Conodonts and the Devonian–Carboniferous transition in the Dyer Formation, Colorado

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ABSTRACT

Conodont assemblages from shallow platform carbonate strata of the Dyer Formation in northwestern Colorado indicate that the unit spans the Devonian–Carboniferous transition, and include four new taxa, described herein. The underlying Parting Formation and most of the Broken Rib Member of the Dyer Formation are in the Palmatolepis expansa Zone. The upper portion of the Broken Rib Member and the lower part of the Coffee Pot Member of the Dyer Formation are in the Bispathodus aculeatus Zone to the Bispathodus ultimus Zone, and associated with an ~6‰ positive δ13C shift identified as the end-Devonian Hangenberg excursion. Upper Coffee Pot Member conodonts are equivocally Tournaisian, and cap the δ13C excursion. Collectively, these observations suggest that the Devonian–Carboniferous boundary is in the upper Coffee Pot Member of the Dyer Formation, and thus the overlying Gilman Sandstone is Carboniferous.

KEY WORDS: Chaffee Group, conodonts, Devonian–Carboniferous transition, Dyer Formation, Famennian, Hangenberg Crisis, Patrognathus, Pelekysgnathus, Pseudopolygnathus.

INTRODUCTION

The end-Devonian–earliest Carboniferous (D–C) was a time of significant global change marked by glaciation in the Americas—southern Laurentia and western Gondwana (Isaacson et al., 1999, 2008; Brezinski et al., 2010; Ettensohn et al., 2020), and sea level fluctuation (Myrow et al., 2013). These changes were associated with the multiphasic Hangenberg Crisis interval that includes a major mass extinction (Walliser, 1984; Kaiser et al., 2016). Notable changes occur in conodont, brachiopod, goniatite, palyynomorph, trilobite, and vertebrate faunas, as well as a carbon isotope excursion of up to +7‰ (Caplan and Bustin, 1999; Kaiser, 2009; Filipiak and Racki, 2010; Sallan et al., 2010; Cole et al., 2015; Stolfo et al., 2020). The D–C boundary in the United States lies often within a disconformable interval (Over, 2020). In the Dyer Formation, conodonts from 24 productive horizons spread across five measured sections provide biostratigraphic constraint for a measured carbon isotope excursion consistent with the Hangenberg event. The conodonts and carbon isotope shifts allow placement of the Devonian–Carboniferous boundary within a shallow-water carbonate platform setting.

GEOLOGIC SETTING

The Chaffee Group (Campbell, 1970) in Colorado is composed of the lower Parting Formation (Emmons, 1882), consisting primarily of quartz sandstone and subsidiary shale and sandy dolostone, carbonates of the overlying Dyer Formation (Behre, 1932), and dolomitic sandstone of the Gilman Sandstone (Tweto and Lovering, 1977; Beaty et al., 1988). Campbell (1970) subdivided the Dyer Formation into the Broken Rib Member and the overlying Coffee Pot Member. These strata were deposited on a tropical carbonate platform south of the paleo-equator of the western interior of Laurentia, inboard of the Antler orogenic belt (Fig. 1). The Broken Rib Member is composed of dark gray, medium to thick irregularly bedded to nodular bioturbated, dolomitic, bioclastic wackestone to grainstone. The Coffee Pot Member is generally thicker, composed of light to dark gray, thin to thickly bedded, finely crystalline dolomudstones interbedded with intraclastic rudstones, stromatolitic intervals, cherty laminated to micritic dolostone, and local to regional karst surfaces. Regional time equivalent strata, separated from the Dyer by the Uinta and the Uncompahgre uplifts, include the Ouray Limestone in...
southwest Colorado and other formations to the west, the Pilot Shale and equivalents in the Antler foreland basin in eastern Nevada, as well as the Bakken and Englewood formations in the Williston Basin of Montana, North Dakota, South Dakota, Manitoba, and Saskatchewan (Sandberg and Poole, 1977; Over, 2020). Conodonts from the Parting and Dyer formations were first described by Sandberg (1976), Sandberg and Poole (1977), and Sandberg and Dreesen (1984) from east Glenwood Canyon (= Glenwood Canyon section of Myrow et al., 2011, 2013). The Parting and Dyer were considered the most nearshore and possessing the most restricted conodont faunas of the western United States' localities in the Upper Devonian conodont biofacies models (Sandberg and Dreesen, 1984).

**METHODS**

Sections of the Dyer Formation at Bear Scat Creek, Bison Lake, Crane Park, and Monument Lake (Appendix 1) were measured, using a steel tape and Jacob’s staff. Bulk 2+ kg samples were collected for conodonts and δ¹³C_carb chemostratigraphy. To replicate the Broken Rib Member–Coffee Pot Member interval at Bear Scat Creek, a supplementary section was logged and collected for biostratigraphy nearby, at Deep Creek Side Canyon. Data from Sandberg (1976), Sandberg and Poole (1977), and Myrow et al. (2011) from Glenwood Canyon were also incorporated into this study (Figs. 1 and 2). Conodont samples were crushed to 1 cm maximum dimension, and dissolved in buffered
10% formic acid following the method of Jeppsson and Anehus (1995). The acid digestion residues were collected on a 120 μm screen, density separated using 2.78 sg lithium metatungstate, and the heavy fraction scanned for microfossils. Selected conodonts were coated with Au-Pd, and imaged using secondary electron or backscatter detectors on a ZEISS EVO scanning electron microscope.

