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UNIVERSITY OF CALIFORNIA
RIVERSIDE

Morphological Variation Among Nearshore Late Cambrian Trilobites and Their
Sequence Stratigraphic Context in Northern Upper Mississippi Valley

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Geological Sciences

by

Shravya Srivastava

June 2025

Dissertation Committee:
Dr. Nigel Hughes, Chairperson
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I would like to dedicate this thesis to my grandmother, Smt. Prema Srivastava.
Thank you for believing that I can make you proud and make all your dreams for
me come true. I miss you.

ABSTRACT OF THE DISSERTATION

Morphological Variation Among Nearshore Late Cambrian Trilobites and Their Sequence
Stratigraphic Context in Northern Upper Mississippi Valley

by

Shravya Srivastava

Doctor of Philosophy, Graduate Program in Geological Sciences
University of California, University of California, Riverside, June 2025
Dr. Nigel Hughes, Chairperson

Nearshore environments have been invoked as the sites where novelties commonly evolve in extant and extinct taxa studies. This project looks in detail at one such area on the Laurentian craton, northern Upper Mississippi Valley where during the middle Cambrian to Lower Ordovician interval there is a record of marine sedimentary rocks deposited in shallow waters. As a result of this, a high-resolution record of the local sequence stratigraphic evolution is present in this epicontinental basin. The evolutionary relationships of late Cambrian trilobite fossils of the Dikelocephalidae were studied in this region and interpreted in the context of the sediment accumulation history to delineate patterns controlled by changes in sediment deposition from those revealing the true biological signatures of tempo and mode of morphological evolution. The fossil specimens included in this study were collected from 1852 to the present, and included both museum collections and those made during this study. Geometric morphometrics software and various relevant packages in R were used to analyze patterns of morphological variation in relevant taxa following specimen preparation and imaging. Parsimony-based phylogenetic analysis was used to as-

sess evolutionary relationships among the various relevant taxa of dikelocephalids, which was supplemented by Bayesian maximum likelihood approach where possible. The parsimony phylogenetic analysis elucidates important clades within the family Dikelocephalidae, further confirming which characters control the evolutionary relationships at each level of the tree while also implying presence of a division between osceolimorphs and dikelomorphs, the latter of which commonly achieved large body size, perhaps related to the larger volume available in the stomach capsule (glabella) of trilobites in this clade. Detailed analysis of two genera revealed morphological stasis in *Osceolia osceola* for approximately 400,000 years, but did not shed light on its regional origin because it's first appearance is at a maximum flooding surface. *Walcottaspis vanhornei*, on the other hand is restricted to one or possibly two parasequences within the early part of a falling stage systems tract. It's abrupt appearance and disappearance from the record suggest that it briefly flourished in the area, but was later displaced by its relatives in the genus *Dikelocephalus*. Given its phylogenetic position in sister taxon relationship to *Dikelocephalus* species, it's origin is a plausible example of punctuated equilibria.

TABLE OF CONTENTS

LIST OF FIGURES	xii
LIST OF TABLES	xv
1 Introduction	1
1.1 Figures	7
2 Morphology, variation, and systematics of the late Cambrian Laurentian dikelocephalid trilobite <i>Walcottaspis vanhornei</i> (Walcott, 1914)	12
2.1 Abstract	12
2.2 Introduction	13
2.3 Geological Setting	14
2.3.1 Localities	14
2.3.2 Taphonomy	16
2.3.3 Sedimentology	18
2.3.4 Co-occurrent fossils and biostratigraphy	19
2.3.5 Sequence stratigraphic setting	20
2.4 Published views on <i>Walcottaspis vanhornei</i> morphology and systematic affini- ties	22
2.5 Phylogenetic position	25
2.6 Shape Variation	28
2.7 Results	30
2.7.1 Cranidial shape changes	30

2.7.2	Pygidial shape variation	31
2.8	Materials	36
2.8.1	Repositories and institutional abbreviations	36
2.9	Systematic paleontology	36
2.10	Data availability statement	45
2.11	Table	46
2.12	Figures	47
3	Occurrence, morphology, and taxonomy of the late Cambrian Laurentian dikelocephalid trilobite <i>Osceolia</i> Walcott, 1914	71
3.1	Abstract	71
3.2	Non-technical Abstract	72
3.3	Introduction	73
3.4	Geological Setting	74
3.4.1	Localities	74
3.4.2	Sedimentology/Taphonomy	76
3.4.3	Co-occurrent fossils and biostratigraphy	80
3.4.4	Sequence stratigraphic setting	82
3.5	Published views on <i>Osceolia</i> species and systematic affinities	84
3.6	Shape variation among <i>Osceolia</i> cranidia and pygidia	86
3.7	Results	88
3.7.1	Shape variation within an individual collection	88
3.7.2	Shape variation within the entire <i>Osceolia osceola</i> collection	90
3.7.3	Ulrich and Resser type specimens	92
3.7.4	Classification by anterior border ledge morphology	92
3.7.5	Comparison of <i>O. osceola</i> cranidia with homeomorphic taxa	94
3.8	Materials	96
3.9	Systematic Paleontology	97
3.10	Conclusions	115

3.11	Data availability statement	115
3.12	Figures	116
4	Phylogeny of the late Cambrian trilobite family Dikelocephalidae Miller, 1889	156
4.1	Abstract	156
4.2	Introduction	157
4.2.1	Initial assessment	158
4.2.2	Forms with similar overall proportions	158
4.2.3	Forms with shared details of glabellar and palpebral structure	161
4.2.4	Outgroup Selection	164
4.3	Materials and Methods	166
4.3.1	Character and Taxon Selection	166
4.4	Results	174
4.5	Conclusions	177
4.6	Table	179
4.7	Figures	180

LIST OF FIGURES

1.1	Evolutionary modes	7
1.2	Stratigraphic architecture and evolutionary patterns	8
1.3	Upper Mississippi Valley sequence stratigraphy	9
2.1	<i>Walcottaspis vanhornei</i> occurrence map	47
2.2	Hokah stratigraphic section	48
2.3	<i>Walcottaspis vanhornei</i> (Walcott, 1914), cranidia	49
2.4	<i>Walcottaspis vanhornei</i> (Walcott, 1914), other sclerites	50
2.5	<i>Walcottaspis vanhornei</i> (Walcott, 1914), pygidia	51
2.6	Parsimony-based phylogeny	52
2.7	<i>Walcottaspis vanhornei</i> reconstruction	53
2.8	<i>Dikelocephalus minnesotensis</i> , pygidium, Hokah, MN	54
2.9	<i>Walcottaspis vanhornei</i> locality map	55
2.10	Morphometrics landmark scheme, cranidium	55
2.11	Morphometrics landmark scheme, pygidium	56
2.12	Procrustes superimposition, cranidia	56
2.13	PCA analysis, cranidia and pygidia	57
2.14	Relative warp TPS grids, cranidia	58
2.15	Partial Procrustes distance plot, cranidia	59
2.16	Allometry grid, cranidia	59
2.17	Relative warp grids, pygidia, 40 landmarks	60

2.18	Partial Procrustes distance plot, pygidia, 40 landmarks	61
2.19	Relative warp grids, pygidia, 256 landmarks	62
2.20	Partial Procrustes distance plot, pygidia, 256 landmarks	63
2.21	Partial Procrustes distance plot, pygidia, 14 landmarks	63
2.22	Relative warp grids, pygidia, 14 landmarks	64
2.23	Partial Procrustes distance plot, pygidia, 14 landmarks	65
2.24	<i>Wilbernia</i> sp., homeomorph	65
3.1	<i>Osceolia</i> occurrence map	116
3.2	Osceola stratigraphic section	117
3.3	Arcadia stratigraphic section	118
3.4	Spring Valley stratigraphic section	119
3.5	<i>Osceolia osceola</i> , cranidia, Osceola, WI and MN, Norwalk Mbr	120
3.6	<i>Osceolia osceola</i> , cranidia, sandstone facies	121
3.7	<i>Osceolia osceola</i> , cranidia, heterolithic facies	122
3.8	<i>Osceolia osceola</i> , cranidial anterior border variation	123
3.9	<i>Osceolia osceola</i> , librigena	124
3.10	<i>Osceolia osceola</i> , hypostome	125
3.11	<i>Osceolia osceola</i> , thoracic segments	126
3.12	<i>Osceolia osceola</i> , pygidia, Osceola, WI and MN, Norwalk Mbr	127
3.13	<i>Osceolia osceola</i> , pygidia, sandstone facies	128
3.14	<i>Osceolia osceola</i> , pygidia, heterolithic facies	129
3.15	<i>Osceolia osceola</i> reconstruction	130
3.16	<i>Osceolia tumerispina</i> , new species, plate	131
3.17	<i>Osceolia tumerispina</i> , reconstruction	132
3.18	<i>Briscoia</i> resembling <i>Osceolia</i>	133
3.19	Cranidial homeomorphs of <i>Osceolia</i>	134
3.20	<i>O. osceola</i> reconstruction, landmark scheme	135

3.21	Lithofacies bivariate plots, cranidia & pygidia	136
3.22	Relative warps plots, Osceola, WI, Norwalk Mbr.	137
3.23	Relative warp vs. centroid size, Osceola, WI, Norwalk Mbr.	138
3.24	Relative warp TPS Grid, Osceola, WI, Norwalk Mbr.	139
3.25	Allometry TPS Grid, Osceola, WI, Norwalk Mbr.	140
3.26	Relative warp vs. centroid size, 62 <i>O. osceola</i> cranidia	141
3.27	TPS Grids, 62 <i>O. osceola</i> cranidia	142
3.28	Bivariate plots, 41 <i>O. osceola</i> cranidia	143
3.29	TPS Grids, 41 <i>O. osceola</i> cranidia	144
3.30	Bivariate plots, <i>Osceolia</i> type cranidia	145
3.31	Bivariate plots, <i>Osceolia</i> type pygidia	146
3.32	<i>O. osceola</i> ledge classes reconstruction	147
3.33	<i>O. osceola</i> bivariate plot, 62 cranidia, ledge classification	148
3.34	<i>O. osceola</i> bivariate plot, 62 cranidia, homeomorphs & relatives	149
4.1	Discrete character matrix tree	180
4.2	Discrete character Bootstrap and Bremer	181
4.3	Mixed character matrix tree	182
4.4	Mixed character Bootstrap and Bremer	183

LIST OF TABLES

2.1	Matrix of character states for selected taxa. See the Supplemental Data 1 for a descriptive list of character, character states and taxa used in this phylogenetic analysis. Columns correspond to character states designation and rows contain taxa names.	46
4.1	Matrix of discrete character states for analyzed taxa. See the Materials and Methods section for a descriptive list of character and character states coded in this matrix. Columns correspond to character states designation and rows contain taxa names. '?' corresponds to missing character states and '-' corresponds to inapplicable tokens.	179

Chapter 1

Introduction

Recent research into the extent to which the fossil record provides an accurate chronicle of the evolution of animal life provides encouraging results in the cases where the fidelity of record is relatively high. For example, among Paleozoic rocks, recent estimates associated with the best-preserved groups such as graptoloids show that as many as 75% of species that ever existed in the sampled areas sites are currently known ([Foote et al., 2019](#)). It has also been established that the known temporal ranges of such species are accurate to a surprisingly high degree. Factors that control paleontological completeness include amount of sampling within local sections, number of sections sampled, and the time span covered by these sections. Although preservational quality tends to decrease with age, a good quality of ancient fossil record can be at par, in terms of resolution of morphological change time series, with that of the prehistorically focused microevolutionary studies of extant species ([Patzkowsky and Holland, 2012](#)). This suggests that detailed analyses of the fossil record of select ancient fossil groups can provide reliable information about their patterns and modes of evolutionary change.

Trilobites are a major group of biomineralized Paleozoic marine arthropods with a copious fossil record and localized habitat preferences. The trilobite fossil record is among the most comprehensive of any Paleozoic skeletonized animal clade, and it is particularly important in the Cambrian, given the comparatively depauperate nature of the biomineralized fauna at that time. In paleontology, the view that onshore environments are the sites of origin of many evolutionary innovations is supported by the recorded first appearances of new morphologies in fossil forms at the nearshore settings followed by their subsequent offshore spread ([Jablonski et al., 1983](#); [Bottjer et al., 1988](#)). This is also evident in the contemporary studies of living marine taxa that suggest that habitat fragmentation in onshore settings accelerates evolutionary innovations ([Benzie, 1998](#); [Dolby et al., 2018](#)). Evolutionary innovations are in turn sometimes affected by the sea-level changes in shallow marine settings. Hence, it is essential to study lineage evolution in ancient nearshore settings to gain insights into how major evolutionary innovations may initially have been established. However, it is important to consider that deposition in nearshore environments commonly leads to condensed sediment sections as a result of limited sediment accommodation space. This highlights the possibility that the occurrence of evolutionary novelty in fossil record could be associated with significant breaks in sediment accumulation and thus records an apparent signature of rapid, elevated rates of morphological change. Discussion of the fossil record in nearshore settings should carefully distinguish between the morphological patterns overprinted by stratigraphic accumulation history and the patterns governed by biological processes of evolutionary mode.

In the realm of evolutionary change, the mode of evolution among fossil lineages remains incompletely explored. A key to understanding the evolutionary mode is discovering the pattern of morphological variation across the lineage history. One of the earliest mention of modes of evolution dates back to Darwin when he discussed an evolutionary tree figured in the *Origin of Species* (Darwin, 1859). Darwin suggested a pattern of gradual change within an evolving lineage (phyletic gradualism) in which new species evolved through the transformation of ancestors into descendants via divergent morphological evolution (Fig. 1.1.1). In a stratigraphic sequence with continuous and steady accumulation this mode of evolution would be expected to record a series of transitional forms linking ancestors and descendants. While the fossil record offers factual evidence of the evolution of ancient life, patterns of variation within fossil lineages revealed the absence or scarcity of the transitional life forms as predicted by a gradualistic mode of evolution (Darwin, 1859). Darwin understood that this was due, in part, to the incomplete nature of the stratigraphic record. In 1971, Niles Eldredge and Stephen Gould proposed a model of evolutionary mode, called punctuated equilibria (Eldredge and Gould, 1972), which they argued reconciled patterns of morphological variation seen in the fossil record with both stratigraphic history and evolutionary mode. According to this model, the main reason for the discontinuous record of morphological variation in fossil lineages is that notable morphological change originated in small peripheral populations during allopatric speciation events (Fig. 1.1.2). Gaps in the fossil record were thus inferred to reflect speciation events taking place in an area adjacent to the central stock population. They have also argued that the speciation process associated with punctuated events must be occurring within a range of 50,000 to 100,000

years (Gould, 2002) and that it is followed by subsequent morphological stasis within the established species (Fig. 1.1.2). As common with fossils well-represented in shallow marine settings, trilobites have been part of exemplar studies of evolutionary mode as observed in fossils (Eldredge, 1971; Sheldon, 1987, 1996) considering they have an abundant record and possess a variety of morphological characters (McCormick and Fortey, 2002). This range of punctuated events contrasts with rapid adaptive evolutionary changes observed within living species over a period of tens of years (Weldon, 1899; Reznick et al., 1997; Huey et al., 2000; Thomas et al., 2001). Possible reason for fossils showing a slower rate of punctuated evolution could be the averaging of rates of evolution across varied time intervals in geological record. Gould (2002) argued that the extant species studies focus on changes in local populations which cannot successfully gain any sustained macroevolutionary expression unless they are stabilized into a Darwinian individual that can act as a unit of selection in geological time.

Although examples of both phyletic gradualism and punctuated equilibria have been documented in the fossil record based on patterns of morphological variation, the stratigraphic context of such patterns is commonly poorly resolved. The idea that sea-level changes have a role in generating apparent sudden morphological shifts in marine invertebrate fossils has been studied for some time (Moore, 1954, 1955; Jablonski and Valentine, 1985). Numerical models have shown that sediment accumulation rates can control the pattern of morphological evolution recorded by hypothetical fossil lineage (Scarponi and Kowalewski, 2007). Several numerical models using stratophenetic series, which contain morphological measurements from the stratigraphic succession of fossil samples, have also

explored the likelihood of particular evolutionary modes being favored depending on the stratigraphic architecture of the depositional basin ([Hannisdal, 2006](#); [Roopnarine, 2001](#)). Hence, stratigraphic context and the preservation potential of fossils are pertinent to the discussion of their occurrence, abundance, and morphological variation. Fortunately, the factors controlling the sediment accumulation make predictions as to which patterns of morphological variation in fossils might be expected if they are primarily driven by sedimentary, as opposed to evolutionary, processes. The details of depositional history may be recorded at high resolution in the sequence stratigraphic architecture of the sedimentary basin. Any robust ecological or evolutionary interpretation requires an attached context of its sequence stratigraphic architecture. Therefore, by combining the interpretations of fossil analysis with the sediment accumulation history, it may be possible to filter the effects of stratigraphic processes on morphological variation. When associated with a well-resolved sequence stratigraphic architecture, conclusions about the progress of evolution through a fossil lineage gain more credence if patterns revealed cannot be explained as stratigraphically controlled signatures. For instance, for a lineage evolving in a consistent direction at a constant rate in a clastic systems tracts where the net sedimentation rate is slow, such as the maximum flooding surface of transgressive systems tract, an apparently rapid rate of morphological change might be expected ([Patzkowsky and Holland, 2012](#)) (Fig. 1.2). Conversely, in the highstand systems tract and earlier part of falling stage systems tract, more subtle patterns of morphological change are expected to be apparent because higher sedimentation rates would record intervals of time more faithfully (Fig. 1.2). Accordingly, when attempting to investigate questions about origins of nearshore novelty and evolution-

ary mode, understanding the depositional regime is critical. However, as accommodation space for sediment accumulation is less in nearshore than in deeper water settings, rock record in such settings is condensed. Artefactual, sediment accumulation-related fragmentation of the record of morphological change in such settings can be particularly marked. In this regard, the late Cambrian succession of the Upper Mississippi Valley provides an exceptional opportunity to explore morphological evolution within its best-represented clade of trilobites, the dikelocephalids, in a context of a well-resolved sequence stratigraphic architecture (Fig. 1.3). Here the patterns of morphological dikelocephalid evolution can be evaluated within the context of a single first order transgressive-regressive cycle that comprises a major episode of relative sea-level rise, followed by basinward progradation of the shoreline as the rate of relative sea-level rise slowed (1.3). Although the entire sequence of Upper Mississippi Valley Cambrian succession is markedly thin compared to the more distal settings, the record of individual transgressions and regressions remains well-preserved at high fidelity not only at scale of first-order patterns but also at higher order (fifth-order (10-100 ka) parasequence resolution (Runkel et al., 2007)). Accordingly, a combined phylogenetic and morphometric approach to dikelocephalid trilobite evolution can be utilized to chart how morphological variance is partitioned within a sequence stratigraphic framework and to infer how morphology is expected to have changed if the local stratigraphic accumulation history reflecting the relative sea-level was the primary controlling factor.

1.1 Figures

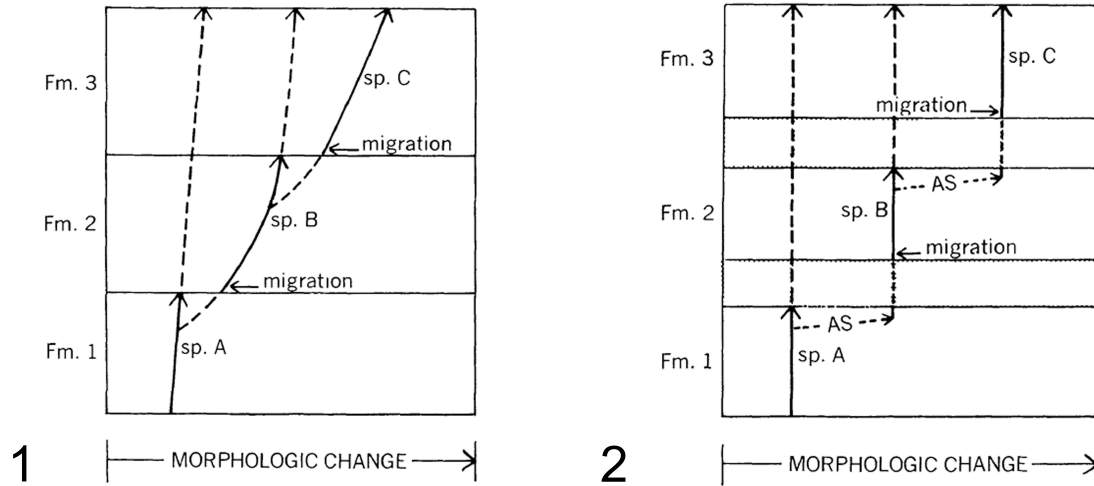


Figure 1.1: Two models of speciation used to explain the occurrence of three species (A-C) in successive bodies of strata (Fms. 1-3) in one local area. **(1)** Gradual morphological divergence model, **(2)** Punctuated equilibria model. Solid lines correspond to species occurrence preserved in local rock unit; dashed lines correspond to species living in same faunal province but outside the local area. AS: allopatric speciation, hiatus in record is marked by stippling. (From [Eldredge, 1971](#))

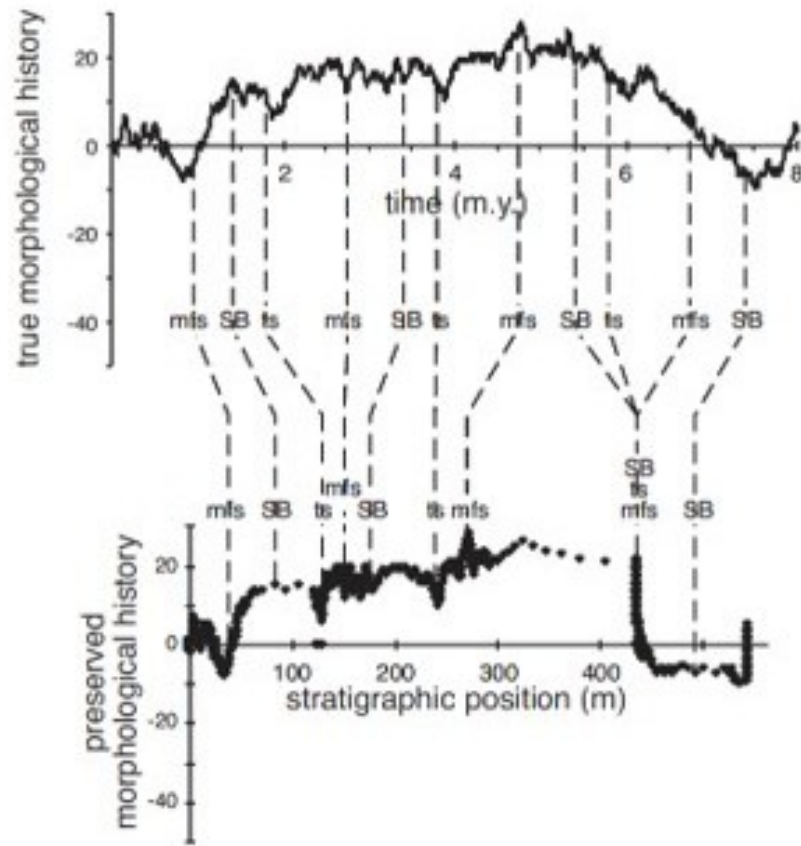


Figure 1.2: Schematic diagram of effects of stratigraphic architecture on histories of morphological evolution. Upper panel shows the actual history of a hypothetical morphological change. Lower panel shows a modelled preservation history of stratigraphic architecture. (From [Patzkowsky and Holland, 2012](#))

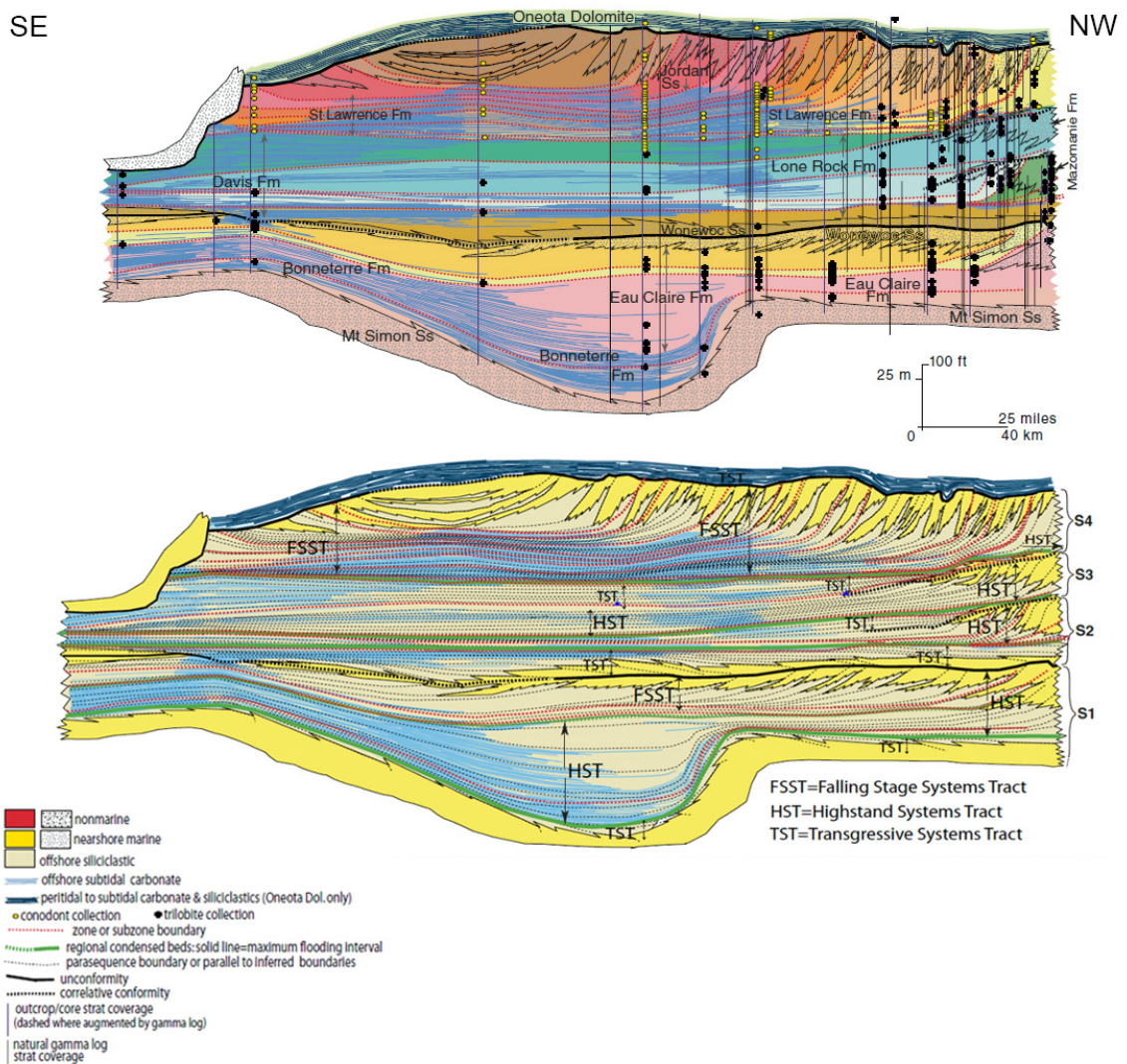


Figure 1.3: Stratigraphic cross sections of middle Cambrian to Lower Ordovician rocks across the Upper Mississippi Valley epeiric ramp. Upper cross section highlights zonal units in this stratigraphic package, colored to correspond to the zonal classification adopted in [Runkel et al., 2007](#) (fig. 5). Lower cross section shows sequence stratigraphic attributes interpreted on the basis of the geometry and stacking of zonal units, in combination with standard sequence stratigraphic techniques based on physical criteria. (modified from [Runkel et al., 2007](#), fig. 6)

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Chapter 2

Morphology, variation, and systematics of the late Cambrian Laurentian dikelocephalid trilobite *Walcottaspis vanhornei* (Walcott, 1914)

2.1 Abstract

Walcottaspis vanhornei (Walcott, 1914) is a large, late Cambrian trilobite with a unique pygidial morphology known only from a narrow outcrop belt of the St. Lawrence Formation in the Upper Mississippi Valley. Found in carbonate-rich layers within heterolithic facies that represent the toesets of a prograding shoreface, it is restricted to a single or small number of parasequences. Only four specimens of any of its sclerites have been illustrated previously. Here holaspid examples of all its biomineralized sclerites are described and illustrated, along with a morphometric analysis of cranidial landmarks and landmarks plus semilandmarks for the pygidium. Ontogenetic allometry accounts for 29% of the variance among holaspid cranidia and includes a relative shortening and narrowing of the palpebral lobe and a reduction in the relative length and width of the frontal area. Notable pygidial

phenotypic variation occurs in the extent of the postaxial region and in the proportion of the structure occupied by the axis. Phylogenetic analysis suggests that *W. vanhornei* is sister taxon to *Dikelocephalus minnesotensis* [Owen et al., 1852](#), which also occurs in the St. Lawrence Formation and has a broadly similar cephalon but distinctive trunk. The holaspide pygidium of *W. vanhornei* is uniquely characterized by the interpleural furrows of the first two segments becoming abruptly obsolete on approaching the axial furrow. Some pygidia show narrow, shallow, flat-bottomed grooves etched into the internal sides of the dorsal surface or doublure that apparently represent infestation of the live trilobite.

2.2 Introduction

Walcottaspis vanhornei ([Walcott, 1914](#)) is a large but little known dikelocephalid trilobite confined to a narrow outcrop belt of the St. Lawrence Formation in the Upper Mississippian Valley. Only four examples of any of its sclerites have previously been illustrated ([Walcott, 1914](#), pl. 62, figs. 1-3; [Ulrich and Resser, 1930](#), pl. 20, figs. 3-5). This paper describes its morphology, ontogeny, and systematics, and also considers aspects of its paleoecology. It complements a forthcoming study of evolutionary patterns among dikelocephalid trilobites from this region. Study of this group is potentially instructive from an evolutionary perspective because the region contains a thin but relatively complete ([Runkel, 1994](#); [Runkel et al., 2007](#)) record of late Cambrian depositional history formed close to the paleoshoreline. During that time a condensed suite of nearshore facies were deposited in the Hollandale embayment ([Mossler, 1992](#)) within the northern part of the Mississippi Valley. The Hollandale embayment reflects an ancient rift basin located between the Wisconsin

arch to the east and the putative “Transcontinental Arch” (Myrow et al., 2003) to the west, two regions of positive relief that were reportedly intermittently exposed during the late Cambrian. This onshore environmental setting, comparable in some ways to modern coastal environments, may have offered opportunity for localized habitat fragmentation and thus enhanced opportunity for speciation, as seen among living marine organisms (e.g. Shen et al., 2011; Dolby et al., 2018). Paleontological evidence suggests that nearshore marine sites were commonly those in which novel morphologies or ecologies first appeared (e.g. Jablonski et al., 1983; Jablonski and Bottjer, 1990; Sepkoski, 1991; Jacobs and Lindberg, 1998). Given this, detailed studies of morphological and ecological evolution in ancient nearshore sites have particular currency but are challenging because such environments are generally poorly preserved. The late Cambrian of the Upper Mississippi Valley provides an important and potentially instructive exception.

2.3 Geological Setting

2.3.1 Localities

Specimens of *Walcottaspis vanhornei* are known from at least three localities (Fig. 2.1) from which most were obtained over a hundred years ago. One of these sites, Hokah (HH), was recollected by the late Gerald O. Gunderson and N.C.H in recent years. It is located at the intersection of Carlson Road and Hwy 16, ~ 4 km west of Hokah, Houston Co., Minnesota (43°46’0.12”N, 91°25’26.4”W) and is apparently the site previously recorded as “Whiteman’s Quarry on Mt Hope”, USGS Locality #346d (Hughes, 1993, p. 25). Previous records also mention another site at Hokah yielding *W. vanhornei* to be “near old railroad

embankment” or “Rail Road Dam” but this is unlikely to have been the HH site because that is at the top of a notable bluff, as are all outcrops of the St. Lawrence Formation in this area.

The specific positions of two other sites that have yielded repositied *W. vanhornei* specimens are unknown but, given the density of settlement in the area at the time they were collected, both localities will have been at most within a few kilometers from the places named. The Winona (WI - see [Hughes, 1993](#)), Winona County, Minnesota site was reported as on the bluffs facing the Mississippi River, immediately west of the town and in the general vicinity of 44°3’N, 91°43’W ([Walcott, 1914](#), p. 373). Bluff Sliding is in Buffalo County, Wisconsin, and lies on the western bank of Mississippi River immediately opposite to Winona. The St. Lawrence Formation crops out in the bluffs above the settlement, for example in an overgrown roadcut at 44°5’8.82”N, 91°37’15.12”W, but the specific locality from which the specimens were collected is also unknown. The only other reported occurrences of *W. vanhornei* known to us are that of Raasch ([1951](#), p. 142) who reported that Charles Bell and Robert Berg made a find near Reno, Minnesota, and Ulrich and Resser’s ([1930](#), p. 66) report of “an imperfect cranidium” from Lodi, Wisconsin. No specimens from near Reno are available, but the settlement at Reno accords with an arc of outcrop defined by the other three localities and Runkel et al.’s ([2007](#)) prograding shoreface model (Fig. [2.1](#)), and we consider this report to be credible. Although to our knowledge we have not seen the Lodi specimen to which Ulrich and Resser ([1930](#)) referred, occurrence of genuine *W. vanhornei* at Lodi is unlikely given its geographical position (and stratigraphic position

as inferred from [Runkel et al., 2007](#)) and, as *Walcottaspis* cranidia strongly resemble those of *D. minnesotensis*, we consider this reported occurrence to be unsubstantiated.

2.3.2 Taphonomy

Sclerites of *W. vanhornei* became disarticulated, apparently completely, prior to recovery, and are somewhat flattened/fractured composite molds. They occur in dolomitic siltstone layers within the heterolithic facies of the St. Lawrence Formation (Fig. 2.2) and are preserved in a manner similar to many examples of their close relative *D. minnesotensis* (see below and [Hughes, 1993](#)). The *W. vanhornei* we have collected lie parallel to bedding, and this appears to be their general condition (in contrast to some beds rich in *Dikelocephalus*, in which specimens may be inclined). The preservation of conjoined free cheeks along with apparently intact genal spines (Fig. 2.4.10, 2.4.11; Fig. 2.7.1) argues against significant reworking at the sediment-water interface. Early ontogenetic stages are missing, perhaps because their sclerites were insufficiently robust to be preserved in this environment or juvenile growth was spatially localized elsewhere (e.g. [Beheregaray and Sunnucks, 2001](#)). Specimens may have derived from assemblages of individuals alive penecontemporaneously, or from post-exuvial trilobite assemblages, followed by some degree of amalgamation among temporally successive assemblages ([Olszewski, 1999](#)). Thus, the “paleontological resolution” ([Kowalewski and Bambach, 2003](#)), the span of time represented between those individuals alive most recently and those alive longest ago, is likely to have been no longer than years to decades at most. It may be that some beds exclusively represent exuvae and/or carcasses of contemporary individuals that have since been only slightly reworked taphonomically. Thus, these assemblages may offer a glimpse of the ambient local seafloor situation at high

temporal resolution, as is increasingly being recognized among such deposits (e.g. Paola et al., 2018).

Westrop (1986, p. 29) considered the effect of compaction on the cranidial morphology of *Walcottaspis*, then known only from one illustrated specimen, and suggested that Lochman's (in Harrington et al., 1959, p. 254-255) diagnosis of its low relief may reflect sediment compaction. Specimens of both *D. minnesotensis* and *W. vanhornei* from the heterolithic facies show similar patterns of flattening and compression-related cracking, with larger specimens such as FMNH-UC14393a (Fig. 2.3.11) showing an overall greater degree of cracking than smaller ones, as is typical among trilobites (Hughes, 1999). However, differences in the cranidial morphologies of these species cannot be primarily assigned to taphonomic effects. While all *W. vanhornei* specimens show effaced S1 and S2 furrows, several such specimens preserve steep-sided, markedly inflated glabellae, that have not suffered significant compaction (Fig. 2.3.1, 2.3.3, 2.3.6, 2.3.9). Accordingly, effacement of the glabellar furrows was an original, biological feature, and serves to distinguish *Walcottaspis* cranidia from those *D. minnesotensis*, in which these furrows are notably incised.

As is also common in *D. minnesotensis* (see Hughes, 1993, p. 15), infestation resulted in shallow, flat bottomed grooves etched into the interior surfaces of both dorsal surface and the doublure of *W. vanhornei*. As the specimens are preserved as composite molds, these original grooves can also appear as ridges when cast on the underside of the dorsal exoskeleton. The organism responsible was presumably exploiting the interface between the internal surface of the exoskeleton and the soft tissues immediately adjacent. Grooves on the interiors of the dorsal and ventral surfaces are between 0.48 and 0.80 mm

wide and do not mirror each other, suggesting independent origin on each surface. As in *D. minnesotensis*, these structures are particularly evident in the pygidium (Fig. 2.5.2, 2.5.3, 2.5.4, 2.5.7) where they, although sinuous or with angular junctions, tend to extend between the axis (where their author presumably gained entrance) and the lateral margin. A possibly similar groove occurs in a free cheek (Fig. 2.4.10). These structures were likely the result of either a metazoan parasite or a scavenger that was mining associated soft tissues and that partially eroded the exoskeleton as it did so. The similar morphologies and width ranges of these trails in both *W. vanhornei* and *D. minnesotensis* suggest the action of a similar author in each and may be evidence of a shared infester.

2.3.3 Sedimentology

The St. Lawrence Formation is a fine-grained mixed carbonate mud – sandstone unit comprising three lithofacies that includes rare stromatolitic dolomite, a laminated feldspathic sandstone facies containing notable flat pebble conglomerates, and a heterolithic facies in which very fine-grained feldspathic sandstone layers are interbedded with dolomitic mudstones (Hughes and Hesselbo, 1997). All *W. vanhornei* specimens yet recovered are preserved in dolomitic mudstone layers of the heterolithic facies. At Hokah specimens were collected towards the top of the St. Lawrence Formation from a 0.95 m thick buff colored dolomitic siltstone bedset located about 6.4 m above the base of the section (Fig. 2.2). *Walcottaspis vanhornei* specimens are concentrated in a level about 15 cm above the base of this layer. A similar ~0.5 m dolomitic siltstone containing *D. minnesotensis*, but apparently no *W. vanhornei*, occurs about one meter above this level, with its base at about 8.2 m in the log (Fig. 2.2, 2.7).

2.3.4 Co-occurrent fossils and biostratigraphy

Both the Hokah bedsets containing the large species *D. minnesotensis* and *W. vanhornei* also yielded disarticulated sclerites of the trilobite *Iliaenurus quadratus*, and linguiliform brachiopods. The aglaspidid *Cycloptes vulgaris* co-occurs with *W. vanhornei*, and specimens belonging to the trilobite genus *Tellerina* occur along with *D. minnesotensis* (Fig. 2.8) in the upper layer, along with fragmentary aglaspidid remains (Fig. 2.2).

Raasch (1951, p. 148) suggested that *W. vanhornei* defines a distinct biostratigraphic level, the 11th within his *Saukia* Zone. This interpretation places *W. vanhornei* as a stratigraphically late form in the area and is supported by recent sequence stratigraphic analysis. More recent work suggests that *W. vanhornei* was represented within a local, informally defined *Saukiella* trilobite subzone (Runkel et al., 2007, figs. 5, 6) that lies within the *Eoconodontus* conodont Zone, and contains the youngest St. Lawrence Formation rocks outcropping in the area. The appearance of *Eoconodontus notchpeakensis* defines the first subzone of the *Eoconodontus* Zone and this species has been found to the east of Hokah but also in sites further to the west but has not been recovered as yet from the Hokah section. The *W. vanhornei* bearing bed at Hokah almost certainly lies within the *Eoconodontus* Zone, but it is not yet clear whether it is within the *Eoconodontus notchpeakensis* subzone or the overlying *Cambrooistodus minutus* subzone, the eponymous species of the latter being a form largely restricted to strongly carbonate-rich facies (A. C. Runkel, personal communication, 2022). *Walcottaspis vanhornei* thus occurs within the younger strata of the St. Lawrence Formation, but not the youngest yet known, which occur further to the southwest.

2.3.5 Sequence stratigraphic setting

The heterolithic facies of the St. Lawrence Formation represents the toesets of progradational parasequences deposited early during the deposition of a falling stage systems tract (Runkel et al., 2007) at ca. 490 Ma. Although recognizing individual parasequences within the St. Lawrence Formation can be challenging (perhaps because these deposits represent the toesets of the prograding shoreline where depositional and preservational events were relatively rare and haphazard), the beds containing *W. vanhornei* and *D. minnesotensis* at Hokah evidently belong to different parasequences and are separated by seven ~10 cm thick beds of parallel laminated feldspathic sandstone with burrowed tops, which may each represent deposition from a notable storm.

During deposition of the highstand and falling stage systems tracts the shoreline in the Upper Mississippi Valley prograded basinward (i.e., toward the southwest) (Runkel et al., 2007). As the rate of relative sea-level rise declined, sediment supply from the land exceeded the generation of accommodation space, leading to deposition of regressive facies and the outward migration of the shoreface. The result was a series of parasequences whose lateral facies coarsened shoreward, the more offshore, distal toesets of which were characterized by carbonate muds of the heterolithic facies. Their proximal equivalent was fine grained sandstones characteristic of the Norwalk Member of the Jordan Formation, but similar lithologies frequently also interbed with the finer grained carbonates within the heterolithic facies of the St. Lawrence Formation, as stated above. Such sandstone beds resulted from depositional events of sufficient magnitude to transport land-derived sediment into this part of the basin and, where concentrated, constitute the feldspathic sandstone

facies of the St. Lawrence Formation. Flat pebble conglomerates are also common in these facies and, in some cases, indicate episodes of marked stratigraphic condensation (Hughes and Hesselbo, 1997).

The geographical positions of the three verified localities from which known *W. vanhornei* specimens have been recovered fall almost exactly along the projected position of the prograding shoreline according to Runkel et al. (2007, fig. 1; Fig. 2.9). In doing so, they provide additional evidence for the validity of this model. This distribution strongly suggests that the temporal range of *W. vanhornei* was notably short, as Raasch's (1951) biostratigraphic scheme anticipated. To date *W. vanhornei* has been localized to only a single parasequence at Hokah, and its distribution among localities does not exclude the possibility of occurrence within a single parasequence throughout the region (Fig. 2.10). This is a minimum, but given the narrow outcrop belt of its occurrence, *W. vanhornei* is unlikely to have been represented at the abundance seen in the bed at Hokah in more than a small number of parasequences, with five being a maximum estimate. Based on an estimate of the rate of deposition of the entire Croixan Series, Runkel et al. (2007, fig. 11) suggested the average duration of a parasequence within the basin to range between 75,000 and 150,000 years. However, during the early falling stage systems tract parasequence duration was likely to have been at the short end of this range, and perhaps closer to 50,000 years (A. C. Runkel, personal communication, 2021). The duration of the known fossil record of *W. vanhornei* thus likely represents an interval not much greater than about 250,000 years, and likely substantially shorter.

Although we have yet to recover trilobites within the St. Lawrence Formation at Hokah below the layer containing *W. vanhornei* (Fig. 2.2), regional relationships show that *D. minnesotensis* occurred widely throughout the region in both the heterolithic and feldspathic sandstone facies, including in areas where St. Lawrence Formation deposition predated that recorded at Hokah. The occurrence of *D. minnesotensis* both in the next fossil bearing bed above those containing *W. vanhornei* (Fig. 2.2, 2.8) and at localities further west, such as Rushford, Minnesota, confirms Raasch’s (1951) view that the range of *W. vanhornei* occupied only a small portion of the regional temporal range of *D. minnesotensis*, and that *D. minnesotensis* evidently regained its local abundance in the heterolithic facies shortly after a time in which *W. vanhornei* apparently had sole local representation.

2.4 Published views on *Walcottaspis vanhornei* morphology and systematic affinities

Dikelocephalus vanhornei was introduced by Walcott (1914, p. 373) who illustrated and described one counterpart cranium, one thoracic segment, and one pygidium. He noted that although its cranium was closely similar to that of the comparably large trilobite *D. minnesotensis*, its pygidium was strikingly different. The genus *Walcottaspis* was established by Ulrich and Resser (1930, p. 66-68), who refigured Walcott’s part cranium and pygidium, along with the illustration of one additional pygidium. Their justification for generic status was the markedly distinct pygidial structure including the termination of the pleural furrow abaxially to the axial furrow, the one fewer clearly defined axial segment, the absence of marginal spines, the transverse anterior pygidial margin and its elliptical posterior margin.

With respect to closest relatives, Walcott (1914) compared *W. vanhornei* only to *D. minnesotensis*, but Ulrich and Resser (1930, p. 64) placed it with species of the genus *Osceolia*, also known only from the Upper Mississippi Valley, in their newly defined subfamily Osceolinae, from which *Dikelocephalus* was excluded. The basis for this grouping was that the pygidial interpleural furrows of *Walcottaspis* and *Osceolia* are partly or wholly obsolete, and that members of both genera have only four clearly defined pygidial axial rings, rather than the five that they considered characteristic of *Dikelocephalus* (Ulrich and Resser, 1930, p. 65-66). They further supported this assertion by reference to unpublished specimens suggested to be allied to *Osceolia* from the “Devil’s Lake Sandstone”, a nearshore facies variant of the Reno Member of the Tunnel City Group, but which lack marginal pygidial spines. The name that Ulrich and Resser (1930, p. 68) gave to that material, “*Osceolina diabolus*”, is a nomen nudum, the whereabouts of its specimens is unclear, and no further material of this kind has subsequently been reported.

Lochman (1956, fig. 2) suggested that *Walcottaspis* was derived from an unspecified species or species lineage within the genus *Briscoia*, which she considered to be explicitly polyphyletic and derived directly, in her view, from two different species of the idahooid *Wilbernia* (Fig. 2.24). She did not provide character-based support for the particular links invoked, but wrote (Lochman, 1956, p. 449) of certain “irreversible trends in the evolution of Dikelocephalidae” some of which, such as the squaring of the anterior glabella and the obsolescence of the anterior border furrow, are present in *W. vanhornei* but others, such as increased eye length and shortened posterolateral border relative to putative ancestors, are not. Given Lochman’s (1956) recognition of explicitly polyphyletic genera

without specification of putative phylogenetically informative characters within these, the reasoning for her association of *W. vanhornei* with a species within *Briscoia* is unclear, as is that justifying her derivation of *Osceolia* and two branches of a polyphyletic *Dikelocephalus* from other unspecified *Briscoia* species.

Westrop's (1986, p. 29) consideration of the effect of compaction (see above) compared *W. vanhornei* directly with St. Lawrence Formation *Dikelocephalus*, and no other taxa.

A report of two cranidia assigned to *Walcottaspis* sp. from substantially older Cambrian rocks in the Himalaya (Shah et al., 1991, p. 91, pl. 1j, n) was based on misidentification. The Himalayan specimens, though effaced, differ in having a trapezoidal glabella, strong eye ridges and, in one case, an anterior border. These authors reported the specimens to be of Guzhangian age, some 7.5–6.0 Ma older than *W. vanhornei*, although in our opinion these forms are likely still older. Their features compare better to Wuliuan forms such as *Paramecephalus* (see Zhang et al., 1980, pl. 117, 118, figs. 1–6; Jell and Hughes, 1997, pl. 12; Luo et al., 2009, pl. 13, figs. 3,4) or *Xingrenaspis dardapurensis* (Jell and Hughes, 1997, pl. 18, figs. 4–11).

Hughes (1994, p. 53) noted that the pygidial axis of *W. vanhornei* displays fewer rings than in *D. minnesotensis* and suggested that the difference in their morphology might be partly explained if holaspid *D. minnesotensis* retained in its pygidium a segment homologous to one released into the thorax in holaspid *W. vanhornei*.

