Conodont Studies Dedicated to the Careers and Contributions of Anita Harris, Glen Merrill, Carl Rexroad, Walter Sweet, and Bruce Wardlaw

Edited by D. Jeffrey Over and Charles M. Henderson
# CONTENTS

D. Jeffrey Over  
Editor’s preface ................................................................. 5

John Repetski and Julie Dumoulin  
Anita G. Harris, researcher and role model .......................... 7–11

Stig M. Bergström and Mark Kleffner  
Walter C. Sweet—Reflections on the scientific work and life of a globally known conodont worker ......................... 13–17

Lewis M. Brown and John C. Steinmetz  
Carl B. Rexroad: In remembrance ..................................... 19–22

Peter von Bitter  
Glen Kenton Merrill, B. Columbus, Ohio, Aug. 28, 1935; D. Houston, Texas, Dec. 2, 2014 — A personal remembrance. ... 23–27

Charles M. Henderson  
Dedication to Bruce R. Wardlaw ......................................... 29–34

Nicholas J. Hogancamp and James E. Barrick  
Morphometric analysis and taxonomic revision of North American species of the *Idiognathodus eudoraensis* Barrick, Heckel, & Boardman, 2008 group (Missourian, Upper Pennsylvanian Conodonts) .................................................. 35–69

Javier Sanz-López and Silvia Blanco-Ferrera  
Conodonts with high potential for correlation in the upper Tournaisian to middle Viséan (Mississippian) of the Cantabrian Mountains, Spain .................................................. 71–87

Michael T. Read and Merlynd K. Nestell  
Cisuralian (Early Permian) sweetognathid conodonts from the upper part of the Riepe Spring Limestone, North Spruce Mountain Ridge, Elko County, Nevada ........................................ 89–113

Martyn L. Golding  
The multielement apparatuses of Guadalupian to Lopingian (Middle-Upper Permian) sweetognathids from North America, and their significance for the phylogeny of Late Paleozoic conodonts .................................................. 115–125

Merlynd K. Nestell and Bruce R. Wardlaw  
Contrasting apparatus reconstructions of the Middle Permian conodont *Pseudohindeodus ramovi* .......................... 127–147

Tea Kolar-Jurkovšek, Carlos Martínez-Pérez, Bogdan Jurkovšek, and Dunja Aljinović  
New clusters of *Pseudofurnishius murcianus* from the Middle Triassic of Slovenia (Dinarides) .......................... 149–163

Michael J. Orchard  
The Lower-Middle Norian (Upper Triassic) boundary: New conodont taxa and a refined biozonation ......................... 165–193

Index .......................................................... 195–198
EDITOR'S PREFACE

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It is with great sadness that I edited (with Charles Henderson) and write a preview to this volume dedicated to the memory and works of five great North American conodont workers—North American in the sense of origin and residence, but not in the scope of work and importance. Several of these papers were first presented in Geological Society of America Pander Society sessions dedicated to Anita Harris—October 2015—and Bruce Wardlaw—September 2016. The dedication grew with the desire to include Carl Rexroad, Walt Sweet, and Glen Merrill as the volume was compiled. I knew all five reasonably well; all hosted me at their homes, offices, labs, or we interacted in the field or at meetings on numerous occasions. I learned essential things from each that have made me a better person, scientist, and teacher.

Carl Rexroad was the first conodont worker, outside of my degree program contacts, to be nice to me. After giving my first Pander Society meeting talk as a graduate student in Knoxville he approached me and offered congratulations. A kind gesture from someone who I had referenced extensively in my masters thesis and typical of Carl as a gentleman and scholar. Walt Sweet was also at the Knoxville meeting. I introduced myself and in the course of our conversation he said: “travel as much as you can, especially now before you get too much responsibility.” I took this advice to heart and apparently never gained responsibility as he recognized it. Anita Harris is my hero – she worked harder than anyone, was generous with her time, famously spoke her mind, and was crazy smart as well as fun. My cohorts, best stated by Mark Kleffner, knew to never look at Anita when giving a talk, as she would invariably be sadly shaking her head at the errors of our identifications and interpretations. Bruce Wardlaw and Glen Merrill were like storms—beautiful and terrifying to behold, especially when in the same room. They taught me that it is fine to disagree—just be able to support your position and proposals—and to be collegial and social as well. Both were outstanding scientists and extremely passionate. So basically: do good science, work hard, be nice (but do not tolerate fools), travel, it is alright to disagree and say what is on your mind, just do it passionately. We miss you all greatly.

D. Jeffrey Over
Geneseo, NY, October 2017
In summer 2014, the Pander Society, and historical geology, lost one of its stars. During the last third of the 20th Century, Anita Harris (Text-figs. 1–3) contributed significantly to the study of conodonts, including making them a key component of thermal maturation assessment in energy and mineral resource evaluations, and of geologic mapping and regional stratigraphic and tectonic history studies. Her energy, work ethic, and scientific vision enabled her to broaden the recognition of the utility of conodonts to a wider range of scientists who previously surely dismissed them as ‘those curious, if sometimes stratigraphically useful microfossils.’

Anita G. Fishman Epstein Harris was born in New York City (10 July 1937) and received her BS degree from Brooklyn College at age 19. As she said many times, she decided that geology was not only interesting, but it also showed her a way to see more of the world. Following Masters degree work in geophysics at Indiana University, Anita took a job with the U.S. Geological Survey in the Washington, DC area, doing geologic mapping for several years in eastern Pennsylvania and in the western US. During one eventful summer (1959), Anita and husband Jack Epstein received a personal demonstration of geologic catastrophism: while mapping in southwestern Montana, they were camped over the epicenter of the major earthquake at Hebgen Lake.

Before long, Anita returned to graduate school, this time at Ohio State University, and pursued a dissertation project on Devonian micropaleontology and stratigraphy with Walter Sweet as her major professor (PhD completed in 1970). As Anita related later, Professor Sweet was not the easiest supervisor for such a broad-minded, independent student. Their disagreements extended beyond his unwillingness to approve her signing up to take such courses as metamorphic petrology, in which she saw potential value for a well-rounded field geologist, all the way to his suspicion that he might be wasting his time supervising a female student who would most likely just go off and abandon science for family life. It must be said, however, that as Anita’s career progressed, her relationship with “Dr. Sweet” (she never could lose that habit) also progressed through mutual respect to genuine friendship. It was during her thesis work that Anita began her conodont studies, and also when she began wondering why her similar-aged conodonts were of different colors across her study area, with consistently darker colors from west to east across northern Ohio and New York State. She and husband Jack began testing whether the color changes might be related to heating by baking conodonts in their home oven at various temperatures for a range of times. Heating produced the effect of color change, but was the change due to tectonic pressure or to simple heat of burial? As her study traverse was across a relatively tectonically stable region, the latter hypothesis seemed to be correct and was supported by isopach maps of overlying strata, but additional evidence was needed. After completing her PhD coursework, Anita returned to the Washington D.C. area in 1967, with hopes of reemployment with the USGS, but there were no positions available for a newly-minted PhD [female] mapping/research geologist, and after a semester of teaching at a Washington-area middle school, Anita took the job as an editor of USGS geologic maps. During her eight years as map editor, Anita not only gained experience and vicarious exposure to the geology of many different regions and terranes, but she also necessarily met and interacted with a broad range of many of the best geologists in the USGS of that time, most of whom appreciated, some grudgingly so, her improvements to their publications. Many of those contacts paid dividends years later, when some of those geologists sought out her stratigraphic expertise. But even during those map-editing years, Anita continued in her spare time to pursue the why and wherefore of conodont color changes. Finally, with the cooperation of the head of the Oil and Gas section of USGS, who had recently been hired from a major oil company and who was familiar with the importance of knowledge of thermal maturation to oil and gas exploration, Anita was able to conduct proper heating experiments in the lab, enabling her to calibrate colors, temperatures, and
time, and to establish the conodont color alteration index, or CAI. In 1974, as she was completing the professional paper documenting the CAI and presenting the scheme to the eager energy industry (Epstein et al., 1977), Anita joined the Paleontology and Stratigraphy Branch of USGS, allowing her to work on conodonts full time.

To Anita, ‘full time’ really meant that: working long days at the office/labs, then late into the evenings picking and writing at home, all the while attending to her other duties and interests, raising her daughter Laura, cooking, gardening, and stamp collecting. Many colleagues, students, and mentees who visited Anita during her time in Washington, when the Paleontology & Stratigraphy Branch of USGS was located in the U.S. National Museum of Natural History, and later at USGS headquarters in Reston, Virginia, can attest to her long days of hard work. And those many lucky ones who were hosted at Anita’s home during their visits, lasting from a day to many weeks, also continued their “Pander Society meetings” late into the night. Case in point: during the North American Paleontology Convention in 1995, Anita chauffeured and hosted at ‘Chez Anita’ at least four fellow Panderers, from at least three countries; the convention expanded to include the morning and evening commutes as well as the after-dinner and into-the-night ‘symposia.’ An Anita mantra: ‘Sleep is overrated.’

Much of the first half of Anita’s career was devoted to conodont biostratigraphy and constructing CAI maps for the eastern U.S. and the Great Basin in the western U.S. The CAI maps of the central and northern Appalachians (Harris, Harris & Epstein, 1978) also record her name change to that of her second geologist husband, Leonard Harris. Her second major paper on the CAI system (Rejebian, Harris & Huebner, 1987) extended the utility of conodont thermal indices into metamorphic temperatures, making our microfossils important tools in mapping, structural, and minerals studies in metasedimentary host-rocks. This paper also was an early study of conodont surface texture alteration. Anita was quite proud of this work, notably that it was the product of a college undergraduate thesis by one of her several mentees, Vivian Rejebian.

Anita’s stratigraphic interests were primarily on the Middle Ordovician through Devonian. As per the duties of USGS paleontologists, however, Anita supplied age-dating support for USGS geologists as well as for geologists and students from universities, industry, state geological surveys, and many other organizations worldwide. Although author/co-author of more than 200 published papers, Anita was not involved with very many taxonomic studies. Her scientific ‘fulfillments’ came from dating the previously undated unit, or picking identifiable conodonts from a residue of mostly tremolite/actinolite crystallites, or producing a CAI and stratigraphic column from a core or cuttings from a new oil or gas field. She produced thousands of pages of reports on many thousands of samples, Cambrian through Triassic; her reports included not only her analysis of age, but also the faunal list, the CAI and its interpretation, biofacies, provinciality, and other bits of valuable data, e.g., notable heavy minerals in the residues. This treasure trove of documents, much of it never published, is preserved and available as scanned digital records in the USGS National Geologic Map Database. As Anita said many times, “I want my data found, and used.”

Anita spent as much time as she could in the field, measur-
ing, describing, and collecting key sections, and visiting other field geologists in their areas with the goal of helping solve their stratigraphic problems. In the second phase of her career, Anita focused most of her research in the two regions that came to interest her the most, the U.S. Great Basin, especially minerals-rich Nevada, and Alaska, the “last frontier” of the U.S. Nevada, with its Paleozoic-hosted gold and other minerals, provided Anita with myriad opportunities to apply conodont biostratigraphic and thermal analyses to the studies of USGS mappers and economic geologists, and even after her retirement both USGS and numerous non-USGS explorationists continued to seek out her help. With Elizabeth Jones Craford, Anita compiled a conodont database for more than 2600 conodont samples known at that time from Nevada, to accompany Craford’s Geologic Map of Nevada (2007).

Many colleagues sent Anita samples from huge and remote Alaska, piquing her interest in the area. In the early 1980s, Anita joined forces with regional geologist and carbonate sedimentologist Julie Dumoulin of the USGS offices in Anchorage. Together, Julie and Anita documented a wide swath of previously poorly-understood Paleozoic and Triassic rocks across the state, contributing to studies of both hydrocarbon and mineral resources. From 1974 to 2006, Anita’s labs processed more than 8000 samples from Alaska. Because so many of the rocks of interest were deformed and/or metamorphosed, Anita strongly encouraged taking big samples – that is, 5 to 10 kg (or more!); conservatively, that is about 40,000 kg of rock. In the mid-1980s, so many conodont samples were collected in support of the 1:250,000-scale quadrangle mapping projects in Alaska that Anita helped set up a processing lab in Anchorage.

About 4000 of the Alaskan conodont samples were productive. Analyses of these samples helped transform understanding of the stratigraphy, depositional settings, paleogeography, and tectonic and thermal histories of Paleozoic-Triassic strata across the state. Conodonts were found in half of the 153 Alaskan 1:250,000 quadrangles, from Dixon Entrance in the south to Barrow in the north. Anita’s conodont studies were fruitful in both metamorphosed and unmetamorphosed rocks. The former included metacarbonate rocks of greenschist and blueschist facies on the Seward Peninsula and through a >700 km-long belt in the western and central Brooks Range; the latter included the Farewell terrane in interior Alaska.

The thermal maturity map of Alaska (Johnson et al., 1992; Johnson & Howell, 1996) incorporates 1500 CAI determinations from more than 1300 locations across the state. Finally, Anita’s work between 1983 and 2006 on the Carboniferous to Permian Lisburne Group, which extends more than 1000 km across northern Alaska, elucidated the stratigraphy, paleogeography, and thermal maturation of this unit that hosts world-class oil, gas, and massive sulfide deposits.

In the early 1990’s, Anita and Julie were able to host Mussa Gagiev from Magadan, Russia, for a month long visit to the U.S. to spend time comparing his conodonts from eastern and northeastern Siberia with collections from the United States. These studies produced insights into paleobiogeographic connections between northeastern Asia, Alaska, and the rest of North America during the Paleozoic. A year or so following Mussa’s visit, Anita traveled to Magadan to present two papers at an arctic geology conference. Due to a perceived problem with her visa, Anita was detained at the Magadan airport for three days, with daily visits from Mussa being her only reliable go-between for news, sustenance, and outside communication. Anita was sent back to Anchorage on the next plane. Afterward, she noted with some pride that she must be one of the rare people deported from Siberia.

Anita loved to share her knowledge. She hosted many students in her lab, from high schoolers to post-docs. They all were expected to work hard, and most of the willing have gone on to successful careers. She took two “sabbaticals” from the USGS, to teach at Duke and Case Western Reserve universities. One of Anita’s favorite ‘teaching’ experiences came when John McPhee asked her to guide him through the geology along a transect from Long Island, New York, to the vicinity of Chicago, Illinois. McPhee crafted his notes from this trip into his 1983 book “In Suspect Terrain,” which subsequently was included in his Pulitzer Prize-winning (1999) 5-book compilation “Annals of the Former World.” These books are recommended for additional interesting, colorful, and enlightening biographical material about Anita.

Always acutely aware that she was a ‘minority’ and pioneer as a female in geology, Anita was a ready mentor and an inspiration to numerous younger females exploring careers in science. She was proud to have been involved in an exhibit at the
Chicago Museum of Science – “My Daughter the Scientist.” In 1991, Anita was awarded the Pander Society Medal, the youngest awardee of that honor. To her argument that she was too young for that medal, Walt Sweet countered that her work opened a whole new aspect of conodont research and indeed had created new career opportunities for Panderers to follow. In 2015, Anita was awarded, posthumously, the Harrison Schmitt Award by the American Association of Petroleum Geologists; the biographical write-up in the May 2015 issue of the AAPG Explorer is well worth reading (Saucier, 2015).

Following her retirement in 1999 and her relocation to Florida, Anita continued her research, with Julie Dumoulin on Alaska projects and with USGS minerals researchers in Denver, as well as consulting on samples submitted to her from many quarters. Tragically, at the early age of 70, she began a slide into Alzheimer’s disease and passed away on 12 July 2014, two days after her 77th birthday. Anita’s legacy in the conodont world is secure, and she will remain a source of inspiration.

LITERATURE CITED


CHRONOLOGICAL SELECTION OF NOTABLE PUBLICATIONS BY ANITA HARRIS


WALTER C. SWEET—REFLECTIONS ON THE SCIENTIFIC WORK AND LIFE OF A GLOBALLY KNOWN CONODONT WORKER

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ABSTRACT
Walter C. Sweet (1927–2015) was one of the internationally most prominent conodont workers during the twentieth century. He spent his pre-college life in Denver and later studied at Colorado College and the University of Iowa, where he received his Ph.D. degree in 1954. His dissertation included a mapping project in the Rocky Mountains and study of the Ordovician Fremont Formation cephalopods and Harding Sandstone conodonts. He was hired as an Instructor at the Ohio State University in 1954 and virtually his entire professional career was spent as a geology professor at this university in Columbus, Ohio, where he was a highly successful teacher who attracted many excellent graduate students. Among these, some became known internationally. His wide-ranging conodont research was particularly focused on the Ordovician and the Permian–Triassic, but he studied conodonts from all the Paleozoic systems. Much of his national and international research was of biostratigraphic nature and he was a pioneer in using conodont-based graphic correlation. He described numerous new conodont and cephalopod taxa from many parts of the world. In cooperation with one of us (SMB), a new approach to conodont classification, namely multielement taxonomy applied to isolated elements, was introduced in the 1960s and had a profound influence on conodont taxonomy. Among his more than 200 publications, perhaps the best known internationally is his conodont book that, thirty years after its publication in 1988, remains a widely used general summary of most aspects of conodonts. His quite comprehensive professional service included Secretary (1976–1982) and President (1983–1985) of the Paleontological Society, and Chief Panderer (=President) of the Pander Society (1975–1985), which is the international organization of conodont researchers.

One of the all-time international leaders in conodont research, Walter C. Sweet, passed away at age 88 on December 4, 2015 after an unsuccessful bypass operation following a heart attack. His death marked the end of a scientifically highly productive life and a distinguished career as a teacher. His instruction career included having been mentor of several dozen graduate students among whom some became internationally known conodont workers, such as T. J. M. Schopf, Anita Epstein (Harris), Jeff Bauer, and Mark Kleffner.

One of us (MK) first met and visited with him when MK was a pre-school fossil-collecting kid in the 1960s. In the 1970s and early 1980s, Walt was both his senior thesis and M.S. thesis advisor and he became Walt’s last Ph.D. student, receiving his degree in 1988, the year of Walt’s retirement from The Ohio State University. MK subsequently continued keeping in touch with Walt during Walt’s retirement years and he was asked by Walt to house his unpublished research notes on graphic correlation.

Although formally not being one of Walt’s university degree advisees, the other author of this account (SMB) was a close friend and co-investigator with Walt on numerous projects during more than a quarter of a century. He first met Walt in the summer of 1960 and served as his Research Assistant in Columbus during the 1960–61 academic year. During the next few years they maintained close contact. SMB spent the summer of 1964 in Columbus, and later made arrangements for Walt to have a paid sabbatical leave at the Lund University in Sweden during the first half of 1966. After SMB’s employment at the Ohio State University in early 1968, Walt and SMB annually team-taught numerous graduate courses and met daily for lunch and other purposes. Hence, the two authors of this account feel that they knew Walt and his work as well as anybody.

As noted in a recent memorial (Bergström & Ausich, 2016), Walt was born in Denver on October 17, 1927 and attended public schools in that city. His family had also a vacation cabin in the Rocky Mountains west of Denver where Walt spent many happy summers and developed his life-long fondness of the nature of the West. After having received his B.Sc. degree at Colorado College, a place that he remembered with affection all his life (he donated his private research microscope to that college after his retirement), Walt continued his education at the

University of Iowa, where Professor A. K. Miller, a prominent and highly productive cephalopod specialist, became his graduate advisor. In view of Miller’s research interests, it was natural that Walt’s thesis work would be a combination of mapping an area in the central Rocky Mountains and an investigation of the Upper Ordovician Fremont Formation cephalopods and the Middle Ordovician Harding Sandstone conodonts. Walt obtained his Harding conodonts by breaking down, washing and boiling shaly interbeds in the Harding successions because of the non-calcareous nature of the sandstone. At that time, isolation of conodonts by the use of weak acids was little employed in North America. Twenty-five years later he processed limestone samples from the Fremont Formation with diluted glacial acetic acid (Sweet, 1979b). Walt received his M.S. degree in 1952 and his Ph.D. degree in 1954 and joined the faculty at The Ohio State University the same year as Instructor. He was promoted to Assistant Professor in 1957, Associate Professor in 1961, and Professor in 1966. Apart from a couple of sabbatical leaves, he spent his entire academic career at The Ohio State University until his retirement in 1988.

As noted by Bergström & Ausich (2016), he was a very successful educator who taught a variety of courses at both the undergraduate and graduate levels. His success is shown by the fact that he was awarded by the graduate students the prestigious Distinguished Teaching Award twice (1971, 1982) and supervised the thesis work of about 40 students. All through his university career, Walt maintained a strong research interest. As a continuation of his Ph.D. dissertation work, he was for several years working with cephalopods. This is shown by, for instance, his comprehensive monograph on Ordovician cephalopods from the Oslo region, Norway (1958) and his authorship of five chapters of the Mollusca 3 volume (Part K) of the Treatise on Invertebrate Paleontology (Teichert et al., 1964). However, there is no doubt that from the late 1950s on, his principal research interest was conodonts. After the publication of his Ph.D. conodont research on the Harding Sandstone conodonts (1955), his next conodont paper was a 1956 study in cooperation with G. A. Stewart on Devonian conodonts from central Ohio (Stewart & Sweet, 1956). In the mid-1950s, he initiated, in cooperation with his colleague M. P. Weiss, an extensive study of the North American Upper Ordovician Standard, the Cincinnatian Series, in its outcrop area around the City of Cincinnati. This project, which came to involve quite a few graduate students, resulted in more than a dozen papers published at irregular intervals through most of his research career. As outlined by Sweet (1979a), he came to the general conclusion that the prevailing old idea that the Cincinnatian succession consists of a series of widespread lithic units deposited in a layer-cake fashion was incorrect and that several of the formations were markedly diachronous. Later work by several workers suggests that his reinterpretation is likely to be correct in some cases, but the general application of his model remains controversial and the problem is in need of further study.

At the invitation of Walt, SMB spent a year (1960–1961) at Ohio State, where he served as Walt’s Research Assistant. This marked the beginning of a close scientific cooperation on Ordovician conodonts that came to last more than a quarter of a century and resulted in more than 14 articles, some of international scope. The first of these, which described the conodonts of the Pratt Ferry Beds of Alabama (Sweet & Bergström, 1962), showed for the first time that latest Darriwilian–Sandbian conodont faunas of the eastern Appalachians contained a significant number of short-ranging conodonts that were previously best known from Baltoscandia, which permitted quite detailed trans-Atlantic correlations. Additional sampling by SMB and his students from many sections in the Southern Appalachians later showed that the detailed conodont biostratigraphy suggested that the prevailing brachiopod biostratigraphy was quite incorrect in several regions. Although Walt was not involved in these studies, he frequently discussed the new results and used some of the interpretations in some of his papers, such as Sweet (1984).

It should be noted that from the beginning in 1960, the joint work of Walt and SMB followed the same arrangement. After initial sample processing, mainly by SMB, SMB and Walt had a general discussion about the organization of the report. When these data were available, SMB produced a draft report that was critically read and edited by Walt, who with a single exception designated himself as senior author. Although our opinions differed occasionally, this was an enjoyable and productive cooperation that came to last some 25 years. Interestingly, in several respects this cooperation was similar to that of Branson and Mehl in their classical conodont work in the 1930s. It should be noted that during this long cooperation, both SMB and Walt also pursued many independent investigations, many with other workers, which resulted in numerous publications with a variety of authors.

A major result of cooperation between Walt and SMB in the 1960s was the development of the multielement conodont taxonomy as a replacement of the prevailing form taxonomy. This involved a taxonomy that was based on the composition of the entire conodont apparatus rather than one based on the appearance of single conodont elements, such as that advocated by Lindström (1955) in his classical monograph. Early attempts of using multielement taxonomy were, for instance, that by Bergström (1962)—who grouped a series of morphologically different coniform elements of Strachanognathus parvus Rhodes into one species—and the reference by Sweet and Bergström (1962) that grouped several morphologically different types of coniform elements of Scolopodus (now Protopanderodus) varicostatus Sweet & Bergström into a single species. Based on morphological similarities and the general co-occurrence of elements in very large conodont collections from the Lexington Limestone of Kentucky and coeval strata in adjacent states, Bergström & Sweet (1966) presented reconstructions of several conodont apparatuses that they regarded as multielement species. Much of this work was done around 1963, SMB spent several months of the 1964 summer in Columbus and during this time, the late Gerald Webers of the University of Minnesota...
paid a visit to The Ohio State University. In his Ph.D. work on the Middle and Upper Ordovician conodont faunas of Minnesota, he had begun applying multielement taxonomy to some of his conodont taxa and SMB and Webers had productive discussions about how to recognize multielement species in Ordovician conodont faunas. For various reasons, the printing of the Lexington Limestone monograph was delayed to 1966 and Webers’ publication appeared during the same year (Webers, 1966). During the rest of the 1960s, the multielement approach was met with skepticism by many workers, especially those concerned that well-known zone designations might have to be changed as a result of using multielement taxonomy. Although some workers continued using form taxonomy well into the 1980s, multielement taxonomy became firmly established internationally in the 1970s. Walt employed this approach in all his papers after 1966. Ironically, it was our experience that graduate students with little conodont experience generally had no problems using multielement taxonomy.

In the late 1960s, Walt became involved in extensive investigations of Permian and Triassic conodonts based on samples collected by the internationally known paleontologists Curt Teichert and Bernhard Kummel. He had cooperated with these paleontologists in the preparations of the nautiloid cephalopod volume of the Treatise on Invertebrate Paleontology so it was natural that he got access to their rock samples from several parts of the world, especially the Salt Range in Pakistan, Kashmir, and several localities in Iran and eastern Greenland. These investigations (e.g., Sweet, 1970, 1979c) established him as an international expert on the taxonomy and biostratigraphy of the then very poorly known late Paleozoic and early Mesozoic conodont faunas. As shown by several publications, he maintained interest in conodonts of that time interval during the rest of his professional life.

