Journal of Paleontology, 90(1), 2016, p. 59–77

0022-3360/16/0088-0906
doi: 10.1017/jpa.2015.71

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

Systematics and paleobiogeographic significance of the Upper Ordovician pterygometopine trilobite *Achatella* Delo, 1935

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Abstract.—Study of type and new material of the pterygometopine *Achatella* Delo, 1935 demonstrates the presence of four species in Upper Ordovician (Katian) strata of Laurentian North America, *A. achates* (Billings, 1860) from the northeastern United States and the St. Lawrence lowlands of Canada, *A. carleyi* (Meek, 1872) from the Cincinnati region, Ohio and Kentucky, *A. katharina* (Bradley, 1930), from Missouri and Oklahoma, and *A. clivosa* Lespérance and Weissenberger, 1998 from the Gaspé Peninsula, Quebec. Perhaps as many as five additional species are present in Sandbian–Katian strata of the Laurentian terranes of Scotland and Northern Ireland, although only three of these are known well enough to code for phylogenetic analysis. The oldest pterygometopines, including species of *Achatella*, are known from Middle Ordovician strata of Baltica. Phylogenetic analysis supports a single migration event from Baltica from Laurentia, followed by a modest diversification in the latter region.

Introduction

Pterygometopine trilobites are well represented in Middle and Upper Ordovician strata of the western European countries of Baltica (Jaanusson and Ramsköld, 1993), but are restricted to species of the youngest genus, *Achatella*, Delo 1935, in Laurentian North America. *Achatella* enters the succession in Laurentia during the Katian, but its record in Baltica extends down into Dariwillian strata (McNamara, 1980; Jaanusson and Ramsköld, 1993) As such, the appearance of *Achatella* is generally viewed as a case of immigration (e.g., Ludvigsen and Chatterton, 1982) associated with the "Trenton transgression" (Shaw and Fortey, 1977; Ludvigsen, 1978b). *Achatella* becomes a persistent element in Upper Ordovician faunas of eastern and central North America, but the most recent revision (Ludvigsen and Chatterton, 1982) was based solely on material from the Lake Simcoe and Ottawa regions of Ontario and Quebec. In this paper, we offer a broader assessment of the genus from new and archival specimens from Oklahoma, Missouri, Illinois, Kentucky, and Ontario.

Ludvigsen and Chatterton's (1982) study of Pterygometopidae proposed a traditional, stratigraphic phylogeny in which Pterygometopinae was represented by *Achatella*, *Pterygometopus*, and *Estoniops*; *Achatella* was interpreted as a descendant of *Pterygometopus*. In this study, we assess the relationship between Baltic and Laurentian species attributed to *Achatella* with a computer-based parsimony analysis. This analysis will place hypotheses of immigration of *Achatella* on a firmer footing, and is a first step toward a more comprehensive revision of Family Pterygometopidae.

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Stratigraphic setting

Achetella has a paleogeographic range that spans Laurentia and Baltica. Geographic and stratigraphic occurrences of Baltic species are reviewed by Jannusson and Ramsköld (1993) and by Pärnaste et al. (2013). Distribution of Laurentian species is discussed below.

Ohio and Kentucky.—*Achatella carleyi* (Meek, 1872) was described from Katian (Maysvillian) strata in the Cincinnati, Ohio, region. The original collecting horizon was listed simply as "the Cincinnati group of the Lower Silurian," but Foerste (1919) considered *A. carleyi* to occur in the Fairmount Member of the Maysville Formation. In current nomenclature, the Fairmount is the younger of two members of the Fairview Formation and (Datillo et al., 2008, fig. 2) and lies in depositional sequence C2. New sclerites of *A. carleyi* were collected from older strata of the Fulton Submember at the base of the Kope Formation (Datillo et al., 2008, fig. 2) at the Blue Licks locality in northern Kentucky (see Bulinski 2007). This new material is fragmentary and generally poorly preserved; it adds no new information on anatomy of the species and is not illustrated. However, they provide important data on stratigraphic occurrence and extend the range of *A. carleyi* down to the lower part of sequence C1.

Missouri and Illinois.—*Achatella katharina* (Bradley, 1930) is from the Upper Ordovician Kimmswick Limestone in this region and, contrary to Ludvigsen and Chatterton's (1982) interpretation, it is a valid species rather than a junior synonym of *A. achates* (Billings, 1860). Bradley's holotype and some paratypes were collected near Batchtown, Calhoun County, Illinois, but other paratypes are from Glen Park, Jefferson County, Missouri. We were unable to gain access to the abandoned quarries at Glen Park, and could not locate the Batchtown site.

New sclerites of *A. katharina* were collected from two previously unstudied localities that will be described in detail elsewhere. Section M was measured and sampled at a large road cut through the uppermost Decorah and Kimmswick formations along County Road M, Jefferson County, Missouri, 200 m southeast of the intersection with Old Lemay Ferry Road, about 6.5 km west of the intersection with Interstate 55, and about 8.5 km west of Bradley's (1930) Glen Park locality. Material was collected about 16 meters from the base of the section. Section 79-M was at a low road cut along State Highway 79, Lincoln County, Missouri, approximately 5.25 km south of the village of Elsbury, about 1.25 km north of the intersection with County Road MO-M, and about 13 km northwest of Bradley's (1930) Batchtown locality. Sclerites of *Achatella* were collected 1 m above the base of the section. At both of the new sections, the sampled horizons are likely near the base of the C1 sequence (Swisher, 2015).

Oklahoma.—Amati and Westrop (2006) reported *Achatella* from the Upper Ordovician (latest Sandbian–Katian) Viola Springs Formation as part of their *Thaleops* Biofacies, and further study demonstrates that it represents *A. katharina*. The species is present in the Katian reference section at State Highway 99, Pontotoc County (Goldman et al., 2007; see Amati, 2014, for a section log), ranging from 38 to 51 m above the base of the Viola Springs, and probably falls in sequence M6 and, possibly C1 (Westrop et al., 2012; Swisher, 2015; see Young et al., 2005 for an alternative interpretation). As such, the occurrence of *A. katharina* probably overlaps with the range in Missouri, where it was sampled from what is likely the lower part of sequence C1.

New York, Ontario, and Quebec.—The type species, *Achatella achates* (Billings, 1860), was initially reported from the "Trenton Limestone" in Ottawa, Ontario, and subsequent work shows that this occurrence lies within upper Trenton Group strata (Ludvigsen and Chatterton, 1982) that are currently assigned to the Lindsay Formation (Dix et al., 2007, fig. 10); archival material at the Royal Ontario Museum from the other side of the Ottawa River in Hull, Quebec, is simply listed as from the "Trenton Group." *Achatella achates* is also known from the underlying Verulam Formation (Wilson, 1947; Ludvigsen and Chatterton, 1982). Archival material from the Royal Ontario Museum included in this study is from the Verulam Formation at various quarries in the Lake Simcoe region, Ontario, about 285 km southwest of Ottawa. These include the well-known quarries at Gambridge, and Lakefield (McFarland et al., 1999). The range of *A. achates* extends into New York as well, with occurrences reported from the Rust Formation (Brett et al. 1999).

A second species, *Achatella clivosa* Lespérance and Weissenberger, 1998, occurs in the Late Ordovician (late Katian; Ashgill) Pabos Formation and the informal, correlative Grande Coupe beds, of the Percé area, Quebec.

Laurentian Britain.—At least five species of *Achatella* have been reported from the Laurentian terranes (Chew and Strachan, 2013, fig. 2) of Scotland and Northern Ireland (Morris, 1988, p. 11), although only three of these are known well enough to merit discussion. In the Girvan area of Scotland, the mostly deep water, Middle to Upper Ordovician succession of the Midland Valley Terrane is a cover sequence above the Ballantrae ophiolite complex. The latter was emplaced on the Laurentian margin during Early-Middle Ordovician continent–arc collision (Chew and Strachan, 2013). *Achatella consobrina* (Tripp 1954) is from the Kiln Mudstone Member of the Craighead Limestone (Tripp, 1980b), which is assigned to the *Dicranograptus clingani* graptolite zone (Tripp, 1980a). This zone correlates into the lower part of the Katian Stage and the M5 or M6 depositional sequences of eastern Laurentia (Goldman et al., 2007, fig. 2). As such, *A. consobrina* is approximately the same age as *A. achates* and *A. katharina* from eastern and central Laurentia. *Achatella retardata* (Reed, 1914) is younger than *A. consobrina*, occurring in the Lady Burn Starfish Beds of the South Threave Formation (Morris and Tripp, 1984; see Harper, 1982 for a review of the stratigraphy). According to Harper (1982), the South Threave Formation falls in the Rawthyan Stage of the Ashgill Series of British nomenclature, which correlates with the upper Katian (Bergström et al., 2009, fig. 1). This means that *A. retardata* is closest in age to *A. clivosa* from Quebec. Even higher in the Girvan succession is a species from the latest Ordovician (Hirnantian) High Mains Formation, identified by Owen (1986) as *A.* cf. *truncatocaudata* (Portlock, 1843). This represents the youngest occurrence of the genus.

Achatella truncatocaudata was originally described (Portlock, 1843) from the Killey Bridge Beds in County Tyrone, Northern Ireland, which is also part of the Midland Valley Terrane (Chew and Strachan, 2013). This unit is assigned to the Cautleyan and, probably, Rawthyan stages of the Ashgill Series (Cripps, 1988; Harper and Parkes, 2000) and thus falls in the upper Katian. A single cephalon from the Knockerk House Sandstone Member of the Knockerk Formation, Gangreeth Terrane, was assigned questionably to *A. truncatocaudata* by Romano and Owen (1993, fig. 5A, F). As Romano and Owen recognized, this specimen is characterized by anteriorly positioned eyes and in our view records a distinct species. The Grangegeeth Terrane is currently interpreted as a peri-Laurentian volcanic arc (McConnell et al., 2010), and the Knockerk House Sandstone Member was correlated into the lower part of the Laurentian Mohawkian Series by both Romano and Owen (1993) and Harper and Parkes (2000). This indicates that "*A. truncatocaudata*" from the Grangegeeth Terrane is likely latest Sandbian in age (e.g., Bergström et al., 2009, fig. 1), and is therefore significantly older than the type material from County Tyrone. It is also older than *A. achates* and *A. katharina*, the earliest species from Laurentian North America.

Phylogenetic analysis

Taxon selection and coding sources.—All species of *Achatella* from Laurentian North America were coded from examination of type or other archival material and sclerites from new field collections (Figs. 3–12), with the exception of *A. clivosa*, which is based on images published by Lespérance and

