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TRILOBITE FAUNAS, SEDIMENTARY FACIES AND SEQUENCE STRATIGRAPHY OF THE UPPER ORDOVICIAN (SANDBIAN-KATIAN) SUCCESSION OF MISSOURI

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TRILOBITE FAUNAS, SEDIMENTARY FACIES AND SEQUENCE STRATIGRAPHY OF THE UPPER ORDOVICIAN (SANDBIAN-KATIAN) SUCCESSION OF MISSOURI

A DISSERTATION APPROVED FOR THE
CONOCOPHILLIPS SCHOOL OF GEOLOGY AND GEOPHYSICS

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Chapter 1: INTRODUCTION

The late Sandbian-Katian interval (Upper Ordovician) was a time of major environmental change across Laurentia with highest recorded sea levels of the Paleozoic (Haq and Schutter, 2008), and the Taconic orogeny was in progress on the eastern margin (present coordinates) of the continent. The flooded midcontinent passed eastward into a foreland basin, generated via thrust-loading, that had wide-ranging sedimentological effects (Holland and Patzkowsky 1996, Holland and Patzkowsky 1997, Kolata et al, 1998). Biotic and environmental changes in the foreland basin are concentrated at the late Sandbian M4-M5 sequence boundary (Holland and Patzkowsky 1998), which is in the vicinity of the well known and widely correlated Deicke and Millbrig K-bentonites (Kolata et al, 1998). The M4-M5 boundary is marked by a pulse of extinction in the brachiopod faunas of eastern Laurentia (Patzkowsky and Holland, 1997) and changes in biofacies composition (Patzkowsky and Holland, 1999). There is growing evidence that the development of the foreland also precipitated changes in the trilobite faunas (Amati and Westrop, 2006; Carlucci and Westrop, 2012). While sequence stratigraphy, environmental change and faunal turnover are generally well studied in the foreland basin of Laurentia, the mid-continent has received less attention. The Upper Ordovician units of eastern Missouri offer the opportunity to examine depositional patterns and trilobite faunas, and this succession has the advantage of secure lines of correlation into the lithologically different successions of the foreland basin via the Deicke and Millbrig bentonites. This dissertation attempts to answer the following questions: 1) How are sedimentary facies and important erosional surfaces

expressed in the shallow continental interior farther away from the Taconic Orogeny? 2) How do the depositional sequence boundaries identified by Holland and Patzkowsky (1996) in eastern Laurentia correlate with the mid-continent? 3) How do trilobite faunas in the mid-continent compare to other basins across Late Ordovican Laurentia? 4) Do they offer new information on the age and correlation of the Upper Ordovician succession? These data also contribute to a larger, NSF-funded project on biotic change in response to foreland basin development in eastern Laurentia.

Chapter 2 focuses on the Upper Ordovician (Sandbian-Katian) sedimentary facies and sequence stratigraphy of the study region. It provides an environmental framework for the trilobite faunas, and also aids in correlation to other regions. This study extends the sequence stratigraphic nomenclature of Holland and Patzkowsky (1996) into the study region from eastern Laurentia, recognizing five third-order depositional sequences, including upper M3 through to perhaps the lower C1. Lower rank, fourth-order depositional sequences and important depositional surfaces (Brett et al. 2004) are also clearly defined. Many carbonate units in the study region appear to occur in a "layer-cake" fashion, where in systems tracts and depositional surfaces can be correlated across the study region, and in some cases up to hundreds of kilometers into other depositional basins.

An unexpected discovery of the poorly known bathyurid *Raymondites* in the lower Kimmswick Limestone prompted a review of the genus that incorporated restudy of types of several previously described species. This is the subject of Chapter 3. A phylogenetic analysis supports monophyly of *Raymondites* but the closely related genus *Bathyurus* is paraphyletic, although some potential apomorphies of the latter could not

be coded due to missing data for most species. Five species, including two that are new, can be diagnosed.

Chapter 4 deals with *Achatella*, a pterygometopine trilobite that appears in the Upper Ordovician of Laurentia but is known from older strata in the continent of Baltica (Jaanusson and Ramsköld, 1993). The arrival of the genus in Laurentia is widely interpreted as a case of immigration as the Iapetus ocean closed, bringing Baltica closer to Laurentia (Ludvigsen and Chatterton, 1982). A phylogenetic analysis that includes Laurentian and Baltican species provides a test of this hypothesis. Species from Laurentia (both from North America and the various terranes of Laurentian Scotland and Ireland) form a derived group, supporting a hypothesis of a single invasive event and subsequent radiation, rather than as a series of invasions of individual species. Study of new material from Missouri and Oklahoma, and types from other regions, demonstrates four readily diagnosable species that occur in Laurentian North America.

Chapter 5 evaluates some Laurentian trilobite species of *Flexicalymene* Shirley 1936, particularly *F. senaria* (Conrad, 1841). It shares some of the characteristics of "wastebasket taxa" (Plotnick and Wagner, 2006), in that it was first described long ago (more than 150 years ago), and has been reported widely across North America (e.g., Bradley 1930, Whittington 1941, Stumm and Kauffman 1958, Davis 1963, Ludvigsen 1979, Chatterton et al., 1990). Previous studies on Laurentian *Flexicalymene* have identified regional groups of species (Stumm and Kauffman 1958; Ross 1967; Dean 1979; Hunda and Hughes 2007); is *F.senaria* truly geographically widespread or does it mask geographic differentiation of species? The systematic description of *F.senaria* is revised based on new specimens collected for this analysis from Ontario, Oklahoma and

Missouri. Material formerly assigned to *F. senaria* from Missouri, as well as new material collected for this analysis is separated as a distinct species, *F. kimmswickensis*. Three other species from Oklahoma are distinct from both *F. senaria* and *F. kimmswickensis*, but are left in open nomenclature, *F.sp. 1*, *F. sp. 2*, and *F.* cf. *meeki*. Material from Ontario represents a valid occurrence of *F. senaria* in a region close to the type area of New York

Chapter 6 examines the trilobite biostratigraphy of the Kimmswick Limestone in the study region. The original work on the faunas of the Kimmswick Limestone was conducted by Foerste in the early 1920s with a more comprehensive analysis later by Bradley in the early 1930s. Little revisionary work has been conducted on the trilobites of the region subsequently. The precise stratigraphic ranges of trilobites within the Kimmswick are currently poorly constrained; this analysis attempts to provide enhanced biostratigraphic resolution for these trilobites. The paper includes a synoptic systematic review of the entire faunas. Two distinct faunas are identified, both of which have closest affinities with the faunas, of the Viola Springs Formation of Oklahoma.

Taken together, the various chapters of the dissertation provide an integrated view of the stratigraphy, sedimentology and trilobite faunas of a classic Upper Ordovician succession in Laurentian North America. This dissertation represents fundamental, field-based research that will facilitate further work on environmental and biotic change during a geologically active period of the continent's history.

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Chapter 2: SEQUENCE STRATIGRAPHY OF A CONTINENTAL INTERIOR CARBONATE SUCCESSION DURING A TIME OF HIGH SEA LEVEL, UPPER ORDOVICIAN (SANDBIAN-KATIAN), MISSOURI, USA

ABSTRACT.— High sea levels of the Upper Ordovician flooded the interior of Laurentian North America, where low depositional dips produced "layer-cake" successions of depositional sequences dominated by highstand systems tracts. Sequences are bounded by irregular unconformities or ravinement surfaces; transgressive systems tracts are variably developed but are typically thin. The upper Plattin—lower Galena groups (Sandbian—Katian) of eastern Missouri exemplify these interior successions. Five third-order depositional sequences can be correlated with those identified in eastern Laurentia (M3–C1) by Holland and Patzkowsky (1996). Lower-rank, high-frequency sequences are components of these third-order sequences. As in other parts of eastern Laurentian, sequences M3 and M4 are composed of tropical carbonates in which thick HSTs are represented by subtidal wackestone–packstone with well-developed *Thalassinoides*-type burrow systems, and may include late HST peritidal carbonates; TSTs are poorly developed. Sequence M5 begins with a mixed carbonate-siliciclastic succession that may record shut-down of carbonate deposition by upwelling of cooler water. The remainder of sequence M5 comprises two high-frequency sequences of subtidal facies with progradational stacking. Sequences M6 and basal C1 are dominated by skeletal carbonates and include well developed TSTs which, in the case of sequence C1, is composed on coarse, cross-bedded grain- and rudstone. Correlation is facilitated by the Deicke and Millbrig K-bentonites, and demonstrates

that sequences can be tracked for a least 140 km without significant changes in systems tracts. Variation in erosional beveling at sequence boundaries may be related to far-field effects of the Taconic orogeny on basement structures.

INTRODUCTION

The highest sea levels of the Paleozoic occurred during the Upper Ordovician (e.g., Haq and Schutter, 2008, fig. 1), with flooding of the continental interior of Laurentian North America. The Taconic Orogeny was also underway in Laurentia and, through foreland basin development, influenced patterns of sedimentation across a broad swath of the eastern (present coordinates) part of the continent. Unlike the expanded, often siliciclastic-rich successions of the foreland basin and adjacent areas, thinner, dominantly carbonate successions characterize much of the continental interior. "Layer-cake" geometries recording deposition during highstands may be cut by irregular, sometimes amalgamated unconformities produced by starvation and submarine erosion (e.g., Kolata et al., 1998) that are the only record of sea level falls; lowstand and falling stage systems tracts are not developed. Depositional sequences comprise packages of strata bounded by flooding or erosional surfaces can be tracked over long distances. In this paper, we document one such succession that exemplifies the sequence architecture characteristic of the flooded continental interior. It comprises the Upper Ordovician (Sandbian–Katian) upper Plattin to lower Galena groups, and is superbly exposed in a series of mostly new road cuts in the St. Louis, Missouri, region.

Study Area

The classic work on the Sandbian–Katian succession in the St. Louis region (Bradley, 1925; Larson, 1951; Templeton and Willman, 1963) relied on quarries that are long-abandoned and inaccessible, and road and railway cuts that have deteriorated and are now in poor condition. During our field work in 2010 and 2011, the well-known exposures along Interstate Highway 55 (e.g., Kolata et al., 1998, locality 36) could not be studied due to extensive, long-term road construction. Fortunately, mostly new cuts in Jefferson County along State Highways 30, M and MM (Fig. 1; see also Metzger and Fike, 2013), provided fresh exposures over a transect of nearly 13 km that facilitated both description of facies and identification of sequence boundaries and other significant surfaces. A well-exposed section about 140 km to the north, near New London (NL), Ralls County (Fig. 1; see also Leslie, 2000, p. 1146; Metzger and Fike, 2013) allowed facies and stratal surfaces to be tracked regionally.

Lithostratigraphic nomenclature

Templeton and Willman (1963) presented a comprehensive revision of the lithostratigraphy of what is now the Sandbian–early Katian succession over much of the Upper Mississippi Valley region, including parts of Illinois, Iowa, and our study area in Missouri. They proposed a complex nomenclature of groups, subgroups, formations and members, some of which were previously established units, but many were new. Subesquent workers (e.g. Kolata et al., 1998) have used many of the units established by Templeton and Willman, but changed their rank and in some cases restricted the geographic area over which they are applied. In this paper, we follow an emerging

consensus (e.g., Emerson et al., 2004; Ludvigson, 2004; Metzger and Fike, 2013) that simplifies the nomenclature by returning traditional, well-established units to their original usage as formations, rather than subgroups, as advocated by Templeton and Willman (Fig. 2). We also follow recent practice in Missouri (e.g., Spreng and McCart, 1994; Kolata et al., 1998; Metzger and Fike, 2013) in using formations established by Larson (1951) for the Sandbian Plattin Group (Fig. 2).

Carbonates of the Plattin Group (Fig. 2) comprise much of the Sandbian succession in the study area (Larson, 1951; Spreng and McCart, 1994), although they are incompletely exposed in our sections, which begin in the upper part of the Beckett Formation. The Beckett is overlain by the Hager Formation (divided into the "lower" and overlying Victory members), which is in turn succeeded by the Macy Formation (Fig. 2). The Galena Group represents the late Sandbian and early Katian part of the succession, and is composed of the Decorah Formation (shale and carbonate) and the overlying Kimmswick Limestone (carbonate).

The Decorah comprises, in ascending order, the Castlewood, Glencoe, Kings Lake, and Guttenburg members (Fig. 3), although the latter is exposed only at our NL section. Decorah members in the St. Louis study region are typically thinner and have reduced shale content relative to their correlative units to the north. In particular, shale development in the Spechts Ferry and Guttenberg members, equivalents of the Glencoe and Kings Lake in Missouri, respectively, to the north of the St. Louis study region in the Hollandale Embayment (Minnesota–Wisconsin), is dramatically more pronounced due to siliciclastic input from the Transcontinental Arch (Simo et al. 2003). The Kings Lake can be divided into two cycles in the St. Louis region, with the upper cycle likely

correlative to the Guttenburg. Indeed, some previous studies have referred to the upper cycle of the Kings Lake in this region as the Guttenburg (Kolata 1998, Metzger and Fike, 2013); however, the interval is reduced in thickness, and is lithologically distinct from the type Guttenberg of the Iowa-Wisconsion region. Accordingly, we retain the Kings Lake as the lithostratigraphic unit for the St. Louis region.

The well known and widely correlated Deicke and Millbrig K-bentonites (Kolata et al., 1998) occur at the base of the Castlewood Member, and just above the base of the Glencoe Member, respectively, and represent important tie points for our sections. The Kimmswick Limestone (Kolata et al., 1998; Metzger and Fike, 2013) is the youngest unit included in the study (Fig. 2), and rests disconformably upon the Decorah. In the St. Louis region, it is truncated by a major unconformity at the base of the Carboniferous, which climbs stratigraphically towards the Mississippi River, revealing increasingly thick Kimmswick successions (Fig. 3). Templeton and Willman (1963) proposed several members for the Kimmswick (under the name Dunleith Formation) but, aside from the coarse-grained, cross-bedded Moredock Member, which is the youngest unit exposed in our sections, we could not recognize them consistently, and the lower Kimmswick is left undifferentiated.

SEDIMENTARY FACIES

The facies of the upper Plattin Group and Decorah Formation have been treated in previous work. Spreng and McCart (1994) published an interpretation of peritidal facies of the upper Plattin Group in three sections to the south and east of Missouri. More recently, Metzger and Fike (2013) included a general treatment of the lithologies

of the Beckett–Decorah formations at the MM and NL sections as part of a study of the carbon isotope stratigraphy. This paper provides a more detailed analysis of the facies and places them in the context of depositional sequences.

Lime mudstone–calcisiltite facies (F1)

Description: This facies consists of lime mudstone with calcisiltite laminae to cm-thick layers and rippled intervals with wavy to lenticular bedding (Fig. 4A); dm-thick bioturbated units are present (Fig. 4B), as well as cm-thick biointraclastic packstone layers with scoured bases (Fig. 4E).

Interpretation: The predominantly mud-grade sediment with intervals of lenticular to wavy bedding points to deposition in a peritidal setting on intertidal flat (Demicco and Hardie 1994, Pratt 2010). Spreng and McCart (1994) made a detailed, cm-scale interpretation of the Hager Formation based on modern environments of Andros Island. They assigned individual beds to such environments such as tidal channels, ponds or algal marshes, and beach ridges. We prefer to take a broader view, recognizing that it may not be possible to provide unique interpretations for individual beds, without assigning lithologies to individual microenvironments (e.g., Pratt, 2010).

Occurrence: Lower Member of the Hager Formation; meter-scale cycle within the HST of depositional sequence M3, sections MM and MM 2

Fenestral lime mudstone (F2)

Description. White to very light gray, poorly fossiliferous to barren lime mudstone forms dm–thick, stylotization within bedded units (Fig. 4C). Sub-ovoid, mm-scale fenestrae filled with calcite cement are ubiquitous (Fig. 4D, arrow-f). Body fossils are restricted to rare gastropods (Fig. 4D, arrow-g, but all units include conspicuous, widely spaced, nearly vertical, spar-filled burrows Figs. 3C, 3D, arrow-b). Facies F2 conformably overlies facies F1.

Interpretation: Abundant fenestrae and limited fauna (e.g., Pratt, 2010), as well as position above facies F2, point to an intertidal flat setting. Although likely occupying a shallower position than facies F2, the vertical burrows and gastropods argue against a supratidal origin.

Occurrence: Upper Victory Member of the Hager Fm. at sections MM and MM 2; subcycle with the HST of sequence M3. The upper contact with overlying Macy Formation (sequence M4) is an undulating erosion surface (Fig. 4C).

Bioturbated lime mudstone–wackestone (F3)

Description: Burrow-mottled (commonly dolomitic) lime mudstone–wackestone (Fig. 4E, F) is volumetrically the most important facies in the Plattin Group. Sharply outlined galleries of *Thalassinoides* (e.g., see Jin et al. 2012) typically contain smaller burrows (Fig. 4F; compare with Jin et al. 2012, figs. 4C, 5C), although some of the small burrows occur outside of the mottles (Fig 3F, arrow-s). When not dolomitized,

the burrow outlines are diffuse (Fig. 4F, arrow-d). Body fossils are restricted to rare molluscs; tabulate corals, stromatoporoids and receptaculitids reported from similar facies elsewhere in Laurentia (Jin et al. 2012; Holland and Patzkowsky 2012) are absent. Centimeter-thick horizons of intraclastic pack–grain–, and rudstone, often superposed on irregular hardgrounds, punctuate the succession; these horizons thicken and become more common upward through an interval of facies F3 that comprises most of the Macy Formation.

Interpretation: We follow previous authors (Thompson 1991; Spreng and McCart 1991; Metzger and Fike 2013; see also Holland and Patzkowsky 2012) in interpreting facies F3 as subtidal in origin; intraclastic horizons record episodic storms. The reduced fauna indicates relatively restricted conditions. This facies comprises the subtidal portion of highstand systems tracts (HST) of sequences M3 and M4.

There is some debate over the origin of *Thalassinoides* burrows (Jin et al. 2012). Kendall (1977) considered the mottles to record large, open burrow systems constructed by arthropods whose fills were reworked by smaller burrows, whereas Gingras et al. (2004) considered the mottles to be secondary diagenetic halos around smaller, primary, worm burrows. Jin et al. (2012) took the middle ground, and interpreted the smaller burrows to represent fills of central, active, open networks, and the dolomitic mottles as diagenetic halos confined to zones of processed sediment plastered onto burrow walls by deposit-feeding arthropods. Our field observations indicate that multiple small burrows are associated with mottles (Fig. 4F) and, contrary to the observations of Jin et

al., occur both at both the margins and centers of burrows. This suggests that Jin et al.'s model for burrow formation is unlikely.

Occurrence. Facies F3 occurs in the Beckett and Macy formations, and in the Castlewood Member of the Decorah Formation throughout the study area. The lithofacies forms the HST of depositional sequences M3 and M4.

Shale with bioclastic rudstone (F4)

Description: Blue-gray shale is a dominant lithology in the Glencoe Member of the Decorah Formation, where it is accompanied by cm– to dm–thick bioclastic carbonate interbeds that include coarse brachiopod rudstone pavements, which may form amalgamated units; mm–thick calcisiltite caps may be present. Thick pack– to rudstone beds are confined to the lower half of the Glencoe, with the upper part composed almost exclusively of shale (Fig. 6a), with minor lenses of calcisiltite. Bioturbation is restricted to *Planolites* burrows in calcisiltite units.

Interpretation: There is little doubt that this facies formed under subtidal conditions, and the shell beds are at least partly the result of storm processes. However, the shale is barren and lacked the raw material needed to produce shell accumulations by simple storm winnowing and concentration (Dattilo et al. 2008). While we cannot rule out diagenetic dissolution of shells in the shale, an epsiodic starvation model (Dattilo et al., 2008, 2012) may provide a better explanation of shell bed genesis. Under this interpretation, shell beds form through long term accumulation at times of low sediment

input; although the developing shell bed may be winnowed from time to time, it is not the primary mechanism for shell concentration. The shale intervals record storm blanketing events that terminate shell bed formation (Dattilo et al., 2008). Under both the storm-winnowing and episodic-starvation models, the loss of limestone interbeds in the upper Glencoe records deepening. With storm-winnowing as the dominant process, disappearance of shell beds records the sea floor reaching depths below the reach of major storms, whereas in the episodic starvation model shell bed production is shut down through an increased frequency of distal storm blanketing events.

Occurrence: Glencoe Member, Decorah Formation; uppermost, symmetrical cycle in sequence M4 (Fig 8C), and lower M5 (M5A).

Shale with bentonite (F5)

Description. The thick, widely correlated Deicke and Millbrig metabentonites (Kolata et al. 1998) are associated with cm to dm-thick shale packages that may include cm-thick planar to nodular carbonate interbeds. The bentonites may sit directly on an irregular hardground at the base of the interval (House Springs K-bentonite; Fig. 6H) or above a cm-thick shale horizon (e.g., Millbrig K-bentonite; Fig. 6F).

Biota, components and bioturbation: Fossils are typically restricted to wackestone interbeds within the shale horizon and record normal marine biotas such as brachiopods and trilobites. The facies is also generally unbioturbated.

Interpretation: Well-developed, widely correlative (Kolata et al., 1998) Upper Ordovician K-bentonites attest to major eruptions that were related to island-arc volcanism off the eastern (present coordinates) margin of Laurentia (Huff et al., 2010). The association of some ashes with hardgrounds (see also Kolata et al. 1998; ver Straaten, 2004) suggests that sediment starvation or at least reduced rates of background sedimentation influence the preservation of the ashes. In such cases, they may well blanket major flooding surfaces, as sediment starvation during transgression would favor accumulation of ash. Deposition of ash over a vast geographic scale – the Millbrig metabentonite has been reported from as far away from the study area as Oklahoma (Rosenau et al., 2012), New York (Mitchell et al., 2004) and Tennessee (Kolata et al., 1998) and may be one of the largest ash eruptions in the Phanerozoic (Huff et al., 2010) – could have even temporarily inhibited carbonate deposition, perhaps explaining the switch to fine siliciclastic deposition above.

Occurrence. Sequences M4, M5 and M6. The Deicke metabentonite is immediately below the Castlewood Member of the Decorah Formation. The Millbrig is near the base of the Glencoe Member, and the House Springs is a short distance above the base of the Kimmswick Formation.

Lime mudstone–packstone with shale (F6)

Description: Light gray, planar- to nodular-bedded lime mudstone and wackestone in cm-thick beds alternating with mm- to cm-thick shale (Fig. 6B, D) are the most common lithologies in the Kings Lake Formation. Fauna includes brachiopods,

gastropods and, less commonly, trilobites; bioturbation is generally minimal (Fig. 6B-D) and limited to diffuse *Planolites* burrows. Graded beds with mm- to cm-thick basal skeletal packstone lags are present (Fig. 6B, C). Thicker skeletal pack- and rudstone layers often have steep-sided scoured bases and possibly with diagenetic underbeds (Fig. 6D); diagenetic enhancement is also suggested by presence of intervals of nodular lime mudstone and marl, particularly in the upper Kings Lake (Fig. 6E). Packstone and bioturbated wackestone also form dm-thick, amalgamated, heterolithic units (Fig. 6B) that mark the bases of meter-scale cycles. In the Guttenberg Formation at NL and in the upper Kings Lake in the House Springs (HS) area, nodular wackestone to packstone is interbedded with mm- to cm-thick recessive, marly layers that may represent diagenetically altered shale (Fig. 6E); gastropods and brachiopods are the dominant taxon (Fig. 6G).

Interpretation: As recognized by Metzger and Fike (2013), this facies records the deepest subtidal environment in the House Springs region. Graded beds are interpreted as distal tempestites, and brachiopod rudstone horizons with strong scoured bases also attest to storm winnowing. Amalgamated intervals of packstone and wackestone form condensed TSTs at the base of meter-scale high-frequency sequences (Zeechin and Catuneanu, 2013), with carbonate-shale facies representing small-scale HSTs. The more strongly nodular version of this facies (Guttenberg Formation) with a gastropod-dominated fauna may represent a shallower, more restricted subtidal setting.

Occurrence: Kings Lake and Guttenberg formations. Sequences M5B and M5C.

(F7) Amalgamated fine grainstone to calcisiltite

Description: The facies is predominantly fine grainstone to calcisiltite with diffuse *Thalassinoides*-type bioturbation. Minor coarse bioclastic packstone layers are also present, commonly occurring at the base of some calcisiltite packages. Indurated lime-mudstone rip-up clasts (cm scale) derived from the underlying Kings Lake or Guttenburg formations are present where this facies form the base of the Kimmswick Limestone. Conspicuous mineralized hardground surfaces divide the succession into dm-thick packages.

Biota, components, and bioturbation: Receptaculitids and gastropods are conspicuous elements of the fauna. Diffuse dolomitized *Thalassinoides* burrows are present throughout, although are seen most clearly on weathered surfaces. Hardgrounds may be bored (e.g., Kolata et al., 1998, fig. 13.

Interpretation: As this forms the base of the Kimmswick Limestone and lies above a conspicuous erosional surface that likely forms the base of sequence M6, this facies is interpreted as a high-energy, transgressive deposit.

Occurrences: The facies is restricted to the base of sequence M6 in the Kimmswick Formation, below the House Springs K-bentonite at section MM, section M, and the HS section.

(F8) Bioturbated lenticular skeletal packstone, grainstone and rudstone

Description: Bioclastic packstones predominate, with grainstone and rudstone intervals interspersed throughout. Bioturbation largely obscures bedding at the outcrop scale (Fig. 7D); however cm- to dm- thick, unbioturbated beds (Fig. 7A, B) and discontinuous lenses (Fig. 7C) are present, the latter commonly with gently scoured bases. Horizons of white, cm-thick, chert nodules appear in the upper two meters of the succession at section M.

Biota, components, and bioturbation: Fossils are diverse, including trilobites, brachiopods, bryozoans, and crinoids; receptaculitids may be present. Bioclasts range from nearly complete, slightly abraded fossils in the grainstone layers, to fragmented, moderately to well sorted debris in the packstone intervals. Bioturbation in the form of dolomitic *Thalassinoides*-type burrows, is more clearly defined on weathered surfaces. Although much of the facies is strongly bioturbated, dm-thick, weakly burrowed units are also present.

Interpretation: Most of the facies comprises bioturbated skeletal sands with mud matrices that are interpreted as having accumulated in subtidal parts of carbonate sand shoals. Unbioturbated beds and lenses may record periodic storm winnowing.

Occurrences: Lower Kimmswick Formation throughout the study region, although it is well represented only at section M. It forms the HST of the M6 sequence.

(F9) Cross-bedded bioclastic grain to rudstone

Description: Bioclastic rudstone to grainstone, commonly cross-bedded, is the primary lithology of the facies. Coarse rudstone beds (Fig. 8D) commonly form basal lags of dm- to m-scale cycles (Fig. 8A, B); lags have scoured bases (Fig. 8A). Cross-bedding occurs in dm-thick sets that may show crude grading. Unidirectional planar sets dominate, but bidirectional cross bedding is locally present (Fig. 8E). Oncoids appear at the top of the succession at section M (Fig. 8F).

Biota, components, and bioturbation: Bryozoan and crinoidal debris is dominant throughout the facies, with cephalopods, trilobites and brachiopods also present. It is generally unbioturbated, with preservation of primary sedimentary structures. Rudstone lags show variable preservation of bioclasts, ranging from heavily abraded debris, to larger and nearly complete fossils (Fig. 8D). Fragments of large bryozoan colonies are typical of both lags and coarse laminae of graded cross-bedded sets (Fig. 8C).

Interpretation: The facies records a shallow shoal environment, probably near fairweather wave base. Cycles with coarse lags and overlying planar cross-bedded skeletal sands suggest a system of migrating dunes and bars separated by channels. The oncoidal units at the top of the succession likely formed in a back-shoal setting (e.g., Aigner, 1985, figs. 60, 63).

Occurrences: This facies is restricted to the youngest parts of Kimmswick Formation (Moredock Member) exposed in the study area, and is best represented at section M. It forms the TST of the C1 sequence.

SEQUENCE STRATIGRAPHY

Holland and Patzkowsky (1996, 1997) developed a sequence-stratigraphic framework for the Middle and Upper Ordovician of eastern Laurentia that has been adapted by other workers in the region (e.g., Brett et al., 2004; Mitchell et al., 2004). The Deicke and Millbrig metabentonites facilitate correlation with Holland and Patzkowsky's divisions. The Deicke lies within, and the Millbrig occurs near the top of, sequence M4 (Holland and Patzkowsky, 1996; Brett et al., 2004; Mitchell et al., 2004). Like Brett et al. (2004), we are able to identify lower-rank subdivisions of Holland and Patzkowsky's sequences and, following Zeechin and Catuneanu (2013), we treat them as high-frequency sequences with small-scale TSTs and HSTs (see also Carlucci et al., 2014 for a similar approach). The oldest sequence identified in the succession is M3, and the youngest is tentatively assigned to C1 (see Holland and Patzkowsky, 1996 for further discussion of nomenclature). They can be tracked throughout the study region.

Sequence M3:

This sequence is not exposed completely in our sections, but includes the Beckett Formation and the Hager Formation of the Plattin Group. At section MM, subtidal bioturbated lime mudstone–wackestone (Facies F3) are interpreted as recording much of the HST of sequence M3. The top of the Beckett Formation is a well-defined, planar surface that forms a low–rank sequence boundary (Fig. 9C). Above are two distinct meter-scale cycles of the Hager Formation (LH and V1 in Fig. 9C) that are separated by a sharp, planar flooding surface. Both cycles begin with cm-thick, plane-

laminated and rippled calcisiltite (Fig. 5A). The lower cycle (lower member of the Hager Formation) is capped by subtidal bioturbated lime mudstone–wackestone, with cm-thick bioclastic packstone layers and lenses (facies F3). The upper cycle (Victory Member of the Hager Formation is composed of peritidal lithologies (facies F1, F2) that include fenestral lime mudstone (Fig. 4D). These two thin cycles comprise the youngest parts of sequence M3 and are interpreted to have formed as accommodation space was reduced during the latest HST. This part of the succession records upward shallowing, with progradation of tidal flats in the youngest cycle. This is consistent with a position late in the HST.

Depositional Sequence M4:

Sequence M4 comprises the Macy Formation and overlying Castlewood Member of the Decorah Formation. The lower boundary is an undulating ravinement surface that separates peritidal carbonates of upper sequence M3 from overlying subtidal carbonates (Fig. 4C). Aside from cm– to dm–thick, fine grainstone that mantles the ravinement surface (Fig. 5B), there is no trace of transgressive facies, and virtually all of the succession in interpreted as an HST of bioturbated wackestone (facies F3). Throughout much of the succession, there is no evidence of lower-rank cyclicity, although a cm-thick shale and probable bentonite (facies F5) 6m above the base of the Macy may record a starved flooding surface.

The Deicke K-bentonite rests on a hardground developed at the top of the Macy Formation, and probably rests on a major flooding surface. The overlying Castlewood Member forms a distinct carbonate ledge that can be traced with little change in

lithology from the St. Louis region to New London (unit Cw in Figs. 7A, B). It is composed largely of bioturbated lime mudstone–wackestone, with cm-thick bioclastic and intraclastic layers. From the dominantly fine-grained lithologies, it seems to be a somewhat condensed subtidal unit, and may represent part of the HST of the lower rank sequence (M4B) that begins with the flooding surface beneath the Deicke that corresponds to omission surface DS1 of Kolata et al. (2001). The M4B sequence is clearly identifiable in the upper Carters Limestone of the Nashville Dome, where its upper boundary is a conspicuous mineralised hardground that marks the M4–M5 sequence boundary at the base of the overlying Hermitage Formation (Swisher unpublished; Holland and Patzkowsky, 1997; Kolata et al.1998, fig. 7).

Depositional Sequence M5:

The M4–M5 sequence boundary has been identified widely across eastern Laurentia, and marks the disappearance of warm-water carbonates over much of the Appalachian basin, perhaps in response to upwelling of cooler waters (Holland and Patzkowsky, 1997; Kolata et al., 2001). There are two likely candidates for the base of M5. One would be the facies offset from carbonates to mixed carbonates and siliciclastics at the base of the Glencoe Member. The lower Glencoe comprises a symmetrical dm- to m-scale cycle of uncertain status (GC1 in Figs. 7A, B), with basal and capping lime mudstone-wackstone beds and a middle interval of shale and lime mudstone and wackestone layers (Fig. 5C); the Millbrig metabentonite rests on the top of the cycle. Alternatively, the M4–M5 boundary may lie at an irregular erosion surface beneath a brachiopod rudstone/grainstone bed that cuts down to the Millbrig. It can be

tracked from the St. Louis region (Fig. 9A) to New London (Fig. 9B). This surface is the preferred candidate because it is similar in age (post-Millbrig) to the M4-M5 boundary in other regions, and appears to correspond to omission surface DS2 of Kolata et al. (2001).

As defined here, the M5 comprises most of the Glencoe Member above the channeled limestone, and all of the Kings Lake Member. The base of the overlying M6 sequence is placed at a significant erosion surface at the base of the Kimmswick Limestone. M5 has an internal architecture of at least three lower-rank cycles that appear to represent high-frequency sequences. They may correspond in part to divisions of M5 identified in the Cincinnati region by Brett et al. (2004; McLaughlin and Brett, 2007).

The upper Glencoe Member seems to represent a single cycle (M5A on Figs. 9A, B, D) that we correlate with M5A of the Cincinnati region, at least in part (Brett et al., 2004). A lower interval of closely spaced rudstone beds, including the basal, erosional shell bed (Fig. 9A), may represent a small-scale TST, with a shale and thin-bedded rudstone succession (Fig. 6A, 7A) recording the HST. The cycle thins dramatically at NL (Fig. 9B), with only about 30 cm of shale and rudstone represented above the basal rudstone. This may record erosional cut-out beneath the ravinement surface at the base of the Kings Lake Formation (unit M5B in Figs. 9A, B, D).

The Kings Lake Formation comprises two meter-scale cycles (M5B and M5C on Figs. 9B, D) with sequence-like architecture that begin with dm-thick, condensed wackestone and skeletal packstone beds that are interpreted as small-scale TSTs. The lower cycle (Fig. 6B) passes upward into thin-bedded carbonate and shale that may

represent the HST. The HST of the overlying cycle starts with carbonate and shale, but passes upward into nodular-bedded carbonate and marly layers (Fig. 6E). The association of gastropod-rich faunas with this nodular-bedded facies suggests stronger upward shallowing in the second cycle. The cycles could be correlative with sequences M5B and M5C of the Cincinnati region (e.g., Brett et al., 2004), although their small scale also raises the possibility that they are low rank divisions of M5B, with M5C missing beneath the erosional base of sequence M6.

Depositional Sequence M6

The base of sequence M6 lies at a conspicuous ravinement surface at the base of the Kimmswick Limestone that can be tracked from the St. Louis region to New London (Figs. 9E, F). It separates shallow subtidal, nodular carbonate (facies F6) from overlying, coarser, high-energy carbonate sands (facies F7) that includes rip-up clasts of the nodular carbonate in the lower 30 cm. The surface has been identified in previous work (e.g., Metzger and Fike, 2013), and Kolata et al. (1998, fig. 13) demonstrated that it is bored by *Trypanites* in the New London area; it corresponds to omission surface DS3 of Kolata et al. (2001). An irregular surface at the base of sequence C1 is the upper boundary of the sequence.

Sequence M6 is composed mostly of thick-bedded to massive, strongly bioturbated carbonates, and internal architecture is obscure. The House Springs K-bentonite is part of a thin, recessive shaly interval developed above a starved hardground in the St. Louis region (e.g., Fig. 7B), but it is absent at New London (Fig. 7E). At the latter locality, the shaly succession is apparently cut out by a sharp surface that separates a lower

interval of weakly bioturbated, somewhat condensed interval with well-developed internal hardgrounds (facies F7; M6A in Fig. 7E) from the overlying more strongly bioturbated facies that comprises most of sequence M6 (facies F8; M6B in Figs. 7D, E). For this reason, the surface is interpreted as a lower-rank sequence boundary that may correlate with the M6A and M6B boundary in the Cincinnati region (e.g. Brett et al., 2004). As is the case for the similarly bioturbated M4 succession, there is little development of a TST in sequence M6B, but it may be represented by a dm-thick package of weakly bioturbated carbonate sands that include fragments of large receptaculitids.

M6A consists mostly of a condensed trangressive succession. It is tempting to suggest that the House Springs K-bentonite accumulated on the maximum flooding surface of this sequence, with the thin, overlying interval of shale and carbonate recording an abbreviated, highstand that may also be partly cut out beneath M6B in the St. Louis region.

Depositional Sequence C1

The base of sequence C6 lies at an irregular erosion surface (Fig. 7F) that separates coarse bioclastic rudstone (facies F9; C1 on Fig. 7F) from underlying bioturbated packstone (facies F8; M6B on Fig. 7F). Within the succession, at least two meter-scale cycles (Fig. 8A) likely record upward shallowing in a belt of migrating dunes. Sequence C1 is incomplete and truncated by a major unconformity beneath the Carboniferous succession. As it consists entirely of shallow, high-energy deposits, it is interpreted as the TST of a thick, third-order sequence.

Structural Controls

The M4–M5 boundary marks the onset of regional changes in thicknesses of sequences between the St. Louis and New London regions. The Deicke K-bentonite, the Castlewood and basal Glencoe members, the Millbrig K-bentonite, and the basal brachiopod shell bed above the M4–M5 boundary itself extend over the study area with little change in thickness and lithologic character (compare Fig. 9A and 9B). However, M5A thins noticeably in New London (Fig. 9B), and is apparently truncated by the planar ravinement surface beneath M5B. M5B is also abbreviated in New London, and the House Springs K-bentonite and associated shale is apparently cut out beneath sequence M6B (Fig. 7E).

The apparent northward erosional beveling could perhaps be a reflection of far-field effects of thrust-loading in the developing Taconic orogen. Quinlan and Beaumont (1984) showed the behavior of cratonic basins, such as the Michigan and Illinois basins, and associated arches could be modeled as the flexural interaction between those basins, the foreland basin and peripheral bulges. A persistent uplift, the Lincoln Fold, occurs at the eastern margin of the Illinois Basin (Koenig, 1961, fig. 1) in Lincoln, Pike and Ralls counties (McQueen et al., 1941), which includes the New London region. The Lincoln Fold has been interpreted as relatively old structural feature dating back to the Precambrian (Rubey 1952, McCracken 1966). However, the early history of the structure is poorly known, and its role in the Ordovician is speculative. The age of the M4–M5 boundary is thought to be close to the onset of the Taconic Orogeny and a major phase of foreland basin development (Holland and Patzkowsky 1997), and the

shift towards erosional cut out over the Lincoln Fold is consistent with flexure at that time.

CONCLUSIONS

Major depositional sequences identified elsewhere in eastern Laurentia can be tracked into the central part of the craton in Missouri. Here, the sequences are dominated by HSTs with abbreviated TSTs; sequence boundaries are well-defined ravinement surfaces. As in eastern Laurentia, the M4–M5 sequence boundary marks a major change in sedimentary style, apparently related to changes in oceanographic conditions associated with the developing Taconic orogen (e.g., Holland and Patzkowsky, 1997), even though eastern Missouri is far from the foreland basin. Expansion of cooler waters across the shelf terminated warm-water "tropical" carbonate deposition, and ushered in a period of mixed carbonate-siliciclastic deposition in sequence M5. The M4–M5 boundary is also characterized by a shift in the nature of erosion at sequence boundaries, with erosional beveling in the northern, New London, region, possibly in response to activation of flexure of the Lincoln Fold.

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CHAPTER 2 APPENDIX. FIGURES



Figure 1. Locality maps for sections in the St. Louis, Missouri, study region. A. General over view of the four sections studied in the St. Louis, Missouri study region; New London Section (NL), House Springs (HS) Section, Section MM, and Section M. B. Overview of southern study region section's locations: HS Section along State Highway 30, near House Springs; Section MM, along State Highway MM; Section M, along State Highway M. All southern sections occur in Jefferson Co., Mo. C. Overview of the northern study region section location, south of New London along State Highway 61, Ralls Co., Mo.

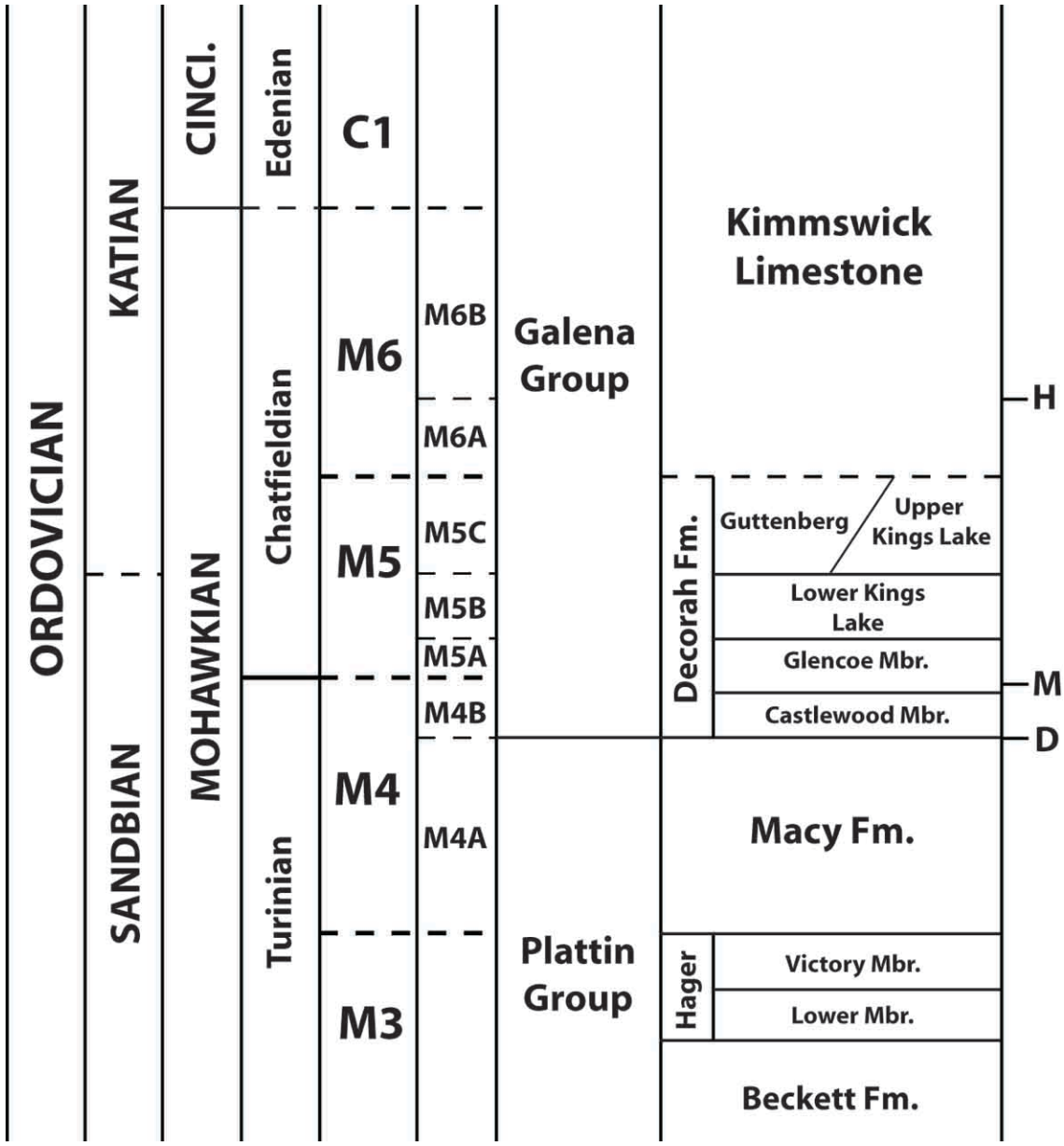

ORDOVICIAN
KATIAN
SANDBIAN
CINCI.
MOHAWKIAN
Edenian
Chatfieldian
Turinian
C1
M6
M5
M4
M3
M6B
M6A
M5C
M5B
M5A
M4B
M4A
Galena Group
Plattin Group
Kimmswick Limestone
Decorah Fm.
Guttenberg
Upper Kings Lake
Lower Kings Lake
Glencoe Mbr.
Castlewood Mbr.
Macy Fm.
Hager
Victory Mbr.
Lower Mbr.
Beckett Fm.
H
M
D

Figure 2. Generalized Upper Ordovician (Sandbian-Katian) stratigraphic nomenclature for St. Louis, Mo, study region. Correlation of the units is facilitated by the presence the Dieke (D), Millbrig (M), and House Springs (H) metabentonites. Depositional sequence nomenclature follows Holland and Patzkowsky (1996, 1997).

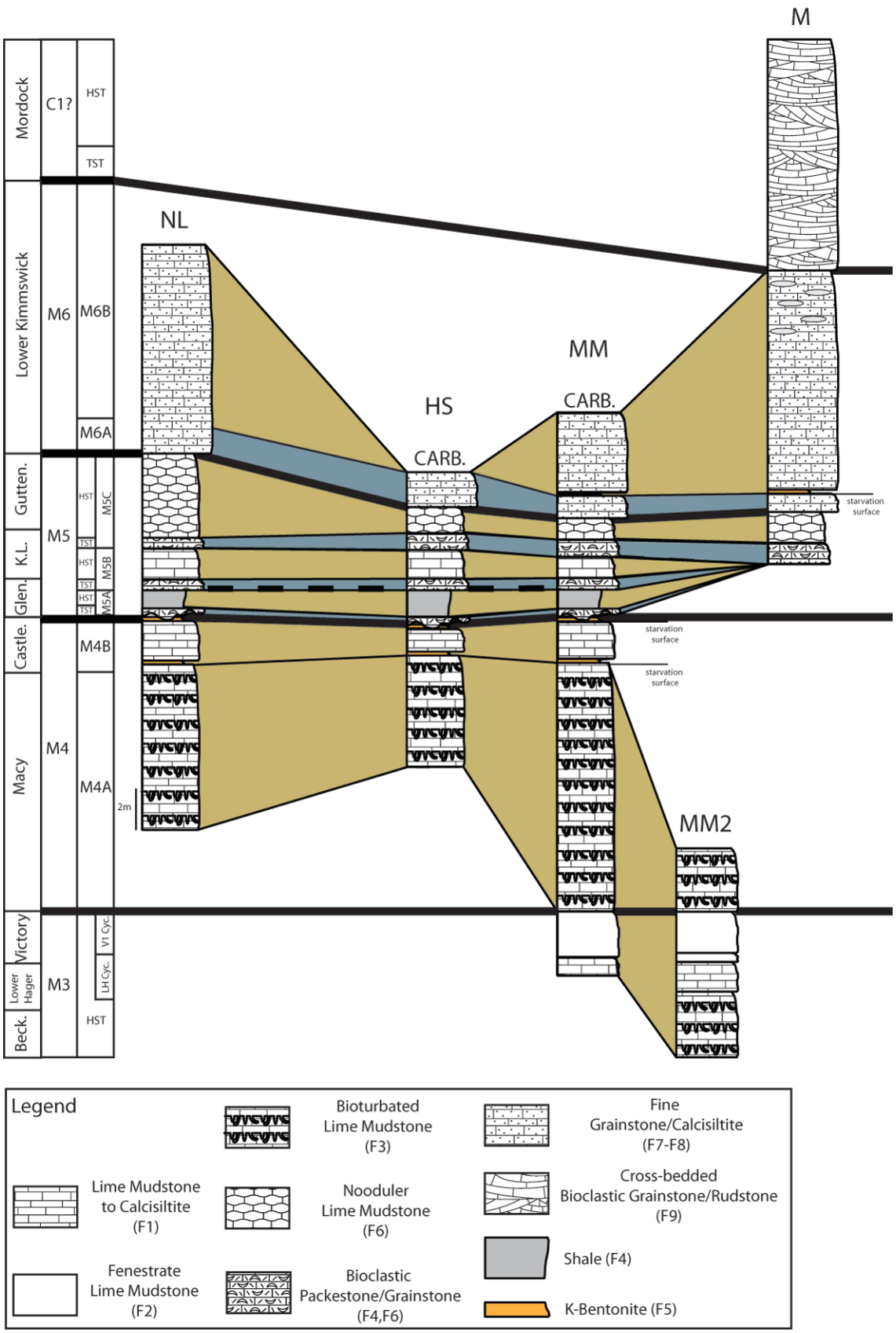
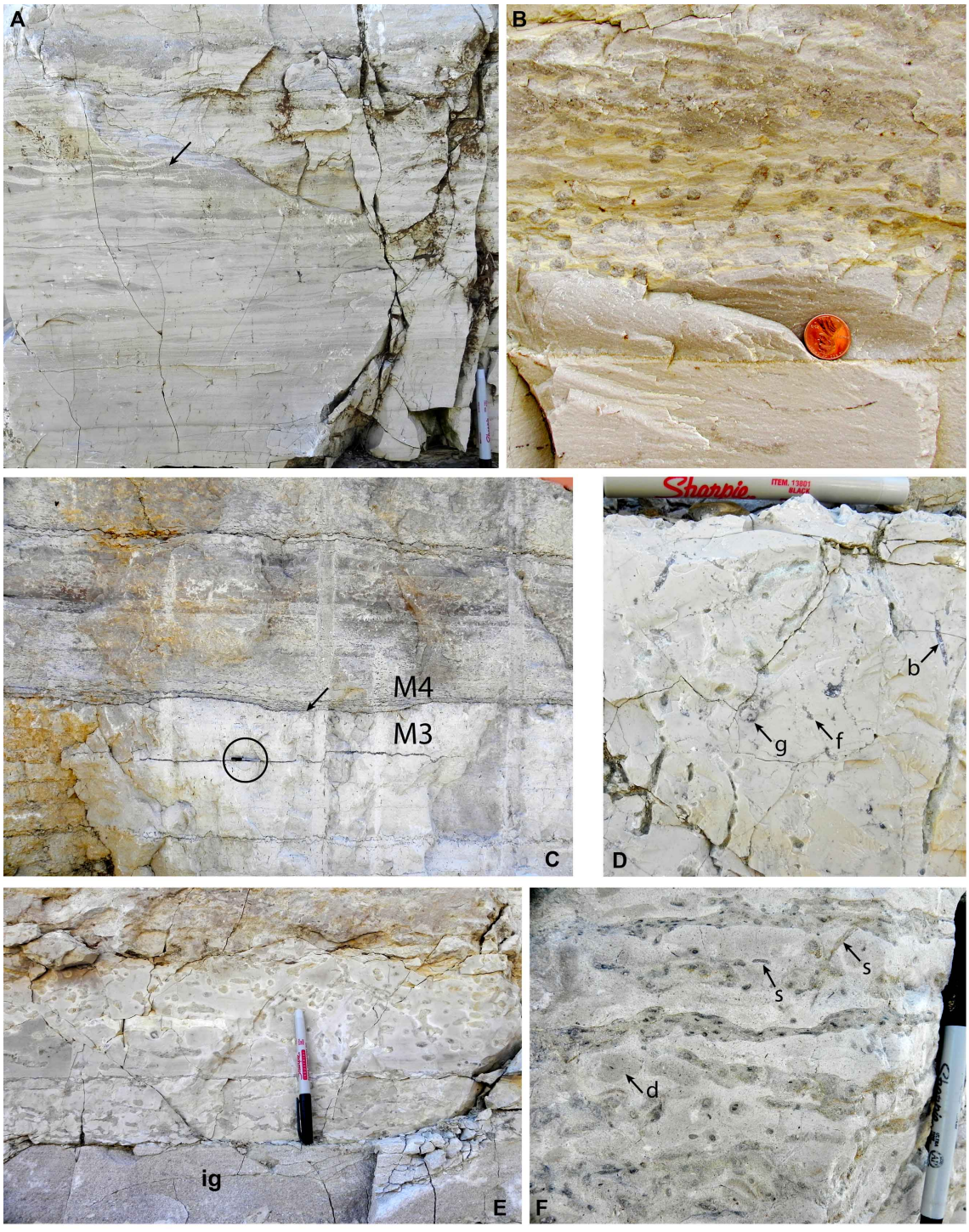

M
NL
HS
CARB.
MM
CARB.
MM2
Mordock
Lower Kimmswick
Gutten.
K.L.
Glen.
Castle.
Macy
Victory
Lower Hager
Beck.
C1?
M6
M5
M4
M3
M6B
M6A
M5C
M5B
M5A
M4B
M4A
V1 Cyc.
LH Cyc.
HST
TST
2m
starvation surface
starvation surface
starvation surface
Legend
Lime Mudstone to Calcisiltite (F1)
Fenestrate Lime Mudstone (F2)
Bioturbated Lime Mudstone (F3)
Nooduler Lime Mudstone (F6)
Bioclastic Packestone/Grainstone (F4,F6)
Fine Grainstone/Calcisiltite (F7-F8)
Cross-bedded Bioclastic Grainstone/Rudstone (F9)
Shale (F4)
K-Bentonite (F5)

Figure 3. Correlation of stratigraphic columns across the St. Louis, Mo, study region. Sections include: NL Section to the north of St. Louis, the HS Section, Section MM, and Section M to the south of St. Louis. Approximately 140 km's separate the NL section from the southern sections. Interpreted depositional sequences marked by thick black lines. System tracts within depositional sequence are indicated as follows: TST, dark blue; HST, tan-brown; Undefined cycle, light grey. Identified intra-sequence cycles include: Lower Hager Cycle, (LH Cyc.); Victory Cycle, (V1 Cyc.); Glencoe Cycle 2, (GC2); Lower King's Lake Cycle, (KL); Guttenberg Cycle, (GB).


A
B
M4
M3
C
Sharpie
ITEM 13001
BLACK
b
g
f
D
ig
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s
s
d
F

Figure 4. (3) Lithofacies of the Plattin Group, section MM. A. Lime mudstone with calcisiltite laminae to cm-thick layers and rippled intervals with wavy to lenticular (arrow) bedding; facies F1, Lower Member, Hager Formation. B, Bioturbated lime mudstone with *Planolites* burrows; facies F1. C. Sharp, undulating transgressive surface (arrow) separating fenestral lime mudstone to wackestone (facies F2, Victory Member, Hager Formation; sequence M3; Fig. 4D) from overlying bioturbated lime mudstone–wackestone (facies F3, Macy Formation; sequence M4; Fig. 4F); pen scale in circle. D. Lime mudstone with irregular fenestrae (arrow-f) and larger, nearly vertical spar-filled burrows (arrow-b); sparse fauna of gastropods (arrow-g); facies F2, Victory Member, Hager Formation. E. Intraclastic grainstone overlain by bioturbated lime mudstone–wackestone; facies F3, Macy Formation. F. Bioturbated wackestone with diffuse, dolomitic burrow-mottles (arrow-d) and more sharply defined, irregular *Thalassinoides*-type galleries. Smaller *Planolites* burrows are most conspicuous inside the galleries, but are also present in more diffusely burrowed wakestone (arrow-s). Facies F3, Macy Formation.

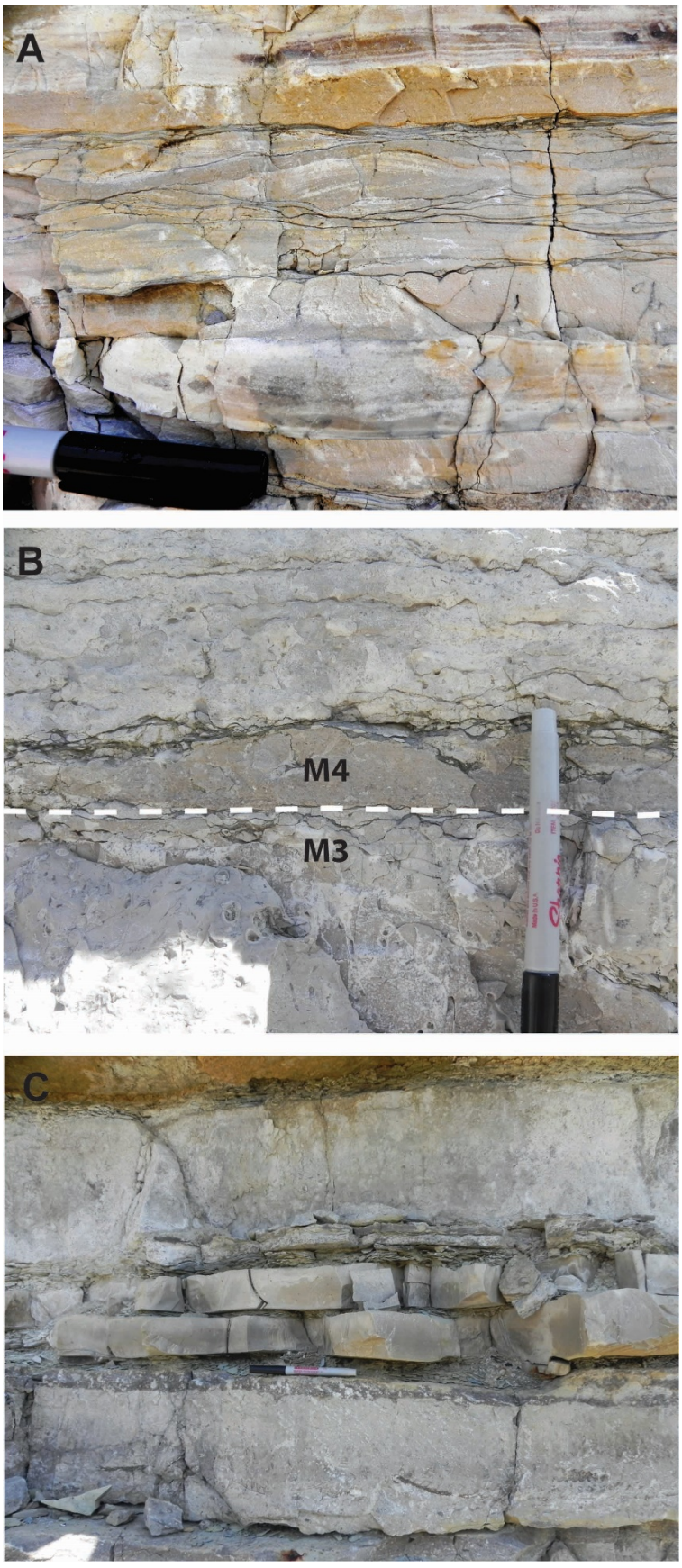
A
B
M4
M3
C

Figure 5. Plattin and Galena Group lithologies, all section MM, except C (NL). A. Plane-laminated to rippled calcisiltite, basal portion of meter-scale cycle of Victory Member, Hager Formation (cycle V1 of Fig. 9C). B. Cm-thick fine grainstone (at upper third of pen-scale) mantling ravinement surface (Fig. 4C) at base of sequence M4. C. Symmetrical cycle at the base of the Glencoe Member, Decorah Formation (GC1 on Fig. 9B), with Deicke metabentonite immediately above. When traced to section MM (Fig. 9A), the middle shaly interval thickens.

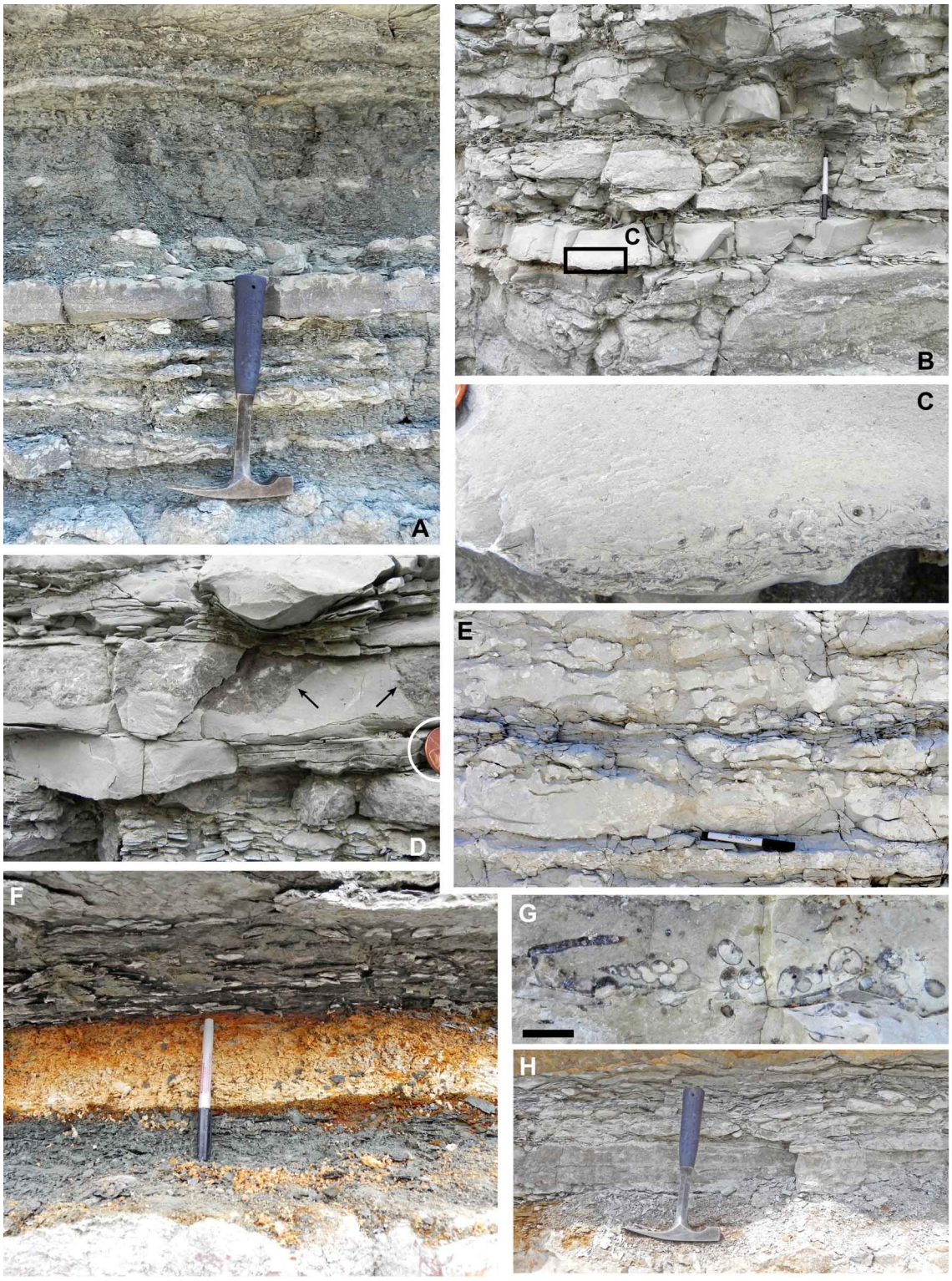
A
B
C
C
D
E
F
G
H

Figure 6. Galena Group lithofacies; all section MM, except G (NL) and H (section M). A. Shale and brachiopod rudstone; facies F4, upper Glencoe Member, Decorah Formation. The carbonate interbeds in the lower part of the image are mostly brachiopod rudstones. B. Part of sequence M5A within the Kings Lake Member, Decorah Formation (facies F6). Basal condensed carbonate with cm-thick wackestone and packstone layer overlain by interbedded shale, wackestone and packstone. Cycle has architecture suggestive of high-frequency sequence, with the condensed basal unit representing a small-scale TST, and the upper shaly interval forming a small-scale HST. Rectangle shows graded bed of Fig. 4C. C. Graded bed (distal tempestite) with cm-thick basal bioclastic lag overlain by lime mudstone–wackestone; Kings Lake Member, facies F6. D. Bioclastic packstone with steep-sided, scoured base (arrows); Kings Lake Member, facies F6; coin scale in semicircle. E. Nodular lime mudstone–wackestone with recessive marly layers and minor cm-thick bioclastic packstone (below pen); Kings Lake Member, Decorah Formation, facies F7. F. Millbrig metabentonite, Decorah Formation; facies F5. Underlying cm-thick shale sits on hardground at the top of a dm-thick wackestone bed within the lower Decorah. G. Gastropod rudstone horizon within lime mudstone–wackestone; Guttenburg Member (facies F7); scale bar, 2 cm. H. House Springs metabentonite (mostly covered at hammer head) overlain by cm-thick bioclastic packstone and shales with nodular lime mudstone; facies F5.

