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PHYLOGENETICS, SYSTEMATICS, PALEOECOLOGY, AND EVOLUTION OF THE TRILOBITE GENERA *PALADIN* AND *KASKIA* FROM THE UNITED STATES

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ABSTRACT—Late Mississippian and earliest Pennsylvanian trilobite faunas of North America are dominated by the *Paladin* and *Kaskia* clades. Phylogenetic analysis of middle Carboniferous species of these clades demonstrates the close ancestral relationship between these groups. The *Kaskia* clade consists of eight species: *K. chesterensis* Weller, 1936, *K. osagensis* (Cisne, 1967), *K. longispina* (Strong, 1872), *K. wilsoni* (Walter, 1924), *K. genevievensis* (Walter, 1924), *K. rosei* (Cisne, 1967), *K. gersnai* n. sp., and *K. rollinsi* n. sp. *Kaskia* Weller, 1936 ranges from late Osagean to middle Chesterian (early Visean-early Serpukhovian) and is restricted to cyclothemic shelf and nearshore deposits. Species of *Kaskia* appear to have evolved in areas of shallow water and high environmental stress. The *Paladin* clade consists of 12 species including previously named species *P. morrowensis* (Mather, 1915), *P. girtyianus* Hahn and Hahn, 1970, *P. rarus* Whittington, 1954, *P. helmsensis* Whittington, 1954, and *P. moorei* (Branson, 1937). New species belonging to this clade are *Paladin moorefieldensis* n. sp., *P. pleisiomorphus* n. sp., *P. imoensis* n. sp., *P. mangeri* n. sp., and *P. wapanukaensis* n. sp. This group ranges from the early Chesterian to early Morrowan (late Visean-late Bashkirian). Species of *Paladin* appear to be confined to outer shelf shelf-edge and off-shelf facies where presumably deeper water environments existed. This is manifested in their paleogeographic distribution, which is paleoenvironmentally controlled.

INTRODUCTION

While morphologic diversification characterizes the evolution of North American trilobites during the early Mississippian, dramatic reductions in morphologic variability during the late Mississippian produced a marked drop in generic and species diversity (Brezinski, 1999). The gradational morphologies that characterize late Mississippian trilobites made traditional taxonomic methods difficult and identification of individual species challenging. The difficulty of separating the plethora of apparently intermediate or ontogenetic morphologies resulted in a taxonomic conundrum that might be called the *Paladin-Kaskia* problem (Whittington, 1954). Morphologies exhibited by larger holaspid individuals of one species are observed in smaller individuals of different species assigned to these two genera. Traditional taxonomic methods confounded this problem by lumping intergrading morphologies of separate species into a single species, as well as combining groups of morphologically variable species into one genus, *Paladin* Weller, 1936. Through phylogenetic analysis, Brezinski (2003) demonstrated that 19 of the more widespread species assigned to *Paladin* from North America and Europe can be separated into four clades that spanned much of the middle and upper Carboniferous. The 11 North American species included in that analysis formed two distinct branches. Brezinski (2003) referred one branch to the genus *Paladin* and the other to a re-erected and re-diagnosed genus, *Kaskia* Weller, 1936. The success of the initial phylogenetic analysis prompted a more comprehensive evaluation of late Mississippian North American species, the results of which are reported herein.

Phylogenetic study of middle Carboniferous species of the *Paladin* and *Kaskia* clades of the United States necessitates a revision of the evolutionary model proposed by Brezinski (1999). Stage 2 of that model was composed solely of species of *Paladin.* The findings of Brezinski (2003, 2005) has shown that not only are North American species of Stage 2 assignable to *Paladin,* but also two sister groups, *Kaskia* and *Weberides* Reed, 1942. Consequently, what was previously interpreted as a long-ranging pandemic genus is under the new interpretation a highly provincial group of genera. Moreover, these taxa provide an important evolutionary step to the low diversity identified in Late Carboniferous and Early Permian genera.

TAXONOMIC BACKGROUND

Since their erection by Weller (1936), *Paladin* and *Kaskia* have become consistently confused primarily, but not solely, because of insufficient diagnoses that were presented to separate the two taxa. This led to the synonomizing of the two genera so that all species were conveniently housed in the purported senior synonym *Paladin.* Additionally, other genera were lumped within the genus *Paladin,* which at one time had more than 50 Carboniferous and Permian species assigned to it (Brezinski, 2003). The history of this taxonomic problem was summarized by Brezinski (2003, 2005) and will not be repeated here. Phylogenetic analysis has shown that *Paladin* is restricted to the late Mississippian and earliest Pennsylvanian strata of North America. Detailed study of more than 500 collections from late Mississippian and early Pennsylvanian strata of the United States indicates that more than 20 species are assignable to these two genera and most are confined to the eastern United States.

Material studied and illustrated herein are reposited in the collections of the University of Iowa (SUI), University of Michigan (UM), Chicago Field Museum of Natural History (CFM), Yale Peabody Museum (YPM), University of Missouri–Columbia Paleontology Collections (UMC), University of Arkansas (UA), and Carnegie Museum of Natural History (CM). Taxonomic descriptions conform to Whittington (1997).

PHYLOGENETIC ANALYSIS

Brezinski (2003) discussed an interpreted ancestral lineage for *Paladin* and *Kaskia* based upon phylogenetic analysis. The current analysis utilizes the same presumed ancestor, but an additional five morphological characters (Table 1) were determined to be useful in examining the ingroup of 18 species (Table 2). The analysis was conducted using PAUP 4.0b10 (Swofford, 2002) employing a branch and bound search command. Accelerated transformation (ACCTRAN) optimization was employed. The analysis produced a single most parsimonious tree of length 83 steps and reaffirmed two separate sister groups consistent with the *Paladin* and *Kaskia* clades (Fig. 1). This tree had a consistency index of 0.43, and retention index (RI) of 0.74.

As in the previous analyses, the ingroup species form two distinct clades similar, but not identical, to that shown by Brezinski (2003, 2005). The one clade consists of eight species and includes several species that Weller (1936) assigned to *Kaskia, K. chesterensis* Weller, 1936, *Griffithides wilsoni* (Walter, 1924), *G. longispina* Strong, 1872, and *G. genevievenesis* Walter, 1924. *Paladin osagensis* Cisne, 1967 and *P. rosei* Cisne, 1967 also are part of this branch, as well as two new species *K. gersnai* n. sp., and *K. rollinsi* n. sp. The new species notwithstanding, this group is consistent with Clade A of Brezinski (2003). Synapomorphies that characterize *Kaskia* are given below.

TABLE *1*—Listing of morphological characters and character states utilized in phylogenetic evaluation of species of *Kaskia* and *Paladin* using *Thigriffides roundyi* (Girty, 1926) as the outgroup.

Character	0	1	2
1. Anterior border	distinct	narrow indistinct	
2. Anterior furrow	present	absent	
3. Base of glabella	rectangular	subrounded	rounded
4. Palpebral position	posterior (<0.35 length)	medial (>0.35 length)	
5. Palpebral shape	semicircular	crescentic	narrow
6. S1 profile	wide-shallow	narrow-deep	
7. Lateral border	subquadrate profile	rounded at margin	
8. Occipital furrow	narrow	V-shaped	
9. L2–3 present	no	yes	
10. Posterior facial sutures	short curved	short straight	long straight section
11. Pygidium border slope	$<$ pleural field slope	$=$ pleural fields	flanged
12. L1 inflation	depressed	distinct	inflated
13. Pygidium axial profile	rounded	subtrapezoidal	
14. Relative δ, β widths	$\delta > \beta$	$\delta = \beta$ or $\delta < \beta$	
15. Shape of β	broadly rounded	acutely rounded	
16. Glabellar width at β	$>\gamma$	$=\gamma$ or $<\gamma$	
17. Pygidium axial prosopon	none	granules	
18. Glabella outline	pyriform	subcylindrical	
19. Genal spine length	to 3rd or 4th segment	$>$5th segment	$<$3rd segment
20. Interpleural furrow ornament	none	granules	
21. L1 shape	suboval	subtriangular	
22. L1 position	sub-even w/glabella base	behind glabella base	
23. S1 trace (outline)	straight	recurved	
24. Pygidium axial ratio	<0.33	>0.33	
25. Pleural furrow	well incised	shallow-narrow	
26. Interpleural furrows	distinct on most ribs	distinct only on anteriormost ribs	
27. Axial terminus	broadly rounded	sharply rounded w/tapered extension	
28. Pygidium outline	parabolic	semielliptical	subtriangular
29. Pygidium border	even	widening posterior	posteriorly extended
30. Pleural field convexity	mildly arched	strongly arched	flattened

The stratigraphic distribution of the species in this clade is totally congruent with their distribution on the cladogram. Figure 2.1 illustrates one possible phylogeny that is consistent with both the species stratigraphic distribution and their arrangement on the cladogram. *Kaskia osagensis* is known from the late Osagean (middle Visean), *K. longispina* from the Meramecian, and *K. wilsoni* and *K. genevievensis* from the basal Chesterian (Asbian, late Visean). *Kaskia chesterensis* and *K. rosei* are known from early and middle Chesterian (late Visean), while *K. gersnai* n. sp. and *K. rollinsi* n. sp. are from the middle Chesterian (late Visean and early Serpukhovian, respectively).

The second clade, which is the similar to Clade B of Brezinski (2003, 2005), is composed of the type species of *Paladin, Griffithides morrowensis* (Mather, 1915), four previously named taxa (*P. helmsensis* Whittington, 1954, *P. rarus* Whittington, 1954, *P. girtyianus* Hahn and Hahn, 1970 (=*Griffithides mucronatus* Girty, 1910), and *G. moorei* Branson, 1937), as well as five new taxa, *P. pleisiomorphus* n. sp., *P. imoensis* n. sp., *P. moorefieldensis* n. sp., *P. mangeri* n. sp., and *P. wapanukaensis* n. sp. Important characters that define *Paladin* are given in the generic diagnosis below.

TABLE *2*—Character states assigned to species of *Kaskia* and *Paladin* of the United States utilizing *Thigriffides roundyi* as an outgroup.

	1234567890	1111111112 1234567890	2222222223 1234567890
Thigriffides roundyi	0000000000	0000000000	0000000000
Paladin morrowensis	0010000101	0101010020	1100111011
Paladin girtyianus	0020100101	0001111111	1100001111
Paladin helmsensis	0010100101	0000001101	1000001011
Paladin rarus	0110100101	0101111001	1100001010
Paladin moorei	0010100101	010111110?	1100001111
Paladin imoensis	1120100101	0000001001	1000000010
Paladin moorefieldensis	0000100001	0101111010	1000000111
Paladin mangeri	0010100111	0101110120	0010110001
Paladin wapanukaensis	1111200001	10010100?0	1100111011
Paladin pleisiomorphus	001010?001	00000011?1	00000000?0
Kaskia chesterensis	2101211012	1201101010	0011110100
Kaskia wilsoni	2101111012	12011011?0	0011100000
Kaskia genevievensis	1101111012	1201110010	0011110000
Kaskia rosei	2101111012	1201101010	0011110100
Kaskia longispina	2101110012	02?1101010	00100001?1
Kaskia osagensis	1101110011	0211001010	101000???0
Kaskia gersnai	2101211012	1201101110	0011110101
Kaskia rollinsi	2101211012	12011011?0	0011010101

The distribution of the species of the *Paladin* clade on the cladogram (Fig. 1), and the proposed phylogeny presented in Figure 3B exhibit only moderate congruence with the known stratigraphic distribution of these species. However, the level of congruence increases if all the species restricted to the Cordilleran are excluded from the phylogram, and only those found in the southern United States are considered. The exception is *P. imoensis,* which exhibits a large number of pleisiomorphic characters. This species has a stratigraphic occurrence much later than a number of more derived species. It is also important to note that the most derived species of this clade, *P. moorei,* is known from Wyoming, and tends to support the paleobiogeographic inferences of Brezinski (2005) that the genus *Weberides* was derived from a northern Cordillera *Paladin* ancestor.

