

CONODONT BIOSTRATIGRAPHY AND PALEOECOLOGY OF THE
LOWER DEVONIAN HELDERBERG GROUP OF VIRGINIA

by

Elizabeth G. Cook

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APPROVED:

Dr. C. G. Tillman, Chairman

Dr. W. D. Lowry /

Dr. J. F. Read

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INTRODUCTION

Lower Devonian conodonts have been described from many parts of the world, in particular from Europe, western North America, and Australia. Zonations based on conodonts have been established and, particularly in western North America, successfully used for correlation (Lane and Ormiston, 1979). Conodonts have been used to correlate the Silurian-Devonian boundary worldwide (Klapper et al., 1971; Ziegler, 1971).

The Helderberg Group of the Appalachian Basin is of latest Silurian to Early Devonian age in Virginia and is entirely Early Devonian in New York (Head, 1969). The Helderberg Group consists of formations with time-transgressive boundaries (Rickard, 1962; Head, 1969). In Virginia, the formations change facies and thickness between southeastern and the northwestern exposures (Swartz, 1929). Most biostratigraphic correlations within the Helderberg Group have been made using brachiopods and corals (Swartz, 1929; Swartz, 1939; Head, 1969). Many of these have distributions which are controlled by facies, reducing the value of time correlations made using them. Most of the Helderberg conodonts, on the other hand, are present in a wide range of facies.

Conodonts in the lower part of the Lower Devonian tend to be provincial (Klapper and Johnson, 1980), and this is true of the Helderberg conodonts. The Helderberg fauna is sufficiently different from the faunas on which conodont zonations have been based that not

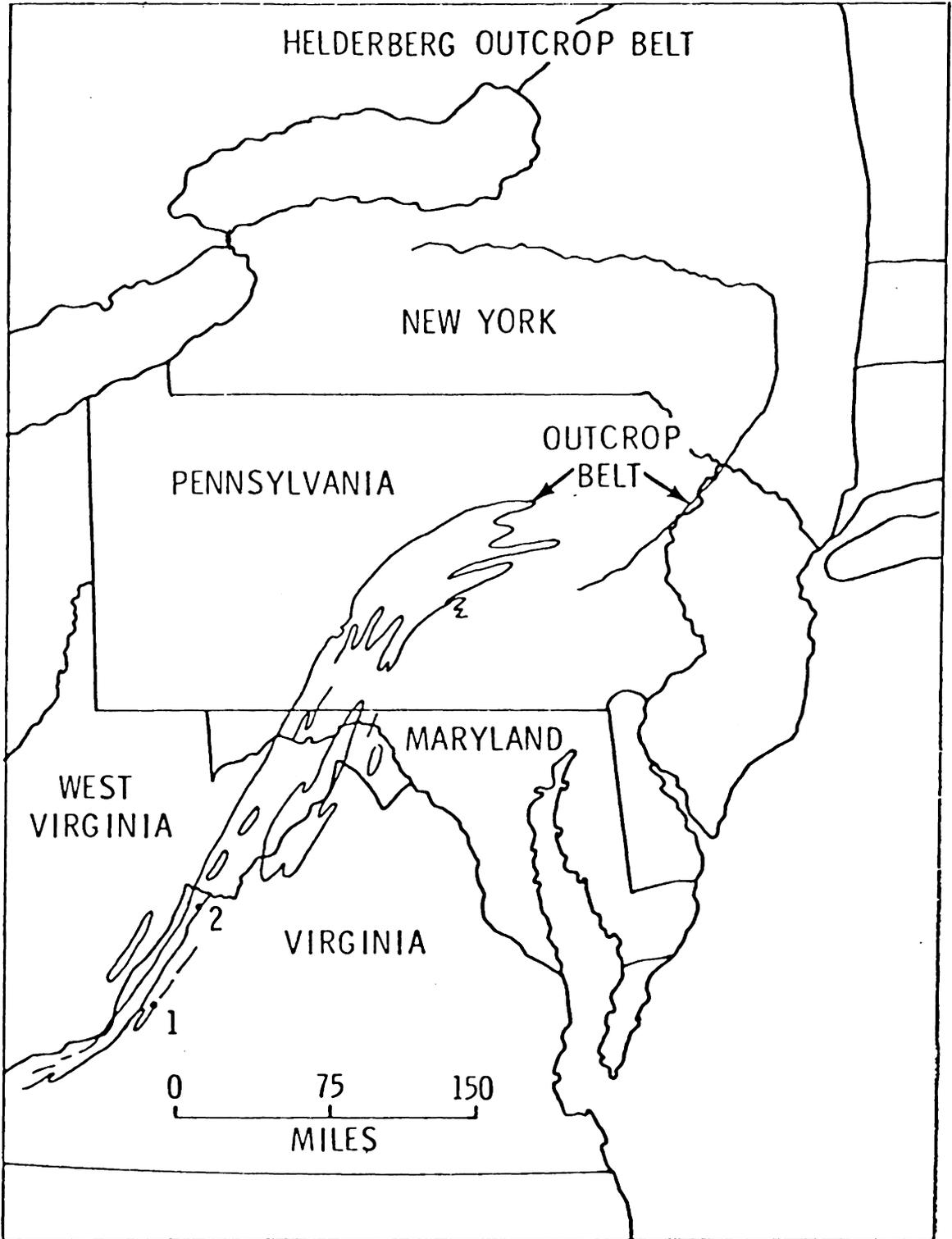
all of the Helderberg Group may be assigned to the standard zones. However, there are enough zonal species present in the Helderberg to correlate it in part with the standard zonation, and in particular to assist with the definition of the Silurian-Devonian boundary in the Appalachians.

Those species which are not useful for correlation of the Helderberg with Lower Devonian strata elsewhere may be used for correlation within the basin. Several conodont species defining an approximate time plane were found at both sections sampled in this study, and the same species are present in the Helderberg of New York (Epstein, 1970; Barnett, 1971). It may therefore prove possible, if conodont species ranges are established across the basin, to use conodonts for more precise Helderberg biostratigraphy.

LOCATION OF SECTIONS

The two sections sampled for conodonts are continuous through most of the Helderberg Group. The sections are about fifty miles apart. The southern section is at Prices' Bluff, along the Chesapeake and Ohio Railway tracks above the James River, about 1 mile north of Gala, Virginia, west of Eagle Rock, Virginia. The Prices' Bluff section was described by Swartz (1929) and its lower part was studied by Barwis and Makurath (1978). The northern section is in the Seybert Hills along Virginia State Route 629, which parallels Strait Creek, about $1\frac{1}{4}$ miles southeast of its intersection with U.S. Route 220, $3\frac{1}{2}$ miles north of Monterey, Virginia. The lower part of the Strait Creek section was sampled for conodonts by Helfrich (1978). The locations of the two sections are shown in Figure 1.

Figure 1. Index map showing Helderberg outcrop belt and sections.
1 = Price's Bluff section, 2 = Strait Creek section. After Head,
1969.



METHODS

The two sections were measured using a Jacob staff. About thirty samples, most of them weighing 4 to 7 kilograms, were collected from each section. The sample interval was irregular but averaged about 10 feet at Price's Bluff and about 15 feet at Strait Creek in the Keyser and Licking Creek Formations; sample locations were chosen to include a variety of lithologies. The sample interval was smaller in the thinner formations, in particular the New Creek Limestone, the Healing Springs Sandstone, and the Corriganville Limestone, so that at least three or four samples were taken from each formation. Additional material was later collected from some sample locations which had yielded a well-preserved fauna, and a few additional samples were taken.

The samples were dissolved in 10% acetic acid. Formic acid was also used on samples which did not break down readily in acetic acid. The insoluble residue was washed through screens, and the fraction between 20 and 120 mesh was dried in an oven at low temperature. Undissolved rock fragments were weighed. In some cases, especially in the Clifton Forge Sandstone and the Licking Creek cherts at Strait Creek, this was a large percentage of the original weight of the sample. The screened material was separated using acetylene tetrabromide, and the heavy fraction was picked for conodonts using a binocular microscope.

A total of 310 kilograms of rock was processed, yielding 13,360 conodonts. Sixty-four separate samples were taken, of which 48 yielded

conodonts. The number of conodonts per kilogram of rock dissolved in these samples ranged from .5 to 444.

STRUCTURAL SETTING

The study area is in the Appalachian Ridge and Valley Province, which consists of Paleozoic rocks folded into northeast trending folds and cut by northeast striking thrust faults. The Strait Creek section is in the western Lower Devonian strike belt, about 50 miles north of the Price's Bluff section, which is located in the eastern strike belt (Figure 1).

The Strait Creek section is on the southeast limb of the Jack Mountain Anticline (Kettren, 1971). The rocks dip slightly south of east at an angle ranging between 15° and 30° . There is nearly continuous exposure from the base of the Keyser Formation through about half of the Licking Creek Formation. The underlying Tonoloway Formation is covered immediately below the base of the Keyser but is exposed farther down the road and in the woods above the road cut.

The Price's Bluff section is at the southwest end on the Big Hill Anticline, a small plunging fold which brings up Silurian and lowermost Devonian rocks in the middle of the Craig Creek synclinorium. The synclinorium is for the most part floored with Devonian shales (Lesure, 1957). The rocks dip to the southeast at about 35° . Formations exposed range from the Tonoloway through the Helderberg Group and the unconformably overlying Ridgeley Sandstone, which is only 1.5 feet thick, to the base of the overlying Needmore Shale. The exposure is essentially continuous and is about 256 feet thick from the base of the Keyser to the top of the Licking Creek Formation.

STRATIGRAPHY

Introduction

The Helderberg Group extends from New York south across northwestern New Jersey, Pennsylvania, and western Maryland to western Virginia, and west as far as the subsurface of West Virginia and southeastern Ohio. Its outcrop is shown in Figure 1. It reaches 250 feet in thickness in New York, thinning to the west under the overlying pre-Oriskany unconformity. To the south, in the central part of the basin in Pennsylvania and Maryland, it thickens to 300-500 feet (Head, 1969). In Virginia the Helderberg Group ranges in thickness from 500 feet in the north to 250 feet near the James River. It is dominated throughout this area by shallow water limestones and also includes chert near the center of the basin and sandstone near the eastern basin margin.

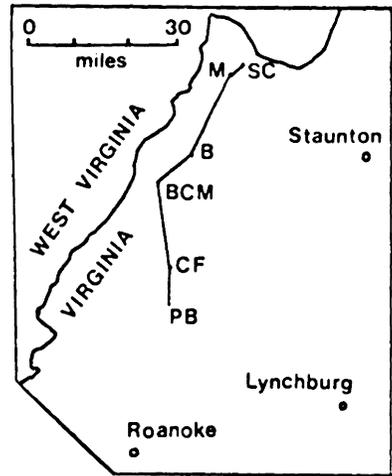
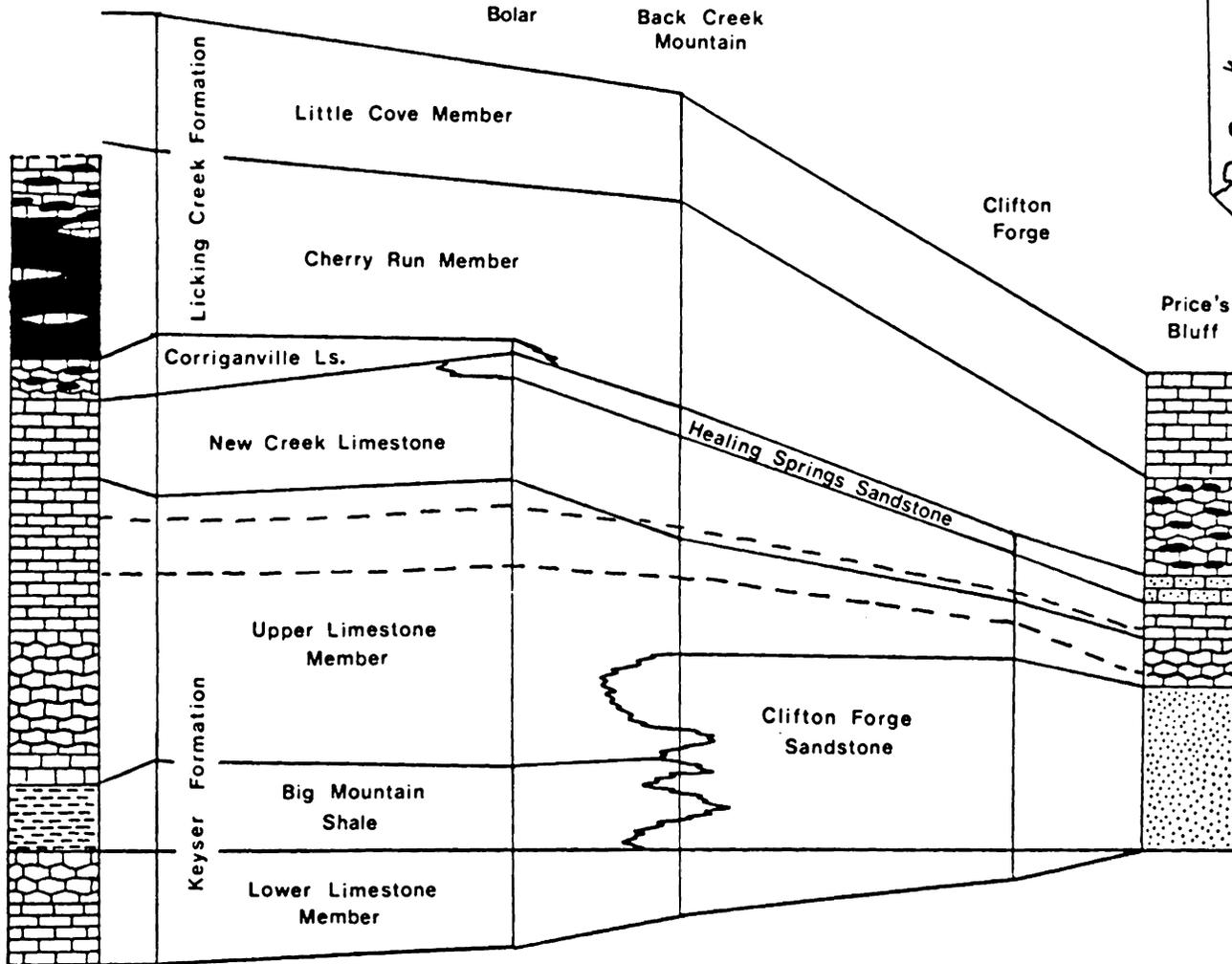
In the study area, the Helderberg Group includes in ascending order the Keyser Formation, the New Creek Limestone, the Corriganville Limestone to the north and the Healing Springs Sandstone to the south, and the Licking Creek Formation (Figure 2). It is underlain by the Tonoloway Formation and overlain unconformably by the Ridgeway Sandstone.

Previous Work

In the past twenty years, there have been several studies clarifying the stratigraphy of the Helderberg Group in the northern part of the Appalachian Basin; less work has been done in the southern

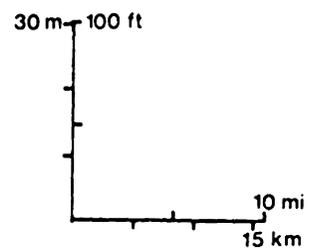
Figure 2. Helderberg Group stratigraphy from Price's Bluff to
Strait Creek. Intermediate sections and map after Swartz, 1929.

Strait Creek
Monterey



— first *I. helderbergensis* n. sp.

— first *D. e. cristagalli*



part. Rickard (1962) showed that the formations of the Helderberg Group in central and eastern New York, which previously had been thought of as time-stratigraphic units, were westward-younging, time transgressive facies which interfinger and grade into each other laterally, and which migrated in response to transgression and regression. Laporte (1969) studied the facies of the New York Helderberg in detail, showing the environmental relationships of the different facies. Epstein et al. (1967) extended this stratigraphic framework into northeastern Pennsylvania and western New Jersey.

The Helderberg Group has been studied in West Virginia and Pennsylvania by Swartz and Swartz (1941), Swartz (1939), and Woodward (1943); for the most part, all dealt with the formations as time-stratigraphic units. The most detailed study of the Helderberg of Virginia was by Swartz (1929), who documented facies changes across the state and described the Helderberg macrofauna. Head (1969) put together a reconstruction of Helderberg basin paleogeography, including generalized environmental interpretations and correlation of the Virginia section with the New York section. Depositional environments of parts of the Keyser Formation have been studied by Makurath (1975, 1977), Barwis and Makurath (1978), and Smosna and Warshauer (1979).

Description of Formations in the Study Area

Keyser Formation.--The Keyser Formation is named for exposures near Keyser, West Virginia (Swartz et al., 1913), and can be traced

from central Pennsylvania to western Virginia. In the study area, the Keyser thins from 250 feet in the north to 110 feet in the south.

The Keyser Formation includes four members in the study area (Swartz, 1929). In the north these include the lower limestone member, the Big Mountain Shale, and the upper limestone member. In the south, the Clifton Forge Sandstone replaces the Big Mountain Shale and part of the upper limestone member, and the lower limestone member pinches out below it (Figure 2).

The lower limestone member thins southward from 60-80 feet in the north, pinching out under the Clifton Forge Sandstone between Clifton Forge and the Price's Bluff section. Both limestone members consist largely of skeletal or pelletal wackestone and mudstone with nodular bedding; also included are skeletal packstone and grainstone and stromatoporoid biostromes.

The Clifton Forge Sandstone was named by Swartz (1929) for the section at Clifton Forge, Virginia. It averages about 80 feet in thickness, and consists of cross-bedded calcareous quartz sandstone. It is present in the southeastern part of the area of Helderberg outcrop in Virginia and interfingers with the Big Mountain Shale and the lower part of the upper limestone member near Warm Springs, Virginia.

The Big Mountain Shale extends from Warm Springs north to Petersburg, West Virginia, pinching out north of that section. It was named by Swartz (1929) for exposures on Big Mountain in Pendleton

County, West Virginia. This grey shale contains limestone interbeds in some places and averages 25-30 feet in thickness in the study area.

The upper limestone member ranges from 150 feet in thickness in the northern part of the study area to 30-35 feet in the southern part. Part of this decrease in thickness is due to a regional thinning of the Keyser to the south, but part is also due to the replacement of the lower part of the upper limestone member by the Clifton Forge Sandstone. The contact of the upper limestone member with the overlying New Creek Limestone is sharp.

New Creek Limestone.--The New Creek Limestone extends from central Pennsylvania to western Virginia. It was named by Bowen (1967) for exposures in Mineral County, West Virginia, and includes rocks in that area which were previously known as the Coeymans Formation. The type Coeymans is in New York and cannot be traced in outcrop to the New Creek. The New Creek Limestone is only 11 feet thick at the type section (Head, 1969), but ranges in the study area from 40-60 feet thick in the north to 20-25 feet in the south. It consists of coarse crinoidal grainstone and packstone.

Healing Springs Sandstone.--The Healing Springs Sandstone was named by Swartz (1929) for exposures near Healing Springs, Virginia. It consists of 10-20 feet of cross-bedded very calcareous sandstone. The Healing Springs is present in the southern part of the study area. It pinches out to the north between the underlying New Creek Limestone and the southern edge of the Corriganville Limestone near Warm Springs,

Virginia, and is elsewhere overlain by the Licking Creek Formation (Figure 2).

Corriganville Limestone.--The Corriganville Limestone (Head, 1969), whose type section is in Maryland, includes strata in the southern part of the basin previously known as the New Scotland Limestone. The type New Scotland, in New York, is not the same facies as the Corriganville Limestone and is not traceable to it in outcrop. The Corriganville Limestone includes approximately 25 feet of light-colored, cherty skeletal packstone or wackestone. The Corriganville is present in the northern part of the study area and overlies the New Creek Limestone except near its southern limit, where it pinches out between the northern edge of the Healing Springs Sandstone and the overlying Licking Creek Formation.

Licking Creek Formation.--The Licking Creek Formation was named by Swartz (1939) for exposures along Licking Creek, in Franklin County, Pennsylvania, to include strata previously known as the Becraft Formation. It extends from the eastern strike belt of central Pennsylvania to western Virginia. To the northwest, in the western strike belt of Pennsylvania, Maryland, and West Virginia, it grades into the Shriver Chert (Swartz, 1929; Head, 1969). The Licking Creek Formation includes a lower member, the Cherry Run Member, and an upper, the Little Cove Member (Head, 1969, 1974).

Cherry Run Member.--The Cherry Run Member (Head, 1969, 1974) was named for exposures in Morgan County, West Virginia. In the study area, it thins from about 100 feet in the north to about 55 feet in

the south. The Cherry Run consists of dark-colored, cherty, argillaceous skeletal packstone and wackestone in the southern part of the study area, grading north to interbedded dark chert and lime mudstone.

Little Cove Member.--The Little Cove Member (Head, 1974) was named for exposures in Franklin County, Pennsylvania. In the study area it thins from 90 feet in the north to about 55 feet in the south. It consists of light-colored skeletal grainstone and packstone, sandy to the south. It is overlain unconformably by the Ridgeley Sandstone; the hiatus decreases in magnitude toward the center of the basin (Dennison and Head, 1975).

The lithologies typical of the Cherry Run and the Little Cove interfinger. The boundary between the two members is herein drawn at the top of the highest typical Cherry Run lithology.

Regional Correlation

Head (1969, 1974) has summarized correlation for the Helderberg Group from New York to southwestern Virginia. Criteria for correlation included (1) recognition of basin-wide transgressions and regressions; (2) consideration of facies patterns, including which facies would exist contemporaneously; (3) biostratigraphy, in particular the use of brachiopod ranges; (4) lithologic markers, such as terrigenous tongues in the largely carbonate basin and thin regressive dolomites. Time lines based on such data tend to be parallel which suggests that sedimentation rates were similar across the basin. Thus beds that lie the same distance above or below a particular datum are likely to be

the same age. For this reason, thickness data were also used in correlation (Head, 1969). This is less reliable in areas of coarse clastic deposition.

According to these correlations, the base of the Helderberg Group is older in the southern part of the basin, from south-central Pennsylvania south to western Virginia, than in New York. Although the upper part of the Keyser Formation correlates with the older New York Helderberg formations, i.e., the Manlius Formation in central New York and Manlius and Coeymans Formations in eastern New York, the lower part of the Keyser correlates with pre-Helderberg strata in New York.

Through Helderberg time, the basin axis ran northeast through West Virginia to central Pennsylvania, from there curving more to the east to southeastern New York (Head, 1969). The upper part of the Keyser Formation in the northern part of the study area was deposited during a regression. This regression is also recognizable in central New York, where it is shown by a tongue of the Manlius extending east into the Coeymans Formation, and in southeastern New York and northeastern Pennsylvania, where it is represented by the Stormville Sandstone (Head, 1969). Above that the formations through the New Scotland Formation of New York and the lower Licking Creek Formation of Virginia were deposited under transgressive conditions. These formations are therefore oldest near the basin axis and younger away from it. Since the basin axis runs through West Virginia, neither of the sections considered in this study is at the axis. The line between

the sections is slightly oblique to the basin axis, with the Strait Creek section closer to the axis. One would therefore expect deeper water facies at the Strait Creek section than at the Price's Bluff section at any particular time, which would result in time-transgressive facies, although not as strongly time-transgressive as in New York where the line of outcrop cuts directly across the basin axis.

DEPOSITIONAL ENVIRONMENTS

Introduction

The Helderberg Group of western Virginia was deposited in shallow water environments, ranging from intertidal to below wave base. The sediment was largely carbonate, with some clastic sediment supplied at the eastern basin margin.

Depositional environments of the Helderberg Group have been considered by Head (1969, 1974); in addition, the Keyser Formation or parts of it have been studied by Makurath (1975, 1977), Barwis and Makurath (1978), and Smosna and Warshauer (1979). Beyond this, little has been done on defining the depositional environments of the Helderberg formations of western Virginia.

Helderberg facies and depositional environments are summarized in Table 1.

Keyser Formation

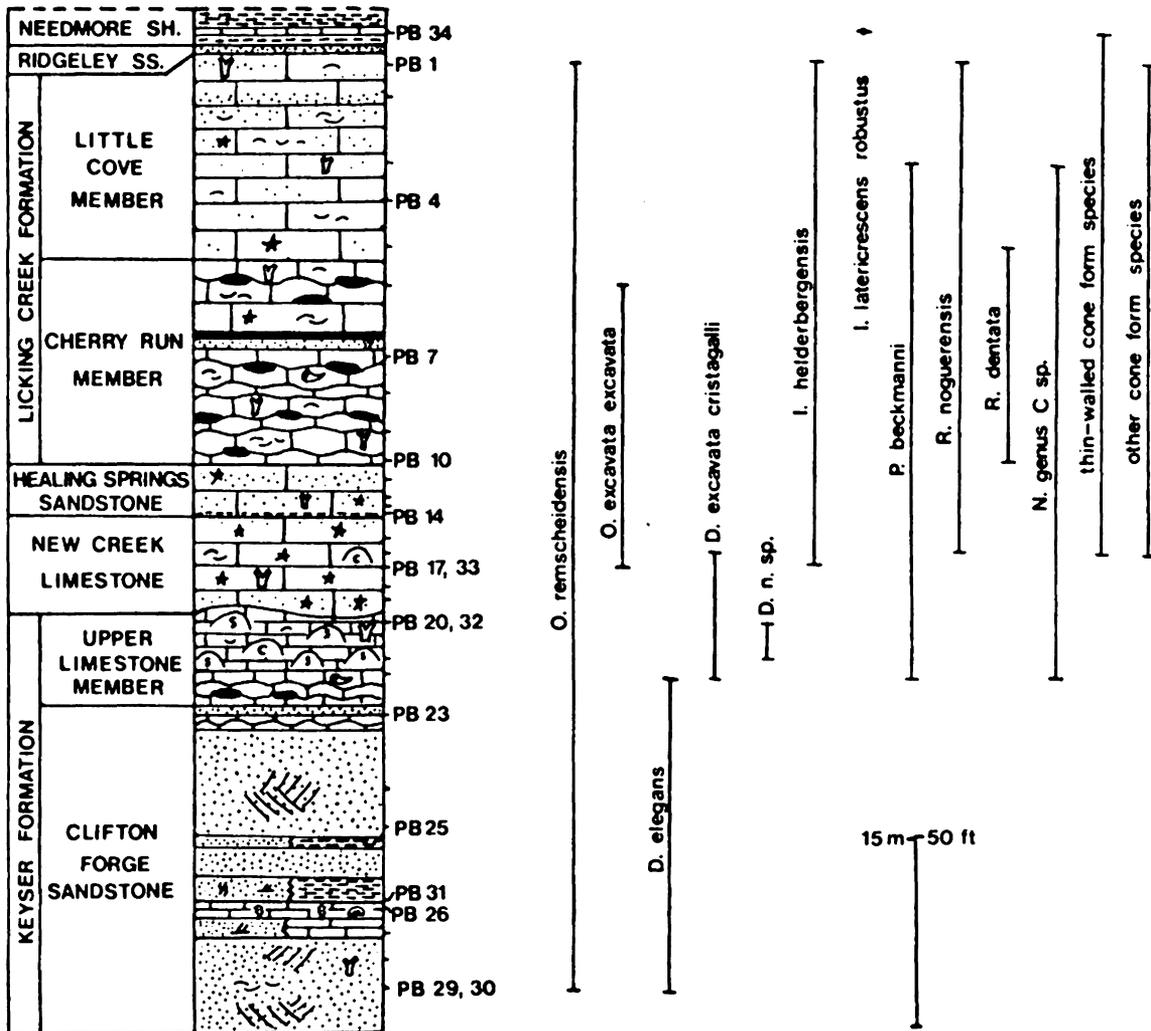
Makurath (1975, 1977), in a study of the Keyser Formation from central Pennsylvania south to Botetourt County, Virginia, divided the formation into six lithofacies. Four of these lithofacies are present in the two sections sampled in this study.

