SEXUAL DIMORPHISM IN THE DEVONIAN TRILOBITE PHACOPS RANA

Thesis for the Degree of M. S.

MICHIGAN STATE UNIVERSITY
MICHAEL TUCKEY

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ABSTRACT

SEXUAL DIMORPHISM IN THE DEVONIAN TRILOBITE

PHACOPS RANA

By

Michael Tuckey

Quantitative analysis of the cephalons of the Devonian trilobites *Phacops rana milleri* and *Phacops rana crassituberculata* from the Silica shale, Sylvania, Ohio, reveal significant morphological differences between the two subspecies, and dimorphism within each of the two subspecies characterized by variation in glabellar and cephalic shape. The dimorphism is interpreted to be sexual in nature with the females having relatively longer and narrower glabellas and cephalons and the males having relatively shorter and wider glabellas and cephalons.

SEXUAL DIMORPHISM IN THE DEVONIAN TRILOBITE

PHACOPS RANA

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Michael Tuckey

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

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1975

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Sexual dimorphism has been recognized as an important problem in paleontology, and among trilobites it has been commonly inferred. Morphological variations in the cephalon, glabella, libriginae, occipital ring, eye, genal area, pygidium, ornamentation, and hypostome, among others have been attributed to sexual dimorphism in several trilobite species by many authors [Lochman and Hu, 1959, 1962; Hu, 1964, 1971; Wittington, 1963, 1965; Selwood, 1965; Selwood and Burton, 1969; Clarkson, 1966, 1969; Webby, 1973). Often the problem of sexual dimorphism is intertwined with the problem of speciation, or subspeciation, as in this study where it is difficult to tell whether the two groups are different taxa or sexual dimorphs.

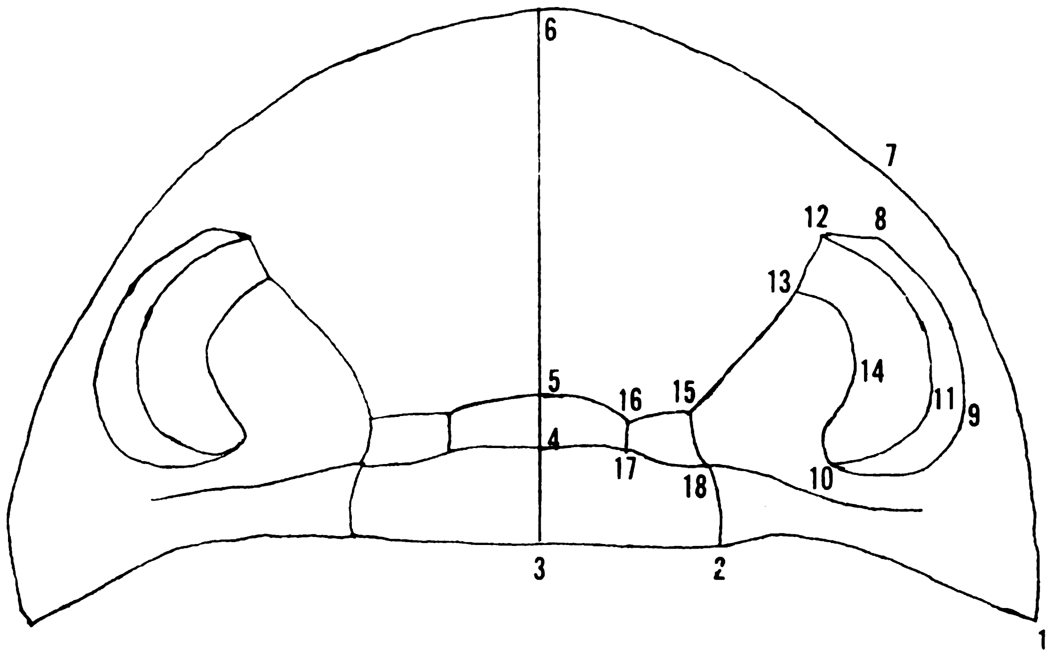
The trilobite species _Phacops rana_ [Green, 1832] has been divided into several subspecies, two of which, _P. rana milleri_ [Steward, 1927] and _P. rana crassituberculata_ [Stumm, 1953] are morphologically similar and occur together in the Silica Shale (Devonian) at Sylvania, Ohio. The main morphological difference between the two subspecies is in eye structure, with _P. r. milleri_ having more lenses, and a less highly inflated interlensar schlera. Because of their close morphological similarity, and mutual occurence in the Silica Shale, Clarkson [1966] has suggested that the two subspecies may be sexual dimorphs. Eldredge [1971] has argued against sexual dimorphism, stating that P. r. milleri and P. r. crassituberculata are usually not found together at the same locality (Table 7, Eldredge, 1971). Even within the Silica Shale itself, although P. r. milleri and P. r. crassituberculata are occasionally found together in the same beds, in general, the beds contain only one of the two subspecies, or an overwhelming majority of one of the subspecies over the other [Ehlers, Stumm and Kesling, 1951]. This has also been confirmed through personal communication with Larry Magrum, a hobbyist who has done extensive collecting at the Medusa Portland Cement quarry at Sylvania (1.5 miles north of Silica, SE 1/4, Section 7, T9S, R6E). Furthermore, "the eyes of all small post-larval instars of P. rana collected from the Silica shale appear to be of the milleri variety" [Eldredge, 1971]. It is also possible that environmental differences play a part in the distribution of the two subspecies, as P. r. milleri is generally found in more argillaceous rocks, while P. r. crassituberculata is usually found in more calcareous rocks.

This study is designed to clarify the relationship between the two subspecies through extensive quantitative analysis of the cephalons of specimens of P. rana milleri and P. rana crassituberculata from the Silica Shale at Sylvania. Through mathematical techniques including principal components analysis, clustering, and use of the discriminant function, morphological differences both within and between the two subspecies will be analyzed to attempt to find discrete clusters of individuals and thus shed light on the problem of whether P. rana milleri and P. rana crassituberculata are sexual dimorphs, and also to investigate the possibility of sexual dimorphism within the two subspecies.

METHOD

This study is based on 99 specimens, 40 of which are P. rana milleri and 59 of which are P. rana crassituberculata. All of the specimens represent the holaspid stage of growth. Thirty specimens were obtained from the Museum of Paleontology, University of Michigan, and the remaining 69 specimens were obtained from the collection of Larry Magrum of Toledo, Ohio. The specimens were photographed and the photographic negatives were mounted in slide mounts. By means of an overhead projector, the cephalons were magnified four times and measurements were recorded from the drawings of the projected images. Because many of the trilobites used in this study were in an enrolled or incomplete state, only the cephalons were used.

Eldredge [1971] listed a number of measurements he made on trilobite cephalons in his study. It was found that if the locations of 18 key points on one side of the trilobite cephalon were known, most of Eldredge's measurements could be duplicated. These 18 key points (Figure 1) were then marked on one side of each drawing, either on the right side or left side, depending on which half was more clearly delineated. Drawings on which the 18 points were marked on the left side were reversed to their mirror image to correspond to the right



1. Corner of genal angle
2. Corner of occipital ring
3. Intersection of vertical axis and rear of occipital ring
4. Intersection of vertical axis and occipital furrow
5. Intersection of vertical axis and glabellar furrow
6. Intersection of vertical axis and front of glabellar
7. Intersection of axial furrow and cephalic margin
8. Lower front corner of eye
9. Point on lower eye margin extended farthest to right
10. Upper rear corner of eye
11. Point on upper eye margin extended farthest to right
12. Upper front corner of eye
13. Intersection of axial and palpebral furrows
14. Point on palpebral furrow extended farthest to right
15. Rear edge of axial furrow
16. Front corner of glabellar lobe
17. Rear corner of glabellar lobe
18. Front corner of occipital ring

Figure 1. Locations of the 18 key points.

half of the cephalon. The coordinates of the 18 points were then plotted, with respect to a common zero point, by means of an electronic digitizer and then punched on computer cards, with a x and y cordinate for each point, thus providing 36 coordinate values.

