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PALEOBIOGEOGRAPHIC PATTERNS IN LATE MISSISSIPPIAN TRILOBITES OF THE UNITED STATES
WITH NEW SPECIES FROM MONTANA

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ABSTRACT

Two new species of trilobites, *Weberides chamberlaini* new species and *Weberides samwaysi* new species, are described from the Heath Formation (Serpukhovian, Mississippian) of Montana. Based upon phylogenetic analysis, the assignment of these species to the genus *Weberides* represents the first recognition of this genus in North America. Brooks Parsimony Analysis of the single phylogenetic tree suggests that the northern Cordillera acted as an ancestral area for the typically European genus *Weberides*. Thus, the North American vicariants of *Weberides* share a common ancestral area with the genus *Paladin*. Vicariance patterns suggest that interchange with the type *Weberides* areas of Europe was through the northern Cordilleran region rather than through the Rheic Ocean, as others have suggested.

KEY WORDS: Mississippian, trilobites, biogeography, evolution

INTRODUCTION

Brezinski (2003) demonstrated, through phylogenetic analysis, that the previous definition of the Carboniferous and Permian trilobite genus *Paladin* consists of no less than four distinct clades that represent separate genera. The species comprising Brezinski's Clade A are restricted to the interior area of the United States and were reassigned to *Kaskia* Weller. A second clade is distributed through the southern and western United States, includes the type species, *Paladin morrowensis* (Mather 1915), and conforms to the diagnosis of *Paladin* Weller. Clade C consists of Early Carboniferous species restricted to western and eastern Europe and was reassigned to the genus *Weberides* Reed. Finally, Clade D consists of Late Carboniferous species from the Ukraine, western Russia, and Spitsbergen and were referable to a yet unnamed genus. Brooks Parsimony Analysis (Wiley 1988) of the most parsimonious tree defining Brezinski's four clades delineated four geographically separate sister groups that paralleled the generic assignments.

Three late Mississippian trilobite clades (A, B, and C) existed during Brezinski's (1999) Stage 2 of North American late Paleozoic trilobites. While as many as fifty genera are known from this time interval worldwide, all previously recognized North American late Mississippian trilobite species belong to the genera *Paladin* or *Kaskia*. However, discernment of two new trilobites from the Heath Formation of Montana calls into question this assertion because they do not conform to either *Kaskia* or *Paladin*. The purposes of this paper are to describe and illustrate two new Montana trilobite species, to evaluate their phylogenetic position, and to compare them to contemporary species from the central and eastern United States.

The two new species from Montana are very similar to specimens that Chamberlain (1969) illustrated and

assigned to *Paladin* (i.e., *Kaskia*) *chesterensis* (Weller 1936), and *Paladin mucronatus* (Girty) (i.e., *P. girtyianus*, Hahn and Hahn 1970). Chamberlain's specimens were recovered from the upper Great Blue Limestone and Manning Canyon Shale of Utah and appear to be contemporaneous with the Montana material. The Utah material is interpreted to be the same species as those from Montana. This suggests that these two species were relatively widespread throughout the northern Cordillera during the late Mississippian.

COLLECTION LOCATIONS

The trilobites described herein were recovered from three localities of the Heath Formation (late Mississippian) of central and southwestern Montana (Fig. 1). Locality 1 is in the Little Snowy Mountains of Fergus County, Montana (Carnegie Museum Sampling Locality 6130) and was collected by the author and A.D. Kollar in 2001. The stratigraphic section exposed at this locality is illustrated in Figure 2. The section is present along Hamilton Creek Road, section 24, T14N, R19E, Heath Quadrangle. Locality 3 is in the Tendoy Mountains of Beaverhead County, in southwestern Montana (Carnegie Museum Sampling Locality 579). This locality is within the Whiskey Spring 7.5 minute quadrangle (NE 1/4, Section 23, T12S, R6W). Locality 2 is within the Little Snowy Mountains of Fergus County of central Montana (Carnegie Museum Sampling Locality 576). This locality is within the Becket 7.5 minute quadrangle at NW 1/4, NW 1/4, Section 29, T14N, R22E. Both Localities 2 and 3 were collected by Dr. Richard Lund and Bryan Snyder in 1984.

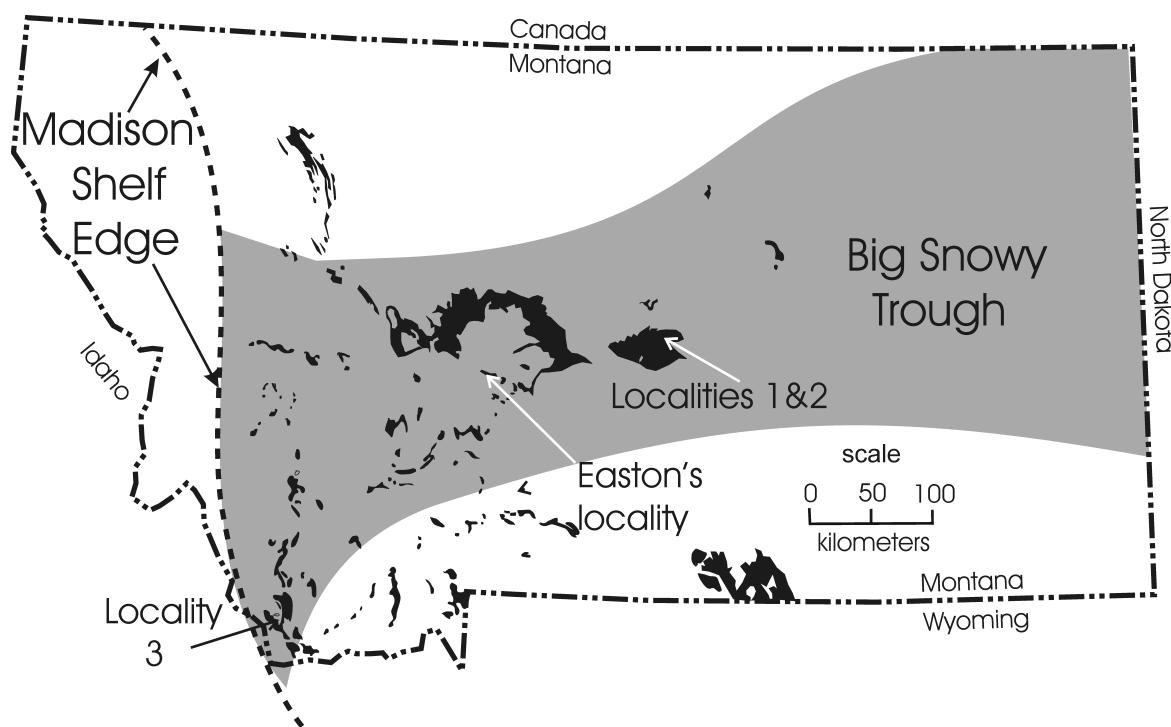


Fig. 1.—Distribution of outcrops of Carboniferous rocks (black) in Montana with location of trilobite localities and their distribution with respect to paleoenvironmental features such as the Big Snowy Trough, and the edge of the Madison Shelf (from Smith and Gilmore 1979).

