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The University of Nebraska

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ABSTRACT

Biometrical Study of Morphology and Development of the Pennsylvanian Trilobite *Ameura sangamonensis* (Meek and Worthen) from Nebraska

ROGER K. PABIAN   J. A. FAGERSTROM

Biometrical study of morphology and development in a sample of 100 cranidia, 94 pygidia, 26 free cheeks, and 9 complete specimens of the trilobite *Ameura sangamonensis* (Meek and Worthen) from the Bonner Springs Shale (Pennsylvanian; Missouri Series) in eastern Nebraska indicates that the dominant growth pattern was isometric. Evidence supporting this conclusion consists of rectilinear size relations among eight pairs of cranidial dimensions, three pairs of pygidial dimensions, and three pairs of dimensions of the free cheeks. Qualitative changes in pygidial morphology during development include a progressive decrease in prominence of the border, increasing width of the posterior border relative to the lateral borders, and a progressive change in outline from a smoothly rounded semi-circular margin to one that is subtriangular or sub-parabolic.

All the complete specimens in the sample are holaspides. There is some indication of point clustering on scatter diagrams among the smallest cranidia which suggests that the sample may contain a few late meraspides. However, if meraspid cranidia and free cheeks are present, they are morphologically very similar to the small holaspides.

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Fagerstrom[1]

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INTRODUCTION

Although trilobites are not abundant in the rocks of the Pennsylvanian System in eastern Nebraska, they are not so rare as has been commonly assumed. During the summer of 1962, an unusually rich fossil population of the trilobite species *Ameura sangamonensis* (Meek and Worthen) was collected from the Bonner Springs Formation (Upper Pennsylvanian, Missouri Series; see Condra and Reed, 1959, p. 51) exposed in an abandoned quarry near the center of the SE¼, SE¼, Sec. 7, T12N, R12E, Cass County, Nebraska, about 1½ miles southwest of the village of Cedar Creek. The trilobites are associated with at least sixteen other species of fossil invertebrates (Fagerstrom and Boellstorff, 1964; Fagerstrom, 1965) in a one foot thick layer of interbedded yellowish brown shale and light gray crystalline limestone located between one and two feet below the upper contact of the Bonner Springs Formation. The larger specimens were collected loose on the surface of the outcrop or on the bedding surfaces of the limestone layers; the small specimens were picked from boiled and washed bulk samples of the shale which were examined for microfossils under a binocular microscope.

The exuviae of *A. sangamonensis* have been altered by minor pre-burial currents, scavengers, etc., and by post-burial crushing from the weight of the overlying rocks (Fagerstrom, 1965). As a result, the fossil trilobite population consists largely of disarticulated and broken parts. Only nine complete specimens were collected and four of these were too poorly preserved for biometrical study. All of the specimens (229) have been deposited in the invertebrate paleontological collection of the University of Nebraska State Museum (UNSM) and are numbered UNSM 5201-5429.

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ACKNOWLEDGMENTS

BIOMETRICAL DATA

UNIVARIATE ANALYSIS

Some of the more important univariate measures which were computed from the sample are given in Table 1; the dimensions measured are illustrated in Fig. 1. One of the most interesting features of the sample is the very great range in size of the individuals (observed range, Table 1). The very small size of many of the
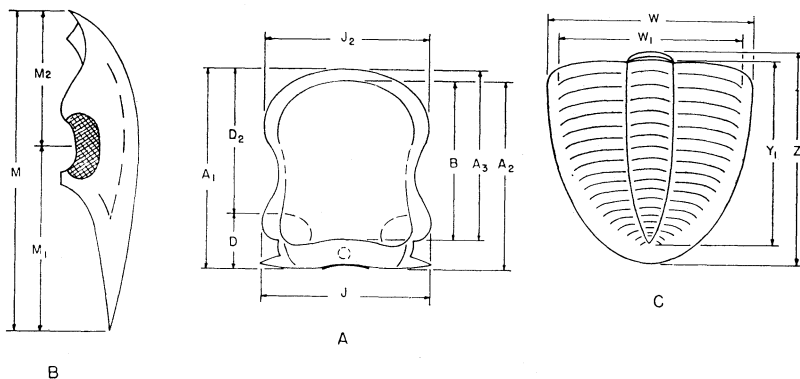
FIG. 1. Outline drawings showing dimensions measured on cranidia (A), free cheeks (B), and pygidia (C) of *Ameura sangamonensis* (Meek and Worthen).

fragments suggests that some may represent larval stages. Review of the literature on the ontogeny of North American Carboniferous trilobites indicates that larvae are rare and wherever present are very thin and fragile. Weller (1935) has described the "adolescent" development of species of *Ditomopyge* and Whittington (1954) has described very small specimens (presumably late meraspides; see p. 4) of two species of *Paladin*. No descriptions of Carboniferous protaspides are known to the present authors.

Table 1.   Univariate measures computed from samples of cranidia, free cheeks, pygidia, and complete specimens of <u>Ameura</u> <u>sangamonensis</u> (Meek and Worthen). All measurements in mm.   Symbols for dimensions mostly after Shaw (1957).

Dimension	Observed Range	Mean	Standard Deviation
CRANIDIA (see Fig. 1A) (N = 100)			
Total cranidial length, A_1	3.0 - 10.7	7.05	2.10
Occipital intra-marginal cephalic length, A_2	2.6 - 9.7	6.30	1.90
Preoccipital cranidial length, A_3	2.3 - 9.0	5.95	1.81
Occipital mid-palpebral distance, D	1.0 - 4.2	2.22	0.22
Anterior cranidial mid-palpebral distance, D_2	1.7 - 8.0	4.82	1.51
Maximum width, frontal area, J_2	2.2 - 9.2	5.80	1.88
Palpebral cranidial width, J	2.2 - 9.6	5.96	1.92
Total glabellar length, B	1.9 - 8.7	5.20	1.62
FREE CHEEKS (see Fig. 1B) (N = 26)			
Total length, free cheek plus genal spine, M	2.5 - 16.7	9.80	3.34
Vertex of genal angle mid-eye lobe distance, M_1	1.8 - 10.8	6.29	4.72
Anterior free cheek mid-eye lobe distance, M_2	0.7 - 5.8	3.60	1.89
PYGIDIA (see Fig. 1C) (N = 94)			
Total pygidial length, Z	1.7 - 11.5	6.51	2.88
Intra-articulating rhachis length, Y_1	1.5 - 9.8	5.56	2.57
Maximum pygidial width, W	2.4 - 13.7	8.05	3.33
Maximum intra-marginal pygidial width, W_1	2.0 - 11.2	7.02	2.95
COMPLETE SPECIMENS (N = 5)			
Total exoskeletal length, P	15.9 - 28.8	21.50	5.31

