

**PATTERNS OF FAUNAL CHANGE AT AN UPPER CAMBRIAN
TRILOBITE EXTINCTION EVENT, NOLICHUCKY FORMATION,
TENNESSEE AND VIRGINIA**

by

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ABSTRACT

During the Upper Cambrian there were three mass extinctions, each of which eliminated at least half of the trilobite families living in North American shelf seas. The Nolichucky Formation preserves the record of one of these extinction events at the base of the Steptoean Stage.

Sixty-six trilobite collections were made from five sections in Tennessee and Virginia. The lower Steptoean faunas are assigned to one low diversity, *Aphelaspis*-dominated biofacies, which can be recognized in several other parts of North America. In Tennessee, the underlying upper Marjuman strata contain two higher diversity biofacies, the *Coosella-Glaphyraspis* Biofacies and the *Tricrepicephalus*-Norwoodiid Biofacies. At least four different biofacies are present in other parts of North America: the *Crepicephalus* -*Lonchocephalus* Biofacies, the *Kingstonia* Biofacies, the *Cedaria* Biofacies, and the *Uncaspis* Biofacies.

A new, species-based zonation for the Nolichucky Formation includes five zones, three of which are new. These zones are the *Crepicephalus* Zone, the *Coosella perplexa* Zone, the *Aphelaspis buttsi* Zone, the *A. walcotti* Zone and the *A. tarda* Zone.

The Nolichucky Formation was deposited within a shallow shelf basin and consists largely of subtidal shales with storm-generated carbonate interbeds. A relative deepening is recorded

in the Nolichucky Formation near the extinction, and is indicated in some sections by the appearance of shale-rich, distal storm deposits above a carbonate-rich, more proximal storm deposit sequence. A comparable deepening-upward sequence occurs near the extinction in the Great Basin of southwestern United States and in central Texas, and this suggests a possible eustatic control.

In other parts of North America, the extinction is recorded in a variety of environmental settings that range from near-shore to slope. In shelf environments, there is a marked decrease in diversity, and a sharp reduction in biofacies differentiation. Although extinctions do take place in slope environments, there is no net reduction in diversity because of the immigration of several new taxa.

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CHAPTER 1

INTRODUCTION

During the Upper Cambrian, there were three mass extinctions (i.e., bioturbation events), each of which eliminated at least 50% of the trilobite families living in North American shelf seas (Palmer 1965b; Stitt 1971, 1977; Westrop and Ludvigsen 1987). This study will examine the pattern of extinction and the changes in trilobite biofacies at one of these events (Marjuman-Steptoean Stage boundary) in Tennessee and Virginia, and the paleoenvironmental constraints on these faunas. Analysis of the Upper Cambrian extinction events has been extensive (e.g., Palmer 1965b, 1984; Stitt 1971, 1977; Westrop and Ludvigsen 1987; Thomas 1995). Most of these earlier studies have ignored the large-scale facies relationships of these events (Palmer 1965b, 1984; Stitt 1971, 1977) and have usually concentrated only on a few meters of section immediately adjacent to the extinction event (Palmer 1984). Biofacies changes associated with the extinctions have been studied only for the late Sunwaptan event (Westrop and Ludvigsen 1987). Explanations for the extinction events have included such factors as changes in oxygen levels or decreases in temperature (Palmer 1979, 1984, Stitt 1971, 1977). However, no consensus has been reached on the mechanisms causing the extinctions.

The trilobites of the Upper Cambrian Nolichucky Formation were originally studied by Resser (1938), and more recently

examined in their stratigraphic framework by Rasetti (1965) in Tennessee, and by Derby (1966) in Virginia. All of these previous studies have concentrated on the systematics, but no attention was paid to the facies relationships and the patterns of extinction across the Marjuman-Steptoean boundary. This thesis does not deal with the systematics of the trilobites of the Nolichucky Formation (see Rasetti, 1965 for the most recent treatment), although species synonymies are included in Appendix I. The sedimentology of the Nolichucky Formation has been well established in recent work by Markello and Read (1981, 1982).

This study will examine the facies relationships, biofacies and biostratigraphy across the Marjuman-Steptoean boundary in the Nolichucky Formation. The spatial and temporal relationships of the trilobites will be examined to produce a detailed zonation for correlation with strata across North America. This information will also be used to document faunal changes in the extinction interval in the southern Appalachians and comparisons will be made with other localities across North America.

Field work was carried out in the summer of 1992. Three sections were measured and collected in northeastern Tennessee and two sections were measured and collected in southwestern Virginia (Fig. 1).

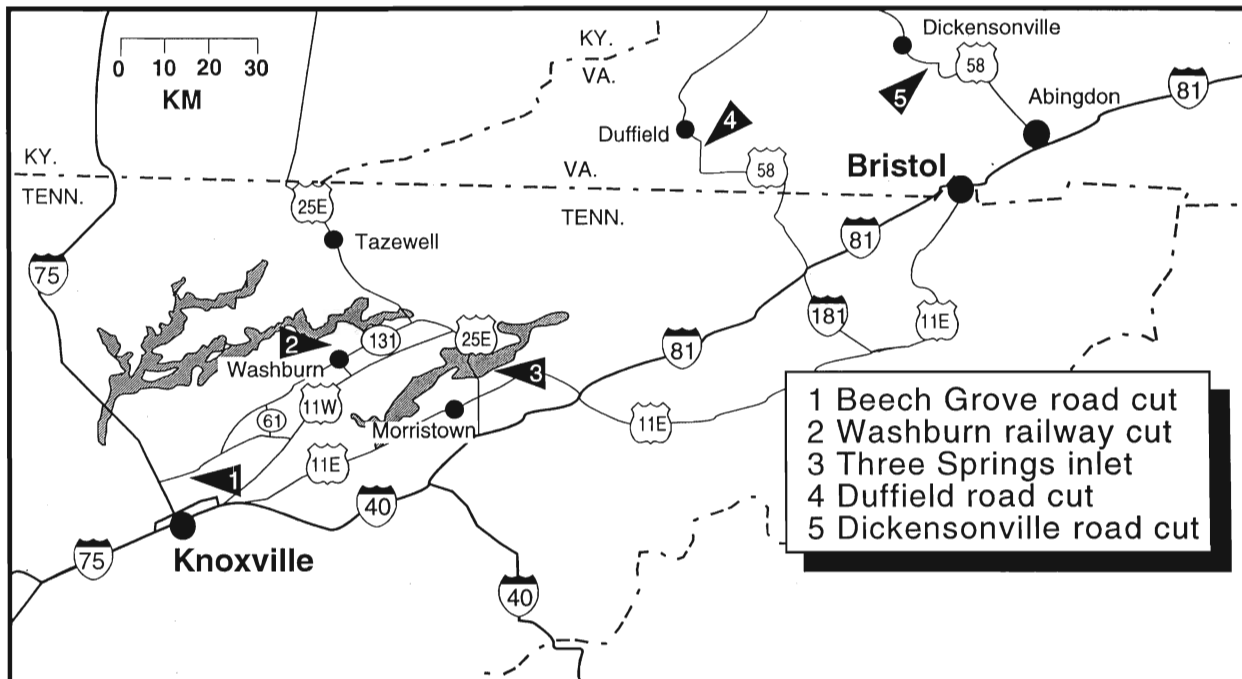


Figure 1- Location of sections used in this study.

CHAPTER 2

STRATIGRAPHIC AND PALAEOENVIRONMENTAL SETTING

Introduction

The southern Appalachians of the eastern United States include some of the best exposures of Paleozoic rocks in eastern North America. The lithostratigraphy of the Cambrian and Ordovician sequence has received considerable attention over the last fifteen years, primarily from J.F. Read and his students in Virginia and K. Walker and his students in Tennessee (e.g., Markello and Read 1981, 1982; Koerschner and Read 1989; Kozar *et al.*, 1990; Walker *et al.*, 1990; Foreman *et al.*, 1991; Osleger and Read 1991; Srinivasan and Walker 1993). They emphasised the cyclic alteration of thick, shale-dominated and carbonate-dominated intervals (Hasson and Haase 1988), which is similar to the grand cycles described from the southern Canadian Rocky Mountains (Aitken 1966, 1978; Westrop 1989a). Each of these grand cycles comprises a lower, recessive, shaly half-cycle that passes graditionally upward into a resistant, carbonate half-cycle (Aitken 1966, 1978). The latter is abruptly overlain, in turn, by the shaly half-cycle of the succeeding grand cycle. According to Aitken (1966, 1978), each grand cycle was terminated by the flooding of the carbonate bank and this led to deposition of the shaly half-cycle. The carbonate half-cycle reflects subsequent recovery and progradation of the carbonate bank (Aitken 1966, 1978; Westrop 1989a).

Stratigraphic setting

The study area (Figs. 2 and 3) lies in the northeast - southwest trending Valley and Ridge Province of the Appalachian Mountains (Palmer 1971; Markello and Read 1981, 1982; Hatcher 1987; Hasson and Haase 1988). The rocks are exposed in imbricate thrust sheets that moved from the southeast to the northwest (Markello and Read 1981, 1982; Hasson and Haase 1988). The Nolichucky Formation (Campbell 1894; Markello and Read 1981, 1982; Hasson and Haase 1988) is a shale and limestone unit that interfingers with Elbrook-Honaker-Maryville carbonates both to the northeast (along strike) and to the southeast (toward the regional shelf edge). These units rest on the Lower Cambrian Rome Formation and are overlain by the Upper Cambrian Copper Ridge-Conococheague formations (Markello and Read 1981, 1982; Hasson and Haase 1988).

The Nolichucky Formation is made up of interfingering shale-and limestone-dominated members: the Lower Shale Member, the Bradley Creek Limestone Member and the Upper Shale Member (Hasson and Haase 1988). This study deals primarily with the Bradley Creek Limestone Member and the Upper Shale Member. The Lower and Upper Shale members have been used informally (Markello and Read 1981, 1982; Hasson and Haase 1988), and both contain shales and siltstones interbedded with coarse- and fine-grained carbonates. The Bradley Creek

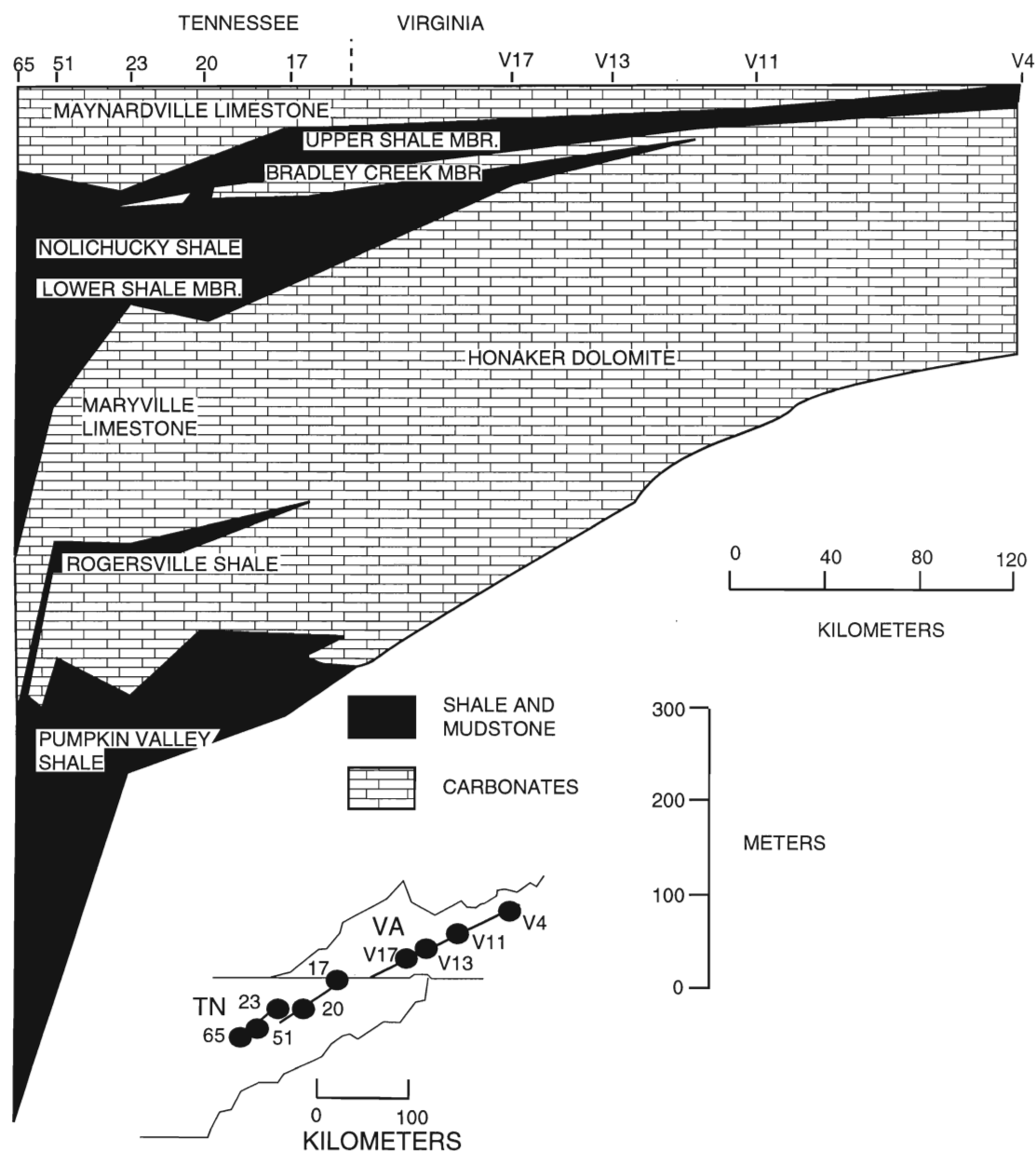


Figure 2- Section along strike through the Nolichucky Formation, showing the Lower Shale Member, the Bradley Creek Limestone Member, and the Upper Shale Member (modified from Hasson and Haase 1988).

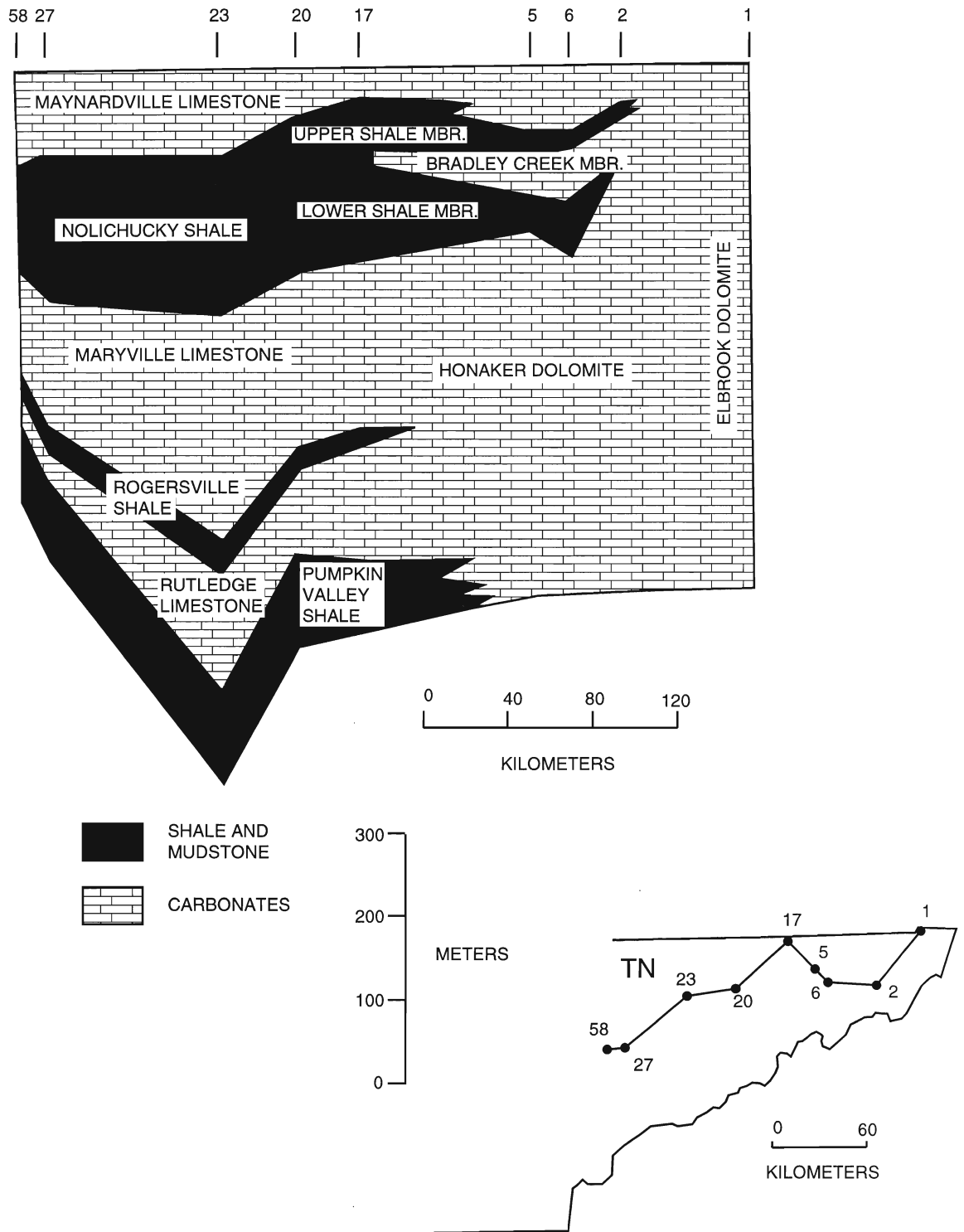


Figure 3- Section across strike through the Nolichucky Formation, showing the Lower Shale Member, the Bradley Creek Limestone Member and the Upper Shale Member (modified from Hasson and Haase 1988).

Limestone Member varies across the study area, and consists of thick thrombolitic buildups or bioclastic rudstones to packstones.

The general environment of the Nolichucky Formation is that of an intrashelf basin on a carbonate-rimmed miogeocline (Palmer 1971; Markello and Read 1981, 1982; Hasson and Haase 1988; Fig. 4). The intrashelf basin was bordered along strike and toward the regional shelf edge by a rim of peritidal carbonates and by near-shore clastics toward the craton (Markello and Read 1982). The peritidal carbonates passed into the intrashelf basin by way of a gently sloping carbonate ramp (Markello and Read 1981, 1982). The regional carbonate shelf passed south-east into deep water pelitic sediments of the Piedmont (Markello and Read 1981). The regional shelf has been compared to an Atlantic-type continental shelf (Markello and Read 1981).

The intra-shelf basin appears to be located over a persistent Cambrian-Ordovician depocentre which later evolved into a deep foreland basin in the Middle Ordovician (Markello and Read 1981). The Nolichucky basin appears to have many similarities to the 'inshore basins' described from the Cambrian of western Canada, and the Great Basin of the western United States (Aitken 1978), many of which were sites of fine clastic deposition and were bounded on their seaward side by shallow-water carbonates (Markello and Read 1981). Hasson and Hasse (1988) have examined the basin topography for the Nolichucky Formation in Tennessee and have identified a region of particular high

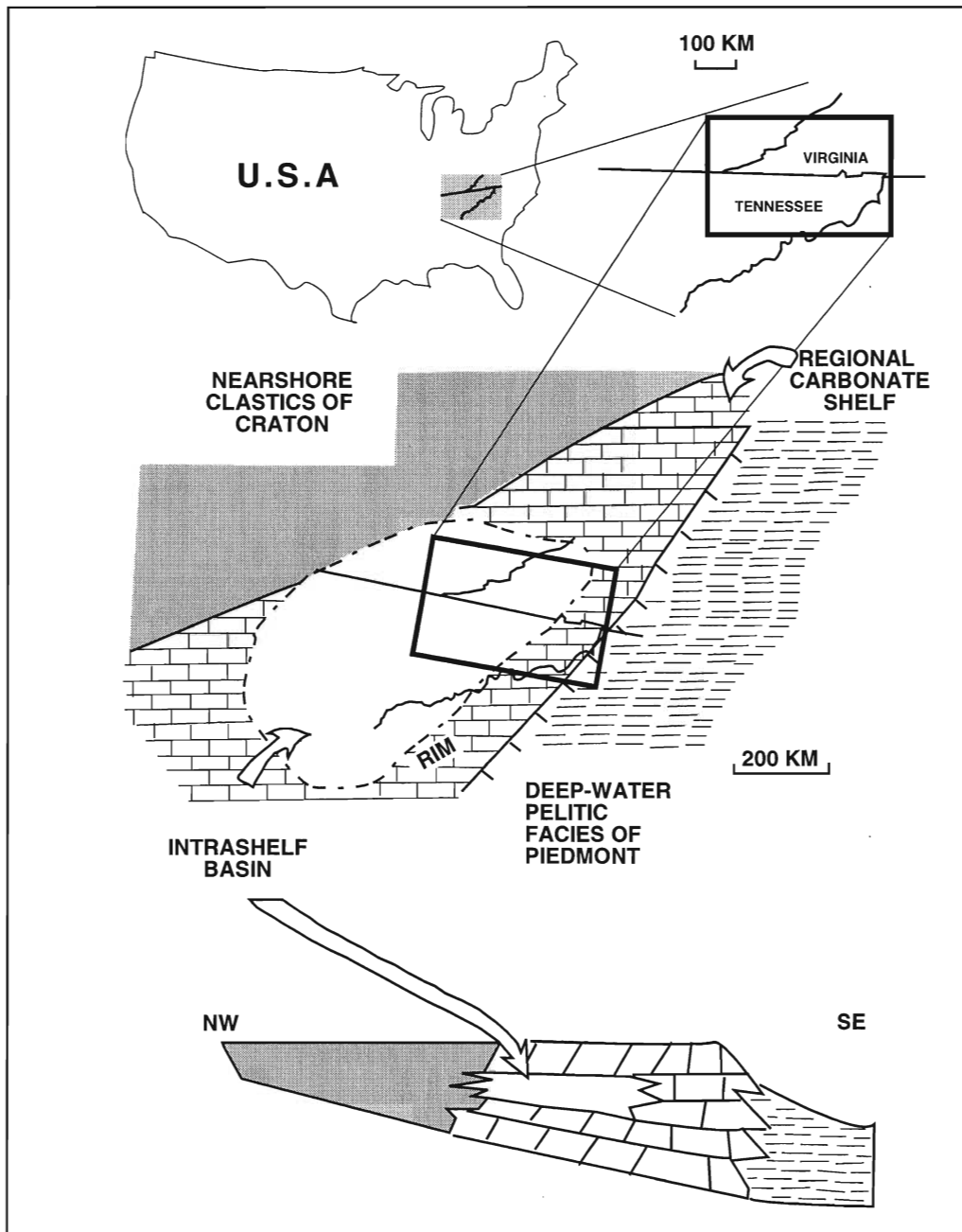


Figure 4- Late Cambrian regional palaeogeography of the southern Appalachians showing the Nolichucky intrashelf basin in the regional carbonate shelf (modified from Markello and Read 1981).

subsidence, the Luttrell Sub-Basin, that was in the centre of the basin.

The transition from peritidal shelf carbonates into the Nolichucky basin facies appears to have many of the characteristics of a carbonate ramp. The slope was extremely low, which inhibited the development of gravity flows, but instead favoured storm-generated sequences over wide areas (Markello and Read 1981). Secondly, grainstones developed in up-dip positions peripheral to the peritidal facies, and linear build-up trends are absent (Markello and Read 1981). Facies that comprise the transition from shelf to basin include oncoid and ooid grainstones, "ribbon carbonates" (nodular bioclastic limestones with fining upward layers and dolomitized layers) of the deep ramp, and limestone conglomerates and siltstones of the shallow basin (Markello and Read 1981).

The thin conglomerate, siltstone and shale sequences of the Nolichucky Formation appear to be largely storm-generated sequences that formed in relatively shallow (above storm wave base) settings on a gently sloping ramp and in the shallow intrashelf basin (Markello and Read 1981). Although these facies may be superficially similar to those of tidal-flat deposits, they lack features typical of emergence and show abundant evidence of deposition below fair-weather wave base (Markello and Read 1981).

Sedimentary Facies

Introduction

A detailed study of the sedimentology of the Nolichucky Formation is unnecessary because of the recent work that has been published by Markello and Read (1981, 1982) and Hasson and Haase (1988). However, observations made during the course of field work do allow the facies to be described and provide the palaeoenvironmental context for the discussion of the faunal changes.

The Nolichucky Formation is divided into three basic lithofacies, which are distributed among two recurrent facies associations; individual lithofacies may occur in more than one association. The descriptive terminology for these carbonate rocks follows Embry and Klovan (1971). The lithofacies and their associations are adapted from Westrop (1989a).

Description of Lithofacies

Medium to dark grey calcareous mudstones and shales

-This is the most common lithofacies in the Lower and Upper Shale members of the Nolichucky Formation (Fig. 5). It has been described previously from Virginia by Markello and Read (1981), and very similar shales and mudstones occur in the younger Bison Creek Formation of Alberta (Westrop 1989a). These shales and



Figure 5- Facies Association A, Lower Shale Member, Washburn section. An interval (5m) of shales with thin, resistant carbonaceous interbeds. The thicker interbeds in the middle of the exposure are intracrudites.

mudstones occur in all sections and are interbedded with thin (1-5 cm) interbeds, lenses, and nodules of grey lime mudstone, calcisiltite, and bioclastic pack- to rudstones (Fig 6). Many of these carbonate interbeds also contain ooids. The proportion of calcareous shales and mudstones within this lithofacies varies from thin partings that separate relatively continuous limestone beds up to thicker intervals (> 15 cm) that lie between discontinuous limestone lenses and nodules.

The bioclastic pack- to rudstones contain abundant, commonly abraded, trilobite and inarticulate brachiopod bioclasts. In some beds, irregular intraclasts or ooids are present. The bed thickness ranges from 10 to 60 cm, and the bases of the beds are often erosional. They are common throughout the Nolichucky Formation and have been described in detail by Markello and Read (1981).

