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CAMBRIAN (JIANGSHANIAN; SUNWAPTAN) TRILOBITES FROM THE UPPER HONEY CREEK FORMATION, WICHITA MOUNTAINS REGION, OKLAHOMA

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SEAN ROBERT BLACKWELL
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CAMBRIAN (JIANGSHANIAN; SUNWAPTAN) TRILOBITES FROM THE UPPER HONEY CREEK FORMATION, WICHITA MOUNTAINS REGION, OKLAHOMA

A THESIS APPROVED FOR THE SCHOOL OF GEOSCIENCES

BY

Dr. Stephen Westrop, Chair

Dr. Richard Cifelli

Dr. Richard Lupia

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Abstract

The Upper Cambrian (Jiangshanian; Sunwaptan) Honey Creek Formation of Oklahoma is a succession of sandy limstone and minor sandstone that was deposited under shallow subtidal conditions in an achipelago of rhyolite islands. This thesis revised the trilobite fauna of the upper Honey Creek at Bally Mountain, Kiowa County, and Ring Top Mountain, Comanche County, using new collections from three measured sections, and archival museum collections. The faunas are assigned to four species based biostratigraphic zones, three of which are new. In ascending order, these are the *Orygmaspis* (*Orgmaspis*) *llanoensis*, *Taenicephalus wichitaenis*, and *Idahoia lirae* zones, and an informal unit, the *Monocheilus reginae* Fauna. The lower three zones can be correlated readily to succession in central Texas. Genera treated in the thesis are *Conaspis*, *Idahoia*, *Monocheilus*, *Orygmaspis*, *Ptychaspis*, *Taenicephalus* and *Wilbernia*. New species are *Idahoia czukay*, *Monocheilus reginae*, *Ptychaspis richardi*, *P. occulta*, and *Taenicephalus kallisti*.

Chapter I: Introduction

The Cambrian succession of southern Oklahoma is well known for its trilobite faunas (e.g., Frederickson, 1948, 1949; Stitt, 1971b, 1977; Westrop et al., 2007, 2010; Westrop and Adrain, 2008, 2009), and includes the record of two major extinction events (Stitt, 1971a, 1977). One of these extinctions, at the end of the Steptoean Stage of the Laurentian nomenclature, can be identified in the Honey Creek Formation. Pre-extinction faunas (Westrop et al., 2007, 2010; Westrop and Adrain, 2009) and those of the extinction interval (Westrop and Adrain, 2008) are under study by S.R. Westrop and colleagues. This thesis documents part of the post-extinction interval in the upper Honey Creek at Ring Top Mountain in Comanche County (Westrop et al., 2010) and at Bally Mountain in Kiowa County (Donovan et al., 1986). It is based mainly on section logs and collections made by Westrop and Roger Burkhalter in 2011, with additional material collected by Blackwell and Westrop in 2014. Some specimens from the J.H. Stitt collection of trilobites from the Honey Creek Formation of the Arbuckle Mountains (Stitt, 1971b), now housed at the Sam Noble Oklahoma Museum of Natural History, were also incorporated into the study.

This chapter provides background information on sample localities and the general stratigraphic setting of the Honey Creek Formation, as well as a new, species-based zonation for the upper part of the formation. The remaining chapters document the trilobite faunas. Chapter two describes a new fauna from the Honey Creek–Fort Sill boundary interval that is dominated by a new species of *Monocheilus*. Chapter three focuses on *Taenicephalus*, which is the most abundant genus in the upper Honey Creek. Finally, Chapter four provides a brief treatment of other, less common genera.

Stratigraphic Setting

The Honey Creek Formation outcrops in the Wichita and Arbuckle Mountains areas of Oklahoma, and forms the Timbered Hills Group with the underlying Reagan Sandstone (Stitt, 1971b). The Timbered Hills onlaps the Carlton Rhyolite, which was exposed in late Cambrian Oklahoma as a volcanic archipelago with at least 300 m of relief (Donovan, 1986; Donovan and Bucheit, 2000; Donovan et al. 2000). Following Donovan and Ragland (1986), the base of the Honey Creek is placed at the lowest occurrence of bioclastic carbonate. Lithologically, the formation is a pelmatzoan-rich, glauconitic, bioclastic grainstone and rudstone with thin siliciclastic drapes. Cross-bedding and ripple marks are common, as are sandstone interbeds. Heterolithic intervals comprise fine to medium grained sandstone with recessively weathering bioclastic carbonate lenses (Westrop et al., 2010, fig. 1). Donovan and Bucheit (2000) interpreted the Honey Creek as a tidally influenced deposit that formed as sandbars between rhylolite islands.

The Fort Sill Formation (lowest unit of the Arbuckle Group) succeeds the Honey Creek Formation, and is composed of lime mudstone–wackestone (Stitt, 1971b; Donovan and Ragland, 1986). Intraclastic rudstone is also present, and microbial buildups occur in the upper part of the formation (Stitt, 1971b). Quartz sand and glauconite are minor components, suggesting that the archipelago was largely flooded during deposition of the Fort Sill.

Study Area

The study area lies in the Slick Hills, immediately north of the Wichita Mountains. A composite section through most of the Honey Creek Formation is available at locality KR, at Ring Top Mountain on the Kimbell Ranch, Comanche County (Fig. 1A). Three sections were measured, logged and sampled by Westrop and R. Burkhalter (sections KR1–KR3), with additional sampling by Blackwell and Westrop. The sections were physically correlated by tracing a resistant, meter scale limestone unit around the flanks of Ring Top Mountain (Westrop et al., 2010, fig. 1); the upper *Elvinia–Taenicephalus* zones are not exposed in KR2, so that section is not included in this study. The succession at Ring Top Mountain was deposited in the vicinity of a rhyolite island (Donovan and Bucheit, 2000), and Westrop et al. (2010, fig. 1) document rapid facies changes in the proportion of sandstone and carbonate along the transect between sections KR1 and KR3. The succession thickens noticeably at KR1 and is more carbonate-rich (Fig. 6). As a result, it yielded the most complete set of trilobite faunas (Fig. 3).

The type material of *Taenicephalus wichitaensis* Resser, 1942 was collected from the Honey Creek Formation in Blue Creek Canyon (Smithsonian locality 9q), which is the narrow valley on the west side of Ring Top Mountain and is the route of Highway 58 (Fig. 1A). The exact location is not specified, but it may correspond to one Frederickson's (1949) localities (6, 7 or 8) from Blue Creek Canyon.

The succession in the Bally Mountain region (locality BM) of Kiowa County was also deposited near a rhyolite island (Donovan and Bucheit, 2000). The section was measured, logged and sampled by Westrop and Burkhalter, with additional sampling by Blackwell and Westrop. It is located on the west-facing slope of an unnamed ridge about one kilometer to the east of Bally Mountain (Fig. 1B). *Elvinia* Zone faunas are well represented in a carbonate unit about 52.5 m above the base of the section. An overlying 12 m sandstone unit did not yield trilobites, but *Taenicephalus* and *Conaspis* are present in the succeeding carbonate unit, between 70.5m and 72m above the base of the section (Fig. 5). A newly discovered fauna dominated by *Monocheilus reginae* n. sp. occurs higher in the section, in the Honey Creek–Fort Sill boundary interval (Fig. 5).

The upper half of the Honey Creek Formation at BM is dominated by limestone, and a 6–11m unit of sandstone with carbonate lenses at KR is absent (Fig. 6).

Some material from the Arbuckle Mountains in Murray County, Oklahoma, is also included in the study. Sclerites of *Taenicephalus gouldi* (Frederickson, 1949) and *Orygmaspis* (*Orygmaspis*) *llanoensis* (Walcott, 1890) from the Honey Creek Formation at Stitt's (1971b) Royer Ranch section (collection RR 150) are treated in chapters 3 (Pl. 19) and 4 (Fig. 1), respectively. Cranidia of *Taenicephalus kallisti* n. sp. from Stitt's (1971b) US Highway 77 section (collection HS 61) are included in Chapter 3 (Fig. 1). The type material of *Ptychaspis richardi* n. sp. (Chapter 2) was collected from the Fort Sill Formation, 4.4 km south-east of Hennepin.

Comparative material from outside Oklahoma is also treated in this thesis. Sclerites of *Ptychaspis* (Chapter 2) and *Taenicephalus* (Chapter 3) that were illustrated previously by Bell and Ellinwood (1962) are from the Morgan Creek Member of the Wilberns Formation Burnet, Gilespie, Mason, McCulloch and San Saba counties in central Texas. The types of *Ptychaspis bullasa* Lochman and Hu, 1959 are from the St. Charles Formation at Mink Creek, southern Idaho.

Introductory Biostratigraphy

The trilobite zonation used for the Cambrian (Sunwaptan; Jiangshanian– "Stage 10"; Peng et al., 2012, fig. 2) succession in the south-central United States has its origin in the correlation chart assembled by Howell et al., (1944), with subsequent modifications by Grant (1965) and Longacre (1970), among others (see Longacre, 1970, p. 6–12 for nomenclatural history). The study interval in the upper Honey Creek Formation belongs to the *Taenicephalus* and *Saratogia* zones (Stitt, 1971b; in Texas, the correlatives of the lower half of the *Saratogia* Zone is assigned to the *Idahoia* Zone -- see Longacre, 1970 and Fig. 7). Stitt (1971b) followed Grant (1965) and Longacre (1970) in defining a lower subzone of the *Taenicephalus* Zone, the *Parabolinoides* Subzone (Fig. 7), which is based on the local range of *Orygmaspis* (*Parabolinoides*). Both Longacre (1970) and Stitt (1971b) also separated the basal part of the *Idahoia* and *Saratogia* zones, respectively, as the *Idahoia lirae* Zone. Stitt also defined the *Drumaspis* Subzone, based on the local range of the name-bearing genus. Although this zonation is used widely, it is based largely on the ranges of genera. Species based zonations offer more biostratigraphic resolution simply because the stratigraphic ranges of species are typically shorter than those of genera (Westrop, 1986). One goal of this thesis is to develop a high-resolution zonation using species ranges that can also be applied to the succession in central Texas (Fig. 2).

Zonation

The traditional *Taenicephalus* zone is a relatively low diversity interval in the aftermath of the trilobite extinction at the base of the Sunwaptan Stage, with collections typically yielding fewer than five species (e.g., Westrop and Cuggy, 1999). However, turnover of taxa remained brisk (Westrop, 1996), so that there is considerable potential for development of a species-based zonation. A new set of zones that can be applied to the successions in Oklahoma and Texas is proposed below (Figs. 2, 7).

Orygmaspis (*Parabolinoides*) *contracta Zone*.— The lower part of the traditional *Taenicephalus* Zone is the *Parabolinoides* Subzone (Longacre, 1970; Stitt, 1971b; Fig. 7). Westrop (1986) redefined it as the *Orygmaspis* (*Parabolinoides*) *contracta* Subzone, with the lower boundary defined at the first appearance of the name-bearing species. Southern Oklahoma is the type area of *O*. (*P*.) *contracta*, so this datum can be recognized in both the Wichita and Arbuckle Mountains. This species is also present in Texas (e.g. Bell et al., 1962) and in the southern Canadian Rocky Mountains (Westrop, 1986), so that the base of the zone can be correlated widely. This interval is under study by Westrop and will not be considered further.

Orygmaspis (*Orygmaspis*) *llanoensis Zone*.— The oldest species of *Taenicephalus* in the Arbuckle Mountains is *T*. *gouldi* (Frederickson, 1949), and it occurs in Stitt's (1971b) Royer Ranch (RR) and US Highway 77 (HS) sections. Unfortunately this stratigraphic interval is unfossiliferous in all sections studied in the Wichita Mountains region, including Stitt's (1977) Chandler Creek section. Stitt's collections from the Arbuckle Mountains, housed in the Sam Noble Oklahoma Museum of Natural History, record the lowest occurrence of *T*. *gouldi* in collection RR 150, where it enters the succession with *Orygmaspis* (*Orygmaspis*) *llanoensis* (Walcott, 1890). Specimens from this collection are illustrated in this thesis (Ch. 4, Fig. 1; Pl. 19) to document the base of the zone, which is defined in this thesis by the lowest occurrence of *O*. (*O*.) *llanoensis*. The base of the zone can be correlated into central Texas, where both *T*.

gouldi and *O*. (*O*.) *llanoensis* occur in the Morgan Creek Member of the Wilberns Formation (Bell et al., 1962; Longacre, 1970).

Taenicephalus gouldi has a short stratigraphic range. In Stitt's (1971b, p. 66) section RR, the species is recorded through only 3 feet (0.91 m; collections RR 150, 153), but *O*. (*O*.) *llanoensis* occurs through 33 feet (10.06 m; collections RR 150–183). Above the unfossiliferous interval in section KR1 at Ring Top Mountain, *O*. (*O*.) *llanoensis* is associated with *T. kallisti* n. sp. and *Conaspis testudinata* Ellinwood, in Bell and Ellinwood, 1962 (Fig. 3). In Stitt's collections from the Arbuckles, I have identified *T. kallisti* in collection HS 61 (Chapter 3, Fig. 1; misidentified as *T. shumardi* by Stitt, 1971b, p. 57), where it co-occurs with *O*. (*O*.) *llanoensis* at a level that is 11 feet (3.35 m) above the entry of *T. gouldi* into the succession (collection HS 50). These data confirm that *T. kallisti* lies above *T. gouldi* in southern Oklahoma, and it occurs in the upper half of the *O*. (*O*.) *llanoensis* Zone. The co-occurrence of *O*. (*O*.) *llanoensis* and *C. testudinata* in collection KR1 29.9 indicates a correlation into the lower half of the post-*Parabolinoides* interval of the *Taenicephalus* Zone in Texas (Longacre, 1970, text-fig. 2; Fig 7), and this is consistent with the position of *T. kallisti* in the Honey Creek Formation.

Taenicephalus wichitaensis Zone.—The base of the zone is defined by the lowest occurrence of *T. wichitaensis* Resser (1942), and the upper boundary is the base of the overlying *Idahoia lirae* Zone. In addition to the name-bearing species, *Orygmaspis* (*Orygmaspis*) *llanoensis* (Walcott, 1890) and *Conaspis testudinata* Ellinwood, in Bell and Ellinwood also occur in the zone (Figs. 4, 5) Based on its stratigraphic position below the *I. lirae* Zone at section KR1 (Fig. 3), the *T.*

wichitaensis Zone must correlate with the upper half of the *Taenicephalus* Zone of Texas (Longacre, 1970; Fig. 7) and Montana–Wyoming (Grant, 1965), and the upper half of the *T. shumardi* Subzone in the southern Canadian Rocky Mountains (Westrop, 1986).

Idahoia lirae Zone.— The *Idahoia lirae* Zone was first proposed as a subzone of the *Idahoia* Zone of Texas by Longacre (1970), and was subsequently used as a subzone of *Saratogia* Zone in Oklahoma (Stitt, 1971b). As noted by Longacre (1970, p. 10), the composition of this unit is almost identical in Texas and Oklahoma, and the base is defined by the lowest occurrence of *I. lirae*. The *I. lirae* Zone is a thin stratigraphic interval that is only 1.83 m (6 ft) thick in Texas (Longacre, 1970, p. 10), and 7.92 m (26 ft) in the US Highway 77 section in the Arbuckle Mountains (Stitt, 1971b, p. 57). Thickness of the Honey Creek Formation varies laterally in thickness in the Wichita Mountains area (Fig. 6), but the *I. lirae* Zone cannot be more than about 7 m in thickness at section BM (Fig. 5), where the *T. wichitaensis* Zone is represented in collection BM-72, and the lowest occurrence of the *M. reginae* Fauna is in BM-79.4T. In addition to *I. lirae*, *I. czukay* n. sp. is also present.

Monocheilus reginae Fauna.— The *Monocheilus reginae* Fauna is an informal biostratigraphic unit that is known only from section BM (Fig. 5), where it occurs in the Honey Creek–Fort Sill boundary interval. The base is defined by the lowest occurrence of *M. reginae*, with *Wilbernia* cf. *diademata* and *Ptychaspis* sp. indet. *Drumaspis* Resser, 1942 and *Minkella* Lochman and Hu, 1959 enter the succession 1.1 m above the base of the Fort Sill Formation (S.R. Westrop, unpublished data). The age and correlation of the fauna is discussed in more detail in Chapter 2.

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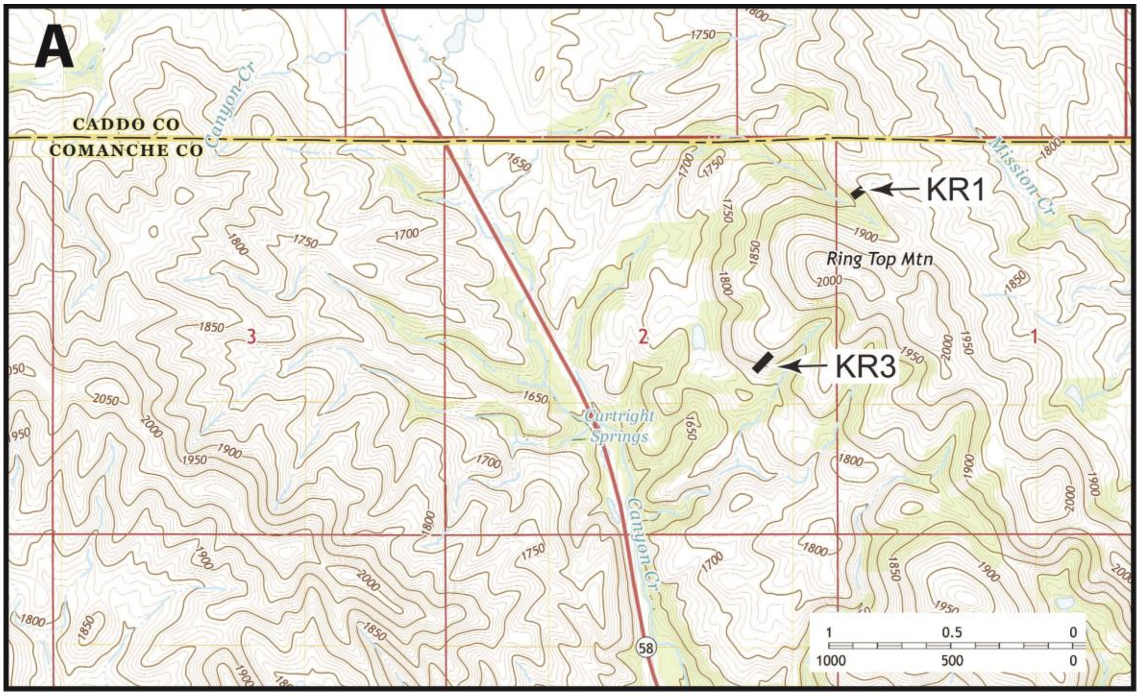
Figure 1

Maps showing the location of stratigraphic sections on the north flank of the Wichita Mountains.

A. Sections KR1 and KR3 are located on the flanks of Ring Top Mountain in Comanche County

B. Section BM is on the west slope of an unnamed ridge opposite Bally Mountain in Kiowa County.


A
CADDO CO
COMANCHE CO
KR1
KR3
Ring Top Mtn
Curtright Springs
Canyon Cr
Mission Cr
1
0.5
0
1000
500
0

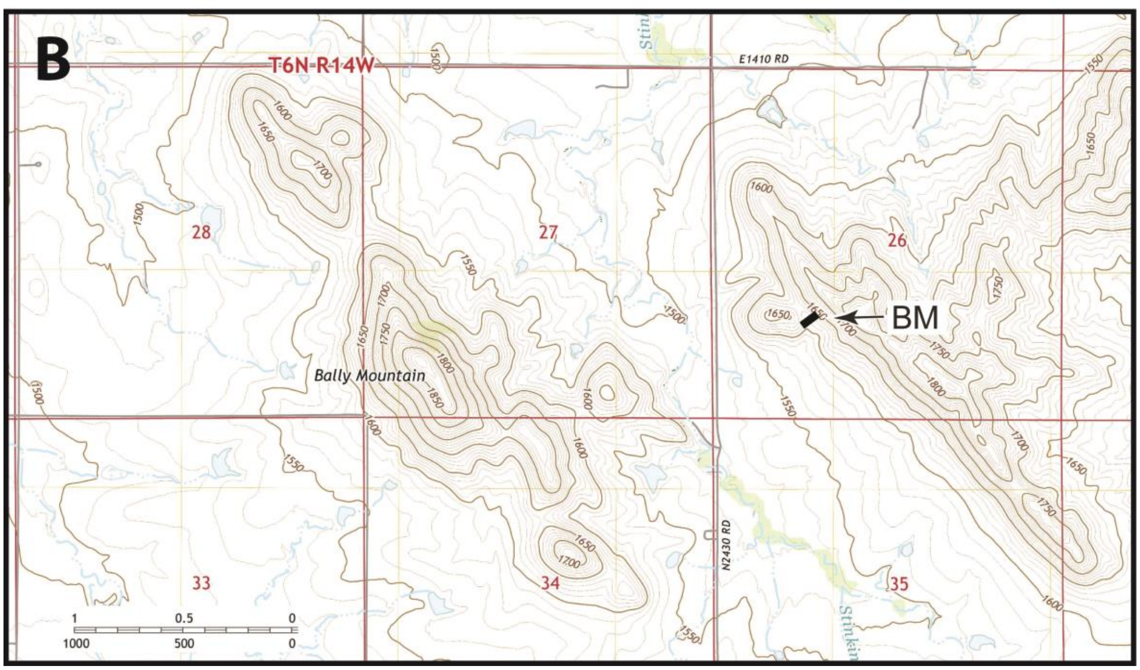

B
T6N R14W
E1410 RD
BM
Bally Mountain
N2430 RD
1
0.5
0
1000
500
0

Figure 2

Species-based trilobite zones defined in this study. The interval below the *Orygmaspis* (*Orygmaspis*) *llanoensis* Zone is from unpublished work by S.R. Westrop.

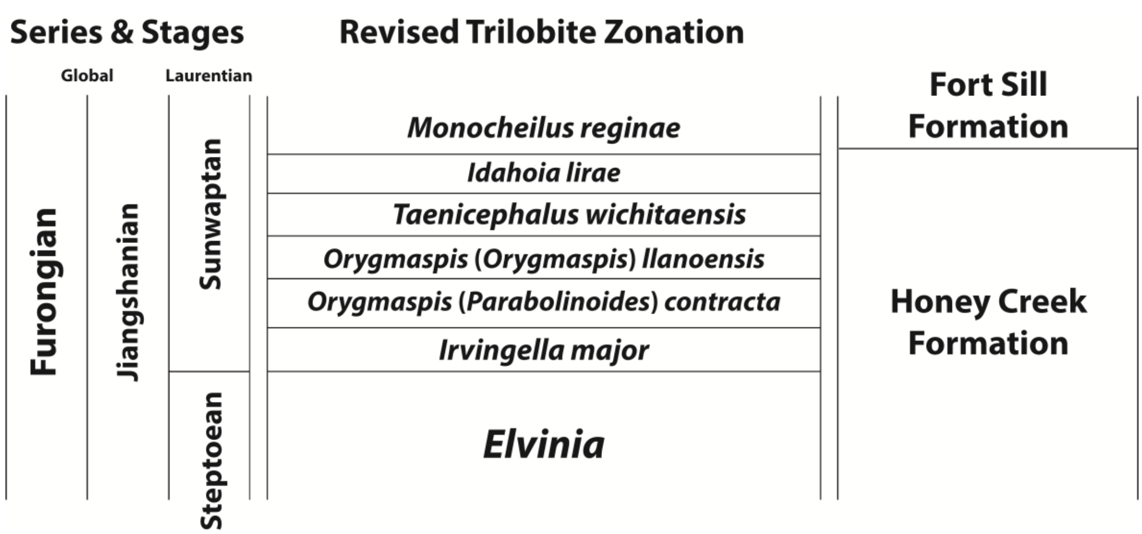

Series & Stages
Revised Trilobite Zonation
Global
Laurentian
Furongian
Jiangshanian
Sunwaptan
Steptoean
Monocheilus reginae
Idahoia lirae
Taenicephalus wichitaensis
Orygmaspis (Orygmaspis) llanoensis
Orygmaspis (Parabolinoides) contracta
Irvingella major
Elvinia
Fort Sill Formation
Honey Creek Formation

Figure 3

Stratigraphic distribution of trilobite species at section KR1 plotted against an unpublished lithologic log of the upper Honey Creek and lower Fort Sill formations provided by S.R. Westrop. Boundaries of zones in the lower six meters of the section [*Elvinia*, *Elvinia* Zone; major, *Irvingella major* Zone; *contracta*, *Orygmaspis* (*Parabolinoides*) *contracta* Zone] from unpublished work by S.R. Westrop.

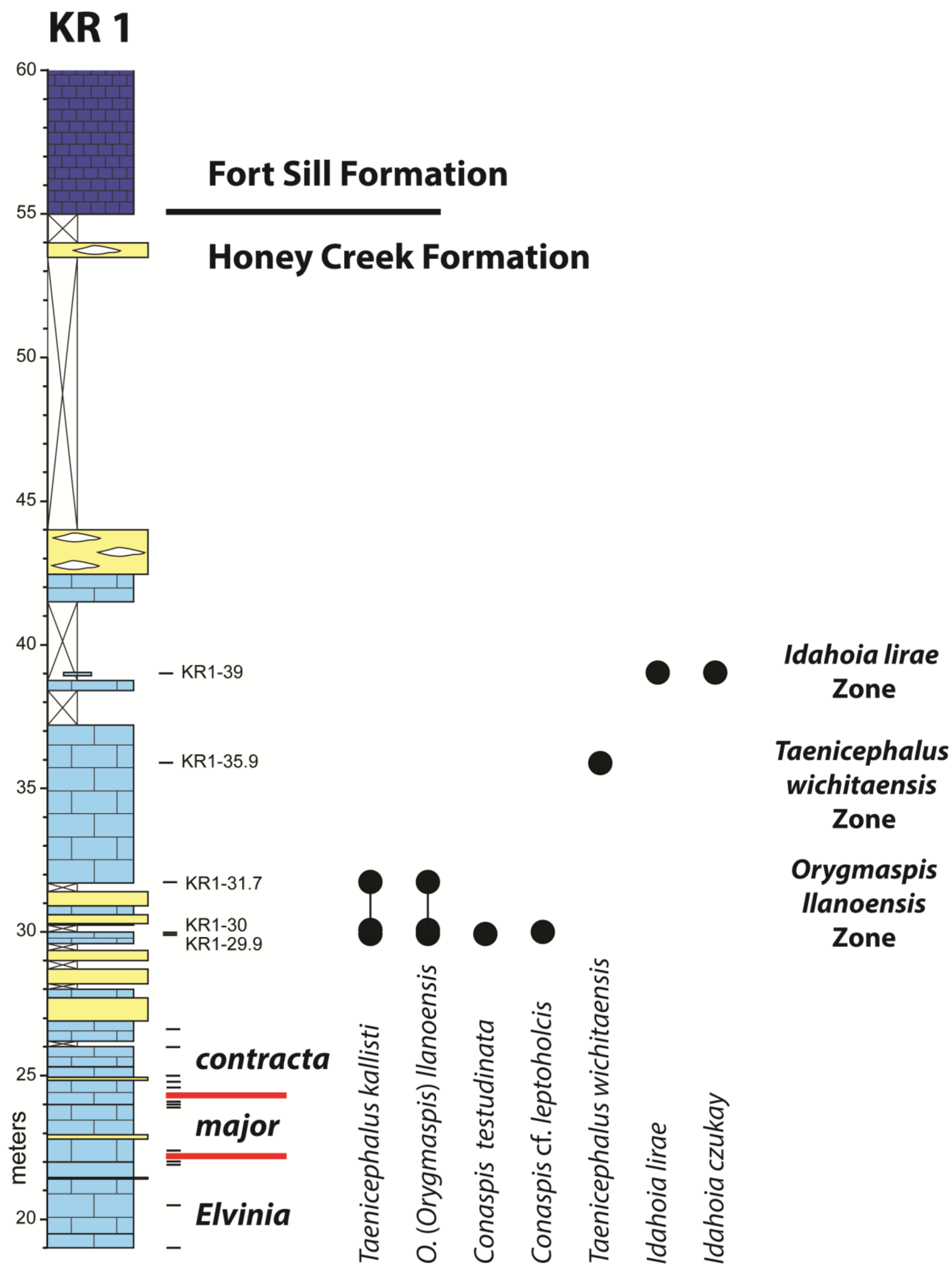

KR 1
60
55
50
45
40
35
30
25
20
meters
Fort Sill Formation
Honey Creek Formation
KR1-39
KR1-35.9
KR1-31.7
KR1-30
KR1-29.9
contracta
major
Elvinia
Taenicephalus kallisti
O. (Orygmaspis) llanoensis
Conaspis testudinata
Conaspis cf. leptoholcis
Taenicephalus wichitaensis
Idahoia lirae
Idahoia czukay
Idahoia lirae Zone
Taenicephalus wichitaensis Zone
Orygmaspis llanoensis Zone

Figure 4

Stratigraphic distribution of trilobite species at section KR3 plotted against an unpublished lithologic log of the upper Honey Creek and lower Fort Sill formations provided by S.R. Westrop.