During the "meraspid" development of pygidia of *Ditomopyge olsoni* (Weller, 1935, p. 506–509, Text-figs. 4–8) there is a progressive decrease in the relative size of the pair of posterior spines and in the width of the posterior border. By definition, holaspid development in this species begins with those stages lacking spines (Weller, 1935, p. 506). Small specimens of *Paladin* and *Ameura sangamonensis* lack pygidial spines but there is a progressive reduction in the relative width of the border in *A. sangamonensis* that is similar to the meraspid development of *D. olsoni* as noted above. However, despite this similarity in the development of *A. sangamonensis* and meraspides of *D. olsoni* it is impossible to determine whether the small pygidia in the present sample actually are larval stages. If they are larvae, their morphology is essentially the same as the morphology of the adults, except for smaller size. The smallest complete early holaspid specimen, with nine thoracic segments (UNSM 5201), is morphologically similar to cranidial and pygidial fragments of the same and smaller sizes. A few of the important dimensions (in mm.) of this specimen are as follows (see Fig. 1 for the dimensions indicated): total cranidial length (A_1)=4.9; anterior cranidial mid-palpebral distance (D_2)=3.2; occipital mid-palpebral distance (D)=1.7; total glabellar length (B)=3.9; maximum width, frontal area (J_2)=4.2; palpebral cranidial width (J)=4.2; preoccipital cranidial length (A_3)=4.3; occipital intra-marginal cephalic length (A_2)=4.5.

BIVARIATE ANALYSIS

The chief disadvantage of univariate analysis is that it gives no information concerning morphological change during growth. This study of the development of *A. sangamonensis* is based largely upon bivariate measures for the paired dimensions indicated in Table 2. The choice of paired dimensions for bivariate analysis of cranidia and pygidia is largely based upon the suggestions of Shaw (1957, p. 193). Bivariate analysis of the development of free cheeks has not been undertaken by previous workers so the dimensions selected for measurement and the terminology and symbols (Table 1 and Fig. 1B) are used for the first time in the present paper. The use of Bartlett's "best fit" lines in Table 2 rather than reduced major axes follows the recommendations of Simpson, Roe, and Lewontin (1960, p. 401–402).

Scatter diagrams were prepared for each pair of dimensions listed in Table 2 and in all cases the general trend of points was rectilinear (see Text-figs. 2–7). Therefore, the dominant growth pattern for cranidia, free cheeks, and pygidia was isometric. Isometric pat-

Table 2. Bivariate measures computed from samples of cranidia, pygidia and free cheeks of Ameura sangamonensis (Meek and Worthen). $\underline{r}$ = total correlation coefficient; "Best Fit" lines after Simpson, Roe, and Lewontin (1960). Symbols for paired dimensions as in Fig. 1 and Table 1.

Paired Dimensions (Y, X)	$\underline{r}$	"Best Fit" Line	95% Confidence Intervals (for slope)	(for Y-intercept)
CRANIDIA (N = 100)				
J, A_1	.98	J $= .894A_1 - .338$	.888 - .910	$\pm .025$
B, A_1	.98	B $= .741A_1 - .033$	.739 - .751	$\pm .039$
B, A_2	.99	B $= .840A_2 - .096$	.811 - .857	$\pm .080$
J_2, A_1	.99	$J_2 = .854A_1 - .235$	.784 - .928	$\pm .031$
J, J_2	.98	J $= 1.020J_2 + .032$	.879 - 1.240	$\pm .004$
D, D_2	.84	D $= .384D_2 - .393$	.348 - .415	$\pm .124$
D_2, A_1	.98	$D_2 = .708A_1 - .174$	.690 - .726	$\pm .014$
A_3, A_1	.99	$A_3 = .850A_1 - .046$	.840 - .860	$\pm .108$
FREE CHEEKS (N = 26)				
M_2, M	.91	$M_2 = .402M - .340$	.359 - .438	$\pm .061$
M_1, M	.98	$M_1 = .631M + .110$	.502 - .737	$\pm .023$
M_2, M_1	.83	$M_2 = .637M_1 - .407$	.585 - .683	$\pm .049$
PYGIDIA (N = 94)				
Z, W	.96	Z $= 1.131W + .692$	1.103 - 1.157	$\pm .062$
Z, W_1	.96	Z $= 1.008W_1 + .462$	.992 - 1.022	$\pm .034$
Y_1, Z	.96	$Y_1 = .859Z - .025$	.821 - .893	$\pm .095$

terns indicate that the dimensions being compared were increasing at the same relative rate, even though their absolute sizes may have been considerably different.