2.5 Phylogenetic position

Herein we have primarily used parsimony-based phylogenetic analysis, supplemented by a Bayesian maximum likelihood approach, to assess phylogenetic relationships between the various taxa of dikelocephalids bearing an extended cephalic doublure. The cladistic analysis of Dikelocephalidae conducted here uses a branch and bound search of 38 characters, divided into a total of 98-character states, across 16 ingroup taxa and one outgroup (Table 2.1 and Supplementary Data 1). As some characters varied along a continuous scale, we also conducted a separate parsimony-based analysis treating them as such, rather than with user-imposed, discretized character state divisions used in the first analysis. Eleven out of a total of 38 characters were continuous and were measured using the most complete sclerites of each species considered (see table in the Supplementary Data 1 for the character states of continuous characters). For both the discretized dataset, and the mixed continuous character and discrete character dataset, the outgroup was *Prosaukia misa* chosen for its close similarity with dikelocephalids in having a quadrate glabella and elliptical pygidium, but not showing the extended doublure. The species used in the phylogenetic analysis are listed in Supplementary Data 1 with references to their published figures and unpublished images from our image library.

The parsimony analyses were run using Tree Analysis Using New Technology (TNT; Goloboff et al., 2008) and Winclada (Nixon, 2002) was used to map transitions in discrete characters states (Fig. 2.6.1, 2.6.2) and to calculate support indices (Supplementary Data 2, Fig. 1, 2). For the discretized character-state analysis an implicit enumeration

search in TNT resulted in 4 most parsimonious trees, of which the strict consensus tree is depicted in figure 2.6.1, and a tree length of 141, consistency index of 39 and retention index of 33. Although overall tree resolution is poor, relationships between most well-represented dikelocephalids from the Upper Mississippi Valley are supported by unambiguous synapomorphies and suggest common ancestry among *Dikelocephalus* species and *W. vanhornei*, with *W. vanhornei* as sister taxon to *D. minnesotensis*. Bootstrap resampling was calculated by the GC method for 1000 replicates with the implicit enumeration search option (Supplementary Data 2, Fig. 1). Bremer support (Bremer, 1988, 1994) was calculated by default TBR branch swapping setting the suboptimal limit to 6 steps. Both these metrics suggest that relationships of *W. vanhornei* reported above receive the strongest support within the analysis. Maximum likelihood analysis of the same dataset using MrBayes yields consistent with this parsimony-based analysis (Supplementary Data 6), specifically that *D. freeburgensis* Feniak in Bell et al., 1952 is the sister taxon to a clade bearing *W. vanhornei* and *D. minnesotensis*, and that these relationships have posterior probability support comparable to that of other morphological character-based analyses.

For the combined discrete and continuous character-based analysis, TNT implicit enumeration search resulted in a single tree. The 27 discrete characters from this dataset were mapped onto the most parsimonious tree found by TNT (Fig. 2.6.2) with tree length of 72, consistency index of 48 and retention index of 50. Overall tree resolution is improved and maintains shared ancestry among *Dikelocephalus* species and *W. vanhornei*, with *W. vanhornei* as sister taxon to *D. minnesotensis*. Again, Bremer support and bootstrap resampling show these relationships to receive relatively high levels of support (Supplementary

Data 2, Fig. 2). This analysis confirms that these phylogenetic conclusions are not the result of arbitrary character state divisions imposed during the discretization of continuous variables.

The results of both the parsimony-based phylogenetic analysis (and of maximum likelihood analyses conducted to date) all suggest *W. vanhornei* to be sister taxon to *Dikelocephalus minnesotensis*, whose stratigraphic range encompasses that of *W. vanhornei* (Fig. 2.6) and support Walcott’s (1914) original comparison between these taxa. The older *Dikelocephalus* form from the transgressive systems tract in the Reno Member, Tunnel City Group, *Dikelocephalus freeburgensis*, is sister taxon to the clade comprising *D. minnesotensis* and *Walcottaspis vanhornei*. *Osceolia* species lie outside the clade bearing *Dikelocephalus* and *Walcottaspis* and this result predicts that *Osceolia* or its closest relatives will occur in the stratigraphic record prior to the appearance of the *Dikelocephalus*–*Walcottaspis* clade. Neither Ulrich and Resser’s (1930) and Lochman’s (1956) proposed relationships of *W. vanhornei* are supported, and *Briscoia* remains either an association of plesiomorphic species with unresolved relationships (Fig. 2.6.1) or polyphyletic (Fig. 2.6.2). Most *Briscoia* species are based on small numbers of specimens and occurrences widely scattered across Laurentia. A more extensive phylogenetic analysis of dikelocephalids and their relatives is forthcoming but beyond the scope of this paper.

Ulrich and Resser (1930) justified *Walcottaspis* among dikelocephalids largely on the basis of its phenetically distinctive pygidium (see above), and this opinion has not been challenged by any subsequent worker to date. One implication of our phylogenetic analyses is that, if the genus *Walcottaspis* is maintained, the genus *Dikelocephalus* is paraphyletic

(Fig. 2.6). We note this implied paraphyly but defer further consideration until we complete a comprehensive investigation of dikelocephalid morphometry and systematics.

2.6 Shape Variation

Although specimens assigned to *Walcottaspis vanhornei* share definitive features, morphological variation is evident among its members. Here we use semilandmark- and landmark-based geometric morphometric analysis to explore such variation. Specimens were imaged in dorsal view with the palpebral lobe surface mounted horizontally and the axial pygidial furrow mounted horizontally. A set of landmarks were selected: 22 in the cranidium (Fig. 2.10) and 40 landmarks and 240 semilandmarks in the pygidium, with semilandmarks used to capture information about the pleural and interpleural furrows (Fig. 2.11.1, 2.11.2). A pygidial analysis with only the 14 landmarks present on the axial lobe and the axial posterior margin was also conducted (Fig. 2.11.3). Except where prohibited, specimens were coated with ammonium chloride sublimate prior to being photographed. The image library was assembled intermittently between 1986 and 2021, and mostly using a Nikon SRL camera with images captured either as 35 mm black and white negatives, or directly as digital images. Most were taken within the specimen's host institution. Negatives were digitally scanned with a Polaroid SprintScan 35 plus or an Epson Perfection V700 scanner. Cartesian X and Y coordinates of morphological landmarks for each specimen of cranidia and pygidia were recorded using the freely available software tpsDig (<http://www.sbmorphometrics.org/soft-dataacq.html>) and ImageJ (<https://imagej.nih.gov/ij/download.html>). Morphometric analysis of the landmark

dataset was conducted using RStudio interface in R (<https://www.rstudio.com>). In R, the package used for statistical analysis were geomorph (Baken et al., 2021; Adams et al., 2021) for most of the morphometric functions and prWarp (Mitteroecker et al., 2020; Grunstra et al., 2021) for partial warp analysis. For fitting linear regression models, Residual Randomization Permutation Package (Collyer and Adams, 2018, 2021) was used as RRPP has a high statistical power to identify patterns in data (Anderson and Braak, 2003). Preservation in dolomitic siltstone resulted in specimen compaction, which inflates variance due to taphonomic, as opposed to biological, reasons. While we are confident that such variance does not overwhelm the original biological signal, it conflates it in such a way that we cannot confidently interpret the biological significance of very small differences among specimen shape. Accordingly, rather than some of the more sophisticated estimates of measurement error used in recent analyses (see Hughes et al., 2021), we used a simple estimate of measurement error involving multiple remounting, reimaging and redigitizing of three crania (Supplemental Data 4). The result of this analysis is that measurement error accounted for 4.84% of the total cranial variance and thus was not a major contributor to the within group or intergroup variance observed (see Supplementary Data 5). Bookstein (1991, p. 63-66) defined “type 1” landmarks when three surfaces intersect (“discrete juxtapositions of tissues”), and “type 2” landmarks when two surfaces intersect (“maxima of curvature”), noting that arguments for positional homology are stronger for type 1 landmarks than for type 2. This study utilizes both these landmark types (Fig. 2.10, 2.11) but because *W. vanhornei* is somewhat effaced the majority are “type 2”. Although we preferred to use type 1 landmarks where possible, measurement error in shape is broadly comparable to

those of trilobites with a higher proportion of type 1 landmarks (e.g., [Hong et al., 2014](#)), a finding echoed by a recent comparative analysis among landmarks categories ([Wärmländer et al., 2019](#)). The high proportion of type 2 landmarks used herein does not appear to have notably inflated observed variance.

2.7 Results

2.7.1 Cranidial shape changes

The occipital-glabellar length of available *W. vanhornei* cranidia ranges from 1.40 mm to 4.30 mm and, across this span, analysis of cranidial shape change was based on 22 cranidial landmarks superimposed using General Procrustes superimposition of shape configurations of 17 cranidial specimens (Fig. [2.12](#)).

A PCA of the partial warp scores (derived from the thin-plate spline analysis of Procrustes aligned landmarks based on the mean shape of the whole sample) shows that 68.44% of the shape variance is captured by the first three relative warps: Relative Warp 1 (RW 1), RW 2 and RW 3 respectively explain 38.34%, 18.73% and 11.37% of the total shape variance (Fig. [2.13.1](#)). Other 13 RWs each account for less than 10.00% of the total variance and are not considered further (Supplementary Data 3). The deformation grids for the principal components were obtained by comparing minimum to maximum scores on each RWs. Relative warp 1 depicts an increase in relative length of the frontal area (sag.) and an overall contraction of the proportions of the glabella and of the eye (tr.) compared to other structures (Fig. [2.14.1](#)). Relative warp 2 depicts change in curvature of the frontal area, extension (sag.) of the L2 glabellar lobe, and contraction (sag.) of the L1 glabellar

lobe (Fig. 2.14.2). Relative warp 3 reflects widening of the fixigena (tr.) and of the frontal area (tr.) (Fig. 2.14.3).

To investigate whether any of these patterns reflect ontogenetic change, the partial Procrustes distance of individual specimens from the mean of the smallest two cranidia specimens in the dataset were calculated and plotted against the natural log of centroid size as estimated by the generalized Procrustes analysis (Fig. 2.15). A significant positive relationship exists between partial Procrustes distance and $\ln$ CCS (the natural log of centroid size, slope = 0.0486, $p = 0.002267$, $r = 0.7241$). Regression of partial warp scores from the mean shape of smallest two cranidia specimens against $\ln$ CCS is significant ($p = 0.003996$ for 1,000 bootstraps) and suggests that 16.39% of overall shape variance captures ontogenetic variation. A deformation plot was computed by regression of Procrustes aligned landmark data onto the $\ln$ CCS and using the predicted shapes from the regression model. Size-related shape change (Fig. 2.16) includes a relative decrease in frontal area length particularly sagittally accompanied by slight rearward migration of its widest point, slight negative allometry and abaxial migration of the palpebral lobe, and minor relative shortening of the occipital ring. According to sum squared calculation of predicted values from this regression, 28.64% of the cranidial shape variation is ontogenetic.

2.7.2 Pygidial shape variation

The size range for the pygidium is from 2.00 mm to 5.50 mm in terms of total pygidial length (sag.).

We conducted three analyses of variation in pygidial shape for a total of 10 pygidia. One was a landmark-based analysis of landmarks on the axis and pygidial margin that also

included landmarks representing both the adaxial and abaxial extents of the pleural and interpleural furrows. The second was similar but also included semi-landmarks interpolated along the course of each of these furrows, and a third analysis that was limited to the axial landmarks only. In all cases, the smallest well-preserved pygidium specimen was used as the sole ontogenetic reference in this analysis because its centroid size was far smaller than that of all other specimens such that the normal procedure of averaging several specimens to produce a small-sized reference form was not feasible. In no case did we find evidence of significant allometry among the pygidia, although this result may reflect the fact that only ten specimens were part of the analysis. Nevertheless, the analysis did highlight notable patterns of morphological variation among these pygidia that deserved comment and given no evident support for ontogeny-related variation, these can be summarized together. The main results are:

1. The principal morphological variation among pygidia is related to the proportions of the pygidial terminal piece, the length of the postaxial region and the location of where the pygidium is widest. Together these summarize the proportion of the pygidium occupied by the axis.
2. Despite some arbitrariness in exact placement of the adaxial extents of pleural and interpleural furrows due to differential flattening, their positions and courses are notably stable among *W. vanhornei*, and especially so in the better defined, more anterior furrows.
3. In specimens in which the terminal piece is expanded, the third axial ring is notably contracted sagittally.

Pygidial shape variation based on 40 landmarks

These include landmarks marking the abaxial and adaxial margins of 6 furrow left-right pairs (Fig. 2.11.1).

A PCA of the partial warp scores shows that 71.60% of the shape variance is captured by the first three relative warps: RW 1, RW 2 and RW 3 respectively explain 32.15%, 21.14% and 18.31% of the total shape variance (Fig. 2.13.2). Other 6 principal components each contain less than 15.00% of total variance (Supplementary Data 4). Relative warp 1 mostly captures variation in the position of the abaxial extent of the last interpleural furrow, and this may be influenced by differential flattening, but also suggests some variation in the ratio of axial to postaxial length (Fig. 2.17.1). Other than that, RW 1 also captures variation in the relative width of the axis. Relative warp 2 shows variation in the proportions of the axial terminal piece with respect to the third axial ring and in the relative length of the postaxial field (Fig. 2.17.2). Relative warp 3 shows variation in the position of pygidial maximum width and in the relative length of the postaxial field (Fig. 2.17.3).

The relationship between partial Procrustes distance and $\ln$ CCS is not significant (slope=0.02274, $P=0.72000$, $r=0.14170$) (Fig. 2.18). Regression of partial warp scores against $\ln$ CCS is not significant at $P=0.3726$ (at 1,000 bootstraps) but captures 12.23% of the total variance. Accordingly, while limitations of the sample preclude exclusion of any role for ontogeny in generating observed variance among holapsid *W. vanhornei* pygidia, its influence did not dominate observed variation.

Analysis of pygidial semilandmarks

The traces of furrows on the pleural region of *Walcottaspis* pygidium invite investigation via semilandmarks (20 semilandmarks distributed along each of 6 left-right paired pleural furrows, Fig. 2.11.2).

Principal component analysis of general Procrustes aligned landmarks shows that 75.36% of the shape variance is captured by the first three relative warps (RW). Relative warp 1 depicts 37.83% of the shape variance in form of expansion of the postaxial region and change in extent of the posterior most pleural furrows, which is likely influenced partly by degree of compaction (Fig. 2.19.1). Relative warp 2 contains 22.76% of the shape variance and expresses minor variation in positions of the pleural and interpleural furrows (Fig. 2.19.2). Relative warp 3 (14.77% of shape variance) depicts expansion of postaxial region and contraction of third axial ring (Fig. 2.19.3). The six additional RWs each contain less than 10.00% of the shape variance (Supplementary Data 4).

A non-significant negative relationship exists between these variables (slope = -0.02518, $P=0.2753$, $r=0.4083$) (Fig. 2.20). The regression of partial warp scores from reference smallest specimen shape against the $\ln$ CCS is also not significant ($P=0.4456$ at 1,000 bootstraps).

Axial pygidium landmarks

A subset of the previous data comprising 14 landmarks along the pygidial axis was chosen to explore variation therein (Fig. 2.11.3). The 10-specimen dataset was superimposed by generalized Procrustes analysis (Fig. 2.21).

Principal component analysis of Procrustes aligned shape configurations shows that first two relative warps (RWs) capture almost the entire shape variance (84.38%): Relative warp 1 captures more than half of the shape variance (54.61%) and RW 2 explains 29.77% of the variance. The remaining six RWs each capture less than 15.00% of the shape variance in the dataset (Supplementary Data 4). RW 1 shows contraction of the length of the third axial segment while the posterior margin is extended and an overall contraction (tr.) of the axis is captured (Fig. 2.22.1). In contrast, RW 2 depicts expansion of the terminal axial piece which decreases the relative length of the postaxial region (Fig. 2.22.2). The contraction of the third axial segment is consistently shown by both relative warps. The relationship between partial Procrustes distance and $\ln$ CCS is not significant at $P=0.183$ (slope=0.2455, $r=0.488$) (Fig. 2.23). When partial warp scores from reference shape of smallest specimen were regressed against the $\ln$ CCS, the regression is not significant ($P=0.1598$ at 1,000 bootstraps)

Overall, despite the low specimen abundance, *W. vanhornei* shows notable intraspecific variation in both the cranidium and pygidium, with most of this occurring in samples derived from a single locality, Hokah (HH), and there apparently from a single bed (Figs. 2.2, 2.13). The cranidium, known from more specimens, shows evident ontogenetic variation, something not confirmed for the pygidium. Pygidial morphological variation is nonetheless marked, particularly with respect to the length of the postaxial region and, again, this varies markedly within the collection made from the layer at about 6.6 m above the section base at Hokah (Fig. 2.13.2).

2.8 Materials

All specimens of *W. vanhornei* came from the heterolithic facies of the St. Lawrence Formation and are from Hokah, MN unless otherwise specified.

2.8.1 Repositories and institutional abbreviations

Types, figures and other specimens are deposited in the following institutions: University of Minnesota Paleontological Collection (UMPC, now part of the Cincinnati Museum Center [CMCIP] collection); Museum of Comparative Zoology, Harvard (MCZ); Field Museum of Natural History, Chicago (FMNH); University of Wisconsin, Madison (UWGM); United States National Museum of Natural History (USNM) and Yale Peabody Museum (YMP).

2.9 Systematic paleontology

Below we employ the synonymy list notations of Matthews (1973).

Class Trilobita [Walch, 1773](#)

Subclass Libristoma [Fortey, 1990](#)

Order Asaphida [Salter, 1864](#); emended [Fortey, 1990](#)

Superfamily Dikelocephalacea [Miller, 1889](#) (emended [Ludvigsen et al., 1989](#))

Family Dikelocephalidae [Miller, 1889](#); emended [Ludvigsen et al., 1989](#))

While higher level systematic relationship among members of this family and with its relatives will be discussed by us elsewhere, here we reject Ulrich and Resser's (1930) concept of

Osceolinae because our phylogenetic analysis does not support a sister taxon relationship between *W. vanhornei* and species of *Osceolia*. We consider *W. vanhornei* to be part of a clade containing those dikelocephalids with an extended cephalic doublure (see above), and thus not part of the paraphyletic subfamily Dikelocephalinae as conceived of by Ludvigsen et al. (1989, p. 28), which contains taxa traditionally considered to be sauikiid.

Genus *Walcottaspis* Ulrich and Resser, 1930

Type species.— *Walcottaspis vanhornei* (Walcott, 1914) from the heterolithic facies of the St. Lawrence Formation.

Diagnosis.— as for type species by monotypy.

Walcottaspis vanhornei (Walcott, 1914)

Figures 2.3-2.5

v*1914 *Dikelocephalus vanhornei* Walcott, p. 373, pl. 62, figs. 1-3.

v*1930 *Walcottaspis vanhornei* Ulrich and Resser, p. 65, pl. 20. figs. 3-5

1935 *Walcottaspis vanhornei* Twenhofel et al., 1935, p. 1712

1940 *Walcottaspis vanhornei* Richter and Richter, p. 24, pl. 25, fig. 4.

1951 *Walcottaspis vanhornei* Raasch, p. 141, 142, 150.

1959 *Walcottaspis vanhornei* Lochman in Harrington et al., p. 254-255, fig. 191, 1a.

non v*1991 *Walcottaspis* sp. Shah et al., p. 91, pl. 1, figs. j, n.

Lectotype.— Selected herein: Pygidium FMNH-UC14393-b from heterolithic facies of St. Lawrence Formation, Hokah (HH), Minnesota ([Walcott, 1914](#), pl. 62, fig. 3).

Paralectotypes.— Cranidium (FMNH-UC14393-a) and thoracic segment (FMNH-UC14393-c) ([Walcott, 1914](#), pl. 62, figs. 1, 2), paralectotypes from the same bed as lectotype at Hokah (HH), Minnesota.

Diagnosis.— S1 glabellar furrow isolated, transversely weakly incised, effaced in largest specimens. S2 and additional glabellar furrows absent. Fixigena wide relative to other derived dikelocephalids. Pygidium with three clearly incised axial rings and long (sag.) terminal piece. Anterior pygidial margin fulcrate, transverse adaxially, posterior margin elliptical. Interpleural furrows of first two segments abruptly obsolete within pleural platform before approaching axial furrow. Postaxial region of variable length, but short (sag.).

Occurrence.— *Eoconodontus* Zone, heterolithic facies of the St. Lawrence Formation within narrow outcrop belt including Hokah, Winona, and Reno, Minnesota and Bluff Siding, Wisconsin.

Description.— Mature exoskeletons large, largest likely longer than 50 cm sagittally. Cephalon convex, outline semicircular, pygidium lateral margin shape matches that of anterior cephalon.

Glabella quadrate in smaller holaspids, trapezoidal in largest holaspids, inflated, maximum width just posterior to S1 furrow, expressed as slight bulge in L1. Glabellar anterior margin rounded. SO deepest adaxially, isolated in some specimens, shallowing transversely to yield slit-like furrow appearance. S1 isolated, variably incised but deepest

axially where it forms an open U shape, running obliquely slightly forward abaxially. S2 obsolete. Median occipital tubercle present. Low, semicircular to transverse ridge shortly anterior to posterior margin of occipital ring. Axial furrow sharply incised. Frontal area long (sag.), broad (tr.), not less than 35% of occipital-glabellar length, flat to downsloping. Frontal area width is not less than 46% of the occipital lobe width. Anterior margin rounded to slightly angular axially, border absent. Frontal area width (tr) wider than maximum cranial width between palpebral lobes (tr.) in smaller specimens, equal in larger. Opisthoparian, dorsal cephalic suture marginal sagittally, laterally sweeps posteriorly at an angle of 20° to 41° to sagittal axis. Fixigenae wide for family, narrowest preocularly, shortly anterior to S1 where wider (tr.) than occipital lobe length (sag.). Intraocular fixed cheek inflated against palpebral furrow, sloping downward toward axial furrow (tr.). Palpebral lobes relatively short (exsag.) and narrow (tr.), midpoint opposite L1 bulge, relatively longer in smaller specimens. Palpebral furrow crescentic, deeply and evenly incised, eye ridge obsolete but ocular platform inflated to height of palpebral lobe distally. Posterior border area spatulate, terminating in blunt point abaxially, abaxial posterior portion with transverse ridge that parallels course of posterior border furrow. Posterior border furrow evenly incised, anterior face steeper than posterior, running transversely and posteriorly from point where SO projects to meet axial furrow.

Free cheeks arcuate, conjoined. Broad, undivided genal field, gently convex near the margin rising steeply concavely toward flat ocular platform. Posterior border furrow sigmoidal, curving posteriorly into base of narrow, long genal spine. Ocular incisure arcuate, bounded adaxially by shallow arcuate furrow and raised marginal flange forming

eye socle. Terrace ridges on ocular platform inosculate. Doublure wide, extending about nine-tenths of distance from margin to ocular incisure, with flexure in its anterior portion that accommodates the anterior edge of hypostome. Doublure curves upward adaxially, remaining close beneath dorsal surface. Terrace ridges on doublure straight.

Hypostome subquadrangular, wider (tr.) than long (sag.); median body large, oval, inflated; anterior lobe convex, round; posterior lobe short (sag.), wide (tr.). Median furrow pit-like abaxially, shallow axially; maculae oval, small; pit-like furrows are developed at posterolateral margin of posterior lobe; border furrow weakly incised; lateral border triangular, widest (tr.) opposite midpoint of posterior lobe. Posterior border lip-like, gently arched anteriorly in axial portion. Terrace ridges on lateral border straight to sinuous, cuestaform, steep slopes facing adaxially.

Axial region of thoracic segments convex, articulating furrow transverse. Margins of thoracic pleurae transverse adaxially from axial furrow, curving posteriorly abaxial of fulcrum; anterior facet long (exsag.) abaxially of fulcrum; pleural furrow diagonal, firmly incised adaxially, reaching almost to tip of pleura; propleura and opisthopleura of equal length (exsag.) at fulcrum; pleural spine tip blunt. Fulcrum no more abaxial than one third (tr.) of pleural width.

Pygidium anterior margin transverse adaxially, extending posterolaterally abaxial to fulcrum; posterior margin entire, semielliptical. Axis convex, 60 – 72% of pygidial length (sag.) with anterior articulating half-ring, three distinct axial rings defined by narrow and well-incised inter-ring furrows, long (sag.) terminal piece. Ridge arches anteriorly from posterior border of first axial ring, occupying medial three-quarters of ring width (tr.) and

extending across one-half of ring length (sag.) Each axial ring with pair of swollen nodes located anterior of segment midline (exsag.) near axial furrow, two additional pairs of the lobes extend onto terminal piece in lectotype, which also shows one additional incomplete rachial furrow. Terminal piece may be inflated, posterior margin blunt, rounded to bullet-shaped. Pleural furrows entire, extending to near margin in anterior segments; interpleural furrows of first two segments abruptly obsolete on pleural platform approaching axial furrow; third interpleural furrow connects to axis at posterior of third axial ring. Postaxial region short (sag.) but of variable length. Petaloid terraces developed on articulating facet of first pleura. Doublure extends to pleural platform lying close beneath dorsal surface, with faint paradoublural line, terrace ridges on it straight, relief high, steeper slopes facing outwards; some 25 terraces from top of pleural platform to margin.

Other material.— All from Hokah, MN unless otherwise stated. 21 cranidia (FMNH-PE-39216-c, FMNH-PE-39214, FMNH-PE-39215, FMNH-UC-23314-a, FMNH-UC-23314-b, FMNH-UC-23314-c, FMNH-UC-23314-d, CMC-IP-87565x, CMC-IP-89411h, CMC-IP-89411i, CMC-IP-87565j, CMC-IP89411m, CMC-IP-87565n, CMC-IP-87565t, CMC-IP-95630, UWGM 7150, UWGM 7151, UWGM 7152, UWGM 7155, UWGM 7156, YMP73152), 19 pygidia (FMNH-PE-39216-a, FMNH-PE-39216-b, FMNH-PE-39210, FMNH-PE-39312, FMNH-UC-23314-e, FMNH-UC-14393-b, MCZ-IP910 from Bluff Siding WI, CMC-IP-89411a, CMC-IP-89411b, CMC-IP-89411c, CMC-IP-87565d, CMC IP97568, USNM-PAL-72687A from Winona, MI, USNM-PAL-72687B from Winona, MN, UWGM 7157, UWGM 7158, UWGM 7159, UWGM 7160, UWGM 7161), 5 disarticulated free cheek specimens (FMNH-UC-23314-h2, FMNH-UC-23314-h, FMNH-UC-23314-h1, FMNH-UC-23314-i, CM

C-IP-89411y), 3 hypostomes (FMNH-UC-23314-f, FMNH-UC-23314-f, FMNH-UC-23314-g), 1 conjoined free cheek (MCZ-IP-917 from Bluff Siding, WI) and 2 thoracic segment specimens (FMNH-PE-82162, FMNH-UC-14393-c). Other previously figured material includes 1 pygidium (USNM-PAL-72687A) from Winona, MN. (Ulrich and Resser, 1930, pl. 20, fig. 6; Fig. 2.5.4) and 1 plastotype cranidium (USNM-PAL 58608-a) and 1 plastotype pygidium (USNM-PAL 58608-b) cast from Walcott's (1914) figured specimens (FMNH-UC-14393-a and FMNH-UC-14393-b; Ulrich and Resser, 1930, pl. 20, fig. 3, 4).

Remarks.— The proportions of the posterior trunk in our reconstruction are based on a pygidial size in which the marginal outline best matches the shape of the anterior cephalic doublure, which it does closely and that may also suggest spheroidal enrolment in this trilobite. Proportioning the pygidium in this way and assuming 12 thoracic segments in maturity, as known in *D. minnesotensis*, yields an overall body plan that seems realistic (Fig. 2.7.2). However, the number of thoracic segments in holaspid *W. vanhornei* is unknown. Given that *W. vanhornei* has one less clearly defined holaspid pygidial segment than *D. minnesotensis*, one possibility is that the total number of trunk segments was common to both species and that the evolution of *W. vanhornei* from a *minnesotensis*-like ancestor reflected release of the leading pygidial segment into the mature thorax (see Hughes, 1994, p. 53). If the pygidial spines in *D. minnesotensis* were related to this leading segment, then the striking morphological difference between their pygidia might be explained without invoking major body repatterning because the two species may have had quite similar trunk forms, their principal difference being where the pygidial boundary was situated. Although this suggestion is speculative, it illustrates how the trilobite trunk region, with its variations

not only in the form and degree of integration between segments but also in their overall number and allocation to the mature thorax or pygidium, offered more “degrees of freedom” to vary than the cephalon, and may in part explain why the cranidia of *W. vanhornei* and *D. minnesotensis* remain much more similar than their pygidia. On the other hand, in the posterior of the thorax of *D. minnesotensis* segments lost the fulcrum and became markedly more siculate, whereas in *W. vanhornei* the fulcrum was maintained throughout the trunk, as it is present both in the holaspid posterior cephalic and anterior pygidial margins. This suggests a lower gradient of thoracic segment shape change in *W. vanhornei* than in *D. minnesotensis*. A number of determinants of trunk structure were evidently adjusted during the evolution of *W. vanhornei*.

Walcott’s (1914, pl. 62, fig. 3) illustration of the lectotype pygidium of *W. vanhornei* was “retouched”, an ink-based outlining technique used at will to emphasize subtle features. His figure suggests that the terminal piece bears possibly as many as four additional transverse furrows, in addition those defining the three clear axial segments. These additional furrows are not visible in the image of the same specimen provided by Ulrich and Resser (1930, pl. 20, fig. 4), but our illustrations (Figs. 2.5.7, 2.7.1) confirm some transverse structures within the terminal piece. Recognition of an incompletely expressed fourth segment is warranted based on the nodes and furrow expressed, and there may be a fifth set of nodes, but we do not see evidence for all the four additional segments that Walcott (1914, fig. 3) depicted. Furthermore, furrows expressed in the pleural region relate only to the first three axial segments. Such imprecision in segment counts is not surprising. The terminal piece housed the zone of teloblastic cells from which new segments derived and

trilobites varied in the ways in which new trunk segments were expressed with, for example, mismatches known between the numbers of ventral appendages and segments expressed in the exoskeleton (Hughes, 2003). However, there is no evidence of a change in the number of well-expressed segments during the part of the holaspid ontogeny of *W. vanhornei* available for analysis: it is three in all specimens, as opposed to the four segments clearly expressed in both axis and pleural region in most *D. minnesotensis*, a species that also has additional, indistinctly expressed segments in its terminal piece. Accordingly, we consider the two species to differ in the number of firmly expressed pygidial segments, and that this difference between them is not simply variation in the prominence with which the most posterior segments are expressed.

The distinctive elliptical pygidial shape of *W. vanhornei* is homeomorphic with that of several other trilobites. Examples from the same region include *Briscoia pertransversa* Lochman (1956) from the *Prosaugia* Zone of the Tunnel City Group and likewise *Wilbernia* sp. occurring in the “Hudson Member” of the Lone Rock formation in lower stratigraphic units (Fig. 2.24). Both these other examples also bear three clearly expressed segments in the axis, and matching pleural and interpleural furrows that mimic those of the thorax (i.e., all trunk segments are homonomous in structure; Hughes, 2003). Such pygidia must link articulating thoracic segments to the terminal piece across a short interval of three pygidial segments. If the postaxial region is short, then an elliptical shape for the pygidial posterior shape is required in order to produce the necessary pleural width at the anterior of the pygidium to allow integration with the thorax. Accordingly, it is not unexpected that pygidial shape and furrow structure arose iteratively in various groups at

that time. However, *W. vanhornei* is clearly distinguished from such homeomorphs by its unique termination of the anterior interpleural furrows, and by the features that place it as sister taxon to *D. minnesotensis*, which bore a more segment-rich pygidium.

2.10 Data availability statement

Data available from the Dryad Digital Repository:

<https://doi.org/10.5061/dryad.h70rxwdpd>.

2.11 Table

Table 2.1: Matrix of character states for selected taxa. See the Supplemental Data 1 for a descriptive list of character, character states and taxa used in this phylogenetic analysis. Columns correspond to character states designation and rows contain taxa names.

Taxon	Character and Character State																																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
<i>Prosaukia misa</i> (Owen, 1852)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Prosaukia hartii</i> (Walcott, 1879)	0	0	0	1	0	0	0	1	1	0	1	1	0	0	2	0	1	0	0	?	0	0	0	0	0	0	0	0	1	2	0	0	0	1	2	2	0	0	0	0
<i>Briscoia schucherti</i> Ulrich and Resser, 1930	1	0	0	1	2	?	0	2	1	2	2	1	0	0	0	0	1	0	0	?	0	?	?	?	?	0	0	0	?	1	0	0	0	0	1	?	0	0	0	0
<i>Briscoia angustilimba</i> Westrop, 1986	0	0	0	0	2	?	0	0	0	2	1	1	0	0	2	0	1	0	0	?	?	?	?	?	?	0	0	0	2	1	0	0	0	0	1	1	1	0	0	0
<i>Briscoia sinclairiensis</i> Walcott, 1924	1	0	0	0	0	1	1	1	1	2	1	1	0	0	0	0	1	0	0	0	0	1	1	?	?	0	0	0	2	1	0	0	0	1	2	2	1	0	0	0
<i>Briscoia dalyi</i> Walcott, 1914	1	0	0	1	0	1	0	0	1	1	0	0	0	2	0	1	1	0	0	0	1	?	?	?	?	0	1	0	1	1	0	0	0	0	2	2	1	0	0	0
<i>Briscoia llanoensis</i> Winston and Nicholls, 1967	1	0	1	?	?	?	0	0	1	2	1	0	0	0	0	1	2	0	1	?	?	?	?	?	?	0	0	0	1	2	0	0	0	0	?	0	2	0	0	0
<i>Briscoia septentrionalis</i> Kobayashi, 1935	1	0	0	1	2	1	0	2	2	0	1	0	0	0	0	0	0	1	0	?	0	?	?	?	?	0	0	1	1	0	0	0	0	?	0	2	0	0	0	
<i>Briscoia pertransversa</i> Lochman, 1956	1	0	0	2	3	?	0	1	2	?	1	1	1	2	0	0	?	0	0	?	?	?	?	?	?	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Briscoia coloradoensis</i> Walcott, 1914	1	0	0	2	2	1	0	0	1	2	2	1	0	1	0	0	0	?	0	?	?	?	?	?	?	0	0	0	2	1	0	0	0	1	0	2	0	0	0	
<i>Briscoia nevadensis</i> Resser, 1937	1	0	0	1	0	?	0	1	2	2	1	1	0	1	0	0	0	?	0	?	?	?	?	?	?	0	0	0	1	2	0	0	0	0	1	2	0	0	0	
<i>Dikelocephalus minnesotensis</i> Owen, 1852	1	0	0	2	2	1	1	1	0	1	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	2	1	1	1	0	0	1	2	2	1	0	1	
<i>Dikelocephalus freeburgensis</i> Feniak in Bell et al., 1952	1	0	0	2	2	1	1	1	1	2	1	1	0	0	0	1	1	1	0	?	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	2	1	1	0	1
<i>Walcottaspis vanhorni</i> (Walcott, 1914)	2	0	1	?	3	1	1	2	1	1	0	0	0	1	0	1	1	2	1	0	1	1	1	1	1	0	1	1	2	0	1	0	1	1	2	2	1	0	0	
<i>Osceolia sensu lato</i>	1	0	0	0	0	1	0	1	2	2	2	1	0	1	0	0	1	1	0	0	1	?	?	?	?	0	0	0	1	0	0	2	0	1	0	1	1	0	2	
<i>Elkia nasuta</i> Walcott, 1884	1	0	0	1	1	?	0	2	2	0	0	0	0	1	1	0	0	0	0	1	?	1	0	?	?	0	0	0	1	1	0	0	0	1	0	2	1	2	0	
<i>Hamashania pulchra</i> Kobayashi, 1942	2	0	0	2	0	?	?	1	1	1	0	1	1	0	1	0	0	0	0	?	0	?	?	?	?	1	0	0	0	3	0	1	0	1	0	1	0	0	0	

2.12 Figures

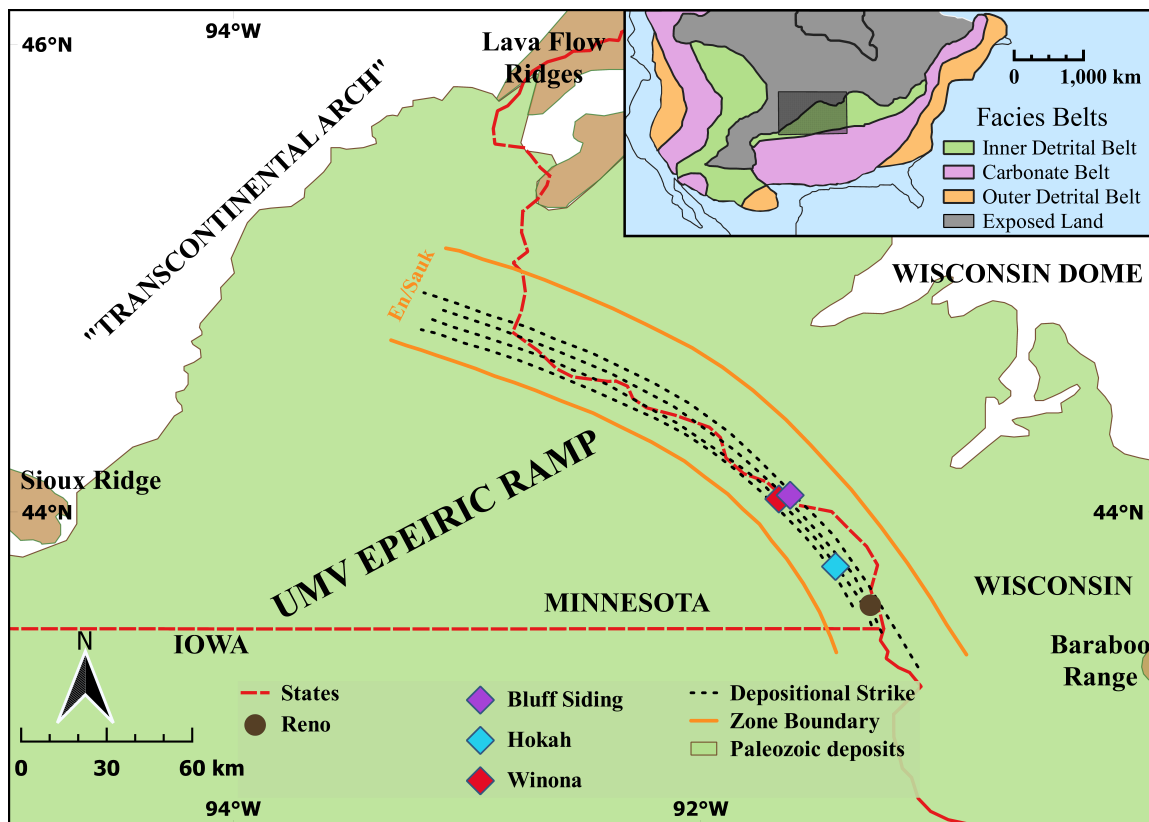


Figure 2.1: Location of Upper Mississippi Valley (UMV) region of the North American cratonic interior showing where lower Paleozoic strata are present. Localities yielding *Walcottaspis vanhornei* are shown with diamond shaped symbols, i.e., Bluff Siding, WI, Winona and Hokah, MN. Reno, MN is shown with a brown circle. Inset shows the location of UMV region (shaded area) with respect to the Late Cambrian continental lithofacies belts of Palmer, 1960. Depositional strike lines are based on Runkel et al., 2007 and *Eoconodontus notchpeakensis-Saukiella* (En-Sauk) subzone boundary is based on Bell et al. (1956); Nelson (1956); Miller et al. (2003)

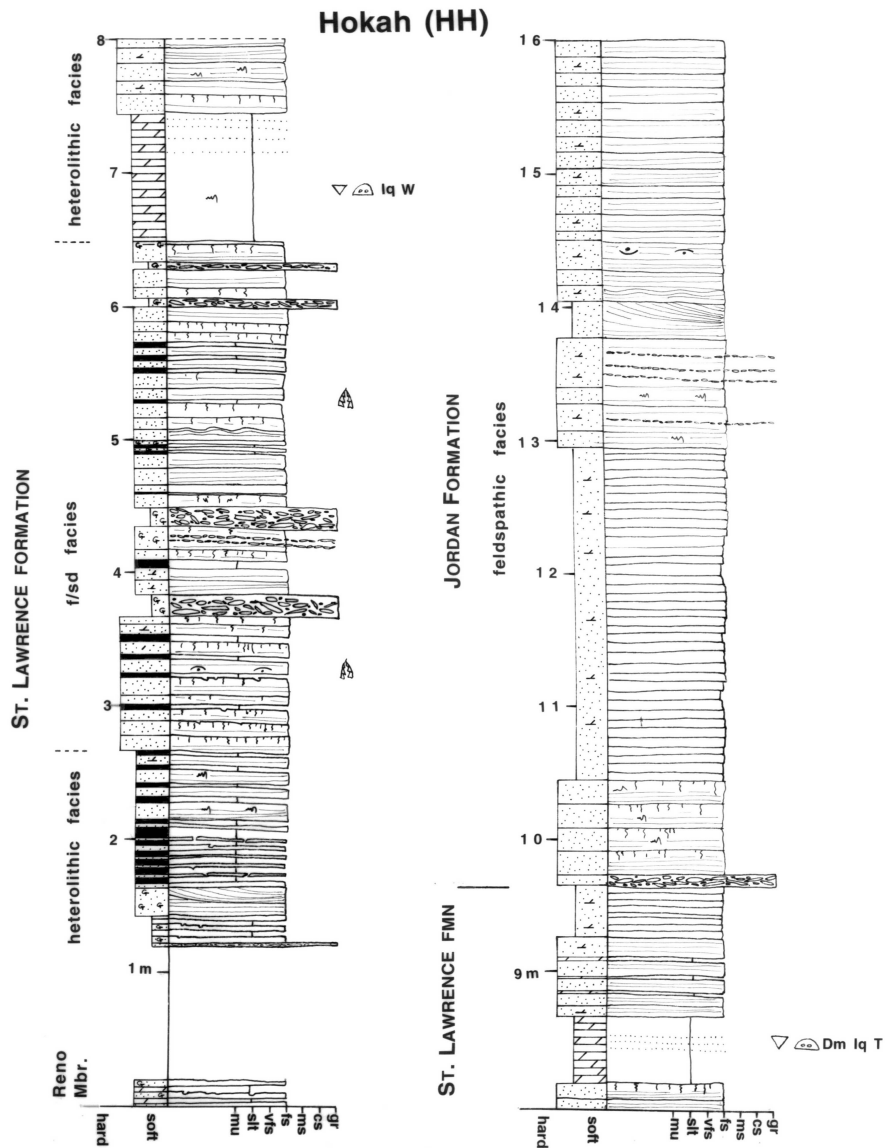


Figure 2.2: Stratigraphic section of St. Lawrence Formation and adjacent units at locality Hokah (HH), Houston Co., Minnesota. Left column depicts lithology and degree of induration with G: glauconite and black: mudstone. Symbols on right side of the log refer to presence of dendroid graptolites, inarticulate brachiopods ('▽') and aglaspids. The trilobite occurrences marked on the log include: *Iliaenurus quadratus* (Iq), *Dikelocephalus minnesotensis* (Dm), *Walcottaspis vanhornei* (W), *Tellerina* (T). Mbr: member, Fmn: formation, f/sd facies: feldspathic facies. (see [Hughes and Hesselbo, 1997](#) for further details).

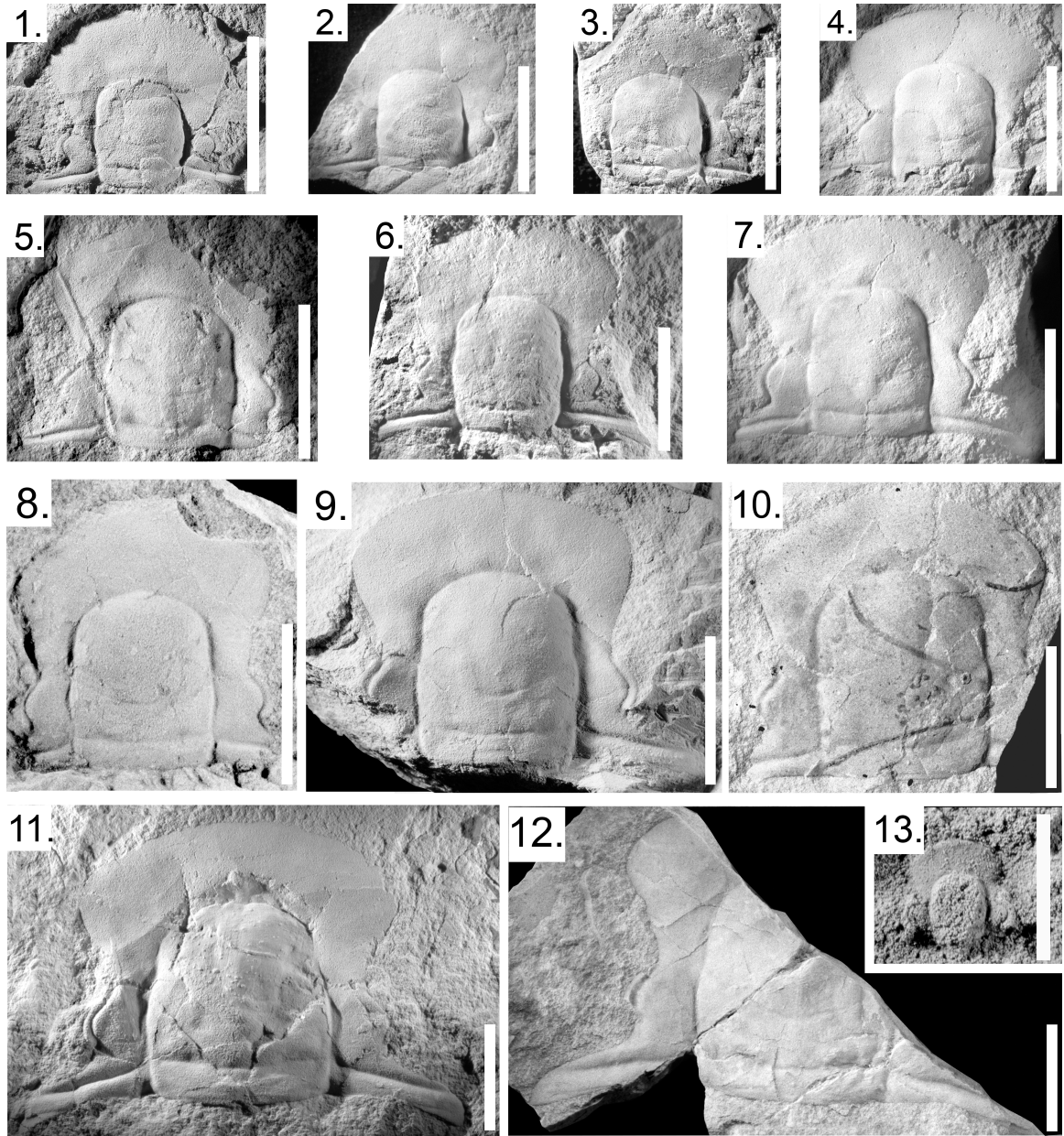


Figure 2.3: *Walcottaspis vanhornei* (Walcott, 1914) cranidia from the heterolithic facies of the St. Lawrence Formation at Hokah, Minnesota in the Upper Mississippi Valley except for (13). (1) FMNH-UC23314c; (2) FMNH-PE39215; (3) FMNH-PE39214; (4) CMC-IP-89411i (formerly UMPC2443i); (5) CMC-IP-87565j (formerly UMPC2443j); (6) FMNH-UC23314a; (7) CMC-IP-89411h (formerly UMPC2443h); (8) CMC-IP-87565x (formerly UMPC2443x); (9) CMC-IP-95630 (formerly UMPC3689); (10) UWGM 7151 (formerly UW4006-491); (11) FMNH-UC14393a, paralectotype; (12) CMC-IP-87565t (formerly UMPC2443t); (13) Small holaspisid cranium, likely *Dikelocephalus*, from Trempealeau, Wisconsin, holotype of *D. juvenalis* Ulrich and Resser, 1930, USNM-PAL-58601. Scale bars are 20 mm (1-12); 10 mm (13).