STRATIGRAPHY OF MONTANA TRILOBITES

The Heath Formation is a Serpukhovian (late Chesterian, Lower Carboniferous) deposit that was formed along the edge of the Madison Shelf of western Montana and within the Big Snowy Trough of central Montana. The Big Snowy Trough was a deep marine embayment that connected the Williston Basin of eastern Montana with the main Madison Shelf in the western part of the state (Rose 1976). The Heath Formation accumulated during foraminifera biozone 18 of Mamet's biostratigraphic scheme (see Sando 1984, fig. 3). This indicates that the Heath was deposited during the very latest Chesterian (Serpukovian) (Smith and Gilmour 1979; Sando and Bamber 1985).

The Heath Formation of the Big Snowy Group is important because it represents some of the youngest Mississippian strata known from North America. A worldwide drop in sea level during the late Mississippian left extensive areas of North America either subaerially exposed or relegated to nonmarine deposition. The sparse marine deposits of this age are preserved only within basinal deposits or at the very margins of the ancestral North American continent. This worldwide sea level drop was the result of the beginning of Late Carboniferous continental glaciation (Saunders and Ramsbottom 1986; Stanley and Powell 2004).

At Localities 1 and 2 the Heath Formation was deposit-

ed along the margin of the Big Snowy Trough, and consists of interbedded, dark gray, fossiliferous limestone and dark gray unfossiliferous, nonmarine shale (Fig. 2). This interval was deposited during repeated and incremental deepening episodes of a coastal onlap sequence. Based on the progressive increases up section in faunal content and relative faunal diversity, each succeeding marine layer appears to represent a more open marine environment. The onlap sequence appears to demonstrate that the maximum period of deepening occurred during the deposition of the thicker limestone units at the top of the section (Figure 2). Thus, the trilobites collected from these localities appear to have lived under normal marine conditions, but within a relatively nearshore milieu.

The specimens from locality 3 and conspecific material from Utah were preserved in a very different geological setting. Locality 3 consists of well over 100 m of discontinuously exposed very dark gray, thinly bedded, fine-grained limestone with black shaly partings. The limestone strata emit a petroliferous odor when broken. The fauna consists primarily of thin-shelled bivalves and diminutive brachiopods. Strata at this location appear to have been deposited in discernibly deeper, more oxygen deficient environments of deposition than those in central Montana. Consequently, these specimens appear to have lived very near the edge of the late Mississippian shelf (= Madison Shelf of Gutshick and Sandberg, 1983). Farther to the west

coeval rocks were deposited in very deep waters of the Deseret Basin (Rose 1976; Gutschick et al. 1980; Gutshick and Sandberg 1983). The age of the Utah material is consistent with the Montana forms described herein (Sando and Bamber 1985, fig 10).

LATE MISSISSIPPIAN SISTER GROUPS

Morphologic attributes, such as a forwardly expanding glabella, posteriorly located palpebral lobes, broad anterior border, and bordered pygidium, epitomize middle to late Mississippian trilobites. Several contemporary genera such as *Particeps*, *Eocyphyinium*, *Exochops*, *Kaskia*, and *Weberides* display these characters, but none so well as the genus *Paladin*. Weller (1936) erected the genus *Paladin* based on *Griffithides morrowensis* Mather 1915 from northern Arkansas. Whittington (1954) interpreted the similar but varying morphological differences between *Kaskia* and *Paladin* as a gradation and chose to consider *Kaskia* a subgenus of *Paladin*. Furthermore, he considered the European genus *Weberides* Reed (1942) to be a synonym of *Paladin*. Cisne (1967) considered *Kaskia* and *Paladin* to be congeneric; Hahn and Hahn (1970) and Osmolska (1970) subsequently followed by making *Kaskia* and *Weberides* junior synonyms of *Paladin*. As a result, *Paladin*, by virtue of priority and these synonymies, became a broad taxon into which all similar forms were placed. Recently, Brezinski (2003) demonstrated by phylogenetic analysis that the junior synonyms *Kaskia* and *Weberides* were sister groups of sufficient geographic restriction and morphological distinctness to also be considered genera. These sister groups, like *Paladin*, were interpreted as having common ancestry with the early Mississippian genus *Thigriphides* Hessler. Herein the Montana and Utah species are added to Brezinski's (1999) phylogenetic analysis in an effort to determine the relationship of these species to *Paladin* and *Kaskia*.

PHYLOGENETIC ANALYSIS

Brezinski (2003) included several species from Late Carboniferous strata in his phylogenetic analysis (e.g., *Paladin lutugeni* [Weber 1933], *P. cervilatus* [Weber 1933], and *P. trigonopyge* [Osmolska 1968]). These non-contemporary species were excluded from the current study so as to focus on the Late Mississippian sister groups only. One of the goals of the current phylogenetic examinations is to evaluate late Mississippian vicariance and dispersal patterns. This necessitates nearly contemporary occurrences. Consequently, with the inclusion of the Montana species, an ingroup of 18 species was analyzed in this current study. *Thigriphides roundyi* (Girty 1926) was used as the outgroup for the reasons documented in Brezinski (2003). Species were compared utilizing the following 25 morphological characters.

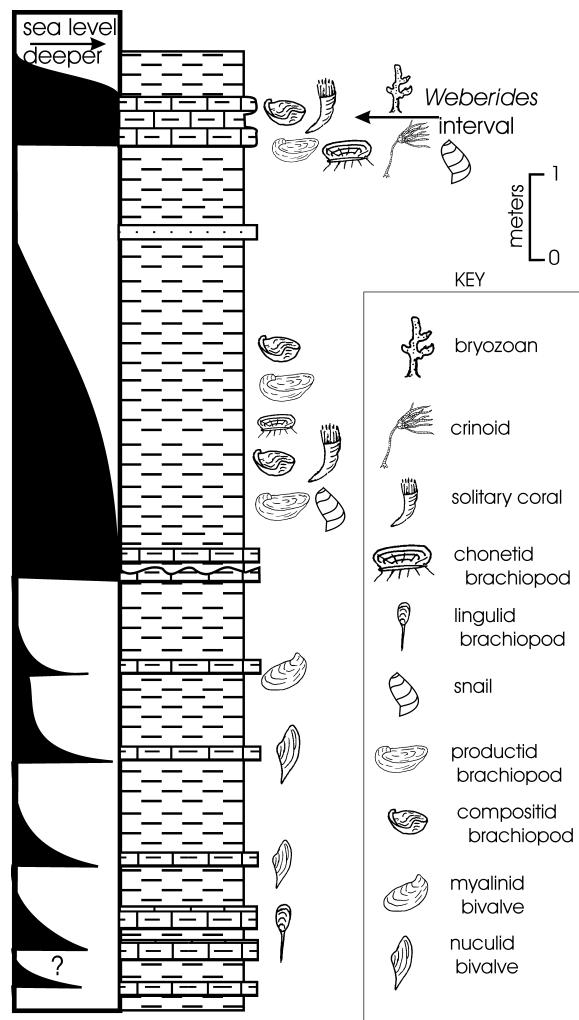


Fig. 2.—Measured stratigraphic section and faunal distribution of the Heath Formation at Locality 1 (CM locality 6130). Interbedding within the section reflects iterative late Mississippian deepening along the edge of the Big Snowy Trough. Relative increases up stratigraphic section appear to reflect the progressive character of individual deepening episodes.

Character 1.—Anterior border is distinct and wide (0), narrow but distinct (1), or indistinct so that it is continuous with the anterior part of the frontal lobe (2).

Character 2.—The anterior border furrow is shallow and distinct (0), or absent (1).