There is some evidence of clustering of points among the smallest cranidia on the scatter diagrams (Text-figs. 2–5). This clustering may be indicative of individual molt stages (see Whittington, 1957, p. 449). Since, in many trilobite species, clustering is more prevalent among larval forms than among holaspides (*e.g.* Hunt, 1967, p. 204–206), the suggested clustering in the present sample of *A. sanga-monensis* indicates that the smallest individuals may be late mera-
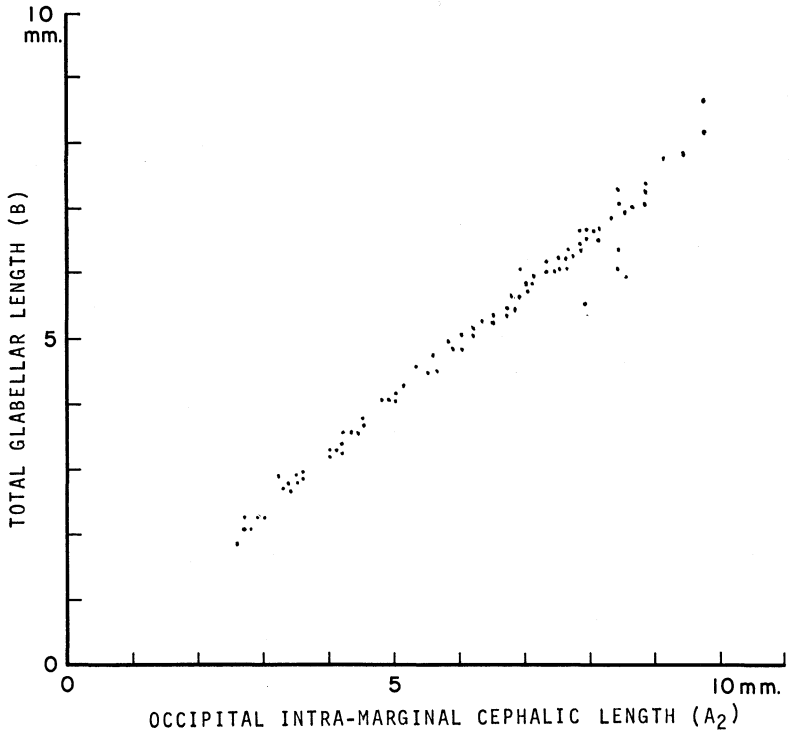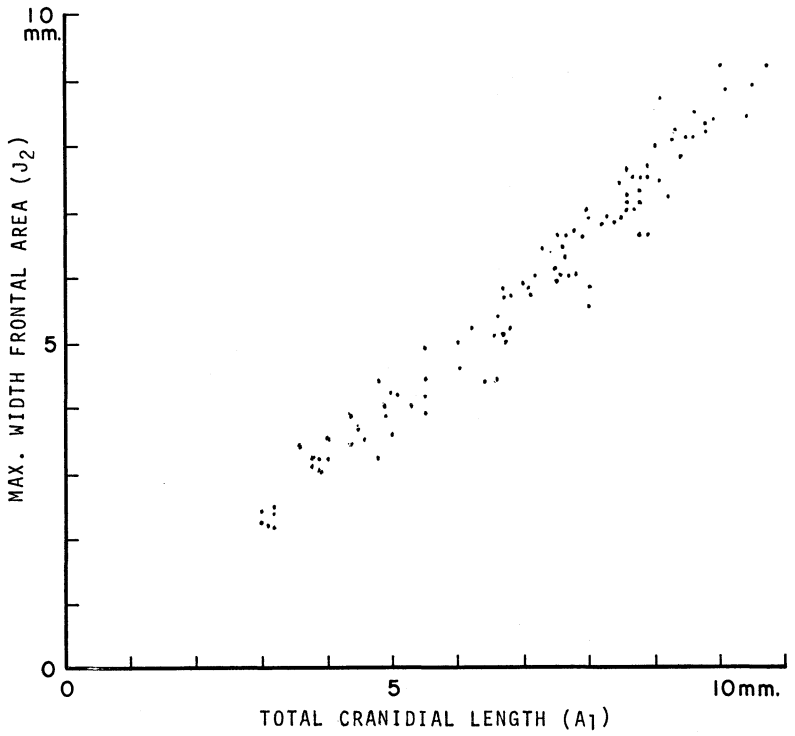
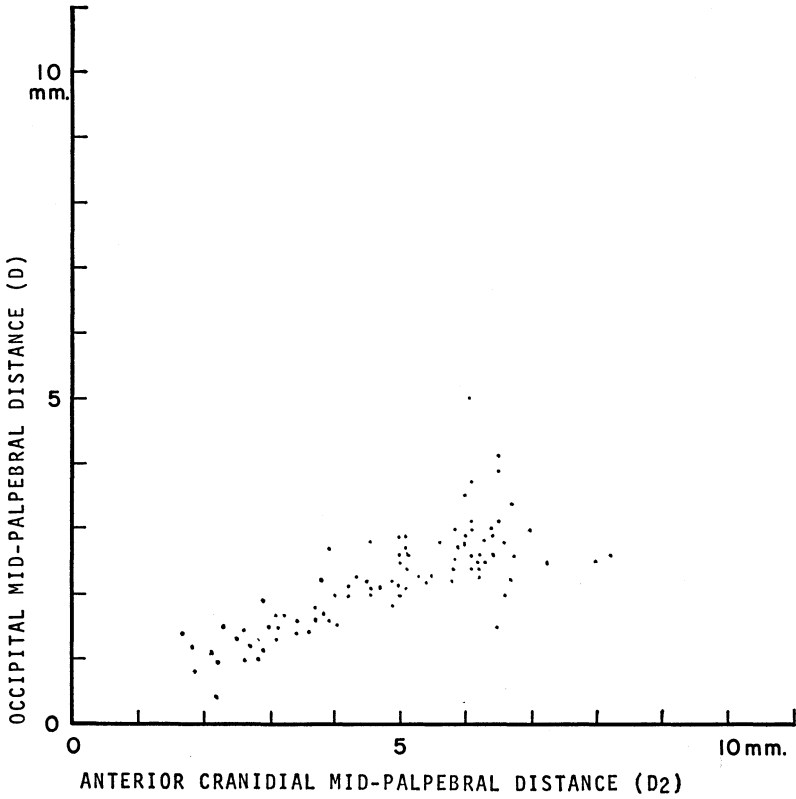FIG. 2. Scatter diagrams for paired cranidial dimensions of *A. sangamonensis*.
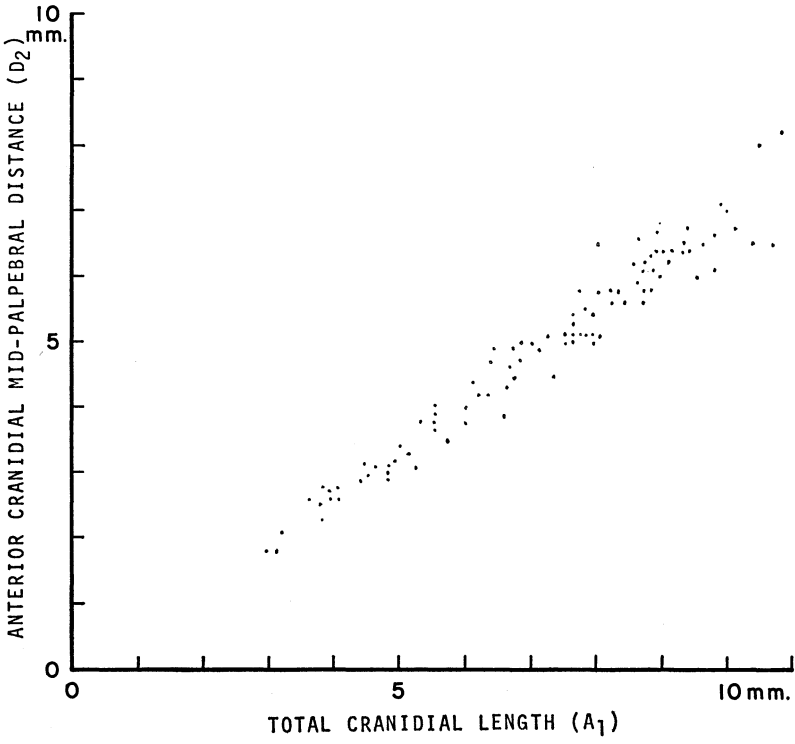
Fig. 3. Scatter diagrams for paired cranidial dimensions of *A. sangamonensis.*

FIG. 4. Scatter diagrams for paired cranidial dimensions of *A. sangamonensis*.