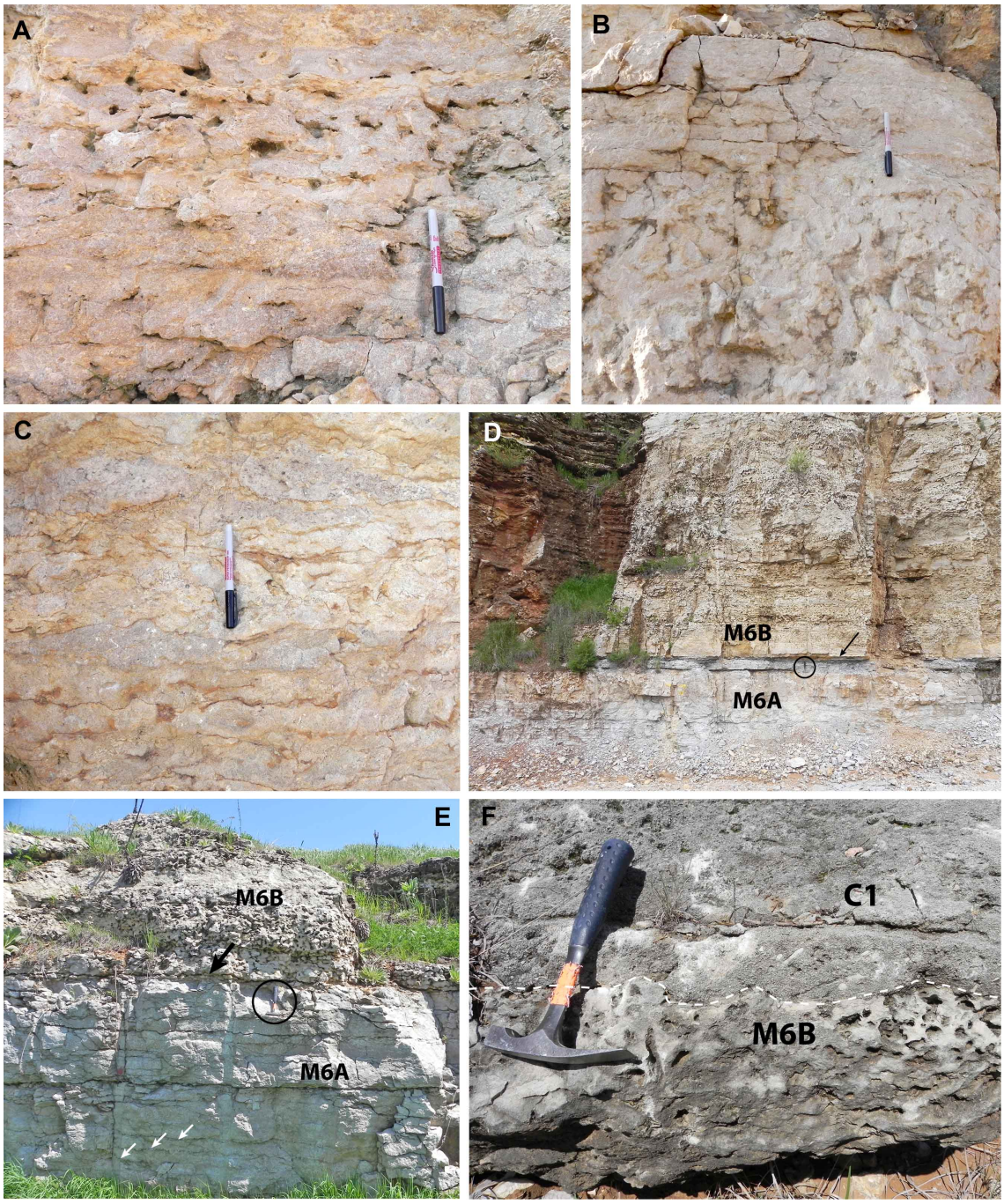
A
B
C
D
M6B
M6A
E
M6B
M6A
F
C1
M6B

Figure 7. Kimmswick Limestone lithofacies. All from section M except E (NL). Variably bioturbated, bioclastic pack- and grainstone; facies F9. B. Bioturbated bioclastic pack- and grainstone with dolomitic galleries of *Thalassinoides* type burrow systems, overlain by less bioturbated packstone; facies F8. C. Lenticular, cm-thick, bioclastic pack- and grainstone interbedded with cm- to dm-thick bioturbated horizons; facies F8, D. Lower half of roadcut at section M, showing pitted weathered surfaces of bioturbated bioclastic carbonates with *Thalassinoides*-type burrow systems (facies F8). The lowest part of the roadcut exposes less bioturbated bioclastic carbonates of the basal Kimmswick (facies F7). The recessive interval at hammer (circle) includes the House Springs metabentonite (Fig. 6H). M6A and M6B are depositional sequences within the Kimmswick. E. Contact between depositional sequences M6A and M6B (facies F7 and F8, respectively) in the NL section. Note that the House Springs metabentonite of section M (Fig. 7D) is cut out by the base of sequence M6B (Black arrow). White arrows show closely-spaced, mineralized hardgrounds. Hammer scale (circle). F. Irregular erosion surface (white dashed line) separating packstone with *Thalassinoides*-type burrows from coarse bioclastic grain- to rudstone that forms the base of sequence Km3.

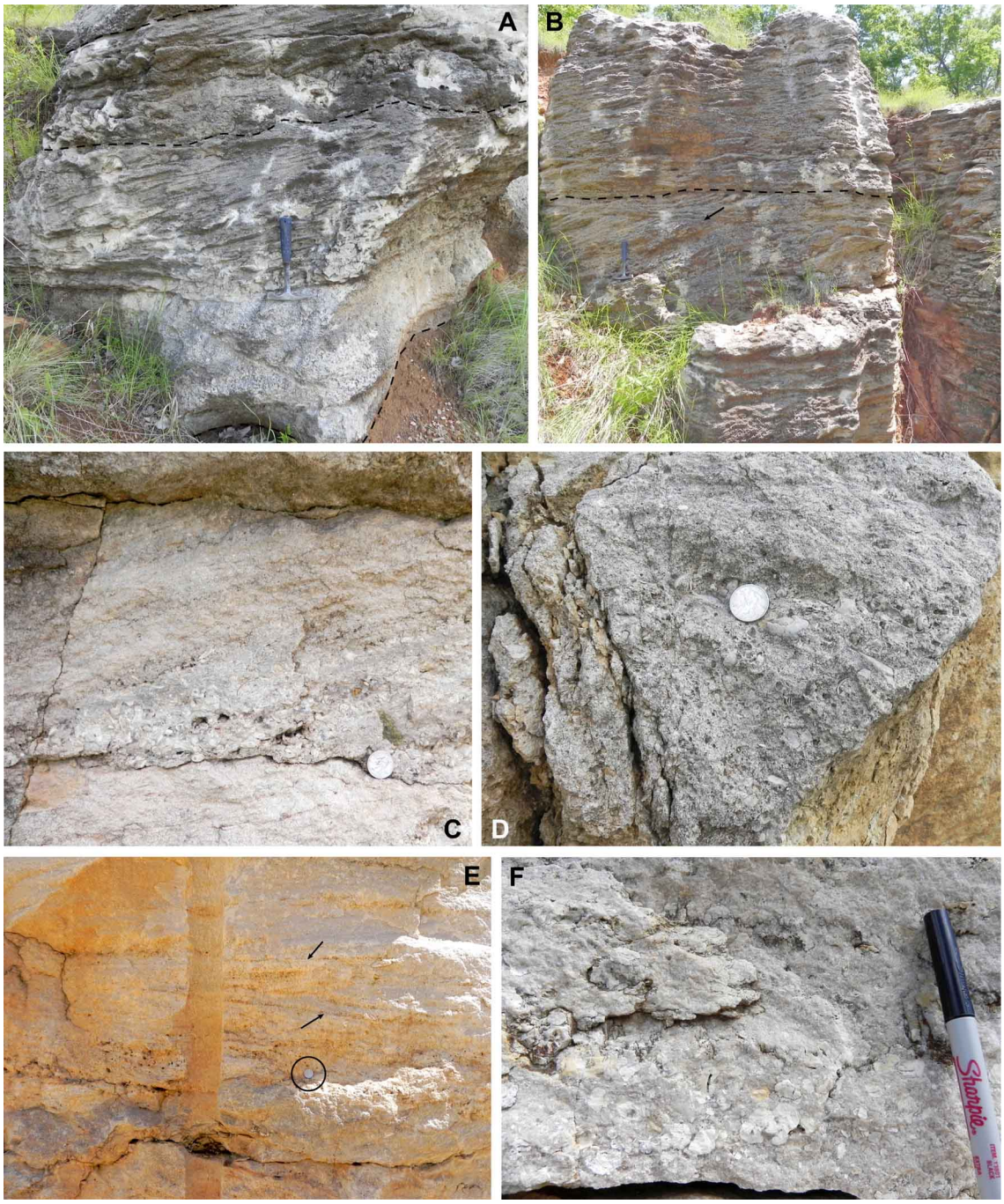
A
B
C
D
E
F
Sharpie

Figure 8. Kimmswick Limestone lithofacies (facies F9). All from section M. A, Two cycles in lower sequence C1, each with basal, massive bioclastic rudstone sharly overlain by cross-bedded bioclastic grain- and rudstone. Dashed line marks erosional base of second cycle. B. Thick sets (dm-scale) of cross-bedded, bioclastic grain- and rudstone (internal erosion surface at arrow), overlain by rippled to low angle planar cross-bedded bioclastic grain- and rudstone. C. Fining upward set of cross-beds, with abundant cm-sized bryozoan debris in basal layers. D. Massive bioclastic rudstone with cm-sized trilobite, brachiopod and bryozoan fragments. E. Bidirectional sets of low angle, planar cross beds; coin scale (circle). F. Crudely graded intra-oncoidal packstone.


A
M5B (base)
M5A
M4–M5?
Mi
Gc1
M4B
Di
M4A
B
M5C
M5B
M5A
Mi
Gc1
Cw (M4B)
Di
C
V1
LH
Bk
D
M5C (base)
M5B
M5A
M4–M5?
Mi
Gc1
E
M6A
M5C
F
M6A
M5–M6
M5C

Figure 9. Significant surfaces and cycles. All from section MM except B (NL). A. Lower Decorah succession. Deicke metabentonite (Di) sits on hardground at the top of the Macy Formation (M4A). The overlying Castlewood Member of the Decorah (M4B) is a condensed unit of mostly wackestone with cm-thick bioclastic and intraclastic layers. The base of the lowest package of the Glencoe Member is a symmetrical cycle (Gc1) with cm-thick carbonates and shale comprising the deepest, mid-point; both the base and the top of the cycle are flooding surfaces. The Millbrig metabentonite (Mi) and associated shale abruptly overlie the lower Glencoe. An irregular erosion surface at the base of a dm-thick brachiopod rudstone cuts down into the Millbrig, and may record the M4–M5 sequence boundary recognized over much of eastern North America (Holland and Patzkowsky, 1996). The upper Glencoe (M5A) has a sequence-like architecture, with a lower interval rich in bioclastic carbonate beds (small-scale TST), and upper shale-rich interval (small-scale HST). The base of the Kings Lake Member (M5B) is a significant ravinement surface. B. Lower Decorah at New London, about 140 km north of Fig. 9A. The Deike metabentonite (Di), Castlewood Member (Cw), lower symmetrical cycle of the Glencoe Member (Gc1) and Millbrig metabentonite (Mi) are similar to section MM. As at MM, the basal brachiopod rudstone of the upper Glencoe (M5A) has an irregular erosional base that cuts down to the Millbrig, but almost all of the rest of the cycle is cut out beneath the Kings Lake Member. As at MM (Figs. 4B, 9D), the lower Kings Lake consists of two cycles M5B, M5C), each with a lower condensed carbonate base and an upper interval of shale and carbonate. C. The Hager Formation comprises two cycles that form a upwardly shallowing succession above the bioturbated subtidal facies of the Beckett Formation (Bk), possibly recording

late HST sequence M3. The lower cycle (lower member; LH) consist of plane-laminated to rippled calcisiltite and overlying bioturbated lime mudstone–wackestone with cm-thick bioclastic packstone layers and lenses. The succeeding cycle comprises the Victory Member, and also begins with plane-laminated to rippled calcisiltite. This interval is overlain by wavy to lenticular bedded lime mudstone and packstone (Fig. 4A) and fenestral lime mudstone (Fig. 4D). D. Sharp contact between Kings Lake and Glencoe members, showing the lower cycle Kings Lake (M5B) and the base of the overlying cycle (M5C). Photographed about 400 m south of Fig. 9A; abbreviations as for Fig 7A. E. Contact between the upper Decorah (upper Kings Lake (M5C) and Kimmswick Limestone (M6A dashed line, M5–M6 sequence boundary); arrows show mineralized hardgrounds in basal Kimmswick. F. As for E; M5C is assigned to the Guttenburg Member; basal Kimmswick includes reworked clasts of Guttenburg.

Chapter 3: The UPPER ORDOVICIAN TRILOBITE *RAYMONDITES* SINCLAIR, 1944 IN NORTH AMERICA

ABSTRACT.— The Upper Ordovician (Sandbian-Katian) bathyurid trilobite *Raymondites* Sinclair is revised using new collections from Missouri and Ontario, and archival material from Illinois, Wisconsin, New York, and Ontario. Phylogenetic analysis supports monophyly of *Raymondites*, but recognition of this genus renders *Bathyurus* Billings paraphyletic. We treat *Raymondites* as a subgenus of *Bathyurus* and label the paraphylum of species traditionally assigned to the latter as *Bathyurus* sensu lato. *Bathyurus* (*Raymondites*) comprises five previously named species, *B*. (*R*.) *spiniger* (Hall), *B*. (*R*.) *longispinus* (Walcott), *B*. (*R*.) *ingalli* (Raymond), *B*. (*R*.) *bandifer* Sinclair, and *B*. (*R*.) *trispinosus* (Wilson), and two new species, *B*. (*R*.) *clochensis*, and *B*. (*R*.) *missouriensis*; an eighth species is placed in open nomenclature. All species share tuberculate sculpture on the glabella, a relatively short palpebral lobe whose length is less than half of preoccipital glabellar length, and a pygidial outline that is well rounded posteriorly. Aside from the most basal species, *B*. (*R*.) *longispinus*, they also possess occipital spines and, where the pygidium is known, axial pygidial spines.

INTRODUCTION

BATHYURID TRILOBITES are widespread and diverse in Lower Ordovician strata of Laurentian North America (e.g., Fortey, 1979; Brett and Westrop, 1996; Adrain and Westrop, 2005; Loch, 2007; Adrain et al., 2009; Fortey and Bruton, 2013). However, by the Upper Ordovician, the family was reduced to a handful of species

(Ludvigsen, 1979a, b; Tremblay and Westrop, 1991) that are assigned to *Bathyurus* Billings, 1859 and *Raymondites* Sinclair, 1944, and most of these occurred in shallow water, peritidal settings. Many species of *Bathyurus* have been documented in detail from silicified sclerites (Ludvigsen, 1979a; Tremblay and Westrop, 1991) but *Raymondites* remains by comparison poorly known. Whittington's (1953) review, now sixty years old, is the most recent treatment of the genus to have included study of type material. Species of *Raymondites* are, however, distinctive, with most bearing long occipital and axial pygidial spines. In this paper, we revise *Raymondites* using new collections from Missouri and Ontario, undescribed archival material from Ontario and New York, and restudy of type and figured material of all previously named species.

There is little doubt that *Bathyurus* and *Raymondites* are closely related. Indeed, Sinclair (1944) originally established *Raymondites* as a subgenus of *Bathyurus* although studies published over the last 35 years have considered them to be distinct genera (Ludvigsen, 1979a, b; DeMott, 1987). Here we provide an assessment of monophyly of these genera with a phylogenetic analysis that includes all adequately documented species of *Raymondites* and nine species of *Bathyurus* that could be coded from silicified sclerites (Ludvigsen, 1979a; Tremblay and Westrop, 1991). Based on these results, discussed later in the text, we treat *Raymondites* as a subgenus of *Bathyurus* and assign a paraphylum of more basal species to *Bathyurus* sensu lato.

STRATIGRAPHIC SETTING

Bathyurus **(***Raymondites*) is restricted to Laurentian North America, and has been reported from Ontario, New York, and the Upper Mississippi Valley. A brief outline of

stratigraphic occurrences of the various species treated in systematics section is presented below, along with an assessment of their biostratigraphic significance. Species ranges are summarized in Fig. 1.

Illinois and Wisconsin.— *Bathyurus* **(***Raymondites*) *longispinus* (Walcott, 1876) is well documented in Wisconsin and Illinois, and material figured previously by Whittington (1953) and DeMott (1987) is illustrated here (Figs. 7-9). This species ranges throughout the Plattin Subgroup (DeMott, 1987, fig. 10.3), and figured material comes both from the Quimbys Mill Formation at the top of the subgroup, and the Mifflin Formation at the base. All occurrences in this region are below the Deicke K-bentonite, indicating that they are no younger than the *Phragmodus undatus* conodont Zone (Leslie, 2000, fig. 2) and the M4 depositional sequence of Holland and Patzkowsky (1997, 1998). In eastern Iowa (Ludvigson et al., 2004, fig. 2), a complex hardground at the base of the Quimbys Mill is a candidate for the base of M4, and similar hardgrounds at the top and base of the Mifflin may represent the lower boundaries of M3 and M2, respectively. Thus, *B*. **(***R*.) *longispinus* is a long-ranging species that likely crosses two third-order sequence boundaries.

A second, younger species in Wisconsin and Illinois was originally identified by DeMott (1987) as *B*. (*R*.) *spiniger* (Hall, 1847), but is assigned here to *B*. (*R*.) cf. *B*. (*R*.) *ingalli*. It occurs in the Guttenburg Formation of the Decorah Subgroup, which is well above the Millbrig K-bentonite, and correlates with the *Plectodina tenuis* conodont Zone (Leslie, 2000, fig. 2) and the M5 depositional sequence.

Missouri.—*Bathyurus* (*Raymondites*) *missouriensis* n. sp. occurs in coarse bioclastic carbonate of Katian age exposed in a major road cut along Missouri State Highway MM, about 2.8 km east of House Springs, Jefferson County (see Metzger and Fike, 2013 for additional locality information). We follow Kolata et al. (1998) and Metzger and Fike (2013) in assigning these carbonates to the Kimmswick Formation, rather than the Dunleith Formation of Templeton and Willman (1963). Most of the material was collected from a 50 cm interval of bioturbated crinoidal-bryozoan-trilobite grain- and rudstone located 26.1 m above the base of the section and about two meters above the well-known House Springs K-bentonite (Kolata et al., 1998, fig. 8). One specimen was collected from the equivalent horizon approximately 11.5 km east of House Springs on Missouri State Highway M. The presence of the House Springs K-bentonite near the base of the Kimmswick Formation, as well as an unconformable boundary with the underlying King's Lake Member of the Decorah Formation (M4- M5 depositional sequences), suggest that at least the lower Kimmswick correlates with the M6 depositional sequence of Holland and Patzkowsky (1997, 1998). This interpretation would place the Kimmswick Formation within the *Belodina confluens* conodont Zone (e.g. Mitchell at al., 2004, fig. 7).

Ontario.—*Bathyurus* (*Raymondites*) has been reported from the Lake Simcoe and Ottawa areas (e.g., Wilson, 1947), and Ludvigsen (1979b) illustrated sclerites from exposures along the Moira River in Belleville. The majority of these occurrences lie in the Bobcaygeon Formation (Liberty, 1969), which is largely assigned to the *Plectodina. tenuis* Zone, but with its lower part extending down into *Phragmodus undatus* Zone

(Leslie, 2000, fig. 2). As such, this formation straddles the M4–M5 sequence boundary, with most of it lying in M5. The Bobcaygeon Formation replaced a tangled nomenclature of various units, including the Coboconk, Kirkfield, Rockland, Leray and Hull formations (Liberty, 1969), but many of the earlier reports of the genus (e.g., Wilson, 1947) are expressed in terms of these now obsolete names.

The holotype of *B*. (*R.*) *ingalli* (Raymond, 1913) is from the middle or upper Bobcaygeon ("Hull beds" of Wilson, 1947), but the species has also been recorded from the lower Bobcaygeon ("Leray-Rockland beds"; Wilson, 1947, p. 20), and the overlying Verulam Formation (Ludvigsen, 1979b, fig. 22C). *Raymondites trispinosus* (Wilson, 1947) was collected from strata correlative with the lower Bobcaygeon, whereas the only known specimen of *B*. (*R.*) *bandifer* Sinclair, 1944 is from somewhat older strata ("Leray beds"; Wilson, 1947, p. 19) that are probably equivalent to the upper Gull River Formation.

We collected sclerites of *B*. (*R.*) *longispinus* (Walcott, 1876) and *B*. (*R.*) *clochensis* n. sp., from a single horizon the Cloche Island Formation on Cloche Island. The locality is a road cut along HW 68 that exposes about 10 m of various carbonates, and corresponds to Leslie's (2000, p. 1147) section 27. The trilobites were collected 3.75 m above the base of the section, in a heterolithic interval of nodular to planar bedded, bioturbated lime mudstone to wackestone, with cm-thick bioclastic packstone to rudstone. The associated fauna includes the trilobites *Isotelus* Dekay, 1824, *Thaleops* Conrad, 1843, *Bumastoides* Whittington, 1954, and an undescribed cheirurid allied with *Ceraurinella* Cooper, 1953, along with abundant leperditocopid arthropods. From Leslie's (2000, fig. 2) correlation chart, this fossiliferous interval likely falls in the upper

part of the *Phragmodus undatus* Zone, and is correlative with strata that lie between the Deicke and Millbrig K-bentonites in other regions. This means that the record of *B*. (*R.*) *longispinus* in the Cloche Island Formation is somewhat younger than the highest occurrence in Wisconsin and Illinois, although it is still within depositional sequence M4.

An enrolled individual (Fig. 11.1-11.4) and a cranidium (Fig. 13.4-13.6) from St. Joseph Island (Ontario, not Quebec, as stated by Whittington, 1953, p. 673), about 160 km west of the Cloche Island locality, appear to be conspecific with *B*. (*R.*) cf. *B.* (*R.*) *ingalli* from Wisconsin and Illinois. The collecting locality (northeastern corner of the island) lies in either the Swift Current Formation or the Cloche Island Formation.

New York.— DeMott (1987, p. 68) relocated the old Buck Quarry near Poland, Herkimer County, New York, that yielded Walcott's type material of *B*. (*R.*) *longispinus*, and showed that it was collected from the Chaumont Formation. We follow Liberty (1969) and Salad Hersi and Dix (1999) in correlating the Chaumont with the upper Gull River Formation of Ontario, although Mitchell et al. (2004, fig. 7) equated the Chaumont with the lower part of the overlying Bobcaygeon Formation. The Chaumont underlies the Selby Formation (Salad Hersi and Dix, 1999, fig. 2), a unit that includes the Millbrig K-bentonite at the Dexter Quarry, New York (Mitchell et al., 2004). The Chaumont Formation and its trilobite fauna thus fall into the *Phragmodus undatus* conodont zone and sequence M4, and record an occurrence of *B*. (*R.*) *longispinus* near the top of the range of the species in Wisconsin and Illinois. One incomplete, flattened exoskeleton (Fig. 8.1, see also Whittington, 1953, pl. 65, fig. 16)

is from the Larabee Member of the Glen Falls Formation (see Kay, 1937, p. 262, for details of this unit). According to Kay (1937), the Larabee Member correlates with the "Hull Formation" of the Ottawa region (= middle and upper Bobcaygeon). If both the stratigraphic information and correlation are correct, then this occurrence is likely a little younger than the new record from the Cloche Island Formation of Ontario (see above), and may lie in strata of the lower part of the M5 sequence.

There is little detailed information on the stratigraphic occurrence of the holotype of *B*. (*R.*) *spiniger*, which is from the Mohawk Valley (Kay, 1937). Kay (1937, p. 300) considered the lithology of the host limestone to be characteristic of the Rockland Formation (Napanee Formation of the current New York nomenclature; Brett and Baird, 2002). However, an additional cranidium illustrated by Kay (1937, fig. 9) may represent *B*. (*R.*) cf. *B*. (*R.*) *ingalli* as it possesses tuberculate sculpture, rather than terrace ridges, on the palpebral area. Two previously undescribed cranidia (Fig. 5.5–5.10) from the "Trenton Limestone", 1.6 km north of the Mohawk Valley town of Amsterdam (USNM loc 322a), are very similar to Hall's holotype of *B*. (*R.*) *spiniger*. They almost certainly represent the same species, and are likely from the same general geographic area.

Biostratigraphic significance of B. (Raymondites).—In the Mississippi Valley region of northern Missouri and southern Illinois and Wisconsin, a composite Plattin–Kimmswick succession yields a sequence of three species (Fig. 2) that may have some biostratigraphic utility, albeit limited due to the general rarity of the genus. *Bathyurus* (*Raymondites*) *longsipinus* is the oldest of these; indeed it is the oldest known species,

with all occurrences in strata below the Millbrig K-bentonite. It is confined to the Plattin Subgroup in the Mississippi Valley and, although it likely ranges into slightly younger strata in the Manitoulin Island area of Ontario (Fig. 2), it is entirely Sandbian in age. *Bathyurus* (*Raymondites*) cf. *B*. (*R.*) *ingalli* appears in the upper Decorah Subgroup, and is likely Katian in age, probably occupying a position high in sequence M5. As such, it overlaps in age with *B*. (*R.*) *ingalli* in Ontario. The youngest species, *B*. (*R.*) *missouriensis* is known from the basal Kimmswick Formation and is broadly coeval with the youngest occurrences of *B*. (*Raymondites*) in southern Ontario.

Setting aside species that are known from limited material and/or are geographically restricted [*B*. (*R.*) *spiniger*, *B*. (*R.*) *bandifer*, *B*. (*R.*) *trispinosus* and *B*. (*R.*) *clochensis*], there is a two-fold division of the Ontario-New York succession (Fig. 2). *Bathyurus* (*R.*) *longispinus* is present in pre-Millbrig strata, with *B*. (*R.*) *ingalli* appearing above, and extending into lower Katian strata.

According to Patzkowsky and Holland (1999, p. 318, table 2), *B*. (*Raymondites*) is restricted to the M4 sequence boundary in the Nashville Dome region of Tennessee. Our revision shows that the youngest species of the genus range into the M5 and M6 sequences (i.e., well above the Millbrig K-Bentonite) outside of the Appalachian Foreland Basin in the Mississippi Valley of Missouri, Illinois, and Wisconsin, and over the Algonquin Arch of Ontario. Thus, the disappearance of *B*. (*Raymondites*) at the M4-M5 sequence boundary in Tennessee records regional extirpation rather than complete extinction.

PHYLOGENETIC ANALYSIS

Taxon selection and coding sources.— *Bathyurus* (*Raymondites*) is widespread but generally rare, and much of this study is based on previously described specimens. We borrowed type and other archival material of as many species as possible, all of which is illustrated and revised in this paper. *Bathyurus* (*Raymondites*) *spiniger*, *B*. (*R.*) *longispinus* and *B*. (*R.*) *ingalli* were included in the analysis, along with two new species, *B*. (*R.*) *missouriensis* and *B*. (*R.*) *clochensis*. *Bathyurus* (*Raymondites*) cf. *B*. (*R.*) *ingalli*, although left in open nomenclature, is represented in the analysis by material assigned previously to *B*. (*R.*) *spiniger* by DeMott (1987) and to *B*. (*R.*) *ingalli* by Whittington (1953). All of these species were coded from direct examination of specimens and from new, high-resolution digital images (Figs. 3-16). We excluded two species, *B*. (*R.*) *bandifer* and *B*. (*R.*) *trispinosus*, which are known from limited, incomplete material, although both are treated in the systematics section.

Many species of *Bathyurus* sensu lato from the eastern United States Ontario, and Québec, including the type species, *Bathyurus extans* (Hall, 1847), remain poorly known and are in need of revision. However, such a revision is beyond the scope of this study, and questions of monophyly of *Bathyurus* and *Raymondites* will be addressed with a representative sample of species of the former genus. We selected nine species from northern Canada that are well documented from silicified sclerites and could be coded adequately from photographs published by Ludvigsen (1979a) and Tremblay and Westrop (1991): *B. nevadensis* Ross, 1967; *B. angustus* Ross, 1970; *B. ulu* Ludvigsen, 1979a, *B. esbataottinensis* Ludvigsen, 1979a; *B. granulosus* Ludvigsen, 1979a; *B*. *platyparius* Ludvigsen, 1979a; *B. mackenziensis* Tremblay and Westrop,

1991; *B. sunbloodensis* Tremblay and Westrop, 1991; and *B. margareti* Tremblay and Westrop, 1991. *Acidiphorus brighti* (Hintze, 1953), also based on silicified material, was employed as the outgroup.

Characters.— The data matrix (Table 1) includes 15 ingroup species, 14 binary characters and 3 unordered multistate characters; all characters are described in detail in the appendix. Parsimony uninformative characters (autapomorphies of individual species and states that are shared by all ingroup species) were excluded.

Ludvigsen (1979a, p. 13) considered rostral plate morphology to be diagnostic of *Bathyurus*. Unfortunately, this sclerite is known only for one species of *Raymondites* (Fig. 8.1) and is unknown for the outgroup. The narrow (tr.) anterior portion in species of *Bathyurus* (e.g., Ludvigsen, 1979a, pl. 1, fig. 36; pl. 2, figs. 10, 28; pl. 4, fig. 12) contrasts with the much wider (relative to the width of the medial "waist" of sclerite) anterior portion in *Raymondites*. As rostral plate morphology can be coded to all intents and purposes only for *Bathyurus*, inclusion of a character that describes the narrow anterior portion has no impact on the outcome of the analysis (14 trees are retrieved, as described below). Consequently, we did not include this character in the final analysis, but it is conceivable that rostral plate morphology might play a more decisive role when known for more species of *Raymondites*, *Acidiphorus*, and other related species.

Results.—Parsimony analysis was performed in PAUP* (Swofford, 2001) and the results were checked with TNT (Golobloff et al., 2008). Tree support metrics were calculated with TNT, and character optimization was performed with both PAUP* and

Winclada (Nixon, 2002). A branch-and-bound search (implicit enumeration; branch-collapsing rules were not enforced) discovered 14 equally parsimonious trees (length, 34; CI, 0.61; RI, 0.81; RC, 0.49); the strict consensus is shown in shown in Fig. 2.1, and character optimization (unambiguous transformations that optimize to the same node under the assumptions of ACCTRAN and DELTRAN) is shown in Fig. 2.2. Support indices are generally low, with only one node with Bremer support greater than 1, and one node with GC and/or conventional bootstrap values of 50% or higher.

The results confirm monophyly of (*B*.) *Raymondites*, but recognition of this genus renders *Bathyurus* paraphyletic. Species assigned traditionally to "*Bathyurus*" form a pectinate array that is basal to *Raymondites* (Fig. 2.1). One approach to classification of the ingroup would simply treat *Raymondites* as a junior synonym of *Bathyurus*. The latter would be diagnosed by loss of the anterior border of cranidium, a state that is parsimony uninformative for the ingroup and was not included in the phylogenetic analysis. However, the traditional concept of *Raymondites* represents a derived group of species that is, as discussed below, readily diagnosed. As an alternative, we suggest that it be treated as a subgenus of *Bathyurus*, with the paraphylum of species at lower nodes simply labeled as *Bathyurus* sensu lato. We view this as a more appropriate action than synonymy, given that there are characters, such as rostral plate morphology (see above) that could eventually support monophyly of *Bathyurus*.

Bathyurus (*Raymondites*) is diagnosed by tuberculate sculpture on the glabella (character 4, state 0; see appendix), a relatively short palpebral lobe that is equal to less than half of preoccipital glabellar length (character 8, state 0), and a pygidium that is

well rounded posteriorly (character 14, state 1); all but one species (*R. longispinus*) has a axial spine on the pygidium and possesses an occipital spine.

All species assigned to *Bathyurus* by previous workers are characterized by relatively long palpebral lobes (character 8, state 1). In addition, they share a roughly triangular pygidial outline (character 14, state 0), although in the context of this analysis it is interpreted as a conserved plesiomorphic state. However, *B*. (s.l.) *platyparius* is more closely related to species of *Raymondites* than it is to other *Bathyurus* (s.l.) species on the basis of the long frontal area (character 6. State 0) and, along with *B*. (s.l.) *esbataottinesis*, also shares a relatively narrow glabella (character 1, state 1) with (*B*.) *Raymondites* species. Two species, *B. sunbloodensis* and *B. angustus* retain a marginal pygidial spine (character 15, state 0), and occupy basal positions within "*Bathyurus*".

SYSTEMATIC PALEONTOLOGY

Repositories for figured material are indicated by the following acronyms: AMNH, American Museum of Natural History, New York; GSC, Geological Survey of Canada, Ottawa; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; OU, Oklahoma Museum of Natural History, Norman; ROM, Royal Ontario Museum, Toronto; USNM, National Museum of Natural History, Washington DC.

Morphological terminology follows Whittington et al. (1997); however, the occipital ring and 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 100–500 micron 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 BATHYURIDAE Walcott, 1886

Discussion.—Fortey and Bruton (2013) split Bathyuridae into the two traditionally recognized subfamilies, Bathyurinae and Bathyurellinae, even though they realized that one of these is almost certainly paraphyletic. We prefer to leave the family undivided.

Genus BATHYURUS Billings, 1859

Type species.—*Asaphus*? *extans* Hall, 1847 from the Black River Group of New York State (by original designation).

Discussion.—Although *Bathyurus* as defined by all recent authors (e.g., Ludvigsen, 1979a; Tremblay and Westrop, 1991) is paraphyletic in our analysis (Fig. 2), when rostral plate morphology is known more widely among species of Bathyuridae, it could perhaps support monophyly of the genus (see discussion earlier in text). The large palpebral lobe that is equal to more than half of preoccipital glabellar length (character

8, state 1) is also characteristic of *Bathyurus* species, but originates at the basal node in our analysis. It is possible that it could play a more decisive role in a more comprehensive analysis of Bathyuridae. The classification that we use in this paper, with *Raymondites* treated as a subgenus of *Bathyurus*, and species of the traditional concept of the latter simply assigned to *Bathyurus* sensu lato, is best viewed as an interim step. Species of *Bathyurus* (*Raymondites*) and *Bathyurus* sensu lato are united by the loss of the anterior border on the frontal area [with a reversal in *R.* (*B.*) *clochensis*].

Subgenus RAYMONDITES Sinclair, 1944

Type species.—*Bathyurus ingalli* Raymond, 1913 from the Bobcaygeon Formation near Kirkfield, Ontario, Canada (by original designation).

Diagnosis.—Glabella with tuberculate sculpture on glabella [4(0)]; palpebral lobe length less than half of preoccipital glabellar length [8(0)]; pygidium with well-rounded posterior margin [14(1)]. Aside from most basal species, *R. longispinus*, occipital spine present [3(1)] and, where known, pygidium with long, stout axial spine [16(1)].

Discussion.— Sinclair (1944) established *Raymondites* as a subgenus of *Bathyurus* whose species were characterized by the presence of a stout occipital spine, tuberculate sculpture on the cranidium, and an axial spine on the pygidium. Whittington (1953; Whittington, in Moore, 1959) subsequently developed the modern concept of

Raymondites (e.g., Ludvigsen, 1979b; DeMott, 1987) as a distinct genus that included non-spinose species. He placed emphasis on such features as the shorter palpebral lobe that does not extend as far forward on the cranidium, and the broad cephalic border as separating *B*. (*Raymondites*) from *Bathyrurus* s.l.

Our analysis (Fig. 2.2) identifies several synapomorphies of *B*. (*Raymondites*) as defined by Whittington (1953), including tuberculate sculpture on the glabella, a comparatively short (exsag.) palpebral lobe, and a well-rounded posterior pygidial margin that contrasts with the strongly triangular, often spinose margins of *Bathyrus* sensu lato. Some characters thought to diagnostic by Whittington, particularly the broad cephalic borders, appear in derived species of *Bathyurus* sensu lato (e.g., Ludvigsen, 1979a, pl. 2, figs. 20, 30, 32, 33). The occipital and pygidial axial spines emphasized by Sinclair (1944) occur in all but the oldest, most basal (Fig. 1) species, *B*. (*R*.) *longispinus*. It is also clear that species of *B*. (*Raymondites*) are nested within *Bathyurus* s.l., so that there is some degree of vindication for Sinclair's (1944) original classification.

BATHYURUS (RAYMONDITES) INGALLI (Raymond, 1913)

Figures 3-4

1913 *Bathyurus ingalli* RAYMOND, p. 57, pl. 7, fig. 7.

1921 *Bathyurus ingalli*; RAYMOND, p. 31, pl. 9, figs. 3-5;

1947 *Bathyurus ingalli*; WILSON, p. 19, pl. 2, figs. 15-18.

1944 *Bathyurus (Raymondites) ingalli*; SINCLAIR, p. 16, pl. 1, figs. 9-11.

1953 *Raymondites ingalli* WHITTINGTON, p. 654, pl. 69, figs. 16-21.

1979b *Raymondites spiniger* (Hall); LUDVIGSEN, p. 39, fig. 22B, C.

Diagnosis.— Occipital and axial pygidial spines present. Frontal area equal to 21 % (18-23) of preoccipital glabellar length. Palpebral area of fixigena smooth or with scattered, barely perceptible low tubercles. Pygidium with sculpture of terraces ridges; may include barely perceptible tubercles on axial rings in front of axial spine.

Holotype.— A cranidium (GSC 4318; Fig. 3.6) from the Bobcaygeon Formation near the lift-lock on the Trent-Severn Waterway, about three kilometers north of Kirkfield, Victoria County, Ontario.

Other material.— One exoskeleton and two cranidia from the middle and upper Bobcaygeon Formation, from the Kirkfield area, Victoria County, Ontario; one exoskeleton from the middle or upper Bobcaygeon Formation, Eganville, Renfrew

County, Ontario; two pygidia from the Verulam Formation, Belleville, Hastings County, Ontario.

Description. – Cephalon exclusive of genal spines semielliptical in outline with strongly curved lateral margins. Cranidium subrectangular to subovate in outline, maximum width (tr.) at palpebral lobes equal to 91 % (86-93) of length. Axial and preglabellar furrows are shallow grooves. Glabella convex, elevated well above fixgenae and comprises 86 (84-87) % of cranidial length; well rounded anteriorly. Glabellar width at LO 63 (57-67) % of preoccipital glabella length, but expands slightly forward, reaching maximum width in front of palpebral lobe. LO represents 16 (14-18) % of glabella length; stout occipital spine with broad base, tapering evenly towards tip, length slightly less than preoccipital glabellar length. Spine broken off on smallest specimen (Fig. 3.5), but apparently with a narrower base, and presumably shorter, than on larger cranidia. SO moderately impressed, transverse medially, gently curves anteriorly towards glabellar margin. Glabellar furrows faintly impressed and often expressed only by absence of glabellar sculpture. S1 furrow angled obliquely backward; S2 barely identifiable on most cranidia, nearly transverse. Frontal area lacks border furrow, slopes slightly forward, length equal to 21 % (18-23) of preoccipital glabellar length; anterior margin gently curved forward. Palpebral lobe upturned arcuate band, length 37 % (31-45) of preoccipital glabellar length; strongly developed palpebral furrow separates lobe from weakly arched palpebral area. Anterior branch of facial suture directed gently outward anteriorly along relatively straight course before curving inward towards anterior margin; curved portion begins at point just behind level of

anterior tip of glabella. Preoccular area narrow (tr.), expands slightly forward. Posterior branch of suture initially nearly transverse but curves towards posterior margin distally. Posterolateral projection of fixigena very short (exsag.) and narrow (tr.), extending only slightly beyond level of abaxial tip of palpebral lobe; posterior border furrow is shallow groove. Sculpture of rounded tubercles, moderately developed across glabella, except for occipital spine. Palpebral area may have a few low, indistinct tubercles on otherwise smooth surface.

Librigena with long genal spine equal to 50 % of librigenal field. Lateral border broad anteriorly but narrows progressively backward on spine. Border furrow expressed largely as change in slope between border and librigenal field or between border and inner (adaxial) portion of spine. Librigenal field narrow (tr.), weakly inflated, rises steeply from border. Circumocular suture arcuate. External surface smooth aside from scattered indistinct tubercles on librigenal field.

Thorax with nine segments. Axial furrows strongly impressed, outlining convex axis that narrows backward so that width (tr.) at ninth segment is 77 % of width at first segment. Axial rings transversely subrectangular in outline. Pleura curved downward at fulcrum located at midpoint between axial furrow and small, backwardly directed, hook-shaped pleural spine; broad (tr.) articulating facet present. Deep interpleural furrow extends abaxially from axial furrow to point just beyond fulcrum. Convex posterior pleural band about twice length (exsag.) of anterior band. Coarse turberculate sculpture on axial ring, with pair of conspicuous tubercles present medially. Pleurae smooth.

Pygidium subovate in outline, strongly arched in both lateral and posterior profiles. Pygidium moderately wide, length is approximately 54 % of maximum width. Axial furrows distinct grooves anteriorly, becoming faint towards posterior tip of axis. Axis distinctly vaulted, width approximately 30 % of pygidial width at anterior; narrows backward with four axial rings, three expressed over the crest of the axis, with fourth evident on flanks of axis below spine, and a long, posteriorly narrowing unfurrowed region behind spine. Ring furrows moderately impressed and reach axial furrows. Axial spine with circular to subovate base extending from third axial ring to anterior third of unfurrowed rear portion of axis; spine longer than axis, curving upward and backward, and tapers gradually towards pointed terminus. Pleural field steeply arched with narrow pygidial border defined by change in slope near pygidial margin. Anterior pleural segment defined over distal half of width (tr.) by distinct interpleural furrow, which becomes faint abaxially; interpleural furrow firmly impressed groove. Behind first segment, pleural furrows merge with distal part of interpleural furrows, forming three composite furrows that terminate short of pygidial margin; faint, oblique abaxial portion of interpleural furrow recognizable on external surface of well preserved specimens (e.g., left pleural field of Fig. 4.6). Sculpture of fine terrace ridges on pleural field may be augmented by indistinct tubercles on axial rings.

Discussion.— *Bathyurus* (*Raymondites*) *ingalli* is similar to *B*. (*R*.) *spiniger* (Fig. 5) and recent studies (e.g., Ludvigsen, 1979b) have either treated them as synonyms or restricted the former to the holotype (DeMott, 1987). In our view, these actions are premature because *B*. (*R*.) *spiniger* in particular is poorly known, and there are clear

differences between it and *B*. (*R*.) *ingalli*. Our new images of the holotype of *B*. (*R*.) *spiniger* (Fig. 5.1-5.4) show that it has a relatively long and narrow glabella, and a weakly inflated, upsloping palpebral area of the fixigena that carries sculpture of very fine terrace ridges. Two additional, previously unfigured cranidia (Fig. 5.5-5.10) from "Trenton Limestone", 1.6 km north of Amsterdam, New York (USNM loc. 322a), share these features, which contrast with the relatively shorter and narrower glabella and more inflated, nearly smooth palpebral area of *B*. (*R*.) *ingalli*. Other characters used to separate *B*. (*R*.) *ingalli* and *B*. (*R*.) *spiniger* in earlier studies are of doubtful value. For example, Raymond (1921), Kay (1937, p. 300) and Wilson (1947) emphasized the presence of a larger occipital spine in the former. However, comparisons are difficult because all cranidia that can be attributed to *B*. (*R*.) *spiniger* with any confidence (Fig. 5), including the holotype, have incompletely preserved spines. The holotype of *B*. (*R*.) *ingalli* (Fig. 3.6) has a long, stout occipital spine, although it is also a large sclerite, but the basal portions of the spines of other, smaller specimens (e.g., Fig. 3.1) are not appreciably larger than the preserved portions of those of *B*. (*R*.) *spiniger*. Similarly, we can discern no difference in the lengths of the frontal areas of these species (compare Figs. 3 and 5), although Raymond (1921) believed that the two species could be separated on this basis.

As discussed later, material from St Joseph Island, Lake Huron, that was assigned to *B*. (*R*.) *ingalli* by Whittington (1953), and sclerites from Wisconsin identified as *B*. (*R*.) *spiniger* by DeMott (1987) show persistent sculptural differences from *B*. (*R*.) *ingalli*, and are placed in open nomenclature. *Bathyurus* (*Raymondites*) *trispinosus* (Fig. 10) has smooth palpebral areas of the fixigenae that resemble those of *B*. (*R*.) *ingalli*.

However, the former has a distinctive trifid occipital spine that comprises a long central element and two lateral subsidiary spines; large, spinose tubercles are present at the distal tips of the posterolateral projection. In contrast, *B*. (*R.)ingalli* has a conventional occipital spine (Fig. 3.2, 3.6, 3.7) and lacks the spinose tubercles on the posterolateral projection (Fig. 3.1, 3.5).

BATHYURUS (RAYMONDITES) SPINIGER (Hall, 1847)

Figure 5

1847 *Acidaspis* spiniger HALL, p. 241, pl. 64, fig. 5.

?1894 *Bathyurus spiniger*; CLARKE, p. 723, figs. 38-40.

?1902 *Bathyurus spiniger*; RAYMOND, p. 35, pl. 19, fig. 1.

?1910 *Bathyurus spiniger*; RAYMOND AND NARRAWAY, p. 48, Pl. 15, figs. 4-6

?1920 *Bathyurus spiniger*; FOERSTE, p. 222, pl. 22, fig. 20

?1937 *Bathyurus spiniger*; SCHROCK and RAASCH, p. 577, pl. 10, fig. 14.

non 1937 *Bathyrus spiniger*; KAY, p. 300, pl. 9 [? = *B*. (*R.*) cf. *B*. (*R.*) *ingalli*].

1953 *Raymondites spiniger*; WHITTINGTON, 1953, p. 655.

non 1979b *Raymondites spiniger*; LUDVIGSEN, p. 39, fig. 22B, C [=*B*. (*R.*) *ingalli*].

non 1987 *Raymondites spiniger*; DEMOTT, p. 76, pl. 8, figs. 1-9 [=*B*. (*R.*) cf. *B*. (*R.*) *ingalli*].

Diagnosis.— Long, narrow glabella, with width at SO equal to about 60% of preocipital length. Weakly inflated, upsloping palpebral area of fixigena with sculpture of very fine terrace ridges.

Holotype.— A cranidium (AMNH 854; Fig. 5.1-5.4) from "building stone" (probably the "Rockland Formation" [= Napanee Formation] according to Kay, 1937), Mohawk Valley, New York.

Other material.—Two cranidia from "Trenton Limestone", 1.6 km north of Amsterdam, Mohawk Valley, Montgomery County, New York.

Discussion.—Although numerous sclerites have been identified as *B*. (*R*.) *spiniger* for more than a century (e.g., Raymond, 1902, p. 288, 289, pl. 19, figs. 1-2; Raymond and Narraway, 1910, p. 48, pl. 15, figs. 4-6; Ludvigsen, 1979a, fig. 22B, C), among those that we have been able to examine, only the holotype and two similar cranidia from the Mohawk Valley (Fig. 5) are assigned to this species. Some other occurrences are misidentifications but most are so poorly documented as to questionable at best (see synonomy), As noted earlier, *B*. (*R*.) *spiniger* is differentiated from the otherwise similar *B*. (*R*.) *ingalli* by a somewhat longer and narrower glabella and a weakly inflated, upsloping palpebral area that carry very fine terrace ridges that may be barely perceptible without a microscope.

Kay (1937, p. 300) suggested that the lithology of the matrix surrounding the holotype of *B*. (*R*.) *spiniger* is indicative of the “Rockland Formation” (Napanee Formation of current nomenclature). However, the cranidium (Kay, 1937, pl. 9) that he attributed to this species has tuberculate sculpture on the palpebral area and may in fact represent *B*. (*R*.) cf. *B*. (*R*.) *ingalli*. Interestingly, Kay (1937, p. 300) also noted that *R*.

spiniger "is most similar to a species in the lower Decorah (Guttenberg) limestone of the Upper Mississippi Valley", and given the morphology of his specimen, this unnamed species may well be represented by sclerites from Wisconsin that we assign to *B*. (*R.*) cf. *B*. (*R.*) *ingalli* (Fig. 12).

BATHYURUS (RAYMONDITES) LONGISPINUS (Walcott, 1876)

Figures 6.2–6.7, 7–9

1876 *Bathyurus longispinus* WALCOTT, p. 94.

1910 *Bathyurus longispinus* RAYMOND and NARRAWAY, p. 47, pl. 16, figs. 12-14.

1953 *Raymondites longispinus* WHITTINGTON, p. 625, pl. 65, figs. 10, 14-16, 19, pl. 69, figs. 29.

1987 *Raymondites longispinus* DEMOTT, p. 75, pl. 7, figs. 1-17.

Diagnosis.— Axial pygidial spine and occipital spine absent; array of large, pointed tubercles along posterior margin of LO. Faint anterior border furrow expressed on preocular area, defined most clearly by change in sculpture from tubercles on preocular field (often weak on external surface of exoskeleton; Fig. 7.3) to mostly terrace ridges on the border (e.g., Fig. 6.2). Anterior branches of facial sutures curved outwards, with maximum width of preocular area behind border furrow. Palpebral area of fixgena with sculpture of coarse terrace ridges. Pygidium transversely subelliptical in outline, length equal to about 45 % of width. Only one well defined axial ring on external surface of axis (Fig. 8.4).

Holotype.—A nearly complete exoskeleton (MCZ 107237, Fig. 6.1-6.4) from the Chaumont Formation, Buck's Quarry, Poland, Herkimer County, New York (DeMott, 1987, p. 68).

Other material.—One nearly complete exoskeleton and a cephalon from the Chaumont Formation, New York; a nearly complete, compacted exoskeleton from the Larabee Member, Glen Falls Formation, New York; one cranidium and one librigena from the Cloche Island Formation, Cloche Island, Ontario; one cranidium and one pygidium from the Mifflin Formation and one cranidium possibly from the Quimbys Mill Formation, Illinois; two cephala and one cranidium from the Quimbys Mill Formation, Wisconsin.

Description.—Cephalon (excluding genal spines) semielliptical in outline and strongly vaulted. Cranidium subrectangular in outline with anterior margin bowed gently forward; maximum width across the palpebral lobes about 95 % of length. Axial and preglabellar furrows narrow, relatively shallow but clearly defined. Glabella occupies 84 % of cranidial length, parallel sided posteriorly but slightly expanded and well rounded anteriorly. LO long, accounts for 17 % of glabellar length, with posterior margin curved strongly backwards. Occipital spine absent but array of large, pointed tubercles present along posterior margin of LO. SO firmly impressed, nearly transverse medially but curved gently forward near axial furrow. Glabellar furrows largely obsolete. S1 identifiable as smooth patch of exoskeleton opposite anterior end of palpebral furrow but lacks appreciable incision even on internal mold. Faint anterior

border furrow expressed on preocular area, defined most clearly by change in sculpture from tubercles on preocular field (often weak on external surface of exoskeleton; Fig. 7.3) to mostly terrace ridges on the border (e.g., Fig. 6.2, 6.3). Border distinctly concave anteriorly. Palpebral lobe forms narrow rim (Fig. 7.7) around margin of upsloping (Fig. 6.4) palpebral area of fixgena; extends from LO to S1 and equal (exsag.) to 38 % of preoccipital glabellar length. Palpebral furrows obsolete. Anterior branches of facial sutures curved outwards, with maximum width of preocular area behind border furrow, then curve inward along anterior cranidial margin. Posterior branches strongly divergent; posterolateral projection very short (exsag.) and narrow (tr.), extending only slightly beyond outer edge of palpebral lobe, apparently lacks border furrow. Connective sutures (Fig. 8.1) converge obliquely backward before turning abruptly to become roughly parallel near posterior margin of doublure. Rostral plate broad anteriorly, subtriangular in outline, with short (sag.), narrow (tr.) rectangular projection posteriorly. Glabella and preocular field with scattered tubercles, augmented with fine terrace ridges on glabella; palpebral area of fixgena carries coarser terrace ridges. Anterior border with terrace ridges and scattered coarse granules.

Librigena with conspicuous genal spine longer than cranidium. Wide, flattened lateral border defined largely by sharp reduction in slope and change from tuberculate sculpture of librigenal field to mostly terrace ridges; narrows backward along genal spine and disappears near tip. Posterior border furrow distinct groove adaxially but terminates short of lateral border. Librigenal field tall and steeply sloping; visual surface of eye mounted on vertical eye socle (Fig. 6.4); eye socle furrow absent.

Thorax of nine segments. Axial furrows well defined grooves; axis moderately convex, occupying 40 % of total thoracic width at anterior but narrowing backwards, with posterior width about 79 % of anterior width. Axial rings subrectangular to subovate in outline. Pleura elongate, flexed down distally; pleural tips, including articulating facet not preserved on available material. Strongly impressed pleural furrows extend across at least half of pleural width; incision decreases abaxially. Sculpture of terrace ridges, with small, faint tubercles on axial ring.

Pygidium transversely subelliptical in outline, length equal to about 45 % of width, and arched in posterior view. Axis moderately convex, gently tapered and well rounded posteriorly; width at anterior 28 % (26-31) of maximum pygidial width. Only one well defined axial ring on external surface of axis (Fig. 8.4); single axial ring furrow transverse and reaches axial furrow. Articulating furrow also transverse and firmly impressed; articulating half-ring semielliptical and short, length (sag.) a little less than half length of first axial ring. Pleural field moderately arched, nearly flat and wide adaxially, but flexed gently downward towards narrow, weakly concave border. Anterior pleural rib with well-incised pleural furrow separating subequal anterior and posterior pleural bands; interpleural furrow well defined distally but becomes increasingly faint adaxially. Behind the anterior rib, pleural and interpleural furrows merge, connected by short, sigmoid segment. Entire surface with sculpture of terrace ridge; three pairs of smooth oval patches of exoskeleton along flanks of axis (Fig. 6.5) apparently mark vestigial axial rings.

Discussion.— *Bathyurus* (*Raymondites*) *longispinus* differs from all other members of the subgenus in lacking both an occipital spine on the cranidium and an axial spine on the pygidium, and occupies a basal position in the clade in the phylogenetic analysis (Fig. 2). Other diagnostic features include outwardly bowed anterior branches of the facial sutures (Figs. 6.2, 7.1), conspicuous sculpture of terrace ridges on the palpebral area (internal molds are smooth; Figs. 6.2, 7.1), and a broad, semielliptical pygidium that has only one well defined axial ring anteriorly (Fig. 8.4). The figured material encompasses a broad stratigraphic range that crosses at least one, and likely two, third order sequence boundaries. However, the diagnostic character states listed above are evident in specimens from the lower (Figs. 7.1-7.4, 8.4) and upper (Figs. 6.2-6.5, 8.2, 8.3) parts of this range, and we assign them all to *B*. (*R*.) *longispinus* without hesitation.

Bathyurus (s.l.) *platyparius* Ludvigsen (1979a, pl. 2, figs. 20-43) is most closely related to *B*. (*Raymondites*) among *Bathyurus* (s.l.) species, and sits one node down-tree from *B*. (*R*.) *longispinus* (Fig. 2) Like other *Bathyurus* (s.l.) species, it resembles *B*. (*R*.) *longispinus* in lacking both an occipital spine and a pygidial axial spine. It is also unique among *Bathyurus* (s.l.) in possessing a relatively long frontal area on the cranidium that approaches the morphology of *B*. (*R*.) *longispinus*. However, the latter differs in having tuberculate sculpture on the glabella, including large, pointed tubercles along the posterior margin of LO (e.g., Fig. 7.7), proportionately shorter palpebral lobes, and a faint anterior border furrow on the anterior areas of the fixigenae. The pygidium of *B*. (s.l.) *platyparius* is dramatically different in being triangular in outline with a bluntly pointed posterior terminus (Ludvigsen, 1979a, pl. 2, figs. 24, 25, 31).

BATHYURUS (RAYMONDITES) BANDIFER Sinclair, 1944

Figure 6.1

1944 *Bathyurus* (*Raymondites*) *bandifer* SINCLAIR, p. 17, pl. 1, figs. 12-13.

1947 *Bathyurus bandifer*; WILSON, p. 19, pl. 2, fig. 7

Diagnosis.— Short, bifurcate occipital spine on LO. Frontal area relatively short, roughly equal in length to LO (excluding spine).

Holotype. – A cranidium (GSC 13249; Fig. 6.1) from the "Leray Beds" (= Chaumont Formation; Salad Hersi and Dix, 1999, fig. 2), 11.25 km west of Cobden, Renfrew County, Ontario.

Discussion.— The species is currently only known from the holotype, an incomplete ventral surface of a cranidium (Fig. 6.1). It possesses a distinctive, short, stout, bifurcate occipital spine. As far as can be determined, glabellar outline, density of tuberculation, and the morphology of the frontal area are comparable to *B*. (*R*.) *ingalli* (Fig. 3). Although the cephalic doublure is visible, it is crumpled and broken medially, so that the rostral plate and rostral sutures cannot be indentified with any confidence.

BATHYURUS (RAYMONDITES) TRISPINOSUS (Wilson, 1947)

Figure 10

1947 *Bathyurus trispinosus* WILSON, p. 21, pl. 2, figs. 8-9.

Diagnosis.— Cranidium with trifid occipital spine comprising long central element and smaller lateral spines. Large, spinose tubercle at tip of posterolateral projection. External surface of palpebral area of fixigena smooth. Palpebral lobe strongly elevated, rising well above crest of glabella. Pygidium with long axial spine.

Holotype.—A cephalon (GSC 11304; Fig. 10.1-10.4) from the "Leray-Rockland Beds" (lower Bobcaygeon Formation), east of Packenham, Lanark County, about 47 km east of Ottawa, Ontario.

Other material.—A pygidium (GSC 11304a; paratype) from the same locality as the holotype.

Discussion.— The unique holotype cephalon of *B.* (*R.*) *trispinosus* is closest to *B*. (*R.*) *ingalli*, with which it shares a smooth palpebral area and a long axial pygidial spine. It differs most noticeably from *B*. (*R.*) *ingalli*, and all other species of *B*. (*Raymondites*), in having a trifid occipital spine and a conspicuous spinose tubercle on the distal tip of the posterolateral projection. The palpebral lobes of *B*. (*R.*) *trispinous* rise well above the level of the crest of the glabella, contrasting with the lower elevation of the lobes in

other species (e.g., Figs. 6.4, 11.2). The associated pygidium (Fig. 10.5-10.7) is distorted by differential compaction and we cannot entirely rule out some degree of compaction of the cephalon as there appears to be a fracture along the left axial furrow (Fig. 10.1, 10.4). However, the right side appears to be intact and we interpret the cephalon as faithfully recording the elevation of the palpebral lobe.

BATHYURUS (RAYMONDITES) cf. B. (R.) INGALLI (Raymond, 1913)

Figures 11–13

?1937 *Bathyrus spiniger* (Hall); KAY, p. 300, pl. 9.

1987 *Raymondites spiniger*; DEMOTT, p. 76, pl. 8, figs. 1-9.

Material. —One enrolled exoskeleton and one cranidium from Upper Ordovician strata (Gull River Formation or Cloche Island Formation), northeast corner of St. Joseph Island, Algoma District, northwestern Lake Huron, Ontario. Three cranidia and a pygidium from the Guttenberg Formation, Fennimore West road cut, Grant County, Wisconsin (DeMott, 1987).

Discussion.— Material assigned here to *B*. (*R*.) cf. *B*. (*R*.) *ingalli* includes specimens that were identified as *B*. (*R*.) *ingalli* by Whittington (1953; Figs. 11.1-11.4,13.4-13.6) and as *B*. (*R*.) *spiniger* by DeMott (1987; Figs. 12, 13.1-13.3). These specimens are united by details of the sculpture, particularly on the cephalon. The external surface of

the palpebral area of the fixigena has large, closely spaced tubercles (e.g., Figs. 12.1, 13.4) that are subdued on internal molds (e.g., Fig. 12.6); the librigenal field also carries numerous conspicuous tubercles anteriorly (Fig. 11.1, 11.3). In contrast, these regions of the cephalon of *B*. (*R*.) *ingalli* are virtually smooth (Fig. 3). These sculptural differences extend to the pygidia, which are tuberculate in *B*. (*R*.) cf. *ingalli* (Fig. 13.1-13.3) but smooth in *B*. (*R*.) *ingalli*.

