30	1.0	.95	.50	.21	.88	.25	.70	2.27	1.70	1.37
60811	1.35	1.00	1.00	.42	.13	1.16	.19	.81	2.44	1.75	1.35
60812	1.60	1.16	1.09	.48	.22	1.15	.20	.82	2.77	1.86	1.34
60813	1.80	1.21	1.17	.48	.21	1.11	.21	.61	2.70	1.91	1.29
60814	1.47	1.12	1.01	.40	.18	.92	.15	.70	2.48	1.78	1.22
60815	1.52	1.17	1.00	.45	.12	1.10	.15	.65	2.84	1.97	1.28
60816	1.57	1.35	1.20	.50	.21	1.15	.11	.75	2.81	2.26	1.52
60817	1.76	1.30	1.23	.60	.21	1.21	.30	.71	3.18	2.18	1.84
60818	1.75	1.41	1.40	.90	.38	1.10	.59	.90	3.30	2.41	2.17
60819	1.50	1.11	1.18	.61	.26	1.04	.34	.70	2.94	1.81	1.74
60820	1.64	1.42	1.48	.80	.30	1.26	.42	.92	3.50	2.36	2.1
60821	1.49	1.20	1.27	.65	.38	1.16	.40	.71	3.21	1.99	1.76
60822	2.18	1.46	1.50	.76	.20	1.45	.35	1.00	3.73	2.54	2.14
60823	2.06	1.65	1.62	.88	.26	1.5	.56	.94	4.09	2.71	2.20
60824	.95	.66	.65	.28	.10	.75	.07	.45	1.64	1.12	.81
60825	1.88	1.39	1.30	.60	.21	1.05	.39	.68	3.29	2.29	1.70
60826	.75	.65	.60	.22	.11	.55	.10	.32	1.37	1.04	.70
60827	1.49	1.09	.90	.40	.10	1.05	.16	.55	2.60	1.76	1.26
60828	.95	.72	.65	.32	.12	.65	.09	.40	1.70	1.14	.88
60829	.85	.57	.50	.22	.08	.70	.05	.58	1.65	.92	.71

areas. Points were scattered continuously, not separated into two clusters representing the conical and the flat forms.

Next, we used the direct method of comparing the maximum diameter of the cup against the height as measured between a plane through the bottom of the RR circlet and a plane through the upper edges of the IIIBrBr. This told, of course, whether a specimen was flat or not, but it did not disclose much about the flattening process during growth. There was a simple explanation of why this procedure was not much good: three cups with the same height/diameter ratio might have very different volumes because the sides of the first were convex, the sides of the second were nearly straight, and the sides of the third were resupinate -- S-shaped -- steep at the base, then flared sharply out-

TABLE 11 -- CDGRs of Other Parameters Compared to H in Tennessee Population.

Parameter-Pair	Juv.	Adult	Parameter-Pair	Juv.	Adult	Parameter-Pair	Juv.	Adult
Diam:H	0.85	1.34	IAx$_4$:H	0.83	1.28	IIAx$_1$:H	0.78	1.46
R_4:H	0.91	0.91	ISBr$_1$:H	0.91	0.91	IIAx$_2$:H	0.75	1.11
IBr$_1$:H	1.18	1.18	ISBr$_2$:H	0.73	1.16	IIAx$_4$:H	0.62	1.32
IBr$_2$:H	1.30	1.30	ISBr$_3$:H	0.90	0.90	InBr$_1$:H	1.12	0.94
IBr$_3$:H	1.02	1.02	ISBr$_5$:H	1.02	1.02	InBr$_2$:H	0.84	1.06
IBr$_4$:H	1.02	1.02	IIBr$_1$:H	0.98	1.10	InBr$_3$:H	0.75	1.22
IBr$_5$:H	0.90	1.20	IIBr$_2$:H	0.80	1.36	InBr2$_1$:H	1.00	1.14
IAx$_1$:H	1.00	1.00	IIBr$_3$:H	0.82	1.16	InBr2$_3$:H	0.94	0.94
IAx$_2$:H	1.04	1.04	IIBr$_4$:H	1.03	1.13	InBr2$_5$:H	1.08	1.08
IAx$_3$:H	1.18	0.77	IIBr$_6$:H	1.00	1.26			

TABLE 12 -- CDGRs of Selected Parameter-Pairs in Tennessee Population.

Parameter-Pair	Juv.	Adult	Parameter-Pair	Juv.	Adult	Parameter-Pair	Juv.	Adult
Diam:Total 1	0.85	1.40	IIAx$_2$:IBr$_4$	0.88	1.28	InBr2$_2$:InBr$_3$	1.12	0.80
Diam:R_4	0.87	1.48	IBr$_3$:IBr$_1$	0.68	1.14	InBr2$_3$:IIBr$_5$	0.83	0.83
Total 2:R_4	0.77	2.15	IBr$_4$:IBr$_1$	0.65	1.29	InBr2$_3$:InBr2$_5$	0.80	1.16
Total 2:Total 1	1.10	1.10	IBr$_5$:IBr$_1$	0.64	1.23	IIBr$_2$:IIBr$_1$	0.94	0.94
Diam:IBr$_4$	0.92	1.36	IAx$_1$:IBr$_5$	1.27	0.95	IIBr$_3$:IIBr$_1$	1.02	1.16
R_4:IBr$_4$	0.97	0.97	ISBr$_1$:ISBr$_2$	1.01	1.01	IAx$_4$:IIBr$_5$	0.91	1.14
ISBr$_2$:IBr$_4$	0.83	1.54	InBr$_2$:InBr$_1$	0.94	0.94	IIAx$_2$:IIAx$_1$	1.14	0.75
InBr$_2$:IBr$_4$	0.97	0.97	InBr$_3$:InBr$_1$	0.89	1.10			

ward, and curved back strongly near the top (even back toward the central axis of the cup).

In another scheme, we compared the vertical height against the distance up the side of the cup. Again, the differences in the shape of the cup made the results dubious, at best. It appeared that the flattening process had not started in all crinoids at the same stage of development. Some began expanding laterally very early in life, whereas others went through a period of conical growth before flaring outward. In those crinoids which curved back toward the central axis at the top of the cup, we have no idea what the tegmen was like. Seemingly, it must have been very low. The sutural surfaces of the ISBr, IIIBr, and InBr2 plates in such specimens are strongly slanted inward.

CDGRs and Their Interpretation

Shape of the cup. -- To study how the cup develops during ontogeny, we selected three of the parameters used for the Indiana population: R_4, Total 1, and Total 2. R_4 is the maximum width of the radial plate. Total 1 is the sum of the width across the top of the primibrachial and the maximum width of the first interbrachial (Total 1 = IBr$_5$ + InBr$_2$); and Total 2 is the sum of half the width of the second interbrachial, the width of the secundaxil, and the width of the second interbrachial (Total 2 = $\frac{1}{2}$ISBr$_2$ + IIAx$_2$ + InBr2$_1$). Because the base of the cup is irregularly preserved and hard to measure accurately, we decided not to use R_3 (the width at the base of the radial plate).

In early stages of development, until the cup reaches 3.7 cm in diameter, R_4

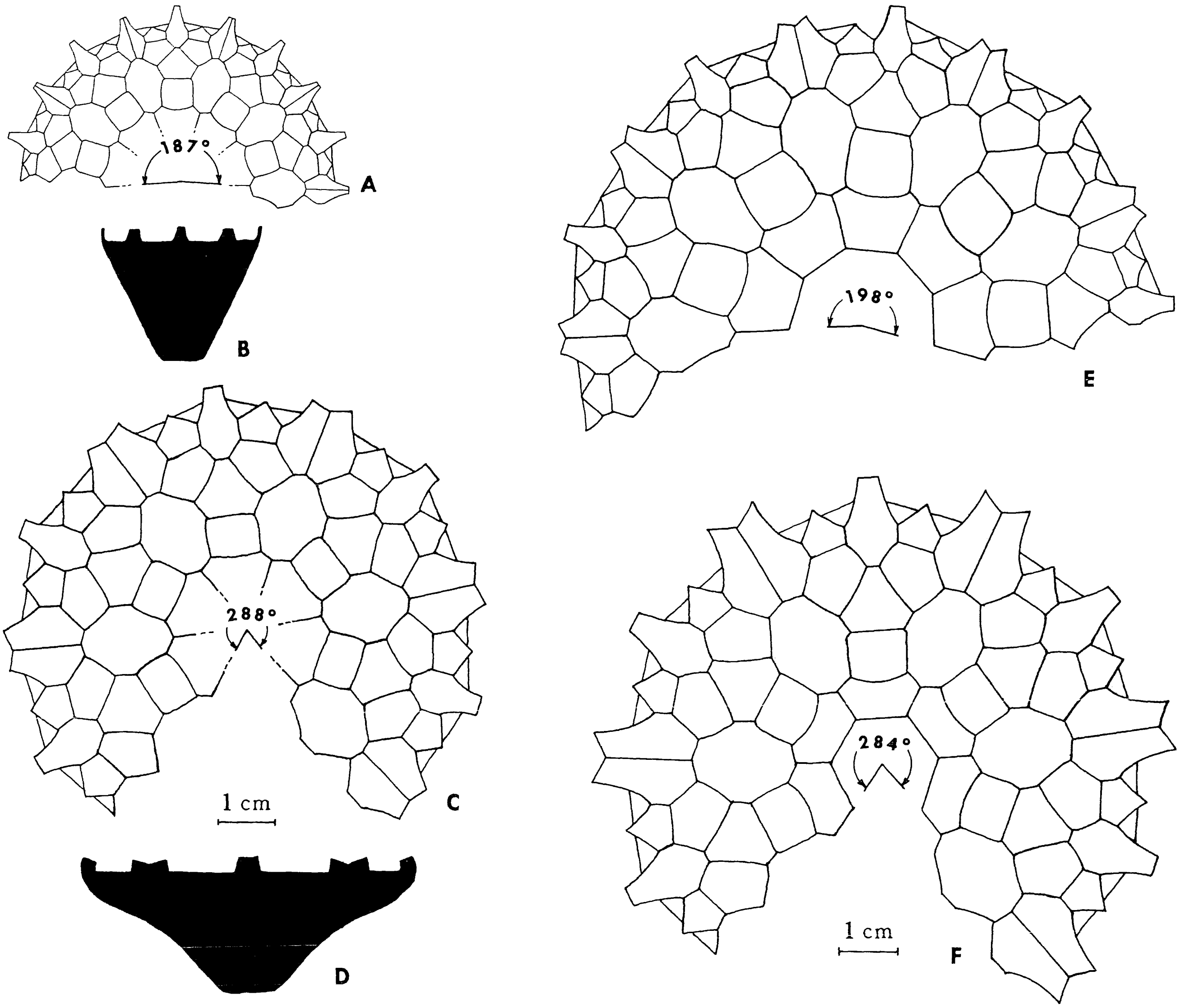
TABLE 13 -- CDGRs of Selected Parameters in the Two Populations Compared to the Standard Parameter. For Indiana population, averages are taken below and above 7.2 mm in diameter of cup.