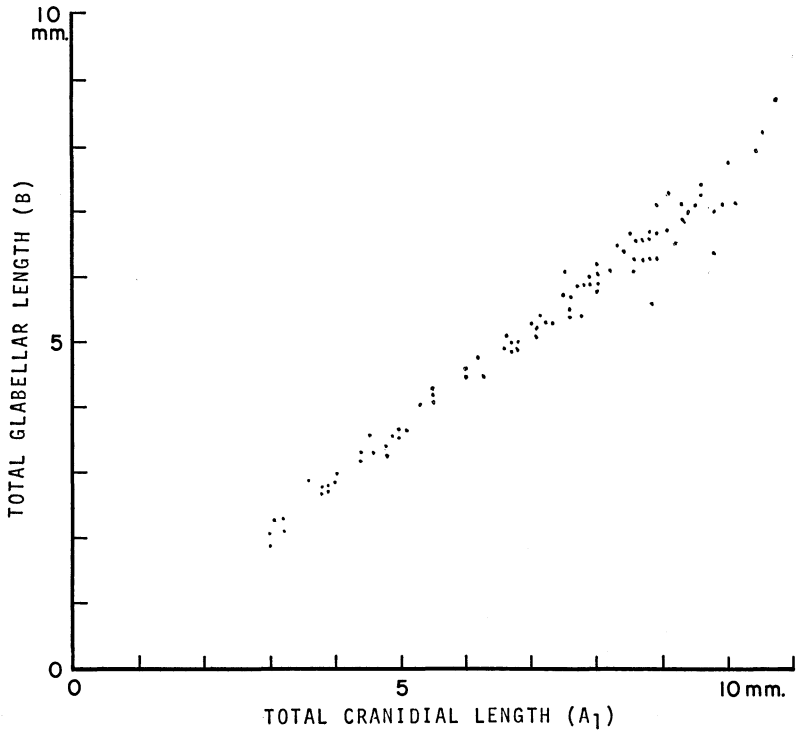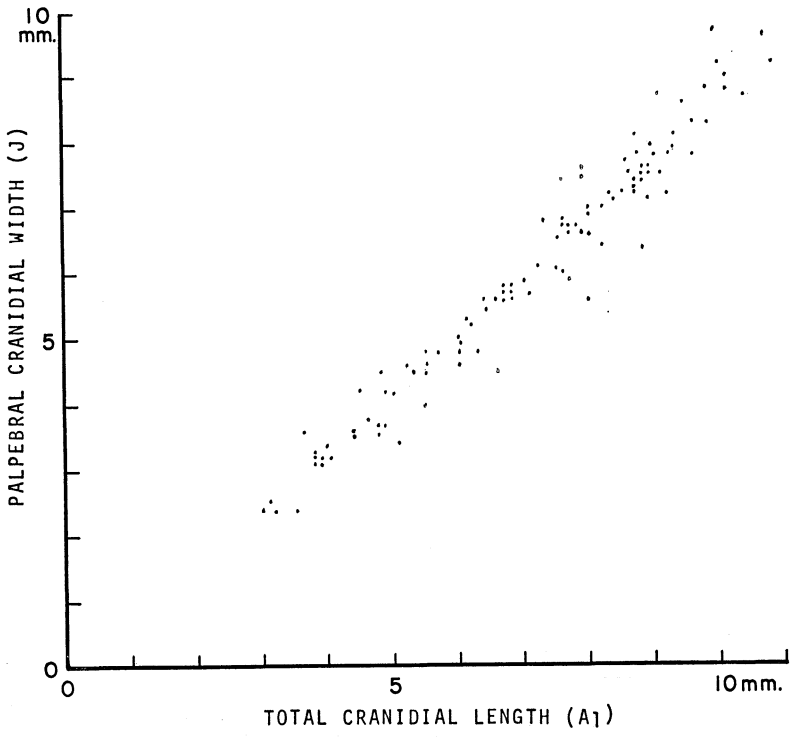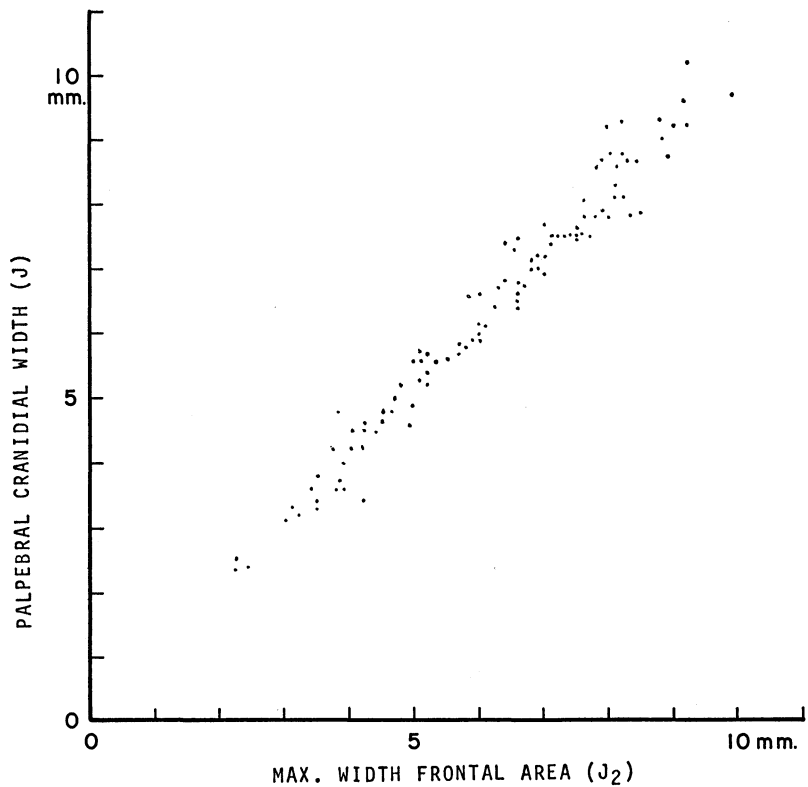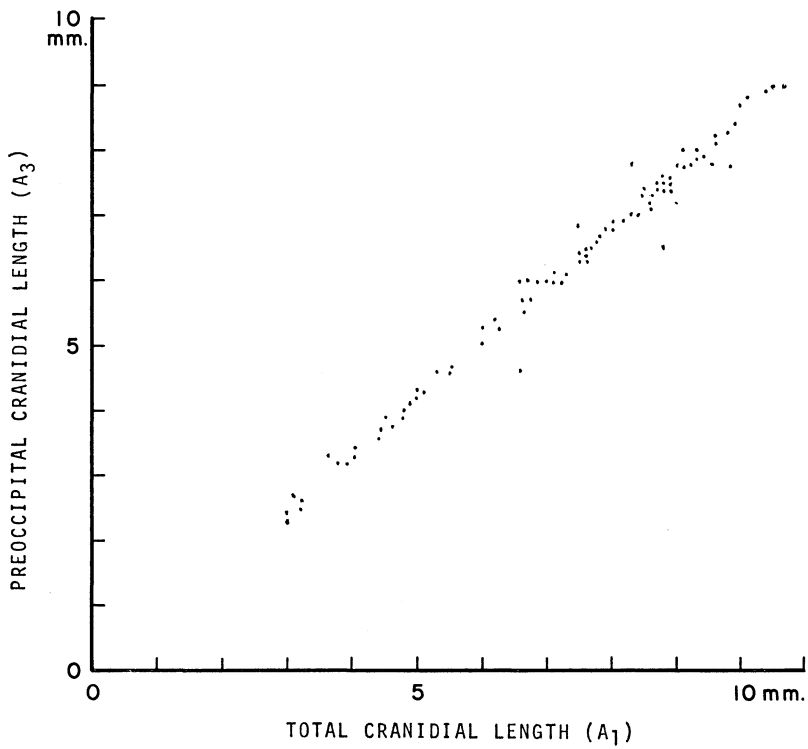FIG. 5. Scatter diagrams for paired cranidial dimensions of *A. sangamonensis*.
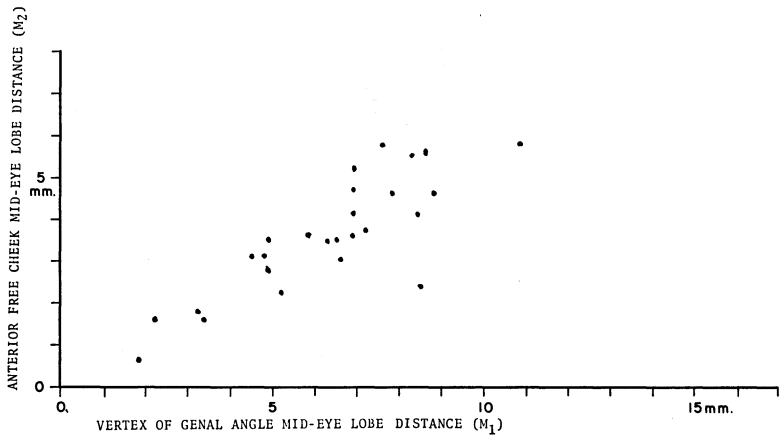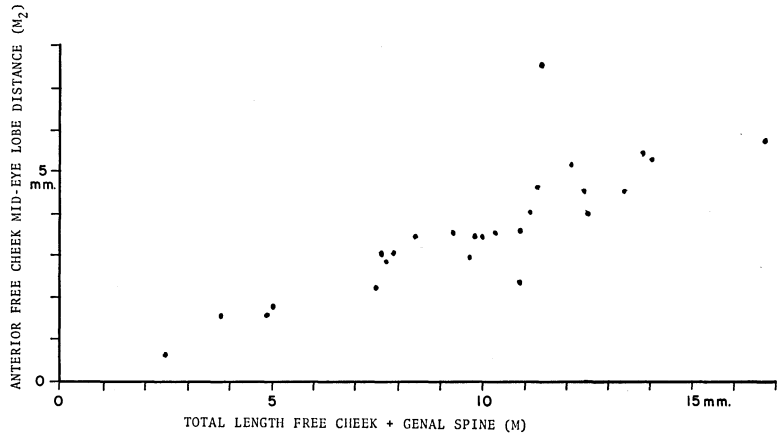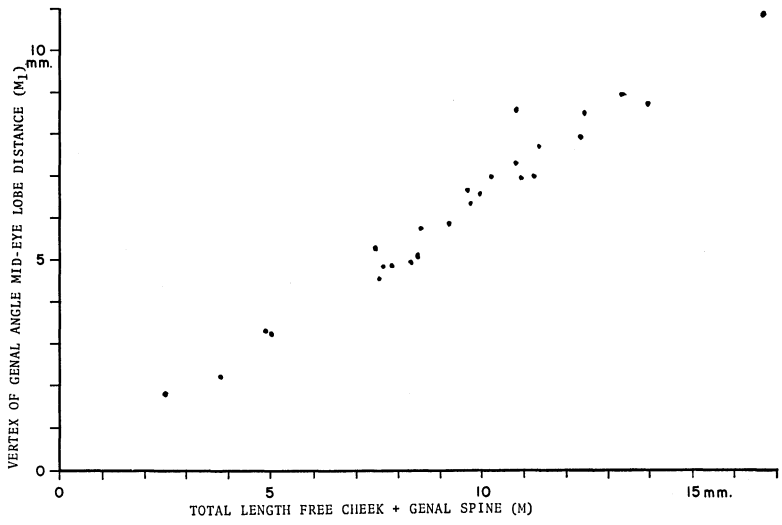
FIG. 6. Scatter diagrams for paired dimensions of free cheeks of *A. sangamonensis*.