Fourier analysis, a mathematical technique to describe shape quantitatively, has begun to be used in geology, notably by Ehrlich and Weinberg [1970] and their students to measure the shape of sand grains, and Anstey and Delmet [1972; 1973] in measuring the shapes of bryozoan zooecia. In this study, 29 Fourier harmonics were calculated to describe the shape of each cephalon. This was done by plotting the coordinates of 60 equiangular points on the outline of each cephalon by means of the electronic digitizer, and having them punched on computer cards. The harmonic coefficients were then calculated by means of the Fourier analysis computer program devised by Ehrlich and Weinberg. Along with the harmonic amplitudes, were calculated 29 harmonic phase angles, measuring the orientation of the individual harmonics with respect to the cephalon, and the normalized roughness coefficient [Ehrlich and Weinberg, 1970], measuring the total Fourier deviation from a circle, and the mean radius for each shape.

Based on cases of sexual dimorphism described in the literature, eleven potentially sexually dimorphic indicator variables were determined and defined by use of the coordinates of the 18 key points (Table 1). Twenty of the phase angles

Table 1. Eleven potentially sexually dimorphic indicator variables

	Variable	Description	Reference
1.	Glabellar length	y_6-y_5	Lochman and Hu, 1962; Hu, 1964; Hu, 1971
2.	Glabellar width	$2(x_7)$	Hu, 1964; Hu, 1971
3.	Librigineal length	$\sqrt{(y_7-y_9)^2+(x_y-x_9)^2}$	Whittington, 1965; Hu, 1971
4.	Genal prolongation	y_3	Whittington, 1963
5.	Occipital ring length	$2(x_2)$	Selwood and Burton, 1969
6.	Occipital ring width	y_4-y_3	Selwood and Burton, 1969
7.	Cephalic length	y_6	Hu, 1971
8.	Cephalic width	$2(x_1)$	Hu, 1971
9.	Glabellar shape	$(y_6-y_5)/2(x_7)$	Lochman and Hu, 1959; Lochman and Hu, 1962; Hu, 1964; Hu, 1971
10.	Cephalic shape	$y_6/2(x_1)$	Hu, 1971
11.	Phalpebral lobe position	$((y_{12}-y_{10})/2)-y_3$	Hu, 1971

were then deemed insignificant because of inordinately high or low values of their vector sums in the sample [Christopher and Waters, 1974], and dropped from use, and seven of the 36 point coordinates were also dropped because five of them lay on the axis and had zero values in all specimens, and two of them were duplicated by the sexually dimorphic indicator variables. It was decided that each of the 29 remaining x and y coordinates be used as an independent variable so that point locations along the width and length of the cephalon could be defined separately. This left a total of 78 variables (Table 2).

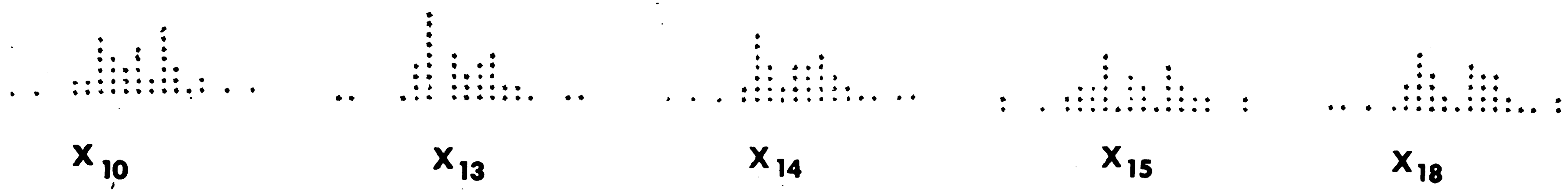
ONTOGENY

Computer drawn histograms (Figure 2) revealed many clearly and slightly bimodal distributions present among several of the variables. It was found that the variables x_{10}, x_{13}, x_{14}, x_{15}, x_{18}, and the mean radius formed clusters in each of the two subspecies, in which large trilobites were grouped into one cluster and small trilobites were grouped into the other cluster. In SPSS principal components analysis with varimax rotation [Nie, Bent and Hull, 1970], the variables all had extremely high scores on factor one (Table 3), which is interpreted to be the size of growth factor, because the mean radius, a measure of absolute size, expressed its greatest degree of variation along this axis. It is therefore assumed that the bimodality present among those variables is of an ontogenetic nature forming clusters

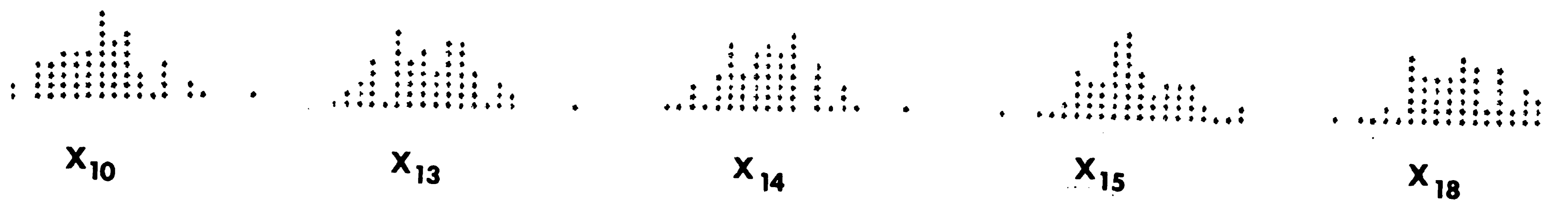
Table 2. List of morphological characters measured. x and y coordinates refer to points in Figure 1. HA indicates Fourier harmonic amplitude. PA indicates Fourier harmonic phase angle.

1. Glabellar length	27. x_{12}
2. Glabellar width	28. y_{12}
3. Librigineal length	29. x_{13}
4. Genal prolongation	30. y_{13}
5. Occipital ring length	31. x_{14}
6. Occipital ring length width	32. y_{14}
7. Cephalic length	33. x_{15}
8. Cephalic width	34. y_{15}
9. Glabellar shape	35. x_{16}
10. Cephalic shape	36. y_{16}
11. Palpebral lobe position	37. x_{17}
12. x_1	38. y_{17}
13. x_2	39. x_{18}
14. y_2	40. y_{18}
15. y_4	41-67. HA 2 - 28
16. y_5	68. Mean radius
17. x_7	69. Normalized roughness coefficient
18. y_7	70. PA 4
19. x_8	71. PA 7
20. y_8	72. PA 11
21. x_9	73. PA 12
22. y_9	74. PA 14
23. x_{10}	75. PA 15
24. y_{10}	76. PA 17
25. x_{11}	77. PA 18
26. y_{11}	78. PA 21

Figure 2. Computer drawn histograms revealing ontogenetic distributions of *P. rana milleri* and *P. rana crassituberculata* in variables; x_{10}, x_{13}, x_{14}, x_{15}, and x_{18}.



P rana milleri



P rana crassituberculata

Table 3. Principal components analysis results for first five factors. Variable numbers correspond to variables in Table 2. x = deleted variable.