A major event in conodont biostratigraphic research was the Symposium on Conodont Biostratigraphy, which was organized by Walt and SMB and took place at The Ohio State University on May 15–16, 1969 and attended by numerous national and international conodont workers. It resulted in a 499-page, widely cited memoir, edited by Walt and SMB, that for the first time gave a global view of conodont biostratigraphy from the Cambrian to the Triassic (Sweet and Bergström, 1971). Walt was the senior author of a chapter on North American Middle and Upper Ordovician conodont faunas that summarized much widely scattered published information as well as a wealth of new data. In this chapter, the authors recognized for the first time 12 Middle and Upper Ordovician biostratigraphic units, referred to as Faunas, based on detailed range data. The Faunas became widely used up to the 1980s, particularly in the North American Midcontinent. In the same volume, Walt was also the senior author of an article entitled Conodont Biostratigraphy of the Triassic, in which 20 named conodont zones were recognized and correlated with the ammonoid zones. Walt had a particularly productive period during the 1970s and early 1980s when he published quite a few significant studies. During that decade, he also was a frequent participant in international symposia in Europe and elsewhere (Text-fig. 1). Joint papers with SMB during this period include, among others, papers on conodont provincialism (Sweet & Bergström, 1972; 1984), multielement taxonomy (Sweet & Bergström, 1972), and conodont biostratigraphy of the North American Midcontinent (Sweet & Bergström, 1976). Walt’s extensive work on the Upper Ordovician conodont biostratigraphy of the Cincinnati region was summarized with many new data in Sweet (1979a). In the same year, he published a similar monographic study on the Upper Ordovician conodonts of the Western Interior (Sweet, 1979b). In this study, he recognized many new taxa that subsequently have proved to have a wide distribution. A few years later (Sweet, 1984) he introduced a modified conodont zonation of the Middle and Upper Ordovician of North America that was largely based on graphic correlation. From reading A. B. Shaw’s book Time in Stratigraphy (Shaw, 1964), Walt had been strongly inspired to use the graphic correlation technique and he employed this method, beginning in 1979, for all papers dealing with conodont biostratigraphy (for instance, Sweet, 1979a, 1979b, 1979c). Sweet’s 1979 papers were the first in a series of papers using the graphic correlation technique to correlate Ordovician strata of the North American Midcontinent Province that continued through 2005 (e.g., Sweet, 1984, 2000). Sweet (1979c) was the first of several papers using graphic correlation on Permian-Triassic strata of the Middle East and Asia (e.g., Sweet, 1992). His final paper using this technique, and apparently his last article as senior author, correlated Lower/Middle Ordovician sections in the Argentine Precordillera with coeval ones in North America (Sweet & Albanesi, 2006).

In the 1980s, Walt (Text-fig. 2) started work on his opus magnum, the book The Conodonta: Morphology, Taxonomy, Paleontology, and Evolutionary History of an Extinct Animal Phylum.
long-time friends and colleagues, and did not attend national and international meetings. Contributing to this was undoubtedly an eye problem that prevented him from using a microscope and his wife’s increasingly serious health problems that made it difficult for him to leave home.

During much of his professional career, Walt was quite active in professional service. Apart from being a widely used manuscript reviewer, he was Secretary (1976–1982) and President (1983–1985) of the Paleontological Society. He was also long-time Chief Panderer (=President) (1975–1985) of the Pander Society, the international association of conodont workers. For many years, he also spent much time on the activities of the Ordivician, Permian, and Triassic subcommisions of the International Commission on Stratigraphy.

In view of his important scientific contributions, it is not surprising that Walt received a number of major professional awards. These include the Pander Gold Medal (1985), the highest international award in conodont research; the Raymond C. Moore Medal (1988), the most prestigious award in soft-rock geology and paleontology in North America; and the Paleontological Society’s Medal (1994), the foremost American paleontology award. Only one other person has received all these three awards.

Walt had a somewhat complex personality and his actions sometimes were difficult to understand even to persons who had known him closely for decades. For instance, he was a big fan of Ohio State football and he and his wife always had season tickets and attended all home games in the Ohio Stadium and occasionally also Big Ten games in Michigan and elsewhere. However, as was the well-known practice of the Ohio State ticket office, after his retirement his seats near the 50-yardline ticket on the A deck were degraded to seats around the 10-20 yard line. Walt took this move as a serious personal insult and never again bought season tickets or even attended another football game in the Ohio Stadium.

Walt was a well-organized and highly active worker, who got even extensive tasks done on schedule. He tended to be demanding to students as well as to co-workers and had little patience with what he felt was sloppy or incomplete work. This sometimes led to unnecessary minor or major conflicts. When in a good mood, he could be quite happy and enjoyable company (Text-fig. 2). He had an obvious temper and had quite strong opinions about a variety of matters, which he rarely changed. If he felt something was wrong, he did not hesitate to express his opinions orally or to write overly critical letters, particularly to university administrators. This is likely to have prevented him from becoming department chairman or receiving the university awards for which he was well qualified. However, in the case of matters that he felt ought to be done, he was generally exceedingly helpful. He also had a peculiar secret side. For instance, he did not tell long-time colleagues that in a couple of weeks he would retire, and his closest friends did not find out that he and his wife had decided to move permanently to Tucson, Arizona until after they moved there from Columbus in 2013. Finally, it should be

Text-fig. 2. Walter C. Sweet circa 2010.
noted that he was a true dog-lover, who took great pride in having one or two dogs during most of his many years in Columbus.

SMB had his last contact with Walt on October 17, 2015 when he telephoned him on Walt’s birthday. Walt was in a good mood and recalled a number of past joint experiences. He also stated that he expected to break the longevity record of any individual of the extended Sweet family, which was 90 years. Sadly, this turned out to be impossible because he passed away less than three weeks later. However, it is safe to suggest that many of his more than 200 publications will be of lasting value to future generations of geologists. His place in the paleontological history is also safe in view of the fact that at least four fossil genera (Sweetognathus, Sweetodus, Sweetina, Sweetocrinitatus) and several species (e.g. Cahabagnathus sweeti, Panderodus sweeti) have been named for him.

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Carl B. Rexroad is remembered by colleagues as an outstanding scientist and biostratigrapher and is considered by many to have been a dean of conodont researchers, but he was above all a loving husband, father, grandfather, great grandfather, and a loyal and supportive friend. He was highly ethical and inclined to help and assist. Moreover, he was accepting and tolerant of all people. In addition to his scientific expertise, he was an avid reader, particularly of mysteries, a strong supporter of Indiana University athletics, particularly men’s and women’s basketball, a dedicated opera fan who rarely missed an Indiana University production, a birder and animal lover, a very decent cook who enjoyed frequent visits to barbeque and ethnic restaurants, and in his later years, a connoisseur of Long Island ice tea.

Carl traveled extensively with his parents and visited the 48 contiguous states as a youngster. He spent many summer holidays with his family in a cabin at Estes Park, Colorado, and always considered Rocky Mountain National Park to be his favorite. When he was about 12 years old he traveled to Europe with his aunt and that probably sparked life-long interest in travel. These travels provided Carl with an appreciation of diverse cultures, a first-hand understanding of unique geological phenomena and, perhaps most importantly, the opportunity to assemble a large and diverse sweater collection.

Carl graduated from University High School in 1943. He then entered the army where he served in the field artillery from 1943–1946. He wrote letters home almost daily while stationed in the Philippine Islands. These letters are deposited at the Missouri Historical Society, Columbia, Missouri, and are available to the public. The letters contain detailed descriptions of local physiography, rocks, and birds that Carl observed; they show that Carl’s observation skills and attention to detail were already developing in his late teens and early 20’s. They also reveal the early years of his lifelong interest in various sports, both as a participant and an observer. Carl continued spelunking into his 70’s and to play softball in an organized league into his 80’s.

Upon returning from his stint in the army, Carl began undergraduate education at Dennison University in Granville, Ohio, where he studied for one year. He then transferred to the University of Missouri where he earned his bachelor’s degree (1949) and Master of Science degree (1950). Carl was very appreciative of his years at “Mizzou” and later established the Carl B. Rexroad Geological Sciences Endowment Fund at the university to support the study of paleontology, “soft rock” geology, and to promote professional development among undergraduate students and faculty.

After completing his M.S. degree, Carl accepted a position at Louisiana Polytechnical Institute, now Louisiana Tech University, where, as Instructor of Geology, he taught for three years (1950–1953). While in Ruston, Carl met Edythe Rose Evans who was an alumna of Louisiana Polytech. They married on April 7, 1951 and one son, Carl E., was born on September 23, 1952 in Ruston.

Carl B. and his young family moved to the University of Iowa in 1953 to pursue a Ph.D. in conodont studies under the direction of W. M. Furnish. His dissertation, “Conodonts from the type Chester, Illinois” (Rexroad, 1955) marked the completion of his degree in 1955. He presented this work at the 1956 meeting of the Society of Economic Paleontologists and Mineralogists in Chicago (Rexroad, 1956) and published it one year later (Rexroad, 1957). Thus began his career as a micropaleontologist specializing in conodont biostratigraphy and paleobiology.

Carl B. Rexroad is remembered by colleagues as an outstanding scientist and biostratigrapher, and is considered by many to be a dean of conodont research.

Charlie are credited with showing that the presence of conodonts in Mississippian rocks provided geologists with a high degree of accuracy in correlation of those rocks over global distances.

Carl began his long and illustrious career with the Indiana Geological Survey in 1961 (Text-fig. 1) and remained actively engaged in research there for more than 50 years. He also held the rank of Professor in the Department of Geological Sciences at Indiana University in Bloomington during his years with the Survey. A one-year leave from the Survey during the 1967–1968 academic year, in order to serve as visiting professor at the University of Iowa, returned him to full-time teaching for the final time in his career. After retirement in the summer of 2003, Carl continued working at his office and laboratory at the Survey until 2015 and later from his home in Bloomington. He published his final paper in 2016 (Brown, Rexroad & Zimmerman, 2016).

Carl’s research addressed all aspects of the paleontology of conodonts including biostratigraphy, paleoecology, biogeography, taxonomy, and systematics. His research resulted in 124 publications and 73 abstracts and he presented papers and attended field trips and field conferences domestically and around the world. Carl truly enjoyed writing papers and was always thrilled to receive notice of a paper accepted for publication.

Carl was active in many professional societies including the American Association of Petroleum Geologists, Geological Society of America, Indiana Academy of Science, Society of Economic Paleontologists and Mineralogists, and the International Union of Geological Sciences. Foremost among his professional society activities was his involvement in the Pander Society, an international organization founded in 1967 for the study of conodonts. He regularly attended its yearly meetings for which he authored and co-authored field trip road logs and guidebook papers. He served as Chief Panderer, essentially president of the organization and newsletter editor, from 1985 to 1990. He was highly honored and genuinely surprised to receive the Pander Medal in recognition of his exemplary research and service in 1992 at the thirtieth anniversary meeting of the Pander Society at Iowa City, Iowa. The medal was presented by Carl’s good friend and long-time collaborator, Glen Merrill. To paraphrase a comment that Glen made at that Pander Medal presentation: “behind Carl’s soft-spoken ways lies a mind like a steel trap. What goes in there, stays there, never forgotten”.

In 1998, the Professional Geologists of Indiana awarded Carl its first Lifetime Achievement Award for his exemplary professionalism during his career. At Carl’s retirement reception in June 2003, he was delightfully surprised to receive “The Sagamore of the Wabash”, Indiana’s highest honor bestowed by then governor Frank O’Bannon.

Carl worked with many collaborators from around the world, and many of his international and domestic colleagues visited with him at his office and laboratory in Indiana. These collaborations spanned Silurian through Pennsylvanian strata and discovered much of what is now known about faunal associations in conodont biofacies, provincialism, and phylogenetic lineages. The results largely benefited high-resolution interregional and intercontinental correlations of Paleozoic strata.

Carl spent most of his career studying taxonomy and biostratigraphy of Midwestern conodonts (Text-fig. 2). He was a well-organized, meticulous and skillful laboratory technician whose project planning, fieldwork, sample collecting and preparation reflected those characteristics (Text-fig. 3). In addition, he was an excellent writer and editor and a skilled photographer in the field and in the lab. He created outstanding slides for conference talks and excellent plates for publication.

Carl assembled the primary conodont reference collection for Silurian biostratigraphy in eastern North America and it remains one of the largest and most comprehensive collections of Silurian conodonts in the United States. As such, it serves as a primary reference for all chronostratigraphic stud-
ies involving Silurian carbonates, which are notorious for their low yields of conodonts. Its excellence in terms of recovered individual specimens, diversity, and geographic coverage is a demonstration of the care, diligence, and skill that defined his career.

Carl also invested a great deal of time and effort with Pennsylvanian conodonts. He and Lewis M. Brown sampled outcrops in Indiana, Illinois, Kentucky, Missouri, Kansas, New Mexico, Oklahoma and Spain. Carl was co-principal investigator for a National Geographic grant and he was advisor to National Science Foundation grants awarded to Lew for geoscience education and conodont studies.

Carl and colleagues recognized and named 11 new genera and 74 new species of conodonts in their numerous publications. Details are available in the excellent detailed compilation of Carl’s work published by John C. Steinmetz (2017). Fellow conodont paleontologists honored Carl by naming three conodont taxa after him, the early Silurian genus *Rexroadus* named by Zhang and Barnes (2002); the Mississippian-Pennsylvanian species *Spathognathodus rexroadi* named by Webster (1969); and the subspecies *Neoprioniodus erectus rexroadi* named by Elias (1966).

Carl was interested in geoscience education; he visited local high schools to talk about geoscience careers, worked with high-school students in programs with IGS, and engaged in collaborative research with motivated high school and undergraduate students. He co-authored several geoscience education papers and served as a resource and advisor to several geoscience education grants, including a complete restructuring of an undergraduate geoscience curriculum. He served as a teacher and mentor to high school students including Robert Nicoll and Alexander Zimmerman and many undergraduates from Indiana University and Lake Superior State University, Sault Ste. Marie, Michigan. He also advised graduate students at Indiana University at both the Master’s and Ph.D. levels. At the Master’s level, he supervised theses for Robert Burton, Charles Clarke, Mary Jarrell, Richard Liebe, Robert Nicoll, Jan Wade, and Arthur Waterman. He supervised Ph.D. dissertations for Mira Kirka, Sandy McCracken, Glen Merrill, Robert Nicoll, and William Orr. In addition, he sponsored post-doctoral fellows Lewis M. Brown, Jong Deick Lee, and Charles Pollack.

Lew Brown, a geology professor at Lake Superior State University spoke at Carl’s retirement party sponsored by the Indiana Geological Survey (Text-fig. 4). Following are some of the comments from that talk.

“It all started with a telephone call. I [Lew] was interested in conodont work in Indiana because somebody named Carl Rexroad had already worked with the conodonts in the rocks around Sault Ste. Marie, Michigan and here was Carl, the “Chief Panderer” himself, offering to teach me to be a professional conodonter!”

“I learned something about conodonts over these years, yes. But I also learned that Carl was a fantastically valuable partner in undergraduate geology education as well. I began to rely heavily on his advice, and I began to earnestly solicit his opinions. This led to a series of geo-education projects, papers and abstracts and I think Carl was at least mildly surprised to find himself a co-author of several Journal of Geoscience Education publications.”

“I came to rely on Carl’s incredible editing ability, many of us have over the years, and this person who is involved with projects worldwide—he never says he’s “too busy” to read
something over. And whatever it is, it always comes back not only much improved, but with detailed editorial comments."

"I think of how often Carl described to me in detail every turn and twist in the road we took to every collecting site, the details of every outcrop. And of course what we had for dinner that night was always part of the discussion. The dinners are fairly easy to remember though. It was always barbeque, or Mexican, or Asian, it was 'let's share a beer.' But for some reason it was never catfish! Fish was not allowed on the table!"

"Many snapshots of my experiences with Carl in the field come to mind. For example, a late afternoon, in a hurry, driving around some fields in Missouri, we were looking for an elusive outcrop, but the roads did not match the map. We drove towards some pickups parked in a field. Carl jumped out of the car and asked the drivers where we were relative to where we wanted to go, and he showed them a map or two. And then he came back to the car and stuck his head in the window and proclaimed loudly and directly, 'they think we're nuts'. Then there was Oviedo, north-central Spain, Carl singing the Marseilles, to the delight and loud applause of a roomful of Spaniards, after a huge steak dinner and of course several bottles of the local sidra. And then on a planned bus trip to Churchill Downs in 1997 he began to attend University Club after Edythe Rose's passing in her memory on the Indiana University campus. Carl began to fail. Carol worked hard and tirelessly as she cared for Carl through his various infirmities until his passing on 27 October 2016. Carl is survived by Carol, her three children, and his son, Carl E. Rexroad of Carbondale, Illinois."

John C. Steinmetz, now retired as the Indiana State Geologist, enjoyed Carl's greatest respect, not easily earned. John interviewed Carl extensively and compiled a comprehensive bibliography of his published works (2017). He stated that Carl Rexroad provided an enduring legacy in Midwestern biostratigraphy. The care with which Carl collected and documented his samples serves as a model for future paleontologists and geoscientists and the literature that he and his colleagues produced has lasting value. The concise recording of location and detailed stratigraphic field descriptions of the examined sections, the presentation of data and careful attention to illustrative plates and figures, the documentation of the archival disposition of the specimens, and the scientific conclusions reached all attest to the work of an exemplary scientist. Future generations of geoscientists will benefit from the remarkable quality of Carl's science. That sentiment is surely shared by all who had the fortune to know Carl as a scientist and as a man. He liked to play with words and phrases and his quips were indirect yet to the point. Those who knew Carl may wonder what quips he would have made in response to this memoir.

LITERATURE CITED


GLEN KENTON MERRILL, B. COLUMBUS, OHIO, AUG. 28, 1935; D. HOUSTON, TEXAS, DEC. 2, 2014 — A PERSONAL REMEMBRANCE

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Glen Merrill was the son of railway mail clerk Lee D. Merrill and his second wife Gladys Jaquith Merrill. Glen grew up in central Ohio, and attended Bellpoint and Scioto Valley High schools in Delaware Co. and then entered Ohio University in Athens, Ohio, crediting Myron Sturgeon, a well-respected paleontologist and teacher of the old school, with awakening his interest in paleontology and stratigraphy. Sturgeon had, with Walter Youngquist, previously published a 1949 paper on Allegheny (Pennsylvanian) conodonts from eastern Ohio. While at Ohio University, Glen added to these collections, several years later using them as the core of his own Ph.D. research. In 1954, Glen married Martha L. Metzer of Columbus; however, their marriage was short lived, and they had no children. Glen completed and received his Bachelor of Science degree in Geology in 1957.

Glen served on active duty as a first lieutenant in the United States Army between 1957–1959, and in the subsequent two years until he entered the University of Texas in Austin in Sept. 1961, he worked with the U.S. Corps of Engineers in Huntington, West Virginia. At Texas, Glen’s teacher and advisor was Samuel Ellison Jr., whose own Ph.D. at the University of Missouri in the early 1940’s was a pioneering work on Pennsylvanian conodonts of the American Midcontinent. Glen graduated from Texas in 1964, and his M.A. thesis, apparently drawn from his Ohio background and the biostratigraphic interests he had developed at Ohio University, was entitled “Zonation of Platform Conodont Genera in Conemaugh [Pennsylvanian] Strata of Ohio and Vicinity”, with Samuel Ellison Jr., supervisor, and W. Charles Bell and Alan J. Scott committee members.

It was during a short teaching stint in 1964 at Northwestern State College of Louisiana at Natchitoches that Glen met Stina Margareta Hellberg of Gamlakarleby, Finland; they married in 1964, and Stina was a pivotal and crucial part of his life, until her death on Jan. 1, 2011.

Although Glen would normally have continued at Texas for his Ph.D., he was even at this relatively early stage a man of strongly held and strongly defended convictions; thus differences between him and Samuel Ellison Jr. led him instead to enter the Louisiana State University in the fall of 1964. There, his Ph.D. supervisor was John C. Ferm, a Pennsylvanian stratigrapher and sedimentologist, and Glen became a strong and devoted ‘Fermite’. At Louisiana, Glen enjoyed the support and friendship of committee member palynologist George F. Hart, and benefitted from the taxonomic quality control of outside committee member Carl Rexroad. Glen was awarded his Ph.D. by Louisiana State in 1968, with a dissertation entitled “Allegheny (Pennsylvanian) Conodonts”.

I first met a young and intense Glen at the first Pander [Conodont] Society meeting in Iowa City in 1968, where he impressed with his knowledge of Pennsylvanian conodonts. Of particular interest to me was his insistence that the distribution of Pennsylvanian conodonts was environmentally controlled, the possibility of which had been suggested to...
him by D.A. Drake's unpublished master's thesis on the microfauna of the Cisco Series of Brown and Coleman counties, Texas (University of Texas, 1958). Glen apparently rather quickly understood the implications of Drake's alternating *Streptognathodus*/*Cavusgnathus* faunas for documenting or measuring environmental control on the distribution of Pennsylvanian conodonts; in fact, a year after entering the university, he published an abstract “Facies relationships in Pennsylvanian conodont faunas” in the 1962 Texas Journal of Science, subsequently continuing and strengthening his observations on environmental control of Pennsylvanian conodonts in both his 1964 M.A. thesis and his 1968 Ph.D. dissertation. By the late 1960's, environmental controls on faunal distributions was a ‘hot’ topic in paleontology, and I had the perfect outdoor laboratory of repeating environments that are the Pennsylvanian cyclothsms of eastern Kansas, literally outside my door in Lawrence, Kansas. Thus, I decided as a part of my Ph.D. to test Glen's thesis that particular conodont taxa were either restricted to, or were dominant in, specific lithologies, *i.e.* environments. My results were published in 1972 and used cluster and relative abundance analyses of the distribution of 29,026 conodonts that I recovered and identified from the Pennsylvania of eastern Kansas; because my work corroborated and supported Glen's conclusions based on his work further east, it made possible, or at least eased, our subsequent friendship and collaboration. Our first joint paper published in 1976 by the Royal Ontario Museum as Life Science Contribution 108, was entitled “Revision of conodont biofacies nomenclature and interpretations of environmental controls in Pennsylvanian rocks of eastern and central North America”, and attempted to reconcile and integrate the patterns and nomenclature of conodont biofacies in two geologically separate regions, the cyclothsms of eastern Kansas with those of the more eastern United States.

Glen's politics, military experience, and bearing were not universally popular in the late 1960's and early 1970's, not with the Vietnam War raging and wide-spread protest on American university campuses. At one meeting of the Pander Society, ironically the one at Kent State in 1974, first Chief Panderer John Huddle explained to me that it was because Glen was politically and militarily a ‘Hawk’ that he had, and was having, such a difficult time landing a permanent teaching job. Whatever the reason, Glen persevered, initially obtaining a teaching position in 1968–1971 as an Assistant Professor of Geology at Monmouth College in Illinois, followed in 1971–1972 by a similar position at the University of Texas at Arlington, before being unemployed for two years. One of the happiest periods of Glen's early teaching career may have been between 1974–1982, when he taught Geology at the College of Charleston, while there being promoted to Associate Professor and receiving tenure. He would likely have stayed in Charleston had it not been that Stina, herself a strong and gifted Ph.D. in Sports Education, felt stymied and frustrated by the Charleston school system. With the great devotion he always had for Stina, Glen reluctantly decided to leave South Carolina, so that his wife could better pursue her career. That move led them to Houston, Texas, where Glen was appointed Associate Professor of Geology at the University of Houston Downtown in 1982. He was promoted to Professor and received tenure there in 1987.

Glen served on active and reserve duty in the U.S. Army Airborne for over 25 years, achieving the rank of major, and his military background and his interest in military history and things German came together in his study of World War I aviation. He was an avid airplane modeler and an early member of Cross & Cockade, a group that got its start about 1964; their publication Cross & Cockade contain many of Glen's contributions on WW I aviation. In the summer of 1982, with his geology student Charles Hart, he founded American/ Gryphon to painstakingly produce decal sets of camouflage and markings that were otherwise not available for airplane modelers. The A/G range grew to over 200 decal sets covering the aircraft of most or all of the European nations involved in World War I, as well as those of the Ottoman Empire, Russia, and the United States. Glen wrote and contributed articles to Windscock, to the book *Gotha!*, and authored a comprehensive two volume history of *Jasta 5*, the Royal Prussian Jagdstaffel 5, a WW I fighter squadron that included the later infamous Hermann Goering among its aces. Glen inevitably applied the same painstaking methods and reliance on primary sources in this historical research, as he was trained and used to doing in his geological and paleontological work.

The Merrills were active people, who for much of their lives were part of a group of cave explorers in Kentucky. Glen and friends began their exploration and survey of Jesse James Cave near Park City, Kentucky in the mid- to late-1950's. They made numerous trips into the cave, surveying and mapping the upper level, before finding deep pits, some over 100 feet deep, that they used to descend to lower levels, which they explored and mapped. On at least one occasion, they camped at the bottom of a deep pit for several days in passages only a few feet in diameter and many hundreds of feet long. Although commercialization of the cave in the mid-1960's facilitated access, exploration and survey trips to the lower levels could (and did!!) easily run to more than 24 hours, and required great stamina. Glen, as project leader, and his team discovered many new passages, eventually mapping an approximately 12 miles long cave system under about 40 acres of land, a remarkable density of cave passages. Glen was the spirit behind many years of cave exploration, and the project is still active. Glen also conducted geologic studies, in one instance collecting small calcareous concretions from the cave...
floor and, undoubtedly drawing on his years of dissolving carbonate rock for conodonts, then used weak acid to discover and etch out bat skulls and wing bones at the core of some of the concretions. He published at least one paper on his observations in caves (Merrill, 1960).

Professionally, Glen could be a formidable opponent who did not suffer anybody, including fools, gladly. A ‘Fermite’ to the end, one of his last publications was a joint paper that included his student Steve Kivett: Wilkinson, Merrill, and Kivett (2003). His view, based on his experience in Illinois and states further east, was that the order and ability to trace individual units of cyclothems was more imaginary than real, and that because of rapid facies changes, individual units could not be traced or correlated for any great distance, certainly not those claimed by the Kansas school of the late Raymond C. Moore, based on the almost perfectly repeating environments in Kansas. This not only created challenges, but also a need for diplomacy and forbearance by this Kansas graduate who for decades was not only Glen’s room-mate at conferences, but also his friend, co-author and co-presenter. It also led to sometimes very lively and well attended debates between Glen and colleagues, some of the liveliest and most memorable being between Glen and friend and colleague Philip Heckel of the University of Iowa.

