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SYSTEMATICS AND PALEOECOLOGY OF TRILOBITES FROM THE LATE ORDOVICIAN VIOLA GROUP, SOUTH-CENTRAL OKLAHOMA

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SYSTEMATICS AND PALEOECOLOGY OF TRILOBITES FROM THE LATE ORDOVICIAN VIOLA GROUP, SOUTH-CENTRAL OKLAHOMA

A Dissertation APPROVED FOR THE
SCHOOL OF GEOLOGY AND GEOPHYSICS

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TABLE OF CONTENTS

Chapter 1: Introduction 1

Chapter 2: Sedimentary facies and trilobite biofacies along an Ordovician shelf to basin gradient, Viola Group, south-central Oklahoma 6

Chapter 3: A systematic revision of *Thaleops* (Trilobita: Illaenidae) with new species from the Middle and Late Ordovician of Oklahoma and New York 58

Chapter 4: Isoteline trilobites of the Viola Group (Ordovician: Oklahoma): phylogenetic relationships and stratigraphic occurrence 210

Chapter 5: Cheirurids from the Late Ordovician Viola Group, south-central Oklahoma 394

Chapter 6: Remaining trilobites of the Viola Group 457

Appendix 1: Trilobite abundance data 523

CHAPTER 1:

INTRODUCTION

The Viola Group is an important oil and gas reservoir that has been producing since at least 1913 (Northcutt and Johnson, 1997). Although economic factors are easiest to measure, the highly fossiliferous Viola Group is also of scientific interest in a number of areas. In south-central Oklahoma, deposition in a tectonically subsiding basin preserved a nearly continuous Upper Ordovician succession (see chapter 2). The Viola Group offers a textbook example of depositional systems along a carbonate ramp. The Viola Group and its correlatives in the Ouachita trough are biostratigraphically important because they allow correlation of laterally equivalent graptolite biofacies (Finney, 1986). Fossils from Oklahoma provide a critical biogeographic link between the western and eastern United States. In addition, the high diversity and abundance of organisms in the Viola Group provide significant taxonomic information. Graptolites (Ruedemann and Decker, 1934), conodonts (Oberg, 1966), chitinozoans (Jenkins, 1969) and silicified articulate brachiopods (Alberstadt, 1973) have been studied, but many other groups remain to be investigated.

H. B. Whittington described the first Viola Group trilobites – several species of cryptolithines – in 1941. Since that time, Shaw (1991) revised the cryptolithines of the Viola but did not conduct a more comprehensive assessment of the trilobite fauna. The diversity of trilobites in the Viola has been drastically underestimated in the past. This is due in part to the tendency of workers to focus on outer-ramp deposits of the

aulacogen. The little field work that has been done did not include inner-ramp strata of the aulacogen margins. Shaw and Fortey (1977) reported trilobite diversity across Laurentia based on a compilation of data from the literature. They listed 12 genera from the Viola Group, most with tentative or vague identifications, which is in sharp contrast to the 36 trilobite genera I identified in this study. I attribute this increase to focus on inner-ramp deposits in addition to outer-ramp facies and to a field-oriented approach.

I conducted field work in south-central Oklahoma over the course of three summers. Eleven localities were surveyed and, of these, I measured, described and sampled eight sections (see appendix to Chapter 4). From each measured section, I recovered lithologic samples that were later slabbed, polished and sectioned. I also collected trilobites from each fossiliferous horizon and samples of other components of the fauna. In addition to assembling material for systematic research, I gathered abundance data for paleoecological analysis. My research shows that trilobites of the Viola Group are most closely related to those described by Bradley (1930) from the Kimmswick Limestone in eastern Missouri and western Illinois. Most taxa from Bradley are in need of revision and several taxa are addressed in this dissertation.

Chapter 2 of this dissertation deals with the depositional environments and trilobite paleoecology of the Viola Group. I describe five lithofacies of the Viola Group and interpret the depositional environments that they represent in the context of a carbonate ramp setting. A paleoecological analysis was conducted by applying cluster analysis techniques to trilobite abundance data for each collecting horizon. My results indicate that trilobite fossil assemblages most likely record original

environmental distributions across various habitats of the carbonate ramp. I also document a sharp change in trilobite species diversity between shallower environments of the platform and the deep ramp of the aulacogen.

In Chapter 3, I use parsimony analysis to reassess the status of two trilobite genera. *Nanillaenus* and *Thaleops* are common trilobites in the Middle and Late Ordovician of Laurentia. Many species had been named in the 160 years since the erection of *Thaleops* but no one had a clear idea of what defined either genus, or what separated the two. My analysis demonstrates that there is no unambiguous difference between *Nanillaenus* and *Thaleops* and the former name is now considered a junior synonym of the latter. Further, the relationship of *Thaleops* to its nearest relative, *Illaneus*, is suggested in the results and provides a starting point for a future reevaluation of that genus. Most *Thaleops* species were described and named between 60 and 160 years ago and were figured as "interpretive" illustrations or small, unclear photographs. I refigure type material of seventeen species, and describe and name one new species from New York and four new species from Oklahoma.

Chapter 4 addresses an even more problematic trilobite group. Isotelines are very common throughout the Ordovician in Laurentia and beyond. *Isotelus* is among the most widely recognized Ordovician trilobite genera in North America, but its relationships with other isotelines are uncertain. Revision of North American isoteline trilobites would be a subject for an entire dissertation, and a parsimony analysis was not attempted herein. The purpose of this chapter is to take the first steps necessary toward clarifying isoteline relationships by evaluating the four

isoteline genera represented in the Viola Group and discussing their possible relationships to each other. Eight species from the Viola are new.

Cheirurid trilobites, the topic of Chapter 5, are locally very abundant, especially in shallow-water settings. A comprehensive revision of this diverse group is beyond the scope of this dissertation. As in chapter 4, I simply address the genera that occur in the Viola Group, and nine new species are described.

During my three years of field work, I discovered more trilobite taxa in the Viola Group than can adequately be dealt with in the time constraints of a dissertation. Twenty-two of these taxa are documented in Chapter 6 and will be treated more completely in subsequent work. Appendix I is a table providing the original abundance data I used in my cluster analysis.

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CHAPTER 2:

SEDIMENTARY FACIES AND TRILOBITE BIOFACIES ALONG AN ORDOVICIAN SHELF TO BASIN GRADIENT, VIOLA GROUP, SOUTH-CENTRAL OKLAHOMA

ABSTRACT

The Upper Ordovician Viola Group of south-central Oklahoma records deposition on a carbonate ramp that extended from platform settings to a basin within the Southern Oklahoma aulacogen. Lithofacies analysis allows inner, mid- and outer ramp environments to be identified in the Viola Springs Formation, each of which housed a distinct trilobite biofacies. A sharp break occurs in both composition and species diversity of biofacies between the outer ramp within the aulacogen and shallower environments outside the margins of the aulacogen. The outer ramp Cryptolithine Biofacies is characterized by low species diversity, whereas both the mid-ramp *Thaleops* Biofacies and the inner ramp *Bumastoides* Biofacies lack cryptolithines and contain up to four times as many trilobites species. Comparisons with Cambrian and older Ordovician shelf-to-basin trilobite distributions suggest that the pattern recorded in the Viola Springs is temperature-related. The overlying Welling Formation includes two biofacies in inner to mid-ramp environments, with the faunas of the aulacogen less diverse than those of the platform. The high trilobite species diversity in shallow-water environments of the Viola Group supports a dilution model for community reorganization during the Ordovician.

INTRODUCTION

The Middle-Late Ordovician was a critical interval in the history of trilobites. The great Ordovician Radiation was underway, and trilobite-dominated paleocommunities of the Cambrian Evolutionary Fauna gave way to brachiopod-rich paleocommunities of the Paleozoic Evolutionary Fauna (Sepkoski, 1981; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). There is little doubt that trilobites underwent a decline in *relative* importance during the latter half of the Ordovician. However, there is debate over the actual patterns and underlying processes. Some authors suggest that trilobites underwent a real decline in absolute abundance and/or diversity, and were displaced offshore during the Ordovician Radiation (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985; Droser et al., 1996). Others argue that the apparent decline in trilobites within habitats during the Ordovician is an artifact of dilution as other groups of organisms (e.g., articulate brachiopods; bryozoans) increased in diversity and abundance (Westrop et al., 1995; Westrop and Adrain, 1998).

The dilution hypothesis is supported by the compilations of Westrop and Adrain (1998) and Adrain et al. (2000), which show that trilobite species diversity within all shelf habitats (alpha diversity) was maintained at Late Cambrian levels through the Ordovician and most of the Silurian. There is no evidence for Ordovician displacement of trilobites from shallow-water settings. The diversity gradients used in these studies are mosaics of data compiled from environments at different localities across Laurentia. The next step in the evaluation of trilobite environmental distribution patterns during the Ordovician is the analysis of a single gradient in a

single area. Local analyses test the reliability of composite gradients assembled from data at provincial to global scales. Ludvigsen's (1978b; see also Chatterton and Ludvigsen, 1976) work on Middle-Late Ordovician trilobite faunas of northern Canada is the only available quantitative treatment of a single, complete, shelf to basin gradient in Laurentian North America. However, Ludvigsen's (1978b) study provides minimal supporting data on sedimentary facies, and the relative bathymetric positions of trilobite assemblages were established largely from faunal replacements in stratigraphic sections that were inferred to record sea-level fluctuations (Ludvigsen, 1978b, fig. 11).

In this paper, we document a shelf-to-basin transect recorded by the Viola Group in south-central Oklahoma that includes abundant and diverse trilobite assemblages. The Viola Group is Late Ordovician in age and thus preserves faunas that lived at a time when the Ordovician Radiation was well underway and the Paleozoic Evolutionary Fauna was well established in Laurentia. Interpretation of the long-term patterns of trilobite distribution and diversity is complicated over much of eastern North America by profound environmental and faunal changes associated with development of the Appalachian foreland basin (Patzkowsky and Holland, 1993, 1996). Indeed, many of the initial data supporting displacement of trilobites from Late Ordovician shallow-water environments (Sepkoski and Sheehan, 1983, p. 710, sources 87-94) were derived from this region. Oklahoma lay outside the Appalachian basin and should provide a more representative record of Late Ordovician trilobite environmental distribution patterns for comparison with Cambrian data.

GEOLOGIC SETTING

The Viola Group (Mohawkian to Cincinnatian) is composed of the Viola Springs Formation and overlying Welling Formation (Fig. 1). It is unconformable with the Bromide Formation below and is unconformably overlain by the organic-rich Sylvan Shale. Nearly pure carbonates of the Viola Group were deposited along a storm-dominated, homoclinal carbonate ramp extending from the shallow carbonate platform of the Oklahoma basin (Fig. 2) into the Southern Oklahoma aulacogen.

The Southern Oklahoma aulacogen (Fig. 2) was a structural basin that extended from the Texas panhandle southeast through Oklahoma to eastern Texas. It formed during a phase of rifting along the southern margin of Laurentia in the latest Precambrian to Early Cambrian (Keller and Baldridge, 1995). Episodic reactivation of the Washita Valley fault along the northeastern margin of the aulacogen created accommodation space for thick sequences of early Paleozoic sediments (Hoffman et al., 1974). The Bromide Formation (Mountain Lake and Pooleville members; Fig. 1) is the uppermost unit of the carbonate-dominated Simpson Group and is mainly a shallowing-upward succession that represents filling of the aulacogen (Longman, 1982a, b). The Pooleville Member contains lime mudstone deposited as distal tempestites and shallows upward into storm-generated shell pavements (Karim and Westrop, 2002). The Corbin Ranch Submember of the Poolville Member (Fig. 1) consists of microbial laminites and mudcracked lime mudstone interpreted as peritidal in origin (Amsden and Sweet, 1983).

Deposition of the Viola Group began following a rapid subsidence event within the Southern Oklahoma aulacogen (Finney, 1986). Thick successions of the

Figure 1—Mohawk - Cinncinnati stratigraphy of the Arbuckle Mountains, south-central Oklahoma (modified from Derby et al., 1971, with stadial nomenclature from Leslie and Bergström, 1995, and Webby, 1998). CRS, Corbin Ranch Submember of the Poolevelle (Amsden and Sweet, 1983). The bar labeled SRF shows the approximate correlation with the Sugar River Formation of New York, which provided comparative data for biofacies analysis.

Figure 1

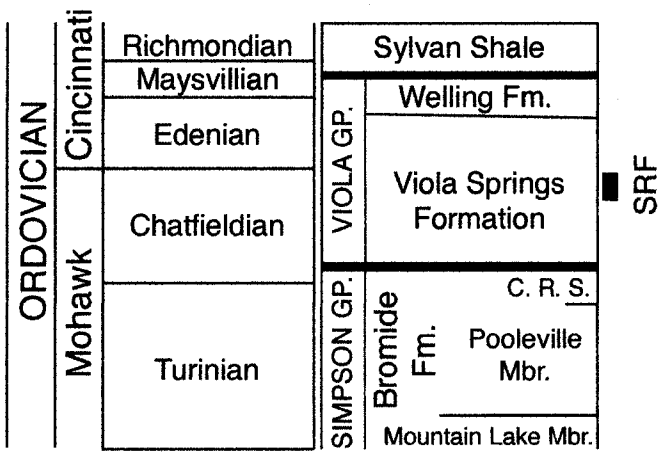
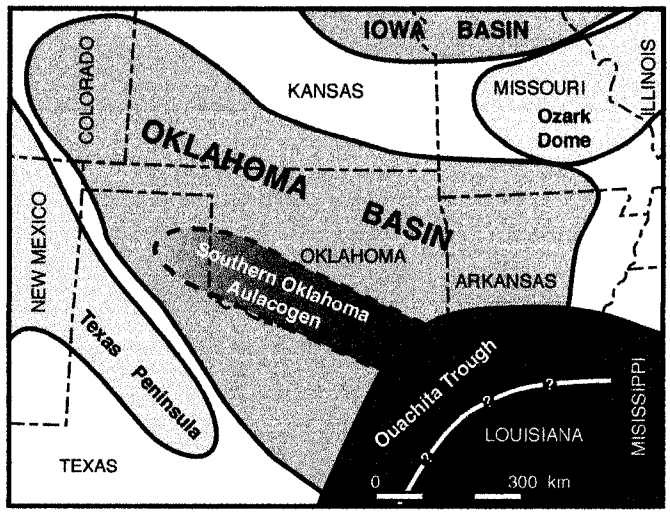

ORDOVICIAN
Cincinnati
Mohawk
Richmondian
Maysvillian
Edenian
Chatfieldian
Turinian
Sylvan Shale
VIOLA GP.
Welling Fm.
Viola Springs Formation
SRF
SIMPSON GP.
Bromide Fm.
C. R. S.
Pooleville Mbr.
Mountain Lake Mbr.

Figure 2—Ordovician depositional basins of the south-central United States (modified from Johnson, 1991).

Figure 2

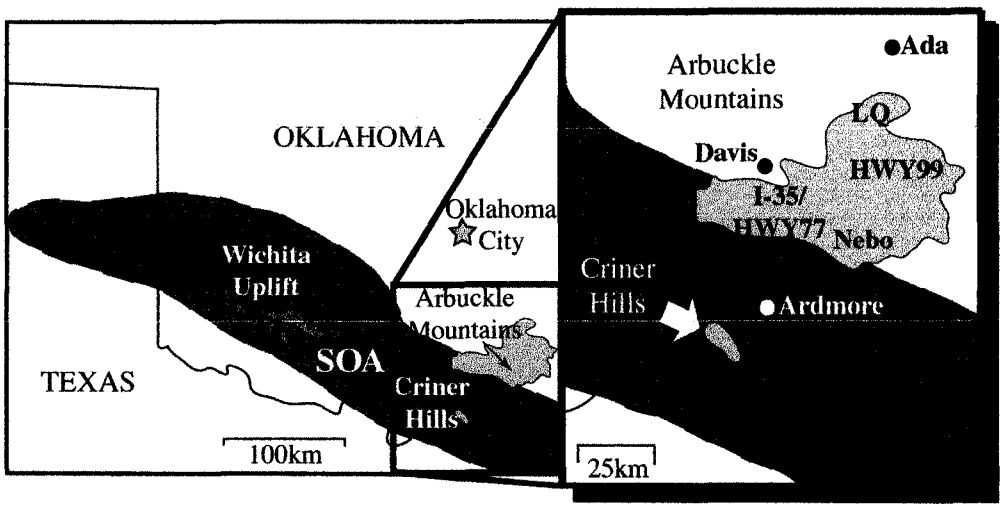

IOWA BASIN
ILLINOIS
COLORADO
KANSAS
MISSOURI
Ozark
Dome
OKLAHOMA
BASIN
NEW MEXICO
OKLAHOMA
ARKANSAS
Southern Oklahoma
Aulacogen
Texas Peninsula
Ouachita Trough
LOUISIANA
MISSISSIPPI
TEXAS
0
300 km

Viola Springs Formation in the aulacogen pinch out over the Ozark dome to the northeast and the Texas arch to the southwest (Suhm, 1997) (Fig. 2). The restricted distribution and lateral thinning of the Viola Springs outside the aulacogen indicate that deposition occurred during a short-lived relative sea-level lowstand (Finney, 1986). Following subsidence within the aulacogen, the Viola Springs carbonate factory caught up with tectonic subsidence and then kept up with eustatic sea-level rise. Siliciclastic sediment was trapped near source areas such as the transcontinental arch and the Ozark dome, allowing formation of relatively pure carbonates (Suhm, 1997). The Welling Formation (Cincinnatian) was deposited during maximum Tippecanoe transgression and is laterally continuous both inside and outside the aulacogen (Finney, 1997). Viola Group deposition ended with influx of organic-rich clay of the Sylvan Shale.

My study focuses on the thick Viola Group sequence from the Southern Oklahoma aulacogen where a shelf-to-basin transect is exposed in the Arbuckle Mountains. We investigated seven localities across the paleo-depth gradient (Fig. 3). Two localities in the Criner Hills record deposition within the basin of the aulacogen and consist of mainly outer ramp deposits. Three localities on the southern flank of the Arbuckle Anticline preserve sediments that accumulated along the margin of the aulacogen. Three localities on the Hunton Uplift were deposited on the shallow carbonate platform outside the margins of the aulacogen and shallow rapidly upward. The Welling Formation caps the Viola Springs in all sections. It is thinner and finer-grained within the basin and coarsens and thickens toward the margins. In northeastern Oklahoma, the Viola Springs is not preserved, most likely due to eustatic

Figure 3—Map of Oklahoma showing the general locations of stratigraphic sections relative to the Southern Oklahoma aulacogen (SOA; dark gray shading). LQ, Lawrence Quarry, 10 km southwest of Ada, Oklahoma. HWY99, roadcut 5 km south of Fittstown, Oklahoma along the west side of U.S. Highway 99. I-35, about 17 km south of Davis, Oklahoma along the east and west sides of the northbound lanes of Interstate 35. HWY77, about 17 km south of Davis, Oklahoma along the east side of U.S. Highway 77. Nebo, about 2.5 km west of Nebo, Oklahoma and about 1.5 km south of section-line road along stream cut. Criner Hills southwest of Ardmore, Oklahoma: Burns Quarry, 5 km south and 2.5 km west of the I-35/I-70 interchange and South Quarry, 1.5 km west of I-35 and 9 km south of I-70.

Figure 3


OKLAHOMA
TEXAS
Wichita
Uplift
SOA
Oklahoma
City
Arbuckle
Mountains
Criner
Hills
100km
Arbuckle
Mountains
Ada
LQ
Davis
HWY99
I-35/
HWY77
Nebo
Criner
Hills
Ardmore
25km

sea-level lowstand during that time interval (Finney, 1986). Presence of a thick Viola Springs sequence outside the margins of the aulacogen in south-central Oklahoma suggests that tectonic subsidence downwarped the edges of the platform in the region of the aulacogen (Keller and Baldridge, 1995).

LITHOFACIES ANALYSIS AND PALEOENVIRONMENTAL INTERPRETATION

Four sedimentary facies are confined to the Viola Springs Formation and the overlying Welling Formation comprises a fifth facies. Below, we describe each facies and interpret their environments of deposition, using the general carbonate ramp model proposed by Burchette and Wright (1992). The facies vary in stratigraphic position and thickness in each region of the aulacogen, as discussed in the next section, but constitute a dominantly shallowing-upward succession.

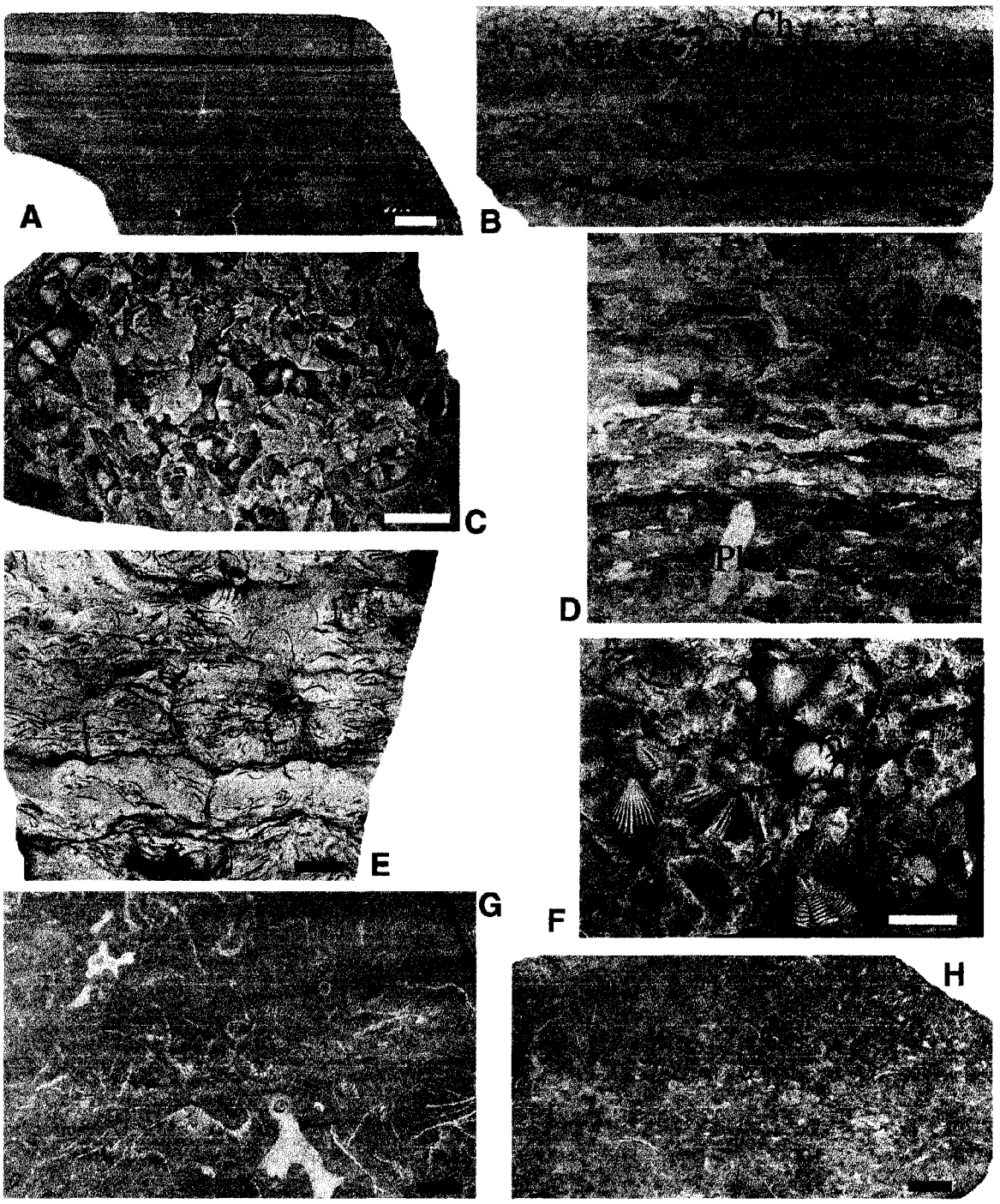
Viola Springs Formation

Carbonate Mudstone Facies

Description: This facies contains two sub-facies defined by degree of disruption of laminations by bioturbation. Abundant chert occurs throughout the facies as nodules, lenses and discontinuous beds. Organic content, as indicated by color, varies between localities and beds but is generally high. In the laminated carbonate mudstone subfacies, millimeter-scale couplets are formed by a light layer of fine carbonate mud paired with a layer of slightly coarser (silt-grade) carbonate material that appears darker in polished slabs (Fig. 4A). Faint interruptions in

Figure 4—Representative polished slabs of lithofacies in the Viola Springs and Welling formations. All scale bars are 1 cm. A-D, Outer ramp. A, Millimeter-scale laminated, unbioturbated carbonate mudstone likely deposited by contour currents under dysaerobic, possibly cool-water, conditions; coarser laminae are calcisiltite grade; B, Carbonate mudstone (upsection from A) with millimeter to centimeter-scale laminations increasingly disrupted by bioturbation (mainly *Chondrites* [Ch]); thicker layers probably indicate deposition by distal, fine-grained ebb or turbidity currents; C, Bedding plane-parallel surface of thin rudstone composed of cryptolithine sclerites sorted by storm winnowing near maximum storm wave base; D, Thicker layers (2 – 10 cm) of lime mud to wackestone representing distal tempestites or turbidites; heavy bioturbation, including *Chondrites* and *Planolites* [Pl] suggests increasing oxygen levels. E, F, Mid-ramp. E, Interlayered bioturbated pelletal wackestone and brachiopod-rich float- to rudstone; convex-up brachiopod valves in rudstone indicate condensation by storm winnowing between mean storm and fair-weather wave bases; thin, dark layers more organic rich, accentuated by diagenesis. F, Bedding plane-parallel rudstone pavement showing predominantly convex-up brachiopod valves and trilobite sclerites. G, Inner ramp shoal. Bryozoan-rich grain- to rudstone containing little to no lime mud; cross-bedding, large clast size and random orientation suggest high energy near mean fair-weather wave base. H, Platform. Well-washed pelmatazoan-rich grain- to rudstone cross-beds separated by scour surfaces; deposited near fair-weather wave base.

Figure 4



laminae provide the only evidence for bioturbation and subtle upward deflections in laminae are interpreted as water- or gas-escape structures. The preserved fauna consists of graptolites, which occur as isolated rhabdosomes or as oriented accumulations on bedding planes, with benthos restricted to rare cryptolithine trilobites.

The bioturbated carbonate mudstone subfacies contains millimeter to centimeter-scale couplets of lime mud and calcisilt laminae with superimposed bioturbation that increases in intensity upward in stratigraphic section (Fig. 4B). Bedding-plane exposures were unavailable for study so trace fossils were identified using polished vertical slabs. *Chondrites* is the most abundant ichnotaxon, and traces increase in size (as measured by diameter of burrows) upward in the section. *Diplocraterion* (small, <1 cm wide, vertically-oriented burrows with spreite) and *Terebellina* (slightly compressed, lined tubes] occur rarely.

Interpretation: The laminated carbonate mudstone facies represents the deepest-water environments in the Viola Group and occurs at the base of the Viola Springs Formation in every section. Millimeter-scale laminations indicate deposition below maximum storm wave base in an outer ramp setting (Fig. 5), and their preservation suggests an infauna limited by dysaerobic to anoxic conditions. Increasing bioturbation and burrow diameter up-section is evidence for increased oxygenation as the sections shallow upward (e.g., Pratt, 1984; Savrda and Bottjer, 1986).

In the absence of calcareous plankton as major sources of pelagic carbonate prior to the Jurassic (Coniglio and Dix, 1992), carbonate mud in the outer ramp of the Viola Group must have been exported from the shallow subtidal "carbonate factory"

Figure 5—Environmental interpretation of lithofacies of the carbonate ramp succession of the Viola Springs Formation. Ramp terminology follows Burchette and Wright (1992). Figure also shows environmental distributions of trilobite biofacies defined by cluster analysis (Fig. 8).

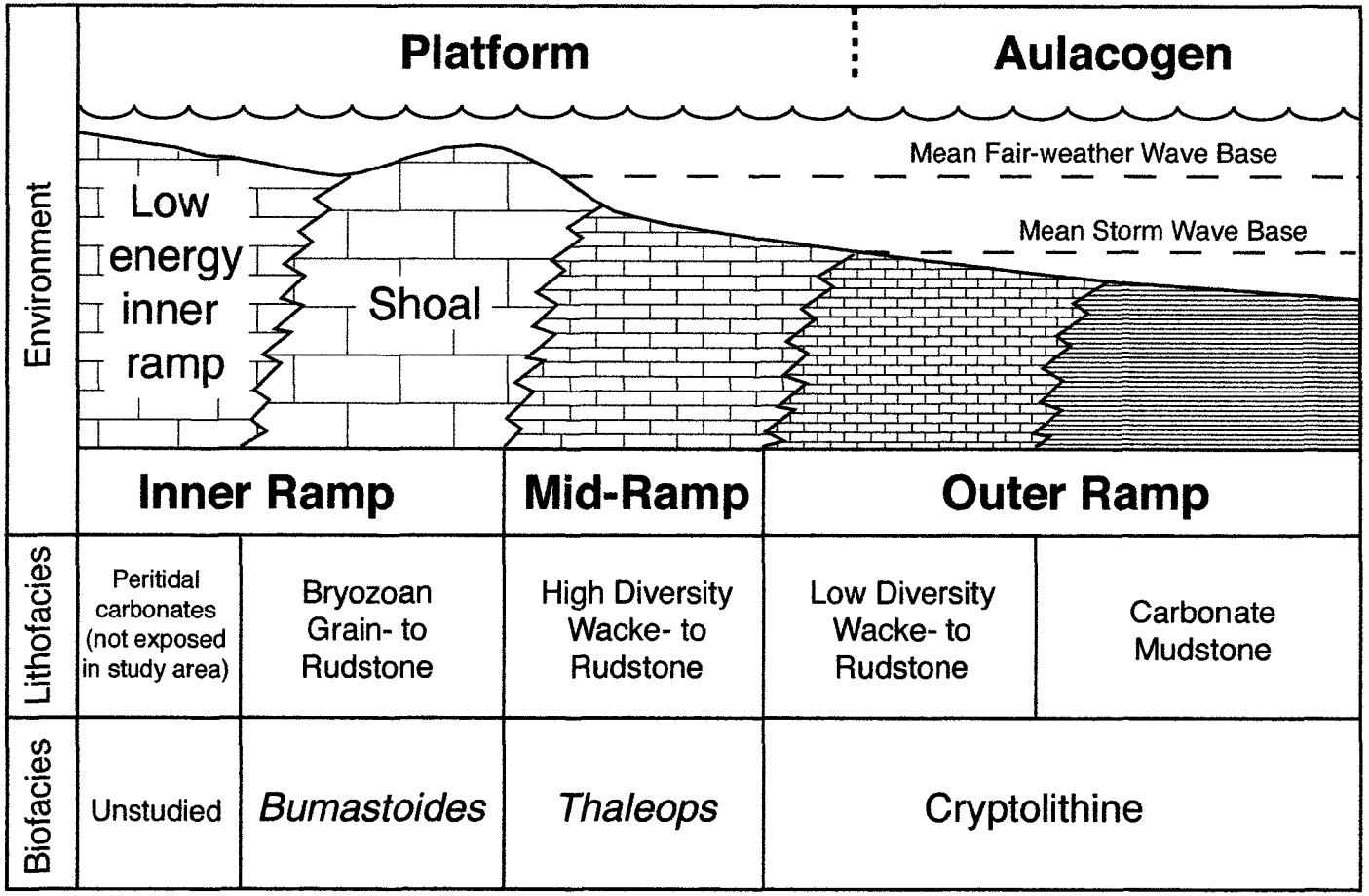

Platform
Aulacogen
Mean Fair-weather Wave Base
Mean Storm Wave Base
Low energy inner ramp
Shoal
Environment
Inner Ramp
Mid-Ramp
Outer Ramp
Lithofacies
Peritidal carbonates (not exposed in study area)
Bryozoan Grain- to Rudstone
High Diversity Wacke- to Rudstone
Low Diversity Wacke- to Rudstone
Carbonate Mudstone
Biofacies
Unstudied
Bumastoides
Thaleops
Cryptolithine

Figure 5

(James and Kendall, 1992) by storm-ebb or turbidity currents (e.g., Reinhardt, 1977; Aigner, 1982, 1985; Elrick and Snider, 2002). The laminated carbonate mudstone facies contains fine-grained, thin laminae that are well sorted and are separated by micro-scours. These characteristics conform to those described by Bouma (1972) for contour-parallel current deposits. We speculate that variations in contour current strength at different times of year produced coarse and fine laminae. Reworking by contour currents is supported by bedding planes covered by graptolites that are oriented parallel to the long axis of the Southern Oklahoma aulacogen (Gentile et al., 1984; Eriksson and Reczko, 1998).

In the bioturbated carbonate mudstone subfacies, depositional packages become thicker upward and were most likely deposited by distal turbid clouds that were remnants of turbidity currents or from unidirectional return flows following storms (Einsele and Seilacher, 1991). Increasing oxygen levels, as indicated by higher diversity infauna and macrofauna, may have been accentuated by influx of well-oxygenated water with these currents.

Low Diversity Wackestone to Rudstone Facies

Description: Pelletal wackestone is the dominant lithology in this facies with rare monotaxic, bioclastic float- to rudstone horizons. Diversity and abundance of trace fossils is higher than in the carbonate mudstone facies, with most beds completely homogenized by bioturbation. Individual depositional units average 5-10 cm thick. Those that preserve primary fabric fine slightly upward to mudstone with bioturbation concentrated near the upper surfaces. Parting surfaces at 10-30 cm intervals are formed by erosion along thin (1 mm - 6 cm), diagenetically enhanced marl layers.

Chert, as nodules and lenses, is more abundant at partings.

Up-section in this facies, some beds are inversely graded, with pelletal wackestone coarsening upward to float- to rudstone composed of sclerites of the isoteline trilobite, *Anataphrus*. These sclerites are unsorted by size and shape, and the majority are preserved in concave-up orientation. Cryptolithine trilobite fragments, especially fringes, are concentrated at parting surfaces at the tops of beds (Fig. 4C).

Tiering of trace fossils is indicated where *Chondrites* overprints homogenized wackestone (Bromley and Ekdale, 1984) (Fig. 4D). Larger, horizontally oriented burrows, attributable to *Thalassinoides*, are filled with differently colored sediment than the surrounding matrix, lack a lining and are slightly compacted. *Planolites* consists of isolated, oblique burrows with lighter color infilling of sediment lacking spreite.

At stratigraphically lower levels in this facies, cryptolithine trilobites and graptolites are abundant. Isoteline trilobites including *Isotelus*, *Stegnopsis* and especially *Anataphrus* occur in abundance at some stratigraphically higher horizons. Small crinoid ossicles are conspicuous components of wackestone; articulate and small inarticulate brachiopods are rare.

Interpretation: The low-diversity wacke- to rudstone lithofacies was deposited near mean storm wave base in an outer ramp environment (Fig. 5). Homogenization of the sediment by an infauna and increased diversity and abundance of ichno- and macrofossils indicate increased oxygenation both above and below the sediment/water interface (Savrda and Bottjer, 1986).

Anataphrus rudstone is unusual among bioclastic accumulations in the Viola

Group in displaying inverse grading of sclerites in mostly concave-up orientation. Inverse grading can be produced by deposition from turbid flows with high concentrations of sedimentary particles (Reineck and Singh, 1980). Interestingly, experiments by Allen (1984; see also Lask, 1993 for additional discussion) showed that bivalve shells adopt a concave-up orientation when settling out of dense flows with abundant suspended sediment. The *Anataphrus* rudstone does not include any of the trilobite genera typical of biofacies of inner ramp or mid-ramp environments (*Thaleops* and *Bumastoides* biofacies; see below), suggesting that flows did not originate in shallow ramp settings. Rather, the *Anataphrus* rudstone was probably deposited by flows that originated locally in the outer ramp (Mehrtens, 1989).

Accumulations of cryptolithine fringes at bedding surfaces were probably generated by winnowing and sorting of bioclastic debris by storm waves. Partings between beds formed as a result of primary heterogeneity due to accumulation of organic or other non-carbonate debris during pelagic sedimentation between event deposits (Bathurst, 1987).

High Diversity Wackestone to Rudstone Facies

Description: Five to fifteen centimeter thick pack- to rudstone layers, separated by thinner intervals of pelletal wackestone, dominate this facies (Fig. 4E). Rudstone is commonly in the form of trilobite and articulate brachiopod pavements (Fig. 4F) composed of convex up bioclasts with shelter spar below. This facies yields the highest diversity fauna in the Viola Group including gastropods, inarticulate brachiopods, bryozoa, receptaculitids, solitary rugose corals, crinoids, ostracods, rare

bivalves, and abundant trilobites and articulate brachiopods. *Planolites* and large *Thalassinoides* burrows disrupt shell accumulations. Primary heterogeneity of organic content is preserved as diagenetically enhanced limestone/marl alternations (Bathurst, 1987).

Interpretation: This facies was deposited in a mid-ramp environment between mean fair-weather and storm wave bases (Fig. 5). Preservation of brachiopod shells and trilobite sclerites in a hydrodynamically stable, convex-up orientation with spar-filled shelter porosity indicate condensation by storm-winnowing (Kreisa, 1981; Kreisa and Bambach, 1982). Deposition under tropical conditions is indicated by high levels of carbonate mud (Nelson, 1988), abundance of peloids (James, 1997), presence of *Girvanella* (Pratt, 2001) and evidence for a high diversity benthic macrofauna.

Bryozoan Grainstone to Rudstone Facies

Description: Bioclasts consist mainly of fenestrate and dome-shaped bryozoa with abundant crinoids, articulate brachiopods and effaced trilobites (Fig. 4G). Coarse sediment is well-washed, cemented with sparry calcite and often cross-bedded. Multiple, commonly iron-stained, hardgrounds and scour surfaces separate 10-20 cm thick cross-bedded rudstone horizons and thinner (5-7 cm thick) grainstone beds. Large *Thalassinoides* burrows (4 cm in diameter) and smaller *Palaeophycus* burrows (~1 cm in diameter) are common.

Interpretation: Abundant cross bedding, coarse clast size and absence of carbonate mud indicate deposition near mean fair-weather wave base in a shoal environment (Fig. 5). Scalloped hardgrounds stained with oxidized iron may have

been exposed subaerially. The high energy of the environment is indicated by broken fenestrate bryozoa and tumbled domal bryozoan colonies.

Bryozoan-dominated assemblages have been used to indicate cool-water conditions (Nelson, 1988; Beauchamp, 1994). In the Viola Group, lack of phosphate deposits, abundance of carbonate mud and presence of photozoan components (corals, peloids) suggest that this lithofacies developed as a result of its position near mean fair-weather wave base and is not linked to temperature.

Models of carbonate ramp depositional systems (e.g., Read, 1985; Burchette and Wright, 1992) indicate that high energy, inner-ramp shoal environments pass landward into peritidal carbonates. These are not expressed in the sections studied because of a relative sea level rise in the Southern Oklahoma aulacogen: bryozoan-rich grain- and rudstone of the shoal are succeeded by mid-ramp wackestone and storm-generated bioclastic pack- and rudstone. However, in eastern Oklahoma, the condensed Mohawkian succcession includes the Fite Formation, which is correlative with the lower Viola Group (Bauer, 1989). The Fite is composed of peritidal carbonates (Amsden and Sweet, 1983) that resemble those of the upper Bromide Formation.

Welling Formation

During deposition of the Welling Formation, filling of the basin resulted in the presence of only a single facies across the platform and in the aulacogen. Subtle differences between these two regions probably reflect bathymetric setting.

Crinoidal Packstone, Grainstone and Rudstone Facies

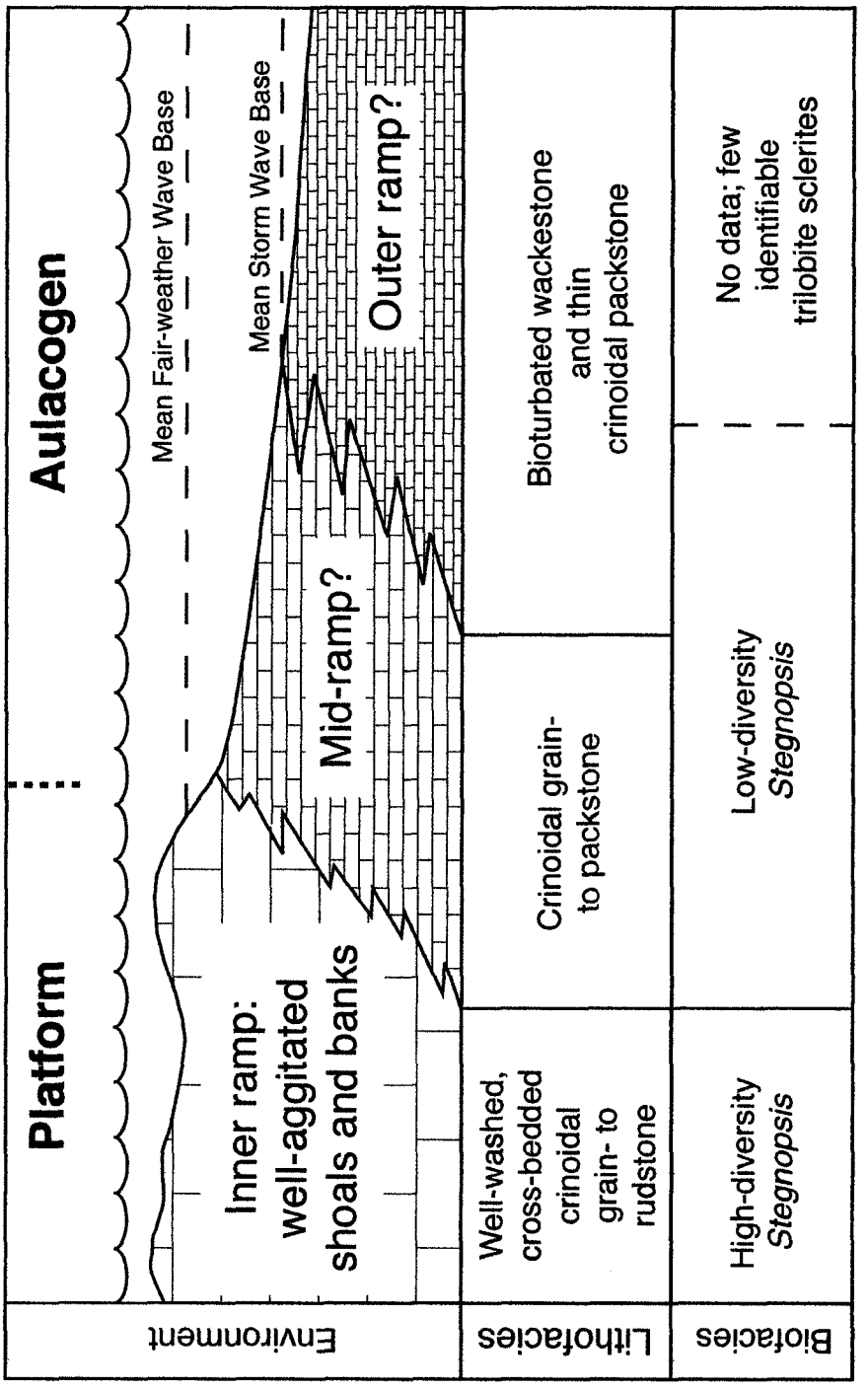
Description: At all localities, the Welling Formation is a bioclastic unit that is rich in crinoidal debris, but the bryozoa that characterize shoal environments of the Viola Springs Formation are rare or absent. On the platform, the Welling is composed of a well-washed, cross-bedded, coarse crinoidal grain- to rudstone with sparry calcite cement; abundant scour surfaces separate sets of cross beds. The associated fauna includes diverse trilobites and articulate brachiopods. The contact with the underlying Viola Springs Formation is gradational and expressed by upward coarsening from packstone to rudstone through an interval of 0.5 meters.

At marginal sites (sections I-35, HWY77 and Nebo; Fig 3) the Welling contains carbonate mud and is composed largely of crinoidal packstone. Bioclasts are large enough for identification but are smaller than the average size on the platform. As discussed below, the associated trilobite fauna is significantly lower in diversity than on the platform. The Viola-Welling boundary interval is transitional through several meters of interbedded bioturbated wackestone and crinoidal pack- or grainstone. In some cases, the crinoidal beds overlie burrowed firmgrounds developed on the wackestone. In the most distal sections in the Criner Hills, the Welling is poorly exposed but appears to consist exclusively of alterating wackestone and crinoidal grainstone in which bioclasts are finely comminuted.

Interpretation: The Welling of the platform records laterally extensive crinoidal banks and shoals (Fig. 6), perhaps similar to those described by Aigner (1985) from the Triassic of Germany. However, the well-washed grainstone to rudstone of the

Figure 6—Environmental interpretation of lithofacies of the carbonate ramp succession of the Welling Formation. Ramp terminology follows Burchette and Wright (1992). Figure also shows environmental distributions of trilobite biofacies defined by cluster analysis (Fig. 8).

Figure 6


Platform
Aulacogen
Mean Fair-weather Wave Base
Mean Storm Wave Base
Inner ramp: well-aggitated shoals and banks
Mid-ramp?
Outer ramp?
Environment
Lithofacies
Biofacies
Well-washed, cross-bedded crinoidal grain- to rudstone
Crinoidal grain- to packstone
Bioturbated wackestone and thin crinoidal packstone
High-diversity *Stegnopsis*
Low-diversity *Stegnopsis*
No data; few identifiable trilobite sclerites

Welling was probably deposited closer to fair-weather wave base than the Triassic examples, which are composed dominantly of packstone (Aigner, 1985, p. 69).

More distally, the alternation of wackestone and crinoidal limestone in the Viola Springs-Welling transition suggests that much of the bioclastic debris may have been transported down-ramp. The packstone of the Welling itself may record the distal margins of the banks and shoals (e.g., Aigner, 1985, figs. 60, 61). Down-ramp migration of coarse skeletal debris can occur under either low-stand or high-stand conditions (Tucker et al., 1983). In eastern Oklahoma, the Welling is a persistent, unconformity-bounded unit that probably formed during a period of high sea level (Finney, 1986). Thus, the more distal Welling most likely represents progradation of a highstand systems tract (e.g., Reid and Dorobek, 1993). Bathymetric setting of the Welling in central parts of the aulacogen is difficult to estimate, but probably lay between fair-weather and mean storm wave base. Bioclastic beds most likely consist of allochthonous material exported down-ramp from the platform.

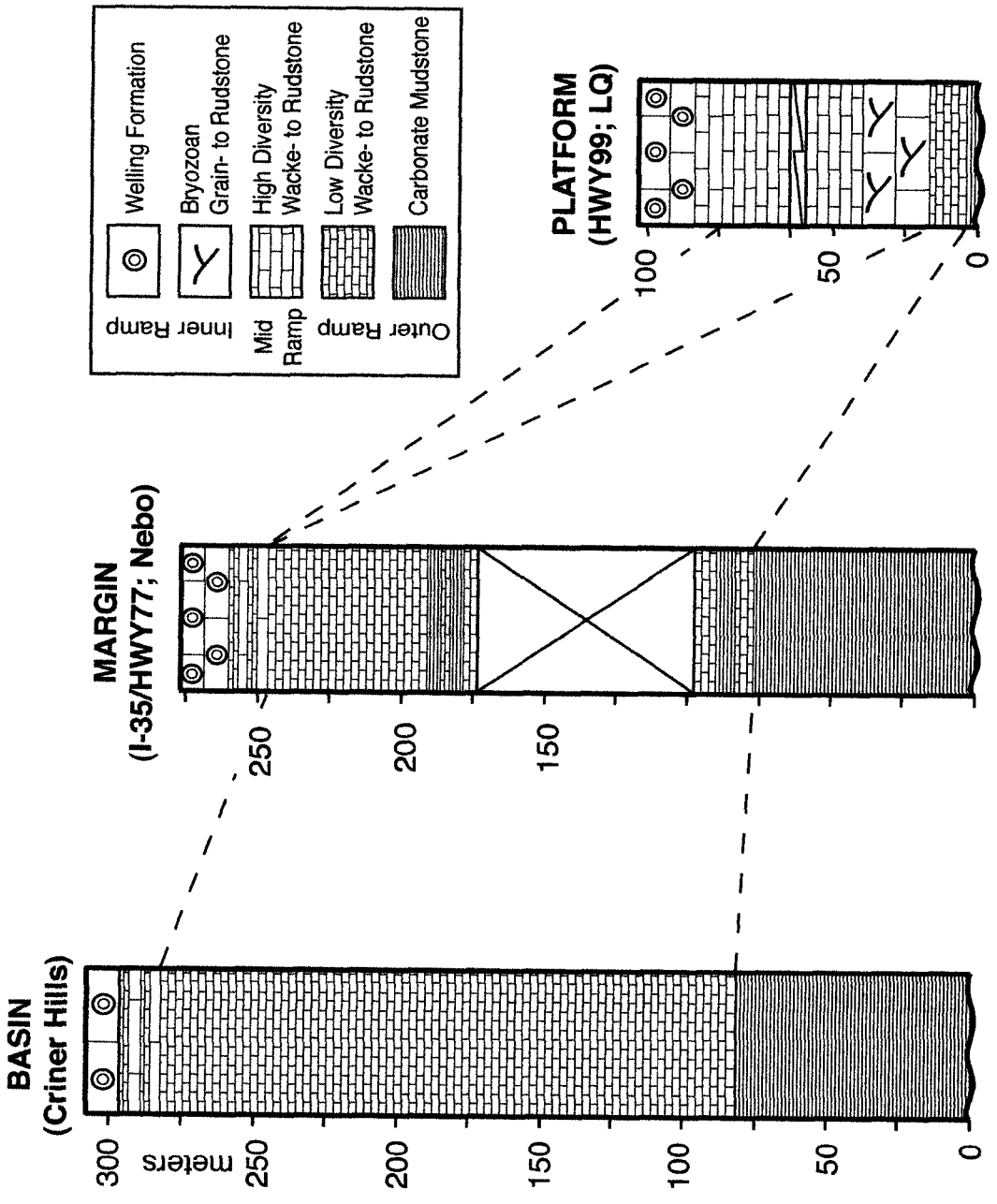
STRATIGRAPHIC DISTRIBUTION OF LITHOFACIES

The Viola Group records an overall shallowing upward sequence following subsidence within the Southern Oklahoma aulacogen. Contact with the underlying Bromide Formation is abrupt everywhere, with erosional relief up to 8 cm in some platformal sections. Within the group, contact between the Viola Springs and Welling formations is gradational through an interval of up to 3 m of alternating wackestone and grainstone.

Basinal sections (Criner Hills; Fig. 7) are thicker (average 300 m) than those on

Figure 7—Composite stratigraphic columns for localities on the platform, near the margins of the aulacogen and within the basin of the aulacogen, showing the distribution of lithofacies. A complete stratigraphic section outside the aulacogen was unavailable for study so the column on the right is a composite from two sections with an unknown combined thickness. Total thickness and thickness of outer ramp lithofacies is greatest within the aulacogen and thins outside the margins. Lithofacies deposited on the inner ramp pinch-out towards the margins of the aulacogen and crinoidal rudstone of the Welling Formation is coarsest and thickest outside the aulacogen.

Figure 7


Welling Formation
Bryozoan Grain- to Rudstone
High Diversity Wacke- to Rudstone
Low Diversity Wacke- to Rudstone
Carbonate Mudstone
Inner Ramp
Mid Ramp
Outer Ramp
BASIN (Criner Hills)
MARGIN (I-35/HWY77; Nebo)
PLATFORM (HWY99; LQ)
meters
300
250
200
150
100
50
0

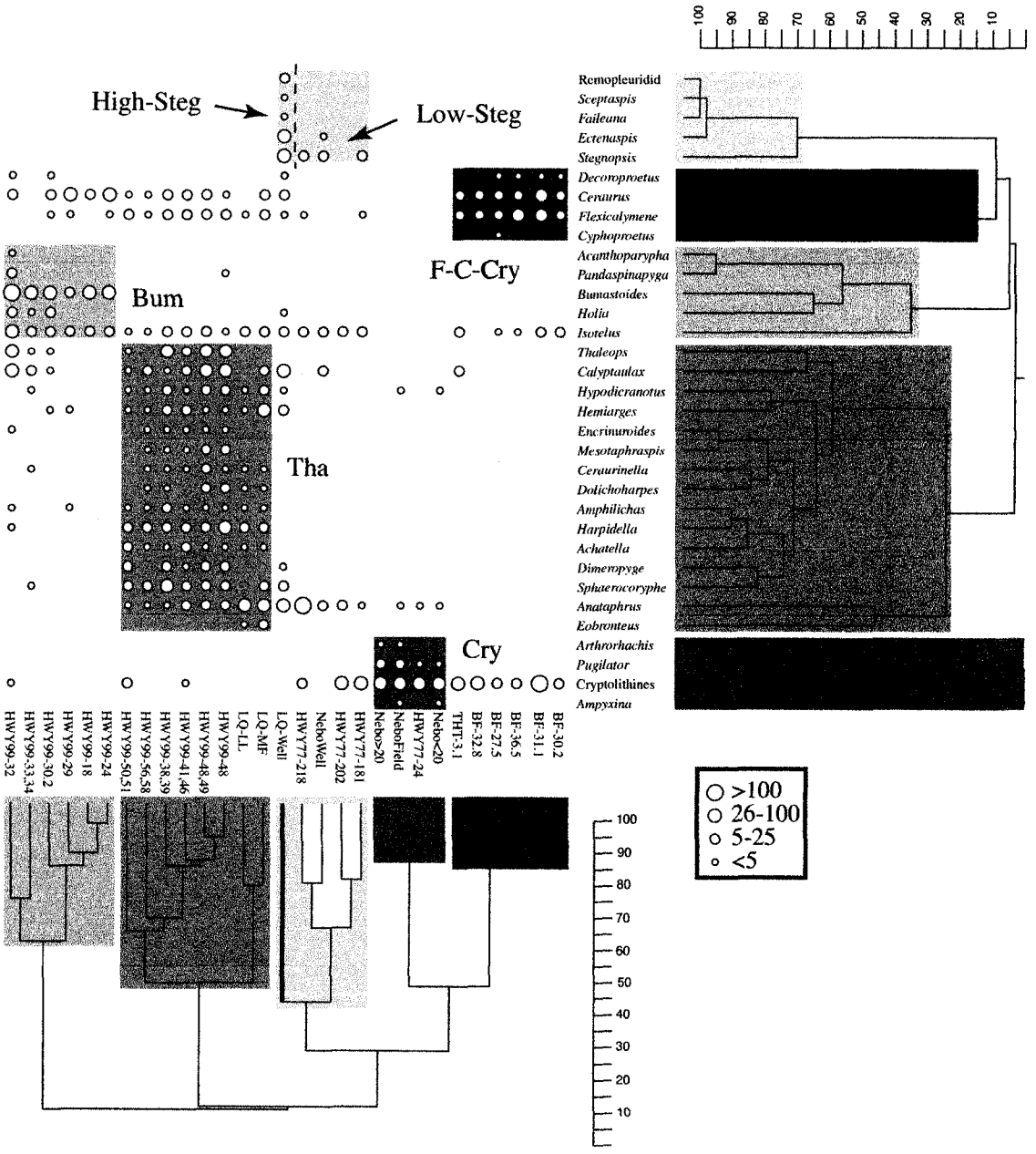
the margin (HWY77/I-35, Nebo; Fig. 7; average 250 m) and both consist almost exclusively of deep water facies (outer ramp environments; Fig. 8). Bioturbation increases up-section, reflecting an overall shallowing-upward trend. All five facies are represented on the platform, but deeper water lithofacies are restricted to relatively thin intervals at the base of the Viola Springs Formation (Fig. 7).

TRILOBITE BIOFACIES

During the course of this study, we collected over 5500 trilobite sclerites, representing more than 4100 individuals, that were assigned to 52 species and 36 genera. Other invertebrate taxa were collected to aid in description of lithofacies and interpretation of depositional environments. From the earliest phases of field work, it was apparent that each of the lithofacies of the Viola Group contained different assemblages of trilobites. Here, we use Q- and R-mode cluster analyses as a simple and convenient method of presenting our conclusions (e.g, Ludvigsen and Westrop, 1983; Westrop, 1996). The data set consists of 23 large collections (average size: 90 individuals) from Oklahoma along with six samples from the Late Ordovician Sugar River Formation of New York, which provided data for cryptolithine-rich assemblages from the Appalachian foreland basin (see below). Generic abundance data were normalized by log transformation before analysis using SPSS version 10 for the Macintosh (SPSS, 2000). We used Pearson's Correlation Coefficient as an index of similarity, and the clusters were formed using the average linkage method. Trilobite biofacies, named for the dominant genus present, are defined by the intersection of Q- and R-mode clusters (Fig. 8). Five biofacies are recognized in the

Figure 8—Results of Q- and R-mode cluster analyses of 29 collections from Oklahoma (HWY99, LQ, HWY77 and Nebo prefixes) and New York (BF and THT prefixes). Collections are in Q-mode clustering order, taxa are in R-mode clustering order, and abundance (number of individuals) is expressed as a graded series of circles; data were log-transformed prior to analysis. "Cryptolithines" combines *Cryptolithus* and *Cryptolithoides*; "*Flexicalymene*" combines *Flexicalymene* and *Gravicalymene*. Biofacies defined by intersections of Q- and R-mode cluster analyses are: Cry, Cryptolithine Biofacies; *Tha*, *Thaleops* Biofacies; *Bum*, *Bumastoides* Biofacies; *F-C*-Cry, *Flexicalymene-Ceraurus*-cryptolithine Biofacies. Collections from the Welling Formation formed a single cluster, which was divided into two biofacies based on species richness (Fig. 9): High-*Steg*, High-diversity *Stegnopsis* Biofacies; Low-*Steg*, Low-diversity *Stegnopsis* Biofacies. New York collections are from the Sugar River Formation at Buttermilk Falls (BF-; see Kay, 1953 for locality and stratigraphic information) and the Tribes Hill railroad cut (THT; see Whittington, 1968 for locality information).

Figure 8


High-Steg
Low-Steg
F-C-Cry
Bum
Tha
Cry
Remopleuridid
Sceptaspis
Failleana
Ectenaspis
Stegnopsis
Decoroproetus
Ceraurus
Flexicalymene
Cyphoproetus
Acanthoparypha
Pandaspinapyga
Bumastoides
Holia
Isotelus
Thaleops
Calyptaulax
Hypodicranotus
Hemiarges
Encrinuroides
Mesotaphraspis
Ceraurinella
Dolichoharpes
Amphilichas
Harpidella
Achatella
Dimeropyge
Sphaerocoryphe
Anataphrus
Eobronteus
Arthrorhachis
Pugilator
Cryptolithines
Ampyxina
HWY99-32
HWY99-33,34
HWY99-30.2
HWY99-29
HWY99-18
HWY99-24
HWY99-50,51
HWY99-56,58
HWY99-38,39
HWY99-41,46
HWY99-48,49
HWY99-48
LQ-LL
LQ-MF
LQ-Well
HWY77-218
NeboWell
HWY77-202
HWY77-181
Nebo>20
NeboField
HWY77-24
Nebo<20
THT-3.1
BF-32.8
BF-27.5
BF-36.5
BF-31.1
BF-30.2
100
90
80
70
60
50
40
30
20
10
>100
26-100
5-25
<5

Viola Group, with a sixth occurring in the Sugar River Formation. To facilitate comparisons of diversity between biofacies, we employed rarefaction (Tipper, 1979; Westrop and Adrain, 1998) using Analytic Rarefaction v. 1.3. (Holland, 2000).

Results

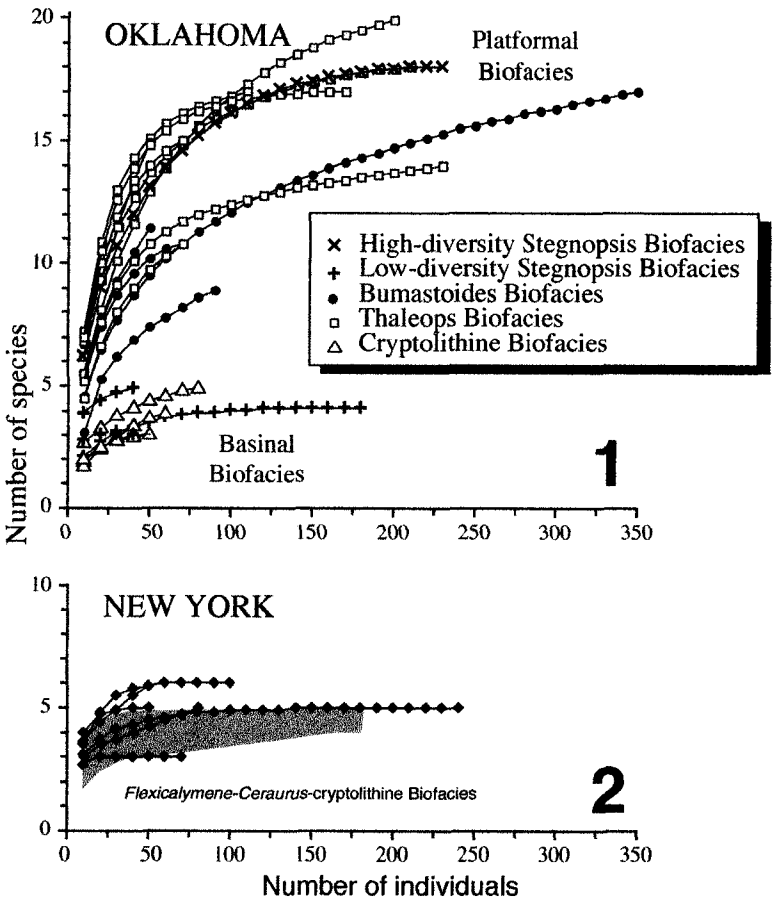
Inner-ramp shoal and mid-ramp environments of the Viola Springs Formation each contain a unique trilobite biofacies, with a third biofacies occupying outer-ramp settings (Fig. 9). The Welling Formation contains a single biofacies composed of similar genera, but species diversity differs profoundly with depth. The strong linkage between biofacies and lithofacies suggests that the original habitat distributions of living organisms is preserved in the recorded pattern. As with other time-averaged (Walker and Bambach, 1971; Kidwell and Bosence, 1991) assemblages, diversity is likely to be elevated relative to the original life assemblages (e.g., Warme et al., 1976).

Viola Springs Formation

Cryptolithine Biofacies: Cryptolithine trilobites (*Cryptolithus* and *Cryptolithoides*) are the dominant skeletalized benthic organisms in outer ramp environments of the Viola Springs Formation (Fig. 5). They are rare in the laminated lime mudstone subfacies, but increase in abundance as oxygen levels (as indicated by the extent of bioturbation) rise. Diversity is higher in shallower settings of the outer ramp (low diversity wacke- to rudstone lithofacies) with the appearance of isoteline trilobites (*Isotelus* and *Anataphrus*), but does not exceed five species (Fig. 9).

Figure 9—Rarefaction curves for collections from Oklahoma and New York. 1. Collections from Oklahoma fall into two groups: high-diversity assemblages from platformal sites outside of the Southern Oklahoma aulacogen (*Thaleops*, *Bumastoides* and High-diversity *Stegnopsis* biofacies) and low diversity assemblages from basinal sites within the aulacogen (Cryptolithine and Low-diversity *Stegnopsis* biofacies). 2. Collections from New York (*Flexicalymene-Ceraurus*-cryptolithine Biofacies) are of low diversity and are comparable to the basinal biofacies of Oklahoma (shaded area shows the field occupied by basinal biofacies of Oklahoma).

Figure 9


OKLAHOMA
Platformal Biofacies
High-diversity Stegnopsis Biofacies
Low-diversity Stegnopsis Biofacies
Bumastoides Biofacies
Thaleops Biofacies
Cryptolithine Biofacies
Basinal Biofacies
1
NEW YORK
Flexicalymene-Ceraurus-cryptolithine Biofacies
2
Number of species
Number of individuals
0
5
10
15
20
50
100
150
200
250
300
350

Thaleops *Biofacies*: A dramatic increase in trilobite species diversity (Fig. 9) characterizes the mid-ramp environment (Fig. 5). The *Thaleops* Biofacies occurs in storm-generated pack- and rudstone, and includes up to 20 species of trilobites. In addition to the eponymous genus, calymenid (*Flexicalymene*), pterygometopid (*Achatella* and *Calyptaulax*), isoteline (*Isotelus*), harpetid (*Dolichoharpes*) and aulacopleurid (*Harpidella*) trilobites are important components of the biofacies.

Bumastoides *Biofacies*: Trilobite diversity remained high in the *Bumastoides* Biofacies (Fig. 9) of the inner-ramp shoal environment (Fig. 5). Bioclasts composing the shoal grainstone and rudstone show more evidence for transportation than those from other environments, and larger trilobite sclerites are commonly broken. However, many trilobite genera are restricted to the shoal environment (including *Bumastoides* itself, which is the most abundant genus present), so that extensive lateral transportation of sclerites is unlikely. That is, the trilobite assemblage can be considered parautochthonous and representative of the original fauna inhabiting the shoal.

Welling Formation

Five collections from the Welling Formation and the Welling-Viola Springs transition interval cluster together in the Q-mode analysis (Fig. 8). However, they vary dramatically in species diversity and their association in the cluster analysis most likely reflects similarities in age, rather than ecology. The collections include genera (e.g., *Ectenaspis*) that do not occur in any lithofacies of the older Viola Springs

Formation. Two environmentally segregated biofacies are recognized from diversity patterns (Fig. 9): high-diversity *Stegnopsis* and low-diversity *Stegnopsis* biofacies.

High-diversity Stegnopsis *Biofacies*: As the name implies, the high-diversity *Stegnopsis* Biofacies includes far more trilobite species than the low-diversity *Stegnopsis* Biofacies (Fig. 9). It occurs only in the well-washed grain- and rudstone of the extensive crinoidal banks and shoals that occupied the platform (Fig. 5). The level of diversity is comparable to those of the other shallow-water biofacies (*Thaleops* and *Bumastoides* biofacies) that are developed on the platform (Fig. 9).

Low-diversity Stegnopsis *Biofacies*: Confined to the aulacogen, this biofacies attains no more than about 25 percent of the trilobite species richness of the coeval High-diversity *Stegnopsis* Biofacies of the platform (Fig. 9). It occupied the most distal, down-ramp portions of the crinoidal bank and adjacent areas of the outer ramp (Fig. 5).

The low-diversity *Stegnopsis* Biofacies occupied the shallowest-water environments within the aulacogen, perhaps overlapping in bathymetic range with the older mid-ramp *Thaleops* Biofacies of the platformal regions outside the aulacogen. However, trilobite species diversity of the *Thaleops* Biofacies is four to five times greater than in the low-diversity *Stegnopsis* Biofacies. The pervasive differences between the faunas of the platform and aulacogen hint at persistent environmental contrasts, possibly in the form of cooler water (Pope and Steffen, 2003), in the aulacogen.

Discussion

Prior to this study, Late Ordovician trilobite biofacies of Laurentian North America had been documented only in a shelf-to-slope transect in northern Canada (Ludvigsen, 1978b; Chatterton and Ludvigsen, 1976). The accompanying sedimentological data are limited so that it is difficult to make detailed comparisons with the environments and biofacies of the Viola Group. In terms of diversity, the mid-ramp and inner ramp shoal biofacies of the Viola are similar to "Trentonian" Biofacies II and III of the Whittaker Formation (Ludvigsen, 1978b, fig. 10). It is more difficult to compare compositions of biofacies because Ludvigsen's analysis was based upon binary, rather than relative abundance, data. However, with a few exceptions (e.g., *Achatella*), all of the genera present in the Viola mid-ramp and shoal environments are among those listed by Ludvigsen (1978b, fig. 12) as occuring in the "Trentonian" biofacies II and III.

As anticipated by Ludvigsen (1978a), the most distal biofacies of the Whittaker Formation, Biofacies IV from slope environments (Ludvigsen, 1978b), resembles the outer ramp cryptolithine biofacies of the Viola Group. Both are low-diversity associations (e.g. Ludvigsen, 1978b, fig. 4, collections G4460, CN-34 and GSC58482) that, with the exception of *Anataphrus*, are composed of genera that are rare or absent from the coeval shallow-water biofacies. In addition to cryptolithines, both are characterized by raphiophorid (*Ampyxina*); agnostoid (*Trinodus*) and remopleuridid (*Pugilator* and *Robergia*) trilobites. Following Taylor's (1977) work on Late Cambrian trilobite biogeography, Ludvigsen (1978b) interpreted the sharp

contrast between the shelf biofacies and Biofacies IV as temperature-related, with the latter occupying cooler water below the permanent thermocline.

The recent compilations of Westrop and Adrain (1998) and Adrain et al. (2000) provide more extensive comparative species diversity data for trilobite biofacies in various environments through much of the lower Paleozoic. The environmental gradient used by these authors is not completely comparable to the one recorded by the Viola Group. Although their shallow subtidal environment (between mean fair-weather and storm wave bases) clearly corresponds to my mid-ramp and shoal, Adrain et al. (2000) divided the region below mean storm wave base into deep subtidal and basinal environments instead of outer ramp. In the Viola Group, the mid-ramp of the platform passes into outer ramp environments of the aulacogen that are most similar to Adrain et al.'s basinal settings. Using frequency distributions of expected species number [E(Sn)] rarefied to a standard sample size of 90 individuals (see Westrop and Adrain, 1998), there is no significant difference (Mann-Whitney U-test, $p = .70$) between Middle-Late Ordovician shallow subtidal species richness in Oklahoma and the other parts of Laurentia documented by Adrain et al. (2000). The Oklahoma samples are, however, more diverse than Late Cambrian shallow subtidal carbonate collections from Adrain et al.'s data set ($p < .01$), supporting the notion that species richness of trilobites in shallow water did not decline during the Ordovician.

Data for Ordovician slope-to-basin environments are too limited for statistical analysis, but the mean (non-rarefied) species richness (four species) for this setting in Adrain et al.'s data set (2000, fig. 11) is in line with the values obtained from the outer ramp of the Viola (three to five species).

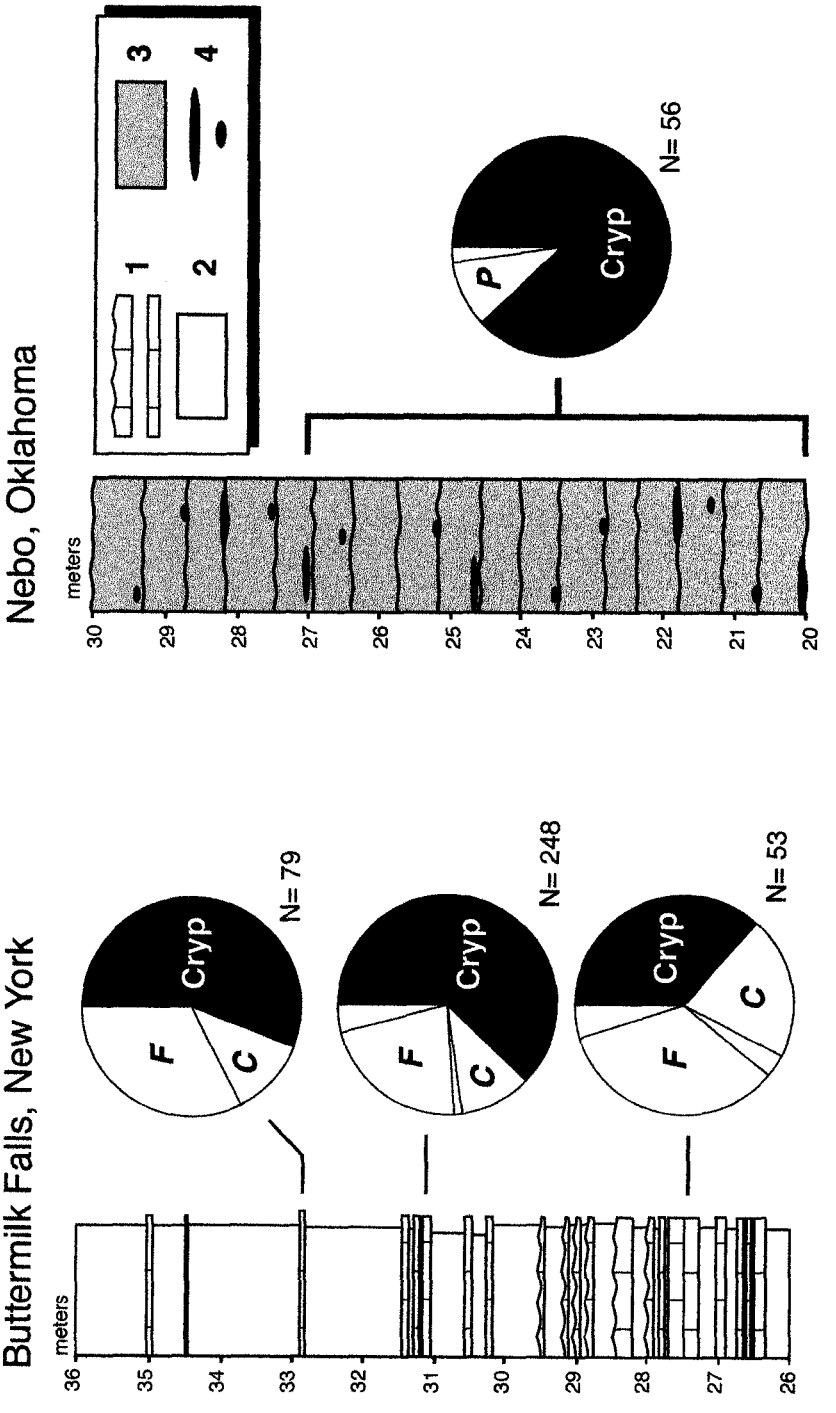
A preliminary comparison with the Appalachian foreland basin, New York

The low diversity of cryptolithine-dominated faunas present in the outer ramp of the Viola Group suggest that the waters of the Southern Oklahoma aulacogen may have been cooler than those of the adjacent platform. Cryptolithines also have been documented from Mohawkian strata of the Applachian foreland basin in New York (e.g., Whittington, 1968), although their paleoenvironmental and paleoecologic contexts are poorly known. Trilobite distribution in that area is of interest because the foreland basin has been interpreted as a site of cool-water carbonate deposition (e.g., Brookfield, 1988; Lavoie, 1995). Indeed, the shift from warm- to cool-water conditions during evolution of the basin has been implicated as a contributing factor to regional extinction among brachiopod and coral faunas in eastern North America (Patzkowsky and Holland, 1993, 1996). Here, we present some preliminary data on a cryptolithine-rich trilobite biofacies from the Sugar River Formation in central New York (Fig. 10)

The Sugar River Formation was sampled at several sites in central New York and Figure 10 shows a segment of a representative stratigraphic section. Seven collections included in the cluster analysis represent a biofacies dominated by cryptolithines, *Flexicalymene* and *Ceraurus* (Fig. 8). Trilobite species richness is low and is comparable to the low diversity Cryptolithine Biofacies in the outer ramp of the Viola Springs Formation (Fig. 9). However, the Sugar River collections are from bioclastic tempestites, many of which have wave-rippled tops (Fig. 10). In terms of depositional environment, they record a bathymetric setting (between mean fair-

Figure 10—Segments of stratigraphic sections through the Sugar River Formation, Buttermilk Falls, New York and the lower Viola Springs Formation, Nebo, Oklahoma, showing occurrences of cryptolithine-dominated trilobite assemblages. Lithologic symbols: 1, bioclastic pack- and rudstones with wave-rippled tops (upper) and planar tops (lower); 2, nodular bioclastic wackestones and packstones; 3, weakly laminated lime mudstone to wackestone with thin, argillaceous partings; 4, chert nodules and lenses. Taxa on pie charts: Cryp, cryptolithines; *P*, *Pugilator*; *F*, *Flexicalymene*; *C*, *Ceraurus*.

Figure 10


Nebo, Oklahoma
meters
30
29
28
27
26
25
24
23
22
21
20
1
2
3
4
Cryp
P
N= 56
Buttermilk Falls, New York
meters
36
35
34
33
32
31
30
29
28
27
26
Cryp
F
C
N= 79
Cryp
F
C
N= 248
Cryp
F
C
N= 53

weather and storm wave base) similar to that of the mid-ramp of the Viola Springs Formation. However, the latter is characterized by a high-diversity trilobite biofacies (Fig. 9) that lacks cryptolithine trilobites. In Oklahoma, cryptolithine-rich, low-diversity faunas occur in deeper parts of the ramp that lay below mean storm wave base (Figs. 5, 9). The emergence of low-diversity, cryptolithine-rich trilobite faunas into shallower water in New York compared to Oklahoma could well be an expression of changing paleoceanographic conditions during evolution of the foreland basin. From interpretations of the paleoecology of cryptolithines in other areas (e.g., Ludvigsen, 1978b), an influx of cooler water is plausible, although we cannot rule out the influence of other factors, such as salinity or siliciclastic influx, on faunal changes.

The data from New York are clearly preliminary, but they raise the possibility that diversity and composition of Middle and Upper Ordovician trilobite assemblages can provide information on such paleoceanographic parameters as water temperature and salinity. More work is needed, preferably in tandem with geochemical analysis. At minimum, the data presented herein underscore the pitfalls of interpreting the ecological history of trilobites from a limited range of environmental and geographic settings. Comprehensive surveys (e.g., Westrop and Adrain, 1998; Adrain et al., 2000) are needed to separate pervasive trends from local environmental noise.

The extinctions across eastern North America recorded by Patzkowsky and Holland (1993, 1996) occurred at their M4-M5 sequence boundary, which is roughly correlative with the boundary between the Bromide and Viola Springs formations in central Oklahoma. Although the laminated carbonate mudstone facies of the lower

Viola Springs records a brief incursion of cooler, dysoxic waters onto the platform, warm water carbonate sedimentation was re-established quickly in these areas outside the aulacogen. Consequently, there is no significant trilobite extinction in Oklahoma, which lay outside the Appalachian foreland basin. Seventy-five percent of the genera recorded from the underlying Pooleville Member of the Bromide Formation (Shaw, 1974; Westrop and Amati, unpublished data) reappear in mid-ramp and shoal environments of the Viola Springs (Fig. 11). This provides some support for the suggestion (Patzkowsky and Holland, 1993, 1996) that biotic turnover in the Appalachian foreland basin was a consequence of tectonically induced environmental change.

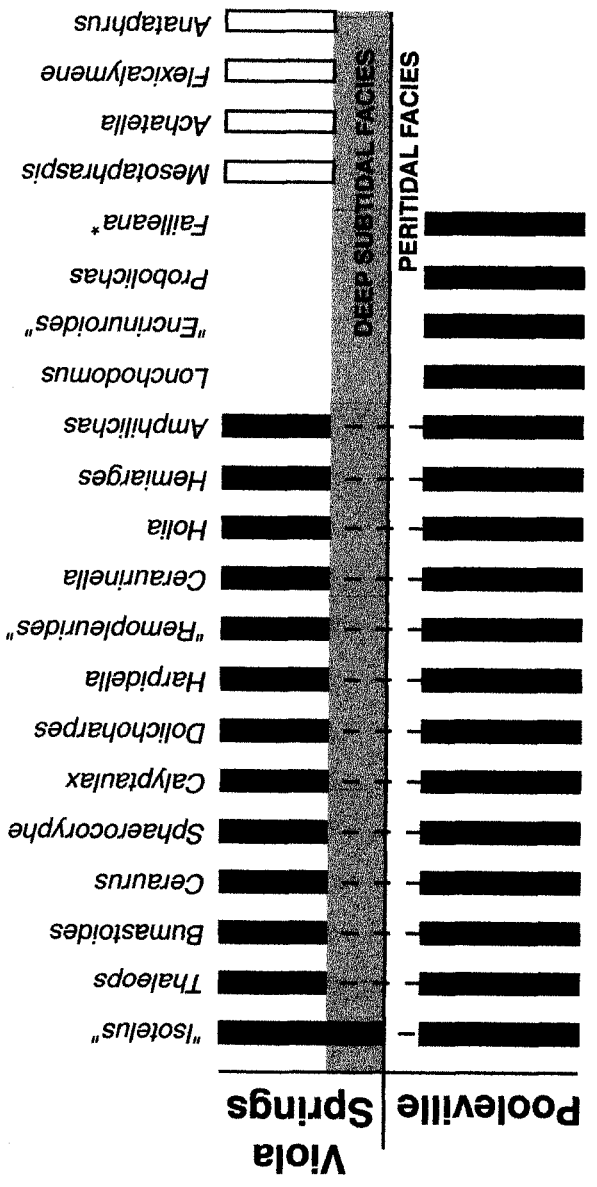
CONCLUSIONS

The Middle-Late Ordovician carbonate ramp extending from the shallow platform to the deeper portions of the Southern Oklahoma aulacogen was occupied by a spectrum of trilobite biofacies. Trilobite species diversity in shallow water environments was high and comparable to diversity in similar environmental settings during the Late Cambrian. Down-ramp, trilobite diversity decreased rapidly and attained no more than about 25 percent of species richness in more proximal settings. Trilobite species richness in the outer ramp is similar to that reported from both younger and older basinal environments (e.g., Adrain et al., 2000). Other taxa followed the same trend, and such groups as articulate brachiopods and bryozoans are rare to absent in outer-ramp environments.

With maximum richness in shallow subtidal, mid-ramp to shoal enviroments, the

Figure 11—Schematic diagram showing survival and regional extinction of trilobite genera in shallow subtidal facies between the upper Bromide (Pooleville Member) and Viola Springs formations, southern Oklahoma. Most of the genera recorded from shallow subtidal facies of the Pooleville (Shaw, 1974; Westrop and Amati, unpublished data) disappear throughout the study area with the appearance of unfavorable facies (peritidal carbonates; outer ramp lime mudstones), but re-enter the succession with the return of shallow subtidal (mid- to inner ramp) conditions. *Failleana reappears in the Welling Formation.

Figure 11


Viola Springs
Pooleville
"Isotelus"
Thaleops
Bumastoides
Ceraurus
Sphaerocoryphe
Calyptaulax
Dolichoharpes
Harpidella
"Remopleuridies"
Ceraurinella
Holia
Hemiarges
Amphilichas
Lonchodomus
"Encrinuroides"
Probolichas
Failleana*
Mesotaphraspis
Achatella
Flexicalymene
Anataphrus
DEEP SUBTIDAL FACIES
PERITIDAL FACIES

distribution of trilobites is exactly opposite to the expectations of models that predict off-shore displacement of trilobites during the Ordovician (e.g., Sepkoski and Sheehan, 1983; Droser et al., 1996). However, these shallow-water environments also contain the greatest taxonomic richness of the various elements of the Paleozoic Evolutionary Fauna, suggesting that a dilution model (Westrop et al., 1995; Westrop and Adrain, 1998) provides a better description of the Middle-Late Ordovician ecological history of trilobites.

Preliminary data suggest that emergence of trilobite biofacies of deep water aspect into shallow subtidal settings in such regions as the Appalachian foreland basin may provide evidence of incursions of cool water.

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CHAPTER 2:

A SYSTEMATIC REVISION OF *THALEOPS* (TRILOBITA: ILLAENIDAE) WITH NEW SPECIES FROM THE MIDDLE AND LATE ORDOVICIAN OF OKLAHOMA AND NEW YORK

ABSTRACT *Illaenus* Dalman 1827 has long served as a garbage can for effaced species, and the problem has been compounded in North America by the addition of *Thaleops* Conrad 1843 and *Nanillaenus* Jaanusson 1954. This study takes the first step toward defining the relationships of Laurentian taxa within this group using cladistic methods. *Parillaenus* Jaanusson 1954 forms a monophyletic group based on pygidial morphology that is distinct from *Illaenus*. Our analysis indicates that *Illaenus* is paraphyletic and requires major revision. *Thaleops* is a large group of species whose monophyly is supported by an unambiguous apomorphy: the presence of long articulating facets on the pygidium that are oriented at a high angle to the anterior margin of the pygidium. All but one basal member of the clade possesses a second apomorphy, posteriorly positioned palpebral lobes. *Nanillaenus* is not monophyletic and is synonymized with *Thaleops*. Several Laurentian species originally identified as *Illaenus* are reassigned to *Thaleops*. Seventeen previously named species are revised and re-illustrated, four of which (*I. arcturus* Hall 1847; *I. clavifrons* Billings 1859; *I. punctatus* Raymond 1905; *I. americanus* Billings 1859) are restricted to the type material. In addition, four new species, *T. anusacerbissima*, *T. jaanussoni*, *T. mobydicki* and *T. laurentiana*, are described from the Middle and

Upper Ordovician Bromide and Viola Springs formations of Oklahoma and the Trenton Group of New York.

INTRODUCTION

Illaenus Dalman 1827, encompasses a broad range of convex, effaced species that possess relatively few characters that might be used to resolve relationships within the genus. This problem has been discussed by several authors over the last 50 years, but little progress has been made (e.g., Jaanusson 1954, 1957; Šnajdr, 1957; Whittington, 1963; Shaw, 1968; Bruton & Owen 1988). *Thaleops* Conrad 1843 was erected for Laurentian illaenids with stalked eyes, genal spines and well-defined axial lobes, but problems arose as additional Laurentian species were discovered that possess only some of these traits, or similar characters that are developed to a lesser degree. Jaanusson (1954) erected *Nanillaenus* to accommodate those species with morphologies intermediate between *Illaenus* and *Thaleops*. Although *Illaenus*, *Nanillaenus* and *Thaleops* seem to be defined by distinct characters, the characters often are manifested as points along a gradient between two more extreme end members.

In this paper, we describe new illaenid species from the Middle to Late Ordovician of Oklahoma and New York, and provide a review of the history of thought regarding the relationships between *Illaenus*, *Nanillaenus* and *Thaleops*. Seventeen other Laurentian species are revised using type and other material. A cladistic analysis describes the ingroup relationships within a monophyletic *Thaleops* that encompasses *Nanillaenus*. In addition, our phylogenetic analysis indicates that *Illaenus* is paraphyletic and lends support to a monophyletic *Parillaenus* Jaanusson 1954, which serves as a starting point for a more detailed revision of those genera in

the future.

GEOLOGICAL SETTING OF NEW MATERIAL

Middle to Late Ordovician trilobites from Oklahoma described in this paper were collected from exposures in the Arbuckle Mountains of south-central Oklahoma (Fig. 1). The Southern Oklahoma aulacogen was the depocenter for the larger Oklahoma basin during the Ordovician. Subsidence within this topographic feature allowed deposition of thick sedimentary units at varying depths along an environmental gradient on a carbonate ramp leading into the aulacogen (e.g., see Longman 1982a, b).

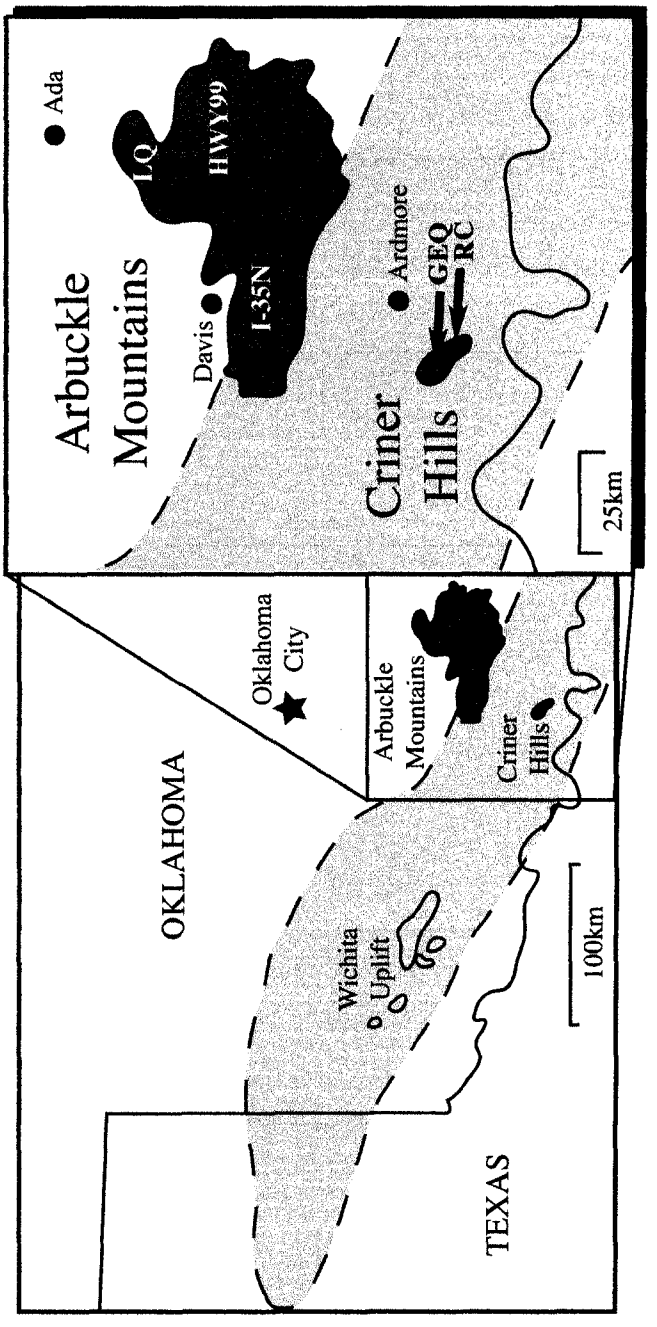
The Bromide Formation is the uppermost unit of the Middle Ordovician Simpson Group and is well exposed in the Arbuckle Mountains. At least five species of illaenid are present in the Bromide Formation. *Thaleops* sp. A is restricted to rudstones in the lower, Mountain Lake Member 36 metres above the base of the I-35N section (Fig. 1). These deposits are interpreted to represent deposition in a shoal environment. Three species, *T.* sp. A, *T. jaanussoni* sp. nov. and an undescribed species of *Illaenus* occur in packstones to rudstones in both the Mountain Lake and Poolville members at I-35N and GEQ. *Thaleops mobydicki* sp. nov. is only found in rudstones to packstones near the top of the Poolville Member at GEQ.

Two species of illaenid, *T. depressicapitata* Bradley 1930 and *T. anusacerbissima* sp. nov. are present in the Upper Ordovician (Mohawkian – Cincinnatian) Viola

FIGURE 1

Map of Oklahoma showing the position of the Arbuckle Mountains and Criner Hills relative to the inferred outline of the Southern Oklahoma aulacogen. Inset shows position of main collecting localities for new species from Oklahoma. **LQ**, Lawrence Quarry, operated by Holnam, Inc. 10 km southwest of Ada, Oklahoma. **HWY99**, roadcut along west side of U.S. Highway 99, 5 km south of Fittstown, Oklahoma. **I-35N**, roadcut on the east side of Interstate 35, on the north flank of the Arbuckle Mountains, 8 km south of Davis, Oklahoma. **GEQ**, Dunn Quarry operated by Geological Enterprises Ltd., 8 km southwest of Ardmore, Oklahoma in the Criner Hills. **RC**, Rock Crossing, creek bed in Criner Hills, 9 km southwest of Ardmore, Oklahoma. (Modified from Perry 1989.)

Figure 1


Ada
LQ
HWY99
I-35N
Davis
Arbuckle
Mountains
Ardmore
GEQ
RC
Criner
Hills
25km
Oklahoma
City
OKLAHOMA
Arbuckle
Mountains
Criner
Hills
Wichita
Uplift
100km
TEXAS

Springs Formation (Fig. 2). The Viola Springs is a nearly pure carbonate unit that was deposited at varying depths on a carbonate ramp following tectonic activation of faults and rapid subsidence within the aulacogen. The majority of sites preserve facies that formed below wave base on distal portions of the ramp, although two localities provide exposure of sediments that were deposited on the proximal ramp near the margins of the aulacogen. Each species of *Thaleops* is restricted to a different facies representing distinct depositional environments.

Thaleops anusacerbissima is restricted to a cross-bedded, bryozoan-rich rudstone 18-38 metres above the base of section HWY99 (Fig. 1) that is interpreted as having been deposited in a high-energy, localized shoal environment. *Thaleops depressicapitata* appears 38 metres stratigraphically above *T. anusacerbissima* at the same locality. It is preserved in winnowed packages of packstone to rudstone interbedded with wackestone that are thought to represent a shallow subtidal environment between fair-weather and storm wave base. *Thaleops depressicapitata* also occurs in a similar lithofacies at a second locality (LQ) near the margins of the Southern Oklahoma aulacogen (Fig. 1).

Thaleops laurentiana sp. nov. is erected for specimens previously referred to *I. americanus* Billings 1859. Type material is from the Upper Ordovician, middle to upper Trenton Group near Trenton Falls, NY where complete trilobites are preserved in fine-grained carbonate representing distal storm event deposits. Other figured specimens are from the upper Black River Group near Poland, NY and the lower Trenton Group near Watertown, NY.

FIGURE 2

Relative geologic and geographic distribution of species of *Thaleops*. Solid lines indicate ranges that are known with some confidence; dashed lines show extent of formation for which occurrence was reported. Graptolite zones from Riva (1972, 1974). **1**, *T. adunca*, *T. mackenziensis* (Chatterton & Ludvigsen 1976), Upper Ordovician Esbataottine Formation, Nahanni River Area, District of Mackenzie. **2**, *T. utahensis* (Hintze 1952), Middle Ordovician Kanosh Shale and Lehman Formation, western Utah and eastern Nevada. **3**, *T.* cf. *utahensis* (Shaw 1974), Middle Ordovician Oil Creek Formation, Arbuckle Mountains, Oklahoma. **4**, *T.* sp. 2 described herein, Upper Ordovician Mountain Lake Member, Bromide Formation, I-35N at 36.6m, Arbuckle Mountains, Oklahoma. **5**, *T.* sp. 1, described herein, *T. jaanussoni* sp. nov., Upper Ordovician Mountain Lake and Pooleville members, Bromide Formation, I-35N at 47-48m and GEQ, Oklahoma. **6**, *T. mobydicki* sp. nov., Upper Ordovician Pooleville Member, Bromide Formation, GEQ and RC, Oklahoma. **7**, *T. anusacerbissima* sp. nov, Upper Ordovician Viola Springs Formation 13-34m interval at HWY99, Oklahoma. **8**, *T. depressicapitata* (Bradley 1930), Upper Ordovician Viola Springs Formation 38-51m interval at HWY99 and near quarry base at LQ, Oklahoma. **9**, *T. ovata* (Conrad 1843), Upper Ordovician Maquoketa Group, Iowa. **10**, *T. laurentiana* sp. nov., Upper Ordovician Galena Formation, Minnesota and Illinois. **11**, *T. ovata*, *T. depressicapitata* (type occurrence) Upper Ordovician Kimmswick Formation, eastern Missouri and western Illinois. **12**, *T. ovata* (type occurrence), Upper Ordovician Galena Formation, Mineral Point, Wisconsin. **13**, *T. ovata* and *T. angusticollis* (Billings 1859) Upper Ordovician

Platteville Group, Illinois and Wisconsin. **14**, *T. angusticollis* (type occurrence), Upper Ordovician Ottawa Formation, St. Joseph Island, Lake Huron. **15**, *T. angusticollis*, *T. latiaxiata* (Raymond & Narraway 1908) (type locality), *T. conradi* (Billings 1859), Upper Ordovician Black River Formation near Ottawa. **16**, *T. ovata*, Upper Ordovician Black River and Ottawa formations near Ottawa. **17**, *T. laurentiana*, Upper Ordovician Trenton Formation near Ottawa. **18**, *T. fieldi* (Raymond 1925) Upper Ordovician Holston Formation, Catawba Valley, Virginia. **19**, *T. arctura* (Hall 1847), *T. laurentiana*, Middle Ordovician Chazy Formation near Chazy, New York. **20**, *T. angusticollis*, Upper Ordovician Glens Falls Formation, Mohawk Valley, New York. **21**, *T. longispina* Shaw 1968, Upper Ordovician Crown Point and Valcour formations, Valcour Island, New York. **22**, *T. laurentiana* (type occurrence) upper Black River to Trenton Groups, New York. **23**, *T. raymondi* (Shaw 1968), Middle to Upper Ordovician uppermost Day Point and Crown Point formations, Valcour Island, New York. **24**, *T. latiaxiata* Upper Ordovician Black River Group, New York. **25**, *T.* sp. 3 described herein, Upper Ordovician Crown Point Formation, Valcour Island, New York. **26**, *T. conradi*, Upper Ordovician Black River Group near Mechanicsville, Ontario. **27**, *T. latiaxiata*, Upper Ordovician Cobourg Formation, Bowmanville, Ontario. **28**, *T. conradi*, Upper Ordovician Black River Formation near Hull, Quebec. **29**, *T. conradi* (type occurrence), Upper Ordovician Leray Formation near Hull, Quebec. **30**, *T. vindex* (Billings 1865) , *T. clavifrons* (Billings 1859), *T. conifrons* (Billings 1859) Middle to Upper Ordovician Mingan Formation, Mingan Islands, Quebec. **31**, *T. conifrons* (type occurrence) Upper Ordovician Black River Group, Mingan Islands, Quebec. **32**, *T. marginalis*

(Raymond 1925) Middle Ordovician lower Table Head Formation, Table Point and Pointe Riche, western Newfoundland. **33**, *T. viator* (Raymond 1925) Upper Ordovician Lourdes Limestone, Long Point, Port Au Port Peninsula, Newfoundland. **34**, *T. lacerta* (Whittington 1954), *T. baffinlandica* (Roy 1941), *T. nunivutica* sp. nov., *T. groenlandica*(?)(Troedsson 1928) Upper Ordovician Amadjuak Formation, Silliman's fossil mount, Frobisher Bay, southern Baffin Island, Nunavut. **35**, *T. borealis* Teichert 1937 Upper Ordovician Kap Jackson Formation, North Greenland. **36**, *T. groenlandica* (type occurrence) Upper Ordovician Cape Calhoun Formation, Cape Calhoun, North Greenland.

*tere, *G.* cf. *teretiusculus* zone; *amer, *C. americanus* zone; *rued, *O. ruedemanni* zone; *pyg, *C. pygmaeus* zone; *mani, *C. manitoulinensis* zone; *comp, *C. complanatus* zone; *inuit, *A. inuiti* zone.

+ indicates type occurrence when species is known from multiple localities

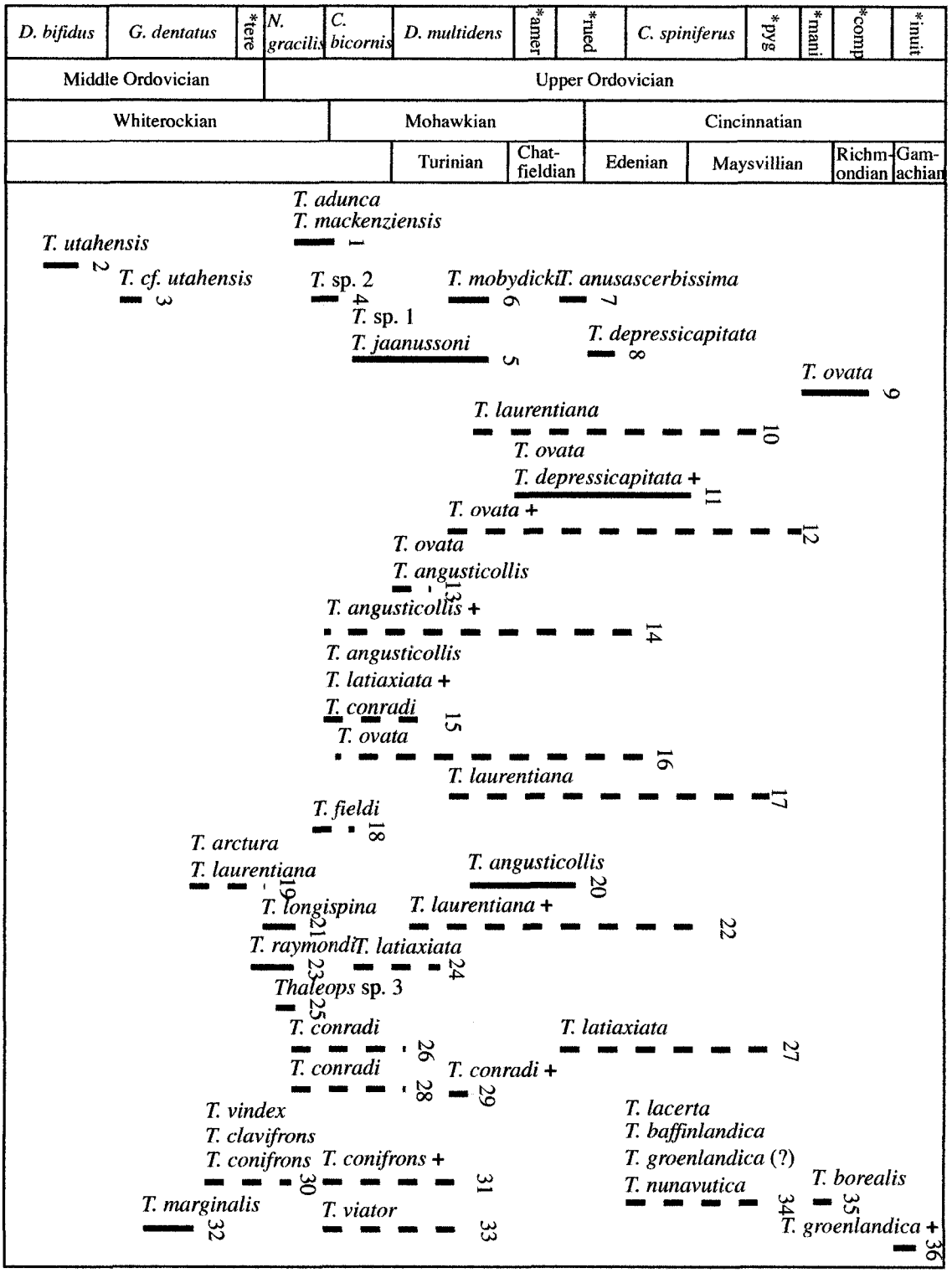

D. bifidus
G. dentatus
*tere
N. gracilis
C. bicornis
D. multidens
*amer
*rued
C. spiniferus
*pyg
*mani
*comp
*inuit
Middle Ordovician
Upper Ordovician
Whiterockian
Mohawkian
Cincinnatian
Turinian
Chat-fieldian
Edenian
Maysvillian
Richm-ondian
Gam-achian
T. adunca
T. mackenziensis
1
T. utahensis
2
T. cf. utahensis
3
T. sp. 2
4
T. mobydickiT. anusascerbissima
6
7
T. sp. 1
T. jaanussoni
5
T. depressicapitata
8
T. ovata
9
T. laurentiana
10
T. ovata
T. depressicapitata +
11
T. ovata +
12
T. ovata
T. angusticollis
13
T. angusticollis +
14
T. angusticollis
T. latiaxiata +
T. conradi
15
T. ovata
16
T. laurentiana
17
T. fieldi
18
T. arctura
T. laurentiana
19
T. angusticollis
20
T. longispina
21
T. laurentiana +
22
T. raymondiT. latiaxiata
23
24
Thaleops sp. 3
25
T. conradi
26
T. latiaxiata
27
T. conradi
28
T. conradi +
29
T. vindex
T. clavifrons
T. conifrons
30
T. conifrons +
31
T. lacerta
T. baffinlandica
T. groenlandica (?)
T. nunavutica
34
T. borealis
35
T. marginalis
32
T. viator
33
T. groenlandica +
36

Figure 2

PREVIOUS WORK

Thaleops was erected by Conrad (1843) in response to discovery of Laurentian illaenids that bore a strong resemblance to typical Scandinavian species of *Illaenus*, but with some distinct differences. In his description, Conrad emphasized the definition of the axial lobe, the stalk-like nature of the palpebral lobes and the high angle that the articulating facets of the pygidium form with the anterior margin of the pygidium as diagnostic features. Later workers (Billings, 1859; Billings, 1861; Raymond & Narraway 1908; Raymond, 1925; Troedsson, 1928; Bradley, 1930; Teichert, 1937; Twenhofel, 1938; Roy, 1941; Wilson, 1947; Whittington, 1954; Shaw, 1968; Chatterton & Ludvigsen 1976) described new species that were recognized as belonging to a group of illaenids with characters similar to those used to diagnose *T. ovata* Conrad 1843. These species display a range of morphologies grading between strongly furrowed forms, like *T. ovata* with a very well-defined axial lobe and distinct eye stalks, and species like *I. americanus* that exhibit greater effacement and narrower (tr.) palpebral lobes.

Raymond & Narraway (1908) suggested that *I. angusticollis* Billings 1859 and *I. conradi* Billings 1859 had an intermediate morphology between *Illaenus* and *Thaleops*.

Since its erection by Jaanusson in 1954, *Nanillaenus* (type species: *N. conradi*) has been used for these intermediate forms (Shaw, 1968; Chatterton & Ludvigsen 1976). Unfortunately, the characters used by Jaanusson to diagnose *Thaleops* and *Nanillaenus* have overlapping distributions and do not define distinct groups. For

example, *I. latiaxiatus* Raymond & Narraway 1908 has 10 thoracic segments (a character of *Thaleops*, according to Jaanusson), but also possesses relatively short palpebral lobes and the moderately vaulted pygidium typical of *Nanillaenus*. The stalked and elevated palpebral lobes of *N. aduncus* Chatterton & Ludvigsen 1976 conform to the diagnosis of *Thaleops*, but the shallow axial furrows of the cephalon are features considered by Jaanusson to be diagnostic of *Nanillaenus*.

Whittington (1954) recognized two groups of Laurentian illaenids. He pointed out that the narrow cranidial axis, elevation and posterior position of the palpebral lobes, and anterior convergence of the facial sutures allied *I. punctatus* Roy 1941 (a junior homonym of *I. punctatus* Raymond 1905) with *Thaleops*. A second group including *I. lacertus* Whittington 1954, *I. groenlandicus* Troedsson 1928, *I. americanus*, *I. latiaxiatus*, *I. fieldi* Raymond 1925, and *I. depressicapitatus* was characterized by Whittington (1954, p. 138) as being united by a "sharp angle at anterolateral margin of pygidium".

Shaw (1968) commented on the gradational nature of Laurentian illaenid morphology and the need for more concise limits on genera. Chatterton & Ludvigsen (1976) tentatively assigned two new species from northern Canada with intermediate morphologies to *Nanillaenus*, although they noted that both *Nanillaenus* and *Thaleops* might be synonomized eventually with *Illaenus*.

PHYLOGENETIC ANALYSIS

Thaleops has been weakly defined since its diagnosis in 1843 by characters that are

gradational with other genera or are probably plesiomorphic for the Illaenidae. Erection of *Nanillaenus* by Jaanusson in 1954 only served to exacerbate the problem. We conducted a cladistic analysis of 28 species in order to evaluate *Thaleops* and its relationships with other illaenid genera.

TAXA USED IN THE ANALYSIS

Outgroup. We chose a styginid for the outgroup because they are plesiomorphic members of Illaenida and *Raymondaspis* Pŕibyl in Prantl and Pŕibyl 1949 is a well-documented species available from the Whiterockian of Laurentia. Coding of cranidial, pygidial and librigenal characters is based on *Raymondaspis vespertina* Ross 1967, as illustrated by Fortey (1980, pl. 6, figs 1-8, 11). This was supplemented by information on other sclerites from *R. recticulatus* Whittington (1965, pl. 55, figs 2, 3, 5-9, pl. 56, figs 1-10, pl. 57, pl. 58, figs 1, 7) and *R. tennesseensis* Cooper (1953, pl. 9, fig. 11). To evaluate the influence of outgroup selection, we repeated the analysis using an outgroup that is more closely related to *Thaleops* and *Nanillaenus*, *Illaenus oscitatus* Fortey, 1980. As discussed below, this change in rooting had no significant impact on the results.

Illaenus. One goal of this analysis is to explore the relationship between *Illaenus* and *Thaleops*. Jaanusson (1954) divided European species of *Illaenus* into two groups, *Illaenus sensu strictu* and a *Parillaenus* group, mainly based on the shape of the inner margin of the pygidial doublure. Although doubts have been expressed about the utility of this trait (Whittington, 1963; Shaw, 1968), most subsequent authors have

treated *Parillaenus* as a subgenus (Ingham, 1970; Dean, 1979; Owen & Bruton 1980; Bruton & Owen 1988). In 1957, Jaanusson increased the number of *Illaenus*-groups to five through a four-fold division of *Illaenus sensu strictu*, based on the shape of the anterior margin of the pygidial doublure. He then outlined other morphological features of each group using one or more representative species. Jaanusson recognized the difficulty in defining taxa on a single character in isolation and did not formally name any of his *Illaenus*-groups. In this analysis, at least one taxon was chosen to represent each of Jaanusson's (1957) *Illaenus*-groups. *Illaenus sarsi* Jaanusson 1954 and *I. aduncus* Jaanusson 1957 are included from the *I. sarsi*-group, *I. praecurrens* Jaanusson 1957 represents the *I. excellens*-group, and *I. planifrons* Jaanusson 1957 is from the *I. sulcifrons*-group. The *I. crassicauda*-group is represented by the eponymous species, and *I. roemeri* Volborth 1864 and *I. fallax* Holm 1882 are from the *Parillaenus*-group. Because *Thaleops* is known only from Laurentia, we also coded *I. oscitatus* Fortey 1980 from the Whiterockian of Spitsbergen as a Laurentian representative of *Illaenus*.

Nanillaenus and Thaleops. During preliminary stages of the analysis, we recognized a single character (long articulating facets of pygidium that form a high angle with the anterior margin) as a potential apomorphy uniting *Nanillaenus* and *Thaleops.* This character also occurs in some species that have been classified previously as *Illaenus*, including *I. lacertus*, *I. utahensis* Hintze 1952 and *I. marginalis* Raymond 1925, and these were also assigned to the ingroup. Species that have been classified as *Nanillaenus* and *Thaleops* in the past were included wherever adequate material for

coding was available.

TAXA NOT INCLUDED IN ANALYSIS

A number of species in the literature appear to have affinities with *Thaleops* but were not be included in the analysis because they are known only from a few, often poorly preserved sclerites. These include *I. arcturus* Hall 1847, *I. clavifrons* Billings 1859, *I. vindex* Billings 1865, *T. borealis* Teichert 1937, *I. punctatus* Raymond 1905, *I. punctatus* Roy 1941, and *I. baffinlandicus* Roy 1941. *Illaenus groenlandicus* Troedsson 1928 was unavailable for loan and the published illustration was inadequate for coding.

Hammann (1992) erected *T. inflata* and later (Hammann & Leone 1997) established *Amphoriops* as a subgenus of *Thaleops*, adding a second species, *Thaleops (Amphoriops) zoppii*. The well-defined axial furrows of the cranidia of both species bear a resemblance to those of such derived species of *Thaleops* as *T. longispina* (Shaw, 1968), but the pygidial morphology allies them with Scandinavian species of *Illaenus*.

EXPLANATION OF CHARACTERS AND CHARACTER STATES

We used seven binary and 13 multistate characters, with a total of 40 apomorphic states. Character states and codings are listed in Appendix 1, and those characters that require additional explanation are discussed below. The data matrix used for this analysis is presented as Appendix 2.

Length and orientation of articulating facets. This character was described indirectly by Conrad (1843) in his diagnosis of *Thaleops* when he observed that the outer half of the pleural lobes of the thorax are suddenly depressed dorso-ventrally. The length and angle of deflection of the outer portions of the thoracic segments are reflected in the length and shape of the articulating facets of the pygidium. As noted above, Whittington (1954) recognized the utility of this character in his definition of a group of Laurentian species of "*Illaenus*" (e.g., Whittington 1954, pl. 61, figs 5-6). However, this state also occurs in *Thaleops*, which has a long articulating facet that is directed at a steep angle, averaging 75°, to the anterior margin of the pygidium. The greatest width (tr.) of the pygidium is located at the posterior termination of the articulating facet. In contrast, *I. fallax* and *I. praecurrens* (Jaanusson, 1957, pl. 7, fig. 7, pl. 8, figs 1-5; Bruton & Owen 1988, fig. 8) have short articulating facets oriented at a very low angle to the anterior margin of the pygidium. Other species of *Illaenus* treated by Jaanusson (1957) and *Raymondaspis* (Fortey, 1980, pl. 6, figs 3-4) have short articulating facets on the pygidium that form an angle with the anterior margin of the pygidium that is roughly 45°.

In order to quantify the length and angle of the articulating facet, we measured the distance from the anterior margin of the pygidium to the point of maximum width (tr.) of the pygidium and express this as a percentage of the total length (sag.) of the pygidium. Transformations between character states are based on gaps in the distribution of percentages.

Shape of pygidial doublure. The use of the pygidial doublure in the classification of

illaenid trilobites has had a checkered history. Doublure shape figured prominently in the work of Jaanusson (1954, 1957) and Šnadjr (1957), whereas other workers doubted its value (e.g., Whittington, 1963). Illaenids show a wide range of doublure morpholgies. For example, Jaanusson (1957, figs 11-12) illustrated two different doublure shapes for *Dysplanus* Burmeister 1843 and no less than 7 shapes for *Illaenus* (his figure 14). The most common doublure shape in *Thaleops* (two sharp anterior projections bracketing the posterior termination of the pygidial axis; Jaanusson, 1957, fig. 14 A) is also found in many species of *Illaenus* (Jaanusson, 1954, fig. 10A), *Stenopariea* Holm 1886 (Jaanusson, 1954, fig. 10E) and *Bumastoides* (Chatterton & Ludvigsen 1976, figs 9, 17, 25). For this analysis, doublure shapes were grouped into four categories: anterior margin of doublure is smooth or has a faint embayment (e.g., Nielsen, 1995 fig. 224D; Jaanusson, 1957 pl. 7, fig. 7); a sharp, anteriorly directed projection on either side of the termination of the pygidial axis (e.g., Jaanusson, 1957 pl. 6, fig. 6; Chatterton & Ludvigsen 1976 pl. 4, fig. 37), including those taxa with a second, shorter (exsag.) pair of anterior projections between the larger pair (e.g., Pl. 11, Figs 4, 5); a deep, U-shaped incision in the anterior margin of the doublure exhibited only by *I. utahensis* (e.g., Hintze, 1952 pl. 28, fig. 9a); and a rounded, medial, anterior projection identified only in *I. planifrons* (e.g., Jaanusson, 1957 pl. 10, fig. 1).