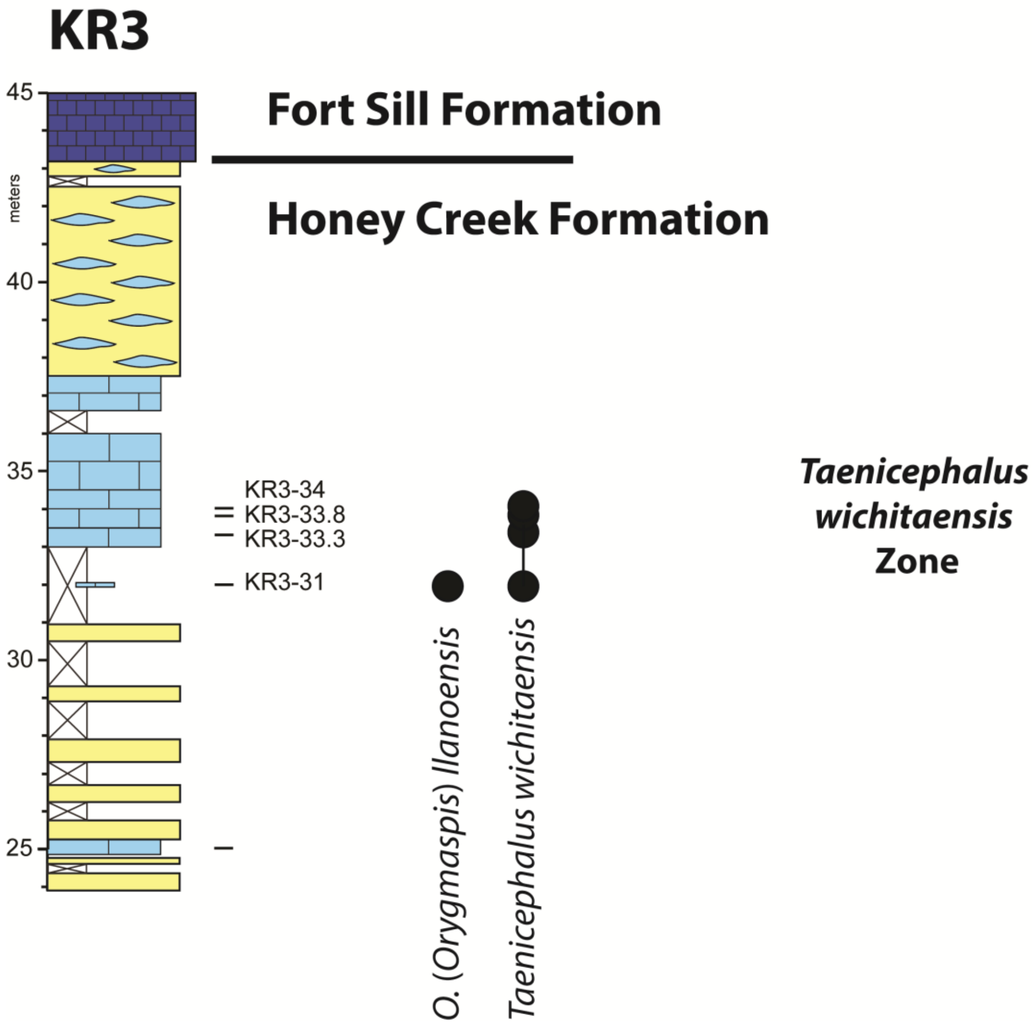

KR3
45
40
35
30
25
meters
Fort Sill Formation
Honey Creek Formation
KR3-34
KR3-33.8
KR3-33.3
KR3-31
O. (Orygmaspis) llanoensis
Taenicephalus wichitaensis
Taenicephalus wichitaensis Zone

Figure 5

Stratigraphic distribution of trilobite species at section BM plotted against an unpublished lithologic log of the upper Honey Creek and lower Fort Sill formations provided by S.R. Westrop.

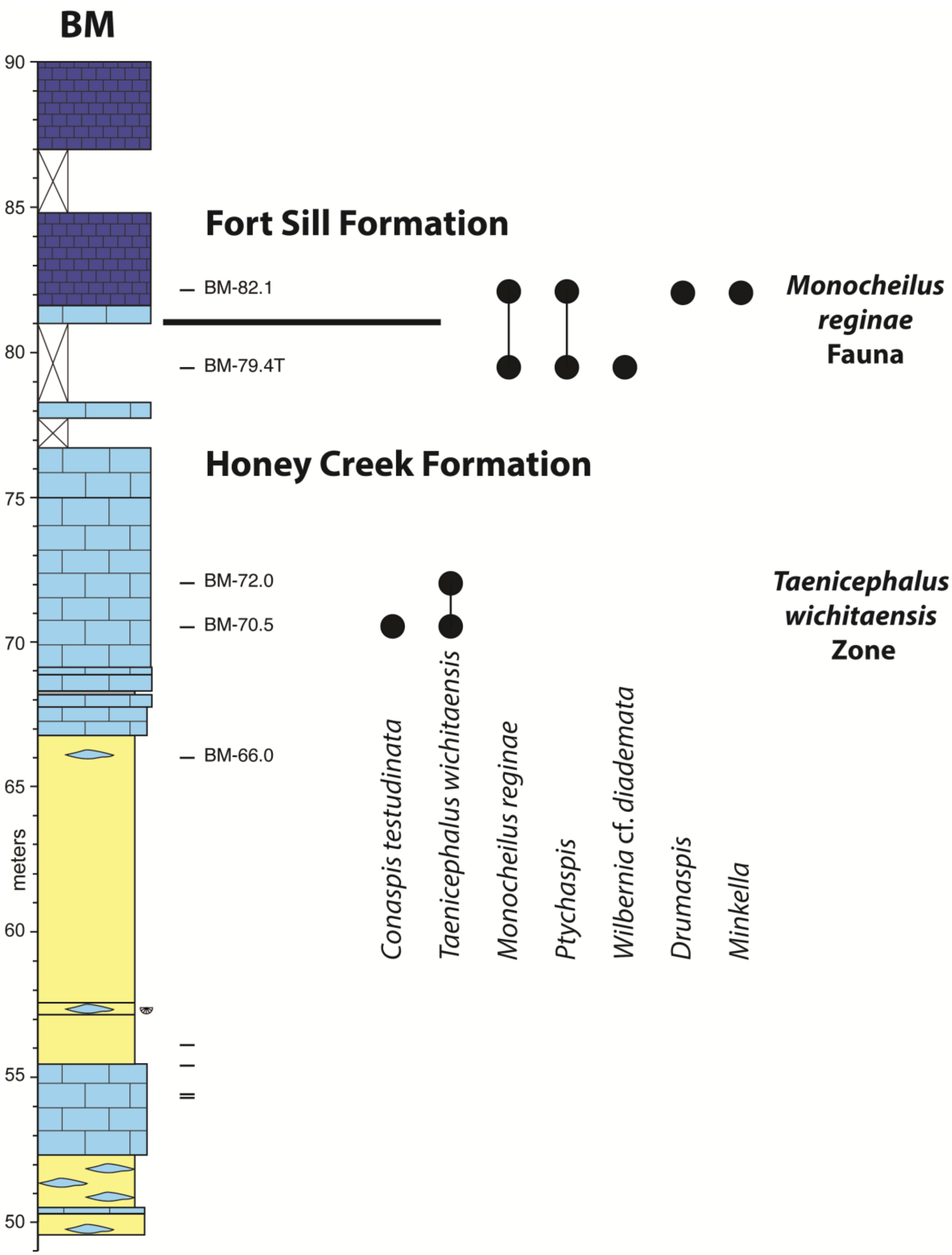

BM
90
85
80
75
70
65
60
55
50
meters
BM-82.1
BM-79.4T
BM-72.0
BM-70.5
BM-66.0
Fort Sill Formation
Honey Creek Formation
Monocheilus reginae Fauna
Taenicephalus wichitaensis Zone
Conaspis testudinata
Taenicephalus wichitaensis
Monocheilus reginae
Ptychaspis
Wilbernia cf. diademata
Drumaspis
Minkella

Figure 6

Correlation of section KR1, KR3 and BM. Black lines show correlation of major lithologic units (based on unpublished work by S.R. Westrop); red dashed lines correlate zones.

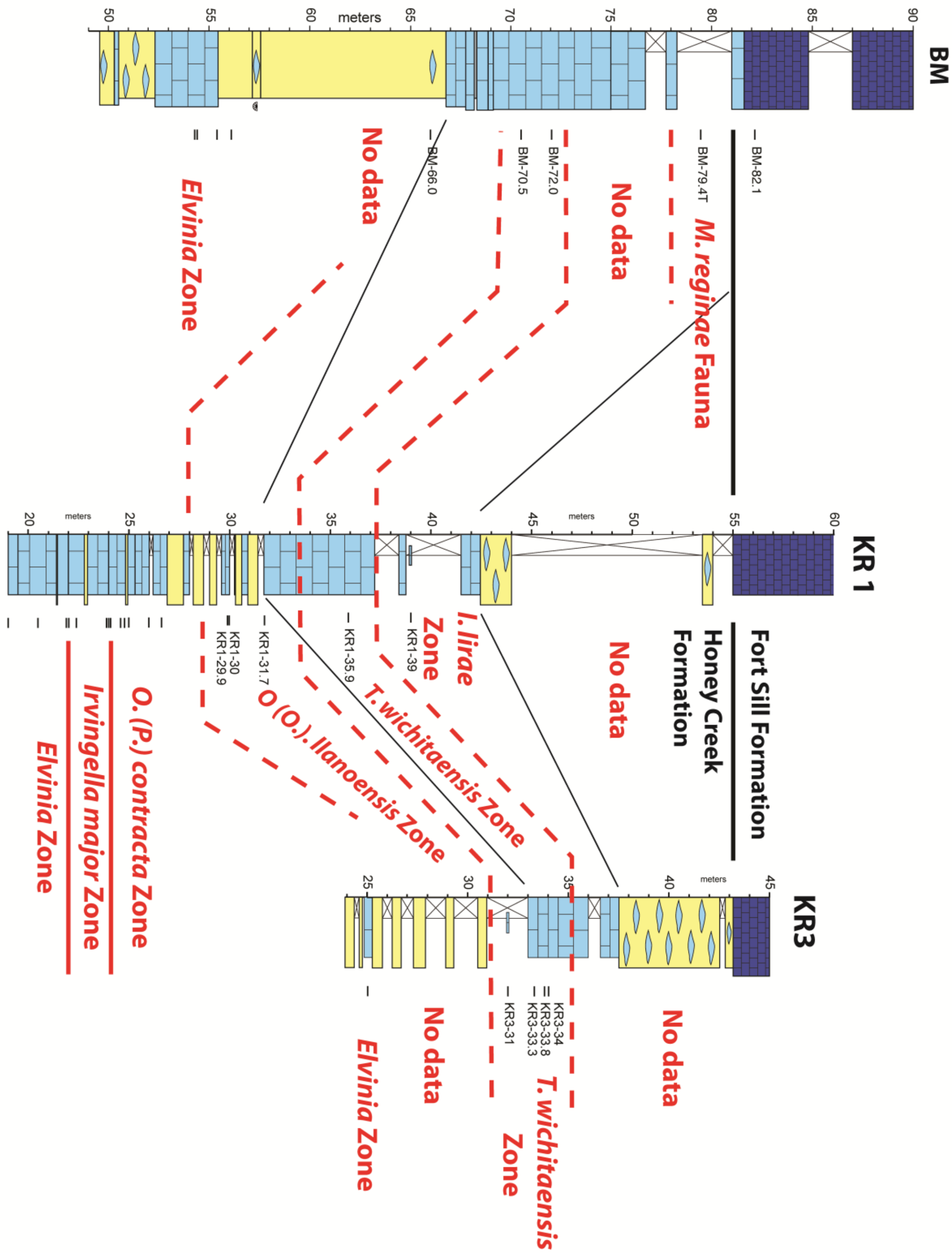
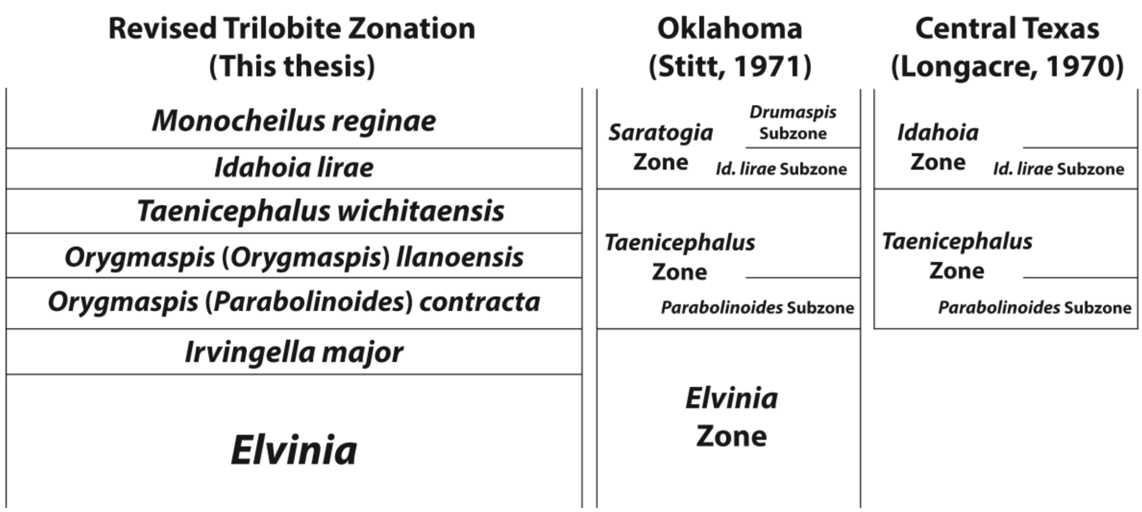

BM
KR 1
KR3
meters
Fort Sill Formation
Honey Creek Formation
BM-82.1
BM-79.4T
BM-72.0
BM-70.5
BM-66.0
M. reginae Fauna
No data
No data
Elvinia Zone
I. lirae Zone
T. wichitaensis Zone
O (O.) llanoensis Zone
O. (P.) contracta Zone
Irvingella major Zone
Elvinia Zone
KR1-39
KR1-35.9
KR1-31.7
KR1-30
KR1-29.9
No data
KR3-34
KR3-33.8
KR3-33.3
KR3-31
No data
T. wichitaensis Zone
No data
Elvinia Zone

Figure 7

Correlation of the trilobite zonation with zonations proposed for Oklahoma (Stitt, 1971b) and Texas (Longacre, 1970).


Revised Trilobite Zonation
(This thesis)
Monocheilus reginae
Idahoia lirae
Taenicephalus wichitaensis
Orygmaspis (Orygmaspis) llanoensis
Orygmaspis (Parabolinoides) contracta
Irvingella major
Elvinia
Oklahoma
(Stitt, 1971)
Saratogia Zone
Drumaspis Subzone
Id. lirae Subzone
Taenicephalus Zone
Parabolinoides Subzone
Elvinia Zone
Central Texas
(Longacre, 1970)
Idahoia Zone
Id. lirae Subzone
Taenicephalus Zone
Parabolinoides Subzone

Chapter II: A new trilobite fauna from the Honey Creek–Fort Sill boundary interval and its biostratigraphic significance.

Introduction

The Cambrian trilobites of Oklahoma have been studied intensively for 70 years (Frederickson 1948, 1949; Stitt, 1971b, 1977), so it is surprising to discover an entirely new fauna in the succession. This fauna is of interest because it includes early representatives of two major clades (Ptychaspididae and Eurekiidae) that radiated in Laurentia during the Sunwaptan Stage. The composition of the fauna, which is dominated by *Monocheilus* Resser, 1937 and also containing *Ptychaspis* Hall, 1863, resembles assemblages that occur in the same homotaxial position in Minnesota and Wisconsin (e.g. Nelson, 1951) and in the southern Canadian Rocky Mountains (Westrop, 1986). As such, these assemblages may mark a distinct biostratigraphic interval in a transition from low diversity faunas in the aftermath of the end-Steptoean extinction to more diverse Sunwaptan faunas (e.g., Westrop and Cuggy, 1999).

The fauna occurs in the boundary interval of the Honey Creek and Fort Sill formations at Bally Mountain (Section BM; Chapter 1, Fig. 5) in Kiowa County, Oklahoma (see Chapter 1 for stratigraphic setting and detailed locality information). *Monocheilus* (considered here to be a senior synonym of *Stigmacephalus* Resser, 1937; see Systematic Paleontology, below) is the earliest representative of Family Eurekiidae, and the occurrence of *Ptychaspis* is likely the oldest record of Family Ptychaspididae. Early representatives of *Ptychaspis* have often been assigned to a single species, *P*. *bullasa* Lochman and Hu, 1959 (e.g. Bell and Ellinwood, 1962; Stitt, 1971, 1977). Restudy of type material shows that there is in fact a plexus of species that are differentiated readily by cranidial and pygidial anatomy (see Systematic Paleontology, below).

Age and Correlation of the Fauna

The fauna occurs in two collections. The lower of these (BM 79.4T) is a float sample from a covered interval 1.6 m below the base of the Fort Sill Formation (Chapter 1, Fig. 5). It includes abundant sclerites of *Monocheilus* (Pl. 1, Pl. 2) and rare specimens of *Ptychaspis* (Pl. 10, Fig. 7) and *Wilbernia* Walcott, 1924 (Pl. 10, figs. 1–3). Collection BM 82.1 was recovered in place, 1.1 m above the base of the Fort Sill. *Monocheilus* and *Pychaspis* are both minor components, with *Drumaspis* Resser, 1942 and *Minkella* Lochman and Hu, 1959 dominating. The latter two genera are under study by S.R. Westrop as part of broader revisionary systematic works and will not be treated in this chapter.

The new species of *Monocheilus* described in this chapter, *M*. *reginae*, is related to *M*. *oweni* (Hall, 1863). This species (under the genus name, *Stigmacephaloides*) is abundant in a collection (B57) from the Bison Creek Formation of Alberta (Westrop, 1986), which, as in Oklahoma, also includes *Ptychaspis* and a species of *Wilbernia*. Westrop (1986, p. 17) placed this collection in his *Stigmacephalus oweni* Fauna, which encompassed a poorly fossiliferous interval whose base was defined broadly by the first occurrences of either the name bearing species, *Idahoia* cf. *lirae* (Frederickson, 1949) or *Taenicephalina* sp. 1. *Idahoia* cf. *lirae* is distinct from Frederickson's types (Pl. 26) from Oklahoma by virtue of, among other characters, a long occipital spine (Westrop, 1986, p. 42). This species does not co-occur with *M*. *oweni* in any of Westrop's (1986) sections: *I*. cf. *lirae* occurs in his section D, whereas *M*. *oweni* is from his sections B and S. As a result, there is some uncertainty about the relative ranges of these two species, although *M. oweni* seems to extend into younger strata (see Westrop, 1986, p. 18 for discussion). In Oklahoma, the *M. reginae* Fauna lies above the *I. lirae* Zone. The evidence suggests that the ranges of *M. reginae* and *M. oweni* likely overlap, and the *M. oweni* Fauna and the *M. reginae* Fauna may be broadly correlative.

In the Minnesota–Wisconsin border region of the St. Croix Valley (Nelson, 1951), *M. oweni* occurs above the *Conaspis* Zone (= *Taenicephalus* Zone; Grant, 1965), confirming that this species is among the older representatives of the genus. Sections farther to the south, along the bluffs of the Mississippi (Grant, 1962), apparently lie above the local range of *M. oweni*, and instead contain *M. anatinus* (Hall, 1863) in association with *Ellipsocephaloides curtus* (Whitfield), and *Idahoia wisconsinesis* (Owen) [e.g., Grant, 1962, text-figs. 3, 6] among others. Both of these species enter the succession in Alberta above the *M. oweni* Fauna (Westrop, 1986).

Systematic Paleontology

Figured specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU) and at the National Museum of Natural History (USNM). All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop ™. To maximize depth of field, all digital images were rendered from stacks of images focused at 100 micron intervals using Helicon Focus 4.0 for the Macintosh <http://www.heliconsoft.com>.

Family EUREKIIDAE Hupé, 1953

Discussion.— Adrain and Westrop (2004, p. 19) raised the possibility that *Monocheilus* Resser, 1937 and *Stigmacephalus* Resser, 1937 were related to younger Sunwaptan genera assigned to Family Eurekiidae. As discussed below, these genera are considered to be synonyms, and *Monocheilus* has page priority in Resser's (1937) publication.

Genus MONOCHEILUS Resser, 1937

Type species.—*Conocephalites anatinus* Hall, 1863 from the Lone Rock Formation, Wisconsin (by original designation).

Diagnosis.—Eurekiidae with transversely subelliptical pygidium bearing one to four pairs of short, flat marginal spines. Short, convex axis comprised of one axial ring and terminal piece composed of at least two segments. Pygidial pleural field is flat. Preglabellar field of cranidium separated from anterior border by weak anterior border furrow in small cranidia that becomes nearly impossible to discern in larger holaspids. Palpebral furrows well incised; palpebral lobes semi-lunate and distinct. Glabella parallel sided to gently tapered anteriorly with very weakly incised glabellar furrows barely perceptible in larger holaspids.

Discussion.— Previous authors (e.g., Grant, 1962; Westrop, 1986) have treated *Monocheilus* and *Stigmacephalus* as distinct genera, although the type species of the latter, *S. oweni* (Hall, 1863), is known only from cranidia. *Monocheilus reginae* n. sp. (Pl. 1, Pl. 2) from the uppermost Honey Creek Formation and basal Fort Sill Formation is clearly related to *S. oweni* and provides information on the librigena and pygidium. It also provides character support for synonymy of *Monocheilus* and *Stigmacephalus*. Sclerites of *M. reginae* show that the pygidium attributed to *S. oweni* by Nelson (1951, pl. 109, fig. 9) is almost certainly misassigned, and use of pygidial characters to separate *Monocheilus* and *Stigmacephalus* (e.g., Westrop, 1986, p. 87) can no longer be justified. Pygidia of *M. reginae* (Pl. 2, figs. 1–4) are similar to those of *M. anatinus* (Hall, 1863; Westrop, 1986, pl. 14, fig. 3) and *M. micros* (Walter, 1924; Westrop, 1986, pl. 15, fig. 4). In particular, they share triangular spines on the posterior corners, a single pair of broad, shallow pleural furrows on a relatively flat pleural field, and short axes with one well defined axial ring, and a second ring that is partly fused with the terminal piece; they differ only on overall outline, with *M. reginae* being relatively shorter and wider. Librigenae of *M. micros* (e.g., Westrop, 1986, pl. 15, fig. 9) and *M. reginae* (Pl. 2, figs. 12, 13) are very similar, with long genal spines, and are separable only on the basis of sculpture: like the rest of the cephalon, the former has a smooth external surface, whereas the latter is pitted. Aside from sculpture, cranida of these two species are differentiated primarily on the position of the palpebral lobe. *Monocheilus reginae* resembles *S. oweni* (e.g., Westrop, 1986, pl. 15, figs. 11, 13) in possessing a palpebral lobe that is separated from the glabella both anteriorly and posteriorly by a distinct, continuous band of fixigena (Pl. 1, figs. 1–12, Pl. 2, figs. 5–7). In contrast, larger cranidia of *M. micros* (e.g., Westrop, 1986, pl. 15, fig. 1) have palpebral lobes that are located closer to the glabella, so that the palpebral furrows and axial furrows merge anteriorly, and only the posterior tip of the lobe is separated by a narrow strip of fixigena; similar palpebral lobe positions characterize *M. anatinus* (e.g., Westrop, 1986, pl. 14, fig. 1), *M. truncatus* Bell and Ellinwood (e.g., Westrop, 1986, pl. 14, figs. 3–5) and *M. orestes* Westrop (1986, pl. 15, figs. 14–17). However, small cranidia of *M. micros* clearly have palpebral lobes that are farther from the glabella (Westrop, 1986, pl. 15, fig.

7), resembling the condition in *M. reginae*, and the palpebral lobe shifts towards the glabella during holaspid ontogeny. The polarity of ontogenetic change indicates that a palpebral lobe and, therefore, eye that are located close to the glabella is the apomorphic condition. This is also supported by potential outgroups like *Minkella* (e.g., Westrop, 1986, pl. 14, figs. 7–16), in which the palpebral lobe is separated from the glabella by a broad, continuous band of fixigena. *Stigmacephalus* appears to rest only on the retention of this plesiomorphic character state, and recognition of *Monocheilus* on the basis of a palpebral lobe that abuts the glabella likely makes *Stigmacephalus* paraphyletic; the latter is therefore treated as a junior synonym of the former. As revised here, *Monocheilus* includes, at minimum, *M. anatinus*, *M. oweni*, *M. oweni* var. A of Nelson, 1951 (which represents a distinct species; see Westrop, 1986, p. 89), *M. micros*, *M. truncatus*, *M. orestes*, and *M. reginae*. Pygidial characters, including the flat pleural field, and short axis, are potential apomorphic characters supporting monophyly.

MONOCHEILUS REGINAE n. sp.

Plate 1, figs. 1–12; Plate 2, figs. 1–6

Diagnosis.— *Monocheilus* with large palpebral lobe about 22% of glabellar length; both anterior and posterior ends separated from glabella by narrow strips of fixigenae. Faint anterior border furrow curved backward; anterior border roughly triangular in outline. Cephalon with pitted sculpture augmented by caecal network that is best expressed on smaller specimens (e.g., Pl. 2, figs. 5–7). Pygidium short and wide, with single pair of short, flat, triangular marginal spines.

Description.— Cranidium exclusive of posterolateral projection subrectangular outline with gently rounded anterior margin; width across palpebral lobes equal to about 92% of length. Axial and preglabellar furrows finely etched grooves. Glabella large, accounting for about 81% of cranidial length, about 60% of cranidial width, and gently convex. Anterior margin rounded and lateral margins nearly straight. Occipital furrow (SO) shallow, curved gently backward, terminating short of axial furrow. Occipital lobe (LO) occupies about 14% of glabellar length. Short anterior border expressed on some specimens; border furrow faint and curved backward. Palpebral lobe forms nearly flat, arcuate band centered in front of glabellar mid-length, with length equal to about 22% of glabellar length; palpebral furrow lightly impressed curved groove. Narrow palpebral area accounts for about 15% of cranidium width. Anterior branches of facial sutures nearly parallel before curving inward along anterior cranidial margin; posterior branches diverge backward in faintly sigmoid curve. Posterior border convex, expands abaxially, with maximum length (exsag.) equal to about 10% of glabellar length; posterior border furrow is clearly defined groove directed obliquely forward from axial furrow. Sculpture of irregular pits on external surface except for furrows and palpebral lobes; overprinted with weak caecal network on frontal area.

Libragena with long genal spine. Librigenal field well inflated; carries same pitted sculpture as the cranidium, which also extends to the anterior sections of the librigenal border. Librigenal border furrow weakly impressed; border gently convex. Faint terrace ridges on posterior librigenal border and genal spine.

Pygidium short, length equal to about 46% of maximum width and with short, triangular spines at posterior corners. Axis short, occupying about 60% of pygidial length, convex, tapered posteriorly; extended into weak post-axial ridge that terminates short of posterior margin. One distinct, short axial ring occupies about one third of axis length and separated from longer terminal piece composed of at least two segments by shallow, transverse ring furrow; articulating half-ring short. Pleural field nearly flat and unfurrowed aside from single pair of wide, shallow pleural furrows that curve sharply backward.

Ontogeny.— Small cranidia (e.g., Pl. 2, figs. 5–7) have a roughly triangular anterior border and backwardly curved border furrow. The border furrow is lost in larger specimens, and the border becomes identifiable only by a change in surface sculpture from caecal markings to a generally pitted sculpture. (Pl 1, figs. 1-3). The frontal area in smaller specimens (Pl. 2 figs. 5-7) is more prominently sculpted in an anastomosing pattern of caecal ridges, which fades in larger specimens (Pl. 1 figs. 1-3). The palpebral lobe becomes shorter, with length dropping from about 35% of glabellar length to 23%. Glabellar furrows also exhibit ontogenetic variation. Smaller specimens have an SO that is transverse medially, whereas the SO of larger specimens weakly curved backward. Faint S1-S3 furrows are evident on smaller specimens (Pl. 2, figs. 5, 6) and relatively fainter in the larger ones (Pl. 2, figs. 8–9).

Etymology.— Named for Regina Blackwell, the author's mother

Holotype.— A cranidium (Plate 1, figs. 4-6; OU 238158) from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Paratypes.— Five cranidia (OU 238157, OU 238159, OU 238160, OU 238163, OU 238164), one librigena (OU 238166), one incomplete thoracic segment OU 238165), and two pygidia (OU

238162, OU 238163), all from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Occurrence.—Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collections BM 79.4T and BM 82.1, *Monocheilus reginae* Fauna

Discussion.— *Monocheilus reginae* is similar to sclerites from the Bison Creek Formation, southern Alberta, that were assigned to *M*. *micros* (Walter, 1924) by Westrop (1986, pl. 15, figs. 1–9). As noted earlier, free cheeks can be distinguished only on the basis of sculpture (smooth in *M*. *micros*; pits on *M*. *reginae*; a difference that extends to the cranidia), and pygidia differ in outline. The position of the palpebral lobe is also diagnostic, and is much closer to axial furrow in *M*. *micros*, particularly at the anterior tip of the lobe (compare Pl. 1 with Westrop, 1986, pl. 15, figs. 1–2) a consequence of this position in *M*. *micros* is a relatively narrower (tr.) frontal area that is also longer than in *M*. *reginae*. *Monocheilus anatinus* (Hall, 1863; e.g., Westrop, 196, pl. 14, fig. 1), *M*. *truncatus* Ellinwood, in Bell and Ellinwood, 1962 (e.g., Westrop, pl. 14, figs. 3, 4) and *M*. *orestes* Westrop (1986, pl. 15, figs. 14–17) also differ from *M*. *reginae* in having larger palpebral lobes that are much closer to the glabella.

The pitted sculpture is a diagnostic feature of *M*. *reginae*. The cranidia are similar to the types and other specimens of *M. oweni* (Hall, 1863) from the Upper Mississippi Valley region (e.g., Nelson, 1951, pl. 109, figs. 1, 2). Unfortunately, all of the specimens from the Upper Mississippi Valley are preserved as sandstone internal molds, and the nature of the sculpture cannot be determined. It is impossible to compare M. oweni completely with other species that preserve the skeleton. For this reason, I recommend that the name *M. oweni* should thus be restricted to the types, and internal molds from other collections in the Upper Mississippi Valley should be placed in open nomenclature (*M.* cf. *oweni*).

Family PTYCHASPIDIDAE RAYMOND, 1924

Genus PTYCHASPIS Hall, 1863

Type species.— Dikelocephalus miniscaensis Owen, 1852 from the Lone Rock Formation, Minnesota (subsequent designation by Miller, 1889; see Bell et. al., 1952)

PTYCHASPIS BULLASA Lochman and Hu, 1959

Plates 3–6

1959 *Ptychaspis bullasa* Lochman and Hu, p. 422, pl. 58, figs. 21-42.

non 1962 *Ptychaspis bullasa*; Bell and Ellinwood, p. 405, pl. 58, figs. 14–17.

non 1970 *Ptychaspis bullasa*; Longacre, p. 44, pl. 2, figs. 4, 5.

1970 *Ptychaspis bullasa* Lochman and Hu, Hu, p. 97, pl. 17, figs. 1-34; text fig. 46.

non 1977 *Ptychaspis bullasa* Lochman and Hu, Stitt, p. 43, pl. 2, fig. 4

non 1986 *Ptychaspis bullasa*? Westrop, pl. 8, figs. 9-12

non 1997 *Pychaspis bullasa* Lochman and Hu, Stitt and Straatmann, p. 90, fig. 7.16.