BATHYURUS (RAYMONDITES) CLOCHENSIS new species

Figure 14.1-14.9

Diagnosis. —Frontal area subequally divided into gently convex anterior border and slightly longer preglabellar field; anterior border furrow poorly defined. Palpebral area of fixgena with sculpture of fine tubercles, best defined on smaller specimen. Occipital spine present.

Holotype. —A cranidium (part and counterpart, ROM 61465a, b; Fig. 14.1-14.6) from the Cloche Island Formation, road cut on HW 68, Cloche Island, about 9 km south of Birch Island (section 27 of Leslie, 2000, p. 1147), Manitoulin District, Ontario, 3.5 m above the base of the section.

Other Material. — One cranidium (ROM 61466; paratype) associated with holotype.

Description. — Cranidial outline (excluding palpebral lobes) generally subrectangular, with forwardly curved anterior margin; maximum width at palpebral lobes equal to 88 % (87-90) of cranidial length (sag.). Axial and preglabellar furrows shallow grooves. Glabella convex, standing above level of palpebral lobe; expands slightly forward, well rounded anteriorly, occupies 86 % (85-87) of cranidial length. SO curved backward, firmly impressed on external surface, more so on internal mold. LO with long occipital spine; excluding spine, LO accounts for 14 % (13-15) of glabellar length. S1 and S2 expressed as oblique smooth bands on external surface; S1 weakly impressed on internal mold. Frontal area subequally divided into gently convex anterior border and slightly longer preglabellar field; anterior border furrow poorly defined. Palpebral lobe strongly upturned, arcuate band extending from SO to S1; anterior tip close to axial furrow but posterior tip separated from glabella by narrow strip of fixigena. Palpebral area inflated, bounded abaxially by shallow, strongly curved palpebral furrow. Anterior branches of the facial suture diverge gently forward along straight paths, then curve sharply inward along anterior cranidial margin. Preocular field of fixigena narrow posteriorly but expands forward, largely due to curvature of anterior end of glabella. Posterior branches of sutures diverge obliquely backward. Posterolateral projection very short (exsag.) and narrow, extending only a little beyond outer tip of palpebral lobe. Posterior border narrow (exsag.), convex rim. Posterior border furrow firmly impressed, truncated abaxially by sutural margin short of tip of posterolateral projection. Evenly distributed tuberculate sculpture on glabella and palpebral area; tubercles becomes slightly larger and more spinose on LO. Preglabellar, preocular and posterior fields smooth; anterior border with fine terrace ridges.

Discussion. —*Bathyurus* (*Raymondites*) *clochensis* is unique in possessing a frontal area that is divided into a distinct anterior border and preglabellar field, and although the material available is limited, we are confident that it represents a new species. The sculpture of tubercles on the palpebral area is shared with *B*. (*R*.) cf. *B*. (*R*.) *ingalli* but the frontal area, aside from being undifferentiated, appears to be relatively shorter (e.g., Figs. 12.8, 13.4).

Bathyurus (*Raymondites*) *longispinus* has weak border furrow that is defined in part by a sharp change in sculpture from tubercles on the preocular field to terrace ridges on the border; it merges adaxially with the preglabellar furrow (e.g., Fig, 6.1-6.4). As such, it differs from *B*. (*R*.) *clochensis* through backward expansion of the border and concomitant loss of the preglabellar field. Other species of *B*. (*Raymondites*) lack any trace of the border furrow or sculptural differentiation between the frontal area and preocular field, so it is unclear whether their uniform morphology originated from effacement of a configuration resembling that of *B*. (*R*.) *clochensis* or of *B*. (*R*.) *longispinus*.

BATHYURUS (RAYMONDITES) MISSOURIENSIS new species

Figures 15-16

Diagnosis.— Occipital and axial pygidial spine present. Long frontal area, length equal to 28 % (22-32); lower values in largest specimens) of preoccipital glabellar length; anterior border furrow obsolete. Glabella well rounded anteriorly and with conspicuous

taper in front of S2. Palpebral area of fixigena smooth. Anterior branches of facial suture nearly straight, slightly divergent.

Holotype.—A cranidium (OU 12656; Fig. 15.6-15.8), Kimmswick Formation, Section MM, road cut on Missouri State Highway MM, 2.7 km southeast of House Springs, Jefferson County, Missouri, collection MM 26.1-26.6.

Other material.— One paratype cranidium (OU 12657) from section M, 10.8 km southeast of House Springs. Five paratype cranidia (OU 12653–12656, 12658), one paratype hypostome (OU 12665), one paratype librigena (OU 12659) and five paratype pygidia (OU12660–12664) from section MM. Additional, non-type material includes four cranidia and three pygidia from section MM.

Description. – Cranidium subrectangular in outline, with maximum width (across palpebral lobes) equal to 79 % of length. Strongly convex glabella outlined by shallow axial and preglabellar furrows and occupies 77 % of cranidium; nearly parallel-sided posteriorly, but tapered and well rounded in front of S2, with both taper and rounding best expressed in smaller specimens (e.g., Figs. 15.5). LO (excluding spine) accounts for 15 % of glabellar length; long, stout occipital spine equal to at least 23 % of preoccipital glabellar length. SO firmly impressed, curved gently backward. Oblique S1 and S2 barely expressed as smooth areas that interrupt sculpture. Frontal area long, length equal to 28 % (22-32; lower values in largest specimens) of preoccipital glabellar length, and flat (Fig.15.5) to gently concave (Fig.15.9); border furrow and border

obsolete. Palpebral lobe arcuate in outline and slopes upward; centered opposite L1 and extends from LO to S1, length equal to 39 % of preoccipital glabellar length; anterior and posterior tips located close to axial furrow. Palpebral area gently inflated and separated from palpebral lobe by shallow, arcuate palpebral furrow. Anterior branches of facial sutures diverge gently forward along nearly straight course before curving inward along anterior cranidial margin; posterior branches and posterolateral projection not preserved. Preocular fixigena narrow (tr.) posteriorly but expands anteriorly to more than double width; postoccular fixigena very short (exsag.), limited to posterior border and border furrow. On internal mold, tubercles evenly distributed over preoccipital glabella, except for lateral furrows; LO with scattered large tubercles, including four along posterior margin. Palpebral area of fixgena smooth.

Librigena with elongate genal spine and strongly curved lateral margin; genal spine length about 140 % of length (exsag.) of librigenal field. Lateral border flattened, broad (tr.) anteriorly but narrows backward along genal spine, terminating just short of spine tip.

Hypostome excluding anterior wings semicircular in outline; bases of a pair of spines preserved on posterior corners. Median body outlined posteriorly and laterally by firmly impressed border furrows, but ill-defined anterior and not differentiated from anterior border. Middle furrows deep abaxially but not connected across median body; maculae indistinct. Posterior lobe of median body semicircular in outline. Posterior border convex, maintains even width (sag., exsag.) between spines; lateral border constricted in front of spines, forming concave embayment of lateral margin, then expands, reaching maximum width (tr.) just behind level of middle furrow.

Pygidium subovate in outline, with strongly curved lateral and posterior margins, length approximately 55 % of maximum width. Axis strongly convex, long accounting for 85 % of pygidial length, and wide, occupying approximately 36 % of pygidial width. Axial furrows lightly impressed, more clearly defined anteriorly. Semielliptical articulating half-ring and two axial rings expressed in front of axial spine; remainder of axis unfurrowed. Ring furrows transverse, weakly impressed. Base of axial spine ovate in outline with anterior end on third axial ring; spine long (at least equal to pygidial height), directed steeply upward and slightly curved posteriorly, originating in the third axial ring and continues onto unfurrowed rear portion of axis. Pleural field flexed downward with a steep slope to narrow border. Anteriormost pleural and interpleural furrows separated; pleural furrow developed adaxially and interpleural furrow expressed distally, extending onto border. Three additional pleural and interpleural furrows confluent, with narrowing (exsag.) and shallowing at junction (Fig. 16.8, 16.9). External surface of exoskeleton and internal mold smooth.

Discussion.— The long frontal area separates *B*. (*R*.) *missouriensis* from all other members of the genus. In other respects, including the smooth palpebral area and tuberculate glabellar sculpture, it is most like *B*. (*R*.) *ingalli*, from which it also differs in having a relatively narrower, elongate glabella (e.g., Fig. 15.1, 15.4-15.6). In addition to a clearly shorter frontal area (compare Fig. 5.1 and 5.5 with Fig. 15.1 and Fig. 15.6), *B*. (*R*.) *spiniger* has a steeply upsloping palpebral area (Fig. 5.3, 5.4) that contrasts with the inflated, but nearly horizontal, palpebral area (Fig. 15.7). Unlike *B*. (*R*.) *clochensis* (Fig. 14), *B*. (*R*.) lacks any trace of a border or border furrow.

Bathyurid gen. and sp. indet.

Figure 17

1974 *Raymondites*? sp. 1974, p. 21, pl. 5, figs. 9-11, 13, 15, 16.

Material.—Two well preserved pygidia from the Oil Creek Formation, Highway 77 section, Carter County, southern Oklahoma (Shaw, 1974). This locality is essentially the same as the section that yielded the conodonts studied by Bauer (2010). The range of "*B*. (*Raymondites*)" sp. indet. (161–171 m above the base of the Joins Formation) likely falls in Bauer's (2010) *Histiodella labiosa* Zone (Whiterockian; Darriwilian). Two incomplete pygidia from the same formation at the Washita River section, Murray County, (Shaw, 1974, p. 48, pl. 5, figs. 9, 13) may also represent this species.

Discussion.— Pygidia from the Middle Ordovician (Darriwilian) Oil Creek Formation resemble *B*. (*Raymondites*) in possessing what must be, judging from the preserved bases, long, stout axial spines. However, the spine is centered on the second axial ring (Fig. 17.1, 17.6), with forward and backward deflection of the ring furrows, so that this ring is subhexagonal in outline. This contrasts with the more posterior position in *B*. (*Raymondites*), where the anterior end is at the third ring (Figs. 4, 10.5-10.7, 11.4, 13.1-13.3), and the spine extends backward across at least three segments (rings 3-5; Fig. 4.5). The Oil Creek pygidia also differ from *B*. (*Raymondites*) in having a narrow rim-like border and a border furrow that forms a shallow gutter (e.g., Fig. 17.2, 17.3). The

border in *B*. (*Raymondites*) is expressed by a distal change in slope of the pleural field (Figs. 4.5, 13.3).

As recognized by Shaw (1974, p. 22) many bathyurid trilobites have interpleural furrows that are expressed distally, but become progressively effaced towards the axis. Behind a well-defined anterior pleural segment, the pleural and interpleural furrows merge, and each composite furrow has a faintly sigmoid course (e.g., Fig. 8.4). The Oil Creek specimens possess this type of composite furrow on a relatively narrow pleural field. However, these furrows are also connected by additional furrows, presumably paradoublural in nature, that run roughly parallel to the pygidial margin (Fig. 17.1, 17.6); a feature that is unknown in *B*. (*Raymondites*). Given the various differences in the Oil Creek pygidia, we agree with Shaw that an assignment to *B*. (*Raymondites*) is at best questionable, and they may represent an undescribed bathyurid genus.

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CHAPTER 3 APPENDIX. CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

1. Glabellar width. 0, wide (glabellar length/glabellar width at SO ≥ 0.65; e.g., Fig. 5.1; Ludvigsen, 1979a, pl. 2, fig. 20) 1, narrow (glabellar length/glabellar width at SO < 0.60; e.g., Ludvigsen, 1979, pl. 2, figs. 5, 18).
2. S1 lateral glabellar furrow. 0, absent (e.g., Hintze, 1953, pl. 26, fig. 4a; Fig. 7.1, 7.4); 1, present (e.g., Ludvigsen, 1979a, pl. 4, fig. 21).
3. Occipital spine. 0, absent (e.g., Hintze, 1953, pl. 26, fig. 4a; Fig. 7.1); 1, present (e.g., Fig. 3.2).
4. Glabellar sculpture. 0, tuberculate (e.g., Hintze, 1953, pl. 26, fig. 4a; Fig. 3.2); 1, granulose (e.g., Ludvigsen, 1979a, pl. 2, fig. 2); 2, terrace ridges in the form of "scales" (e.g., Ludvigsen, 1979a, pl. 6, fig. 2).
5. Expansion of glabella at 2L. 0, absent (e.g., Hintze, 1953, pl. 26, fig. 4a); 1, present (e.g., Ludvigsen, 1979a, pl. 4, figs. 1, 21).
6. Frontal area length. 0, long (at minimum, roughly equal to LO; e.g., Fig. 7); 1, short (much shorter than LO; e.g., Ludvigsen, 1979a, pl. 5, figs. 1, 6, 7).
7. Variability of short frontal area ([state 6(1)]. 1, preglabellar area narrows medially (sag.) relative to width (tr.) of preocular area (e.g., Tremblay and Westrop, 1991, fig. 14.1, 14.4); 2, preglabellar area continuous with preocular area (e.g., Ludvigsen, 1979a, pl. 1, figs. 6, 7). The condition in *Raymondites* and some species of *Bathyurus* (e.g., *B. platyparius*) involves expansion of the border relative to the

preocular area. As this state essentially duplicates state 6(0), it was not coded (i.e., entered into the matrix as an inapplicable state).

8. Palpebral lobe length. 0, less than half of preoccipital glabellar length (e.g., Fig. 7); 1, more than half of preoccipital glabellar length (e.g., Ludvigsen, 1979a, pl. 1, figs. 1, 4).

9. Palpebral lobe configuration. 0, flat to gently convex (e.g., Ludvigsen, 1979a, pl. 1, figs. 1-3); 1, strongly upturned (e.g., Fig. 5.3.).

10. Sculpture of palpebral area. 0, tubercles (e.g., Fig. 12.1); 1, granules (e.g., Ludvigsen, 1979a, pl. 2, figs. 2, 4, 5); 2, terrace ridges (e.g., Fig. 7.6; Ludvigsen, 1979a, pl. 6, fig. 2); 3, smooth (e.g., Fig. 3.1). Sculpture of the palepbral area may differ from glabellar sculpture in species of *Raymondites* (e.g., Fig. 7) and was coded separately.

11. Librigenal border furrow. 0, little or on extension onto genal spine (e.g., Tremblay and Westrop, 1991, fig. 13.41, 13.42); extends along most or all of genal spine (e.g., Figs. 3.6, 6.1-6.4).

12. Spines on posterior corners of hypostomal border. 0, present (e.g., Tremblay and Westrop, 1991, fig. 12.14); 1, absent (e.g., Ludvigsen, 1979a, pl. 6, figs. 9, 14). This character was polarized using ontogeny, as spines may be lost in larger holaspids in some species (e.g., Tremblay and Westrop, 1991, fig. 11.10, 11.20, 11.26, 11.33). Coding was based on the condition in the largest available hypostome.

13. Configuration of hypostomal borders. 0, posterior and lateral borders separated by a zone of narrowing (indentation of margin), and with some expansion of the lateral

border (e.g., Ludvigsen, 1979a, pl. 5, figs. 27, 29); 1, borders continuous with little variation in width (e.g., Tremblay and Westrop, 1991, fig. 9.35, 9.46).

14. Pygidial outline. 0, subtriangular (e.g., Ludvigsen, 1979a, pl. 2, figs. 25, 31, 35); 1, well-rounded posteriorly (e.g., Fig. 13.1).

15. Marginal pygidial spine. 0, present (e.g., Hintze, 1953, pl. 26, figs. 1, 2a); 1, absent (e.g., Fig. 13.1). Some *Bathyurus* species lose the spine during ontogeny (e.g., Tremblay and Westrop, 1991, fig. 14.9-14.23), so this character is not simply a restatement of character 14.

16. Axial pygidial spine. 0, absent (e.g., Hintze, 1953, pl. 26, figs. 1, 2a; Fig. 8.4); 1, present (e.g., Fig. 4.1-4.3).

17. Pygidial axial rings (larger holaspids). 0, at least two rings well defined anteriorly (e.g., Hintze, 1953, pl. 26, figs. 1, 2a; Ludvigsen, 1979a, pl. 4, figs. 4, 7, 33; Fig. 4.6); 1, no more than one, and may be mostly to entirely effaced (e.g., Ludvigsen, 1979a, pl. 1, figs. 17-20).

Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
A. brighti	0	0	0	0	0	0	?	0	0	0	0	?	?	0	0	0	0
R. longispinus	1	0	0	0	0	0	?	0	0	2	1	?	?	1	1	0	1
R. spiniger	1	0	1	0	0	0	?	0	1	2	?	?	?	1	1	1	0
R. ingalli	1	0	1	0	0	0	?	0	1	3	1	?	?	1	1	1	0
R. cf. ingalli	1	0	1	0	0	0	?	0	1	0	?	?	?	1	1	1	0
R. missouriensis	1	0	1	0	0	0	?	0	0	3	1	0	0	1	1	1	0
R. clochensis	1	0	1	0	0	0	?	0	1	0	?	?	?	?	?	?	?
B. angustus	0	0	0	1	0	1	2	1	0	1	1	1	1	0	0	0	1
B. platyparius	1	0	0	2	0	0	?	1	0	2	1	0	0	0	1	0	1
B. esbataottinensis	1	0	0	2	0	1	2	1	0	2	1	1	0	0	1	0	1
B. granulosus	0	0	0	1	0	1	2	1	0	1	1	1	0	0	1	0	1
B. ulu	0	1	0	2	1	1	1	1	0	2	1	0	0	0	1	0	0
B. nevadensis	0	0	0	1	0	1	2	1	0	1	1	0	0	0	1	0	1
B. sunbloodensis	0	0	0	1	0	1	2	1	0	1	0	1	1	0	0	0	0
B. mackenzieneis	0	0	0	1	0	1	1	1	0	1	1	0	1	0	1	0	0
B. margareti	0	1	0	1	1	1	1	1	0	1	0	1	1	0	1	0	1

Table 1.—Data matrix used in the phylogenetic analysis (Fig. 1).

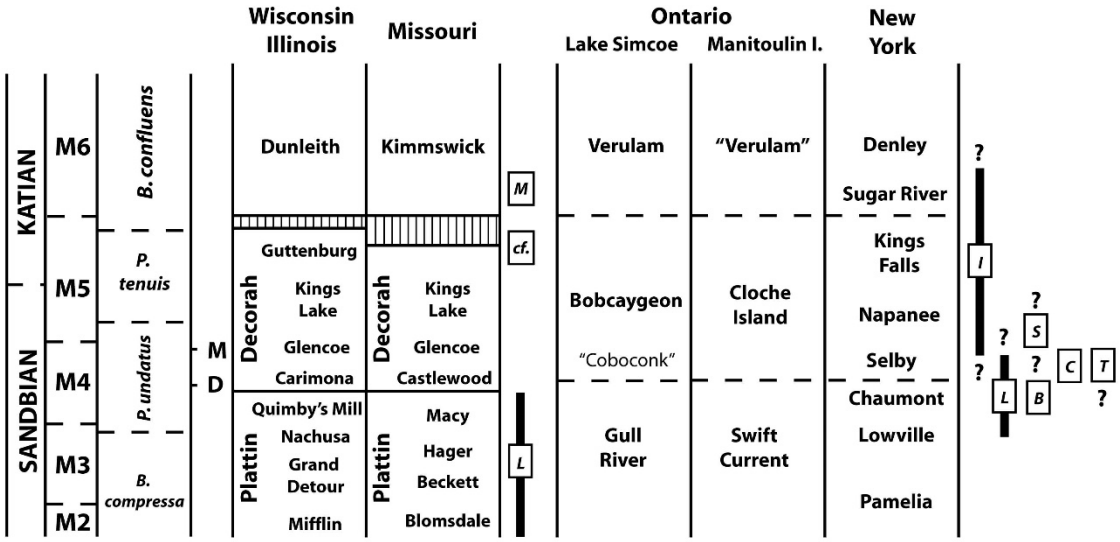
Wisconsin
Illinois
Missouri
Ontario
Lake Simcoe
Manitoulin I.
New
York
KATIAN
SANDBIAN
M6
M5
M4
M3
M2
B. confluens
P. tenuis
P. undatus
B. compressa
M
D
Dunleith
Kimmswick
Verulam
"Verulam"
Denley
Sugar River
Guttenburg
Kings
Lake
Glencoe
Carimona
Decorah
Kings
Lake
Glencoe
Castlewood
Decorah
Bobcaygeon
"Coboconk"
Cloche
Island
Kings
Falls
Napanee
Selby
Chaumont
Quimby's Mill
Nachusa
Grand
Detour
Mifflin
Plattin
Macy
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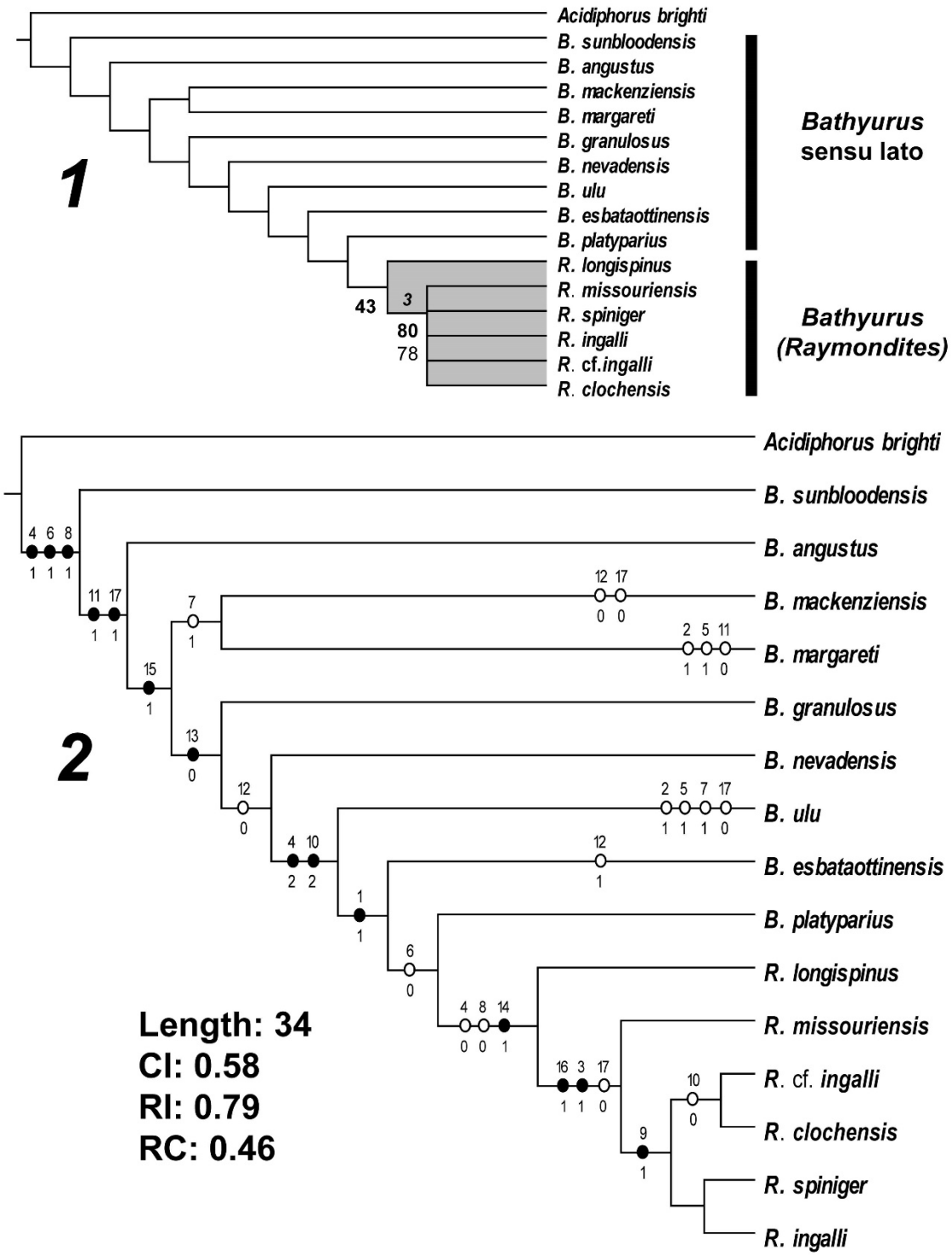
Figure 1—Species ranges, Mississippi Valley region, Missouri, Illinois and Wisconsin, and Ontario-New York State, plotted against lithostratigraphic units, conodont zones and major depositional sequences identified by Holland and Patzowsky (1997, 1998). Dashed lines reflect uncertainties in correlation. D, M indicate the positions of the Deicke and Millbrig K-bentonites, respectively. Lithostratigraphy and correlation of the successions of Wisconsin, Illinois and Missouri are modified from Larson (1951), Templeton and Willman (1963), Leslie (2000), and Metzger and Fike (2013); ranges of species are based on DeMott (1987) and unpublished field data. Lithostratigraphy and correlation of the successions of Ontario and New York are modified from Kay (1937), Liberty (1969), Salad Hersi and Dix (1999), Leslie (2000), Brett and Baird (2002), Mitchell et al. (2004); ranges of species are based on Wilson (1947) and unpublished field data. Species are identified by the following abbreviations: *L*, *B.* (*R.*) *longispinus*; cf., *B.* (*R.*) cf. *B.* (*R.*) *ingalli*; *M*, *B.* (*R.*) *missouriensis*; *I*, *B.* (*R.*) *ingalli*; *B*, *B.* (*R.*) *bandifer*; *S*, *B.* (*R.*) *spiniger*; *C*, *B.* (*R.*) *clochensis*; *T*, *B.* (*R.*) *trispinosus*.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Acidiphorus brighti
B. sunbloodensis
B. angustus
B. mackenziensis
B. margareti
B. granulosus
B. nevadensis
B. ulu
B. esbataottinensis
B. platyparius
R. longispinus
R. missouriensis
R. spiniger
R. ingalli
R. cf.ingalli
R. clochensis
43
3
80
78
Bathyurus sensu lato
Bathyurus (Raymondites)
2
Length: 34
CI: 0.58
RI: 0.79
RC: 0.46

Figure 2.—Results of phylogenetic analysis of the matrix (Table 1; see appendix for list of characters). *1*, strict consensus of 14 trees discovered with a branch-and-bound search (implicit enumeration), and showing the suggested classification of *Bathyurus* and *Raymondites*. Support metrics shown by numbers are Bremer support (italics; only values greater than 1 are shown), GC bootstrap support (bold face) and conventional bootstrap support (roman type). *Raymondites* is a recognizable clade that is classified as a subgenus of *Bathyurus*; *Bathyurus* itself is paraphyletic and the paraphylum of species occupying successive nodes below *B*. (*Raymondites*) is simply assigned to *Bathyurus* sensu lato. *2*, Optimized character distribution plotted on one of the three most parsimonious trees; upper numbers indicate characters, lower numbers indicate particular states (see Appendix). Only unambiguous state changes (i.e. show the same transformations at the nodes under the assumptions of ACCTRAN and DELTRAN) are shown. Filled circles show states that originate at a single node; open circles indicate those that show homoplasy.

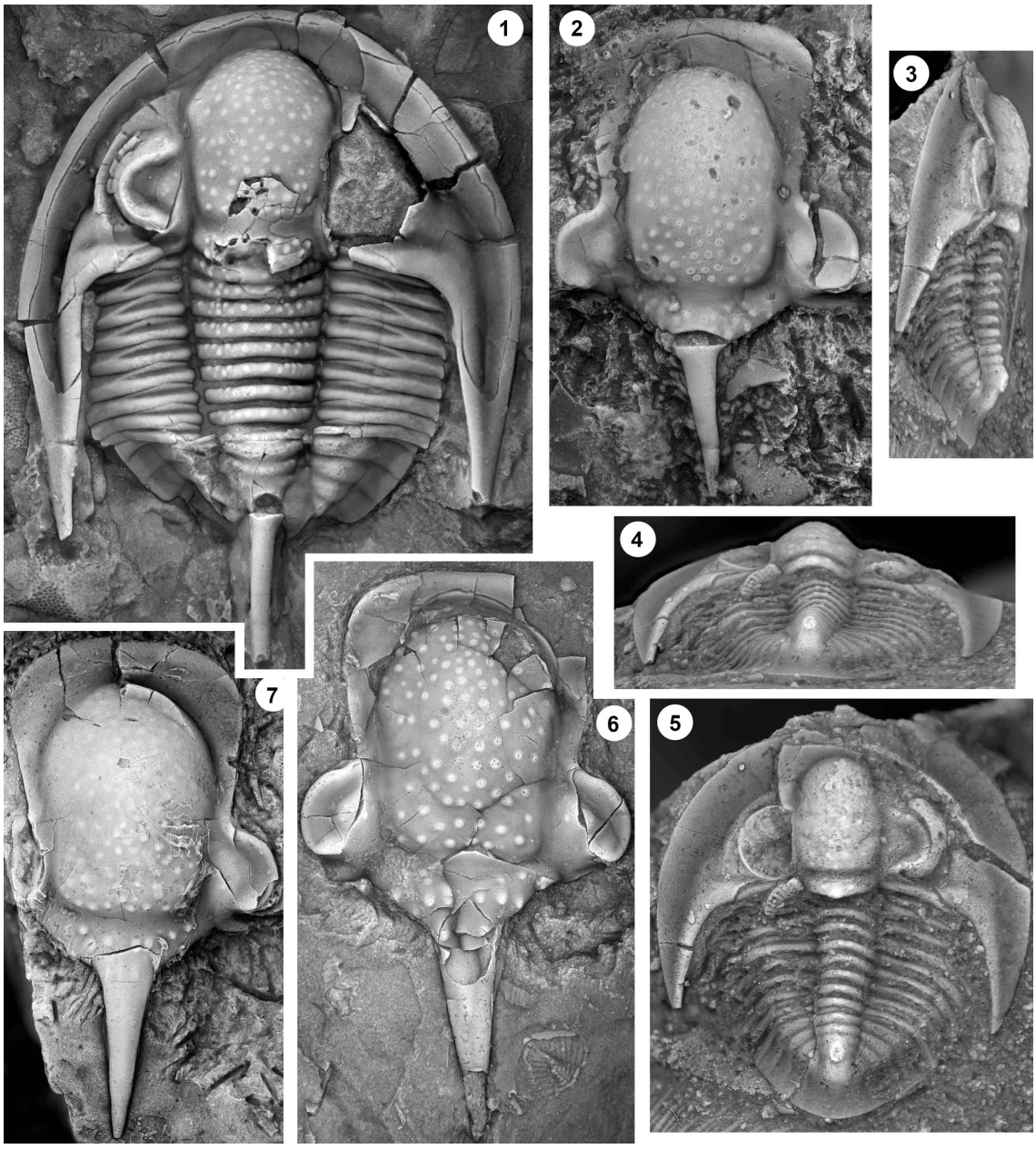
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Figure 3.—Bathyurus (*Raymondites*) *ingalli* (Raymond, 1913), Bobcaygeon Formation, Lake Simcoe region, southern Ontario. *1*, complete exoskeleton (ROM 48582), dorsal view, x4.5, Carden Quarry; *2*, cranidium (ROM 54394), dorsal view, x3.25, Carden Quarry, 9.5 km west of Kirkfield, Victoria County; *3-5*, complete exoskeleton (ROM 23962), lateral, posterior, and dorsal views, x11, Gull River-Bobcaygeon Formations (undifferentiated), Eganville, Renfrew County, about 110 km west of Ottawa; *6*, cranidium (GSC 4318; holotype), dorsal view, x2.7, near the lift-lock on the Trent-Severn Waterway, about 3 km kilometers north of Kirkfield, Victoria County (illustrated previously by Ludvigsen, 1979b, fig. 22C); *7*, cranidium (ROM 34648), dorsal view, x3, Old Kirkfield Quarry, about 3.3 km north of Kirkfield, Victoria County.

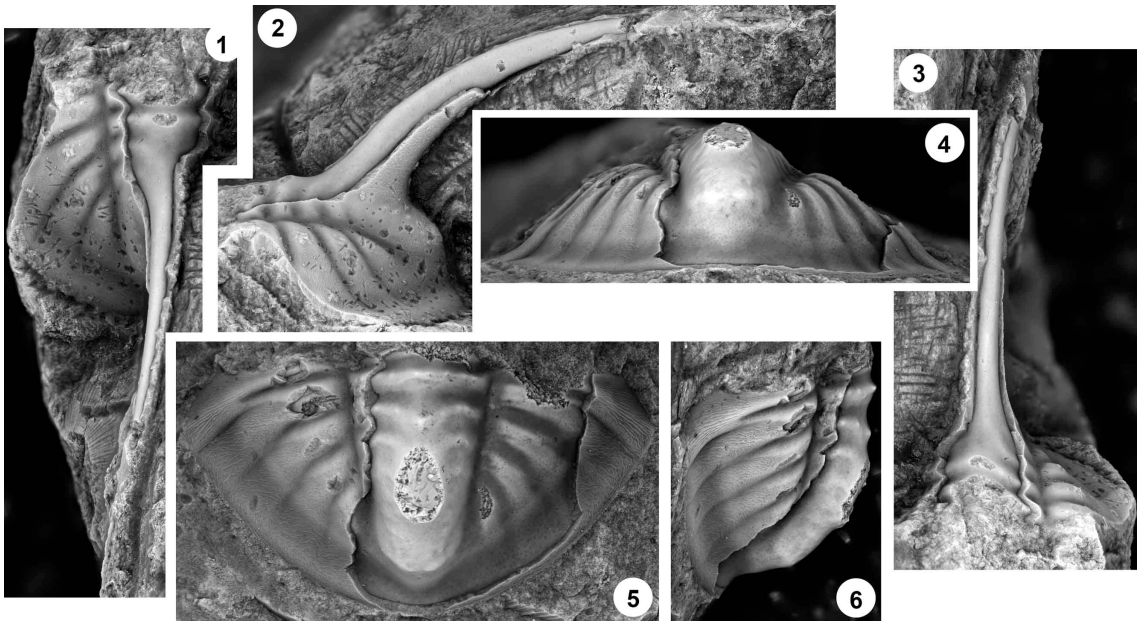
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Figure 4.—Bathyurus (*Raymondites*) *ingalli* (Raymond, 1913), Verulam Formation, right bank of the Moira River, Belleville, Hastings County, southern Ontario. 1-3, incomplete pygidium showing axial spine (ROM 35352), dorsal, lateral and anterior views, x5; 4-6, pygidium (ROM 35353), posterior, dorsal and lateral views, x5.

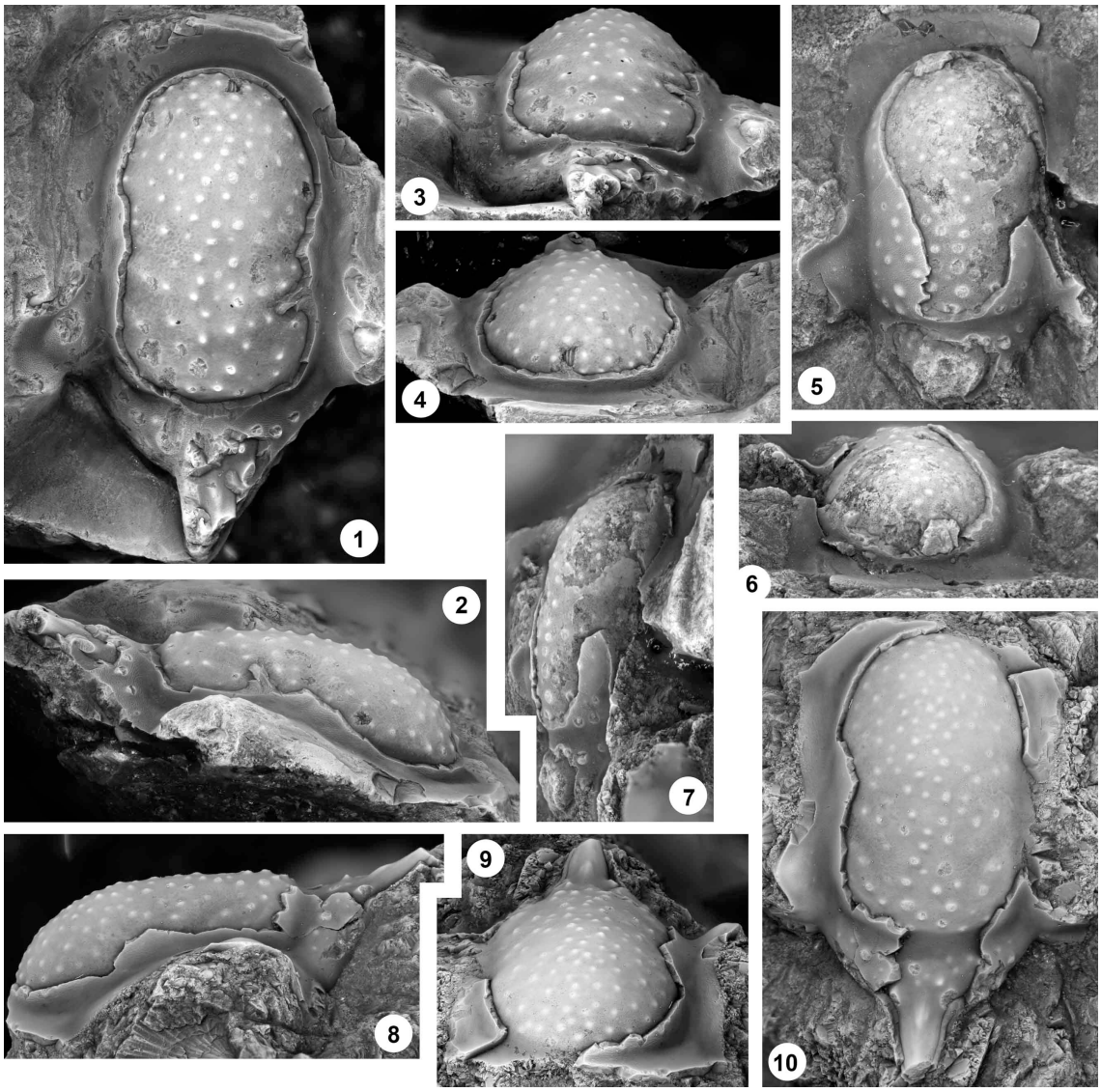
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Figure 5.—Bathyurus (*Raymondites*) *spiniger* (Hall, 1847). All from "Trenton Limestone", 1.6 miles north of Amsterdam, Montgomery County, New York (USNM loc. 322a), except for Figs. 1-4 (?Napanee Formation, Mohawk Valley, New York). *1-4*, cranidium (AMNH 854; holotype), dorsal, lateral, posterior and anterior views, x3.75; *8-10*, cranidium (USNM 595076), lateral, anterior and dorsal views, x5; *5-7*, cranidium (USNM 595076), dorsal, anterior and lateral views, x6.

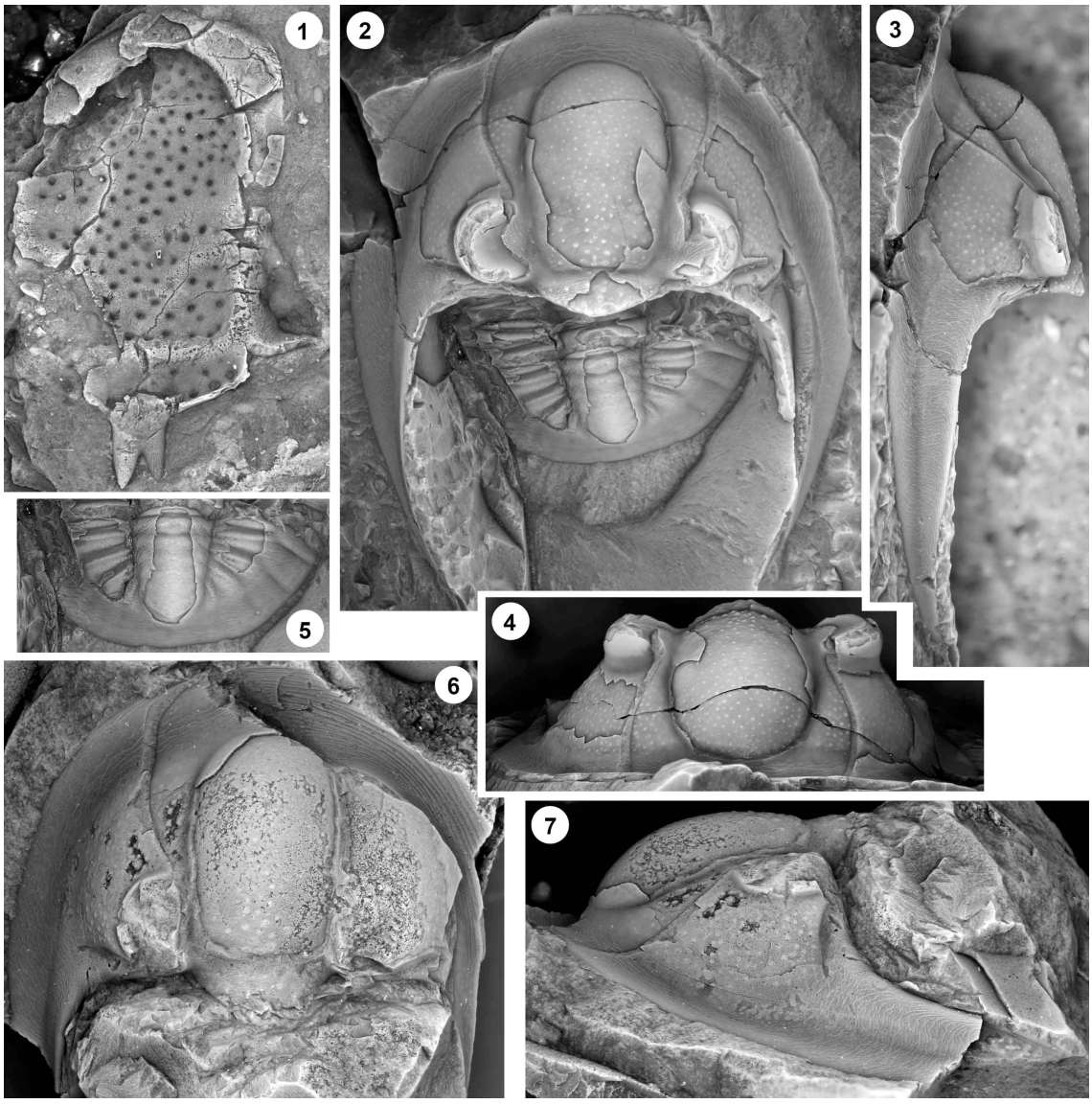
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Figure 6.— Bathyurus (*Raymondites*) from Canada and the United States. *1*, *B*. (*Raymondites*) *bandifer* Sinclair, 1944, cranidium (GSC 13249; holotype), ventral view, x5, "Leray Beds" (= Chaumont Formation; Salad Hersi and Dix, 1999, fig. 2), 11.25 km west of Cobden, Renfrew County, Ontario (illustrated previously by Wilson, 1947, pl. 2, fig. 7). *Bathyurus* (*Raymondites*) *longispinus* (Walcott, 1876). All from the Chaumont Formation, Buck's Quarry, 0.6 km north Poland, Herkimer County, New York, except Figs. 6, 7 ("Black River Limestone" [likely Chaumont Formation], 1.6 km north of Poland). 2–5, nearly complete exoskeleton (MCZ 107237; holotype), cephalon in dorsal view, lateral view, anterior view, dorsal view of pygidium x2 (illustrated previously by Whittington, 1953, pl. 65, figs. 10, 14, 15); 6, 7, cephalon (USNM 340622), lateral and dorsal views, x5 (Whittington, 1953, pl. 65, fig. 19, inked in the course of the rostral suture on his photograph, but we could find no trace of this feature on the specimen; there is, however, a fracture in the doublure).

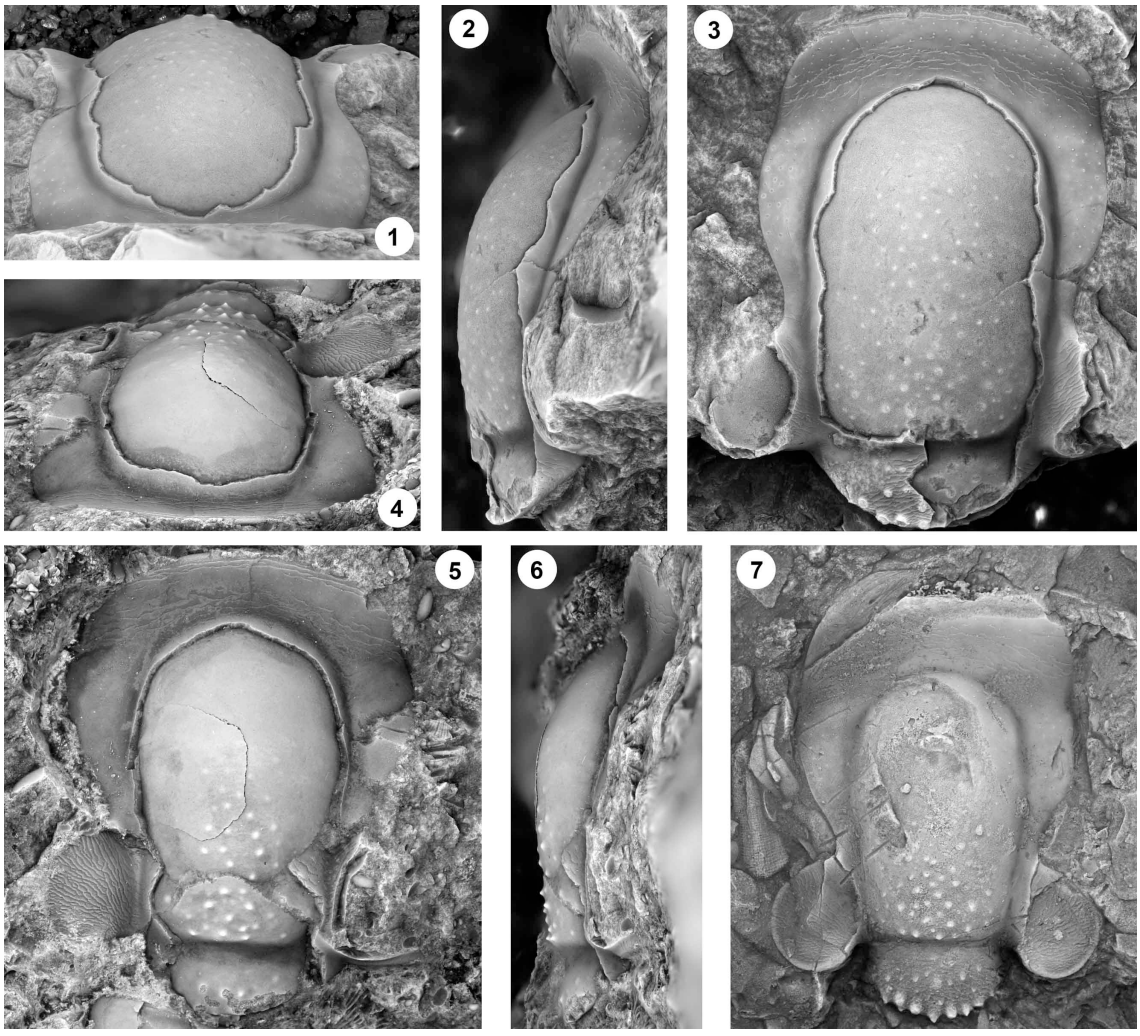
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Figure 7.—Bathyurus (*Raymondites*) *longispinus* (Walcott, 1876) from Wisconsin and Illinois. *1-3*, cranidium (MCZ 107241), anterior, lateral, and dorsal views, x3.5, Mifflin Formation, Dixon North Quarry Section, Lee County, Illinois (illustrated previously by DeMott, 1987, pl. 7, figs. 12, 13; see his fig. 10.1 and table 10.1 for locality information). *4-6*, cranidium (MCZ 107243), anterior, dorsal and lateral views, x4, Quimbys Mill Formation, Quimbys Mill Quarry section, Lafayette County, Wisconsin (illustrated previously by DeMott, 1987, pl. 7, fig. 17; see his fig. 10.1 and table 10.1 for locality information). *7*, cranidium (USNM 340624), dorsal view, x4, "Upper Black River" (likely Quimbys Mill Formation from the implied stratigraphic position), Phelan and Jordon quarries, Dixon, Lee County, Illinois (note that Whittington [1953, pl. 69, fig. 22) inadvertently cropped out the anterior part of the frontal area).

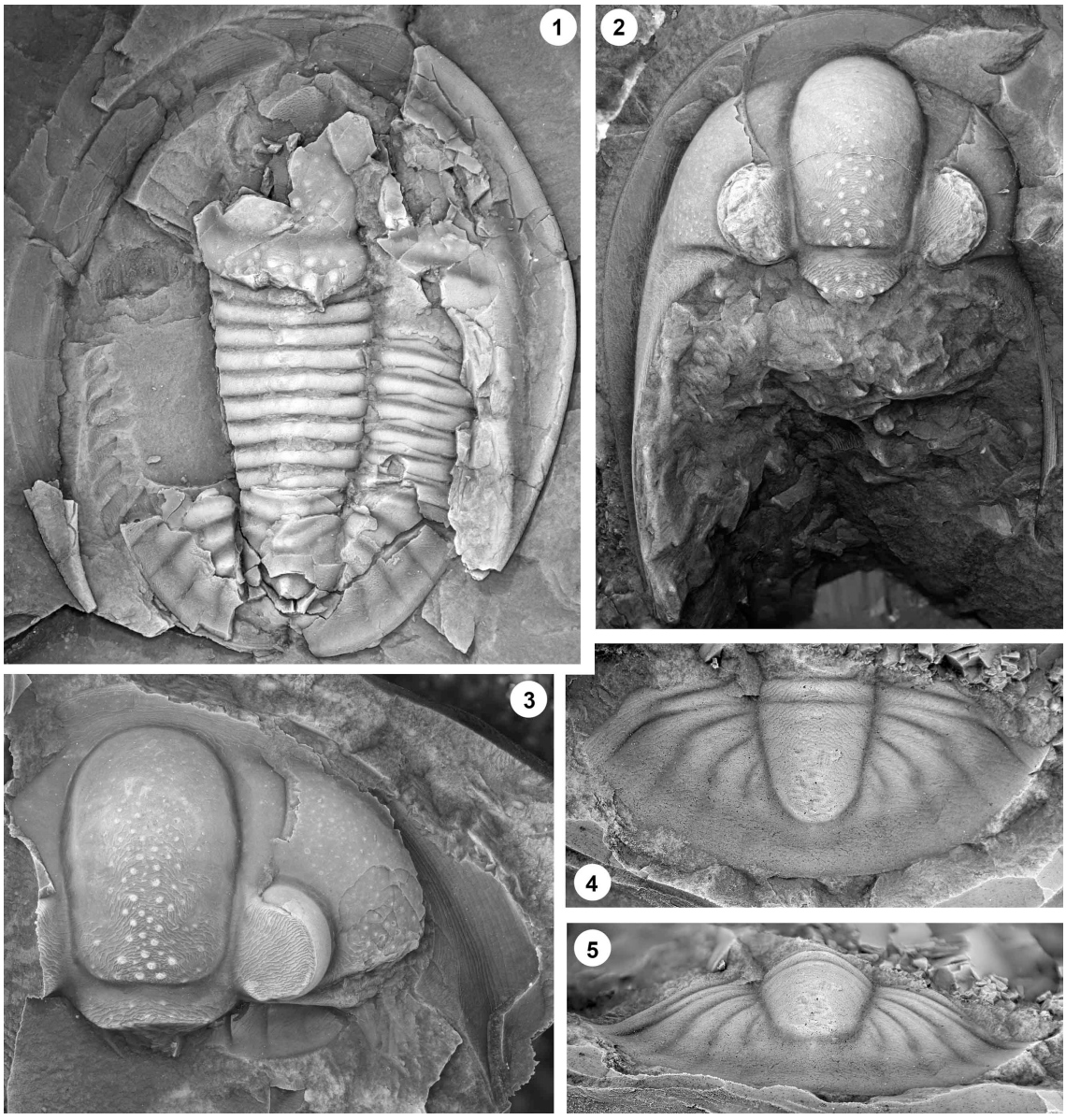
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Figure 8.—Bathyurus (*Raymondites*) *longispinus* (Walcott, 1876), New York, Illinois and Wisconsin. *1*, nearly complete exoskeleton (USNM 379365), dorsal view, x4, Larabee Member, Glens Fall Formation (see Kay, 1937, p. 262 for stratigraphic nomenclature), Rowland's Mill, 6.4 km west of Saratoga Springs, Saratoga County, New York (illustrated previously by Whittington, 1953, pl. 65, fig. 16). *2*, cephalon (MCZ 107240), dorsal view of latex cast from external mold, x5, Quimbys Mill Formation, Quimbys Mill Quarry section, Lafayette County, Wisconsin (illustrated previously by DeMott, 1987, pl. 7, fig. 8-11; see his fig. 10.1 and table 10.1 for locality information). *3*, cephalon (MCZ 107238), dorsal view of latex cast of external mold, x4, Quimbys Mill Formation, Quimbys Mill Quarry section, Lafayette County, Wisconsin (illustrated previously by DeMott, 1987, pl. 7, figs. 1, 2; see his fig. 10.1 and table 10.1 for locality information). *4*, *5*, pygidium (MCZ 107239), dorsal and posterior views of latex cast of external mold, x8, Mifflin Formation, Dixon North Quarry Section, Lee County, Illinois (illustrated previously by DeMott, 1987, pl. 7, fig. 8; see his fig. 10.1 and table 10.1 for locality information).

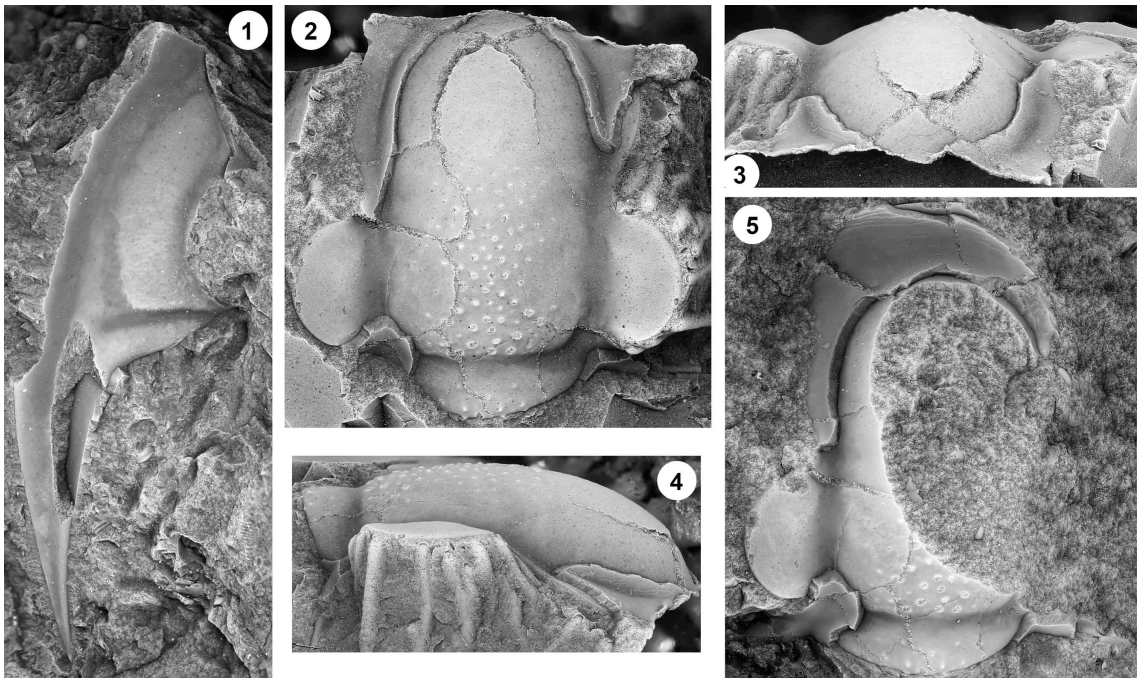
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Figure 9.—Bathyurus (*Raymondites*) *longispinus* (Walcott, 1876), Cloche Island Formation, road cut on HW 68, Cloche Island, about 9 km south of Birch Island (section 27 of Leslie, 2000, p. 1147), Manitoulin District, Ontario. 1, librigena (ROM 63007**),** dorsal view, x4; 2-5, cranidium, dorsal, anterior and lateral views of latex cast from mold (ROM 63006a), and dorsal view of counterpart (ROM 63006a) showing frontal area, x8.

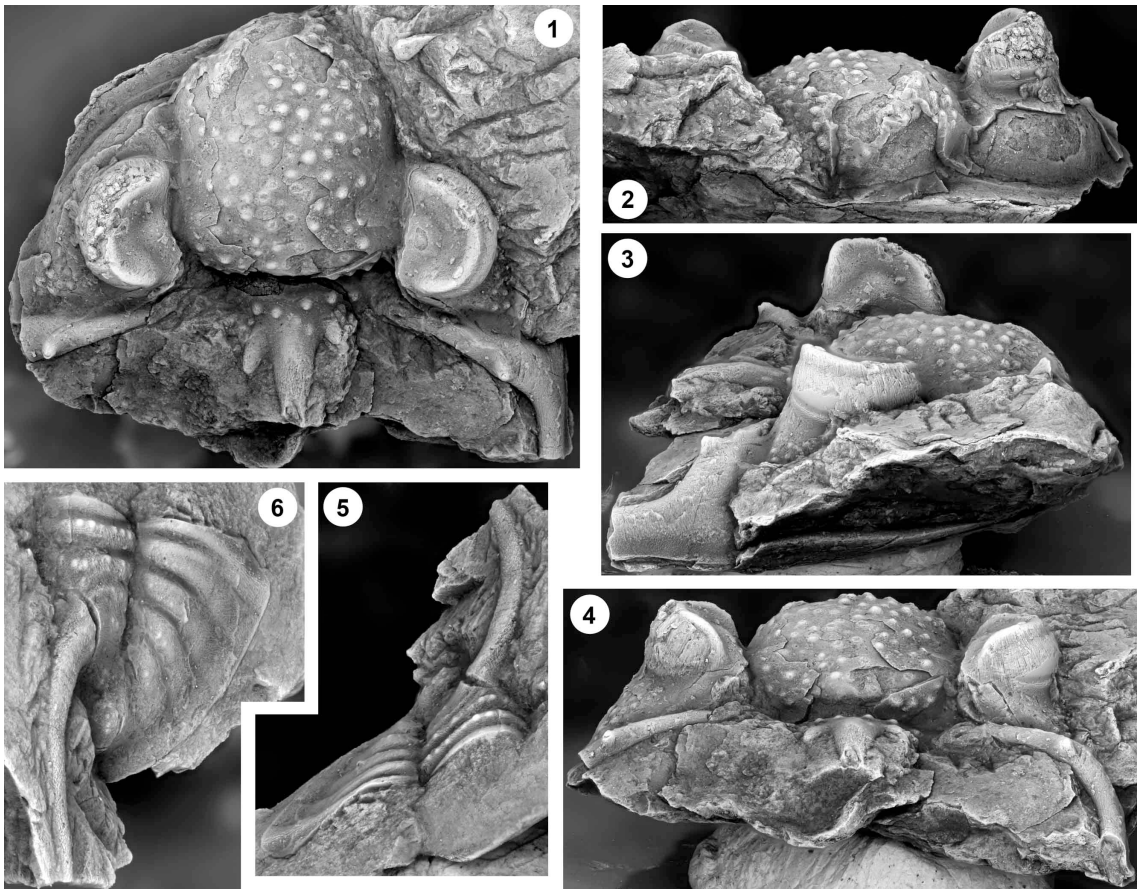
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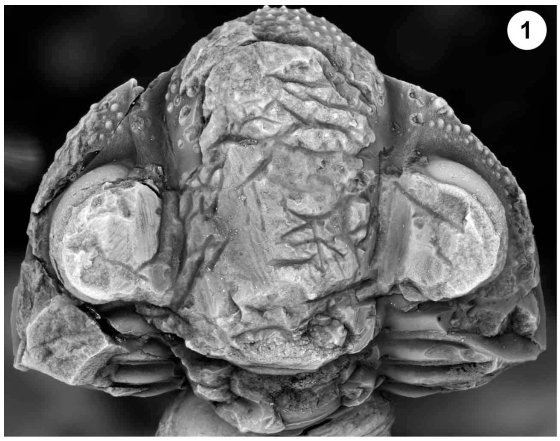
Figure 10.—Bathyurus (*Raymondites*) *trispinosus* (Wilson, 1947), "Leray-Rockland Beds" (lower Bobcaygeon Formation), east of Packenham, Lanark County, about 47 km east of Ottawa, Ontario (sclerites illustrated previously by Wilson, 1947, pl. 2, figs. 8-9). *1-4*, cephalon (GSC 11304; holotype), dorsal, anterior, lateral, and posterior views, x5.5; *4, 5*, pygidium (GSC 11304a; paratype), lateral and dorsal views, x6.5.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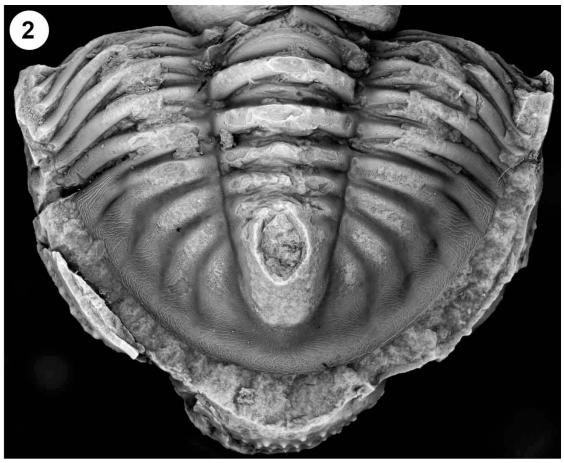
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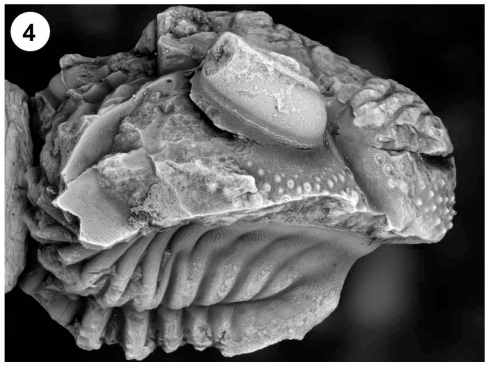
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Figure 11.—*Bathyurus* (*Raymondites*) cf. *B*. (*R*.) *ingalli* (Raymond, 1913), Upper Ordovician strata (Gull River Formation or Cloche Island Formation), northeast corner of St. Joseph Island, Algoma District, northwestern Lake Huron, Ontario 1–4, enrolled exoskeleton (USNM 166731), dorsal (cephalon), dorsal (pygidium), anterior and lateral views, x6 (illustrated previously by Whittington, 1953, pl. 69, figs. 16, 17, 19–21).