Degree of definition of pygidial axis. Conrad (1843) described the pygidium of *Thaleops* as being "profoundly trilobed" while that of *Illaenus* is effaced. A well-defined axial lobe of the pygidium (delimited by deep furrows and/or high vaulting)

has been considered a character of *Thaleops* and *Nanillaenus* by nearly every author who has discussed these genera (Conrad, 1843; Clarke, 1897; Raymond & Narraway 1908; Jaanusson, 1954; Jaanusson *in* Moore 1959; Shaw, 1968), while the pygidial axis of *Illaenus* is characterized as recognizable, but poorly defined. In our analysis, pygidial axes are coded as effaced if the posterior margin of the axis is not defined (e.g., *I. utahensis* Hintze, 1952, pl. 28, fig. 9b). Pygidial axes coded as "defined" are weakly outlined by shallow furrows around the entire circumference of the axis but are not vaulted to a great degree above the pleural fields (e.g., *N. conradi* Pl. 7, Fig. 1d, 4a-b). Well-defined pygidial axes are those in which the axial furrows are deeply incised and the axis is highly vaulted (e.g., *T. ovata* Pl. 1, Fig. 1a-c, 3c, 4a, c).

Width (tr.) of pygidial axis. The maximum width (tr.) of the axis of the pygidium was measured as a percentage of the maximum width (tr.) of the pygidium. Transformations between character states are based on gaps in the distribution of percentages.

Number of thoracic segments. Segment number has been used to diagnose illaenid genera by previous workers. Both *Thaleops* and *Illaenus* include species with ten thoracic segments (Conrad, 1843; Jaanusson, 1954; Jaanusson *in* Moore 1959) while *Nanillaenus* is characterized by eight (Jaanusson, 1954; Jaanusson *in* Moore 1959). *Illaenus angusticollis* has been reported as varying in segment number. As originally described by Billings, this species has eight thoracic segments. However, Raymond & Narraway (1908) attributed twelve specimens to *I. angusticollis*, ten of which had

eight thoracic segments and two had nine. It is not clear whether Raymond & Narraway's material represents a single species, and we coded *I. angusticollis* as having eight thoracic segments, as in Billings' types.

Thorax shape. Several authors (Jaanusson, 1954, Jaanusson *in* Moore 1959, Shaw, 1968) have pointed out that the pygidia of species in *Nanillaenus* and *Thaleops* are considerably smaller than the cephala. This character is also reflected in the shape of the thorax, which tapers markedly in species with relatively small pygidia. We used thorax shape, expressed as the width (tr.) of the posterior-most thoracic segment as a percentage of the width (tr.) of the first thoracic segment. Character states were defined using gaps in the distribution of percentages.

Position of palpebral lobes. Whittington (1954) noted that taxa he considered to belong to *Thaleops* had palpebral lobes positioned near the posterior margin of the cranidium.

Definition of anterior margin of glabella. Jaanusson (1954) described the axial furrows of the cephalon as well developed in *Thaleops*. This character is coded in terms of strength of furrows around the anterior margin of the glabella, with well-defined anterior furrows present in *I. angusticollis* and *T. longispina* and weakly-defined but visible furrows in *N. raymondi* Shaw 1968 and *I. crassicauda.*

CHARACTERS EXCLUDED FROM ANALYSIS

Rostral plate. Jaanusson (1954, 1957) and Šnajdr (1957) both considered the morphology of the rostral plate to be important in the classification of illaenid trilobites. Rostral plates are unknown for all but a few of the species under study and, given the extent of missing data, this sclerite was not included in the analysis.

Hypostome. Hypostome morphology was also emphasized by Jaanusson (1954, 1957) and Šnajdr (1957) in their classifications of illaenids. For example, the broad, subquadrate anterior wing is a potential apomorphy for *Illaenus.* Shortly after Jaanusson and Šnajdr published their work, Whittington (1963, p. 66) noted that the absence of information on the hypostome for most illaenid species meant that this sclerite "can scarcely be used in classification" and the state of knowledge is essentially unchanged.

Stalk-like palpebral lobes. The width (tr.) of the palpebral lobes was difficult to measure and to code discretely. We chose instead to analyze the orientation of the palpebral lobes (ventrally directed, horizontal, or directed upward). This allowed us to address the "stalk-like" nature of the eyes without attempting to quantify width.

RESULTS

We conducted a parsimony analysis using PAUP version 4.0b10 (Swofford, 2000); all characters were unordered (nonadditive) and equally weighted. A branch-and-bound search retrieved 14 equally parsimonious trees with length of 70, C. I. of 0.57,

R. I. of 0.76 and R. C. of 0.43. The strict consensus tree is shown in figure 3. Successive approximations weighting of characters using the rescaled consistency indices yielded a single tree with length 32.17 (Fig. 4) that was topologically identical to one in the original set of 14 trees. The optimized character distributions for the weighted tree under both ACCTRAN and DELTRAN are compared in Table 1. The results are robust to changes in the outgroup. An alternate analysis in which *I. oscitatus* was designated as the outgroup retrieved 14 trees, the strict consensus of which was identical to the tree shown in figure 3.

Thaleops (node 9) is defined as a large monophyletic group that includes some species (e.g., *T. utahensis* and *T. lacerta*) that lack features (such as stalked eyes and genal spines) traditionally used to characterize the genus. At node 9, character 1, state 2, pygidial outline in which long articulating facets are inclined backward at a steep angle to the anterior margin, is an unambiguous apomorphy for *Thaleops*, with a C. I . of 1.0. Other characters (under DELTRAN, a thorax shape that is slightly tapered and under ACCTRAN glabellar furrows that are convergent from the posterior margin and a cranidium with length that is approximately 75% of width) arising at the same node are ambiguous. Node 10, immediately above node 9 within *Thaleops*, is defined by two additional unambiguous apomorphies (character 13, state 2 and character 18, state 3 in Appendix 1), palpebral lobes that are located close to the posterior margin (at a distance of less than 25% of total cranidial length) and facial sutures that are weakly convergent. These states apply to all species of *Thaleops* except *T. marginalis*.

FIGURE 3

Strict consensus of 14 equally parsimonious trees of length 70 found in a branch-and-bound search. All characters were unordered and the tree was rooted using *Raymondaspis* as the outgroup. The tree statistics are: C. I., 0.57, R. I., 0.76 and R. C., 0.43. Bremer support indices are indicated in italics.

Figure 3

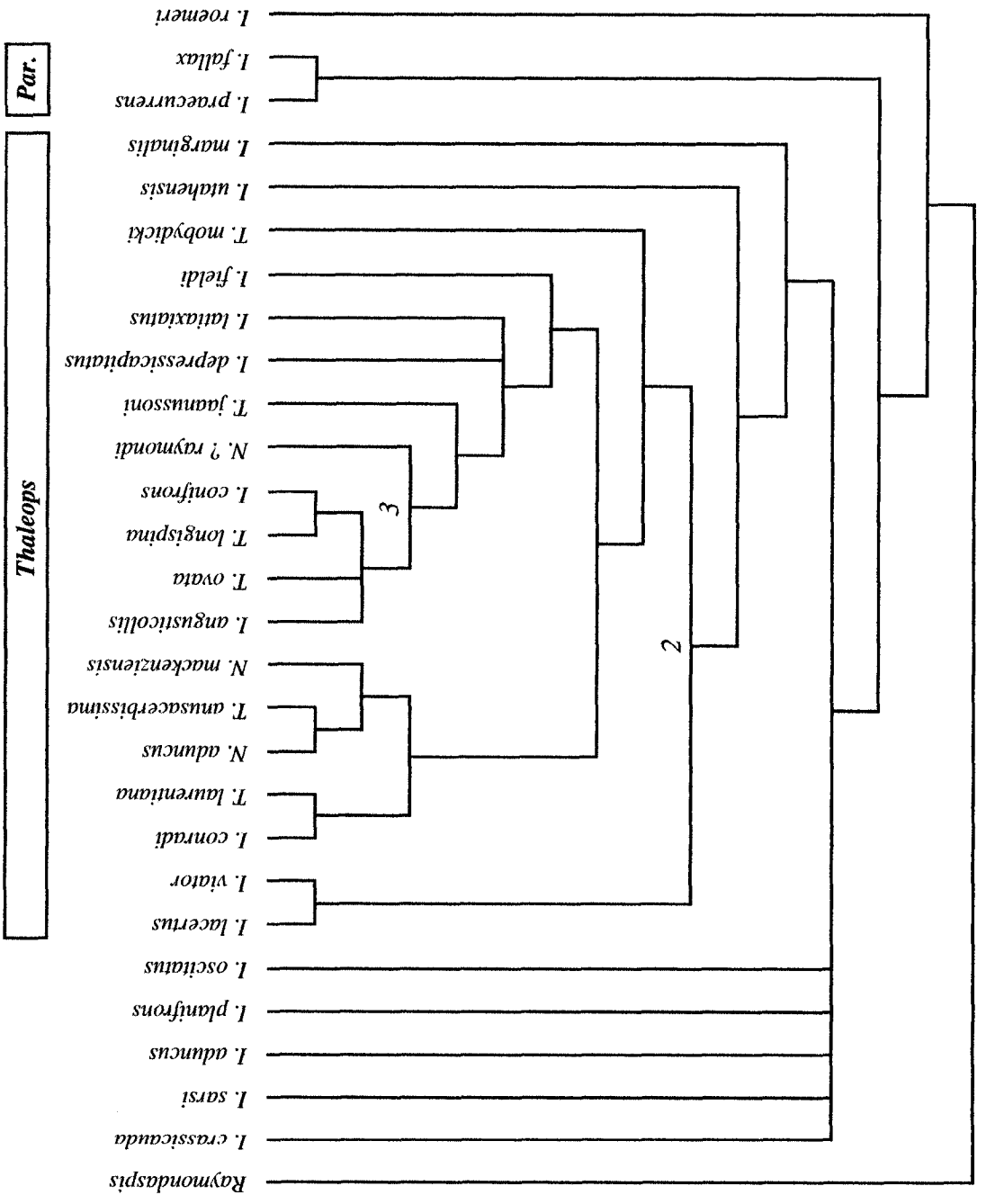

Raymondaspis
I. crassicauda
I. sarsi
I. aduncus
I. planifrons
I. ocsitatus
I. lacertus
I. viator
I. conradi
T. laurentiana
N. aduncus
T. ausacerbissima
N. mackenziensis
I. angusticollis
T. ovata
T. longispina
I. conifrons
N. ? raymondi
T. jaanussoni
I. depressicapitatus
I. latiaxiatus
I. fieldi
T. mobydicki
I. utahensis
I. marginalis
I. praecurrens
I. fallax
I. roemeri
Par.
Thaleops
3
2

FIGURE 4

The single most parsimonious tree (length 32.17) produced following successive approximations weighting of characters using the rescaled consistency indices. This tree is identical to one of the original 14 trees. Optimized character distributions under both ACCTRAN and DELTRAN for the tree are shown in Table 1.

Figure 4

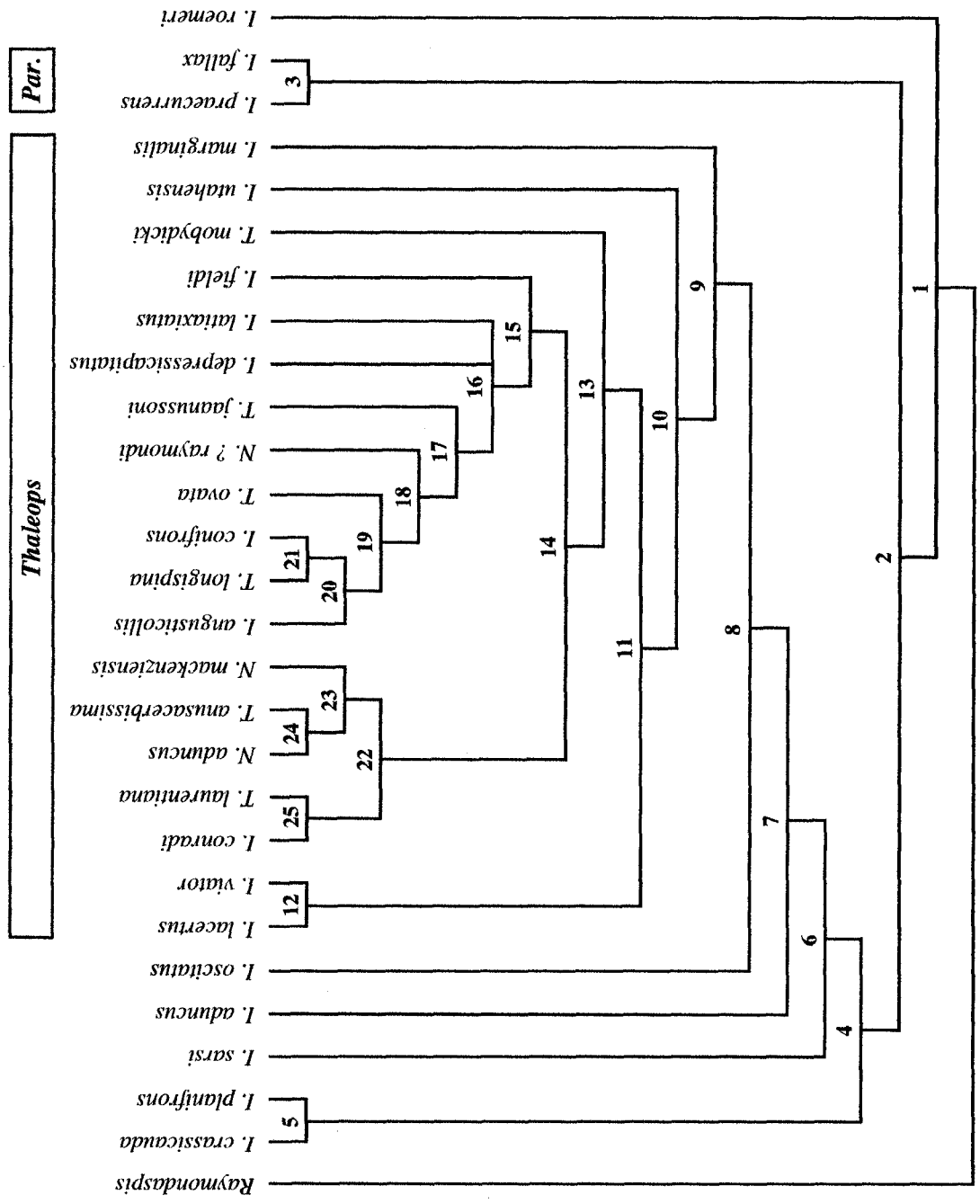

Raymondaspis
I. crassicauda
I. planifrons
I. sarsi
I. aduncus
I. oscitatus
I. laceratus
I. viator
I. conradi
T. laurentiana
N. aduncus
T. anusacerbissima
N. mackenziensis
I. angusticollis
T. longispina
I. conifrons
T. ovata
N. ? raymondi
T. jaanussoni
I. depressicapitatus
I. latiaxiatus
I. fieldi
T. mobydicki
I. utahensis
I. marginalis
I. praecurrens
I. fallax
I. roemeri
Par.
Thaleops
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TABLE 1

Synapomorphies at nodes on the tree in figure 4 under ACCTRAN and DELTRAN optimization. Asterisks indicate character states with ambiguous optimization.

Table 1

Node	ACCTRAN Synapomorphies	Node	DELTRAN Synapomorphies
1	5(2), 7(1), 8(1)*, 10(1), 11(1), 13(1), 14(1), 16(2)	1	5(2), 7(1), 10(1), 11(1), 13(1), 14(1), 16(2)
2	3(1)*, 6(1)	2	6(1), 8(1)*
3	1(1), 2(1)	3	1(1), 2(1)
4	18(1)	4	3(1)*, 18(1)
5	9(1)*, 15(2)	5	15(2)
6	4(1)	6	4(1)
7	20(4)	7	20(4)
8	9(1)*, 18(2)	8	18(2)
9	1(2), 15(2)*, 20(2)*	9	1(2), 9(1)*
10	13(2), 18(3)	10	13(2), 18(3)
11	6(0), 9(2)	11	6(0), 9(2), 20(2)*
12	7(2)	12	7(2)
13	5(1)	13	5(1), 15(2)*
14	11(3)	14	11(3)
15	17(1)	15	17(1)
16	19(1)	16	19(1)
17	5(0)	17	5(0)
18	12(1), 14(0), 16(1)	18	12(1), 14(0), 16(1)
19	10(0), 15(1)*, 17(2)*	19	10(0)
20	15(3)*, 18(4)	20	15(3)*, 18(4)
21	16(0), 17(0)*	21	16(0)
22	15(1)	22	15(1)
23	18(4)	23	18(4)
24	12(1)	24	12(1)
25	11(2)	25	11(2)

Two nodes have Bremer support > 1 (Fig. 3), and one of these defines *Thaleops*, excluding *T. marginalis* and *T. utahensis*, at node 11. Two unambiguous apomorphies, a pygidial axis that is longer (exsag.) than the post-axial field (character 6, state 0 in Appendix 1) and a thorax that is much narrower (tr.) toward the posterior (character 9, state 2 in Appendix 1) define the node under both ACCTRAN and DELTRAN optimization and an ambiguous apomorphy (character 20, state 2) is added under DELTRAN.

Node 18, uniting *Thaleops raymondi*, *T. ovata*, *T. angusticollis*, *T. longispina* and *T. conifrons* Billings 1859, forms a subgroup that is supported by a Bremer index of 3. Well-defined axial furrows, glabellar furrows defined on the anterior portion of the cranidium and palpebral lobes angled upward unite these taxa.

All other nodes have Bremer indices of one and are less well supported. However, three subgroups within the ingroup occur in all trees (Figs 3, 4). The first is node 18, discussed above. The monophyletic group consisting of *T. lacerta* and *T. viator* Raymond 1925 is defined by a pygidial axis that is exceptionally wide. A third subgroup arises at node 23 in this analysis and includes *T. mackenziensis* Chatterton & Ludvigsen 1976, *T. anusacerbissima* and *T. adunca*. These taxa are united by anterior facial sutures that are angled strongly medially and the presence of genal spines.

Illaenus sensu Jaanusson (1954, 1957) is spread out over five nodes and is clearly paraphyletic. The results suggest that additional monophyletic groups might be identified within *Illaenus* with further study, although they do not appear to correspond exactly to Jaanusson's (1957) *Illaenus*-groups. For example, Jaanusson

(1954) designated *I. fallax* as the type species of his "*Parillaenus* group", and several subsequent workers have treated this group as a subgenus. In our analysis, *I. fallax* and *I. praecurrens* form a monophyletic group defined by two pygidial apomorphies: a pygidium that is long relative to width (character 2, state 1 in Appendix 1) and orientation of the relatively short articulating facets at a low angle to the anterior margin of the pygidium (character 1, state 1 in Appendix 1). *Illaenus crassicauda* and *I. planifrons* form a monophyletic group at node 5 that is defined by axial furrows that converge from the posterior margin (character 15, state 2 in Appendix 1). This grouping is determined by glabella shape (character 15) but this has a low C. I. of only 0.375.

SYSTEMATIC PALEONTOLOGY

Specimens from nine institutions are refigured: NYSM – New York State Museum, Albany; GSC – Geological Survey of Canada, Ottawa; AMNH – American Museum of Natural History, New York; CM – Carnegie Museum, Pittsburgh; MCZ – Museum of Comparative Zoology, Cambridge; ROM – Royal Ontario Museum, Toronto; YPM – Peabody Museum of Natural History, New Haven; P, UC and WM – The Field Museum, Chicago; GM – Geological Museum, Copenhagen. Type material of *T. anusacerbissima*, *T. mobydicki*, *T. jaanussoni*, *T.* sp. A and *T.* sp. B from the Viola Group of Oklahoma and figured material of *T. depressicapitata* from the Viola Group and the Kimmswick Limestone of Missouri are housed in the type and figured collections at the Oklahoma Museum of Natural History (OU). The collection

localities are indicated in figure 1.

Suborder **ILLAENINA** Jaanusson 1959

Superfamily **ILLAENOIDEA** Hawle & Corda 1847

Family **ILLAENIDAE** Hawle & Corda 1847

Genus ***Thaleops*** Conrad 1843

TYPE SPECIES

Thaleops ovata Conrad 1843 from the Upper Ordovician Galena Formation, Mineral Point, Wisconsin by original designation.

EMENDED DIAGNOSIS

A genus of Illaenidae with long articulating facets of the pygidium oriented at a high angle with respect to the anterior margin of the pygidium. Most species with palpebral lobes positioned at less than 25% the total length (sag.) of the cranidium anterior to the posterior margin.

Thaleops ovata Conrad 1843 Pl. 1, Pl. 2, Pl. 3, Figs 1, 2

1843. *Thaleops ovata*; Conrad, P. 332.

1847. *Thaleops (Illaenus) ovatus*; Hall, p. 259, pl. 67, figs 6a-6b.

1882. *Illaenus ovatus*; Whitfield, p. 238, pl. 5, figs 1-2.

1887. *Illaenus herricki*; Foerste, p. 479. fig. 2.

1894. *Thaleops ovata*; Clarke, p. 716, text-figs 25-28.

non 1902. *Illaenus ovata*; Raymond, pl. 18, fig. 9 (*Thaleops longispina*, Shaw).

non 1905. *Thaleops ovata*; Raymond, pl. 13, fig. 5 (*Thaleops longispina*, Shaw).

1908. *Thaleops ovata*; Raymond & Narraway, p. 247, pl. 60, figs 11-13, pl. 61, figs 6-7.

1913. *Thaleops ovatus;* Slocom, p. 56, pl. 14, figs 7-8 not fig. 6.

1927. *Thaleops ovata*; Walter, p. 224, pl. 17, figs 3-5.

?1928. *Thaleops* cf. *ovatus*; Troedsson, p. 48, pl. 14, fig. 8.

1930. *Thaleops ovata*; Bradley, p. 256, pl. 30, figs 15-16.

?1937. *Thaleops ovatus*; Shrock & Raasch, p. 578, pl. 10, figs 2a-e.

1947. *Thaleops ovatus*; Wilson, p. 36, pl. 7, figs 16a-b.

1963. *Thaleops ovata*; DeMott, p. 85, pl. 5, figs 1-23.

1979. *Thaleops ovata*; Ludvigsen, fig. 20C.

TYPES

Two complete exoskeletons (Lectotype, AMNH 29516, designated herein; paralectotype, AMNH 29517).

DIAGNOSIS

A species of *Thaleops* with long, curving genal spines that bear a dorsal carina. Pygidial axis well-defined and with pitted ornament oriented in transverse bands. Ventral surface of pygidium with traces of segmentation both on axis and pleural regions. Palpebral lobes elongate laterally and directed weakly upward. Central, anterior portion of cranidium with a longitudinal depression.

OCCURRENCE

The type material is from the Upper Ordovician (Mohawkian-Cincinnatian: Turinian-Maysvillian) Galena Formation, Mineral Point, Wisconsin. Other Upper Ordovician occurrences are: the Black River and Ottawa formations near Ottawa, Ontario (Mohawkian-Cininnatian); the Platteville Formation in Illinois and Wisconsin (Mohawkian: Turinian); the Kimmswick Formation in Missouri (Mohawkian-Cincinnatian: Chatfieldian-Edenian) and the Maquoketa Group in Iowa (Cincinnatian: Maysvillian-Richmondian).

DESCRIPTION

Longitudinal convexity strong over most of length (sag.); anterior 1/3 of cranidium slightly flattened. Axial furrows well defined; directed outward from posterior margin for half distance to lunettes then curving inward giving lateral margins of glabella a convex outward shape. Axial furrows faint in front of lunettes on dorsal surface but expressed clearly on internal moulds; diverging from lunettes then converging around anterior margin of glabella before becoming totally effaced. Occipital furrow weakly defined. Occipital ring longest (sag.) medially. Posterior branch of facial suture directed laterally and posteriorly at approximately 45° to transverse line. Anterior branch of facial suture follows outwardly convex course to anterior margin. Anterior margin moderately convex. Anterior rim strongly elevated, long (sag.) for genus and tapering slightly laterally, ornamented with terrace ridges. Glabella elevated slightly above level of fixigenae; flat-topped in anterior view.

Palpebral area of fixigena moderately convex and sloping gently downward laterally. Behind palpebral lobes, posterior margin of cranidium directed backward. Distal portion of posterior fixigenae short (exsag.) and deflected ventrally. Palpebral lobes positioned well back on cranidium, close to posterior margin. Palpebral furrow wide and shallow. Palpebral lobes wide (tr.) relative to length (exsag.) and oriented weakly upward. Outline of palpebral lobes sub-triangular; posterior margin nearly transverse; anterior margin convex and convergent on posterior margin; distal termination of palpebral lobe rounded. Lunettes large and deep both on internal moulds and dorsal surface. Ornament of wide, shallow pits, transversely elongate over glabella but with more rounded outline over other parts of cranidium. Ornament lacking or greatly reduced on palpebral lobes and most convex portion of cranidium. In some specimens, muscle scars exhibited as pairs of globular, raised areas on either side of a shallow depression running longitudinally down the middle of the cranidium (e.g. Pl. 1, Figs 3a, c, d). In other specimens (e.g. Pl. 2, Figs 2a, b, c), muscle scars present as irregularly shaped areas lacking ornament. In both cases, the longitudinal depression between muscle scars continues well forward to the anterior part of the cranidium.

Librigena triangular in outline, tapering distally into long, stout, curved spine. In dorsal view, anterior margin curved inward, posterior margin curved outward. Eye projects upward and outward from dorsal surface of cheek. Visual surface tall (dorsoventrally) compared to other species; visual field of eye nearly horizontal at palpebral lobe then flexed steeply downward. Genal spine arched gently toward posterior and deflected slightly ventrally. Anterior and posterior surfaces of genal

spine converge dorsally to form sharp dorsal carina, making cross-section of spine triangular; spine tapers distally to sharp termination; cheek and spine ornamented by pits except on carina. Genal spines (measured from base of spine) equal to just over half of maximum width (tr.) of cephalon (measured across cephalon from base of genal spines). Hypostome unknown. Rostral plate roughly crescentric in outline with medial posterior projection; longest (sag.) medially, becoming much shorter (exsag.) abaxially. Ornamentation of subparallel terrace ridges parallel anterior margin. Rostral flange, if present, not exposed on types.

Thorax of 10 segments. Axis moderately convex; width (tr.) of axis approximately 37% total width of thorax. Axial furrows well defined. Distal portions of pleurae only slightly wider (tr.) than proximal and deflected strongly ventrally. Each successive thoracic segment more narrow (tr.) toward posterior. Faint pleural furrows expressed only on internal moulds (e.g., Pl. 2, Fig. 2d). Scattered wide, shallow pits preserved on dorsal surfaces of thoracic segments.

Pygidium almost half as long as wide; length (sag.) 55% of width (tr.). Axis convex but narrow, making up only 35% total width (tr.) of pygidium. Axial furrows deeply impressed, weakly tapering backward; posterior margin of axis well-defined. Anterior margin of axis with articulating half ring. Posterior margin of pygidium rounded. In lateral profile, axis slopes downward to posterior; post-axial field dives steeply downward. Articulating facets moderately long and steeply inclined; maximum width (tr.) of pygidium located at approximately 65% total length (sag.) of pygidium from anterior margin. Pygidial ornament similar to that on cranidium; size of pits decreases away from the axis on pleural areas and post-axial field. Ornament

on axis arranged into five transverse bands connected by single longitudinal band running down center of axis. Cuticle in areas between the bands completely smooth (e.g., Pl. 3, Figs 2a, c), may correspond to areas of muscle attachment. Termination of axis divided into two by longitudinal band of ornament; these two areas slightly inflated to form two, posterior projecting lobes, probably indicating sites of muscle attachment (e.g., Pl. 3, Figs 1a, b, 2b). Internal moulds preserve faint transverse bands across the axis are suggestive of relict axial rings (e.g., Pl. 1, Fig. 4a). Internal moulds of pleural regions show traces of pleural furrows (e.g., Pl. 2, Fig. 2d). Anterior margin of doublure with two short, sharp anterior projections and ornamented with terrace ridges. A shallow, longitudinal furrow arises at anterior margin of doublure, terminating in front of posterior margin.

REMARKS

Thaleops ovata has a relatively wide geographic range, having been described from Iowa to Ontario in Upper Ordovician deposits. Slight variation between individuals is found in the size of pits on the cuticle and expression of muscle scars on the dorsal surface. The dorsal carina on the genal spine and relict segmentation of the pygidial axis are distinctive and are preserved in all specimens examined for this study.

Thaleops raymondi (Shaw 1968; pl. 20, figs 1-16) resembles *T. ovata* in pattern and distribution of cephalic ornament and the presence of bold lunettes but the shape of the glabella is different in the two species. The pygidia of these species are similar in outline and axis shape, but the axis of *T. ovata* is much longer (sag.). The pygidial outline of *T. angusticollis* (Billings 1859; pl. 4, figs 4, 5; pl. 5, fig. 3) is nearly

identical to *T. ovata* and the axes have the same shape and bear similar ornamentation. The cranidia of the two species are very different; *T. angusticollis* has a glabella that is very narrow (tr.) posteriorly and the relatively narrow (tr.) palpebral lobes are directed slightly downward (Pl. 4, Figs 1-3, 5a, b, f; Pl. 5, Figs 1, 2). *Thaleops conradi* (Billings 1859; pl. 7, figs 1a, c, 2, 3b, c) shares large lunettes and a posteriorly wide (tr.) glabella with *T. ovata*, but has narrow (tr.) palpebral lobes that are directed downward and a cranidium that is dorsoventrally compressed. The pygidia of *T. ovata* (e.g., Pl. 1, Figs 1a, 4a, c; Pl. 3, Figs 1-2) and *T. conradi* (Pl. 7, Figs 1d, 3a, b, 4a, b) are similar in outline but the axis of the latter is not as well-defined and the ornament is weaker. *Thaleops nunavutica* nom. nov. [= *T. punctata* (Roy 1941), non *T. punctata* (Raymond 1905), preoccupied] has similar ornament and glabella shape but the palpebral lobes are longer (tr.) and oriented upward at a higher angle (Pl. 14, Figs 1-3, 5). The glabella of *T. vindex* (Billings 1859; pl. 6, fig. 3) is divided longitudinally by a median depression, but the anterior half of the glabella is better defined in *T. vindex*. In lateral view, the lateral profile of the cranidium is roughly horizontal posteriorly but is nearly vertical anteriorly. In contrast, the lateral profile of *T. ovata* is more evenly curved (Pl. 1, Fig. 3b).

Thaleops arctura (Hall 1847) Pl. 3, Fig. 3

1847. *Illaenus arcturus*; Hall, p. 23, pl. 4, fig. 12.

non 1910. *Thaleops arctura*; Raymond, p. 227, pl. 35, fig. 5.

1968. *Thaleops arctura*; Shaw, pl. 21, figs 3, 11.

TYPE

A single, poorly preserved cranidium (Holotype, NYSM 4499).

OCCURRENCE

Hall (1847) reported the locality for the type as a "fine semi-oolitic limestone (at) the base of the formation at Chazy village". Shaw (1968) introduced the possibility that the locality is not in the Chazy.

DISCUSSION

The type of this species consists of a single, poorly preserved, partial cranidium for which the stratigraphic occurrence is uncertain. It is similar to *T. conifrons* but is too fragmentary for reliable identification. We recommend restricting the species to the type. Other specimens attributed to this species have been reassigned to *T. longispina* (see Shaw, 1968).

Thaleops angusticollis (Billings 1859) Pl. 4, Pl. 5, Figs 1-3

1859. *Illaenus angusticollis*; Billings, p. 376, fig. 10a-d.

1863. *Illaenus angusticollis*; Billings, p. 151, figs 113a-d.

1908. *Illaenus angusticollis*; Raymond & Narraway, p. 245, pl. 61, figs 1-5.

1947. *Illaenus angusticollis*; Sinclair, figs 5-7.

1963. *Thaleops divericata*; DeMott, p. 90, pl. 6, figs 1-6.

1987. *Thaleops* sp. "A"; DeMott, pl. 6, figs 1-6.

TYPES

A nearly complete cephalon (Holotype, GSC 1314b), a slightly crushed cranidium (Paratype, GSC 1314c), two exfoliated cranidia (Paratypes, GSC 1314a, 1314) and a well preserved pygidium (Paratype, GSC 1314d).

DIAGNOSIS

A species of *Thaleops* with very narrow (tr.) glabella behind lunettes. Occipital ring marked by shallow occipital furrow. Glabella defined for short distance in front of lunettes. Palpebral lobes short (exsag.) and narrow (tr.). Pygidial axis with sharp, scale-like terrace ridges that are curved gently forward.

OCCURRENCE

The type material is from the Upper Ordovician (Mohawkian-Cincinnatian) Ottawa Formation, St. Joseph Island and "the island west of Grant's Islands", Lake Huron. It is also known from the Upper Ordovician Black River Formation near Ottawa, Ontario (Mohawkian: pre-Turinian), from the Platteville Group in Illinois and Wisconsin (Mohawkian: Turinian) and from the Glens Falls Limestone in the Mohawk Valley, New York (Mohawkian: Turinian-Chatfieldian).

DESCRIPTION

Longitudinal convexity moderate and even anterior to occipital ring. Axial furrows deeply impressed behind lunettes and weakly discernable on dorsal surface in front of lunettes. On internal moulds, axial furrows extend forward for more than 1/2 distance

between palpebral lobes and anterior margin. Behind lunettes, axial furrows are curved strongly inward, making posterior portion of glabella very narrow. In front of lunettes, axial furrows diverge strongly before becoming effaced. Occipital furrow defined by change in convexity from arched occipital ring to much more weakly convex glabella. Posterior branch of facial sutures directed laterally and posteriorly at about 45° to horizontal. Anterior branch strongly convergent in front of palpebral lobes to nearly flat anterior margin. A short (sag.) anterior rim bears closely spaced terrace ridges running parallel to the anterior margin and is elevated a short distance above the level of the anterior area of the cranidium. Glabella narrow (tr.) with moderate convexity between and behind lunettes. Fixigenae convex and sloping outward to ventrally depressed palpebral lobes. Palpebral lobes positioned near posterior margin of cranidium. Palpebral furrow not visible. Palpebral lobes short (exsag.) and narrow (tr.) for genus, with rounded termination. At level of palpebral lobes, posterior margin of cranidium angles toward posterior. Posterior portion of fixigena narrow (tr.), sub-triangular and deflected ventrally. Lunettes visible on dorsal surface as subtle widening of axial furrows. On internal moulds, lunettes are deep and broad (tr.). Ornament strongest on glabella. Coarse pits cover occipital ring, fixigenae and librigenae, becoming less dense and weaker toward anterior of cranidium. Glabella from occipital ring to point just anterior to lunettes ornamented with laterally elongate, shallow, flat-bottomed pits that merge together in convex-forward lines. Muscle scars visible on dorsal surface of some specimens (e.g. Pl. 4, Figs 5a-c) are only weakly expressed on internal moulds (e.g. Pl. 4, Figs 3a, b; Pl. 5, Figs 1a, b); scars ovate with long axis longitudinal and positioned near lateral margins

of glabella leaving flat area in between over dorsal surface of glabella. A narrow (tr.), median, longitudinal ridge can be seen running almost the entire length of the pre-occipital glabella on some internal moulds (e.g. Pl. 4, Figs 3a, b; Pl. 5, Fig. 1a).

Outline of librigenae strongly triangular; posterior margin curved slightly toward anterior; anterior margin gently rounded and directed more strongly toward posterior. Cheek tapers laterally to form elongate (tr.) genal "flap". Lateral termination of cheek broken in available specimens but Billings illustrated a sharp point at the termination of the flap. Eyes projecting only slightly laterally from dorsal surface of librigena. Rostral plate and hypostome unknown.

Thorax of eight segments (see discussion under "Explanation of character and character states"). Width (tr.) of thoracic segments gradually decreasing toward posterior. Axis convex and relatively narrow (tr.), accounting for only 35% total width (tr.) of thorax. Axial furrows firmly impressed. Proximal portion of pleurae nearly flat and relatively wide (tr.), making up 45% total width (tr.) of pleurae. Angle from proximal to distal segments of pleurae high. Thoracic segments ornamented with coarse pits.

Pygidium 58% as long as wide. Axis strongly convex and well-defined by deep axial furrows. Furrows converge only slightly toward posterior then curve abruptly to give axis a blunt termination. Width (tr.) of axis approximately 40% total width (tr.) of pygidium. Anterior margin of axis convex; anterior margins of pleural regions nearly transverse. Posterior margin of pygidium rounded. In lateral profile, convexity of axis is independent of convexity of post-axial field. Articulating facets moderately long and steeply inclined relative to anterior margin of pygidium;

maximum width (tr.) of pygidium located posterior to anterior margin at a distance that is 68% total pygidial length (sag.). Pleural regions, post-axial field and center of axis ornamented with shallow, flat-bottomed pits. Four scale-like, transverse ridges arise on the pleural fields adjacent to the axial furrows and run across top of axis. These resemble terrace ridges with steep slopes forming sharp ridges that have been deflected toward the posterior. Doublure not exposed on available specimens.

REMARKS

The pygidium of *T. angusticollis* (e.g., Pl. 4, Figs 4a, b, 5d, e) resembles that of *T. ovata* (Pl. 1, Figs 1a, 3e, f, 4a; Pl. 3, Figs 1-2) in the ornamentation and shape and degree of definition of the axis but, as discussed above, the cranidial characters of the two species are very different. *Thaleops longispina* Shaw 1968 (pl. 20, fig. 20; pl. 21, figs 1, 2, 4-10) is similar to *T. angusticollis* in that it has a narrow glabella posterior to the lunettes but the axis of the pygidium of *T. longispina* is much shorter and more triangular in outline. The posterior area of the glabella is narrow in *T. conifrons* (Billings 1859) (e.g., Pl. 5, Figs 5-6; Pl. 6, Fig. 1) but it has wider (tr.) eyes than *T. angusticollis* and a glabella with a well-defined anterior furrow.

T. clavifrons (Billings 1859) Pl. 5, Fig. 4

1859. *Illaenus clavifrons*; Billings, p. 379.

1925. *Thaleops clavifrons*; Raymond, p. 113.

1938. *Illaenus clavifrons*; Twenhofel, pl. 11, fig. 16.

TYPE

A single, exfolilated cranidium missing most of the right side and some of the left side (Holotype, GSC 1323).

OCCURRENCE

The only known specimen is from the Middle Ordovician (Whiterockian: *G. dentatus-N. gracilis* zone) Mingan Formation, Mingan Islands, Quebec.

REMARKS

This species is known from one extremely fragmentary cranidium and is here restricted to the type. Raymond (1925) attempted to synonymize *T. clavifrons* with *T. vindex* but we do not feel this can be justified given the incomplete nature of the former.

Thaleops conifrons (Billings 1859) Pl. 5, Figs 5-6, Pl. 6, Figs 1-2

1859. *Illaenus conifrons*; Billings, p. 378, fig. 11.

1863. *Illaenus conifrons*; Billings, p. 151, fig. 111.

1938. *Thaleops conifrons*; Twenhofel, p. 73, pl. 11, fig. 10.

TYPE

A single exfoliated cranidium with part of left fixigena broken (Lectotype, GSC 1322).

DIAGNOSIS

A species of *Thaleops* with a glabella that is narrow posteriorly and well defined anteriorly by complete axial and preglabellar furrows. Anterior facial sutures directed toward anterior for approximately 1/2 distance to anterior margin then angled strongly toward median. Palpebral lobes directed upward.

OCCURRENCE

The type specimen is from the Upper Ordovician (Mohawkian: pre-Turinian) Black River Group, Mingan Islands, Quebec. Additional material is from the Middle Ordovician (Whiterockian: *G. dentatus-N. gracilis* zone) Mingan Formation, Mingan Islands.

DESCRIPTION

Longitudinal convexity very low over posterior 1/3 of cranidium so that longitudinal profile slopes gently toward anterior; convexity high over remainder of cranidium; glabella overhanging anterior margin of cranidium. Axial furrows well impressed, curving inward from posterior margin to lunettes; directed outward to maximum glabella width (tr.) at 60% distance from posterior margin, then curving inward to anterior margin of glabella. Occipital furrow weak; occipital ring inflated. Posterior branch of facial suture directed toward posterior and only slightly laterally. Posterior half of anterior branch directed forward from palpebral lobes, anterior half turning strongly inward. Anterior margin of cranidium weakly convex. Anterior rim short (sag.), composed of two very well defined terrace ridges. Transverse convexity of

glabella high over entire glabellar length (sag.). Width (tr.) of glabella behind lunettes approximately 60% maximum width (tr.) in front of lunettes. Fixigenae convex, sloping upward to palpebral furrow. Posterior margin of cranidium directed slightly backward at lateral margins of cranidium. Fixigenae behind palpebral lobes wide (tr.). Palpebral lobes almost at posterior margin of cranidium. Palpebral furrow broad. Palpebral lobe very wide (tr.) and short (exsag.), tapering laterally with rounded termination, directed sharply upward. Lunettes broad and moderately deep. Ornament of densely distributed, wide, shallow pits evenly distributed over most of cranidium, slightly smaller in diameter toward anterior. Muscle attachment sites not expressed. Librigenae, rostral plate, hypostome and thorax unknown.

Preservation of pygidium poor. Length (sag.) approximately 60% of width (tr.). Axis moderately convex; axis 40% total width (tr.) of pygidium. Axial furrows wide, moderately deep, converging toward posterior. Posterior margin of pygidium moderately rounded. Articulating facets moderately long; maximum width (tr.) of pygidium at 65% total length (sag.) of pygidium from anterior. Ornament of wide, shallow pits preserved only along anterior margin of pygidium. Anterior margin of doublure with forward projecting, sharp points on each side of the axis. Terrace ridges sub-parallel to each other and to anterior margin of doublure; longitudinal furrow arising between forward projections narrowing backward, terminateing at 3/4 distance to posterior margin.

REMARKS

Thaleops arctura resembles *T. conifrons* (see discussion above). *Thaleops vindex*

(Billings 1865) is very similar to *T. conifrons* and the two species will most likely be synonymized when more material is known. See remarks below.

Thaleops vindex (Billings 1865) Pl. 6, Fig. 3

1865. *Illaenus vindex*; Billings, p. 179, fig. 160.

1925. *Thaleops clavifrons*; Raymond, p. 113.

1938. *Thaleops conifrons*; Twenhofel, p. 73, pl. 11, fig. 9.

TYPE

A nearly complete cephalon (Holotype, GSC 1088).

DIAGNOSIS

A species of *Thaleops* with very well-defined glabella. In lateral view, posterior of cranidium nearly horizontal and anterior roughly vertical so that maximum convexity does not overhang anterior margin. In anterior view, anterior portion of glabella quadrate in outline.

OCCURRENCE

The only specimen assigned to this species was collected from the Middle Ordovician (Whiterockian: *G. dentatus-N. gracilis* zone) Mingan Formation, Mingan Islands, Quebec.

DESCRIPTION

Thaleops vindex is very similar to *T. conifrons*. Dorsal surface of glabella in *T. vindex* less convex transversely. In lateral view, posterior 2/3 of cranidium nearly flat, intersecting with convex anterior surface at nearly 90° so that point of maximum convexity is above anterior margin. Axial furrows of *T. vindex* deeper than in *T. conifrons*. Most of posterior margin of glabella missing, but occipital furrow appears to be effaced. Anterior branch of facial suture difficult to distinguish without high magnification, directed sharply medially at approximately 45° to anterior margin. Wide, shallow pits ornamenting surface of *T. vindex* slightly larger than in *T. conifrons*. Lateral margins of glabella form slightly raised, swollen ridges that become wider toward anterior, terminating just posterior to ventral deflection in the cranidium; ridges separated by a shallow depression most likely representing dorsal expression of areas of muscle attachment on ventral surface.

Librigenae roughly triangular in outline. Anterior and posterior margins converge on genal spine. Spine broken off proximally but thickness at preserved base suggests that it was long and stout. Spine at base oriented laterally and slightly toward the posterior. Eye elevated above level of fixigena; eye projecting upward and outward from librigena. Ornament of wide, shallow pits slightly smaller than those on dorsal surface of glabella, more similar in size to those on anterior of cranidium. Hypostome, thorax and pygidium unknown.

REMARKS

Raymond (1925) considered that *T. vindex* was a synonym of *T. clavifrons*

(Billings 1859). Although the material of *T. clavifrons* is incomplete, it is clearly different from *T. vindex*. For example, the axial furrows of *T. clavifrons* are bowed outward rather than inward behind the lunettes and continue for only a short distance in front of the lunettes. *Thaleops vindex* is more similar to *T. conifrons* than to any other species. It is likely that *T. vindex* will prove to be a synonym of the latter, but more material is required for a confident evaluation.

Thaleops vindex and *T. conifrons* are similar to *T. longispina* in the definition and outline of the glabella, cranidial ornament, and stalked eyes. *Thaleops longispina* differs mainly in having a well-rounded, uniformly convex lateral profile and in the lower elevation of the eye stalks. In *T. borealis* (Teichert 1937) the axial furrows diverge uniformly from the lunettes to the anterior margin so that the widest (tr.) point of the glabella is at the anterior margin (Pl. 13, Figs 3-4). In *T. vindex* and *T. conifrons*, the axial furrows diverge rapidly in front of the lunettes and then converge again before reaching the anterior margin so that the widest (tr.) point of the glabella is reached only a short distance anterior to the lunettes.

Thaleops conradi (Billings 1859) Pl. 7

1859. *Illaenus conradi*; Billings, p. 372, figs 7-9.

1863. *Illaenus conradi*; Billings, p. 151, figs 110a-c.

1908. *Illaenus conradi*; Raymond & Narraway, p. 245, pl. 60, figs 9-10.

1947. *Illaenus conradi*; Sinclair, p. 534, pl. 1, fig. 1.

1947. *Illaenus conradi*; Wilson, pl. 7, figs 14-15.

TYPES

A complete, enrolled specimen (Holotype, GSC 1320a) and a pygidium (Paratype, GSC 1320).

DIAGNOSIS

A species of *Thaleops* with eight thoracic segments. Axial furrows bowed outward, forming a glabella that is very wide behind the lunettes. Lunettes shallow, very wide (tr.). Posterior thoracic pleurae with greater ventral deflection than anterior.

OCCURRENCE

The type material is from the Upper Ordovician (Mohawkian: Turinian) Leray Formation near Hull, Quebec. This species also occurs in the Upper Ordovician (Whiterockian-Mohawkian: *N. gracilis* zone-Turinian) Black River Formation near Hull and in the Black River Group near Mechanicsville, Ontario.

DESCRIPTION

Longitudinal convexity strong; convexity over dorsal surface of cranidium slightly lower than toward anterior so that height (dorsoventral) of cranidium is less than width (tr.) as seen in anterior view. Axial furrows moderately well defined behind lunettes and effaced in front of lunettes. Furrows diverge strongly immediately from posterior margin then begin to converge at level of palpebral lobes so that glabella reaches maximum width (tr.) behind lunettes. Occipital furrow effaced; presence of occipital ring suggested in some specimens by reduction of ornament (e.g. Pl. 7, Fig.

2c). Posterior branch of facial suture directed backward and weakly laterally. Anterior branches of facial suture converge forward and merge with anterior margin to form continuous curve. Anterior rim only slightly elevated, long (sag.) medially, becoming shorter (exsag.) toward lateral margins. Glabella with strong transverse convexity. Fixigenae placed below glabella, moderately convex, and slope laterally down to palpebral lobes. Posterior margin of cranidium initially transverse then directed weakly backward to lateral margin. Posterior fixigenae short (exsag.), deflected slightly ventrally. Palpebral lobes placed near posterior margin of cranidium. Palpebral furrow defined as change in convexity from fixigena to palpebral lobe. Palpebral lobes short (exsag.), narrow (tr.), deflected slightly downward, with rounded lateral margin. Lunettes defined on dorsal surface as broad, shallow depressions devoid of ornament. Dorsal surface of cranidium ornamented with wide, shallow pits. Two large pairs of muscle scars indicated by lack of ornament (e.g. Pl. 7, Figs 2c, 3c); some specimens with slightly inflated areas of muscle attachment (e.g. Pl. 7, Fig. 1c).

Librigenae sub-triangular in outline. In dorsal view, anterior margin curved out, posterior margin weakly curved in. Anterior and posterior margins nearly equal in length, converging laterally, meeting at short, blunt, backwardly directed point. Eye projects only slightly outward. Ornament of shallow pits concentrated near anterior margin of cheek. Rostral plate and hypostome unknown.

Thorax of eight segments tapering towards posterior. Axis moderately convex; 37% of total thoracic width (tr.). Axial furrows shallow. Proximally, pleurae nearly flat. Pleurae deflected ventrally at just under 1/2 distance from axial furrows; distal

portions of pleurae on more posterior thoracic segments deflected more strongly than those on more anterior thoracic segments resulting in greater angle of ventral deflection on articulating facets of pygidium than angle of ventral deflection on librigenae of the cephalon (e.g. Pl. 7, Fig. 3a). Thoracic segments with pits roughly arranged into transverse rows.

Pygidium wider (tr.) than long (sag.); length approximately 57% of width. Axis moderately convex and narrow; width (tr.) 35% total width of pygidium. Axial furrows well defined, converging very slightly toward posterior then turning sharply to form blunt posterior termination of axis. Anterior margin of axis very gently rounded; anterior margin of pleural regions nearly transverse. Posterior margin of pygidium moderately rounded. In lateral profile, pygidium with even longitudinal convexity, axis elevated only slightly above post-axial field. Articulating facets long. Angle of articulating surface relative to anterior margin of pygidium relatively high. Maximum width (tr.) of pygidium found at distance from anterior margin that is 68% the total length (sag.) of pygidium. Pygidium ornamented with wide, shallow pits over axis, on pleural fields and for short distance posterior to axis. Scale-like terrace ridges cross axis transversely. Doublure not fully exposed but anterior margin appears scalloped with a sharp forward projection on each side of the axis; ornament of terrace ridges. Median longitudinal furrow not evident.

REMARKS

The pygidium of *T. angusticollis* resembles that of *T. conradi* in the shape of the axis and ornament but, as noted above, the axial glabellar furrows are bowed in rather than

out behind the lunettes in *T. angusticollis*. The axial glabellar furrows in *T. ovata* are curved strongly outward behind the lunettes as in *T. conradi*, but *T. ovata* has much wider (tr.) palpebral lobes, coarser cranidial pitting and more distinct lunettes. The axial furrows of the cranidium are bowed outward more weakly on *T. laurentiana* sp. nov. (e.g., Pl. 15, Figs 1c, 2a, 3a) and the palpebral lobes are much larger than those of *T. conradi*. In addition, the pygidial axis of *T. laurentiana* is sub-triangular rather than sub-rectangular in outline.

Thaleops punctata (Raymond 1905) Pl. 8, Fig. 1

1905. *Illaenus punctatus*; Raymond, p. 347, pl. 13, fig. 10.

1910. *Illaenus punctatus*; Raymond, p. 226, pl. 35, fig. 10.

1968. *Nanillaenus? punctatus*; Shaw, p. 49, pl. 20, fig. 19.

non 1968. *Nanillaenus? punctatus*; Shaw, p. 49, pl. 20, figs 17, 21-28.

non 1974. *Nanillaenus?* cf. *N. punctatus*; Shaw, p. 16, pl. 4, figs 3, 4, 8, 10-18.

TYPE

A crushed complete individual (Holotype, CM 1278).

REMARKS

Raymond erected a new species based on a single complete specimen that is crushed badly. Following our own examination of the type specimen, we conclude that it is preserved too poorly to provide reliable taxonomic information and restrict the species to the type. Shaw (1968) tentatively reassigned the species to *Nanillaenus*

and illustrated additional material collected from Raymond's original locality that Shaw presumed to represent the same species. Four of the specimens figured by Shaw (NYSM 12501, NYSM 12503, NYSM 12505, NYSM 12506) are examples of *T. fieldi* or *T. depressicapitata*. One cranidium (NYSM 12504) resembles *I. bayfieldi* Billings 1859. The remaining specimen (NYSM 12502) is nearly complete and rather well preserved but has not been described previously in the literature. Although this specimen may represent a new species, we do not feel it should be named until additional material can be collected (see *Thaleops* sp. 3 below).

Thaleops latiaxiata (Raymond & Narraway 1908) Pl. 8, Figs 2-4

1908. *Illaenus latiaxiatus*; Raymond & Narraway, p. 243, pl. 60, figs 4-8.

1947. *Illaenus latiaxiatus*; Wilson, p. 33, pl. 7, figs 5-6.

1979. *Nanillaenus latiaxiatus*; Ludvigsen, figs 20D, E.

2002. *Nanillaenus latiaxiatus*; Whiteley *et al.*, p. 122, pl. 9.

TYPE

A well-preserved cranidium (Holotype, ROM 18754C). The type material was originally part of Narraway's private collection. Other material used by Raymond in his description may never have been reposited at the ROM.

DIAGNOSIS

A species of *Thaleops* in which central area of cranidium protrudes well anteriorly, overhanging anterior margin to a relatively high degree. Articulating facets on

pygidium exceptionally long, oriented at very high angle to anterior margin.

OCCURRENCE

Type material is from the Upper Ordovician (Mohawkian: pre-Turinian) Black River Group, near Ottawa, Ontario. The species is also reported from the Black River Group in Pattersonville and Newport, New York (Mohawkian: pre-Turinian) and the Cobourg Formation in Bowmanville, Ontario (Mohawkian-Cincinnatian: Chatfieldian-Maysvillian).

DESCRIPTION

Longitudinal convexity uneven; posterior 1/3 with low convexity but sloping steeply toward anterior, medial 1/3 convex, anterior 1/3 moderately convex. Axial furrows moderately well impressed, directed weakly adaxially behind lunettes, effaced within short distance in front of lunettes. Occipital furrow effaced; occipital ring indicated by absence of ornament in transverse band parallel with posterior margin. Posterior branch of facial suture short, directed strongly laterally before curving back to intersect posterior margin. Anterior branch of facial suture following broadly rounded course, making smooth transition to similarly rounded anterior margin. Anterior rim short (sag.), consisting of three parallel terrace ridges, with no perceptible elevation above rest of cranidium. Glabella with moderate transverse convexity behind lunettes, not defined in front of lunettes where axial furrows effaced. Fixigenae moderately convex, standing below elevation of glabella, sloping down only slightly towards palpebral lobes. Posterior margin of cranidium transverse

then deflected gently backward behind palpebral lobes. Posterior portion of fixigenae very short (exsag.); width (tr.) not discernable on figured specimens. Palpebral lobes positioned very near posterior margin. Palpebral furrow indicated by change in convexity between fixigena and palpebral lobe. Palpebral lobes sub-triangular in outline, anterior margin angled toward posterior, posterior margin nearly transverse, directed outward. On dorsal surface, lunettes equal in width (tr.) to axial furrows, expressed as slight depressions without ornament. Ornament consisting of irregularly shaped, wide, shallow pits on glabella; pits narrower over remainder of cranidium. Ornament lacking on protruding central portion of cranidium, occipital ring and palpebral lobes. Muscle scars appear on dorsal surface as ovoid pairs of relatively smooth areas on either side of mid-line of glabella. Librigena, hypostome and rostral plate unknown.

According to Raymond and Narraway (1908) the thorax consists of 10 segments, although the type material does not include a complete thorax. Measurements used in the following description are estimates made using ROM 18754C (Pl. 8, Fig. 3). Axis convex, approximately 50% total width (tr.) of thorax. Pleurae horizontal over proximal 45% of thoracic width (tr.) then deflected sharply ventrally.

Pygidium rather long for genus, length (sag.) 65% of width (tr.). Axis moderately convex, axis wide, nearly 50% maximum width (tr.) of pygidium. Axial furrows wide and shallow, converging gently toward posterior then converging more sharply to form blunt termination. Axis elevated only short distance above pleural fields. Posterior margin rounded. Convexity in lateral profile low over most of length (sag.), increasing to slope steeply to posterior margin. Articulating facets very long even for

genus and nearly parallel; maximum width (tr.) of pygidium at a distance from the anterior margin 77% total length (sag.) of pygidium. Ornament concentrated on axis and medial portions of pleural areas; consisting of shallow grooves that appear to have formed from elongation and merging of shallow pits. Irregular, shallow pits similar to those on glabella occurring on pleural areas near termination of shallow grooves. Doublure not exposed.

REMARKS

The cranidial ornament of *T. depressicapitata* (Bradley 1930) resembles that of *T. latiaxiata* but the shallow pits are less densely distributed on the former (Pl. 12, Fig. 4). The shape of the cranidia of these two species are similar but *T. depressicapitata* lacks an inflated central portion of the cranidium overhanging the anterior margin (Pl. 12, Figs 1b, 2c). The pygidia have similar ornament (Pl. 12, Fig. 5; Pl. 13, Fig. 1) but the articulating facets on *T. depressicapitata* are shorter and at a lower angle to the anterior margin of the pygidium. The pygidium of *T. viator* (Raymond 1925) is similar in outline to that of *T. latiaxiata* but is not ornamented with shallow grooves (Pl. 9, Figs 6, 8; Pl. 10, Fig. 1c). In addition to lacking an overhanging anterior protuberance on the cranidium, the cranidium of *T. viator* has greater dorsoventral compression. *Thaleops lacerta* (Whittington 1954) possesses a similar pygidial outline and ornament (pl. 61, figs 1-6), but the cranidium is more effaced than that of *T. latiaxiata* and is ornamented with shallow depressions rather than pits. The eyes of *T. lacerta* are much smaller, in both length (exsag.) and width (tr.) than those of *T. latiaxiata*. The pygidium of *T. raymondi* is long (sag.) with long articulating facets,

but the axis of the pygidium is narrower and more rectangular in shape than in *T. latiaxiata* and bears shallow pits as ornament rather than shallow grooves.

Thaleops fieldi (Raymond 1925) Pl. 8, Fig. 5, Pl. 9, Figs 1, 2

1925. *Illaenus fieldi*; Raymond, p. 107, pl. 7, figs 1-4.

TYPES

A well-preserved cranidium (Lectotype, MCZ 101145, designated herein), an exfoliated cranidium (Paralectotype MCZ 101143, designated herein) and an exfoliated pygidium (Paralectotype MCZ 101144, designated herein).

DIAGNOSIS

A species of *Thaleops* with shallow axial furrows and cranidial ornament of extremely fine, narrow punctae. Sites of muscle attachment preserved as very low, longitudinal ridges on internal moulds. Pygidium with long, steeply inclined articulating facets.

OCCURRENCE

Thaleops fieldi was collected from the Upper Ordovician (Whiterockian-Mohawkian) Holston Limestone in the Catawba Valley, Virginia.

DESCRIPTION

Cranidium with even longitudinal convexity. Axial furrows shallow, converging

slightly from posterior margin half the distance to lunettes then parallel to lunettes. On internal moulds, axial furrows strongly divergent for short distance in front of lunettes before becoming obsolete. Occipital furrow effaced. Posterior branch of facial suture short, directed laterally and posteriorly at approximately 45° from horizontal. Anteriorly, facial sutures parallel for short distance then weakly convergent to rounded anterior margin. Anterior rim moderately long (sag.); composed of three or four parallel terrace ridges but with little to no elevation above anterior portion of cranidium. Glabella convex transversely, elevated above fixigenae. Fixigenae convex, sloping down very gradually abaxially. Posterior margin of cranidium transverse behind glabella and palpebral region of fixigenae then angled sharply toward posterior behind palpebral lobes. Posterior fixigenae small, triangular in outline, deflected downward. Palpebral lobes placed far toward posterior of cranidium. Palpebral furrow weakly identifiable as change in convexity between fixigena and palpebral lobe. Palpebral lobes narrow (tr.) but long (exsag.), directed slightly downward. Distal termination of palpebral lobes evenly rounded. Lunettes visible on dorsal surface as expansion of axial furrows. Except for anterior region of glabella, dorsal surface ornamented with very fine, densely packed, shallow pits. Pairs of raised areas barely perceptible on internal moulds correspond to areas of muscle attachment. Librigenae, rostral plate, hypostome and thorax unknown

Single known pygidium preserved mainly as internal mould. Pygidial length (sag.) 58% of width (tr.). Width (tr.) of moderately convex axis 43% maximum width (tr.) of pygidium. Axial furrows appear to be shallow and converge posteriorly to form blunt termination. Posterior margin not completely prepared. Articulating

facets long, forming steep angle with anterior margin of pygidium. Distance from front of pygidium to point of maximum width (tr.) could not be measured because posterior margin not excavated. Raymond (1925) described terrace ridges on surface of pygidium but type material does not include a pygidium with preserved cuticle, pygidial doublure is not exposed.

REMARKS

Thaleops fieldi is morphologically very similar to *T. depressicapitata.* The cranidial ornamentation of *T. depressicapitata* is much better developed and the palpebral lobes are directed horizontally rather than slightly downward. The axial glabellar furrows of *T. depressicapitata* are slightly deeper and the articulating facets of the pygidium appear to be slightly shorter and at a lower angle to the anterior margin of the pygidium. The paucity and poor quality of *T. fieldi* sclerites prevent further comparison.

T. viator (Raymond 1925) Pl. 9, Figs 3-8, Pl. 10, Fig. 1

1925. *Illaenus viator*; Raymond, p. 111, pl. 6, figs 16-17.

1979. *Illaenus kayi*; Dean, pl. 10, figs 10, 12, pl. 12, figs 1, 2, 4-5, 8-10, pl. 13, figs 1-10.

TYPES

Three external moulds of complete but compressed individuals (Lectotype, YPM 13032, designated herein; Paralectotypes, YPM 26995 and YPM 26996, designated

herein) and an articulated thorax and pygidium and external mould (Paralectotype, YPM 13033, designated herein).

OCCURRENCE

Raymond (1925) collected the type material of *T. viator* from the Upper Ordovician (Whiterockian-Mohawkian) Lourdes Limestone on the west shore of Long Point on the Port Au Port Peninsula, Newfoundland. Dean (1979) described *T. kayi* from Geological Survey of Canada localities in the Lourdes Limestone on Long Point.

REMARKS

Although Dean did not mention *T. viator*, the material of *T. kayi* that he collected came from the west side of Long Point (Loc. 84824) or the east side of The Bar, the northeasterly extension of Long Point that is less than 1 km wide. Raymond's material is not well preserved, but the pygidium of YPM 13033 (Pl. 9, Fig. 5) is nearly identical to that of *T. kayi*. The fact that *T. viator* and *T. kayi* were collected from the same area and the close morphologic similarity of the two species leads us to suggest that *T. kayi* is a junior synonym for *T. viator*. Dean recognized the similarity between this species and *T. latiaxiata* and other species (*I. americanus*, *T. lacerta*, *T. groenlandica* etc.) included herein in *Thaleops*. *Thaleops viator* and *T. lacerta* are similar in that both have very wide pygidial axes and very subdued ornament. The palpebral lobes of *T. viator* are wider (tr.) and are directed more laterally than those of *T. lacerta*.

Two other illaenids were collected by Dean on Long Point. *Thaleops* sp. A is

represented by a single partial cranidium. The glabella of *Thaleops* sp. A is much narrower (tr.) than that of *T. viator*. It is similar to *T. fieldi*, but with axial furrows that are more deeply impressed. A second unnamed illaenid, *Thaleops* sp. B, has a very narrow (tr.) glabella that is elevated well above the level of the fixigenae. The glabella of this specimen is not as narrow (tr.) as that of *T. angusticollis*. The outline of the glabella is similar to that of *T. raymondi* but the dorsal surface of the glabella of the latter species is nearly flat rather than strongly convex. *Thaleops* sp. B is very similar to *T. longispina* with the exception of the glabella of the former expanding more gradually toward the anterior and being elevated higher above the fixigenae. We agree with Dean that the strength of the axial furrows, position of the palpebral lobes near the posterior margin of the cranidium and width (tr.) of the palpebral lobes confirm assignment of both specimens to *Thaleops*.

Thaleops depressicapitata (Bradley 1930) Pl. 10, Figs 2-4, Pl. 11, Pl. 12, Pl. 13, Figs 1-2

1930. *Illaenus depressicapitatus*; Bradley, p. 252, pl. 28, figs 11-14.

1947. *Illaenus depressicapitatus*; Sinclair, figs 2-4.

TYPES

Two exfoliated cranidia (Holotype, UC 28895; Paratype, UC 28898).

DIAGNOSIS

A species of *Thaleops* with strong longitudinal convexity. Muscle scar attachment

sites well defined on internal moulds as two longitudinal ridges along the lateral margins of the glabella with a shallow depression between. Relict segmentation present on ventral surface of pygidial axis. Anterior margin of pygidial doublure with second, smaller pair of forward projections between larger pair of forward projections on either side of axis.

OCCURRENCE

Type material is from the Upper Ordovician (Mohawkian-Cincinnatian: Chatfieldian-Edenian) Kimmswick Formation in Missouri and Illinois. Additional material is figured from the Upper Ordovician (Cincinnatian: Edenian) Viola Springs Formation in Oklahoma from HWY99 locality (Fig. 1) between 38m and 51m above the base of the Viola Springs Formation. The species also occurs at LQ (Fig. 1) near the base of the exposure of Viola Springs. Reference material was collected from four localities in the Kimmswick Formation in eastern Missouri.

DESCRIPTION

Longitudinal convexity strong and even. Axial furrows shallow but wide, directed slightly adaxially from posterior margin; on internal moulds, furrows directed outward for short distance in front of lunettes before becoming effaced. Occipital furrow effaced. Facial sutures short behind palpebral lobes, directed laterally and posteriorly at approximately 45°. Anterior branch of facial suture gently rounded, continuing without inflection around anterior margin, creating broad, sub-circular outline to anterior of cranidium. Glabella with moderate transverse convexity.

Convexity of palpebral portion of fixigena very low, nearly horizontal. Posterior margin of glabella straight; posterior margin of fixigena straight for most of length then directed abruptly toward posterior for distance equal to width of palpebral lobe. Posterior fixigena short, sub-triangular, directed ventrally. Palpebral lobes positioned very near posterior margin of cranidium. Palpebral furrow faint. Palpebral lobes wide (tr.) with rounded termination, directed outward. Lunettes large on internal moulds (e.g. Pl. 12, Fig. 2b); expressed on external surface as ovate depressions devoid of ornament (e.g. Pl. 12, Fig. 4d). Ornamentation consisting of irregularly-shaped shallow pits with flat bottoms, elongate laterally, arranged in rows arching toward anterior over glabella. Pits continue over anterior of cranidium except in narrow (tr.) band; finer on proximal portion of palpebral lobe then disappear distally. Muscle scars preserved on glabella as three or four pairs of weak, rounded nodes with slight depression between. Scars most obvious on internal moulds (e.g. Pl. 11, Fig. 1), discernable on external test only as deflections in arched pattern of pits (e.g. Pl. 12, Fig. 4d).

A single, illaenimorph librigena found in Viola Springs collections from which this species is known (e.g. Pl. 13, Fig. 2) tentatively assigned to this species. Anterior margin rounded to point opposite mid-point of eye; lateral margin nearly flat and angled posteromedially; posterior margin short (tr.), nearly transverse. Eye raised above gently convex dorsal surface of cheek, directed slightly outward. Visual surface forming short (dorsoventral) arch spanning nearly 180°.

An illaenimorph rostral plate preserved as an internal mould from a Viola Springs collection bearing *T. depressicapitata* tentatively assigned to this species (e.g. Pl. 12,

Fig. 6). Anterior margin rounded. Posterior margin with central, sharp, posterior projection lacking flange. Posterior margin without curvature from lateral margin to posterior projection. Terrace ridges roughly parallel anterior margin. Hypostome and thorax unknown.

Pygidium wider than long, length 60% of width. Axial lobe vaulted above pleural fields, defined by wide, shallow furrows. Axial furrows converging sharply to rounded point, forming sub-triangular pygidial axis with all three sides about equal length. Width (tr.) of axis about 40% total width (tr.) of pygidium. Ventral surface of axis with three or four shallow, transverse grooves interpreted as relict segmentation (e.g. Pl. 11, Fig. 6a, b); also preserved on internal moulds (e.g. Pl. 11, Figs 3b, c, 4a, b). Anterior margin of axis weakly rounded, extending forward beyond anterior margins of pleural fields. Anterior margins of pleural fields transverse. Intersection with articulating facet rounded. Posterior margin evenly and strongly rounded. Maximum width (tr.) of pygidium at distance from anterior margin about 55% total length (sag.) of pygidium. Intersection of articulating facet with posterior margin sharp. Ornament of shallow pits near posterior of pygidium. Pits become elongate at 1/3 distance from posterior, becoming connected at 1/2 length of pygidium to form anastomosing grooves and ridges which arch up onto axis. Elongate pits present on mid-line of axis. Lateral portions of anterior margin of doublure strongly scalloped, extending into sharp anterior projections on either side of axis with two very short (exsag.) projections present between them. A narrow, deep, median furrow extending from anterior margin of doublure to 2/3 length of doublure. Internal moulds preserve sharp ridge from posterior tip of pygidial axis to posterior of pygidium, indicating

thinning on ventral surface of cuticle of pygidium directly above furrow in doublure.

REMARKS

In his original description of *T. depressicapitata*, Bradley recognized a "concavity" on the glabella which is deeper near the posterior end and becomes obsolete at half the length of the cranidium. We interpret this concavity to be equivalent to the depression described herein between the rounded muscle scars on the posterior of the glabella (Pl. 10, Fig. 2d; Pl. 11, Figs 1, 2). Muscle scars are more distinct on larger individuals and especially where cuticle has been preserved which may explain Bradley's failure to describe them. Sinclair (1947) described the scars in greater detail using a specimen from one of Bradley's localities and explained their functional significance as insertion points for muscles.

Bradley described a "sharp narrow ridge" running from the posterior margin of the axial lobe of the pygidium nearly to the posterior margin of the pygidium. This feature is not present on the external cuticle and is preserved only on internal moulds of the pygidium (e.g. Pl. 11, Figs 3b, c), which indicates the presence of a sharp narrow depression in the underside of the cuticle of the pygidium (e.g. Pl. 11, Fig. 6a). In comparing *T. depressicapitata* to *I. americanus* and *T. latiaxiata*, Bradley commented that ornamentation consisting of "fine lines radiating from the axial lobe" of the pygidium is absent in *T. depressicapitata*. This feature is well preserved on specimens both from the Viola Group and the Kimmswick where cuticle is preserved and indicates that Bradley apparently did not realize that he was describing the species from internal moulds.

Sinclair (1947) described the neck-ring and occipital furrow (neck-furrow) of *T. depressicapitata* from a single exfoliated sample. On samples with cuticle preserved, an occipital furrow, and therefore an occipital ring, is not present.

Thaleops conradi resembles *T. depressicapitata* in the length of the eye stalks and presence of rounded nodes on the glabella at the level of the palpebral lobes (e.g., Pl. 7, Fig. 2c) but *T. conradi* has axial furrows of the glabella that are bowed outward to a greater degree, a much shorter (exsag.) pygidium, and a longer and more quadrate pygidial axis (e.g., Pl. 7, Fig. 1b, d) .

Thaleops borealis Teichert 1937 Pl. 13, Figs 3-4

1937. *Thaleops borealis*; Teichert, p. 39, pl. 4, fig. 4.

TYPE

An exfoliated cranidium with right fixigena missing (Holotype, GM 3310). Three additional specimens were known to Teichert but were not designated as types.

DIAGNOSIS

A species of *Thaleops* with well-defined occipital ring. Axial furrows diverge evenly forward in front of lunettes to anterior margin. Longitudinal convexity very low.

OCCURRENCE

Thaleops borealis was collected from the Gonioceras Bay limestone (Wright Bay Formation of Teichert) (Troelsen 1950). The Gonioceras Bay Member of the Kap

Jackson Formation has been dated as Ashgill (late Maysvillian) using chitinozoan biostratigraphy (Grahn & Nøhr-Hansen 1989). The specimens were collected at Cape Webster and between Cape Webster and Cape Calhoun on the south coast of Washington Land, North Greenland and also from Princess Mary Bay, Norman Lockyer Island off the east coast of Grinnell Land, Ellesmere Island.

REMARKS

Thaleops borealis is very similar to *T. longispina* Shaw 1968 in the definition of the glabella and presence of an occipital ring (e.g., pl. 21, figs 1, 2). The axial furrows of *T. longispina* diverge more abruptly in front of the lunettes, giving the glabella a quadrate outline in anterior aspect (e.g., pl. 21, figs 4, 6, 8). In *T. borealis*, the glabella and especially the occipital ring are elevated much higher above the fixigenae than in *T. longispina* (e.g., Pl. 13, Figs 3a, c). The internal mould of *T. borealis* preserves a median ridge on the anterior half of the glabella, indicating the presence of a sharp depression in the ventral surface of the cuticle (Pl. 13, Fig. 3a).

Thaleops baffinlandica (Roy 1941) Pl. 13, Figs 5-6

1941. *Illaenus baffinlandicus*; Roy, p. 156, fig. 117.

1954. *Illaenus baffinlandicus*; Whittington, pl. 62, figs 19, 23.

2000. *Illaenus* cf. *groenlandicus*; Bolton, pl. 30, fig. 2.

TYPES

A complete pygidium (Lectotype, P 28703, designated by Whittington 1954) and a

partial cranidium preserving a small portion of cuticle (Paralectotype, P28703, designated herein).

DIAGNOSIS

A species of *Thaleops* with almost completely effaced axial furrows on pygidium; articulating facets of pygidium relatively short for genus, posterior margin very well-rounded.

OCCURRENCE

Upper Ordovician (Cincinnatian: Edenian-Maysvillian) Silliman's Fossil Mount, Frobisher Bay, Baffin Island, Nunavut.

DESCRIPTION

Longitudinal convexity moderate. Axial furrows shallow, directed inward behind lunettes; directed abaxially for short distance before becoming effaced in front of lunettes on internal mould. Occipital furrow effaced. Posterior margin of cranidium directed backward at about 45° to posterior margin from level of palpebral lobe. Posterior branch of facial suture long, oriented at 45° to horizontal. Anterior branch of facial suture, anterior margin of cranidium and anterior rim not preserved. Glabella moderately convex transversely. Fixigenae moderately convex. Posterior fixigenae sub-triangular, long (exsag.), directed strongly ventrally. Palpebral lobes positioned near posterior of cranidium. Palpebral lobes longer (exsag.) than wide (tr.) with round termination. Lunettes expressed on dorsal surface as widening of axial

furrows. No evidence of muscle scars preserved. Small preserved portion of cranidial cuticle appears weathered. Hypostome, rostral plate and thorax unknown.

Pygidium relatively long, length (sag.) 60% maximum width (tr.). Axis moderately convex and wide; width (tr.) 48% maximum width of pygidium. Axial furrows very wide and shallow, converging sharply backward to form rounded point. Posterior margin of pygidium more rounded than is common for genus. In lateral profile, pygidium evenly convex except at depression that marks posterior termination of axis. Articulating facets short for genus. Angle of facets to anterior margin of pygidium higher than in *Illaenus* but relatively low for *Thaleops*. Maximum width (tr.) of pygidium at 50% length (sag.). Ornament of terrace ridges running transversely across axis then radiating out over pleural regions. Doublure not exposed.

REMARKS

The status of *T. baffinlandica* is uncertain because of the poor quality of the type material, which consists of a poorly preserved, partial cranidium and a pygidium. Roy (1941) designated both specimens as the holotype and gave the two samples a single specimen number. Whittington (1954) selected the pygidium as the lectotype and suggested that the cranidium is indistinguishable from that of *T. lacerta*. We disagree with Whittington because the cranidium collected by Roy has much wider (tr.) palpebral lobes than the type of *T. lacerta* figured by Whittington (1954). The pygidium of *T. baffinlandica* is easily distinguished from that of *T. lacerta* by the presence of very short articulating facets that are oriented at a relatively low angle to

the anterior margin of the pygidium.

Thaleops baffinlandica bears a strong resemblance to *T. groenlandica* (Troedsson 1928), but we were unable to secure a loan of type material of the latter. None of the few features preserved in the only known cranidium of *T. baffinlandica* is inconsistent with those figured by Troedsson for *T. groenlandica*. Of the pygidia figured by Troedsson, seven (his pl. 13, figs 8a, 12-14, 16-18) are nearly identical to the lectotype of *T. baffinlandica*. Two (his pl. 13, figs 11, 15) appear to have the long articulating facets characteristic of *T. lacerta*. Roy distinguished *T. baffinlandica* from *T. groenlandica* on the basis of pygidial proportions and ornamentation, but we find this distinction questionable. Bolton (2000) illustrated additional material that he assigned to both species. The pygidium attributed to *T. baffinlandica* (GSC 113679, pl. 30. fig. 3) appears to be a specimen of *T. lacerta* with the pygidial ornamentation obscured by weathering. A pygidium assigned to *T.* cf. *groenlandica* (GSC113680, pl. 30, fig. 2) is indistinguishable from the lectotype of *T. baffinlandica*. Although a definitive conclusion cannot be made at present, it is likely that *T. baffinlandica* will prove to be a synonym of *T. groenlandica* upon collection of further material.

Thaleops nunavutica nom. nov. Pl. 14

1941. *Illaenus punctatus*; Roy, p. 157, Fig. 118.

1954. *Thaleops? punctatus*; Whittington, p. 140, pl. 62, figs 28, 30, 31.

2000. *Nanillaenus punctatus*; Bolton, pl. 24, fig. 6; pl. 30, fig. 4; pl. 31, fig. 8; pl. 36, fig. 25; pl. 37, fig. 12

?2000. *Illaenus* sp.; Bolton, pl. 29, fig. 3.

TYPE

A nearly complete, partially exfoliated cranidium (Holotype, P 28704).

ETYMOLOGY

A new name is required for *Thaleops punctata* (Roy 1941), non Raymond 1905, preoccupied. The new name is for Nunavut, the Canadian territory from which the material was collected.

DIAGNOSIS

A species of *Thaleops* with wide (tr.) palpebral lobes directed upward. Anterior facial sutures angled sharply toward mid-line. Ornament on glabella of wide, closely spaced pits.

OCCURRENCE

The holotype was collected from the Upper Ordovician (Cincinnatian: Edenian-Maysvillian) at Silliman's Fossil Mount, Frobisher Bay, Baffin Island, Nunavut. Additional material was collected from talus in the Amadjuak(?) Formation at Sylvia Grinnell Lake (GSC locality O-104480) by Bolton. Bolton (2000) figured an unidentified pygidium from the locality from which he collected his other material of *T. nunavutica*. The pygidium does not match those described for other species from the region (*T. lacerta*, *T. baffinlandica*, *T. groenlandica*) and bears punctate ornamentation similar to that preserved on the cranidium of *T. nunavutica*.

Accordingly, we tentatively assign it herein to *T. nunavutica*.

DESCRIPTION

Longitudinal convexity of cranidium strong. Axial furrows deep and broad for genus, bowed weakly outward behind lunettes, effaced in front of lunettes on exterior surface, internal moulds not available for study. Occipital furrow effaced; occipital ring defined as area raised slightly above elevation of rest of glabella. Posterior branch of facial suture not preserved on available specimens. Anterior branch of facial suture angled strongly toward mid-line. Anterior margin of cranidium weakly rounded. Anterior rim short (exsag.) with well-defined terrace ridges. Glabella with strong transverse convexity. Fixigenae with low convexity in palpebral region, without abaxial slope. Palpebral lobes positioned near posterior margin of cranidium. Palpebral furrows shallow and wide. Fixigenae behind palpebral lobes not exposed. Palpebral lobes wide (tr.), directed upward for about 1/2 length then oriented horizontally. Lunettes wide and deep. Ornament of closely-spaced, wide, shallow pits on glabella and palpebral regions of fixigenae; pits becoming smaller toward anterior and lateral margins of cranidium. Muscle scars not preserved on dorsal surface. Librigenae, hypostome, rostral plate and thorax unknown.

Pygidium length (sag.) 53% width (tr.). Axis narrow (tr.), 33% total width (tr.) of pygidium. Convexity of axis moderate. Posterior margin of axis defined by narrow, deep furrows; furrows converging weakly toward posterior giving axis sub-rectangular shape. Anterior margin of axis extending forward beyond anterior margin of pleural regions. Posterior margin of pygidium rounded. Articulating facets

oriented at moderately steep angle to anterior margin. Maximum width (tr.) of pygidium at 64% total length (sag.) from anterior margin. Ornament of moderately narrow, evenly-spaced pits. Doublure not exposed.

REMARKS

Thaleops nunavutica differs from *T. lacerta* in having much wider (tr.) palpebral lobes, greater transverse convexity of the glabella, and strongly punctate ornamentation. *Thaleops groenlandica* and *T. baffinlandica* are ornamented with terrace ridges rather than punctae. The course of the axial glabellar furrows is similar in *T. anusacerbissima* sp. nov. (e.g., Pl. 17, Figs 4d, 5a, 6c), but the palpebral lobes are directed upward more strongly and the longitudinal convexity is lower in the latter species.

Thaleops laurentiana sp. nov. Pls 15,16

1859. *Illaenus americanus*; Billings, p. 371.

1865. *Illaenus americanus*; Billings, p. 329, figs 316a-d.

1894. *Illaenus americanus*; Clarke, p. 714, figs 20-23.

1908. *Illaenus americanus*; Raymond & Narraway, pl. 60, figs 1-4.

1947. *Illaenus americanus*; Wilson, p. 31, pl. 7, figs 3-4.

1979. *Nanillaenus americanus*; Ludvigsen, p. 37.

1983. *Illaenus americanus*; Westrop & Ludvigsen, p. 17, pl. 3, figs 2, 4-6.

2002. *Nanillaenus americanus*; Whiteley, *et al.*, p. 122, pl. 8.

TYPES

The type material of *I. americanus* Billings 1859 from the Trenton Limestone near Ottawa was reported lost by Wilson (1947) and it is not currently housed at the GSC (J. Dougherty, pers. comm). Without a standard for comparison, it is unclear if specimens collected from numerous localities and ascribed to *I. americanus* represent the same species. We propose restricting *I. americanus* to the missing types and erect a new species, *T. laurentiana*, using well-preserved specimens from the Trenton Group of New York. The type material consists of three complete exoskeletons (Holotype, NYSM 15235; paratypes, NYSM 15236, 15238). Additional specimens examined in the course of this study are NYSM 15237, 15239-15241.

ETYMOLOGY

For Laurentia, in reference to the geographic distribution of this species.

DIAGNOSIS

A species of *Thaleops* with short, sharp projections from lateral margins of otherwise broadly rounded genal angles. Axial furrows of glabella arched outward behind lunettes. Pygidial axis only weakly defined; ornamented with wide, shallow grooves radiating out onto pleural regions.

OCCURRENCE

The type material of *T. laurentiana* is from the Upper Ordovician (Mohawkian-Cincinnatian: Turinian-Maysvillian) Trenton Group near Trenton Falls, New York.

Additional Upper Ordovician material is figured from near Watertown, New York and a Middle Ordovician (Whiterockian) occurrence in the Chazy Formation near Chazy, New York. Specimens representing *T. laurentiana* also occur in the Galena Formation (Mohawkian-Cincinnatian: Turinian-Maysvillian) of Minnesota and Illinois.

DESCRIPTION

Longitudinal convexity relatively low. Axial furrows moderately well impressed behind lunettes, bowed gently laterally. Furrows effaced in front of lunettes. Occipital furrow effaced; position of occipital ring indicated by area of effaced ornamentation. Posterior branch of facial suture directed backward and slightly laterally. Anterior branches of facial suture nearly parallel for short distance in front of palpebral lobes then converge weakly to rounded anterior margin. Anterior rim longest (sag.) medially, consisting of two or three widely spaced, parallel terrace lines; anterior rim not elevated above anterior of cranidium. Glabella moderately convex transversely behind lunettes, undefined in front of lunettes. Fixigenae moderately convex , sloping gently down abaxially. At level of palpebral lobes, posterior margin of cranidium directed toward posterior. Posterior portion of fixigenae sub-triangular, deflected ventrally. Palpebral lobes located far back on cranidium. Palpebral furrow relatively well defined by distinct change in convexity. Palpebral lobes narrow (tr.), directed outward, with evenly rounded termination. Lunettes defined on dorsal surface both as expansion (tr.) of axial furrows and disruption of ornament. Ornament composed of shallow, flat-bottomed pits over

most of cephalon; pits arranged in anteriorly-arched rows over glabella, with some pits merging together. Muscle scars not visible on dorsal surface, internal moulds not available.

Librigenae broadly U-shaped in outline. Anterior and posterior margins with nearly uniform rounding. Posterior margin directed toward anterior; anterior margin directed more strongly toward posterior. Anterior and posterior margins intersect at small, sharp projection at farthest lateral point of cheek. Eye forming convex, horizontal band projecting slightly outward from cheek. Anterior rim of cranidium continuing for short distance onto anterior margin of cheek. Ornament same as on cranidium. Hypostome and rostral plate unknown.

Thorax of ten segments. Axis moderately convex, wide (tr.), 43% total width (tr.) of thorax. Axial furrows shallow, marked mainly by change in convexity from axis to pleurae. Adaxial portions of pleurae nearly flat; approximately 45% total width (tr.) of pleurae. Lateral portions of pleurae strongly deflected. Posterior thoracic segments narrower (tr.) than those toward anterior. Dorsal surface of thoracic segments without ornament.

Pygidial length (sag.) 55% of width (tr.). Axis moderately convex, elevated only short distance above pleural fields. Axial furrows shallow, wide, converging toward posterior to form blunt point at posterior of axis. Anterior margin of axis weakly rounded; anterior margins of pleural regions nearly transverse. Posterior margin of pygidium rounded. Longitudinal convexity of pygidium low over axis, very low to nearly flat posterior to axis then steeply deflected 1/4 total length (sag.) from posterior margin. Articulating facets moderately long, oriented at fairly high angle to

anterior margin of pygidium. Maximum width (tr.) of pygidium approximately 55% its total length (sag.) from anterior margin. Ornament of shallow, wide grooves arising in center of axis and radiating out over pleural regions. Elongate, shallow pits at termination of grooves. Two large, sub-ovate muscle scars visible on pygidial axis. Posterior margin of muscle scars located at posterior margin of axis, widening toward anterior, becoming narrower and terminatinh at 1/2 to 2/3 distance from posterior margin of axis. Muscle scars separated by area approximately 1/2 total width (tr.) of each scar. Doublure with pair of sharp forward projections straddling posterior termination of pygidial axis; two much smaller, sharp forward projections directly posterior to termination of the axis. Ornament of terrace ridges on doublure roughly paralleling anterior margin of doublure. Central, longitudinal furrow on doublure widest anteriorly, narrowing toward posterio, terminating at 2/3 distance to posterior margin.

REMARKS

The cranidium of *T. laurentiana* is similar to that of *T. conradi* except that the latter has more strongly bowed axial furrows and shorter palpebral lobes (e.g., Pl. 7, Figs 1c, 2c). The pygidium of *T. depressicapitata* is remarkably similar to that of *T. laurentiana* in both shape and ornamentation (e.g., Pl. 13, Fig. 1). The cranidia of the two species differ in that the palpebral lobes of *T. laurentiana* are directed slightly upward rather than outward or slightly downward and *T. laurentiana* has much more strongly arched axial furrows of the cranidium. *Thaleops utahensis* (Hintze 1952; pl. 28, figs 8-12) resembles *T. laurentiana* in pygidial outline but has a pygidial axis that

is better defined. The pygidium of *T. marginalis* (Whittington 1954; pl. 48, figs 3, 8, 10) is similar but the anterior margin of the doublure has a single pair of very long (exsag.) forward projections rather than two, relatively short pairs.

Thaleops anusacerbissima sp. nov. Pls 17, 18

TYPES

A nearly complete but exfoliated cranidium (Holotype, OU 11729) a cranidium and two transitory pygidia (Paratypes, OU 11726-11728) two partially to completely exfoliated cranidia (Paratypes, OU 11730, 11731), an exfoliated rostral plate (Paratype, OU 11732), a partially exfoliated pygidium with doublure exposed (Paratype, OU 11733), three partially to completely exfoliated pygidia (Paratypes, OU 11734, 11737, 11738), two partial, exfoliated librigenae (Paratypes, OU 11735, 11736) and the cuticle of a pygidium (Paratype, OU 11739).

ETYMOLOGY

From Latin for excruciating pain in the rectum, a metaphor for the senior author's frustration in dealing with illaenid systematics.

DIAGNOSIS

A species of *Thaleops* with wide (tr.), strongly elevated palpebral lobes. Intersection of articulating facet with posterior margin of pygidium sharply pointed. Genal spines long, slender, curved over entire length, dorsoventrally compressed, directed posterolaterally for about half length, then curving abruptly backward and downward.

OCCURRENCE

Fifty-four cranidia, 20 pygidia, 5 librigenae and 1 rostral plate were collected from the Upper Ordovician (Mohawkian: Chatfieldian) Viola Springs Formation, Oklahoma at the HWY99 locality (13m, 30m-34m). Specimens are all disarticulated and usually preserved as internal moulds.

DESCRIPTION

Cranidium wider than long with low longitudinal convexity. Axial furrows moderately shallow behind lunettes; directed weakly abaxially from posterior margin for about 1/2 distance to lunette then directed inward to lunette, which is positioned just in front of level of palpebral lobe. On internal moulds, axial furrows visible for short distance in front of lunettes, directed abaxially before becoming effaced. Occipital furrow obsolete. Posterior branch of facial suture short (exsag.), directed postero-laterally. Anterior branch gently rounded for 1/2 distance to anterior margin, then nearly straight and angled sharply adaxially. Anterior margin of cranidium very gently rounded with short anterior border covered by two or three terrace ridges. Posterior margin of glabella straight, transverse convexity strong. Fixigenae highly vaulted, positioned well below elevation of glabella, sloping downward abaxially to wide, shallow palpebral furrow. Posterior margins of fixigenae straight, directed only slightly toward posterior. Posterior fixigenae narrow (tr.), long (exsag.), sub-triangular, deflected ventrally. Palpebral lobes nearly at posterior margin of cranidium, oriented upward to a point well above level of fixigenae. Posterior margin

of palpebral lobe straight to termination; anterior margin straight then converging toward posterior margin at 1/3 distance from termination, forming rounded point. Lunettes only slightly wider (tr.) than axial furrows, weakly impressed. Ornamentation of very fine shallow pits.

Librigenae broken proximally. Preserved portion sub-triangular then tapering into spine. Anterior margin of cheek rounded; posterior margin curving gently inward; inflection at intersection with spine. Spine slender over entire length, dorsoventrally compressed, directed posterolaterally for half of preserved distance, then directed toward posterior and deflected ventrally. Rostral plate not preserved in place on any specimen. An exfoliated illaenimorph rostral plate (Pl. 17, Fig. 7) collected from a horizon containing specimens of *T. anusacerbissima* and resembling a rostral plate tentatively assigned to *T. depressicapitata* tentatively assigned to this species. Anterior margin rounded; distinct furrow parallels anterior margin. Posterior margin with central posterior projection mostly broken off. Hypostome and thorax unknown.

Pygidium wider (tr.) than long (sag.), length 60% of width. Axis vaulted well above pleural region, narrow (tr.), width 35% total width of pygidium. Axial furrows shallow, wide, converging very slightly toward posterior then turning abruptly to form blunt posterior margin, giving axis sub-rectangular shape. Ventral surface of axis with two well-defined muscle attachment sites. Anterior margin of axis rounded, extending forward beyond anterior margins of pleural region. Pleural region vaulted, anterior margins very gently rounded. Intersection of anterior margin with articulating facet rounded. Posterior margin evenly rounded. Intersection of articulating facet with posterior margin of pygidium sharp, forming point.

Articulating facets moderately long (exsag.) reaching 65% total length (sag.) of pygidium from anterior margin of pygidium. Cuticle of pygidium with very fine pits. Doublure long (exsag), originating at articulating facet 1/3 distance behind anterior margin. Anterior margin of doublure gently curved inward then forming two sharp forward projections at level of axial furrows. Anterior margin of doublure between forward projections strongly curved inward, marking posterior margin of pygidial axis. A wide, shallow furrow bisects doublure, extending from anterior margin of doublure for 2/3 its length.

REMARKS

Thaleops anusacerbissima closely resembles *T. adunca* (Chatterton & Ludvigsen 1976; pl. 3, figs 40-55), especially in cranidial characteristics. The fixigenae of *T. adunca* are sloped strongly downward abaxially while those of *T. anusacerbissima* are more uniformly vaulted. The genal spines of *T. adunca* do not narrow as abruptly at the intersection with the rest of the cheek, are more strongly curved, and are directed ventrally at a shorter distance from the rest of the cheek than in *T. anusacerbissima*. The pygidial axis of *T. adunca* is wider and the axial furrows converge more sharply toward the posterior. A sharp point at the intersection of the articulating facet with the posterior margin is not present in *T. adunca*. *Thaleops mackenziensis* (Chatterton & Ludvigsen 1976; pl. 4, figs 1-39) differs from *T. anusacerbissima* in the horizontally oriented, rather than elevated, palpebral lobes, shorter genal spines, and the presence of roughly transverse ridges on the pygidial axis. *Thaleops raymondi* (Shaw 1968; pl. 20, figs 1-16, 18) resembles *T.*

anusacerbissima in the blunt posterior margin of the pygidial axis. The axial furrows of the glabella of *T. raymondi* are nearly parallel rather than outwardly bowed, the lunettes of *T. raymondi* are larger, the axial furrows are weakly defined in front of the palpebral lobes, and the ornamentation consists of shallow, flat-bottomed pits. The presence of genal spines in *T. ovata* and blunt posterior margin of the pygidial axis resemble *T. anusacerbissima*. *Thaleops ovata* has a carina on the genal spine, a pygidial axis that is more sharply defined and crossed by transverse ridges, larger lunettes in the axial furrows, and coarsely pitted rather than finely punctate ornamentation (Pls 1-3).

Thaleops mobydicki sp. nov. Pls 19, 20

TYPES

A complete cephalon (Holotype, OU 11741), a partially weathered cranidium (Paratype, OU 11742), two slightly crushed complete exoskeletons (Paratypes, OU 11743, 11746), a partial cephalon (Paratype, OU 11744), an articulated thorax and pygidium (Paratype, OU 11745), a complete pygidium (Paratype, OU 11747), a pygidium prepared to expose doublure (Paratype, OU 11748), articulated, partially enrolled posterior thorax and pygidium (Paratype, OU 11749).

ETYMOLOGY

At times, the senior author's analysis of relationships among illaenid trilobites felt like Ahab's pursuit of the Great White Whale.

DIAGNOSIS

A species of *Thaleops* with broad (tr.) cranidium ornamented by extremely fine, shallow pits. Dorsal surface of fixigenae even with or only slightly below dorsal surface of glabella. Axial furrows of pygidium deep and broad.

OCCURRENCE

This species occurs in the Upper Ordovician (Mohawkian: Turinian) Bromide Formation of Oklahoma at localities GEQ and RC. Most are preserved with cuticle intact and some are partially articulated.

DESCRIPTION

Cranidium wider (tr.) than long (sag.). Longitudinal convexity strong. Posterior 1/3 of cranidium with low convexity and sloping steeply forward; convexity strong and even over remaining distance, becoming overturned at approximately 2/3 total length (sag.) from posterior margin. Axial furrows deep, relatively narrow, curving inward from posterior margin to lunette then diverging for short distance in front of lunette before becoming effaced. Occipital furrow effaced. Posterior branch of facial suture short, directed laterally and posteriorly at approximately 45° to posterior margin. Anterior branches of facial sutures weakly rounded and weakly convergent. Anterior margin very gently rounded. Anterior rim long (sag.), narrowing slightly abaxially; composed of three well-defined, parallel terrace ridges; rim without independent elevation. Transverse convexity of glabella very low. Palpebral regions of fixigenae with low convexity approximately equal to that of glabella, located at nearly equal

elevation. Posterior margin of cranidium transverse to palpebral lobe then deflected toward posterior. Posterior portions of fixigenae small, sub-triangular, deflected ventrally. Palpebral lobes placed far back on cranidium, only slightly in front of posterior margin. Palpebral furrow wide, shallow. Palpebral lobes relatively wide (tr.), directed outward or slightly downward, with uniformly rounded termination. Ornament of very shallow pits not visible without magnification. Horizontal terrace ridges run parallel to anterior margin.

Librigena with semicircular outline; anterior margin gently rounded; posterior and lateral margins evenly rounded around genal angle. Vaulting of dorsal surface of cheek low. Eyes oriented outward from dorsal surface of cheek, located slightly below convexity of fixigenae. Visual surface strongly convex laterally. Anterior rim continuing onto anterior margin of cheek for short distance. Hypostome and rostral plate unknown.

Thorax of 10 segments, tapering toward posterior. Axis convex, approximately 45% width (tr.) of thorax. Axial furrows broad, defined mainly by change in convexity between axis and pleurae. Articulating furrows effaced; anterior 1/3 of axial rings deflected toward anterior. Adaxial portions of pleurae sub-horizontal; approximately 40% total width (tr.) of each pleura. Abaxial sections of pleurae bear articulating facets, deflected ventrally at sharp angle. Ornament of widely scattered shallow pits.

Pygidium wider than long; length (sag.) approximately 60% of width (tr.). Axis only raised slightly above level of pleural fields; width (tr.) of axis just over 40% maximum width (tr.) of pygidium. Axial furrows moderately effaced, convergent

toward posterior. Anterior margin of axis gently rounded. Anterior margins of pleural regions nearly transverse, directed slightly toward anterior from axial furrows toward lateral margin. Posterior margin of pygidium gently and evenly rounded. Convexity in lateral profile even over most of length (sag.), then steepening abruptly to posterior margin. Articulating facets long, oriented at high angle to anterior margin of the pygidium; distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 70% total length (sag.) of pygidium. Pits shallower and more widely scattered than on cranidium. Doublure ornamented with terrace ridges which parallel scalloped anterior margin. Anterior margin of doublure similar to that of *T. depressicapitata* with two pairs of sharp anterior projections. Central longitudinal furrow uniform in width (tr.), reaching 2/3 distance to posterior margin.

REMARKS

Thaleops mobydicki resembles *T. fieldi* in the outline of the cranidium, placement and shape of the palpebral lobes, pygidial outline and ornamentation (Pl. 8, Fig. 5; Pl. 9, Fig. 2). The axial furrows of the cranidium are more effaced in *T. fieldi*. In lateral profile, the curvature of the cranidium in *T. fieldi* is more even. The punctae of *T. fieldi* are more pronounced and more densely spaced. The pygidium of *T. viator* is very similar to that of *T. mobydicki* and both share weak ornamentation (Pl. 10, Figs 1b, c, d). The fixigenae of *T. viator* are depressed below the glabella and the cranidium is more evenly convex (Pl. 9, Fig. 7).

Thaleops jaanussoni sp. nov. Pl. 21

1974. *Nanillaenus*? cf. *N. punctatus*; Shaw, p. 16, pl. 4, figs 3-4, 8, 10-18.

TYPES

A complete exoskeleton (Holotype, OU 11750), two complete cranidia (Paratypes OU 11751, 11752), a pygidium prepared to expose the doublure (Paratype, OU 11753), a complete pygidium (Paratype, OU 11754), and a nearly complete librigena (Paratype, OU 11755).

ETYMOLOGY

The trivial name pays homage to Valdar Jaanusson for his efforts to empty the *Illaenus* garbage can.

DIAGNOSIS

A species of *Thaleops* with densely pitted cuticle; lunettes expressed on dorsal surface of cuticle as depressed areas devoid of ornament. Genal spines long, curved, evenly tapering to sharp point.

OCCURRENCE

This species is from the Upper Ordovician (Mohawkian: pre-Turinian) Bromide Formation of Oklahoma at GEQ and I-35N (47-48m).

DESCRIPTION

Longitudinal convexity relatively low, even across entire length (sag.). Axial furrows parallel to slightly divergent behind lunettes, becoming effaced in front of lunettes. Occipital furrow effaced. Posterior branch of facial sutures short, directed toward posterior and strongly laterally. Anterior branches of facial sutures follow gently curved path, converging weakly forward to anterior margin. Anterior margin of cranidium weakly rounded. Anterior rim moderately long(sag.), consisting of four terrace ridges raised slightly above elevation of anterior of cranidium. Lateral margin of cranidium in front of palpebral lobes with same curvature as anterior margin, forming evenly rounded frontal portion of cranidium. Transverse convexity of glabella moderate behind lunettes, indistinguishable from fixigenae in front of lunettes. Palpebral region of fixigenae with low convexity and at an elevation below that of glabella. Palpebral furrow effaced. Posterior margin of cranidium directed very slightly backward behind palpebral lobes. Posterior portions of fixigenae very short (exsag.), directed laterally and ventrally. Palpebral lobes located far back on cranidium, nearly at posterior margin. Palpebral lobes short (exsag.) relative to width (tr.), creating sub-triangular outline, with rounded termination. Palpebral lobes directed weakly downward. Lunettes visible on dorsal surface of cuticle as shallow depressions without ornament. Ornament of densely distributed, coarse pits over entire surface of cuticle except in lunettes, on extremity of palpebral lobes and on posterior extension of fixigenae. Muscle scars suggested on dorsal surface where ornament is slightly effaced.

Librigenae sub-triangular, tapering distally into long, curving spine. Anterior

margin evenly rounded along entire length. Posterior margin nearly straight proximally, directed anterolaterally then curving inward along posterior margin of spine. Spine directed posterolaterally, tapering to sharp termination. Anterior and posterior margins of spine converge dorsally to form dorsal carina. Dorsal portion of gena convex; eye directed slightly outward. Dorsal surface of gena densely covered by pits; terrace ridges of anterior rim continue onto anterior surface of cheek for short distance. Hypostome and rostral plate unknown.

Thorax of 10 segments, tapering toward posterior. Each segment ornamented with a row of punctae. Width (tr.) of axis approximately 32% total width (tr.) of thorax. Adaxial portion of pleurae nearly 50% total width (tr.) of pleurae, nearly horizontal; abaxial portions deflected sharply ventrally.

Length (sag.) of pygidium approximately 60% of width (tr.). Axis strongly convex, arching well above elevation of pleural regions. Width (tr.) of axis approximately 35% maximum width (tr.) of pygidium. Axial furrows wide, well-defined around posterior margin of axis. Axial furrows converge only slightly backward; posterior termination of axis bluntly rounded. Anterior margin of axis gently rounded, extending short distance in front of anterior margin of pleural regions. Posterior margin gently rounded, extending abaxially for short distance beyond articulating facet so articulating facet curves abaxially to intersect posterior margin forming short, laterally projecting point. Longitudinal convexity of pygidium strong and even. Articulating facets shorter and at slightly lower angle than those of *T. mobydicki*. Maximum width (tr.) of pygidium located at distance from anterior margin approximately 65% total length (sag.) of pygidium. Pygidial ornament

similar to that of cranidium. Pygidial doublure long (sag.) with two sharp forward projections, one on either side of a short, rounded forward projection. Terrace ridges of doublure roughly parallel. Longitudinal furrow in center of doublure shallow, extending 2/3 distance to posterior margin.

REMARKS

Thaleops depressicapitata is similar to *T. jaanussoni*, but has larger pits on the surface of the cuticle of the cranidium and radiating terrace ridges on the pygidium rather than pits. The pygidial axis of *T. depressicapitata* is sub-triangular rather than sub-rectangular (Pl. 12, Figs 4a, 5a, b). The ornament of *T. fieldi* is much more obscure than in *T. jaanussoni*. *Thaleops fieldi* has fixigenae located below the elevation of the glabella, weaker axial furrows of the cranidium and a sub-triangular pygidial axis (Pl. 8, Fig.5; Pl. 9, Fig. 2). The cuticle of *T.viator* is only weakly pitted, the pygidial axis is relatively wider and the articulating facets of the pygidium are oriented at a higher angle to the anterior margin (Pl. 9, Fig. 7; Pl. 10, Fig. 1c) . The genal spines of *T. ovata* are similar in shape to those of *T. jaanussoni* and bear a dorsal carina. *Thaleops ovata* differs from *T. jaanussoni* in the possession of upwardly directed palpebral lobes, more strongly defined axial furrows and presence of relict segmentation on the axis and pleural regions of the pygidium (Pl. 2, Figs 1a, 1c, 1h; Pl. 3, Figs 1, 2).

***Thaleops* sp. 1** Pl. 22, Figs 1-5

MATERIAL

Material consists of three moderately well-preserved cranidia (OU 11756-11758) and an exfoliated cranidium (OU 11759).

DIAGNOSIS

A species of *Thaleops* with densely distributed, deep but narrow pits. Anterior branches of facial sutures sub-parallel for short distance in front of palpebral lobes before becoming weakly convergent. Palpebral lobes long (exsag.) and wide (tr.).

OCCURRENCE

This species is found in the Upper Ordovician (Mohawkian: pre-Turinian) Bromide Formation of Oklahoma at GEQ and I-35N (6.85m, 47-48m.

DESCRIPTION

Longitudinal convexity strong and even. Axial furrows moderately well incised, directed inward behind lunettes, directed slightly abaxially in front of lunettes then becoming effaced within a short distance. Occipital furrow effaced. Posterior branch of facial sutures short, directed toward posterior and only slightly laterally. Facial sutures sub-parallel in front of palpebral lobes for short distance then converge weakly until intersecting nearly transverse anterior margin. Anterior rim short (sag.) and low. Glabella weakly arched behind lunettes, becoming obsolete in front of lunettes. Fixigenae at slightly lower elevation than glabella, weakly convex.

Posterior margin of cranidium nearly transverse for most of width (tr.), at level of palpebral lobes directed toward posterior at approximately 45°. Fixigenae behind palpebral lobes small, sub-triangular, weakly deflected ventrally. Palpebral lobes positioned near posterior of cranidium. Palpebral furrow weakly indicated by change in convexity. Palpebral lobes wide (tr.), long (exsag.), directed outward from fixigenae. Termination of palpebral lobes rounded. Lunettes weakly expressed on dorsal surface where axial furrows change direction, represented by only slight widening of axial furrows on internal moulds. Ornament of densely packed pits of moderate width. Muscle scars not visible on exterior of cuticle or on internal moulds of glabella. Librigenae, hypostome, rostral plate, thorax and pygidium unknown.

REMARKS

This species occurs in the same collection as *T. jaanussoni* but differs in a number of significant ways. *Thaleops jaanussoni* has a lower longitudinal convexity of the cranidium, axial furrows with greater effacement and coarser pitting of the dorsal exoskeleton. The anterior facial sutures of *T.* sp 1 are parallel for a short distance in front of the palpebral lobes and the palpebral lobes are longer (exsag.) and wider (tr.) than in *T. jaanussoni*.

***Thaleops* sp. 2** Pl. 22, Fig. 6, Pl. 23, Figs 1-3

MATERIAL

Material of this species consists of a slightly exfoliated cranidium (OU 11762), a mostly exfoliated cranidium (OU 11763), a partial, exfoliated pygidium (OU 11764)

and a distorted and partially exfoliated pygidium (OU 11765).

DIAGNOSIS

A species of *Thaleops* with wide, deeply impressed lunettes on dorsal surface of cuticle. Longitudinal convexity nearly flat over posterior 1/3 of cranidium. Axis of pygidium very narrow (tr.). Relict segmentation on ventral surface of axial and pleural regions of pygidium.

OCCURRENCE

This species occurs in the Upper Ordovician (Whiterockian: *N. gracilis* zone) Bromide Formation of Oklahoma at locality I-35N (36.6m) in a coarse rudstone interpreted as a shoal environment.

DESCRIPTION

Posterior 1/3 of cranidium without longitudinal convexity; middle 1/3 of cranidium with strong convexity; anterior 1/3 with very low convexity. Axial furrows wide, deep, directed straight forward or very slightly abaxially from posterior margin to lunettes; effaced in front of lunettes, even on internal moulds. Occipital furrow only weakly visible on external surface (e.g. Pl. 23, Fig. 1c), slightly better expressed on internal moulds (e.g. Pl. 23, Fig. 2c); represented by slight change in convexity from more convex occipital region to nearly flat glabella. Posterior branch of facial suture directed posterolaterally at less than 45° to posterior margin. Anterior branch of facial suture curving inward to weakly rounded anterior margin. Anterior rim short

(sag.), raised slightly above elevation of frontal portion of cranidium. Glabella with low transverse convexity behind lunettes. Fixigenae in palpebral region with low convexity, situated only slightly below elevation of glabella, sloping gently down to wide, shallow palpebral furrows. Posterior margin of cranidium directed toward posterior at level of palpebral lobes. Posteriorly, fixigenae short (exsag.), deflected weakly ventrally. Palpebral lobes placed very near posterior margin of cranidium. Palpebral lobes long (exsag.), narrow (tr.), directed outward or weakly downward. Lunettes wide, deeply impressed on dorsal surface, profound on internal moulds. Ornament of densely distributed, wide, shallow pits; pits become finer and then effaced distally on palpebral lobes, posterior fixigenae and around anterior projection of cranidium. Posterior pair of muscle scars preserved as dorsal bulge on cuticle (e.g. Pl. 23, Fig. 1c) and on internal moulds (e.g. Pl. 23, Fig. 2c). Longitudinal depression between muscle scars more prominent on internal moulds. Librigenae, hypostome, rostral plate and thorax unknown.

Pygidium incompletely preserved. Axis narrow (tr.), approximately 31% total width (tr.) of pygidium. Axial furrows converge slightly backward; termination of axis blunt. Posterior margin not complete. Articulating facets oriented at high angle to anterior margin of pygidium. Ornament of densely distributed, coarse pits. Doublure with pair of sharp forward projections straddling posterior termination of axis. Terrace ridges roughly parallel anterior margin of doublure. Longitudinal furrow not preserved.

REMARKS

Thaleops sp. 2 is similar to *T. jaanussoni* but is ornamented with broader, more widely spaced pits, has a narrower (tr.) pygidial axis and the lateral profile of the cranidium is not evenly convex.

***Thaleops* sp. 3** Pl. 23, Fig. 4

1968. *Nanillaenus*? cf. *N. punctatus*; Shaw, p. 49, pl. 20, figs 21-23.

1997. *Nanillaenus*? *punctatus*; Whittington, p. 894, fig. 9, 5-7.

MATERIAL

A single, mostly exfoliated but nearly complete exoskeleton (NYSM 12502).

DIAGNOSIS

A species of *Thaleops* with short (dorsoventrally) cranidium relative to width (tr.); lunettes on internal moulds very large, deeply impressed. Transverse convexity of cranidium low; dorsal surface of fixigenae at only slightly lower elevation than dorsal surface of glabella.

OCCURRENCE

A single, partially exfoliated but otherwise complete specimen is known from the Middle Ordovician (Whiterockian: *N. gracilis* zone) Crown Point Formation, Sloop Bay, Valcour Island, New York.

DESCRIPTION

Longitudinal convexity strong. In anterior view, height of cranidium low relative to width (tr.). Cuticle on cranidium not preserved. Axial furrows behind lunettes wide, parallel; effaced in front of lunettes. Occipital furrow effaced. Posterior branch of facial suture long for genus, angled laterally and toward posterior at approximately 45°. Anterior branches of facial sutures rounded, directed strongly adaxially. Anterior margin of cranidium weakly rounded; anterior rim not preserved on internal mould. Dorsal surface of glabella with very low convexity. Fixigenae with low convexity, sloping gently downward toward palpebral lobes. Posterior margin of cranidium nearly transverse except where directed backward behind palpebral lobes. Fixigenae behind palpebral lobes relatively large, sub-triangular. Palpebral lobes placed very short distance in front of posterior margin. Palpebral furrow expressed as change in convexity between fixigenae and palpebral lobes. Palpebral lobes narrow (tr.), short (exsag.), directed outward, with rounded termination. Lunettes on internal mould wide (tr.), deep. Ornament not preserved on cranidium. Two slightly elevated, rounded ridges run along lateral margins of glabella with very shallow depression in center; ridges most likely represent areas of muscle attachment.

Librigenae semicircular in outline; both anterior and posterior margins rounded. Eye protrudes only slightly outward from dorsal surface of librigena. Visual surface short (dorsoventral) band. Ornament of narrow, shallow pits. Hypostome unknown. Rostral plate not fully exposed; relatively short (sag.) for genus.

Thorax of 10 segments; thoracic segments narrower (tr.) toward pygidium. Axis moderately convex, 41% total width (tr.) of thorax. Axial furrows wide, moderately

well impressed. Adaxial portions of pleurae flat, approximately 50% total width (tr.) of segments. Abaxial portions of pleurae deflected sharply ventrally.

Pygidium length (sag.) approximately 60% maximum width (tr.). Axis moderately convex. Axial furrows on internal moulds wide, shallow; converging sharply backward to form relatively sharp termination. Posterior margin of pygidium rounded. Longitudinal convexity rather low. Articulating facets fairly long. Maximum width (tr.) of pygidium at 64% total length (sag.) of pygidium. Ornament not preserved. Doublure not fully exposed but preserves sharp forward projection on right side of axis. Doublure ornamented with sub-parallel terrace ridges. Longitudinal furrow narrows (tr.) posteriorly, terminates at approximately 1/2 distance to posterior margin.

REMARKS

The width (tr.) of the cranidium of *T.* sp. 3 is similar to that of *T. mobydicki* and the dorsal surfaces of the fixigenae are only slightly lower than the dorsal surface of the glabella in both species. Smaller lunettes and longer (exsag.) and wider (tr.) palpebral lobes distinguish *T.* sp. 3 from *T. mobydicki. Thaleops* sp. 3 is very similar to *T. raymondi* but the cranidium of the former has lower longitudinal convexity.

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APPENDIX 1

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS OF THALEOPS

Examples listed for each character state employ names used by author providing figure.