Parameter		Indiana		Tennessee	
		Juv.	Adult	Juv.	Adult
	Diam	0.97	0.66	0.85	1.34
Width	R_4	1.24	0.76	0.91	0.91
Height	IBr_1	1.59	1.13	1.18	1.18
Side	IBr_2	1.23	1.16	1.30	1.30
Width	IBr_4	1.67	0.78	1.02	1.02
Height	IAx_1	1.58	0.92	1.00	1.00
Diagonal	IAx_2	1.39	0.81	1.04	1.04
InBr suture	IAx_3	0.99	0.91	1.18	0.77
IIBr suture	IAx_4	1.60	0.91	0.83	1.28
Height	ISBr_1	0.95	0.81	0.91	0.91
Width	ISBr_2	2.09	0.75	0.73	1.16
IIBr suture	ISBr_3	1.02	0.80	0.90	0.90
Upper side	ISBr_5	1.72	0.83	1.02	1.02
Height	IIBr_1	1.08	0.88	0.98	1.10
Diagonal	IIBr_2	1.20	0.80	0.80	1.36
Diagonal	IIBr_3	1.00	0.88	0.82	1.16
InBr suture	IIBr_4	1.68	0.92	1.03	1.13
IIAx suture	IIBr_6	0.73	0.73	1.00	1.26
Height	IIAx_1	0.25	0.86	0.78	1.46
Width	IIAx_2	0.60	0.60	0.75	1.11
IIIBr suture	IIAx_4	0.70	0.70	0.62	1.32
Height	InBr_1	1.20	0.92	1.12	0.94
Lower width	InBr_2	0.97	0.74	0.84	1.06
Upper width	InBr_3	1.00	0.64	0.75	1.22
Width	$\mathrm{InBr2}_1$	1.20	0.68	1.00	1.14
Height	$\mathrm{InBr2}_3$	1.63	0.85	0.94	0.94
Upper side	$\mathrm{InBr2}_5$	2.36	0.77	1.08	1.08

increases faster than the cup diameter. Then a change in growth pattern occurs, and thereafter the diameter increases faster than R_4 (see table 11 and text-fig. 17). A similar relationship exists between Total 1 and the diameter, except the change-over occurs at a diameter of 4.0 cm (see table 11 and text-fig. 17). In juvenile stages R_4 increases faster than Total 2, whereas in adult stages the opposite is true (text-fig. 17). A small difference in CDGRs exists between Total 1 and Total 2, with Total 1 being slightly less than Total 2. From these we learn that the crinoids from Tennessee altered the shape of their cups at about the time they reached 4.0 cm in diameter; hence, the ontogeny can be easily divided into a juvenile stage (pre-4.0 cm) and an adult stage (post-4.0 cm). We can also conclude that the cup expands at a faster rate in the lower part during the juvenile stage, and faster in the upper part during the adult stage.

The same conclusion can be reached by comparing H (roughly, the height measured along the side) and the maximum diameter of the cup (text-fig. 14). Until the diameter reaches 3.9 cm, it increases slower than H; thereafter, it increases faster. Simply stated: above a critical diameter of about 4 cm, the cup flares outward.

Changes in the cup shape are further shown in text-figure 13. Juvenile crinoids have relatively steep sided parabolic cups. UMMP 60799 shows typical characteristics of the juvenile stage; text-figure 13 shows a roll-out plate diagram (A) and a silhouette (B) of this specimen. Some indication of the steepness of the sides can be obtained in the two-dimensional drawing of the rolled-out cup, which sweeps through an arc of only 187°. Later, the cup begins to mushroom outward. UMMP 60819 shows characteristics found in many adult cups; it is shown as a roll-out plate diagram (C) and a silhouette (D) in text-figure 13. The diagram (C), sweeping through an arc of 288°, presents a rather dramatic picture of how width has increased more than height.



TEXT-FIG. 13 -- Roll-out plate diagrams of four specimens and silhouettes of two of them. A, B, roll-out and silhouette of young specimen, UMMP 60799. C, D, roll-out and silhouette of adult specimen, UMMP 60819. E, F, roll-outs of two specimens of different shape, UMMP 60825 and 60818. All to same scale.

Relative size of plates. -- The contribution made by each plate to the overall height and width of the cup does not stay constant throughout ontogeny (text-fig. 12A and 13C). The proof lies in the CDGRs listed in table 11 (plate parameters vs. H) and table 12 (other parameter-pairs).

Let us look at plate width first. We selected IBr_4 (the width of the primibrachial) as a standard for comparing other plate widths. IBr_4 is not only fairly consistent with H, but it also grows at about the same rate as H (text-fig. 14). It also increases faster than the diameter of the cup (text-fig. 17) until the cup reaches 4.0 cm in diameter, but in later stages increases much slower than the diameter. From our study of the "Shape of the cup" (above) we already know that the lower and upper parts of the cup grow differently; now we want to find out whether *all* the lower plates grow one way and *all* the upper plates grow another way. As listed in table 12, R$_4$:IBr$_4$ has a CDGR = .97 throughout ontogeny, identical with the CDGR of InBr$_2$: IBr$_4$. Hence, the three plates comprising the lower part of the cup -- R, IBr, and InBr -- all expand in width at about the same rate throughout the crinoid's life. Now, for some of the plates in the upper part of the cup, we go to text-figures 15, 16, and 18 and to tables 11 and 12. Two of the upper plates -- ISBr and IIAx -- grow in width at a slower rate than H in juvenile crinoids, but at a faster rate than H in adults (text-figs. 15, 16; table 11); a third upper plate -- InBr2 -- also grows faster in the adult stage than in the juvenile (text-fig. 16). As compared to the growth in width of the primibrachial, the growths in width of both IIAx and ISBr are slower in the juvenile stage (IIAx$_2$:IBr$_4$ = .88; ISBr$_2$:IBr$_4$ = .83) and much faster in the adult stage (IIAx$_2$:IBr$_4$ = 1.28; ISBr$_2$: IBr$_4$ = 1.54), as can be seen in text-figure 18. From these CDGRs it is clear that the upper plates achieve their great final width (relative to lower plates) by expansion during only the adult stage; in the juvenile stage, these upper plates were actually shrinking in width as compared to the lower plates.

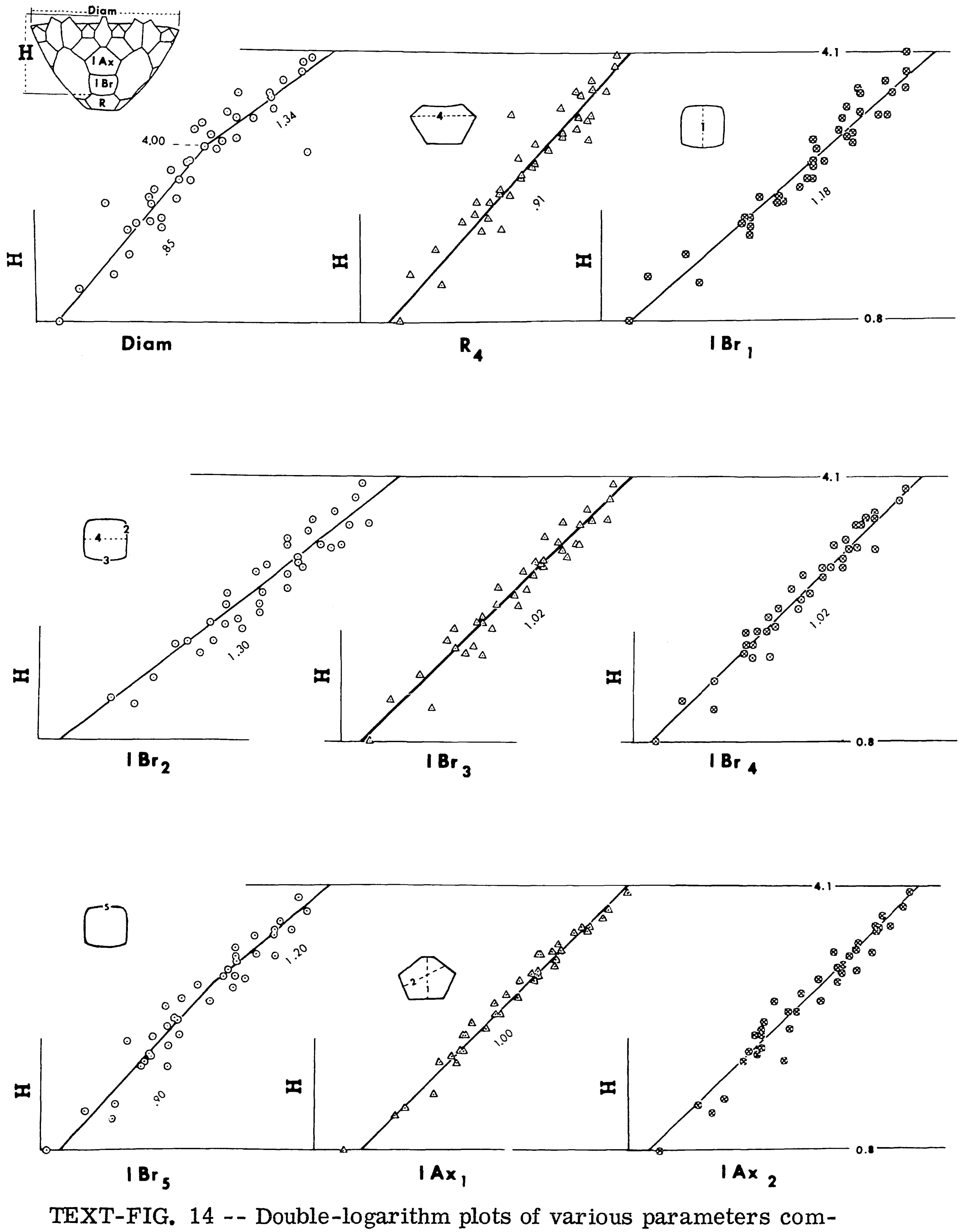
The "flattening" of the cup can now be explained as the natural and necessary result of expansion of the upper plates in later stages of growth. With the CDGRs of width in the upper plates -- low in early youth, high in later life -- *Eucalyptocrinites crassus* had to assume the shapes shown for young (text-fig. 13B) and for old (text-fig. 13D) individuals. But the CDGRs tell only *how* the flattening occurred, nothing about *why* it happened. We have the mechanics of the process but not the cause. At least, we now know what was involved in the crinoid achieving its flattened adult form.