Laminated limestone lithofacies.--This facies includes cryptalgal laminates, more thickly laminated limestone, fenestral mudstone, and thin intraclast-skeletal packstone, with low-diversity faunas dominated by leperditiid ostracods and stromatoporoids. It is present at Price's Bluff (Figure 3) as a unit within the Clifton Forge Sandstone, where it

Table 1. Summary of Helderberg facies.

Formation/Member	Lithology	Biota	Interpreted Environment
Little Cove Member	arenaceous skeletal grainstone, light grey, cross bedded	crinoids, brachiopods, bryozoans	shallow water, above wave base, high energy (Head, 1969)
Cherry Run Member (north)	partially silicified argillaceous lime mudstone, dark grey, interbedded with black chert	rare brachiopods	quiet open marine, below wave base (Head, 1969)
Cherry Run Member (south)	argillaceous skeletal packstone or wackestone, dark grey, nodular, with black chert nodules	brachiopods, bryozoans, crinoids, rugose corals	usually quiet open marine, slightly below wave base (Head, 1969)
Corriganville Limestone (north)	skeletal packstone, with white or grey chert nodules and beds	brachiopods, bryozoans, rugose corals	usually quiet open marine, slightly below wave base (Head, 1969)
Healing Springs Sandstone (south)	arenaceous skeletal grainstone to calcareous quartz sandstone, light grey to reddish brown, cross bedded	crinoids, bryozoans	shallow water, high energy
New Creek Limestone	crinoidal grainstone or packstone, pinkish light grey	crinoids, brachiopods, bryozoans, corals	shallow water, moderately high energy (Head, 1969)
Keyser Upper and Lower Limestone Members (facies are repeatedly interbedded)	lime mudstone, light grey, laminated or fenestral stromatoporoid biostrome, stromatoporoids in a skeletal wackestone matrix pelletal argillaceous lime mudstone or wackestone, with nodular bedding crinoidal or skeletal grainstone, massive or cross bedded	ostracods stromatoporoids, colonial corals, brachiopods, bryozoans ostracods, rare brachiopods, rugose corals crinoids, bryozoans, brachiopods	tidal flat (Makurath, 1977) lagoonal stromatoporoid mound (Makurath, 1977) lagoon (Makurath, 1977) barrier (Makurath, 1977)
Clifton Forge Sandstone Member	cross bedded or massive sandstone, white to reddish brown, few vertical burrows interbedded burrowed or ripple cross laminated sandstone and shale clay-rich lime mudstone, light grey, massive, laminated or fenestral	rare brachiopods, bryozoans ostracods	shallow subtidal barrier (Barwis and Makurath, 1978) sand and mud flat (Barwis and Makurath, 1978) tidal flat (barwis and Makurath, 1978)
Big Mountain Shale Member	grey shale or shale with thin limestone interbeds	rare brachiopods	quiet water

Figure 3. Lithology, sample locations, and species ranges at Price's Bluff. "Thin-walled cone form species" includes Belodella spp., Coelocerodontus spp., and Haplobelodella sp.; "other cone form species" includes Acodina spp., Acodus sp., and gen. indet. spp.



Fauna		Rock Types		Sedimentary Structures	
	stromatoporoids		lime mudstone or wackestone		scoured surface
	colonial corals		lime packstone or grainstone		fenestrae
	rugose corals		nodular limestone		ripple cross lamination
	bryozoans		chert		cross bedding
	brachiopods		interbedded shale and sandstone		burrowing
	crinoids				
	ostracods				

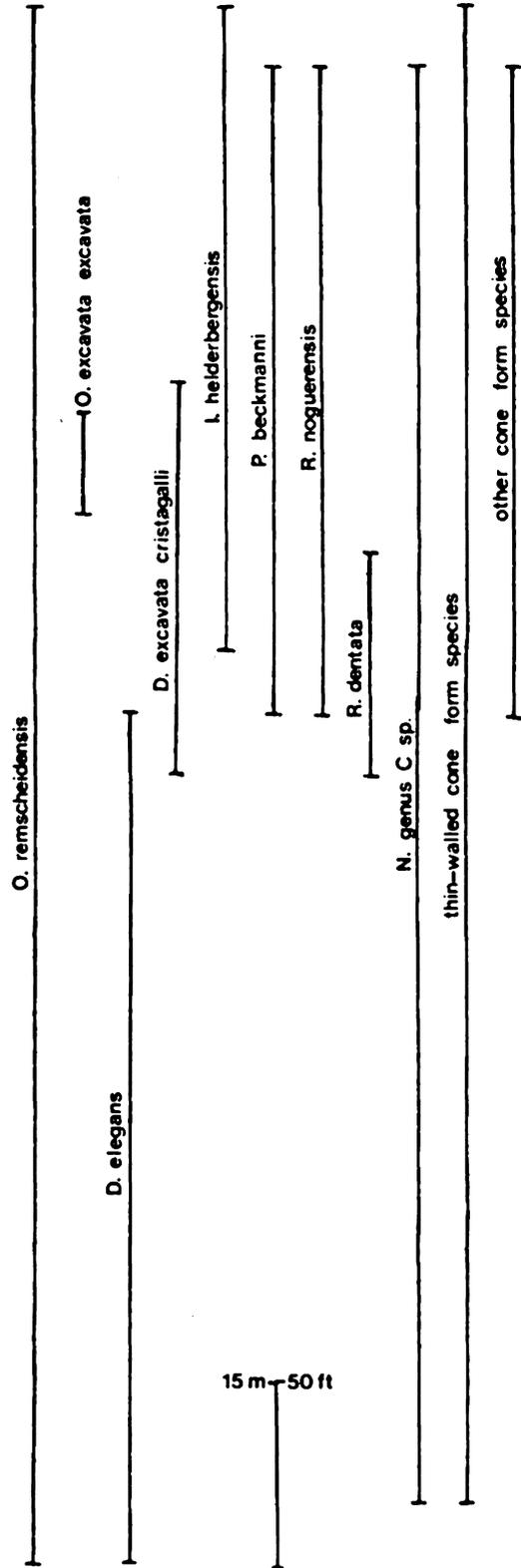
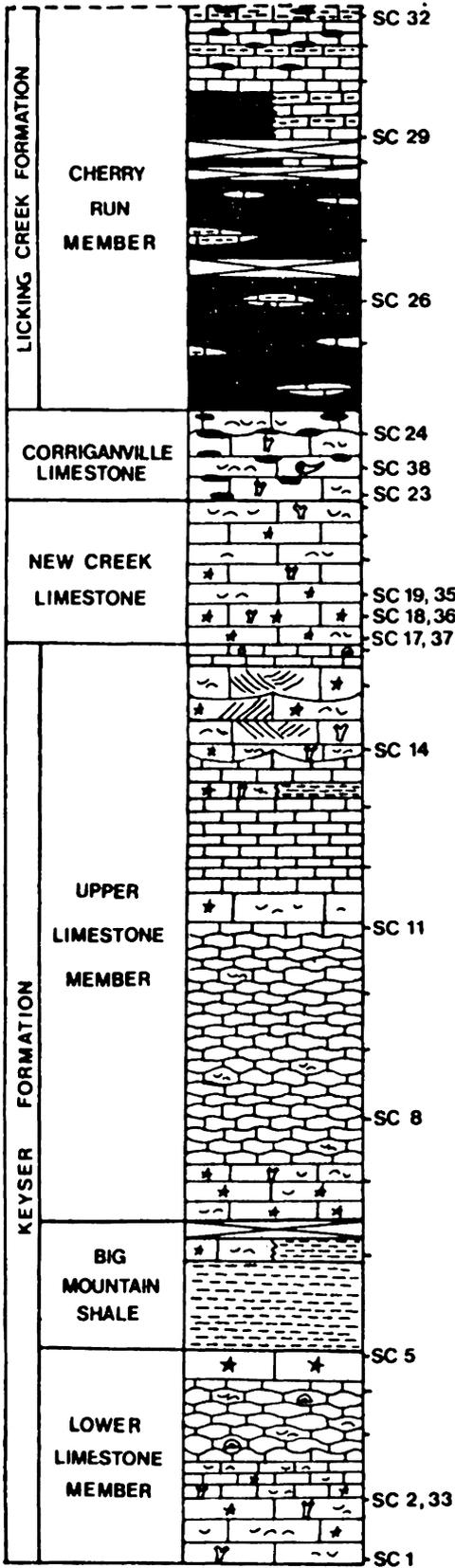
includes 9 feet of very clay-rich lime mudstone, which is thinly interbedded with sandstone in the lower part and in the upper part is fenestrate and contains leperditiid ostracods as its only fauna. This is overlain by a thin bed of skeletal grainstone. At Strait Creek (Figure 4) this facies is present at the top of the formation, including both thinly laminated and fenestral lime mudstone.

The laminated limestone lithofacies is interpreted as tidal flat sediments (Makurath, 1975, 1977). The thin skeletal grainstone at the top of the unit at Price's Bluff is considered to have been deposited during a storm which washed skeletal material up from deeper water onto the tidal flat.

Nodular limestone lithofacies.--This facies consists of nodular-bedded mottled pelletal limestone, often fossiliferous, in a dark organic-rich shaly matrix. Other lithologies include thin pellet-skeletal grainstone and stromatoporoid biostromes with packed stromatoporoids surrounded by lime mudstone or wackestone. Faunal diversity in the facies is generally low. Rocks of this facies are present at Strait Creek in the lower limestone member and in the lower part of the upper limestone member (Figure 4). At Price's Bluff they form the entire upper limestone member which consists of nodular limestone below and a stromatoporoid biostrome above (Figure 3).

The nodular limestone lithofacies is interpreted as lagoonal (Makurath, 1975, 1977). Thin grainstone or sandstone beds within it were deposited as washover sands from the barrier. The stromatoporoid biostromes are considered to be lagoonal buildups rather than wave-

Figure 4. Lithology, sample locations, and species ranges at Strait Creek. For explanation of symbols see Figure 3.



resistant reefs forming part of the barrier facies because of the fine-grained matrix and their persistent association with nodular limestones.

Cross-stratified sand lithofacies.--Makurath (1977) included both carbonate and quartz sandstone in this lithofacies. The quartz sandstone is restricted to the southern end of the study area where it comprises the Clifton Forge Sandstone. It ranges from massive or cross-bedded sandstone with a fauna of moderate-diversity to thin-bedded burrowed or ripple cross-laminated sandstone with shale partings and little or no preserved fauna. This facies forms most of the lower three-quarters of the Keyser at Price's Bluff (Figure 3). The carbonate sand is massive or cross-bedded skeletal grainstone or packstone, in many cases composed largely of crinoid fragments, with a diverse fauna. In the lower limestone member and the lower part of the upper limestone member at Strait Creek this facies is present as massive beds 10-15 feet thick. Near the top of the upper limestone member is a cross-bedded skeletal grainstone 21 feet thick with an internal scoured surface with several inches of relief. A 9-inch boulder of the grainstone which rests on the surface shows that the grainstone was at least partially cemented at the time of the erosion.

The cross-stratified sand lithofacies is interpreted by Makurath (1977) as barrier deposits which separated lagoonal and tidal flat facies from deeper water deposits. The quartz sandstone facies ranges from shallow subtidal to intertidal (Barwis and Makurath, 1978). The carbonate sands occupy a similar position, but are entirely subtidal.

About 9.5 miles south along strike from Strait Creek, at Mustoe, Virginia, a stromatoporoid reef in the upper part of the Keyser corresponds to the cross-bedded skeletal grainstone at Strait Creek. A wave-cut erosional surface within the reef (Smosna and Warshauer, 1979) corresponds to the scoured surface within the grainstone at Strait Creek; this represents a small drop in relative sea level. The reef, like the grainstone, fines up to tidal-flat mudstone overlain by New Creek crinoidal grainstone (Smosna and Warshauer, 1979).

Shale lithofacies.--This facies consists of poorly fossiliferous grey shale, weathering tan. Faunal diversity is low (Head, 1969). This facies is present only in the Big Mountain Shale at Strait Creek, where near the top it is interbedded with thin beds of skeletal packstone. Head (1969) and Makurath (1975, 1977) both considered this facies to have been deposited in quiet water environments during a time when clastic sediment was being supplied to the basin. The lagoonal and open marine limestone facies are distinguished by the higher faunal of the open marine facies (Makurath, 1975, 1977), but, as an influx of terrigenous mud into the open marine environment might well reduce faunal diversity, low diversity does not identify the lagoonal environment under conditions of shale deposition. The shale at Strait Creek could therefore have been deposited either in a lagoonal environment or in an open marine environment below wave base.

Deeper water facies.--Makurath (1975, 1977) described two deeper water facies, neither of which has been definitely identified in the two sections here studied. The shaly limestone lithofacies tends to

overlie barrier sediments and consists of thin beds of whole-fossil wackestone or packstone separated by thin beds and partings of shale. Faunal diversity is high and delicate fossils may be well preserved. Some beds in the upper limestone member at Strait Creek may be assignable to this facies. The thin-bedded muddy calcarenite lithofacies consists of thin beds with a scoured base, coarse skeletal material at the base and laminated sand-sized material above, grading up to burrowed muds (Makurath, 1975, 1977). This facies is interpreted as storm deposits, being similar to those described by Kreisa (1979). It is not present in the two sections studied.

Summary of Keyser facies in study area.--The Keyser Formation at Price's Bluff (Figure 3) has a basal subtidal quartzose barrier facies, grading up to lime mud and clay tidal flat facies, overlain by more subtidal to intertidal quartz sandstone barrier facies. This is overlain by lagoonal nodular limestone, overlain by a stromatoporoid biostrome. The Keyser at Strait Creek (Figure 4) consists largely of an alternation of subtidal carbonate barrier facies and nodular lagoonal facies, perhaps with some deeper water shale or shaly limestone. At the top is a thick unit of barrier grainstone, laterally equivalent to a coral-stromatopoid reef a few miles away; this unit grades up at the top to tidal flat facies.

New Creek Limestone

The New Creek Limestone is composed of massive or cross-bedded, coarse-grained, light-colored crinoidal grainstone or packstone. Some crinoidal columnals are pink, giving the rock a pinkish grey color.

The rock consists largely of disarticulated crinoid columnals, but some parts of the formation, which lack cross bedding, may have articulated sections of crinoid stem. Brachiopods, bryozoans, and corals are also present.

At Price's Bluff the New Creek is cross-bedded at the base, but most of the formation is massive, with some articulated pieces of crinoid stem. At the top it becomes sandy, grading up to the Healing Springs Sandstone. At Strait Creek the New Creek is coarsest at the base and fines up, grading into the overlying Corriganville Limestone.

The New Creek Limestone was deposited in shallow, open marine water under high energy conditions (Head, 1969). The cross-bedded grainstone represents the highest energy conditions. Like the Keyser grainstone, the New Creek probably formed a barrier which separated upper Keyser lagoons from deeper water. As most of the sediment was provided by crinoids, the barrier apparently was formed by a crinoidal meadow with crinoids serving as baffles and as major sediment source. At Strait Creek the energy wanes upward toward the Corriganville as a result of steadily deepening water. At Price's Bluff the lower part of the New Creek was deposited under higher energy conditions than the middle part, but the sandy top of the formation represents renewed increased energy.

Healing Springs Sandstone

The Healing Springs Sandstone is a cross-bedded sandstone unit, with mixed quartz and carbonate sand and quartz pebbles. The carbonate sand is skeletal, dominated by broken crinoid columnals. At Price's

Bluff it grades up from the New Creek Limestone; the boundary is drawn at the base of a 9-inch shale bed. Above this the Healing Springs Sandstone alternates between predominately quartz sand and predominately carbonate sand, with quartz pebbles in the lower part. The Healing Springs was deposited in a shallow, high energy environment. The presence of pebbles and the cross-bedding suggest a higher energy environment than most of the underlying New Creek.

Corriganville Limestone

The Corriganville Limestone includes cherty skeletal packstone and wackestone, fining up from the underlying New Creek grainstone. Shells tend to be unbroken and may be articulated. The chert replaces original carbonate material; the source for the silica may be sponge spicules (Head, 1969). The fauna is very diverse. The Corriganville at Strait Creek grades up from the New Creek Limestone, the base of the Corriganville being drawn at the lowest chert bed. It becomes finer and more argillaceous upward. The Corriganville is interpreted to have been deposited near wave base, deepening upward (Head, 1969).

Licking Creek Formation

Cherry Run Member.--The Cherry Run Member of the Licking Creek consists in the southern part of the study area of cherty dark grey interbedded limestones and shales. The limestones are nodular as a result of sedimentary boudinage (Head, 1969) and are generally skeletal packstones and wackestones. The fauna is diverse and includes brachiopods, trilobites, crinoids, bryozoans, and rugose corals. The Cherry

Run becomes darker, finer grained, and more cherty to the north, and grades to the north of the study area into the Shriver Chert. In the northern part of the study area the Cherry Run consists of dark grey or black lime mudstones, largely replaced by chert, both in beds and disseminated throughout the rock. Faunal diversities are commonly low but the sediment was extensively burrowed (Head, 1969).

The southern Cherry Run is similar to the Corriganville Limestone, although the Cherry Run contains more terrigenous and organic material, and it is interpreted as having been deposited in a similar environment of moderately deep water, slightly below wave base. As the sediment was burrowed, it is unlikely that the lack of fauna was due to anoxic conditions; instead, a very soft substrate may have prevented attachment of epifaunal filter feeders such as brachiopods or bryozoans (Head, 1969).

Little Cove Member.--The Little Cove Member consists of light-colored, cross-bedded skeletal grainstone and packstone with a diverse fauna of brachiopods, bryozoans, crinoids, and corals. At Price's Bluff, the grainstone is sandy, particularly near the top of the member. At the top of the underlying Cherry Run Member, the grainstone lithology interfingers with the dark argillaceous packstone typical of the Cherry Run. Above that the grain size increases upward.

The Little Cove was deposited in a shallow, high energy, normal marine environment. The transition from the deeper water Cherry Run and the upward increase in grain size at Price's Bluff suggests increase in energy and shallowing upward through the member.

CONODONT PALEOECOLOGY

General Conodont Distribution

Conodonts are unevenly distributed among the facies. In particular, conodonts are present in the moderately deep water skeletal packstone and wackestone, in most barrier skeletal grainstone, and in most of the deep water mudstone. Conodonts are present in only a few samples of lagoonal limestone, shallow subtidal to intertidal sandstone, and tidal flat limestone.

This distribution is similar to the distribution of crinoids in the Helderberg Group. A X^2 test of association based on the presence or absence of conodonts and crinoids in the samples shows conodonts and crinoids to be significantly associated; 34 of the 48 conodont-bearing samples are from units with crinoids, and 4 of the 16 barren samples are from units without crinoids. Crinoids, like other echinoderms, are sensitive to variation in salinity.

The avoidance of lagoonal and tidal flat lithologies and the association with crinoids indicates that Helderberg conodonts as a group were not tolerant of restricted conditions. This may have resulted from variable salinity, variable temperature, or both.

Conodont Associations

Associations of conodont species and form species were tested by means of a X^2 test on the presence and absence of each pair of species in the samples within their overlapping ranges (Table 2).

Associations of Delotaxis elegans and D. excavata cristagalli could

	Ozarkodina remscheidensis	O. excavata excavata	Pseudooneotodus beckmanni	Icriodus helderbergensis	Rotundacodina noguerensis	Acodina curvata	Acodus sp.	Belodella devonica	B. resima	B. triangularis	Haplobelodella sp.	Coelocerodontus biconvexus	C. reductus	N. genus C
N. genus C	o	/	+	+	+	+	+	+	+	+	+	+	+	+
Coelocerodontus reductus	+	/	o	+	+	+	+	o	o	o	o	+		
C. biconvexus	o	o	o	+	+	+	+	+	+	+	+			
Haplobelodella sp.	o	o	+	o	+	+	+	+	+	+				
Belodella triangularis	o	/	+	o	o	o	o	+	+					
B. resima	o	o	+	o	o	o	o	+						
B. devonica	o	/	+	+	+	o	+							
Acodus sp.	o	o	o	+	+	+								
Acodina curvata	o	o	o	+	+		+	+: significant association						
Rotundacodina noguerensis	o	-	o	+				-: Significant avoidance						
Icriodus helderbergensis	o	o	o					o: random with respect to each other						
Pseudooneotodus beckmanni	o	+						/: insufficient data for significant results						
Ozarkodina excavata	o													

Table 2. Associations between species significant at the 95% level, based on X^2 tests on presence/absence data within the overlapping ranges of the species.

not be tested, as there were not enough samples from the range of either species for significant results.

Members of a group of species and form species which includes Icriodus helderbergensis, Rotundacodina elegans, and members of the simple cone form genera Acodina, Acodus, Coelocerodontus, and N. gen. C, are strongly associated with each other (Table 2). Some of the form species in the association probably belong together as elements of multielement species, so that the number of biological species associated is probably smaller than the number of "species" considered here. However, the large number of different form species, the variation of the ratios of the numbers of many of the form species, including some which are very abundant, and evidence from the occurrence elsewhere of some of the species demonstrate that the group does not represent a single multi-element species but instead an ecological association of several species.

Members of the genera Belodella and Haplobelodella form a second group of strongly associated conodonts (Table 2). These four form species may be a single multi-element species, but do not always occur together in approximately the same proportions, and they are therefore here treated as separate form species. That tend to occur with members of the Icriodus helderbergensis group, in particular with Coelocerodontus biconvexus and N. gen. C sp.

Ozarkodina excavata and Pseudooneotodus beckmanni are associated, with P. beckmanni present in all samples containing O. excavata.

P. beckmanni is also associated with the Belodella group. O. excavata tends not to occur with the Icriodus helderbergensis group.

Effects of Sorting

The major effect on conodont distribution that would be expected from sorting is the loss by breakage or transportation elsewhere of the lighter and more fragile elements. These include simple cones, the bar elements of Ozarkodina remscheidensis, and all of the Delotaxis elegans elements.

Two species, Icriodus helderbergensis and O. remscheidensis, can be used for recognition of this effect. Both species include both relatively light and relatively heavy elements. The S₂ element of I. helderbergensis, which is a simple cone, and the bar elements (M, Sa, Sb, and Sc elements) of O. remscheidensis are thinner and more fragile than the blade elements (Pa and Pb elements). The natural ratio of elements within an apparatus can be calculated approximately using samples from low-energy facies. A higher than normal proportion of heavy elements in either apparatus indicates loss of light elements through mechanical sorting. Loss of the S₂ element of I. helderbergensis was observed in the upper two samples in the Little Cove Member at Price's Bluff. Loss of the bar elements of O. remscheidensis was observed in the lower part of the New Creek Limestone at both sections and in the storm-deposited grainstone above the tidal flat facies in the Keyser Formation at Price's Bluff. The ratios are not strongly distorted in the Keyser grainstones at Strait Creek or the lower three samples of the Little Cove grainstones at Price's Bluff.

Distribution of Conodont Species

Idriodus helderbergensis group.--I. helderbergensis and its associated species occur irregularly within their stratigraphic range, in numbers ranging from zero to hundreds of conodonts per kilogram. Samples yielding this association were taken from the lower part of the New Creek at Strait Creek, part of the Licking Creek at Strait Creek, and most of both facies of the Licking Creek at Price's Bluff. Samples within the range of the species but lacking these conodonts include the New Creek and the Healing Springs Sandstone at Price's Bluff, and the upper New Creek and parts of the Corriganville and Licking Creek at Strait Creek. Thus, these conodonts are present in the high-energy coarse skeletal facies in the New Creek at Strait Creek and the Little Cove at Price's Bluff, but not similar facies in the New Creek at Price's Bluff; they are present in the deeper water muddy skeletal packstone of the Cherry Run at Price's Bluff, but not in that of the upper New Creek and most of the Corriganville at Strait Creek; and they are present in large numbers in part of the relatively deep water dark cherty lime mudstone from the Licking Creek at Strait Creek, but absent from other samples from that unit. The species appear to be irregularly distributed within seemingly uniform facies in the study area, over an environmental range from barrier to quiet water below wave base. The irregularity of the distribution suggests that some environmental factor or factors exert a strong control on the occurrence of Icriodus helderbergensis and the species associated with it, but this factor is neither depth nor substrate.

Belodella group.--Members of this group are present in abundance in some samples from the northern Cherry Run dark cherty mudstone, in two samples at the top of the southern Cherry Run muddy skeletal packstone, in one sample from the New Creek crinoidal grainstone, and in the single sample from a shaly limestone bed in the Needmore Shale. They are also present in small numbers in most of the remaining samples from the Cherry Run at both sections, in the lower part of the Little Cove, and in a few samples from the Keyser Formation at Strait Creek, in facies including tidal flat lime mudstone, barrier skeletal packstone and grainstone, and interbedded skeletal limestone and shale. They are absent from most of the New Creek Limestone, the Keyser Formation at Price's Bluff and most of the Keyser at Strait Creek, the Healing Springs Sandstone, and the Corriganville Limestone. In summary, they occur in facies ranging from tidal flat to deep water, although they are usually absent from tidal flat and lagoonal facies and are not present in all barrier and deeper water units, and they occur in rocks ranging from lime mudstone to grainstone. These conodonts are missing from the highest energy facies, but all of them are small and light and this could be merely an effect of sorting. As in the case of the Icriodus helderbergensis group, neither depth nor substrate appears to be a factor determining the occurrence of these conodonts.