Intraclastic rudstones -These widespread intrarudites of the Nolichucky Formation have been described in detail by Markello and Read (1981). In the study region, the clasts are typically lime mudstones and tend to form pavements and fans in which the long axis are orientated approximately horizontally (Fig. 7) or show low angle imbrication. The rudstones typically form units 10 - 40 cm thick, commonly with erosional bases, and also occur as thinner interbeds in the mudstone and shale lithofacies. Similar rudstones have been described from the Bison Creek Formation

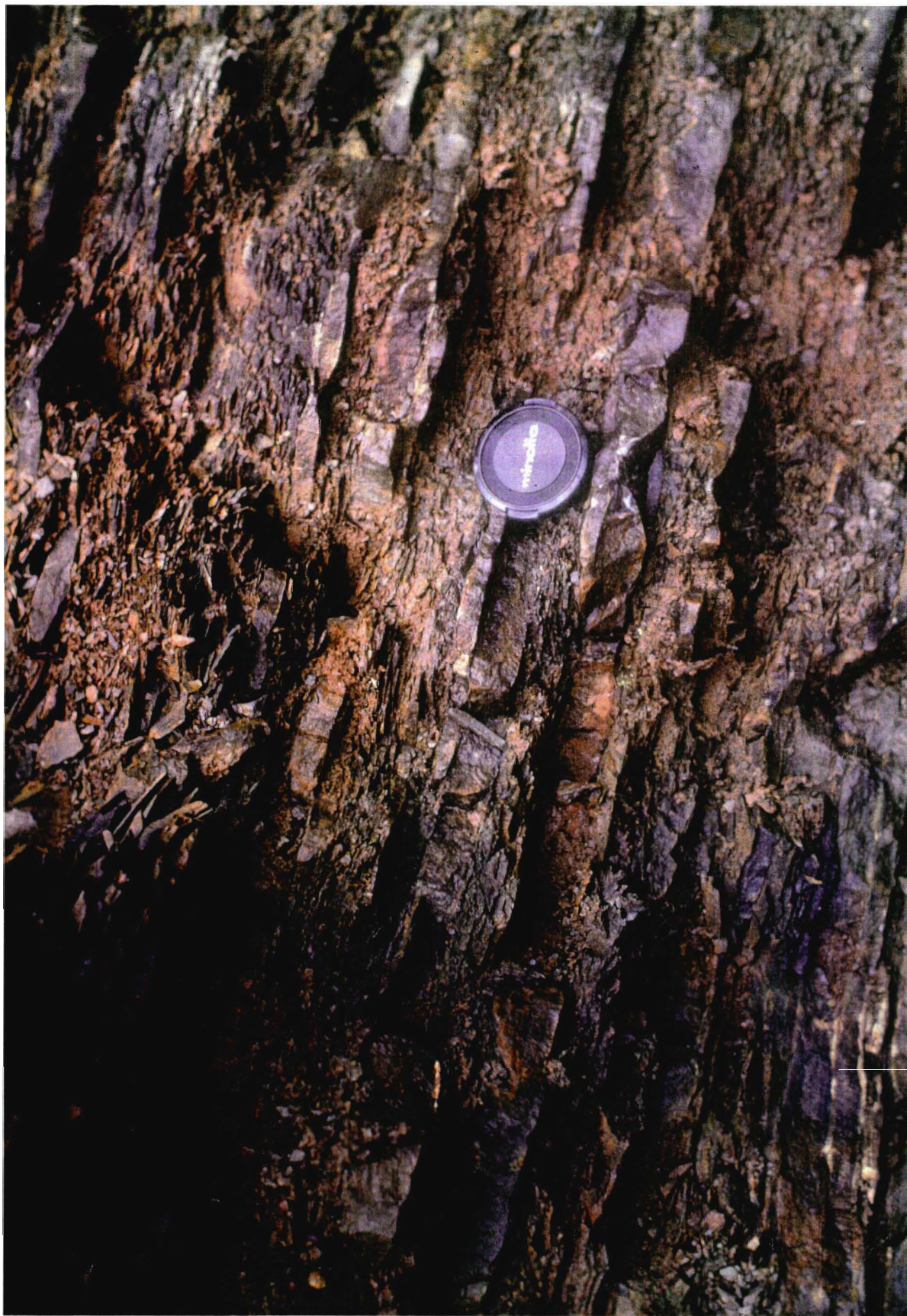


Figure 6- Carbonate interbeds, Upper Shale Member, Washburn section. Interbeds are bioclastic packstones and grainstones.



Figure 7- Base of intraclastic rudstone, Lower Shale Member, Beech Grove section. Showing horizontally orientated, tabular clasts of lime mudstone.

of Alberta (Westrop 1989a) and from other Upper Cambrian localities in the western United States (Sepkoski 1982).

Thrombolitic buildups - Thrombolitic buildups (Aitken 1967; Kennard and James 1986) are well-developed in the Lower and Middle Member of the Nolichucky Formation (Markello and Read 1981) and virtually identical buildups occur in the younger Bison Creek Formation of Alberta (Westrop 1989a). In common with these examples, the buildups at Dickensonville range from low domes and hemispheres to subspherical forms greater than 1 m in diameter (Fig. 8). At Three Springs, low domes and hemispheres with thicknesses of less than 1 m are present. Many of the thrombolites were built on rudstones.

Facies associations

Facies association A

The Lower Shale Member and the Upper Shale Member of the Nolichucky Formation consist largely of an association of shales and mudstones with interbeds of rudstones to grainstones (Fig. 5). These constitute the shale facies of the intrashelf basin of Markello and Read (1981). The association records an alternation of high (rudstones and grainstones) and lower (shales and mudstones) energy conditions. Markello and Read (1981) have argued that this association is best interpreted as the deposit of a storm-influenced, subtidal, marine environment, that lay between



Figure 8- Thrombolitic buildups, Bradley Creek Limestone Member, Dickensonville section.
A small buildup is to the right of the individual and a larger one to the left.

fair weather and storm-wave base. A similar palaeoenvironmental setting was also proposed by Westrop (1989a) for a comparable facies association in the younger Bison Creek Formation of Alberta.

Association A does not include features that are diagnostic of exposure on tidal flats (e.g., mudcracks; see Chow and James 1987). Sepkoski (1982) used these criteria to demonstrate a subtidal origin for similar Cambrian shale-limestone sequences in Montana. Association A also includes the shaly cycles capped by flat-pebble conglomerates that were described by Osleger and Read (1991) (Fig 10). These cycles have been interpreted as shallowing-upward cycles, with the intrarudites representing the shallowest water phase (Osleger and Read 1991). However, this cyclicity could also be the result of periodic passage of major storms under relatively constant water depth conditions.

Facies association B

Facies Association B reflects a more proximal setting and includes a lower proportion of shale than Association A. Unlike Association A, it is not uniformly developed over the study area. This association is best represented at Three Springs, Tennessee, where the undifferentiated Nolichucky Formation lacks the more shaly Association A (Appendix II). Association B at this locality includes cycles that have bases of thin shales often resting on rudstones. Above this are bioclastic grain to packstones, often interbedded with lime mudstones. The cycles are usually capped by



Figure 9-- Facies Association B, Bradley Creek Limestone Member, Three Springs section. An interval (3m) of shales with more resistant carbonates.

thrombolitic buildups (Figs. 9 and 11). This association is the cyclic algal bioherm facies of Markello and Read (1981), and is similar to the cycles capped by thrombolitic bioherms in the Notch Peak Formation of Utah (Osleger and Read 1991). Osleger and Read (1991) considered both of these to be shallowing upward cycles.

At Beech Grove, Tennessee (Appendix II), Association B lacks thrombolitic buildups and the cycles are capped by bio-oid pack- and grainstones. These oolites are high energy, shallow water carbonate sands (Markello and Read (1982). This contrasts sharply with the development of this association at Dickensonville VA (Appendix II) where thrombolites dominate. At this locality there are two cycles in Association B each capped by thrombolites that are greater than 1.5m in maximum thickness. This section is probably shallower than Beech Grove. The other sections measured (Washburn and Duffield) do not include association B.

Lithofacies changes across the Marjuman-Steptoean Boundary

Recent work on sea level history and facies changes through the Nolichucky Formation in the southern Appalachians of Virginia has been published by Markello and Read (1981) and Osleger and Read (1993). They argued that the buildup-bearing Bradley Creek Limestone Member (their "Middle Limestone Member"; Fig. 13) records a regional shallowing. The appearance

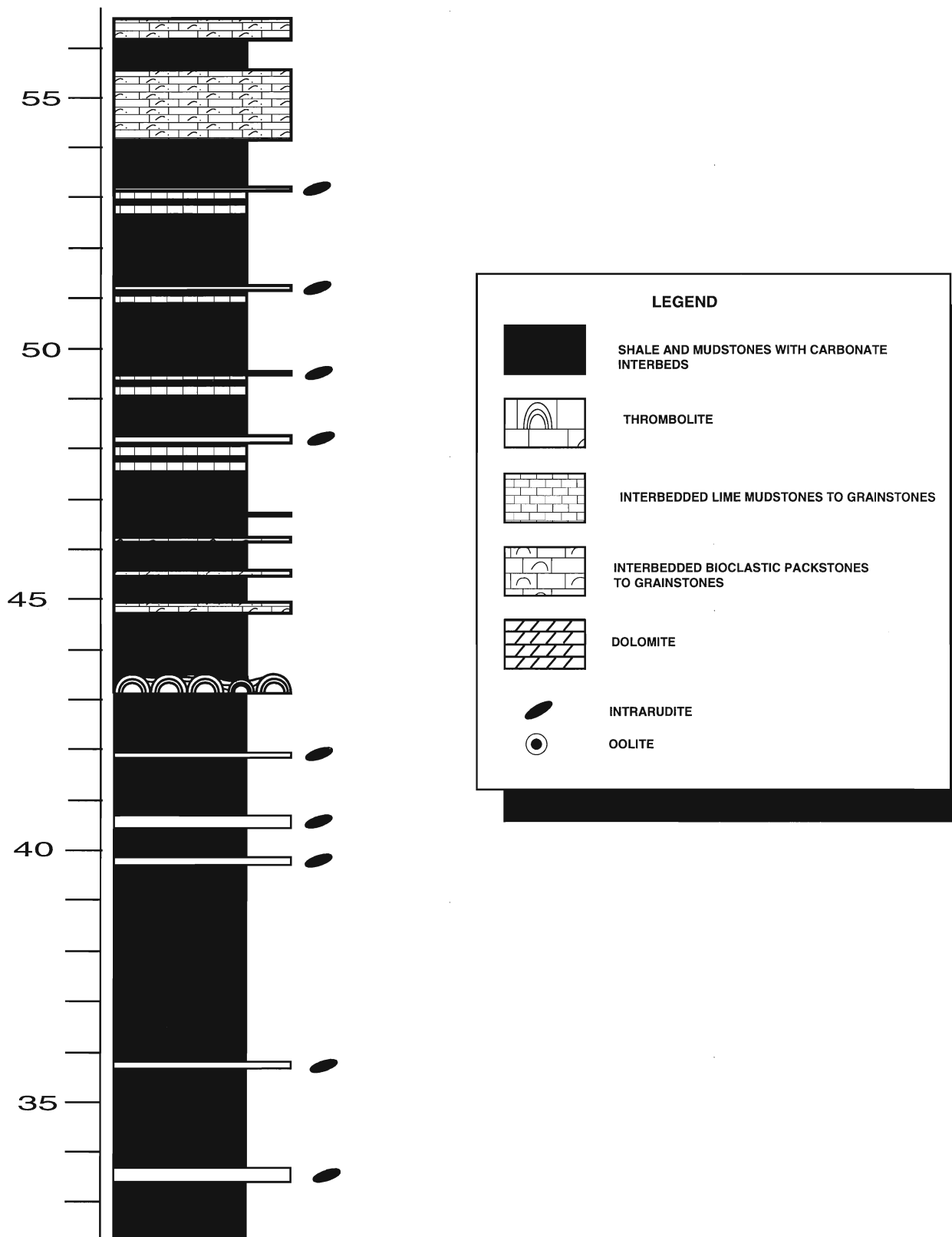
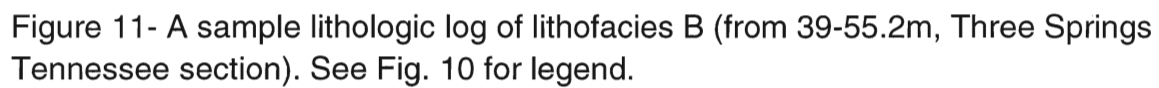


Figure 10- A typical lithologic log of Association A (from 33-56.7m, Dickensonville Virginia section).



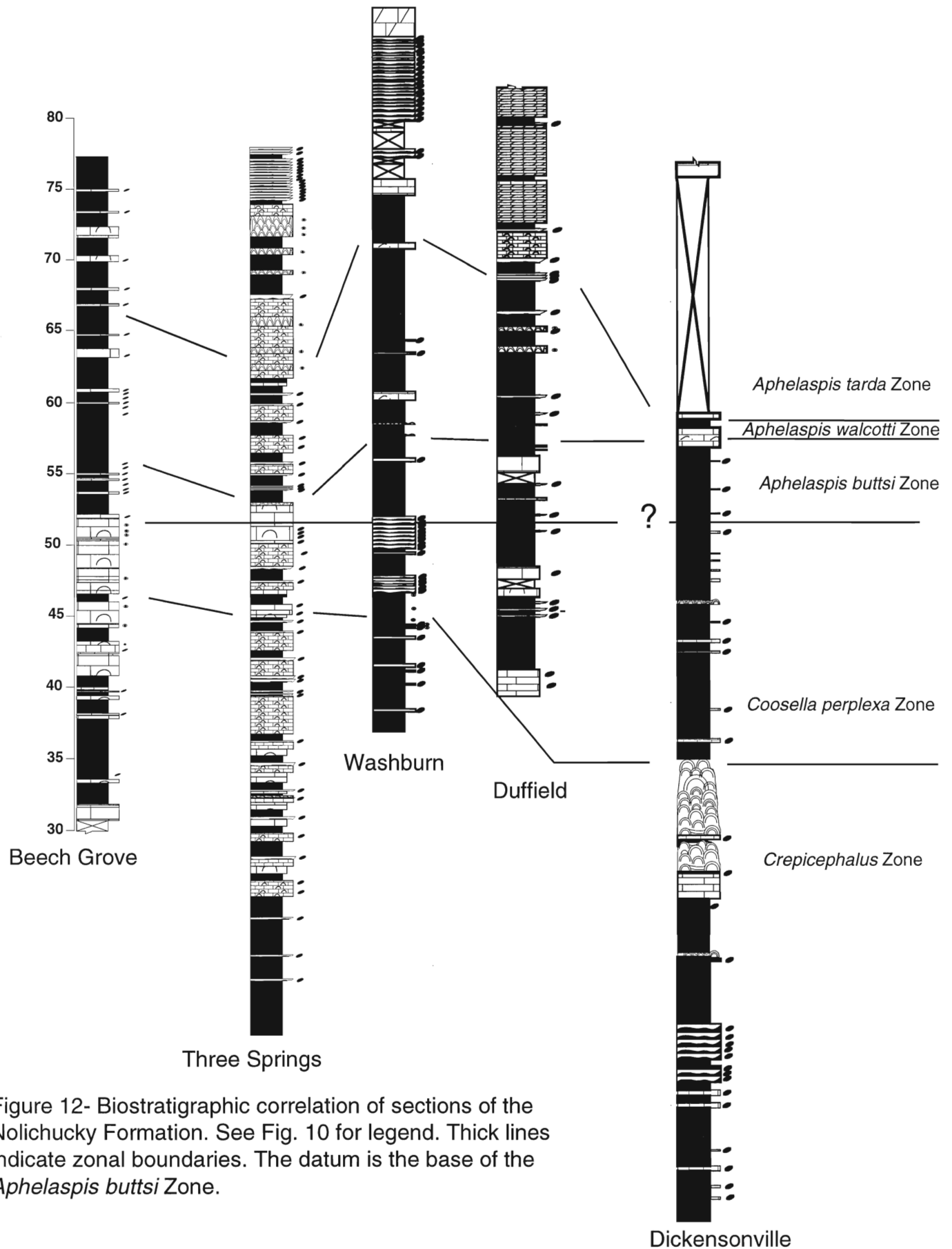


Figure 12- Biostratigraphic correlation of sections of the Nolichucky Formation. See Fig. 10 for legend. Thick lines indicate zonal boundaries. The datum is the base of the *Aphelaspis buttsi* Zone.

of shales and carbonates of the Upper Shale Member above the Bradley Creek Limestone Member (Fig. 13) was interpreted as evidence for a relative deepening that occurred in the Early Steptoean (*Aphelaspis* Zone). From a comparison between Utah, Texas, and Virginia, Osleger and Read (1993) argued that the base of the *Aphelaspis* Zone is a major sequence boundary that reflects a eustatic deepening. In Tennessee, the interpretation of facies change and sea level history is hindered by a complex basin topography. From an analysis of isopach maps, Hasson and Haase (1988) identified a region of higher subsidence and, consequently, thick Nolichucky sequences in the Lutrell Sub-basin (Fig. 14). Other regions were characterized by lower subsidence rates and, consequently, thin Nolichucky sequences (Hasson and Hasse, 1988).

The Bradley Creek Limestone Member is not developed within the Lutrell Sub-basin, although an interval with numerous rudstones in the *Coosella perplexa* Zone at Washburn (the section in the thickest part of the Nolichucky in this study) might record a regional shallowing, with subsequent deepening near the base of the Steptoean (*Aphelaspis buttsi* Zone; Appendix II). Around the margins of the sub-basin as at Beech Grove (Appendix II), the Bradley Creek Limestone Member is developed and the deepening associated with the appearance of the Upper Shale member (Fig. 12) occurs in the Marjuman-Steptoean boundary interval (*A. buttsi* Zone). In regions of relatively thin Nolichucky (Three Springs), the Marjuman-Steptoean boundary interval lies

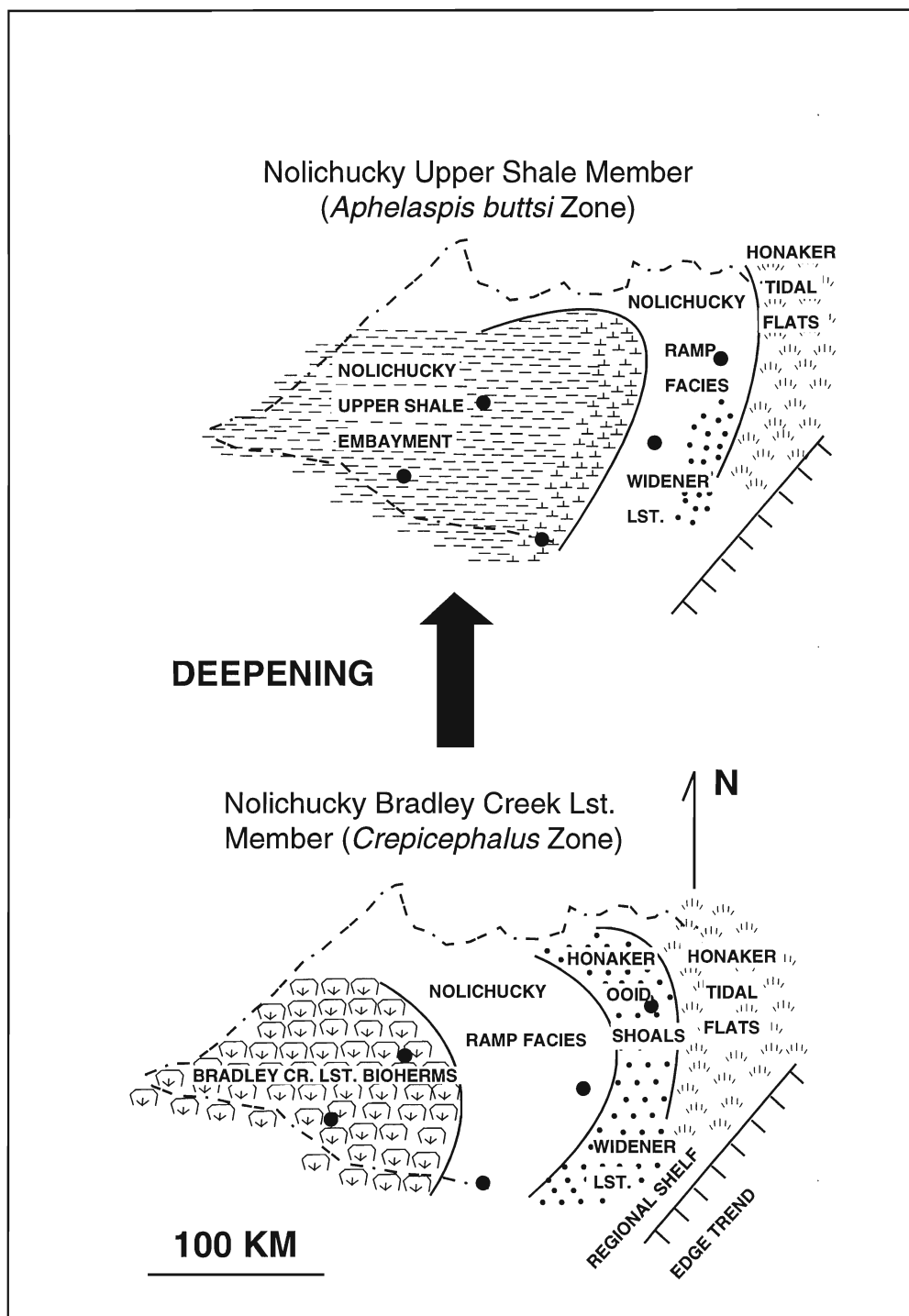


Figure 13- Geographic distribution of lithofacies during Noliichucky deposition in Virginia (modified from Markello and Read 1981).

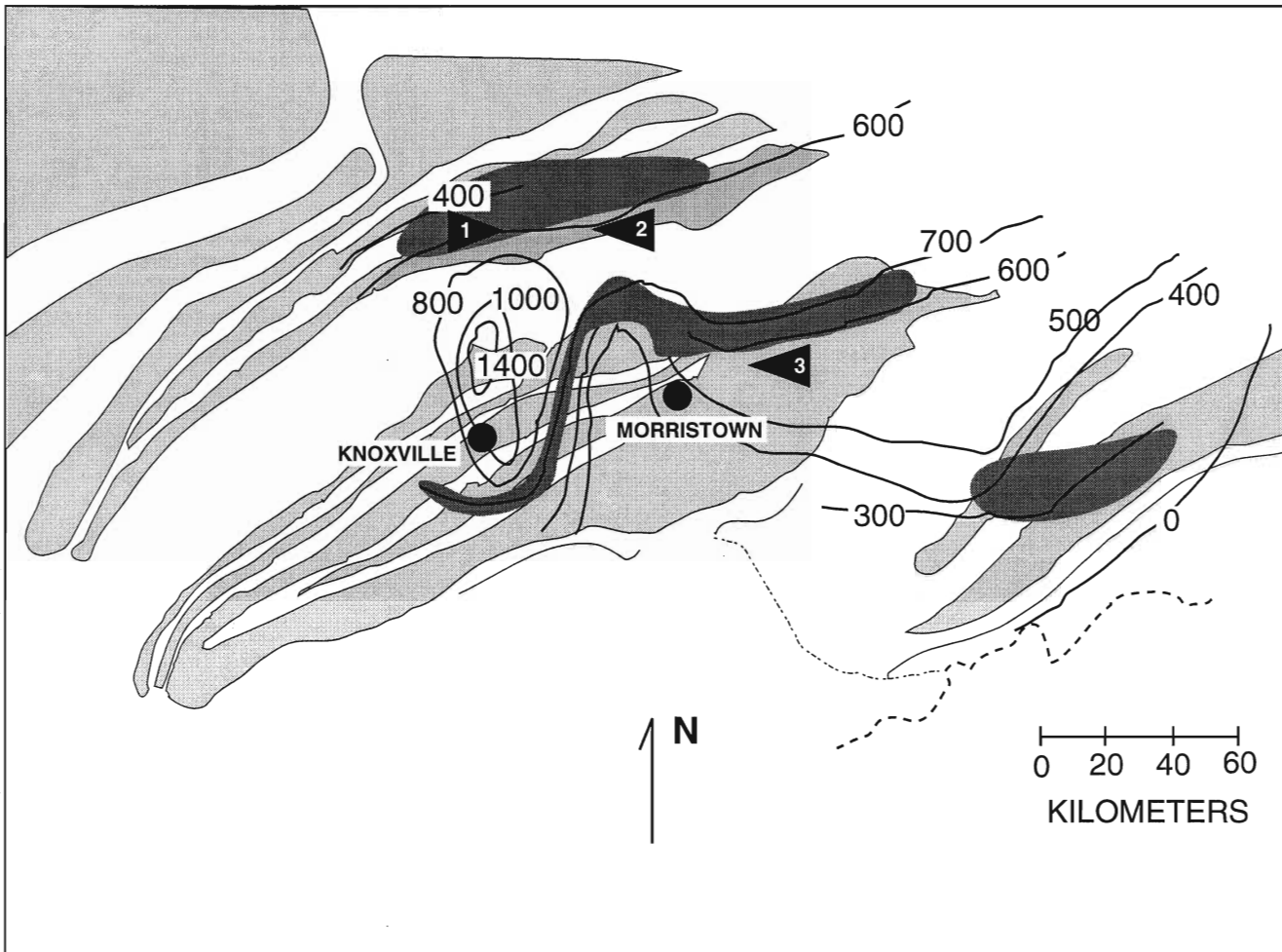


Figure 14-- Isopach trends of the Nolichucky Formation within east Tennessee. Data plotted on palinspatic base map. Dark stipple indicates distribution of Bradley Creek Limestone Member; light stipple shows outcrop belt of the Nolichucky Formation (modified from Hasson and Haase 1988).

entirely within relatively proximal limestone facies and there is no evidence for a deepening (Appendix II). Finally, at Dickensonville, Virginia, relative deepening at the base of the *Coosella perplexa* Zone (Fig. 12) is indicated by the change from buildups of facies Association B to more distal shales and storm deposits of facies Association A (Appendix II).

In conclusion, the data from Tennessee are consistent with the hypothesis of a relative deepening near the base of the Steptoean. The facies change appears to be diachronous and begins in the *C. perplexa* Zone in some sections and occurs in the overlying *A. buttsi* Zone at other section. The data generated by this study do not allow for the separation of subsidence from eustasy as potential controls of the relative sea level change.

CHAPTER 3

BIOSTRATIGRAPHY

INTRODUCTION

The "standard" biostratigraphic framework for the Upper Cambrian of North America (Palmer 1971a; Lochman-Balk 1971; North 1971; Cowie 1971) uses genus-based zones. This presents some problems because genera tend to be less precise for correlation than species since they commonly display diachronous first appearances (Ludvigsen et al. 1986).

A sequence of five zones is established here from species range data (see figs. 15-20). The upper Marjuman consists of the *Crepicephalus* Zone and the *Coosella perplexa* Zone. The basal Steptoean sequence is divided into three zones. In ascending order, these are the *Aphelaspis buttsi*, *A. walcotti*, and *A. tarda* zones. This zonation is used to establish a relative time framework to discuss the extinction that occurs at the top of the Marjuman Stage.