spides. The absence of point clustering among the larger cranidia, and all of the free cheeks and pygidia (Text-figs. 6, 7) simply means that there is some overlap in size between large individuals in earlier molt stages and small individuals in later stages.

In contrast to the relatively great variation in size among individuals of the same molt stage, there is relatively little variation in general morphology during development, *i.e.* small cranidia, free cheeks, and pygidia have essentially the same shape as large ones (*cf.* Robison, 1967, p. 215–216). Evidence for this in the present sample consists of the generally high values for all the correlation coefficients (*r*, Table 2) and the isometric growth patterns for all pairs of dimensions studied (Text-figs. 2–7). The absence of distinct

FIG. 7. Scatter diagrams for paired pygidial dimensions of *A. sangamonensis.*

shape differences between small and large specimens suggests that the sample includes only holaspides.

<div align="center">COMPARISON OF SAMPLES</div>

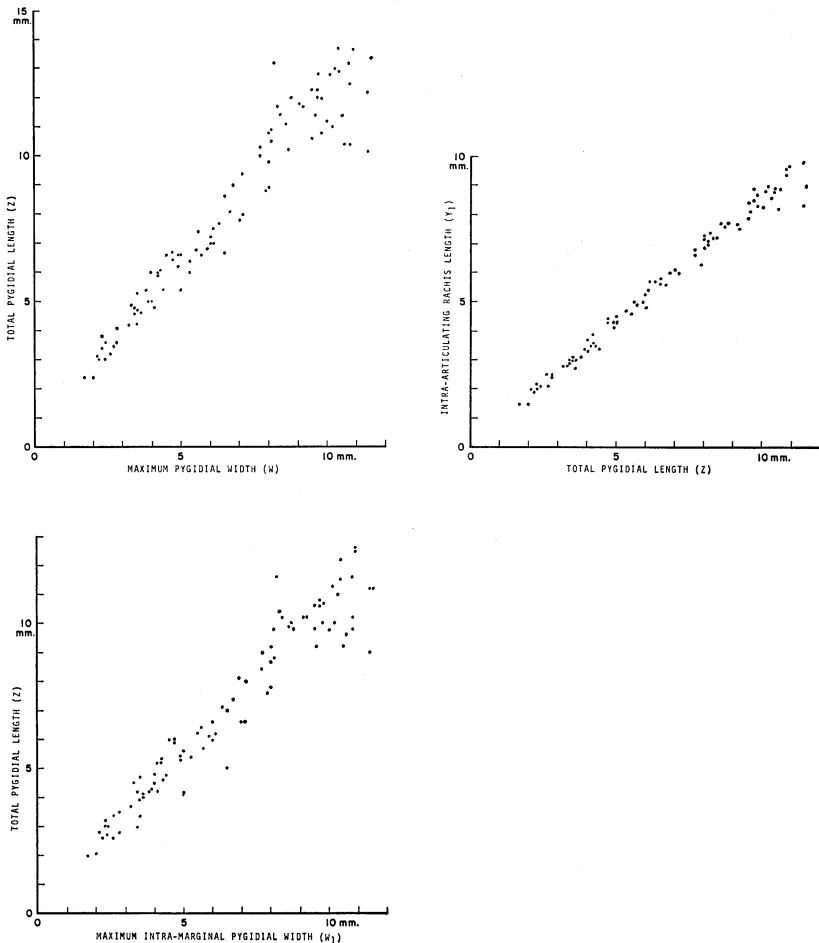Future workers may wish to compare other samples of *A. sanga-monensis* with the present sample. For such comparisons it is suggested that *t*—tests for the significance of the difference between two values of slope and Y-intercept described by Simpson, Roe, and Lewontin (1960, p. 237) be used except $s_B{}^2$ is given by