Ozarkodina excavata.--O. excavata is restricted to a small range in both sections (Figures 3 and 4), which includes at Strait Creek the upper New Creek and lower Corriganville, and at Price's Bluff the upper New Creek and lower Cherry Run. Elsewhere O. excavata ranges from the

Silurian patula zone (Walliser, 1971) through the Emsian gronbergi zone (Klapper and Johnson, 1980). As this span of time covers the deposition of the entire Helderberg Group, the limitation on the occurrence of O. excavata in the Helderberg is not chronostratigraphic. It occurs in similar facies at the two sections, in the lower energy parts of the New Creek and the muddy skeletal packstone of the Corriganville and southern Cherry Run. The cross-bedded quartz and carbonate sandstone of the Healing Springs, which lies between the New Creek and the Cherry Run, does not contain O. excavata; neither does skeletal packstone in the Keyser which is similar to the rocks with O. excavata higher in the section. It is possible, therefore, that O. excavata is limited to moderate-energy facies, being excluded from both very high energy and low energy conditions, and that by its time of migration into the basin or by climate. Climate may influence the occurrence of this species in Europe (Jeppsson, 1974).

Pseudooneotodus beckmanni.--P. beckmanni occurs in the same moderate-energy facies as O. excavata and also in the higher energy facies of the lower part of the New Creek Limestone at Strait Creek and the lower three samples of the Little Cove Member at Price's Bluff. It therefore ranges from muddy skeletal packstones to skeletal grainstones, and is absent or rare in very high energy rocks, such as cross-bedded sandstones and grainstones of the lower New Creek, the Healing Springs, and the top of the Little Cove, and also in the deeper water mudstones of the Cherry Run at Strait Creek. It is also usually missing from all facies of the Keyser, including facies similar to those in

which it is present higher in the section, although the species ranges elsewhere through the Silurian (Cooper, 1977). Its absence from the very high energy facies may be due to mechanical sorting, as it is relatively small. Its distribution does not closely follow that of the Icriodus helderbergensis group, as P. beckmanni is present in the upper New Creek and Corriganville Limestones at Strait Creek, where I. helderbergensis and the species associated with it are missing. In the post-Keyser Helderberg, P. beckmanni is apparently limited to the moderate-energy, moderate-depth facies, but is independent of the factors which control the distribution of I. helderbergensis.

Ozarkodina remscheidensis.--This species is present, often in great abundance, in all of the Keyser samples which yielded conodonts, in the lower part of the New Creek at both sections, and in the three Corriganville samples. In the rest of the section, which includes the upper half of the New Creek at Strait Creek and most of the New Creek at Prices' Bluff, the Healing Springs Sandstone, and all facies of the Licking Creek Formation, O. remscheidensis is sporadically present in small numbers. Thus O. remscheidensis is present in facies from tidal flat to deep water mudstone, and abundant in some but not all lagoonal, barrier, and moderately deep water facies.

Although most tidal flat and many lagoonal samples lack conodonts, there are several samples from such environments in the Keyser, including SC7, SC12, SC16, and PB31, which contain a few O. remscheidensis and no other conodonts. O. remscheidensis therefore appears to be more tolerant of restricted conditions than most conodont species.

O. remscheidensis is rare in or absent from the deeper water facies of the Cherry Run Member at both sections. However, the sequence at Strait Creek from the New Creek through as much of the Licking Creek as is exposed, which was deposited under steadily deepening conditions, does not show the pattern of occurrence of O. remscheidensis that would be produced by simple depth control. Instead, O. remscheidensis is abundant in the lower New Creek, rare or absent in the upper New Creek, abundant again in the overlying Corriganville, and rare or absent in the Licking Creek.

Delotaxis elegans.--D. elegans ranges from the upper Tonoloway Formation (Helfrich, 1975) through most of the Keyser Formation. It is generally absent from the more restricted facies and present elsewhere. In the Tonoloway, which consists of restricted limestone facies, D. elegans is extremely rare, known only from one specimen from one sample (Helfrich, 1975). In the Keyser D. elegans is present in barrier grainstone and packstone, interbedded limestone and shale, and some lagoonal limestone, and is absent from tidal flat lime mudstone, sandstone, and shale, and from most of the lagoonal limestone.

Delotaxis excavata cristagalli.--This species is sporadically present from the upper Keyser through the Corriganville at Strait Creek and through most of the New Creek at Price's Bluff. The samples in which it occurs are from rocks which range from skeletal wackestone to cross-bedded skeletal grainstone and include lagoonal, carbonate barrier, and quiet offshore facies. Control of occurrence or abundance of D. e. cristagalli within this range by lithofacies is not apparent.

Delotaxis n. sp.--Delotaxis n. sp. is present only in two adjacent samples at Price's Bluff; one is from a cross-bedded crinoidal grainstone at the base of the New Creek, the other from the top of the lagoonal stromatoporoid biostrome at the top of the Keyser. The species therefore occurs in both low-energy and high-energy facies.

Models of Conodont Ecology

Two models of conodont ecology have been proposed to explain conodont distribution. Seddon and Sweet (1971) suggested a vertical segregation model, based on late Devonian and Ordovician conodont distributions, according to which conodonts were pelagic and restricted to certain depth ranges. The pattern of conodont distribution predicted by this model is that any species is present wherever the water depth was greater than the minimum water depth required by that species. The relative abundance of a species decreases where the water depth was greater than the maximum depth at which the species could live and other, deeper-water species could appear. Diversity therefore increases with increasing depth.

Barnes and Fähræus (1975) proposed a model involving horizontal segregation, based on work with Ordovician conodonts. A few wide ranging simple cone species are considered pelagic, but most species are thought to be benthic or nektobenthic. A species or small group of species forming a community occupies a depth zone, with zones of adjacent communities overlapping slightly. In the Ordovician, three or four communities existed at any given time, ranging from the littoral zone seaward.

Both the horizontal segregation model and the vertical segregation model are based on control of conodont distribution by factors directly related to depth. This is not the case with the Helderberg Group conodonts, with the exception of Pseudooneotodus beckmanni and perhaps Ozarkodina excavata. Conodonts tend to be excluded from restricted nearshore environments, but water depth and energy do not seem to control the distribution of most species in normal marine facies. Moreover, the same factors do not seem to control all Helderberg conodonts. O. remscheidensis and O. excavata are distributed independently of each other, of I. helderbergensis, and of the Belodella group, and D. e. cristagalli shows no strong tendency to avoid or to associate with any of them. This suggests that different factors affect the different conodont species.

CONODONT BIOSTRATIGRAPHY

Zonation of the Upper Silurian and Lower Devonian

Conodont zonations have been proposed for the uppermost Silurian and the Lower Devonian, based largely on European and North American sections. Correlation among these zonations is, in some instances, still in dispute, particularly in the lower part of the Lower Devonian, where many species are endemic to one region. Figure 5 shows the correlation of the most widely applicable zonation to the standard uppermost Silurian and Lower Devonian stages.

Uppermost Silurian zonation.--Walliser (1964) erected a series of zones based largely on a section at Cellon, Austria, in the Carnic Alps, for most of the Silurian and the lowermost Devonian. This zonation has, with some modification, been used worldwide (Walmsley et al., 1974; Klapper and Murphy, 1975; Aldridge, 1975; Helfrich, 1975; and Cooper, 1977). The three highest of these zones, in ascending order, are the crispus and eosteinhornensis zones, which are Silurian, and the woschmidti zone, which is largely lowermost Devonian.

In North America, the crispus and eosteinhornensis zones have been reported in sequence from central Nevada (Klapper and Murphy, 1975) and the Appalachians of Virginia and West Virginia (Helfrich, 1975, 1978), and the eosteinhornensis zone from Nova Scotia (Legault, 1968) and the Canadian Arctic islands (Walliser, 1960).

Silurian-Devonian boundary.--The Silurian-Devonian boundary was defined by international agreement (McLaren, 1973) to be at the base of

a bed which is the lowest bed containing Monograptus uniformis in the section at Klonk, Czechoslovakia. Conodonts have not been described from the boundary stratotype at Klonk. However, at Cellon, Austria, Icriodus woschmidti woschmidti appears 2.2 meters below the lowest occurrence of M. uniformis, and at the Birch Creek section, Eureka County, Nevada, I. woschmidti hesperius appears 1.8 meters below the lowest M. uniformis (Klapper and Murphy, 1975). In both cases I. woschmidti s.l. appears just above the overlap of Ozarkodina remscheidensis eosteinhornensis and O. r. remscheidensis as defined by Klapper and Murphy (1975). If the lowest occurrence of M. uniformis is taken as the best indicator of the boundary, then it appears that the bases of the woschmidti zone of Europe and the hesperius zone of western North America are just below the Silurian-Devonian boundary.

Lower Devonian zonation.--Lower Devonian conodont biostratigraphy is complicated by provincialism. In the lower part of the Lower Devonian there are few cosmopolitan species, and, with the exception of the lowest zone, many endemic species (Klapper and Johnson, 1980). As a result of this, although local conodont sequences are known from several areas, correlating these with each other is difficult because zonally diagnostic species are often restricted to one area. Therefore, no zonation which is applicable worldwide exists for the lower part of the Lower Devonian. The zonation developed for the upper part of the Lower Devonian and the Middle Devonian (Klapper, Ziegler, and Mashkova, 1978; Weddige and Ziegler, 1977) can be applied much more widely.

The most nearly complete zonation of the Lower Devonian (Figure 5) is based on sections in western North America, in particular in Nevada (Klapper, 1977), the Yukon Territory (Klapper, 1969, 1977; Fahraeus, 1971), and eastern Alaska (Lane and Ormiston, 1979). The nominal species of the lowest four zones, starting with the lowest, are Icriodus woschmidti hesperius, Ozarkodina eurekaensis, O. delta, and Pedavis pesavis pesavis. Each of the zones has approximately the range of its nominal species. Ranges of these and other species of those genera and of Ancyrocelloides, which are also diagnostic of the zones, are shown in Figure 6. Most of the characteristic species are restricted to western North America.

A second conodont sequence, from Spain (Figure 6), has been described but not formally zoned (Carls and Gandl, 1969; Carls, 1969, 1975; Bultynck, 1971). The same sequence of faunas has been reported from Turkey (Ziegler, 1971). The sequence is characterized largely by Icriodus species, most of them endemic. Species of Ozarkodina, Pedavis, and Ancyrodelloides are also present. The widespread species I. w. woschmidti is at the base of the section, followed by I. postwoschmidti.

Mashkova (1979) has described conodont zones through the Lower Devonian of the Soviet Union. The lower three of these, the woschmidti, postwoschmidti, and eolatericrescens zones, are based on related Icriodus species and occur in sequence in Podolia (Mashkova, 1968, 1970, 1979). The woschmidti zone extends from the first appearance of I. w. woschmidti to the first appearance of I. postwoschmidti. The

CONODONT ZONES	SERIES AND STAGES		
	RHENISH AND BRITISH	BOHEMIAN	
<i>costatus costatus</i>	EIFELIAN	COUVINIAN	DEVONIAN
<i>patulus</i>			
<i>serotinus</i>	EMSIAN	— ? —	
<i>inversus</i>		DALEJAN	
<i>gronbergi</i>		ZLICHOVIAN	
<i>dehiscens</i>		— ? —	
<i>kindlei</i>			
<i>sulcatus</i>	SIEGEMIAN AND GEDINNIAN	— ? —	
<i>pesavis</i>		LOCHKOVIAN	
<i>delta</i>			
<i>eurekaensis</i>			
<i>hesperius/woschmidti</i>		— ? —	
<i>eosteinhornensis</i>	LUDLOVIAN	PRIDOLIAN	
<i>crispa</i>		— ? —	
<i>latialatus</i>		KOPANINAN	
<i>siluricus</i>		?	

Figure 5. Correlation of conodont zones with Upper Silurian and Lower Devonian series and stages. Devonian after Klapper and Johnson, 1980; Silurian conodont zones after Walliser, 1964; Ludlovian after Aldridge, 1975; Pridoli and Kopanina after Walmsley, Aldridge, and Austin, 1974.

postwoschmidti zone has both I. w. woschmidti and I. postwoschmidti at the base and extends above this to the first appearance of I. eolatericrescens and I. angustoides bidentatus, which marks the base of the eolatericrescens zone. I. postwoschmidti ranges through the postwoschmidti zone into the base of the eolatericrescens zone. The fourth of Mashkova's conodont zones, the optima-pesavis zone, is named for Pandorinella optima and Pedavis pesavis. It does not occur in direct sequence with the lower zones, so that it is possible that a gap exists in the zonal scheme between the eolatericrescens zone and the optima-pesavis zone.

Conodonts of lowermost Devonian age are also known from central Europe and from eastern Australia (Klapper and Ziegler, 1979), but not in continuous sequences that could be used to establish a zonation.

Correlation among zonations.--As discussed above in the section on the Silurian-Devonian boundary, it appears that the first appearance of Icriodus woschmidti woschmidti and I. w. hesperius correlate with each other. The bases of the woschmidti zone of Europe and the hesperius zone of western North America are therefore equivalent.

Conodonts of the overlying postwoschmidti and eolatericrescens zones are present in Spain as well as in Podolia. In Podolia I. postwoschmidti first appears below the first appearance of I. eolatericrescens and I. angustoides bidentatus, which occur together with I. postwoschmidti at the base of the eolatericrescens zone (Mashkova, 1970, 1979). In Spain I. postwoschmidti and I. a. bidentatus appear together (Carls, 1975). This may be due to a gap in the section

Figure 6. Zonation and species ranges, Nevada and Spain, for the lower part of the Lower Devonian. The hesperius zone is the lowest zone. After Klapper and Ziegler, 1979.

HESPERIUS		EUREKA-ENSIS	DELTA	PESAVIS	SULCATUS	KINDLEI	ZONE AREA	
			<i>I. woschmidti hesperius</i>				N E V A D A	
			<i>O. n. sp. E</i>					
			<i>O. remscheidensis remscheidensis</i>					
			<i>O. n. sp. F</i>					
			<i>O. eurekaensis</i>					
			<i>Pedavis n. sp. C</i>					
			<i>I. n. sp. G</i>					
				<i>O. delta</i>				
				<i>O. n. sp. C</i>				
				<i>Pedavis pesavis n. subsp. A</i>				
				<i>O. remscheidensis repelitor</i>				
				<i>O. transitans</i>				
				<i>O. stygia</i>				
				<i>O. johnsoni</i>				
			<i>Pedavis pesavis pesavis</i>					
			<i>I. steinachensis eta</i>					
			<i>O. n. sp. I</i>					
			<i>O. linearis</i>					
			<i>E. sulcatus sulcatus</i>					
				<i>I. n. sp. B</i>				
				<i>Pedavis n. sp. A</i>				
			<i>I. huddlei curvicauda</i>					
				<i>E. sulcatus kindlei</i>				
LUESMA (part)		NOGUERAS			SANTA CRUZ (part)		FORMA- TION	
1bβ	1c a-β	1cγ	2αα	2αβ 2b	2c	3a	3b	MEMBER
			<i>I. woschmidti woschmidti</i>					S P A I N
			<i>O. remscheidensis remscheidensis</i>					
			<i>I. postwoschmidti</i>					
			<i>I. rectangularis rectangularis</i>					
			<i>I. angustoides bidentatus</i>					
			<i>- Pelekysgnathus serratus elongatus</i>					
			<i>O. remscheidensis repelitor</i>					
			<i>O. transitans</i>					
			<i>- I. angustoides alcolea</i>					
			<i>- I. rectangularis lotzei</i>					
			<i>- I. vincorum</i>					
			<i>- I. fallax</i>					
			<i>- A. trigonicus</i>					
			<i>- Pedavis pesavis n. subsp. A</i>					
			<i>I. angustoides angustoides</i>					
			<i>I. angustoides castilianus</i>					
			<i>I. simulator</i>					
			<i>I. huddlei curvicauda</i>					

in Spain, so that the postwoschmidti zone is entirely missing there, or to a delay in the appearance of I. eolatericrescens and I. a. bidentatus in Podolia, in which case the postwoschmidti zone and the eolatericrescens zone may overlap completely. Correlation between Europe and western North America in this interval is not possible, except on the basis of correlation of underlying and overlying zones. On this basis, the postwoschmidti and eolatericrescens zones of Podolia and Spain together correlate with all or part of the upper hesperius and eurekaensis zones of Nevada.

The delta zone of Nevada overlies the eurekaensis zone. It is characterized in Nevada by five species (Klapper, 1977; Klapper and Johnson, 1980). Ozarkodina delta and O. eleanorae are restricted to western North America, but Pedavis pesavis n. subsp. A Klapper and Phillip, Ancyrodelloides trigonicus, and A. kutscheri are more widespread (Klapper and Johnson, 1980). P. pesavis n. subsp. A and A. trigonicus are present in the Spanish sequence above Icriodus postwoschmidti and I. angustoides bidentatus (Carls, 1975). Ozarkodina transitans, which ranges through the delta and pesavis zones in western North America, is also present with species characteristic of the delta zone in Spain and elsewhere (Klapper and Johnson, 1980). Thus, the delta zone correlates with strata above the postwoschmidti and eolatericrescens zones as represented in Spain.

Pedavis pesavis pesavis characterizes both the western North American pesavis zone and the optima-pesavis zone of the Soviet Union. However, Pandorinella optima is not restricted to the pesavis zone in

the Yukon Territory, ranging both above and below it (Klapper, 1977). The correlation of the optima-pesavis zone with the western North American sequence therefore depends on exactly how the zone is defined, which Mashkova (1979) unfortunately does not specify.

Helderberg Conodont Biostratigraphy

The conodont fauna of the Helderberg Group differs from lowermost Devonian faunas described from other areas both in including species endemic to the area and in lacking species present elsewhere. Most of the characteristic zonal forms from other areas do not occur in the Helderberg Group. The fauna does not appear to differ much between southeastern New York (Epstein, 1970; Barnett, 1971) and Virginia; most of the same species are present in both areas.

Biostratigraphically important species in the Helderberg Group of the study area include Delotaxis elegans, Ozarkodina remscheidensis, Delotaxis excavata cristagelli, Icriodus helderbergensis, Rotundacodina noguerensis, and Rotundacodina dentata.

Delotaxis elegans.--D. elegans has been reported from the siliuricus through eosteinhornensis zones, and in the Carnic Alps from the lowermost woschmidti zone (Jeppsson, 1974). In the study area, D. elegans is present through most of the Keyser Formation, and is also present in the underlying Tonoloway Formation north of the study area (Helfrich, 1975). Its highest occurrences are in the Keyser at 30 feet and 15 feet below the base of the New Creek Limestone at Strait Creek and Price's Bluff, respectively (Figures 3 and 4).

Jeppsson (1972, 1974) has reported D. elegans elements with large denticles regularly alternating with one or more small denticles from the uppermost eosteinhornensis and lowermost woschmidti zones in Europe and North Africa. In the study area, only one such Pb element was found, which came from the top of the Big Mountain Shale, in the highest sample with abundant D. elegans at either section.

Ozarkodina remscheidensis.--O. remscheidensis eosteinhornensis is restricted to the eosteinhornensis zone. It appears at the base of the zone and grades into O. r. remscheidensis at the top of the zone, just below the appearance of I. woschmidti, which marks the base of the overlying woschmidti zone. This transition takes place just below the Silurian-Devonian boundary in both Europe and western North America (Klapper and Murphy, 1975).

In New York O. r. remscheidensis has been reported from the Helderberg Group as high as the Kalkberg Formation, and from upper Silurian rocks as low as the Syracuse Formation (Rickard, in Klapper, Berry, and Boucot, 1970; Barnett, 1971, 1972) and O. r. eosteinhornensis has not been reported. This anomolous distribution is apparently due to the difficulty of distinguishing the two subspecies, which differ only in the denticulation of the Pa element. It is generally agreed that the transition is gradational and the range of variation of any given population is wide; few authors distinguish the two in exactly the same fashion (cf. Walliser, 1964; Klapper and Murphy, 1975; and Mehrtens and Barnett, 1976). In the case of the New York specimens, the lowest specimens illustrated by Barnett (1971) as O. r.

remscheidensis fall within the range of variation of O. r. eosteinhornensis according to Klapper and Murphy (1975). The location of the transition between O. r. remscheidensis and O. r. eosteinhornensis therefore does not appear to be precisely reproducible by different workers, and should be used for biostratigraphic purposes only with caution.

O. r. remscheidensis ranges up into the delta zone in Nevada and up to the base of that zone in Spain (Figure 6).

Barnett (1971, 1972) measured several characters of many Pa elements of O. remscheidensis s.l. and determined which appeared to be environmentally controlled. He then used the stratigraphic variation of the remaining characters for correlation both within the northern Appalachian Basin (Barnett, 1971) and from there to reference sections in Nevada and Czechoslovakia (Barnett, 1972). The correlation between Nevada and Czechoslovakia determined by this method differs from that determined by Klapper and Murphy (1975), who used the first occurrences of Monograptus uniformis, Warburgella rugulosa, and Icriodus woschmidti s.l. and the transition from O. r. eosteinhornensis to O. r. remscheidensis.

O. remschiedensis eosteinhornensis occurs through most of the Keyser Formation, grading up into O. r. remschiedensis in the upper part of the formation. The two subspecies intergrade over some distance, with forms present typical of both subspecies and intermediate between them. At Strait Creek, the lowest typical O. r. remscheidensis is in the Keyser at 29 feet below the base of the New

Creek, and the highest typical O. r. eosteinhornensis is 37 feet higher in the New Creek; most of the specimens in this interval are intermediate. At Price's Bluff, there are fewer samples with large populations of the species, but the observed interval of overlap of the two subspecies is approximately from 15 feet below the base of the New Creek to 4 feet above it. O. r. remschiedensis ranges up from there through the rest of the Helderberg Group at both sections.

Delotaxis excavata cristagalli.--D. e. cristagalli has been reported in Europe from the base of the woschmidti zone of the Carnic Alps (Walliser, 1964), the Rhenish Slate Mountains (Ziegler, 1960), and Bohemia (Walmsley et al., 1974). It has also been reported from the upper e-gamma limestone of the Karawankan Alps (Schulze, 1968), in which it is associated with Ozarkodina transitans. This occurrence therefore correlates with either the delta or the pesavis zone. The hitherto established total range of D. e. cristagalli is therefore from the base of the woschmidti zone to the delta zone and perhaps the pesavis zone. In southeastern New York and New Jersey it ranges from the Thatcher Member of the Manlius Formation to the lower New Scotland Formation (Epstein, 1970).

Delotaxis excavata cristagalli is the youngest member of a lineage which begins at least as early as the Silurian sagitta zone. Two of the older subspecies, D. e. excavata and D. e. novexcavata, occur in the siluricus and lower eosteinhornensis zones, respectively, in Gotland (Jeppsson, 1972). Three subspecies distinguished chiefly on differences in the Pb element occur in the Mifflintown and Wills

Creek Formations of West Virginia and Maryland. These subspecies were described by Helfrich (1975) in form taxonomy, although he noted the association of the Pa and Pb elements as his group V. Of these three subspecies, D. e. aequalis occurs in the Ozarkodina sagitta bohemica zone, D. e. tenuiramaea in the O. bicornuta and O. snajdri zones, and D. e. sinuosa in the O. tillmani zone; this sequence covers roughly the same span of time as the sagitta through siluricus zones (Helfrich, 1975). D. e. sinuosa, the youngest of the Appalachian subspecies, is apparently a contemporary of D. e. excavata, the older of the two Swedish subspecies, but the relationship between them is not clear and would have to be resolved by study of the original material.

D. e. cristagalli first appears in the upper part of the Keyser Formation, 15 feet below the base of the overlying New Creek Limestone at Price's Bluff and 45 feet below the base of the New Creek at Strait Creek, and it ranges up into the Corriganville Limestone at Strait Creek and into the New Creek at Price's Bluff.

Due to environmental restriction, no Delotaxis excavata of any subspecies has been found in the southern Appalachian in the upper Wills Creek, Tonoloway, and lower Keyser Formations. The only exception to this, in the Tonoloway in Maryland, does not include the Pb element which would be necessary to distinguish the subspecies (Helfrich, 1975). The transition to D. e. cristagalli from its immediate ancestor, which would be a more precise time marker than the first appearance of the subspecies, therefore cannot be observed.

However, D. e. cristagalli has not been reported from below the woschmidti zone, and its first appearance is therefore an approximation to the base of that zone.

Rotundacodina noguerensis.--This species occurs in the dlc-gamma d2c-alpha beds of the Gedinnian of Spain (Carls and Gandl, 1969). This interval includes approximately the postwoschmidti through the delta or perhaps lower pesavis zones (Klapper and Ziegler, 1979). The lower limit of its range in Spain is not known, as Carls and Gandl (1969) did not recover conodonts from beds below the postwoschmidti zone. R. noguerensis is also present in southeastern New York in the Coeymans and lower Kalkberg Formations (Epstein, 1970).

In the Helderberg Group of the study area R. noguerensis first appears 30 feet below the top of the Keyser Formation at Strait Creek and within the New Creek Limestone at Price's Bluff.

Icriodus helderbergensis.--I. helderbergensis n. sp. has been previously reported only from the Helderberg Group of the Appalachians, under the name of Icriodus woschmidti. As the specimens illustrated as "I. woschmidti" differ from typical I. woschmidti in possessing transverse rows of denticles instead of fused transverse bars, in having, in many cases, more transverse rows than I. w. woschmidti has bars, and in having processes not as well developed as in I. w. hesperius, they are here assigned to I. helderbergensis. They have been reported from the main Helderberg outcrop belt of southeastern New York, New Jersey, and eastern Pennsylvania from the Thatcher Member of the Manlius Formation up into the lower New Scotland

Formation (Epstein, 1970; Barnett, 1971), from the Helderberg outlier to the east as low as the Roundout Formation (Barnett, 1971), and from West Virginia in the top of the Keyser Formation (Helfrich, 1978). However, all illustrated specimens from the New York-New Jersey area are from the Coeymans Formation, and it is possible that some of the unillustrated reports of the species from older formations may in fact be I. woschmidti.

In the study area, the first appearance of I. helderbergensis is in the Keyser Formation 11 feet below the base of the New Creek Limestone at the Strait Creek section, and at Price's Bluff in the New Creek 9 feet above its base.

Some of the lowest specimens of Icriodus helderbergensis have transverse bars instead of the typical transverse rows of denticles, which suggests a transition from I. woschmidti. These occur together with the typical forms, intergrading with them, in the lowest 19 feet of the range of the species at Strait Creek. Whether the same is true of I. helderbergensis at Price's Bluff cannot be determined, because of the rarity and poor condition of the specimens in the lower part of the species range. Since the occurrence and abundance of I. helderbergensis are to some extent environmentally controlled, its first occurrence may be an unreliable time marker; if, however, these specimens indeed represent an evolutionary development, the level at which they grade into typical I. helderbergensis will be a good marker for correlation.