Character 3.—The rear of the glabella is straight at the occipital furrow and forms the subrectangular base (0), base is slightly rounded (1), or base is distinctly rounded (2).

Character 4.—The midline of the palpebral lobes is located very far to the posterior of the cranidium, usually located much less than 0.35 the total cranidial length, (0) the

palpebral lobes are located to the anterior at greater than 0.35 the total cranidial length(1).

Character 5.—The outline of the palpebral lobes is wide and semicircular (0), medium crescents (1), or very narrow and broad arches (2).

Character 6.—The S1 glabellar furrow is shallow to indistinct (0), or deeply incised and narrow (1).

Character 7.—The lateral cephalic border furrow is distinct, deep, with a sharp outer margin (0), or broad, shallow, and rounded into the margin (1).

Character 8.—The occipital furrow is narrow and deeply incised in longitudinal profile (0), or broadly V-shaped in longitudinal profile (1).

Character 9.—The L2 and L3 glabellar furrows are absent (0), or present (1).

Character 10.—The posterior facial sutures are very short and curved (0), possess a short straight section (1), or have a long straight section (2).

Character 11.—The shape of the L1 (basal) lobe is suboval (0), or subtriangular (1).

Character 12.—The positions of the rear of the L1 lobes, with respect to the posterior end of the glabella, are even (0), or hang into the occipital furrow behind the rear end of the base of the glabella, giving the occipital furrow a sinuous trace (1).

Character 13.—The trace of the S1 glabellar furrow is diagonal and straight (0), or arched, curved, or obtusely angular (1).

Character 14.—The width of the pygidial axis is less than or equal to 0.33 of the maximum pygidial width (0), or is greater than 0.33 of the pygidial width (1).

Character 15.—The pleural furrows are distinct along the entire length (0), or the furrows shallow towards the margin, and to the posterior are very narrow to poorly defined (1).

Character 16.—Interpleural furrows are present on all but the most posterior two or three ribs (0), or interpleural furrows are present on only the two or three anteriormost ribs (1).

Character 17.—The posterior terminus of the pygidial axis is bluntly rounded (0), or acutely rounded with faint tapering extension (1).

Character 18.—Outline of the pygidium is parabolic (0), semielliptical (1), or subtriangular (2).

Character 19.—The pygidial border is of even width around entire pygidium (0), is slightly wider behind the axis (1), or is distinctly widened behind the axis (2).

Character 20.—The transverse profile of the pleural fields is strongly arched (0), or has a low to moderate convexity (1).

Character 21.—The slope of the pygidial border, when examined in transverse profile, slopes at a gentler angle than the abaxial part of the pleural ribs (0), is the same as the pleural ribs, forming a continuous slope (1), or is flange-like, nearly horizontal at the end of the pleural fields, and nearly vertical at the margin (2).

Character 22.—The L1 (basal lobe) is depressed in height relative to the adjacent posterior part of the glabella (0), or is inflated so that it is of about the same height as the rear of the glabella (1).

Character 23.—The transverse profile of the pygidial axis is broadly rounded to semicircular (0), or is flattened on top, giving it a subtrapezoidal profile (1).

Character 24.—The width of the cranidium between the palpebral lobes (Δ) is greater than the width at maximum divergence of the anterior facial sutures (β) (0), or the cranidial width between the maximum divergence of the anterior facial sutures (β) is greater than the palpebral width (Δ) (1).

Character 25.—The shape of the anterior facial sutures at the point of maximum divergence (β) is broadly rounded (0), or is sharply rounded (1).

The 18 ingroup taxa were evaluated using the beta version of PAUP 4.0 employing a heuristic search command with simple step-wise addition and 100 random replications. All characters were unordered, of equal weight, and parsimony informative. The analysis produced a single most parsimonious tree (Fig. 3) with a length of 58 steps, a consistency index of 0.52, and a retention index (RI) of 0.81.

The topology of the tree is similar to the most parsimonious tree defined by Brezinski (2003, text fig. 2). While clades A (*Kaskia*) and B (*Paladin*) are identical, the exclusion of the three Late Carboniferous species and the addition of the two Montana species produced a Clade C (*Weberides* clade) with a slightly different topology than that of the earlier study. Clade C of this study comprises a branch made up of the polytomous species *W. mucronatus* (McCoy), *W. eichwaldi* (Fischer v. Waldheim), *W. czarnieckii* (Osmolska), and *W. chamberlaini* new species; a branch made up of *W. cuspidatus* (Reed), *W. samwaysi*