Hand samples for chemostratigraphy were collected in each of the study sections, thin-sectioned, stained, and petrographically screened. The least altered phases (principally

Figure 2. Graphic logs of studied sections of the Dyer Formation in northwest Colorado showing general lithology, key surfaces or sedimentary structures, and position of productive conodont samples (bold numbers and arrowheads). Dashed lines indicate where the zone boundaries are hypothesized; undulatory lines indicate unconformities. Only the upper portion of the underlying Parting Formation is depicted. Composite graphic log for Glenwood Canyon adapted from Hauck (1954), Bass and Northrop (1963), Campbell (1966), and Strauss (2006). One sample (4*) came from the Deep Creek Side Canyon section, which is adjacent and parallel to the Bear Scat Creek section. Rather than plot this supplementary section separately, we have indicated the equivalent stratigraphic position of this sample within the Bear Scat Creek section. Biostratigraphy samples are keyed to Tables 1–5; arrowheads indicate samples that only contained unidentifiable conodont elements and fragments; samples with numbered arrowheads contained identifiable taxa; samples 16–19 are from Sandberg (1976).
micrite, dolomicrite, and oolite) were micro-drilled, avoiding late-stage spar, fossils, and allochems. Stable isotope ratios ($\delta^{18}O$ and $\delta^{13}C$) were measured using a Thermo Fisher Scientific Kiel III automated carbonate preparation device coupled to a Finnigan MAT 252 gas-ratio mass spectrometer. Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. The isotope ratio measurement was calibrated based on repeated measurements of NBS-19, NBS-18, and CAR2, an in-house carbonate standard. The following isotope ratios were assigned to these standards ($\delta^{18}O$ followed by $\delta^{13}C$): NBS-19, -2.20, +1.95; NBS-18, -23.20, -5.01; CAR2, -1.41, +2.03. Analytical precision was ± 0.10‰ for $\delta^{18}O$, and ±0.08‰ for $\delta^{13}C$ (1σ). Chemostratigraphic analysis of the Dyer succession, including $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ work on carbonate phases and selected conodont separates, will be treated in greater detail in a separate paper.

RESULTS

Twenty-six of 46 samples from the Dyer Formation yielded conodonts (Fig. 2; Tables 1–5). Of these, 17 samples, as well as four horizons from Glenwood Canyon collected and described by Sandberg (1976, table 1), Sandberg and Poole (1977, fig. 15), Sandberg and Dreesen (1984, fig. 5), and some illustrated in Sandberg and Zielger (1979) and Sandberg and Dreesen (1984), had recognizable taxa representing eight genera and 19 species, of which one new species and three new subspecies are described. Eleven of the 20 barren samples came from the Coffee Pot Member of the Dyer Formation, four samples were from carbonates within the underlying Parving Formation, and five samples were from sandy carbonates within the overlying Gilman Sandstone. Carbon isotope data show a 6‰ positive excursion starting in the upper Broken Rib Member of the Dyer Formation or lower Coffee Pot Member (Fig. 3).

DISCUSSION: IMPLICATIONS AND IMPORTANCE OF THE CONODONTS

Conodonts are generally well preserved in the Dyer (Figures 4–7), although commonly marred by dolomite crystal impressions and overgrowths (e.g., Figs. 4.9 and 4.12). Conodont color alteration index (CAI) of 2 to 3 indicates thermal heating between 60 and 200 degrees Celsius (Epstein et al., 1977).

The Parving Formation, based on the identification of Cladognathus ormistoni Beinert, Klapper, Sandberg, and Ziegler, 1971, from Glenwood Canyon (Sandberg, 1976, table 1), is placed in the Palmatolepis expansa Zone (= former Lower expansa Zone) using the zonation scheme proposed by Spalletta et al. (2017).

The lower portion of the Broken Rib Member yielded a fauna that includes Aptognathus varians Branson and Mehl, 1934a; Pandorinollina cf. P. insita Stauffer 1940, of Sandberg and Ziegler, 1979; Polygnathus semicostatus Branson and Mehl, 1934a, morphotype 5 of Dreesen and Orichard, 1974; and Polygnathus subirregularis Sandberg and Ziegler, 1979. These taxa range into or through the expansa Zone.