var	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4	FACTOR 5
1.	.02546	-.17032	-.15758	-.00795	-.02495
2.	-.33393	.08916	.06954	.00788	.00579
3.	.84832	-.09553	.03257	.03397	-.07541
4.	.39477	.76061	.18564	.08430	.14440
5.	.34170	.05870	.02609	-.05921	.01674
6.	.80152	.10652	.10987	.01301	-.03196
7.	.37337	.16158	-.02324	.02523	.02074
8.	-.31471	-.09312	-.08174	.02415	-.00940
9.	-.12305	-.11925	-.30059	-.07290	-.07628
10.	-.02800	.30912	-.52349	.13951	.04605
11.	.02094	-.12424	.06416	.06381	-.10690
12.	.96317	.04917	.13073	-.03176	.01553
x	.15751	-.00059	-.02120	.03576	.11575
13.	.34170	.05870	.02609	-.05921	.01674
14.	.43703	.74592	.23497	.10232	.13522
x	.11842	.02018	.11649	.02181	.04232
x	-.01270	.03334	.08074	.02205	.01378
15.	.61211	.65334	.19094	.07235	.10497
x	.06497	.05335	.15708	.05172	.01522
16.	.74664	.56001	.15432	.06235	.07504
x	.09347	.04372	.04593	.01953	.03592
17.	.36071	-.12750	-.01802	.01761	-.00179
18.	.94314	.19681	.00374	.03658	.05604
19.	.30915	-.00074	.11906	-.05444	-.08430
20.	.93564	.25295	.03808	.01647	.10548
21.	.38422	-.01615	.06497	-.03493	-.00390
22.	.92521	.41012	.03528	.00535	.13742
23.	.97755	.00153	.01697	-.02576	.00495
24.	.71020	.57587	.16121	.01875	.03077
25.	.38422	-.00747	.02349	-.01215	-.01219
26.	.80701	.47922	.07772	.07016	.07907
27.	.36887	-.00552	.07234	-.02714	-.05696
28.	.90801	.34971	.10123	.03296	.04548
29.	.97867	.00310	.03771	-.02210	-.02254
30.	.87314	.40356	.11351	.02696	.06035
31.	.98118	.00618	.03231	-.02618	-.04357
32.	.78246	.49642	.12245	.07601	.09342
33.	.33099	.02270	.03897	-.05194	-.06209
34.	.73100	.58108	.12655	.07449	.08927
35.	.93455	.11935	.08539	-.03483	.00091
36.	.68283	.58521	.10292	.09214	.03381
37.	.79278	.07159	.08153	-.07953	.03660
38.	.61605	.62179	.11732	.11207	.05596
39.	.94569	.03260	.06058	-.03724	.02104
40.	.55238	.64193	.15651	.07000	.09436
41.	.04053	-.01247	.59478	.09325	.06540
42.	.12980	.73985	.09967	-.01821	.10945
43.	.09414	-.39722	.65438	-.06171	.20314
44.	.07640	.26544	.59337	-.01259	-.10248
45.	-.02345	.77341	-.11849	.03346	.10557
46.	.22236	-.33646	.58066	.00195	.49216
47.	.11465	.28224	.73113	-.03112	-.24522
48.	.02166	.86954	.00809	.04515	.06788
49.	.04119	.07532	.11550	.03886	.94251
50.	.11702	.32649	.80273	-.03592	-.20555
51.	.08720	.92216	.11324	.03537	.05335
52.	.00413	.37456	-.30752	.08555	.80900
53.	.03038	.17233	.93763	-.01446	-.11736
54.	.07444	.90456	.24058	-.07056	-.18484
55.	.02033	.64545	-.39134	.09626	.51775
56.	.12046	.01792	.94839	.02622	.11936
57.	.11035	.83189	.41574	-.04856	-.23295
58.	.01626	.82392	-.27476	.06473	.29058
59.	.01972	.10788	.83455	.11070	.28125
60.	.09651	.73184	.60335	-.03376	-.15285
61.	-.02430	.91416	-.16615	.00233	.06723
62.	-.00809	.19405	.44152	.11766	.52650
63.	.09441	.56671	.71977	-.03263	-.06250
64.	.06362	.93379	-.02838	.00465	.01686
65.	-.05676	.39549	.12978	.11812	.37398
66.	.03322	.48150	.75091	-.01589	-.01398
67.	.05686	.90135	.18983	-.03869	.01986
68.	.97864	-.09950	-.04664	-.00554	-.02267
x	-.00000	-.00000	-.00000	.00000	.00000
69.	.09110	.77167	.40770	.05436	.40704
70.	.06784	-.15250	.04174	-.47957	.01345
71.	.08261	-.23805	.40028	.09060	-.34873
72.	-.05086	.02250	-.03513	.93215	.22253
73.	-.00089	.06412	-.02113	-.66449	.00667
74.	.05161	.01935	-.04029	-.59497	-.02017
75.	-.01625	.08148	-.01067	.95325	-.10174
76.	-.09141	-.22926	.30188	.31726	-.36236
77.	-.01192	.06052	.01555	.97631	.03720
78.	.07088	-.12109	.10263	-.21683	.02944

of young and old individuals. As to why there seem to be clusters of old and young, rather than a gradient between the two, could be explained either by a biased sample, or by the fact that during growth, trilobites go through a series of molt stages, with discrete jumps from one size to the next. It is possible that a sample may contain a high relative proportion of one or two different instars due to differential preservation, differential collection, or if a large number of trilobites tend to die during the same molt states.

In *P. r. milleri*, which had 21 older individuals and 19 younger ones, use of the discriminant function using the above variables, confirmed the validity of the ontogenetic clustering (Table 4). In *P. r. crassituberculata*, which had 36 older trilobites and 23 younger ones, the discriminant function reclassified two individuals into the opposite group (Table 5).

Graphs, plotting the mean radius against size of the individual variables show that increase of the individual variables proceeds in a linear fashion with respect to overall growth, and if the overall size, as indicated by the mean radius, is taken to be correlated to a certain extent with age, then the growth of the individual variables has proceeded in a linear fashion throughout ontogeny. Only the graph of variable x_{10} is shown (Figures 3 and 4) as the others show the same results and are redundant.

Table 4. Discriminant function results for ontogenetic clusters in *P. rana milleri*. Specimen numbers below 300 are from U of M collection. Specimen numbers above 300 are from Magrum collection.

MAHALANOBIS DSQUARE= 8.26785

F(6, 33)= 11.96559

POP. NO.	SAMPLE SIZE	MEAN Z	VARIANCE Z	STD. DEV. Z
1	19	-.57616	.00683	.08265
2	21	-.79426	.00476	.06898

D(0) = -.69564

PROBABILITY OF ERROR = (.0749) FOR GROUPS ONE AND TWO

RANK	FIRST GROUP VALUES	SECOND GROUP VALUES	FIRST GROUP SPECIMEN NO.	SECOND GROUP SPECIMEN NO.	
1	-.39221		354		
2	-.41754		114		
3	-.47527		313		
4	-.50606		106		
5	-.52619		307		
6	-.56121		336		
7	-.56491		303		
8	-.56863		309		YOUNG
9	-.58475		103		
10	-.58942		348		
11	[illegible]		312		
12	-.59748		302		
13	-.63701		321		
14	-.64061		333		
15	-.64382		318		
16	-.65753		331		
17	-.66044		346		
18	-.66576		310		
19	-.67722		328		
20		-.69372		349	
21		-.71325		327	
22		-.71861		107	
23		-.73429		322	OLD
24		-.73809		338	
25		[illegible]		301	
26		-.74377		325	
27		[illegible]		340	
28		-.77424		311	
29		-.77650		347	
30		-.78120		352	
31		-.78530		306	
32		-.78809		319	
33		-.80283		350	
34		-.81652		345	
35		-.81762		316	
36		-.83715		317	
37		-.85721		332	
38		-.86401		308	
39		-.91318		343	
40		-.98340		344	

Table 5. Discriminant function results for ontogenetic clusters in P. rana crassituberculata. Specimen numbers below 300 are from U of M collection. Specimen numbers above 300 are from Magrum collection.

MAHALANOBIS DSQUARE= 4.30602

F(6, 52)= 9.18823

POP. NO.	SAMPLE SIZE	MEAN Z	VARIANCE Z	STD. DEV. Z
1	36	.33395	.00105	.03250
2	23	.25931	.00175	.04187

D(C) = .30034

PROBABILITY OF ERROR = (.1539) FOR GROUPS ONE AND TWO

RANK	FIRST GROUP VALUES	SECOND GROUP VALUES	FIRST GROUP SPECIMEN NO.	SECOND GROUP SPECIMEN NO.	
1		.40169		427	
2	.39601		216		
3	.39113		215		OLD
4	.38045		219		
5	.37382		418		
6	.37594		434		
7	.37308		217		
8	.37064		413		
9	.36916		235		
10	.36617		410		
11	.35914		206		
12	.35116		423		
13	.35760		209		
14	.35162		409		
15	.34139		429		
16	.34111		431		
17	.34[illegible]		234		
18	.33[illegible]5		230		
19	.33[illegible]3		403		
20	.33303		242		
21	.33321		411		
22	.32743		243		
23	.32127		437		
24	.32[illegible]6		406		
25	.31329		439		
26	.31765		438		
27	.31[illegible]0		229		
28	.30713		424		
29	.30470		221		
30	.30223		201		
31	.30175		416		
32		.29929		412	
33	.29505		415		
34	.29435		428		
35	.29[illegible]4		421		
36	.28[illegible]2		237		
37	.2[illegible]314		407		
38		.28764		205	
39		.28681		232	
40		.28355		238	
41		.27707		433	
42		.27203		440	
43		.26643		419	YOUNG
44	.26428		231		
45		.26133		240	
46		.26103		220	
47		.26023		414	
48		.25[illegible]		430	
49		.25037		228	
50		.24934		417	
51		.24654		402	
52		.24647		236	
53		.23975		425	
54		.23655		404	
55		.23401		223	
56		.21839		408	
57		.21691		222	
58		.20362		405	
59		.18555		227	

Figure 3. Graph of mean radius against variable x_{10} for *P. rana milleri*. Measurements are in millimeters.