PALEOECOLOGIC IMPLICATIONS

Brezinski (2005, fig. 5) showed that North American species of the *Paladin*-*Kaskia* clades produced a recognizable geographic separation. He showed that species of *Paladin* are distributed in the southern United States from Alabama to West Texas and in the Cordilleran. In contrast, the six species of *Kaskia* are restricted to interior regions of the central and eastern United States (Brezinski, 2005, fig. 5). This geographic segregation is interpreted as being both paleobiogeographical and paleoecological in nature. *Paladin* is interpreted as having inhabited the ancient shelf edge or off-shelf areas, whereas species of *Kaskia* were present in cyclothemic deposits that formed in nearshore or marginal marine settings. When plotted on the late Mississippian paleoenvironmental reconstruction of the United States (McKinney and Gault, 1980; Cook and Bally, 1975) this segregation demonstrated by the species studied herein is even more apparent. Of the nearly

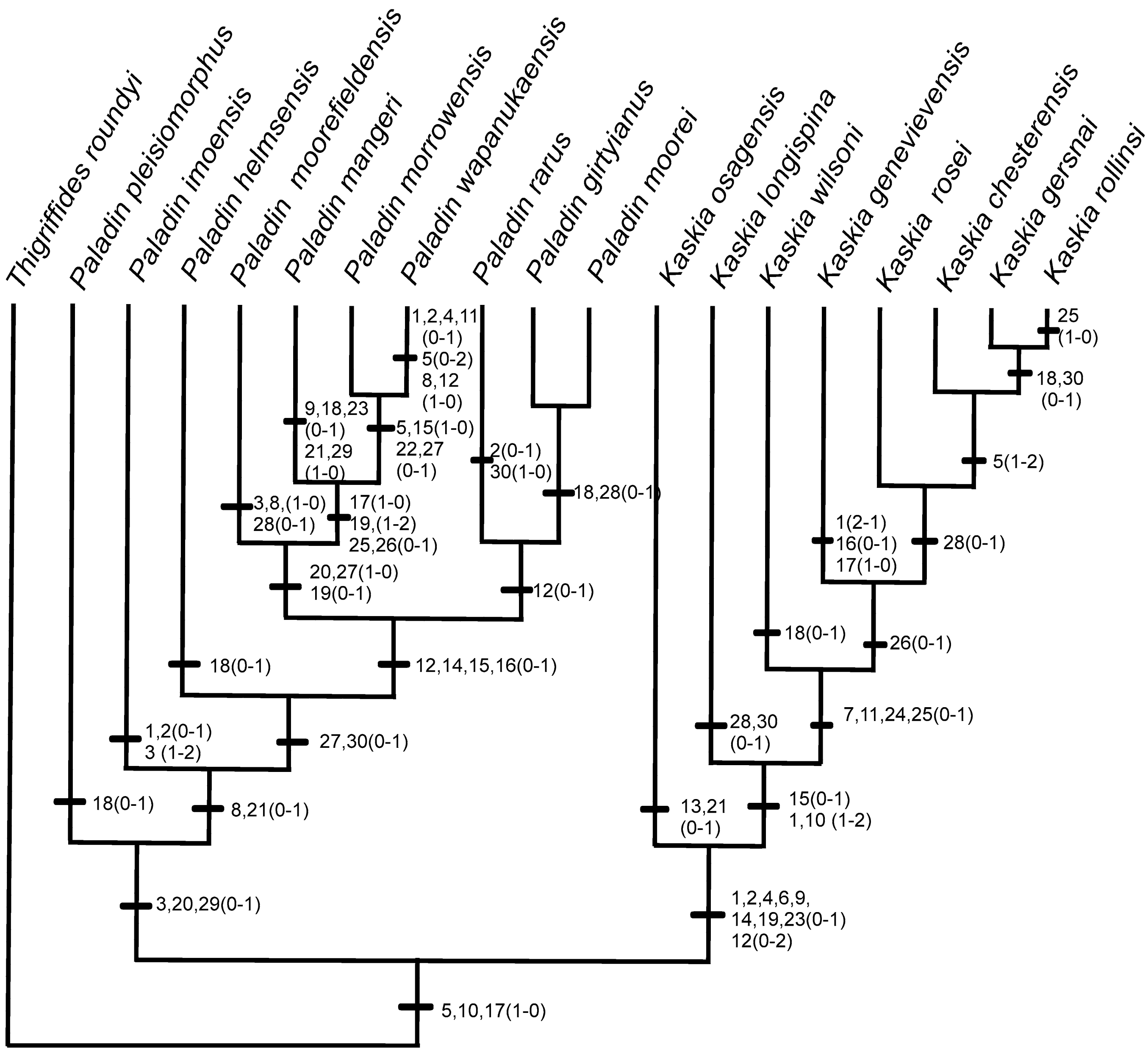

FIGURE 1—Single most parsimonious tree saved from a branch and bound search of 18 species of the genera *Kaskia* and *Paladin* in the United States.

400 collections examined, essentially all of the occurrences of *Kaskia* clade species are within the interpreted cyclothemic deposits and nearshore deposits from the Upper Mississippi Valley, the Illinois, Michigan, or central Appalachian basins. These strata are characterized by rapid vertical lithologic changes from marine to nonmarine in a cyclothemic character (Swann, 1964; Brezinski, 1989). Such ephemeral environments would have been wrought with severe ecological stresses such as salinity variations, turbidity, and substrate mobility. Indeed, some of the characters used to define this clade may have arisen from coping with such stresses. The wider pygidial axis (character 24-1), more strongly vaulted profile to the pleural fields of the pygidium (character 30-1), and more deeply incised glabella furrowing (character 6-1) can be attributed to the increased musculature needed for inhabiting high energy, shallow water environments. Brezinski (1983) observed a distribution within populations of *Kaskia chesterensis* in the central Appalachian Basin that suggests an environmental preference for nearshore settings.

Species of *Paladin,* on the other hand, are found to have occurred in quite different environments. Nearly all of the occurrences of species assigned herein to the *Paladin* clade are from either the southern or western edge of the shelf areas present in North America during the late Mississippian or early Pennsylvanian (Fig. 3). Although some of these deposits were obviously formed in shallow water environments, such as the Pitkin Formation of Arkansas, many can be attributed to lower energy, deeper water environments of deposition near or at the shelf edge (Sutherland and Manger, 1979). The Fayetteville and Moorefield Formations in Oklahoma and Arkansas from which species of *Paladin* were recovered are dark gray organic-rich shale that is suggestive of deep-water settings.

The distribution of the *Paladin* clade in deep water deposits parallels that of the presumed ancestor *Thigriffides roundyi* (Girty, 1926) (Brezinski, 1998, 2003, 2005). Of the collections studied, only a single occurrence can be ascribed to cyclothemic deposits. That particular location is within the latest Mississippian of

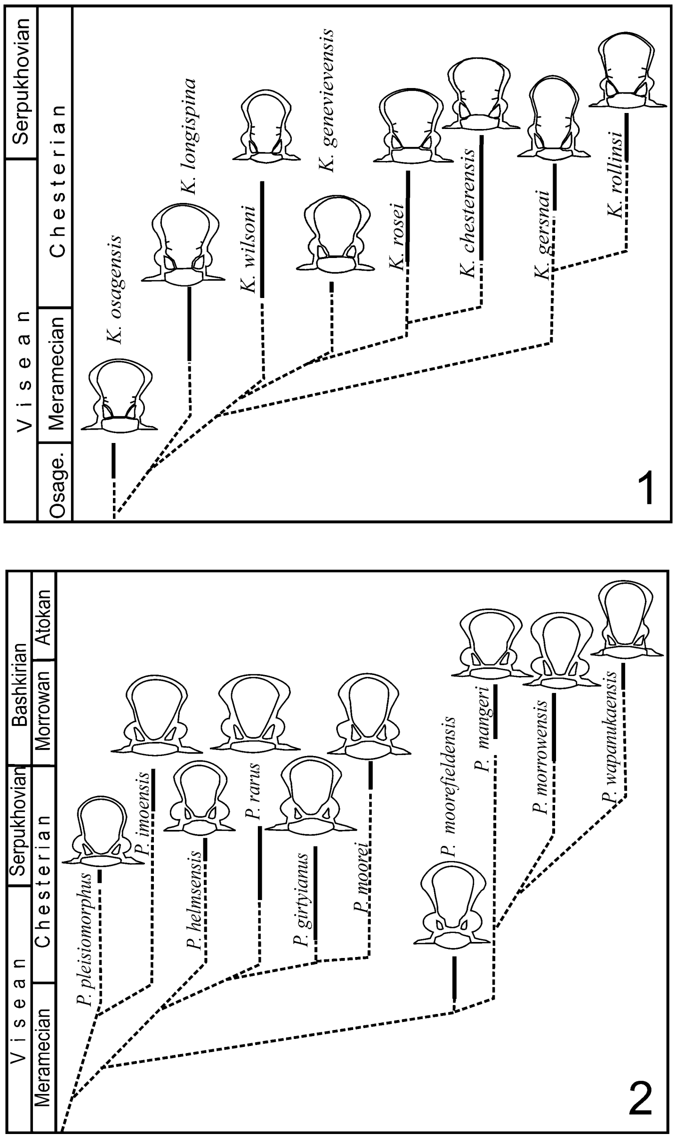

FIGURE 2—Proposed phylogenies of species of the *Kaskia* 1 and Paladin 2 clades based upon key morphological characteristics, distribution on the cladogram presented in Figure 1, and their known stratigraphic ranges.

southern West Virginia. All the remaining occurrences of the *Paladin* clade are from non-cyclothemic settings near or at the shelf edge. The *Paladin* clade restriction to stable settings suggests that species of this group preferred the low environmental stress of these deep-water habitats.

Figure 3 illustrates the possible phylogram-facies relationships of species of *Kaskia* and *Paladin* within an idealized shelf to basin transect. The phylogram is based on the cladogram presented in Figure 1. Cordilleran species have been omitted.

SYSTEMATIC PALEONTOLOGY

Genus PALADIN Weller, 1936

Diagnosis.—Glabella base subrounded (character state 3-1), L1 depressed (character state 22-1), palpebral lobe large, broadly crescentic to semicircular, posteriorly located on cranidium. Anterior border distinct, of variable width, shallow border present on some species. Lateral margin subquadrate in transverse profile. Pygidium outline parabolic with slight posterior widening of the pygidial border (character state 29-1).

Assigned species.—*Paladin girtyianus* Hahn and Hahn, 1970, *P. moorei* (Branson, 1937), *P. helmsensis* Whittington, 1954, *P. rarus* Whittington, 1954, *P. mangeri* n. sp., *P. imoensis* n. sp., *P. wapanukaensis* n. sp., *P. moorefieldensis* n. sp., and *P. pleisiomorphus* n. sp.

Discussion.—While Weller's (1936) main distinguishing characteristic of *Paladin* was the presence of a wide anterior cephalic border, Whittington (1954) noted that various levels of development could be demonstrated on different species, an interpretation concurred with by Cisne (1967). The current study recommends that a number of other characters be used in the identification of this genus, such as the presence of a narrow anterior border furrow, a very short posterior section to the facial sutures, a subrounded base to the glabella, and a distinct lateral cephalic border with a squared-off profile to the margin. The current revision of this genus severely limits its range to the middle Carboniferous, from early Chesterian (middle Visean) to late Morrowan (earliest Westphalian).

The partial paratype cranidium of *P. retrolatus* Chamberlain exhibits several features that are inconsistent with an assignment to *Paladin.* For instance, there is a preocciptial furrow suggesting the presence of a medial preoccipital lobe, and that in conjunction with a partial rounded anterior border indicates that this species is not a *Paladin* congenitor.

Range.—Early Chesterian (middle Visean) through Morrowan (late Bashkirian) in North America.

PALADIN MORROWENSIS (Mather, 1915)
Figure 4.1–4.8

Griffithides morrowensis MATHER, 1915, p. 244–246, pl. 16, figs. 13–14.
Paladin morrowensis WELLER, 1936, p. 707; OSMÓLSKA, 1970, p. 127; BREZINSKI, 2003, text-fig. 4E, F, I, J, M, N, text-fig. 5-2.
Paladin (*Paladin*) *morrowensis* WHITTINGTON, 1954, p. 6, 7, pl. 1, figs. 1–6, 9; HAHN AND HAHN, 1970, p. 277–278.

Diagnosis.—Glabella strongly laterally expanded anteriorly, palpebal lobes semicircular. Anterior facial sutures widely divergent and broadly rounded at β, with relatively long straight section from β to α. Pygidium outline parabolic, axis lacking ornament, tapering at posterior border.

Material illustrated.—Holotype, a partial cephalon from the Brentwood Limestone (Morrowan) of Arkansas, CFM 16174. Paratype, a pygidium from the same location, CFM 16174B. Three cranidia, CM 41724, 41726, 41728, and three pygidia, CM 41725, 41727, 41729, from the Brentwood Limestone of Arkansas.

Distribution.—Morrowan of the southern United States midcontinent, Hale and Bloyd Formations of Arkansas.

Discussion.—*Paladin morrowensis* (Mather), the type species, is recognized by the pyriform glabella, deeply incised 1s glabellar furrows, and flat cephalic border that extends around the entire cephalon. This species is one of the most derived members of the genus *Paladin,* and represents one of only two forms to survive the end of the Mississippian extinction episode. As such it appears to be a Lazarus taxon that may be an important ancestral taxon for later Pennsylvanian species.

PALADIN GIRTYIANUS Hahn and Hahn, 1970
Figure 4.9–4.19

Griffithides mucronatus GIRTY, 1910, p. 230; 1915, p. 133–134.
Paladin mucronatus WELLER, 1936, p. 707; EASTON, 1943, p. 152, pl. 24, fig. 15; GORDON, 1969, p. 35–38, pl. 5, figs. 1–23.
Paladin (*Paladin*) *girtyianus* HAHN AND HAHN, 1970, p. 269–270.
Paladin girtyi OSMÓLSKA, 1970, p. 127.
Paladin girtyianus BREZINSKI, 2003, p. 370.