Rotundacodina dentata.--R. dentata occurs with R. noguerensis in the dlc-gamma beds of the Geninnian of Spain (Carls and Gandl, 1969), which lie within the postwoschmidti and/or eolatericrescens zones. As with R. noguerensis, the lower limit of its range in Spain is not known. In the Appalachians it occurs in the Coeymans Formation of southeastern New York and New Jersey (Epstein, 1970; Barnett, 1971). In the study area it was found in the Licking Creek at Price's Bluff and in the upper Keyser and New Creek at Strait Creek. Helfrich (1978) also found it lower in the Keyser, in and just above the Big Mountain Shale.

Icriodus latericrescens robustus.--I. l. robustus is endemic to North America, having hitherto been found in New York and Nevada. The range of this species in New York, from the uppermost Schoharie Formation through the Ononodaga Limestone, includes the patulus and costatus costatus zones (Klapper and Ziegler, 1967; Klapper, 1971), as well as some strata below the patulus zone which lack diagnostic conodonts but which may correlate with the serotinus zone (Klapper and Johnson, 1980). This range spans approximately the late Emsian and early Eifelian (Figure 5).

I. l. robustus was found in the only sample taken from the Needmore Shale, 4 feet above the base of the formation at Price's Bluff (Figure 3).

Correlation Between Sections

The two sections sampled in this study are about 50 miles apart. Major facies changes take place over that distance, and the Helderberg

section doubles in thickness, which complicates correlation of the two sections. It has been demonstrated that the formations of the Helderberg Group of New York are time-transgressive along a line oblique to the basin axis. Since the line between the sections studied here also is slightly oblique to the basin axis, with the Strait Creek section closer to the center of the basin, one might expect the formations to be time-transgressive but not as strongly as in New York.

Some correlations can be based on physical evidence. A tongue of clastic sediment extending into a carbonate basin from a short-lived sediment source is an approximation to a time plane. The Clifton Forge Sandstone and the Big Mountain Shale, which interfingers with the lower part of the Clifton Forge, form such a tongue (Figure 2). The lower part of the Clifton Forge Sandstone at Price's Bluff therefore correlates with the Big Mountain Shale at Strait Creek. The Healing Springs Sandstone, a second clastic tongue, does not reach Strait Creek, pinching out between Bolar and Monterey. The Healing Springs diverges from the lower clastic tongue, demonstrating that Head's (1969) assumption of constant rates of sedimentation across the basin is not true in the study area.

Times of maximum transgression and regression can also be correlated from one section to another. The greatest extent of the post-Keyser transgression is represented at both sections by the Cherry Run Member of the Licking Creek Formation. The Cherry Run at

Price's Bluff therefore correlates at least in part with the Cherry Run at Strait Creek.

The only faunal change that could be used for correlation takes place in the upper Keyser and New Creek formations. In that part of the section four separate faunal events take place in both sections, in about 25-35 feet at the top of the Keyser at Strait Creek and the top of the Keyser and base of the New Creek at Price's Bluff, in the following order beginning with the lowest: the appearance of Delotaxis excavata cristagalli, the last D. elegans, the appearance of Rotundacodina noguerensis, and the appearance of Icriodus helderbergensis. The appearance of D. e. cristagalli may be delayed, as most of the samples directly below it in both sections are barren, but this is not the case with the other three. The transition from Ozarkodina remscheidensis eosteinhornensis to O. r. remscheidensis also takes place in approximately the same interval. This transition is not precisely located, but takes place in the upper and lower New Creek at both Strait Creek and Price's Bluff. Since the transition is a phyletic event, rather than an appearance or disappearance like the other events, it cannot be environmentally controlled. It therefore lends some confidence that the other events are close approximations to the actual times of origination or extinction of the species rather than being controlled by the local environment.

In summary, the Big Mountain Shale at Strait Creek correlates with the Clifton Forge Sandstone at Price's Bluff, so that the lower limestone member of the Keyser at Strait Creek apparently correlates

with the top part of the Tonolway at Price's Bluff. The top of the Keyser and base of the New Creek are close to the same age at the two sections, according to the conodont ranges. The exact relationship of the New Creek, Corriganville and Healing Springs Formations are not known, but the Cherry Run Member is approximately the same age at both sections.

Zonal Assignment of the Helderberg Group

Correlation with the standard conodont zonation is summarized in Figure 7.

Most of the Keyser Formation, like the upper part of the underlying Tonolway Formation, contains Ozarkodina remscheidensis eosteinhornensis and Delotaxis elegans and therefore belongs to the eosteinhornensis zone.

The nominal species of the overlying woschmidti zone, Icriodus woschmidti, is not present. Near the top of the Keyser, 45 feet below the top at Strait Creek and 15 feet below the top at Price's Bluff, Delotaxis excavata cristagalli first appears. The highest occurrence of D. elegans is in the same sample as the lowest D. e. cristagalli or in the next higher sample. The transition from Ozarkodina remscheidensis eosteinhornensis to C. r. remscheidensis is difficult to define precisely, but takes place in the upper part of the Keyser and the overlying basal New Creek. In Europe D. e. cristagalli appears at the base of the woschmidti zone; D. elegans dies out at the top of the eosteinhornensis zone or in the base of the woschmidti zone; and

the transition from O. r. eosteinhornensis to O. r. remscheidensis, although it is too slowly gradational for precise biostratigraphic use, takes place at the top of the eosteinhornensis zone. Together, these occurrences suggest that the top of the upper limestone member of the Keyser Formation, above the first occurrence of D. e. cristagalli, belongs to the woschmidti zone.

The fauna of the upper part of the Helderberg Group, from a little below or above the top of the New Creek Limestone to the top of the Licking Creek Formation is characterized by Ozarkodina remschiedensis remscheidensis, Icriodus helderbergensis, and Rotundacodina noguerensis. The lowest occurrences of I. helderbergensis and R. noguerensis are near the top of the Keyser Formation at Strait Creek, R. noguerensis appearing slightly lower, and at Price's Bluff in the same sample within the New Creek. Rotundacodina dentata and Delotaxis excavata cristagalli are sporadically present in this fauna, neither species ranging to the top of the Helderberg Group.

This fauna appears above the base of the woschmidti zone. Although R. noguerensis and R. dentata have not been reported below the postwoschmidti or eolatericrescens zone in Spain, conodonts were not collected from lower strata in that study (Carls and Gandl, 1969), so that it is not known whether or not these species occur in the woschmidti zone. The other species in the upper Helderberg fauna either occur in the woschmidti zone or have not been reported outside the Appalachians. The lower age limit is therefore the woschmidti zone.

Both R. noguerensis and D. e. cristagalli range up into the delta zone and possibly into the pesavis zone. O. r. remscheidensis occurs in the lower part of the delta zone in western North America and has not been reported higher. As O. r. remscheidensis ranges up to the top of the Helderberg Group in at least the southern part of the study area, the top of the Helderberg in that area is no younger than the delta zone. The upper part of the Helderberg Group therefore may span some part of the upper woschmidti zone, the eurekaensis zone, and the delta zone.

The Ridgeley Sandstone was not sampled. The base of the overlying Needmore Shale contains Icriodus latericrescens robustus and therefore correlates with the serotinus zone, the patulus zone, or the costatus costatus zone of upper Emsian or lower Eifelian age (Figure 5). Since the top of the Licking Creek is no younger than the delta zone, and the base of the Needmore Shale is no older than the serotinus zone, at least the intervening six conodont zones are represented by the Ridgeley Sandstone and the unconformities which lie above and below it (Figure 7). Head (1969) suggested that the top of the Helderberg becomes younger toward the center of the basin. Since the top of the Licking Creek Formation at Strait Creek was not sampled, it is possible that this is true and that the upper Licking Creek is younger than the delta zone in the northern part of the study area.

Figure 7. Summary of Helderberg conodont biostratigraphy and correlation with uppermost Silurian-lowermost Devonian sections in Nevada and Austria.

WESTERN VIRGINIA			CELLON, AUSTRIA (Walliser, 1964)		NEVADA (Klapper and Murphy, 1975)	
FORMATION	SPECIES RANGES	CONODONT ZONES	ZONES	SPECIES RANGES	ZONES	SPECIES RANGES
NEEDMORE SHALE (lowermost)		serotinus, patulus, or costatus costatus zone				
RIDGELEY SANDSTONE		includes the pesavis, sukka- tus, kindlei, dehiscens, gronbergi, and inversus zones and perhaps some of the underlying and overlying zones				
LICKING CREEK FORMATION	<u>O. r. remscheidensis</u> <u>D. elegans</u> <u>D. e. cristagalli</u> <u>I. helderbergensis</u> <u>R. noguerensis</u>	may include all or part of the eurekaensis and delta zones	<u>woschmidti</u> zone (lower part)	<u>O. r. remscheidensis</u> <u>I. w. woschmidti</u> <u>Monograptus uniformis</u> <u>D. e. cristagalli</u>	hesperius zone (lower part)	<u>O. r. remscheidensis</u> <u>I. w. hesperius</u> <u>M. uniformis</u>
HEALING SPRINGS SANDSTONE/ CORRIGANVILLE LIMESTONE		?				
NEW CREEK LIMESTONE		woschmidti/hesperius zone				
KEYSER FORMATION		eosteinhornensis zone	eosteinhornensis zone		eostein- hornensis zone	ROBERTS MOUNTAINS FM.
TONOLOWAY FORMATION (upper part)						

SYSTEMATIC PALEONTOLOGY

Introduction

Where possible, disjunct conodonts have been assigned to multi-element species. Criteria for such groupings include consistent co-occurrence; similarity of details such as denticulation, shape of the basal cavity, or shape of the cusp; similarity of size or range of sizes within a sample; resemblance of the pattern of an associated group of elements to the patterns of established multi-element species; consistency of ratios between elements in large samples which show no evidence of sorting; and, where the elements have been reported before, co-occurrence elsewhere. Most types of elements were assignable to biological species, either multi-element or single-element; the remainder, for which the evidence was insufficient either to justify assignment to a multi-element species or to demonstrate that no other elements were associated, are listed as form species with the letters s.f. (*sensu formo*) after the name, following the suggestion of Barnes and Poplawski (1973). The letter designations for elements proposed by Sweet and Schonlaub (1975) have been used for the genera Delotaxis and Ozarkodina, which have six or seven-member bar or blade apparatuses, and the letter designations of Klapper and Philip (1971) for the genus Icriodus.

Species are treated as including considerable variation in morphology of elements, particularly in cases where large collections permit the observation of intergradation between similar forms. Because it is difficult to know the range of variation of a species

without large collections, new species were not recognized unless such collections were available.

As suprageneric taxonomy of Silurian and Devonian conodonts is still in a state of flux (Klapper and Philip, 1972; Cooper, 1977), no attempt was made to assign genera to families. Biological genera are here followed by form genera, both in alphabetical order.

Synonymies of multi-element species include separate listings of references to each of the isolated elements, followed by a list of multi-element references. Only references with illustrations of the conodonts are included. If a complete synonymy already exists, this is noted after the reference to the paper which includes it, and only more recent references and the reference to the original description of each element are included here.

Order Conodontophorida Eichenberg, 1930

Genus DELOTAXIS Klapper and Philip, 1971

Type species. Ligonodina elegans Walliser, 1964.

Emended diagnosis. An apparatus with six or seven distinct elements: Pa element slightly twisted, lonchodiniform or ozarkodini-form; Pb element more strongly twisted lonchodiniform (detortiform or oulodiform); M element neoprioniodiform; Sa element trichonodelliform; Sb element ligonodiniform; Sd element (where present) similar to Sa element with processes set at different angles to the cusp. Denticles tend to be peg-like and stand separated.

Remarks. The original diagnosis of Klapper and Philip (1971) included an O_2 (aversiform) element. However, Lonchodina walliseri s.f., listed as the O_2 element of the type species, D. elegans, is not part of that apparatus (Jeppsson, 1974; Sweet and Schonlaub, 1975; and herein). In addition, their B_3 element, "a variation from a detortiform to an asymmetrical trichonodellan element" (Klapper and Philip, 1971, p. 101), includes three or four distinct elements, the Pb, Sa, Sb, and Sd elements of Sweet and Schonlaub (1975) and this report.

Oulodus Branson and Mehl was defined by Sweet and Schonlaub (1975) to have Pa, Pb, Sa, and Sb elements essentially as described above, and M and Sc elements as above or prioniodiniform or cordylodiform, respectively. However, the Ordovician forms generally differ from younger species; the M elements of the Ordovician species are not neoprioniodiform and the Sc elements, with the exception of O. robustus, are cordylodiform. This difference seems sufficient for the separation of Delotaxis from Oulodus; Delotaxis is therefore here retained for species with ligonodiniform Sc elements. Further study will be necessary to resolve the relationship between the two genera.

Jeppsson (1969, 1972, 1974) has used the name Ligonodina for this genus. It has, however, been argued (Klapper and Philip, 1971; Walliser, 1972) that as Ligonodina pectinata Bassler 1925, the type species of Ligonodina, is an Upper Devonian species which has not been described as part of any apparatus, and as there is no reason to believe that it belongs to an apparatus of this type, the name Ligonodina should not be used for apparatuses of this type unless the

apparatus of Ligonodina pectinata proves to be similar. Although Jeppsson (1974) argues that forms contemporary with L. pectinata have been described which might be the associated M and Pb elements, a Delotaxis-type apparatus still has not been established for this species, and Ligonodina is therefore not used here. If, however, Jeppsson is correct, Ligonodina has priority over Delotaxis and, if the separation of Delotaxis from Oulodus is not accepted, over Oulodus as well.

DELOTAXIS ELEGANS (Walliser)

Pl. 3, fig. 9, 10, 12-18

Pa element

Ozarkodina ortuformis Walliser, 1964, p. 59, Pl. 9, fig. 18, Pl. 24, fig. 7, 8, 10-13.

Pb element

Lonchodina detorta Walliser, 1964 (partim), p. 43, Pl. 9, fig. 20, Pl. 30, fig. 34, 35, 37.

Lonchodina detorta Walliser. Helfrich, 1975, p. A15-A16, Pl. 15, fig. 14.

M element

Neoprioniodus bicurvatus (Branson and Mehl). Walliser, 1964 (partim), p. 46, Pl. 29, fig. 31-33.

Neoprioniodus arisaigensis Legault, 1968, p. 14, Pl. 2, fig. 5-7.

Sa element

Trichonodella inconstans Walliser. Legault, 1968, p. 18, Pl. 1, fig. 7-9.

Sb element

Lonchodina sp. indet. Legault, 1968, p. 13, Pl. 1, fig. 13.

Sc element

Ligonodina elegans Walliser, 1964, p. 41, Pl. 9, fig. 19, Pl. 32, fig. 16-21.

Sd element

Lonchodina detorta Walliser, 1964 (partim), p. 43, Pl. 9, fig. 20, Pl. 30, fig. 36.

Multi-element

Ligonodina elegans Walliser, 1964, sensu Jeppsson, 1969. Jeppsson, 1974, p. 19-22, Pl. 3, fig. 1-15, Pl. 8, fig. 4 (includes synonymy through 1973).

? Delotaxis elegans (Walliser)?. Klapper and Murphy, 1975 (partim), p. 45, Pl. 10, fig. 18-20.

? Oulodus elegans (Walliser). Sweet and Schönlaub, 1975, p. 51, Pl. 1, fig. 7-12.

Ozarkodina excavata (Branson and Mehl). Helfrich, 1978 (partim), Pl. 2, fig. 1, 2, 3, 5.

Delotaxis elegans (Walliser). Helfrich, 1978 (partim), Pl. 2, fig. 16-20 (non 14, 15).

non Delotaxis elegans (Walliser). Mehrtens and Barnett, 1976, p. 496, Pl. 1, fig. 23.

non Ozarkodina ortuformis Walliser. Helfrich, 1975, p. A30-A31, Pl. 12, fig. 5, 9, 21, 25, 28.

Description. D. elegans has seven elements, which have in common a strong cusp; narrow basal grooves which run the length of the processes; a basal cavity generally either broadly expanded or with a laterally compressed extension on the posterior side under the cusp; flattened processes; and denticles which are oval in cross section, somewhat flattened in the plane of that process, and except in the case of the M element, separated by U-shaped spaces.

Pa element. The element is twisted, with a laterally compressed anterior and posterior processes. The anterior process is arched and slightly curved inward; the posterior process is twisted, so that the denticles are rotated outward, and is curved inward, except for the tip, which in the single specimen in which this process remains unbroken, curves outward again. The cusp is strong, oval in cross section, and curves back and inward. The basal cavity is expanded beneath the cusp. The anterior process is higher than the posterior process; it bears 5 to 8 closely spaced, slightly reclined denticles.

The posterior process is somewhat longer, the single unbroken example bearing 8 denticles.

Pb element. The element is sufficiently twisted that determining orientation is difficult; the cusp, however, is more consistently inclined away from the process which Walliser (1964) calls posterior but which will therefore here be called anterior. The anterior process is almost identical to that of the Pa element, but is less arched; the posterior process is bent, just beyond the cusp, more or less sharply outward and down, so that it may be almost perpendicular to the cusp, and is twisted to rotate the denticles inward. The anterior process curves inward, the posterior process outward. The cusp, while larger than the other denticles, is not as strong as that of the Pa element; it curves back and inward over an expanded basal cavity. The anterior process is higher and shorter than the posterior process; the former has 5 to 7 denticles, the latter 8 or 9 denticles.

M element. The element is pick-shaped, with a short anterior process, a strong cusp at an angle of about 150° with the process, and an unusually undenticulated anticusp. The strongly laterally compressed cusp is about four times as wide as the denticles on the process and is 3 to $3\frac{1}{2}$ times as long as it is wide. The basal cavity is expanded under the cusp. The process is narrow, less than half the width of the cusp, and bears denticles which are flattened and fused at the base near the cusp and usually stand separate farther along the process. No specimens found had an unbroken process; the longest remnant had

7 denticles. The short anticusp is usually undenticulated, but bears one or two very weak denticles in a few specimens.

Sa element. This is a symmetrical element with two lateral processes which join initially at an angle of slightly less than 90° and curve down and back. The cusp is long and tapering, and its greatest basal diameter is about three times that of the largest other denticles. It is laterally compressed and oval in cross section. It curves back, most strongly near the base. The basal cavity has a high, laterally compressed extension on the posterior side, its lips projecting back. The denticles are largest and the processes are highest away from the cusp. Each process bears 6 to 8 denticles, inclined slightly toward the cusp.

Sb element. The element is asymmetrical with two unequal lateral processes, with the longer and lower process at a greater angle to the cusp in posterior view than the shorter and higher process. The two are at an angle of slightly more than 90° to each other. The cusp and basal cavity are like those of the Sa element. The longer process bears 8 to 10 denticles, slightly inclined back and toward the cusp; the shorter curves down, becoming higher away from the cusp, and bears 3 to 5 closely spaced denticles which increase in size away from the cusp.

Sc element. This element consists of a long, straight posterior process, a strong cusp, and a short, high inner lateral process. The cusp is two or three times as broad at the base as the other denticles and is much longer, curving back and tapering. It is over a small oval

basal cavity which, as in the other elements, extends as grooves running the length of the aboral sides of the processes. The posterior process is straight; in all specimens it is broken, the longest fragments bearing 8 denticles. The denticles are reclined and increase in size away from the cusp; the spaces between them are at least as wide as the denticles. The lateral process bends inward just anterior to the cusp, initially almost perpendicular to the posterior process and curving back, with the short aboral edge projecting down and slightly back, and the denticles on the longer oral edge tending to fan out. It bears 3 to 5 denticles which are smallest near the cusp and which curve back.

Sd element. The element consists of a strong, posteriorly inclined cusp, an anterior process, and a lateral process which branches off perpendicular to the anterior process just in front of the cusp. The anterior process curves down and slightly toward the lateral process; the lateral process curves down and back. The cusp and basal cavity are as in the Sa element, so that the element resembles an Sa element in which one of the lateral processes has been bent straight back. On the few specimens with unbroken processes, the anterior bears 8 or 9 denticles and the lateral bears 5 to 7 denticles.

Remarks. This reconstruction of the Delotaxis elegans apparatus differs from previous reconstructions in including seven elements. Some earlier reconstructions have omitted either the Sa (Klapper and Philip, 1971) or the Sb element (Jeppsson, 1969, 1974), and both these reconstructions and that of Sweet and Schonlaub (1975) did not describe

the Sd element as a separate form; while the Sd element has been illustrated from collections with the other D. elegans elements, it has been given the same name, Lonchodina detorta s.f., as the Pb element (Walliser, 1964; Jeppsson, 1974, Pl. 3, fig. 12). In addition, the percentage of detortiform elements in a large sample reported by Sweet and Schonlaub (1975) agrees well with the combined percentages of Pb and Sd elements observed here. As has been observed before (Jeppsson, 1974; Sweet and Schonlaub, 1975), the O₂ element of Klapper and Philip (1971), Lonchodina walliseri s.f., does not occur consistently with the elements of Delotaxis elegans; it is instead the Pa element of various subspecies of Delotaxis excavata (Branson and Mehl) (Jeppsson, 1972).

Regularly alternating denticulation as described by Jeppsson (1972, 1974) was observed in one Pb element in sample SC6, and a few other specimens had one or two small denticles inserted between large ones, but the characteristic is not common.

DELOTAXIS EXCAVATA CRISTAGALLI (Ziegler)

Pl. 2, fig. 1-7

Pa element

Lonchodina walliseri Ziegler, 1960, p. 188-189, Pl. 14, fig. 2, 6, 7.

Lochodina walliseri Ziegler. Epstein, 1970 (partim), p. 179-181, Pl. 4, fig. 16, Pl. 5, fig. 3, 4.

Lonchodina walliseri Ziegler. Barnett, 1971, pl. 37, fig. 16.

Delotaxis elegans (Walliser). Helfrich, 1978 (partim), Pl. 2, fig. 14, 15.

Pb element

Lonchodina cristagalli Ziegler, 1960, p. 189-190, Pl. 14, fig. 1, 3, 5.

Lonchodina cristagalli Ziegler. Walliser, 1964, p. 43, Pl. 9, fig. 23.

Lonchodina cristagalli Ziegler. Schulze, 1968, p. 196, Pl. 17, fig. 23.

Lonchodina cristagalli Ziegler. Epstein, 1970, p. 174-176, Pl. 5, fig. 1, 2.

M element

Prioniodina excavata (Branson and Mehl). Ziegler, 1960, p. 192, Pl. 15, fig. 5.

Neoprioniodus multiformis Walliser. Schulze, 1968 (partim), p. 201, Pl. 18, fig. 4.

Lonchodina walliseri Ziegler. Epstein, 1970 (partim), p. 179, Pl. 4, fig. 15.

Lonchodina greilingi Walliser. Barnett, 1971, Pl. 37, fig. 5.

Sa element

Trichonodella inconstans Walliser. Ziegler, 1960, p. 197, Pl. 14, fig. 14, 17.

Trichonodella inconstans Walliser. Epstein, 1970, p. 232-235, Pl. 6, fig. 7-10.

Trichonodella inconstans Walliser. Barnett, 1971, Pl. 37, fig. 18.

Sb element

Lonchodina greilingi Walliser. Ziegler, 1960, p. 188, Pl. 14, fig. 15, 16, 18, 20.

Lonchodina greilingi Walliser. Epstein, 1970, p. 176-179, Pl. 5, fig. 5-12.

Sc element

Ligonodina diversa Walliser. Ziegler, 1960, p. 186-187, Pl. 14, fig. 8, 12.

Ligonodina n. sp. Walliser. Ziegler, 1960, p. 187, Pl. 14, fig. 9, 10.

Ligonodina n. sp. a Ziegler, 1960, p. 187, Pl. 14, fig. 13.

Ligonodina salopia Rhodes. Epstein, 1970 (partim), p. 170-174, Pl. 7, fig. 1, 2, 6, 7.

Multi-element

Ozarkodina excavata (Branson and Mehl). Helfrich, 1978 (partim), Pl. 2, fig. 4 (sb), 6 (M), 7 (Sc).

Description. D. e. cristagalli has six elements. All elements have denticles separated by U-shaped to V-shaped spaces. Denticles are round to oval in cross section, with both denticles and processes becoming more flattened toward the end of a process. The basal cavity is inverted away from the cusp, so that the outer edges of the cavity become ridges on the sides of the processes along all or most

of their lengths, particularly in older individuals; in some elements this produces a flattened underside on a process. With the exception of the Pb element, the cusp is long and tapering.

Pa element. The element is strongly arched, with the processes joining at an angle of about 110° and curving down slightly. It is also somewhat twisted, so that the anterior process curves inward and is slightly twisted to rotate the denticles outward, and the posterior process curves slightly outward. The cusp is strong and leans inward and back; it is oval in cross section, with its longest diameter in the direction in which it leans. The basal cavity is expanded toward the inner side under the cusp and extends to each side as narrow grooves running partway along both processes. It is inverted, which produces ridges along the sides of the processes, particularly in large elements. The posterior ridge is stronger and in large elements the aboral surface of the posterior process may become a flattened surface slanting up toward the inner side. The anterior process bears 3 to 5 laterally compressed denticles, the posterior process 5 to 7 somewhat less strongly compressed denticles; denticles on both processes are largest in the middle of the process.

Pb element. The element is here considered to be oriented so that the straighter of the two processes is anterior, and is slightly concave inward. The element consists of a nearly straight anterior process which is gently curved inward and a posterior process which, two or three denticles away from the cusp, bends outward and to some extent down through 90° or more, and is twisted so that the denticles are

rotated inward. The cusp is only slightly posteriorly inclined. Although larger than the adjacent denticles, it is in mature specimens smaller than the denticles on the posterior process at its greatest curvature. The basal cavity is largest under the cusp, extending as a narrow groove along both processes; this ends before the curve of the posterior process and about halfway down the anterior process. The basal cavity is inverted away from the cusp, which produces a weak ridge on the side of the anterior process near the base and turns the aboral side of the posterior process into a broad, flattened surface slanting up inwards. The anterior process bears 5 to 7 laterally compressed denticles which are largest in the center of the process, and the posterior process bears 7 to 10 denticles which are largest and roundest at the curve.

Juvenile elements have relatively larger cusps, a less inverted basal cavity, and a less strongly curved posterior process.

M element. This resembles closely a Pa element with a very short anterior process, a somewhat twisted posterior process, and a cusp more inclined inwards. The posterior process is curved inward and down and twisted so that the denticles are rotated outward. The cusp is strong, curved inward and slightly back, almost round in section near the base and flattened farther up, with its longest diameter pointing in and slightly forward. The basal cavity is expanded to the inside under the cusp, and its inner lip is raised on the posterior side of the cusp. It extends as a groove along the posterior process, as far as any of the specimens, which are all broken, extend. The

longest remnants have four denticles. The posterior process is not flattened and bears denticles nearly round to oval in cross section, which are usually separated by U-shaped spaces, particularly in smaller elements. The shorter anterior process bears one or two strongly flattened denticles, which may be as large as those of the posterior process.