The *Crepicephalus* Zone:

This is the lowest zone recognized in this study of the Nolichucky Formation, and the contact with the underlying *Cedaria* Zone (Rasetti 1965) was not encountered in any of the

BEECH GROVE RANGE CHART

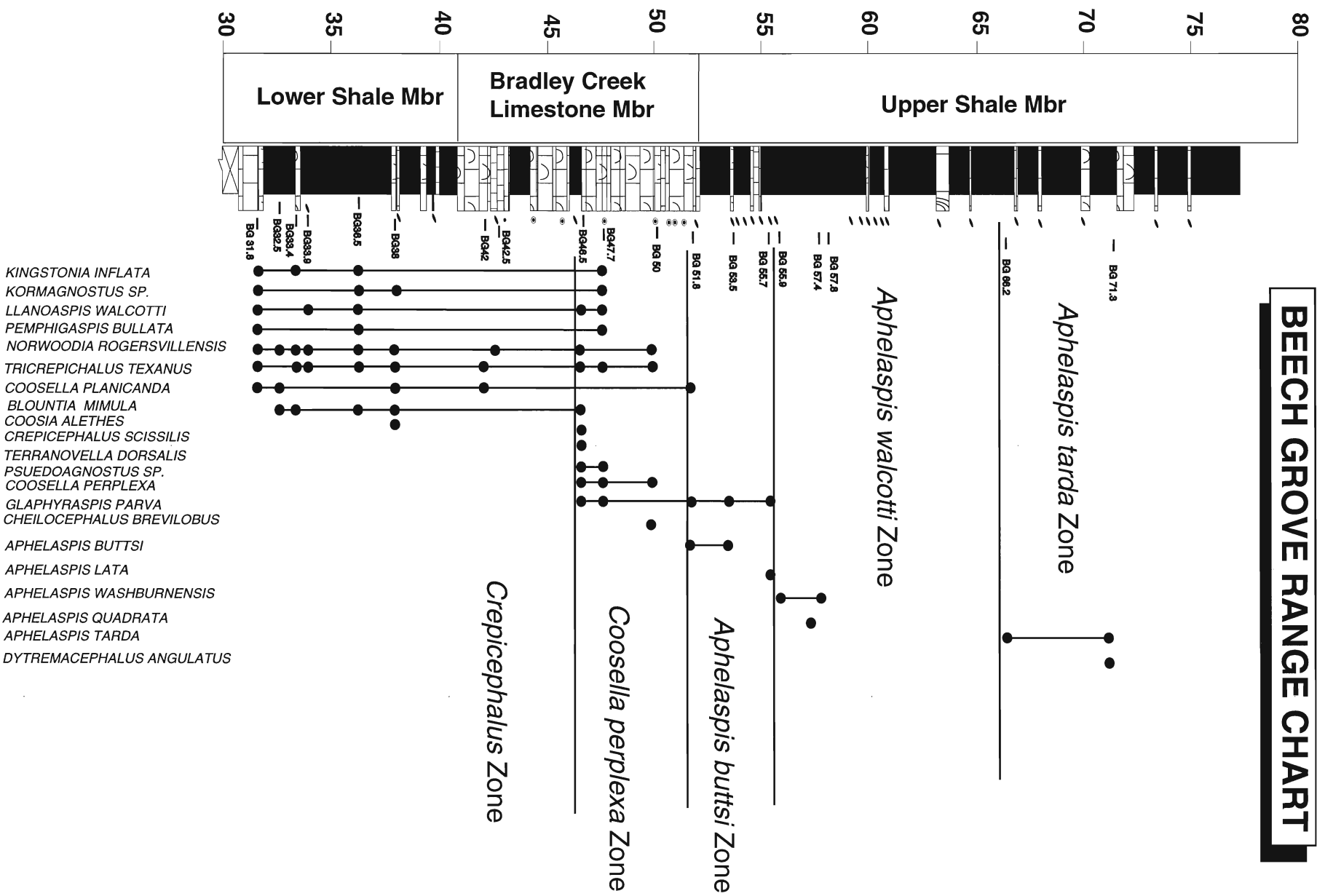


Figure 16 - Species range chart, Beech Grove. See Fig. 10 for legend.

WASHBURN

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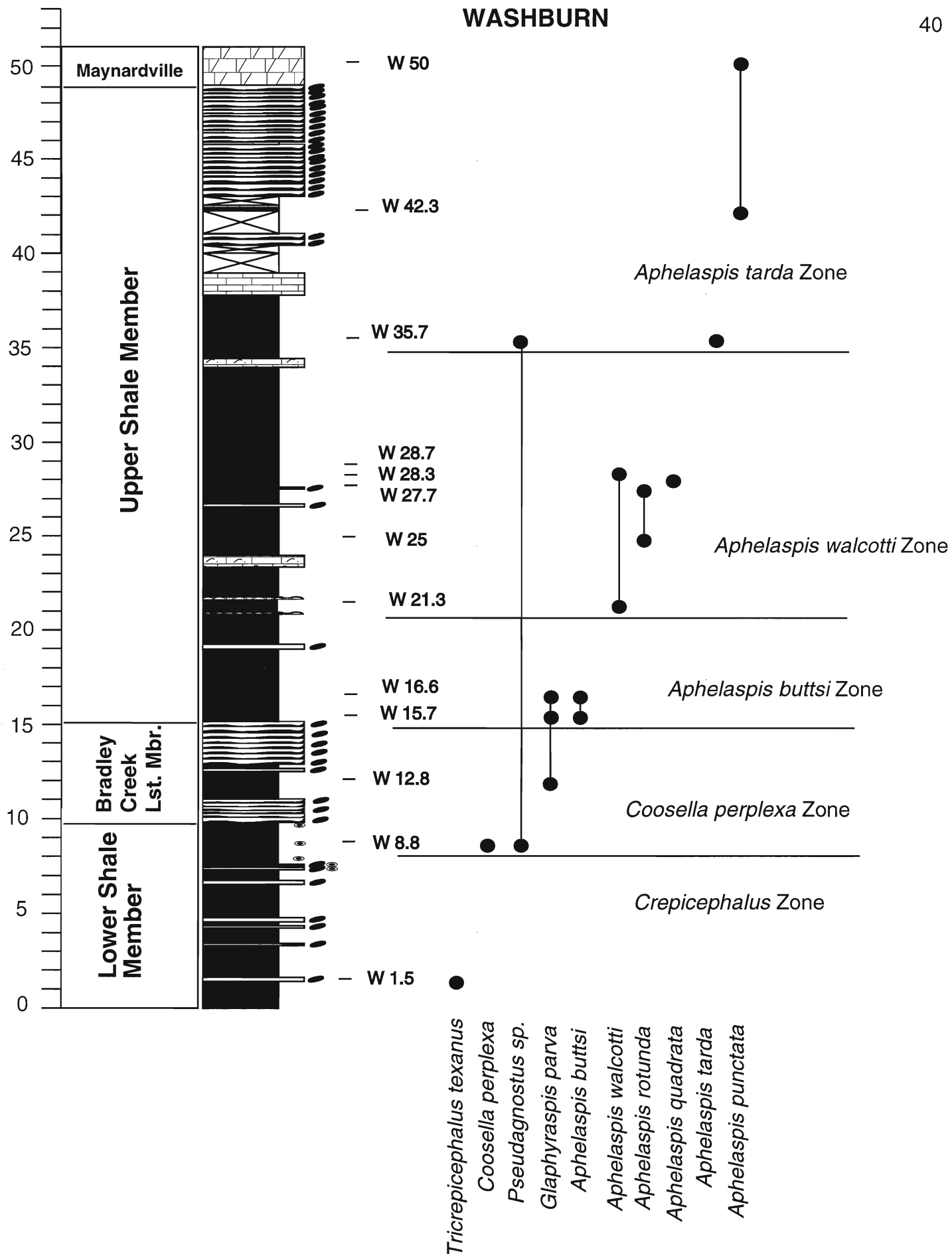


Figure 17 - Species range chart, Washburn. See Fig. 10 for legend.

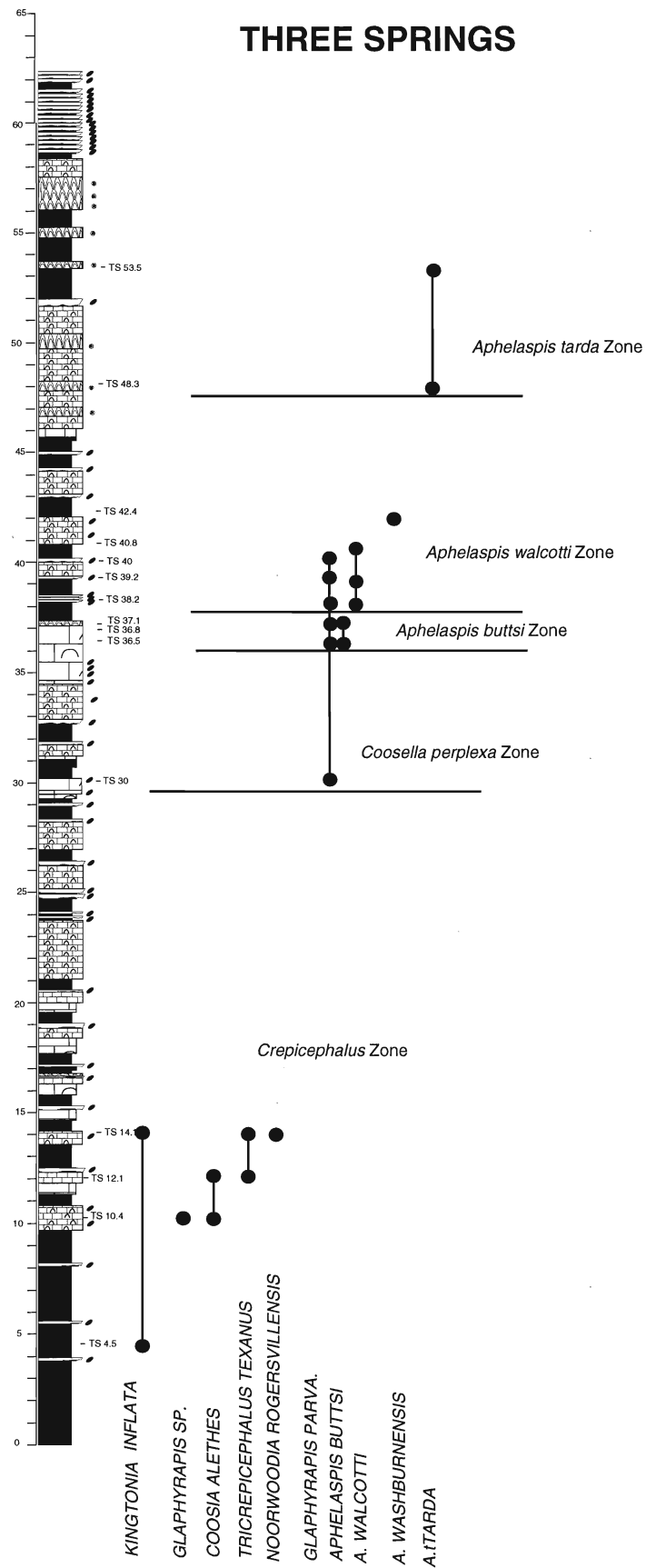


Figure 18 - Species range chart, Three Springs. See Fig. 10 for legend.

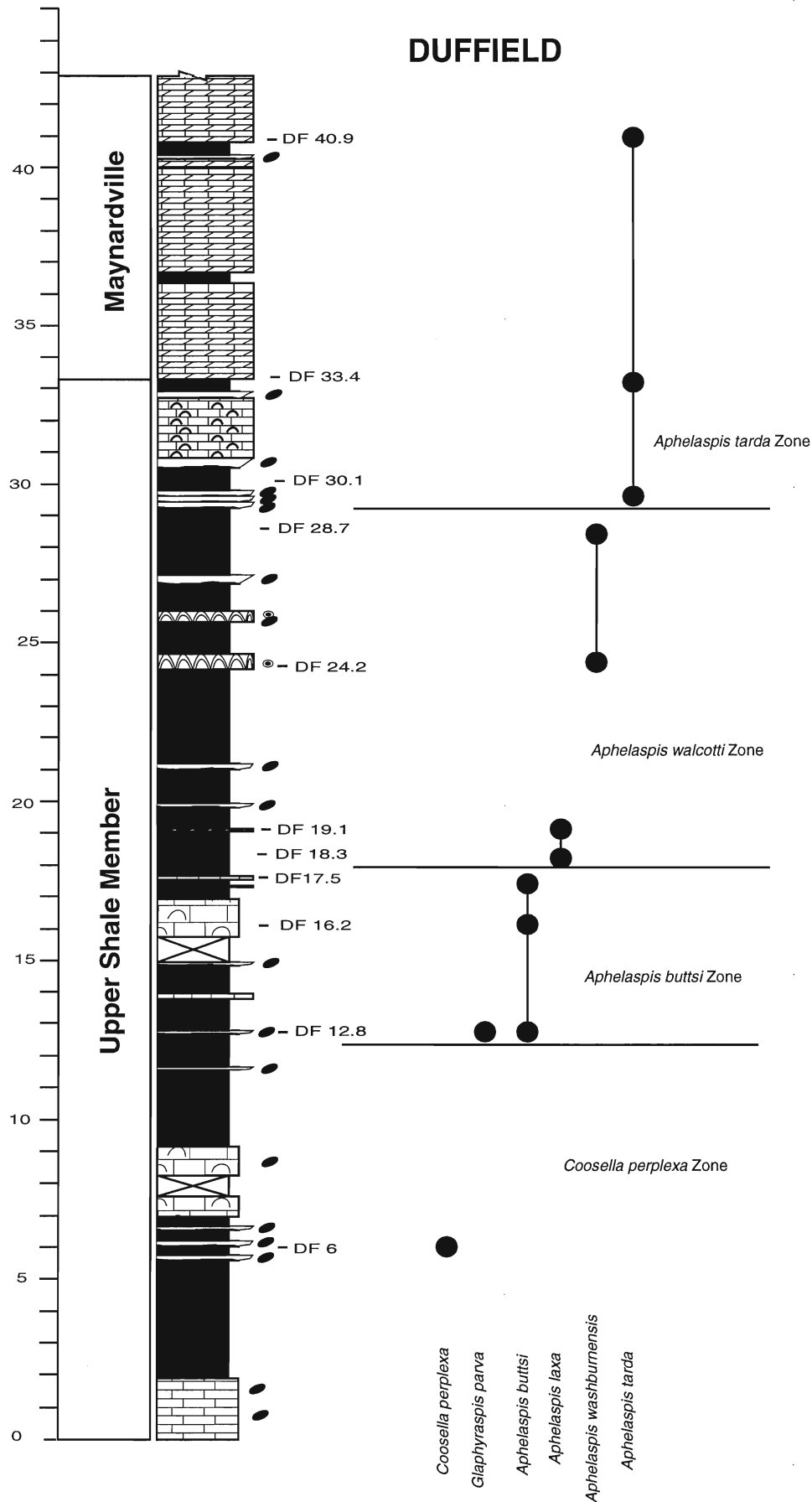


Figure 19 - Species range chart, Duffield. See Fig. 10 for legend.

DICKENSONVILLE

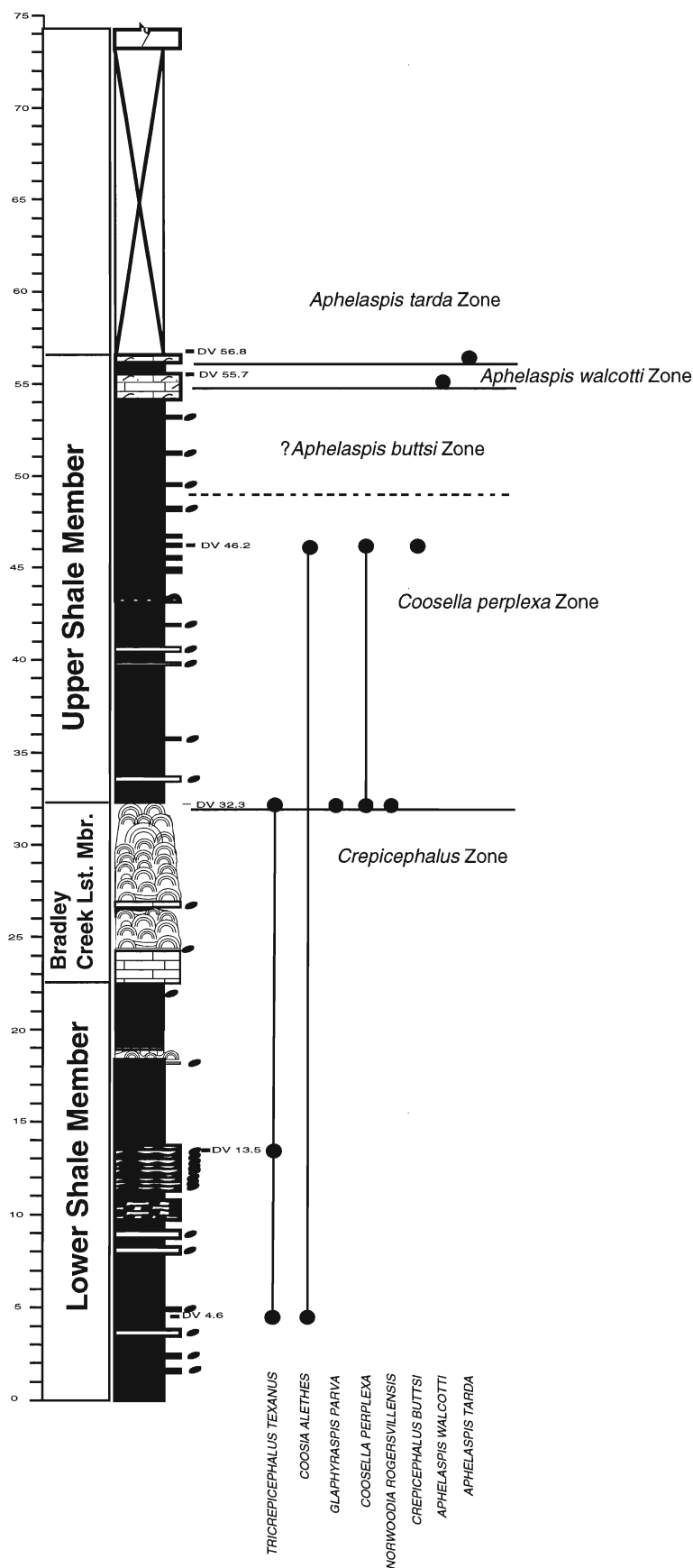


Figure 20. Species range chart, Dickensonville. See Fig. 10 for legend.

sections. The concept of the *Crepicephalus* Zone follows Rasetti (1965) except that the *Coosella perplexa* fauna defines an overlying zone.

The following taxa occur in the *Crepicephalus* Zone:

Tricrepicephalus texanus (Shumard)

Kingstonia inflata Resser

Coosia alethes (Walcott)

Norwoodia rogersvillensis Resser

Kormagnostus sp.

Llanoaspis walcotti (Resser)

Pemphigaspis bulata Hall

Blountia mimula Walcott

Coosella planicanda Rasetti

Pseudagnostus sp.

Crepicephalus buttsi Resser

The *Crepicephalus* Zone has been correlated to other Cambrian sections across North America and has been used as one of the North America-wide genus-based zones (Lochman-Balk 1971). The *Crepicephalus* Zone in the Nolichucky Formation can be correlated with the *Coosella* and *Maryvillia* Zones of central Texas (Palmer 1954) on the bases of the presence of *Tricrepicephalus texanus*. The *Crepicephalus* Zone can be correlated with the same zone in the Eau Claire Formation in Wisconsin based on shared taxa *Coosia* and *Terranovella dorsalis* (Nelson 1951). The presence of *Terranovella dorsalis* also allows it to be broadly correlated into the *Terranovella dorsalis* Fauna interval of the Felix Member of

the Port au Port Formation in western Newfoundland (Westrop 1992). It can also be correlated broadly to the *Crepicephalus* Zone in central Montana (Lochman and Duncan 1944) and Utah (Palmer 1979) based on the presence of a shared assemblage of genera. Shared genera also suggest that the *Crepicephalus* Zone of the Nolichucky Formation is coeval with the exposure of the Conasauga Formation at Woodstock, Alabama (Palmer 1962). Correlation to the Upper Cambrian deep shelf to slope facies of the Rabittkettle Formation of the Mackenzie Mountains in the Northwest Territories (Pratt 1992) is much more difficult due to the sharp differences in trilobite biofacies. However, the presence of *Tricrepicephalus texanus* indicates that the *Crepicephalus* Zone is roughly coeval with the *Cedaria selwyni* through *Cedaria brevifrons* Zones.

The *Coosella perplexa* Zone:

The lower boundary of the *Coosella perplexa* Zone is defined by the first occurrence of the eponymous species. The *Coosella perplexa* Zone was first proposed by Palmer (1979) as a subzone.

The following taxa occur in the *Coosella perplexa* Subzone:

Coosella perplexa (Palmer)

Tricrepicephalus texanus (Shumard)

Glaphyraspis parva (Walcott)

Kingstonia inflata Resser

Coosia alethes (Walcott)

Norwoodia rogersvillensis Resser

Crepicephalus scissilis Resser

Pseudagnostus sp.

Llanoaspis walcotti (Resser)

Pemphigaspis bulata Hall

Cheilocephalus brevilobus (Walcott)

Terranovella dorsalis (Hall)

The *Coosella perplexa* Subzone was first defined by Palmer (1979) from the Great Basin, although the eponymous species had been described earlier from strata that had been assigned to the basal part of the *Aphelaspis* Zone in Texas (Palmer 1954). A collection from Logan Mountain, Montana (Lochman and Hu 1962) may be of the same age based on the presence of *Cheilocephalus brevilobus* and *Glaphyraspis parva* and the absence of *Aphelaspis*.

The *Aphelaspis buttsi* Zone:

The lower boundary of the *Aphelaspis buttsi* Zone is defined by the first appearance of *A. buttsi*. The following species occur in the *Aphelaspis buttsi* Zone:

Aphelaspis buttsi (Kobayashi)

A. lata (Rasetti)

Glaphyraspis parva (Walcott)

Coosella perplexa (Palmer)

The *Aphelaspis buttsi* Zone is recognized as the base of the Steptoean Stage in the Nolichucky Formation and it can be correlated to basal portions of the *Aphelaspis* Zone in other localities in North America. The eponymous species occurs in the basal beds of the *Aphelaspis* Zone in the Conasauga Formation at Cedar Bluff, Alabama (Palmer 1962), and in the Great Basin (Palmer, 1965a). In the central Texas area, it is difficult to be more confident in the correlation because there are no shared species from this zone. The presence of the *A. buttsi* Zone cannot be demonstrated because *Aphelaspis walcotti* is the stratigraphically lowest species of the genus in Texas. However, there is typically a gap of a few meters of unfossiliferous rock separating the lowest appearance of *A. walcotti* from the highest occurrence of the *C. perplexa* Zone fauna (Palmer 1954). The *A. buttsi* Zone is probably correlative with a fauna from the upper part of the Eau Claire Formation of Wisconsin (Nelson 1951) which consists of *Aphelaspis* sp. and *Glaphyraspis* sp. cf. *G. parva*. In Montana and Wyoming, the *Aphelaspis* faunas are poorly known, but the *A. buttsi* Zone may be represented by a few collections which contain *Glaphyraspis parva* in association with the first appearance of *Aphelaspis* (Lochman and Duncan 1944; Shaw 1956). The *Glyptagnostus reticulatus* Zone of the Rabbitkettle Formation, Mackenzie Mountains (Pratt 1992), marks the first appearance of *Aphelaspis* with *Glaphyraspis parva* and *Glyptagnostus reticulatus* and may be correlative with the *A. buttsi* Zone. This is further supported by the association of *G. reticulatus* with *A. buttsi* at Cedar Bluff Alabama (Palmer 1962).

The *Aphelaspis walcotti* Zone:

The base of the *Aphelaspis walcotti* Zone is defined by the first occurrence of *A. walcotti* or *A. washburnensis*. The following species occur in the *Aphelaspis walcotti* Zone:

Aphelaspis walcotti Resser

A. rotunda Rasetti

A. laxa Resser

A. quadrata Resser

A. washburnensis Rasetti

A. walcotti is present in the Riley Formation of central Texas (Palmer 1954) and suggests that the entire *Aphelaspis* Zone of that region is correlative with the *A. walcotti* Zone of Tennessee and Virginia. Direct correlation between the Great Basin (Palmer 1965a) and the *A. walcotti* Zone of the Nolichucky Formation is difficult due to the absence of shared species. However, from the presence of *Glaphyraspis ornata* with *A. walcotti* in Texas (Palmer 1954), the *A. walcotti* Zone can be correlated to an interval straddling the boundary between the lower and upper *Aphelaspis* Zone as recognized in the Great Basin (Palmer 1965a). The absence of shared species also means that the *A. walcotti* Zone can only be roughly correlated into the Rabbitkettle Formation. By using the Great Basin as an intermediary, an approximate correlation can be made because *A. subditus* occurs both at the

base of the upper *Aphelaspis* Zone in the Great Basin (Palmer 1965a) and in the *Olenaspella regularis* Zone of the Rabbitkettle Formation (Pratt 1992). This suggests that the *A. walcotti* Zone of Tennessee and Virginia is correlative with the *O. regularis* Zone.

The *Aphelaspis tarda* Zone:

The first appearance of *Aphelaspis tarda* marks the base of this zone. The zone is characterized by the following species:

Aphelaspis tarda Rasetti

A. punctata Rasetti

Dytremacephalus angulatus Rasetti

The *A. tarda* Zone can be correlated with strata outside the study region only with great difficulty. The lowest appearance of *Dytremacephalus* occurs in this zone and suggests that it is at least partly equivalent to the "post-*Aphelaspis*" Zone in Texas (Palmer 1954), the *Dunderbergia* Zone in the Great Basin (Palmer 1965a) and the *Olenaspella evansi* Zone of the Mackenzie Mountains (Pratt 1992).