$$\text{(i)} \quad s_B{}^2 = s_x{}^2 - 2Bs_{xy} + B^2s_y{}^2$$

<div align="center">or</div>

$$\text{(ii)} \quad s_{B'}{}^2 = s_y{}^2 - 2Bs_{xy} + B^2s_x{}^2$$

Table 3.   Data for use in comparing other samples of A. sangamonensis with the sample described herein. (See Simpson, Roe, and Lewontin, 1960, p. 237).

Paired Dimensions (Y, X)	$\bar{X}_3 - \bar{X}_1$	$s_b{}^2$	B	A
CRANIDIA (N = 100)				
A_1, J	4.780	.032	.894	-.338
B, A_1	4.780	.049	.742	-.033
B, A_2	4.062	.024	.840	-.096
J_2, A_1	4.780	.001	.856	-.235
J, J_2	4.182	.001	1.020	+.032
D, D_2	3.612	.194	.814	-.212
D_2, A_1	4.780	.112	.708	-.174
A_3, A_1	4.780	.021	.850	-.046
FREE CHEEKS (N = 26)				
M_1, M	6.930	.901	.402	-.340
M_2, M	6.930	1.438	.631	+.110
M_2, M_1	4.380	.504	.637	-.407
PYGIDIA (N = 94)				
Z, W	7.519	1.250	1.131	+.692
Z, W_1	6.703	.034	1.008	+.462
Y_1, Z	6.646	.077	.859	-.025

where the unprimed symbols refer to one sample and the primed symbols refer to the other sample. The quantity $(a-b)(a-b)$ is $a^2-2ab+b^2$ when x and y are a and b respectively. In equation (i), $x=a$ and $y=b$; in equation (ii) $x=b$ and $y=a$.

The data of Table 3 are presented for making these comparisons of samples.

<div align="center">RATIOS BETWEEN VARIATES</div>

The use of the ratio between two dimensions has been a common practice in trilobite taxonomy for many years. However, evidence from the present study indicates that some ratios may be rather unsatisfactory taxonomic criteria and that their continued use should be critically reviewed for each species.

The standard form for an equation in two unknowns (x and y) is given by

$$\text{(iii)} \; y = b\,x + a$$

The equations for Bartlett's "best fit lines" in Table 2 are given in this same form: x and y in equation (iii) are two different dimensions of the dorsal carapace, b is the growth rate, or slope of the growth line, and a is the initial growth index, or the value of y when x equals zero.

The relations between these same four variables may be expressed in the form

$$\text{(iv)} \; \frac{y - a}{x} = b$$

As the value of a approaches zero, the ratio y/x approximates b and is relatively constant regardless of the absolute values of y, x, and b. Conversely, the greater the difference between a and zero, the greater the difference between the ratio y/x and b. Thus, if the values of a and b remain constant, the value of the ratio y/x depends upon the absolute values of y and x and is not constant.

These mathematical concepts can be expressed in terms of their biological significance as follows:

1. If growth is isometric, the greater the difference in the value of the initial growth index (a) and zero, the more the value of the ratio between the dimensions (y and x) will change during ontogeny.

2. The greater the variation in the value of the ratio between two dimensions (y/x), the less suitable it is as a taxonomic criterion (Shaw, 1956, p. 1212–1213).

3. The greatest variation in the value of the ratio occurs when the dimensions (y and x) are small. Thus, the ratio between two dimensions may change considerably during early ontogenetic stages and have only limited taxonomic significance, whereas the ratio

between the same two dimensions may be relatively constant during later ontogeny and therefore become a useful taxonomic criterion.

These generalizations can be applied rather easily to the taxonomic understanding of *A. sangamonensis*. The values of *a* for the A_1–B and J–J_2 paired dimensions (Table 2) most closely approach zero of all the pairs investigated. Therefore, the ratios B/A_1 and J/J_2 are nearly constant throughout development (Figs. 8 and 9B)
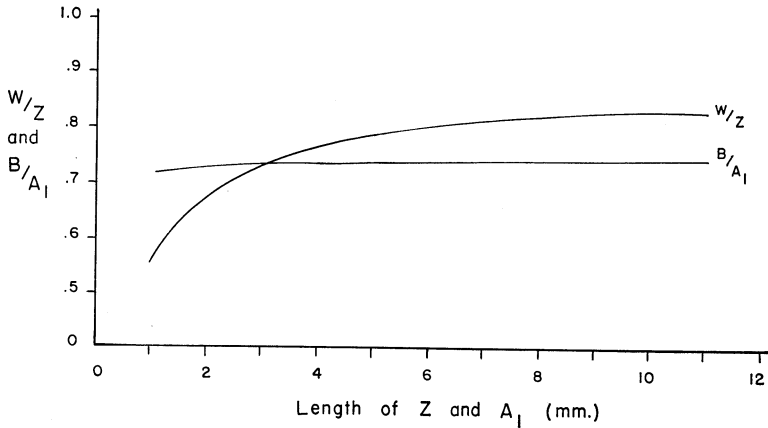

FIG. 8. Graph showing relatively great change in the ratio W/Z for values of Z less than about 5 mm. and relatively constant values for the ratio B/A_1 for all values of A_1 for cranidia and pygidia of *A. sangamonensis*.

and are useful taxonomic criteria in the identification of cranidia of all sizes.

The ratio J/A_1 varies significantly among small specimens but is relatively constant for specimens in which A_1 is greater than about 4 mm. (Fig. 9A).

Although the value of *a* for the Z-W paired dimensions appears relatively large (Table 2), study of the change in the W/Z ratio (Fig. 8) during development indicates that even this ratio has taxonomic significance for pygidia longer than about 5mm. Thus, on the basis of the present investigation it appears as though the ratios between all the paired dimensions of cranidia, free cheeks, and pygidia of *A. sangamonensis* are useful taxonomic criteria in the identification of large specimens.