Diagnosis.—Glabella short, subpyriform, cylindrical in larger specimens, rounded at the base with well-defined anterior border furrow; basal lobes small, strongly depressed; long, straight anterior section of the facial sutures that are sharply rounded. Pygidium subtriangular with broad, flattened, border flange.

Description.—See Gordon, 1969, p. 35–38 for *Paladin mucronatus* (Girty, 1910).

Material illustrated.—Lectotype, cranidium from the lower Fayetteville

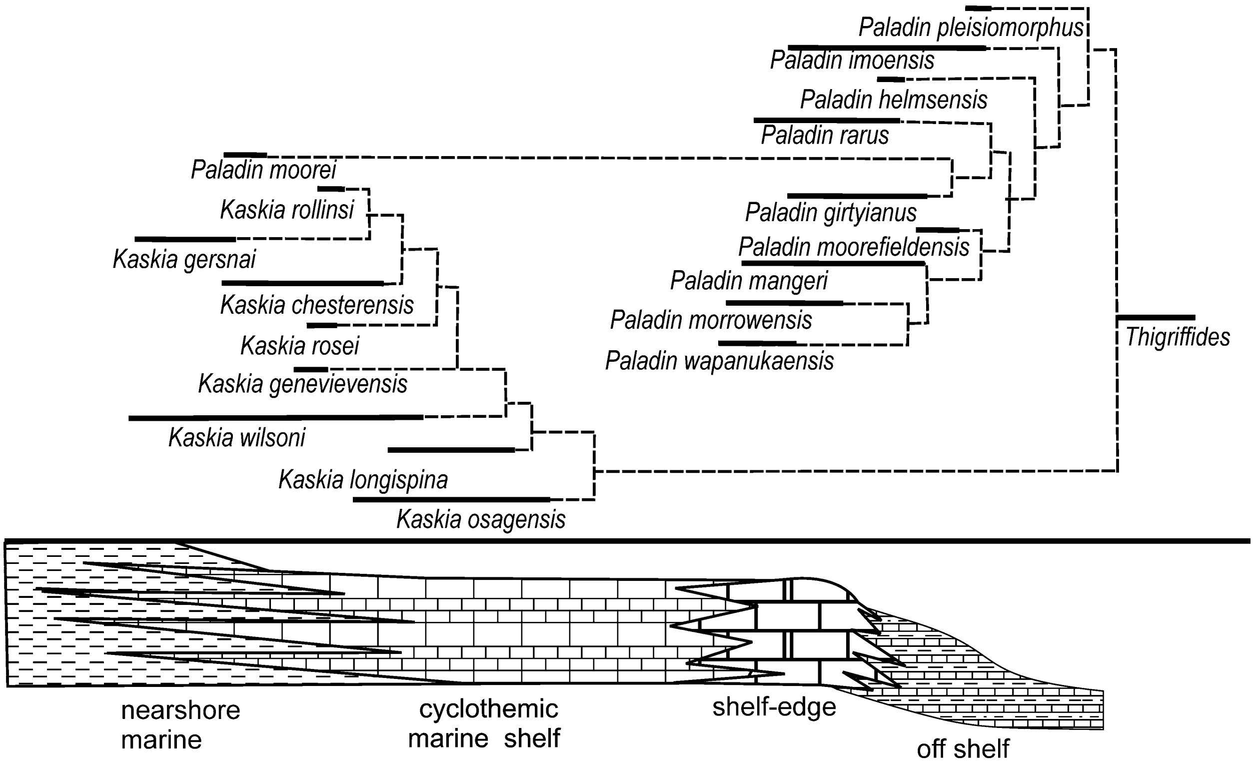

FIGURE 3—Idealized shelf to basin transition in the southern United States during the late Mississippian and early Pennsylvanian and interpreted phylogeny of the *Paladin* and *Kaskia* clades. Ecologic range or breadth of niche inhabited based on variety of environments in which species were observed. Ecologic assignment of *Thigriffides* is from Brezinski (1998).

Shale of Arkansas, USNM 160902. Paralectotypes, from the Fayetteville Shale, USNM 160912, 160914. Two enrolled specimens from the upper Fayetteville, UA 93-600-2, UA 93-600-7.

Distribution.—Known from the Hindesville Limestone, Batesville Sandstone, and the Fayetteville Shale of Arkansas and Oklahoma.

Discussion.—Hahn and Hahn (1970) showed that *P. mucronatus* (Girty, 1910) was a junior homonym of a European species of the same genus, and therefore erected the new species *P. girtyianus.* Chamberlain (1969, pl. 12, figs. 1–6) assigned a specimen from the Manning Canyon Shale of Utah to this species. However, the Utah specimen lacks the definitive anterior border, posteriorly located palpebral lobes, depressed L1, and mucronate pygidial border that characterize the Arkansas specimens of this species. As such the Utah specimen is probably assignable to a different species.

Other species which might be confused with *P. girtyianus* include *P. moorei* (Branson) and *P. imoensis* n. sp. Although *P. moorei* exhibits gross cranidial characters similar *P. girtyianus,* the latter species has greatly depressed L1, and a distinctly rounded glabella. *Paladin imoensis* differs from *P. girtyianus* by lacking an anterior border furrow, more inflated L1 that are subparallel with the base of the glabella, and a poorly defined lateral border.

PALADIN HELMSENSIS Whittington, 1954
Figure 5.1–5.2

Paladin (*Paladin*) *helmsensis* WHITTINGTON, 1954, p. 7–11, pl. 2, figs. 1–45, pl. 3, figs. 1–17; HAHN AND HAHN, 1970, p. 270–271.
Paladin helmsensis BREZINSKI, 2003, p. 371.

Diagnosis.—Glabella nearly parallel-sided to constricted at γ. Anterior border wide, flat. Anterior branch of facial sutures strongly diverging and rounded at β. Palpebral lobes large, semicircular, wider than cranidial width at β. Pygidial axis sharply posteriorly tapering, border wide.

Description.—See Whittington, 1954, p. 7–9.

Material examined.—Holotype, a cranidium from the Helms Formation of Texas, USNM 116513. Paratypes, a pygidium, USNM 116514b.

Distribution.—Known from the late Chesterian Helms Formation of Texas.

Discussion.—Smaller specimens of *Paladin helmsensis* Whittington is similar to *P. moorefieldensis* n. sp. in that both species possess a narrow glabella that is subcylindrical in outline, a wide anterior cranidial border, large, posteriorly located, semicircular palpebral lobes, and anterior facial sutures that are broadly rounded at β. The latter species does not possess the semicircular pygidium of *P. helmsenis. Paladin helmsensis* can be differentiated from other species assigned to the genus by its larger palpebral lobes, broadly rounded anterior facial sutures and very minor inflation to the frontal glabellar lobe.

PALADIN MOOREI (Branson, 1937)
Figure 5.3–5.7

Griffithides moorei BRANSON, 1937, p. 659–660, pl. 89, figs. 28–31.
Paladin (*Paladin*) *moorei* HAHN AND HAHN, 1970, p. 277.
Paladin moorei GORDON AND YOCHELSON, 1975, p. F24–F26, pl. 1, figs. 23–32; BREZINSKI, 2003, p. 367.

Diagnosis.—Glabella mildly anteriorly expanding, slightly constricted at δ; palpebral lobes, large crescentic, posteriorly located. Pygidium semielliptical in outline, border moderately wide. Axis elevated, somewhat flattened on top.

Description.—See Gordon and Yochelson, 1975, p. 24–25.

Material examined.—Holotype, a partial cranidium from the Amsden Formation of Wyoming, UMC 6605. Paratypes, three pygidia from the Amsden Formation of Wyoming, UMC 6605, 6625, 6592. Other specimen, pygidium illustrated by Gordon and Yochelson (1975), USNM 173617.

Distribution.—Known from the late Chesterian Amsden Formation of Wyoming.

Discussion.—This species is recognized by the slight medial constriction to the glabella that has a subcylindrical outline, and the semielliptical outline to the pygidium. Based on these characters *P. moorei* is similar only to *P. girtyianus,* except that the latter species has depressed L1 and a rounded base to the glabella.

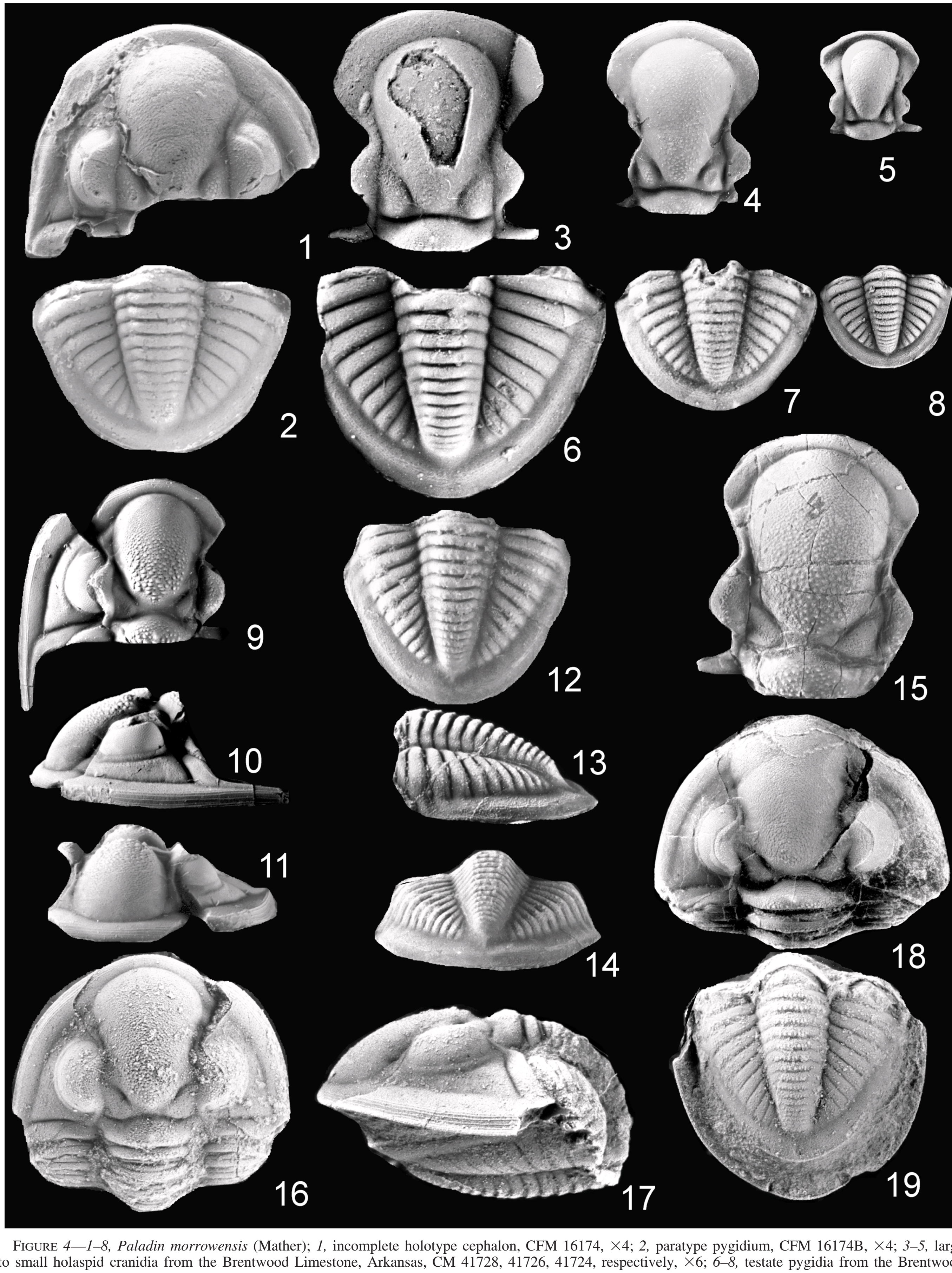

FIGURE 4—*1–8, Paladin morrowensis* (Mather); *1,* incomplete holotype cephalon, CFM 16174, ×4; *2,* paratype pygidium, CFM 16174B, ×4; *3–5,* large to small holaspid cranidia from the Brentwood Limestone, Arkansas, CM 41728, 41726, 41724, respectively, ×6; *6–8,* testate pygidia from the Brentwood

PALADIN RARUS Whittington, 1954
Figure 5.8–5.15

Paladin (*Kaskia*) *rarus* WHITTINGTON, 1954, p. 12–13, pl. 1, figs. 7, 8, 10–35.
Paladin (*Paladin*) *rarus* HAHN AND HAHN, 1970, p. 283–284.
Paladin rarus BREZINSKI, 2003, p. 367.