○ = young females
♤ = young males
◆ = old females
♠ = old males

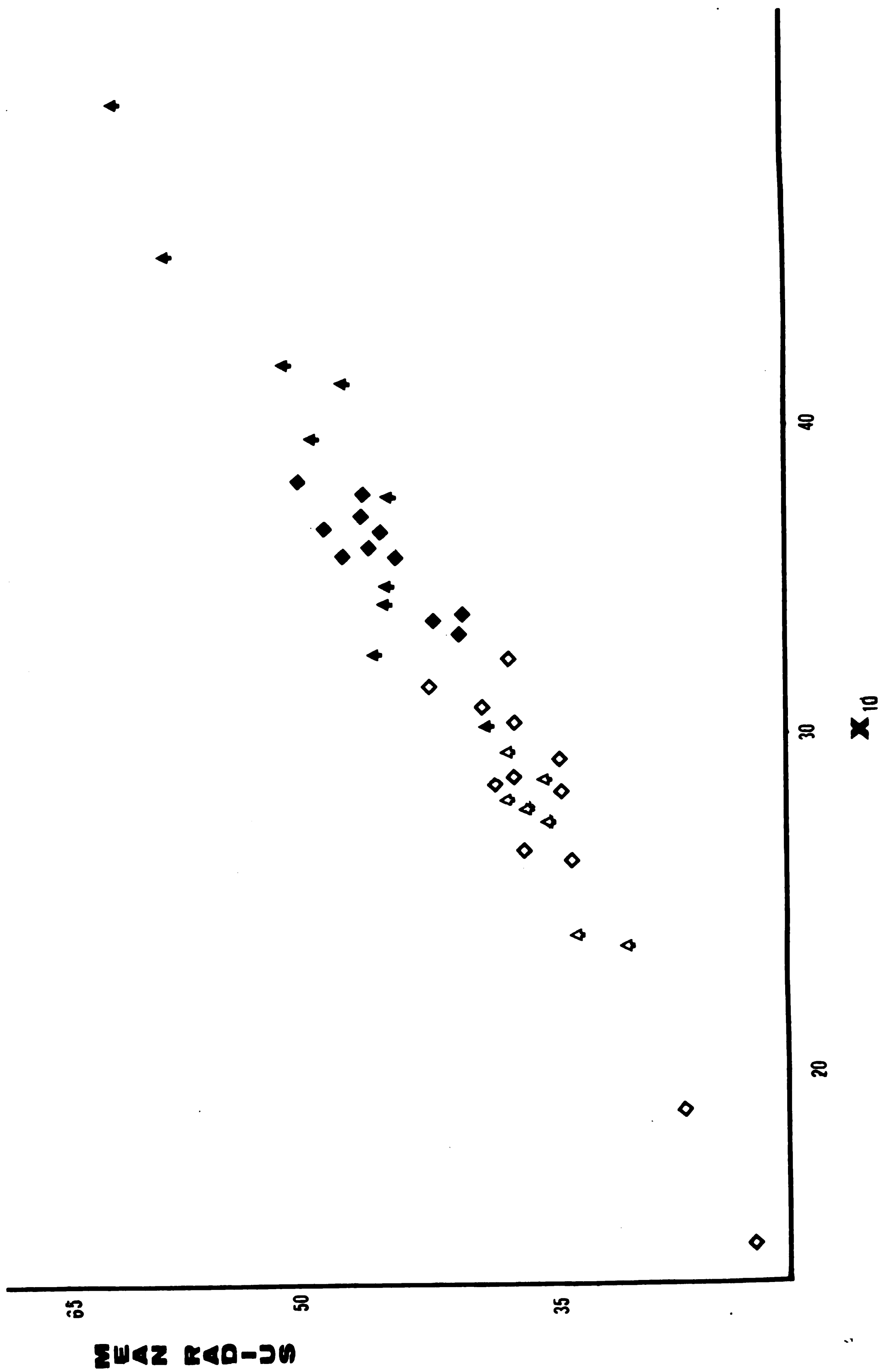
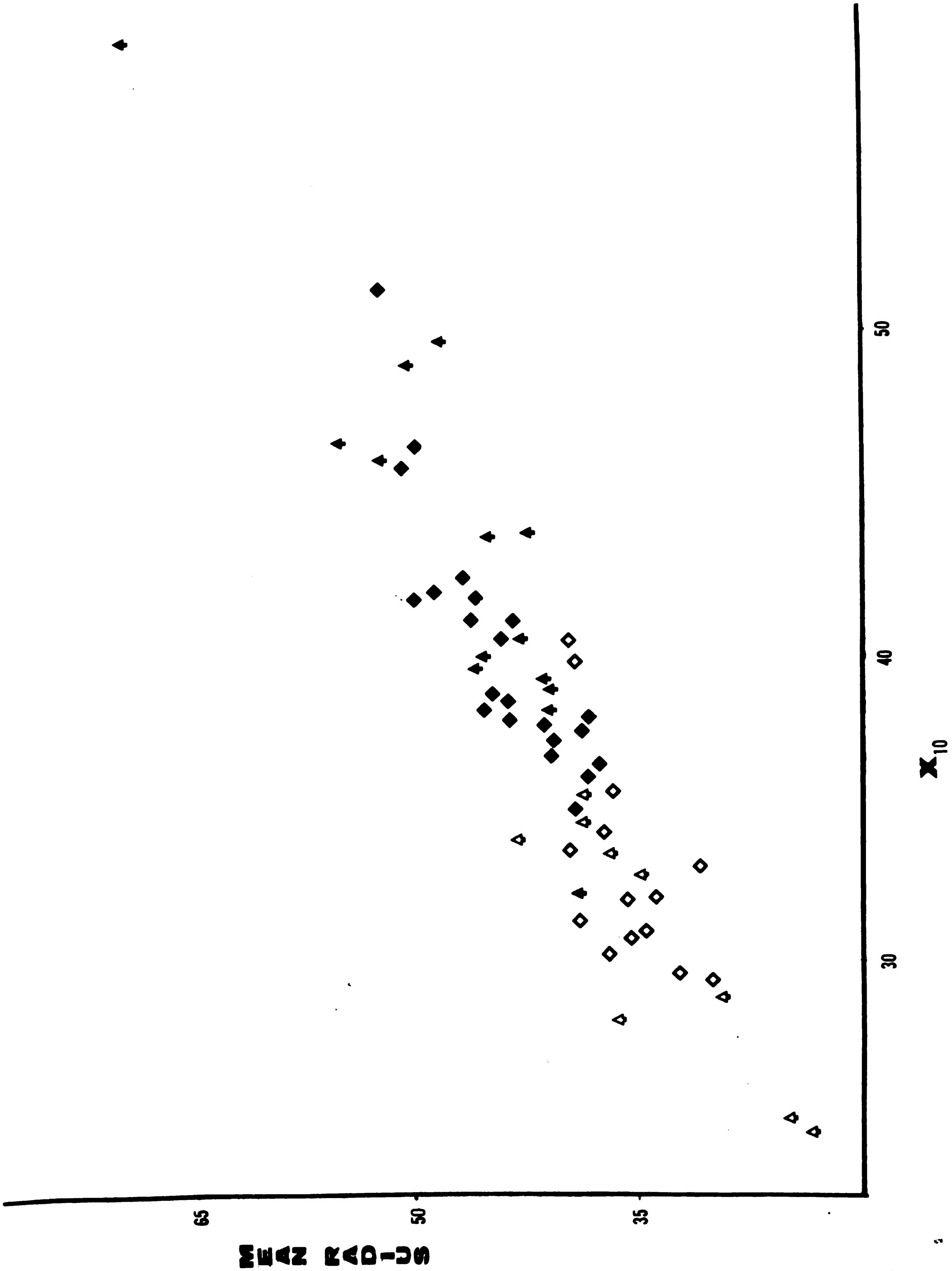

65
50
35
MEAN RADIUS
20
30
40
X_{10}

Figure 4. Graph of mean radius against variable x_{10} for *P. rana crassituberculata*. Measurements are in millimeters.