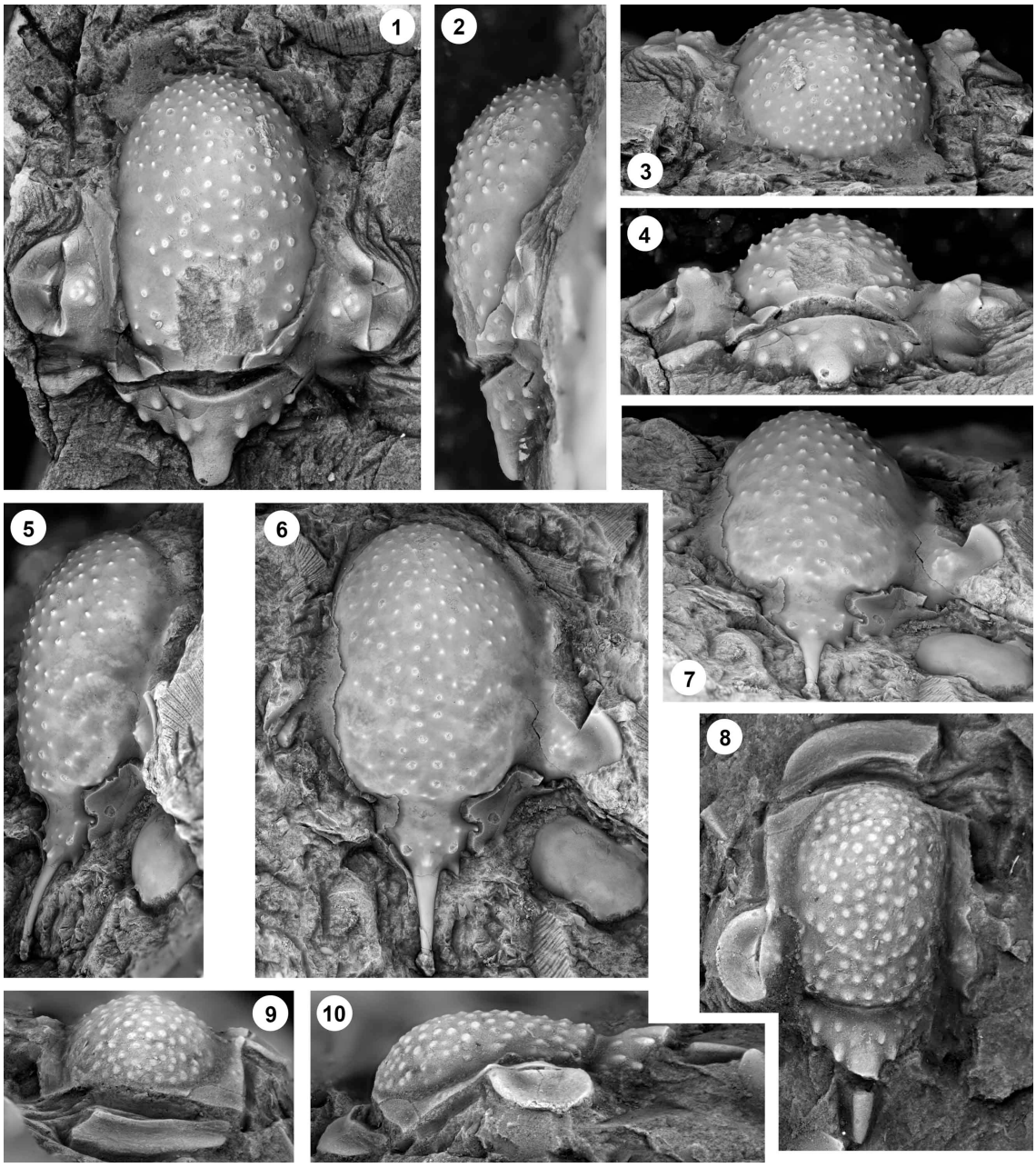
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Figure 12.—Bathyurus (*Raymondites*) cf. *B*. (*R*.) *ingalli* (Raymond, 1913), Guttenberg Formation, Fennimore West road cut, Grant County, Wisconsin (sclerites illustrated previously by DeMott, 1987, pl. 8, figs. 1-3, 7-9; see his fig. 10.1 and table 10.1 for locality information). *1-4*, cranidium (MCZ 107427), dorsal, lateral, anterior and posterior views, x3.5; 5-7, cranidium, MCZ 107244, x3.5; 8-10, cranidium (MCZ, 107246), dorsal, anterior and lateral views, x6.5.

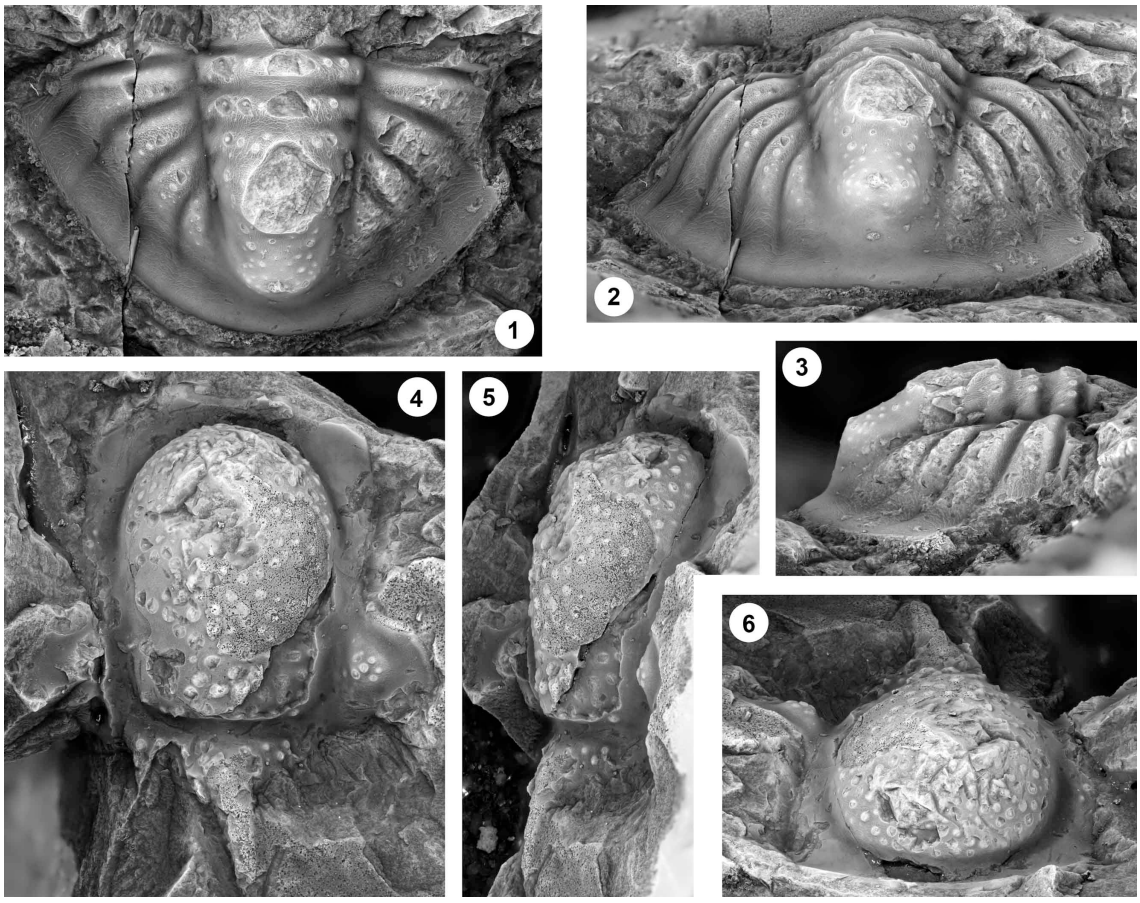
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Figure 13.—Bathyurus (*Raymondites*) cf. *B*. (*R*.) *ingalli* (Raymond, 1913), Wisconsin and Ontario. *1-3*, pygidium (MCZ 107245), dorsal, posterior and lateral views, x5, Guttenberg Formation, Fennimore West road cut, Grant County, Wisconsin (illustrated previously by DeMott, 1987, pl. 8, figs. 4-6; see his fig. 10.1 and table 10.1 for locality information); *4-6*, cranidium (USNM 166732), dorsal, lateral and anterior views, Upper Ordovician strata (Gull River Formation or Cloche Island Formation), northeast corner of St. Joseph Island, Algoma District, northwestern Lake Huron, Ontario (note that Whittington's [1953, pl. 69, fig. 18] original photograph of this specimen crops out the left palpebral lobe, the occipital spine and gives a misleading impression of the shape of the anterior cranidial margin).

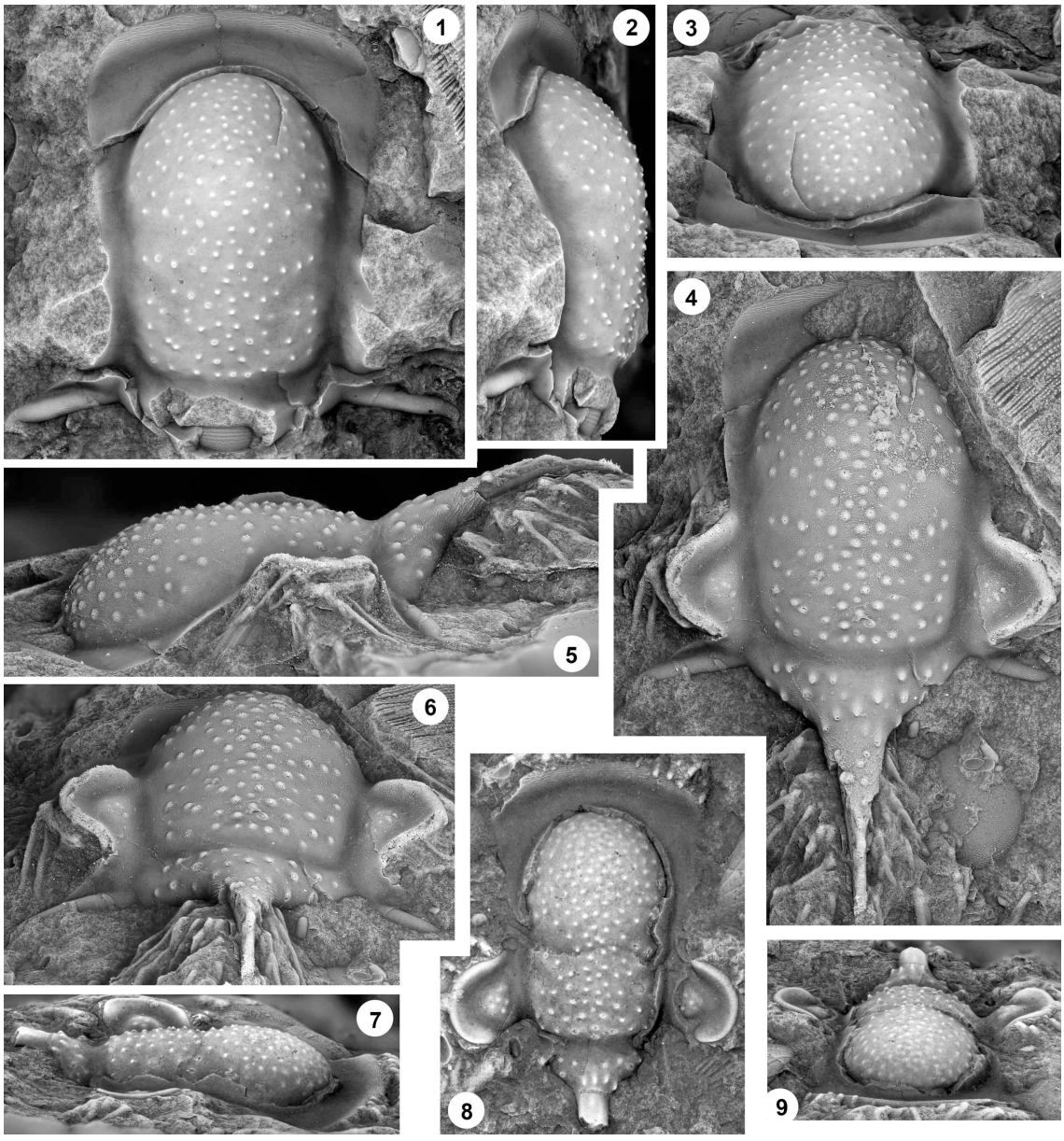
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Figure 14.—Bathyurus (Raymondites) clochensis n. sp., Cloche Island Formation, road cut on HW 68, Cloche Island, about 9 km south of Birch Island (section 27 of Leslie, 2000, p. 1147), Manitoulin District, Ontario. *1-6*, cranidium (holotype), dorsal, lateral and anterior views (ROM 61465a), and dorsal, lateral and posterior views of latex cast of counterpart external mold (ROM 61465b); 7-9, cranidium (ROM 61466), lateral, dorsal and anterior views of latex cast from external mold, x7.

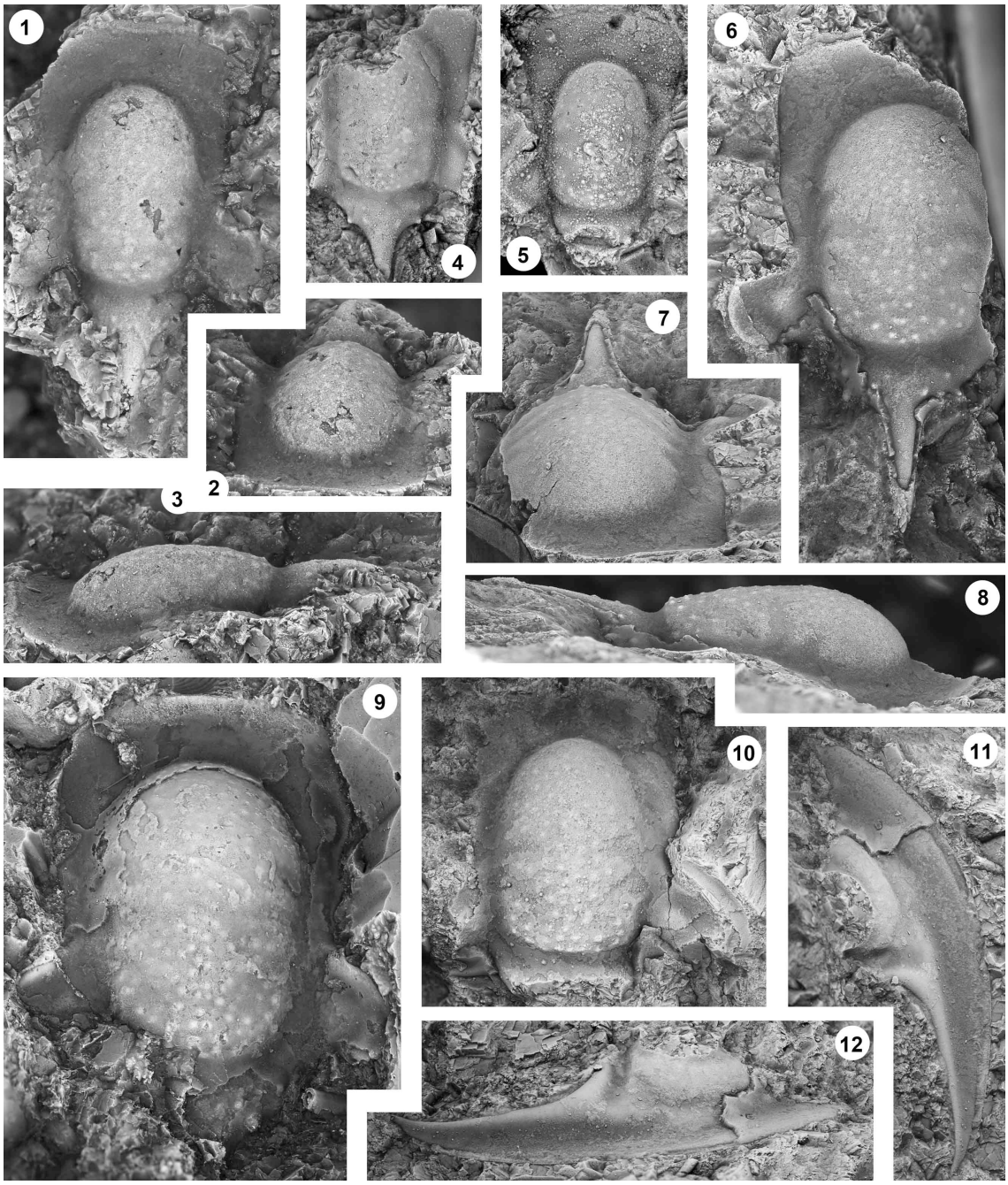
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Figure 15.—Bathyurus (*Raymondites*) *missouriensis,* Kimmswick Formation, Jefferson County, Missouri. All from 26.1-26.6 m above the base of section MM, road cut on Missouri State Highway MM, 2.7 km southeast of House Springs, except 15.9 (5-6 m above the base of section M, road cut on Missouri State Highway M, 10.8 km southeast of House Springs. *1-3*, cranidium (OU 12653), dorsal, anterior, and lateral views, x7; *4*, cranidium (OU 12654), dorsal view, x6; *5*, cranidium (OU 12655), dorsal view, x6; *6-8*, cranidium (OU 12656; holotype), dorsal, anterior, and lateral views, x6; *9*, cranidium (OU 12657), dorsal view of latex cast of external mold, x4.5; *10*, cranidium (OU 12658), dorsal view, x4.5; *11-12*, librigena (OU 12659), dorsal and lateral views, x5.

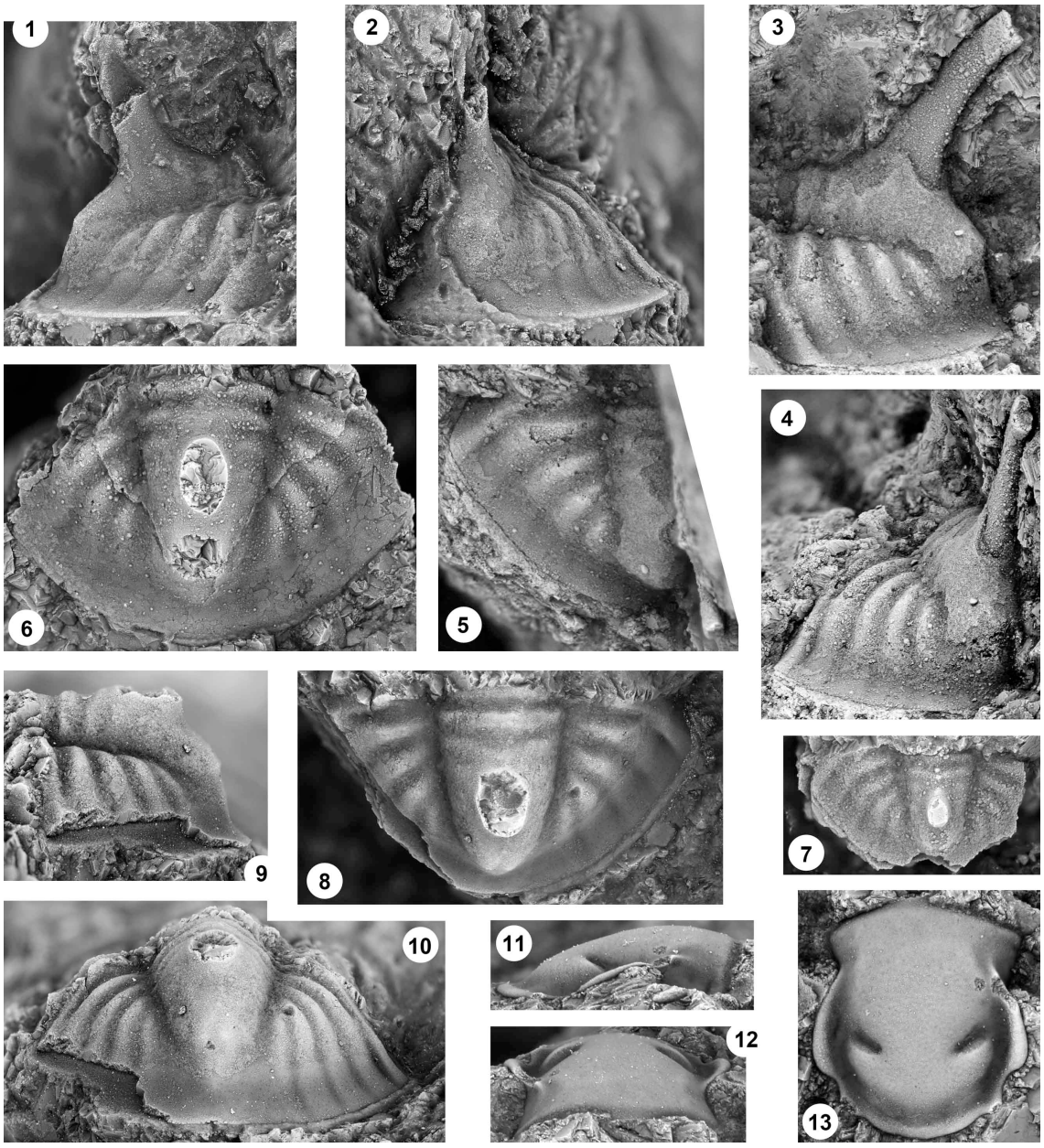
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Figure 16.—Bathyurus (*Raymondites*) *missouriensis,* Kimmswick Formation, 26.1-26.6 m above the base of section MM, road cut on Missouri State Highway MM, 2.7 km southeast of House Springs, Jefferson County. *1-2*, pygidium (OU 12660), lateral and posterior views, x7; *3-5*, pygidium (OU 12661), lateral, dorsal, and posterior views, left half of specimen unprepared to preserve occipital spine, x6; *6*, pygidium (OU 12662), dorsal view, x6; *7*, pygidium (OU 12664), dorsal view, x8; *8-10*, pygidium (OU 12663), dorsal, lateral, and posterior views, x7; *11-13*, hypostome (OU 12665), lateral, anterior and dorsal views, x11.

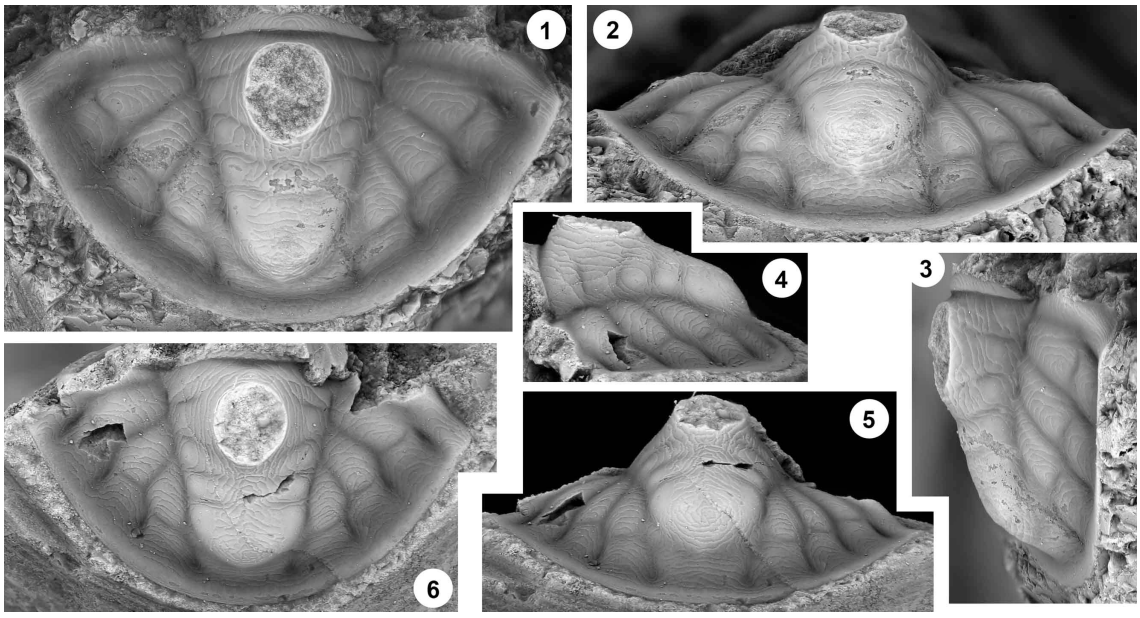
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Figure 17.—Bathyurid gen. and sp. indet. All from the Oil Creek Formation, Highway 77 section, Carter County, southern Oklahoma (illustrated previously by Shaw, 1974, pl. 5, figs. 10, 11, 15, 16). 1-3, pygidium (OU 8010), dorsal, posterior, and lateral views, x10, collection SP-1-68, 171 m (561 feet) above the base of the Joins Formation; *3-6*, pygidium (OU 8008), lateral, posterior, and dorsal views, x12, collection SP-1-65, 161 m (528 feet) above the base of the Joins Formation.

Chapter 4: SYSTEMATICS AND BIOSTRATIGRAPHIC SIGNIFICANCE OF THE UPPER ORDOVICIAN PTERYGOMETOPINE TRILOBITE *ACHATELLA* DELO, 1935

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 & Chatterton's (1982) study of Pterygometopidae proposed a traditional, stratigraphic phylogeny in which Pterygometopinae were 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 also a first step towards a more comprehensive revision of Family Pterygometopidae.

STRATIGRAPHIC SETTING

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

Ohio and Kentucky.— *Achatella carleyi* (Meek, 1872) was described from Katian (Maysvillian) strata in the Cincinnati, Ohio. The original collecting horizon was listed

simply as was collected "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 Fairmont 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 fragmentary and generally poorly preserved; they add no new information on anatomy of the species and are 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 katherina* (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 some 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. katherina* 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 measured at 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 collection. At both of the new sections, the sampled horizons are likely near the base of the C1 sequence.

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. katherina*. 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 38–51 m above the base of the Viola Springs, and probably falls in sequence M6 (Westrop et al., 2012; see Young et al., 2005 for an alternative interpretation). As such, the occurrence of *A. katherina* is somewhat older than in Missouri, where it was sampled from what is likely the lower part of sequence C1. However, the upper M6 succession in Missouri that correlates with the range of *A. katharina* in Oklahoma did not yield trilobite samples. Taken together, data from Oklahoma and Missouri indicates that *A. katharina* has a range that straddles the M6–C1 sequence boundary.

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 & 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 & 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 south-west 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. katherina* from eastern and central Laurentia. *Achatella retardata* (Reed 1914) is younger than *A. consobrina*, occurring in the Lady Burne 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 Threve Formation falls in the Rawthyan Stage of the Ashgill Series of British nomenclature, which correlates with the upper Katian (Bergström et al., 2008, 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, possibly, Rawthyan stages of the Ashgill Series (Cripps, 1988) and thus falls in the upper Katian. However, the species is too poorly known for critical evaluation. 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, text-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 Romano and Owen (1993). This indicates that "*A. truncatocaudata*" from the Grangegeeth Terrane is likely Sandbian in age (e.g., Bergström et al., 2008, fig. 1), and is therefore significantly older than the type material from County Tyrone. It is also older than *A. achates* and *A. katherina,* 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 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 sclerites illustrated in Owen (1986). *Achatella* species from Baltica, *A.schmidti* (Warberg, 1925) and *A. kukersianus* (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) comprises 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 (Golobloff et al., 2008) and yielded the same set of 50 trees, with length, 30, C.I., 0.80, R.I, 0.82; R.C., 0.65; 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 (esag.) than L1 and L2 [8(1)], and a posterior branch of the facial suture that is nearly straight [16(1)]. *Achatella kukersianus* 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 100–500 micron 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)]; longer (exsag.) than L1 and L2 [8(1)]. Posterior branch of facial suture nearly straight [16(1)]. Pygidium elongate, subtriangular in outline.

Discussion.— 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*, *Vironiaspis*, with *Phacops* (*Pterygometopus*) *kuckersianus* Schmidt, 1881, from Baltica (northern Estonia), as the type species. As this species, the only one assigned to *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.

Four 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), and 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* (Warberg) 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. katherina*, 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, text-fig. 3) trilobites, it is 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 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.

?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. 4 a and b.

1978a *Achatella achates*, LUDVIGSEN, p1. 5, fig. 47.

1979 *Achatella achates*, LUDVIGSEN, fig. 47 a 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.— Small palpebral lobe 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.

Holotype. — An incomplete, flattened exoskeleton (GSC 1784; Fig. 3.5), probably from the Cobourg 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 length. Glabella outline pinches inward towards L1 between L0 and L2; L0 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, more faintly impressed across the anterior portion of the librigena. Glabellar furrows moderately to strongly developed as well, tending to become shallower toward the axis. S0 approximately transverse, strongly developed near the axial furrows, more shallowly impressed axial; L0 protrudes above the sharply defined furrow. S1 variable in appearance, relatively transverse near the axial furrows, then slightly curves anteriorly toward the axis; variably branches axially forming a poorly to well defined secondary

furrow that produces a secondary inflation in lateral portion of L1. S2 relatively linear, angled slightly to moderately posteriorly. S3 approximately linear, but more variable in appearance due to pinching between L3 and the anterior lobe; angled slightly anteriorly. L0 subrectangular in outline, inflated rectangular area in the middle, pinched laterally by the shift in S0 furrow depth; L0 slope inward anteriorly. L1 relatively transverse, variable inflation on the lateral portions of the lobe. L2 slightly thicker near the axis, but pinched slightly before the axis; angled slightly posteriorly. L3 approximately triangular in outline, longest side along S3. Anterior lobe wide, but relatively narrow in length, producing an elongate subovate outline along the curved anterior margin of the lobe. A triangular inflation present on the anterior lobe expands towards the anterior margin; anterior tips mark by two distinct projects or sculptural elements with a moderate concave curvature present in-between. A narrow but well defined anterior margin present, marked by a change of sloped in the glabella and the anterior suture of the librigena. Palpebral lobe relatively small, strongly raised and angled sharply towards the ocular suture. Outline is arcuate, with a small slightly raised palpebral area surrounded by moderate palpebral furrow and a relatively large, flat palpebral border. Anterior branch of the facial suture strongly curved, expands outward laterally from below the anterior tip of L3 and the anterior lobe, curves strongly inward around the anterior portion of the anterior lobe toward the narrow anterior margin. Posterior branch of the facial suture angled slightly posteriorly away from the eye, marked by a strong posterior change in slope approaching the lateral margin. Posterior lateral protection relatively large, flat, subtriangular in outline, curves gently inward towards the axial furrow; a strongly developed posterior furrow develop along the posterior margin. Genal spine

relatively long, greater than the glabella's length, and relatively flat laterally where it merges with the lateral margin anteriorly; genal spine becomes narrower to a thin rounded tip posteriorly. Sculpture well developed along the glabella and posterior lateral fixigena; tubercle sculpture large well rounded, sculpture is large anteriorly on the glabella, becoming smaller fainter by the LO.

Librigena field strongly curved, raised towards the suboccular furrow; furrow strong, slightly raised, flat, subcircular in outline. Relatively broad, flat lateral margin present; librigena lacks a true lateral furrow but is mark by a change in slope between the strong curvature of the librigena field and the lateral margin. Lateral margin becomes thinner, and narrower anteriorly, grading into the anterior border.

Pygidium approximately triangular in outline and relatively wide, tapers to the posterior tip at approximately a 45 degree angle. Axis relatively thin, approximately 37 percent of total pygidial width at maximum point; tapers gradually toward the posterior. Axial furrow present but weakly developed. Axial lobes and furrows relatively transverse; anterior most lobes and furrows moderately curved anteriorly along the lateral margins the lobes. Axial lobes taper in thickness posteriorly, with axial furrows becoming weaker as well. Approximately 11 to 12 well defined axial lobes and furrows present, with lobes and furrows becoming blended near the posterior tip. Pleural region all defined by strong, well defined pleural furrows; anterior most pleural furrows angled slightly posteriorly with subsequent furrow becoming angled more posteriorly gradually until nearly running entirely posteriorly. Pleural furrows relatively linear at the axis, becoming more curved posteriorly along the lateral margin. Faint intrapleural impressions present, originating from the axial furrow near the posterior tip of a pleural

rib then expand outward towards the middle of the pleural rib laterally. 9-10 well defined pleural ribs present. Pleural field relatively flat near the axis, curves strongly downward near the lateral margin. Faint tubercle sculpture present across the pygidium.

Discussion.— Ludvigsen and Chatterton (1982) considered *Achatella katherina* 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 katherina* 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.), *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 Ramskold, 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 muscles scar is also variable, as is the median embayment of the anterior glabellar margin. The latter feature is generally more weakly expressed than in *A. katherina* 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)

Figure 6-7

1872 *Dalmanites carleyi*, MEEK, p. 424-426.

1873 *Dalmanites carleyi*, MEEK, p. 170-173, 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 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).

Other material – Five cephala (CM 51280) (CM 51280, CM 51280, CM 31699, CM 31699) and two pygidia (CM 51280, CM 31699).

Description — Cephalon is relatively wide, semielliptical outline (excluding genal spines); the cranidium is approximately subtrapezoidal in outline. Cranidium length is approximately 47 percent of the cranidial width across the posterolateral fixigena and genal spines. Axial furrow generally shallowly impressed with a gentle slope around the margins; the furrow tends to weaken and shallow anteriorly along the L3 margin. A distinct axial pit is developed along the axial furrow at the anterior tip of L3 and the posterior margin of the anterior lobe. Glabella outline pinches inward from the L0 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 percent of cranidial width; glabella has a low convexity, relatively flat adaxially. LO relatively wide and long; generally subovate in outline but more rectangular along nearly flat posterior margin that expands outward past the posterolateral fixigena. LO is approximately 19 percent of total glabella 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, but relatively narrow, only slightly extending past L3; subovate in outline, rounded anteriorly especially along the lateral margins. S0 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 more strongly developed adaxial and slightly wider; furrow becomes pinch laterally by L2 and L3. S3 is pinch out adaxially between L3 and the anterior lobe; becomes wider and more strongly impressed abaxially towards the axial furrow pit. Anterior branch of the facial suture originates approximately across from S3; curves inward to the anteriolateral margin of the anterior lobe. Posterior branch of the facial suture poorly preserved. Genal spine moderately long, less than 50 % of total librigena length and slightly less than glabella length. Well-developed tubercles cover the entire cephalon. A distinct, larger protrusion is present along the posterior margin of the LO, along the axis.

Librigenal lateral border and lateral furrow well defined; furrow expressed as a relatively wide trough like break in slope between the librigena field and lateral border. Librigena field moderately convex; suboccular furrow is raised very slightly above the librigena field. Circumocular suture arcuate, distinctly below the top of the glabella in anterior view. Strongly developed tubercles across the librigena.

Pygidium elongate, triangular to subtriangular in outline, length approximately 90 percent of width. Axis outlined by a moderate to strong furrow, composed of 11 to 12

well defined ribs and furrows. Axial ribs and furrows slightly convex along the lateral portions near the axial furrow. Pleural field relatively flat, gently slopes lateral, marked by a strong change in slope laterally towards a weak lateral border. Pleural furrow angle slightly off from transverse anteriorly, becomes strongly angled posteriorly by the posterior tip; 11 to 12 pleural ribs and furrows developed. Weak lateral border present, more distinct at the moderately rounded posterior tip. Moderate tubercle sculpture developed along the axis.

Discussion.— 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 have 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.a, 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*. *katherina* from Missouri and Oklahoma. However, it differs from *A*. *katherina* 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 Weisenberger, and *A*. *retardarta* (Reed) have eyes that extend forward to reach the axial furrow.

ACHATELLA KATHERINA (Bradley, 1930)

Figure 8-12

1930 *Dalmanites katherina*, BRADLEY, p. 286, pl. 30, figs. 19-28.

1940 *Dalmanites katherina*, DELO, p. 112, pl. 13, figs. 26-29.

Diagnosis.— Small palpebral lobe 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 Co. IL.

Other material.—Paratypes: three cephala (UC 33780a, 33780c, 33780e), a hypostome (UC 28975a) and two pygidia (UC 33780b,,UC 28977 [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 222768, OU 222769); 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 towards a gently rounded anterior margin. Cranidial length approximately 48 percent of maximum cranidial width. Axial furrow sides gently curve towards fixigena and more sharply upward along the lobes of the glabella. Conspicuous pit in axial furrows at S3. Glabella moderately convex expands evenly forward from S1, so that width at L1 is approximately 53 percent of the width at anterior lobe. LO slightly curves inward to L1, then outward from L1 to L2, with the lateral tips of LO and L2 being approximately equal in width. The glabella rapidly expands from L3 to its maximum width across the anterior lobe; glabella maximum width approximately 45 percent of maximum cranidium width. SO nearly

transverse, deepest adaxially and curved slightly forward, but shallows medially. S1 also transverse, expands adaxially. S2 strongly incised, proceeds obliquely forward from axial furrow; width (tr.) equal to 71% of glabellar width at L3. S3 angled slightly anteriorly away from the axis. S3 shallower than S2; extends obliquely backward from prominent pit at axial furrow, terminates adaxially at shallow pit. LO curved gently backward, increasing in length (sag., exsag.) towards midline; maximum length approximately 17.5 percent of glabella length; posterior portion raised above the rest of the glabella, gently grades downward towards SO. L1 approximately transverse expands forward weakly near axial furrow. L2 with transverse posterior and oblique anterior margins; expands adaxially. L3 subtriangular in outline with adaxially convergent margins so that length (exsag.) becomes reduced by about 50% away from axial furrow. Anterior lobe approximately subovate; with increased thickness anteriorly and a moderate to strong marginal curve. Anterior border very short, separated from glabella by shallow preglabellar furrow; narrows abaxially and eventually cut out entirely by suture. Palpebral lobe arcuate in outline sloping sharply upward with a well developed palpebral margin; palpebral margin relatively wide, slightly convex. A relatively flat top surrounds a raised cone like palpebral area with a faint palpebral furrow; furrow marks the shift from the pointed, slightly raised palpebral area and relatively wide palpebral margin that slopes upward to the ocular suture. The anterior tip of the palpebral lobe is slightly behind the anterior tip of L3. Anterior branch of the facial suture runs approximately transverse to the axis of the 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 posteriorly towards genal

spine. Posterolateral projection of fixigena is wide (tr.) with strong posterior border furrow that gently curves towards the genal spine. Lateral portion of fixigena above the genal spinal slightly protrudes above posterior facial suture and extends outward beyond posterior tip of librigena. Genal spine relatively long, slightly greater than 50% of cephalon length. Posterolateral fixigena furrow initially convex towards axial furrow then quickly becomes convex posteriorly. Sculpture of rounded tubercles developed moderately across glabella and fixigena. A small raised posteriorly angled protrusion is developed along the axis of the posterior margin of LO.

Librigena lateral border widest (tr.) opposite anterior part of librigenal field, but becomes greatly reduced anteriorly to near obsolescence along the anterior margin of glabella, and backwards towards posterior branch of suture. Border furrow weak and expressed largely by change in slope between the librigena field and lateral border. Librigena field strongly convex; a shallow suboccular furrow extends above glabella, minus L0. Circumocular suture arcuate; slightly angled anteriorly adaxially. Visual surface of the eye arranged in an hexagonal stacking pattern, with 8-9 circular lens per column and approximately 8-9 rows of lens at the base tapering to 5-6 by the top of the eye. Cicular lens composed of a raised margin with a deeper circular, pitted area inside. Faint hexagonally stack pits surround the area around each lens. Eye relatively tall, tapers gently towards the flatted top along the palpebral suture.

Pygidium relatively narrow, long and triangular in outline with maximum width approximately 90 percent of pygidial length. Lateral and posterior profiles strongly convex. Axial furrow well defined, shallows towards the posterior tip. Axis moderately

convex and tapers backwards towards a pointed posterior tip; width approximately 39 percent of pygidial width across the anterior most ring; includes twelve well defined axial rings and a short (sag.) tip 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. Pleural ribs defined by shallow, oblique interpleural furrows that curve backward distally. Pleural furrows deep, and nearly parallel to interpleural furrows. Slight dorsal flexure present along the axis of the pygidium, raising the posterior tip, readily apparent in lateral view (e.g. Fig.). Sculpture is generally smooth and lacking large tubercles. Doublure, where exposed, relatively smooth and strongly curved dorsally; curvature mimics the outer most edge of the overlying pleural field. Doublure appears to extend inward toward the approximate inflection point of the pleural field or to the approximate termination point of the interpleural furrows.

Discussion.—The short (exsag.), tall eye (e.g., Fig. 8.8–8.11) separates *A*. *katherina* 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.

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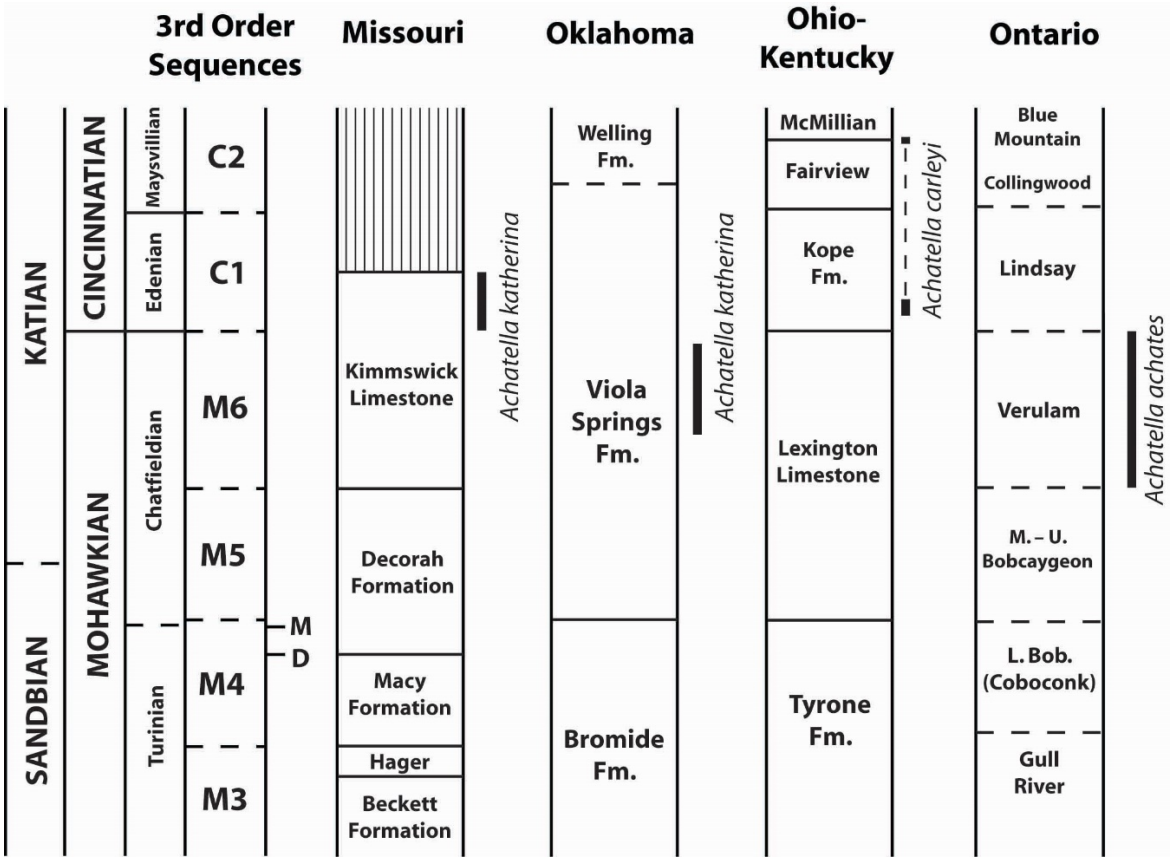
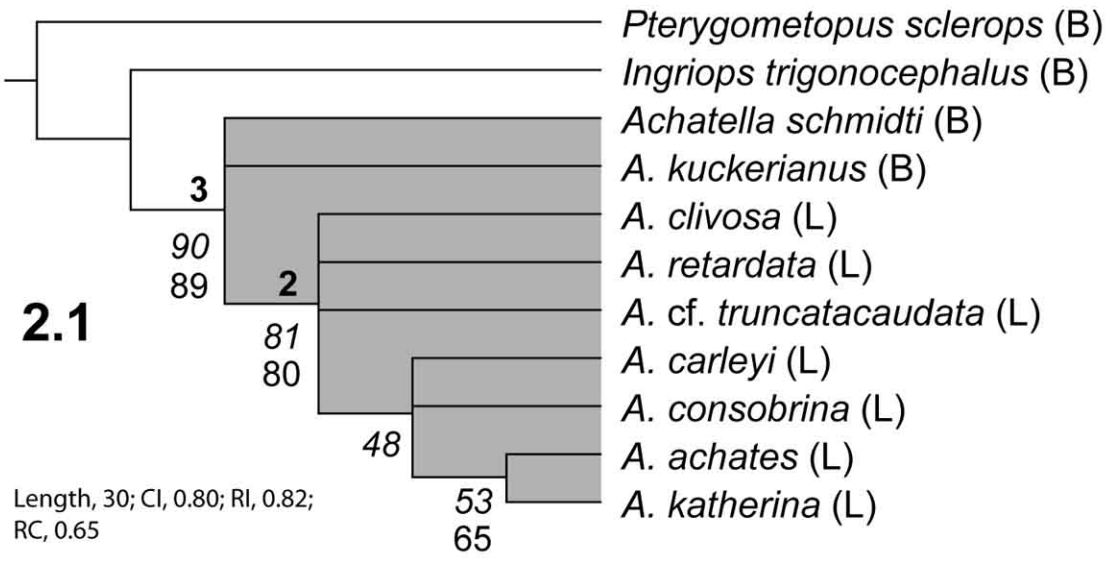

3rd Order Sequences
Missouri
Oklahoma
Ohio-Kentucky
Ontario
KATIAN
SANDBIAN
CINCINNATIAN
MOHAWKIAN
Maysvillian
Edenian
Chatfieldian
Turinian
C2
C1
M6
M5
M4
M3
M
D
Kimmswick Limestone
Decorah Formation
Macy Formation
Hager
Beckett Formation
Achatella katherina
Welling Fm.
Viola Springs Fm.
Bromide Fm.
Achatella katherina
McMillian
Fairview
Kope Fm.
Lexington Limestone
Tyrone Fm.
Achatella carleyi
Blue Mountain
Collingwood
Lindsay
Verulam
M.–U. Bobcaygeon
L. Bob. (Coboconk)
Gull River
Achatella achates

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


Pterygometopus sclerops (B)
Ingriops trigonocephalus (B)
Achatella schmidti (B)
A. kuckerianus (B)
A. clivosa (L)
A. retardata (L)
A. cf. truncatacaudata (L)
A. carleyi (L)
A. consobrina (L)
A. achates (L)
A. katherina (L)
3
90
89
2
81
80
48
53
65
2.1
Length, 30; CI, 0.80; RI, 0.82;
RC, 0.65

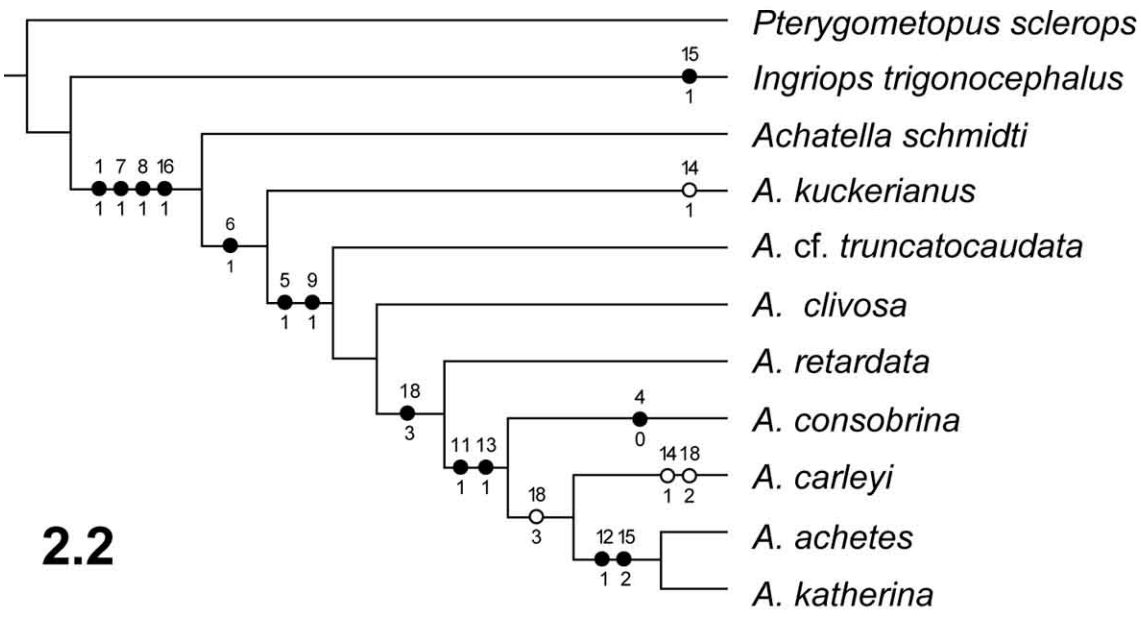

Pterygometopus sclerops
Ingriops trigonocephalus
Achatella schmidti
A. kuckerianus
A. cf. truncatocaudata
A. clivosa
A. retardata
A. consobrina
A. carleyi
A. achetes
A. katherina
15
1
1 7 8 16
1 1 1 1
14
1
6
1
5 9
1 1
18
3
11 13
1 1
4
0
14 18
1 2
18
3
12 15
1 2
2.2

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 50 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.

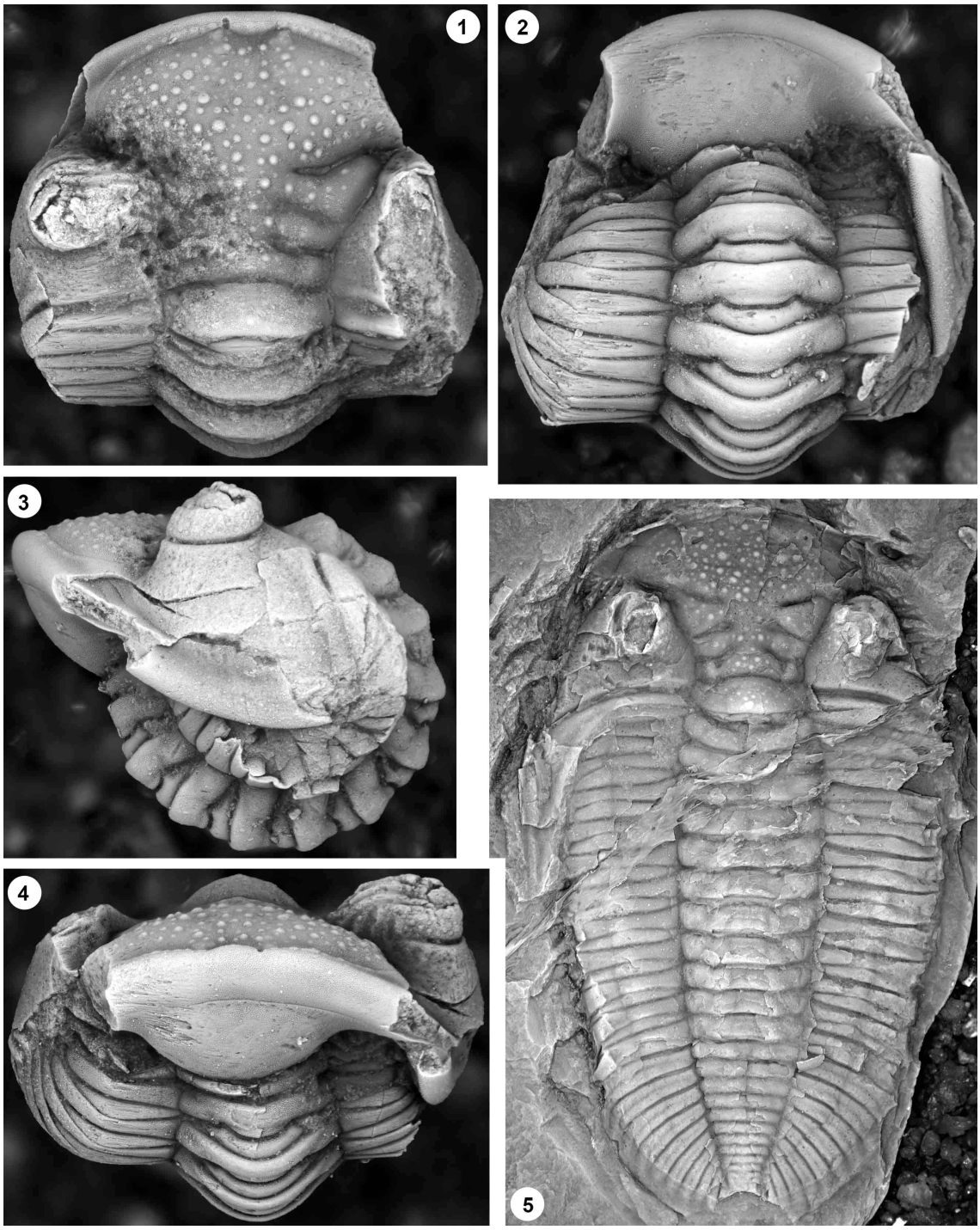

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Figure 3.— *Achatella achates* (Billings, 1860) from Ontario. *1–4*, enrolled exoskeleton (ROM 49475), dorsal, ventral, lateral and anterior views, x7, Verulam Formation, Gamebridge Quarry, Gamebridge. *5*, complete, somewhat compacted exoskeleton (GSC 1784, holotype), x3.75, Lindsay Formation, Ottawa.

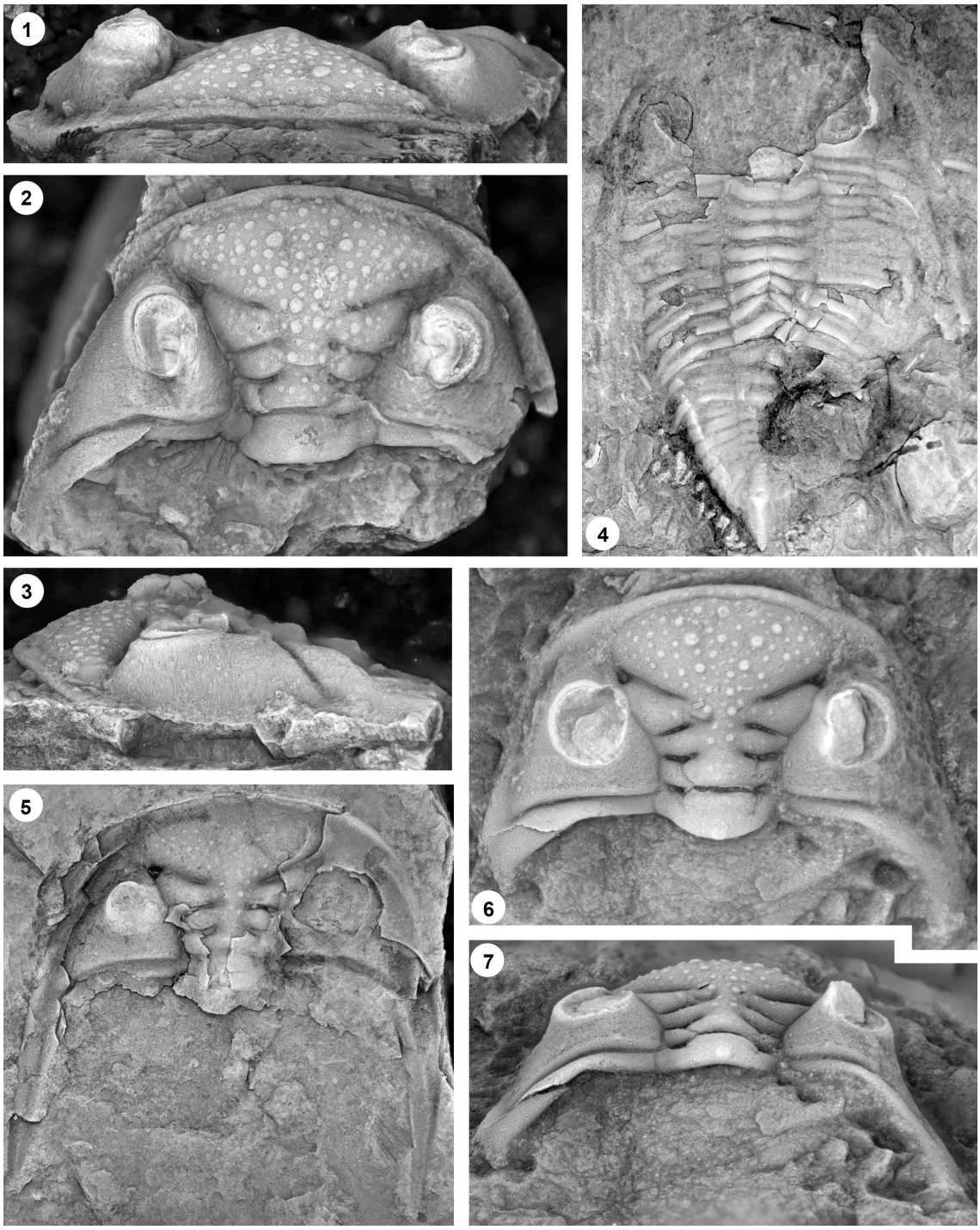
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Figure 4.— *Achatella achates* (Billings, 1860) from Canada. *1–3*, cephalon (ROM 63163), anterior, dorsal and lateral views, x5.5, Trenton Group, Hull, Quebec. *4*, Incomplete exoskeleton (ROM 63161), dorsal view, x4.5, Trenton Group, Hull, Quebec. *5*, cephalon (ROM 18747), dorsal view, x4.5, Trenton Group, Hull, Quebec (illustrated previously by Ludvigsen and Chatterton, 1982, pl. 1, fig. 2). *6, 7,* cephalon (ROM 63160), dorsal and posterior views, x10, Verulam Formation, Lakefield Quarry, Lakefield, Ontario.

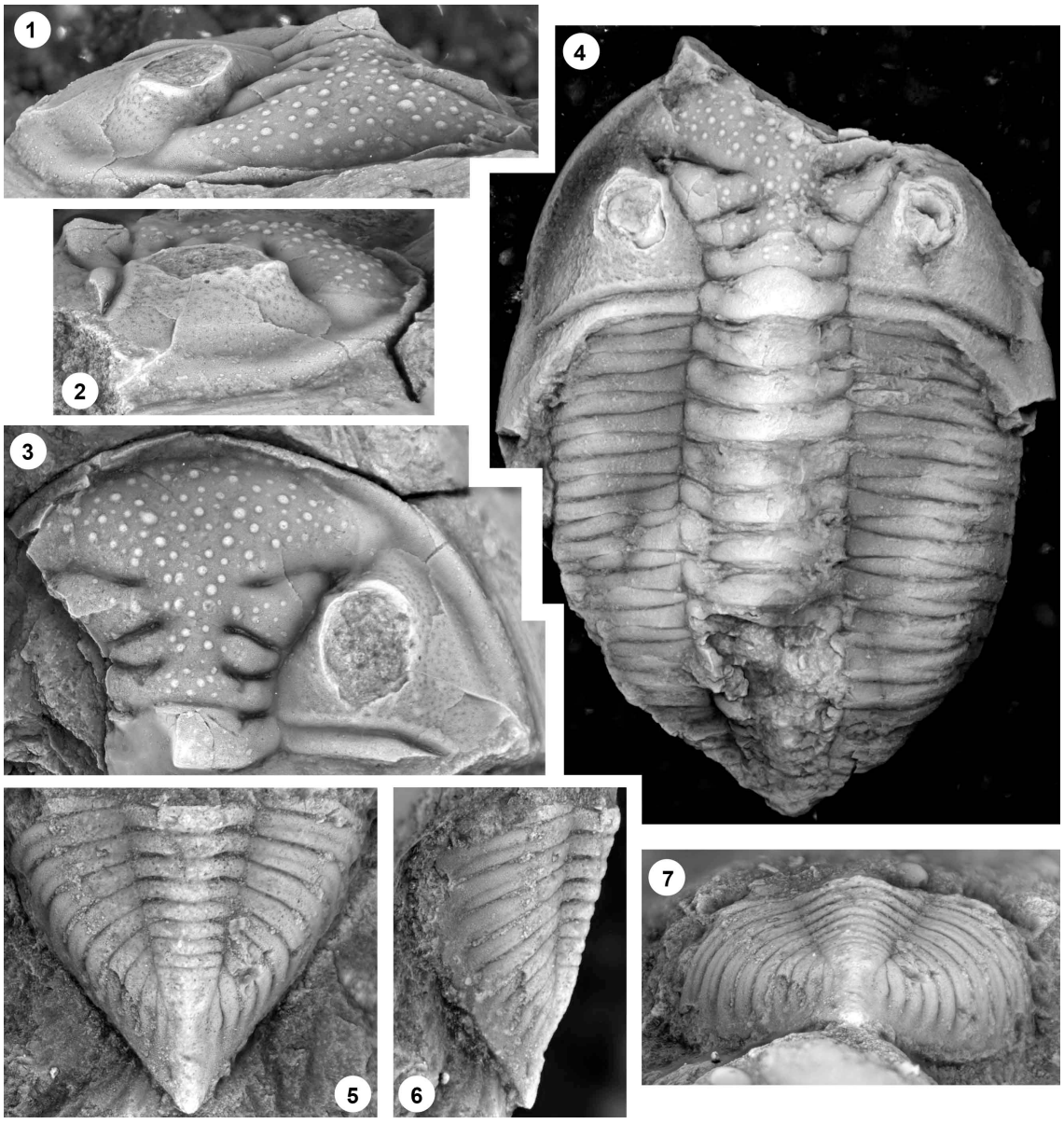
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Figure 5.— *Achatella achates* (Billings, 1860), Canada. 1–3, cephalon (ROM 35371), anterior, lateral and dorsal views, x6.5, Lakefield Quarry, Lakefield, Ontario. 4, nearly complete exoskeleton (ROM 63162), dorsal view, x4, Trenton Group, Hull, Quebec. 5-7, pygidium (ROM 63159), dorsal, lateral and posterior views, x10, Verulam Formation, Gamebridge Quarry, upper face.