Glen was not materialistic, and was not interested in wealth or possessions; thus, he and Stina lived comfortably, but not ostentatiously. Glen liked Mexican and Asian food, the hotter the better; in restaurants he sometimes caused his friends or colleagues to squirm, by practicing his Spanish, Thai, or whatever the language or culture a particular restaurant happened to be, with the wait staff. Glen liked and was knowledgeable about baseball, watching this sport (along with a beer) being one of few leisure-time activities in which he truly relaxed; he was initially a Brooklyn Dodgers fan, but later when they became the L.A. Dodgers, he shifted most of his support to the Texas Rangers. Like many academics, Glen did not really know how to relax by doing nothing; I well remember his visible discomfiture when faced with an entire weekend of socializing and doing ‘nothing’ at Nancy’s and my home in the Beaver Valley of Ontario. A few years later, when Stina was still well, I casually suggested that they consider retiring to Fredericksburg, in his beloved Texas hill country. Glen was not having any of that, snorting that he needed to be in Houston, and that he would teach until he dropped. Which, of course, is just about what he did.

A well-known truism is that people often choose dogs whose appearance mimics their own. That was certainly the case with Glen and the succession of boxers that he and Stina, being childless, lavished their affections on. Glen’s appearance, build and temperament were that of a boxer, and his entrance at a meeting or a social occasion could be intimidat-
ductive, original scientist in spite, or maybe even because, of that adversity. His professionalism and drive will be missed; he was a unique individual and it is fair to say that there will not be another Glen Merrill.

I am indebted to and thank Charles and Catherine Bishop (Versailles, Kentucky) for details of Glen’s cave explorations, Dayton Smith (Houston, Texas) for his reflections on Glen the person, Phillip Anz-Meador (Houston, Texas) for pictures of Glen and help with his military career and aviation interests, Charles Hart (Columbus, Ohio) for information regarding their joint business venture and Glen’s passion for aviation history, and the late Joan Burke (Toronto, Ontario) for sharing her recollections and memories of Glen and Stina’s many visits to Toronto, and for help editing this remembrance.

**LITERATURE CITED**


**SELECTION OF THE PUBLICATIONS BY G. K. MERRILL, EXCLUSIVE OF FIELD TRIP GUIDEBOOKS, CONODONT RECOVERY TECHNIQUES, AND TAXONOMY**


DEDICATION TO BRUCE R. WARDLAW

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INTRODUCTION
This special issue of Bulletins of American Paleontology is dedicated to a number of pioneer conodont workers including Anita Harris, Glen Merrill, Carl Rexroad, Walt Sweet, and Bruce Wardlaw; there are lessons to learn about our science, and about life, from knowing a little more about each of them. I knew each of them, but especially Bruce. I visited D.C. in 1989 to deliver a manuscript to Dick Grant and arranged a visit with Anita Harris hoping to secure a color alteration index (CAI) slide; I did, but I also got a whole lot more, including dinner with Anita and a pep-talk for my career, which was about to begin. During future Pander field trips she would always ask of my progress. In 1993, I gave a talk at my first Pander Meeting at Rolla, Missouri on Visean conodonts in which I tried to explain the apparent diachronity between the foraminifer and conodont zones. Walt Sweet approached me afterward and said “it was a good talk and good luck with your career, but you must remember that it is easy to explain the discrepancy when you start with the knowledge that the conodonts are always right”. I have always remembered that encouragement and advice.

Bruce Wardlaw was perhaps too young to be truly considered a pioneer, but he was, from my perspective. Only a little was known about Permian conodont biostratigraphy when he did his graduate work and wrote his first papers. His work with the Subcommission on Permian Stratigraphy (SPS) was instrumental in the development of the Permian Time Scale and, in particular, of the definitions for the Middle Permian stages. Some of his early papers influenced my understanding of conodonts during my own graduate work.

I was shocked when I heard the news of his death – it was a tragedy to his family, who were very important to him, and I had expected many more opportunities to debate our science, at times fueled with good single malt whisky. In the pages to follow, I offer some of my own reflections of Bruce and his work, as well as comments from others. Somehow, the Permian is just a little bit quieter with his passing, but his influence on our discipline will live on for years to come.

FROM HIS OBITUARY
On Wednesday, March 23, 2016 Bruce Richardson Wardlaw (Age 68) passed away at INOVA Fairfax Hospital from injuries due to a fall. He was the beloved husband of Jeanne E. Wardlaw of Herndon, VA, loving and devoted father of Kristen Deanne Frankforter of Beaumont, CA, Andrea Jean Radics of Budapest, Hungary, Jane Wardlaw and Erin Michelle Wardlaw, both of San Diego CA. He is also survived by his brother Kirk Wardlaw of Marysville, CA and four grandchildren.

Dr. Wardlaw was the Chief Paleontologist of the US Geological Survey, which allowed him to travel to remote places around the world to investigate important sedimentary deposits. He was an internationally known expert in Paleozoic fossils and stratigraphy authoring many research papers in scientific journals and serving as editor of newsletters and proceedings volumes. During his 40-year research career Dr. Wardlaw was recognized for his exceptional service to the USGS in helping to understand various complex geological problems and managing teams of research scientists. He also served as liaison between the USGS and the Smithsonian’s Museum of Natural History helping to curate unique collections of fossils from across the world.

Dr. Wardlaw was also active in coaching youth basketball.

BIOGRAPHY AND PERSONAL COMMENTS
Bruce received his B.S. in Geology from the University of California-Riverside in 1969 and his Ph.D. from Case Western Reserve University in 1975 with his dissertation on “The biostratigraphy and paleoecology of the Gerster Formation (Upper Permian) in Nevada and Utah”. Bruce started his career with the USGS as a post-doctoral fellow in 1975 and became a full-time research geologist in 1976. Over his career, he contributed to USGS science in stratigraphy, carbonate petrology, upper Paleozoic and Triassic conodont and brachiopod biostratigraphy and paleoecology, thermal maturity, coal geology, and nuclear explosive test craters. Although much of his research was in the western U.S., he reached out internationally in the Middle East, Pakistan, the Pacific atoll of Eniwetok, and South China. More recently, Bruce was an integral part of a proposal to map the geology of Qatar for his expertise in carbonate petrology and paleontology. Also, Bruce was a prolific writer with over 200 publications on his broad knowledge of geology. His legacy will include editorship of volumes of Micropaleontology, Stratigraphy, and Smithsonian Contributions. He was honoured at the Pander Session at GSA in Denver, 25 September 2016.

Randy Orndorff (USGS): “I will miss him greatly. I had many interactions with Bruce from my early career starting at the

Note: This contribution is partially modified from a memorial to Bruce Wardlaw in Permophiles 63 (October 2016; pp. 52–56).
Text-fig. 1. Bruce and me at a conference in Chaohu, China in 2005. 2. Bruce and the late Heinz Kozur at Stratotype Canyon, Guadalupe National Park, sitting on the base of the Roadian in 2007. 3. A barbeque at my home in Calgary following Permophiles work in 2008; from left to right, Charles Henderson, Shuzhong Shen, Shilong Mei, and Bruce Wardlaw. 4. Bruce Wardlaw and Merlynd Nestell sitting on the Cherry Canyon Sandstone in the Apache Mountains in 2012. 5. Bruce and I with conodont samples from the Shangsi section in 2003.
National Museum of Natural History (NMNH), and have relied on his knowledge and expertise in my current position as center director. Bruce would never hesitate to offer his help and never complained about any assignment he was given. Over the last several years, he had stepped up to work with the Smithsonian on inventorying, compacting, and evaluating over 120 years of USGS paleontological collections at NMNH. In doing so, he has worked with many student interns, sharing his knowledge and mentoring them. As Chief Paleontologist and the last chief of the USGS Branch of Paleontology and Stratigraphy, he was the man for the job.”

Nancy Stamm (USGS): “You guys (referring to Bruce and me) had some fabulous adventures together, and the best scientific discussions over refreshing beverages! It was a real treat for me just to hang out and listen to a few of them.”

Tyler Beatty (former graduate student at University of Calgary): “I have some good memories of Bruce - in particular the BBQ you and Elizabeth hosted in the fall of 2006, where Bruce turned me green with envy with his stories of seeing all of my favorite rock bands (Zeppelin, Stones, Deep Purple) back in the 70s. It seems to be a tough couple of years for both pioneering conodont workers and 70’s rock legends. Perhaps they get to share a special place upstairs.”

Shilong Mei (China University of Geosciences Beijing; now Alberta Geological Survey): “I remember my time in D.C. hosted by Bruce and later when Bruce came to China – several papers resulted from our collaboration and we enjoyed some great Sichuan food.”

Shuzhong Shen (Nanjing Institute of Geology and Palaeontology and current SPS Chair): “Bruce Wardlaw was a trusted colleague, an outstanding scientist, and a good friend to the Nanjing Group. In 2004, Bruce provided the Chinese Group with a guided tour of the Permian sequences in western USA and the Guadalupe and Apache mountains in West Texas. During that trip we had a flat tire in the desert around the Hogup Mountains near Salt Lake City and only managed to make it out by Bruce's ingenuity. We enjoyed numerous field collaborations with Bruce in South China, where he had the chance to experience some of the spicy local cuisine. Bruce was such a big fan that he once guided a hotel chef on how to make the dish even more spicy and numbing. Bruce was an easy going character and was the first to establish the well-known custom to run his SPS business meetings with a beer in his hand and a smile on his face. Bruce will be missed as an inspiration, an intellectual leader, and most of all, as a friend in times of need.”

Merlynd Nestell (University of Texas, Arlington): “Bruce Wardlaw and I first met in the spring of 1976 in the Paleobiology Department of the Smithsonian Institution and began what was to be a 40 year collaboration resulting in over 45 joint publications of papers or abstracts on various aspects of Pennsylvanian and Permian conodonts and biostratigraphy from such diverse places as Greece (Nestell & Wardlaw, 1987), Vietnam (Wardlaw et al., 2015a; Nestell et al., 2015), Mexico, Oregon, Kansas, Iowa (Nestell et al., 2016), and Texas. In that spring, we discussed our common interest in the Permian and decided to collaborate on a field trip the following summer to visit the well-known Permian section at Las Delicias in the state of Coahuila in Mexico. William Furnish of the University of Iowa was also invited to be a participant on this trip. The section is very remote and requires camping, and Nestell's four wheel drive vehicle was used to gain access. This trip was the first of three that Wardlaw and Nestell took to this section and eventually results were presented in two publications (Wardlaw et al., 1979, 2000). In our next field trip together in the summer of 1978 we met in Los Angeles with our two 12 year old daughters for a memorable joint camping and field work trip to central Oregon to examine the Permian rocks of the Grindstone terrane. Thomas Dutro of the USGS met us in central Oregon and a resulting paper was later published (Wardlaw et al., 1982).

Our collaboration continued after participating in the Symposium on the Permian Guadalupian held in Alpine, Texas in 1996. One of the field trips was to the Apache Mountains northeast of Van Horn in West Texas and at one of the stops, Wardlaw, Nestell, Garner Wilde, and Lance Lambert recognized that there was a very substantial and unstudied section of the uppermost part of the Bell Canyon Formation and lowermost part of the Castile Formation exposed on a public road in the Apaches (Text-fig. 1.4). On the day after the trip, Nestell returned to the field trip site to examine this section and incidentally met one of the ranch landowners in the area who, after some discussion, graciously agreed to allow future geological field work by Nestell and his students on his very large ranch. Later we were joined my wife Galina, Gordon Bell (geologist for Guadalupe Mountains National Park), and Lance Lambert on several projects on the study of Permian microfauna of the Guadalupe and Apache mountains area, because three sites in the Guadalupe Mountains were being proposed as Guadalupian (Middle Permian) stratotypes (Text-fig. 1.2). A number of joint publications and meeting presentations resulted from this collaboration (Lambert et al., 2002; Nestell et al., 2006; Nestell & Wardlaw, 2010; Wardlaw & Nestell, 2010; Ellwood et al., 2012; Nestell et al., 2015b; Wardlaw & Nestell, 2015; Nestell & Wardlaw, 2015). Work still continues at the present time to finish several papers on which Bruce is an author or coauthor.

In the 1990’s Darwin Boardman and I initiated a study of the latest Pennsylvanian and Early Permian conodont faunas of Kansas and northern Oklahoma, as well as north-central Texas. We later invited Bruce to participate in the project (Boardman et al., 1998). The Kansas study resulted in a Kansas Geological Survey publication (Boardman et al., 2009). One paper on two occurrences of Streptognathodus isolatus in Pennsylvanian/Permian boundary strata in Texas was published in Permophiles (Wardlaw & Nestell, 2014).

Soon after the Apache Mountains work, Bruce was included on several UT-Arlington student thesis committees as an adjunct professor. He began to come regularly to Arlington for week long visits to work on papers, meet with students, and do field work in West Texas or Nevada. At the time of his death he was serving
on the committees of four graduate students. We worked very well together as a team and his careful and thoughtful work will be greatly missed.”

A PERSONAL DEDICATION

A paper on the youngest Permian conodonts in the Great Basin and Rocky Mountain region by Wardlaw & Collinson (1979) greatly influenced my M.Sc. studies completed in 1981 at the University of British Columbia on cool-water Middle Permian conodonts from the Sverdrup Basin. One quote in their paper provided the seeds to what we now call the “sample-population” approach to naming taxa. They said “…rare individuals within a population of a particular species may exhibit one or several characteristics that are thought to be diagnostic of different species”. This distinction between a “population species” with variability and “form species” for each morphotype continues to be debated in the literature. Later, papers by Wardlaw & Collinson (1984, 1986) were cited in my Ph.D. dissertation on Early Permian conodonts from the Sverdrup Basin. Bruce was a major influence on my formative years as a conodont worker.

I met Bruce at numerous meetings, but one stands out in particular. It was the 20–21 March 1997 GSA South-Central/Rocky Mountain meeting in El Paso, Texas. I departed Calgary in a snowstorm and arrived to an air conditioned conference hall that was even colder. I presented a talk on the Middle to Upper Permian of Arctic Canada and made the mistake of suggesting the significance of accessory denticles on the posterior carina. At the end, Bruce stood up and screamed at me “you should know by now that this is simply a gerontic character”! The room became chiller, but we discussed it more calmly later, when Bruce took me on a fantastic trip, my first, to the Guadalupes and to Carlsbad Caverns. A friendship was forged. Bruce and I really got to know each other well when I served as his Secretary for SPS beginning in 2000. He visited Calgary in the summer (Text-fig. 1.3) and I visited Washington D.C. in the winter (much more sensible than the other way around) so that we could prepare Permiphiles. This work was usually fueled with a few drinks of some fine scotch. It may surprise some, but as conodont workers we did not always agree. We had many heated scientific debates that occasionally resulted in a compromise. Our conversations went well into the night, much to the consternation of our respective wives. Thanks to Elizabeth and Jeanne for putting up with us! I will always remember one trip to D.C. in which I joined him on the basketball court. One of his daughters was playing basketball and he had to referee. He asked me to be the timekeeper, but probably questioned the wisdom of his request when I asked “how long is a game?” It is apparently shorter than the three 20 minute periods of hockey. I did learn during that visit how much he loved coaching basketball, especially his girls, and how much he loved his family. This was truly his first priority.

Bruce contributed enormously to SPS of the International Commission on Stratigraphy (ICS) as the Secretary and later two terms (1996 to 2004) as Chair of SPS. He included me in his 10-year group, often remarking that he was influenced by Claude Spinosa who was 10 years older and Brian Glenister who was an additional 10 years older. I was 9 ‘Canadian’ years younger. It turns out that his most cited paper (according to Google Scholar) was a paper establishing the Permian chronostratigraphic subdivisions (Jin et al., 1997) that was also greatly influenced by Brian Glenister. Another top-20 cited paper was the proposal by Glenister et al. (1999) to name the Roadian, Wordian, and Capitanian stage GSSPs. The Smithsonian Contribution related to the Guadalupian Symposium will be cited for a long time to come (Wardlaw, 2000) and the papers in that volume form the definitive work on the Permian faunas of the Guadalupes. Bruce was also instrumental in resolving the base of the Permian (Chernykh et al., 1997) and the Upper Permian stages (Jin et al., 2001, 2006).

His work on Permian conodonts forms a lasting legacy! Both of us have numerous papers on conodonts from China (Mei et al., 1990a, 1990b, 1991, 1992, 1993a, 1993b, 1994, 1998, 2002; Henderson et al., 2002) with the common link being Shilong Mei who completed “post-docs” with both of us. On one occasion we collected numerous samples at the Shangsi section in Sichuan province (Text-fig. 1.5), which meant that every evening we would have spicy Sichuan food. One night, to the horror of our hosts, we kept saying that the food was not spicy enough, and the waiters would return each time with a slightly spicier version. Some cold Chinese beers proved essential eventually. Some trips were to conferences like that at Chaochu, China (Text-fig. 1.1), which somehow always seemed like celebrations. On another long road trip in China, Bruce regaled us with stories of his work on Enewetak Atoll (Wardlaw, 1991) and “religious experiences” in Pakistan (Pogue et al., 1992; Wardlaw & Pogue, 1995). I remember Sam Bowring saying “Bruce you have to write this stuff down in a book”, but unfortunately that will not happen now. It is important to remember that each of us have stories worth telling and that we should not wait too long to tell them. I will miss those stories and I miss Bruce. The Permian community really is a little bit quieter now!

ACKNOWLEDGMENTS

This contribution is partially modified from a memorial to Bruce in Permiphiles 63 (October 2016; pp. 52–56).

LITERATURE CITED

Note: Top 19 publications cited over 35 times are marked by an asterisk (*).


MORPHOMETRIC ANALYSIS AND TAXONOMIC REVISION OF NORTH AMERICAN SPECIES OF THE IDIOGNATHODUS EUDORAENSIS BARRICK, HECKEL, & BOARDMAN, 2008 GROUP (MISSOURIAN, UPPER PENNSYLVANIAN CONODONTS)

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ABSTRACT

The platform landmark analysis (PLA) for Idiognathodus is used to analyze morphological variability in the I. eudoraensis group and compare it with the I. simulator and I. magnificus groups. The I. eudoraensis group comprises four species, I. eudoraensis, I. centralis n. sp., I. abdinitus n. sp., and I. aff. I. luganicus, based on analysis of material from New Mexico and Iowa. Idiognathodus abdinitus n. sp. has the same distinct feature as I. simulator (the index of the base of the Gzhelian Stage) the isolated caudal adcarinal ridge, but the two species are differentiated on the basis of platform and adcarinal ridge shape. Another species of Idiognathodus, I. sweeti n. sp., occurs with the I. eudoraensis group, but does not have an eccentric groove and is assigned to the I. magnificus group. All four species of the I. eudoraensis Zone show the same style of P₁ element asymmetry observed in the I. simulator and I. magnificus groups. This style of asymmetry is named simulator-style asymmetry and is identified by the sinistral element having a broadly curved rostral platform margin that has a more dorsal location of the curvature maxima, and the dextral element having a wider, tapered rostral margin with a more ventral location of the curvature maxima. The shared character of platform asymmetry style across multiple species with different platform structures (lobes, grooves, ridges) suggests that the I. magnificus, I. eudoraensis, and I. simulator groups represent a distinct clade of idiognathodids that were derived from typical Idiognathodus, first by the development of P₁ element asymmetry, and later by the development of an eccentric groove during the Missourian (Kasimovian) Stage.

INTRODUCTION

Barrick and Boardman (1989) recognized that P₁ elements with an eccentric groove assigned to Idiognathodus simulator (Ellison, 1941) from the Missourian Eudora Shale were distinct from the specimens of I. simulator from the younger Virgilian Heebner Shale, the holotype level (Text-fig. 1). For this reason, the specimens from the Eudora Shale were later referred to as I. aff. I. simulator, and were considered to be ancestral to I. simulator (Barrick et al., 2004). Barrick et al. (2008) later named the Eudora species I. eudoraensis and provided a detailed taxonomic history and description of both I. eudoraensis and I. simulator. In the most recent summary of the Midcontinent Pennsylvania conodont zonation by Barrick et al. (2013a), the first occurrence of I. eudoraensis from the Eudora Shale of the Stanton cyclothem marks the base of the upper Missourian I. eudoraensis Zone and the first occurrence of I. simulator in the Heebner Shale of the Oread cyclothem marks the base of the Virgilian I. simulator Zone, as well as the base of the Gzhelian Stage (Heckel et al., 2008).

The Idiognathodus simulator group from the Heebner Shale was studied in more detail using morphometric analysis by Hogancamp et al. (2016). The group was determined to be composed of five distinct morphological species: I. auritus, I. lateralis, I. luganicus, I. praenuntius, and I. simulator (Pl. 1). All five species demonstrate the same pattern of strong P₁ element dextral-sinistral asymmetry, and all have an eccentric groove. Using the terminology of Lane (1968), this P₁ element asymmetry is referred to as Class IIIb symmetry, which is strongly asymmetrical mirror-image pairing. The dextral elements of the species of the I. simulator group have a wide, triangular rostral platform margin, and the sinistral elements have a smooth, curved rostral platform margin.

Hogancamp et al. (2017) performed the same morphometric analyses on specimens of Idiognathodus magnificus Stauffer and Plummer, 1932 from the Missourian Beeman Formation of the Sacramento Mountains in New Mexico.
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<th>STAGE</th>
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Text-fig. 1. Ranges of better-known and significant species are plotted against cyclothems and the New Mexico formations. Conodont zones are for Upper Pennsylvanian strata in Midcontinent North America. Major cyclothems are denoted by capital letters; lesser cyclothems by upper and lower-case letters. I. = Idiognathodus; S. = Streptognathodus. Modified from Barrick et al. (2013a) by the addition of the species discussed in the text and species proposed by Roscoe and Barrick (2013).
Mexico. They identified two distinct morphotypes of *Idiognathodus magnificus*, both of which showed the same style of dextral-sinistral platform asymmetry observed in the *I. simulator* group. The *I. magnificus* group, which also characterizes the Quivira Shale Member of the Dewey cyclothem in the Midcontinent region (Barrick *et al.*, 2013a), has no eccentric groove and has much larger and more nodose lobes than any species of the *I. simulator* group, making the two groups morphologically very different and easy to distinguish based on platform structures (lobes, grooves). Variability in platform structures is observed to change through ontogenetic series in both groups of *Idiognathodus* and can represent interspecies variation, intraspecies variation, or both (Hogancamp *et al.*, 2016; Hogancamp *et al.*, 2017).

The persistence of the same style of platform asymmetry through time and across different combinations of platform structures suggests that platform symmetry is a higher-level taxonomic character than the platform structures. If this is true, it suggests that the *Idiognathodus magnificus* and *I. simulator* groups are more closely related to one another than they are to species with similar platform structures, but nearly symmetrical P₁ element pairs. Asymmetrical P₁ element pairs have been shown to affect P₁ element occlusion processes (Donoghue & Purnell, 1999; Martínez-Pérez *et al.*, 2014). If symmetrical pairs of *Idiognathodus* P₁ elements occlude differently than asymmetrical pairs, this would justify the use of symmetry style as a higher-level taxonomic character than platform structures. Because the *I. eudoraensis* group occurs stratigraphically above the *I. magnificus* group and below the *I. simulator* group, it likely represents the transitional set of morphologies between these two groups in a lineage of species with asymmetrical platform pairs. Here, the *I. eudoraensis* group is morphometrically analyzed using the same landmark-based technique used to study the *I. magnificus* and *I. simulator* groups. The analysis aids in determination of how many distinct morphological species exist in the *I. eudoraensis* group, what style of platform asymmetry the group has, and how the *I. eudoraensis* group compares to the older *I. magnificus* group and the younger *I. simulator* group.

**Previous work using platform landmark analysis (PLA)**

The PLA procedure was first used by Hogancamp *et al.* (2016) to study geometric morphometric variability in the *I. simulator* group. The procedure was formally named by Hogancamp *et al.* (2017) in their study of the *I. magnificus* group. A modified version of the PLA was used by Hogancamp and Barrick (2016) in their study of ungrooved *Idiognathodus* from the Heebner Shale. In this modification, the landmarks defined by the internal terminations of the transverse ridges were removed because none of the specimens had an eccentric groove. Later, Hogancamp *et al.* (2017) modified the definitions of the internal landmarks so that when a groove is absent, the landmark is placed at the notch or midpoint along the transverse ridge. This modified definition allows for the groove and transverse ridge landmarks to be included in the PLA of all *Idiognathodus* regardless of groove presence. Another version of the PLA was used by Hogancamp *et al.* (2017) that added eight additional landmarks defined by the lobes and was called the bi-lobed landmark analysis (BLA). The BLA provides a more complete geometric reconstruction of the biological form, but can only be used on P₁ elements with two lobes. Because the *I. eudoraensis* group contains species with 0, 1, or 2 lobes, the BLA was not used in this study. Other workers have used landmarks to study conodont platforms for other groups, including Chen *et al.*, (2016) in their study on Triassic conodonts, and Hogancamp and Manship (2016) in their study on Devonian *Palmatolepis*. Although PLA is an abbreviation for ‘Platform Landmark Analysis,’ it is only used here to refer to the specific method applied to *Idiognathodus*. It seems likely that if morphometric studies on conodonts become more common, a more specific set of revised nomenclature for different standardized analyses will be required.