1. Length and orientation of articulating facets: 0, distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 25% to 39% total length (sag.) of pygidium (e.g., *I. sarsi* in Jaanusson 1957; pl. 4, fig. 5; 1, distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 14% to 18% total length (sag.) of pygidium (e.g., *I. praecurrens* Jaanusson 1957; pl. 8, fig. 2); 2, distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 51% to 77% total length (sag.) of pygidium (e.g., *T. mobydicki*; Pl. 20, Fig. 4b).
2. Maximum length (sag.) of pygidium relative to maximum width (tr.): 0, pygidium wider (tr.) than long (sag.) (e.g., *I. aduncus* Jaanusson 1957; pl. 6, fig. 6); 1, length (sag.) and width (tr.) of pygidium nearly equal (e.g., *I. (P.) fallax* in Bruton & Owen 1988, fig. 8F).
3. First pleural furrow: 0, present (e.g., *R. vespertina* in Fortey 1980; pl. 6, fig. 3); 1, absent (e.g., *T. ovata*; Pl. 3, Fig. 2a).
4. Pygidial doublure: 0, smooth or with faint embayment (e.g., *I. (P.) roemeri* in Bruton & Owen 1988; fig. 7G); 1, two sharp forward projections reaching anterior to either side of posterior border of pygidial axis (e.g., *I. oscitatus* Fortey 1980; pl. 10, fig. 12); 2, strong, U-shaped medial embayment (*I. utahensis*

Hintze 1952; pl. 28, fig. 9a); 3, central forward projection with no central embayment (*I. planifrons* Jaanusson 1957; pl. 10, fig. 1).

5. Degree of definition of pygidial axis: 0, entire pygidial axis well defined by strong furrows (e.g., *T. ovata*; Pl. 3, Fig. 1); 1, entire pygidial axis defined by weak axial furrows (e.g., *T. conradi*; Pl. 7, Fig. 4a); 2, posterior portion of axial furrows effaced (e.g., *T. viator*; Pl. 10, Fig. 1c).
6. Length of pygidial axis: 0, length (sag.) of axis greater than length of post-axial field (e.g., *T. angusticollis*; Pl. 4, Fig. 4), 1, length (sag.) of axis less than length of post-axial field (e.g., *T. latiaxiata*; Pl. 8, Fig. 3).
7. Width of pygidial axis: 0, width (tr.) less than 30% maximum width (tr.) of pygidium (*R. vespertina* in Fortey 1980; pl. 6, fig. 4); 1, width (tr.) 33% to 44% maximum width (tr.) of pygidium (e.g., *T. laurentiana*; Pl. 15, Fig. 1f); 2, width (tr.) 47% to 50% maximum width (tr.) of pygidium (e.g., *T. latiaxiata*; Pl. 8, Fig. 4b).
8. Number of thoracic segments: 0, seven (*R. tennesseensis* Cooper 1953; pl. 9, fig. 11); 1, ten (e.g., *T. ovata*, Pl. 1, Fig. 1a); 2, eight (e.g., *T. conradi*; Pl. 7, Fig. 3a).
9. Thorax shape: 0, width (tr.) of posterior-most thoracic segment equal to or only slightly narrower than width (tr.) of first thoracic segment (e.g., *I. sarsi* in Jaanusson 1957; pl. 4, fig. 7); 1, width (tr.) of posterior-most thoracic segment 87% to 89% width (tr.) of first thoracic segment (e.g., *I. utahensis* Hintze 1952; pl. 28, fig. 12b); 2, width (tr.) of posterior-most thoracic segment 71% to 82% width (tr.) of first thoracic segment (e.g., *T. jaanussoni*; Pl. 21, Fig. 1c).

10. Occipital ring: 0, occipital ring well defined by occipital furrow (e.g., *T. angusticollis*; Pl. 4, Fig. 5b); 1, occipital furrow effaced (e.g., *T. mobydicki*; Pl. 19, Fig. 1c).
11. Genal spine: 0, short spine directed backward (R. vespertina in Fortey 1980; pl. 6, fig. 6); 1, rounded genal angle (e.g., *T. mobydicki*; Pl. 19, Fig. 1d); 2, rounded genal angle elongated into genal flap (e.g., *T. conradi*; Pl. 7, Figs 2a, 2c, 3b); 3, genal spine directed posterolaterally (e.g., *T. ovata*; Pl. 2, Fig. 1a).
12. Elevation of palbebral lobes: 0, palpebral lobes directed outward or slightly downward (e.g., *T. depressicapitata*; Pl. 12, Fig. 4a); 1, palpebral lobes directed upward (*T. anusacerbissima*; Pl. 17, Fig. 4a).
13. Position of palpebral lobes: 0, located well in front of posterior margin of cranidium (*R. reticulatus* Whittington 1965; pl. 56, fig. 1); 1, located short distance in front of posterior margin of cranidium (e.g., *I. oscitatus* Fortey 1980; pl. 10, fig. 1); 2, located almost even with posterior margin of cranidium (e.g., *T. anusacerbissima*; Pl. 17, Fig. 6d).
14. Strength of axial glabellar furrows: 0, strong (e.g., *T. ovata*; Pl. 1, Fig. 3a); 1, effaced (e.g., *T. fieldi*; Pl. 8, Fig. 5a).
15. Shape of glabella posterior to lunettes: 0, glabellar furrows subparallel (e.g., *N. mackenziensis* Chatterton & Ludvigsen 1976; pl. 4, fig. 30); 1, glabellar furrows bowed out (e.g., *T. conradi*; Pl. 7, Fig. 1c); 2, glabellar furrows curved in (e.g., *T. mobydicki*; Pl. 19, Fig. 1a); 3, glabellar furrows directed sharply in, then sharply out (e.g., *T. angusticollis*; Pl. 4, Fig. 5b).

16. Definition of anterior margin of glabella: 0, well-defined (e.g., *T. conifrons*; Pl. 5, Fig. 6a); 1, weakly defined (e.g., *I. crassicauda* in Jaanusson 1954; pl. 1, fig. 2); 2, effaced (e.g., *T. depressicapitata*; Pl. 12, Fig. 4a).
17. Glabellar muscle scars visible on exterior of cranidium: 0, absent (e.g., *T. laurentiana*; Pl. 15, Fig. 2a); 1, present as irregularly shaped, smooth areas in sculpture (e.g., *T. latiaxiata*; Pl. 8, Fig. 2d) or as lateral ridges on margins of glabella (e.g., *T. depressicapitata*; Pl. 11, Fig. 1); 2, present as raised areas on dorsal surface of exoskeleton (e.g., *T. ovata*; Pl. 1, Fig. 3a).
18. Course of anterior facial sutures: 0, strongly divergent (e.g., *R. vespertina* in Fortey 1980; pl. 6, fig. 5); 1, directed weakly laterally (e.g., *I. crassicauda* in Jaanusson 1954; pl. 1, fig. 2); 2, nearly parallel (e.g., *I. oscitatus* Fortey 1980; pl. 10, fig. 3); 3, directed weakly medially (e.g., *T. conradi*; Pl. 7, Fig. 2a); 4, angled sharply toward mid-line (e.g., *T. anusacerbissima*; Pl. 17, Fig. 4a).
19. Cephalic ornamentation: 0, punctae faint to absent (e.g., *T. mobydicki*; Pl. 19, Fig. 1e); 1, punctae present (e.g., *T. ovata*; Pl. 1 Fig. 3a).
20. Maximum length (sag.) of cranidium versus maximum width (tr.): 0, length 82% to 88% of width (e.g., *I. crassicauda* in Jaanusson 1954; pl. 1, figs 2, 4); 1, length 64% of width (*T. ovata*; Pl. 1, Figs 3b, c); 2, length 71% to 79% of width (e.g., *T. conradi*; Pl. 7, Figs 2a, b); 3, length 92% of width (*I. marginalis* in Whittington 1965; pl. 47, figs 3, 6); 4, length 103% to 104% of width (e.g., *I. oscitatus* Fortey 1980; pl. 10, figs 2, 3).

APPENDIX 2

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Raymondaspis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I. crassicauda	0	0	1	0	2	1	1	1	1	1	1	1	1	1	2	1	0	1	0	0
I. sarsi	0	0	1	1	2	1	1	1	0	1	1	0	1	1	0	2	0	1	0	0
I. aduncus	0	0	1	1	2	1	1	1	0	1	2	0	1	1	0	2	0	1	0	4
I. planifrons	0	0	1	3	2	1	1	?	?	1	?	0	1	1	2	2	0	1	0	0
I. oscitatus	0	0	1	1	2	1	1	?	?	1	1	0	1	1	0	2	0	2	1	4
I. praecurrens	1	1	1	0	2	?	1	1	0	1	1	0	1	1	0	2	0	0	0	?
I. fallax	1	1	0	0	2	1	1	1	0	1	1	0	1	1	0	2	0	0	0	?
I. roemeri	0	0	0	0	2	0	1	?	0	1	1	0	1	1	0	2	0	0	0	0
I. lacertus	2	0	1	1	2	?	2	1	2	1	1	0	2	1	?	2	0	3	0	?
I. viator	2	0	1	1	2	0	2	1	2	1	1	0	2	1	?	2	0	3	0	2
I. utahensis	2	0	1	2	2	1	1	1	1	1	2	0	2	1	0	2	0	3	0	?
I. marginalis	2	0	1	1	2	1	1	1	1	1	1	0	1	1	2	2	0	2	0	3
I. conradi	2	0	1	1	1	0	1	2	2	1	2	0	2	1	1	2	2	3	1	2
I. angusticollis	2	0	1	?	0	0	1	2	2	0	2	0	2	0	3	1	2	4	1	2
I. depressicapitatus	2	0	1	1	1	0	1	?	?	1	?	0	2	1	2	2	1	3	1	2
I. latiaxiatus	2	0	1	?	1	1	2	1	?	1	?	0	2	1	2	2	1	3	1	2
I. fieldi	2	0	1	?	?	0	1	?	?	1	?	0	2	1	2	2	1	3	0	2
I. conifrons	2	0	1	1	?	?	1	?	?	0	?	1	2	0	3	0	0	4	1	2
N. ? raymondi	2	0	1	1	0	0	1	1	2	1	?	1	2	0	2	1	1	3	1	0
N. aduncus	2	0	1	1	1	0	1	?	?	1	3	1	2	1	1	2	0	4	?	2
N. mackenziensis	2	0	1	1	1	0	1	?	?	1	3	0	2	1	0	2	0	4	1	2
T. ovata	2	0	1	1	0	0	1	1	2	0	3	1	2	0	1	1	2	3	1	1
T. longispina	2	0	1	1	?	0	1	1	2	0	3	1	2	0	3	0	1	4	1	2
T. anusacermissima	2	0	1	1	1	0	1	?	?	1	3	1	2	1	1	2	0	4	0	2
T. laurentiana	2	0	1	1	1	0	1	1	2	1	2	0	2	1	1	2	0	3	0	2
T. jaanussoni	2	0	1	1	0	0	1	1	2	1	3	0	2	1	0	2	1	3	1	2
T. mobydicki	2	0	1	1	1	0	1	1	2	1	1	0	2	1	2	2	0	3	0	2

PLATE 1

Figs 1-4 *Thaleops ovata* Conrad, 1843 **1a-d**, lectotype, complete exoskeleton (AMNH 29516), Upper Ordovician Galena Formation, Mineral Point, Wisconsin x3. **1a**, dorsal view **1b**, posterior view **1c**, lateral view **1d**, anterior view. **2a-b**, paralectotype, complete exoskeleton (AMNH 29517), Upper Ordovician Galena Formation, Mineral Point, Wisconsin x3. **2a**, dorsal view **2b**, lateral view. **3a-f**, complete exoskeleton (CM 5415) Upper Ordovician Black River Formation, Tetrauville, Quebec. **3a**, enlargment of glabella in palpebral view showing muscle scars, x6 **3b**, lateral view x3 **3c**, anterior view x3 **3d**, palpebral view x3 **3e**, posterior view x3 **3f**, dorsal view x3. **4a-c**, complete exoskeleton (GSC 1321) Upper Ordovician Ottawa Formation, Mechanicsville, Ontario x2. **4a**, dorsal view **4b**, anterior view **4c**, lateral view.

Plate 1

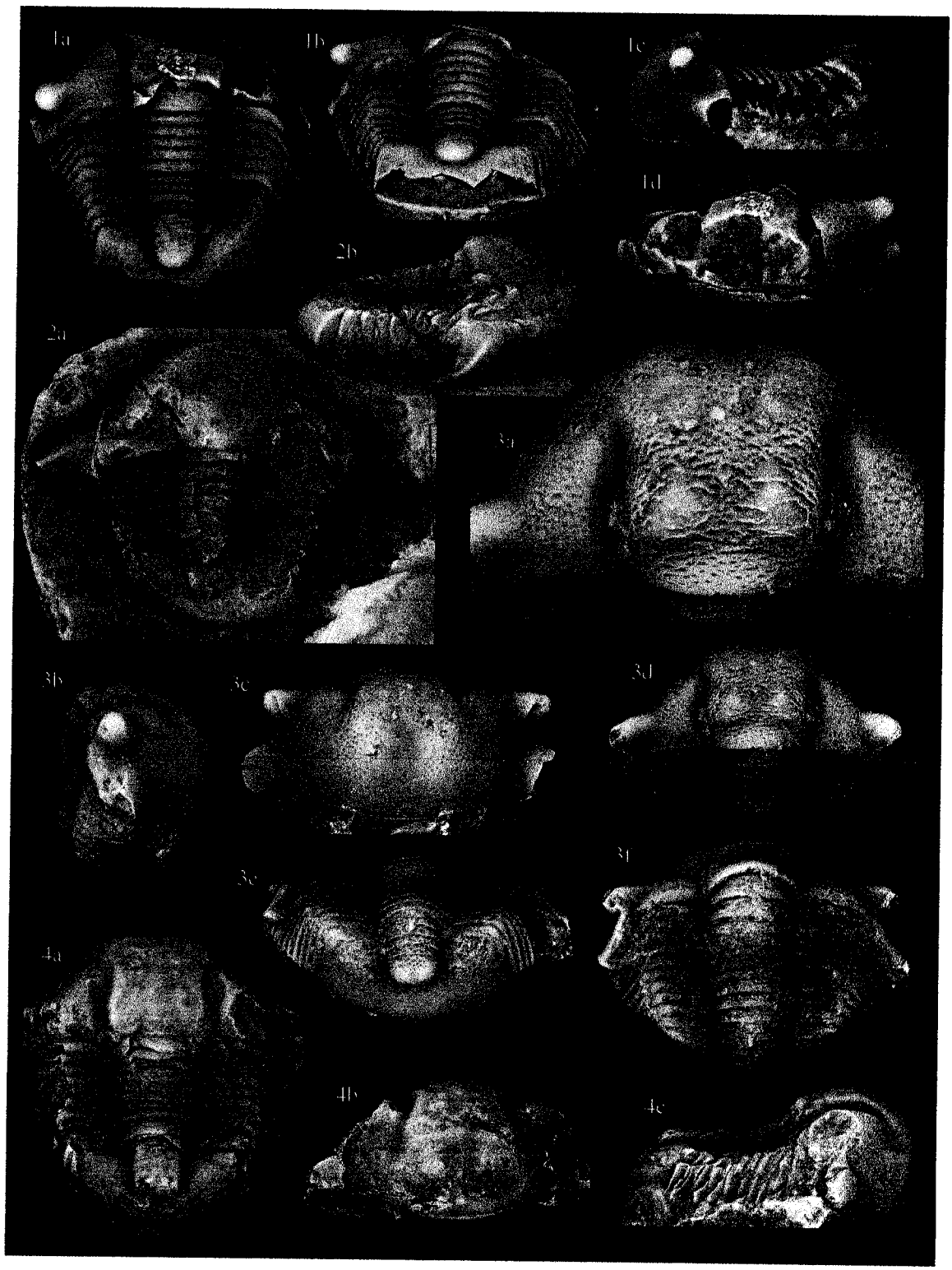


PLATE 2

Figs 1-2 *Thaleops ovata* Conrad, 1843 **1a-h**, complete exoskeleton (WM 6900), Upper Ordovician Kimmswick Limestone, Batchtown, Illinois. **1a**, palpebral view x3 **1b**, lateral view x3 **1c**, oblique view x3 **1d**, anterior view x3 **1e**, enlargement of genal spine showing dorsal carina x6 **1f**, enlargement of muscle scars on internal mold x6 **1g**, ventral view of rostral plate x3 **1h**, posterior view x3. **2a-d** complete exoskeleton (CM 5416) Upper Ordovician Black River Group, Pelton's Quarry near Ottawa, Ontario x3. **2a**, palpebral view **2b**, dorsal view showing dorsal carina on spine and muscle scars on cuticle **2c**, anterior view **2d**, posterior view showing relict segmentation on pleural fields of pygidium.

Plate 2

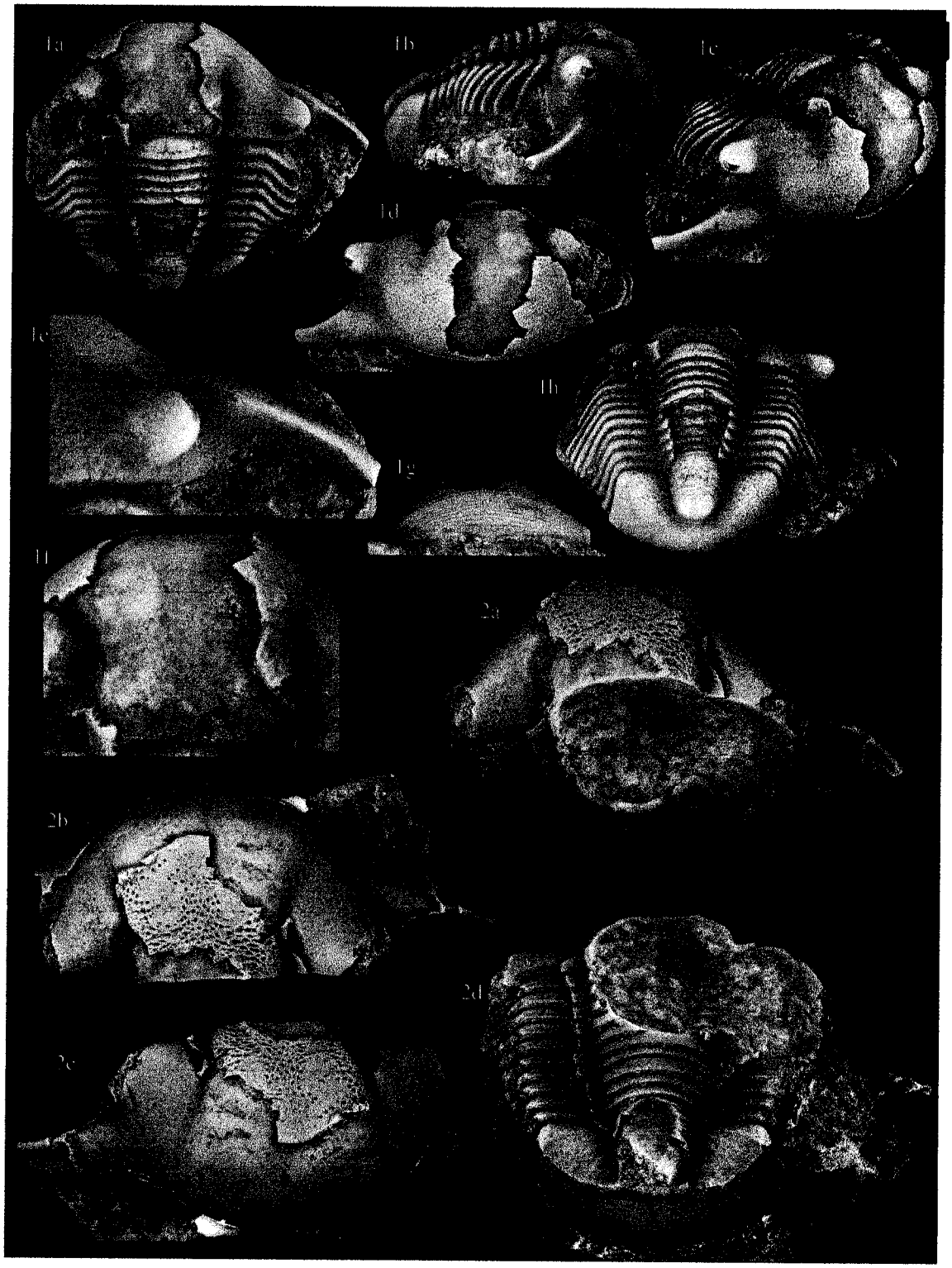


PLATE 3

Figs 1-2 *Thaleops ovata* Conrad, 1843 Upper Ordovician Platteville Formation, Winnebago Co., Illinois. **1a-b**, articulated thorax and pygidium (MCZ107221) x3 **1a**, oblique view showing pair of swollen posterior extensions at termination of pygidial axis **1b**, dorsal view. **2a-d**, posterior thorax and pygidium in articulation (MCZ 107220) **2a**, dorsal view x3 **2b**, posterior view x3 **2c**, enlargement of dorsal view showing detail of ornament on pygidial axis x5 **2d**, lateral view.

Fig 3 *Thaleops arctura* Hall, 1847 Middle to Upper Ordovician Chazy Limestone, Chazy, New York. **3a-e**, Holotype, cranidium (NYSM 4499) **3a**, anterior view x4 **3b**, oblique view x4 **3c**, palpebral view x4 **3d**, lateral view x4 **3e**, enlargement of sculpture on posterior of glabella x8.

Plate 3

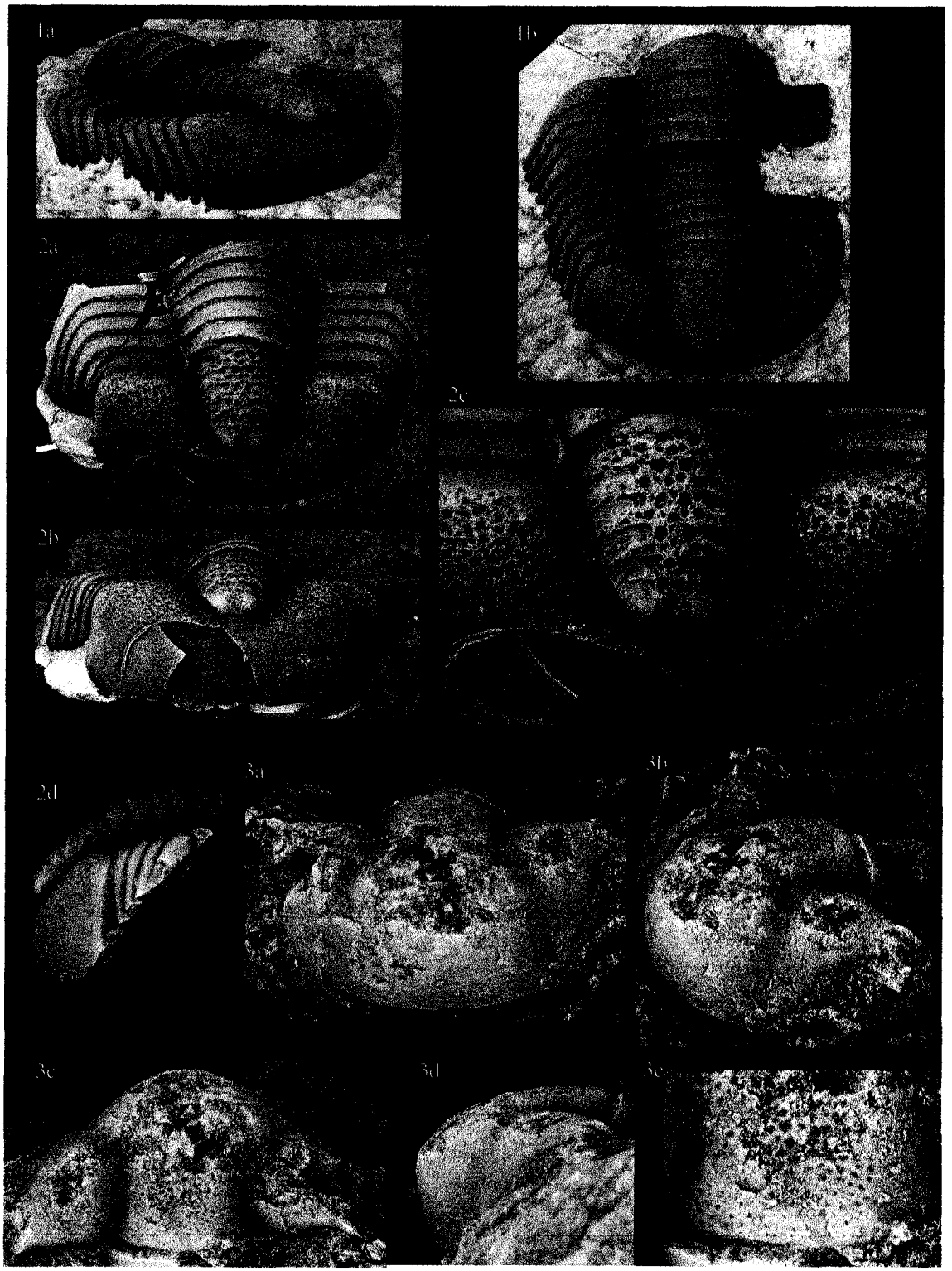


PLATE 4

Figs 1-5 *Thaleops angusticollis* (Billings, 1859) **1a-c**, holotype, cephalon (GSC 1314b) Upper Ordovician Ottawa Formation, St. Joseph Island, Lake Huron, Canada x5 **1a**, anterior view **1b**, palpebral view, occipital ring not excavated **1c**, lateral view. **2a-c**, paratype, cranidium (GSC 1314c) x9 **2a**, anterior view **2b**, palpebral view, occipital ring not excavated **2c**, lateral view. **3a-c**, paratype, exfoliated cranidium (GSC 1314) x4 **3a**, anterior view **3b**, palpebral view with occipital ring exposed **3c**, lateral view. **4a-c**, paratype, pygidium (GSC 1314d) x9 **4a**, dorsal view **4b**, posterior view **4c**, lateral view. **5a-f**, complete enrolled individual (CM 5417) Upper Ordovician Black River Group, Pelton's Quarry near Ottawa, Canada **5a**, anterior view x5 **5b**, palpebral view x5 **5c**, enlargement of 5b showing muscle scars on glabella x8 **5d**, dorsal view of thorax x5 **5e**, dorsal view of pygidium x5 **5f**, lateral view x5.

Plate 4

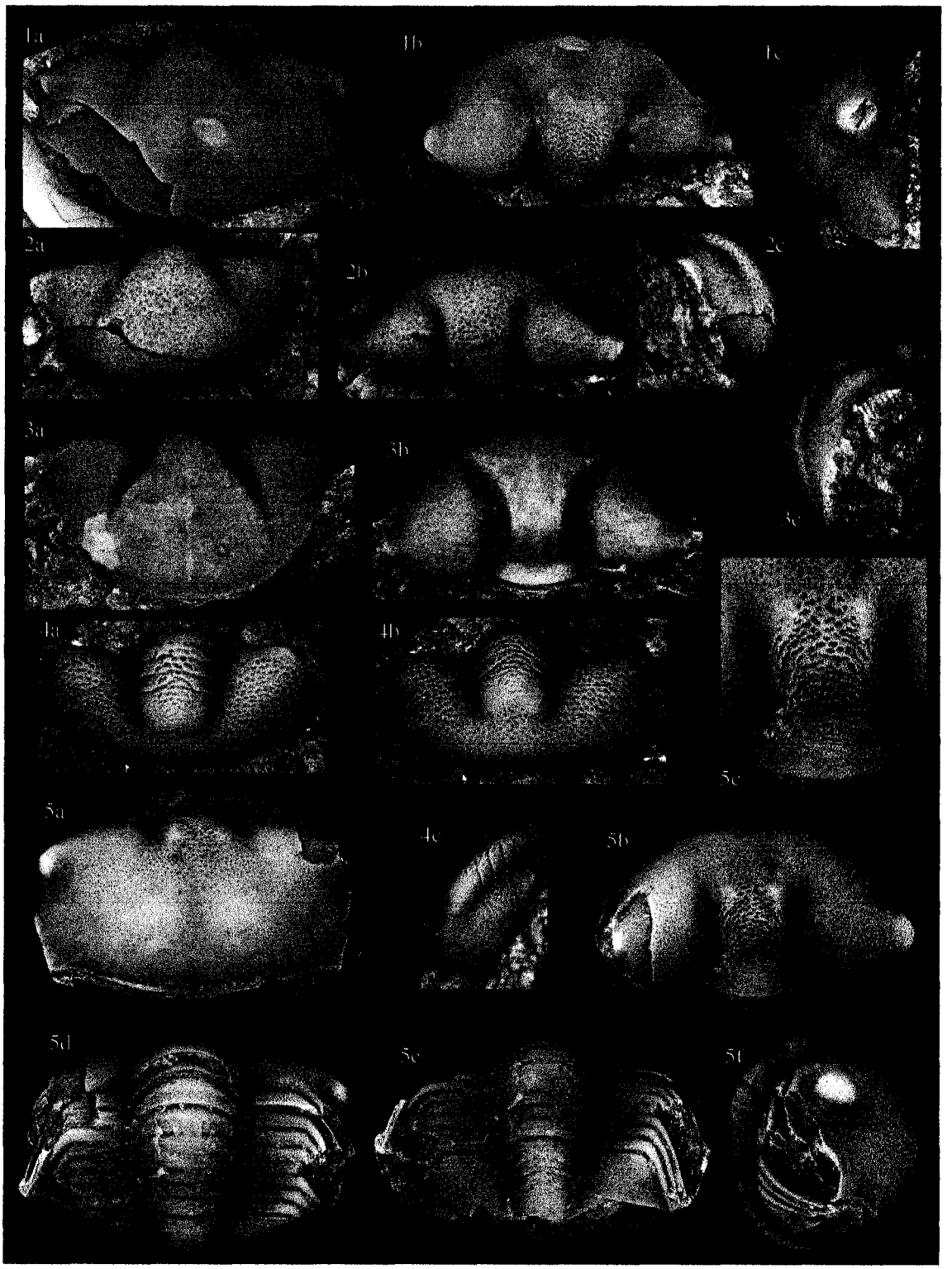


PLATE 5

Figs 1-3 *Thaleops angusticollis* (Billings, 1859) Upper Ordovician Glens Falls Formation, Manny Corners, New York. **1a-b,** partially exfoliated cranidium (NYSM 15242) x5 **1a**, anterior view **1b**, posterior view showing posterior margin of fixed cheeks **2a-b**, exfoliated cranidium (NYSM 15243) x8 **2a**, anterior view **2b**, posterior view showing posterior portion of fixed cheeks and occipital ring **3a-c**, pygidium (NYSM 15244) x8 **3a**, posterior view **3b**, lateral view **3c**, dorsal view.

Fig 4 *Thaleops clavifrons* (Billings, 1859) Middle Ordovician Mingan Formation, Mingan Islands, Quebec. **4a-c**, holotype, partial weathered cranidium (GSC 1323) x1.5 **4a**, lateral view **4b**, palpebral view **4c**, anterior view.

Figs 5-6 *Thaleops conifrons* (Billings, 1859) Mingan Islands, Quebec. **5a-d**, lectotype, partial exfoliated cranidium (GSC 1322) Upper Ordovician Black River Group x2 **5a**, palpebral view **5b**, oblique view 5c, anterior view **5d**, lateral view. **6a-e**, cranidium with exoskeleton (YPM 119468) Middle Ordovician Mingan Formation x3 **6a**, anterior view **6b**, palpebral view **6c**, posterior view showing posterior portion of fixed cheeks **6d**, oblique view **6e**, lateral view.

Plate 5

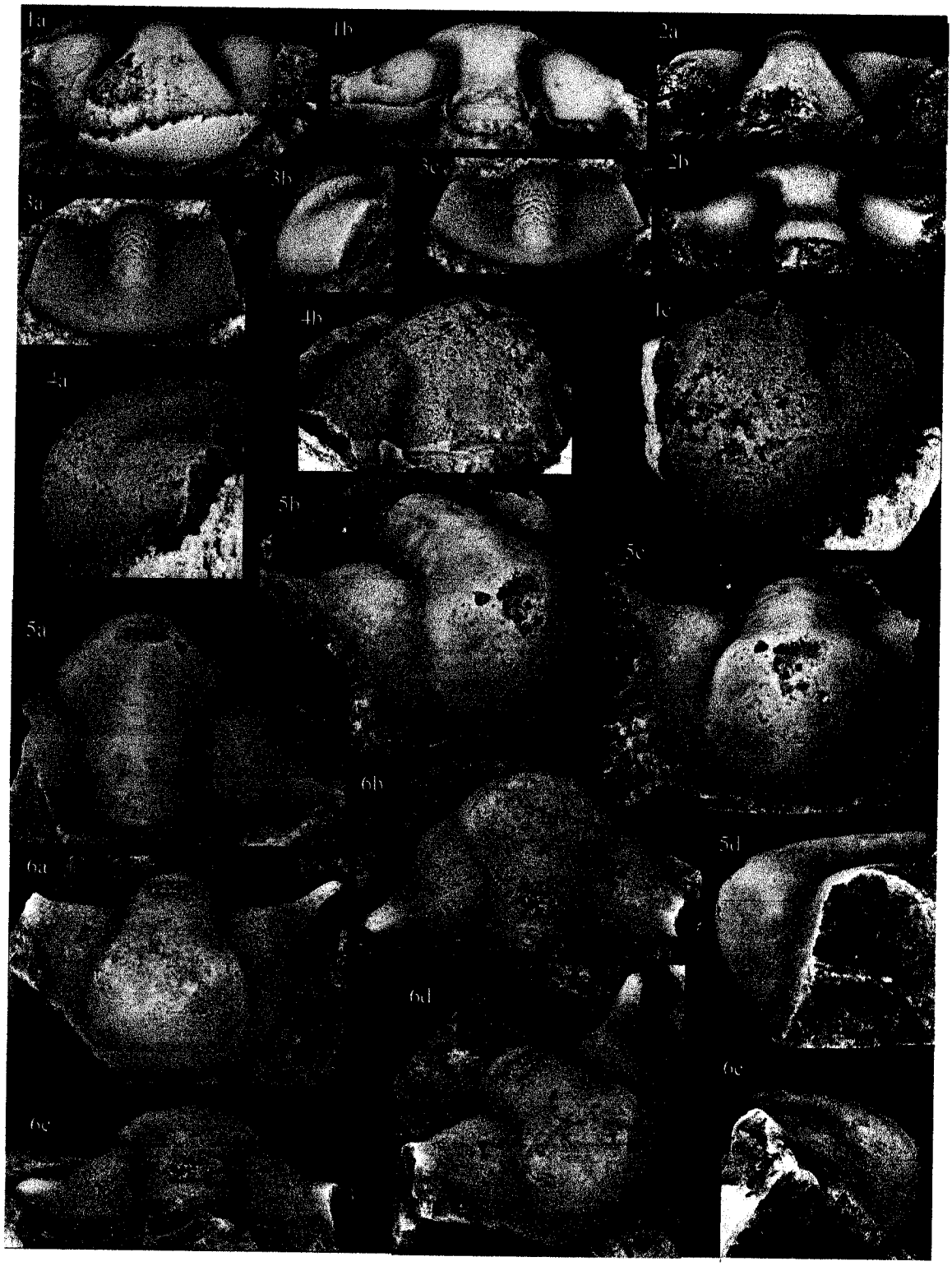


PLATE 6

Figs 1-2 *Thaleops conifrons* (Billings, 1859) Middle Ordovician Mingan Formation, Mingan Islands, Quebec. **1a-d**, partially exfoliated cranidium (YPM 119466) x3 **1a**, anterior view **1b**, lateral view **1c**, palpebral view **1d**, oblique view . **2a-b**, partially exfoliated pygidium with exposed doublure (YPM 119465) x3 **2a**, dorsal view **2b**, lateral view.

Fig 3 *Thaleops vindex* (Billings, 1865) Middle Ordovician Mingan Formation, Mingan Islands, Quebec. **3a-e**, holotype, cephalon (GSC 1088) x3 **3a**, lateral view **3b**, anterior view **3c**, oblique view **3d**, palpebral view **3e**, anterior/ventral view showing rostral plate.

Plate 6

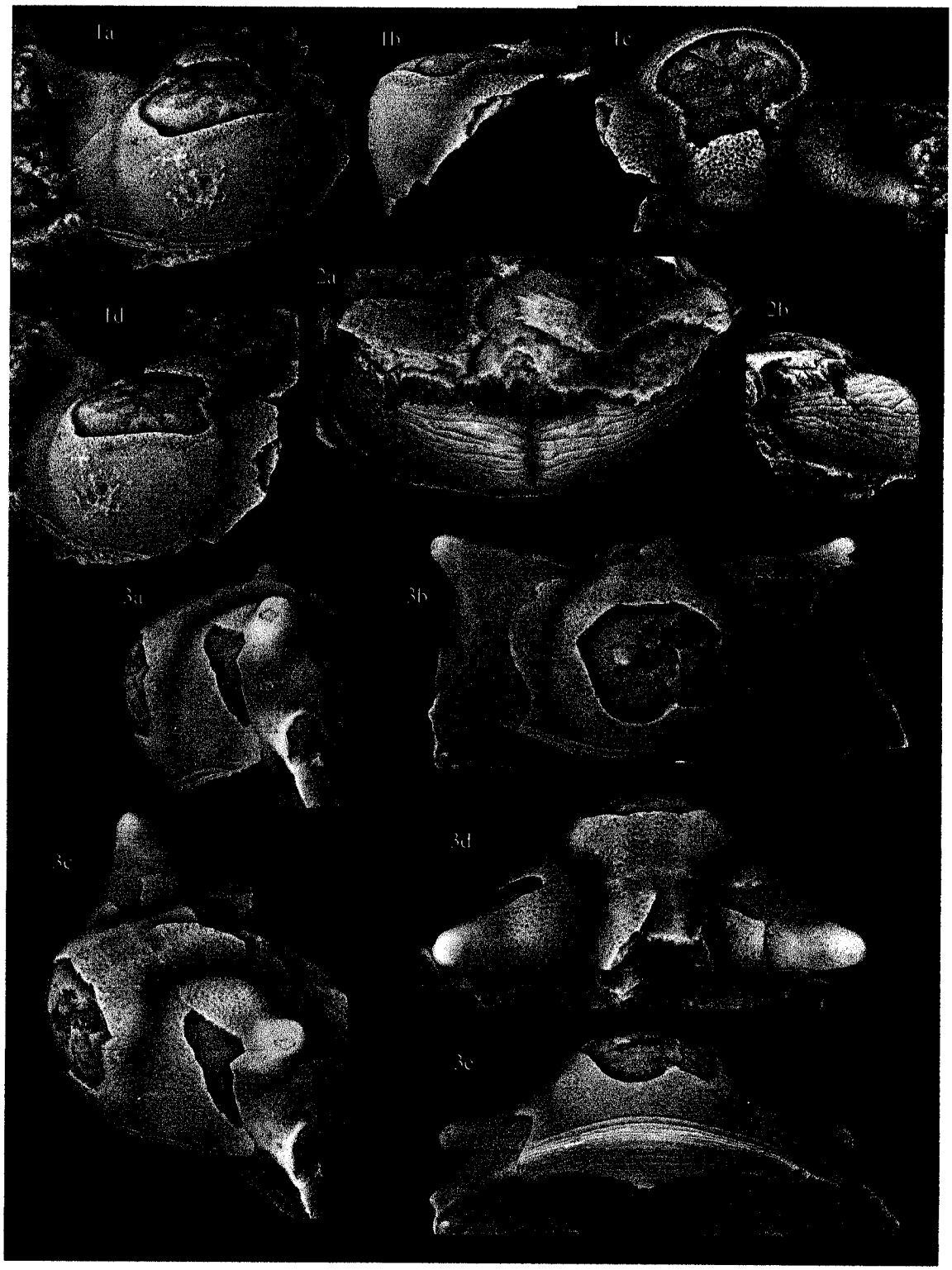


PLATE 7

Figs 1-4 *Thaleops conradi* (Billings, 1859) **1a-d**, holotype, complete enrolled specimen (GSC 1320a) Upper Ordovician Leray Formation near Hull, Quebec x4 **1a**, anterior view **1b**, dorsal view **1c**, palpebral view **1d**, posterior view. **2a-d**, complete enrolled individual (ROM 18691) Upper Ordovician Black River Formation near Hull, Quebec x3 **2a**, anterior view **2b**, lateral view **2c**, palpebral view **2d**, oblique view **3a-c**, complete specimen (CM 5413) Upper Ordovician Black River Group, Mechanicsville, Ontario x3 **3a**, dorsal view **3b**, lateral view **3c**, anterior view **4a-b**, paratype, pygidium (GSC 1320) Upper Ordovician Leray Formation near Hull, Quebec x3 **4a**, dorsal view **4b**, lateral view.

Plate 7

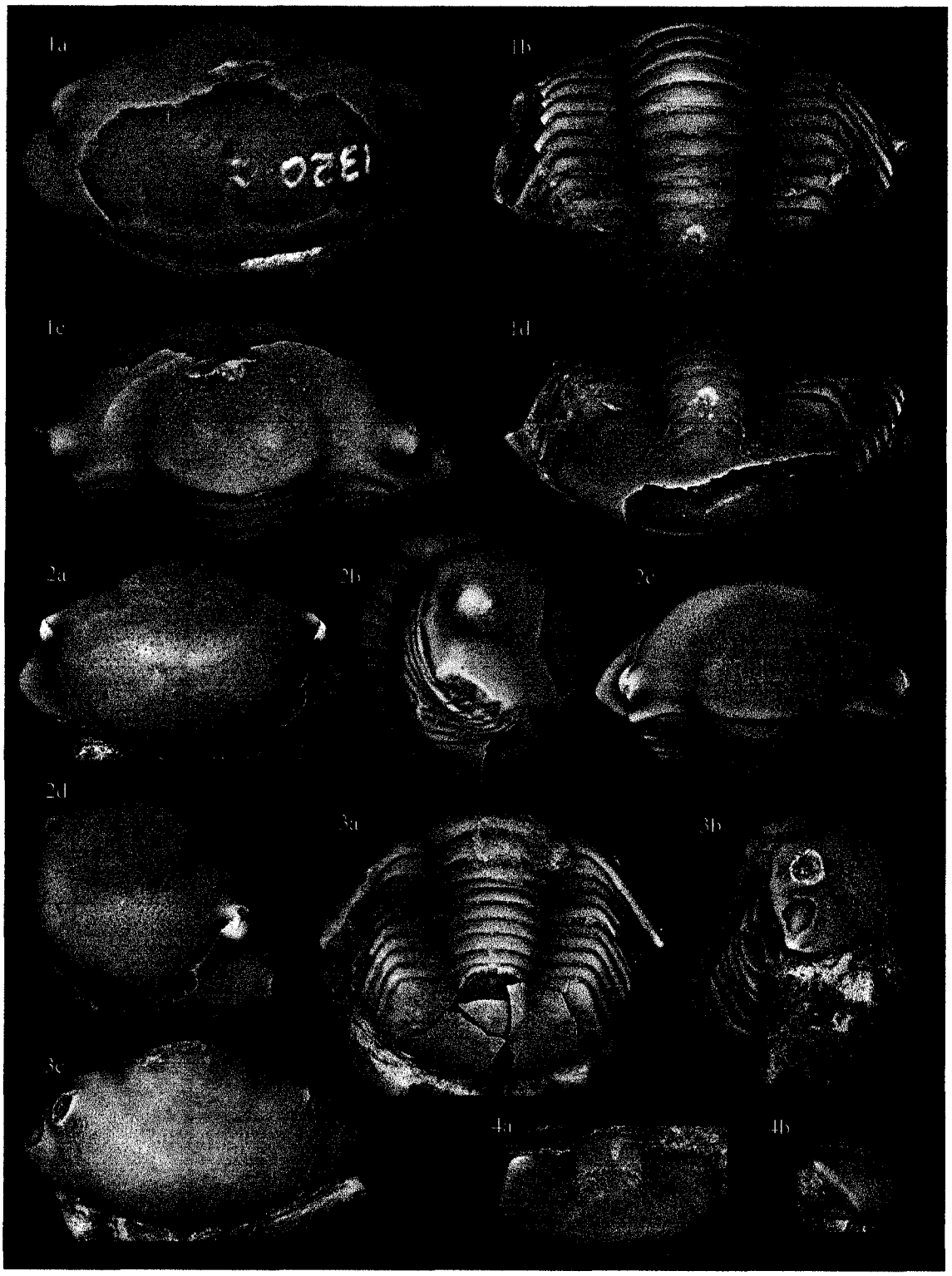


PLATE 8

Fig 1 *Thaleops punctata* (Raymond, 1905) Middle to Upper Ordovician Chazy Formation, Crown Point, New York. **1a-c**, holotype, complete crushed specimen (CM 1278) x4 **1a**, dorsal view **1b**, posterior view **1c**, anterior view.

Figs 2-4 *Thaleops latiaxiata* (Raymond & Narraway, 1908) Upper Ordovician Black River Group, near Ottawa, Ontario. **2a-e**, lectotype, cranidium (ROM 18754) **2a**, anterior view; anterior rim not visible in this view due to strong convexity x2 **2b**, palpebral view x2 **2c**, oblique view x2 **2d**, enlargement of glabella showing ornament and muscle scars x4 **2e**, lateral view x2. **3a-b**, paralectotpye, articulated partial thorax and pygidium (ROM 18754) x2 **3a**, dorsal view **3b**, lateral view **4a-b**, paralectotype, pygidium (ROM 18754) x2 **4a**, lateral view **4b**, posterior view.

Fig 5 *Thaleops fieldi* (Raymond, 1925) Upper Ordovician Holston Limestone, Catawba Valley, Virginia. **5a-d**, lectotype, cranidium (MCZ 101145) **5a**, palpebral view x4 **5b**, anterior view x4 **5c**, enlargement of cuticle to show ornament x8 **5d**, lateral view x4.

Plate 8

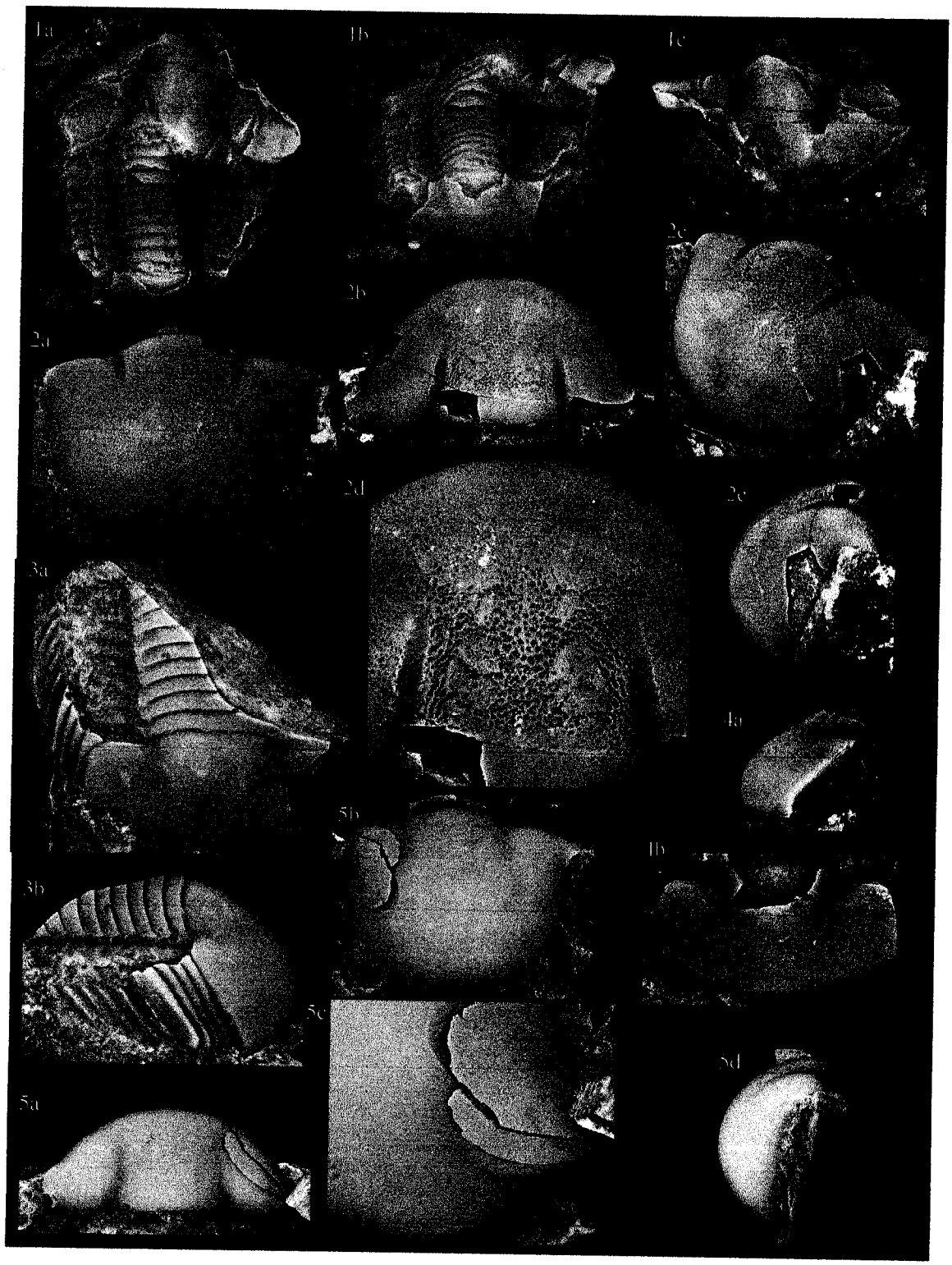


PLATE 9

Figs 1-2 *Thaleops fieldi* (Raymond, 1925) Upper Ordovician Holston Limestone, Catawba Valley, Virginia. **1a-c**, paralectotype, exfoliated cranidium (MCZ 101143) x2 **1a**, anterior view **1b**, lateral view **1c**, palpebral view. **2a-b**, paralectotype, exfoliated pygidium (MCZ 101144) x 4 **2a**, dorsal view **2b**, lateral view.

Figs 3-8 *Thaleops viator* (Raymond, 1925) Upper Ordovician Lourdes Limestone, Long Point, Port Au Port Peninsula, Newfoundland. **3**, paralectotype, cast of dorsoventrally compressed complete specimen (YPM 26995) x1.5 dorsal view **4**, paralectotype, cast of dorsoventrally compressed complete exoskeleton (YPM 26996) x1.5 dorsal view **5**, paralectotype, cast of dorsoventrally compressed articulated thorax and pygidium (YPM 13033) x1.5 dorsal view **6**, lectotype, dorsoventrally compressed exoskeleton (YPM 13032) x1.5 dorsal view of cast. **7a-d**, cranidium (GSC 38692) x1.5 **7a**, palpebral view **7b**, anterior view **7c**, lateral view **7d**, oblique view **8**, pygidium (GSC 38689) x3 ventral view of pygidial doublure.

Plate 9

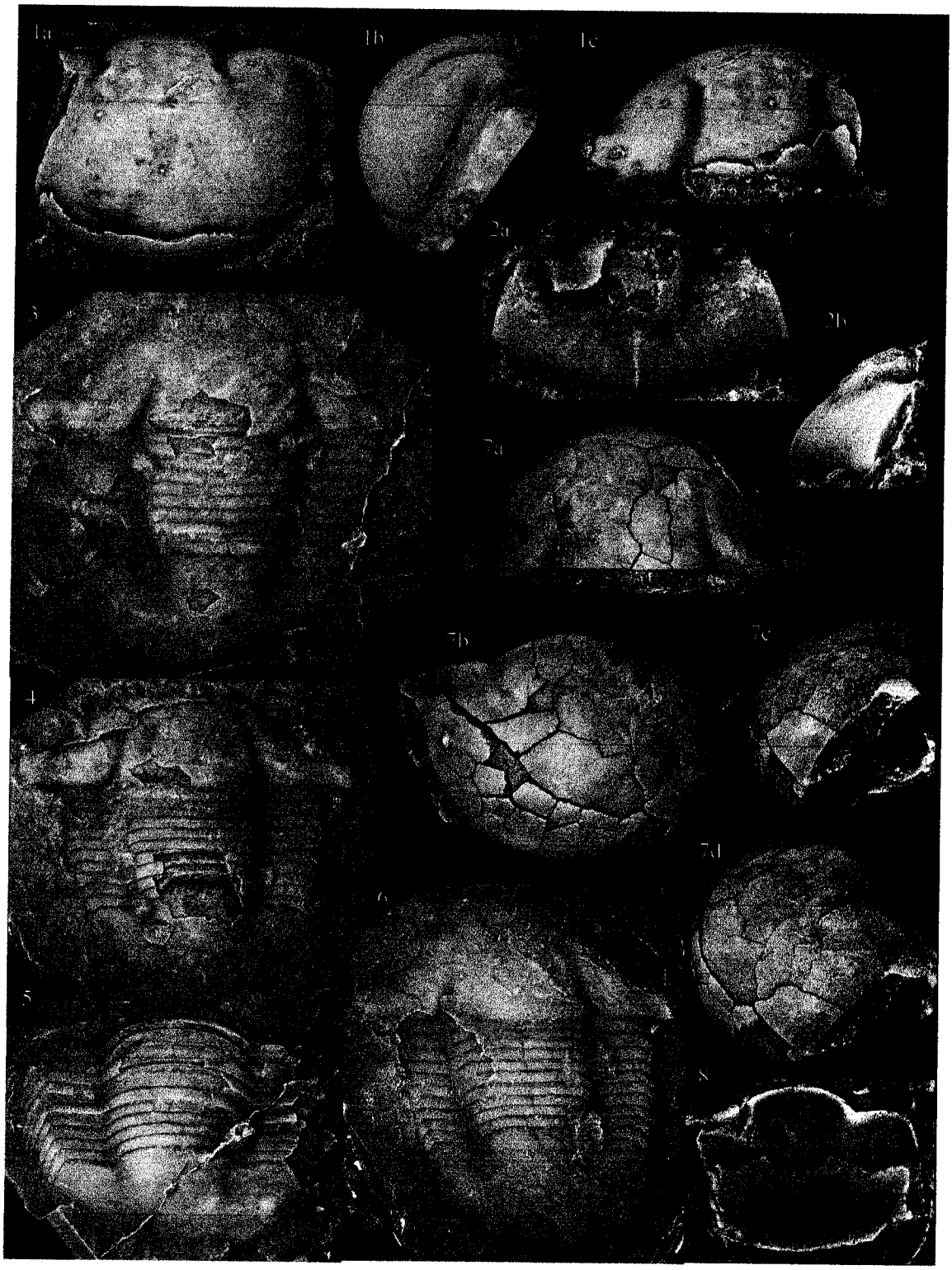


PLATE 10

Fig 1 *Thaleops viator* (Raymond, 1925) Upper Ordovician Lourdes Limestone, Long Point, Port Au Port Peninsula, Newfoundland. **1a-d**, complete exoskeleton (GSC 38687) x2 **1a**, palpebral view **1b**, lateral view **1c**, posterior view **1d**, anterior view.

Figs 2-4 *Thaleops depressicapitata* (Bradley, 1930) Upper Ordovician Kimmswick Formation **2a-d**, holotype, exfoliated cranidium (UC 28895) Glen Park, Missouri x2 **2a**, anterior view **2b**, palpebral view **2c**, lateral view **2d**, posterior view with oblique illumination to maximize appearance of muscle scars **3a-c**, paratype, exfoliated cranidium (UC 28898) near Batchtown, Illinois x2.5 **3a**, anterior view **3b**, lateral view **3c**, palpebral view **4a-b**, exfoliated pygidium (UC 20701) near Batchtown, Illinois x2 **4a**, lateral view **4b**, posterior view.

Plate 10

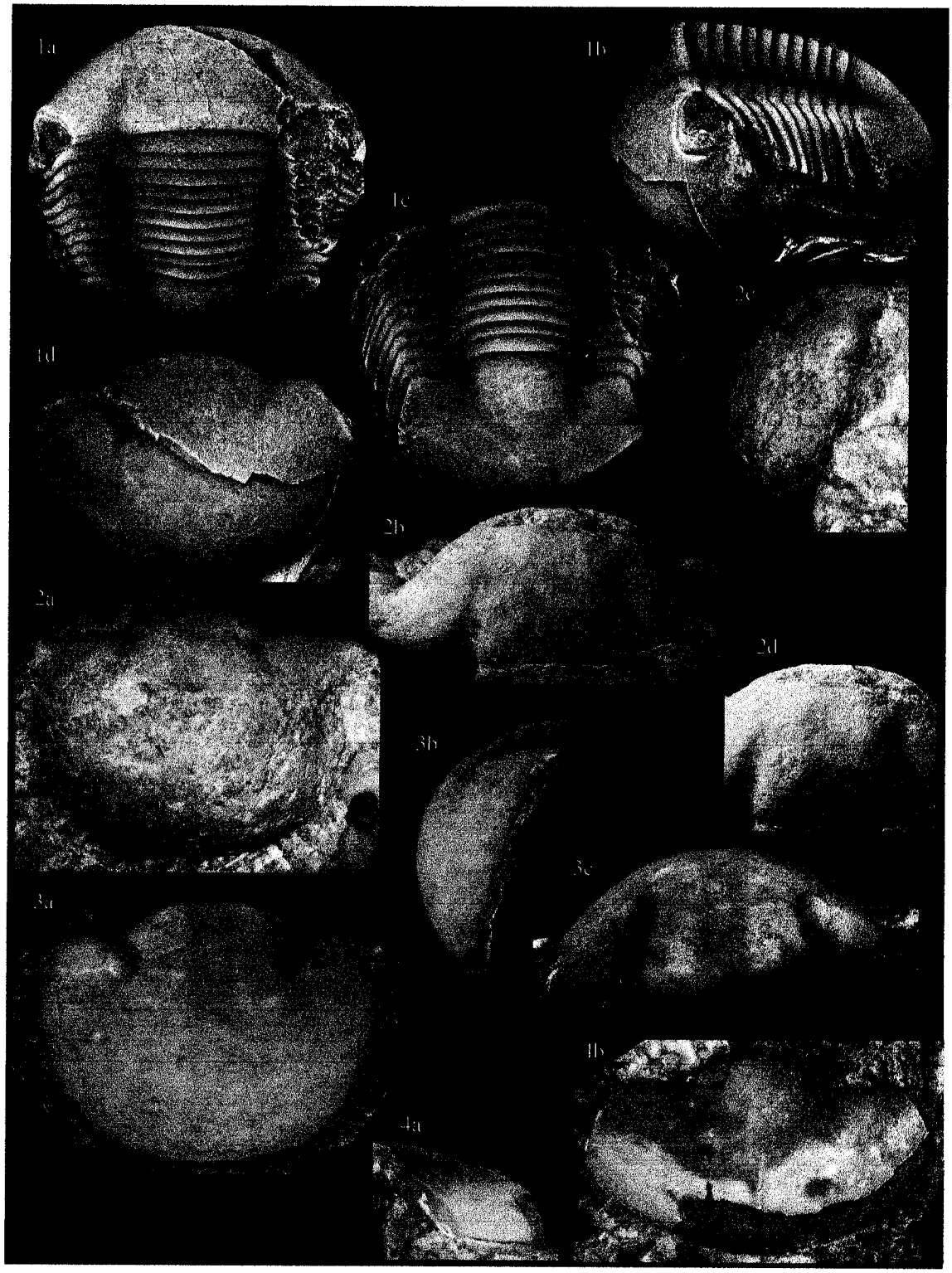


PLATE 11

Figs 1-6 *Thaleops depressicapitata* (Bradley, 1930) **1**, cast of cranidium (OU 11714) Upper Ordovician Kimmswick Formation, Troutman Quarry, Pevely, Missouri, dorsal view of internal mold showing muscle scars, x3. **2**, partial cranidium (OU 11715) Upper Ordovician Kimmswick Formation, Holnam Quarry near Clarksville, Missouri, ventral view showing attachment sites for muscles, x4. **3a-c**, exfoliated pygidium (UC 20701) Upper Ordovician Kimmswick Formation, near Batchtown, Illinois x2.5 **3a**, lateral view **3b**, dorsal view **3c**, posterior view **4a-b**, exfoliated pygidium with doublure exposed (OU 11716) Upper Ordovician Kimmswick Formation, Holnam Quarry near Clarksville, Missouri **4a**, dorsal view x5 **4b**, enlargement of 4a showing relict segmentation on ventral side of pygidial axis and second pair of projections on anterior margin of doublure between larger pair of anterior projections. **5a-b**, exfoliated pygidium with doublure exposed (OU 11717) Upper Ordovician Viola Springs Formation, HWY99 at 48m, Oklahoma **5a**, dorsal view x4 **5b**, enlargement of 5a showing detail of anterior margin of doublure x8. **6a-b**, pygidium (OU 11718) Upper Ordovician Viola Springs Formation, HWY99 at 46.5m, Oklahoma **6a**, ventral view of cuticle on pygidium x5 **6b**, enlargement of axial region of ventral cuticle showing relict segmentation x10.

Plate 11

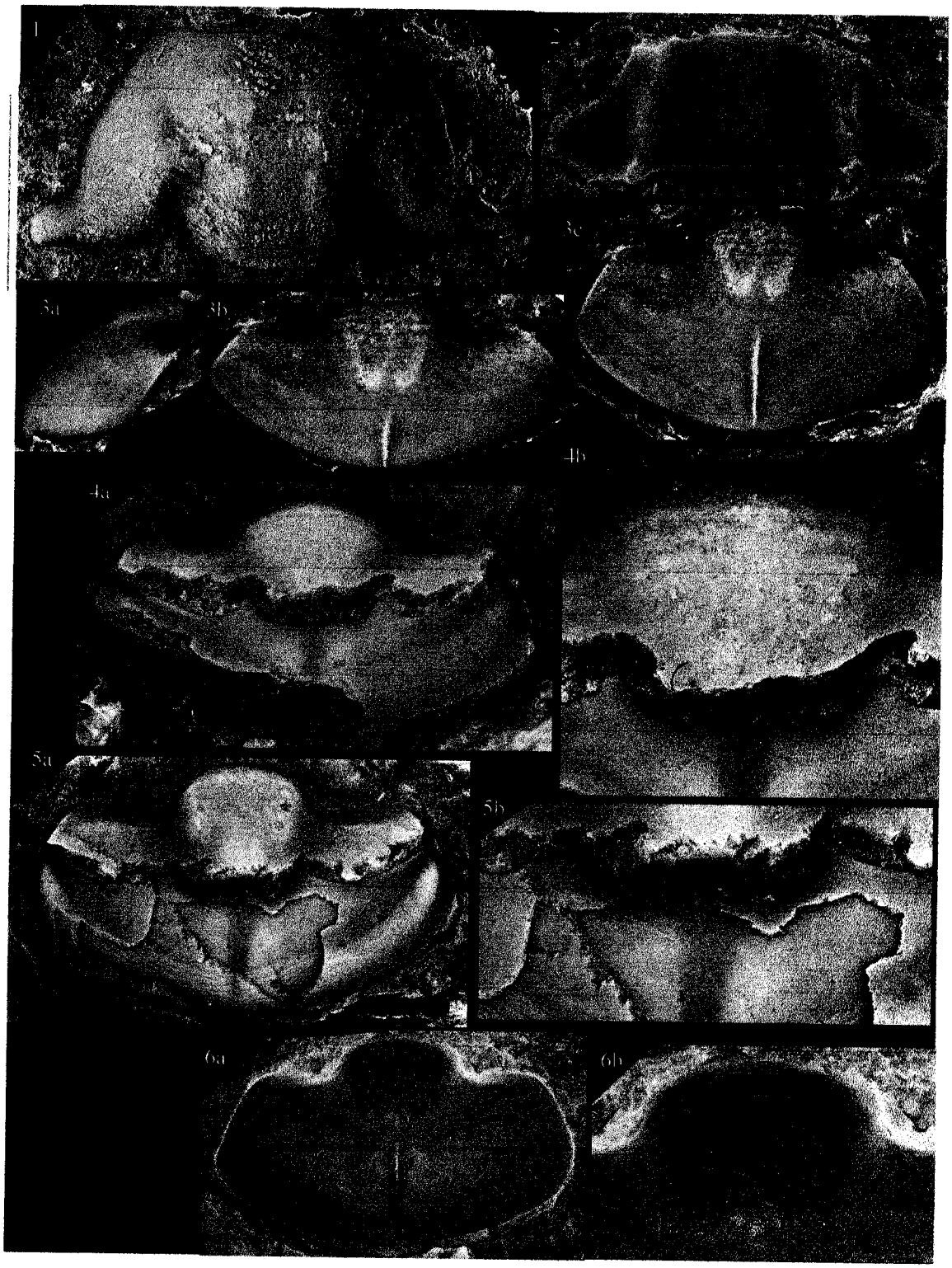


PLATE 12

Thaleops depressicapitata (Bradley, 1930) Upper Ordovician Viola Springs Formation, Oklahoma. **1a-c**, exfoliated cranidium (OU 11719) HWY99 at 48m x10 **1a**, anterior view **1b**, lateral view **1c**, palpebral view. **2a-c**, partially exfoliated cranidium (OU 11711720) HWY99 at 48m x6 **2a**, anterior view **2b**, palpebral view **2c**, lateral view. **3a-c**, pygidium (OU 11721) HWY99 at 48m x10 **3a**, dorsal view **3b**, posterior view 3c, lateral view. **4a-d**, cranidium (OU 11722) HWY99 at 46m **4a**, anterior view x6 **4b**, palpebral view x6 **4c**, oblique view x6 **4d**, enlargement showing detail of ornament over glabella x8. **5a-b**, partially exfoliated pygidium (OU 11723) HWY99 float **5a**, enlargement showing detail of ornament on pygidium x3 **5b**, x2 showing whole pygidium. **6**, internal mold of rostral plate (OU 11724) HWY99 at 48m x3 ventral view.

Plate 12

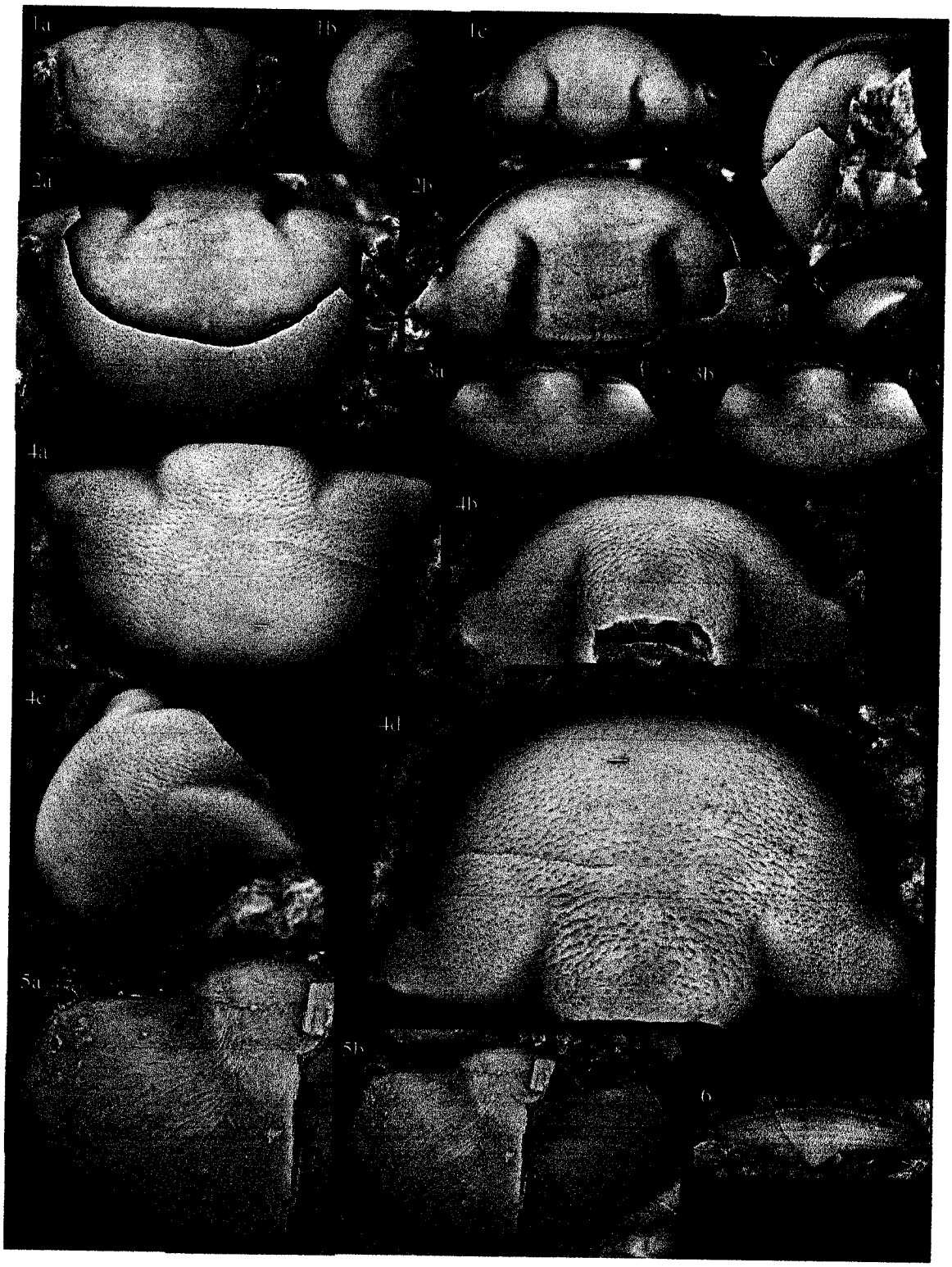


PLATE 13

Figs 1-2 *Thaleops depressicapitata* (Bradley, 1930) Upper Ordovician Viola Springs Formation, Oklahoma. **1a-b**, pygidium (OU 11725) HWY99 at 49.5m **1a**, dorsal view x3 **1b**, enlargement of ornament x5 **2a-c**, librigena (OU 11740) HWY99 at 49.5m x4 **2a**, lateral view **2b**, palpebral view **2c**, anterior view.

Figs 3-4 *Thaleops borealis* Teichert, 1937 Upper Ordovician Kap Jackson Formation, Cape Webster and Cape Calhoun, Washington Land, North Greenland. **3a-c**, cranidium, cast of holotype (GM 3310) x3 **3a**, anterior view **3b**, palpebral view **3c**, lateral view **4**, cast of paratype (GM 3309) x10 anterior view.

Figs 5-6 *Thaleops baffinlandica* (Roy, 1941) Upper Ordovician Silliman's Fossil Mount, Frobisher Bay, southern Baffin Island, Nunavut. **5a-b**, partial cranidium, paralectotype (P 28703) x3 **5a**, palpebral view **5b**, anterior view **6a-c**, pygidium, lectotype (P 28703) **6a**, posterior view x3 **6b**, lateral view x3 **6c**, enlargement of ornament on pygidial axis x6.

Plate 13

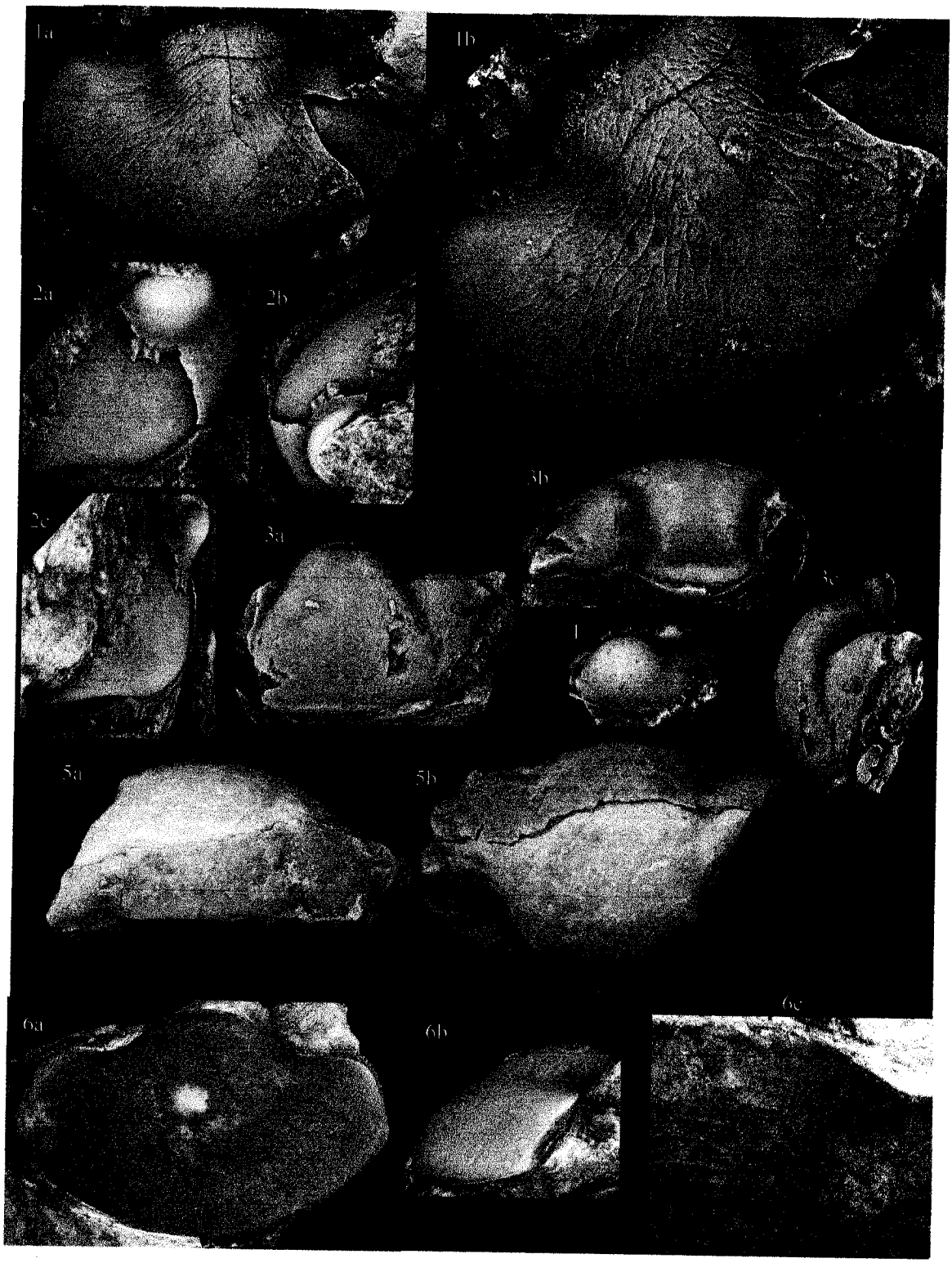


PLATE 14

Figs 1-4 *Thaleops nunavutica* (Roy, 1941) Upper Ordovician Silliman's Fossil Mount, Frobisher Bay, southern Baffin Island, Nunavut. **1a-e**, partially exfoliated cranidium, holotype (P28704) **1a**, anterior view x3 **1b**, enlargement of 1c showing ornament on posterior of glabella x6 **1c**, palpebral view x3 **1d**, lateral view **1e**, oblique view **2a-d**, partially exfoliated cranidium (GSC113629) x5 **2a**, anterior view **2b**, lateral view **2c**, oblique view **2d**, palpebral view **3a-c**, pygidium (GSC113674) x8 **3a**, lateral view **3b**, dorsal view **3c**, posterior view **4a-d**, cranidium (GSC113683) x5 **4a**, anterior view **4b**, oblique view **4c**, lateral view **4d**, palpebral view.

Plate 14

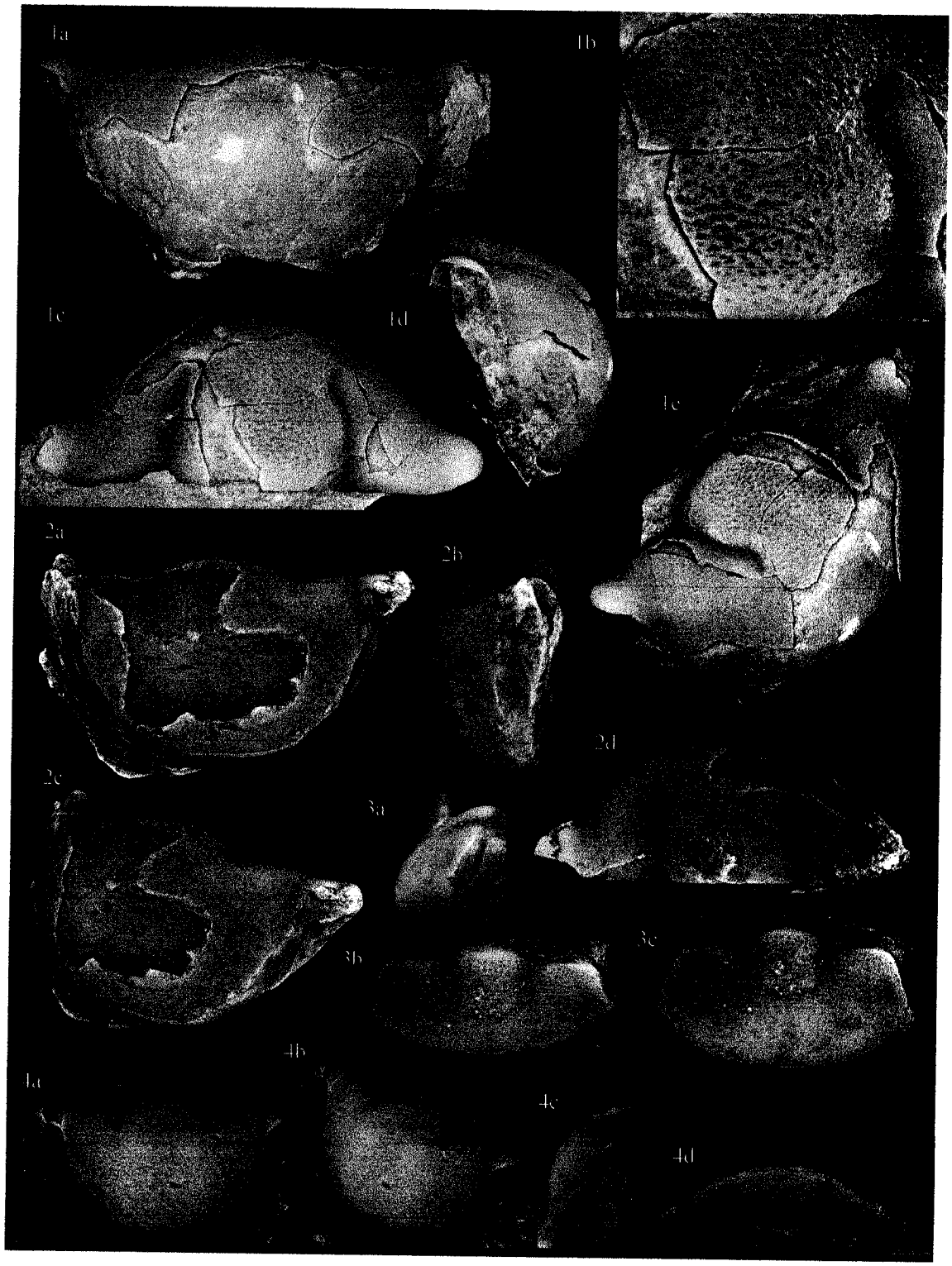


PLATE 15

Figs 1-3 *Thaleops laurentiana,* new species, Upper Ordovician Trenton Group, New York. **1a-f**, complete exoskeleton, holotype (NYSM 15235) Trenton Falls **1a**, dorsal view x3 **1b**, posterior view x3 **1c**, palpebral view x3 **1d**, anterior view x3 **1e**, lateral view x3 **1f**, enlargement of posterior of pygidium showing ornament x5 **2a-d**, complete exoskeleton, paratype (NYSM15236) Trenton Falls **2a**, palpebral view x3 **2b**, anterior view x3 **2c**, lateral view x3 **2d**, posterior view of pygidium showing shape of anterior margin of pygidial doublure x6. **3a-d**, complete exoskeleton (NYSM15237) Buck's Quarry, Herkimer Co. x4 **3a**, palpebral view **3b**, lateral view **3c**, anterior view **3d**, lateral/oblique view.

Plate 15

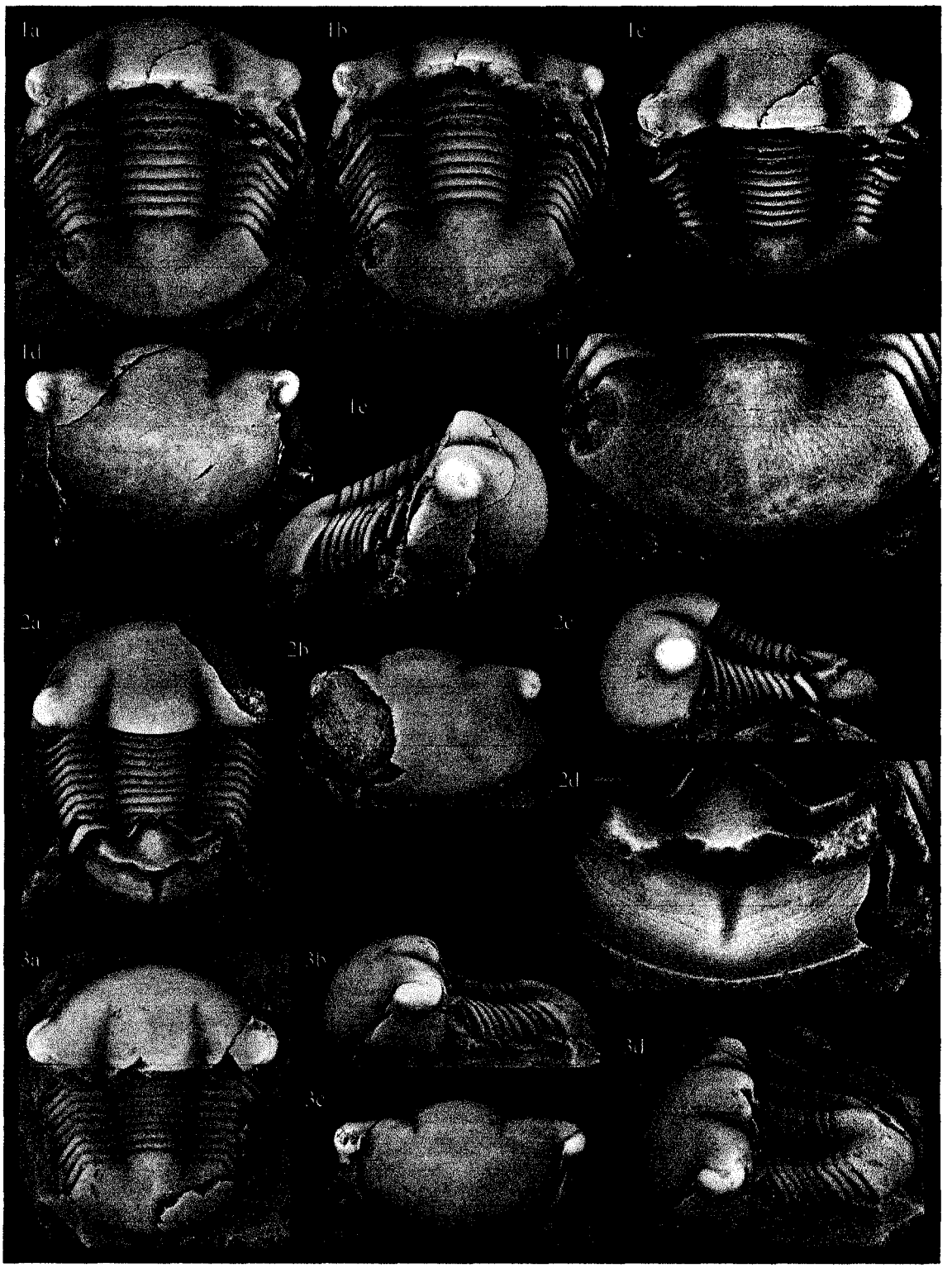


PLATE 16

Figs 1-4 *Thaleops laurentiana,* new species. **1a-d**, complete exoskeleton, paratype (NYSM15238) Upper Ordovician Trenton Group, Watertown, New York x2. **1a**, dorsal view **1b**, anterior view **1c**, palpebral view **1d**, lateral view **2a-c**, complete exoskeleton (YPM182903) Upper Ordovician Trenton Group, Trenton Falls, New York x1.5 **2a**, dorsal view **2b**, anterior view **2c**, palpebral view. **3a-b**, complete exoskeleton with partially exfoliated cranidium (YPM 37282) Upper Ordovician Trenton Group, Trenton Falls, New York x2 **3a**, oblique view showing sharp angle at intersection of lateral and posterior margin of librigena **3b**, palpebral view **4a-c**, complete exoskeleton with dorsal surface of cranidium weathered (YPM 19190) Middle to Upper Ordovician Chazy Group, Chazy, New York **4a**, dorsal view x3 **4b**, enlargement of posterior view of pygidium showing sculpture and muscle scars on axis x6 **4c**, oblique view showing intersection of lateral and posterior margins of librigena x3.

Plate 16

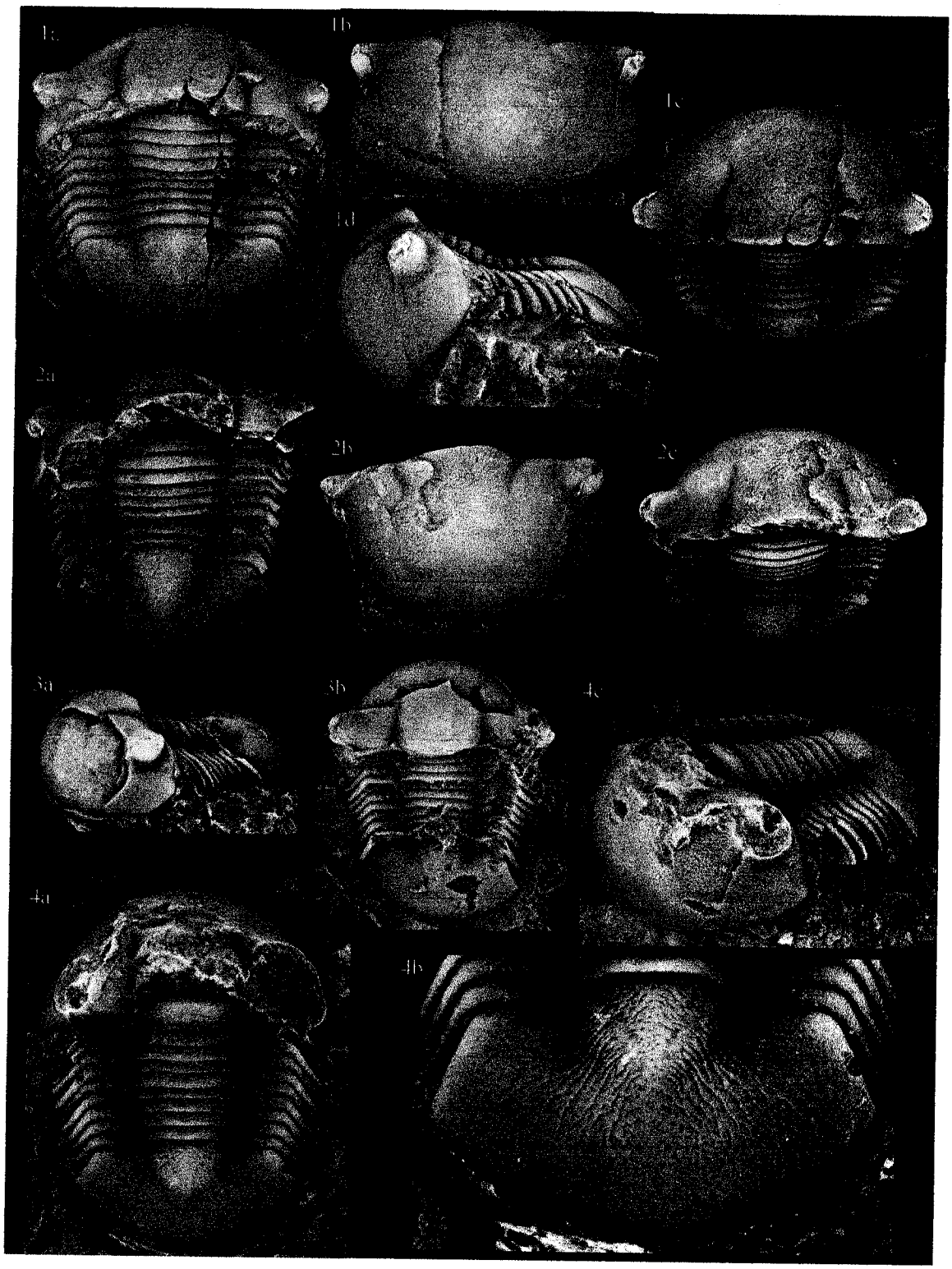


PLATE 17

Figs 1-8 *Thaleops anusacerbissima*, new species, Upper Ordovician Viola Springs Formation, Oklahoma. **1**, meraspid cranidium (OU 11726) HWY99 at 32m, dorsal view x15 **2a-b**, meraspid pygidium (OU 11727) HWY99 at 34m x15 **2a**, dorsal view **2b**, oblique view **3a-b**, meraspid pygidium (OU 11728) HWY99 at 34m x15 **3a**, dorsal view **3b**, oblique view **4a-d**, exfoliated cranidium, holotype (OU 11729) HWY99 at 32m x5 **4a**, anterior view **4b**, oblique view **4c**, lateral view **4d**, palpebral view **5a-d**, partially exfoliated cranidium, paratype (OU 11730) HWY99 at 32m **5a**, palpebral view x4 **5b**, anterior view x4 **5c**, lateral view x4 **5d**, enlargement of palpebral region of fixigena showing sculpture x8 **6a-e**, exfoliated cranidium, paratype (OU 11731) HWY99 at 32m x3 **6a**, anterior view **6b**, oblique view **6c**, palpebral view **6d**, posterior view showing posterior portions of fixigenae **6e**, lateral view **7**, exfoliated rostral plate, paratype (OU 11732) HWY99 at 32m x6 **8**, partially exfoliated pygidium with doublure exposed, paratype (OU11733) HWY99 at 32m posterior view showing anterior margin of pygidial doublure x5.

Plate 17

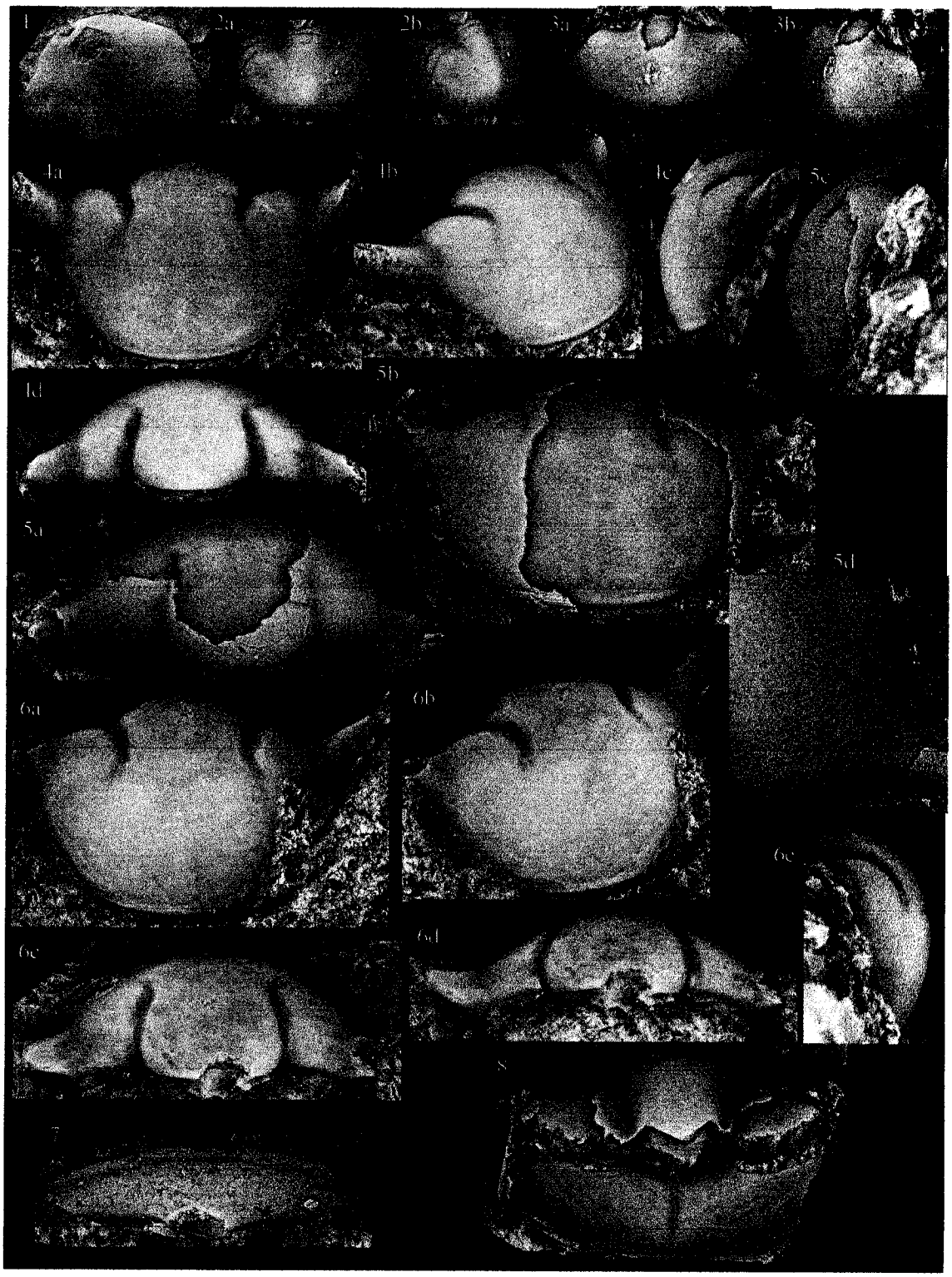


PLATE 18

Figs 1-6 *Thaleops anusacerbissima*, new species, Upper Ordovician Viola Springs Formation, Oklahoma. **1a-c**, partially exfoliated pygidium, paratype (OU 11734) HWY99 at 32m **1a**, posterior view x3 **1b**, lateral view x3 **1c**, oblique view showing sculpture and sharp posterolateral corner x5 **2a-c**, exfoliated librigena with broken proximal margin, paratype (OU 11735) HWY99 at 32m x4 **2a**, dorsal view **2b**, lateral view **2c**, posterior view **3a-c**, exfoliated librigena with broken proximal margin, paratype (OU11736) HWY99 at 32m x4 **3a**, dorsal view **3b**, lateral view **3c**, posterior view **4a-b**, partially exfoliated pygidium, paratype (OU 11737) HWY99 at 32m x3 **4a**, posterior view **4b**, lateral view **5**, exfoliated pygidium in dorsal view showing sharp posterolateral corners, paratype (OU 11738) HWY99 at 31.5m x4 **6a-b**, ventral view of pygidium showing muscle scars on axis, paratype (OU 11739) HWY99 at 32m **6a**, x5 **6b**, enlargement of axis x10.

Plate 18

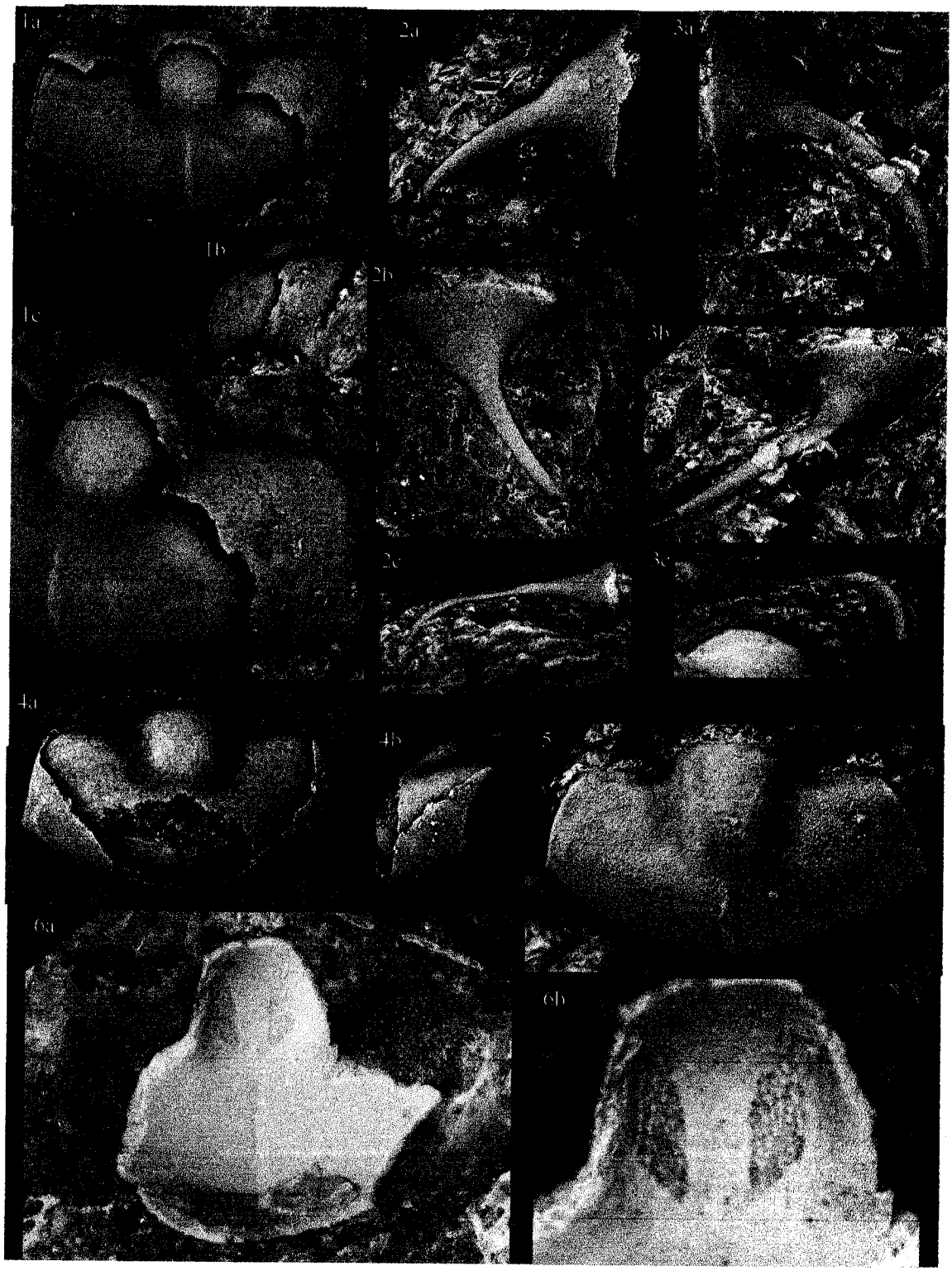


PLATE 19

Figs 1-3 *Thaleops mobydick*i, new species, Upper Ordovician Bromide Formation, Criner Hills, Oklahoma. **1a-e**, cephalon, holotype (OU 11741) Geological Enterprises Quarry x2 **1a**, palpebral view **1b**, anterior view **1c**, posterior view **1d**, lateral view **1e**, oblique view **2a-d**, cranidium, paratype (OU 11742) Rock Crossing x2 **2a**, palpebral view **2b**, oblique view **2c**, anterior view **2d**, lateral view **3a-b**, slightly crused complete exoskeleton (OU 11743) Rock Crossing x2 **3a**, lateral view **3b**, dorsal view.

Plate 19

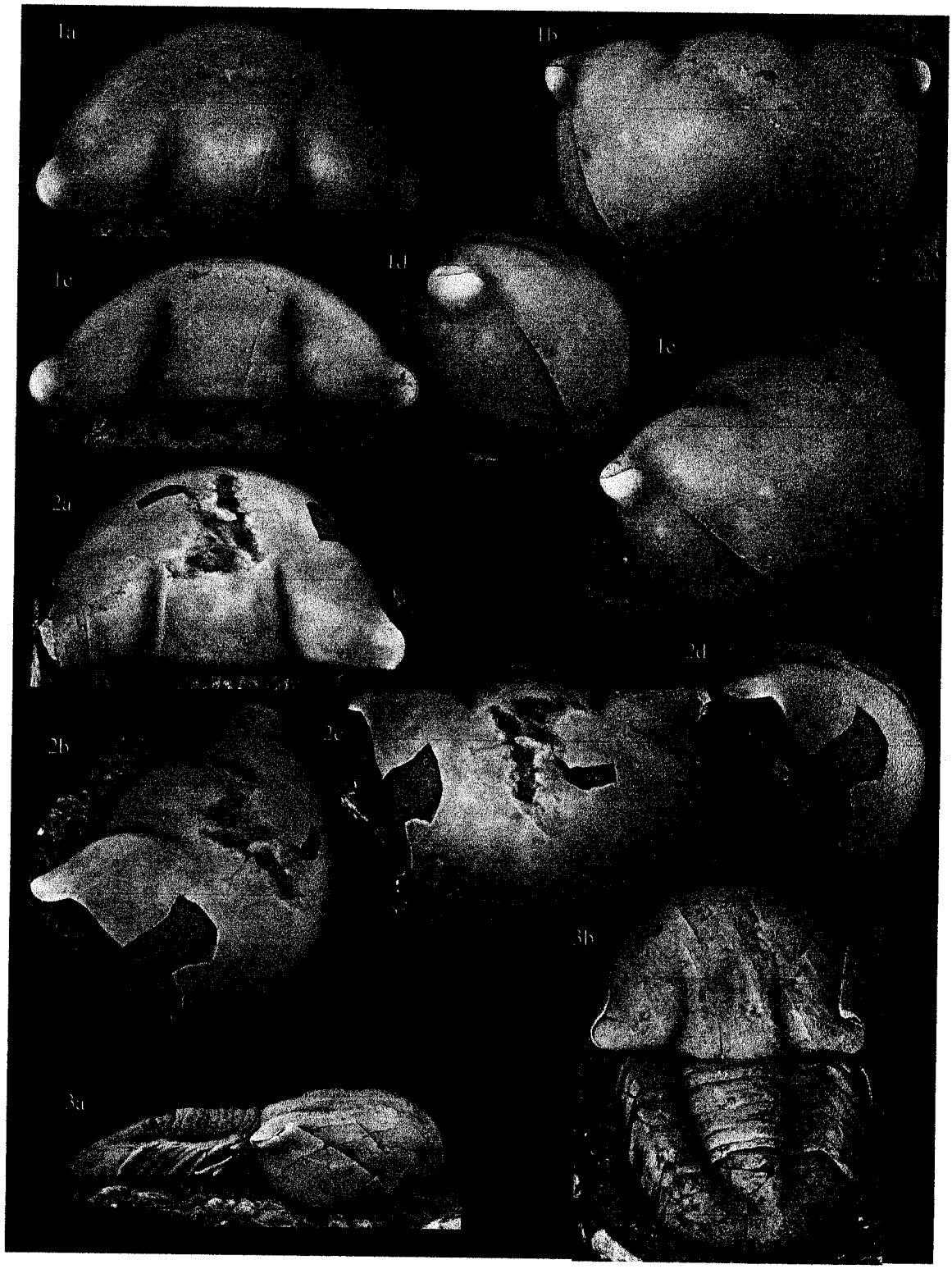


PLATE 20

Figs 1-6 *Thaleops mobydicki*, new species, Upper Ordovician Bromide Formation, Criner Hills, Oklahoma. **1a-e**, partial cephalon, paratype (OU 11744) Rock Crossing x2 **1a**, palpebral view **1b**, lateral view **1c**, anterior view **1d**, posterior view showing posterior portions of fixigenae **1e**, oblique view **2a-b**, articulated thorax and pygidium, paratype (OU 11745) Geological Enterprises Quarry x2.5 **2a**, posterior view **2b**, lateral view **3**, crushed complete exoskeleton in dorsal view, paratype (OU 11746) Geological Enterprises Quarry x4 **4a-c**, pygidium, paratype (OU 11747) Geological Enterprises Quarry x4 **4a**, dorsal view **4b**, posterior view **4c**, lateral view **5**, pygidium with doublure exposed, paratype (OU 11748) Geological Enterprises Quarry, x6 **6a-b**, posterior thorax and articulated pygidium, paratype (OU 11749) Geological Enterprises Quarry x4 **6a**, posterior view **6b**, lateral view.

Plate 20

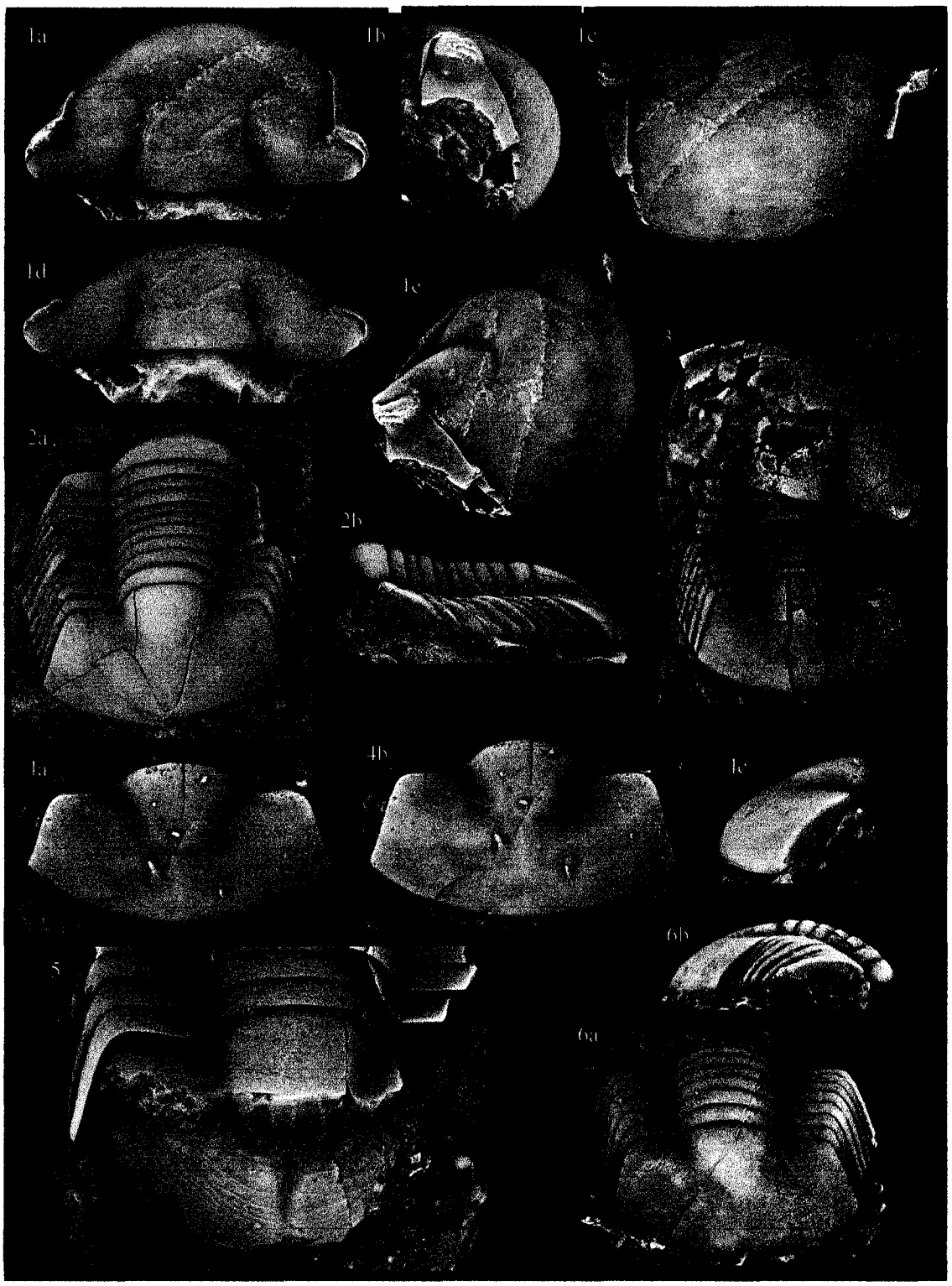


PLATE 21

Figs 1-6 *Thaleops jaanussoni*, new species, Upper Ordovician Bromide Formation, Oklahoma. **1a-f**, complete exoskeleton, holotype (OU 11750) Geological Enterprises Quarry, Criner Hills x6 **1a**, anterior view **1b**, palpebral view **1c**, dorsal view **1d**, posterior view **1e**, oblique view **1f**, lateral view **2a-d**, cranidium, paratype (OU 11751) Geological Enterprises Quarry, Criner Hills x5 **2a**, dorsal view **2b**, oblique view **2c**, lateral view **2d**, palpebral view **3a-e**, cranidium, paratype (OU 11752) I-35N at 47-48m, x4 **3a**, anterior view **3b**, oblique view **3c**, palpebral view **3d**, posterior view showing fixigenae posterior to palpebral lobes **3e**, lateral view **4**, pygidium with doublure exposed, paratype (OU 11753) I-35N at 47-48m, x4 **5a-c**, pygidium, paratype (OU 11754) I-35N at 47-48m, x4 **5a**, dorsal view **5b**, posterior view **5c**, lateral view **6a-c**, fixigena, paratype (OU 11755) I-35N at 47-48m, x5 **6a**, lateral view **6b**, anterior view **6c**, dorsal view.

Plate 21

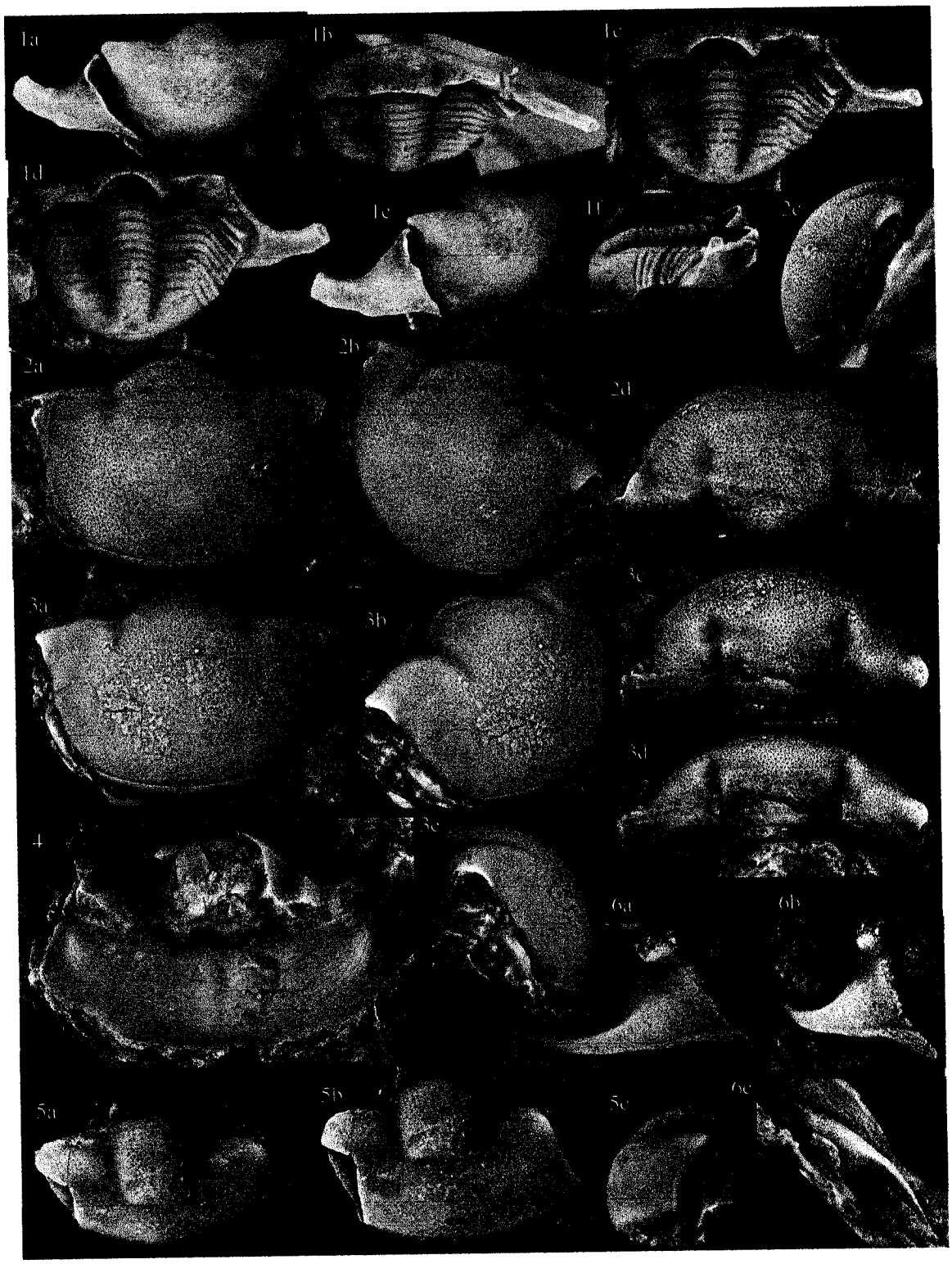


PLATE 22

Figs 1-5 *Thaleops* sp. 1, Upper Ordovician Bromide Formation, Oklahoma. **1a-d**, cranidium (OU 11756) Geological Enterprises Quarry, Criner Hills, x5 **1a**, anterior view **1b**, palpebral view **1c**, oblique view **1d**, lateral view **2a-e**, slightly weathered cranidium, (OU 11757) I-35N at 47-48m x5 **2a**, anterior view **2b**, palpebral view **2c**, posterior view **2d**, oblique view **2e**, lateral view **3a-d**, cranidium (OU 11758) Geological Enterprises Quarry, Criner Hills x4 **3a**, anterior view **3b**, palpebral view **3c**, lateral view **3d**, oblique view **4a-d**, exfoliated cranidium (OU 11759) I-35N at 6.85m x3 **4a**, anterior view **4b**, palpebral view **4c**, lateral view **4d**, oblique view **5**, enlargement of glabella in 2b showing detail of ornament x8.

Fig. 6 *Thaleops* sp. 2, Upper Ordovician Bromide Formation, I-35N at 36.6m, Oklahoma. **6a-d**, exfoliated cranidium, x4 (OU 11763) **6a**, palpebral view **6b**, oblique view **6c**, lateral view **6d**, anterior view.