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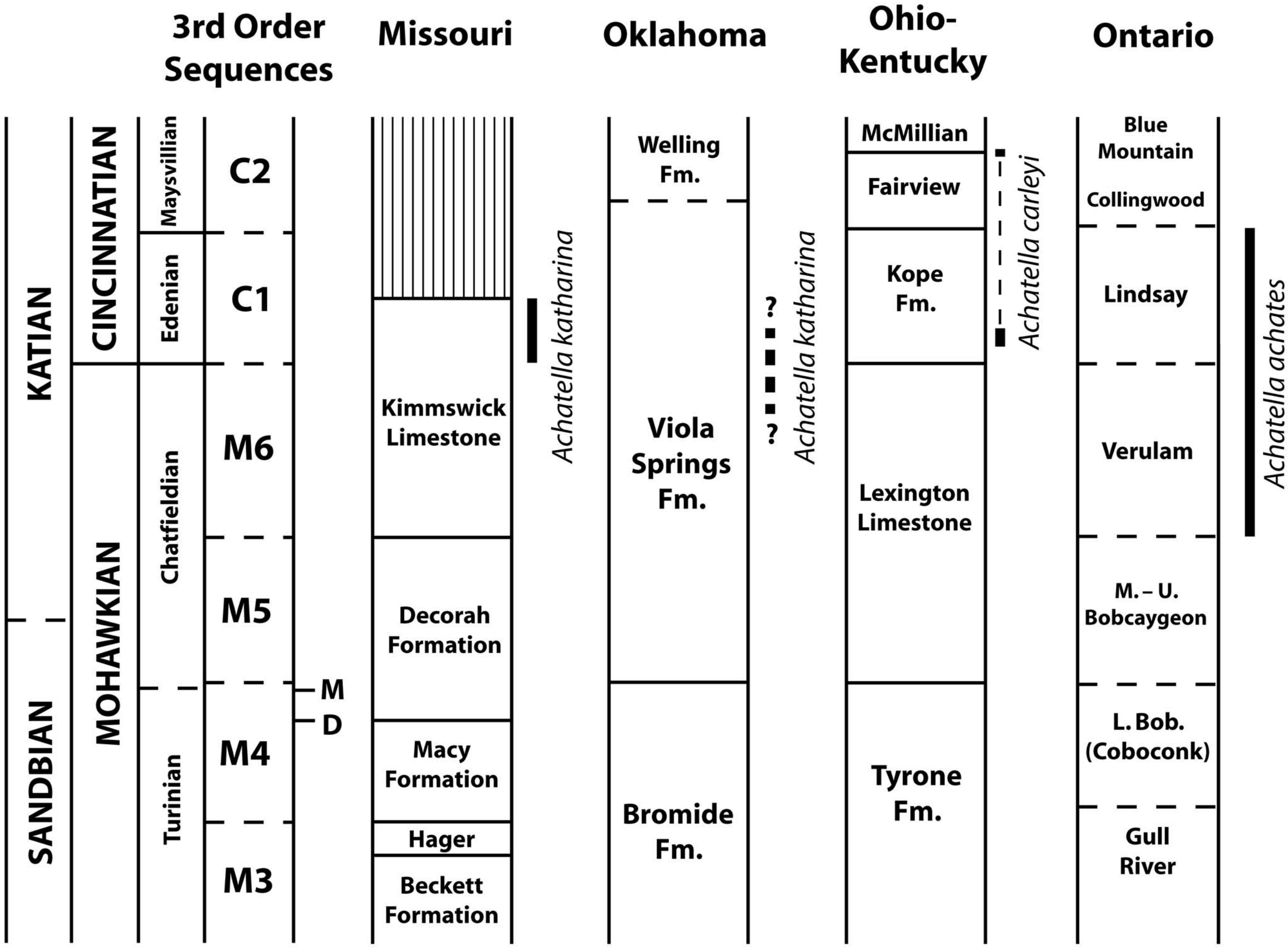

Figure 1. Stratigraphic distribution of *Achatella* species from Laurentian North America. Third order depositional sequences from Holland and Patzkowsky, 1996. Sources of regional stratigraphic data: Missouri, Swisher, 2015; Oklahoma, Amati, 2014, Carlucci et al., 2014, Westrop et al., 2012; Cincinnati, Brett et al., 2004, Datillo et al., 2008; Ontario, Mitchell et al., 2004, Sharma et al., 2003, Amati and Westrop, unpublished.

Weissenberger (1998). Coding of *A. retardata* and *A. consobrina* from the Midland Valley Terrance of Scotland used images published by Morris and Tripp (1986) and by Tripp (1954, 1980b), and *A. truncatocaudata* was coded from high-resolution images of Portlock's syntypes (GSM 13988, 19194, 19195; British Geological Survey, Keyworth, Nottingham) that are available on-line from the British Geological Survey (http://www.3d-fossils.ac.uk). *Achatella* cf. *truncatocaudata* of Owen (1986) does not differ from *A. truncatocaudata* in coding of observable character states and was not included in the analysis. *Achatella* species from Baltica, *A.schmidti* (Warburg, 1925) and *A. kuckersianus* (Schmidt, 1881) were coded using illustrations in Jaanusson and Ramsköld (1993); *Ingriops trigonocephalus* (Schmidt, 1881), which has a somewhat elongate pygidium similar to *Achatella*, was also included in the analysis and was coded largely from images in Jaanusson and Ramsköld (1993). Previous workers (e.g., Whittington, 1966; McNamara, 1980; Ludvigsen and Chatterton, 1982) have considered *Pterygometopus* to occupy a basal position in Pterygometopinae, and *P. sclerops* (Dalman, 1827) was selected as the outgroup (coding based on images in Jaanusson and Ramsköld, 1993).

Character coding.—The data matrix (Table 1) is composed of 10 ingroup species, 15 binary characters, and four unordered multistate characters (Appendix). Inapplicable character states (e.g., character 3) were handled by reductive coding (Strong and Lipscomb, 1999). Autapomophies of individual species were excluded except where parts of multistate characters (e.g., character 19), and branch collapsing rules were not enforced.

Results.—Parsimony analysis was conducted using both PAUP* (Swofford, 2001) and TNT (Goloboff et al., 2008) and yielded the same set of 42 trees, with length, 31, C.I., 0.77, R.I, 0.79; R.C., 0.62; the strict consensus tree is shown in Fig. 2.1. Tree support metrics (Fig. 2.1) were calculated using TNT and character optimization (Fig. 2.2) was performed with both PAUP* and Winclada (Nixon, 2002). Support for individual nodes was low, with only two with Bremer support greater than one; three nodes have GC values above 50, and three nodes have standard boostrap values above 50.

Achatella is defined by several synapomorphic characters (Fig. 2.2), including a relatively flat cephalon with a weak anterior arch [1(1)], subtriangular L3 lobe with conspicuous adaxial taper [7(1)] and is also longer (exsag.) than L1 and L2 [8(1)]; almost all

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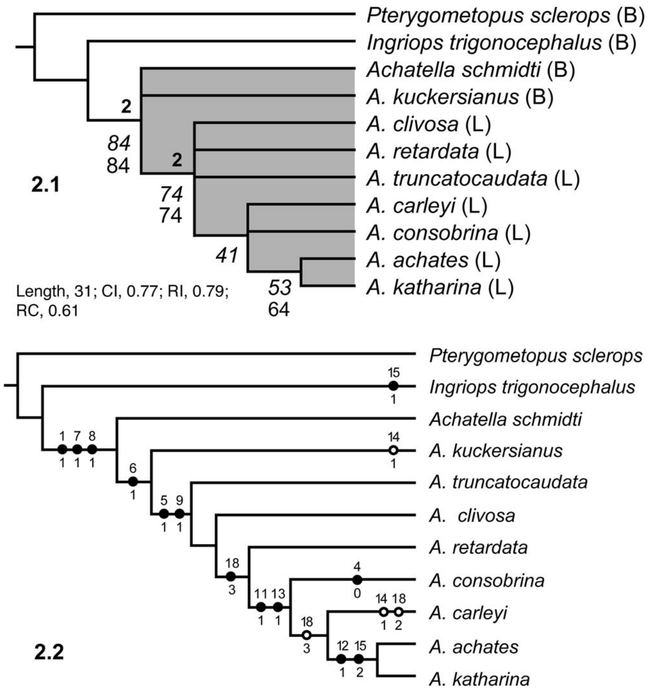

Figure 2. Results of a phylogenetic analysis of a character matrix (Table 1; see appendix for list of characters) for *Achatella* species. (**1**) Strict consensus of 42 trees discovered with a branch-and-bound search (implicit enumeration). Support metrics (calculated in TNT; Goloboff et al., 2008) show by numbers are Bremer support (boldface; only values >1 are shown), GC bootstrap support (italics) and conventional bootstrap support (roman font). Shaded region comprises species of *Achatella* as diagnosed in this study. B, species from Baltica; L, species from Laurentian North America and Britain; (**2**) optimized character distribution plotted on one of the most parsimonious trees. Numbers above circles refer to characters and those below identify particular states (Appendix). Only unambiguous transformations (i.e., optimize to the same nodes under the assumptions of both ACCTRAN and DELTRAN) are shown; filled circles show states that originate at a single node, and open circles indicate states that are homoplastic.

species possess a posterior branch of the facial suture that is nearly straight [16(1)]. *Achatella kuckersianus* (Schmidt, 1881), the type species of of *A.* (*Vironiaspis*) Jaanusson and Ramsköld, 1993, is part of a polytomy in our strict consensus tree and, accordingly, we leave *Achatella* undivided at the subgeneric level. The Laurentian species form a distinct, derived group within *Achatella*, with the representatives from Baltica lying in a basal position (Fig. 2.1). This result is consistent with a single invasion of Laurentia with subsequent radiation, rather than multiple invasions of species from Baltica.

Systematic paleontology

Repositories for figured material are indicated by the following acronyms: CM, Cincinnati Museum of Natural History, Cincinnati, OH; UC, Field Museum of Natural History, Chicago, IL; GSC, Geological Survey of Canada, Ottawa; OU, Oklahoma Museum of Natural History, Norman; ROM, Royal Ontario Museum, Toronto.

Morphological terminology follows Whittington et al. (1997); however, the occipital ring is designated LO (lobus occipitalis) and the occipital furrow is designated SO (sulcus occipitalis). Proportions expressed as percentages in the descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop.

To maximize depth of field, all digital images were rendered from stacks of images focused at 100- to 500-μm intervals using Helicon Focus 4.0 for the Macintosh <http://www.heliconsoft.com>. All specimens were coated with a sublimate of ammonium chloride prior to photography.

Family Pterygometopidae Reed, 1905

Subfamily Pterygometopinae Reed, 1905

Genus *Achatella* Delo, 1935

Diagnosis.—Cephalon relatively flat with a weak anterior arch [1(1)]. L3 lobe subtriangular with conspicuous adaxial taper [7(1)], and longer (exsag.) than L1 and L2 [8(1)]. Posterior branch of facial suture nearly straight [16(1)]. Pygidium elongate, subtriangular in outline.

Remarks.—In our analysis, *Achatella* is a clade that includes both Baltic and Laurentian species, with species from the former continent occupying a basal position in the cladogram (Fig. 2). Jaanusson and Ramsköld (1993) named a new subgenus of *Achatella*, *A.* (*Vironiaspis*), with *Phacops* (*Pterygometopus*) *kuckersianus* Schmidt, 1881, from Baltica (northern Estonia), as the type species. As this species, the only one assigned to *A.* (*Vironiaspis*) with any confidence (Jaanausson and Ramsköld, 1993, p. 766), forms part of a polytomy at the base of *Achatella* in the strict consensus tree (Fig. 2.1), subgenera are not used in this paper.

Three characters states are unambiguous synapomorphies of *Achatella* in the phylogenetic analysis (Fig. 2.2): a relatively flat cephalon with weak anterior arch [1(1)] (e.g., Figs. 5.1, 8.2, 8.5); a subtriangular L3 lobe that exhibits a conspicuous adaxial taper (7[1]), and which is longer (exsag.) than L1 and L2 (8[1]; e.g., Figs. 3.1, 8.1, 8.7). With the exception of *A. truncatocaudata*, which retains the plesiomorphic state seen in *Pterygometopus* (16[0] in the Appendix), all species of *Achatella* possess a posterior branch of the facial suture that is nearly straight (16[1]) (e.g., Fig. 8.1, 8.4). Where known, a long genal spine is present (e.g., Figs. 4.5, 8.1; *A. schmidti* [Warburg] is an exception that lacks a genal spine), and the pygidium is elongate and subtriangular in outline, with a gently rounded to pointed posterior terminus (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 2a; Figs. 5.5, 12.1, 12.4).

