

Silurian conodont biostratigraphy of the east-central Appalachian Basin (eastern USA): Re-examination of the C.T. Helfrich Collection

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The conodont biozonation for the Silurian succession in the Appalachian Basin was established by C.T. Helfrich nearly half a century ago. Herein, we re-examined and updated the taxonomy of the conodont fauna and the consequent biozonation of the upper Rose Hill, Mifflintown, Wills Creek, and lower Tonoloway formations in the east-central Appalachian Basin. While these strata span the upper Telychian Stage (Llandovery Series) to the upper Pridoli Series, a major stratigraphic gap representing most of the Ludlow Series (from the lower part of the Gorstian to the upper part of the Ludfordian stages) was identified. The new conodont biozonation consists of: the *Pterospathodus amorphognathoides amorphognathoides* Zonal Group, an Unzoned Interval of the Sheinwoodian Stage, the *Kockelella walliseri* Zonal Group, the *Ozarkodina bicornuta* Zone, an Unzoned Interval of the Homerian Stage, the *Ozarkodina bohémica* Interval Zone, the *Ozarkodina crispa* Zone, and the *Ozarkodina eosteinhornensis sensu lato* Interval Zone. This refined biozonation permits enhanced global correlation of the Silurian within the east-central Appalachian Basin. • Key words: Appalachian Basin, Wenlock, Ludlow, Pridoli, conodont biostratigraphy, global zonation, Helfrich collection.

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The largest and stratigraphically most comprehensive collection of conodonts from middle to upper Silurian (uppermost Llandovery–Pridoli series) strata in the Appalachian Basin was produced by Charles T. Helfrich during the 1970's. Most of the work was completed as part of his Ph.D. dissertation (Helfrich 1972) and published in a series of papers (Helfrich 1975, 1978, 1980) that laid the foundation for Silurian conodont biostratigraphy in the Appalachian Basin. In total, more than 15,000 specimens were recovered from six sections in the West Virginia, Virginia, and Maryland tri-state area, with which he established the conodont biozonation for the Silurian succession of the east-central Appalachian Mountains.

Helfrich's work was carried out at the dawn of a major transition in conodont systematics, from form taxonomy to multi-element taxonomy, and relied on the original Silurian conodont biozonation of Walliser (1964) to establish a biostratigraphic zonation for the Appalachian Basin consisting of eight zones for uppermost Llandovery through Pridoli strata. Most reported specimens were identified as form species, typically with tentative multi-

element species designations in open nomenclature. Silurian conodont taxonomy and biostratigraphy have advanced tremendously in the intervening decades (e.g., Barrick & Klapper 1976; Bischoff 1986; Aldridge & Schönlaub 1989; Kleffner 1989, 1995; Nowlan 1995; Jeppsson 1997; Männik 1998, 2007; Corradini & Serpagli 1999; Jeppsson & Aldridge 2000; Calner & Jeppsson 2003; Murphy *et al.* 2004; Jeppsson *et al.* 2006; Carls *et al.* 2007; Slavík 2014; Corradini *et al.* 2015; Männik *et al.* 2015; Mathieson *et al.* 2016; Waid & Cramer 2017a, b), however, no modern systematic revision to the conodont biozonation of the uppermost Llandovery to Pridoli interval of the east-central Appalachian Basin has been undertaken. Herein, we provide a modern and revised conodont biozonation for the central axis portion of the Appalachian Basin based upon the conodont collection of C.T. Helfrich (Helfrich 1972, 1975, 1980) that was re-examined by the authors at the University of Iowa from 2015–2018. The Helfrich collection is housed at the Museum of Geosciences at Virginia Tech (Virginia Polytechnic Institute and State University).

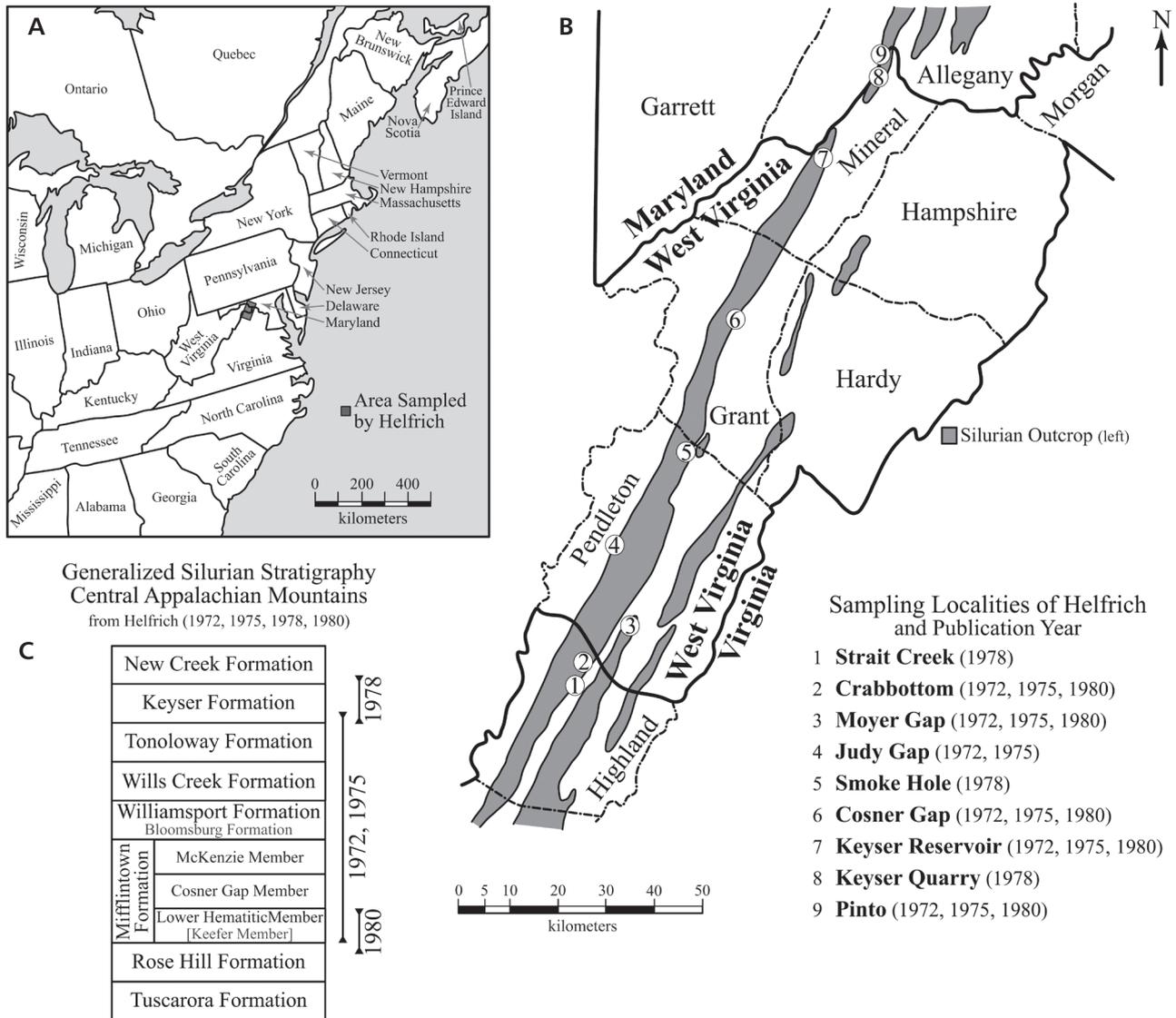


Figure 1. A – general map of eastern North America, the area Helfrich sampled (Virginia, West Virginia, and Maryland) is highlighted. • B – outcrop map of Silurian strata in the east-central Appalachian Basin showing localities included in the collection. • C – lithostratigraphic chart showing formations included in the investigation and the dates of publication for manuscripts associated with the collection (the 1972 publication is Helfrich’s dissertation document, which was published in 1975 as *Geological Society of America Special Paper 161*). Modified from Helfrich (1975).

Geologic Setting

The successive accretion of island arcs and continental fragments onto the eastern margin (present orientation) of the Laurentian paleocontinent from the Ordovician through Devonian provided sufficient flexural subsidence and the creation of accommodation space for extensive Silurian deposition along an area several thousand kilometers long, stretching from Nova Scotia in the north to North Carolina, South Carolina, Georgia, and Alabama in the south (e.g., Hibbard 2000, Ettensohn & Brett 2002, Van Staal *et al.* 2014, Pinet 2016). This series of collisional tectonic events, variably termed the Taconic,

Salinic, and Acadian orogenies (Goodman & Brett 1994, Ettensohn & Brett 2002, Cramer *et al.* 2011a, Van Staal *et al.* 2014), produced the Appalachian Foreland Basin that recorded nearly the entire Silurian succession (e.g., Horvath 1969, Berry & Boucot 1970, Goodman & Brett 1994, Brett *et al.* 1995, Sullivan *et al.* 2016). The area originally studied by Helfrich (1972) follows the Silurian outcrop belt (Fig. 1) where the states of West Virginia, Virginia, and Maryland converge. This narrow belt was likely on the highland-proximal side of the basin axis during the Silurian (Goodman & Brett 1994, Sullivan *et al.* 2016) and is much more clastic rich than the carbonate-dominated western margin of the basin.

European Conodont Zones (Walliser – 1964)	North American Conodont Zones (Nicoll & Rexroad – 1968) (Pollock, Rexroad, & Nicoll – 1970) (Helfrich – 1975)
<i>eosteinhornensis</i>	<i>Spathognathodus steinhornensis eosteinhornensis</i>
<i>crispus</i>	<i>Spathognathodus crispus</i>
<i>latialatus</i>	<i>Spathognathodus tillmani</i>
<i>siluricus</i> <div style="border-left: 1px solid black; border-right: 1px solid black; height: 10px; width: 10px; display: inline-block;"></div> <div style="display: inline-block; vertical-align: middle; margin-left: 5px;"> <i>snajdri</i> horizon </div> 	<i>Spathognathodus snajdri</i>
<i>ploeckensis</i>	Unzoned Interval
<i>crassa</i>	<i>Spathognathodus bicornutus</i>
<i>sagitta</i>	<i>Spathognathodus sagitta bohemicus</i>
<i>patula</i>	unreported
<i>amorphognathoides</i>	<i>Pterospathodus amorphognathoides - Spathognathodus ranuliformis</i> (1968)
<i>celloni</i>	<i>Neospathognathodus celloni</i> (1968)
Bereich I	<i>Icriodina irregularis</i> (1968)
	<i>Panderodus simplex</i> (1970)

Figure 2. Comparison of European (Walliser 1964) and North American conodont biozones used by Helfrich (1975). Figure modified from Helfrich (1975).