♤ = young females
♤ = young males
♠ = old females
♠ = old males


MEAN RADIUS
65
50
35
X10
30
40
50

SUBSPECIFIC DIFFERENCES

Eldredge [1971] has rejected Clarkson's [1966] idea with the statement, "Sexual dimorphism must also be rejected in view of the stratigraphic and geographic distributions of the two variants. The precise nature of the relationship between milleri and crassituberculata seems an insoluble problem with the given data as the correct explanation appears to lie in the realm of population genetics. Perhaps the ontogeny of the eye was flexible and capable of reaction to the peculiar environmental conditions obtaining at a given place at a given time. Alternately, a more strictly genetically based adaptation to local environments may underlie the distributions of the two variants."

The quantitative measurements of the morphology of the cephalon taken in this study clarify the relationship between the two subspecies. Sixty-seven variables (the 78 listed in Table 2 minus the nine phase angles, the occipital ring length, and the libriginial length) were used in a discriminant analysis to distinguish the two subspecies. The discriminant function successfully separated the two subspecies, misclassifying only one specimen (Table 6). Use of fewer than 67 variables produced a greater degree of misclassification; this indicates that the difference between the two subspecies are an overall effect of a large number of morphological differences. The fact that the subspecies differ significantly in a large number of morphologic characteristics

Table 6. Discriminant function results for subspecific clusters in P. rana. Specimen numbers below 300 are from U of M collection. Specimen numbers above 300 are from Magrum collection.

MAHALANOBIS DSQUARE= 19.30910

F(57, 31)= [illegible].19560

POP. NO.	SAMPLE SIZE	MEAN Z	VARIANCE Z	STD. DEV. Z
1	40	2.58017	.00234	.04833
2	59	2.39919	.00174	.04170

D(0) = 2.48572

PROBABILITY OF ERROR = (.0179) FOR GROUPS ONE AND TWO

RANK	FIRST GROUP VALUES	SECOND GROUP VALUES	FIRST GROUP SPECIMEN NO.	SECOND GROUP SPECIMEN NO.
1	[illegible]		312	
2	2.66783		32[illegible]	
3	[illegible]		303	
4	2.65725		11[illegible]	
5	[illegible]		343	
6	[illegible]		3[illegible]3	
7	[illegible]		350	
8	[illegible]		332	
9	[illegible]		306	
10	[illegible]		354	
11	2.61221		317	
12	[illegible]		309	
13	2.61168		336	
14	2.60769		311	
15	[illegible]		307	
16	[illegible]		321	
17	2.60345		103	
18	[illegible]		327	
19	2.59925		316	
20	[illegible]		325	
21	[illegible]		310	
22	[illegible]		1[illegible]6	
23	[illegible]		317	
24	2.56661		30[illegible]	
25		2.56530		419
26	2.56457		302	
27	2.56232		319	
28	[illegible]		352	
29	[illegible]		344	
30	2.55716		322	
31	2.55309		308	
32	[illegible]		333	
33	2.54657		318	
34	[illegible]		345	
35	2.54397		313	

P rana
milleri

Table 6. Continued.

36	2.53695		346		
37	2.53122		331		
38	2.52847		107		
39	2.52536		338		
40	2.52017		340		
41	2.50395		349		
42		2.46446		406	
43		2.46065		412	
44		2.455[illegible]		41[illegible]	
45		2.45217		407	
46		2.44[illegible]		424	
47		2.44[illegible]		217	P. rana crassituberculata
48		2.43[illegible]		438	
49		2.43[illegible]		423	
50		2.43720		440	
51		2.43476		240	
52		2.43[illegible]		237	
53		2.43[illegible]		222	
54		2.42[illegible]		421	
55		2.42[illegible]		232	
56		2.42[illegible]		405	
57		2.42[illegible]		209	
58		2.42[illegible]		433	
59		2.42[illegible]		[illegible]	
60		2.42[illegible]		250	
61		2.41742		206	
62		2.41714		404	
63		2.41549		416	
64		2.40949		221	
65		2.40735		425	
66		2.40486		411	
67		2.39[illegible]		205	
68		2.39[illegible]		436	
69		2.39[illegible]		228	
70		2.39[illegible]		229	
71		2.39205		235	
72		2.39281		427	
73		2.39063		417	
74		2.38867		220	
75		2.38667		242	
76		2.38[illegible]		431	
77		2.38[illegible]7		243	
78		2.38575		219	
79		2.39079		201	
80		2.37[illegible]13		413	
81		2.37[illegible]		406	
82		2.37174		215	
83		2.37144		216	
84		2.37137		238	
85		2.36777		236	
86		2.35[illegible]		428	
87		2.36[illegible]84		223	
88		2.34[illegible]		227	
89		2.34[illegible]		234	
90		2.35779		409	
91		2.35713		231	
92		2.35563		429	
93		2.34767		410	
94		2.34941		402	
95		2.34667		434	
96		2.34395		418	
97		2.33429		430	
98		2.33334		437	
99		2.32017		403	

combined with the fact that they are rarely found at the same locality does not support Clarkson's hypothesis of sexual dimorphism. Rather, the data suggest that their recognition as subspecies is tentatively valid, until more is known about the population genetics of these animals. Despite Eldredge's observation concerning eye pattern, the two subspecies are sufficiently distinct at the Sylvania locality to represent two phenetically differentiated populations.

SEXUAL DIMORPHISM

Histograms and cluster analysis of the _milleri_ and _crassituberculata_ populations reveal another set of clearly and slightly dimorphic clusters within each of the two subspecies (Figures 5 and 6). This dimorphism is expressed by glabellar shape, cephalic shape, and the amplitudes of the Fourier harmonics 4, 7, 10, 16 and 20. Individuals with high values for glabellar shape, cephalic shape, and harmonic 16, and low values for harmonics 4, 7, 10 and 20 form one cluster (cluster A), and individuals with low values for glabellar shape, cephalic shape, and harmonic 16, and high values for harmonics 4, 7, 10, and 20 form the other cluster (cluster B). In _crassituberculata_, there were 36 trilobites in cluster A and 23 trilobites in cluster B. In _milleri_, there were 23 trilobites in cluster A and 17 in cluster B. Use of the discriminant function confirms the validity of dimorphic clusters within both the _milleri_ and _crassituberculata groups_ (Tables 7 and 8). In principal components

Figure 5. Computer drawn histograms revealing sexually dimorphic distributions of _P. rana milleri_ in variables; glabellar shape, cephalic shape, and Fourier harmonic amplitudes 4, 7, 10, 16 and 20.