Diagnosis.—Cranidium with narrow, distinct anterior border, anterior facial sutures sharply rounded at β, palpebral lobes large, crescentic. Pygidium, parabolic, with strongly arched pleural fields, pleural furrows deep.

Description.—See Whittington, 1954, p. 12.

Material illustrated.—Holotype, a cranidium from the Helms Formation of the Hueco Mountains, Texas, USNM 116511. Paratype, a pygidium from the same location as holotype, USNM 116512a. A cranidium and two pygidia from the Pitkin Formation of Arkansas, CM 55304, 55305, 55306 from USGS localities PC 7173, and PC 1240.

Distribution.—Known from the Chesterian Helms Formation of West Texas, and the Pitkin and Imo Formations of Arkansas and Oklahoma.

Discussion.—Previously this species was known only from the type material from the Helms Formation of Texas. Specimens of *Paladin* from the Pitkin Formation of Oklahoma and Arkansas exhibit the same sharply rounded facial sutures at β and narrow anterior border on the cranidium, and the strongly arched pleural fields with deeply incised pleural furrows on the pygidium. The Pitkin specimens are herein assigned to this species because of these similar characteristics. Furthermore, a single pygidium from the late Chesterian Imo Formation of Arkansas also appears similar to this species and is assigned to it.

The phylogeny presented in Figure 2.2 suggests that *P. rarus* belongs to late Mississippian sister group composed of it, *P. girtyianus*, and *P. moorei,* and that the Pennsylvanian species of *Paladin* form a quite different sister group. The stratigraphic position of the Arkansas specimens assigned to *P. rarus* is consistent with that of the type material from west Texas.

PALADIN MOOREFIELDENSIS new species
Figure 5.16–5.26

Diagnosis.—Glabella, narrow, subrectangular at base, faintly indicating medial preoccipital lobe. Maximum glabellar width 0.57 to 0.58 the maximum cranidal width at β. Anterior border furrow distinct, relatively wide. Dorsal furrow deep, wide. S1 arcuate. Pygidium long, semielliptical in outline, widening at terminus.

Description.—Cranidium deeply furrowed. Glabella relatively narrow, mildly forwardly inflated, about 0.57 of the maximum cranidial width at β, evenly convex in transverse profile, posteriorly flattened in longitudinal profile, covered with granular prosopon. Posterior part of glabella much lower in height than adjacent palpebral lobes, subrectangular in outline with faint indication of separation into medial preoccipital lobe. Anterior border furrow distinct, broadening and deepening laterally; border narrow, sharply rounded. S1 shallow, narrow, with arcuate trace. S2 and S3 only very faintly evident on larger specimens. L1 depressed, subtriangular, rounded at base, extending slightly behind the base of the glabella. Occipital furrow deep, wide, becoming narrow axially. Palpebral lobes large, semicircular. Anterior facial sutures strongly divergent from γ to β, broadly rounded at β. Posterior facial sutures with very short straight section.

Pygidium long, semielliptical, approaching subtriangular in outline, width 1.10 times pygidial length. Distinctly shouldered axis narrow, 0.32 of the maximum pygidial width. Low, evenly rounded in transverse profile; straight, very mildly arched in longitudinal profile. Composed of 17 to 18 rings, ornamented with two or more rows of fine granules, separated by narrow, deep ring furrows. Pleural fields mildly arched in transverse profile, flat near the sagittal line, straight in longitudinal profile, composed of 10 straight ribs separated by narrow, deep pleural furrow, and covered by fine granules. Five anteriormost ribs divided into narrow posterior, and broader anterior bands divided by a shallow interpleural furrow that extends to mid-rib in posterior ribs, but along entire rib in anterior segments; posteriormost ribs marked by a row of fine granules. Border slightly wider at the posterior terminus, otherwise of even width, slightly less steep than posterior ends of pleural ribs.

Type material.—Holotype, a cranidium, CM 55308, from the Moorefield Formation along the banks of Baron Creek at road bridge immediately south of Welling, Cherokee County, SE corner, SE¼, sec. 7, T16N, R23E, Park Hill Quadrangle, Oklahoma. Paratypes, two partial cranidia, CM 55309, 55300, and 4, partial pygidia, CM 55310, 55301, 55307, and 55311, all from the same locality as the holotype.

Distribution.—Known only from the Moorefield Formation (upper Meramecian and lower Chesterian) of Oklahoma.

Etymology.—Named for the Moorefield Formation.

Discussion.—*Paladin moorefieldensis* n. sp. differs from all currently recognized congeners by its small glabella that reaches a distinct anterior border furrow and is less than 0.6 the maximum cranidial width at β, by the arcuate trace to S1, by the deeply incised cranidial border furrow, and a semielliptical pygidial outline that verges on subtriangular. Another character that is unusual is the subrectangular base of the glabella, which suggests an incipient medial preoccipital lobe.

Paladin moorefieldensis is the earliest representative of this genus currently known.

It is present within strata that are only 2–3 m above the stratum where Ormiston (1966) recovered a species of *Australosutura.* These lower strata also contain *Hesslerides pustulosus* (Snider, 1915) and a yet unidentified species of *Phillibole.* These beds may be earliest Chesterian or perhaps latest Meramecian.

PALADIN IMOENSIS new species
Figure 6.1–6.15

Diagnosis.—Glabella anteriorly wide, 0.75 maximum cranidial width at β, reaching narrow anterior border, rounded at base. Posterior section of facial sutures with a relatively long straight section. Pygidium approaching subtriangular in outline, but still parabolic.

Description.—Glabella forwardly expanded, pyriform in outline, rounded at the base, evenly rounded in the frontal lobe, mildly convex in transverse and longitudinal profiles, extending to narrow anterior border, covered by fine prosopon, especially near the base. Frontal lobe 0.75 times the maximum cranidial width at β. S1 straight, shallow, narrow. L1 subtriangular in outline, base of triangle sub-even with the base of the glabella. Occipital furrow straight, V-shaped in longitudinal profile. Occipital ring narrow, with a row of granules along posterior margin. Dorsal furrow shallow, narrow, straight. Palpebral lobes crescentic in outline, lower in height than adjacent part of glabella. Anterior facial sutures straight, mildly diverging from γ to β, acutely rounded at β. Posterior facial sutures with a relatively long straight section. Eyes medium, reniform, with distinct ocular platform gently inclined to shallow inflection at lateral border furrow. Lateral margin bent sharply to vertical margin.

Thorax of nine unornamented segments.

Pygidium parabolic in outline, moderately convex. Axis 0.31–0.33 the maximum pygidial width; sharply posteriorly tapering, sharply rounded at terminus; of low even convexity in transverse profile; of very low convexity in longitudinal profile; composed of 14–15 narrow rings; ornamented with a row of fine granules at the apex; and separated by straight, narrow, deep ring furrow. Dorsal furrow narrow, straight. Pleural fields of low, even convexity in transverse profile, nearly straight in longitudinal profile; composed of 10 to 11 recurved ribs made up of a broad anterior, forward sloping band, delineated from a narrow posterior-sloping posterior band by a row of fine granules. Pleural furrows deep and distinct, even on posterior ribs. Border narrow laterally, slightly wider behind axis, inclined at a slightly lower angle than adjacent pleural fields.

Type material.—Holotype, nearly complete, enrolled specimen from the Imo Formation, along U.S. 65 at Peyton Creek, NE¼, sec. 11, T13N, R15W, Van Buren County, Arkansas, CM 55313. Paratypes, an enrolled specimen from the Pitkin Formation, Washington County, Arkansas, collected by Craig

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Limestone, Arkansas, CM 41729, 41727, 41725, respectively all ×7. *9–19, Paladin girtyianus* Hahn and Hahn; *9–11,* dorsal, lateral, and anterior views of testate paralectotype cephalon, USNM 160912, ×5; *12, 13,* dorsal, lateral, and posterior view of testate paralectotype pygidium, USNM 160914, ×4; *15,* partial testate lectotype cranidium, USNM 160902, ×5; *16, 17, 19,* dorsal, lateral and pygidial views of testate enrolled specimen from the upper Fayetteville Shale, Arkansas, UA 93-600-2, ×4; *18,* incomplete specimen from the upper Fayetteville Shale, UA 93-600-2, ×4.

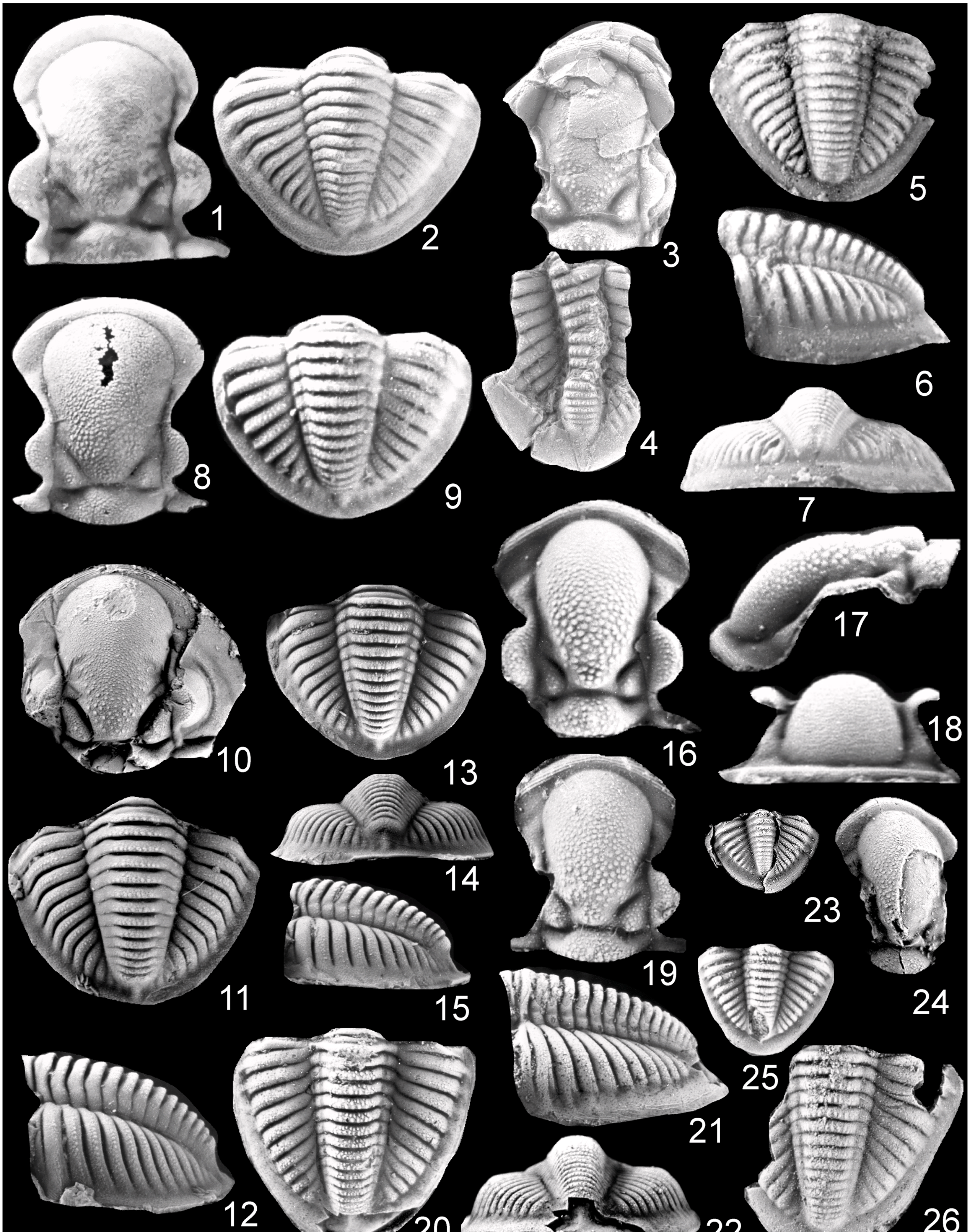

FIGURE 5—*1, 2, Paladin helmsensis* Whittington; *1,* incomplete holotype cranidium, USNM 116513, ×5; *2,* paratype pygidium, USNM 116514b, ×4. *3–7, Paladin moorei* (Branson); *3,* partial crushed holotype cranidium, UMC 6605, ×4; *4,* incomplete, crushed paratype pygidium, UMC 6605, ×4; *5–7,* dorsal,

Brown, CM 55314; two nearly complete enrolled specimens from the type locality UA 75-831-3, 75-831-4; a partial cranidium from the type locality, CM 55315.

Distribution.—Known from the Pitkin and Imo Formations (late Chesterian, late Serpukhovian) of Arkansas.

Etymology.—Named for the Imo Formation.