Sa element. This is an arched symmetrical or almost symmetrical element, with two flattened lateral processes which join at an angle of slightly over 90° and curve down and gently back. The cusp curves strongly back and is generally oval in section, flattened laterally near the base but anteroposteriorly near the tip. The basal cavity has an extension on the posterior side under the cusp shaped like an inverted U; the basal grooves die out close to the cusp, but ridges on both sides of the processes, extending from the edges of the basal cavity to the ends of the processes, are present on large specimens. Each process bears six or seven denticles, smallest near the cusp and largest just past the middle of the process.

Sb element. This element is very similar to the Sa element, except that one process is shorter and higher than the other and forms a slightly smaller angle with the cusp, and the cusp and the extension of the basal cavity under it are slightly twisted toward the longer process. The longer process, cusp, and basal cavity are otherwise like those of the Sa element. The shorter process bears three or four denticles, which away from the cusp are larger than the denticles of the longer process.

Sc element. The element consists of a long, straight posterior process, a strong, reclined cusp, and a shorter down-curved anterolateral process. The cusp is long and several times the basal diameter of the other denticles. It is posteriorly inclined and flattened in the plane of the posterior process at base but is closer to round in section farther up. Under it is an oval basal cavity which may continue as a narrow groove along the aboral side of part of the posterior process. The outer edge of the basal cavity becomes a ridge on the sides of the posterior process and on larger specimens on the sides of the anterolateral process, dying out toward the ends of the processes. The posterior process becomes higher and thinner away from the cusp. It bears about ten reclined denticles which increase in size and become more strongly reclined away from the cusp. The anterolateral process is at an angle greater than 90° to the posterior process and curves downward, often slightly twisted so that the denticles are rotated forward. It bears 5 to 7 denticles.

Comparison. D. e. cristagalli is distinguished from the other subspecies of D. excavata most clearly by its Pb element, which is more strongly twisted than the Pb elements of any of the other subspecies. In addition, M elements of older subspecies lack the large anterior denticles of the M elements described here, the Pa element of D. e. cristagalli is more strongly arched than in the older subspecies, and the basal cavity is more inverted in all elements of D. e. cristagalli.

The Pa, Pb, and M elements of D. e. cristagalli are quite different from the equivalent elements of D. elegans, but the Sa, Sb, and Sc elements of the two taxa resemble each other. However, these elements are consistently more robust and have inverted basal cavities in D. e. cristagalli. The denticles of the Sa and Sb elements are more widely spaced in D. elegans, and the posterior extension of the basal cavity under the cusp in these elements is more compressed laterally in D. elegans. The Sc elements are distinguished by the shape of the anterolateral process. In D. elegans this process is almost fanshaped with 3 to 5 denticles and bends back to form an angle of less than 90° with the posterior process, but in D. e. cristagalli it is longer, bearing 5 to 7 denticles, and forms an angle of more than 90° with the posterior process.

Remarks. Delotaxis excavata cristagalli is part of a lineage extending at least from the Silurian (Wenlockian) sagitta zone to the Lower Devonian delta or pesavis zone. Jeppsson (1972) described multi-element "Ligonodina" excavata, with two Silurian subspecies, the type from the siluricus zone and the other from the eosteinhornensis zone. Helfrich (1975) described in form taxonomy the elements of three more Silurian subspecies under the names Lonchodina walliseri (Pa element); Ozarkodina aequalis, O. tenuiramaea, and O. sinuosa (Pb elements of the three subspecies); Neoprioniodus excavatus (M element); Trichonodella excavata (Sa element); Plectospathodus extensus (Sb element); and Ligonodina silurica or Hindeodella equidentata (Sc element). Another Lower Devonian (delta or pesavis zone) subspecies

is represented in the material of Bischoff and Sannemann (1958), described by them as Lonchodina n. sp. a Walliser 1957 (Pa element), Lonchodina cf. n. sp. b Walliser 1957 (Pb element), Prioniodina excavata (M element), Trichonodella inconstans (Sa and probably Sb elements), and Ligonodina diversa (Sc element).

D. e. cristagalli has not been previously described in multi-element taxonomy; however, Jeppsson (1972) remarked that a Lower Devonian subspecies of Delotaxis excavata was represented in the material of Ziegler (1960), and Ziegler (1972) suggested that some of the elements here included should be considered an apparatus, although he proposed a different M element. Of the elements in this apparatus, only two are assignable to form species whose types belong to this subspecies. These are Lonchodina walliseri and L. cristagalli, both published in the same paper (Ziegler, 1960). As the name L. cristagalli has been used only for the distinctive Pb element of this subspecies, while L. walliseri has been more generally used for Pa and, probably, Pb elements of various D. excavata subspecies, the former is hereby selected.

DELOTAXIS n. sp.

Pl. 2, fig. 8-15

Pb element

Lonchodina n. sp. Epstein, 1970 (partim), p. 182-183, Pl. 6, fig. 20-22.

Sb element

Plectospathodus sp. Walliser, 1964, Pl. 30, fig. 20.

Plectospathodus extensus Rhodes. Epstein, 1970 (partim), p. 200-202, Pl. 4, fig. 9, 10.

Plectospathodus flexuosus Branson and Mehl. Epstein, 1970, p. 203-205, Pl. 4, fig. 5-7.

Multi-element

Ozarkodina steinhornensis scanica Jeppsson, 1974. Helfrich, 1978 (partim), Pl. 2, fig. 23 (Sa), 24 (sb), 31 (Sc).

Description. This species is characterized by a relatively short, thick, straight cusp and peglike denticles separated by V-shaped to U-shaped spaces, some or all of which may be occupied by a small denticle set between two large ones, particularly in the Sa element. Large elements often have ridges on the sides of the processes resulting from the inversion of the basal cavity; the lip of the basal cavity projects out strongly under the cusp in all elements except for the Sc element and sometimes the Sb element.

Pa element. Only a few broken specimens of this element were found. It is a twisted element with two flattened processes; the anterior process is twisted to rotate the denticles slightly inward, and the posterior is twisted slightly in the opposite direction. Both processes are somewhat curved inward. The initial angle between them in lateral view is about 120° . The cusp leans in and slightly back; the basal cavity is broadly expanded under it. The denticles are round to oval in cross section.

Pb element. The element is twisted, consisting of a short, somewhat flattened anterior process and a longer posterior process which is round in cross section; the initial angle between the processes in lateral view is slightly less than 90° . The anterior process forms an angle of 120° or more with the cusp, and its end may curve slightly inward. The posterior process is twisted so that the denticles are rotated slightly outward, and it curves down and inward. The anterior

process bears about four flattened denticles. The posterior process bears denticles round to oval in section. It is broken in all specimens, and the longest remaining piece bears seven denticles. The basal width of the cusp is about half its height. It leans in and alightly back. In cross section is is round to oval, one specimen having sharp anterior and posterior edges.

M element. Only two broken specimens were found. These have the thick cusp that characterizes the species; an anticusp, undenticulated or with one denticle; and an anterior process which is nearly round in section. The denticles are closely spaced and round to oval in cross section, in both specimens broken off short.

Sa element. The two lateral processes of the symmetrical element are nearly straight, in some specimens curved slightly down and back; the angle between them in posterior view is about 90° . The cusp curves back over a slightly expanded basal cavity. The basal cavity has a lip extended straight back, in some cases to a point, and has in lower posterior view an opening shaped like an inverted U about twice as high as wide. Near the cusp the processes are oval in section and the denticles on them are nearly round. Both processes and denticles become more flattened near the tip of the processes. There are generally some small denticles present between large ones, and some specimens have regularly alternating denticulation.

Sb element. The element is arched, so that the processes meet in lateral view at an angle of about 140° , and is usually slightly bowed inward. Both processes are oval in cross section, becoming more

flattened toward the end. The anterior process is lower and longer than the posterior and nearly straight in lateral view; in most specimens it is broken. The last third of the posterior process is hooked down and in some specimens back. The cusp is reclined, at an angle of about 75° to the posterior process, and is nearly round at the base. The denticles are fairly regular in size on the anterior process, but the denticles of the posterior process are largest at the greatest curvature of the process. These denticles may be nearly as large in lateral view as the cusp, although they are laterally compressed and are therefore much thinner.

Sc element. The element consists of a straight posterior process, a strong cusp, and a downward-angled anterolateral process which curves inward to form an angle of slightly over 90° with the posterior process. The cusp is short, straight, thick, and slightly reclined. The posterior process is in all specimens broken after up to 4 denticles; these are round in section, more or less reclined, and separated by V-shaped spaces, and they increase rapidly in size away from the cusp. The anterolateral process bears 4 to 6 denticles which may curve back slightly. Small denticles between large ones are occasionally present. Ridges on the sides of both processes are well developed on most specimens.

Comparison. The Sa-Sc transition series and the M element are easily homologized with the other species of Delotaxis in the Helderberg Group. The Sb element differs from the homologous elements of D. elegans and D. e. cristagalli in that it is plectospathodan instead

of almost trichonodellan. The Sa and Sc elements resemble closely the corresponding elements of Delotaxis excavata cristagalli, but the Sa element of D. e. cristagalli has a higher posterior extension of the basal cavity, its cusp and denticles tend to be longer, and alternating denticulation is not developed; and the Sc element has a longer, more curved cusp. The homologous elements of D. elegans are less robust, have longer, curving denticles spaced more widely, and differ in the shape of the basal cavity. The M element is quite different from the M element of D. e. cristagalli; the M element of Delotaxis n. sp. has an anticusp rather than a short denticulated process and its cusp leans away from rather than toward the long process. It differs from the M element of D. elegans in that its cusp is round in cross section and is smaller relative to the size of the process than in D. elegans. The Pa element is less arched than in D. e. cristagalli. It is similar in shape to the Pa element of D. elegans: in both cases, the cusp is inclined backward and inward and the posterior process is twisted so that the denticles are rotated outward. The twisted element here considered to be the Pb element is quite distinctive, not closely resembling the homologous elements of either of the other two Delotaxis species from the Helderberg Group.

Remarks. The elements described above occur together in two samples from the Keyser and New Creek Formations at Price's Bluff and show considerable similarity in size, denticulation, and shape of the cusp and the processes; they are therefore considered to belong to

one biological species. This species is not named, since two of the elements included, the Pa and M elements, were found only in poor condition and in small numbers, and therefore cannot be adequately described.

Genus ICRIODUS Branson and Mehl, 1938

Type species. Icriodus expansus Branson and Mehl, 1938

Remarks. Members of the form genus Icriodus often occur in association with simple cones assigned to Acodina or sometimes to Acodus (Barnett, 1971; Ziegler, 1972), and Lange (1968) described an Upper Devonian coprolitic cluster containing the two in a ratio of about one pair of Icriodus to about 30 Acodina. Klapper and Philip (1971, 1972) proposed that the apparatus of Icriodus contains an acodiniform element as well as an icriodiform element, probably with larger numbers of the latter; and various authors (Klapper and Murphy, 1975; Savage, 1976; Mehrtens and Barnett, 1976; and Chatterton and Perry, 1977) dealing with Lower Devonian species of Icriodus have followed this. However, Bultynck (1972) has argued that in Middle Devonian faunas, species of Acodina do not occur consistently with Icriodus, and the numbers of the two do not form small, consistent ratios; as Panderodus spp. may be present where Acodina is lacking, loss of simple cones by sorting or laboratory sieving is unlikely. Carls (1975) has reported similar results in connection with Lower Devonian icriodids. Both Carls and Bultynck dealt with members of the Icriodus latericrescens group, among others.

Both species of Icriodus considered here belong to the Icriodus latericrescens group (Klapper and Ziegler, 1967). The icriodiform element of I. helderbergensis is associated with a large group of simple cones (Table 2) including forms assignable to Acodina s.f. as well as other genera, which consistently occur in the same samples at both sections, but which, with one exception, do not occur in constant proportions with the icriodiform element. An element similar to Acodina plicata, here considered to be the acodiniform element of I. helderbergensis, is usually present in a 2:5 ratio with the icriodiform element; of the three samples where the proportion of the latter was much higher, two are from high-energy sandy grainstones where selective removal of the smaller elements might well have taken place, although the third is from a cherty lime mudstone where such sorting is less likely. In addition, Klapper and Philip (1971, fig. 8) illustrated an apparatus from Nevada containing icriodiform and acodiniform elements both of which are very similar to the Helderberg forms, which is evidence that the same two types of elements occur together in a closely related species of Icriodus.

Icriodus latericrescens robustus was recovered from a bed near the base of the Needmore Shale. In this sample and another collected by Dr. C. G. Tillman from the same bed, a total of 71 icriodiform elements and no acodiniform elements were found. The presence of abundant Belodella spp. suggests that the lack of Acodina s.f. is not due to laboratory techniques or to depositional sorting that would selectively remove simple cones. In Lower and Middle Devonian rocks

from Ontario, Acodina s.f. does not occur consistently with Icriodus latericrescens robustus and is usually strongly outnumbered when it is present; again, in some samples lacking Acodina, Belodella and/or Panderodus may be present in abundance (Telford, von Bitter, and Tarrant, 1977).

Thus, the older I. helderbergensis has both icriodiform and acodiniform elements, while the younger I. latericrescens robustus has only icriodiform elements, although both species are considered members of the latericrescens group within the genus Icriodus (Klapper and Philip, 1971; Klapper and Ziegler, 1967). While this may indicate a change over time of the Icriodus apparatus, apparatuses of more species of Icriodus will have to be documented before generalizations can be made.

ICRIODUS HELDERBERGENSIS n. sp.

Pl. 1, fig. 1-9

I element

Icriodus woschmidti woschmidti Ziegler. Epstein, 1970, p. 165-169, Pl. 2, fig. 1-4.

Icriodus woschmidti ssp. cf. I. w. postwoschmidti Mashkova. Epstein, 1970, p. 169-170, Pl. 2, fig. 5.

Icriodus woschmidti Ziegler. Barnett, 1971, Pl. 37, fig. 14, 17.

Icriodus woschmidti Ziegler. Helfrich, 1978, Pl. 2, fig. 10, 11.

S₂ element

Acodina plicata Carls and Gandl. Epstein, 1970, p. 154-155, Pl. 8, fig. 8, 9.

Acodus sp. transitional to Acodina plicata Carls and Gandl. Epstein, 1970 (partim), p. 155-156, Pl. 9, fig. 6.

Acodus sp. Barnett, 1971 (partim), Pl. 37, fig. 4.

Holotype. The holotype is an I element (Pl. 1, figure 5) from the Licking Creek Formation 69 feet above its base in the section at Price's Bluff 1 mile north of Gala, Virginia.

Paratypes. The paratypes are: two S_2 elements (Pl. 1, figures 3, 4) from the same locality as the holotype; and an I element (Pl. 1, figure 9) from the Coeymans Formation 8 feet above its base at the Strait Creek section on Virginia Route 629 3 miles north of Monterey, Virginia.

Description. The apparatus includes I (icriodiform) and S_2 (acodiniform) elements, both of which occur as right- and left-handed forms.

I element. The spindle is gently curved in to almost straight; it is four to five times as long as its greatest width, which is located a third to almost half the length of the spindle from the posterior end. A posteriorly directed outer lateral process branches off from the spindle at the last denticle at an angle of $105-135^\circ$, bearing a ridge which is undenticulated or has up to four small, laterally compressed denticles. A lobe on the inner side extending forward from the denticle behind the last transverse row is angled slightly forward of the continuation of the line of the lateral process; this lobe rarely bears a faint ridge. There may also be an anteriorly directed outer lobe and a very small posterior inner lateral lobe.

The spindle bears up to 10 transverse rows of three rounded denticles. The lateral denticles are distinct and circular in cross section. The median denticles are smaller and less distinct near the

anterior end, and may be either circular in cross section or laterally compressed. The denticles are linked by transverse ridges which stand a little lower than the denticles; at the anterior end, the first row of denticles and their connecting ridge may be nearly fused into a transverse bar. The rows are separated by transverse troughs, anteriorly deep and wider than the rows, and posteriorly shallow and narrower. A thin median longitudinal ridge running through the troughs connects the median denticles, strongest at the posterior end, and usually dying out by the anterior-most trough. There is usually a single node, which is the first stage of a developing transverse row, at the anterior end, and two or rarely three single denticles along the longitudinal ridge at the posterior end, equal in size or with the last largest, with the lateral denticles missing.

In small growth stages (Pl. 1, figure 1, 2), there are fewer transverse rows of denticles, the smallest individuals having only two. The lateral process is shorter and undenticulated and, as the lower platform is much thinner, is usually broken off. The posterior-most denticle stands distinctly higher than the rest, and all denticles are pointed and stand somewhat more separate.

In some specimens in the lowest Icriodus-containing samples at the Strait Creek section (up to samples SC18 and SC36) the denticles are fused into transverse bars instead of rows of linked denticles (Pl. 1, figure 8); the longitudinal ridge is weaker and does not reach as far forward. In other respects these are identical to the more

common type, which occurs in the same samples; intermediates between the two types exist.

S₂ element. In lateral view, the conodont is a long, curved simple cone, slightly expanded at the base. The basal width is about half the height. The cusp is thick and blunt, curved back and slightly inward, and is unequally biconvex in section, the inner side being flatter. Anterior and posterior edges are sharp and may be keeled at the base, the anterior edge more so. The basal cavity is about half the height of the conodont, extending up just past the expanded base. The inner side of the base is convex, sometimes with a distinct break between the cusp and the base, and the outer side has a fold, approximately in the middle, which dies out above the base.

Comparison. Of the previously described latericrescid Icriodus species, I. steinachensis Al-Rawi eta morphotype of Klapper and Johnson (1980), I. postwoschmidti Mashkova, and I. beckmanni Ziegler are most similar to I. helderbergensis. I. steinachensis eta morphotype differs from I. helderbergensis in that the angle between the spindle and the lateral process is smaller (about 95°); the lateral process is usually longer and has better developed denticulation, often with short transverse bars across the process; and the S₂ element (Klapper and Philip, 1971) is more expanded laterally. The S₂ element of neither of the other two species mentioned above has been described. I. postwoschmidti has been described both from the type area in Podolia and, as "I. woschmidti transiens", from Spain (Carls and Gandl, 1969). Based on descriptions and illustrations of both these populations, I.

postwoschmidti differs from I. helderbergensis in that the transverse rows of denticles of I. postwoschmidti are more fused into bars and there are fewer of them than in I. helderbergensis, these bars in mature specimens are broader than the intervening troughs, and the base is strongly expanded with, usually, a ridge which may be weakly denticulated on the inner-anterior lobe. In I. beckmanni, the inner lobe is developed into a ridged process which may be denticulated, and the denticulation of the outer lateral process is better developed than in I. helderbergensis.

I. helderbergensis has been reported as the zonal form I. woschmidti, but may be distinguished by the development of linked transverse rows of denticles instead of transverse bars, and by the larger number of rows; I. woschmidti has no more than 5 transverse rows and I. helderbergensis has up to 10 rows.

Remarks. The tendency of some of the earliest specimens toward fused bars instead of rows of denticles may be evidence of descent from I. woschmidti. Typical I. woschmidti, of either subspecies, has not yet been illustrated from the Appalachians, as all illustrated specimens of "I. woschmidti" appear to be I. helderbergensis.

ICRIODUS LATERICRESCENS ROBUSTUS Orr

Pl. 1, fig. 10, 11

- Icriodus latericrescens n. subsp. A. Klapper and Ziegler, 1967, p. 75, Pl. 8, fig. 7, 9, Pl. 9, fig. 1-7.
Icriodus latericrescens robustus Orr, 1971, p. 37-38, Pl. 2, fig. 14-17.
Icriodus latericrescens robustus Orr. Klapper and Johnson, 1980, p. 448 p. 448, Pl. 3, fig. 16 (includes synonymy through 1978).

Remarks. The specimens from the Needmore Shale at Price's Bluff are very similar to the original material described by Orr from the Dundee Limestone of Ontario but differ in several respects from the forms described by Klapper and Ziegler from the Schoharie Formation and the Onondaga Limestone of New York. The major difference is that the process of the New York specimens consistently bears three or four transverse bars, often connected by a thin longitudinal ridge, while the forms described here and those illustrated by Orr have a simply denticulated process. In addition, the process of the New York specimens is often more strongly curved back, and denticles in the posterior part of the spindle in larger New York specimens tend to be elongated perpendicular to the length of the spindle. Part of the difference might be due to difference in maturity; all New York specimens illustrated are at least as long as the largest specimens collected from the Needmore Shale, and larger than Orr's illustrated specimens. However, although there is some overlap in size between the New York and the Virginia specimens, there is no overlap in type of denticulation of the process.

Genus OZARKODINA Branson and Nehl, 1933

Type species. Ozarkodina confluens (Branson and Mehl, 1933)

OZARKODINA EXCAVATA EXCAVATA (Branson and Mehl)

Pl. 3, fig. 1-8, 11

Pa element

Prioniodella inclinata Rhodes, 1953, p. 324, Pl. 23, fig. 233-235.

Spathognathodus cf. S. inclinatus (Rhodes). Telford, 1975, p. 68, Pl. 11, fig. 2, 3.

Spathognathodus inclinatus (Rhodes). Miller, 1978, Pl. 2, fig. 22.

Pb element

Ozarkodina media Walliser, 1957, p. 40, Pl. 1, fig. 21-25.

Ozarkodina c.f. O. media Walliser. Telford, 1975, p. 35, Pl. 11, fig. 10-11.

Ozarkodina media Walliser. Miller, 1978, Pl. 3, fig. 20.

M element

Prioniodus excavatus Branson and Mehl, 1933, p. 45, Pl. 3, fig. 7, 8.

Neoprioniodus excavatus (Branson and Mehl). Miller, 1978, Pl. 2, fig. 16.

Sa element

Trichonodella aboroflexa Rhodes, 1953, p. 312, Pl. 23, fig. 231, 241, 242.

Trichonodella excavata (Branson and Mehl). Walliser, 1957, p. 48-49, Pl. 3, fig. 3, 4, 6-8.

Sb element

Plectospathodus extensus Rhodes, 1953, p. 323, Pl. 23, fig. 236-240.

Plectospathodus extensus Rhodes. Miller, 1978, Pl. 3, fig. 24.

Sc element

Hindeodella equidentata Rhodes, 1953, o. 303, Pl. 23, fig. 248, 252-254.

Multi-element

Hindeodella excavata excavata (Branson and Mehl) sensu Jeppsson, 1969. Jeppsson, 1974, p. 25-31, Pl. 4, fig. 1-17 (includes synonymy through 1973).

Ozarkodina excavata excavata (Branson and Mehl). Klapper and Murphy, 1975, p. 34-37, Pl. 6, fig. 1-20.

Ozarkodina excavata (Branson and Mehl). Aldridge, 1975, Pl. 2, fig. 9-14.

Ozarkodina excavata excavata (Branson and Mehl). Barrick and Klapper, 1976, p. 78-79, Pl. 4, fig. 13-23, 26.

Ozarkodina excavata wurmi (Bischoff and Sannemann). Savage, 1976, p. 1182, Pl. 1, fig. 16-31.

Ozarkodina excavata Fähræus. Mehrtens and Barnett, 1976, p. 497, Pl. 1, fig. 11, 12, 14, 18, 21.

Ozarkodina excavata (Branson and Mehl). Cooper, 1977, p. 188, Pl. 16, fig. 8-15.

Ozarkodina excavata excavata (Branson and Mehl). Rexroad et al., 1978, p. 9-10, Pl. 1, fig. 17-22.

Ozarkodina excavata excavata (Branson and Mehl). Lane and Ormiston, 1979, Pl. 2, fig. 30, 31, Pl. 9, fig. 18-23.

Description. All elements have been fully described elsewhere (Walliser, 1964; Jeppsson, 1974); only additional information is

included here. Both the Pa and Pb elements lack the ledge at the top of the processes produced by the abrupt narrowing of the process just below where the denticles begin, which has often been described from collections elsewhere. The basal cavity of the Pa element is small, with the lips very little flared, and the element is narrow. The denticle over the basal cavity may or may not be larger than the others. Denticulation on all elements varies from quite even to slightly irregular, and denticles tend to be closely spaced. The Pa element bears about 20 denticles, the Pb element 4 to 8 on the anterior process and up to 12 on the posterior process; this is many fewer than on the corresponding elements in the type material of O. excavata wurmi (Bischoff and Sannemann, 1958). The M, Sa, Sb, and Sc elements all have ridges on the sides of the processes from the inversion of the basal cavity. The processes of the Sa element are at a high angle, about 130° to 150° .

Comparison. Some of the elements resemble the corresponding elements of Delotaxis excavata cristagalli. In general, the elements of O. excavata have more even denticulation. In addition, the M element of D. e. cristagalli is distinguished by its better developed anterior process and, usually, by U-shaped spaces between the denticles. The Sa element of D. e. cristagalli has more arched processes. The Sc element of O. excavata is distinguished from the Sc element of D. e. cristagalli by the fact that the anterior process of the latter is strongly bent down and the denticles on the posterior process increase in size away from the cusp. The Sb element resembles

that of Delotaxis n. sp., but has more even denticulation and lacks the sharp hook in the posterior process which characterizes the Sb element of Delotaxis n. sp.

OZARKODINA REMSCHEIDENSIS (Ziegler)

Pl. 4, fig. 1-16

Pa element

Spathognathodus remscheidensis Ziegler, 1960, p. 194-196, Pl. 13, fig. 1, 2, 4, 5, 7, 8, 10, 14.

Spathognathodus steinhornensis eosteinhornensis Walliser, 1964, p. 85-86, Pl. 9, fig. 15, Pl. 20, fig. 7-16, 19-25.

Spathognathodus remscheidensis Ziegler. Savage, 1973, p. 329, Pl. 34, fig. 19-29, 33-42, text-fig. 28.

Spathognathodus steinhornensis remscheidensis Walliser. Feist and Schonlaub, 1974, Pl. 8, fig. 1-6, 8, 10, 12-14.

Spathognathodus steinhornensis eosteinhornensis Walliser. Feist and Schonlaub, 1974, Pl. 7, fig. 5, Pl. 8, fig. 9.

Spathognathodus eosteinhornensis Walliser. Telford, 1975, p. 56, Pl. 12, fig. 9-11.

Pb element

Ozarkodina denckmanni Ziegler. Ziegler, 1960, p. 190, Pl. 15, fig. 13-15.

Ozarkodina typica denckmanni Ziegler. Savage, 1973, p. 322, Pl. 33, fig. 1, 7-10, text-fig. 17.

M element

Prioniodina bicurvata pronoides Walliser. Ziegler, 1960, p. 193, Pl. 15, fig. 8, 9.

Sa element

Trichonodella n. sp. aff. T. symmetrica (Branson and Mehl). Ziegler, 1960, p. 197-198, Pl. 15, fig. 1, 2.