The upper Broken Rib Member and lower Coffee Pot Member contain a diverse fauna that includes: Aptognathus varians; Bispathodus aculeatus aculeatus Branson and Mehl, 1934a; B. cf. B. ac. plumeric Rhodes, Austin, and Druce, 1969; Bispathodus stabilis Branson and Mehl, 1934a; Icriodus costatus coffeeopotensis n. ssp.; Icriodus costatus darybenis Klapper, 1958; Pandorinollina cf. P. insita; Patrognathus donbasicus Lipnjagov, in Kozitskaya et al. (1978); Pelekygnathus

| Unit | Broken Rib Mbr | Coffee Pot Mbr |
|------|----------------|----------------|
| Conodont Zone | expansa | aculeatus |
| Broken Rib Mbr | 17.4 | 19.7 | 27.0 | 27.3 |
| Coffee Pot Mbr | 2 | 2.6 | 2 |
| Broken Rib Mbr | 1 | 2 | 3 |
| Coffee Pot Mbr | 1 | 1 |
| Broken Rib Mbr | 3 | 3 |
| Coffee Pot Mbr | 2 | 2 |
| Broken Rib Mbr | 3 | 3 |
| Coffee Pot Mbr | 2 | 2 |
| Broken Rib Mbr | 10 | 32 |

Table 1. Bear Scat Creek (DMNH 7542) sample horizons, conodont-bearing horizons (bold), and conodonts recovered.
### Table 2. Deep Creek Side Canyon (DMNH 7541) sample horizons, conodont-bearing horizons (bold), conodonts recovered.

| unit | Broken Rib Mbr | Coffee Pot Mbr |
|------|----------------|----------------|
|      | no conodonts (expansus) | aculeatus       |
| m above base | 0.0 | 1.0 | 6.7 | 10.2 | 17.5 | 21.0 | 22.6 | 23.6 |
| sample size (kg) | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| label on graphic log | 4 |     |       |       |       |       |       |       |
| *B. cf. B. aculeatus plumulus |     |       |       |       |       |       |       |       |
| other elements and fragments |     |       |       |       |       |       |       |       |

* uncertain if this is Broken Rib Member or Coffee Pot Member

### Table 3. Part 1. Bison Lake (DMNH 4257) sample horizons, conodont-bearing horizons (bold), conodonts recovered.

| unit | Parting | Broken Rib Mbr | Coffee Pot Mbr |
|------|---------|----------------|----------------|
|      | expansus | aculeatus       |                |
| m above base | -3.9 | -3.7 | -2.5 | 1.5 | 6.5 | 13.5 | 22 | 28.5 | 32.85 | 34.0 | 35.7 | 39.0 |
| sample size (kg) | 2 | 2 | 1.9 | | 1 | | 1 | 3 | 1.8 | 12.1 | 3.9 |
| label on graphic log | < | < | 5 | | < | 6 | | 7 | < | 8 | |
| *Apatognathus varians* | | 2 | | | | | | 1 | |
| *B. cf. B. aculeatus plumulus* | | | 2 | | 17 | | |
| *Bisphodus stabili* | | | | | | | | 6 | |
| *Pelekynognathus inclinatus* | | | | | | | | 2 | |

### Table 3. Part 2. Bison Lake sample horizons, conodont-bearing horizons (bold), conodonts recovered. Gil. = Gilman Sandstone.

| unit | Coffee Pot Mbr |
|------|----------------|
|      | expansus to ultimus | Tournaisian | Gil. |
| m above base | 44.2 | 44.5 | 45.5 | 49.5 | 50.5 | 52.0 | 55.7 | 58.5 | 59.3 | 59.9 | 62.3 | 62.7 | 67.0 |
| sample size (kg) | 2 | 8.8 | 2 | 1.9 | 2 | 1.9 | 2 | 2 | 12.1 | 13.8 | 2 | 5.5 | 2 |
| label on graphic log | 9 | 10 | 11 | 12 | | | | | | | | | |
| *Apatognathus varians* | 1 | 3 | | | | | | | | | | |
| *Iridodus costatus* sp. | | | | | | | | | | | | 1 | |
| *Pandorinella cf. P. invita* | 3 | 1 | | | | | | | | | | |
| *Pelekynognathus* sp. | 1 | 1 | | | | | | | | | | |
| *Polynathus communis* palvanensis | 2 | 2 | 4 | | | | | | | | | | |
| *Polynathus perplexus* | | | | | | | | | | | | 1 | |
| *Polynathus urmicostatus* M5 | 4 | 4 | 8 | | | | | | | | | | |
| *Polynathus subirregularis* | 1 | | | | | | | | | | | | |
| *Polynathus* sp. | | | | | | | | | | | | 2 | |
| *Pseudopolynathus* sp. | 1 | | | | | | | | | | | | 1 | |
| *Siphonodella* sp. | | | | | | | | | | | | 1 | |
| other elements and fragments | 5 | 23 | 13 | 3 | | | | | | | | | 6 | |
inclinitus Thomas, 1949; Pelekygnathus soarei n. sp.; Polygnathus communis pahvantensis n. sp.; Polygnathus perplexus Sandberg and Ziegler, 1979; Polygnathus perplexus Thomas, 1949; Polygnathus semicostatus Thomas, 1949; Polygnathus subirregularis Sandberg and Ziegler, 1979; Polygnathus sp. in the inornatus group of Hogancamp and Rodriguez (2020); and Pseudopolygnathus primus craneparkensis n. sp. The first occurrence of Bispathodus ac. aculeatus and Bi. cf. Bi. ac. plumulus indicate the Bispathodus aculeatus Zone (lower portion of former Middle expansa Zone). These two taxa range into the Tournaisian (Spalletta et al., 2017). Polygnathus perplexus ranges to the end of the Bispathodus costatus Zone; P. semicostatus ranges into the Bispathodus ultimus Zone, an indication that the middle Coffee Pot Member could be younger than the Bispathodus aculeatus Zone.