CHAPTER 4

BIOFACIES CHANGES ACROSS THE MARJUMAN-STEPTOEAN BOUNDARY

INTRODUCTION

During the Upper Cambrian, there were three mass extinctions of North American shelf trilobites. These mass extinctions have been used to define the boundaries of units called 'biomeres' and have been the subject of considerable research (e.g., Palmer 1965b, 1979, 1984; Stitt 1971, 1975, 1977; Westrop and Ludvigsen 1987; Westrop 1988, 1989b, 1990, 1991; Thomas 1995; Saltzman *et al.* 1995; Backus and Thomas 1995). Despite this attention, no consensus has been reached concerning the merits of the various explanations that have been put forward. The most popular explanatory theories include cooling of the shelf waters (Stitt 1971, 1975; Palmer 1979; Backus and Thomas 1995; Thomas 1995), a decrease in oxygen (Palmer 1984; Saltzman *et al.* 1995), elimination of biofacies due to onlap in the outer shelf (Westrop and Ludvigsen 1987), and a complex scenario which invokes a sea level fall over the craton, accompanied by subsidence-related deepening in miogeoclinal regions seaward of a "hingeline" (Backus and Thomas 1995; Thomas 1995).

The biofacies, diversity, and lithologic patterns associated with the mass extinction event in the Nolichucky Formation will be compared to patterns at other localities in North America (Fig. 21). Comparisons will also be made with the available data from other "biomere" extinction events to attempt to determine the merits of the various extinction models.

The extinction events in the Upper Cambrian were first identified and used as the boundaries of biomes by Palmer (1965b). Biomes were originally defined as regional biostratigraphic units bounded by abrupt "non-evolutionary" changes in the dominant faunal elements (Palmer 1965b). Palmer (1965b) argued that biome boundaries differed from those of conventional biostratigraphic units because they were diachronous. It has subsequently been demonstrated that diachroneity is minimal (Palmer 1984) and biomes have been reinterpreted as stages (Ludvigsen and Westrop 1985). This interpretation will be followed here.

BIOFACIES PATTERNS

The literature on trilobite biofacies has increased in recent years (e.g., Fortey, 1975; Ludvigsen, 1978; Thomas, 1979; Mikulic and Watkins, 1981; Westrop, 1986a,1995; Chlupac, 1987; Owen et al., 1991; Melzak and Westrop, 1994). This work has shown that the distributional ecology of latest Cambrian trilobites was similar both to younger trilobite faunas and to Paleozoic brachiopod-rich

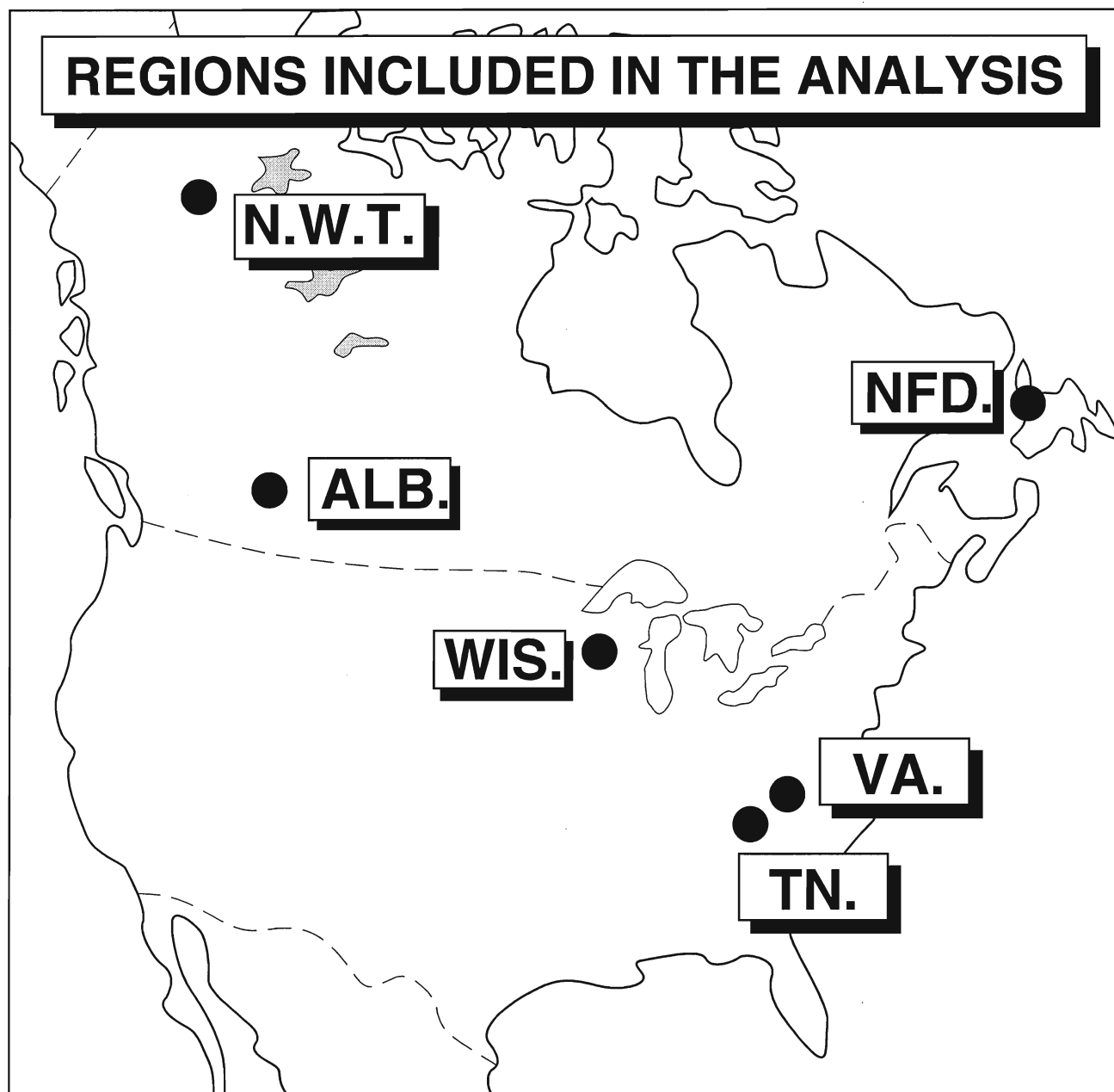


Figure 21 - Map of localities used in the study: Alb., Sullivan Formation southern Canadian Rockies; N.W.T., Rabbitkettle Formation, North West Territories; Wis., Eau Claire Formation, Wisconsin; NFD., Cow Head Group, Newfoundland; Tn., and Va., Nolichucky Formation, Tennessee and Virginia.

faunas (Bambach 1986; Patzkowsky 1995). In common with previous work, trilobite biofacies are defined in this study on the basis of relative abundances of genera and higher taxa in large collections (more than fifty individuals). Thirty collections from the Nolichucky Formation and twenty-one collections from other localities in North America were analyzed using cluster analysis (Jones, 1988). The collections from outside the study area are representatives of large, undescribed collections (B. Mills; S.R. Westrop, unpublished data), or a portion of published data sets (Pratt, 1992). This material is used to contrast the *Aphelaspis* Zone faunas with those from the upper Marjuman, in a preliminary way. Analysis (Fig. 22) was performed on percent abundance data using SYSTAT 5.2 (SYSTAT, 1992) using the index of similarity, Pearson's Product Moment correlation, coefficient and clusters formed using the average linkage method (Jones, 1988).

Upper Marjuman Biofacies

Six biofacies are recognized in the upper Marjuman Stage of North America (Fig. 22). These are the *Coosella-Glaphyraspis* Biofacies, *Tricrepicephalus*-Norwoodiid Biofacies, *Kingstonia* Biofacies, *Uncaspis* Biofacies, *Cedaria* Biofacies and the *Crepicephalus-Lonchocephalus* Biofacies. Of these the *Coosella-Glaphyraspis* Biofacies and the *Tricrepicephalus*-Norwoodiid Biofacies are recognized in the Nolichucky Formation.

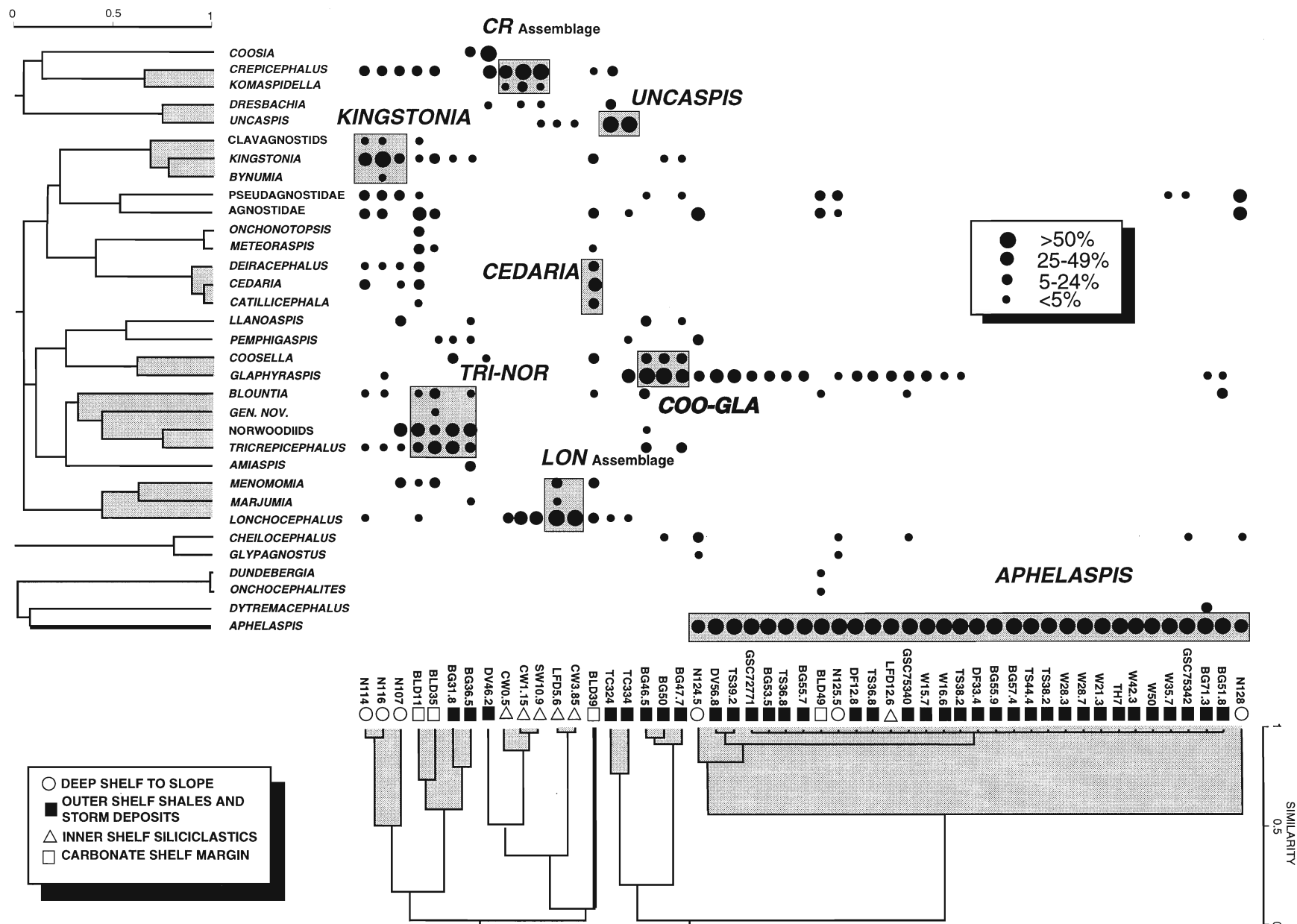


Figure 22 - Q- and R-mode cluster analysis of 30 collections from the Nolichucky Fm. and 21 from other localities in North America (Appendix). The biofacies are defined by the intersection of Q- and R-mode cluster; relative abundances of taxa are indicated by a series of graded dots and gross lithofacies are represented by symbols.

Kingstonia Biofacies

Composition. Cluster analysis (Fig. 22) grouped together three collections from deep shelf and slope facies of the Rabbitkettle Formation of the Northwest Territories that are characterized by a high abundance of *Kingstonia* (Fig. 23). This biofacies was first described by Pratt (1992).

Assigned collections. Rabbitkettle Formation N107, N114, N116 and other collections assigned to it by Pratt (1992).

Tricrepicephalus-Norwoodiid Biofacies

Composition. The cluster analysis (Fig. 22) grouped together four collections from the Nolichucky Formation and from the carbonate shelf margin facies of the Cow Head Group of western Newfoundland (James and Stevens 1986). This biofacies is dominated by *Tricrepicephalus* and norwoodiids and also contains *Blountia* (Fig. 24). The collections from the Cow Head Group are more diverse (15 species) than those from the Nolichucky Formation (7 species) and contain several genera (e.g., *Catillecephala* and *Deiracephalus*) that are not present in Tennessee. Additional data may well separate the Cow Head and Nolichucky faunas into more distinct biofacies groupings.

KINGSTONIA BIOFACIES

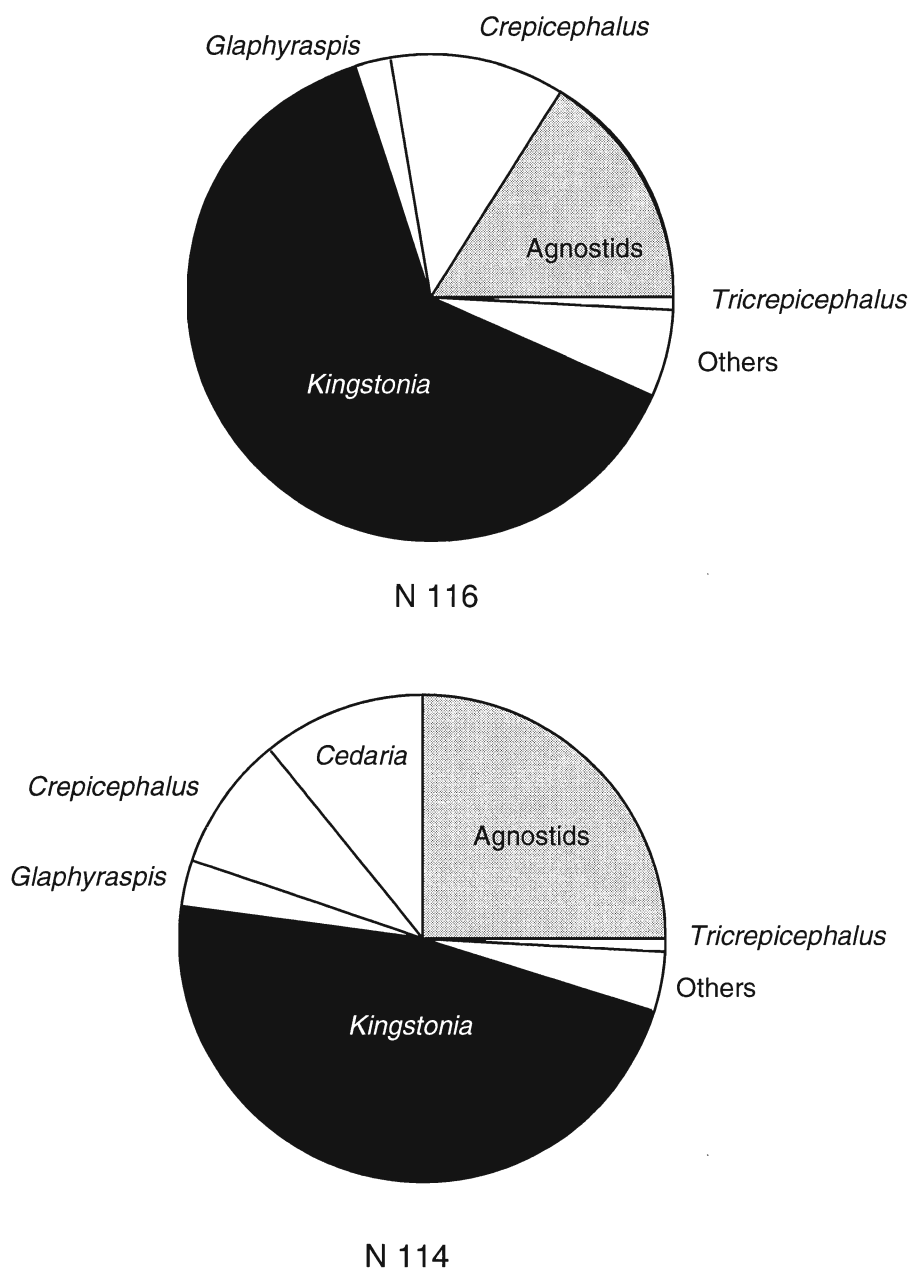
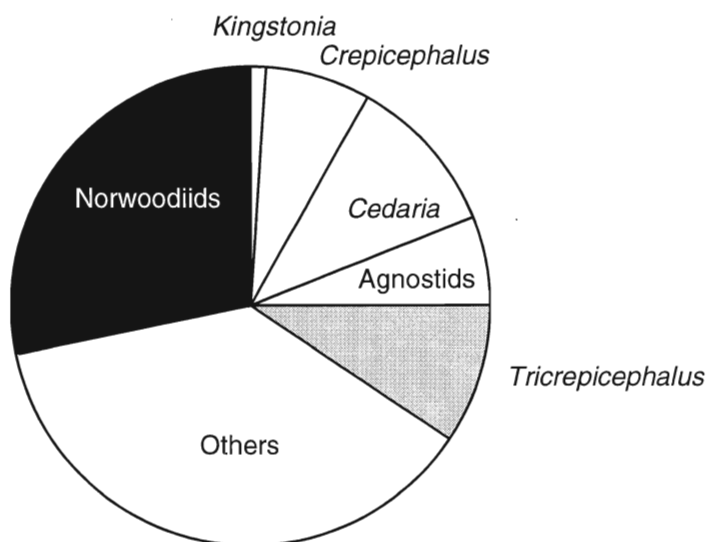
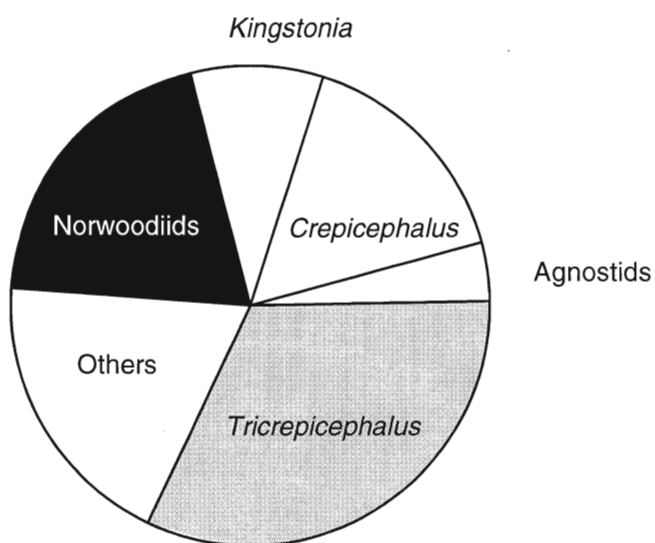


Figure 23- Relative abundances of taxa in representative collections of the *Kingstonia* Biofacies. See Appendix III for full description of collections.

Tricrepicephalus- Norwoodiid Biofacies



Boulder 11



Boulder 35

Figure 24- Relative abundances of taxa in representative collections of the *Tricrepicephalus*-Norwoodiid Biofacies. See Appendix III for full description of collections.

Assigned collections. Cow Head Group Boulder 11, Boulder 35, Nolichucky Formation BG 31.8, BG 36.5.

Crepicephalus-Lonchocephalus Biofacies

Composition. The *Crepicephalus-Lonchocephalus* biofacies includes five collections from near shore siliciclastics (Driese *et al.* 1981) of the Eau Claire Formation in Wisconsin (Figs. 22 and 25). The *Crepicephalus-Lonchocephalus* biofacies collections are low diversity (4-5 species) assemblages that are dominated by *Crepicephalus* or *Lonchocephalus*. This biofacies grades from being a *Lonchocephalus*-dominated assemblage to a *Crepicephalus*-dominated assemblage (Fig. 22), and they are probably end members in a spectrum produced by size-sorting by storm waves and currents (Westrop pers. comm.; see Westrop 1986 for influence of size sorting on abundances of trilobite sclerites in other Cambrian sequences).

Assigned collections. *Crepicephalus-Lonchocephalus* Biofacies. Eau Claire Formation SW10.9, CW 0.5, CW 1.15, LFD 5.6 and CW 3.85.

Cedaria Biofacies

Composition. This biofacies is represented by a single collection from shelf-margin derived carbonate boulders (James and Stevens 1986) of the Cow Head Group in western Newfoundland (Fig. 22). This biofacies is dominated by *Cedaria* but is also rich in

CREPICEPHALUS-LONCHOCEPHALUS BIOFACIES

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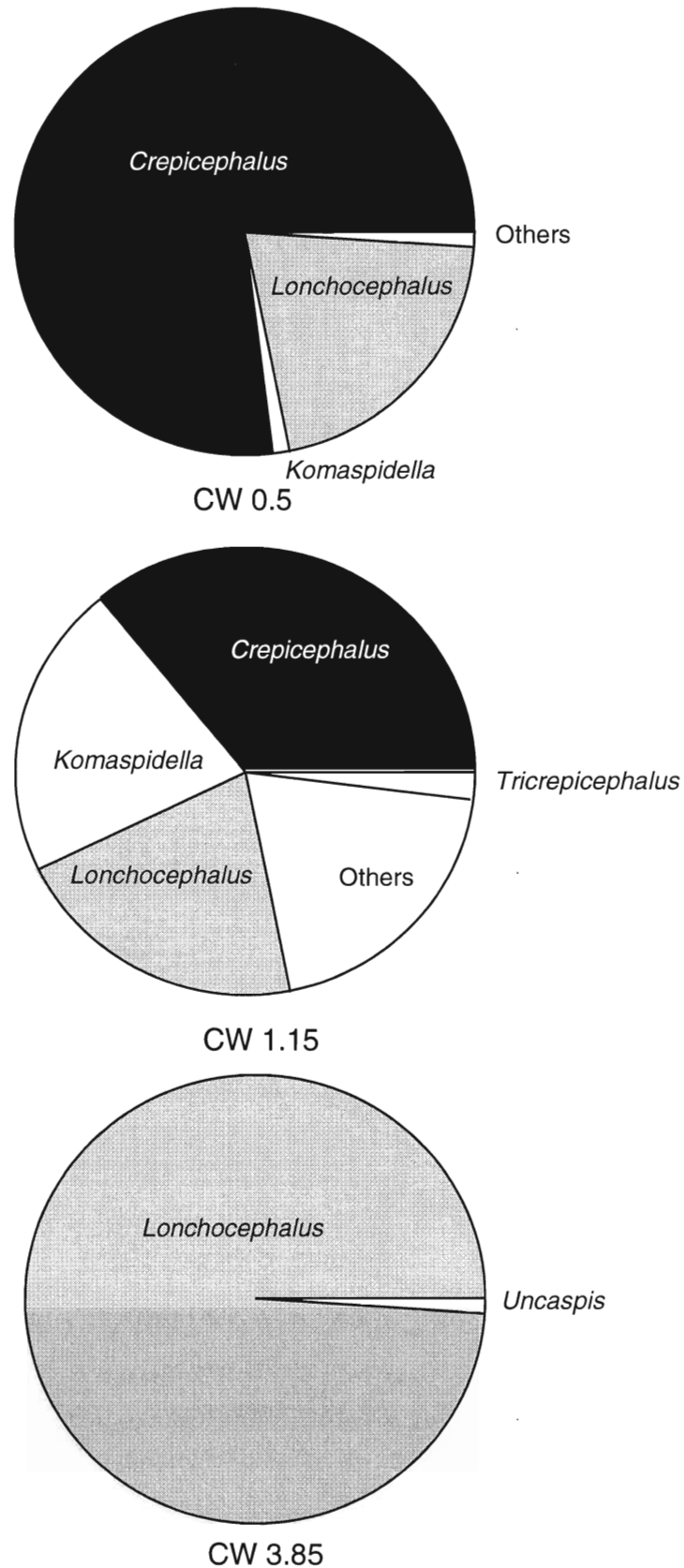


Figure 25- Relative abundances of taxa in representative collections of the *Crepicephalus-Komaspidella* Biofacies and the *Lonchocephalus* Biofacies. See Appendix III for full description of collections.

Deiracephalus and *Catillicephalus* (Fig. 26).

Assigned collections. Cow Head Group Bld. 39.

Uncaspis Biofacies

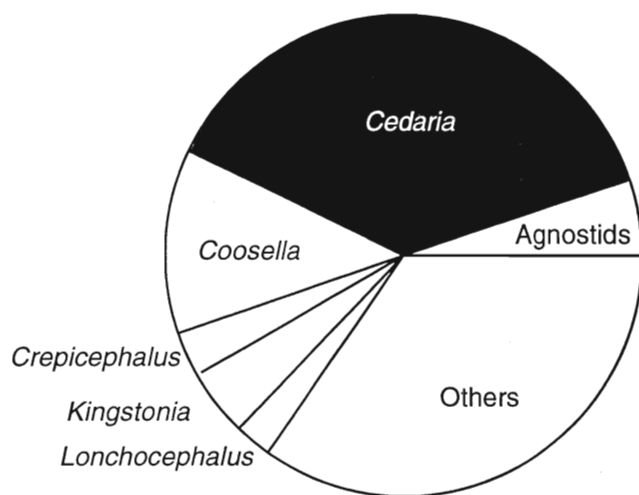
Composition. Cluster analysis (Fig. 22) grouped together two collections from the outer shelf shales and storm deposits of the Sullivan Formation (Aitken 1978, Cuggy and Westrop unpublished data) from Alberta into this biofacies. These collections are moderately diverse (5 species) and dominated by *Uncaspsis* (Fig. 27).

Assigned collections. Sullivan Formation TC 324 and TC 334.

Coosella-Glaphyraspis Biofacies

Composition. The *Coosella-Glaphyraspis* Biofacies is based on three collections from the *Coosella perplexa* Zone of the Nolichucky Formation (Fig. 22). They are dominated by *Glaphyraspis*, and all contain modest numbers of *Coosella* (Fig. 28). Diversity is high (8 species), and the collections also include *Tricrepicephalus* and *Kingstonia*. Quantitative abundance is not available for the correlative intervals in other parts of North America, although faunal lists also indicate that this biofacies occurs in Texas (Palmer, 1954).

Cedaria Biofacies



Boulder 39

Figure 26- Relative abundances of taxa in representative collection of the *Cedaria* Biofacies. See Appendix III for full description of collections.