Let us now examine plate height. Three plates are of special interest -- IBr, IAx, and ISBr -- because the sum of their heights was chosen as the standard for comparing other parameters, H. The three did not ever grow at the same rate. IBr$_1$ always grew faster than H, IAx$_1$ always grew at exactly the same rate as H, and ISBr$_1$ always grew slower than H (table 11). The height of the second interbrachial (InBr2$_3$) increased consistently slower than H (text-fig. 17). InBr, one of the lower plates, at first extended its height (InBr$_1$) faster than H; then, when H reached 2.5 cm, InBr rather abruptly slowed down its rate of growth in height and never again kept pace with respect to H (text-fig. 16). Heights in two upper plates followed the reverse pattern of growth: IIBr$_1$ and IIAx$_1$ both grew slower than H in the juvenile stage and faster than H in later life (table 11). The difference in juvenile and adult CDGRs is fairly small in IIBr, but exceptionally large in IIAx. It will be worth our while at this point to summarize how plates grew in height with respect to H:

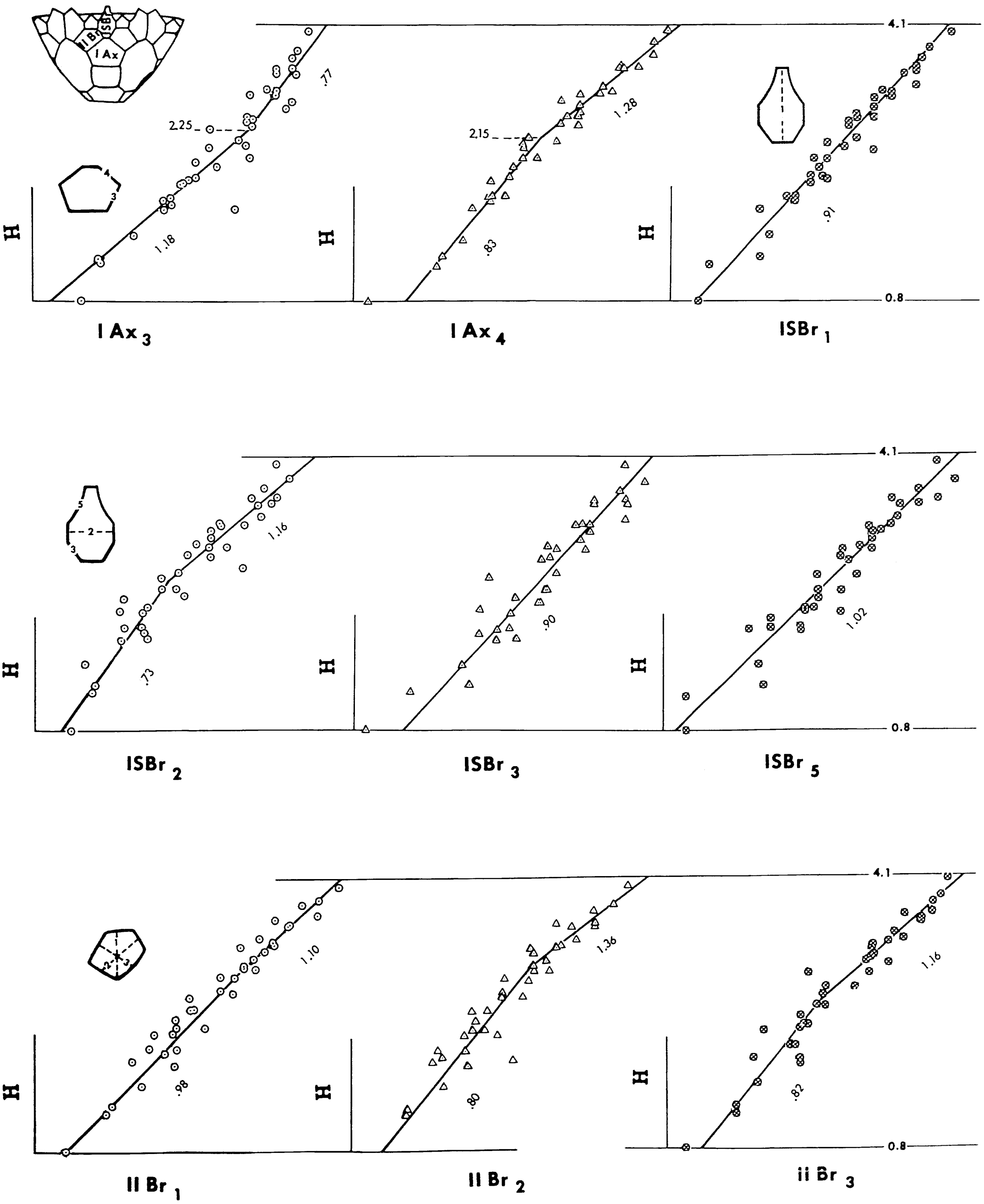
Growth rate	Juvenile	Adult
Much slower than H	IIAx	
Slightly slower than H	ISBr, InBr2	ISBr, InBr, InBr2
About the same as H	IAx, IIBr	IAx
Slightly faster than H	IBr, InBr	IBr, IIBr
Much faster than H		IIAx

The growth pattern of height now seems to fit very nicely with the change in shape of the cup. Above, we note that the plate which increases most in height is IIAx. It is the plate most responsible for pushing the upper part of the cup outward during the late stages of growth. Oddly enough, the plates at the very top of the cup -- ISBr and InBr2 -- do not take part in this lateral extension. This explains how the sides of the cup assume the peculiar resupinate outline which characterizes the large specimens. The cup flares out most at about the level of the IIAx plates; it even contracts at the tips of the ISBr and InBr2 plates.

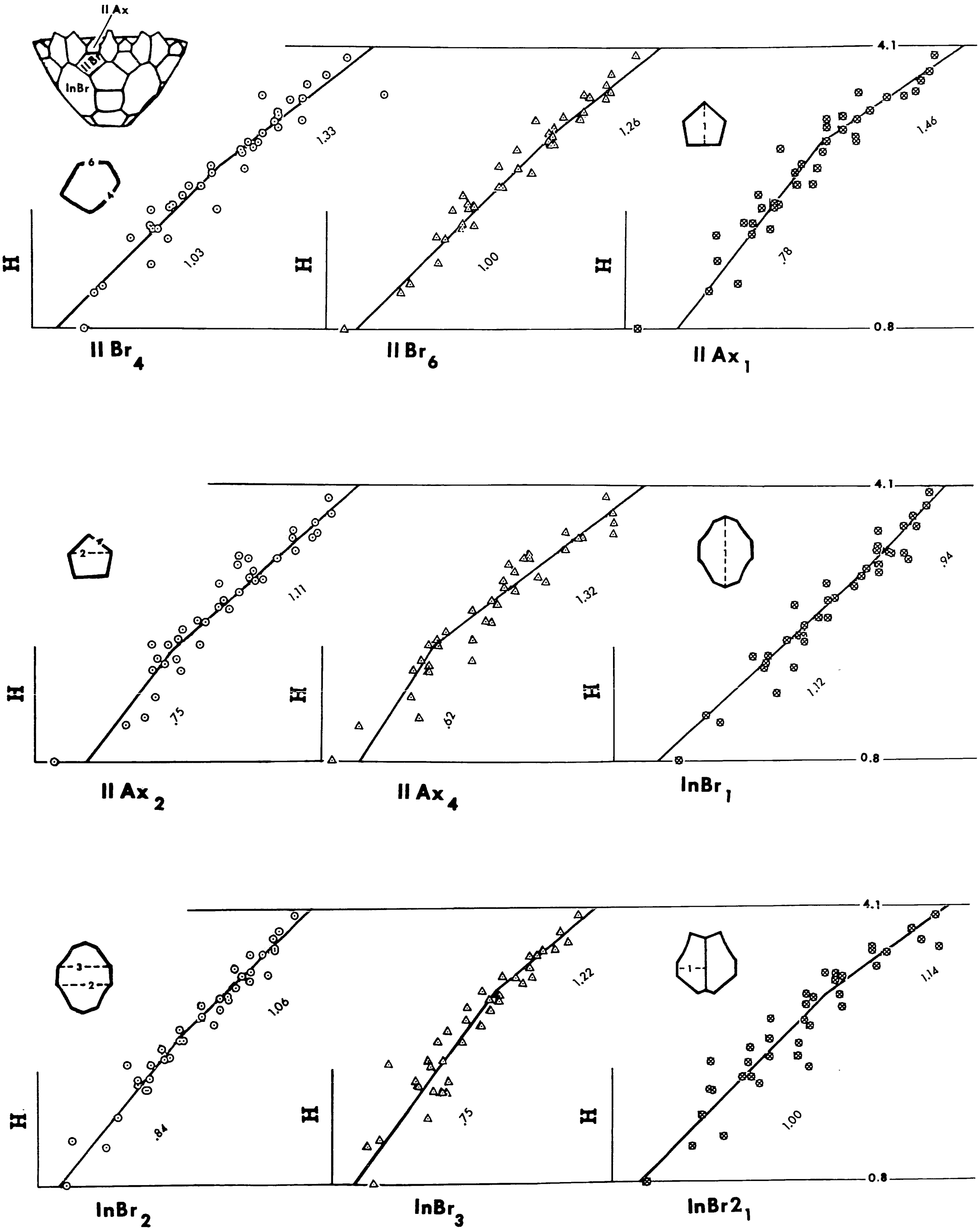
Proportions of plates. -- In this section, various parameters of a particular plate are compared by their CDGRs with respect to



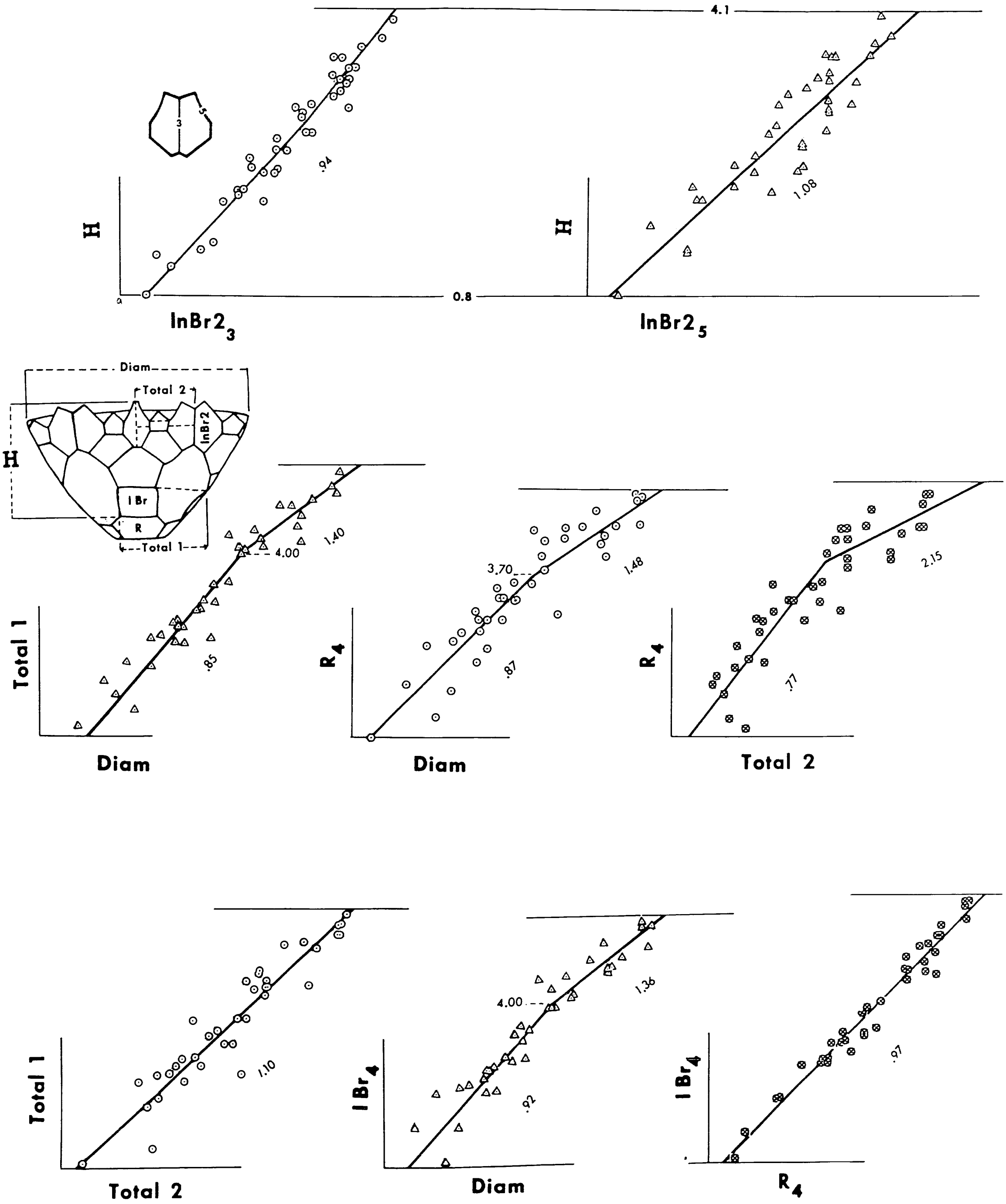
TEXT-FIG. 14 -- Double-logarithm plots of various parameters compared to H. Data from table 10. Mean lines labeled with CDGR values.