Laurentian species share weak expansion (tr.) of the anterior glabellar lobe (5[1]) and an apodemal pit at intersection of L3 and axial furrow (9[1]). A derived group of four Laurentian species, *A. consobrina*, *A. carleyi*, *A. katharina*, and *A. achates*, are characterized by a median embayment on the anterior glabellar margin (11[1]; e.g., Figs. 3.1, 6.4, 6.5, 8.7), and eyes that do not reach the axial furrows anteriorly (13[1]; e.g., Figs. 6.1, 6.6, 8.11). The median embayment appears to be associated with a weakly inflated, often barely perceptible, subtriangular region on the frontal lobe (e.g., Figs. 4.2, 9.5, 9.8) that corresponds to the pterygometopid cephalic muscle insertion scar as defined by Eldredge (1971). As this scar also occurs on chasmopine (Eldredge, 1971, fig. 2H) and eomonorachine (Eldredge, 1971, fig. 3) trilobites, it is

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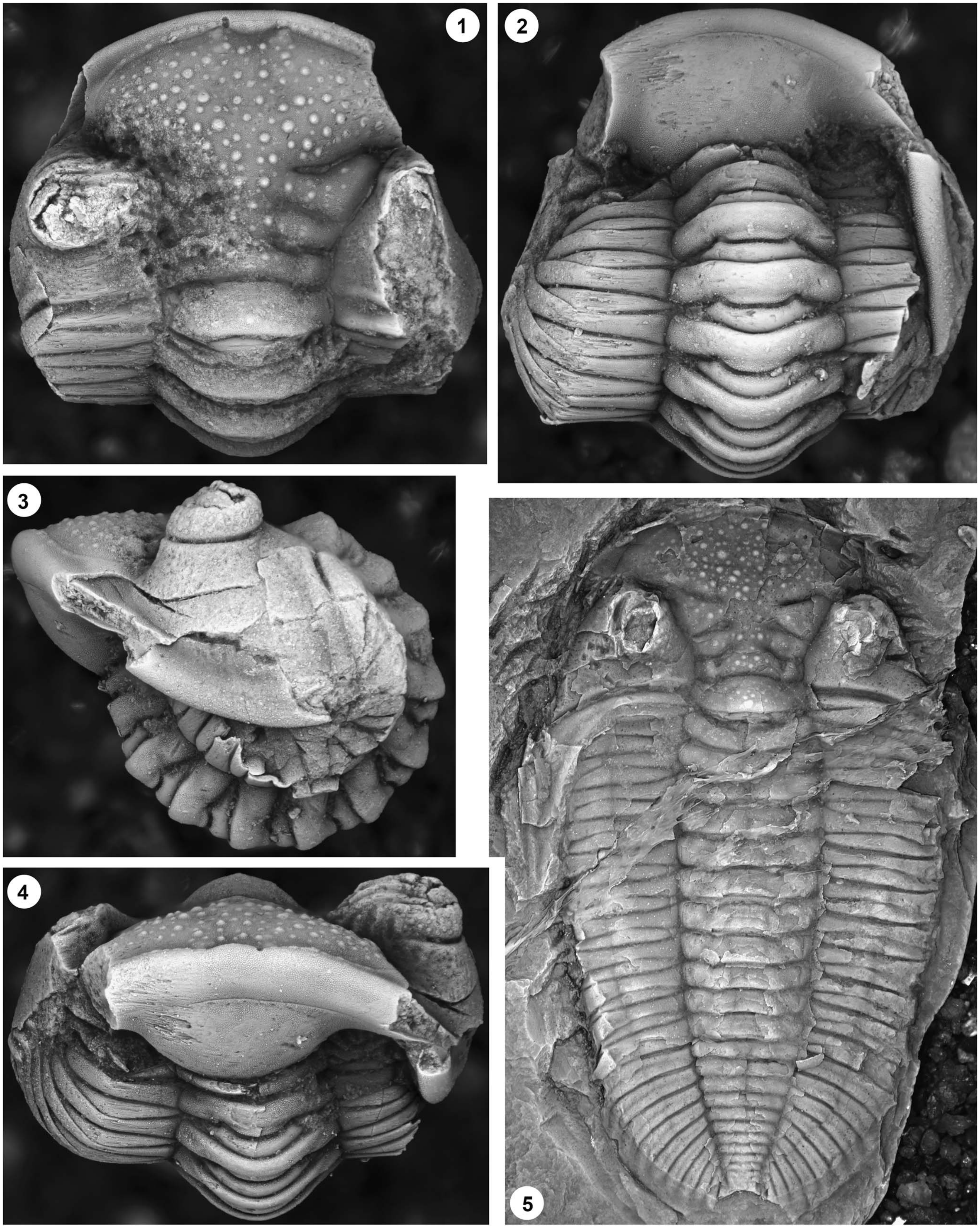

Figure 3. *Achatella achates* (Billings, 1860) from Ontario. (**1–4**) Enrolled exoskeleton (ROM 49475), dorsal, ventral, lateral and anterior views, ×7, Verulam Formation, Gamebridge Quarry, Gamebridge; (**5**) complete, somewhat compacted exoskeleton (GSC 1784, holotype), ×3.75, Lindsay Formation, Ottawa.

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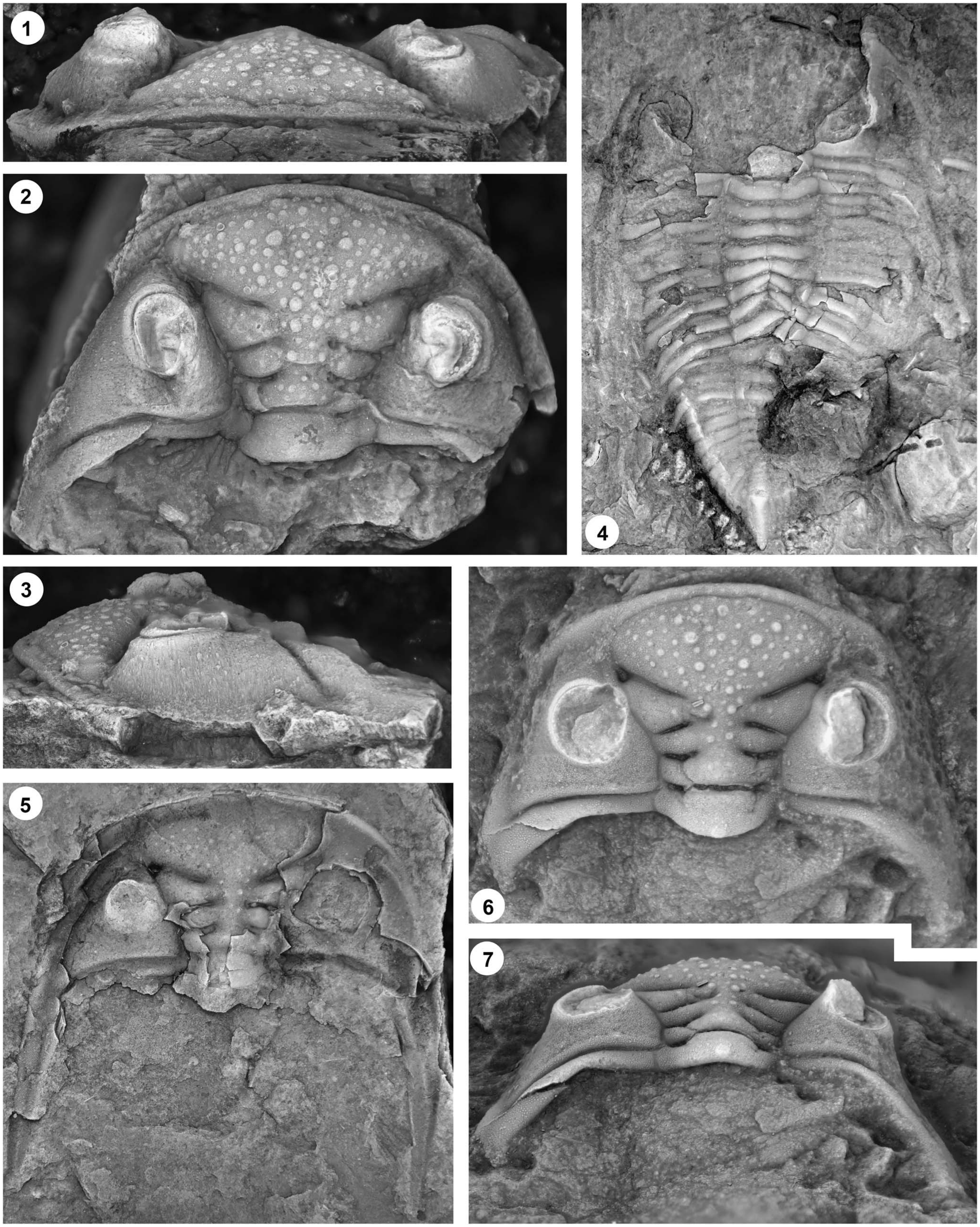

Figure 4. *Achatella achates* (Billings, 1860) from Canada. (**1–3**) Cephalon (ROM 63163), anterior, dorsal and lateral views, ×5.5, Trenton Group, Hull, Quebec; (**4**) Incomplete exoskeleton (ROM 63161), dorsal view, ×4.5, Trenton Group, Hull, Quebec; (**5**) cephalon (ROM 18747), dorsal view, ×4.5, Trenton Group, Hull, Quebec (illustrated previously by Ludvigsen and Chatterton, 1982, pl. 1, figs. 2); (**6, 7**) cephalon (ROM 63160), dorsal and posterior views, ×10, Verulam Formation, Lakefield Quarry, Lakefield, Ontario.

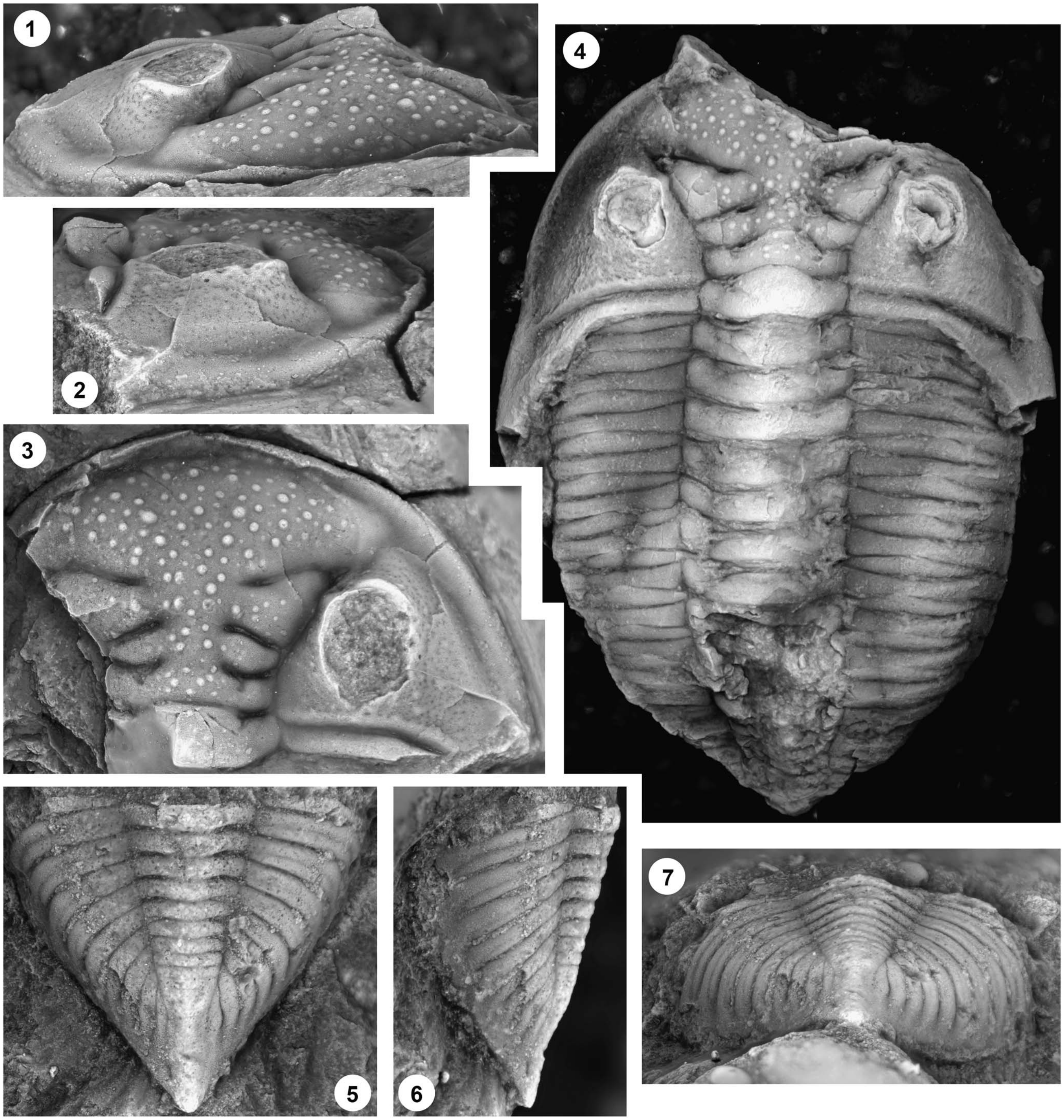

Figure 5. *Achatella achates* (Billings, 1860), Canada. (**1–3**) Cephalon (ROM 35371), anterior, lateral and dorsal views, ×6.5, Lakefield Quarry, Lakefield, Ontario; (**4**) nearly complete exoskeleton (ROM 63162), dorsal view, ×4, Trenton Group, Hull, Quebec; (**5–7**) pygidium (ROM 63159), dorsal, lateral and posterior views, ×10, Verulam Formation, Gamebridge Quarry, upper face.

very likely plesiomorphic for *Achatella*. However, similar triangular scars occur without a median embayment in other species of *Achatella* (e.g., Owen, 1986, fig. 2a), so that the embayment itself is interpreted as an apomorphic state. In some species, the edges of the embayment are marked by conspicuous tubercles (e.g., Figs. 3.1, 9.5, 9.7. 9.8).