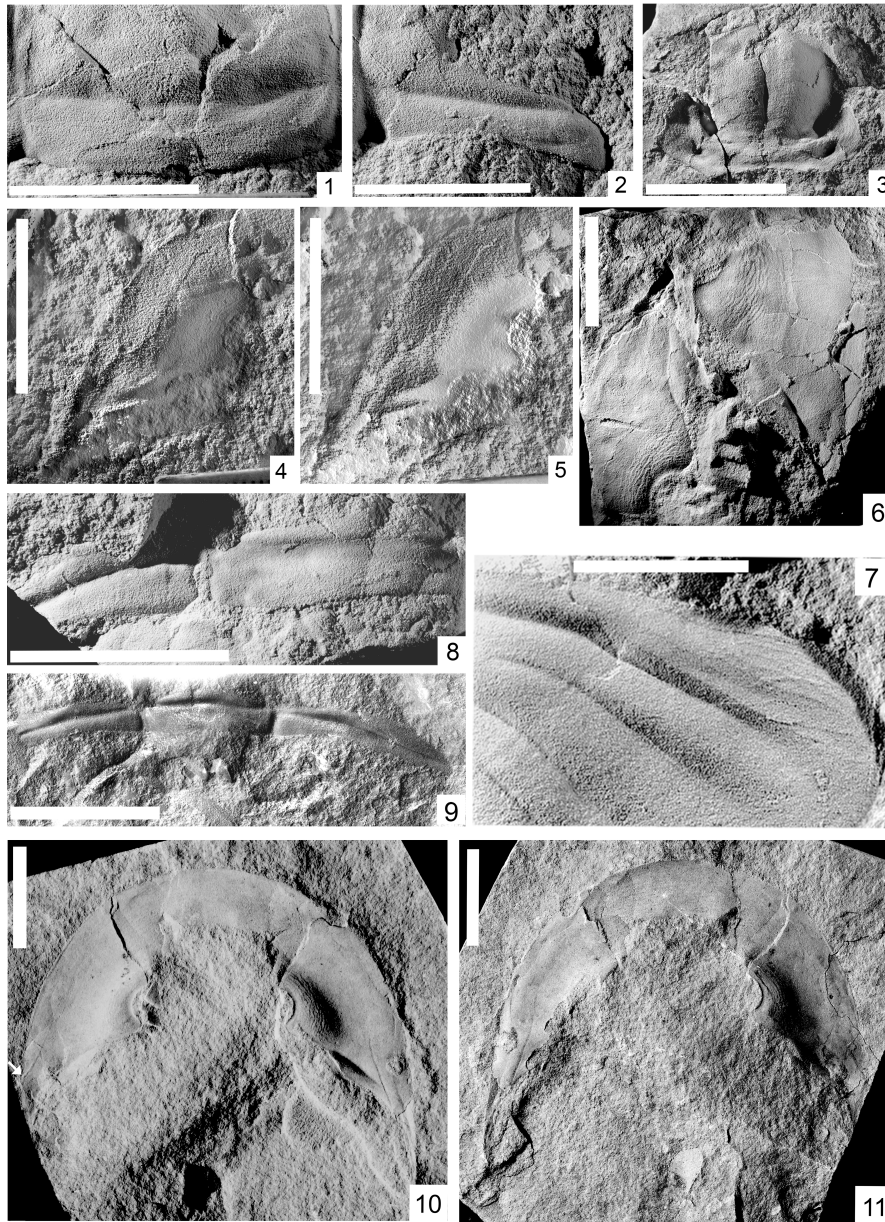


Figure 2.4: *Walcottaspis vanhornei* (Walcott, 1914) sclerites from the heterolithic facies of the St. Lawrence Formation at Hokah, Minnesota in the Upper Mississippi Valley except (9). (1) detail of glabella of FMNH-UC14393a, paralectotype; (2) detail of posterolateral border, FMNH-UC14393a, paralectotype; (3) hypostome, FMNH-UC23314f; (4a) counterpart of right librigena, FMNH-PE82161; (4b) pixel inversion of fig. 4a; (5) two right librigena on same slab, FMNH-UC23314h; (6) detail of FMNH-UC14393b showing terrace ridges, lectotype; (7) axial part of thoracic segment, FMNH-PE82162; (8) pixel inversion of counterpart thoracic segment, FMNH-UC14393c, paralectotype; (9a) conjoined free cheek from Bluff Siding, Wisconsin, MCZ-IP917; (9b) counterpart of conjoined free cheek from Bluff Siding, Wisconsin, MCZ-IP917. Scale bar = 20 mm in all images. Arrow points to an example of a sinuous structure interpreted to reflect infestation.

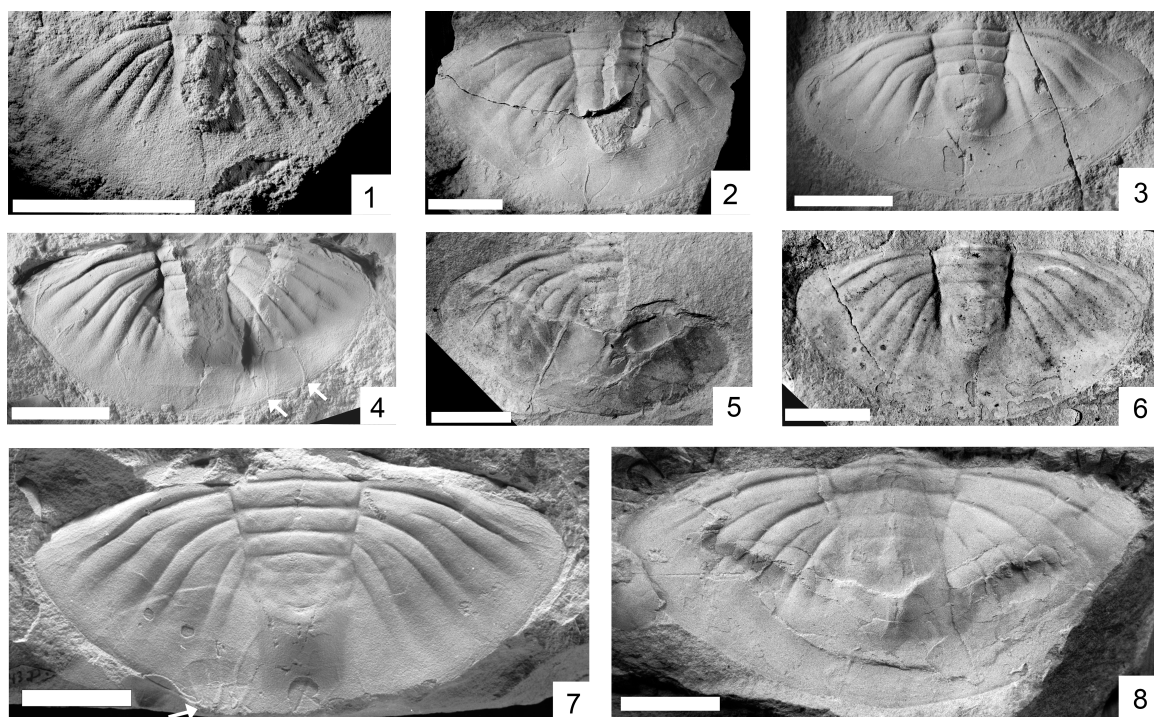


Figure 2.5: *Walcottaspis vanhornei* (Walcott, 1914) pygidia from the heterolithic facies of the St. Lawrence Formation at Hokah, Minnesota in the Upper Mississippi Valley except (4) and (6). (1) FMNH-PE39210; (2) CMC IP97568 (formerly UMPC6352); (3) CMC-IP 89411c (formerly UMPC2443c); (4) from Winona, Minnesota, USNM-PAL 72687A; (5) UWGM 7161 (formerly UW4006-501); (6) from Bluff Siding, Wisconsin, MCZ-IP910; (7) FMNH-UC14393b, lectotype; (8) CMC-IP 89411a (formerly UMPC2443a). Scale bar = 20 mm in all images. Arrow points to examples of sinuous structures interpreted to reflect infestation.

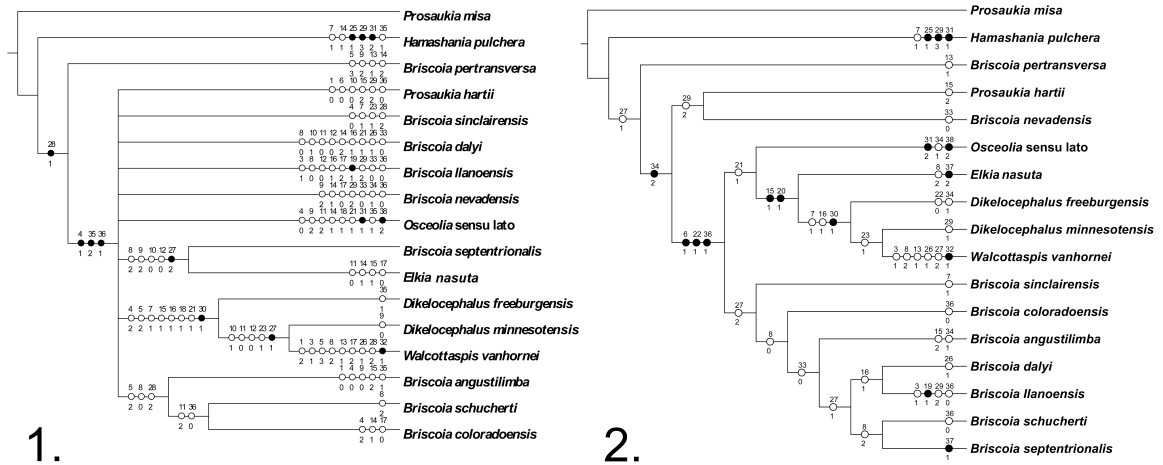


Figure 2.6: Parsimony-based phylogeny of dikelocephalids using *Prosaukia misa* as the outgroup. (1) Strict consensus tree of the 4 most parsimonious tree found for this character matrix using all characters divided into discretized character states. (2) Single tree found for the character matrix using a mixture of discretized and continuous characters. Numbers on top of node branches show the character number and numbers on bottom show the state for that character. Filled circles indicate unambiguous derived character states while open circles indicate convergent derived character states. Refer to Supplementary Data 1 for list of characters, character states and selected taxa and Supplementary Data 2 for Bremer support and bootstrap resampling results.

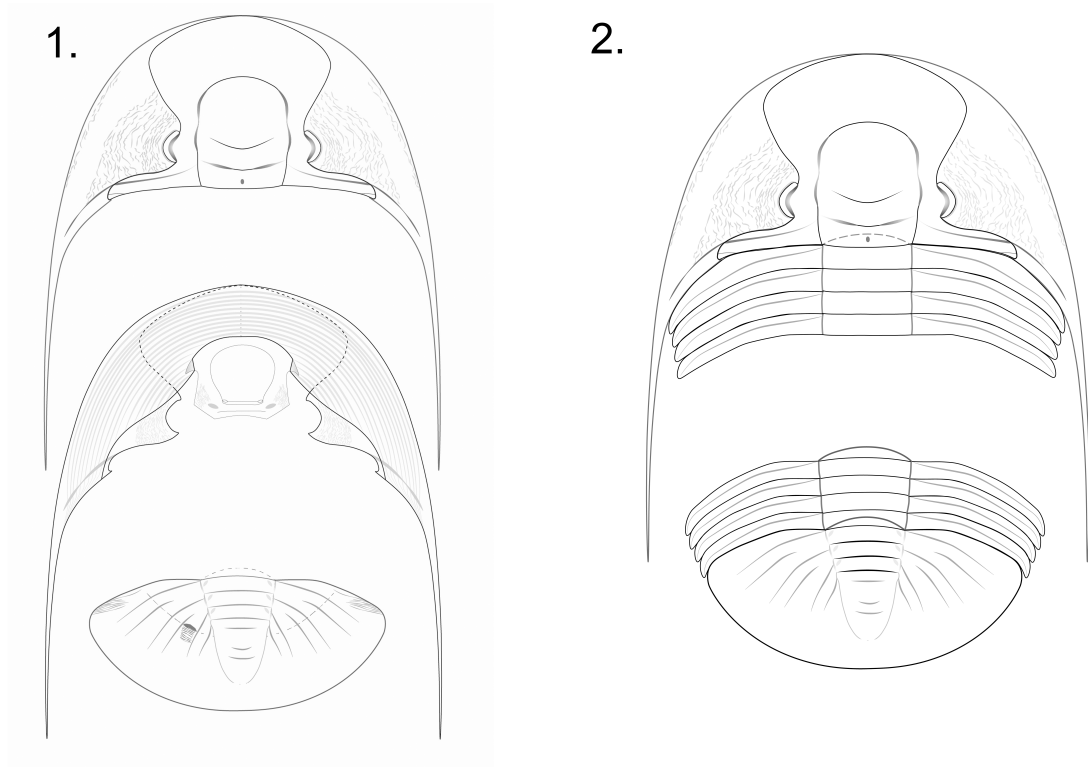


Figure 2.7: Reconstruction of *Walcottaspis vanhornei*. **(1)** dorsal view of cranidium with median tubercle, free cheek with eye platform and surface ornamentation; ventral view of conjoined free cheek with terrace ridges and hypostome with surface ornamentation; and dorsal view of pygidium showing petaloid facet, paradoublural line (dashed) and terrace ridges on the dorsal surface of the venter ventral side of pygidium. **(2)** Dorsal view of holaspis with estimated trunk proportions. The relative sizes of the cephalon and pygidium are drawn such that, upon putative enrollment their marginal outlines match optimally in shape (see text for details).

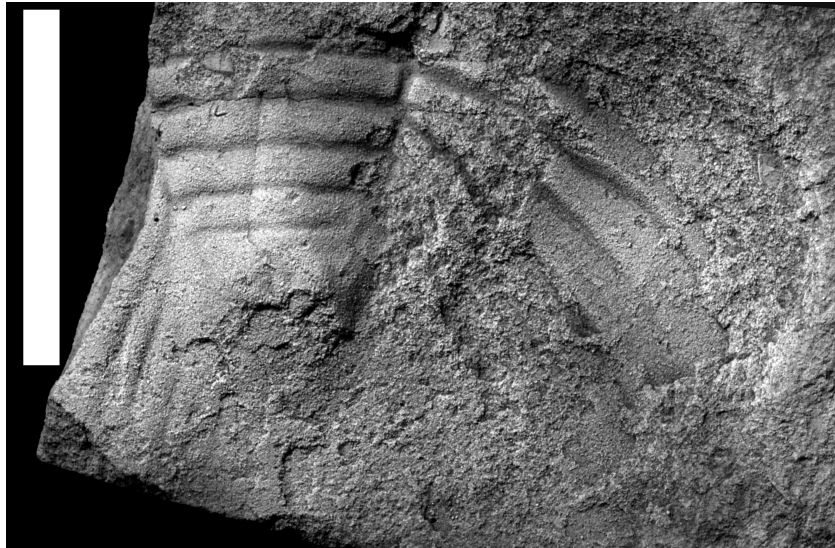


Figure 2.8: *Dikelocephalus minnesotensis* pygidium (UWGM7065) recovered from a dolomitic siltstone bed the base of which is at about 8.2 m in the Hokah (HH) outcrop section, approximately one meter above the level containing the *Walcottaspis vanhornei* specimens collected in this study. This helps demonstrate that *W. vanhornei* occurs within the temporal range of *D. minnesotensis*. Scale bar = 20 mm.

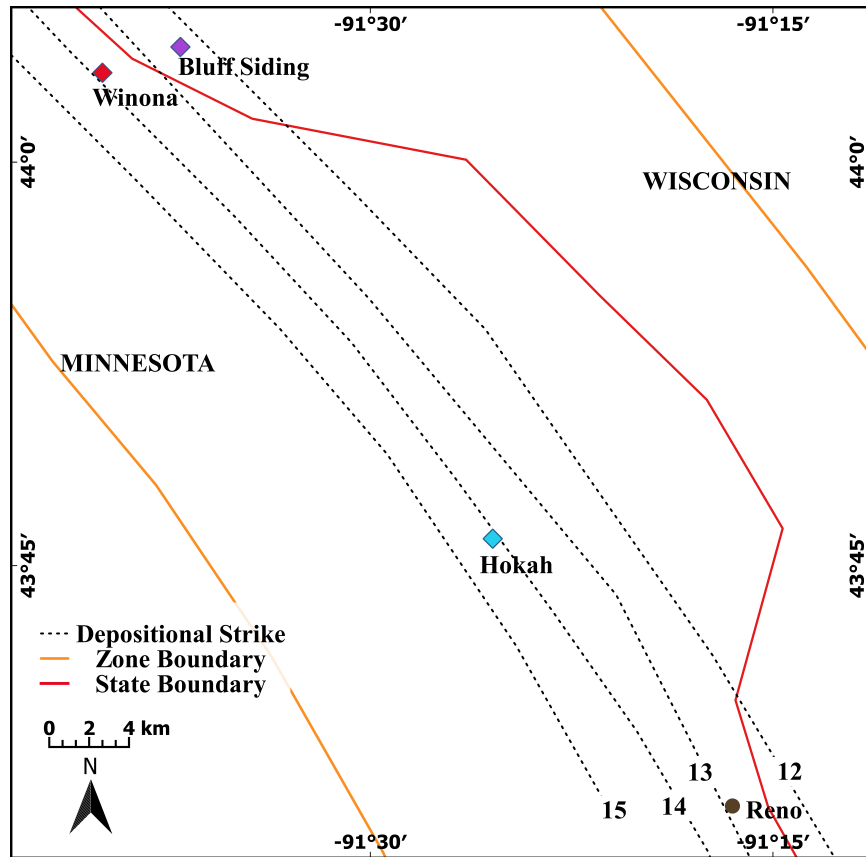


Figure 2.9: Spatial distribution of *Walcottaspis vanhornei* in the four localities from figure 1, consistent with occurrence possibly restricted to the geographical range of single parasequence of the En-Sauk subzone boundary as defined by [Runkel et al., 2007](#).

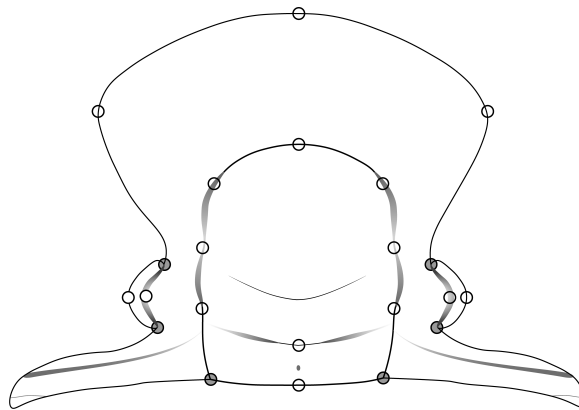


Figure 2.10: Reconstruction of *Walcottaspis vanhornei* cranium showing the set of 22 landmarks selected to optimally capture variation among the specimens available. Specimens had to preserve all 4 axial landmarks, and at least one of each of the paired abaxial landmarks to be included in the dataset. Type 1 landmarks ([Bookstein, 1991](#)) are shown as grey shaded circles, Type 2 landmarks as open circles.

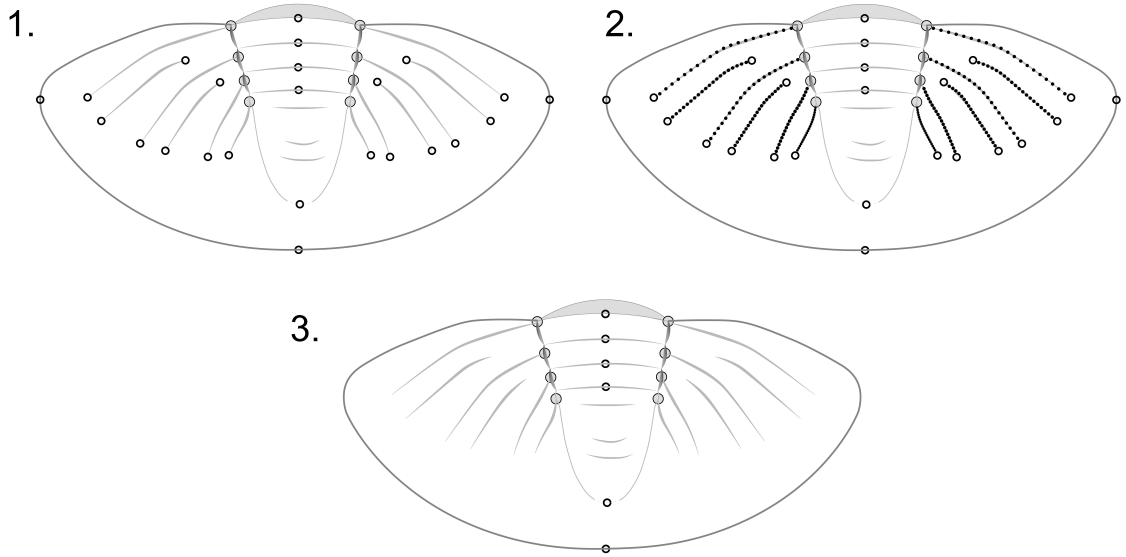


Figure 2.11: Reconstruction of *Walcottaspis vanhornei* pygidium showing the landmarks used to assess morphological variation in a set of 10 specimens. **(1)** landmark scheme comprising 40 landmarks capturing features of the axis, the pygidial margin and extent of pleural and interpleural furrows; **(2)** landmarks scheme of 256 landmarks, including the 40 landmarks mentioned above combined with 216 semilandmarks used to trace the positions of the pleural and interpleural furrows; **(3)** landmark scheme of 14 landmarks capturing only the axial features of the pygidium. Type 1 landmarks are shown as grey shaded circles, Type 2 landmarks as open circles.

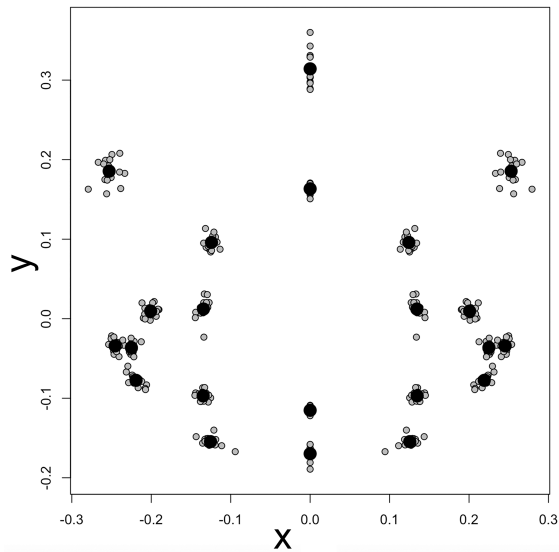


Figure 2.12: Procrustes superimposition of 22 landmarks for holaspid crania of *W. vanhornei*, (N=17).

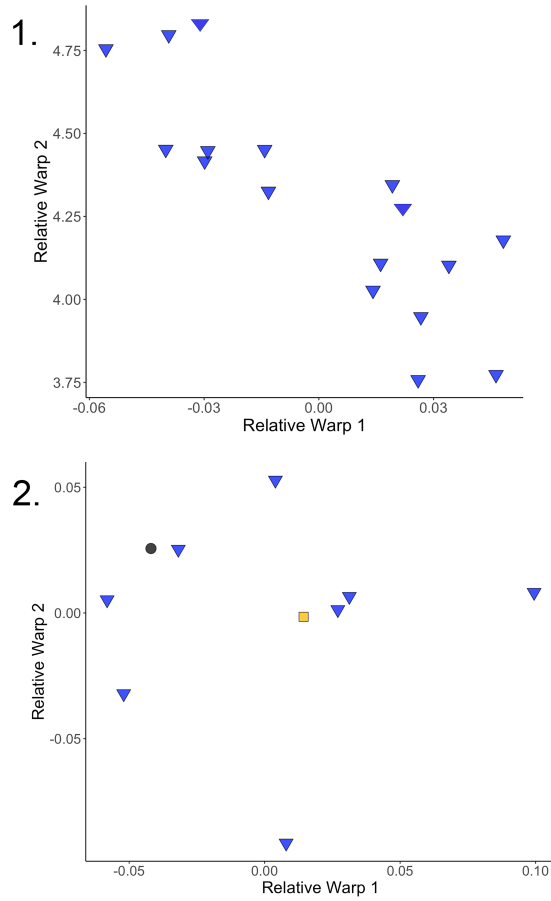


Figure 2.13: Bivariate scatter plots of first two principal components showing *Walcottaspis vanhornei* cranidia and pygidia categorized according to occurrence in the three localities. **(1)** plot of principal component 1 and 2 for cranidial dataset showing 17 specimens from Hokah, MN (blue inverted triangle); **(2)** plot of principal components 1 and 2 for pygidial dataset showing 8 specimens from Hokah, MN (blue inverted triangle), one specimen from Winona, MN (black circle) and one specimen from Bluff Siding, WI (yellow square).

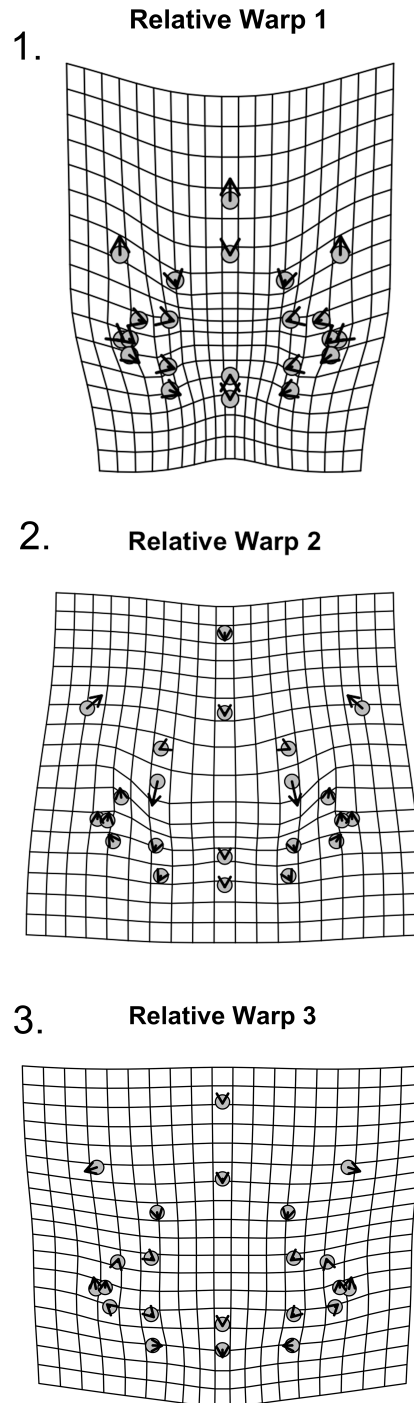


Figure 2.14: Thin-plate spline deformation grid of relative warps for 22 landmarks for holaspid crania of *W. vanhornei*, (N=17). **(1)** shape variation related to RW1; **(2)** shape variation related to RW2; **(3)** shape variation related to RW3.

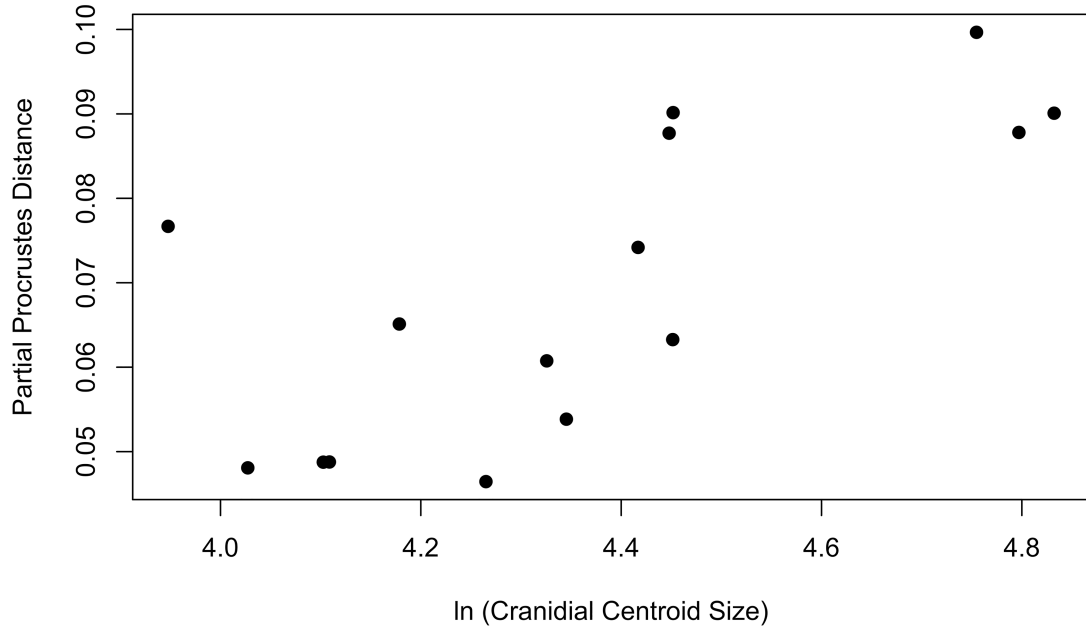


Figure 2.15: Partial Procrustes distance from the reference (mean shape of the smallest two crania) of 22 cranial landmarks of *W. vanhornei*, (N=17).

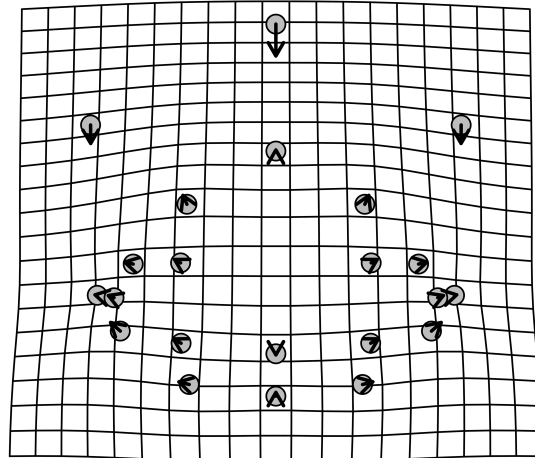


Figure 2.16: Thin-plate spline deformation grid of shape changes with growth for the 22 cranial landmarks of *W. vanhornei*, (N=17).

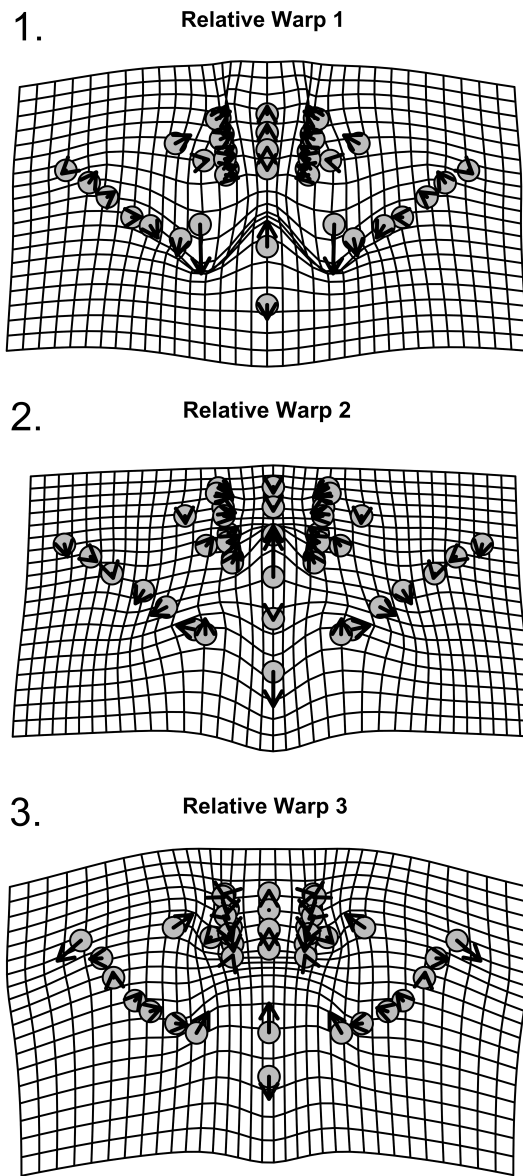


Figure 2.17: Thin-plate spline deformation grid of relative warps for 40 landmarks for pygidia of *W. vanhornei*, (N=10). (1) shape variation related to RW1; (2) shape variation related to RW2; (3) shape variation related to RW3.

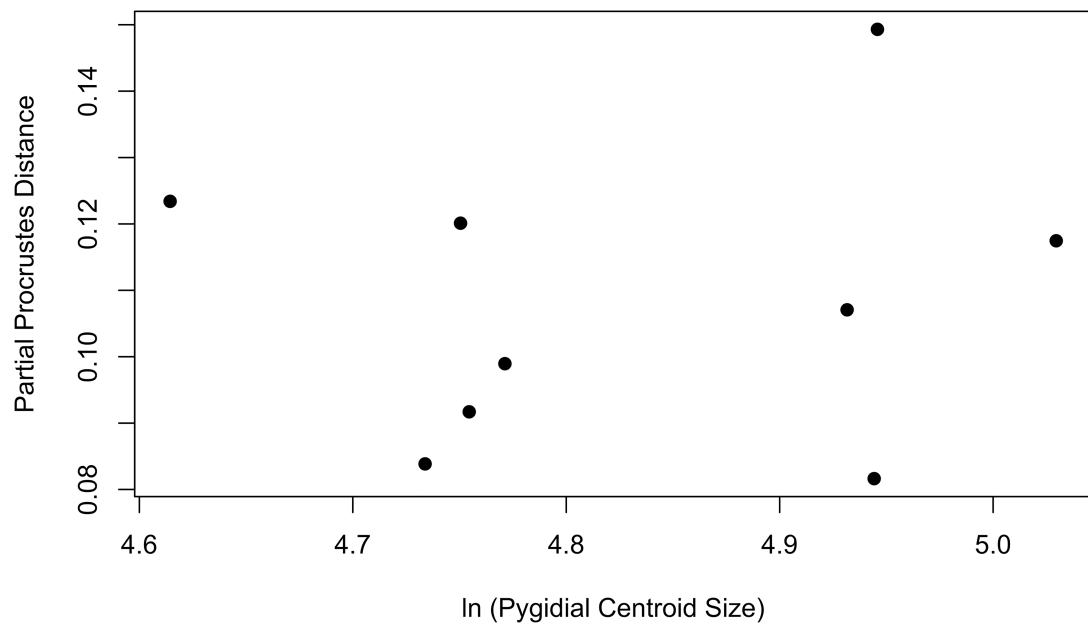


Figure 2.18: Partial Procrustes distance from the reference (mean shape of the smallest pygidium) of 40 pygidial landmarks of *W. vanhornei*, (N=10).

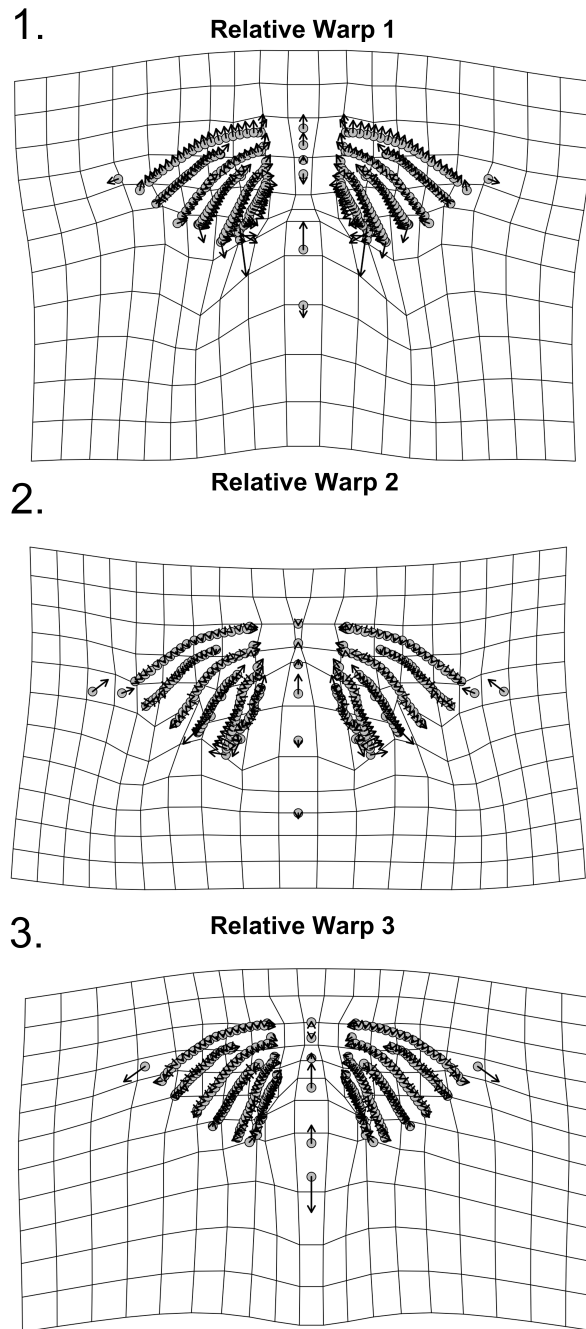


Figure 2.19: Thin-plate spline deformation grid of relative warps for 256 landmarks for pygidia, of *W. vanhornei*, (N=10). **(1)** shape variation related to RW1; **(2)** shape variation related to RW2; **(3)** shape variation related to RW3.

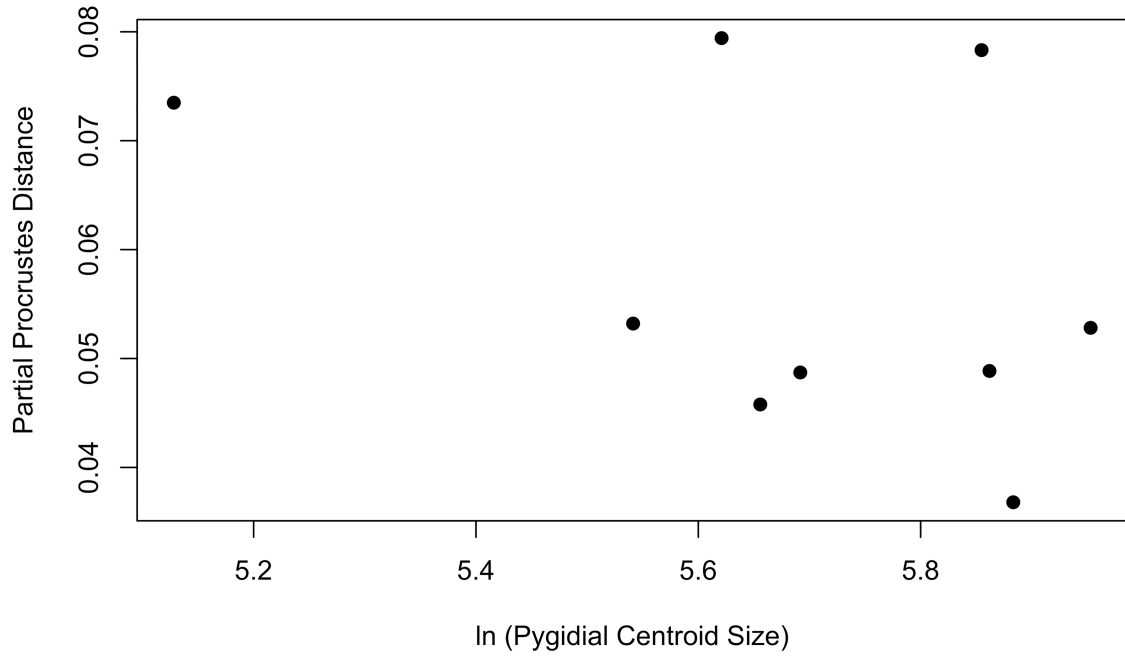


Figure 2.20: Partial Procrustes distance from the reference (mean shape of the smallest pygidium) of 256 pygidial landmarks of *W. vanhornei*, (N=10).

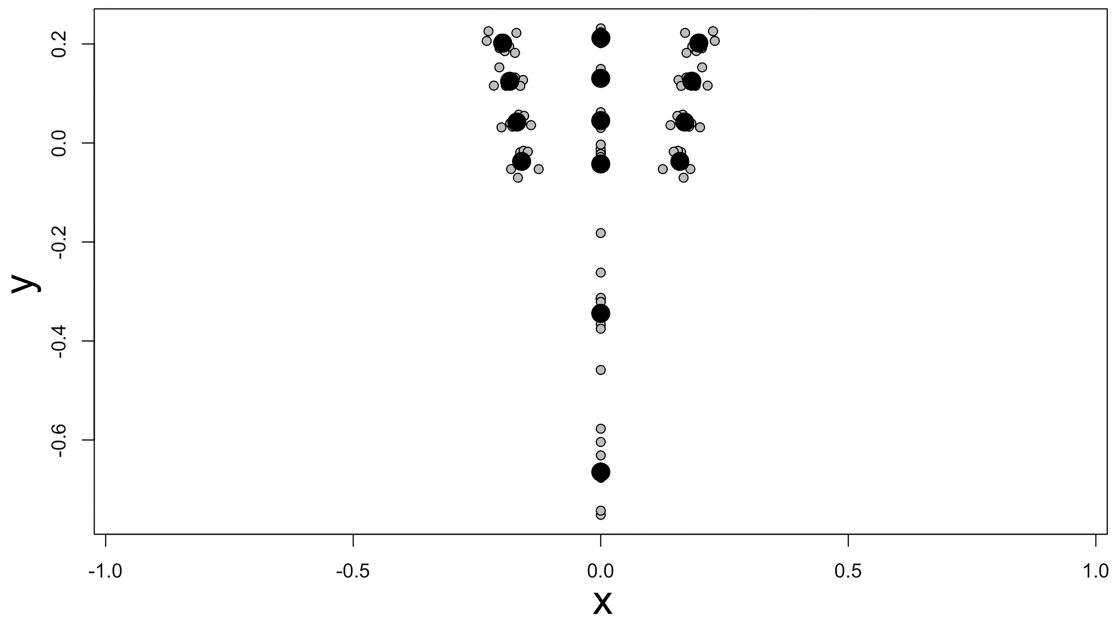


Figure 2.21: Procrustes superimposition of 14 landmarks for pygidia including axis and posterior margin of *W. vanhornei*, (N=10).

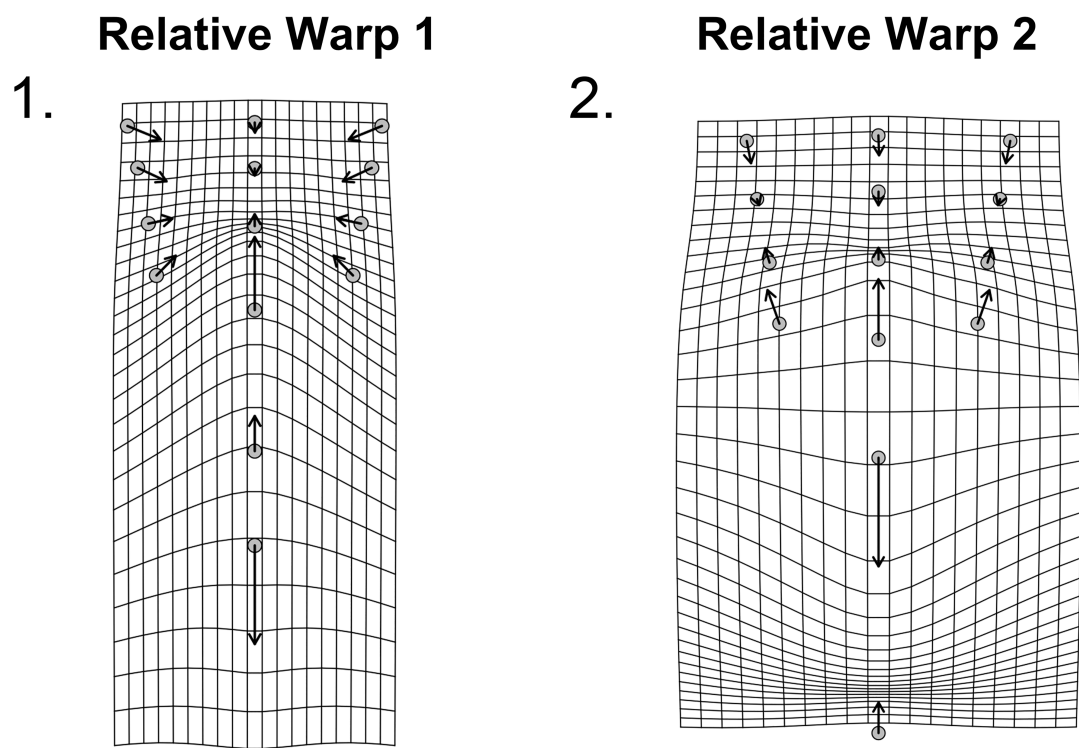


Figure 2.22: Thin-plate spline deformation grid of relative warps for 14 landmarks for pygidia of *W. vanhornei*, (N=10). **(1)** shape variation related to RW1; **(2)** shape variation related to RW2.

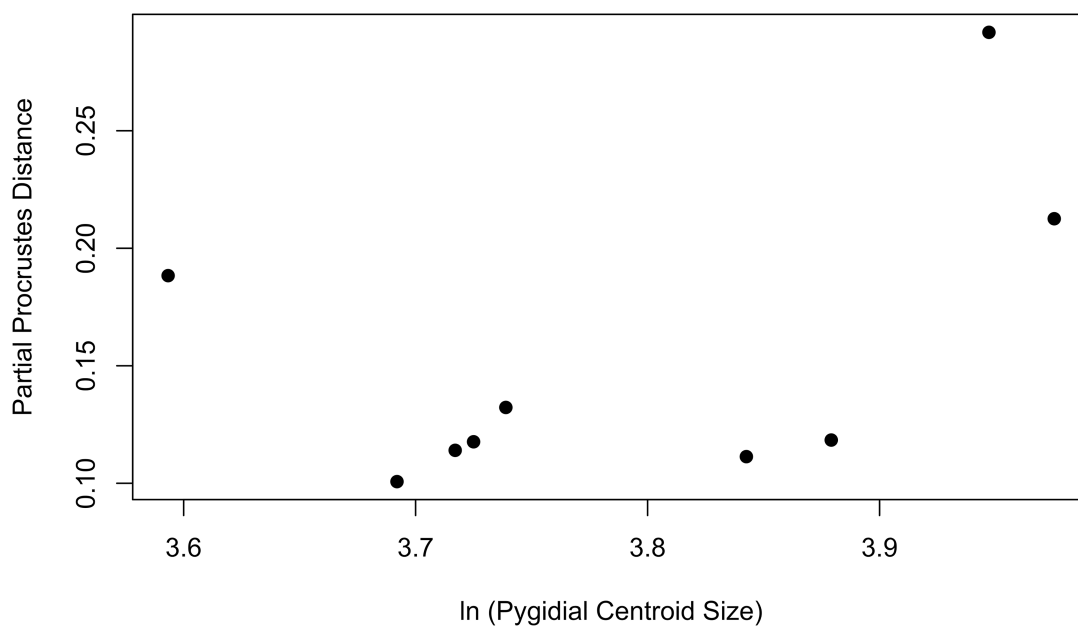


Figure 2.23: Partial Procrustes distance from the reference (mean shape of the smallest pygidium) of 14 pygidial landmarks of *W. vanhornei*, (N=10).

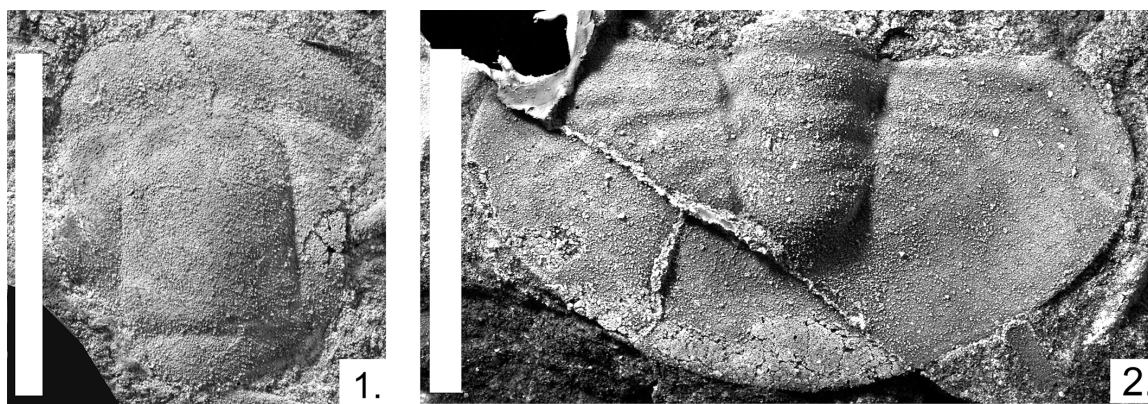


Figure 2.24: *Wilbernia* sp. from the “Hudson Member” of the Lone Rock Formation in the Upper Mississippi Valley from the Winona (MN)/Fountain City (WI) region showing notable homeomorphy with *W. vanhornei*. (1) UWGM7069, cranidium; (2) UWGM7070, pygidium. Scale bar = 20 mm in both images.