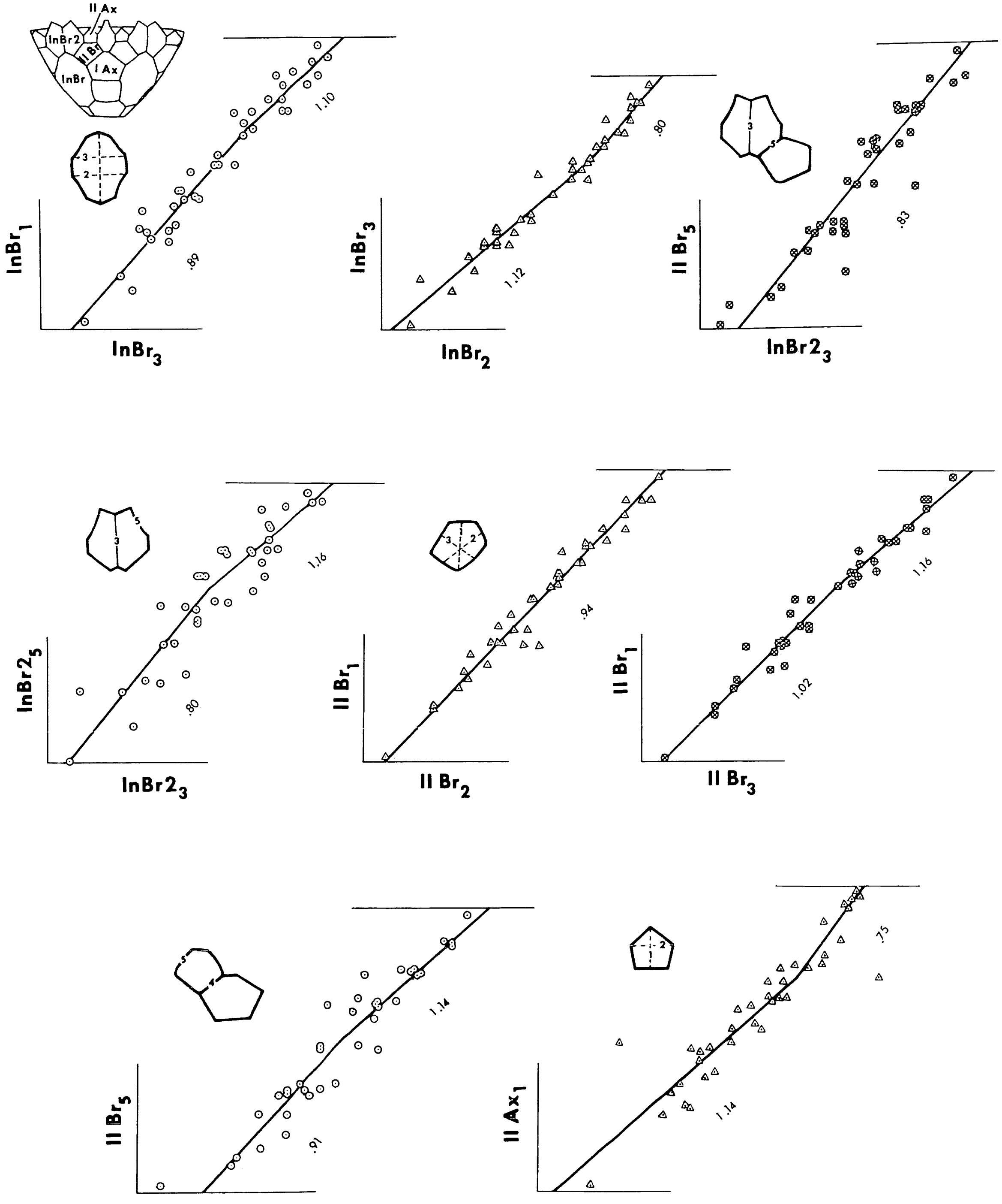
TEXT-FIG. 15 -- Double-logarithm plots of various parameters compared to H. Data from table 10. Mean lines labeled with CDGR values.



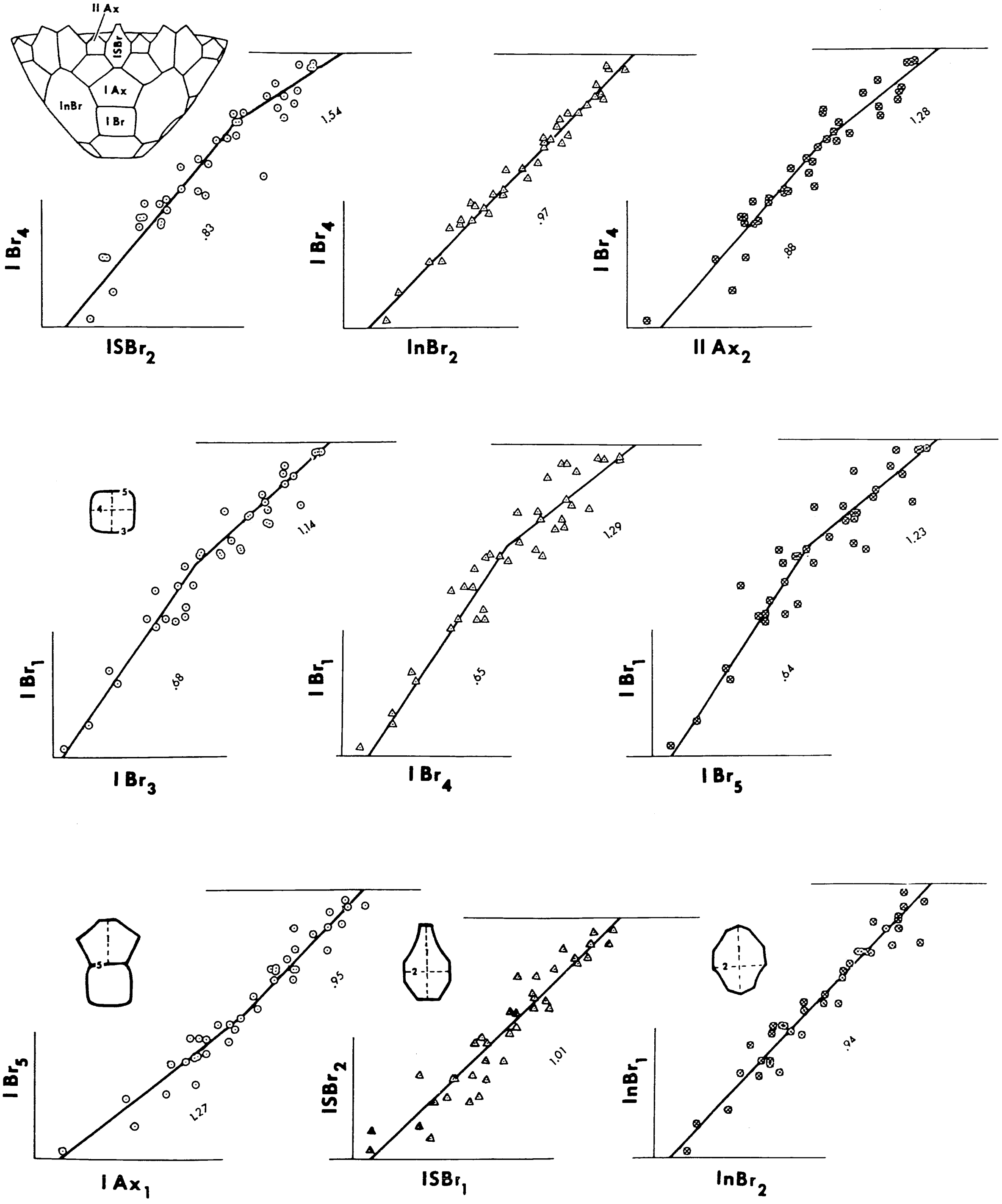
TEXT-FIG. 16 -- Double-logarithm plots of various parameters compared to H. Data from table 10. Mean lines labeled with CDGR values.



TEXT-FIG. 17 -- Double-logarithm plots of various parameters compared to H. Data from table 10. Mean lines labeled with CDGR values.



TEXT-FIG. 18 -- Double-logarithm plots of parameter-pairs in certain plates, showing changes in proportions.



TEXT-FIG. 19 -- Double-logarithm plots of parameter-pairs in certain plates, showing changes in proportions.

H and by the CDGRs of selected pairs of its parameters. We found that more precise determination of proportions came from the parameter-pairs (table 12) than from the parameter:H ratios (table 11).

Radial (R) plate: Because of the generally poor preservation of these plates, only the maximum width (R$_4$) could be reliably measured. It increases a little slower than H during ontogeny (CDGR = .91). After looking at more than 300 specimens we think the proportions of R stay about the same, but we are not sure.

Primibrachial (IBr) plate: The length of the side (IBr$_2$) increases faster than any other parameter of the plate (text-fig. 14), much faster than H. When the width across the base (IBr$_3$), the median width (IBr$_4$), and the width across the top (IBr$_5$) are each plotted against the height (IBr$_1$), a striking change in proportion of the plate is disclosed. All three widths increase much slower than the height in earlier stages of development, and much faster than height in later stages (text-fig. 18; table 12). Simply stated: in young crinoids IBr becomes progressively higher, in old crinoids it becomes wider at all levels.

Primaxil (IAx) plate: Throughout ontogeny, the median height (IAx$_1$) and the diagonal length (IAx$_2$) increase at almost exactly the same rate as H (text-fig. 14; table 11). The length of the IAx:InBr suture (IAx$_3$) and the IAx:IIBr suture (IAx$_4$) grow in opposite ways in early and in late stages, switching their patterns at 2.25 and 2.15 cm respectively (text-fig. 15); as compared with H,

Parameter	Juvenile	Adult
IAx$_3$	Faster than H; CDGR = 1.18	Slower than H; CDGR = .77
IAx$_4$	Slower than H: CDGR = .83	Faster than H; CDGR = 1.28

For direct comparison, the width across the bottom of IAx (IBr$_5$) is plotted against the height (IAx$_1$) in text-figure 18; the result shows that height grows faster than basal width (CDGR = 1.27) during early stages and then slows down (CDGR = .95) during late stages. Because acceleration and deceleration do not change over in each parameter at exactly the same size of cup, actually more than two stages could be distinguished in the growth pattern; we could make a new stage for each possible combination of CDGRs during ontogeny. This would not be very significant, since inflection points in the plots fall fairly close together; from a practical standpoint, we feel reasonably certain that another sample of this population might produce a slightly different set of inflection points.