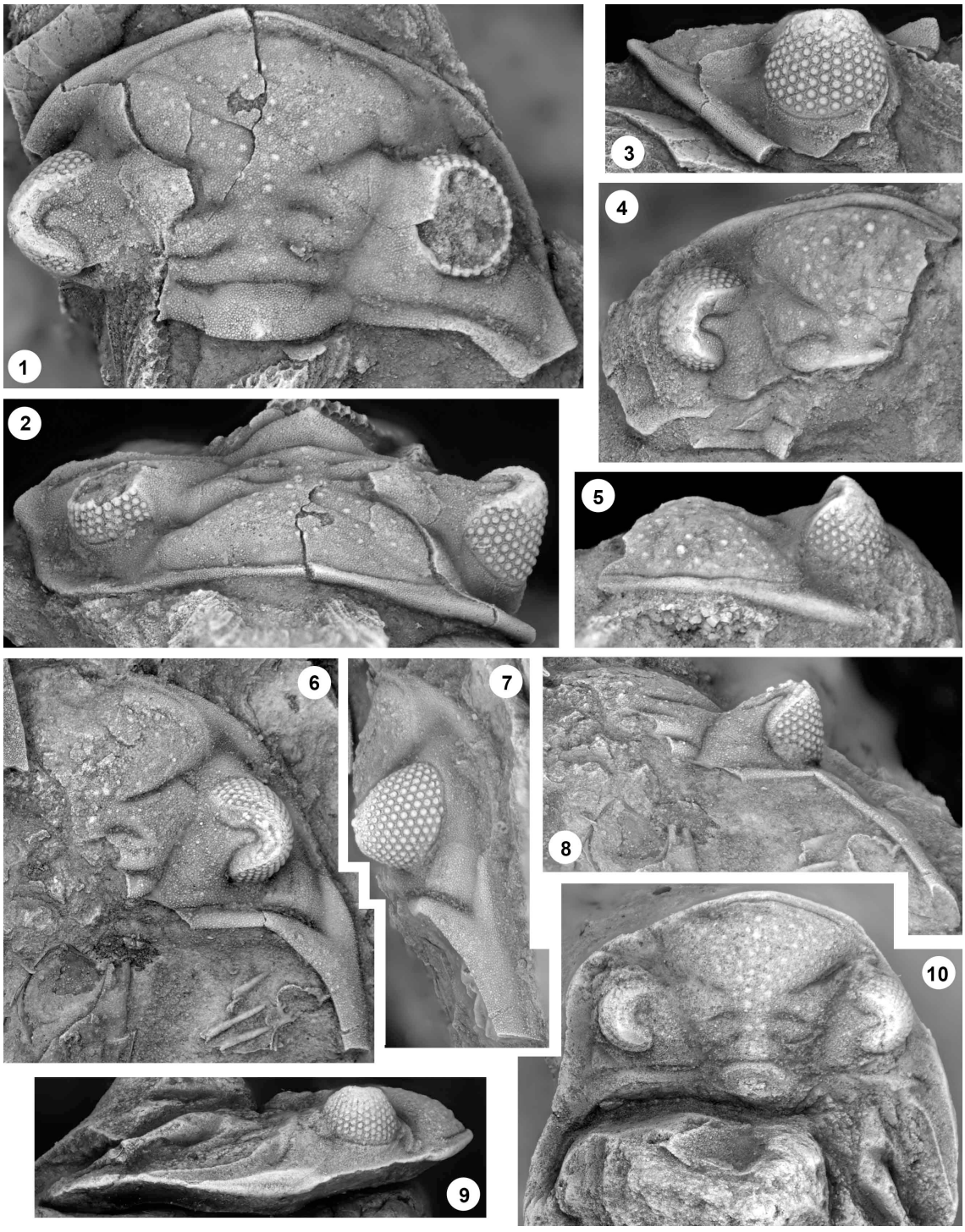
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Figure 6.—Achatella carleyi (Meek, 1872), Cincinnati region, Ohio. *1–3*, cephalon (CM 51280), dorsal, anterior and lateral views, x8, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Does Road at intersection with Ocean. *4, 5*, cephalon (CM 31699), dorsal and anterior views, x12, "Lorraine Group" Formation, Cincinnati, Hamilton County, Ohio; *6–8*, cephalon (CM 51280), dorsal, lateral and posterior views, x8, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Does Road at intersection with Ocean. *9, 10*, cephalon (UC 965;lectotype), lateral and dorsal views, Fairview Formation, Cincinnati.

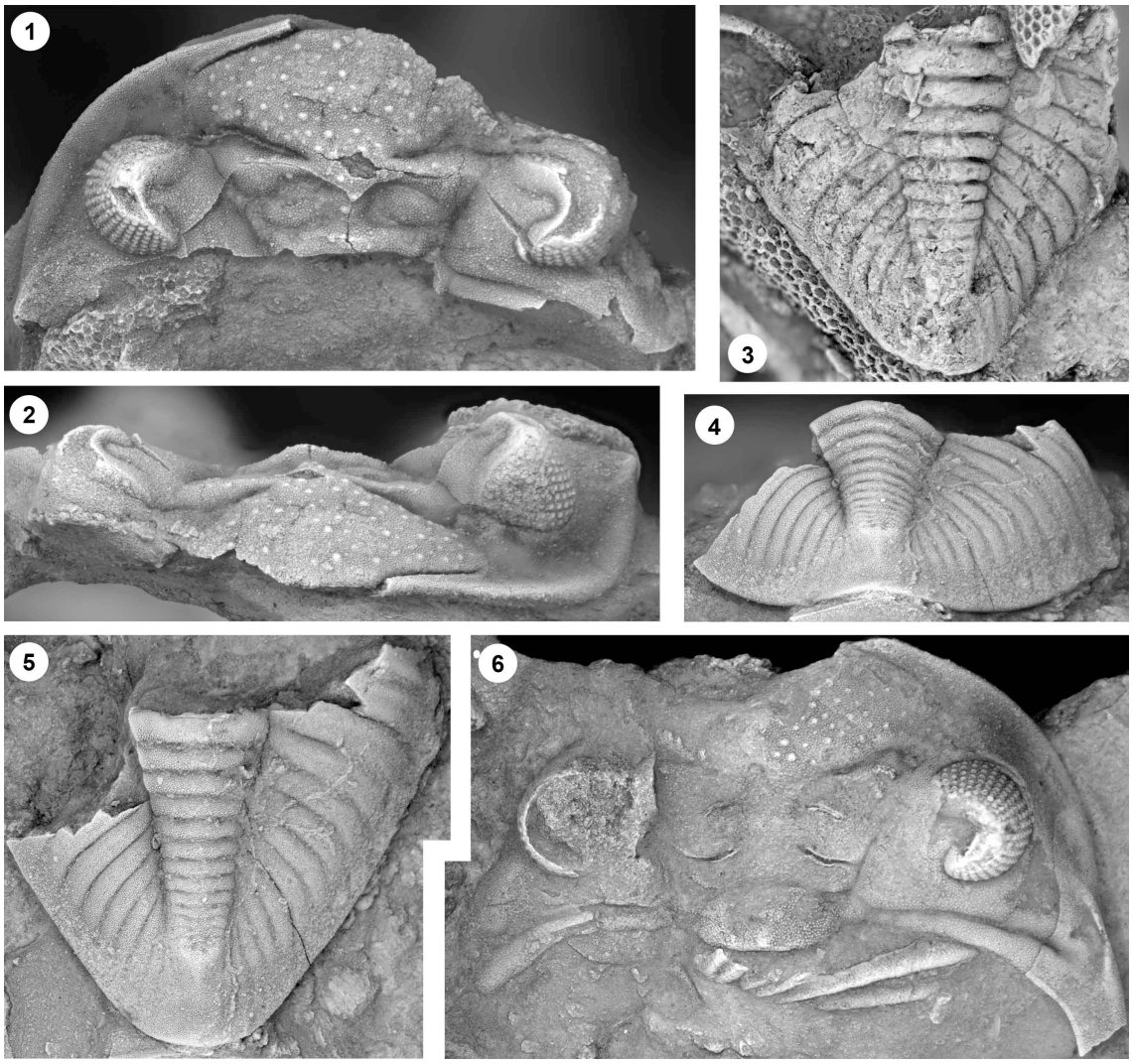
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Figure 7.— *Achatella carleyi* (Meek, 1872), Cincinnati region, Ohio. 1, 2, cephalon (CM 51280), dorsal and anterior views, x9, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Does Road at intersection with Ocean. 3, pygidium (CM 31699), dorsal view, x10, Lorraine Group", Cincinnati, Ohio. 4, 5, pygidium (CM 51280), posterior and dorsal views, x7, middle Fairview Formation, Cincinnati, Hamilton County, Ohio, off 747 on Does Road at intersection with Ocean. 6, cephalon (CM 31699), dorsal view, x6, "Lorraine Group", Cincinnati, Ohio.

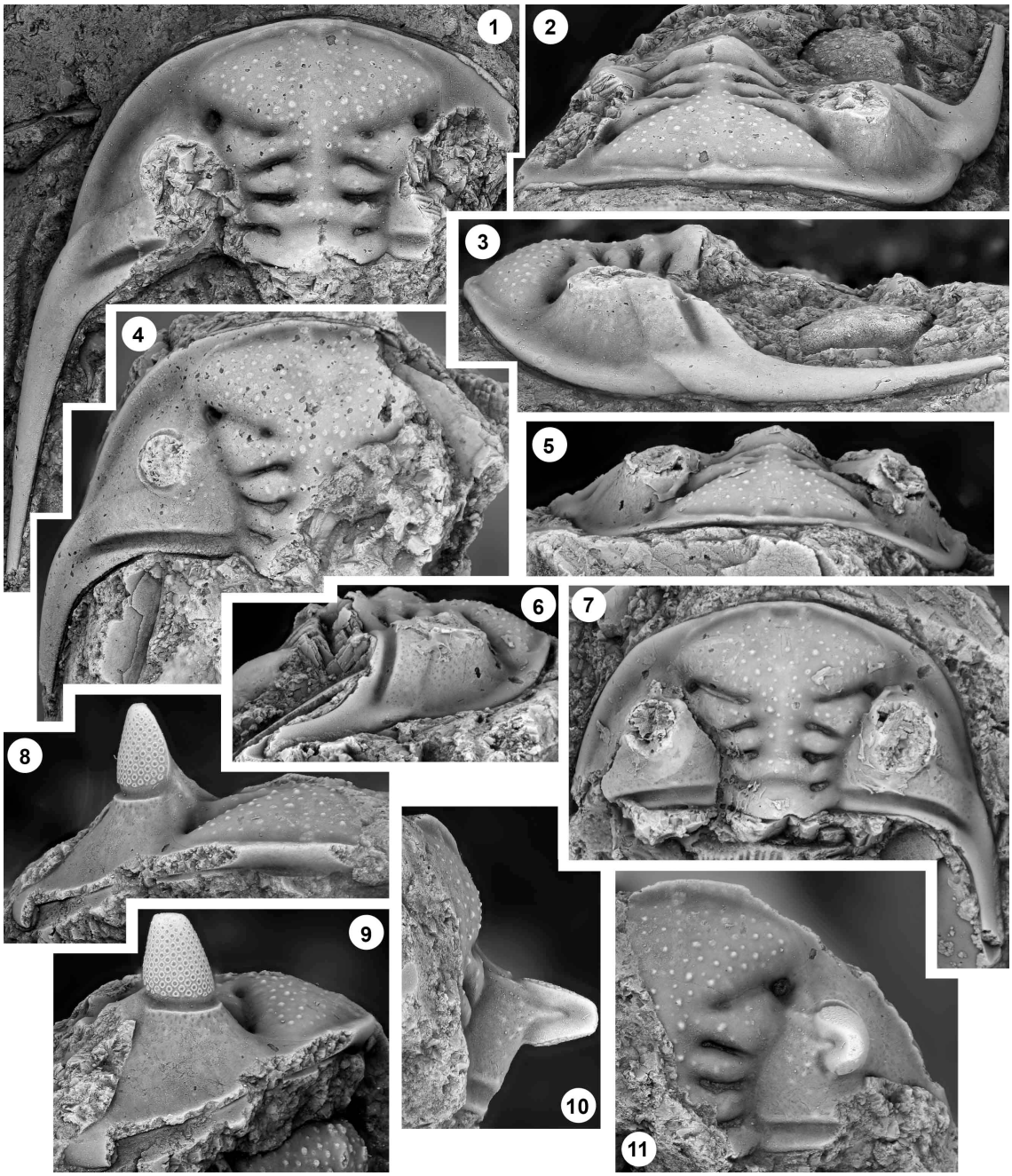
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Figure 8.—*Achatella katherina* (Bradley, 1930), Kimmswick Formation, Batchtown, Illinois. *1–3*, cephalon (UC 33780a; paratype), dorsal, anterior and lateral views, x4.5. *4*, cephalon (UC 337380a; paratype), dorsal view, x4.5. *5–7*, cephalon (UC 20685; holotype), anterior, lateral and dorsal views, x6.5. *8–11*, cephalon (UC 33780e; paratype), anterior, lateral-exterior, lateral-interior and dorsal views, x6.5.

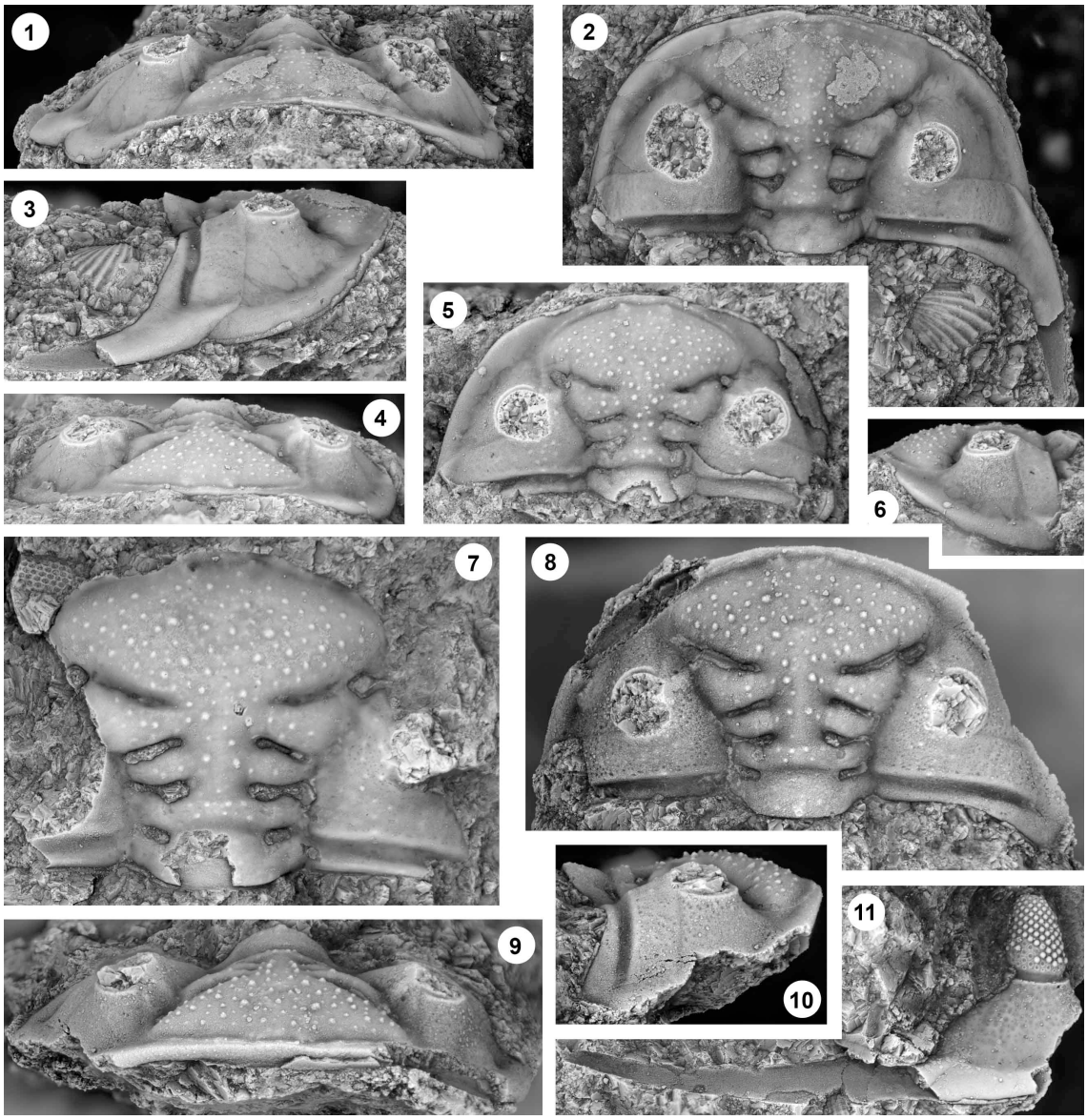
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Figure 9.—Achatella katherina (Bradley, 1930), Kimmswick Formation, Missouri. All from a road cut along State Highway 79, Lincoln Co., MO, approximately 5. 25 km south of the village of Elsbury, except 1–3 (road cut on County Road M, Jefferson Co., Missouri, 200 m southeast of the intersection with Old Lemay Ferry Road). *1–3*, cephalon (OU 222760), anterior, dorsal and lateral views, x6.5, collection M19. *4–6*, cephalon (OU 222761), anterior, dorsal and lateral views, x6.5, collection 79M-1m. *7*, cranidium, (OU 222762), dorsal view, x6.5, collection 79M-1m. *8–10*, cephalon (OU 222763), dorsal, anterior and lateral views, x10, collection 79M-1m. *11*, free cheek (OU 222764), lateral view, x12, collection 79M-1m.

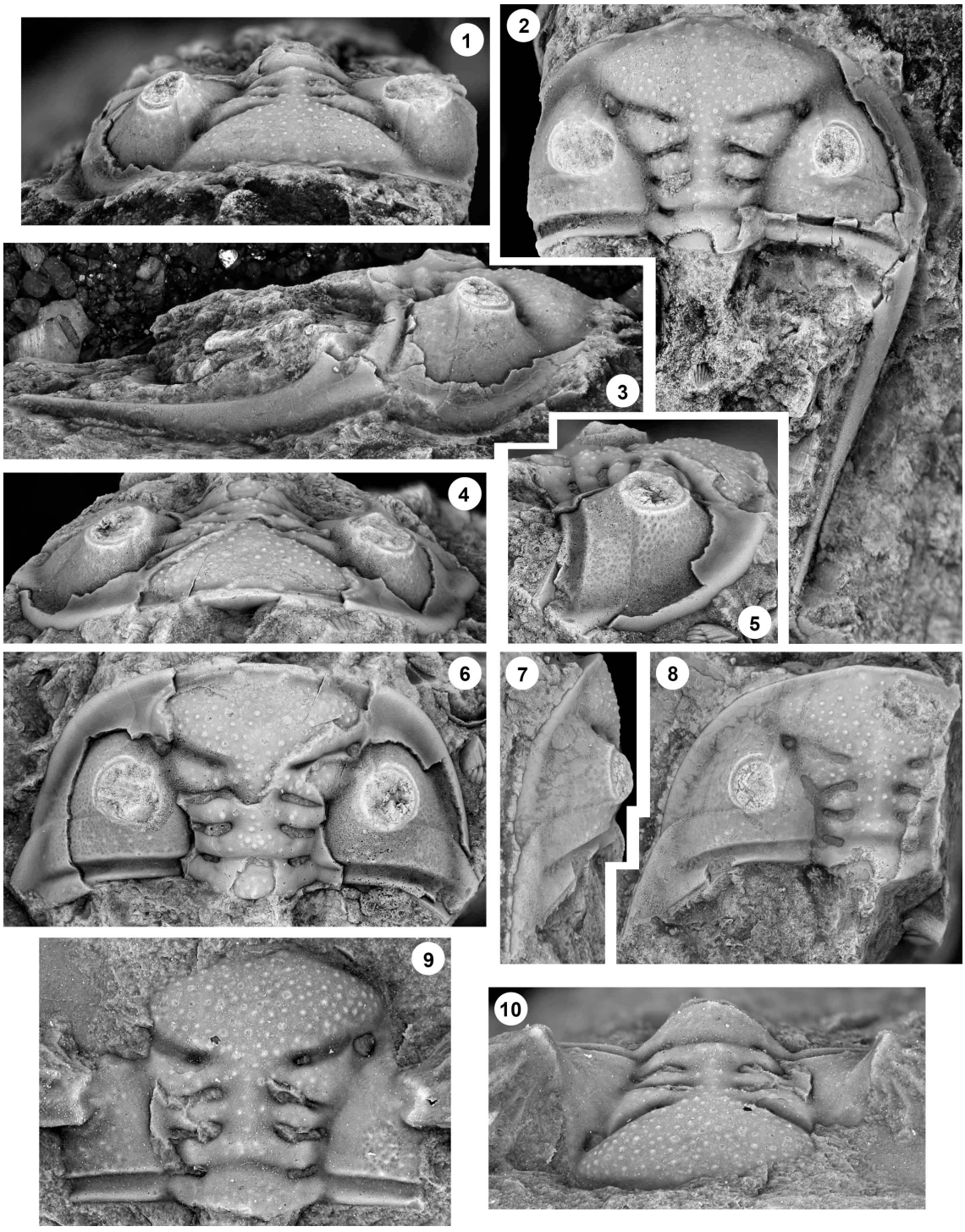
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Figure 10.—Achatella katherina (Bradley, 1930), all from Viola Springs Formation, roadcut along west side of U.S, Highway 99, 5 km south of Fittstown, Pontotoc County, Oklahoma (except 9, 10, Lawrence Quarry, about 10 km southwest of Ada, Pontotoc County).. *1*–3, cephalon (OU 12121), anterior, dorsal and lateral views, x5.25, collection 99-51. *4–6*, cephalon (OU 12123), anterior, lateral and dorsal views, x6, collection 99-float. *7, 8*, cephalon (OU 222765), lateral and dorsal views, x5.5, collection HW99-51. 9, 10, cranidium (OU 12124), latex cast from external mold, dorsal and anterior views, x5.25.

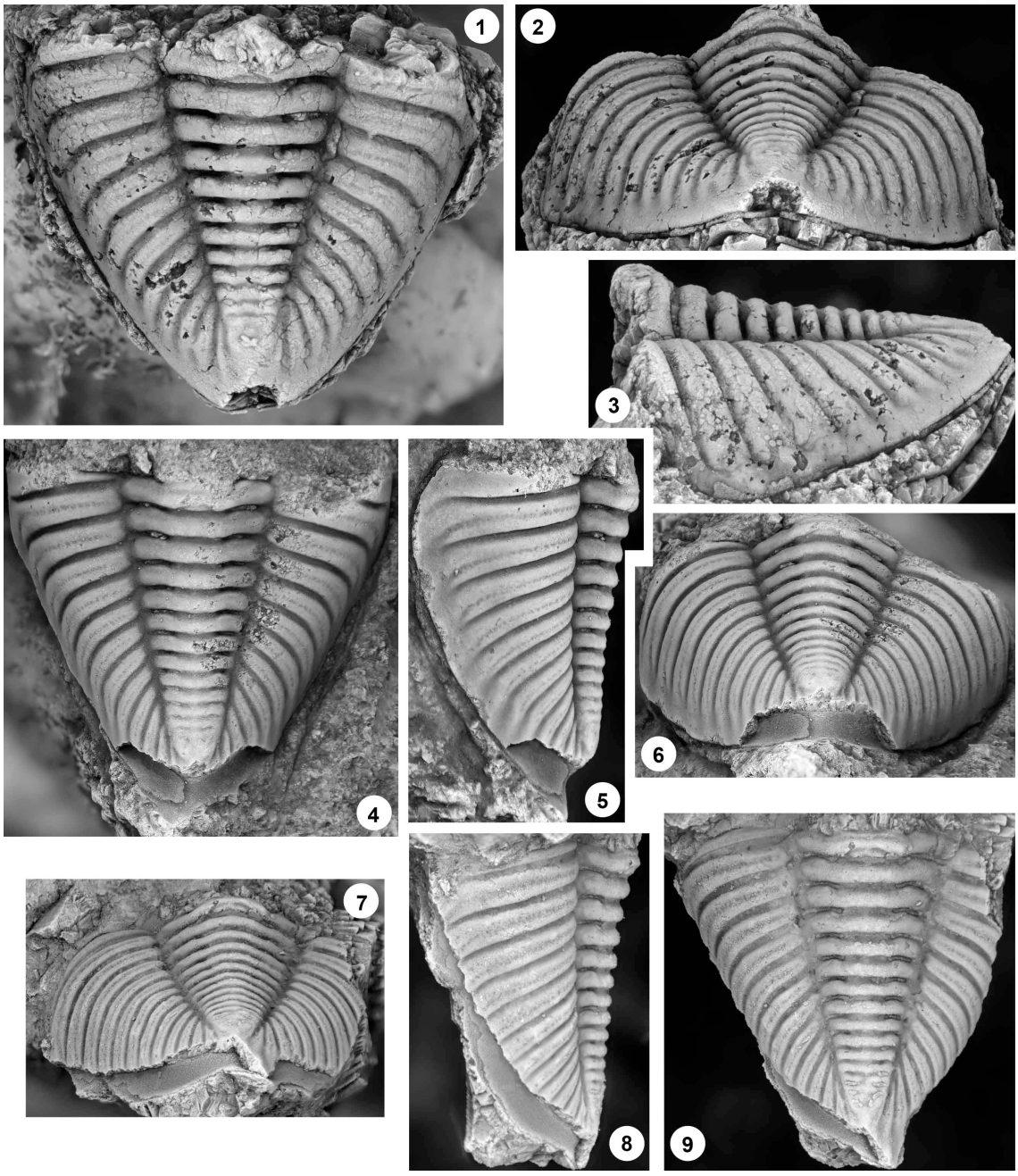
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Figure 11.—*Achatella katherina* (Bradley, 1930), Kimmswick Formation, near Batchtown, IL. *1–3*, Pygidium (UC 28977; paratype of *A*. *katherina* but assigned doubtfully to that species in this paper), dorsal, posterior and lateral views, x7. *4–6*, pygidium (UC 33780b, paratype), dorsal, lateral and posterior views, x7. *7–9*, pygidium (OU 222766), posterior, lateral and dorsal views, x7, collection 79M-1m.

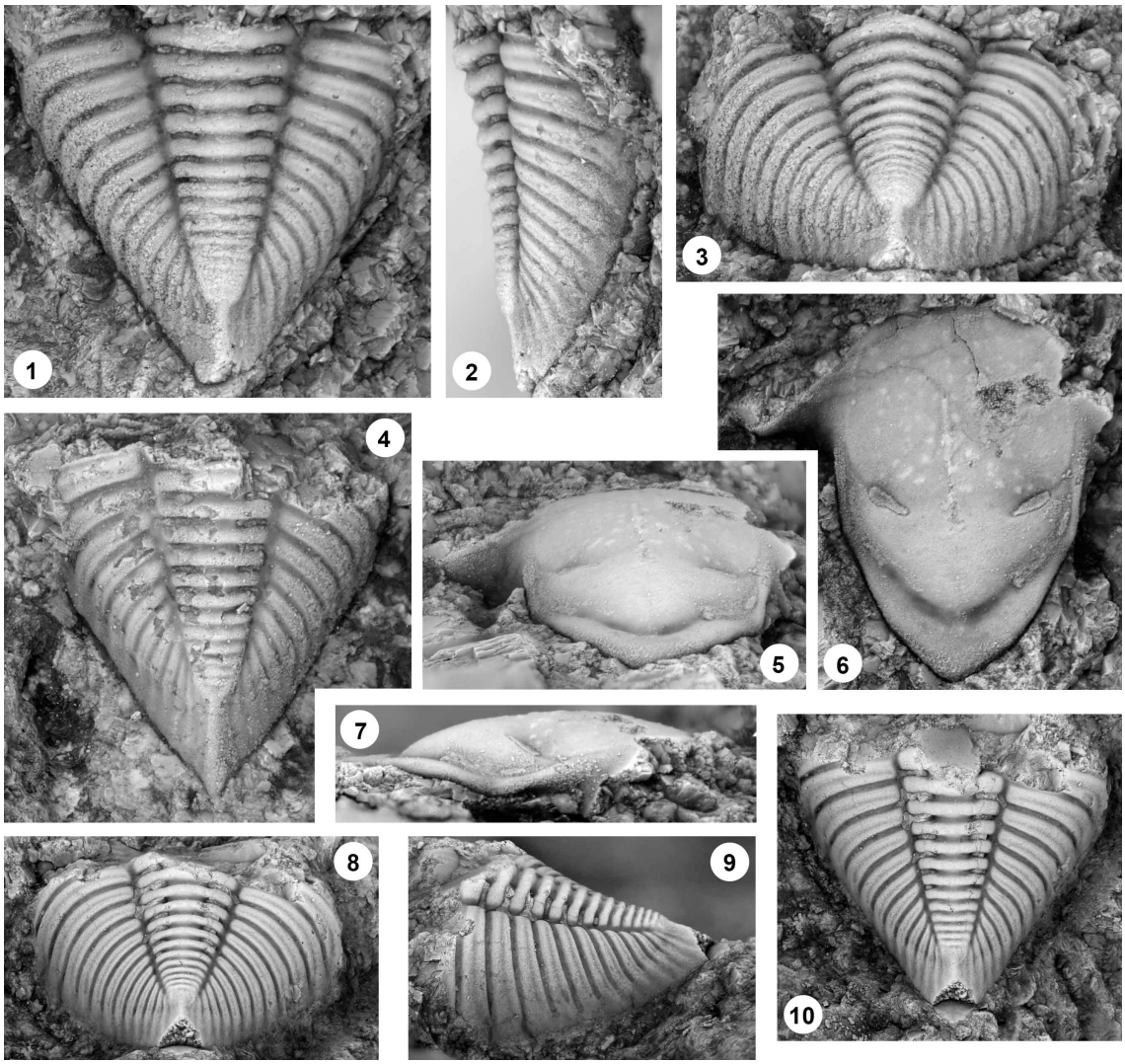
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Figure 12.—*Achatella katherina* (Bradley, 1930). All from the Kimmswick Formation, road cut along State Highway 79, Lincoln Co., Missouri, approximately 5.25 km south of the village of Elsbury except 8-10 (Viola Springs Formation, roadcut along west side of U.S, Highway 99, 5 km south of Fittstown, Pontotoc County, Oklahoma, collection 222767). *1–3*, pygidium (OU 222768) dorsal, lateral and posterior views, x15, collection 79M-1m. *4*, pygidium (OU 222769), dorsal view, x15, collection 79M-1m. *5–7*, hypostome (UC 28975a, paratype), posterior, ventral and lateral views, x16. *8–10*, pygidium (OU 12125), posterior, lateral and dorsal views, x10.

CHAPTER 4 APPENDIX. CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

1. Cephalic convexity. 0, strongly convex with conspicuous anterior arch; 1, relatively flat with weak arch.
2. Genal spine. 0, absent; 1, present
3. Genal spine length. 0, short (equal to less than cranidial length [sag.]); 1, long (length greater than cranidal length).
4. Preglabellar furrow. 0, firmly impressed; 1, border separated from glabella largely by change in slope; 2, effaced, although may be marked by change in sculpture.
5. Anterior expansion of glabella beyond L3. 0, strong (*Pterygometopus*; *Ingriops*); 1, weak.
6. Minimum glabellar width. 0, at L2; 1, at L1 (e.g., *Achatella*).
7. Shape of L3 lobe. 0, roughly even in length (exsag.) and subtrapezoidal in outline; 1, conspicuous adaxial taper in length (exsag.), with minimum adaxial length half or less of length at axial furrow, and subtriangular in outline.
8 Lengths (exsag.) of L1–L3 lobes. 0, roughly equal in length; 1, L3 noticeably longer.
9. Apodemal pits in L3. 0, absent; 1, present. [note, often infilled with matrix]
10. Tuberculate sculpture on glabella. 0, weak or absent; 1, well defined.
11. Anterior glabellar embayment. 0, absent; 1, present (see text for further discussion).
12. Pair of conspicuous tubercles at edges of glabellar embayment. 0, absent; 1, present.

13. Eye position. 0, abuts glabella anteriorly; 1, separate from glabella anteriorly by strip of fixigena. Lésperance and Weissenberger (1998, p. 312) 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; 1, finely etched groove.

15. Palpebral lobe length. 0, extends from S3 to anterior tip of L1; 1, extends from L3 to posterior tip of L1 (*Ingriops*); 2, extends from L3 to S2 or anterior tip of L2 (*A. achetes*; *A. katherina*).

16. Posterior branches of sutures. 0, curved forward abaxially; 1, nearly straight.

17. Outward curvature of cephalic margin behind suture. 0, absent; 1, present.

18. Pygidial length. 0, short, rounded posteriorly; 1, intermediate, rounded posteriorly (Ingriops); 2, long, rounded posteriorly; 3, long, pointed posteriorly.

19. Pleural field. 0, gently arched distally; 1, nearly vertical flanks (*Achatella*); 2, gently concave flanks (*Veroniaspis*).

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 trigonoceplus	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. katherina	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. kuckerianus	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. cf. *truncatocaudata*	1	1	?	?	1	1	1	1	1	1	0	0	?	0	0	?	0	?	1
A. consobrina	1	1	2	0	1	1	1	1	1	1	1	0	1	0	0	1	0	3	1

Chapter 5: *FLEXICALYMENE SENARIA* (CONRAD 1841) AND RELATED TRILOBITES FROM OKLAHOMA, MISSOURI AND ONTARIO

INTRODUCTION

Like other trilobite species named in the early history of geological investigations of North America, *Flexicalymene senaria* (Conrad, 1841) has been reported widely in the literature for more than 150 years (e.g., Anthony and Lyell, 1847). More recent work has segregated *Flexicalymene* into a number of temporally and geographically segregated species (eg., Stumm and Kauffman 1958; Ross 1967; Dean 1979; Hunda and Hughes 2007), but there remain many occurrences of *F. senaria* in such regions as Missouri (Bradley, 1930), Michigan (Stumm and Kauffman, 1958), New Jersey (Davis, 1963), Ontario (Ludvigsen, 1979) and Virginia (Whittington, 1941; Chatterton et al., 1990) that have yet to be evaluated fully. Indeed, the characteristics of *F. senaria* (described long ago; widely distributed) resemble those of "wastebasket taxa" (Plotnick and Wagner, 2006), raising the possibility that the published record of the species masks geographic differentiation. Discovery of abundant, well-preserved sclerites of *Flexicalymene* in the Kimmswick Limestone of Missouri prompted a review of *F. senaria* that also incorporates new material from Oklahoma and Ontario.

STRATIGRAPHIC SETTING

Missouri and Illinois — Flexicalymene senaria was initially described from sclerites from an unspecified position within the Kimmswick Limestone near Batchtown, Calhoun Co., IL (Bradley 1930). Although we were unable to relocate Bradley's collecting locality, we obtained new material from Section 79M, which was measured at

low road cut along State Highway 79, Lincoln County, Missouri, approximately 5. 25 km south of the village of Elsbury, and about 13 km northwest Batchtown. Together with Bradley's figured specimens, the additional sclerites demonstrate that a new species, *Flexicalymene kimmswickensis*, is in fact present in the Kimmswick Limestone. The stratigraphic range of the species is shown in Fig. 1.

Oklahoma — In an unpublished dissertation, Amati (2004) showed that several species of *Flexicalymene* were present in the Viola Springs and Welling formations, although no species were given formal systematic treatment. In this paper, at least four species are documented, mostly from restudy of Amati's specimens, although sample sizes are too small to allow any of them to be named. *Flexicalymene* sp. 1 and *F*. sp. 2 from the lower Viola Springs Formation at Bromide Quarry and Highway 99 (see Amati, 2014 for locality information). *Flexicalymene* cf. *senaria* occurs in the upper Viola Springs Formation at Lawrence Quarry and appears 51 m above the base of the Highway 99 section, whereas *Flexicalymene* cf. *F. meeki* Foerste 1910 occurs in the Welling Formation, Lawrence Quarry (see Amati, 2014 for locality information). A single cranidium of an indeterminate species of *Flexicalymene* (not illustrated) was collected from a thin grainstone that forms part of the transgressive systems tract of a thin cycle with sequence-like architecture (possibly correlative with sequence M5A in the Cincinnati region; Brett et al., 2004) at the base of the Viola Springs at Highway 99. Stratigraphic ranges of Oklahoman species illustrated in Fig. 1.

Ontario, *Canada — Flexicalymene senaria* has been reported from the Verulam Formation (Ludvigsen, 1979), and new material of the species is described and illustrated from this formation at Gamebridge Quarry, Gamebridge, Ontario. A second species from Ontario, *F. croneisi* (Roy 1941), was described from the Upper Ordovician Hillier Member of the Cobourg Formation at Port Colborne, Ontario, Canada. In current nomenclature, this would place the species within the Lindsay Formation (Liberty, 1969), and it is younger than *F. senaria*. *Flexicalymene granulosa* (Foerste 1909) occurs in the upper Katian (Richmondian) Georgian Bay Formation (Ludvigsen, 1979) and is the youngest species represented in Ontario. Stratigraphic ranges of Ontario species illustrated in Fig. 1.

SYSTEMATIC PALEONTOLOGY

Family **CALYMENIDAE** Burmeister 1843

Genus **FLEXICALYMENE** Shirley, 1936

Type species.—*Calemene blumenbachi* var. *caratacti* Salter, 1865 from Caradoc strata of Shropshire (by original designation)

FLEXICALYMENE SENARIA (Conrad, 1841)

Figure 2.1-2.18

1841 *Calymene senaria* CONRAD, p. 38, 49.

1847 *Calymene senaria*; HALL, p. 238, pl. 64, figs. 3a-n.

1941 *Flexicalymene senaria*; WHITTINGTON, p. 493.

1946 *Flexicalymene senaria*; WILSON, p. 48, pl. 10, figs. 11a, 11b, 12.

1953 *Flexicalymene senaria*; EVITT AND WHITTINGTON, pl. 9, figs. 1–16, pl. 10, fig. 1

1958 *Flexicalymene senaria*; STUMM AND KAUFFMAN, p. 949, pl. 123, figs. 1-11.

1967 *Flexicalymene senaria*; ROSS, p. B14, pl. 4, figs. 1-6.

1979 *Flexicalymene senaria*; LUDVIGSEN, p. 46, fig. 29A-D.

1990 *Flexicalymene senaria*; CHATTERTON ET AL., p. 266, figs. 1.10–1.15, 2.1, 2.2, 5.1–5.18, 6.1–6.21

1999 *Flexicalymene senaria*; BRETT ET AL., p. 301, fig. 9.1, 9.2

2002 *Flexicalymene senaria*; WHITELEY ET AL., p. 133, pl. 68, ? pl. 70.

Diagnosis — Cranidium outline subtriangular, with a rounded subtrapezoidal outline to the glabella. A relatively narrow, but strongly developed preglabellar furrow; with a reduced anterior border. Fixigena are moderately convex. Fine tubercles cover the entire cranidium. Pygidium as a relatively wide axis with a reduced pleural field width, but with a strong ventral slope and length. Faint tubercles cover the entire pygidium.
Neotype — A complete specimen (AMNH 843/1), Trenton Limestone, Middleville N.Y, designated and illustrated by Ross (1967, pl. 4, figs. 1-6).

Other material — Three nearly complete cranidia and three complete pygidium from Gambridge Quarry, Ontario, Canada are figured. 22 additional unfigured cranidia, pygidia, and librigena were also available.

Other Occurrences —Flexicalymene senaria appears to be long ranging within the Upper Ordovician Trenton Group of the New York, reported from the Lower Trenton directly above the Lowville Limestone and into the overlying Utica Shale, Dolgeville Formation and Denley Limestone (Cisne et. al 1982). Material from the Upper Ordovician of Michigan assigned to *F. senaria* are also recorded throughout the entirety of the Trenton (Stumm and Kauffman 1958). Silicified material attributed to *F. senaria* from the Spring Hill area of Virginia (Whittington 1941) is apparently from the Martinsburg Formation (Chatterton et al., 1990).

Description —Cephalon subtrapezoidal to subtriangular in outline, rounded anteriorly; maximum cephalic length measured from the occipital lobe, approximately 55 percent of the maximum width across the posterior lateral projections. Cephalon lateral convexity relatively strong; glabella and posterior laterally projections approximately equal in degree of convexity. Axial furrows deep posteriorly, but relatively narrow, shallow anteriorly towards small pits opposite S3. Axial furrows outline contours around the lobes of the glabella, pinching inward towards glabellar furrows. Preglabellar furrow deep, relatively narrow but wider than axial furrows; curved gently forward. Glabella outline subtrapezoidal to subtriangular, with a distinct lateral bulge in the outline at L2. Glabella length approximately 78 percent of cranidial length from the posterior margin of LO. Minimum glabella width measured across the posterior margin of the anterior lobe approximately 55 percent of maximum glabella width across L1. Glabella slightly curved from SO to L2 in lateral profile, becoming strongly curved from S2 into the preglabellar furrow; raised well above the fixigena. SO deepest

adjacent to L1 lobes, shallows and pinched forward medially. LO has a distinct anterior bulge medially, laterally pinched behind L1. L1 lobe outline rounded posteriorly, less so laterally, becoming relatively straight along S1. S1 deep, geniculate, initially inclined at 30 degrees, but reaching about 60 degrees adaxially. L2 well-rounded in outline, shorter and narrower than L1. L3 reduced, separated from the base of anterior lobe by shallow, nearly transverse S3 furrow that does not reach axial furrow. Anterior lobe is approximately subtrapezoidal, but well rounded and relatively wide; the length is approximately 16 percent of total glabella length. Anterior tip of palpebral lobe opposite S2 or L3; posterior tip reaches posterior edge of L2 or S1. Anterior border relatively long, upturned at about 45 degrees, and gently rounded anteriorly. Border furrow slot-like and curved gently forward. Anterior branch of the facial suture relatively straight, angled inward; posterior branch of the facial suture nearly transverse at palpebral lobe before sharp, approximately 60 degree angle backward turn along gently curved path. Posterolateral projection approximately triangular in outline .Gently curved border furrow shallows distally; border widens abaxially, so that width (exsag.) at sutural margin is more than twice width at axis. Fine tuberculate sculpture present across the entire cranidium.

Outline of pygidium approximately subtriangular, rounded along the posterior, straight along lateral margin, with distinct notch becoming parallel to axial plane approaching anterior margin. Ratio of maximum pygidial length to maximum width approximately 60 percent. Pygidium strongly convex in both lateral and posterior profiles axis. Axial furrow well developed, becomes weak at the posterior tip. Axis long, accounting for approximately 94 percent of total pygidial length. Axial width,

measured at the anterior most axial ring, is approximately 50 percent of maximum pygidial width. Axis has 5 axial rings and a terminal piece of at least two segments; distinct semielliptical articulating half-ring, slightly narrower than anteriormost axial ring. Axis tapers posteriorly, becoming rounded approaching the terminal piece. Axial width across the anterior end of the posterior tip approximately 59 percent of the width across the anterior most axial ring. Pleural field strongly curved, continuing downward ventrally until becoming nearly vertical; relatively tall in posterior profile. Pleural field composed of 4 pleura with strong pleural furrows that become progressively shallower towards rear; interpleural furrows expressed distally, but disappear near axis. Border expressed as narrow, unfurrowed band bounded anteriorly by row of fine pits. Fine tuberculate sculpture present across the entire pygidium.

Discussion — As diagnosed here, *Flexicalymene senaria* remains broadly destributed, occurring in northeastern (present coordinates) Laurentia (e.g., Stumm and Kauffman, 1958, Ludvigsen, 1979, Brett et al., 1999) and parts of the Applachian Foreland Basin (Whittington, 1941; Chatterton et al., 1990). Occurrences of in the mid-continent region of Missouri and in the southern Oklahoma aulacogen represent different but related species, including *F. kimswickensis* sp. nov. from the Kimmswick Limestone The cranidium of *F. senaria* can be readily distinguished from *F. kimmswickensis* and a second species from the Viola Springs Formation of Oklahoma, *F.* sp. 2*,* based on the following morphological traits: 1) The fixigena along the anterior branch of the facial suture runs inward toward the anterior margin at a greater angle, 2) The preglabellar furrow is reduced in length though still relatively deep; with short anterior border, 3)

The anterior border is especially distinct with strong anterior curvature, 4) The posterior lateral projections curve downward at a decreased angle, creating a flatter lateral and anterior profile. Though most similar to the pygidium of *F.* sp. 2, *F. senaria* can be distinguished by a more steeply sloping pleural field.

Cisne et al. (1980, 1982) reported an increase in pygidial segmentation in *F. senaria* along an apparent depth gradient in the Trenton Group of central New York. These changes included a shift in the number axial and pleural segments that was also expressed over time, which led Cisne an colleagues to speculate that the pattern might record a case of parapatric speciation. The interpretation hinged in part on physical correlation of sections by the use of bentonites. However, there are alternative interpretations of the stratigraphy, and ages of K-bentonite beds of this region demonstrates that are congruent with graptolite biostratigraphy (Mitchell et al. 1994). This undermines Cisne et al. (1982)'s morphocline for *F.senaria*. In any event, pygidia of F. senaria from Gambridge quarry have five axial rings appear to fall within the older segment of morphocline, with (Cisne et al., 1982). The neotype of *F.senaria* (Ross, 1967, pl. 4, fig. 5) also appears to fall within the lowest range of Cisne's morphocline as well, with 5 distinct axial rings on the pygidium. Future work on samples from the upper portions of Cisne's morphocline, pygidia with up to 8 axial rings, may lead to recognition of a distinct species; following the current trend of systematic treatment within the genus (Hunda and Hughes 2007).

FLEXICALYMENE cf. SENARIA (Conrad, 1841)

Figure 3.1-3.18

Material — OU12077-OU12092, from the upper horizons of the Viola Springs Formation at Lawrence Quarry and the Highway 99 section, Oklahoma. Material includes nearly complete cranidia, pygidia, a hypostome and two librigenae.

Discussion — Specimens assigned to *F.* cf. *senaria* show similarities with *F. senaria*, particularly with the similarly short (sag.) and strongly upturned anterior border. However, the border is more transverse, so that the anterior margin of the cranidium is nearly straight. In addition, the sculpture is more strongly granulose. More material will be needed to determine if *F. senaria* and *F.* cf. *senaria* represent different species.

FLEXICALYMENE KIMMSWICKENSIS

Figure 4-5

1930 *Calymene senaria*, BRADLEY, p. 273, pl. XXIX.

Diagnosis — Anterior border relatively broad in length and width, relatively thick, with strong anterior convexity. Pygidium relatively wide, with a narrow axis of low convexity .

Holotype — A nearly complete cephalon (UC 20687), Kimmswick Limestone, Batchtown, Illinois .

Other material — Six cranidia, including one late meraspis; four pygidia.

Description — Cephalon outline subtrapezoidal with maximum length approximately 60 percent of the maximum width across the cephalon. In lateral profile cephalon is strongly convex across the substantially curved posterolateral projections. Axial and preglabellar furrows strongly incised, wide and equally developed, axial furrows slightly shallow anteriorly, forming an area of distinct separation from the preglabellar furrow. Glabella outline elongate subtrapezoidal; lateral profile steeply curved from L2 to the preglabellar furrow, relatively flat from L0 to L2. Glabella length approximately 75 percent of cranidial length; minimum width across the posterior margin of the anterior lobe approximately 58 percent of maximum glabella width across L1. Glabella convex, rising well above the fixigena in lateral profile. SO strongly incised, wide, deeper adjacent to L1 lobes; curved slightly forward medially. LO has a slight anterior bulge across the axis. L1 extends laterally slightly beyond LO; rounded at posterior corner, relatively long and straight along the axial furrow. S1 strongly incised, angled at approximately 30 degrees towards the axial furrow, with a distinct adaxial bend slightly off from parallel to the glabella. L2 approximately less than a third of the maximum length of L1, rounded along the lateral margin, reduced in width compared to L1. S2 strongly incised near the axial furrow, shallows toward glabella; angled at approximately 30 degrees. L3 expressed as weak rounded lateral protrusion; bounded anteriorly by faint S3. Anterior lobe subovate to subtrapezoidal, rounded, length approximately 18 percent of total glabella length. Palpebral lobe extends from anterior tip of L1 to the anterior tip of L2. Anterior branch of the facial suture directed slightly

inward along nearly straight path towards anterior margin of cranidium. Anterior border broad (sag., tr.), well rounded anteriorly, with strong convexity; in lateral profile the anterior border upturned at approximately 60 degrees. Posterior branch of the facial suture runs nearly laterally from the palpebral lobe before a sharp posterior curve originating slightly past the palpebral lobe. Posteriolateral projection subtriangular in outline, strongly convex with a wide, strong furrow near the posterior margin. Posterior border furrow curved gently forward becomes constricted as it approaches axial furrows. Anterior border narrow near axial furrow but expands considerably (exsag.) as it approaches sutural margin. Most specimens are exfoliated or with poorly preserved external surfaces; one small individual (Fig. 4.7) has well defined sculpture of fine tubercles, but apparently subdued on larger specimens.

Pygidium outline subtriangular, rounded at anterior-lateral tips and posterior tip but straight along the margins, relatively wide with length approximately 58 percent of maximum pygidial width. Pygidium strongly convex in posterior profile, axis and pleura both convex. Axis relatively long, approximately 93 percent of total pygidial length, while axial width, taken from the anterior most axial ring, approximately 41 percent of total pygidial width. Axial furrow well developed anterior, shallows posteriorly, becoming faint to indistinct around the posterior tip of the axis. 4-5 distinct axial rings present with a terminal piece; axial furrows linear, well defined anteriorly, becoming shallower and indistinct by the terminal piece. Axis tapers distinctly, with the width across the anterior end of the posterior tip approximately 62 percent of the width across the anterior most axial ring. Semielliptical articulating half-ring rounded, separated by a wide furrow and is angled slightly dorsally inward away from the axis.

Pleural field strongly convex with 3-4 slightly rounded pleura; furrows more lightly impressed compared to the axial furrows, and similarly become fainter, less distinct posteriorly. Interpleural furrows strongly impressed, when visible on samples, well developed even approaching the lateral margin.

Discussion —Morphological traits that can be used to readily distinguished *F. kimmswickensis* from the morphologically similar *F. senaria* and *F.* sp. 2, as well as other members of the genus include: 1) A relatively convex, long and wide anterior border. The preglabellar field is well-developed and slot-like, 2) A wider pygidium, with a narrower axis differentiates *F. kimmswickensis* from both *F. senaria* and *F.sp 2*. *Flexicalymene* sp. 1 has a much wider pygidium with laterally extended pleural fields. 3) In the posterior view of the pygidium, the plueral field height is severely reduced when compared to *F. senaria* and *F.* sp 2. For further comparisons and a review of the distinguishing features between *F. kimmswickensis*, and the morphologically similar *F. sp. 2* see the discussion below for *F.* sp. 2.

A series of presumed instars is recorded for the species from the same horizon at 1.0 m at section 79-M. In the earliest holaspid or meraspid phase (fig. 4.7-4.9) convexity in lateral profile appears stronger than in holaspid cephalon, with height much greater than length. The glabella also appears taller; this is most readily in lateral profile with the anterior lobe where the height difference between instars is most distinct. The anterior lobe has the strongest difference in height, where it is much taller, slopes downward at a steep angle then slightly inward before the preglabellar furrow. Anterior border slightly reduced in convexity. The entire cranidium is covered with

uniformly-sized tubercles. A similar disparity between larger tubercle development in protapsid verse holaspid cranidia has been reported from silicified material of *F.senaria* (Whittington 1941). Comparison of the meraspid to early holaspid phases of *F. kimmswickensis* and *F.senaria* reveals a variety of differences including: 1) *F. kimmswickensis* has a glabella with a more triangular outline, while the similar ontogenetic phase in *F.senaria* are more elongate and rectangular in outline; 2) *F. kimmswickensis* appears to have a longer, sligthy wider and distinctly thicker anterior boarder compared to the earlier instars of *F.senaria*, 3) *F. kimmswickensis* appears to lack a true genal spine, while *F. senaria*'s earliest instars retain and thin, spine like genal spine. The absent of this characteristic in *F. kimmswickensis* may be a result of poor preservation; however there does not appear to be a broken tip at the lateral genal margin in the available sample. This further supports the separation of the two species; despite some similarities holaspid samples, the species have distinct ontogenetic development pathways.

FLEXICALYMENE Sp. 1

Figure 6.1-6.10

Holotype — OU 12071, a nearly complete cranidium.

Other material — OU12072, partial hypostome, paratype; OU12073, a complete pygidium, paratype.

Discussion — The morphology of *F.* sp. 1 is unique within the genus, with the most distinct morphological features being: 1) Relatively broad, wide, and flat posterior lateral projections; this creates a relatively flat lateral and anterior profile when accompanied by the shallower angle of the anterior fixigena/anterior branch of the facial suture, 2) A reduced width and length of the preglabellar field and anterior border, 3) A distinctly wide (tr.) and short (sag.) pygidium with a greatly expand pleural field. Morphologically, *F.* sp. 1 appears most similar to *F. griphus* (1967, pl. 4, figs. 16–21; pl. 5, figs. 1–3) sharing flatter lateral and anterior profiles, accompanied with a reduction in the length and width of the preglabellar field/anterior border. The following distinctions are present between *F.* sp. 1 and *F. griphus*: 1) Increase length in the preglabellar field and the anterior border in *F.* sp. 1 compared to *F. griphus*. 2) The posterior branches of the facial future of *F. griphus* continue to diverge as they reach the posterior cranidial margin, whereas those of *F.* sp. 1 become roughly parallel at the border furrow. 3) Palpebral lobe placement is opposite L2 in *F.* sp. 1, while in *F. griphus* the palpebral lobe begins near the middle of L2 and extends beyond S3. 4) The axial furrows of the glabella taper gently anteriorly in *F.* sp. 1, forming a subtrapezoidal outline with the anterior lobe of the glabella only a little narrower than the base. In contrast, glabellar outline of *F. griphus* narrows more distinctly anteriorly. 5) The pygidium of *F.* sp. 1 is distinctly wider with laterally expanded pleural fields when compared with *F. griphus*.

FLEXICALYMENE Sp. 2

Figure 7.1-7.6

Holotype — OU12074, partial, mostly exfoliated cranidium.

Other material — OU12075, complete librigena, OU12076,complete pygidium.

Discussion — Flexicalymene sp. 2 is sufficiently similar in morphology to *F. kimmswickensis* that a comparison will be presented instead of description. Differences include: 1) A more convex, upturned anterior border, visible in anterior and lateral profiles, in *F. sp. 2*, 2) tuberculate sculpture in cranidia of *F. kimmswickensis*, 3) The palpebral lobe appears larger in *F.* sp. 2, and angled more sharply upward dorsally., *Flexicalymene.* sp. 2 and *F. kimmswickensis* can be distinguished readily with the following pygidial differences: 1) The axis in *F.* sp. 2 is wider and shorter in length compared to *F. kimmswickensis*, while the pleural field appears to be slightly wider in *F. kimmswickensis*; this may be function of the difference in axis width however, 2) The pygidium appears slightly wider in *F. kimmswickensis* than *F.* sp. 2.

FLEXICALYMENE CF. MEEKI (Foerste, 1910)

Figure 8.1-8.6

Material — A partial, exfoliated cranidium, (OU12095), A complete librigena, (OU12096), and a complete pygidium, (OU12098).

Discussion — This species is separable from other species from Oklahoma on the basis of a very short anterior border and a narrow (sag.) border furrow. The pygidial axis is

relatively broad (tr.), are there is an abrupt steepening of the pleural field close to the axis. *Flexicalymene meeki* itself (e.g., Ross, 1967, pl. 5, figs. 4–7) has a shallower anterior border furrow, longer anterior border, and a wider pygidium with relatively broader pleural fields.

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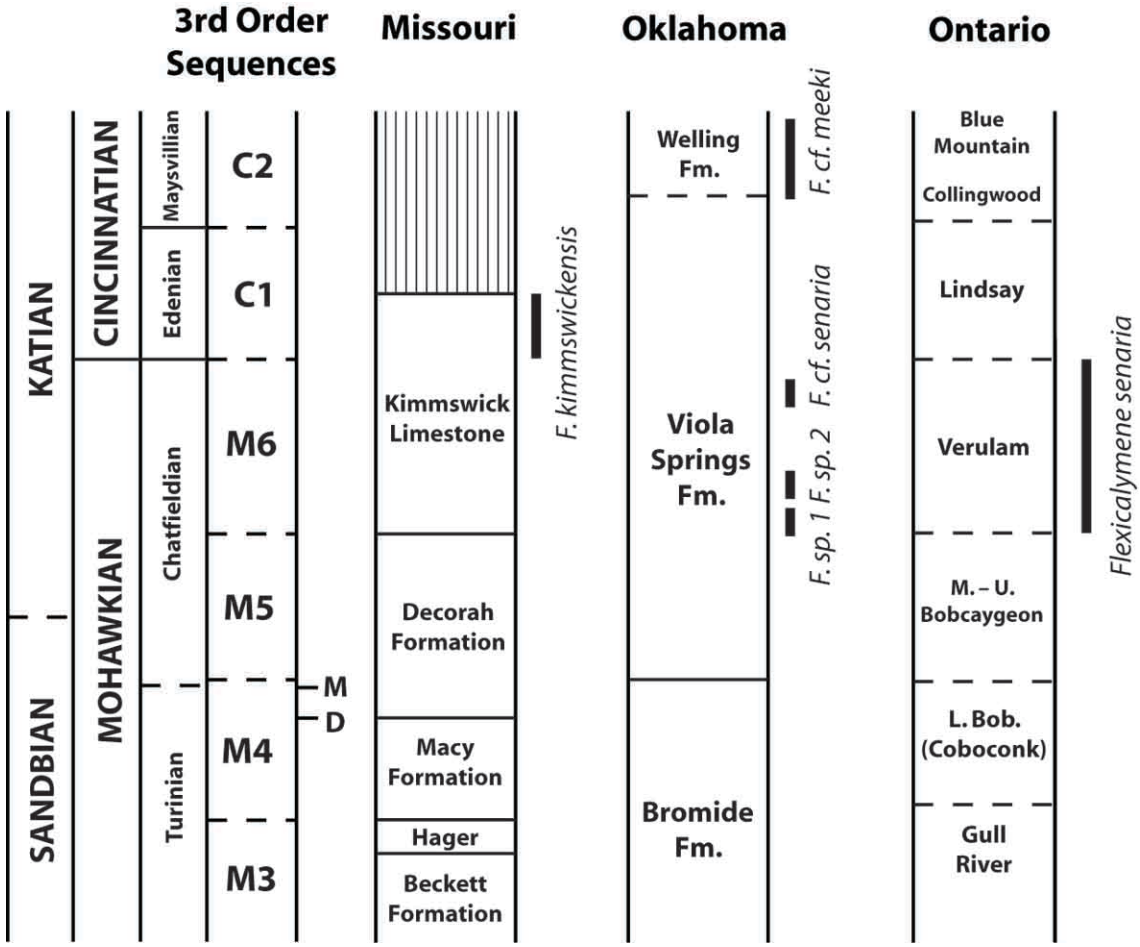
3rd Order Sequences
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CINCINNATIAN
MOHAWKIAN
Maysvillian
Edenian
Chatfieldian
Turinian
C2
C1
M6
M5
M4
M3
M
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Kimmswick Limestone
Decorah Formation
Macy Formation
Hager
Beckett Formation
F. kimmswickensis
Welling Fm.
Viola Springs Fm.
Bromide Fm.
F. cf. meeki
F. cf. senaria
F. sp. 1 F. sp. 2
Blue Mountain
Collingwood
Lindsay
Verulam
M. – U. Bobcaygeon
L. Bob. (Coboconk)
Gull River
Flexicalymene senaria

Figure 1.—Stratigraphic distribution of *Flexicalymene* in Laurentian North America. Third order deposition sequences from Holland and Patzkowsky, 1996. Sources for generalized regional stratigraphy: Missouri, Swisher and Westrop unpublished; Oklahoma, Amati Disseration, 2004; Ontario, Kay, 1937, Liberty, 1969, Salad Hersi and Dix, 1999, Leslie 2000, Brett and Baird, 2002, Mitchell et al., 2004. Species ranges identified by black bars.