Silurian Conodont Biozonation

Walliser (1964) produced the first recognizably modern conodont biozonation scheme for the Silurian System based primarily upon sections in the Carnic Alps region of Central Europe. The two decades that followed Walliser’s original work transformed our understanding of conodont paleobiology, and as a result, also transformed the practice of conodont biostratigraphy (e.g., Sweet & Bergström 1970, Aldridge & von Bitter 2009). The transition from form taxonomy to multi-element taxonomy had already begun by the time of Helfrich’s doctoral work in the early 1970’s, and some of the earliest efforts towards erecting a North American Conodont Zonation had recently been completed (Nicoll & Rexroad 1968, Pollock

Series	Stage	Cramer et al. (2011b)	Corradini et al. (2015) Cellon	McAdams et al. (2019)	This Study Appalachian Basin
Pridoli		<i>Ou. elegans detortus</i>	Upper <i>Ou. el. detortus</i>	<i>Ou. elegans detortus</i>	
			Lower <i>Ou. el. detortus</i>		
Ludlow	Ludfordian	<i>Oz. eostein-hornensis s.l.</i> Interval Zone	<i>Oz. eostein-hornensis s.l.</i> Interval Zone	<i>Oz. eostein-hornensis s.l.</i> Interval Zone	<i>Oz. eostein-hornensis s.l.</i> Interval Zone
		<i>Oz. crispus</i>	<i>Oz. crispus</i>	<i>Oz. crispus</i>	<i>Oz. crispus</i>
		<i>Oz. snajdri</i> Interval Zone	<i>Oz. snajdri/ Ped. latialata</i> Interval Zone	<i>Oz. snajdri/ Ped. latialata</i> Interval Zone	
	Gorstian	<i>Po. siluricus</i>	<i>Po. siluricus</i>	<i>Po. siluricus</i>	
		<i>A. ploeckensis</i>	<i>A. ploeckensis</i>	<i>A. ploeckensis</i>	
		<i>K. variabilis</i> Interval Zone	<i>K. variabilis</i> Interval Zone	<i>K. variabilis</i> Interval Zone	
Wenlock	Homerian	<i>K. crassa</i>	<i>K. crassa</i>	<i>K. crassa</i>	
		<i>K. ortus absidata</i>		<i>K. ortus absidata</i>	<i>Oz. bohemia</i> Interval Zone
		<i>Oz. bohemia longa</i>		<i>Oz. bohemia longa</i>	
	Sheinwoodian	<i>Oz. sagitta sagitta</i>	<i>Oz. sagitta sagitta</i>	<i>Oz. sagitta sagitta</i>	Unzoned Interval
		<i>K. ortus ortus</i>	<i>K. ortus ortus</i>	<i>K. amsdeni/ K. walliseri</i> Superzone	<i>Oz. bicornuta</i> <i>K. walliseri</i> Zonal Group
		<i>K. walliseri</i>	<i>K. patula</i>		
Tely.	<i>Oz. s. rhenana</i>		<i>Oz. s. rhenana</i>		
	<i>K. ranuliformis</i> Superzone		<i>K. ranuliformis</i> Superzone	Unzoned Interval	
Lland.		<i>Pt. p. pro. S.Z.</i>	<i>Pt. p. pro. S.Z.</i>		
		<i>Pt. am. amorph.</i> Zonal Group	<i>Pt. am. amorph.</i> Zonal Group	<i>Pt. am. amorph.</i> Zonal Group	

Figure 3. Comparison of conodont biozonations used by Cramer et al. (2011b), Corradini et al. (2015), McAdams et al. (2019), and this study. Cramer et al. (2011b) and McAdams et al. (2019) were intended to be global biostratigraphic charts. Corradini et al. (2015) shows the biozonation they developed for the classical Cellon Section in the Carnic Alps. The grey areas denote missing stratigraphic section and we followed this in our column at the far right. Where section is clearly missing, we have a gray area. Where strata exist but are devoid of biostratigraphically important specimens, we refer to it as an Unzoned Interval. Abbreviations: Lland. – Llandovery; Tely. – Telychian; A. – *Ancyrodella*; am. or amorph. – *amorphognathoides*; el. – *elegans*; K. – *Kockelella*; o. – *ortus*; Ou. – *Oulodus*; Oz. – *Ozarkodina*; p. – *pennatus*; P. – *Polygnathoides*; Ped. – *Pedavis*; pro. – *procerus*; Pt. – *Pterospathodus*; s. – *sagitta*; s.l. – *sensu lato*; I.Z. – Interval Zone; S.Z. – Superzone.

et al. 1970). Helfrich (1972) added to these studies and erected a new suite of conodont biozones for the upper Llandovery, Wenlock, Ludlow, and Pridoli series of North America (Fig. 2). Since that time, considerable progress has been made integrating global advances in conodont biostratigraphy into Silurian chronostratigraphy of North America (see discussion in Cramer et al. 2011b). With the exception of a handful of studies (e.g., Denkler & Harris 1988a, b; Kleffner et al. 2009) however, most

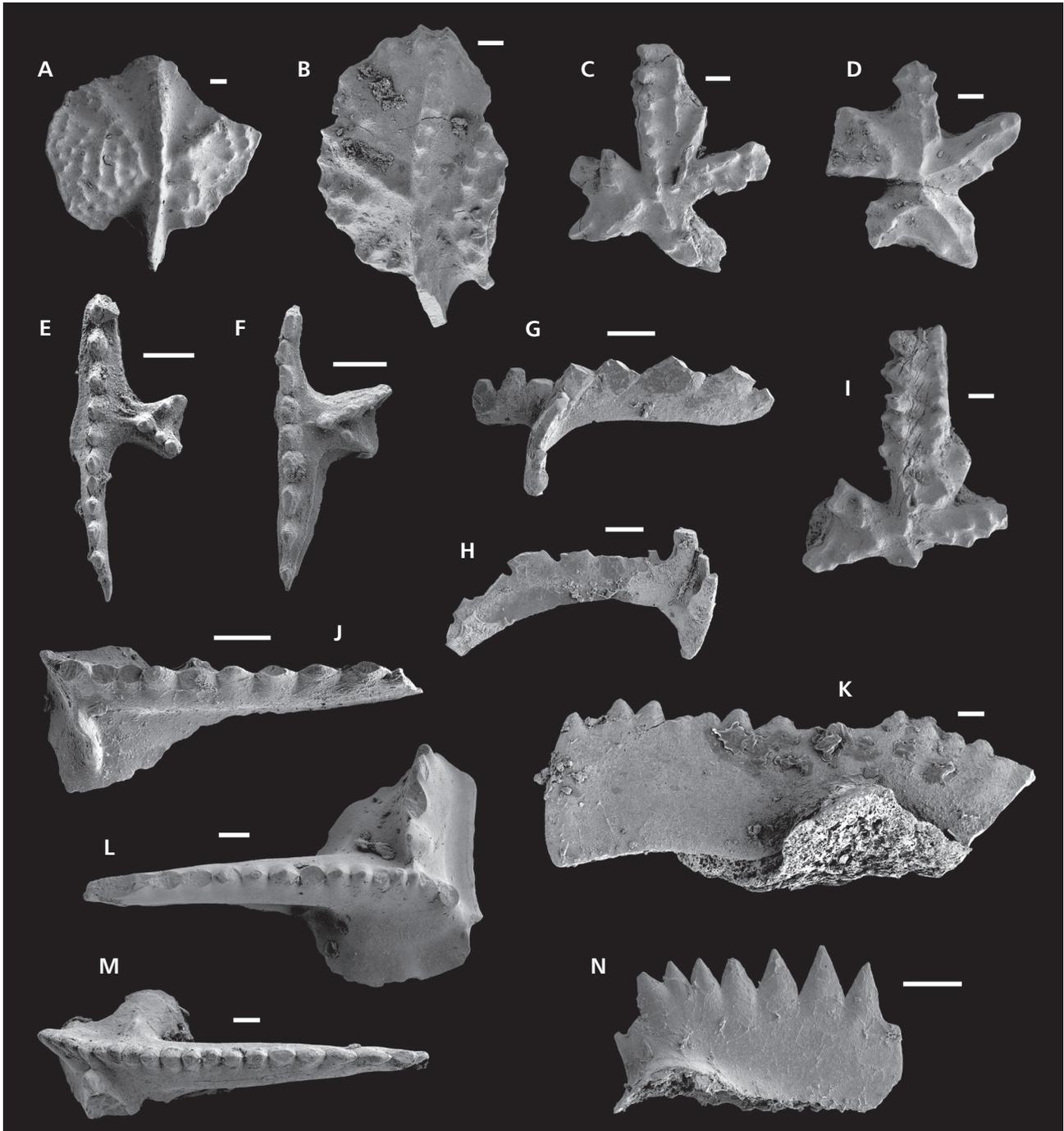


Figure 4. A, B – *Apsidognathodus tuberculatus* Walliser, 1964; A – Cosner Cap Section, Rose Hill Formation (CG-RH1) [VPIL 3706] (Helfrich 1980, pl. 1, fig. 29); B – Cosner Cap Section, Rose Hill Formation (CG-RH1) [VPIL 3754]. • C, D, I – *Distomodus staurognathoides* (Walliser, 1964); C – Pinto Section, Rose Hill Formation (P-RH5) [VPIL 3698] (Helfrich 1980, pl. 1, fig. 22); D – Pinto Section, Rose Hill Formation (P-RH5) [VPIL 4764]; I – Pinto Section, Rose Hill Formation (P-RH5) [VPIL 4764]. • E, F – *Pterospathodus amorphognathoides amorphognathoides* Walliser, 1964; E – Keyser Reservoir Section, Rose Hill Formation (KR-RH4) [VPIL 3722] (Helfrich 1980, pl. 2, fig. 18); F – Keyser Reservoir Section, Rose Hill Formation (KR-RH3) [VPIL 4756]. • G, H – *Pseudolonchodina fluegeli fluegeli* (Walliser, 1964); G – Keyser Reservoir Section, Rose Hill Formation (KR-RH4) [VPIL 3691] (Helfrich 1980, pl. 1, fig. 11); H – Keyser Reservoir Section, Rose Hill Formation (KR-RH6) [VPIL 3689] (Helfrich 1980, pl. 1, fig. 9). • J – *Kockelella ?ranuliformis* (Walliser, 1964), Pinto Section, Rose Hill Formation (P-RH1) [VPIL 3722] (Helfrich 1980, pl. 2, figs 15, 16). • *Ozarkodina gulletensis* (Aldridge, 1972), Moyer Gap Section, Lower Hematitic Member, Mifflintown Formation (MG-LMH1) [VPIL 3753]. • L–N – *Kockelella walliseri* (Helfrich, 1975); L – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG6) [VPIL 1222] holotype (Helfrich 1975, pl. 1, fig. 21); M – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG5) [VPIL 1221] paratype (Helfrich 1975, pl. 1, fig. 19); N – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG1) [VPIL 1218] paratype (Helfrich 1975, pl. 1, fig. 1). Scale bars = 100 microns.