Intersecundibrachial (ISBr) plate: Plotting of the height (ISBr$_1$) directly against the width (ISBr$_2$) seems to show that growth maintains the same proportions of the parameters throughout ontogeny (text-fig. 18); however, the scattered distribution of points shows that plates in individual crinoids depart considerably from the mean. Plotting of ISBr$_1$ and ISBr$_2$ each against H (text-fig. 15) tells a somewhat different story: ISBr$_1$ continues to grow somewhat slower than H (CDGR = .91), but ISBr$_2$ grows appreciably slower than H early in ontogeny (CDGR = .73) and faster than H in later stages (CDGR = 1.16). So there is a general trend for the plate to shift from heightening to widening after all. The length of the ISBR:IIBr suture at the base of the plate (ISBr$_3$) increases a little slower than H -- nearly matching the growth of height (ISBr$_1$). The upper side of the plate (ISBr$_5$) increases at nearly the same rate as H (text-fig. 15; table 11).

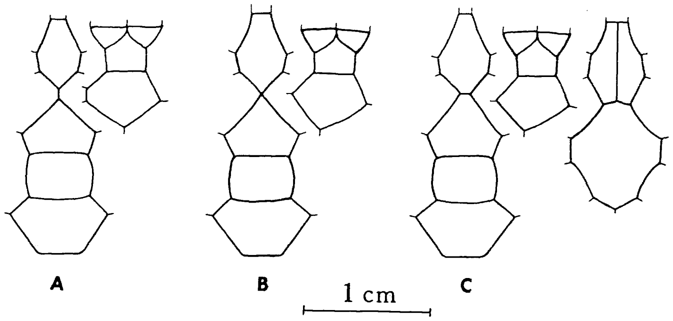
Secundibrachial (IIBr) plate: In young crinoids, three parameters of this plate -- the height (IIBr$_1$), the length of the suture with InBr (IIBr$_4$), and the length of the suture with InBr2 (IIBr$_5$) -- all increase at essentially the same pace as H; but two parameters -- the two diagonals (IIBr$_2$ and IIBr$_3$) -- increase appreciably slower than H (text-figs. 15 and 16). In older crinoids, all parameters increase faster than H (table 11). When we plot each of the two diagonals against height (text-fig. 19) we find that one diagonal (IIBr$_2$) consistently lags a little behind height (IIBr$_1$), whereas the other (IIBr$_3$) at first keeps pace with height and later speeds up to a CDGR of 1.16. The differences in the CDGRs of the two diagonals can only mean one thing: the secundibrachial becomes lopsided with growth. Further evidence of this tendency can be found by plotting the base of the plate (IAx$_4$) against the edge next to InBr2 (IIBr$_5$), as in text-figure 19. Here we see that the base grows slower for a time (IAx$_4$:IIBr$_5$ CDGR = .91), then faster than the edge (CDGR = 1.14).

Secundaxil (IIAx) plate: The height (IIAx$_1$), width (IIAx$_2$), and the side next to IIIBr (IIAx$_4$) follow the same general pattern of growth as compared to H. At first all three parameters grow much slower than H, later all three grow faster (text-fig. 16). But in the adult stage, height increases much faster than H (CDGR = 1.46) and width only a little faster (CDGR = 1.11). The change in proportions of the plate are emphasized by plotting width directly against height (text-fig. 19). The IIAx$_2$:IIAx$_1$ CDGRs (table 12) reveal that the secundaxil becomes proportionally wider for a time and then puts most of its increase into height.

First interbrachial (InBr) plate: In contrast to the heights of other plates, the height of this plate (InBr$_1$) increases at a faster rate in younger intervals (CDGR = 1.12) and decreases with respect to H in older intervals (CDGR = .94), as shown in text-figure 16. The two widths (InBr$_2$ and InBr$_3$) both grow slower than H at first (CDGRs = .84 and .75); later, both grow faster than H (CDGRs = 1.06 and 1.22). From direct plotting of one width against height (InBr$_2$:InBr$_1$ in text-fig. 18), we learn that during ontogeny the first interbrachial becomes slowly and persistently higher with respect to its lower width. But from direct plotting of the other width (InBr$_3$) against height (InBr$_1$), we see a very different pattern of growth during the adult stage (text-fig. 19): in that stage the width in the upper part of the plate increases faster than the height (CDGR = 1.10). When we compare the two widths (InBr$_2$ and InBr$_3$) by direct plotting (text-fig. 19), we discover that the plate in young specimens expands most in its lower part (InBr$_2$) but in older specimens expands most in its upper part (InBr$_3$). This plan of growth might have been anticipated from the change in shape of the cup. With respect to its upper width (InBr$_3$), the InBr plate in big crinoids is shorter and tapers more toward the base than it does in little crinoids.

Second interbrachial (InBr2) plate: During the early period of growth, the width of this plate (InBr2$_1$) increases at exactly the same rate as H (text-fig. 16). Later, it increases faster than H (CDGR = 1.14). The long vertical side of the plate (InBr2$_3$) is a good index of the height. Compared to H, InBr2$_3$ grows at a constant slower rate (Text-fig. 17; table 11). InBr2$_5$ (the length of the upper side, facing IIIBr) grows just a little faster than H. We can discriminate more closely how growth in height is related to growth of this upper side by plotting one against the other (text-fig. 19). The resulting CDGRs of InBr2$_3$:InBr2$_5$ show that height starts off slower than the side but finishes at a faster rate, changing from .80 to 1.16 (table 12). The plot of height (InBr2$_3$) against one of the lower sides (IIBr$_5$) shows that throughout ontogeny the height grows slower, with CDGR = .83 (text-fig. 19). Throughout the lifetime of the crinoid, its second interbrachial plate is being continuously distorted, becoming wider in the process.

Variability in plate junctions. -- Several cups have plates arranged in a pattern very different from that in all other crinoids. The different pattern involves the junctions of IAx, ISBr, and IIBr plates. Some extreme variations can be seen in one cup (UMMP 60800, illustrated in text-fig. 20). The normal relationship is shown in set C in the figure: a six-sided IAx lies in contact with an eight-sided ISBr, the top of IAx and the bottom of ISBr are horizontal, and the two plates separate the adjacent IIBr plates. In set B in the figure, all four plates meet at one point -- IAx, ISBr, and the two IIBrBr. In set A, the encroachment of the IIBrBr plates has brought them in contact to form a IIBr:IIBr suture, separating the IAx from the ISBr above. In this case, the top of IAx is pointed and so is the base of ISBr, resulting



TEXT-FIG. 20 -- Plate diagrams from UMMP 60800, showing variability in plate junctions. Plate sets labeled A, B, and C.

in a five-sided IAx and a seven-sided ISBr. We suspect that this anomaly existed from the time the crinoid first secreted cup plates. There is no indication that the unusual relationships were produced by differential growth during later ontogeny.

Another cup (UMMP 60804, illustrated in text-fig. 21) has the primaxil in one ray divided into two plates.

Summary of Part II

Before comparing the two populations, we may profitably review the findings on the Tennessee crinoids.

1. Adults vary more in shape than young crinoids. All small cups are conical. Some large cups are also conical, only slightly modified from the small ones, but most are markedly flattened. And among the cups that are flattened, there is a variety of profiles.

2. The flattening process has been proved to begin at about the time when the diameter of the cup reaches 4.0 cm. In text-figure 17 we noted that in young crinoids the increase in diameter lags behind the increase in R_4 and Total 1 (indices of the cup diameter at lower levels) and Total 2 lags behind R_4. In this interval, therefore, the cup was becoming progressively higher. Beyond the 4.0-cm stage, the situation drastically reverses: the maximum diameter grows much faster than either R_4 or Total 1, and Total 2 grows more than twice as fast as R_4. The adult crinoid mushrooms outward.

3. Plates do not continue to occupy the same relative amount of height or width in the cup -- some expand, some contract. In youth, plates grow at about the same pace except IIAx, which actually shrinks in both height and width as a component of the cup, and ISBr and InBr, which contract in width (table 11). In later growth, the lower plates (R, IBr, and IAx) and one upper plate (InBr2) continue growth with little departure from the average. The story is different for the other upper plates. In adulthood ISBr increases the CDGR of its width from .73 to 1.16, IIBr increases its diagonal width from .80 to 1.36, and InBr increases its upper width from .75 to 1.22. The most astonishing change occurs in Ax -- its height growth-rate suddenly shifts from a youthful CDGR of .78 to a mature CDGR of 1.46 and its width rate from the youthful .75 to the mature 1.11. Briefly, then, lower plates keep their size; IIAx shrinks and then rapidly expands; and other upper plates (except InBr2) start their great expansion as cup elements after a steady young stage.

4. Plates do not maintain their height/width ratios. IBr becomes higher as a juvenile, wider as an adult. IAx comes close to keeping its height/width ratio throughout ontogeny. ISBr has a general shift from narrowing to widening. IIAx does the opposite, at first becoming proportionally wider and later becoming proportionally higher. InBr becomes narrower at all levels in the juvenile stage, but expands the width of the upper part of the plate in the adult stage. InBr2 becomes just a little wider during the late growth interval.

5. Other parameters than height and width change within a plate to alter the shape, often differently in the juvenile stage than in the adult stage. In relation to the height, the base of IAx at first decreases and then slightly expands. The lower and upper sides of this plate change their proportions greatly; in the juvenile stage the lower side (IAx_3) grows much faster than the upper (IAx_4), but after-

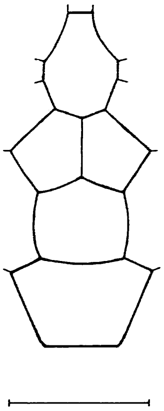
ward it is the upper side which grows at a rapid rate. As a result, the smallest crinoid, a middle-size crinoid, and the largest crinoid have three different outlines. IIBr becomes lopsided with growth, with different CDGRs in its two diagonals. The differential growth in width at different levels in InBr produces a plate that progressively tapers more sharply toward the base.

6. The sites of rapid and slow growth change from the juvenile to the adult stage. The juvenile stage is characterized by slow growth in width of ISBr, the diagonals of IIBr, height and width of IIAx, the length of the upper side of IIAx, and the upper width of InBr. The adult stage is marked by rapid growth in many parameters, most of them in the upper plates of the cup. In particular, growth is strong in the IIBr diagonals, the height of IIAx, the upper width of InBr, and in the lengths of the following sutures: IAx: IIBr, IIBr:IIAx, and IIAx:IIIBr. In the adult stage growth is notably slow only in the length of the IAx:InBr suture.