**Methods**

**Materials**

Several thousand conodont elements from four different outcrop locations were available for study, and 281 *Idiognathodus* P₁ elements were used in the morphometric analyses. Most specimens were obtained from limestones from the middle of the Tinajas Member of the Atrasado Formation, Socorro County, New Mexico (Cerros de Amado, Minas de Chupadera, and Ojo de Amado sections; see Appendix 1 for localities). The composition of conodont faunas from the middle part of the Tinajas Member varies by locality. The Cerros de Amado B sample, from a limestone bed (Bed 10) in a siliciclastic-dominated section, is dominated by elements of the *I. eudoraensis* group and includes a smaller number of elements of *Streptognathodus firmus* Kozitskaya, 1978 (in Kozitskaya *et al.*, 1978) (Lucas *et al.*, 2009). At the Minas de Chupadera section, in two samples also from limestone beds in a siliciclastic-dominated section (Bed 2 and Bed 4), *S. firmus* is the more abundant species and the *I. eudoraensis* group is less common. In contrast, samples from the Ojo de Amado section come from the lower limestones in a 12 m thick limestone unit with minor shale interbeds. In the lower samples (Beds 64 and 65), elements of the *I. eudoraensis* group are subordinate to different forms of *Streptognathodus* that may be transitional from *S. isakovae* Goreva & Alekseev, 2006 to *S. firmus* (Barrick *et al.*, 2013b). A slightly higher bed (Bed 68) is dominated by *Idiognathodus* elements, many
of which belong to the *I. eudoraensis* group, as well as other forms assigned here to *I. sweeti* n. sp.

These New Mexico samples have been correlated with the Eudora Shale of the Midcontinent succession (Barrick et al., 2013b). The Eudora Shale at the Winterset, Iowa section comprises three major successive units (Heckel and Pope, 1992). The basal dark gray clay shale (10 cm) is dominated by *Streptognathodus* species, *S. elegantulus*, *S. gracilis*, and *S. excelsus*, and the *Idiognathodus eudoraensis* group and *Idioprioniodus* are poorly represented. The middle black shale and upper dark gray shale samples are dominated by elements of the *I. eudoraensis* group, *Idioprioniodus*, and *Gondolella*. The lower 10 cm of the overlying Stoner Limestone has a sparse fauna of *Hindeodus* elements and the *I. eudoraensis* group.

Limestone samples were crushed into small pieces (1 to 3 cm in diameter) and dissolved in a 10% buffered formic acid solution to dissolve carbonate material. Black shale samples were submersed in a 12% bleach solution (sodium hypochlorite) to break down the organic constituents. The mixture was poured off every month and replaced with new bleach until the shale began to lighten in color and break apart into a fine residue. Once the organic material was removed and the solution was consistently a light color, the samples were dried and then submersed in kerosene for approximately 4 to 5 hours to aid in the deflocculation of the clay particles. After the kerosene was poured off, the sample was submersed in hot water and allowed to sit overnight to thoroughly disaggregate. Samples were sieved to a small size (120 μm). When necessary, the residues were placed in heavy liquids for density separation.

**Platform Landmark Analysis (PLA) for *Idiognathodus***

*Specimen images.*—The platform landmark analysis (PLA) developed by Hogancamp et al. (2016) was used to morphometrically analyze the *Idiognathodus eudoraensis* group and compare them to the *I. simulator* and *I. magnificus* groups. A more detailed explanation of the PLA morphometric procedure can be found in Hogancamp et al. (2016) and Hogancamp et al. (2017), but the steps are explained briefly here for clarity. First, digital images were taken of the P<sub>1</sub> elements at the same orientation, resolution, and magnification using a Nikon SMZ1500 light microscope camera. Second, all the dextral element images were mirrored to remove natural shape bias due to chirality. Two hundred and forty-five P<sub>1</sub> elements of the *I. eudoraensis* group and 36 P<sub>1</sub> elements of *I. sweeti* n. sp. from four different localities were photographed.

*Placement of landmarks.*—The images were converted to TPS files using the software TpsUtil (Rohlf, 2010a). Landmarks were placed on the TPS files using the software TpsDig (Rohlf, 2010b). The PLA procedure uses 18 landmarks on *Idiognathodus* P<sub>1</sub> elements to represent the morphological shape of the platform, carina, and adcarinal ridges (Text-fig. 2). These landmarks are the ventral ends of the adcarinal ridges (1, 3), the midpoint of the adcarinal ridges (17, 18), the dorsal termination of the carina (2), the dorsal tip of the element (16), the rostral and caudal ends of the most dorsal transverse ridge on the rostral side (4–7), the most dorsal transverse ridge (12–15), and the transverse ridges nearest to the point of maximum platform margin curvature (8–11).

*Assignment of groups.*—Each individual specimen was assigned a variety of group classifiers including chirality (sinistral or dextral), lobe type (0, 1, 2, or disconnected adcarinal ridge), groove (present or absent), locality, and species. Species assignment for the P<sub>1</sub> elements were based on lobe and groove criteria. *Idiognathodus eudoraensis* has an eccentric groove and
two lobes. *Idiognathodus centralis* n. sp. has an eccentric groove and one lobe on the caudal side. *Idiognathodus aff. luganicus* has an eccentric groove and no lobes. *Idiognathodus abdibitus* n. sp. has an eccentric groove and a caudal adcarinal ridge that is separated from the platform margin by the adcarinal trough. *Idiognathodus sweeti* n. sp. has no eccentric groove and two lobes.

The file created from TpsDig that contains the raw X and Y landmark coordinates for each specimen was then imported into the software MorphoJ (Klingenberg, 2011). The group classifier list was then added to the table in MorphoJ using the group classifiers as filters. For some analyses, specimens from the *I. eudoraensis* data set were compared to specimens from the *I. simular* data set of Hogancamp et al. (2016) and the *I. magnificus* data set of Hogancamp et al. (2017) using the same landmark configuration.

**Procrustes superimposition and calculation of a covariance matrix.**—A Procrustes superimposition analysis was calculated for each dataset created in MorphoJ. This analysis translates, scales, and rotates all the specimens to a best fit. This removes shape bias affiliated with size, image position, and image rotation. The analysis provides an additional matrix of X and Y coordinate points that are referred to as the Procrustes coordinate points, and the original X and Y coordinates are referred to as the raw coordinate points. Because the Procrustes analysis calculates an average value for each landmark position, an average shape can be constructed by combining all the average locations for each landmark.

A covariance matrix can then be calculated using the sums of square roots and cross products of the deviations from the column means for each Procrustes coordinate point. The covariance matrix contains data that is calculated from how each landmark for any individual varies from the average location of that landmark as represented by the Procrustes form. Subsequent eigen analyses can be calculated from the covariance matrix.

**Eigen analysis as a tool to analyze multidimensional data.**—Eigen analyses are statistical analyses that use vector geometries to determine direction and magnitude of co-linear variation in multi-dimensional statistical space. Canonical variance analysis (CVA) is a discriminatory eigen analysis that determines the linear direction in multidimensional statistical space that best separates pre-selected groups. The number of canonical variate axes (*i.e.*, the eigenvectors) depends on the number of groups in the analysis and the independence of those groups. There will always be a maximum of one less canonical variate axis than there are groups. Each eigen vector has an eigenscore that represents how much of the variation is represented by that particular eigenvector. Because the canonical variate axes are eigenvectors, they are mutually orthogonal, and their eigenscores will sum to 100% of the total variation. The intersection of all eigenvectors is where all eigenscores equal zero, which is represented by the average shape calculated from the Procrustes analysis.

Each landmark coordinate for each specimen has a scaling for each eigenvector. Each individual specimen has a single score for any eigenvector. The eigenscore for each specimen is calculated by taking the sum of the products for each raw landmark coordinate multiplied by its respective eigenvector scaling for that landmark. Plots can be created using the eigenvectors as axes and placing specimens on the plots based on their eigenscores. Because the eigenvectors are oriented in the direction of maximum variation, the eigenvector cross plots provide a two-dimensional window into multidimensional space that shows the most variation in the data.

**Translating statistical variability into morphological variability using wireframe models.**—Morphological change in the P1 elements can be determined for any value of any eigenvector. This is used to translate statistical variability into morphological variability. For example, if canonical variate 1 (CV1) separates two groups of specimens in morphospace, so that one group is located around a CV1 value of -3 and the other group plots around a CV1 value of +2, there is still the missing piece explaining what a value of -3 or +2 means morphologically. Because a CV1 value of 0 would represent the average form calculated from the Procrustes analysis, wireframe models can be constructed using the average location of the landmarks. To determine what the wireframes look like at a scale of +2, the scaling for CV1 = 2 is applied to the Procrustes shape landmarks, thus moving them in geometric space based on the scaling. This procedure is used to visually construct wireframes on either end of any particular eigenvector to determine what morphological change is associated with movement in statistical space along either direction of the eigen vector.

**RESULTS**

**Idiognathodus eudoraensis group — CVA, chirality**

A CVA using chirality as the group classifier was calculated for all species of the *I. eudoraensis* group to determine whether or not the group as a whole contains asymmetrical P1 element pairs recognizable by using PLA. The sinistral and dextral elements are separated into two different groups along the CV1 axis (Text-fig. 3). Sinistral elements are concentrated on the positive side of CV1, and dextral elements are concentrated on the negative side of CV1. Movement in the positive
direction of the CV1 axis corresponds with more symmetrical platform margins, a narrower rostral side, a longer caudal adcarinal ridge, and a more ventral position of the dorsal termination of the carina. Specimens with negative values of CV1 correspond with a wider rostral platform margin with a ventrally shifted point of maximum curvature, a straighter caudal side, and a more dorsally extensive carina. The degree of chirality is similar to that found in the *I. magnificus* and *I. simulator* groups.

**Idiognathodus eudoraensis group sinistral elements – CVA, species**

A CVA using species as the group classifier was calculated for all sinistral elements of the *Idiognathodus eudoraensis* group to determine if the lobe-based groups could be differentiated from one another using PLA. Separate analyses were run for the sinistral and dextral elements because we already determined that sinistral and dextral elements are morphologically different and did not want to include the noise associated with chirality variation in these analyses. CV1 separates *I. abdixitus* n. sp. from the other three species (Text-fig. 4). All specimens of *Idiognathodus abdixitus* n. sp. except for two have CV1 values less than -1, and the other three species, *I. aff. I. luganicus*, *I. centralis* n. sp., and *I. eudoraensis*, have CV1 values greater than -1, except for two specimens of *I. eudoraensis*. Specimens with negative values of CV1 correspond with an outwardly extended caudal adcarinal ridge, and those with positive values of CV1 correspond with a concave caudal adcarinal ridge.

*Idiognathodus eudoraensis* and *I. centralis* n. sp. are slightly separated along the CV2 axis. *Idiognathodus eudoraensis* mostly has positive values of CV2, and *I. centralis* n. sp. mostly has negative values of CV2, with only one specimen of *I. centralis* overlapping into positive CV2 values, and 12 specimens of *I. eudoraensis* overlapping into negative CV2 values. The overlapping region between *I. eudoraensis* and *I. centralis* on the CV2 axis is from +0.5 to -1.5. Specimens with positive values of CV2 correspond with a wider platform and a more ventral location of the maximum curvature of the platform margin. Specimens with negative values of CV2 correspond with a narrower platform, a straighter rostral adcarinal ridge, and a more dorsal location of the maximum curvature of the platform margin.

The three sinistral specimens of *Idiognathodus aff. I. luganicus* are separated from the other three species along the CV3 axis. The other three species cannot be differentiated based on their CV3 values and show almost complete overlap in CV3 value ranges. *Idiognathodus aff. I. luganicus* have CV3 values higher than 2.5, and the other species all have CV3 values less than 2.5. Higher CV3 values correspond with longer adcarinal ridges and a more dorsal location of maximum curvature of the platform margin.

**Idiognathodus eudoraensis group dextral elements – CVA, species**

A CVA using species as the group classifier was calculated for all dextral elements of the *Idiognathodus eudoraensis* group to determine if the lobe-based groups could be differentiated from one another using PLA. CV1 separates *Idiognathodus abdixitus* n. sp. from the other three species, whereas values for *I. abdixitus* n. sp. specimens are typically less than -2, except for one specimen, and values for the other three species are greater than -2 (Text-fig. 5). Specimens with negative values of CV1 correspond with an outward expansion of the caudal adcarinal ridge and positive values of CV1 correspond with a concave caudal adcarinal ridge.

*Idiognathodus aff. I. luganicus* is slightly separated from the other three species along the CV2 axis, whereas *I. aff. I. luganicus* specimens typically have CV2 values greater than zero, and CV2 values for the other three species are typically less than zero, although significant overlap between the clusters is observed. Only when CV1 and CV2 values are combined does the cluster of *I. aff. I. luganicus* seem to separate from the *I. eudoraensis* and *I. centralis* n. sp. cluster, although some overlap remains. Positive CV2 values correspond with a narrower platform, a straight caudal adcarinal ridge, and a more dorsal location of the maximum curvature on the rostral side. Negative CV2 values correspond with a wider platform, a concave caudal adcarinal ridge, and a more ventral location of the maximum curvature on the rostral side.

*Idiognathodus eudoraensis* is most separated from *I. centralis* n. sp. along the CV3 axis, whereas many *I. eudoraensis* specimens have positive CV3 values, and most *I. centralis* n. sp. specimens have negative CV3 values. Despite the differences in where the majority of specimens for each of those two groups lie on the plot, a significant amount of overlap between the two is still observed. Specimens with positive values of CV3 correspond with an outwardly flaring caudal adcarinal ridge, sub-parallel transverse ridges on both sides of the platform, and a more dorsally extensive carina. Specimens with negative values of CV3 correspond with a more inwardly located caudal adcarinal ridge, oblique transverse ridges on the rostral side of the platform, and a less dorsally extensive carina.

**Idiognathodus abdixitus n. sp. and I. simulator sinistral elements – CVA, species**

A CVA using species as the group classifier was calculated for all the sinistral elements of *Idiognathodus simulator* specimens from the Heebner Shale, midcontinent North America (Hogancamp *et al.*, 2016) and all the sinistral elements of *I. abdixitus* specimens from this study to determine if the two species could be distinguished from one another using PLA. Both species possess an eccentric groove and a caudal adcarinal ridge that is separated from the platform margin by the adcarinal trough. The two species are separated from each
Text-fig. 3. CVA analysis using chirality as the group classifier for the Idiognathodus magnificus group (Hogancamp et al., 2017), the I. eudoraensis group, and the I. simulator group (Hogancamp et al., 2016). Light gray wireframes represent the Procrustes shape where all CV values equal zero. Black wireframes represent the shape at the designated eigenscore. Percentages refer to the amount of variation accounted for by the eigenvector. Blue = sinistral elements. Red = dextral elements.
other along the CV1 axis; *I. simulator* has positive values of CV1 and *I. abdivitus* n. sp. has negative values of CV1 (Text-fig. 6). Specimens with positive values of CV1 have a more asymmetrical platform, with the rostral side almost twice as wide as the caudal side. Specimens with negative values of CV1 have a more symmetrical platform where the platform area on either side of the eccentric groove is similar in size. Specimens with positive values of CV1 have more asymmetrical adcarinal ridges, where the rostral adcarinal ridge is shorter than the caudal ridge and curves inwards at the ventral end. Specimens with negative values of CV1 have more symmetrical adcarinal ridges of similar length and similar orientation subparallel to the carina.

**Text-fig. 4. CVA analysis cross plots for the Idiognathodus eudoraensis group sinistral elements using species as the group classifier.** Light gray wireframes represent the Procrustes shape where all CV values equal zero. Black wireframes represent the shape at the designated eigenscore. Percentages refer to the amount of variation accounted for by the eigenvector. Yellow = *I. abdivitus* n. sp. Blue = *I. aff. luganicus*. Red = *I. centralis* n. sp. Gray = *I. eudoraensis*.

**Idiognathodus abdivitus n. sp. and I. simulator**

**Dextral elements — CVA, species**

A CVA using species as the group classifier was calculated for all the dextral elements of *Idiognathodus simulator* specimens from the Heebner Shale, midcontinent North America (Hogancamp *et al.*, 2016) and all the dextral elements of *I. abdivitus* specimens from this study to determine if the two species could be distinguished from one another using PLA. Both species possess an eccentric groove and a caudal adcarinal ridge that is separated from the platform margin by the adcarinal trough. The two species are separated from each other along the CV1 axis, whereas *I. simulator* has negative values of CV1 and *I. abdivitus* n. sp. has positive values of
CV1 (Text-fig. 6). Specimens with negative values of CV1 have a more asymmetrical platform, with the rostral side more than twice as wide as the caudal side, especially in the ventral part. Specimens with positive values of CV1 have a more symmetrical platform where the platform area on the rostral side of the eccentric groove is still wider than the caudal side, but by a lesser amount, and the location of maximum curvature on the rostral margin is in a more medial location on the platform. Specimens with negative values of CV1 have more asymmetrical adcarinal ridges, whereas the rostral adcarinal ridge is shorter than the caudal ridge and curves inwards at the ventral end. Specimens with positive values of CV1 have more symmetrical adcarinal ridges of similar length and similar orientation subparallel to the carina.

**Idiognathodus sweeti n. sp. – CVA, chirality**

A CVA using chirality as the group classifier was calculated for the *Idiognathodus sweeti* n. sp. specimens from this study to determine whether or not this species exhibits asymmetrical $P_1$ element pairs. The sinistral and dextral elements are separated from each other on the CV1 axis, whereas dextral elements have negative CV1 values and sinistral elements have positive CV1 values (Text-fig. 7). Specimens with negative values of CV1 have a wider rostral platform margin, and those with
positive values of CV1 have a narrower rostral platform margin.

**Idiognathodus magnificus group morphotypes sinistral elements – CVA, species**

A CVA using species as the group classifier was calculated for the sinistral elements of the *Idiognathodus magnificus* group, including specimens of *I. sweeti* n. sp. from this study, and all sinistral specimens of *I. magnificus* morphotypes 1 and 2 from the Beeman Formation, New Mexico (Hogancamp *et al.*, 2017) to determine if they can be differentiated from one another using PLA. *Idiognathodus sweeti* n. sp. is separated from the other two morphotypes along the CV1 axis, whereas *I. sweeti* n. sp. typically has CV1 values less than -1, and the other two morphotypes have CV1 values greater than -1 (Text-fig. 8). Specimens with negative values of CV1 correspond with straight adcarinal ridges that taper slightly towards the carina ventrally with a more dorsal termination of the carina, and those with positive values of CV1 have more concave adcarinal ridges and ventral platforms, with adcarinal ridges that flare outwards at the ventral ends with a more ventral termination of the carina.

The *Idiognathodus magnificus* morphotype 1 and 2 clusters are slightly separated from one another by CV2. Although some overlap between the two clusters is observed, all but one specimen of *I. magnificus* morphotype 2 have negative values of CV2 and most *I. magnificus* morphotype 1 specimens have positive values of CV2. Specimens with negative values of CV2 correspond with a more dorsally extensive curvature maxima on the rostral platform margin, and those with positive values of CV2 correspond with a more ventral position of the curvature maxima on the rostral platform margin. More discussion about the differences between *I. magnificus* morphotypes 1 and 2 can be found in Hogancamp *et al.* (2017) (also see Pl. 1, Figs. 19-22).

**Idiognathodus magnificus group morphotypes dextral elements – CVA, species**

A CVA using species as the group classifier was calculated for the dextral elements of the *Idiognathodus magnificus* group,
including specimens of *Idiognathodus sweeti* n. sp. from this study, and all dextral specimens of *Idiognathodus magnificus* morphotypes 1 and 2 from the Beeman Formation, New Mexico (Hogancamp et al., 2017) to determine if they can be differentiated from one another using PLA. *Idiognathodus sweeti* n. sp. is separated from the other two morphotypes along the CV1 axis, whereas *I. sweeti* n. sp. has CV1 values greater than +1, and the other two morphotypes have CV1 values typically less than -1 (Text-fig. 8). Specimens with positive values of CV1 correspond with straight adcarinal ridges that taper slightly in the caudal direction ventrally with a more dorsal termination of the carina, and those with negative values of CV1 have more concave adcarinal ridges and ventral platforms, with adcarinal ridges that flare outwards at the ventral ends and a more ventral termination of the carina.

The *Idiognathodus magnificus* morphotype 1 and 2 clusters are slightly separated from one another by CV2. Although some overlap between the two clusters is observed, most specimens of *I. magnificus* morphotype 2 have negative values of CV2 and most *I. magnificus* morphotype 1 specimens have positive values of CV2. Specimens with negative values of CV2 correspond with a more dorsally extensive curvature maxima on the rostral platform margin with longer adcarinal ridges, and those with positive values of CV2 correspond with a more ventral position of the curvature maxima on the rostral platform margin with shorter adcarinal ridges. More discussion about the differences between *I. magnificus* morphotypes 1 and 2 can be found in Hogancamp et al. (2017) (also see Pl. 1, Figs. 19-22).

**Idiognathodus sinistral elements, asymmetrical platform groups – CVA, species group**

A CVA using species group as the group classifier was performed for all sinistral elements for all members of the *Idiognathodus magnificus* group, the *I. eudoraensis* group, and the *I. simulator* group to determine how the sinistral elements vary between the three groups. The three groups are separated from one another along the CV1 axis, whereas the *I. magnificus* group has negative CV1 values, the *I. simulator* group has positive CV1 values, and the *I. eudoraensis* group lies between them with CV1 values between -2 and +2 (Text-fig. 9). Specimens with negative values of CV1 have longer adcarinal ridges, symmetrical platform margins, no eccentric groove, and shorter platforms. Specimens with positive values of CV1 have shorter adcarinal ridges of differing lengths, asymmetrical platform margins, an eccentric groove, and longer platforms.

The *Idiognathodus eudoraensis* group is separated from the other two groups by the CV2 axis, whereas the *I. eudoraensis* group has CV2 values greater than -1, and the other two groups have CV2 values between -4 and +2. Specimens with positive values of CV2 have longer adcarinal ridges and a wider caudal platform. Specimens with negative values of CV2 have shorter adcarinal ridges and a narrower caudal platform margin.

**Idiognathodus dextral elements, asymmetrical platform groups – CVA, species group**

A CVA using species group as the group classifier was performed for all dextral elements for all members of the *Idiognathodus simulator* group, *I. eudoraensis* group, and the *I. magnificus* group to determine how the dextral elements vary between the three groups. The three groups are separated from one another along the CV1 axis, whereas the *I. magnificus* group has negative CV1 values, the *I. simulator* group has positive CV1 values, and the *I. eudoraensis* group is in between them, with CV1 values between -2 and +2 (Text-fig. 9). Specimens with negative values of CV1 have longer adcarinal ridges of similar length, a rostral adcarinal ridge that
flares outward, a strongly concave rostral and caudal side, and no eccentric groove. Specimens with positive values of CV1 have shorter adcarinal ridges of different lengths, a rostral adcarinal ridge that flares inward, a convex rostral side, and an eccentric groove.

The *I. eudoraensis* group is partially separated from the other two groups by the CV2 axis, whereas the *I. eudoraensis* group has CV2 values greater than -1, and the other two groups mostly have CV2 values between -4 and +2. Specimens with positive values of CV2 have longer adcarinal ridges of similar length, more symmetrical platform margins, and a wider caudal platform. Specimens with negative values of CV2 have shorter adcarinal ridges of different lengths, asymmetrical platform margins, and a narrower caudal platform margin.

**SYSTEMATIC PALEONTOLOGY**

Illustrated specimens from Iowa are reposited at the University of Iowa Paleontology Repository (SUI) and specimens from New Mexico at the New Mexico Museum of Natural History (NMMNH). All specimens included in the morphometric analyses were assigned a separate morphometric identification number (TTU).

Class **CONODONTI** Branson, 1938  
Order **OZARKODINIDA** Dzik, 1976  
Superfamily **POLYGNATHACEA** Bassler, 1925  
Family **IDIOGNATHODONTIDAE** Harris & Hollingsworth, 1933
Genus *IDIOGNATHODUS* Gunnell, 1931

Type species.— *Idiognathodus claviformis* Gunnell, 1931.

*Idiognathodus eudoraensis* Barrick, Heckel & Boardman, 2008

Pl. 1, Figs. 17, 24; Pl. 2, Figs. 1–4, 9–21

*Idiognathodus eudoraensis* Barrick, Heckel & Boardman, 2008: p. 130, pl. 1, figs. 6, 7, pl. 2, figs. 3, 5, 7, 13, 18, 19, 22.

Amended Diagnosis.—*P₁* elements form an asymmetrical pair. An eccentric groove on the dorsal surface is shifted caudally or is medial in position. Rostral lobes and medial-restricted caudal lobes are restricted on both elements. Adcarinal ridges are relatively long with ventral extensions.

Description.—Sinistral element: The rostral adcarinal ridge is moderate in length and is concave along most of its length, curving in towards the carina. The caudal adcarinal ridge is slightly longer than the rostral ridge and has the same style of curvature. Both adcarinal ridges form continuous boundaries with the platform margins, which are typically twice as long as the adcarinal ridges. The maximum platform curvature for both margins is near the midpoint of the platform, forming nearly symmetrical platform margins. The eccentric groove
is caudally shifted slightly or medial in position, resulting in a rostral platform surface that is larger in area than the caudal platform surface. The eccentric groove is typically well-defined and shallow. The eccentric groove is usually larger and better developed on smaller specimens. The carina is short and terminates near the most ventral transverse ridges. The oral platform surface dips in towards the groove and the entire surface is typically slanted towards the caudal side. The transverse ridges intersect the eccentric groove at a slightly oblique angle and some ridges may curve slightly. Straight transverse ridges may be present. There is a lobe on the caudal and rostral side of the margins and adcarinal ridges. The rostral lobe is either reduced or medial in length and is thin. The caudal lobe does not extend as far down the platform but is wider than the rostral lobe. Both lobes extend close to the ventral ends of the adcarinal ridges and because the caudal ridge is longer, the caudal lobe usually appears larger, despite the fact that it does not extend far along the platform margin. Both lobes are decorated with small subspherical nodes that are typically discrete, but may fuse to create irregularly shaped nodular bodies. The number of nodes increases with the size of the lobe, but typically 2–4 nodes are common.