Discussion.—*Paladin imoensis* n. sp. can be readily differentiated from other species assigned to this genus by the very narrow anterior border, relatively long posterior section of the facial sutures, and rounded base to the glabella. The last of these three characters is more consistent with the European genus *Weberides,* while the long straight section to the posterior facial sutures is characteristic of *Kaskia.* With the exception of a medial preoccipital lobe, this species is more similar to the Pennsylvanian genus *Ditomopyge* than to most other species of *Paladin. Paladin imoensis* may in fact represent an ancestral species of this long-lived late Carboniferous and Permian genus.

Paladin mangeri new species
Figure 7.1–7.12

Diagnosis.—Glabella bluntly rounded in frontal lobe, widening between the palpebral lobes. Pygidium subparabolic, axis narrow.

Description.—Cranidium short, wide. Glabella short; bluntly rounded in the frontal lobe; reaching shallow, indistinct, anterior border furrow; sharply rounded laterally; constricted at γ nearly as wide or wider between the palpebral lobes as in frontal lobe; covered by fine granular prosopon; subquadrate at the base. Anterior border sharply rounded, widening laterally, sharply bent ventrally at margin. S1 wide, arcuate, deepest at its midpoint, shallowing towards the dorsal and occipital furrow. S2-3 short, very shallow, faint. L1 subelliptical, rounded at base that extends slightly posterior of the glabella base. Dorsal furrow narrow, sinuous, deep. Palpebral lobes crescentic, nearly as wide as cranidium at β. Anterior facial sutures widely divergent between γ and β, acutely rounded at β. Occipital furrow narrow, sinuous, V-shaped in longitudinal profile. Occipital ring of medium width, sloping into occipital furrow. Posterior facial sutures with short straight section that are parallel to dorsal furrow. Eyes medium in size, with distinct eye socle. Librigenae with distinct, narrow, subocular groove; steeply downsloping to inflection marking lateral border; sharply bent at margin. Genal spine short, extending to second or third thoracic segment.

Pygidium semielliptical in outline. Axis 0.32 maximum pygidial width; low; rounded in transverse profile; composed of 14 narrow, rounded rings covered by fine granular prosopon. Axis mildly posteriorly convergent, straight sided, reaching wide posterior border. Ring furrows narrow, deep, straight. Pleural fields of low convexity in both longitudinal and transverse profiles, composed of 10 ribs ornamented by fine granular prosopon. Border noticeably wider to the posterior than laterally.

Type material.—Holotype, a cephalon from the Prairie Grove Member of the Hale Formation (Morrowan, Bashkirian) of Arkansas, UA 93-600-08. Paratypes, four partial cranidia, CM 55324, 55325, 55302, 55328, and a partial pygidium, CM 55327, from the Prairie Grove Member of the Hale Formation of Arkansas and Brentwood Member of the Bloyd Formation of Arkansas, and a pygidium, CM 55326, from the Braggs Member of Sausbee Formation of Oklahoma.

Etymology.—Named in honor of Dr. Walter L. Manger of the University of Arkansas.

Distribution.—Present in the Morrowan Hale and Bloyd Formations (Bashkirian) of Arkansas and Oklahoma.

Discussion.—*Paladin mangeri* n. sp. is distinguished from the other species assigned to this genus by the short, bluntly anteriorly rounded glabella that broadens between the palpebral lobes and is constricted at γ, the sharply rounded facial sutures at β, and the posterior broadening of the pygidial border.

The combination of characters such as the medial glabellar constriction that makes the glabella nearly as wide between the palpebral lobes as the frontal lobe, the incision of the anterior border, inflation of L1, the posterior elongation of the pygidial border, and the shallowing of the pleural furrows are suggestive of the Pennsylvanian and Early Permian genus *Ameura. Paladin mangeri* is known from the Morrowan (early Bashkirian) Hale and Bloyd Formations of Arkansas and thus predates the widespread genus *Ameura* that ranges from the Atokan (late Bashkirian) to Wolfcampian (Sakmarian). While further evaluation is needed, it is postulated herein that *P. mangeri* may represent an ancestral taxon for this Pennsylvanian and Permian North American genus.

Paladin wapanukaensis new species
Figure 7.13–7.21

Diagnosis.—Cranidium of low relief and vaulting, furrowing shallow to poorly defined. Palpebral lobes short and very narrow. Cranidium relatively wide at β. Posterior section of facial sutures with long straight section. Pygidium parabolic with poor definition of segmentation.

Description.—Cranidium of low vaulting. Glabella pyriform, mildly laterally inflated in the frontal lobe, nearly flattened in longitudinal profile, subrounded at base. Dorsal furrow deepest between palpebral lobes then shallowing both to the front and rear, nearly obsolete near anterior margin. S1 shallow, narrow, indistinct; L1 subtriangular, dorsally depressed. Anterior border furrow very shallow; anterior margin sharply rounded. Palpebral lobes small, short, and narrow (transverse). Occipital furrow narrow, and deeply incised. Anterior facial sutures mildly anteriorly divergent from γ, broadly rounded at β. Posterior facial sutures with a long straight section. Occipital ring narrow. Librigenae smooth, with shallow lateral border, angular at the margin.

Pygidium somewhat smooth, parabolic in outline, low in relief and vaulting. Axis strongly posteriorly tapering, with smooth surface so that the posterior axial rings are not discernable, composed of more than 10 rings. Ring furrows shallow and narrow; rings wide and smooth. Axial furrow distinct and relatively narrow and deep. Pleural fields with little longitudinal or transverse arching, composed of 7 to 9 ribs. Pleural furrows shallow, narrow, becoming indistinct to the posterior. Border slightly wider behind the axis, smooth.

Type material.—Holotype, an incomplete cranidium from the Wapanuka Limestone of Oklahoma, USGS locality PC 19524, CM 55319. Paratypes, two fragmentary cranidia, CM 55323, 55303, from the same locality as the holotype, and three pygidia, CM 55320, 55321, 55322, from the same local as the holotype.

Etymology.—Named for the Wapanuka Formation of Oklahoma.

Distribution.—Currently known only from the late Morrowan Wapanuka Limestone of Oklahoma.

Discussion.—Grayson (1979) has shown that the Wapanuka Limestone is late Morrowan to earliest Atokan (late Bashkirian) in age. With an occurrence as earliest Atokan, *Paladin wapanukaensis* n. sp. is the youngest species assigned to this genus. The distribution of this species on Figures 1 and 3 suggests that it is the most derived form of *Paladin* currently recognized. A number of its characters are unlike those of any other species assigned to this genus. These include the near total obscuring of cranidial and pygidial furrowing, the presence of a long straight section to the posterior facial sutures, and a narrow, deeply incised occipital furrow. So different is *P. wapanukaensis* from its congeners that it could be interpreted to represent a new genus. However, so few specimens are available for study that such an interpretation at this juncture would be imprudent.

The poorly defined furrowing to the cranidium and pygidium

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lateral, and posterior views of testate pygidium from the Amsden Formation, Wyoming, USNM 173617, ×4. *8–15, Paladin rarus* Whittington; *8,* holotype cranidium, USNM 116511, ×5; *9,* paratype pygidium, USNM 116512a, ×5; *10,* incomplete, testate cranidium from the Pitkin Formation, Arkansas, CM 55304, ×4; *11, 12,* dorsal and lateral view of testate pygidium from the Pitkin Formation of Arkansas, CM 55305, ×4; *13–15,* dorsal, lateral, and posterior views of testate pygidium from the Pitkin Formation, Arkansas, CM 55306, ×4. *16–26, Paladin moorefieldensis* n. sp.; *16–18,* dorsal, lateral, and anterior views of partial testate holotype cranidium, CM 55308, ×4; *19,* dorsal view of testate paratype cranidium, CM 55309, ×4; *20–22,* dorsal, lateral, and posterior view of testate paratype pygidium, CM 55310, ×3; *23,* dorsal view of small testate pygidium, CM 55301, ×6; *24,* small fragmentary paratype cranidium, CM 55300; *25,* dorsal view of small testate pygidium, CM 55307, ×5; *26,* dorsal view of small testate pygidium, CM 55311.

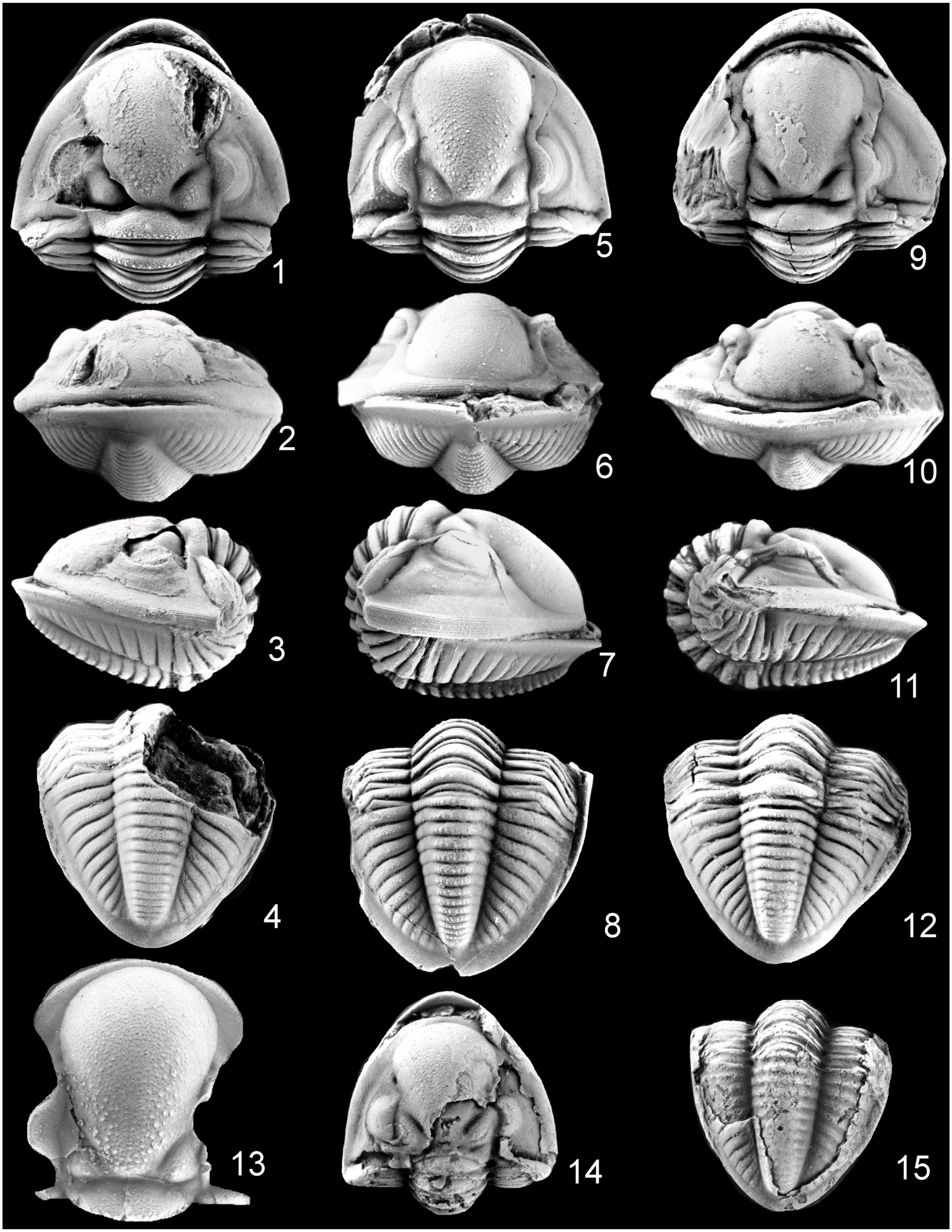

FIGURE 6—*1–15, Paladin imoensis* n. sp.; *1–4,* dorsal, anterior, lateral, and pygidial views of enrolled paratype specimen from the Pitkin Formation, Arkansas, CM 55314, ×4; *5–8,* dorsal, anterior, lateral, and pygidial views of enrolled holotype specimen, from the Imo Formation of Arkansas, CM 55314,

of *Paladin wapanukaensis* n. sp. may represent an ecologically induced character. Grayson (1979) has shown that the limestone strata of the Wapanuka represent high-energy, shoal-water deposits. This type of environment has been interpreted by Brezinski (1987) to induce a reduction in surface features in the Mississippian trilobite genus *Spergenaspis* from Indiana.

PALADIN PLEISIOMORPHUS new species
Figure 7.25–7.30

Diagnosis.—Glabella subcylindrical in outline, exhibiting little anterior broadening, attaining 0.80 the cranidial width at β. Cranidial width at γ wider than at β.

Description.—Cranidium narrow; anterior border distinct, narrow, of even width. Glabella mildly anteriorly expanded in the frontal lobe, posteriorly flattened, mildly convex in longitudinal profile, evenly convex and low in transverse profile, covered with fine granulose prosopon. S1 narrow, shallow. L1 small, low in relief, subtriangular in outline, posterior end even with posterior terminus of glabella. Occipital furrow narrow, deep, straight. Anterior facial sutures straight, only slightly anteriorly divergent between γ and β, evenly rounded at β. Width of cranidium at β nearly same as at γ. Palpebral lobes semicircular, flattened distally; dorsal furrow shallow, narrow. Posterior facial sutures with a very short straight section. Occipital ring narrow, straight.