Plate 22

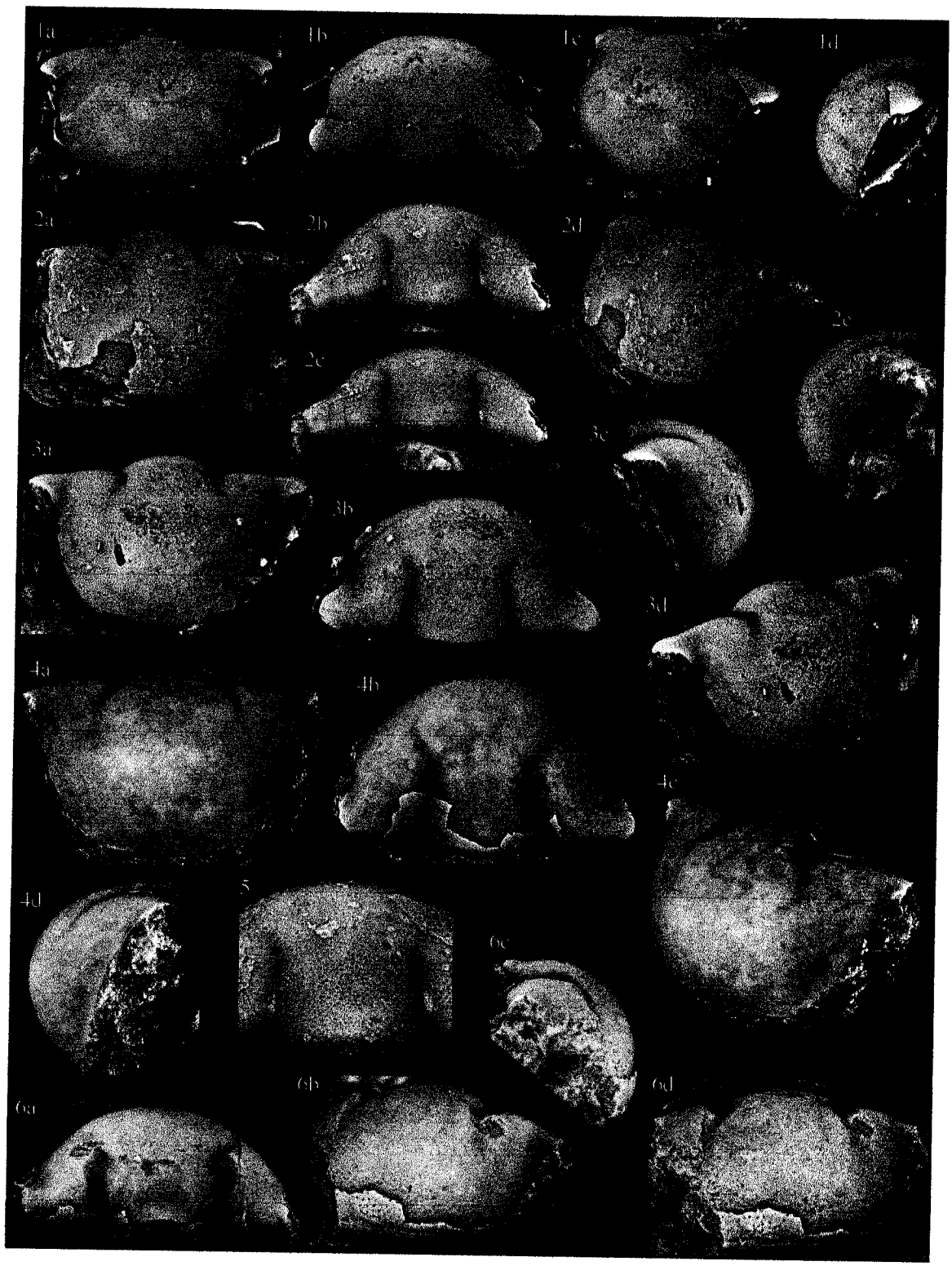
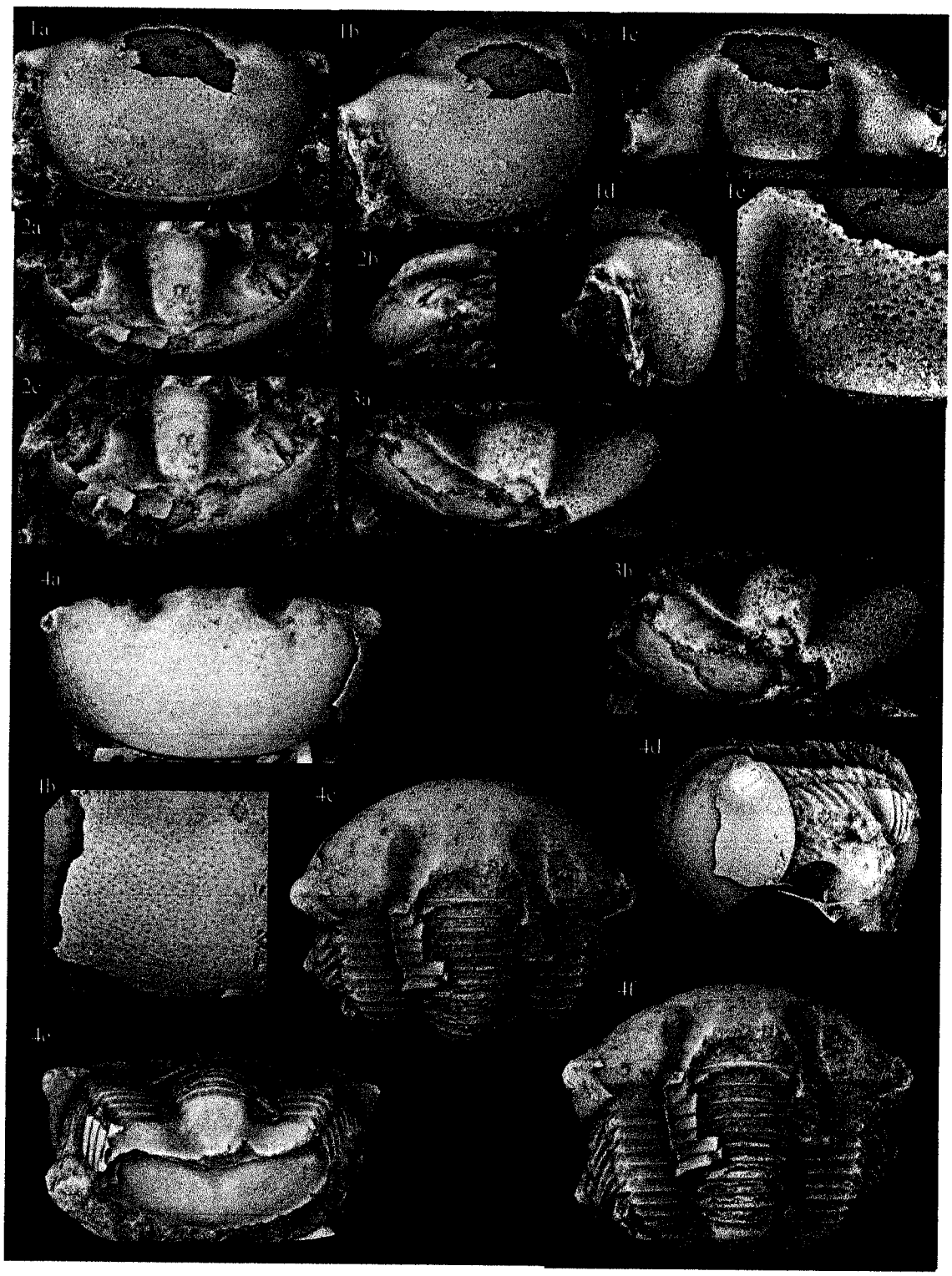


PLATE 23

Figs 1-3 *Thaleops* sp. 2, Upper Ordovician Bromide Formation, I-35N at 36.6m, Oklahoma. **1a-e**, cranidium, x4 (OU 11762) **1a**, anterior view **1b**, oblique view **1c**, palpebral view **1d**, lateral view **1e**, enlargement of ornament over glabella x8 **2a-c**, partial, exfoliated pygidium, x6 (OU 11764) **2a**, dorsal view **2b**, lateral view **2c**, posterior view **3a-b**, partially exfoliated pygidium showing relict segmentation on internal mold over pleural region, x5 (OU 11765) **3a**, dorsal view **3b**, posterior view.

Fig 4 *Thaleops* sp. 3 (NYSM 12502) Upper Ordovician Crown Point Formation, Vacour Island, New York. **4a**, anterior view x2.5 **4b**, enlargement of sculpture on free cheek x8 **4c**, palpebral view x2.5 **4d**, lateral view x2.5 **4e**, posterior view x2.5 **4f**, dorsal view x2.5.

Plate 23



CHAPTER 4:

ISOTELINE TRILOBITES OF THE VIOLA GROUP (ORDOVICIAN: OKLAHOMA): PHYLOGENETIC RELATIONSHIPS AND STRATIGRAPHIC OCCURRENCE

ABSTRACT

The Upper Ordovician (Mohawkian-Cincinnatian) Viola Group of south-central Oklahoma was deposited on a shallow carbonate ramp in the area of the Southern Oklahoma aulacogen. Five lithofacies superimposed in a shallowing-upward succession record filling of the aulacogen. Eleven species of isoteline trilobites occur in the Viola Group and are used to correlate sections across lithostratigraphic boundaries. Six species of *Isotelus* (*I. kimmswickensis* Bradley, 1930, *I. violaensis* new species, *I. bradleyi* new species, *I. skapaneidos* new species, *Isotelus* cf. *I. walcotti* Walcott, 1918, *Isotelus* cf. *I. iowensis* Owen, 1852), *Ectenaspis* (*E. abothros* new species), two species of *Stegnopsis* (*S. wellingensis* new species, *S. byzanteneidos* new species) and two species of *Anataphrus* (*A. megalophrys* new species, *A. kermiti* new species) are described. The phylogenetic context of the four genera occurring in the Viola Group are discussed in terms of their relationships with closely related genera.

INTRODUCTION

Isotelines are large and conspicuous trilobites that are familiar to most paleontologists. Indeed, *Isotelus* Dekay, 1824 includes the largest known species of trilobite (Rudkin and others, 2003). Isotelines can be found in most exposures of the Viola Group in south-central Oklahoma, where they occur in a variety of lithofacies. They are also widely distributed across North America (e.g., northwestern Canada, Chatterton and Ludvigsen, 1976; Nevada, Ross and Shaw, 1972; Missouri, Bradley, 1930; Manitoba, Westrop and Ludvigsen, 1983; Ontario, Wilson, 1947; Virginia, Tripp and Evitt, 1986; Newfoundland, Whittington, 1965), so they will likely be useful in regional and inter-regional correlation. However, their biostratigraphic utility is undermined by the absence of modern systematic treatment of most genera and species. For example, *I. gigas* Dekay, 1824, the type species of *Isotelus*, and *I. walcotti* Walcott, 1918 were revised recently by Rudkin and Tripp (1989), but most other members of the genus remain poorly known. Here, I document eleven isoteline species from the Viola Group and evaluate species described by Bradley (1930) from the coeval Kimmswick Limestone of Missouri and Illinois. Viola Group isotelines include six species of *Isotelus*, two species of *Anataphrus* Whittington, in Miller and others, 1954, two species of *Stegnopsis* Whittington, 1965, and a single species of *Ectenaspis* Raymond, 1920; seven of these species are new. A phylogenetic analysis of isoteline trilobites is long overdue but is beyond the scope of this monograph. However, some of the taxonomic problems that need to be addressed are discussed at various points in the text.

GEOLOGIC SETTING

The Viola Group consists of Upper Ordovician (Mohawkian – Cincinnatian) carbonates that were deposited in shallow epeiric seas covering the southern mid-continent. The Southern Oklahoma aulacogen (Hoffman and others, 1974) was a narrow, fault-bounded basin running from the Texas panhandle southeast through Oklahoma to eastern Texas that formed as a result of Early Cambrian rifting (Fig. 1). Periodic reactivation of faults along the hingeline of the aulacogen provided accommodation space that allowed deposition and preservation of a thick sequence of early Paleozoic sediment (Ham and others, 1964). These units are now well-exposed in the Arbuckle Mountains of south-central Oklahoma.

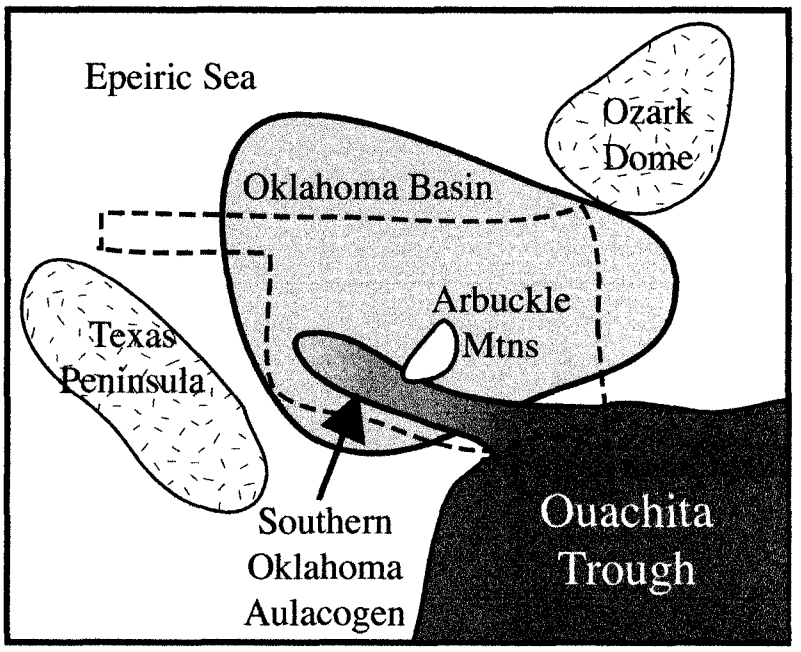
Two formations make up the Viola Group, the Viola Springs Formation and the overlying Welling Formation (Fig. 2). The base of the Viola Group in south-central Oklahoma is disconformable with the underlying Bromide Formation and is marked by finely-laminated mudstone indicating onset of deep-water deposition following rapid subsidence within the aulacogen. A general shallowing-upward trend is recorded at all sections, with areas nearer the platform shallowing more abruptly than those well within the margins of the basin. Overall section thickness, as well as thickness of deep-water deposits, increases toward the center of the basin.

LITHOFACIES ANALYSIS

Four lithofacies characterize the Viola Springs Formation in south-central Oklahoma and represent deposition at different depths along an environmental gradient from the shallow carbonate platform to a deep ramp environment within the

Figure 1. Generalized paleogeographic map showing the location of the Arbuckle Mountains in relation to the margins of the Southern Oklahoma aulacogen.

Figure 1


Epeiric Sea
Ozark
Dome
Oklahoma Basin
Arbuckle
Mtns
Texas
Peninsula
Southern
Oklahoma
Aulacogen
Ouachita
Trough

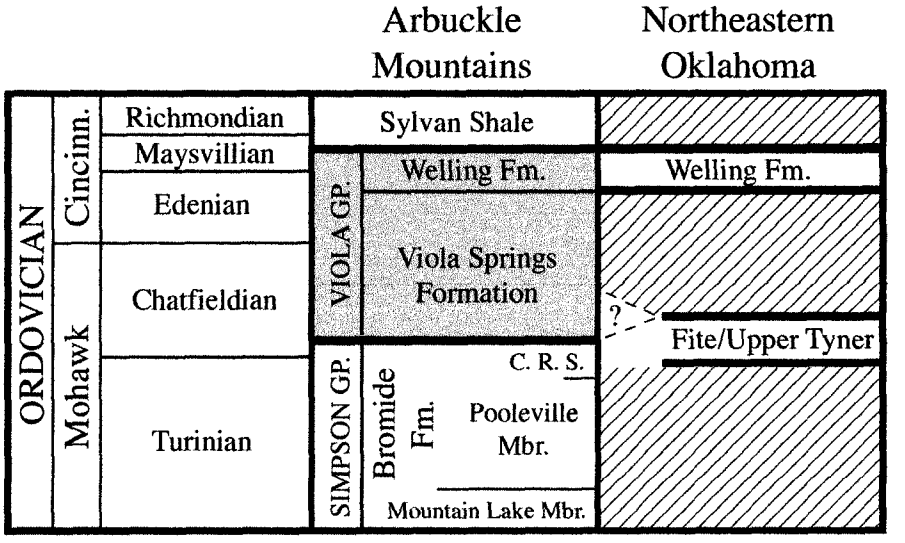
Southern Oklahoma aulacogen. These facies are superimposed through the Viola Springs Formation indicating shallowing as the aulacogen slowly filled with sediment. A fifth lithofacies defines the Welling Formation and represents relatively shallow deposition across the environmental gradient. Following is a brief outline of Viola Group facies; a more detailed treatment can be found in Amati and Westrop (submitted manuscript).

Carbonate Mudstone Lithofacies

This facies is divided into two subfacies based on sedimentary structures. The laminated carbonate mudstone subfacies consists of millimeter- to centimeter-scale laminae. Darker laminae are made up of slightly coarser-grained (silt grade) material and lighter laminae are nearly pure carbonate mud. Carbonate layers 10-40 cm thick are separated by thin, 0.5-3 cm thick marl partings. Limestone/marl alternations reflect original heterogeneity that has been enhanced by diagenesis (Bathurst, 1987). Nodules, lenses and discontinuous beds of chert are concentrated along marl partings. The fauna is limited to rare cryptolithine trilobites and graptolites, which are abundant at some parting surfaces and are oriented parallel to the hingeline of the aulacogen (Gentile and others, 1984). Absence of bioturbation, high organic content of the sediment (indicated by dark color) and limited benthic fauna suggest deposition occurred in a low-oxygen environment (Allison and others, 1995). Thin laminae, regularity of laminae thickness, low oxygen levels, presence of small scours and small-scale ripples are evidence suggesting that deposition occurred by contour currents (Eriksson and Reczko, 1998).

Figure 2. Late Ordovician stratigraphy for the Arbuckle Mountain region and northeastern Oklahoma. C.R.S. – Corbin Ranch Submember of the Pooleville Member of the Bromide Formation. Correlation of the Fite and Upper Tyner formations is in doubt (see text for more information).

Figure 2


Arbuckle Mountains
Northeastern Oklahoma
ORDOVICIAN
Cincinn.
Mohawk
Richmondian
Maysvillian
Edenian
Chatfieldian
Turinian
Sylvan Shale
VIOLA GP.
Welling Fm.
Viola Springs Formation
SIMPSON GP.
Bromide Fm.
C. R. S.
Pooleville Mbr.
Mountain Lake Mbr.
Welling Fm.
?
Fite/Upper Tyner

The bioturbated carbonate mudstone subfacies consists of centimeter-scale laminae similar to those of the laminated subfacies but slightly thicker on average. Degree of bioturbation increases upward in the section, indicating increased oxygen levels. This is supported by an increase in the abundance of cryptolithine trilobites. Greater thickness of laminae (centimeter-scale) and increased oxygenation suggest that transportation of carbonate mud into the environment was from turbid flows.

Low-diversity Wacke- to Rudstone Lithofacies

Wackestone, completely homogenized by bioturbation, occurs in 20-50 cm thick beds separated by thin marl partings. Thickness of beds and general fining-upward trend suggest deposition by distal turbid flows. *Anataphrus* trilobites are locally abundant in thick (3-10 cm) float- to rudstone layers at the tops of beds. Sclerites are very abundant within these layers and consist almost exclusively of *Anataphrus*. Nearly every preservable body part is present (cranidia, librigenae, thoracic segments, hypostomes, pygidia) and jumbled in random orientation. Storm winnowing is unlikely to have produced these accumulations because the majority of sclerites are not found in the hydrodynamically stable, convex-up position. *Anataphrus* float- to rudstone more probably represents settling of sclerites from suspension. Karim and Westrop (2002) and Speyer and Brett (1985) provided examples of monotaxic trilobite accumulations resulting from rapid burial of biologic aggregations. The *Anataphrus* floatstone differs in that the sclerites are not preserved *in situ*, but behavioral aggregations may explain the presence of so many individuals of a singe species in one place at one time. Cryptolithine fringes occur as storm-

winnowed accumulations at partings between beds.

High-diversity Pack- to Rudstone Lithofacies

This facies consists of centimeter-scale packages of articulate brachiopod and trilobite float- to rudstone separated by pelletal packstone layers of similar thickness. Brachiopod shells and trilobite sclerites oriented mainly in the hydrodynamically stable convex-up position indicate concentration by storm winnowing (Aigner, 1982). Marl layers are much thinner (millimeters to few centimeters) and bioturbation is ubiquitous. Faunal diversity is very high with articulate brachiopods and trilobites the most abundant bioclasts. Ostracodes, gastropods, bivalves, inarticulate brachiopods, receptaculitids, solitary corals, crinoids and cephalopods are all also common.

Bryozoan Grain- to Rudstone Lithofacies

Well-washed, coarse skeletal debris accumulated in 15-40 cm thick packages separated by scour surfaces. Fenestrate, branching and domal bryozoan colonies dominate bioclasts, although articulate brachiopods, crinoids and trilobites are also abundant and diverse. Iron staining at scour surfaces suggest frequent, brief subaerial exposure.

Crinoid Pack- to Rudstone Lithofacies

This facies defines the Welling Formation. Bioclasts are dominated by crinoid columnals with abundant articulate brachiopod shells and trilobite sclerites.

Outside the margins of the aulacogen, bioclasts reach up to 9 cm in diameter. Cross-bedding is common and little to no carbonate mud is preserved. Closer to the margins of the aulacogen, bioclasts become smaller (maximum 4 cm in diameter) and carbonate mud is more common. Within the basin of the aulacogen, bioclasts too small for identification make up a smaller proportion of sediment relative to carbonate mud.

STRATIGRAPHIC DISTRIBUTION OF LITHOFACIES

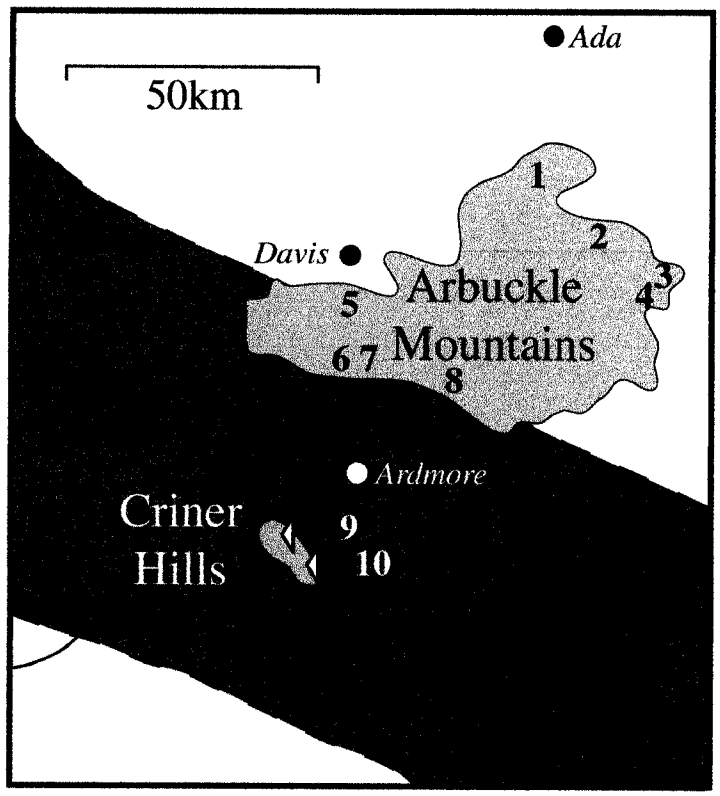
The Viola Group records an overall upward shallowing succession following subsidence within the Southern Oklahoma aulacogen. Basinal sections are thicker than those on the margin and consist exclusively of a succession of deep-water facies (outer ramp environments). All of the facies are represented on the platform, but lithofacies from deeper water are relatively thin (Fig. 3; Appendix).

Basinal Sections (9-10 in Fig. 3; SQ, CN in Appendix)

Viola Group sections deposited in basinal environments average 300 m in total thickness, with the Welling Formation accounting for about 20 m. The entire Viola Springs succession consists of limestone/marl alternations in relatively fine-grained carbonate. The Pooleville Member of the Bromide Formation in the area of the Criner Hills consists of sparsely to highly fossiliferous lime mudstone deposited in a subtidal environment. A shallowing-upward trend culminates in a floatstone rich in articulate brachiopods and receptaculitids at the top of the Pooleville. Contact with the overlying Viola Springs is abrupt and erosional but without significant relief.

Figure 3. Viola Group collecting localities. Dark grey shading indicates inferred outline of Southern Oklahoma aulacogen. 1, Lawrence Quarry (LQ), Holcim (US) Inc. quarry 10 km southwest of Ada, OK. 2, U.S. Highway 99 (99), roadcut, along west side of U.S. Highway 99, 5 km south of Fittstown, OK. 3, Mosely Creek (MC), creek bed 5 km north of Bromide, OK. 4, Bromide Quarry (BQ), abandoned quarry about 0.5 km west of Bromide, OK. 5, Camp Classen (CC), exposure near top of hill, about 7 km south west of Davis, OK near Lake Classen. 6, Interstate 35 (I-35), roadcut along east and west sides of northbound lanes of Interstate 35, 17 km south of Davis, OK. 7, U.S. Highway 77 (77), roadcut along east side of U.S. Highway 77, about 17 km south of Davis, OK. 8, Nebo (Nebo), hillside exposure and stream cut, aobut 2.5 km west of Nebo, OK and about 1.5 km south of section-line road. 9, Burns Quarry (CN), abandoned quarry in northern part of Criner Hills, 5 km south and 2.5 km west of I-35/I-70 interchange, southwest of Ardmore, OK. 10, South Quarry (SQ), abandoned quarry in southern part of Criner Hills, 1.5 km west of I-35 and 9 km south of I-70, southwest of Ardmore, OK.

Figure 3


Ada
50km
1
2
3
Davis
Arbuckle
4
5
Mountains
6 7
8
Ardmore
Criner
Hills
9
10

The lower 17 m of the Viola Springs Formation consists of millimeter-scale laminae of the carbonate mudstone lithofacies. Degree of disturbance of laminae varies from faint interruptions by minimal infauna to small-scale scours, ripples and more disruptive bioturbation. This variation in abundance and type of sedimentary structures reflects changes in bottom oxygenation most likely due to minor fluctuations in relative sea level or severity in storm activity. The interval is covered from 28.5-33 m then again from 34-49.5 m. An overall increase in bioturbation upward through the section records a shallowing-upward trend. Complete burrow homogenization of carbonate mud- to wackestone by about 140 m marks the transition to the low-diversity wacke- to rudstone lithofacies. The high-diversity wacke- to rudstone and bryozoan grain- to rudstone lithofacies are absent in the basin. Exposure is limited at both sections above 192 m. The transition from the Viola Springs to the Welling Formation consists of meter-scale coarsening-upward packages of wackestone to grainstone over about a 3 m interval. This transition zone represents progradation of coarser debris from shallower environments during highstand.

Skeletalized benthic macrofossils, consisting mainly of trilobites and articulate brachiopods, are rare throughout the section. In the lower 60 m, graptolites are the only fossils preserved. Cryptolithine trilobites appear at about 60 m above the base and become more abundant up section as sclerites of the isoteline *Anataphrus* and the remopleuridid *Hypodicranotus* Whittington, 1952 are added. Articulate brachiopods and gastropods occur in low abundance in few horizons high in the section.

Marginal Sections (5-8 in Fig. 3; I-35, 77, Nebo in Appendix)

The Viola Group reaches a total thickness of about 250 m at marginal sections with about 10 m of Welling. As in basinal sections, the high diversity wacke- to rudstone and bryozoan grain- to rudstone lithofacies are absent. Marginal sections shallow upward more quickly than in the basin and preserve a greater abundance of macrofossils. Limestone/marl alternations occur throughout the Viola Springs.

The Pooleville Member of the Bromide Formation underlies the Viola Springs at sections located near the margins of the aulacogen. Moderately large (8 cm diameter) receptaculitids and solitary rugose corals are common just below the contact. A low relief erosional surface marks the contact with the Viola Springs and is topped by a thin (<1 cm) iron- and phosphate-rich layer. Overlying this is a 2 m interval consisting of rippled, ostracod-rich wacke- to packstone assigned to the Viola Springs. At about 2 m, a thin (2 cm) layer of pyrite nodules on a phosphate crust marks a transition to very dark colored, millimeter-scale laminated carbonate mudstone. Limited bioturbation at 30 m signals increased oxygenation and graptolites are more common as accumulations at partings. The low-diversity wacke- to rudstone lithofacies at marginal sections begins where *Chondrites* becomes so abundant as to nearly obscure layers (75 m). Poorly defined, meter-scale shallowing-upward packages consist of laminated layers grading upward into increasingly bioturbated layers. Shallowing-upward packages are more distinct above the covered interval at 180 m where they are also slightly coarser and shallow upward from wacke- to grainstone.

Contact with the Welling Formation is gradational over a 1 m interval. Firmgrounds developed at the surface of Viola Springs wackestone are succeeded by grainstone of the Welling Formation. Welling lithology at marginal localities combines elements characteristic of both the basin and the platform. The matrix resembles that in the basin, with well-washed grainstone consisting of bioclasts too small for identification, but very large (up to 8 cm) trilobite bioclasts are more similar to what is preserved on the platform.

Diversity and abundance of skeletalized benthic organisms is slightly higher than in basinal sections. The carbonate mudstone lithofacies contains graptolites and rare cryptolithines as well as *Pugilator deckeri* Cooper, 1953, which is abundant at some horizons. Isotelines appear at 48 m and become more abundant upward in the section. At about 180 m, the isoteline trilobite *Anataphrus* occurs in high abundance forming dense accumulations of monotaxic float- to rudstone.

Platform Sections (1-4 in Fig. 3; LQ and 99 in Appendix)

A complete Viola Group section was not accessible outside the aulacogen but total thickness ranges from 90-110 m with 15-25 m of Welling (Puckette and others, 2000; API Well #12300123; API Well #12370042; #1 Cummings Well, NRIS Well Database). All lithofacies are present on the platform with those representing outer ramp environments thinnest.

The contact between peritidal carbonates of the Corbin Ranch Submember (Amsden and Sweet, 1983) at the top of the Bromide and the Viola Springs is erosional with up to 8 cm of relief. The laminated carbonate mudstone facies overlies

the contact and contains abundant graptolite fragments oriented parallel to bedding. Laminae are completely obscured by bioturbation within 0.5 m of the contact, with the entire facies only 1.5 m thick. *Isotelus* trilobites are present in the carbonate mudstone facies in addition to cryptolithine trilobites and graptolites.

Skeletalized macrofossils are limited to cryptolithine and isoteline trilobites in the low-diversity wacke- to rudstone facies, which extends from 1.5-13 m above the Bromide. Planar-bedded float- to rudstone between 18 m and 23 m grades upward into the bryozoan grain- to rudstone facies. Oxidized iron at some hardground surfaces may have formed during periods of subaerial exposure.

The high-diversity wacke- to rudstone lithofacies is present only at platform localities and is at least 30 m thick. Trilobite and articulate brachiopod pavements are separated by finer pelletal wacke- to packstone layers. Trilobite biostratigraphy allows correlation to a similar lithofacies at the LQ locality (see next section for details). Higher wackestone content at this locality is responsible for formation of more distinct limestone/marl alternations, although they are not as well developed as in marginal and basinal settings. Contact between the high-diversity wacke- to rudstone facies and the Welling is gradational over 0.5 m. The Welling Formation on the platform is a coarse-grained, well-washed rudstone consisting mainly of crinoidal debris with abundant large articulate brachiopod and trilobite clasts and is similar in lithology to the Welling Formation in northeastern Oklahoma (Amsden and Sweet, 1983).

Platform sections contain the highest diversity of organisms, including trilobites. Trilobite diversity and abundance are highest in the high-diversity wacke-

rudstone. The bryozoan grain- to rudstone has lower trilobite diversity but the highest abundance. Trilobite diversity and abundance are high in the Welling but lower than in slightly shallower lithofacies.

SEQUENCE STRATIGRAPHY

Application of sequence stratigraphic methods to studies of faunal change through time has demonstrated the importance of documenting the response of faunas to environmental fluctuations (Holland and Patzkowsky, 1996, 1999; Patzkowsky and Holland, 1993, 1996, 1999; Holland, 1999; Dattilo, 1996; Harris and Sheehan, 1997). Understanding the sequence stratigraphic architecture of the Southern Oklahoma aulacogen is especially important because tectonics within the aulacogen created a local stacking pattern that is very different from successions in surrounding areas that were affected mainly by eustatic changes. Eustatic influence is more difficult to identify within the aulacogen where it must be distinguished from tectonic control. Identification of systems tracts in the Viola Group is based on vertical stacking patterns in outcrop. Although the detail available from seismic data or analysis of continuous outcrop is not possible, the general observations below can be made.

The contact between the Bromide and Viola Springs formations in south-central Oklahoma marks a major deepening event and represents a short hiatus (less than one conodont biozone) (Derby and others, 1991, O'Brien and Derby, 1997). The lowstand systems tract (LST) and, in some areas the transgressive systems tract (TST), are not preserved, so the surface at the base of the Viola Springs is a composite of at least the sequence boundary (SB) and first flooding surface (Vail and

others, 1991). Formation of this condensed section in much of the aulacogen indicates that either relative sea level rise was much greater than carbonate production, or the carbonate factory was shifted too far landward for sediment to reach the area via offbank transport.

Conodont biostratigraphic data from Bauer (1989) indicate that the Upper Tyner and Fite formations in northeastern Oklahoma are no younger than Kirkfieldian in age. O'Brien and Derby (1997) used wireline logs and well cores and cuttings to correlate the Upper Tyner and Fite with the lower Viola Springs in the Arbuckle Mountains. Their correlation, if correct, has interesting implications for Viola deposition. It indicates that shallow subtidal conditions, represented by the Upper Tyner and Fite, persisted in northeastern Oklahoma during deposition of deep subtidal Viola strata in the region of the Southern Oklahoma aulacogen. Furthermore, an extensive (about 1 conodont biozone) unconformity above the Upper Tyner and Fite in northeastern Oklahoma indicates eustatic low stand. Shallowing indicative of a regression may have been masked by tectonic subsidence within the aulacogen. It is possible that the bryozoan shoals preserved on the platform near the aulacogen formed as a result of the eustatic sea level fall recorded outside the aulacogen, but better biostratigraphic correlation is required to determine this hypothesis.

Sequence Boundary and Lowstand Systems Tract

Within basinal successions of the aulacogen, the condensed section at the base of the Viola represents a SB, and a LST is not preserved. At marginal sections, the low-relief erosional surface at the contact between the Viola Springs and Bromide

formations is highlighted by a thin layer of iron and phosphate which represents the exposure surface of the SB. As in the basin, the LST is not preserved. Greater erosional relief at the contact between the Bromide and Viola Springs may represent both the SB and the maximum flooding surface (MFS), with the (LST) absent between.

Transgressive Systems Tract

In places, the condensed section in the basin is overlain by 1.5 m of crinoidal packstone. Finney (1986) considers this the remnants of a transgressive sequence and it is most likely the preserved portion of a (TST). The TST on the margin makes up the lower 2 m of the Viola Springs and is composed of ostracod-rich wacke- to packstone, most likely carried into the environment from more proximal environments. The TST, as observed at marginal and basinal sections, is not preserved on the platform within the region of the Southern Oklahoma aulacogen.

Maximum Flooding Surface

In the Criner Hills, the MFS consists of a thin (5 mm) horizon of iron-rich carbonate located about 7 cm above the contact with the Bromide. A condensation surface at 2 m above the Bromide on the margin is composed of a 2 cm interval of phosphatic and pyritic nodules. As mentioned above, the MFS on the platform may be encompassed by the condensed section at the base of the Viola Springs. This has been suggested by Ruedemann and Decker (1934) and Sweet (in Amsden and Sweet) 1983, but graptolite data from Finney (1986) indicate that the basal Viola Springs is

older at platform localities than within the aulacogen. Movement of the fault along the margins of the aulacogen may have dragged the edges of the platform down, allowing establishment of relatively deep-water conditions and deposition of laminated, graptolitic mudstone at the base of Viola Springs sequences on the platform.

Highstand Systems Tract

The condensation surface representing the MFS is succeeded by finely laminated, unbioturbated, organic-rich carbonate mud to siltstone across the entire study area. Very thin laminae indicate limited sediment supply from proximal settings. Tectonic subsidence within the aulacogen, coupled with a eustatic sea level fall, may have decreased the surface area of optimum environments for carbonate production. Even without eustatic sea level fall, subsidence (and the corresponding relative sea level rise) would have shifted the carbonate factory farther landward and deposition of significant amounts of sediment would require progradation of material down the ramp.

The laminated carbonate mudstone subfacies represents the catch-up phase of sedimentation, when distal tempestites and turbidites slowly filled accommodation space and the carbonate factory prograded farther into basin. Catch-up is indicated by lack of evidence of reworking and bypass. The basin filled more quickly during the keep-up phase, as meter-scale shallowing upward sequences recorded either sea-level fluctuations or minor episodes of increased subsidence within the aulacogen (Kendall and Schlager, 1981). Although a thick succession of carbonate is preserved and well-

exposed, parasequences are rare. This is partly due to the nature of carbonate parasequences below wave base, in which shallowing-upward from laminated mudstone to bioturbated wackestone is hard to recognize. In addition, lack of extensive ice caps in the Late Ordovician greenhouse climate likely resulted in minimal small-scale eustatic sea level changes of the type that form meter-scale parasequence sets (Lehrmann and Goldhammer, 1999).

Outside the aulacogen, a gradual eustatic sea-level rise culminating in maximum Tippecanoe transgression is indicated by deposition of the Welling Formation in northeastern Oklahoma. Within the aulacogen, sedimentation outpaced eustasy and coarse grain- to rudstone of the Welling Formation prograded out into the basin during sea-level highstand. Viola Group deposition ended with the influx of organic rich mud of the Sylvan Shale.

STRATIGRAPHIC DISTRIBUTION OF ISOTELINES

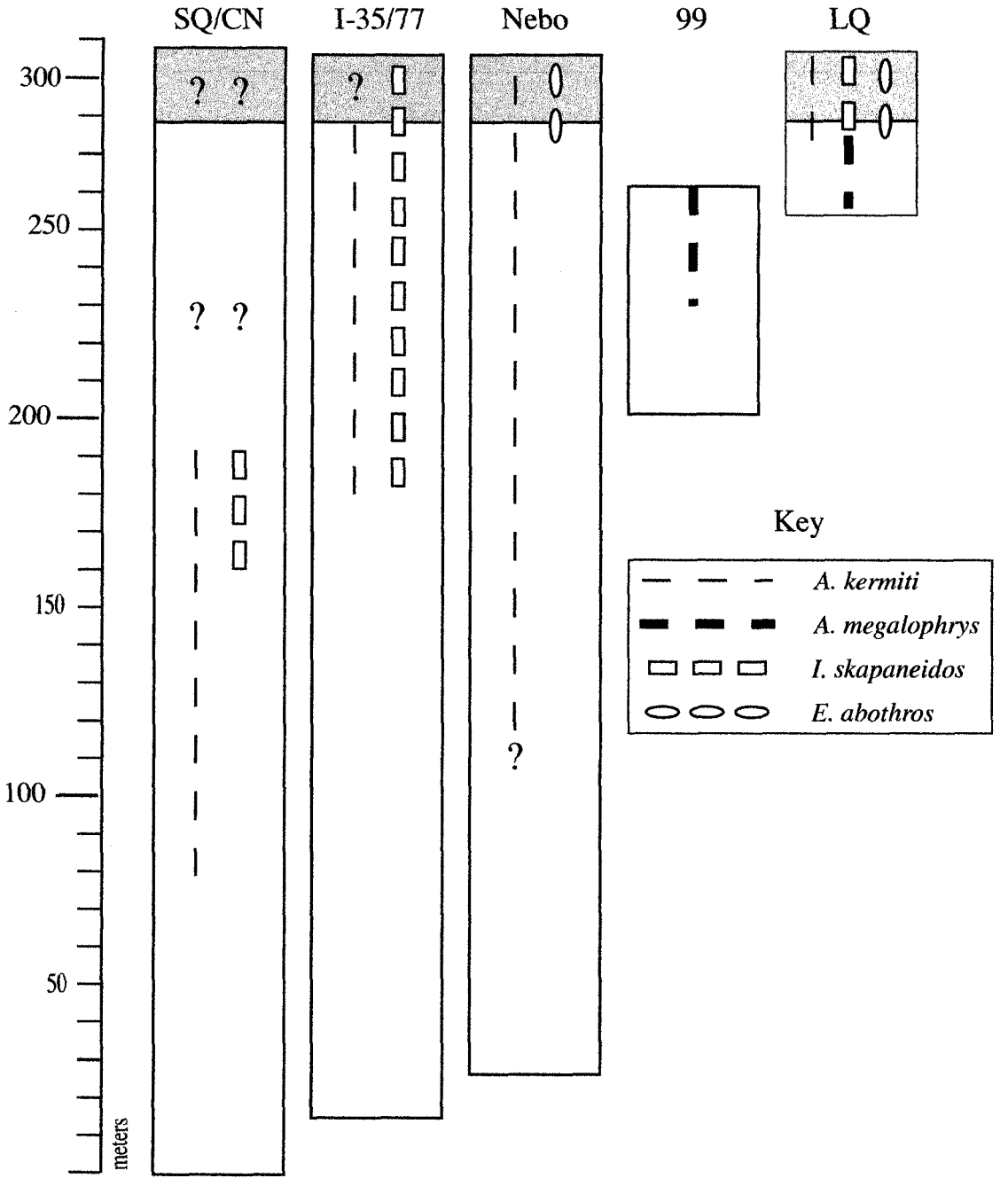
Lithofacies of the Viola Group record changing environmental conditions along the environmental gradient from the platform into the basin. Each lithofacies preserves a unique trilobite assemblage that reflects the trilobite community that inhabited that environment (Amati and Westrop, submitted manuscript). Some trilobite genera apparently were not restricted by narrow environmental tolerances and occur in multiple lithofacies. These genera can be used to correlate different but contemporaneous habitats. Trilobites provide biostratigraphic data from shallow subtidal to peritidal environments where graptolites are rare to absent. In anaerobic zones however, graptolites must be used instead of trilobites.

Isoteline trilobites inhabited the greatest range of environments in the Viola Group. Below storm wave base, a greater abundance of cryptolithine trilobites makes them more useful for correlation but isotelines provide higher resolution at shallower paleo-depths. *Stegnopsis wellingensis* and *Anataphrus kermiti* (new species described herein) dominate the fauna in the low-diversity wacke- to rudstone lithofacies of the Viola Springs Formation. Both of these species also occur in high numbers in the crinoidal grain- to rudstone lithofacies of the Welling Formation on the platform. They thus permit correlation across lithofacies boundaries (Fig. 4).

Trilobite assemblages defined for each lithofacies can be used for correlation with assemblages from similar environments in other parts of Laurentia. Trilobite occurrences from the Viola Group are proving to be key in correlating western Laurentia (northwest Canada, western U.S.) with eastern Laurentia (Trenton Group and equivalents). *Isotelus bradleyi* (new species described herein) is most similar to *I. parvirugosus* Chatterton and Ludvigsen, 1976 from the Esbataottine Formation in the Mackenzie Mountains, and *I. violaensis* (new species described herein) bears a strong resemblance to *I. copenhagenensis* (Ross and Shaw, 1972) of the Copenhagen Formation in Nevada. These provide a biogeographic, and therefore biostratigraphic, connection between western and central Laurentia. *Isotelus kimmswickensis* (Bradley, 1930), originally described from the Kimmswick Formation in Missouri and Illinois, is also present in the Viola Group. The Trenton Group shares *I. walcotti* with a close relative in the Viola. Although data from these few species are weak, this study demonstrates the potential for greater correlation using trilobite faunas from Oklahoma.

Figure 4. Stratigraphic distribution of Viola Group isotelines at sections within the southern Oklahoma aulacogen (CN, SQ), near the margins of the aulacogen (I-35/77, Nebo) and outside the margins of the aulacogen (99, LQ). Sections are hung on the base of the Welling.

Figure 4


SQ/CN
I-35/77
Nebo
99
LQ
300
250
200
150
100
50
meters
Key
A. kermiti
A. megalophrys
I. skapaneidos
E. abothros

SYSTEMATIC PALEONTOLOGY

Ten species of isoteline trilobite from the Viola Group are assigned to four genera. Eight species are new, and all species are described and illustrated. All figured specimens of new species are stored at the Oklahoma Museum of Natural History (OU). Several specimens from the Field Museum, Chicago (P, UC) are refigured herein.

A locality map is provided as Figure 3. Abbreviations for locality and horizon information are as follows; Lawrence Quarry: undifferentiated Viola Springs Formation (LQ-VS), undifferentiated Welling Formation (LQ-WF). Highway 99: stratigraphic level of each collection is designated as X meters above the base of the section (99-X). Mosely Creek: stratigraphic information not available (MC). Bromide Quarry: pavement at quarry floor (BQ-Pave), each collection horizon is designated as X meters above the pavement (BQ-X). Camp Classen: collections are from a single horizon near the top of the Viola Springs (CC). Interstate 35: all collections are labeled by horizon in meters above the contact with the Bromide (I-35-X). U.S. Highway 77: all collections are designated in meters above the base (77-X). Nebo: collections from the Viola Springs Formation are designated in X meters above the base (Nebo-X), Welling Formation collections are undifferentiated (NeboWell). Burns Quarry: (Northern Criner Hills) each collection is designated in meters above the base (CN-X). South Quarry: collections are labeled in meters above the base (SQ-X).

Additional material of *I. kimmswickensis* is figured both from the Viola Group of Oklahoma and the Kimmswick Limestone of Missouri. Material from Missouri

figured herein (Clark) is from an active quarry operated by Holcim (US) Inc., located near the town of Clarksville about 95 km northwest of St. Louis near the Mississippi River.

Order Asaphida Burmeister, 1843

Suborder Asaphina Salter, 1864

Family Asaphidae Burmeister, 1843

Subfamily Isotelinae Angelin, 1854

Discussion: Current concepts of the Asaphidae go back to Jaanusson (in Moore, 1959), with a more recent emendation by Fortey (1980), who focused on features of the glabella. A major revision of the group is long overdue but is well beyond the scope of this paper. Here, I follow Fortey's scheme. According to Fortey, the isoteline glabella is plesiomorphic, suggesting that the Isotelinae may not form a monophyletic group. At present, the absence of asaphine glabellar characters is the only criterion available to define the Isotelinae. Before relationships within the Isotelinae can be fully understood, the concepts of its constituent genera need to be better delimited. Rudkin and Tripp (1989) redescribed and reillustrated type material of *I. gigas* (the type species if the genus) and *I. walcotti.* In this paper, I describe three new species of *Isotelus* and discuss the relationships of *Isotelus*, *Ectenaspis*, *Stegnopsis* and *Anataphrus* with their presumed close relatives. For all characters discussed in the following sections, the plesiomorphic condition was determined based on comparison with asaphines such as *Asaphus* Brongniart, 1822, *Ogyginus* Raymond, 1912 and *Megistaspis* Jaanusson, 1956 and niobines like *Niobe* Angelin,

1851 and *Golasaphus* Shergold, 1971. Among closely related genera, states in *Isoteloides* Raymond, 1910a were also used to polarize characters, as were ontogenetic data, where available.

Genus *Isotelus* Dekay, 1824

Type species: *Isotelus gigas* Dekay, 1824

Discussion: *Isotelus* and *Ectenaspis* share derived features that suggest they form a monophyletic group. The pygidium is triangular in outline with lateral margins that converge toward the posterior and length (sag.) that is greater relative to width (tr.) than in other closely related isotelines. The frontal region is long (sag.), and effacement of both the cranidium and pygidium is greater than in *Isoteloides*. Also unlike *Isoteloides*, the glabella expands in front of the palpebral lobes. *Ectenaspis* is a derived group defined by hyper-elongate eye-stalks and a frontal region that tapers into a dorsally curving proboscis. Elongation of the pygidium is developed to a greater degree than in *Isotelus*, and long, thin genal spines are retained in large holaspids. It is possible that recognition of a monophyletic, derived *Ectenaspis* will make *Isotelus* paraphyletic, but until a phylogenetic analysis has been performed, it is best that they are retained as separate genera. I am uncertain about the relationship between *Isotelus*, *Ectenaspis* and *Trigonocerca* Ross, 1951 and *Trigonocercella* Hintze, 1952.

Species of *Isotelus* discussed below fall into two groups based on the course of the facial sutures in front of the palpebral lobes. In Group I, the cranidium narrows slightly in front of the palpebral lobes but widens again abruptly as the facial sutures

are directed laterally; the facial sutures are roughly parallel until angling inward to intersect at the mid-line. *Isotelus gigas*, *I. copenhagenensis*, *I. kimmswickensis*, *I. homalonotoides* Walcott, 1877 and *I. violaensis* new species belong to this group. Based on a comparison with the course of the facial sutures in other asaphines, this group is apomorphic. In Group II, the cranidium narrows strongly in front of the palpebral lobes and widens gradually as the facial sutures curve gently forward and outward; the widest point of the cranidium in front of the palpebral lobes is at the inflection point where the facial sutures turn to become directed inward to the mid-line. This facial suture pattern appears to be plesiomorphic and is found in *I. parvirugosus*, *I. iowensis* Owen, 1852, *I. walcotti*, *I. giselae* Tripp and Evitt, 1986, *I. ottawaensis* Wilson, 1947, *I. bradleyi* new species and *I. skapaneidos* new species are members of the second group.

A third group of species assigned to *Isotelus* have the plesiomorphic anterior suture pattern of Group II *Isotelus* but are also very wide (tr.) relative to length (sag.) and have rounded pygidia with broad borders. This group consists of: *I. latus* Raymond, 1913, *I. maximus* Locke, 1838, *I. rex* Rudkin and others, 2003 and possibly *I. platycephalus* Stokes, 1824. I suspect that a phylogenetic analysis will produce a clade including *Isotelus* and *Ectenaspis* that is defined by a pygidium that tapers strongly posteriorly. The species mentioned above will be excluded from the clade and will be referred to as "*Isotelus*".

Isotelus kimmswickensis Bradley, 1930

1930. *Isoteloides kimmswickensis*, Bradley, p. pl. 27, fig. 1, 2, 11.

not 1930. *Isoteloides kimmswickensis*, Bradley, pl. 27, fig. 3, 4.

not 1930. *Isoteloides* cf. *kimmswickensis*, Bradley, p. 27, 5-7.

Pls 1-2; Pl. 3, Figs 1-5

Type Material: An incomplete internal mold of a cranidium (Holotype, UC28851A), a second incomplete internal mold of a cranidium from the same rock (Paratype, UC28851B), an incomplete internal mold of a pygidium from the same rock (Paratype, UC28851C), a nearly complete but exfoliated pygidium (Paratype, UC28853), a broken and exfoliated pygidium (Paratype UC28855). Two additional specimens, a cranidium preserving a portion of cuticle on the right posterior fixigena (UC28854) and an exfoliated librigena (UC28851D), listed by Bradley as paratypes are more similar to *I. bradleyi*, new species and are figured on plate 7 as *Isotelus* cf. *I. bradleyi*. Additional material from the Viola Group is also figured.

Stratigraphic Occurrence: Type material is from the Upper Ordovician Kimmswick Limestone in Glen Park, Missouri. Additional figured material is from the Upper Ordovician Viola Springs Formation of Oklahoma (99-20 to 99-36) (Appendix).

Diagnosis: A species of *Isotelus* with very short (sag.) cranidium, only slightly longer than maximum width (tr.) in front of palpebral lobes. Facial sutures nearly parallel for short distance in front of palpebral lobes. Pygidium with long border, longest directly behind axis.

Description: Cranidium only slightly longer (sag.) than wide (tr.), maximum width in front of palpebral lobes about 90% of length. Longitudinal convexity low over posterior three quarters, then sloping steeply down to frontal area. Transverse convexity low. Axial furrows shallow, directed slightly inward from posterior margin to level of palpebral lobes; directed laterally for approximately one half distance in front of palpebral lobes creating "waisted" shape to glabella. Axial furrows curve inward to become preglabellar furrow. Anterior margin of glabella rounded. Occipital furrow effaced, seen faintly on internal molds (Pl. 1, Figs 3c, 4a, 6a, 8). Occipital ring longer (sag.) medially, expressed as thin band lacking ornament. Glabellar furrows S2 and S3 more visible than S1 on some internal molds, most obvious in smaller individuals (Pl. 1, Figs 3c, 4a). Median tubercle located at front edge of occipital furrow, behind posterior margin of palpebral lobes, visible on internal molds, not expressed on dorsal surface of cuticle. Width of glabella half that of posterior margin of cranidium. Palpebral regions of fixigenae taper upward into eye-stalks. Eye-stalks wider (tr.) than long (sag.), located at one third total length (sag.) in front of posterior margin, elevated slightly above maximum height of cranidium. Palpebral furrow visible on internal molds (Pl. 1, Fig. 7). Anterior branches of facial sutures running directly forward in front of palpebral lobe for short distance before curving gently inward toward sagittal line; approach sagittal line at angle of 50° to horizontal; form strong point at intersection; suture diverges from anterior margin of glabella so frontal area longest sagittally; length (sag.) of frontal area about 15% total length. Fixigena in front of palpebral lobe wider (tr.) than in

Isotelus of Group II because sutures directed forward rather than inward. Facial sutures do not converge as strongly as preglabellar furrow so frontal area longest exsagittally. Posterior branch of facial suture directed toward posterior at nearly 45° to posterior margin then curving abruptly backward to join posterior. Posterior margin of cranidium horizontal then directed toward posterior at lateral extremity. Termination of posterior portion of fixigena rounded and deflected backward. Posterior border furrow deeply impressed, closer to posterior margin abaxially. Surface of cuticle without ornament.

Librigenae subtriangular in outline, without genal spines in moderately large holaspids. Posterior margin of librigena straight, directed backward. Genal angle sharp. Widest (tr.) point just behind eye. Gena tapering anteriorly, inner margin converging on lateral margin just in front of eye. Lateral margin gently rounded; inner margin gently incised. Dorsal surface of librigena sloping gently down to lateral margin. Posterior border furrow continuing from fixigena on to librigena, still deeply impressed, fading at about one half lateral distance across librigena. Lateral border absent. Eye socle furrow well-developed Ornament not preserved. Visual surface tall, tapering upward, placed on short stalk, directed slightly outward. Hypostome and thorax unknown.

Pygidium subtriangular, width (tr.) only slightly greater than length (sag.), height approximately one half of length. Facets prominent. Axial furrows weak; pleural furrows visible on small holaspids and well-preserved internal molds of larger individuals (Pl. 2, Fig. 4c, Pl. 3, Fig. 5). Pleural furrow of first segment deeply impressed. Articulating half ring visible on some internal molds (Pl. 3, Fig. 5), axial

rings not expressed. Pleural regions gently sloping, become abruptly much steeper just before lateral margin. Border furrow very shallow, arising at approximately one third distance from anterior margin, running very close to lateral margin for most of length; longer behind posterior point of pygidium producing a short platform posterior to termination of axis. Ornament of faint, wide, shallow pits.

Ontogeny: Smallest cranidium (OU11764; Pl. 1, Fig. 3) 4.5 mm long (sag.). Length (sag.) of frontal area decreases through ontogeny; length (sag.) in smallest cranidium 22% total length vs. 15% in largest cranidium (Pl. 1, Fig. 8). S1 broad, deep on internal molds, becoming effaced through development, weakly distinguishable on largest specimens. Anterior facial sutures curving around maximum glabellar width in front of palpebral lobes, become less curved, more parallel in larger individuals. Smallest pygidium (OU11771; Pl. 2, Fig. 2) 3.0 mm long (sag.). Length (sag.) just under 60% width (tr.), pygidial outline subcircular; length increases greatly through ontogeny to 81% relative to width, pygidial outline subtriangular. Lateral border of pygidium with uniform width in smaller individuals, becoming effaced laterally and more elongate behind axis. Pleural furrows increasingly effaced with size. Axial furrows become broader.

Discussion: Among species of Group I, *I. kimmswickensis* resembles *I. copenhagenensis* mainly in the course of the facial sutures and axial furrows (Ross and Shaw, 1972, pl. 2, figs 4, 8, pl. 3, fig. 1). The anterior facial sutures in the former approach the mid-line at a lower angle (near 45°) than in *I. copenhagenensis*

(approximately 60°). The pygidium of *I. copenhagenensis* (Ross and Shaw, 1972, pl. 2, figs 6, 10) is shorter (sag.) and wider (tr.) than in *I. kimmswickensis* and the posterior border continues forward for a greater distance. In *I. gigas*, the facial sutures in front of the palpebral lobes are directed strongly inward for a short distance (Rudkin and Tripp, 1989, fig. 1.1). The cranidium of *I. gigas* is longer than wide while the cranidial dimensions of *I. kimmswickensis* are nearly equal. The posterior border of the pygidium in *I. gigas* is more uniform in width while that of *I. kimmswickensis* is much longer immediately behind the axis.

Isotelus violaensis, new species

?1987. *Isotelus homalonotoides* (Walcott, 1877) in DeMott, pl. 3, figs. 21-26.

Pl. 3, Figs 6-8, Pl. 4, Pl. 5, Figs 1-3, ?4

Etymology: This species is very similar to *I. kimmswickensis* and is named for the correlative Viola Springs from which it comes.

Type Material: An exfoliated cranidium (Holotype, OU11782), a small, partly exfoliated cranidium (Paratype, OU11781, two partial, mostly exfoliated cranidia (Paratypes, OU11783, OU11788), two casts (Paratypes, OU11784, OU11785), four pygidia of various sizes (Paratypes, OU11786, OU11787, OU11789, OU11791), an internal mold of a librigena (Paratype, OU11790). A hypostome from the same collection most likely belongs to this species (OU11792).

Stratigraphic Occurrence: The type material is from the Upper Ordovician Viola Springs Formation of Oklahoma (99-39 to 99-49).

Diagnosis: A species of *Isotelus* with facial sutures nearly parallel for short distance in front of palpebral lobes. Frontal area very long (sag.), length 20% total length of cranidium. Eye-stalks tall, extending well above maximum height of glabella. Lateral border of pygidium strongest over posterior 1/3 of pygidium, becoming much wider directly behind axis.

Description: Very similar to *I. kimmswickensis* except for following features. Cranidium longer (sag.) than wide (tr.), maximum width in front of palpebral lobes just under 80% of length. Eye-stalks directed upward at steeper angle, reaching greater elevation above maximum height of cranidium, directed slightly backward. Frontal area longest exsagittally, relatively longer than in *I. kimmswickensis* (20% vs. 15% total length of cranidium). Palpebral furrow not preserved. Anterior branch of facial suture running generally forward with slight adaxial deflection for short distance followed by slight abaxial deflection in front of palpebral lobe before curving gently inward toward sagittal line. Angle of convergence of facial sutures slightly higher than in *I. kimmswickensis* (45° to horizontal vs. 50°). Posterior portion of fixigenae tapering more sharply than in *I. kimmswickensis*, deflected backward more sharply. Dorsal cuticle virtually without ornament; faint pitting observable with magnification.

Librigena as in *I. kimmswickensis*. Thorax unknown. Hypostome from same collection (Pl. 5, Fig. 4) may belong to this species.

Pygidium very similar to *I. kimmswickensis* except: height lower; greater effacement of pleural furrows on internal molds; border furrow of pygidium more pronounced behind axis. Cuticle without ornament.

Ontogeny: Smallest cranidium (OU11781; Pl. 3, Fig. 6) 6.9 mm long (sag.). Length (sag.) of frontal area 17% total length, becoming longer through ontogeny to about 20%. Occipital and S1 furrows visible on internal molds of small individuals become effaced with growth, obsolete in most large individuals. Anterior branch of facial suture more sinuous in smaller specimens (compare Pl. 3, Fig. 6 to Pl. 4, Fig. 5a). Smallest pygidium (OU11786, Pl. 4, Fig. 3) 3.7 mm. Ratio of length (sag.) to width (tr.) (62%) increases through ontogeny to 79%; lateral margins of pygidium become tapered to posterior. Well-developed lateral border furrow becomes effaced laterally, more elongate behind axis. Straight lateral margins grow to be curved in toward near posterior margin of axis. Effacement of axial and pleural furrows progressive.

Discussion: Of other Group I species, *I. violaensis* is most similar to *I. kimmswickensis*; differences are described above. *Isotelus violaensis* differs from *I. copenhagenensis* in that the pygidium of the former tapers more strongly toward the posterior and the angle of the anterior branch of the facial sutures to the sagittal line is higher (45° in *I. violaensis* versus 30° in *I. copenhagenensis*). The facial sutures of *I. violaensis* follow a similar course to those of *I. gigas* (see Rudkin and Tripp, 1989,

fig. 1) but are initially directed inward to a lesser degree in front of the palpebral lobes and the cranidium of *I. violaensis* has a lower convexity than *I. gigas*. The cranidium of *I. violaensis* is longer (width just under 80% length) than *I. kimmswickensis* (width about 90% length) but shorter than *I. gigas* (width about 65% length). The lateral portions of the posterior fixigenae taper more strongly than in either *I. kimmswickensis* or *I. gigas* and are directed backward more strongly. The posterior border of the pygidium in *I. violaensis* is wider than in *I. gigas*, especially behind the axis.

The pygidium of *I. homalonotoides* (Pl. 5, Figs 5, 6) is very similar to that of *I. violaensis*. In *I. homalonotoides*, the posterior border is slightly longer (exsag.) and maintains a uniform width to the articulating facet while the border of *I. violaensis* becomes effaced anteriorly. The anterior border of the cranidium of *I. homalonotoides* is longer (exsag.) (24% total length of cranidium) than in *I. violaensis* (20% total length) and weak S1 glabellar furrows are retained in a relatively large individual.

Isotelus bradleyi, new species

?1930. *Isoteloides kimmswickensis*, Bradley, pl. 27, fig. 3, 4.

Pl. 6, Pl. 7, Figs 1-3, Pl. 8, Figs 1-3

Etymology: Named in honor of J. H. Bradley, Jr.

Type Material: A small, mostly exfoliated cranidium missing a posterior fixigena and palpebral lobe (Holotype, OU11796), a cast of a small cranidium (Paratype, OU11793), four small cranidia (Paratypes, OU11794, OU11795, OU11797, OU11801), a cast of a cranidium missing the posterior fixigenae (Paratype, OU11798), an external mold of a cranidium showing the ornament on the dorsal cuticle (Paratype, OU11800), a cranidium with distinct glabellar furrows (Paratype, OU11803), an exfoliated librigena (Paratype, OU11799), a partly exfoliated librigena with the visual surface preserved (Paratype, OU11802), two exfoliated pygidia (Paratypes, OU11804, OU11805), and an external mold of a partial pygidium showing ornament of the cuticle (Paratype, OU11806).

Stratigraphic Occurrence: Type material is from the Upper Ordovician Viola Springs Formation (99-08 to 99-33) of Oklahoma.

Diagnosis: A species of *Isotelus* with anterior branch of facial suture directed inward in front of palpebral lobe then curving outward so that lateral margins of cranidium in front of palpebral lobes strongly sinuous. Anterior branches of facial sutures curving abruptly forward just before intersecting making anterior margin of cranidium sharply pointed. Ornament of coarse pits. Pygidium short (sag.) for genus and without border furrow.

Description: Longitudinal convexity of glabella low, nearly flat over posterior 3/4 of cranidium then sloping steeply down to anterior margin. Axial and preglabellar

furrows weak, expressed mainly as change in convexity from glabella to fixigenae and frontal area. Axial furrows directed weakly adaxially from posterior margin to level of palpebral lobes; directed strongly laterally in front of palpebral lobes to widest margin of cranidium at half distance from palpebral lobes to front of cranidium. Preglabellar furrow directed anteromedially so that anterior margin of glabella subangular medially. Occipital furrow very weak, only visible on some internal molds; very near posterior border abaxially, longer sagittally. Glabellar furrows S1, S2 and S3 visible to varying degrees on internal molds of some specimens (Pl. 6, Figs 1, 2a, 4b, 5a; Pl. 7, Fig. 3c). Median tubercle slightly in front of occipital furrow, behind posterior margin of palpebral lobes, visible on internal molds. Width (tr.) of glabella approximately half width (tr.) of posterior margin of cranidium. Fixigenae tapering upward into eye-stalks. Eye-stalks in front of posterior margin 1/3 total length (sag.) of cranidium, angled sharply upward above cranidium, then oriented horizontally; length (sag.) moderate, nearly equal to width (tr.). Palpebral furrow weak (Pl. 6, Fig. 6); termination of palpebral lobe evenly rounded. Facial suture directed strongly inward just in front of palpebral lobe then curving anterolaterally, making lateral margin of cranidium distinctly sinuous in front of palpebral lobe. Maximum width (tr.) of cranidium in front of palpebral lobes located at 2/3 distance from posterior margin. From widest point, facial sutures converge at 60° then curve abruptly forward just before intersecting at sagittal line. Sutures parallel preglabellar furrow until diverging forward just before intersecting, creating frontal area that is longer sagittally than exsagittally. Posterior branch of facial suture directed posterolaterally to point twice width (tr.) of eye-stalk then

directed backward to intersect with posterior margin. Posterior margin of cranidium directed slightly backward from level of palpebral lobes so that posterior fixigenae directed slightly backward at lateral extremity. Weak posterior border furrow visible only on internal molds (Pl. 7, Fig. 1a, 3c), placed very near posterior border, positioned horizontally so closer to posterior margin axially, becoming effaced abaxially. Ornament of densely packed, coarse pits (Pl. 6, Fig. 8). Weak sagittal ridge arising at level of S2, continuing to anterior margin of glabella.

Librigenae without genal spines in moderately small holaspids; unknown for smaller holaspids. Posterior margin directed only slightly backward, intersecting sharply with lateral margin. Lateral margin strongly convex. Widest point of gena at point just behind eye. Facial suture in front of eye directed strongly laterally then curving to run anteromedially. Dorsal surface of gena gently convex. Eye socle furrow wide, shallow. Visual surface tall, taller anteriorly than posteriorly, directed slightly laterally from dorsal surface of gena. Posterior border furrow shallow, becoming effaced at 1/2 distance to lateral margin. Border furrow wide, shallow, arising short distance in front of posterior margin, widening slightly anteriorly. Ornament not preserved. Hypostome and thorax unknown.

Pygidium subtriangular, short for genus with length (sag.) approximately 75% of width (tr.). Inflation moderate, height 60% of length. Dorsal surface of pygidium sloping gently away from anteromedian for 3/4 distance, then slope abruptly becoming much steeper to lateral and posterior margins. Articulating facets prominent. Pleural furrows of first segment deeply impressed. Axial and pleural furrows weakly impressed on internal molds. Border furrow absent. Ornament of

densely packed, medium-sized pits.

Ontogeny: Smallest well-preserved cranidium (OU11794; Pl. 6, Fig. 2) 5.3 mm long (sag.). Length (sag.) of frontal area decreases through ontogeny, shape retained. S1 furrows generally more effaced with greater size with rare exceptions (Pl. 7, Fig. 3). Very fine, shallow pits increase in size and depth with growth. Small pygidia not known.

Discussion: Among Group II species, *I. bradleyi* most closely resembles *I. parvirugosus*, especially in cranidial characters. The frontal area of *I. bradleyi* is much longer sagittally than exsagittally instead of becoming only slightly longer adaxially. The angle of convergence of the anterior facial sutures is higher in *I. bradleyi* than in *I. parvirugosus*. In *I. bradleyi*, the longitudinal convexity is lower, especially over the posterior 3/4 of the cranidium and the eye-stalks are slightly less elevated. The pygidia of *I. bradleyi* and *I. parvirugosus* are similar in outline, but a posterior border is present in the latter. *Isotelus bradleyi* has an ornament of coarse pits and lacks genal spines in holaspids. The cranidial outline of *I. giselae* is similar to *I. bradleyi*, but the posterior fixigenae of the former are longer (exsag.) and wider (tr.). The holaspid pygidium of *I. giselae* is unknown. The cranidium and librigenae of *Isotelus* cf. *I. harrisi* Raymond, 1905 figured by Tremblay and Westrop, 1991 (fig. 9.10-9.14) are very like *I. bradleyi*, but the facial sutures of the latter converge at a lower angle. *Isotelus instabilis* Reed, 1904 has a similar cranidial outline and lacks genal spines, but details of the anterior border aren't clear in the illustrations.

Bradley (1930) figured material of an isoteline similar to *I. bradleyi*, but attributed it to *I. gigas* (Pl. 7, Fig. 4) and *I. kimmswickensis* (Pl. 7, Fig. 5). I include it here under *Isotelus* cf. *I. bradleyi*.

Isotelus skapaneidos, new species

Pl. 8, Figs 4, 5; Pls 9, 10; Pl. 11, Figs 1, 2; Pl. 12, Fig. 1?

Etymology: The outline of the cranidium is in the form of a spade or shovel.

Type Material: A partly exfoliated cranidium (Holotype, OU11809), a nearly complete cranidium with the left librigena (Paratype, OU11811), four cranidia (Paratypes, OU11810, OU11814, OU11816, OU11817), one nearly complete, weathered individual (Paratype, OU11813), a cranidial doublure with parts of both librigenae attached (Paratype, OU11815), two large pygidia and one small pygidium (Paratypes, OU11808, OU11812, OU11807).

Stratigraphic Occurrence: The type material is from the Upper Ordovician Viola Springs (77-202 to 77-216; CN-float) and Welling formations (LQ-WF).

Diagnosis: A species of *Isotelus* sharply pointed frontal area of cranidium; length (sag.) of frontal area about 25% total length of cranidium. Posterior portion of fixigenae long (exsag.), deflected sharply backward.

Description: Glabella very gently convex over 3/4 of length from posterior margin then sloping sharply down to frontal area. Axial, preglabellar furrows shallow, wide. Behind palpebral lobes, axial furrows very faint, directed slightly adaxially; directed forward lateral to palpebral lobes; directed abaxially in front of palpebral lobes then curving toward center to become preglabellar furrow. Anterior margin of glabella rounded. Occipital furrow, glabellar furrows effaced. Median tubercle not expressed on only available exfoliated specimen. Glabellar width more than 1/2 total width of posterior margin. Palpebral lobes at approximately 1/4 total length in front of posterior margin. Palpebral region of fixigena tapering upward into eye-stalk; extending upward from cranidium at low angle for short distance then oriented horizontally. Palpebral furrow not preserved. Length (exsag.) of eye-stalk greater than width (tr.); termination of palpebral lobe evenly rounded. Facial suture directed inward in front of palpebral lobe, then deflected gradually outward to form long (tr.) indentation in lateral margin of cranidium. Suture curving inward at about 60% length of cranidium, continuing toward sagittal line at high angle (40° from horizontal). Sutures parallel axial furrows, continue at high angle as preglabellar furrows converge at low angle forming frontal area with length (sag.) 25% total cranidial length. Posterior branch of facial suture directed abaxially and backward for 2/3 length then directed abruptly backward to intersect posterior margin. Posterior margin of cranidium curved outward behind glabella; curved inward behind axial furrows and posterior portion of fixigenae. Fixigenae behind palpebral lobes tapering laterally and directed backward. Posterior border furrow absent. Dorsal surface of cuticle without ornament.

Librigenae subrectangular in outline, without genal spines in moderately large holaspids. Posterior margin straight, directed backward. Genal angle sharp. Widest (tr.) point just behind eye. Gena tapering anteriorly, inner margin converging strongly on lateral margin in front of eye. Lateral margin gently rounded. Dorsal surface of librigena convex. Posterior border furrow absent. Lateral border furrow arising just in front of posterior margin, widening (tr.) gradually anteriorly to widest (tr.) point in front of eye. Thin (tr.) anterior portion of gena nearly flat. Visual surface short, but more than 180° in circumference. Librigenae without ornament. Hypostome unknown.

Thorax of eight segments. Axis wide (tr.), about 50% total width (tr.) of thorax, convex. Articulating furrows effaced. Adaxial 1/3 of pleural portions of thoracic segments horizontal, abaxial 2/3 deflected strongly ventrally. Articulating facets of pleurae oriented anterolaterally; extend for distal 2/3 of pleurae.

Pygidium subtriangular, length (sag.) nearly equal to width (tr.), moderately inflated. Articulating facets at lower angle to horizontal than in other Viola Group species. Pleural furrows of first segment well defined; pleural furrows of other segments, furrows and axial rings effaced. Axial furrows very weak. Border furrow shallow but wide, very near lateral margin, reaching nearly to anterior margin. Posterior margin of pygidium behind axis deflected upward. Cuticle without ornament.

Ontogeny: Smallest cranidium (OU11810; Pl. 9, Fig. 2) 26.6 mm long (sag.). Smallest pygidium (OU11807; Pl. 8, Fig. 4) 9.8 mm long (sag.). Intraspecific

variation evident; two general morphotypes. Morphotype A (Pl. 9, Figs 1, 2; Pl. 10, Fig. 1) with large palpebral lobes, posterior fixigenae short (exsag.), especially in larger individuals; axis of pygidium weakly defined (Pl. 8, Fig. 5). Morphotype B (Pl. 9, Fig. 3; Pl. 10, Fig. 2; Pl. 11, Figs 1, 2) with smaller palpebral lobes, posterior fixigenae very long (exsag.); axis of pygidium almost completely effaced (Pl. 9, Fig. 4).

Discussion: Compared to other species in Group II, the lateral margins of cranidia in *I. skapaneidos* are very sinuous. The exceptionally well-developed anterior border of the cranidium is similar to *I. walcotti* but is much longer sagittally than exsagittally instead of being more uniform in length. *Isotelus iowensis* also has a large cranidial border but retains genal spines in the holaspids. The frontal area of *I. gigas* is moderately long (sag.) and the pygidium tapers strongly toward the posterior but the facial sutures are those of trilobites in Group I.

Isotelus cf. *I. iowensis*

Pl. 12, Figs 2, 3

Stratigraphic Occurrence: Material of this species is from the Upper Ordovician Viola Springs Formation (BQ-float; I-35-75).

Description: Longitudinal convexity very low; posterior 3/4 of cranidium flat to slightly concave; sloping steeply to anterior margin over anterior 1/4 of length. Axial and preglabellar furrows effaced even for genus; axial furrows effaced lateral and

posterior to palpebral lobes; directed abaxially in front of palpebral lobes. Glabellar furrows preserved as broad, shallow, poorly-defined depressions. Eye-stalks, palpebral lobes not preserved. Anterior branch of facial suture curving outward and forward in front of palpebral lobe, continuing in broad, strongly rounded arch around lateral margin of cranidium then directed forward and adaxially. Sutures and axial furrows roughly parallel. Lateral border furrow wide on cranidium. Posterior branch of facial suture directed abaxially and slightly backward for 2/3 length, then directed abaxially and backward at about 45° to posterior margin. Posterior margin, and therefore posterior fixigenae, directed backward at lateral extremities. Posterior border furrow absent. Ornament lacking.

Librigenae wide (tr.), subtriangular in outline. Genal spines present in large holaspids; narrow (tr.), tapering rapidly, broken distally. Posterior margin curved backward, nearly transverse in orientation. Posterior border furrow absent. Widest (tr.) point just behind eye-stalk, narrowing (tr.) behind and toward anterior. Inner margin in front of eye converging strongly on lateral margin. Border furrow strong along entire lateral margin of gena, widest in front of eye. Anterior portion of gena nearly very narrow (tr.). Lateral margin very gently rounded from genal spine forward to point in front of eye, then curved slightly inward lateral to maximum width of cranidium in front of palpebral lobes. Dorsal surface of librigena weakly convex. Eye-stalk and visual surface broken. Dorsal surface without ornament. Hypostome unknown.

Thorax of eight segments, wide (tr.), low convexity. Axis <45% total width of thorax. Adaxial 1/3 of pleurae nearly flat, abaxial 2/3 deflected ventrally. Pleural

furrows well-defined, arising at front of segment, running laterally and backward for about 1/2 width (tr.) of pleurae then becoming effaced. Articulating facets long (exsag.), covering nearly entire length (exsag.) of abaxial 1/2 of pleurae.

Pygidium subtriangular, low, long (sag.), length (sag.) 82% of width (tr.). Lateral border wide (tr.), extending at about equal width around entire margin of pygidium. Posterior margin of pygidium upturned. Articulating facets prominent, oriented at low angle to anterior margin of pygidium. Pleural furrows of first segment well defined. Axial furrows weakest toward anterior, slightly better defined toward posterior and around posterior of axis; pleural furrows effaced. Small areas of preserved cuticle without ornament.

Discussion: This species resembles *I. iowensis* in the width of the body, course of the anterior facial sutures, broad lateral border furrows on both the cephalon and pygidium and retention of genal spines in large holaspids. Further comparison is hindered by lack of preservation of the anterior of the cranidium in the Viola specimen. Pygidia from the Viola Springs are distinctive in that the posterior point of the pygidium is upturned; this feature cannot be assessed for the type specimen because it is crushed.

Isotelus cf. *I. walcotti*

Pl. 13

Stratigraphic Occurrence: Material of *Isotelus* cf. *I. walcotti* comes from the Upper

Ordovician Viola Springs (99-33 to 99-49.5).

Description: Longitudinal convexity low. Posterior 2/3 of cranidium nearly flat, anterior 1/3 sloping gently to anterior margin. Axial and preglabellar furrows expressed as change in convexity from glabella to lateral and frontal areas. Axial furrows directed inward from posterior margin to point just in front of palpebral lobes, curving outward then inward parallel with lateral margin of cranidium formed by facial sutures. Anterior margin of glabella rounded. Occipital region incompletely preserved; weak glabellar furrows (S2, S3) preserved on internal molds (Pl. 13, Fig. 1). Anterior branch of facial suture directed outward and forward in front of palpebral lobe, continuing in broad, strongly rounded arch around lateral margin of cranidium then directed forward and toward mid-line at an angle of nearly 60° to sagittal line. Sutures parallel axial furrows until point of maximum width of cranidium in front of palpebral lobes then diverge from preglabellar furrow so that frontal region is longest sagittally. Lateral border (between facial suture and axial furrow at point of maximum width in front of palpebral lobes) much wider (tr.) than in most other species. Posterior portion of cranidium including posterior branch of facial suture, posterior fixigenae and posterior portion of glabella not preserved. Ornament of very fine pits only visible under magnification.

Librigenae subrectangular in outline; narrow (tr.) and tall. Genal spines present in moderately large holaspids (Pl. 13, Fig. 2). Posterior margin directed strongly backward. Posterior border furrow continuing for 1/2 distance across gena. Widest (tr.) point just behind eye-stalk. Gena tapering toward anterior; inner margin

converging strongly on lateral margin just in front of eye. Border furrow strong from point just behind eye forward; anterior portion of gena nearly flat. Lateral margin very gently rounded. Dorsal surface of librigena convex. Eye-stalk extending dorsally and laterally for short distance; visual surface much taller than in *I. walcotti*. Dorsal surface without ornament. Hypostome and thorax unknown.

Pygidium subtriangular, short, length (sag.) 77% of width (tr.). Height low, 42% of length. Very gently concave lateral border extending around entire margin of pygidium. Articulating facets prominent, oriented at low angle to anterior margin of pygidium. Pleural furrows of first segment well defined. Axial furrows very weak, even on internal mold; pleural furrows absent. Ornament not preserved.

Discussion: The strength and width of the cranidial border furrow strongly resemble *I. walcotti* but material is too sparse for confident identification. Pygidia of the species from the Viola Group and *I. walcotti* are indistinguishable. *Isotelus* cf. *I. walcotti* is the only isoteline from the Viola Group that retains genal spines as a holaspid.

Genus *Ectenaspis* Raymond, 1920

Type species: *Megalaspis beckeri* Slocom, 1913

Discussion: Westrop and Ludvigsen (1983) redescribed the type of *Ectenaspis* and provided a reconstruction of the nearly complete individual. Because complete eye-stalks were unknown, those in the reconstruction are not accurate. Based on the

length of the eye-stalks in the new species from the Viola Group, it is probable that those of *E. beckeri* were longer than estimated. The holotype is refigured on Plate 14 herein.

Ectenaspis abothros

Pls 15, 16; Pl. 17, Figs 1-4

Etymology: The trivial name, "without trough" refers to the lack of a wide, concave border furrow, especially behind the axis as is typical of *E. beckeri.*

Type Material: A cranidium with the left eye-stalk and palpebral lobe preserved (Holotype, OU11827), a crushed cranidium with a well-preserved palpebral lobe showing the ornament on the cranidium (Paratype, OU11828), two partial cranidia (Paratypes, OU11829, OU11830), portions of two librigenae (Paratypes, OU11831, OU11832), four pygidia of varying sizes with cuticle preserved (Paratypes, OU11833, OU11834, OU11835, OU11836).

Stratigraphic Occurrence: The type material is from the Upper Ordovician Welling Formation, Oklahoma (LQ-WF, Nebo-Well).

Diagnosis: A species of *Ectenaspis* with border furrow of pygidium becoming obsolete through holaspid ontogeny. Weak axial rings and pleural furrows present.

Description. Longitudinal convexity of cranidium low, nearly horizontal for 3/4 distance from posterior margin then sloping gently to frontal area. Frontal area tapering anteriorly, curving dorsally; anterior margin of all specimens broken. Palpebral lobes short distance behind transverse mid-line. Axial furrows effaced; lateral margins of glabella indicated by change in convexity rather than discrete furrow. Occipital furrow obsolete. Posterior branch of facial sutures sinuous; directed posteromedially then posterolaterally to posterior border furrow making front margin of posterior fixigena curved in; lateral margin of posterior fixigena rounded. Anterior branch of facial sutures very gently rounded inward for short distance then rounded outward to anterior prolongation; directed anteromedially at approximately 30° to sagittal line. At frontal area, sutures directed more strongly toward anterior then broken. Glabella weakly convex behind palpebral lobes; lateral margins of glabella obscured at level of palpebral lobes by inflated base of eye-stalks. In front of palpebral lobes, convexity of glabella slightly lower and tapering toward anterior; anterior margin of glabella narrow and rounded. Fixigenae narrow (tr.); posterior portion narrow (tr.) and concave. Posterior border furrow indicated by change in convexity. Posterior border short (exsag.), strongly convex, deflected slightly backward distally. Palpebral areas of fixigenae with swellings oriented about 25° to horizontal, tapering dramatically abaxially, extending dorsolaterally to form long, thin eye-stalks (Pl. 16, Figs 1a, 2a, 2b). Eye-stalks directed slightly forward at about 35° to horizontal; distal extremity of eye-stalk directed suddenly more vertically. Palpebral lobe subcircular in outline; posterior margin more strongly rounded than anterior or lateral margins, giving the impression that the entire palpebral lobe is

twisted backward. Dorsal surface of palpebral lobe strongly concave with lowest point at anteromedial edge. Palpebral furrow runs near lateral margins of lobe around entire circumference except where palpebral lobe attaches to eye-stalk. Muscle scars not expressed on dorsal or ventral surface of exoskeleton. Ornament of widely scattered, fine pustules (Pl. 15, Figs 2a, 2e). Occipital tubercle appears absent although internal molds not well preserved.

Librigenae long (exsag.), with long (exsag.) genal spines. Posterior margin sloping laterally and backward into curve of genal spine. Spines long, bowed outward, presumably to hug lateral margin of thorax, broken posteriorly. Posterior border furrow deep, long (exsag.); continuing across gena to spine. Widest point of librigena behind eye. Dorsal surface weakly convex. Eye-stalk very thin, long; directed outward and upward from dorsal surface. Termination and visual surface not preserved. Librigena much narrower (tr.) anteriorly. Inner margin converging gradually on lateral margin then broken. Lateral margin rounded. Cuticle of librigenae without ornament. Hypostome and thorax unknown.

Pygidium subtriangular in outline; lateral margins converging on posterior margin at about 30° to sagittal. Posterior margin rounded. Maximum length (sag.) approximately 75% maximum width (tr.). Axis weakly convex. Articulating facets prominent. Axial furrows weakly defined. Pleural furrows visible on dorsal surface. Pleural furrow of the first segment deeply impressed. Articulating half ring preserved as flattened forward extension of axis; axial rings weakly expressed. Pleural regions gently convex then abruptly steepen to lateral margin. Border furrow absent on large holaspids; smaller individuals with remnant of border (Pl. 16, Fig. 5). Cuticle of

pygidium without ornament.

Ontogeny: Smallest cranidium (OU11830; Pl. 16, Fig. 2) 13.7 mm wide (tr. across posterior fixigenae). Greater effacement of posterior border furrow, decreased convexity with development. Smallest pygidium (OU11833; Pl. 16, Fig. 5) 15.6 mm long (sag.). Short (sag.) posterior border (Pl. 16, Fig. 5b) becoming shorter through growth (Pl. 17, Fig. 2b) until obsolete (Pl. 17, Fig. 4b).

Discussion: *Ectenaspis abothros* differs from *E. beckeri* mainly in the absence of a pygidial border furrow. Pustules on the cranidium are coarser and more extensively distributed in *E. abothros* and pleural furrows of the pygidium show less effacement.

Genus *Stegnopsis*, Whittington, 1965

Type species: *Stegnopsis solitarius*

Diagnosis: A genus of isoteline with broadly divergent anterior facial sutures. Glabella without anterior expansion; frontal area broad both laterally and anteriorly. Palpebral lobes positioned far back on cranidium. Pygidium highly effaced, subcircular in outline with broad border continuing to anterior margin.

Discussion. Whittington (1965) diagnosed *Stegnopsis* as an isoteline with wide cranidial and pygidial borders, weak axial furrows of the cranidium and strongly divergent anterior facial sutures. He speculated that *Stegnopsis* is most closely

related to *Isoteloides* but differs from the latter in having palpebral lobes that are located much closer to the posterior margin and in having more divergent anterior facial sutures. *Stegnopsis* is otherwise very similar to *Isoteloides* in retention of plesiomorphic features [a short (sag.), subcircular pygidium, wide border furrows of cranidium and pygidium, wide (tr.) librigenae, genal spines in holaspids, minimal anterior expansion of glabella, relict segmentation of pygidium] in comparison with asaphines and niobines. *Stegnopsis* is distinguished from *Isoteloides* by two features in addition to those mentioned by Whittington. The cranidium has uncommonly high convexity and the anterior lobe of the hypostome lacks a border. These features may be apomorphies of *Stegnopsis*, but the monophyly of the genus is currently unclear

Stegnopsis huttoni, described by Whittington from the same formation as the type species, *S. solitarius*, has the anteriorly expanding glabella typical of *Isotelus*. It is similar to "*Isotelus*" *maximus* in possessing wide librigenae, holaspid genal spines and a rounded pygidium but is unique in having an extremely narrow axial lobe (Whittington, 1965, pl. 22, fig. 14). Although the appropriate taxonomic position of this species is currently unknown, its inclusion in *Stegnopsis* confuses the definition of that genus and the following discussion doesn't include it. I recommend calling it "*Isotelus*" *huttoni* for now. Whittington suggests some affinity of *Stegnopsis* with *Lachnostoma* Ross, 1951 but the shape of the glabella of the latter suggests that it is an asaphine (Fortey, 1980).

Shaw (1968) remarked on the similarities between *Stegnopsis* and *I. harrisi* Raymond, 1905. He differentiated them based on characters that are present in *S. huttoni* but lacking in the type, *S. solitarius*. *Isotelus harrisi* is nearly

indistinguishable from *S. solitarius*, with the exception that the palpebral lobes are slightly farther forward in the former, and it is here reassigned to that genus. The two species share the following characters: anterior lobe of the hypostome without a lateral border, palpebral lobes located behind the mid-line of the glabella, strongly divergent anterior facial sutures, a wide cranidial border, a glabella that does not expand anteriorly, high convexity of the glabella, wide (tr.) librigenae, genal spines in holaspids, a short (exsag.) pygidium with a rounded posterior margin and a wide border furrow. Shaw (1968) reassigned several individuals of *I. platymarginatus* figured by Raymond (1910b, 1910c) to *S. harrisi.* Some of Raymond's figures are too poor to identify (1910b pl. 17, figs 1-3; 1910c pl. 37, figs 1-3) and others are examples of *Isoteloides* rather than *Stegnopsis* based on the anterior facial sutures that do not reach abaxially beyond the lateral limit of the palpebral lobes (1910b, pl. 19, fig. 3; 1910c pl. 39, fig. 3). Some of Shaw's reassignments (1910b pl. 17, figs 4, 5; 1910c pl. 34, figs 3-7, pl. 37, figs 4, 5) appear to be valid.

Two isotelines from the upper Viola Springs and Welling formations are assigned to *Stegnopsis* on the basis of the following characters. The palpebral lobes are located well behind the mid-line of the glabella and the posterior fixigenae are therefore short (exsag.), but wide (tr.) (Pl. 17, Fig. 5; Pl. 21, Fig. 1). The palpebral lobes are large as in *S. solitarius*, the facial sutures are nearly straight and strongly divergent for a long distance in front of the palpebral lobes, and the convexity of the cranidium is very high. In both, the glabella does not expand anteriorly. The pygidia of the Viola Group species are subcircular in outline with rounded posterior margins and broad border furrows (Pl. 19, Fig. 1; Pl. 21, Fig. 3). The Viola Group species,

unlike *S. solitarius*, appear to lack genal spines in holaspids (Pl. 20, Fig. 1). Acquisition and study of additional material, especially hypostomes, will help to improve the definition of this genus.

Stegnopsis wellingensis, new species

Pl. 17, Fig. 5; Pl.18; Pl. 19, Figs 1-4

Etymology: from the Welling Formation

Type Material: A cast of a cranidium (Holotype, OU11837), two partial cranidia, one partly and the other completely exfoliated (Paratypes, OU11838, OU11839), four pygidia of varying sizes, mostly exfoliated (Paratypes, OU11840, OU11844, OU11846, OU11847), and a cast of a pygidium showing details of the cuticle (Paratype, OU11845).

Stratigraphic Occurrence: The type material is from the Upper Ordovician Welling Formation (LQ-WF).

Diagnosis: A species of *Stegnopsis* with facial sutures converging at anterior of cranidium at low angle; maximum width anterior to palpebral lobes near anterior margin. Convexity of cranidium very high.

Description: Glabella very convex transversely and longitudinally over posterior 3/4

of length. Frontal area nearly horizontal (Pl. 18, Fig. 1b). Axial and preglabellar furrows very shallow, broad, expressed only as change in convexity from glabella to fixigenae and frontal area, only faintly impressed at level of palpebral lobes; not discernable behind palpebral lobes. Outline of glabella broadly rounded, without expansion in front of palpebral lobes. Occipital furrow very weak, only visible on internal molds (Pl. 17, Fig. 5a). Glabellar furrows not expressed. Median tubercle absent. Palpebral lobes far back on cranidium about 1/4 total length (sag.) in front of posterior margin. Palpebral region of fixigena tapering into laterally and slightly posteriorly directed eye-stalk. Palpebral lobe oriented horizontally, directed slightly backward; slightly longer (exsag.) than wide (tr.); lateral margin broadly rounded. Palpebral furrow deep and wide. Anterior branches of facial sutures directed first inward then outward and around maximum width (tr.), converging toward sagittal line at low angle to horizontal. Suture path "s"-shaped with posterior curve shorter (exsag.) than anterior curve. Maximum width (tr.) of cranidium at posterior margin. Maximum width (tr.) in front of palpebral lobes at 3/4 distance from posterior margin. Facial sutures follow similar course to preglabellar furrow but separated by distance about 1/6 total length forming broad, flat frontal area. Posterior branch of facial suture running laterally, only slightly posteriorly to distance nearly equal to width (tr.) of palpebral lobe before curving abruptly to meet posterior margin. Posterior border furrow absent. Posterior margin nearly flat, laterally deflected only slightly backward. Posterior fixigenae only slightly shorter (exsag.) distally than medially. Surface of cuticle without ornament.

Librigenae wide (tr.); widest point just behind eye-stalk. Genal angle

rounded. In front of eye-stalk, inner margin of librigena converges strongly on lateral margin then is broken in the only known specimen. Posterior margin directed posterolaterally. Eye-stalks directed dorsolaterally; visual surface not preserved. Only known specimen is exfoliated. Hypostome and thorax unknown.

Pygidium subovate in outline, wider (tr.) than long (sag.), length approximately 65% of width. Convexity very low, height approximately 35% of length. Articulating facets prominent, oriented at a low angle to horizontal. Axial furrows and pleural furrows of first segment moderately well-defined; axial rings and pleural furrows faintly preserved on internal molds (Pl. 18, Figs 3a, 7a; Pl. 19, Fig. 2). Border furrow wide; expressed as change in slope from pleural regions to margin. Dorsal surface of exoskeleton without ornament.

Ontogeny: Small cranidium not available. Smallest pygidium (OU11840; Pl. 18, Fig. 3) 20.5 mm long (sag.) Progressive effacement of axial furrows, posterior border furrow through ontogeny.

Discussion: *Stegnopsis wellingensis* bears some resemblance to *I. levis* Chugaeva, 1958 in the course of the anterior facial sutures. The poor preservation of the figured specimen and lack of additional material makes further comparison impossible. *Stegnopsis wellingensis* is similar to *S. solitarius* in the course of the facial sutures and high convexity of the cranidium but the anterior border of the type is longer (sag.) and more steeply sloped. The posterior margin of the pygidium of *S. solitarius* is more broadly rounded and the border furrow is longer (sag.). The frontal area and

lateral border of *S. harrisi* are much broader and the facial sutures converge at a lower angle than in *S. wellingensis*; the glabella appears to contract anteriorly in the former. The concave lateral border present in *S. harrisi* is absent in large individuals of *S. wellingensis*.

Stegnopsis byzanteneidos, new species

Pl. 18, Figs 4-6?; Pl. 19, Figs 4?, 5; Pls 20, 21

Etymology: The trivial name describes the resemblance of the outline of the cranidium to a Byzantine dome.

Type Material: A nearly complete, small cranidium (Holotype, OU11853), three partial cranidia of varying sizes (Paratypes, OU11849, OU11852, OU11854), a cast of a partial cranidium (Paratype, OU11851), a nearly complete, weathered individual (Paratype, OU11850), two nearly complete pygidia (Paratypes, OU11855, OU11856) and a cast of a broken pygidium showing ornament of the cuticle (Paratype, OU11857). A meraspid cranidium (OU11841), two meraspid librigenae (OU11842, OU11843), and a meraspid pygidium (OU11848) are tentatively assigned to this species.

Stratigraphic Occurrence: The type material is from the Upper Ordovician Viola Springs (77-181.5 to 77-183) and Welling formations (Nebo-Well) of Oklahoma. Meraspid material tentatively assigned to this species is from the upper part of the

Viola Springs Formation (BQ-12 to BQ-18).

Diagnosis: A species of *Stegnopsis* with very wide, evenly rounded cranidial border; anterior facial sutures directed abruptly forward at intersection to form sharp point. Palpebral lobes large. Librigenae without genal spines in large holaspids.

Description: Cranidium with high longitudinal convexity. Glabella sloping upward from posterior margin to level of eyes. Longitudinal convexity lower from palpebral lobes to point 3/4 distance in front of posterior margin then sloping steeply down to frontal area. Transverse convexity low. Axial and preglabellar furrows expressed as transition from convex glabella to flat border and frontal areas. Glabella without expansion in front of palpebral lobes. Anterior margin of glabella broadly rounded. Axial furrows at level of palpebral lobes very shallow, becoming obsolete to posterior. Occipital furrow broad, shallow, located very close to posterior margin. Glabellar furrows visible only on small specimens (Pl. 19, Fig. 5a). Palpebral lobes behind mid-point of cranidium. Palpebral regions of fixigenae extending upward forming short (d.-v.), long (exsag.) eye-stalk, elevated only slightly above maximum height of glabella. Palpebral lobes oriented horizontally; length (exsag.) about equal to width (tr.). Palpebral furrow very weak, located at top of eye-stalk, paralleling lateral margin of palpebral lobe. Anterior facial sutures diverging to point nearly equal to anterior margin of glabella then running toward sagittal line at high angle to horizontal. In front of palpebral lobes, maximum width of cranidium located 2/3 distance from posterior margin. Broad, flat, spade-shaped frontal area between the

glabella and margins of cranidium. Posterior branch of facial suture running abaxially and slightly posteriorly well past lateral margin of palpebral lobe then deflected backward at high angle to meet posterior margin. Posterior border furrow not present. Posterior fixigena short (exsag.), narrowing only slightly abaxially. Posterior margin nearly horizontal. Ornament of wide, shallow pits not visible without magnification. Very faint sagittal line visible on internal molds (Pl. 20, Fig. 4c).

Librigenae wide (tr.), widest point at posterior margin. Genal angle rounded. Lateral margin evenly rounded. Inner margin rounded, converging on lateral margin in front of eye. Anterior portion of librigena narrow (tr.). Dorsal surface weakly convex. Eye-stalk and visual surface not preserved.

Thorax wide (tr.), composed of eight segments. Axial furrows broad, deep. Axis wide (tr.), about 50% total width of thorax. Adaxial 1/2 of pleurae nearly horizontal; abaxial 1/2 deflected ventrally. Articulating facets wide (tr.), located on abaxial 1/2 of pleurae, becoming longer (exsag.) to lateral margins. Hypostome unknown.

Pygidium subovate in outline, length (sag.) about 75% of width (tr.). Inflation moderate, height 60% of length. Border furrow wide; continuing with equal width forward to articulating facet. Articulating facets prominent, oriented at low angle to horizontal. Pleural furrows of first segment deeply impressed. Axial and pleural furrows well defined on internal molds (Pl. 21, Fig. 3a); axial rings weak. Ornament if densely packed, fine pits.

Ontogeny: Smallest (unequivocal) cranidium (OU11849; Pl. 19, Fig. 5) 6.3 mm long (sag.). S1, occipital furrows effaced during growth. Possible librigena indicates loss of genal spines. Ontogenetic series of pygidia not available.

Discussion: The glabella of *S. solitarius* is similar to that of *S. byzanteneidos*, but the anterior facial sutures in the latter are more evenly curved around the point of maximum width. Holaspid genal spines are present in *S. solitarius* but lacking in the Viola species. Pygidia of *S. byzanteneidos* have relict pleural furrows and well defined axis while those of *S. soliatarius* have greater effacement and are more rounded posteriorly. *Stegnopsis byzanteneidos* is similar to *S. harrisi* in the course of the facial sutures but the widest point of the cranidium in the former is evenly rounded rather than angled. The Viola species has a parallel-sided glabella with a rounded anterior margin rather than an anterior constriction. The pygidia of *S. harrisi* and *S. byzanteneidos* are similar in outline and border width, but the pygidium is more effaced in the former. This species differs from *S. wellingensis* in having a wider (tr.) cranidial border, and a frontal area that is formed by a lateral deflection of the facial sutures in front of the palpebral lobes and a high angle of convergence of the sutures toward the sagittal line.

Genus *Anataphrus* Whittington, 1954

Type species: *Anataphrus borraeus* Whittington, 1954

Discussion: Chatterton and Ludvigsen (1976) regarded *Anataphrus*, *Nahannia*

Chatterton and Ludvigsen, 1976, *Protopresbynileus* Hintze, 1954, *Vogdesia* Raymond, 1910c and *Homotelus* Raymond, 1920 as a closely related group of isoteline genera. I consider them to be a derived group united by potential apomorphies including: a glabella that reaches the anterior margin of the cranidium; effacement of the axial furrows, especially on the cranidium; and wide pygidial axes. The poorly known *Nileoides* Raymond, 1920 possesses these features and may also belong to this group.

Nahannia may be monophyletic based on the short (sag.) median body of the hypostome and, possibly, the retention of genal spines in holaspids. The wide border on the pygidium, which is present in the ontogeny of *Anataphrus*, is likely to be plesiomorphic.

The status of *Anataphrus*, *Protopresbynileus* and *Nileoides* is uncertain, but all show greater effacement than *Nahannia*. Effacement of the thorax in *Anataphrus* may prove to be apomorphic. In *Anataphrus glomeratus* Dean, 1979, the position of the palpebral lobes close to the posterior margin of the cranidium and large size of the palpebral lobes make it look superficially like *Nahannia*. Absence of both a border furrow on the pygidium and of holaspid genal spines assignment to *Anataphrus*. *Isotelus spurius* Phleger, 1933 (see Ross, 1967 pl. 4, figs 6-9; 1970 pl. 13, figs 3, 5, 7, 10) is highly effaced and lacks a border on the pygidium and is here reassigned to *Anataphrus*. The effacement of *Nileoides* seems to match that of *Anataphrus*, but the eyes are apparently in a more posterior position. *Protopresbynileus* is comparable to *Anataphrus* in cranidial and pygidial effacement but the thorax is unknown. A median border spine on the hypostome could be an apomorphy but it is possible that

recognition of *Protopresbynileus* will create paraphyly in *Anataphrus* and/or *Nileoides*. Until the status of these genera can be evaluated through a phylogenetic analysis, I recommend retaining all genera.

Vogdesia is distinct among this group mainly in having a pygidium that is elongate and posteriorly tapering rather than subcircular in outline. The lesser degree of effacement of the axial furrows of the cranidium behind the palpebral lobes and narrower axial lobe are also distinctive. *Vogdesia* is especially problematic because the types of the type species, *V. bearsi*, have been lost. Shaw (1968) figured topotype material and designated a neotype. This genus is another candidate for revision. *Isotelus simplex* Raymond and Narraway, 1910 (also see DeMott, 1987) lacks a frontal area but also has a short (exsag.) tapering pygidium with only moderate effacement typical of *Vogdesia* and is here tentatively reassigned to that genus. Whittington (1954) attributed some species originally assigned to *Vogdesia* to *Anataphrus* including *A. gigas*, *A. vigilans* and *A. raymondi*.

Homotelus was erected by Raymond (1920) for isotelines lacking genal spines but with wide cranidia, weak axial furrows, elevated palpebral lobes and a lateral border. Jaanusson (in Moore, 1959) added that a frontal area is lacking and the palpebral lobes are positioned slightly in front of the transverse mid-line of the cranidium. Whittington (1950) noted that the differences between *Homotelus* and *Isotelus* are small and recommended restricting the genus to the type. I agree that the genus should be restricted but feel that the lack of a frontal area on the cranidium allies *Homotelus* more closely with *Vogdesia* than *Isotelus*. Some species previously assigned to *Homotelus* (e.g., *H. bromidensis*, Esker, 1964) may belong in *Vogdesia*.

Anataphrus megalophrys, new species

Pls 22-24; Pl. 25, Figs 1-6

Etymology: This species is named for the large size of the palpebral lobe.

Type material: A nearly complete, testate cranidium (Holotype, OU11866), eight cranidia of varying sizes, all with at least some cuticle preserved (Paratypes, OU11858, OU11859, OU11860, OU11861, OU11862, OU11863, OU11864, OU11865), two librigenae (Paratypes, OU11868, OU11869), three hypostomes (Paratypes, OU11867, OU11870, OU11871), an articulated thorax and pygidium (Paratype, OU11873), two meraspid pygidia (Paratypes, OU11879, OU11883), a small pygidium (OU11872), and eight larger pygidia (Paratypes, OU11874, OU11875, OU11876, OU11877, OU11878, OU11880, OU11881, OU11882).

Stratigraphic Occurrence: The type material is from the Upper Ordovician Viola Springs Formation (99-39 to 99-49.5; LQ-VS).

Diagnosis: A species of *Anataphrus* with long (exsag.), wide (tr.) palpebral lobes. Pygidium long (sag.) relative to width (tr.); axial lobe weakly defined on internal molds.

Description. Longitudinal convexity of cranidium low; anterior 1/4 of cranidium

sloping at about 45° to anterior margin. Palpebral lobes at about 40% total length (sag.) from posterior margin. Axial furrows effaced except from just behind to just in front of palpebral lobes. Occipital furrow effaced on dorsal surface; preserved on internal molds (Pl. 22, Figs 7a, 8). Occipital ring longest sagittally reaching almost to occipital tubercle; furrow converging on posterior margin laterally; occipital ring very short (exsag.) on posterior fixigenae. Posterior branch of facial sutures directed backward for short distance then running posterolaterally at 25°, steepening to 35° before turning abruptly at termination of posterior fixigenae to intersect posterior margin. Anterior branch of facial suture directed slightly adaxially and forward for short distance; abruptly directed anterolaterally for to maximum width then curving abruptly around point of maximum width; directed anteriorly and strongly adaxially to intersect at anterior margin. Anterior margin of cranidium with short (sag.), sharp point at intersection of facial sutures. Glabella poorly defined; only weakly convex transversely. Posterior fixigenae becoming shorter (exsag.) laterally, directed weakly backward and downward. Palpebral lobes large, wide (tr.) and long (exsag.); lateral termination evenly rounded; oriented horizontally, elevated only slightly above height of glabella. Occipital tubercle well defined on internal molds (Pl. 22, Fig. 2a), positioned just in front of occipital furrow. Ornament absent on dorsal surface of exoskeleton in large holaspids (Pl. 23, Fig. 1b). Small holaspids with fine pits (Pl. 22, Fig. 3). Faint terrace ridges on anterior of cranidium present in small holaspids (Pl. 22, Fig. 2c) become fainter with increasing size (Pl. 22, Fig. 6a), absent in larger individuals (Pl. 23, Fig. 1b, 1c).

Librigenae subtriangular in outline; widest point just behind eye. Genal angle

rounded in holaspids. Posterior margin rounded, lateral margin weakly convex. Inner margin converging strongly on lateral margin in front of eye then nearly parallel to lateral margin, converging only weakly until intersecting with lateral margin at anterior. Dorsal surface of gena only weakly convex. Furrow at base of visual surface well defined. Visual surface continuing for about 170°, tall, becoming shorter toward anterior.

Hypostome wider (tr.) than long (sag.), length about 90% of width. Lateral margins bowed strongly outward; maximum width (tr.) across posterior lobe nearly equal to maximum width (tr.) across anterior margin. Maculae well-defined; positioned about 1/2 distance from anterior border to posterior border (exclusive of forks). Fork deep, making up about 50% total length (sag.) of hypostome; inner margins of fork nearly parallel; posterior termination of fork rounded. Terrace ridges roughly parallel lateral margins and inner margins of fork. Middle body and posterior lobe with widely scattered fine pits.

Thorax of eight segments. Axis wide (tr.), about 65% total width (tr.) of thorax, weakly convex. Articulating furrow effaced. Pleural portions of thoracic segments deflected strongly ventrally. Articulating facets of pleurae oriented anterolaterally; extend entire width (tr.); non-articulating portion becoming shorter (exsag.) distally. Short (exsag.), subtriangular process extending backward from posterior margin of thoracic segments at intersection of axial and pleural regions; process articulates with corresponding shallow facet on anterior margin of segments.

Pygidium length (sag.) about 65% of width (tr.). Axis without independent convexity, raised to slightly higher elevation on internal molds (Pl. 24, Fig. 5b).

Axial furrows effaced. Axis wide (tr.), about 50% total width (tr.) of pygidium, tapering toward posterior. Anterior margin transverse to very weakly rounded. Posterior margin evenly rounded. Inflation of pygidium moderate, height 55% of length (sag.). Articulating facets well-defined. Ornament of fine terrace ridges most pronounced near articulating facets. Doublure arising just behind anterior margin of articulating facet; length (exsag.) roughly uniform around entire posterior margin of pygidium. Dorsal surface of doublure parallel to dorsal surface of pygidium; anterior margin of doublure deflected toward posterior to form relatively wide (tr.) notch at level of posterior termination of axis. Ornament of terrace ridges subparallel to anterior margin of doublure.

Ontogeny: Smallest cranidium (OU11858) 1.9 mm long (sag.). Pitting of cuticle (Pl. 22, Fig. 3) decreases with growth. Smallest pygidium (OU11872; Pl. 23, Fig. 7) 1.0 mm long (sag.). Posterior margins become more rounded through ontogeny; increasing effacement pleural furrows, axial rings; axial rings better defined with large size. Border furrow of pygidium lost early in ontogeny.

Discussion: *Anataphrus megalophrys* is very similar to *A. borraeus* but has larger palpebral lobes, the cranidium in front of the palpebral lobes is narrower (tr.) and the cranidium widens (tr.) more abruptly in front of the palpebral lobes. The glabella of *A. martinensis* Ross and Shaw, 1972 is narrower and the pygidium is shorter (exsag.) than in *A. megalophrys*. *Anataphrus spurius* has a very short (exsag.) cranidium.

Anataphrus kermiti, new species

Pl. 25, Figs 7-10; Pls 26-31

Etymology: Named for Kermit the Frog, whom this species resembles in anterior view.

Type material: A nearly complete, enrolled individual (Holotype, OU11889), a second nearly complete enrolled individual (OU11937), two nearly complete individuals (OU11938, OU11939), three cranidia with strap-like palpebral lobes (OU11884, OU11887, OU11908), three casts of cranidia with strap-like palpebral lobes (OU11885, OU11909, OU11910), two cranidia with waisted palpebral lobes (OU11888, OU11911), three casts of cranidia with waisted palpebral lobes (OU11892, OU11893, OU11897, three cranidia missing palpebral lobes (OU11899, OU11906, OU11940), three small cranidia (OU11914, OU1195, OU11920), two librigenae (OU11898, OU11912), two hypostomes (OU11900, OU11901), four pygidia (OU11895, OU11896, OU11907, OU11941), five small pygidia (OU11886, OU11890, OU11894, OU11904, OU11905), two meraspid cranidia (OU11918, OU11919), four meraspid librigenae (OU11916, OU11921, OU11922, OU11923), two meraspid hypostomes (OU11924, OU11925), fifteen meraspid pygidia (OU11891, OU11902, OU11903, OU11917, OU11926, OU11927, OU11928, OU11929, OU11930, OU11931, OU11932, OU11933, OU11934, OU11935, OU11936).

Stratigraphic Occurrence: Type material is from the upper Viola Springs Formation (77-218 to 77-219, BQ-pave to BQ-24, CC, MC) and Welling Formation (LQ-WF, Nebo-Well).

Diagnosis: A species of *Anataphrus* with small palpebral lobes. Cuticle densely pitted; anterior margin of cranidium with coarse, parallel terrace ridges. Lateral margins of hypostome only slightly curved outward. Eyes on long stalks, directed dorsally and slightly abaxially.

Description. Longitudinal convexity of cranidium very low, nearly flat over posterior 3/4 then sloping abruptly to anterior margin. Palpebral lobes slightly behind transverse mid-line of cranidium. Axial furrows mainly effaced; weakly expressed in palpebral region. Occipital furrow effaced on dorsal surface; preserved on some internal molds (Pl. 28, Fig. 10). Occipital ring longest sagittally. Posterior border furrow absent. Posterior branch of facial sutures directed backward at about 45° for half length of posterior fixigenae then directed more sharply backward to intersect posterior margin. Posterior margin directed backward abaxially so that lateral extremities of posterior fixigenae directed backward. Anterior branch of facial suture directed adaxially so that cranidium just in front of palpebral lobe narrower (tr.) than just behind. Sutures curving forward and abaxially around maximum width (tr.) in front of palpebral lobes then directed forward and adaxially to intersect at sharp point at mid-line. Glabella not defined; weakly convex transversely. Palpebral lobes wider

(tr.) than long (sag.), exhibit two distinct morphologies. Most individuals (especially small holaspids) with strap-like eye-stalks: nearly equal length (sag.) over entire width (tr.), rounded termination (Pl. 25, Figs 7, 8a, 10b; Pl. 26, Fig. 2; Pl. 29, Figs 2, 3a). Some individuals (especially large holaspids) with waisted eye-stalk: base of eye-stalk where intersects with fixigena narrow, widening upward to termination, rounded terminal piece directed slightly backward (Pl. 26, Figs 1a, 1c; Pl. 27, Figs 1a, 1d, 2; Pl. 28, Figs 1; Pl. 29, Fig. 5). Occipital tubercle weak, visible only on internal molds, located in front of occipital furrow. Ornament of fine, densely scattered pits becoming more obscure through ontogeny. Well-defined, parallel, transverse terrace ridges cover anterior 1/4 of cranidium.

Librigenae subrectangular in outline; widest point just behind eye, only slightly narrower (tr.) toward posterior margin. Genal angle and posterior margin rounded; lateral margin rounded more weakly. Inner margin converging sharply on lateral margin just in front of eye socle. Anterior portion of librigena very thin. Dorsal surface of gena weakly convex. Visual surface tall, inflated, covering about 270° field of view.

Hypostome narrow (tr.) for genus, without broad lateral flare between level of maculae and posterior margin between forked projections. Lateral margins weakly rounded. Maculae well-defined; located between anterior border and posterior margin between fork. Fork deep, wide (tr.), inner margins of fork nearly parallel, posterior terminations of fork broken. Terrace ridges parallel lateral margins of fork. Anterior wings long (exsag.). Ventral surface of hypostome nearly flat, curving slightly downward near anterior margin.

Thorax of 8 segments. Axis wide (tr.), greater than 60% total width (tr.) of thorax, weakly convex. Articulating furrow effaced. Pleural portions of thoracic segments curve evenly downward. Articulating facets of pleurae oriented anterolaterally; extend entire width (tr.), becoming shorter (exsag.) medially. Posterior margin of thoracic segments at intersection of axial and pleural regions with short, subtriangular posterior process; correspond to facets on anterior margin of segments.

Pygidium length (sag.) about 60% of width (tr.). Axis without independent convexity. Axial furrows effaced, faintly visible on internal molds. Axis width (tr.) about 60% total width (tr.) of pygidium. Anterior margin transverse; posterior margin evenly rounded. Convexity strong, height 90% of length (sag.). Articulating facets well-defined. Ornament of deep, densely packed pits less pronounced over axis; coarse terrace ridges across pleural regions and on articulating facets.

Ontogeny: Smallest cranidium (OU11918; Pl. 30, Fig. 1) 1.3 mm long (sag.). Axial, preglabellar, occipital, posterior border furrows well-developed in meraspids, progressive effacement through ontogeny to obsolescence in large holaspids (except axial furrows in palpebral region). Laterally directed palpebral lobes become elevated into stalks; relative size of palpebral lobes decreases (Pl. 27, Fig 2a). Narrow glabella widens through growth. Smallest librigena (OU11921; Pl. 30, Fig. 4) 1.2 mm wide behind eye. Genal spine lost in holaspids. Smallest hypostome (OU11924; Pl. 30, Fig. 7) 1.3 mm wide (tr.) across maculae. Sharp lateral projections behind maculae lost during growth. Smallest pygidium (OU11928; Pl. 30, Fig. 11)

0.8 mm long (sag.). Posteromedian notch lost in early stage. Strong axial, pleural furrows, axial rings gradually become effaced, also well-defined border furrow. Wide axis becomes wider.