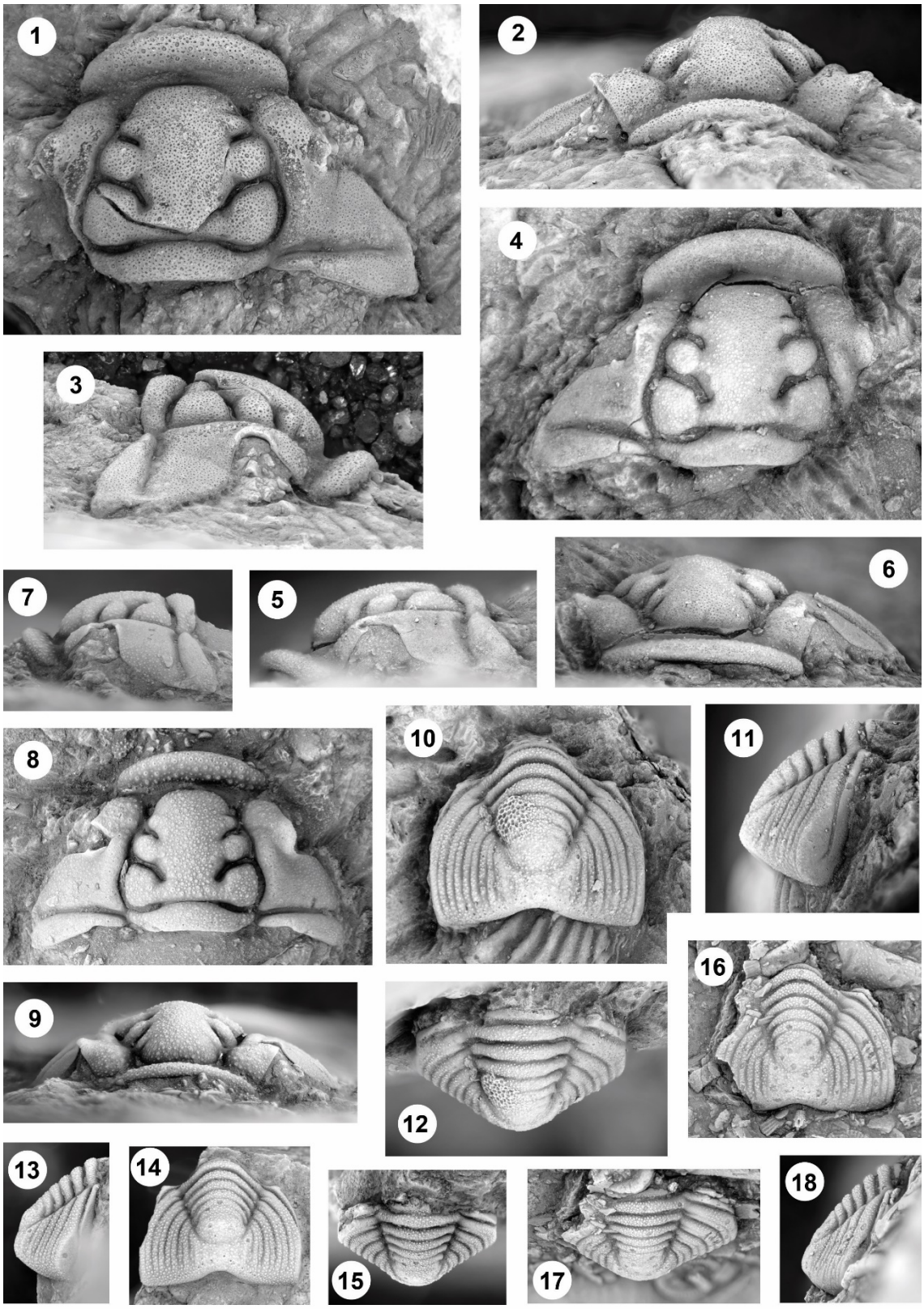
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Figure 2.— *Flexicalymene senaria* (Conrad, 1841) from Gambridge Quarry, Ontario. *1-3*, partial cranidium, (OU 222770), dorsal, anterior, lateral, views, x5, Verulam Formation, Gamebridge Quarry, Gamebridge; *4-6*, partial cranidium, (OU 222771), dorsal, lateral and anterior views, x5, Verulam Formation, Gamebridge Quarry, Gamebridge; *7-9*, nearly complete cranidium, (OU 222772), lateral, dorsal, anterior views, x10, Verulam Formation, Gamebridge Quarry, Gamebridge; *10-12*, nearly complete cranidium, (OU 222773), posterior, lateral and dorsal views, x10, Verulam Formation, Gamebridge Quarry, Gamebridge; *13-15*, nearly complete cranidium, (OU 222774),, lateral, posterior and dorsal views, x10, Verulam Formation, Gamebridge Quarry, Gamebridge; *16-18*, nearly complete cranidium, (OU 222775), posterior, dorsal, lateral views, x10, Verulam Formation, Gamebridge Quarry, Gamebridge.

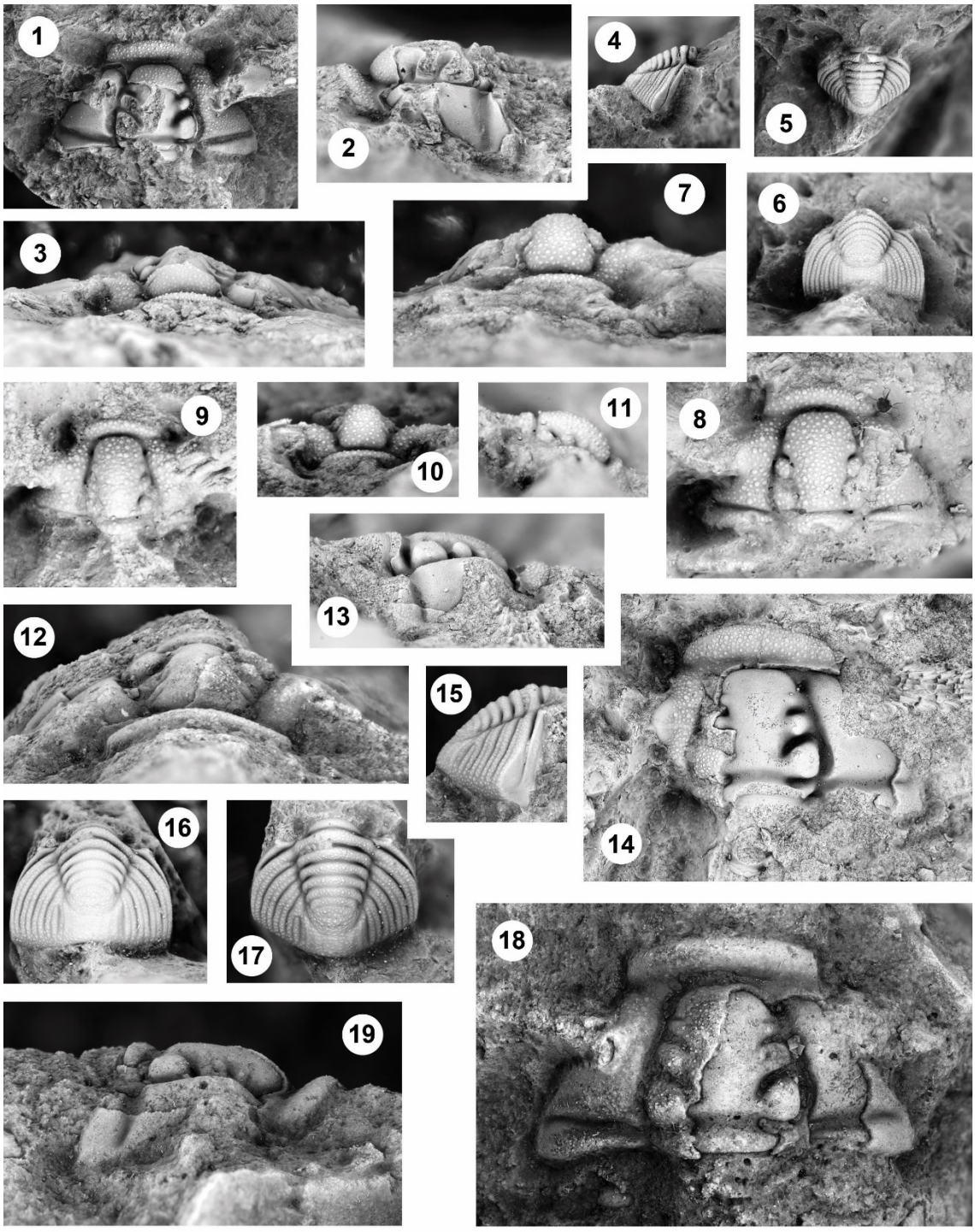
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Figure 3.— *Flexicalymene* cf, *senaria* (Conrad, 1841) from the Viola Springs Formation, Oklahoma. *1-3*, partial cranidium, (OU 12081), dorsal, lateral, and anterior views, x10, Viola Spring's Formation; *4-6*, complete pygidium, (OU 12082), lateral, dorsal and posterior views, x10, Viola Spring's Formation; *7-8*, nearly complete cranidium, (OU 12079), anterior and dorsal views, x10, Viola Spring's Formation. *9-11*, nearly complete cranidium, (OU 12078), dorsal, anterior, lateral views, x10, Viola Spring's Formation; *12-14*, partial cranidium, partially exfoliated, (OU 12087), anterior, lateral, and dorsal views, x5, Viola Spring's Formation; *15-17*, complete pygidium, (OU 12092), lateral, posterior and dorsal views, x10, Viola Spring's Formation. *18,* complete cranidium, partially exfoliated, (OU 12090), dorsal, views, x5, Viola Spring's Formation.

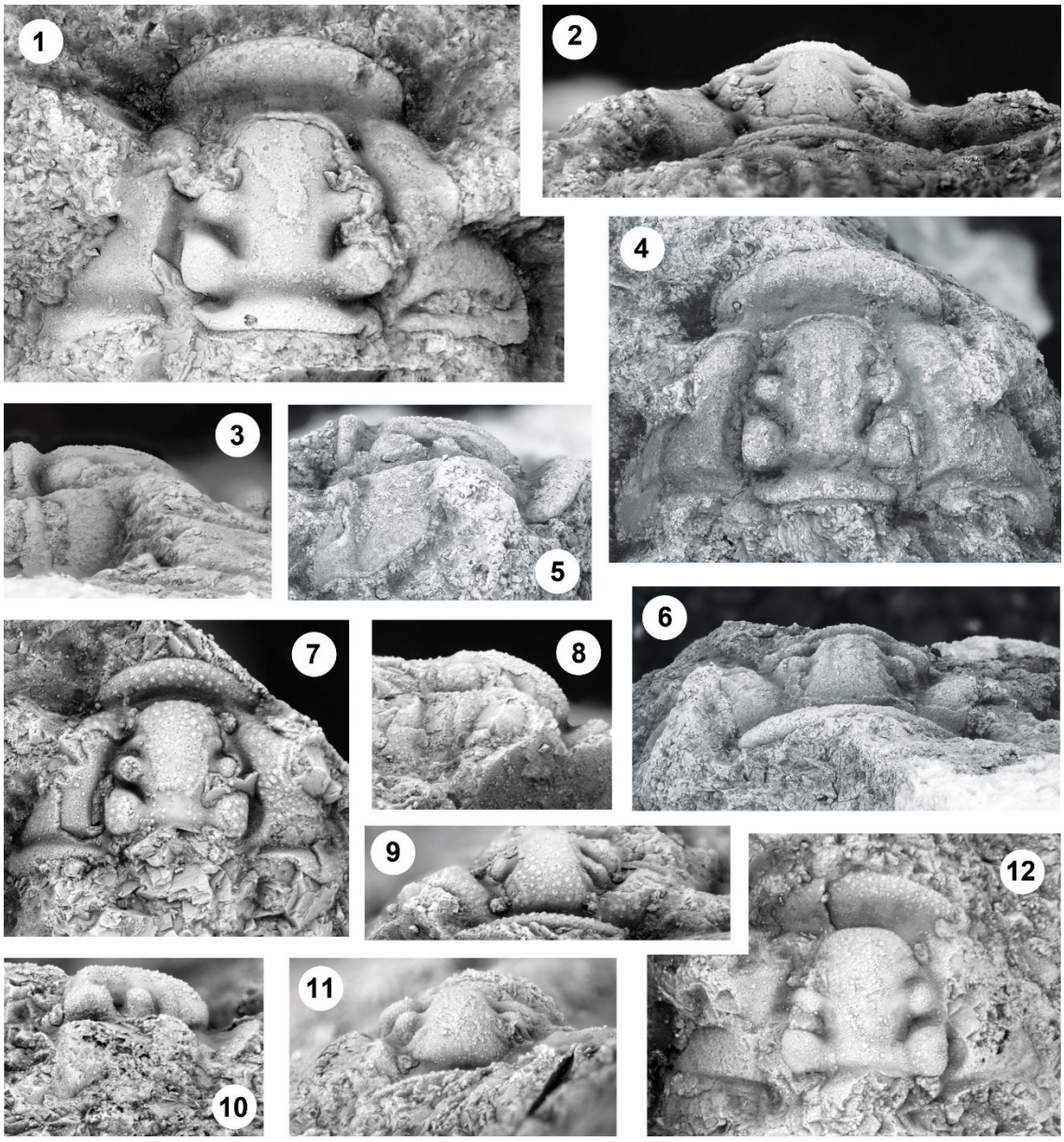
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Figure 4.— *Flexicalymene kimmswickensis* from the upper Kimmswick Limestone (Mordock), Missouri. *1-3*, nearly complete cranidium, mostly exfoliated, (OU 222776), dorsal, anterior, and lateral views, x5; *4-6*, nearly complete cranidium, mostly exfoliated, (OU 222777), dorsal, lateral, and anterior views, x5; *7-9*, nearly complete cranidium, partially exfoliated, (OU 222778), dorsal, lateral, and anterior views, x5; *10-12*, nearly complete cranidium, mostly exfoliated, (OU 222779), lateral, anterior, and dorsal views, x5.

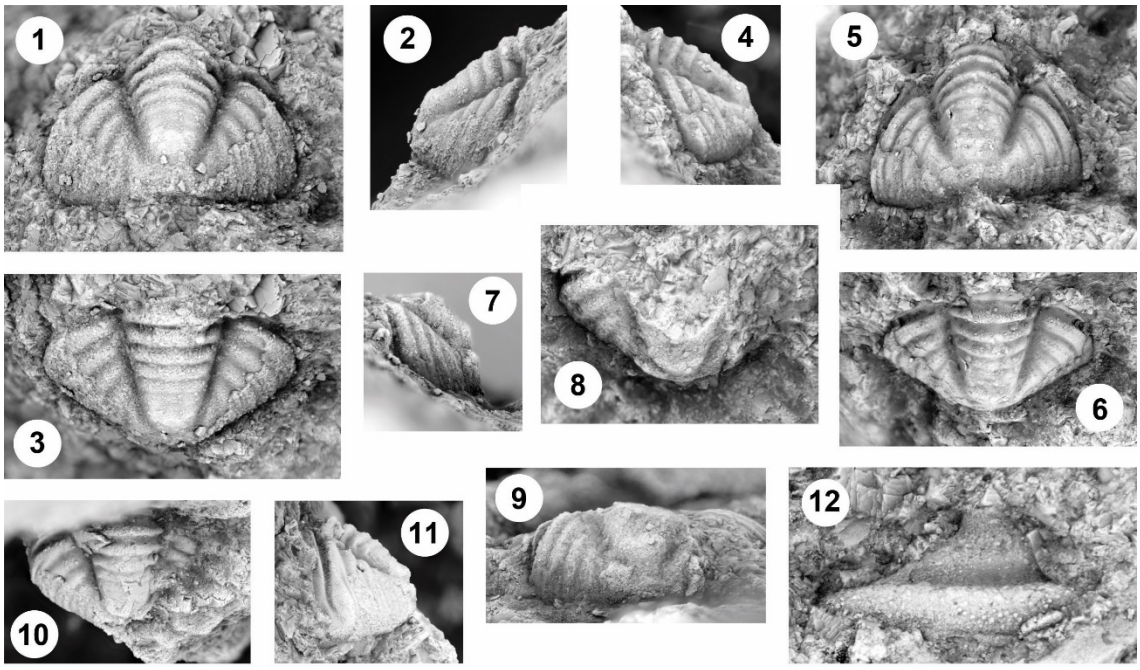
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Figure 5.— *Flexicalymene kimmswickensis* from the upper Kimmswick Limestone (Mordock), Missouri. *1-3*, nearly complete, partially exfoliated pygidium, (OU 222780), posterior, lateral, and dorsal views, x 10; *4-6*, nearly complete, partially exfoliated pygidium, (OU 222781), lateral, posterior, and dorsal views, x 10; *7-9*, partial pygidium, exfoliated, (OU 222782), lateral, dorsal, and posterior views, x10; *10-11*, partial pygidium, (OU 222783), dorsal and lateral views, x10; *12*, librigena, (OU 222784), lateral view, x10.

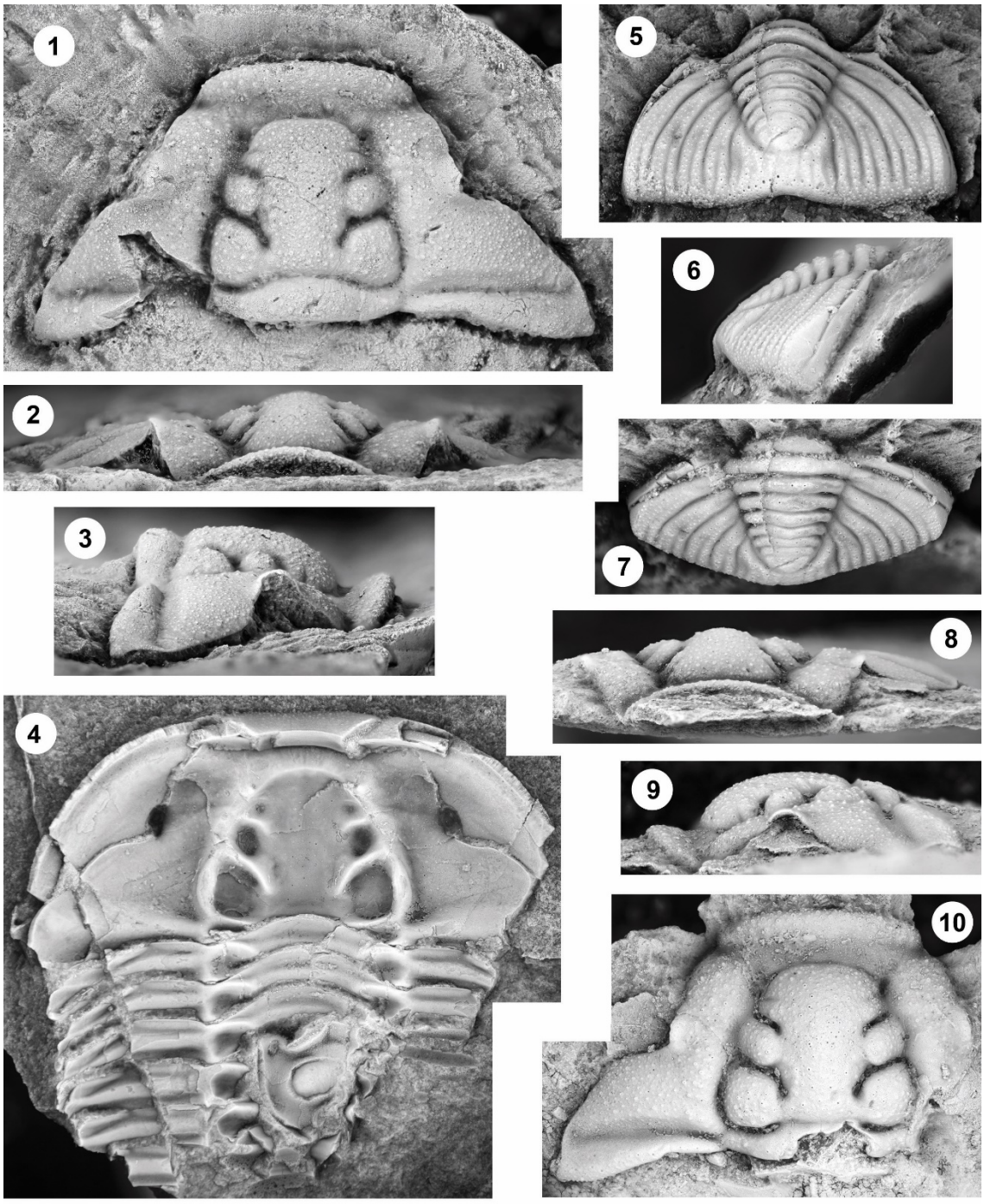
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Figure 6.— *Flexicalymene* sp. 1 from the Viola Springs Formation, Oklahoma. *1-3*, nearly complete cranidium, (OU 12071), dorsal, anterior, and lateral views, x5; *4*, cephalon and thoracic segments, (OU 12072) ventral view, x5; 5-7, pygidium, (OU 12073), posterior, lateral, and dorsal views; *8-10*, nearly complete cephalon, (OU 222785), anterior, lateral, and dorsal views, x5.

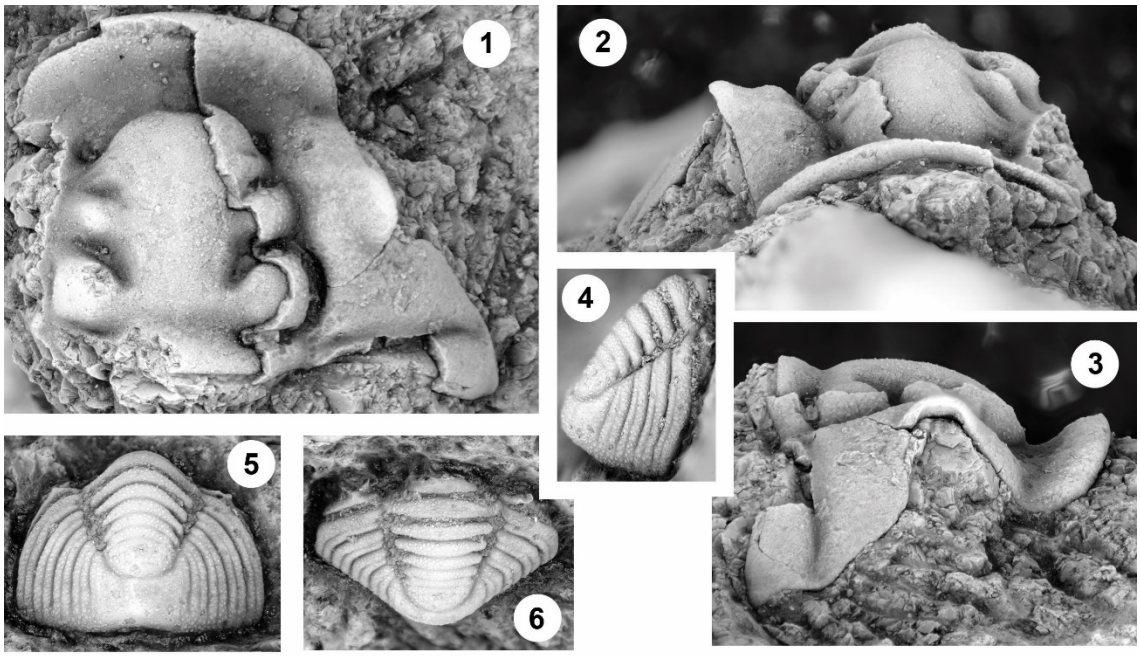
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Figure 7.— Flexicalymene sp. 2 from the Viola Springs Formation, Oklahoma. *1-3*, partial cranidium, partially exfoliated, (OU 12074), dorsal, anterior, and lateral views, x5; *4-6*, pygidium, (OU 12076), lateral, posterior, and dorsal views x10.

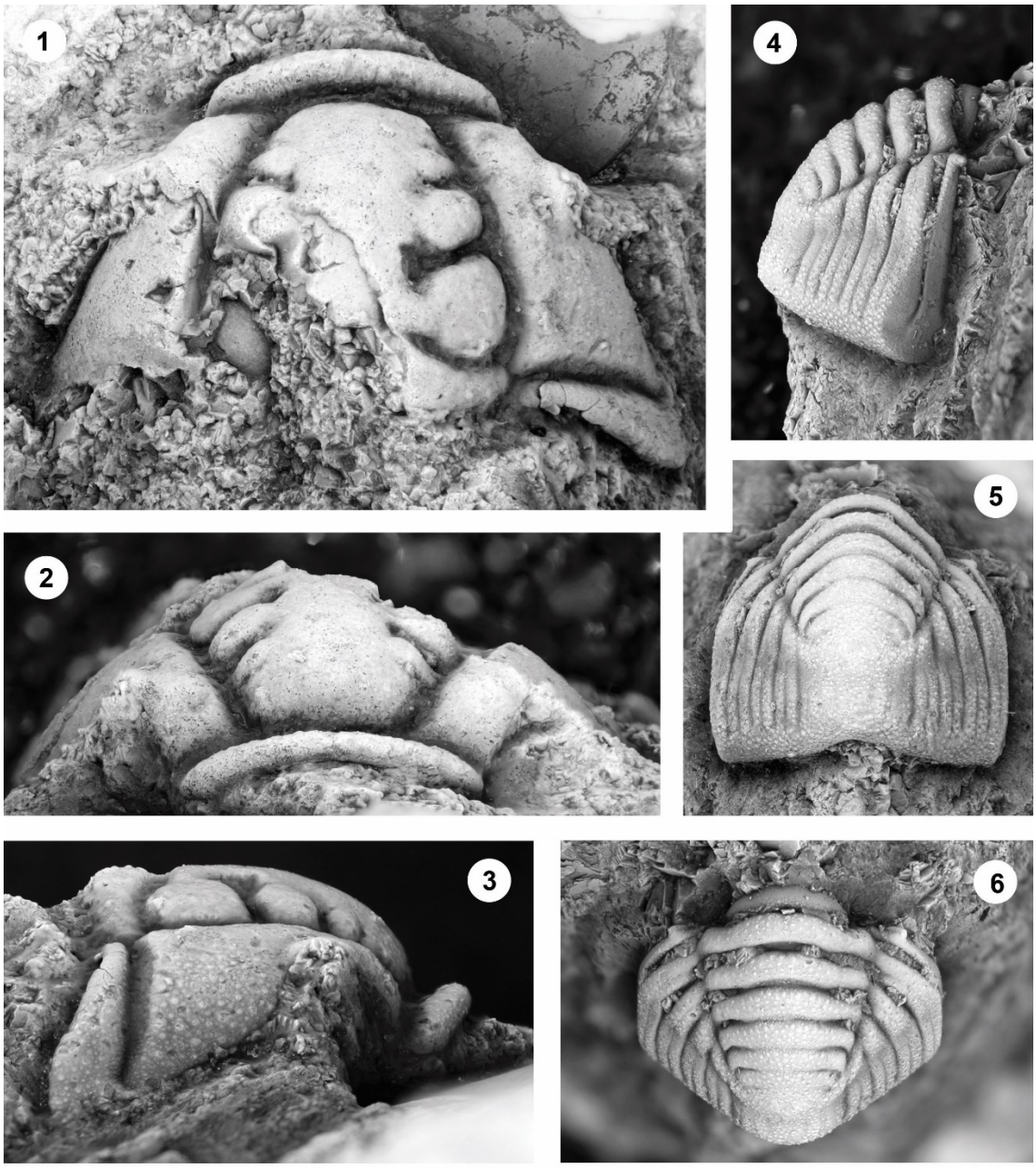
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Figure 8.— *Flexicalymene* cf. *meeki* from the Viola Springs Formation, Oklahoma. *1-3*, nearly complete cranidium, partially exfoliated, (OU 12095), dorsal, anterior, and lateral views, x5; *4-6*, pygidium, (OU 12098), lateral, posterior, and dorsal views x10.

Chapter 6: TRILOBITE BIOSTRATIGRAPHY OF THE KIMMSWICK LIMESTONE (UPPER ORDOVICIAN; KATIAN), MISSOURI

INTRODUCTION

The initial work on the faunas of the Upper Ordovician of Missouri was conducted by Foerste (1920) on the Plattin Limestone and lower portions of the Kimmswick Limestone, with a more extensive study on the Kimmswick trilobites by Bradley, (1925, 1930). Since these early examinations, little work has been conducted on the trilobites of the Kimmswick Limestone beyond the inclusion of type material in broader systematic studies (Amati and Westrop 2004, Amati 2014). In particular, little is known on the stratigraphic ranges of trilobite genera and species and this represents a distinct gap in Upper Ordovician trilobite biostratigraphy of Laurentian North America.

This analysis attempts to better understand the trilobite biostratigraphy of the Kimmswick Limestone in the type area of St. Louis, Missouri, using new collections. The lower portions of the Kimmswick (undifferentiated at the member level) were sampled at section MM, a large road cut along Missouri State Highway MM, about 2.8 km east of House Springs, Jefferson County. The upper Kimmswick (Moredock Member) was examined at sections M, 79-M, and B. 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. Section 79-M was measured 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. Section B

was measured at a small road cut along County Road B, approximately 6.5 kilometers (4 miles), west of the village of Elsbury.

For this analysis, bulk samples were collected in the field and broken up for detailed examination in the lab. In total, 961 sclerites were recovered from the Kimmswick Limestone, representing 524 individual trilobites. In addition, Bradley's type and figured material was also available for study. As recognized by Amati (2004, 2014), closest similarities lie with the faunas of the Viola Springs Formation of Oklahoma. Two assemblages, in ascending order, the *Whittakerites* sp. nov. and *Achatella katharina* faunas, are defined below and occur in the lower Kimmswick and the Moredock Member, respectively. They can also be identified in the Viola Springs Formation, Oklahoma.

TRILOBITE BIOSTRATIGRAPHY

Trilobites of the Lower Kimmswick

Genus composition and abundances.—The lower Kimmswick as defined here comprises all Kimmswick strata below the coarse, cross-bedded grainstone and rudstone of the Moredock Member. Ten trilobite genera are present in the fauna: *Bathyurus* (*Raymondites)*, *Calyptaulax*, "*Whittakerities"*, *Ceraurus*, *Isotelus*, *Bumastoides*, *Paraproetus*, *Hemiarges*, "*Encrinuroides"*, and *Sphaerocoryphe*. Cheirurid trilobites (*Ceraurus* and "*Whittakerities"*) dominate, composing approximately 34 percent of the fauna. Other common taxa include *Raymondites* (approximately 20 percent) and *Calyptaulax* (approximately 18 percent). Samples were collected from Section MM at 24m and 26m, and from Section M at 5-6m.

"Whittakerites" sp. nov. Fauna.—Species restricted to the lower Kimmswick, are:

Calyptaulax sp. 2

Ceraurus sp. 1

"Encrinuroides" sp. 1

Isotelus bradleyi Amati, 2014

Paraproetus sp. 1

Bathyurus (Raymondites) missouriensis sp. nov.

Whittakerites sp. nov.

The following species range into the younger *Achatella katharina* Fauna of the Moredock Member:

Ceraurus globulobatus Bradley, 1930

Isotelus kimmswickensis (Bradley, 1930)

Bumastoides kimmswickensis Carlucci et al., 2012

Paraproetus canalis (Bradley, 1930)

Hemiarges paulianus (Clark, 1894)

Sphaerocoryphe arachniformis Bradley, 1930

Failleana rowleyi (Bradley, 1930)

Correlation.—"*Whittakerites*" sp. nov. was recognized as new by Amati (2004), and occurs between 18 and 32 meters above the base the Viola Springs Formation at her Highway 99 section at Fittstown, Oklahoma. As in the Kimmswick, it appears in the lowest occurrence of bryozoan-trilobite rudstone in the succession; in both cases, this lithofacies is part of a transgressive systems tract that likely marks the base of Holland

and Patzkowsky's sequence M6. Other species shared with the Viola Springs Formation (Amati, 2004, 2014) are *Ceraurus globulobatus* Bradley, 1930 and *Isotelus kimmswickensis* (Bradley, 1930). *Hemiarges paulianus* (Clarke, 1894) occurs commonly in the Trenton Group of New York State (e.g. Whitely et al., 2002) and New York (e.g., Ludvigsen, 1979), in Shermanian–Edenian strata (Westrop and Ludvigsen, 1983); that is, in strata probably assignable to the M6–C1 depositional sequences (Brett et al. 2004).

Trilobites of the Upper Kimmswick (Moredock Member)

Genus composition and abundances.—Sixteen trilobite genera were recovered from the Moredock Member of the upper Kimmswick; *Calyptaulax*, *Ceraurus*, *Isotelus*, *Bumastoides*, *Paraproetus*, *Hemiarges*, *Sphaerocorpyphe*, *Hypodicranotus*, *Flexicalymene*, *Achatella*, *Failiana*, *Thaleops*, *Amphilichas*, *Dimeropyge*, *Eobronteus*, and *Harpidella*. *Ceraurus* again dominates, composing approximately 18 percent of the fauna. Other notable taxa include *Hypodicranotus, Flexicalymene* and *Calyptaulax*, which compose approximately 15 percent, 12 percent, and 10 percent, respectively, of the upper trilobite fauna. These percentages were calculated from individuals within the "course-grained" horizons at Section M and 79-M. The composition of the Upper Kimmswick drastically shifts when sampled from the "fined-grained" facies at 19.0m, Section M. Within this facies *Paraproetus* dominates, composing approximately 65 percent of the fauna with the second most abundant taxa, *Hypodicranotus*, composing 15 percent of the fauna. Other taxa in the facies compose less than 10 percent of the fauna. Samples were primarily collected from two localities across the St. Louis study

region; Section M at 16.3-16.8m, 16.5-18m, and 19m and at Section 79-M in Lincoln County at 0.5m and 1.0m. These localities occur on opposite ends of the study region, approximately 140 km apart, and demonstrate that faunal assemblages can be found regionally.

Achatella katharina Fauna.—As noted above, several species are shared with the underlying "*Whittakerites*" sp. nov. Fauna. Species restricted to the *A. katharina* Fauna are:

Achatella katharina (Bradley, 1930)

Amphilichas sp. 1

Calyptaulax sp. 1

Ceraurinella tenuisculpta (Bradley, 1930)

Dimeropygie tumidus (Bradley, 1930)

Flexicalymene kimmswickensis sp. nov.

Harpidella globosa

Hemiarges leviculus Bradley, 1930

Holia magnispina Bradley, 1930

Hypodicranotus missouriensis (Foerste, 1920)

Thaleops depressicapitata (Bradley, 1930)

Correlation.—In addition to those mentioned above, under "*Whittakerites"* sp. nov. Fauna, several species of the *Achatella katharina* Fauna are shared with the Viola Springs Formation of Oklahoma, including *A. katharina* (Bradley, 1930), *Thaleops depressicapitata* (Bradley, 1930) *Ceraurinella tenuisculpta* (Bradley, 1930) and *Dimeropyge tumidus* (Bradley, 1930). As in Missouri, assemblages with *Achatella*

katharina (Bradley, 1930) and *Thaleops depressicapitata* (Bradley, 1930) occur above those with "*Whittakerites*" sp. nov. and *Isotelus kimmswickensis* in Oklahoma. However, in Oklahoma, the two assemblages occur in different lithofacies and biofacies ("*W*." sp. nov. Fauna in coarse, bryozoan-rich, bioclastic rudstone; *A*. *katharina* Fauna in interbedded wackestone and packstone; Amati and Westrop, 2004, 2006; Amati, 2014), raising the possibility that their superposition is at least partly related to facies shifts. In contrast, the *A*. *katharina* Fauna in Missouri occurs in a bryozoan-rich, bioclastic rudstone facies that is closely similar to the facies that houses the "*W"*. sp. nov. Fauna in Oklahoma. This shows that species extend across facies boundaries (although may vary in abundances between facies), and that there is in fact a temporal signal in the stratigraphic distribution of the trilobites.

Trilobites of the Kings Lake Member of the Decorah Formation.

Composition.—Trilobites are rare, and generally poorly preserved in the underlying Decorah Formation, but a fauna from Kings Lake Member provide an additional constraint on the age and correlation of the Kimmswick. Trilobite diversity is exceptionally low, with only three genera, *Eomonorachus*, *Isotelus* and *Ceraurus* present. *Eomonorachus intermedius* (Walcott, 1877) predominates, accounting for approximately 84 percent of the total trilobite individuals (sample size of approximately 100 individuals). Trilobite faunas in the King's Lake appear to be restricted to the brachiopod/trilobite wacke/packestones in the lower cycle, with only gastropods and minor brachiopods faunas found in nodular lime mudstone and wackestone facies (see chapter 2 for details of the stratigraphy and sedimentary facies).

Correlation.—*Eomonorachus intermedius* also occurs throughout the Decorah Formation in Illinois and Wisconsin, and is most abundant in the Guttenburg Member (DeMott, 1987, fig. 10.3), which is broadly correlative with the Kings Lake Member in the St. Louis region. The species seems to be restricted to sequence M5, and has not been recorded from the Kimmswick Limestone or from the Viola Springs Formation in Oklahoma. In Ontario, *E. intermedius* is reported from the Bobcaygeon Formation (early Chatfieldin and Rocklandian) of Manitoulin Island (Ludvigsen and Chatterton, 1982), which is consistent with an occurrence in sequence M5.

DISCUSSION

Strong similarities in trilobites faunas at the species level, including homotaxial ordering of key species that is unrelated to facies successions, provide strong support for correlation between shallow water facies of the Viola Springs Formation at the Highway 99 section, Pontotoc County, Oklahoma (Amati, 2004, 2014; Amati and Westrop, 2004, 2006) and the Kimmswick Limestone of the St. Louis regions, Missouri. This raises further questions about correlation of carbon isotope excursions between the two regions (Westrop et al., 2012).

In Missouri, the Kimmswick Limestone overlies the Kings Lake Member of the Decorah Formation (M5 sequence), which contains Guttenberg (GICE; Ludvigson et al., 2004) positive carbon isotope excursion (Metzger and Fike, 2013). Young et al. (2005) studied carbon isotope stratigraphy at the Highway 99 section in Oklahoma, and reported a positive excursion that they equated with the GICE. The interval with the putative GICE excursion is essentially the succession that yields the "*W*." sp. nov. and

A. *katharina* faunas, which begins around 20 meters above the base of the Viola Springs Formation. That is, the trilobite faunas that appear above the GICE in the M6 sequence in Missouri co-occur with what is supposedly the same excursion, and in strata that Young et al. (2005) correlate with sequence M5.

There are two possible solutions to this correlation conundrum. Either the carbon isotope excursions are miscorrelated, or the first appearances of the trilobite faunas are strongly diachronous between Oklahoma and Missouri (Westrop et al., 2012). The latter hypothesis is not appealing as it implies not only that the same trilobite faunas appear later, in M6, in Missouri, but also in the same order as in the supposedly older strata of Oklahoma, even though the facies successions are different.

New work on the sequence stratigraphy at the Highway 99 section (Westrop et al., 2012; Carlucci et al., 2014) supports the hypothesis that the carbon isotope excursions are miscorrelated. The base of the Viola Springs Formation represents the M4–M5 sequence boundary (Carlucci et al., 2014); the trilobite faunas correlative with the Kimmswick appear in a younger sequence that can be correlated with the M6 sequence (Westrop et al., 2012). The base of this sequence is marked by a TST of coarse, cross-bedded bioclastic grain- to rudstone facies and appears to correlate with the base of Kimmswick in the St. Louis area. Limited graptolite data for the Viola Springs at Highway 99 indicate that the upper half of the section is no older than M6, which is in accord with the trilobite biostratigraphy and sequence stratigraphy (Westrop et al., 2012). The published record of conodont biostratigraphy for the section (Young et al., 2005) conflicts with an assignment to M6 and is more consistent with the M5 sequence. However, the conodont species are long ranging, and identification of zonal boundaries

hinges upon the first appearance of index species in stratigraphic sections. Young et al. (2005, fig. 3) place the base of the *Belodina confluens* Zone within 10 m of the top of the Highway 99 section. However, if this occurrence records a "late" occurrence of *B. confluens* (implying some degree of environmental/ecological control), conflict with the sequence stratigraphy, trilobite and graptolite biostratigraphy is resolved (Westrop et al., 2012).

The balance of biostratigraphy and sequence stratigraphic data supports the idea of a miscorrelation of carbon isotope excursions in Oklahoma with the GICE of Missouri; the "GICE" in Oklahoma becomes a late, M6 or potentially even a C1 excursion younger than the excursions recorded in M5 in Iowa (Ludvigson et al., 2004) and Missouri (Metzger and Fike, 2013). More data on isotope geochemistry of the M6 to C1 succession in Missouri are needed to test this hypothesis.

SYSTEMATIC SYNOPSIS OF THE TRILOBITE FAUNA

The systematics of the trilobites will be dealt with elsewhere, but a brief synopsis of the fauna is presented below. The systematics of species of *Raymondites*, *Achatella* annd *Flexicalymene* are treated in detail in chapters three, four and five, respectively.

Order Asaphida **ASAPHIDA** Brumeister, 1843

Suborder Asaphina **ASAPHINA** Salter, 1864

Family **ASAPHIDAE** Brumeister, 1843

Subfamily **ISOTELINAE** Angelin, 1854

Genus **ISOTELUS** Dekay, 1824

ISOTELUS KIMMSWICKENSIS (Bradley, 1930)

Pl. 1, Figs. 1-7

Stratigraphic occurrence.— Occurs within all samples in the study region. It also occurs in the Viola Springs Formation of Oklahoma (Amati, 2014).

Discussion.— The species has been revised by Amati (2014), and requires no further comment. Figures illustrate examples of new material recovered during the course of this study.

ISOTELUS BRADLEYI Amati, 2014

Stratigraphic occurrence.— Sampled from the Lower Kimmswick 26.0 meter horizon, Section MM. Species level identification of *Isotelus* material is dependent on complete cranidia and pygidia, but sclerites are often fragmentary and abraded in the Kimmswick. Identifiable samples were relatively rare, only occurring within the coarsest-grained horizons. As a result, the stratigraphic range of the species may be underestimated. The species also occurs in the Viola Springs Formation of Oklahoma (Amati, 2014)

Discussion.— . Described and named for material from Oklahoma; new collections confirm that *I. bradleyi* also occurs in Missouri.

Superfamily **REMOPLEURIDIOIDEA**

Family **REMOPLEURIDIDAE** Hawle and Corda 1847

Genus **HYPODICRANOTUS** Whittington 1952

HYPODICRANOTUS MISSOURIENSIS (Foerste, 1920)

Pl. 2, Figs. 1-14

Stratigraphic occurrence.— Restricted to the upper Kimmswick (Moredock Member) at Section M and Section 79-M.

Discussion.— Originally described from Missouri, the species' distribution may extend into Oklahoma, with similar material attributed to *H.* cf. *missouriensis* occurring in upper portion of the Viola Springs Formation. New collections document some differences between new Kimmswick (Moredock Member) sclerites and previously illustrated Viola Springs material: 1) A shorter, slightly wider and more rounded anterior portion of the cranidium in *H.missouriensis* 2) An occipital lobe that is slightly shorter in length in *H. missouriensis*.

Order **ILLAENIDA**

Suborder **ILLAENIA** Jaanusson, 1959

Superfamily **ILLAENOIDEA** Hawle and Corda, 1847

Family **ILLAENIDAE** Hawle and Corda, 1847

Subfamily **ILLAENINAE** Hawle and Corda, 1847

Genus **BUMASTOIDES** Whittington, 1954

BUMASTOIDES KIMMSWICKENSIS (Carlucci *et al*. 2012)

Pl. 3, Figs. 1-2

Stratigraphic occurrence.— Occurs within all sampled stratigraphic horizons in the study region.

Discussion.— The species was named Carlucci *et al*. 2014 and requires no revisions in this analysis. Figures illustrate examples of new material recovered during the course of this study.

Genus **THALEOPS** Conrad 1843

THALEOPS OVATA (Conrad, 1843)

Stratigraphic occurrence.— No new material was recovered over the course of this analysis; however Bradley did report small cranidia occurring from an unspecified horizon within the Kimmswick Limestone, near Batchtown, Illinois.

Discussion.— The species was revised by Amati and Westrop (2004), who re-illustrated Bradley's types.

THALEOPS DEPRESSICAPITATA (Bradley, 1930)

Pl. 3, Figs. 3-8

Stratigraphic occurrence.— Sampled from the 16.5-18.0 meter interval at Section M, within the Upper Kimmswick. Amati and Westrop (2004) reported this species from the Viola Springs Formation of Oklahoma.

Discussion.— The recent revision of T. depressicapitata by Amati and Westrop (2004) is followed in this paper. Figures illustrate examples of new material recovered during the course of field work.

Subfamily **BUMASTINAE** Raymond, 1916

Genus **FAILLEANA** Chatteron and Ludvigsen, 1976

FAILLEANA ROWLEYI (Foerste, 1920)

Pl. 4, Figs. 1-6

Stratigraphic occurrence.— The species ranges through the entire Kimmswick exposed in the St. Louis region. It was sampled within the lower Kimmswick at Section MM, 26.0 meters and the upper Kimmswick within the 16.5-18.0 meter interval at Section M. Identifiable sclerites were relatively rare, typically occurring within coarse-grained horizons.

Discussion.— Cranidia of *F. rowleyi* are characterized by axial furrows angled inward, followed by a sharp bend towards the anterior suture at approximately 130 degrees. Axial furrows shallows anteriorly, becoming indistinct towards the lunette impressions. Lunette developed close to the anterior suture, deeper adaxially. Specimens are generally exfoliated, but terrace ridge sculpture is well developed in testate sclerites.

Family **STYGINIDAE** Vogdes, 1890

Subfamily **SCUTELLUINAE** Richter and Richter, 1955

Genus **EOBRONTEUS** Reed, 1928

EOBRONTEUS SLOCOMI (Bradley, 1930)

Pl. 4, Figs. 7-9

Stratigraphic occurrence.— Collected from a fine grained facies from Section M, at the 19.0m horizon.

Discussion.— This species is represented only by pygidia that possess five distinct pleural furrows that become shallower towards the lateral margin. The anterior two most pleural furrows merge adaxially near the pygidial axis. Terrace ridge sculpture developed across the entire pygidium.

Order **PHACOPIDA** Salter, 1864

Suborder **CHEIRURINA** Harrington and Leanza, 1957

Family **CHEIRURIDAE** Hawle and Corda, 1847

Subfamily **CHEIRURINAE** Hawle and Corda, 1847

Genus **CERAURUS** Green, 1832

CERAURUS GLOBULOBATUS (Bradley, 1930)

Pl. 5, Figs. 1-9

Stratigraphic occurrence.— Occurs within the Lower Kimmswick at Section MM 24 meters and Section M 5-6 meters. Also collected within the Upper Kimmswick (Mordock) at Section M at 16.5-18.0 and 19 meters, and Section 79-M 1.0m.

Discussion.— *Ceraurus globulobatus* is readily distinguished by the follow characteristics: 1) A long, slender genal spine, 2) A pair of parallel tubercles developed within the raised area of the fixigena, 3) Distinct tubercles along the lateral portions of the anterior suture, 4) Large tubercle development across the glabella.

"CERAURUS" SP. 1

Pl. 6, Figs. 1-8

Stratigraphic occurrence.— Occurs within the Lower Kimmswick at Section MM 24 meters.

Discussion.— This species is differentiated from *C. globulobatus* on the following morphological characteristic: 1) A sharply hooked, broad and flat genal spine, 2) A pygidium with two robust spines, 3) Four smaller spines along the lateral margin of the pygidium that are associated with the pleural ribs.

Genus **WHITTAKERITES** Ludvigsen, 1976

"WHITTAKERITES" SP. NOV

Pl. 6, Figs. 9-14

Stratigraphic occurrence.— Sampled from the 24 meter horizon at Section MM, within the Lower Kimmswick. It also occurs in the Viola Springs Formation of Oklahoma (Amati, 2004).

Discussion.— Material from Missouri and Oklahoma share a distinctive "trapezoidal" anterior border, a relatively straight sided glabella, and a large, broad and flat genal spine. It represents a new species that is related to *Whittakerites* Ludvigsen, 1976 from the Upper Ordovician of northern Canada. However, other species of the genus (e.g., Ludvigsen, 1976, pl. 1, figs. 1-3) have well-rounded, rather than transverse, anterior cranidial margins, so the assignment is tentative.

Genus **CERAURINELLA** Cooper, 1953

CERAURINUS TENUISCULPTA Bradley, 1930

Pl. 7, Figs. 1-4

Stratigraphic occurrence.— Collected from Section B, approximately correlates to the upper Kimmswick (Mordock). The species is also reported from the Viola Springs Formation of Oklahoma in Amati's 2004 dissertation.

Discussion.— The species is rare within the Missouri study region. Sclerites are generally poor in quality, complicating species comparisons. However, we are confident that it is conspecific with material from the Viola Springs Formation of Oklahoma (Amati, 2004).

Subfamily **ENCRINURIDAE** Angelin, 1854

Genus **ENCRINUROIDES** Reed, 1931

"ENCRINUROIDES" SP. 1

Stratigraphic occurrence.— Rare in the lower Kimmswick at Section MM, approximately 24 meters. Bradley reported a pygidium from exposures at Batchtown, Il, which most likely correlate with the upper Kimmswick; however, both an exact stratigraphic correlation or exact stratigraphic horizon for Bradley's sample are uncertain.

Discussion.— Due to the limited quantity and quality of recovered material, no sclerites are illustrated in this paper.

Subfamily **ACANTHOPARYPHINAE** Whittington and Evitt, 1954

Genus **HOLIA** Bradley, 1930

HOLIA MAGNASPINA Bradley, 1930

Pl. 7, Figs. 5-7

Stratigraphic occurrence.— Collected from Section 79-M at the 1.0m interval.

Discussion.— Material recovered from this analysis is limited in both quality and quantity; however the distinct genal spine and short, transvere anterior suture readily distinguish the species.

Subfamily **DEIPHONINAE** Raymond, 1913

Genus **SPHAEROCORYPHE** Angelin, 1854

SPHAEROCORYPE ARACHNIFORMIS (Bradley, 1930)

Pl. 7, Fig. 8

Stratigraphic occurrence.— Collected from the Kimmswick throughout the study region.

Discussion.— The species is rare in the lower Kimmwick, but slightly increases in abundance in the upper Kimmswick (Mordock). Sclerites are often broken and limited to the anterior glabella bulb, complicating detailed comparisons with other species.

Suborder **PHACOPINA** Richter, Richter and Struve, 1959

Superfamily **PHACOPOIDEA** Hawle and Corda, 1847

Family **PTERYGOMETOPIDAE** Reed 1905

Subfamily **EOMONORACHINAE** Pillet, 1954

Genus **CALYPTAULAX** Cooper, 1930

CALYPTAULAX SP. 1

Pl. 8, Figs. 1-11

Stratigraphic occurrence.— Occurs within the upper Kimmswick (Mordock) at Section MM and Section 79-M.

Discussion.— *Calyptaulax sp.* 1 is readily distinguished from "*Calyptaulax*" *sp.* 2 by the following: 1) Relatively straight glabellar furrows, 2) A distinct triangular outline of L3. Material collected by Bradley, 1930 was assigned to the species *C. callicephala*; however it appears unlikely based on new collections from this study that the sclerites are conspecific with the type material of *C. callicephala*.

"CALYPTAULAX" SP. 2

Pl. 8, Fig. 12

Stratigraphic occurrence.— Restricted to the lower Kimmswick intervals at Section MM and Section M.

Discussion.— This species is readily identified based on the following morphological traits: 1) Rounding of glabella lobes along the axial furrow, 2) Fusion of the posterior tip of L3 and the anterior tip of L2; pinching out the S2 furrow. It may also share an affinity with *Eomonorachus*; however, any decision must await comprehensive systematic revision of Subfamily Eomonorachinae as a whole.

Order **LICHIDA**

Subfamily **TETRALICHINAE** Phleger, 1936

Genus **AMPHILICHAS** Raymond, 1906

AMPHILICHAS SP. 1

Pl. 9, Figs. 1-6

Stratigraphic occurrence.— Collected from Section M, at the 19.0m horizon.

Discussion.— Rare, broken Amphilichas sclerites were collected from the lower Kimmswick but were not identifiable to the species level

Subfamily **CERATARGINAE** Tripp, 1957

Genus **HEMIARGES** Gürich, 1901

HEMIARGES LEVICULUS (Bradly, 1930)

Pl. 9, Figs. 7-12

Stratigraphic occurrence.— Occurs within the upper Kimmswick (Mordock) interval at Section 79-M.

Discussion.— *Hemiarges leviculus* is distinguished from *H. paulianus* by: 1) Longer and wider anterior border, 2) Reduced convexity in the fixigena and glabella, 3) Finer sculpture.

HEMIARGES PAULIANAUS (Clarke, 1894)

Pl. 10, Figs. 1-14

Stratigraphic occurrence.— Material is reported across the entire Kimmswick across the study region at Section MM, Section M and Section 79-1.

Discussion.— We follow Rudkin et al. (1994) in considering *H. bartoni* Raymond, 1925, which was reported from the Kimmswick Limestone by Bradley, 1930, to be a junior synonym of *H. paulianus*.

Order **PROETIDA**

Family **PROETIDAE** Salter, 1864

Genus **PARAPROETUS** Pribyl, 1946

PARAPROETUS CANALIS (Bradley, 1930)

Pl. 11, Figs. 1-15

Stratigraphic occurrence.— Ranges throughout the lower and upper Kimmswick across the entire study region at Section MM, Section M, and Section 79-M. Collected extensively from Section M, at 19m, from a fine grained graionstone, where the high abundance of the species may be a product of taphonomic sorting.

Discussion.— The species is distinguished from *Paraproetus sp.* 1 by possession of a longer frontal area that includes a distinct preglabellar field. A wide degree of ontogenetic variation is present within earlier instars including: 1) A longer, narrower glabella; 2) A l distinct S2 glabellar furrow; 3) Distinctly broader anterior border and fixigena.

PARAPROETUS SP. 1

Pl. 11, Figs. 16-18

Stratigraphic occurrence.— Collected from the approximately 24m horizon at Section MM. Though the species is relatively rare within the lower Kimmswick, the genus *Paraproetus* is well sampled within the upper Kimmswick. If the *Paraproetus sp.*1 occurs within the upper Kimmswick, it is likely it would have been collected.

Discussion.— Comparisons with *P. canalis* were presented above.

Family **DIMEROPYGIDAE** Hupé 1953

Genus **DIMEROPYGE** Öpik 1937

DIMEROPYGE TIMIDUS (Bradley, 1930)

Pl. 12, Figs. 1-6

Stratigraphic occurrence.— Sampled from the Mordock at Section M, 16.5-18m. A complete cranidium was reported by Bradley 1930, collected near Batchtown, Il. Bradley's locality likely correlates with the upper Kimmswick of this analysis; however an exact stratigraphic correlation or exact stratigraphic horizon for Bradley's sample is uncertain. Cranidia with the distinctive coarse, tuberculate sculpture are rare in the Viola Springs Formation (Amati, 2004).

Discussion.— Coarse tubercle sculpture and a relatively wide fixigena field distinguish the species.

DIMEROPYGE SP. 1

Pl. 12, Figs. 7-9

Stratigraphic occurrence.— Recorded at Section 79-M, approximately 0.5m.

Discussion.— Though material is exfoliated, it appears that the fixigena field is distinctly narrower than in *Dimeropyge timidus*.

Family **AULACOPLEURIDAE** Angelin 1854

Subfamily **OTARIONINAE** Richter and Richter 1926

Genus **HARPIDELLA** M'Coy 1849

HARPIDELLA GLOBOSUS (Bradley, 1930)

Pl. 12, Figs. 10-15

Stratigraphic occurrence.— Rare in the upper Kimmswick at Section M, 16.5 meters, within the "coarse facies".

Discussion.—The identification is based on direct comparison with Bradley's (1930) types.

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CHAPTER 6 APPENDIX. FIGURES AND PLATES

Raymondaties missouriensis
Whitikerities sp.
"Cerarus" sp.1
"Calyptaulax" sp. 2
Paraproetus sp. 1
"Encrinuroides" sp. 1
Isoteius bradleyi
Ceraurus globulobatus
Isoteius kimmswickensis
Bumastoides kimmswickensis
Paraproetus canalis
Hemiarges paulianus
Sphaerocorypke arachniformis
Failleana rowleyi
Thaleops dpressicapita
Eobronteus slocomi
Ceraurinus tenuisculpta
Holia magnaspina
Amphilichas sp. 1
Hemiarges levicuius
Dimeropyge timidus
Dimeropyge sp. 1
Harpidella globosus
Flexicalymene kimmswickensis
Achatella katherina
Hypodicranotus missouriensis
Calyptaulax sp. 1
Lower Kimmswick
Mordock
H
MM 26m
M 5-6m
MM 24m
79-M ?
M 19m
M 16.5-18m

Figure 1.— Stratigraphic range of sampled trilobite species from the Kimmswick Limestone in the Missouri study region. Samples are divided into two groups the Lower Kimmswick and the Mordock (Upper Kimmswick). Black rectangles indicate well sampled species with relatively confindent stratigraphic range assignments. Gray rectangles indicate rare species that may have incomplete stratigraphic ranges.