Only two samples in the upper Coffee Pot yielded conodonts. A sample at 50.5 m in our measured section at Bison Lake contained Icriodus costatus sp., a Devonian taxon, and three small fragments. A sample from 59.9 m at Bison Lake contained conodonts in fused clusters of sand and fragments, possibly coprolitic in origin. The conodonts include Polygnathus sp., Pseudopolygnathus?, and Siphonodella?, which have affinities to Tournaisian forms (see Systematic Paleontology, Appendix 2).
These conodonts suggest the *Siphonodella duplicata* Zone and indicate that the Devonian–Carboniferous (D–C) boundary is between 50.5 m and 60 m in the section at Bison Lake. This interval also corresponds to the decline in the positive δ13C shift at the end of the Hangenberg isotope excursion and the D–C boundary (Myrow et al., 2011; Kaiser et al., 2016; Fig. 3 this paper).

Numerous conodont taxa in the Dyer are similar to species described elsewhere from the high Famennian of Laurentia (Branson and Mehl, 1934a, 1934b; Klapper, 1958, 1966; Sandberg and Ziegler, 1979; Sandberg and Dreesen, 1984; Johnston and Chatterton, 2001; Hogan-camp and Rodriguez, 2020). Their presence indicates faunal
Figure 4. Scanning electron microscope images of conodonts from the upper Broken Rib Member and the lower Coffee Pot Member of the Dyer Formation (see Figure 2 for stratigraphic context). Scale bars = 0.1 mm. 1–4, 6, 7, *Patrognathus donbassicus* Lipnjagov, 1978; 1–3, 6, 7, Crane Park Quarry 31.5 m (24 on Figure 2), DMNH EPV.136312 - EPV.136316; 4, new image of holotype, Donets Basin, Ukraine, 68/481 IGS AS UkrSSR. 5, *Bispathodus stabils* (Branson and Mehl, 1934a), Crane Park Quarry 31.5 m (24 on Figure 2), DMNH EPV.136317. 8, 12, *Bispathodus cf. B. aculeatus plumulus* Rhodes, Austin, and Druce, 1969, Bear Scat Creek 19.7 m (3 on Figure 2), DMNH EPV.136318, EPV.136319. 9, 10, *Pandorinellina cf. P. insita* (Stauffer, 1940) of Sandberg and Ziegler (1979); 9, Bear Scat Creek 19.7 m (3 on Figure 2), DMNH EPV.136320; 10, Crane Park Quarry 25.5 m (22 on Figure 2), DMNH EPV.136321. 11, *Bispathodus aculeatus aculeatus* (Branson and Mehl, 1934a), Crane Park Quarry 25.5 m (22 on Figure 2), DMNH EPV.136322.
Figure 5. Scanning electron microscope images of conodonts from the upper Broken Rib Member and the Coffee Pot Member of the Dyer Formation (see Figure 2 for stratigraphic context). Scale bars = 0.1 mm. 1–4, 8, *Polygnathus communis pahvantensis* new subspecies, Crane Park Quarry 25.5 m (22 on Figure 2), DMNH EPV.136323 - EPV.136327. 5, 10, *Polygnathus subirregularis* Sandberg and Ziegler, 1979; 5, Bison Lake 44.2 m (9 on Figure 2), DMNH EPV.136328; 10, Bear Scat Creek 7.4 m, (1 on Figure 2), DMNH EPV.136329. 6, *Polygnathus semicostatus* "5" Branson and Mehl, 1934a of Dreesen and Orchard (1974), Bison Lake 44.2 m (9 on Figure 2), DMNH EPV.136330. 7, *Polygnathus semicostatus* "2" Branson and Mehl, 1934a of Dreesen and Orchard (1974), Crane Park Quarry 27 m (23 on Figure 2), DMNH EPV.136331. 9, *Polygnathus experplexus* Sandberg and Ziegler, 1979, Crane Park Quarry 27 m (23 on Figure 2), DMNH EPV.136332. 11, *Polygnathus* sp. in *P. inornatus* group of Hogancamp and Rodriguez (2020), Crane Park Quarry 31.5 m (24 on Figure 2), DMNH EPV.136333. 12, *Polygnathus perplexus* Thomas, 1949, Bison Lake 44.5 m (10 on Figure 2), DMNH EPV.136334. 13–14, *Polygnathus* sp. P. elements, associated with *P. perplexus* and *P. semicostatus*, Bison Lake 44.5 m (10 on Figure 2), DMNH EPV.136335, EPV.136336. 15, *Polygnathus*? sp., Bison Lake 44.5 m (10 on Figure 2), DMNH EPV.136337.
Figure 6. Scanning electron microscope images of conodonts from the upper Broken Rib Member and the Coffee Pot Member of the Dyer Formation (see Figure 2 for stratigraphic context). Scale bars = 0.1 mm. 1–4, Icriodus costatus coffeepotensis new subspecies; 1, 2, 4, Bear Scat Creek 19.7 m (3 on Figure 2), DMNH EPV.136338, EPV.136339, EPV.136341; 3, Crane Park Quarry 25.5 m (22 on Figure 2), DMNH EPV.136340. 5–6, Icriodus costatus darbyensis Klapper, 1958, Crane Park Quarry 25.5 m (22 on Figure 2), DMNH EPV.136342, EPV.136343. 7–9, Apatognathus varians Branson and Mehl, 1934a; 7, S-element, 9, M-element, Crane Park Quarry 27 m (23 on Figure 2), DMNH EPV.136344, EPV.136346; 8, S-element, Bison Lake 44.2 m (9 on Figure 2), DMNH EPV.136345. 10, Pelekysgnathus soarae new species, Crane Park Quarry 31.5 m (24 on Figure 2), DMNH EPV.13631947. 11–12, Pelekysgnathus inclinatus Thomas, 1949, Bison Lake 39.0 m (8 on Figure 2), DMNH EPV.136348, EPV.136349. 13, fused cluster of sand grains and conodonts, Bison Lake 59.9 m (13 on Figure 2), DMNH EPV.136350.
Figure 7. Scanning electron microscope images of conodonts from the upper Broken Rib Member and the Coffee Pot Member of the Dyer Formation (see Figure 2 for stratigraphic context). Scale bars = 0.1 mm. 1–5, *Pseudopolygnathus primus craneparkensis* new subspecies, Crane Park Quarry 27 m (23 on Figure 2), DMNH EPV.136351 - EPV.136355. 6, *Siphonodella?* sp., fused cluster, Bison Lake 59.9 m (13 on Figure 2), DMNH EPV.1363156. 7–8, *Pseudopolygnathus?* sp., fused clusters, Bison Lake 59.9 m (13 on Figure 2); 7, specimen processed for Sr/Sr analysis; 8, DMNH EPV.136350. 9–10, *Polygnathus* sp., fused cluster, Bison Lake 59.9 m (13 on Figure 2), DMNH EPV.136357.
communication with the interior basins of Laurentia, or
migration and exchange around the periphery of the paleocontinent. Notable is the occurrence of *Patrognathus donbasicus* from 31.5 m at Crane Park Quarry (lower Coffee Pot Member). This taxon is also known from Ukraine (Kozitskaya et al., 1978), which at this time was on the eastern margin of Laurentia–Laurussia, where it is associated with similar conodont taxa. This indicates global migration around the continental margin, at least some of the time, even into the more restricted shallow platform environments represented by the Dyer Formation. This would be much more likely during times of higher sea level before the onset of extensive glaciation in the *Bispathodus ultimus* Zone. Such communication is also supported by the presence of pterygoid tooth plates, holocoelalian tooth plates, and *Orodus* teeth from the Dyer that are most similar to forms from the Famennian of Turkey, Western Australia/Poland, and Ireland/England, respectively (Schultze et al., in press). Other taxa seem to be endemic to the Dyer or western Laurentia, such as *Polygnathus communis pahvantensis*, which occurs in the upper Broken Rib and lower Coffee Pot, which was also reported by Sandberg and Ziegler (1979) from the Pinyon Peak Limestone in Utah, illustrated as *P. com. carina* Hass, 1959. It is unclear if this taxon occurs anywhere else. *Pseudopolygnathus primus craneparkensis* and *Icriodus costatus coffeepotensis* may also be endemic to the Dyer Formation.