Discussion: *Anataphrus kermiti* is most similar to *A. martinensis*, especially in the outline of the cranidium. The eye-stalks of *A. martinensis* are taller than in *A. kermiti* and the depressions in the palpebral regions of the fixigenae are deeper. *Anataphrus kermiti* has much smaller palpebral lobes than *A. borraeus*. The cranidium of *A. kermiti* is longer (sag.) and the posterior fixigenae are much wider (tr.) than in *A. spurius*. This species differs from *A. megalophrys* mainly in having smaller, more elevated palpebral lobes and a shorter pygidium with a more poorly-defined axis.

REFERENCES

API Well #12300123 (Morris #1): T3N, R6E, Sec18, about 5 km NNE of locality LQ.

API Well #12370042 (Fittswest Unit TR40-7): T2N, R6E, Sec 36, about 3 km N of locality 99.

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Plate 1 *Isotelus kimmswickensis*

1. UC28851A Paralectotype: broken, exfoliated cranidium x2 a) dorsal b) anterior c) lateral
2. UC28851B Paralectotype: broken, exfoliated cranidium x2 a) dorsal b) anterior c) lateral
3. OU11764 (99-30.5) mostly exfoliated transitory cranidium x8 a) anterior b) lateral c) dorsal
4. OU11765 (99-20) mostly exfoliated cranidiuim x5 a) dorsal b) lateral c) anterior
5. OU11766 (99-29) mostly exfoliated cranidium x3 in dorsal view
6. OU11767 (99-29) exfoliated cranidium x4 in dorsal view
7. OU11768 (99-08) cast of cranidium preserving palpebral lobe and furrow x4 in dorsal view
8. OU11769 (99-29) cast of cranidium x4 a) oblique b) dorsal
9. OU11770 (99-32) small, exfoliated pygidium x7 a) dorsal b) lateral

Plate 1

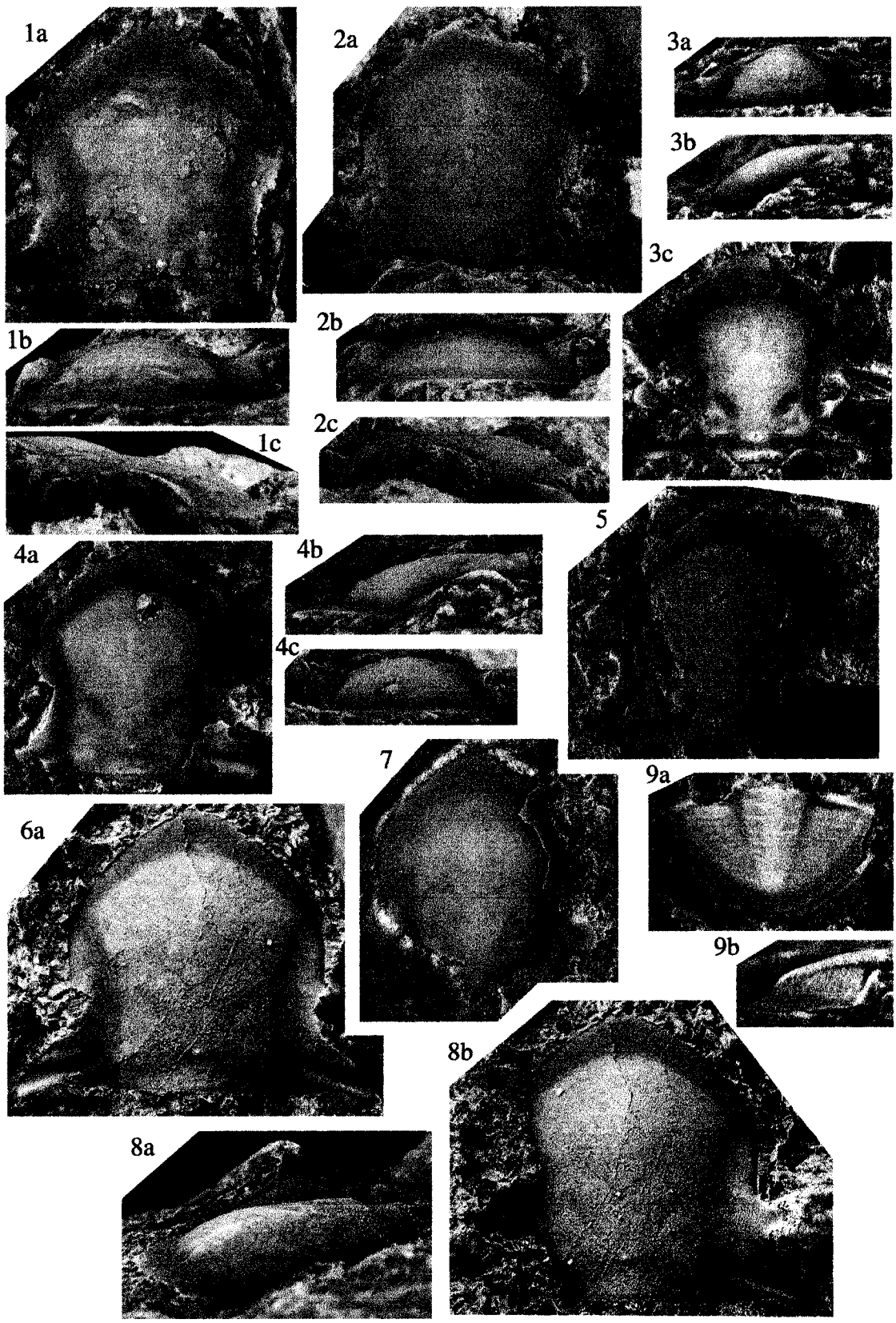


Plate 2 *Isotelus kimmswickensis*, *Isotelus kimmswickensis*?

1-5 *Isotelus kimmswickensis*

1. UC28853 Paratype exfoliated pygidium x1.5 a) dorsal b) posterior c) lateral
2. OU11771 (99-10) small pygidium x8 a) lateral b) dorsal
3. UC28851C Paralectotype broken, exfoliated pygidium x2.5 a) dorsal b) lateral c) posterior
4. OU11772 (99-13) small exfoliated pygidium x6 a) posterior b) lateral c) dorsal
5. UC28855 Paratype broken, exfoliated pygidium x2 a) dorsal b) lateral

6 *Isotelus kimmswickensis*?

6. OU11773 (99-29) mostly exfoliated hypostome x1 a) dorsal b) lateral

7-8 *Isotelus kimmswickensis*

7. OU11774 (99-30.25) small, partly exfoliated pygidium x5 a) posterior b) lateral c) dorsal
8. OU11775 (99-32) mostly exfoliated librigena with visual surface x3 a) lateral b) dorsal

Plate 2

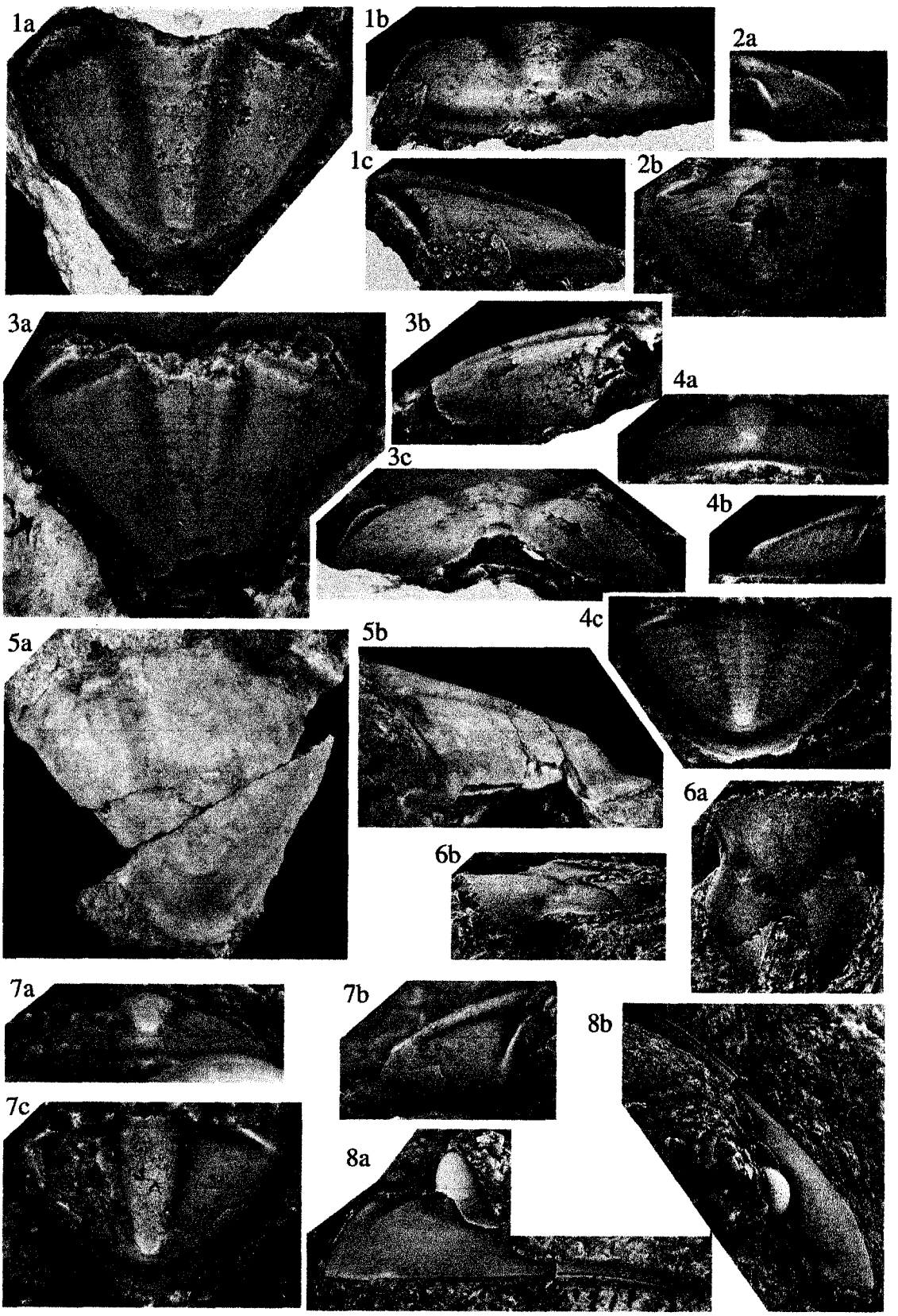


Plate 3 *Isotelus kimmswickensis, Isotelus violaensis*

1-5 *Isotelus kimmswickensis*

1. OU11776 (99-20) partially exfoliated pygidium x6 a) dorsal b) posterior c) lateral
2. OU11777 (99-18) partially exfoliated pygidium x4 a) lateral b) posterior c) dorsal
3. OU11778 (99-29) broken, exfoliated pygidium x3 a) posterior b) lateral c) dorsal
4. OU11779 (99-30.25) partial, partially exfoliated pygidium a) dorsal x3 b) cuticle x6
5. OU11780 (99-32) broken, exfoliated pygidium in dorsal view showing relict segmentation on internal mold x2.5

6-8 *Isotelus violaensis*

6. OU11781 (99-46.5) small, partially exfoliated cranidium in dorsal view showing lateral glabellar furrows on internal mold x5
7. OU11782 Holotype: (99-48) exfoliated cranidium x2 a) dorsal b) oblique
8. OU11783 (99-40sFloat) mostly exfoliated cranidium x2 a) anterior b) dorsal

Plate 3

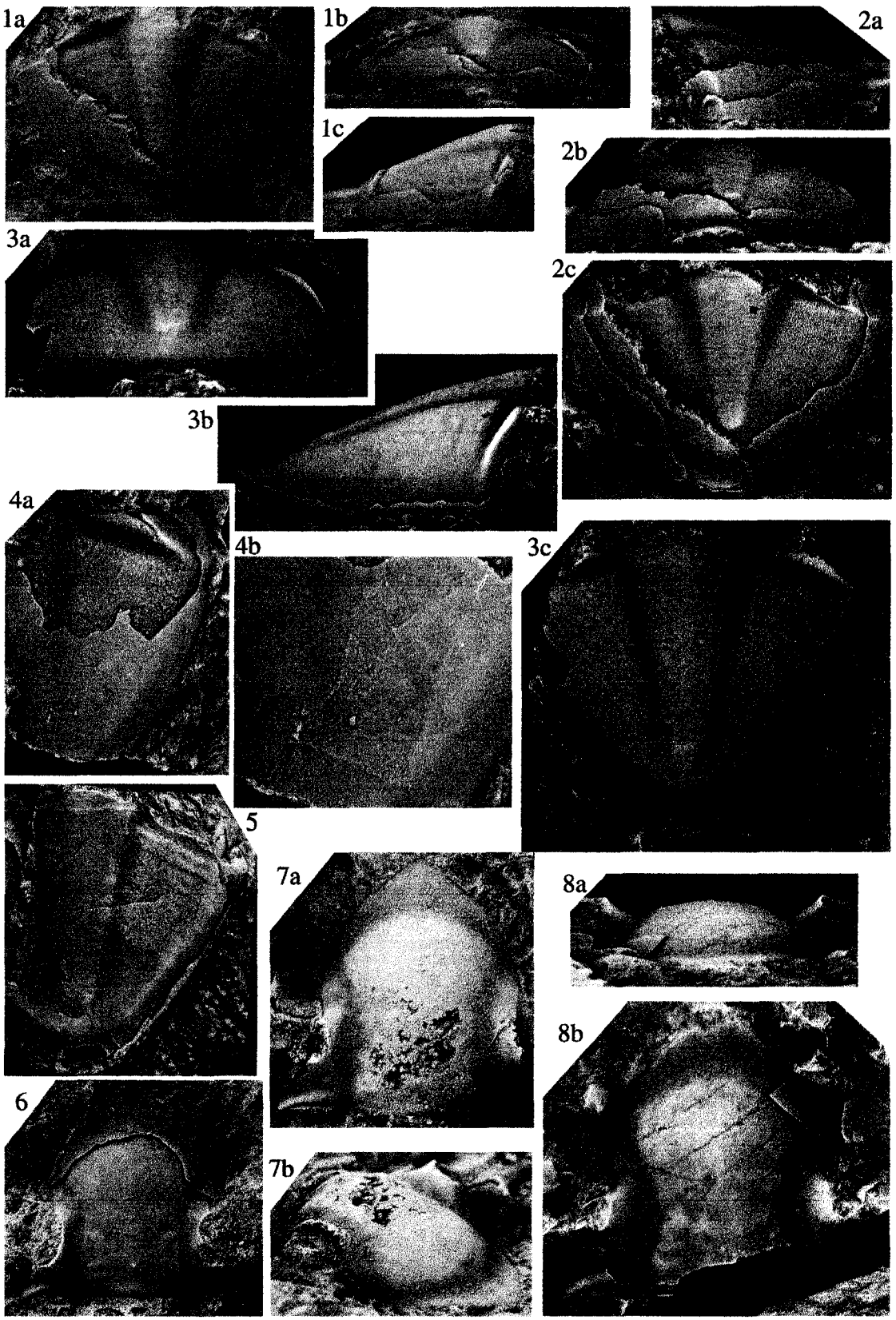


Plate 4 *Isotelus violaensis*

1. OU11784 (99-39) cast of cranidium x2 a) dorsal b) oblique c) anterior
2. OU11785 (99-48) cast of cranidium x2 a) dorsal b) anterior
3. OU11786 (99-46) small, exfoliated pygidium x6 a) lateral b) dorsal
4. OU11787 (99-46) mostly exfoliated pygidium x5 a) posterior b) dorsal c) lateral
5. OU11788 (99-39) exfoliated cranidium x2 a) dorsal b) oblique

Plate 4

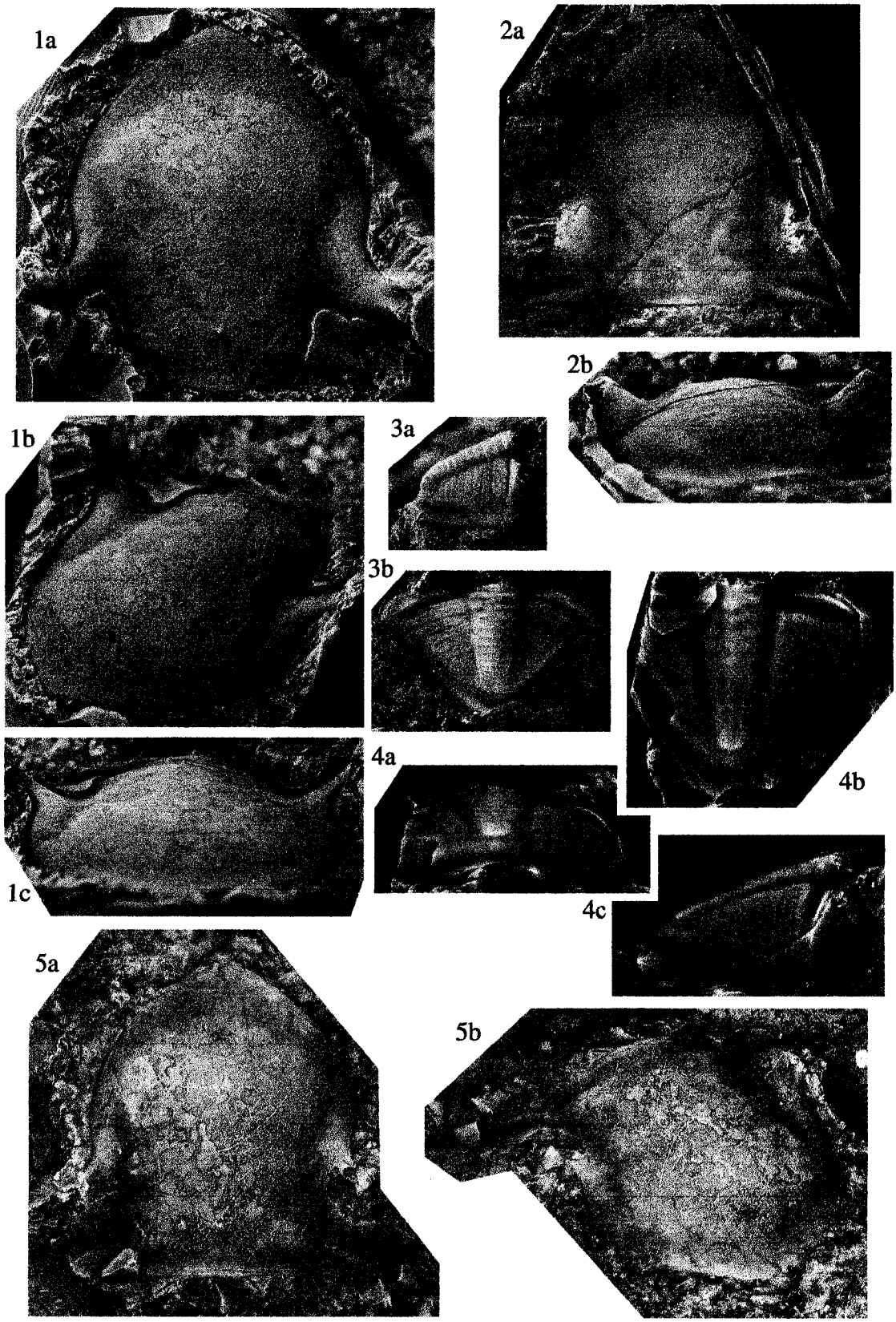


Plate 5 *Isotelus violaensis, Isotelus homalonotoides*

1-4 *Isotelus violaensis*

1. OU11789 (99-40sFloat) partially exfoliated pygidium x5 a) dorsal b) posterior c) lateral
2. OU11790 (99-46.5) cast of librigena without visual surface x3 a) dorsal b) anterior c) lateral
3. OU11791 (99-49) partly exfoliated, broken pygidium x4 a) dorsal b) close-up of cuticle x8
4. OU11792 (99-40sFloat) ventral view of broken hypostome tentatively attributed to this species x1

5-6 *Isotelus homalonotoides*

5. UC12324 Lectotype (designated herein): mostly exfoliated cranidium with missing palpebral lobes x3 a) dorsal b) lateral c) anterior
6. UC12324 Paralectotype (designated herein) complete, exfoliated pygidium x3 a) lateral b) posterior c) dorsal

Plate 5

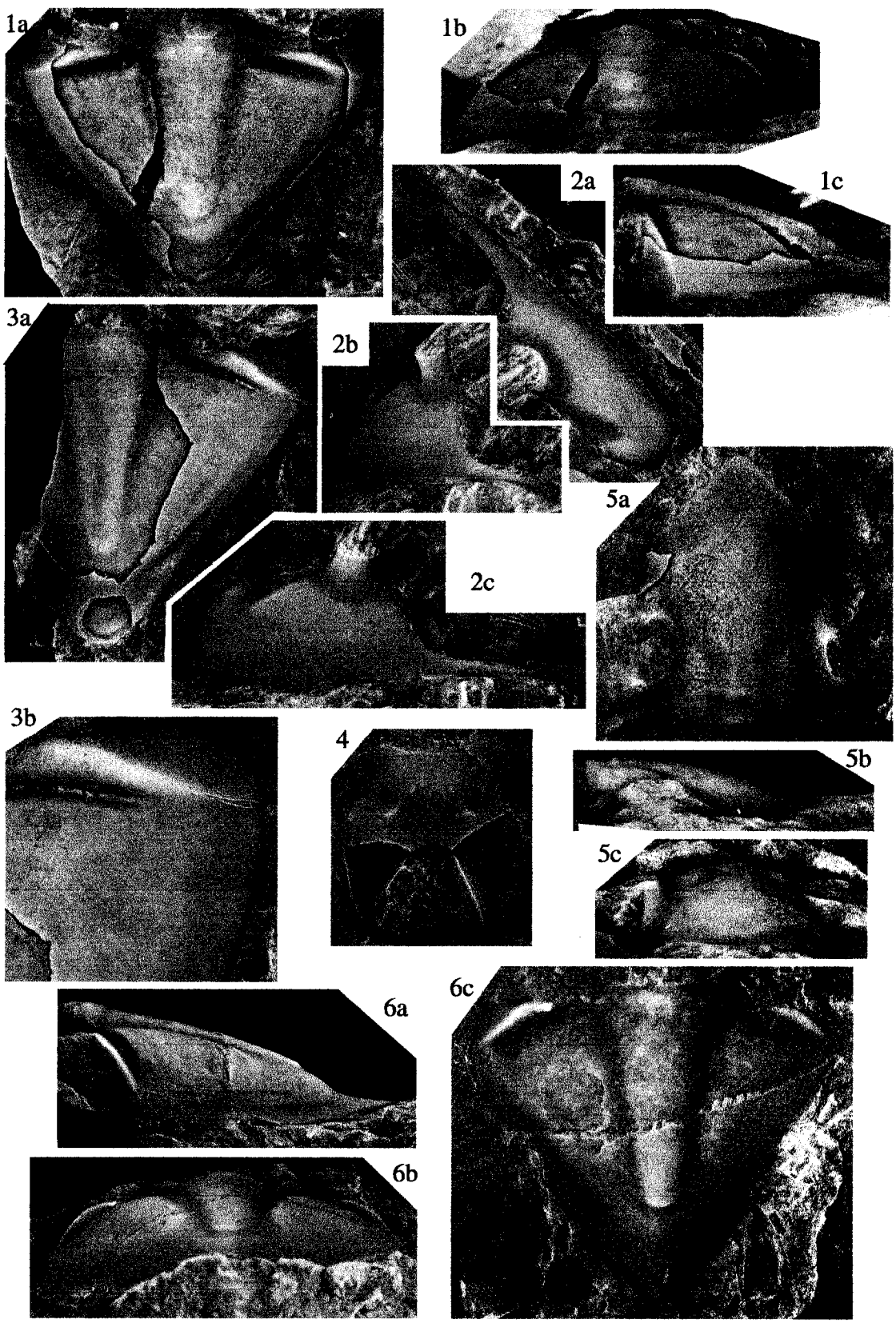


Plate 6 *Isotelus bradleyi*

1. OU11793 (99-08) cast of cranidium in dorsal view x8
2. OU11794 (99-13) partial, testate cranidium x8 a) dorsal b) oblque c) anterior
3. OU11795 (99-33) exfoliated cranidium x5 a) anterior b) dorsal c) lateral
4. OU11796 (99-13) partly exfoliated cranidium x5 a) anterior b) dorsal c) oblique
5. OU11797 (99-33) exfoliated, broken cranidium x3 a) dorsal b) lateral
6. OU11798 (99-32) cast with palpebral lobes and furrows preserved, in dorsal view x3
7. OU11799 (99-31.5) internal mold of librigena without eye stalk x4 a) dorsal b) anterior c) lateral
8. OU11800 (99-32) cast of cranidium showing pitted cuticle in dorsal view x3

Plate 6

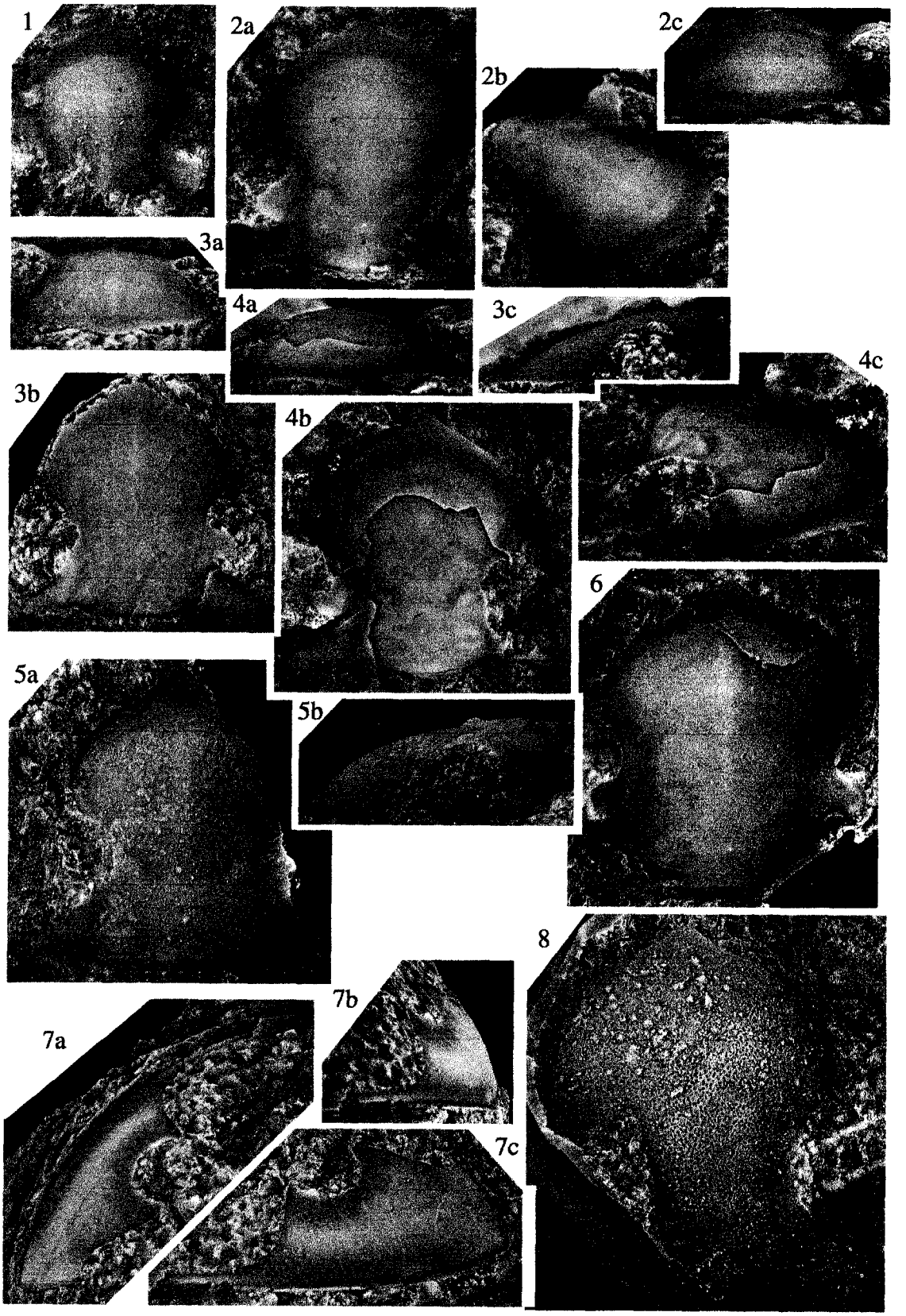


Plate 7 *Isotelus bradleyi*, *Isotelus* cf. *I. bradleyi*

1-3 *Isotelus bradleyi*

1. OU11801 (99-32) broken, mostly exfoliated cranidium x3 a) dorsal b) anterior c) cuticle x8 d) lateral
2. OU11802 (LQ-VS) mostly exfoliated librigena with visual surface x2 a) lateral b) anterior c) dorsal
3. OU11803 (99-32) exfoliated cranidium with lateral glabellar furrows x3 a) lateral b) anterior c) dorsal

4-6 *Isotelus* cf. *I. bradleyi*

4. UC28871 mostly exfoliated librigenae, part of visual surface preserved; labeled *I. gigas* but facial sutures match pattern for *I.* cf. *I. bradleyi* x1.5 a) anterior b) lateral c) dorsal
5. UC28854 labeled as a paratype of *I. kimmswickensis*; exfoliated cranidium x2.5 a) anterior b) lateral c) dorsal

Plate 7

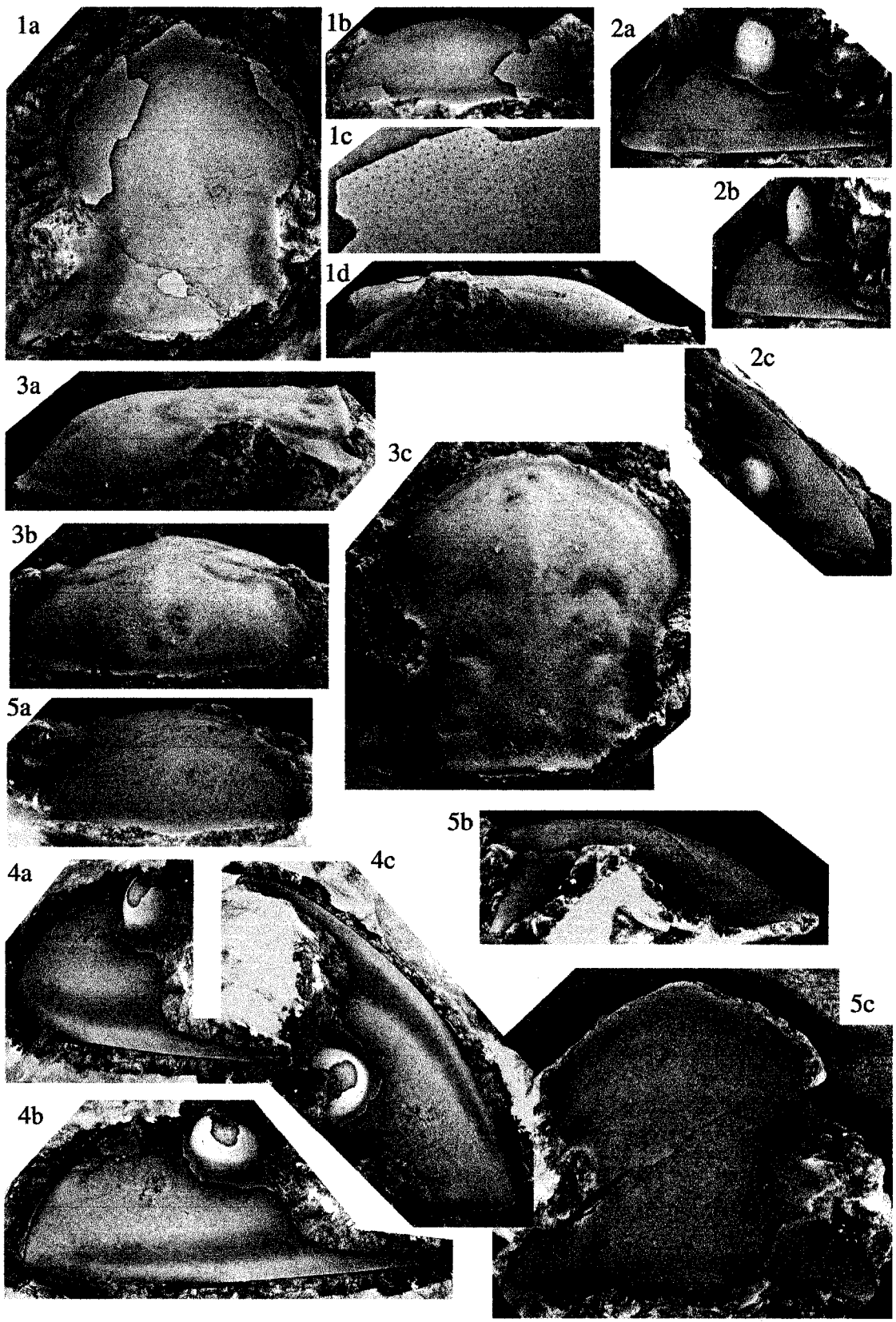


Plate 8 *Isotelus bradleyi, Isotelus skapaneidos*

1-3 *Isotelus bradleyi*

1. OU11804 (99-32) exfoliated broken pygidium x2 a) dorsal b) posterior c) lateral
2. OU11805 (99-32) exfoliated broken pygidium x3 a) dorsal b) posterior c) lateral
3. OU11806 (99-32) cast of broken pygidium a) dorsal x2 b) close-up showing pitting on cuticle x6

4-5 *Isotelus skapaneidos*

4. OU11807 (LQ-WF) broken pygidium x3 a) dorsal b) lateral
5. OU11808 (LQ-WF) mostly exfoliated, broken pygidium x1 a) dorsal b) lateral

Plate 8

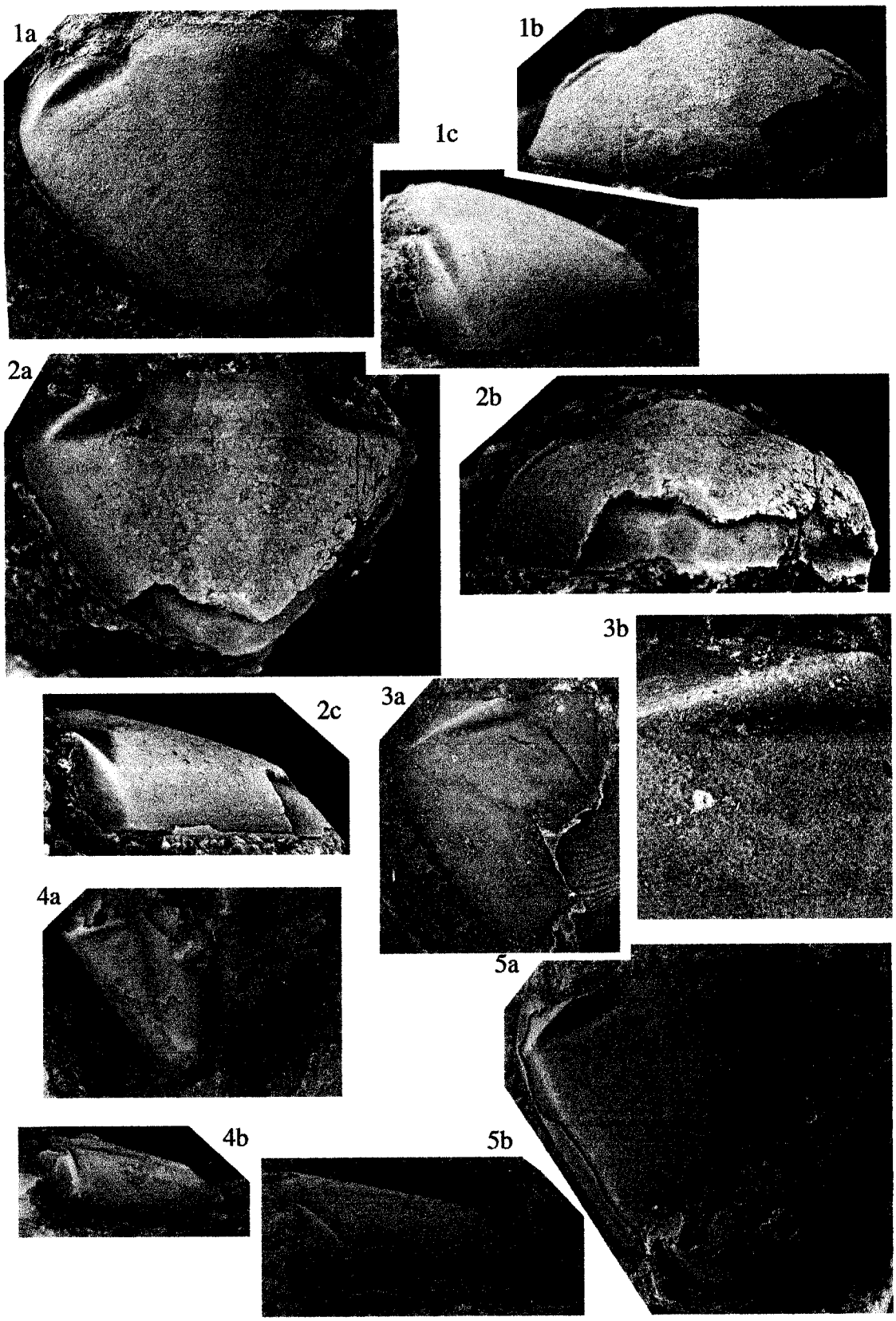


Plate 9 *Isotelus skapaneidos*

1. OU11809 (LQ-WF) mostly exfoliated, nearly complete cranidium in dorsal view x1
2. OU11810 (LQ-WF) nearly complete, testate cranidium x2.5 a) lateral b) dorsal
3. OU11811 (CN-Float) testate cephalon with right side broken x1 a) dorsal b) anterior
4. OU11812 (77-216) exfoliated pygidium x1.5 a) dorsal b) lateral c) posterior

Plate 9

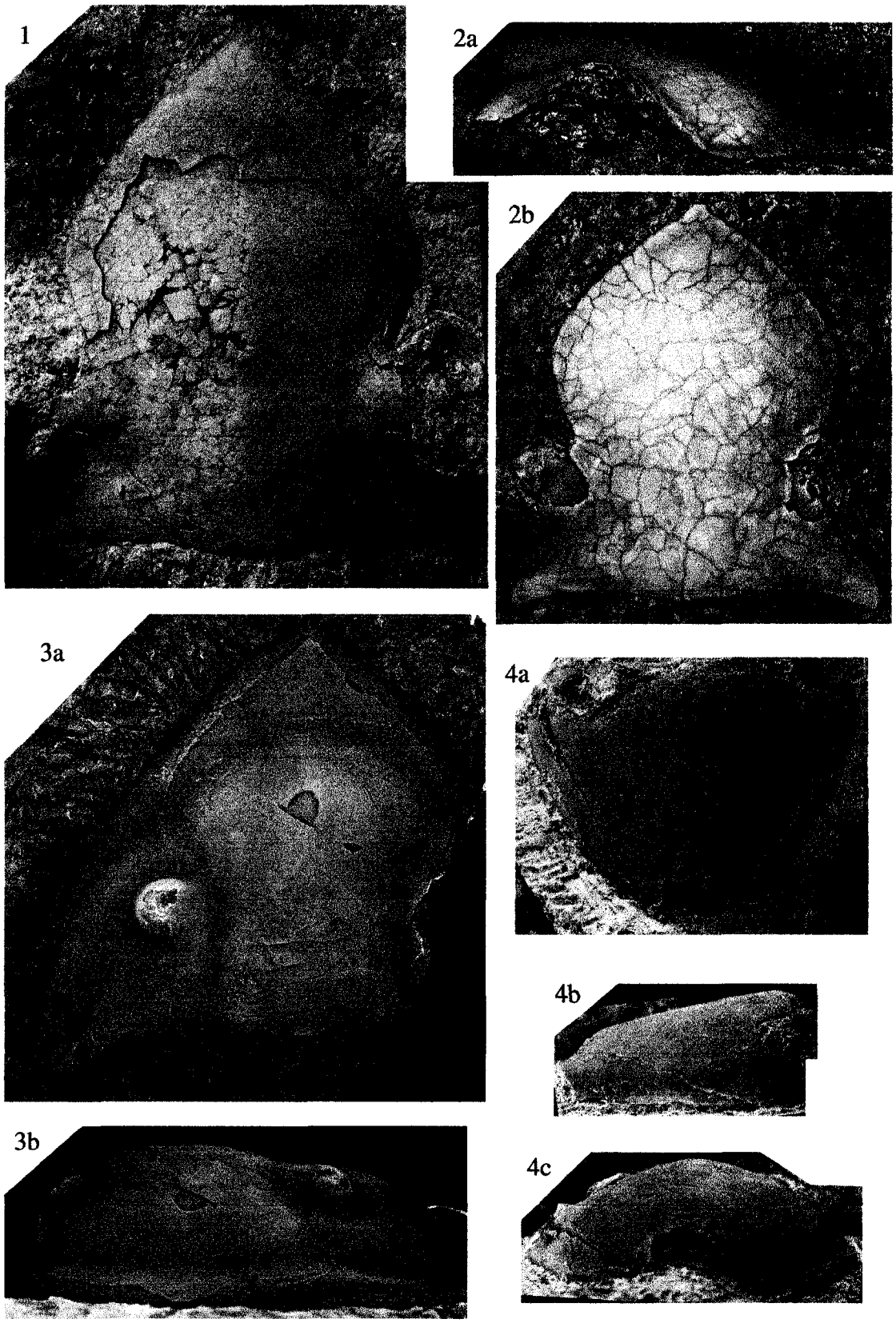


Plate 10 *Isotelus skapaneidos*

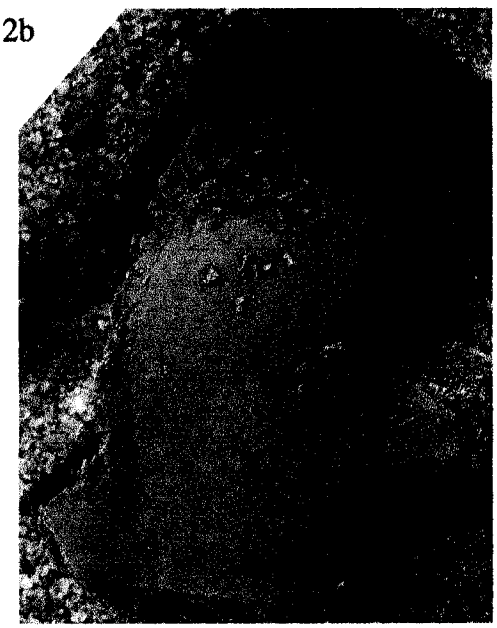
1. OU11813 (77-Float) nearly complete individual with front of cephalon broken off, dorsal surface of pygidium weathered x1 a) lateral b) dorsal
2. OU11814 (LQ-WF) broken cranidium with cuticle x1.5 a) lateral b) dorsal c) anterior
3. OU11815 (LQ-WF) cephalic doublure with portions of librigenae in dorsal view x1.5

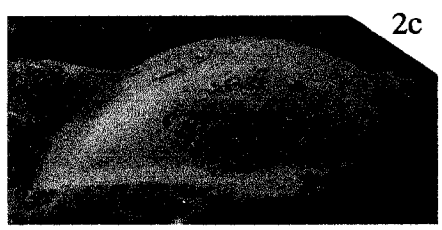
Plate 10











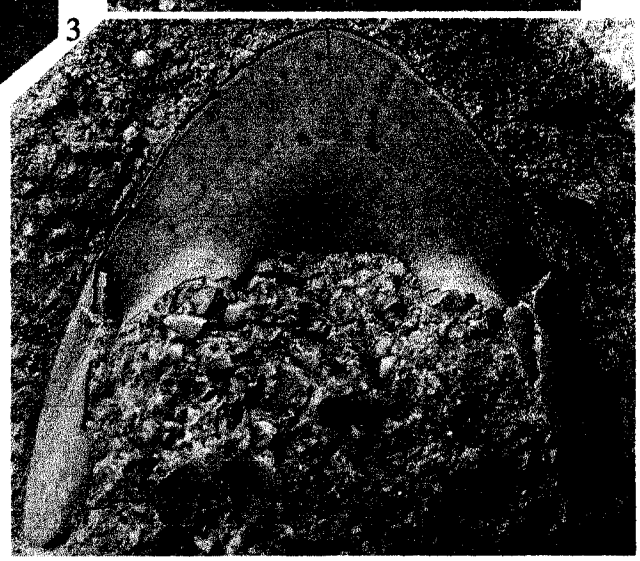


Plate 11 *Isotelus skapaneidos*, *Isotelus iowensis*

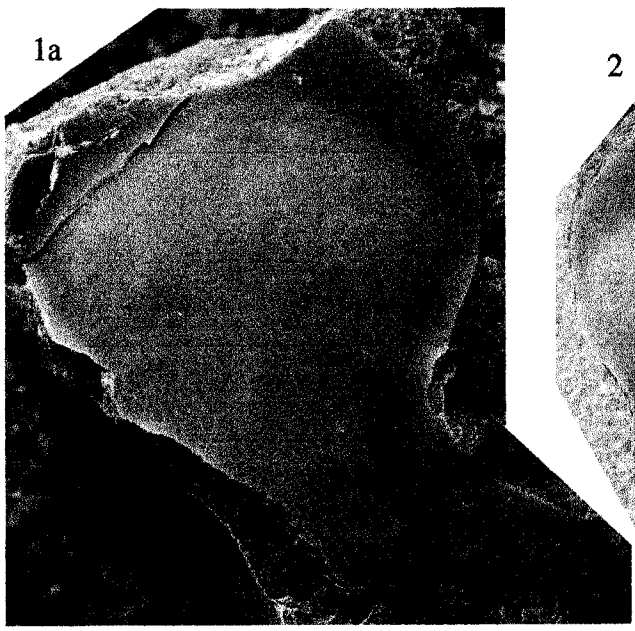
1-2 *Isotelus skapaneidos*

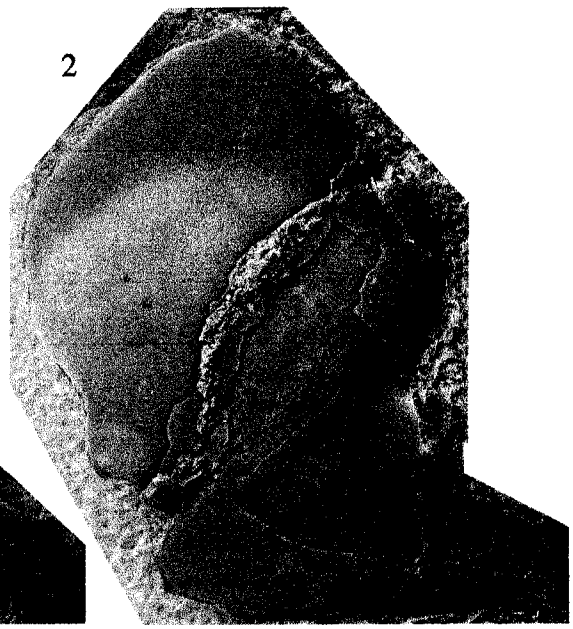
1. OU11816 (77-Float) (Amoco collection) broken, testate cranidium x3 a) dorsal b) lateral
2. OU11817 (77-202.5) broken, testate cranidium in dorsal view x1.5

3-4 *Isotelus iowensis*

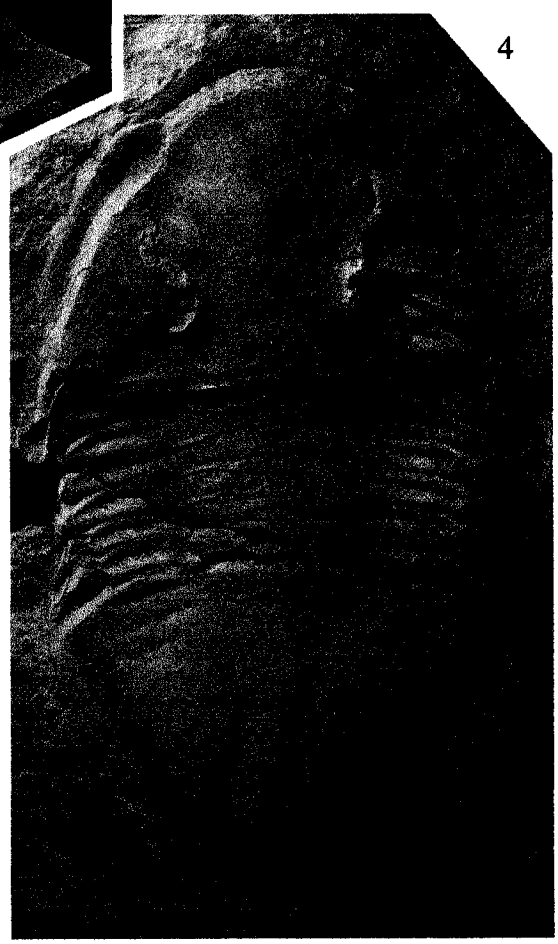
3. P11241 *Isotelus iowensis* ventral exoskeleton x1 (refigured from Slocum 1913, pl. 13, fig. 1)
4. UC6308 Holotype: *Isotelus iowensis* Owen 1852 x1.5

Plate 11









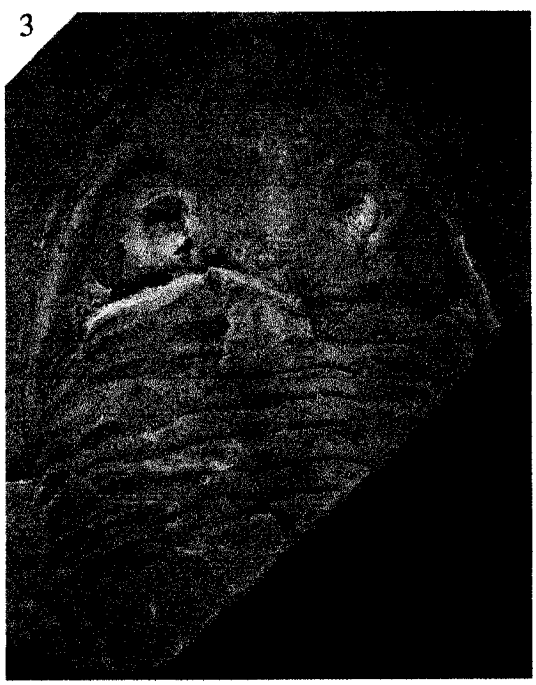


Plate 12 *Isotelus skapaneidos*?, *Isotelus* cf. *I. iowensis*

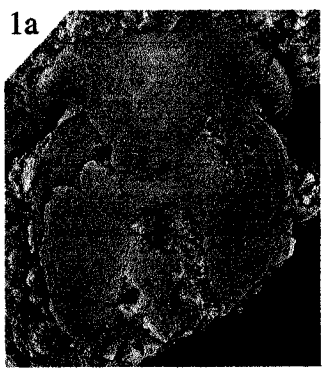
1 *Isotelus skapaneidos*?

1. OU11818 (LQ-WF) nearly complete hypostome tentatively assigned to this species x3 a) dorsal b) lateral/oblique c) lateral

2-3 *Isotelus* cf. *I. iowensis*

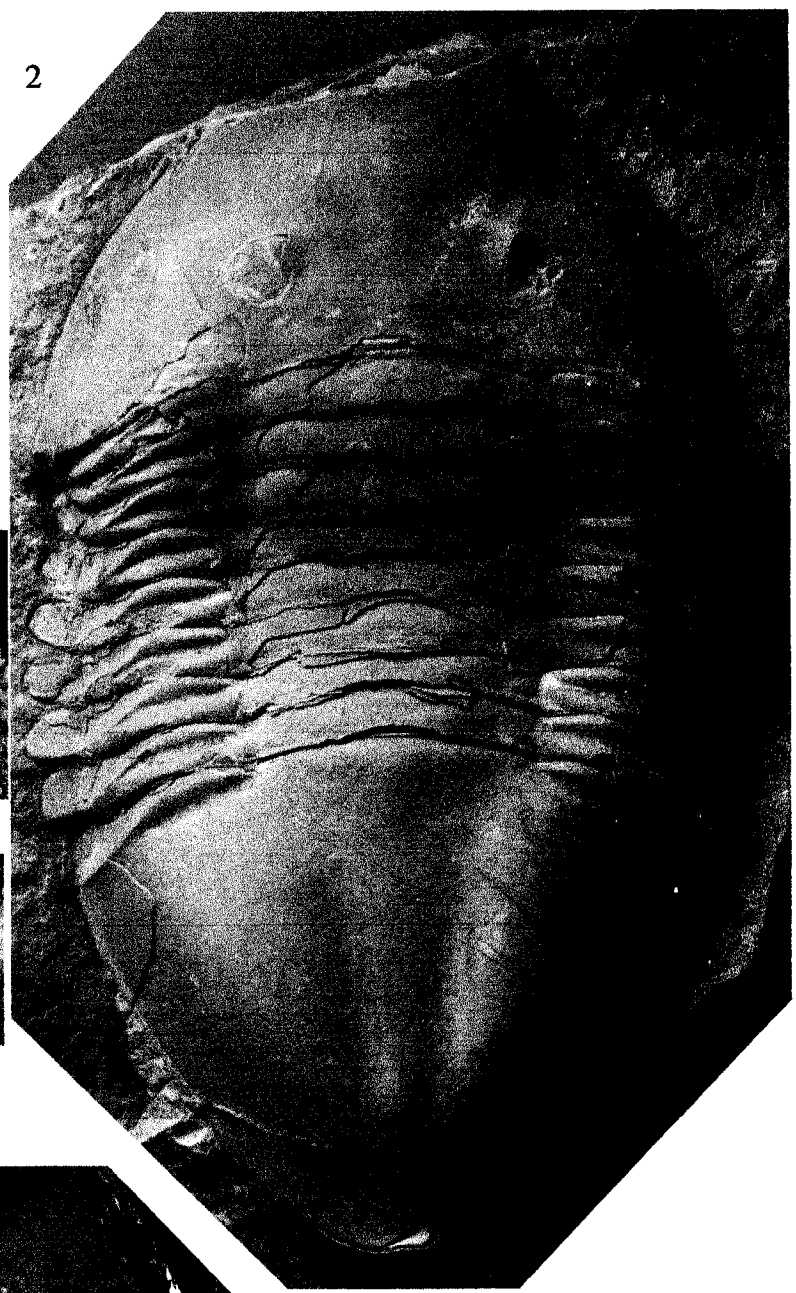
2. OU3119 (BQ-Float) nearly complete individual, front of cephalon and rear of pygidium broken x0.75 in dorsal view
3. OU11819 (I-35-75) broken, testate pygidium x1 a) dorsal b) lateral

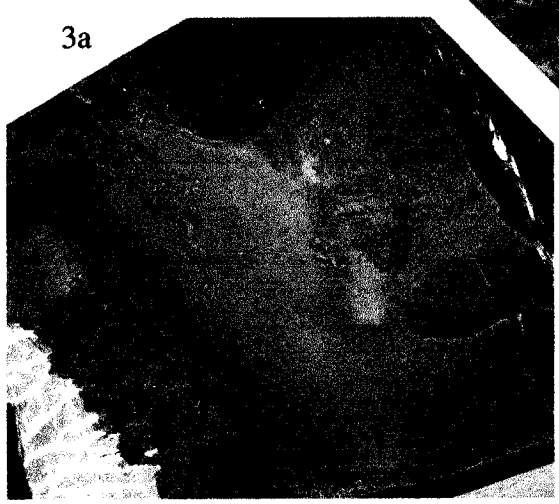
Plate 12


1a


1b


1c


2


3a


3b

Plate 13 *Isotelus* cf. *I. walcotti*

1. OU11820 (99-49.5) exfoliated anterior of cranidium in dorsal view x3
2. OU11821 (99-47) partly exfoliated librigena with visual surface x4 a) anterior b) dorsal c) lateral
3. OU11822 (99-49.5) anterior portion of cranidium x3 a) dorsal b) anterior
4. OU11823 (99-33) cast of broken cranidium in dorsal view x1.5
5. OU11824 (99-39) cast of pygidium x1.5 a) dorsal b) posterior
6. OU11825 (99-49.5) exfoliated pygidium x1.5 a) dorsal b) lateral

Plate 13

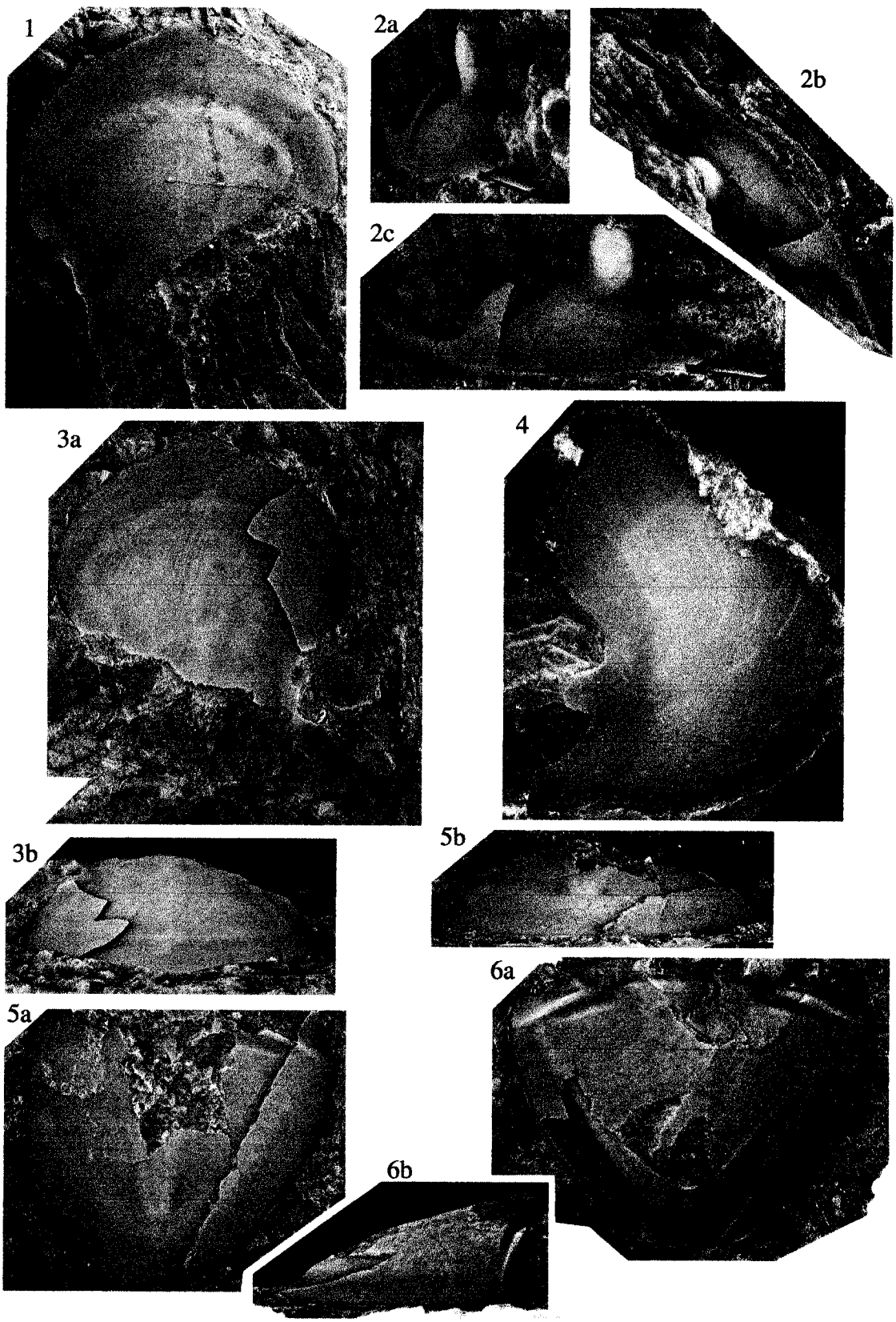


Plate 14 *Ectenaspis beckeri*, *Ectenaspis abothros*?

1 *Ectenaspis beckeri*

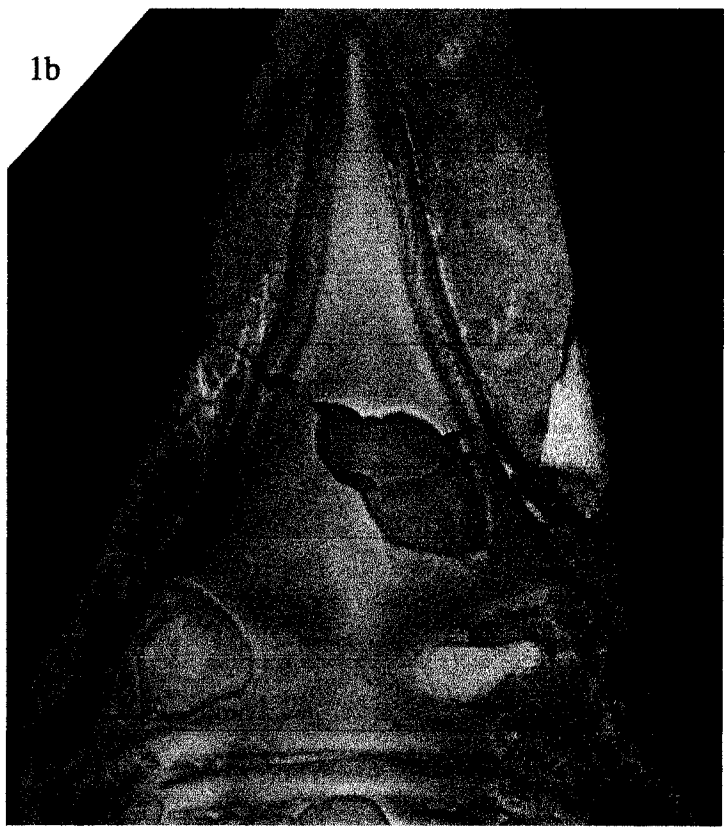
1. UC41151 Holotype: nearly complete, testate individual a) dorsal x1 b) dorsal of cephalon x2 c) lateral/oblique x1 d) lateral x1 e) proboscis showing details of ornament x4

2 *Ectenaspis abothros*?

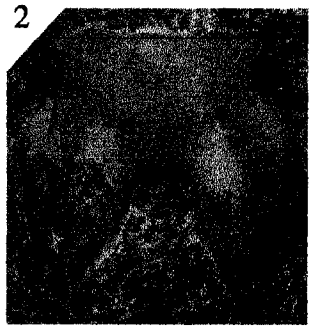
2. OU11826 (Nebo-Well) possible hypostome of *E. abothros* in ventral view x5

Plate 14











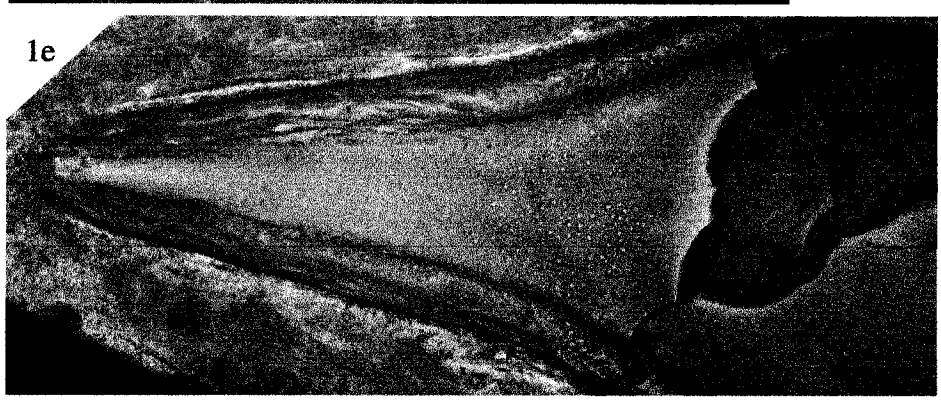
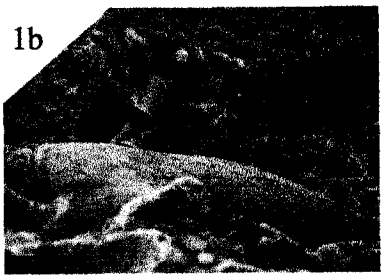


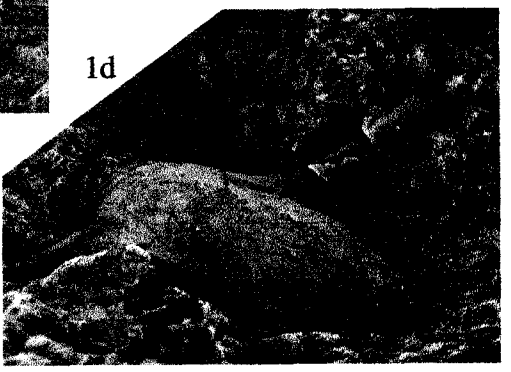
Plate 15 *Ectenaspis abothros*

1. OU11827 (Nebo-Well) exfoliated cranidium with proboscis and right eye stalk broken a) dorsal x4 b) lateral x4 c) anterior x4 d) oblique x4 e) lateral view of palpebral lobe x8
2. OU11828 (LQ-WF) broken, crushed cranidium with one eye stalk well-preserved a) dorsal x3 b) dorsal view of palpebral lobe and eye stalk x6 c) anterior oblique x3 d) anterior of cranidium just behind where proboscis is broken off showing pustules x6

Plate 15

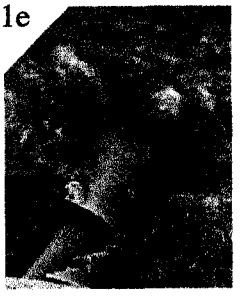

1a


1b

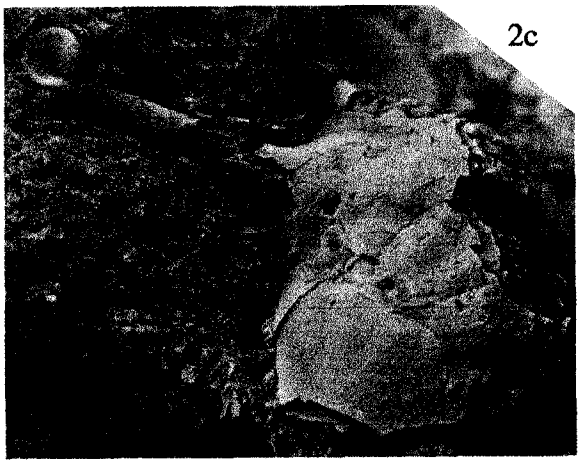

1d


1c


2a


1e


2b


2c


2d

Plate 16 *Ectenaspis abothros*

1. OU11829 (LQ-WF) partial, testate cranidium x2 a) dorsal b) lateral
2. OU11830 (LQ-WF) partial cranidium x3 a) dorsal b) anterior oblique
3. OU11831 (LQ-WF) exfoliated anterior portion of librigena, including ventral part of eye stalk x1.5 a) posterior oblique b) lateral
4. OU11832 (LQ-WF) partly exfoliated, broken librigena missing eye stalk and most of anterior portion, with part of genal spine x1 a) lateral b) dorsal
5. OU11833 (LQ-WF) broken, testate pygidium x3 a) dorsal b) lateral

Plate 16

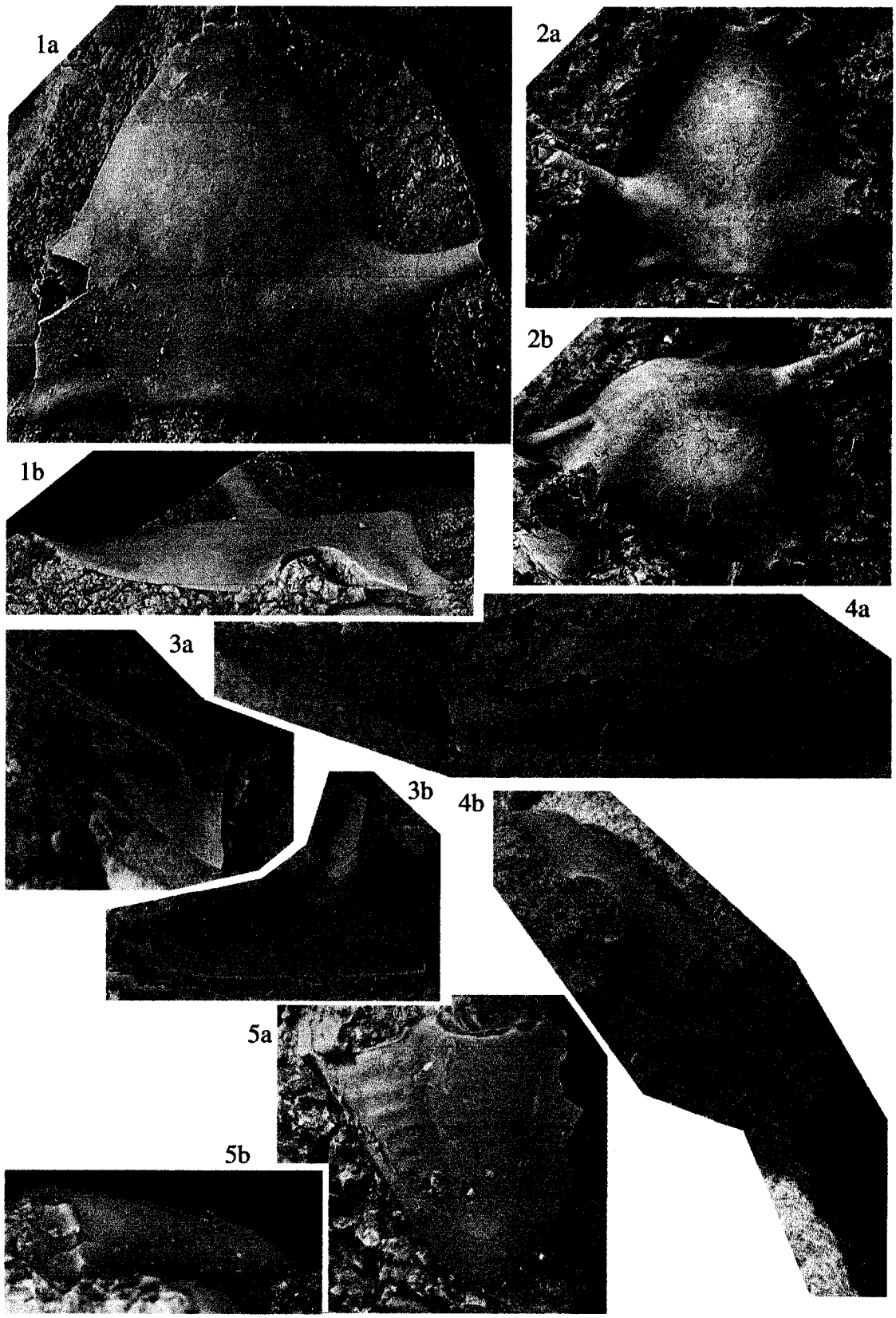


Plate 17 *Ectenaspis beckeri*, *Ectenaspis abothros*, *Stegnopsis wellingensis*

1 *Ectenaspis beckeri*

1. UC41151 Holotype: pygidium x2 a) dorsal b) lateral

2-4 *Ectenaspis abothros*

2. OU11834 (LQ-WF) nearly complete, testate pygidium x2 (a dorsal b) lateral
3. OU11835 (LQ-WF) testate pygidium with posterior broken x2 a) lateral b) dorsal
4. OU11836 (LQ-WF) nearly complete, testate pygidium x1.5 a) dorsal b) lateral

5 *Stegnopsis wellingensis*

5. OU11837 (LQ-WF) cast of broken cranidium x1.5 a) dorsal b) anterior c) lateral

Plate 17

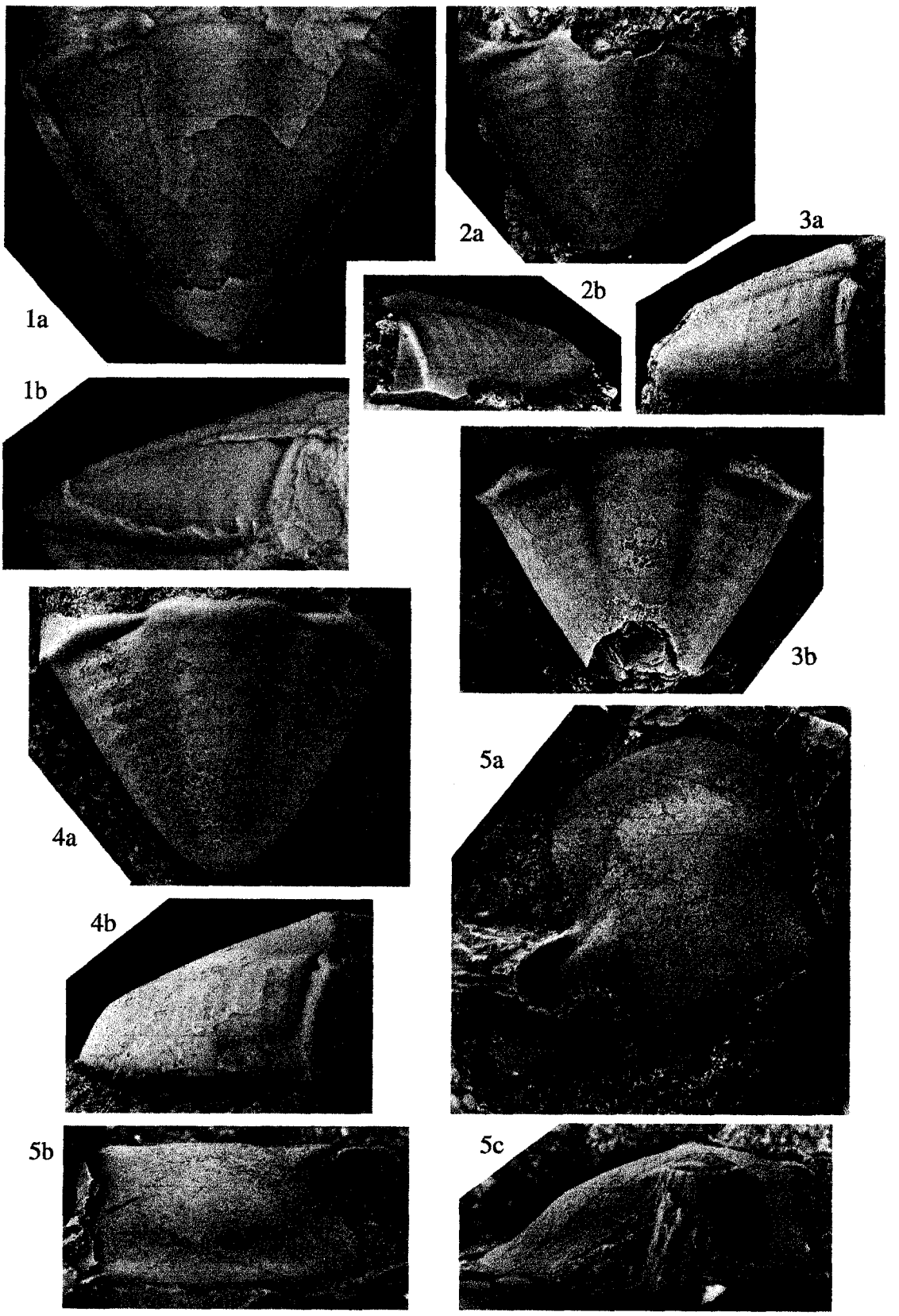


Plate 18 *Stegnopsis wellingensis*, *Stegnopsis byzanteneidos*?

1-3 *Stegnopsis wellingensis*

1. OU11838 (LQ-WF) partial cranidium, partly testate x3 a) dorsal b) lateral c) anterior
2. OU11839 (LQ-WF) partial, exfoliated cranidium x2 a) dorsal b) anterior
3. OU11840 (LQ-WF) mostly exfoliated pygidium broken along posterior margin x1.5 a) dorsal b) posterior c) lateral

4-6 *Stegnopsis byzanteneidos*?

4. OU11841 (BQ-18) meraspid cranidium tentatively assigned to this species x12 a) oblique b) lateral c) dorsal c) anterior
5. OU11842 (BQ-12) meraspid librigena tentatively assigned to this species x10 a) dorsal b) lateral
6. OU11843 (BQ-12) meraspid librigena tentatively assigned to this species, in dorsal view x10

7 *Stegnopsis wellingensis*

7. OU11844 (LQ-WF) mostly exfoliated pygidium, broken along posterior and left margins x1 a) dorsal b) posterior c) lateral

Plate 18

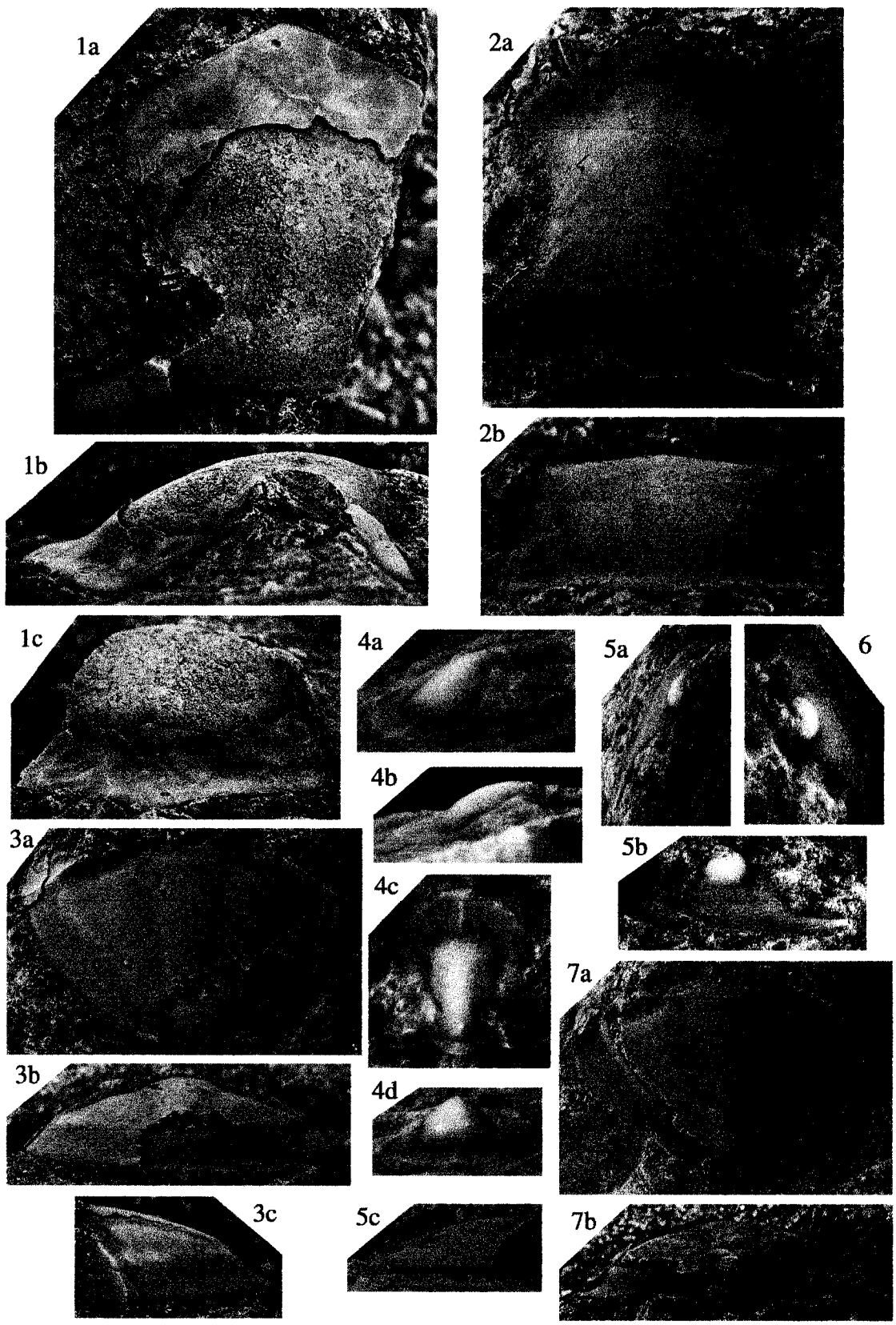


Plate 19 *Stegnopsis wellingensis*, *Stegnopsis byzanteneidos*

1-3 *Stegnopsis wellingensis*

1. OU11845 (LQ-WF) cast of nearly complete pygidium x2 a) dorsal b) lateral c) posterior
2. OU11846 (LQ-WF) exfoliated pygidium in dorsal view x1.5
3. OU11847 (LQ-WF) mostly exfoliated pygidium x1.5 a) dorsal b) lateral c) posterior d) close-up of cuticle showing absence of ornament x6

4-5 *Stegnopsis byzanteneidos*

4. OU11848 (BQ-24) small pygidium tentatively assigned to this species x8 a) dorsal b) posterior
5. OU11849 (77-183) nearly complete (meraspid?) cranidium x7 a) dorsal b) oblique c) lateral

Plate 19

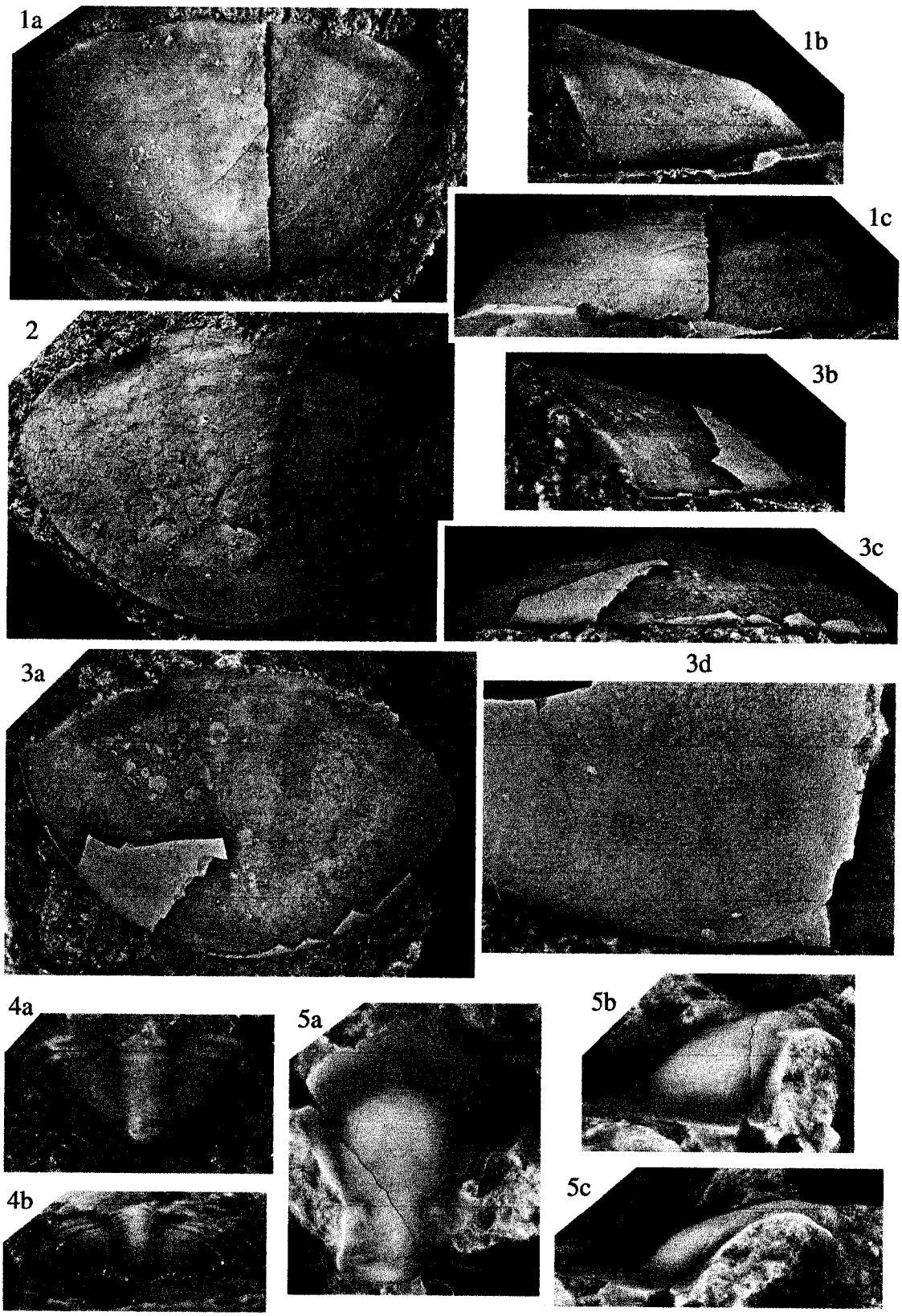
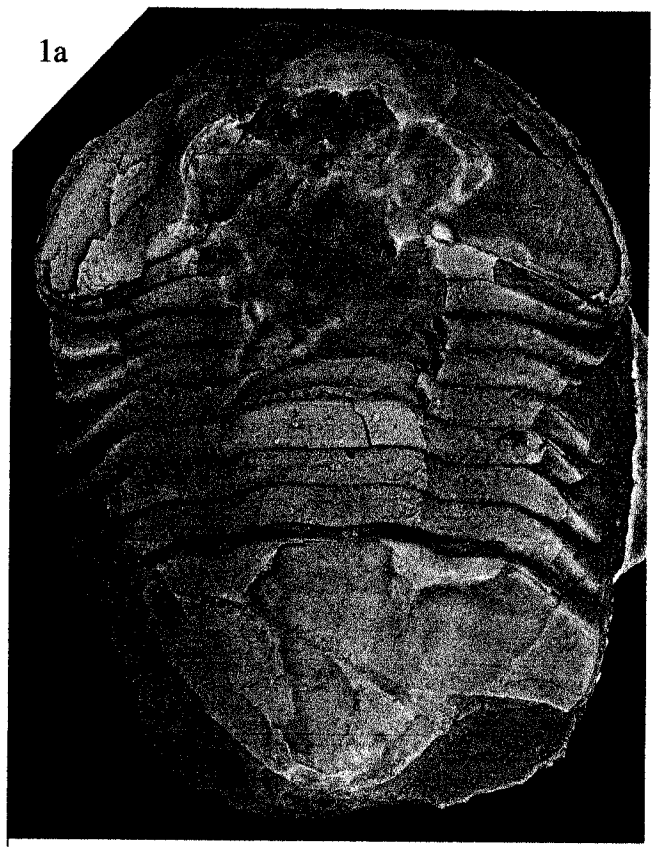
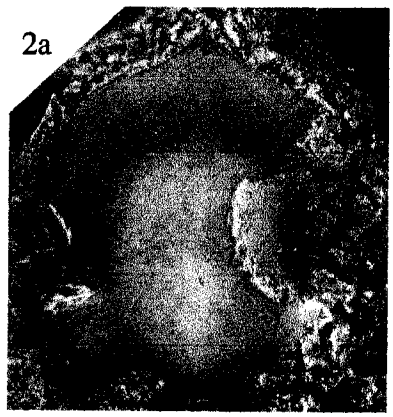


Plate 20 *Stegnopsis byzanteneidos*

1. OU11850 Loc. G of Glaser, along Little Buckhorn Creek near the south-east margin of the Arbuckle Reservoir, Chickasaw National Recreation Area; nearly complete individual missing posterior margin of pygidium and with dorsal surface of cranidium badly weathered x1 a) dorsal b) oblique c) lateral
2. OU11851 (Nebo-Well) cast of cranidium showing palpebral lobes x4 a) dorsal b) anterior c) lateral
3. OU11852 (Nebo-Well) cranidium in dorsal view x5
4. OU11853 (Nebo-Well) small (meraspid?) cranidium with some cuticle x6 a) oblique b) lateral c) dorsal

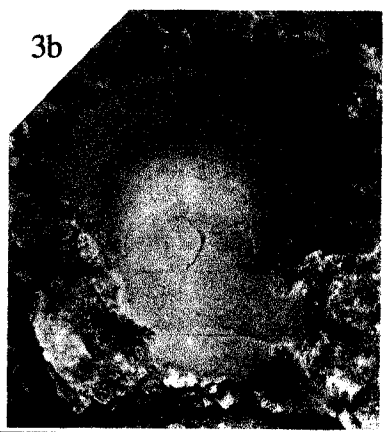
Plate 20















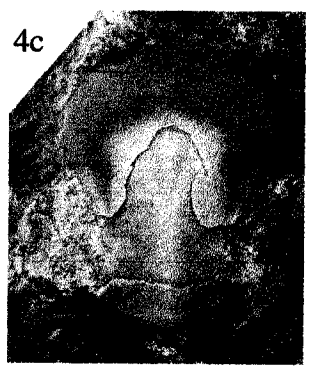






Plate 21 *Stegnopsis byzanteneidos*

1. OU11854 (Nebo-Well) testate cranidium with broken anterior margin x4 a) dorsal b) anterior c) lateral
2. OU11855 (Nebo-Well) nearly complete, exfoliated pygidium x1.5 a) posterior b) dorsal
3. OU11856 (Nebo-Well) testate pygidium x1.5 a) dorsal b) lateral c) posterior
4. OU11857 (77-183) cast of pygidium showing sculpture a) dorsal x1.5 b) close-up x6

Plate 21

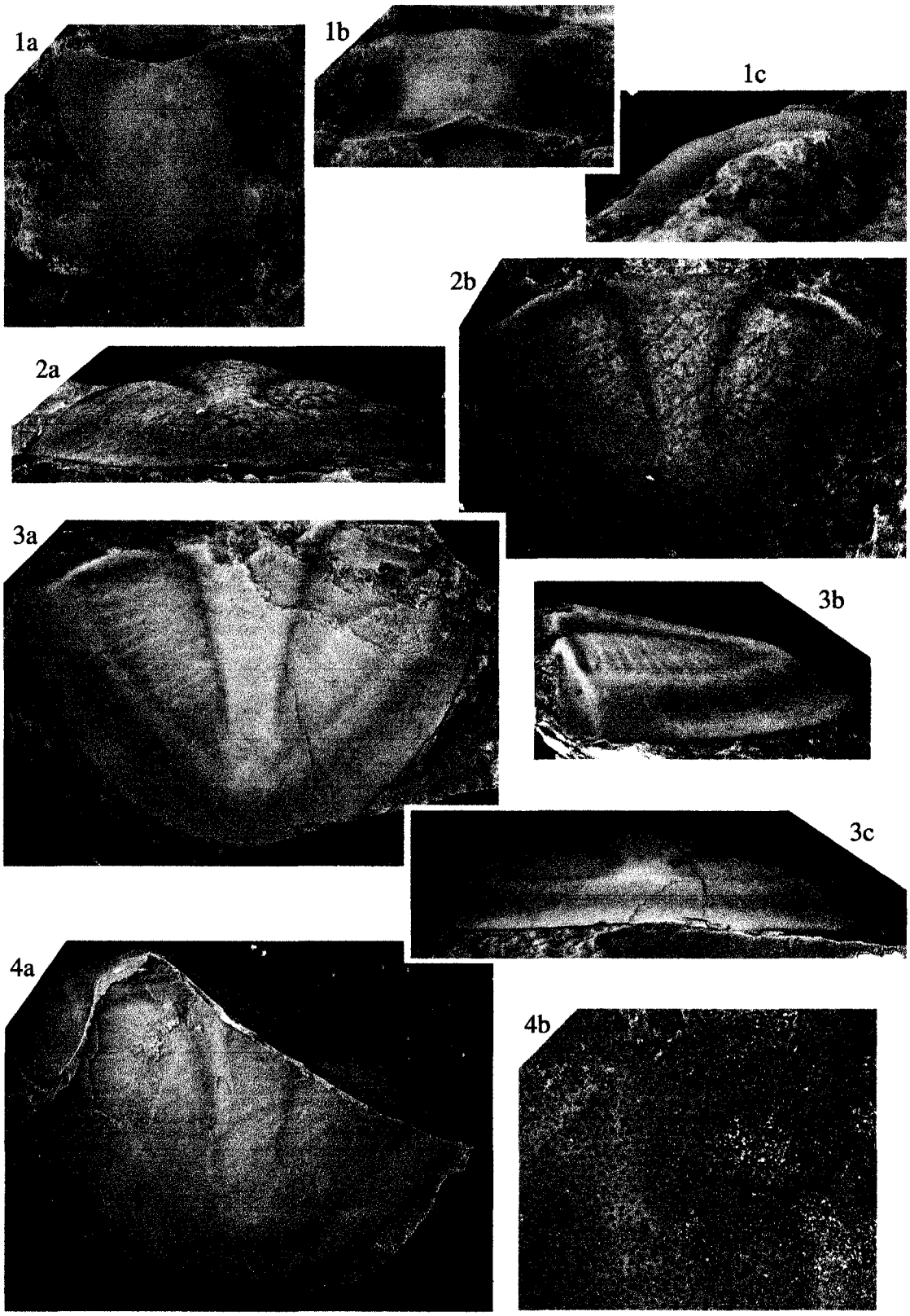


Plate 22 *Anataphrus megalophrys*

1. OU11858 (LQ-VS) small (meraspid?) cranidium in dorsal view x12
2. OU11859 (LQ-VS) small (meraspid?) cranidium, testate on anterior x12 a) dorsal b) lateral c) close-up of cuticle x15 d) anterior
3. OU11860 (LQ-VS) small, testate cranidium x10 a) dorsal b) anterior/dorsal c) lateral
4. OU11861 (LQ-VS) small, partially testate cranidium x8 a) dorsal b) lateral c) anterior
5. OU11862 (LQ-VS) testate cranidium x7 a) dorsal b) close-up of palpebral lobe and cuticle x15
6. OU11863 (LQ-VS) testate cranidium x7 a) anterior b) dorsal
7. OU11864 (LQ-VS) large, testate cranidium x4 a) dorsal b) lateral c) anterior
8. OU11865 (99-49) large cranidium in dorsal view x4

Plate 22

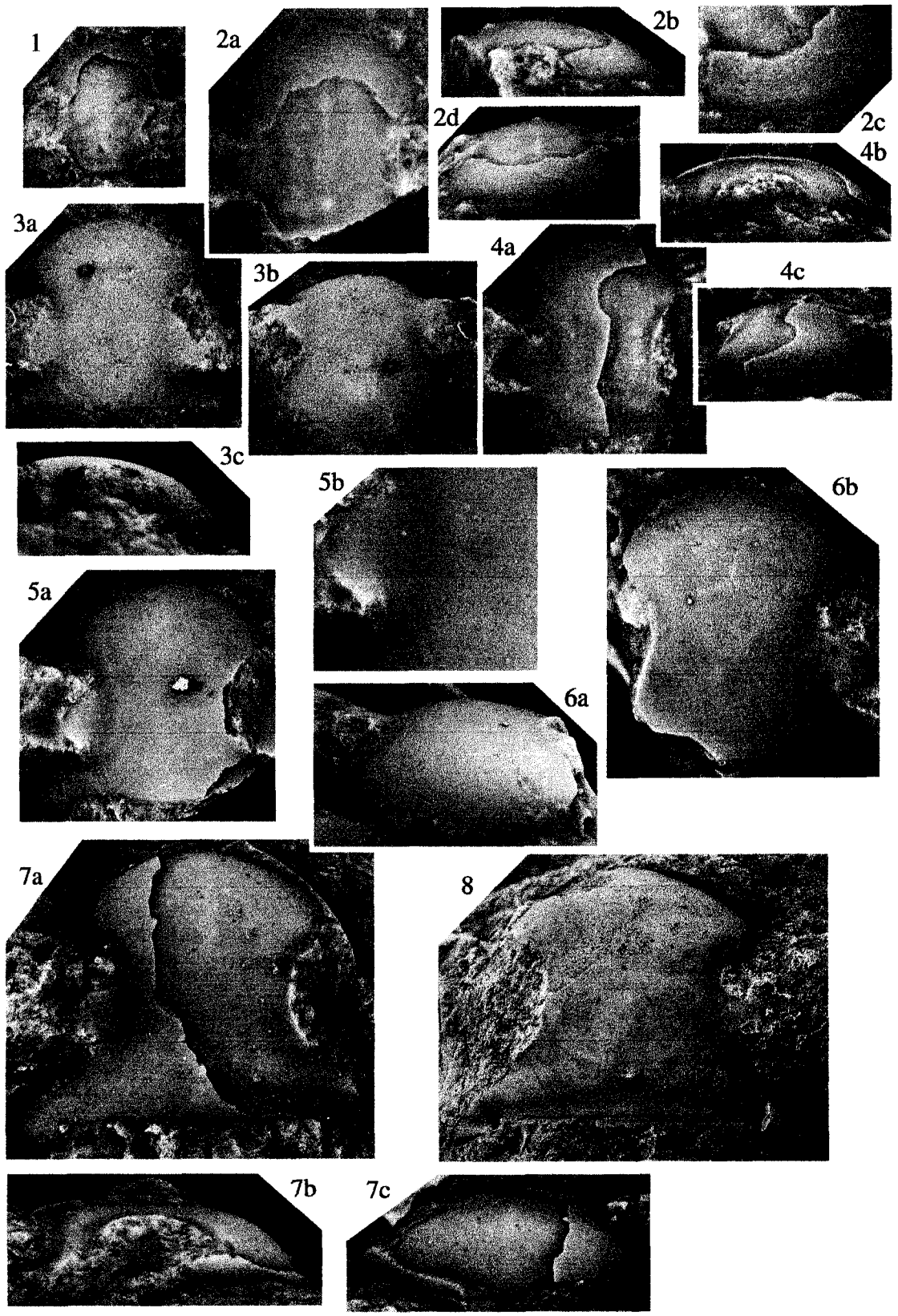


Plate 23 *Anataphrus megalophrys*

1. OU11866 Holotype (LQ-VS) testate cranidium missing only right posterior fixigena a) dorsal x7 b) anterior right portion of cranidium showing lack of sculpture x12 c) anterior/dorsal
2. OU11867 (LQ-VS) nearly complete, testate hypostome x6 a) ventral b) lateral/oblique c) lateral
3. OU11868 (99-48) mostly testate librigena with visual surface x4 a) lateral b) dorsal c) anterior
4. OU11869 (99-49) mostly exfoliated librigena with visual surface x4 a) lateral b) dorsal c) anterior
5. OU11870 (LQ-VS) testate hypostome x6 a) ventral b) lateral
6. OU11871 (99-48) partly exfoliated hypostome x6 a) dorsal b) lateral
7. OU11872 (LQ-VS) partly exfoliated, transitory pygidium x10 a) lateral b) dorsal c) posterior

Plate 23

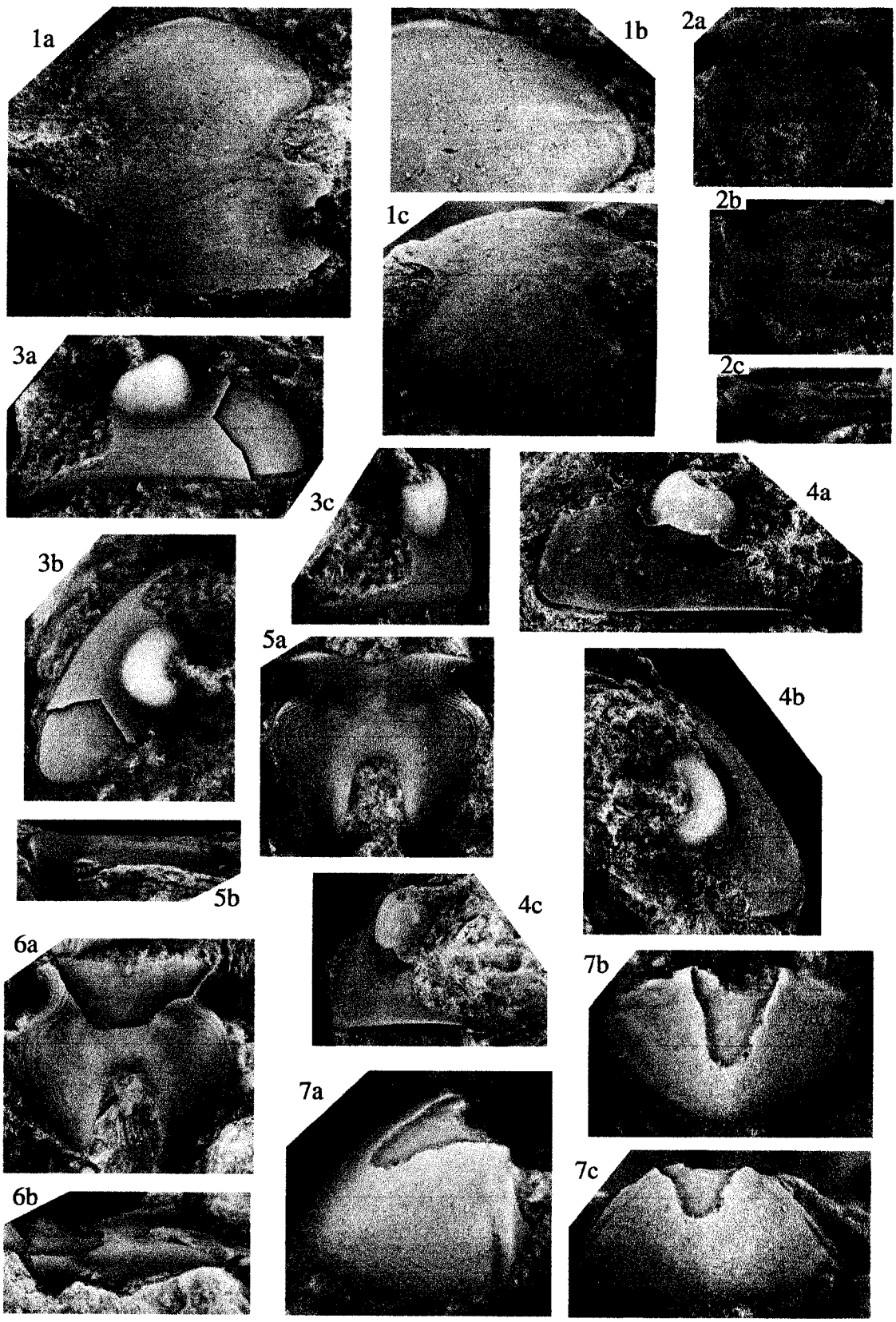


Plate 24 *Anataphrus megalophrys*

1. OU11873 (LQ-VS) partly exfoliated thorax and exfoliated pygidium x4 a) dorsal b) lateral
2. OU11874 (LQ-VS) small, testate pygidium x6 a) dorsal b) posterior c) maximum view with lighting to show faint axial furrows d) lateral
3. OU11875 (99-48) partly exfoliated pygidium missing posterior margin x6 a) dorsal b) posterior c) lateral
4. OU11876 (LQ-VS) exfolilated pygidium showing relict segmentation of axis x5 a) posterior b) maximum c) lateral
5. OU11877 (LQ-VS) mostly exfoliated pygidium showing relict segmentation of axis x5 a) dorsal b) posterior c) lateral

Plate 24

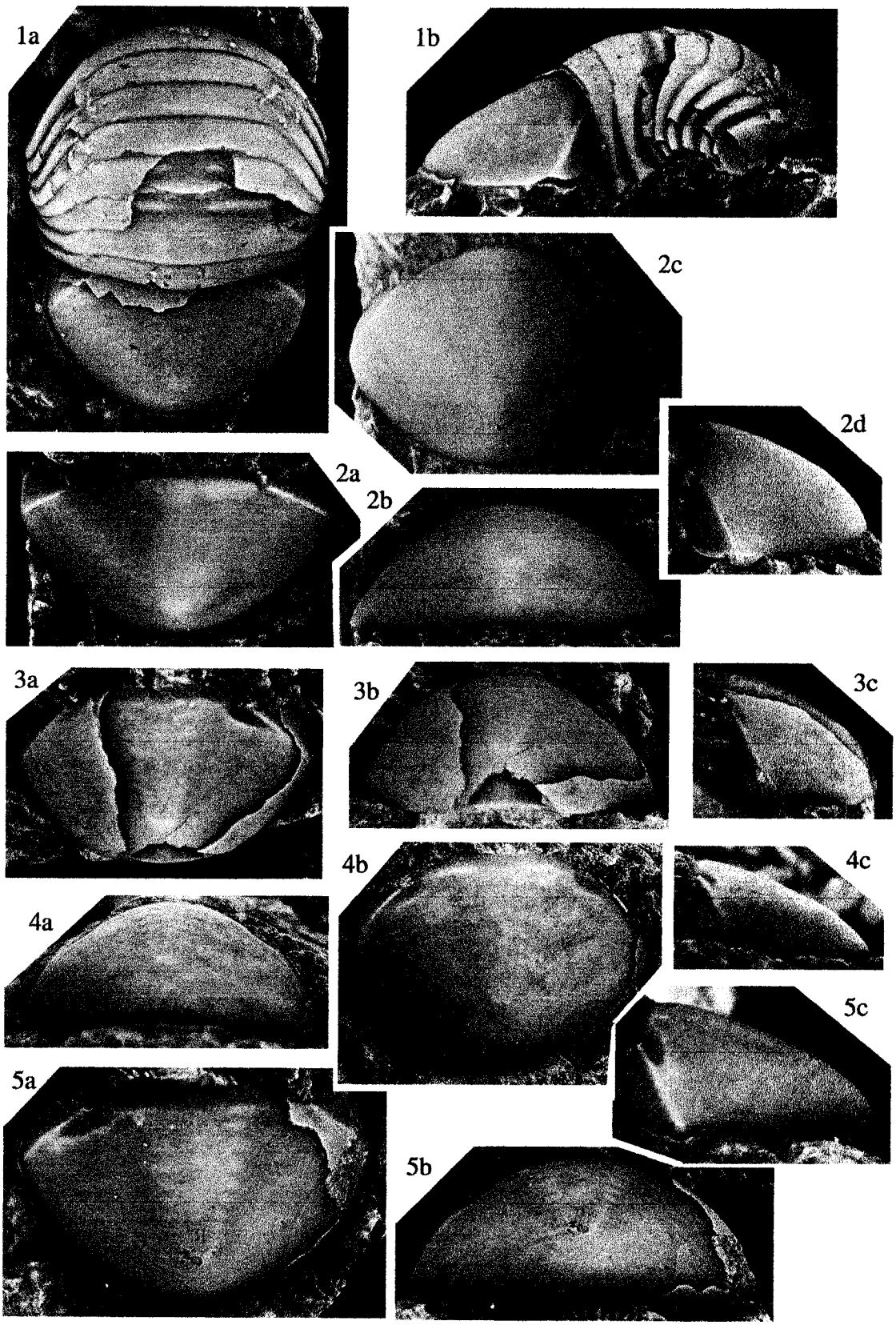


Plate 25 *Anataphrus megalophrys, Anataphrus kermiti*

1-6 *Anataphrus megalophrys*

1. OU11878 (LQ-VS) partly exfoliated, broken pygidium with right and posterior part of doublure exposed a) dorsal x4 b) close-up showing sculpture x8
2. OU11879 (LQ-VS) transitory pygidium x12 a) dorsal b) posterior c) lateral
3. OU11880 (99-48) partly exfoliated pygidium x3 a) dorsal b) posterior
4. OU11881 (99-49.5) exfoliated pygidium showing part of doublure in dorsal view x4
5. OU11882 (99-48) dorsal view of exfoliated large pygidium showing axial segmentation x4
6. OU11883 (99-48) transitory pygidium x12 a) dorsal b) posterior c) lateral

7-10 *Anataphrus kermiti*

7. OU11884 (77-218) complete, testate cranidium in dorsal view x10
8. OU11885 (77-219) cast of cranidium x7 a) dorsal b) anterior c) lateral
9. OU11886 (77-219) small, testate pygidium x8 a) dorsal b) posterior c) lateral
10. OU11887 (77-219) small, nearly complete testate cranidium x4 a) anterior b) dorsal

Plate 25

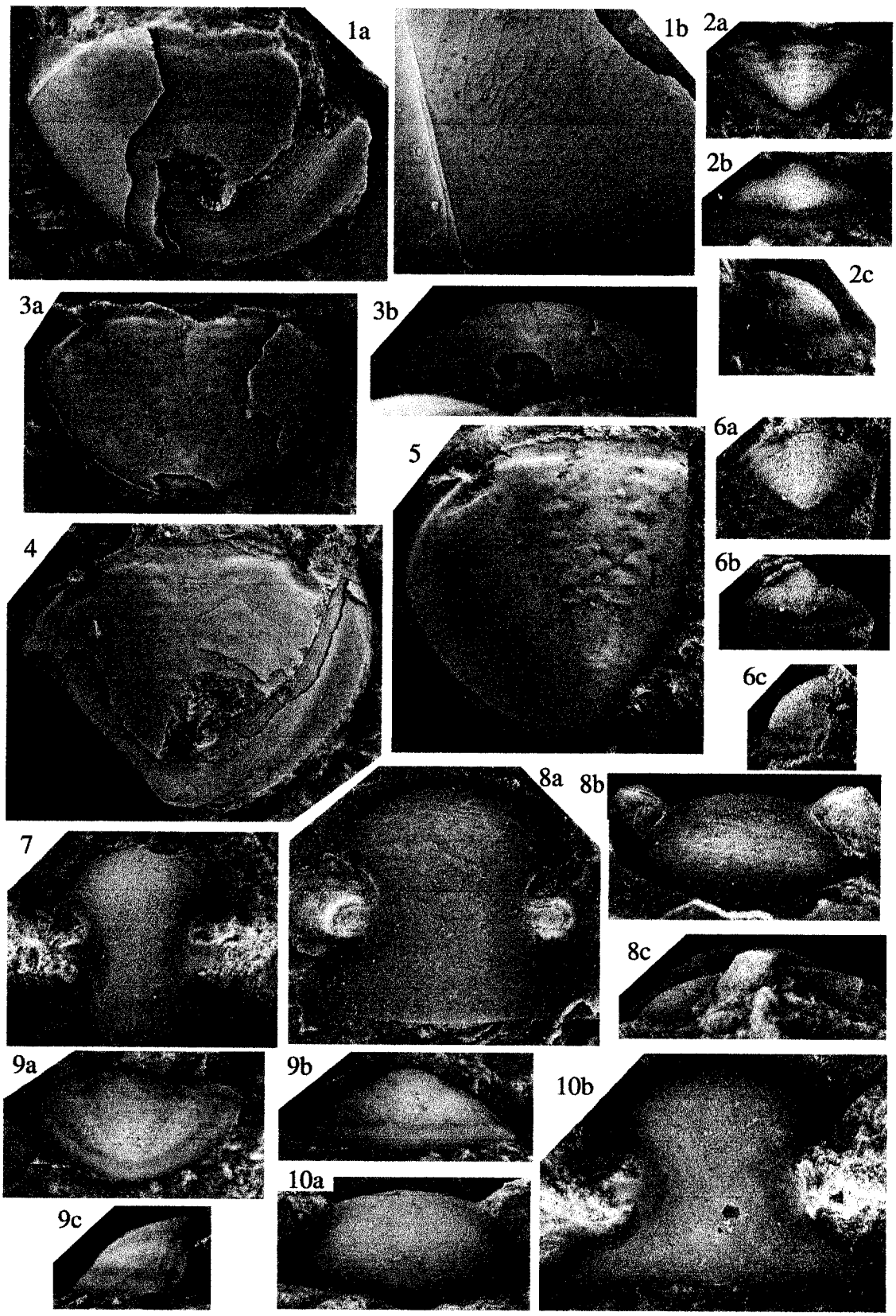


Plate 26 *Anataphrus kermiti*

1. OU11888 (77-218) cast of cranidium shoing strap-like palpebral lobes a) dorsal x4 b) lateral x4 c) palpebral lobe x8 d) anterior x4
2. OU11889 Holotype (77-Float) nearly complete enrolled individual x4 a) anterior b) dorsal view of pygidium c) dorsal view of cephalon d) lateral e) dorsal view of thorax
3. OU11890 (77-219) small, exfoliated pygidium with posterior margin broken to show part of doublure x7 a) posterior b) dorsal
4. OU11891 (77-219) mostly exfoliated, transitory pygidium x10 a) dorsal b) posterior c) lateral