Sb element

Plectospathodus cf. P. extensus Rhodes. Ziegler, 1960, p. 191-192, Pl. 51, fig. 6, 7.

Plectospathodus alternatus Walliser, 1964, p. 64, Pl. 9, fig. 17, Pl. 30, fig. 23-25.

Plectospathodus aff. P. alternatus Walliser. Savage, 1973, p. 325, Pl. 34, fig. 16-18, text-fig. 24.

Sc element

Hindeodella priscilla Stauffer. Walliser, 1964, p. 36, Pl. 9, fig. 12, Pl. 32, fig. 12, 13.

Multi-element

Ozarkodina remscheidensis (Ziegler, 1960). Klapper and Murphy, 1975, p. 38-43, pl. 7, fig. 1-5, 7, 8, 11-30 (includes synonymy through 1972).

Ozarkodina steinhornensis eosteinhornensis (Walliser). Aldridge, 1975, Pl. 2, fig. 23, 34.

Ozarkodina remscheidensis (Ziegler). Carls, 1975, Pl. 2, fig. 16-18.

Ozarkodina remscheidensis (Ziegler). Mehrtens and Barnett, 1976, p. 497, Pl. 1, fig. 6-10, 13, 15, 16.

Ozarkodina remscheidensis (Ziegler). Savage, 1976, p. 1182, Pl. 1, fig. 1-15.

Ozarkodina remscheidensis (Ziegler). Chatterton and Perry, 1977, p. 785-791, Pl. 3, fig. 24, 26, 28-35, Pl. 4, fig. 1-3, 7-9, 23-26, 31, 33-36.

Ozarkodina remscheidensis (Ziegler). Uyeno, 1977, Pl. 41.1, fig. 11, 12.

Ozarkodina steinhornensis eosteinhornensis (Walliser). Helfrich, 1978, Pl. 1, fig. 4-38.

Ozarkodina remscheidensis remscheidensis (Ziegler). Lane and Ormiston, 1979, p. 57, Pl. 1, fig. 3-5, 8, 15, 17, 18, 34-36, 43.

Description. All elements have been previously described (Walliser, 1964, and references above), and will be only briefly described here.

The Pa element is spathognathodiform. It consists of a thin, approximately rectangular blade bearing a single row of 10 to 20 denticles which tend to be triangular and are compressed in the plane of the blade. The basal cavity is a thin groove for most of the length of the conodont but expands under the cusp, at or slightly posterior to the middle of the blade, to produce heart-shaped or semicircular lobes on both sides. This element is most characteristic of the species, as all of the other elements are very similar to the equivalent elements of related species of Ozarkodina. Variation in the Pa element has also been used to distinguish the subspecies O. r. remscheidensis and O. r. eosteinhornensis.

The other elements include the ozarkodiniform Pb element, the neoprioniodiniform M element, and a symmetry transition series ranging from the symmetrical trichonodellan Sa element through the plectospathodan Sb element to the hindeodellan Sc element. The Pb element is an arched laterally compressed blade with a large cusp and small, even denticles, all flattened in the plane of the blade; the basal cavity flares out slightly to form small lobes under the cusp on both sides of the blade, although not to the degree to which it does in the Pa element. The M element consists of a cusp which is oval in cross section, a long, flattened, slightly curving anterior process bearing many small denticles, and an anticusp which may or may not bear two or three very small denticles. The Sa, Sb, and Sc elements all have two flattened processes bearing many small denticles, a cusp which is oval in cross section and is two or three times the diameter of the largest of the small denticles, and a small basal cavity. In the Sa element, the processes are symmetrical, both relatively short, and at an angle just over 90° to each other in posterior view; the cusp curves back between them and the basal cavity has a small opening on the posterior side projecting back under the cusp. In the Sb element, the posterior process is about twice as long as the anterior process, the cusp leans inward and backward, and the small opening of the basal cavity on the inner side under the cusp is also asymmetrical. The whole element is curved, concave inward, most strongly at the anterior end. In the Sc element, the posterior process is about four times as long as the anterior process, the cusp leans back along the

posterior process, and there is no opening of the basal cavity on the inner side. The anterior process is bent down and inward.

Variation. The Pa element collected range from elements typical of O. remscheidensis eosteinhornensis, with even denticulation, to those typical of O. remscheidensis remscheidensis, with the denticle over the basal cavity and two or three denticles at the anterior end enlarged and the rest rather uneven, although typical O. r. remscheidensis is rare. More common in the upper part of the section are forms with a somewhat enlarged median denticle which is often flanked by denticles smaller than average, and with the other denticles nearly even except that the anteriormost denticles are sometimes slightly enlarged. The lobes of the basal cavity are somewhat heart-shaped, with the point toward the posterior end; they are usually about equal in size, although a few are asymmetrical. A few specimens near the base of the Strait Creek section, in the lower part of the Keyser Formation (SC2), have the ridge on one of the lobes which is present in the type material of O. r. eosteinhornensis (Walliser, 1964).

Two variants of the Pa element found in the lower part of the Keyser at Strait Creek are included in O. remscheidensis because transitional forms between these and the typical forms exist. The first (Pl. 4, fig. 3) is a form with many (about 20) fine, very even denticles, fused at the base, with the line formed by the base of the denticles straight; the blade is long relative to its height, and the aboral edges of the anterior and posterior halves are inclined upward

away from the basal cavity. The Pa elements in sample SC4 and some of those in SC5 are this form. The second variant (Pl. 4, fig. 1) is in some respects similar to Ozarkodina sp. nov. E. Klapper and Murphy, 1975; three to six denticles posterior to the cusp are much reduced, usually followed by one or two normal-sized denticles, and the posterior. Intermediate forms (Pl. 4, fig. 4) have less strongly reduced denticles, only one or two denticles reduced, or both. These forms with reduced posterior denticles differ from Ozarkodina sp. nov. E in that the aboral margin in these forms is nearly straight or sigmoidally curved, while in O. sp. nov. E. the aboral margin curves up away from the cusp at both ends. This variant of O. remscheidensis occurs in samples SC2 and SC33, SC5, and SC6, all in the lower Keyser Formation at Strait Creek.

Alternation of large and small denticles is characteristic of the M, Sa, Sb, and Sc elements of Ozarkodina remscheidensis, but is not equally developed in all elements. Alternating denticulation is consistently present in the Sb and Sc elements; there are usually three or four small denticles between a pair of large ones, but there may be anywhere from one to six. The number is not constant for an individual element, often decreasing away from the cusp. The M and Sa elements often have even denticles or have small denticles between only a few of the larger denticles; but some have regularly alternating denticulation, and a few specimens have two or three small denticles between a pair of large ones. Again, this is better developed away from the cusp.

Fåhraeus (1971) separated M elements with alternating denticulation from those lacking it. However, there are intermediates in the form of specimens with a few small denticles; this characteristic does not appear to be correlated with any other or with position in the section; and in many samples, there is no second apparatus present of which a second group of M elements could be part. Both forms are therefore here considered to be part of O. remscheidensis.

Remarks. Ozarkodina remscheidensis has been considered to consist of two subspecies, the younger O. r. remscheidensis and the older O. r. eosteinhornensis, which differ only in the denticulation of the Pa element. Although typical specimens of the two subspecies are easily distinguished, all intermediate variants exist, and populations near the transition from one subspecies to the other may show the full range of variation (Klapper and Murphy, 1975, p. 42); separating the two subspecies requires large collections and is somewhat arbitrary. To complicate matters further, Barnett (1971) offered evidence that the height of the denticle above the basal cavity is environmentally controlled, although it is unclear whether this is also true of its breadth.

As might be expected, taxonomic treatment and therefore biostratigraphic use of these subspecies has varied considerably. Walliser (1964) arbitrarily separated the two at the base of the woschmidti zone; however, deciding the taxonomic status of one species by the occurrence of an unrelated species does not make sense biologically, and also prevents the distinction from being made where

Icriodus woschmidti does not occur. The two have also been treated as separate subspecies, with a zone of overlapping ranges slightly below the base of the woschmidti zone (Klapper and Murphy, 1975). Mehrtens and Barnett (1976) argued that O. r. eosteinhornensis does not occur in New York at levels which correlate with the eosteinhornensis zone in Czechoslovakia; they suggest that the two are geographical subspecies, although it is hard to see why in that case such genetically isolated populations should show the parallel evolutionary trends that Mehrtens and Barnett demonstrate, and on which they base their correlation. However the subspecies are treated, their variability and integradation requires caution in their biostratigraphic use.

The two subspecies are not here separated, as determining the status of a population requires large numbers of specimens with the denticles unbroken, and the conodonts collected from the Helderberg are often poorly preserved in that respect. At Strait Creek, the lowest typical O. r. remscheidensis Pa element observed was collected from 30 feet below the base of the New Creek Limestone (sample SC14) and the highest overlapping typical O. r. eosteinhornensis Pa element from 7 feet above the base of the New Creek (sample SC18); transitional forms, lacking strongly enlarged anterior denticles but with the cusp distinctly larger than the adjacent denticles, occur over the entire range of the species and are particularly abundant in the upper part.

Genus PSEUDOONEOTODUS Drygant, 1977

Type species. Oneotodus (?) beckmanni Bischoff and Sannemann, 1958.

PSEUDOONEOTODUS BECKMANNI (Bischoff and Sannemann)

Pl. 5, fig. 10

Oneotodus (?) beckmanni Bischoff and Sannemann, 1958, p. 98, Pl. 15, fig. 22-25.

Pseudooneotodus beckmanni (Bischoff and Sannemann). Cooper, 1977, p. 1068-1069, Pl. 2, fig. 14, 17 (includes synonymy through 1975).

Remarks. Cooper (1977) considered P. beckmanni to have a single-element apparatus, and its occurrence in the Helderberg Group supports that conclusion; although it is present in abundance in many samples, so that any other elements in the apparatus would be expected also to be present, no other elements occur with it consistently. P. beckmanni tends to occur in the same samples as Ozarkodina excavata excavata, n. gen. C sp., and all three species of Belodella s.f., but it is more widespread than any of those and does not occur in constant proportions with them; some samples (for example, SC20 and SC22) contain large numbers of P. beckmanni and few other conodonts of any species.

Genus ROTUNDACODINA Carls and Gandl, 1969

Type species. Rotundacodina noguerensis Carls and Gandl, 1969

ROTUNDACODINA NOGUERENSIS (Carls and Gandl)

Pl. 5, fig. 1-3, 5-8, 11, 12

Lenticular element

Rotundacodina elegans Carls and Gandl, 1969, p. 208-209, Pl. 20, fig. 10-12.

Rotundacodina sp. cf. R. elegans Carls and Gandl. Epstein, 1970, p. 206-207, Pl. 8, fig. 10-13.

Triangular element

Rotundacodina noguerensis Carls and Gandl, 1969, p. 207-208, Pl. 20, fig. 17-19.

Bicostate element

Acodina retracta Carls and Gandl, 1969, p. 203, Pl. 20, fig. 8, 9.

Tricostate element

Paltodus sp. Epstein, 1970, p. 196-197, Pl. 8, fig. 6, 7.

Quadricostate element

Distacodus sp. Epstein, 1970, p. 162, Pl. 8, fig. 16, 17.

Diagnosis. A species of Rotundacodina with six simple cone elements, distinguished by basal cross section and by number of costae on the base; the elements include lenticular, triangular, plano-convex, bicostate, tricostate, and quadricostate elements. All elements have a long, slender, reclined cusp, a base more or less distinctly set off from the cusp and bearing one or more keeled ridges, and fine longitudinal striations running the length of the cone.

Description. All six elements have fine longitudinal striations, visible only under very high magnification (X900) (Pl. 5, fig. 11, 12); in the specimens in which these were examined in detail (plano-convex and bicostate elements), individual striations run the full length of the conodont. All elements also have a basal cavity which extends through the expanded basal portion of the cone.

Lenticular element. The cusp is long and slender, curving back most strongly just above the base and also curving slightly inward, with sharp anterior and posterior edges and a biconvex cross section. It is often slightly twisted, so that the inner surface of the cusp is turned partly back. The edges become keeled near the base and often project slightly below the rest of the base. The base is expanded

anteriorly and posteriorly; the height of the base is about one third of the height of the conodont, and its basal width is a little less. The basal cross section is biconvex, with the inner surface usually somewhat flattened and the outer surface often showing a peak which does not, however, develop into a sharp edge or ridge.

Triangular element. The cusp is slender and just above the base is bent back and slightly inward; anterior and posterior edges are sharp and the cross section is biconvex. The basal width is about the same as in the lenticular element, but the base is over half the height of the conodont. A ridge runs down the outer surface of the base, in the middle or near the anterior edge. The posterior edge is keeled; the anterior edge and the ridge on the outer side are rarely keeled, and if keeled, not as strongly as the posterior edge. The inner side is convex, but is not as much expanded as the outer side.

Plano-convex element. The cusp is slender and not sharply distinguished from the base. It curves back above the base but does not curve inward. Anterior and posterior edges are sharp to somewhat rounded on the cusp, and the cross section is unequally biconvex, with the inner side flatter. On the base, the anterior edge is sharp and the posterior edge becomes keeled. The basal width is only about one quarter of the height of the conodont, and the height of the base is about half the height of the conodont. The outer surface of the base is strongly convex, either symmetrical or with the posterior margin steeper; the inner surface is nearly flat to slightly sigmoidal, convex posteriorly

and flat to slightly concave anteriorly. This element is usually smaller than the lenticular and triangular elements.

Bicostate element. The cusp is long and slender, bent slightly back just above the base and bent and twisted inward. Two posterolateral ridges run most of the way up the cusp; these become broad keels on the lower part of the base. The base is about half the height of the conodont; it is slender, not sharply set off from the cusp. The cross section is round or nearly so throughout the length of the conodont; the basal cross section may be slightly elongated toward the anterior, in which case the keels are symmetrically disposed with respect to the elongation. The conodont is usually at least as long as the lenticular and triangular elements but is less wide.

Tricostate element. The cusp is slender and curves back, sometimes strongly, and slightly inward. It is round or nearly round in section, with the outer and anterior ridges persisting up much of the cusp. The base has three keeled ridges, posterior, anterior, and outer. In some specimens the anterior and outer ridges nearly form a pair of anterolateral ridges, symmetrical with respect to the curvature of the cusp and the posterior ridge; however, the conodont is never quite symmetrical. All three surfaces of the base are convex, the outer anterior surface least so. The base is between one-half and one-third the height of the conodont, and the basal width is a little less.

Quadricostate element. The cusp is long, somewhat thicker than the cusps of the other elements, and nearly straight, bent to the posterior just above the base. The cusp bears two lateral ridges and its cross

section is unequally biconvex to nearly round, the posterior side being flatter. The base is expanded; its height is under one-third the height of the conodont, and the basal width is about the same. The base has keeled ridges anteriorly, posteriorly, and on both sides; the anterior and posterior ridges are more strongly keeled. The basal cross section is approximately elliptical, with the long direction of the ellipse running anterior to posterior.

Remarks. These six elements occur together quite consistently, are similar in shape, depth of basal cavity, and micro-ornament, and tend to occur in about the same proportions in all samples. The plano-convex element has not previously been described. They occur in ratios of approximately ten pairs of lenticular elements to one pair of triangular elements to one pair of plano-convex elements to three pairs of bicostate elements to three pairs of tricostate elements to one quadricostate element (10:1:1:3:3:5). The quadricostate is the only symmetrical element and is probably unpaired. In addition, Epstein (1970) commented that some of the same elements tend to occur together in the Helderberg Group of southeastern New York and northeastern Pennsylvania. Although some other simple cones, including Acodina curvata s.f. and Acodus sp. s.f., tend to associate with R. noguerensis, no others share the similarity of the six elements or occur in constant ratios with them.

ROTUNDACODINA (?) DENTATA n. sp.

Pl. 5, fig. 4, 9, 13

Cordylodus n. sp. Ziegler, 1960, p. 181, Pl. 14, fig. 19a, b.

n. gen. A n. sp. a van Adrichem Boogaert, 1967, p. 187-188, Pl. 3, fig. 28, 29, text-fig. 68.

Rotundacodina dubia (Rhodes, 1953). Carls and Gandl, 1969, p. 208, Pl. 20, fig. 13-16.

Genus undetermined A sp. Epstein, 1970, p. 239-240, Pl. 7, fig. 15, 16.

Genus undetermined B sp. Epstein, 1970, p. 240-241, Pl. 7, fig. 8, 9.

Genus undetermined C sp. Epstein, 1970, p. 241-243, Pl. 7, fig. 10, 11.

Neoprioniodus brevirameus Walliser. Barnett, 1971, Pl. 36, fig. 6.Oepikodus sp. Barnett, 1971, Pl. 37, fig. 9.Rotundacodina dubia (Rhodes). Savage, 1973, p. 328, Pl. 32, fig. 23, 24, text-fig. 26.

Genus et species indet. Helfrich, 1978, Pl. 2, fig. 8, 9.

non Cordylodus (?) dubius Rhodes, 1953, p. 299, Pl. 23, fig. 221-224.

Holotype. The holotype is a smooth element (Pl. 5, fig. 4) from the New Creek Formation 2 feet above its base at the Strait Creek section on Virginia Route 629 about three miles north of Monterey, Virginia.

Paratype. The paratype is a costate element (Pl. 5, fig. 9) from the same locality as the holotype.

Description. The apparatus contains two elements which are very similar but differ in the presence or absence of a longitudinal costa. These are here called the costate element and the non-costate element, respectively.

In both elements, the cusp is slender and is round in cross section; it is curved back and slightly inward and is slightly twisted so that its inner surface is turned to face backward. The anterior and posterior edges of the conodont are sharp. The base is expanded anteriorly and posteriorly; the posterior margin bears one to three

small, laterally compressed denticles, and the base is extended back under each denticle rather than having its posterior margin continue down in a smooth curve. The basal cavity extends up about half the height of the conodont; it has a small branch extending into the base of each denticle. The surface of the conodont is covered with fine longitudinal striations, visible only under high magnification (Pl. 5, figure 13), each of which runs only a short distance.

In both elements the base under the denticles is separated from the main part of the base by a gentle vertical furrow on both sides of the conodont. On the non-costate element, the main part of the base is unequally biconvex in section, with the inner side flatter. The base of the costate element bears a keeled ridge on the outer side, in the middle of the main part of the base or closer to the anterior edge; the surface anterior and posterior to the ridge meet at a sharp angle.

Comparison. R. dentata has been identified as Cordylodus (?) dubius of Rhodes (Carls and Gandl, 1969; Savage, 1973). Rhodes' Cordylodus (?) dubius, however, is part of the Distomodus dubius apparatus (Jeppsson, 1972). R. dentata differs from this element in that the width of the base increases sharply under each denticle, rather than having small denticles which project out from the base at right angles; and the outline of the conodont is somewhat different. The other elements of Distomodus dubius were not found in the Virginia Helderberg rocks, although some of them occur lower in the section in the Appalachians (Helfrich, 1975).

Remarks. This species was included in Rotundacodina by Carls and Gandl (1969); this practice is followed here although the type species of Rotundacodina is an apparatus of simple cones, because R. dentata resembles the type species in having elements with a recurved slender cusp, a somewhat expanded base containing a basal cavity half the height of the conodont or slightly less, one or more keeled ridges on the base with the number of ridges distinguishing the different elements, and fine longitudinal striations on the surface of the elements. R. dentata resembles R. noguerensis sufficiently, in fact, that one might suppose R. dentata to be a denticulate element of R. noguerensis; however, the pattern of occurrence of the two species is not consistent with their forming one apparatus. R. dentata usually occurs in samples containing R. noguerensis, but the ratio of the lenticular element of R. noguerensis to both elements of R. dentata ranges from 485:5 to 7:10, and there are several samples with many R. noguerensis and no R. dentata, including some with hundreds of R. noguerensis elements (samples PB4, PB6, and PB7).

Genus ACODINA Stauffer, 1940 s.f.

Type species. Acodina lanceolata Stauffer, 1940

Remarks. Some elements which have previously been assigned to the form genus Acodina are S₂ elements of Icriodus, but others are not associated with Icriodus, and must therefore be part of a different sort of apparatus. In the Helderberg Group, for instance, neither Acodina curvata s.f. nor A. aragonica s.f. occurs in constant

proportions with Icriodus helderbergensis. The form genus Acodina is here retained for elements which cannot be assigned to any multi-element species.

ACODINA ARAGONICA Carls and Gandl, s.f.

Pl. 6, fig. 5

Acodina aragonica Carls and Gandl, 1969, p. 201, Pl. 20, fig. 5-7.
Acodina curvata Stauffer. Epstein, 1970 (partim), p. 153, Pl. 8,
 fig. 24-26.

Description. The conodont is fairly short, with a base that is slightly expanded to the inside but not anteriorly or posteriorly, so that it is not sharply set off from the cusp. The cusp curves inward and slightly back; it has sharp anterior and posterior edges and is biconvex in cross section. The edges become keeled on the base. The basal cavity is about half the height of the conodont, and the basal width is a little less; the cross section of the base is unequally biconvex, with the outer side slightly convex and the inner side more strongly convex and somewhat flattened in the center.

ACODINA CURVATA Stauffer s.f.

Pl. 6, fig. 6

Acodina curvata Stauffer, 1940, p. 418, Pl. 60, fig. 3, 14-16.
Acodina curvata Stauffer. Ziegler, 1956, p. 98, Pl. 7, fig. 25.
Acodina curvata Stauffer. Carls and Gandl, 1969, p. 201-202, Pl. 19,
 fig. 25-26
Acodina curvata Stauffer. Epstein, 1970 (partim), p. 153, Pl. 8,
 fig. 23.

Description. The cusp is relatively short and broad and curves inward and back. It has a biconvex cross section with the anterior and posterior edges sharp. The base is about one-third of the height

of the conodont; it is expanded inward, forward, and backward, and the anterior edge is drawn out, so that the basal width is over half the height of the conodont. The basal cross section is plano-convex, with the outer side flat to slightly concave and the inner side strongly convex; the angle where the two sides meet is greater at the posterior edge than at the anterior edge.

Comparison. A. curvata resembles A. aragonica in having a short, thick cusp and an outer side which is flatter on the base than the inner side. A. curvata, however, has a more expanded base, a greater anterior/posterior asymmetry, and a completely flat basal outer surface.

Genus ACODUS Pander, 1856 s.f.

Type species. Acodus erectus Pander, 1856

ACODUS sp. s.f.

Pl. 6, fig. 8, 9

Acodus sp. transitional to Acodina plicata Carls and Gandl. Epstein, 1970 (partim), p. 155-156, Pl. 8, fig. 14, 15, Pl. 9, fig. 7-9.
Acodus sp. Barnett, 1971 (partim), Pl. 37, fig. 10.

Description. The cusp is straight, inclined slightly back. Its cross section is subtriangular, with anterior, posterior, and outer edges which become sharper closer to the base; the inner side is slightly convex. The base is expanded, so that is distinctly set off from the cusp; it is about one-third the height of the conodont, and the basal width is close to half the height of the conodont. Its cross section is lenticular to subtriangular, with three ridges, the outer

ridge ranging from halfway between the anterior and posterior ridges to closer to the posterior ridge. All three ridges become keeled at the base, the posterior most weakly.

Genus BELODELLA Ethington, 1959 s.f.

Type species. Belodus devonicus Stauffer, 1940

Remarks. An apparatus consisting of a symmetry transition series of two or more belodelliform elements ranging from triangular to lenticular in cross section has been proposed for several species of Belodella, including Belodella erecta of Ordovician age (Serpagli, 1967), B. anomalis of Upper Silurian age (Cooper, 1974), and Belodella devonica of Silurian and Devonian age (Serpagli, 1967; Fahraeus, 1971). Although Serpagli (1967, p. 25, text-figure 5) described a continuous variation from lenticular to triangular elements in B. erecta, his figured series of cross sections show a sharp distinction between the triangular and lenticular elements; and various authors (Savage, 1973; Telford, 1975) have observed two or three distinct types of cross section in Belodella elements in their collections. Wilson (1977) described two species of Belodella which, in addition to a symmetry transition series of three and five belodelliform elements, respectively, each include an acodiform element similar to Haplobelodella s.f. and an oistodiform element.

Elements in the Helderberg Group which might be part of a Belodella apparatus include Belodella devonica s.f., B. resima s.f., B. triangularis s.f., three form species of Coelocerodontus, and one form species of Haplobelodella. These are all thin-walled cones with

very deep basal cavities which reach most of the way to the tip; all tend to be lighter in color than other conodonts in the same sample. They tend to occur together, but not in constant proportions; the ratio of B. devonica s.f. to B. triangularis s.f., for example, varies from 1:37 to 29:6. Even though the samples are relatively small, this sort of variation in ratios is puzzling if one assumes these conodonts to have formed a single apparatus; as all of them are similar in size and shape, one would not expect the original ratios to be so greatly disturbed by breakage or mechanical sorting. Even if one assumes that at least some of the elements belong together, it is not clear whether one or more apparatuses are involved, or, if several apparatuses are involved, which elements within the group are likely to be part of the same apparatus. For these reasons, all seven elements are here left in form taxonomy until there is sufficient evidence to show apparatus composition.

BELODELLA DEVONICA Stauffer s.f.

Pl. 6, fig. 16

Belodus devonicus Stauffer, 1940, p. 420, Pl. 59, fig. 47-48.

Belodella devonica (Stauffer). Savage, 1973, p. 312, Pl. 32, fig. 19, 20, 25, 26, text-fig. 4.

Belodella devonica (Stauffer). Chatterton, 1974 (partim), p. 1469-1470, Pl. 2, fig. 11-14.

Belodella devonica (Stauffer). Telford, 1975, p. 10-11, Pl. 1, fig. 5-9 (includes synonymy through 1971).

Belodella devonica (Stauffer). Mehrtens and Barnett, 1976, Pl. 1, fig. 4.

"Belodella devonicus" Orchard, 1978, Pl. 108, fig. 34.

BELODELLA TRIANGULARIS (Stauffer) s.f.

Pl. 6, fig. 15

- Belodus triangularis Stauffer, 1940, p. 420, Pl. 59, fig. 49.
Belodella triangularis (Stauffer). Savage, 1973, p. 313, Pl. 32, fig. 21, 22, text-fig. 6.
Belodella devonica (Stauffer). Chatterton, 1974 (partim), p. 1469-1470, Pl. 2, fig. 10.
Belodella triangularis (Stauffer). Telford, 1975, p. 11-12, Pl. 1, fig. 1-4, Pl. 2, fig. 1, 2 (includes synonymy through 1971).
Belodella triangularis (Stauffer). Mehrstens and Barnett, 1976, Pl. 1, fig. 2.
Belodella devonica (Stauffer). Savage et al., 1977 (partim), p. 2935, Pl. 2, fig. 23, 24.
 "Belodella triangularis" Orchard, 1978, Pl. 108, fig. 40, 44.
Belodella triangularis Stauffer. Lane and Ormiston, 1979, Pl. 1, fig. 23.