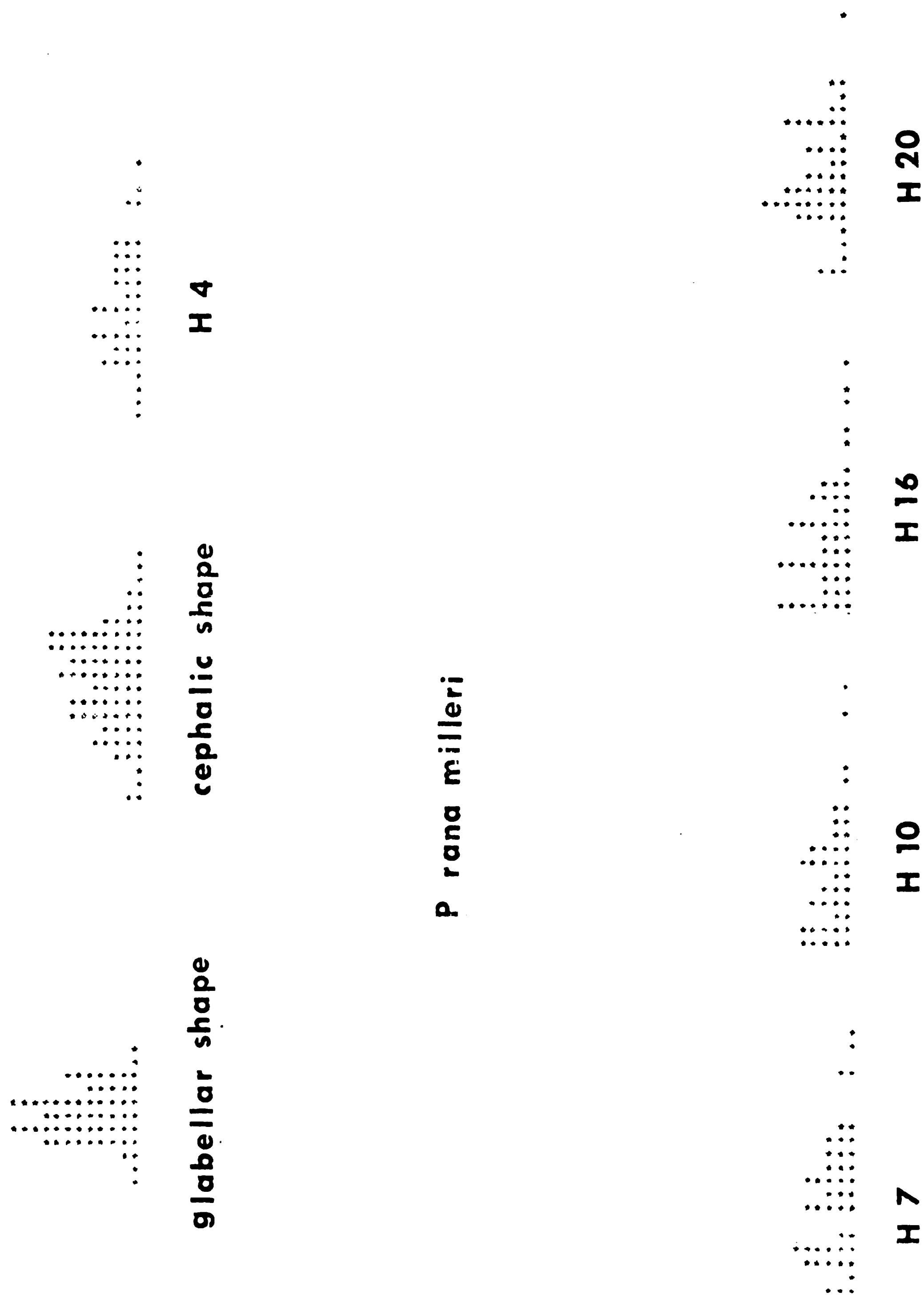
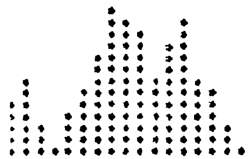
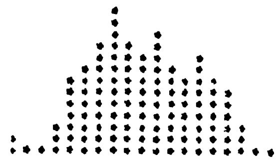

glabellar shape
cephalic shape
H 4
P rana milleri
H 7
H 10
H 16
H 20

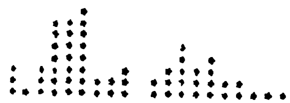
Figure 6. Computer drawn histograms revealing sexually dimorphic distributions of _P. rana crassituberculata_ in variables; glabellar shape, cephalic shape, and Fourier harmonic amplitudes 4, 7, 10, 16 and 20.



glabellar shape

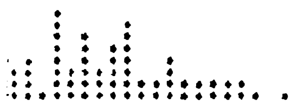


cephalic shape

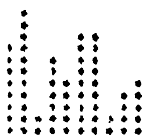


H 4

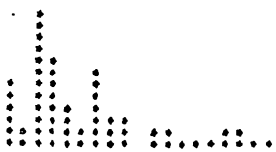
P rana crassituberculata



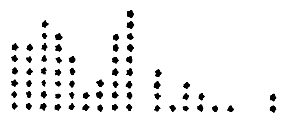
H 7



H 10



H 16



H 20

Table 7. Discriminant function results for sexually dimorphic clusters in P. rana milleri. Specimen numbers below 300 are from U of M collection. Specimen numbers above 300 are from Magrum collection.

MAHALANOBIS DSQUARE= 16.39736

F(7, 32)= 19.28231

POP. NO.	SAMPLE SIZE	MEAN Z	VARIANCE Z	STD. DEV. Z
1	23	1.97314	.00936	.09676
2	17	1.54163	.01410	.11873

D(0) = 1.77934

PROBABILITY OF ERROR = (.0222) FOR GROUPS ONE AND TWO

RANK	FIRST GROUP VALUES	SECOND GROUP VALUES	FIRST GROUP SPECIMEN NO.	SECOND GROUP SPECIMEN NO.	
1	[illegible]		[illegible]		
2	[illegible]		114		
3	[illegible]		343		
4	[illegible]		319		
5	[illegible]		325		
6	[illegible]		336		
7	2.01170		301		
8	1.93172		307		
9	[illegible]		354		♀
10	[illegible]		347		
11	[illegible]		[illegible]		
12	[illegible]		107		
13	[illegible]		348		
14	[illegible]		346		
15	[illegible]		350		
16	[illegible]		106		
17	1.91189		331		
18	[illegible]		349		
19	[illegible]		340		
20	[illegible]		333		
21	1.83?01		103		
22	[illegible]		328		
23	1.81975		316		
24		1.70194		312	
25		[illegible]		313	
26		1.64?41		343	
27		1.61136		309	♂
28		[illegible]		327	
29		1.58476		344	
30		[illegible]		303	
31		[illegible]		321	
32		[illegible]		306	
33		[illegible]		302	
34		[illegible]		316	
35		[illegible]		332	
36		[illegible]		317	
37		[illegible]		308	
38		1.37869		311	
39		1.31094		322	
40		1.29802		310	

Table 8. Discriminant function results for sexually dimorphic clusters in P. rana crassituberculata. Specimen numbers below 300 are from U of M collection. Specimen numbers above 300 are from Magrum collection.

```
1    MAHALANOBIS DSQUARE=        19.30910
     F( 7, 51)=         35.53369
     POP. NO.     SAMPLE SIZE      MEAN Z          VARIANCE Z        STD. DEV. Z
        1             36           .49512           .03647            .06018
        2             23           .14750           .05557            .07462
     Z(0) =        .31511
     PROBABILITY OF ERROR = ( .0122) FOR GROUP. ONE AND TWO
```

RANK	FIRST GROUP VALUES	SECOND GROUP VALUES	FIRST GROUP SPECIMEN NO.	SECOND GROUP SPECIMEN NO.	
1	.63968		428		
2	.60036		431		
3	.59408		425		
4	.5[illegible]729		406		
5	.5[illegible]484		434		
6	.55343		23[illegible]		
7	.55276		416		
8	.55083		429		♀
9	.55032		222		
10	.54552		409		
11	.54178		424		
12	.53437		242		
13	.53372		217		
14	.52759		237		
15	.52756		231		
16	.5275[illegible]		421		
17	.52534		415		
18	.52099		433		
19	.51359		413		
20	.51282		236		
21	.49757		232		
22	.49051		221		
23	.48593		419		
24	.48566		436		
25	.48194		414		
26	.46987		205		
27	.448[illegible]		410		
28	.44[illegible]37		229		
29	.42756		209		
30	.42662		436		
31	.41728		430		
32	.3798[illegible]		411		
33	.37469		405		
34	.33139		404		
35	.32217		243		
36	.30743		408		
37		.28710		417	
38		.27140		402	
39		.22152		418	
40		.21811		230	
41		.21413		440	
42		.21052		216	
43		.19752		223	
44		.19720		412	
45		.17244		407	♂
46		.15979		235	
47		.15244		220	
48		.15014		2[illegible]5	
49		.14941		227	
50		.13440		438	
51		.12790		240	
52		.12547		234	
53		.09739		2[illegible]6	
54		.06626		219	
55		.05742		201	
56		.05274		423	
57		.05075		427	
58		.04856		403	
59		.00212		228	

analysis, the variables denoting this bimodality scored high values on factor three and low values on factor one, the size or growth factor (Table 3). Thus these variables depict a bimodality that is independent of ontogeny, but instead depicts various aspects of cephalic and glabellar shape.