Plate 26

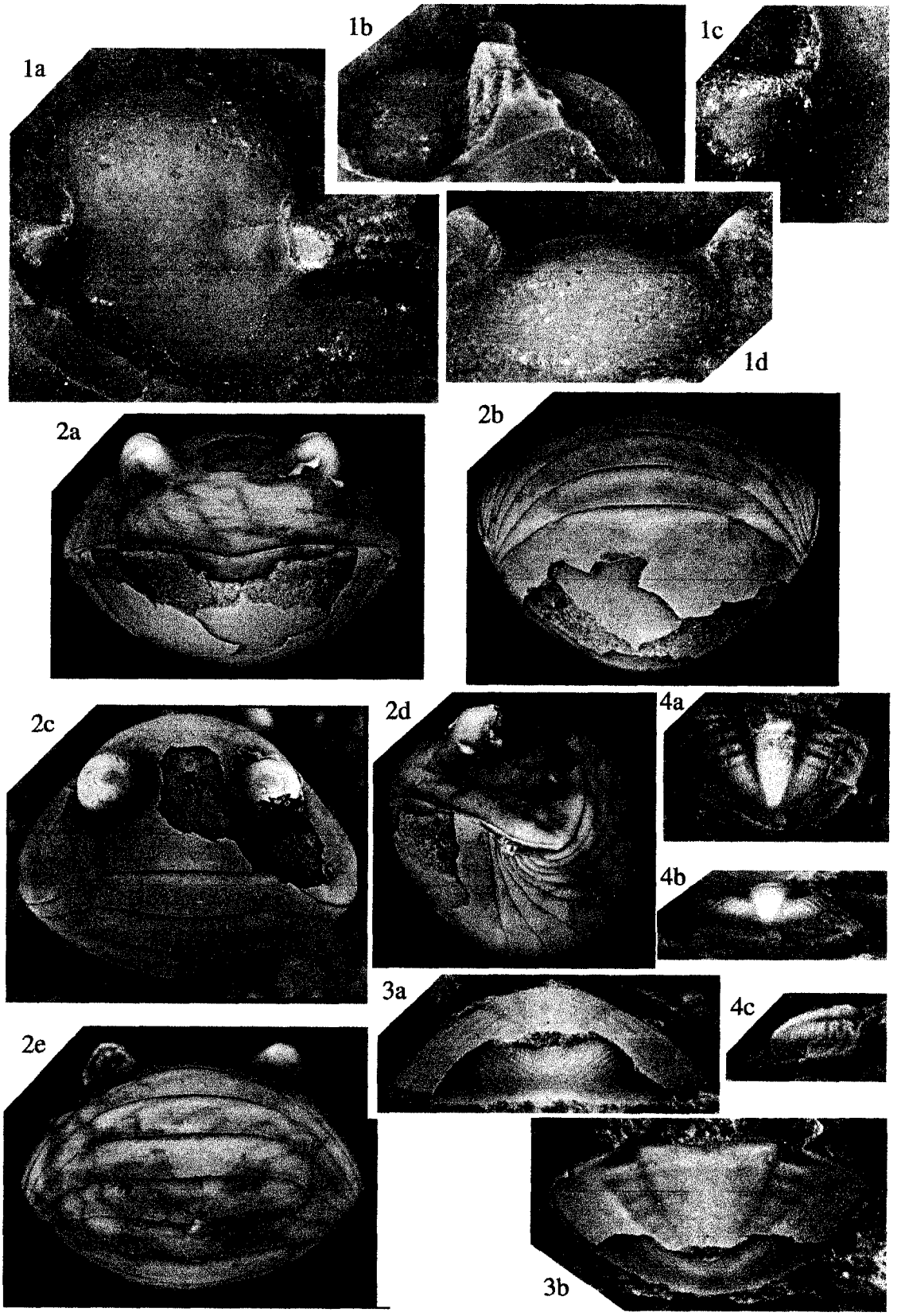


Plate 27 *Anataphrus kermiti*

1. OU11892 (77-219) cast of nearly complete cranidium a) dorsal x3 b) anterior showing terrace ridges x3 c) lateral x3 d) detail of waisted palpebral lobe, pitted cuticle, terrace ridges x6
2. OU11893 (77-219) cast of cranidium missing lateral posterior fixigenae and anterior of cranidium a) dorsal x3 b) dorsal view of waisted palpebral lobe x8 c) lateral view of waisted palpebral lobe x8
3. OU11894 (77-219) small, testate pygidium x7 a) posterior b) maximum c) lateral
4. OU11895 (LQ-WF) testate pygidium x7 a) dorsal b) lateral c) posterior
5. OU11896 (LQ-WF) complete, testate pygidium a) maximum x2.5 b) lateral x2.5 c) detail of cuticle showing pitting and ridges x5

Plate 27

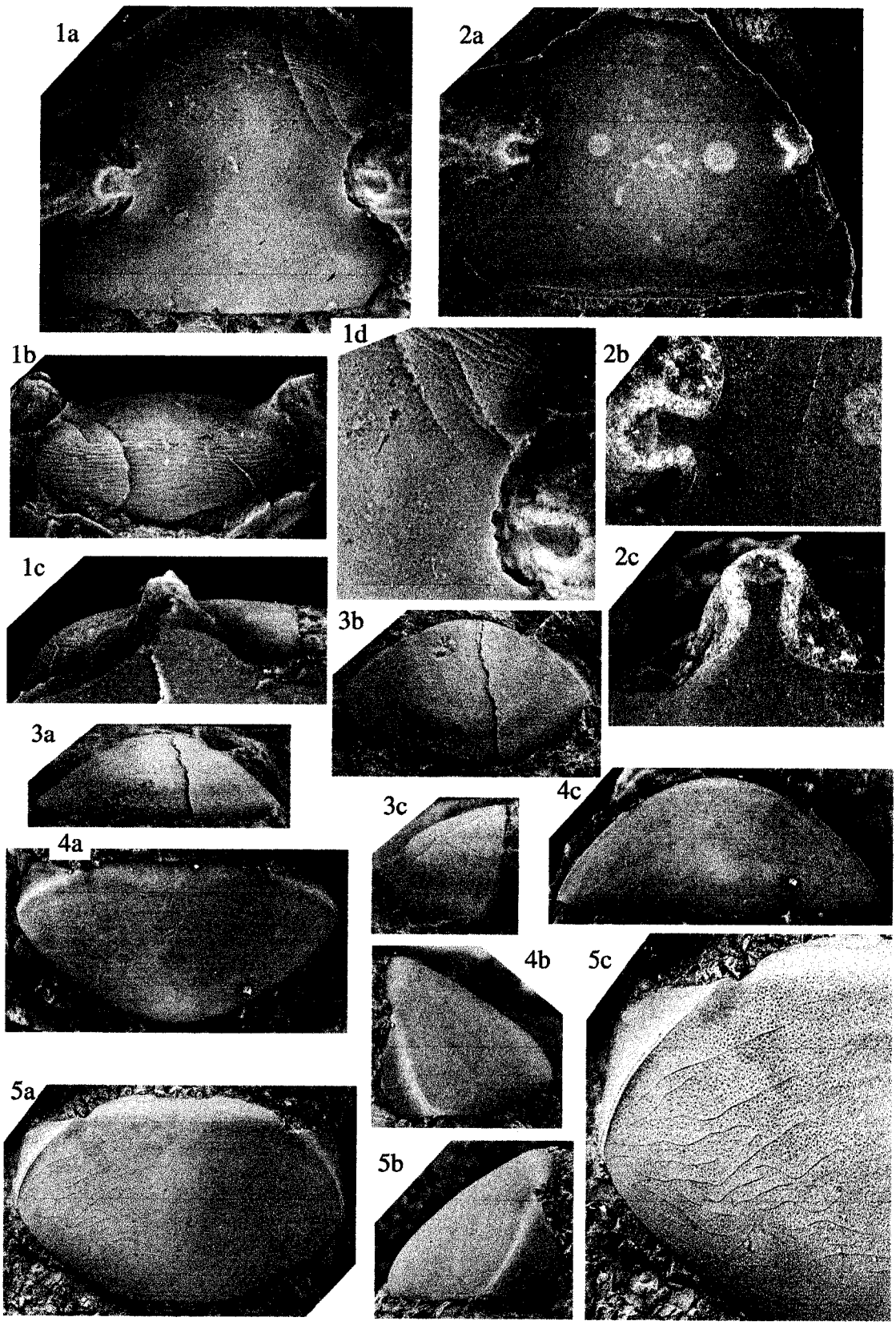


Plate 28 *Anataphrus kermiti*

1. OU11897 (LQ-WF) cast of partial cranidium a) dorsal x5 b) waisted palpebral lobe x8
2. OU11898 (LQ-WF) nearly complete librigena x8 a) anterior b) dorsal c) lateral
3. OU11899 (LQ-WF) nearly complete, testate cranidium x6 a) dorsal b) anterior/oblique
4. OU11900 (Nebo-Well) testate hypostome in ventral view x4
5. OU11901 (LQ-WF) exfoliated hypostome x4 a) ventral b) lateral
6. OU11902 (LQ-WF) testate, transitory pygidium x8 a) dorsal b) posterior c) lateral
7. OU11903 (CC) testate transitory pygidium x12 a) dorsal b) lateral c) posterior
8. OU11904 (Nebo-Well) exfoliated pygidium x6 a) lateral b) posterior c) dorsal
9. OU11905 (LQ-WF) exfoliated pygidium showing axial segmentation x7 a) posterior b) lateral c) dorsal
10. OU11906 (CC) exfoliated cranidium in dorsal view x4

Plate 28

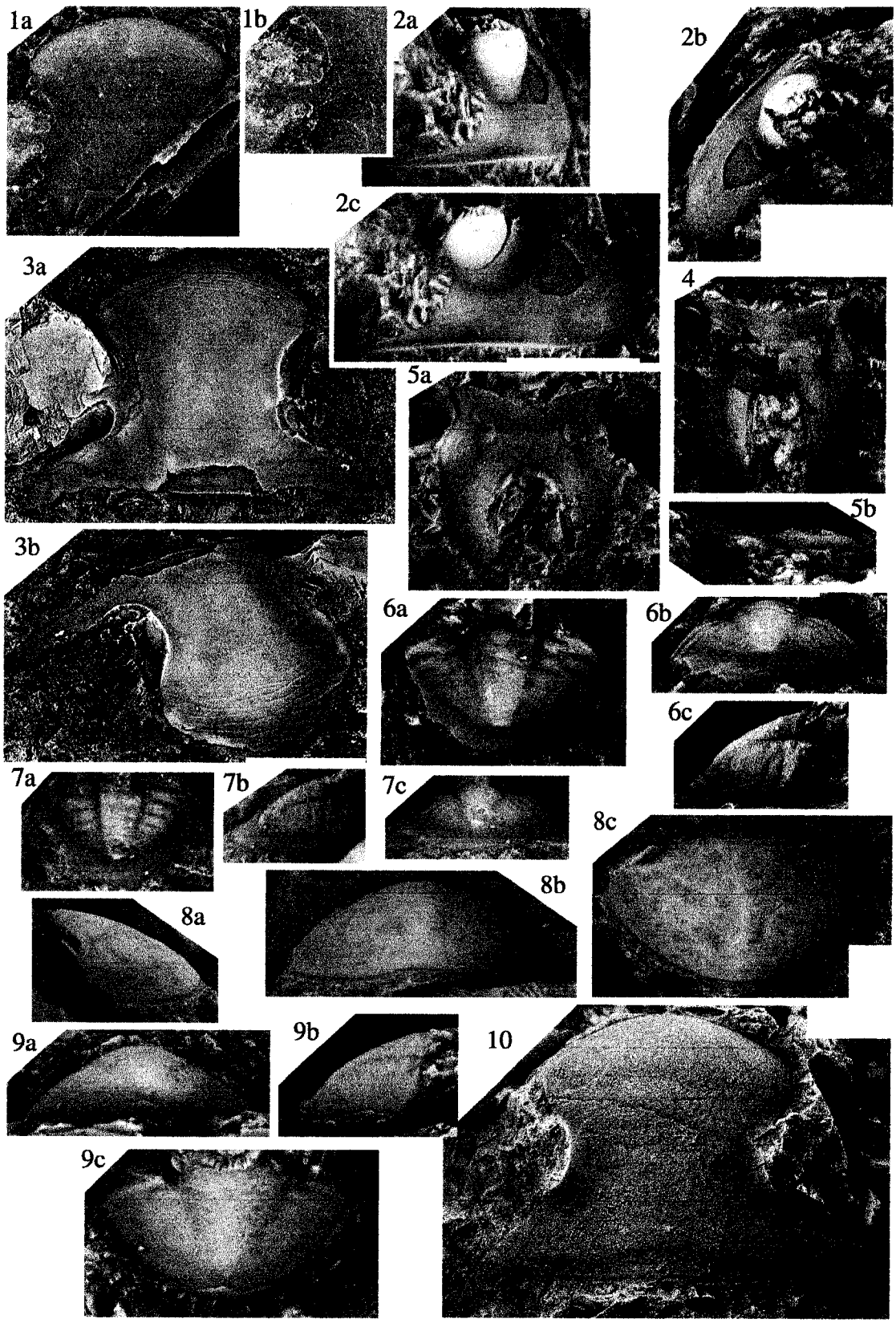


Plate 29 *Anataphrus kermiti*

1. OU11907 (CC) exfoliated pygidium x6 a) maximum b) posterior c) lateral
2. OU11908 (BQ-24) small, testate cranidium x8 a) dorsal b) lateral/dorsal showing strap-like palpebral lobe
3. OU11909 (BQ-18) cast of cranidium showing strap-like palpebral lobe x8 a) dorsal b) anterior c) lateral
4. OU11910 (BQ-24) cast showing strap-like palpebral lobe in dorsal view x8
5. OU11911 (BQ-18) distorted, testate cranidium showing waisted palpebral lobe in dorsal view x5
6. OU11912 (BQ-24) testate librigena with visual surface x4 a) anterior b) dorsal c) lateral
7. OU11913 (BQ-18) exfoliated pygidium x3.5 a) dorsal b) posterior c) lateral
8. OU11914 (77-219) small, nearly complete, partly exfoliated cranidium in dorsal view x10
9. OU11915 (77-219) small, partly exfoliated cranidium x10 a) dorsal b) anterior c) lateral
10. OU11916 (77-219) meraspid librigena in lateral view x10
11. OU11917 (CC) transitory pygidium x10 a) posterior b) lateral c) dorsal

Plate 29

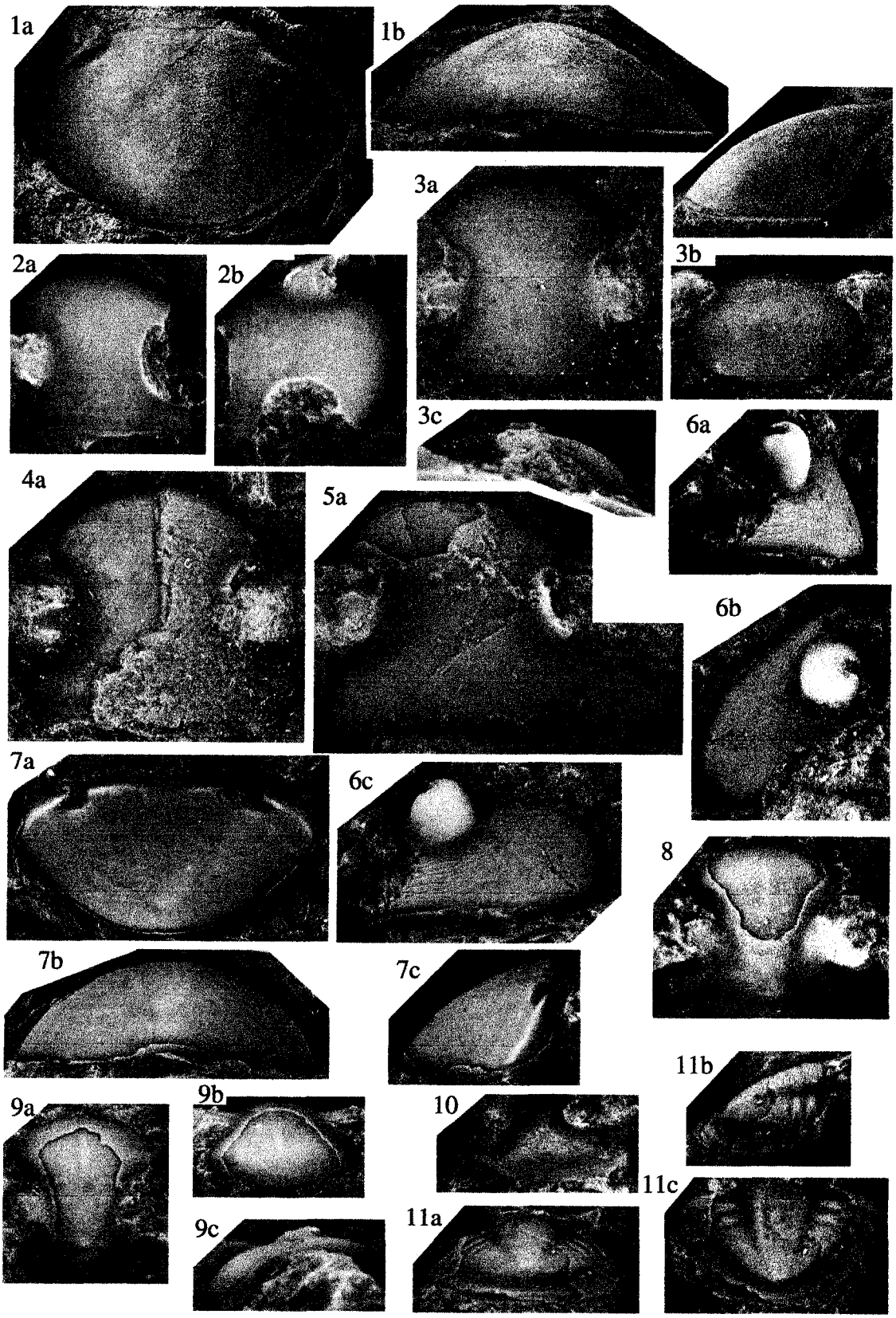


Plate 30 *Anataphrus kermiti* ontogeny

1. OU11918 (BQ-12) meraspid cranidium x15 a) dorsal b) anterior c) lateral c) oblique
2. OU11919 (BQ-18) meraspid cranidium x12 a) dorsal b) anterior c) lateral d) oblique
3. OU11920 (BQ-12) small cranidium x10 a) dorsal b) oblique c) anterior d) lateral
4. OU11921 (BQ-12) meraspid librigena x10 in lateral view
5. OU11922 (BQ-24) meraspid librigena x8 in lateral view
6. OU11923 (BQ-24) meraspid librigena x8 a) anterior b) dorsal c) lateral
7. OU11924 (BQ-12) meraspid hypostome x14 in ventral view
8. OU11925 (BQ-12) meraspid hypostome x12 a) lateral/ventral b) ventral
9. OU11926 (BQ-24) meraspid pygidium x8 in dorsal view
10. OU11927 (BQ-24) meraspid pygidia x12
11. OU11928 (BQ-18) meraspid pygidium x15 a) dorsal b) lateral c) posterior
12. OU11929 (BQ-12) meraspid pygidium x15 a) dorsal b) lateral c) posterior
13. OU11930 (BQ-12) meraspid pygidium x15 a) dorsal b) lateral c) posterior
14. OU11931 (BQ-24) meraspid pygidium x12 a) dorsal b) posterior
15. OU11932 (BQ-24) meraspid pygidium x8 a) dorsal b) maximum c) lateral
16. OU11933 (BQ-12) meraspid pygidium x12 a) dorsal b) lateral c) posterior
17. OU11934 (BQ-12) meraspid pygidium x10 a) dorsal b) lateral c) posterior
18. OU11935 (BQ-24) meraspid pygidium in dorsal view x12
19. OU11936 (LQ-WF) meraspid pygidium x8 a) dorsal b) lateral c) posterior

Plate 30

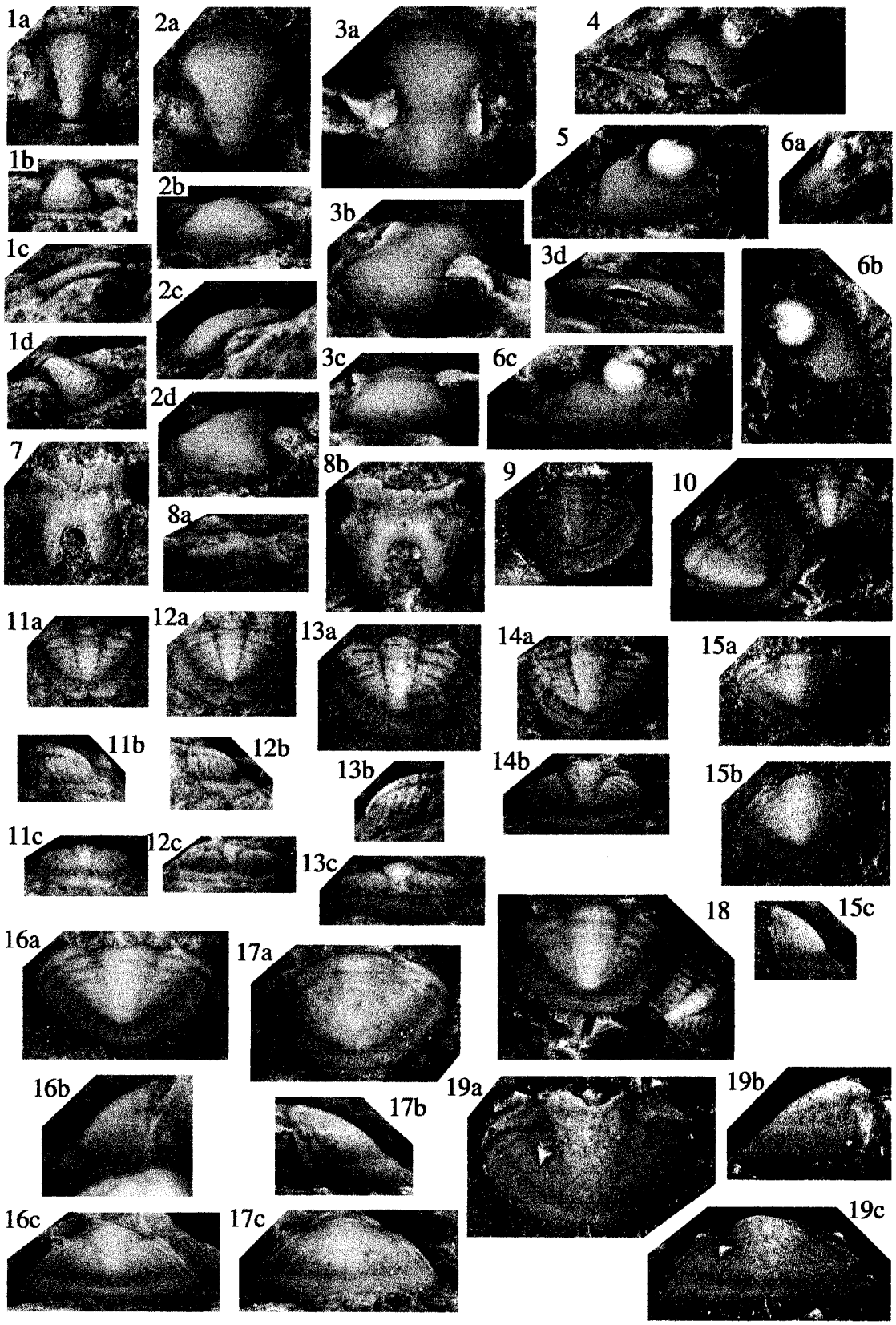
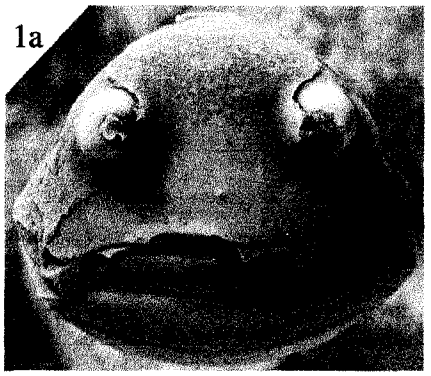

1a
2a
3a
4
1b
2b
5
6a
3b
1c
3d
6b
2c
1d
3c
6c
2d
7
8b
9
10
8a
11a
12a
13a
14a
15a
11b
12b
13b
14b
15b
11c
12c
13c
18
15c
16a
17a
16b
17b
19a
19b
16c
17c
19c

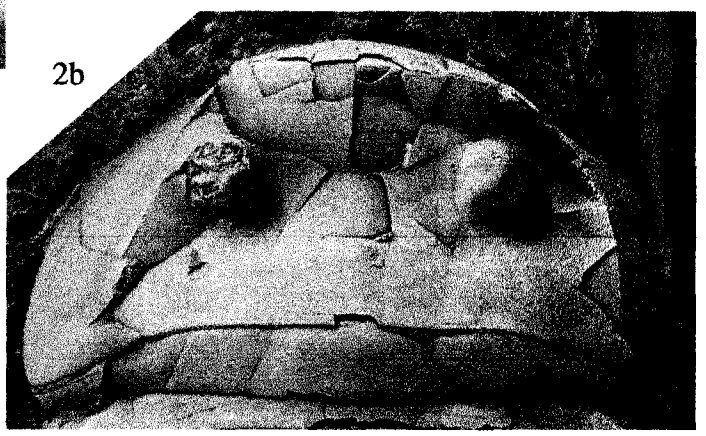
Plate 31 *Anataphrus kermiti*

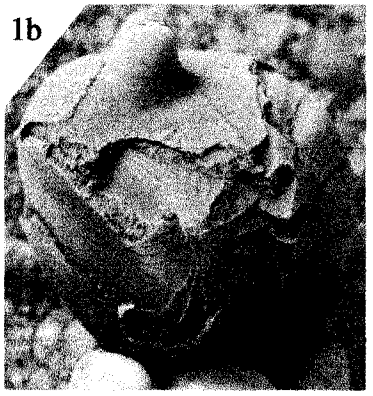
1. OU11937 (MC) nearly complete, partly exfoliated, enrolled individual x2.5 a) dorsal b) lateral c) anterior
2. OU11938 (BQ-Pave) complete, testate individual with slightly crushed cranidium a) lateral/dorsal x1 b) cephalon x2 c) dorsal x1
3. OU11939 (BQ-Pave) crushed, weathered complete individual x1 a) dorsal b) lateral/dorsal
4. OU11940 (LQ-WF) testate cranidium indorsal view, unblackened, dark areas indicate muscle attachment sites on ventral surface of cuticle x2
5. OU11941 (LQ-WF) testate pygidium, unblackened x2 a) dorsal view, dark areas along axis indicate sites of muscle attachment on ventral surface of cuticle b) dorsal view, lighting maximized to show faint relict segmentation on pleural regions

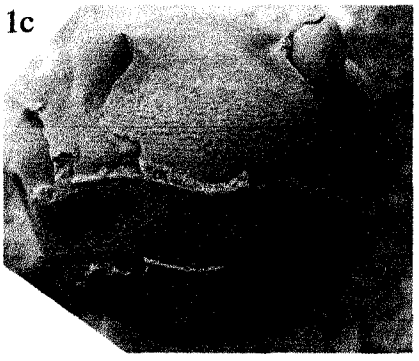
Plate 31


1a

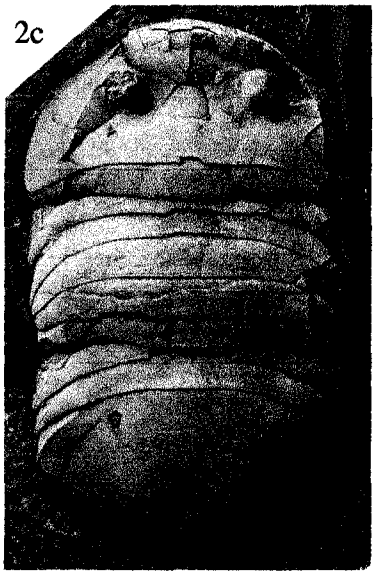

2a

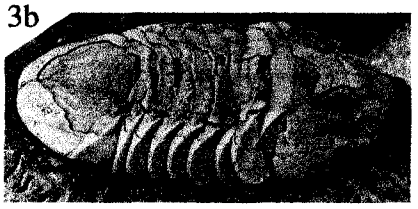

2b

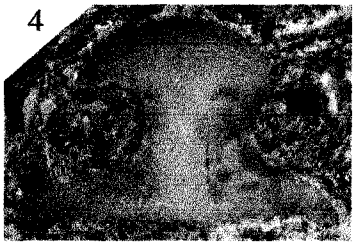

1b

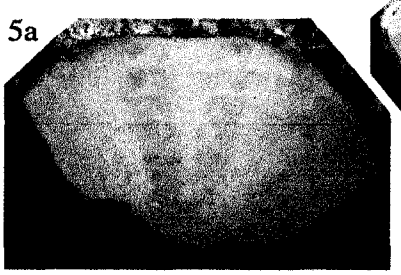

1c

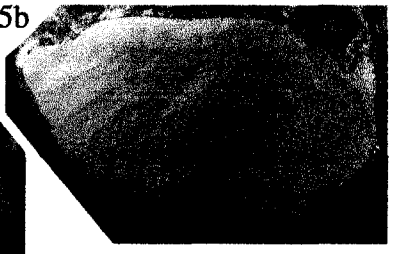

3a


2c


3b


4

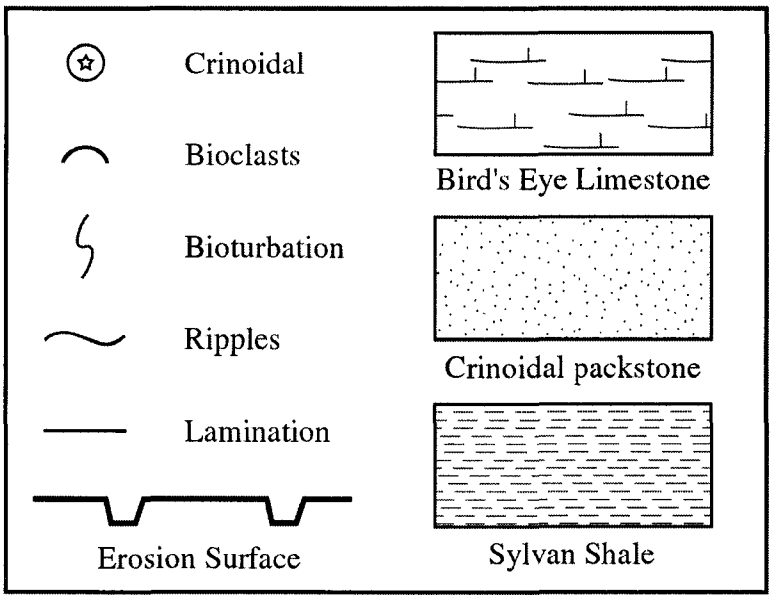

5a

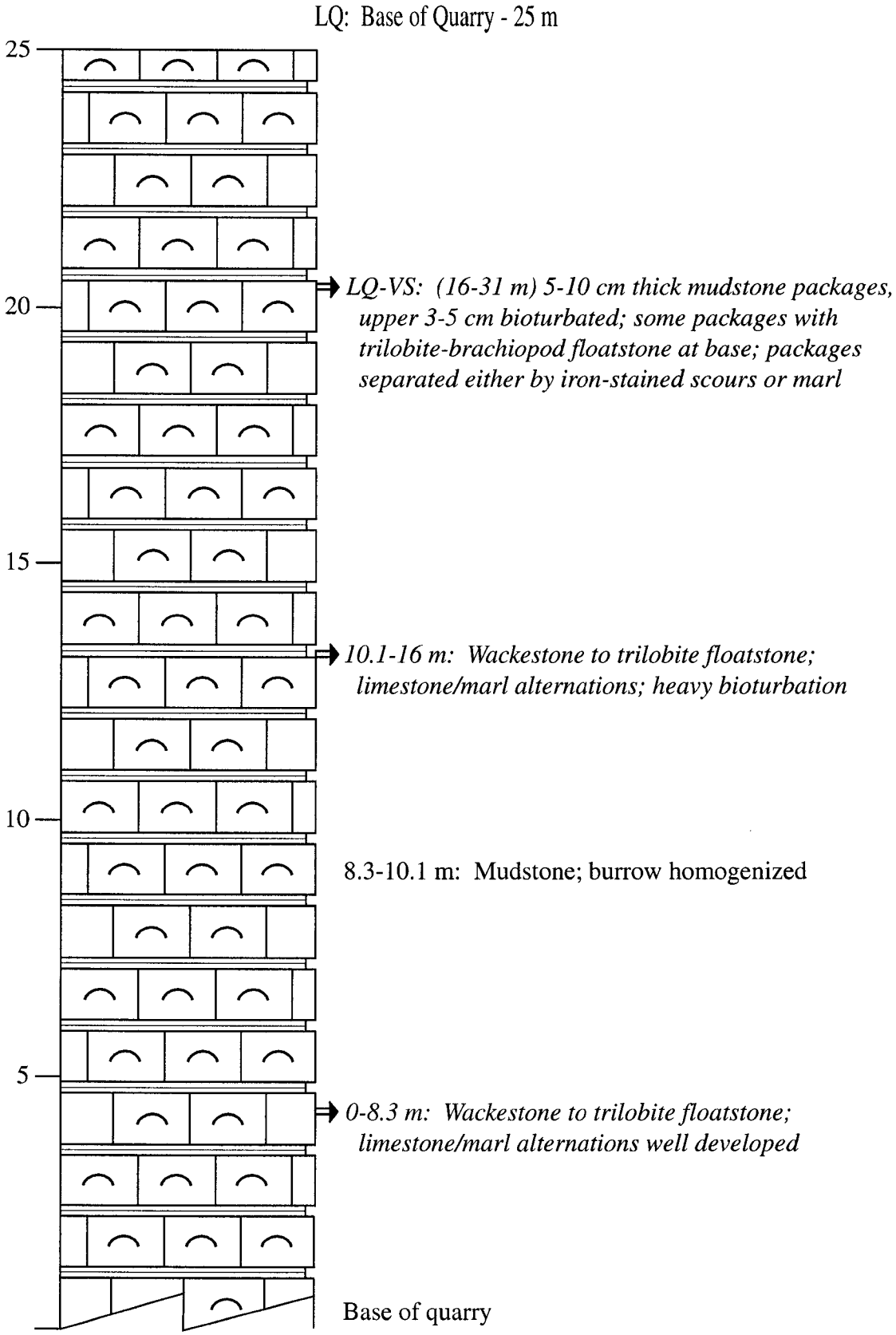

5b

Appendix

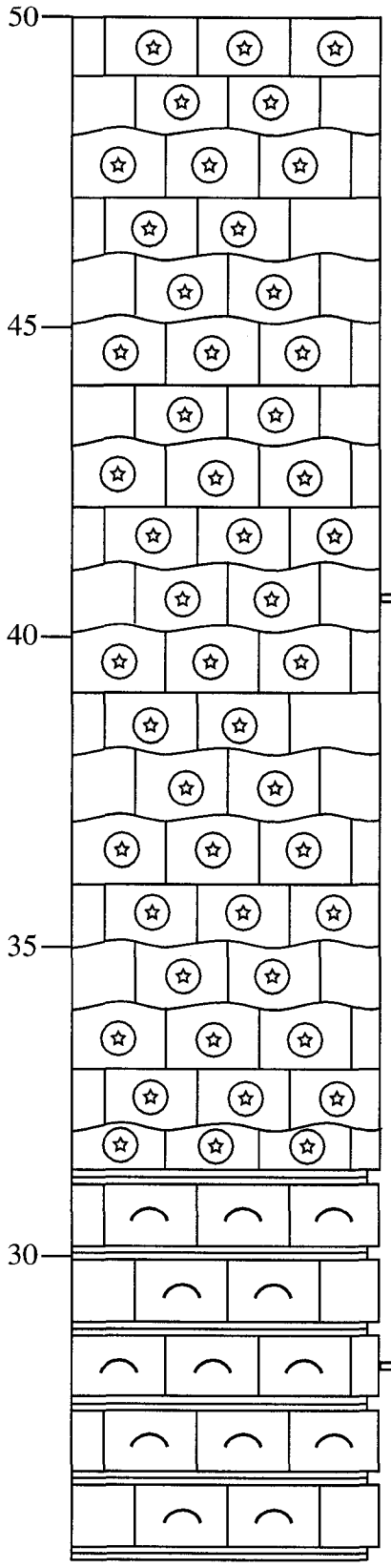
I measured and logged eight stratigraphic sections of the Viola Group in the Arbuckle Mountains and Criner Hills (Fig. 3). These are figured as stratigraphic columns on the following pages. The key below explains symbols used in the columns. Trilobite collecting horizons are indicated in each column by arrows.

Stratigraphic Column
Key




LQ: Base of Quarry - 25 m
25
20
15
10
5
LQ-VS: (16-31 m) 5-10 cm thick mudstone packages, upper 3-5 cm bioturbated; some packages with trilobite-brachiopod floatstone at base; packages separated either by iron-stained scours or marl
10.1-16 m: Wackestone to trilobite floatstone; limestone/marl alternations; heavy bioturbation
8.3-10.1 m: Mudstone; burrow homogenized
0-8.3 m: Wackestone to trilobite floatstone; limestone/marl alternations well developed
Base of quarry

LQ: 25-50 m

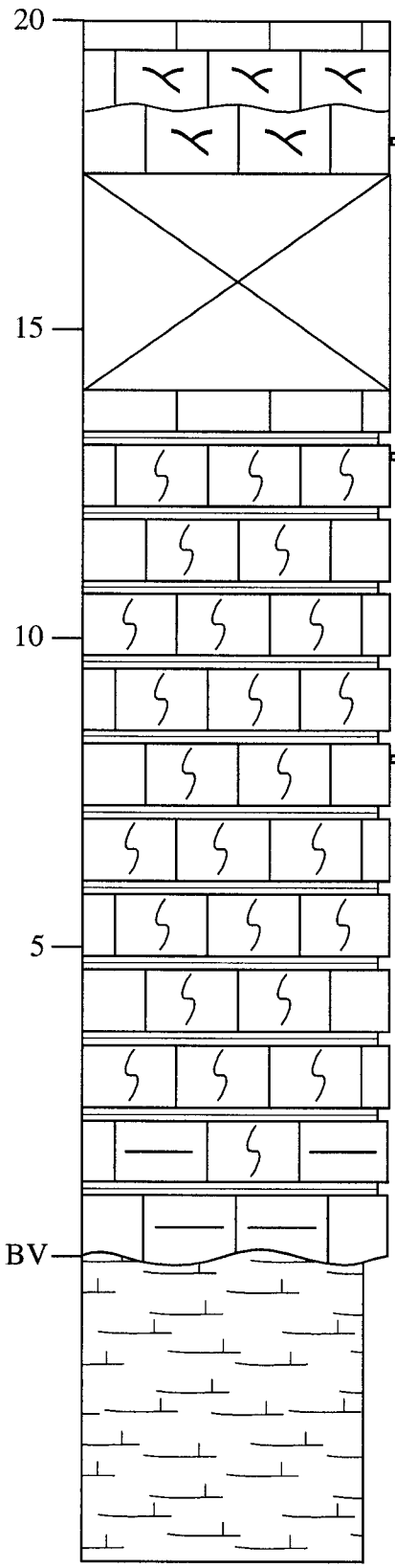


LQ-WF: (31-50 m) Welling Formation; well-washed, crinoid-rich grain- to rudstone; cross-bedding; scours between 10-40 cm thick packages

Viola Springs/Welling contact: gradational; wacke- to floatstone coarsens upward to grain- to rudstone over 0.5 m

LQ-VS: (16-31 m) 5-10 cm thick mudstone packages, upper 3-5 cm bioturbated; some packages with trilobite-brachiopod floatstone at base; packages separated either by iron-stained scours or marl

99: Bromide to 20m



18-20 m: Wacke- to rudstone interbedded with mud- to grainstone

99-18: 5-10 cm thick, wacke- to rudstone; parallel-bedded; convex-up brachiopods; shelter-spar; marl partings absent

14-18 m: Covered interval

99-13: Wacke- to floatstone; patchy silicification; crinoid ossicles, short columns, silicified brachiopods, fenestrate bryozoa, cryptolithine trilobites

99-8: Thin 4-8 cm interval brachiopod-trilobite wacke- to floatstone

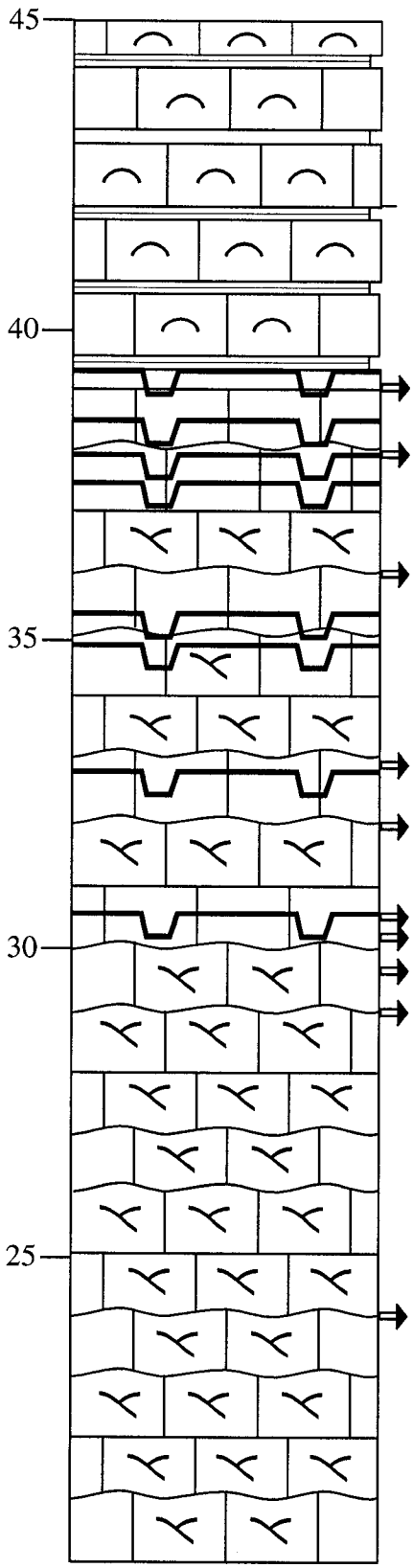
0.5-12 m: bioturbated lime mud- to wackestone; limestone/marl alternations; beds 5-15 cm thick; chert in nodules, lenses, discontinuous beds; graptolites, cryptolithine and isoteline trilobites

0-0.5 m: laminated lime mud- to wackestone, small graptolite fragments in layers, chert

Bromide/Viola Contact: unconformable; up to 8 cm erosional relief; phosphate crust

Bromide Formation: fine carbonate mud; microbial laminites; shrinkage cracks; limited fauna

99: 20-45 m



39.5-51m: 5-15 cm thick beds; pelletal wacke- to packstone interbedded with pack- to rudstone; clasts convex-up; bioturbation pervasive; marl/ limestone alternations; marl partings 0.5-3 cm thick; brachiopods, trilobites abundant; also crinoids, ostracodes, bivalves, gastropods, solitary corals, receptaculitids, bryozoa, conulariids

99-39

99-38

36.5 m: bench; floatstone interbeds above

99-36

30-39 m: Iron-stained erosion surfaces common; largest clasts (bryozoan mounds) at bases of beds; many lenses pinch laterally;

99-33

99-32

99-30.25, 99-30.5

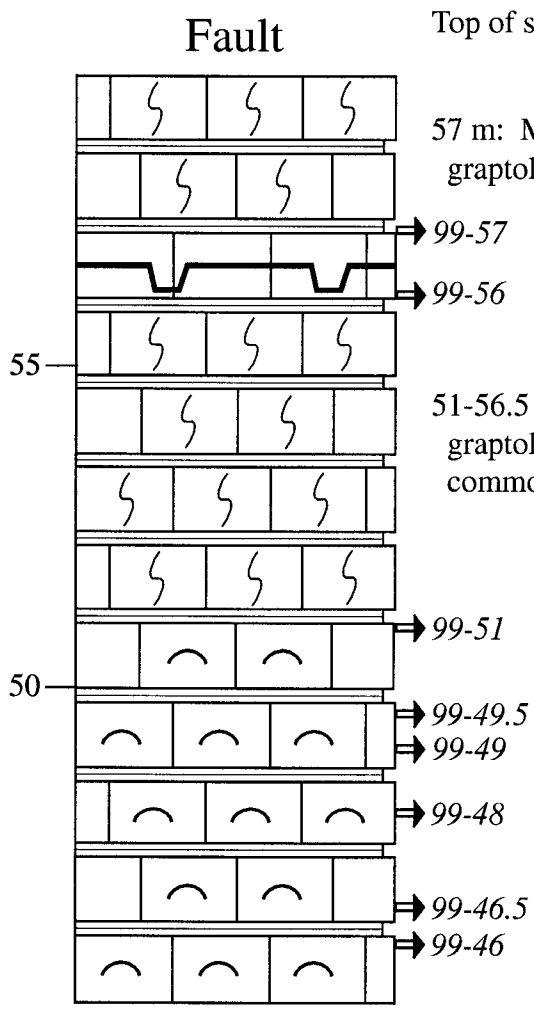
99-29.75

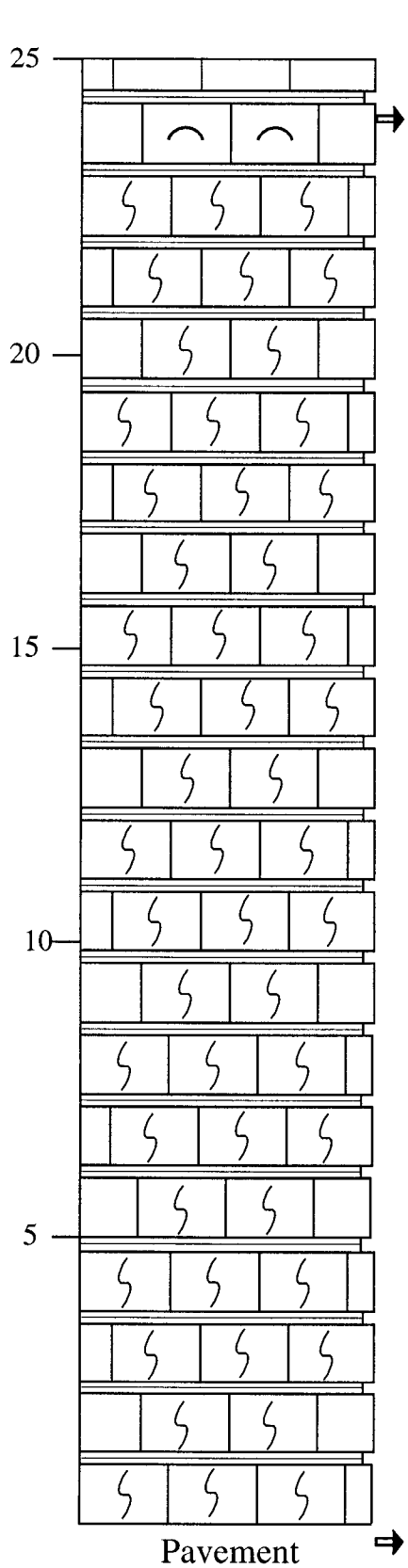
99-29

99-24

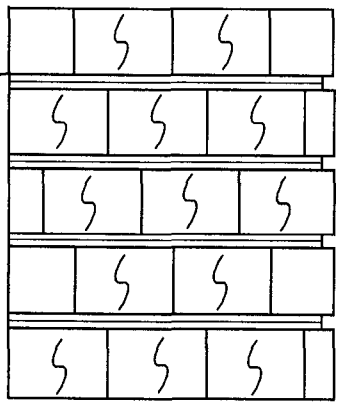
20-30 m: Grain- to rudstone; crinoid ossicles, mounded bryozoa at partings; thin 5-7 cm interbeds grainstone; cross-bedding common; trilobites, bryozoa abundant

99: 45-58 m


Fault
Top of section faulted out
57 m: Mud- to wackestone; large bioclasts rare graptolites common
99-57
99-56
55
51-56.5 m: 10-20 cm wacke- to floatstone beds; graptolites, conulariids, cryptolithine trilobites common; other trilobites present
99-51
50
99-49.5
99-49
99-48
99-46.5
99-46


BQ: Pavement-25 m
25
20
15
10
5
Pavement
BQ-24: 15-20 cm thick package; fining-upward, trilobite floatstone to wackestone
15-24 m: beds thicker, up to 40 cm thick; bioclasts up to 2 cm diameter; increased bioturbation
10.5-15 m: fining-upward packages; coarsest fraction coarser than below
6-10.5 m: fining-upward packages; limestone/marl alternations
6 m: Upper pavement: fossil hash, most bioclasts <2 cm
Pavement - 6 m: 10-30 cm thick limestone/marl alternations; 5-20 cm thick beds, packestone fining upward to lime mudstone; bioturbation minimal, concentrated at tops of packages
Pavement; quarry floor; finer shell debris on top; large (20 cm diameter) chert nodules

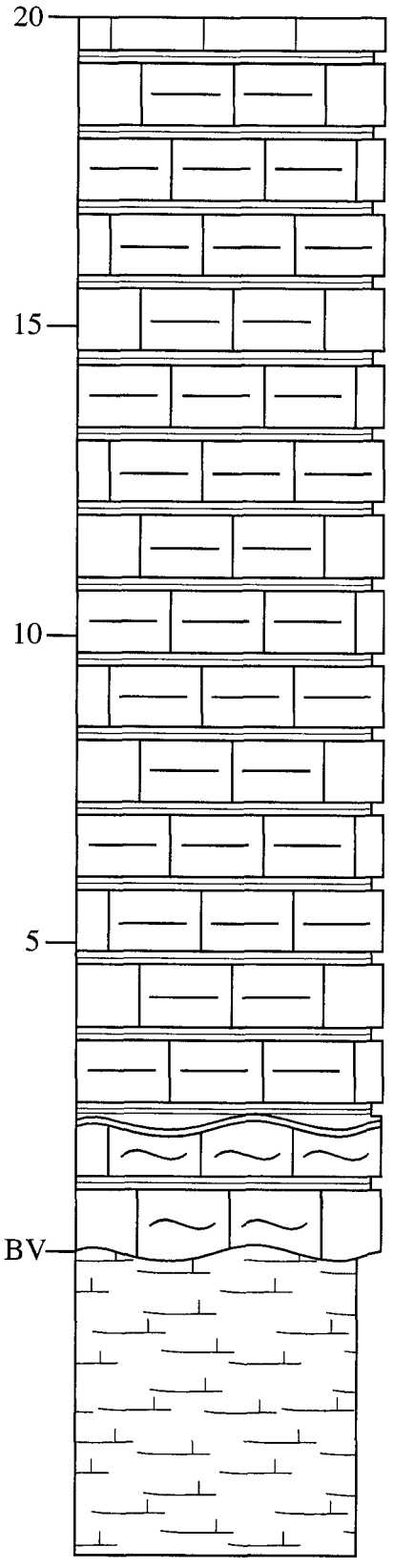
BQ: 25-31 m



29-31 m: highly weathered

25-29 m: wacke- to packstone; isolated large (4 cm) bioclasts; rare thin (0.5 cm) packstone lenses in mudstone

35: Bromide - 20 m



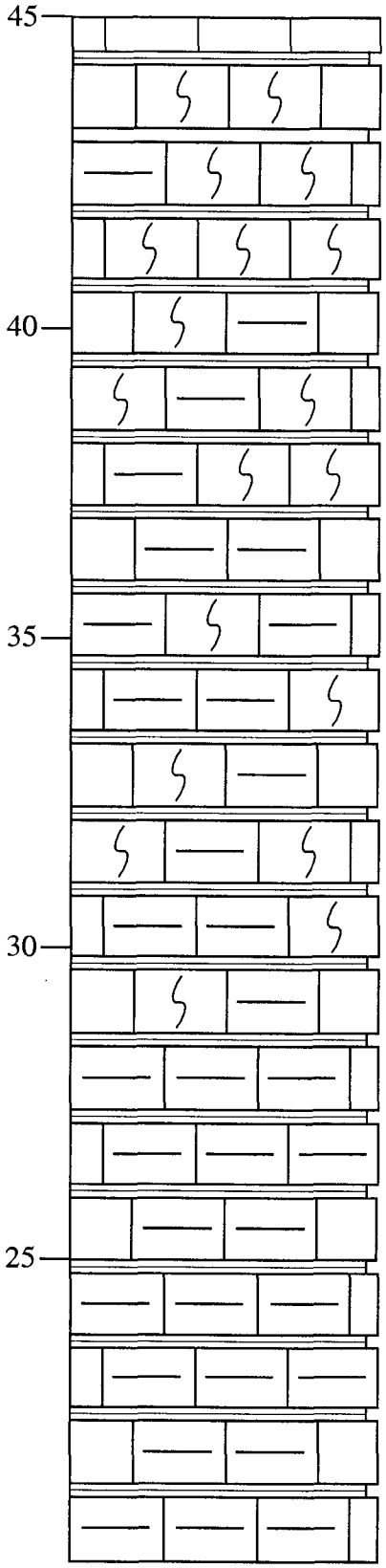
7-28 m: Lime mudstone to wackestone; laminae thicker upwards (mm to cm-scale); bioturbation rare; limestone/marl alternations

2-7 m: Very dark lime mudstone; mm-scale laminae; bioturbation, scours absent; limestone/marl alternations

2 m: surface rich in iron, phosphate
0-2 m: ostracode-rich wacke- to packstone; mm-scale laminae; ripple cross-beds; scour surfaces
Contact: low relief surface; small (<1cm diamter) iron nodules, phosphate

Corbin Ranch Submember, Pooleville Member: fine carbonate mud; shrinkage cracks; brachiopods, receptaculitids abundant

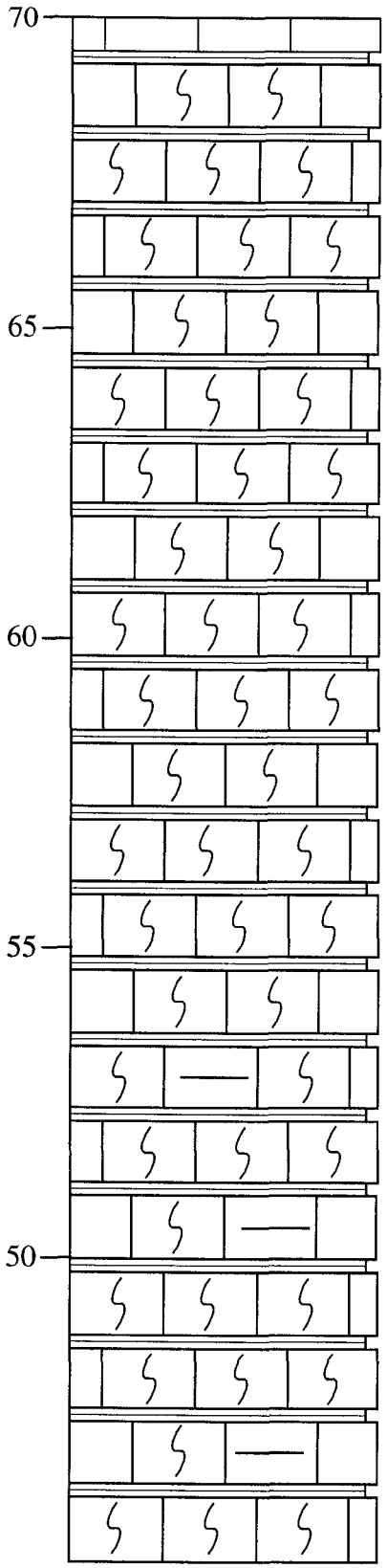
35: 20-45 m



28-55 m: Increasing bioturbation upward

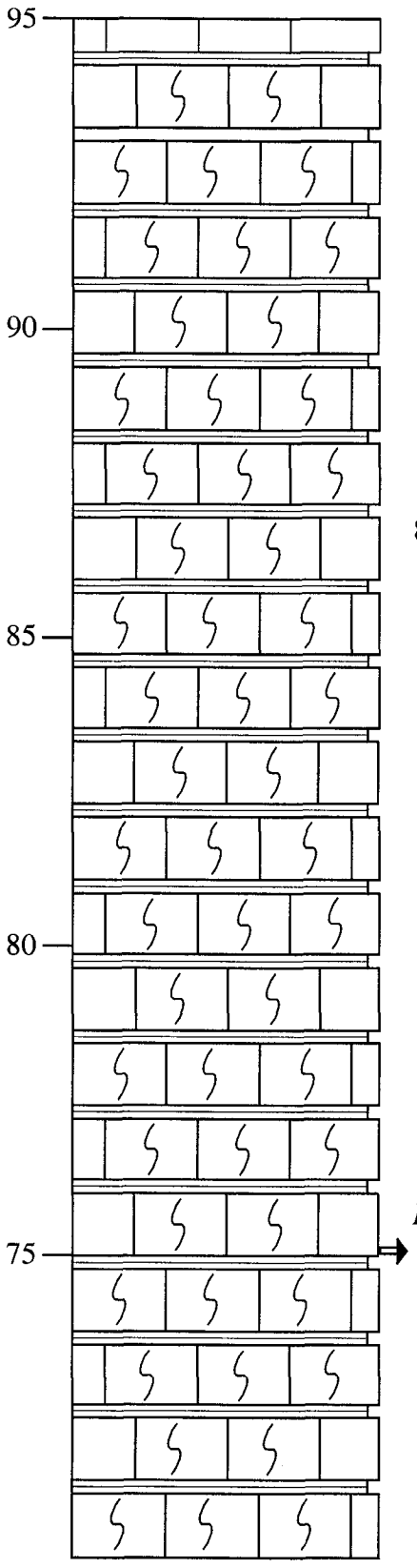
7-28 m: Laminated wacke- to packstone; laminae thicker upwards (mm to cm-scale); bioturbation rare

35: 45-70 m



55m: *Chondrites* abundant; wacke- to packestone burrow homogenized; cryptolithines at marl partings

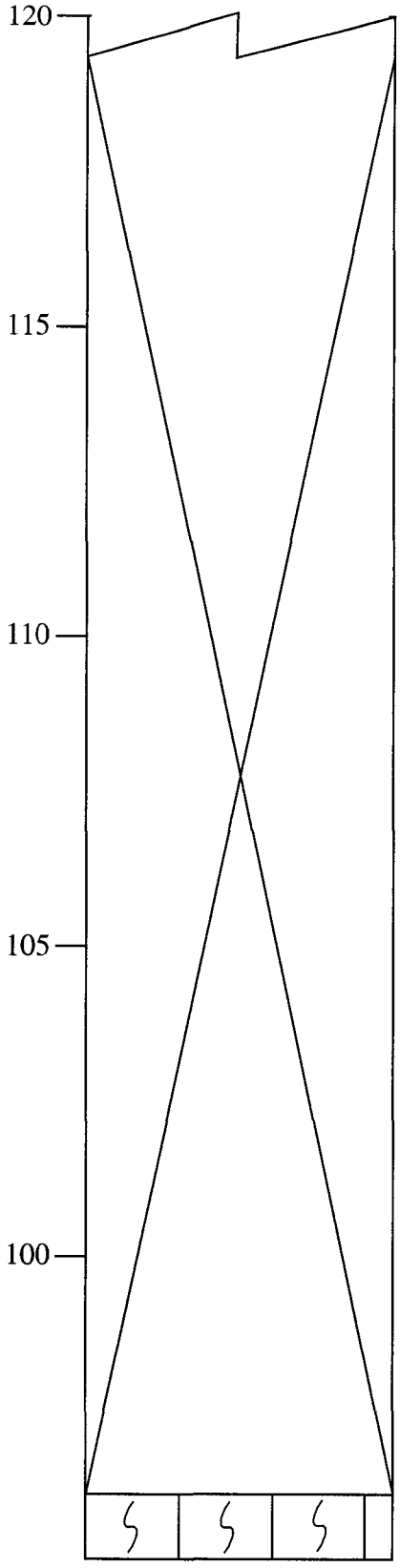
35: 70-95 m



83-96 m: Wacke- to packstone; rare articulate brachipods, isoteline fragments with cryptolithines at partings

I-35-75: Homogenized wacke- to packstone; isoteline floatstone horiozons rare; cryptolithines at marl partings

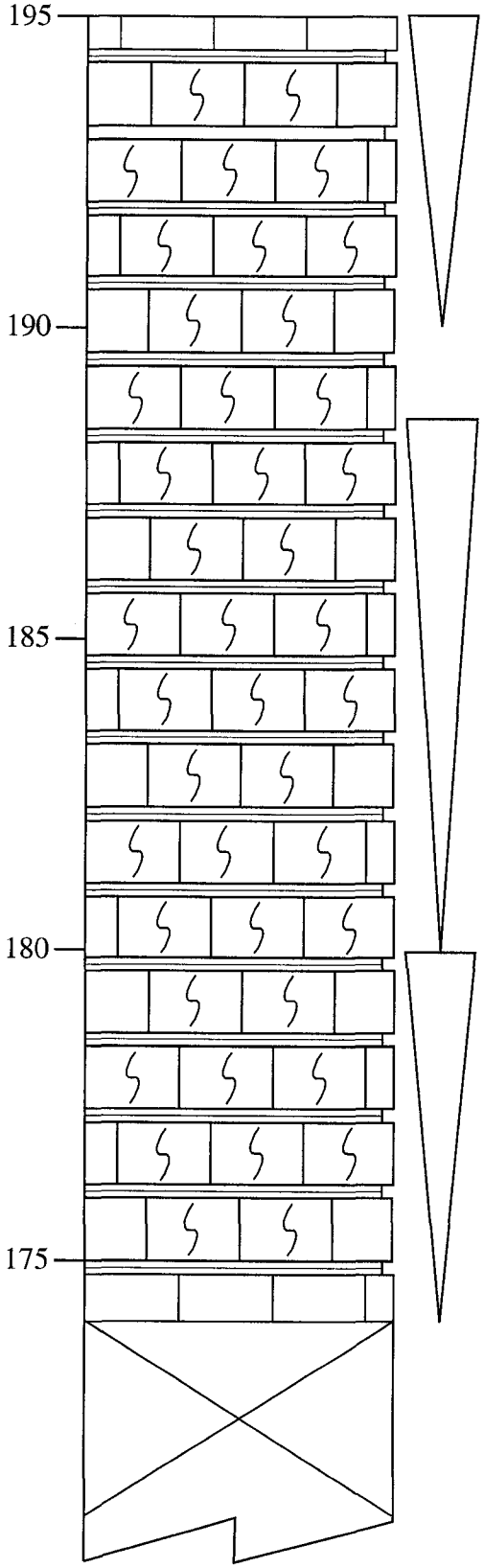
35: 95-96 m



Covered 96-174 m

Wacke- to packstone; burrow homogenized; rare large isoteline fragments

35: 174-195 m

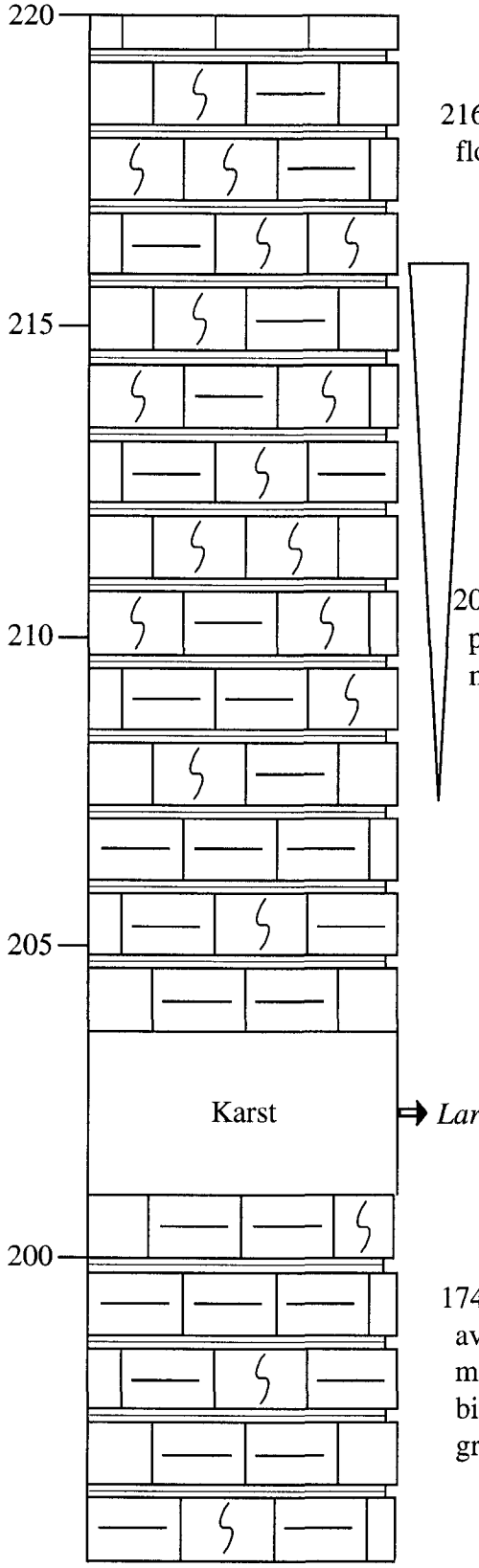


192 m: Packstone, coarse isoteline, brachiopod debris

189 m: Recessed marl parting; fine, dark mudstone above; graptolite-rich

174-201 m: Coarsening-upward packages; average 4 m thick; separated by recessed, marly partings; fine, dark mudstone, heavily bioturbated; coarsens up to crinoidal grainstone

35: 195-220 m



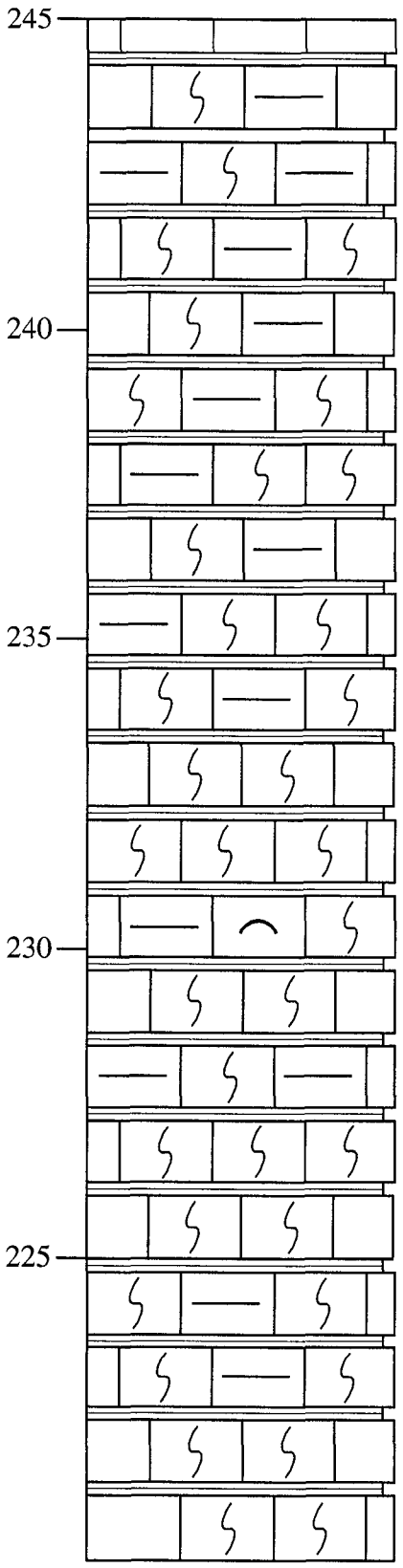
216-246.5 m: Burrow-homogenized wacke- to floatstone

204-216 m: Partings between coarsening-upward packages with iron staining; pack- to floatstone more common

Large isoteline fragments weathering out of karst

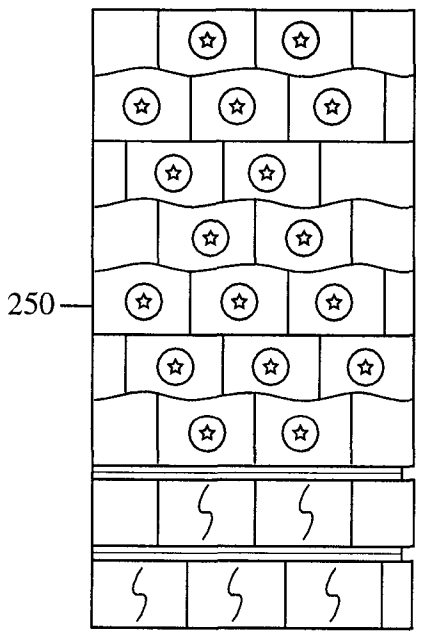
174-201 m: Coarsening-upward packages; average 4 m thick; separated by recessed, marly partings; fine, dark mudstone, heavily bioturbated; coarsens up to crinoidal grainstone

35: 220-245 m



216-246.5 m Burrow-homogenized wacke- to floatstone

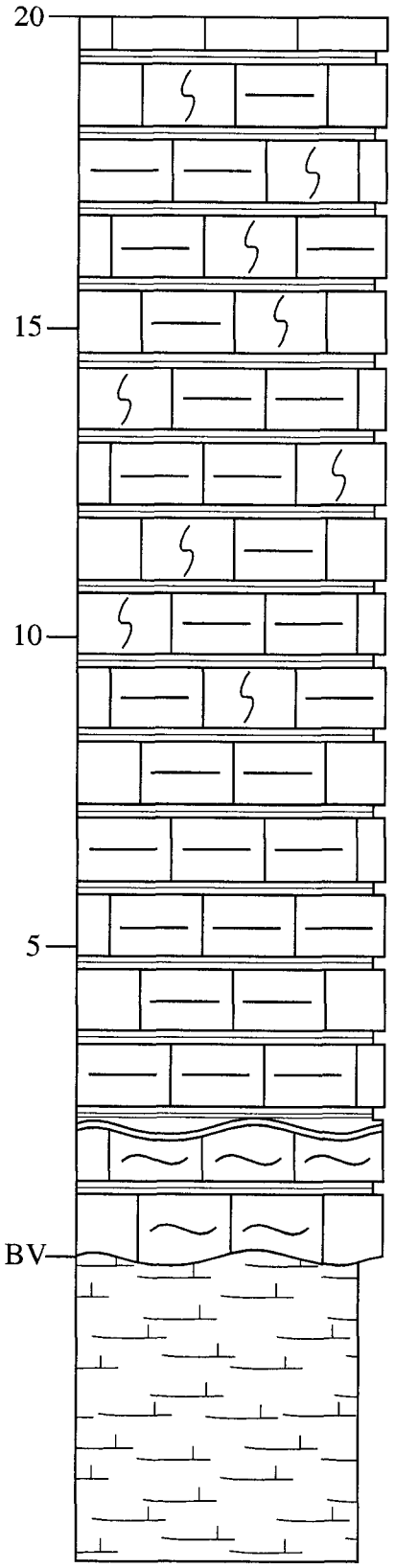
35: 245-256 m



247.5-256 m: Welling Formation; crinoidal grainstone

246-247.5 m: Four coarsening-upward packages; fine lime mudstone coarsens upward to crinoidal grainstone of Welling Formation

77: Bromide - 20 m



7-30 m: mm-scale laminae increase to cm-scale gradually up section; increasing bioturbation upwards; limestone/marl alternations

2-7 m: Very dark, mm-laminated carbonate mudstone; bioturbation absent; limestone/marl alternations

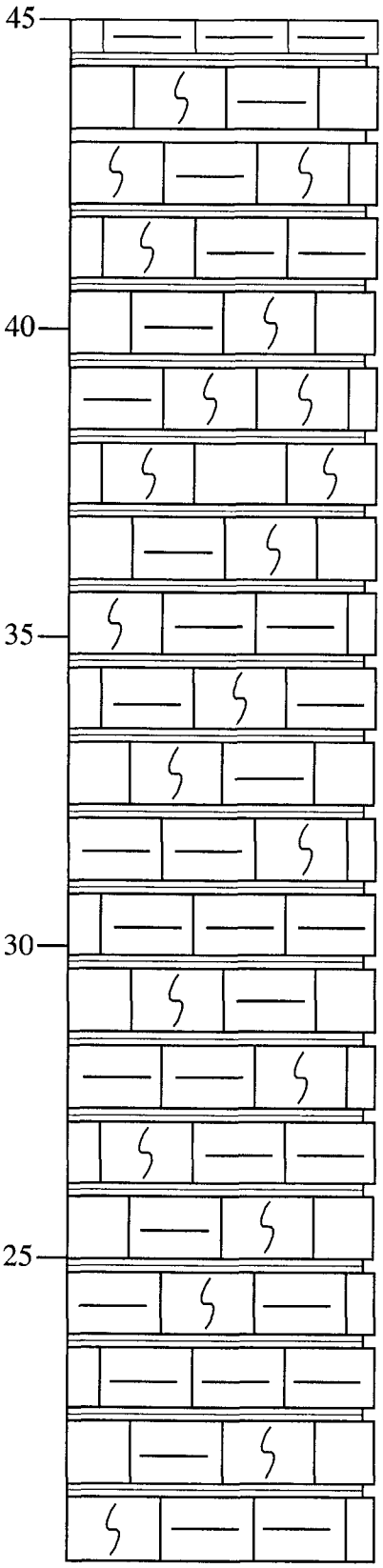
Condensed surface: pyrite, phosphate at low-relief erosion surface

0-2 m: ostracod-rich wacke- to packstone; cm-scale laminations; rippled

Contact: low relief; iron, phosphate at surface

Corbin Ranch Submember, Pooleville Member; receptaculitids, rugose corals common

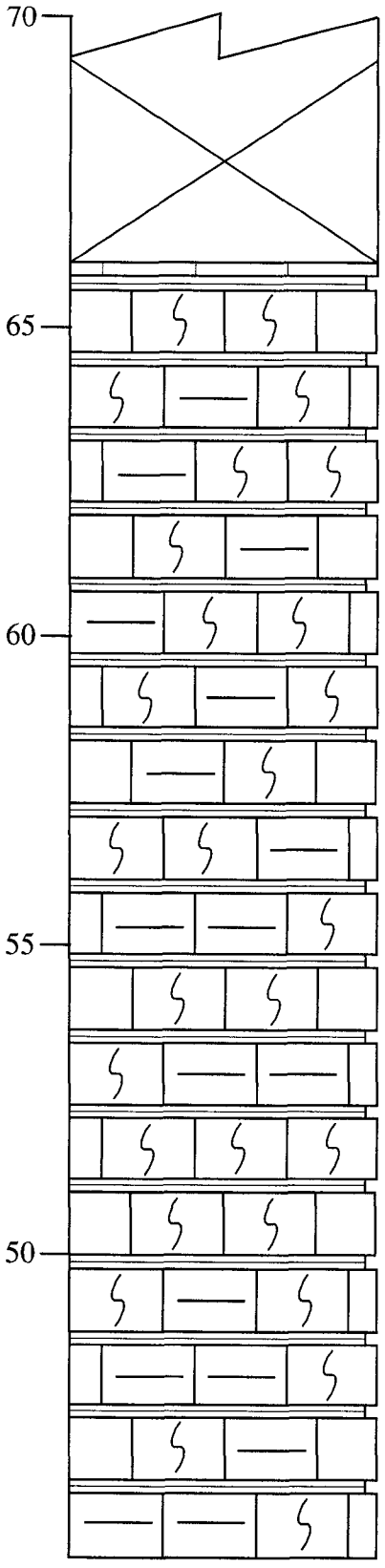
77: 20-45 m



30-70 m: cm-scale laminae, increasingly bioturbated

7-30 m: mm-scale laminae increase to cm-scale gradually up section; increasing bioturbation upwards; limestone/marl alternations

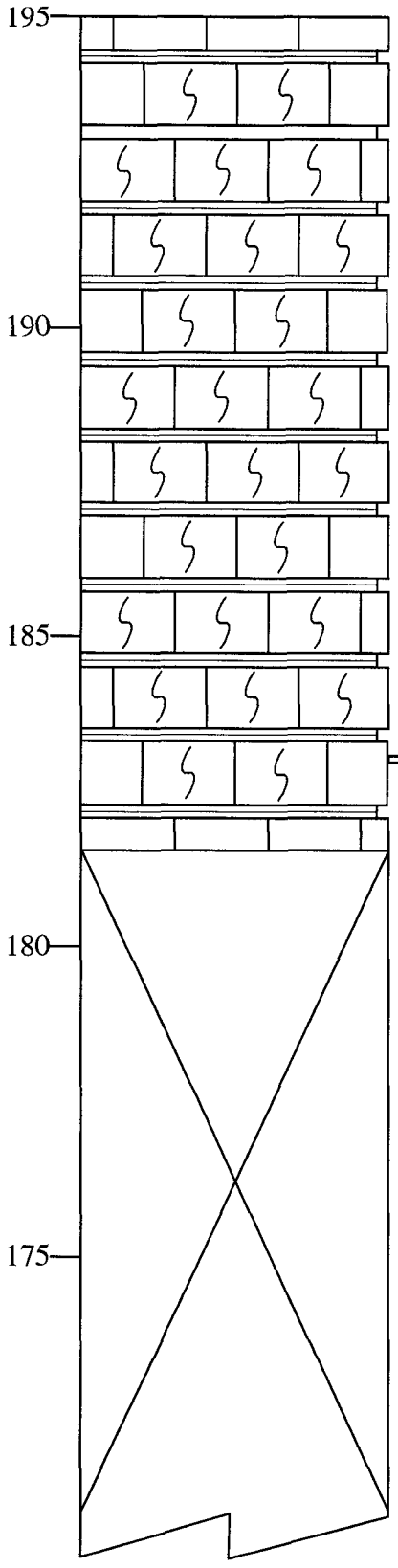
77: 45-66 m



Covered 66-182 m

30-66 m: rare cryptolithines at marl parting surfaces; bioturbation increasing until nearly homogenized at 55 m

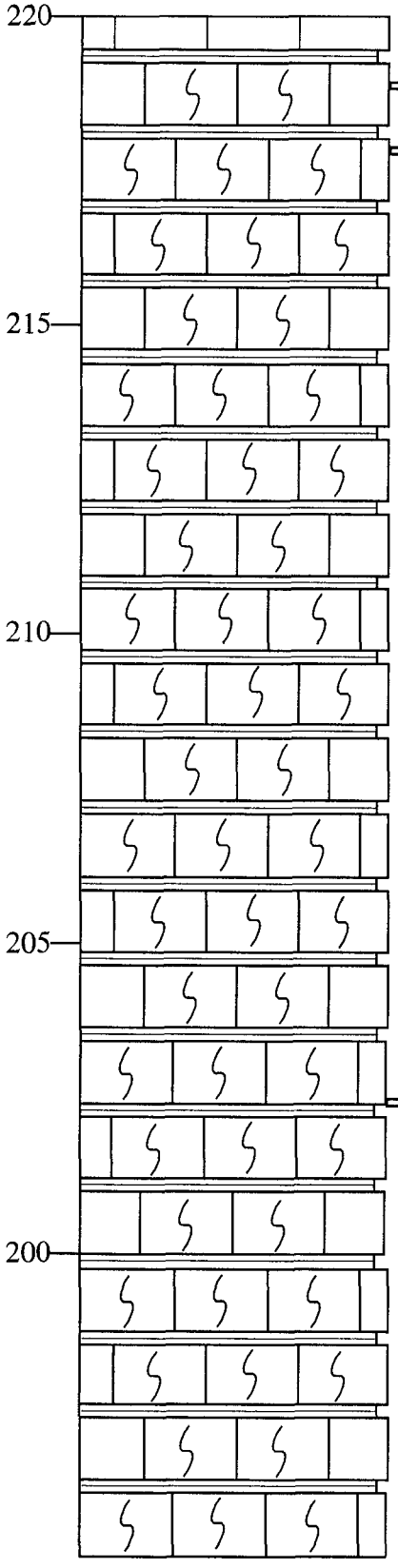
77: 182-195 m



182-243m: 20-50 cm thick event beds; burrow-homogenized wacke- to packstone; coarsening upward to isoteline-rich float- to rudstone; cryptolithine fringes at marl partings

77-183 Collection from isoteline float- to rudstone

77: 195-220 m



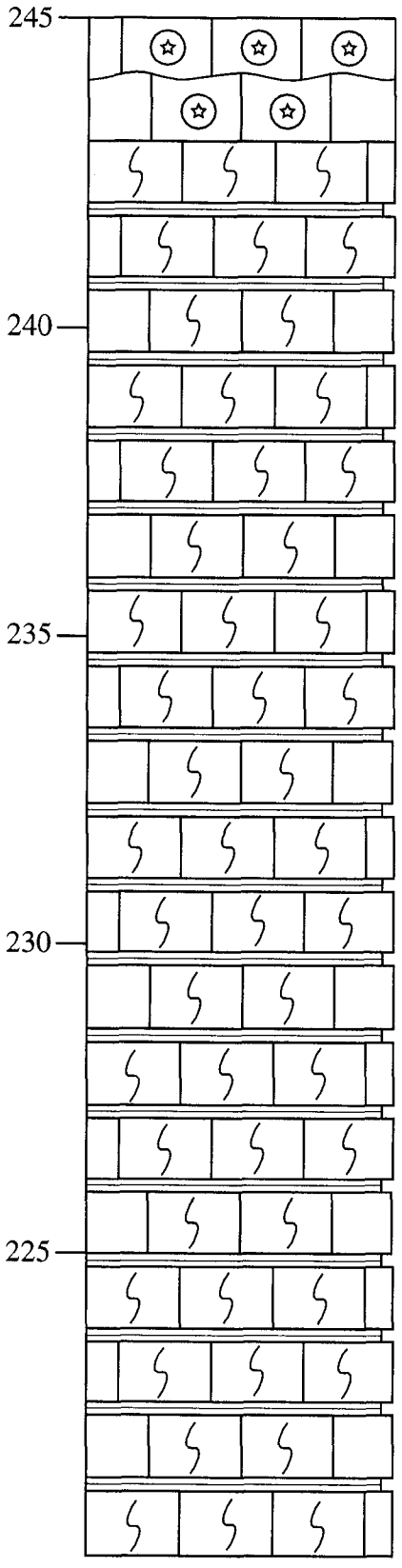
77-219 Collection from isoteline float- to rudstone

77-218 Collection from isoteline float- to rudstone

182-243m: 20-50 cm thick event beds; burrow-homogenized wacke- to packstone; coarsening upward to isoteline-rich float- to rudstone; cryptolithine fringes at marl partings

77-202.5 Collection from isoteline float- to rudstone

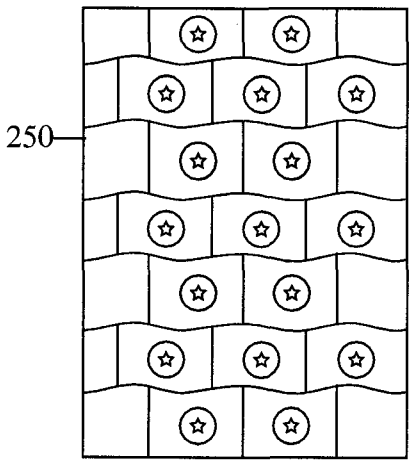
77: 220-245 m



243m: Contact with Welling Formation; contact gradational; about 30 cm packages of wackestone grading upward to grainstone over 3 m interval

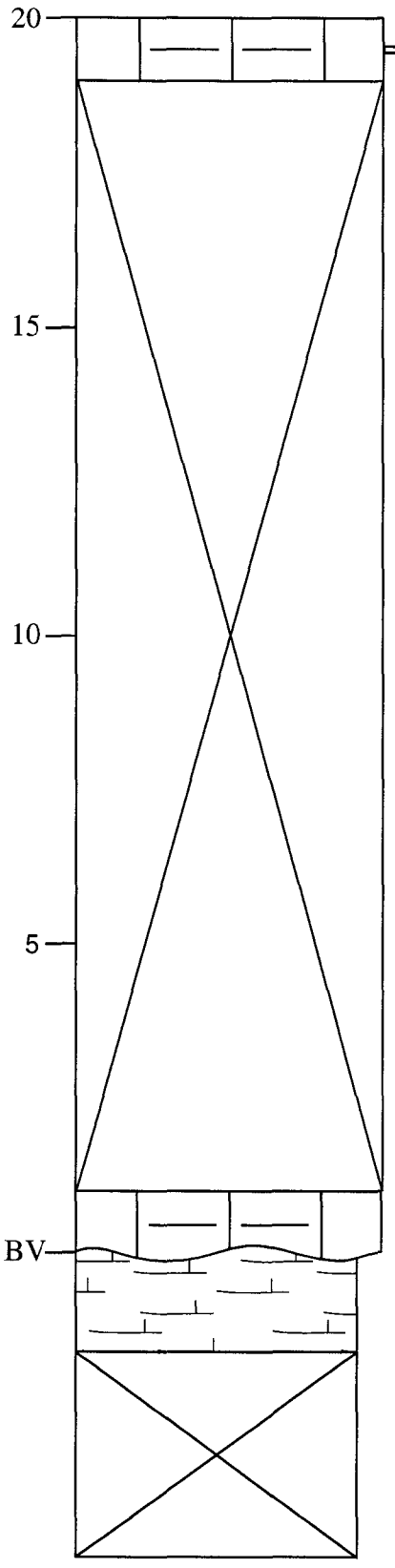
182-243m: 20-50 cm thick event beds; burrow-homogenized wacke- to packstone; coarsening upward to isoteline-rich float- to rudstone; cryptolithine fringes at marl partings

77: 245-252 m



Welling Formation: crinoidal grainstone; beds separated by scours; large bioclasts (8 cm diameter) occur rarely

Nebo: Bromide - 0.5 m, 19-20 m



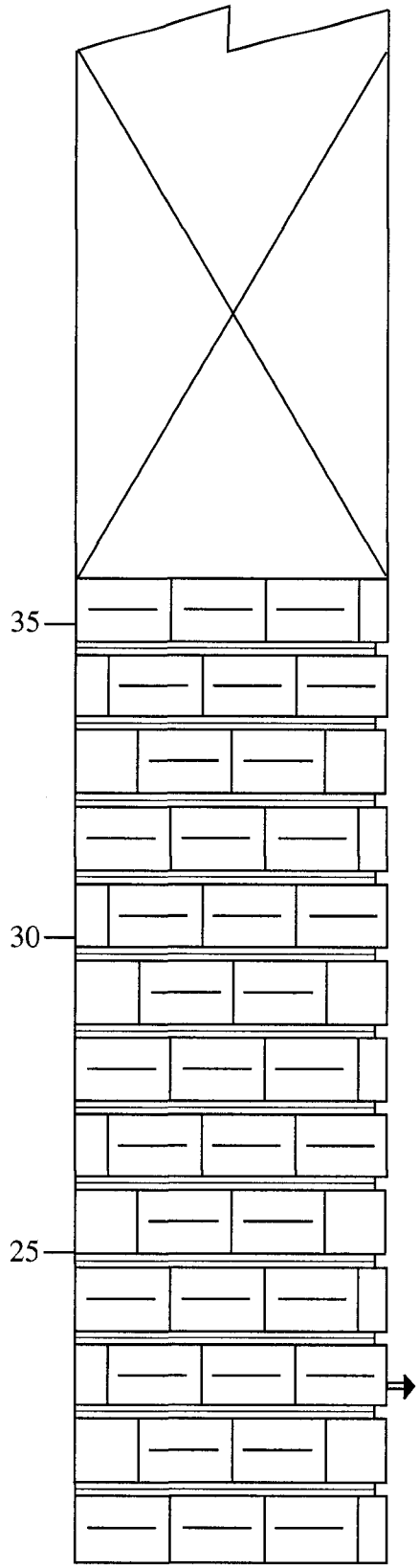
Nebo 20 m: Cryptolithines from parting surfaces between 1-6 cm thick laminated mudstone

0-0.5 m: laminated mudstone

Bromide/Viola Springs contact: low relief

Bromide Formation: bioturbated mud- to wackestone

Nebo: 20-36 m

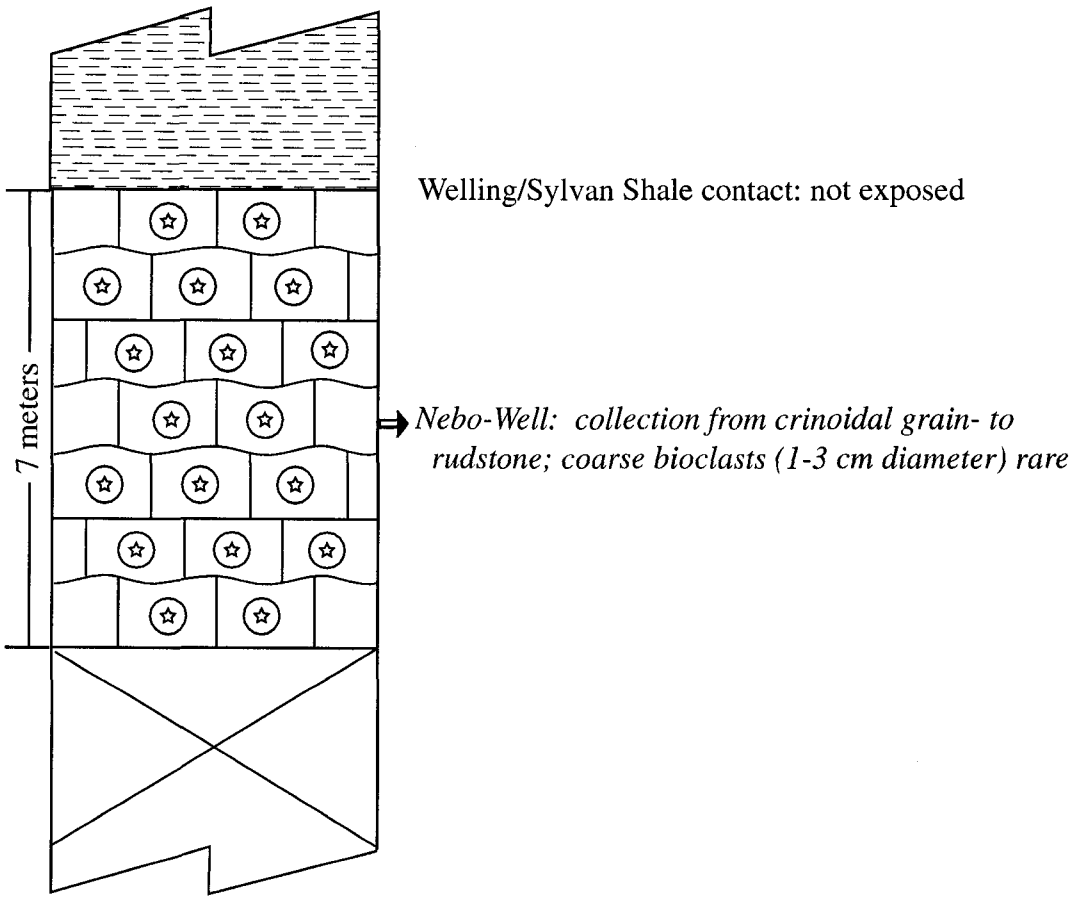


Covered and faulted

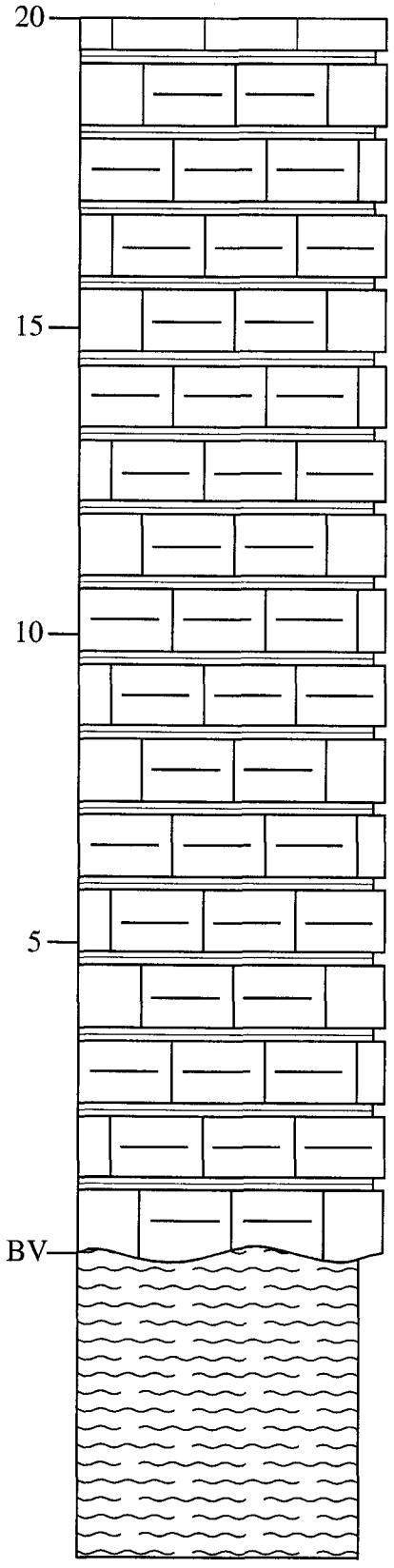
19-35.5 m: Lime mudstone, 1-6 cm thick; thin (<1 cm) partings; graptolites, cryptolithines concentrated at partings; bioturbation rare

Nebo 23 m: Cryptolithines from parting surfaces between laminated mudstone

Nebo: Upper 7 m - Sylvan Shale



CN: Bromide - 20 m



17-20 m: laminae disrupted by scours, ripples, low-level bioturbation

4-17 m: mm-laminated lime mudstone

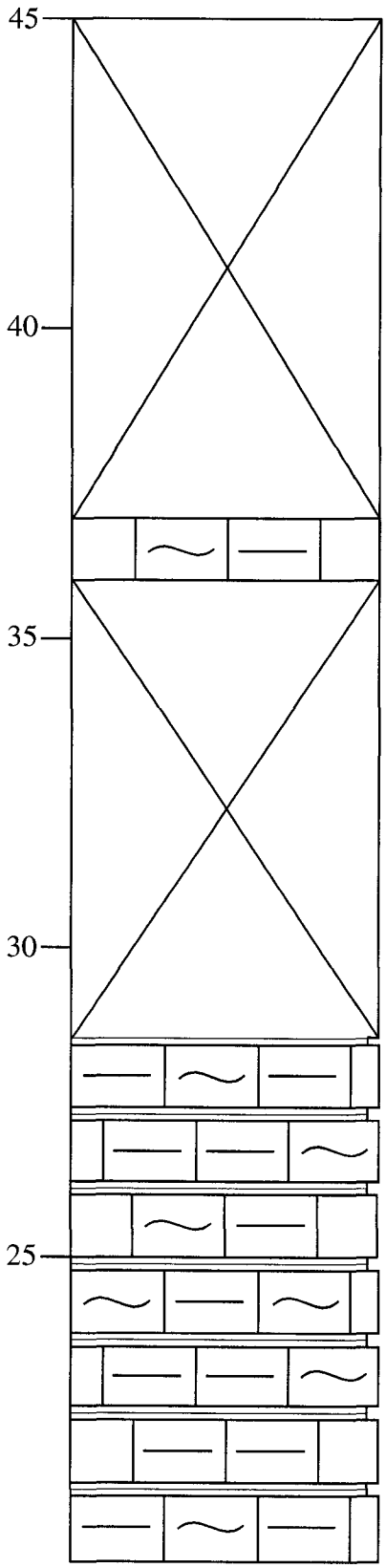
1.8-4 m: mm-sclae laminae, lighter laminae lime mud, darker laminae silt-grade carbonate; small-scale scours, ripples, bioturbation

0-1.8 m: faint laminae in lime mudstone

Bromide-Viola Contact: erosional, low relief

Bromide Formation (Pooleville Member): fine lime mudstone; articulate brachiopods, receptaculitids common

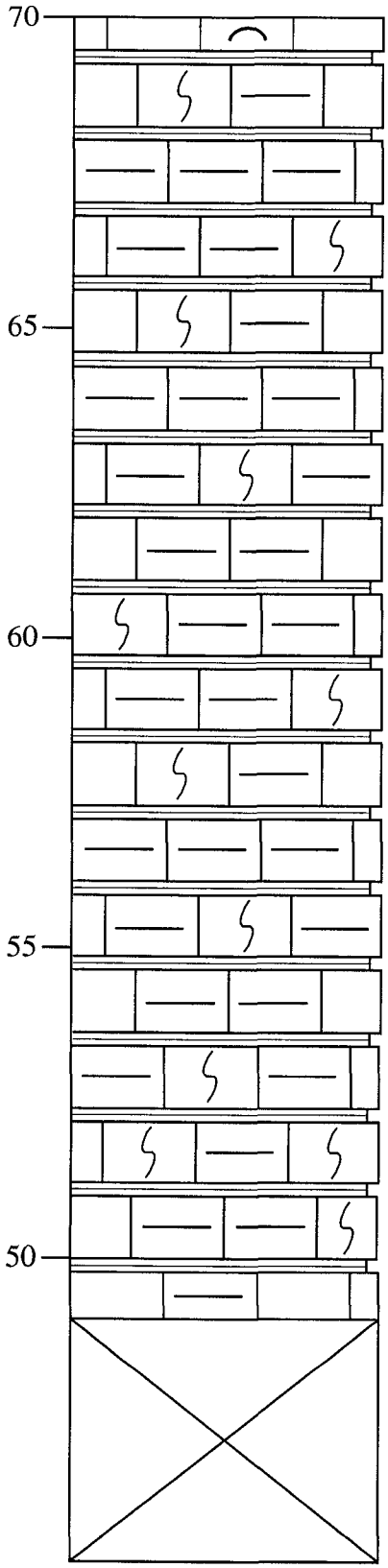
CN: 20-45 m



33-33.5 m: laminated lime mud to wackestone; abundant bioturbation

20-28.5 m: laminated carbonate mudstone; scours, ripples, bioturbation increase in scale and frequency upward

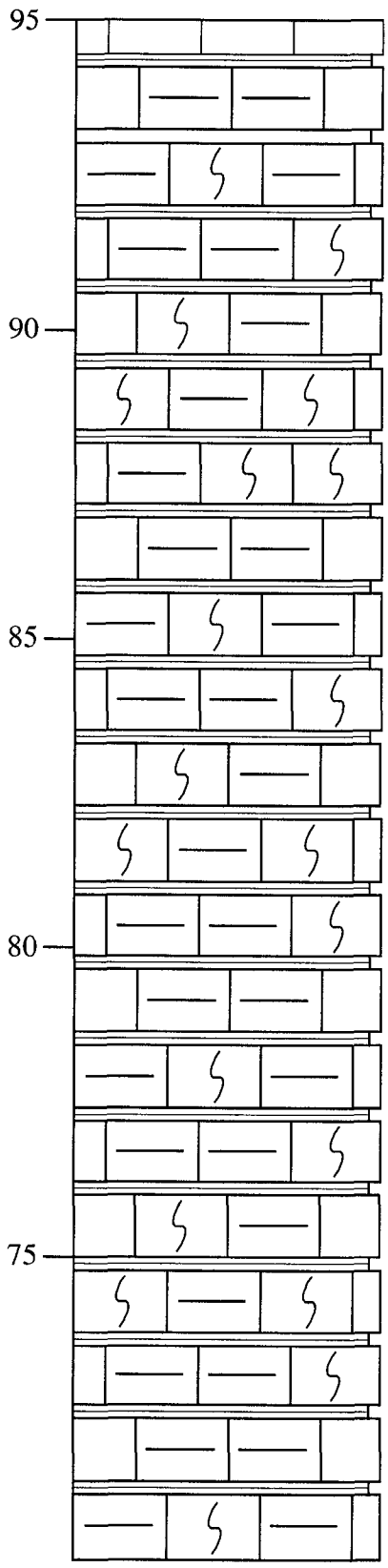
CN: 49-70 m



69 m: west edge of quarry

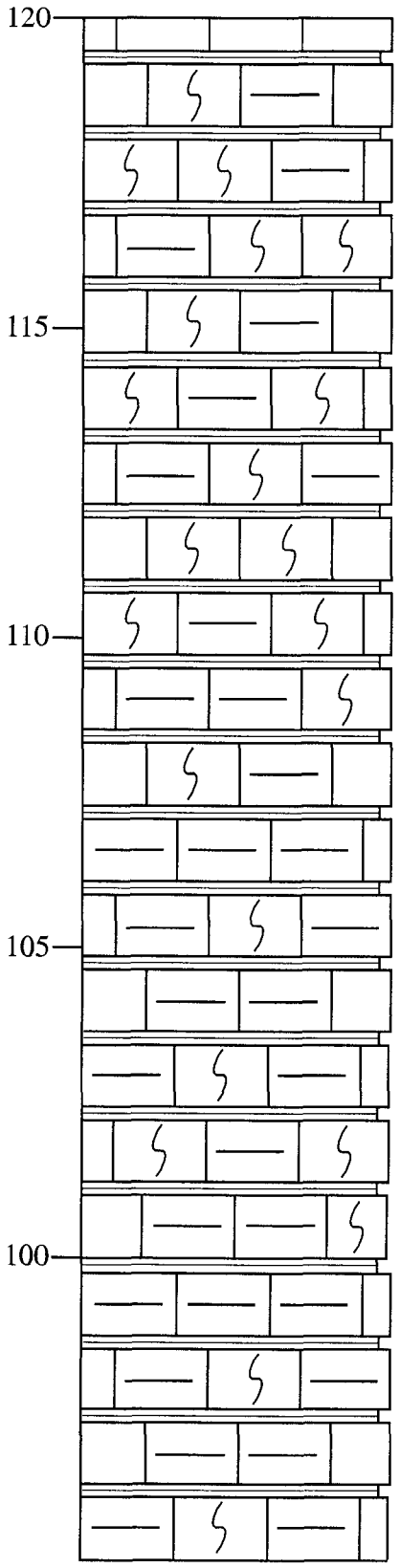
49.5-69 m: laminated lime mudstone; bioturbation increases upward

CN: 70-95 m



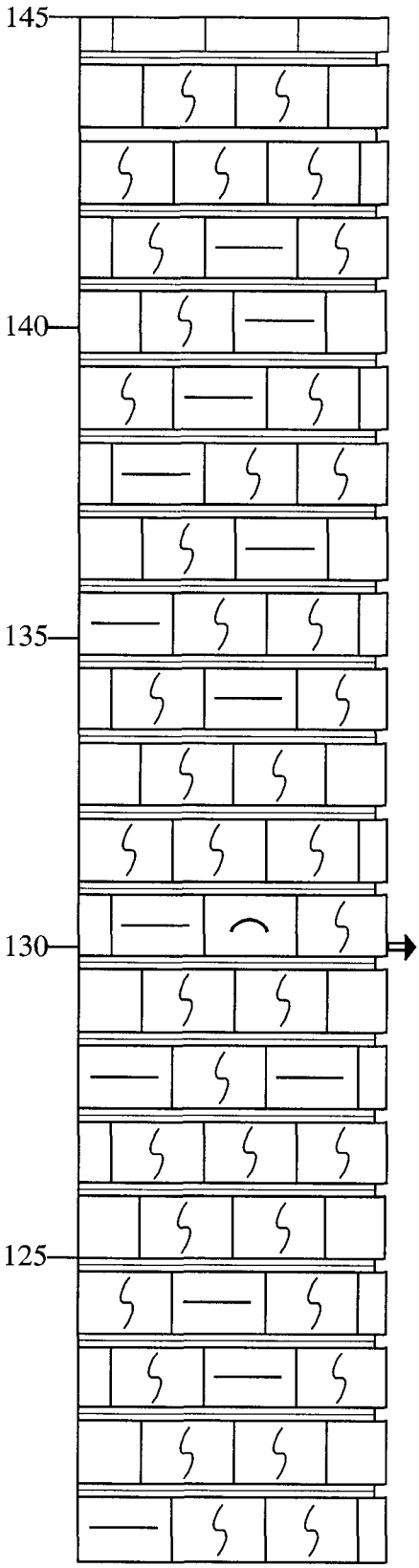
70-95 m: laminated lime mud to wackestone; limestone/marl alternations; rare cryptolithine and isoteline bioclasts; increasing bioturbation upward

CN: 95-120 m



95-120 m: laminated lime mud to wackestone; cm-scale packages; increasing bioturbation; greater trace fossil diversity; bioclasts rare

CN: 120-145 m

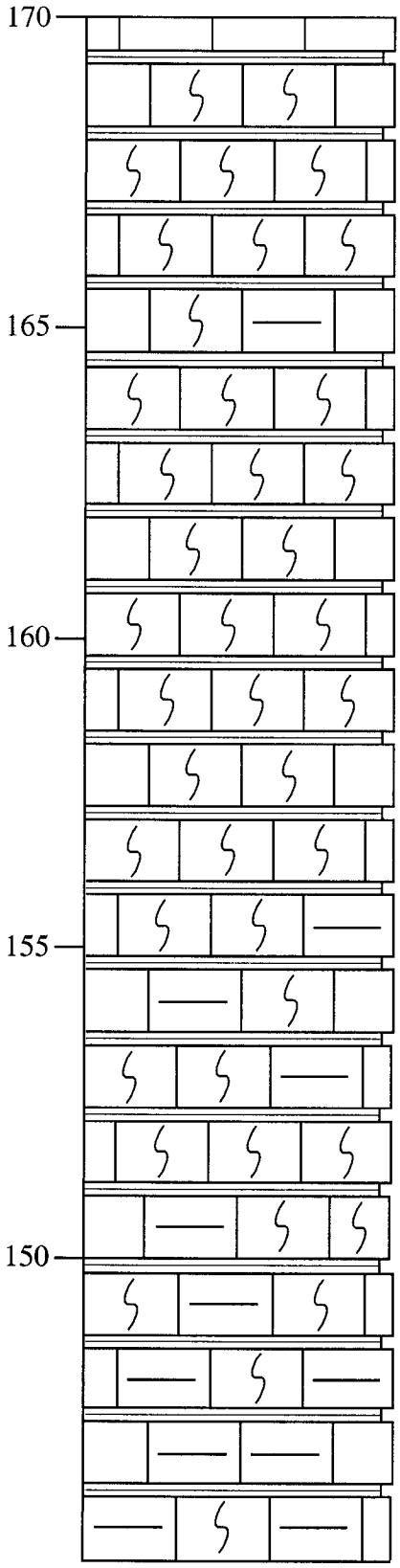


130-145 m: burrow homogenized wacke- to floatstone; gastropods locally abundant

130 m: wacke- to floatstone; brachiopod shell hash

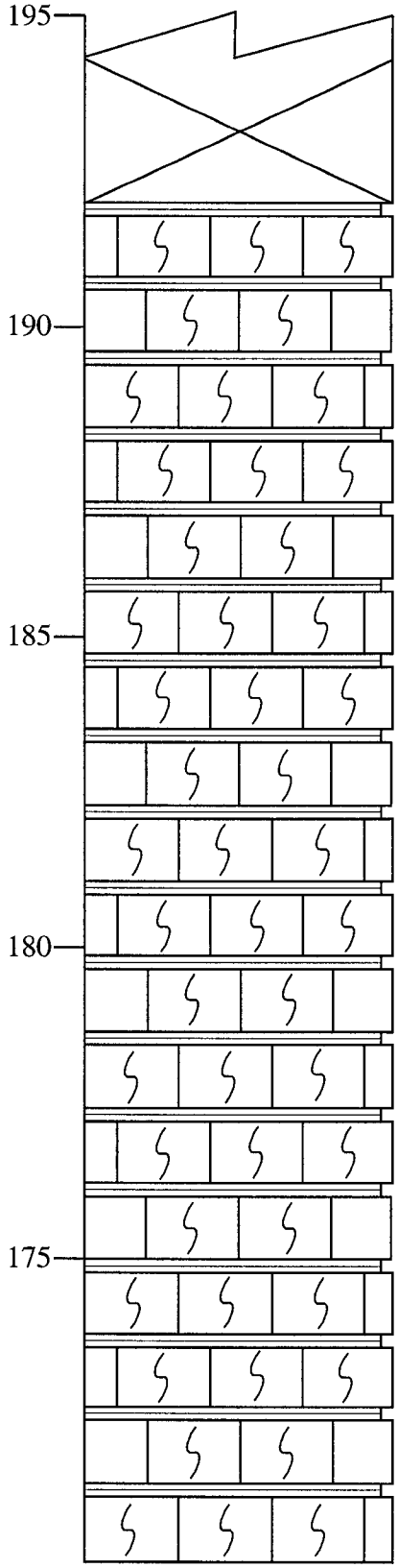
120-126 m: cm-scale packages almost completely burrow homogenized

CN: 145-170



145-170 m: burrow homogenized wacke- to floatstone; large isoteline bioclasts rare

CN: 170-193 m

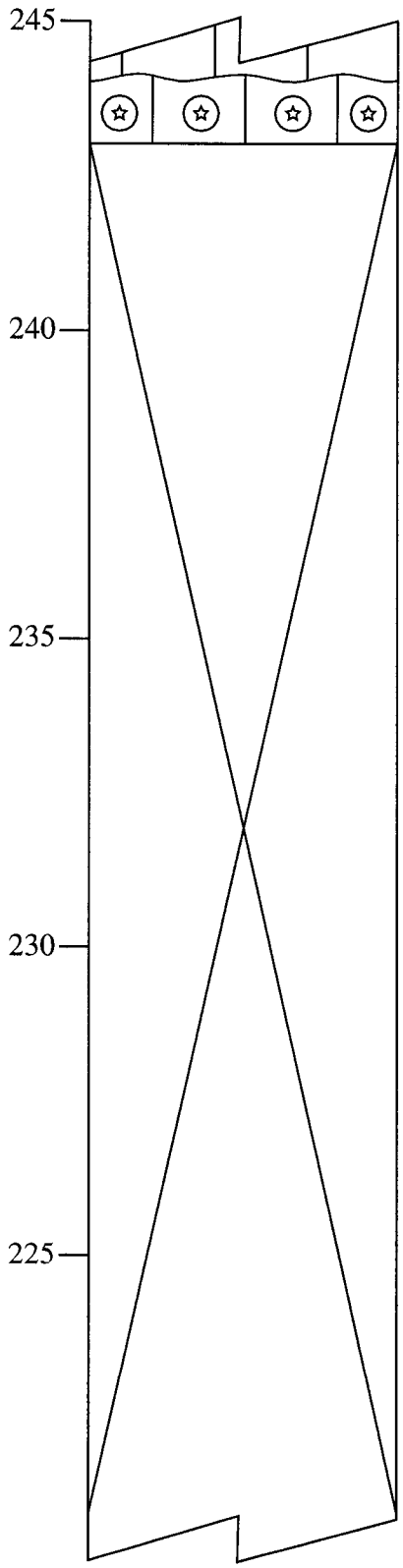


Covered 193-243 m

193 m: east edge of quarry

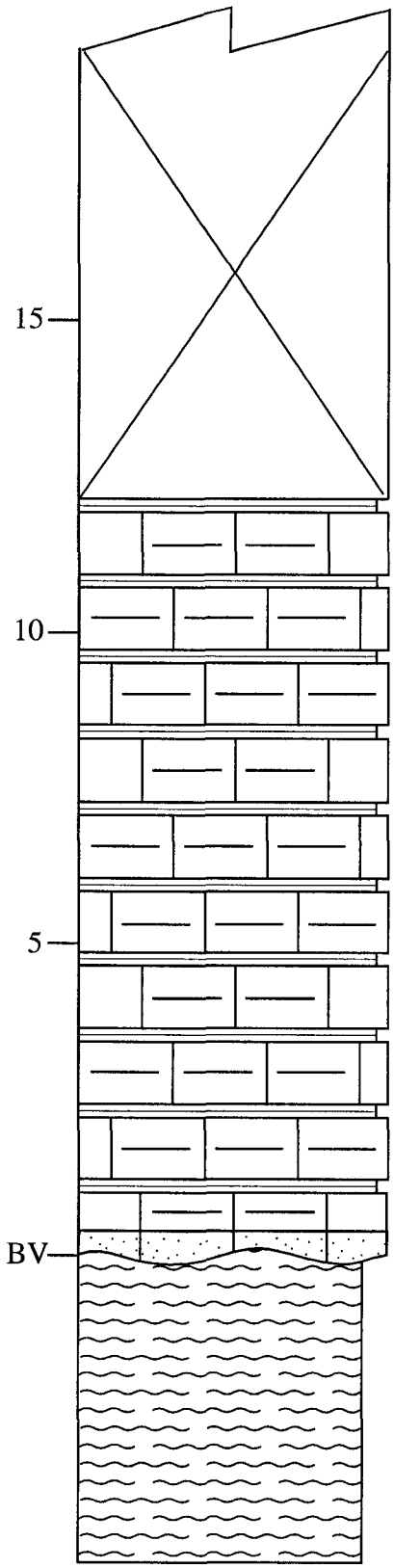
170-193 m: burrow homogenized pelletal wacke- to floatstone

CN: 243-245 m



Welling Formation; crinoidal grainstone exposed on slope of hill outside quarry; thickness unknown

SQ: Bromide - 20 m



Covered 12-47 m

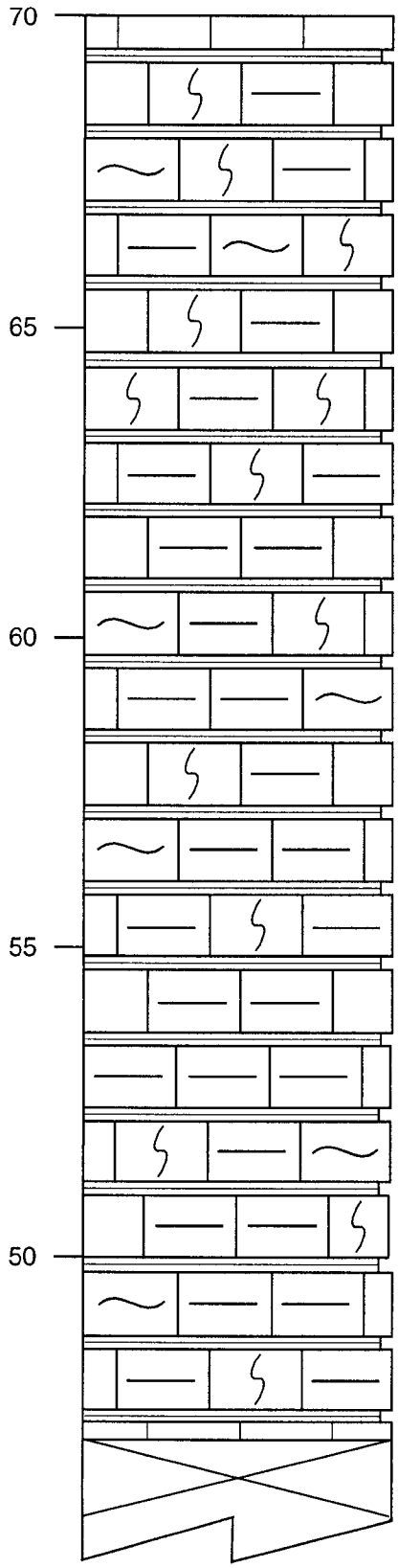
1.25-12 m: mm-scale laminae; light colored layers carbonate mudstone; darker laminae silt-grade carbonate; graptolites rare, other fauna absent

0-1.25 m: crinoidal packstone

Bromide - Viola Contact: unconformable; no significant relief

Bromide Formation (Pooleville Member): fine lime mudstone; articulate brachiopods, receptaculitids common

SQ: 47-70 m



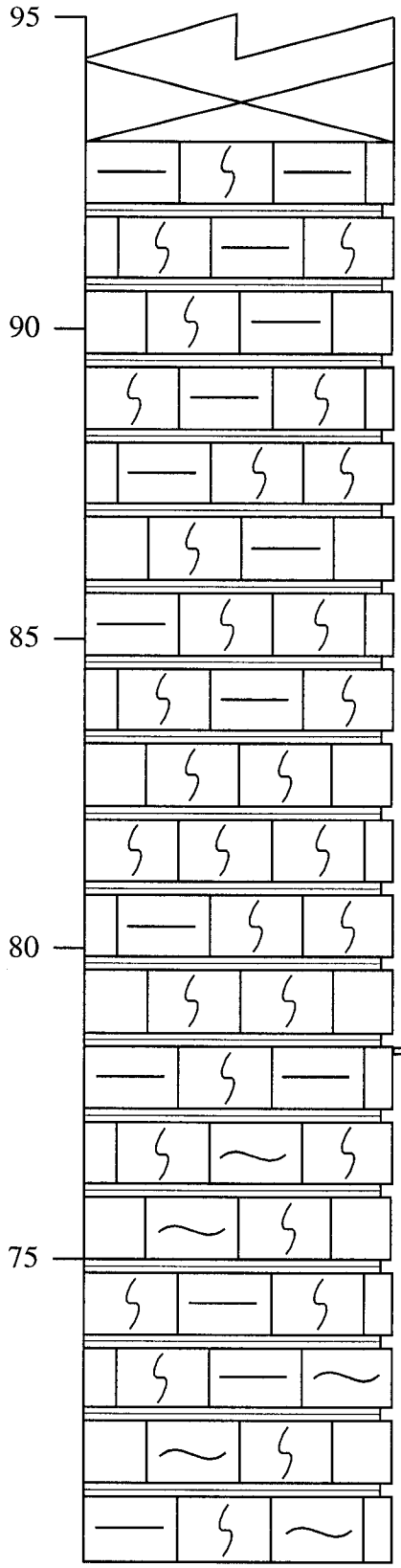
69 m: rare cryptolithine trilobite fragments

61-69 m: increasing bioturbation (mainly *Chondrites*)

47-61 m: laminated mud- to wackestone; limestone/marl alternations; mm to cm-scale scours; bioturbation as disruptions in laminae

47 m: west edge of quarry

SQ: 70-95 m



Covered 93-148 m

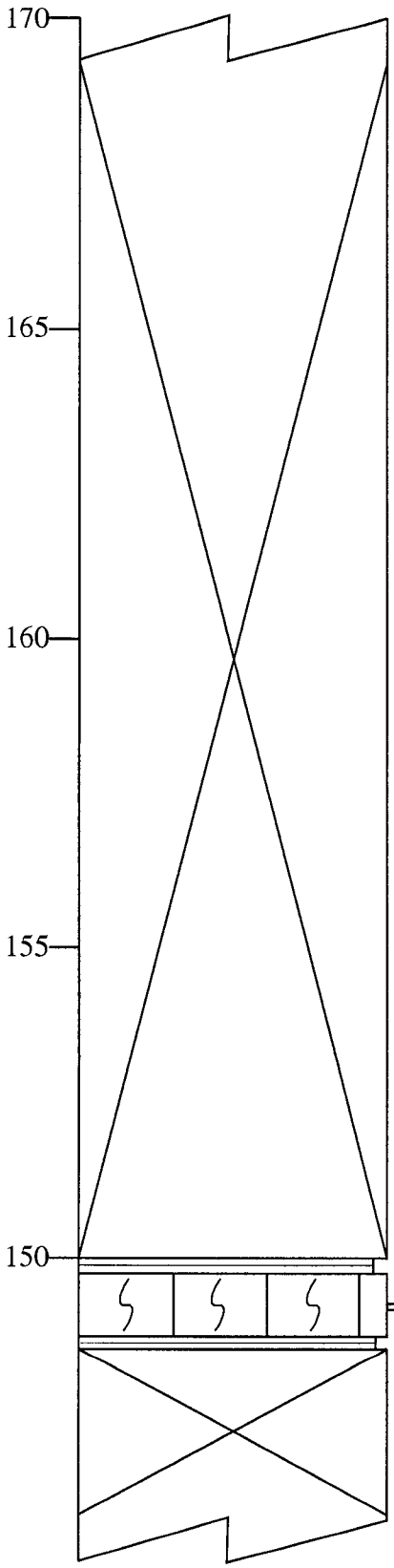
93 m: West edge of quarry; cryptolithines, isotelines more abundant in marl between packages

81-93 m: thicker (cm-scale) packages; increased bioturbation and trace fossil diversity, *Chondrites* plus *Planolites*, spreiten-filled vertical burrows

CH-78

70-81 m: laminated lime mudstone; limestone/ marl alternations; scours, bioturbation increase upward; rare pack- to grainstone lenses; graptolites, rare cryptolithine trilobites

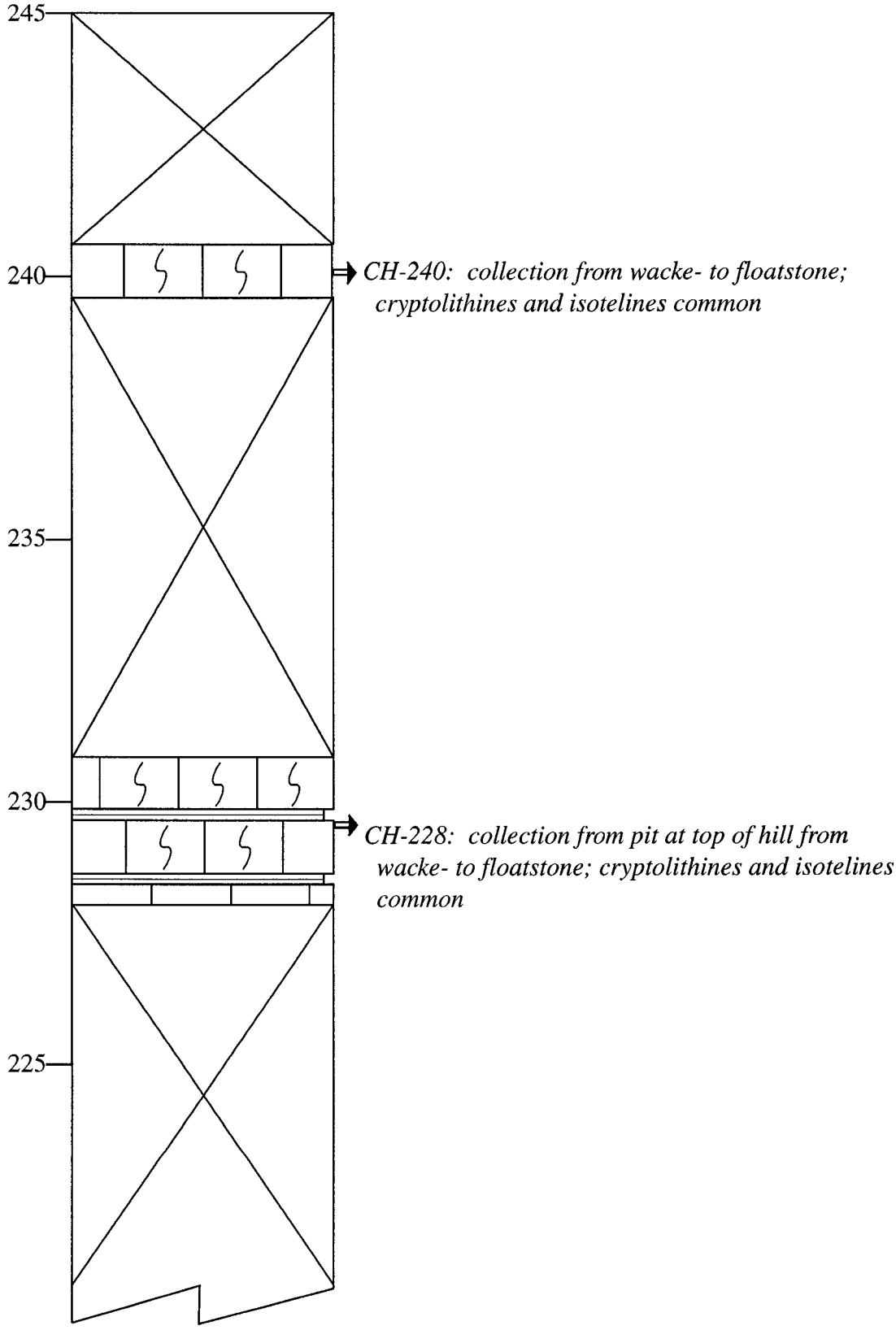
SQ: 148.5-150 m



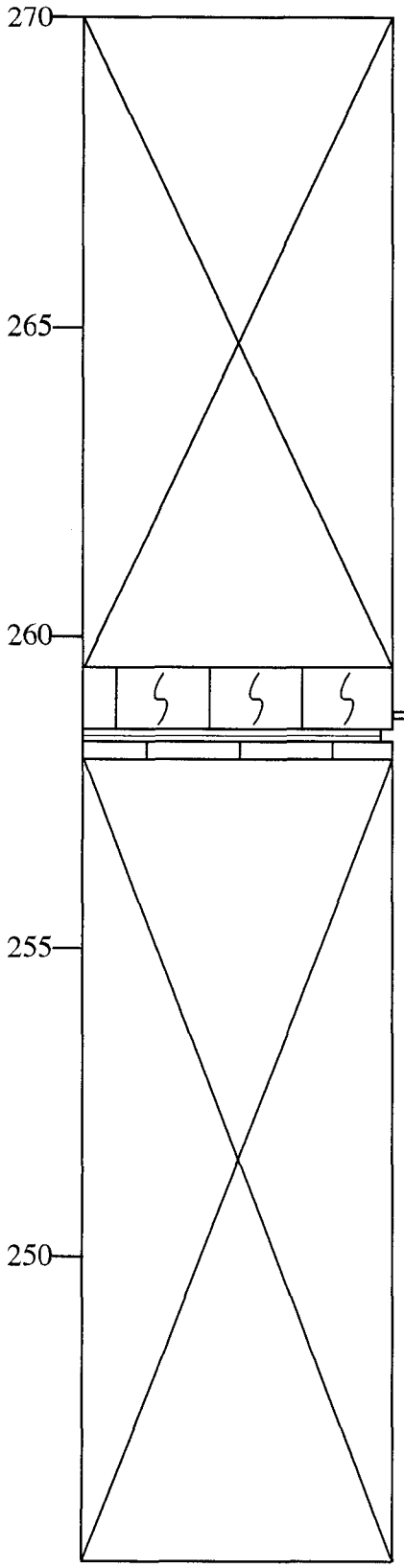
Covered 150-228

CH-148.5: exposure on hillside; collection from wacke- to floatstone; cryptolithines common

SQ: 228-231m, 239.5-240.5 m

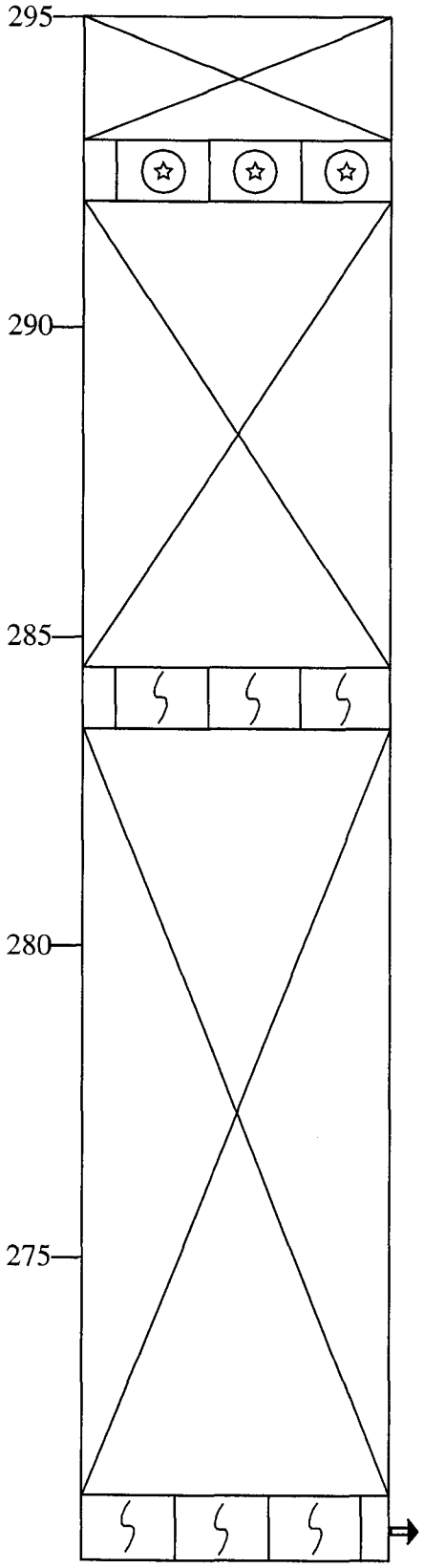


SQ: 258-259.5 m



CH-258: collection from wacke- to floatstone; isoteline trilobites abundant

SQ: 270-271 m, 283-284.5 m, 293-294 m

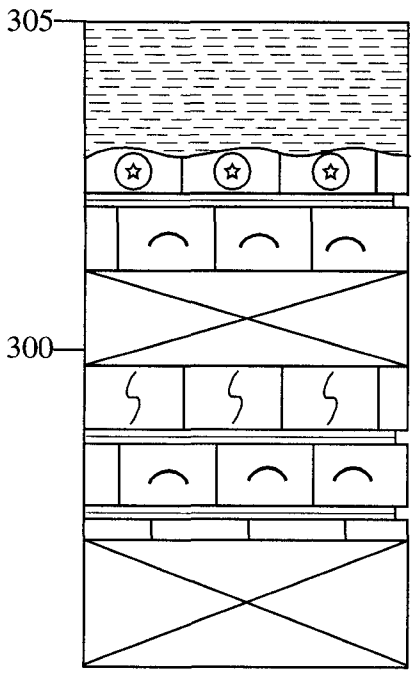


Crinoidal grainstone

282-295 m: bioturbated wacke- to floatstone alternating with crinoidal grainstone

Bioturbated wacke- to floatstone

CH-270: wacke- to floatstone; mainly isoteline trilobites



303 m: Sylvan Shale

Welling/Sylvan contact not exposed

296-303 m: bioturbated wacke- to floatstone packages alternating with grainstone; grainstone more abundant upward

CHAPTER 5:

CHEIRURID TRILOBITES FROM THE LATE ORDOVICIAN VIOLA GROUP, SOUTH-CENTRAL OKLAHOMA

ABSTRACT

Nine species assigned to six cheirurid genera are documented from the Upper Ordovician (Mohawkian-Cincinnatian) Viola Group of south-central Oklahoma. Two species (*Ceraurinella tenuisculpta*, *Ceraurus globulobatus*) are shared with the correlative Kimmswick Limestone in eastern Missouri and Illinois, and three new species are named (*Ceraurinella gracilispina*, *Whittakerites*? *trapezoidantyx*, *Borealaspis marilynoides*). The remaining species are placed in open nomenclature. The relationships of *Ceraurus* with the closely related genera, *Gabriceraurus*, *Whittakerites* and *Borealaspis* are discussed within a phylogenetic context. *Leviceraurus* is regarded as a junior synonym of *Ceraurus* and *Bufoceraurus* is a junior synonym of *Borealaspis*.