Among other pterygometopines, *Ingriops* Jaanusson and Ramsköld, 1993, is likely the closest relative of *Achatella* from the presence of a distinct genal spine and a relatively long pygidium (Jaanusson and Ramsköld, 1993, pl. 5, fig. 1; see also Schmidt 1881, pl. 1, figs. 9, 10).

Achatella achates (Billings, 1860)
Figures 3–5

1860 *Dalmanites achates* Billings, p. 63, fig. 9.
1897 *Dalmanites achates*; Clarke, p. 726, fig. 44.
?1910 *Dalmanites carleyi-rogersensis* Foerste, p. 85.

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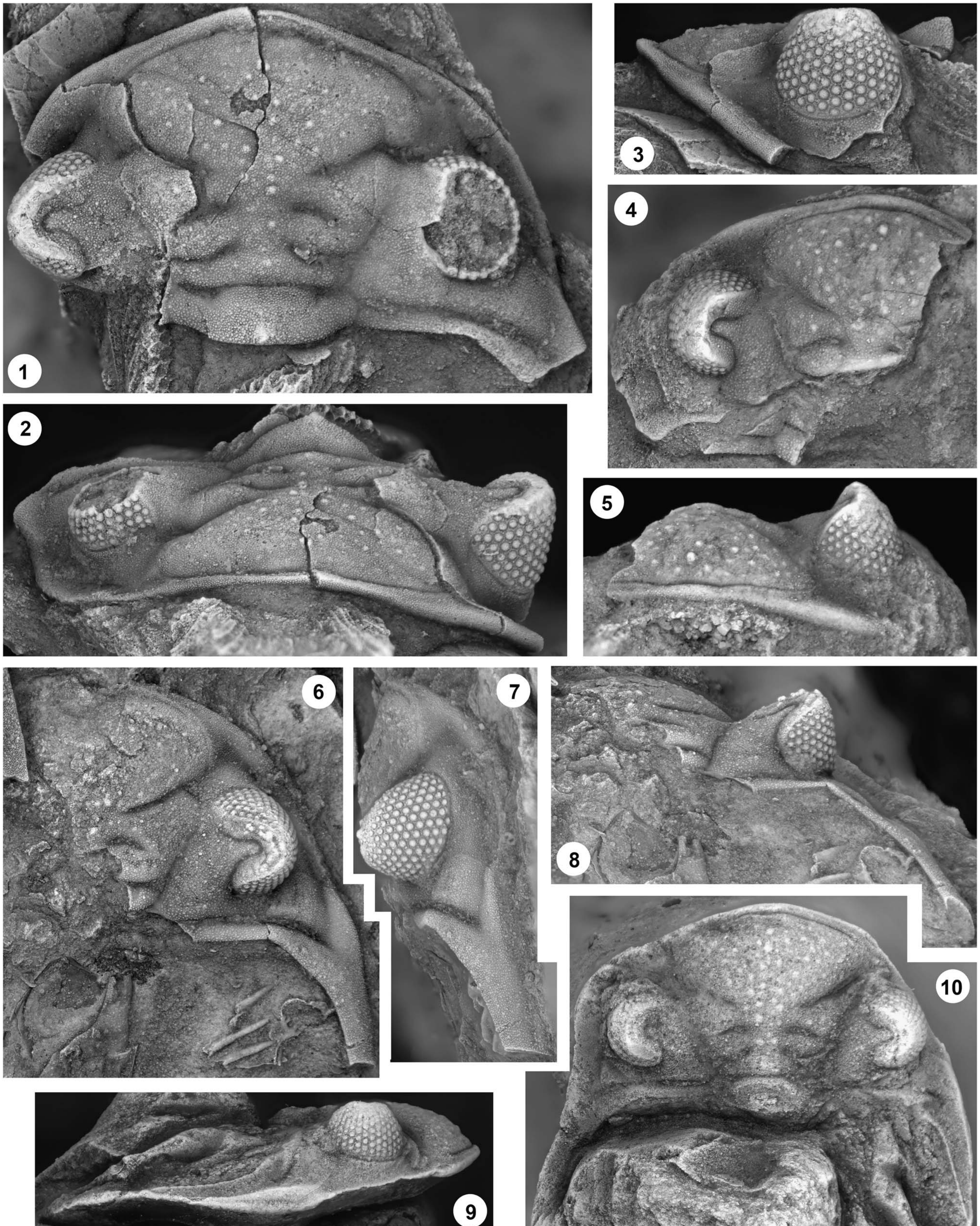

Figure 6. *Achatella carleyi* (Meek, 1872), Cincinnati region, Ohio. (**1–3**) Cephalon (CM 51280a), dorsal, anterior and lateral views, ×8, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Dues Road at intersection with Ocean Road; (**4, 5**) cephalon (CM 31699a), dorsal and anterior views, ×12, "Lorraine Group" Formation, Cincinnati, Hamilton County, Ohio; (**6–8**) cephalon (CM 51280b), dorsal, lateral and posterior views, ×8, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Dues Road at intersection with Ocean Road; (**9, 10**) cephalon (UC 965; lectotype), lateral and dorsal views, ×8, Fairview Formation, Cincinnati.

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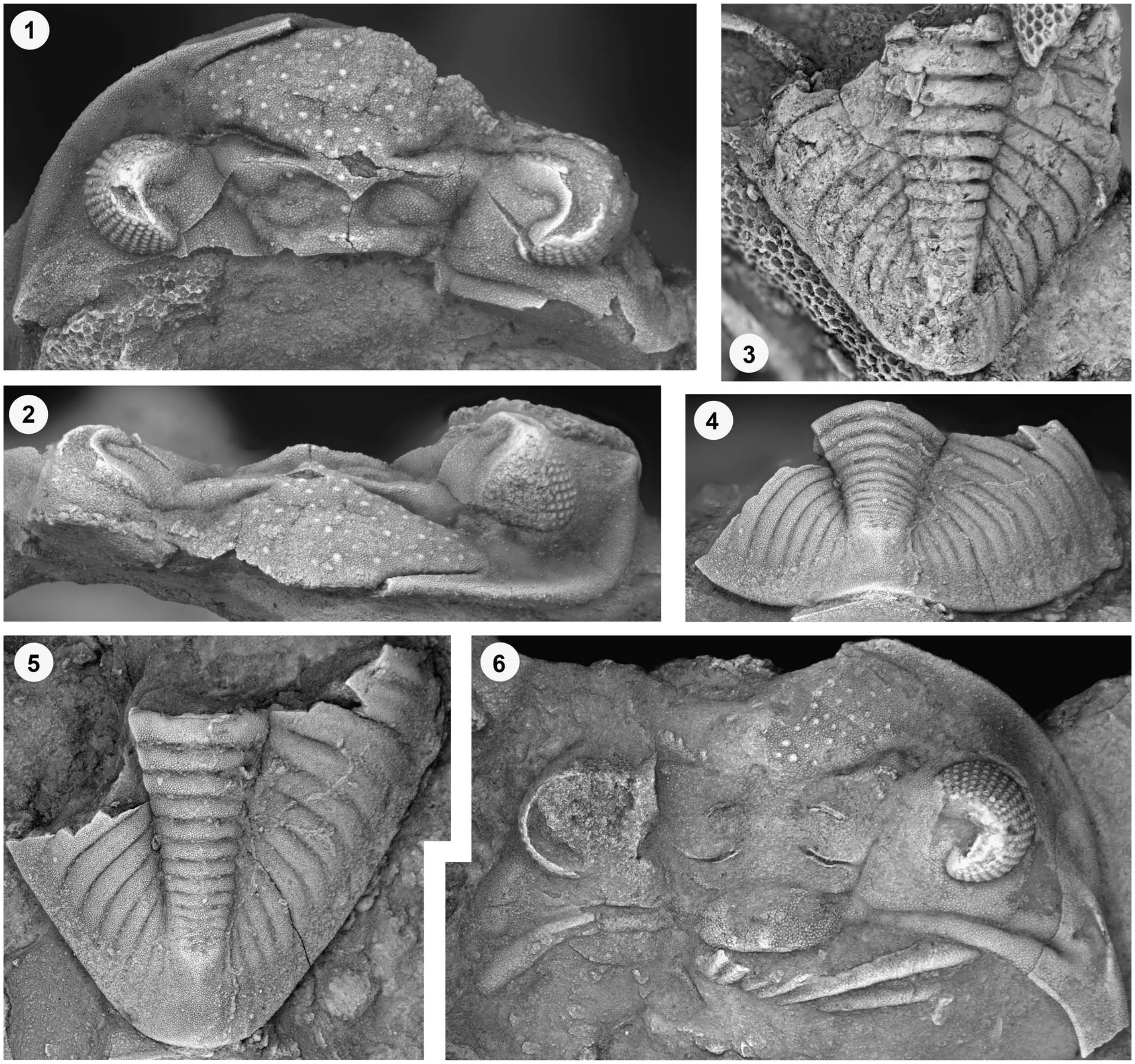

Figure 7. *Achatella carleyi* (Meek, 1872), Cincinnati region, Ohio. (**1, 2**) Cephalon (CM 51280c), dorsal and anterior views, x9, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Dues Road at intersection with Ocean Road; (**3**) pygidium (CM 31699c), dorsal view, ×10, Lorraine Group", Cincinnati, Ohio; (**4, 5**) pygidium (CM 51280d), posterior and dorsal views, ×7, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Dues Road at intersection with Ocean Road; (**6**) cephalon (CM 31699b), dorsal view, ×6, "Lorraine Group," Cincinnati, Ohio.

?1914 *Dalmanites achates;* Foerste, p. 147, pl. 1, fig. 18.
1919 *Pterygometopus achates*; Foerste, p. 397, pl. 19, fig. 8.
?1919 *Pterygometopus carleyi-rogersensis*; Foerste, p. 398, pl. 19, figs. 18a, b.
1921 *Dalmanites achates*; Raymond, p. 38, pl. 11, fig. 3.
1935 *Achatella achates*, Delo, p. 416, figs. 38, 39.
1940 *Achatella achates*, Delo, p. 110, p1. 13, figs. 19-21.
?1940 *Achatella carleyi* var. *rogersensis*; Delo, p. 111, p1. 13, figs. 25.
1942 *Achatella achates*; Okulitch, p. 104, p1. 1, fig. 1.
1944 *Achatella billingsi* Sinclair, p. 17, p1. 1, figs. 1, 2.
1947 *Achatella achates*; Wilson, p. 60, p1. 10, fig. 16.
1947 *Pterygometopus billingsi*; Wilson, p. 55, p1. 10, figs. 4a and b.
1978a *Achatella achates*; Ludvigsen, p1. 5, fig. 47.
1979 *Achatella achates*; Ludvigsen, fig. 47a and b.
1982 *Achatella achates*; Ludvigsen and Chatterton, p. 2183, pl. 1, figs. 1–7, fig. 3.
1999 *Achatella achates*; Brett et al., p. 300, fig. 8.4
2002 *Achatella achates*; Whitely et al., p. 145, pl. 115.

Diagnosis.—Eye extending from L3 to S2 or anterior tip of L2; located very close to glabella anteriorly, so that palpebral ridge barely recognizable. Conspicuous glabellar tubercles on each side of anterior glabellar embayment. Lateral cephalic margin evenly curved. Pygidium with pointed posterior margin.