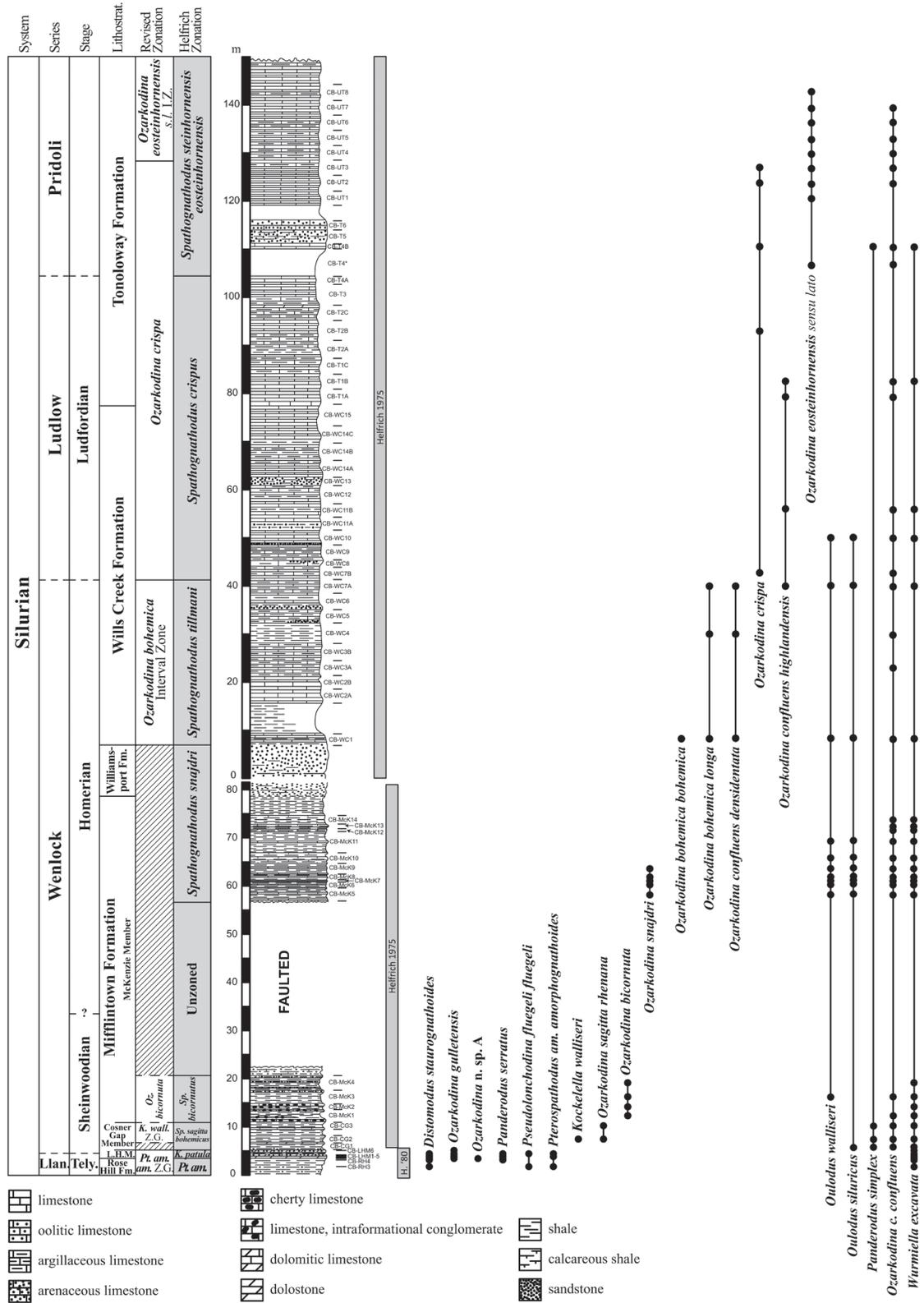


Figure 5. Stratigraphic column for the Crabbottom Section, Highland County, Virginia, combined from Helfrich (1980) and Helfrich (1975). The original biozonations of Helfrich are shown against the new biozonation designations made herein. Lithologic key at the bottom of this figure applies to all other lithologic columns in the manuscript. Diagonal hatching in the biozone column indicates an unzoned interval because of a lack of diagnostic fauna. Abbreviations: Llan. – Llandovery; Tely. – Telychian; Fm. – Formation; L.H.M. – Lower Hematitic Member; am. – *amorphognathoides*; K. – *Kockellella*; Oz. – *Ozarkodina*; Pt. – *Pterospathodus*; s.l. – *sensu lato*; Sp. – *Spathognathodus*; wall. – *walliseri*; I.Z. – Interval Zone; Z.G. – Zonal Group.

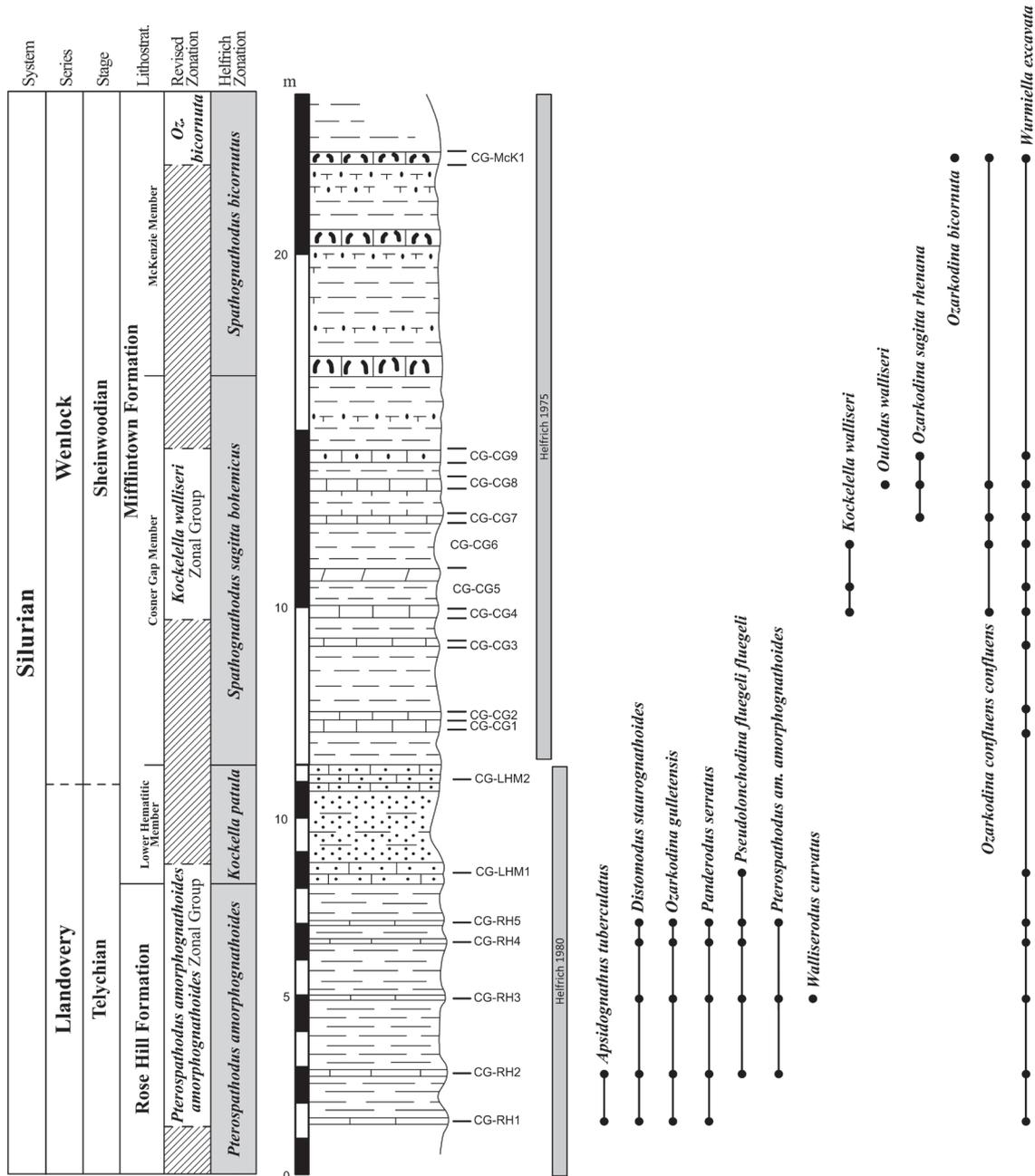


Figure 6. Stratigraphic column for the Cosner Gap Section, Grant County, West Virginia, combined from Helfrich (1980) and Helfrich (1975). The original biozonations of Helfrich are shown against the new biozonation designations made herein. Lithologic key can be found in the caption to Fig. 5. Diagonal hatching in the biozone column indicates an unzoned interval because of a lack of diagnostic fauna. Abbreviation: *Oz.* – *Ozarkodina*.

of the conodont work in North America in the past 50 years has been either limited to the western margin of the Appalachian Basin or outside of the Appalachian Basin altogether. As a result, the placement of modern global Silurian conodont biozones within the strata of the Appalachian Basin remains unclear.

Conodont biozonations established during the past decade advanced our ability to correlate sections globally

(e.g., Cramer *et al.* 2011b), as well as improved our understanding of some of the historically most important Silurian conodont collections (Corradini *et al.* 2015). Here, we attempt to apply global Silurian conodont biozones (Cramer *et al.* 2011b, Corradini *et al.* 2015, McAdams *et al.* 2019) to the C.T. Helfrich collection from the Appalachian Basin succession (Fig. 3). We provide new and updated occurrence range charts for each outcrop