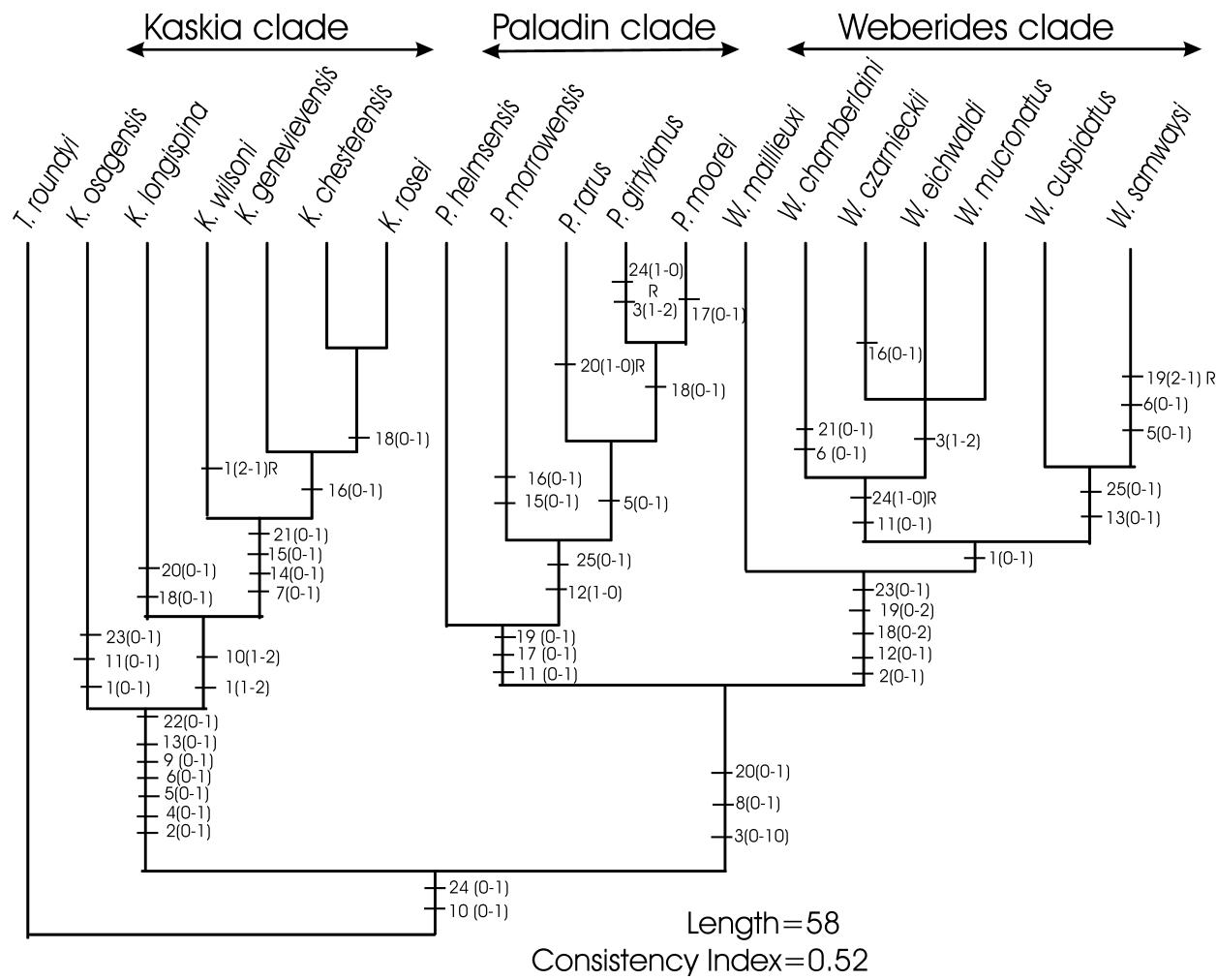


Fig. 3.—Single most parsimonious tree determined by a heuristic search using Paup 4.0. Sister groups are interpreted to represent the genera *Kaskia* Weller, *Paladin* Weller (*sensu strictum*), and *Weberides* Reed. Tree length is 58 steps with a consistency index of 0.53.

new species, and a sister taxon, *W. mailleuxi* (Demanet). The new branch topology is consistent with suggestions by Brezinski (2003) that the clade C of that study may represent more than one taxonomic group (i.e., genus). The possibility of multiple taxonomic groups is indicated on the current tree by the separation of the type species of *Weberides* (branch composed of *W. mucronatus* [McCoy] *W. eichwaldi* [Fischer v. Waldheim], *W. czarnieckii* [Osmolska], and *W. chamberlaini* new species), and a second group composed of *W. cuspidatus* (Reed) and *W. samwaysi* new species. While it is beyond the scope of the current study to determine the validity of separating these seven species into two or even three genera, two conclusions can be forwarded. Firstly, *W. chamberlaini* new species has a close common ancestry with the true *Weberides* (polytomous branch) of Europe, and should be

maintained within that genus. Secondly, *W. mailleuxi*, *W. cuspidatus*, and *W. samwaysi* may ultimately not be referable to *Weberides*, but further comparison of the relationship of these taxa with other European congenitors is necessary.

Paleobiogeographic Analysis

The North American species of *Weberides* were examined for paleobiogeographic affinities utilizing the phylogenetic tree illustrated in Figure 3. This analysis employed procedures to determine whether either vicariance or geodispersal had the dominant paleobiogeographic effect on producing the currently recognized distribution of species. To determine if vicariance played a significant role in the dis-

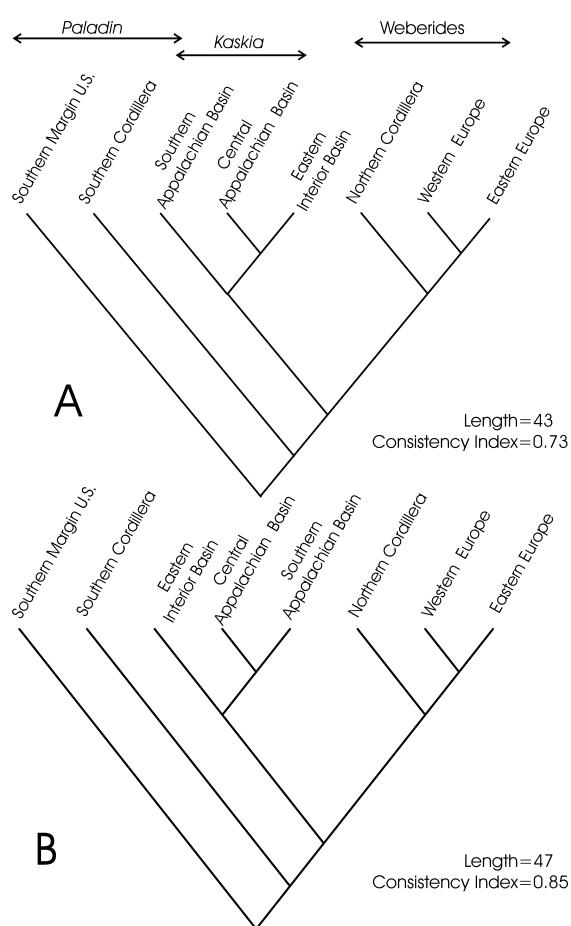


Fig. 4.—Single most parsimonious area trees retrieved from an exhaustive search of PAUP 4.0 and employing Brooks Parsimony Analysis (A) for vicariance analysis (A) and geodispersal analysis (Lieberman 2000) (B), and based on phylogenetic tree illustrated in Figure 2.

tribution of species of these three clades, Brooks Parsimony Analysis was utilized (Wiley 1988). Further, in an effort to delineate possible species dispersal patterns, geodispersal analysis was also conducted (Lieberman and Eldredge 1996; Lieberman 2000).

Eight areas were delineated for the paleobiogeographic analysis. For both of these procedures the ancestral geographic area was considered to be the area inhabited by the putative ancestor *Thigriphides roundyi*. This area extends from eastern Texas to southern Illinois. During the early Mississippian this region represented a suite of deep-water environments that bordered the southern margin of the North American continental shelf (Brezinski 1998). This area, later in the Mississippian, was to be the site inhabited by most of the currently recognized species of the *Paladin* clade. Species of *Paladin* extended outside of the ancestral area into southern New Mexico and western

Wyoming to the west and southern West Virginia to the east. A second group of species belonging to the *Kaskia* clade contemporaneously inhabited the Eastern Interior Basin (Illinois, Michigan, and Iowa). A small contingent of these species is also known from the semi-isolated central Appalachian Basin (eastern Ohio, Pennsylvania, and Maryland) (Brezinski 1988). Whereas, in the southern Appalachians (Alabama to southern Virginia) the *Kaskia* and *Paladin* clades appear to overlap. Species of *Weberides* are well known from western Europe (England, Belgium, France, and Spain) and eastern Europe (Poland and Russia). During the late Mississippian these two areas of Europe were separated by the Variscan orogenic belt (Brezinski 2003, text fig. 4).

The vicariance and geodispersal analysis conducted on the phylogenetic tree produced two area trees that are quite similar in topology (Figure 4). The single most parsimonious vicariance tree is 43 steps in length with a consistency index 0.73. The geodispersal analysis produced a slightly longer single most parsimonious tree of 47 steps with a consistency index of 0.77. Both analyses were conducted using the exhaustive search command in PAUP 4.0.