COMPARISON OF THE TWO POPULATIONS

For nearly everyone it is impossible to keep all these figures in mind. Even so, we need to have the CDGRs handy to compare growth in the Indiana and Tennessee populations. Table 13 was assembled for this purpose. It contains just the same data as tables 2 and 11, but makes it easier to spot similarities and differences.

A quick inspection of table 13 pinpoints the first big difference between the two populations. High values of CDGRs are in general concentrated in the Juvenile column for the Indiana crinoids, but in the Adult column for the Tennessee crinoids. Keep in mind that many parameters of the Indiana juveniles owe their high CDGRs to the inclusion of a very small specimen in the population. No comparably small crinoid was available in the Tennessee collection. If one were found and measured, we are pretty sure the CDGRs would be appreciably changed for Tennessee juveniles. Be that as it may, there are obviously some differences in the growth pattern of juvenile crinoids in the two populations. The differences in the pattern of the two adult groups cannot be questioned.



TEXT-FIG. 21 -- Plate diagram from UMMP 60804, showing a median suture dividing the primaxil (IAx) into two plates.

It would be still more convenient to synthesize some of the data in table 13. Let us divide, somewhat arbitrarily, the cup into zones of lower, middle, and upper plates. The lower zone would include R, IBr, and the lower half of InBr; the middle zone IAx, IIBr, and the upper half of InBr; and the upper zone ISBr, IIAx, IIIBr, and InBr2. Now we can average the CDGRs of plates within each zone to get some figures for comparison. Width and height are significant parameters. For width we find:

	Indiana		Tennessee	
Zone	Juvenile	Adult	Juvenile	Adult
Upper	1.30	.68	.83	1.14
Middle	1.15	.78	.85	1.20
Lower	1.29	.78	.85	1.20

and for height we find:

	Indiana		Tennessee	
Zone	Juvenile	Adult	Juvenile	Adult
Upper	.94	.84	.88	1.10
Middle	1.29	.91	1.03	1.01
Lower	1.40	1.03	1.15	1.06

Looking at the columns in these syntheses, we may allow ourselves a few conclusions. First, growth gradients in the cup are not equally distributed. None of the stages displays a gradient for width. For height, however, the Indiana juvenile and adult crinoids and the Tennessee juveniles show increased rates toward the base of the cup. Second, without exception growth rates of width and height in the Indiana population decrease from juvenile to adult stage -- in all zones of the cup. Third, without exception growth rates of width in the Tennessee population increase from juvenile to adult stages, in all zones. Fourth, growth rates of height do not show consistent changes from juvenile to adult stages in the Tennessee crinoids. Instead, the growth rate appears to slow somewhat in the lower zone and to speed up in the upper zone.

Much of the change in shape of the cup between the two populations can be attributed to the mid-ontogenetic reversals in growth rates of width. In the switch-over from juvenile to adult, the Indiana crinoids start narrowing their cup plates (relative to cup height); the Tennessee crinoids start expanding theirs.

The simplest and most direct revelation of the difference in adults is the first line of table 13. With respect to height of the cup, the Indiana crinoids contract in maximum diameter as soon as they reach the adult stage, but the Tennessee crinoids continuously expand. All the other CDGRs in the study only serve to fill in the details -- which plates are most responsible for increasing height and which are least responsible, which plates contribute to the width of the cup and which do not, which plates add to the size of the crinoid and which subtract, which plates change their growth pattern and when, how plates alter their shape from one stage to another in ontogeny, and so on.

We now have answers. But our answers apply only to the mechanics of ontogeny. They give a plate-by-plate and stage-by-stage account of the moves made by Eucalyptocrinites crassus in two games of growth -- one played in Indiana, the other in Tennessee. At this point we might ask two questions: Would other crinoid species play by the same rules and make the same moves, maintaining their youthful shape in Indiana and becoming flattened in Tennessee? And is the game entirely under the control of environment, determining the whole course of growth?

To the first question we must reply that growth studies must be made for many species before generalizations can be drawn on how much of the pattern can be duplicated in other crinoids. Perhaps ontogenetic patterns will prove to be like morphologic characteristics, with many similarities at the generic level, some at the family level, and a few at the next higher taxon. For the present, we would just be guessing.

To the second question, we strongly suspect that factors in the environment do indeed affect the living habits of a species. That seems a logical reason why the two localities produced such different populations of Eucalyptocrinites crassus. So we take a look at some possible controlling factors.

WHY CRINOIDS DIFFER IN THE TWO POPULATIONS

We might say that the Indiana crinoids are normal and that the Tennessee crinoids are modified, keeping in mind that the young cups are conical in both. However, we are well aware that "normal" is a modern-day tabu. Use the word in any group and someone will remind you that with the same genetic inheritance, the same environment, the same internal chemistry, the same expenditure of energy, the same experiences from egg to old age -- the whole lot of it -- any two individuals would respond alike; and if one of the pair does not respond the same and does not grow up to look like the first, then it was all because he did not have the same genetic inheritance, the same environment, the same.. ... So let us avoid calling the Indiana population "normal" and the Tennessee population "abnormal." Be that as it may, it does seem a bit more intriguing why the Tennessee crinoids changed from their conical youth than why the Indiana crinoids failed to change.

Of course, individuals were successful in both places. Otherwise there would have been no populations to study. So the environment in Indiana permitted its population to survive, and the environment in Tennessee permitted its population to survive. But survival does not mean ideal conditions. And the burial ground may not have been the living area.

One clue to the differences in the environments is the rock itself. The Waldron Shale in Indiana is a claystone, uniform in color, bedding, and texture. Such a claystone, we think, was deposited in quiet, fairly deep water. The Waldron Shale in Tennessee is not a shale at all; it is an impure carbonate rock, irregularly bedded, the product of limy mud cement mixed with varying amounts of ground-up shell fragments -- what once would have been called a calcarenite or simply a limestone, but now would be said to be a biomicrite. It was undoubtedly formed under high-energy conditions, within the shallow water affected strongly by wave action. The crinoids are so numerous that they must have lived nearby, if not actually in this rather violent and abrasive environment.

Another clue might be the faunal diversity. The Waldron locality in Indiana has been a famous collecting ground for years, and still new species show up from time to time. On the other hand, to judge from our collections, the Newsome locality yields very few species. Again, shallower water is indicated for the Tennessee deposit.

Preservation of the fossils is even better for contrasting the two environments. The Indiana crinoids are near-perfect specimens. Their tegmens and arms are almost always intact, with every little plate in place. Even the tiny little specimen found by the Lancasters, only 8 mm from base to crown, is remarkably well preserved. In contrast, the Tennessee crinoids are a sorry lot. Their tegmens and arms are almost always missing, their bases are nicked and worn, and many are too poorly preserved to allow measurements of the plates. The Indiana specimens were buried in such quiet water that at least one has been found with calyx, stem, and root all perfectly articulated. The Tennessee specimens obviously suffered severe buffeting before burial.

Hence, several lines of evidence point to a connection between the flattening process and turbulence in the environment. Yet the problem remains of why some individuals in the Tennessee population were more flattened than others of the same size.

Possibly, we have the key. In the early stages of research, we considered using the diameter of the columnar facet as one of the parameters. Then we found that in the Tennessee crinoids this facet, which lies down in an indentation in the base of the cup, was obscured with hard matrix. And when we tried to clean out the matrix with airdent abrasion, the removal was very slow and the matrix did not separate cleanly from the facet. After a few disappointing trials we gave up. Nevertheless, we did note some discrepancies in the diameter of the facet. Since the facet is generally proportional to the diameter of the basal indentation, we looked at the bottoms of all 315 specimens in the collection. Even though poor preservation and adhering matrix make the exact boundary somewhat hard to discern, we are convinced that the flattened specimens had unusually small facets. We might even go so far as to say that the flatter the cup, the smaller the facet.

After discussing this shape-facet relationship among ourselves and with members of the Friends of the Museum of Paleontology, we present this hypothesis. In Tennessee, the population of Eucalyptocrinites crassus lived both in fairly deep and in shallow turbulent water. All baby crinoids settled in the deeper water and started growing stems. Any which were lucky enough to stay there, probably matured into adults like those in the Indiana population. Most of the year the water was calm. But from time to time, storms hit the area. Waves generated tremendous force. Turbulence extended downward, reaching to the crinoid garden. Some of the crinoid heads were torn from their stems, carried along, and thrown closer to shore. Many of these survived, severed heads resting on the sea floor and subjected to buffeting in rough water. Flattening was a necessary response. Only the flat forms, spread laterally like a pancake, could keep their arms uppermost and avoid being turned upside-down. After the stem had been torn off, the facet grew no more. In a flattened crinoid, therefore, the size of its facet is an index to how big it was when it was torn from its stem -- and started a new stage in its growth and development. From the presence of small cups, still retaining their conical shape, we can surmise that not all heads did manage to survive. These young individuals may have been injured too badly, or they may have landed in an inverted position and smothered. Probably, the unwilling settlers which healed and grew to adulthood were not all the same size at the time they were thrust into these unfavorable surroundings. Or the population may have been brought in by several storms, a few individuals at a time. Anyhow, from the variety of cup shapes and the irregular distribution of stem facets, we postulate that individuals were swept into their second environment at different sizes and presumably at different ages.

As we begin to understand one problem, others appear. We wish we could find the Tennessee locality where the crinoids first grew, and where many probably lived out their lives. Would they have the same growth patterns as the Indiana population? Is there any way to determine how long one of the Tennessee crinoids spent in each of the two environments? What stimulated the torn-off heads to start spreading out in growth? Was the abrasion they suffered before burial characteristic of the conditions in which they managed to survive? If we could be provided with instant answers, paleontology might not be so exciting.

REFERENCES

HUXLEY, J. S., 1924, Constant differential growth-ratios and their significance: Nature, v. 114, p. 895.

__________ 1932, Problems of relative growth: London, Methuen & Co., Ltd., p. 6-8.

KESLING, R. V., Mechanical solution of formulas for growth rates: Contrib. Mus. Paleontology Univ. Mich., v. 8, no. 10, p. 231-237, 3 figs.

MACURDA, D. B., Jr., 1968, Ontogeny of the crinoid Eucalyptocrinites: Paleontol. Soc., Mem. 2, p. 99-118, 10 text-figs.

Observations on Evolution of Calycine Appendages in the Crinoid *Gilbertsocrinus*

Jeanette M. Fini

INTRODUCTION

CALYCINE APPENDAGES make Gilbertsocrinus a unique camerate crinoid. Otherwise, this genus is not very different from others in the family Rhodocrinitidae. It is dicyclic with a subglobular cup. The RR are separated all around the calyx and the median ray ridges are weak or, commonly, absent. Interbrachials are regular and not depressed. In most species, the anal region is reduced and lacks a median ridge. Infrabasals lie in a concavity (Moore & Laudon, 1943).

Calycine appendages are prominent tubular structures originating in the interradial regions and projecting from the edge of the tegmen. In some species, they hang down alongside the cup. These extensions are formed by uniserial rows of cylindrical ossicles or by multiserial rows of plates. The appendages are joined in pairs along the midline of the interray. The fused sections are joined along the edges of two plates in some species, six plates in others. Each appendage may bifurcate after it diverges from the joined section. The tubes themselves are pierced to their full extent by a central canal which, upon entering the calyx, connects with subtegminal grooves (Wachsmuth & Springer, 1897).