Uncaspis Biofacies

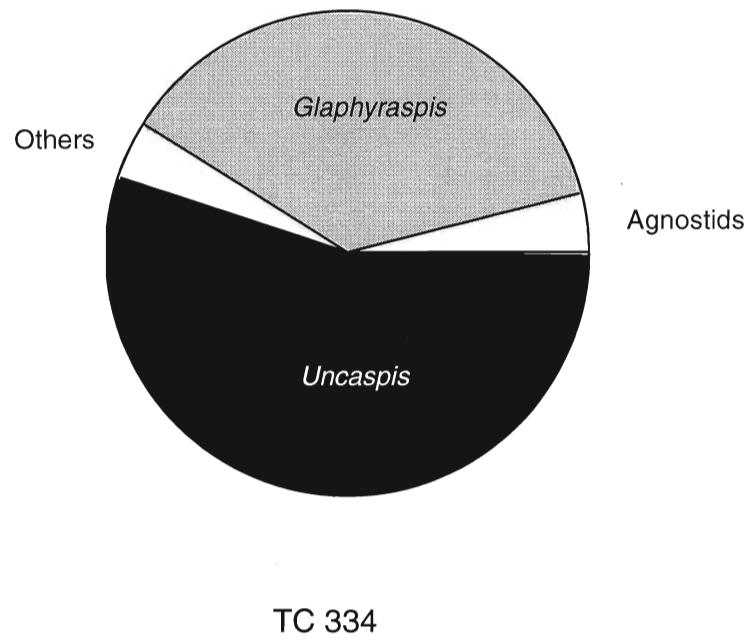
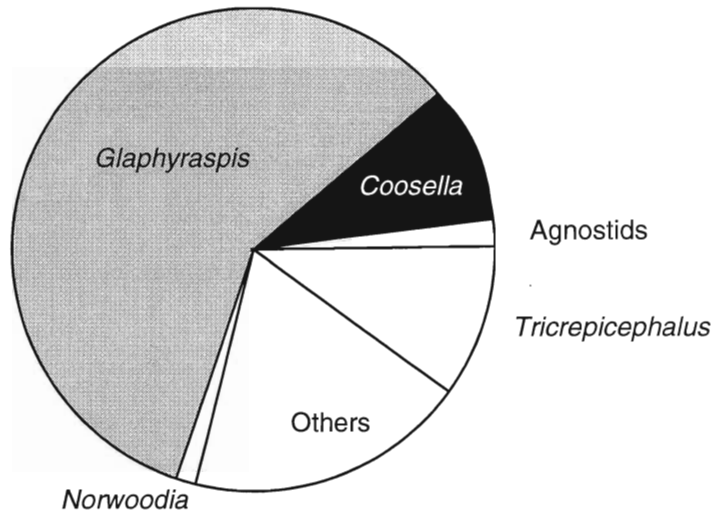
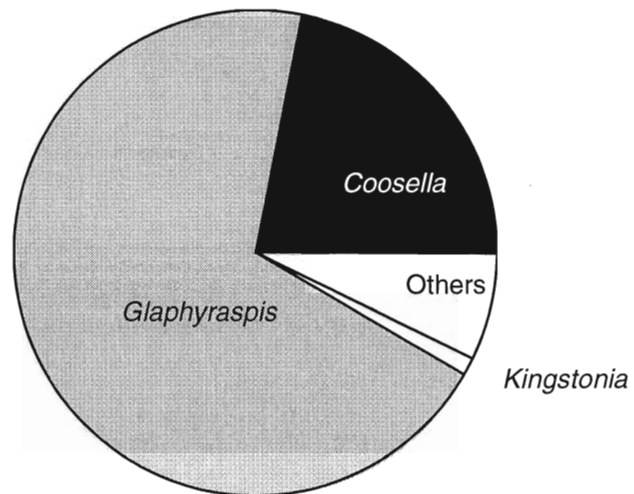


Figure 27- Relative abundances of taxa in representative collection of the *Uncaspis* Biofacies. See Appendix III for full description of collections.

Coosella-Glaphyraspis Biofacies



BG 46.5



BG 50

Figure 28- Relative abundances of taxa in representative collections of the *Coosella-Glaphyraspis* Biofacies. See Appendix III for full description of collections.

Assigned collections. Nolichucky Formation BG 46.5, BG 47.7, BG 50.

Lower Steptoean Biofacies

In contrast to the Marjuman, the lower Steptoean is dominated by a single *Aphelaspis* Biofacies (Fig. 22) that is recognized in all localities examined from North America. This demonstrates that the extinction involved a sharp reduction in biofacies differentiation (beta diversity; Sepkoski, 1988) from the late Marjuman to early Steptoean (Fig. 29). This is indicated by the drop from four biofacies in the upper Marjuman down to a single biofacies in the lower Steptoean.

A similar pattern is seen at the top of the Sunwaptan Stage (Ludvigsen and Westrop, 1983), where the *Missisquoia* Biofacies becomes dominant throughout carbonate shelf facies following the extinction. This is in striking contrast to an earlier shelf that had a number of biofacies before the end Sunwaptan extinction event (Ludvigsen and Westrop 1983; Westrop and Ludvigsen 1987). The pattern is repeated again following the late Steptoean extinction, when a single, low diversity biofacies (*Parabolinoides* Biofacies) (Westrop 1986; Ludvigsen *et al.* 1989) replaces several more diverse biofacies (Pratt 1992).

<i>Aphelaspis buttsi</i> Zone			Aphelaspis		No Data	Aphelaspis
<i>Coosella perplexa</i> Zone	Coo-Gla	No Data	Coosella-Glaphyraspis	No Data	No Data	Kingstonia
<i>Crepicephalus</i> Zone	Uncaspis, and Tri-Nor	Cr- Lon	No Data	Tri-Nor & Ced	No Data	Kingstonia

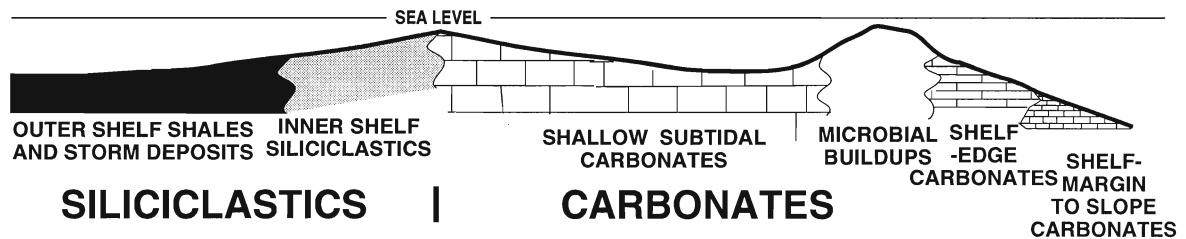


Figure 29 - Schematic transect across the North American shelf across the upper marjuman - Lower Steptoean showing the distribution of biofacies. Abbreviations: Coo-Gla., *Coosella-Glaphyraspis* Biofacies; Tri-Nor., *Tricrepicephalus*-Norwoodiid Biofacies; Cr-Lon., *Crepicphalus*-*Lonchocephalus* Biofacies; Ced., *Cedaria* Biofacies.

Aphelaspis Biofacies

Composition. Cluster analysis (Fig. 22) grouped together thirty-two collections from localities and lithofacies across North America. All of the collections have low diversity (less than 9 species) and are dominated by *Aphelaspis* (Fig. 30). Many of the collections also include a significant number of *Glaphyraspis* specimens.

Assigned collections. Nolichucky Formation BG 51.8, BG53.5, BG 55.7, BG 55.9, Bg 57.4, BG 71.3, DV 56.8, TS 36.5, TS 36.8, TS 38.2, TS 39.2, TS 44.4, TS 46.1, DF 12.8, DF 33.4, W15.7, W16.6, W21.3, W 28.3, W28.7, W35.7, W 42.3, W 50, TH 35.2, Rabbitkettle Formation N 124.5, N125.5, N128, Sullivan Formation GSC 72771, GSC 75340, GSC 75342, Cow Head Group Boulder49, Eau Claire Formation LFD12.6.

DIVERSITY PATTERNS OF BIOFACIES

A marked decline in species diversity takes place across the Marjuman-Steptoean boundary in the Nolichucky Formation. This is most competely documented in the Beech Grove section (Fig. 31). Here, diversity in the upper Marjuman *Crepicephalus* Zone is high with the number of species per collection in the range of 6 to 8. There is a modest decline in the overlying *Coosella perplexa* Zone, with a dramatic reduction in the *Aphelaspis buttsi* Zone to only one or two species per collection. Because sample sizes are

APHELASPIS BIOFACIES

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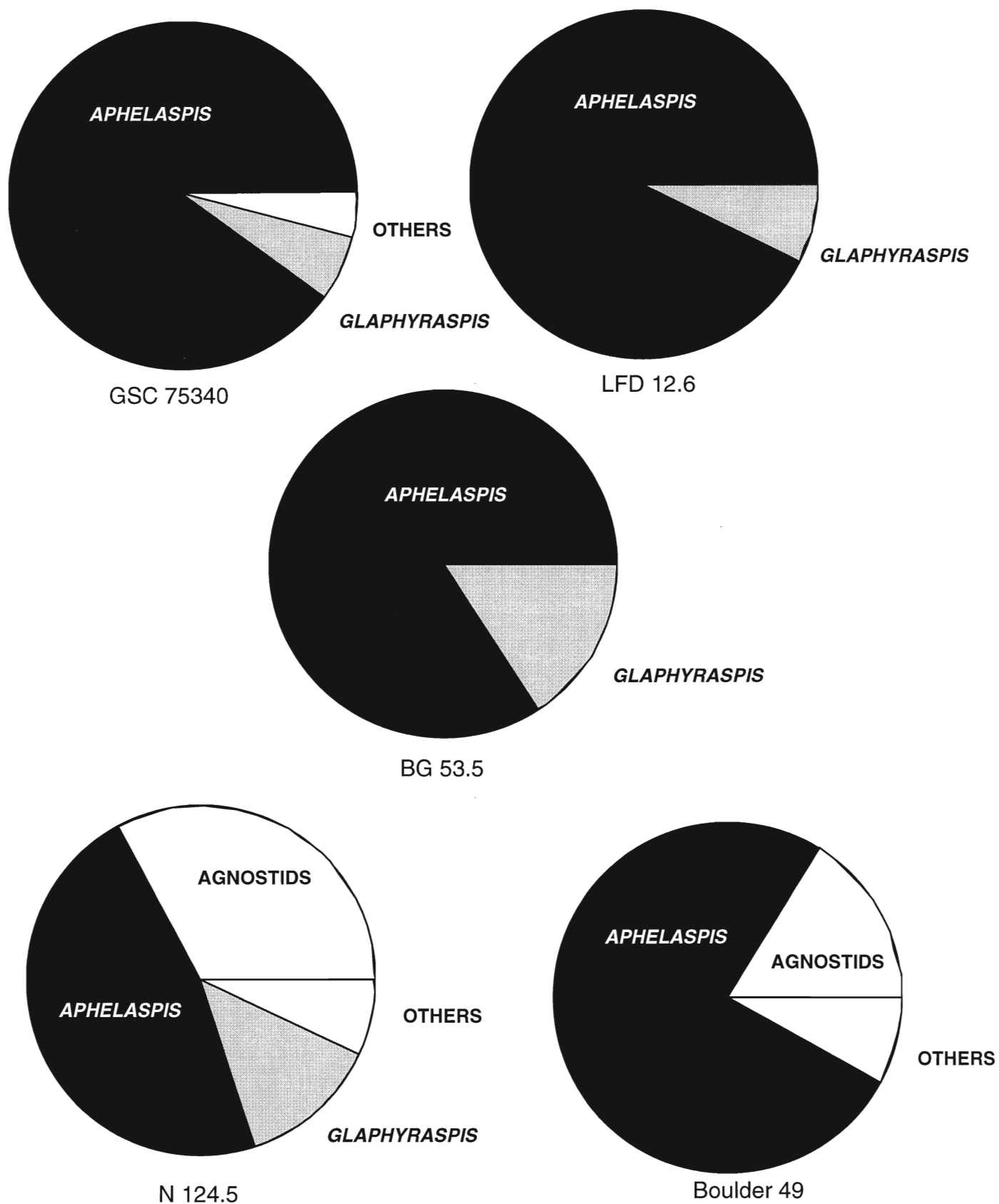


Figure 30- Relative abundances of taxa in representative collections of the *Aphelaspis* Biofacies. See Appendix III for full description of collections.

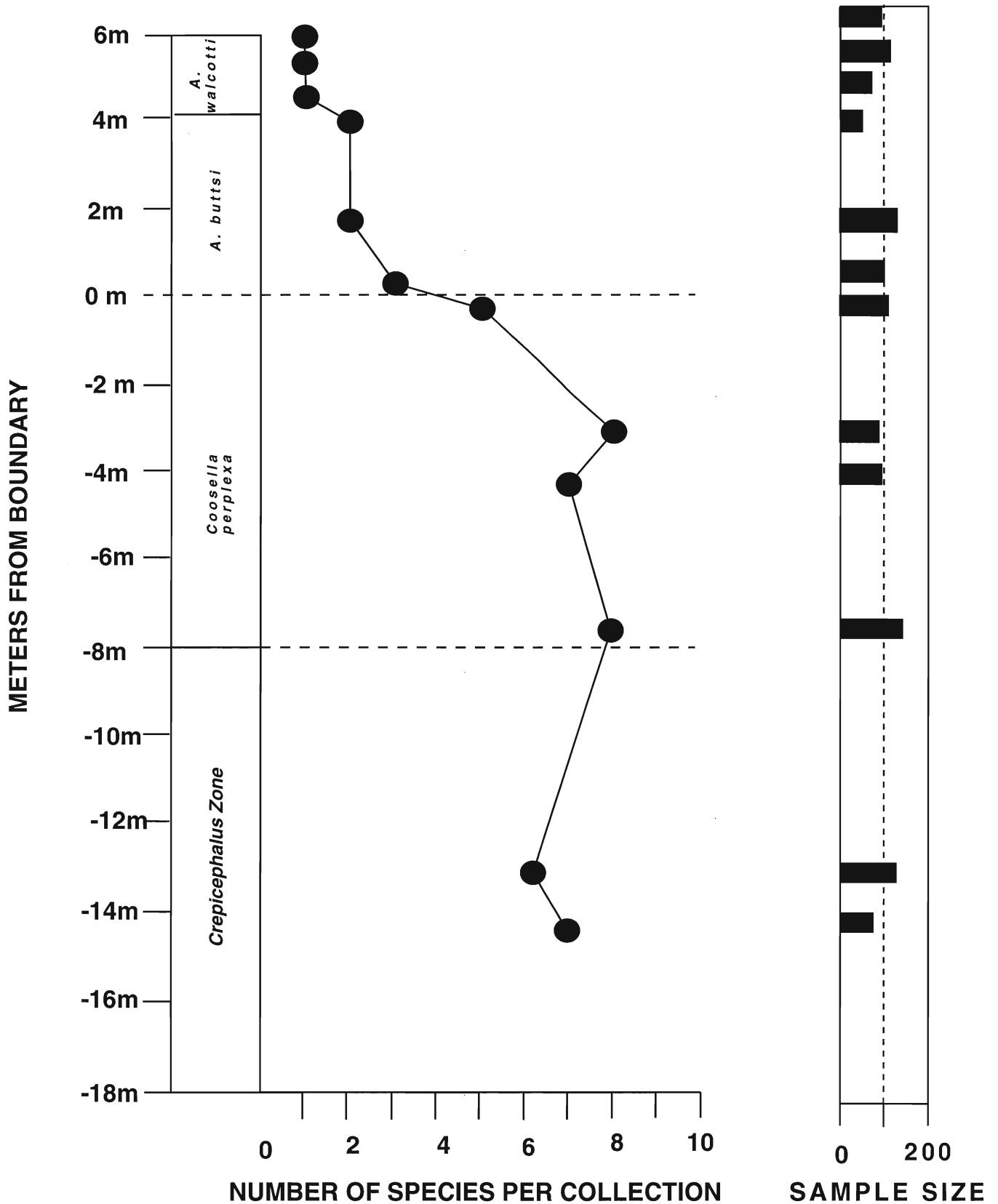


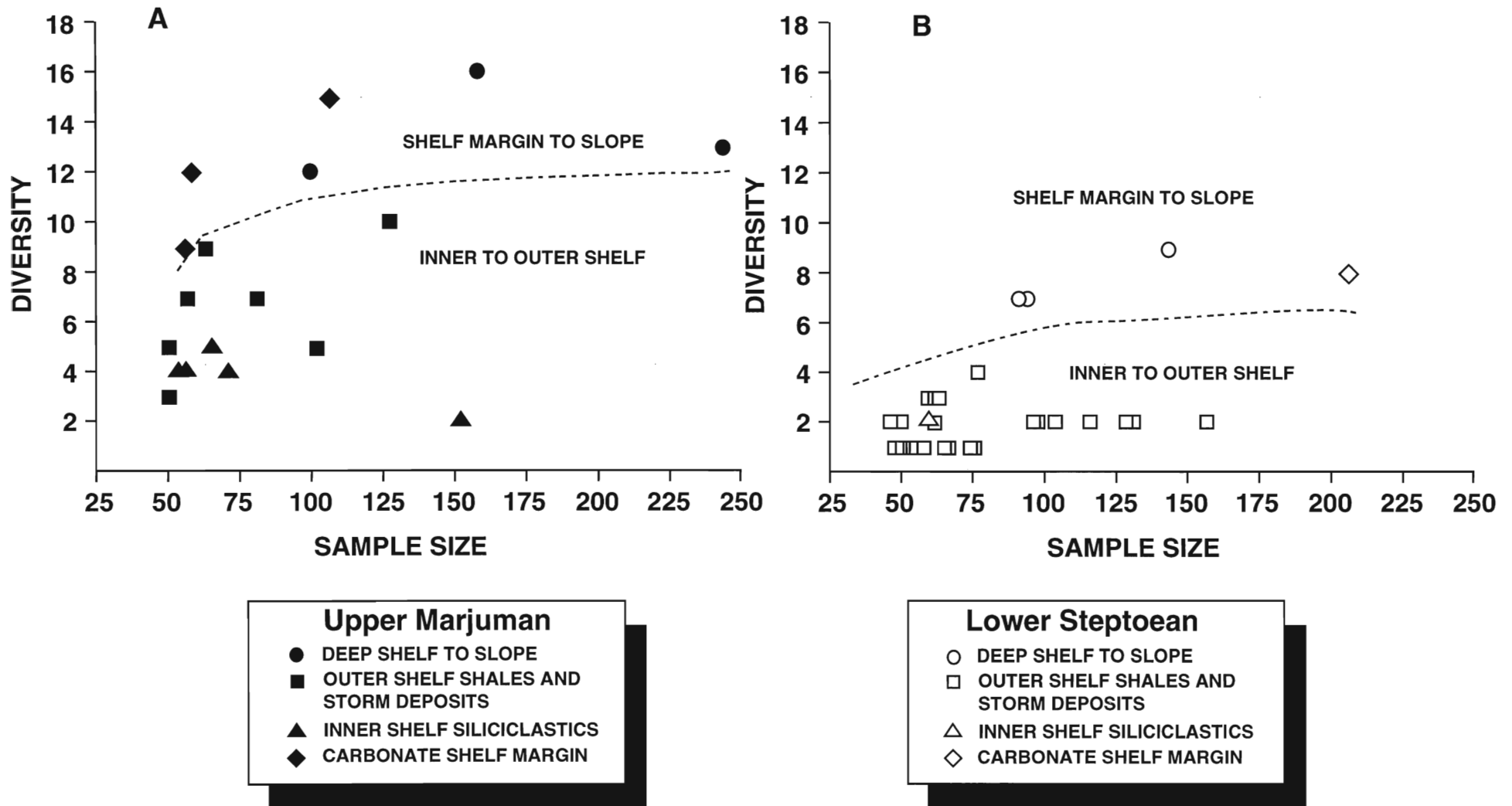
Figure 31- Plot of the number of species per collection and collection size across the Marjuman-Steptoean boundary at Beech Grove.

comparable throughout the section, this decline cannot be dismissed as a sampling artifact.

A comparable diversity decline is evident in all other North American localities included in this study. Upper Marjuman diversities are relatively high, with most of the collections containing between six and fifteen species (Figure 32a). This is in sharp contrast to the lower Steptoean, where diversity in collections is usually in the range of one to ten species per collection (Figure 32b). The drop in diversity in this situation represents a decrease in within-habitat or alpha diversity (Sepkoski, 1988) and demonstrates that both alpha and beta diversity drop across the upper Marjuman-lower Steptoean boundary.

The data also indicate that slope and shelf margin collections have higher diversities than shelf collections, both before and after the extinction. In the upper Marjuman collections, the slope and shelf margin collections have a mean diversity of 10 species compared to a mean diversity of 5 in the shelf. In the lower Steptoean, the mean slope and shelf margin diversity is 8 species, whereas mean shelf diversity is 2 (Figs. 32a and b). Bambach (1977) described the lower diversity found in shelf habitats ('epeiric' seas), compared it to that shelf margins throughout the Phanerozoic, and determined that lower shelf diversities were possibly due to differences in environmental stability and resource supplies.

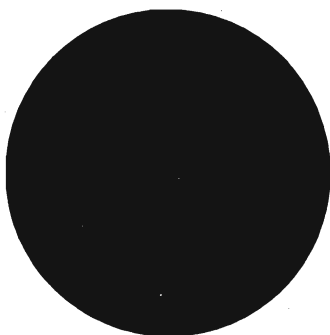
DIVERSITY PATTERNS



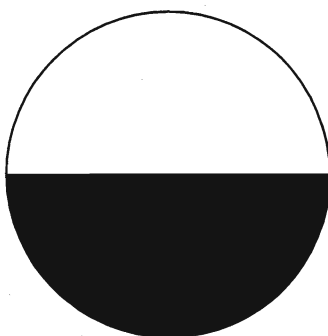
The drop in diversity across the Marjuman-Steptoean boundary is accompanied by extensive immigration of taxa from off-shelf sites. Figure 33 shows the proportion of immigrant taxa in the biofacies during each biostratigraphic unit. During the *Coosella perplexa* Zone, immigrant species from off-shelf sites make up 9% of the composition of the zone. In the *Aphelaspis buttsi* Zone, immigrant species make up 50% of the species present, and finally, in the *A. walcotti* Zone, they make up 100% of the species present (Fig. 33). A similar pattern has been observed for the Sunwaptan-Ibexian extinction event (Westrop, 1990), where the extinction was believed to be due to a major biogeographic and ecologic reorganization of the shelf.

NOLICHUCKY FORMATION

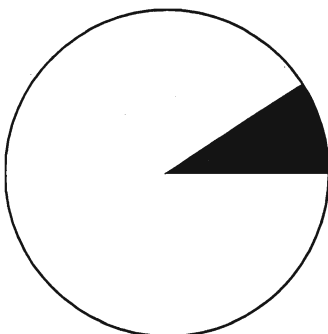
A. walcotti



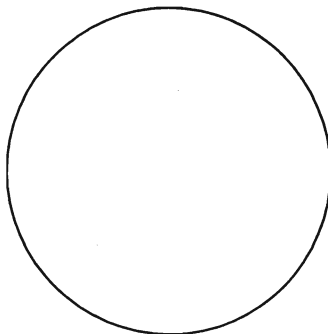
A. buttsi



Coosella perplexa



Crepicephalus



LEGEND



Species characteristic
of shelf environments
prior to extinctions



Species characteristic
of off-shelf environments
prior to extinctions

Figure 33- Pie diagrams showing the proportion of immigrant taxa versus "hold-over" taxa across the Marjuman-Steptoean boundary in the Nolichucky Formation based on all collections.

CHAPTER 5

CONCLUSIONS

In this study a new biostratigraphic and biofacies framework was established for the Nolichucky Formation in Tennessee and Virginia. Five new species-based zones are recognized: *Crepicephalus*, *Coosella perplexa*, *Aphelaspis buttsi*, *A. walcotti*, and *A. tarda* zones. Analysis of generic relative abundance data indicates that three biofacies were present in the Nolichucky Formation. The lower Steptoean faunas are assigned to one low diversity, *Aphelaspis*-dominated biofacies, whereas the underlying upper Marjuman strata contain two higher diversity, stratigraphically separate biofacies, the *Coosella-Glaphyraspis* Biofacies and the *Tricrepicephalus*-Norwoodiid Biofacies. In addition, four other biofacies were recognized from other upper Marjuman localities in North America.

In the study area, the extinctions are associated with a deepening (Osleger and Read, 1993) and shifts of lithofacies. This deepening is seen in some localities by the replacement of the carbonate-rich facies of Association B (Fig. 11) of the Bradley Creek Limestone Member by the shale-rich facies of Association A (Fig. 10) of the Upper Shale Member (see Fig.16 for an example at Beech Grove, Tennessee). This deepening and lithofacies shift is

slightly diachronous in the Nolichucky Formation and occurs in some sections in the *C. perplexa* Zone and in the overlying *A. buttsi* Zone in other sections. Osleger and Read (1993) considered the deepening to mark a sequence boundary and identified the same sequence boundary in the Orr Formation of Utah and the Riley Formation of Texas. They suggested that the sea level change was eustatic in nature. This interpretation has been challenged recently by Thomas (1995), who argued that deepening is restricted to miogeoclinal facies. He interpreted sequences cratonward of the miogeocline as recording a shallowing during the extinction interval (Thomas 1995). However, Thomas' data has not yet been fully published and cannot be evaluated.

The extinctions at the Marjuman-Steptoean boundary involve both a diversity decline within habitats (alpha diversity) (Fig. 32a&b) and in differentiation between habitats (beta diversity) (Fig. 29). These low diversities following the extinction lead to a remarkable uniformity in both diversity and composition across the entire shelf. This is evident from the continent-wide distribution of the low diversity *Aphelaspis* Biofacies. The pattern of declining alpha and beta diversity is comparable to that documented for the extinctions across the Sunwaptan-Ibexian boundary (Westrop and Ludvigsen 1987; Westrop 1988).

The three trilobites mass extinctions of the Upper Cambrian have been the subject of considerable research (e.g., Palmer 1965a, 1979, 1984; Stitt 1971, 1975, 1977; Westrop and

Ludvigsen 1987; Westrop 1988, 1989b, 1990, 1991; Thomas 1995) and a variety of explanatory theories have been proposed. The evidence for a sea level rise at the upper Marjuman-lower Steptoean Boundary raises the possibility that the extinctions involved habitat destruction and the elimination of biofacies, as suggested by Westrop and Ludvigsen (1987) for the extinction at the top of the Sunwaptan Stage. However, the available data from the Nolichucky cannot exclude the possibility of a decline in shelf water temperature or level of dissolved oxygen. Additional work on lithofacies and biofacies changes in other regions is required.