Dextral element: The rostral adcarinal ridge is typically straight and parallel with the carina but curved in the dorsal end near the lobe. The caudal adcarinal ridge is similar in ventral length to the rostral adcarinal ridge but always extends further. The caudal adcarinal ridge is more curved than the rostral ridge and curves in towards the carina. The caudal platform margin is relatively straight, with the maximum curvature located in the ventral region. The rostral adcarinal ridge is wider and the maximum curvature is also located in the ventral region. Dorsal of these inflection points, the margins for both sides taper into the dorsal tip. The eccentric groove is thin but typically well-developed throughout all growth stages. The carina is short and terminates near the most ventral transverse ridges. The transverse ridges are typically straight on the caudal side of the groove and dip dorsally away from the groove on the rostral side. The rostral lobe barely extends along the platform margin and is so small that it may only be represented by one spherical node located outside the adcarinal ridge. The caudal lobe is also restricted but may extend further along the platform margin and is typically slightly larger. Nodosity of a lobe appears to correlate with the size of the lobe. Nodes are subspherical and typically discrete, but may fuse slightly at their bases when in close proximity.

Remarks.—Barrick et al. (2008) outlined the morphological tendencies of the *Idiognathodus eudoraensis* group, but did not discriminate morphotypes. We provide this updated description to serve as a supplement to improve taxonomic clarity. Barrick et al. (2008) discussed the potential phylogenetic relationships between *I. simulator* and *I. eudoraensis*. The presence of *I. abdivitus* with the other *I. eudoraensis* group taxa described here provides conclusive evidence of *I. simulator*-like morphologies occurring with the older *I. eudoraensis* fauna. These are the oldest documented occurrences of *I. simulator*-like morphologies from North America.

The other Upper Pennsylvanian species of *Idiognathodus* that has an eccentric groove and lobes on both sides of the platform is *I. auritus* Chernykh, 2005. This species has smaller adcarinal ridges without ventral extensions, a more caudally shifted eccentric groove, and more strongly asymmetrical *P*₁ elements than *I. eudoraensis* (Hogancamp et al., 2016).

**Occurrence.**—*P*₁ elements of *Idiognathodus eudoraensis* used in this study were recovered from the middle Tinajas Member of the Atrasado Formation in New Mexico at Cerros de Amado B (Bed 10), Chupadera (Beds 2 & 4), and Ojo de Amado (base of Bed 64 and top of Bed 65). Specimens from the Winterset section, Iowa, came from the basal Eudora Shale and the basal 10 cm of the Stoner Limestone. Barrick et al. (2008) reported *I. eudoraensis* from the Eudora Shale at several locations in the Midcontinent, as well as the Upper Winchell cyclothem in north-central Texas, the Little Vermilion cyclothem in the Illinois basin, and rare occurrences in the South Bend cyclothem in Kansas.

*Idiognathodus abdivitus* n. sp.
Pl. 1, Figs. 2, 7; Pl. 3, Figs. 1–15

*Idiognathodus eudoraensis* Barrick, Heckel, & Boardman, 2008: p. 130, pl. 1, fig. 8, pl. 2, figs. 2, 12; 17, 20, 21.

*Holotype.*—NMMNH P-79380; Pl. 3, Fig. 3.

*Etymology.*—Latin meaning removed or separated, referring to the diagnostic caudal adcarinal ridge that is separated from the platform margin.

*Type locality.*—Cerros de Amado B section, Socorro County, New Mexico (Lucas et al. 2009).

*Type stratum.*—Bed 10, middle Tinajas Member, Atrasado Formation (Barrick, 2013b).

*Diagnosis.*—Asymmetrical *P*₁ element pair, a slightly caudally shifted eccentric groove, a disconnected caudal adcarinal ridge, and the absence of a rostral lobe.

*Description.*—Sinistral element: Rostral adcarinal ridge is short to moderate in length and oriented subparallel to the
carina. The rostral adcarinal ridge is connected with the rostral platform margin and forms a continuous boundary. The caudal adcarinal ridge is longer than the rostral adcarinal ridge and is separated from the caudal platform margin by the caudal adcarinal trough. The ventral part of the caudal adcarinal ridge is subparallel to the carina and the dorsal part typically flares away from the carina. The maximum platform margin curvature for both rostral and caudal platform margins is located around midlength. The eccentric groove is shifted slightly to the caudal side or is in a near median position. The groove is typically thin and shallow. The carina ends close to the most ventral transverse ridge. Oral platform surface may dip in towards the eccentric groove or be relatively flat. The transverse ridges on opposite sides of the groove are parallel. The platform margins are typically three to four times longer than the adcarinal ridges.

Dextral element: Rostral adcarinal ridge may be subparallel to the carina or dip towards it. The rostral adcarinal ridge forms a continuous boundary with the platform margin. The caudal adcarinal ridge is separated from the caudal platform margin by the adcarinal trough. The caudal ridge is subparallel to the carina on its ventral portion and the dorsal end flares away from the platform. The maximum curvature for the platform margins is typically near midlength for the caudal margin and in the ventral portion for the rostral margin. The eccentric groove is typically thin and not complete along the length of the platform. The groove can be truncated by as many as half of the adcarinal ridges, but sometimes these ridges appear notched along the trajectory of the groove. The carina terminates before or near the most ventral transverse ridge. The oral platform surface is relatively flat but may dip in towards the groove in the dorsal region. The transverse ridges are straight across the platform on both sides, but occasionally the most dorsal ridges dip dorsally away from the groove. The platform margins are typically three to four times longer than the adcarinal ridges.

Remarks.—Idiognathodus abdivitus n. sp. shows similar patterns of P₁ element asymmetry to I. simulator and also has the isolated caudal adcarinal ridge just like I. simulator. This species is discriminated from I. simulator by having longer adcarinal ridges that are typically subparallel to the carina, a more central and less prominent eccentric groove, no rostral lobes, and more symmetrical platform margins. The dextral element is wider than the sinistral element, the maximum curvature on the rostral margin is ventrally shifted on the dextral element, and the eccentric groove is better developed on the sinistral element. The eccentric groove for this species is weakly developed compared the groove seen on specimens of I. simulator, especially for the dextral elements. The adcarinal ridges of I. abdivitus n. sp. are longer relative to the platform length than specimens of I. simulator from the Heebner Shale. The isolated adcarinal ridge on the sinistral elements is more parallel to the carina in I. abdivitus n. sp. than it is in I. simulator. Large specimens of I. simulator grow a rostral lobe that is typically ornamented with one or two nodes, but specimens of I. abdivitus n. sp. do not grow rostral lobes at any size. It is because of these multiple morphological differences that we propose the designation of I. abdivitus n. sp. for these specimens that vary from I. simulator from the Heebner Shale.

Occurrence.—P₁ elements of Idiognathodus abdivitus n. sp. were recovered from the middle Tinajas Member of the Atrasado Formation in New Mexico at Cerros de Amado B (Bed 10), Chupadera (Bed 4), Ojo de Amado (top of Bed 65), and from the Winterset, Iowa section from the upper Eudora Shale.

Idiognathodus centralis n. sp.
Pl. 1. Figs. 10, 15; Pl. 4. Figs. 1–21

Idiognathodus eudoraensis Barrick, Heckel, & Boardman, 2008: p. 130, pl. 2, figs. 1, 6, 8–11, 14, 15.

Holotype.—NMMNH P-79398; Pl. 4. Fig. 8.

Etymology.—Latin meaning central, or medial in position, referring to the more central location of the eccentric groove in this species.

Type locality.—Cerros de Amado B section, Socorro County, New Mexico (Lucas et al. 2009).

Type stratum.—Bed 2, middle Tinajas Member, Atrasado Formation (Barrick, 2013b).

Diagnosis.—Asymmetrical P₁ element pair with a near-medial eccentric groove, one caudal lobe, moderately long adcarinal ridges, and relatively straight platforms.

Description.—Sinistral element: The rostral adcarinal ridge is sub-parallel to the carina and is usually one-third to one-half the length of the platform margin. The caudal adcarinal ridge is longer than the rostral ridge and is typically curved in the dorsal region near the lobe. The maximum curvature of both platform margins is located near midlength. The eccentric groove is medial in position, but can be shifted caudally slightly. The groove is better developed in smaller specimens than in larger ones. The transverse ridges on the oral platform surface are parallel across the groove in larger specimens, but typically deflect dorsally from the groove in small specimens.
The oral platform surface may dip in towards the groove and the entire surface is typically slanted downwards towards the caudal side. There is only a small lobe on the caudal side that does not extend far down the platform margin. The lobe is typically decorated with one to three subspherical nodes.

Dextral element: The rostral adcarinal ridge is subparallel to the carina and is typically short. The caudal adcarinal ridge is longer and typically flares away from the carina. The maximum curvature of the platform margins are in the most ventral region for both sides, but may be closer to the midpoint on the caudal side. The eccentric groove is medial in position but may be shifted slightly to the caudal side. The groove is best developed in smaller specimens, and may become incomplete in larger specimens. When the groove is truncated by complete transverse ridges they are typically located on the ventral half. The transverse ridges on the ventral half of the platform are subparallel on both sides of the groove, whereas the ridges on the dorsal half tend to deflect dorsally away from the groove. The rostral platform margin is much wider than the caudal margin, making the rostral platform area larger than the caudal platform area. This is one of the most apparent asymmetrical features between the sinistral and dextral element. The caudal lobe is small and does not extend far along the platform margin.

Remarks.—The other *Idiognathodus* species with an eccentric groove and a caudal lobe are *I. lateralis* Hogancamp, Barrick, and Strauss, 2016 and *I. praenuitius* Chernykh, 2005. Some specimens resembling *I. praenuntius* (Hogancamp et al., 2016; Pl. 1, Figs. 19, 20), but differ from that species based on their much longer adcarinal ridges and more curved platform margins. Many *I. centralis* specimens are similar to *I. lateralis* because the platforms of both are much longer than they are wide. *P₁* element asymmetry is similar in *I. centralis* and *I. lateralis* because the sinistral element has a more slender and oblique platform, and the dextral element has a straighter, more triangular shaped platform with a much wider rostral side. The features that most distinguish *I. centralis* from *I. lateralis* are the more medial position of the groove, the longer adcarinal ridges, straighter sinistral elements, thinner dextral elements, the less developed eccentric groove, and the slightly less apparent *P₁* element asymmetry of the former species.

Occurrence.—*P₁* elements of *Idiognathodus centralis* were recovered from the middle Tinajas Member of the Atrasado Formation in New Mexico at Cerros de Amado B (Bed 10), Chupadera (Beds 2 and 4), and Ojo de Amado (base of Bed 64 and top of Bed 65), as well as from the Winterset, Iowa section, from the middle and upper Eudora Shale.

**Idiognathodus aff. I. luganicus** Kozitskaya, 1978, in Kozitskaya et al., 1978

Pl. 1. Figs. 4, 5; Pl. 2. Figs. 5–8

**Idiognathodus eudoraensis** Barrick, Heckel, and Boardman, 2008: p. 130, pl. 2, figs. 4, 16.

Description.—Most of the known elements are dextral elements. The rostral and caudal adcarinal ridges are subparallel to the carina and moderate in length, approximately one-third to one-half the total length of the respective platform margin. The eccentric groove is variable in its development, and a weakly developed groove corresponds with straighter transverse ridges across the platform. The carina is short and terminates near the most ventral transverse ridge. The caudal platform margin is relatively straight for both sinistral and dextral elements. The rostral platform margin is wider, and the maximum curvature is located on the ventral platform region for the dextral elements and closer to midpoint for the sinistral elements. The oral platform surface is relatively flat for dextral elements and caudally slanted for sinistral elements. There are no lobes on either side of the element.

Remarks.—Although there are just a few specimens, both the sinistral and dextral elements appear similar to *Idiognathodus luganicus* Kozitskaya, 1978 (in Kozitskaya et al., 1978). *P₁* elements designated here as *I. aff. I. luganicus* are similar to *I. luganicus* from the Heebner Shale in Kansas and Missouri (Hogancamp et al., 2016; Pl. 1, Figs. 3, 6). The *I. luganicus* specimens have longer adcarinal ridges and the eccentric groove appears more medial in position. The low number of sinistral elements relative to the greater number of dextral elements makes it difficult to assign a symmetry class to these specimens, but the strong similarities to *I. luganicus* would suggest that this species also has similar *P₁* element symmetry patterns.

Occurrence.—*P₁* elements of *Idiognathodus aff. I. luganicus* were recovered from the middle Tinajas Member of the Atrasado Formation in New Mexico at Cerros de Amado B (Bed 10), Chupadera (Beds 2 and 4), and Ojo de Amado (base of Bed 64 and top of Bed 65), as well as from the Winterset, Iowa section, from the middle and upper Eudora Shale.

**Idiognathodus sweeti** n. sp.

Pl. 1. Figs. 18, 23; Pl. 5. Figs. 1–17

Holotype.—NMMNH P-79359; Pl. 5. Fig. 9.

Etymology.—A tribute to Walt Sweet, who recognized the taxonomic complications in the *Idiognathodus*–*Streptognathodus* plexus and believed that biometric studies
would be necessary to understanding their evolutionary and biostratigraphic relationships.

“That is, stratigraphic intervals dominated by Streptognathodus alternate with those dominated by Idiognathodus through the Pennsylvanian. This has surely complicated understanding of this plexus and represents a major unsolved problem in conodont taxonomy… If such an evolutionary program was followed in the developmental history of this important group of conodonts, I suspect it involved several lineages, which may have been affected to different degrees and at different times. Sorting this out will require careful biometric studies of collections from rock sequences.” Sweet, 1988, pp. 114–115.

**Type locality.**—Cerros de Amado B section, Socorro County, New Mexico (Lucas et al. 2009).

**Type stratum.**—Bed 2, middle Tinajas Member, Atrasado Formation (Barrick, 2013b).

**Diagnosis.**—P₁ element pairs appear slightly asymmetrical in platform shape. The oral platform surface lacks a groove. Both lobes are restricted and do not extend far into the platform. The caudal lobe is smooth and ovular in shape and does not protrude strongly from the platform.

**Description.**—Sinistral element: Both adcarinal ridges are concave on their dorsal half and are either subparallel to the carina or deflect in towards the carina on their ventral half. The location of the ridge concavity is near the lobe for both sides, and the ridges straighten ventral of the lobes, forming ventral extensions. The carina terminates near the most ventral transverse ridge and typically does not extend beyond it. The rostral platform margin forms a broad smooth curve from the dorsal end of the adcarinal ridge to the dorsal tip of the element. The caudal platform margin is widest in its ventral region and then tapers straightly in towards the dorsal tip. These different margin shapes give the platform an oblique and asymmetrical outline relative to the carina. The transverse ridges are variable in their orientation, but are either straight across the platform and sub-perpendicular to the carina, or they deflect dorsally away from the center of the platform. When the transverse ridges are deflected, the geniculation points are aligned following the line of the carina. The rostral lobe is either restricted or extends downwards near the midpoint of the margin. The caudal lobe does not extend far into the platform and is located outside the caudal adcarinal ridge. Both lobes are decorated with small, subspherical nodes that may fuse at their bases and form irregularly shaped nodular bodies. The nodosity increases with the size of the lobe.

Dextral element: Both adcarinal ridges are sub-parallel to the carina in their ventral regions and are typically concave on their dorsal regions near the lobes. The carina terminates near the most ventral transverse ridge and rarely extends beyond it. The maximum curvature of each platform margin is located in the ventral region. Both margins taper to the dorsal point and give the platform a triangular shape. The transverse ridges typically deflect dorsally from the middle of the platform but may be straight across the platform. The rostral lobe is small and does not extend far along the platform margin. Sometimes the rostral lobe is so small it may comprise only one or two nodes on the side of the platform. The caudal lobe extends farther down the platform, but does not extend beyond the midpoint of the margin. The nodosity of the lobes increases as lobes increase in size.

**Remarks.**—Idiognathodus sweeti n. sp. is different from *I. magnificus* morphotypes 1 and 2 described from New Mexico by Hogancamp et al. (2017), and from the Midcontinent material described by Rossco (2008). *Idiognathodus sweeti* n. sp. can be distinguished from *I. magnificus* morphotypes 1 and 2 because it has a caudal lobe that does not protrude strongly from the platform, and a rostral lobe that is restricted so that it does not extend to the midpoint along the platform margin; morphotypes 1 and 2 are described as having strongly asymmetrical P₁ element pairs, and although asymmetry is observed in morphotype 3, it is less obvious.

**Occurrence.**—P₁ elements of *Idiognathodus sweeti* n. sp. were recovered from the middle Tinajas Member of the Atrasado Formation in New Mexico, at Cerros de Amado B (Bed 10), Beds 2 and 4 at Chupadera (Beds 2 and 4), and Ojo de Amado (base of Bed 64). From the Winterset, Iowa section, it was recovered from the basal part of the Eudora Shale.

**DISCUSSION**

**Morphological variation in the *Idiognathodus eudoraensis* group**

Four different species of the *Idiognathodus eudoraensis* group are defined based primarily on differences between their lobes and adcarinal ridges. The morphometric analyses showed that both sinistral and dextral elements of *I. abdixitus* n. sp. can be separated from the other three species of the group using the PLA (Text-figs. 4 and 5). Dextral elements of *I. centralis* n. sp. and *I. eudoraensis* show little to no separation from each other using PLA (Text-fig. 5), but sinistral elements can be differentiated from each other using PLA (Text-fig. 4). These results suggest that based on the shape of the platform and adcarinal ridges alone (the features used in the PLA), the dextral elements between these two species cannot be...
Text-fig. 10. Identification flow chart showing the major morphological criteria used to differentiate between all species of the asymmetrical idiognathid clade.
confidently differentiated, but the sinistral elements can. All but three specimens of *I. aff. I. luganicus* were dextral elements and appeared to cluster separately from the other three species using PLA (Text-fig. 5). The element shapes as modeled by the PLA seem to support the differentiation of these species, most notably with the sinistral elements, as the dextral elements of *I. centralis* n. sp. and *I. eudoraensis* could not be confidently distinguished by the analysis.

**Idiognathodus sweeti** n. sp.

One species of *Idiognathodus* occurs with the *I. eudoraensis* group but is not assigned to the *I. eudoraensis* group because it did not have an eccentric groove. This species also has nodose lobes on the caudal and rostral side that are larger than the lobes seen on *I. eudoraensis* group specimens. This species is more similar to specimens from the *I. magnificus* group, but has significantly smaller lobes than typical *I. magnificus* (Text-fig. 10). It was classified as *I. sweeti* n. sp. and was compared to *I. magnificus* morphotypes 1 and 2 from Hogancamp et al. (2017). CVA shows that sinistral and dextral elements of *I. sweeti* n. sp. differ from *I. magnificus* morphotypes 1 and 2 by the presence of longer and less concave adcarinal ridges and ventral platform margins, with a more dorsal termination of the carina (Text-fig. 8). A CVA of *I. sweeti* n. sp. using chirality as the group classifier shows that *I. sweeti* n. sp. also has asymmetrical P₁ element pairs, with the dextral elements having a wider rostral platform margin. The asymmetry observed in *I. sweeti* n. sp. is less apparent than it is in *I. magnificus* morphotypes 1 and 2.

**Simulator-style asymmetry in *Idiognathodus* P₁ elements**

On the basis of platform structures and platform shape, the *Idiognathodus magnificus* group, the *I. eudoraensis* group, and the *I. simulator* group are easily distinguished from one another (Text-fig. 9). The CVA plots for the sinistral and dextral elements suggest that the dextral elements are more distinctive than the sinistral elements because the clusters on the dextral element cross-plot show less overlap between the three groups. Each of the three groups is composed of several species that are differentiated from each other by their platform structures (Text-fig. 10). Despite the diverse combinations of platform structures, all of the species from these three groups have the same style of P₁ element asymmetry. This asymmetry is here referred to as simulator-style P₁ element asymmetry because it was first described in detail in the *I. simulator* group. Simulator-style asymmetry is defined by differences on the rostral platform between sinistral and dextral P₁ elements. In particular, the sinistral element has a broadly curved rostral platform margin with a more dorsal location of the curvature maxima, and the dextral element has a wider, tapered rostral margin with a more ventral location of the curvature maxima. The magnitude of asymmetry appears more pronounced in larger specimens. In juvenile growth stages (platforms less than 0.5 mm), both elements resemble the adult sinistral form. As specimens get larger, the distinctive dextral element morphology becomes more pronounced and the sinistral element maintains juvenile characteristics but becomes larger. The dextral elements typically have a flatter platform surface than the sinistral elements, which typically have a caudally tapered platform surface.

**A distinct Idiognathodus clade with asymmetrical platforms**

We propose that the species of the *I. magnificus* group, the *I. eudoraensis* group, and the *I. simulator* group represent a distinct clade of *Idiognathodus* that was derived from typical *Idiognathodus* species with nearly symmetrical P₁ element pairs (Text-fig. 11). Strongly asymmetrical pairs in Late Pennsylvanian conodonts first appear in the *Idiognathodus magnificus* group (Rosscoe, 2008). Older species, such as the possible ancestor, *I. harkeyi* Gunnell, 1931, display only weak platform asymmetry (Rosscoe, 2008). When the asymmetrical clade first appears, as represented by *Idiognathodus magnificus* in the Dennis cyclothem, it occurs with other typical symmetrical *Idiognathodus* species such as *I. corrugatus*, *I. cherryvalensis*, and similar forms (Rosscoe, 2008). No symmetrical *Idiognathodus* species were recovered in our collections with the *I. eudoraensis* fauna. The other *Idiognathodus* species present, *I. sweeti* n. sp., lacks a groove—as does its ancestor, *I. magnificus*—but has more symmetrical sinistral and dextral elements than *I. magnificus* morphotypes 1 and 2 (Hogancamp et al., 2017).

The next younger fauna of asymmetrical *Idiognathodus* species is the *Idiognathodus eudoraensis* fauna, which is composed completely of species with the same asymmetrical platform symmetry, and with the addition of an eccentric groove. The youngest fauna, the *I. simulator* group, maintains the eccentric groove and strongly asymmetrical P₁ elements, but differs from the *eudoraensis* group in platform shape and features of the adcarinal ridge. *Idiognathodus boardmani* Hogancamp & Barrick, 2016 also appears with the *I. simulator* group and has simulator-style asymmetry, but lacks the eccentric groove. In contrast, the *I. tersus* group is a distinct group of symmetrical and ungrooved *Idiognathodus* that occur with the *I. simulator* group in North America (Hogancamp & Barrick, 2016). It is possible that the *I. tersus* group represents descendants of *I. sweeti* n. sp. that continued to become more symmetrically paired through time, or the *I. tersus* group in North America represents migrants from another region, potentially the Urals where similar species are described from coeval stratigraphic levels (Davydov et al. 2008).
Possible pattern of evolution of Late Pennsylvanian *Idiognathodus* species in North America

**Simulator clade**

- *Idiognathodus* simulator group
  - Groove maintained.
  - Asymmetry gets more apparent. Platform margins get more asymmetrical.
  - Adcarinal ridges get slightly shorter.

- *Idiognathodus* boardmani
  - Groove lost.

- *Idiognathodus* eudoraensis group
  - Asymmetry more apparent. Groove develops. Adcarinal ridges get slightly shorter.

- *Idiognathodus* sweeti
  - Asymmetry less apparent. No groove.

- *Idiognathodus* magnificus
  - Platform asymmetry becomes apparent.

**Idiognathodus tersus group**

- Asymmetry lost. Adcarinal ridges long

**Migrant *Idiognathodus* from Eurasia**

Only two specimens of the asymmetrical *Idiognathodus* clade have been documented from the *Streptognathodus zethus* Zone, the zone in between the *I. eudoraensis* and the *I. simulator* Zone (Barrick et al., 2008, pl. 1, figs. 1, 2). Both specimens are from the Little Pawnee Shale Member of the Cass cyclothem and have short adcarinal ridges, two lobes, and most resemble *I. auritus*. The presence of a simulator group species in the Cass cyclothem combined with the extreme rarity of *Idiognathodus* in the S. zethus Zone in the Midcontinent suggests the possibility that all simulator group species may first appear at an earlier time than the Oread cyclothem, but are not present or preserved in the Midcontinent.

The rise of asymmetry and a grooved platform in *Idiognathodus* described here represents another example of the independent evolution of distinct clades of species with a groove on the platform surface of *Idiognathodus*, similar to the proposed origins of *Streptognathodus* Stauffer and Plummer, 1932 (Rosscoe & Barrick, 2009), and *Swadelina* Lambert, Heckel, and Barrick, 2003. Although Merrill & von Bitter (1976) recognized the multiple appearances of idiognathodids with grooved platforms during the Middle and Late Pennsylvanian, they chose to attribute the appearances to ecological responses within a complex plexus of a single *Idiognathodus* group. We interpret the appearance of grooved platforms, as well as platform asymmetry, to represent multiple evolutionary events with each forming a new clade of species.

Donoghue & Purnell (1999) performed an occlusion study of *Idiognathodus* elements preserved in-situ from bedding plane assemblages from a black shale unit in the Desmoinesian Modesto Formation of Illinois. The *Idiognathodus* from their study also have a groove, but it appears more trough-like and is not as discrete as the eccentric groove observed in the *I. simulator* and *I. eudoraensis* groups. The transverse ridges from their specimens also appear more nodose than those observed in our three species groups. Despite these differences, the elements from their study and the elements of this study are quite similar when considering
the diverse array of morphological variation possible in conodont $P_i$ elements. Donoghue & Purnell (1999) noted that the rostral side of the dextral elements were wider than the rostral side of the sinistral elements. The simulator-style of asymmetry can be seen in the pair of elements labeled A and B in Donoghue & Purnell (1999, fig. 2) although it is not as prominent as the asymmetry observed in the three groups studied here. Donoghue & Purnell (1999) also showed that element damage is focused in the ventral part of the platform near the dorsal tip of the carina, and from a macro-scale optical view, similar trends of ‘duller’ ridges and nodes in that region are observed in all three groups studied here. Typically, the dullest platform surfaces are observed on the largest specimens. Based on these similarities it appears likely that the $I. magnificus$ group, the $I. eudoraensis$ group, and the $I. simulator$ group occluded in a similar fashion to the Idiognathodus studied by Donoghue & Purnell (1999). However, one complication to this interpretation is that the $I. magnificus$ group does not have any groove on the platform surface. According to Donoghue & Purnell (1999), the development of the groove seems to play a critical role in providing interlocking topography for the element pairs in the ventral region. Ventral ornament is also shown to be very important in the occlusion of Polygnathus (Martínez-Pérez et al., 2016) and Gnathodus (Martínez-Pérez et al., 2014). More work is required to confidently compare the occlusion styles of different Idiognathodus groups with different platform surfaces and to synthesize these observations.