My study was undertaken as a special class project under the direction of Professor Robert V. Kesling. He intends to pursue the problem further and, as soon as the photography room at the Museum of Paleontology is remodeled, to illustrate the various kinds of calycine appendages occurring in Gilbertsocrinus. This paper, therefore, can be regarded as an advance announcement of the features which we discovered in the Winter term of 1973.

MIDDLE DEVONIAN SPECIES

The Middle Devonian species studied were Gilbertsocrinus ohioensis Stewart and G. alpenensis Ehlers. Specimens in the collection came from northern Ohio and northeastern Michigan, from the Silica Formation and the Bell Shale, respectively. Adult calyces in both species range from 8 to 14 mm in width and from 8 to 10 mm in height. The basal pit is wide and moderately deep, enclosed by large basals and the lower halves of the radials. The radials, largest plates of the cup, extend into long spines. In G. alpenensis, long spines are also developed on the primibrachials. Ten arms arise from the inner side of the secundibrachials. They are zigzag biserial and bear long pinnules. Many arms bifurcate on the fourth or fifth plate.

Calycine appendages arise from the outer edges of the secundibrachials along the interray (Stewart, 1940). They are short and nearly the same diameter as the arms. Those of G. ohioensis join along the midline of the interray for the length of two plates, then separate again to assume their individual identities. To this general arrangement, the appendages arising from the C-ray and

D-ray are exceptions. A row of large anal plates extends the full height of the cup along the middle of this interray, interceding between the calycine appendages on the sides.

These extensions of the tegmen in Devonian species seem even stranger because of the torsion. Apparently, the calyx was too small to accommodate the rather stout arms and calycine appendages of the same size. Arms developed first and preempted the space. To fit between the arms in the interray, the calycine appendages twisted into a nearly vertical plane at their joined section.

Appendages in G. alpenensis are very much like those in G. ohioensis, being nearly the same size as the arms. The joined portion of each appendage is the length of two plates. Torsion is pronounced. Aside from the number of spines on the cup, the main difference between the two species is the absence of prominent anal plates in G. alpenensis. This makes it possible for the appendages of the C-ray and D-ray to join, just like those of the other interrays.

MISSISSIPPIAN SPECIES

From their descriptions, all Mississippian species of Gilbertsocrinus are very different from the Middle Devonian species. But I have only had the opportunity to examine specimens of G. tuberosus Lyon & Casseday. It is appreciably larger than the Devonian forms. Its calyx is slightly wider than high. The subcylindrical cup is somewhat constricted at the arm level, and the rather flat tegmen is marked with deep interradial depressions. The radials are drawn out into elongate nodes, directed downward. The arms are fairly long, pendant, and frequently branching; they bear well-developed pinnules. The whole structure of the arms, however, seems frail compared to the size of the calyx; arms are scarcely as large as those of the Devonian species in actual measurements. Arms in each ray are widely spaced, separated by two or three interdistichals.

The ten calycine appendages meet in pairs at the midlines of the interrays. They are in contact for about 12 mm from the calyx, about the length of five or six plates. Upon separation, appendages turn sharply outward. Distally they become pendant, overhanging the sides of the cup. Each tube is composed of three rows of plates, two of them ventral and the third dorsal (Wachsmuth & Springer, 1897). Calycine appendages of G. tuberosus are very large compared to the size of the arms and are without question the most prominent features of the crinoid. In relation to the size of the calyx, appendages of the Mississippian species are much longer than those of the Middle Devonian species. Furthermore, they have a longer sutured area between pairs and show no torsion. Each appendage is triserial instead of uniserial, as in G. ohioensis and G. alpenensis.

ONTOGENY OF APPENDAGES

I studied a few examples of calycine appendages in juvenile individuals of G. ohioensis. They begin as small "buds" on the interradial plates beside the arms, little more than a slightly swollen node of the plate itself. Presumably, growth of the appendages consists of additional plates to these original "buds," joining onto the interradial plates and extending toward the middle of the interray. When the two appendages meet (at about the second and third plates), they fuse for a short section. Fusion involves only the outer part of each appendage, and the central tube retains its identity at all times. At this place, the interray can scarcely accommodate the fused section and lateral diversion of the appendages is impeded by the arms. As the appendages resume their separate growth by additional plates, torsion in the fused section diverts one appendage upward and the other downward and outward.

LITERATURE CITED

MOORE, R. C., & LAUDON, L. R., 1943, Evolution and classification of Paleozoic crinoids: Geol. Soc. Am. Spec. Papers, No. 46, 153 p., 14 pls. 18 figs.

STEWART, G. A., 1940, Crinoids from the Silica Shale, Devonian of Ohio: Ohio Jour. Sci., v. 40, no. 2, p. 53-59, 1 pl.

WACHSMUTH, C., & SPRINGER, F., 1897, The North American Crinoidea Camerata: Harvard Coll. Mus. Comp. Zoology, mem. 20 and 21, 897 p., 83 pls., 21 text-figs.

A Cystoid Plate from the Lower Part of the Petoskey Formation

Robert V. Kesling

INTRODUCTION

THIS IS A SHORT NOTE about a little fossil I picked up in the northern part of the Lower Peninsula of Michigan. The time was late July of this year, in the middle of a hot, muggy Wednesday morning. The rocks were Middle Devonian in age. The fossil was obviously a cystoid plate, for it bore half of a long montidisjunct pectinirhomb -- the half surrounded by a rim. No other plates could be found in the vicinity.

Now there is nothing particularly exciting about finding one cystoid plate in the Middle Devonian strata of Michigan. Cystoids have been known for many years in the Traverse Group along the northeastern margin of the peninsula, in Alpena County. But this one was found along the northwestern margin of the peninsula, in Emmet County -- a region notorious for its few echinoderms of any kind. The plate represents the first cystoid from that section of our state.

Mr. Karoly Kutasi and I were on a reconnaissance trip to the Charlevoix-Petoskey area. I had not been back for over ten years, although I can't recall missing a single field season there during the 1950's. Every summer I had collected fossils and mapped strata, always in company with Professor George M. Ehlers (now retired) and sometimes joined by Professor Erwin C. Stumm (now deceased). By the end of that period I knew the exposures as well as I knew the floor plan of the Museum of Paleontology. This year was different.

Everyone knows that man is changing the landscape. News media constantly remind us that cities are swallowing up the surrounding farm land, that the expanding population needs more homes and factories, and that natural resources are being used at an alarming rate. No one disputes these facts. Nevertheless, the return to an area after an absence of more than a decade can be quite a shock.

For instance, the operations of the Medusa Portland Cement Company, started in the mid-1960's, have strongly changed the exposures southwest of Charlevoix. On Tuesday (the day before I found the cystoid plate) Kutasi and I met with Mr. Harry O. Sorensen of the Michigan Geological Survey to look over the geology there. On my previous visits, the No. 1 quarry of the Charlevoix Rock Products Company was the most conspicuous feature thereabouts. As we approached, even the roads were new and unfamiliar. I had to ask the quarry foreman how to locate the old access road. After some searching in the rain, I found the old concrete bases of the No. 1 quarry hoist, crusher, and buildings. But there was no quarry. The ground was very level -- filled in completely with waste from the new Medusa Quarry.

Near Petoskey, the old Bell Quarry had provided us with excellent collecting in the "upper blue" shale (at the top of the Gravel Point Formation) for a long time. The quarry was known to R. A. Smith in 1916. When G. O. Raasch and E. R. Pohl visited the locality in the late 1920's, the quarry had been aban-

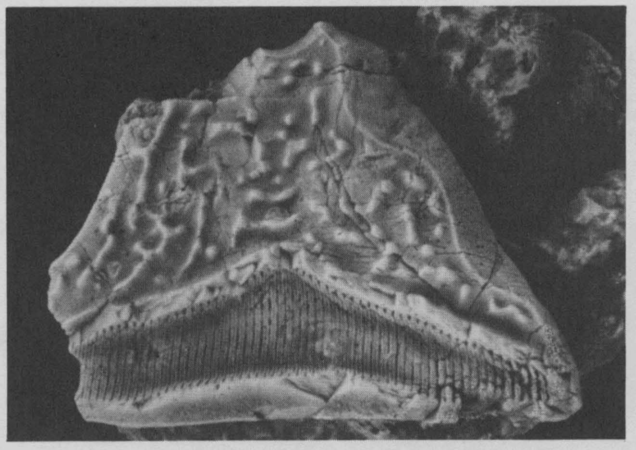


FIG. 1 -- The isolated and incomplete plate of Lipsanocystis found in the Petoskey Formation, UMMP 60830. x 4.

doned. Now, the quarry cannot even be recognized as such. It has been incorporated into the shale pit of the Penn-Dixie Cement Corporation.

For still another example, the old Jarman Quarry on the west edge of Petoskey was a fine locality to study the contact of the Gravel Point and Charlevoix Formations. The Antrim Lime Company had operated a kiln there long ago. I knew about where the quarry should be, but the surroundings seemed strange. Finally, I asked an elderly caretaker at the Greenwood Cemetery across the road.

He was delighted to find someone interested in the local history. "You must go back quite a few years to ask about the old Jarman Quarry, eh?" I admitted that I did go back more than a few years, and explained why I was anxious to locate it -- anxious enough to be wandering around in the rain. "Well," he told me, "you were right. That's just where it was. They tore down the old kiln some years back and filled in most of the quarry when they built the new supermarket." He added, "Boys used to swim in it -- but not any more."

A closer look at the site was not rewarding. Slump from the widened road bed has covered all the west wall of the quarry; the parking lot for the new Grant City shopping center is perched on fill over the east part of the quarry; and all that is left to mark the Jarman Quarry is a small muddy pond partly filled with sand and debris. No rock can be seen. A few timbers from the construction activities of a few years ago float on the scummy surface.

Having read thus far, you must be convinced that my nostalgic tour of the region was all a series of frustrations and disappointments. Not so. Some new and exciting exposures have come into being, mostly from expanded quarrying operations. One new exposure yielded the cystoid plate described below.

We were hunting for the abandoned Kegomic Quarry about a mile east of Bay View in Emmet County on that Wednesday morning. As I remembered, the quarry was water-filled, represented by a little elongate pond in the sector between two main highways -- US-31 leading to Mackinac City and M-131 following the shore northward to the vicinity of Sturgeon Bay. A little earth dam led across the north end of the pond to some small low exposures on the east shore.

When we got there, however, the pond was much wider than I expected. Surely, I thought, the junction of two major highways cannot have been shifted. Following a gravel road around the south end of the pond -- a road not shown on the land plat map -- we stopped near the site of the old onshore exposure of the Petoskey Formation. To my joy, bulldozing activity had laid bare much more rock than I had ever seen there. In fact, the strata were exposed over a large enough area to clearly show a strong change in dip. Later, we learned that the dredging and scraping were started to provide an access channel from Lake Michigan to one of the inland lakes nearby. Legal action by dissatisfied land owners along the projected path of the channel, however, had thwarted the action and all work stopped. So the new exposures were just waiting to be collected. About that time the new owner came by and wanted to know what we were doing. When we explained, he kindly gave his permission for us to proceed.