Paleobiogeographic Implications

The two area cladograms exhibit distinct similarities as well as differences. There are distinctly similar branches separating the *Kaskia* and *Weberides* areas. This may indicate that the factors controlling the origin of these clades acted early in their evolutionary history of each individual clade allowing them to develop, through time, as distinct monophyletic groups. As a result each of these monophyletic groups dispersed into and evolved within separate geographic areas. The earliest recognized representative of the *Kaskia* clade is known from Osagean strata (early Viséan), while the earliest member of *Weberides* is late Chesterian (late Viséan). While both area trees demonstrate the distinctness of the area inhabited by the *Kaskia* clade, the vicariance tree suggests that the clade's ancestry is within the southern Appalachian Basin, while the geodispersal tree suggests an ancestral area in the Eastern Interior Basin. The known stratigraphic record exhibits a greater level of congruence with this latter interpretation. Furthermore, both trees indicate that the *Weberides* clade's ancestral area is within western North America. The stratigraphic record for this geographic region is less well known than that in the eastern United States, however, there is no incongruence with the currently recognized species ranges, and geographic distribution. Neither tree exhibits a more robust congruence with the stratigraphic distribution of species than the other. However, both trees tend to suggest that either by vicariance or geodispersal means the ancestral stocks of the European species of *Weberides* may have arrived in Europe by way of Alaska, the Canadian Arctic, and Spitsbergen rather than through

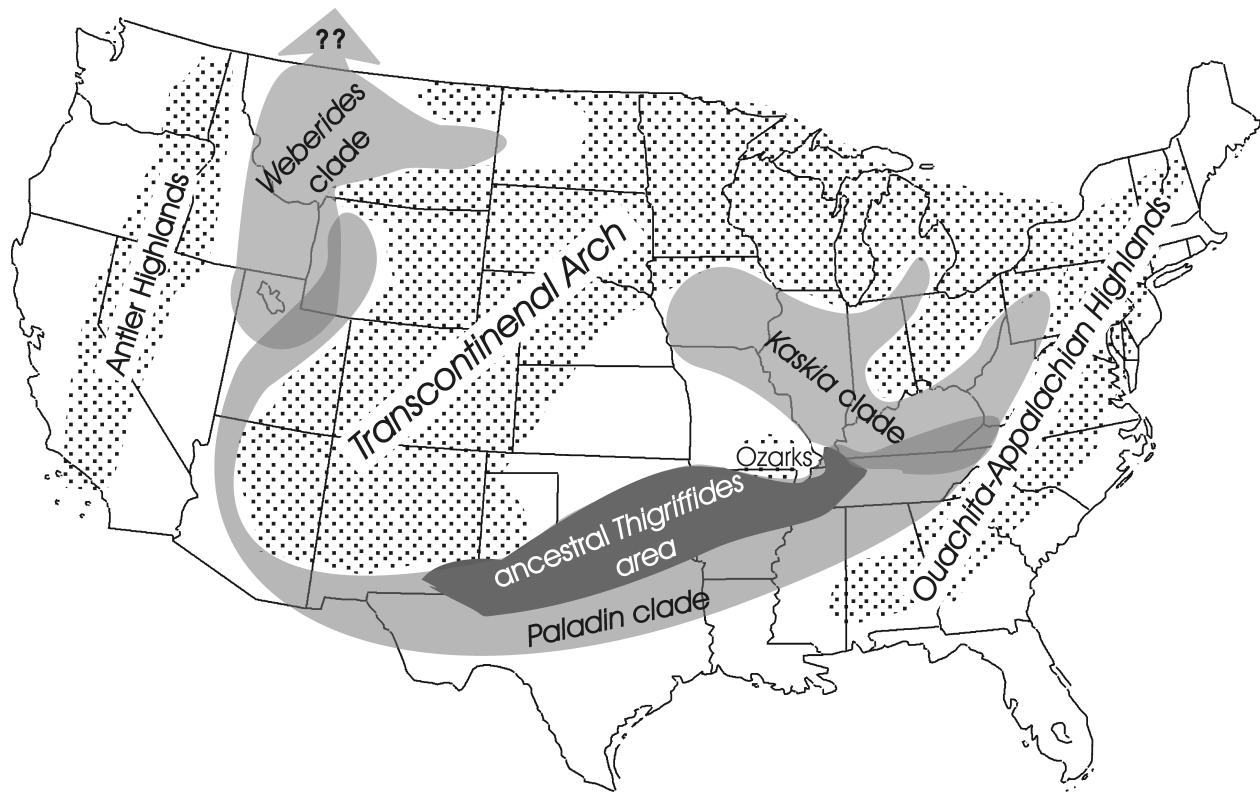


Fig. 5.—Paleobiogeographic map of the late Mississippian (late Visean-Serpukovian) trilobite clades of the United States. Map illustrates the distribution of the *Kaskia-Paladin-Weberides* sister groups and their relative areas of habitation with respect to the ancestral area of *Thigriphides*. Sympatric areas are may be interpreted to represent possible areas of barrier creation or removal for species interchange.

the subequatorial Rheic Ocean (Owens and Hahn 1993; Brezinski 2003, text fig. 4).

That both trees display closely related topologies indicates that neither vicariance nor dispersal forces had a greater influence on the evolution of these groups (Lieberman 2000). Thus, it appears that the geologic conditions producing this paleobiogeographic pattern may have been created by alternations of vicariance and geo-dispersal. This could have been accomplished by cyclical factors that repeatedly alternated the creation and destruction of geographic barriers. Interestingly, the Late Mississippian is characterized by the onset of cyclothemtic sedimentation that typifies all of the Late Carboniferous (Smith and Read 2000). This type of sedimentation is indicative of periods of rapid sea level change resulting from the waxing and waning of continental glaciers. Consequently, the evolution of the *Kaskia*, *Paladin* and *Weberides* clades took place during a period in Earth's history when sea level fluctuated rapidly and repeatedly. These iterative sea level changes would have allowed episodes of vicariance during periods of glacial advance and sea level lowering and geodispersal during periods of retreating ice and sea level rise. Even minor topographic features could have been substantial geographic barriers

with such a rapidly fluctuating global sea level. Indeed, the Cincinnati Arch is strategically located near the southern end of the Illinois and Appalachian basins. This low-lying feature was probably exposed during periods of sea level drop, while readily submerged during sea level rise (Ettenson 1980; McKinney and Gault 1980). Thus, the biogeographic patterns observed between the ancestral area, that inhabited by species of *Paladin*, and that inhabited by *Kaskia* can be explained by the repeated submergence and emergence of this geographic feature (Figure 5). Furthermore, a similar scenario can be employed in the northern Cordillera where repeated sea level fluctuations could have repeatedly isolated and flooded the Big Snowy Trough and the Williston Basin (Rose 1976).

SYSTEMATIC PALEONTOLOGY
 Class Trilobita, Walch, 1771
 Order Proetida, Fortey and Owens, 1975
 Family Phillipsiidae, Oehlert, 1886
 Genus *Weberides* Reed, 1942

Revised Diagnosis.—*Gabella* long, rounded to subrounded at base; L1 small, depressed, anterior border furrow

absent in larger holaspids; cranidium wider at α than at β ; pygidium triangular with posterior border broader than lateral border; pleural furrows present on all but most posterior ribs.

Remarks.—Based on phylogenetic analysis of late Mississippian species of *Paladin* Weller, Brezinski (2003) resurrected the genus *Weberides* Reed. *Weberides* comprised a clade of five European species: *W. mucronatus* (McCoy 1844), *W. cuspidatus* Reed, 1942, *W. maillieuxi* (Demanet 1938), *W. czarnieckii* (Osmolska 1970), and *W. eichwaldi* (Fisher v. Waldheim, 1825). Brezinski (2003) found an unresolved polytomy created by *W. eichwaldi*, *W. mucronatus*, and *W. czarnieckii* and suggested these three species represented a separate clade from the other two species, *W. cuspidatus* and *W. maillieuxi*; these two clades may represent two genera. The analysis presented here tends to verify those inferences. The current study suggests that the polytomous species are sister species to *W. chamberlaini* new species, while *W. samwaysi* new species is the sister species with *W. cuspidatus* Reed, 1942. Phylogenetic study of European species currently assigned to *Paladin* is needed to determine whether they are indeed assignable to that genus or possibly representatives of *Weberides*. Recent studies demonstrate the breadth of characters displayed by some of these taxa (Tilsley and Owens 2003). It is highly likely that several genera would be delineated by such examination.