QUALITATIVE MORPHOLOGY

In addition to the quantitative aspects of morphology and development described above, there are some features of the dorsal carapace of *A. sangamonensis* that are not amenable to measurement and so must be qualitatively described.
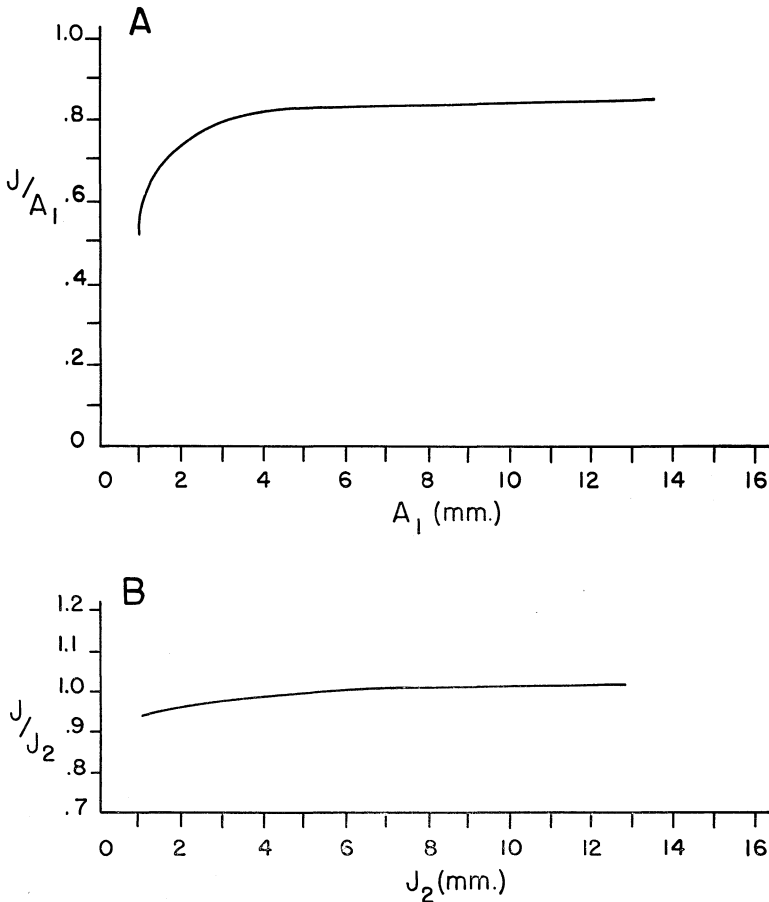
Fig. 9. *Ameura sangamonensis* (Meek and Worthen). 9A. Graph showing relatively great change in ratio J/A_1 for values of A_1 less than about 4mm. 9B. Graph showing relatively constant values for the ratio J/J_2 for all values of J_2.

The prominence of the glabellar furrows is highly variable and independent of the size or convexity of the glabella. In some specimens the glabellar furrows are deeply incised whereas in others the furrows are shallow and broad or entirely absent. The ventral surfaces of some glabellae are furrowed and yet the dorsal surfaces of the same specimens are smooth.

An important qualitative aspect of the pygidium is the progressive decrease in the prominence of the border from early to late molt stages. On small specimens the border is well-defined whereas on larger specimens the border becomes increasingly indistinct (see Fig. 10).
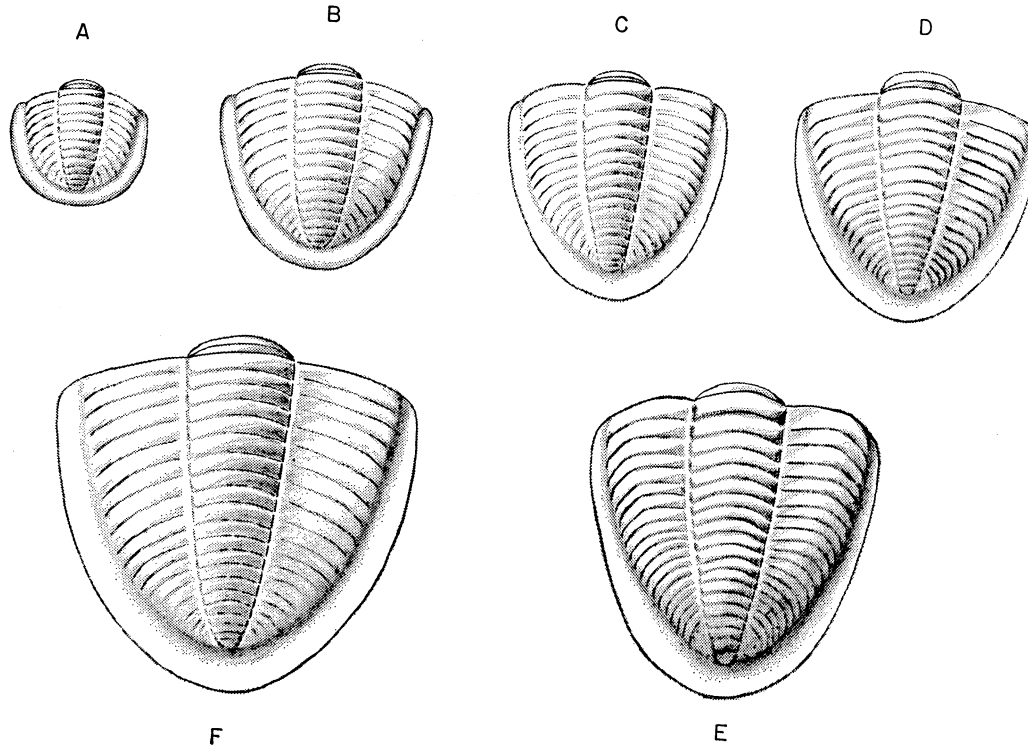
FIG. 10. *Ameura sangamonensis* (Meek and Worthen). A sequence of pygidia showing changes in morphology during ontogeny. The most significant changes are: (1) decreasing prominence of the pygidial border due largely to a merging of the inner margin of the border with the outer margin of the pleural lobes, (2) increasing width of the posterior portion of the pygidial border in relation to the posterolateral and anterolateral portions, and (3) a progressive change in the outline of the pygidium from smoothly rounded lateral and posterior margins in very small individuals to a subtriangular to subparabolic outline in large individuals. Fig. 10A, UNSM 5202, X 10; fig. 10B, UNSM 5203, X 10; fig. 10C, UNSM 5204, X 10; fig. 10D, UNSM 5205, X 5; fig. 10E, UNSM 5206, X 5; fig. 10F, UNSM 5207, X 5.

SYSTEMATIC DESCRIPTION

Phylum Arthropoda
Class Trilobita
Order Ptychopariida
Suborder Illanenina
Superfamily Proetacea
Family Phillipsiidae, Oehlert, 1886

Genus *Ameura* Weller, 1936, p. 713–714

Type species.—Phillipsia sangamonensis Meek and Worthen, 1865, p. 271–272. *Other species included.—Phillipsia major* and *P. missouriensis* Shumard, 1858. *Diagnosis.—*See Harrington, H. J., *et al.*, 1959, p. 0401, fig. 308.