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PLATES

Plate 1

Figs. 1-2 *Crepicphalus buttsi* Resser

1 Dorsal view of cranidium, DV 46.2, 5x

2 Dorsal view of pygidium, DV 46.2, 4x

Fig. 3 *Crepicephalus scissilis* Resser Dorsal view of pygidium, BG 46.5, 4.5x

Figs. 4-5 & 13 *Pseudagnostus* sp.

4 Dorsal view of cranidium, BG47.7, 6x

5 Dorsal view of pygidium, BG 47.7, 9x

13 Dorsal view of pygidium, BG46.5, 6x

Fig. 6 *Kingstonia inflata* Resser Dorsal view of cranidium, BG 31.8, 9x

Fig. 7 *Pemphigaspis bulata* Hall Dorsal view of cranidium, BG 31.8, 6x

Fig. 8 *Coosella planicanda* Rasetti Dorsal view of cranidium, BG 46.5, 6x

Figs. 9-11 *Tricrepicephalus texanus* (Shumard)

9 Dorsal view of cranidium, BG 47.7, 6x

10 Dorsal view of pygidium, BG 31.8, 5x

11 Dorsal view of free cheek, BG 47.7, 4.5x

Fig. 12 *Llanoaspis walcotti*(Resser) Dorsal view of cranidium, BG 31.8, 5x

Plate 1

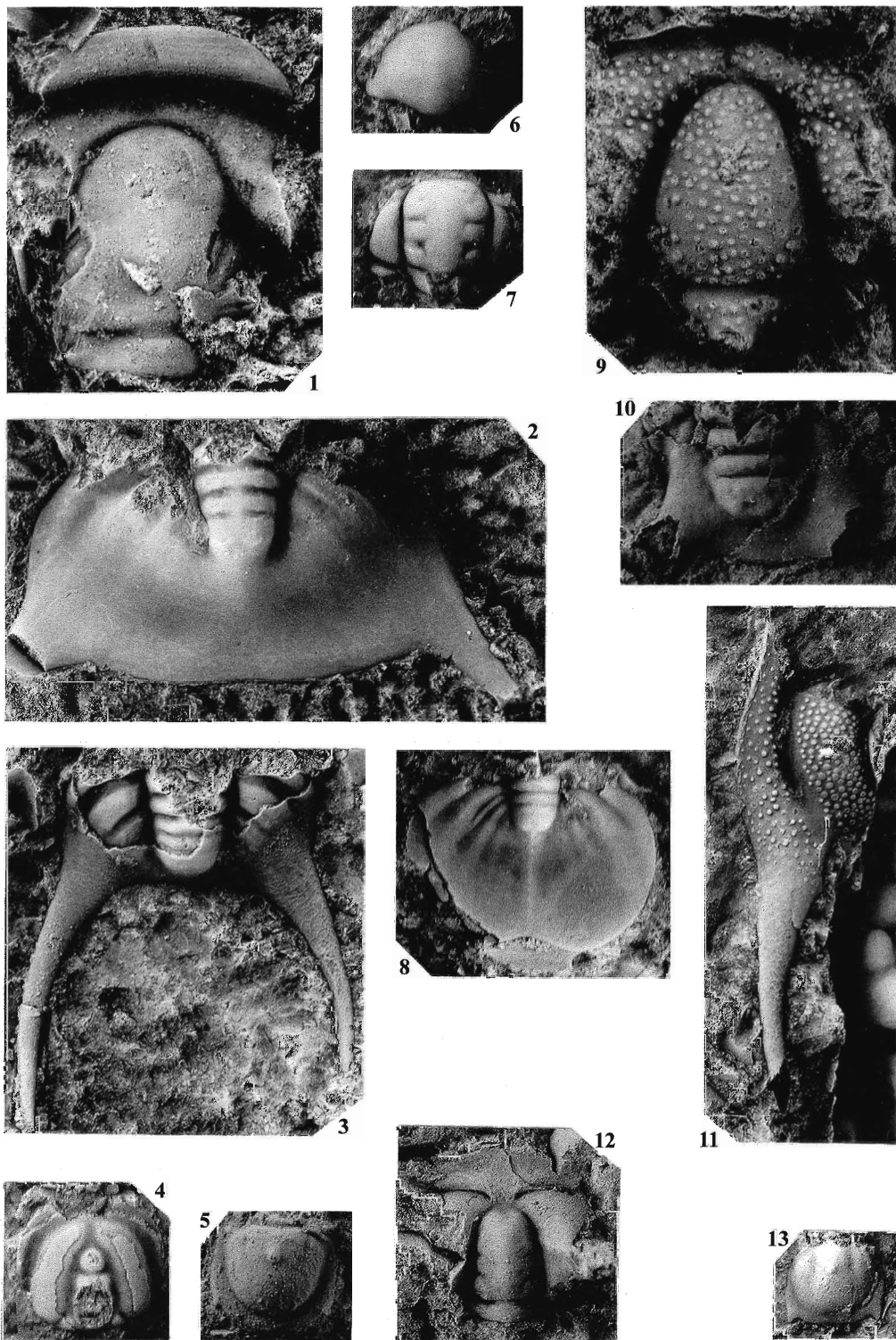


Plate 2**Figs. 1-5** *Coosella perplexa* (Palmer)

- 1 Dorsal view of cranidium, TS 36.5, 7x
- 2 Dorsal view of cranidium, BG 47.7, 9x
- 3 Dorsal view of cranidium, DV 32.3, 7.5x
- 4 Dorsal view of pygidium, BG 47.7, 6x
- 5 Dorsal view of pygidium, BG 46.5, 6x

Figs. 6&7 *Glaphyraspis parva* (Walcott)

- 6 Dorsal view of cranidium, BG 50, 9x
- 7 Dorsal view of pygidium, BG 50, 12x

Fig. 8 *Cheilocephalus brevilobus* (Walcott) Dorsal view of pygidium, BG 50, 7x**Figs. 9-13.** *Aphelaspis buttsi* (Kobayashi)

- 9 Dorsal view of cranidium, TS 36.8, 7x
- 10 Dorsal view of pygidium, TS 36.8, 9x
- 11 Dorsal view of cranidium, TS 36.8, 9x
- 12 Dorsal view of free cheek, BG 51.8, 6x
- 13 Dorsal view of cranidium, TS 37.1, 9x

Fig. 14 *Aphelaspis walcotti* Resser Dorsal view of cranidium, W 21.3, 12x

Plate 2

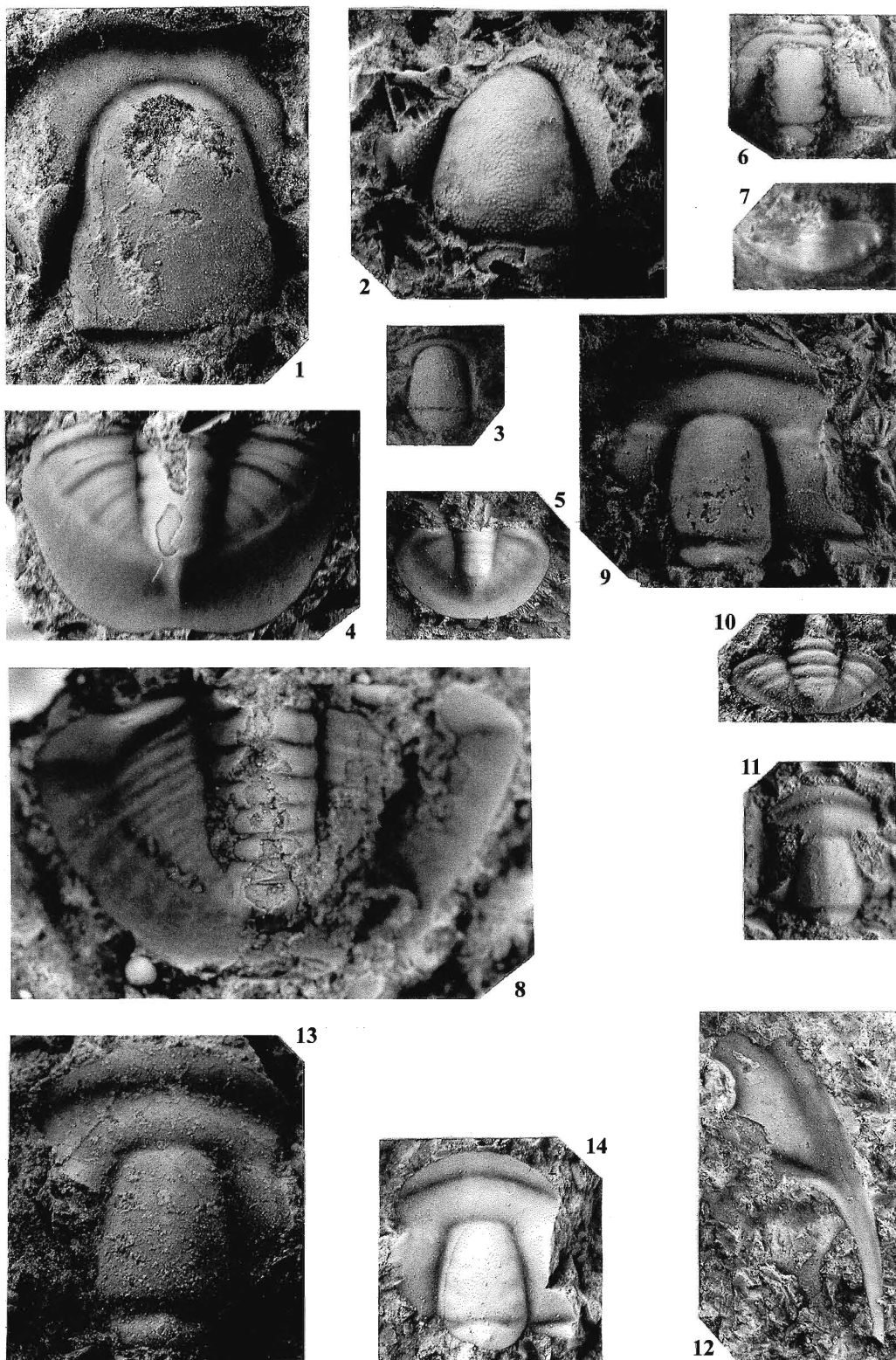


Plate 3

Figs. 1 & 2 *Aphelaspis walcotti* Resser, TS 39.2, 9x

1 Dorsal view of pygidium, TS 39.2, 9x

2 Dorsal view of free cheek, DV 55.7, 9x

Figs 3-6 *Aphelaspis washburnensis* Rasetti

3 Dorsal view of cranidium, BG 57.8, 12x

4 Dorsal view of pygidium, BG 57.8, 9x

5 Dorsal view of pygidium, BG 55.9, 9x

6 Dorsal view of free cheek, BG 57.8, 9x

Figs. 7-9 *Aphelaspis tarda* Rasetti

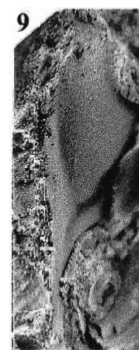
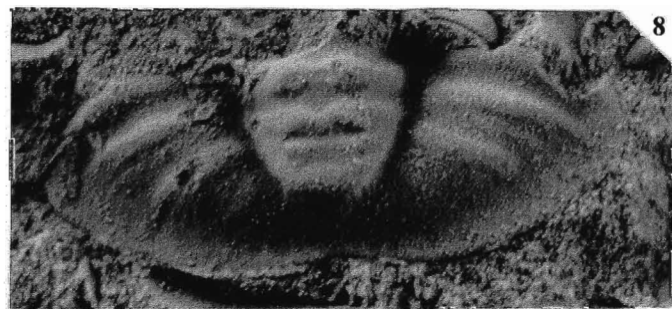
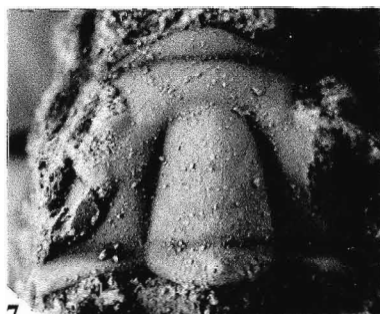
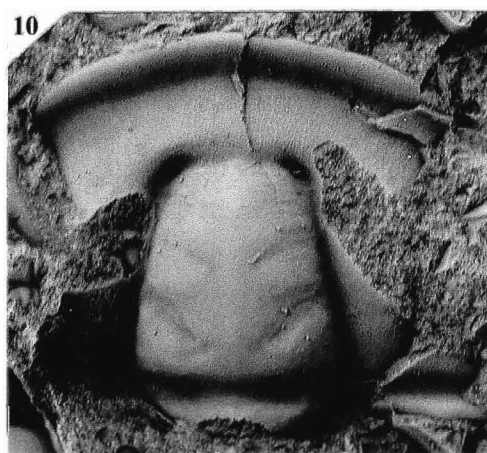
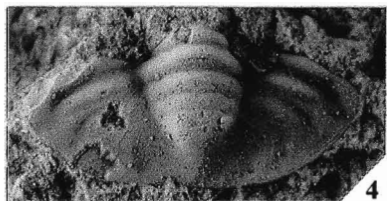
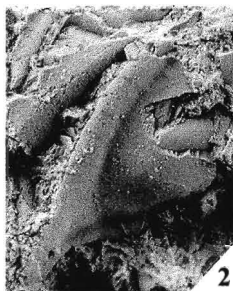
7 Dorsal view of cranidium, BG 66.2, 9x

8 Dorsal view of pygidium, BG 66.2, 9x

9 Dorsal view of free cheek, W 35.7, 7x

Fig. 10 *Aphelaspis punctata* Rasetti Dorsal view of cranidium, W 42.3 6x

Plate 3



APPENDIX 1

SPECIES PRESENT IN COLLECTIONS

Order AGNOSTIDA Kobayashi, 1935

Superfamily AGNOSTACAE Henningsmoen, 1951

Family AGNOSTIDAE M'Coy, 1849

Subfamily KOMAGNOSTINAE Pratt, 1992

Genus *Kormagnostus* Resser, 1938a

Type Species. *Agnostus seclusus* Walcott, 1884, Nolichucky Formation, Tennessee (by synonymy with *Kormagnostus simplex* Resser, 1938a; see Robison, 1988, p.45).

Kormagnostus sp.

Occurrence. From the *Crepicephalus* Zone and *Coosella perplexa* Zone of Beech Grove Tn, collection BG 31.8, BG 36.5, BG 38, Bg 47.7.

Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

Genus *Pseudagnostus* Jaekel, 1909

Type species. *Agnostus cyclopyge* Tullberg, 1880, Andrarum Limestone, Sweden (by original designation).

Pseudagnostus sp. A

Pl. 1, figs. 4, 5 & 13

Occurrence. Nolichucky Formation, Beech Grove and Washburn TN collections BG 46.5, BG 47.5, W 8.8, W35.7.

Discussion. Cranidium as *Pseudagnostus communis* Hall and Whitfield, 1877. Pygidium effaced and inflated. Has a broad border, with two small spines.

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1933

Family ELVINIINAE Kobayashi, 1935

Subfamily APHELASPIDINAE Palmer, 1960

Genus *Aphelaspis* Resser, 1935

Type species. *Aphelaspis walcotti* Resser, 1938a, Nolichucky Formation, Virginia (By original designation).

Aphelaspis buttsi Kobayashi, 1936

Pl. 2, figs. 9-13

1926 *Olenus* cf. *truncatus* (Brunnich) Butts, pl. 9, figs. 6,7.1936 *Proaulacopleura buttsi* Kobayashi, p. 93, pl. 15, fig. 6.

- 1938a *Proaulacopleura buttsi* Kobayashi, Resser, p. 95. pl. 16,
fig. 18.
- 1962b *Aphelaspis buttsi*, Palmer, p. 35, pl. 4, figs. 23, 26,
31, 32; pl. 6. fig. 15.
- 1965 *Aphelaspis buttsi*, Rasetti, p. 87, pl. 16, figs. 1-7.

Occurrence. Nolichucky Formation, occurring in most localities in the *Aphelaspis buttsi* Zone, collections BG 51.8, BG 53.5, W 15.7, W 16.6, TS 36.5, TS 37.1, DF 12.8, DF 16.2, DF 17.5.

Aphelaspis lata Rasetti, 1965

- 1965 *Aphelaspis lata*, Rasetti, p. 87, pl. 16, figs. 8-20.

Occurrence. Nolichucky Formation from Beech Grove in the *Aphelaspis buttsi* Zone collection BG 55.7.

Aphelaspis laxa Resser, 1938

- 1938 *Aphelaspis laxa*, Resser, p. 60, pl. 13, fig. 18.
- 1965 *Aphelaspis laxa*, Rasetti, p. 80-81, pl. 12, figs. 18-21;
pl. 13, figs 8-15.

Occurrence. Nolichucky Formation from the *Aphelaspis walcotti* Zone of Duffield Va. collection DF 18.3, DF19.1.

Aphelaspis punctata Rasetti, 1965

Pl. 3, fig. 10

1965 *Aphelaspis punctata*, Rasetti, p. 92, pl. 18, figs. 21-29.

Occurrence. Nolichucky Formation from Washburn TN in the *Aphelaspis tarda* Zone collections W 42.3, W 50.

Aphelaspis quadrata Resser, 1938 a

1938a *Aphelaspis quadrata* Resser, p. 59, pl. 13, figs. 16-17.

1965 *Aphelaspis quadrata*, Rasetti, p. 78, pl. 18, figs. 1-9.

Occurrence. From the *Aphelaspis walcotti* Zone of the Nolichucky Formation collections BG 57.4, W 28.3.

Aphelapis rotunda Rasetti 1965

1965 *Aphelaspis rotunda* Rasetti, p. 84-85, pl. 14, figs 1-12.

Occurrence. From the *Aphelaspis walcotti* Zone of the Nolichucky Formation at Washburn Tn. collections W 25, W 27.5.

Aphelaspis tarda Rasetti 1965

Pl. 3, figs. 7-9

1965 *Aphelaspis tarda* Rasetti, p. 79-80, pl 20, figs. 1-18.

Occurrence. Common in all localities in the Nolichucky Formation, from the *Aphelaspis tarda* Zone collections BG 66.2, BG 71.3, W 35.7, TS 48.3, TS 53.5, DF 30.1, DF 33.4, DF 60.9, DV 56.8.

Aphelaspis walcotti Resser 1938a

Pl. 2, fig. 14, Pl. 3, figs. 1, 2

1938a *Aphelaspis walcotti* Resser, p. 59, pl. 13, fig. 14.

1962b *Aphelaspis walcotti*, Palmer, p. 33, pl. 4, figs. 24, 28, 33.

1938a *Aphelaspis simulans* Resser, p. 59, pl. 13, figs. 19-21.

1965 *Aphelaspis walcotti*, Rasetti, p. 76, pl. 18, figs. 10-20.

Occurrence. Common in the *Aphelaspis walcotti* Zone of the Nolichucky Formation from collections W 21.3, W 28.7, TS 38.2, TS 39.2, TS 40.8, DV 55.7.

Aphelaspis washburnensis Rasetti, 1965

Pl. 3, figs. 3-6

1965 *Aphelaspis washburnensis* , Rasetti, p. 85, pl. 17, figs.
15-23.

Occurrence. Nolichucky Formation, from many localities in
the *Aphelaspis walcotti* Zone from collections BG 55.9, BG 57.8, TS
44.4, DF 24.2, DF 28.7.

Subfamily ELVINIIDAE Kobayashi, 1935

Genus *Dytremacephalus* Palmer, 1954b

Type species. *Dytremacephalus granulatus* Palmer, 1954b, Riley
Formation Texas (by original designation).

Dytremacephalus angulatus Rasetti, 1965

1965 *Dytremacephalus angulatus* Rasetti, p. 98-101, fig. 2a,
pl. 21 figs. 1-9.

Occurrence. From the *Aphelaspis tarda* Zone of the Nolichucky
Formation, at Beech Grove TN collection BG 71.3.

Superfamily UNCERTAIN

Family TRICREPICEPHILIDAE Palmer, 1954b

Genus *Tricrepicephalus* Kobayashi, 1935

Type species. Arionellus (Bathyurus) texanus Shumard, 1861,
Riley Formation, Texas (by original designation).

Tricrepicephalus texanus (Shumard, 1861)

Pl. 1, figs. 9-11

1965 *Tricrepicephalus thoosa* (Walcott); Rasetti, p. 54, pl.
6, figs. 1-4.

1992 *Tricrepicephalus texanus*, Pratt, p. 62, pl. 21, figs. 1-7
(see for synonymy).

Occurrence. Nolichucky Formation in the *Crepicephalus* Zone and the *Coosella perplexa* Zone from collections BG 31.8, BG 33.4, BG 33.9, BG 36.5, BG 38, BG 42, BG 46.5 BG 47.7, BG 50, W 1.5, TS 12.1, TS 14.1, DV 4.6, DV 13.5, DV 32.3. Also widespread in North America during the *Cedaria* and *Crepicephalus* Zones, and in the Upper Cambrian of Argentina.

Genus *Crepicephalus* Owen, 1852

Type species. Dikelocephalus iowensis Owen, 1852, Eau Claire Formation, Minnesota (designated by Walcott, 1886).

Crepicephalus buttsi Resser, 1938a

Pl. 1, figs. 1-2

- 1938a *Crepicepalus buttsi*, Resser, p. 72, pl. 11, figs. 28, 29, 49, 50.
- 1938a *Crepicepalus expansus*, Resser, p.73, pl. 11, fig. 36.
- 1965 *Crepicepalus buttsi*, Rasetti, p. 45, pl. 6, figs. 5, 6.

Occurrence. The *Coosella perplexa* Zone of the Nolichucky Formation at Dickensonville Va. from collection DV 46.2.

Crepicephalus scissilis Resser, 1938

- 1938 *Crepicephalus scissilis*, Resser, p. 72, pl. 11, figs. 34, 35.

Occurrence. Nolichucky Formation from the *Coosella perplexa* Zone of Beech Grove Tn, BG 46.5.

Genus *Coosella* Lochman, 1936

Type species. *Coosella prolifica* Lochman, 1936, Bonneterre Dolomite, Missouri (by original designation).

Coosella perplexa (Palmer, 1954)

Pl. 2, figs1-5

1954 *Crepicephalus? perplexa*, Palmer, p. 733, pl. 77, figs.
1, 2, 4.

1965 *Coosella perplexa*, Rasetti, p. 50, pl. 15, figs. 19-26.

Occurrence. The *Coosella perplexa* Zone of the Nolichucky Formation from collections BG 46.5, BG 47.7, BG 50, W 8.8, DF 6, DV 32.3, DV 46.2. Also found in the Riley Formation of Texas.

Coosella planicauda Rasetti, 1965

Pl. 1, fig. 8

1965 *Coosella planicauda* Rasetti, p. 49, pl. 7, figs. 1-5.

Occurrence. From the *Crepicephalus* Zone of the Nolichucky Formation at Beech Grove Tn. from collections BG 31.8, BG 32.5, BG 38, BG 42.

Genus *Coosia* Walcott, 1911

Type species. *Coosia superba* Walcott, 1911, Conasauga Formation, Alabama (by original designation).

Coosia alethes (Walcott, 1916b)

1916b *Blountia alethes*, Walcott [part], p. 397, pl. 64, figs. 1,
1a [only].

- 1938a *Coosia alethes*, Resser, p. 71.
 1965 *Coosia alethes*, Rasetti, p. 52, pl. 6, figs 15-18; pl. 7,
 figs. 6-13.

Occurrence. Common in the upper *Crepicephalus* Zone and *Coosella perplexa* Zone of the Nolichucky Formation found in collections from BG 38, TS 10.4, TS 12.1, DV 4.6, DV 46.2.

Family ASAPHISCIDAE Raymond, 1924

Subfamily BLOUNTIINAE Lochman *in* Lochman and Duncan, 1944

Genus *Blountia* Walcott, 1916b

Type species. *Blountia mimula* Walcott, 1916a, Maryville Formation, Tennessee (by original designation).

Blountia mimula Walcott, 1916b

- 1916b *Blountia mimula*, Walcott, p. 399, pl. 61, figs. 4, 4a-c.
 1938a *Blountia mimula*, Resser, p. 63, pl. 12, figs. 18, 19.
 1965 *Blountia mimula*, Rasetti, p. 59. pl. 10, figs. 3-7.

Occurrence. The *Crepicephalus* Zone and *Coosella perplex* Zone from Beech Grove from collections BG 32.5, BG 33.4, BG 36.5, BG 38, BG 46.5.

Subfamily KINGSTONIINAE Kobayashi, 1933

Genus *Kingstonia* Walcott, 1924

Type species. Kingstonia apion Walcott, 1924, Maryville Formation, Tennessee (by original designation).

Kingstonia inflata Resser, 1938a

Pl. 1, fig. 6

1938a *Kingstonia inflata*, Resser, p. 84, pl. 12, figs. 5, 6.

1938a *Kingstonia rotundata*, Resser, p. 83, pl. 12, figs. 9, 10.

1965 *Kingstonia inflata*, Rasetti, p. 60, pl. 8, figs. 21-28.

Occurrence. Common in the *Crepicephalus* Zone and the *Coosella perplexa* Zone of the Nolichucky Formation found in collections BG31.8, BG 33.4, BG 36.5, BG 47.7, TS 4.5, TS 14.1.

Family CHEILOCEPHALIDAE Shaw, 1956

Genus *Cheilocephalus* Berkey, 1898

Type species. Cheilocephalus st. croixensis Berkey, 1898, Upper Cambrian, Minnesota (by original designation)

Cheilocephalus brevilobus (Walcott, 1916b)

Pl. 2, fig. 8

- 1916b *Lisania? breviloba* Walcott, p. 404, pl. 66, figs. 3, 3a
 1965 *Cheilocephalus brevilobus*, Rasetti, p. 103, pl. 17, figs
 1-5.
 1992 *Cheilocephalus brevilobus*, Pratt, p. 69, pl. 24, figs.
 18-28 (see for complete synonymy).

Occurrence. From the *Coosella perplexa* Zone of the Nolichucky Formation, from Beech Grove Tn., collection BG 50.

Family LONCHOCEPHALIDAE Hupe, 1955

Remarks. The concept of this family is following that of Pratt (1992).

Genus *Terranovella* Lochman, 1938b

Type species. *Terranovella obscura* Lochman, 1938b, Cow Head Group, Newfoundland (by original designation).

Terranovella dorsalis (Hall, 1863)

- 1863 *Chonocephalities? (Arionellus?) dorsalis* Hall, p.22.
 1965 *Terranovella dorsalis*, Rasetti, p. 40, pl. 6, fig. 7.
 1992 *Terranovella dorsalis*, Pratt, p. 70, pl. 26, figs. 1-4
 (see for synonymy).