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Chapter 3

Occurrence, morphology, and taxonomy of the late Cambrian Laurentian dikelocephalid trilobite *Osceolia* Walcott, 1914

3.1 Abstract

Abrupt appearance of the dikelocephalid trilobite genus *Osceolia* in later Cambrian strata of the upper Mississippi Valley immediately above a flooding surface is succeeded by widespread regional occurrence among approximately 8 parasequences in the early part of a falling stage systems tract. For the first time all *Osceolia*'s sclerite types are illustrated. The taxonomy is revised to recognize two species, of which *O. tumerispina* is new and known only from a dolomitic horizon at a single locality. All five of Ulrich and Resser's (1930) *Osceolia* species are synonymized within *O. osceola* (Hall, 1863), a species widespread in regional dolomitic mudstones and feldspathic sandstones. *Osceolia osceola* shows notable polymorphism in the presence of an axial ledge in the anterior cranial border. Holaspid ontogenetic variation evident within bedding plane collections of *O. osceola* scales with that occurring among collections and across facies. Collection-related morphological differences among the samples beyond those related to size are subtle. The occurrence of larger individuals in more

distal settings may reflect ontogenetically related habitat preference. Osceolinae Ulrich and Resser, 1930 is rejected and the closest relatives of the two *Osceolia* species may occur outside of the upper Mississippi Valley. Material of a local, stratigraphically older, and possibly related Ulrich and Resser, 1930 nomen nudum is figured and described for the first time. *Osceolia*'s cranidial morphotype was converged upon several times during the evolution of Cambrian trilobites among relatives both phylogenetically close and distant.

Zoobank UUID: <http://zoobank.org/bdd2cf1b-331f-4204-8957-eadce195610d>

3.2 Non-technical Abstract

Morphological novelties commonly evolve in nearshore marine environments but the stratigraphic record of such settings is sparse. Where these environments are preserved, detailed sequence stratigraphy can help differentiate between stratigraphic and biotic controls on patterns of morphological variation. Latest Cambrian dikelocephalid trilobites from nearshore deposits of the Laurentian upper Mississippi Valley are sufficiently abundant and widespread to permit insights into evolutionary tempo and mode in its sequence stratigraphic context. Here the relatively small sized dikelocephalid genus *Osceolia* is shown to appear regionally immediately above a maximum flooding surface in the oldest part of the subsequent early falling stage systems tract and to endure for approximately 0.4 Ma., where it commonly co-occurs with its relative *Dikelocephalus*. Its regional first appearance is thus stratigraphically controlled. Within *O. osceola* locality-related morphological variation reflects differences in mean specimen size, with larger individuals common in finer-grained sedimentary rocks, deposited in more distal environments. Such variation is thus primarily ontogenetic. Phe-

notypic variation in the presence of a ledge in the anterior cranial border occurs in all well represented bedding plane collections. Despite additional minor character variation within the sample, no other trends in the morphology of *O. osceola* are evident during its range, although a distinctive new species, *O. tumerispina*, is recognized in a rarely exposed, offshore facies.

3.3 Introduction

Osceolia [Walcott, 1914](#) is a distinctive genus of dikelocephalid trilobites relatively common only as disarticulated sclerites in the northeastern outcrop area of latest Cambrian rocks in the upper Mississippi Valley of the midwestern United States (Fig. [3.1](#)). Despite being represented by several hundred cataloged specimens spread among at least 7 US museums, it has not been the subject of comprehensive evaluation for almost an hundred years. Completing such an evaluation is a component of ongoing efforts to examine the evolutionary tempo and mode of the family Dikelocephalidae [Miller, 1889](#) in sequence stratigraphic context, of which [Srivastava and Hughes \(2024\)](#) on *Walcottaspis* [Ulrich and Resser, 1930](#) is also a part. Here we consider the geographical and stratigraphic setting of *Osceolia*'s occurrence, assess patterns of morphological variation within the genus and their inferred controls, reconstruct the exoskeletal components, revise the systematics, and consider some paleoecological aspects of the genus.

3.4 Geological Setting

Osceolia occurs in all the various lithofacies of the St. Lawrence Formation including in fine grained dolomitic siltstones of the heterolithic facies, in the stromatolitic dolomite facies, and in the laminated sandstones of the flat-pebble conglomerate and laminated sandstone facies (Hughes and Hesselbo, 1997). It is also found in the feldspathic sandstones of the Norwalk Member of the overlying Jordan Formation (Figs. 3.2, 3.3, 3.4). Within this area the *Osceolia osceola* Subzone (Nelson, 1956) is recognized stratigraphically immediately beneath the local incoming of *Eoconodontus notchpeakensis* and contemporary representative species of the trilobite genus *Saukia* (Runkel et al., 2007). *Osceolia osceola*'s regional occurrence is likely coincident with the *Proconodontus muelleri* conodont Zone, and its range possibly extends into the subjacent *Proconodontus posterocostatus* conodont Zone (Hughes and Hesselbo, 1997; Runkel et al., 2007).

3.4.1 Localities

Within the upper Mississippi Valley specimens of *Osceolia* are presently reported from 15 localities (Fig. 3.1) and were mostly collected early in the last century. Reposited specimens are available for all localities except Franklin, Wilton and Norwalk, WI (Supplementary Data 1). *Osceolia*'s geographical restriction to the northern part of upper Mississippi Valley reflects the position of shoreface deposition during the early part of a falling stage systems tract (Runkel et al., 2007). In those localities closest to the cratonic interior, *Osceolia* is present in fossil-bearing horizons throughout much of the St. Lawrence Formation, and in the overlying Norwalk Member of the Jordan Formation (Fig. 3.2). In localities toward

the southwest of its regional occurrence, such as Arcadia and Spring Valley, the genus is restricted to only the lower fossil-yielding beds of the St. Lawrence Formation (Figs. 3.3 and 3.4). This presumably is because at these localities the genus was regionally extinct during the interval in which most of the St. Lawrence Formation was deposited, and thus absent from the higher fossil-bearing beds of this unit. Considering the southwestward progradation of the shoreline during this interval, it is likely that the oldest *Osceolia* regionally are those occurring stratigraphically lowest in the northeastern sections of the outcrop region, such as specimens in the dolomitic mudstones and laminated sandstones of the St. Lawrence Formation in Osceola and Ridgeland. *Osceolia*'s stratigraphic occurrence is thus regionally markedly diachronous (Nelson, 1956).

Where *Osceolia* is preserved, it is common among trilobites. It has been recorded at almost all fossil-bearing outcrops of the St. Lawrence Formation and Norwalk Member within the limits of its geographical range (Fig. 3.1) (also see Supplementary Data 2a and 2b). A new record is at Howe Quarry, 44°52'53" N, 092°5'13" W, about 200 m south of the Highway 29 near the intersection of Road 150 and Route 560, some 13 km east of Spring Valley (SV) Dunn Co, WI (Figs. 3.1, 3.4) and located within a short distance of the "Lucas (MT), Dunn Co, WI" locality of Hughes and Hesselbo (1997), located at 44°52'39" N, 092°5'58" W. Grid coordinates for occurrences of other *Osceolia* reported by Hughes and Hesselbo (1997) are Osceola (OA), Polk Co., WI: 45°19'11.67" N, 92°42'28.70" W, and Arcadia (AAa) Trempealeau Co., WI: 44°13'57" N, 091°28'17" W. Geographical restriction of *Osceolia* to northern localities appears sharply defined (Fig. 3.1), with no occurrences known south of Coon Valley, WI. Whether this was for stratigraphic (Hughes and Hesselbo,

1997, p. 5-7), paleoecological, or sampling reasons remains unclear, but the occurrence of *Saukia* low in the St. Lawrence Formation in inboard, southeastern locations favors the first reason, and *Osceolia*'s near consistent appearance at localities within its geographic range (Fig. 3.1) argues against the last.

3.4.2 Sedimentology/Taphonomy

Osceolia appears in all major lithofacies represented within these units, which are interpreted to represent shoreface deposits (sandstones) and their somewhat deeper water, dolomite-rich lateral equivalents, all deposited in an equatorial, shallow water, epicontinental “inner detrital belt” setting.

In all facies *Osceolia* occurs as intact but disarticulated sclerites (Figs. 3.5-3.17) (as are many of its close relatives and homeomorphs [Figs. 3.18, 3.19], one exception being an articulated dorsal cephalic shield from the Norwalk Member at Osceola [Fig. 3.5.16]). As is general within these stratigraphic units, trilobites occur with moderate abundance in particular beds, and those occurring in the sandstones apparently formed thin shell beds now comprised mainly of internal and external molds (Figs. 3.5, 3.6, 3.12, 3.13). Within the dolomitic mudstones of the St. Lawrence Formation isolated specimens lie parallel to bedding, are composite molds, and commonly show a degree of compaction, including sclerite fracture (e.g., Figs. 3.7.4, 3.7.10, 3.14.6, 3.14.17). While such flattening has likely inflated shape variance in samples from this facies the extent of such flattening is difficult to ascertain. It was apparently insufficient to mask some biologically related patterns of shape change (see below) and, due to the lateral confining pressure along the bedding plane, its influence appears confined to fractures within sclerites that accommodated flattening locally,

rather than wholesale compressional splaying of sclerite form (also see [Hughes, 1999](#)). While flattening apparently increased shape variance in samples from dolomitic mudstone, it does not seem to have imparted a consistent bias upon the forms of these sclerites, and some specimens from dolomitic mudstone faithfully preserve high relief features (e.g., Fig. [3.7.4](#), [3.7.11](#), [3.7.14](#)).

For our morphometric investigation of cranidial shape (see below for details) we divided specimens ($n = 62$) bearing sufficient landmarks (Fig. [3.20.1](#)) for analysis from 9 localities, including both those from dolomitic mudstones and from very fine sandstones, into two groups based on an assessment of their overall preservational quality considering their completeness and degree of fracturing. Exact positioning of landmarks was judged harder to pinpoint in Grade 2 specimens due to factors such as only a single landmark preserved of those that were paired and somewhat reduced confidence in the exact positions of Type I and II landmarks (see below). We then conducted analyses of shape variance within these two groups using the Two Group 8 module within the Integrated Morphometrics Package Suite ([Sheets, 2014](#)), of which Grade 1 was judged to be the better preserved (e.g., Figs. [3.5.1](#), [3.5.11](#); [3.7.10](#), [3.7.16](#)). As expected, within group variance was higher in Grade 2 (0.00291, $n = 36$, e.g., Figs. [3.5.13](#), [3.5.15](#); [3.7.7](#), [3.7.13](#)) than in Grade 1 (0.00246, $n = 26$), which was anticipated to show less taphonomically-related variance. However, as the difference in group variance (0.00045) was of similar magnitude to the largest error associated with measuring the same specimen multiple times (0.00037 and see Supplementary Data 3) and because of this also because we could not exclude other explanations such as random factors, sample size differences, or differences in degrees of ontogenetically-related change within the

samples, we saw no benefit in restricting our morphometric analyses to only those specimens belonging to Grade 1. We conclude that the combined Grade 1 and Grade 2 sample used to assess cranidial morphological variation below, although not free from taphonomic influence, is as good as is available to us.

One lithologically-related distinction among *Osceolia* specimens is that the mean sclerite size is larger in specimens from the dolomitic mudstones of the heterolithic facies than among those from the laminated sandstones of the Norwalk Member of the Jordan Formation (Fig. 3.21). This difference applies to all sclerite types sufficiently common to be assessed. Possible explanations include either 1) a pattern of lithofacies-related hydrodynamic sclerite sorting in which size rather than shape played a dominant role, or 2) different habitat preference for trilobites of different mean size. The markedly different shapes of the sclerites casts doubt on the first explanation, as physical models of the hydrodynamic behavior of trilobites sclerites suggest varied responses among sclerite types (Hesselbo, 1987). Additionally, sclerites of other co-occurring taxa can be of markedly different mean size to those of *Osceolia*, arguing against strong size-related sorting. Furthermore, out-of-habitat transport of fossil material in shallow marine settings is generally rare (Patzkowsky and Holland, 2012). Size-related habitat differentiation, on the other hand, may explain why immature or small individuals of many trilobite taxa are absent in the dolomitic mudstones despite the apparently high preservation potential for such material. The occasional occurrence of large dikelocephalid sclerites within the laminated sandstones is consistent with this explanation, arguing directly against size-related sorting, and consistent with anticipated mortality/molting of some large individuals while onshore. This is also congruent with

the behaviors of the four extant species of horseshoe crab ([Sekiguchi, 1988](#); [Brockmann, 2003](#)), mature individuals of which live in somewhat deeper water, coming briefly ashore to mate, while younger individuals develop in shallow water before migrating into deeper water when further developed. A similar explanation may also apply to the sclerites of *D. minnesotensis*, which also tend to be smaller in sandstones than in the mudstones ([Hughes, 1993](#)). Accordingly, it is plausible that in this area dikelocephalid trilobites moved into shallow waters to deposit their eggs and that these environments served as nurseries before larger individuals moved further offshore for most of their mature lives. Comparable explanations for the occurrences of other trilobites have been invoked previously (e.g., [Paterson et al., 2007](#)), although in the case of *Osceolia* no pre-holaspid specimens are known from any locality.

Free cheeks and pygidia of fellow dikelocephalids *Dikelocephalus minnesotensis* Owen, 1852 and *Walcottaspis vanhornei* ([Walcott, 1914](#)) preserved in the dolomitic mudstones of the St. Lawrence Formation commonly show evidence of an infestor that excavated shallow, flat-bottomed grooves etched into the internal surfaces of the dorsal exoskeleton and doublure in both species (see [Hughes, 1993](#), p. 15; [Srivastava and Hughes, 2024](#), p. 615). These are interpreted as the work of metazoan parasites or scavengers that mined associated soft tissues, and these two taxa may have shared a common infestor. The number of *Osceolia* pygidia preserved in the heterolithic facies exceeds that available for *W. vanhornei*, yet evidence of such infestation in *Osceolia* is generally absent and, where it might occur, is equivocal (see Fig. [3.14.10](#), [3.14.16](#)). A common infestor was perhaps specific to the two large sister species, but less effective within their more distant relative. Degree

of infestation may also relate both to available exoskeletal area for infestation and rate of molting, which likely slowed in large animals (Hartnoll, 1982). In such a case, evidence of infestation might be more common in the larger trilobites because a larger area of live tissue lining the exoskeleton was exposed to infestors for a longer interval of time.

3.4.3 Co-occurrent fossils and biostratigraphy

In multiple localities *Osceolia* occurs in bedding plane assemblages that also yield *Dikelocephalus* sclerites, along with those of a number of other trilobite taxa (Raasch, 1951; Nelson, 1956). Thus, *Osceolia* and *Dikelocephalus* evidently coexisted within the same ecological community. Such co-occurrence is known in both the dolomitic mudstones of the St. Lawrence Formation at Osceola (Fig. 3.2) and Arcadia (Fig. 3.3), and also in the very fine sandstones of the Norwalk Member at Osceola on the Minnesota side of the St. Croix River (Fig. 3.12.17). Given their difference in morphology and maximum size, ecological partitioning between these forms is likely, but this pattern contrasts with the distributions of *Walcottaspis* and *Dikelocephalus*, for which there are no records of co-occurrence between these similarly large and cephalically closely comparable genera. This is despite *Dikelocephalus* occurring in beds shortly beneath and almost immediately above *Walcottaspis* in the section at Hokah, MN. In addition to *D. minnesotensis*, *Osceolia* is recorded to co-occur with species of the trilobite genera *Saukiella*, *Tellerina*, *Eurekia*, *Corbinia*, *Triarthropsis*, *Macronoda* and *Euptychaspis*, and with *Illaenurus quadratus* (Raasch, 1951; Nelson, 1956; Hughes and Hesselbo, 1997), along with various aglaspids, linguiliform brachiopods, and other more rarely represented groups including graptolites, mollusks and serpulids.

Although the upper Mississippi Valley Cambrian trilobite faunas have a long history of investigation, several factors have hindered establishing an adequate trilobite biostratigraphy for the region. These include the marked diachroneity of fossil occurrences that led to the proposal that rock-based units be based on biostratigraphic criteria (e.g., [Raasch, 1951](#)), disagreements on the species-level taxonomy of the more common genera and, within the late Sunwaptan, fossil occurrence commonly being restricted to only single or few horizons within any given section. That *Osceolia* only occurs in the oldest deposits of the St. Lawrence Formation was highlighted by Raasch ([1951](#)) in his 14 “zonal unit” division of the *Saukia* Zone of the upper Mississippi Valley. Nelson ([1956](#)) proposed the *O. osceola* Subzone, a unit that defines the lowest subzone of the *Saukia* Zone in the upper Mississippi Valley. Following recognition that the regional ranges of *O. osceola* and *Rasettia* (commonly referred to by earlier authors as *Platycolpus*) are at least partially coincident ([Nelson, 1956](#), p. 172), the *O. osceola* Subzone has been biostratigraphically succeeded by the “upper *Dikelocephalus* Subzone” (e.g., [Runkel et al., 2007](#)). The *O. osceola* Subzone has been referred to as an assemblage zone ([Nelson, 1956](#)), but of its trilobite fauna only *Osceolia* is readily recognizable as diagnostic of the unit, making the subzone effectively the range of this taxon (see below). The name of overlying “upper *Dikelocephalus*” Subzone suggests it not to be based on the incoming of a distinctive novel form. However, as Raasch’s ([1951](#)) zonal units indicated, the genus *Saukia* apparently makes its first regional appearance in rocks just younger than those bearing *Osceolia* (e.g., [Hughes and Hesselbo, 1997](#), p. 37), and we know of no collection in which these two genera co-occur. It was for this reason that Hughes and Hesselbo ([1997](#), p. 4) suggested recognition of a *Saukia*

Subzone beginning shortly above the observed range of *Osceolia*. The incoming of *Saukia* may correlate with the base of the *Eoconodontus notchpeakensis* Zone in the region (Runkel et al., 2007).

Following the taxonomic revision proposed herein, *Osceolia osceola* occurs throughout the stratigraphic and geographic range of the genus within the upper Mississippi Valley, its range remaining useful in the definition of a regional subzone.

3.4.4 Sequence stratigraphic setting

Outcrops bearing *Osceolia* directly overlie a prominent maximum flooding surface that separates a transgressive systems tract represented by the upper part of the Tunnel City Group from the latest highstand and earliest falling stage systems tracts represented by the St. Lawrence and Jordan formations (Runkel et al., 2007, 2008). There is no evidence of *Osceolia* in the Tunnel City Group, although its close relatives may occur within that unit (Fig. 3.19.3-3.19.6). *Osceolia*'s apparently sudden appearance in the upper Mississippi Valley as a distinct dikelocephalid morphotype is thus apparently related to the stratigraphic condensation and hiatus associated with the maximum flooding surface. It might have evolved within the interval of that hiatus, possibly in further inboard settings for which no sedimentary record remains preserved today. Alternatively, and especially so if *Prosaukia lochmani* Straatmann in Stitt and Straatmann (1997) from South Dakota (Fig. 3.19.10-3.19.14) is confirmed to belong to the genus (see below), earlier *Osceolia* may be represented elsewhere in shallow seas bordering the Laurentian cratonic interior.

Records from the Osceola and Ridgeland localities suggest *Osceolia* occurrences at multiple beds within the St. Lawrence Formation and Norwalk Member, with as many as

4 separate collection levels occurring in the St. Lawrence Formation at Ridgeland (Nelson, 1956, p. 180), and with a 15 meter interval between beds bearing the genus at Osceola (Nelson, 1956, p. 177-178) (Fig. 3.2) that includes a number of flat pebble conglomerate beds that may represent hiatuses in local accumulation history. Given prior estimates of the numbers of parasequences within individual sections and the average parasequence in these rocks being of 50,000 years in duration (Srivastava and Hughes, 2024), we estimate that *Osceolia* was represented with individual sections for an interval of 8 parasequences, or approximately 400,000 years (see Runkel et al., 2007). We are not currently able to trace individual parasequences across the outcrop belt, and this hinders evaluation of whether the southern and westerly prograding architecture of the system increases the duration of the preserved record of *Osceolia* (and thus the duration of the *O. osceola* Subzone) in the region. *Osceolia* occurs in dolomite mudstones near the base of the St. Lawrence Formation in Wisconsin localities at Spring Valley/Lucas (SV/MT) and Arcadia (AAa), and in stromatolitic dolomite at Coon Valley (CN). These may represent the toesets of coarser grained units in more proximal locations. In conclusion, the regional temporal range was likely minimally approximately 400,000 years. This temporal range estimate contrasts with the markedly shorter temporal range of *Walcottaspis vanhornei*, whose represented temporal range is estimated to have been between 50,000 to 250,000 years, and apparently toward the shorter end of this estimate (Srivastava and Hughes, 2024, p. 618).

3.5 Published views on *Osceolia* species and systematic affinities

Dikelocephalus osceola was introduced by Hall (1863) who noted five specimens available to him, of which pygidium AMNH 342 he questionably but correctly assigned to the species (Fig. 3.12.6) and AMNH 39114 which he did not figure and that in our opinion belongs to *Saukiella pyrene* (Walcott, 1914) (Fig. 3.19.9). Walcott (1914, p. 386) established the genus *Osceolia*, illustrating additional specimens of *O. osceola* from the upper Mississippi Valley and reported expansion of the species's geographical range to both Nevada and Texas. These southern and western occurrences are discussed and rejected in the Systematic Paleontology section below.

Walcott (1914, p. 355) also referred to pygidia from the Devil's Lake Member, Sauk Co., WI (USNM locality 81b) as *O. cf. osceola*. These specimens were subsequently assigned by Ulrich and Resser (1930, p. 68) to their nomen nudum "*Osceolina diabolus*". This material is figured here for the first time (Fig. 3.19.3-3.19.6) and is also reassessed below.

Ulrich and Resser (1930, p. 15, 64) established the subfamily Osceolinae to accommodate species of both *Osceolia* and *Walcottaspis* based largely on supposed homology in the pattern of effacement of the pygidial interpleural furrows in both genera. Raasch (1951, p. 141) questioned the status of the subfamily Osceolinae, suggesting that *Walcottaspis* is a descendant of *Dikelocephalus* while viewing *Osceolia* species as a "probably terminal offshoot of *Briscoia*", but provided no character support for this assertion. Lochman (1956,

fig. 2) illustrated a similar view, and suggested basal species of *Dikelocephalus*, *Walcottaspis*, and *Osceolia* to each be derived from a separate lineage within *Briscoia*.

We reject the putatively homologous pattern of effacement of the pygidial interpleural furrows in *Osceolia* and *Walcottaspis* because rare specimens of *Osceolia* with remnant interpleural furrows show that its effacement occurred evenly along the entire interpleural furrow (Figs. 3.12.13, 3.13.14, 3.13.20, 3.14.6, 3.14.15, 3.14.16), whereas in *Walcottaspis* deeply incised interpleural furrows remain evident in the distal parts of all well-developed pygidial segments, with effacement abruptly confined to the adaxial part of the anterior interpleural furrows (Srivastava and Hughes, 2024, fig. 5). This notable difference between persistent, sharply localized and inconsistent entire furrow effacement undermines the putatively synapomorphic basis for this subfamily (Srivastava and Hughes, 2024), with relationships instead suggesting that *Walcottaspis vanhornei* has its sister taxa within *Dikelocephalus*, and with *Osceolia* sensu lato occupying a more basal position (Srivastava and Hughes, 2024, fig. 11). (The presence of a relatively long pygidial postaxial region in some *W. vanhornei* [see Srivastava and Hughes, 2024, fig. 5.5] also questions putative *W. vanhornei*–*Osceolia* sensu lato synapomorphy based on a short postaxial region.) This paper provides a revision of *Osceolia* that will allow us to undertake a more complete phylogenetic analysis of Dikelocephalidae when systematic revisions of *Briscoia* and *Dikelocephalus* species are completed.

In addition to the type species, *O. osceola*, Ulrich and Resser (1930) established five more species, two of which included distinct varieties both recognized on the basis of

an adaxial ledge in the anterior border. Raasch (1951) proposed synonymy of most but not all Ulrich and Resser’s *Osceolia* species (see Systematic Paleontology section below).

3.6 Shape variation among *Osceolia* cranidia and pygidia

Morphological variation among *Osceolia* beyond that taphonomically induced was the basis for much of the finely resolved species and variety designations of Ulrich and Resser (1930), their subsequent near wholesale synonymy (Raasch, 1951) notwithstanding. In order to explore morphological variation within the genus, our approach has been to first assess patterns of intracollectional variation (c.f., Hughes, 1994), and then compare such patterns more broadly among different collections. This was applied to both cranidia and pygidia, as other sclerites were either too poorly represented or preserved, or too difficult to represent with homologous landmarks. Individual collections likely provide the highest temporal resolution among individuals available to us and were used to assess whether patterns seen across the sample as a whole mimic those seen within individual collections. We used landmark-based geometric morphometrics to explore such variation. All *Osceolia* specimens were imaged in dorsal view with the palpebral lobe surface mounted horizontally and the pygidial axial furrow mounted horizontally. Except where prohibited, in order to reveal the morphology more clearly, specimens were coated with ammonium chloride sublimate prior to being photographed. The image library was assembled intermittently between 1986 and 2024 and acquired mostly using a Nikon SLR camera with images captured either as 35 mm black and white negatives, or directly as digital images. Images were taken within the specimen’s host institution or at the University of California, Riverside.

Negatives were digitally scanned with a Polaroid SprintScan 35 plus or an Epson Perfection V700 scanner. Cartesian X and Y coordinates of morphological landmarks for each specimen of cranidia and pygidia were measured using the freely available software tps-Dig (<http://www.sbmorphometrics.org/soft-dataacq.html>). Morphometric analysis of the landmark dataset was conducted using RStudio interface in R (<https://www.rstudio.com>). The R packages used for statistical analysis were Geomorph ([Adams et al., 2021](#); [Baken et al., 2021](#)) for most of the morphometric functions, Residual Randomization Permutation Package ([Collyer and Adams, 2018, 2021](#)) for calculating linear regression models and ggplot2 package to plot specimens as classified according to certain relevant parameters ([Wickham and Chang, 2016](#)). Here we defined “Type I” landmarks at juxtapositions of three surfaces/tissues (“discrete juxtapositions of tissues” of Bookstein [[1991](#), p. 63-66]), and “Type II” landmarks as points of maximum of a curvature along a boundary (“maxima of curvature”). Arguments for positional homology are stronger for Type I landmarks than for Type II and this study utilizes both kinds (Fig. [3.20](#)), with the majority being Type II. This notwithstanding, the landmark scheme does not appear to have unduly influenced the observed overall variance, as measurement error in shape is broadly comparable to those of trilobites with a higher proportion of Type 1 landmarks (Supplementary Data 3, e.g., [Hong et al., 2014](#)). This finding is echoed by a recent comparative analysis among landmarks categories ([Wärmländer et al., 2019](#)).

The analysis of cranidial shape was based on 28 cranidial landmarks (Fig. [3.20.1](#)) and pygidial analysis was based on 13 landmarks (Fig. [3.20.2](#)). Of a total of several hundred *Osceolia osceola* cranidia and pygidia available to us, a total of 62 cranidia (Taphonomic

Grades 1 and 2 combined) and 41 pygidia preserved a sufficient number of landmarks to provide morphometric coverage capturing most major aspects of sclerite shape. As the sample sizes of suitable specimens for most individual localities are small (>10 specimens), we present only:

1. Analyses from the most prolific individual collection, that from the Norwalk Member at Osceola, WI
2. An analysis that combines all measurable specimens of *Osceolia osceola* available to us.

3.7 Results

3.7.1 Shape variation within an individual collection

Osceola, WI, Norwalk Member collection. This collection yielded 20 cranidia and 14 pygidia ($n = 14$) and is from USNM locality 78 (see below for details).

A PCA of the Procrustes aligned coordinates of the cranidia shows that 50.2% of the total shape variance is captured by the first two relative warps with Relative Warp 1 (RW 1) and RW 2 explaining 31.7% and 18.5% of the total shape variance respectively (Fig. 3.22.1). The other 17 RWs each contain 10% or less of the total shape variance (see Supplementary Data 5) and are not to be considered further herein. Centroid size was plotted against RW 1 to explore whether the principal variation in the sample might be ontogenetically-related (Fig. 3.23.1). While no clear trend relates these variables, variance along RW 1 increased among larger sized individuals. A thin-plate spline grid of Relative

Warp 1 captures variation in frontal area width and in the relative length (sag.) of the L1 lobe (Fig. 3.24.1). A regression of Procrustes aligned landmark configurations onto the natural log of centroid size ($\ln$ CCS) suggests that 6.7% of the total shape change in the sample is ontogenetic. Size-related shape change according to this regression is widening of the frontal area (Fig. 3.25.1), and the deformation grids of ontogenetic allometry and RW 1 are comparable in showing reduction of the relative palpebral lobe length, and widening and lengthening of the frontal area, with the polarity observed along RW 1 with respect to overall size being arbitrary. It is notable that although ontogeny accounts for a small component of shape change within this sample, similar shape changes nevertheless mark the major morphological variations in the sample (as captured by RW 1), suggesting phenotypic variation about ontogenetically variable trends. The relatively small ontogenetic component likely reflects the limited size range of the cranidia within this sample.

A PCA of 14 pygidia shows that 78.9% of the total shape variance is captured by the first two relative warps: RW 1 contains 59.4% and RW 2 contains 19.5% of the total shape variance (Fig. 3.22.2). The remainder of the 9 RWs contain 10% or less shape variance (see Supplementary Data 5) and are not considered further. Larger size pygidia score low on RW 1 (Fig. 3.23.2), and a thin-plate spline reveals the major shape change along this vector as variation in the width between the posterolateral spine bases (Fig. 3.24.2). Procrustes aligned landmarks configurations were regressed onto the natural log of centroid size ($\ln$ CCS) in this dataset. The major size-related shape change according to the regression shows that the distance between the spine bases increases during ontogeny (Fig. 3.25.2), with the reversed polarity observed in RW 1 with respect to overall size being

arbitrary. According to the sum squared calculation of the regression predicted values, 40.6% of the total shape change is ontogenetic. (For an additional analysis of the combined Osceola Norwalk collections from WI and MN localities, see Supplementary Data 4.)

3.7.2 Shape variation within the entire *Osceolia osceola* collection

62 cranidia and 41 pygidia from all collections of *O. osceola* were pooled to analyze the shape variation in the species as a whole. A PCA of Generalized Procrustes superimposed cranidia landmark configurations was then classified according to which collections the specimens belong (Fig. 3.26). The total shape variance contained in the first two relative warps was 45.2% (26.3% in RW 1 and 18.9% in RW 2) and the remaining 24 RWs contain less than 12% of shape variance (see Supplementary Data 5). The scatter of specimens from the pooled Osceola collections in the RW 1/ RW 2 plot (blue square in Fig. 3.26.1) covers much of the total area occupied. The most striking result is that the larger specimens are mostly preserved in dolomitic mudstone, and smaller ones in feldspathic sandstone (Fig. 3.21.1) and that there is a transitional overlap in shape and size among specimens from these lithofacies. Smaller cranidia score lower on RW 1 than larger ones, and the pattern of size-related shape change weakly present within the Norwalk Member collection from Osceola (Supplementary Data 4, fig. 4.1.1) is consistent with the stronger pattern seen across the sample as a whole (Fig. 3.26.2). The major shape change captured by RW 1 is a marked ontogenetic decrease in the relative width (tr.) and slight decrease in the relative length (exsag.) of the palpebral lobe, an increase in the relative length and width of the frontal area, and a relative contraction in the anterior part of the glabella (Fig. 3.27.1). The pattern of allometric shape change is broadly consistent with the shape changes captured

by RW 1 (Fig. 3.27.2). A regression of superimposed landmark configurations onto natural log of centroid size suggests that in the pooled sample 17.7% of the total shape variance is ontogenetic. It effectively captures size-related differences in shape and any collection-related shape variation apparently largely reflects differences in mean specimen size among collections. Variation on RW 2 is not apparently size related.

A PCA of the pygidial landmark dataset showed that 70.5% of the shape variance was contained in the first two relative warps (RW1 = 46.7%, RW 2 = 23.8%). The remaining 9 RWs account for 12% or less of total shape variance (see Supplementary Data 5) and are not considered further. Much of the morphological variation within the entire *O. osceola* pygidial dataset mimicked that within that of the pooled Osceola sample (blue square in Fig. 3.28.1), as in the cranial analysis. The pygidia with higher scores on RW 1 are larger than those with low scores (Fig. 3.28.2). The RW 1 thin-plate spline grid reflects a relative increase in the width between the posterolateral spine bases (Fig. 3.29.1). Regression of the Procrustes superimposed landmarks onto ln CCS shows that 6.1% of the total shape variance is ontogenetic. The allometry grid shows shape change that is consistent with that seen in the RW 1 grid (Fig. 3.29.2).

None of the analyses presented above suggest shape-related subgrouping other than the facies-related size partitioning. Phenotypic variation is commonly associated with characters showing a component of ontogenetic variation. Below we consider these results from other perspectives, including prior systematic assignments and the variation of notable nominal or ordinal character states.

3.7.3 Ulrich and Resser type specimens

Several syntype cranidia and pygidia for the six species recognized by Ulrich and Resser (1930) were included in the above analyses. These specimens fall within the spread of continuous variation seen in the sample as a whole (Fig. 3.30.1). The centroid size versus RW 1 plot for all cranidia shows that there is an ontogenetic trend in the complete dataset that encompasses the distribution of the type specimens (Fig. 3.30.2). It is clear that some of the shape differences among these *Osceolia* species were ontogenetically-related. For example, specimens assigned by Ulrich and Resser (1930) to *O. osceola* were of distinctly smaller size than those assigned to other species (pink diamond in Fig. 3.30.2). As Ulrich and Resser (1930) also used other features, not captured within the morphometric analysis, to justify their *Osceolia* species, this result alone does not discount their validity, but it questions it because this analysis of shape variation does capture several features that they used to differentiate among species. For the pygidial dataset, a notable result depicted in the plot comparing RW 1 and RW 2 scores is an outlier among the type specimens: a pygidium assigned to *Osceolia lodensis* Ulrich and Resser, 1930 (star symbol in Fig. 3.31.1). This is discussed in the Systematic Paleontology section below. The plot comparing pygidial RW 1 and centroid size shows that specimens follow a general ontogenetic trend and, consistent with the pattern seen among cranidia, no marked clustering is apparent (Fig. 3.31.2).

3.7.4 Classification by anterior border ledge morphology

Many of *Osceolia* cranidial anterior borders possess a marked, axially developed, anterior ledge that appears impressed (Fig. 3.8). To assess variation in this character we devised

three classes of ledge condition (Fig. 3.32, 3.33): strongly impressed ledge present (black square), weakly impressed ledge present (blue triangle) and no ledge present (pink dot). When ledge occurrence is compared to specimen size it is evident that all three forms occur across similar size ranges throughout much of holaspid growth except, perhaps, for the smallest holaspid specimens in which no ledge is known (Fig. 3.33.2). Examples of all three conditions occur in both feldspathic sandstone (Figs. 3.6.7, 3.6.14, 3.8.1) and in dolomitic mudstone (Figs. 3.7.12, 3.7.13, 3.8.12) and thus there is no evident relationship between ledge occurrence and lithology.

Ulrich and Resser (1930) designated two intraspecific “varieties” of *Osceolia* based on this character, *Osceolia obsoleta reversa* (herein Figs. 3.6.20, 3.8.13) and *Osceolia lodensis reflexa* (herein Fig. 3.8.25), both complemented by forms of the same proposed species that lack the ledge condition. As these authors commonly based species on subtle putative differences in morphology (see Hughes and Labandeira, 1995) their choice to recognize varieties in these cases was notable, but unexplained. Ledge occurrence within the entire sample is notably more common than Ulrich and Resser’s (1930) descriptions imply but, as their variety names suggest, the structure does vary notably in form and prominence. It is possible that the ledge is a dimorphic rather than polymorphic character, and also that its occurrence is related to the bearer’s gender. While sexual dimorphism remains a plausible explanation for the occurrence of this feature, conditions for invoking it as a strongly supported explanation for patterns observed (see Hughes and Fortey, 1995) are not met. There is also a possibility that it was incised behaviorally in some manner. Here we

treat the expression of this character as an intraspecific variant that does not merit formal designation as a subspecific variety.

3.7.5 Comparison of *O. osceola* cranidia with homeomorphic taxa

The long glabella, long-eyed, narrow fixigenae, notable anterior border cranial form of *Osceolia osceola* is shared both with various other dikelocephalids and also with occasional species from families considered to be far removed phylogenetically. To date, little morphometric exploration of such homeomorphy has been conducted in trilobites. Here we use the combined *O. osceola* cranidial dataset to explore phenetic similarity to various species judged by eye to be its homeomorphs. These included dikelocephalid species with comparably shaped cranidia (Figs. 3.19, 3.34) including the new species *Osceolia tumerispina* (Figs. 3.16, 3.34), and also with homeomorphs from taxa generally considered to be phylogenetically (and also commonly stratigraphically) distantly related forms. These candidate homeomorphs were selected based on our general knowledge of Cambrian trilobite literature and are surely not exhaustive.

Overall, the morphometric analysis is effective in distinguishing *O. osceola* from its homeomorphs (dark blue upside-down triangle in Fig. 3.34) as there is little overlap between the *O. osceola* sample and other taxa. Among forms considered dikelocephalid, the sole *O. tumerispina* cranidium (light blue triangle in Fig. 3.34, Fig. 3.16) plots adjacent to the *O. osceola* sample but not within it, a result consistent with shape differences described below. The sole cranidium of the Gondwanan late Cambrian *Hamashania pulchra* (Kobayashi, 1942) (star symbol in Fig. 3.34.2, Fig. 3.19.15) suitable for morphometric consideration with *O. osceola* is strikingly similar, with the type of *H. pulchra* lying within the envelope of

O. osceola specimens in the centroid size versus RW 1 plot, although it is distinct in scores on RW 2 (Fig. 3.34.1). Other subtle differences in cranial morphology not captured morphometrically permit the further distinction between these forms. These include slight expansion of the anterior glabella (Fig. 3.19.15) and striations in the anterior border furrow that parallel the sagittal axis, possibly suggesting a plectrum (Sohn and Choi, 2005, fig. 3B) in *H. pulchra*. Furthermore, the pygidia of these species are strikingly different (Fig. 3.19.16, 3.19.17) with a recent phylogenetic analysis placing these forms far apart within a broadly defined dikelocephalid clade (Srivastava and Hughes, 2024, fig. 11) (also see Sohn and Choi, 2005). The similarity in cranial form between *O. osceola* and *H. pulchra* is such that Jell and Adrain (2003) placed them in a restricted family Dikelocephalidae that only included forms with extended frontal areas (but with variable degrees of doublure width). Our results rather suggest a more distant relationship, with strikingly convergent cranial form. A similar morphometric result occurs with the cranidium of the middle Cambrian Altay Sayan form *Pseudoanomocarina eldachica* Bognibova et al., 1971 as figured by Savitsky (1976, pl. 38, fig. 15) (open circle in Fig. 3.34, Fig. 3.19.2), which falls just within the field of *O. osceola* on RW 1 but is also quite distinct on RW 2. Again, the cranial similarity appears to be the result of strong cranial shape convergence, in this case in a then geographically distant and significantly older earlier middle Cambrian form.

All other homeomorphs selected plot close to but outside the variation envelope of *O. osceola*. Several mid-sized homeomorphs show RW 1 scores comparable to those that *O. osceola* acquired only at its largest sizes. These also show RW 2 scores that equal or exceed the largest RW 2 scores of any *O. osceola*. Results suggest that the geometric morphometric

scheme used is of help in distinguishing *O. osceola* from similar forms. These also include forms such as *Prosaugia lochmani* (Fig. 3.19.10-3.19.14, grey dot in Fig. 3.34), *Briscoia coloradoensis* (Walcott, 1914) (Fig. 3.18.1-3.18.4, black square in Fig. 3.34) and *Briscoia* sp. (Fig. 3.18.15-3.18.19, square plus symbol in Fig. 3.34) that are likely dikelocephalid relatives of *O. osceola*, but also forms such as *Formosocephalus savitzkyi* Pegel in Egorova et al., 1982 from the *Tomagnostus fissus* biozone of the Lena River section (Fig. 3.19.1, red diamond in Fig. 3.34), also likely phylogenetically distant.

Although these taxonomically and stratigraphically varied homeomorphs of *O. osceola* cranidia differ detectably in shape from Hall's species, the degree of intraspecific shape variation within the *O. osceola* collection is notable, with its scores on RW 1 spanning the morphological gap between various of the homeomorphs selected (Fig. 3.34.2). Despite some of the variation among *O. osceola* being taphonomically induced (see above), these results suggest that morphological variation within trilobite species can occupy significant morphospace.

3.8 Materials

Repositories and institutional abbreviations: Types, figures, and other specimens of *Osceolia* are repositied in the following institutions: University of Michigan Museum of Paleontology (UMMP); University of Minnesota Paleontological Collection (UMPC, now part of the Cincinnati Museum Center [CMCIP] collection); Museum of Comparative Zoology, Harvard (MCZ); Natural History Museum of Los Angeles (LACMIP); University of Wisconsin, Madison (UWGM); Smithsonian United States National Museum of Natural History (USNM),

or American Museum of Natural History, New York (AMNH). See Supplementary Data 1 for list of cataloged specimens at each repository.

3.9 Systematic Paleontology

In the following, we employ the synonymy list notations of Matthews ([1973](#)).

Class Trilobita [Walch, 1773](#)

Subclass Libristoma [Fortey, 1990](#)

Order Asaphida [Salter, 1864](#); emended [Fortey, 1990](#)

Superfamily Dikelocephalacea [Miller, 1889](#) (emended [Ludvigsen et al., 1989](#))

Family Dikelocephalidae [Miller, 1889](#); emended [Ludvigsen et al., 1989](#))

Genus *Osceolia* [Walcott, 1914](#)

Type species.—*Osceolia osceola* ([Hall, 1863](#)) from the St. Lawrence Formation and the Norwalk Member of the Jordan Formation of the upper Mississippi Valley.

Diagnosis.—Dikelocephalid trilobite with rectangular to subtrapezoidal glabella with transverse SO firmly incised and open, V-shaped S1 continuous, either firmly or weakly incised. L1 with slight lateral anterior bulge. Extended (sag.) preglabellar field and short (sag.) anterior border, frontal area width comparable to maximum width between palpebral furrows or palpebral lobes, long (exsag.), wide (tr.) palpebral lobes with rear posterior to SO and anterior opposite S2 in large specimens, with firmly and evenly incised palpebral

furrow, markedly narrow fixigenae, and free cheeks with conterminant doublure extending to median suture. Elongate hypostome with paired lateral swellings in posterior lobe. Associated thoracic segments fulcrate, some but not all with extended, posterolaterally directed pleural spines. Holaspid pygidium with 3 or 4 relatively narrow (tr.) axial rings defined by firmly incised ring furrows. Terminal piece posterior blunt. Postaxial region short for dikelocephalid: rachis about 80% of pygidial sagittal length. Three or four pairs of firmly incised pleural furrows, interpleural furrows usually entirely effaced, remnants continuous across pleural surface where rarely preserved. Pygidial anterior margin extends into pair of robust marginal spines that extend well posterior to sagittal posterior border. Pygidial doublure wide (tr.), extending to pleural platform.

Remarks.—Occurrences of *Osceolia* outside of the upper Mississippi Valley suggested previously can be rejected, because no instances of taxa bearing the diagnostic characteristics listed above are known at present. Walcott (1914, p. 386) reported *Osceolia* in both Nevada and Texas, having previously assigned a cranidium from Nevada (Walcott, 1884, pl. 9, fig. 25) to *Dikelocephalus osceola* (herein Fig. 3.18.10-12), along with cranidia and pygidia from Texas figured herein for the first time (Fig. 3.18.5-3.18.9) that were not assigned at the species level but attributed by Walcott (1914) to the genus. *Briscoia texana* (Walcott, 1914, p. 372, pl. 65, fig. 4), based on a single incomplete cranidium (herein Fig. 3.18.7) from the Wilburns Formation at Baldy Mountain, northwest of Burnet, is co-occurrent with material that Walcott considered *Osceolia*. One relatively complete cranidium from this locality (Fig. 3.18.5-6) does resemble *Osceolia* in its elongated glabella and extended but relatively narrow frontal area. However, associated pygidia, illustrated here for the first time, show

interpleural furrows and lack marginal spines (Fig. 3.18.8-9), characters which exclude this material from *Osceolia*. We thus agree with Ulrich and Resser (1930, p. 68, 70) that all the material considered belongs within *Briscoia texana*. *Briscoia* Walcott, 1924 is here considered to encompass a paraphyletic group of species at best (see Srivastava and Hughes, 2024, fig. 11), but we retain it until more thorough dikelocephalid phylogeny allows us to better resolve lineages within the group and thus to propose wider revision of generic concepts. When that is completed apomorphy-based diagnoses for derived genera may be possible.

Resser (1937, p. 5) erected a new species, *Briscoia nevadensis*, to accommodate Walcott's (1884) Nevadan *D. osceola* specimens. Additional previously unfigured material from the same locality also includes pygidia with interpleural furrows and lacking marginal spines (Fig. 3.18.13-14), likewise excluding it from *Osceolia*.

Osceolia brevifrons Clark, 1924, p. 30, pl. 4, fig. 4 (herein Fig. 3.19.8) was reassigned by Rasetti (1944, p. 254, pl. 39, fig. 34) to *Pseudosaukia*, and may be a junior synonym of *P. sesostris* (Billings, 1865). The lack of an extended frontal area and anterior position of the palpebral lobes excludes this form from *Osceolia* and from the extended doublure-bearing dikelocephalids.

Other material from outside the upper Mississippi Valley might belong within *Osceolia*. *Prosaukia lochmani* Straatmann in Stitt and Straatmann (1997), described on the basis of four cranidia (two of which were figured) from the upper part of the *Ellipsocephalooides* Zone in the Englewood section of the Deadwood Formation in South Dakota, show features characteristic of *Osceolia* cranidia (see Fig. 3.19.10-3.19.14), although their proportions are slightly different (grey dot in Fig. 3.34). As no candidate associated pygidia

are known, membership of *Osceolia* cannot presently be confirmed, but these cranidia are closely similar to that currently assigned to *Briscoia* sp. from the Dotsero Formation of Colorado, which is *Illaelenurus* Zone in age (J.F. Taylor pers. com., 2025) (Fig. 3.18.15). Although specific association of these Dotsero Formation cranidia with pygidia is not well resolved, with likely candidate pygidium showing either equally divided pleura or those with reduced propleurae (Fig. 3.18.16-19), both forms resemble those known among species attributed to *Briscoia*, and do not show the effaced interpleural furrows or marginal spine pair characteristic of *Osceolia*. Phylogenetic analyses assessing relationships among these forms more comprehensively will be presented elsewhere.

Osceolia osceola (Hall, 1863)

Figures 3.5-3.15

v*1863 *Dikelocephalus osceola* Hall, p. 146, pl. 10, figs. 18-19.

v*1863 *Dikelocephalus osceola?* Hall, p. 146, pl. 7, fig. 49.

non v*1884 *Dikelocephalus osceola* Walcott, p. 40, pl. 9, fig. 25 (rejected by Ulrich and Resser, 1930, p. 67, 69 and assigned to *Briscoia nevadensis* by Resser, 1937, p. 5).

1886 *Conokephalina osceola* Brøgger, p. 205.

non v*1914 *Osceolia* cf. *osceola* Walcott, p. 355 (considered below as Genus and Species indeterminate).

v*1914 *Osceolia osceola* Walcott, p. 356, 359, 361-362, 382, 385-386, pl. 68, figs. 4-10.