CONCLUSIONS

The Dyer Formation conodonts, while not the most diverse or prolific for this interval, are important, because they provide a connection between biostratigraphically better constrained offshore to deeper-water D–C successions and shallower successions that are typically more depauperate in conodonts, yet diverse with macroscopic fossils. As an example, the Dyer lies geographically between thin exposures of the Ouray, Williams Canyon, and Temple Butte formations of Colorado and Arizona, and thicker coeval units to the west in the Pinyon Peak Limestone and Leatham Formation of Utah, and to the north in the Sappington and Bakken formations. Our new Dyer biostratigraphy offers opportunities to compare and correlate between these strata.

The occurrence of biostratigraphically relevant conodonts in suspected coprolites also highlights how fused clusters are a useful search image for paleontologists seeking biostratigraphic or ecologic control in otherwise “barren” stratigraphic successions like the intermittently lagoonal to peritidal facies of the Coffee Pot Member. Such records are relatively common in the American West and midcontinent, and may house a more complete record of these biotic events than previously recognized.

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APPENDIX 1. LOCALITY INFORMATION

Bear Scat Creek – DMNH 7542 - very small gully on north side of Deep Creek Canyon, 13S 0317955(E) 4395075(N) WGS 1984, Parting Formation to Leadville Limestone.

Deep Creek Side Canyon – DMNH 7541 - small tributary to Deep Creek on north side of Deep Creek Canyon, 13S 0319423(E) 4394935(N) WGS 1984, Broken Rib and Coffee Pot members.

Bison Lake – DMNH 4257 - hillside exposures 0.7 km northwest of Bison Lake, north of Forest Service Road 640 (Ute Trail), 13S 0298360(E) 4404590(N) WGS 1984, Parting Formation to Leadville Limestone.

Monument Lake – DMNH 4288 - hillside exposures 0.5 km west and southwest of Monument Lake, west of Forest Service Road 602 (Transfer Trail), 13S 0299450(E) 4396775(N) WGS 1984, Parting Formation to Leadville Limestone.