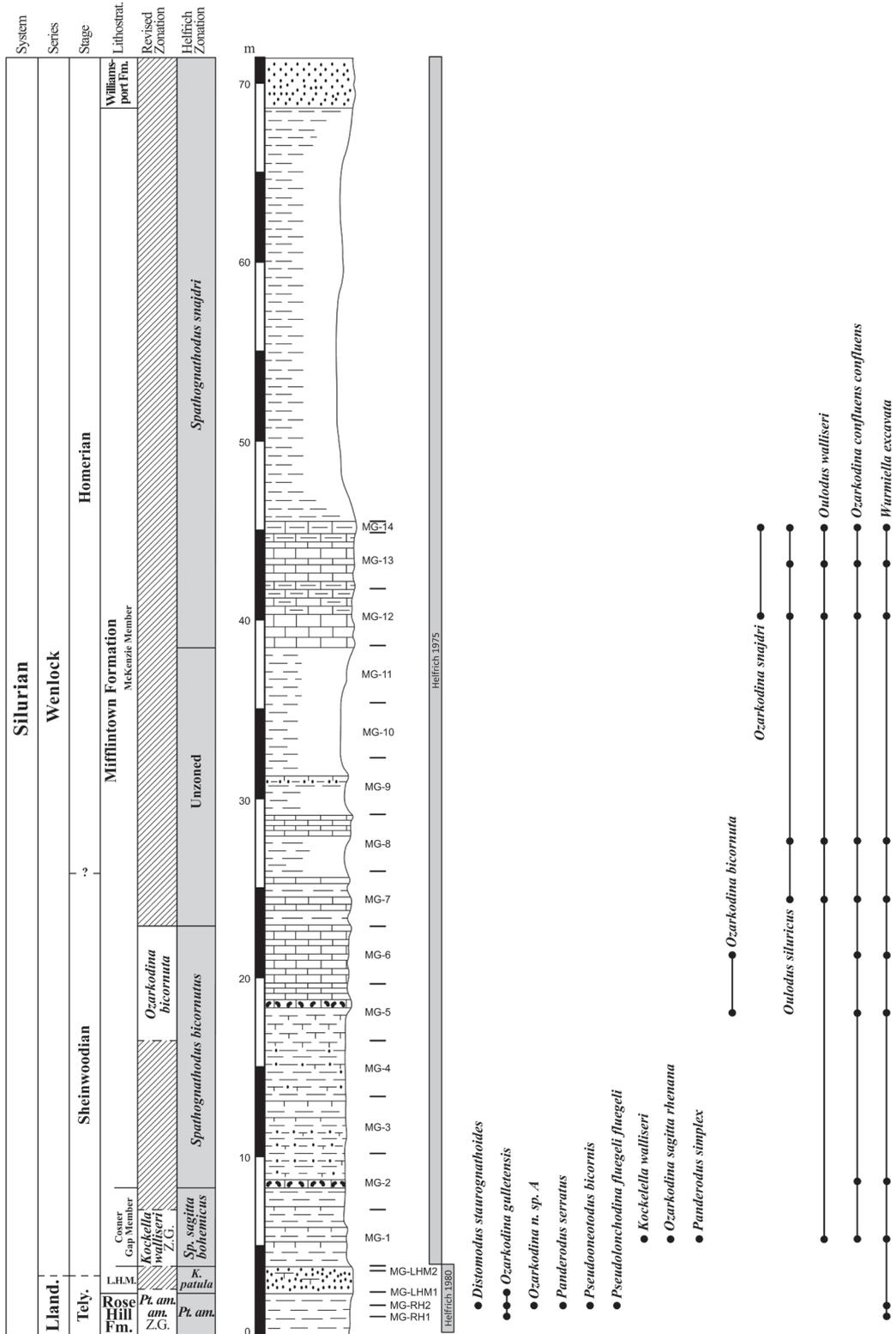


Figure 7. Stratigraphic column for the Moyer Gap Section, Pendleton County, West Virginia, combined from Helfrich (1980) and Helfrich (1975). The original biozonations of Helfrich are shown against the new biozonation designations made herein. Lithologic key can be found in the caption to Fig. 5. Diagonal hatching in the biozone column indicates an unzoned interval because of a lack of diagnostic fauna. Abbreviations: Lland. – Llandover; Tely. – Telychian; Fm. – Formation; L.H.M. – Lower Hematitic Member; am. – *amorphognathoides*; K. – *Kockella*; Pt. – *Pterospathodus*; Sp. – *Spathognathodus*; Z.G. – Zonal Group.

studied, and we re-illustrated a number of specimens included in Helfrich (1972, 1975, 1980) in addition to new images of material not previously illustrated from the collection. The result is an improved global correlation that considerably alters the chronostratigraphic position of strata within the Appalachian Basin.

Pterospathodus amorphognathoides *amorphognathoides* Zonal Group (Jeppsson 1997)

The *Pterospathodus amorphognathoides amorphognathoides* Zonal Group consists of a series of zones as originally defined by Jeppsson (1997) that are effectively the taxon-range zone for *Pt. am. amorphognathoides*. This zonal group occurs throughout the studied sections in the uppermost part of the Rose Hill Formation and extends through most, if not all, of the Lower Hematitic Member (LHM) of the Mifflintown Formation. The *Pt. am. amorphognathoides* Zonal Group in the study area contains the eponymous species, *Distomodus staurogathoides*, *Ozarkodina gulletensis*, *Pseudolonchodina fluegeli fluegeli*, and *Apsidognathus tuberculatus* (Fig. 4). The upper boundary of the zone should be placed no higher than the top of the LHM of the Mifflintown Formation.

Helfrich (1975, 1980) correlated the LHM with the *Kockelella patula* conodont Biozone of Walliser (1964) not based on the presence of *K. patula*, but because this interval was, in part, above the disappearance of *Pt. am. amorphognathoides* and below what he identified as *Ozarkodina sagitta bohémica* in the overlying Cosner Gap Member of the Mifflintown Formation. *Pt. am. amorphognathoides* disappears in all sections below the top of the LHM. The highest occurrence is in the second to highest sample in the Crabbottom locality (Fig. 5). However, because many sections did not include continuous sampling through the LHM or had very poor conodont yields owing to the clastic-rich nature of the strata, it is difficult to determine the precise position.

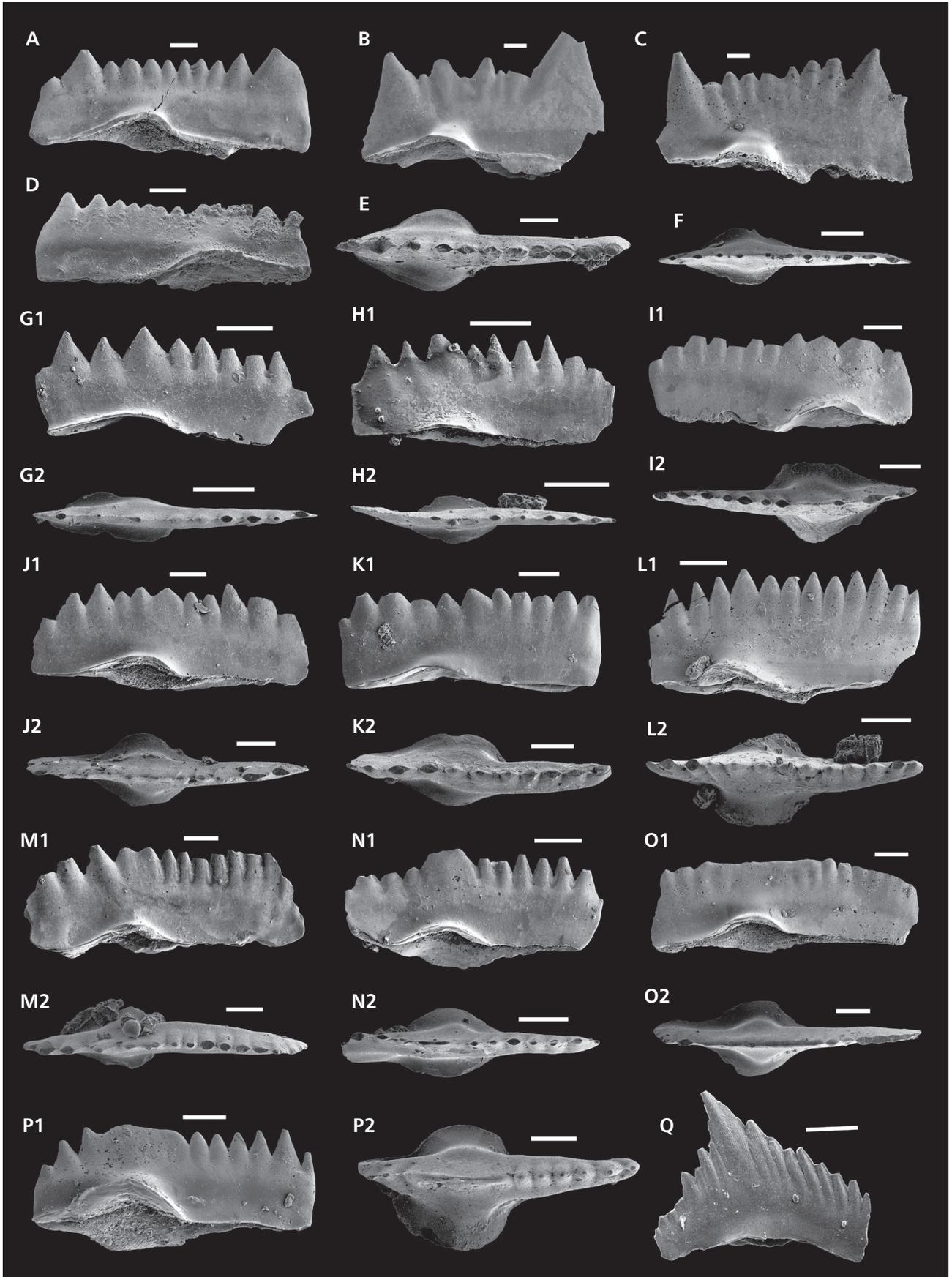
Unzoned Interval of the Sheinwoodian Stage

From the disappearance of *Pt. am. amorphognathoides* to the first appearance of *Kockelella walliseri* there are no zonally diagnostic conodonts in the studied collection utilizing current biozonal schemes. The typical globally recognized zonal indicators (Fig. 3) *Pterospathodus pennatus procerus* and *Kockelella ranuliformis* were not recovered, and although *Ozarkodina sagitta rhenana* does occur in the collection, its first occurrence is either stratigraphically above or coeval with the first occurrence of *K. walliseri* in all sections where they co-occur (Crabbottom – Fig. 5, Cosner Gap – Fig. 6, Moyer Gap – Fig. 7). Based upon the disappearance of *Distomodus staurogathoides* it is most likely that this interval belongs to the Upper *K. ranuliformis* Zone and the *Oz. s. rhenana* Zone of Jeppsson (1997). However, because of the lack of the diagnostic taxa we have chosen to designate this as an Unzoned Interval. This interval spans the uppermost Lower Hematitic Member to the lowermost Cosner Gap Member of the Mifflintown Formation.

Kockelella walliseri Zonal Group (modified from Jeppsson 1997)

The taxon-range zone for *Kockelella walliseri* was defined as the *K. walliseri* Zonal Group (Jeppsson 1997) to include four zones based upon the overlap and disappearance of *Oz. sagitta rhenana* and *K. patula* within the range of *K. walliseri*. This zonal group occurs throughout the remainder of the Cosner Gap Member of the Mifflintown Formation. The lower boundary of the zone is placed at the base of the first appearance of *K. walliseri* (see Cramer *et al.* 2010) and the upper boundary is placed at the last appearance of *Oz. s. rhenana*. Strictly speaking, this is the definition of the Lower *K. walliseri* Zone of Jeppsson (1997). However, under Jeppsson's original range definitions, *Oz. s. rhenana* should appear before *K. walliseri* and disappear before the last appearance datum (LAD)

Figure 8. A–C – *Ozarkodina bicornuta* (Helfrich, 1975); A – Crabbottom Section, McKenzie Member, Mifflintown Formation (CB-McK3) [VPIL 1117] holotype (Helfrich 1975, pl. 1, fig. 11); B – Cosner Gap Section, McKenzie Member, Mifflintown Formation (CG-McK1) [VPIL 1119] paratype (Helfrich 1975, pl. 1, fig. 14); C – Keyser Reservoir Section, McKenzie Member, Mifflintown Formation (KR-McK5) [VPIL 1120] paratype (Helfrich 1975, pl. 1, fig. 15). • D–Q – *Ozarkodina sagitta rhenana* (Walliser, 1964); D – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362FF]; E – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362]; F – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362FF]; G – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG2) [VPIL 1357]; H – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG2) [VPIL 1357]; I – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362]; J – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362]; K – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362]; L – Moyer Gap Section, Cosner Gap Member, Mifflintown Formation (MG-CG5) [VPIL 1340]; M – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG2) [VPIL 1357]; N – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG2) [VPIL 1357]; O – Cosner Gap Section, Cosner Gap Member, Mifflintown Formation (CG-CG7) [VPIL 1362]; P – Moyer Gap Section, Cosner Gap Member, Mifflintown Formation (MG-CG5) [VPIL 1177] (Helfrich 1975, pl. 1, fig. 3); Q – Crabbottom Section, Cosner Gap Member, Mifflintown Formation (CB-CG2) [VPIL 987] (Helfrich 1975, pl. 4, fig. 1). Scale bars = 100 microns.



of *K. walliseri*. Neither of these two orders of events are true in the studied sections, and the range of *Oz. s. rhenana* extends above *K. walliseri* in several sections. We therefore consider this a likely upwards range extension of *Oz. s. rhenana* and mark the top of this Zonal Group at the highest occurrence of either *K. walliseri* or *Oz. s. rhenana* (*Oz. s. rhenana* in the studied sections).