- v*1914 *Dikelocephalus? limbatus* (pars) Walcott, p. 369, pl. 65, fig. 5.
- v*1930 *Osceolia osceola* Ulrich and Resser, p. 69-71, 74, pl. 22, figs. 1-9, pl. 23, figs. 1-8, 11, 16-18, 22.
- v*1930 *Osceolia arguta* Ulrich and Resser, p. 71, pl. 23, fig. 11.
- v*1930 *Osceolia lodensis* Ulrich and Resser, p. 72, pl. 23, figs. 19-21.
- v*1930 *Osceolia lodensis reflexa* Ulrich and Resser, p. 74, pl. 23, fig. 22.
- v*1930 *Osceolia obsoleta* Ulrich and Resser, p. 70, pl. 23, figs. 1-8.
- v*1930 *Osceolia obsoleta reversa* Ulrich and Resser, p. 70, pl. 23, figs. 9-10.
- v*1930 *Osceolia praecepta* Ulrich and Resser, p. 74, pl. 23, figs. 16-18.
- v*1930 *Osceolia separata* Ulrich and Resser, p. 71, pl. 23, figs. 12-15.
- v*1935 *Osceolia osceola* Twenhofel, Raasch and Thwaites, p. 1713.
- v*1951 *Osceolia osceola* Nelson, p. 783, pl. 110, figs. 9-10.
- 1951 *Osceolia osceola* Raasch, p. 141, 145, 147, 149.
- 1951 *Osceolia arguta* Raasch, p. 141 (reassigned to *Osceolia osceola*).
- 1951 *Osceolia lodensis* Raasch, p. 138 (reassigned to *Osceolia osceola*).
- 1951 *Osceolia lodensis reflexa* Raasch, p. 141 (reassigned to *Osceolia osceola*).
- 1951 *Osceolia praecepta* Raasch, p. 141 (reassigned to *Osceolia osceola*).
- 1951 *Osceolia obsoleta* Raasch, p. 141 (reassigned to *Osceolia osceola*).

1954 *Osceolia osceola* Berg, p. 878.

1956 *Osceolia osceola* Nelson, p. 172, 177-178, 180-181.

1959 *Osceolia osceola* Lochman in Harrington et al., p. 254, figs. 191, 2a, b.

1994 *Osceolia osceola* Hughes, p. 9, 53.

1997 *Osceolia osceola* Hughes and Hesselbo, p. 1, 4-5, 7, 9.

1997 *Osceolia osceola* Stitt and Straatmann, p. 92.

2007 *Osceolia osceola* Runkel et al. 2007, fig. 5 (subzone shown in zonation chart)

Lectotype.—Selected herein: cranidium AMNH 99388 (Hall, 1863, pl. 10, fig. 18) (Fig. 3.5.3) from the very fine grained feldspathic sandstone of the Norwalk Member at USNM site 78 “quarry near St. Croix River, in suburbs of Osceola”, WI (see Walcott, 1914, p. 386). Walcott’s field notebook of 1883 records this location as “Osceola Mills, in the northern suburbs of the village, near St Croix River”. C.W. Schuchert’s field notes of 1893 and those of E.O. Ulrich in 1919 confirm that the *Osceolia*-bearing sandstone were located directly above the waterfall on Osceola Creek, which is the stratigraphic position of the ~3.5 m thick Norwalk Member at this locality, 45° 19’10.96” N, 92°42’12.30” W (see Supplementary Data 6 for copies of these fieldnotes).

Paralectotype.—Counterpart free cheek AMNH 39115 (Hall, 1863, pl. 10, fig. 19) (Fig. 3.9.1), counterpart pygidium AMNH 342 (Hall, 1863, pl. 7, fig. 49) (Fig. 3.12.6) from the very fine grained feldspathic sandstone of the Norwalk Member at USNM site 78, Osceola, Polk County, WI.

Diagnosis.—*Osceolia* species with cranidial frontal area length (sag.) less than 47% of occipital-glabellar length. Species includes morphs with and without an incised platform in the medial part of the cranidial anterior border. Pygidium with three or four firmly incised axial rings, and three firmly incised pleural furrows. Rachis around 65% of pygidial axial length (sag). Pygidial marginal spines narrow evenly toward sharp terminus.

Occurrence.—*Osceolia osceola* Subzone, heterolithic and feldspathic sandstone facies of the St. Lawrence Formation and the Norwalk Member of the Jordan Formation of the upper Mississippi Valley, at localities in the northern and eastern parts of the outcrop area.

Description.—Mature exoskeleton relatively small for dikelocephalid, largest likely not larger than about 20 mm occipital glabellar length (sag.). Cephalon transversely convex, outline crescentic. Likely isopygous or subisopygous. Pygidium lateral margin shape incongruent with shape of anterior cephalic margin. Glabella rectangular to subtrapezoidal, inflated, maximum width posterior to SO furrow, L1 inflated just posterior to S1 furrow. Glabellar anterior margin transverse to slightly rounded. SO furrow entire, deeply incised, shallowing notably in central portion. S1 less firmly incised than SO, deepest abaxially, running obliquely slightly forward at confluence with lateral margin. S2-S4 faint where present, S2, slightly oblique forward abaxially, short (tr.) S3 and S4 furrows transverse. Occipital lobe widens subtly posteriorly. Occipital lobe posterior with short (sag.) anteriorly-arched doublure. Median occipital tubercle apparent in some specimens. Axial furrow firmly incised. Frontal area length less than 47% of occipital-glabellar length, preglabellar field length 10-40% of occipital-glabellar length (sag.). Occipital lobe width (tr.) 53-89% of frontal area width (tr.). Anterior border varies from slightly narrower (tr.) than distance

(tr.) between midpoints of palpebral furrow to as wide as distance (tr.) between midpoints of palpebral lobes. Preglabellar field gently convex to gently concave, anterior border furrow long (sag.). Fixigenae narrow, narrowest preocularly, maximum fixigenal width (tr.) opposite L1 lobe midpoint, less than occipital lobe length (sag.). Palpebral lobes extending just posterior of SO to opposite S2, wide (tr.). Posterolateral border short (sag.), strap-like, narrow (tr.) with transverse ridge that parallels posterior margin.

Free cheeks arcuate. Broad genal field, gently convex near margin defining low border and shallow border furrow, rising steeply concavely toward flat ocular platform. Opisthoparian dorsal suture marginal sagittally at anterior, laterally initially sweeping abaxially at angle of approximately 60° , then curves adaxially at 30° - 40° to sagittal axis. Ocular incisure arcuate, bounded abaxially by raised marginal eye socle and adjacent shallow arcuate furrow. Posterior border furrow curves evenly posteriorly, merging with lateral border furrow, and continuing into genal spine base. Genal spine length approximately equal to cranial length (sag.). Doublure wide, extending at least 60% of distance from margin to midpoint of ocular incisure, with anterior flexure accommodating hypostome. Terrace ridges on ocular platform inosculate. Terrace ridges on doublure continuous, parallel margin. Doublure curves upward adaxially, close beneath dorsal surface.

Associated hypostome subquadrangular, longer (sag.) than wide (tr.), median body ovoid, inflated medially. Anterior lobe convex, rounded; posterior lobe short (sag.), convex. Median furrow slit-like abaxially, shallow axially; maculae apparent in one compressed specimen, confluent with lateral posterior lobe in uncompressed forms. Anterior

border short (sag.), curving into anterior wing with processes. Lateral border triangular, widest (tr.) about midpoint of posterior lobe. Posterior border evenly short (sag., exsag.).

Associated thoracic segments with firmly incised axial furrows. Articulating half rings crescentic, articulating furrow transverse, shallower in medial portion. Anterior pleural margin transverse adaxially for short distance (tr.) to fulcrum, then curves posteriorly abaxially. Pleural furrow deeply incised, curving evenly posterolaterally, anterior face steeper than posterior face, extending toward pleural tip. Pleural region anterior margin concavely scalloped abaxial to fulcrum, posterior margin continuous. Pleural region abaxial to fulcrum varied among specimens, nearly transverse in some extending into short or longer posteriorly directed pleural spine, or more evenly curving posteriorly.

Pygidium subelliptical with anterior margin extending into pair of long, robust, progressively thinning posterolateral spines that project beyond pygidial sagittal posterior by up to approximately half pygidial sagittal length. Anterior margin evenly curved or with subtle fulcrum present close to axis. Axis convex, 70-80% of pygidial length (sag.) with anterior articulating half-ring, three distinct axial rings defined by broad and deeply incised inter-ring furrows, fourth ring occasionally well defined. Terminal piece bullet shaped, extending into postaxial ridge in rare specimens, but sagittal posterior border usually flat. Postaxial posterior border evenly curved or with slight inflection sagittally. Three pairs of firmly incised pleural furrows extending to base of concave pleural slope, fourth pair of weakly incised pleural furrows present in most specimens. Interpleural furrows entirely effaced in most specimens, but remnants rarely preserved as continuous, shallow furrows. Border flat, narrow (tr, sag). Faint paradoublural line. Doublure extends to pleural platform

top, and to end of terminal piece. Double terrace ridges sparsely spaced, continuous, parallel border.

Remarks.—In erection of the species Hall (1863, p. 146) mentioned only his figured cranidium AMNH 99388 (herein Fig. 3.5.3) as definitively belonging to it, with his figured pygidium AMNH 342 (herein Fig. 3.12.6) questionably referred to the species. This would seem to imply that AMNH 99388 is the holotype. However, Hall also figured free cheek AMNH 39115 (herein Fig. 3.9.1) under the same species name in the accompanying plate caption (Hall, 1863, pl. 10, fig. 19), but did not mention this sclerite in his description of the species. As two specimens were figured by Hall (1863) under the name *Dikelocephalus osceola*, we choose the cranidium as lectotype because of Hall's clear intent that this specimen bears species-diagnostic characters. In a footnote Hall (1863, p. 146) also mentioned that “at least five individuals of this peculiar species have been seen” and AMNH 39114 (Fig. 3.19.9) is one of these that was not figured by Hall (1863). The distinctly short prelabellar field of this specimen excludes it from *O. osceola* and allies it to *Saukiella pyrene* (Walcott, 1914), a form well known from this collection.

In their description of *Osceolia* Ulrich and Resser (1930) drew attention to notable variation in the form of the axial part of the cranidial anterior border that we describe above as having a ledge-like morphology in some specimens. Among the five new species of *Osceolia* that those authors established, two showed varieties (their *Osceolia obsoleta reversa* from the Norwalk Member at Osceola [OA] and Eleva [EA], and their *Osceolia lodensis reflexa* from the dolomitic mudstones of the St. Lawrence Formation at Osceola) based on the presence of the ledge. These occurred within the same collections as closely similar, and in

their view conspecific, forms that lacked the ledge. As discussed above, we agree with Ulrich and Resser (1930) that this variation in ledge presence is an important intra-collectional variation among *Osceolia* specimens that does not appear size-related within the available sample (Fig. 3.33).

Most, but not all, of the morphological differences suggested by Ulrich and Resser (1930) to distinguish species and variants, can be discerned when reviewing both images and descriptions of the six species described by them. However, we conclude, as Raasch (1951) apparently also intended to, that all are conspecific. (Raasch [1951] made no comment on the status of *O. obsoleta reversa* but that may have been because, unlike their *O. lodensis reflexa*, Ulrich and Resser [1933, p. 71, pl. 23, figs. 9-10] did not give *O. obsoleta reversa* an individual variety heading in their systematic text, although they distinguished it by name in their figure caption. Likewise, for reasons unclear, Raasch [1951] also omitted discussion of Ulrich and Resser's [1930] *O. separata*.) Of the Ulrich and Resser species preserved, like the type species, in very fine sandstone, *O. obsoleta* was based on material in which the S1 and more anterior furrows were effaced, and also on relatively large cranidia and pygidia (Figs. 3.30, 3.31) whereas their concept of *O. osceola* emphasized small pygidia with relatively wide and robust marginal spines. Expression of the incision of these glabellar furrows is continuously variable within collections, and the narrower pygidial marginal spines reflect later ontogeny, the curvature of which is also variable intracollectionally. *Osceolia arguta* was based on a single cranidium (herein Fig. 3.6.22) that is exceptional in no characters other than its relatively large size (Fig. 3.30), and as *O. separata* (herein Figs. 3.6.18, 3.8.14, 3.13.16, 3.13.21) was considered by those authors as intermediate between *O.*

osceola and *O. obsoleta*, it is also a synonym. Specimens preserved in dolomitic mudstones are generally larger (see above) and Ulrich and Resser (1930, p. 73) suggested that all these had consistently wider frontal areas than those preserved in sandstones. Although some specimens from dolomitic mudstone do have wider frontal areas, others do not (Fig. 3.7). Ulrich and Resser's (1930) *Osceolia lodensis* (herein Figs. 3.7.12, 3.14.8, 3.14.9) contains those that are wider in this feature, and this form also has pygidia with a relatively short and narrow axis with four axial rings clearly expressed, and a more transverse overall shape. We considered maintaining *O. lodensis* as a separate species confined to the earlier part of the range of *O. osceola* in this region but decided against this for reasons given below.

No shape-based grounds for the recognition of Ulrich and Resser's (1930) species emerged from this study of those type specimens complete enough for inclusion in the morphometric analysis. Rather, any clustering among the types of their species in shape space reflected characters that varied ontogenetically (Figs. 3.31, 3.32), with the specimens from the dolomitic shales generally being larger (Fig. 3.21). Accordingly, as there are also no consistent differences based on meristic characters other than ledge occurrence, all specimens of *Osceolia* from the Norwalk Member and from the heterolithic facies and laminated sandstone facies of the St. Lawrence Formation are here considered conspecific. This is done acknowledging observable variation in specimen shape and features, taphonomic differences between sandstone- and mudstone-preserved specimens, and perhaps minor locality-related differences in mean form. If the quality of specimen preservation were higher, more refined morphospecies determination among *O. osceola* might be possible. Given what is available, a conservative approach to species recognition is warranted, and maintaining species

that are apparently ontogenetic variants or have no valid diagnostic features is likely to hinder rather than advance future understanding of these organisms. Hence the proposed synonymy.

There is some question concerning the association of hypostomes and thoracic segments with this species. In the case of the hypostomes, each illustrated seems likely to belong to *O. osceola* because their shape and size is consistent with the elongated glabellar form, and differences among them may represent their different lithologies of preservation (Fig. 3.10). On the other hand, the hypostome preserved in the dolomitic mudstone (Fig. 3.10.2) shows particular characters resembling other dikelocephalid hypostomes including maculae, a transverse posterior border with deep lateral pits and a wide posterior lateral border, whereas in the two in sandstone these features are obscure (Figs. 3.10.1, 3.10.3, 3.10.4). For this reason, the dolomitic mudstone specimen will be the primary source for character state coding in subsequent phylogenetic analysis. Association of the illustrated thoracic segments with this species is also insecure because some (such as Fig. 3.11.4, 3.11.9) might belong to other co-occurrent dikelocephalid/saukiid taxa. However, given both similarities in adaxial segment form and taxon abundance in collections based on cranidia and pygidia, it is likely that some *O. osceola* thoracic segments had long pleural spines and others shorter spines.

Unlike in *Walcottaspis vanhornei*, the more highly curved pygidial posterior border does not match the gentle curve of the cephalic anterior, with the result that if the animal enrolled these structures could not have formed a fully encapsulated structure (Fig. 3.15.2).

On the other hand, upon enrolment the pygidial spines would have protruded forward of the remaining enrolled exoskeleton, possibly affording alternative protection.

Osceolia tumerispina new species

Figures 3.16, 3.17

Holotype.—Selected herein: pygidium UWGM 7452 (Fig. 3.16.17-3.16.20) from the stromatolitic dolomite facies of the St. Lawrence Formation, 4 km west of Coon Valley, WI, in the vicinity of 43°42'27" N, 91°03'02" W, 290 m altitude.

Paratypes.—Cranidium part and counterpart UWGM 7455 (Fig. 3.16.3-3.16.5) and UWGM 7459 (Fig. 3.16.1-3.16.2), free cheek UWGM 7456 (Fig. 3.16.6), thoracic segments UWGM 7454 (Fig. 3.16.1.8-3.16.10), UWGM 7457 (Fig. 3.16.7), pygidia UWGM 7453 (Fig. 3.16.13-3.16.14), UWGM 7458 (Fig. 3.16.11), UWGM "L201" (specimen currently missing, Fig. 3.16.12), all from same locality as holotype.

Diagnosis.—*Osceolia* species with distally swollen pygidial pleural spines, long cranidial frontal area and long/wide cephalic border.

Occurrence.—Known only from carbonate-rich rocks of the stromatolitic dolomite facies of Hughes and Hesselbo (1997) that likely represent the most distal St. Lawrence Formation environment preserved within the upper Mississippi Valley. Presently known only from a single locality, Raasch's locality number 141.24 (417.1), fieldmap x 57.103 – Bed 6, along Hwy 14, approximately 4 kilometers west of Coon Valley, Vernon County, WI. Its relatively

southwestern occurrence may suggest temporal equivalence to the later part of the range of *O. osceola* or possibly shortly thereafter.

Description.—Frontal area ~50% of occipital-glabellar length, with long (sag.), low anterior border lacking ledge and weakly incised anterior border furrow. Glabella rectangular. SO entire, firmly incised, S1 entire, shallowing medially. Frontal area diverges preocularly at 20° angle. Free cheek with wide border and relatively narrow pleural slope. Confluence of lateral and posterior border furrows adaxial to genal spine base. Hypostome unknown. Thoracic segments with narrow transverse anterior pleural margin until fulcrum, gently posterolaterally inclined thereafter. Pygidium with three or four well defined axial rings and triangular or bullet shaped terminal piece, postaxial region short (sag.), rachis 75-85% of pygidial axial length minus sagittal spine. Anterior pleural border an even curve. Posterior pygidial margin with short sagittal spine in large specimens. Three or four deeply incised pleural furrows terminate before narrow, flat border. Pleural spines with broad (tr.) bases widening distally and strongly inflated on abaxial side to form a swollen (tr. and dorso-ventrally) club-like structure. Sharp terminal spine at distal, adaxial tip present in holotype, tip rounded in another specimen.

Etymology.—From the Latin: *tumer* meaning swollen and *spina* spine, for the inflated, club-like pygidial marginal spines.

Remarks.—The most obvious difference between *O. tumerispina* and *O. osceola* is the club-like pygidial marginal spines in the new species, although cranidial proportions and form also differ (Fig. 3.34). However, the form of the pygidial spines shows notable variety within the small sample of *tumerispina* available. Whereas in the holotype the inflated spine ends

in a sharp tip, in a paratype it ends in a rounded inflated club on the left side spine, but in a broad-based, non-inflated, *osceola*-like spine on the right side of the same specimen. It is possible that this range of form includes teratologies of some kind, but the presence of swollen features on all pygidial specimens with spines preserved confirms that this character is taxonomically diagnostic. This is supported by the other, more subtle differences listed in the diagnosis. *Osceolia tumerispina* is readily distinguished from *O. osceola* based on these characteristics and thus merits recognition as a new species within the same genus.

The notably long frontal area and low elevation of the anterior border resemble the condition of some of the largest specimens of *O. osceola* but in *tumerispina* this condition is achieved at smaller size. While this character (which might be phylogenetically basal) could be hypermorphic compared to the *osceola* condition, the robust spines in large *tumerispina* more closely resemble those of smaller *osceola*. Hence, any allometric repatterning in *Osceolia* evolution is likely complex.

Genus and species indeterminate

Figures [3.19.3-3.19.6](#)

v*[1914](#) *Osceolia* cf. *osceola* Walcott, p. 355.

v*[1930](#) *Osceolina diabolus* nomen nudum, Ulrich and Resser, p. 68.

Material.—USNM PAL 791890 (counterpart pygidium, Figs. [3.19.3-3.19.4](#)) and pygidium USNM PAL 791891 (Figs. [3.19.5-3.19.6](#)) from the Devil's Lake Member, USNM site 81b, 4 km southwest of Baraboo, WI, apparently in the vicinity of 43°26'12.13" N, 89°46'22.30" W (see Supplementary Data 7).

Remarks.—In 1884, working under the direction of Charles Walcott, Cooper Curtice made a collecting excursion to the upper Mississippi Valley. One of his collections was from the Devil’s Lake Member, a red quartzose sandstone with rounded grains exposed between Baraboo and Devil’s Lake, WI (see Supplementary Data 7). This unit is interpreted to have been deposited in a nearshore, island archipelago setting (Wanenmacher et al., 1934; Dalziel and Dott Jr., 1970), and the various trilobite faunas found sporadically within it suggest that in the Baraboo district the Devil’s Lake Member lithology may have been deposited episodically over an extended interval of the late Cambrian. The collection from USNM site 81b was apparently one of the stratigraphically highest of these episodes of deposition, and one that for some time E.O. Ulrich considered to lie stratigraphically above the latest Cambrian deposition in the region and to represent the now abandoned, so-called “Ozarkian” System (Merk, 1985; Weiss, 1992; Weiss and Yochelson, 1995; Weiss and White, 1998). Currently these rocks are thought have been deposited in a nearshore setting temporally equivalent to the feldspathic-sandstone rich Mazomanie Formation and the glauconite-rich Reno Member of the Tunnel City Group during the later part of the transgressive systems tract that is regionally immediately overlain by rocks the St. Lawrence Formation (Wanenmacher et al., 1934; Runkel et al., 2007). It is thus considered likely temporally equivalent to the rocks bearing *Dikelocephalus freeburgensis* Feniak in Bell et al., 1952, and *Dikelocephalus postrectus* Ulrich and Resser, 1930, and thus deposited prior to the first regional records of *Osceolia*. This correlation is based on co-occurrence of the pygidia discussed below with species of *Prosaukia*, *Briscoia*, *Rasettia*, and *Illaenurus*.

Faunas recovered from the Devil's Lake Member reveal differences from those of their putative more offshore correlates (Wanenmacher et al., 1934), which partially explains Ulrich's mistaken view that at least some of them were temporally distinct. Of particular interest to this study are two pygidia recovered from USNM site 81b that were mentioned by Walcott (1914, pp. 355, 386) as *O. cf. osceola* and by Ulrich and Resser (1930, p. 68) as the nomen nudum "*Osceolina diablo*". These specimens (Figs. 3.19.3-3.19.6) have not been illustrated previously. As Ulrich and Resser (1930, p. 67-68) stated, they resemble *Osceolia* in overall pygidial shape and proportions of axis and pleural regions, and in the extended doublure. A notable similarity is that they also lack the expression of interpleural furrows, while the pleural furrows are firmly incised, and it was this character that suggested to these earlier workers particular affinity with *Osceolia*. On the other hand, these pygidia differ from *Osceolia* in two notable ways. Firstly, they lack the prominent marginal pleural spines seen in association with the first pygidial segment in *Osceolia* and, secondly, they also have 5, as opposed to 3 or 4 axial rings and have 5, as opposed to 3 or 4, firmly incised pleural furrows.

Although USNM site 81b yielded a diverse range of fossils (see Supplementary Data 6), no cranidium or other sclerite recovered there is obviously associated with these pygidia. Given that only the pygidium of this form is currently known, we choose not to formally recognize a new taxon, nor can we affirm definitively that these pygidia are dikelocephalid. On the other hand, this form is apparently the closest relative of the members of *Osceolia* known from the upper Mississippi Valley. If so, the origin of *Osceolia* involved reduction

in the number of holaspid pygidial segments and the gain of the prominent marginal spine pair.

3.10 Conclusions

Following comprehensive review of *Osceolia* specimens and their occurrence, six previously described and illustrated species of *Osceolia*, two with designated varieties, are revised into the regionally relatively long-ranged species *O. osceola* (Hall, 1863) that may have occurred locally for some 400,000 years. During this time *O. osceola* persisted in relatively nearshore settings, exhibiting notable morphological variation but shows little collection-related variation beyond a tendency for larger specimens to be found in slightly deeper water settings. Morphs either with or without a prominent ledge in the medial anterior cranial border are both present in most collections from single beds, and detectable ontogenetic variation occurs within such collections. A new species of *Osceolia* with highly distinctive pygidial spine morphology is erected and is known only in the most offshore facies. The abrupt appearance of *Osceolia* species in the upper Mississippi Valley sedimentary record immediately postdates a maximum flooding surface. During the early part of the subsequent falling stage systems tract preserved in the region two congeneric species co-existed for a short period, one confined only to the most distal facies.

3.11 Data availability statement

Data available from the Dryad Digital Repository:

<https://doi.org/10.5061/dryad.xwdbrv1rd>.

3.12 Figures

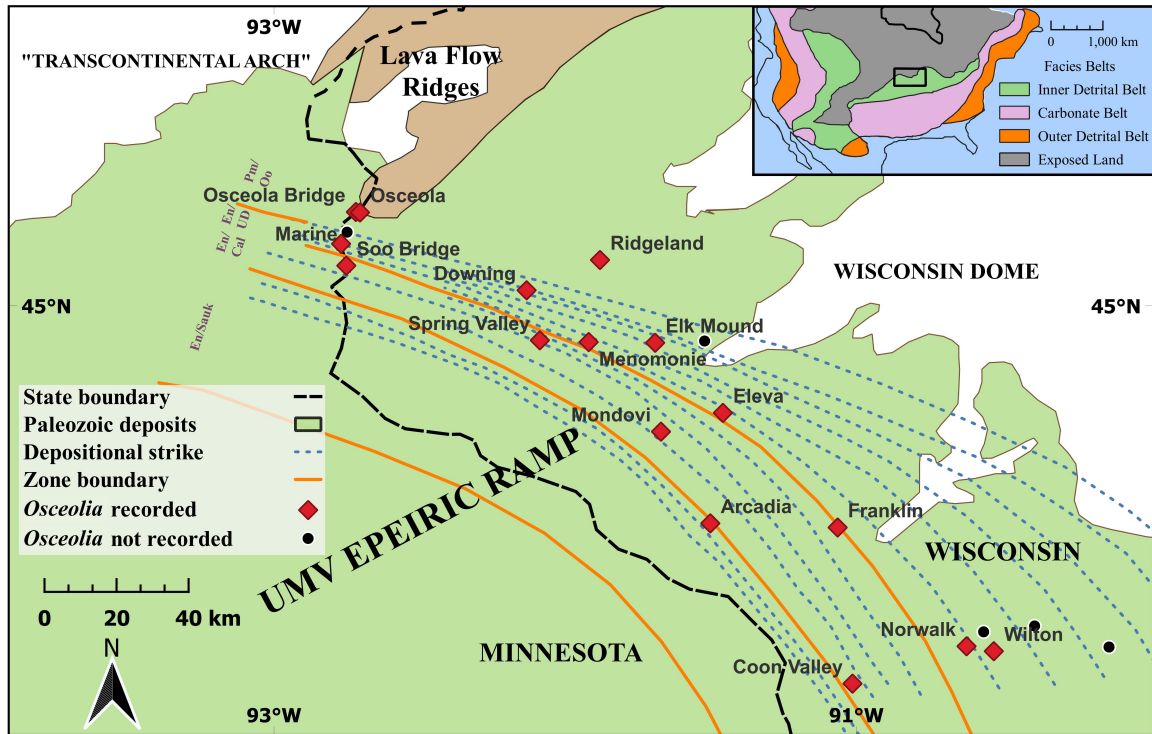


Figure 3.1: Locality map of upper Mississippi Valley (UMV) region of the Laurentian cratonic interior showing *Osceolia*-bearing strata occur. Inset shows the location of UMV region (boxed area) with respect to the late Cambrian lithofacies belts of Palmer (1960). Depositional strike lines are shown in black lines and are based on Runkel et al. (2007). *Eoconodontus notchpeakensis-Saukiella* (En-Sauk) Subzone, *Eoconodontus notchpeakensis-Calvinella* Subzone, *Eoconodontus notchpeakensis*-Upper *Dikelocephalus* Subzone and *Proconodontus muelleri*-*Osceolia osceola* Subzone boundaries are shown with orange curves and are based on Bell et al. (1956), Nelson (1956) and Miller et al. (2003).

Osceola (OA)

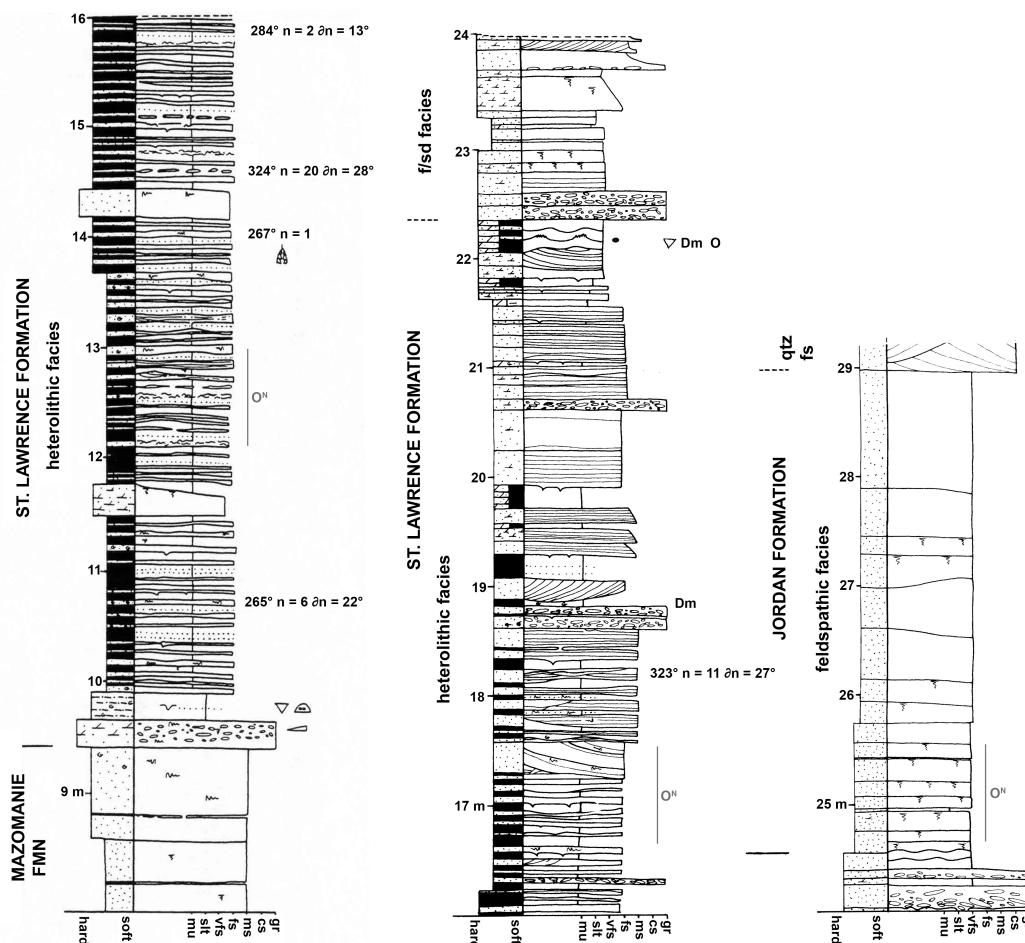


Figure 3.2: Stratigraphic section in the cascade and along the south side of MN State Highway 243 at Osceola (OA), Polk Co, Wisconsin. The left column depicts lithology and degree of induration with G: glauconite. Symbols on right side of the log refer to presence of dendroid graptolites (tuning fork-like symbol), linguliiform brachiopods ('∇'), hyolithids (right-angled triangle symbol) and aglaspids (half-moon-like symbol). The trilobite occurrences marked on the log include: *Dikelocephalus minnesotensis* (Dm) and *Osceolia* (O). O^N and the vertical gray line next to the symbol refers to approximate range of *Osceolia* collection made by Nelson (1956) at this locality. The uppermost of these, at ~25 m, is almost certainly equivalent to the horizon of the USNM site 78 collection. Fmn: formation, f/sd facies: feldspathic facies, qtz fs: quartzose facies (see Hughes and Hesselbo, 1997 for further details).

Arcadia (AAa), north section

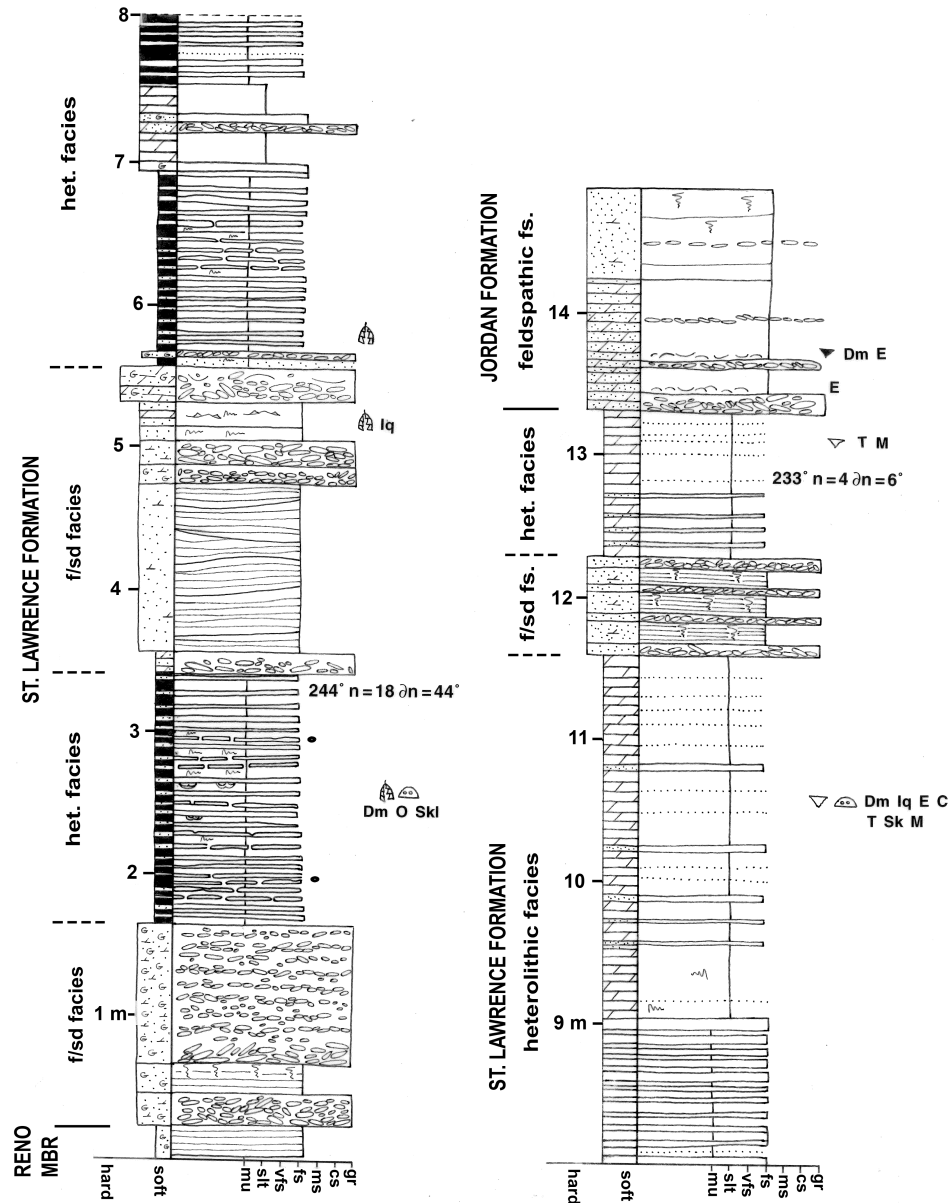


Figure 3.3: Stratigraphic section at Arcadia (AAa), north section, Trempealeau Co., Wisconsin. In addition to symbols described in figure 2, symbols on right side of the log also refer to presence of wrinkle marks (flat-oval-like symbol) and rhyconelliform brachiopods (filled-inverted-triangle symbol). The trilobite occurrences marked on the log include: *Dikelocephalus minnesotensis* (Dm), *Saukiella* (Sk), *Eurekia* (E), *Illaenurus quadratus* (Iq), *Tellerina* (T), *Macronoda* (M), *Calvinella* (C), *Saukia* (Sk) and *Osceolia* (O). Mbr: member (see Fig. 3.2 and Hughes and Hesselbo, 1997 for further details).

Spring Valley (SV) Howe Quarry

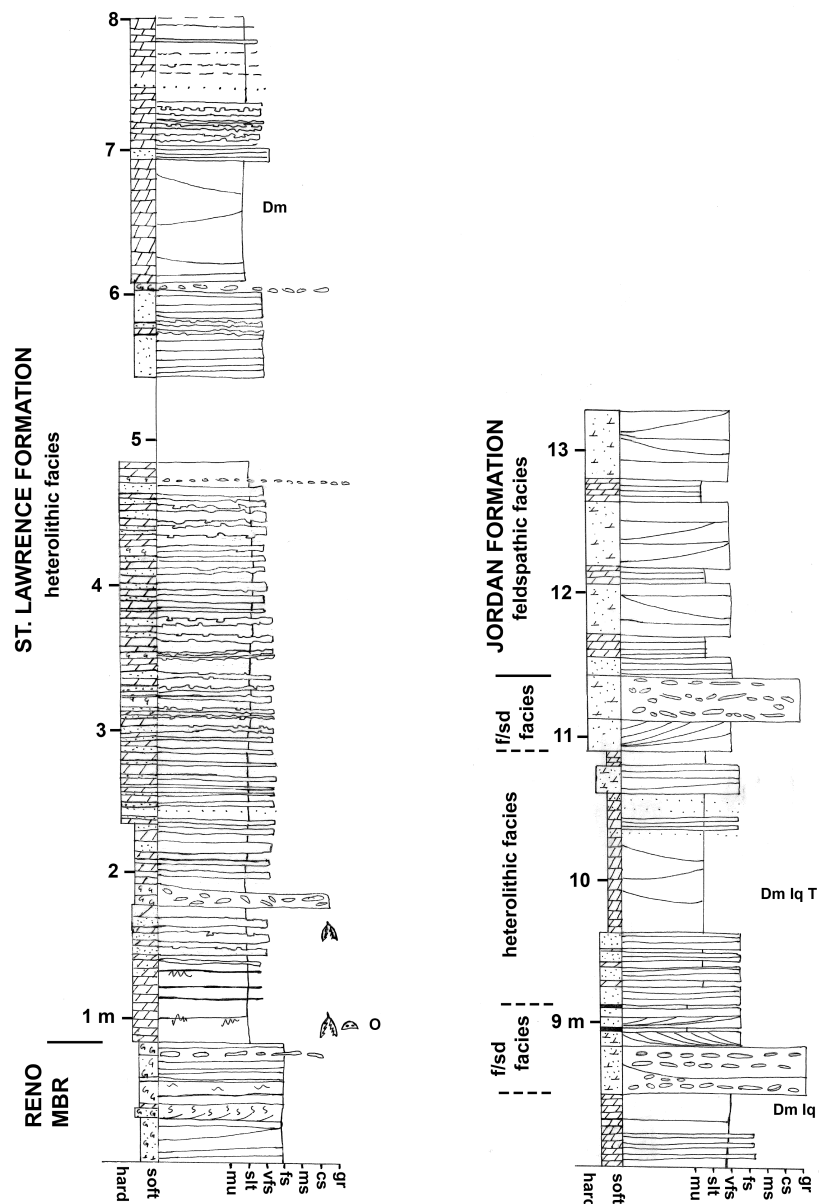


Figure 3.4: Stratigraphic section 13 km east of Spring Valley (SV), Howe Quarry, Dunn Co., Wisconsin. Symbols as described in Figs. 3.2 and 3.3.

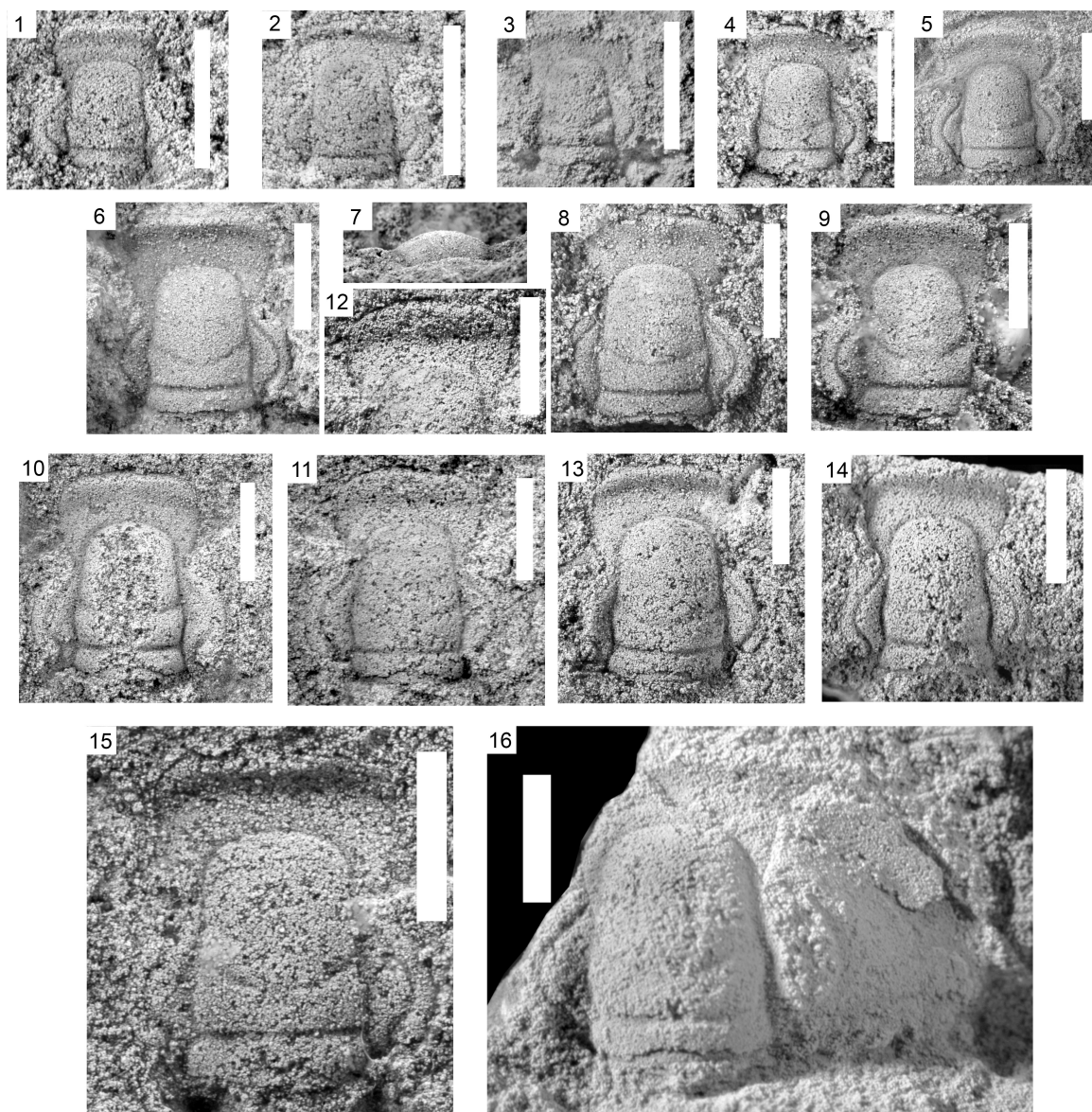


Figure 3.5: *Osceolia osceola* (Hall, 1863) cranidia from the Norwalk Member of the Jordan Formation collected at stratigraphically equivalent beds on both sides of the St. Croix River at Osceola, Wisconsin (WI) and Minnesota (MN) in the upper Mississippi Valley. (1) CMC-IP 91763b, WI (formerly UMPC 8040); (2) USNM-PAL 789889, WI; (3) AMNH 99388, WI (lectotype, Hall, 1863, pl. 10, fig. 18); (4) USNM-PAL 789887, WI; (5) USNM-PAL 58666, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 3); (6) LACMIP 29240.20, MN; (7) anterior view of (6); (8) USNM-PAL 789869, WI; (9) LACMIP 29240.19, MN; (10) LACMIP 29237.12, MN; (11) LACMIP 9681.1, MN; (12) anterior portion of (11); (13) USNM-PAL 789872, WI; (14) CMC-IP 91820b, WI (formerly UMPC 9410b); (15) LACMIP 12793.1, MN; (16) cephalon USNM-PAL 58667, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 1). Scale bar = 5 mm in all images.

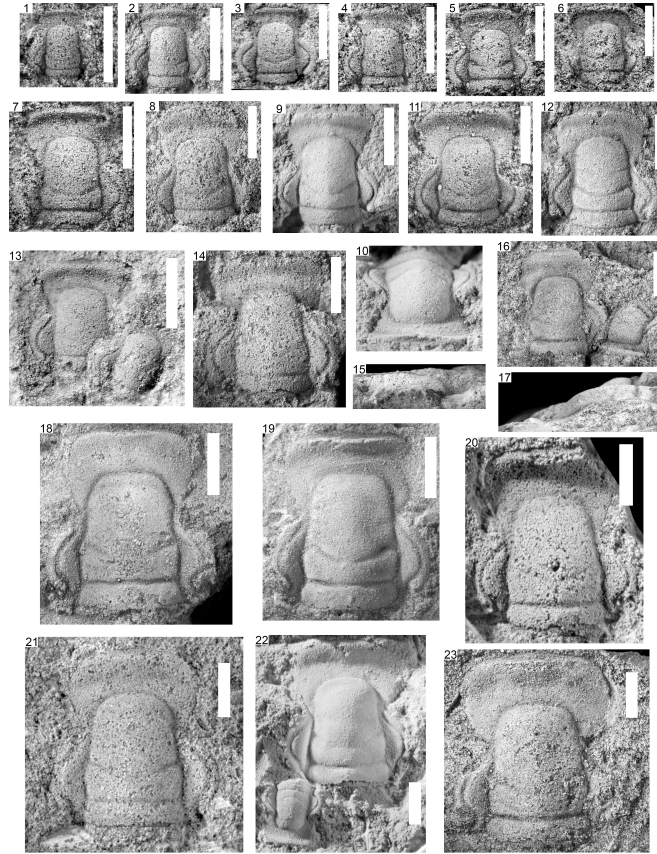


Figure 3.6: *Osceolia osceola* (Hall, 1863) cranidia from sandstone facies illustrating ontogenetic variation from small to larger specimens. (1) USNM PAL 789877 from Norwalk Member, Osceola, WI; (2) USNM PAL 9555A from the Norwalk Member, Mondovi, WI; (3) LACMIP 29274.5 from the laminated sandstone facies of the St. Lawrence Formation, Ridgeland, WI; (4) USNM PAL 789879 from the Norwalk Member, Osceola, WI; (5) LACMIP 29240.27 from the Norwalk Member, Osceola, MN; (6) LACMIP 29240.30 from the Norwalk Member, Osceola, MN; (7) LACMIP 29240.21 from the Norwalk Member, Osceola, MN; (8) USNM PAL 789892 from the laminated sandstone facies of the St. Lawrence Formation, Eleva, WI; (9) CMC-IP 82027a from the laminated sandstone facies of the St. Lawrence Formation, Osceola, MN (formerly UMPC T6604a, figured as *O. osceola* by Nelson, 1951, pl. 110, fig. 9); (10) anterior view of (9); (11) USNM PAL 789899 from the laminated sandstone facies of the St. Lawrence Formation, Eleva, WI; (12) USNM PAL 9561B from the Norwalk Member, Mondovi, WI; (13) LACMIP 29246.4 from the laminated sandstone facies of the St. Lawrence Formation, Ridgeland, WI; (14) USNM PAL 340603C from the Norwalk Member, Osceola, MN; (15) right lateral view of (14); (16) USNM PAL 789901 from the Norwalk Member, Eleva, WI; (17) left lateral view of (16); (18) USNM PAL 78495 from the Norwalk Member, Mondovi, WI (syntype of *O. separata* Ulrich and Resser, 1930, pl. 23, fig. 12); (19) latex of counterpart USNM PAL 9546 from the Norwalk Member, Mondovi, WI; (20) USNM PAL 78492 from the Norwalk Member, Eleva, WI (syntype of *O. obsoleta reversa* Ulrich and Resser, 1930, pl. 23, fig. 9); (21) UWGM “L14” from the laminated sandstone facies of the St. Lawrence Formation, Osceola, WI (specimen currently missing); (22) USNM PAL 78494 from the Norwalk Member, Eleva, WI (syntype of *O. arguta* Ulrich and Resser, 1930, pl. 23, fig. 11); (23) USNM PAL 789895A from the Norwalk Member, Eleva, WI. Scale bars on all images = 5 mm.