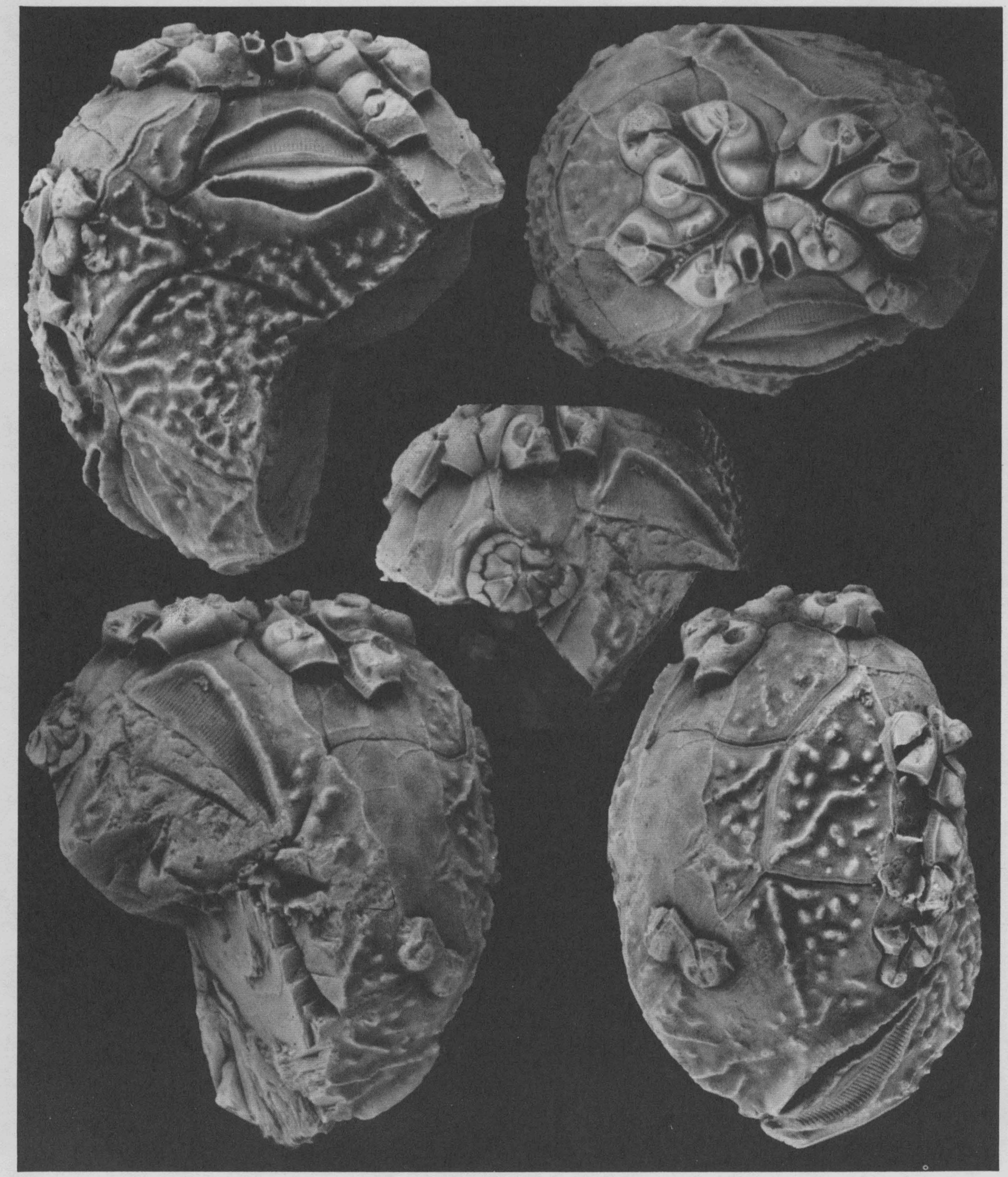


FIG. 2 -- Holotype of Lipsanocystis magnus Stumm, two lateral views (left), end view (lower right), top view (upper right), and periproct region (center). All x 4.

Some day, a complete cystoid may be discovered in this expansion of the Kegomic Quarry. I hope so. Until that time, it seems advisable to publish on this first find of a cystoid in the Middle Devonian strata of Charlevoix and Emmet Counties, Michigan.

LOCALITY

Extension of the old Kegomic Quarry, SE¼ SW¼ sec. 27, T 35 N, R 5 W, just north of Pickerel Lake Road, between US-31 and M-131 highways, south of the Pennsylvania Railroad tracks. Lower part of Petoskey Formation.

The plate was picked up midway between the road and the edge of the pond. The spot is topographically about ten feet above water level; because of the strong westward dip in part of the strata, however, I suspect that it is stratigraphically only a few feet above the zone of Pentamerella petoskeyensis, which crops out at water level. The section consists of alternating thin limestone and shale units. The plate came from a shale near the top of the exposure.

THE PLATE

The plate, UMMP 60830, is incomplete (fig. 1). The preserved part is subtrapezoidal, about 18 mm wide and 14 mm high, with one corner beveled. It has a pectinirhomb along the base. Although one end is broken from the pectinirhomb, the preserved part is over 16 mm long and about 3½ mm in its widest part. Both the projected outline and the symmetry of the rhomb suggest that it was over 18 mm in length. The closely spaced slits number 59 in the actual specimen; they probably reached 65 in the original plate. The rim around the rhomb is about ½ mm wide. Low irregular nodes and ridges give the rest of the plate a somewhat rugose appearance.

Even though we have only one plate, we can tell something about the cystoid to which it belonged and about its position in the theca. The classification followed here is the one I outlined in the Contributions (1963) and followed in the Treatise (1967). First, the presence of the rhomb shows that the cystoid belonged in the order Rhombifera. Second, the development of the rhomb as a pectinirhomb further places it in the superfamily Glyptocystitida. We can now try, by elimination, to assign the cystoid to a family.

From the shape of the plate, we can easily and certainly say that it is not in the Pleurocystitidae, Cystoblastidae, or Rhombiferidae. In the family Glyptocystitidae (so far known only from the Middle Ordovician), the only plates bearing rimmed halves of montidisjunct pectinirhombs, with no other half-rhombs on the plate, are IL1, IL2, and L5 -- and the middle of each of these plates is crossed by the scar of a long recumbent ambulacrum. Since our plate has no such scar it cannot belong to the Glyptocystitidae. In the family Cheirocrinidae (L. Ord.-L. Sil.), only Cheirocrinus and Homocystites have disjunct pectinirhombs; and both these genera have a characteristic ornamentation of ridges radiating from the center to the sides of each plate. So our specimen cannot be put into the Cheirocrinidae. This brings us down to the Echinoencrinitidae and the Callocystitidae.

The Echinoencrinitidae, reported only from Ordovician and Silurian rocks, has some genera with montidisjunct pectinirhombs. These include Prunocystites, Schizocystis, and Scoliocystis. In all three, however, the rhombs are small and considerably shorter than the edge they border upon.

The family Callocystitidae fits all the requirements. It extends into the Devonian, it has many genera with long montidisjunct rhombs, and it contains plates shaped like the one we are investigating. One genus of this family is already reported from the Middle Devonian of Michigan and it possesses all the characteristics of our plate -- Lipsanocystis. I have no doubt that our specimen does indeed belong in the genus Lipsanocystis.

Even though Lipsanocystis has been known for over 50 years, it is still a rare genus. All the known specimens could be held in one hand. Ehlers & Leighley created the genus in 1922 and described only the type species, Lipsanocystis traversensis. Stumm added three more species in 1955. No more have been found. Chris Paul (1967) made a detailed investigation of the type species and discovered that the supposed generic hallmark -- one thecal plate (L5) surrounding most of the periproct -- was not a reliable criterion, since he had specimens from the type locality with more than one plate bordering the periproct in that region of the theca. He suggested more emphasis on the large size of the pectinirhombs and the close spacing of their slits. With all the attention paid to Lipsanocystis, no specimen has previously been found outside the borders of one county -- Alpena County, Michigan. This is particularly strange because species have been recorded there from three distinct formations.

There is scarcely any question about where our specimen fitted in the original theca. Only IL2, L1, and L4 have rimmed pectinirhombs; and IL2 can immediately be dismissed from consideration because it is hexagonal. Both L1 and L4 are nearly trapezoidal. Two features favor L4 as the identity of our specimen: (1) the lack of ornamentation along one margin, and (2) the acuminate center of the rhomb. In known species of Lipsanocystis, L1 is not crossed by any of the four recumbent ambulacra, whereas L4 has part of its junctions with R4 and IL4 obscured by a long ambulacrum that extends down to the center of B4 (or thereabouts). Our specimen has an unornamented, somewhat sinuous area along the edge, set off by a thin crest, where, in complete cystoids, the ambulacrum crosses over L4. Furthermore, in all complete or nearly complete specimens of Lipsanocystis that I have seen, the rhomb on L1 tends to be sausage-shaped, more nearly elliptical than triangular, whereas the rhomb on L4 is subtriangular and has a definite peak at its middle. Hence, the evidence from complete cystoids supports the designation of our isolated plate as L4.

I am reluctant to say that this plate is Lipsanocystis magnus, even though it has the same kind of ornamentation. The holotype of this species, described in 1955 by Stumm, is still the only known specimen (see fig. 2); and it has a large chunk of the theca missing below the periproct, including part of the base. It was found in the Four Mile Dam Formation in Alpena County. The plate from the Petoskey Formation was about 20 mm wide in its entirety, whereas the L4 in the holotype is only about 11 mm wide. The slits in the plate are spaced at about 3.6 per mm, whereas those in the holotype are spaced at 5.0 per mm. With only one known theca (and that one incomplete), of course, we have no way of knowing what was the range in size, what were the ontogenetic changes in slit spacing, or what individual variations occurred in the population of the species.

So, for the present, my conclusion is to call the plate:

Lipsanocystis sp. cf. L. magnus Stumm.

LITERATURE CITED

EHLERS, G. M., & LEIGHLEY, J. B., 1922, Lipsanocystis traversensis, a new cystid from the Devonian of Michigan: Papers Mich. Acad. Sci. Arts, v. 2, p. 155-160, pl. 10.

KESLING, R. V., 1963, Key for classification of cystoids: Contrib. Mus. Paleontology Univ. Mich., v. 18, no. 6, p. 101-116.

________ 1967, Cystoids, in R. C. MOORE, ed., Treatise on Invertebrate Paleontology, pt. S (Echinodermata 1), v. 1, p. S85-S267, figs. 32-157.

PAUL, C. R. C., 1967, A redescription of the cystoid Lipsanocystis traversensis: Contrib. Mus. Paleontology Univ. Mich. v. 21, no. 9, p. 205-217, 2 pls.

STUMM, E. C., 1955, Three new species of the cystid genus Lipsanocystis from the Middle Devonian Traverse Group of Michigan: Contrib. Mus. Paleontology Univ. Mich., v. 12, no. 6, p. 97-103, 2 pls.

PAPERS ON PALEONTOLOGY : No. 6

Kesling, Abdul-Razzaq, Devore, & Lattanzi:
Eucalyptocrinites crassus

Jeanette M. Fini: *Gilbertsocrinus*

Robert V. Kesling: A Cystoid Plate