- 1992 *Terranovella dorsalis*, Westrop, p. 249, figs. 15.10-15.14.

Occurrence. *Crepicephalus* Zone of the Nolichucky Formation from Beech Grove TN, collection BG 46.5, Eau Claire Formation of Wisconsin, Orr Formation of Utah, and the Boothia Felix Formation of the the Canadian Artic Islands and Felix Member of the Port au Port Formation of Newfoundland. Also found in the *Cedaria prolifica* and *Cedaria brevifrons* zones of the Rabbitkettle Formation of the N.W.T..

Genus *Glaphyraspis* Resser, 1937

Type species. *Liostracus parvus* Walcott, 1899, Upper Cambrian Wyoming (by original designation).

Glaphyraspis parva (Walcott, 1899)

pl. 2, figs. 6, 7

- 1899 *Liostracus parvus* Walcott, p. 463, pl. 65, fig. 6.
 1937 *Glaphyraspis parva*, Resser, p. 12.
 1965 *Glaphyraspis parva*, Rasetti, p. 40, pl. 10, figs. 9-17.
 1965 *Glaphyraspis ornata*, Rasetti, p. 41, pl. 10, fig. 8, pl. 11, figs. 13, 14.
 1992 *Glaphyraspis parva*, Pratt, p. 71, pl. 26, figs. 13-22
 (see for synonymy).

Occurrence. *Coosella perplexa* Zone, *Aphelaspis buttsi* and *A. walcotti* zones of the Nolichucky Formation from collections BG 46.5, BG 53.5, W 12.8, W 15.7, W 16.5, TS 30, TS 36.5, TS 37.1, TS 38.2, TS 39.2, TS 40, DF 12.8, DV 32.3. Also widespread in North America in these zones.

Glaphyraspis sp.

1968 *Glaphyraspis ornata*, Lochman, p. 1157, pl. 149, figs. 12-19, 22.

Occurrence. *Crepicephalus* Zone of the Nolichucky Formation TS 10.4 and the Bonneterre Dolomite of Missouri.

Discussion. This species was identified as *G. ornata* by Lochman (1968), but it differs from *G. ornata* due to the presence of an occipital spine. Therefore it is considered tentatively a new species. The specimens from the Nolichucky Formation differ from those illustrated by Lochman (1968), in that they have a smooth prosopon, but this may be due to preservation, or intraspecific variation since the amount of ornamentation varies greatly in *G. parva* (Pratt, 1992).

Family CATILLICEPHALIDAE Raymond, 1938

Genus *Pemphigaspis* Hall, 1863

Type species. Pemphigaspis bullata Hall, 1863, Eau Claire Formation, Wisconsin (by original designation).

Pemphigaspis bullata Hall, 1863

Pl. 1, fig. 7

- 1863 *Pemphigaspis bullata* Hall, p. 221, pl. 5a, figs. 3-5.
- 1951 *Pemphigaspis bullata*, Palmer, p. 763, pl. 105, figs. 3-6
[see for synonymy].
- 1954 *Pemphigaspis bullata*, Rasstti, p. 603, figs. 1f.
- 1965 *Pemphigaspis* sp., Rasetti, p. 44, pl. 7, figs. 23-25.
- 1968 *Pemphigaspis bullata*, Lochman, p. 1160, pl. 150, figs.
21, 26, 28-31.

Occurrence. From the *Crepicephalus* Zone and the *Coosella perplexa* Zone of the Nolichucky Formation from collections BG 31.8, BG 36.5, BG 47.7 from Beech Grove Tn. and widespread in *Crepicephalus* Zone rocks of North America.

Family NORWOODIIDAE Walcott, 1916a

Genus *Norwoodia* Walcott, 1916a

Type species. Norwoodia gracilis Walcott, 1916a, Conasauga Formation, Alabama (by original designation).

Norwoodia rogersvillensis Resser, 1938a

- 1938a *Norwoodia rogersvillensis*, Resser, p. 91, pl. 9, figs.
25, 26.
- 1938a *Norwoodia harlanensis*, Resser, p. 91, pl. 9, fig. 31.
- 1965 *Norwoodia rogersvillensis*, Rasetti, p. 64, pl. 4, figs.
25, 26.

Occurrence. *Crepicephalus* Zone and *Coosella perplexa* Zone of the Nolichucky Formation found in collections BG 31.8, BG 32.5, BG 33.9, BG 36.5, BG 38, BG 42.5, BG 46.5, BG 50, TS 14.1, DV 32.3.

Family LLANOASPIDIDAE Lochman *in* Lochman and Duncan, 1944.

Subfamily LLANOASPIIDINAE Lochman *in* Lochman and Duncan, 1944.

Genus *Llanoaspis* Lochman, 1938a

Type species. *Llanoaspis modesta* Lochman, 1938a, Riley Formation, Texas (by original designation).

Llanoaspis walcotti (Resser, 1938a)

Pl. 1, fig. 12

- 1938a *Gienevievella walcotti* Resser, p. 77, pl. 15, figs. 3-5.
- 1938a *Gienevievella rogersvillensis* Resser, p. 78, pl. 15,
figs. 16-18.

- 1953 *Rogersvillia rogersvillensis* Hupe, p. 182, fig. 159.
1965 *Llanoaspis walcotti*, Rasetti, p. 70, pl. 8, figs. 14-16.

Occurrence. From the *Crepicephalus* Zone and *Coosella perplexa* Zone of the Nolichucky Formation from the Beech Grove Tn. locality from collections BG 31.8, BG 33.9, BG 36.5, BG 46.5, BG 47.7.

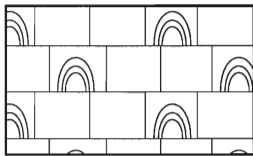
APPENDIX II

LITHOLOGIC LOGS

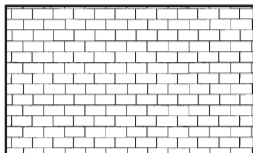
LEGEND



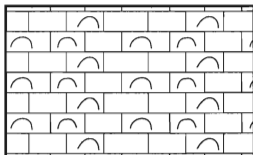
**SHALE AND MUDSTONES WITH CARBONATE
INTERBEDS**



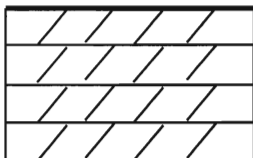
THROMBOLITE



INTERBEDDED LIME MUDSTONES TO GRAINSTONES



**INTERBEDDED BIOCLASTIC PACKSTONES
TO GRAINSTONES**



DOLOMITE

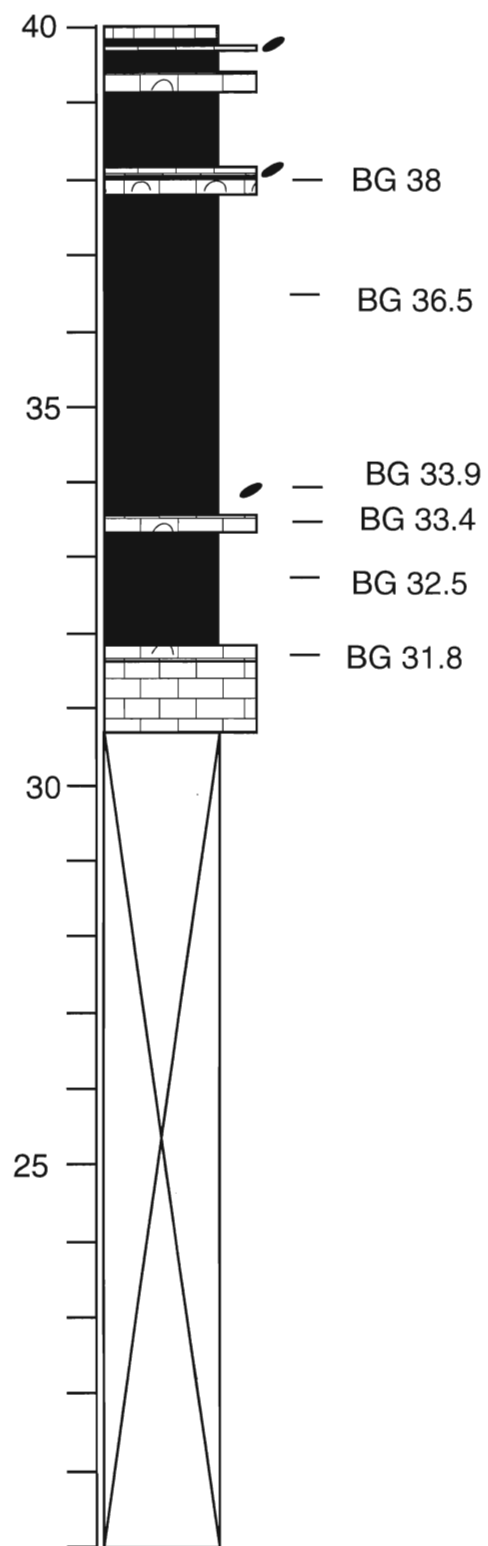
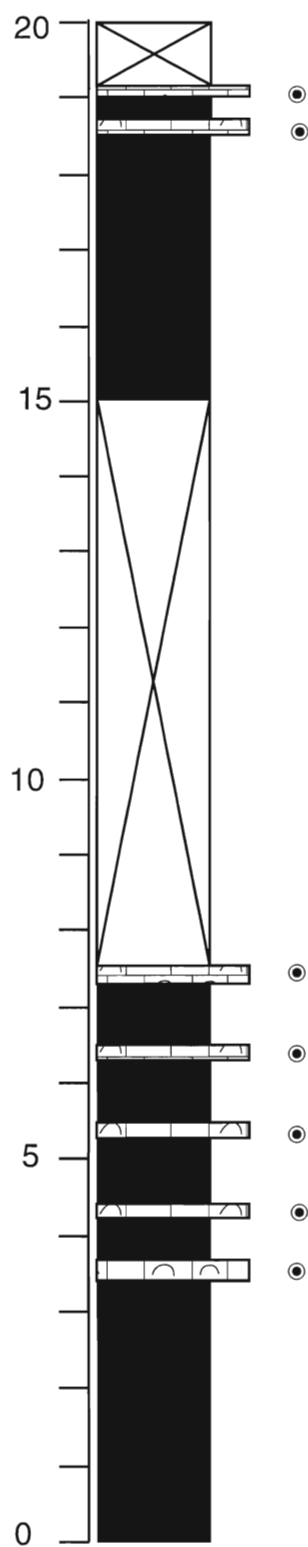