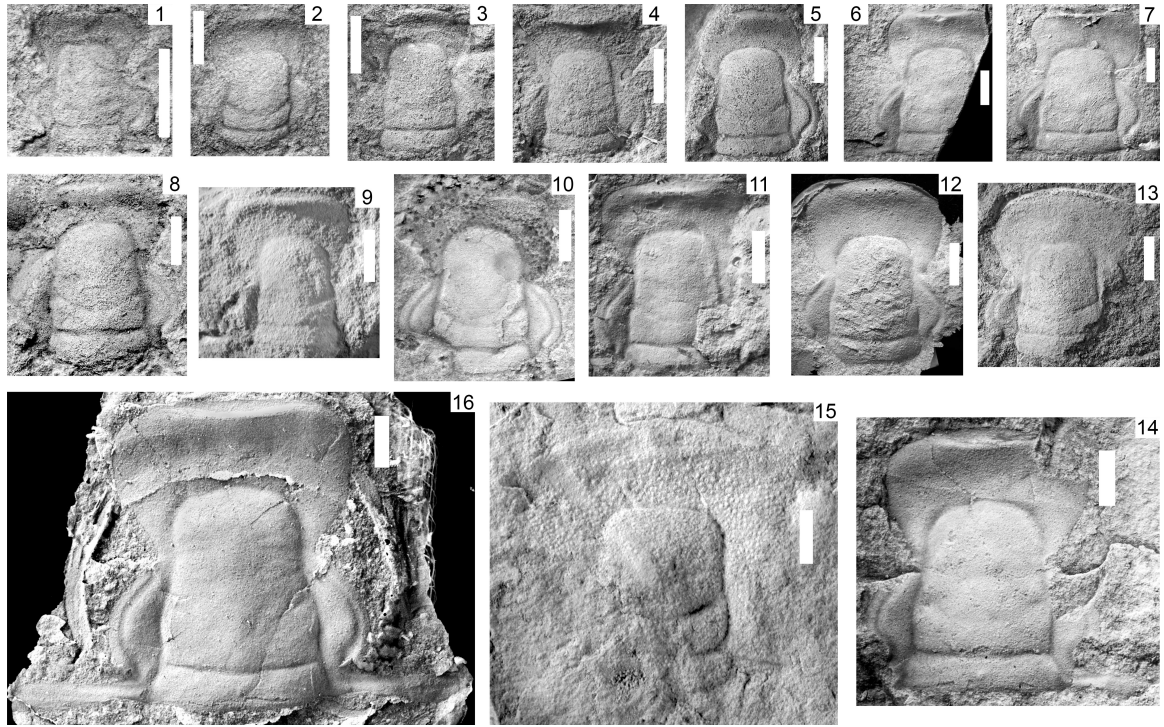


Figure 3.7: *Osceolia osceola* (Hall, 1863) cranidia from the heterolithic facies of the St. Lawrence Formation from several localities in the upper Mississippi Valley. (1) LACMIP 29246.7 from Ridgeland, WI; (2) LACMIP 29239.8 from Osceola, WI; (3) LACMIP 29236.3 from Soo Bridge, MN; (4) LACMIP 29239.6 from Osceola, WI; (5) USNM-PAL 792115 from Elk Mound, WI; (6) CMC-IP 96960A from 1 m above the base of the formation, Spring Valley, WI; (7) latex of counterpart CMC-IP 96960B from 1 m above the base of the formation, Spring Valley, WI; (8) LACMIP 29235.17 from Soo Bridge, MN; (9) USNM-PAL 78499 from Osceola, WI (syntype of *O. praecepta* Ulrich and Resser, 1930, pl. 23, fig. 16); (10) UWGM 7148 from Arcadia, WI; (11) latex of counterpart LACMIP 29246.9 from Ridgeland, WI; (12) latex of counterpart USNM-PAL 58622 from Osceola, WI (syntype of *O. lodensis* Ulrich and Resser, 1930, pl. 23, fig. 19); (13) USNM-PAL 789885 from Osceola, WI; (14) LACMIP 29246.1 from Ridgeland, WI; (15) LACMIP 29239.1 from locality unspecified within Dunn County, WI, with fragment of aglaspidid cuticle (pustulated) superimposed; (16) latex of counterpart UWGM 7548 from Ridgeland, WI. Scale bar = 5 mm in all images.

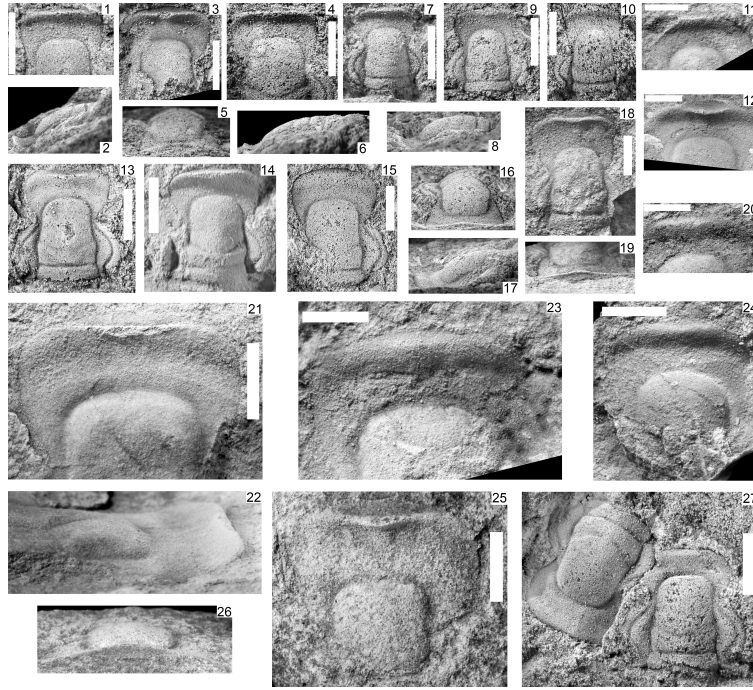


Figure 3.8: Variation in morphology of cranial anterior border among *O. osceola* (Hall, 1863) cranidia. (1) anterior border of LACMIP 29240.26 from the Norwalk Member, Osceola, MN (strong ledge); (2) left lateral view of (1); (3) anterior border of LACMIP 29240.25 from the Norwalk Member, Osceola, MN (strong ledge); (4) anterior border of LACMIP 29240.23 from the Norwalk Member, Osceola, MN (strong ledge); (5-6) anterior and left lateral views of (4); (7) LACMIP 29240.22 from the Norwalk Member, Osceola, MN (intermediate ledge); (8) left lateral view of (7); (9) LACMIP 29237.11 from the Norwalk Member, Osceola, WI (strong ledge); (10) USNM PAL 789876 from the Norwalk Member, Osceola, WI (intermediate ledge); (11) anterior border of LACMIP 29235.16 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN (intermediate ledge); (12) latex of counterpart anterior border of LACMIP 29236.5 from the heterolithic facies of St. Lawrence Formation, Soo Bridge, MN (strong ledge); (13) USNM PAL 78493 from the Norwalk Member, Eleva, WI (strong ledge; syntype of *O. obsoleta reversa* Ulrich and Resser, 1930, pl. 23, fig. 10); (14) USNM PAL 78496 from the Norwalk Member, Mondovi (strong ledge; syntype of *O. separata* Ulrich and Resser, 1930, pl. 23, fig. 13), WI; (15) MCZ-IP 202510 from the Norwalk Member, Osceola, WI (ledge absent); (16-17) anterior and left lateral views of (15); (18) LACMIP 29239.7 from the heterolithic facies of the St. Lawrence Formation, Osceola, WI (strong ledge); (19) anterior view of (18); (20) anterior border of LACMIP 29235.17 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN (strong ledge); (21) anterior border of LACMIP 29275.1 from the heterolithic facies of the St. Lawrence Formation of Ridgeland, WI (strong ledge); (22) oblique anterior view of (21); (23) anterior border of LACMIP 29235.9 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN (strong ledge); (24) latex of counterpart anterior border of LACMIP 29235.15 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN (strong ledge); (25) anterior border of USNM PAL 78503 from the heterolithic facies of the St. Lawrence Formation, Osceola, WI (strong ledge; syntype of *O. lodensis reflexa* Ulrich and Resser, 1930, pl. 23, fig. 22); (26) anterior view of (25); (27) USNM PAL 789896A (ledge absent) and USNM PAL 789896B (intermediate ledge) (from left) from the Norwalk Member, Eleva, WI. Scale bars on all images = 5 mm.

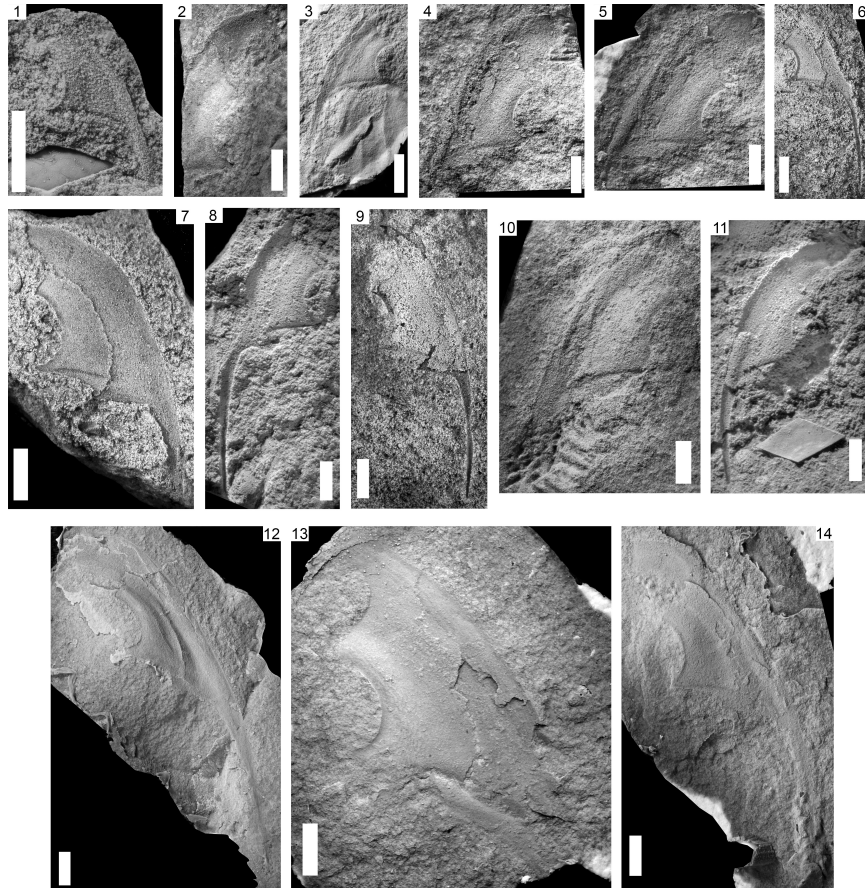


Figure 3.9: *Osceolia osceola* (Hall, 1863) free cheeks from various localities. (1) latex of counterpart AMNH 39115 from the Norwalk Member, Osceola, WI (paralectotype, Hall, 1863, pl. 10, fig. 19); (2) LACMIP 29235.10 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN; (3) latex of counterpart LACMIP 29246.8 from the heterolithic facies of Ridgeland, WI; (4) LACMIP 29239.5 from the heterolithic facies the St. Lawrence Formation of Osceola, WI; (5) latex of counterpart LACMIP 29239.5 from the heterolithic facies the St. Lawrence Formation of Osceola, WI; (6) USNM PAL 789894 from the Norwalk Member, Eleva, WI; (7) USNM PAL 789900 from the Norwalk Member, Eleva, WI; (8) USNM PAL 78488 from the Norwalk Member, Osceola, WI (syntype of *O. obsoleta* Ulrich and Resser, 1930, pl. 23, fig. 5); (9) MCZ-IP 926 from the Norwalk Member, Osceola, WI; (10) LACMIP 29235.11 from the heterolithic facies of the St. Lawrence Formation, Soo Bridge, MN; (11) USNM PAL 58665 from the Norwalk Member, Osceola, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 4); (12) latex of counterpart CMC-IP 96961 from the heterolithic facies of the St. Lawrence Formation, Spring Valley, WI; (13) latex of counterpart CMC-IP 96979 from the heterolithic facies the St. Lawrence Formation, Spring Valley, WI; (14) latex of counterpart CMC-IP 96962 from the heterolithic facies of the St. Lawrence Formation, Spring Valley, WI. Scale bars = 5 mm in all images.

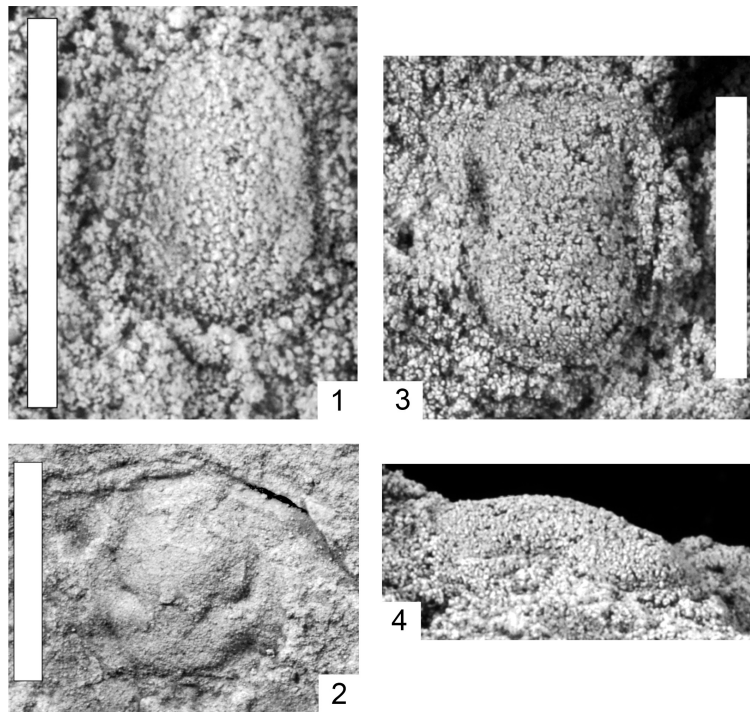


Figure 3.10: *Osceolia osceola* (Hall, 1863) associated hypostomes from various localities. (1) latex of counterpart MCZ-IP 202512 from the Norwalk Member, Osceola, WI; (2) LACMIP 29246.6 from the heterolithic facies of the St. Lawrence Formation of Ridgeland, WI; (3) USNM PAL 58668B from the Norwalk Member, Osceola, WI; (4) left lateral view of (3). Scale bars = 5 mm in all images.

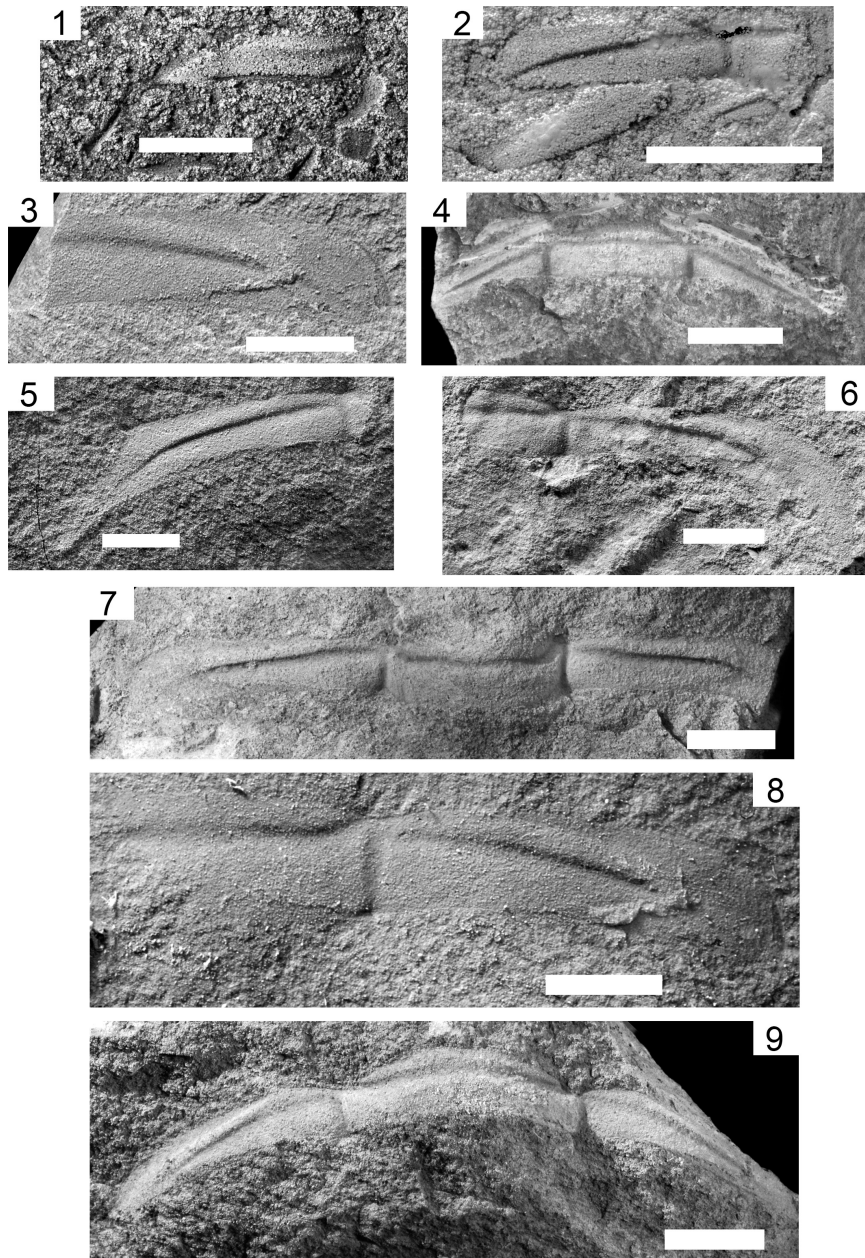


Figure 3.11: *Osceolia osceola* (Hall, 1863) associated thoracic segments from various localities. (1) USNM PAL 72689B from the Norwalk Member, Osceola, WI; (2) LACMIP 29274.3 from the heterolithic facies of the St. Lawrence Formation at Ridgeland, WI; (3) CMC-IP 96970 from the heterolithic facies of the St. Lawrence Formation, Spring Valley, WI; (4) USNM PAL 340608A from the Norwalk Member, Osceola, WI; (5) CMC-IP 96969 from the heterolithic facies of the St. Lawrence Formation, Spring Valley, WI; (6) LACMIP 29245.5 from the heterolithic facies of the St. Lawrence Formation, Menomanie, WI; (7) USNM PAL 789886 from the heterolithic facies of Osceola the St. Lawrence Formation, WI; (8) latex of counterpart CMC-IP 96968 from the heterolithic facies, the St. Lawrence Formation, Spring Valley, WI; (9) USNM PAL 340608B from the Norwalk Member, Osceola, WI. Scale bars = 5 mm in all images.

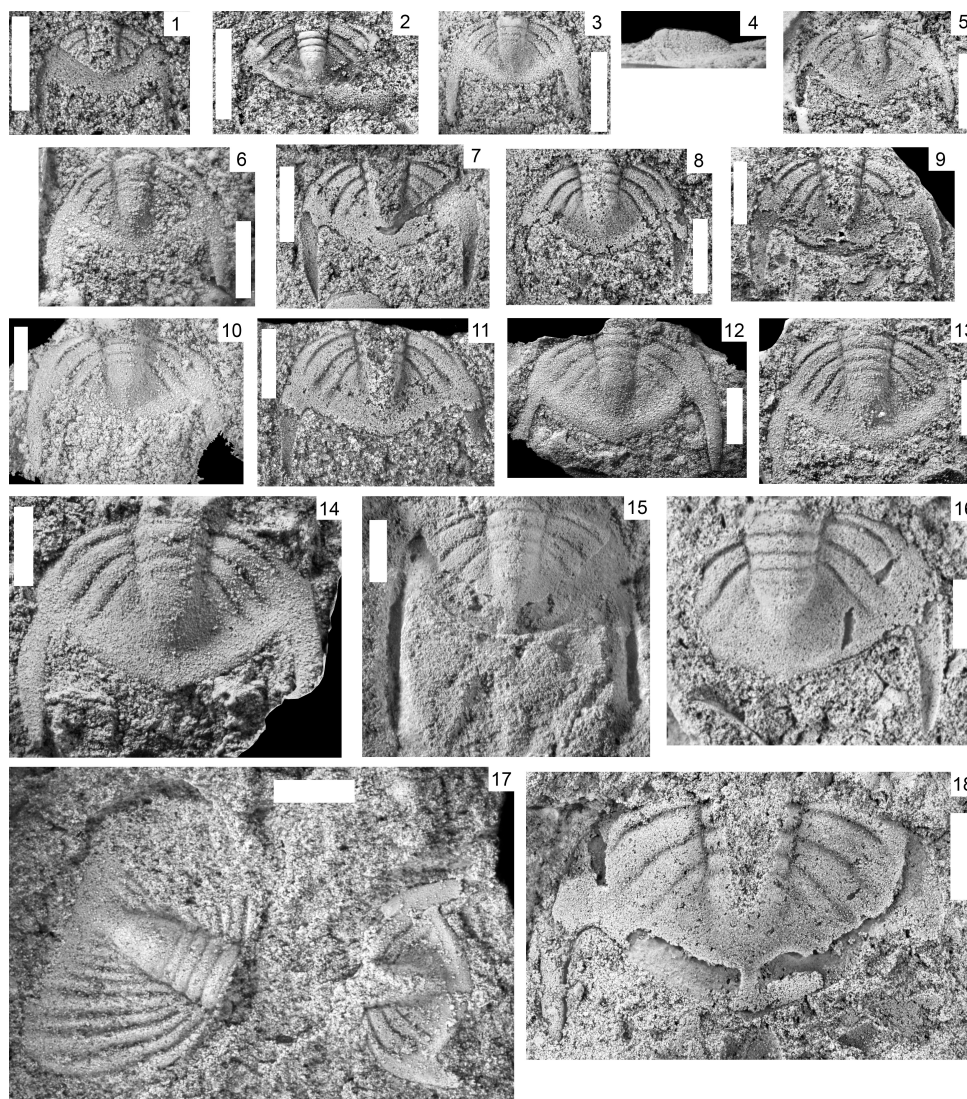


Figure 3.12: *Osceolia osceola* (Hall, 1863) pygidia from the Norwalk Member of the Jordan Formation at Osceola, on both Wisconsin (WI) and Minnesota (MN) sides of the St. Croix River in the upper Mississippi Valley. (1) USNM-PAL 789888, WI; (2) LACMIP 29240.31, MN; (3) latex of counterpart USNM-PAL 58669, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 8); (4) left lateral view of (3); (5) latex of counterpart USNM-PAL 789881, WI; (6) latex of counterpart AMNH 342, WI (paralectotype, Hall, 1863, pl. 7, fig. 49); (7) USNM-PAL 72689A, WI (formerly USNM 72689; figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 9); (8) USNM-PAL 789874, WI; (9) LACMIP 29240.24, MN; (10) latex of counterpart USNM-PAL 58670, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 7); (11) USNM-PAL 789880, WI; (12) latex of counterpart MCZ-IP: 202514, WI; (13) latex of counterpart LACMIP 29240.3, MN; (14) latex of counterpart LACMIP 29240.18, MN; (15) USNM-PAL 78491, WI (syntype of *O. obsoleta* Ulrich and Resser, 1930, pl. 23, fig. 8); (16) CMC-IP 94405b, WI (formerly UMPC 8040); (17) USNM-PAL 789882A with *Dikelocephalus minnesotensis* Owen, 1852 pygidium (left) on same slab, MN; (18) USNM-PAL 78489, WI (syntype of *O. obsoleta* Ulrich and Resser, 1930, pl. 23, fig. 6). Scale bar = 5 mm in all images.

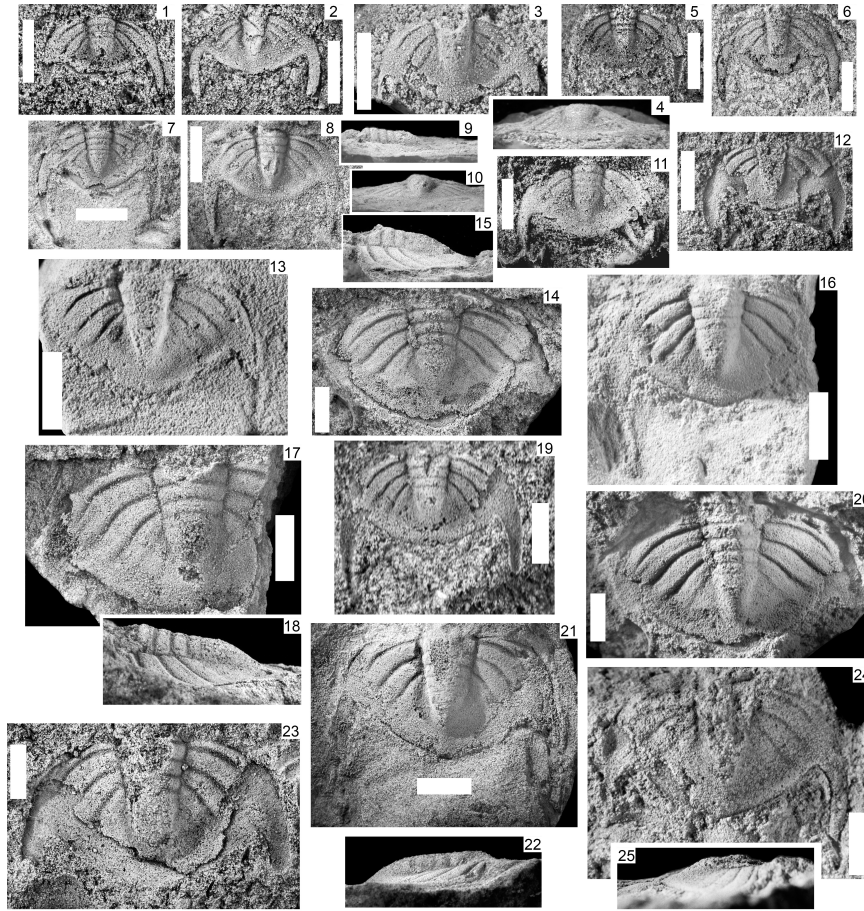


Figure 3.13: *Osceolia osceola* (Hall, 1863) pygidia from sandstone facies from various localities illustrating ontogenetic variation from small to larger specimens. (1) USNM PAL 789875 from the Norwalk Member, Osceola, WI; (2) latex of counterpart USNM PAL 789884 from the Norwalk Member, Osceola, WI; (3) Posterolateral view of (2); (4) USNM PAL 789897 from the Norwalk Member, Eleva, WI; (5) MCZ 202513 from the Norwalk Member, Osceola, WI; (6) latex of counterpart USNM PAL 9555B from the Norwalk Member, Mondovi, WI; (7-8) Left lateral and posterolateral views of (6); (9) USNM PAL 9561A from the Norwalk Member, Mondovi, WI; (10) USNM PAL 789891 from the Norwalk Member, Eleva, WI; (11) latex of counterpart USNM PAL 789895B from the Norwalk Member, Eleva, WI; (12) USNM PAL 58668A from the Norwalk Member, Osceola, WI; (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 5); (13) CMC-IP 87992 from Norwalk Member, Mondovi, WI (formerly UMPC 3150); (14) CMC-IP 82027b from laminated sandstone of St. Lawrence Formation, Osceola, MN (formerly UMPC T6604b; figured as *O. osceola* by Nelson, 1951, pl. 110, fig. 10); (15) Right lateral view of (14); (16) USNM PAL 789902 from the Norwalk Member, Osceola, WI; (17) Left lateral view of (16); (18) latex of counterpart USNM PAL 78497 from the Norwalk Member, Mondovi, WI (syntype of *O. separata* Ulrich and Resser, 1930, pl. 23, fig. 14); (19) USNM PAL 72688 from the Norwalk Member, Osceola, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 22, fig. 6); (20) USNM PAL 789891A from the Norwalk Member, Eleva, WI; (21) USNM PAL 78498 from the Norwalk Member, Mondovi, WI (syntype of *O. separata* Ulrich and Resser, 1930, pl. 23, fig. 15); (22) Right lateral view of (21); (23) USNM PAL 340603A from the Norwalk Member, Osceola, WI; (24) Left lateral view of (23). Scale bars = 5 mm in all images.

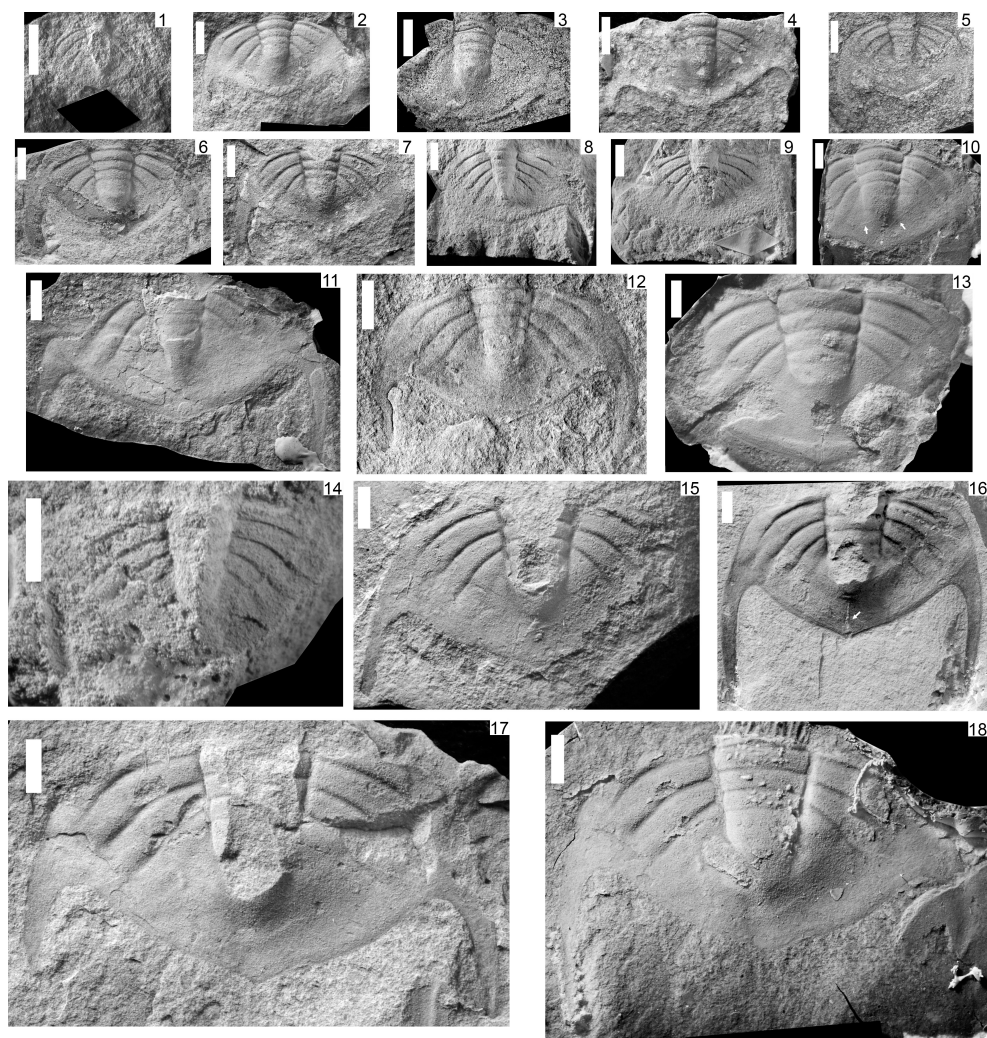


Figure 3.14: *Osceolia osceola* (Hall, 1863) pygidia from the heterolithic facies of St. Lawrence Formation from several localities in the upper Mississippi Valley. (1) USNM-PAL 78501 from Osceola, WI (syntype of *O. praecipta* Ulrich and Resser, 1930, pl. 23, fig. 18); (2) latex of counterpart LACMIP 29234.3 from Soo Bridge, MN; (3) latex of counterpart USNM-PAL 789893 from Eleva, WI; (4) LACMIP 29235.14 from Soo Bridge, MN; (5) LACMIP 29239.5 from Osceola, WI; (6) LACMIP 29234.4 from Soo Bridge, MN; (7) LACMIP 29235.12 from Soo Bridge, MN; (8) USNM-PAL 58605 from Osceola, WI (figured as *O. osceola* by Ulrich and Resser, 1930, pl. 23, fig. 20); (9) USNM-PAL 78502 from Osceola, WI (syntype of *O. lodensis* Ulrich and Resser, 1930, pl. 23, fig. 21)); (10) latex of counterpart LACMIP 29235.5 from Soo Bridge, MN; (11) latex of counterpart LACMIP 29246.8 from Ridgeland, WI; (12) UWGM “L204” from Ridgeland, WI (specimen currently missing); (13) latex of counterpart LACMIP 29245.2 from Menomanie, WI; (14) USNM-PAL 78500 from Osceola, WI (syntype of *O. praecipta* Ulrich and Resser, 1930, pl. 23, fig. 17); (15) CMC-IP 96972 from 1 m above the base of the formation, Spring Valley, WI; (16) CMC-IP 96971 from Spring Valley, WI; (17) CMC-IP 96973 from 1 m above the base of the formation, Spring Valley, WI; (18) latex of counterpart CMC-IP 96975 from Spring Valley, WI. Scale bar = 5 mm in all images. White arrow points to sinuous structures possibly reflecting infestation.

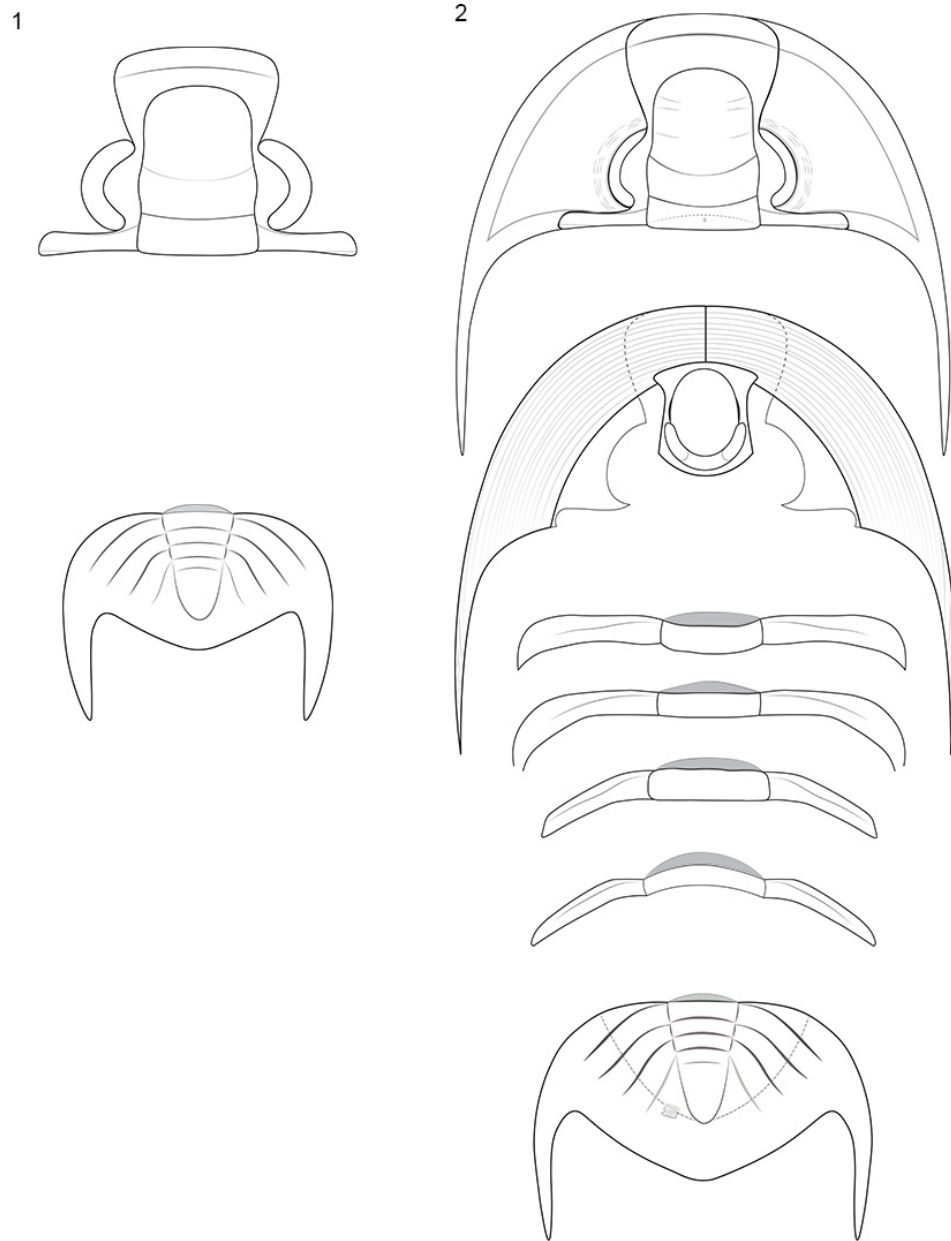


Figure 3.15: Reconstruction of *Osceolia osceola* representing the generalized shape of the exoskeletal components. **(1)** dorsal view of small sized holaspid *O. osceola* cranium and pygidium; **(2)** dorsal view of large sized holaspid, cranium with median tubercle, free cheek with eye platform and surface ornamentation, ventral view of free cheek with terrace ridges, surface ornamentation and median suture, dorsal view of pygidium showing paradoublural line (dashed), and terrace ridges projected on the dorsal surface from the ventral side of pygidium (cutout view with zigzag outline), with associated thoracic segments and hypostome.

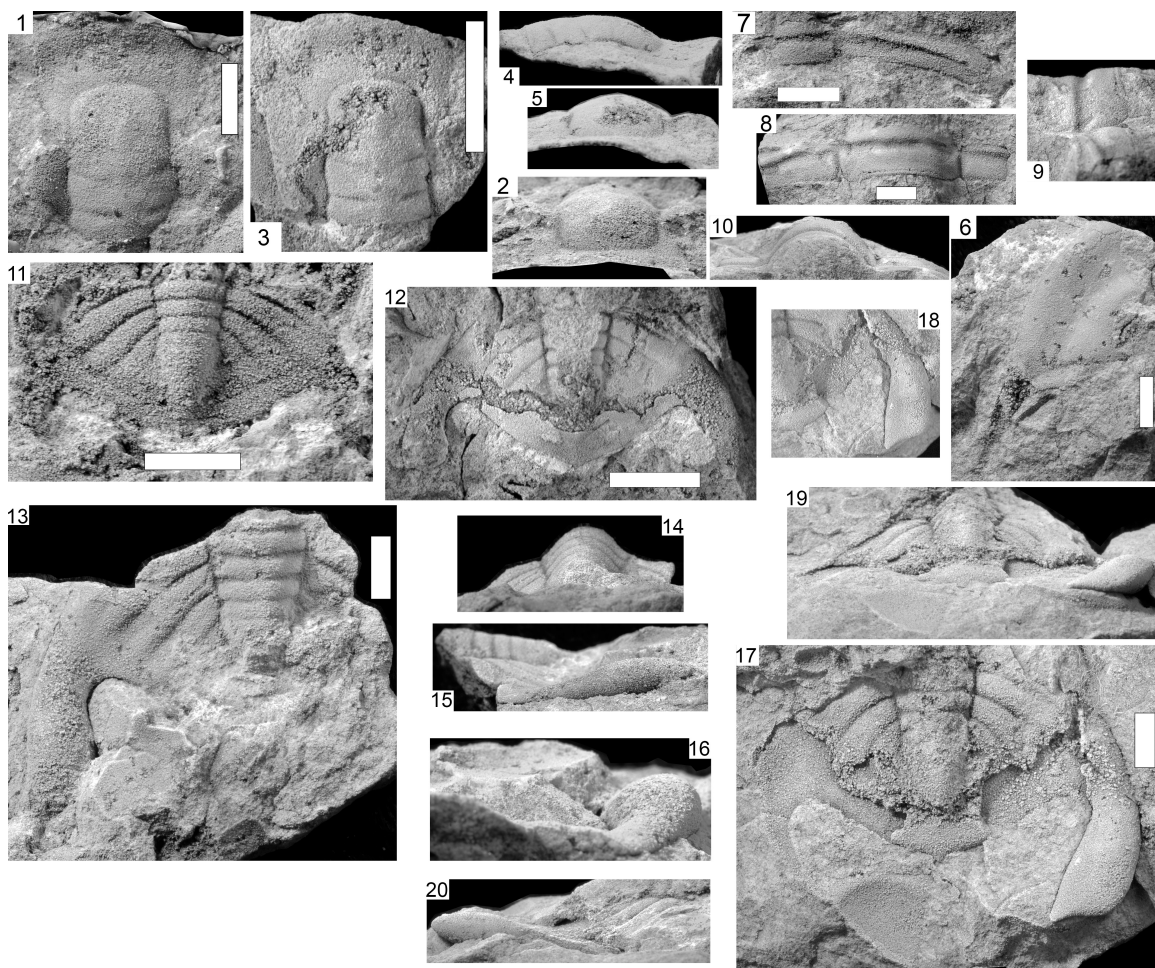


Figure 3.16: *Osceolia tumerispina* new species from the dolomitic facies of the St. Lawrence Formation, Coon Valley, WI. (1) paratype, latex of counterpart cranidium UWGM 7459; (2) anterior view of (1); (3) paratype, cranidium UWGM 7455; (4-5) right lateral and anterior views of (3); (6) paratype, free cheek UWGM 7456; (7) paratype, thoracic segment UWGM 7457; (8) paratype, thoracic segment UWGM 7454; (9-10) left lateral and anterior views of (8); (11) paratype, pygidium UWGM 7458; (12) paratype, pygidium UWGM “L201” (specimen currently missing); (13) paratype, pygidium UWGM 7453; (14-16) posterior, left lateral and anterior views of (13); (17) holotype, pygidium UWGM 7452; (18-20) right spine, posterior and right lateral views of (17). Scale bars = 5 mm for 1-2, 6-11, 13-17, 10 mm for 3-5, 12.

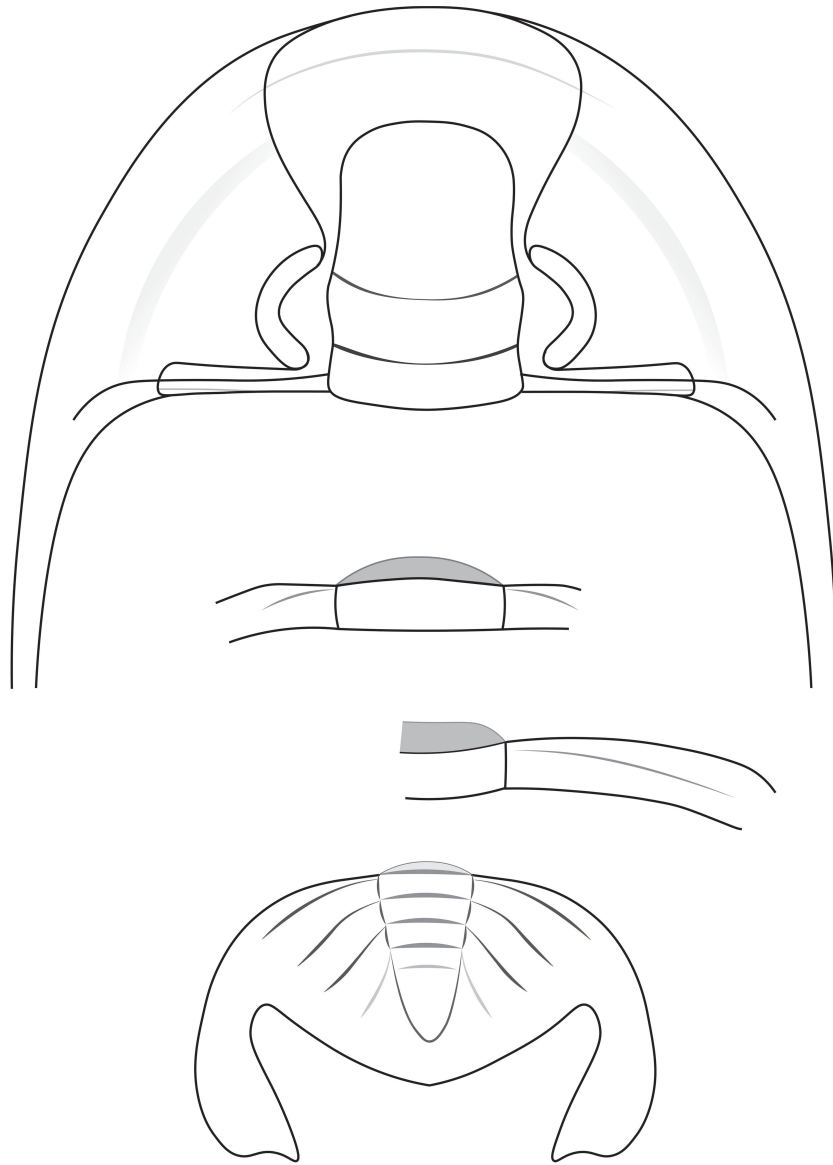


Figure 3.17: Reconstructions of *Osceolia tumerispina* exoskeleton, cephalon with long frontal area, thoracic segments, and pygidium with club-like posterolateral spines. Lightly shaded region within the pleural platform of the free cheek indicates break in slope.

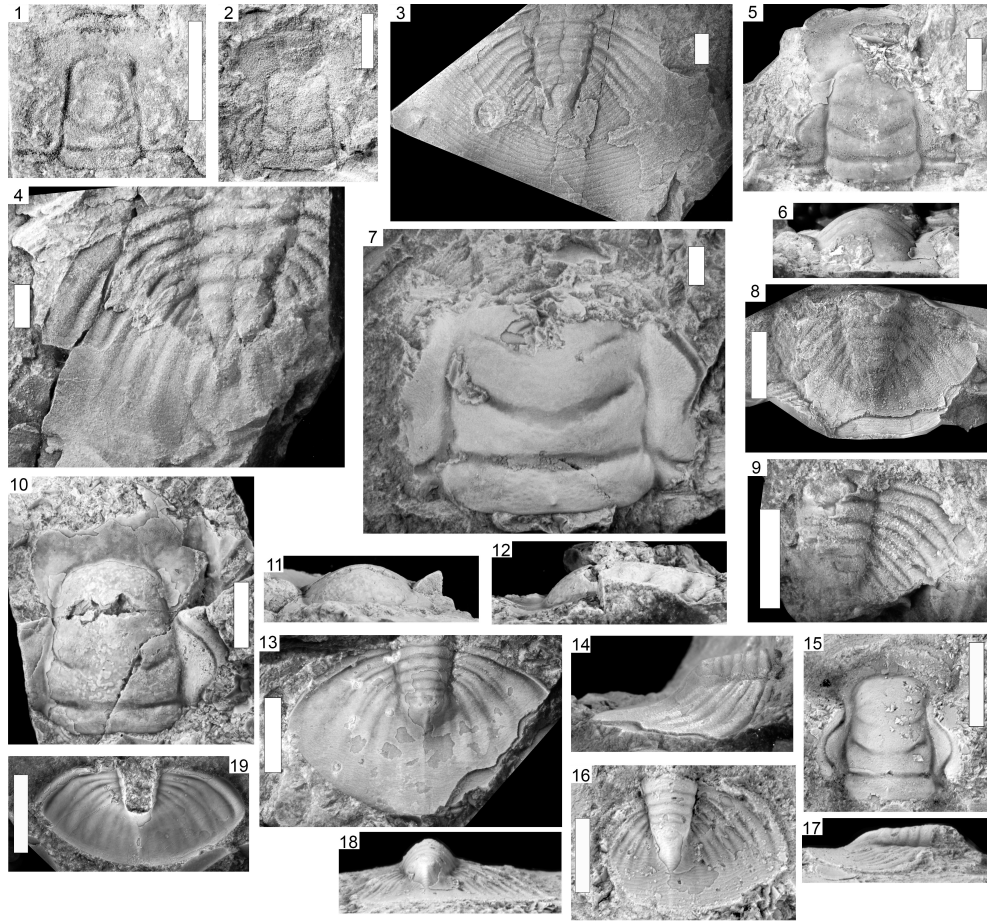


Figure 3.18: *Briscoia* species resembling members of *Osceolia*. (1) cranidium, *Briscoia coloradoensis* Walcott, 1914, USNM PAL 795972, Sawatch, CO; (2) cranidium, *Briscoia coloradoensis* Walcott, 1914, USNM PAL 60673, Sawatch, CO (figured as *Saukia coloradoensis* by Walcott, 1914, pg. 376, fig. 13); (3) pygidium, *Briscoia coloradoensis* Walcott, 1914, USNM PAL 60676, Sawatch, CO (figured as *Saukia coloradoensis* by Walcott, 1914, pg. 376, fig. 16); (4) pygidium, *Briscoia coloradoensis* Walcott, 1914, USNM PAL 60675, Sawatch, CO (figured as *Saukia coloradoensis* by Walcott, 1914, pg. 376, fig. 15); (5) cranidium, *Briscoia texana* Walcott, 1914, USNM PAL 795968, Burnet Co., TX; (6) anterior view of (5); (7) cranidium, *Briscoia texana* Walcott, 1914, USNM PAL 58621, Burnet Co., TX (figured as *Dikelocephalus texanus* by Walcott, 1914, p. 372, pl. 65, fig. 4); (8) pygidium, *Briscoia texana* Walcott, 1914, USNM PAL 795945c, Burnet Co., TX; (9) pygidium, *Briscoia texana* Walcott, 1914, USNM PAL 795945b, Burnet Co., TX; (10) cranidium, *Briscoia nevadensis* (Walcott, 1884), USNM PAL 24659A, Eureka, NV (figured as *Dikelocephalus osceola* by Walcott, 1884, pl. 9, fig. 25; (11-12) anterior and left lateral views of (10); (13) pygidium, *Briscoia nevadensis* (Walcott, 1884), USNM PAL 792120, Eureka, NV; (14) right lateral view of (13); (15) cranidium, *Briscoia* sp., CMC-IP 102303 (PH 242), Dotsero Formation, at 17.33 m in South Bush Creek section, CO; (16) pygidium, *Briscoia* sp., CMC-IP 102304 (PH 2491), Dotsero Formation, at 16.6 m in Lime Creek section, CO; (17-18) right lateral and posterior views of (16); (19) pygidium, *Briscoia* sp., CMC-IP 102305 (PH 524), Dotsero Formation, at 15.65 m in South Bush Creek section, CO. Scale bars = 5 mm in all images.