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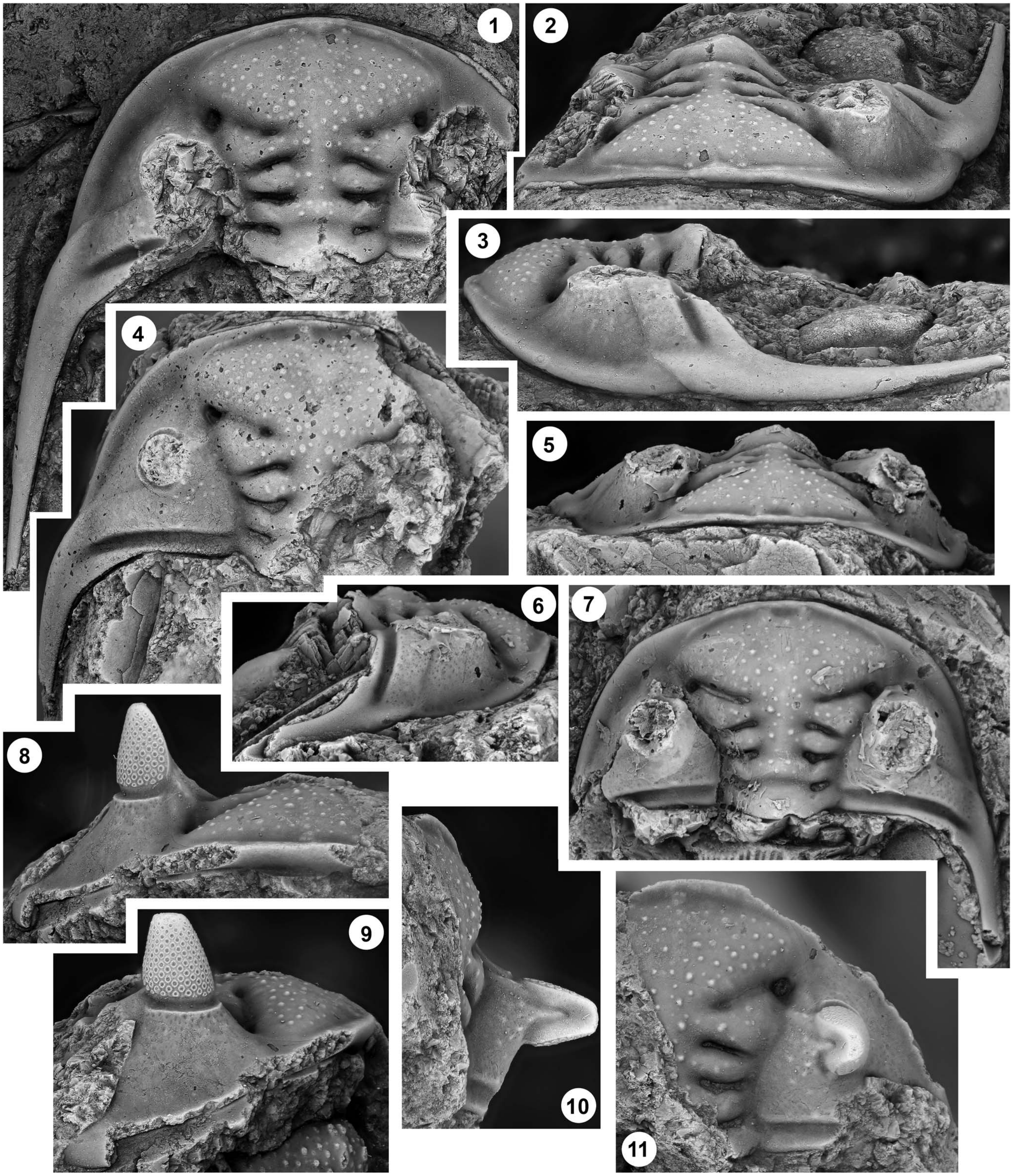

Figure 8. *Achatella katharina* (Bradley, 1930), Kimmswick Formation, Batchtown, Illinois. (**1–3**) Cephalon (UC 33780a; paratype), dorsal, anterior and lateral views, ×4.5; (**4**) cephalon (UC 337380a; paratype), dorsal view, ×4.5; (**5–7**) cephalon (UC 20685; holotype), anterior, lateral and dorsal views, ×6.5; (**8–11**) cephalon (UC 33780e; paratype), anterior, lateral-exterior, lateral-interior and dorsal views, ×6.5.

Holotype.—An incomplete, flattened exoskeleton (GSC 1784; Fig. 3.5), probably from the Lindsay Formation of Ottawa, Ontario.

Other material.—An enrolled exoskeleton missing the pygidium (ROM 49475), two nearly complete exoskeletons (ROM 63161, ROM 63162), four cephala (ROM 18747, ROM 63163, ROM 35371, ROM 63160), and a pygidium (ROM 63159).

Description.—Cephalon well rounded, subcircular to subovate in outline; maximum width approximately two times maximum

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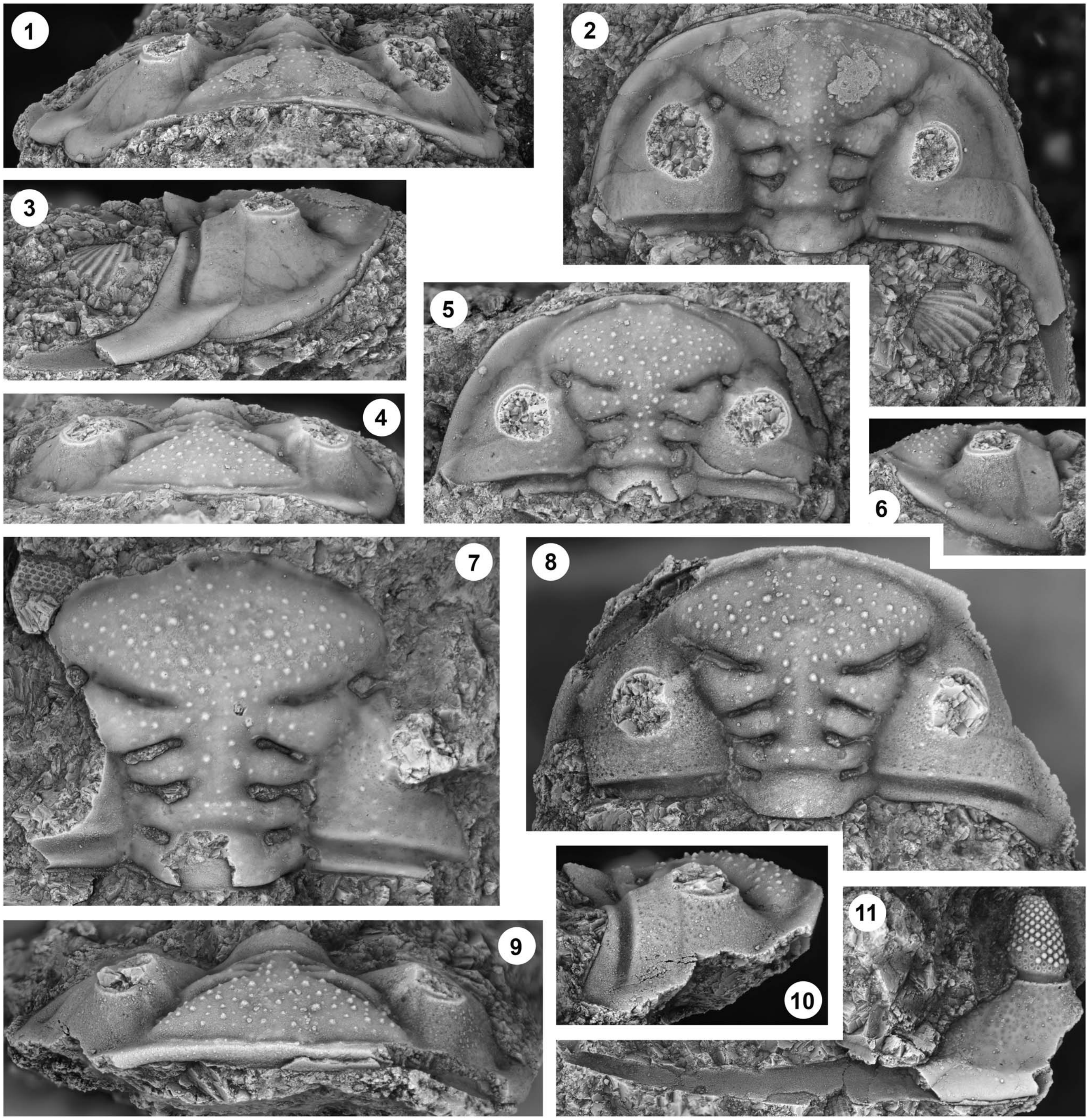

Figure 9. *Achatella katharina* (Bradley, 1930), Kimmswick Formation, Missouri. All from a road cut along State Highway 79, Lincoln Co., Missouri, approximately 5.25 km south of the village of Elsbury, except (**1–3**) (road cut on County Road M, Jefferson Co., Missouri, 200 m southeast of the intersection with Old Lemay Ferry Road). (**1–3**) Cephalon (OU 222760), anterior, dorsal and lateral views, ×6.5, collection M19; (**4–6**) cephalon (OU 222761), anterior, dorsal and lateral views, ×6.5, collection 79 M-1 m; (**7**) cranidium, (OU 222762), dorsal view, ×6.5, collection 79 M-1 m; (**8–10**) cephalon (OU 222763), dorsal, anterior and lateral views, ×10, collection 79 M-1 m; (**11**) free cheek (OU 222764), lateral view, ×12, collection 79 M-1 m.

length. Glabella outline pinches inward toward L1 between LO and L2; LO slightly wider than L2, while L2 is only marginally wider than L1. Outline expands rapidly laterally from L2 to the widest point across the anterior lobe. Axial furrow moderately to strongly developed around the glabella. Glabellar furrows also moderately to strongly developed, tending to become shallower adaxially. SO approximately transverse to forwardly curved medially; strongly developed near the axial furrows, more shallowly impressed adaxially. S1 variable in appearance, relatively transverse near the axial furrows, then slightly curved anteriorly toward the axis; weakly bifurcate adaxially with short, posteriorly directed, shallow, secondary furrow. S2 relatively straight, angled inward and forward; terminates short of axial furrow in some specimens. S3 also nearly straight, directed more steeply inward and backwards; may deepen slightly adaxially; well-developed apodemal pit at intersection with axial furrow (e.g., Fig. 4.5, 4.6). LO with conspicuous backward curvature. L1 relatively transverse, but with weak forward