Diagnosis.— *Ptychaspis* with palpebral lobes short and narrow, with midpoint situated roughly opposite S2 glabellar furrow. Anterior cranidial margin gently curved so that frontal area maintains nearly even width (sag, exsag.). Cranidial sculpture of tubercles extends forward to point just in front of anterior tip of palpebral lobe and in smaller cranidia extends back to posterior border furrow (e.g., Pl. 4, figs. 4, 10); tubercles are lost on posterior fixigenae on larger specimens (e.g., Pl. 3, fig. 6, Pl. 4, fig, 1). Frontal area lacks tubercles and has up to two striate ridges running parallel to anterior cranidial margin. Pygidial pleural and interpleural furrows extend nearly transversely from axis before curving backward shallowly near pygidial margin.

Holotype.— A cranidium (USNM 137099) from the St. Charles Formation, Idaho (Pl. 3, figs. 1–3).

Occurrence.— St. Charles Formation, ridge north of Mink Creek, near Preston, southern Idaho (Lochman and Hu, 1959).

Description.— Cranidium wider than long. Glabella long and broad with glabellar furrows S0 through S2 well impressed and connected across glabella. Glabellar lobes L0 and L1 similar in length (sag.), nearly transverse medially, but curved forward near axial furrows. L3 occupies about a third of glabellar length and sub-spheroidal in outline. Frontal area short and lacks border furrow. Anterior cranidial margin gently curved so that frontal area maintains nearly even width (sag., exsag.). Palpebral lobes short, narrow, and co-latitudinal with S2; palpebral furrow firmly impressed. Palpebral area of fixigenae very gently inflated. Posterior branches of facial suture strongly divergent; anterior branches nearly parallel in front of palpebral lobe before swinging inward along anterior cranidial margin. Posterior border furrow well incised; posterior border strongly convex. Cranidial sculpture of tubercles extends forward to point just in front of anterior tip of palpebral lobe and in smaller cranidia extends back to posterior border furrow (e.g., Pl. 4, figs. 4, 10); tubercles are lost on posterior fixigenae on larger specimens (e.g., Pl. 3, fig. 6, Pl. 4, fig, 1). Frontal area lacks tubercles and has up to two striate ridges running parallel to anterior cranidial margin.

Librigena with stout genal spine. Lateral border furrow well defined and merges posteriorly with posterior border. Lateral border narrow and descends steeply at cephalic margin. Librigenal field strongly inflated. Borders, spine and abaxial parts of librigenal field carry coarse striate ridges; adaxially, librigenal field with tubercles.

Pygidium semi-elliptical in outline, wider than long. Axis convex, extending almost entire pygidial length and narrow, occupying less than a third of pygidial width; composed of 3 axial rings and terminal piece. Axial ring furrows transverse; posteriormost shallower than others. Articulating half ring short. Deep pleural and shallower interpleural furrows extend nearly transversely from axis before curving backward near pygidial margin; anterior pleural bands longer than posterior bands. Pygidial border narrow, rising vertically from weakly convex pleural field.

Discussion.— Restudy of the type material of *Ptychaspis bullasa* Lochman and Hu (1959; Pl. 3–6) show that this species is characterized by an anteriorly positioned palpebral lobe that is centered opposite the S2 glabellar furrow, and pygidial pleural and interpleural furrows that are nearly transverse over most of their length. This allows several records of *P. bullasa* from outside the type area in southern Idaho to be evaluated critically.

As noted by Longacre (1970, p. 44), cranidia that both she and Bell and Ellinwood (1962) identified as *P. bullasa* from Texas (Pl. 9) have palpebral lobes that are larger and more posteriorly located than those of the types (e.g., Pl. 3). There are other differences in the cranidia from Texas, including a longer frontal area with a more rounded anterior cranidial margin, more densely packed tuberculate sculpture, and striate ridges that are more closely spaced on the anterior border (Pl. 9). The Texas material is assigned to a new species, *P*. *occulta*.

The cranidium attributed to *P*. *bullasa* by Stitt (1977, pl. 2, fig. 4) from Oklahoma has been damaged since it was photographed and can no longer be evaluated fully. However, sclerites from the same stratigraphic interval in the lower Fort Sill Formation represent a distinct species characterized by curved pleural and interpleural furrows on the pygidium, among other characters (see following discussion of *P*. *richardi* n. sp.). The record of *P*. *bullasa* from the Deadwood Formation of South Dakota (Stitt and Straatmann (1997, fig. 7.16) is supported by a single illustrated librigenae, and is difficult to evaluate. This specimen has far greater development of striate ridges, and a smaller area of tuberculate sculpture than either librigena in the type lot of *P*. *bullasa* (Pl. 5, figs. 4, 5; Pl. 6, fig. 4), and the identification cannot be corroborated. Finally, Westrop (1986, pl. 8, figs. 9–12) assigned sclerites from the Bison Creek Formation in the southern Canadian Rockies questionably to *P*. *bullasa*, noting that the cranidial sculpture of highly irregular tubercles of the Canadian material contrasted with the more conventional, subcircular tubercles of the latter. Restudy of the types confirms this difference, and the sclerites from the Bison Creek Formation likely record and undescribed species.

Rather than a single, widespread species, detailed comparisons of putative occurrences of *P*. *bullasa* indicate that there is in fact a geographically structured plexus of related species. Westrop et al. (2018) have recently documented a similar pattern in the Middle Cambrian trilobite *Eodiscus*, noting that such groups of "pseudocryptic" species are comparable to groups of modern species that are now recognized routinely in studies that integrate morphometric and genomic data.

PTYCHASPIS RICHARDI n. sp.

Plates 7–8

Diagnosis.— Ptychaspsis with predominately tuberculate cephalic sculpture yielding to sparse striate ridge sculpture along crandial and librigenal margins. In front of transglabellar S2 furrow, glabella subcircular in outline, divided by faint S3 and S4 lateral furrows (most clearly visible in lateral view; Pl. 7, fig. 2,). Palpebral lobe small and roughly co-latitudinal with S2. Bacula present on fixigena opposite L1. Pygidium possesses gently inflated pleural field and axis composed of three axial rings and terminal piece. Pygidial pleural and interpleural furrows deflected obliquely backward at angle of about 45° from transverse plane. Pygidial border forms distinct narrow upturned rim that thickens toward axis.

Holotype.— A cranidium (OU 4268; Pl. 7, figs. 1–3) from the Fort Sill Formation, about 4.4 km south-east of Hennepin (SE Sec. 4, T1S, R1W), Murray County Oklahoma, 60 feet above the base of zone 1a (Matuszak 1957).

Derivation of name.— Named for Richard Blackwell, the name of the author's father and grandfather.

Paratypes.— A cranidium (OU 238168; Pl. 8, Figs. 1-3), two incomplete free cheeks (OU 238167, OU 4269: Plts. 7,8, Figs. 4, 4-5), and two pygidia (OU 4270, OU 238169: Plts. 7,8, Figs. 5, 6-7).

Occurrence.— Fort Sill Formation, Oklahoma, 4.4 km south-east of Hennepin (SE Sec. 4, T1S, R1W), Murray County Oklahoma, 60 feet above the base of zone 1a).

Description.—Cranidium sub-rounded and semi-ovoid in outline. Short posterior lateral projections. Anterior border furrow absent. Frontal area is short, accounting for about 10% of cranidial length, and slopes almost vertically forward. Axial and preglabellar furrows firmly impressed grooves. Glabella well rounded and inflated, comprising about 89% of cranidial length and about 49% of cranidial width. SO firmly impressed and of even incision across glabella; curved gently backwards. LO occupies about 12% of glabellar length and curved forward abaxially; carries small median node on internal mold. S1 and S2 glabellar furrows connected across glabella. S1 nearly transverse medially but curves forward and deepens abaxially. L1 also curved forward and occupies about 10% of medial glabellar length. S2 shorter (sag.; exsag) shallower than S1, maintaining nearly even depth; less strongly curved. L2 accounts for about 17% of glabellar length medially, but narrows slightly abaxially. S3 and S4 lateral furrows gently impressed, defined in part by absence of sculpture, and nearly transverse. L3 and L4 similar in length (exsag.) to L2.

Palpebral lobes short and narrow. Situated along the length of the cranidium roughly perpendicular with S2. Palpebral area of fixigena semi-elliptical. Width equal to about 30% of length. Surface sculpture uniformly tuberculate throughout glabella, palpebral area, post-palpebral area, and posterior later borders; terminates just shy of posterior border furrow. Anterior branches of facial suture converge forward in even curve. Posterior branches diverge gradually backward along a nearly straight path. Posterior border furrow deeply incised and broad with a narrow rim-like border.

Free cheek with long, stout genal spine. Inflated librigenal field occupies 68% of width opposite eye. Lateral border furrow well incised anteriorly, but shallows near genal spine; lateral border furrow narrow in dorsal view; descends nearly vertically from border furrow. Librigenal field with conspicuous tubercles that are lost distally, near border furrow. Border with elongate, widely spaced striate ridges running parallel to lateral cranidial margin. .

Pygidium subelliptical in outline, width greater than length; gently arched in posterior view. Axis narrow, convex, occupies 67% of pygidial length. Three axial rings and terminal piece of at least two segments separated by well defined, transverse ring furrows; shallower furrow present on terminal piece. Articulating half-ring short; articulating furrow nearly transverse. Pleural field crossed by at least four pairs of broad (exsag.), oblique pleural furrows that separate subequal, convex anterior and posterior pleural bands; interpleural furrows narrower but well-defined grooves. Lateral and posterior borders form short (sag.; exsag), weakly upturned rim. External surface smooth; internal molds with pits; closely spaced on pleural field and border but widely spaced on crest of axis.

Discussion.-- Cranidia of *Ptychaspis richardi* are similar to those of *Ptychaspis bullasa*, Lochman and Hu, 1959 (Plates 3-6). Both have tuberculate sculpture but there are fewer, more widely spaced tubercles in P. bullasa (compare *P. richardi* [Pl. 7-8] with *P. bullasa* [Pl. 3-6]), which also has well defined striate ridges on the frontal area. Both species have relatively small, anteriorly-placed palpebral lobes that are centered near S2, and the overall proportions of the glabellar lobes are comparable. *Ptychaspis richardi* differs in having a well-defined bacula next to L1. In addition, cranidia of *P. bullasa* possess less rapidly diverging posterior suture branches, resulting in narrower (tr.) posterolateral projections. Pygidia share a raised, rim-like border, with those of *P*. *richardi* (Pl. 7, fig. 5) differing from *P*. *bullasa* (Pl. 5, figs. 6–8) most clearly in having shorter axes and pleural and interpleural that are deflected strongly backward rather than being nearly transverse.

Cranidia of *P*. *striata* (Whitfield, 1878) and *P*. cf. *miniscaensis* (Owen, 1852) from the Bison Creek Formation of Alberta (e.g., Westrop, 1986, pl. 8, figs. 1–3, 6, and pl. 7, figs. 1–4, respectively) are differentiated easily from *P*. *richardi* in having prosopon of coarse striate ridges that is expressed on both the external surface and the internal mold; tubercles are absent. Additionally, the glabella of *P* cf. *miniscaensis* in front of S2 is tapered and subtrapezoidal, whereas the equivalent part of *P*. *richardi* is more rounded and subcircular in outline. S2 lateral furrows are connected across the glabella by a firmly impressed furrow in the latter species, whereas S2 furrows are barely connected in *P*. cf. *miniscaensis*. The raised, rim-like pygidial borders of both *P*. *richardi* and *P*. cf. *miniscaensis* (e.g., Westrop, 1986, pl. 7, figs. 6, 11, 14) set them apart from *P*. *striata*, which has a flat pygidial border. *Ptychaspis* cf. *miniscaensis* has four axial rings in front of the terminal piece, whereas *P. richardi* has only three.

Ptychaspis miniscaensis is known only from sandstone internal molds from Lone Rock of Minnesota and Wisconsin (e.g., Westrop, 1986, pl. 8, fig. 15; Bell et al., 1952, pl. 36, fig. 1a) that are smooth or at best very weakly ridged even when well preserved. *Ptychaspis tuberosa* (e.g., Westrop, 1986, pl. 8, fig. 14) also has a smooth internal mold.

Ptychaspis granulosa is known only from poorly preserved sandstone internal molds from the Upper Mississippi Valley. Superficially it is quite similar to *P. richardi* and *P. bullasa* in terms of tuberculate sculpture of the cranidium. However the pygidial border in *P*. *granulosa* is broad and flat whereas the border of *P. richardi* is narrow and forms an upturned rim.

PTYCHASPIS OCCULTA n. sp.

Plate 9

1962 *Ptychaspis bullasa* Lochman and Hu; Bell and Ellinwood, p. 405, pl. 58, figs. 14–17.

1970 *Ptychaspis bullasa*; Longacre, p. 44, pl. 2, figs. 4, 5.

Diagnosis.— A species of *Ptychaspis* with relatively densely packed tuberculate cephalic prosopon yielding anteriorly to robust striate ridge prosopon toward the anterior margin. Rounded glabella with sub-spheroid L4 and well incised glabellar furrows. S3 faintly impressed and not transverse. Palpebral lobes short and narrow with robust palpebral border and situated more posteriorly in comparison with the other species of *Ptychaspis* discussed here, roughly co-latitudinal with L2.

Holotype..— A cranidium (U.S.N.M. 185472; Pl. 9, figs. 6-8) from the Morgan Creek Member, Wilberns Formation, Little Llano River section, collection LL 725, San Saba County (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 16).

Paratypes.— Two cranidia (U.S.N.M. 185437, 185470; Pl. 9, figs. 1–5) from the Morgan Creek Member, Wilberns Formation, central Texas.

Derivation of name. —The species takes its name from the Latin past participle meaning “having been hidden” in reference to the species lurking unrecognized within the literature for many decades.

Occurrence.— Morgan Creek Member, Wilberns Formation, central Texas, (see Longacre, 1970, p. 44 for a detailed list of collection numbers and localities).

Discussion.— *Ptychaspis occulta* is sufficiently similar to *P. richardi* that a full description is unnecessary; a comparison of these species is presented instead. These species are superficially similar yet differ in detail. *Ptychaspis occulta* exhibits more robust sculpture than *P. richardi* in both the size and packing density of tubercules, as well as the striate ridge sculpture on the frontal area. *Ptychaspis occulta* also lacks a bacula, and the anterior branches of the facial suture are more rapidly convergent, so that the frontal area is subtriangular in anterior view (e.g., Pl. 9, fig. 6).

As is the case for *P*. *richardi*, *P*. *occulta* clearly differs from *P*. *miniscaensis*, *P*. cf. *miniscaensis*, *P*. *striata* and *P*. *tuberosa* in the type of cranidial sculpture. All four of these species lack tubercles; external surfaces and internal molds of *P*. *striata* and *P*. cf. *miniscaensis* have coarse striate ridges over the frontal area, glabella and fixed cheeks, whereas internal molds of both *P*. *minscaensis* and *P*. *tuberosa* are mostly smooth.

Genus WILBERNIA Walcott, 1924

Type species.—*Ptychoparia pero* (Walcott, 1890) from the Wilberns Formation of central Texas (by original designation).

WILBERNIA cf. DIADEMATA (Hall, 1863)

Plate 10, figs. 1–3

cf. 1863 *Conocephalites diadematus* Hall, p. 167, pl. 7, fig. 36, pl. 8, fig. 21 (only)

cf. 1962 *Wilbernia diademata* (Hall), Bell and Ellinwood, p. 365, pl. 34, figs. 9-10 (synonymy to date)

cf. 1970 *Wilbernia diademata* (Hall), Longacre, p. 32 (synonymy to date)

cf. 1971b *Wilbernia diademata* (Hall), Stitt, p. 33, pl. 3, fig. 2

cf. 1986 *Wilbernia diademata* (Hall), Westrop, p. 44, pl. 13, figs. 13-14

Holotype.—A cranidium from the Lone Rock Formation, Minnesota, illustrated by Nelson (1951, pl. 109, fig. 11).

Material and occurrence.— A cranidium from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T, *Monocheilus reginae* Fauna.

Discussion.—A single, nearly complete cranidium possesses large palpebral lobes that are equal to about 36% of glabellar length with firmly impressed palpebral furrows. The frontal area consists of a weakly inflated preglabellar field that is slightly shorter than the weakly convex anterior border. It is most like *W. diademata* (Hall, 1863; e.g., Nelson, 1951, pl. 109, figs. 8, 11), but has a shorter border and, consequently, a somewhat shorter frontal area. Cranidia identified as *W. diademata* by Bell and Ellinwood (1962, pl. 54, fig. 9) have shorter palpebral lobes than *W.* cf. *diademata*. Small cranidia attributed to the poorly known *W. halli* Resser, 1937 by both Bell et al. (1952, pl. 32, fig. 5a) and Bell and Ellinwood (1962, fig. 14) approach *W.* cf. *diademata* in frontal area morphology but also have relatively short palpebral lobes. *Wilbernia explanata* (Whitfield, 1880; Bell et al., 1952, pl. 34, figs, 4b–d; Westrop, 1986, pl. 13, figs. 1, 3) has a longer frontal area, whereas *W. pero* (Walcott, 1890) possesses a preglabellar field that is very short (e.g., Bell and Ellinwood, 1962, pl. 54, fig. 19).

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Chapter III: The trilobite genus *Taenicephalus* Ulrich and Resser from the Honey Creek Formation, Oklahoma and correlative strata in central Texas

Introduction

As noted in Chapter 1, the most widely used trilobite zonation of the Laurentian Sunwaptan Stage (Jianshanian–"Stage 10" of the global nomenclature) developed over a roughly 30-year period, with Grant (1965), Winston and Nicholls (1967), Longacre (1970) and Stitt (1971) making significant contributions. Above the thin, basal *Irvingella major* Zone (proposed by Chatterton and Ludvigsen, 1998), the *Taenicephalus* Zone has been identified in Montana–Wyoming (Grant, 1965), Texas (Longacre, 1970), Oklahoma (Stitt, 1971, 1977), the southern Canadian Rockies (Westrop, 1986), and South Dakota (Stitt and Straatmann, 1997). Although the associated species vary, *T. shumardi* (Hall, 1863), the type species of the genus, has been identified in all of these regions. And yet, the type material of *T. shumardi* (Westrop, 1986, pl. 21, figs. 5, 6) and other sclerites from the type area in the Upper Mississippi Valley (e.g., Berg, 1953, pl. 59, figs. 11–13) are preserved as sandstone internal molds that provide no information on the sculpture of the external surface. This was recognized by Bell and Ellinwood (1962, p. 402), who followed what was at the time unpublished work by Grant (1965) that used ratios of cranidial dimensions to define species of *Taenicephalus*. This approach has influenced much of the subsequent research on Sunwaptan biostratigraphy (e.g., Longacre, 1970; Stitt, 1971). However, sclerites of *Taenicephalus* from new collections from Oklahoma (Pl. 13–16, 23) and restudy of Bell and Ellinwood's figured specimens from Texas (Pl. 16, 17, 20–22), indicate that there are in fact sculptural differences between species, and this information should not be ignored. As discussed below, *T. shumardi* cannot be identified with confidence, and the name should be restricted to the types.

Putative occurrences of *T. shumardi* in the literature need to be reevaluated. This chapter begins this task by revising *Taenicephalus* from Oklahoma and Texas using type material and new collections. *Taenicephalus gouldi* (Frederickson, 1949) is also restudied from the types and archival collections made by J.H. Stitt (1971) that are now housed at the Oklahoma Museum of Natural History.

Systematic Paleontology

Figured specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU) and at the National Museum of Natural History (USNM). All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop ™. Proportions expressed in percentages in descriptions and diagnoses are means. To maximize depth of field, all digital images were rendered from stacks of images focused at 100-micron intervals using Helicon Focus 4.0 for the Macintosh <http://www.heliconsoft.com>.

Family PARABOLINOIDIDAE Lochman, 1956

Genus TAENICEPHALUS Ulrich and Resser in Walcott, 1924

Type species.—Conocephalites shumardi Hall, 1863 from the Lone Rock Formation, Wisconsin (by original designation)

Diagnosis.— Parabolinoididae with trapezoidally shaped glabella that narrows anteriorly, a triangular and convex anterior border, and well-incised furrows throughout, except for the palpebral furrow, which is poorly defined. Palpebral lobes generally located near glabellar mid-length, roughly co-latitudinal with S2. Frontal area roughly one-fourth to one-third length of cranidium. Pygidium sub-elliptical and convex. Strongly defined pleural and interpleural furrows (modified from Westrop, 1986).

Discussion.— Revision of species from Oklahoma and Texas shows that surface sculpture is an important diagnostic criterion, particularly in smaller holaspids. External surfaces of cranidia of various species may have networks of fine anastomosing ridges that produce irregularly pitted surfaces (e.g., *Taenicephalus wichitaensis*, Pl. 13), larger, elongate tubercles (e.g., *T. gouldi*, Pl. 20, figs. 4–6; *T. kallisti*, Pl. 23) or rounded tubercles (e.g., *T. granulosus* Resser, 1942, pl. 20, figs. 4–7). These characters cannot be determined in specimens preserved in sandstone internal molds that represent the normal condition of sclerites from inner shelf siliciclastic facies of the Upper Mississippi Valley region. I recommend that species that are based on type material from this region, including *T. shumardi* (Hall, 1863) and *T. altus* Nelson, 1951.

TAENICEPHALUS WITCHITAENSIS Resser, 1942

Plates 11–17

1942 *Taenicephalus wichitaensis* Resser p. 105, pl. 21, figs., 13-17

1949 *Taenicephalus wichitaensis* Frederickson p. 362, pl. 72, figs., 1-2

1962 *Taenicephalus shumardi*, Bell and Ellinwood p. 402, pl. 57, figs., 10-21

1970 *Taenicephalus shumardi*, Longacre p. 31,

1971 *Taenicephalus shumardi*, Stitt p. 32, pl. 2, fig., 17

Diagnosis.— *Taenicephalus* with well inflated preglabellar field and three pairs of well incised, posteriorly angled glabellar furrows. Glabella subtrapezoidal with fossulae at anterior. Anterior border long, roughly 112% the length of the preglabellar field. Anterior border, preglabellar field, and posterior lateral projections bear sculpture of fine anastomosing ridges, although it becomes muted in the largest specimens. Associated pygidia are transversely subelliptical with axis composed of two axial rings, and terminal piece.

Holotype — A cranidium (USNM No. 108837a) from the Honey Creek limestone; (loc. 9q) Blue Creek Canyon, 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

Paratypes.— USNM Nos. 108837b-d

Occurrence.— Honey Creek limestone, Wichita Mountains area Oklahoma, collections BM-70.5, -72.0, KR1-35.9; KR3-31, -33.3, -33.8, -34. *Taenicephalus wichitaensis* Zone.

Description.— Cranidium subtrapezoidal in outline. Long posterior lateral projections accounting for 29% of cranidial width. Anterior border furrow well-incised. Frontal area accounts for about 24% of cranidial length with well inflated preglabellar field. Glabella subtrapezoidal in outline with conspicuous anterior tapering, comprising about 69% of cranidial length and about 61% of cranidial width. SO relatively narrow (sag., exsag.) but firmly and evenly impressed; transverse medially but curving gently forwards at margins. LO curves forward abaxially. Oblique S1 well impressed compared with subsequent glabellar furrows. S2 and S3 also oblique, becoming progressively shorter than S1. Palpebral lobes comprise 18% of cranidial length. Anterior tip of palpebral lobe roughly co-latitudinal with anterior end of S3 and posterior terminus roughly co-latitudinal with anterior end of of S1. Palpebral area of fixigena semi-elliptical, with width equal to about 9% of total cranidial width. Posterior border furrow well incised. Posterior border convex, broadening abaxially. Facial suture anterior of palpebral lobe nearly parallel to outwardly bowed. Posterior branches diverge in a weakly sigmoid shape. Surface sculpture of cranidium uniformly composed of fine anastomosing ridges.

Pygidium subelliptical in outline, width greater than length; gently arched in posterior view. Axis narrow, convex, accounting for 83% of pygidial length and 35% of pygidial width. Two axial rings and terminal piece of two segments separated by well defined, transverse ring furrows; shallower furrow present on terminal piece. Long articulating half ring occupies18% of pygidial axis; transverse articulating furrow. Pleural field crossed by at least four pairs of broad (exsag.), oblique pleural furrows that separate subequal, convex anterior and posterior pleural bands; interpleural furrows narrower but well-defined grooves. Lateral and posterior borders resting noticeably lower than the inflated pleural field. External surface sculpture equivalent to the finely threaded anastomosing sculpture of the cranidium.

Discussion.—Restudy of sclerites from the Wilberns Formation of Texas (Pl. 16, 17), illustrated under the name *Taenicephalus shumardi* by Bell and Ellinwood (1962) shows that that are closely comparable to the types of *T. wichitaensis* from Oklahoma (Pl. 11, 12) in all cranidial proportions and in having a sculpture of fine anastomosing ridges that become subdued in the largest specimens. I interpret them as recording a single species.

In comparing the cranidia of *T. wichitaensis* (Pl. 11–14) and *T. gouldi* (Pl. 15–18), an easily recognizable difference is that of relative width, with *T. gouldi* being notably wider across the palpebral lobes than it is long, as a result of a short anterior border and preglabellar field. Together, the border and preglabellar field account for about 25% total cranidial length in *T. gouldi*, whereas in *T. wichitaensis* they are longer and occupy about 32% of total cranidial length. The external surface of the cranidium consists of fine, anastomosing ridges (e.g., Pl. 13) that contrast with the coarser sculpture of cranidia of *T. gouldi* (Pl. 20, figs. 4–6). In addition, the palpebral lobe is farther forward, with posterior tip opposite mid-point of glabellar lobe L2 (e.g., Pl. 11, figs. 2, 6) rather than opposite the anterior tip of the S1 furrow (e.g., Pl. 18, fig. 1). The pygidium of *T. wichitaensis* has two distinct axial rings in front of the terminal piece (e.g., Pl. 15, figs. 1, 3), whereas *T. gouldi* has three (Pl. 20, figs. 7–9). The pleural and interpleural furrows are relatively effaced on *T. gouldi*, although this could be a result of the size difference between the sclerites.

Taenicephalus leei (Chatterton and Gibb, 2016, pl. 58, figs. 6, 9) is extremely similar to *T. wichitaensis*. Similarities in the cephalon include sculpture pattern, frontal area size and inflation, and size and position of the eyes. Pygidia are likewise very similar, with an articulating half-ring, two axial rings, a terminal piece, subelliptical shape, and small size. The most prominent character distinction between the two species is that *T. leei* possesses a small occipital spine whereas *T. wichitaensis* lacks this feature.

Cranidia attributed to *T. nasutus* by Westrop (1986, pl. 22, figs. 1, 2, 5, 7) differ from *T. wichitaensis* most notably in having a shorter preglabellar field and weakly inflated anterior border. *Taenicephalus nasutus* also has smaller and narrower palpebral lobes. Pygidia of *T. nasutus* (e.g., Westrop, 1986, pl. 22, figs. 6, 9) have very weak spines that give the pygidial margin a distinctive scalloped appearance. In contrast, the margin of the pygidium of *T. wichitaensis* is nearly smooth (Pl. 15, figs. 1–4).

Taenicephalus granulosus Resser, 1942 (pl. 20, figs. 4–7), and its probable synonym *T. ornatus* Resser (1942, pl. 20, figs. 11, 20) differs clearly from *T. wichitaensis* in having fine tuberculate sculpture across all cranidial surfaces. Also, the preglabellar field of *T. granulosus* is relatively longer, with a more strongly tapered glabella, which is thus more trapezoidal in outline.

Taenicephalus altus Nelson (1951, pl. 107, figs. 2,4, 7), from the Lone Rock Formation of the Upper Mississippi Valley, is known only from sandstone internal molds lacking sculpture for comparison with other species. Nelson's type cranidia possess extremely well tapered trapezoidal glabellae, as does a specimen attributed to the species by Bell et al. (1952, pl. 31, fig 6). Both sets of specimens are also readily distinguished from *T. wichitaensis* by way of their larger palpebral lobes.

Taenicephalus westropi Chatterton and Gibb (2016, pl. 57, figs. 1–5, 7) is distinguishable from *T. wichitaensis* on the basis of a longer preglabellar field. Palpebral lobes in *T. westropi* are also set further forward on the cranidium, with posterior terminus of the lobe set roughly opposite to the middle of L2. Pygidial axis, as with *T. leei*, is composed of two axial rings and a terminal piece. However, the most distinctive characteristic of *T. westropi* is the smooth surface, which contrasts with the sculpture of fine anastomosing ridges in *T. wichitaensis*.

TAENICEPHALUS GOULDI (Frederickson, 1949)

Plates 18–22

1949 *Bemaspis gouldi* Frederickson p. 357, pl. 71, figs. 11-14

1962 *Taenicephalus gouldi* Bell and Ellinwood, p. 401, pl. 57, figs. 1-9

1965 *Taenicephalus gouldi* Grant, p. 137, pl. 12, figs. 1-2

1970 *Taenicephalus gouldi* Longacre, p. 31

1971 *Taenicephalus gouldi* Stitt, p. 31-32, pl. 2, fig. 16

Diagnosis.— *Taenicephalus* with cranidial width across palpebral lobes greater than length. Preglabellar field weakly inflated and occupies about 13% of cranidial length. Glabella gently tapered, weakly rounded anteriorly. Three pairs of oblique lateral glabellar furrows; most posterior two pairs well impressed; most anterior pair faintly impressed. Anterior corners of glabella lack fossulae. Sculpture of large, irregular, elongate tubercles on glabella, ocular and postocular fixigena, with anastomosing ridges on frontal area. Pygidium transversely elliptical with axis composed of three distinct rings and terminal piece of two short segments. Pygidial sculpture of very fine anastomosing ridges on crest of axial rings, with very fine granules in ring furrows; Pleural field with anastomosing ridges, with irregular, elongate ridges on either side of faint interpleural furrows.

Holotype..— A cranidium (OU 5364; Pl. 18, Figs. 4-6) from the Honey Creek Formation, Murray County, Oklahoma (Frederickson, 1949 locality 14).

Occurrence.—Honey Creek Formation, Arbuckle Mountains, collections RR 150, 153; HS 50 (Stitt, 1971b). *Orygmaspis* (*Orygmaspis*) *llanoensis* Zone.

Description.—Cranidium sub-rectangular in outline. Posterior lateral projections about 26% as wide as the rest of the cranidium. Anterior border furrow well-incised. Frontal area accounts for about 25% of cranidial length and is well inflated in the pre-glabellar field. Glabella sub-trapezoidal with anterior tapering, widest near base around SO, comprising about 25% of cranidial length and about 56% of cranidial width. SO relatively thin but firmly impressed and of mostly even incision across glabella; curving gently forwards at margins. LO occupies about 18% of glabellar length and curved forward abaxially. S1 curves posteriorly at wide angle about half-way along length. S2 shorter and straighter than S1 with higher angled posterior initial glabellar incision; less strongly curved. L2 narrows slightly abaxially. S3 more weakly impressed and roughly as linear as S2, instead angled anteriorly at a comparable initial incision angle.