Jeppsson (1997), based on the published photographs in Helfrich (1975), clearly identified that the specimens Helfrich (1975) referred to as *Spathognathodus sagitta bohemicus* were not the same species as Walliser's (1964) *Sp. s. bohemicus*. Jeppsson (1997, p. 101) also pointed out that specimens closely similar to those illustrated as *Sp. s. bohemicus* by Helfrich (1975) occur on Gotland, Sweden, within the *Oz. sagitta rhenana* Biozone, that Aldridge (1985) illustrated a similar early Sheinwoodian subspecies from the United Kingdom, and that due to the co-occurrence with *K. walliseri* in his sections, Helfrich's (1975) specimens do not indicate a placement within the Homeric Stage. We agree with Jeppsson (1997) that the zone identified by Helfrich (1975) as *Sp. sagitta bohemicus* should instead be referred to the *K. walliseri* Zonal Group.

The taxonomic definitions of Walliser's (1964) original subspecies of *Spathognathodus sagitta* leave much to be desired. Originally designated as *Spathognathodus sagitta rhenanus*, *Spathognathodus sagitta sagitta*, and *Spathognathodus sagitta bohemicus*, they have since all been placed within the genus *Ozarkodina* (see Aldridge 1975), however, their diagnoses remain imprecise and overlap to a great extent. As the name implies, one of the major diagnostic features is an arrow-shaped outline in oral view. Walliser (1964, p. 83) originally stated that *Oz. s. rhenana* usually contained 9 to 16 denticles, *Oz. s. sagitta* contained 15 to 22 denticles, and that *Oz. s. bohemicus* was "approximately between the two others, as far as development of the denticles is concerned. The blade is relatively high in relation to the length." Jeppsson in Calner & Jeppsson (2003) elevated *bohemicus* to a species designation and erected a new subspecies, *Ozarkodina bohemicus longa*, which could be differentiated from *Ozarkodina bohemicus bohemicus* based on its overall blade length to blade height ratio.

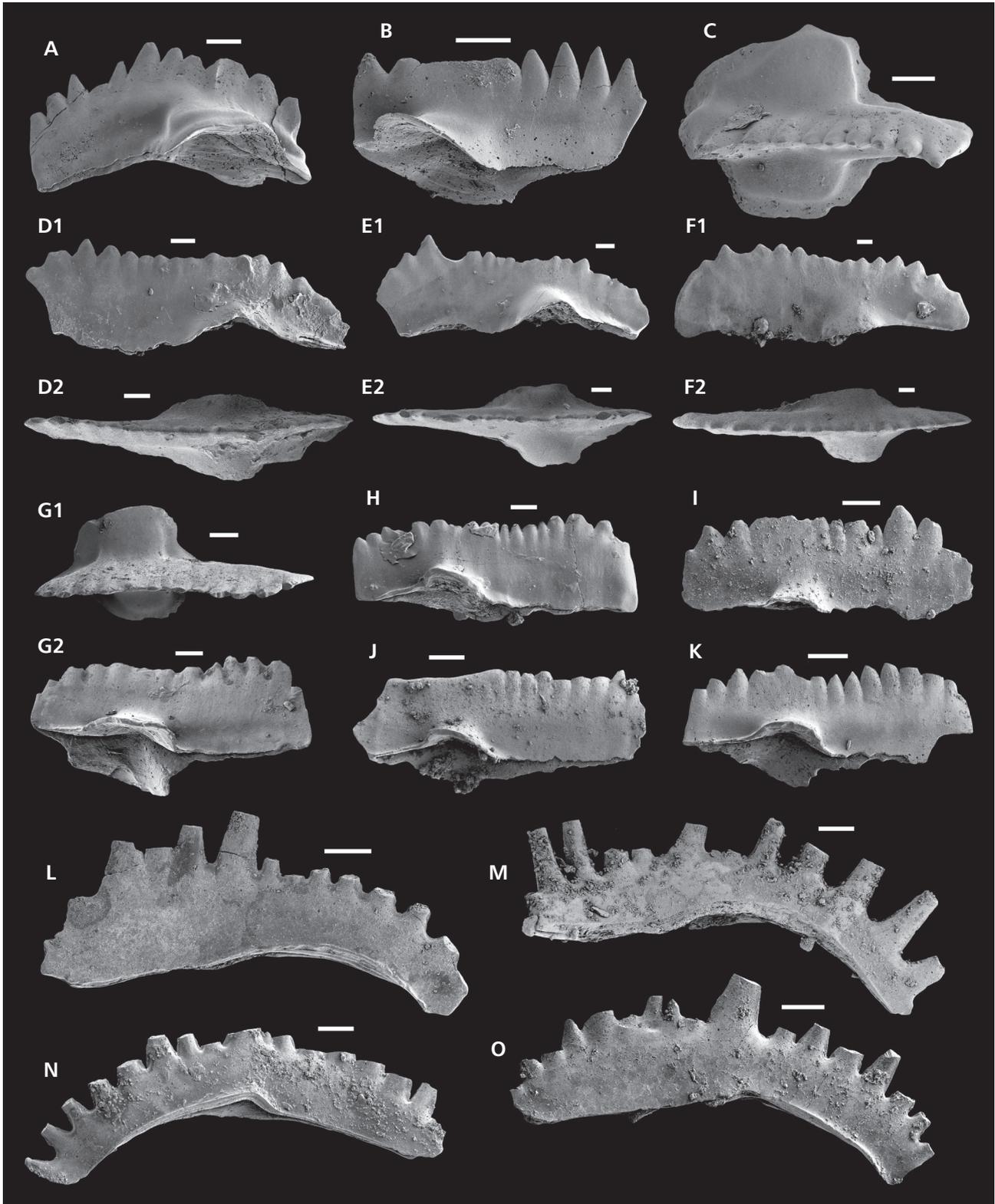
Several samples in the studied collection contain abundant specimens originally referred to as *Sp. sagitta*

bohemicus. Many are clearly *Oz. sagitta rhenana* and have an obvious arrow-shaped basal cavity in oral view and bear 10 to 12 denticles (Fig. 8, specimens D–F, I). However, specimens in these collections, particularly those from Cosner Gap and Moyer Gap (samples CG-CG2, CG-CG7, and MG-CG5), contain an unexpected range of variability. In particular, there is a wide range of both spatulate and denticulate forms in addition to extensive variation in the placement of the basal cavity from fully posterior to nearly central (Fig. 8, specimens J–P). Almost all samples that yielded *Oz. s. rhenana* also contain what Helfrich (1975) referred to as a new subspecies *Ozarkodina edithae marie* (Fig. 8Q). As early as Walliser (1964, p. 83) it was generally accepted that *Ozarkodina edithae* was part of the same "conodont assemblage" as *Sp. sagitta*, and we now consider the form element *Oz. edithae* to be the P₂ element of *Oz. sagitta* (Aldridge 1972). Within the population of *Oz. s. rhenana* recovered from the east-central Appalachian Basin there are also multiple examples of extremely unique forms as well (Fig. 9A–C).

Ozarkodina bicornuta Zone (Helfrich 1975)

Originally defined as the taxon-range zone for *Spathognathodus bicornutus* (Helfrich 1975), this species (Fig. 8A–C) appears to have been endemic to the central Appalachian Basin. With the exception of a single report of *Ozarkodina* aff. *bicornuta* from the Homeric of Estonia (Viira & Aldridge 1998), this species has not been illustrated outside of the Helfrich collection. Here, we also use this zone primarily because of the lack of other zonally diagnostic conodonts in this interval (e.g., *Kockelella patula*, *Kockelella ortus ortus*, *Ozarkodina sagitta sagitta*). The base of this zone was placed at the base of the McKenzie Member of the Mifflintown Formation by Helfrich, but *Oz. bicornuta* only occurs this low in one (Crabbottom – Fig. 5) of the four outcrops from which it was recovered (Cosner Gap – Fig. 6, Moyer Gap – Fig. 7, Keyser Reservoir – Fig. 10). This zone appears to be correlative to the upper part of the *K. walliseri*/*K. amsdeni* Superzone and the lowermost part of the *Oz. sagitta sagitta* Zone of McAdams *et al.* (2019). This zone corresponds with the uppermost part of the Sheinwoodian Stage and

Figure 9. A–C – *Ozarkodina* sp. (?*rhenana*); A – Moyer Gap Section, Cosner Gap Member, Mifflintown Formation (MG-CG5) [VPIL 1182] (Helfrich 1975, pl. 1, fig. 20); B – Moyer Gap Section, Cosner Gap Member, Mifflintown Formation (MG-CG5) [VPIL 1340]; C – Moyer Gap Section, Cosner Gap Member, Mifflintown Formation (MG-CG5) [VPIL 1340]. • D–F – *Ozarkodina snajdri* (Walliser, 1964); D – Crabbottom Section, McKenzie Member, Mifflintown Formation (CB-McK7B) [VPIL 1318]; E – Crabbottom Section, McKenzie Member, Mifflintown Formation (CB-McK7) [VPIL 1186] (Helfrich 1975, pl. 2, fig. 11); F – Crabbottom Section, McKenzie Member, Mifflintown Formation (CB-McK7A) [VPIL 1191] (Helfrich 1975, pl. 2, fig. 17). • G – *Ozarkodina bohemicus bohemicus* (Walliser, 1964), Crabbottom Section, Will Creek Formation (CB-WC1DUB) [VPIL 1213] (Helfrich 1975, pl. 13, fig. 6 – holotype of *Spathognathodus tillmani*). • H–K –; H – Crabbottom Section, Will Creek Formation (CB-WC1) [VPIL 1217] (Helfrich 1975, pl. 13, fig. 11 – paratype of *Spathognathodus tillmani*); I – Crabbottom Section, Will Creek Formation (CB-WC1D) [VPIL 1391];



J – Crabbottom Section, Will Creek Formation (CB-WC1D) [VPIL 1209] (Helfrich 1975, pl. 13, fig. 1 – paratype of *Spathognathodus tillmani*); K – Crabbottom Section, Will Creek Formation (CB-WC1D) [VPIL 1210] (Helfrich 1975, pl. 13, fig. 2 – *Ozarkodina bohémica longa* Jeppsson in Calner & Jeppsson, 2003, paratype of *Spathognathodus tillmani*). • L–O – ?*Ozarkodina sinuosa* Helfrich, 1975; L – Crabbottom Section, Will Creek Formation (CB-WC1) [VPIL 1012] paratype (Helfrich 1975, pl. 16, fig. 18); M – Crabbottom Section, Will Creek Formation (CB-WC1DUB) [VPIL 1017] holotype (Helfrich 1975, pl. 16, fig. 30); N – Crabbottom Section, Will Creek Formation (CB-WC1DUB) [VPIL 1016] paratype (Helfrich 1975, pl. 16, fig. 28); O – Crabbottom Section, Will Creek Formation (CB-WC1DUB) [VPIL 1393]. Scale bars = 100 microns.