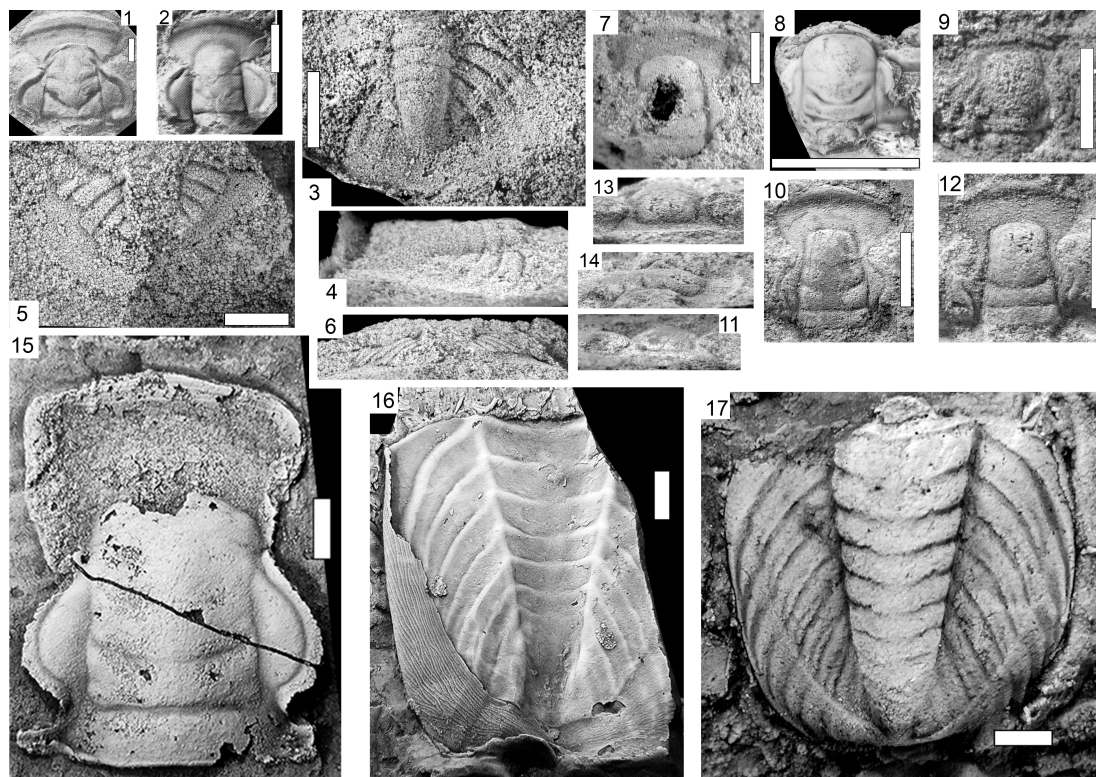


Figure 3.19: Cranidial homeomorphs of *Osceolia*, cranidia previously incorrectly assigned to the genus, and indeterminate pygidia from the Devil's Lake Member. (1) homeomorphic cranidium, *Formosocephalus savitzkyi* Pegel in Egorova et al. (1982, pl. 51, fig. 6), sample 34/5, Lena River section, Siberia; (2) homeomorphic cranidium, *Pseudoanomocarina eldachica* Bognibova et al., 1971, figured in Savitsky, 1976, pl. 38, fig. 15, sample 44/143, Siberia; (3) Gen. et sp. indeterminate, pygidium, USNM PAL 791890, Devil's Lake Member, Devil's Lake, WI; (4) right lateral view of (3); (5) Gen. et sp. indeterminate pygidium, USNM PAL 791891, Devil's Lake Member, Devil's Lake, WI; (6) posterior view of (5); (7) cranidium, cf. *Osceolia*, CMC-IP 87150, Marine, MN (formerly UMPC 9407); (8) cranidium previously referred to *Osceolia*, *Pseudosaukia brevifrons* (Clark, 1924), MCZ-IP 101227, Beekmantown series, Lévis, Québec; (9) cranidium previously referred to *O. osceola* by Hall (1863, pg. 146, not previously figured), *Saukiella pyrene* (Walcott, 1914), AMNH 39114, Osceola, WI; (10) homeomorphic cranidium, *Prosaukia lochmani* Stitt and Straatmann, 1997, UMC 17170, Black Hills, SD; (11) anterior view of (10); (12) homeomorphic cranidium, *Prosaukia lochmani* Stitt and Straatmann, 1997, UMC 17171, Black Hills, SD; (13-14) anterior and right lateral views of (12); (15) homeomorphic cranidium, *Hamashania pulchra* (Kobayashi, 1942), SNUP4004, Taebaeksan Basin, Korea; (16) pygidium, *Hamashania pulchra* (Kobayashi, 1942), SNUP 4007, Taebaeksan Basin, Korea; (17) pygidium, *Hamashania* sp. cf. *H. busiris* (Walcott, 1905), SNUP 4013, Taebaeksan Basin, Korea. Scale bars = 5 mm (3, 5, 7-10, 12, 15-17), or 10 mm (1, 2).

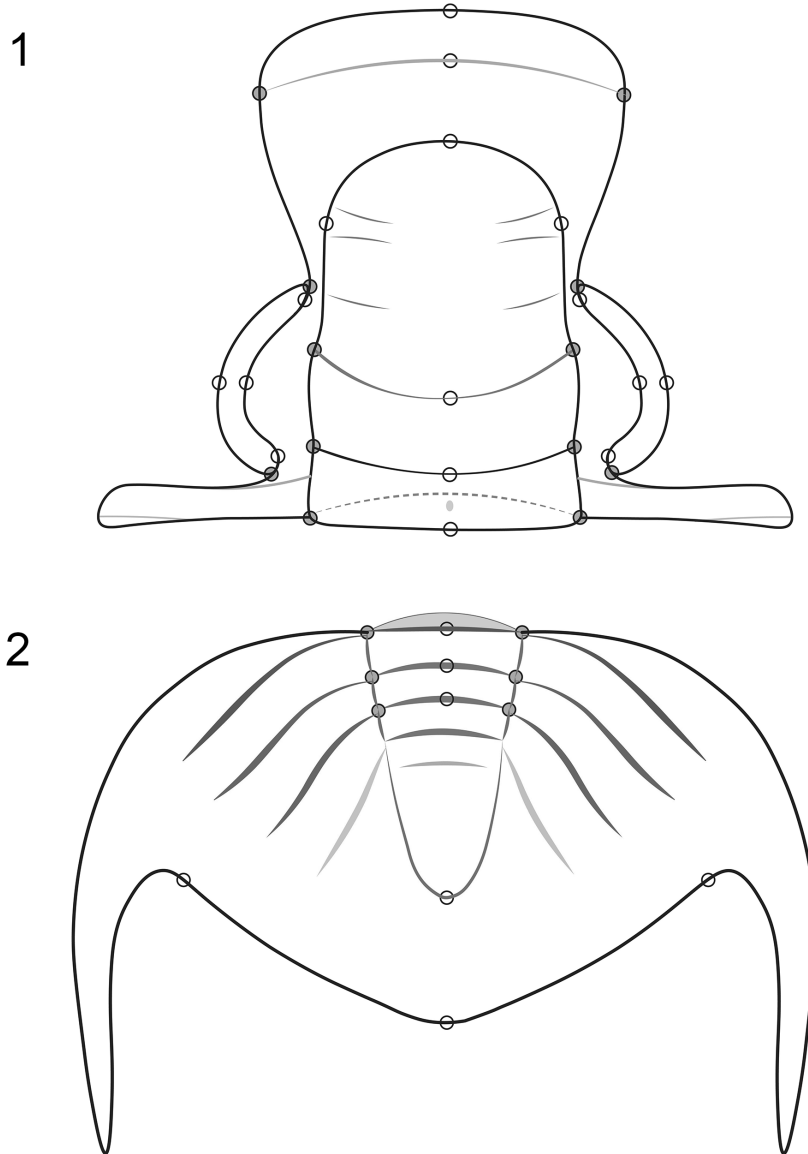


Figure 3.20: Reconstruction of *Osceolia osceola* cranidium and pygidium showing the set of landmarks used to assess geometric morphological variation. **(1)** Cranidium reconstruction with the set of 28 landmarks selected. Eligible specimens had to preserve all 6 axial landmarks, and at least one of each of the paired abaxial landmarks; **(2)** Pygidium reconstruction with the set of 13 landmarks selected. Eligible specimens had to preserve all 5 axial landmarks, and at least one of each of the paired abaxial landmarks. Type I landmarks (Bookstein, 1991) are shown as grey shaded circles, Type II landmarks as open circles.

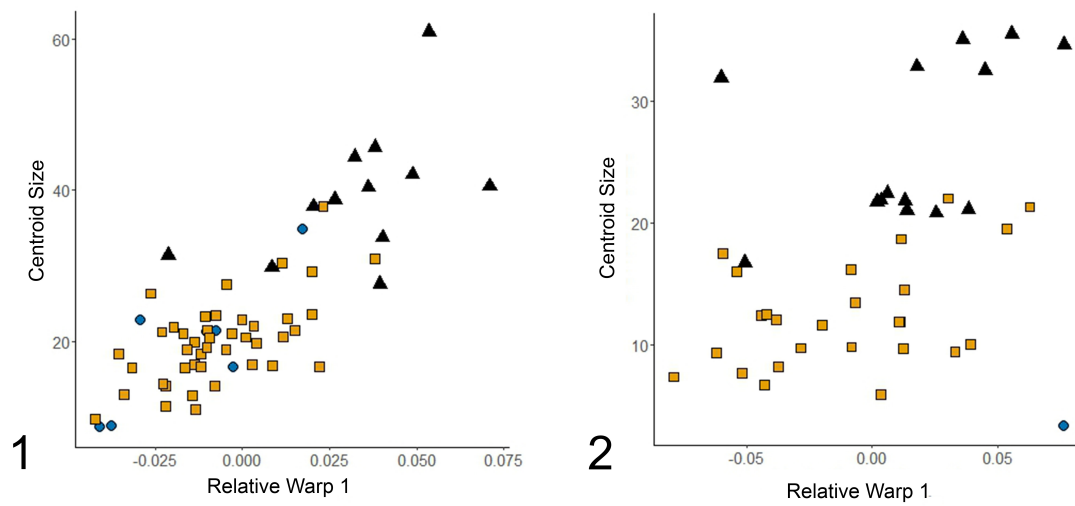


Figure 3.21: Bivariate scatter plots of first principal component versus centroid size for *Osceolia osceola* (1) 62 cranidia and (2) 41 pygidia categorized according to occurrence in different lithofacies. The lithofacies are represented as: heterolithic facies dolomitic mudstone from the St. Lawrence Formation (black triangle), sandstone facies of the Norwalk Member from the Jordan Formation (yellow square), and laminated sandstone from the St. Lawrence Formation (blue dot).

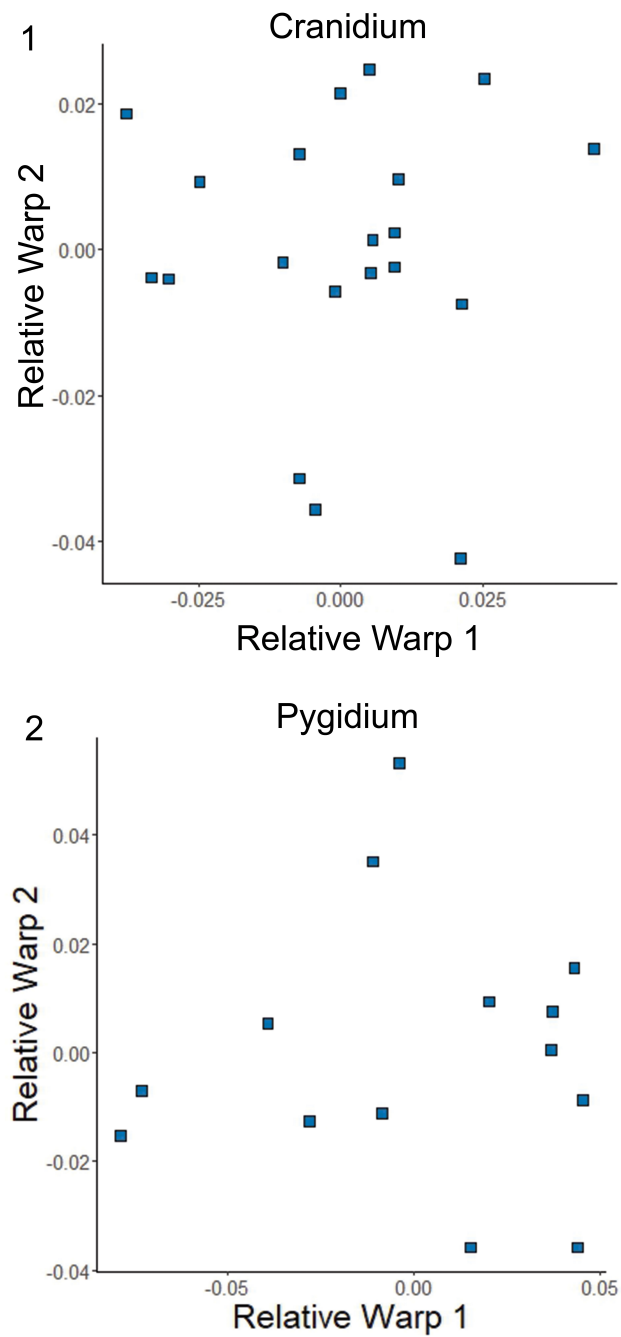


Figure 3.22: Bivariate scatter plots of first two relative warps showing *Osceolia osceola* cranidia and pygidia from only Osceola, WI, Norwalk Member collection. (1) plot of RW 2 and RW 1 for 20 cranidia; (2) plot of RW 2 and RW 1 for 14 pygidia.

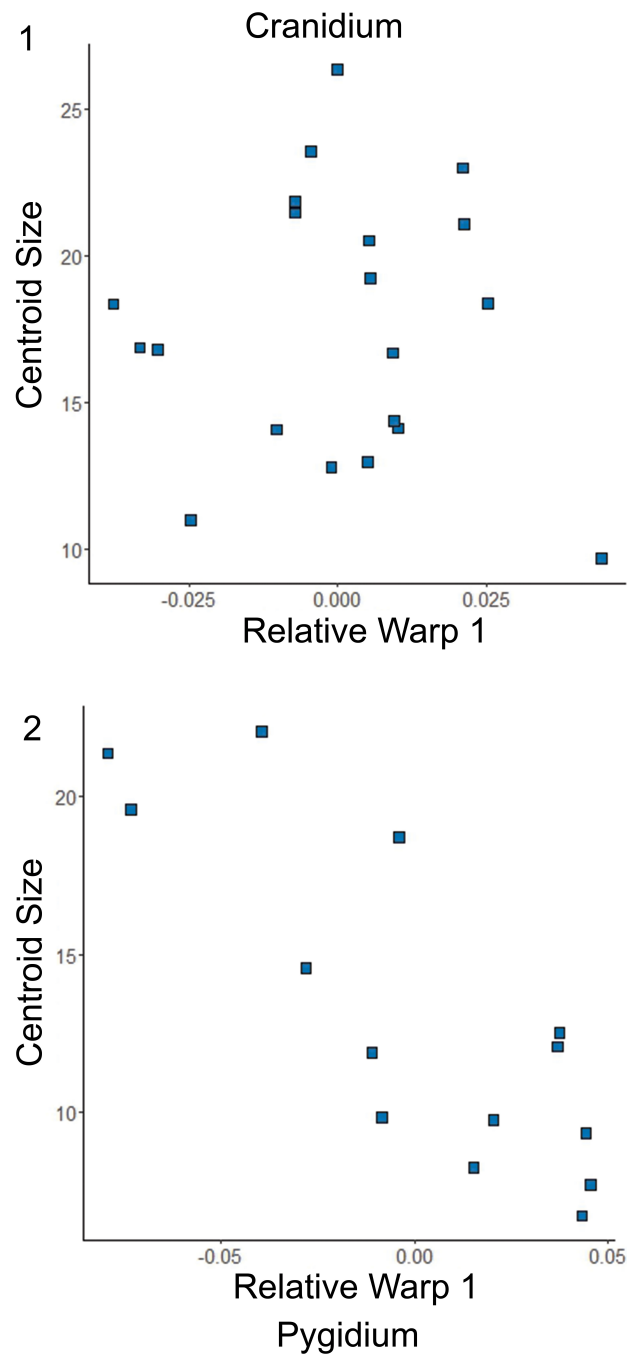


Figure 3.23: Bivariate scatter plots of centroid size versus relative warp 1 showing *O. osceola* cranidia and pygidia from only Osceola, WI, Norwalk Member collection. **(1)** plot of centroid size and RW 1 for 20 cranidia; **(2)** plot of centroid size and RW 1 for 14 pygidia.

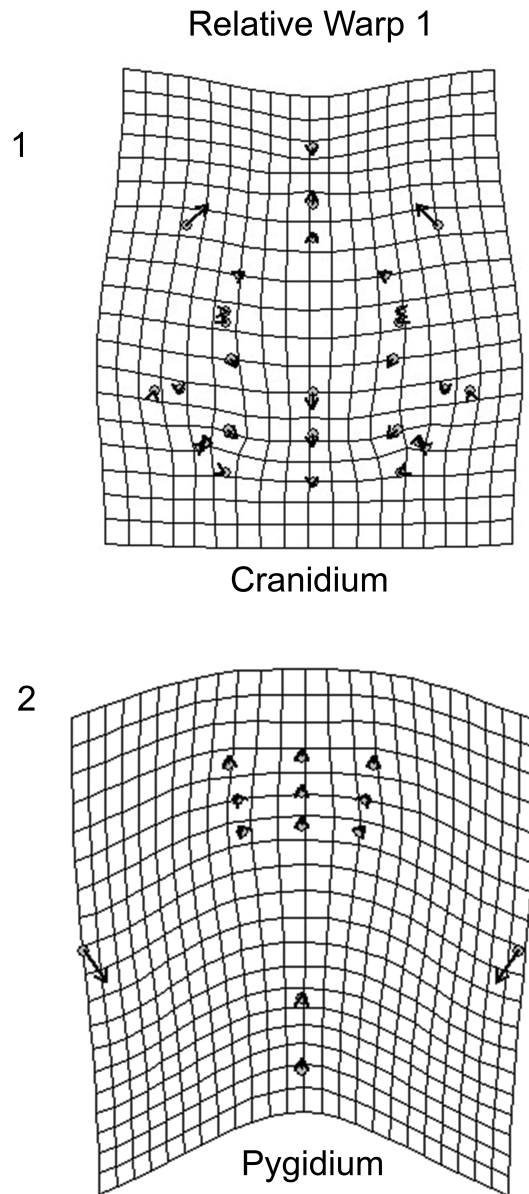
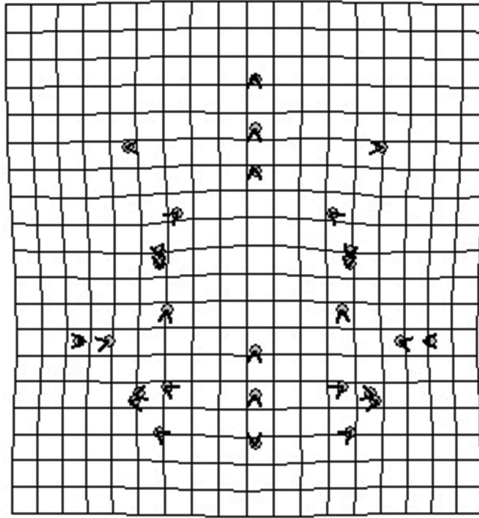


Figure 3.24: Thin-plate spline deformation grid of relative warp 1 for *O. osceola* cranidia and pygidia from only Osceola, WI Norwalk Member collection. (1) shape variation captured by RW 1 for cranidia; (2) shape variation captured by RW 1 for pygidia.

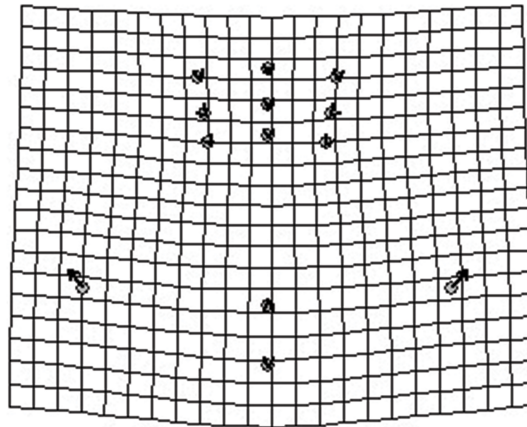
Size Related Shape Change

1



Cranidium

2



Pygidium

Figure 3.25: Thin-plate spline deformation grid of size related shape change for *O. osceola* cranidia and pygidia from only Osceola, WI Norwalk Member collection. (1) allometric changes for cranidia; (2) allometric changes for pygidia. Arrows indicate direction of change from small to larger specimens.

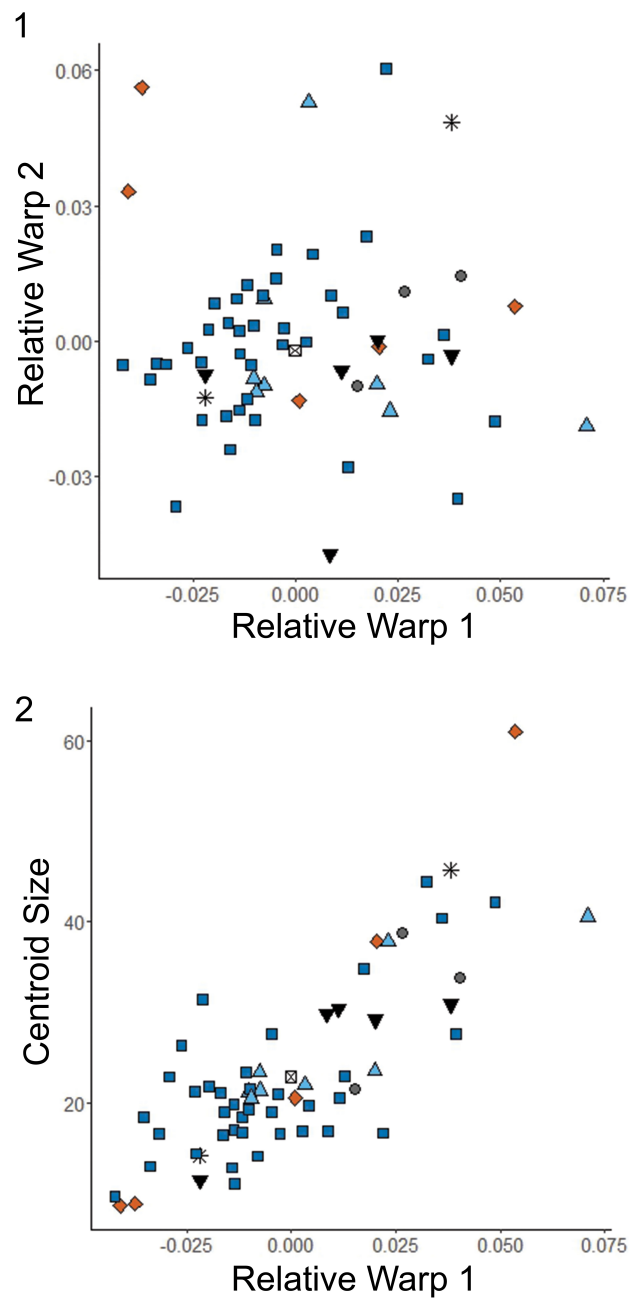
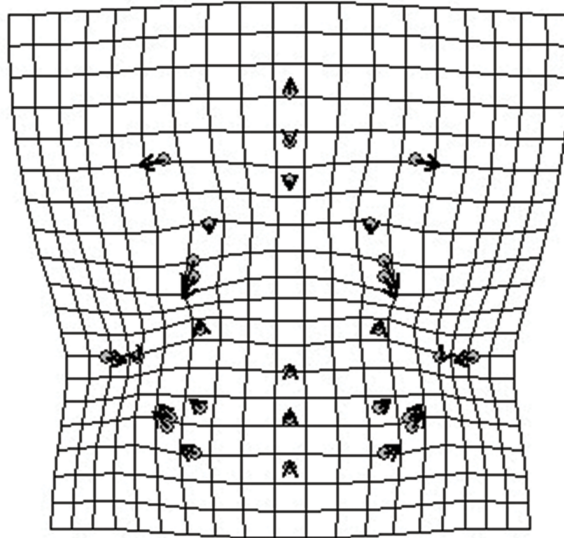


Figure 3.26: Bivariate scatter plots of centroid size and relative warps showing 62 *O. osceola* crania pooled from the entire collection categorized according to locality. (1) plot of RW 2 vs. RW 1; (2) plot of centroid size and RW 1. Different collections are color coded as- Mondovi: black inverted triangle, Osceola: blue square, Elewa: blue triangle, Spring Valley: star, Ridgeland: red diamond, Soo Bridge: grey dot, Elk Mound: square with cross.

1 Relative Warp 1



2 Size Related Shape Change

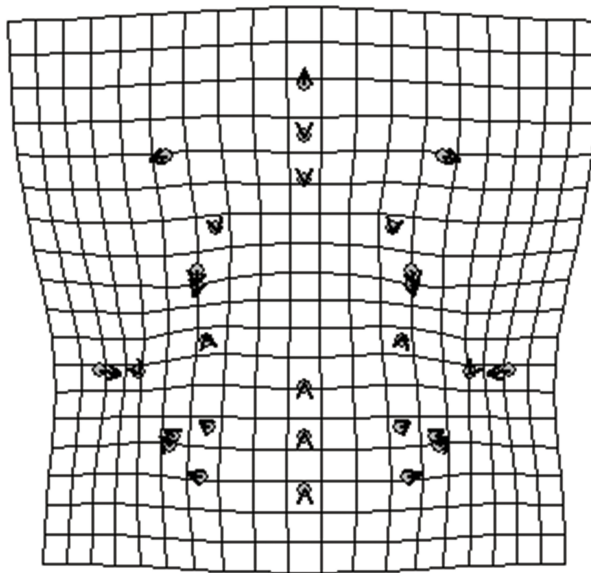


Figure 3.27: Thin-plate spline deformation grids for *O. osceola* cranidia pooled from the entire collection. (1) Size related shape change shown by a deformation grid for cranidia, vector arrows indicate direction of change from small to larger specimens; (2) Relative Warp 1 shape change depicted in a deformation grid for cranidia.

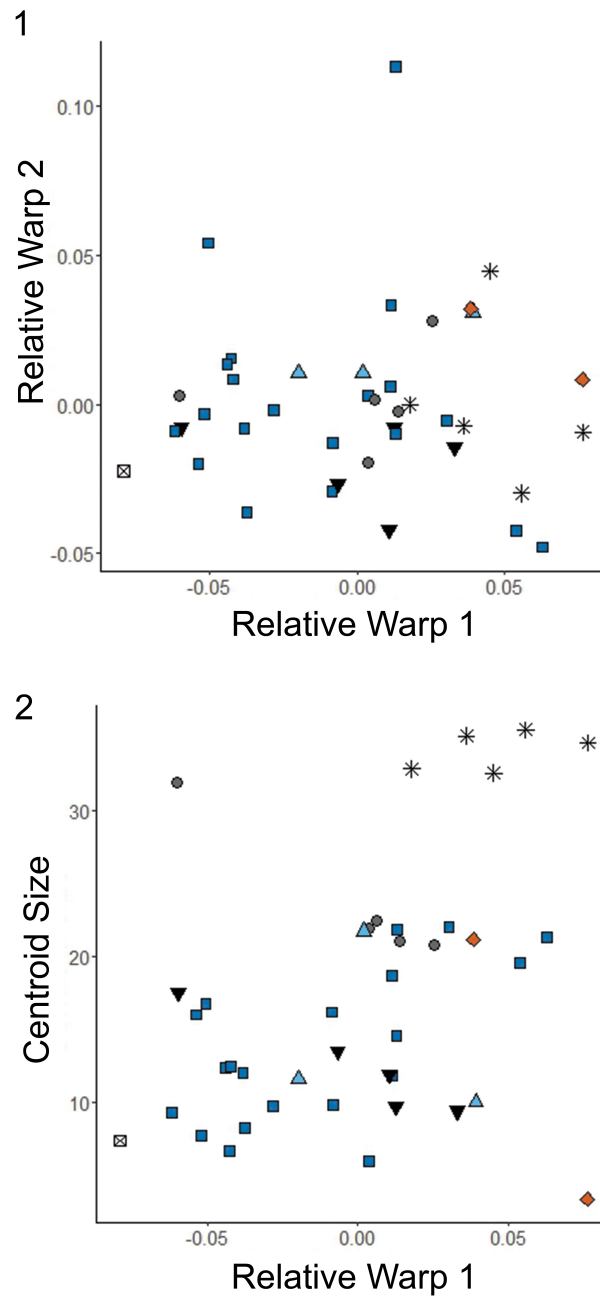
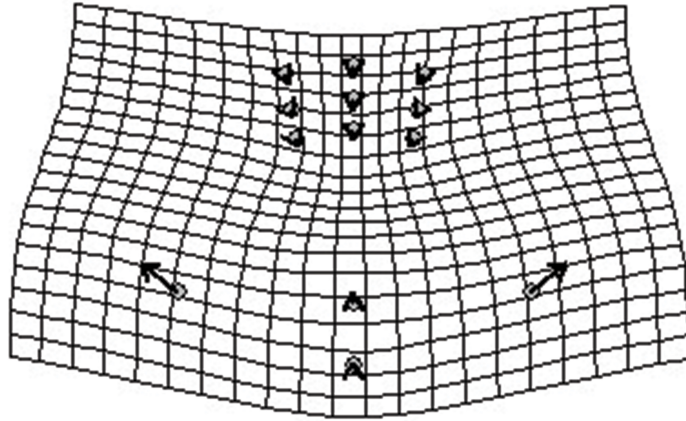


Figure 3.28: Bivariate scatter plots of centroid size and relative warps showing 41 *O. osceola* pygidia pooled from the entire collection categorized according to locality. **(1)** plot of RW 2 and RW 1; **(2)** plot of centroid size and RW 1. Different collections are color coded as– Mondovi: black inverted triangle, Osceola: blue square, Elewa: blue triangle, Spring Valley: star, Ridgeland: red diamond, Soo Bridge: grey dot, Downing: square with cross.

1 Relative Warp 1



2 Size Related Shape Change

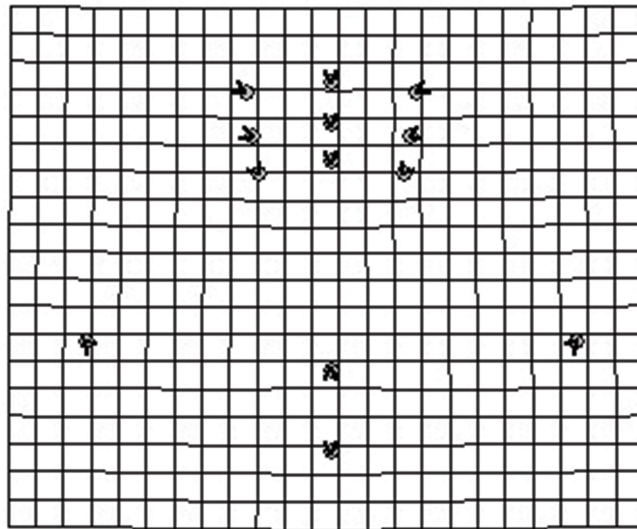


Figure 3.29: Thin-plate spline deformation grids for *O. osceola* pygidia pooled from the entire collection. (1) Relative Warp 1 shape change depicted in a deformation grid for pygidia; (2) Size related shape change shown by a deformation grid for pygidia, vector arrows indicate direction of change from small to larger specimens.

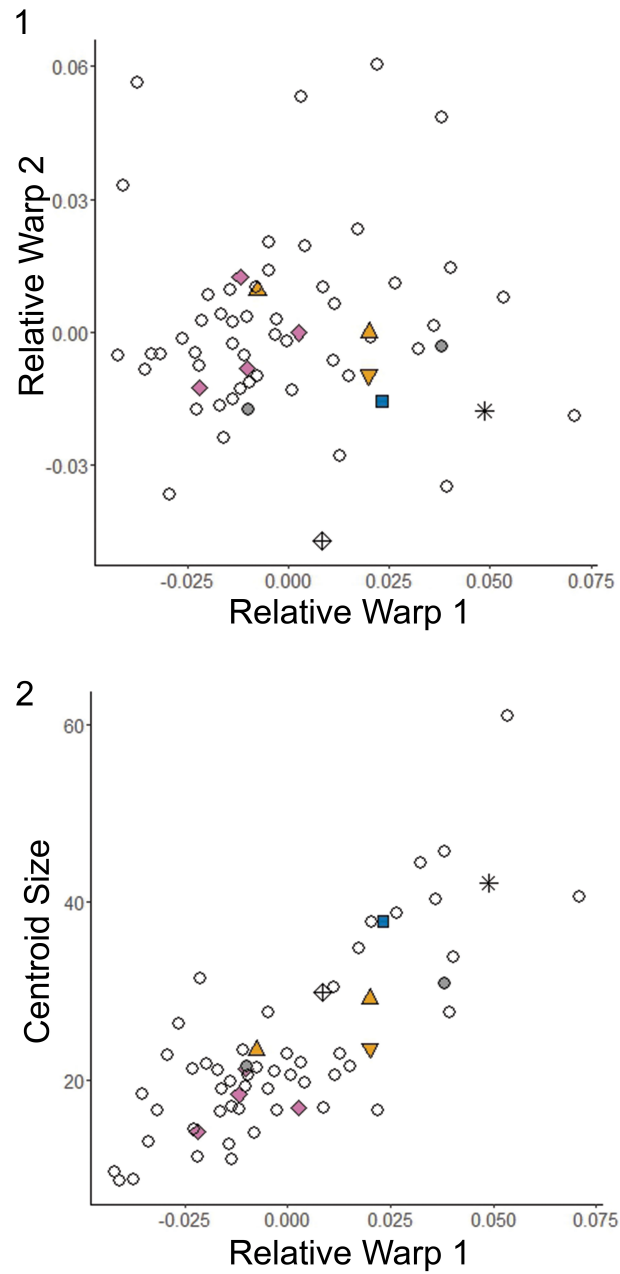


Figure 3.30: Bivariate plots of centroid size and relative warps for *O. osceola* cranidia pooled from the entire collection distinguishing *O. osceola* lectotypes of Hall (1863), syntypes of Ulrich and Resser's (1930) new *Osceolia* species, and their figured material of *O. osceola*. Colored data points are syntype specimens while open circles are non-type specimens from the rest of the collection. (1) plot of RW 2 and RW 1; (2) plot of centroid size and RW 1. Cranidia are classified as – non-type: open circles, *O. arguta*: blue square, *O. osceola*: pink diamond, *O. obsoleta*: orange inverted triangle, *O. obsoleta reversa*: orange triangle, *O. separata*: grey dot, *O. lodensis*: star, *O. praecipta*: diamond with plus.

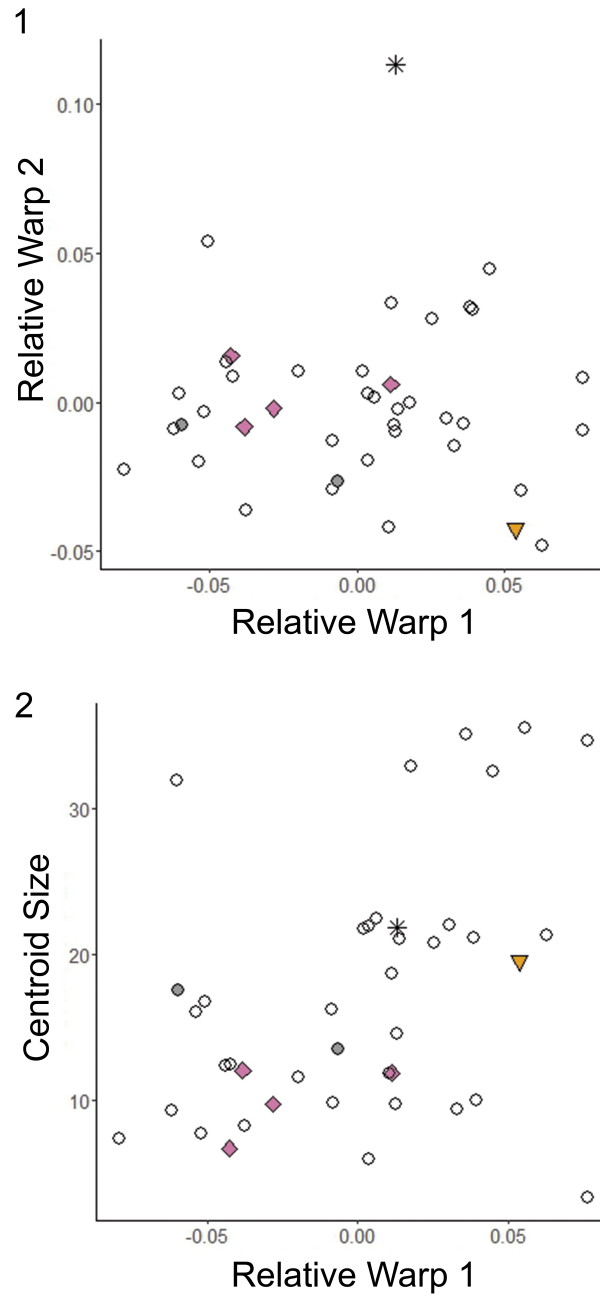


Figure 3.31: Bivariate plots of centroid size and relative warps for *O. osceola* pygidia pooled from the entire collection distinguishing *O. osceola* lectotypes of Hall (1863), syntypes of Ulrich and Resser's (1930) new *Osceolia* species, and their figured material of *O. osceola*. (1) plot of RW 2 and RW 1; (2) plot of centroid size and RW 1. Pygidia are classified as non-type: open circles, *O. osceola*: pink diamond, *O. obsoleta*: orange inverted triangle, *O. separata*: grey dot, *O. lodensis*: star.

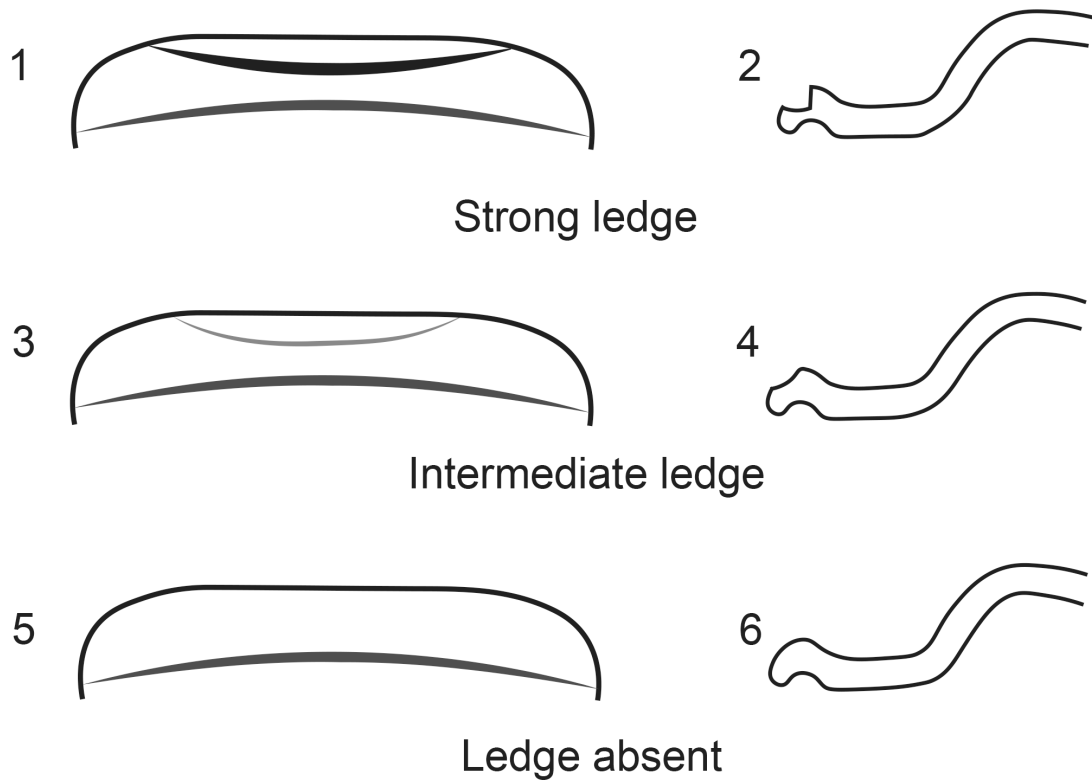


Figure 3.32: Reconstruction of *O. osceola* cranial anterior border ledge morphology illustrating classification used for morphometric analysis of this characteristic. (1) dorsal reconstruction of anterior border with strong ledge class; (2) cross section profile of (1); (3) dorsal reconstruction of anterior border with weak ledge class; (4) cross section profile of (3); (5) dorsal reconstruction of anterior border with no ledge; (6) cross section profile of (5).

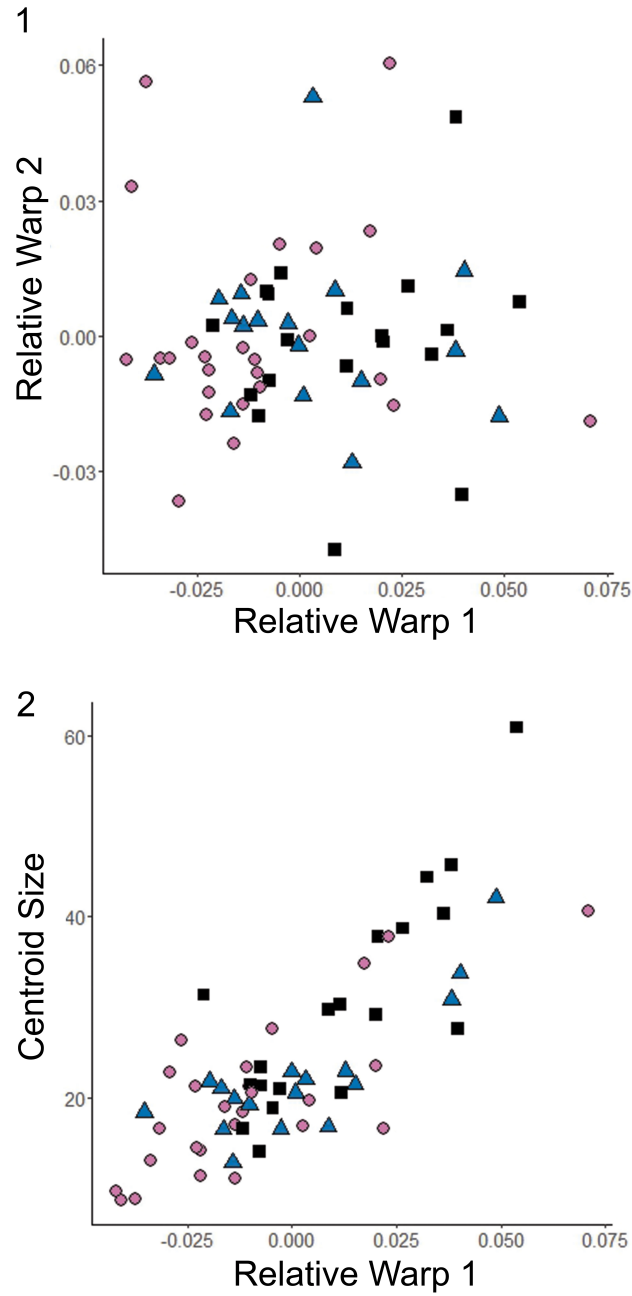


Figure 3.33: Bivariate plots between centroid size and relative warps for *O. osceola* cranidia categorized according to anterior ledge morphology class. (1) plot of RW 2 and RW 1; (2) plot of centroid size and RW 1. Ledge morphology is color coded as– strong ledge: black square, weak ledge: blue triangle, ledge absent: pink dot.

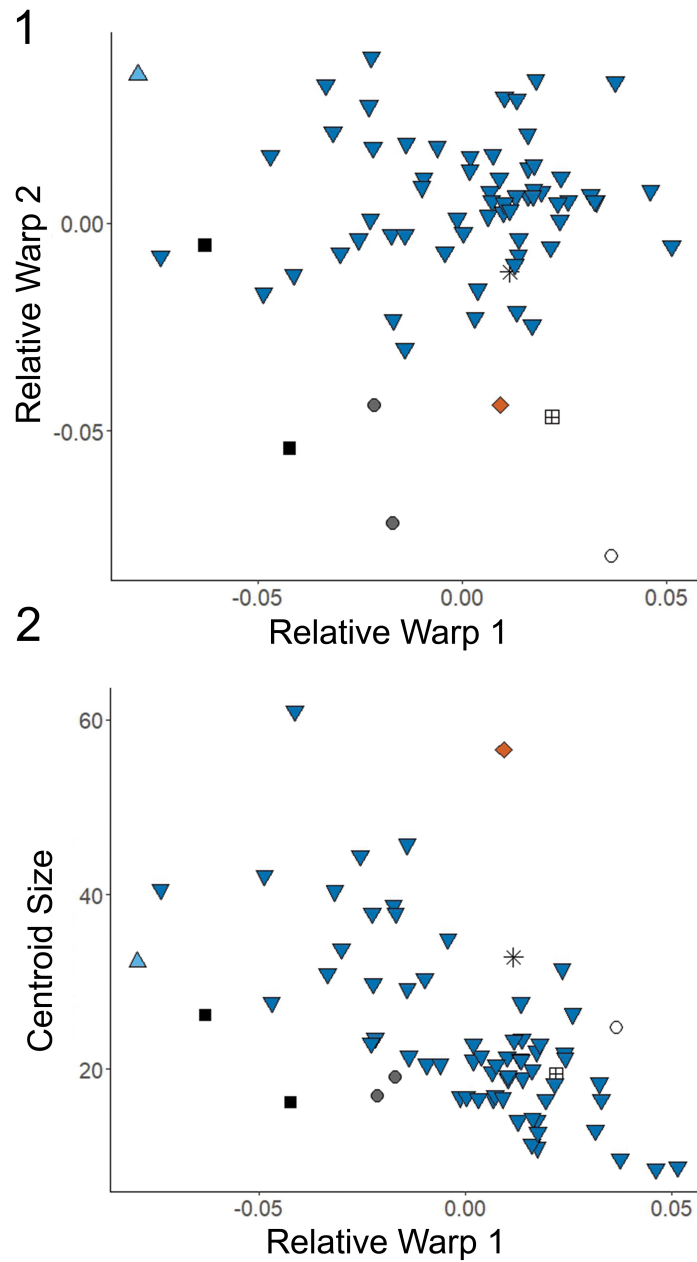


Figure 3.34: Bivariate plots between centroid size and relative warps of *O. osceola* cranidia compared with homeomorphs and close relatives. (1) plot of RW 2 and RW 1; (2) plot of centroid size and RW 1. Cranidia are color coded as— *O. osceola*: dark blue inverted triangle, *O. tumerispina*: light blue triangle, *Briscoia coloradoensis*: black square, *Formosocephalus savitzkyi*: red diamond, *Prosaukia lochmani*: grey dot, *Hamashania pulchra*: star, *Pseudoanomocarina eldachica*: open circle.