Pygidium parabolic in outline, of medium vaulting. Axial lobe narrow, straight-sided, mildly posteriorly tapering, rounded in transverse profile, straight in longitudinal profile, composed of 17 narrow rings ornamented with a row of small granules along posterior apex, and separated by narrow, deep, straight ring furrows. Pleural fields of even, low convexity in transverse profile; straight in longitudinal profile; composed of ten ribs made up of broad, flat anterior bands and narrow posterior bands that are separated by shallow, narrow pleural furrow. Interpleural furrows narrow, deep, straight, extending to inflection suggestive of a border furrow. Border slightly wider near posterior terminus than along lateral margins.

Type material.—An incomplete cranidium from the upper Fayetteville Formation of Arkansas, USGS locality PC 1616, CM 55316. Paratypes, two pygidia, CM 55317, 55318, from the same location as the holotype.

Etymology.—Named for the preponderance of pleisiomorphic characters present in this species.

Distribution.—Known from the upper Fayetteville Shale of Arkansas.

Discussion.—*Paladin pleisiomorphus* n. sp. exhibits many of the morphological characters that are indicative of the presumed ancestral genus *Thigriffides* Hessler, 1965. The narrow cranidium at β that is narrower than between the palpebral lobes at δ; the narrow, straight occipital furrow; semicircular outline to the palpebral lobes; and low convexity to the glabella are suggestive of *Thigriffides.* However, the narrow, distinct S1 and short straight section to the posterior facial sutures are characteristic of *Paladin.* Because of the discrepancy between these characters, assignment of this species to either of these genera is tenable. The fact that this species is found in the Chesterian (late Visean-early Serpukhovian) tends to indicate that it is better left within *Paladin* rather than *Thigriffides,* since no representatives of the latter genus have yet been recognized in rocks younger than early Osagean (late Tournaisian).

Genus KASKIA Weller, 1936

Type species.—*Kaskia chesterensis* Weller, 1936.

Assigned species.—*Kaskia osagensis* (Cisne, 1967), *K. longispina* (Strong, 1872), *K. wilsoni* (Walter, 1924), *K. genevievensis* (Walter, 1924), *K. rosei* (Cisne, 1967), *K. gersnai* n. sp., *K. rollinsi* n. sp.

Diagnosis.—Glabella reaching an indistinct anterior border or margin (character state 1-2), subrectangular at base. Posterior facial sutures with long, straight section (character state 10-2), S1 narrow and deeply incised, arcuate in outline (character state 23-1). L1 large, suboval in outline (character state 12-1). Palpebral lobes small, located nearly mid-length of cranidium. Lateral border indistinct, broad, margin rounded, genal spine long. Pygidial axis wide, greater than one-third total pygidial width.

Range.—Species currently assigned to this genus range from late Osagean (middle Visean) to late Chesterian (early Serpukhovian).

Discussion.—The *Kaskia* clade is characterized by more deeply incised cranidial furrowing and stronger vaulting than the *Paladin* clade. Early representatives of this clade (*K. osagensis* Cisne and *K. longispina* (Strong)) share a number of characters with the putative ancestor, *Thigriffides,* that are not present on subsequent representatives. These include the presence of a distinct anterior border and intrapleural furrow.

The *Kaskia* clade exhibits a high level of correspondence between the cladogram and the stratigraphic distribution of individual species (Fig. 2). Clearly, this group of species represents a monophyletic group whose stratigraphic and geographic distribution is consistent. This genus is geographically restricted to the Appalachian and Illinois Basins, and upper Mississippi Valley region of the central United States.

KASKIA CHESTERENSIS Weller, 1936
Figure 8.1–8.4

Kaskia chesterensis WELLER, 1936, p. 708, pl. 95, fig. 4A–6; SHIMER AND SHROCK, 1944, p. 649, pl. 275, figs. 29–33; WELLER, 1959, p. 0399, fig. 305-1A, B; BREZINSKI, 2003, p. 370, text-fig. 1-C, D, G, H, K, L.
Paladin chesterensis CISNE, 1967, p. 1268; CHAMBERLAIN, 1969, p. 51–54, pl. 11, figs. 26–39, pl. 12, fig. 6; BREZINSKI, 1983, p. 2–7; BREZINSKI, 1988, p. 940, fig. 2.28, 2.29, 2.31, 2.32, 2.34.
Paladin (*Kaskia*) *chesterensis* HAHN AND HAHN, 1970, p. 254–255.

Diagnosis.—Glabella strongly inflated laterally and in transverse profile, meeting anterior margin. Palpebral lobes narrow, anteriorly located. Pygidium strongly vaulted, with broad axis, semielliptical in outline.

Amended description.—Glabella broadly laterally inflated in the frontal lobe, reaching anterior margin of cranidium. Base of glabella subquadrate; S1 and occipital furrows narrow and deep; S1 straight, S2-3 shallow, short, sharply oblique to dorsal furrow. Posterior facial sutures with long straight section. Palpebral lobes small, crescentic. Lateral border furrow represented by shallow inflection to librigenae, margin rounded. Pygidial axis more than 0.35 maximum pygidial width. Pleural fields strongly distally sloping, continuous with border.

Material examined.—Holotype, a complete enrolled exoskeleton, CFM 34437.

Discussion.—*Kaskia chesterensis* is a pervasive species of late Mississippian trilobite of the United States. It is found in the Appalachian Basin, midcontinent, and tentatively the northern and southern Cordillera.

Distribution.—Common in early to middle Chesterian of the eastern and central United States.

KASKIA OSAGENSIS (Cisne, 1967)
Figure 8.5–8.10

Paladin osagensis CISNE, 1967, p. 1268–1270, text-fig. 1A–F.
Paladin chesterensis LEVI-SETTI, 1975, pl. 75.
Kaskia osagensis BREZINSKI, 2003, p. 370.

Diagnosis.—Glabella strongly anteriorly and laterally inflated, anterior branch of facial sutures with long straight section from γ to β, bluntly rounded at β. Palpebral lobes very posteriorly located. Pygidial axis slightly flattened on top.

Description.—See Cisne, 1967, p. 1268–1270.

Material examined.—Holotype, an incomplete exoskeleton from Indiana, YPM 24872. Paratype, a pygidium, YPM 24873.

Distribution.—Late Osagean Keokuk Limestone of Indiana.

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×4; *9–12,* dorsal, anterior, lateral, and pygidial views of enrolled paratype specimen from the Imo Formation, Arkansas, UA 75-83-4, ×4; *13,* partially exfoliated paratype cranidium, CM 55315, ×4; *14, 15,* dorsal and pygidial views of partially exfoliated enrolled paratype specimen, UA 75-831-3, ×3.

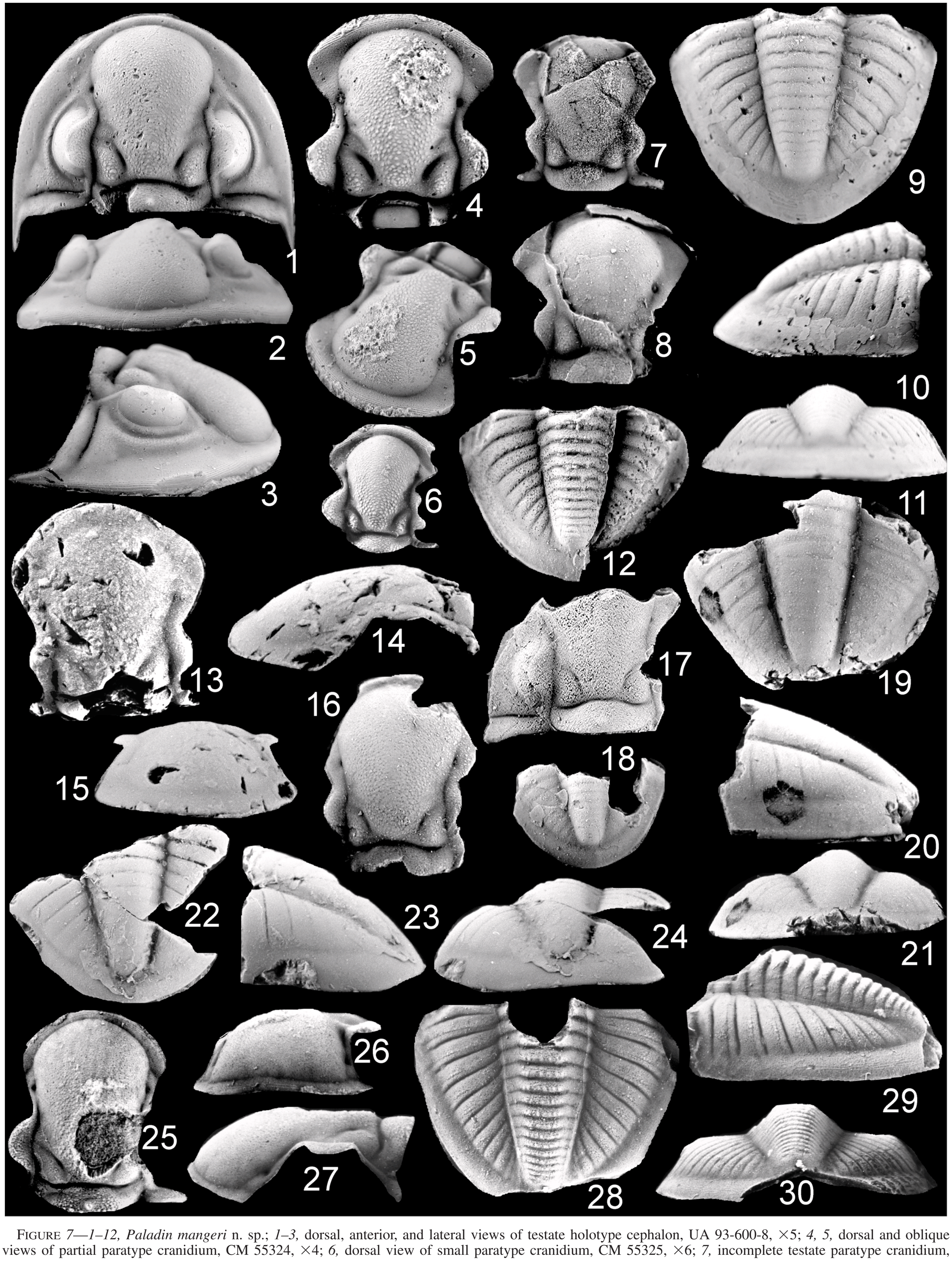

FIGURE 7—*1–12, Paladin mangeri* n. sp.; *1–3,* dorsal, anterior, and lateral views of testate holotype cephalon, UA 93-600-8, ×5; *4, 5,* dorsal and oblique views of partial paratype cranidium, CM 55324, ×4; *6,* dorsal view of small paratype cranidium, CM 55325, ×6; *7,* incomplete testate paratype cranidium,

Discussion.—This species is the earliest known species of *Kaskia* currently recognized. The posteriorly located palpebral lobes and presence of interpleural furrows indicate common ancestry with species assigned to *Paladin.* However, the narrow palpebral lobes, subrectangular base to the glabella, and rounded lateral cephalic margin are unquestionably characteristic of *Kaskia.* A specimen from the late Osagean of Crawfordsville, Indiana, and assigned to *Kaskia chesterensis* by Levi-Setti (1975, pl. 75) exhibits the interpleural furrow to the pygidium and subrectangular base to the glabella seen in *K. osagensis* (Cisne). Additionally, this specimen occurs within the stratigraphic interval characterized by *K. osagensis,* and is herein reassigned to *K. osagensis.*

KASKIA LONGISPINA (Strong, 1872)
Figure 8.11–8.14

Phillipsia longispina STRONG, 1872, p. 3.
Kaskia longispina EHLERS AND HUMPHREY, 1944, p. 127–129, pl. 3, figs. 1–3 (4–7); BREZINSKI, 2003, p. 370.
Paladin (*Kaskia*) *longispina* HAHN AND HAHN, 1970, p. 256–257.

Diagnosis.—Glabella with deep, well-defined 1p and 2p glabellar furrows, faint medial preoccipital furrow. Palpebral lobes anteriorly located. Genal spine very long, extending to anterior of pygidium. Pygidium subtriangular with broad border.

Description.—See Ehlers and Humphrey, 1944, p. 127–129.

Material examined.—Holotype, a nearly complete exoskeleton from the Point au Gres Limestone (Bayport Limestone) (Chesterian) of Michigan, UM 21223. Paratype, an enrolled specimen from the Point au Gres Limestone, UM 21222. A cranidium from the St. Genevieve Limestone from St. Genevieve, Missouri, CM 55341.