Donoghue & Purnell (1999) also discussed the dramatic morphological change in Idiognathodus elements during ontogeny. The major change is that the smallest specimens are comprised mostly of a blade, with only a small platform. In larger Idiognathodus specimens, the platform becomes larger and the platform structures become more developed. If the platform structures played a critical role in element occlusion, then it would appear the juvenile elements may have occluded differently than the adults. Donoghue and Purnell (1999) suggested that if this is true, this could force a change in prey items during different life stages. Similar ontogenetic trends were observed in the three species groups studied here. Hogancamp et al. (2016) also showed that the lobes do not fully develop until after the platform is developed and suggested that lobe-based taxonomic identification can only be applied to specimens with a platform length longer than 0.4 mm. In the $I. simulator$ and $I. eudoraensis$ groups, the groove on the platform is maintained at all stages, suggesting that lobe development is more influenced by growth than the groove. The step-wise ontogenetic development of Idiognathodus $P_i$ elements should continue to be considered in future work due to the implications these changes likely have on element occlusion and function, as well as phylogenetic relationships.

**CONCLUSIONS**

The platform landmark analysis (PLA) technique was used to study morphological variations in the Idiognathodus eudoraensis group, and to compare them to the $I. simulator$ and $I. magnificus$ groups. The $I. eudoraensis$ group comprises four species with strongly asymmetrical $P_i$ element pairs and an eccentric groove that are differentiated from one another based on their platform structures. The same pattern of $P_i$ element asymmetry is observed in the $I. eudoraensis$, $I. magnificus$, and $I. simulator$ groups and is here referred to as simulator-style asymmetry. In simulator-style asymmetry, the sinistral element has a broadly curved rostral platform margin with a more dorsal location of the curvature maxima, and the dextral element has a wider, tapered rostral margin with a more ventral location of the curvature maxima. The consistent pattern of strong $P_i$ element asymmetry across multiple combinations of platform structures suggests that $P_i$ element symmetry is of higher taxonomic ranking than the platform structures and suggests that the three groups are related. The three groups comprise a distinct clade of idiognathodids derived from typical Idiognathodus first by the development of strong $P_i$ element asymmetry in $I. magnificus$ and later by the development of an eccentric groove on the platform surface in the $I. eudoraensis$ and $I. simulator$ groups. This clade represents another instance of independent evolution of a grooved platform surface in idiognathodids similar to that proposed for Streptognathodus and Sucadelina. Idiognathodus abdavisit us n. sp. from the $I. eudoraensis$ group is similar to the Gzhelian marker species $I. simulator$, but the two can be differentiated based on their adcarinal ridges, platform shape, and position of the eccentric groove.

**ACKNOWLEDGMENTS**

We would like to thank Carlos Martínez-Pérez and Yanlong Chen for very helpful reviews that enhanced the quality of this manuscript.

**LITERATURE CITED**


Barrick, J. E., P. H. Heckel, & D. R. Boardman. 2008. Revision of the conodont Idiognathodus simulator (Ellison 1941), the marker species for the base of the Late Pennsylvania global Gzhelian Stage. Micropaleontology, 54: 125–137.
APPENDIX 1: LOCALITY INFORMATION

**Cerros de Amado B**
Middle of Tinajas Member, Atrasado Formation, Socorro County, New Mexico; sample number is bed number shown in the following publications, bed 10: Lucas *et al.* (2009, fig. 12); Barrick *et al.* (2013b, fig. 6); Lucas *et al.* (2013, fig. 16, Second Day Road Log, Stop 3B, p. 60–62).

**Minas de Chupadera (Chupadera)**
Middle of Tinajas Member, Atrasado Formation, Socorro County, New Mexico; sample numbers are bed numbers shown in the following publications, beds 2 and 4: Lucas *et al.* (2009, fig. 13); Barrick *et al.* (2013b, fig. 60).

**Ojo de Amado**
Middle of Tinajas Member, Atrasado Formation, Socorro County, New Mexico; sample numbers are bed numbers shown in the following publications, beds 64 base and 65 top: Barrick *et al.* (2013b, fig. 6); Lucas *et al.* (2013, fig. 7, Second Day Road Log, Stop 1B, p. 47–49).

**Madison County, Iowa**
Stream bank near Madison-Adair County line, Iowa: Stanton Limestone Formation. Eudora Shale Member: basal dark gray shale, middle black shale; upper dark gray shale; Stoner Limestone Member - lower 10 cm. Heckel & Pope (1992, Stop 8, p. 36–37).
PLATES
### Plate 1

Species of the asymmetrical *Idiognathodus* clade. Scale is 0.25 mm. All are upper views of P1 elements. SUI = specimens reposed at University of Iowa. NMMNH = specimens reposed at the New Mexico Museum of Natural History. TTU = identification number for morphometric analysis.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 8.</td>
<td><em>Idiognathodus simulator</em> Ellison, 1941. Re-illustrated from Hogancamp et al. (2016).</td>
<td>35</td>
</tr>
<tr>
<td>1.</td>
<td>SUI 141038, Sedan 16, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td>SUI 141040, Clinton 12, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>2, 7.</td>
<td><em>Idiognathodus abdiveitus</em> n. sp.</td>
<td>48</td>
</tr>
<tr>
<td>2.</td>
<td>NMMNH P-79351, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 165.</td>
<td></td>
</tr>
<tr>
<td>7.</td>
<td>NMMNH P-79352, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 058.</td>
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</tr>
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<td>3.</td>
<td>SUI 141101, Clinton 14, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>6.</td>
<td>SUI 141103, Sedan 12, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>NMMNH P-79353, Ojo de Amado, base of Bed 64, middle Tinajas Member, Atrasado Formation, TTU 235.</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td>NMMNH P-79354, Chupadera, Bed 4, middle Tinajas Member, Atrasado Formation, TTU 148.</td>
<td></td>
</tr>
<tr>
<td>9.</td>
<td>SUI 141052, Clinton 12, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>16.</td>
<td>SUI 141054, Sedan 23, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>10, 15.</td>
<td><em>Idiognathodus centralis</em> n. sp.</td>
<td>49</td>
</tr>
<tr>
<td>10.</td>
<td>NMMNH P-79355, Cerros de Amado bed 10, middle Tinajas Member, Atrasado Formation, TTU 055.</td>
<td></td>
</tr>
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<td>15.</td>
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</tr>
<tr>
<td>11.</td>
<td>SUI 141077, Sedan 23, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>14.</td>
<td>SUI 141079, Clinton 29, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>12.</td>
<td>Holotype, SUI 141070, Clinton 19, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>13.</td>
<td>SUI 141073, Clinton 37, Heebner Shale.</td>
<td></td>
</tr>
<tr>
<td>17, 24.</td>
<td><em>Idiognathodus eudoraensis</em> Barrick, Heckel &amp; Boardman, 2008.</td>
<td>47</td>
</tr>
<tr>
<td>17.</td>
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<td></td>
</tr>
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</tr>
<tr>
<td>18, 23.</td>
<td><em>Idiognathodus sweeti</em> n. sp.</td>
<td>50</td>
</tr>
<tr>
<td>18.</td>
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<td></td>
</tr>
<tr>
<td>23.</td>
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<td></td>
</tr>
<tr>
<td>19, 22.</td>
<td><em>Idiognathodus magnificus</em> morphotype 1. Re-illustrated from Hogancamp et al. (2017).</td>
<td>44</td>
</tr>
<tr>
<td>19.</td>
<td>NMMNH P-77597, Space History B, Bed 229, Beeman Formation.</td>
<td></td>
</tr>
<tr>
<td>22.</td>
<td>NMMNH P-77594, Space History B, Bed 235, Beeman Formation.</td>
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</tr>
<tr>
<td>20.</td>
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Plate 2

Idiognathodus P1 elements, upper views. Scale bar is 0.25 mm. SUI = specimens repositioned at University of Iowa. NMMNH = specimens repositioned at the New Mexico Museum of Natural History. TTU = identification number for respective morphometric analyses.

Figure

Table

<table>
<thead>
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<th>Figure</th>
<th>Page</th>
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<tbody>
<tr>
<td>1–4, 9–21. <em>Idiognathodus eudoraensis</em> Barrick, Heckel &amp; Boardman, 2008.</td>
<td>47</td>
</tr>
</tbody>
</table>

1. NMMNH P-79361, Ojo de Amado, base of Bed 64, middle Tinajas Member, Atrasado Formation, TTU 237.
2. NMMNH P-79362, Chupadera, Bed 4, middle Tinajas Member, Atrasado Formation, TTU 151.
3. NMMNH P-79363, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 033.
4. NMMNH P-79364, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 216.
5. NMMNH P-79365, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 071.
6. NMMNH P-79366, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 039.
7. NMMNH P-79367, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 031.
8. NMMNH P-79368, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 025.
9. NMMNH P-79369, Ojo de Amado, top of Bed 65, middle Tinajas Member, Atrasado Formation, TTU 244.
10. NMMNH P-79370, Chupadera, Bed 4, middle Tinajas Member, Atrasado Formation, TTU 146.
11. NMMNH P-79371, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 206.
12. SUI 145772, Winterset, Eudora basal shale, TTU 009.
13. NMMNH P-79372, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 083.
14. NMMNH P-79373, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 189.
15. SUI 145773, Winterset, Eudora basal shale, TTU 010.
16. NMMNH P-79374, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 176.
17. SUI 145774, Winterset, Eudora basal shale, TTU 012.


5. NMMNH P-79375, Chupadera, Bed 4, middle Tinajas Member, Atrasado Formation, TTU 148.
6. SUI 145775, Winterset, Eudora upper shale, TTU 004.
7. NMMNH P-79376, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 188.
8. NMMNH P-79377, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 110.
Figure

*Idiognathodus* P, elements, upper views. Scale bar is 0.25 mm. SUI = specimens repositioned at University of Iowa. NMMNH = specimens repositioned at the New Mexico Museum of Natural History. TTU = identification number for respective morphometric analyses.

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<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
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<tbody>
<tr>
<td>1–15.</td>
<td>48</td>
</tr>
</tbody>
</table>

*Idiognathodus abdivitus* n. sp. 

1. NMMNH P-79378, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 091.
2. NMMNH P-79379, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 155.
3. Holotype, NMMNH P-79380, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 029.
4. NMMNH P-79381, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 222.
5. NMMNH P-79382, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 108.
6. NMMNH P-79383, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 172.
7. NMMNH P-79384, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 075.
8. NMMNH P-79385, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 165.
9. NMMNH P-79386, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 057.
10. NMMNH P-79387, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 058.
11. NMMNH P-79388, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 118.
12. NMMNH P-79389, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 133.
13. SUI 145776, Winterset, Eudora upper shale, TTU 001.
14. NMMNH P-79390, Chupadera, Bed 4, middle Tinajas Member, Atrasado Formation, TTU 144.
15. NMMNH P-79391, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 174.
Plate 4

*Idiognathodus* P, elements, upper views. Scale bar is 0.25 mm. SUI = specimens repositioned at University of Iowa. NMMNH = specimens repositioned at the New Mexico Museum of Natural History. TTU = identification number for respective morphometric analyses.

**Figure**

1–23. *Idiognathodus centralis* n. sp. ................................................................. 49

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. NMMNH P-79392, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 111.</td>
<td>49</td>
</tr>
<tr>
<td>2. SUI 145777, Winterset, Eudora middle shale, TTU 005.</td>
<td></td>
</tr>
<tr>
<td>3. NMMNH P-79393, Ojo de Amado, top of Bed 65, middle Tinajas Member, Atrasado Formation, TTU 239.</td>
<td></td>
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<td>4. NMMNH P-79394, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 103.</td>
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<td>5. NMMNH P-79395, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 224.</td>
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<td>6. NMMNH P-79396, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 208.</td>
<td></td>
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<tr>
<td>7. NMMNH P-79397, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 028.</td>
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<tr>
<td>8. Holotype, NMMNH P-79398, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 192.</td>
<td></td>
</tr>
<tr>
<td>9. NMMNH P-79399, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 049.</td>
<td></td>
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<tr>
<td>10. NMMNH P-79400, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 055.</td>
<td></td>
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<tr>
<td>11. NMMNH P-79401, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 086.</td>
<td></td>
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<tr>
<td>12. NMMNH P-79402, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 054.</td>
<td></td>
</tr>
<tr>
<td>13. SUI 145778, Winterset, Eudora upper shale, TTU 002.</td>
<td></td>
</tr>
<tr>
<td>14. NMMNH P-79403, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 052.</td>
<td></td>
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<tr>
<td>15. NMMNH P-79404, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 130.</td>
<td></td>
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<tr>
<td>16. NMMNH P-79405, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 119.</td>
<td></td>
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<tr>
<td>17. NMMNH P-79406, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 115.</td>
<td></td>
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<tr>
<td>18. NMMNH P-79407, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 166.</td>
<td></td>
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<tr>
<td>19. NMMNH P-79408, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 038.</td>
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<tr>
<td>20. NMMNH P-79409, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 032.</td>
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<tr>
<td>21. NMMNH P-79410, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 162.</td>
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</tbody>
</table>
**Figure**  
*Idiognathodus* P1 elements, upper views. Scale bar is 0.25 mm. SUI = specimens reposited at University of Iowa. NMMNH = specimens reposited at the New Mexico Museum of Natural History. TTU = identification number for respective morphometric analyses.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
</table>
| 1–17. *Idiognathodus sweeti* n. sp. | 50
| 1. NMMNH P-79411, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 079. | |
| 2. NMMNH P-79412, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 221. | |
| 3. NMMNH P-79413, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 219. | |
| 4. NMMNH P-79414, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 218. | |
| 5. NMMNH P-79415, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 092. | |
| 6. NMMNH P-79416, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 214. | |
| 7. NMMNH P-79417, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 204. | |
| 8. NMMNH P-79418, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 175. | |
| 9. Holotype, NMMNH P-79359, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 169. | |
| 10. NMMNH P-79420, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 171. | |
| 11. NMMNH P-79421, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 198. | |
| 12. NMMNH P-79422, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 168. | |
| 13. NMMNH P-79423, Cerros de Amado, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 041. | |
| 14. NMMNH P-79424, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 157. | |
| 15. NMMNH P-79425, Chupadera, Bed 2, middle Tinajas Member, Atrasado Formation, TTU 170. | |
| 16. NMMNH P-79426, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 094. | |
| 17. NMMNH P-79427, Cerros de Amado B, Bed 10, middle Tinajas Member, Atrasado Formation, TTU 072. | |
Hogancamp and Barrick: Morphometric analysis of *Idiognathodus*
CONODONTS WITH HIGH POTENTIAL FOR CORRELATION IN THE UPPER TOURNAISIAN TO MIDDLE VISÉAN (MISSISSIPPIAN) OF THE CANTABRIAN MOUNTAINS, SPAIN

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ABSTRACT

The first occurrence datums of several biostratigraphically relevant conodont taxa are revised in the Cantabrian Mountains, Spain. Tournaisian conodonts from the condensed cephalopod-bearing limestones of the Alba Formation, Cantabrian Mountains, Spain, include nearly globally distributed taxa such as Scaliognathus anchoralis and Gnathodus pseudosemiglaber. Gnathodus mirousei n. sp. has a high potential for correlation due to its occurrence in upper Tournaisian rocks of Europe, North America, and Asia. The first occurrence datum of Pseudognathodus homopunctatus in six stratigraphic sections in the Cantabrian Mountains is the best marker for recognition and correlation of the base of the Viséan. The datum is also related to ammonoid occurrences in the Cantabrian Mountains.

The first occurrences of index species such as Gnathodus praebilineatus, G. romulus, and G. bilineatus are discussed to demonstrate the diachronous nature of the boundaries between the nodular limestone and the chert-shale lithostratigraphic units (Gorgera, Lavandera, and Canalón members of the Alba Formation). Radiometric ages from the Lavandera Member and from beds of the Donets, Namur-Dinant and Southern Urals basins are integrated with the biostratigraphic zonal scheme.

INTRODUCTION

The base of the global Viséan Stage was defined at the base of bed 85 at the Pengchong GSSP section in Guangxi, south China, by the first appearance of the foraminifera Eoparastaffella simplex Vdovenko, 1954 in the lineage Eoparastaffella ovalis Vdovenko, 1954–E. simplex (Devuyst et al., 2003). The GSSP was correlated with the base of the Moliniacian Regional Substage, revised and discussed in the Belgian Dinant-Namur Basin by Devuyst et al. (2006) and Poty et al. (2006). The Tournaisian–Viséan boundary is below the entry of the conodont Pseudognathodus homopunctatus (Ziegler, 1960), which is considered a secondary marker for worldwide correlation. This horizon is above the last occurrences of the conodonts Scaliognathus anchoralis Branson and Mehl, 1941, Doliognathus latus Branson and Mehl, 1941, and the first occurrences of Polygnathus bischoffi Rhodes, Austin, & Druce, 1969, Mestognathus praebecmanni Sandberg, Johnston, Orchard, & von Bitter (in von Bitter et al., 1986), and M. beckmanni Bischoff, 1957 in south China and Belgium (Groessens, 1975; Conil et al., 1977, 1989, 1991; Tian & Coen, 2005; Devuyst et al., 2003, 2006).

In the Alpine chain of the Cantabrian Mountains, Paleozoic rocks correspond with the so-called Cantabrian Zone (CZ) after Lotze (1945). Mississippian carbonates were deposited in a deep marine setting that was almost free of shallow-water foraminifera in the CZ. Consequently, the base of the Viséan should be recognized from the first occurrence of the conodont Ps. homopunctatus. However, this species was rarely reported in the lower Viséan beds of the CZ. Higgins & Wagner-Gentis (1982) defined the Gnathodus typicus Zone in the lower beds of the Viséan, which they recognized in many sections of the CZ by the occurrence of G. typicus Cooper, 1939, G. antetexanus Rexroad and Scott, 1964, and G. texanus pseudosemiglaber Thompson and Fellows, 1980. This zone was correlated with the Ps. homopunctatus Subzone described by Groessens (1975) in Belgium, because Higgins & Wagner-Gentis (1982) found very scarce specimens of Ps. homopunctatus, one or two in two samples from different sections. The
systematics of *Gnathodus* species were being significantly revised during the nineteen eighties: Lane *et al.* (1980) had restricted the occurrence of *G. typicus* to the upper Tournaisian and invalidated *G. antetexanus*. *Gnathodus pseudosemiglaber* occurred from the upper Tournaisian. Alternatively, Lane *et al.* (1980) proposed the first occurrence of *Gnathodus texanus* Roundy, 1926 to correlate the base of the *G. texanus* Zone. This was applied by Park (1983), although in practice the recognition of the lower boundary of the zone was based on the last occurrence of *Scaliognathus anchoralis*. The concept of *G. texanus* was also equivocal, and doubtful specimens were recovered below the lower boundary of the *G. texanus* Zone (Lane *et al.*, 1980). Belka & Korn (1994) followed the same disappearance datum of *S. anchoralis* to define the lower boundary of their so-called “*G. texanus*” Zone. Raven (1983) correlated the lower boundary of the Viséan with a bed in the *S. anchoralis*–*D. latus* Zone in the CZ. However, the ranges of stratigraphic distribution of conodont taxa were wider in this work than in other studies. Hence, *S. anchoralis* coexisted with *P. bischoffi* and *Ps. homopunctatus* in the upper beds of Raven’s (1983) *S. anchoralis*–*D. latus* Zone.

The location of the Tournaisian/Viséan boundary in the Alba Formation was also discussed on the basis of ammonoid occurrences, mainly in Kullmann (1961, 1963, 1985) and Higgins & Wagner-Gentis (1982). The associations correspond to the *Merocanites–Ammonelliptites* Assemblage after Korn *et al.* (2012), which characterizes beds of the Tournaisian–Viséan interval.

Merino-Tomé *et al.* (2017) provided radiometric ages from two ash horizons interbedded in the lower–middle Viséan beds (Lavandera Member). They correlated these ash beds with the *G. texanus* and *G. praebilineatus* conodont zones.

The aim of this work is the revision of the occurrences of biostatigraphically significant conodont taxa, such as *Ps. homopunctatus*, *G. praebilineatus*, *G. romulus*, and *G. bilineatus*, in the upper Tournaisian to middle Viséan succession of the CZ. The chronostratigraphic scale is discussed for the key conodont taxa and known radiometric age dates from Viséan beds.

**GEOLOGIC SETTING**

The CZ corresponds to a thrust and fold belt in the southwestern branch of the Variscan chain. Concretely, the CZ is in the core of the so-called Ibero-Armorican (or Asturian) arc in the northwestern part of the Iberian Peninsula (Text-fig. 1; Lotze, 1945). Pre-orogenic paleogeographic reconstruction of the CZ produces a more or less arcuate disposition in accordance with the distinct model of formation. All the hypotheses suggest a passive margin (Gondwana continent) where Cambrian to Devonian shallow water, mainly marine...
clastic and carbonate deposits, change westwards, or west-southwards, to deep water facies. They form a wedge that thins progressively eastward, because the westward tilting of the platform during the Late Devonian gave rise to erosion and a regional unconformity. The associated hiatus increased in duration towards the core of the Asturian arc where it lies on middle Cambrian rocks (Adrichem Boogaert, 1967). The unconformity was postdated by a condensed sedimentation event between the latest Famennian (Devonian) and the late Serpukhovian (Carboniferous) in the pre-orogenic, or transition between pre- and syn-orogenic, series (Marcos & Pulgar, 1982). The Mississippian succession in the CZ was described by Comte (1959), who named the Ermita, Vegamián, and Alba formations.

The Ermita Formation (Comte, 1938) consists of 5–75 m of cross-bedded sandstones with thin shale layers. Locally, the top or all of the formation is replaced by 1 to 12 m of sandy, or bioclastic limestones of the Baleas Formation (Wagner et al., 1971). Conodonts and brachiopods indicate a latest Famennian to late Tournaisian age for the Ermita and Baleas formations (García-Alcalde & Menéndez-Álvarez, 1988; Sanz-López & Blanco-Ferrera, 2012).

The Vegamián Formation (Comte, 1959) consists of 2–5 m of black to grey shales with chert beds, and nodules of silico-phosphate and marcasite. The base of the formation is an unconformity (Winkler Prins, 1968; Sanz-López & Blanco-Ferrera, 2012). The formation is laterally replaced by upper Tournaisian limestone or sandstone of the Baleas and Ermita formations (Text-fig. 2).

The Alba Formation is composed of 20–30 m of red, nodular, cephalopod-bearing limestones deposited between the upper Tournaisian and the Serpukhovian. These limestones are similar to other Palaeozoic pelagic limestones in Western Europe, such as the Devonian ‘Griotte’ in the Montagne Noire and the Pyrenees, or as the German ‘Cephalopodenkalk’ (Tucker, 1974). A Mississippian shallow-water carbonate platform was only recently located in the eastern outcrops of the CZ, assigned to the Valdediezma Limestone (Text-fig. 1; Sanz-López et al., 2018b). High subsidence and stepped margins of this platform suggested a vast, starved, deep basin where very condensed sedimentation of the Alba Formation occurred.

The Alba Formation was subdivided into the Gorgera, Lavandera, and Canalón members based on the occurrence of radiolarian cherts and shales in the middle member (Wagner et al., 1971); three additional members may be locally differentiated above the Canalón Member (Sanz-López et al., 2004). The Gorgera Member is usually 1.2 to less than 2.5 m thick and consists of light grey, fine-grained carbonate nodules and beds included in mudstone or marl at the base, and red nodular limestone with red shales near the top. Limestones show an early episode of cementation (Balthasar & Amler, 2003) and bed surfaces include firm-ground horizons with small, patchy accumulations of bioclasts and intraclasts. The lowermost beds of the member included reworked bioclasts, iron-rich coated grains, and less than 1 mm sub-angular to sub-rounded quartz grains. Shale content is high. The varied fauna indicates a deep, but more or less oxygenated, setting in contrast to underlying black shales of the Vegamián Formation.
Greenish and reddish shales above the grey and black shales of the Vegamián Formation are included in the Gorgera Member of the Alba Formation (Winkler Prins, 1968; Wagner et al., 1971). The fauna of the greenish and reddish shales consists of entomozoid and benthic ostracods, articulate brachiopods of the Chonetispula–Plicochonetes Zone, bivalves, trilobites, pelmatozoan plates, bryozoan fragments, solitary corals, ammonoids, conodonts, and fish remains (Winkler Prins, 1968; Jordan & Bless, 1970; Wagner et al., 1971; Gandl, 1973; Amler & Winkler Prins, 1999; Winkler Prins & Martínez Chacón, 1999; Sánchez de Posada et al., 2002). The carbonate beds of the Gorgera Member yielded silicified agglutinated foraminifera (Balthasar & Amler, 2003), small brachiopods such as Rugosochonetes, Curthides, and Chonetispula (Winkler Prins, 1968; Martínez Chacón & Winkler Prins, 1993; Sánchez de Posada et al., 2002), corals of the Gyathosanxia Fauna (Küllmann, 1966), crinoids, gastropods, and trilobites of genera Griffithides and Liobole (Winkler Prins, 1968; Gandl, 1977), which are related at a generic level with those in the Kulm Facies of Central Europe.

The Lavandera Member consists of 1–10 m thick shale and chert with a few ash horizons. Chert beds preserved radiolarians and poriferan spicules. Ash layers were derived from originally basaltic composition volcanics, and have been altered to kaolinite and sudoite (Loeschke, 1983; Frankenfeld & Lippmann, 1985).

The Lavandera Member occurs in the deeper parts of the basin (Raven, 1983; Eichmüller & Seibert, 1984), whereas a fully condensed carbonate succession of the Alba Formation occurs on paleotopographic highs. This carbonate succession shows a more argillaceous lower part (3.5–7 m thick) correlated with the Gorgera Member, which may include abundant intraformational breccia beds interpreted as debris flows in relation to instability at the margins of sedimentary paleotopographic highs (Raven, 1983; Wendt & Aigner, 1985). The Canalón Member consists of 15–25 m of pink and reddish grey limestone with thin shale layers. This member is above the Lavandera or the Gorgera members (Text-fig. 2).