INTRODUCTION

This is the third in a series of papers dealing with the systematics and paleoecology of trilobites from the Upper Ordovician (Mohawkian-Cincinnatian) Viola Group. Amati and Westrop (in press) and Amati (in review) provide an overview of the stratigraphic and depositional setting. A more detailed analysis of the depositional environments and trilobite paleoecology is available in Amati and Westrop (in review).

Cheirurids were important components of shallow subtidal Ordovician trilobite communities in Laurentia and Baltica where they often accounted for a significant proportion of species present in carbonate build-ups (Ludvigsen, 1978; Mikulic, 1981). The Viola Group in south-central Oklahoma was deposited along a homoclinal carbonate ramp that extended from the shallow carbonate platform in the Oklahoma basin into the basin of the Southern Oklahoma aulacogen. Six cheirurid genera in the Viola Group (*Ceraurus* Green, 1832; *Ceraurinella* Cooper, 1953; *Borealaspis* Ludvigsen, 1976; *Acanthoparypha* Whittington and Evitt, 1954; *Pandaspinapyga* Esker and Levin, 1964; *Holia* Bradley, 1930) occur in inner ramp, bryozoan-dominated carbonate shoals and account for 17% of the total trilobite abundance. Diversity and abundance are comparatively lower in shallow subtidal, mid-ramp settings, but cheirurids remain a conspicuous component of the fauna (*Ceraurus*, *Ceraurinella*, *Pandaspinapyga*). The Welling Formation in south-central Oklahoma consists of coarse, crinoidal grain- to rudstone and cheirurids, although present, are less diverse and make up only 4% of trilobite abundance.

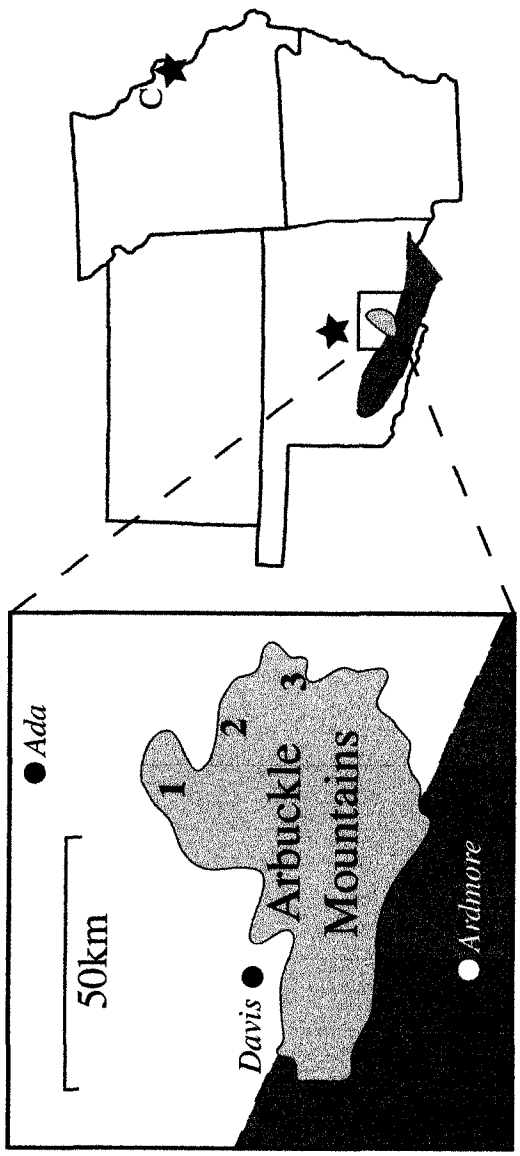
Two cheirurid species are shared with the Kimmswick Limestone of Missouri (*Ceraurinella tenuisculpta* Bradley, 1930 and *Ceraurus globulobatus* Bradley, 1930). Beyond the mid-continent, cheirurids from the Viola Group are similar to those from the Mackenzie Mountains including *Whittakerites*, *Borealaspis* and *Ceraurus mackenziensis* Ludvigsen, 1979.

SYSTEMATIC PALEONTOLOGY

Type material from Bradley, 1930, borrowed from the Field Museum (UC), is refigured as necessary for comparison. Material from the Viola Group is reposited at the Oklahoma Museum of Natural History (OU). Cheirurids were collected from three localities in the Arbuckle Mountains of Oklahoma (Figure 1). Lawrence Quarry (LQ) is operated by Holcim (US) Inc. and is located about 10 km southwest of Ada, Oklahoma. Collections from the Viola Springs (LQ-VS) and Welling Formations (LQ-WF) are undifferentiated. The stratigraphic level of each collection from a roadcut along the west side of U.S. Highway 99, 5 km south of Fittstown, Okahoma is designated as X meters above the base of the section (99-X). Bromide Quarry (BQ) is abandoned and is located about 1 km west of Bromide, Oklahoma. Collections are from a pavement on the quarry floor (BQ-Pave), and from horizons above the pavement, which are designated in X meters above the pavement (BQ-X). Additional material from the Kimmswick Limestone was collected from a quarry operated by Holcim (US) Inc. near the town of Clarksville, Missouri, about 95 km northwest of St. Louis (Clark).

Figure 1. Map of south-central United States showing collecting localities for this study in Missouri and Oklahoma. Stars indicate state capitals, St. Louis and Oklahoma City. C, Clarksville Quarry, 95 km northwest of St. Louis. Inset shows proximity of Arbuckle Mountains to Southern Oklahoma aulacogen and three collecting localities in northeastern Arbuckles. 1, Lawrence Quarry (LQ), about 10 km southwest of Ada, Oklahoma 2, Highway 99 (99) roadcut about 5 km south of Fittstown, Oklahoma 3, Bromide Quarry (BQ), about 1 km west of Bromide, Oklahoma.

Figure 1



Order Phacopida Salter, 1864

Suborder Cheirurina Harrington and Leanza, 1957

Family Cheiruridae Hawle and Corda, 1847

Subfamily Cheirurinae Hawle and Corda, 1847

Discussion.—In the following discussions, plesiomorphic conditions were determined by outgroup comparison with pilekiids (*Pilekia* Barton, 1916, *Parapilekia* Kobayashi, 1934, *Anacheirurus* Reed 1896 and *Macrogrammus* Whittard 1966). The following sources of information on pilekiid characters were used: *Pilekia*, Přibyl et al., 1985, pl. 1, fig. 8; *Parapilekia*, Přibyl et al. 1985, pl. 1, figs 1-4 and Fortey, 1980 pl. 17, figs 1-6; *Anacheirurus*, Přibyl et al. 1985 pl. 1, fig. 8; *Macrogrammus*, Lane 1971, pl. 7, fig. 21 and Edgecombe et al., 1999, figs 7.1-7.19, 8.1-8.20, 9).

Among cranidial characters, low convexity glabellae (e.g., *Parapilekia* in Fortey, 1980, pl. 17, figs 2, 6), large (exsag. and tr.) lateral glabellar lobes (e.g., *Anacheirurus* in Přibyl et al., 1985, pl.1, fig. 5) and wide (tr.) lateral glabellar furrows are plesiomorphic states occurring in pilekiids, as is isolation of L1 from the glabella. Long (sag.) and nearly transverse anterior borders are also plesiomorphic, as is the position of the palpebral lobes far forward on the cranidium, across from or in front of S2. Plesiomorphic genal spines are short and narrow (e.g., *Macrogrammus* in Edgecombe et al., 1999, figs 7.5-7.6, 7.8-7.9). In pilekiids, the anterior lobe is either narrower (tr.) than L3 or parallel-sided, so that forwardly expanding glabellae (e.g., *Ceraurus*) are apomorphic. S2 and S3 furrows are commonly arched forward,

but transverse orientation, where abaxial and adaxial ends of furrows are in a transverse plane, is an apomorphic feature (e.g., as in *Ceraurinella*). Increasing length (sag.) of the anterior lobe and presence of a break in slope between the lateral lobes and the center of the glabella (as in *Gabriceraurus*, see Ludvigsen, 1979, pl. 12, figs 9, 10; pl. 14, figs 1, 2) are also apomorphic states that are unknown among pilekiids. An occipital spine, paired frontal nodes, median preoccipital node, longitudinal medial glabellar furrow and well-developed paired pits on the anterior lobe are also apomorphic traits. Pustulose ornament is apomorphic relative to granular. Pilekiid pygidia have four rather than three segments. Spines are present on all segments and tend to be nearly the same length. They are also short, slender, round in cross-section and directed backward.

Genus *Ceraurinella* Cooper, 1953

Type species.—*Ceraurinella typa* Cooper, 1953, from the Edinburg Formation, Virginia (by original designation).

Discussion.—Chatterton and Ludvigsen (1976) provided a detailed diagnosis and discussed the status of the genus. Ludvigsen (1979, p. 20-22) divided species of *Ceraurinella* into two groups based on convexity of the glabella, isolation of L1, size of palpebral lobes and width and orientation of first pygidial spines. Assessment of the phylogenetic significance of these groups requires a cladistic analysis that is beyond the scope of this paper.

As discussed by Ludvigsen (1977), *Ceraurinus* Barton, 1916, *Ceraurinella* Cooper, 1953 and *Xylabion* Lane, 1971 resemble each other in both cranidial and pygidial morphology. All three possess smooth to finely granulose, parallel-sided glabellae with well-defined lateral furrows. Pygidia have three distinct segments and up to three pairs of marginal spines. The monophyly of *Ceraurinus* is supported by the presence of carina on the first pair of pygidial spines (e.g., see Ludvigsen, 1977). The status of *Xylabion* and *Ceraurinella* is less clear. Like *Ceraurinus*, the poorly known *Xylabion* appears to possess an anteriorly truncate, rectangular glabella (e.g., Lane, 1971, pl. 6, fig. 15), and Ludvigsen (1977, p. 965) noted that these two genera are difficult to distinguish based on cephalic characters. The absence of carina on pygidial spines in *Xylabion*, a feature emphasized by Ludvigsen (1977) is, by comparison with such outgroups as the Pilekiidae, a plesiomorphic state. Where known, the anterior spine pair of *Xylabion* is curved outward and, apparently, posteriorly pointed (Lane, 1971, pl. 2, figs 12-13). This morphology differs from the condition in both *Ceraurinus* and *Ceraurinella*, although there are some similarities with *Hadromeros* Lane, 1971 (e.g., Lane, 1971, pl. 3, figs 2, 7). *Ceraurinella* appears to lack unequivocal apomorphic states and may prove to be paraphyletic. It is retained in this paper (see Chatterton and Ludvigsen, 1976, for diagnosis), pending phylogenetic analysis. Any analysis will also need to consider the relationship between *Ceraurinella* and *Hadromeros*. Although the latter possesses an anteriorly expanding glabella that would appear to ally it with such Silurian cheirurines as *Ktenora* Lane, 1971, Chatterton and Perry (1984, p. 22) suggested an ancestor-

descendant relationship between *Ceraurinella* and *Hadromeros*. This would also imply paraphyly in *Ceraurinella*.

Ceraurinella tenuisculpta Bradley, 1930

1930. *Ceraurinus tenuisculptus*, Bradley, p. 278, pl. 30, fig. 14

Pl. 1; Pl. 2, Figs 1, 2

Additional material.—Additional material of this species was collected from the Kimmswick in eastern Missouri and the Viola Group. A partial, mostly exfoliated cranidium (OU11942) from the Kimmswick and two partial, exfolilated cranidia from the Viola Group (OU11943-OU11944).

Stratigraphic occurrence.—This species was collected from undifferentiated material at Clarksville Quarry in Missouri and from 56 to 58 meters above the Bromide at Highway 99.

Diagnosis.—A species of *Ceraurinella* with long but slender genal spines. Pits on fixigenae fine, widely spaced. Glabella and fixigenae with extremely fine granules.

Description.—Glabella expanding slightly at anterior lobe; transverse vaulting low; longitudinal convexity moderate and even along length (sag.). Occipital furrow narrow, deep, transverse behind middle of glabella, arched backward and directed posterolaterally behind L1. Occipital ring longest (exsag.) medially, becoming

shorter abaxially; posterior margin of ring transverse. Three pairs glabellar furrows; each furrow extending about 1/3 width (tr.) of cranidium; S1 deep, oblique near axial furrow, curving back adaxially to intersect occipital furrow; S2, S3 weakly impressed, equally arched forward. L1 lobe constricted adaxially, isolated from glabella by S1; L2, L3 equal length (exsag.); anterior lobe length exsagittaly equal to length of L2 and L3 together. Anterior margin of glabella evenly rounded. Axial furrows deep, narrow, nearly parallel between occipital furrow and S3 then deflected gently outward. Preglabellar furrow very narrow, deep, widening at S3 to form shallow anterior pit. Anterior border short (sag.), becoming slightly longer abaxially, dorsoventrally compressed. Fixigenae subtriangular in outline, posterior margin angled slightly forward from axial furrow. Palpebral lobes horizontal; reach height even with top of fixigenae; postitioned at about 1/2 maximum width (tr.) of fixigenae and opposite L2. Palpebral lobe crescentric in outline, widest at base, tapering upward. Palpebral furrow wide, shallow. Palpebral ridge without ornament, continues around margin of palpebral lobe. Visual surface not preserved. Anterior branch of facial suture short, directed forward and adaxially to anterior border. Posterior branch of facial suture longer, directed laterally and slightly forward to lateral border furrow then directed laterally and posteriorly. Lateral border furrow, deep wide. Posterior border furrow deep, wide, expands abaxially, intersection with lateral border furrow sharp. Lateral border, posterior border widening to genal spine. Genal spine long for genus, about 1/2 length (sag.) of cranidium; tapering quickly toward posterior; ending in sharp point. Entire surface of cranidium including genal

spines covered by very fine, closely spaced granules; fixigenae also with widely spaced fine pits. Librigena, hypostome, rostral plate and thorax, pygidium unknown.

Discussion.—The original material used by Bradley (1930) for his description is supplemented with additional material from the Viola Group (99 above 51 m). Bradley described the cuticle of the glabella as being smooth, but re-examination of his material shows that it is exfoliated. Description of the cuticle here comes from Viola Group specimens and material collected by the author from the Kimmswick Limestone in Missouri (Clarksville Quarry).

Ludvigsen (1979) includes *C. tenuisculpta* in a group with *C. trentonensis* Barton, 1913 and *C. longifrons* Troedsson, 1928 based on the depth of S1 compared to relatively shallow S2 and S3, and the inflation of L1. The pygidia of all three of these species are unknown and comparison between cranidia is hampered by the limited information available for both *C. trentonensis* and *C. longifrons.*

The long, thin, tapering genal spines of *C. tenuisculpta* are distinctive. The genal spines of *C. latipyga* Shaw, 1968 are longer, more robust and directed more strongly backward. The genal spines of *C. nahanniensis* Ludvigsen, 1979 are also relatively long, but the glabella expands slightly at the anterior lobe and the narrow (tr.) fixigenae bear moderately fine pits. The granulation of the glabella of *C. nahanniensis* is slightly coarser, the palpebral lobes are positioned across from L2 rather than S2 and the genal spines are stouter than in *C. tenuisculpta.*

Ceraurinella gracilispina, new species

Pl. 2, Figs 3, 4; Pl. 3, Figs 1-3

Type material.—A nearly complete, mostly exfoliated cranidium (OU11945, Holotype), a testate cranidium with broken genal spines (OU11946, Paratype), a cast of a partial cranidium (OU11947, Paratype), an exfoliated pygidium with first spine pair broken (OU11948, Paratype), and a partial, testate galbella (OU11949, Paratype).

Stratigraphic Occurrence.—This species is from mid-ramp deposits of the Viola Springs Formation at Highway 99 and Lawrence Quarry (LQ-MF, 99-48 to 99-49.5).

Diagnosis.—A species of *Ceraurinella* with long but slender genal spines. Pits on fixigenae moderately coarse, densely packed. Second and third segments of pygidium bearing spines.

Description.—Cranidium very similar to *C. tenuisculpta*. Palpebral lobes positioned farther forward, opposite S2 rather than L2. Genal spine about 1/2 length of cranidium from front of anterior border to back of occipital ring. Entire surface of cranidium including genal spines covered by fine granules, larger and less closely spaced than in *C. tenuisculpta*. Librigena, hypostome, rostral plate and thorax unknown.

Pygidium roughly rectangular in outline, length (sag. without spines) about 40% width (tr.). Axis trapezoidal in outline, convexity low. Axial furrows very faint.

Articulating half ring broken; three axial rings plus small subcircular terminal piece. Axial ring furrows broad, deep, nearly transverse. First axial ring broken dorsally. Second axial ring weakly convex, nearly transverse, slightly narrower (tr.) than first. Third axial ring similar to second, width (tr.) about 3/4 that of second. First axial ring furrow connects at about 55° angle to broad, deep interpleural furrow. Second axial ring furrow connects at nearly 80° angle to longitudinally elongate apomemal pits. Third axial ring furrow curved slightly backward, curve continuous into apodemal pits. Terminal piece small, about 1/2 width (tr.) of third axial ring. Spines of first segment widest (tr.) adaxially; beginning to taper then broken. Spines of second segment short, about 35% estimated length (sag.) of pygidium, taper to dull point. Spines of third segment shorter than those of second but long for genus, about 24% estimated length (sag.) of pygidium. Spines slightly flattened in cross-section. Ornament not preserved.

Discussion.—*Ceraurinella gracilispina* is most similar to *C. tenuisculpta*; differences are described above. The pygidium of *C. seriata* Ludvigsen, 1979 bears three pairs of pygidial spines, with those of third segment only slightly shorter (exsa.) than those of second segment. However, the genal spines of *C. gracilispina* are longer and more slender. *Ceraurinella latipyga* from the Chazy of New York has long genal spines and three distinct spine pairs on the pygidium. The genal spines of *C. latipyga* are much broader, granulation of the glabella is coarser, and the palpebral lobes are farther back (middle of the lobe across from S1 rather than S2) than in *C. gracilispina*. *Ceraurinella scofieldi* Clarke, 1897 (see DeMott 1987) is similar in

glabella shape and position of palpebral lobes but lacks strong pitting on fixigenae. Most other species, including *C. typa*, *C. chondra* Whittington and Evitt, 1954 and most species from Mackenzie Mountains (Ludvigsen, 1979) have much shorter genal spines. *Ceraurinella nahanniensis* from the Mackenzie Mountains is an exception, with genal spines approaching the length of *C. gracilispina*, however the genal spines of the Canadian species are much stouter and the third pygidial spines are merged.

Ceraurus Green, 1832

Type species.—*Ceraurus pleurexanthemus* Green, 1832, from the Trenton Group, New York (by original designation).

Discussion.—*Ceraurus* has a number of characters that serve to distinguish it from *Ceraurinella* and pilekiids, including a forwardly expanding glabella that reaches maximum width at the frontal lobe, small lateral glabellar lobes defined by narrow (tr.) furrows, long, wide genal spines directed outward and back, a tendency toward more varied ornament on the cephalon. However, none of these is an unambiguous apomorphy as they occur in other cheirurine genera. According to Lespérance and Desbiens (1995), *Ceraurus* is diagnosed by lateral glabellar furrows that are strongest adaxially, a short anterior border that is usually overhung by the glabella, and a pygidium with a tendency toward a subtriangular posterior margin. These three features are possible apomorphies, although the dorsally visible border in *C. globulobatus* must be considered a reversal. Palpebral lobes in an anterior position

opposite L3 is also used in their diagnosis, but this is the plesiomorphic condition (see *Parapilekia* in Fortey 1980, pl. 17, figs 1, 4). *Ceraurus* is distinct from *Gabriceraurus* in having small lateral glabellar lobes, a short anterior border and lacking spines on the second and third pygidial segments.

Přibyl et al. (1985) provided a diagnosis of *Gabriceraurus* that emphasized the forward expansion of the glabella, subtetragonal 1L that is isolated by a well-developed 1S and a distinct anterior border that is visible in dorsal view. Lespérance and Desbiens (1995) added reduction of all but the first pair of pygidial spines to this diagnosis. Although absent from pilekiids, these features are ambiguous because they can also be shared with *Ceraurus* (forward expansion of the glabella, reduction second and third pygidial spine pairs) or *Whittakerites* (anterior border visible in dorsal view). A change in slope from the lateral glabellar lobes to the lower convexity of the median portion of the glabella creates a shallow longitudinal depression that serves as a possible apomorphy for *Gabriceraurus*, as does a tendency toward a transverse posterior pygidial margin. Shallow, longitudinal furrows on the glabella of *Paraceraurus ruedemanni* Raymond, 1916 (see Shaw, 1968 pl. 15, fig. 34, pl. 16, figs 1-11), although developed more strongly, suggest that this species may be a basal member of *Gabriceraurus*.

Leviceraurus Hessin, 1988 was diagnosed as a cheirurine with a nearly parallel-sided glabella and ornament consisting of fine granules and few tubercles. The first feature occurs in other cheirurines as well as in some pilekiids and is plesiomorphic. Sculpture similar to that of *Leviceraurus* can be found in other species of *Ceraurus*, including *C. matranseris* Sinclair, 1947 (see Lespérance and

Desbiens 1995, figs 4.6, 4.10). *Leviceraurus* appears to be paraphyletic and may be considered a synonym of *Ceraurus*.

Přibyl et al. (1985) assigned *C. bispinosus* Raymond and Barton, 1913 to *Borealaspis*. Hessin (1989) subsequently erected *Bufoceraurus* for this species based on new material from Ontario and synonymized a number of species under *Bufoceraurus*. However, the type of *Borealaspis bispinosus*, refigured by Ludvigsen, 1978, has a shorter (exsag.), more convex glabella with narrower (tr.) lateral glabellar lobes and a long (sag.) anterior border visible in dorsal view and should be retained in *Borealspis*. Hessin's material probably represents a new genus and species. It is similar to *Gabriceraurus* in having wide (tr.) glabellar furrows and an isolated L1, although both features are probably plesiomorphic. The glabella is otherwise similar to *Ceraurus* except for small spines projecting backward from the posterior margin just inside the genal spines. Although the pygidium is poorly preserved, it appears to be very distinctive and may support monophyly. The pygidium is wide (tr.) relative to the width of the thorax. Well-developed spine pairs on each segment are also very wide (tr.) with the first pair longest and the second and third pairs shorter but nearly equal to each other in length. The pygidial spines also appear to be dorso-ventrally compressed.

Ceraurus cetus Dean, 1979 may belong to the new genus represented by Hessin's material (although it is difficult to determine without pygidial material) but is not conspecific with Hessin's species. Most obviously, the genal spines of *C. cetus* are more slender and are curved more strongly outward.

Ceraurus globulobatus Bradley, 1930

Pl. 3, Figs 4-7; Pl. 4

1930. *Ceraurus globulobatus*, Bradley, p. 274, pl. 30, figs 33-36, 41-42.

?1930. *Ceraurus globulobatus*, Bradley, p. 274, pl. 30, figs 39, 40.

non 1930. *Ceraurus globulobatus*, Bradley, p. 274, pl. 30, fig. 38.

non *Ceraurus* cf. *C. globulobatus* Bradley, Hessin 1989, p. 1217, pl. 4, figs 1-7,

1995. *Ceraurus globulobatus* Bradley, Lespérance and Desbiens, p. 13, figs 4.14-4.23

Additional Material.—A nearly complete, exfoliated cranidium from the Kimmswick Limestone of eastern Missouri (OU11950), a nearly complete, testate cranidium and an exfoliated cranidium missing a genal spine from the Viola Group (OU11951-OU11952).

Stratigraphic Occurrence.—Viola Group material is from the upper part of the Viola Springs Formation at Highway 99 and Bromide Quarry (99-51, BQ-24).

Discussion.—Lespérance and Desbiens (1995) refigured the type material of this species and also provided a diagnosis. Additional material from the Viola Group is figured herein, as is a previously unnoticed feature of the holotype (discussed below). The anterior border of *C. globulobatus* is visible in dorsal view, a character which is unique to this species of *Ceraurus* and perhaps acquired in parallel by *Gabriceraurus*.

Very weak to indistinguishable eye ridges and hypostomata with equal length (sag.) and width (tr.) are additionally diagnostic (Lespérance and Desbiens 1995).

Ceraurus globulobatus is similar to both *C. pleurexanthemus* and *C. whittingtoni* Evitt, 1953. *Ceraurus globulobatus* differs from both species in having a longer (exsag.) glabella relative to width (tr.), greater forward expansion of the glabella and broader (tr.) lateral glabellar lobes. The anterior margin of the cranidium of *C. matranseris* is very flat, making the anterior lobe short (sag.) and the genal spines are arched more strongly outward. *Ceraurus milleranus* Miller and Gurley, 1897 has shorter genal spines, narrower (tr.) fixigenae and a shorter anterior border. The anterior lobe of the holotype of *C. globulobatus* is subdivided into two anterior nodes by shallow transverse and longitudinal depressions (Pl. 3, Fig. 4d). This features is also present in a specimen from the Viola Group (Pl. 4, Fig. 6d).

Bradley (1930) figured two pygidia (pl. 30, figs 39, 40; Pl. 4, Figs 1, 2) as paratype material of *C. globulobatus*. However, he also figured a cheirurid cranidium (pl. 30, fig. 38) designated as paratype material that is obviously not *C. globulobatus*, making the affinities of the figured pygidia questionable.

Ceraurus sp. 1

Pl. 5, Figs 1-3

Material.—A nearly complete cranidium (OU11953), a pygidium with broken spines (OU11954), and a partly exfoliated hypostome (OU11955).

Stratigraphic Occurrence.—All specimens from the Welling Formation at Lawrence quarry (LQ-WF).

Description.—Cephalon with subtrapezoidal outline; longitudinal and transverse convexity high. Glabella expanding strongly forward to greatest width (tr.) across base of L3. Occipital ring convex transversely, nearly flat longitudinally; posterior margin curves forward behind middle of glabella. Occipital furrow deep, wide, nearly transverse behind middle of glabella, curves strongly backward behind L1 lobes; pits deep, transversely elongate. Three pairs of lateral glabellar furrows short (tr.), deep, widest adaxially; all three furrows becoming shallow, curving backward to intersect with next furrow to posterior, isolating glabellar lobes from middle of glabella. S1 very deep and long (exsag.), nearly circular adaxially; S2 shortest (exsag.) of three; S3 long (exsag.), subcircular adaxially. Lateral glabellar lobes 1-3 narrow (tr.), width (tr.) nearly equal to length (exsag.); all three isolated from middle of glabella, L1 with greatest isolation. Anterior lobe widest across posterior margin, length (sag.) greater than L2, L3 together, anterolateral corners strongly rounded, anterior margin very weakly rounded. Axial furrows moderate in depth, wide, divergent, especially from S1 forward to anterior pit. Anterior pit subcircular, adjacent to posterior margin of anterior lobe. Preglabellar furrow deep, very short (exsag.). Anterior border short (sag.), not visible in dorsal view, nearly flat across anterior margin, bearing coarse tubercles. Outline of fixigenae subtriangular; convexity moderately high. Palpebral lobe far out on fixigena, nearly 3/4 distance from glabella, across from L3; directed strongly upward, termination broken.

Palpebral ridge short (exsag.), moderately convex. Anterior branch of facial suture running inward and slightly forward to anterior border. Posterior branch of facial suture nearly transverse, running slightly backward. Posterior border furrow deep, short (exsag.). Posterior border convex; arched backward then running slightly forward to genal spine. Genal spines long, length (exsag.) over 50% total length of cephalon, slender, curving weakly outward, directed mainly backward, tapering distally to point. Ornament of glabella, fixigenae coarse and very coarse tubercles. Fixigenae also with coarse pits. Anterior border, genal spines with coarse tubercles. Posterior margin with two posteriorly elongate tubercles. Occipital ring with at least five coarse tubercles positioned at posterior margin. Hypostome ovoid; length (sag.) nearly equal to width (tr. across shoulders). Middle body ovoid, width (tr. across anterior margin) nearly 90% of length, convexity moderate. Lateral margins of anterior lobe flexed weakly inward. Posterior lobe small, subtriangular. Maculae very faint. Lateral border furrow narrow, shallow. Lateral border convex, broadens to shoulder. Anterior margin arched forward; anterior border very short (sag.), becoming longer (exsag.) toward anterior wings. Lateral margins convex, bowed outward at shoulders, converge toward posterior without flexure. Posterior margin convex, rounded. Anterior margin of anterior wings continuation of arch of anterior margin. Ornament of densely packed, moderately large tubercles. Librigenae, thorax unknown.

Pygidium subtriangular in outline excluding spines; length (sag.) roughly 80% width (tr.). Axis short, weakly convex (tr.). Axial furrows effaced. First axial ring convex, arched forward, well-defined by deep, broad first axial ring furrow. Second

axial ring slightly shorter (sag.) than first, arched forward parallel to first, second axial ring furrow very shallow, short (sag.), narrow (tr.), consisting mainly of elongate apodemal pits, tapering adaxially. Third axial ring very short (sag.), arched forward more strongly than first or second ring; third axial ring furrow very short (sag.), very narrow (tr.); apodemal pits elongate, taper adaxially. Terminal piece small, subtriangular with narrowest (tr.) point at anterior end. Anterior margin of pygidium not preserved. First spine base subcircular in cross-section, directed upward. Second and third spine pairs absent. Posterior margin smooth, rounded, weakly triangular. Ornament of large granules.

Discussion.—This specimen is similar to *C. globulobatus* in glabella shape and the hypostome is short (sag.) relative to width (tr.), but the anterior border is not visible in dorsal view. *"Ceraurus" cetus* is similar to this species in having small, posteriorly projecting spines from the posterior border and very coarse pustules but has more forwardly positioned palpebral lobes and genal spines that are curved outward more strongly. The individual from the Viola Group has a longer (sag.) anterior lobe. The genal spines of the new species are more slender than those of *C. matranseris* and the anterior margin of the glabella is much more rounded, although the shape of the lateral glabellar lobes and glabellar ornamentation are similar in the two species.

"*Ceraurus*" sp. 1

Pl. 5, Figs 4-9

Material.—Four partial, mostly exfoliated cranidia (OU11956-OU11959), and two pygidia, both partially exfoliated, one nearly complete (OU11960-OU11961).

Stratigraphic Occurrence.—Material is from the Viola Springs Formation at Highway 99 (99-24 to 99-48).

Descripton.—Cranidium with trapezoidal outline; longitudinal and transverse convexity high. Glabella expanding forward; greatest width (tr.) across base of L3. Occipital ring convex transversely, very short (sag.); convex longitudinally; posterior margin transverse. Occipital furrow deep, very broad behind middle of glabella; posterior pits small, deep, subcircular. Three pairs of lateral glabellar furrows very short (tr.), moderately deep; widen abaxially; S1 deepest, becoming shallow adaxially, curving backward to intersect with occipital furrow, isolating L1 from middle of glabella. Lateral glabellar lobes lower than height of glabella. L1 small, subcircular , isolated. L2, L3 narrow (tr.), width (tr.) nearly equal to length (exsag.). Anterior lobe widest across posterior margin, length (sag.) greater than L2, L3 together, anterolateral corners strongly rounded, anterior margin very weakly rounded. Axial furrows moderately shallow, wide, divergent from S1 forward to anterior pit. Anterior pit deep, subcircular, located at level of S3. Preglabellar furrow deep, short (exsag.). Anterior border long (sag.), becoming only slightly longer abaxially, nearly flat; anterior margin of border very weakly curved forward; entire anterior border and most of preglabellar furrow visible in dorsal view. Fixigenae subtriangular; moderately convex. Palpebral lobes far out on fixigenae; positioned

across from S2. Palpebral ridge weak. Anterior branch of facial suture directed inward and weakly forward; posterior branch not clearly preserved. Posterior border short (exsag.), convex, curved backward then forward. Genal spines not preserved. Ornament on glabella coarse turbercles, mainly in two parallel, longitudinal rows, smaller tubercles randomly scattered. Occipital ring with one small, central tubercle. Fixigenae pitted. Hypostome, librigenae, thorax unknown.

Pygidium subrectangular in outline, length (sag.) about 50% width (tr.) (without spines). Axis short, transverse convexity moderate; longitudinal convexity weakly negative; axial furrows effaced; consists of 3 axial rings and small terminal piece; articulating half ring not preserved. First axial ring moderately convex (tr.); width (tr.) about 24% total width of pygidium. Second axial ring slightly shorter (sag.) and narrower (tr.) than first; transverse convexity lower, nearly effaced. Third axial ring not clearly defined. First axial ring furrow very shallow; connects to apodemal pits/interpleural furrows at about 50° angle; pits longitudinally elongate, reach to level of posterior margin of third axial ring. Second axial ring furrow very shallow, connects to apodemal pits/interpleural furrow at about 70° angle; pits longitudinally elongate, reach nearly to posterior margin. Third axial ring furrow effaced; apodemal pits subcircular, posterior margin slightly behind termination of second apodemal pit pair. Terminal piece small, without independent convexity. Anterior margin of pygidium directed laterally and slightly backward; anterolateral corners angular. First pygidial segment with weak pleural furrow. First spine very broad, long, weakly flattened in cross-section; initially directed backward and outward at about 50° to horizontal; curving gently inward until termination of spine

directed slightly inward; anterior 1/2 angled weakly upward, posterior 1/2 directed more strongly dorsally. Second and third spine pairs absent; position indicated by weakly scalloped posterior margin. Ornament of very fine granules.

Discussion.—This species is superficially similar to *Ceraurus*, but lateral glabellar furrows that widen abaxially (rather than being strongest adaxially) and a long (sag.), flat anterior border completely visible in dorsal view prevent inclusion in the genus. In addition, the posterior margin of the pygidium is transverse rather than subtriangular. The broad first pygidial spines are unlike *Ceraurus* and are much more similar to the first spines of *Whittakerites planatus* Ludvigsen, 1976, which also has a transverse posterior pygidial margin. It is possible that the long, flat anterior border will ally this species with *Whittakerites*, but more detailed relationships must wait for a cladistic analysis. It is likely that as yet unrecognized monopyletic groups are currently encompassed within *Ceraurus*. For example, *"Ceraurus" mackenziensis* is a problematic species that possesses characters of both *Whittakerites* and *Borealaspis* but has a forwardly expanding glabella that is unlike both. The long anterior border, posteriorly positioned palpebral lobes and reduced pygidium suggest an affinity with *Whittakerites*, but the extremely reduced lateral glabellar lobes are similar to *Borealaspis*. "*Ceraurus*" sp. 1 shares a forwardly expanding glabella, reduced lateral glabellar furrows, and a long (sag.) anterior border with "*C*". *mackenziensis*, and these species may prove to be closely related.

Whittakerites Ludvigsen, 1976

Type species.—*Whittakerites planatus* Ludvigsen, 1976 from the lower Whittaker Formation, District of Mackenzie, Canada (by original designation).

Discussion.—In *Whittakerites*, the glabella expands from L1 to L3 then becomes very slightly narrower (tr.) at the anterior lobe (bulb-shaped glabella). Ludvigsen (1979) diagnosed *Whittakerites* mainly on plesiomorphies, but the posterior position of the palpebral lobe opposite S1 and the long, flat anterior border are apomorphic. A pygidium that has been reduced mainly to long, robust first spines with a small, subrectangular axial region is also likely to be apomorphic. A new species from the Viola Springs Formation, described below, possesses one of these apomorphies (a long, flat, anterior border) and is assigned questionably to *Whittakerites*.

Whittakerites? *trapezoidantyx* new species

Pls 6, 7

Etymology.—The anterior border is in the shape of a trapezoid.

Type material.—A nearly complete but exfoliated cephalon (OU11962), two small, nearly complete, exfoliated cranidia (OU11963, OU11965), one small, partial, testate cranidium (OU11964) two small, partial, mostly exfoliated cranidia (OU11968, OU11971), five large, partial crandia, some partly testate (OU11966, OU11967,

OU11969, OU11970, OU11973), two partial pygidia one mostly testate (OU11972), one exfoliated (OU11974), two partial, exfoliated hypostomes (OU11975, OU11976).

Stratigraphic Occurrence.—Specimens are from the Viola Springs Formation at U.S. Highway 99 (99-18 to 99-32).

Diagnosis.—A species of *Ceraurus* with gently forwardly expanding glabella lacking coarse tubercles. Anterior border long (sag.), flat, distinctly trapezoidal in outline. Pair of deep pits just in front of S3 visible on dorsal surface of cuticle and internal molds of most specimens. Genal spines robust, especially in larger holaspids, flattened in cross-section.

Description.—Cephalon roughly trapezoidal in outline, vaulting low. Glabella expanding weakly forward, narrowing slightly from L1 to L2, widest point across L3; convexity (longitudinal, transverse) low. Glabella with three pairs of furrows; furrows deep, narrow (tr.); S1 directed in and back, widening (exsag.) adaxially; S2 transverse to slightly anteriorly directed, uniform width (exsag.); S3 widest (exsag.) abaxially, directed slightly toward anterior. L1 separated from glabella by shallow furrow, longest (exsag.) abaxially. L2, L3 lobes similar in length (exsag.), width (tr.). Anterior lobe only slightly wider than L3, anterolateral corners more strongly rounded than anterior margin. Sagittal ridge visible on internal molds, narrow (tr.), sharp, arises at L2, running to point just behind anterior margin. Posterior margin of glabella just in front of occipital furrow with raised area consisting of paired, nearly

merged lobes; visible on external surface and internal molds; raised area slightly narrower (tr.) than width of glabella at that point just in front of L1 lobes; short (sag.) forming transverse ridge. Axial furrows deep, only weakly divergent. Anterior pit adjacent to, slightly deeper than, S3 furrow. Preglabellar furrow deep, broad, joins border furrow of librigena at anterior pit. Anterior border well-developed, dorso-ventrally compressed in cross-section, length (exsag.) about equal to length of L3; anterior and anterolateral components form roughly trapezoidal outline; anterior component nearly transverse to level of adaxial margin of S3 furrow, anterolateral component directed posterolaterally at about 45° to some part of fixigena; width of border generally narrowing slightly at 1/2 distance to fixigena; anterolateral components arched dorsally. Occipital furrow moderately deep, shallower than axial furrows, running behind glabella to pits behind L1. Pits deep, elongate, width (tr.) about equal to width of L1; length (exsag.) about 1/2 length of L1 at longest point. Occipital ring shorter (exsag.) abaxially behind pits; posterior margin of ring directed forward abaxially. Fixigenae roughly triangular in outline, deeply pitted; longest (exsag.) adaxially. Palpebral lobe at 2/3 width (tr.) of fixigenae from axial furrow; located opposite L2 as measured from center of lobe; directed upward and outward; raised above fixigena to height of visual surface but without stalk; length (exsag.) of lobe greater than width (tr.); subtriangular in outline. Palpebral furrow weak. Palpebral ridge short (exsag.), low convexity, only faintly visible on some specimens. Visual surface bulbous, projecting well beyond palpebral lobe laterally; covering slightly less than 180° field of view. Anterior branch of facial suture directed slightly more anterior than adaxially to posterolateral corner of anterior border. Posterior

branch of facial suture directed laterally, arching gently forward to lateral margin. Lateral and posterior border furrows deep, broad, intersect sharply. Posterior border about equal in length (exsag.) to anterior border; widening (exsag.) slightly abaxially. Genal spines long, length (exsag.) about 60% total length of cephalon, at base directed outward and backward at about 40° to horizontal, curving gradually to become directed more strongly backward; broad at base, dorsoventrally compressed in cross-section, tapering distally, becoming more rounded in cross-section; end in sharp point. Glabella and anterior border covered by fine, densely space granules. Fixigenae with deep pits. Occipital ring, posterior border, genal spines without ornament. Librigena subtriangular in outline, anterior margin steep, posterior margin steep, more gently sloping along lateral border, single row of pits below eye, deep, narrow furrow below row of pits. Rostral plate and thorax unknown.

Hypostome subtriangular in outline. Middle body subrectangular; width (tr.) across anterior margin only slightly less than length (sag.), about 95%; convexity moderate. Anterior lobe with weakly curved-in lateral margins, convexity about equal to posterior lobe; posterior lobe small, subtriangular. Maculae small, located very far back, at lateral margins of middle body; weakly elongate parallel to lateral margins. Lateral border furrow deep, narrow, weakly sinuous. Lateral border convex, narrow, widening slightly to shoulder. Anterior margin arched forward; anterior border short (sag.), slightly longer (exsag.) abaxially. Lateral margins directed inward toward posterior. Posterior margin rounded. Anterior margin of anterior wings continuation of arch of anterior margin. Ornament not preserved.

Pygidium subrectangular in outline, length (sag.) about 50% width (tr.) without spines. Axis subrectangular, length (sag.) about 80% width (tr.); transverse convexity at front low, becoming negative across middle, nearly flat across posterior. Longitudinal convexity strongly negative. Axial furrows effaced. Articulating half ring mostly missing. Articulating furrow deep, broad. First axial ring short (exsag.), wide (tr.), weakly convex, nearly transverse. Second axial ring shorter (exsag.), narrower (tr.) than first. Third axial ring without independent convexity. First axial ring furrow deep, slightly shorter (sag.) than first axial ring, curved weakly backward; connects to apodemal pits/interpleural furrows at about 40° to horizontal; pits elongate. Second axial ring furrow moderately deep, slightly shorter (sag.) than second axial ring, curved backward; connects to elongate apodemal pits at about 60° angle. Third axial ring furrow nearly completely effaced; connects to subcircular apodemal pits. Terminal piece identified as area between third pair of apodemal pits. Anterior margin of pygidium broken. Pleural region of first segment with narrow (tr.) pleural furrow. First spine very robust; proximal portion directed strongly outward at about 45° to horizontal, curving upward very weakly; distal 1/2 curving strongly dorsally and backward; entire spine tapering gradually to sharp point. Second and third spine pairs absent. Posterior margin of pygidium weakly arched to posterior, faintly scalloped behind second and third segments. Ornament of very fine granules.

Discussion.—*Whittakerites*? *trapezoidantyx* differs from *W. planatus* in having a glabella that expands weakly forward. The lateral glabellar furrows are narrower (tr.) than in *W. planatus*, the anterior border is transverse across the front rather than

rounded, and the axial region of the pygidium is not as reduced. Discovery of this species and its obvious affinities with *Ceraurus* lends support to Ludvigsen's claim that *Whittakerites* is closely related to *Ceraurus*. This species and *Whittakerites*? sp. 1 described below might be basal members of a *Whittakerites* clade.

Whittakerites? sp. 1

Pl. 8, Figs 1, 2

Material.—A nearly complete, partly exfoliated cranidium (OU11977), and a nearly complete, testate hypostome (OU11978).

Stratigraphic Occurrence.—Both specimens are from the Welling Formation at Lawrence Quarry (LQ-WF).

Description.—Cephalon trapezoidal in outline; transverse convexity moderate, longitudinal convexity moderately low. Glabella expanding weakly forward to L3, slightly narrower (tr.) across posterior margin of anterior lobe. Occipital ring transversely convex; nearly flat across dorsal surface; posterior margin arched backward; longest sagitally, tapering abaxially. Occipital furrow shallow, long (exsag.); roughly transverse behind middle of glabella, curved backward behind posterior pits. Lateral glabellar furrows moderately deep, narrow (tr.), short (exsag.); S1 appears to curve backward to connect to occipital furrow; S3 longest (exsag.). Lateral glabellar lobes narrow (tr.); L1 incompletely preserved; L2, L3 nearly equal in

size. Anterior lobe long, sagitally longer than length of L2, L3 combined; tapers only slightly forward; anterior margin gently curved. Axial furrows deep, narrow, weakly divergent from posterior to anterior pits. Anterior pits small, located in front of anterior margin of L3. Preglabellar furrow deep, narrow. Anterior border long (exsag.), visible in dorsal view, longer exsagitally, nearly flat across anterior, rounded around anterolateral corners. Fixigenae with triangular outline, moderately high convexity. Palpebral lobes at about 2/3 distance across fixigenae from glabella; positioned across from L3. Palpebral ridge very weak. Anterior branch of facial suture running inward and slightly forward. Posterior branch of facial suture running mainly laterally, slightly forward. Posterior border furrow deep, wide. Posterior border curved sharply backward, then curved weakly forward behind palpebral lobe. Genal spines long, about 60% total length (exsag.) of cephalon; very broad at base, tapering sharply, bowed strongly outward. Ornament of glabella, anterior border, posterior border, occipital ring, genal spines fine granules. Fixigenae with regularly spaced, moderately deep pits.

Hypostome subtriangular in outline; length (sag.) less than width (tr.) (about 92%). Width (tr.) of middle body across anterior margin nearly equal to length (sag.) (about 98%); convexity moderately low. Anterior lobe with moderate convexity, lateral margins curved weakly inward. Posterior lobe smaller, subtriangular. Maculae small, located far toward posterior. Lateral border furrow shallow, narrow, deepens toward anterior. Lateral border weakly convex, narrowest at level of maculae, widening to shoulders. Anterior margin arched forward. Lateral margins

tapers toward posterior, weakly bowed outward. Posterior margin rounded; posterior border wider than lateral border at level of maculae. Ornament of fine granules. Librigenae, thorax, pygidium unknown.

Discussion.—As in *W.? trapezoidantyx*, this specimen has a large, flat anterior border resembling *Whittakerites* and broad, widely arched genal spines. Unlike *W.? trapezoidantyx*, this specimen shares a weakly bulb-shaped glabella with *Whittakerites*. The hypostome of this specimen (Pl. 8, Fig. 2) is comparable to the hypostome of *W. planatus* (see Ludvigsen, 1979, pl. 16, fig. 38). As with *W.? trapezoidantyx*, it seems likely that a cladistic analysis will place this species as a basal member of the *Whittakerites* clade.

Borealaspis Ludvigsen, 1976

Type species.—*Borealaspis whittakerites* Ludvigsen, 1976 from the Whittaker Formation, District of Mackenzie, Canada (by original designation).

Discussion.—Ludvigsen (1976) diagnosed *Borealaspis* partly based on the strongly bulb-shaped glabella, which is developed to a greater degree than in *Whittakerites*. The forward position of the palpebral lobes opposite L3 or S3 is plesiomorphic. I follow Hessin (1989) in rejecting the division by Přibyl et al. (1985) of *Borealaspis* into two subgenera based on the presence or absence of paired anterior nodes. Presence of occipital spines, preoccipital spines and paired frontal nodes are possible

apomorphies, as is the reduction in width (tr.) and adaxial length (exsag.) of the lateral glabellar lobes. According to this diagnosis, *Ceraurus* cf. *C. maewestoides* (Ludvigsen, 1979, pl. 17, figs 34-35) is herein reassigned to this genus and represents a new species. *Ceraurus maewestoides* Ludvigsen, 1979 has an evenly expanded, rather than bulb-shaped glabella and is retained as a questionable member of *Ceraurus* pending phylogenetic analysis.

Borealaspis marilynoides new species

Pl. 8, Figs 3-10; Pl. 9, Figs 1-3

Etymology.—The trivial name indicates the similarity of this species to *Borealaspis* cf. *B. maewestoides* and gives recognition to a similarly busty woman.

Type Material.—A nearly complete, exfoliated cephalon (OU11987), seven broken cranidia, mostly exfoliated (OU11979-OU11983, OU11986, OU11989), one pygidium consisting of a spine and the external mold of the axis and second spine (OU11988), and two mostly exfoliated hypostomes (OU11984, OU11985).

Stratigraphic Occurrence.—All specimens are from the Viola Springs Formation at Highway 99 (99-30.25 to 99-32).

Diagnosis.—A species of *Borealaspis* with anterior lobe divided into two, massively inflated nodes. Paired anterior nodes with three large pustules; two pairs of large

pustules forming square on top of glabella. Pustules with small opening roughly on dorsal surface. Smaller pustules scattered across surface of glabella and occipital ring.

Description.—Cephalon subtriangular in outline. Glabella narrowing from L1 to L2, widest across L3, narrowing slightly to anterior lobe. Longitudinal convexity strong; transverse convexity moderate. Three pairs of glabellar furrows deep, long (exsag.); furrows narrow (tr.), each reaching about 1/5 width (tr.) of glabella. S1 longest (exsag.), becoming longer adaxially, directed slightly backward; S2, S3 furrows narrower (tr.), nearly transverse. L1 lobe constricted adaxially, completely separated from glabella by well-developed furrow; longest (exsag.) area of lobe abaxial, equal to length of L2 and L3. L2 and L3 subequal in length (exsag.) and width (tr.). Anterior lobe with very high convexity, subdivided into two lobes by longitudinal furrow; subsidiary lobes taper upward into cone in smaller individuals, with about 3 large pustules on top in larger specimens. Posterior margin of glabella with paired median preoccipital lobes, merged laterlally to form bi-lobed, transverse ridge. Axial furrows deep, wide, sinuous, curving inward from posterior margin to L2, curving outward to anterior pit. Preglabellar furrow shallow, moderately wide, widens abaxially to anterior pit at intersection with axial furrow. Anterior border short (exsag.), becoming longer abaxially, dorsoventrally flattened. Occipital furrow deep, wide, transverse behind glabella, curved backward behind L1. Occipital ring longest (sag.) sagittaly, shorter behind L1; posterior margin of ring curved backward. Fixigenae subtriangular in outline, posterior margin very weakly sinuous, directed

slightly forward. Palpebral lobe subtriangular, directed very slightly upward from surface of fixigena; positioned at 1/2 width (tr.) of fixigena, opposite front edge of L3. Palpebral furrow moderately deep, wide. Palpebral ridge without ornament, continues around margin of palpebral lobe. Visual surface not preserved. Anterior branch of facial suture nearly transverse. Posterior branch of facial suture directed posterolaterally. Lateral, posterior border furrows deep, wide, parallel lateral, posterior margins, intersect at acute angle. Lateral, posterior borders convex, broaden to genal spine. Genal spine length (exsag.) about 60% total length of cephalon; curved strongly outward, tapers rapidly, distal portions very thin, terminates in sharp point. Glabellar ornament of large, randomly scattered granules; four large pustules arranged in square with small opening on dorsal surface; three large pustules with dorsal openings on anterior lobes. Fixigenae with coarse pits; one pustule near posterior border furrow at about 1/2 width (tr.) of fixigena; second pustule at level of posterior margin of palpebral lobe, slightly closer to glabella than posterior pustule. Posterior border with pustule nearly in line with pustules of fixigena. Occipital ring with coarse granules.

Librigena with long (exsag.) lateral border, curving backward just lateral to intersection with anterior border. Lateral border furrow deep, wide. Eye stalk, visual surface not preserved.

Hypostome subtriangular in outline. Width (tr.) across front of middle body about 80% length (sag.); convexity moderate. Anterior lobe widest across front, tapering sharply for short distance, then tapering very weakly to maculae. Posterior lobe small, subtriangular, lateral margins tapering sharply to posterior; weak ridge

running from maculae around posterior margin. Maculae small, located at .75 total length (sag.) of middle body from anterior margin of middle body; elongate, parallel lateral margins. Lateral border furrow deep, narrow, sinuous. Lateral border only partly preserved; widest (tr.) shoulder, tapering toward posterior. Anterior margin arched strongly forward; anterior border short (sag.), uniform in length. Lateral margins weakly curved outward, taper strongly backward from level of shoulder. Posterior margin blunt point. Ornament of two to three parallel lines of tubercles from anterior margin of middle body to level of maculae; fine granules on lateral border. Rostral plate and thorax unknown.

Pygidium subtriangular in outline (without spines), length (sag.) about 80% width (tr.). Axis subtriangular in outline, negative convexity. Axial rings short (sag.), convex. Axial ring furrows deep, very short (sag.), arch strongly forward. Apodemal pits deep, elongate. Terminal piece small, subcircular. First spine very long, thin, tapering quickly to become very thin; directed outward and strongly upward. Second and third spines absent. Posterior margin of pygidium tapering slightly backward, scalloped. Ornament not preserved.

Discussion.—*Borealaspis marilynoides* is most similar to *Borealapis* cf. *B. maewestoides* in glabella shape, size of lateral glabellar lobes, and outline of paired anterior nodes. The new species resembles *C.*? *maewestoides* in having two pustule pairs on the glabella forming a square. In comparison to the new species, *C.*? *maewestoides* has more convex, better defined paired anterior nodes lacking tubercles, lateral glabellar lobes that are isolated from the glabella and more robust

genal spines. *Borealaspis whittakerensis* has a preoccipital spine, a shorter (sag.) glabella and lacks two paired pustules on the glabella, but the long, thin first pygidial spines are similar to *B. marilynoides*. The glabellar outline of *B. biformis* Ludvigsen, 1976 is similar to that of *B. marilynoides* and some specimens (Ludvigsen, 1979, pl. 17, fig. 19) have four glabellar tubercles in a square. *Borealaspis biformis* is unique in having an occipital spine.

Order Phacopida Salter, 1864

Suborder Cheirurina Harrington and Leanza, 1957

Family Cheiruridae Hawle and Corda, 1847

Subfamily Acanthoparyphinae Whittington and Evitt, 1954

Holia Bradley, 1930

Type species.—*Holia magnaspina* Bradley, 1930 from the Kimmswick Limestone of eastern Missouri (by original designation).

Discussion.—According to the analysis of Adrain (1998) *Holia* is the basal clade of the Acanthoparyphinae.

Holia sp., new species

Pl. 9, Fig. 6

Material.—A single, exfoliated glabella (OU11990).

Stratigraphic Occurrence.—The single specimen is from the Viola Springs Formation at Highway 99 (99-32).

Discussion.—The species of *Holia* from the Viola Group is distinctive in possessing large pustules on the posterior margin of the occipital ring that are elongated backward. This feature is lacking in *H. anacantha* Ludvigsen, 1979, which is the only other species lacking an occipital spine.

Pandaspinapyga Esker and Levin, 1964

Type species.—*Pandaspinapyga projecta* Esker, 1961 from the Kimmswick Limestone of Missouri.

Discussion.—The results of a cladistic analysis conducted by Adrain (1998) indicate that the status of *Acanthoparypha* and the poorly known *Pandaspinapyga* is unresolved at a node and Tripp (1993) considered *Pandaspinapyga* a junior subjective synonym of *Acanthoparypha*. Because the type material of *Pandaspinapyga* is of poor quality (in fact, the pygidium has never been figured beyond a line drawing), it is likely that the genus will eventually be restricted to type.

"*Pandaspinapyga*", new species

Pl. 10, Figs 2-4

Material.—Two exfoliated glabellae (OU11991, OU11992) and a broken, exfoliated pygidium (OU11993).

Stratigraphic Occurrence.—The material is from a single horizon in the Viola Springs Formation at Highway 99 (99-32).

Discussion.—A pygidium from the Viola Group resembles pygidia that have been assigned to *Pandaspinapyga* in that they are wide (tr.) with long, broad, flat spine pairs. I am tentatively assigning the pygidium, and associated cranidia, to "*Pandaspinapyga*" based on the presence of three segments on the pygidium. The pygidium of the new species is similar to "*P*". *projecta*, but the segments are arched only weakly forward and the terminal piece is subtriangular instead of circular. "*Pandaspinapyga*" *salsa* Esker, 1964 is very similar in the shape of the pygidial segments and overall shape of the terminal piece, but the terminal piece of the new species is more sharply triangular and the proximal portions of the pygidial spines are broader. The glabellae of the two species are similar in shape and position and curvature of lateral glabellar furrows.

Acanthoparyphine indet.

Material.—Two nearly complete, testate cranidia (OU11994, OU11995).

Stratigraphic occurrence.—Both cranidia are from the Welling Formation at Lawrence Quarry (LQ-WF).

Discussion.—Without an associated pygidium, it is currently impossible to determine if the acanthoparyphine cranidia from the Welling Formation belong in *Acanthoparypha* or "*Pandaspinapyga*". Esker and Levin (1964) suggested that S2 and S3 were parallel in *Acanthoparypha* and not in *Pandaspinapyga*, however, the furrows of "*P*". *salsa* and "*Pandaspinapyga*" new sp. above appear to be parallel. It is clear that these genera need reassessment, but that is beyond the scope of the present paper.

Acanthoparypha perforata Whittington and Evitt, 1954 differs from the Welling species in having long, robust genal spines. The genal spines of *A. chiropyga* Whittington and Evitt, 1954 are shorter than in *A. perforata*, but are still more robust than those of the Oklahoma species. *Acanthoparypha echinoderma* Chatterton and Ludvigsen, 1976 are of a similar length but the glabella tapers less strongly forward and is more well-rounded around the anterior margin. The cranidium of "*P*". *salsa* is most similar to the Welling Formation species in both glabellar outline and genal spine length and width, although the former has greater convexity of the glabella and finer tuberculate ornamentation.

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Plate 1. *Ceraurinella tenuisculpta* Bradley, 1930

1. UC20691 (Holotype), broken, exfoliated cranidium x4 a) dorsal b) anterior c) lateral d) oblique e) sculpture of fixigena x8
2. UC28945 (Paratype), partial, exfoliated cranidium x4 a) dorsal b) anterior c) lateral
3. UC28945 (Paratype), partial, exfoliated cranidium in dorsal view x4
4. OU11942 (Clark), partly exfoliated cranidium missing genal spine x4 a) dorsal b) lateral c) oblique d) anterior

Plate 1

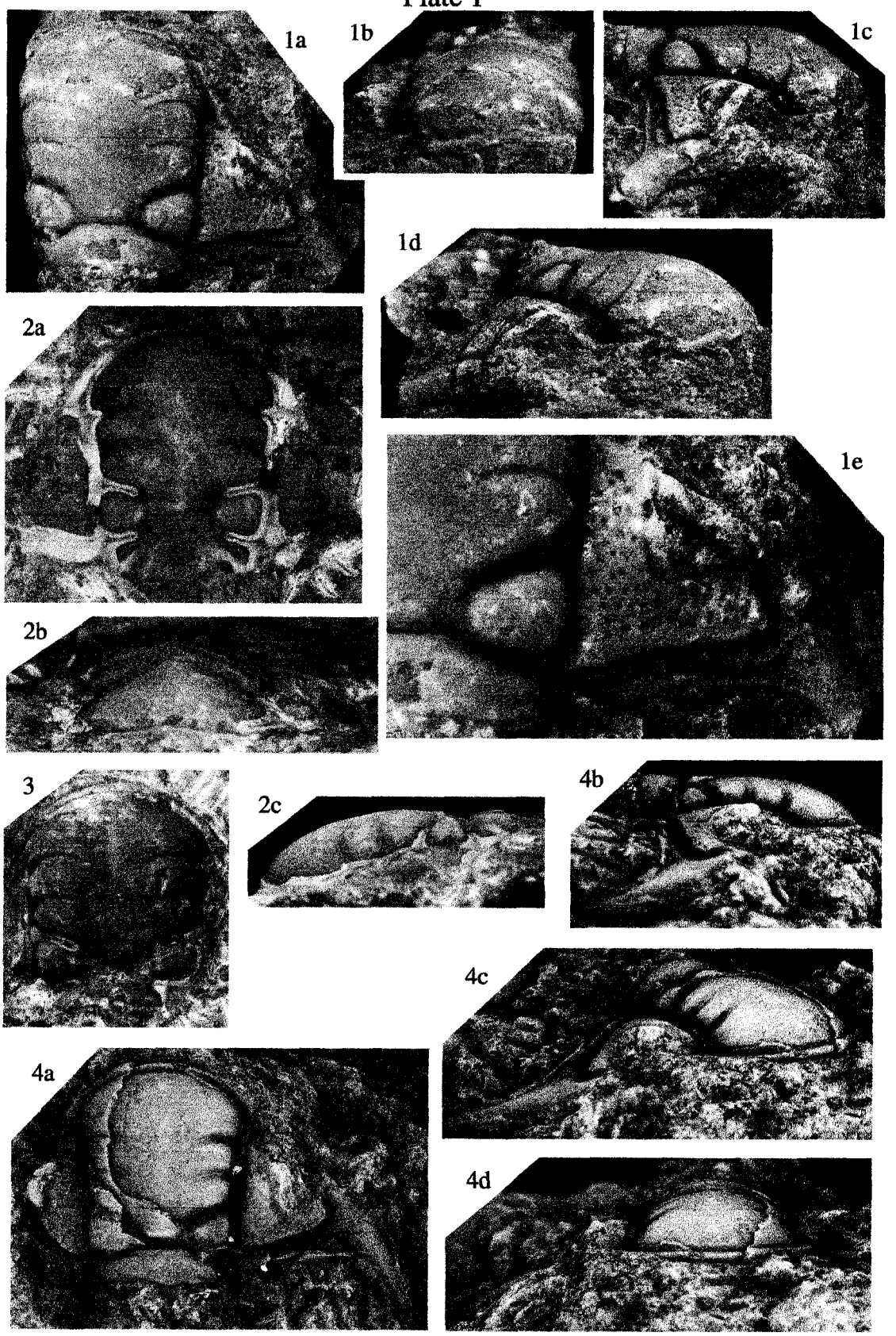


Plate 2. *Ceraurinella tenuisculpta*, *Ceraurinella gracilispina*, new species

1-2 *Ceraurinella tenuisculpta*

1. OU11943 (99-58), exfoliated cranidium missing genal spine x4 a) dorsal b) anterior c) oblique d) lateral
2. OU11944 (99-56), nearly complete, mostly exfoliated cranidium with partially repaired injury to right fixigena x3 a) dorsal b) anterior c) oblique d) lateral e) repaired genal spine x6

3-4 *Ceraurinella gracilispina*

3. OU11945 (LQ-MF), nearly complete, mostly exfoliated cranidium x7 a) dorsal b) lateral
4. OU11946 (99-48), cranidium with broken genal spines x7 a) anterior/oblique b) lateral c) dorsal

Plate 2

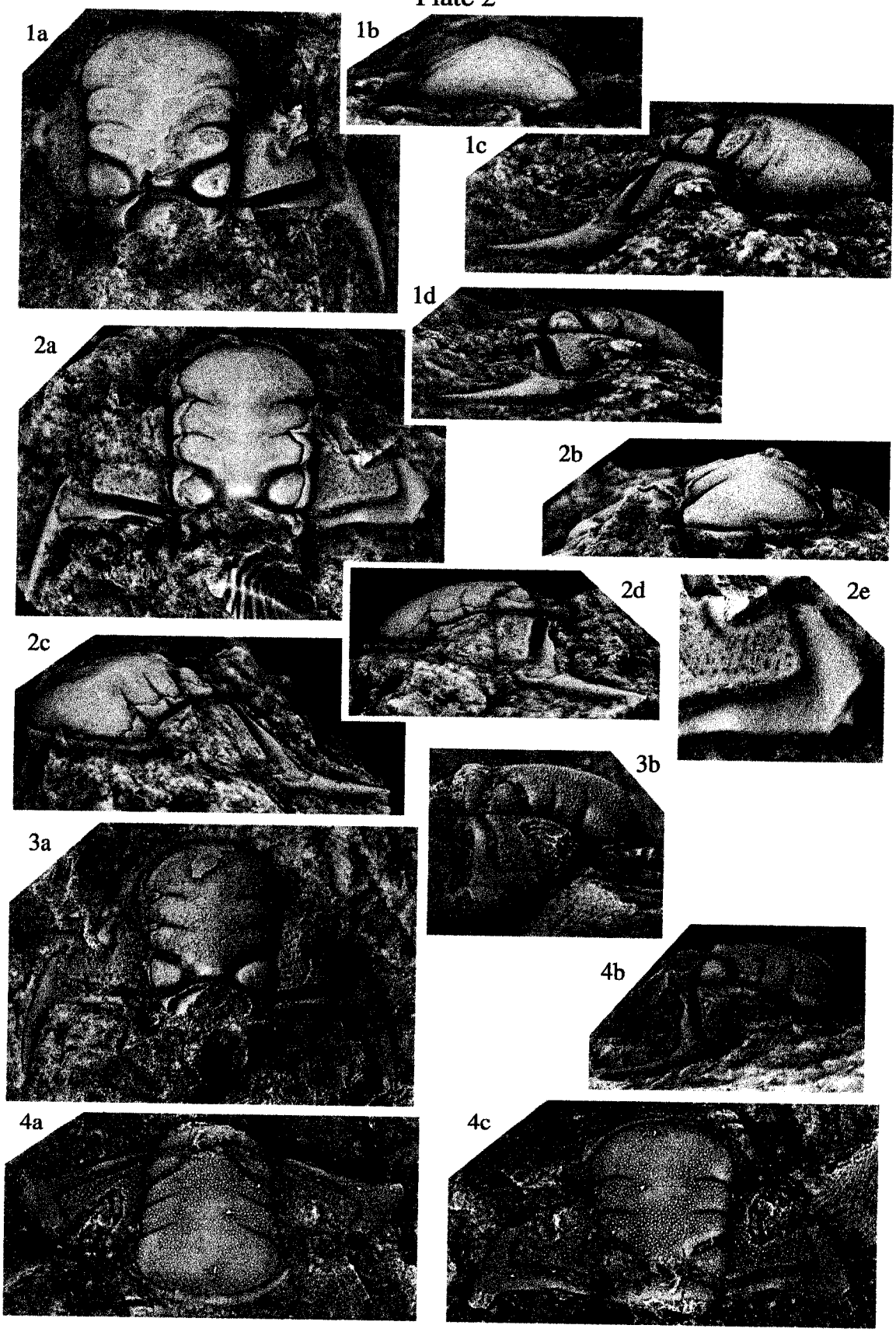


Plate 3. *Ceraurinella gracilispina, Ceraurus globulobatus*

1-3 *Ceraurinella gracilispina*

1. OU11947 (LQ-MF), cast of broken cranidium x8 in dorsal view
2. OU11948 (99-49.5), broken, exfoliated pygidium in dorsal view x5
3. OU11949 (99-49.5), partial glabella in dorsal view x7

4-7 *Ceraurus globulobatus*

4. UC20709 (Holotype), broken, exfoliated cranidium x3 a) dorsal b) anterior c) lateral d) anterior lobe x6 e) oblique
5. UC28956 (Paratype), exfoliated cranidium missing one genal spine x3 a) dorsal b) anterior c) oblique d) lateral
6. UC20695 (Paratype), partial, exfoliated cranidium x4 a) dorsal b) lateral
7. UC20719A (figured specimen from Bradley, 1930), exfoliated glabella in dorsal view x2

Plate 3

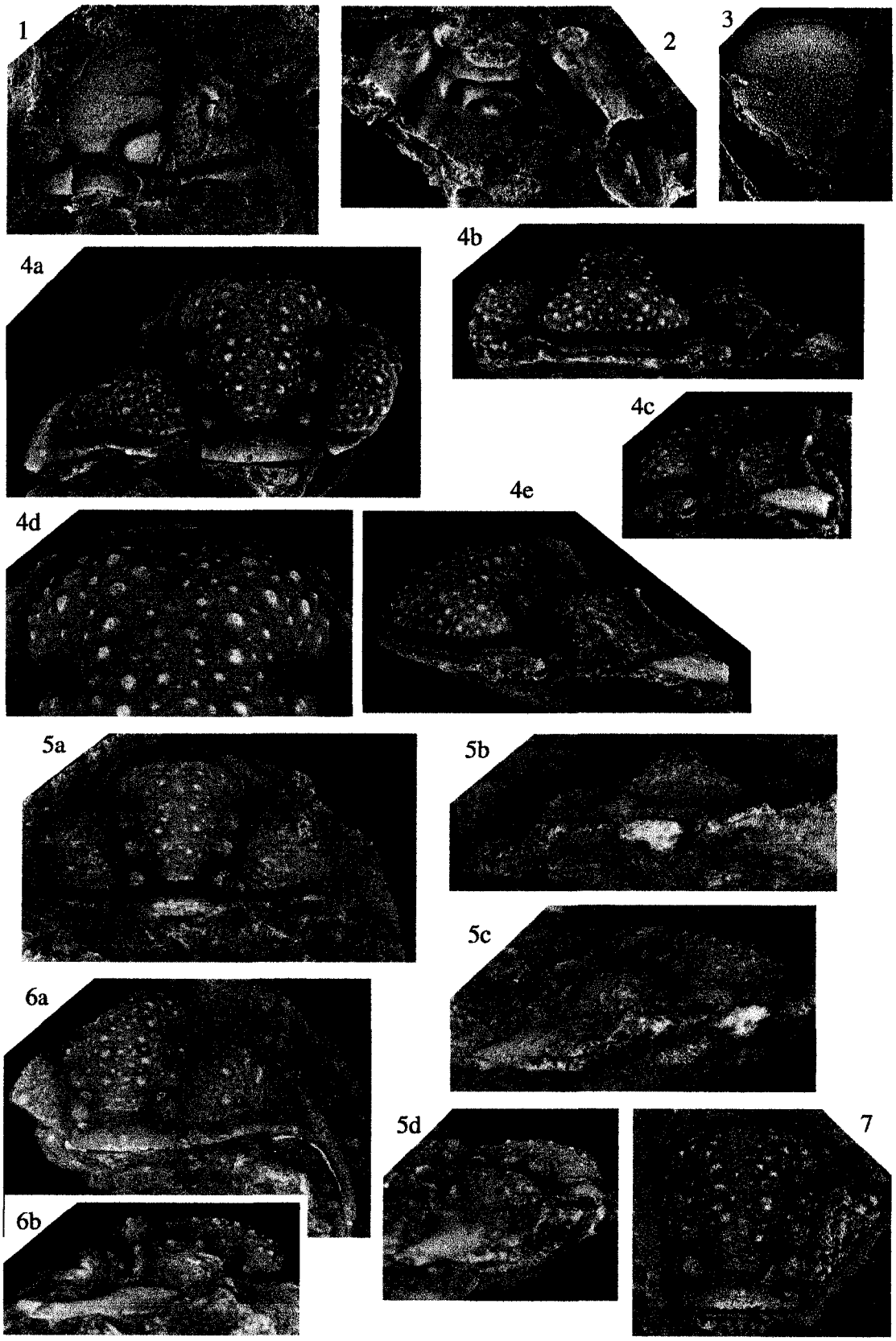


Plate 4 *Ceraurus globulobatus*

1. UC20695 (Paratype), exfoliated pygidium missing most of both spines in dorsal view x4
2. UC20695 (Paratype), external mold of pygidium in ventral view x5
3. UC20709B (Paratype), exfoliated hypostome x6 a) ventral b) lateral
4. OU11950 (Clark), nearly complete, exfoliated cranidium x6 a) dorsal b) oblique c) anterior
5. OU11951 (BQ-24), nearly complete cranidium x6 a) dorsal b) anterior c) oblique d) lateral
6. OU11952 (99-51), exfoliated cranidium missing one genal spine x3 a) dorsal b) anterior c) lateral d) division of anterior lobe x6 e) oblique

Plate 4

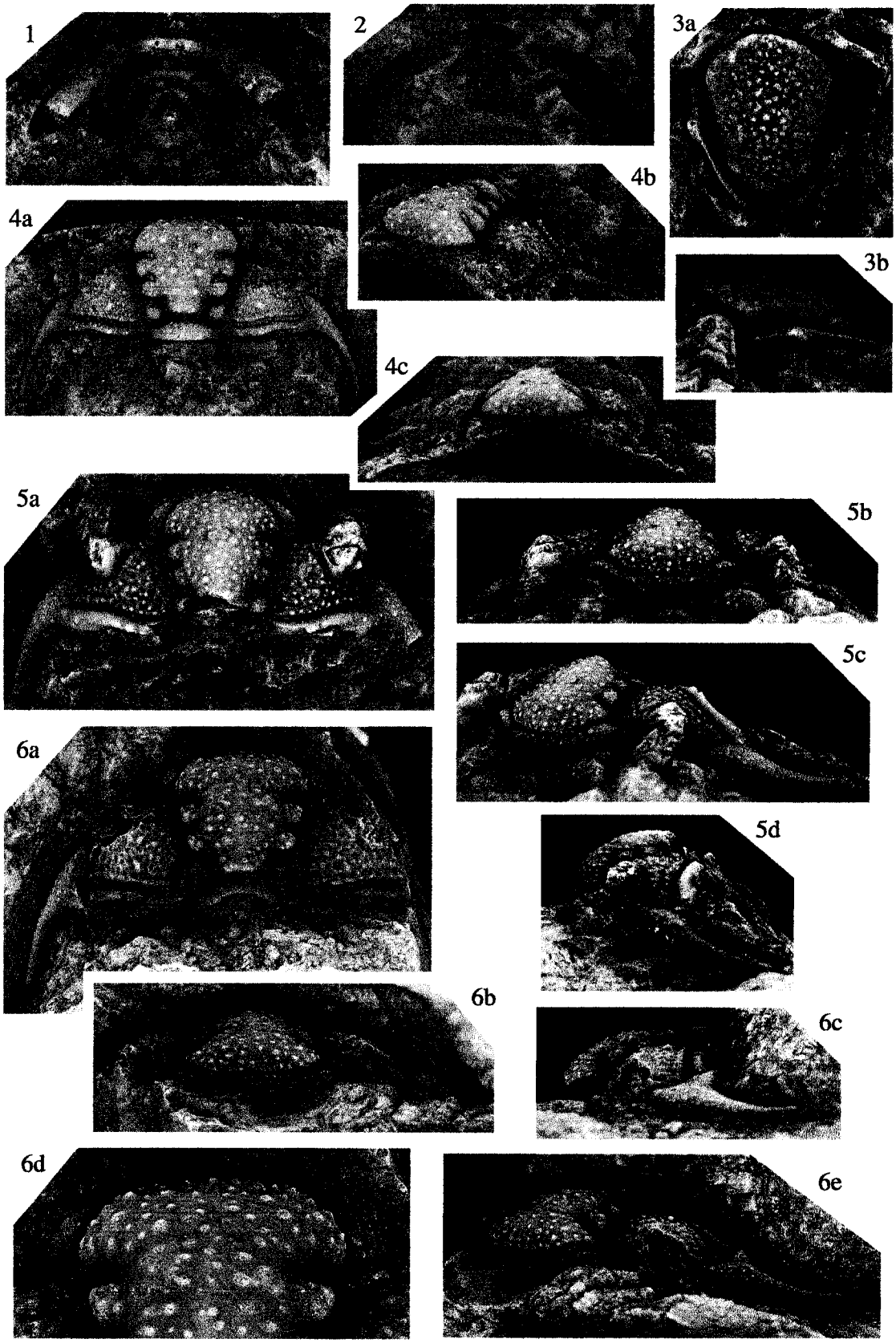


Plate 5 *Ceraurus* sp. 1, "*Ceraurus*" sp. 2

1-3 *Ceraurus* sp. 1

1. OU11953 (LQ-WF), complete cranidium x3 a) dorsal b) lateral c) oblique d) anterior/oblique
2. OU11954 (LQ-WF), pygidium missing spines in dorsal view x6
3. OU11955 (LQ-WF), partially exfoliated hypostome in ventral view x6

4-9 "*Ceraurus*" sp. 1

4. OU11956 (99-30.25), exfoliated glabella, exfoliated partial fixigenae in dorsal view x6
5. OU11957 (99-24), exfoliated glabella, fixigenae in dorsal view x4
6. OU11958 (99-29), partially exfoliated glabella, partial fixigenae in dorsal view x5
7. OU11959 (99-29), partially exfoliated glabella, partial fixigena x4 a) dorsal b) anterior/oblique
8. OU11960 (99-24), partially exfoliated pygidium missing one spine in dorsal view x6
9. OU11961 (99-29.75), partially exfoliated pygidium missing one half spine x5 a) dorsal b) anterior c) lateral d) sculpture x10

Plate 5

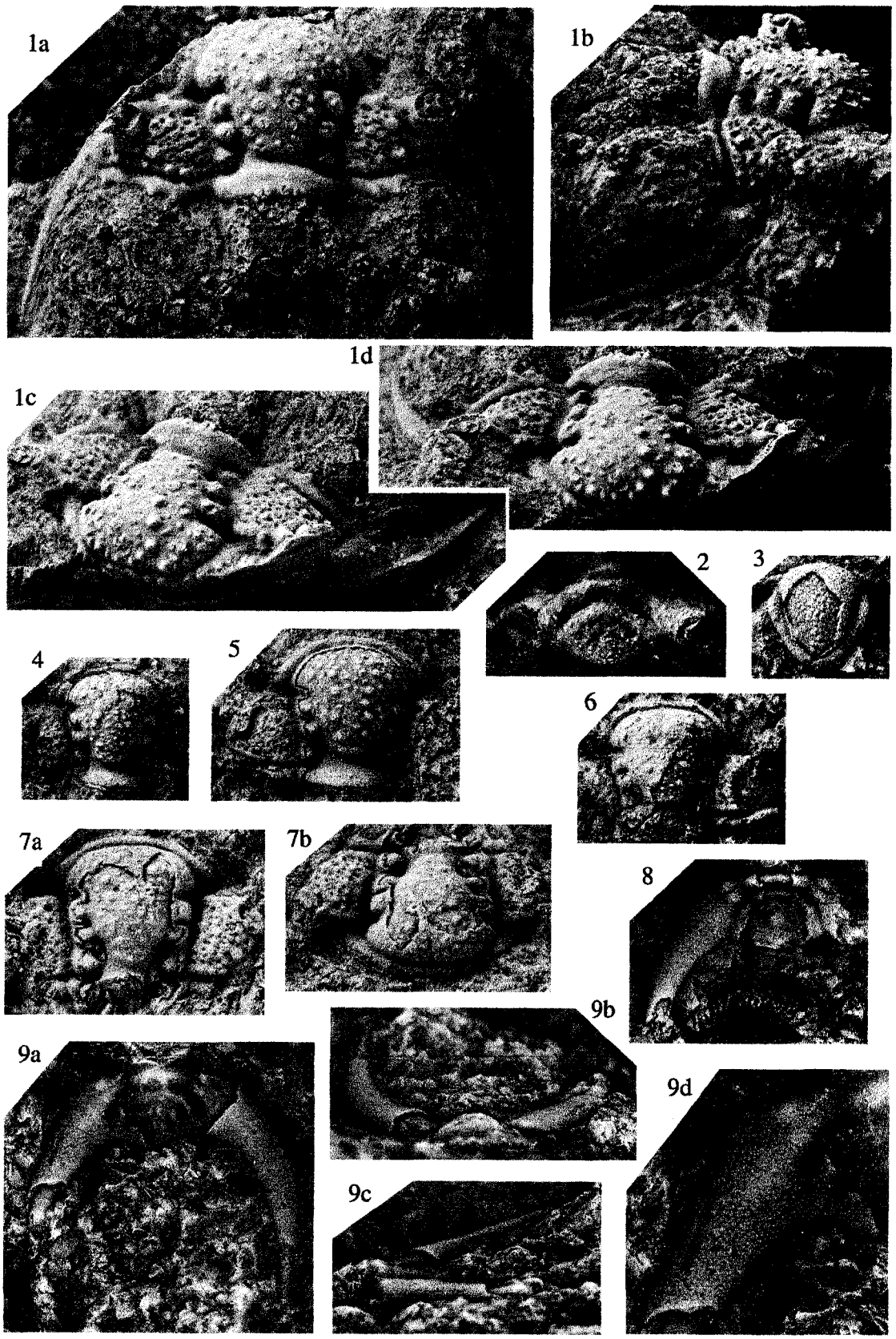


Plate 6 *Whittakerites*? *trapezoidantyx*, new species

1. OU11962 (99-30.25), nearly complete, exfoliated cephalon x4 a) dorsal b) lateral c) anterior/dorsal d) oblique
2. OU11963 (99-18), exfoliated cranidium missing one genal spine; note especially rounded anterior border x4 a) dorsal b) oblique c) anterior d) lateral
3. OU11964 (99-30.5), partial glabella, retaining cuticle x5 a) dorsal b) oblique
4. OU11965 (99-32), nearly complete, exfoliated cranidium x5 a) oblique b) lateral c) anterior d) dorsal
5. OU11966 (99-29), large, mostly exfoliated cranidium in dorsal view x4

Plate 6

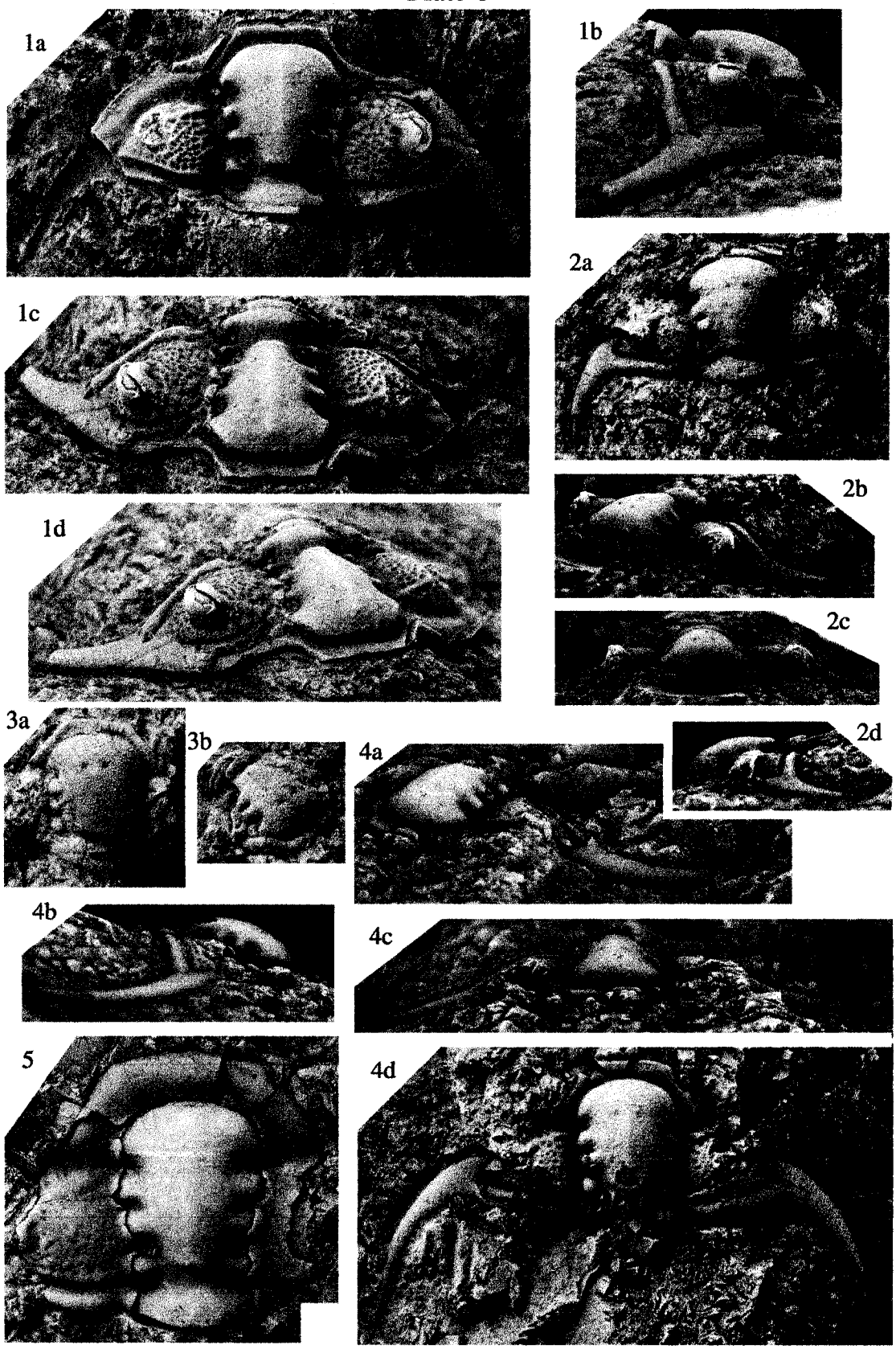


Plate 7 *Whittakerites*? *trapezoidantyx*, new species

1. OU11967 (99-29), partial cranidium x4 a) dorsal b) lateral c) oblique d) anterior
2. OU11968 (99-18), small, partly exfoliated glabella, part of one fixigena x5 in dorsal view
3. OU11969 (99-32), large, partially exfoliated glabella, partial fixigenae x4 a) dorsal b) oblique
4. OU11970 (99-29.5), large, broken cranidium x4 a) anterior b) dorsal c)oblique
5. OU11971 (99-24), small, partially exfoliated glabella in dorsal view x5
6. OU11972 (99-29.75), partly exfoliated pygidium missing parts of spines x5 a) dorsal b) anterior
7. OU11973 (99-30.5), large, partial cranidium in dorsal view x3
8. OU11974 (99-29), exfoliated, partial pygidium x5 a) dorsal b) anterior
9. OU11975 (99-29), partial, exfoliated hypostome ventral view x5
10. OU11976 (99-18), exfoliated, broken hypostome in ventral view x5

Plate 7

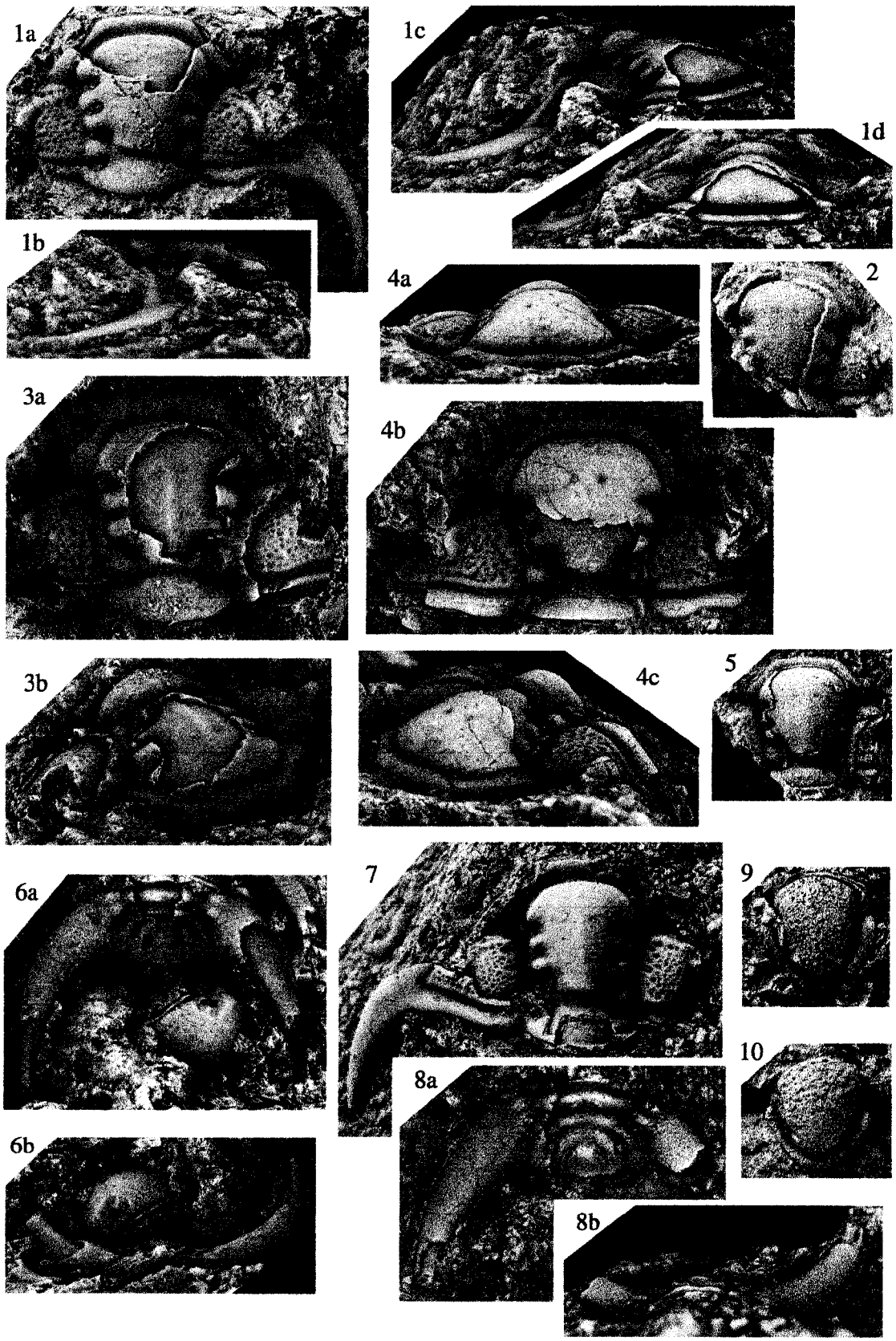


Plate 8 *Whittakerites*? sp. 1, *Borealaspis marilynoides*, new species

1-2 *Whittakerities*? sp. 1

1. OU11977 (LQ-WF), nearly complete, partially exfoliated crandium x6 a) dorsal b) anterior c) oblique d) lateral
2. OPU11978 (LQ-WF), exfoliated hypostome x5 a) ventral b) lateral

3-10 *Borealaspis marilynoides*

3. OU11979 (99-32), small, partial, exfoliated crandium x8 in dorsal view
4. OU11980 (99-32), exfoliated glabella x5 dorsal view
5. OU11981 (99-32), small, mostly exfoliated glabella and part of one fixigena x8 a)lateral b) dorsal c) anterior
6. OU11982 (99-32), partially exfoliated, broken cranidium x5 a) dorsal b) lateral c) oblique d) glabella x10 e) anterior
7. OU11983 (99-32) an image of a very small glabella in dorsal view
8. OU11984 (99-32), exfoliated hypostome in ventral view x5
9. OU11985 (99-30.25), mostly exfoliated hypostome in ventral view x4
10. OU11986 (99-32), small exfoliated glabella and parts of fixigenae x8 a) lateral b) dorsal

Plate 8

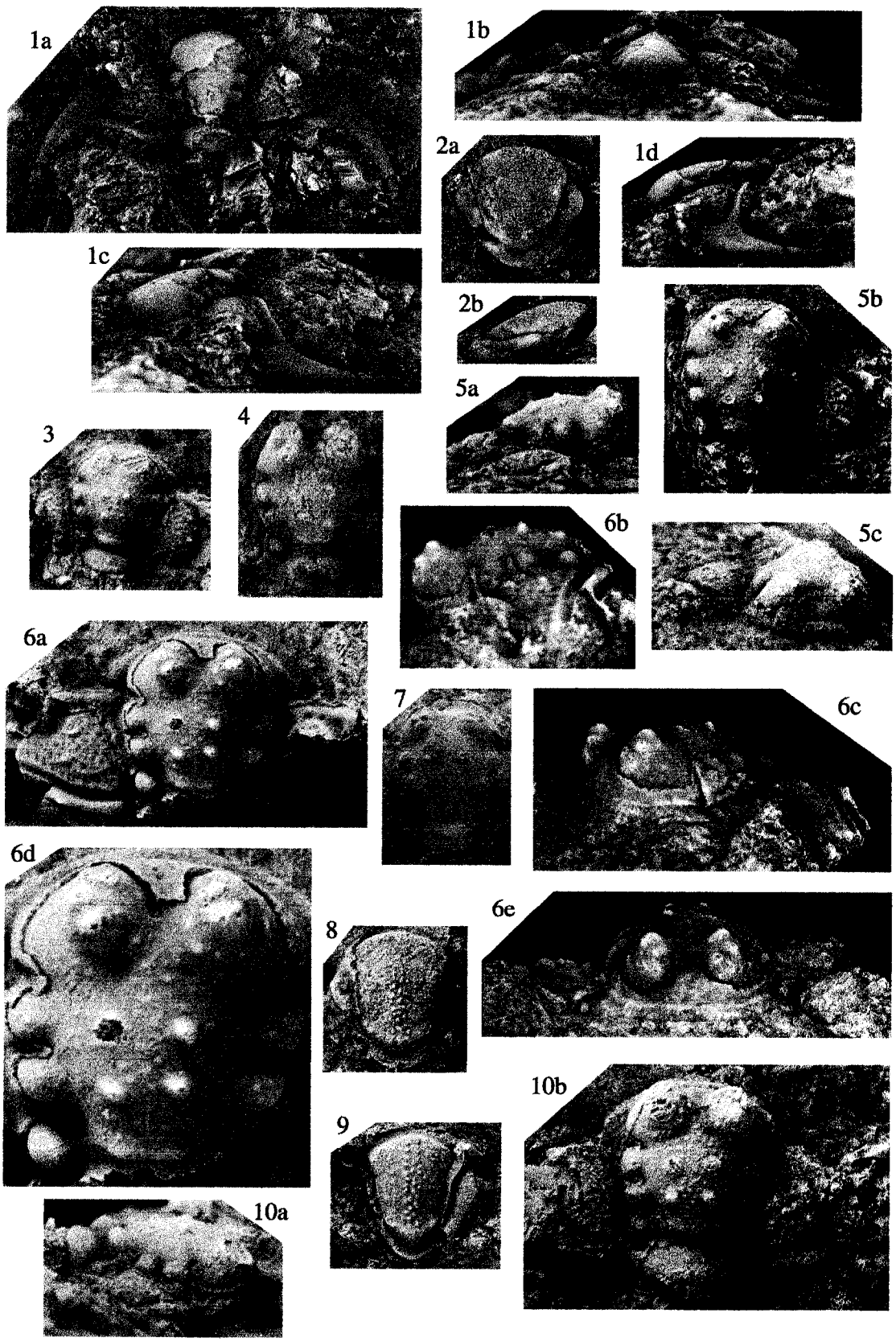


Plate 9 *Borealaspis marilynoides*, *Holia magnaspina*, *Holia* sp. 1

1-3 *Borealaspis marilynoides*

1. OU11987 (99-32), nearly complete, exfoliated cephalon x5 a) dorsal b) anterior c) oblique
2. OU11988 (99-32), external mold of pygidium and part of one spine x6 a) ventral b) anterior
3. OU11989 (99-32), exfoliated glabella and parts of fixigenae x4 anterior/dorsal view

4-5 *Holia magnaspina*

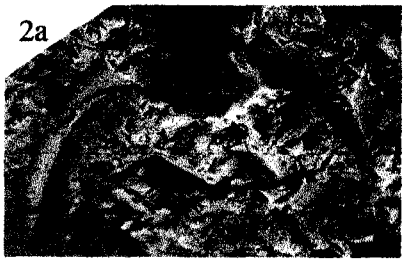
4. UC20688B (Holotype), partial, exfoliated glabella x5 a) dorsal b) anterior c) lateral d) oblique
5. UC20688A (Paratype), cast of partial glabella x5 a) lateral b) dorsal c) oblique d) anterior

6 *Holia* sp. 1

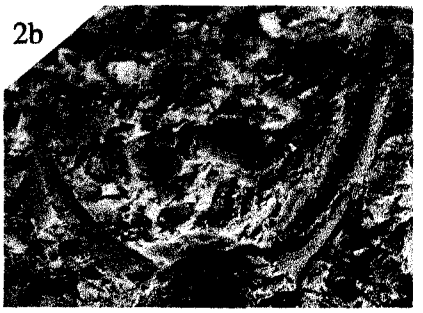
6. OU11990 (99-32), exfoliated glabella x6 a) anterior b) dorsal

Plate 9







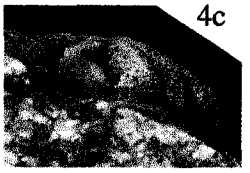




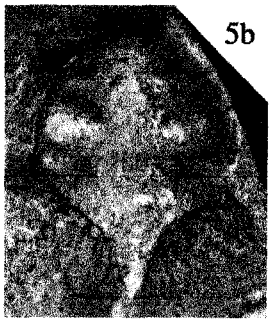






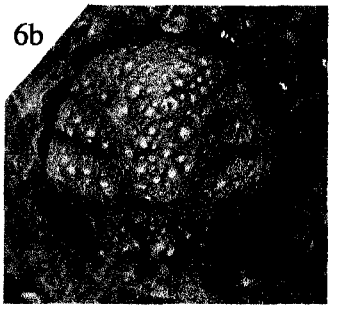


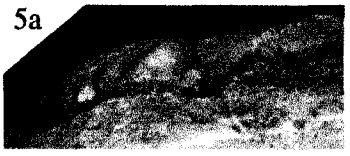












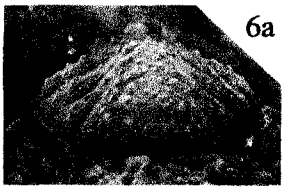
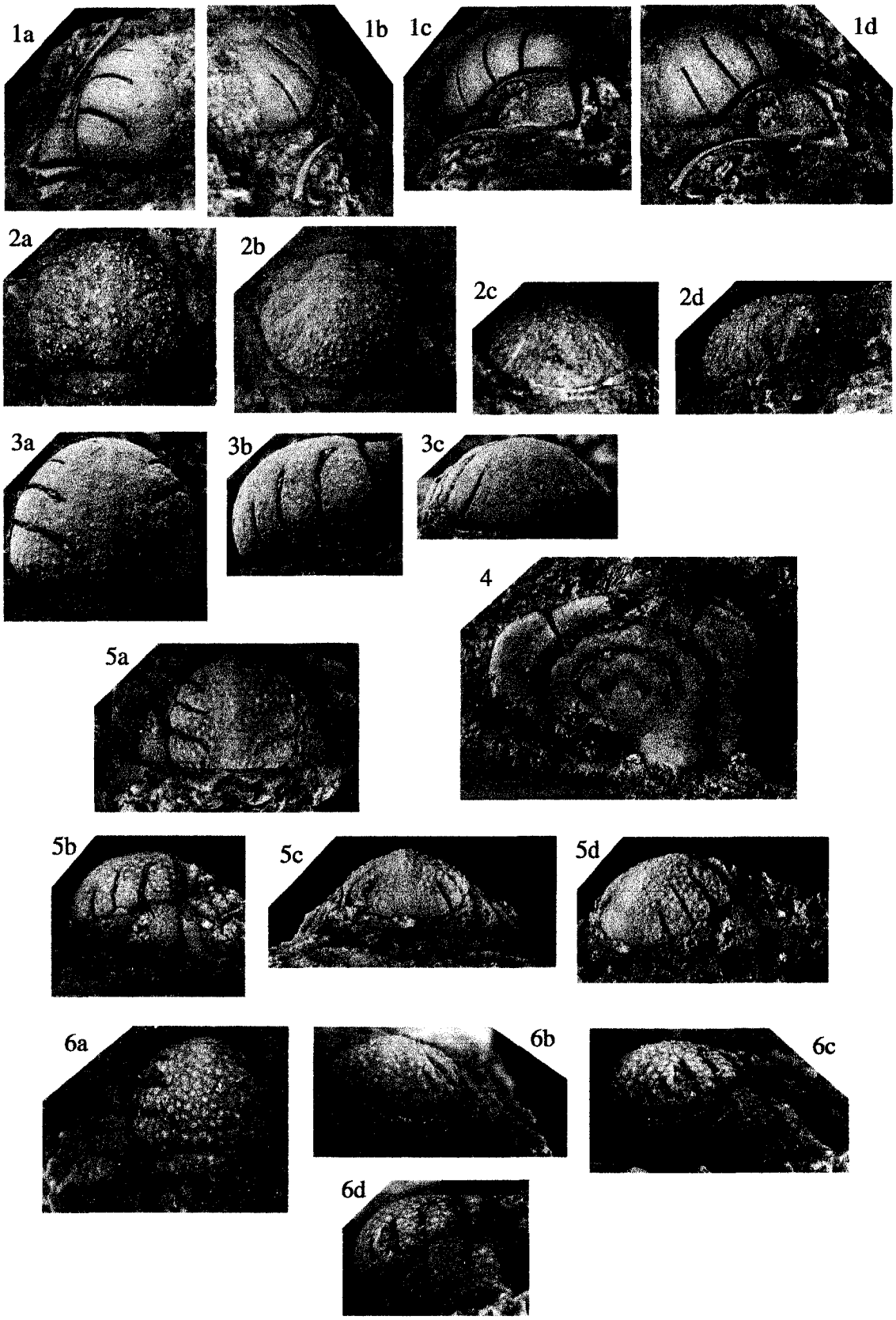


Plate 10



Chapter 6:

REMAINING TRILOBITES OF THE VIOLA GROUP

I identified 33 trilobite genera from the Viola Group. Of these, I have provided detailed systematic treatment for eleven (*Thaleops*, *Isotelus*, *Stegnopsis*, *Ectenaspis*, *Anataphrus*, *Ceraurinella*, *Ceraurus*, "*Whittakerites*", *Borealaspis*, *Holia*, "*Pandaspinapyga*"). The following annotated, illustrated faunal list provides documentation of trilobite diversity within the Viola Group and supports abundance data used in the paleoecological study. Taxa in this section will be treated more completely in subsequent work.