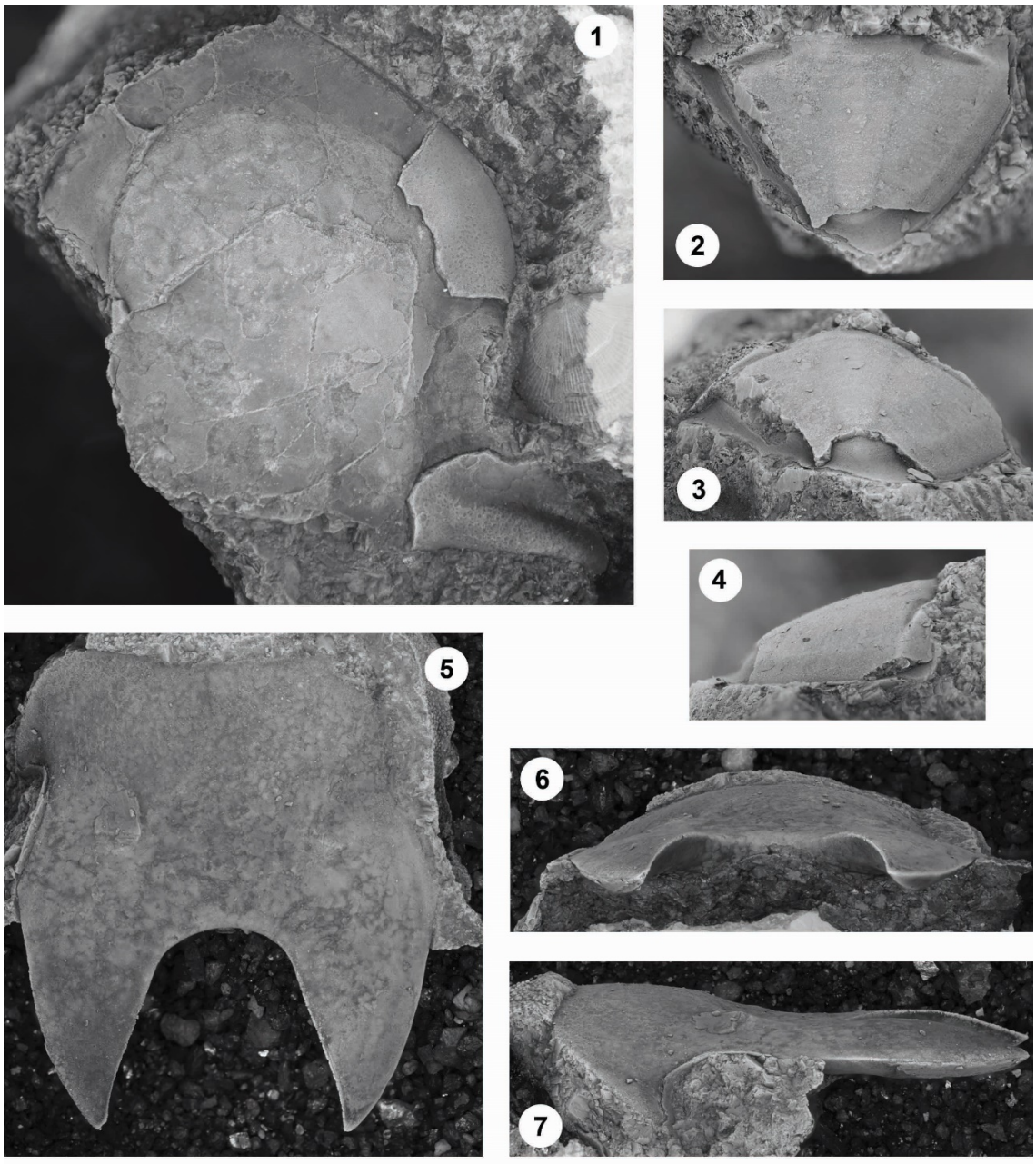
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Plate 1 *Isotelus kimmswickensis*

1-7 *Isotelus kimmswickensis*

1. OU 222786 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, dorsal view x4
2. OU 222787 (79-M 1.0m) nearly complete, exfoliated pygidium, dorsal view, x4
3. OU 222787 (79-M 1.0m) nearly complete, exfoliated pygidium, posterior view, x4
4. OU 222787 (79-M 1.0m) nearly complete, exfoliated pygidium, lateral view, x4
5. OU 222788 (79-M 1.0m) complete, exfoliated hypostome, dorsal view, x3
6. OU 222788 (79-M 1.0m) complete, exfoliated hypostome, posterior view, x3
7. OU 222788 (79-M 1.0m) complete, exfoliated hypostome, lateral view, x3

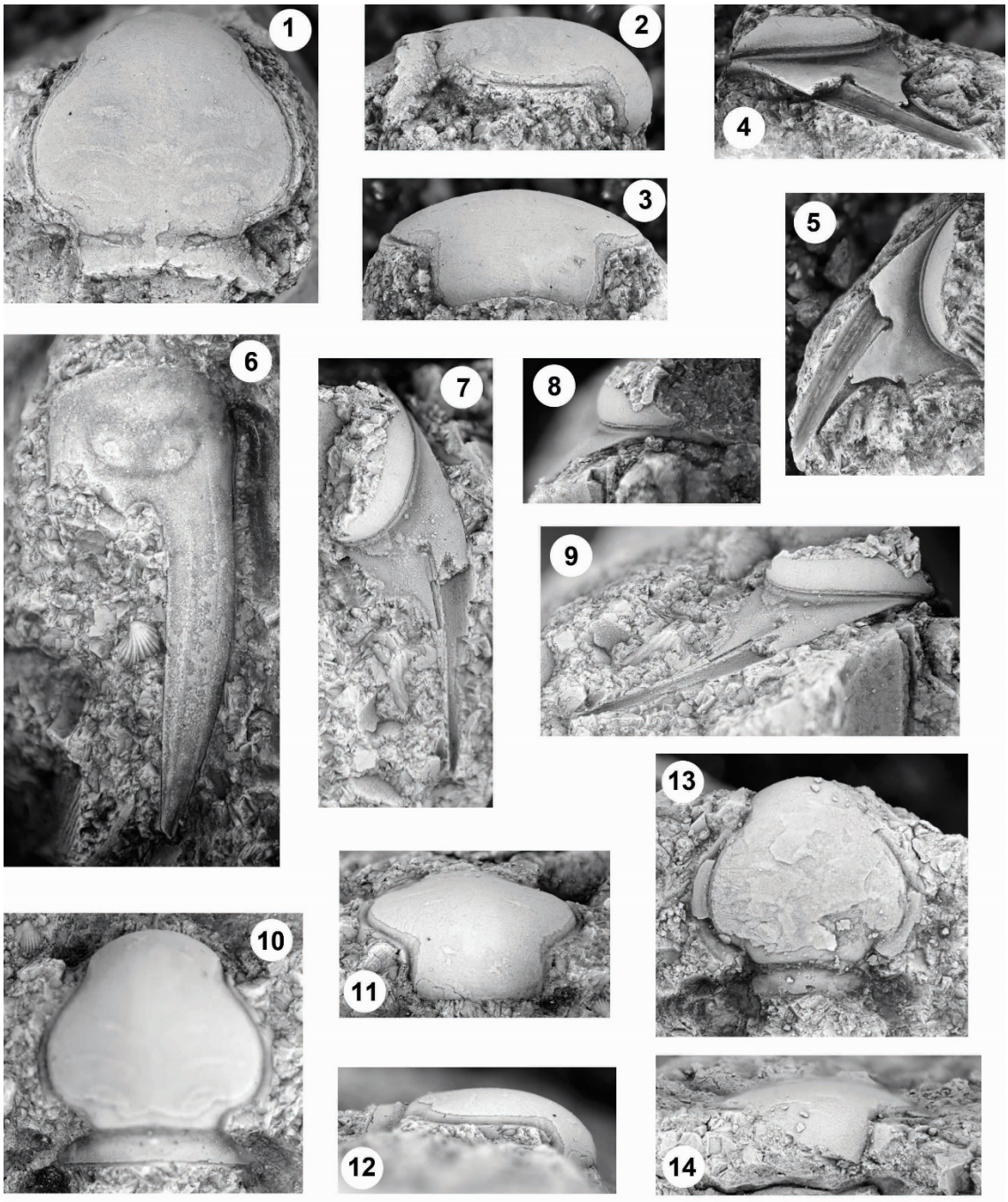
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Plate 2 *Hypodicranotus missouriensis*

1-14 *Hypodicranotus missouriensis*

1. UC28906a nearly complete, exfoliated cranidium, dorsal view x4.5
2. UC28906a nearly complete, exfoliated cranidium, lateral view, x4.5
3. UC28906a nearly complete, exfoliated cranidium, anterior view, x4.5
4. UC28906b partial librigena with visual surface, lateral view, x4.5
5. UC28906b partial librigena with visual surface, dorsal view, x4.5
6. OU 222789 (79-M 1.0m) nearly complete, exfoliated hypostome, dorsal view, x4.5
7. OU 222790 (79-M 1.0m) nearly complete, exfoliated librigena with visual surface, dorsal view, x5
8. OU 222790 (79-M 1.0m) nearly complete, exfoliated librigena with visual surface, anterior view, x5
9. OU 222790 (79-M 1.0m) nearly complete, exfoliated librigena with visual surface, lateral view, x5
10. OU 222791 (79-M 1.0m) nearly complete, exfoliated cranidium, dorsal view, x5
11. OU 222791 (79-M 1.0m) nearly complete, exfoliated cranidium, anterior view, x5
12. OU 222791 (79-M 1.0m) nearly complete, exfoliated cranidium, lateral view, x5
13. OU 222792 (79-M 1.0m) nearly complete, exfoliated cranidium, dorsal view, x7

14. OU 222792 (79-M 1.0m) nearly complete, exfoliated cranidium, anterior view, x7

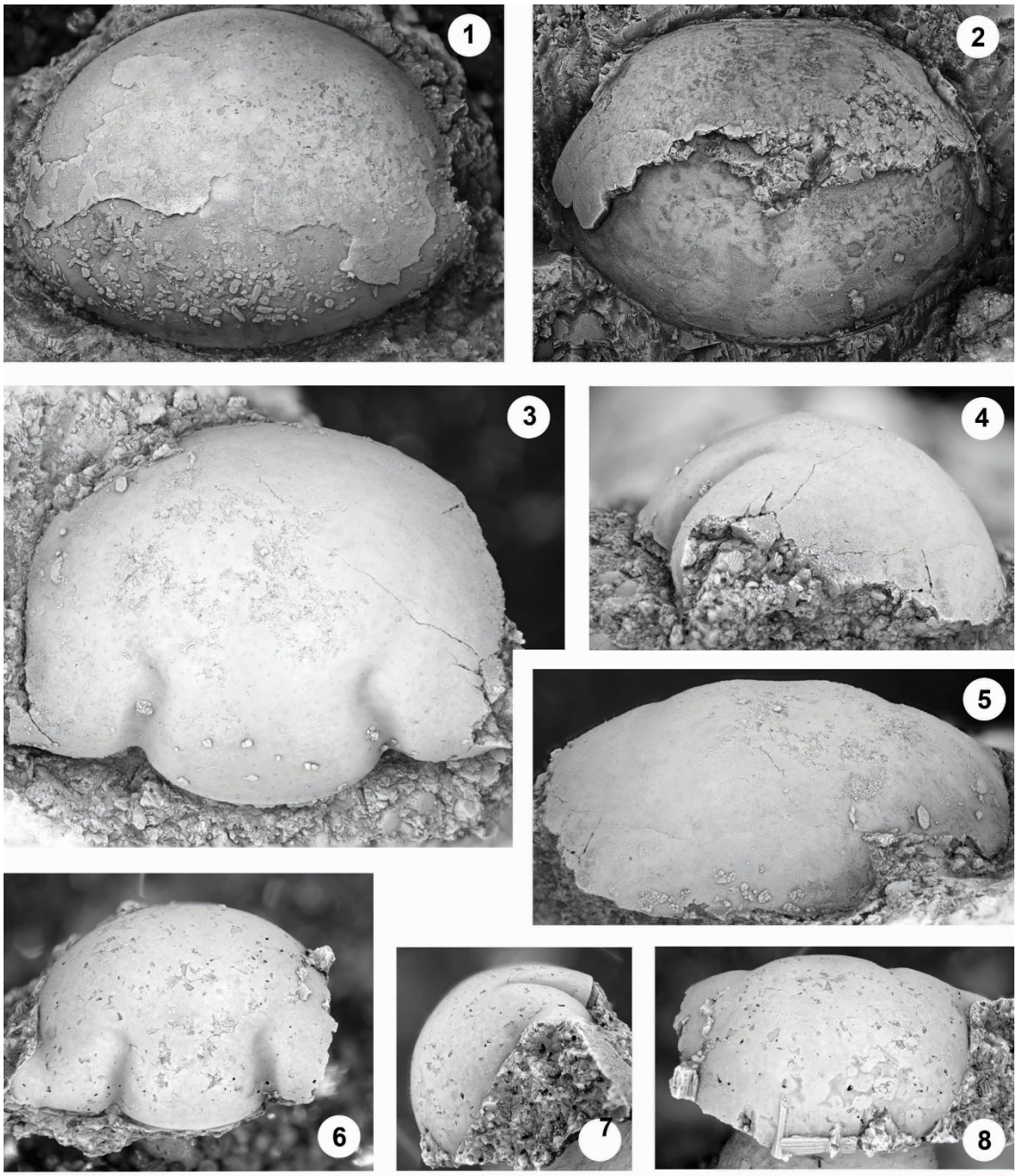
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Plate 3 *Bumastoides kimmswickensis*, *Thaleops depressicapitata*

1-2 *Bumastoides kimmswickensis*

1. OU 222793 (M 16.5-18.0m) nearly complete, mostly exfoliated cranidium, dorsal view x7
2. OU 222794 (MM 24.0m) nearly complete, exfoliated pygidium, dorsal view x7

3-8 *Thaleops depressicapitata*

3. OU 222795 (M 16.5-18.0m) nearly complete, exfoliated cranidium, dorsal view x3.5
4. OU 222795 (M 16.5-18.0m) nearly complete, exfoliated cranidium, lateral view x3.5
5. OU 222795 (M 16.5-18.0m) nearly complete, exfoliated cranidium, anterior view x3.5
6. OU 222796 (M 16.5-18.0m) nearly complete, exfoliated cranidium, dorsal view x3.5
7. OU 222796 (M 16.5-18.0m) nearly complete, exfoliated cranidium, lateral view x3.5
8. OU 222796 (M 16.5-18.0m) nearly complete, exfoliated cranidium, anterior view x3.5


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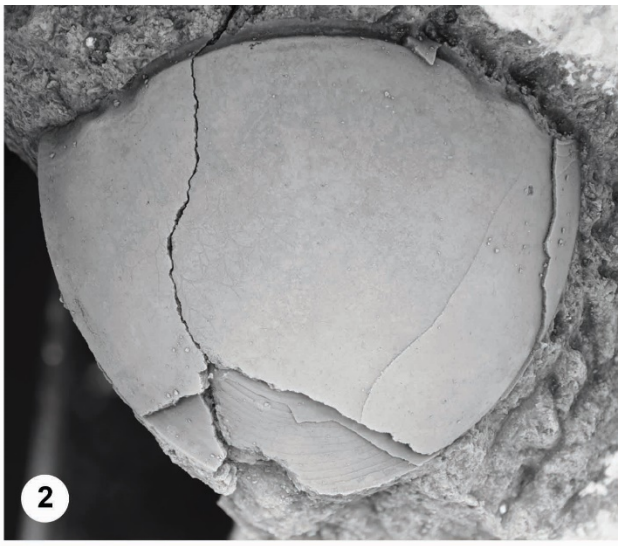
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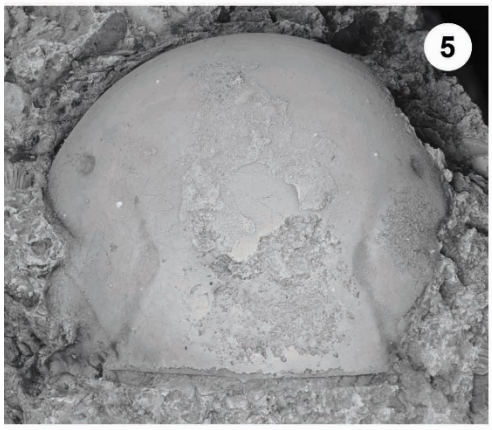
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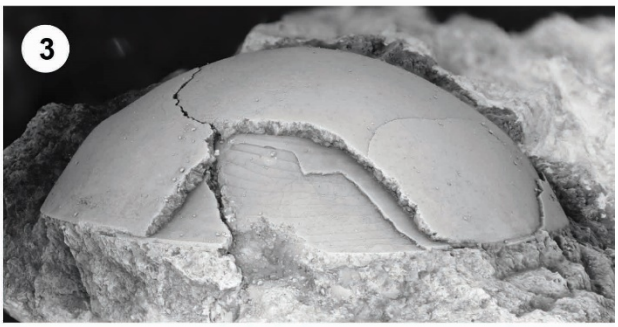
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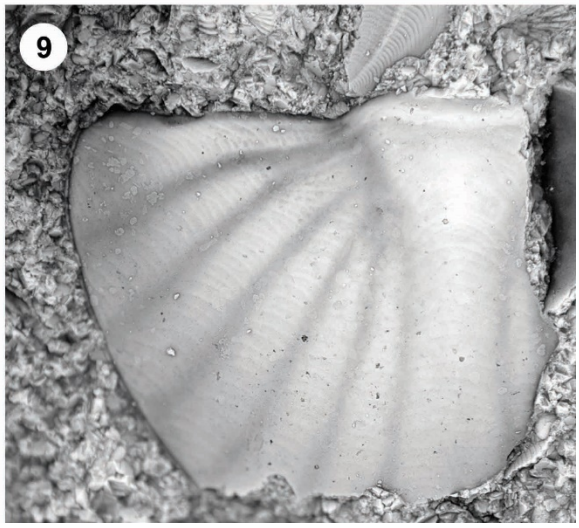
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Plate 4 *Failleana rowleyi*, *Eobronteus slocomi*

1-6 *Failleana rowleyi*

1. OU 222797 (M 16.5-18.0m) nearly complete, mostly exfoliated pygidium, lateral view x2
2. OU 222797 (M 16.5-18.0m) nearly complete, mostly exfoliated pygidium, dorsal view x2
3. OU 222797 (M 16.5-18.0m) nearly complete, mostly exfoliated pygidium, posterior view x2
4. OU 222798 (M 16.5-18.0m) nearly complete, exfoliated cranidium, lateral view x2
5. OU 222798 (M 16.5-18.0m) nearly complete, exfoliated cranidium, dorsal view x2
6. OU 222798 (M 16.5-18.0m) nearly complete, exfoliated cranidium, anterior view x2

7-9 Eobronteus slocomi

7. OU 222799 (M 19.0m) partial pygidium, posterior view x5
8. OU 222799 (M 19.0m) partial pygidium, lateral view x5
9. OU 222799 (M 19.0m) partial pygidium, dorsal view x5

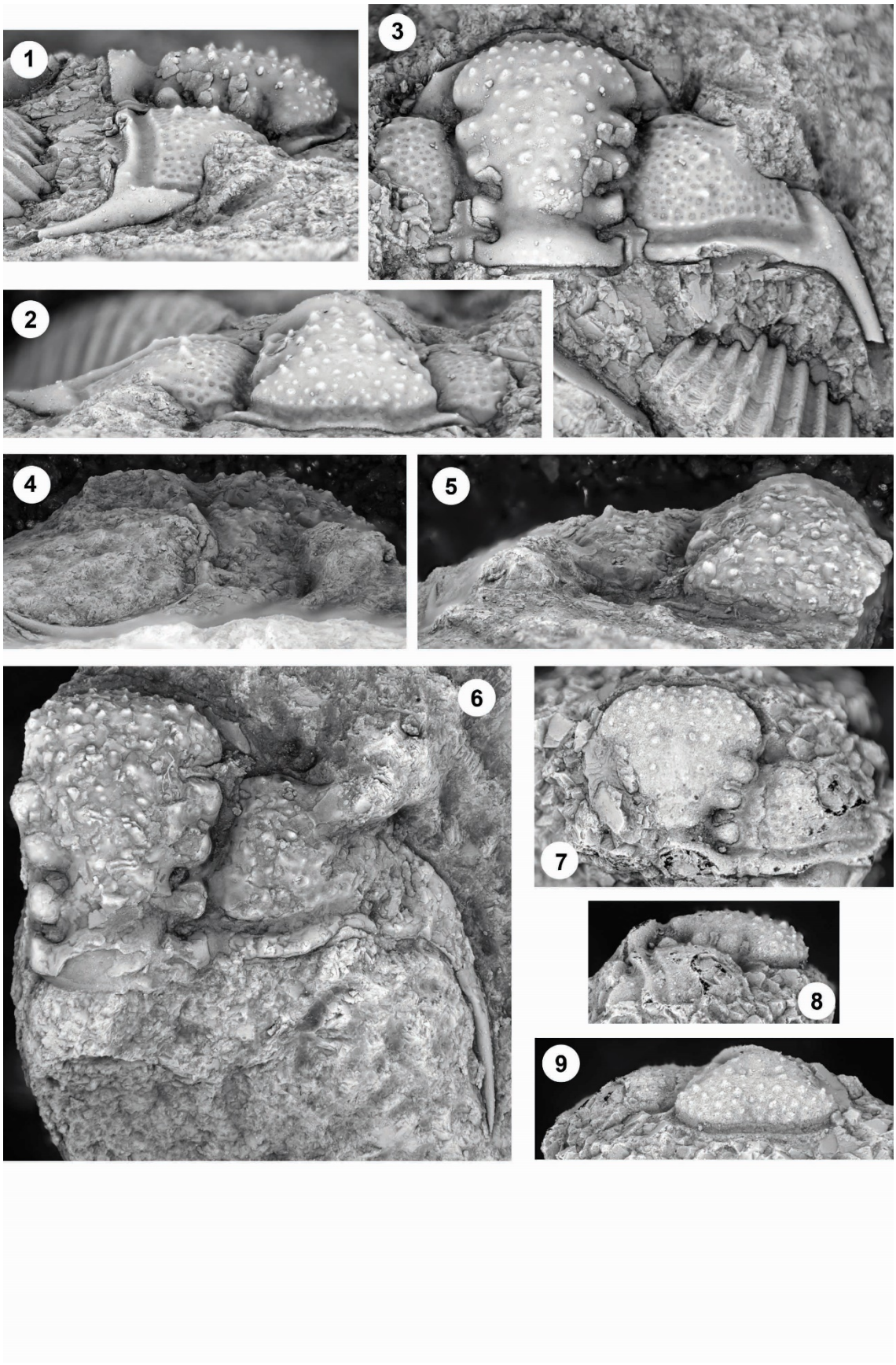
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Plate 5 *Ceraurus globulobatus*

1-9 *Ceraurus globulobatus*

1. OU 222800 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
2. OU 222800 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, anterior view x5
3. OU 222800 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5
4. OU 222801 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
5. OU 222801 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, anterior view x5
6. OU 222801 (79-M 1.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5
7. OU 222802 (MM 24.0m) partial, mostly exfoliated cranidium, dorsal view x6
8. OU 222802 (MM 24.0m) partial, mostly exfoliated cranidium, lateral view x6
9. OU 222802 (MM 24.0m) partial, mostly exfoliated cranidium, anterior view x6

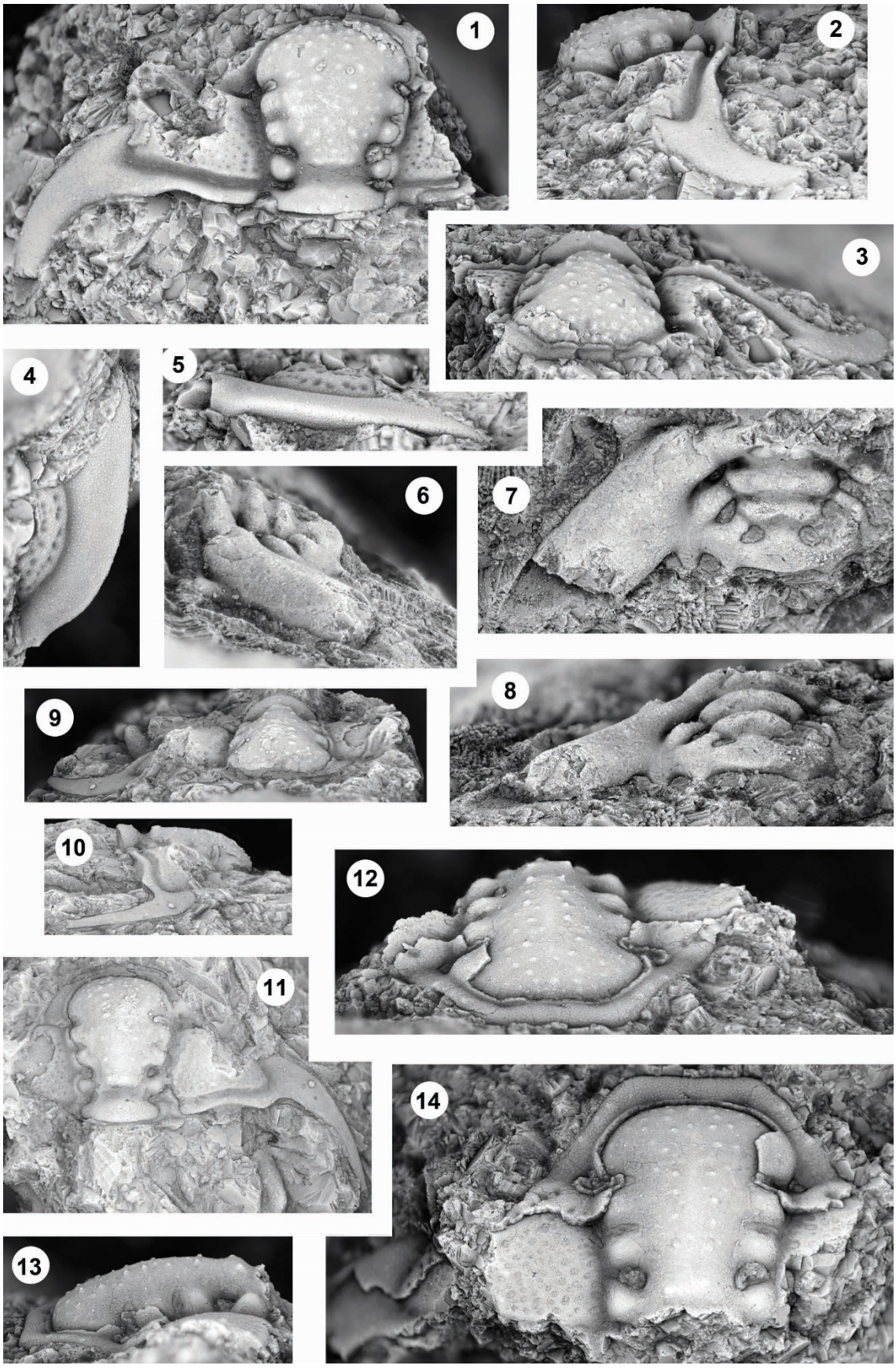
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Plate 6 *"Ceraurus" sp.1, "Whittakerites" sp.*

1-8 *"Ceraurus" sp.1*

1. OU 222803 (MM 24.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5
2. OU 222803 (MM 24.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
3. OU 222803 (MM 24.0m) nearly complete, mostly exfoliated cranidium, anterior view x5
4. OU 222804 (MM 24.0m) nearly complete librigena, dorsal view x5
5. OU 222804 (MM 24.0m) nearly complete librigena, lateral view x5
6. OU 222805 (MM 24.0m) partial, exfoliated pygidium, lateral view x5
7. OU 222805 (MM 24.0m) partial, exfoliated pygidium, dorsal view x5
8. OU 222805 (MM 24.0m) partial, exfoliated pygidium, anterior view x5

9-14 *"Whittakerites" sp.*

9. OU 222806 (MM 24.0m) nearly complete, mostly exfoliated cranidium, anterior view x5
10. OU 222806 (MM 24.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
11. OU 222806 (MM 24.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5
12. OU 222807 (MM 24.0m) nearly complete, mostly exfoliated cranidium, anterior view x5

13. OU 222807 (MM 24.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
14. OU 222807 (MM 24.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5

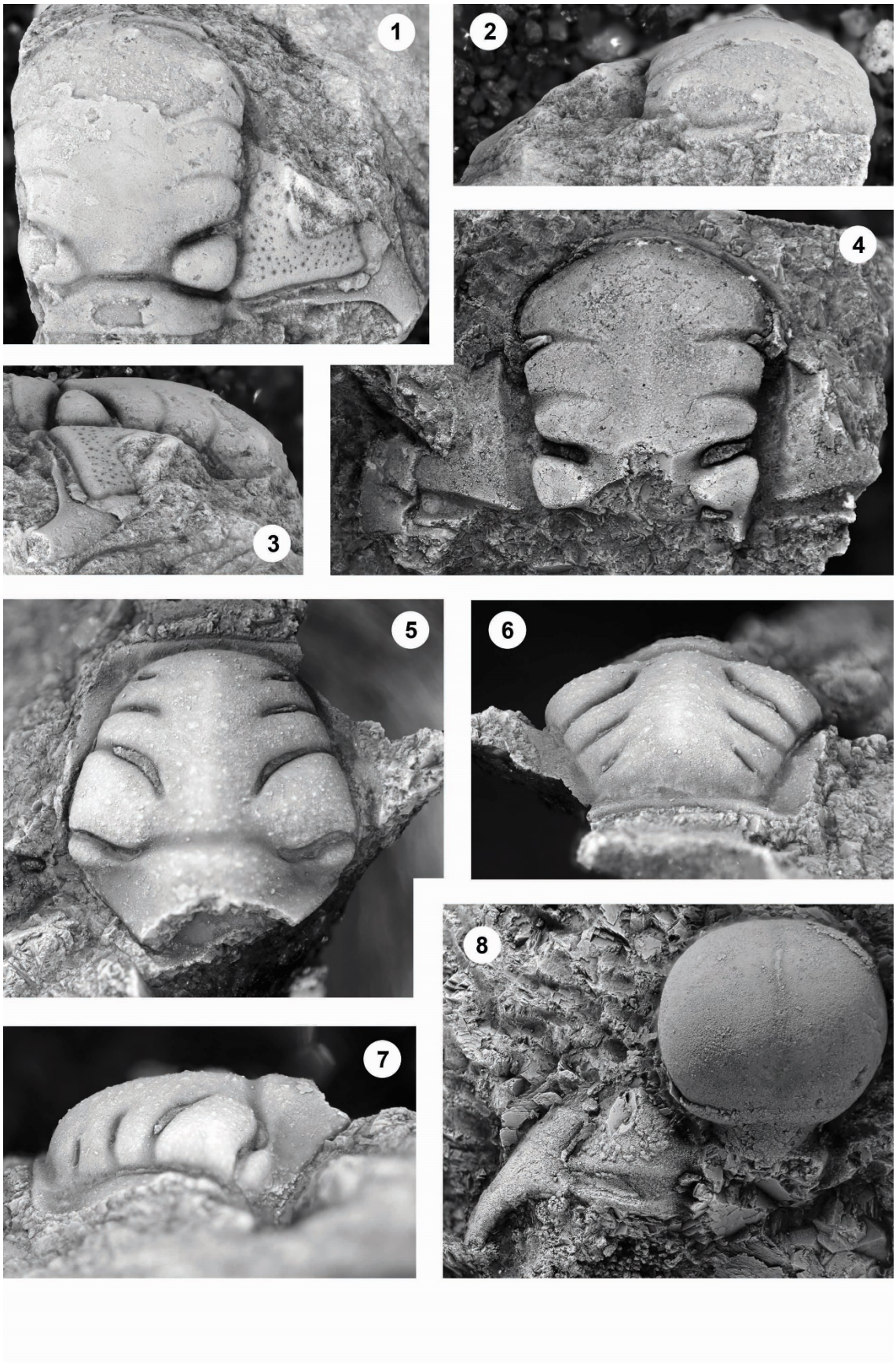
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Plate 7 *Ceraurinus tenuisculpta, Holia magnaspina, Sphaerocorype arachniformis*

1-4 *Ceraurinus tenuisculpta*

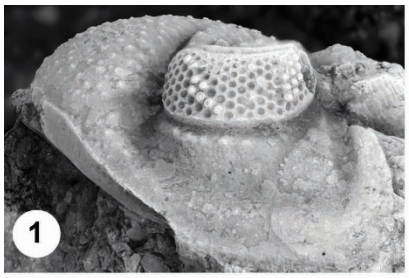
1. UC20691 nearly complete, mostly exfoliated cranidium, dorsal view x5
2. UC20691 nearly complete, mostly exfoliated cranidium, anterior view x5
3. UC20691 nearly complete, mostly exfoliated cranidium, lateral view x5
4. OU 222808 (SB 1.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5

5-7 *Holia magnaspina*

5. OU 222809 (79-M 1.0m) nearly complete, exfoliated cranidium, dorsal view x5
6. OU 222809 (79-M 1.0m) nearly complete, exfoliated cranidium, anterior view x5
7. OU 222809 (79-M 1.0m) nearly complete, exfoliated cranidium, lateral view x5

8 *Sphaerocorype arachniformis*

8. OU 222810 (79-M 1.0m) partial, mostly exfoliated cranidium, dorsal view x8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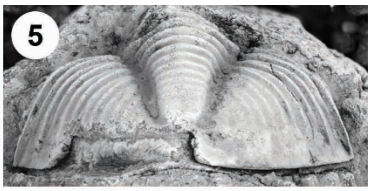
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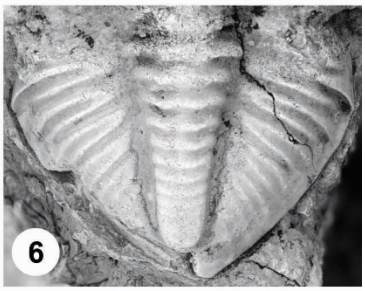
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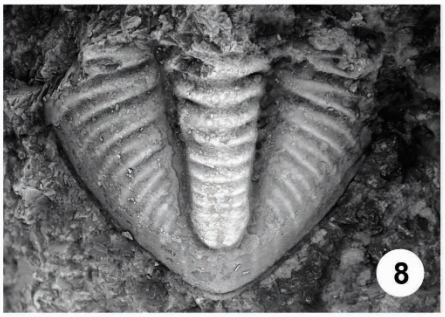
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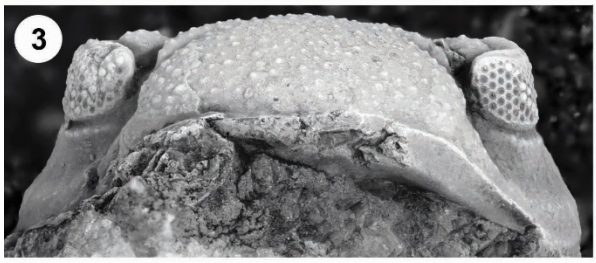
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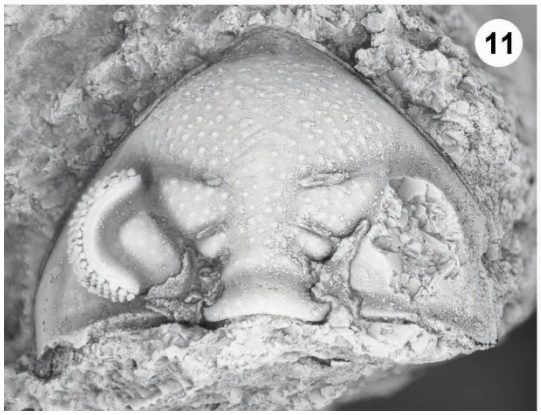
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Plate 8 *Calyptaulax sp. 1*, *"Calyptaulax" sp. 2*

1-5 *Calyptaulax sp. 1*

1. UC28920 nearly complete, mostly exfoliated cranidium, lateral view x4.5
2. UC28920 nearly complete, mostly exfoliated cranidium, dorsal view x4.5
3. UC28920 nearly complete, mostly exfoliated cranidium, anterior view x4.5
4. UC28920 nearly complete, mostly exfoliated pygidium, lateral view x4.5
5. UC28920 nearly complete, mostly exfoliated pygidium, posterior view x4.5
6. UC28920 nearly complete, mostly exfoliated pygidium, dorsal view x4.5
7. OU 222811 (79-M 1.0m) nearly complete, mostly exfoliated pygidium, lateral view x5
8. OU 222811 (79-M 1.0m) nearly complete, mostly exfoliated pygidium, dorsal view x5
9. OU 222812 (M 16.5-18.0m) nearly complete, mostly exfoliated cranidium, lateral view x5
10. OU 222812 (M 16.5-18.0m) nearly complete, mostly exfoliated cranidium, anterior view x5
11. OU 222812 (M 16.5-18.0m) nearly complete, mostly exfoliated cranidium, dorsal view x5

12 *"Calyptaulax" sp. 2*

12. OU 222813 (MM 24.0m) partial, exfoliated cranidium, dorsal view x8

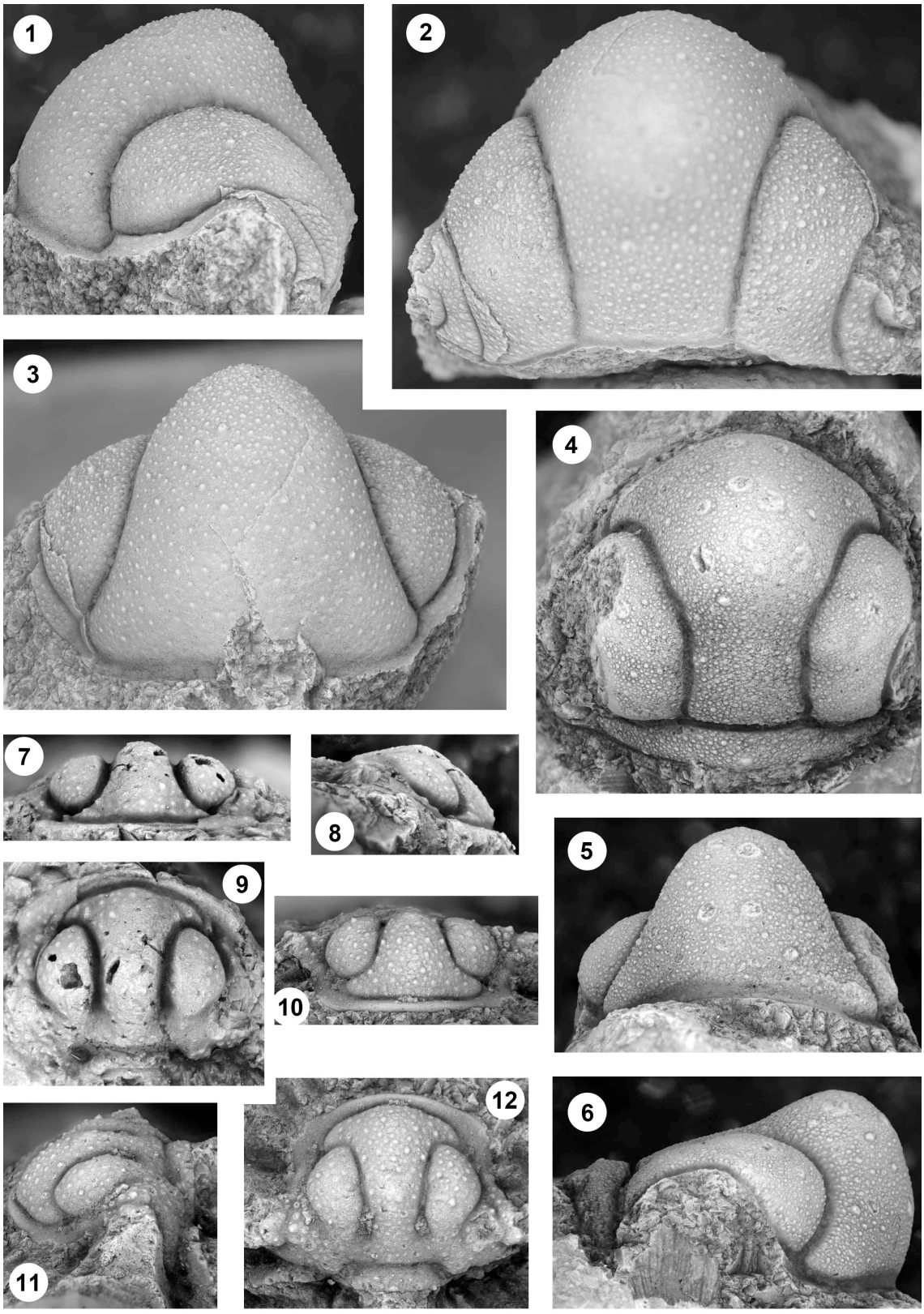
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Plate 9 *Amphilichas sp. 1*, *Hemiarges leviculus*

1-6 *Amphilichas sp. 1*

1. OU 222814 (M 19.0m) nearly complete, mostly exfoliated cranidium, lateral view x3.5
2. OU 222814 (M 19.0m) nearly complete, mostly exfoliated cranidium, dorsal view x3.5
3. OU 222814 (M 19.0m) nearly complete, mostly exfoliated cranidium, anterior view x3.5
4. UC20675a nearly complete, exfoliated cranidium, dorsal view x3.5
5. UC20675a nearly complete, exfoliated cranidium, anterior view x3.5
6. UC20675a nearly complete, exfoliated cranidium, lateral view x3.5

7-12 *Hemiarges leviculus*

7. UC28942 nearly complete, partially exfoliated cranidium, anterior view x8
8. UC28942 nearly complete, partially exfoliated cranidium, lateral view x8
9. UC28942 nearly complete, partially exfoliated cranidium, dorsal view x8
10. OU 222815 (79-M 1.0m) nearly complete cranidium, anterior view x7
11. OU 222815 (79-M 1.0m) nearly complete cranidium, lateral view x7
12. OU 222815 (79-M 1.0m) nearly complete cranidium, dorsal view x7

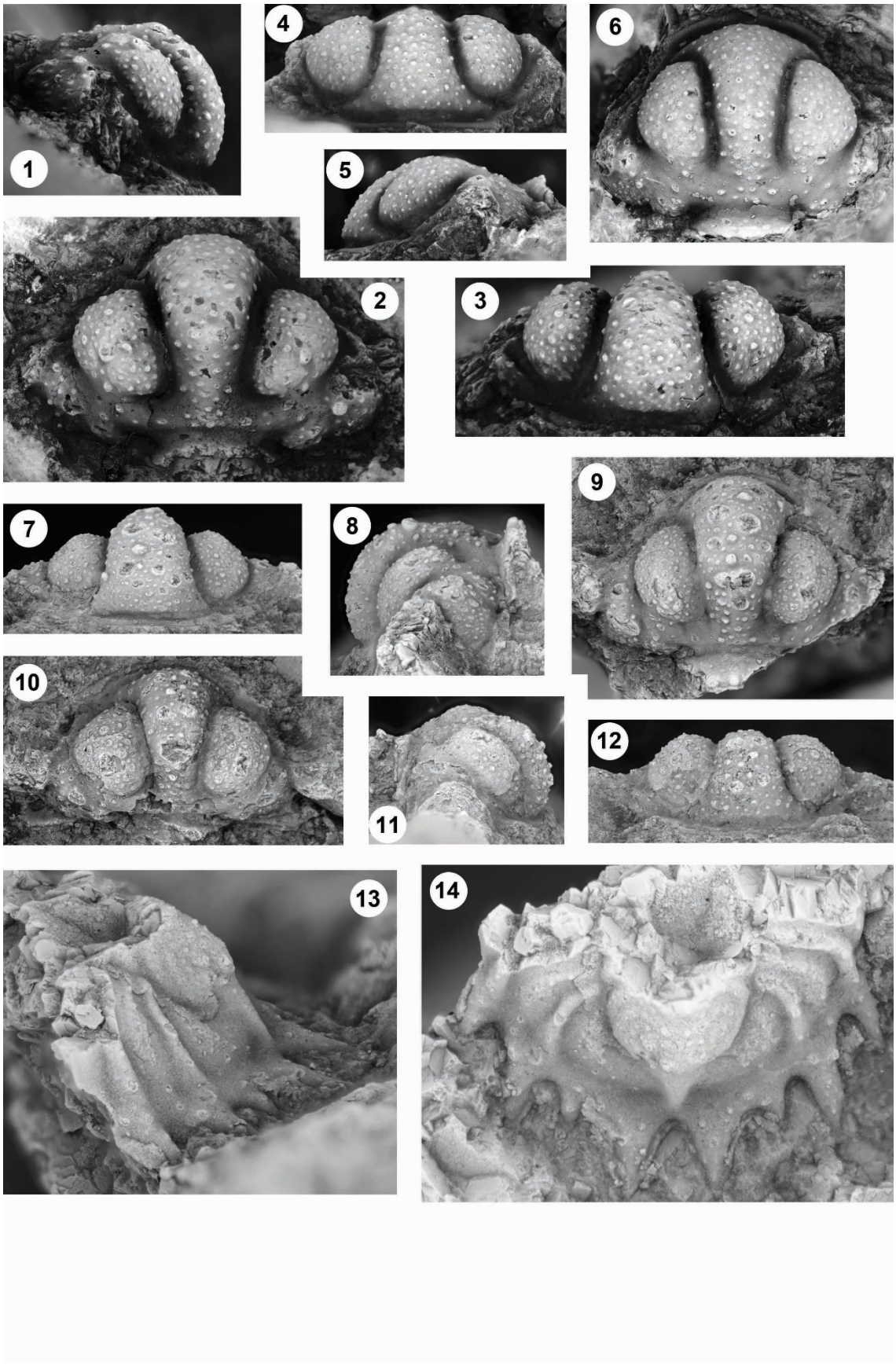
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Plate 10 *Hemiarges paulianus*

1-14 *Hemiarges paulianus*

1. UC28935 nearly complete cranidium, lateral view x8
2. UC28935 nearly complete cranidium, dorsal view x8
3. UC28935 nearly complete cranidium, anterior view x8
4. UC20716 nearly complete cranidium, anterior view x8
5. UC20716 nearly complete cranidium, lateral view x8
6. UC20716 nearly complete cranidium, dorsal view x8
7. OU 222816 (79-M 1.0m) nearly complete cranidium, anterior view x8
8. OU 222816 (79-M 1.0m) nearly complete cranidium, lateral view x8
9. OU 222816 (79-M 1.0m) nearly complete cranidium, dorsal view x8
10. OU 222817 (79-M 1.0m) nearly complete cranidium, anterior view x8
11. OU 222817 (79-M 1.0m) nearly complete cranidium, lateral view x8
12. OU 222817 (79-M 1.0m) nearly complete cranidium, dorsal view x8
13. OU 222818 (MM 24.0m) partial pygidium, mostly exfoliated, lateral view x10
14. OU 222818 (MM 24.0m) partial pygidium, mostly exfoliated, dorsal view x10

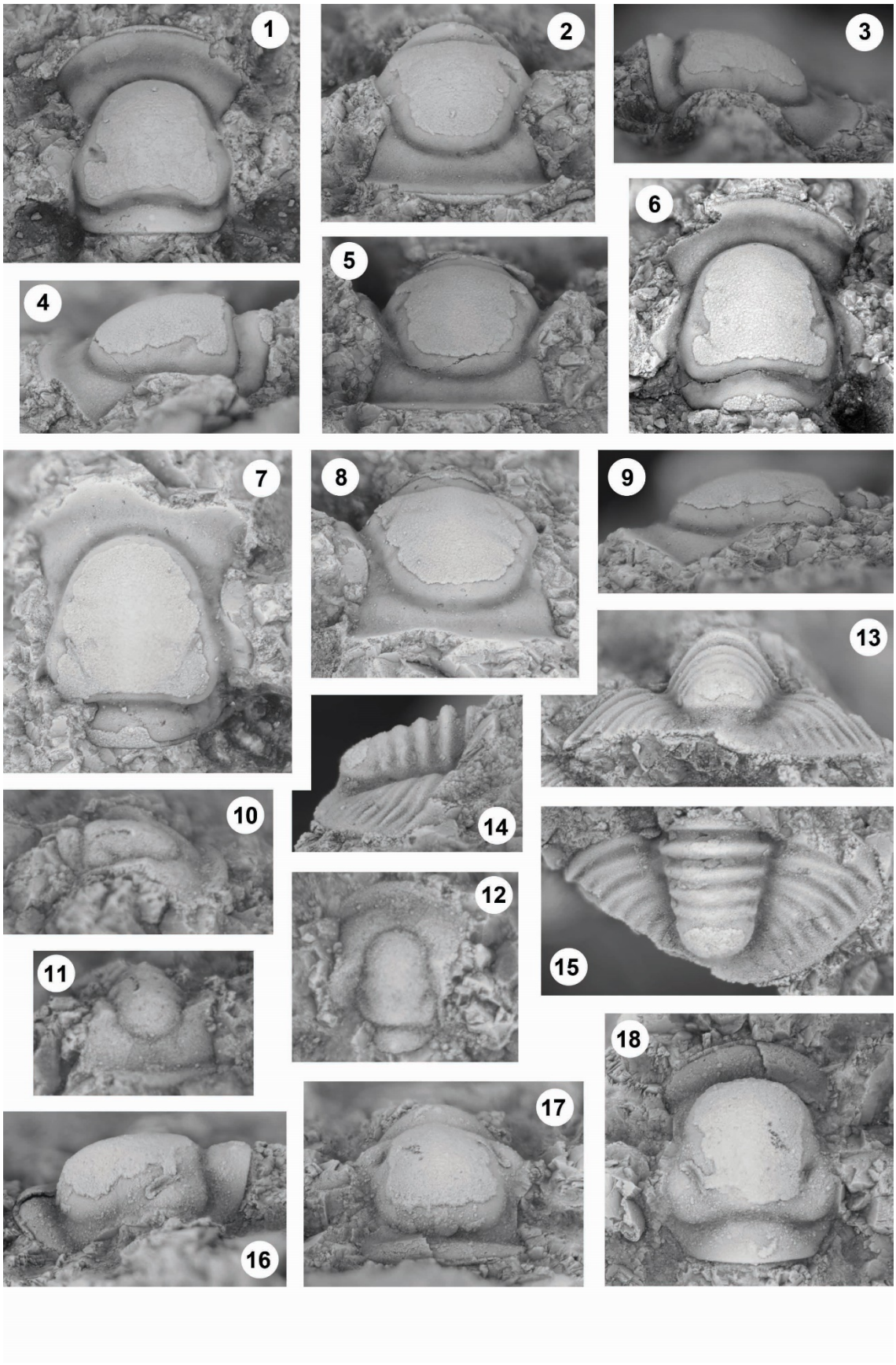
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Plate 11 *Paraproetus canalis*, *Paraproetus sp. 1*

1-15 *Paraproetus canalis*

1. OU 222819 (M 19.0m) nearly complete, mostly exfoliated cranidium, dorsal view x10
2. OU 222819 (M 19.0m) nearly complete, mostly exfoliated cranidium, anterior view x10
3. OU 222819 (M 19.0m) nearly complete, mostly exfoliated cranidium, lateral view x10
4. OU 222820 (M 19.0m) nearly complete, mostly exfoliated cranidium, lateral view x10
5. OU 222820 (M 19.0m) nearly complete, mostly exfoliated cranidium, anterior view x10
6. OU 222820 (M 19.0m) nearly complete, mostly exfoliated cranidium, dorsal view x10
7. OU 222821 (M 19.0m) nearly complete, mostly exfoliated cranidium, dorsal view x10
8. OU 222821 (M 19.0m) nearly complete, mostly exfoliated cranidium, anterior view x10
9. OU 222821 (M 19.0m) nearly complete, mostly exfoliated cranidium, lateral view x10
10. OU 222822 (M 19.0m) nearly complete, exfoliated cranidium, lateral view x25

11. OU 222822 (M 19.0m) nearly complete, exfoliated cranidium, anterior view x25
12. OU 222822 (M 19.0m) nearly complete, exfoliated cranidium, dorsal view x25
13. OU 222823 (M 19.0m) nearly complete, exfoliated pygidium, posterior view x15
14. OU 222823 (M 19.0m) nearly complete, exfoliated pygidium, lateral view x15
15. OU 222823 (M 19.0m) nearly complete, exfoliated pygidium, dorsal view x15

16-18 *Paraproetus sp. 1*

16. OU 222824 (MM 24.0m) nearly complete, mostly exfoliated cranidium, lateral view x10
17. OU 222824 (MM 24.0m) nearly complete, mostly exfoliated cranidium, anterior view x10
18. OU 222824 (MM 24.0m) nearly complete, mostly exfoliated cranidium, dorsal view x10

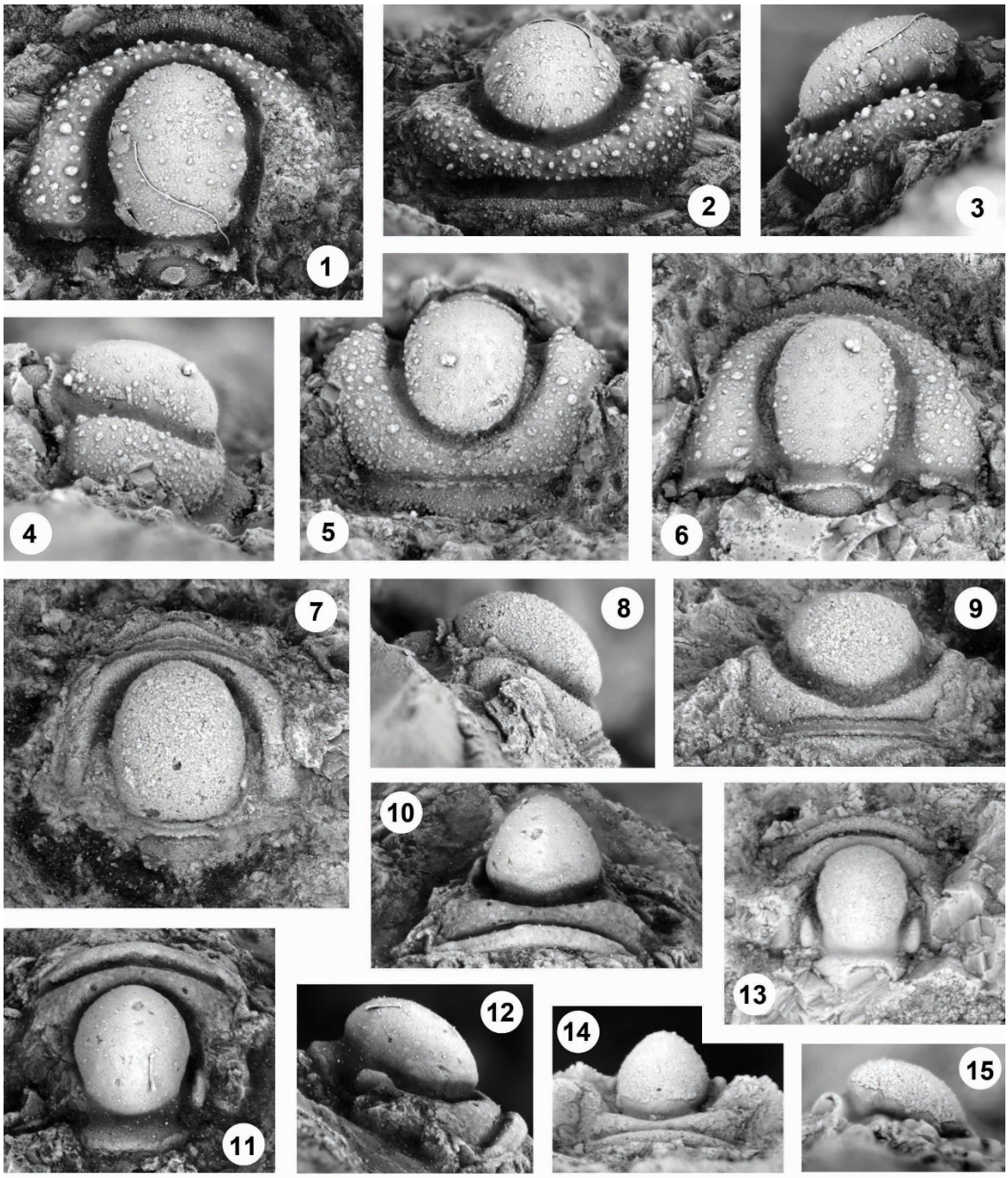
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Plate 12 *Dimeropyge timidus*, *Dimeropgye sp. 1*, *Harpidella globosus*

1-6 *Dimeropyge timidus*

1. UC28916 nearly complete cranidium, dorsal view x12
2. UC28916 nearly complete cranidium, anterior view x12
3. UC28916 nearly complete cranidium, lateral view x12
4. OU 222825 (M 16.5-18.0m) nearly complete cranidium, lateral view x12
5. OU 222825 (M 16.5-18.0m) nearly complete cranidium, anterior view x12
6. OU 222825 (M 16.5-18.0m) nearly complete cranidium, dorsal view x12

7-9 *Dimeropyge sp. 1*

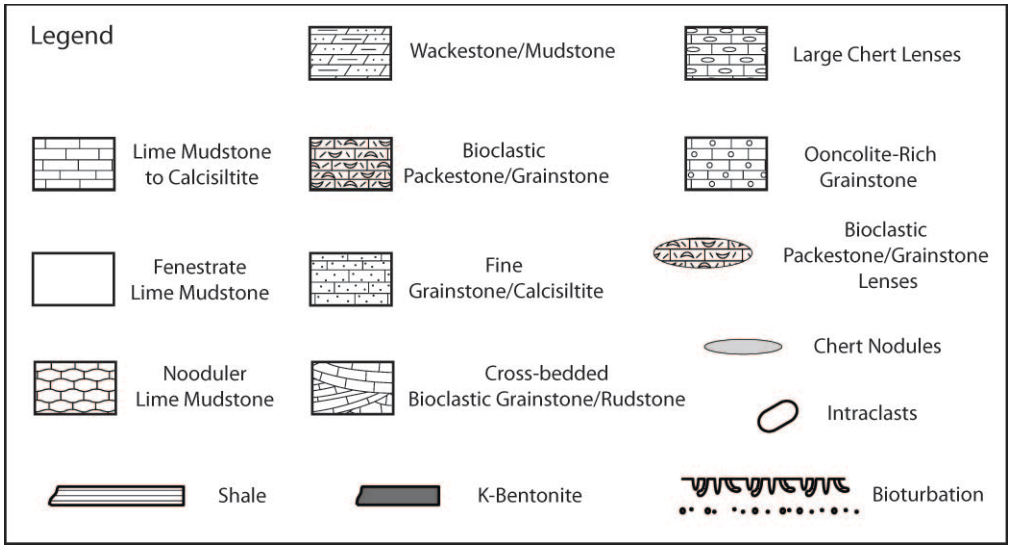
7. OU 222826 (79-M 0.5m) nearly complete cranidium, dorsal view x12
8. OU 222826 (79-M 0.5m) nearly complete cranidium, lateral view x12
9. OU 222826 (79-M 0.5m) nearly complete cranidium, anterior view x12

10-15 *Harpidella globosus*

10. UC20679 nearly complete cranidium, anterior view x15
11. UC20679 nearly complete cranidium, dorsal view x15
12. UC20679 nearly complete cranidium, lateral view x15
13. OU 222827 (M 16.5m “Coarse Facies”) nearly complete, mostly exfoliated cranidium, dorsal view x15
14. OU 222827 (M 16.5m “Coarse Facies”) nearly complete, mostly exfoliated cranidium, anterior view x15
15. OU 222827 (M 16.5m “Coarse Facies”) nearly complete, mostly exfoliated cranidium, lateral view x15

Appendix 1: Stratigraphic Columns

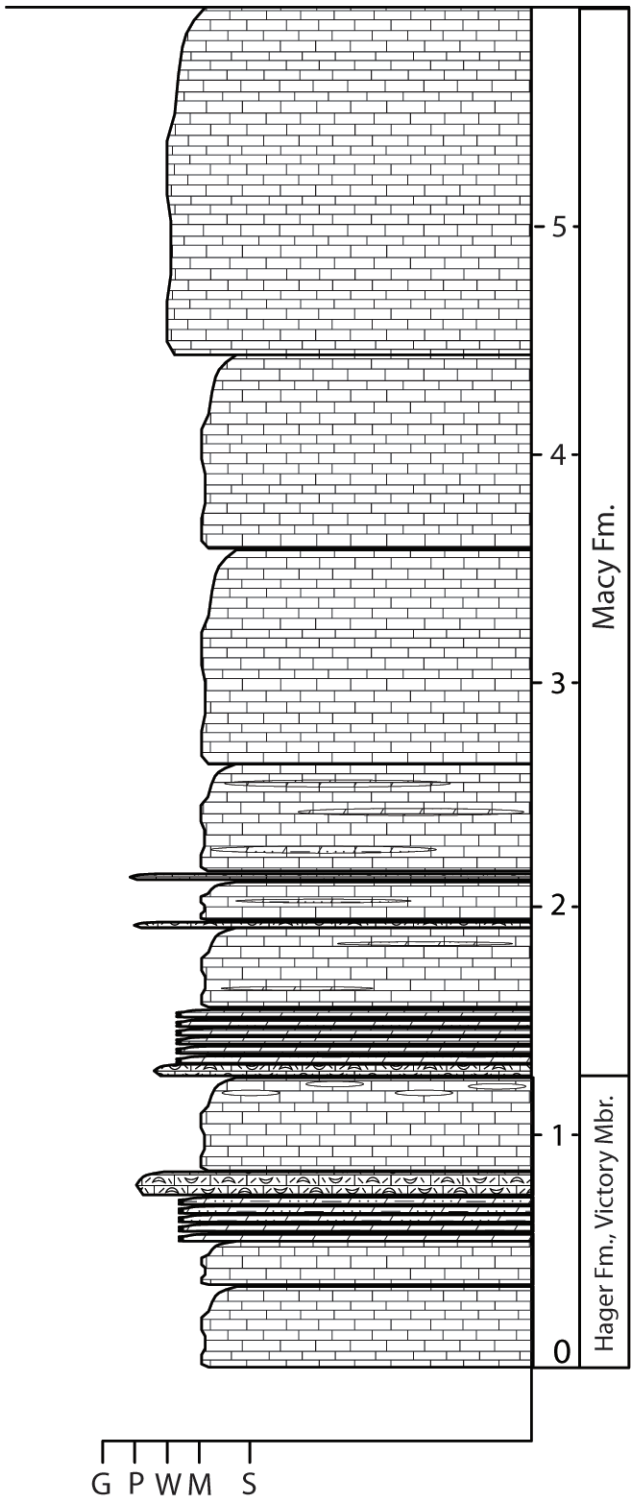
Appendix 1 illustrates detailed lithostratigraphic sections measured over the course of this study. Sections are present in approximately 5 meter intervals. Oldest strata appear on the first page for each section, with younger strata presented on each subsequent page.



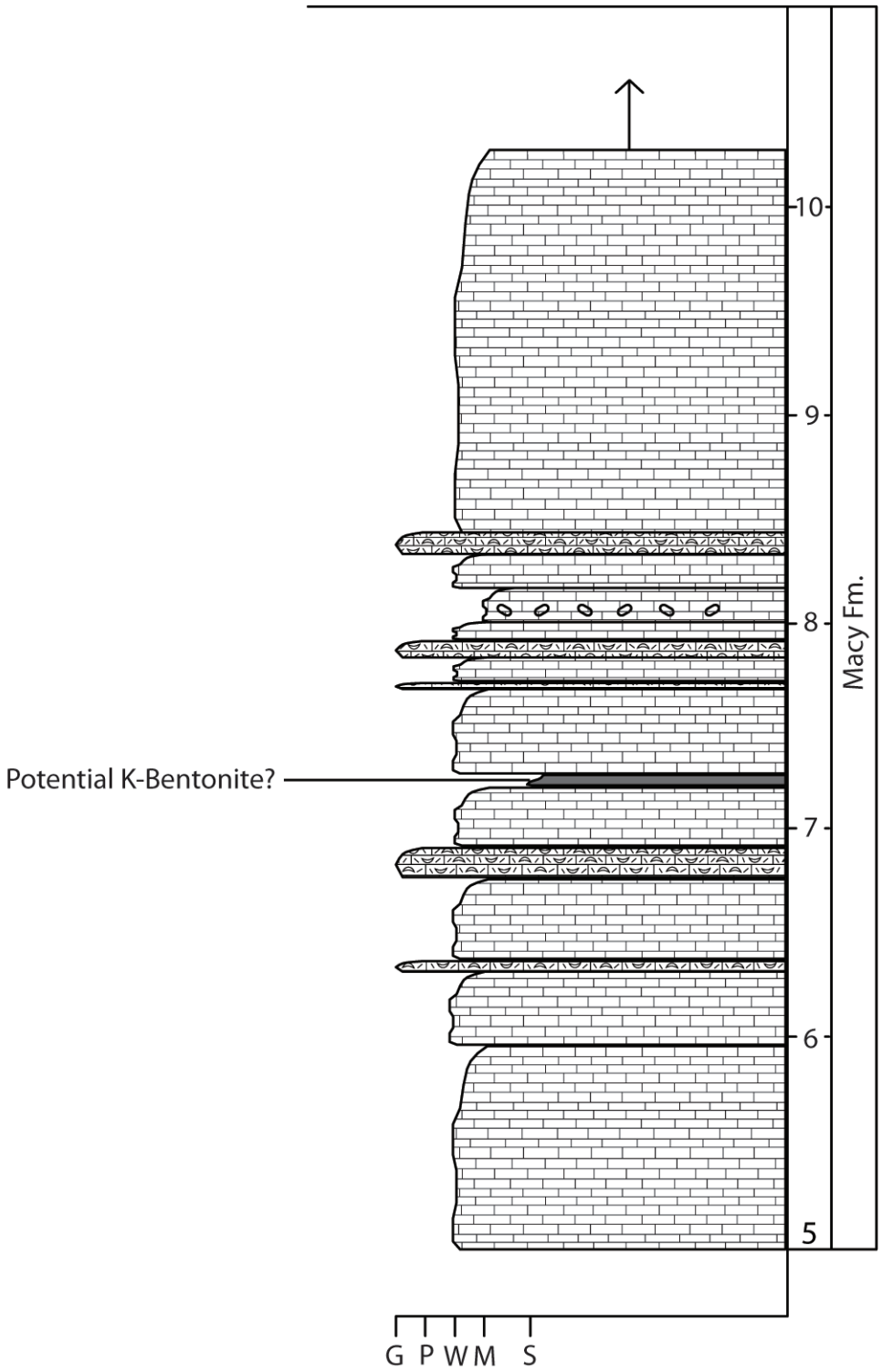
Section MM (SMM)

Section MM is measured along State Highway MM, approximately 3 km's east of House Springs, Jefferson Co., Missouri.