Sexual dimorphism is often expressed by shape differences in many animals, including trilobites. Hu [1971] found dimorphism in the glabellas and cephalons of 9 species of trilobites, and attributed it to sexual differences. In 6 species, Hu described the female as having a longer and narrower glabella than the male; in one species, the female was described as having a narrower and more conical glabella; in one species, the female was described as having both a longer and narrower glabella and cephalon; and in one species, the female was described as having a more elongate cranidum. As rationale for these sexual designations, Hu states, "It is the assumption here that the most abundantly represented specimens were males, either having relatively small bodies without special prosopon, or large bodies with strongly modifying prosopon. The less numerous females are large-bodied without special prosopon or small-bodied with slightly modifying prosopon. These morphologic and sexual ratio differences seem to correlate with sexual dimorphism in Recent Arthropoda, such as Insecta, Crustacea, and Merostomata" [Hu, 1971].

The dimorphism found in *P. r. milleri* and *P. r. crassituberculata* is similar to that found by Hu, in that the individuals in cluster A have relatively longer and narrower glabellas and cephalons than the individuals in cluster B. The individuals in cluster A also had a greater degree of 16-rayed symmetry in their cephalic shape, but a lesser degree of 4, 7, 10 and 20-rayed symmetry, than the individuals in cluster B, as expressed by the bimodality in the Fourier harmonics. Based on similarities with Hu's study, I attribute the dimorphism to be of a sexual nature, with cluster A being the females and cluster B being the males. A possible discrepancy in this judgment is that in each of the subspecies, the females outnumber the males (36 to 23 in crassituberculata and 23 to 17 in milleri). However, judging by the fact that the samples were not random, the sexual ratio may not be too applicable. In terms of actual quantitative shape differences in the glabellas and cephalons, the morphologic differences involved here are subtle. The extreme cases can easily be visually differentiated as being male or female, but with many of the average and gradational individuals it is difficult to determine the sex on a visual basis alone. Figure 7 shows an example of the extreme male and female types of each subspecies. By summing up the coordinates of the 18 points and averaging them out for the group, eight "average" trilobites, each representing its own group, were determined and reconstructed. The eight "average" trilobites are, the average younger milleri female, the average younger milleri male, the average older milleri female, the average older milleri male, the average younger crassituberculata female, the average younger crassituberculata male, the average older crassituberculata female, and the average older crassituberculata male (Figure 8). These "average" trilobites then, give an indication of the mean differences between sexes throughout ontogeny within both subspecies, and as Figure 8 indicates, the younger individuals of each sex are quite similar, while the mature individuals are more clearly sexually dimorphic. This, along with Eldredge's statement about the eyes of all small post-larval instars being of the milleri variety, indicates that, just as in many other animals, the differences between males and females, as well as possible genetic differences, become more pronounced as they reach maturity. A possible explanation as to why sexual dimorphism seems to manifest itself in cephalic and glabellar shape is found in the Treatise on Invertebrate Paleontology, "Barrande, in 1872, described and illustrated a specimen of Barrandia crassa from the Middle Ordovician of Bohemia bearing a mall of tiny ovoid bodies located below the integument of the frontal glabellar lobe. The bodies were regarded as eggs still in place in ovaries below the cephalic exoskeleton." If Barrande's interpretation is correct, the glabellas of the females may be longer and narrower than the glabellas of the males in order to provide space for the ovaries contained within.

Figure 7. Extreme males and females of *P. rana milleri* and *P. rana crassituberculata*. *Milleri* male = specimen no. 322, *milleri* female = specimen no. 338, *crassituberculata* male = specimen no. 403, *crassituberculata* female = specimen no. 428.

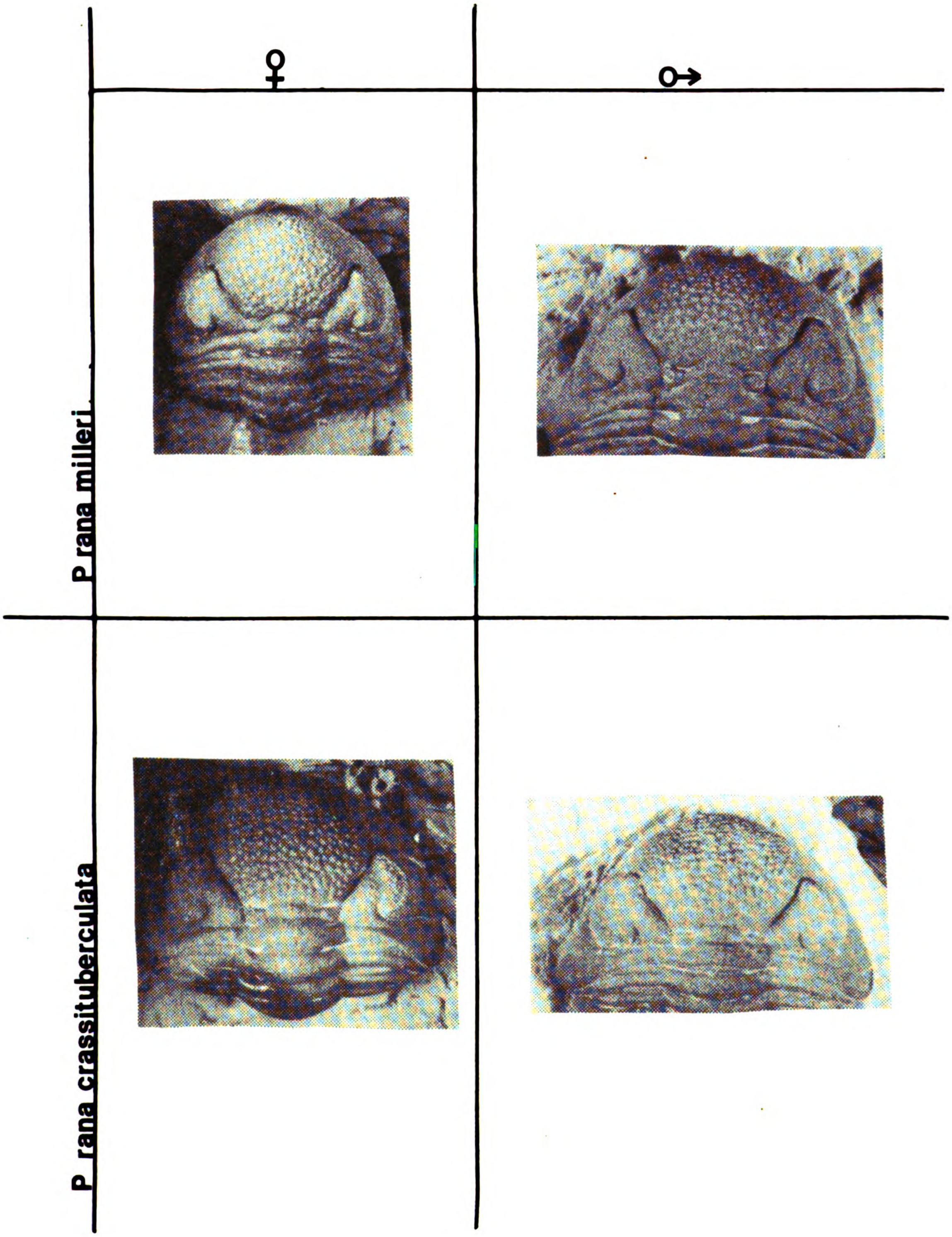

♀
♂
P rana milleri
P rana crassituberculata

Figure 8. The eight "average" trilobites.

CONCLUSION

The trilobites examined in this study were found to contain four natural clusters in each of the two subspecies. Two of the clusters were ontogenetic, consisting of clusters of younger and older individuals based on size differences. The variables which were found to be most useful in determining the ontogenetic clusters were the mean radius, and the x coordinates of the points 10, 13, 14, 15 and 18 on the cephalon. Graphs of mean radius, which could be taken as an indication of age, against size, revealed that growth proceeded at a constant rate rather than exponentially.