Glenwood Canyon – DMNH 8985 - section of Bass and Northrop (1963); also see Hauck (1954), Campbell (1966), Strauss (2006), and Myrow et al. (2011, 2013) - hillside exposures 1.2 km west of Glenwood Canyon trailhead parking area, on access road, 4.2 km west of the community of Dotsero, north side of Colorado River and Interstate 70, 13S 0318040(E) 4388415(N) WGS 1984, Parting Formation to Leadville Limestone.

Crane Park Quarry – DMNH 4258 - quarry and hillside exposures on both sides of Forest Service Road 600 (Coffee Pot Road), 5 km southeast of Owl Lake, 13S 0307345(E) 4399420(N) WGS 1984, Parting Formation to lower Coffee Pot Member.

APPENDIX 2. CONODONTS: SYSTEMATIC PALEONTOLOGY OF NEW AND SELECTED TAXA BY JEFFREY OVER.

The higher taxonomic categories of Sweet (1988) and element notation and terminology of Purnell et al. (2000) are followed herein. Figured specimens and accessory materials are repositioned at the Denver Museum of Nature & Science (DMNH). The holotype of *Patrognathus donbassicus* Lipnjagov, 1978 is in the Institute of Geology Sciences (IGS) at the National Academy of Sciences of Ukraine (AS) in Kyiv, Ukraine. The holotype of *Polygnathus communis pahvantensis* new subspecies is in the United States National Museum (USNM) in Washington, D.C.

*Patrognathus donbassicus* Lipnjagov, 1978
Figures 4.1–4.4, 4.6, 4.7
*Patrognathus donbassicus* Lipnjagov in Kozitskaya et al., 1978, p. 78–79, pl. 5, figs. 1 and 2; Lipnjagov, 1979, pl. 1, figs. 12a–12c (reillustration of holotype).

**Holotype:** 68/481 IGS AS UkrSSR, borehole 932, near the town of Dokuchaevsk, Upper Devonian, Famennian (C1’a Zone), the Donets Basin—reillustrated in Figure 4.4.

**Original description** (translated by T. Nemirovskaya from Kozitskaya et al., 1978):
Platform is straight and narrow in small specimens; it is wider and strongly curved in large specimens, with maximum width in the ventral part. The dorsal end is pointed. The upper surface of the platform is ornamented by low transverse ridges (ribs), which can grow together in the axial part and form a thin low ridge. The length of the blade is one-third of the total length of the element or slightly longer. The blade is formed by several denticles of almost equal height and the very large last denticle (cusp). This denticle is usually shifted inward. The basal cavity of small specimens is almost symmetrical and elongated. It is strongly asymmetrical in large specimens. It is very wide in the ventral third, with protruding edges. In the dorsal part, the basal cavity is narrower than the platform.

**Remarks:** No other elements in the apparatus can be unequivocally assigned to the taxon. Other features noted in the P1 element are that the large posterior cusp of the free blade is always on the right side of the element and the small ventral-most denticle disappears in larger specimens. In juvenile specimens a thin, axial ridge connects the denticles on the platform. This ridge persists in the dorsal portion of the platform in larger specimens. An axial groove may be present between the marginal middle and ventral platform denticles where the transverse ridges are not completely developed in larger specimens. *Patrognathus donbassicus* differs from the morphologically similar Late Devonian taxon *P. ourayensis* Sandberg and Ziegler, 1979, in that the basal cavity of *P. donbassicus* is tapered dorsally, more smoothly convex, and not as widely flared under the cusp; the cusp is reclined dorsally, and the dorsal platform has an axial ridge connecting the denticles and transverse ridges. In the Donets Basin, *P. donbassicus* occurs above the first occurrence of *Bispathodus costatus* and *Bi. ziegleri*, yet before *P. andersoni* and *Siphonodella aff. S. sulcata*.

*Polygnathus communis pahvantensis* new subspecies
Figures 5.1–5.4, 5.8
*Polygnathus communis carina* Hass, 1959, of Sandberg and Ziegler, 1979, p. 188, pl. 5, figs. 12 and 13.

**Holotype:** USNM 257660 SEP 77/1174, LDD-2, Pinyon Peak Limestone, ~10 m above the base of the unit, Pahvant Range, Utah, plate 5, fig. 12 of Sandberg and Ziegler (1979).

**Diagnosis:** Subspecies of *Polygnathus* (Neopolygnathus) communis Branson and Mehl, 1934—P element distinguished by a moderately curved dorsal carina and platform, raised margins of the platform in small specimens form a ventral rostrum in larger specimens where the platform out-
side the rostral ridges may have raised margins as well, especially on the caudal side, resulting in three to four short longitudinal ridges.

**Description:** P₁ element, carminiplanate, long free blade equal to length of platform in small specimens, two thirds to half the length in larger specimens; the ovoid platform, widest about mid-length, and carina are moderately curved with deep ventral adcarinal troughs. The platform margins are raised in the ventral portion, forming a rostrum in large specimens where the platform outside the rostral ridges may also have raised margins, especially on the caudal side, resulting in three to four short longitudinal ridges. The carina consists of fused denticles in the ventral portion that become more discrete dorsally, and they terminate before the tip of the platform. On the abaxial side the basal pit is small and symmetrical, with raised lips, starting at the end of the free blade in the ventral portion of the platform; dorsal from the pit is an elongate shallow depression; a narrow keel extends from the pit to the dorsal tip, widening slightly.