Palpebral lobes fairly long and narrow, comprising about 22% of cranidial length. Anterior of palpebral lobe roughly co-latitudinal with abaxial origin of S3 and posterior terminus roughly co-latitudinal with abaxial origin of S1. Palpebral area of fixigena semi-elliptical equal to only about 9% of length. Surface sculpture uniformly tuberculate throughout glabella, palpebral area, post-palpebral area, and posterior lateral borders. Tuberculate structure becomes increasingly anastomosing on pre-glabellar field and anterior border. Posterior border furrow well incised and broad, broadening abaxially, with convexly inflated border. Facial sutures diverge gently away in a sigmoid fashion in the posterior lateral projections. Anterior to the palpebral lobes facial sutures diverge outward before turning back in and converging toward anterior margin.

Free cheek with short, robust genal spine. Inflated librigenal field occupies about 55% of width opposite eye. Lateral border furrow marginally incised anteriorly, but shallows medially. Librigenal field exhibits anastomosing tuberculate sculpture associated with pre-glabellar field and anterior border of cranidia.

Pygidium sub-elliptical in outline, width greater than length; gently arched in posterior view. Axis narrow, convex, occupies about 88% of pygidial length. Three axial rings and terminal piece of two segments separated by well defined, transverse ring furrows; shallower furrow present on terminal piece. Articulating half-ring short, making up about 11% of pygidial length; articulating furrow nearly transverse. Pleural field crossed by at least four pairs of broad (exsag.), oblique pleural furrows that separate subequal, convex anterior and posterior pleural bands; interpleural furrows narrower but well-defined grooves. Lateral and posterior borders resting noticeably lower than the inflated pleural field. External surface appears to exhibit the same well defined anastomosing structure found on librigena and anterior of cranidia.

Discussion.—The type material of *Taenicephalus gouldi* (Pl. 18, Pl. 20, figs. 4–6) greatly resembles sclerites (Pl. 20–22) from the Wilberns Formation, Texas, that were assigned to this species by Bell and Ellinwood (1962). There are also strong similarities with specimens of *Taenicephalus leei* Chatterton and Gibb (2016, pl. 58, figs. 1–9) from the McKay Group of British Columbia. All three sets of specimens share cranidial sculpture that comprises irregular, subcircular to more elongate tubercles on the glabella and palpebral and postocular fixigenae .

On the preglabellar area, these tubercles are aligned along a caecal network. In larger specimens from Texas (Pl. 20, Figs. 1-3), the sculpture becomes subdued and barely identifiable.

Taenicephalus leei differs from *T. gouldi* in possessing pit-like fossulae in the axial furrows at the anterior corners of the glabella, and the preglabellar field is longer (e.g., Chatterton and Gibb, 2016, pl. 58, figs. 6, 9). Pygidia are not associated with the types of *T. gouldi*, but specimens from Texas (Pl. 20, figs. 7–9) have three distinct axial rings plus a terminal piece composed of at least two segments. In contrast, the pygidium of *T. leei* has only two distinct rings and a terminal piece, and there is also a minute marginal spine on the anteriormost segment (Chatterton and Gibb, 2016, p. 80, pl. 58, figs., 1, 8). However, as the pygidium from Texas is much larger than those from British Columbia, loss of the spine during ontogeny cannot be ruled out for the former.

Comparisons with *Taenicephalus wichitaensis* Resser, 1942, also from the Honey Creek Formation of Oklahoma are presented above, in the discussion of that species.

The holotype of the type species, *T. shumardi* (Hall, 1863; Westrop, 1986, pl. 21, figs. 5, 6), and other cranidia from the Wisconsin and Minnesota Lone Rock Formation (e.g., Berg, 1953, pl. 59, figs. 11–14), differ from the latter in having longer, more inflated preglabellar fields and distinct fossulae at the anterior corners of the glabella. Cranidia from the Bison Creek Formation, Alberta, attributed to *T. shumardi* by Westrop (1986, pl. 21, figs. 8–14, 16, 17) also differ from *T. gouldi* in these respects, and have sculpture that consists of finely anastomosing ridges. The associated pygidia (Westrop, 1986, pl. 21, figs. 7, 15) have two distinct axial rings in front of the terminal piece, rather than three, as in *T. gouldi*.

Taenicephalus gouldi differs from *T. nasutus* (Westrop, 1986, pl. 22. figs, 1-13) in having a relatively shorter preglabellar field, and a more strongly inflated anterior border. Like *T.*

shumardi, *T. nasutus* has a strongly trapezoidal glabella, and has smaller, more anteriorly placed palpebral lobes than those of *T. gouldi*. Type and other material from the Upper Mississippi valley is preserved as sandstone internal molds that provide no information on sculpture. Cranidia from the Bison Creek Formation in Alberta that were assigned to *T. nasutus* by Westrop (1986, pl. 22, figs. 1, 2, 5, 7) have fine anastomosing ridges over the entire surface except for furrows and the posterior border, producing a pitted appearance.

Taenicephalus granulosus Resser, 1942 (pl. 20, figs. 4–7), and its probable synonym *T. ornatus* Resser (1942, pl. 20, figs. 11, 20) differs clearly from *T. gouldi* in having fine tubercles over both testate and exfoliated cranidial surfaces. In addition, the preglabellar field of *T. granulosus* is relatively longer, and the glabella is more strongly tapered, producing a distinctly trapezoidal outline.

Taenicephalus altus Nelson (1951, pl. 107, figs. 2,4, 7), from the Lone Rock Formation of the Upper Mississippi Valley, is known only from sandstone internal molds. Nelson's type cranidia have strongly tapered, distinctly trapezoidal glabellae, as does a specimen attributed to the species by Bell et al., 1952 (pl. 31, fig 6). They also differ clearly from *T. gouldi* in possessing much longer palpebral lobes.

Taenicephalus westropi Chatterton and Gibb (2016, pl. 57, figs. 1–5, 7) is separable from *T. gouldi* on the basis of a longer preglabellar field and fossulae at the anterior corners of the glabella. Palpebral lobes in *T. westropi* are also set somewhat farther forward on the cranidium, with posterior tip of the lobe set roughly opposite to the middle of L2. Pygidial axis, as with *T. leei*, is composed of 2 axial rings and a terminal piece. However, the most distinctive characteristic of this species is the smooth surface.

TAENICEPHALUS KALLISTI

Figure 1, Plate 23, figs. 1–7, Plate 24, figs. 6–8

Diagnosis.— A species of *Taenicephalus* with a cranidium almost as wide as long when measured across palpebral lobes. Frontal area equal to about 30% of cranidial length. Preglabellar field relatively weakly inflated and relatively long, accounting for about 50% of frontal area length. Glabella sub-rounded anteriorly with tapering sides. Three pairs of glabellar furrows. Most posterior two pairs well impressed, most anterior pair weakly impressed. Anterior of glabellar margin lacking fossulae of other *Taenicephalus*. Sculpture of well-developed, irregular tubercles in center and posterior of cranidium, transitioning to anastomosing ridges toward preglabellar field and anterior margin.

Holotype .—A cranidium [OU 238191, Plate 23, figs. 4-6], Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1, collection KR1 29.9.

Derivation of name.— Named for the romanization of inscription on the Golden Apple which the goddess Eris used to begin the Trojan War after being snubbed from a wedding. Translated as "for the fairest."

Occurrence.—Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1, collection KR1 29, KR1-30; Arbuckle Mountains, U.S. Hwy 77 Section, Collection HS 61 (Stitt, 1971b). *Orygmaspis* (*Orygmaspis*) *llanoensis* Zone.

Discussion.— This species, hitherto undescribed, occurs in the upper part of the *Orygmaspis* (*Orygmaspis*) *llanoensis* Zone and bears strong resemblance to the stratigraphically lower species *T. gouldi*, from which it is distinguished most easily by the comparatively long frontal area that occupies about 30%, rather than 25% of cranidial length. The preglabellar field is long, accounting for about half of the frontal area, whereas this feature is equal to only about one-third of frontal area length in *T. gouldi*.

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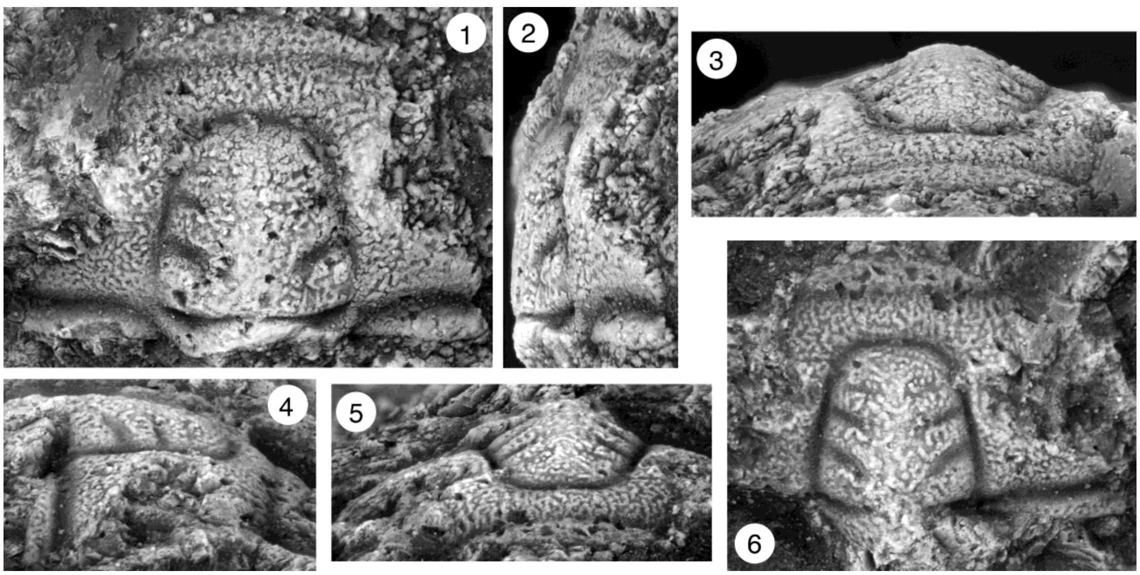
Figure 8

Taenicephalus kallisti sp.nov., Honey Creek Formation, US Highway 77 section, Murray County, Oklahoma, collection HS 61 (Stitt, 1971b). Both cranidia are paratypes.

1–3, OU 120719, dorsal, lateral and anterior views, x18.

4–6, OU 120720, lateral, anterior and dorsal views, x20.



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Chapter IV: Other genera from the upper *Taenicephalus* Zone of the Honey Creek Formation

Introduction

Several, mostly less common taxa are present in the collections from the upper Honey Creek Formation. They are illustrated and given brief treatment largely to support the biostratigraphic component of the thesis (Chapter 1).

Systematic Paleontology

Figured specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU) and at the National Museum of Natural History (USNM). All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop ™. Proportions expressed in percentages in descriptions and diagnoses are means. To maximize depth of field, all digital images were rendered from stacks of images focused at 100-micron intervals using Helicon Focus 4.0 for the Macintosh <http://www.heliconsoft.com>.

Family PARABOLINOIDIDAE Lochman, 1956

Genus ORYGMASPIS Resser, 1937

Type species. Ptychoparia llanoensis Walcott, 1890 from the Morgan Creek Member, Wilberns Formation, central Texas (by original designation).

Subgenus ORYGMASPIS (ORYGMASPIS) Resser, 1937

Discussion.—Most authors (e.g., Longacre, 1970; Stitt, 1971b; Westrop, 1986) have recognized that Parabolinoides Frederickson, 1949 is very similar to Orygmaspis, differing in having a more anteriorly positioned palpebral lobe, and a more convex glabella. Westrop (1986) treated them as subgenera and this is followed here. However, a case could also be made for considering them synonyms. Revision of the classification of these taxa is a larger problem that demands a broader phylogenetic analysis of Parabolinoididae, including genera such as Croixana, Kendallina, Roksaspis and Taenicephalus, and is beyond the scope of this thesis.

ORGYMASPIS (ORYGMASPIS) LLANOENSIS (Walcott, 1890)

Figure 1; Plate 24, figs. 1–5

1890 *Ptychoparia llanoensis* Walcott, p. 272, pl. 21, figs. 3–5

1962 *Orygmaspis llanoensis*; Bell and Ellinwood, p. 398, pl. 55, figs. 11–15 (synonymy to date)

1970 *Orygmaspis llanoensis*; Longacre, p. 26, pl. 1, figs. 7–16

1971b *Orygmaspis llanoensis*; Stitt, p. 28, pl. 2, fig. 14.

Diagnosis.— *Orygmaspis* (*Orygmaspis*) with effaced anterior border furrow with position on internal mold marked by line of small tubercles. Associated pygidia wider than long with short but robust spines extending from border.

Holotype.—A cranidium USNM 23857 (Walcott, 1890, pl. 21, figs. 3-5) from the Morgan Creek Member, Wilberns Formation, central Texas.

Occurrence.— Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, Comanche County, collections KR1-29.9, -31.7, KR3-31.1

Discussion.—Cranidia from the Honey Creek Formation at sections KR1 and BM are identical to type and other material from Texas (Bell and Ellinwood, 1962, pl. 55, figs. 11–15) in possessing a frontal area in which the anterior border is poorly differential and the position of the border furrow is marked by a line of tubercles on internal molds.

ORGYMASPIS (ORYGMASPIS) FIRMA (Frederickson, 1949)

Plate 25

1949 *Orygmaspis firma* Frederickson, p. 859, pl. 71, figs. 19–22.

1962 *Orygmaspis firma* Frederickson, Bell and Ellinwood, p. 398, pl. 55, fig. 16, pl. 56, fig. 1.

Diagnosis.— *Orygmaspis* (*Orygmaspis*) distinguished by a convex anterior border and clearly defined anterior border furrow.

Holotype.— A cranidium (Pl. 25, figs. 1–3) from Honey Creek Formation, Arbuckle Mountains, Murray County, Fredrickson (1949) locality 14.

Discussion.— Frederickson (1949) established *O*. (*Orygmaspis*) *firma* for cranidia that differed from *O*. (*Orygmaspis*) *llanoensis* in having a distinct anterior border and border furrow. Longacre (1970) claimed (but did not illustrate) that there were specimens in the Wilberns Formation of Texas that had morphologies that were intermediate between the two species, and considered them to be synonyms. All of the cranidia in my collections from the Wichita Mountains area are assignable to *O*. (*Orygmaspis*) *llanoensis* (e.g., Pl. 24). Restudy of Frederickson's types (Pl. 25, figs. 1-6) show that they are clearly differentiated by frontal area anatomy, and until intermediate specimens are documented, they should be treated as a distinct species.

Family IDAHOIIDAE Lochman, 1956

Genus IDAHOIA Walcott, 1924

Type species.—*Idahoia serapio* Walcott, 1924 from the St. Charles Formation, Two Mile Canyon, Malad, southern Idaho (by original designation).

Remarks.— The relationships between *Saratogia* Walcott. 1916, *Idahoia* Walcott, 1924, *Psalaspis* Resser, 1937, *Meeria* Frederickson, 1949 and *Minkella* Lochman and Hu, 1959 have been discussed extensively in the literature (e.g., Bell and Ellinwood, 1962; Longacre, 1970;

Ludvigsen and Westrop, 1983). The most recent attempt at a comprehensive revision (Ludvigsen and Westrop, 1983) treated *Saratogia* and *Idahoia* as subgenera of *Saratogia*. *Saratogia* (e.g., Ludvigsen and Westrop, 1983, pls. 7–8) differs from *Idahoia* (e.g., Ludvigsen and Westrop, 1983, pl. 9, figs. 1–3) in possessing much larger palpebral lobes that are located close to the glabella. The glabellar are firmly impressed, as is the palpebral furrow, whereas the glabellar furrows are effaced on species of *Idahoia*. As noted by Ludvigsen and Westrop (1983), the pygidium of *Saratogia* is strikingly different from *Idahoia*, and is characterized by a long axis that extends to the posterior margin to merge with a narrow border. In contrast, *Idahoia* has a short axis and very long border (e.g., Ludvigsen and Westrop, 1983, pl. 9, fig. 3) that resembles some species of *Wilbernia* Walcott, 1924 (e.g., Bell and Ellinwood, 1962, pl. 54, fig. 20; Westrop, 1986, pl. 12, fig. 13), and it is possible that these two genera are more closely related to each other than either is to *Saratogia*. A full evaluation and discussion of *Saratogia*, *Idahoia* and related genera lies beyond the scope of this thesis, and will require a comprehensive phylogenetic analysis. For the purposes of this thesis, *Saratogia* and *Idahoia* will be treated as separate genera, and species assignments will follow Ludvigsen and Westrop (1983, p. 25).

IDAHOIA LIRAE (Frederickson, 1949)

Plate 26

1949 *Meeria lirae*, Frederickson, p. 358, pl. 72, figs. 3-6.

non 1962 *Idahoia lirae* (Frederickson), Bell & Ellinwood, p. 392, pl. 53, figs. 1–9 [= *Idahoia czukay* n. sp.]

1962 Idahoia lirae (Frederickson), var. A Bell & Ellinwood, p. 392, pl. 53, figs. 10-12.

1970 *Idahoia lirae* (Frederickson), Longacre, p. 24 (synonymy to date)

1971b *Idahoia lirae* (Frederickson), Stitt, p. 26, pl. 3, figs. 5-9.

1983 *Meeria lirae* (Frederickson), Ludvigsen and Westrop, p. 25.

1986 *Saratogia* (*Idahoia*) *lirae* (Frederickson), Westrop, p. 42, pl. 16, figs. 5-7.

Diagnosis.—*Idahoia* with strongly effaced frontal area; preglabellar field poorly differentiated from down-sloping anterior border. Cranidium mostly smooth, with faint sculpture of anastomosing ridges on occipital ring and sparsely on glabellar surface. Occipital spine absent.

Holotype.— A cranidium (OU 4277, Pl. 26, figs. 1–3), Honey Creek Formation, Wichita Mountains, west side of Blue Creek Canyon, Comanche County, Fredrickson (1949) locality 6.

Occurrence.—Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, Comanche County, collections KR1-39.

Discussion.— Ludvigsen and Westrop (1983) were uncertain about the status of *Meeria,* but Westrop (1986) followed the long-standing practice (e.g., Bell and Ellinwood, 1962; Longacre, 1970; Stitt, 1971b) of considering it to be a junior synonym of *Idahoia*. There are two distinct morphotypes in Oklahoma, and a similar pattern can be seen in Texas (Bell and Ellinwood, 1962). The types of *I. lirae* (Pl. 26) have an relatively effaced frontal area with little differentiation between the preglabellar field and border, and similar cranidia from Texas were assigned to *I. lirae* variety A by Bell and Ellinwood (1962, p. 393, pl. 35, figs. 10–12). A second species, *I. czukay* n. sp., is present in collection KR1–39 (Pl. 27). It is characterized by a short, thorn-like spine, better differentiation of the upturned anterior border and border furrow, and well developed cranidial sculpture of irregular, anastomosing ridges over the entire external surface except for the furrows. Some of the specimens from Texas assigned to *I. lirae* by Bell and Ellinwood (1962, p. 392, figs. 1–3) have small spines and well-developed anterior borders and border furrow, and may be conspecific with cranidia from KR1–39. Other, similar cranidia from Texas with large nodes rather than spines (Bell and Ellinwood, p. 392, figs. 4–9) may also belong to this species.

IDAHOIA CZUKAY n. sp.

Plate 27

1962 *Idahoia lirae* (Frederickson), Bell & Ellinwood, p. 392, pl. 53, figs. 1–9.

Diagnosis.— *Idahoia* with short, occipital spine or large node. Well-defined anterior border furrow and upturned anterior border. Sculpture of irregular, anastomosing ridges over entire external surface of cranidium except for furrows.

Derivation of name.— Named for the German experimental musician Holger Czukay.

Occurrence.—Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, Comanche County, collections KR1-39.

Description.— Cranidium longer than wide. Weakly convex, trapezoidal glabella with three pairs of shallow, oblique lateral furrows defined in part as smooth areas that lack sculpture. SO transverse medially, but swings forward abaxially. L0 with occipital spine. Frontal area occupies about 30% of length of the cranidium. Broad and well-defined anterior border furrow separates short, gently upturned border from longer, down-sloping preglabellar field. Mid-point of large, flap-like palpebral lobes approximately medially co-latitudinal with L2; palpebral furrow absent. Anterior branches of facial sutures diverge slightly anterior before swinging inward at anterior border furrow; posterior branches strongly divergent in faintly sigmoid curve, so that posterolateral projection short (exsag.). Well-incised posterior border furrow; border short (exsag.) and convex. Sculpture of irregular, anastomosing ridges over the entire external surface except for the furrows

Discussion.— As noted above, two distinct morphotypes of *Idahoia* immediately above the ranges of species of *Taenicephalus* at section KR1 represent distinct species.   Comparisons between *I. lirae* and *I. czukay* n. sp. were presented above.

Family DOKIMOCEPHALIDAE Kobayashi 1935

Genus CONASPIS Hall, 1863

Type species.—*Conocephalites perseus* Hall, 1863 from the Lone Rock Formation, Wisconsin (by original designation).

Discussion.—Assignment of *Conaspis* to Family Dokimocephalidae follows Ludvigsen and Westrop (in Ludvigsen et al., 1989).

CONASPIS TESTUDINATA Ellinwood, in Bell and Ellinwood, 1962

Plate 28, figs. 1–7, Plate 29, figs. 1–4

1962 *Conaspis testudinatus* Ellinwood, in Bell and Ellinwood, p. 404, pl. 58, figs. 10–13.

1970 *Conaspis testudinatis*, Longacre, p. 40, pl. 1, figs. 17, 18.

1971b *Conaspis testudinata*, Stitt, p. 42, pl. 2, fig. 15,

Occurrence.—Honey Creek Formation, Ring Top Mountain, Comanche County, collection KR1-29.9; Bally Mountain, collection BM 70.5. *Orygmaspis* (*Orygmaspis*) *llanoensis* and *T. wichitaenis* zones, See Stitt (1971b) and Longacre (1970) for other occurrences in the Arbuckle Mountains of Oklahoma, and central Texas, respectively.

Discussion.— In their original description, Bell and Ellinwood (1962) characterized the internal mold of the cranidium of *Conaspis testudinata* as smooth, but Longacre (1970, p. 40) disputed this, and illustrated internal molds (1970, pl. 1, figs. 17, 18) that, like those from the Honey Creek Formation, clearly possess sculpture of granules to fine tubercles. Specimens from Oklahoma (Pl. 28) appear to be identical to Longacre's material.

The librigena (Pl. 28, fig. 7) and pygidium (Pl. 29, figs. 1–2) of *C. testudinata* are illustrated here for the first time, and are described as follows: Librigena with stout spine, length equal to about one-fifth to one-fourth the length of the librigenal field. Librigenal field convex, accounts for roughly two-thirds total librigenal width at widest point, and is adorned with tuberculate sculpture in the half of the field nearest the palpebral suture. Border furrow absent. Weakly-defined terrace ridge sculpture present at librigenal border.

Pygidium subelliptical in outline. Axis composed of three axial rings, a terminal piece, and an articulating half-ring. Axis comprises roughly 90% of the axial length of the pygidium and approximately one-third of pygidial width; composed of three rings and terminal piece separated by transverse ring furrows. Pleural and interpleural furrows well defined, with notable posterior curvature. Pleural field appears to curve upward distally, resulting in the pygidium appearing concave with exception of the axial ring.

CONASPIS cf. LEPTOHOLCIS Longacre, 1970

Plate 29, figs. 6–10

cf. 1970 *Conaspis leptoholcis* Longacre, p. 39, pl. 1, figs. 19–21.

Occurrence.— Honey Creek Formation, Ring Top Mountain, Comanche County, collection KR1-30, *Orygmaspis* (*Orygmaspis*) *llanoensis* Zone. See Longacre (1970) for occurrences in central Texas.

Discussion.— Cranidia of *Conaspis* from KR1-30 are very similar to C. *leptoholcis* Longacre, 1970. However, there are enough discrepancies between the few new specimens described here and *C. leptoholcis* that more data will be needed make a confident identification. For example, Longacre diagnoses the exoskeleton of *C. leptoholcis* as smooth, but the sclerites from KR1-30 have weakly tuberculate sculpture on the anterior border and on the glabella. Because of the small number of specimens illustrated by Longacre and the limited sample available from KR1-30, open nomenclature is used here.

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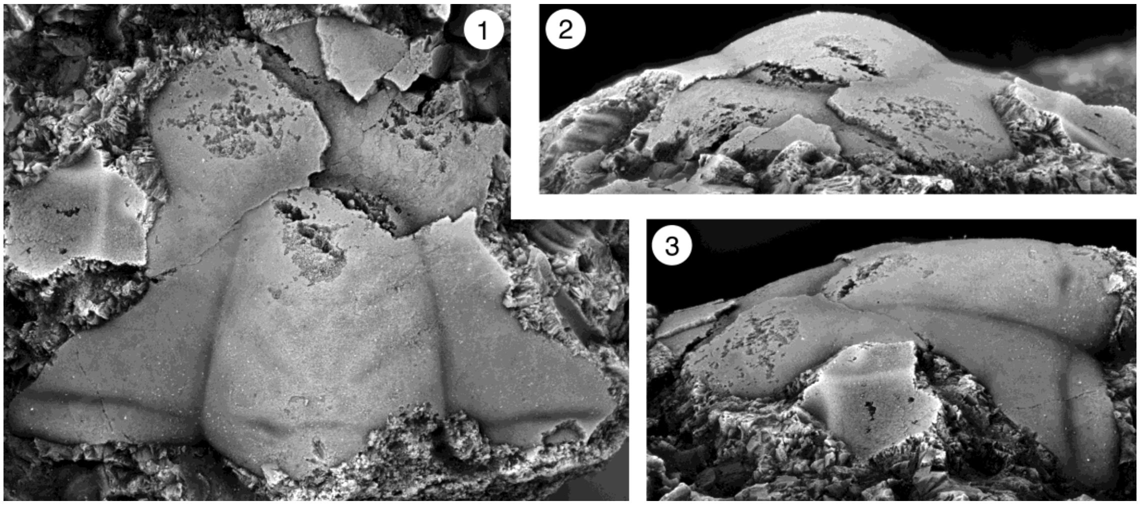
Figure 9

Cranidium (OU 238156) of *Orygmaspis* (*Orygmaspis*) *llanoensis* (Walcott, 1890) from the Honey Creek Formation, Arbuckle Mountains, Royer Ranch section, collection RR-150 (Stitt, 1971b), Murray County, Oklahoma, x12. 1, dorsal view; 2, anterior view; 3, lateral view.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APPENDIX A: Plates

Plate 1

Monocheilus reginae n. sp., Honey Creek Formation, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T. All cranidia and all paratypes except 4–6 (holotype).

1–3, OU 238157, lateral, anterior and dorsal views, x6.66.

4–6, OU 238158 , anterior, lateral and dorsal views, x10.82.

7–9, OU 238159, anterior, lateral and dorsal views, x10.82.

10–12, OU 238160, lateral, dorsal and anterior views, x10.82.

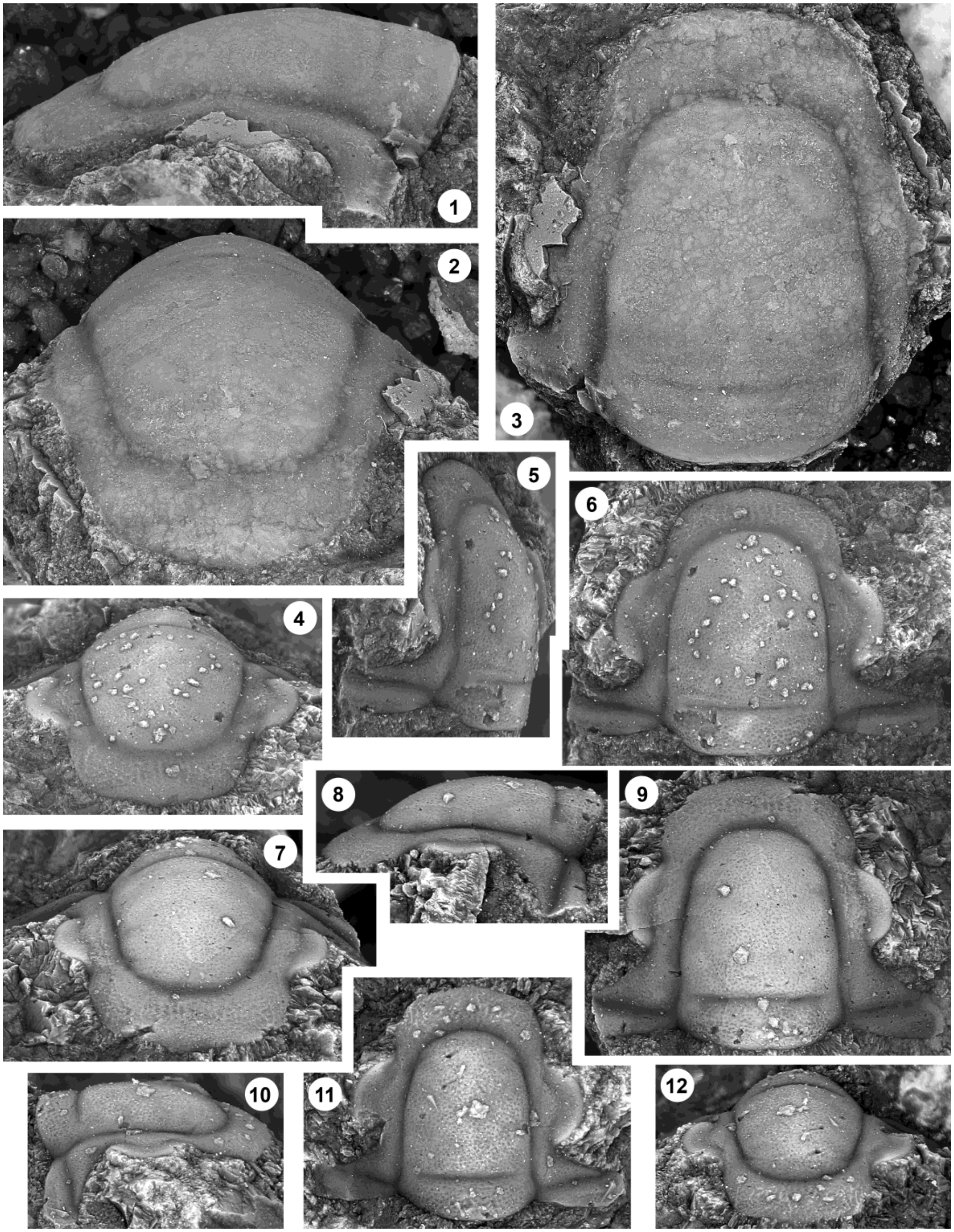
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Plate 2

Monocheilus reginae n. sp., Honey Creek Formation, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T. All paratypes

1, 2, pygidium, OU 238161, dorsal and posterior views, x7.49.