BELODELLA RESIMA (Philip) s.f.

Pl. 6, fig. 14

- Belodus resimus Philip, 1965, p. 98, Pl. 8, fig. 15-17, 19, text-fig. 2e-f.
Belodella resima (Philip). Savage, 1973, p. 312, Pl. 32, fig. 9, 10, text-fig. 5.
Belodella resima (Philip). Cooper, 1973, Pl. 2, fig. 6.
Belodella resima (Philip). Telford, 1975, p. 11, Pl. 1, fig. 10-16, Pl. 2, fig. 3-4.
 "Belodella resimus" Orchard, 1978, Pl. 108, fig. 37, 41.
Belodella resima Philip. Lane and Ormiston, 1979, Pl. 1, fig. 24, 27.

Comparison. Belodella resima s.f. is distinguished from B. triangularis s.f. in that the basal cross section of the former is narrow and symmetrical, with the lateral faces over twice as wide as the anterior face, while that of the latter is broader and asymmetrical, with lateral faces less than twice as wide as the anterior face and the outer later face slightly shorter than the inner; the ratio of the height to the basal width of the conodont is about 3.5:1 to 4.5:1 in the former, but about 2:1 to 3:1 in the latter; and both anterolateral

ridges run almost to the tip in the former, but the outer antero-lateral ridge ends at or below the curve near the tip in the latter.

Genus COELOCERODONTUS Ethington, 1959, s.f.

Type species. Coelocerodontus trigonius Ethington, 1959

Remarks. Devonian form species referred to Coelocerodontus by Bultynck (1970) and Telford (1975) differ from the Ordovician species, including the type species of the genus, which were assigned to the genus by Ethington (1959) in being much broader and more expanded; whether they in fact belong to the same genus is open to question. This may be resolved when apparatuses of Devonian and Ordovician forms are established. For discussion of the apparatus of the Helderberg Coelocerodontus form species, see under Belodella.

COELOCERODONTUS BICONVEXUS Bultynck s.f.

Pl. 6, fig. 18

Coelocerodontus biconvexus Bultynck, 1970, p. 94, Pl. 27, fig. 13-15.

Description. The tip is curved back more or less sharply in most specimens at an angle close to 90° ; the rest of the conodont is also curved back but not as strongly. The basal cavity extends to the point of sharpest curvature. Two ridges run the full length of the conodont, one posterior and the other inner-anterior. The cross section is unequally biconvex, with the outer side more strongly convex; its strongest curvature is anterior.

Comparison. This species differs from C. digonius Sweet and Bergström by its greater curvature, its more rapid widening toward

the base, and the placement of its anterior ridge toward the inner side. It differs from C. *reductus* by the lack of a second anterior ridge.

COELOCERODONTUS REDUNCTUS Telford s.f.

Pl. 6, fig. 17

Coelocerodontus *reductus* Telford, 1975, p. 16, Pl. 3, fig. 1-3.

Description. The tip is sharply curved back, in some cases as much as a 90° angle; the rest of the conodont is gently curved back. The basal cavity reaches up to the sharp curve. The conodont is nearly bilaterally symmetrical. Its basal cross section is an isosceles triangle with the anterior face two-thirds to less than half the length of the lateral faces. The ridges along which the faces join extend from the base approximately to the strongly curved region of the tip; the posterior ridge may be keeled.

COELOCERODONTUS sp. s.f.

Pl. 6, fig. 19

Description. The conodont is bilaterally symmetrical. Its upper half is curved back; the base is more or less expanded laterally and strongly expanded front and back, so that the basal width is over half the height of the conodont. The posterior edge is sharp, the anterior edge sharp to slightly rounded. The basal cavity extends above the expanded base, to about two-thirds to three-quarters of the height of the conodont.

Genus HAPLOBELODELLA Khodalevich and Tsernich, 1973, s.f.

HAPLOBELODELLA sp. s.f.

Pl. 6, fig. 20

Description. The conodont is about three times as high as its basal width; it expands evenly from tip to base and curves back smoothly and may curve slightly inward. It is thin-walled and laterally compressed, with a deep basal cavity and sharp anterior and posterior edges. The basal cavity extends over three-quarters of the height of the conodont, and its tip and anterior edge are close to the anterior edge of the conodont, rather than the tip being centered. There is a fold in the anterior half of both sides, producing an almost keyhole-shaped cross section; the cross section may be bilaterally symmetrical, or the fold on the outer side may be larger.

Comparison. This form species differs from Haplobelodella bicarinata Snigireva, 1975, in that its base is narrower relative to its height, and it lacks the two weak anterior keels of H. bicarinata.

Gen. indet. sp. A

Pl. 6, fig. 2, 10

Description. The cusp is fairly thick, straight, and inclined back slightly. The base is between half and one-third the height of the conodont and is expanded so that the basal width is about half the height of the conodont; it is oval in cross section, with the long dimension running anterior-posterior. In lateral view, the posterior margin of the conodont is concave and the anterior margin is straight

to slightly concave. The cusp bears an anterior ridge and two posterolateral ridges; when these reach the base they may continue onto it, bifurcate to produce ridges, or die out.

Gen. indet. sp. B

Pl. 6, fig. 13

Description. The conodont is a small, evenly tapering cone, slightly flared at the base but with the base not distinctly set off from the cusp. The cusp curves back and is round to biconvex in cross section; the base is also nearly round in section, but may be slightly elongated front to back. The basal width is about one-third of the height of the conodont; the height of the basal cavity is about the same. The conodont bears one or two ridges running its length which may be slightly keeled at the base. one ridge is generally anterolateral; the second, if present, is slightly anterolateral to posterolateral, so that the ridges are not symmetrically disposed with respect to the curvature of the cusp. The two may or may not be equally strong. The surface of the conodont is covered with fine longitudinal striations, visible only under high magnification.

Gen. indet. sp. C

Pl. 6, fig. 1

Description. The conodont is laterally compressed and consists of a long, tapering cusp and a base expanded anteriorly and posteriorly. The cusp curves back and sometimes inward; it may be slightly twisted. There are broad anterior and posterior keels running the

full length of the conodont; these do not project below the base. The keels tend to be transparent. The central part of the base between the keels is equally to unequally biconvex, usually with the widest part somewhat posterior to the middle; if unequally biconvex, the inner side is more expanded. The basal cavity reaches between half and one-third of the height of the conodont. The conodont is finely striated; this is visible only under high magnification.

Comparison. This form is similar to the lenticular element of Rotundacodina noguerensis; the anterior and posterior edges of the latter, however, are keeled only at the base and the keels extend below the base.

Genus indet. sp. D

Pl. 6, fig. 3, 4

Description. The conodont consists of a short, thick cusp and a base which is very little expanded. The cusp has sharp posterior and lateral edges; it is curved slightly back and to the inside. The lateral edges become keeled on the base. The base is in cross section a rounded triangle with the anterior face slightly shorter than the lateral faces. The basal cavity is between half and one-third of the height of the conodont; the basal width is about half the height of the conodont.

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Plate 1

Figs. 1-9 --Icriodus helderbergensis n. sp. 1, 2, icriodiform elements, PB4, 80X; 3, 4, acodiniform elements, PB3, 70X; 5, icriodiform element, PB4, 40X; 6, icriodiform element, SC29, 40X; 7, icriodiform element, SC30, 40X; 8, icriodiform element, SC18, 40X; 9, icriodiform element, SC36, 40X.

Figs. 10, 11 --Icriodus latericrescens robustus Orr. Icriodiform elements, PB34, 80X

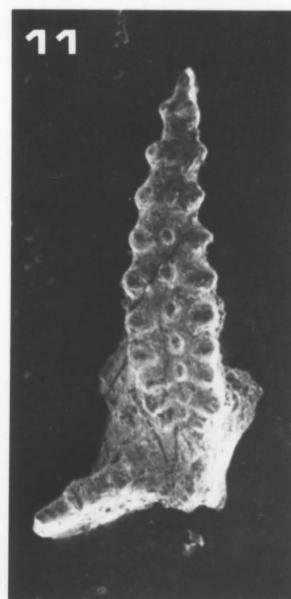
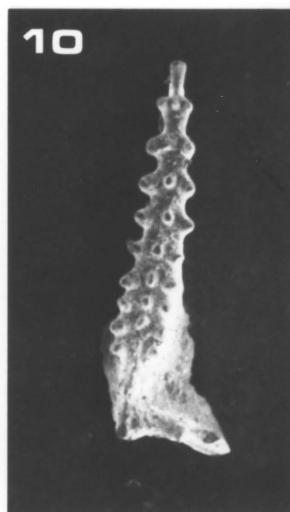
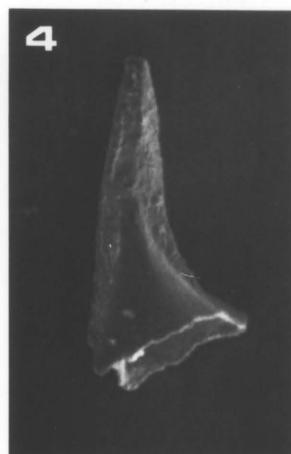


Plate 2

All figures at 45X, except 10, 14 at 90X

Figs. 1-7 --Delotaxis excavata cristagalli Ziegler. 1, Pb element, SC17; 2, Sb element, SC17; 3, Sa element, SC17; 4, Pb element, SC37; 5, M element, SC17; 6, Sc element, SC37; 7, Pa element, SC17.

Figs. 8-15 --Delotaxis n. sp. 8, Sb element, PB20; 9, M element, PB19; 10, 14, Pa elements, PB19; 11, Sb element, PB19; 12, Sa element, PB19; 13, Pb element, PB19; 15, Sc element, PB19.

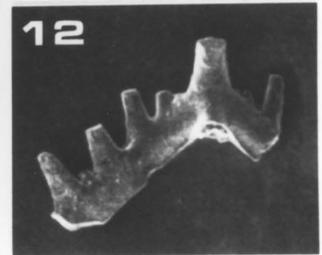
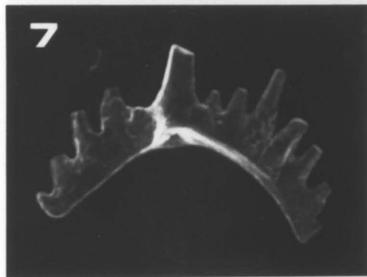
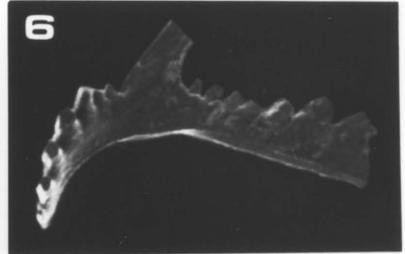
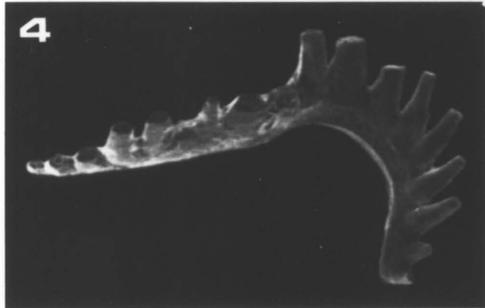
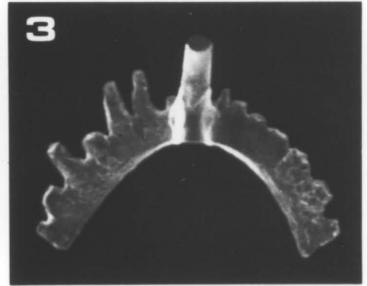
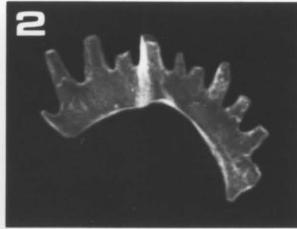
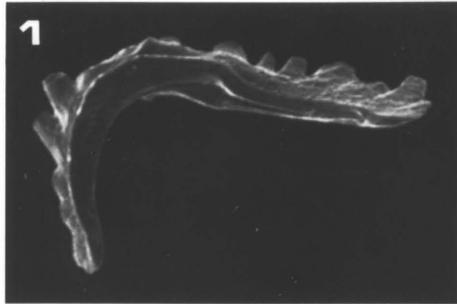


Plate 3

Figs. 1-8, 11 --Ozarkodina excavata excavata (Branson and Mehl). 1, 8, Sc elements, PB33, 45X; 2, M element, PB10, 45X; 3, Pb element, PB17, 45X; 4, Pa element, PB16, 45X; 5, Pb element, PB16, 45X; 6, M element, PB16, 45X; 7, Sa element, PB10, 45X; 11, Pb element, PB17, 45X.

Figs. 9, 10, 12-18 --Delotaxis elegans (Walliser). 9, Pa element, SC6, 70X; 10, Sb element, SC6, 70X; 12, 15, Pb elements, SC6, 70X; 13, 16, M elements, SC6, 70X; 14, Sa element, SC6, 65X; 17, Sd element, SC4, 65X; 18, Sc element, SC6, 70X.

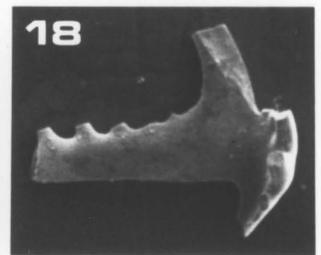
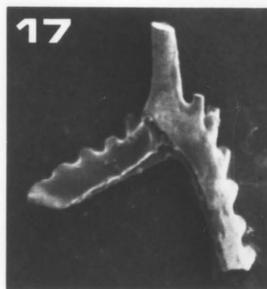
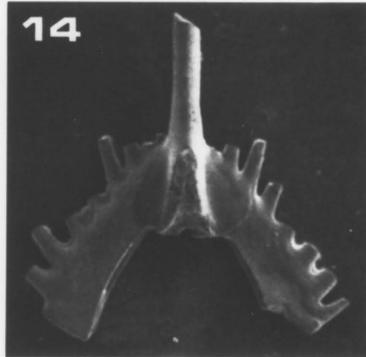
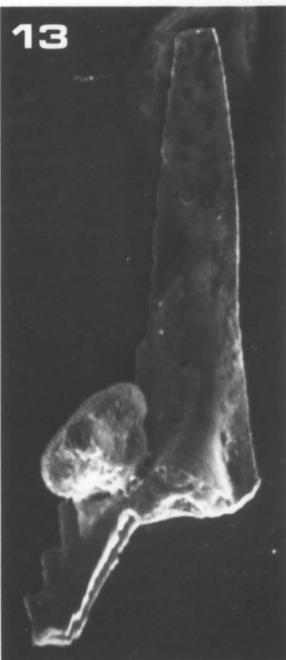
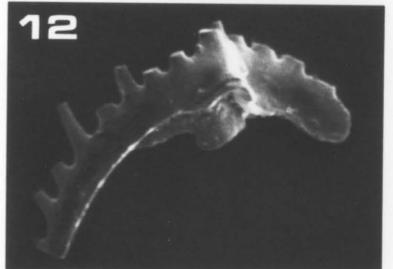
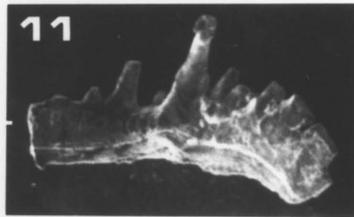
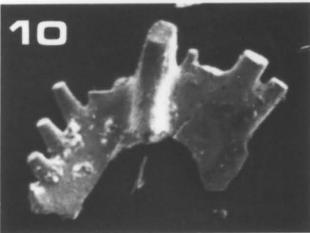
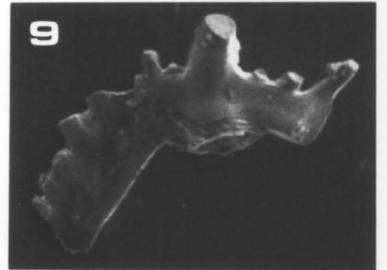
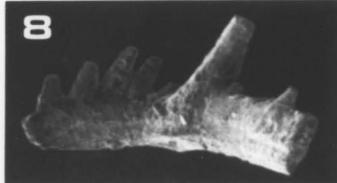
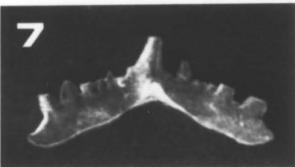
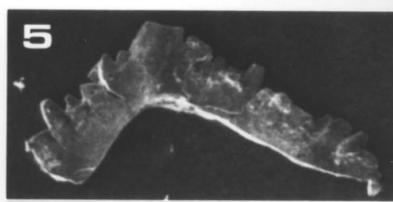
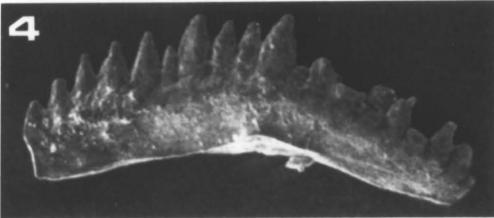
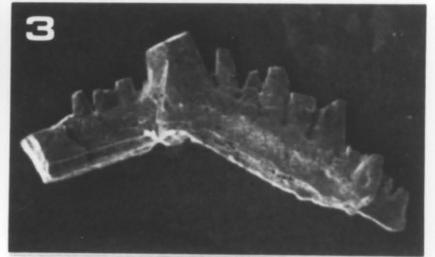
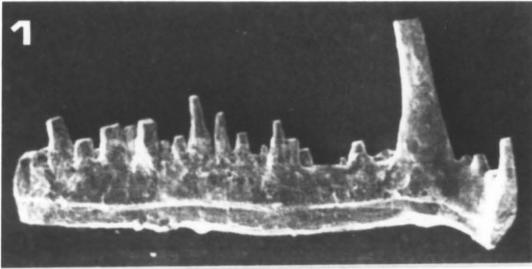


Plate 4

All figures at 65X, except 8 at 90X,
12 at 130X, 16 at 70X

Figs. 1-16 --Ozarkodina remscheidensis (Ziegler). 1, Pa element, SC2; 2, M element, SC13; 3, Pa element, SC4; 4, Pa element, SC6; 5, Pa element, SC36; 6, Pa element, SC5; 7, M element, SC6; 8, Pa element, PB22; 9, Sb element, PB22; 10, Pa element, SC14; 11, Pb element, PB22; 12, Sa element, PB22; 13, Pa element, SC38; 14, Sc element, PB22; 15, Pa element, SC24; 16, Sb element, PB22.

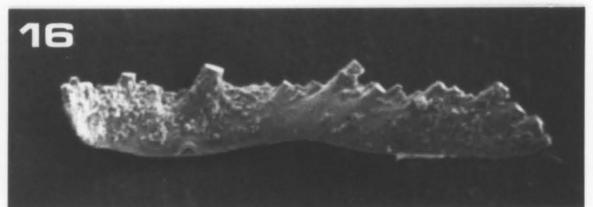
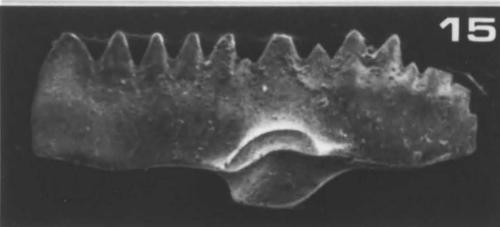
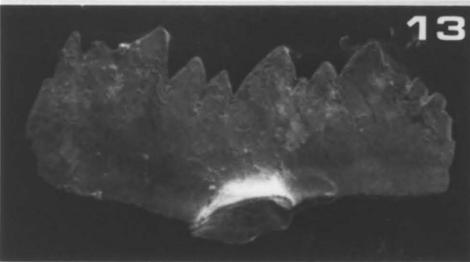
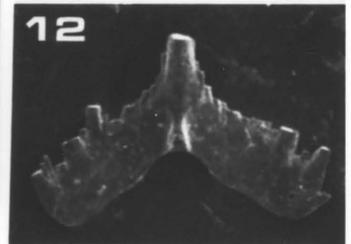
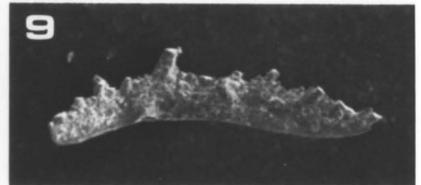
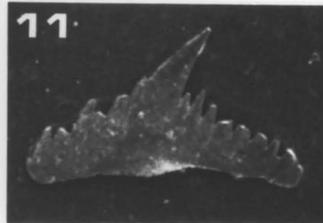
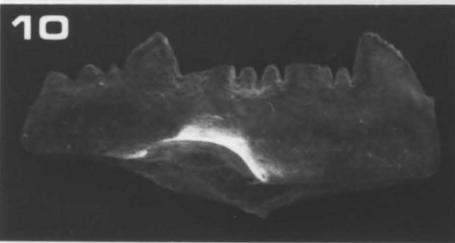
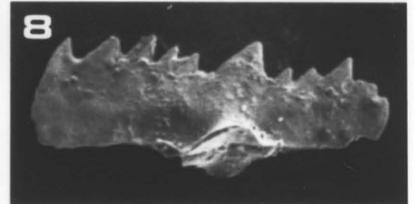
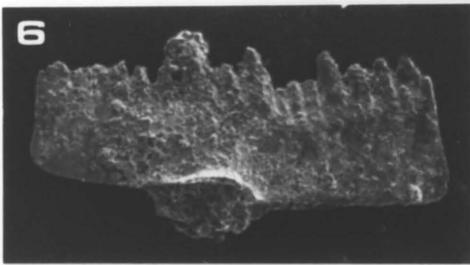
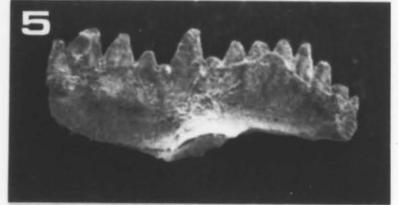
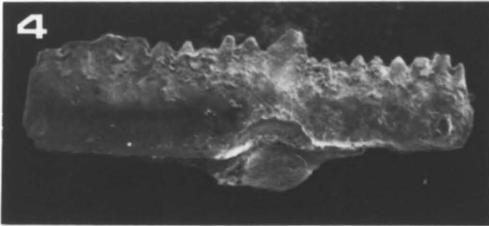
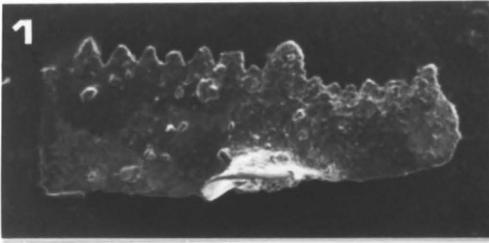


Plate 5

All figures at 90X,
except 11-13 at 900X

Figs. 1-3, 5-8, 11, 12 --Rotundacodina noguerensis Carls and Gandl.
1, triangular element, PB3; 2, 3, lenticular
elements, PB3; 5, 11, bicostrate element,
PB6; 6, quadricostate element, PB5; 7, 12,
plano-convex element, PB6; 8, tricostate
element, PB3.

Figs. 4, 9, 13 --Rotundacodina dentata n. sp. 4, 13, non-
costate element, SC37; 9, costate element,
SC37.

Fig. 10 --Pseudooneotodus beckmanni (Bischoff and
Sannemann), SC35.