Order Agnostida Kobayashi 1935

Suborder Agnostina Salter 1864

Family Metagnostidae Jaekel 1909

Trinodus M'Coy 1846

(= *Arthrorhachis* Hawle and Corda1847; *Metagnostus* Jaekel 1909; *Girvanagnostus* Kobayashi 1939)

Type species.—*Trinodus agnostiformis* M'Coy 1846, Campile Formation, Wexford, Ireland (by monotypy).

Discussion.—Type material of *Trinodus* M'Coy consisted of a single, poorly preserved cranidium. Lack of a pygidium for comparison with *Geragnostus* Howell

1935 and *Arthrorhachis* led to questions about the status of the genus. Fortey (1980) recommended restriction of the genus to type material, but recovery of additional material by Owen and Parkes (2000) from the type locality allowed clarification of the generic diagnosis. Based on this new material, *Arthrorhachis* is considered a junior subjective synonym of *Trinodus*.

Trinodus sp.

Plate 1, Figs 1, 2

Stratigraphic occurrence.—Five specimens are from Nebo and Bromide Quarry in the Viola Springs Formation.

Discussion.—This species is most similar to *T. elspethi* Raymond 1925 in that the length (sag.) and width (tr.) of the pygidium are nearly equal, but the lateral margins of the Viola species are more nearly parallel and the axis tapers more strongly.

Order Asaphida

Suborder Asaphina Salter 1864

Superfamily Remopleuridioidea

Family Remopleurididae Hawle and Corda 1847

Hypodicranotus Whittington 1952

Type species.—*Remopleurides striatulus* Walcott 1875, Denley Formation, Trenton

Falls, New York (by original designation).

Hypodicranotus cf. *H. missouriensis*

Plate 1, Figs 3-8

Stratigraphic occurrence.—This genus occurs in almost every horizon in both the Viola Springs and Welling Formations.

Discussion.—*Hypodicranotus missouriensis* Foerste 1920 differs from the type in having more clearly defined glabellar furrows and a longer (sag.) frontal lobe of the glabella that curves downward more strongly. The Viola species is similar to *H. missouriensis* in these features, but lacks transversely elongate granules that become larger toward the lateral margins of the cranidium. The granular ornament of the Viola species is subcircular and uniform in size across the cranidium.

Robergiella Whittington 1959

Type species.—*Robergiella sagittalis* Whittington 1959, Edinburg Formation, Virginia (by original designation).

Discussion.—The long (exsag.) palpebral lobes that reach back to, but not opposite, the occipital furrow, the epipalpebral furrow and the bulbous frontal lobe of the glabella are characters the Viola species share with *Robergia*. They differ from

Robergia in that the frontal lobe is deflected strongly downward, and L1 is not clearly defined and lacks independent convexity. In species of *Robergia* such as *R. microphthalma* Linnarson 1875, *R. major* Raymond 1920 and *R. schlotheimi* Billings 1865 and in *Robergiella sagittalis*, S3 is directed forward abaxially and terminates near the anterior margin of the palepebral lobe. The Viola species are more similar to *Remopleurides* and *Hypodicranotus* in that the adaxial and abaxial ends of S3 are in a horizontal plane located well behind the anterior margin of the palpebral lobe. Lack of anything but cranidial material prohibits further analysis.

Robergiella sp. 1

Plate 1, Figs 9-11

Stratigraphic occurrence.—This species occurs in the Viola Springs Formation at Bromide Quarry.

Discussion.—The frontal lobe of this species is relatively flat across the anterior margin rather than broadly rounded. *Robergiella sagittalis* and *Robergiella* cf. *sagittalis* of Ludvigsen 1980 are similar in glabellar outline but differ in the orientation of the glabellar furrows.

Robergiella sp. 2

Plate 2, Figs 1-3

Stratigraphic occurrence.—This species is found in the Welling Formation at Lawrence Quarry.

Discussion.—This species is similar to an unnamed species from the Copenhagen Formation of Nevada (*Robergiella* sp. Ross and Shaw 1972) in the great lateral expansion of the frontal lobe of the glabella.

Pugilator Nikolaisen 1991

Type species.—*Robergia yukonensis* Lenz and Churkin 1966, Road River Formation, Yukon Territory, Canada (by original designation).

Pugilator deckeri Cooper 1953

Plate 2, Figs 4-13

Stratigraphic occurrence.—This species is from low in the Viola Springs Formation. Rare specimens are from Highway 77 and Burns' Quarry but most are from float blocks in a field near the Nebo outcrop.

Remopleuridid new genus

Plate 3, Fig. 1

Stratigraphic occurrence.—Stratigraphically low in the Viola Springs Formation at

Nebo and Bromide Quarry.

Discussion.—This specimen exhibits a combination of characters used to define both *Remopleurides* (posterior part of palpebral lobe adjacent to occipital furrow) and *Robergia* (lateral expansion of the frontal glabellar lobe, S1 and S2 angled strongly forward abaxially). It is not assigned to *Robergia* because L1 is not subcircular with independent convexity and an epipalpebral furrow is lacking. It is most similar to *Robergiella* but without the epipalpebral furrow. The S3 furrow is very faint.

Superfamily Trinucleoidea

Family Trinucleidae Hawle and Corda 1847

Cryptolithoides Whittington 1941

Type species.—*Cryptolithoides ulrichi* Whittington 1941 from the Late Ordovician Viola Springs Formation, Arbuckle Mountains, south-central Oklahoma (by original designation).

Cryptolithoides ulrichi Whittington 1941

Plate 3, Figs 2-7

Stratigraphic occurrence.—This species is found near the base of the Viola Springs Formation at Bromide Quarry, Nebo, Highway 77, I-35 and South Quarry.

Cryptolithoides fittsi Ulrich and Whittington in Whittington 1941

Plate 3, Figs 8-9

Stratigraphic occurrence.—The only specimen unambiguously attributed to this species if from 37 meters above the base at Highway 77. A second specimen from 51 meters above the base at Highway 99 is tentatively assigned to *C. fittsi.*

Cryptolithoides carinatus Ulrich and Whittington in Whittington 1941

Plate 4, Figs 1, 2

Stratigraphic occurrence.—This species occurs high in the Viola Springs Formation at Nebo and Highway 77.

Cryptolithus Green 1832

Type species.—*Cryptolithus tessellatus* Green 1832, "Trenton", New York (by original designation).

Cryptolithus convexus Ulrich and Whittington in Whittington 1941

Plate 4, Figs 3-5

Stratigraphic occurrence.—This species is restricted to the Welling Formation at I-35 and Highway 77.

Cryptolithus sp.

Plate 4, Figs 6, 7

Stratigraphic occurrence.—This species is abundant near the base of the exposure at Stoneybroke and may be conspecific with poorly preserved specimens near the base of the section at Highway 99.

Family Raphiophoridae Angelin 1854

Ampyxina Ulrich 1922

Type species.—*Endymionia bellatula* Savage 1917 (subsequent designation by Ulrich 1922).

Ampyxina sp.

Stratigraphic occurrence.—This species is common on the pavement at Bromide Quarry.

Discussion.—This species is similar to *A. powelli* Raymond 1920 and *A. elegans* Cooper 1953 in lacking a frontal glabellar spine. The anterior margins of the fixigenae in the Viola species are much more rounded than in *A. powelli* and the pleural furrows of the pygidium are not arched forward as in both other species. The pygidium of the Viola species is very similar to that of *A. wothertonenesis* Whittard

1955, but the glabella of the latter species expands forward more strongly and the alae are better developed.

Order Illaenida

Suborder Illaenina Jaanusson 1959

Family Illaenidae Hawle and Corda 1847

Subfamily Illaeninae Hawle and Corda 1847

Bumastoides Whittington 1954

Type species.—*Illaenus milleri* Billings 1859, Trenton Group, Ontario (by original designation).

Bumastoides billingsi Raymond and Narraway 1908

Plate 5, Figs 1-3, 5

Stratigraphic occurrence.—This is the most abundant genus in the bryozoan grain- to rudstone facies at Highway 99.

Subfamily Bumastinae Raymond 1916

Failleana Chatterton and Ludvigsen 1976

Type species.—*Failleana calva* Chatterton and Ludvigsen 1976, lower Esbataottine Formation, Sunblood Range, District of Mackenzie (by original designation).

Failleana sp.

Plate 5, Fig. 4

Stratigraphic occurrence.—Two cranidia are known from the Welling Formation at Lawrence Quarry.

Discussion.—In *F. calva*, the maximum width (tr.) of the cranidium in front of the palpebral lobes is nearly as great as the width (tr.) across the palpebral lobes while, in the Viola species, the cranidium is narrower (tr.) anteriorly than the palpebral lobes.

Order Proetida

Family Aulacopleuridae Angelin 1854

Subfamily Otarioninae Richter and Richter 1926

Harpidella M'Coy 1849

Type species.—*Harpes*? *megalops* M'Coy 1849, Kilbride Formation, County Galway, Ireland.

Harpidella new species

Plate 5, Figs 6-8; Plate 6, Figs 1-6

Stratigraphic occurrence.—This species is found high in the Viola Springs Formation at Highway 99 and Lawrence Quarry.

Discussion.—This species is assigned to *Harpidilla* based on characters such as a convex glabella that doesn't overhang the anterior border, an anterior border of nearly uniform length, a short preglabellar field and long genal spines. This species is unique in that the glabella is ovate in outline without "waisting" lateral to L1. This is a feature that is most commonly seen in *Cyphaspis* (see *C. carrolli* Adrain and Kloc 1997), but is also present to a lesser degree in *Harpidella* sp. A Owen and Bruton 1980. The lateral and posterior border furrows of this species merge and continue for a short distance onto the genal spine. This feature is also seen in *H. triloba* Hu 1975 (see Adrain and Chatterton 1995, figs 2.7, 2.13, 2.14) but is better developed in the Viola species.

Family Proetidae Salter 1864

Decoroproetus Pribyl 1946

Type species.—*Proetus decorus* Barrande 1846, Liten Formation, Prague district, Czechoslovakia (subsequent designation by Pribyl 1946).

Decoroproetus new species

Plate 6, Figs 7-9; Plate 7, Figs 1-2

Stratigraphic occurrence.—This species occurs in the Welling Formation at Lawrence Quarry.

Discussion.—This species is similar to *D. furubergensis* Owens 1970 and *D. subornatus* Cooper and Kindle 1936 (see Owens 1973, figs 3-7) in having three glabellar furrows and reticulate ornamentation. The new species is unique in having a short (exsag.) but well impressed S1, it lacks an occipital tubercle, and the preglabellar field is very short (sag.) while the anterior border is very long (sag.). The pygidium consists of only four segments.

Decoroproetus sp.

Plate 7, Fig. 3

Stratigraphic occurrence.—A single cranidium is from the bryozoan grain- to rudstone lithofacies at Highway 99.

Discussion.—A second species from the Viola Springs Formation also has three lateral glabellar furrows, with S1 short (exsag.) but deeply impressed. The preglabellar area is longer (sag.) than in the species from the Welling Formation, with the anterior border shorter and more strongly rounded.

Family Dimeropygidae Hupé 1953

Dimeropyge Öpik 1937

Type species.—*Sphaerexochus minutus* Nieszkowski 1857, Kuckers shale, Estonia (by subsequent designation by Öpik 1937).

Dimeropyge cf. *D. virginiensis*

Plate 7, Figs 4-6

Stratigraphic occurrence.—*Dimeropyge* is rare high in the Viola Springs Formation at Highway 99.

Discussion.—The Viola species is most similar to *D. virginiensis* in length (sag.) of the preglabellar field and orientation of the anterior border. The preglabellar field of *D. raymondi* Roy 1941 is deflected downward strongly so that it is not visible in dorsal view, and the anterior border of *D. clintonensis* Shaw 1968 is nearly horizontal rather than deflected downward as in the Viola species.

Mesotaphraspis Whittington and Evitt 1954

Type species.—*Mesotaphraspis parva* Whittington and Evitt 1954, Edinburg limestone, Virginia(by original designation).

Mesotaphraspis new species

Stratigraphic occurrence.—This species is uncommon high in the Viola Springs Formation at Highway 99.

Discussion.—The Viola species is most similar to *M. parva* in cranidial characters

except the anterior border of the new species is longer sagitally instead of being uniform in length. The pygidium of the new species has a border furrow that is more strongly developed than in *M. parva*, and the pleural furrows are transverse rather than arching forward as in the type. *Mesotaphraspis*? *dalfaskensis* Tripp 1980 has wider (tr.) posterior fixigenae than the new species, and the palpebral lobes are placed much father forward. *Mesotaphraspis bockeliei* Owen and Bruton 1980 possesses shallow furrows running from the anterior margin of the palpebral lobe laterally and slightly backward to the axial furrows which are absent on the Viola species.

A single specimen from a lower stratigraphic level at Highway 99 differs from the species identified from higher in the section at the same locality in that the glabella and preglabellar area are very long (sag.). However, examination of small cranidia from the type series of *M. parva* indicates that the glabella, and the cranidium as a whole, becomes shorter through ontogeny. More material from this horizon, representing a broader range of ontogenetic development, is required for identification of this specimen.

Order Harpida

Family Harpidae Hawle and Corda 1847

Dolichoharpes Whittington 1949

Type species.—*Eoharpes uniserialis* Raymond 1925, Kimmswick Limestone, Missouri (subsequent designation by Whittington 1949).

Dolichoharpes cf. *D. uniserialis*

Stratigraphic Distribution.—*Dolichoharpes* is uncommon high in the Viola Springs Formation at Highway 99.

Discussion.—In lateral profile, the dorsal margin of the fringe slopes downward toward the posterior. In *D. reticulata* Whittinton 1949 (pl. 2, fig. 5) and *D.* aff. *reticulata* Chatterton and Ludvigsen 1976 (pl. 7, fig. 7), the dorsal margin of the fringe is horizontal to the posterior termination.

Order Phacopida Salter 1864

Suborder Calymenina Swinnerton 1915

Family Calymenidae Burmeister 1843

Flexicalymene Shirley 1936

Type species.—*Calymene caractaci* Salter 1865, Caradoc, Shropshire (by original designation).

Discussion.—All calymenids from the Viola Group have three lateral glabellar lobes, with L1 only slightly bigger than L2, forming a parabolic rather than bell-shaped glabellar outline. The anterior margin of the glabella is even with the anterior margin of the fixigenae or projects slightly beyond with one exception, noted below. Palpebral lobes are across from or slightly in front of L2, and buttresses between the

fixigenae and glabellar lobes are lacking. The anterior border slopes upward or is roll-like but no form has a ridge along the dorsal margin of the anterior border. With one exception, pygidia of Viola calymenids have interpleural furrows that reach to, or nearly to, the lateral margins of the pygidium.

Flexicalymene sp.1

Plate 9, Figs 1-3

Stratigraphic occurrence.—This species occurs low in the Viola Springs Formation at Bromide Quarry and Highway 99.

Discussion.—This is the only species from the Viola Group in which the front of the glabella does not reach the anterior margin of the fixigenae. It is most similar to *F. jemtlandica* Thorslund 1940 (see Siveter 1977, figs 4H-4K, 5, 6A-6I) in angle of upturn of the anterior border, low convexity of the pygidium and development of weak intermediate lobes. The Viola species differs in that the palpebral lobes are placed more forward on the cranidium (across from L2 rather than S1), the preocular border furrow is more distinct and the pygidium has six segments rather than five. The librigenae of *F. jemtlandica* are very wide (tr.).

Flexicalymene sp. 2

Plate 9, Figs 4-6

Stratigraphic occurrence.—This species is common at 39 meters above the base of the section at Highway 99.

Discussion.—The anterior border of this species is very long (sag.) and directed strongly upward beyond a deep, broad preglabellar furrow so that the anterior margin of the anterior border reaches the height of the top of the glabella. Lateral borders of the librigenae are broad. The pygidium consists of six segments and the interpleural furrows become effaced toward the lateral margins, forming a narrow marginal border.

Flexicalymene sp. 3

Plate 9, Figs 7-10; Plate 10, Figs 1-6

Stratigraphic occurrence.—This species is common high in the Viola Springs Formation at Highway 99.

Discussion.—The preglabellar furrow of this species is deep, but very short (sag.), and the anterior border is short (sag.), very convex (longitudinally), and arched weakly backward. It is similar to *F. griphus* Ross 1967 except the anterior border is shorter (sag.) on the Viola species and less transverse, and the palpebral lobes are opposite L2 rather than S2. *Flexicalymene senaria* Conrad 1841 also has a short (sag.), strongly upturned anterior border but the border is narrower (tr.) than in the Viola species.

Flexicalymene cf. *F. senaria* Conrad 1841

Plate 10, Figs 7-12

Stratigraphic occurrence.—This species is found high in the Viola Springs Formation at Lawrence Quarry and at 51 meters above the base and higher at Highway 99.

Discussion.—This species is similar to the type except the palpebral lobes are placed slightly farther back on the Viola species and the anterior border is turned upward at a lower angle.

Flexicalymene cf. *F. meeki* Foerste 1910

Plate 11, Figs 3, 4, 6?

Stratigraphic occurrence.—This species occurs in the Welling Formation at Lawrence Quarry.

Discussion.—This species resembles *F. meeki* in the convex (longitudinal), nearly transverse anterior border that is directed strongly upward. The border of the new species is shorter (sag.) than in *F. meeki* and the border is not as strongly arched transversely.

Flexicalymene cf. *F. limba* Shirley 1936

Plate 11, Fig. 7

Stratigraphic occurrence.—The single specimen attributed to this species is from the Welling Formation at Lawrence Quarry.

Discussion.—The narrow (tr.) anterior border of this species is distinctive and similar to that of *F. limba*. Preservation of the single cranidium is too fragmentary for further comparison.

Flexicalymene?

Plate 11, Figs 1-2, 5

Stratigraphic occurrence.—Material of this species is from high in the Viola Springs at Highway 77.

Discussion.—A species from the Viola Group exhibits characteristics of *Calymene* Brongniart 1822. Intermediate lobes are present at the adaxial end of S1, L3 is well-defined and the cephalic ornamentation is a bimodal mix of granules and tubercles. The glabella, however, is parapolic in outline rather than bell-shaped, the glabella does not reach beyond the anterior margin of the fixigenae, and the interpleural furrows on the associated pygidia do not extend quite to the lateral margin.

Suborder Cheirurina Harrington and Leanza 1957

Family Cheiruridae Salter 1864

Family Encrinuridae Angelin 1854

Encrinuroides Reed 1931

Type species.—*Cybele sexcostata* Salter 1848, Shoalshook Limestone, Pembrokeshire, Wales (by original designation).

Encrinuroides cf. *E. capitonis* Frederickson 1964

Plate 12, Figs 1-3

Stratigraphic occurrence.—*Encrinuroides* is rare high in the Viola Springs Formation at Highway 99.

Discussion.—The glabella of the Viola species is narrower (tr.) at the posterior and widens (tr.) less forward than in the type or in most other species. In *E. rarus* Walcott 1877 (see Chatterton and Ludvigsen 1976), the lateral glabellar furrows are also much wider (tr.). This species is most similar to *E. capitonis* from the Simpson Group of Oklahoma, especially in glabellar outline and relatively small size of the glabellar tubercles. The pygidia have the same number of segments (16) and a similar outline.

Suborder Phacopina Struve 1959

Superfamily Phacopoidea

Family Pterygometopidae Reed 1905

Subfamily Pterygometopinae Reed 1905

Achatella Delo 1935

Type species.—*Dalmanites achates* Billings 1860, Coburg beds, Ottawa, Ontario (by original designation).

Achatella new species

Plate 14, Figs 2-6

Stratigraphic occurrence.—*Achatella* occurs high in the Viola Springs Formation at Highway 99 and Lawrence Quarry.

Discussion.—*Achatella katharina* Bradley 1930 from the Kimmswick Limestone of Missouri is similar to the Viola species in having very long genal spines and extremely tall eyes. The genal spines of the new species are longer than those of *A. katharina*, while the eyes of *A. katharina* are slightly taller than those of the Viola species.

Subfamily Eomonorachinae Pillet 1954

Calyptaulax Cooper 1930

Type species.—*Calyptaulax glabella* Cooper 1930, Whitehead Formation, Gaspé Peninsula, Quebec (by original designation).

Calyptaulax cf. *C. callirachis* Cooper 1953

Plate 12, Figs 4-9

Stratigraphic occurrence.—This species is found in the bryozoan grain- to rudstone lithofacies at Highway 99.

Discussion.—The Viola species resembles *C. callirachis* in having sharp genal angles, an anterior border that is longest sagitally and distinctly pointed and the posterior margin of the pygidium is deflected upward. Very short (exsag.), thin genal spines distinguish the new species.

Calyptaulax cf. *C. strasburgensis* Ulrich and Delo, in Delo 1940

Plate 13, Figs 1-7

Stratigraphic occurrence.—This species occurs high in the Viola Springs Formation at Highway 99 and Lawrence Quarry.

Discussion.—*Calyptaulax strasburgensis* is distinguished by the presence of shallow, elongate depressions between the central portion of the glabella and the lateral lobes. Such depressions are present in a Viola species (Pl. 13, Fig. 3) and suggest a relationship with *C. strasburgensis*.

Calyptaulax sp.

Plate 13, Figs 8-11; Plate 14, Fig. 1

Stratigraphic occurrence.—This species is found in the Welling Formation at Lawrence Quarry and Nebo

Discussion.—The Welling Formation *Calyptaulax* differs from the Viola Springs species in having a more sharply triangular pygidium in which the lateral margins converge more sharply backward. The L2 is narrower (tr.) than in the other species, and the abaxial margins of L3 are not as well-rounded.

Sceptaspis Ludvigsen and Chatterton 1982

Type species.—*Pterygometopus lincolnensis* Branson 1909, Plattin Formation, Missouri (by original designation).

Sceptaspis new species

Plate 14, Figs 7-12

Stratigraphic occurrence.—*Sceptaspis* is found high in the Viola Springs Formation at Bromide Quarry and in the Welling Formation at Lawrence Quarry.

Discussion.—The pygidium of the new species is not as deep (dorsoventrally) as in *S.*

lincolnensis, the lateral margins converge evenly backward instead of pinching in at about 75% distance to the posterior margin, and the posterior tip of the pygidium is not directed downward.

Order Lichida

Subfamily Tetralichinae Phleger 1936

Amphilichas Raymond 1905

Type species.—*Platymetopus lineatus* Angelin 1854, Dalarne, Sweden (by original designation).

Amphilichas sp.

Plate 16, Figs 2-6

Stratigraphic occurrence.—This species occurs high in the Viola Springs Formation at Highway 99.

Discussion.—This species is most simlar to *A. subpunctatus* Esker 1964 from the Bromide Formation of Oklahoma. The species are similar in profile and relative size of the median and lateral glabellar lobes, but the Viola species differs in that the posterior margin of the occipital ring arches forward.

Amphilichas cf. *A. cucullus*

Plate 16, Fig. 7

Stratigraphic occurrence.—The only specimen is from the Viola Springs Formation at Lawrence Quarry.

Discussion.—A well-preserved specimen from the Viola Group has a blunt swelling at the front of the median lobe similar to that illustrated for *A. cucullus* (see Bradley 1930, pl. 29, fig. 2). The outline of the cephalon and relative size of the median and lateral lobes are also similar.

Subfamily Ceratarginae Tripp 1957

Hemiarges Gürich 1901

Type species.—*Lichas* (*Arges*) *Wesenbergensis* Schmidt 1885, Rakvere Limestone, Estonia (by original designation).

Hemiarges sp. 1

Plate 15, Figs 1-2

Stratigraphic occurrence.—This species is from the bryozoan grain- to rudstone lithofacies at Highway 99.

Discussion.—This species is similar to *H. paulianus* Clarke 1894 in width (tr.) and anterior expansion of the median lobe and ornament. The antero-lateral lobes of *H. paulianus* are larger.

Hemiarges sp. 2

Plate 15, Figs 8, 11

Stratigraphic occurrence.—This species occurs high in the Viola Springs Formation at Bromide Quarry.

Discussion.—*Hemiarges diadayma* Rudkin, Tripp, Ludvigsen 1994 is similar to this species in that the basal lateral glabellar lobes are long (exsag.) and not clearly defined adaxailly. In the Viola species, the basal lateral glabellar lobes also extend backward to a point lateral to the occipital ring.

Hemiarges cf. *H. turneri*

Plate 15, Figs 3-7, 9-10

Stratigraphic occurrence.—This species is found high in the Viola Springs Formation at Highway 99 and Lawrence Quarry.

Discussion.—This species is similar to *H. turneri* Chatterton and Ludvigsen 1976. Both the Viola species and *H. turneri* are similar to *H. bartoni* Bradley 1930.

Chatterton and Ludvigsen distinguish *H. turneri* as having more triangular antero-lateral glabellar lobes, which is a feature shared with the new species from the Viola. The second spine pair on the pygidium of *H. turneri* is more robust than those of the new species.

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Plate 1 *Trinodus*sp., *Hypodicranotus* cf. *H. missouriensis*, *Robergiella* sp. 1

1-2 *Trinodus*

1. OU11996 (BQ-Pave) pygidium in ventral view x5
1. OU11997 (Nebo78) exfoliated pygidium x4 a) dorsal b) lateral

3-8 *Hypodicranotus* cf. *H. missouriensis*

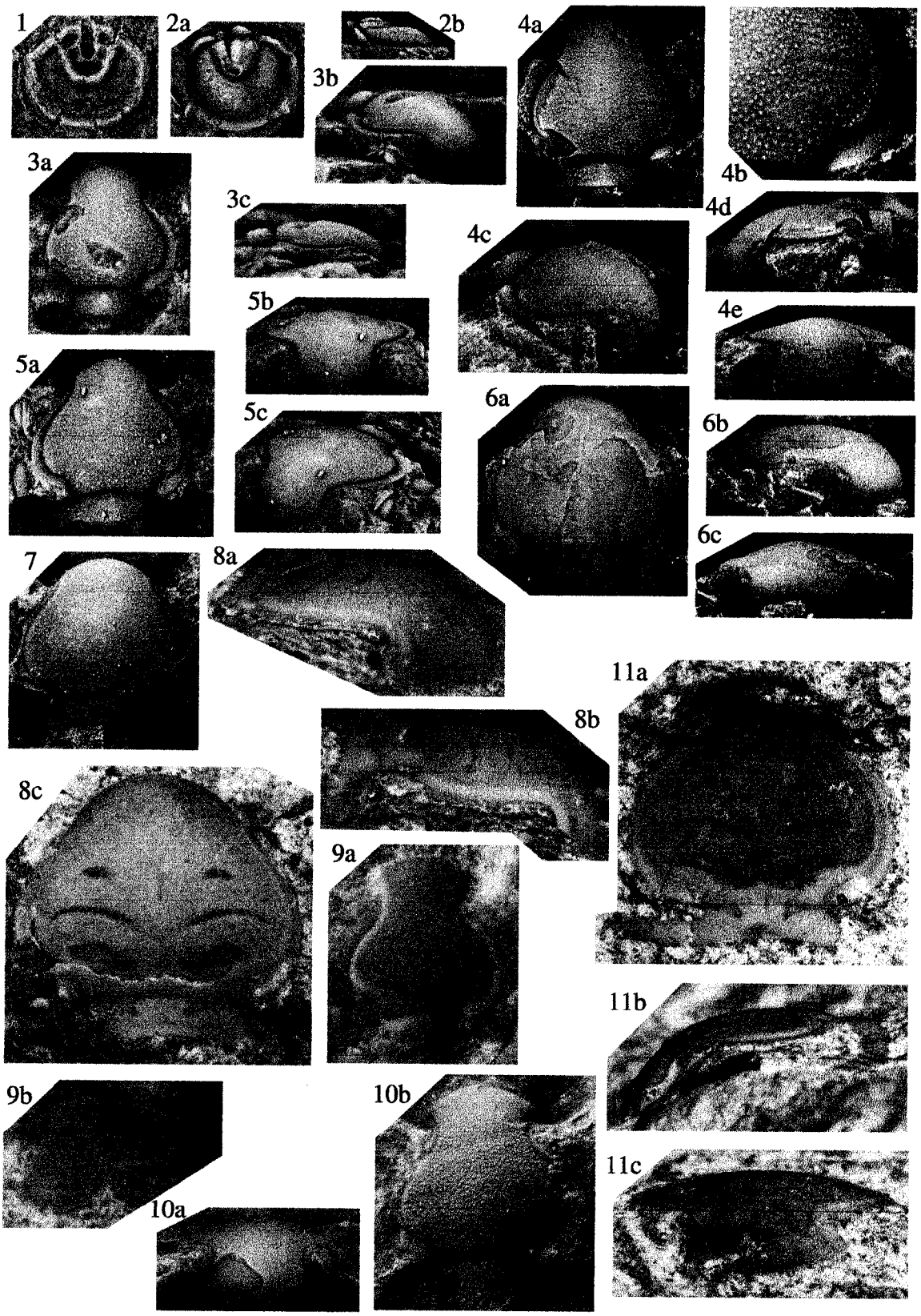
1. OU11998 (99-48) testate cranidium missing left palpebral lobe x12 a) dorsal b) oblique c) lateral
1. OU11999 (99-48) testate cranidium missing left palpebral lobe x10 a) dorsal b) glabella x20 c) oblique d) lateral e) anterior
1. OU12000 (99-48) nearly complete, testate cranidium x10 a) dorsal b) anterior c) oblique
1. OU12001 (99-51) nearly complete, partially testate cranidium x6 a) dorsal b) oblique c) anterior
1. OU12002 (99-46.5) testate cranidium with palpebral lobes partially preserved in dorsal view x8
1. OU12003 (99-56) partial, nearly complete, unwhitened cranidium x6 a) dorsal b) oblique c) lateral

9-11 *Robergiella* sp. 1

1. OU12004 (BQ-18) nearly complete, testate, unwhitened cranidium x12 a) dorsal b) oblique
1. OU12005 (BQ-BaseE) nearly complete, testate crandium x10 a) anterior b) dorsal

1. OU12006 (BQ-1) nearly complete, testate, unwhitened cranidium x6 a) dorsal b) lateral c) anterior

Plate 1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9b
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10a
11c

Plate 2 *Robergiella* sp. 2, *Pugilator deckeri*

1-3 *Robergiella* sp. 2

1. OU12007 (LQ-WF) nearly complete, testate cranidiuim x8 a) dorsal b) anterior c) oblique
1. OU12008 (LQ-WF) nearly complete, testate, unwhitened cranidium x6 a) dorsal b) oblique
1. OU12009 (LQ-WF) nearly complete, testate cranidium x8 a) dorsal b) oblique c) anterior d) lateral

4-13 *Pugilator deckeri*

1. OU12010 (NeboField) slightly crushed, testate cranidium in dorsal view x3
1. OU12011 (NeboField) small, partial, testate cranidium in dorsal view x8
1. OU12012 (NeboField) nearly complete, testate cranidium in dorsal view x5
1. OU12013 (NeboField) ventral view of librigena x4
1. OU12014 (NeboField) ventral view of librigena x4
1. OU12015 (NeboField) ventral view of librigena x4
1. OU12016 (NeboField) nearly complete, testate cranidium in dorsal view x5
1. OU12017 (NeboField) nearly complete, testate cranidium in dorsal view x5
1. OU12018 (NeboField) nearly complete, testate pygidium in dorsal view x5
1. OU12019 (NeboField) broken pygidium in ventral view x5

Plate 2

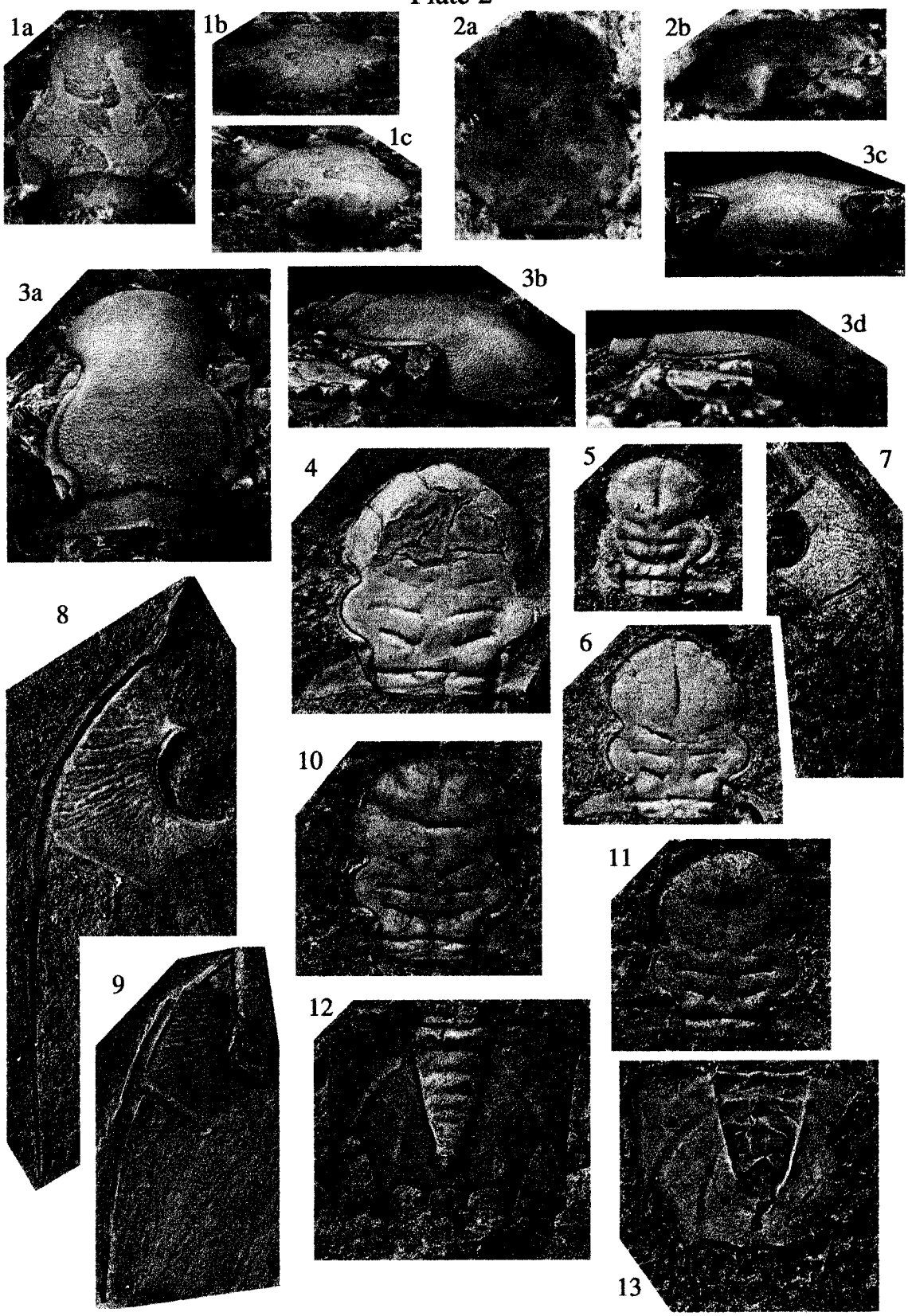


Plate 3 Remopleuridid new genus, *Cryptolithoides ulrichi*, *Cryptolithoides fittsi*

1 Remopleuridid new genus

1. OU12020 (Nebo) complete, testate cephalon x6 in dorsal view

2-7 *Cryptolithoides ulrichi*

2. OU12021 (BQ-12) small cranidium with lateral eye ridges x8 a) dorsal b) oblique c) anterior d) lateral
3. OU12022 (BQ-BaseE) cranidium with occipital spine preserved x4 a) dorsal b) oblique c) anterior d) lateral
4. OU12023 (Nebo-20Float) nearly complete individual with lower lamella and genal spines preserved in dorsal view x3
5. OU12024 (Nebo-20Float) nearly complete, testate individual in dorsal view x3
6. OU12025 (Nebo-Float) hypostome in dorsal view x8
7. OU12026 (Nebo-Float) nearly complete, testate pygidium in dorsal view x4

8 *Cryptolithoides fittsi*

8. OU12027 (77-37) testate individual missing part of glabella and lower lamella x4 a) dorsal b) anterior

9 *Cryptolithoides fittsi*?

9. OU12028 (99-51) nearly complete, testate cranidium x3 a) dorsal b) oblique c) lateral d) anterior

Plate 3

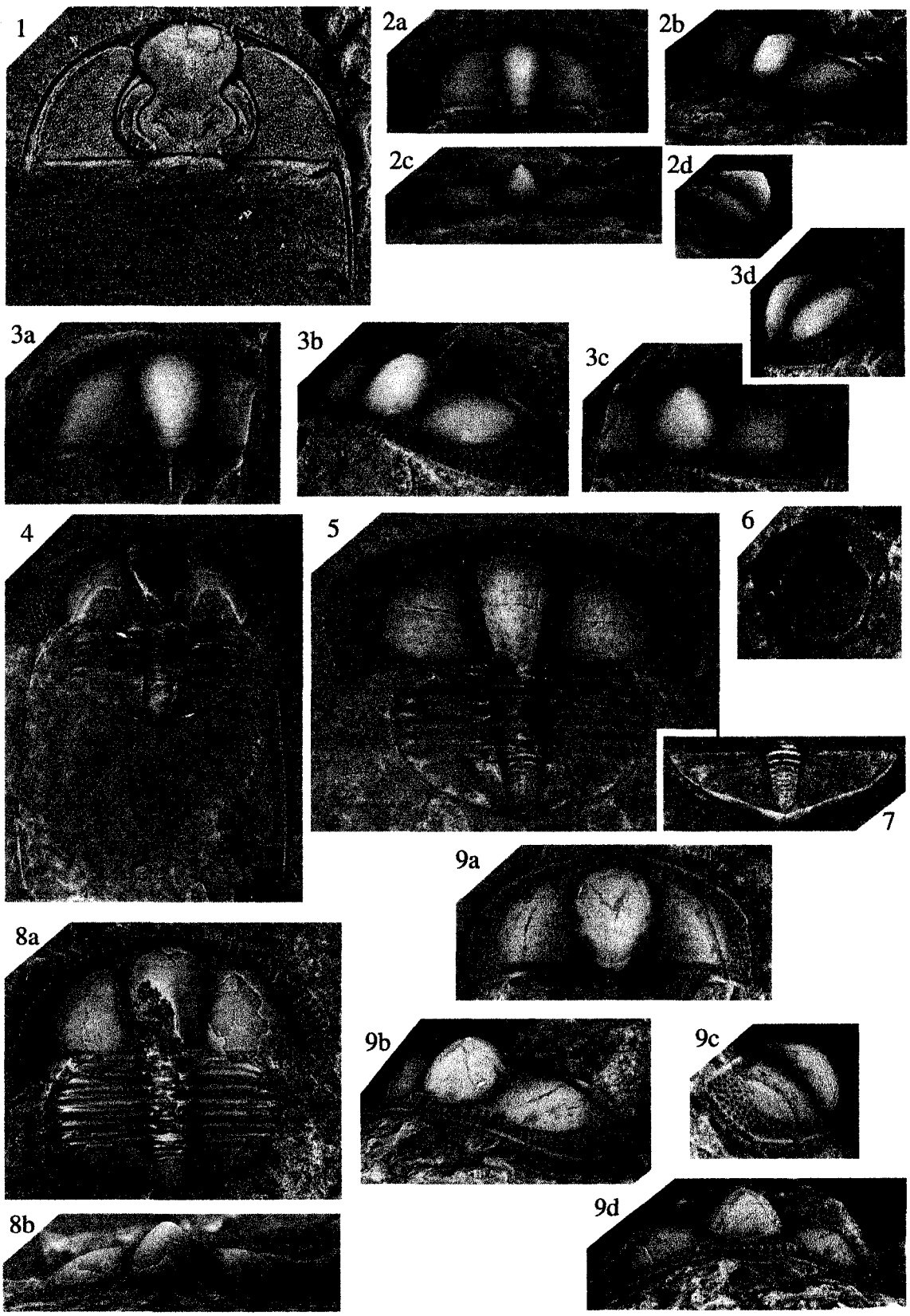


Plate 4 *Cryptolithus convexus*, *Cryptolithus carinatus*, *Cryptolithus* sp., *Ampyxina* sp.

1-2 *Cryptolithus convexus*

1. OU12029 (Nebo-78.5) small, nearly complete, testate cranidium x6 a) dorsal b) oblique c) anterior d) lateral
2. OU12030 (77-208) nearly complete, partially exfoliated cranidium x3 a) dorsal b) lateral c) anterior d) oblique

3-5 *Cryptolithus carinatus*

3. OU12031 (77-235) nearly complete, mostly exfoliated cranidium x3 a) dorsal b) anterior c) lateral d) oblique
4. OU12032 (I-35Well) nearly complete, mostly exfoliated cranidium x3 a) dorsal b) anterior c)lateral d) oblique
5. OU12033 (I-35Well) nearly complete, testate pygidium in dorsal view x5

6-7 *Cryptolithus* sp.

6. OU12034 (SB-2.1) nearly complete, testate cranidium x4 a) dorsal b) lateral c) anterior d) oblique e) glabella x8
7. OU12035 (SB-2.1) partially exfoliated pygidium in dorsal view x6

Ampyxina sp.

8. OU12036 (Nebo-Float) partially exfoliated, slightly weathered individual in dorsal view x6

Plate 4

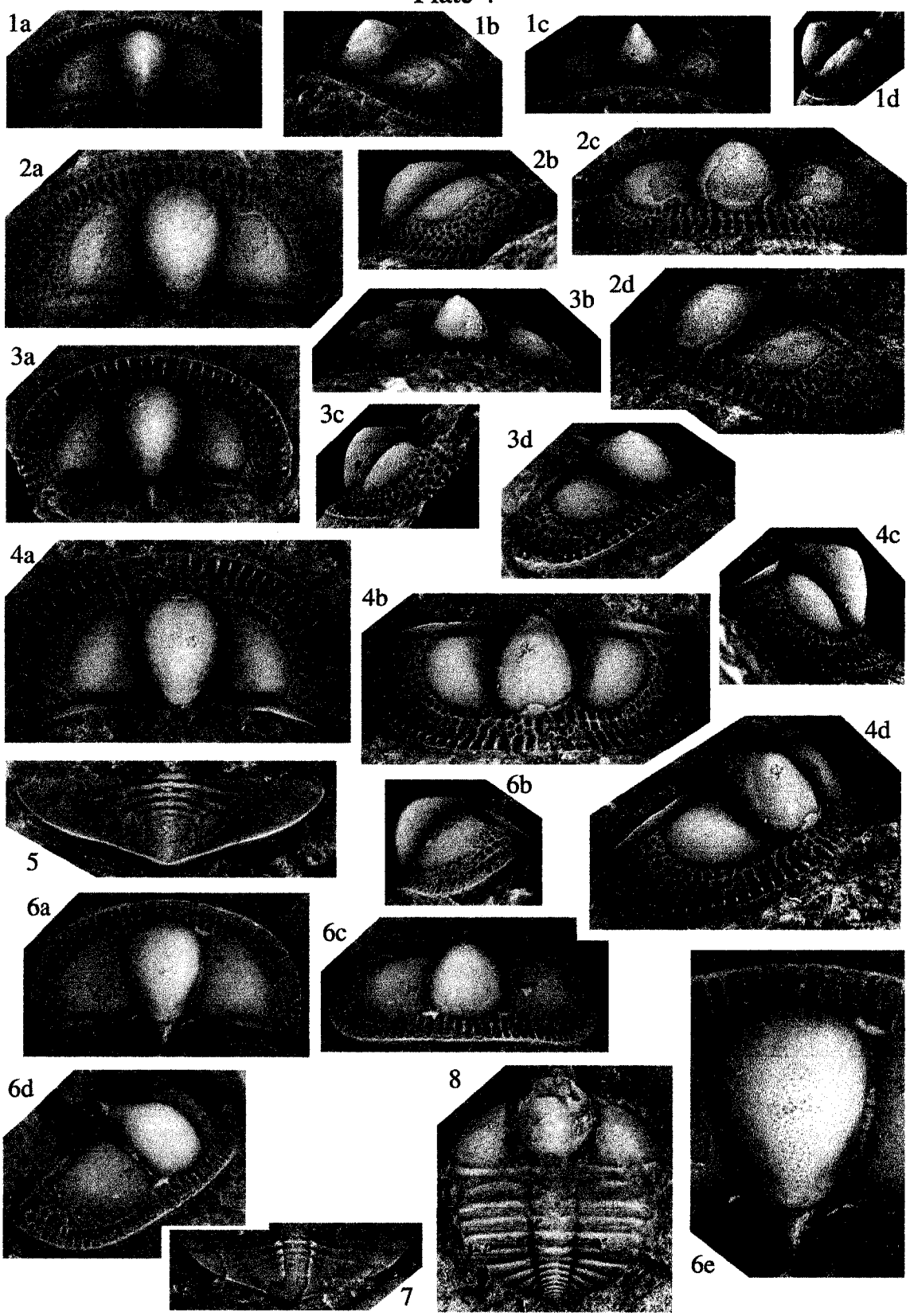


Plate 5 *Bumastoides billingsi, Failleana* sp., *Harpidella* new species

1-3, 5 *Bumastoides billingsi*

1. OU12037 (99-32) exfoliated cranidium x2.5 a) anterior b) maximum c) lateral d) palpebral
2. OU12038 (99-32) partly exfoliated librigena in lateral view x5
3. OU12039 (99-33) partially exfoliated pygidium x3 a) dorsal b) posterior c) lateral

4 *Failleana* sp.

4. OU12040 (LQ-WF) nearly complete, testate cranidium in dorsal view x2

5 *Bumastoides billingsi*

5. OU12041 (99-32) exfoliated pygidium with doublure excavated x3 a) dorsal b) posterior

6-8 *Harpidella* new species

6. OU12042 (LQ-MF) nearly complete, testate cranidiuim x12 a) dorsal b) anterior c) lateral d) oblique
7. OU12043 (LQ-LL) nearly complete, testate cranidium x12 a) anterior b) oblique c) dorsal
8. OU12044 (LQ-MF) testate librigena missing part of genal spine in dorsal view x12

Plate 5

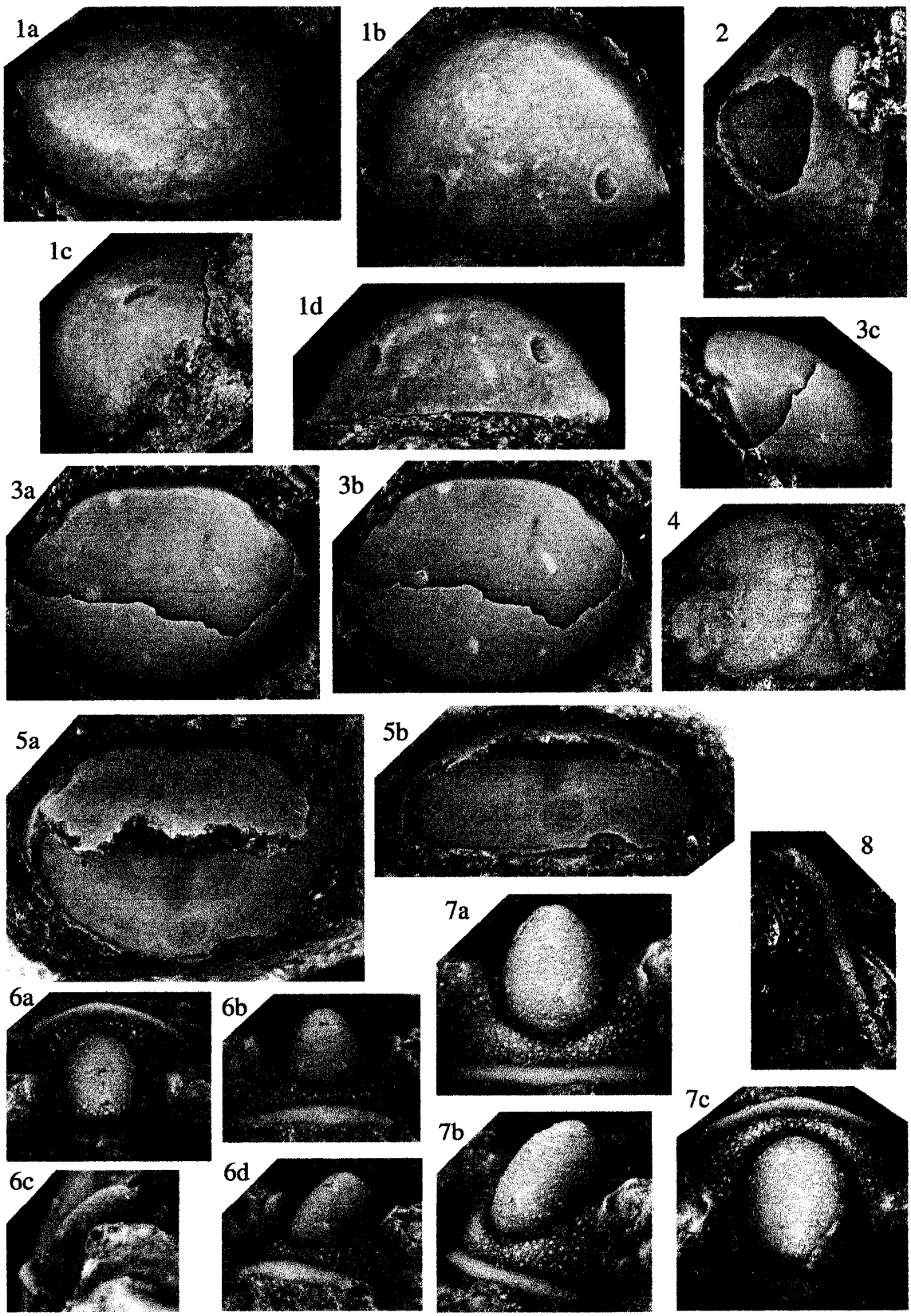


Plate 6 *Harpidella* new species, *Decoroproetus* new species

1-6 *Harpidella* new species

1. OU12045 (99-51) nearly complete, testate cranidium in dorsal view x15
2. OU12046 (99-39) nearly complete, testate cranidium x15 a) dorsal b) anterior
3. OU12047 (99-49.5) nearly complete, testate cranidium x12 a) dorsal b) anterior c) oblique
4. OU12048 (99-48) complete, testate librigena in dorsal view x15
5. OU12049 (LQ-MF) complete, testate librigena x12 a) dorsal b) lateral
6. OU12050 (99-48) small, complete, testate pygidium x18 a) dorsal b) lateral c) posterior

7-9 *Decoroproetus* new species

7. OU12051 (LQ-WF) partial, exfoliated cranidium x10 a) dorsal b) lateral c) anterior
8. OU12052 (LQ-WF) nearly complete, testate cranidium x10 a) dorsal b) glabella x20 c) anterior d) lateral e) oblique
9. OU12053 (LQ-WF) nearly complete, testate pygidium x10 a) posterior b) lateral c) dorsal

Plate 6

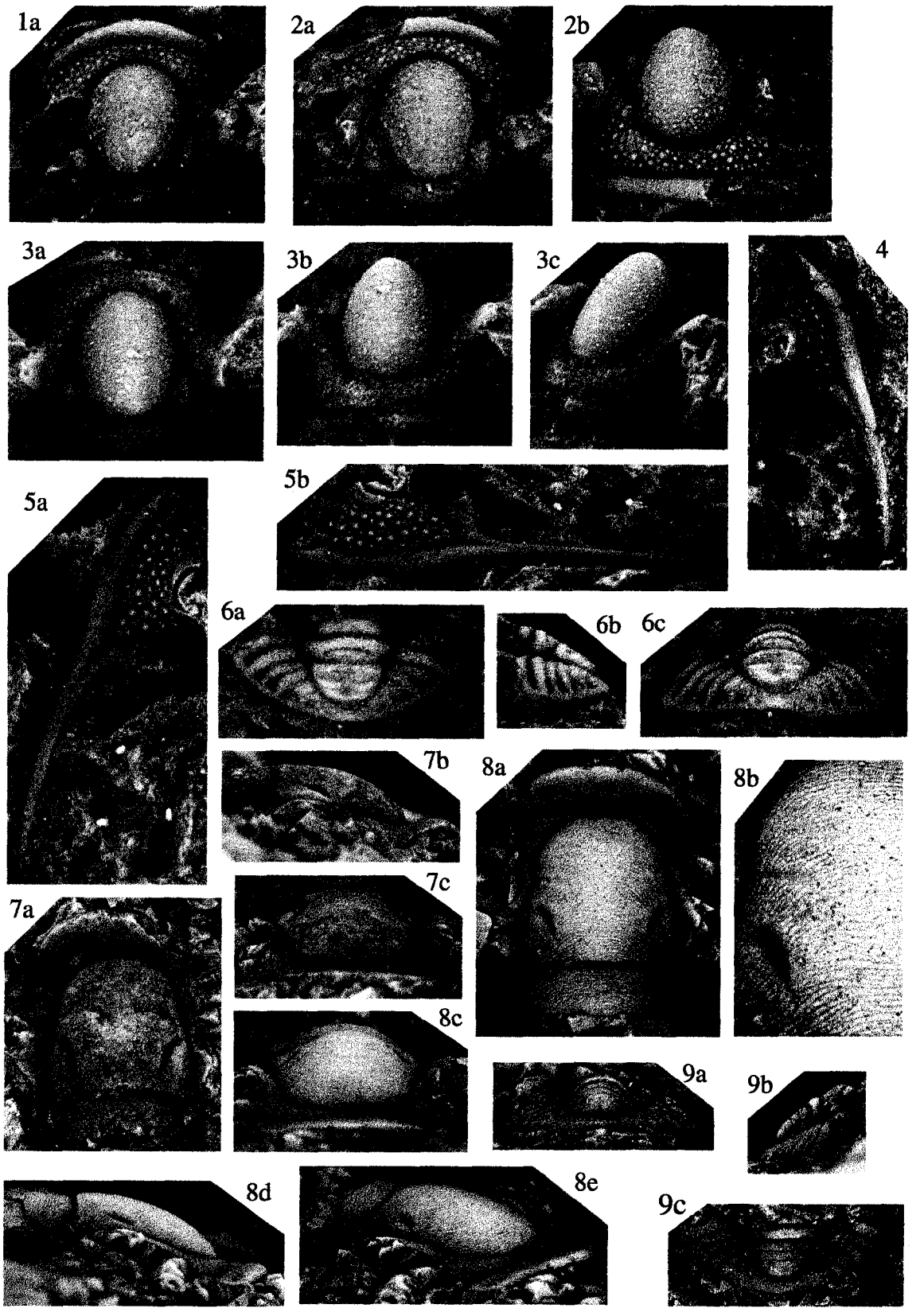


Plate 7 *Decoroproetus* new species, *Decoroproetus* sp., *Dimeropyge* cf. *D. virginiensis*, *Mesotaphraspis* new species

1-2 *Decoroproetus* new species

1. OU12054 (LQ-WF) nearly complete, testate librigena x8 a) dorsal b) lateral
2. OU12055 (LQ-WF) nearly complete, testate pygidium x10 a) dorsal b) posterior

3 *Decoroproetus* sp.

3. OU12056 (99-32) partial, mostly testate cranidium x12 a) anterior b) dorsal c) lateral d) oblique

4-6 *Dimeropyge* cf. *D. virginiensis*

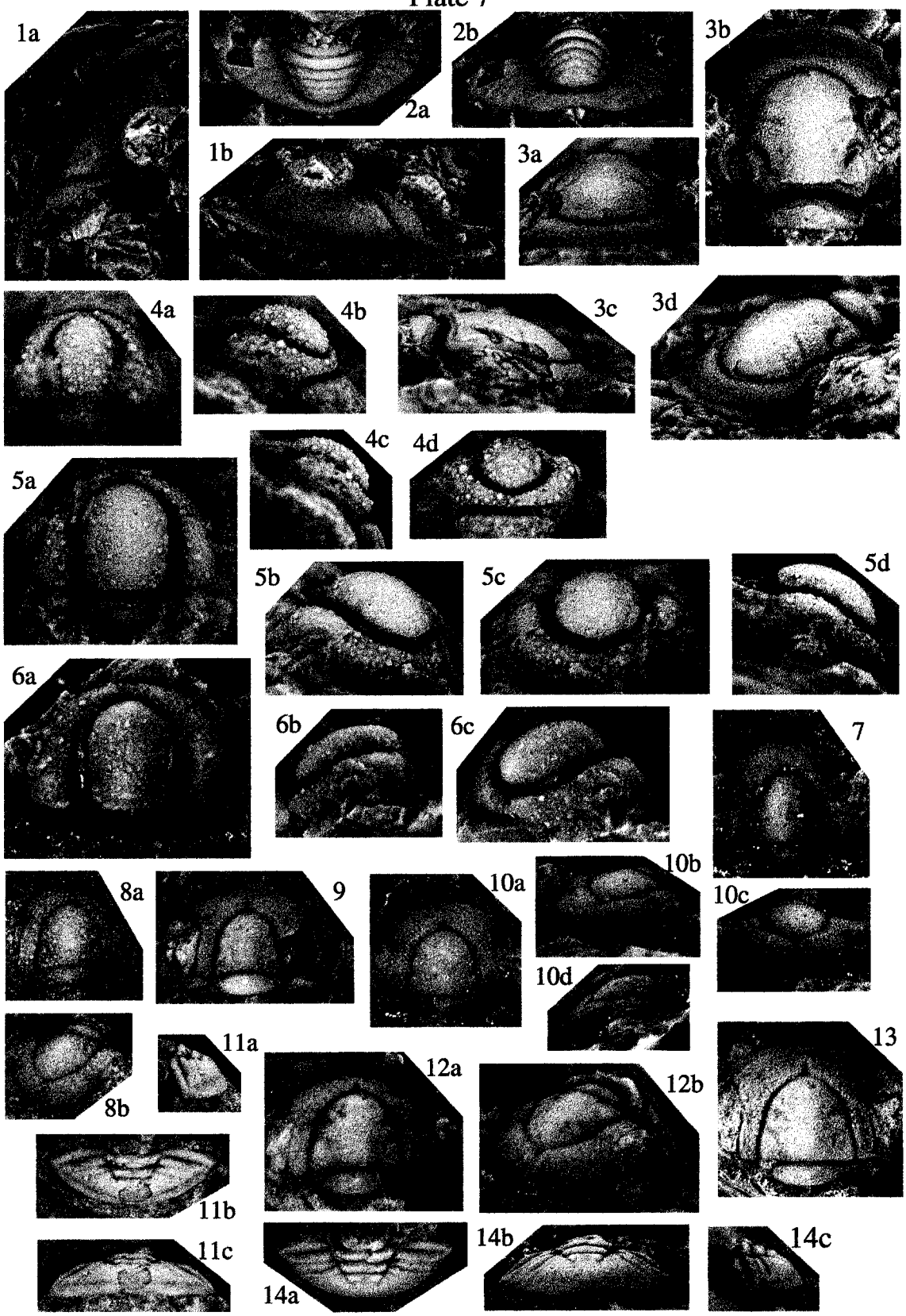
4. OU12057 (99-48) small, partial, testate cranidium x12 a) dorsal b) oblique c) lateral d) anterior
5. OU12058 (99-39) partial, testate cranidium x12 a) dorsal b) oblique c) anterior d) lateral
6. OU12059 (99-49.5) nearly complete, testate crandium x12 a) dorsal b) lateral c) oblique

7-14 *Mesotaphraspis* new species

7. OU12060 (99-38) partial, testate cranidium in dorsal view x12
8. OU12061 (99-48) small, partial, testate cranidium x16 a) dorsal b) oblique
9. OU12062 (99-48) partial, testate cranidium in dorsal view x14
10. OU12063 (99-48) partial, testate cranidium x12 a) dorsal b) oblique c) anterior d) lateral

11. OU12064 (LQ-MF) nearly complete, testate pygidium x12 a) lateral b) dorsal c) posterior
12. OU12065 (99-48) partial, testate cranidium x12 a) dorsal b) oblique
13. OU12066 (99-48) partial, testate cranidiuim in dorsal view x12
14. OU12067 (99-48) nearly complete, testate pygidium x12 a) dorsal b) posterior c) lateral

Plate 7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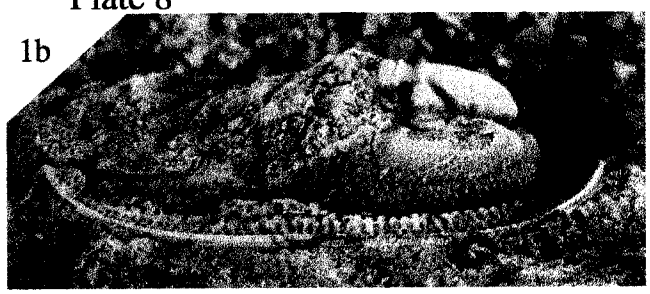
14c

Plate 8 *Dolichoharpes* cf. *D. uniserialis*

1. OU12068 (99-49) partial exfoliated cranidium x4 a) dorsal b) lateral
2. OU12069 (99-48) partial, exfoliated cranidiuim x2.5 a) lateral b) dorsal c) anterior d) lateral of glabellar ornament x8
3. OU12070 (99-48) partial, exfoliated cranidium x3 a) lateral showing palpebral lobe x6 b) anterior c) oblique d) lateral e) dorsal

Plate 8


1a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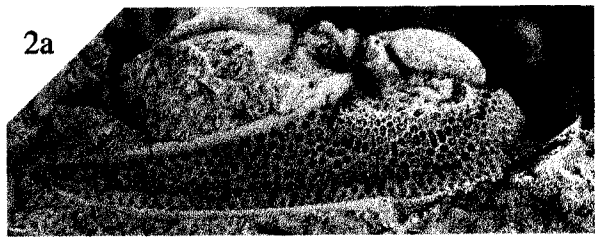
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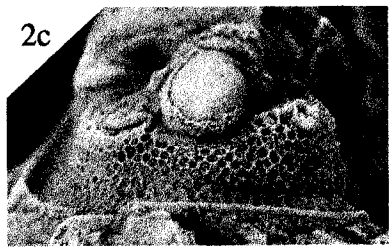
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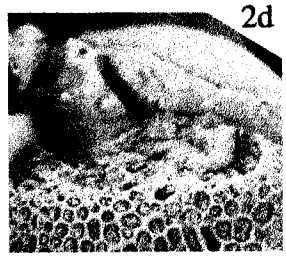
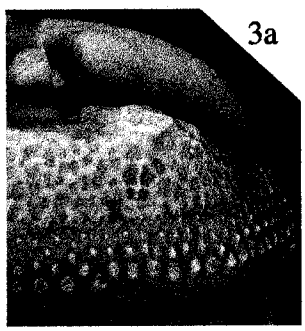

2d


2b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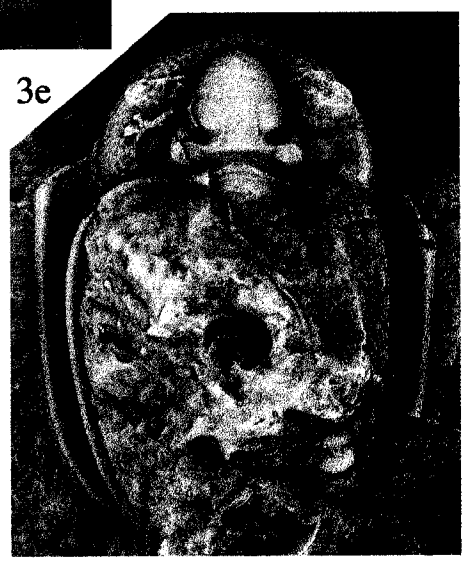
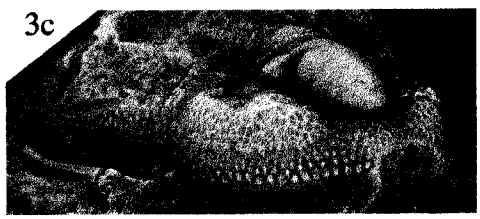
3b


3e


3c


3d

Plate 9 *Flexicalymene* sp. 1, *Flexicalymene* sp. 2, *Flexicalymene* sp. 3

1-3 *Flexicalymene* sp. 1

1. OU12071 (BQ-Pave) nearly complete, testate cranidium x3 a) dorsal b) lateral c) oblique d) anterior
2. OU12072 (BQ-Pave) partial hypostome in ventral view x6
3. OU12073 (BQ-Pave) complete, testate pygidium x3 a) posterior b) lateral c) dorsal

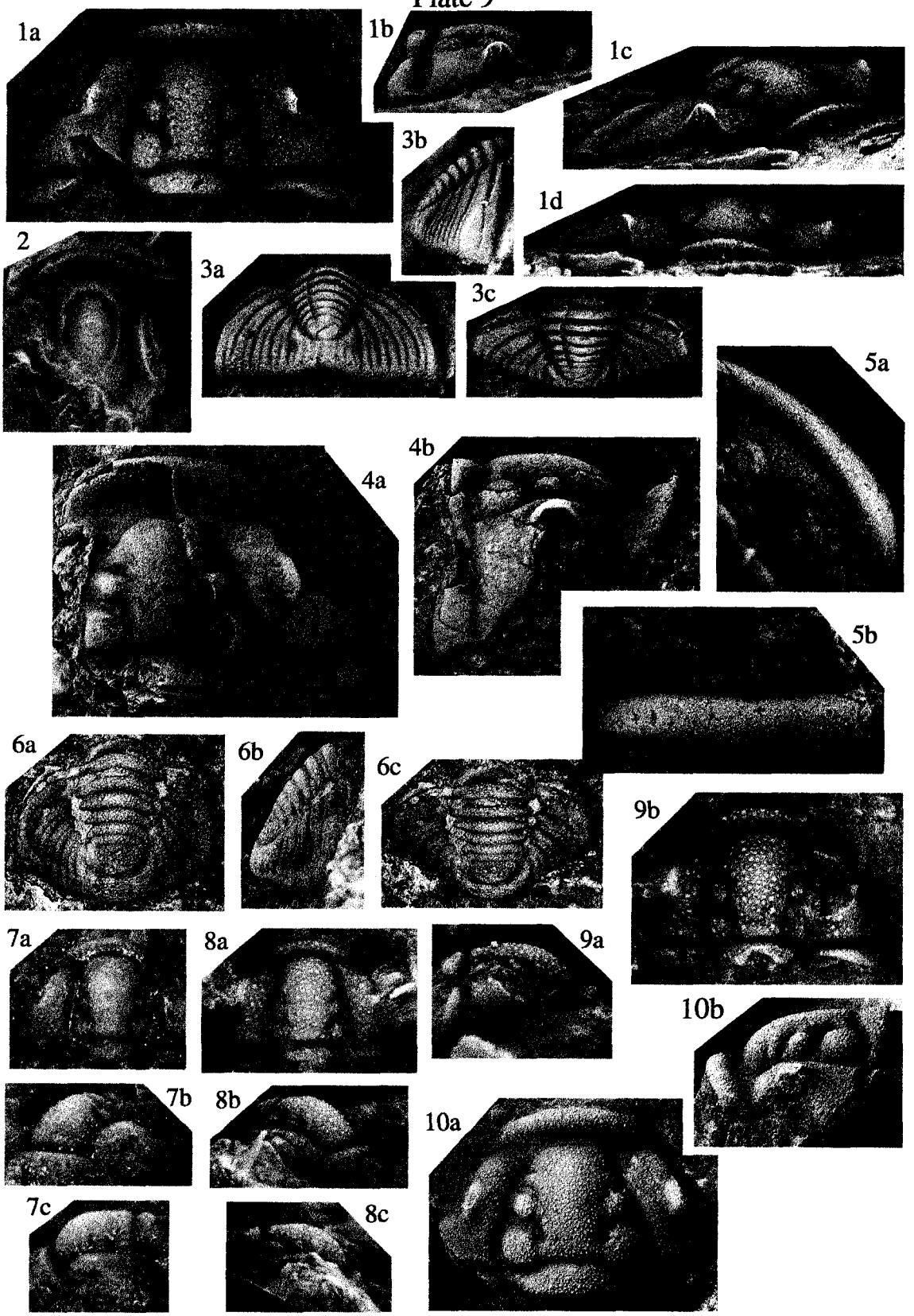
4-6 *Flexicalymene* sp. 2

4. OU12074 (99-39) partial, mostly exfoliated crandium x4 a) dorsal b) lateral
5. OU12075 (99-39) complete, testate librigena x6 a) dorsal b) lateral
6. OU12076 (99-39) complete, testate pygidium x7 a) posterior b) lateral c) dorsal

7-10 *Flexicalymene* sp. 3

7. OU12077 (99-51) small, partial, mostly exfoliated cranidium x12 a) dorsal b) oblique c) lateral
8. OU12078 (99-48) nearly complete, testate cranidium x12 a) dorsal b) oblique c) lateral
9. OU12079 (99-48) partial, testate cranidium x12 a) dorsal b) lateral
10. OU12080 (99-46.5) partial, testate crandium x5 a) dorsal b) lateral

Plate 9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8c
9a
9b
10a
10b

Plate 10 *Flexicalymene* sp. 3, *Flexicalymene* cf. *F. senaria*

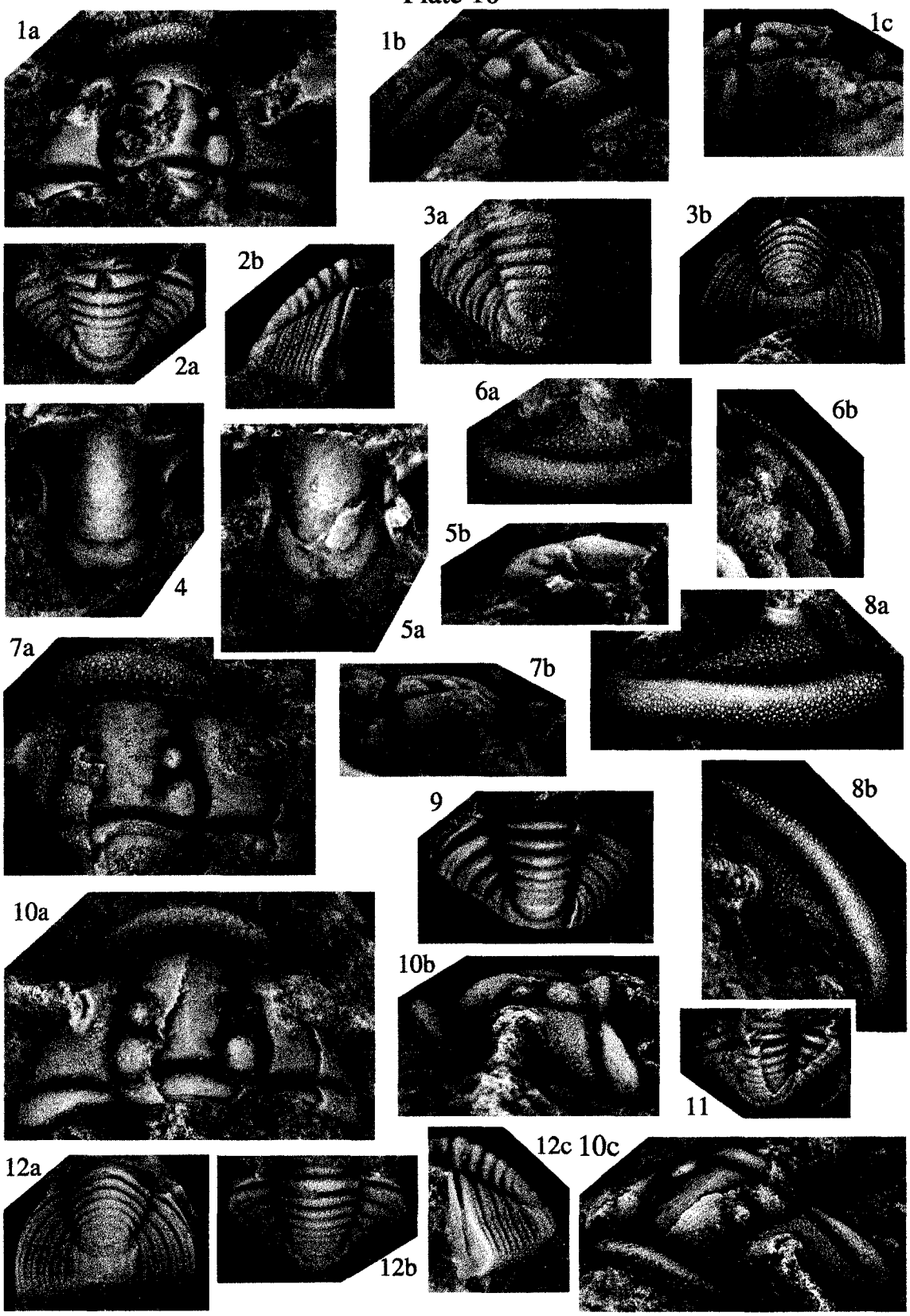
1-6 *Flexicalymene* sp. 3

1. OU12081 (99-48) partial, partially exfoliated cranidium x6 a) dorsal b) oblique c) lateral
2. OU12082 (99-48) nearly complete, testate pygidium x8 a) dorsal b) lateral
3. OU12083 (99-41) nearly complete, testate pygidium x5 a) dorsal b) posterior
4. OU12084 (99-48) partial, testate hypostome in ventral view x8
5. OU12085 (99-49.5) partial, mostly exfoliated hypostome x10 a) ventral b) lateral
6. OU12086 (99-49.5) small, complete, testate librigena x10 a) lateral b) dorsal

7-12 *Flexicalymene* cf. *F. senaria*

7. OU12087 99-51) partial, mostly exfoliated cranidium x6 a) dorsal b) lateral
8. OU12088 (99-51) complete, testate librigena x6 a) lateral b) dorsal
9. OU12089 (99-51) partial, mostly exfoliated pygidium in dorsal view x8
10. OU12090 (LQ-MF) nearly complete, partially exfoliated crandium x5 a) dorsal b) lateral c) oblique
11. OU12091 (LQ-MF) partial, partially exfoliated pygidium in dorsal view x8
12. OU12092 (LQ-LL) complete, testate pygidium x6 a) posterior b) dorsal c) lateral

Plate 10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9
8b
10a
10b
11
12a
12c
10c
12b

Plate 11 *Flexicalymene*?, *Flexicalymene* cf. *F. meek, Flexicalymene* cf. *F. limba*

1-2 *Flexicalymene*?

1. OU12093 (77-219) nearly complete, partly exfoliated cranidium x5 a) dorsal b) oblique c) lateral d) anterior
2. OU12094 (77-219) partial, mostly exfoliated cranidium in dorsal view x5

3-4 *Flexicalymene* cf. *F. meeki*

3. OU12095 (LQ-WF) partial, exfoliated cranidium x3 a) dorsal b) lateral c) oblique
4. OU12096 (LQ-WF) complete, testate librigena x3 a) dorsal b) lateral

5 *Flexicalymene*?

5. OU12097 (77-183) nearly complete, exfoliated pygidium x6 a) posterior b) dorsal

6 *Flexicalymene* cf. *F. meek*

6. OU12098 (LQ-WF) complete, testate pygidium x4 a) lateral b) dorsal c) posterior

7 *Flexicalymene* cf. *F. limba*

7. OU12099 (LQ-WF) partial, testate cranidium x3 a) dorsal b) anterior c) oblique d) lateral

Plate 11

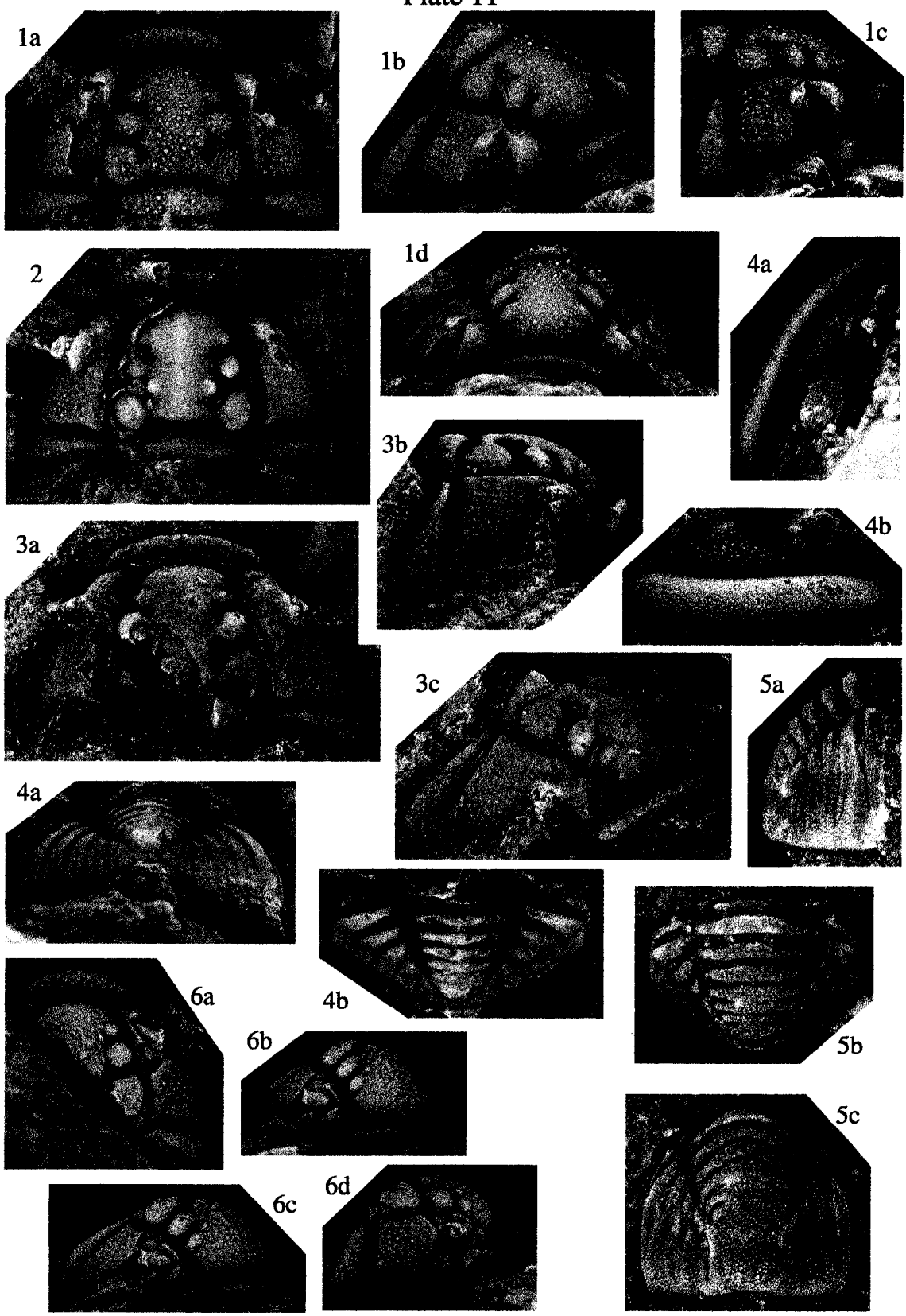


Plate 12 *Encrinuroides* cf. *E. capitonis, Calyptaulax* cf. *C. callirachis*

1-3 *Encrinuroides* cf. *E. capitonis*

1. OU12100 (99-48) partial, testate cranidium x6 a) dorsal b) anterior/dorsal
2. OU12101 (99-39) small, partial, testate cranidium in dorsal view x13
3. OU12102 (99-48) exfoliated pygidium x5 a) lateral b) posterior c) dorsal

4-9 *Calyptaulax* cf. *C. callirachis*

4. OU12103 (99-32) partial, mostly exfoliated cranidium x4 a) dorsal b) anterior c) lateral d) oblique
5. OU12104 (99-32) exfoliated cranidium x4 a) dorsal b) anterior c) lateral
6. OU12105 (99-32) exfoliated pygidium x4 a) posterior b) dorsal c) lateral
7. OU12106 (99-32) partial, exfoliated pygidium in dorsal view x4
8. OU12107 (99-32) nearly complete, exfoliated hypostome x5 a) ventral b) lateral
9. OU12108 (99-32) nearly complete, mostly exfoliated hypostome x6 a) ventral b) lateral

Plate 12

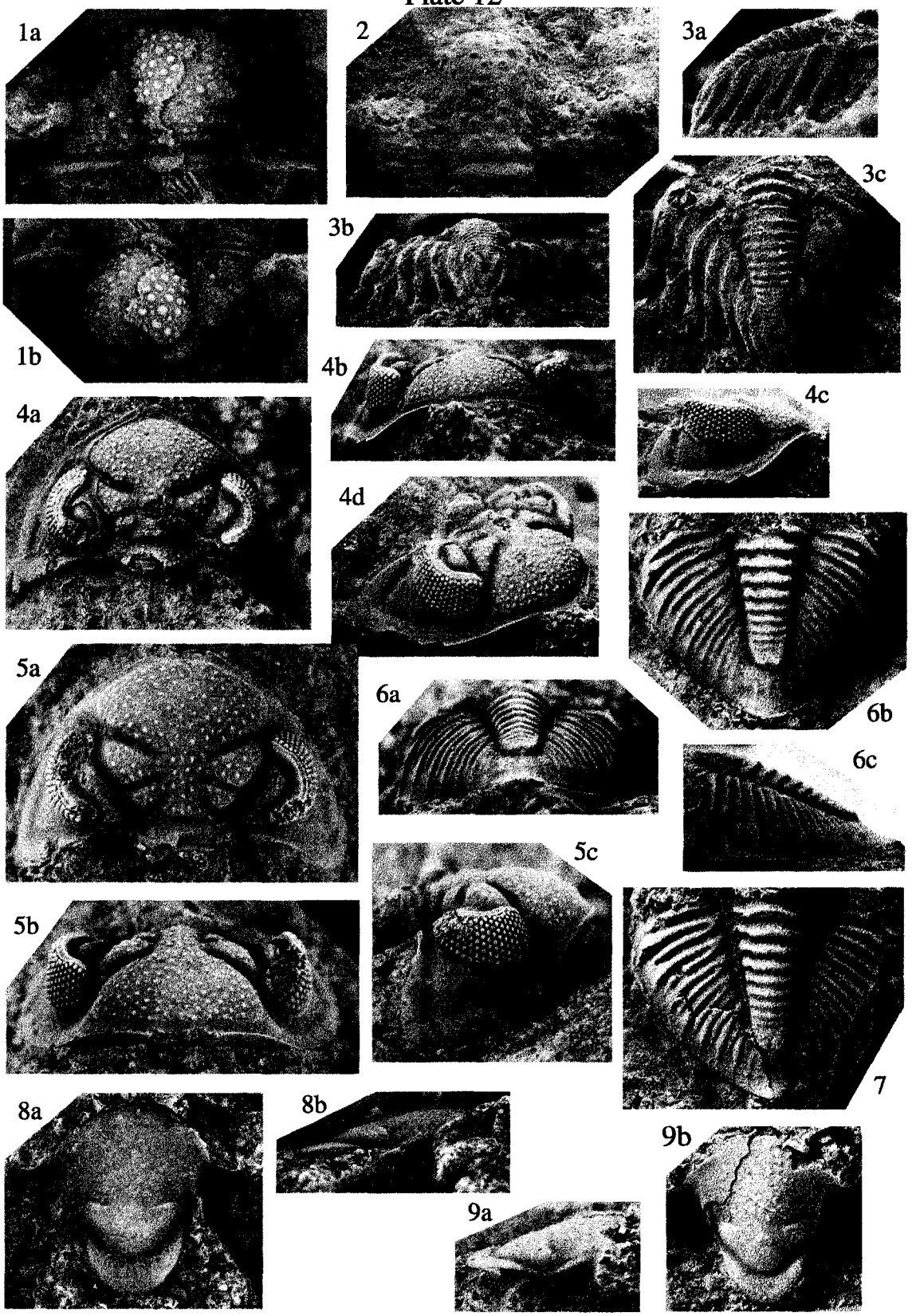


Plate 13 *Calyptaulax* cf. *C. strasburgensis*, *Calyptaulax* sp.

1-7 *Calyptaulax* cf. *C. strasburgensis*

1. OU12109 (99-41) nearly complete, exfoliated cranidium x4 a) dorsal b) oblique c) anterior d) lateral
2. OU12110 (99-48) partial, exfoliated cranidium in dorsal view x4
3. OU12111 (99-46.5) partial, exfoliated cranidium in dorsal view x4
4. OU12112 (99-Fl) nearly complete, exfoliated pygidium in dorsal view x4
5. OU12113 (99-41) partially exfoliated pygidium x4 a) dorsal b) posterior c) lateral
6. OU12114 (99-46.5) nearly complete, exfoliated hypostome in ventral view x4
7. OU12115 (99-57) nearly complete, testate pygidium x5 a) lateral b) dorsal c) posterior

8-11 *Calyptaulax* sp.

8. OU12116 (Nebo-Well) partial, exfoliated cranidium x3.5 a) dorsal b) anterior c) lateral
9. OU12117 (Nebo-Well) partial, exfoliated cranidium in dorsal view x4
10. OU12118 (Nebo-Well) partial, exfoliated cranidium in dorsal view x4
11. OU12119 (Nebo-Well) nearly complete, exfoliated pygidium x5 a) dorsal b) lateral c) posterior

Plate 13

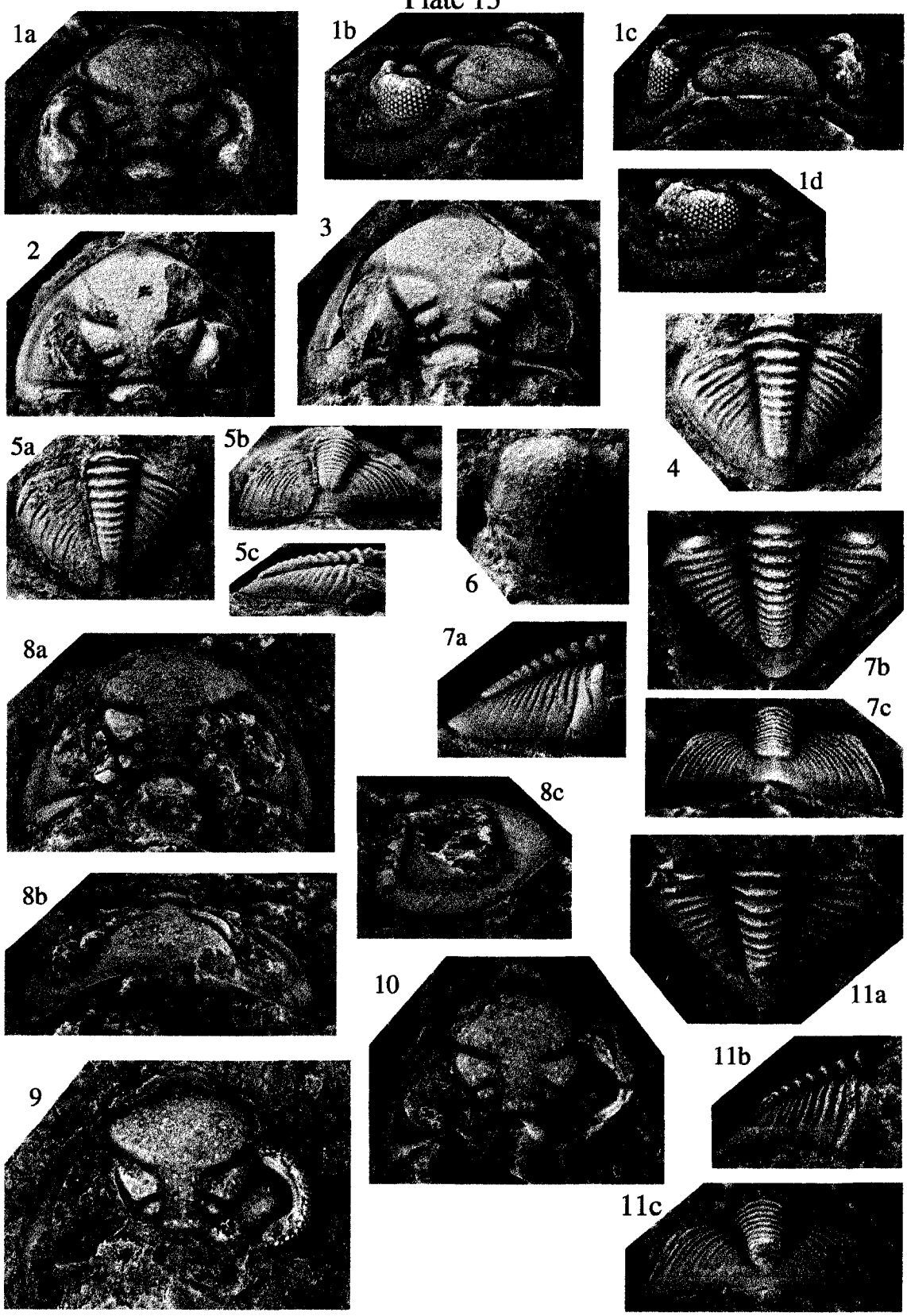


Plate 14 *Calyptaulax* sp. *Achatella* new species, *Sceptaspis* new species

1 *Calyptaulax* sp.

1. OU12120 (LQ-WF) complete, testate pygidium x6 a) dorsal b) posterior c) lateral

2-6 *Achatella* new species

2. OU12121 (99-51) partial, exfoliated cranidium x3.5 a) dorsal b) anterior c) lateral d) oblique
3. OU12122 (99-39) nearly complete, testate pygidium x6 a) posterior b) dorsal c) lateral
4. OU12123 (99-Float) cephalon missing genal spines, mostly exfoliated in dorsal view x3.5
5. OU12124 (LQ-8.3) cast of cranidium x3.5 a) dorsal b) anterior c) lateral/dorsal
6. OU12125 (99-49) nearly complete, testate pygidium in dorsal view x5

7-12 *Sceptaspis* new species

7. OU12126 (BQ-24) partial, exfoliated cranidium in dorsal view x4
8. OU12127 (BQ-24) partial, partly exfoliated pygidium in dorsal view x6
9. OU12128 (LQ-WF) cast of partial cranidium in dorsal view x5
10. OU12129 (BQ-24) partial, exfoliated cranidium in dorsal view x4
11. OU12130 (BQ-24) partial, exfoliated cranidium in dorsal view x6
12. OU12131 (BQ-24) partial, mostly exfoliated pygidium in dorsal view x4

Plate 14

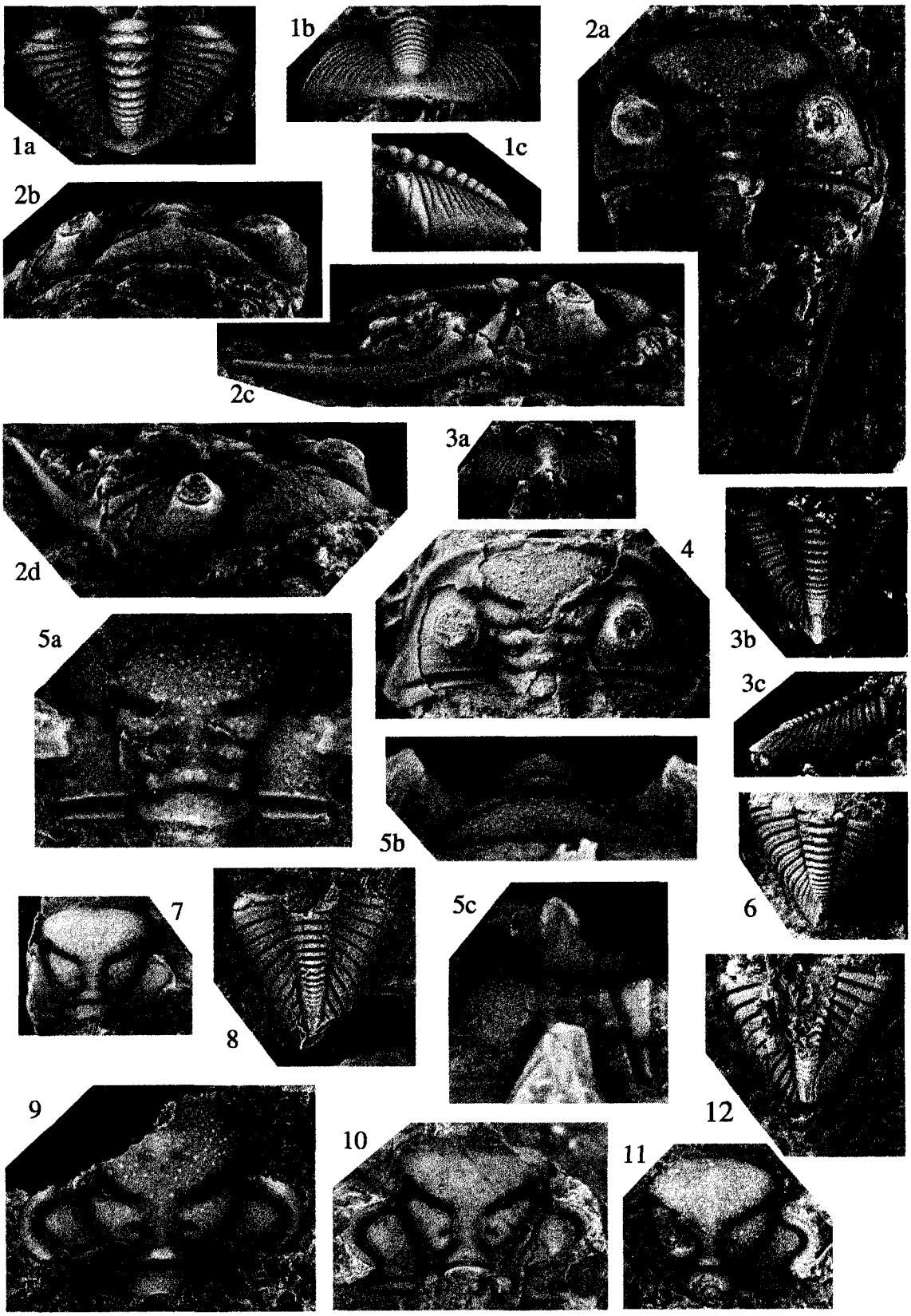


Plate 15 *Hemiarges* sp. 1, *Hemiarges* cf. *H. turneri*, *Hemiarges* sp. 2

1-2 Hemiarges sp. 1

1. OU12132 (99-30.25) testate cranidium x6 a) dorsal b) lateral c) anterior
2. OU12133 (99-30.25) partially exfoliated cranidium x8 a) dorsal b) oblique c) anterior

3-7 *Hemiarges* cf. *H. turneri*

3. OU12134 (99-39) exfoliated cranidium x8 a) dorsal b) lateral
4. OU12135 (99-39) hypostome in ventral view x8
5. OU12136 (99-39) exfoliated pygidium in dorsal view x4
6. OU12137 (99-46.5) partly exfoliated cranidium x8 a) dorsal b) anterior c) lateral d) oblique
7. OU12138 (LQ-MF) pygidiuim with broken axis in dorsal view x7

8 *Hemiarges* sp. 2

8. OU12139 (BQ-24) exfoliated pygidium in dorsal view x4

9-10 *Hemiarges* cf. *H. turneri*

9. OU12140 (LQ-MF) exfoliated cranidiuim x8 a) dorsal b) anterior c) oblique
10. OU12141 (99-46.5) partial cranidium in dorsal view x8

11 *Hemiarges* sp. 2

11. OU12142 (BQ-24) broken, partially exfoliated cranidium x6 a) dorsal b) oblique c) anterior

Plate 15

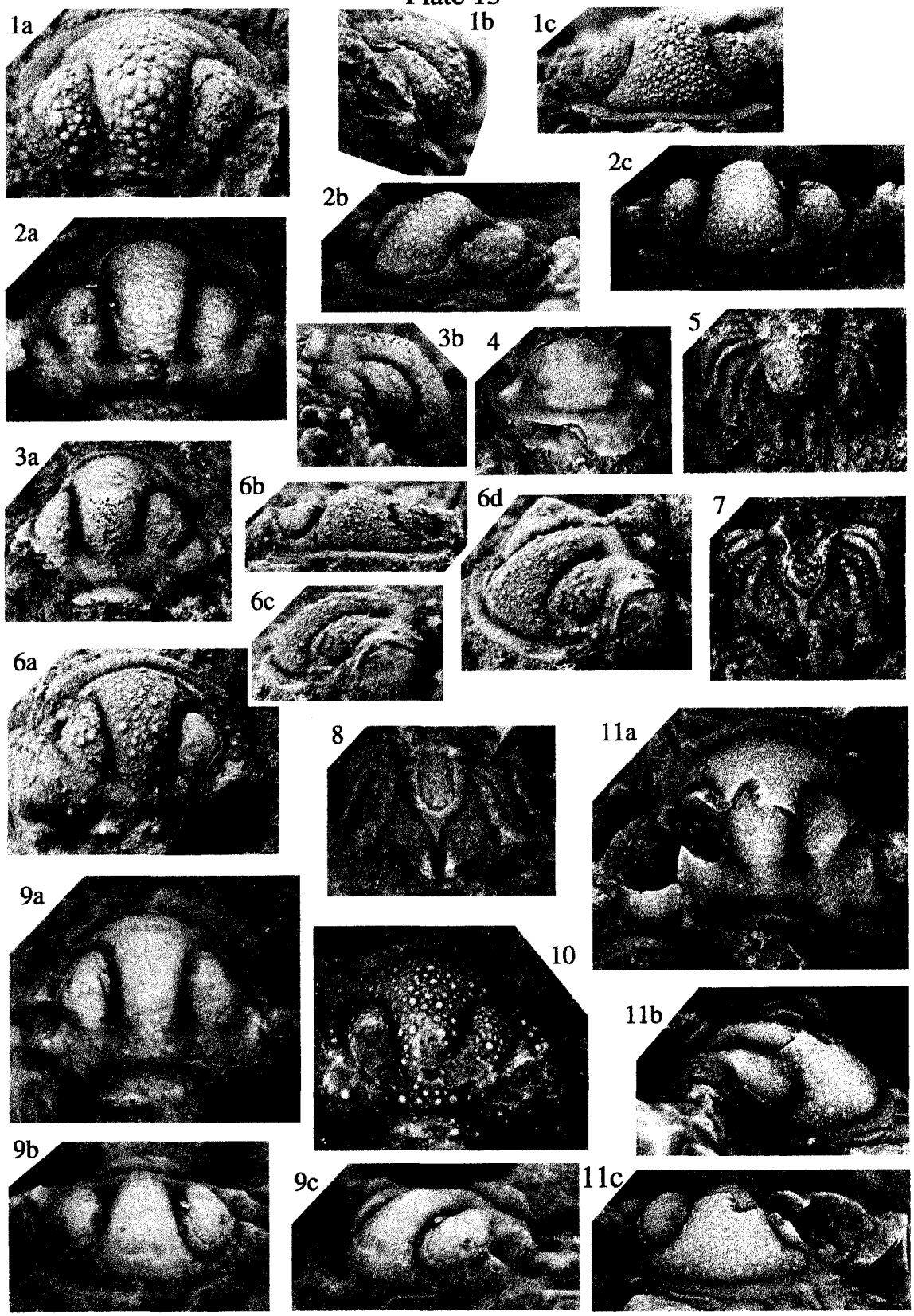


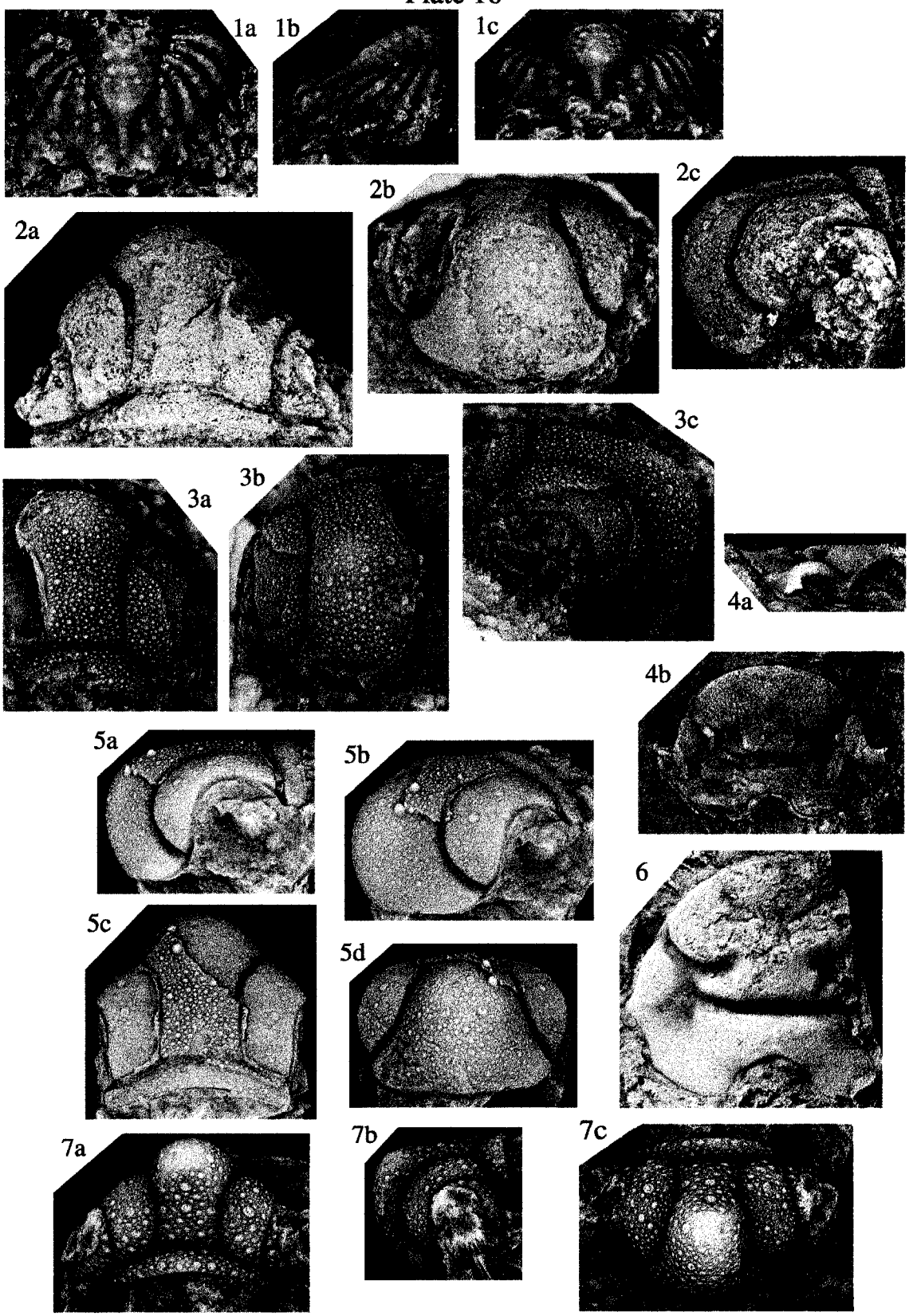
Plate 16 *Amphilichas* sp.

1. OU12143 (LQ-WF) pygidium x6 a) dorsal b) lateral c) posterior
2. OU12144 (99-39) weathered cranidium x2 a) dorsal b) anterior c) lateral
3. OU12145 (99-39) broken, mostly testate cranidium x4 a) dorsal b) anterior c) lateral
4. OU12146 (99-46.5) exfoliated hypostome x2 a) lateral b) ventral
5. OU12147 (99-41) broken, partly exfoliated cranidium x3 a) lateral b) oblique c) dorsal d) anterior
6. OU12148 (99-48) broken, exfoliated hypostome in ventral view x3

7 *Amphilichas* cf. *A. cucullus*

7. OU12149 (LQ-MF) nearly complete, testate cranidium x3 a) dorsal b) lateral c) anterior

Plate 16



APPENDIX:

TRILOBITE ABUNDANCE DATA

I collected trilobites from 11 sections in the Viola Group in south-central Oklahoma. Most specimens were collected by crack-out, and the stratigraphic occurrence of each collection was record. All identifiable trilobite specimens were collected and brought back to the lab at the Oklahoma Museum of Natural History, where they were prepared and counted. All sclerites of all trilobite species were recorded for each horizon that was collected, and abundances were determined using the maximum of cranidia or pygidia for each species. Total abundances for each species were added to obtain generic abundance.

TAXON	99-29	99-30.2	99-24	99-18	99-33to34	99-32	99-38to39	99-56to58	99-48	99-48to49	9941to46	LQ-VS
Ampyxina	0	0	0	0	0	0	0	0	0	0	0	0
Remopleuridid n. g.	0	0	0	0	0	0	0	0	0	0	0	0
Hypodicranotus	0	0	0	0	1	0	5	2	11	6	4	11
Trinodus	0	0	0	0	0	0	0	0	0	0	0	0
Pugilator	0	0	0	0	0	0	0	0	0	0	0	0
Cryptolithines	0	0	0	0	0	3	0	0	0	0	1	0
Decoroproetus	0	2	0	0	0	1	0	0	0	0	0	0
Flexicalymene	3	2	1	0	0	0	17	2	24	23	12	14
Cyphoproetus	0	0	0	0	0	0	0	0	0	0	0	0
Acanthoparypha	0	0	0	0	0	1	0	0	0	0	0	0
Pandaspinapyga	0	0	0	0	0	8	0	0	1	0	0	0
Thaleops	0	1	0	0	4	54	67	0	27	26	9	0
Bumastoides	12	28	56	43	40	167	0	0	0	0	0	0
Holia	0	5	0	0	2	7	0	0	0	0	0	0
Ceraurus	29	23	28	11	0	31	5	1	2	8	5	9
Isoteline	1	0	1	0	0	0	0	0	0	0	0	0
Isotelus	9	13	8	5	8	27	15	2	4	11	7	8
Faileana	0	0	0	0	0	0	0	0	0	0	0	0
Robergiella	0	0	0	0	0	0	0	0	0	0	0	0
Ectenaspis	0	0	0	0	0	0	0	0	0	0	0	0
Anataphrus	0	0	0	0	0	0	2	1	10	11	5	96
Sceptaspis	0	0	0	0	0	0	0	0	0	0	0	0
Eobronteus	0	0	0	0	0	0	0	0	0	0	0	10
Hemiarges	2	3	0	0	0	0	6	1	4	4	5	43
Achatella	0	0	0	0	0	0	3	1	2	2	7	3
Dimeropyge	0	0	0	0	0	0	7	0	11	11	3	0
Amphilichas	1	0	0	0	0	1	6	3	2	3	4	3
Sphaerocoryphe	0	0	0	0	3	0	56	13	17	13	12	7
Ceraurinella	0	0	0	0	1	0	1	4	3	5	1	1
Harpidella	0	0	0	0	0	2	8	11	37	9	10	15
Encrinuroides	0	0	0	0	0	1	2	2	4	4	4	0
Mesotaphraspis	0	0	0	0	0	0	3	1	9	6	3	0
Calyptaulax	0	2	0	0	5	53	3	7	36	30	19	13
Dolichoharpes	0	0	0	0	0	0	3	1	9	7	0	1
Stegnopsis	0	0	0	0	0	0	0	0	0	0	0	0

TAXON	NEBO-W	LQ-WF	LQ-LL13	BQ-24	77-218	CC	99-50to51	BF-36.5	BQ-PAVE	BF-27.5	BF-30.2	BF-32.8
Ampyxina	0	0	0	0	0	0	0	0	47	0	0	0
Remopleuridid n. g.	0	0	0	0	0	0	0	0	2	0	0	0
Hypodicranotus	0	4	4	0	0	0	2	0	17	0	0	0
Trinodus	0	0	0	0	0	0	0	0	2	0	0	0
Pugilator	0	0	0	0	0	0	0	0	7	0	0	0
Cryptolithines	0	0	0	0	6	0	8	12	65	19	24	44
Decoroproetus	0	4	0	0	0	0	0	1	0	1	3	0
Flexicalymene	0	3	4	0	3	0	16	46	18	18	13	25
Cyphoproetus	0	0	0	0	0	0	0	0	0	1	0	0
Acanthoparypha	0	0	0	0	0	0	0	0	0	0	0	0
Pandaspinapyga	0	0	0	0	0	0	0	0	0	0	0	0
Thaleops	0	0	0	0	0	0	2	0	0	0	0	0
Bumastoides	0	0	0	0	0	0	0	0	0	0	0	0
Holia	0	2	0	0	0	0	0	0	0	0	0	0
Ceraurus	0	8	0	8	0	0	3	21	2	12	9	10
Isoteline	0	0	0	0	0	0	0	0	0	0	0	0
Isotelus	8	8	9	3	13	1	4	1	0	2	7	0
Faileana	0	2	0	0	0	0	0	0	0	0	0	0
Robergiella	0	5	0	0	0	0	0	0	0	0	0	0
Ectenaspis	1	29	0	0	0	0	0	0	0	0	0	0
Anataphrus	24	76	42	150	159	68	2	0	6	0	0	0
Sceptaspis	0	3	0	9	0	0	0	0	0	0	0	0
Eobronteus	0	0	1	0	0	0	0	0	0	0	0	0
Hemiarges	0	12	4	4	0	0	3	0	0	0	0	0
Achatella	0	0	2	0	0	0	7	0	0	0	0	0
Dimeropyge	0	2	0	0	0	0	5	0	0	0	0	0
Amphilichas	0	0	1	0	0	0	1	0	0	0	0	0
Sphaerocoryphe	0	9	0	0	0	0	8	0	0	0	0	0
Ceraurinella	0	0	1	0	0	0	0	0	0	0	0	0
Harpidella	0	0	5	4	0	0	8	0	0	0	0	0
Encrinuroides	0	0	0	0	0	0	0	0	0	0	0	0
Mesotaphraspis	0	0	0	0	0	0	0	0	0	0	0	0
Calyptaulax	6	29	0	0	0	0	2	0	0	0	0	0
Dolichoharpes	0	0	2	0	0	0	0	0	0	0	0	0
Stegnopsis	6	39	0	0	8	0	0	0	0	0	0	0

TAXON	RBB	BF-31.1	77-181	I-35WEL	77-202	NEBO-Fld	THT-3.1	THT-2.4	NEBO-20+	NEBO-20-	77-24
Ampyxina	0	0	0	0	0	0	0	0	0	0	0
Remopleuridid n. g.	0	0	0	0	0	0	0	0	0	0	0
Hypodicranotus	0	0	0	0	0	4	0	0	0	2	0
Trinodus	0	0	0	0	0	1	0	0	2	0	0
Pugilator	0	0	0	0	0	20	0	0	5	2	2
Cryptolithines	27	154	33	17	27	59	69	221	49	59	41
Decoroproetus	0	4	0	0	0	0	0	0	0	0	0
Flexicalymene	8	54	1	0	0	0	9	1	0	0	0
Cyphoproetus	0	0	0	0	0	0	0	0	0	0	0
Acanthoparypha	0	0	0	0	0	0	0	0	0	0	0
Pandaspinapyga	0	0	0	0	0	0	0	0	0	0	0
Thaleops	0	0	0	0	0	0	0	0	0	0	0
Bumastoides	0	0	0	0	0	0	0	0	0	0	0
Holia	0	0	0	0	0	0	0	0	0	0	0
Ceraurus	6	27	0	0	0	0	6	1	0	0	0
Isoteline	0	0	0	0	0	0	0	0	0	0	0
Isotelus	3	9	11	3	6	0	7	20	0	0	0
Faileana	0	0	0	0	0	0	0	0	0	0	0
Robergiella	0	0	0	0	0	0	0	0	0	0	0
Ectenaspis	0	0	0	0	0	0	0	0	0	0	0
Anataphrus	0	0	4	4	15	2	0	0	0	1	3
Sceptaspis	0	0	0	0	0	0	0	0	0	0	0
Eobronteus	0	0	0	0	0	0	0	0	0	0	0
Hemiarges	0	0	0	0	0	0	0	0	0	0	0
Achatella	0	0	0	0	0	0	0	0	0	0	0
Dimeropyge	0	0	0	0	0	0	0	0	0	0	0
Amphilichas	0	0	0	0	0	0	0	0	0	0	0
Sphaerocoryphe	0	0	0	0	0	0	0	0	0	0	0
Ceraurinella	0	0	0	0	0	0	0	0	0	0	0
Harpidella	0	0	0	0	0	0	0	0	0	0	0
Encrinuroides	0	0	0	0	0	0	0	0	0	0	0
Mesotaphraspis	0	0	0	0	0	0	0	0	0	0	0
Calyptaulax	0	0	0	0	0	0	5	0	0	0	0
Dolichoharpes	0	0	0	0	0	0	0	0	0	0	0
Stegnopsis	0	0	11	2	0	0	0	0	0	0	0

Plate 10 *Pandaspinapyga projecta*, "*Pandaspinapyga*" sp. 1, Acanthoparyphine indet.

Pandaspinapyga projecta

1. UC28950, exfoliated left half of glabella and part of fixigena x5 a) dorsal b) anterior c) lateral d) oblique

"*Pandaspinapyga*" sp. 1

2. OU11991 (99-32), exfoliated glabella x7 a) dorsal b)anterior/dorsal c) anterior d) lateral
3. OU11992 (99-32), exfoliated glabella x4 a) dorsal b) lateral c) anterior
4. OU11993 (99-32) broken, exfoliated pygidium in dorsal view x3

Acanthoparyphine indet.

5. OU11994 (LQ-WF), nearly complete, testate cranidium x6 a) dorsal b) lateral c) anterior d) oblique
6. OU11995 (LQ-WF), testate cranidium missing one fixigena x10 a) dorsal b) anterior c) oblique d) lateral