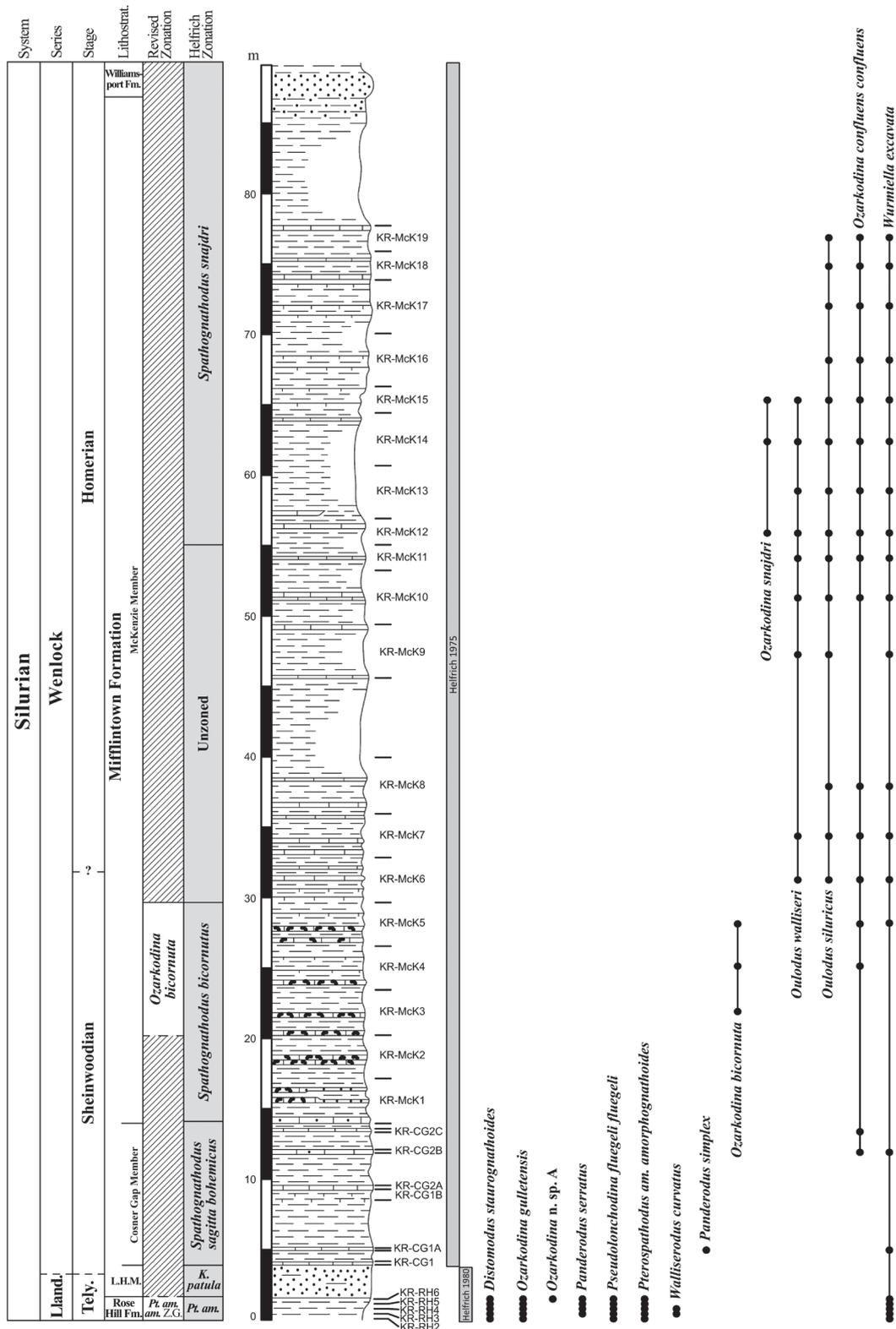


Figure 10. Stratigraphic column for the Keyser Reservoir Section, Mineral County, West Virginia, combined from Helfrich (1980) and Helfrich (1975). The original biozonations of Helfrich are shown against the new biozonation designations made herein. Lithologic key can be found in the caption to Fig. 5. Diagonal hatching in the biozone column indicates an unzoned interval because of a lack of diagnostic fauna. Abbreviations: Lland. – Llandovery; Tely. – Telychian; Fm. – Formation; L.H.M. – Lower Hematitic Member; am. – *amorphognathoides*; K. – *Kockella*; Pt. – *Pterospathodus*; Z.G. – Zonal Group.

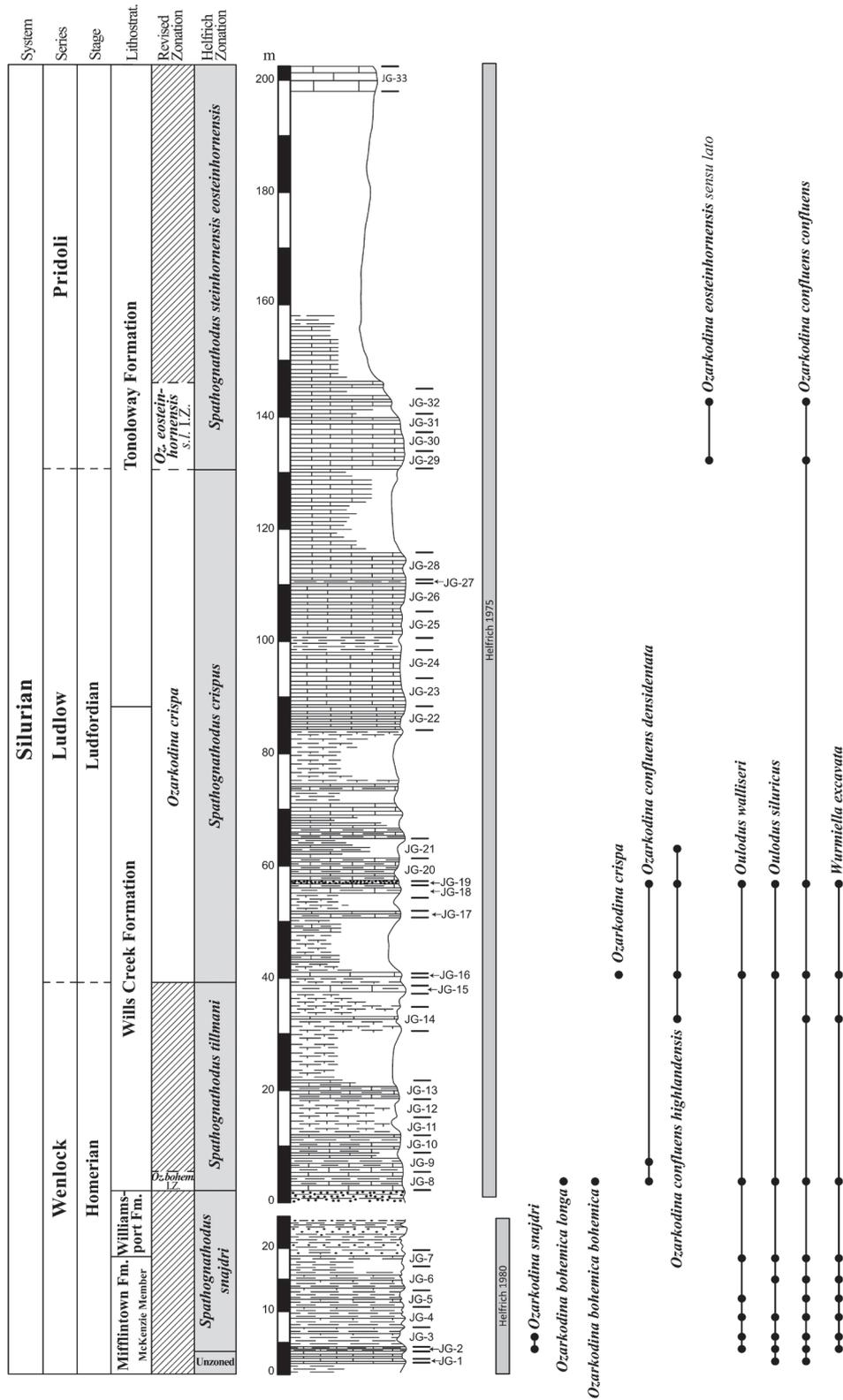


Figure 11. Stratigraphic column for the Judy Gap Section, Pendleton County, West Virginia, combined from Helfrich (1980) and Helfrich (1975). The original biozonations of Helfrich are shown against the new biozonation designations made herein. Lithologic key can be found in the caption to Fig. 5. Diagonal hatching in the biozone column indicates an unzoned interval because of a lack of diagnostic fauna. Abbreviations: Fm. – Formation; *bohem.* – bohemia; *Oz.* – *Ozarkodina*; *s.l.* – *sensu lato*; I.Z. – Interval Zone.

the base of the Homerian Stage is likely above the top of the zone. The long-ranging conodonts *Ozarkodina confluens confluens* and *Wurmiella excavata* are often the only other conodonts to co-occur with *Oz. bicornuta*.

Unzoned Interval of the Homerian Stage

From the disappearance of *Oz. bicornuta* to the appearance of *Ozarkodina bohemica longa* there are no zonally diagnostic conodonts in the studied collection. This interval does contain *Ozarkodina snajdri*, however, the biostratigraphic utility of *Oz. snajdri* has been progressively diminished in the past 30 years. Originally defined as a horizon within the Ludfordian Stage of the Ludlow Series by Walliser (1964), it has been used variably as the designator of an *Oz. snajdri* Zone or the eponymous species for an interval zone, both of which were in the Ludfordian Stage (see review by Corradini *et al.* 2015). The transition away from the use of *Oz. snajdri* as a zonal indicator followed the recognition that its first occurrence was highly variable (Viira & Aldridge 1998), and it has been found at least as low as the lower Hemse Marl (Jeppsson 2005) within the lower part of the Gorstian Stage. This position is just above the highest occurrence of *Ozarkodina bohemica longa* on Gotland (Calner & Jeppsson 2003). Here, we have a further downward range extension of *Oz. snajdri* to a position below *Oz. bohemica longa* within the upper part of the McKenzie Member of the Mifflintown Formation in all four sections in which *Oz. snajdri* occurs (Crabbottom – Fig. 5, Moyer Gap – Fig. 7, Keyser Reservoir – Fig. 10, Judy Gap – Fig. 11). This position places the first occurrence of *Oz. snajdri* in the Homerian Stage in the Appalachian Basin. Viira & Aldridge (1998) assigned all *Oz. snajdri* photographed by Helfrich (1975) to *Oz. snajdri snajdri* (Fig. 9D–F). Helfrich (1975) extended his *Sp. snajdri* zone to the top of the Williamsport Formation, however, the highest occurrence of the species is in the underlying McKenzie Member of the Mifflintown Formation. The top of this unzoned interval is placed at the first occurrence of *Ozarkodina bohemica longa* and contains all of the strata assigned to the unzoned interval and the *Sp. snajdri* Zone by Helfrich (1975).