**MATERIAL AND METHODS**

The study of fifteen conodont samples from the Millaró and Las Portillas del río Nevandi sections of the CZ (Text-figs. 1, 2, M and LP; geographic coordinates of latitude and longitude 42°53′19″ N, 4°18′08″ W, and 4°18′58″ N, 4°46′23″ W, respectively) was focused in the search of the first occurrence of *Pseudognathodus homopunctatus*, or another marker taxon, to differentiate upper Tournaissian and lower Viséan beds. *Pseudognathodus homopunctatus* has been reported in probably lower Viséan beds in the Camplongo and the Venta de Getino sections (Higgins and Wagner-Gentis, 1982) and in the ABX section (Park, 1983), here named the Camperona section (Text-fig. 2, Ca).

A part of the conodont material from the CZ studied by Higgins (1962, 1971), Higgins et al. (1964), and Higgins & Wagner-Gentis (1982) was stored in the Higgins Collection of the National History Museum in London (NHMUK). A first partial study of the housed samples was accomplished during a stay by one of the authors in the museum (J. S-L). It included the re-examination of samples from the lower part of the Alba Formation at the Villabellaco section (Text-fig. 2, V). The geographic coordinates of this section are 42°53′19″ N, 4°18′08″ W.

A new species, *Gnathodus mirousei*, occurred in the upper Tournaissian strata in the Las Portillas del río Nevandi section (Text-fig. 2, LP). A few specimens of this taxon are in samples from the CZ in the A.C. Higgins Collection of the NHMUK. The sample that was the most productive for the new species is from the Catalan Pyrenees, Spain (C-104; geographic coordinates 42°17′48″ N, 1°54′08″ E). The re-examination of samples stored in the R. L. Austin Collection of the NHMUK allowed identification of specimens of *G. mirousei* from the upper Tournaissian (Courceyan Regional Sub-stage) Black Rock Limestone carbonate platform in South Wales and Bristol-Mendips region (England). Other occurrences of *G. mirousei* in unpublished material of the Austin Collection correspond to specimens studied by Hill (1971, 1975) from the Tournaissian and basal Viséan Walsoll Limestone (Limerick Formation) in southern Ireland.

**SYSTEMATIC PALEONTOLOGY**

Illustrated specimens, and additional material, are housed in the Museum of Geology of the University of Oviedo (Abbreviated prefix DGO in the catalog number). Other catalog numbers correspond to specimens stored in the NHMUK with prefix MP X. The notation and orientation applied in the conodont description is according to Purnell et al. (2000).

Order *OZARKODINIDA* Dzik, 1976
Family *GNATHODONTIDAE* Sweet, 1988
Genus *GNATHODUS* Pander, 1856

Type species: *Polygnathus bilineatus* Roundy, 1926, p. 13, pl. 3, fig. 10a–c; emend. Lane & Ziegler, 1984.
**Gnathodus mirousei** n. sp.

Pl. 1, Figs. 6–16

**Gnathodus delicatus** Branson & Mehl, 1938, Higgins *et al.*, 1964: pl. 5, fig. 24; Marks & Wensink, 1970: pp. 261–262, pl. 3, figs. 8–9; Higgins, 1971: pl. 5, figs. 5, 7, 11, and 13 (only); Lane *et al.*, 1980: pl. 3, fig. 17 (only); Austin & Davies, 1984: pl. 2, fig. 16; Belka, 1985: pl. 3, fig. 3 (only); Belka & Groessens, 1986: pl. 4, figs. 8–9; Schönlau & Kreutzer, 1993: pl. 4, fig. 5 (only); Perret, 1993: pl. C8, figs. 25–27, 29–31, 34, 38, 41, and 42; García-López & Sanz-López, 2002: pl. 4, figs. 3–4.


**Gnathodus bulbosus** Thompson, 1967. Butler, 1973: pl. 56, figs. 15, 16, 17, and 19–21 (only); Austin & Davies, 1984: pl. 2, fig. 15.

**Gnathodus cuneiformis** Mehls & Thomas, 1947. Lane *et al.*, 1980: pl. 4, figs. 5 and 13 (only); Belka & Groessens, 1986: pl. 5, figs. 2–3; Perret, 1993: pl. C8, figs. 35–36.

**Gnathodus semiglaber** Bischoff, 1957. Lane *et al.*, 1980: pl. 4, fig. 1 (only); Belka & Groessens, 1986: pl. 6, figs. 1–4, fig. 6.

**Gnathodus semiglaber** Bischoff → *G. texanus* Roundy, 1926. Lane *et al.*, 1980: pl. 5, fig. 3 (only); Belka & Groessens, 1986: pl. 6, figs. 7–9; Tian & Coen, 2004: pl. 1, fig. 32 (only).


**Gnathodus texanus** Roundy, 1926. Belka & Groessens, 1986: pl. 6, fig. 10 (only).

Intermediate form between *G. delicatus* and *Pr. cordiformis* Lane, Sandberg, & Ziegler, 1980. Perret, 1993: pl. C8, fig. 18 (only).

Intermediate form between *G. delicatus* and *G. cuneiformis*. Perret, 1993: pl. C8, fig. 43 (only).

**Gnathodus typicus** Cooper, 1939. Tian & Coen, 2004: pl. 1, fig. 33 (only).

**Gnathodus punctatus** Cooper, 1939. Tian & Coen, 2004: pl. 1, fig. 34 (only).

**Types.**—Holotype, the specimen illustrated in Pl. 1, Fig. 11 (DGO 15.614); paratypes DGO 15.612 and DGO 15.613.

**Type stratum and locality.**—Aspe-Brousset Formation, basal bed, sample C-104, Tosa d’Alp thrust sheet at the south of Amorriador de Cabanes in the Pyrenees (Sanz-López, 2002, fig. 2, section 8).

**Other material examined.**—83 elements from sample C-104 (DGO 15.610–15.611, 15.615, and 15.617); 10 elements from the Alba Formation in the CZ, samples 1364 (Beberino section in Higgins, 1971, NHMUK PM X966), 1519 (Pola de Gordon section in Higgins, 1971), 1166B (Santiago de las Villas section in Higgins *et al.*, 1964, NHMUK PM X857 and X858), J-234 (Olleros de Alba section in García-López & Sanz-López, 2002), and samples LP-5 and J-1986 (DGO 15.618 and 15.619) in Las Fortillas del río Nevandi section (Text-fig. 2); 8 specimens from the Black Rock Limestone of Burrington Combe, England (sample BC3 in Austin & Davies, 1984) and 35 specimens (NHMUK MP X3799 and 3800) from the Country Lietrim, Ireland (Hill, 1975, samples 29, 34, and 68).

**Derivation of name.**—In honor of Professor Dr. Raymond Mirouze, University Paul Sabatier of Toulouse, France.

**Diagnosis.**—Medium and large-sized elements are elongate and triangular, characterized by a high and isolated triangular pillar-like parapet joined to the carina by a transversal ridge. The parapet is followed by a longitudinal caudal row of nodes that reaches the dorsal tip of the element at the caudal cup. The rostral cup is frequently ornamented by a longitudinal row of nodes parallel to the carina and a transverse cross lateral row of nodes at a right angle located just in front of the transversal ridge of the caudal parapet. A longitudinal row of nodes is adjacent to each side of the carina before the dorsal tip.

**Description.**—Large elements of *G. mirousei* n. sp. are characterized by the presence of a high, triangular, pillar-like node (parapet) situated in the ventral part of the caudal platform. The high segment of the pillar joins the carina through a transversal ridge. At the dorsal side of the pillar, a longitudinal row of nodes is parallel to the carina and reaches the dorsal tip of the element. These nodes are small and well differentiated. The rostral platform bears another longitudinal row of nodes parallel to the carina from the ventral-medium part to the dorsal part of the element. The nodes of the rostral row are lower than those of the caudal row and they do not extend to the dorsal tip of the element. Furthermore, there is usually a cross lateral row of nodes forming a right angle with the carina in the ventral part of the rostral platform. The cross lateral row is parallel to the ventral margin of the rostral cup, although it converges with the ventral margin in some elements. The ornamentation in the rostral-dorsal cup may be composed of some small and dispersed nodes, but sometimes a second longitudinal rostral row of nodes can occur.

Immature (small elements) typically show a high pillar without the transverse ridge developed. This pillar is stronger and higher than the other nodes of the longitudinal caudal row. The ornamentation of the rostral cup varies from smooth to one big node, to one node and a dorsal terrace or also small nodes parallel to the carina, and finally to some nodes forming rows with a radial distribution.

**Occurrence.**—*G. mirousei* n. sp. occurs from beds with *Protognathodus cordiformis* Lane *et al.*, 1980, just below the entry of *S. anchoralis fairchildi* Lane & Ziegler, 1984 in the Belgian Salet section (Belka & Groessens, 1986). It occurs nor-
mally in beds of the *S. anchoralis* Zone in the Pyrenees and the CZ, where it co-occurs with *Pr. cordiformis* and *P. bischoffi* (illustrated by Higgins *et al.*, 1964; Marks & Wensink, 1970; Perret, 1993; García-López & Sanz-López, 2002). Elements here considered as *G. mirousei* n. sp. were also observed in the Waulsortian facies in the County Leitrim (Hill, 1975) and were illustrated in studies from the Carnic Alps, Mendips (England), Moravia-Silesia Basin, Illinois (USA), and South China (Butler, 1973; Lane *et al.*, 1980; Belka, 1985; Schönlaub & Kreutzer, 1993; Tian & Coen, 2004).

**Remarks.**—Large or mature elements of *G. mirousei* n. sp. elements are differentiated from *Gnathodus delicatus* by the presence of the triangular and isolated pillar joined to the carina by a transverse ridge. *Protognathodus cordiformis* has a wider caudal platform than *G. mirousei*, and ornamentation of strong nodes is extended on the surface of the cup. A T-shaped ridge composed of semifused high nodes at the ventral part of the caudal platform may occur in specimens of *Pr. cordiformis*, although the ridge is not arriving at the carina. *Gnathodus avonensis* Rhodes, Austin, & Druce, 1969 was defined on the basis of two small specimens with a strong caudal node as that occurring in *G. mirousei* n. sp. (Pl. 1, Fig. 17). In our opinion, a small, immature specimen is not a good choice from which to define a species. The search for other similar specimens in the Avon Gorge section provided a few specimens larger than the holotype in samples Z 36 and Z 37, which are below the type horizon of sample Z 38. However, these elements (Pl. 1, Figs. 20, 21) have a stronger caudal node like a transverse ridge, one or two nodes in the opposite part of the rostral platform, and a thicker platform is adjacent at each side of the dorsal carina. A secondary apatitic overgrowth covers the conodont surface. Their identification is doubtful, although they are closer to immature *G. mirousei* n. sp. than to the holotype of *G. avonensis*. Consequently, we cannot be sure that *G. avonensis* is an immature specimen of *G. mirousei* n. sp., or a small-sized mature element of a related species, whereas large and mature elements will be obtained from the same beds. A few mature elements of *G. mirousei* n. sp. were illustrated by Butler (1973) and Austin & Davies (1984) from some tens of kilometers south of the Avon Gorge from the Main Chert Beds in Halecombe and Burrington Combe quarries, respectively. Butler (1973, pl. 56, figs. 17 and 18) identified “*Gnathodus sp. (juv?)*” for small elements as the morphotype of *G. avonensis*, which should be, in our opinion, a *nomen dubium* of doubtful application.

**Genus PSEUDOGNATHODUS** Perret, 1993

**Type species.**—*Gnathodus commutatus homopunctatus* Ziegler, 1960, p. 5, pl. 4, fig. 3.


**Pseudognathodus homopunctatus** (Ziegler, 1960)

Pl. 1, Figs. 1–5

*Gnathodus commutatus punctatus* Bischoff, 1957, p. 24, pl. 4, figs. 7–11, 14.

*Gnathodus commutatus homopunctatus* Ziegler, 1960, p. 5, pl. 4, fig. 3.

*Pseudognathodus homopunctatus* (Ziegler). Perret, 1993: pp. 349, 351, figs. 122A, 122C; pl. C5, figs. 21–24, and 26 (only);

Nemyrovska, 2005: pp. 45–46, pl. 7, figs. 2 and 3.

**Material examined.**—Sixty one elements from sample CLP-6 in the Las Portillas del río Nevandi (DOG 15.601–15.608 and 15.620) and one element from sample 138C at the Villabellaco section; both samples are from the lower beds of the Alba Formation (Spain).

**Occurrence.**—*Pseudognathodus homopunctatus* is a secondary marker for the recognition and correlation of the lower boundary of the Viséan in Belgium, the British Isles, and China (Conil *et al.*, 1989; Devuyst *et al.*, 2003; Poty *et al.*, 2006). It is globally distributed in Viséan–Serpukhovian beds across Europe, northern Africa, the Moscow Basin, south Urals, central Asia, and China. In North America, a few specimens were studied in Meramecian beds of the Saint Louis Limestone in Kansas and the Tablequah Limestone in Oklahoma (Thompson & Goebel, 1969; Godwin *et al.*, 2010). It was described from the basal Chesterian beds in the Chainman Formation in Nevada and Utah (Sandberg *et al.*, 1980; Tynan, 1980), Virginia (Chaplin, 1984), and Canadian British Columbia (Orchard, 1987). A probable late Osagean (early Viséan) occurrence was reported from Alaska (Dumoulin *et al.*, 2006).

**Remarks.**—Variation in the ornamentation of the P1 elements is associated with the element size in an ontogenetic series. Diagnostic characteristics are well developed in mature elements. A wide morphologic variation is noted in the abundant association in sample CLP-6. Large elements show a row on each side of the cup, which consist of short transverse ridges (Pl. 1, Fig. 1). The two rows taper towards the dorsal termination of the carina through isolated nodes and form a “V” that
opens ventrally. Isolated nodes in the two rows are adjacent to the dorsal part of the carina at the apex of the "V". The ridges are higher and may be offset at the middle part of the row in the large specimens. The rows are formed by a few isolated nodes in the small elements. Rare specimens have a wide veil (extended margin) around a swollen area that is limited to the proximal ventral cup (Pl. 1, Fig. 3). Another morphotype has two differentiated rows of nodes on one side of the cup (Pl. 1, Fig. 4). The specimen from the Villabellaco section shows two aligned nodes between the rostral row of nodes and the carina (Pl. 1, Fig. 5). The wide variability observed in the lower Viséan beds from Spain was also recognized in samples from southwestern Ireland studied by Austin & Husri (1975) and Hill (1975).

NOMENCLATURE ACT
This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is 21DFD786-5A23-48FB-AEC9-EC976C7F9EA3 (Gnathodus mirousei n. sp.).

CONODONTS OF THE GORGERA MEMBER
AND THE FIRST OCCURRENCE OF PSEUDOGNATHODUS HOMOPUNCTATUS
Upper Tournaisian conodonts of the Scadiognathus anchoralis Zone occur within in the basal beds of the Gorgera Member of the Alba Formation (Adrichem Boogaert, 1967; Sanz-López & Blanco-Ferrera, 2012). This zone has been locally reported in beds of the Baleas Formation at the section of Las Portillas del río Nevandi (Raven, 1983; Menéndez-Álvarez, 1991). Gnathodus mirousei n. sp. occurs in the lower beds correlated with the S. anchoralis Zone. This species has a short range with a wide distribution (Pyrenees, Carnic Alps, the British Isles, Namur-Dinant Basin in Belgium, Moravia Silesian Basin, South China, and USA) and high potential for correlation (see Systematic Paleontology section; Pl. 1, Figs. 6–16).

Higgins & Wagner-Gentis (1982) recovered Ps. homopunctatus at the Camplongo and the Venta de Getino sections (Text-fig. 1). Both occurrences were in beds of the Gorgera Member and below the Lavandera Member of the Alba Formation. The marker datum level was located at 2.5 m above the base of the Gorgera Member (the member is 7.9 m thick) at the Camplongo section (sample 3077A), and at the top of the Gorgera Member (sample 1340A; 1.4 m thick) in the Venta de Getino section. The uppermost bed of the Gorgera Member at Las Portillas del río Nevandi (Picos de Europa tectonic unit; Text-figs. 1, 2) yielded 61 specimens of Ps. homopunctatus, and the sample from that bed was the most productive for the species in the CZ (Pl. 1, Figs. 1–4). Other known sections yielded 1–2 specimens at the first occurrence of the species. This low abundance occurs also in sections where the Lavandera Member is absent and replaced by limestone. Park (1983) reported Ps. homopunctatus at 1 m above the base in the Camperona section (Text-fig. 2; ABX section in the Esla parautochthon unit). One specimen of Ps. homopunctatus was identified in the sample 138C of the Villabellaco section stored in the Higgins Collection of the NHMUK (Pl. 1, Fig. 5), although it was not reported in the original publication (Higgins & Wagner-Gentis, 1982, table 3). The sample was collected at 2 m above the base of the Alba Formation (Text-fig. 2).

Specimens of Gnathodus texanus are common in the carbonate beds below and above the Lavandera Member in the Millaró and the Las Portillas de río Nevandi section, confirming the occurrence of this taxon in the CZ. Only one specimen was observed in the basal bed of the Gorgera Member in the Millaró section (Text-fig. 2). This lower occurrence should be re-assessed, because it could be an immature element in the wide variation observed in the prevalent species G. pseudoemglaber.

The top of the Gorgera Member yields conodonts of the Gnathodus praebilineatus Zone in the sections where the Lavandera Member is absent or is very thin (Belka & Korn, 1994; García-López & Sanz-López, 2002). The lowermost beds of the Canalón Member yield conodonts from the G. praebilineatus Zone in the Olleros de Alba section (García-López & Sanz-López, 2002). Gnathodus romulus (Pl. 1, Fig. 18) occurs in the Millaró, the Las Portillas del río Nevandi, and the Villabellaco sections, and indicates correlation with the G. romulus Zone described in the Rhenish Mountains (Korn & Kauffmann, 2009).

LATE TOURNAISIAN TO VISÉAN AMMONOIDS
The lower beds of the Alba Formation yielded ammonoids with high potential for correlation. The genera are nearly globally distributed, such as Eurites, Dzhaprakoceras, and Merocanites, or widely distributed, such as Ammonellipsites and Muensteroceras. These genera correspond to the late Tournaisian–early Viséan Ammonellipsites-Merocanites Assemblage in accordance with Korn et al. (2012). Kullmann (1985) differentiated a Tournaisian Ammonellipsites Fauna and a late Tournaisian to early Viséan Merocanites Fauna in the CZ. The older fauna consisted of Eurites browni McCoy, 1844 at the Olleros de Alba section and Ammonellipsites sp. in a few localities (Higgins et al., 1964; Kullmann, 1966, 2011). The younger ammonoid fauna is relatively abundant and in-
cludes *Dezaprakoceras hispanicum* (Foord & Crick, 1897), *Merocanites applanatus* (Frech, 1899) and *Eurites corpulentum* (Crick, 1899). One of the most diverse ammonoid successions was described in the marly lower part of the Alba Formation at the Villabellaco section by Wagner-Gentis in Higgins & Wagner-Gentis (1982). *Munsteroceras* sp., *Winchellocceras palentinum* Wagner-Gentis, 1982, and *W. marshallensis* (Winchell, 1862) occur below the first appearance of the conodont *Ps. homopunctatus* (Text-fig. 2). *Ammonellipsites kayseri* (Schmidt, 1925), *Dezaprakoceras hispanicum*, *Merocanites hispanicus*, *Muensteroceras parallelum* (Hall, 1860), *Pseudogirtyoceras villabellacoii* Wagner-Gentis (in Higgins & Wagner-Gentis, 1982), and *W. marshallensis* are between 2–5 m above the base of the Alba Formation. The correlation of the ammonoid-bearing beds by Higgins & Wagner-Gentis (1982) with Osagean deposits in Michigan and Indiana (USA) and lower Viséan strata in the Tien Shan Mountains (central Asia) is consistent with the *Ps. homopunctatus* occurrence.

Only one occurrence of the ammonoid *Beyrichoceras* is known in the Nocedo section, just below cherty shales of the Lavandera Member (Kullmann, 1961). This horizon may be correlated with the lower part of the *Beyrichoceras* Genzone in the British Isles (upper Holkerian to lower Asbian, middle Viséan; Waters et al., 2011; Korn et al., 2012).

**RADIOMETRIC AGES IN THE LAVANDERA MEMBER**

Two U–Pb laser ablation inductively coupled plasma mass spectrometry ages (343.5 ± 1.1 Ma and 337 ± 1 Ma) were recently obtained from zircon grains in two ash layers of the Lavandera Member at the Las Baleas section (Merino-Tomé et al., 2017). The lower bed is at the base of the member and the upper bed is one meter below the top of the Lavandera Member (17.5 m from the base of the section).

**DISCUSSION**

The first occurrence of *Ps. homopunctatus* indicates the lower boundary of the *Ps. homopunctatus* Zone and is currently the best datum for location and correlation of the Tournaisian/Viséan boundary in the CZ (Text-fig. 3). The correlation with the GSSP in the Pengchong section in China is not precise because, in that section, the species appears less than 1 m above the boundary, but well above (26.5 m) the last occurrence of *S. anchoralis* (Devuyst et al., 2003). The undefined interval between the disappearance of *S. anchoralis* and the appearance of *Ps. homopunctatus* could be subdivided utilizing the first occurrences of species of *Mestognathus*, but this genus occurs in upper Viséan beds in the CZ.

*Pseudognathodus homopunctatus* seems to occur in low number in the shale carbonates of the deep parts of the basin and is locally abundant in the condensed carbonate strata on the paleotopographic high at the Las Portillas del río Nevandi section.

Occurrences of the ammonoids *D. hispanicum*, *P. villabellacoii*, and maybe *M. applanatus* may be useful to differentiate the Viséan beds, according to their distribution in the sections of the CZ. This ammonoid fauna occurs below the re-examined sequence of the first occurrences of the conodonts *G. praebilineatus*, *G. romulus*, and *G. bilineatus* in the Villabellaco section (Text-fig. 2V).
praequineatus, and the lower boundary of the *G. praequineatus* Zone defined by Menéndez-Alvarez (1991), was reported in the upper part of the argillaceous limestone (Gorgera Member equivalent to the Lavandera Member) in the Peña Roscas section (Belka & Korn, 1994). This zone should be correlated with the upper part of the Lavandera Member, without conodont data. The *Gnathodus romulus* Conodont Zone, between the first occurrences of *G. romulus* and *G. bilineatus* (Korn & Kaufmann, 2009), is recognized at the lowermost beds of the Canalón Member just above the top of the Lavandera Member at the Millaró and Las Portilla del río Nevandi sections (Text-fig. 2). The lower beds of the Canalón Member yielded younger conodonts correlated with the upper Viséan *Lochriella nodosa* Zone in a few Palentian sections (Cardano and Gildar, according to Bwdinger, 1965; Adrichem Boogaart, 1967). Consequently, the boundary between the Lavandera and the Canalón Members is diachronous in the CZ, and local replacement occurred between these members.

Based on the first occurrence of its nominal species (Pl. 1, Fig. 19), the lower boundary of the *Gnathodus bilineatus* Zone, as determined by different authors, is close to the base of the Canalón Member, but it must be locally confirmed. Illustrated specimens in several publications correspond to *G. joseramoni* Sanz-López, Blanco-Ferrera, and García López (pl. 34, fig. 3 in Higgins & Wagner-Gentis, 1982).

Radiometric ages in Las Baleas section correspond, as in the neighborhood Millaró section, to beds from the *Ps. homopunctatus* Zone, the *G. praequineatus* Zone, and perhaps the lower boundary of the *G. romulus* Zone (Text-fig. 3). The ages of 337 Ma and 343.5 Ma after Merino-Tomé et al. (2017) are coincident with the interval from the *G. texanus* to the *G. praequineatus* zones which is close to the lower boundary with the *G. bilineatus* Zone in Davydov et al. (2012, fig. 23.5). This interval corresponds to the global cooling event IV (glaciation) according to Davydov et al. (2012, fig. 23.7). This cooling is represented by chert formation (Lavandera Member) in the deep parts of the CZ basin that formed in cold, nutrient-enriched waters that caused radiolarian blooms.

Existing radiometric data are consistent with those from Merino-Tomé et al. (2017), although the correlation with biostratigraphic units leads to a chronostratigraphic chart (Text-fig. 3) with several differences to that proposed by Davydov et al. (2012, fig. 23.5). Dates of 345.17 ±0.18 Ma and 345.00 ±0.18 Ma were obtained in beds correlated with the MFZ9 and the *Eoparastaffella simplex* Foraminiferal Zone of western Europe in the Donets Basin (Davydov et al., 2010). An age of 342.01 ±0.19 Ma was correlated with the MFZ12 Foraminiferal Zone of western Europe and an interval with the conodont *G. texanus* and *Lochriella aff. L. commutata* in the Donets Basin (Davydov et al., 2010). Pointon et al. (2014) reported an age of 336.22 ±0.06 Ma for a bed correlated with the Foraminifer MFZ12 in the Namur-Dinant Basin (Belgium). This zone occurs in an interval with shallow water conodont genera *Cavognathus* and *Taphognathus*, or an informal unit with taphognathids, and is considered equivalent to the Arundian and Holkerian in Belgium and United Kingdom (Purnell et al., 2002; Poty et al., 2006; Waters et al., 2011). The date of 335.59 ±0.19 Ma from Pointon et al. (2014) is in the lower part of the western European MFZ13. Schmitz & Davydov (2012) obtained a date of 333.87 ±0.18 Ma from a bed of the *L. nodosa* Zone in the southern Urals. The MFZ14 is correlated herein with the *L. nodosa* Zone on basis of the range of *L. nodosa* in Belgium and corresponding data from Conil et al. (1977).