Distribution.—Known only from the Point au Gres (Bayport) Limestone of Michigan.

Discussion.—The holotype of this species exhibits a low vaulting and lack of inflation to the glabella. The paratype possesses a well-defined anterior border that seems to be lacking on the holotype. Furthermore, the paratype possesses a distinct medial preoccipital lobe, which is unknown in the genus *Kaskia.* This character in recognized in many Late Carboniferous genera. It is plausible that this species represents the progenitor to those later Carboniferous genera.

Kaskia longispina is distinguishable by the long genal spine from which it get its name, presence of a medial preoccipital lobe, and 2p and 3p lateral glabellar lobes. No other species of *Kaskia* has this combination of characters.

KASKIA ROSEI (Cisne, 1967)
Figure 8.15–8.21

Paladin rosei CISNE, 1967, p. 1270–1273, text-fig. 1G–N.
Kaskia rosei BREZINSKI, 2003, p. 370.

Diagnosis.—Narrow anterior border present. Palpebral lobes slightly posteriorly located, β sharply rounded. Genal spine long. Pygidial axis flattened on top.

Description.—See Cisne, 1967, p. 1270–1271.

Type material.—Holotype, a cephalon from the lower Chesterian of Illinois, YPM 24861. Paratypes, a cranidium, YPM 24863, and two pygidia, YPM 24869, 24871.

Distribution.—Lower to middle Chesterian of Indiana, Illinois, and Kentucky.

Discussion.—Although Cisne (1967) based his description of this species on a large number of specimens, the characters he used are not diagnostic of individual species of *Kaskia.* When the type specimens of *K. chesterensis, K. wilsoni,* and *K. gersnai* are plotted on his scattergrams, they all fall within the fields produced by *K. rosei.* Consequently, this ill-defined species may actually be synonymous with other species assigned to this genus. The type specimen of this species is almost certainly conspecific with *K. chesterensis,* while one of the paratypes (Cisne, 1967, text-fig. 1J) appears to be *K. wilsoni.* The mixing of these disarticulated tergites produces a distinct species on the cladogram, but whether these parts are from a single species remains in question. If in the future it is found that this is a distinct species, it will almost certainly have close common ancestry with both *K. chesterensis* and *K. wilsoni.*

KASKIA WILSONI (Walter, 1924)
Figure 9.1–9.11

Griffithides wilsoni WALTER, 1924, p. 324–327, pl. 27, figs. 1–6.
Kaskia wilsoni BREZINSKI, 2003, p. 370.

Diagnosis.—Glabella mildly forward expanding, somewhat constricted at γ. Straight section in posterior facial sutures noticeably shorter than most congenitors. Pygidium parabolic, pleural furrows deeply incised.

Description.—Walter (1924), p. 324–325.

Types illustrated.—Holotype, a badly crushed specimen with thoracic segments missing, from the Chesterian ''Pella beds'' of Iowa, SUI 9082. Paratypes, a cranidium, SUI 9100 and two pygidia SUI 9023, 9024.

Other material.—A cranidium and pygidium from the Wymps Gap Limestone Member of the Mauch Chunk Formation of southwestern Pennsylvania, CM 55333, 55334.

Distribution.—Pella beds of Iowa, lower Chesterian of Indiana, Maxville Limestone of Ohio, Wymps Gap Limestone of the Mauch Chunk Formation of Pennsylvania, and the Greenbrier Limestone of Maryland and West Virginia.

Discussion.—In his original description and discussion of *Griffithides wilsoni,* Walter (1924) included a variation, *G. wilsoni* var. *genevievensis,* with this taxon. The current phylogenetic study clearly demonstrates that *G. wilsoni* var. *genevievensis* is a distinct species from *G. wilsoni. Kaskia wilsoni* is a relatively widespread species known from the type area of Iowa and the Illinois and Appalachian basins. It is characterized by a weakly anteriorly broadened frontal glabellar lobe, a relatively short pygidium that has a subtrapezoidal axial profile, and poorly defined interpleural furrows.

KASKIA GENEVIEVENSIS (Walter, 1924)
Figure 9.12–9.17

Griffithides wilsoni var *genevievensis* WALTER, 1924, p. 324–327, pl. 27, figs. 9, 10.
Kaskia genevievensis BREZINSKI, 2003, p. 370.

Diagnosis.—Pygidium strongly vaulted, axis wide, pleural furrows poorly defined. Palpebral lobes large. Cranidial width at β wide, anterior facial sutures strongly divergent between γ and β. β broadly rounded. Posterior facial sutures with short, straight, posteriorly divergent section.

Description.—Glabella moderately laterally inflated in the frontal lobe, reaching poorly defined anterior border. Base of glabella subquadrate. S1 narrow, deep, with an oblique bend so that it intersects occipital furrow at right angle. L1 sub-oval in outline, even with base of glabella. S2 short, faint, strongly oblique to dorsal furrow. Occipital furrow narrow, deep, straight. Dorsal furrow narrow, deep, straight between palpebral lobes, slightly divergent at γ. Palpebral lobes large, nearly semicircular in outline. Anterior facial sutures strongly divergent from γ to β, broadly rounded at β. Posterior facial

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CM 55328, ×4; *8,* dorsal view of partially exfoliated paratype cranidium, CM 55302, ×4; *9–11,* dorsal, lateral, and posterior views of testate paratype pygidium, CM 55326, ×3; *12,* partial paratype pygidium, CM 55327, ×4. *13–24, Paladin wapanukaensis* n. sp.; *13–15,* dorsal, lateral, and anterior views of testate holotype cranidium, CM 55319, ×4; *16,* incomplete testate paratype cranidium, CM 55323, ×4; *17,* dorsal partial testate paratype cranidium, CM 55303, ×4; *18,* dorsal view of partial testate paratype pygidum, CM 55322, ×4; *19–21,* dorsal, lateral, and posterior views of partial testate paratype pygidium, CM 55321, ×4; *22–24,* dorsal, lateral and posterior views of partial testate paratype pygidium, CM 55320, ×3. *25–30, Paladin pleisiomorphus* n. sp.; *25–27,* dorsal, anterior, and lateral views of partial, testate holotype crandium, CM 55316, ×4; *28–30,* dorsal, lateral, and posterior views of partial testate paratype pygidium, CM 55317, ×4.

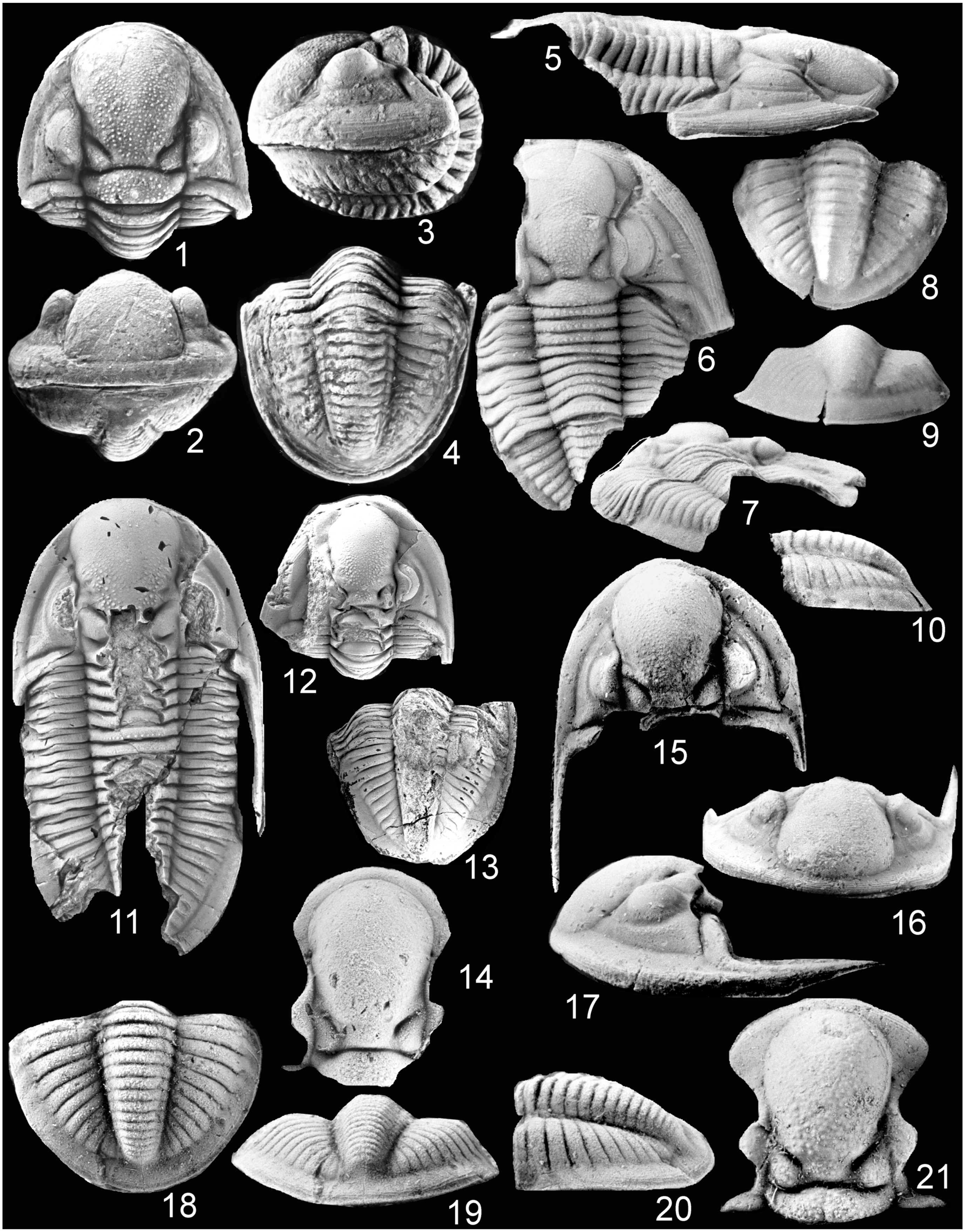

FIGURE 8—*1–4, Kaskia chesterensis* Weller; dorsal, anterior, lateral and pygidial views of enrolled testate holotype cephalon, CFM 34437, ×4. *5–10, Kaskia osagensis* (Cisne); *5–7,* lateral, dorsal, and posterior views of partial holotype exoskeleton, YPM 24872, ×3; *8–10,* dorsal, posterior, and lateral view of testate

sutures with a short, straight, posteriorly divergent section. Occipital ring broad, nearly flat along axial line. Visual surface large, almost hemispherical, with narrow eye socle and furrow below. Librigenae concave, with broad concave, inflection marking border furrow; margin broadly rounded.

Pygidium semicircular in outline, strongly ventrally arched. Axis broad, 0.4 times maximum pygidial width, evenly rounded in transverse and longitudinal profiles, composed of 12–14 broad rings separated by narrow, shallow, straight ring furrows, bluntly posteriorly rounded. Pleural fields narrow, evenly arched in transverse and longitudinal profiles, composed of 7–9 broad, smooth ribs separated by narrow, shallow, straight pleural furrows. Margin arched continuously with pleurae, smooth, of equal width along entire margin.

Type material.—Lectotype, a pygidium from the Pella beds of Iowa, SUI 9056. Paralectotype, a pygidium from the same locality, SUI 9083. Other specimens, a crushed enrolled specimen from the Pella beds, SUI 33530.

Distribution.—Present in the lower Chesterian Pella beds of Iowa.

Discussion.—Walter (1924) believed that the specimens of a variation of *Griffithides wilsoni* he named *genevievensis,* and present within the Pella beds of Iowa, were identical to a species present in the St. Genevieve Limestone of Missouri. The author has collected trilobite specimens from the St. Genevieve Limestone of Missouri, and that species is decidedly different from the type specimens of *K. genevievensis.* The Missouri species has a longer pygidium with more deeply incised pygidial furrowing. The St. Genevieve species may be assignable to *K. longispina* (Strong), but insufficient specimens are currently available to be certain of this interpretation. Consequently, the variation of *K. wilsoni* named *genevievensis* by Walter (1924) is herein elevated to species status even though that species may not be present in the St. Genevieve Limestone.

Kaskia genevievensis is distinguished by the shallow pleural furrows, broad axis which is 0.40 times the maximum pygidial width, and by the strongly forwardly divergent facial sutures that are broadly rounded at β.

Kaskia gersnai new species
Figure 9.18–9.25

Paladin cf. *P. pyriformus* Brezinski, 1988, p. 940, fig. 2.35–2.39.

Diagnosis.—Glabella long, narrow, with little lateral inflation of the frontal lobe; palpebral lobes very narrow, anteriorly located. Cranidial width at β nearly the same as glabellar width. Pygidium narrow, subtriangular in outline.