Ozarkodina bohemica Interval Zone (modified from Slavík 2014)

Originally identified as *Spathognathodus tillmani* by Helfrich (1975), Jeppsson *in* Calner & Jeppsson (2003) classified the name *Sp. tillmani* as a *nomen dubium* and introduced the name *Ozarkodina bohemica longa* including in its description specimens that were originally

classified as *Sp. tillmani* by Helfrich (1975). The original diagnosis of *Oz. b. longa* that differentiated it from *Ozarkodina bohemica bohemica* was the greater length to height ratio of the blade in *Oz. b. longa*. Many of the specimens identified as *Sp. tillmani* in the collection have a high length-to-width ratio (Fig. 9H–K), and are referred to herein as *Oz. bohemica longa*. One significant exception is the holotype (Fig. 9G), which is much taller with a smaller blade length and is better classified as *Ozarkodina bohemica bohemica*. Unfortunately, Jeppsson *in* Calner & Jeppsson (2003) did not give a specific length-to-height ratio to be used to distinguish *Oz. b. longa* from *Oz. b. bohemica*. This lack of taxonomic precision, combined with apparent geographic variability in the order of conodont lowest occurrences within the upper part of the Homerian Stage, led Slavík (2014) to use the *Oz. bohemica* Interval Zone instead of the *Oz. bohemica longa* and *K. ortus absidata* zones (Fig. 3). Slavík (2014) designated the disappearance of *Oz. sagitta sagitta* as the base of the *Oz. bohemica* Interval Zone, but since *Oz. s. sagitta* has not been recovered in the east-central Appalachian Basin, we instead use the first occurrence of *Oz. bohemica longa* or *Oz. bohemica bohemica*, whichever is lowest, as the marker for the base of the *Oz. bohemica* Interval Zone. The original definition of the top of the zone was the first occurrence of *Kockelella crassa*. Once again, this species does not occur in Helfrich's collection, and therefore the top of this zone is difficult to define in the study area.

The *Oz. bohemica* Interval Zone is correlative with the *Oz. bohemica longa* and *K. ortus absidata* zones of Cramer *et al.* (2011b) and McAdams *et al.* (2019) spanning the upper part of the Homerian Stage and is correlative with the entirety of the *Sp. tillmani* Zone as defined by Helfrich (1975). The lowest occurrence of the *Oz. bohemica* I.Z. is at the base of Wills Creek Formation (Crabbottom – Fig. 5, Judy Gap – Fig. 11) and the zone extends into roughly the middle of the Wills Creek Formation. The collection contains *Oz. bohemica longa*, *Oz. bohemica bohemica*, and *Ozarkodina confluens densidentata* within this interval. *Ozarkodina confluens highlandensis* (Figs 9, 12, 13) first occurs within the uppermost part of this interval zone. The name *Spathognathodus primus multidentatus* Helfrich 1975 (Fig. 13) has priority over *Spathognathodus primus densidentatus* Viira (1983) [*Ozarkodina confluens densidentata*], however, for the same reasons as discussed for *Sp. tillmani* by Jeppsson *in* Calner & Jeppsson (2003), *Sp. primus multidentatus* is a *nomen dubium* and is referred to herein as *Ozarkodina confluens densidentata* (Jeppsson 1969, Helfrich 1975, Viira 1983, Jeppsson *et al.* 1995, Calner & Jeppsson 2003). The first occurrence of *Oz. c. densidentata* in both the Gotland and East Baltic succession is within the *Oz. bohemica* I.Z. of the upper Homerian and this matches the occurrence in all sections from

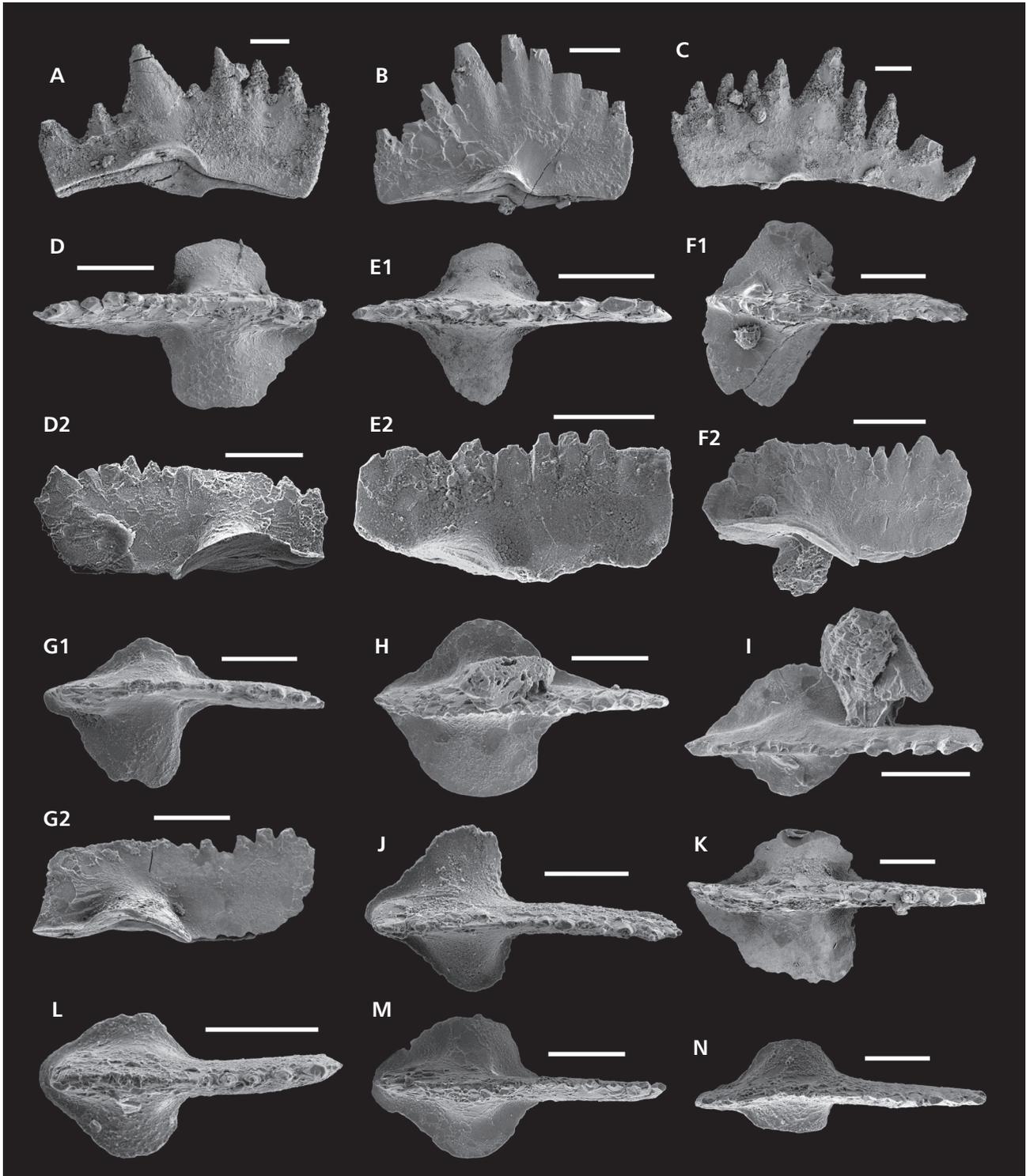


Figure 12. A–C – *Ozarkodina confluens highlandensis* (Helfrich, 1975); A – Crabbottom Section, Wills Creek Formation (CB-WC15) [VPIL 1146] paratype (Helfrich 1975, pl. 14, fig. 26); B – Pinto Section, Wills Creek Formation (P-WC22B) [VPIL 1139] paratype (Helfrich 1975, pl. 14, fig. 11); C – Crabbottom Section, Wills Creek Formation (CB-WC15) [VPIL 1147] paratype (Helfrich 1975, pl. 14, fig. 28). • D–N – *Ozarkodina crispata* (Walliser, 1964); D – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1429]; E – Judy Gap Section, Wills Creek Formation (JG-16B) [VPIL 1431]; F – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1429]; G – Judy Gap Section, Wills Creek Formation (JG-16B) [VPIL 1431]; H – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1429]; I – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1429]; J – Judy Gap Section, Wills Creek Formation (JG-16B) [VPIL 1431]; K – Judy Gap Section, Wills Creek Formation (JG-16B) [VPIL 1431]; L – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1431]; M – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1429BB]; N – Judy Gap Section, Wills Creek Formation (JG-16) [VPIL 1128] (Helfrich 1975, pl. 14, fig. 2). Scale bars = 100 microns.

which it was recovered in the study area (Crabbottom – Fig. 5, Judy Gap – Fig. 11, Pinto – Fig. 14).

The identification of the *Oz. bohémica* Interval Zone marks the largest change to global chronostratigraphic correlation in the study area. Helfrich's (1975) original correlation of his *Sp. tillmani* Zone with Walliser's (1964) *latialata* Zone was not based on the occurrence of any of the zonal indicators of the *latialata* Zone within the study area but rather the fact that this represented an interval above *Oz. snajdri* and below *Ozarkodina crispera*, both of which do occur in the study area. However, the presence of *Oz. bohémica longa*, *Oz. bohémica bohémica*, and *Oz. c. densidentata* clearly demonstrates a Homeric position for these strata. The result is that the occurrence of *Oz. snajdri* in the studied sections is among the chronostratigraphically lowest yet recovered globally and that the lower half of the Wills Creek Formation does not represent the Ludfordian Stage of the Ludlow Series, but rather, the Homeric Stage of the Wenlock Series.

Ozarkodina crispera Zone (Walliser 1964)

The *Ozarkodina crispera* Zone of Walliser (1964) is a taxon-range zone that corresponds to the total range of *Oz. crispera*. Whereas the disappearance of *Oz. crispera* was once considered to be a marker for the base of the Pridoli Series, it is now clear that *Oz. crispera* persists into the lower part of the Pridoli, and as a result, the Ludlow–Pridoli boundary is now placed within the upper part of the *Oz. crispera* Zone (Corradini *et al.* 2015, McAdams *et al.* 2019). Specimens of *Oz. crispera* in the collection exhibit a great degree of morphological variability (Figs 12, 13), and the collection clearly contains all of the morphotypes illustrated by Viira & Aldridge (1998) from the East Baltic succession. *Ozarkodina eosteinhornensis sensu lato* appears in the upper part of the range of *Oz. crispera* within the studied sections and matches well with other co-occurrence data of these two species globally (Viira & Aldridge 1998, Kaljo *et al.* 2015).

The first occurrence of *Oz. crispera* is within the middle part of the Wills Creek Formation in all three locations that contain the Wills Creek (Crabbottom – Fig. 5, Judy Gap – Fig. 11, Pinto – Fig. 14). Surprisingly, at Crabbottom (Fig. 5), *Oz. crispera* appears immediately above the last appearances of both *Oz. b. bohémica* and *Oz. b. longa*, indicating that there is a substantial gap in the

stratigraphic record somewhere near the middle of the Wills Creek Formation at this locality. This hiatus likely spans the entire Gorstian Stage and most of the Ludfordian Stage, likely including the mid-Ludfordian Lau Event and Excursion (Jeppsson *et al.* 2007, Kozłowski 2015, Mergl *et al.* 2018). However, this gap offers an explanation for the complete lack of all typical Ludlow conodonts from the east-central Appalachian Basin (e.g., *Kockelella crassa*, *Kockelella variabilis*, *Ancoradella ploeckensis*, *Polygnathoides siluricus*, *Pedavis latialata*). It is unclear how far this hiatus extends in any direction outside the immediate area studied herein. The last occurrence of *Oz. crispera* is above the first occurrence of *Oz. eosteinhornensis s.l.* within the Tonoloway Formation.