**Etymology:** The subspecies is named for the Pahvant Range, Utah, where the holotype was collected by Sandberg (Sandberg and Ziegler, 1979).

**Remarks:** This taxon was initially identified as *Polygnathus communis carina* Hass, 1959, a Tournaisian taxon and zone indicator quite distinct from this form. Hartenfels and Becker (2018, p. 616) and Hogancamp and Rodriguez (2020, p. 92) gave a thorough review of subspecies and species similar to *Polygnathus* (Neopolygnathus) communis ssp.

*Polygnathus* sp. in *P. inornatus* group of Hogancamp and Rodriguez, 2020

**Figure 5.11**

**Diagnosis:** Species of *Polygnathus* cf. *P. inornatus* Branson and Mehl, 1934b, that has a moderately curved dorsal carina composed of discrete denticles that reach the tip of the platform, the caudal margin is straight with short transform ridges on the raised rim of the platform; the rostral platform is wider and uniformly curved, the raised margin has short transform ridges.

**Description:** P₁ element, carminiplanate with lanceolate platform outline, free blade highest ventrally, less than half the length of the entire element. At mid-length of the platform the carina and outer platform margin curve moderately in the caudal direction; at this point and dorsally, the carina consists of discrete denticles that reach the pointed dorsal tip. Adcarinal troughs are well developed, and wider on the rostral side; the platform margins are raised and ornamented with short transverse ridges. The ventral platform margins merge abruptly at approximately the same position at the start of the free blade. On the abaxial side, the basal cavity is large with a raised rim beneath the ventral third of the platform, and is asymmetrical, grading into a keel with a central groove that extends to the ventral tip.

**Remarks:** The illustrated specimen is relatively small and similar to *Polygnathus* sp. C of Hogancamp and Rodriguez (2020, p. 100, pl. 5, figs. N, O, Q, R) in the curved nature of the ventral carina, differing in that the platform is widest at the dorsal end. The *P. inornatus* group of Hogancamp and Rodriguez (2020) includes several latest Devonian and Tournaisian taxa.

*Icriodus costatus* coffeepotensis new subspecies

**Figures 6.1–6.4**

**Holotype:** Figure 6.3, EPV.136340 from the upper Broken Rib Member, Crane Park Quarry, DMNH 4258, 25.5 m.

**Diagnosis:** Subspecies of *Icriodusalthatus* Thomas, 1949—P₁ element moderately arched, slightly curved, distinguished by a narrow and parallel-sided platform with a wide, asymmetrical basal cavity.

**Description:** P₁ element, segminiscaphate, moderately arched, slightly curved, narrow and parallel sided, cusps low and directed dorsally, medial denticles are low and narrow, marginal nodes are low, rounded, and aligned with the medial denticles. A thin longitudinal ridge connects the medial denticles; aboral surface is characterized by a wide, asymmetrical basal cavity, widest in the dorsal half, continuously convex on the rostral side, concave and narrowing ventrally on the caudal side.

**Etymology:** The subspecies is named for Coffee Pot Springs, Colorado, for which the Coffee Pot Member of Campbell (1970) is presumably named.

*Pelekysgnathus* soarae new species

**Figure 6.10**

*Pelekysgnathus* cf. *P. brevis* Sandberg and Dreesen of John-son and Chatterton, 2001, pl. 4, fig. 15 (only).

**Holotype:** Figure 6.10, EPV.136347 from the lower Coffee Pot Member, Crane Park Quarry, DMNH 4258, 31.5 m.

**Diagnosis:** Species of *Pelekysgnathus*—P₁ element distinguished by a short, high, gently curved blade, reclined dorsal cusp, and wide basal cavity that extends beneath the ventral denticles.

**Description:** P₁ element, segminate, short gently curved blade, slightly arched, large reclined dorsal cusp, several laterally compressed denticles, blade highest mid-length. Basal cavity extends the length of element, widest mid-length to the dorsal tip.

**Etymology:** The subspecies is named in honor of Linda Soar for her exemplary work in the field and contributions to the Denver Museum of Nature & Science.

**Remarks:** No coniform elements were found associated with the P₁ elements. *Pelekysgnathus* soarae has a short blade that is similar to the Givetian taxon *P.brevis* Sandberg and Dreesen, 1984, but the former is characterized by a reclined
cusp, more denticles, and a widening of the basal cavity that extends beneath the ventral portion of the blade. Johnston and Chatterton (2001) illustrated several specimens as *P. brevis* from Famennian carbonate strata in western Canada characterized by only one or two denticles, as well as one similar to *P. soarae*.

**Pseudopolygnathus primus craneparkensis new subspecies**

Figures 7.1–7.5

**Holotype:** Figure 7.3, EVP.136353, upper Broken Rib Member, Crane Park Quarry, DMNH 4258, 27 m.

**Diagnosis:** Subspecies of *Pseudopolygnathus primus* Branson and Mehl 1934b—*P* \(_1^1\) element distinguished by a gently curved free blade, carina, and platform, more obvious in smaller specimens, absence of a distinct caudal lobe, and larger nodes on the right side of the platform, regardless of the direction of curvature.