The second two clusters were independent of the first, and were determined by the glabellar shape, cephalic shape, and Fourier harmonics 4, 7, 10, 16 and 20. These variables are expressive of cephalic and glabellar shape, and one cluster consisted of trilobites with longer and narrower glabellas and cephalons, and the other cluster consisted of trilobites with shorter and wider glabellas and cephalons. These two clusters have been judged to be sexually dimorphic clusters, and, in accordance with previous work done by Hu, the individuals with longer and narrower glabellas and cephalons were judged to be females. The two subspecies, *P. rana milleri* and *P. rana crassituberculata*, were found to be morphologically distinct, and differed from each other by a large number of characters other than eye structure. This tentatively confirms the idea that *milleri* and *crassituberculata* are valid subspecies, although their differences might be ecophenotypic responses to specific local environments represented as a depositional mosaic in the Sylvania area.

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BIBLIOGRAPHY

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APPENDIX

APPENDIX

Data printed as follows: Specimen no.,
Eleven potentially dimorphic indicator variables in same order as in Table 1,
Coordinates of the 18 key points, $x_1, y_1, x_2, y_2, \ldots, x_{18}, y_{18}$,
Fourier Harmonic amplitudes 1-29,
Mean radius multiplied by 100,
The number 60 which was the number of coordinate points taken to determine the Fourier analysis,
Normalized roughness coefficient,
and phase angles 1-29.

Specimen Nos. 103-354 = *P. rana milleri* young females

Specimen Nos. 107-352 = *P. rana milleri* old females

Specimen Nos. 302-321 = *P. rana milleri* young males

Specimen Nos. 306-344 = *P. rana milleri* old males

Specimen Nos. 205-433 = *P. rana crassituberculata* young females

Specimen Nos. 209-437 = *P. rana crassituberculata* old females

Specimen Nos. 220-440 = *P. rana crassituberculata* young males

Speciman Nos. 201-438 = *P. rana crassituberculata* old males

```
103
 40.3827   .0158 28.2957 10.1559 44.4580  7.1147 65.2726   .0105   .6380   .6869
   .0539
 47.5103   .6639 22.2290 10.1312   .3836 10.1559   .2204 17.2706   .3176 24.8899
   .8329 65.2726 31.6465 51.4164 28.9998 43.0675 43.2562 25.6121 30.4374 16.3769
 40.4884 27.6796 26.1509 38.7854 24.5557 33.2174 33.5277 27.5132 15.0192 22.4162
  8.4061 21.7385  9.3571 16.6460 19.2558 16.0116
  .0662  .2994  .1439  .0095  .0637  .0739  .0189  .0266  .0421  .0307  .0055  .
0250  .0217  .0085  .0117  .0148  .0075  .0086  .0103
  .0073  .0021  .0078  .0062  .0033  .0028  .0049  .0054  .0098  .0039
                                   3690.1071      60
 4.6190
  84.43    .00 268.52  57.25 269.06 186.78 126.68 165.82 103.90  22.30
  78.03   6.67 291.83 251.87 251.80 195.76 125.59 144.39  97.34   5.65
  32.83 358.46 266.33 202.27 268.80 189.24 128.08 220.96 116.24
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 37.1693   .0148 24.4289 10.4258 31.8056  8.6509 62.5849   .0112   .5516   .6984
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 302.81 290.12 327.04 228.99 105.18  92.45  84.19  28.01    .63

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 52.0907 27.4808 34.7664 46.5104 32.1667 36.8309 39.6895 30.8913 20.7648 21.4772
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350
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  41.65  98.34 345.34 213.40  49.37 296.44  40.12 308.49 212.27
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  80.80  342.21  91.59  13.11 262.09  21.49 291.57 185.76 315.66
309
 36.3296   .0155 26.0379  9.1475 32.0306  7.8844 59.7094   .0106   .5642   .6350
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 148.83  208.06 156.89  76.14 107.77  74.95 351.24 123.67 339.60
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 102.13 159.60  76.52  22.43  28.49 353.58 276.17  72.90 295.24


312
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321
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 165.94 225.35 164.29  83.95  62.54  77.72  20.98  20.28 318.87
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308
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316
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232
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 45.2728 38.1977 33.0570 53.8737 29.8967 46.2996 37.4259 40.0918 20.0695 34.5054
 11.1693 33.8747 19.0897 29.5722 20.7040 25.8591
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 104.91  11.92 281.29  70.72 288.01 188.49  53.07 207.16 105.49

229
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 45.1095 35.4481 30.3230 49.8796 30.0770 47.3389 37.7178 40.7589 19.9603 33.5910
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476
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 61.4678  -.2776 22.1894 10.4765   .0571  6.6037  -.0848 19.5594  -.5071 29.4694
  -.6109 76.2080 42.8842 53.7331 41.2989 46.6345 50.8120 30.5497 32.6865 20.0380
 44.7229 31.3643 36.2058 45.1545 34.3971 41.6140 39.1505 33.1906 18.5048 24.9869
  9.8712 25.3155 19.0813 20.2335 18.7105 19.3969
  .0689   .3153   .1354   .0656   .1198   .0488   .0360   .0695   .0328   .0110   .0329   .
0248   .0037   .0233   .0156   .0030   .0128   .0129   .0015
  .0079   .0092   .0037   .0058   .0079   .0037   .0031   .0066   .0037   .0014
                                   4599.8982         60
 4.2883
 282.06    .00 275.20 351.23 273.85 186.29 285.21 187.95  83.30 210.12
  93.47   1.07  66.76   4.21 283.36 355.24 283.79 193.63 134.41 185.89
  99.64   6.81  90.57  11.57 288.83 347.29 280.17 206.74 231.40
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 72.3862    .7346 27.2707 16.0255  -.1830 18.0330  -.0708 32.0049    .3470 40.3496
  -.7383 97.7874 49.5471 73.6584 51.6407 67.5334 67.9177 40.5692 47.9507 30.7141
 60.7494 46.0847 44.5497 65.4793 40.3428 54.5141 50.3386 45.7251 25.3073 34.2945
 14.8705 36.4747 13.4163 29.6016 25.1151 28.1963
  .0888  .3415  .1697  .0592  .1059  .0548  .0241  .0515  .0354  .0149  .0342  .
0234  .0032  .0200  .0213  .0033  .0150  .0148  .0051
  .0037  .0113  .0040  .0058  .0090  .0056  .0033  .0071  .0050  .0052
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 4.6351
  83.10     .00 265.39  15.78 264.74 167.60 205.48 180.42  73.20 199.62
  20.08 348.83  73.40 350.27 258.11 241.52 248.10 165.17 103.42 150.63
  62.74  18.97  25.69 328.15 276.02 283.81 227.16 188.26 156.31

403
 48.6121    .0121 30.6846 12.7911 42.4280 10.2686 78.3195    .0080    .5877    .6249
   .6607
 62.6643  -.0134 21.2140 10.9468   .0233 12.7911   .3446 23.0597   .3265 29.7074
   .4656 78.3195 41.3550 59.1088 46.6736 48.7391 54.1165 31.2033 36.5073 22.2170
 46.9482 33.4255 36.1963 50.8261 33.0246 43.0342 37.8216 34.9049 20.4050 26.4520
 14.0479  8.8212 13.6946  3.1526 20.2146 21.5708
  .0920  .3365  .1717  .0551  .1156  .0607  .0330  .0645  .0352  .0221  .0357  .
0228  .0084  .0231  .0188  .0039  .0177  .0140  .0012
  .0124  .0106  .0005  .0077  .0082  .0025  .0053  .0068  .0031  .0034
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 4.9582
 269.29     .00 257.31 357.84 245.04 143.99 241.43 142.84  41.36 126.17
  37.18 294.48  36.31 232.62 185.59 257.81 178.16  84.57 152.50  70.40
 336.12 195.69 314.46 226.91 114.93 204.09 111.22  26.09  80.74
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   .1716
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  .0643  .3320  .1241  .0510  .0881  .0614  .0168  .0506  .0308  .0133  .0249  .
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  52.80 279.13 100.34 331.31 180.81  25.19 218.41  49.60 279.58
418
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 12.8794 32.5574 12.7632 27.2186 35.0036 25.5022
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  82.78 349.94  94.76 341.68 258.48 204.00 249.13 161.87  76.21 153.20
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 355.94 115.62 352.68 254.87 365.07 257.17 178.43 285.31 158.81
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  54.95  83.77  50.49 326.45 319.00 307.02 224.54 139.95 210.25
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