Weberides chamberlaini new species Figure 6A–6N

Paladin chesterensis (Weller): Chamberlain, 1969:51–54, plate 11, figs. 26, 27, 31, 35, 36 [misassigned]

Type Material.—Holotype, a nearly complete, testate cranidium from the Heath Formation, Fergus County, Montana, CM Locality 6130, CM 53200. Paratypes, four nearly complete cranidia CM 53201–53204, from the same location as the holotype; two complete testate, and partial testate pygidia CM 53205–53207, one partial librigena, CM 53208, all from same location as the holotype.

Other Material.—A cranidium and librigenae, BYU 1198, 1199 illustrated by Chamberlain (1969).

Etymology.—Named in honor of C. Kent Chamberlain, first monographer of Cordilleran Carboniferous trilobites.

Diagnosis.—Palpebral lobes posterior position; S1 narrow, deep; base of glabella rounded in smaller individuals, becoming straightened in larger holaspids. Pygidium lanceolate.

Description.—Cranidium pyriform in outline, low in vaulting in smaller holaspids, becoming mildly arched lon-

gitudinally in larger holaspids. Longitudinal and transverse arching low. Frontal glabellar lobe evenly rounded in front, rounded at base in smaller holaspids, straight in larger individuals, covered with fine granular prosopon. Anterior border narrow, rounded; border furrow narrow, shallow in smaller holaspids, faint to indistinct in larger specimens. Dorsal furrow sinuous, shallow, broadest between palpebral lobes. S1 narrow, deep, straight, short. L1 subtriangular in outline, small, depressed with respect to posterior of glabella. Occipital furrow straight, broad, of medium depth. Occipital ring 0.2 of cranidial length of smaller specimens, 0.15 of larger individuals. Palpebral lobes distinctly semicircular in small specimens to slightly crescent-shaped in larger specimens. Anterior facial sutures long and nearly straight between γ and β , rounded at β . Posterior facial sutures with very short curved section. Eyes small, visual field inclined at slight angle; ocular furrow shallow, narrow. Lateral border furrow shallow, narrow, close to visual field, extending well onto long genal spine.

Pygidium lanceolate to subtriangular in outline, of low vaulting and arching in longitudinal and transverse profiles. Axis 0.32 of the total pygidial width, 0.86 total pygidial length; mildly posteriorly tapering, subtrapezoidal in transverse profile at anterior end, rounded in profile at the posterior end, bluntly rounded at terminus; composed of 18–19 narrow rings, each is sharply rounded in transverse profile, apex ornamented with a single row of eight or less granules. Ring furrows narrow, deep, straight. Pleural fields flattened abaxially, mildly arched at fulcrum, inclined to border at less than 45 degree angle, nearly straight in longitudinal profile, composed of 10–11 ribs. Wider anterior and narrow posterior band defined on each rib by row of fine granule prosopon that mark a shallow interpleural furrow. Pleural furrow narrow, deep, of equal depth along entire length, extending slightly onto anterior border. Border distinct along entire pygidium, broadening at the posterior axial terminus.

Remarks.—*Weberides chamberlaini* new species is identical to some specimens illustrated as *Paladin chesterensis* from the late Chesterian of Utah by Chamberlain (1969, pl. 11, figs. 26, 28, 31–35, and 36). While the pygidia illustrated by Chamberlain (1969, pl. 11, figs 29, 30, 33, 34, 39, 39) are dissimilar to those from Montana, the Utah pygidia are much smaller than any of the Heath specimens. Consequently, the former may represent juvenile or smaller holaspid materials. This Utah material lacks the inflated glabellar frontal lobe, the medially located palpebral lobes, the long posterior facial sutures, the enlarged L1, and the arcuate S1 that characterize *Kaskia chesterensis* Weller. Phylogenetic analysis demonstrates that the characters exhibited by the Montana and Utah specimens conform to the European genus *Weberides* (Reed).

Weberides chamberlaini new species may be diagnosed by the posterior location and large size of the palpebral