3, 4, pygidium, OU 238162, dorsal and posterior views, x7.49.

5–7, cranidium, OU 238163, dorsal, anterior and lateral views, x13.31.

8, 9, cranidium, OU 238164, dorsal and lateral views, x9.98.

10, 11, thoracic segment, OU 238165, lateral and dorsal views, x4.16.

12, 13, librigena, OU 238166, dorsal and lateral views, x9.15.

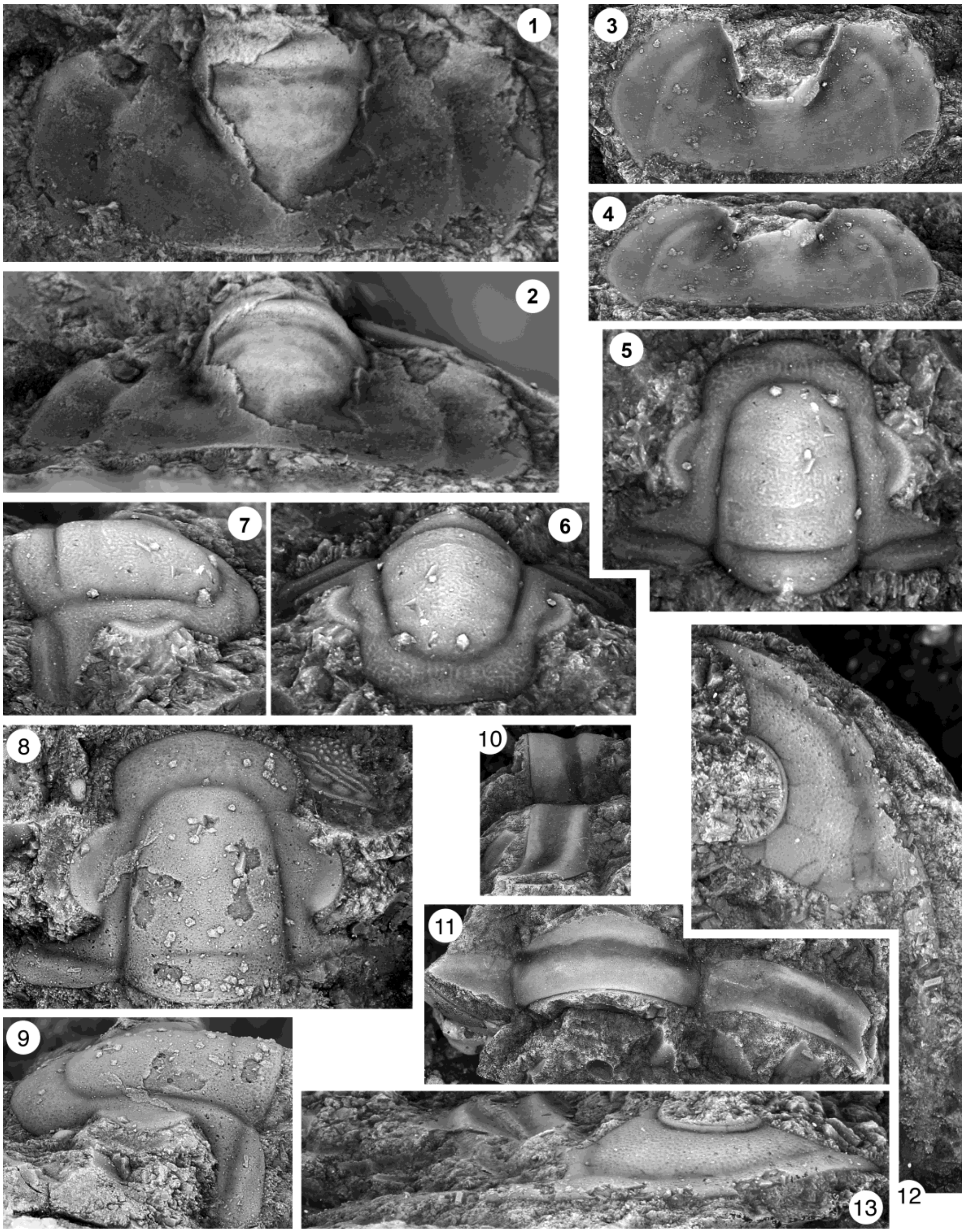
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Plate 3.

Ptychaspis bullasa Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All cranidia and all paratypes except 1–3 (holotype).

1–3, USNM 137099, lateral, dorsal and anterior views, x6.24 (illustrated previously by Lochman and Hu, 1959, pl. 58, figs. 39, 40).

4–6 USNM 137100k, lateral, anterior and dorsal views, x5.41 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 37).

7, USNM 137100, dorsal view, x12.48.

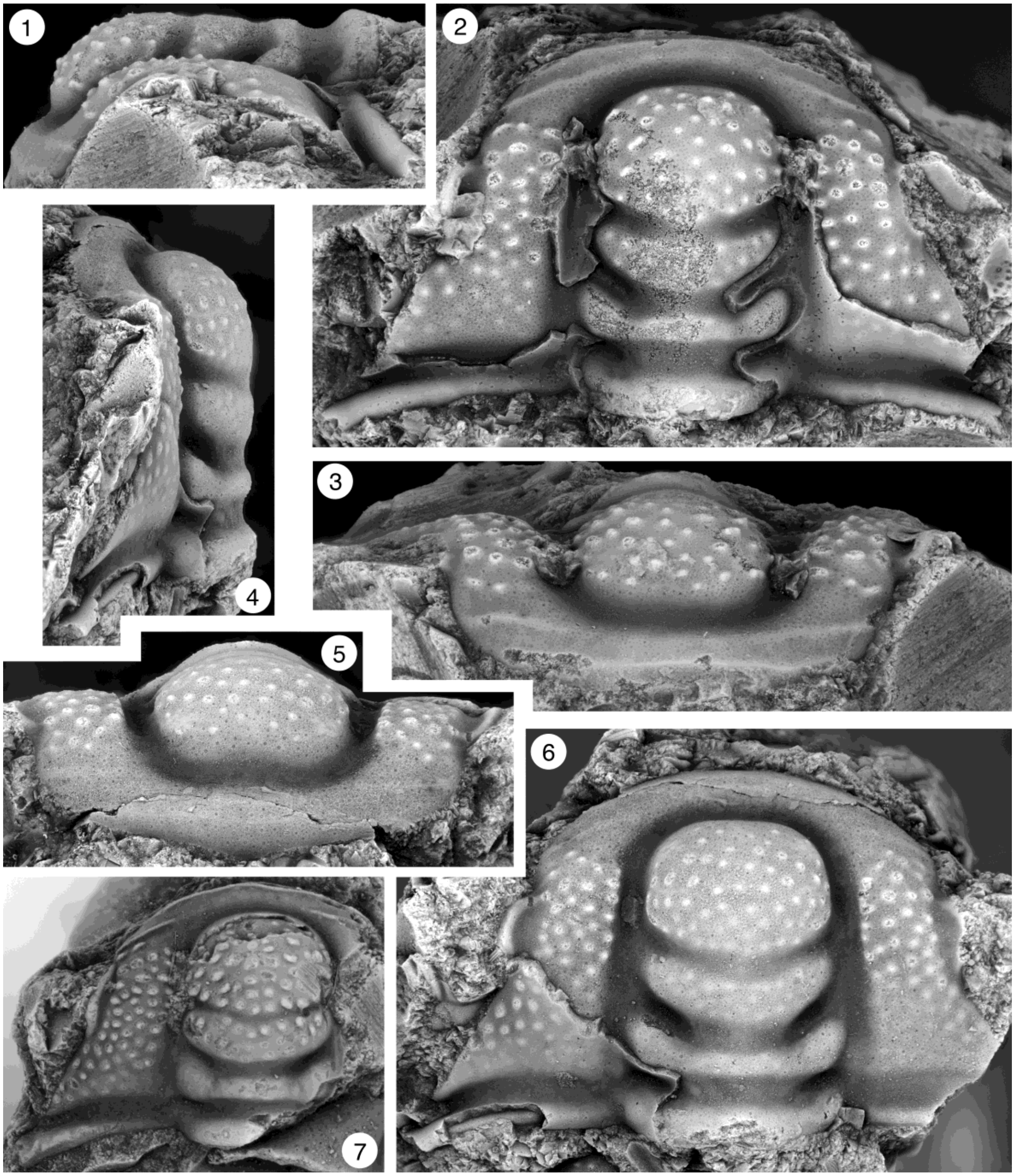
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Plate 4

Ptychaspis bullasa Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All cranidia and all paratypes.

1–3, USNM 135100r, dorsal, lateral and anterior views, x11.65 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 35).

4–6, USNM 137100e, dorsal, lateral and anterior views x19.97 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 26).

7–9, USNM 137100d, lateral, anterior and dorsal views, x18.3 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 24).

10–12, USNM 137100c, dorsal, lateral and anterior views, x24.96 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 23).

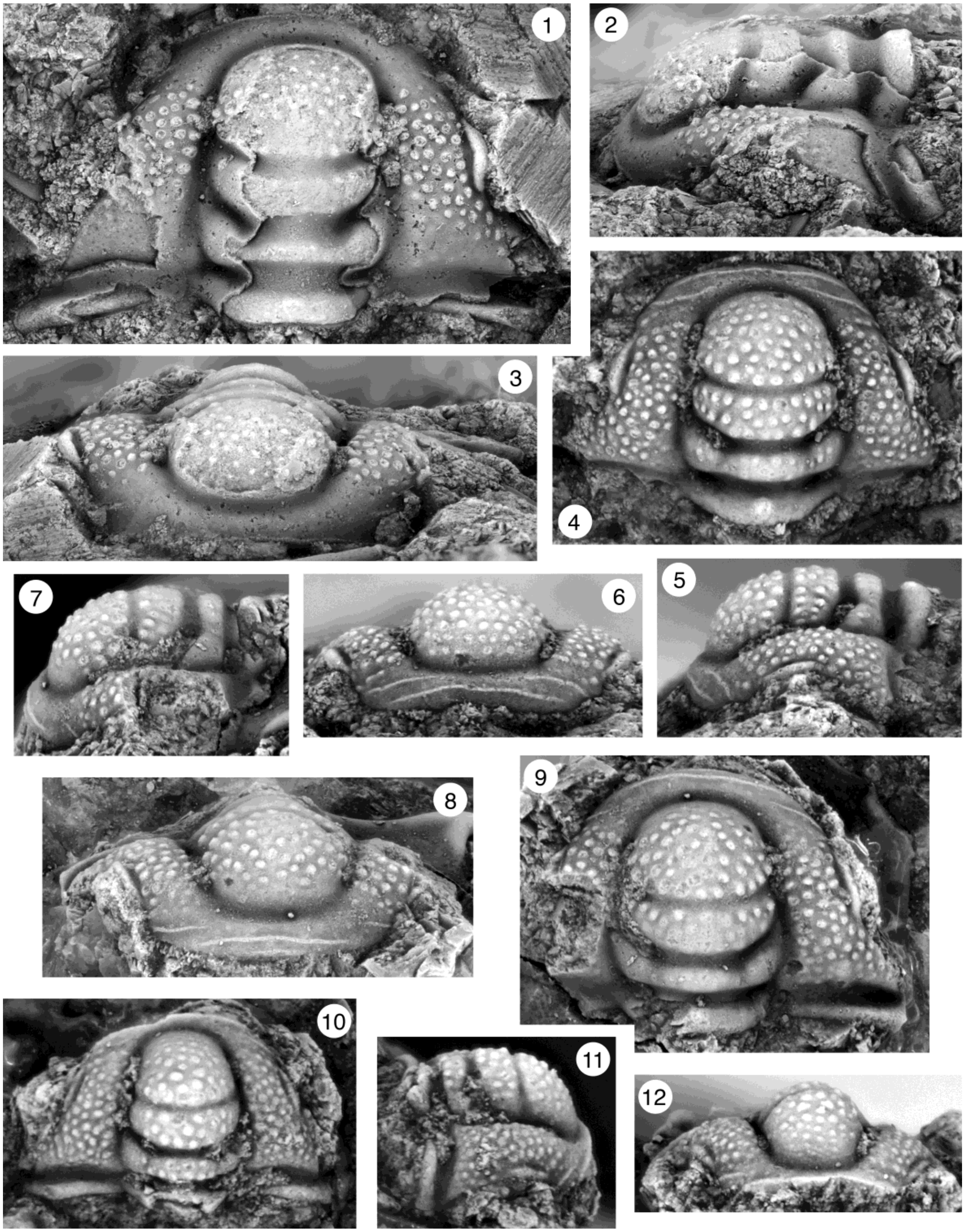
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Plate 5

Ptychaspis bullasa Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho.

1–3, cranidium, USNM 137100n, lateral, dorsal and anterior views, x4.58 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 42).

4, 5, librigena, USNM 137100j, lateral and dorsal views, x4.16 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 36).

6, 7, pygidium, USNM 137100s, dorsal and posterior views, x12.48 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 30).

8, pygidium, USNM 137100p, dorsal view, x14.98 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 31).

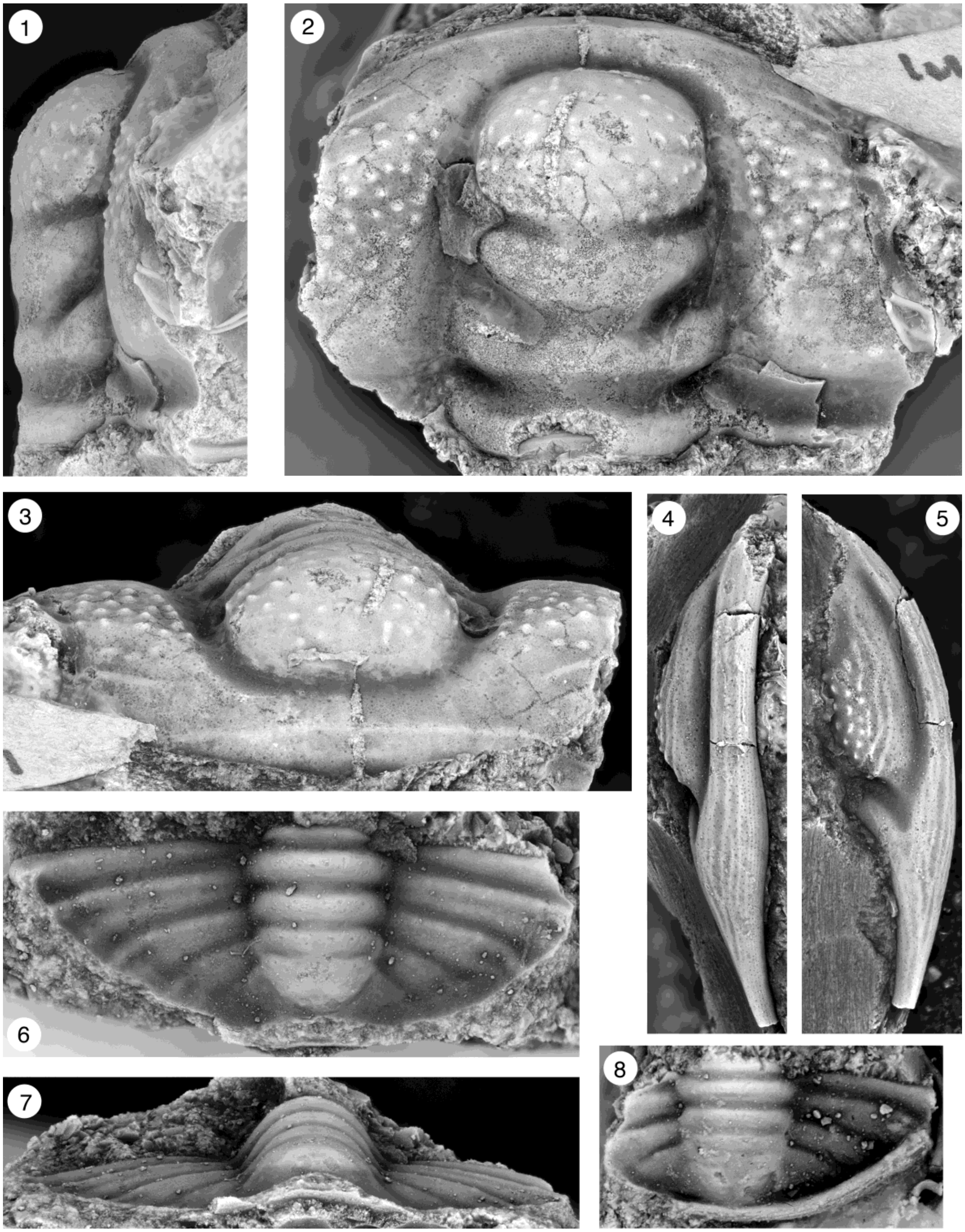
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Plate 6

Ptychaspis bullasa Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All paratypes

1–3, pygidium, USNM 137100L, dorsal, lateral and posterior views, x8.32 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 27).

4, librigena, USNM 137100i, dorsal view, x4.16 (previously unfigured).

5–7, hypostome, USNM 137100m, posterior, lateral and ventral views, x11.65 (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 25).

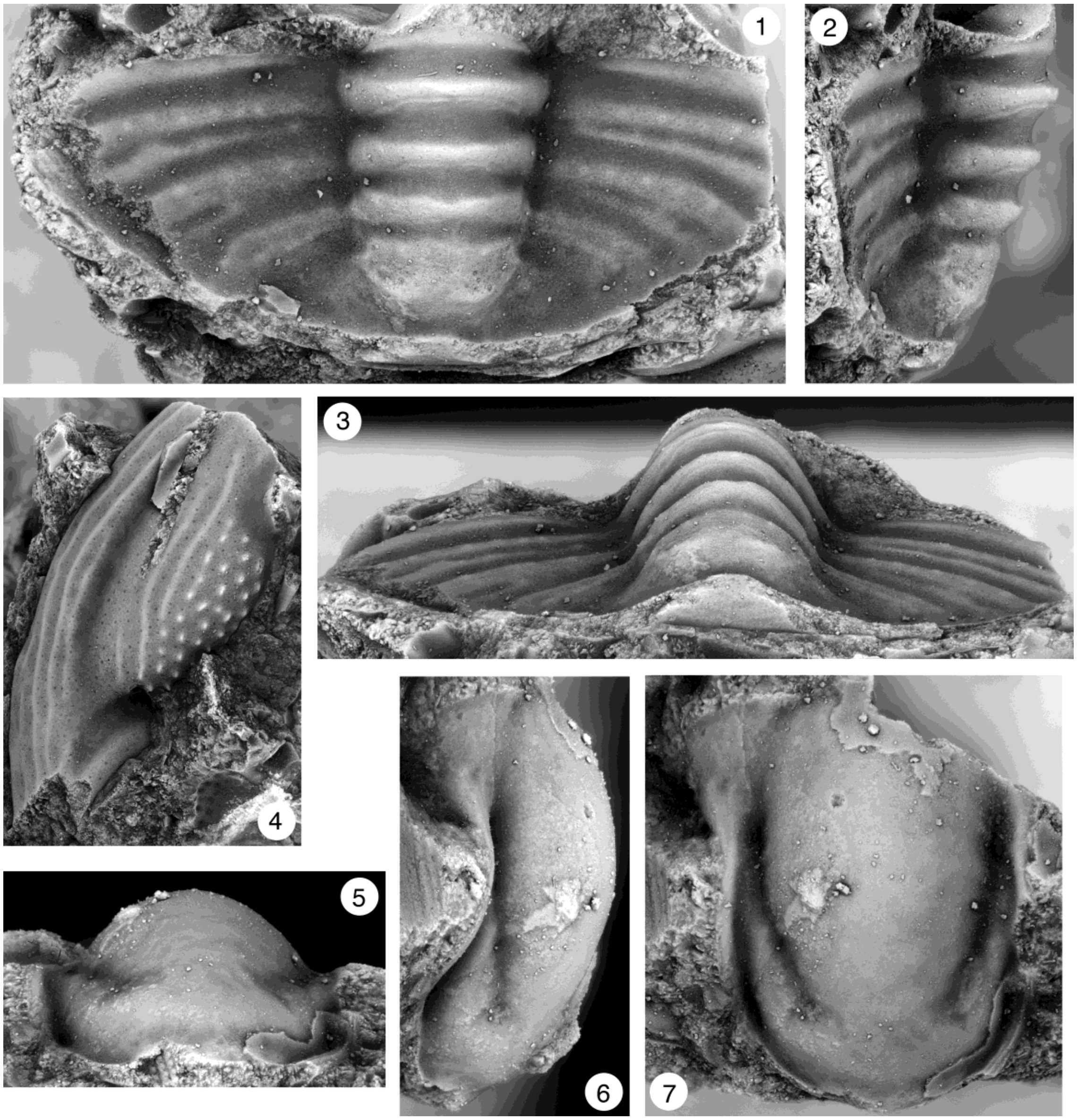
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Plate 7

Ptychaspis richardi n. sp., Fort Sill Formation, about 4.4 km south-east of Hennepin, Murray County Oklahoma, 60 feet above the base of zone 1a). All paratypes, except 1–3 (holotype).

1–3, cranidium, OU 4268, dorsal, lateral and anterior views, x4.16.

4, librigena, OU 238167, dorsal view, x3.33.

5, pygidium, OU 4270, dorsal view, x4.58

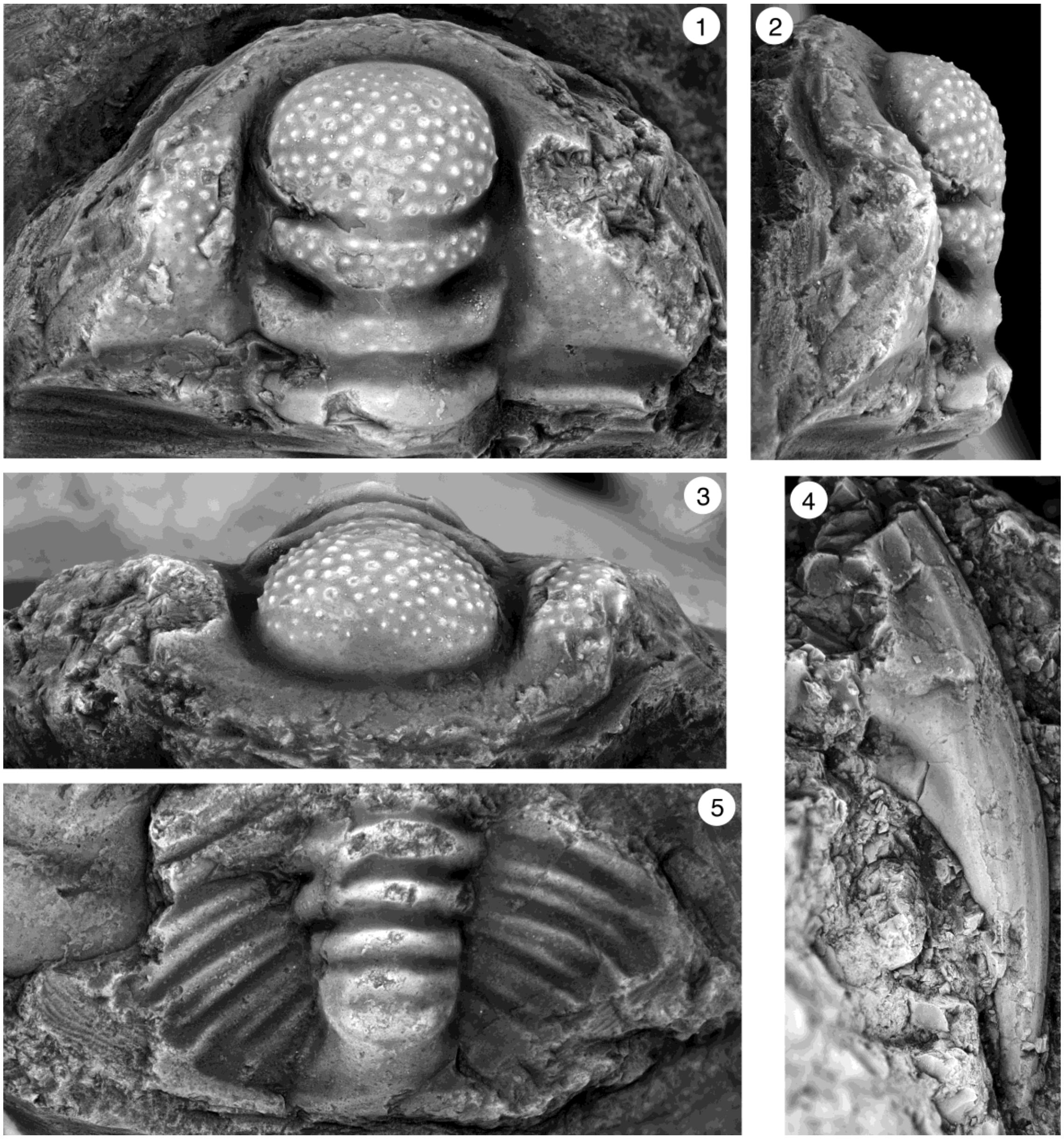
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Plate 8

Ptychaspis richardi n. sp., Fort Sill Formation, about 4.4 km south-east of Hennepin (SE Sec. 4, T1S, R1W), Murray County Oklahoma, 60 feet above the base of zone 1a). All paratypes.

1–3, cranidium, OU 238168, dorsal, lateral and anterior views, x4.16.

4, 5, librigena, OU 4269, lateral and dorsal views, x4.16.

6, 7, pygidium, OU 238169, posterior and dorsal views, x5.41.

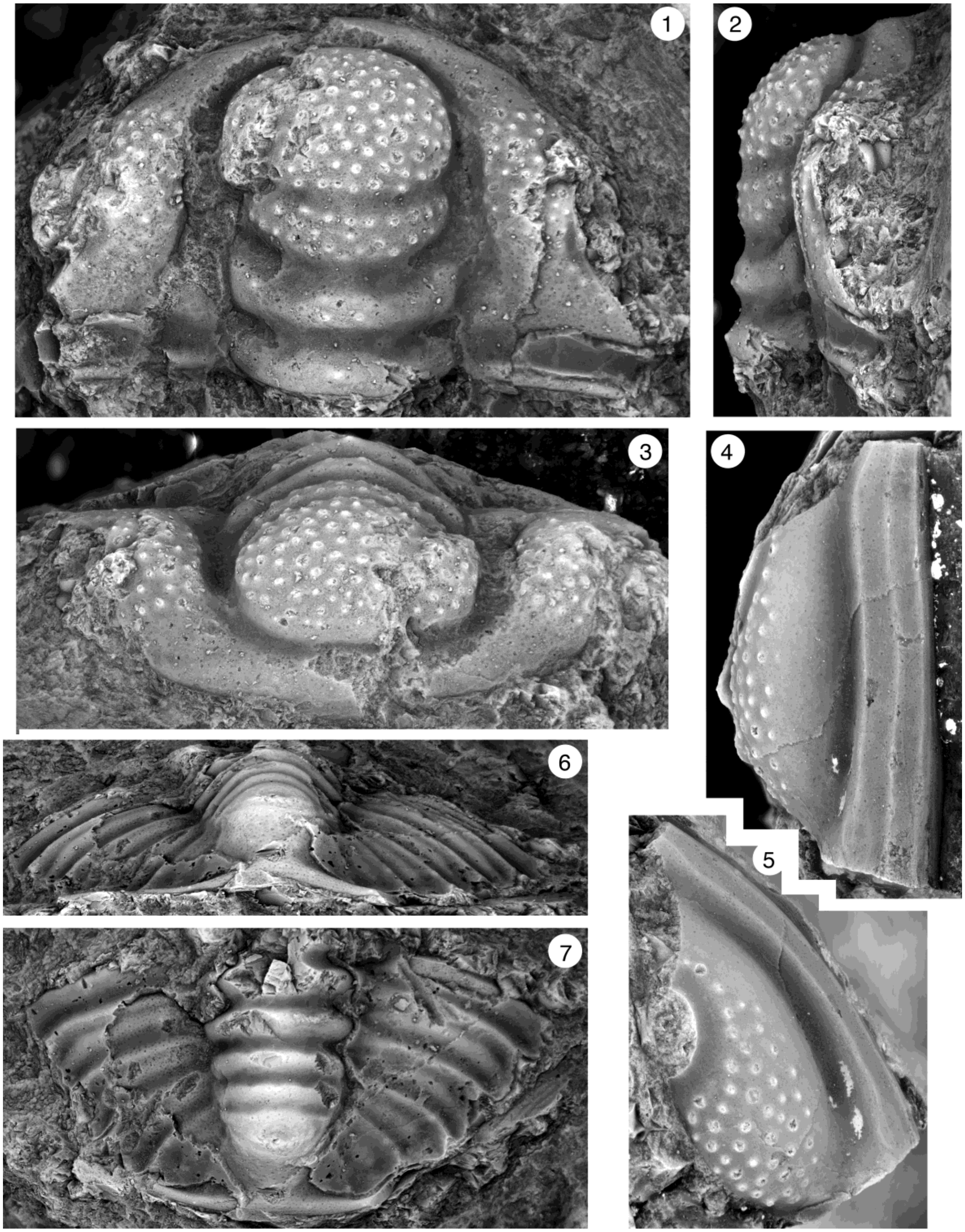
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Plate 9

Ptychaspis occulta n. sp., Morgan Creek Member, Wilberns Formation, central Texas. All cranidia, and all paratypes except 6–8 (holotype).

1–3, USNM 185437, dorsal, lateral and anterior views, x3.33, Sudduth section, collection SU 104, Burnet County (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 17)

4, 5, USNM 185470, dorsal and anterior views, x12.48, White Creek Section, collection WC 950, Blanco County (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 14).

6–8, USNM 185472, anterior, dorsal and lateral views, x9.48, Little Llano River section, collection LL 725, San Saba County (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 16).