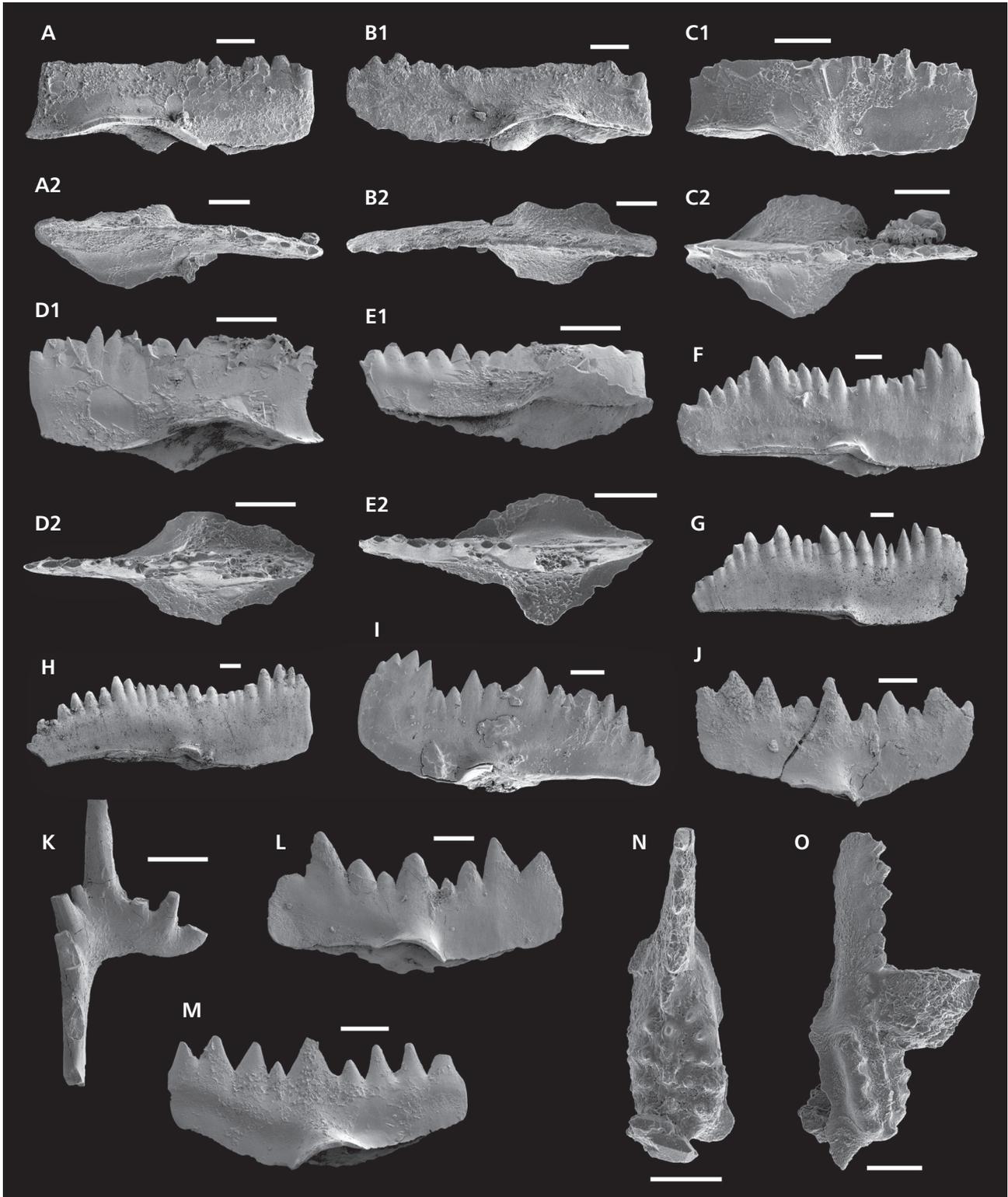
Ozarkodina eosteinhornensis sensu lato Interval Zone (Corriga & Corradini 2009)

The base of the *Ozarkodina eosteinhornensis sensu lato* Interval Zone is placed at the last occurrence of *Oz. crispera* and the top is placed at the first occurrence of *Oulodus elegans detortus*, which does not occur in Helfrich's collection. The lowest occurrence of *Oz. eosteinhornensis s.l.* is 24.29 meters above the base of the Tonoloway Formation at Crabbottom (Fig. 5). A single specimen of *Oulodus elegans elegans* was recovered 86.38 meters above the base of the Tonoloway Formation at Pinto (Fig. 14), coincident with the first occurrence of *Oz. eosteinhornensis s.l.* in this section. *Homeognathodus peniculus* (Fig. 13N, O) occurs in one sample 93.06 meters above the base of the Tonoloway Formation at Pinto (Fig. 14). These three conodont species all occur within the Tonoloway Formation and provide a clear demonstration of the lower part of the Pridoli Series. However, the Helfrich collection does not contain conodonts indicative of the base of the Devonian System within this unit.

Conclusions

The re-examination of the conodont collection of C.T. Helfrich (Helfrich 1972, 1975, 1978, 1980) allows improved global correlation of the Silurian strata within the east-central Appalachian Basin (Fig. 15). A total of six conodont zones/zonal groups/interval zones can be

Figure 13. A–E – *Ozarkodina crispera* (Walliser, 1964); A – Crabbottom Section, Tonoloway Formation (CB-UT3) [VPIL 1133] (Helfrich 1975, pl. 14, fig. 19); B – Crabbottom Section, Tonoloway Formation (CB-T1A) [VPIL 1134] (Helfrich 1975, pl. 14, fig. 21); C – Crabbottom Section, Tonoloway Formation (CB-UT3) [VPIL 1417]; D – Crabbottom Section, Tonoloway Formation (CB-UT3) [VPIL 1131] (Helfrich 1975, pl. 14, fig. 9); E – Crabbottom Section, Tonoloway Formation (CB-UT3) [VPIL 1129] (Helfrich 1975, pl. 14, fig. 3). • F – *Ozarkodina confluens confluens* (Branson & Mehl, 1933), Moyer Gap Section, McKenzie Member, Mifflintown Formation (MG-13) [VPIL 1347]. • G–I – *Ozarkodina confluens densidentata*



(Viira, 1983); G – Crabbottom Section, Wills Creek Formation (CB-WC1D) [VPIL 1152] (Helfrich 1975, pl. 13, fig. 15); H – Crabbottom Section, Wills Creek Formation (CB-WC1DUB) [VPIL 1155] (Helfrich, 1975, pl. 16, fig. 26); I – Crabbottom Section, Wills Creek Formation (CB-WC1) [VPIL 1388]. • J–M – *Ozarkodina eosteinhornensis sensu lato* (Walliser, 1964); J – Pinto Section, Tonoloway Formation (P-T19C) [VPIL 1447]; L – Pinto Section, Tonoloway Formation (P-T19C) [VPIL 1447]; M – Judy Gap Section, Tonoloway Formation (JG-32) [VPIL 1438]. • K – *Oulodus elegans elegans* (Walliser, 1964), Pinto Section, Tonoloway Formation (P-T19C) [VPIL 0945] (Helfrich 1975, pl. 15, fig. 14). • N, O – *Homeognathodus peniculus* Denkler & Harris, 1988b; N – Pinto Section, Tonoloway Formation (P-T21B) [VPIL 1286] (Helfrich 1975, pl. 16, fig. 2); O – Pinto Section, Tonoloway Formation (P-T21B) [VPIL 1285] (Helfrich 1975, pl. 16, fig. 1). Scale bars = 100 microns.

Figure 15. Comparison of chrono-litho-biostratigraphic correlation between Helfrich (1975) and this study. The revised chart at bottom illustrates the position of global chronostratigraphic boundaries within the lithostratigraphic nomenclature of the east-central Appalachian Basin. Abbreviations: N.Y. – New York State, USA; Llan. – Llandovery; Lud. – Ludlow; Ludf. – Ludfordian; Pri. – Pridoli; Shein. – Sheinwoodian; Tely. – Telychian; *eostein.* – *eosteinhornensis*; *K.* – *Kockelella*; *Oz.* – *Ozarkodina*; *Pt.* – *Pterospathodus*; *s.l.* – *sensu lato*; *Sp.* – *Spathognathodus*; I.Z. – Interval Zone; Z.G. – Zonal Group.

Helfrich (1975) Chrono-Bio-Lithostratigraphy

System	Series		Wills Mountain Anticline Lithostratigraphy	Appalachian Basin Conodont Zones (from Helfrich - 1975)	European Conodont Zones (Walliser - 1964)
	Europe	N.Y.			
Silurian	Ludlow	Cayuga	Tonoloway Formation	<i>Sp. steinhornensis eosteinhornensis</i>	<i>eosteinhornensis</i>
			Wills Creek Formation	<i>Spathognathodus crispus</i>	<i>crispus</i>
	Mifflintown Formation	Niagara	Williamsport Formation Bloomsburg Formation	<i>Spathognathodus snajdri</i>	<i>siluricus</i> ^{snajdri horizon}
			McKenzie Member	Unzoned Interval	<i>ploeckensis</i>
			Cosner Gap Member	<i>Spathognathodus bicornutus</i>	<i>crassa</i>
			Lower Hematitic Member [Keeler Member]	<i>Spathognathodus sagitta bohemicus</i>	<i>sagitta</i>
	Wenlock	Niagara	Rose Hill Formation		<i>patula</i>

Revised Chrono-Bio-Lithostratigraphy

System	Series	Stage	Wills Mountain Anticline Lithostratigraphy	Revised Appalachian Conodont Zones	Appalachian Basin Conodont Zones (from Helfrich - 1975)
Silurian	Pridoli	Lud.	Tonoloway Formation	<i>Oz. eosteinhornensis sensu lato</i> Interval Zone	<i>Spathognathodus steinhornensis eosteinhornensis</i>
			Wills Creek Formation	<i>Oz. crispa</i>	<i>Spathognathodus crispus</i>
	Wenlock	Homerian	Williamsport Formation Bloomsburg Formation	Unzoned Interval	<i>Spathognathodus tillmani</i>
			McKenzie Member	Unzoned Interval	<i>Spathognathodus snajdri</i>
			Cosner Gap Member	<i>Oz. bohémica</i> I.Z.	<i>Spathognathodus tillmani</i>
			Lower Hematitic Member [Keeler Member]	<i>Oz. bicornuta</i>	<i>Spathognathodus bicornutus</i>
	Llan.	Tely.	Rose Hill Formation	<i>K. walliseri</i> Zonal Group	<i>Spathognathodus sagitta bohemicus</i>
				Unzoned Interval	<i>Pt. amorphognathoides amorphognathoides</i> Zonal Group

identified in the collection spanning the upper Telychian Stage (Llandovery Series) to at least the lower part of the Pridoli Series. A major stratigraphic gap is identified that spans most of the Ludlow Series from the lower part of the Gorstian Stage to the upper part of the Ludfordian Stage. This gap explains both the need to lower the global chronostratigraphic correlation of the McKenzie Member of the Mifflintown Formation as well as the lack of even the most cosmopolitan of Ludlow species from the collection.

The Llandovery–Wenlock boundary can be confidently placed within the Lower Hematitic Member of the Mifflintown Formation. The base of the Homerian Stage is more difficult to correlate globally, and an unzoned interval in this part of the Appalachian Basin can only refine its position to somewhere within the middle part

of the McKenzie Member of the Mifflintown Formation. There are no clear indicators for the base of the Ludlow Series (Gorstian Stage), nor for the base of the Ludfordian Stage of the Ludlow Series. Within the middle part of the Wills Creek Formation an abrupt transition occurs from an upper Homerian fauna to an upper Ludfordian fauna. The base of the Pridoli can be narrowed down to a small window within the lowermost part of the Tonoloway Formation. There are no indicators of the base of the Devonian System within the collection.

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