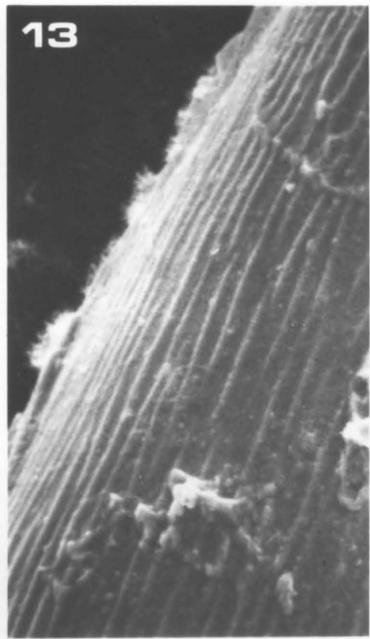
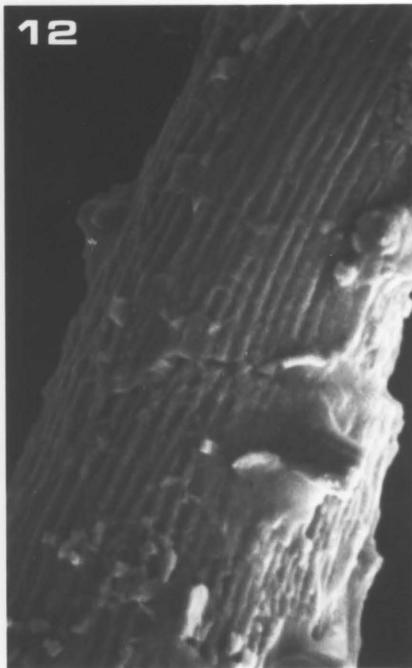
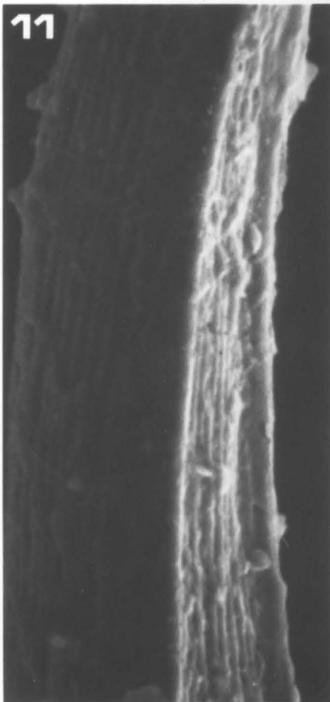
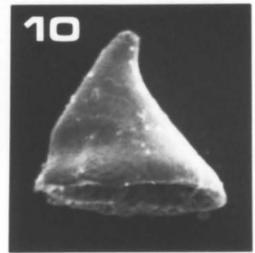
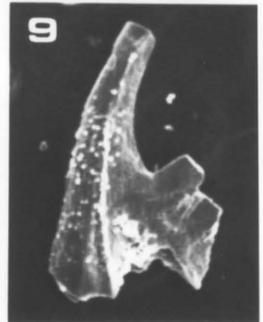
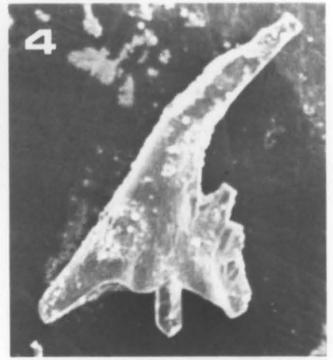
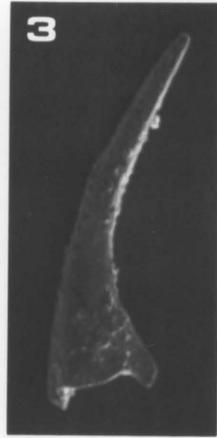
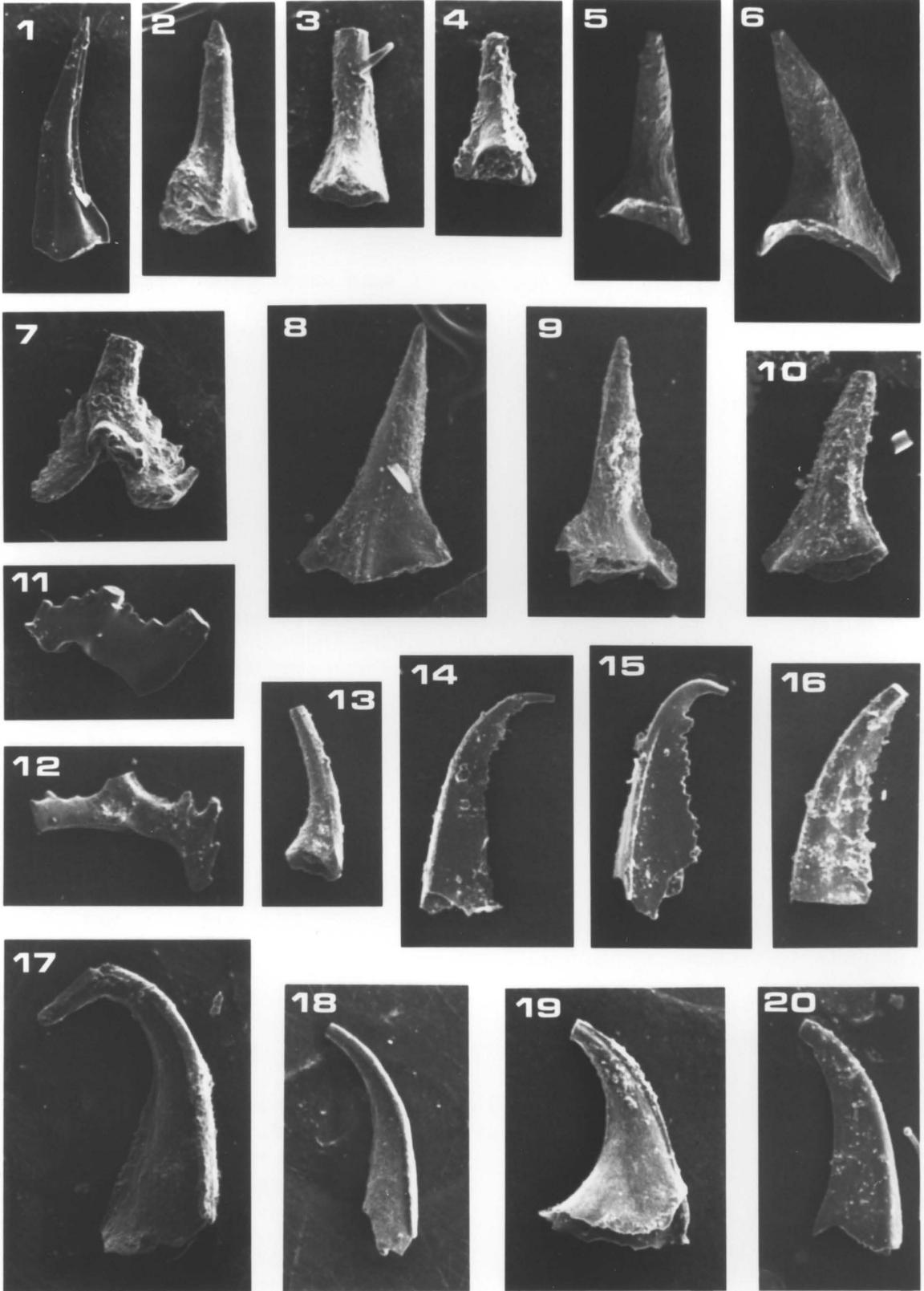


Plate 6

All figures at 90X, except 7,
8, 18, 19 at 70X, 12 at 45X

- Fig. 1 --Gen. indet. sp. C, PB6.
- Figs. 2, 10 --Gen. indet. sp. A. 2, PB6; 10, PB3.
- Figs. 3, 4 --Gen. indet. sp. D. 3, PB5; 4, PB7.
- Fig. 5 --Acodina aragonica Carls and Gandl s.f., PB5.
- Fig. 6 --Acodina curvata Stauffer s.f., PB5.
- Fig. 7 --Synprioniodina sp., PB19.
- Figs. 8, 9 --Acodus sp. s.f., SC35.
- Fig. 11 --Plectospathodus sp. s.f., PB14.
- Fig. 12 --Ligonodina sp. s.f., SC34.
- Fig. 13 --Gen. indet. sp. B, PB16.
- Fig. 14 --Belodella resima (Philip) s.f., SC28.
- Fig. 15 --Belodella triangularis (Stauffer) s.f., SC28.
- Fig. 16 --Belodella devonica (Stauffer) s.f., SC28.
- Fig. 17 --Coelocerodontus redunctus Telford s.f., PB3.
- Fig. 18 --Coelocerodontus biconvexus Bultynck s.f., PB3.
- Fig. 19 --Coelocerodontus sp. s.f., PB3.
- Fig. 20 --Haplobelodella sp. s.f., SC28.



APPENDIX A: MEASURED SECTIONS

Section at Price's Bluff, on the Chesapeake and Ohio Railroad above the James River, near State Route 622, .8 miles from U.S. Route 220, .5 miles north of Gala, Virginia

Unit	Sample	Feet above base of section	Thickness (feet)	Cumulative thickness (feet)
NEEDMORE SHALE (part)				
		Shale, grey		
30.	Argillaceous lime mudstone PB34	261	.7	261.7
29.	Shale, grey		3.5	261
RIDGELEY SANDSTONE				
28.	Quartz sandstone, silica-cemented		1.5	257.5
LICKING CREEK FORMATION LITTLE COVE MEMBER				
27.	Arenaceous skeletal grainstone, in places approaching calcareous quartz sandstone, light grey to reddish brown, massive, stylolitized; brachiopods, bryozoans, crinoids		55.7	256
	PB1	253		
	PB2	244		
	PB3	227		
	PB4	217		
	PB5	206		
CHERRY RUN MEMBER				
26.	Argillaceous skeletal packstone or wackestone, dark grey, nodular bedded, with nodules of black chert; brachiopods, bryozoans		9.6	200.3
	PB6	195		
25.	Skeletal grainstone, light grey; brachiopods, crinoids, bryozoans		7	190.7

24.	Chert, black	1.7	183.7
23.	Quartz sandstone with lenses of carbonate sand, cross bedded; bryozoans	3	182
22.	Argillaceous skeletal packstone, dark grey, nodular bedded, with nodules and irregular, discontinuous beds of black chert; brachiopods, bryozoans, crinoids, rugose corals	31.3	179
	PB7	177	
	PB8	167	
	PB9	157	
	PB10	149	

HEALING SPRINGS SANDSTONE

21.	Crinoidal grainstone, light grey	.7	147.7
20.	Calcareous quartz sandstone, massive or cross-bedded; bryozoans, crinoids	1.5	147
19.	Arenaceous crinoidal grainstone with minor rounded quartz pebbles, massive or cross-bedded, stylolitized; crinoids, bryozoans	9.8	145.5
	PB11	145	
	PB12	140	
	PB13	138	
18.	Shale, black, with thin nodular beds of crinoidal grainstone	.7	135.7
	PB14	135	

NEW CREEK FORMATION

17.	Arenaceous crinoidal grainstone, with thick brown stylolites	1	135
16	Coarse crinoidal grainstone with minor quartz sand near the base, massive, stylolitized, crinoid columnals and a few articulated sections of crinoid stem; also brachiopods, bryozoans, colonial corals	16.7	134

PB15 130
 PB16 126
 PB17, 122
 PB33
 PB18 118

15. Crinoidal grainstone with minor quartz sand, cross bedded 7.8 117.3

PB19 113

KEYSER FORMATION
 UPPER LIMESTONE MEMBER

14. Stromatoporoid packstone, with a matrix of skeletal wackestone; stromatoporoids, few colonial corals, brachiopods, bryozoans; the top of the unit is undulating. 15 109.5

PB20, 109
 PB32
 PB21 98

13. Argillaceous lime mudstone, dark grey, nodular bedded, with black chert nodules; few silicified rugose corals 9.3 94.5

CLIFTON FORGE SANDSTONE MEMBER

12. Quartz sandstone, cross-bedded; silicified colonial corals 3.2 85.2

PB23 82

11. Argillaceous lime mudstone, dark grey, nodular bedded 3.5 82

10. Quartz sandstone, silica-cemented, massive or cross bedded 27.7 78.5

PB24 65
 PB25 54

9. Quartz sandstone, silica-cemented, bioturbated, interbedded with dark grey shale 2.8 50.8

8. Quartz sandstone, silica-cemented, massive 5.3 48

7.	Quartz sandstone, silica-cemented, planar or cross laminated or bioturbated, interbedded with dark grey shale	7.2	42.7
6.	Skeletal grainstone, partially silicified; brachiopods, bryozoans, crinoids	.5	35.5
	PB31 35		
5.	Shale, grey	.7	35
4.	Clay-rich lime mudstone; irregular fenestrae in upper two feet; leperditiid ostracods	5.3	34.3
	PB26 34		
3.	Interbedded laminated clay-rich lime mudstone and cross-laminated sandstone; the sandstone decreases up	3.4	29
	PB27 27		
2.	Quartz sandstone, largely silica-cemented, bidirectionally cross-bedded, with carbonate lenses and thin beds; cross bedding fines up; brachiopods, bryozoans, colonial corals	9.3	25.3
	PB28 20		
1.	Quartz sandstone, largely silica-cemented, bidirectionally cross-bedded	16	16

Section above Strait Creek, on Virginia State Route 629, about 1 mile southeast of its intersection with U.S. Route 220, 3½ miles north of Monterey, Virginia.

Unit	Sample	Feet above base of section	Thickness (feet)	Cumulative thickness (feet)
LICKING CREEK FORMATION (part)				
		covered		
35.		Argillaceous lime mudstone, dark grey, partially silica-replaced, with black chert nodules	24	430
	SC32	426		
	SC31	418		
	SC30	408		
34.		Interbedded black chert and argillaceous lime mudstone, partially silica-replaced	8	406
33.		Covered	2	398
32.		Chert, black, with argillaceous seams	2	396
31.		Argillaceous lime mudstone	1	394
	SC29	393		
30.		Covered	6.5	393
29.		Inbedded black chert and argillaceous lime mudstone, partially silica-replaced	1.5	386.5
	SC28	386		
28.		Covered	4	385
27.		Chert, black, irregularly bedded, with argillaceous seams and nodules and thin beds of lime mudstone	21	381
	SC27	364		

26.	Covered	5	360
25.	Chert, black, irregularly bedded, with argillaceous seams and nodules and thin beds of lime mudstone	38	355
	SC26	345	
	SC25	336	

CORRIGANVILLE LIMESTONE

24.	Argillaceous skeletal packstone with nodules and irregular beds of white or grey chert; brachiopods, bryozoans	12	317
	SC24	311	
23.	Skeletal packstone with nodules and irregular beds of white or grey chert; brachiopods, bryozoans, rugose corals	12	305
	SC38	302	
	SC23	294	

NEW CREEK LIMESTONE

22.	Crinoid-skeletal grainstone, light grey, massive, fining up; crinoids, brachiopods, bryozoans	28.5	293
	SC22	291	
	SC21	283	
	SC20	277	
	SC19, SC35	268	
21.	Coarse crinoidal grainstone, pinkish light grey, massive; crinoids, brachiopods, bryozoans	11	264.5
	SC18, SC36	261	
	SC17, SC37	255	

KEYSER FORMATION

UPPER LIMESTONE MEMBER

20.	Lime mudstone with irregular fenestrae; ostracods	.3	253.5
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19.	Lime mudstone, finely laminated, with ripple cross lamination at the base	4.7	253.2
	SC16 253		
18.	Skeletal fragment grainstone with minor quartz sand, cross bedded, fining up at the top; brachiopods, crinoids, bryozoans; at 240' is an erosional surface with 6" of relief on which rests a 9" boulder of the same material, irregular in shape	21.5	248.5
	SC15 242		
17.	Skeletal-intraclast grainstone, fining up to pelletal(?) lime mudstone or wackestone; at base, crinoids, bryozoans, brachiopods	4	227
	SC14 224		
16.	Pelletal(?) lime mudstone or wackestone	7.5	223
15.	Interbedded shale and skeletal packstone, thin-bedded	3	215.5
14.	Skeletal grainstone or packstone; crinoids, brachiopods, bryozoans	1.5	212.5
13.	Pelletal(?) lime mudstone or wackestone	26	211
	SC13 209		
	SC12 193		
12.	Skeletal packstone and wackestone; brachiopods, crinoids	8	185
11.	Argillaceous lime mudstone, pelletal(?), nodular bedded; few brachiopods	66.5	177
	SC11 175		
	SC10 157		
	SC9 141		
	SC8 123		
10.	Skeletal packstone, massive; crinoids, brachiopods	4.5	110.5

9.	Coarse crinoidal grainstone, massive; crinoids, brachiopods	11	106
BIG MOUNTAIN SHALE MEMBER			
8.	Covered	5	95
7.	Skeletal packstone interbedded with shale; crinoids, brachiopods	6	90
	SC6, 86 SC34		
6.	Shale, grey; few brachiopods	24	84
LOWER LIMESTONE MEMBER			
5.	Skeletal packstone; brachiopods, crinoids	1	60
	SC5 59		
4.	Crinoidal grainstone, fining up; crinoids, brachiopods	8	59
3.	Argillaceous skeletal wackestone, nodular bedded; brachiopods, ostracods	22.5	50
	SC4 48 SC3 36		
2.	Skeletal wackestone, massive; crinoids, brachiopods, bryozoans	10	28.5
1.	Skeletal packstone, thick bedded; brachiopods, crinoids, bryozoans	18.5	18.5

APPENDIX B

Table A1. Abundance data for Strait Creek section. Where two samples were taken from the same level, both sample numbers are given at the top of the table and the total numbers of conodonts from both samples are given in the table.

SPECIES / SAMPLES	SC1	SC2	SC3	SC4	SC5	SC6	SC7	SC8	SC9	SC10	SC11	SC12	SC13	SC14	SC15	SC16	SC17	SC18	SC19	SC20	SC21	SC22	SC23	SC38	SC24	SC25	SC26	SC27	SC28	SC29	SC30	SC31	SC32		
	+33			+34													+37			+36	+35														
OZARKODINA	Pa	81	13	27	161	8						2	184	32	68	9	132	139	8		2		6	76	28								2		
REMSCHIEDENSIS	Pb	34	6	11	92	1						2	117	9	52	5	13	15	2				3	41	16										
	M	11	2	9	50								76	4	37	3	1	2	1				1	20	2							2			
	Sa	1		4	19							1	38		15	3	2		1				1	14									1		
	Sb	1	6		11	35						1	75	1	24	2	2	1					1	18	8								1		
	Sc	1	28	1	14	33	3					1	92	3	24	3	2	7					1	31	7										
O. EXCAVATA	Pa																					2		7	3										
EXCAVATA	Pb																					5		1											
	M																				1	5			3										
	Sa																					1	1		1	1									
	Sb																					1	4		1	3									
	Sc																					3	4	1	2	2									
DELOTAXIS	Pa	6	3	2	37								2																						
ELEGANS	Pb	1	8	2	1	23																													
	M	7	3	11	36																														
	Sa	8	1	2	21																														
	Sb	8		1	24																														
	Sc	31	7	14	89																														
	Sd	5	2	3	13																														
DELOTAXIS	Pa														1		27	1				2			2										
EXCAVATA	Pb												1				17				1				1										
CRISTAGALLI	M																6								2										
	Sa												1				19								4										
	Sb												2				8						1		2	1									
	Sc																32				1	7	1		3										
DELOTAXIS	Pa																																		
N. SP.	Pb																																		
	M																																		
	Sa																																		
	Sb																																		
	Sc																																		
ICRIODUS	I														1		41	44	71						7										
HELDERBERGENSIS	S2														1		22	12	54						3										
I. LATERICRESCENS																																			
ROBUSTUS																																			

Table A1, continued.

SPECIES / SAMPLES	SC1	SC2	SC3	SC4	SC5	SC6	SC7	SC8	SC9	SC10	SC11	SC12	SC13	SC14	SC15	SC16	SC17	SC18	SC19	SC20	SC21	SC22	SC23	SC38	SC24	SC25	SC26	SC27	SC28	SC29	SC30	SC31	SC32				
	+33			+34									+37			+36			+35																		
PSEUDONEOTODUS BECKMANNI														1			43	47	67	172	36	218	74	33	11	1		2		6							
ROTUNDACODINA NOGUERENSIS																																					
LENTICULAR														2	3		17	7	49							5				22	13						
TRIANGULAR																										1				1	2						
PLANOCONVEX														1	1		1													1	1						
BICOSTATE															2		2	5	12							2			2	3							
TRICOSTATE															1		5	5	19											3	1						
QUADRICOSTATE																	3	3	2											2	2						
R. DENTATA SMOOTH																	4	4	7																		
COSTATE														1			4	6	17																		
ACODINA ARAGONICA																	3	3	5																		
A. CURVATA																	7	10	39							4			1		3						
ACODUS SP.														1			8	15	35												2	3					
BELODELLA DEVONICA																			4											7	8	3	2				
B. RESIMA		3				3									1	2		1	20							1	3	1	22	53	21	8					
B. TRIANGULARIS															1				30								3	1	5	30	3	2					
COELOCERODONTUS BICONVEXUS							2										22	6	45		2						2			7	11	3					
C. REDUNCTUS																	4	1	14														2				
C. SP.																	13		2														1				
HAPLOBELODELLA SP.																		1	8								2		5	24	2						
PLECTOSPATHODUS SP.																																					
LIGONODINA SP.																																					
GEN. INDET. SP. A																				12																	
GEN. INDET. SP. B																																					
GEN. INDET. SP. C																			2	2							2	3		2	41	2					
GEN. INDET. SP. D																											1	1									
TOTAL	3	238	0	40	110	638	12	0	0	0	0	7	587	55	232	27	460	337	533	180	70	221	99	258	100	15	2	46	208	126	18	0	0				
SAMPLE WEIGHT (KG.)	4.8	9.5	5.5	5.7	5.1	12	4.9	7.9	7.0	5.3	5.6	3.5	7.8	6.1	7.2	5.9	15.9	8.8	10.2	4.8	5.0	5.3	4.6	6.0	5.0	4.0	4.1	5.7	6.5	4.9	6.5	4.9	5.1				
WEIGHT DISSOLVED	3.3	8.9	1.1	3.4	2.2	9.2	4.4	1.6	1.8	2.6	1.3	2.4	7.8	5.1	6.8	5.9	15.9	8.8	9.9	4.8	5.0	5.3	4.6	4.3	3.6	1.4	.5	3.0	2.8	2.7	3.4	.9	2.3				
COMODONTS/KG. DISSOLVED	1	27	0	12	50	69	3	0	0	0	0	3	75	11	34	5	29	38	54	37	14	42	22	60	28	11	4	15	74	47	5	0	0				
FEET ABOVE BASE OF SECTION	1	18	36	48	59	86	106	123	141	157	175	193	209	224	242	253	255	261	268	277	283	291	294	302	311	336	345	364	386	393	408	418	426				

Table A2. Abundance data for the Price's Bluff section. Where two samples were taken from the same level, both sample numbers are given at the top of the table and the total numbers of conodonts from both samples are given in the table.

SPECIES / SAMPLES	PB29 +30	PB28	PB27	PB26	PB31	PB25	PB24	PB23	PB22	PB21	PB20 +32	PB19	PB18	PB17 +33	PB16	PB15	PB14	PB13	PB12	PB11	PB10	PB9	PB8	PB7	PB6	PB5	PB4	PB3	PB2	PB1	PB34	TOTAL (PB+SC)
OZARKODINA REMSCHIEDENSIS	Pa	5			20				188	42	186			3	12	2							1		1	12	8		3		1461	
	Pb	2			2				111	17	61	1		1	3										1		2			620		
	M	1							80	5	9				3						1		1		2	2	1			325		
	Sa								31	2	7																1			141		
	Sb	1			1				82	2	5					2										3	1			284		
	Sc	2							89	4	7				3										1	3				362		
O. EXCAVATA EXCAVATA	Pa													15	8	1							2								38	
	Pb													9	6						3		2								26	
	M													23	2							2									37	
	Sa													2								1		1							8	
	Sb													22	6							2	3								42	
	Sc													20	6							1	1								40	
DELOTAXIS ELEGANS	Pa								3																						53	
	Pb								1																						36	
	M	1							2																						60	
	Sa								2																						34	
	Sb	1																													34	
	Sc	2							2																						145	
	Sd								1																						24	
D. EXCAVATA CRISTAGALLI	Pa									1				2																	36	
	Pb								1					1																	22	
	M													1																	9	
	Sa													4																	28	
	Sb													2																	15	
	Sc							1						4	1																50	
DELOTAXIS N. SP.	Pa									1	5																				7	
	Pb									1	4																				5	
	M									1	2																				3	
	Sa									3	7																				9	
	Sb									8	17																				25	
	Sc									4	9																				13	
ICRIODUS HELDERBERGENSIS	I											2			1						5	2	18	14	123	227	589	284	20	58	1559	
	S ₂											1									2	2	7	9	37	70	215	157		7	604	
I. LATERICRESCENS ROBUSTUS																															51	51

Table A2, continued.

SPECIES / SAMPLES	PB29	PB28	PB27	PB26	PB31	PB25	PB24	PB23	PB22	PB21	PB20	PB19	PB18	PB17	PB16	PB15	PB14	PB13	PB12	PB11	PB10	PB9	PB8	PB7	PB6	PB5	PB4	PB3	PB2	PB1	PB34	TOTAL (PB+SC)	
	+30										+32			+33																			
PSEUDOOMEOTODUS BECKMANNI									6			1		43	118		6	4				6	4	45	21	12	24	135	80			1216	
ROTUNDACODINA NOCUERENSIS																																	
LENTICULAR													1								11	7	41	237	468	485	126	81	4	3		1582	
TRIANGULAR																					3	2	6	28	68	38	12	8				176	
PLANOCONVEX																					1	2	4	23	50	53	14	1				153	
BICOSTATE																					2	4	10	95	202	151	23	12		3		530	
TRICOSTATE																					3	4	17	88	110	117	31	18				422	
QUADRICOSTATE																							2	6	26	18	12	5				81	
R. DENTATA SMOOTH																																18	
COSTATE																					1											31	
ACODINA ARAGONICA																									49	103	53	8	3				227
A. CURVATA												1									1	7	7	25	77	99	65	31	1				378
ACODUS SP.												1									2	5	6	31	37	77	17	22					262
BELODELLA DEVONICA																					1	1		29	9			2			1	67	
B. RESIMA													1				4				2		1	65	12	3	2	2			23	254	
B. TRIANGULARIS																					2		1	6	12		1	3			37	138	
COELOCERODONTUS BICONVEXUS													3		3		3				9	1	6	273	135	142	33	57	1				765
C. REDUNCTUS												1		1							2		2	26	10	7	5	8		2		85	
C. SP.													1												8	7	4		3			39	
HAPLOBELODELLA SP.																	3				3	1	2	17	9	3				15		95	
PLECTOSPATHODUS SP.											1																						1
GEN. INDET. SP. A																									2	11	28	28	11		1		93
GEN. INDET. SP. B																					2	2		16	24	39	8	2					93
GEN. INDET. SP. C										9		1									9	1	5	100	183	40		1					404
GEN. INDET. SP. D																							3		6	5	26						42
TOTAL	15	0	0	0	23	0	0	0	609	0	91	322	11	150	156	8	38	2	0	0	76	48	190	1175	1730	1717	1343	862	26	77	127	13,360	
SAMPLE WEIGHT (KG.)	10.1	3.4	3.3	4.0	4.0	2.4	3.6	3.2	8.6	5.4	11.9	6.6	5.5	13.4	9.5	6.1	6.4	4.6	8.5	4.4	4.3	4.8	5.8	6.2	4.0	4.0	6.0	5.1	6.2	2.7	4.7		
WEIGHT DISSOLVED	3.1	2.4	2.2	2.7	3.5	.2	.6	.7	7.0	4.7	10.9	6.6	5.5	13.4	9.5	6.1	3.9	4.1	7.2	2.8	3.9	2.8	5.8	6.2	3.9	4.0	6.0	5.1	2.4	2.7	2.1		
CONODONTS/KG. DISSOLVED	5	0	0	0	7	0	0	0	87	0	8	49	2	11	16	1	10	.5	0	0	19	17	33	189	444	429	224	169	11	28	60		
FEET ABOVE BASE OF SECTION	12	20	27	34	35	54	65	82	94	98	109	113	118	122	126	130	135	138	140	145	149	157	167	177	195	206	217	227	244	253	261		

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CONODONT BIOSTRATIGRAPHY AND PALEOECOLOGY

OF THE LOWER DEVONIAN HELDERBERG

GROUP OF VIRGINIA

by

Elizabeth G. Cook

(ABSTRACT)

The occurrences of species of Delotaxis and Icriodus and the Ozarkodina remscheidensis eosteinhornensis--Ozarkodina remscheidensis remscheidensis lineage indicate that (1) most of the Keyser Formation of western Virginia is assignable to the uppermost Silurian eosteinhornensis zone; (2) the top of the upper limestone member of the Keyser is assignable to the basal Devonian woschmidtii zone; (3) the remainder of the Helderberg Group is no younger than the delta zone; and (4) the basal Needmore Shale at the Price's Bluff section is assignable to the serotinus, patulus, or costatus costatus zones, of uppermost lower Devonian and lowermost Middle Devonian age, leaving a gap of at least six conodont zones represented by the Ridgeley Sandstone and its bounding unconformities.

Conodonts tend to avoid tidal flat and lagoonal environments. They are not uniformly distributed through the rest of the section, but the occurrence of all but two species is not related to water depth, energy, or substrate; Ozarkodina excavata and Pseudooneotodus

beckmanni prefer moderate energy environments. Icriodus helderbergensis and most of the simple cone species are associated with each other.

There were 13,360 specimens collected, divided among 10 biological species and 15 form species; of the biological species, 3 are new and 2 are newly reconstructed apparatuses.