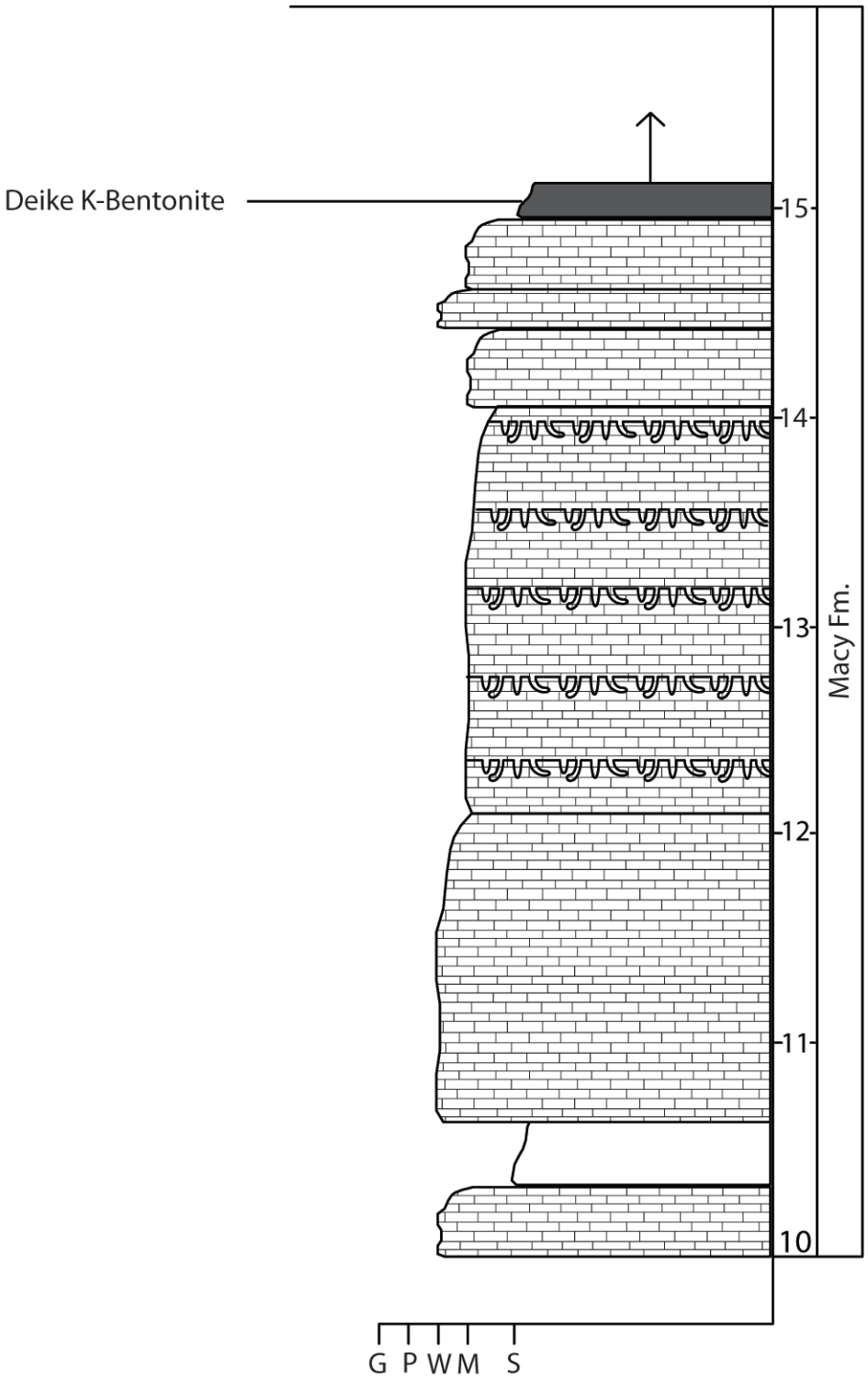
Section MM, Main Section
Part 1



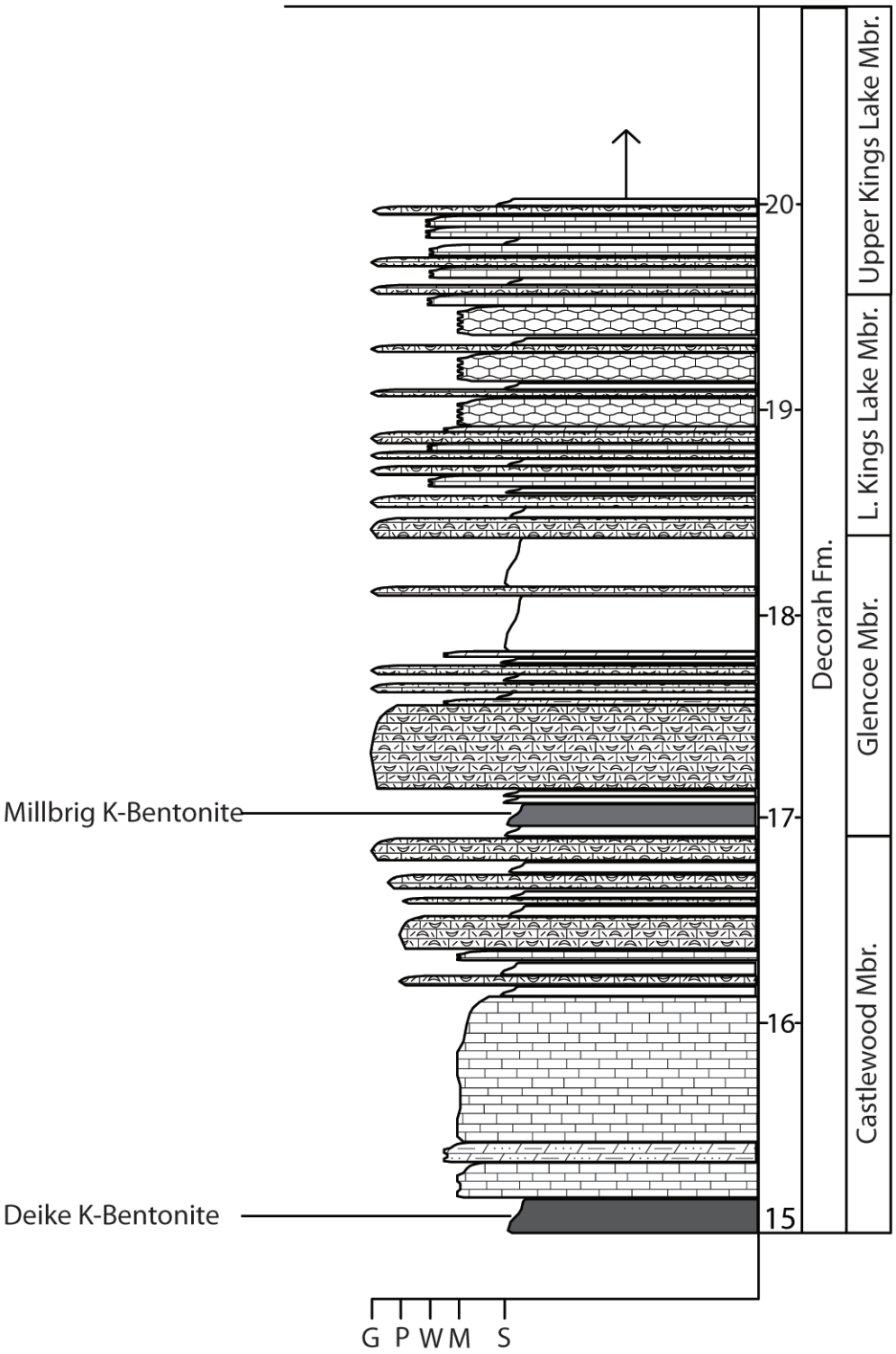
Section MM, Main Section
Part 2



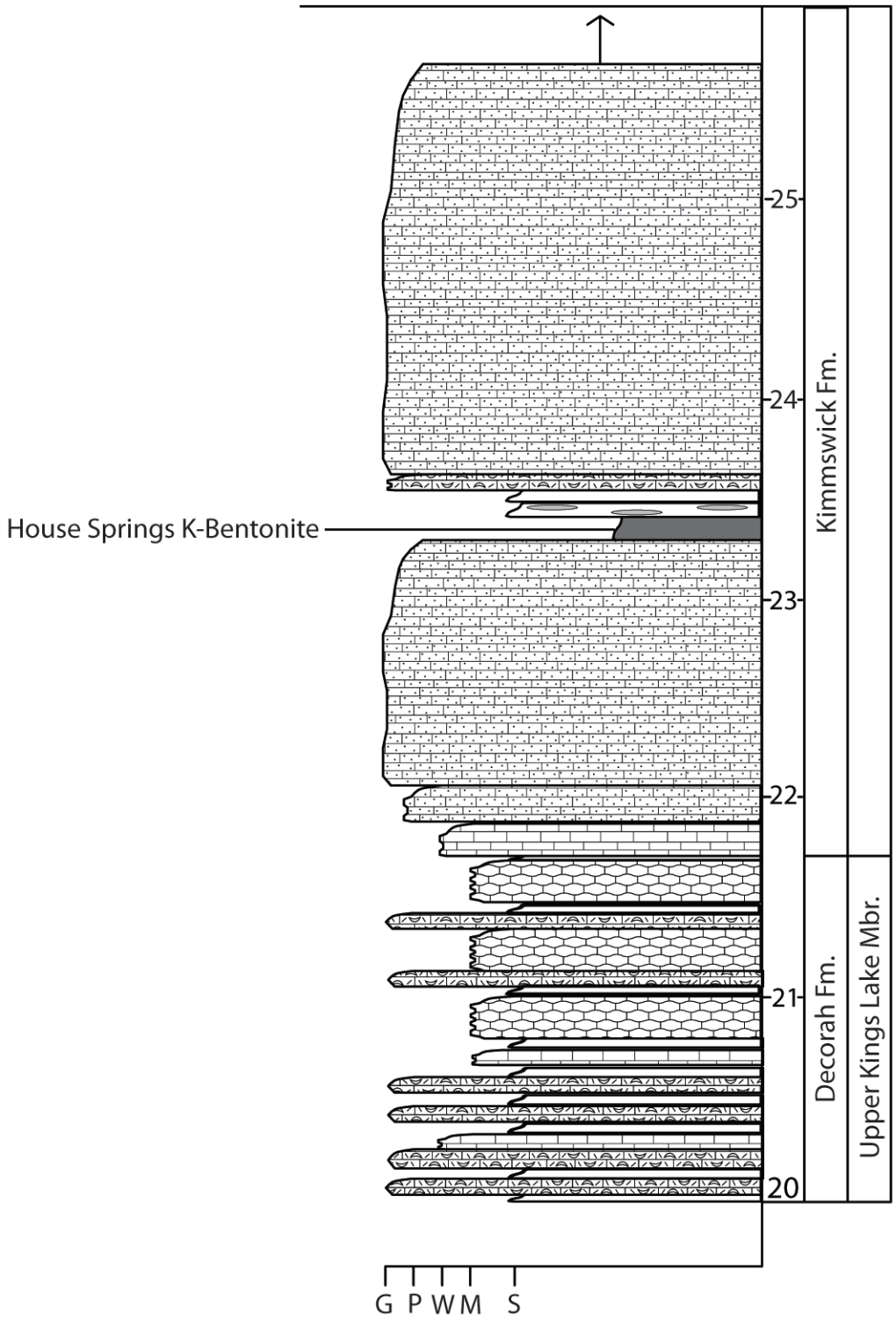
Section MM, Main Section
Part 3



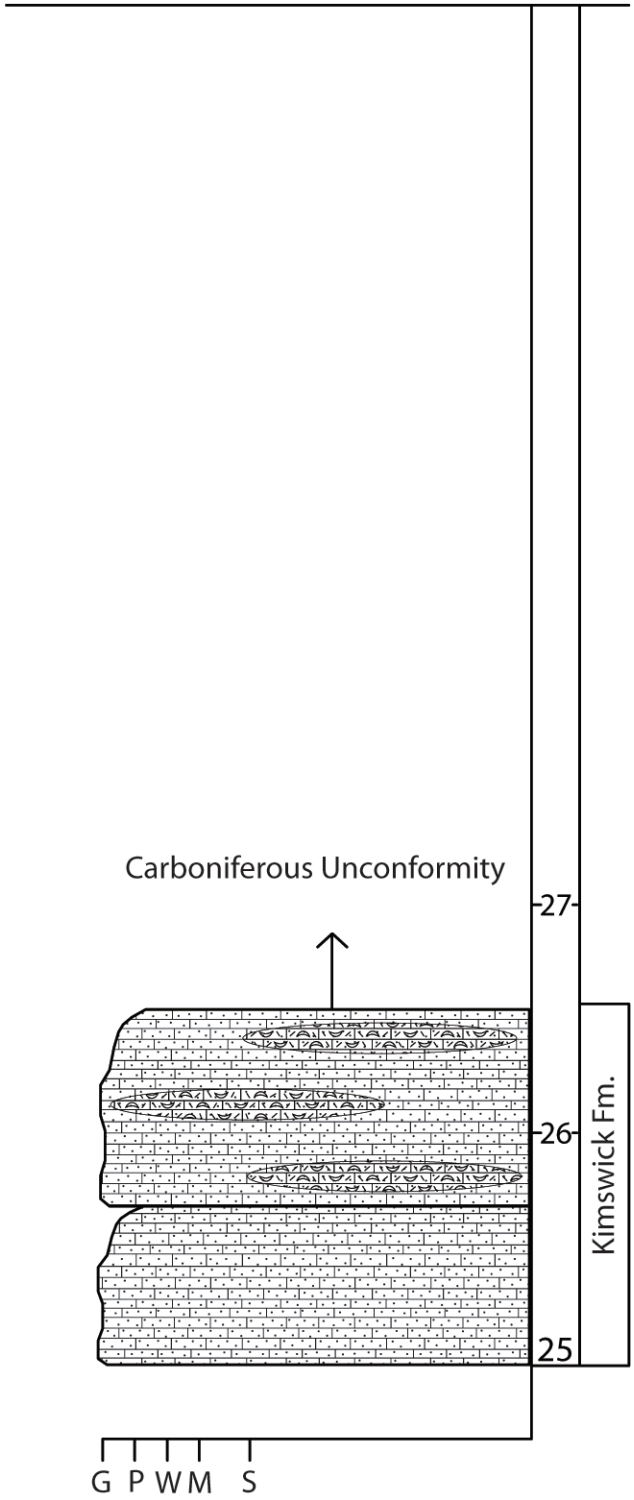
Section MM, Main Section
Part 4



Section MM, Main Section
Part 5



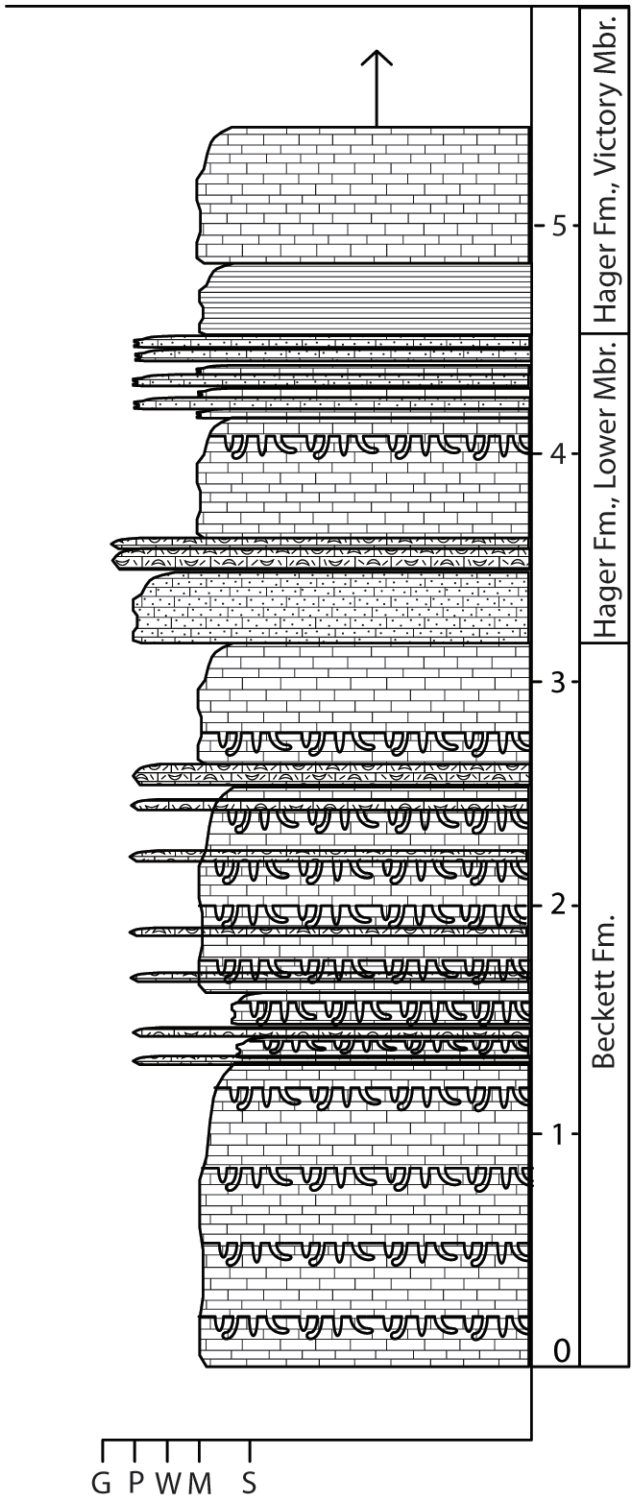
Section MM, Main Section
Part 6



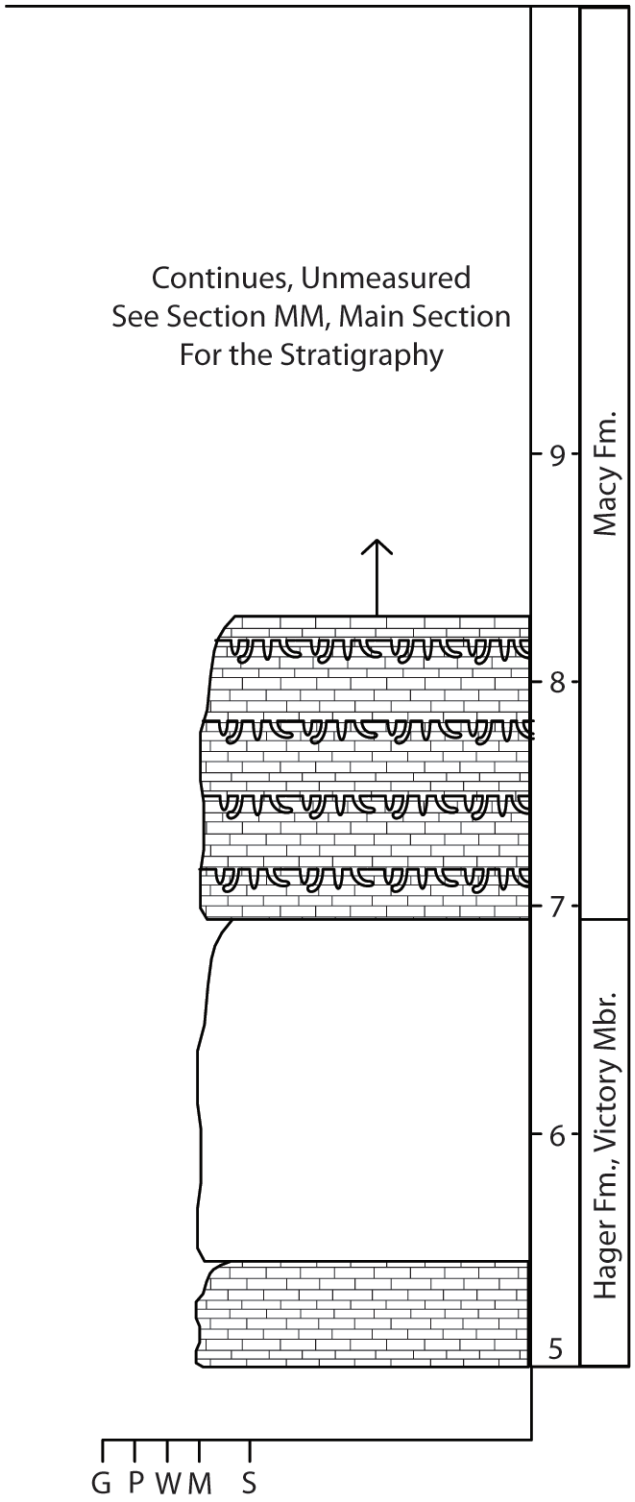
Section MM (SMM) 2nd Smaller, Lower Section

This section occurs just east of Section MM where slightly older strata are exposed that continues into strata measured in Section MM. The section is measured along State Highway MM, approximately 3 km's east of House Springs, Jefferson Co., Missouri.

Section MM, 2nd Section
Lower, Smaller Section
Part 1



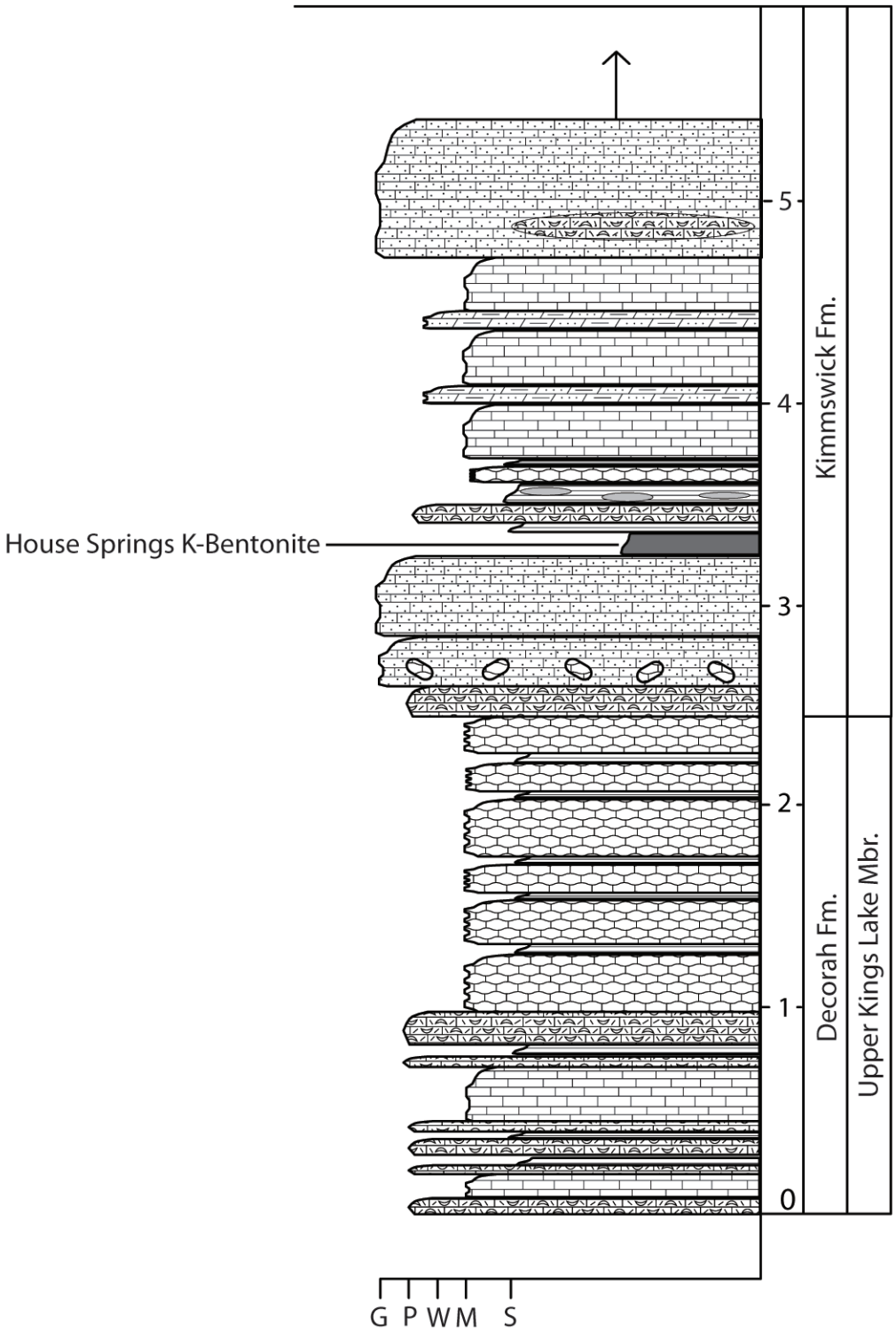
Section MM, 2nd Section
Lower, Smaller Section
Part 2



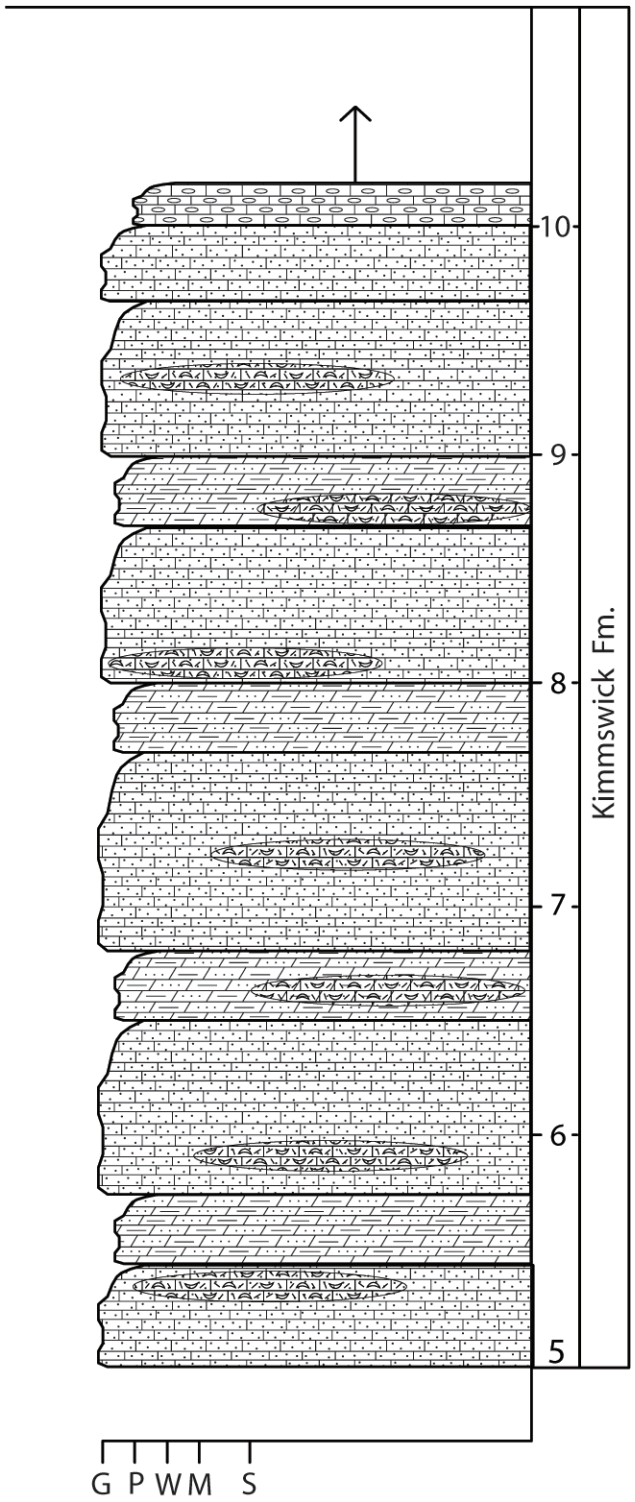
Section M (SM)

Section M was measured along State Highway M, approximately 3.5 km's east of the intersection of State Highway M and State Highway 21, Jefferson Co., Missouri.

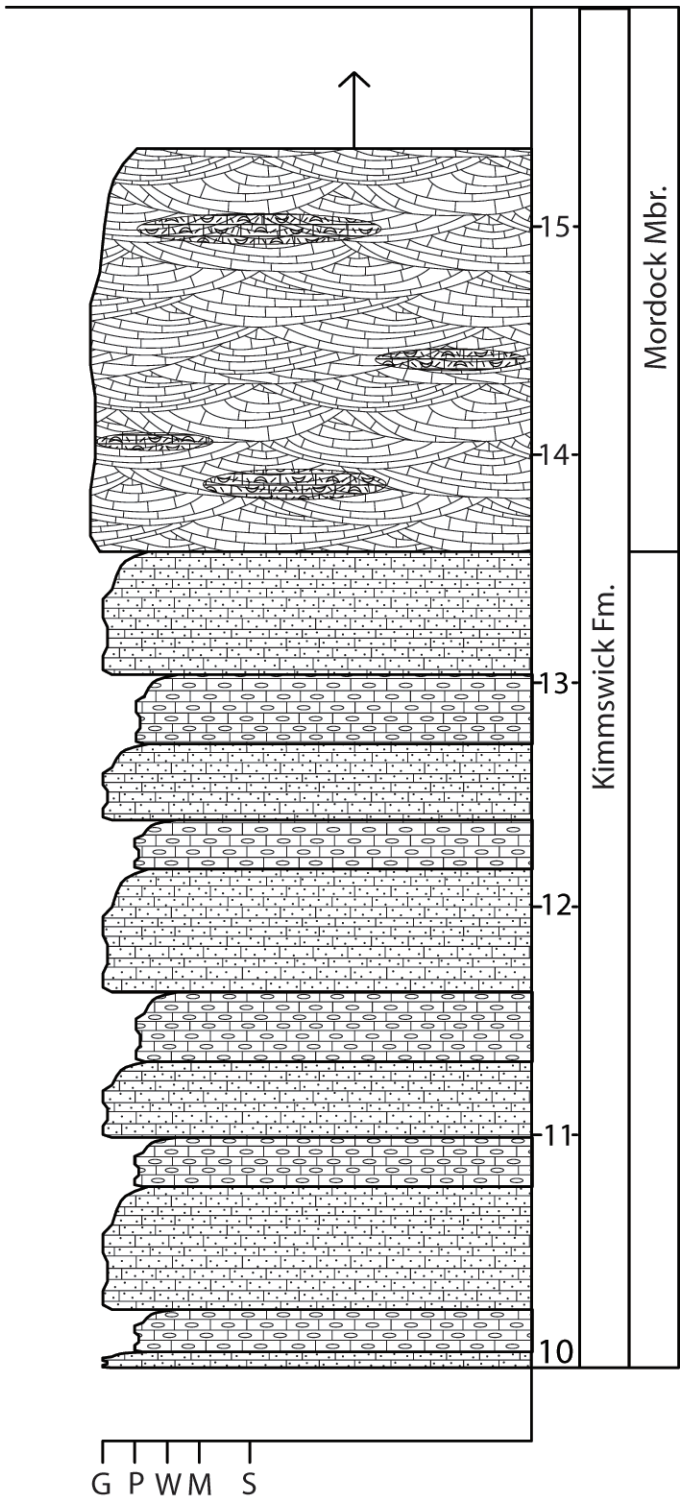
Section M
Part 1



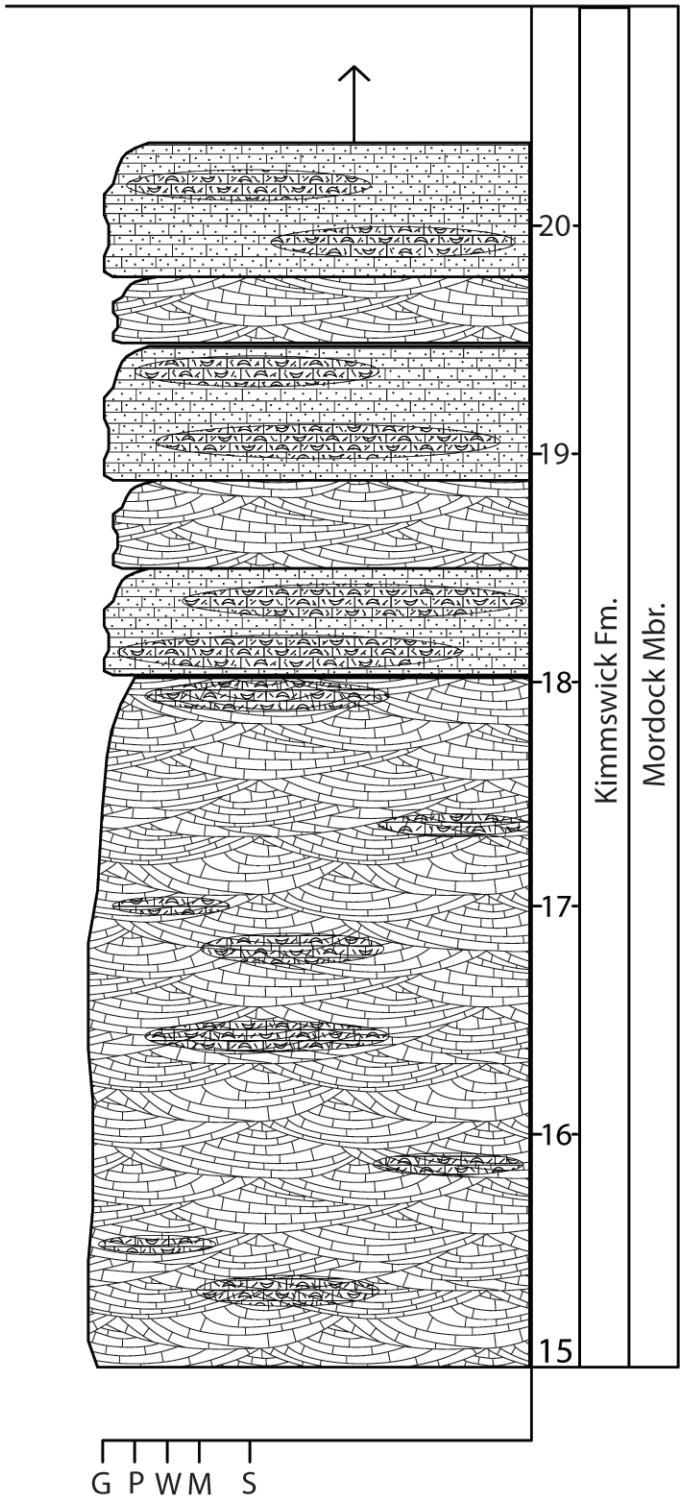
Section M
Part 2



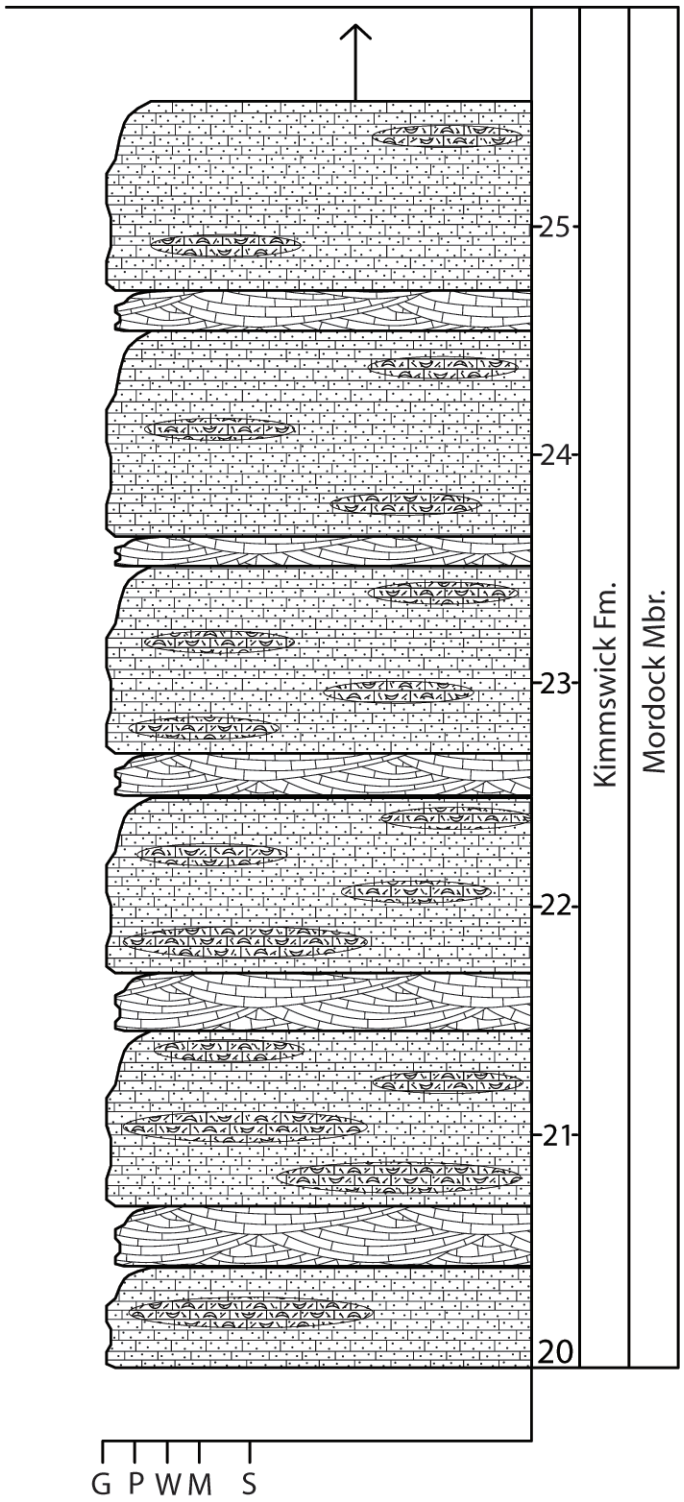
Section M
Part 3



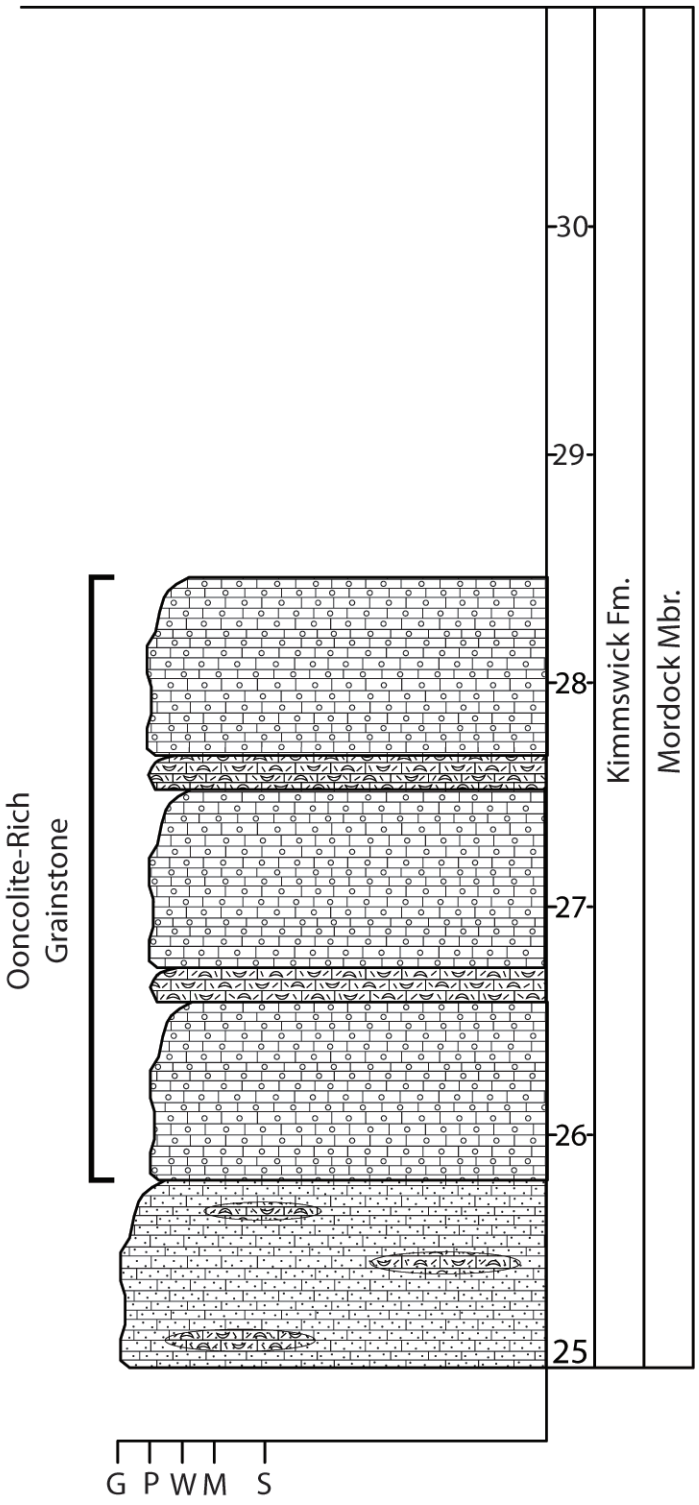
Section M
Part 4



Section M
Part 5



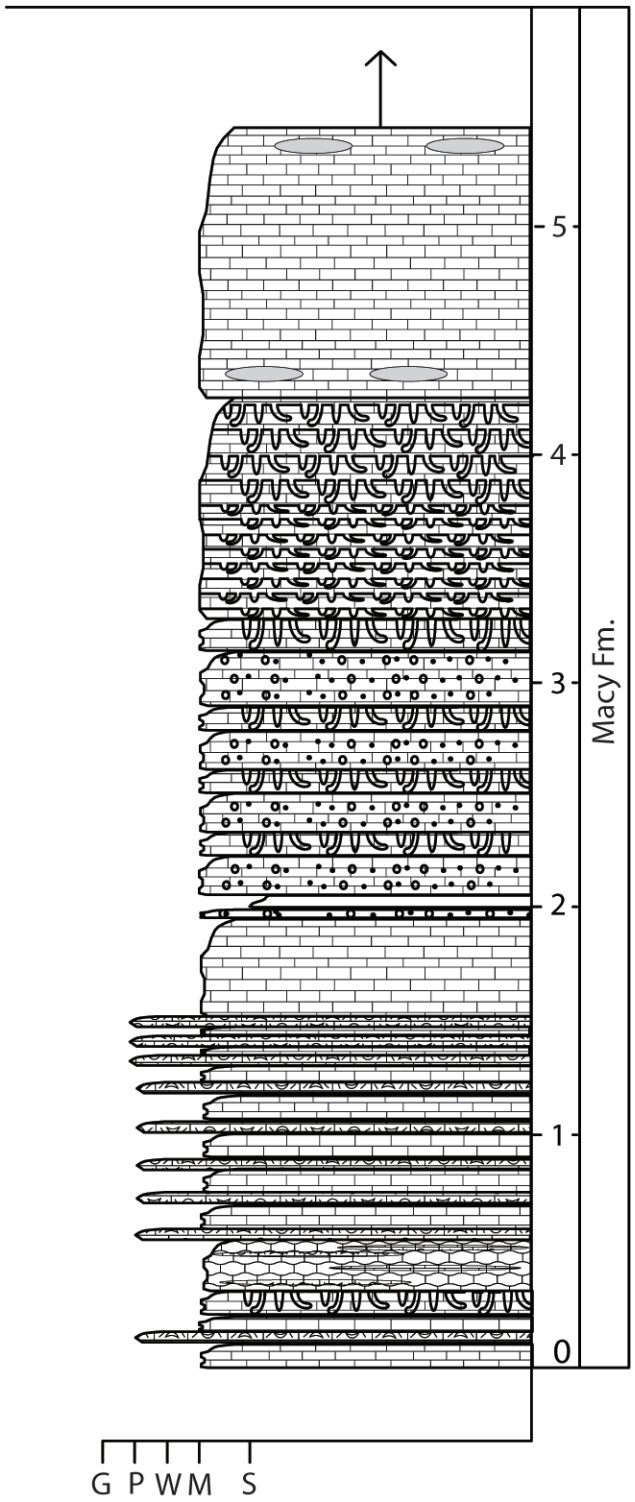
Section M
Part 6



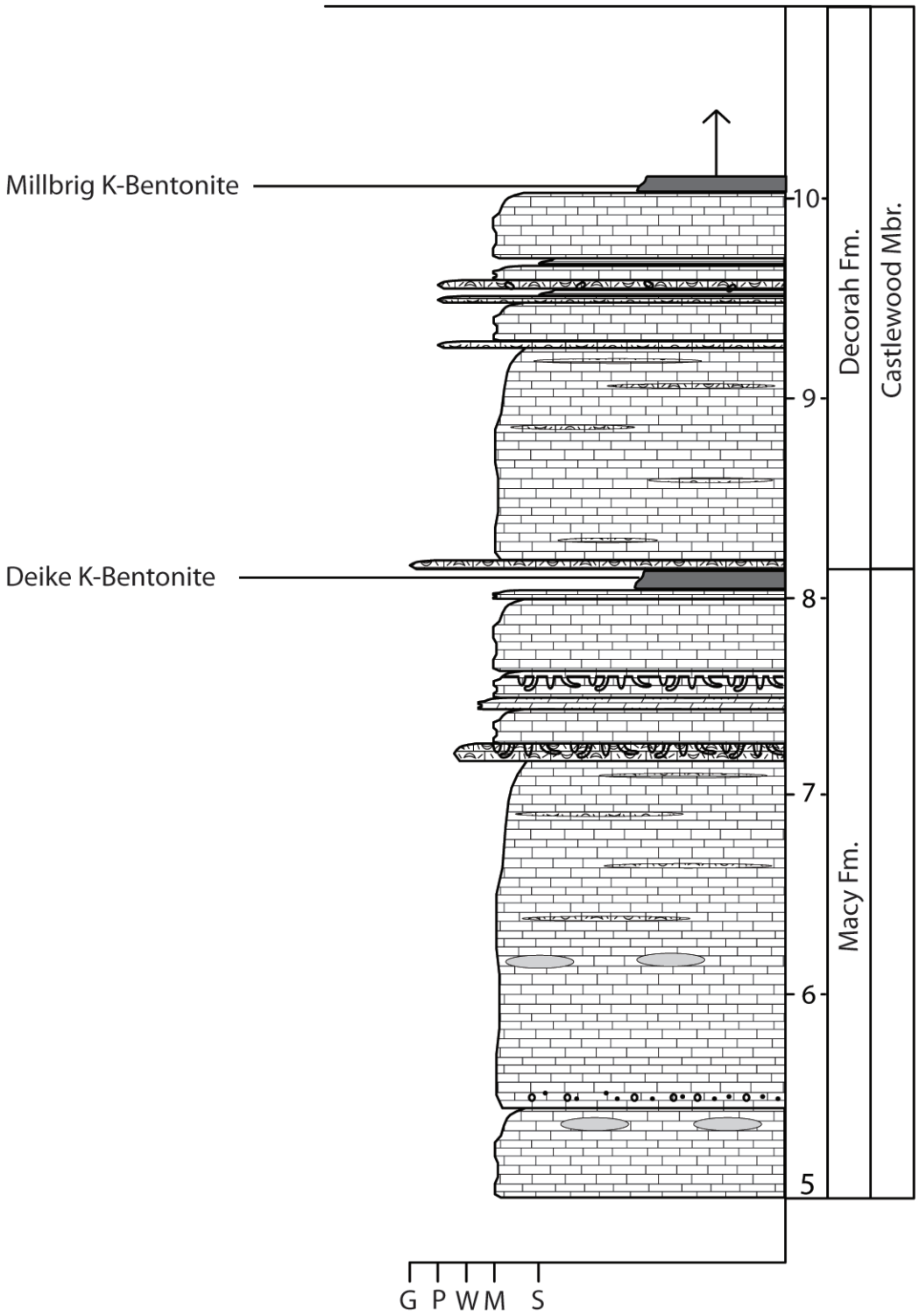
New London Section (NL)

The New London Section was measured near New London (NL), along State Highway 61, Ralls County, Missouri.

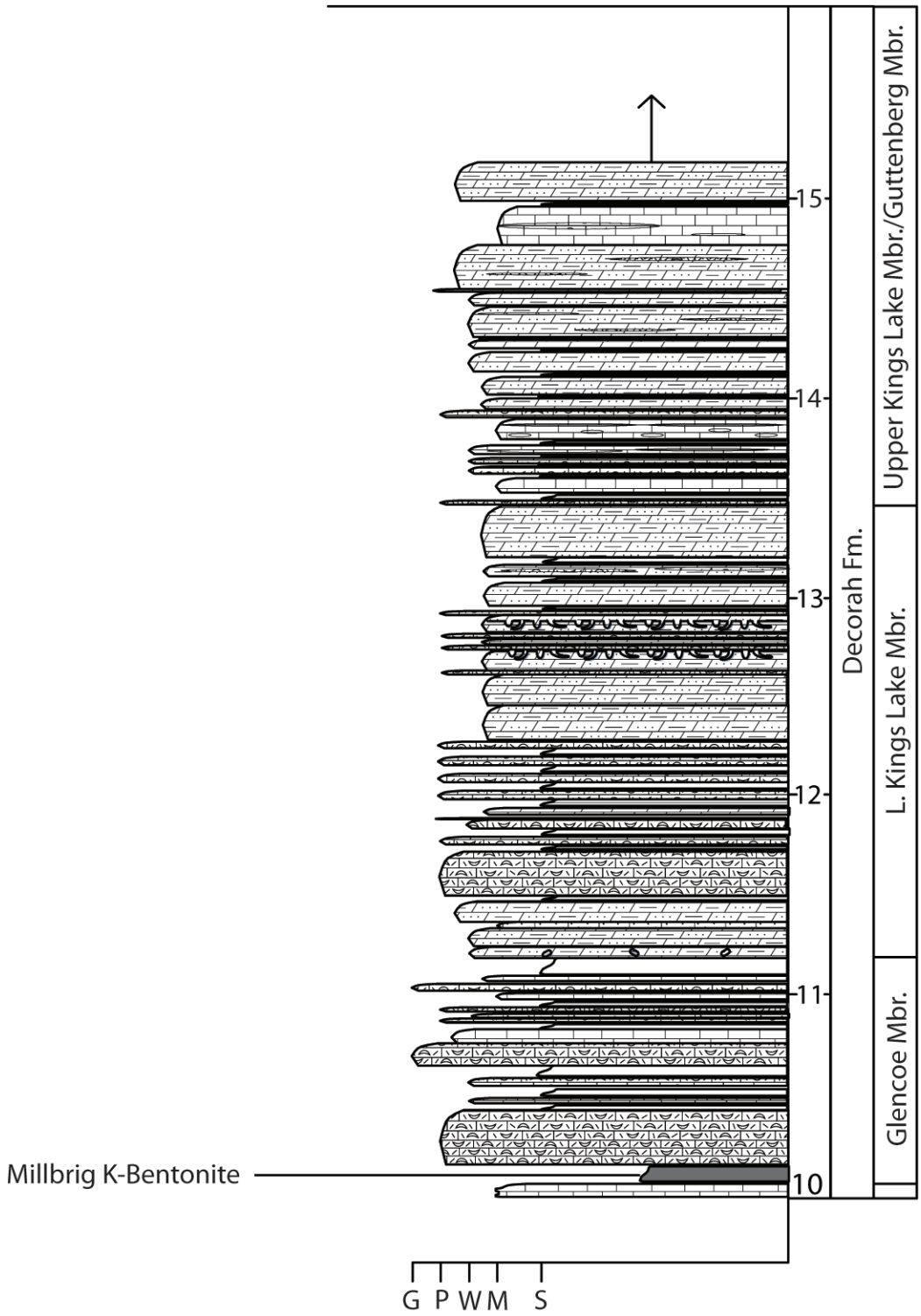
New London Section
Part 1



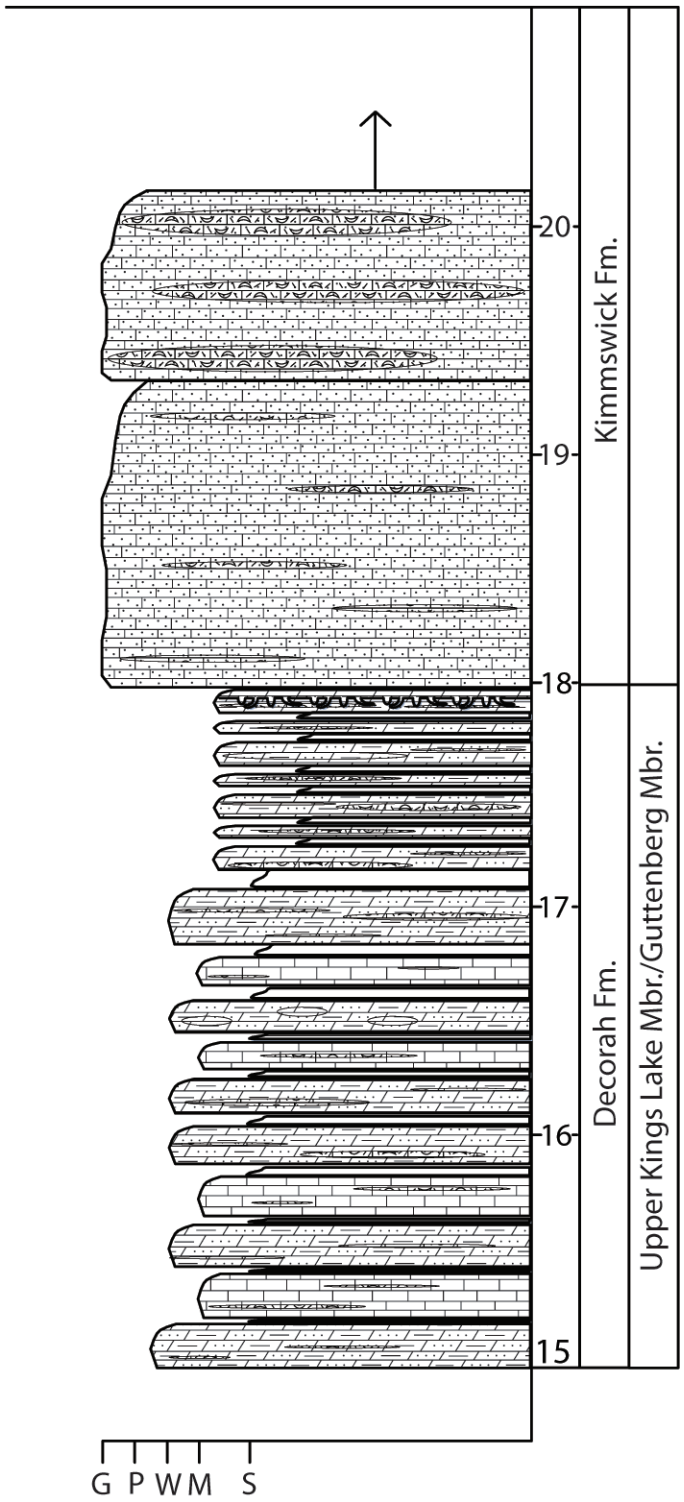
New London Section
Part 2



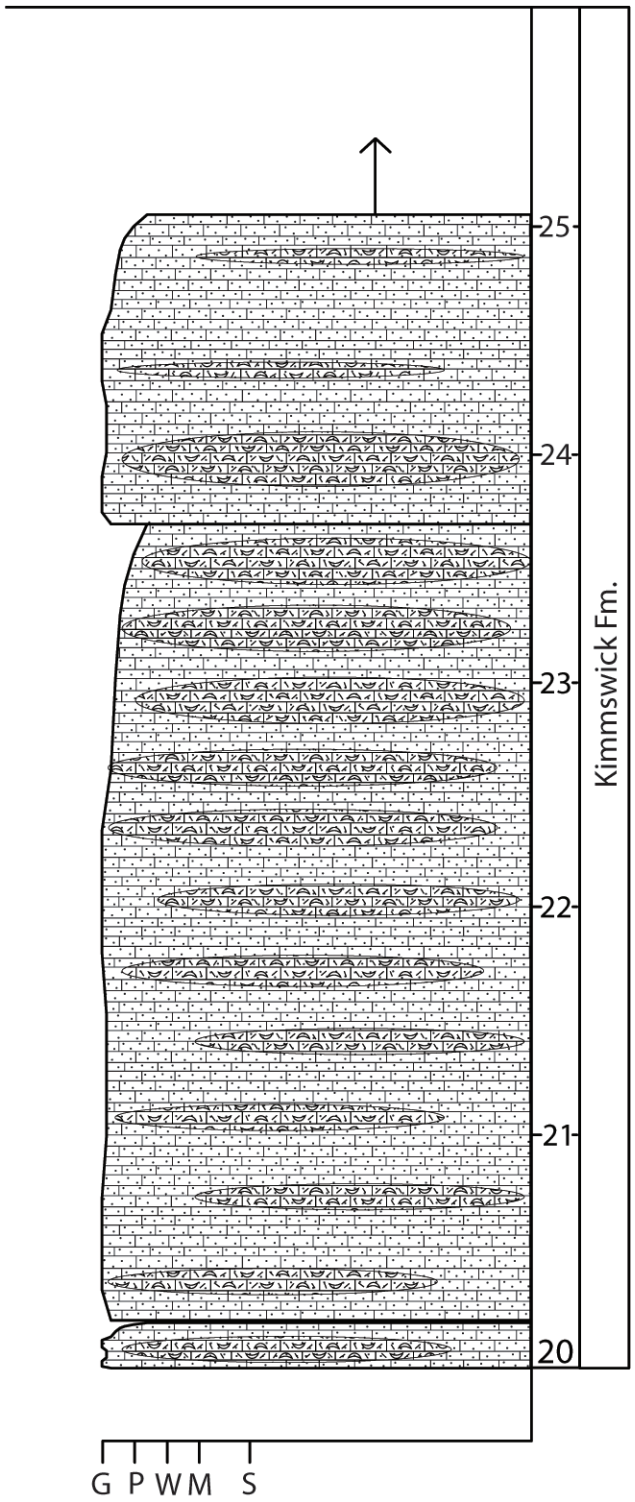
New London Section
Part 3



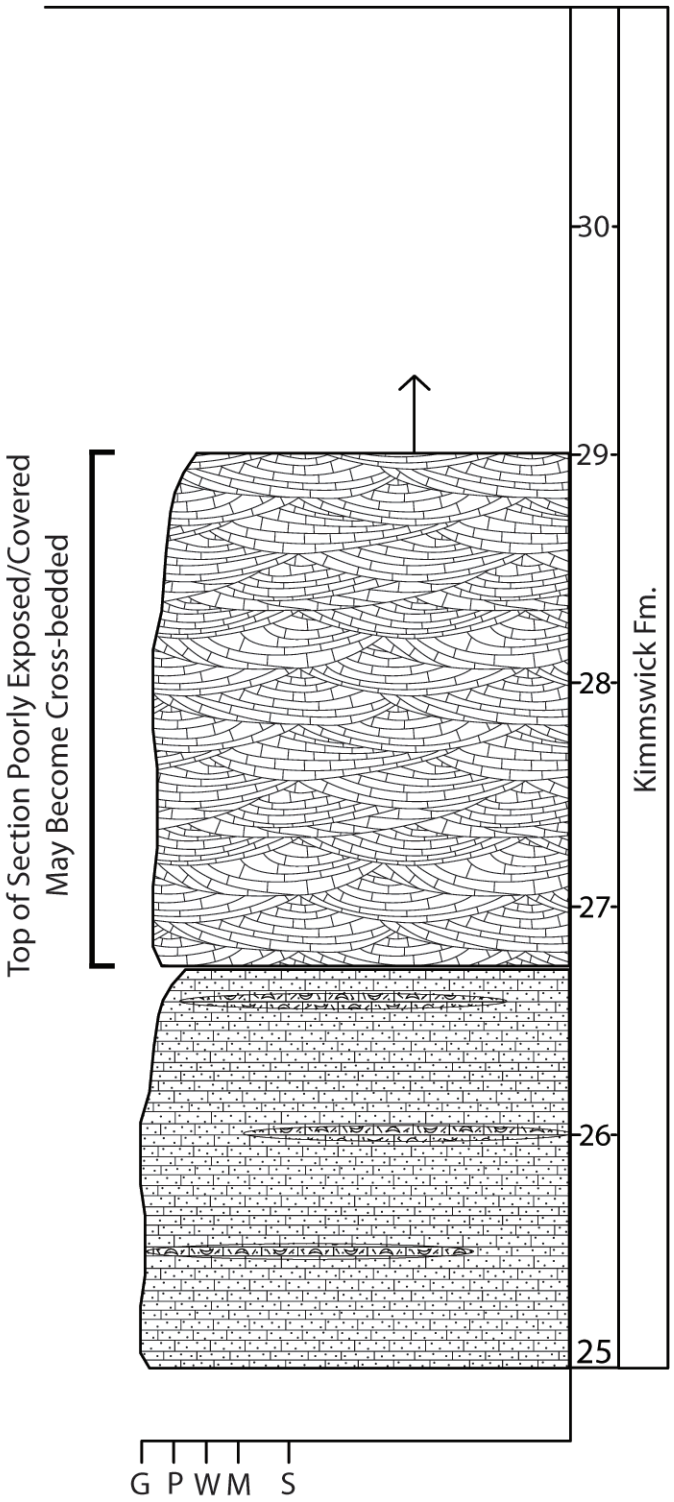
New London Section
Part 4



New London Section
Part 5



New London Section
Part 6



Appendix 2: Trilobite Relative Abundance Data

Appendix 2 contains counts of individual trilobites collected across the Missouri study region over the course of this analysis. Counts are at the genus level. Samples were collected from Section MM, Section M, Section 79-M and Section B.

Genus	Sect. MM 24m	Sect. MM 26.0m	Sect. M 5-6m	Sect. M 16.5-18.0m	Sect. M 16.5m "Coarse Facies"	Sect. M 19.0m	Sect. 79-M 1.0m	Sect .B
Achatella	0	0	0	0	0	1	14	0
Amphilichas	0	0	0	0	1	0	2	1
Bathyurus (Raymondites)	38	0	2	0	0	0	0	0
Bumastoides	17	6	9	1	5	6	4	0
Calyptaulax	46	2	12	3	3	2	12	0
Ceraurinella	0	0	0	0	0	0	0	1
Ceraurus	37	1	9	5	1	4	26	0
Dimeropyge	0	0	0	2	1	1	0	0
"Encrinuroides"	2	0	0	0	0	0	0	0
Eobronteus	0	0	0	0	0	1	0	0
Failleana	0	0	0	1	2	0	0	0
Flexicalymene	0	0	0	1	1	1	20	1
Harpidella	0	0	0	0	1	0	0	0
Hemiarges	1	0	0	3	1	0	3	0
Holia	0	0	0	0	0	0	1	0
Hypodicranotus	0	0	0	6	1	15	20	0
Isotelus	8	2	2	1	1	5	7	0
Paraproetus	12	0	2	13	3	66	0	0
Sphaerocoryphe	1	0	0	3	0	0	9	0
Thaleops	0	0	0	2	0	0	0	0
"Whittakerites"	29	0	1	0	0	0	0	0