Description.—Exoskeleton of moderate relief and vaulting. Glabella longitudinally elongate, only slightly inflated in the frontal lobe, moderately convex in transverse and longitudinal profiles, mildly constricted at γ, and covered by granular prosopon. Anterior portion of the frontal glabellar lobe meets anterior margin at indistinct border that is rounded. L1 small, suboval to subtriangular in outline, with slight posterior inflation. S1 narrow, fairly straight, sharply recurved at occipital furrow; S2 and S3 very shallow, short, faint. Dorsal furrow nearly straight between γ and ζ, deeply incised, follows closely the sides of the glabella from posterior terminus of cranidium to γ, mildly divergent to β. Palpebral lobes very narrow, crescentic in outline, flattened adaxially. Anterior facial sutures with a long straight section from γ to β, sharply rounded at β. Occipital ring broad; occipital furrow, deep, narrow, and sinuous. Posterior section of facial sutures with a very long, straight section.

Thorax of nine segments, axis rounded in transverse profile. Pleural fields flat adjacent to dorsal furrow, sharply arched at fulcrum, nearly vertical at margin.

Pygidium long and narrow, outline subtriangular, vaulting moderately high, length 1.04 to 1.05 times the width. Axis broad, slightly tapering posteriorly, 0.84 to 0.86 the total pygidial length, 0.46 the total width, and composed of 15 to 17 rings; bluntly rounded at terminus. Rings semicircular in transverse profile with 7 fine granules situated along each posterior margin. Interring furrows shallow and narrow. Pleural fields composed of 9 to 11 ribs, flat adjacent to the dorsal furrow, becoming convex and steeply inclined to the border. Well-developed border mildly convex and sloping to the margin.

Etymology.—Named in honor of the late Dr. Charles J. Gersna.

Material.—Holotype, a partial, enrolled specimen from the Savage Dam Member of the Greenbrier Formation, from abandoned quarry along US Route 40, 1.5 km west of Chalkhill, Fayette County, Pennsylvania (39°50′47″N, 79°38′16″W), CM 55329. Paratypes, a partial enrolled exoskeleton from the type locality, CM 55330, and 2 cranidia, CM 55331, 55332, from the Wymps Gap Limestone of the Mauch Chunk along N & S railroad tracks 2 km west of Bolivar, Westmoreland County, Pennsylvania (40°24′34″N, 79°09′18″W).

Distribution.—Known from the Savage Dam Member of the Greenbrier Formation, lower to middle Chesterian (late Visean) of southwestern Pennsylvania and western Maryland.

Discussion.—Specimens assigned to *Paladin* cf. *P. pyriformus* Chamberlain, 1969 by Brezinski (1988) are herein reassigned to *K. gersnai* n. sp. Recent examination of the holotype of *P. pyriformus* Chamberlain has shown that it possesses a medial preoccipital lobe, and a distinct anterior border furrow to the cranidium. These characters are more in keeping with the genus *Pseudophillipsia* (*Carniphillipsia*) Hahn and Brauckmann (1975) rather than *Paladin* (Brezinski, 2003).

Kaskia gersnai n. sp. is most similar to *K. wilsoni* in that both have narrow glabellas that reach the anterior border and approach the anterior facial sutures at β. However, *K. gersnai* differs from *K. wilsoni* as well as all other congenitors by having a distinctly longer cranidium, and an elongate pygidium that is triangular in outline.

Kaskia rollinsi new species
Figure 9.26–9.37

Diagnosis.—Glabella broad, short, constricted at γ; frontal lobe bluntly anteriorly rounded, meeting to overhanging anterior margin. S1 narrow, deeply incised, evenly arcuate. Palpebral lobes very narrow. Pleural fields strongly arched in profile. Lateral cephalic border and pygidial border concave.

Description.—Glabella moderately vaulted, subcylindrical, mildly anteriorly widened, squared at base, constricted in large individuals, covered with fine granular prosopon, frontal lobe bluntly anteriorly rounded. Frontal lobe meeting anterior margin vertically or overhanging it. S1 arcuate, narrow, deeply incised; S2–S3 shallow, short, straight. L1 even with posterior of glabella, inflated, suboval in outline. Dorsal furrow narrow, deep, straight in small specimens, sinuous in large specimens. Occipital furrow narrow, deep, straight. Occipital ring moderately wide. Fixigenae narrow. Anterior facial sutures moderately divergent between γ and β, sharply rounded at β. Posterior facial sutures with very long straight section. Palpebral lobes small, narrow (transverse), crescentic in outline. Librigenae with a wide, convex lateral border.

Pygidium semielliptical in outline. Axis moderately vaulted, arched in longitudinal profile; slightly overhanging, bluntly rounded, posterior terminus of axis; semicircular in transverse profile, 0.43 times maximum pygidial width; composed of 14 to 15 narrow, longitudinally rounded rings with distinct shoulders and a row of granules along apex. Ring furrows narrow, straight, deep. Dorsal furrow straight, shallow, narrow. Pleural fields strongly arched in transverse profile, mildly arched in longitudinal profile, composed of 9 to 10 rounded ribs that are nearly flat adjacent to axial furrow and vertical at border, covered by fine granules. Pleural furrows narrow, deep, straight. Border wide, of equal width, concave in profile.

Etymology.—Named in honor of Dr. Harold B. Rollins.

Type material.—Holotype, an incomplete cranidium from the Vienna Limestone along in bluffs of Mississippi River, NW¼, sec. 30, T7S, R6W, Randolph County, Illinois, CM 55335. Paratypes, two cranidia, CM 55336, 55337, two pygidia, CM 55339, 55340, and a librigenae CM 55338, from same location as the holotype.

Distribution.—Currently known only from the late Chesterian (early Serpukhovian) Vienna Limestone and possibly the Kinkaid Limestone of Illinois.

Discussion.—*Kaskia rollinsi* n. sp. can be distinguished from other congeners by the broad glabella that is bluntly rounded in

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paratype pygidium, YPM 24873. *11–14, Kaskia longispina* (Strong); *11,* dorsal view of incomplete holotype specimen, UM 21223, ×5; *12, 13,* dorsal and pygidial views of enrolled paratype specimen, UM 21222, ×3; *14,* dorsal view of incomplete cranidium from the St. Genevieve Limestone, St. Genevieve, Missouri, CM 55341. *15–21, Kaskia rosei* (Cisne); *15–17,* dorsal, anterior, and lateral views of testate holotype cephalon, YPM 24861, ×4; *18–20,* dorsal, posterior, and lateral views of testate paratype pygidium, YPM 24869, ×3; *21,* dorsal views of partial testate paratype cranidium, YPM 24863, ×3.

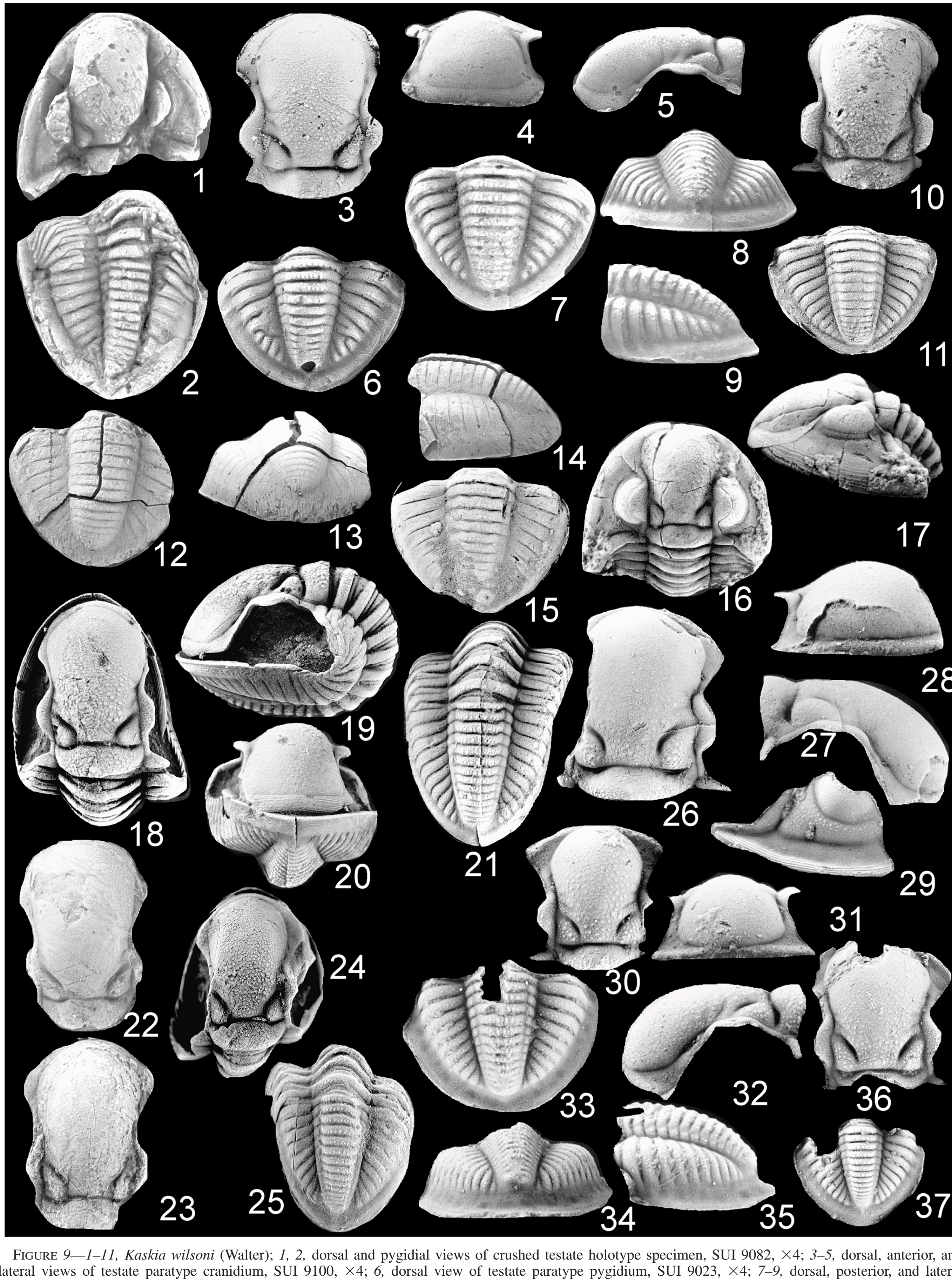

FIGURE 9—*1–11, Kaskia wilsoni* (Walter); *1, 2,* dorsal and pygidial views of crushed testate holotype specimen, SUI 9082, ×4; *3–5,* dorsal, anterior, and lateral views of testate paratype cranidium, SUI 9100, ×4; *6,* dorsal view of testate paratype pygidium, SUI 9023, ×4; *7–9,* dorsal, posterior, and lateral

the frontal lobe, very narrow (transverse) and short palpebral lobes, inflated L1, broadly concave lateral border, highly vaulted pygidium with an axis that is strongly arched in longitudinal profile and overhangs the posterior axial terminus, and concave pygidial border. *Kaskia rollinsi* n. sp. is the youngest taxon currently known from this lineage. The concave lateral and pygidial border are unique to this species within this lineage. The type material is from the late Chesterian (early Serpukhovian) Vienna Limestone. However, several partial pygidia have also been collected from the Kinkaid Limestone. The Kinkaid material has the broad axis and longitudinal axial arching as do the types. Consequently, these specimens can only tentatively be assigned to *K. rollinsi.*

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views of testate paratype pygidium, SUI 9024, ×4; *10,* testate cranidium from the Wymps Gap Member of the Mauch Chunk Formation of Pennsylvania, CM 55333, ×3; *11,* dorsal view of testate pygidium from same location as 10, CM 55334, ×3. *12–17, Kaskia genevievensis* (Walter); *12–14,* testate lectotype pygidium, SUI 9056, ×4; *15,* testate paralectotype pygidium, SUI 9083, ×4; *16, 17,* dorsal and lateral views of testate cephalon from the Pella Formation of Iowa, SUI 33530, ×4. *18–25, Kaskia gersnai* n. sp.; *18–21,* dorsal, lateral, anterior, and pygidial views of enrolled testate holotype, CM 55329, ×5; *22,* incomplete testate paratype cranidium, CM 55331, ×5; *23,* partial testate paratype cranidium, CM 55332, ×5; *24, 25,* incomplete enrolled testate paratype specimen, CM 55330, ×4. *26–37, Kaskia rollinsi* n. sp.; *26–28,* dorsal, anterior, and lateral, views of partial testate holotype cranidium, CM 55335, ×3; *29,* partial testate paratype librigenae, CM 55338, ×3; *30–32,* dorsal, anterior, and lateral views of partial testate paratype cranidium, CM 55336, ×3; *33–35,* dorsal, posterior, and lateral views of testate paratype pygidium, CM 55339, ×3; *36,* partial testate paratype cranidium, CM 55337, ×5; *37,* small testate, paratype pygidium, CM 55340, ×3.