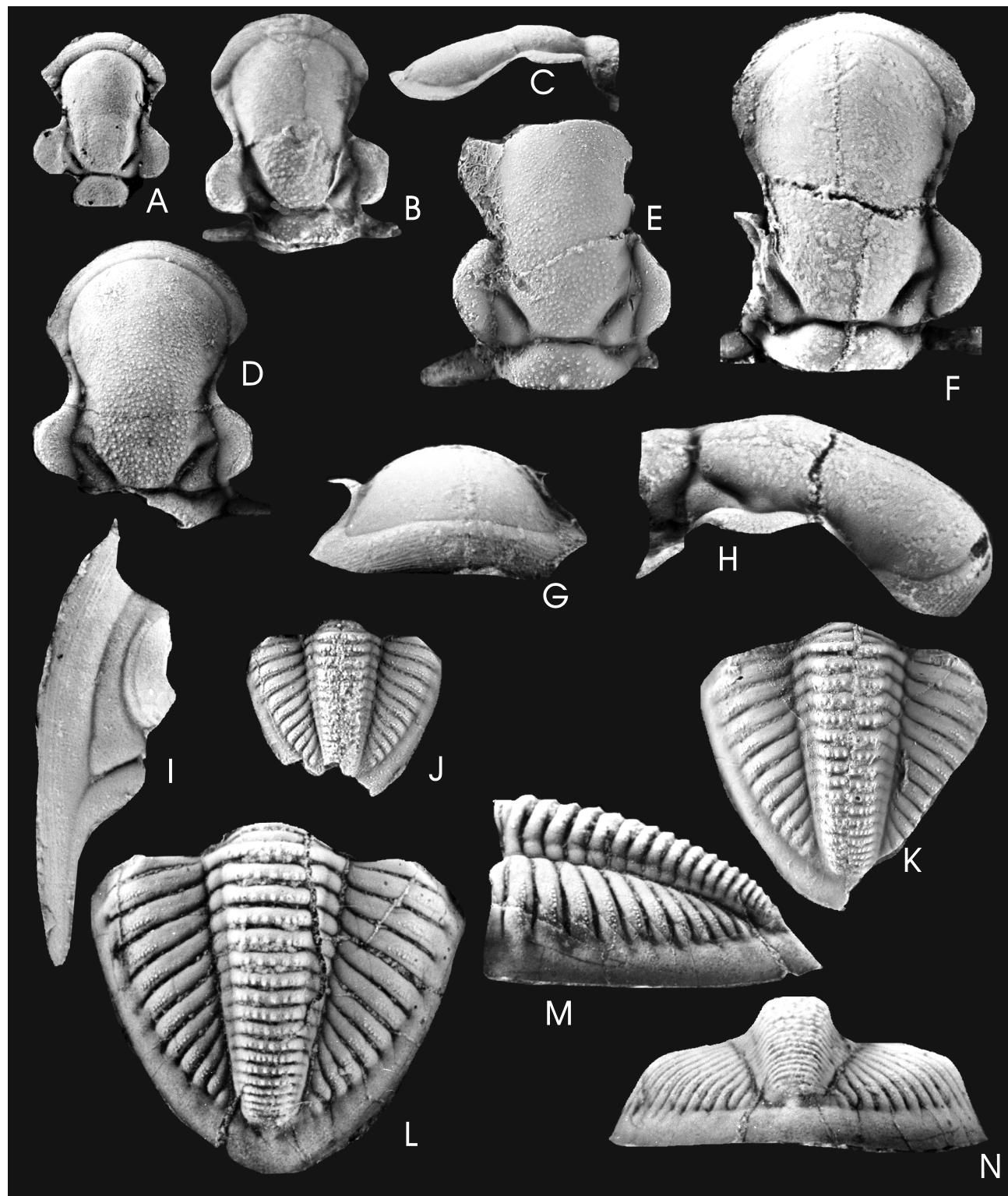


Fig. 6.—6A–6N, *Weberides chamberlaini* new species. A, Small testate paratype cranidium, CM 53201, $\times 3.0$. B, C, Dorsal and lateral views of partial, testate paratype cranidium, CM 53202, $\times 3.0$. D, Dorsal view of incomplete paratype cranidium, CM 53203, $\times 3.0$. E, Fragmentary, testate paratype cranidium from the same locality as holotype, CM 53204, $\times 3.0$. F–H, Dorsal, anterior, and lateral views of holotype cranidium, CM 53200, $\times 4$. I, Testate librigenae, CM 53208, $\times 4.0$. J, Incomplete testate paratype pygidium, CM 53205, $\times 4.0$. K, Incomplete testate paratype pygidium, CM 53206, $\times 4.0$. L–N, Dorsal, lateral, and posterior views of testate paratype pygidium, CM 53207, $\times 4.0$.

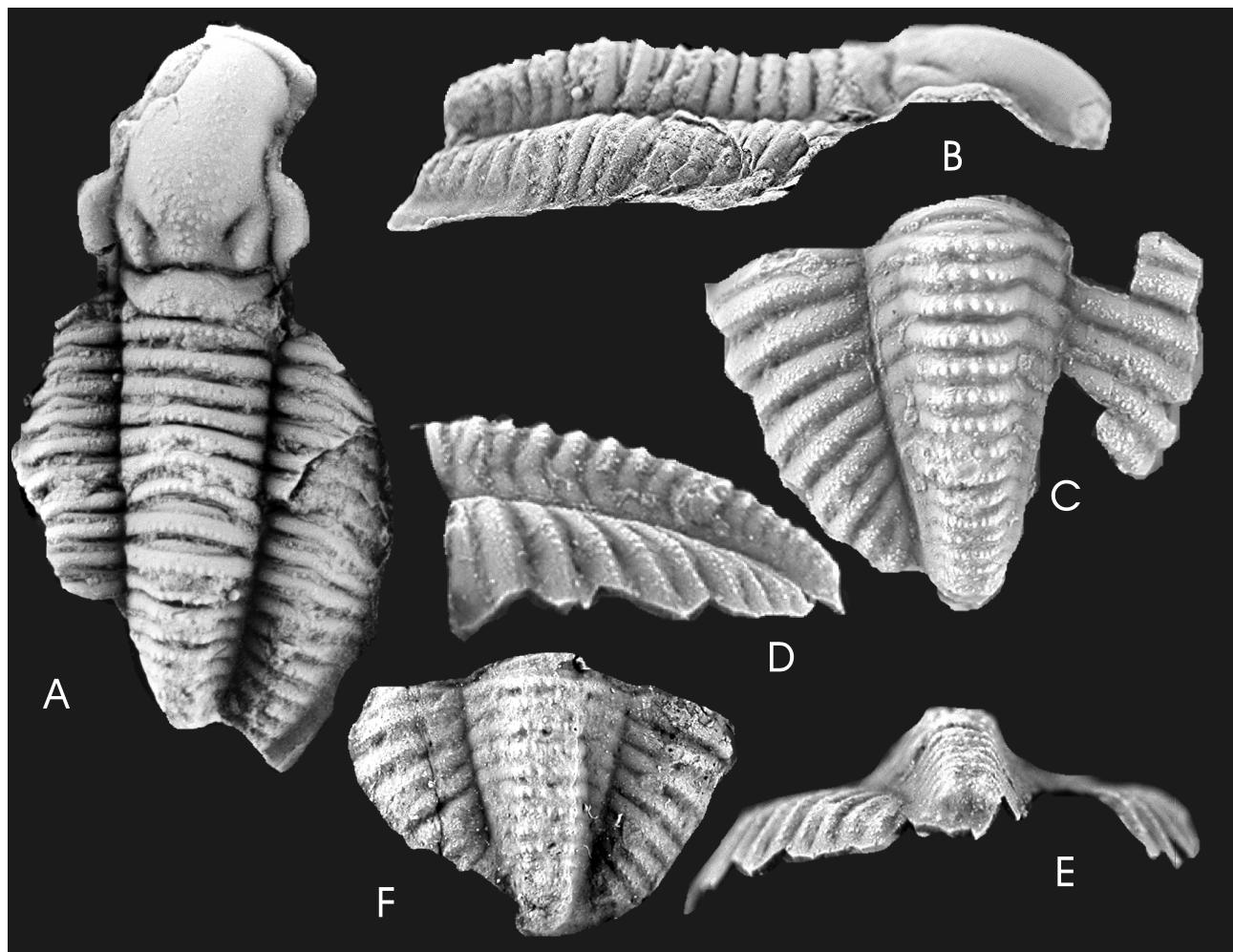


Fig. 7.—*Weberides samwaysi* new species. A, B, Dorsal and lateral views of incomplete holotype exoskeleton, CM 53209, $\times 4$. C–E, Dorsal, lateral, and posterior views of partial testate paratype pygidium from same location as holotype, CM 53210, $\times 3$. F, External latex cast of partial paratype pygidium, CM 53900, $\times 3$.

lobes, straight segment to the base of the glabella, and lanceolate pygidium. This species can be distinguished from all other late Mississippian North American trilobite species by these characters. Smaller cranidial specimens of *Weberides chamberlaini* are very similar to sister species *W. eichwaldi*, *W. czarnieckii*, and *W. mucronatus* in that they possess the rounded base to the glabella, but larger individuals of *W. chamberlaini* exhibit a short straight segment that parallels the occipital furrow. The feature appears to be a primitive, and is present in all species *Paladin* and *Kaskia*, but appears in only one other species of *Weberides*, *W. cuspidatus*. Larger cranidia exhibit a reduction of the narrow anterior border furrow, and slightly more crescentic palpebrae. The pygidia of *W. chamberlaini* do not exhibit the severe posterior extension of their European congeners, but are more markedly extended than any species of *Paladin*.

Stratigraphic Distribution.—Known from the late Chesterian (Serpukovian) Heath Formation, Fergus and Beaverhead Counties, Montana. Stratigraphic position of the Utah specimens is slightly more difficult to determine, but appears to also be late Chesterian (Chamberlain 1969, text fig. 2).

Weberides samwaysi new species Figure 7A–7F

Ameura sp.: Easton, 1962, pl. 13, figs. 28a,b [misidentification].
Paladin mucronatus (Girty): Chamberlain, 1969:54, pl. 12, figs. 1,6 [misidentification].