Remarks. The Pennsylvanian rocks in eastern Nebraska contain specimens of two rather similar genera of phillipsiid trilobites: *Ameura* and *Ditomopyge.* Cranidia can be easily distinguished by the presence of a median preoccipital lobe in *Ditomopyge.* However, isolated holaspid pygidia are somewhat more difficult to separate. Generally, the pygidial border in *Ameura* becomes progressively broader posteriorly whereas the border in *Ditomopyge* is of relatively uniform width around the entire margin. In addition, the axial lobe in *Ditomopyge* is broad and flattened on top (Harrington, *et al.*, 1959, p. 0401).

In our experience in eastern Nebraska, species of these two phillipsiid genera do not normally occur together (Fagerstrom, 1964, p. 1198). Thus, at the Cedar Creek locality no specimens of *Ditomopyge* were collected from the Bonner Springs Shale during the present investigation.

Ameura sangamonensis (Meek and Worthen)

Phillipsia sangamonensis, Meek and Worthen, 1865, p. 271–272.
Ameura sangamonensis, Weller, 1936, p. 713–714; Shimer and Shrock, 1944, pl. 275, figs. 25–27.

Revised description. Frontal area of cranidium crescentic, extending posteriorly to merge with narrow fixed cheeks. Palpebral cranidial width and maximum width of frontal area approximately equal ($J/J_2 \cong 1.0$); palpebral lobes crescentic. Glabella widest between palpebral lobes; glabella oblate and highly inflated, rising sharply from frontal area and reaching its maximum height at position of maximum width of frontal area. Total glabellar length approximately $\frac{3}{4}$ total cranidial length ($B/A_1 \cong 0.75$) and approximately $\frac{4}{5}$ occipital intra-marginal cephalic length ($B/A_2 \cong 0.8$). Glabella may be smooth or contain as many as four pairs of glabellar furrows; glabellar furrows vary considerably in depth and prominence. Occipital lobes nearly oval and located between occipital

ring and palpebral lobes. Occipital furrow deep and narrow. Occipital ring wide. Median pre-occipital lobe absent. Maximum width of frontal area and palpebral cranidial width about $4/5$ total cranidial length ($J_2/A_1 \cong 0.8$; $J/A_1 \cong 0.8$) on specimens where total cranidial length is greater than about 4 mm. Ornamentation absent. No apparent muscle scars on ventral surface of cranidium.

Free cheeks nearly flat toward anterior and lateral margins, rising sharply at the multifaceted eye and tapering posteriorly to a narrow, elongate, genal spine which terminates at the sixth or seventh thoracic segment. In some specimens there is a hook-shaped depression behind the eye that points posteriorly.

Thorax with nine articulating segments. Muscle scars apparently absent from ventral surface and ornamentation absent from dorsal surface.

Pygidium subtriangular to subparabolic. Maximum pygidial length slightly greater than total pygidial width ($W/Z \cong 0.85$) where total pygidial length is greater than about 5 mm. Pygidial border well-defined on small specimens, becoming progressively less well-defined on larger ones. Pleural lobes rise sharply (about 45°) from the pygidial margin and then level off sharply toward the axial lobe. Axial lobe wide and highly arched. Pleural lobes with 11 to 18 segments; axial lobe with 14 to 23 segments. Intra-articulating rhachis length about 9/10 total pygidial length ($Y_1/Z \cong 0.9$). Ornamentation absent. Pygidial doublure prominent, moderately thickened. Muscle scars variably developed; arranged in a single row on each side of the plane of symmetry inside the lateral margins of the axial lobe with one pair of scars per segment.

Remarks. Previous workers (Weller, 1936, p. 714; Whittington, 1954, p. 6; Chamberlain, 1964, p. 234) have described the glabella as widest between the eyes. Such conclusions are probably based upon visual estimation because the boundary between the glabella and the palpebral lobes is not always sharp and well-defined and so the width of the glabella at this position cannot always be measured with consistent results. Nonetheless, we agree with these authors that in most specimens the glabella appears widest between the palpebral lobes. However, measurements of the maximum width of the frontal area (J_2) and of the palpebral cranidial width (J) are consistently reproducible and also are nearly equal ($J_2 \cong J$). Therefore, these features of cranidial morphology appear to be more satisfactory taxonomic criteria than the position of maximum glabellar width.

References

Condra, G. E., and Reed, E. C., 1959. The geological section of Nebraska. *Neb. Geol. Surv.*, 14A, 82p.

Chamberlain, C. K., 1964. A preliminary study of Upper Paleozoic trilobites of central Utah. *The Compass* 41, 227–239.

Fagerstrom, J. A., 1965. Fossil communities in paleoecology: their recognition and significance. *Bull. Geol. Soc. Amer.* 75, 1197–1216.

—————, and Boellstorff, John D., 1964. Taxonomic criteria in the classification of the Pennsylvanian productoid *Juresania nebrascensis. Palaeontology* 7, 23–28, pl. 2.

Harrington, H. J. *et al.* 1959. Trilobita. *Treatise on Invertebrate Paleontology.* Univ. Kansas Press and Geol. Soc. America, pt. 0: 028–0540.

Hunt, A. S., 1967. Growth, variation, and instar development of an agnostid trilobite. *J. Paleont.* 41, 203–208, pl. 22.

Meek, F. B. and Worthen, A. H., 1865. Contributions to the paleontology of Illinois and other western states. *Proc. Acad. Nat. Sci. Philadelphia*, 245–273.

Robison, R. A., 1967. Ontogeny of *Bathyuriscus fimbriatus* and its bearing on affinities of corynexochid trilobites. *J. Paleont.*, 41, 213–221, 1 pl. 24.

Shaw, Alan B., 1956. Quantitative trilobite studies I. The statistical description of trilobites. *J. Paleont.* 30, 1209–1224.

—————. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. Ibid. 31, 193–207.

Shimer, H. W. and Shrock, R. R., 1944. *Index fossils of North America.* John Wiley and Sons, New York: 1–837, 303 pls.

Shumard, B. F., 1858. *in* Shumard, B. F. and Swallow, G. C. Descriptions of new fossils from the Coal Measures of Missouri and Kansas. *Trans. Acad. Sci. St. Louis*, 1, 198–227.

Simpson, G. G., Roe, A., and Lewontin, R. 1960. *Quantitative zoology*, 1–440. New York. Revised ed.

Weller, J. Marvin. 1935. Adolescent development of *Ditomopyge. J. Paleont.* 9, 503–513.

—————. 1936. Carboniferous trilobite genera. Ibid. 10, 704–714.

Whittington, Harry B., 1954. Two silicified Carboniferous trilobites from west Texas. *Smithsonian Misc. Coll.* 122 (10), 1–16, 3 pls.

—————. 1957. The ontogeny of trilobites. *Biol. Reviews* 32, 421–469.

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