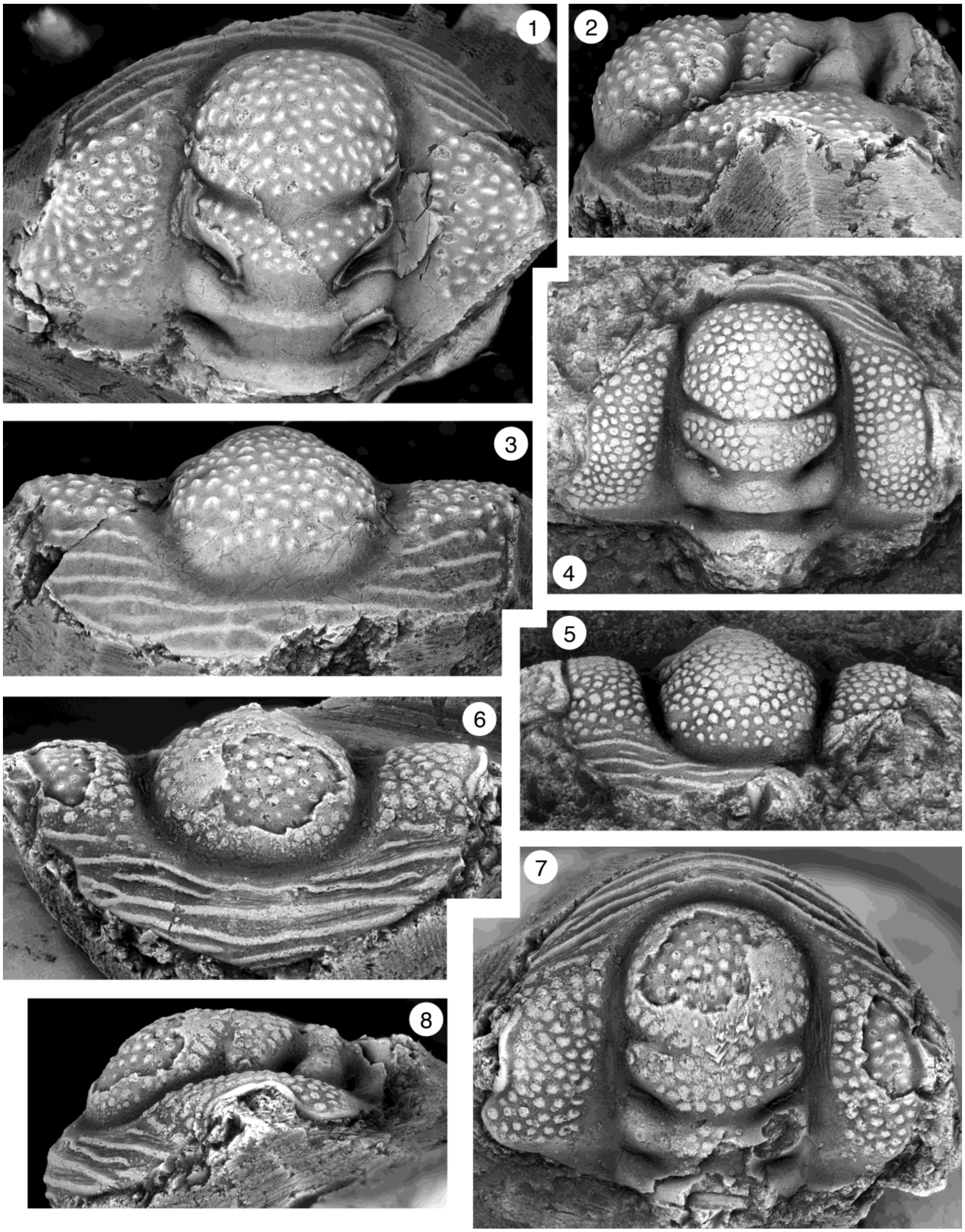
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Plate 10

Wilbernia cf. *diademata* (Hall, 1863) from the Honey Creek Formation, Bally Mountain, Kiowa County, collection BM 79.4T.

1–3, cranidium, OU 238170, dorsal, anterior and lateral views, x7.49.

Ptychaspis from the Honey Creek Formation, Bally Mountain, Kiowa County.

4–6, cranidium, OU 238171, dorsal, lateral and anterior views, x8.32, collection BM 82.1

7, incomplete cranidium, OU 238172, dorsal view, x7, collection BM79.4T.

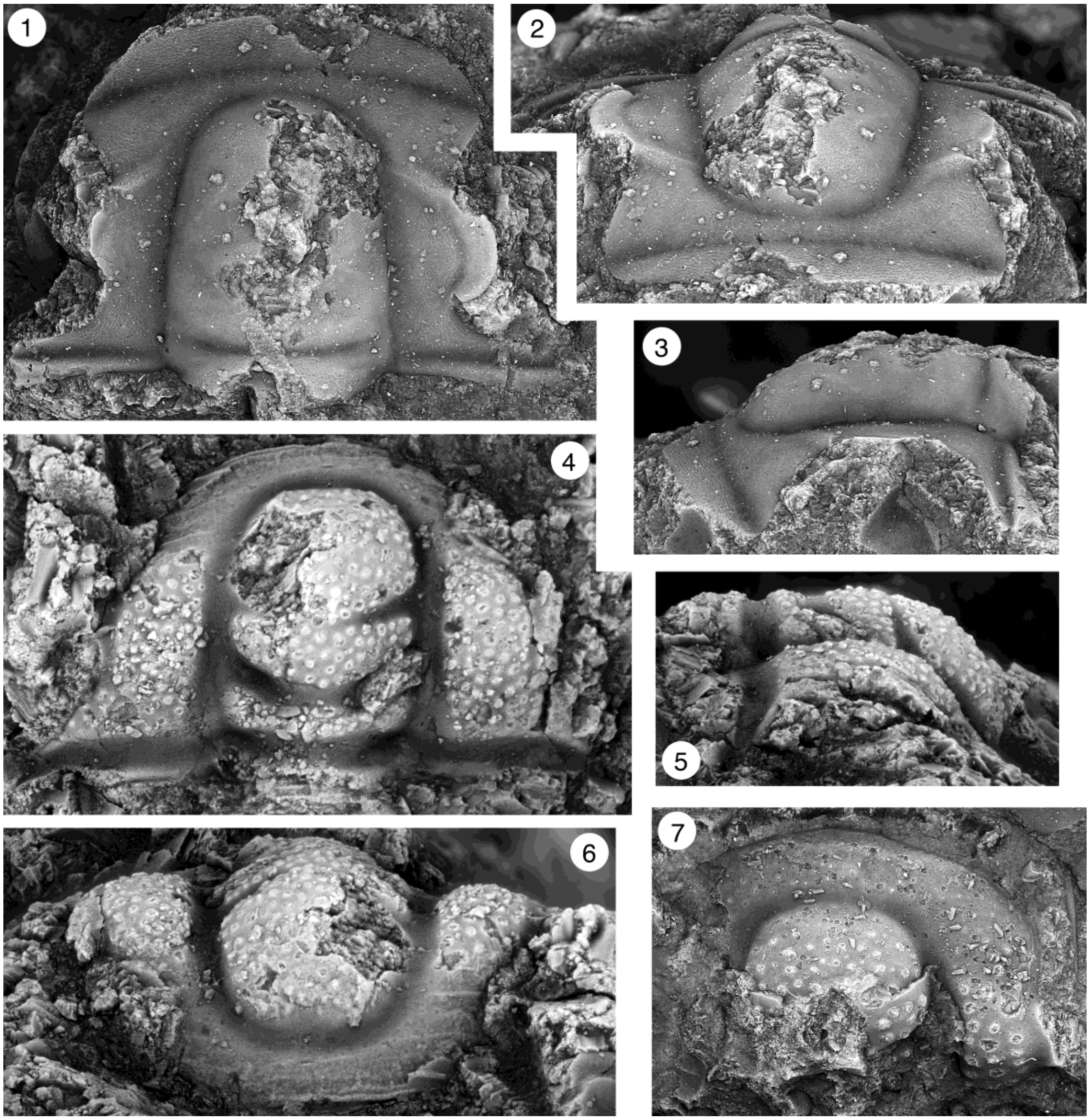
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Plate 11

Taenicephalus wichitaensis Resser, 1942, Honey Creek Formation, Blue Creek Canyon (Smithsonian loc. 9q), Wichita Mountains, Comanche County, Oklahoma. All cranidia.

1–4, USNM 108837c (paratype), anterior, dorsal, lateral and posterior views, x6.66 illustrated previously by Resser, 1942, pl. 21, fig. 13).

5, USNM 108837c (previously unfigured, associated with paratype), dorsal view, x7.49.

6, USNM 108837c (previously unfigured, associated with paratype), dorsal view, x9.98.

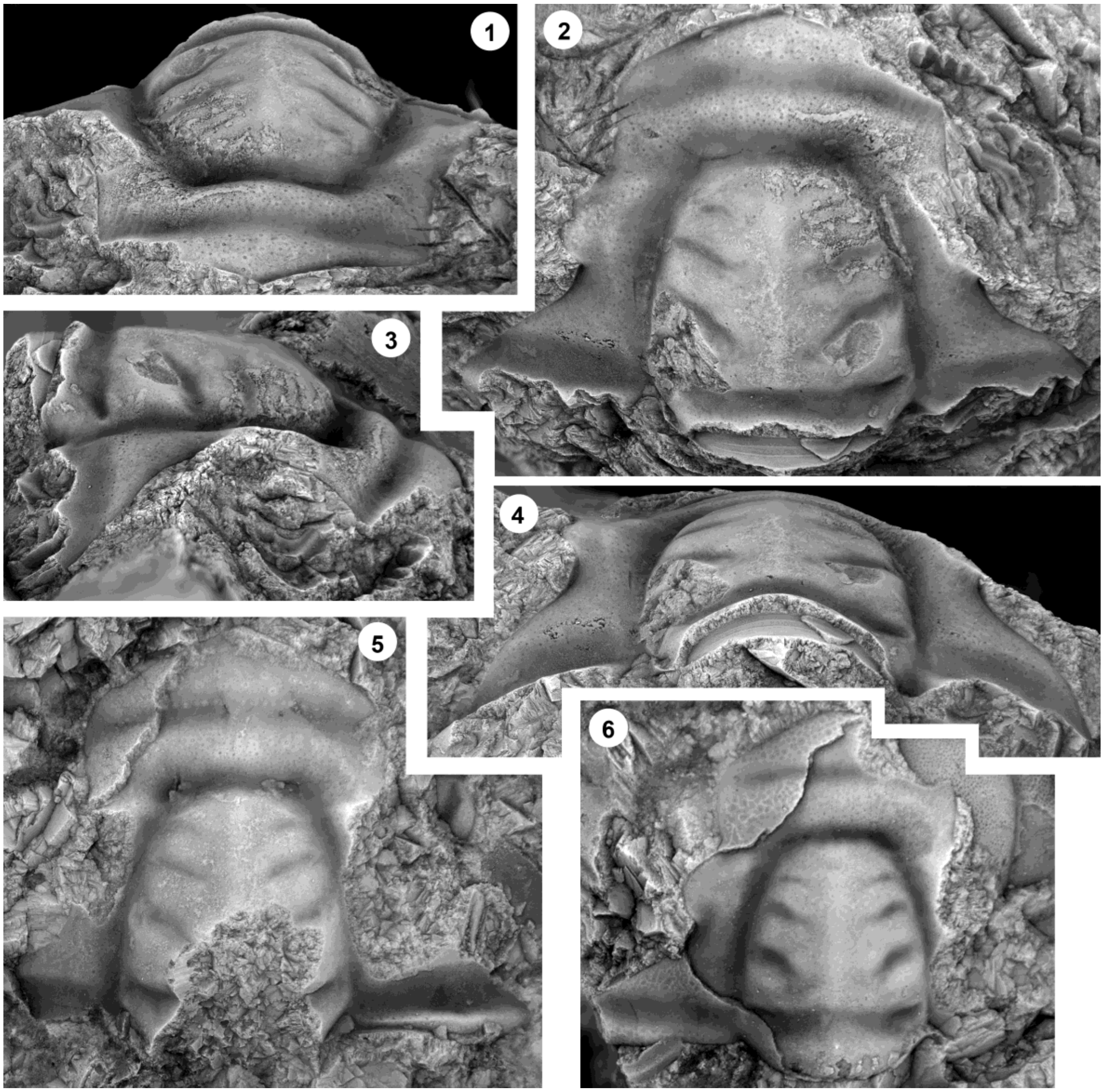
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Plate 12

Taenicephalus wichitaensis Resser, 1942, Honey Creek Formation, Blue Creek Canyon (Smithsonian loc. 9q), Wichita Mountains, Comanche County, Oklahoma. All cranidia except 7–9 (pygidium).

1–3, USNM 108837b (paratype), dorsal, anterior and lateral views, x7.07 (illustrated previously by Resser, 1942, pl. 21, fig. 17).

4–6, USNM 108837a (holotype), dorsal, anterior and lateral views, x7.07 (illustrated previously by Resser, 1942, pl. 21, figs. 14–15).

7–9, USNM 108837b (previously unillustrated specimen associated with paratype), dorsal, lateral and posterior views, x14.98.

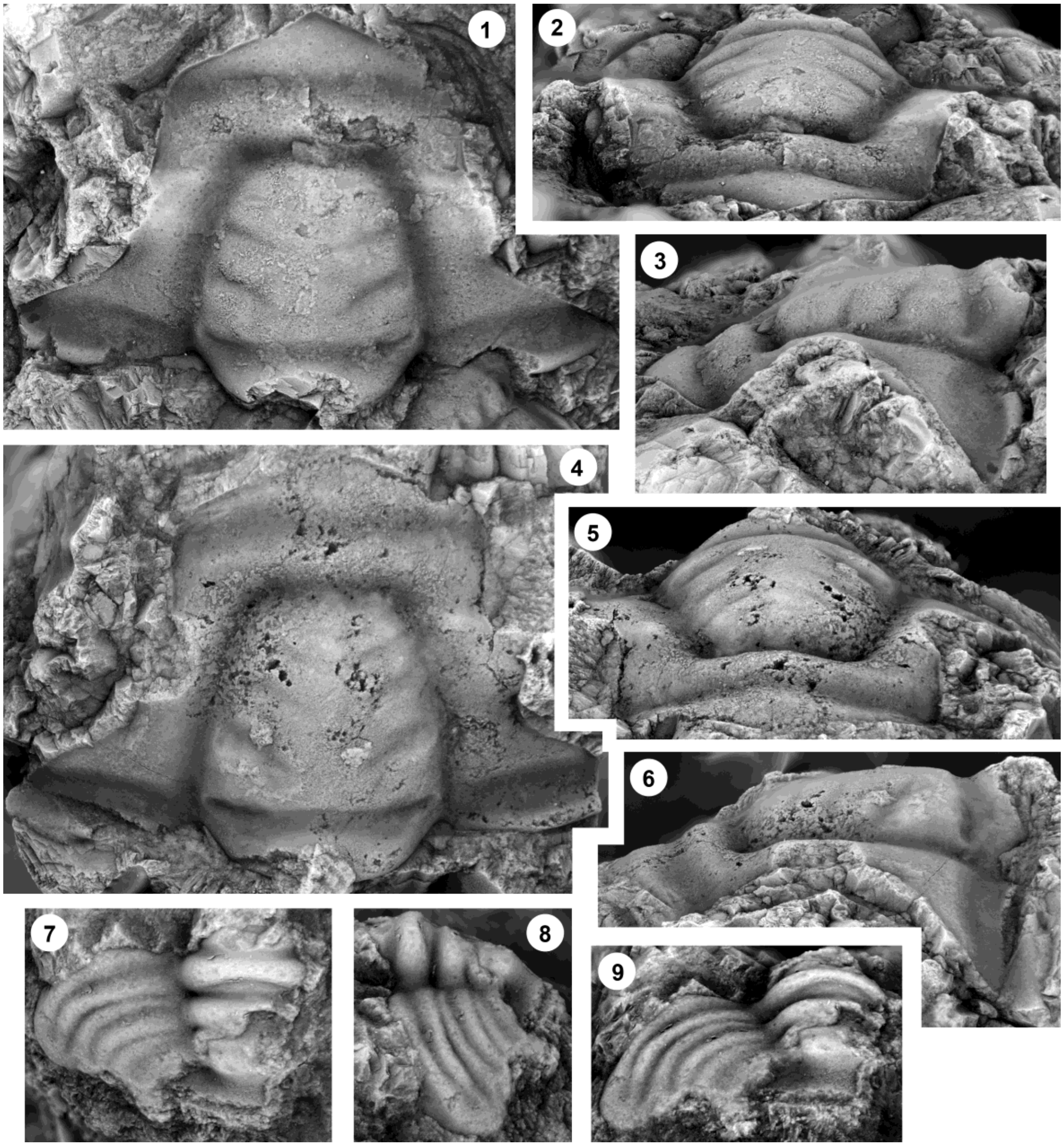
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Plate 13

Taenicephalus wichitaensis Resser, 1942, Honey Creek Formation, Bally Mountain, Kiowa County. All from collection BM 72 except 3–6 (BM 70.5) and all cranidia except 8–9 (librigena).

1, OU 238173, dorsal view, x12.48

2, OU 238174, dorsal view, x12.48

3–4, OU 238175, anterior, dorsal and lateral views, x10.82

6, OU 238176, dorsal view, x14.98.

7, OU 238177, dorsal view, x14.98.

8, 9, OU 238178, lateral and dorsal views, x12.48.

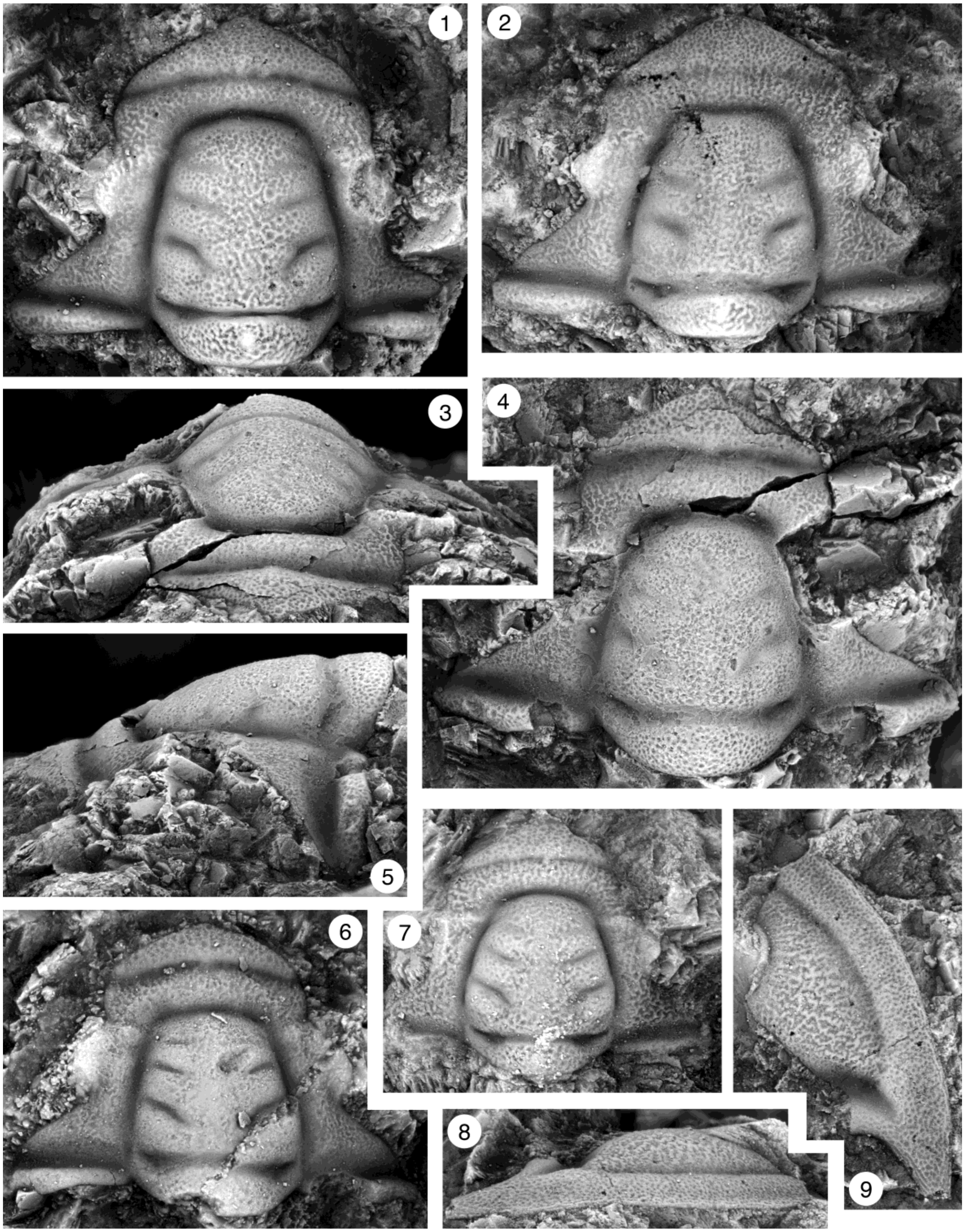
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Plate 14

Taenicephalus wichitaensis Resser, 1942, Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR3, collection KR3 33.3. All cranidia.

1–3, OU 238179, lateral, dorsal and anterior views, x6.66.

4–6, OU 238180, lateral, dorsal and anterior views, x9.98.

7, OU 238181, dorsal view, x9.98.

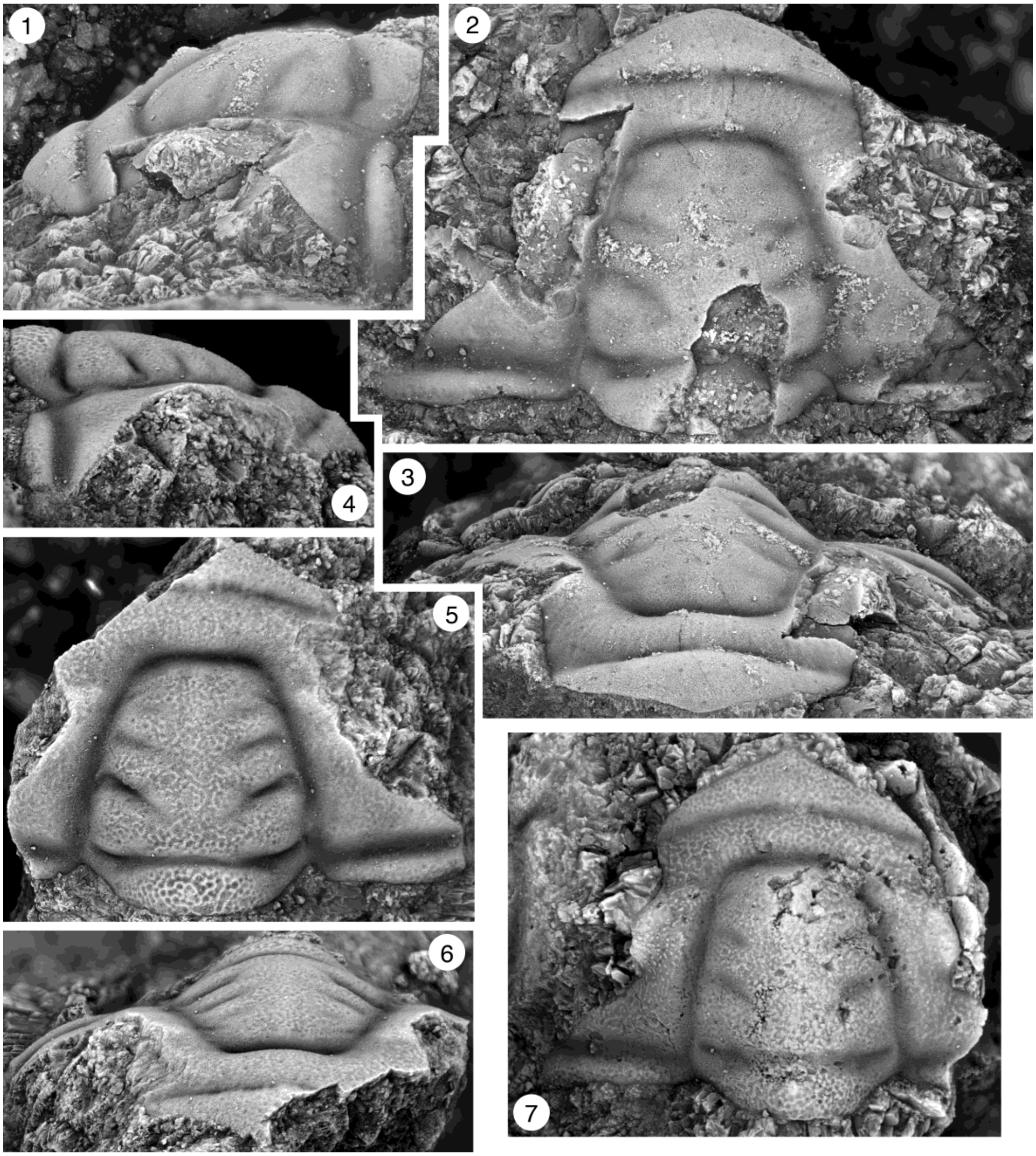
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Plate 15

Taenicephalus wichitaensis Resser, 1942, Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR3. 1–4, pygidia; 5–10, cranidia. All collection KR3 31T except 1, 2 (KR 33.3).

1, 2, OU 238182, dorsal and posterior views, x9.15.

3, 4, OU 238183, dorsal and posterior views, x11.65.

5–7, OU 238184, anterior, dorsal and lateral views, x8.32.

8–10, OU 238185, anterior, lateral, and dorsal views, x12.48.

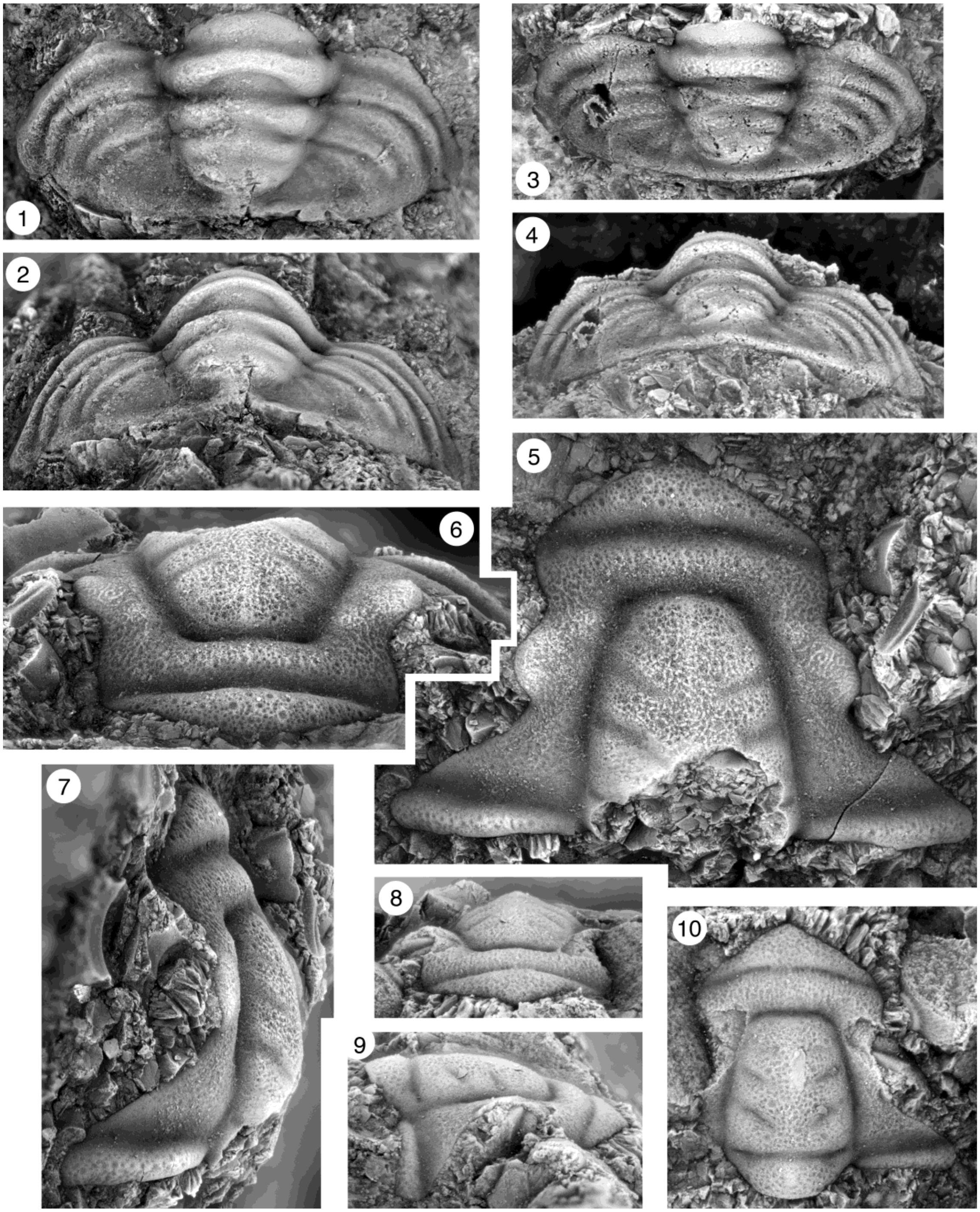
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Plate 16

Taenicephalus wichitaensis Resser, 1942, Morgan Creek Member, Wilberns Formation, central Texas. All cranidia.

1–3 USNM 185441, collection SS-60, Camp San Saba section, McCulloch County, anterior, dorsal and lateral views, x8.74 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 10).

4-6, USNM 185443, collection TC 944.5, Threadgill Creek section, Mason–Gillespie county line, dorsal, anterior and lateral views, x7.07 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 12).

7–9, USNM 185447, collection WC-898, White Creek section, Blanco County, dorsal, anterior and lateral views, x11.65 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 16).