Type Material.—Holotype, an incomplete cranidium and thoracopygon from the Heath Formation CM Locality 579, (locality 3 of this paper), Beaverhead County, Montana, CM 53209. Paratypes, an incomplete pygidium and an

external mold of a partial pygidium from the same location as the holotype, CM 53210, 53900.

Other Material.—An exfoliated pygidium from the Cameron Creek Formation, USGS locality 13362, Meagher County, Montana, USNM 118882B.

Etymology.—Named in honor of Dr. Norman Samways, patron and volunteer of the Section of Invertebrate Paleontology, Carnegie Museum of Natural History.

Diagnosis.—Cranidium long, slightly medially constricted; posterior facial sutures with straight section; S1 arcuate; L1 oval incipient medial preoccipital lobe present. Pygidial axis trapezoidal in transverse profile; border nearly of equal width.

Description.—Cranidium long, moderately arched in longitudinal and transverse profile, 1.29 times as long as wide, mildly constricted at γ , slightly wider between β than δ . Frontal glabellar lobe bluntly rounded in front, subquadrate at base with faint indication of incipient medial preoccipital lobe that is higher in elevation than adjacent occipital ring, covered with granular prosopon. Anterior border narrow, rounded border furrow indistinct to absent. Dorsal furrow narrow, sinuous, broadest between palpebral lobes. S1 trace arcuate, wide, deepest at bend in arc, shallowing at each end. L1 medium, suboval in outline, lower than posterior of glabella, highest at posterior end. Occipital furrow sinuous, broad, medium depth. Occipital ring low, roughly 0.17 the cranidial length. Palpebral lobes long, narrow, crescentic. Anterior facial sutures long, sinuous, rounded at β . Posterior facial sutures with straight section.

Pygidium lanceolate to subtriangular in outline, of low vaulting and arching in longitudinal and transverse profiles. Axis 0.35 the total pygidial width, roughly 0.9 the total pygidial length; mildly posteriorly tapering, distinctly subtrapezoidal in transverse profile, acutely rounded at terminus; composed of 17–18 narrow rings, each is sharply rounded in transverse profile; apex ornamented with single row of = eight granules. Ring furrows narrow, deep, straight. Pleural fields low, flat at dorsal furrow, inclined steeply to border, nearly straight in longitudinal profile, composed of 11 ribs. Wider anterior and narrow posterior band defined on each rib by shallow interpleural furrow on all but most posterior ribs. Pleural furrow wide, deep, straight, of equal depth along entire length, extending slightly onto anterior border. Anterior and posterior bands demarcated by a row of fine granules. Border distinct along entire pygidium, slightly narrower and more steeply inclined at anterior, marked by sharp inclination to margin.

Remarks.—A exfoliated pygidium, illustrated by Easton (1962) as *Ameura*, and recovered from lowest Pennsyl-

vanian Cameron Creek Member of the Tyler Formation from the southern Little Belt Mountains and appears to be assignable to *W. samwaysi* new species. This specimen is slightly younger than the type material, but possesses the trapezoidal profile to the axis, and identical numbers of rings and ribs. This specimen is tentatively assigned to *W. samwaysi*. Moreover, the specimen illustrated by Chamberlain (1969, pl. 12, fig. 1,6) and identified as *Paladin mucronatus* (now considered *P. girtyianus* Hahn and Hahn, 1970) shows many of the characters diagnostic of *W. samwaysi*. Because the glabella is largely eroded it is not possible to precisely determine the shape of the glabella from the Utah specimen. However, all other characters suggest that the Utah specimen is conspecific with *W. samwaysi*. Phylogenetic analysis suggests that *W. samwaysi* shares a closest common ancestry with *W. cuspidatus* Reed from the late Visean of England. Like *W. samwaysi*, *W. cuspidatus* has the straight section of the posterior facial sutures, the widened cranidium at β , the constricted glabella at γ , the incipient medial preoccipital lobe, and the distinctly trapezoidal transverse profile to the pygidial axis. *Weberides samwaysi* differs from this European sister taxon because the former exhibits narrower, more crescentic palpebral lobes, more inflated L1, and more deeply incised, angular S1. The Utah specimen was recovered from the same stratigraphic interval (late Namurian) as the specimen illustrated by Easton (1962), but may be slightly younger than the type material.

Stratigraphic Distribution.—The type material is known from late Chesterian (early Serpukovian) Heath Formation of Montana; the Utah specimen is from slightly younger Serpukovian strata.

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TABLE 1. Character states for ingroup of Mississippian species of the *Paladin-Kaskia-Weberides* clades related to outgroup of *Thigriphides roundyi* (Girty) after Brezinski (2003) and their comparison with new Montana species.

Taxon	Character State				
<i>Thigriphides roundyi</i>	00000	00000	00000	00000	00000
<i>Paladin chesterensis</i>	21011	11012	00111	10100	11011
<i>Paladin wilsoni</i>	21011	11012	00111	00000	11011
<i>Paladin genevievensis</i>	11011	11012	00111	10000	11011
<i>Paladin rosei</i>	21011	11012	00111	10100	11011
<i>Paladin longispina</i>	00100	00101	11001	11011	01010
<i>Paladin girtyianus</i>	00201	00101	11000	01111	00011
<i>Paladin helmsensis</i>	00101	00101	11000	01011	00000
<i>Paladin rarus</i>	01101	00101	10000	01010	00011
<i>Paladin moorei</i>	00101	00101	11000	00111	00011
<i>Weberides czarnieckii</i>	11200	00101	11000	10221	00100
<i>Weberides eichwaldi</i>	11200	00101	11000	00221	00100
<i>Weberides mucronatus</i>	11200	00101	11000	00221	00100
<i>Weberides mucronatus</i>	11200	00101	11000	00221	00100
<i>Weberides cuspidatus</i>	11100	00101	01100	00221	00111
<i>Weberides maillieuvi</i>	01100	00101	0100	00221	00110
<i>Weberides chamberlaini</i>	11100	10101	11000	00221	10100
<i>Weberides samwaysi</i>	11101	10101	01100	00211	00111

TABLE 2. List of character states for Brooks Parsimony Analysis (BPA) and geodispersal analysis (sensu Lieberman and Eldredge 1996) based on phylogenetic tree displayed in Figure 3.

Biogeographic Area	Character (BPA)
Southern US Margin	0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1
Central Appalachian Basin	0 1 1 0 1 1 0 0 0 1 1 0
Southern Appalachian Basin	0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 1 1 0 1 1 0 1 0 1 0 1 1 0
Eastern Interior Basin	0 1 1 1 1 1 1 1 1 1 1 1 0
Southern Cordillera	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 0
Northern Cordillera	1 0 1 0 0 0 0 1 1 1 0 1 1 0 1 0 1 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 1 0
Western Europe	0 1 1 1 1 0 1 0 1 1 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0
Eastern Europe	0 0 0 1 1 1 1 0 1 1 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0
Biogeographic Area	Character (Geodispersal Analysis)
Southern US Margin	1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0
Central Appalachian Basin	0 0 0 0 0 0 2 0 0 0 2 0
Southern Appalachian Basin	0 0 0 0 0 0 2 0 0 0 2 0 0 0 2 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Eastern Interior Basin	0 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
Southern Cordillera	0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 0 1 1 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0
Northern Cordillera	0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 2 0 0 0 1 1 0 1 1 0 0 0 1 0 1
Western Europe	0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 1 1 0 1 0 1 1 1 0
Eastern Europe	0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 2 1 0 1 1 1 0 1 0