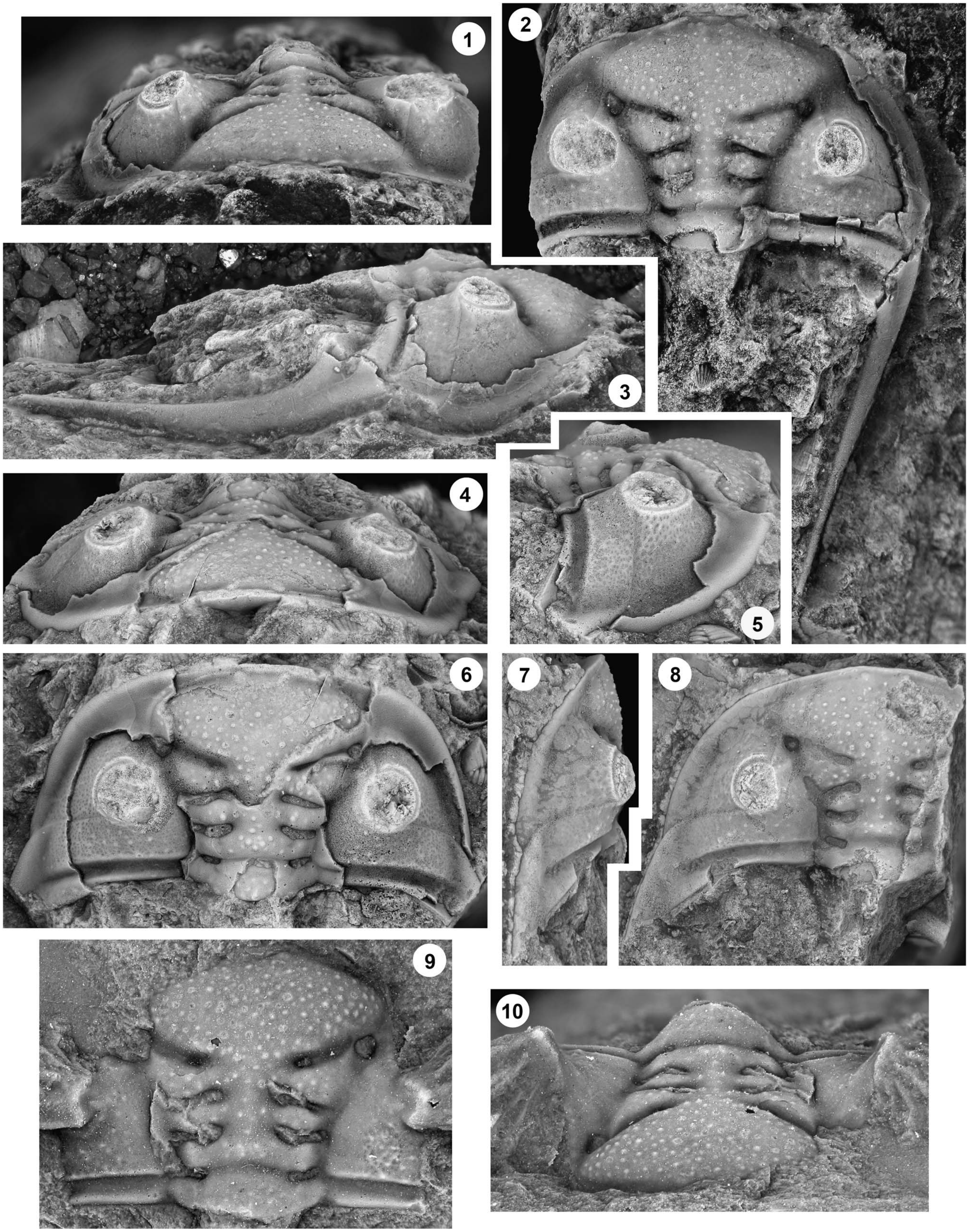

Figure 10. *Achatella katharina* (Bradley, 1930), all from Viola Springs Formation, roadcut along west side of U.S, Highway 99, 5 km south of Fittstown, Pontotoc County, Oklahoma (except **9, 10**, Lawrence Quarry, approximately 10 km southwest of Ada, Pontotoc County). (**1–3**) Cephalon (OU 12121), anterior, dorsal and lateral views, ×5.25, collection 99-51; (**4–6**) cephalon (OU 12123), anterior, lateral and dorsal views, ×6, collection 99-float; (**7, 8**) cephalon (OU 222765), lateral and dorsal views, ×5.5, collection HW99-51; (**9, 10**) cranidium (OU 12124), latex cast from external mold, dorsal and anterior views, ×5.25.

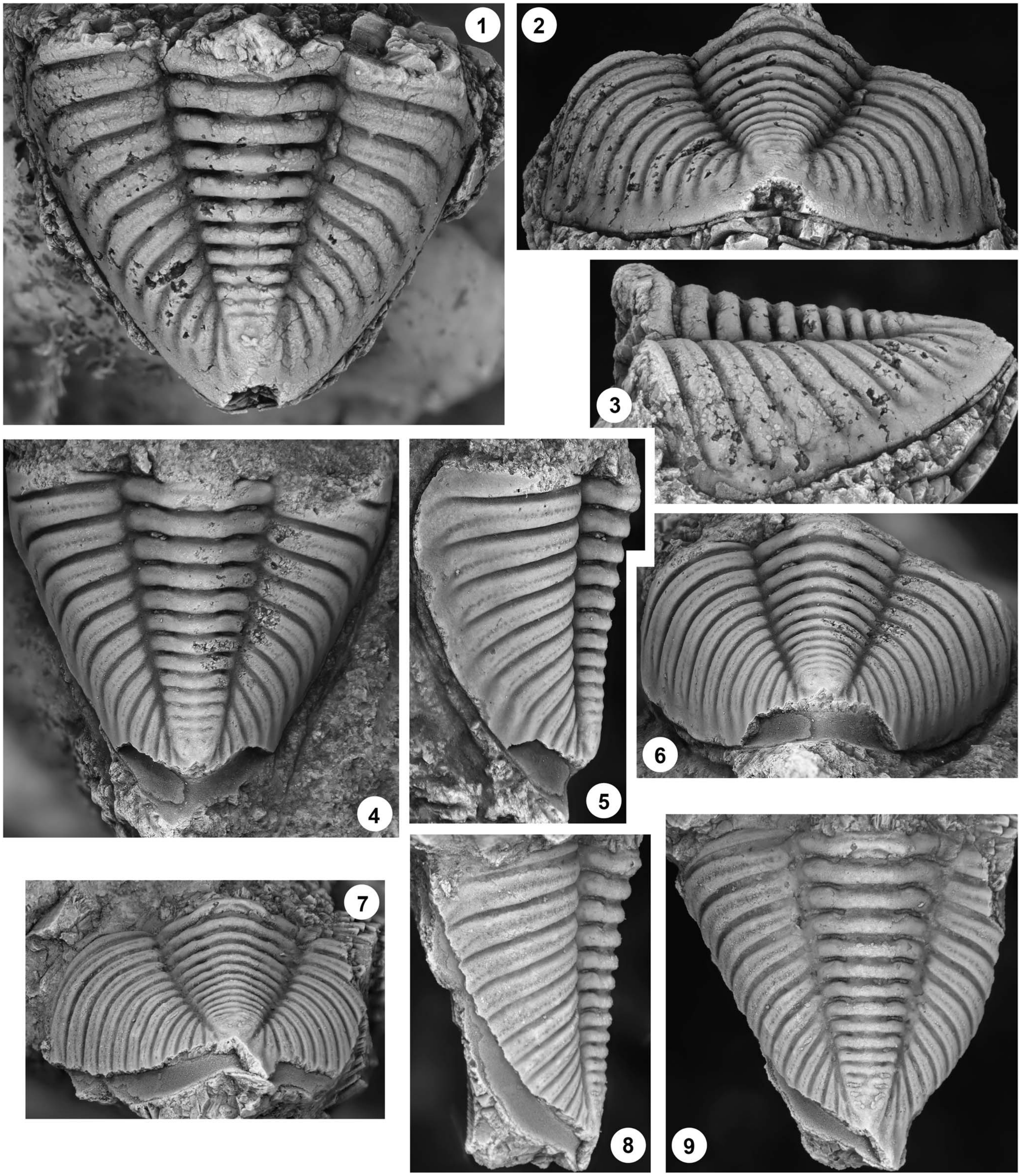

Figure 11. *Achatella katharina* (Bradley, 1930), Kimmswick Formation. (**1–3**) Pygidium (UC 28977; paratype of *A. katharina* but assigned doubtfully to that species in this paper), dorsal, posterior and lateral views, ×7, Glen Park, Missouri; (**4–6**) pygidium (UC 33780b, paratype), dorsal, lateral and posterior views, Batchtown, Illinois, ×7; (**7–9**) pygidium (OU 222766), posterior, lateral, and dorsal views, ×7, collection 79 M-1 m.

projection near axial furrow. L2 expands slightly adaxially. L3 approximately triangular in outline, narrowing conspicuously adaxially. Anterior lobe transversely subovate in outline. Triangular, weakly inflated muscle scar (pterygometopid insertion scar) on anterior glabellar lobe expands forward; anterior end of scar marked by two tubercles separated by gentle median embayment (e.g., Fig. 3.1). Narrow but well-defined anterior border present, marked by a change of slope at anterior end of glabella and finely etched preglabellar furrow. Arcuate palebral lobe relatively small, strongly elevated and centered opposite

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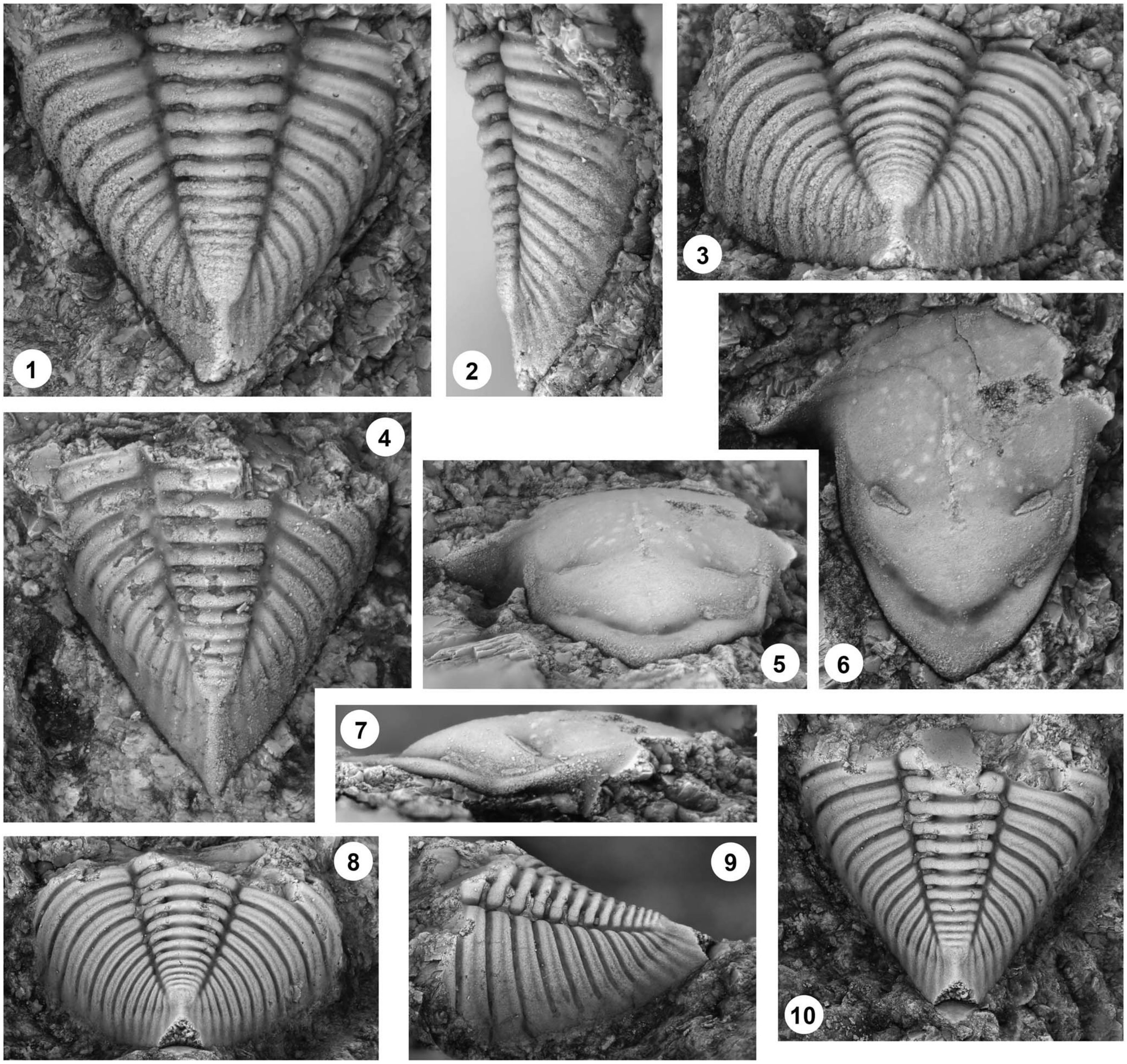

Figure 12. *Achatella katharina* (Bradley, 1930). All from the Kimmswick Formation, road cut along State Highway 79, Lincoln Co., Missouri, approximately 5.25 km south of the village of Elsbury except (**8–10**) (Viola Springs Formation, roadcut along west side of U.S, Highway 99, 5 km south of Fittstown, Pontotoc County, Oklahoma, collection 99-49). (**1–3**) Pygidium (OU 222767) dorsal, lateral, and posterior views, ×15, collection 79 M-1 m; (**4**) pygidium (OU 222768), dorsal view, ×15, collection 79 M-1 m; (**5–7**) hypostome (UC 28975a, paratype), posterior, ventral, and lateral views, ×16; (**8–10**) pygidium (OU 12125), posterior, lateral, and dorsal views, ×10.

posterior tip of L3; anterior end positioned close to anterior tip of L3, and posterior end opposite S1. Anterior branch of the facial suture curves outward laterally from anterior tip of L3, then bends strongly inward along cranidial margin. Posterior branch of the facial suture nearly transverse near eye, then curves gently backward toward lateral cranidial margin. Posterolateral projection relatively broad and flat, with strongly developed posterior border furrow. Genal spine relatively long, exceeds glabellar length, and relatively flat where it merges with the lateral cranidial margin; narrows posteriorly to thin, rounded tip posteriorly. Sculpture of tubercles developed along the glabella and sparsely on posterior fixigena; tubercles largest on anterior lobe of glabella, becoming smaller and fainter toward LO.