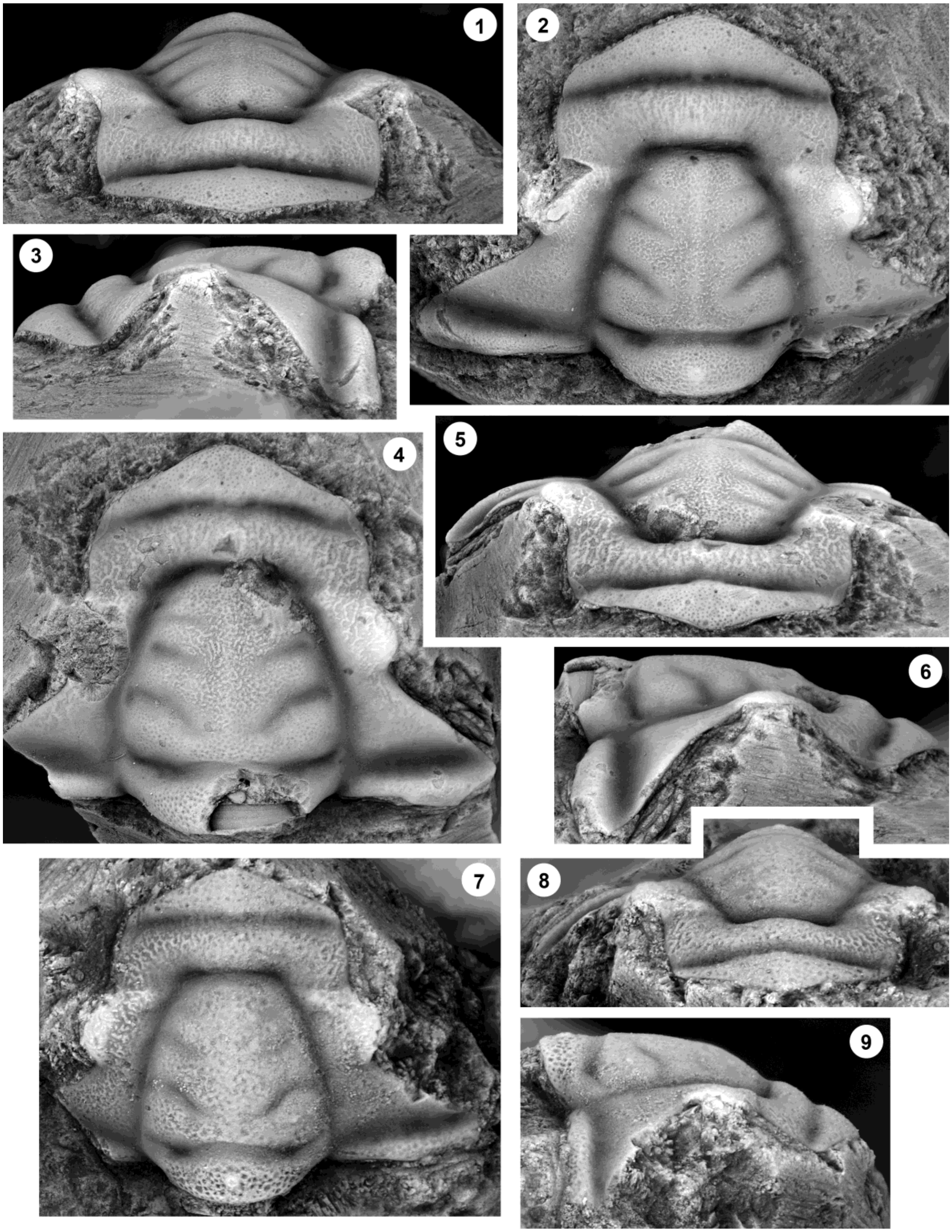
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Plate 17

Taenicephalus wichitaensis Resser, 1942, Morgan Creek Member, Wilberns Formation, central Texas. All cranidia.

1–3, USNM 185442, collection JR-136, James River section, Mason County, lateral, dorsal and anterior views, x5.82 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 11).

4–6, USNM 185445, collection TA-12, Tanyard section, San Saba County, dorsal, anterior and lateral views, x9.98 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 14).

7–9, USNM 185444, collection TA-12, Tanyard section, San Saba County, anterior, lateral and dorsal views, x6.66 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 13).

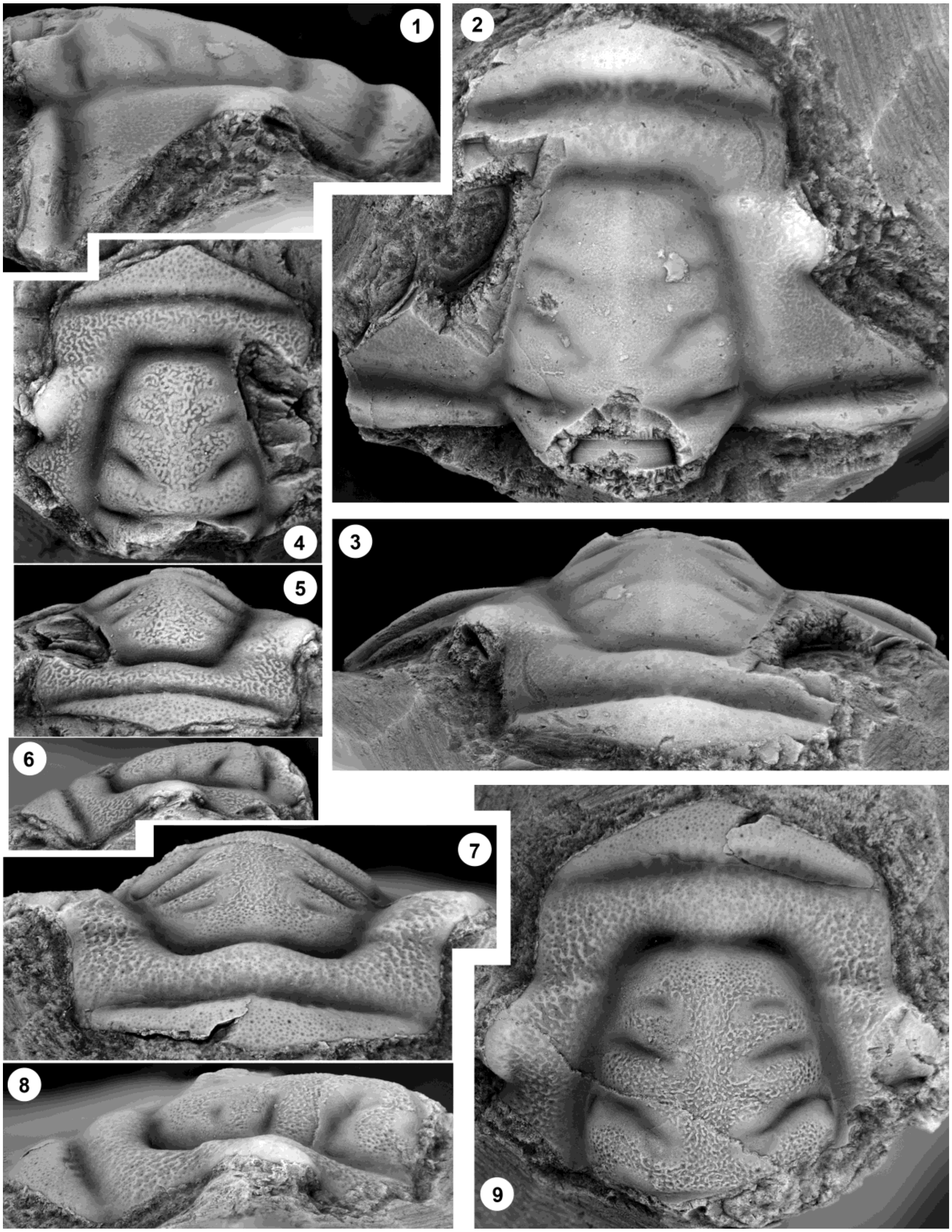
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Plate 18

Taenicephalus gouldi (Frederickson, 1949), Honey Creek Formation, Arbuckle Mountains, locality 14, Murray County, Oklahoma. All cranidia.

1-3, OU 5365 (paratype), dorsal, anterior and lateral views, x10.82 (illustrated by Frederickson, 1949, pl. 71, fig. 13).

4–6, OU 5364 (holotype), anterior, lateral and dorsal views, x13.31 (illustrated by Frederickson, 1949, pl. 71, fig. 11).

7, OU 5367 (topotype collected and identified by Frederickson), dorsal view, x10.82 (previously unfigured).

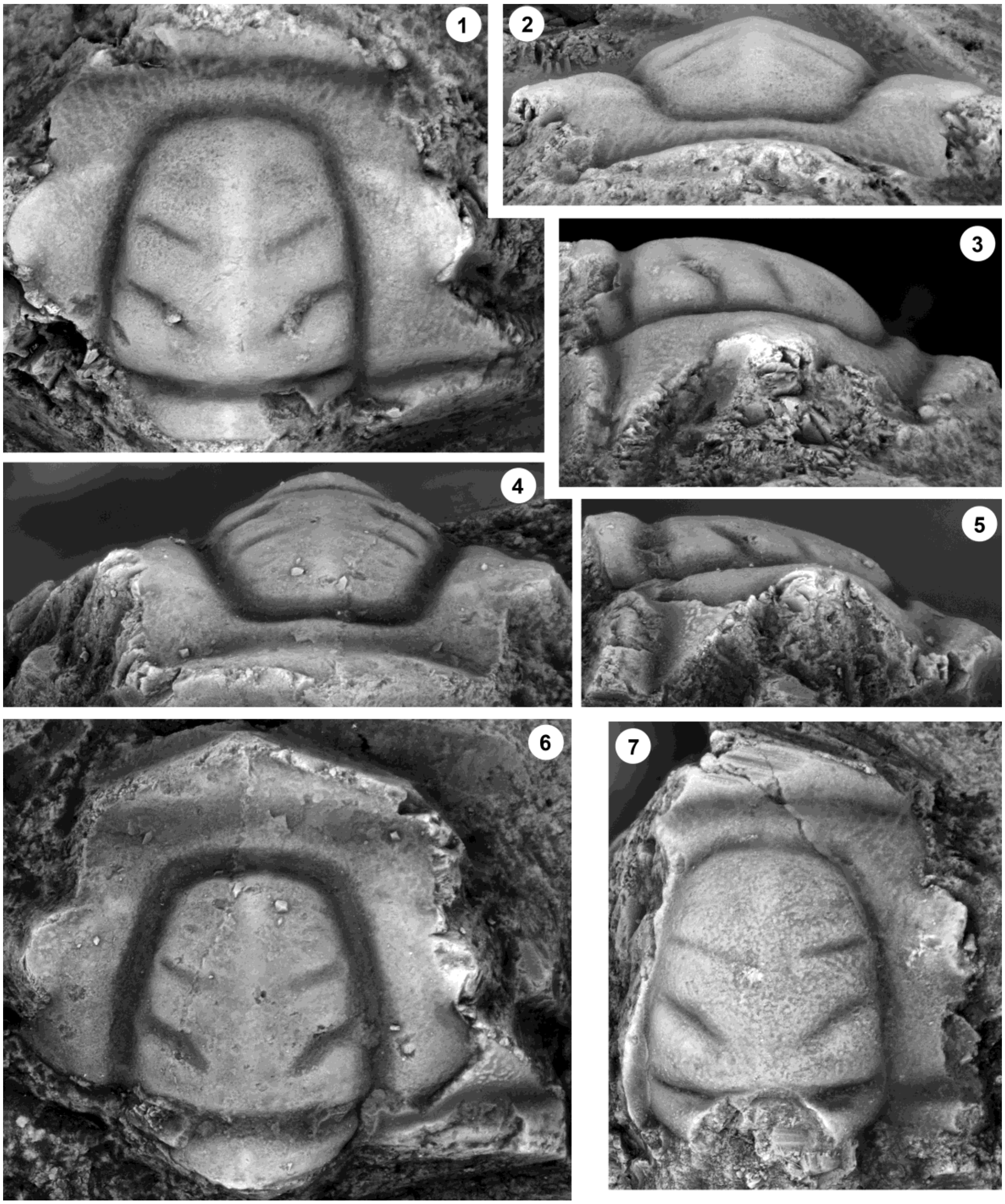
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Plate 19

Taenicephalus gouldi (Frederickson, 1949), Honey Creek Formation, Arbuckle Mountains, Royer Ranch section, collection RR-150 (Stitt, 1971b), Murray County, Oklahoma. 1–6, cranidia; 7–10, pygidia.

1–3, OU 238186, anterior, dorsal and lateral views, x10.82.

4–6, OU 238187, anterior, dorsal and lateral views, x9.98.

7, 8, OU 238188, dorsal and posterior views, x10.82.

9, 10, OU 238189, dorsal and posterior views, x12.48.

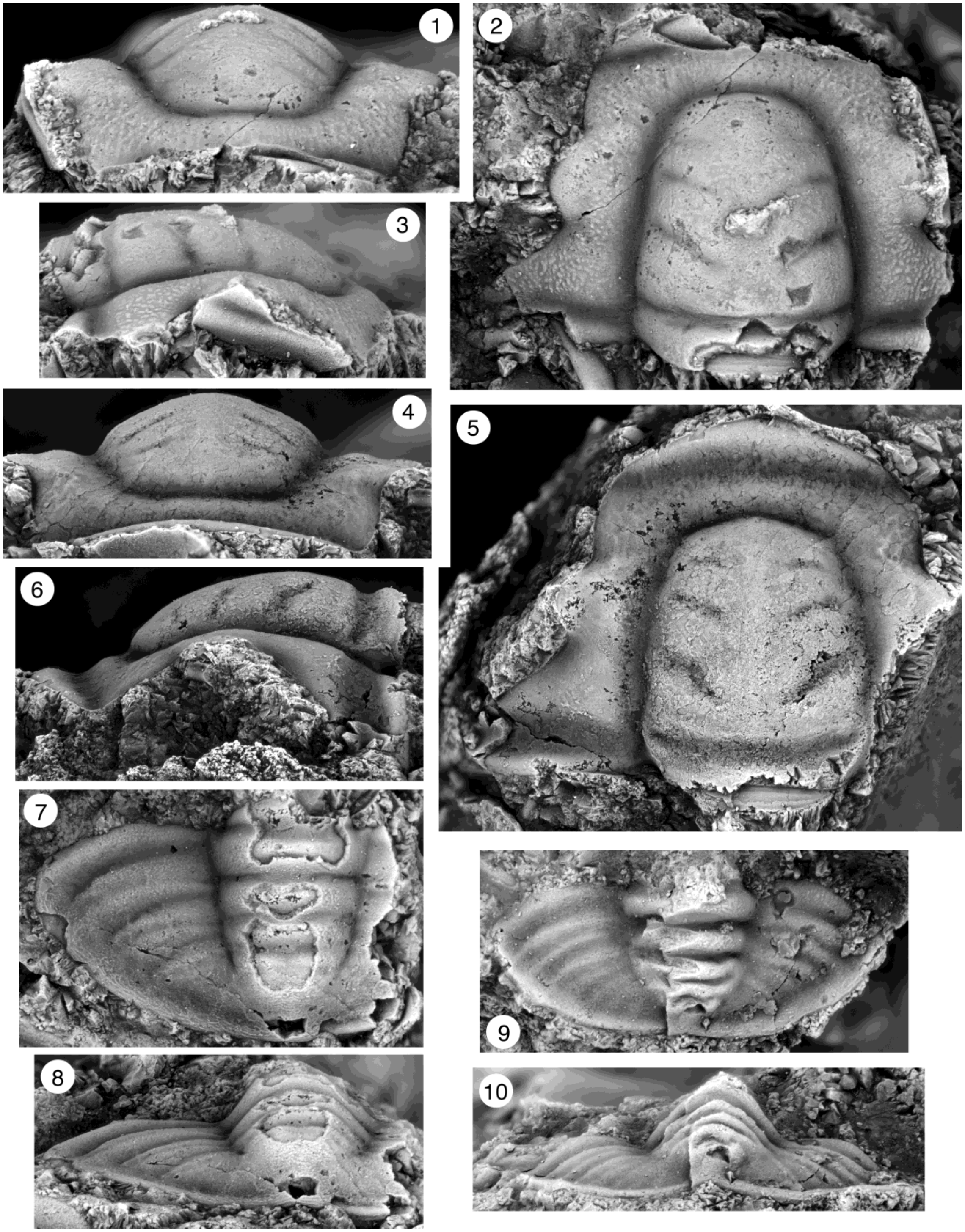
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Plate 20

Taenicephalus gouldi (Frederickson, 1949), from the Honey Creek Formation, Oklahoma (4–6) and the Morgan Creek Member, Wilberns Formation, collection TC 939, Threadgill Creek section, which extends across the Mason–Gillespie county line, central Texas (1–3, 7–9).

1-3, cranidium, USNM 185436, lateral, dorsal and anterior views, x9.98 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 5).

4–6, cranidium, OU 5365 (paratype), lateral, anterior, and dorsal views, x9.15 (illustrated by Frederickson, 1949, pl. 71, fig. 12), Arbuckle Mountains, locality 14, Murray County, Oklahoma.

7–9, pygidium, USNM 185439, lateral, dorsal and posterior views, x6.24 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 8).

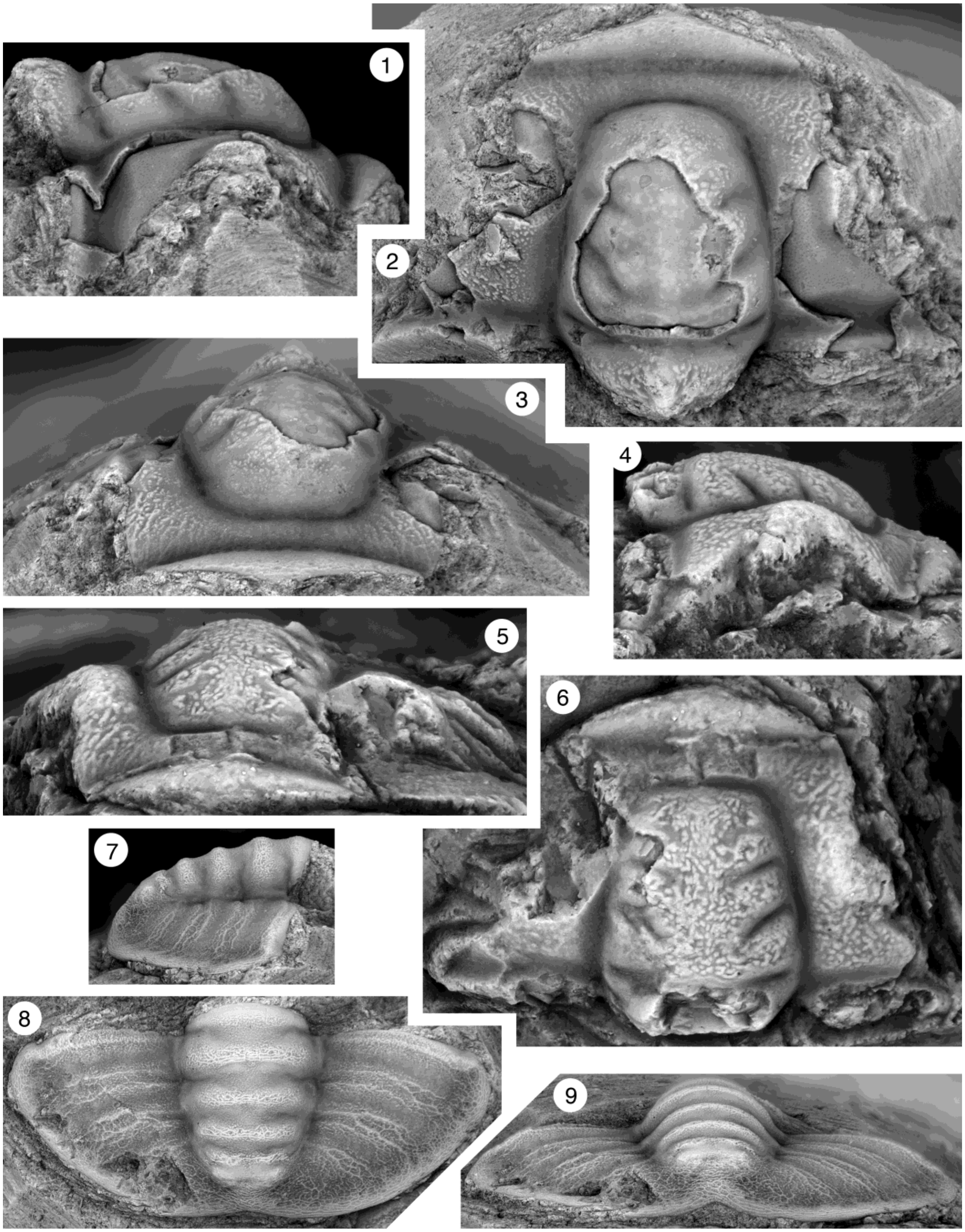
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Plate 21

Taenicephalus gouldi (Frederickson, 1949), Morgan Creek Member, Wilberns Formation, central Texas. All cranidia and all from collection SK 204, Klett–Walker section, western Blanco County.

1–3, USNM 185433, dorsal, lateral and anterior views, x8.32 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 2).

4, USNM 185434, dorsal view, x6.66 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 3).

5–7, USNM 185432, lateral, dorsal and anterior views, x9.15 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 1).

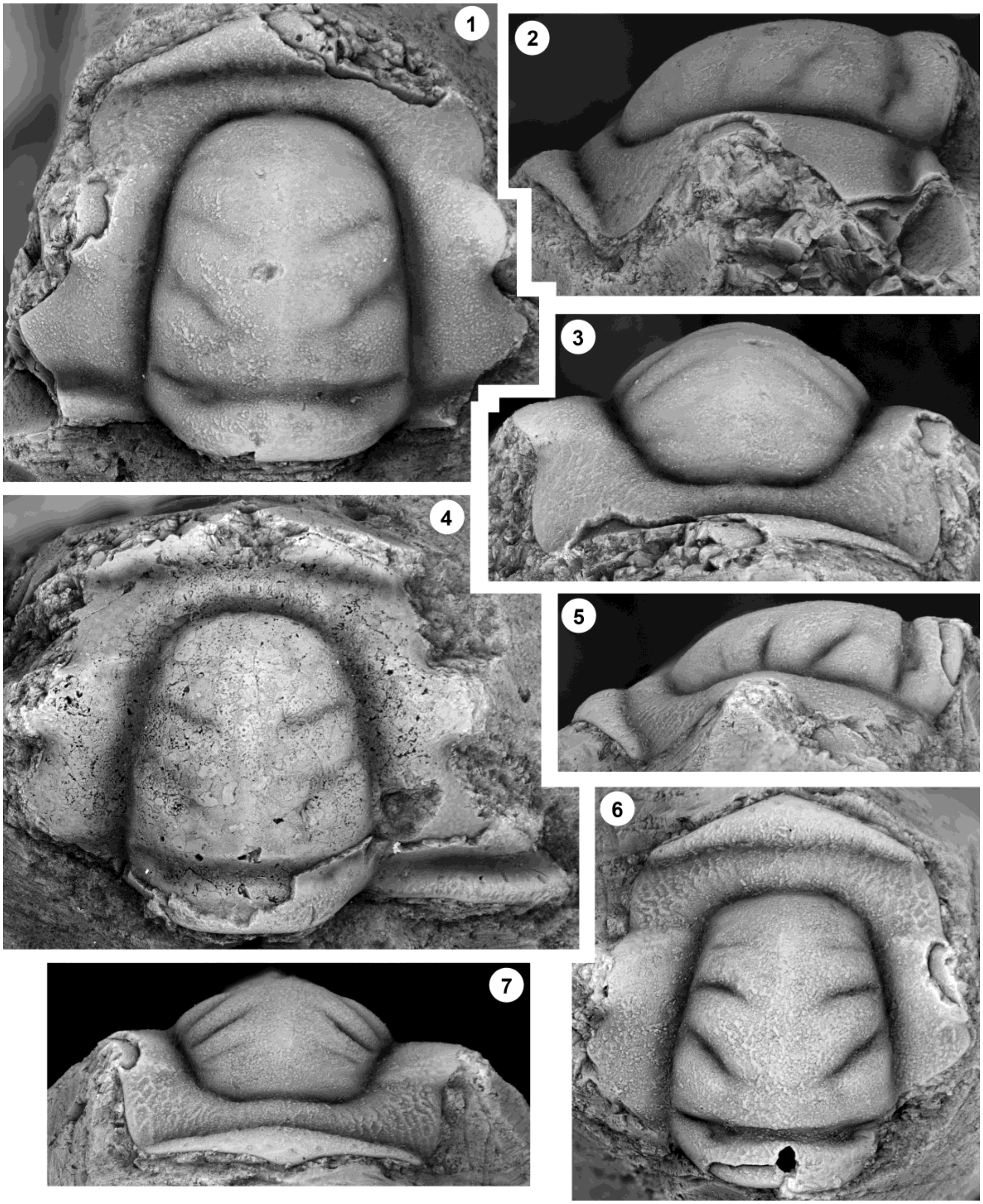
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Plate 22

Taenicephalus gouldi (Frederickson, 1949), Morgan Creek Member, Wilberns Formation, central Texas. All cranidia from collection TC 939, Threadgill Creek section, which extends across the Mason–Gillespie county line, except 7, 8 (librigena from collection JR 126.3, James River section, Mason County).

1–3, USNM 185483, dorsal, lateral and anterior views, x10.82 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 7).

4–6, USNM 185437, lateral, dorsal and anterior views, x10.82 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 6).

7, 8, USNM 185440, lateral and dorsal views, x9.98 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 9).

9, 10, USNM 185435, lateral and dorsal views, x9.98 (illustrated previously by Bell and Ellinwood, 1962, pl. 57, fig. 4).

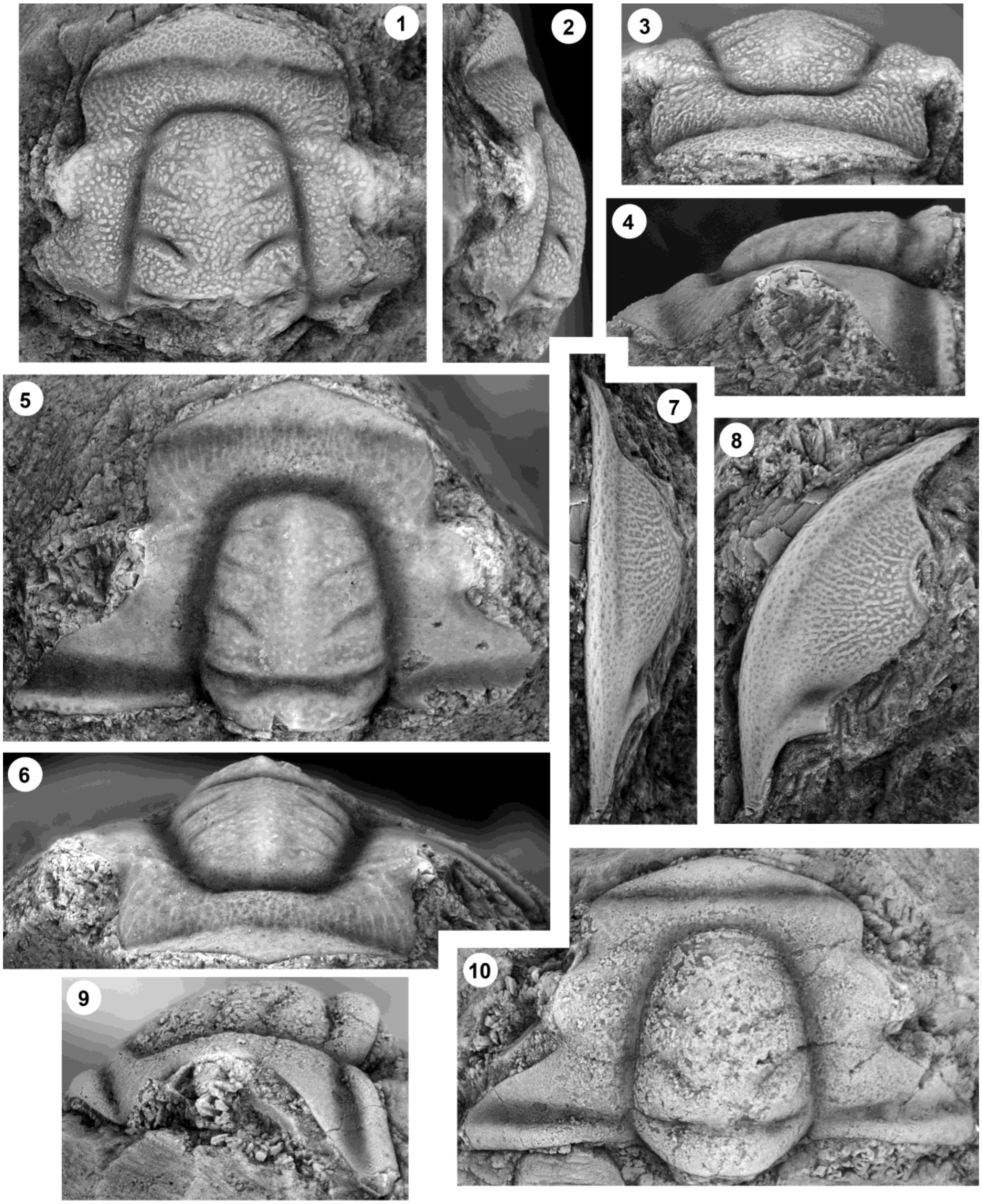
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Plate 23

Taenicephalus kallisti sp.nov., Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1, collection KR1 29.9. All paratypes except 4–6 (holotype).

1–3, OU 238190, lateral, dorsal, and anterior views, x11.65.

4–6, OU 238191, anterior, dorsal and lateral views, x12.48.

7, OU 238192, dorsal view, x12.48.