**Description:** *P* \(_1^1\) element, carminiplanate, free blade less than one-third the length of the element, widening dorsally where it meets the platform. Platform outline is lanceolate in small specimens, irregular in large specimens. The free blade, carina, and platform are gently curved. Denticles on the free blade number 5 to 7. Denticles on the ventral carina are fused and become discrete in the dorsal carina, where they extend to the tip of the platform. Adcarinal troughs are well developed. The rostral platform margin is continuous, or has a sinus in the dorsal half that results in a ventral lobe; nodes on the margin are evenly spaced, larger in the ventral portion. On larger specimens the platform margin bears ridges and elongate nodes that extend perpendicular to the margin; the caudal platform margin is continuous, or there is a small lobe developed over the expanded basal cavity; larger specimens may have an additional dorsal lobe. Nodes on the platform margin, or in larger specimens ridges and elongate nodes that extend perpendicular to the margin, are smaller or absent. Some elongate nodes or ridges may connect to the carina. On the abaxial side the basal cavity is large, asymmetrical, extending from where the free blade widens to the dorsal tip; the cavity is widest below the ventral platform, with a central longitudinal slit and pit.

**Etymology:** The subspecies is named for Crane Park Quarry along the Coffee Pot Road in the White River National Forest, Colorado, where this taxon was collected.

**List of additional Dyer conodonts and key references**

*Apatognathus varians* Branson and Mehl, 1934a, p. 201, pl., 17, figs. 1–3; Hogan camp and Rodriguez (2020), p. 82–84, pl. 1, figs. A–P; Figures 6.7–6.9

*Bispathodus aculeatus aculeatus* Branson and Mehl, 1934a, p. 186, pl. 17, figs. 11 and 14; Ziegler et al., 1974, p. 101, pl. 1, fig. 5, pl. 2, figs. 1–8; Hogan camp and Rodriguez (2020), p. 86, pl. 2, figs. B–G, L, M; Figure 4.11

*Bispathodus cf. Bi. aculeatus plumulus* Rhodes, Austin, and Druce, 1969, p. 229–230, pl. 1, figs. 1, 2, 5, 6; Ziegler et al., 1974, p. 101–102, pl. 2, figs. 10, 11, pl. 3, fig. 24; Hartenfels, 2011, p. 234 (= *Chyagnostus plumulus*), pl. 35, fig. 1; Hogan camp and Rodriguez (2020), p. 86–88; Figures 4.8 and 4.12

*Bispathodus stabilis* Branson and Mehl, 1934a, p. 188, pl. 17, fig. 20; Ziegler et al., 1974, p. 103–104, pl. 1, fig. 10, pl. 3, figs. 1–3; Hartenfels (2011), p. 222–226, pl. 31, figs. 5–8 (= *Bispathodus stabilis vulgaris*); Hogan camp and Rodriguez (2020), p. 88–89, pl. 2, figs. H–K; Figure 4.5

*Icriodus costatus darbyensis* Klapper, 1958, p. 1,086, pl. 141, figs. 9, 11, 12; Hogan camp and Rodriguez (2020), p. 92, pl. 3, figs. N–Q. Klapper (1966) synonymized the taxon in *I. costatus*, which was then re-established by Dreesen and Houlleberghs (1980); Figures 6.5 and 6.6

*Pandorinellina cf. P. initia* Stauffer, 1940, of Sandberg and Ziegler, 1979, p. 192, pl. 7, figs. 8–10, 12, 15; Figures 4.9 and 4.10

*Pelekysgnathus inclinatus* Thomas, 1949, p. 424–425, pl. 2, fig. 10; Sandberg and Dreesen (1984), p. 16–162, pl. 3, figs. 5–7–19, pl. 4, figs. 7–9; Figures 6.11 and 6.12

*Polygnathus experplexus* Sandberg and Ziegler, 1979, p. 185, pl. 4, figs. 2–6; Figure 5.9

*Polygnathus perplexus* Thomas, 1949, p. 418, pl. 2, fig. 23; Sandberg and Ziegler, 1979, p. 185, pl. 4, fig. 1; Figure 5.12

*Polygnathus semicostatus “2”* Branson and Mehl, 1934a, of Dreesen and Orchard, 1974, p. 4, pl. 1, fig. 2a–d; Figure 5.7

*Polygnathus semicostatus “5”* Branson and Mehl, 1934a, of Dreesen and Orchard, 1974, p. 4, pl. 1, fig. 5; Figure 5.6

*Polygnathus subirregularis* Sandberg and Ziegler, 1979, p. 186, pl. 4, figs. 7 and 8; Figures 5.5 and 5.10

*Pseudopolygnathus primus ssp.* Branson and Mehl, 1934a, p. 298, pl., 24, figs. 24 and 25; Hartenfels and Becker (2018), p. 617–620, fig. 20m–u, 22; Figures 7.7 and 7.8

*Siphonodella sp.* Branson and Mehl, 1934b, p. 295; Figure 7.9