INTRARUDITE

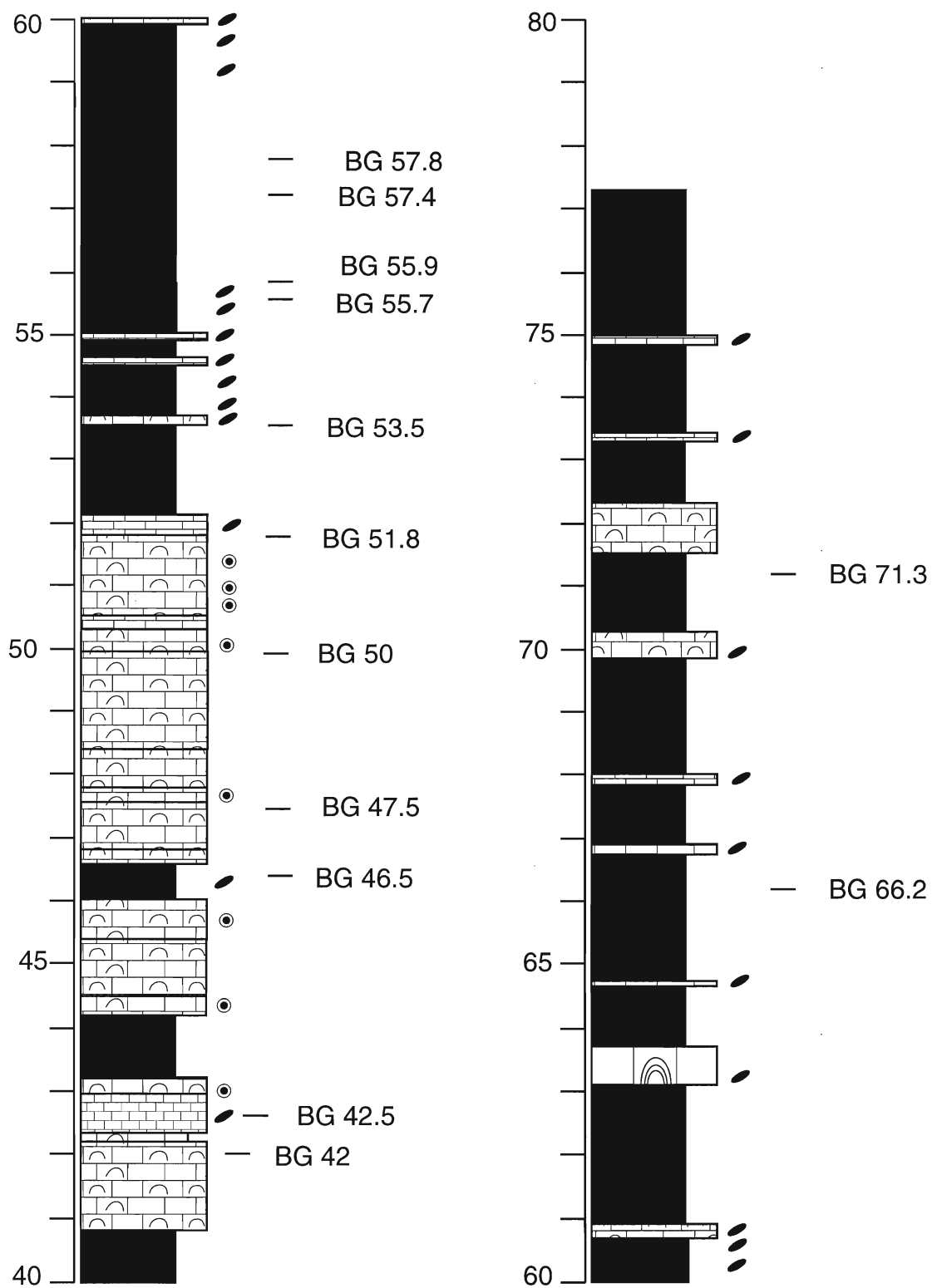


OOLITE

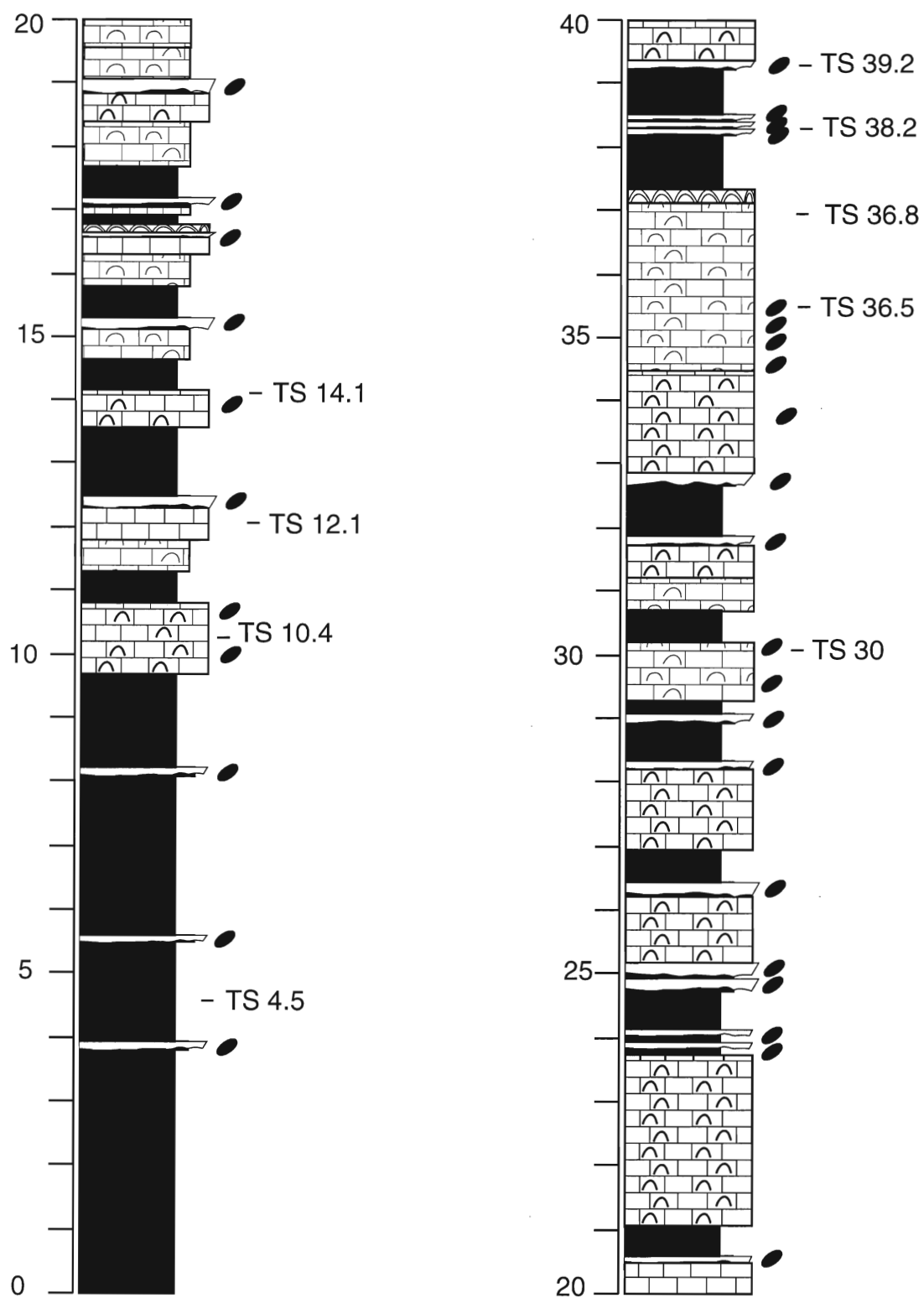
BEECH GROVE LOWER PORTION



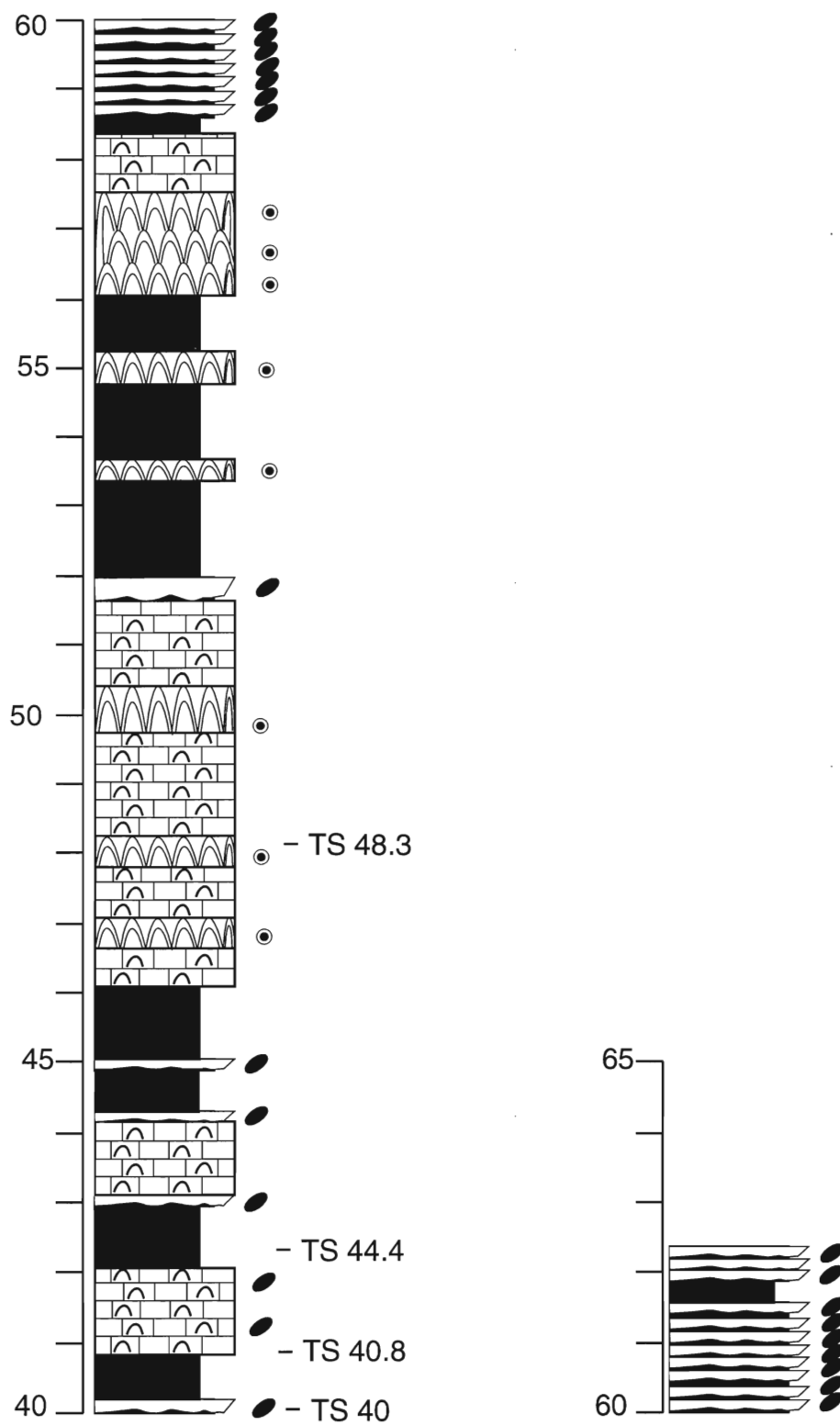
BEECH GROVE UPPER PORTION



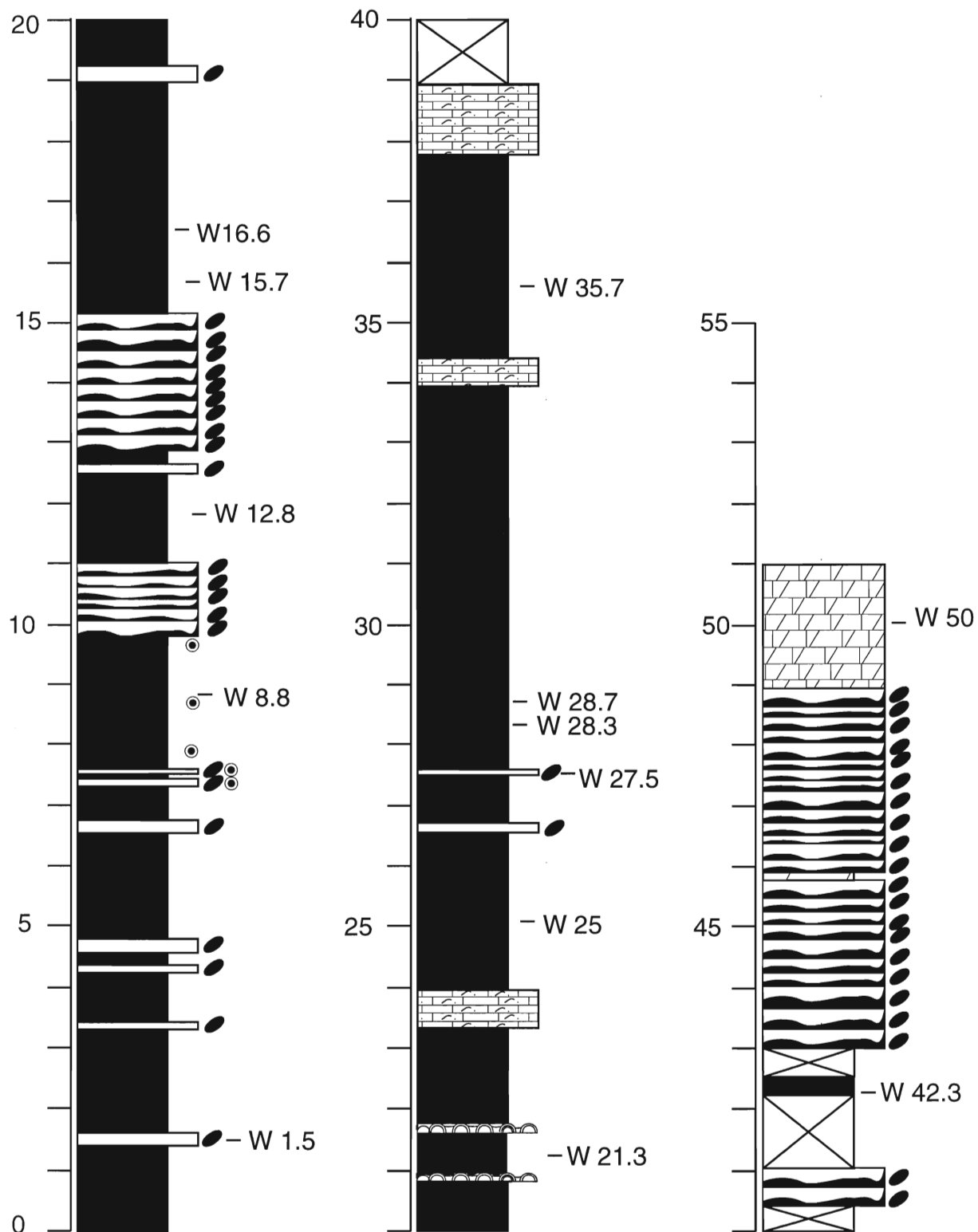
THREE SPRINGS LOWER PORTION



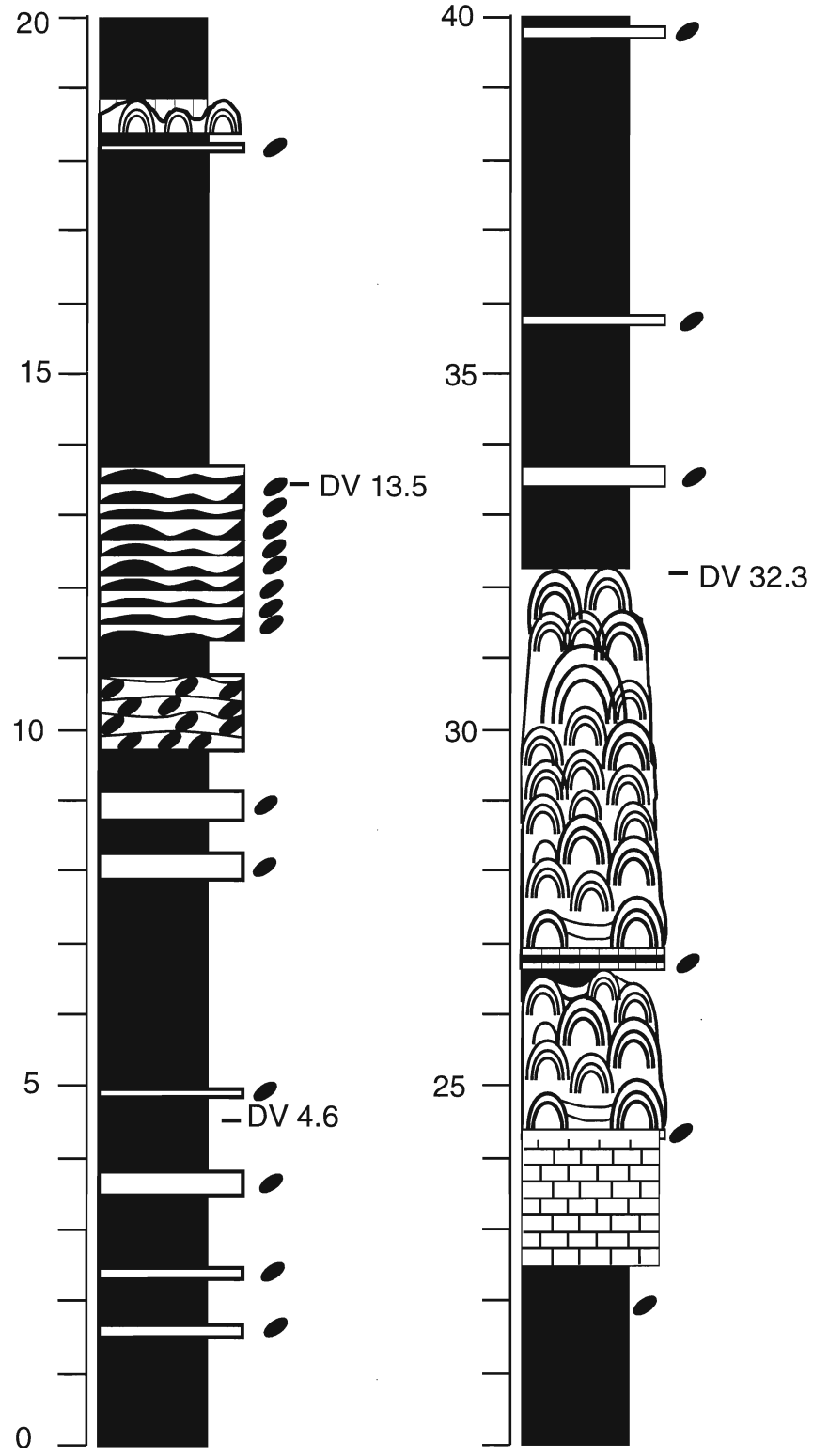
THREE SPRINGS UPPER PORTION

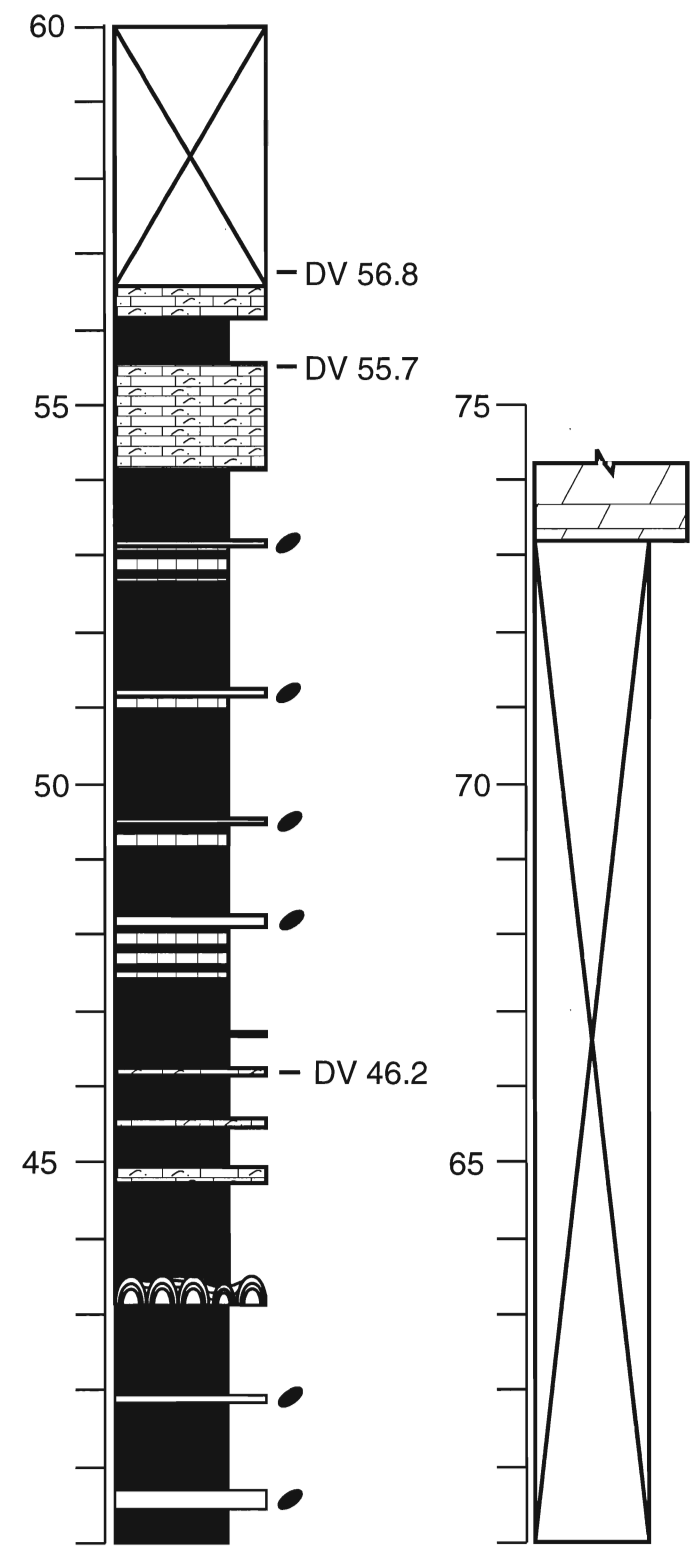


Washburn TN section

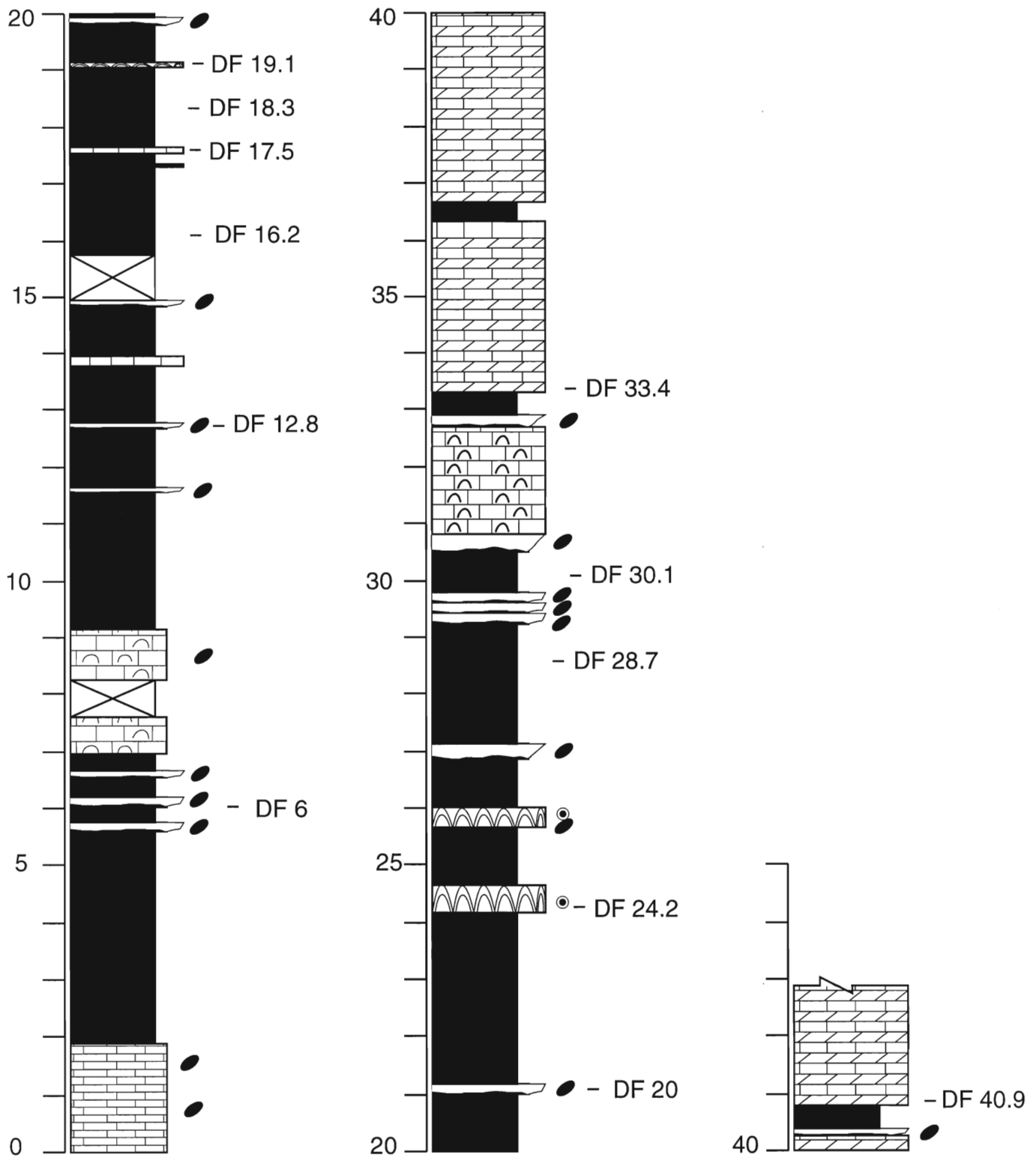


Dickensonville Va lower portion of section





DUFFIELD VA SECTION



APPENDIX III

	Cranidia	Pygidia	Cheeks	Total
BG 31.8				
<i>Kingstonia inflata</i>	1			
<i>Kormagnostus sp.</i>		2		
<i>Llanoaspis walcotti</i>	15	2		
<i>Pemphigaspis bullata</i>	2			
<i>Norwoodia</i>				
<i>rogersvillensis</i>	15			
<i>Tricrepicephalus</i>				
<i>texanus</i>	16	9	2	
<i>Coosella planicanda</i>	6	4		
TOTAL				57
BG 32.5				
<i>Norwoodia</i>				
<i>rogersvillensis</i>	4		1	
<i>Coosella planicanda</i>		3		
<i>Blountia mimula</i>		1		
TOTAL				8
BG 33.4				
<i>Kingstonia inflata</i>		1		
<i>Norwoodia</i>				
<i>rogersvillensis</i>	4			
<i>Tricrepicephalus</i>				

<i>texanus</i>	4	
<i>Blountia mimula</i>	3	
TOTAL		12

BG 33.9

<i>Llanoaspis walcotti</i>	4	
<i>Norwoodia</i>		
<i>rogersvillensis</i>	1	
<i>Tricrepicephalus</i>		
<i>texanus</i>	1	
TOTAL		6

BG 36.5

<i>Kingstonia inflata</i>	1	
<i>Kormagnostus</i> sp.	2	
<i>Llanoaspis walcotti</i>	23	
<i>Pemphigaspis bulata</i>	3	3
<i>Norwoodia</i>		
<i>rogersvillensis</i>	35	
<i>Tricrepicephalus</i>		
<i>texanus</i>	29	
<i>Blountia mimula</i>		6
TOTAL		99

BG 38

<i>Kormagnostus</i> sp.	4	3
<i>Norwoodia</i>		

<i>rogersvillensis</i>	6		
<i>Tricrepicephalus</i>			
<i>texanus</i>	5		5
<i>Coosella planicanda</i>	2	10	
<i>Blountia mimula</i>	1	1	
<i>Coosia alethes</i>	2		
TOTAL			28

BG 42

<i>Tricrepicephalus</i>			
<i>texanus</i>	2		1
<i>Coosella planicanda</i>	1		
TOTAL			3

BG 42.5

<i>Norwoodia</i>			
<i>rogersvillensis</i>	1		
TOTAL			1

BG 46.5

<i>Llanoaspis walcotti</i>		9	
<i>Norwoodia</i>			
<i>rogersvillensis</i>	1	1	
<i>Tricrepicephalus</i>			
<i>texanus</i>	8	3	2
<i>Blountia mimula</i>		6	
<i>Terranovella</i>			

<i>dorsalis</i>	1		
<i>Crepicephalus scissilis</i>		1	
<i>Pseudagnostus</i> sp.	1	2	
<i>Coosella perplexa</i>	4	7	
<i>Glaphyraspis parva</i>	48		
TOTAL			83

BG 47.7

<i>Kingstonia inflata</i>	2		
<i>Kormagnostus</i> sp.	3		
<i>Llanoaspis walcotti</i>	1	3	
<i>Pemphigaspis bullata</i>	2	1	
<i>Tricrepicephalus</i>			
<i>texanus</i>	14	1	2
<i>Pseudagnostus</i> sp.	1	3	
<i>Coosella perplexa</i>	1	10	3
<i>Glaphyraspis parva</i>	29	4	
TOTAL			64

BG 50

<i>Glaphyraspis parva</i>	70	8	
<i>Tricrepicephalus</i>			
<i>texanus</i>			
<i>Coosella perplexa</i>	6	22	
<i>Cheilocephalus</i>			
<i>brevilobus</i>	1	4	
TOTAL			96

BG 51.8

<i>Coosella planicanda</i>	10			
<i>Glaphyraspis parva</i>		2		
<i>Aphelaspis buttsi</i>	51	39	51	
TOTAL				63

BG 53.5

<i>Glaphyraspis parva</i>	21			
<i>Aphelaspis buttsi</i>	110	28	31	
TOTAL				131

BG 55.7

<i>Glaphyraspis parva</i>	10			
<i>Aphelaspis lata</i>	40	6	11	
TOTAL				50

BG 55.9

<i>Aphelaspis</i>				
<i>washburnensis</i>	61	8	25	
TOTAL				61

BG 57.4

<i>Aphelaspis quadrata</i>	40	13	13	
TOTAL				40

BG 57.8

Aphelaspis

<i>washburnensis</i>	58	58	69	
TOTAL				58

BG 66.2

<i>Aphelaspis tarda</i>	6	2	1	
TOTAL				6

BG 71.3

<i>Aphelaspis tarda</i>	49	1	17	
<i>Dytremacephalus</i>				
<i>angulatus</i>	9			
TOTAL				58

W 1.5

Tricrepicephalus

<i>texanus</i>	1			
TOTAL				1

W 8.8

<i>Coosella perplexa</i>		2		
<i>Pseudagnostus</i> sp.	1			
TOTAL				3

W 12.8

<i>Glaphyraspis parva</i>	1			
TOTAL				1

W 15.7

<i>Glapyraspis parva</i>	5			
<i>Aphelaspis buttsi</i>	93	6	23	
TOTAL				98

W 16.6

<i>Glapyraspis parva</i>	2			
<i>Aphelaspis buttsi</i>	47		7	
TOTAL				49

W 21.3

<i>Aphelaspis walcotti</i>	51	1	11	
TOTAL				51

W 25

<i>Aphelaspis rotunda</i>	7		3	
TOTAL				7

W 27.5

<i>Aphelaspis rotunda</i>	42	2	9	
TOTAL				42

W 28.3

<i>Aphelaspis quadrata</i>	75	2	13	
TOTAL				75

W 28.7

<i>Aphelaspis walcotti</i>	54	7	29	
TOTAL				54

W 35.7

<i>Pseudagnostus</i> sp.		1		
<i>Aphelaspis tarda</i>	60	2	24	
TOTAL				61

W 42.3

<i>Aphelaspis punctata</i>	76	1	40	
TOTAL				76

W 50

<i>Aphelaspis punctata</i>	74	1	17	
TOTAL				74

TS 4.5

<i>Kingstonia inflata</i>		1		
TOTAL				1

TS 10.4

<i>Glaphyraspis</i> sp.	5			
<i>Coosia alethes</i>	1	3		
TOTAL				8

TS 12.1

<i>Coosia alethes</i>		1		
<i>Tricrepicephalus</i>				
<i>texanus</i>	2	1		
TOTAL				3

TS 14.1

<i>Kingstonia inflata</i>		1		
<i>Tricrepicephalus</i>				
<i>texanus</i>	1			
<i>Norwoodia</i>				
<i>rogersvillensis</i>	2			
TOTAL				4

TS 30

<i>Glaphyraspis parva</i>	2			
TOTAL				2

TS 36.5

<i>Glaphyraspis parva</i>	30			
<i>Aphelaspis buttsi</i>	127	25	58	
TOTAL				157

TS 36.8

<i>Glaphyraspis parva</i>	10			
<i>Aphelaspis buttsi</i>	119	1	33	
TOTAL				129

TS 38.2

<i>Glaphyraspis parva</i>	9	1		
<i>Aphelaspis walcotti</i>	127		5	
TOTAL				136

TS 39.2

<i>Glaphyraspis parva</i>	26	8		
<i>Aphelaspis walcotti</i>	70	16	11	
TOTAL				96

TS 42.4

Aphelaspis

<i>washburnensis</i>	55	1	6	
TOTAL				55

TS 48.3

<i>Aphelaspis tarda</i>	4	1	1	
TOTAL				4

TS 53.5

<i>Aphelaspis tarda</i>	5	3	4	
TOTAL				5

DF 6

<i>Coosella perplexa</i>		4		
TOTAL				4

DF 12.8

<i>Glaphyraspis parva</i>	9			
<i>Aphelaspis buttsi</i>	95	4	36	
TOTAL				104

DF 16.2

<i>Aphelaspis buttsi</i>	4			
TOTAL				4

DF 17.5

<i>Aphelaspis buttsi</i>	3	1		
TOTAL				3

DF 18.3

<i>Aphelaspis laxa</i>	1	2		
TOTAL				2

DF 19.1

<i>Aphelaspis laxa</i>	5			
TOTAL				5

DF 24.2

<i>Aphelaspis</i>				
<i>washburnensis</i>	22		5	
TOTAL				22

DF 28.7

Aphelaspis

<i>washburnensis</i>	10			
TOTAL				10

DF 30.1

<i>Aphelaspis tarda</i>	20	6	13	
TOTAL				20

DF 33.4

<i>Aphelaspis tarda</i>	53	3	9	
TOTAL				53

DF 40.9

<i>Aphelaspis tarda</i>	2	1		
TOTAL				2

DV 4.6

Tricrepicephalus

<i>texanus</i>	4	1		
<i>Coosia alethes</i>	2			
TOTAL				6

DV 13.5

Tricrepicephalus

<i>texanus</i>	3			
TOTAL				3

DV 32.3

Tricrepicephalus

<i>texanus</i>	3	6
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<i>Glaphyraspis parva</i>	1	
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<i>Coosella perplexa</i>	2	
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Norwoodia

<i>rogersvillensis</i>	1	
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TOTAL		7
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DV 46.2

<i>Coosia alethes</i>		27
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<i>Coosella perplexa</i>		2
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<i>Crepicephalus buttsi</i>	22	19	3
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TOTAL			51
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DV 55.7

<i>Aphelaspis walcotti</i>	4	2	14
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TOTAL			7
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DV 56.8

<i>Aphelaspis tarda</i>	50	3	1
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TOTAL			50
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Collections used in Cluster Analysis

Rabbitkettle Formation. District of Mackenzie, Pratt (1992).

N 107

<i>Pseudagnostina</i>	33	28	
<i>Acmarhachis</i>	9	9	
<i>Nahannagnostus</i>	8	3	
<i>Cedaria</i>	7	4	
<i>Llanoaspis</i>	23	17	
<i>Deiracephalus</i>	2	1	
<i>Kingstonia</i>	44	7	
<i>Crepicephalus</i>	15	17	
<i>Tricrepicephalus</i>	6	1	
<i>Glaphyraspis</i>	2		
<i>Pemphigaspis</i>	14	4	
<i>Hysteropleura</i>	17	2	
<i>Norwoodia</i>	62	3	
TOTAL			244

N 114

<i>Pseudagnostina</i>	13	14	
<i>Nahannagnostus</i>	6	2	
<i>Acmarhachis</i>	2		
<i>Aspidagnostus</i>		1	
<i>Hadragnostus</i>	2	1	
<i>Kormagnostus</i>	2	3	
<i>Connagnostus</i> 2 sp.	9	6	

<i>Cedaria</i>	17	11	
<i>Deiracephalus</i>	5		
<i>Crepicephalus</i>	13	14	
<i>Tricrepicephalus</i>	1		
<i>Kingstonia</i>	75	17	
<i>Blountia</i>	1		
<i>Glaphyraspis</i>	5		
<i>Terranovella</i>	1		
TOTAL			158

N 116

<i>Aspidagnostus</i>		1	
<i>Nahannagnostus</i>	3	1	
<i>Kormagnostus</i>	7	1	
<i>Pseudagnostina</i>	2	4	
<i>Hadragnostus</i>	1	3	
<i>Deiracephalus</i>	4	3	
<i>Kingstonia</i>	63	55	
<i>Bynumia</i>	1		
<i>Crepicephalus</i>	12	6	
<i>Tricrepicephalus</i>	1	2	
<i>Glaphyraspis</i>	2		
<i>Blountia</i>		1	
TOTAL			100

N 124.5

<i>Glyptagnostus</i>	4	2	
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<i>Innitagnostus</i>	12	8	
<i>Homagnostus</i>	11	14	
<i>Aphelaspis</i>	28	6	
<i>Eugonocare</i>	15	9	
<i>Glaphyraspis</i>	12	5	
<i>Cheilocephalus</i>	5	6	
TOTAL			91

N 128

<i>Innitagnostus</i>	4	2	
<i>Homagnostus</i>	29	30	
<i>Pseudagnostus</i>	25	28	
<i>Aphelaspis</i> 2sp.	22	17	
<i>Eugoncare</i>	9	6	
<i>Listroa</i>			1
<i>Cheilocephalus</i>		1	
TOTAL			94

Cow Head Formation. Western Newfoundland, Westrop
(unpublished data).

BLD 11

<i>Deiracephalus</i>	10	3	
<i>Tricrepicephalus</i>	16	2	
<i>Meteoraspis</i>	12	1	
<i>Holacephalus</i>	29	2	
<i>Onchonotopsis</i>	8		

<i>Crepicephalus</i>	1	8	
<i>Kingstonia</i>	1	1	
<i>Pseudagnostina</i>	5	3	
<i>Cedaria</i>	12	1	
<i>Menomonina</i>	2		
<i>Clavagnostus</i>	1		
<i>Lonchocephalus</i>	1		
<i>Catillicephala</i>	1	1	
<i>Blountia</i>	1	1	
TOTAL			107

BLD 35

<i>Tricrepicephalus</i>	18	4	
<i>Blountia</i>		5	
<i>Meteoraspis</i>		1	
<i>Holcacephalus</i>	11	2	
<i>Kingstonia</i>	5	3	
<i>Crepicephalus</i>	9	6	
<i>Menomonina</i>	4		
<i>Pagodia</i>	1		
<i>Kormagnostus</i>		2	
TOTAL			56

BLD 39

<i>Crepicephalus</i>	2	1	
<i>Densonella</i>	3		

<i>Metoraspis</i>	2	2	
Agnostid ?		3	
<i>Unicornensis</i>	8		
<i>Coosella</i>	1	7	
<i>Cedaria</i> 2sp.	1 1	1 1	
<i>Kingstonia</i>	3		
<i>Catillecephela</i>	3		
<i>Blountia</i>	1	1	
<i>Lecanopleura</i>	4		
TOTAL			5 8

BLD 49

<i>Aphelaspis</i>	1 5 6	3 5	3 1
<i>Agnostus</i>	1 0	3	
<i>Blountia</i>	6	2	5
<i>Dundebergia</i>	9	2	
<i>Psuedoagnostus</i>	2 1	1 2	
<i>Homagnostus</i>	1		
<i>Onchocephalities</i>	2		
<i>Innitagnostus</i>	1	1	
TOTAL			2 0 6

Eau Claire Formation. Wisconsin, Westrop (unpublished data)

CW 0.5

<i>Crepicephalus</i>	5 4
<i>Lonchocephalus</i>	1 5

<i>Komaspidella</i>	1		
<i>Dresbachia?</i>	1		
TOTAL			71

CW 3.85

<i>Lonchocephalus</i>	150		
<i>Uncaspis</i>		2	
TOTAL			152

SW 10.9

<i>Lonchocephalus</i>	30		
<i>Crepicephalus</i>	31		
<i>Dresbachia</i>	1		
<i>Komaspidella</i>	1	2	
<i>Uncaspis</i>		2	
TOTAL			65

LFD 5.6

<i>Lonchocephalus</i>	48		
<i>Menomonina</i>	6		
<i>Uncaspis</i>		1	
<i>Modocia</i>	1		
TOTAL			56

LFD 12.6

<i>Aphelaspis</i>	55		
<i>Glaphyraspis</i>	5		

TOTAL 60

Sullivan Formation. Alberta and British Columbia, Cuggy and Westrop (unpublished data)

Totem Creek, Alberta

TC 324

<i>Crepicephalus</i>	9		
<i>Uncaspis</i>	33	15	
<i>Dresbachia</i>	8		
<i>Terranovella</i>	1		
TOTAL			51

TC 334

<i>Uncaspis</i>	23		
<i>Kormagnostus</i>		2	
<i>Glaphyraspis</i>	19		
<i>Pemphigaspis</i>	1		
<i>Teranovella</i>	1		
TOTAL			51

Chaba Creek, Alberta

GSC 72771

<i>Aphelaspis</i>	40	6	2
<i>Glaphyraspis</i>	6		
TOTAL			46

Takakkaw Falls, British Columbia

GSC 75340

<i>Aphelaspis</i>	69	10	13	
<i>Glaphyraspis</i>	5			
<i>Blountia</i>	2			
<i>Cheilocephalus</i>		1	1	
TOTAL				77

Mt. Laussedat, British Columbia

GSC 75342

<i>Aphelaspis</i>	59	8	9	
<i>Cheilocephalus</i>		2		
<i>Pseudagnostus</i>	1			
TOTAL				62