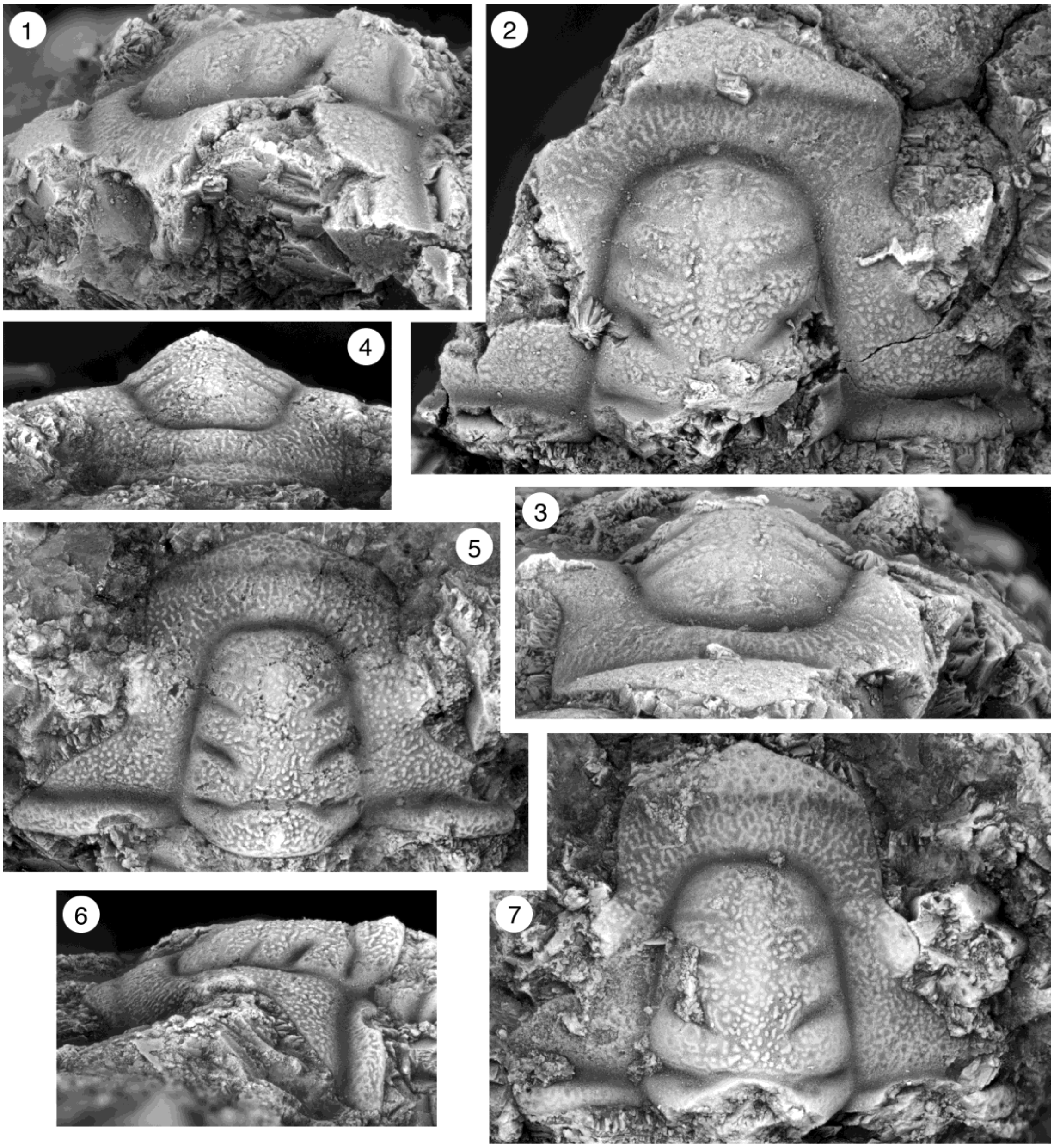
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Plate 24

Orygmaspis llanoensis (Walcott, 1890), Honey Creek Formation, Arbuckle and Wichita Mountains. All cranidia, and all Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1 except 1–3 (Frederickson [1949, p. 346] locality 11, Arbuckle Mountains, Murray County, Oklahoma).

1–3, OU 5335, dorsal, lateral and anterior views, x4.99 (illustrated previously by Frederickson, 1949, pl. 71, fig. 19).

4, OU 238193, dorsal view, x8.32, collection KR1 31.7T.

5, OU 238194, dorsal view, x6.66, collection KR1 30.

Taenicephalus kallisti sp.nov., Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1, collection KR1 29.9. All cranidia except 6 (librigena) and all paratypes.

6, OU 238195, dorsal view, x9.15.

7, OU 238196, dorsal view, x11.65.

8, OU 238197, dorsal view, x12.48.

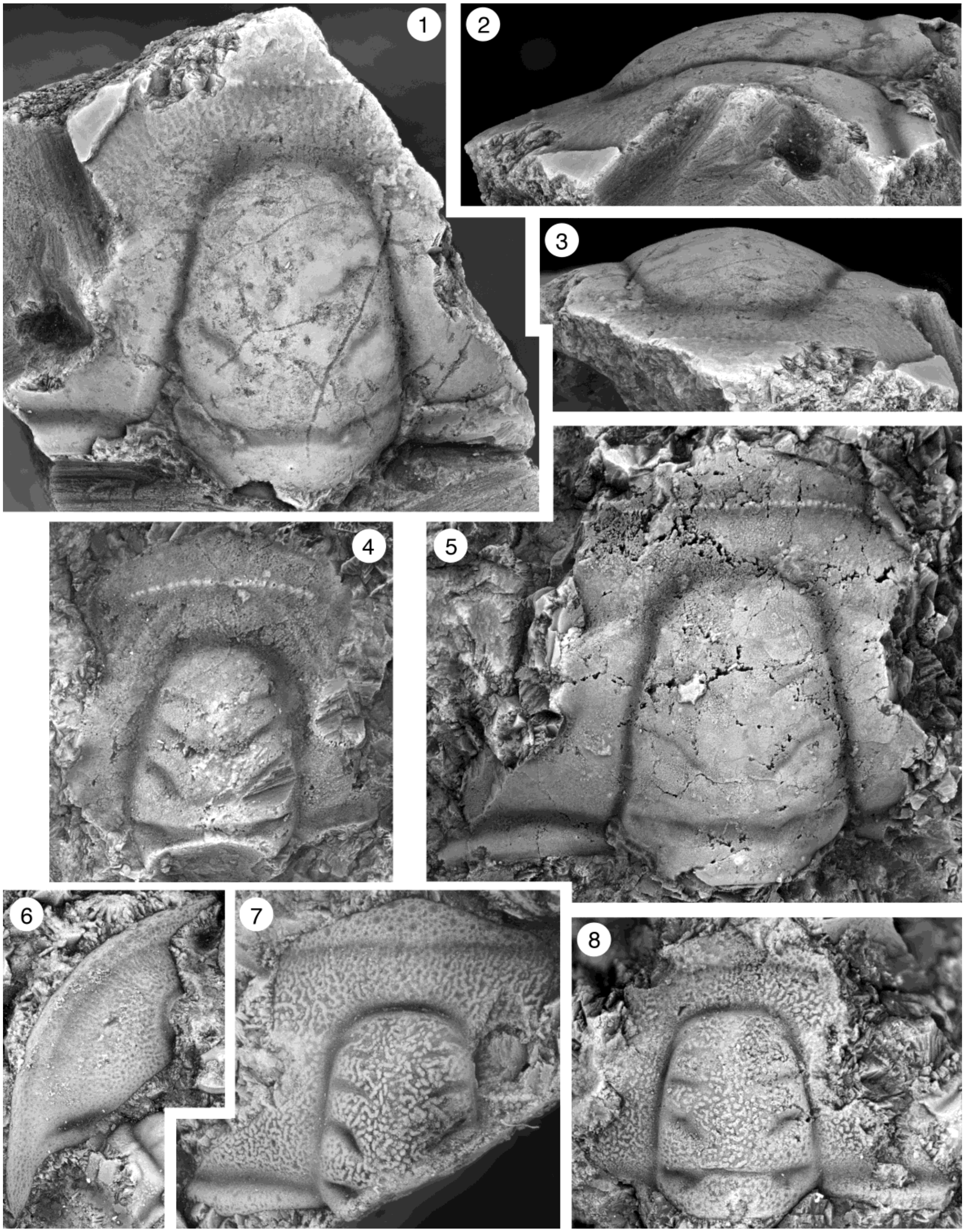
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Plate 25

Orygmaspis (*Orygmaspis*) *firma* Frederickson, 1949, Honey Creek Formation, Arbuckle Mountains, Murray County, Fredrickson (1949) locality 14. Both cranidia.

1–3, OU 5321 (holotype), dorsal, lateral and anterior views, x4.99 (illustrated previously by Frederickson, 1949, pl. 71, figs. 15, 16).

4–6, OU 5294 (paratype) dorsal, lateral and anterior views, x4.16 (illustrated previously by Frederickson, 1949, pl. 71, fig. 18).

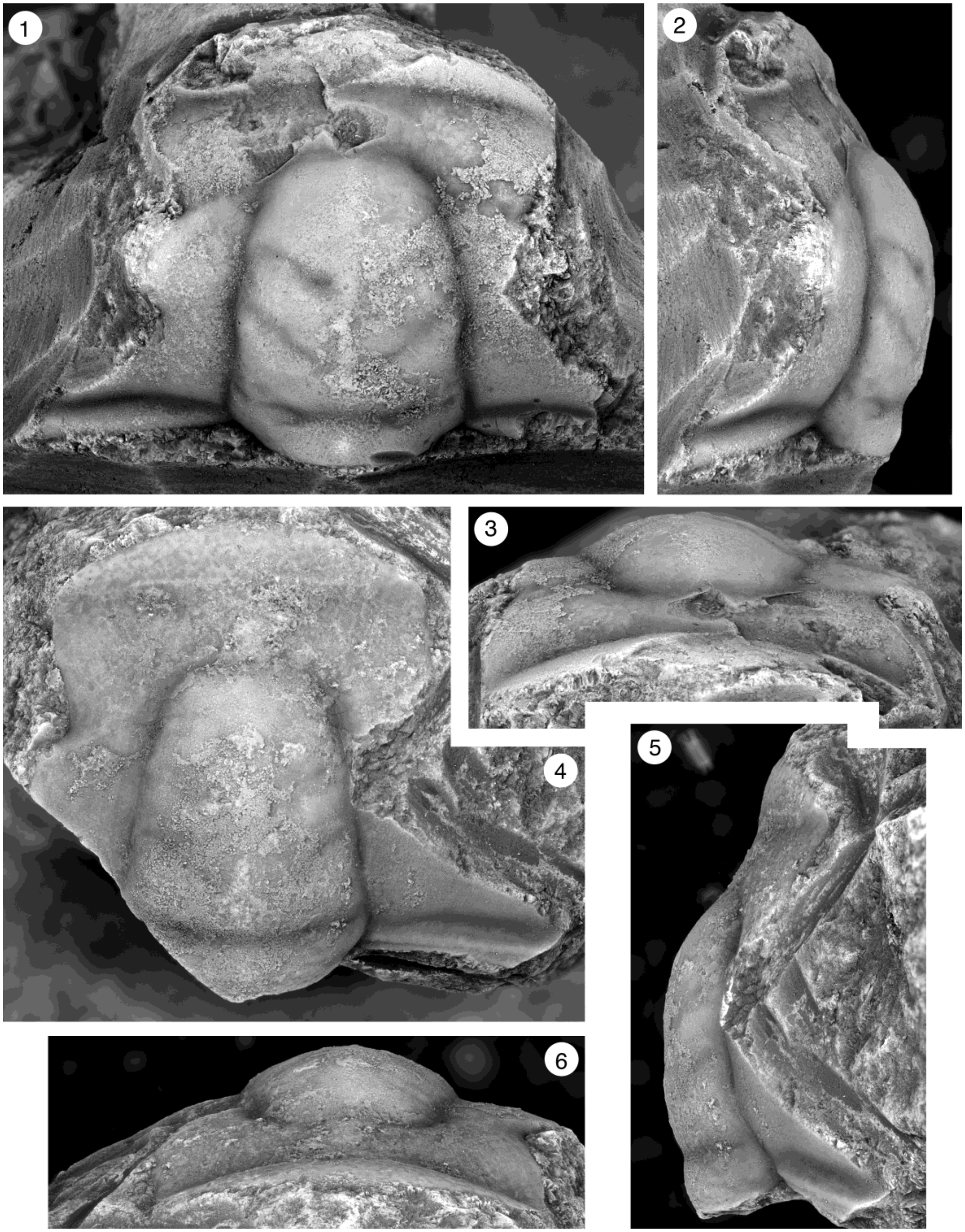
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Plate 26

Idahoia lirae (Frederickson, 1949), Honey Creek Formation, Wichita Mountains, west side of Blue Creek Canyon, Comanche County, Fredrickson (1949) locality 6. Both cranidia.

1–3, OU 4277 (holotype), dorsal, lateral and anterior views, x6.66 (illustrated previously by Westrop, 1986, pl. 16, fig. 5).

4–6, OU 4275, dorsal, lateral and anterior views, x6.66 (illustrated previously by Westrop, 1986, pl. 16, figs. 6, 7).

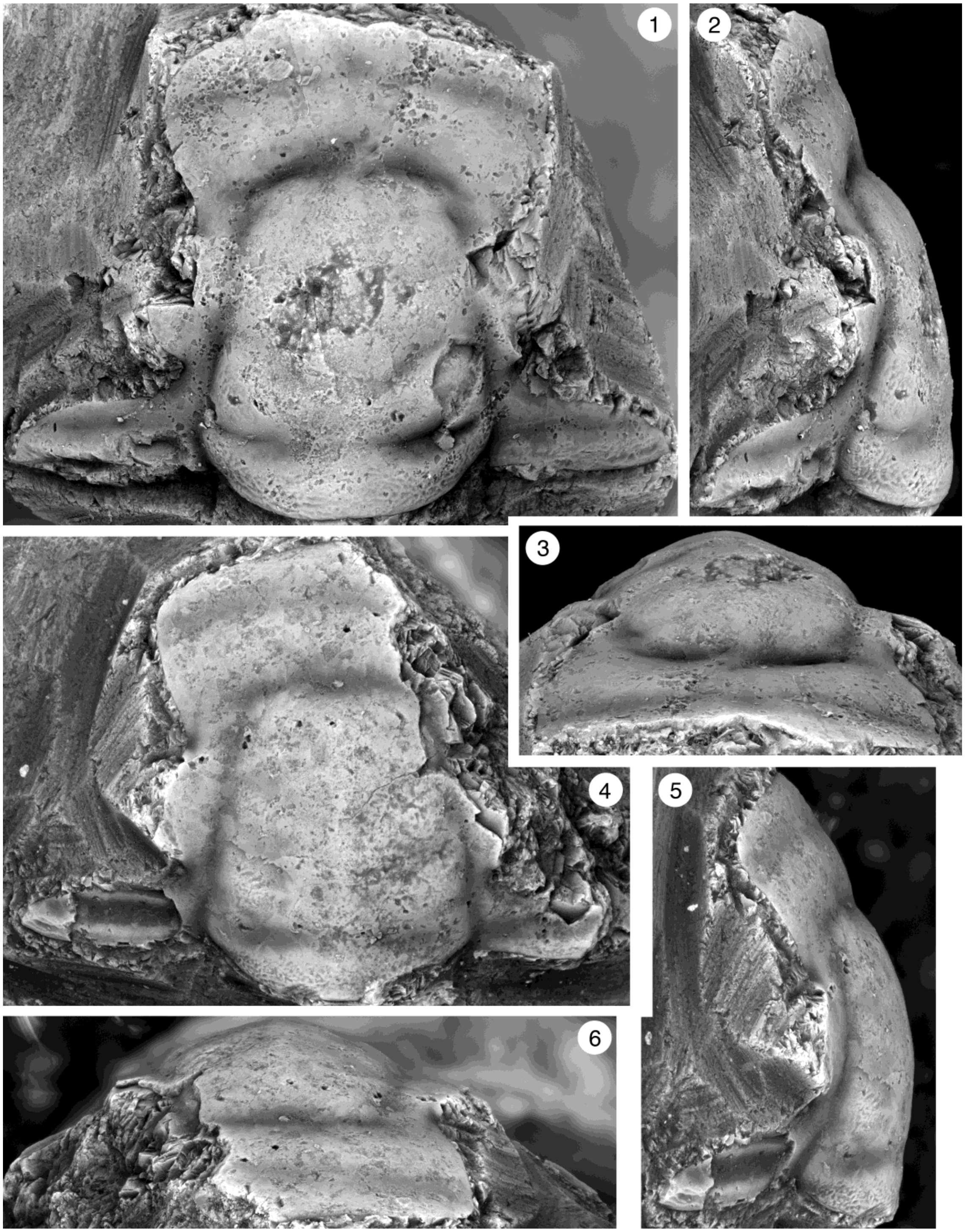
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Plate 27

Idahoia czukayi sp.nov., Honey Creek Formation, Ring Top Mountain, Wichita Mountains, Comanche County, Oklahoma, section KR1, collection KR1 39. All cranidia and all paratypes except 1–3 (holotype).

1–3, OU 238198, dorsal, anterior and lateral views, x6.66.

4, OU 238199, dorsal view, x5.41.

5, OU 238200, dorsal view, x5.2.

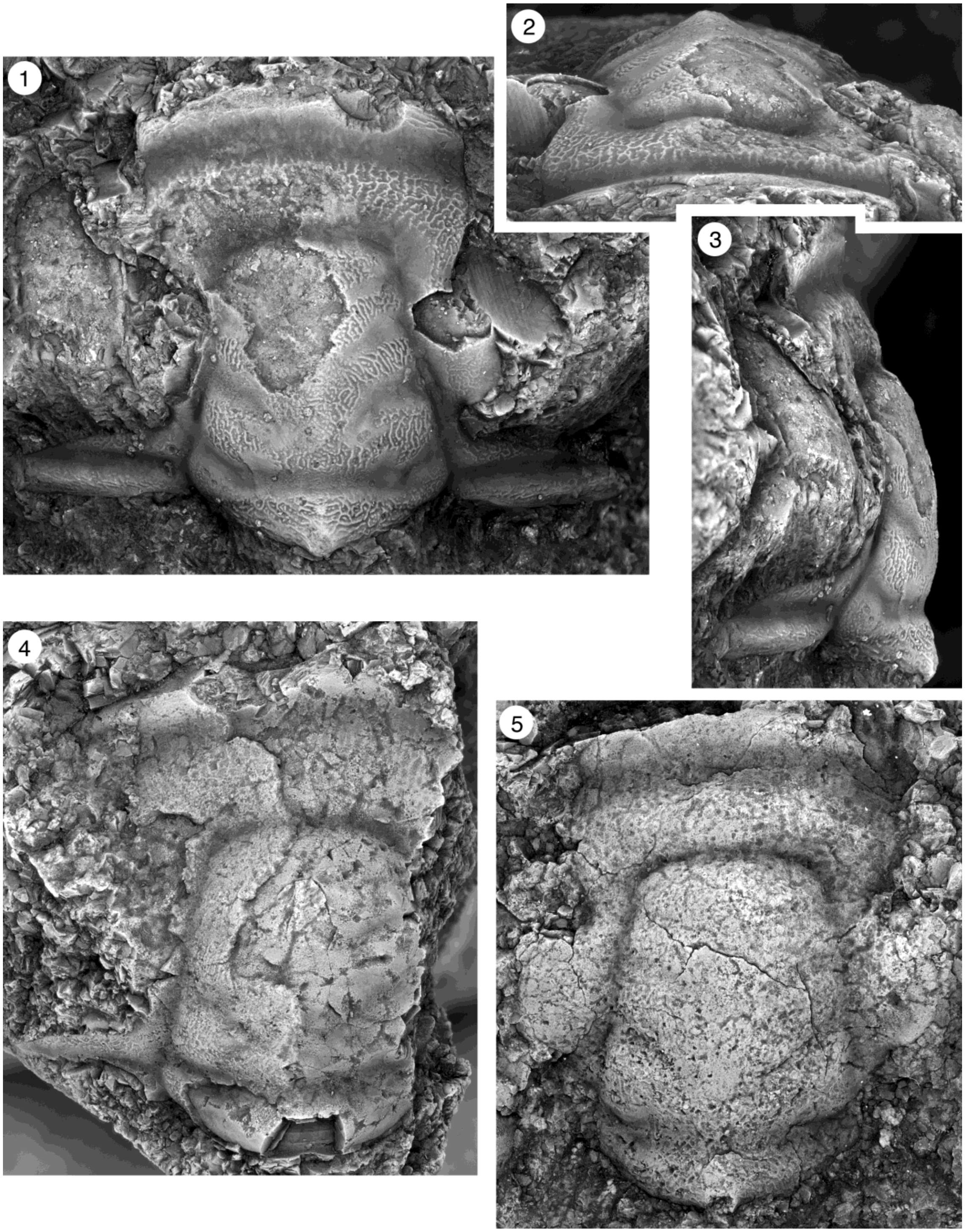
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Plate 28

Conaspis testudinata Ellinwood, in Bell and Ellinwood, 1962, Honey Creek Formation Bally Mountain section, Kiowa County, Oklahoma, collection BM 70.5. All cranidia except 7 (librigena).

1, 2, OU 238201, lateral and dorsal views, x9.98.

3–5, OU 238202, dorsal anterior and lateral views, x11.65.

6, OU 238203, dorsal view, x12.48.

7, OU 238204, dorsal view, x9.98.

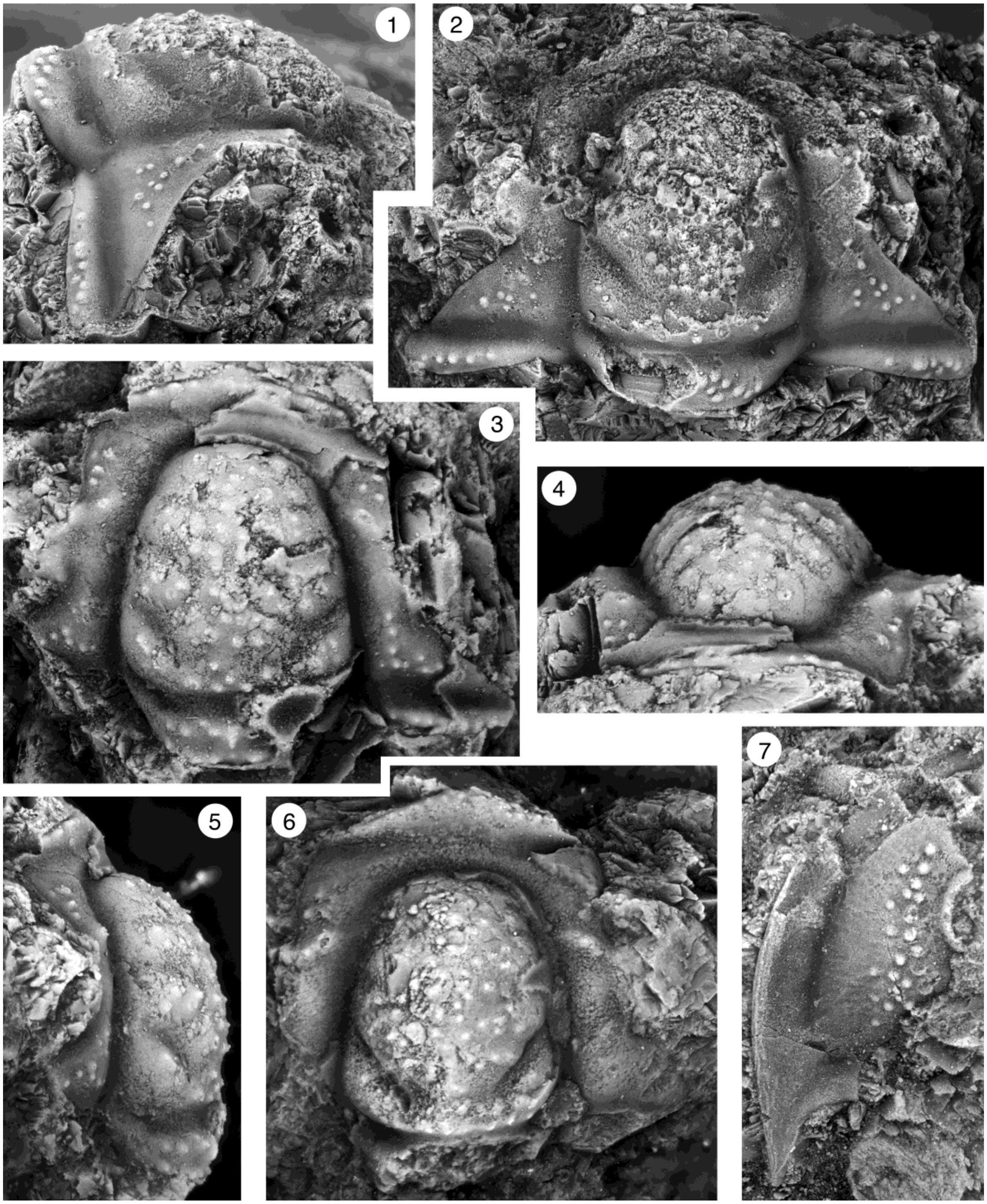
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Plate 29

Conaspis testudinata Ellinwood, in Bell and Ellinwood, 1962, Honey Creek Formation Bally Mountain section, Kiowa County, Oklahoma, collection BM 70.5.

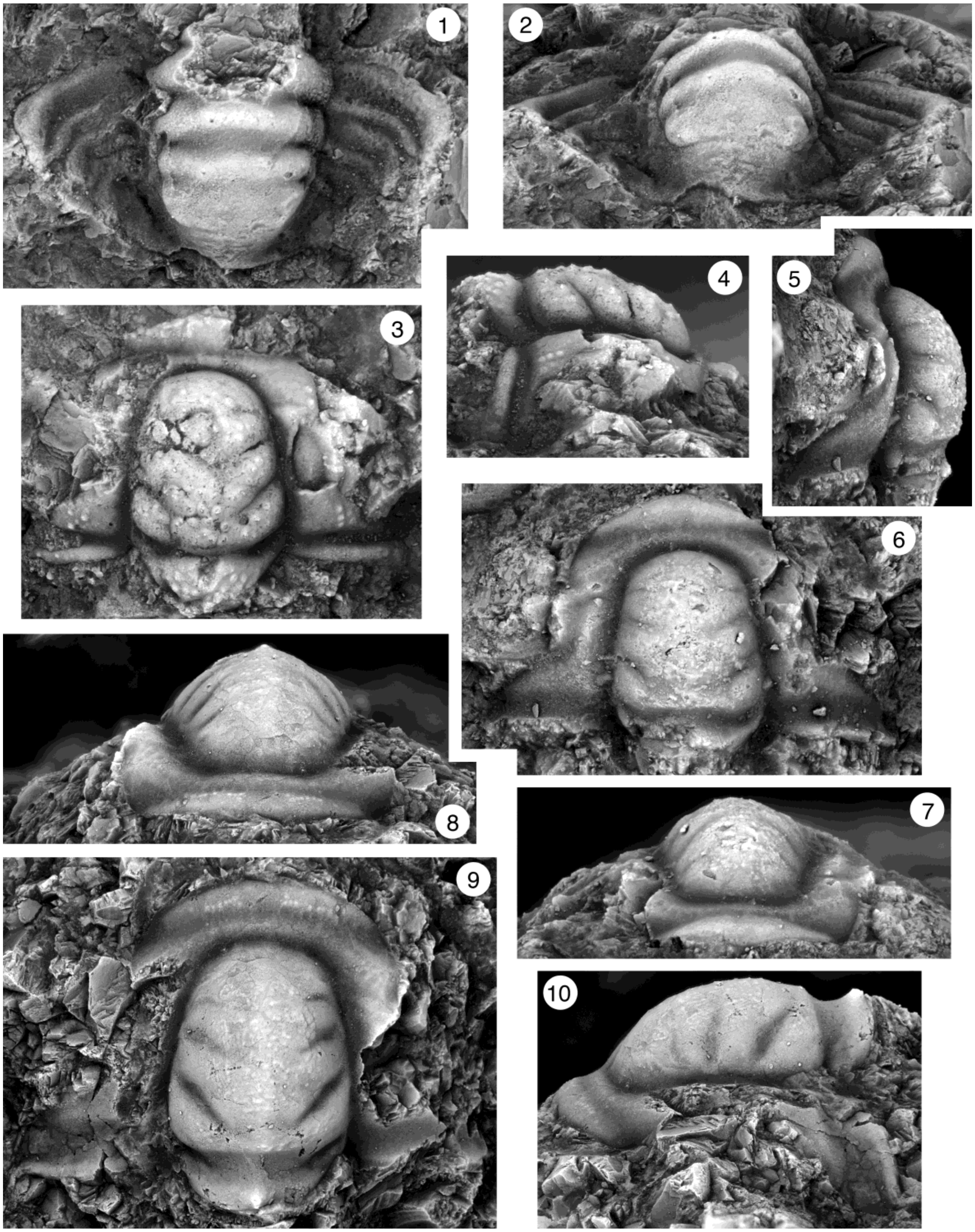
1, 2, pygidium, OU 238205, dorsal and posterior views, x14.98.

3, 4, cranidium, OU 238206, dorsal and lateral views, x13.31.

Conaspis cf. *leptoholcis* Longacre, 1970, Honey Creek Formation, Ring Top Mountain, Comanche County, Oklahoma, section KR1, collection KR1 30.

5–7, cranidium, OU 238207, lateral, dorsal and anterior views, x11.65.

8–10, cranidium, OU 238208, anterior, dorsal and lateral views, x6.66.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APPENDIX B: Collection Composition

KR1 29.9	**Cranidia**	**Pygidia**	**Librigenae**	**Total Sclerites**	**Individuals**
Orygmaspis llanoensis	6	0	0	6	6
Taenicephalus kallisti	20	4	2	26	20
Conaspis testudinata	5	0	1	6	5
					31
KR1 30					
Orygmaspis llanoensis	8	0	0	8	8
Taenicephalus kallisti	37	1	2	40	37
Conaspis testudinata	16	0	3	19	16
				Total:	61
KR1 31.7					
Orygmaspis llanoensis	3	0	0	0	3
Taenicephalus kallisti	5	0	0	0	5
Conaspis tetudinata	3	0	0	0	3
				Total:	11
KR1 35.9					
Orygmaspis llanoensis	0	0	0	0	0
Taenicephalus wichitaensis	6	3	1	10	6
Conaspis testudinata	0	0	1	1	1
				Total:	7
KR1 39					
Idahoia czukay	1	0	1	2	1
Idahoia lirae	1	0	0	1	1

KR3 31	**Cranidia**	**Pygidia**	**Librigenae**	**Total Sclerites**	**Individuals**
Orygmaspis llanoensis	6	0	0	6	6
Taenicephalus kallisti	20	4	2	26	20
Conaspis testudinata	5	0	1	6	5
					31
KR3 33.3					
Orygmaspis llanoensis	8	0	0	8	8
Taenicephalus kallisti	37	1	2	40	37
Conaspis testudinata	16	0	3	19	16
				Total:	61
KR3 33.8					
Taenicephalus wichitaensis	17	2	0	19	17
				Total:	17
KR3 34					
Orygmaspis llanoensis	3	0	0	0	3
Taenicephalus kallisti	5	0	0	0	5
Conaspis tetudinata	3	0	0	0	3
				Total:	11
BM 70.5					
Taenicephalus wichitaensis	14	1	5	20	14
Conaspis testudinata	6	0	1	7	6
				Total:	20
BM 72					
Taenicephalus wichitaensis	15	5	4	24	15
Conaspis testudinata	2	0	1	3	2
				Total:	
BM 79.4 T					
Monocheilus reginae	7	1	5	13	7
Ptychaspis sp. indet.	2	1	0	3	2
Wilbernia cf. diademata	1	0	0	1	1

				Total:	10