Librigenal field strongly curved, raised toward the subocular furrow; subocular furrow firmly impressed. Lateral border broad, flat, defined largely by change in slope.

Pygidium approximately triangular in outline and relatively wide, tapers to posterior tip at approximately 45-degree angle. Axis relatively narrow, approximately 37% of total pygidial width at maximum; tapers gradually toward posterior. Axial furrows present but weakly developed. Nine to 10 well-defined, nearly transverse axial rings and furrows with at least two indistinct segments incorporated into terminal piece. Pleural

Table 1. Character matrix used in the phylogenetic analysis (Fig. 2)

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Pterygometopus sclerops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ingriops trigonocephalus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Achatella achates	1	1	2	1	1	1	1	1	1	1	1	1	1	0	2	1	0	3	1
A. katharina	1	1	2	1	1	1	1	1	1	1	1	1	1	0	2	1	1	3	1
A. clivosa	1	1	?	1	1	1	1	1	1	1	0	0	0	0	0	1	0	2	1
A. retardata	1	1	?	1	1	1	1	1	?	?	0	0	0	?	0	1	0	3	1
A. (s.l.) *schmidti*	1	0	?	0	0	0	1	1	0	1	0	0	?	0	0	1	0	?	?
A. kuckersianus	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	?	0	2	2
A. carleyi	1	1	2	1	1	1	1	1	1	1	1	0	1	1	0	1	1	2	1
A. truncatocaudata	1	1	2	1	1	1	1	1	1	1	?	?	0	0	0	0	0	2	1
A. consobrina	1	1	2	0	1	1	1	1	1	1	1	0	1	0	0	1	0	3	1

Details of characters and character states are given in Appendix 1.

field relatively flat near the axis, curves strongly downward near the lateral margin. Interpleural furrows faint, separating at least nine pairs of pleurae. Pleural furrows firmly impressed, oblique, and terminating short of pygidial margin; separate subequal anterior and posterior bands. Faint tubercle sculpture developed over entire pygidium except for furrows.

Remarks.—Ludvigsen and Chatterton (1982) considered *Achatella katharina* to be a junior synonym of *A. achetes*, but study of type and new material indicates that they are closely related (Fig. 2) but distinct species. Characters shared between *A. achates* and *A. katharina* include a relatively short (exsag.) eye extending from L3 to S2 or the anterior tip of L2, and distinct tubercles on either side of the median embayment of the anterior glabellar margin. *Achatella katharina* differs in having a palpebral lobe that is farther away from the glabella (e.g., compare Fig. 8.4, 8.11 with Figs. 4.2, 4.6 and 5.4), and outward curvature of the lateral cephalic margin behind the intersection with the posterior branch of the facial suture. The latter feature is expressed on well-preserved, uncompacted cephala from both the Kimmswick Limestone (e.g., Figs. 8.1–8.7, 9.1–9.3) and the Viola Springs Formation (e.g., Fig. 10.4–10.8), and appears to be of biological rather than taphonomic significance.

Achatella carleyi is also a distinct species, and is separated from *A. achates* by possession of a larger eye that extends farther back on the cephalon (e.g., Fig. 6.1, 6.6, 6.10), and outward curvature of the lateral cephalic margin behind the posterior branch of the facial suture (e.g., Fig. 6.1, 6.6). S2 is noticeably shorter (tr.) on testate surfaces in *A. carleyi* and does not reach the glabellar margin (e.g., Fig. 6.1, 6.6). The pygidial margin is rounded posteriorly, rather than pointed (e.g., Fig. 7.3, 7.5). The sculpture comprises coarse, closely packed granules with scattered tubercles on the glabella (e.g., Fig. fig. 7.1). *Achatella achates* shares the glabellar tubercles, but these are set in background sculpture of very fine, barely perceptible granules (e.g., Fig. 5.3). *Achatella consobrina* Tripp (1954, pl. 4, figs. 26–33) has eyes that extend back as far as S1, although they do not reach the axial furrow. The median embayment is well developed but tubercles are not developed at the lateral margins. The pygidium of *A. consobrina* has a relatively longer axis that terminates very close to the posterior margin.

Several other species are characterized by larger eyes than *A. achates* and which reach the axial furrow anteriorly, including *A. clivosa* Lespérance and Weissenberger (1998, fig. 4.1), *A. retardata* (Reed, 1914; Morris and Tripp, 1986, pl. 4, fig. 2), and *A. kuckersianus* (Jaanusson and Ramsköld, 1993, pl. 5, fig. 3a–b). The latter species has shorter genal spines than *A. achates*, whereas *A. schmidti* (Warburg, 1925; Jaanusson and Ramsköld, 1993, pl. 5, fig. 4a) lacks genal spines entirely.

Foerste (1910; see also Foerste, 1919) established a new variety of *A. carleyi*, *A. carleyi rogersensis*, for material from the "Cynthiana Formation" (= Point Pleasant Member of the Lexington Formation of modern nomenclature; Osborne, 1968) at Rogers Gap, Scott County, Kentucky. The holotype cranidium (Foerste, 1919, pl. 19, fig. 18a) appears to have an evenly curved lateral cephalic margin and a relatively small eye. It differs from *A. carleyi* in these respects but resembles *A. achates*, to which it is assigned questionably.

As revised here, *A. achates* is variable in several characters, including expression of the large tubercle on the occipital ring, which is barely perceptible in some cranidia (e.g., Fig. 4.2). While faintly developed in some specimens (e.g., Fig. 4.6), all cranidia display a degree of bifurcation of the S1 furrow and a secondary forward inflation of L1 near the axial furrow. The development of the subtriangular pterygometopid cephalic muscle scar is variably expressed, as is the median embayment of the anterior glabellar margin. The latter feature is generally more weakly expressed than in *A. katharina* and *A. consobrina*, and more similar in appearance to the subtly developed embayment of *A. carleyi*. Sculpture across the glabella ranges from large, irregularly spaced globular tubercles set in a background of very fine granules (e.g., Fig. 4.1–4.3, 4.6, 4.7) to smaller, more uniformly sized and spaced tubercles (e.g., Figs. 3.1–3.4, 5.1–5.3).

Achatella carleyi (Meek, 1872)

Figures 6–7

1872 *Dalmanites carleyi* Meek, p. 424.
1873 *Dalmanites carleyi*; Meek, p. 170, pl. 14, figs. 2a–d.
1919 *Pterygometopus carleyi*; Foerste, pl. 19. fig. 17.
1940 *Achatella carleyi*; Delo, p. 111, pl. 13, figs. 22–24.

Diagnosis.—S2 narrow (tr.), terminates short of glabellar margin. Weakly developed median embayment on anterior glabellar margin. Eye does not reach axial furrow; extends from S3 to S1; weakly conical in lateral view. Lateral cephalic margin curved outward behind intersection with posterior branch of suture. Pygidium with rounded posterior margin. External

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surfaces of cephalon and pygidium with finely granulose sculpture, augmented by tubercles on glabella.

Lectotype.—According to Nitecki and Golden (1970), a cranidium (UC 965; Fig. 6.9, 6.10) in the Field Museum was originally part of the collection of U.P. James, and was figured by Meek (1873, pl. 14, fig. 2a) in his description of *Dalmanites carleyi*. We select it as the lectotype. It is most likely from the Fairmount Member of the Fairview Formation (Foerste, 1919) of the Cincinnati region.

Other material.—Five cephala (CM 51280a, CM 51280b, CM 51280c, CM 31699a, CM 31699b), and two pygidia (CM 51280d, CM 31699c).

Description.—Cephalon is relatively wide, semielliptical outline (excluding genal spines); cranidium approximately subtrapezoidal in outline. Cranidial length approximately 47% of the cranidial width across the posterolateral fixigena. Axial furrow generally shallowly impressed; the furrow tends to weaken in front of L3. Well-defined apodemal pit at intersection of S3 and axial furrow. Glabella outline pinches inward from the LO to the narrowest point across L1, slowly expands from L2, then more rapidly across L3 and the anterior lobe. The anterior tip of LO and the posterior tip of L2 are approximately parallel. Maximum width of the glabella across the anterior lobe is approximately 48% of cranidial width; glabella has low convexity, relatively flat adaxially. LO relatively wide and long; generally subovate in outline but posterior margin nearly transverse medially; expands outward beyond level of L1. LO occupies approximately 19% of total glabellar length. L1 relatively transverse, elongate subrectangular in outline. L2 angled slightly posteriorly, middle portion of the lobe is slightly expanded, but outline is otherwise subrectangular. L3 is larger, subtriangular in outline, narrows sharply toward the axis. Anterior lobe is relatively long and narrow, only slightly extending past L3; subovate in outline, rounded anteriorly especially along the lateral margins. SO narrow, shallowly impressed along the axis, then marked by deeper lateral furrows angled very slightly anteriorly. S1 furrow moderately impressed, transverse laterally, curves gently anteriorly adaxially. S2 furrow directed obliquely backward, more strongly developed adaxially, terminating short of lateral glabellar margin. S3 extends oblique forward; becomes more strongly impressed abaxially toward the apodemal pit. Palpebral lobe narrow, arcuate band that tapers abaxially; palpebral furrow is finely etched groove. Eye extends from S3 to S1; does not reach axial furrow anteriorly. Anterior branch of the facial suture curves inward to follow anterolateral margin of the anterior glabellar lobe. Posterior branch of facial suture poorly preserved but apparently nearly transverse. Genal spine moderately long, less than half of total librigenal length and slightly less than glabella length. Coarsely granulose sculpture covers entire cranidial surface, with tubercles on central part of glabella and anterior lobe; on well-preserved specimens, weak median embayment on anterior glabellar margin flanked by indistinct, larger tubercles.

Librigenal lateral border and border furrow well defined; furrow expressed as a relatively wide, trough-like break in slope. Librigenal field moderately convex; subocular furrow gently impressed. Visual surface of eye weakly conical in lateral view, with width approximately three-fourths of height. Twenty-two columns of lenses with up to eight lenses. Strongly developed granular sculpture across the librigena.

Pygidium elongate, triangular to subtriangular in outline, length approximately 90% of width. Axis of 11 to 12 well-defined rings and furrows outlined by distinct axial furrows. Pleural field relatively flat adaxially, but with strong change in slope distally toward weak lateral border defined only by absence of furrows. Up to 12 pairs of oblique, firmly impressed pleural furrows; interpleural furrows obsolete. Granulose sculpture developed along the axis.

Remarks.—In their revision of *Achatella*, Ludvigsen and Chatterton (1982) noted the limited information available for *A. carleyi* (Meek, 1872), although they speculated that it might be a junior synonym of *A. achates*. In addition to the lectotype, we had access to archival specimens from the type area (Figs. 6, 7). They are mostly compacted to varying degrees but demonstrate clearly that *A. carleyi* is a distinct species in the C1 and C2 deposition sequences in southern Ohio and northern Kentucky. Lespérance and Weissenberger (1998, p. 313) interpreted Foerste's (1919, pl. 19, fig. 17) image of *A. carleyi* as showing a small occipital spine. There is no trace of a spine in any of our cephala, although there is an occipital tubercle (e.g., Fig. 6.2), which could perhaps be exaggerated by compaction in Foreste's specimen. Meek (1872, 1873) does not mention either feature in his description. The pygidium that Meek (1873, pl. 14, fig. 2d) attributed to the species has a rounded posterior margin that resembles those illustrated in this paper (Fig. 7.3, 7.5).