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Chapter 4

Phylogeny of the late Cambrian trilobite family

Dikelocephalidae Miller, 1889

4.1 Abstract

Parsimony based phylogenetic analyses are commonly used to explore inferred evolutionary relationships among well-represented fossil and extant taxa. Late Cambrian dikelocephalid trilobites provide a suitable candidate because various systematic hypotheses have been published for their relationships in the last 100 years. A comprehensive review of their evolutionary relationships is long overdue and this chapter attempts to clarify what is, and what is not known of their systematic relationship. The phylogenetic analyses conducted here use two datasets which characterize putative dikelocephalid and outgroup species in terms of both discretized characters, and a mixed character matrix of continuous and discrete characters. The results of the two phylogenetic analyses show two contrasting but plausible phylogenies for the dikelocephalids. The discretized matrix recognizes two major clades, one "osceolimorph" trilobites with elongated glabella and large eyes very close to the glabella, from "dikelomorph" trilobites with more square glabella and relatively smaller

eyes, the latter bearing species that grow to large sizes. On the other hand, the mixed matrix yielded a clade of species occurring in the Upper Mississippi Valley. Previously published phylogenetic analysis of these trilobites is supported by the current. Both cladograms are consistent with the preliminary phylogeny shown in [Srivastava and Hughes, 2024](#) on that there is a sister-taxon relationship between *Walcottaspis* and *Dikelocephalus* species. This relationship is the strongest supported relationship on both phylogenies. This result helps make the argument that *Walcottaspis vanhornei* evolved from a species of *Dikelocephalus*.

4.2 Introduction

While acknowledging that systematic relationships among late Cambrian trilobites are far from being adequately resolved, in the following discussion we use the Linnean ranked group terms in the following manner: Dikelocephalacea ([Miller, 1889](#)) sensu ([Ludvigsen and Westrop, 1983](#)) = ((Dikelocephalidae [Ulrich and Resser, 1930](#) + Saukiidae [Ulrich and Resser, 1933](#))) + Ptychaspidae [Raymond, 1924](#)). This is based on the views of Ludvigsen and Westrop ([1983](#)), Westrop ([1986](#)) and Ludvigsen et al. ([1989](#)), with the acknowledgment that the status of Saukiidae as a monophyletic group requires reconsideration, and that additional groups may belong in the superfamily but that any such connections are not yet well established. Various issues are discussed below, but unless otherwise stated, Dikelocephalidae includes only species assigned to the exclusively Laurentian late Sunwaptan genera *Dikelocephalus* [Owen, 1852](#), *Briscoia* [Walcott, 1924b](#), *Elkia* [Walcott, 1924a](#), *Parabriscoia* [Kobayashi, 1935](#), *Osceolia* [Walcott, 1914](#) and *Walcottaspis* [Ulrich and Resser, 1930](#). When the term “dikelocephalid” is used below, it is referring to this concept of the family.

4.2.1 Initial assessment

Miller's (1889, p. 524) original and later modified designation of the family Dikelocephalidae included three genera: *Dikelocephalus*, *Ptychaspis*, and *Pterocephalia*, all known from the Furongian (i.e. latest Cambrian) of Laurentia. Although the concepts of these genera are now each much changed, Miller's grouping linked large trilobites with prominent glabellae and an extensive frontal area (*Dikelocephalus* and *Pterocephalia*) to smaller trilobites bearing a short anterior border immediately anterior to the glabella (*Ptychaspis*). Linkage with *Ptychaspis* was based on the shared quadrate glabella bearing a firmly incised, V-shaped S1 furrow seen in *Dikelocephalus*, but these features are absent in *Pterocephalia*. Subsequent views on the systematic relationships of *Dikelocephalus* and its close relatives to other trilobites have oscillated between those emphasizing links in maximum size and character relative proportions (as in Miller's *Dikelocephalus* – *Pterocephalia* connection), with those based on more specific structural similarities, such as in the structure of the glabella and ocular regions (the basis of Miller's *Dikelocephalus* – *Ptychaspis* association).

4.2.2 Forms with similar overall proportions

Although no workers have subsequently endorsed Miller's *Dikelocephalus* – *Pterocephalia* link (pterocephaliids being restricted to the Steptoean, some 2 Ma before the first appearance of dikelocephalids in the later Sunwaptan – see [Farrell et al., in press]), the practice of associating dikelocephalids with other trilobites based on general similarities in body proportions including those of the glabella, eyes and fixigenae, accompanied by altering last maximum sizes has endured. Such was the basis for Raasch's (1951, p. 141) and Lochman's

([Lochman, 1956](#) and in [Harrington et al., 1959](#)) derivation of Dikelocephalidae from species of the uppermost lower Sunwaptan Laurentian idahooid genus *Wilbernia*, that occurs stratigraphically shortly below the first dikelocephalaceans. Members of *Wilbernia* are known for their expanded frontal area with a long prelabellar field and short border. Lochman ([1956](#), fig. 2) derived a polyphyletic Dikelocephalidae from different species of *Wilbernia*, suggesting *Dikelocephalus* to have a diphyletic origin from two *Wilbernia* species, *W. diademata* and *W. expanata*. Cranidia of various *Wilbernia* species have proportions comparable to forms within Dikelocephalidae, and some *Wilbernia* pygidia (see [Srivastava and Hughes, 2024](#), fig. 10) are homeomorphic with those of *Briscoia pertransversa* ([Lochman, 1956](#), fig. 2) and *Walcottaspis vanhornei* ([Srivastava and Hughes, 2024](#), fig. 5). However, the rearward arching occipital ring and its inflated lateral margins, isolated S1 furrows, distinctive eye ridges, and relatively wide fixigenae of all *Wilbernia*, differ from the condition in any member of Dikelocephalidae (see [Westrop, 1986](#), pl. 12, 13). Thus, we agree with Ludvigsen and Westrop ([1983](#), p. 28) that the similarity between members of *Wilbernia* and dikelocephalids is homoplastic.

Jell, in Jell and Adrain ([2003](#), p. 469) apparently used a similar taxonomic approach when he proposed a major expansion of Dikelocephalidae to encompass a total of 21 genera, including the six Laurentian genera listed by Westrop ([1986](#)) along with *Hoytaspis*, which had been considered a saukiid ([Ludvigsen and Westrop, 1983](#)) and 14 additional genera previously assigned to other families that included forms from Siberia and Gondwana. No diagnoses of individual families could be provided in this compendium of trilobite genera, nor were relationships among families discussed, and so the basis of Jell's concept

of the family has to be inferred from examination of the taxa assigned. Again, grouping appears to be on the basis of an extended frontal area, prominent glabellae with large eyes situated close to it, and large maximum size, similar to the reasoning used by Raasch (1951) and Lochman (1956), although occurrence evidence apparently played a lesser role in Jell's classification because the genera he grouped are scattered among middle and upper Cambrian strata and paleocontinents. This grouping, apparently based on perceived overall similarity among commonly preserved cranidia and pygidia, is polyphyletic in our view. For example, Jell (in Jell and Adrain, 2003, p. 469) included *Iranella* (Hupé, 1953) in his concept of Dikelocephalidae. This form, now considered as a junior subjective synonym of *Maladiodella abdita* (see Rushton and Hughes, 1996; Jell and Adrain, 2003, p. 388) had both a rostral suture and a natant hypostome, distinguishing it from the conterminant condition ubiquitous in Dikelocephalidae (Fortey and Chatterton, 1988) and implying that it likely only distantly related. *Maladiodella abdita* is characterized by a trapezoidal glabella that narrows markedly anteriorly, isolated pit-like S1 furrows, a marked eye ridge, and a cranidial doublure that extends no further beneath the frontal area than the anterior border furrow (Rushton and Hughes, 1996). The second and fourth of these characters is unknown in any Dikelocephalidae, which questions Jell's grouping based on the characters he considered. Similar arguments based on character incongruence can be made for other genera that Jell included such as *Camarasporoides* Frederickson, 1949 which has a typically ptychopariid cranidial and pygidial form. Additional genera that Jell placed in the family such as *Randicephalus* Ivshin, 1962 and *Kasachstanaspis* Balashova, 1961 are, in our view,

too poorly known to be confidently assigned to any family. *Jell's* suggestion of an association of *Hamashania* [Kobayashi, 1942](#) species is further considered below.

Below I will argue that dikelocephalids derived from close relatives with short preglabellar fields, but a sister-taxon relationship between *Dikelocephalus* and other trilobites with long preglabellar fields between the glabellar and cranidial anterior border including *Hungaia* (commonly considered a remopleurid – see Fortey and Chatterton [\[1988\]](#)) was recently proposed on the basis of phylogenetic analysis by Paterson et al. ([2019](#), fig. 1). The long brimmed monkaspid *Monkaspis* (see [Zhang and Jell, 1987](#), pl. 85, fig. 6) was shown as the sister taxon to both, suggesting a clade sharing long preglabellar fields. However, an alternative analysis of the same dataset places *Dikelocephalus* with *Asioptychaspis* as its sister taxon, a form whose anterior border is extremely short. Sister to this was a clade linking long brimmed *Hungaia* with *Eurekia*, a form with a short border and no preglabellar field ([Paterson et al., 2019](#), fig. 2). Given the low number of taxa considered by Paterson et al. ([2019](#)), neither of these results provide a firm basis for arguing that sister taxa to dikelocephalids bore a long preglabellar field, although it is possible that hungaiids root among dikelocephalids. An argument for this is that the cephalic doublure extends beyond the border in *Hungaia devinei* ([Billings, 1865](#)) (see [Ludvigsen et al., 1989](#), pl. 17, fig. 11), and this possibility will be explored in further work.

4.2.3 Forms with shared details of glabellar and palpebral structure

Westrop ([1995](#), p. 23) grouped together Dikelocephalidae and Saukiidae using specific similarities including the quadrate glabellar with transverse SO, distinctively shaped and transverse S1, and isolated S2, along with the distinctive palpebral structure, that he con-

sidered to be defining homologies of this clade. (Early Cambrian Gondwanan taxa including *Paokannia* [Ho and Li, 1959](#) and *Saukianda* [Richter and Richter, 1940](#) have closely similar glabellar structure to that of sauikiids but, given that these are redlichiid trilobites and thus not libristomate [[Fortey, 1990](#)], we consider this similarity to be convergent.) At a wider level, Ludvigsen and Westrop ([1983](#)) linked these groups to the ptychaspids (as Miller [[1889](#)] had done) based on the share quadrate glabella and glabellar furrow characteristics. Ptychaspids differ from dikelocephalid and sauikiid trilobites in their distinctively wider fixigenae and anteriorly positioned palpebral lobes. Species assigned to Ptychaspidae and Saukiidae are characterized by relatively short frontal areas compared to Dikelocephalidae, with the anterior border confluent with the anterior axial furrow (i.e. without a preglabellar field) in all ptychaspids and in most sauikiids. As discussed below, the presence of a preglabellar field in other sauikiids is the criterion used herein to define the outgroup to dikelocephalids. Currently it remains unclear whether a short preglabellar field is a basal characteristic of the Dikelocephalacea, or whether it is the derived condition within that clade. Despite this lack of resolution, herein it is accepted that dikelocephalids have their closest relatives among those sauikiids with preglabellar fields.

Dikelocephalids and sauikiids also share possession of the “posterior glabellar bulge”, that is developed to a more extreme condition in Remopleuridae and is considered a synapomorphy linking these two families ([Fortey and Chatterton, 1988](#) but also see [Westrop, 1995](#), p. 23). The relatively large, flat, semicircular palpebral lobe and similarly shaped, strongly and evenly incised palpebral furrow among dikelocephalids is another feature shared with the Remopleuridae ([Fortey and Chatterton, 1988](#)), along with other species assigned

to Saukiidae and Eurekaidae (e.g. *Eurekaia ulrichi* in Ludvigsen [1982]). Remopleurids have a preglabellar field, but not with a doublure extending beyond the the extent of border and are characterized by particularly strong expression of the S1 bulge. This autapomorphy excludes their representation among our dikelocephalid outgroup species considered below.

It should also be noted that the firmly incised, entire natures of the SO and S1 furrows characteristic of ptychaspids, sauikiids and dikelocephalids invites comparison with similar structures in earlier Furongian Laurentian trilobites including elviniids such as *Elvinia* and *Irvingella*, and drumaspids, all of which occur in the record some 2 Ma before dikelocephalids first appear (Farrell et al., in press). Characters such as glabellar shape and frontal area development show significant variation among these groups, with drumaspids possessing only a short border with no preglabellar field and so are not considered further herein. *Elvinia* resembles dikelocephalids in the possession of an extended preglabellar field. However, its notably anteriorly convergent cranidial axial furrows and straight anterior glabellar border giving it a notably trapezoidal glabellar form, its cephalic doublure extending only as far as the border (Ludvigsen and Westrop, 1983, pl. 5, fig. 12), its notable transverse eye ridge, the midpoint of its palpebral lobes being opposite S2, the isolation of its anterior border and posterior border furrows on the free cheek, its narrow and short genal spine, the pygidium with only 3 axial rings the third of which is defined by a weakly incised ring furrow at its posterior margin, and the pygidial axis extending almost to the posterior margin of the pygidium without a postaxial ridge are all features that differ from the condition generally seen in dikelocephalids. Its anteriorly placed eyes,

firmly incised anterior border furrow, and wide fixigenae does, however, mimic that seen in forms such as *Thailandum* (see [Wernette et al., 2020](#)).

4.2.4 Outgroup Selection

In this analysis a single species, the preglabellar field-bearing saukiid trilobite *Prosaukia misa* ([Hall, 1863](#)), was used as sole outgroup to the dikelocephalids to determine the polarity of character state changes. While use of species of multiple outgroups is common in phylogenetic analyses (following [Maddison et al., 1984](#)), *P. misa* resembles dikelocephalids in possessing a preglabellar field, a feature most other saukiid lack, and distinguishing between it and some dikelocephalid species assigned to *Briscoia* has been contentious ([Westrop, 1986, 1991](#)). *Prosaukia misa*, however lacks doublure extending beneath the preglabellar field, the presence of which is apparently synapomorphic for Dikelocephalidae ([Ludvigsen et al., 1989](#), p. 27; [Srivastava and Hughes, 2024](#), fig. 2.11, table 2.1), and thus its suggesting outgroup status. It is also a reasonably well characterized species (if Raasch’s [[1951](#)] concept of the species is accepted) permitting all but one of its character states to be coded. Furthermore, this Laurentian form occurs stratigraphically equivalent to or immediately earlier than the first appearance of dikelocephalids and is also the type species for the genus. The choice of this form as an outgroup is thus well justified.

Species assigned to several other saukiid genera such as those known from the Upper Mississippi Valley including *Saukia*, *Calvinella*, *Tellerina*, and those known from Gondwanan localities only, *Eosaukia*, *Pacootasaukia* and *Lophosaukia* for example, all lack a preglabellar field. This condition was likely derived within the group and thus not informative about the basal condition in dikelocephalids. Including such species as potential

outgroups would thus be unwise. There are, however, a number of Gondwanan sauikiid taxa assigned that, like *P. misa* and members of Dikelocephalidae, possess a preglabellar field. Of those sufficiently well known to permit inclusion in this analysis, *Thailandium solum* [Kobayashi, 1957](#) from the Ao Mo Lae Formation of the Sibumasu terrane, has a notably extended preglabellar field although this is not matched by doublure extending beneath it, thus excluding it from the dikelocephalids. A similar Ao Mo Lae Formation example is *Hoytaspis thanisi* [Shergold et al., 1988](#) although its preglabellar field, where discernable, is notably short (see [Wernette et al., 2023](#), fig. 51). Future work will explore considering these species as additional outgroup taxa, along with *P. misa*. Here they are not included on the ground that neither species occurred in Laurentia, although *Hoytaspis* is known from New York State.

In their preliminary phylogenetic analysis of dikelocephalid phylogeny, Srivastava and Hughes ([2024](#), fig. 2.11) included the Stage 10 North China platform species *Hamashania pulchra* [Kobayashi, 1942](#), the cephalon of which closely resembles that of the dikelocephalid *Osceolia osceola* (see [Srivastava and Hughes, in press](#)). That analysis did not ally *H. pulchra* with *O. osceola* but placed it as basal to all other dikelocephalid ingroup species. This placement, along with the fact that information on the extent of the cephalic doublure is missing for this form (and hence the possibility it is not a dikelocephalid), lead me to omit this taxon from further analysis herein.

4.3 Materials and Methods

Herein, I have used parsimony-based phylogenetic analysis to assess the evolutionary relationships between the various well represented taxa of dikelocephalids bearing an extended cephalic doublure. Additional work in this area will also employ Bayesian approaches to further explore phylogenetic context.

4.3.1 Character and Taxon Selection

Dikelocephalid trilobites are well represented across the various facies of the late Sunwaptan part of the Laurentian rock record. The family currently comprises the genera *Dikelocephalus*, *Briscoia*, *Elkia*, *Parabriscoia*, *Osceolia*, and *Walcottaspis*. Of these *Osceolia* and *Walcottaspis* are currently known only from the Upper Mississippi Valley ([Srivastava and Hughes, 2024](#), [Srivastava and Hughes, in press](#)). Species of *Dikelocephalus* and *Briscoia* are found in various parts of the Laurentian continent and occur both in inner detrital lithofacies belt and in the offshore carbonate platform ([Hughes, 1994](#); [Westrop, 1986](#); [Kobayashi, 1935](#)).

The characters and character states used in the phylogenetic analysis are listed below. The characters that vary on a continuous scale and are considered as such in a mixed character matrix are listed in a table in Supplementary Data 1 and are marked with '*' in the list below.

1. *Frontal area length (sag.) divided by occipital-glabellar length (sag.): (0) 15-29%
(1) 30-44% (2) $\geq 45\%$

2. Cranidial anterior margin with respect to cephalic anterior margin: (0) marginal (1) retracted
3. Preglabellar field: (0) absent (1) present
4. Cephalic anterior border furrow: (0) faint (1) distinct
5. *Anterior border length (sag.) divided by prelabellar field length (sag.): (0) <100% (1) =100% (2) >100%
6. *Maximum occipital lobe width (tr.) divided by maximum frontal area width (tr.): (0) <50% (1) 50-69% (2) 70-89% (3) $\geq$ 90%
7. Extent of cephalic doublure: (0) extends beneath anterior border only (1) extends beneath entire frontal area
8. Largest overall body size (expressed as maximum occipital-glabellar length estimate): (0) <2.0 cm (1) 2.0-2.9 cm (2) $\geq$ 3.0 cm
9. Curvature of glabellar anterior margin: (0) transverse (1) intermediate (2) continuously curved
10. *Anterior glabellar width (tr.) (measured at initial inflection point of curve) divided by occipital-glabellar length (sag.): (0) <50% (1) 50-59% (2) 60-69% (3) $\geq$ 70%
11. *Anterior glabellar width (tr.) (measured at initial inflection point of curve) divided by maximum occipital lobe width (tr.): (0) <65% (1) 65-74% (2) 75-84% (3) $\geq$ 85%
12. *Maximum L2 lobe width (tr.) divided by occipital-glabellar length (sag.) (0) <65% (1) 65-69% (2) 70-74% (3) $\geq$ 75%

13. *Maximum L1 lobe width (tr.) divided by occipital-glabellar length (sag.): (0) <70%
(1) 70-74% (2) 75-80% (3) >80%
14. *Maximum occipital lobe width (tr.) divided by occipital-glabellar length (sag.): (0)
<70% (1) 75-79% (2) 80-84% (3) $\geq$ 85%
15. Median tubercle: (0) absent (1) present
16. S1 glabellar furrow incision: (0) faint (1) distinct
17. S2 glabellar furrow incision: (0) faint (1) distinct
18. *Palpebral lobe length (exsag.) divided by occipital-glabellar length (sag.) in largest
specimen available for each taxon: (0) <36% (1) 36-45% (2) 46-55%
19. *Palpebral lobe length (exsag.) divided by maximum occipital lobe width (tr.) in
largest specimen available for each taxon: (0) <40% (1) 40-49% (2) 50-59% (3) $\geq$ 60%
20. *Palpebral lobe width (tr.) divided by palpebral lobe length (exsag.) in largest
specimen available for each taxon: (0) <15% (1) 15-19% (2) 20-24% (3) $\geq$ 25%
21. Exsagittal position of palpebral lobe middle point: (0) opposite S2 (1) anterior to S1
(2) opposite S1 (3) posterior to S1
22. Prominent anterior palpebral lobe thinning (tr.): (0) absent (1) present
23. Eye ridge: (0) absent (1) present
24. *Maximum fixigenal width (tr.) divided by occipital-glabellar length (sag.): (0) <20%
(1) 20-24% (2) $\geq$ 25%

25. *Maximum fixigenal width (tr.) divided by maximum occipital lobe width (tr.): (0) <20% (1) 20-24% (2) 25-29% (3) $\geq$ 30%
26. *Anterior fixigenal width (tr.) divided by occipital lobe length (sag.): (0) <50% (1) 50-59% (2) 60-69% (3) $\geq$ 70%
27. Prominent fixigenal pinched ridge associated with anterior palpebral lobe: (0) absent (1) present
28. *Occipital lobe length (sag.) divided by posterolateral border width (tr.): (0) $\leq$ 85% (1) 86-115% (2) $\geq$ 115%
29. *Occipital lobe length (sag.) divided by posterolateral border length at facial suture inflection (exsag.): (0) <20% (1) 20-24% (2) 25-29% (3) $\geq$ 30%
30. Transverse ridge in abaxial posterior portion of posterolateral border area: (0) absent (1) present
31. Bacculae: (0) absent (1) present
32. Trench adjacent to eye socle: (0) absent (1) present
33. Right-left free cheek junction: (0) median suture present (1) yoked free cheek known
34. Free cheek dorsal border furrow: (0) faint (1) distinct
35. Free cheek lateral and dorsal border furrows: (0) isolated (1) confluent
36. Hypostomal maculae: (0) absent (1) present

37. *Hypostomal posterior body length (sag.) divided by hypostomal anterior body length (sag.): (0) <25% (1) 25-29% (2) $\geq$ 30%
38. *Hypostomal anterior body length (sag.) divided by maximum hypostomal anterior body width (tr.): (0) $\leq$ 100% (1) >100%
39. Hypostomal posterolateral flange: (0) absent (1) present
40. Hypostomal posterior border furrow: (0) continuous (1) shallowing distally (2) pit-like distally
41. Pygidial anterior margin: (0) continuously curved (1) fulcrate
42. Prominent petaloid facet of first pleura of pygidium: (0) absent (1) present
43. *Maximum width of first pygidial axial ring (tr.) divided by maximum pygidial width (tr.): (0) <20% (1) 20-24% (2) 25-29% (3) $\geq$ 30%
44. Number of pygidial axial rings defined by completely incised furrows: (0) 3 (1) 4 (2) 5
45. Pleural expansion in pygidium: (0) propleural (1) equal/subequal (2) opisthoparian
46. Pleural-interpleural furrow incision in pygidium: (0) equally incised (1) interpleural furrow absent
47. Interpleural furrows adaxial expression in pygidium: (0) consistently distinct (1) effaced
48. Incompletely defined posterior-most axial furrow in pygidium: (0) absent (1) present

49. Terminal axial piece shape in pygidium: (0) sharply convex (1) evenly curved (2) blunt
50. Sagittal pygidial marginal spine: (0) absent (1) present
51. *Pygidial postaxial length (sag.) divided by pygidial length (sag.): (0) <30% (1) 30-34% (2) 35-39% (3) $\geq 40\%$
52. Distinct pygidial postaxial ridge: (0) absent (1) present
53. Pygidial posterolateral spines: (0) absent (1) present
54. Position of pygidial posterolateral spine base: (0) anterior to terminal axial piece (1) posterior to terminal axial piece
55. Pairing of pygidial posterolateral spines: (0) single pair (1) multiple
56. Development of multiple pygidial spines: (0) incipient (1) complete
57. Pygidial posterolateral spine association with individual segments: (0) unclear association (1) strong association
58. Pygidial posterolateral spine shape: (0) narrow evenly to a sharp terminus (1) swollen distally

This study builds on the published phylogenetic analyses ([Srivastava and Hughes, 2024](#), fig. 2.11). What is presented here are the results of a more comprehensive survey of characters and character states among dikelocephalids and also observation of a larger number of specimens than previously studied. Instead of only three hypostomal characters

defined, I have now included two new continuous characters (see list above, characters 37 and 38) and two new discrete characters (see list above, characters 39 and 40) in addition to removing the character 'maximum width of hypostome lateral border' (Srivastava and Hughes, 2024, Supplementary Data 1) because it was possible to measure the dimensions of hypostomes more comprehensively given the increased number of specimens surveyed. Similar improvement to the characterization of other sclerites has been made due to increase in number of measurable specimens, especially for the various *Briscoia* species included in the analysis. Two additional *Briscoia* species were included in this analysis, *Briscoia* sp. for which specimens were collected recently from the Dotsero Formation of Colorado (J.F. Taylor pers. com., 2025) and *Briscoia texana* (Walcott, 1914) for which recently figured and discussed material (Walcott, 1914, pl. 65, fig. 4; Srivastava and Hughes, in press, 3.18.5-3.18.9) was referred to *B. texana* by Srivastava and Hughes, in press). *Dikelocephalus* species analyzed now include *Dikelocephalus freeburgensis* Feniak in Bell et al., 1952 and four morphotypes of *Dikelocephalus minnesotensis*: *Dikelocephalus "gracilis"*, *Dikelocephalus "inter-medicus"*, *Dikelocephalus* Arcadia wide fixigena (ArWF) morph and *Dikelocephalus* Arcadia narrow fixigena (ArNF) morph that could be argued to each represent a different species. These were used to see if more light could be thrown on the affinities of *Walcottaspis van-hornei*, a form previously suggested to be sister taxon to *D.minnesotensis* (Srivastava and Hughes, 2024).

As opposed to my previously published phylogeny (see Fig. 2.1), characters and character states that were inapplicable for some species were handled using contingent coding (Forey and Kitching, 2000). This coding strategy makes explicit homology statements

and does not overweight the absences of the inapplicable character states when inferring the trees (Hopkins et al., in review). The character matrix was built using Mesquite software (Maddison and Maddison, 2023). The parsimony analyses were run using Tree Analysis Using New Technology (TNT; Goloboff et al., 2008), and Winclada (Nixon, 2002) was used to map transitions in discrete character states. A heuristic search (“traditional search” in TNT) with tree-bisection-and-reconnection (TBR) swapping algorithm was used to analyze the 58 characters divided into 166 discrete character states across 22 ingroup taxa and one outgroup (Table 4.1) with 100 random addition sequence replicates, holding 100 trees at each step. The three most parsimonious trees (MPTs) from this step were then used as starting trees for another round of branch swapping to obtain the final set of MPTs. Branch-collapsing rules were not enforced. This allowed consideration of all possible most parsimonious trees without imposing a filter against tree branches with low tree length scores. Tree branch support was later surveyed by use of bootstrap resampling and Bremer support as discussed below. Bootstrap resampling involves repeatedly resampling the data with replacement, building multiple trees from these resampled datasets, and then analyzing the frequency with which particular clades appear across those trees. The resulting bootstrap values indicate how often a given branch is recovered in the resampled trees. A bootstrap value of 50% or higher indicates support for a clade and suggests that it may be considered to represent actual evolutionary relationship. Bremer support assesses the integrity of a clade by quantifying the number of additional steps (evolutionary changes) that would have to be added to the MPT for the clade not to be recognized. The Bremer support value is calculated as the difference between the tree lengths of the original MPT

and of the tree lacking the clade in question. A Bremer support value of 3 or higher suggests that the clade is strongly supported by the data and is unlikely to be removed by changes in other parts of the tree. As some characters varied along a continuous scale, we also conducted a separate parsimony-based analysis treating them as such with a traditional search setup same as before, rather than with user-imposed, discretized character state divisions as used in the first analysis. Twenty out of total 58 characters were coded as continuous for this second analysis and the continuous character states were measured using the largest specimen of cranidium, hypostome and pygidium of each species considered, in combination with scaled estimates of characters evident only in smaller specimens of the same taxon (see table in Supplementary Data 1 for the continuous character states).

4.4 Results

The discretized character matrix resulted in 3 most parsimonious trees (of which the strict consensus tree is depicted in Fig. 4.1). The tree length of the consensus tree was 298, consistency index was 32 and retention index was 48. There is an overall improvement in resolution compared to the previous analysis (Srivastava and Hughes, 2024, fig. 2.11) and several synapomorphies support more basal nodes of the tree. The tree implies presence of a division between "osceolimorphs" (including *Briscoia llanoensis*, *Briscoia pertransversa*, *Osceolia osceola*, *Osceolia tumerispina*, *Elkia nasuta*, *Briscoia septentionalis*, *Parabriscoia elegans*, *Briscoia nevadensis* and *Briscoia* sp.) and "dikelomorph" (including *Briscoia schucherti*, *Briscoia angustilimba*, *Briscoia sinclairensis*, *Briscoia texana*, *Dikelocephalus freeburgensis*, *Dikelocephalus "gracilis"*, *Dikelocephalus "intermedicus"*, *Dikelocephalus* Ar-

cadia wide fixigena form, *Dikelocephalus* Arcadia narrow fixigena form and *Walcottaspis vanhornei*). "Osceolimorphs" share an elongated glabella, and large eyes located close to the glabella. Within this putative clade, there is an apparent trend in the pygidial form from a generalized "Briscoia-type" pygidium, shared by the outgroup, to a more embellished pygidium with various marginal spines and modification of the pleural furrow expression. Such trilobites remained relatively small, likely because their glabellar construction constrained the acquisition of a sufficiently large crop (stomach) to permit attaining large size due to size to volume ratio constraints. The "dikelomorphs" putative clade comprises trilobites with a broader glabella and relatively smaller eyes with somewhat wider fixigenae. This clade is characterized by animals that reached larger maximum sizes, likely aided in doing so by the greater potential volume of the crop that could be accommodated under a square-shaped glabella.

In both analyses, in addition to confirming that *Walcottaspis* shares common ancestry with St. Lawrence *Dikelocephalus*, both results also suggest that *W. vanhornei* shares common ancestors with the *Dikelocephalus* Arcadia morphotype, that also possesses a wide fixigena. Bootstrap resampling was undertaken by traditional search by the frequency differences method ("GC" in TNT) for 1,000 replicates (Fig. 4.2). The bootstrap resampling results strongly support (>50% bootstrap support) various nodes in the clade containing *Dikelocephalus*-*Walcottaspis* species, especially the clade containing *Dikelocephalus* "inter-medius", *Walcottaspis vanhornei* and *Dikelocephalus* Arcadia wide fixigena form (61% bootstrap support). Bremer support (Bremer, 1988, 1994) was calculated by default TBR branch swapping, setting the suboptimal limit to six steps. Most of the nodes of the con-

sensus tree have >1 Bremer support, strongest support (Bremer support 3) shown for the clades containing *Dikelocephalus-Walcottaspis* species and that containing *B.angustilimba-B.sinclairensis-B.texana* (Fig. 4.2).

The mixed character matrix resulted in a single most parsimonious tree through a heuristic search of tree length score 125 (Fig. 4.2). The 38 discrete characters from this dataset were mapped onto the MPT yielding a tree with consistency index of 43 and retention index of 63. The better supported tree from this dataset shows a different kind of division between the taxa, where in all the dikelocephalid species found within the Upper Mississippi Valley define a single clade, separated from the species occurring elsewhere in Laurentia. The sister taxon relationships among *Dikelocephalus* species and *W. vanhornei* are maintained, with *W. vanhornei* again revealed as sister taxon to the *Dikelocephalus* morphotype from Arcadia with wide fixigena. Bootstrap resampling and Bremer support calculation show these relationships to receive relatively high levels of support (Fig. 4.4). 59% bootstrap support is calculated for *Dikelocephalus-Walcottaspis* clade, and even higher support (61%) is calculated for the sister taxon relationship of *Dikelocephalus "gracilis"* and *Dikelocephalus* Arcadia morphotype with narrow fixigena. This relationship will be explored further in a forthcoming comprehensive study of the phylogeny of dikelocephalid species which will include a wider selection of outgroup taxa within those "saukiids" possessing a preglabellar field.

4.5 Conclusions

The trees discussed here are the preliminary results of phylogenetic analyses based on an expanded dataset characterizing late Cambrian dikelocephalid trilobites. The two datasets analyzed show contrasting results but each presents a plausible and coherent model of dikelocephalid evolution. Both trees agree on the shared ancestry of *Walcottaspis vanhornei* and *Dikelocephalus* Arcadia morphotype with wide fixigena, but the origin of *Osceolia* is strongly at variance in the two trees. According to the discretized dataset, *Osceolia* may have evolved outside the Upper Mississippi Valley, when its closest relative is indicated to be *B.coloradoensis* (Fig. 4.1). Alternatively, it may have originated more locally with its closest relatives being *B.schucherti* and *B.pertransversa* (Fig. 4.2). Resolving among these solutions is challenging with the present dataset and made more challenging by the absence of a record of *Osceolia*'s origination due to this occurring at a time of maximum flooding, the record of which is not preserved. The division between "osceolimorphs" and "dikelomorphs" (Fig. 4.1), if confirmed, suggests that these morphotypes have a clear phylogenetic basis. In future work, I will test the reasoning behind this division using character mapping techniques that can examine the relationship between the largest body size achievable for these trilobites and the characterization of the shape of stomach capsule (glabella).

The trees shown here contain further exploratory results of phylogenetic analysis into the history of dikelocephalid trilobite evolution. The consistency and retention indices of both trees are toward the low end of a spectrum of values yielded among trilobite phy-

logenetic studies ([Hopkins et al., in review](#)), with one part of the tree consistent between both types of character treatment, but other relationships variable. While a number of additional improvements to the analysis are yet to be explored, including using multiple species to define the outgroup basal node, support levels herein are likely a function of the poor knowledge of many taxa included in the analysis. It may be informative that relationships are best resolved among the best represented species suggesting that when individual species are studied in detail, as I have done in this thesis, relationships with stronger levels of support can be forthcoming. This will be explored in more detail in future work.

4.6 Table

Table 4.1: Matrix of discrete character states for analyzed taxa. See the Materials and Methods section for a descriptive list of character and character states coded in this matrix. Columns correspond to character states designation and rows contain taxa names. '?' corresponds to missing character states and '-' corresponds to inapplicable tokens.

[illegible]

4.7 Figures

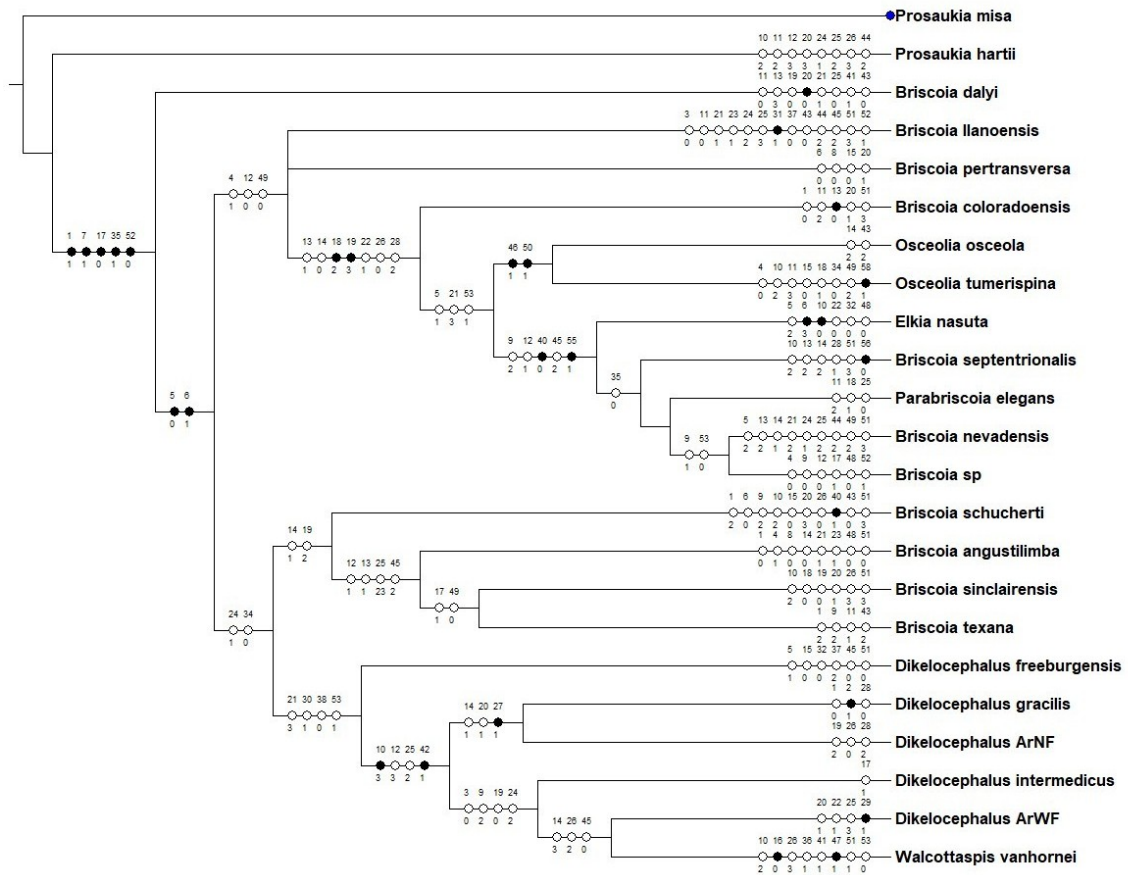


Figure 4.1: Strict consensus tree of the 3 MPTs found for the character matrix were all character states are discretized. Numbers on top of node branches show the character number according to list in text and numbers on bottom show the state for that character. Filled circles indicate unambiguous derived character states while open circles indicate convergent derived character states. Tree score=298, CI=32, RI=48.

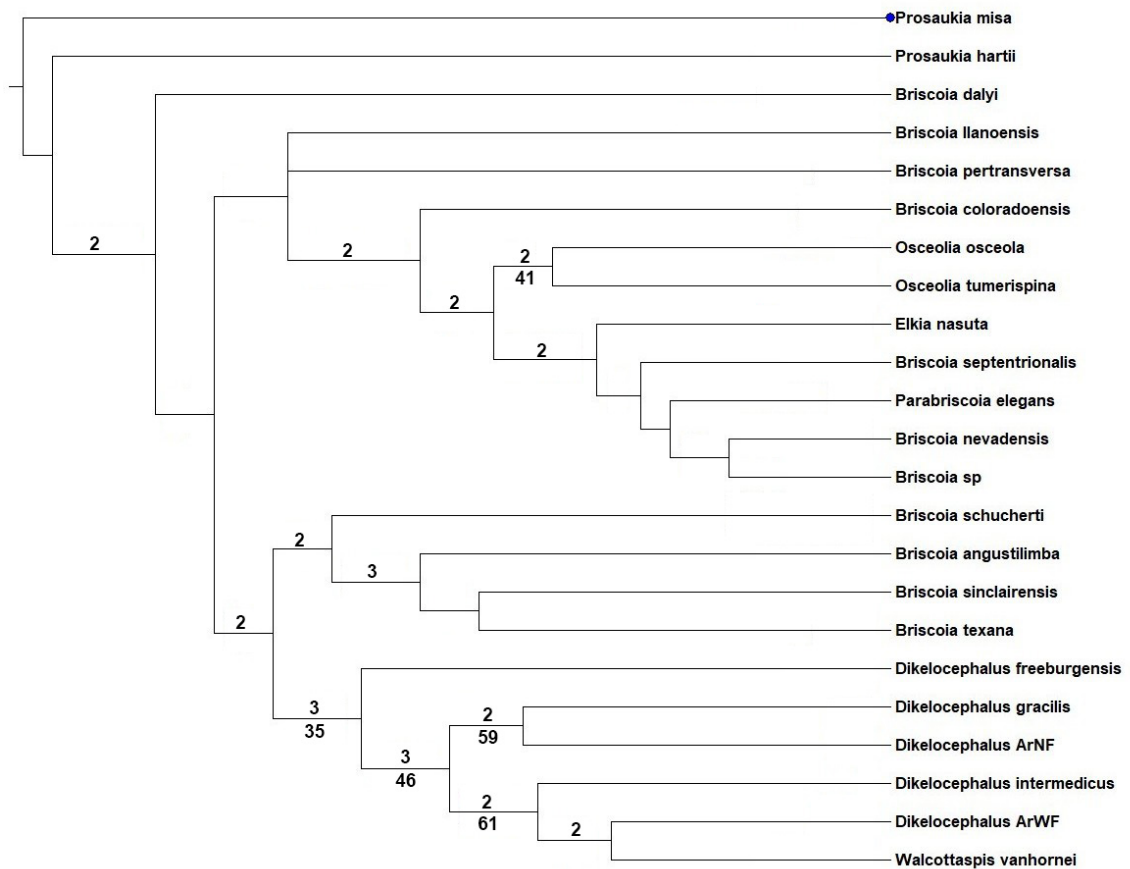


Figure 4.2: Strict consensus tree from Fig. 4.1 using a discretized character-state matrix. The numbers above branches are Bremer supports while the numbers below the branches depict standard bootstrap resampling values.

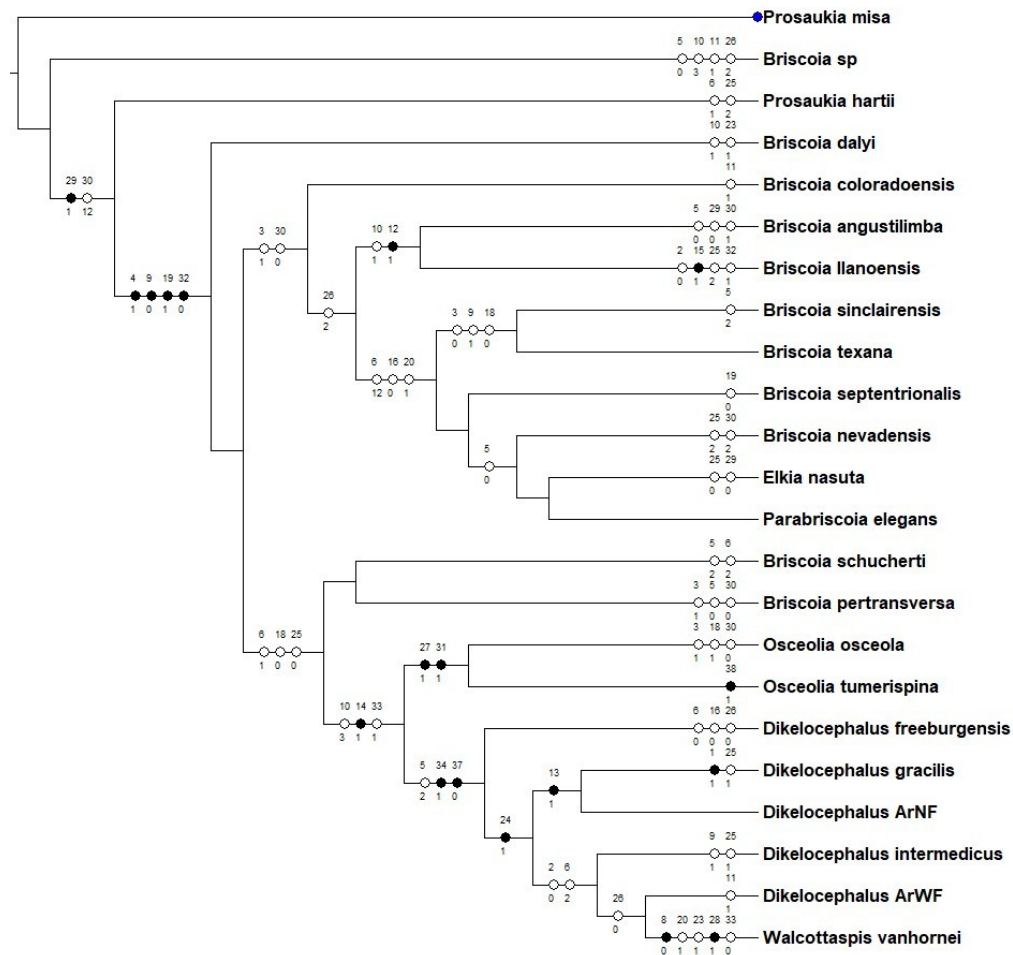


Figure 4.3: Single tree found for the character matrix using a mixture of discretized and continuous characters. Characters mapped are only discrete characters of the dataset. Symbols as described in 4.1. Tree score=125. CI=43, RI=63 according to discrete character mapping.

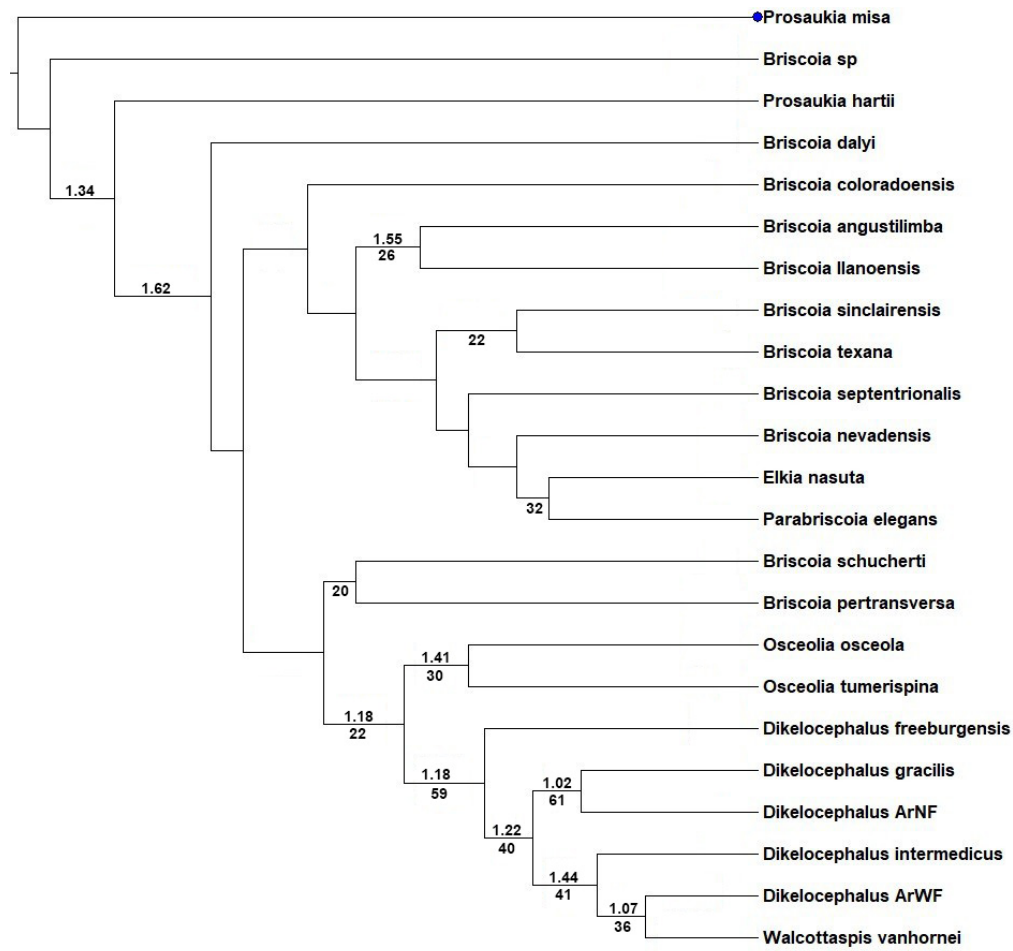


Figure 4.4: Most parsimonious tree from Fig. 4.3 using a mixed character matrix showing bootstrap resampling and Bremer support calculation results. The numbers above branches are Bremer supports while the numbers below the branches depict standard bootstrap resampling values.

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