Achatella carleyi was compared to *A. achates* earlier, under the discussion of the latter. It shares an outwardly curved lateral cephalic margin behind the posterior branch of the suture with *A. katharina* from Missouri and Oklahoma. However, it differs from *A. katharina* in having a much larger palpebral lobe (compare Fig. 6 and Fig. 8.8–8.11), a shorter (tr.) S2 glabellar furrow that terminates well short of the lateral glabellar margin (compare Fig. 6.1, 6.6, and 6.10 with Fig. 10), and a background sculpture of coarser granules; the posterior margin of the pygidium is rounded (Fig. 7.3, 7.5) rather than sharply pointed (Fig. 12.4).

Achatella consobrina (Tripp, 1954, pl. 4, figs. 26–33) has a similarly sized eye to *A. carleyi*, but is closer to the glabella. The lateral margin of the cephalon appears to be evenly curved, rather than curved outward behind the posterior suture. The S2 furrow is better defined and extends to the lateral glabellar margin, and the sculpture of the glabellar surface includes numerous, more closely spaced fine tubercles. Other species, including *A. kuckersianus* (Schmidt), *A. clivosa* Lespérance and Weissenberger, and *A. retardarta* (Reed) have eyes that extend forward to reach the axial furrow.

Achatella katharina (Bradley, 1930)
Figures 8–12

1930 *Dalmanites katharina* Bradley, p. 286, pl. 30, figs. 19–28.
1940 *Dalmanites katharina*; Delo, p. 112, pl. 13, figs. 26–29.

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Diagnosis.—Eye extending from L3 to S2 or anterior tip of L2; located away from glabella anteriorly, with fixigena traversed by short palpebral ridge (e.g., Fig. 8.4, 8.11). Conspicuous glabellar tubercles on each side of anterior glabellar embayment. Lateral cephalic margin curved outward behind intersection with posterior branch of facial suture. Pygidium with pointed posterior margin.

Holotype.—A cephalon (UC 20685; Fig. 8.5–8.7) from the Kimmswick Limestone near Batchtown, Calhoun County, Illinois.

Other material.—Paratypes: three cephala (UC 33780a, 33780c, 33780e), a hypostome (UC 28975a) and two pygidia (UC 33780b, UC 28977 [latter specimen assigned questionably to the species]); additional sclerites from Missouri: three cephala (OU 222760, OU 222761, OU 222763,), a cranidium (OU 222762), a librigena (OU 222764), and three pygidia (OU 222766, OU 222767, OU 222768); sclerites from Oklahoma: three cephala (OU 12121, 12123, OU 222765), a cranidium (OU 12124) and a pygidium (OU 12125)

Description.—Cephalon semielliptical in outline, excluding genal spines. Cranidial outline subtriangular to subtrapezoidial, narrowing toward a gently rounded anterior margin. Cranidial length approximately 48% of maximum cranidial width. Axial furrows are shallow grooves, with conspicuous apodemal pit at intersection with S3. Glabella moderately convex, expands evenly forward from minimum width at S1 to maximum width across the anterior lobe; maximum glabellar width approximately 45% of maximum cranidial width. Median embayment of anterior glabellar margin flanked by conspicuous tubercles. SO nearly transverse, deepest abaxially and curved slightly forward, but shallows medially. S1 also transverse, expands adaxially becoming weakly bifurcate with very shallow, short (exsag.) branch in some specimens (e.g., Fig. 8.7). S2 strongly incised, proceeds obliquely forward from axial furrow; width (tr.) equal to 27% of glabellar width at L3. S3 shallower than S2; extends obliquely backward from prominent apodemal pit at axial furrow; terminates adaxially at second shallower pit. LO curved gently backward, increasing in length (exsag.) toward midline; maximum length approximately 17.5% of glabella length; dorsal surface slopes upward and backward, becoming raised above the rest of the glabella. L1 approximately transverse, expands forward weakly near axial furrow. L2 with straight posterior and oblique anterior margins; expands adaxially. L3 subtriangular in outline with adaxially convergent margins so that length (exsag.) becomes reduced by approximately 50% away from axial furrow. Anterior lobe suboval in outline. Anterior border very short, separated from glabella by shallow preglabellar furrow; narrows abaxially and eventually cut out entirely by suture. Palpebral lobe forms narrow (exsag.), steeply inclined, tapering band (Fig. 8.10); eye short (exsag.), extending from L3 to S2 or anterior tip of L2; located away from glabella anteriorly, with steeply inclined palpebral area of fixigena traversed anteriorly by short palpebral ridge. Palpebral furrow well defined, finely etched groove. Anterior branch of the facial suture runs approximately parallel to margin of glabella before curving inward sharply along the anterior margin of the anterior lobe. Preoccular fixigena is narrow (tr.), tapers anteriorly. Posterior branch of the facial suture curves gently backward toward genal spine. Posterolateral projection of fixigena is wide (tr.) with strong posterior border furrow that gently curves toward genal spine, fading beyond intersection with shallow lateral border furrow. Lateral cephalic margin curved outward behind intersection with posterior branch of facial suture. Genal spine relatively long, slightly greater than 50% of cephalon length. Sculpture of rounded tubercles developed moderately across glabella and fixigena. Conspicuous median tubercle on posterior margin of LO.

Lateral librigenal border widest (tr.) opposite librigenal field, but becomes greatly reduced anteriorly along sutural margin. Border furrow weak and expressed largely by change in slope between the librigena field and lateral border. Librigena field strongly convex; suboccular furrow well defined. Eye raised above level of glabellar crest; strongly curved and subconical; basal width in lateral view equal to approximately 85% of height. Visual surface with 20 columns of domical lenses, with up to nine lenses per column.

Pygidium relatively narrow, long and triangular in outline, with maximum width approximately 90% of pygidial length. Lateral and posterior profiles strongly convex. Axial furrows well defined, shallow toward posterior. Axis moderately convex and tapers backwards toward a bluntly pointed posterior tip; width approximately 39% of pygidial width across the anteriormost ring; includes 12 well-defined axial rings and short (sag.) terminal piece that comprises at least two segments. Axial ring furrows strongly impressed anteriorly, becoming more faintly impressed posteriorly; deepest abaxially, shallowing and becoming slightly longer (sag.) medially. Pleural field strongly convex with steeply sloping lateral margin. Faint interpleural furrows oblique, becoming curved backward distally, and defining up to 12 pairs of pleurae. Pleural furrows deep and oblique; define subequal anterior and posterior bands. Slight dorsal flexure present along pygidial axis, readily apparent in lateral view (e.g., Fig. 12.2), raising posterior tip. External surface generally smooth and lacking large tubercles. Doublure strongly concave in dorsal view and lacks terrace ridges; extends to level of abaxial termination of pleural and interpleural furrows.

Remarks.—The short (exsag.), tall eye (e.g., Fig. 8.8–8.11) separates *A. katharina* from all other members of the genus apart from *A. achates*; these species were compared in detail under the discussion of the latter. One of Bradley's paratype pygidia (Fig. 11.1–11.3) is relatively shorter than all other pygidia (e.g., Fig. 11.4–11.9) and is assigned only questionably to the species.

Acknowledgments

This research was supported by NSF grant EAR 0819715. D.M. Rudkin and P. Fenton at the Royal Ontario Museum, B. Hunda and J. MacKnight at the Cincinnati Museum, M. Coyne at the Geological Survey of Canada, and P. Meyer at the Field Museum arranged loans of type material. T.N. Barker, D.K. Moss, and A. Thomas assisted in fieldwork in Missouri; R. Burkhalter provided invaluable help in the lab and in fieldwork in Oklahoma and Missouri; C.E. Brett guided us to the Blue Licks locality in northern Kentucky. Alan Owen and an anonymous reviewer provided useful comments that improved the paper.

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Appendix

Characters used in the phylogenetic analysis

1. Cephalic convexity. 0, strongly convex with conspicuous anterior arch (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2b); 1, relatively flat with weak arch (e.g., Fig. 8.2, 8.5, 8.8).
2. Genal spine. 0, absent (e.g., Jaanusson and Ramsköld, 1993, pl., fig. 2a); 1, present (e.g., fig. 8.1)
3. Genal spine length. 1, short (equal to less than cranidial length [sag.]) (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 3a); 2, long (length greater than cranidal length) (e.g., Fig. 8.1); ?, inapplicable.
4. Preglabellar furrow. 0, firmly impressed (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, border separated from glabella largely by change in slope (e.g., Fig. 8.1–8.7).
5. Anterior expansion of glabella beyond L3. 0, strong (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, weak (e.g., Fig. 8.1, 8.7).
6. Minimum glabellar width. 0, at L2 (e.g., Jaanusson and Ramsköld, 1993, pl.1, fig. 2a); 1, at L1 (e.g., Fig. 8.1, 8.7, 8.11).
7. Shape of L3 lobe. 0, roughly even in length (exsag.) and subtrapezoidal in outline (e.g., Jaanusson and Ramsköld, 1993, pl., fig. 2a); 1, conspicuous adaxial taper in length (exsag.), with minimum adaxial length half or less of length at axial furrow, and subtriangular in outline (e.g., Fig. 8.1, 8.7).
8. Lengths (exsag.) of L1–L3 lobes. 0, roughly equal in length (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, L3 noticeably longer (e.g., Fig. 8.1, 8.7).
9. Apodemal pits in L3 at axial furrow. 0, absent (e.g., Jaanusson and Ramsköld, 1993, pl.1, fig. 2a); 1, present [note, often infilled with matrix] (Fig. 8.1)
10. Tuberculate sculpture on glabella. 0, weak or absent (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, well defined (e.g., Fig. 8.1).
11. Anterior glabellar embayment. 0, absent (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, present (e.g., Fig. 8.1–8.7) see text for further discussion).
12. Pair of conspicuous tubercles at edges of glabellar embayment. 0, absent (e.g., Jaanusson and Ramsköld, 1993, pl.1, fig. 2a); 1, present (e.g., Fig. 8.1–8.7).
13. Eye position. 0, abuts glabella anteriorly (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, separate from glabella anteriorly by strip of fixigena (e.g., Figs. 6.1, 8.4). Lésperance and Weissenberger (1998, p. 312) first noted that several species of *Achatella* possess eyes whose anterior tip reaches the axial furrow, including *A. clivosa*, *A. retardata* and *A. kuckersianus*. This state is shared with *Ingriops* and *Pterygometopus*, and is plesiomorphic.
14. Subocular furrow. 0, deep, well-defined groove (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2b; Fig. 8.9); 1, narrow, shallow groove (e.g., Fig. 6.7).
15. Palpebral lobe length. 0, extends from anterior tip of L1 to S3 (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, extends from posterior tip of L1 to L3 (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 1a); 2, extends from anterior tip of L2 or S2 to L3 (e.g., Fig. 8.11).
16. Posterior branches of sutures. 0, curved forward abaxially (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, nearly straight (e.g., Figs. 8.1, 9.2).
17. Outward curvature of cephalic margin behind suture. 0, absent (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a; Fig. 5.3); 1, present (e.g., Figs. 6.1, 6.6, 8.1, 8.7, 9.2, 10.6).
18. Pygidial length. 0, short, rounded posteriorly, length/width = 0.65 (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2b); 1, intermediate, rounded posteriorly, length/width = 0.73 (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 1c); 2, long, rounded posteriorly. length/width = 0.85 or greater (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 2a); 3, long, pointed posteriorly, length/width = 0.85 or greater (e.g., Fig. 12.4).
19. Pleural field. 0, gently arched distally (e.g., Jaanusson and Ramsköld, 1993, pl. 1, fig. 2a); 1, nearly vertical flanks (e.g., Fig. 12.3, 12.8); 2, gently concave flanks (e.g., Jaanusson and Ramsköld, 1993, pl. 5, fig. 2c).

Accepted 1 June 2015