The inclusion of the *G. romulus* Zone in the chronostratigraphic scheme in Text-fig. 3 shows its correlation with the late Holkerian, and not only with the Asbian as previous authors have suggested (Korn & Kaufmann, 2009). The first appearance of *G. bilineatus* is unclear. Poty et al. (2006) indicated this occurrence in the middle of the western European foraminifer MFZ13 (Text-fig. 3, II), against the estimated age of Davydov et al. (2012; 336.8 Ma, in Text-fig. 3, I). This inconsistency may be explained by the distinct biostratigraphic and systematic criteria used. Several authors, such as Nemyrovská (2005), located the base of the *G. bilineatus* Zone at the first occurrence of *G. romulus* in the CZ, and the German Rhenish Mountains. The old reports of *G. bilineatus* may correspond to occurrences of species subsequently defined, such as *G. joseramoni*, *G. praequineatus*, and *G. romulus* (e.g., those from Higgins & Wagner-Gentis, 1982).

**CONCLUSIONS**

The first occurrence of *Pseudognathodus homopunctatus* is a useful datum for the recognition and correlation of the Tournaissian/Viséan boundary in the CZ. It is above the last occurrences of *S. anchoralis* and *D. latus*, and close to the local occurrence of *G. texanus*. *Gnathodus mirousei* n. sp. is described from Tournaissian beds correlated with the *S. anchoralis* Zone from the CZ, Pyrenees, and the British Isles. The chert-shale sedimentation (Lavandera Member) show diachronous boundaries with the nodular limestone deposits due to migration of facies in the CZ. The chert-shale unit was initially deposited between the *Ps. homopunctatus* Zone and the *G. praequineatus* Zone (top of the Gorgera Member), and ended between the *G. praequineatus* and the *L. nodosa* zones (base of the Canalón Member). The *G. praequineatus* Zone, below the *G. romulus* Zone, was deposited during a time close to the interval of 337.5–342 Ma.
LITERATURE CITED


PLATE
### PLATE 1

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>DGO 15.605, sample CLP-6, Las Portillas del río Nevandi.</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td>DGO 15.606, sample CLP-6, Las Portillas del río Nevandi.</td>
<td></td>
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<tr>
<td>3.</td>
<td>DGO 15.607, sample CLP-6, Las Portillas del río Nevandi.</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>DGO 15.608, sample CLP-6, Las Portillas del río Nevandi.</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td>NHMUK MP X 3794, sample 138C, Villabellaco section.</td>
<td></td>
</tr>
<tr>
<td>6–16.</td>
<td><em>Gnathodus mirousei</em> n. sp.</td>
<td>75</td>
</tr>
<tr>
<td>6.</td>
<td>DGO 15.609, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>7.</td>
<td>Immature specimen DGO 15.610, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td>Immature specimen DGO 15.611, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>10.</td>
<td>Middle-sized specimen DGO 15.613, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>11.</td>
<td>Large specimen DGO 15.614, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>12.</td>
<td>Immature specimen DGO 15.615, sample C-104, Tosa d’Alp section.</td>
<td></td>
</tr>
<tr>
<td>13.</td>
<td>Large specimen DGO 15.616, sample B-185, Las Portillas del río Nevandi.</td>
<td></td>
</tr>
<tr>
<td>14.</td>
<td>Large specimen NHMUK MP X 966, sample 1364, Beberino section re-illustrated from Higgins (1971, pl. 5, fig. 11).</td>
<td></td>
</tr>
<tr>
<td>15.</td>
<td>NHMUK MP X 3779, sample 29, Ireland, from Hill (1975, pl. 8, fig. 18).</td>
<td></td>
</tr>
<tr>
<td>16.</td>
<td>NHMUK MP X 3780, sample 29, Ireland, from Hill (1975, pl. 8, fig. 10).</td>
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<td>17.</td>
<td><em>Gnathodus avonensis</em> Rhodes, Austin, &amp; Druce, 1969. Small element, holotype NHMUK MP X 411 re-illustrated, sample Z38, Quarry 2 in the Avon Gorge, Bristol, from Rhodes et al. (1969, pl. 19, fig. 4).</td>
<td>76</td>
</tr>
<tr>
<td>20, 21.</td>
<td><em>Gnathodus mirousei</em> n. sp.?</td>
<td>76</td>
</tr>
<tr>
<td>20.</td>
<td>NHMUK MP X 3783, sample Z36, Quarry 2 in the Avon Gorge from Rhodes et al. (1969, fig. 61).</td>
<td></td>
</tr>
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Sanz-López and Blanco-Ferrera: Tournaisian-Viséan Conodonts from Spain
CISURALIAN (EARLY PERMIAN) SWEETOGNATHID CONODONTS FROM THE UPPER PART OF THE RIEPE SPRING LIMESTONE, NORTH SPRUCE MOUNTAIN RIDGE, ELKO COUNTY, NEVADA

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ABSTRACT
The upper part of the Riepe Spring Limestone at North Spruce Mountain Ridge, south of Wells, Nevada, records considerable fluctuations in sedimentation trends and base level along the northern Ferguson Trough in the post-Antler foreland. A thick, mixed carbonate-siliciclastic succession follows an unconformity that spans the Carboniferous-Permian boundary and preserves a shallow-water, Sakmarian through Artinskian age (early to middle Cisuralian) conodont fauna. The low-diversity assemblage is largely composed of cosmopolitan species of the ozarkodinid genus Sweetognathus, dominated by Sweetognathus expansus, S. ‘merrilli’, S. binodosus, and S. ‘whitei’. The recovered conodonts are accompanied by a fusulinid fauna similar to that observed in Cisuralian deposits of the Bird Spring Formation of southeastern California and southern Nevada. The faunal turnover during which ornamented Cisuralian species of Streptognathodus were replaced by Sweetognathus species is not preserved within the section, as this transition appears to coincide with the hiatus. Descriptions are presented for a previously undocumented sweetognathid carinal configuration (Type V group), which exhibits features of both nodose and sulcus-bearing forms. Two new Type V species, S. wardlawi n. sp. and S. duplex n. sp., are described, and the occurrence of Sakmarian age P1 elements that bear a strong resemblance to Neostreptognathodus pequopensis is discussed.

INTRODUCTION
The Riepe Spring Limestone comprises nearly 13,000 square km (approximately 8,000 square mi) of exposed Pennsylvanian and Permian strata across eastern Nevada and adjacent western Utah (Steele, 1960). A recently measured stratigraphic section of the upper part of the Riepe Spring Limestone at North Spruce Mountain Ridge, Elko County, Nevada, is 180 m thick and composed of a variety of lithofacies, representing both marginal and shallow marine environments. The measured section is located 15 km east northeast of the junction of Highway 93 and Spruce Mountain Road, approximately 57 km south of Wells, Nevada (Text-fig. 1). The measured section closely follows Section 1 of Hope (1972), which was previously sampled for fusulinids by Raymond Douglass of the U.S. Geological Survey and Merlynd Nestell in 1969 and 1970. Although nearly 1,300 axially and equatorially oriented thin sections were produced from the collected material, no formal taxonomic identifications or further investigation of the section and formation followed. A number of thin sections from the Smithsonian’s Douglass Collection, along with recently collected and prepared fusulinid specimens from North Spruce Mountain Ridge, have been identified in this study to accompany the conodont biostratigraphy. The pairing of these two critical biostratigraphic indices allows for much-needed, expanded age control of this section.

The assemblage recovered from the lower to middle Cisuralian (Wolfcampian) part of the Riepe Spring Limestone has aided in the identification of an approximate Sakmarian-Artinskian Stage boundary within the section, and has provided new information regarding the iterative evolutionary trends observed within sweetognathid conodont lineages. Previous published investigations of Wolfcampian conodont faunas from the Riepe Spring Limestone have primarily focused on localities near Moorman Ranch, Nevada (Clark & Behnken, 1971; Clark, 1974; Behnken, 1975; Ritter, 1986, 1987) and western Utah (Ritter, 1987; Ritter & Robinson, 2009). Since the work of Ritter (1987), only preliminary conodont work has been conducted on nearby sections of the Riepe Spring Limestone in the Pequop Mountains (Wardlaw et al., 1998; Tierney, 2010).
REGIONAL GEOLOGIC SETTING

During Sakmarian to late Artinskian (middle to late Wolfcampian) time, the Ferguson and Dry Mountain troughs occupied much of northeast and north-central Nevada within the post-Antler foreland (Wardlaw et al., 1995). The Ferguson and Dry Mountain troughs (Text-fig. 2), as well as the preceding Butte Basin (referred to as the Ely Shelf by Stevens and Stone, 2007), were parts of a tectonically controlled and physiographically partitioned trough and shelf complex that may have represented the northern extension of the Bird Spring Platform, better known from exposures in southeastern California and southern Nevada (Stevens & Stone, 2007). The Butte Basin refers to regional marine deposits of Gzhelian (latest Pennsylvanian) and Asselian (earliest Permian) age, and is used to avoid potential confusion with the underlying Ely Basin and Ely Platform of Early to Middle Pennsylvanian age (Larson & Langenheim, 1979; Wardlaw et al., 1995).

The nearly equatorial paleogeographic setting (approximately 12°-15° N latitude) was confined by remnants of the Devonian to Mississippian Antler orogenic belt to the west, the Oquirrh-Uinta Uplift to the northeast, and the Deep Creek-Tintic Uplift to the south (Text-fig. 2) (Stevens, 1979; Scotese, 2014). The succession of shallow to marginal marine strata comprising the upper part of the Riepe Spring Limestone at North Spruce Mountain Ridge was deposited on the northernmost shelf of the Ferguson Trough, or Ferguson-Uinta Basin, portion of the complex between the bounding highlands to the north and south (Text-fig. 2) (Stevens, 1979; Miller et al., 1992).

The architecture and depositional patterns of the Ferguson Trough were dictated by episodes of local to regional uplift and subsidence paired with global sea-level fluctuations attributed to peak Gondwanan glaciation and the ensuing waning stages of the late Paleozoic ice age. Nearly contemporaneous unconformities across the Great Basin region demonstrate the profound, synchronous effects of tectonostratigraphic and glacioeustatic variability on the shallow platforms and marginal basins along the west coast of Pangea. Evidence for localized Pennsylvanian through Permian deformation (post-Antler and pre-Sonoma) has been reported from the nearby Pequop Mountains directly to the east (Marcantel, 1975; Sweet & Snyder, 2003), Carlin Canyon to the west (Dott, 1955; Trexler et al., 2004), east-central Nevada (Snyder et al., 1991; Gallegos et al., 1991), southwest Nevada (Schiappa et al., 1999), southern Idaho (Mahoney et al., 1991; Geslin, 1998), and southeast California (Stevens et al., 1997; Stevens & Stone, 2007). Investigations of glacioeustasy from Midcontinent cyclothems have proposed that the third and final glacial interval of the late Paleozoic ice age produced a base level drop of 60 to 120 m, which led to widespread coastal emergence, and the subsequent erosion and incision.
of exposed Upper Pennsylvanian and Cisuralian marine strata (Rygel et al., 2008). The 60 m range in the approximation of the maximum extent of base level change is ascribed to uncertainties regarding total glacial aerial coverage and the number of independent ice sheets (Isbell et al., 2003). A period of pronounced Gondwanan deglaciation began during the Asselian and persisted intermittently throughout the Cisuralian, with a collapse of continental ice sheets in southwest Gondwana occurring near the Sakmarian-Artinskian boundary (Montañez & Poulsen, 2013).

STRATIGRAPHY

Steele (1960) initially described the Riepe Spring Limestone as a predominantly massive, coralline, fusulinid-bearing limestone unit. The type section is located on the north side of Ward Mountain, White Pine County, Nevada (39°10'33.75"N, 114°55'59.80"W). Prior to the formal description, the strata of the Riepe Spring Limestone were considered to be within the upper part of the underlying Ely Limestone (Spencer, 1917; Pennebaker, 1932). The Riepe Spring Limestone of the Spruce Mountain Quadrangle provides a discontinuous Carboniferous-Permian boundary section, unlike the conventional stratigraphic interpretation of Steele (1960) in which the Cisuralian Riepe Spring Limestone disconformably overlies the nearly lithologically indistinguishable Pennsylvanian Ely Limestone. Such strictly Permian sections of the Riepe Spring Limestone have been described from Burbank Hills, Utah, Moorman Ranch, Nevada, and the Ruth mining district near Rib Hill, Nevada (Steele, 1960; Ritter, 1987). The stratigraphic discrepancy is partially attributed to the southward thinning of the conglomeratic intervals within the Riepe Spring Limestone of Spruce Mountain Ridge and the southern Pequop Mountains (Marcantel, 1975). Further inconsistencies in the regional stratigraphic interpretation of the Riepe Spring Limestone may be attributed to differing definitions of the formation (e.g., Steele, 1960 and Hope, 1972). The USGS geologic map of the Spruce Mountain Quadrangle (Map GQ-942) of Hope (1972) described the Riepe Spring Limestone as the Pennsylvanian-Permian succession of mixed carbonate-siliciclastic strata above the thinner bedded limestone of the Ely Limestone and below the fine, calcareous sandstone of the Rib Hill Formation. The same strata were referred to as the “Riepe Spring Formation” by Marcantel (1975), who suggested that the unit may be genetically related to the Strathearn Formation of the Carlin Canyon, Nevada area. The Pennsylvanian-Permian concept of the Riepe Spring Limestone described by Hope (1972) is used herein because of the priority of USGS Map GQ-942 to the measured section. A forthcoming discussion of the stratigraphy of Section 1 from Hope (1972) is being prepared by the authors.

The base of the measured section within the upper part of the Riepe Spring Limestone at North Spruce Mountain Ridge (40°40'47.08"N, 114°49'35.04"W) is distinguished by a chert-cobble paraglomerate (one meter thick), a lithofacies interpreted as nearshore clastic-wedge deposits that were shed during the discrete episodes of regional uplift to the north (Yochelson & Fraser, 1973; Marcantel, 1975). The top of the conglomerate quickly grades upward into a silty limestone in less than ten centimeters. The limestone transitions to a foraminiferal wackestone and grainstone, overlain by two more thin, quartzose paraglomerate beds at approximately ten meters above the base of the section. A thick quartzose limestone overlies the conglomerate beds, and gradually transitions into a calcareous quartz arenite just above 20 m into the section. The nearly five meter thick arenaceous unit contains small-scale hummocks (two to five centimeters) and laminations that have been interpreted as thin tempestite deposits. Highly abraded fusulinid specimens, many of which are missing outer volutions, are present as well. The remaining strata composing the western face of the ridge up to the crest (approximately 25 m higher) are fairly continuous limestone.
exposures with slightly varying percentages of fine sand-sized terrigenous material. Just beyond the crest of the ridge, at approximately 52 m, the terrigenous component of the limestone increases, and exposure becomes very poor.

Quartzose, sparsely crinoidal limestone composes the majority of the exposed eastern dip-slope of the ridge, where thick intervals are completely obscured by talus (Text-fig. 3.2). The base of the ridge flattens into a saddle where the covered intervals and sporadic limestone beds are interbedded with resistant, platy, yellowish orange-brown sandstone. The adjacent limestone outcrops are darker in color, more crinoidal, and muddier than the coarser, clastic limestone observed between 52 and 85 m above the base of the section. Above the highest, easternmost carbonate bed of the Riepe Spring Limestone lays the Rib Hill Formation (Text-fig. 3.2). The Rib Hill Formation beyond the measured section is similarly poorly exposed and is composed of platy calcareous sandstone talus broken from thin beds approximately one to two centimeters thick.

SYSTEMATIC PALEONTOLOGY
Repository.—All illustrated specimens are reposited in the Paleontology Repository at the University of Iowa (SUI numbers).

Class **CONODONTA** Pander, 1856  
Subclass **CONODONTI** Branson, 1938  
Order **OZARKODINIDA** Dzik, 1976  
Family **SWEETOGNATHIDAE** Ritter, 1986  
Genus **NEOSTREPTOGNATHODUS** Clark, 1972

**Type species.**—Streptognathodus sulcoplicatus (Youngquist et al., 1951).

**Remarks.**—Neostreptognathodus represents the dominant ozarkodinid genus of the late Artinskian and Kungurian Stages of the Permian. The genus shows a strong morphological resemblance to the bifurcated or laterally elongated forms of Sweetognathus, the inferred ancestors of *Neostreptognathodus*. Members of *Neostreptognathodus* display a partially to fully developed dorsoventral sulcus or trough. Carinal margins are occupied by discrete nodes, transverse ridges, or dorsoventral (longitudinal) parapets. Basal representatives of the genus maintain the pustulose microornamentation characteristic of Sweetognathus.

*Neostreptognathodus* aff. *pequopensis* Behnken, 1975  
Pl. 2, Figs. 9–11; Pl. 3, Figs. 1–3
Diagnosis.—A species of *Neostreptognathodus* bearing a carminiscaphate P₁ element with two rows of discrete, irregularly hemispherical carinal denticles separated by a shallow sulcus.

Description.—The P₁ element of *Neostreptognathodus aff. pequopensis* has a free blade of short to moderate length, bearing four to six partially fused ventral denticles. The carina bears five to eight pairs of discrete, pustulose, hemispherical denticles that are separated by a fully developed dorsoventral sulcus. Beyond the paired nodes, a papillary denticle is situated at the dorsal termination of the dorsal process, bringing the sulcus to a close and extending beyond the border of the basal cavity. *N. aff. pequopensis* is classified as a Type IV sweetognathid.

Occurrence.—9.7 m, 30.8 m, 34 m, 36.2 m, 39.7 m, 43.1 m, 51.7 m, 60.5 m, and 65.5 m above the base of the section; level - Sakmarian Stage.

Remarks.—*Neostreptognathodus aff. pequopensis* closely resembles *N. pequopensis* in nearly its full suite of morphological characters. The denticles of specimens collected from North Spruce Mountain Ridge differ slightly from typical specimens of *Neostreptognathodus pequopensis*. Those of *N. aff. pequopensis* are generally lower than the denticles of *N. pequopensis*, and the lateral margins of the former slope more gently toward the basal cup. It should be noted that the orientation of the free blade attachment shows variability in the specimens collected. Some specimens display the typical median attachment at the blade-carina junction (Pl. 2, Figs. 9, 10; Pl. 3, Fig. 2), whereas others have a single auxiliary, lateral denticle positioned at the junction (Pl. 3, Figs. 1, 3). The nature of the free blade attachment is generally not considered a species-level distinction, nor does the presence of the auxiliary node seem indicative of chirality, or “handedness,” in P₁ elements. All four of the specimens imaged represent dextral elements, and both morphotypic variants are observed. The forms described herein are regarded as *Neostreptognathodus aff. pequopensis* rather than *N. pequopensis* primarily on the basis of apparent diachronicity rather than morphological differences.

Genus *PSEUDOHINDEODUS* Gullo & Kozur, 1992

Type species.—*Pseudohindeodus ramosii* Gullo & Kozur, 1992.

Remarks.—An early to middle Permian sweetognathid conodont genus having a carminiscaphate P₁ element with a free blade separated from the narrow carina by a distinctive notch. In most cases the free blade and carina are subequal in length. The carina may be subtly denticulate or adenticulate with faint microornamentation and the dorsal termination is abrupt, dropping steeply to the base of the dorsal process. The basal cavity is broad and deep, occupying more than half of the length of the element, and has a characteristic crimp that runs continuously along the outer margin of the cup.

*Pseudohindeodus stevensi* (Clark & Carr, 1982)

**Pl. 3, Fig. 6**

Diagnosis.—A species of *Pseudohindeodus* having a small P₁ element distinguished by a rhomboidal, broadly flared platform and a narrow carina with a dorsoventral row of faint microornamentation.

Description.—The P₁ element of *Pseudohindeodus stevensi* has a free blade bearing three to five partially fused denticles, often with three smaller accessory denticles located ventrally to the main cusp. Two reduced denticles occupy the notch of the junction between the free blade and the carina. The carina is short, narrow, and displays a single dorsoventral row of fine, chevron-shaped notches. The platform is often slightly asymmetrical and rhomboidal in oral and aboral orientations. The outer one-third of the basal cup is lower than the inner portion following a distinctive crimp.

Occurrence.—177.3 m above the base of the section; level - Artinskian Stage.

Genus *SWEETOGNATHUS* Clark, 1972

Type species.—*Spathognathodus whitei* Rhodes, 1963.

Remarks.—Carminiscaphate P₁ elements may be assigned to one of four carinal configurations (Types I, II, III, and IV) previously described by Ritter (1986), or a new Type V. Sweetognathids with a Type V configuration have either a median sulcus or “dimples” along the ventral half of the carina, and discrete nodes on the dorsal half. The dorsal processes of *Sweetognathus* P₁ elements, regardless of specific denticulation (or lack thereof), are distinctly ornamented with secondary pustules.
**Sweetognathus anceps** Chernykh, 2005  
Pl. 3, Figs. 4, 5

_Sweetognathus behnkeni_ Kozur, 1975. Irwin et al., 1983, p. 1034, fig. 2n.  
_Sweetognathus anceps_ Chernykh, 2005, p. 204, pl. 21, fig. 13.  
_Sweetognathus whitei_ (Rhodes, 1963). Boardman et al., 2009, p. 118, pl. 30, fig. 9; Wardlaw et al., 2015, 379, pl. 1, fig. 15.

**Diagnosis.**—A species of _Sweetognathus_ in which the _P_1 element is characterized by transversely elongated, dumbbell-shaped carinal denticles with pustulose microornamentation.

**Description.**—A sweetognathid with a _P_1 element having a short to moderate free blade bearing four to five partially fused, laterally compressed denticles. The free blade meets the dorsal process in a median position, and the junction is occupied by the first small, pustulose denticles. The carina is laterally expanded and bears six to eight nodose, dumbbell-shaped denticles, which may display asymmetrical irregularities. The lateral margins of the carina drop steeply to the oral surface of the basal cup. Beyond the midpoint, the spacing between individual denticles increases dorsally, and the carina narrows to a single node at the dorsal terminus. _Sweetognathus anceps_ is classified as a Type III sweetognathid.

**Occurrence.**—51.7 m and 59.3 m above the base of the section; level - upper part of the Sakmarian Stage.

**Remarks.**—Although there is a strong morphological resemblance in many regards between _Sweetognathus anceps_ and its immediate descendent, _S. ‘whitei’_, the former lacks the dorsoventral ridge characteristic of the dorsal process of the latter (Chernykh, 2005).

_Sweetognathus behnkeni_ Kozur, 1975  
Pl. 3, Fig. 13

_Sweetognathus whitei_ (Rhodes, 1963). Clark, 1974, p. 716, pl. 2, figs. 15, 17; Riglos Suarez et al., 1987, p. 331, pl. 19.3, figs. 13, 16; Wardlaw et al., 2015, p. 379, pl. 1, figs. 18, 19.  
_Sweetognathus behnkeni_ Kozur. Bando et al., 1980, 43, pl. 4, fig.4; Ritter, 1986, p. 161, pl. 2, figs. 11–15; Riglos Suarez et al., 1987, p. 331, pl. 19.3, figs. 17, 19, 20, 22.

**Diagnosis.**—A species of _Sweetognathus_ bearing a broad _P_ element in which the carina is ornamented with narrow, teardrop-shaped transverse ridges. The ventral and dorsal-most carinal ridges are obliquely deflected toward their respective ends of the dorsal process.

_Description._—A sweetognathid species that, like _Sweetognathus anceps_, bears a general resemblance to _S. ‘whitei’_. The long free blade of _S. behnkeni_ has six to eight partially fused to fused denticles meeting the carina in a median position. The oral surface of the dorsal process is wide, up to nearly one-half the length of the carina, and displays a highly inflated lenticular shape. A sharply raised dorsoventral ridge traverses nearly the entire length of the carina, with peaks occurring in correspondence to the positions of the pustulose lateral denticles. The transversely elongated denticles are perpendicular (or nearly so) to the dorsoventral ridge at the widest portion (midpoint) of the carina, but bow ventrally and dorsally as the carina tapers to its longitudinal margins. The ventral-most ridges may split into two small, bulbous nodes at the marginal extent of the narrow, arcuate denticles. _Sweetognathus behnkeni_ is classified as a Type III sweetognathid.

**Occurrence.**—177.3 m above the base of the section; level - Artinskian Stage.

**Remarks.**—Although several authors (Igo, 1981; Mei et al., 2002) have previously designated _Sweetognathus behnkeni_ a junior synonym of _S. ‘whitei’_ and used the name to describe large, gerontic specimens of the latter species, _S. behnkeni_ is herein regarded as a valid species. _Sweetognathus behnkeni_ is notably absent from the lower range of _S. ‘whitei’_ at both North Spruce Mountain Ridge and Moorman Ranch, Nevada, suggesting that the form is indeed distinct (Kozur, 1975; Ritter, 1986). The occurrence of _S. behnkeni_ at North Spruce Mountain Ridge is 84.5 m higher than the first occurrence of _S. ‘whitei’_ and the approximate base of the Artinskian Stage. Ritter (1986) presented a sound ontogenetic argument for the morphological similarities between _S. behnkeni_ and _S. ‘whitei’_, stating that it is likely that a number of specimens of _S. behnkeni_ must have passed through a juvenile phase that may be hard to distinguish from _S. ‘whitei’_, whereas others exhibit discernible characteristics of _S. behnkeni_ at an immature or subadult level.

_Sweetognathus binodosus_ Chernykh, 2005  
Pl. 1, Fig. 14; Pl. 2, Figs. 1–3

_Sweetognathus inornatus_ Ritter, 1986, p. 163, pl. 3, figs. 12, 14.  
_Sweetognathus aff. whitei_ (Rhodes, 1963). Orchard, 1984, p. 211, pl. 23.1, fig. 1.  
_Sweetognathus whitei_ (Rhodes). Ding & Wan, 1990, p. 151, pl. 2, figs. 5, 9, 11, 15; Holterhoff et al., 2013, p. 116, fig. 4.12.  
_Sweetognathus anceps_ Chernykh, 2005, p. 205, pl. 20, figs. 14, 15.  
_Sweetognathus binodosus_ Chernykh, 2005, p. 203, pl. 20, figs. 5–8.
Diagnosis.—A species of *Sweetognathus* in which the carina of the P element consists of a variable series of semi-obluate, low cross-oval, or depressed dumbbell-shaped pustular nodes.

Description.—The free blade of *Sweetognathus binodosus* is straight to slightly arcuate (in rare instances) and bears three to six laterally compressed, partially fused denticles that increase in height ventrally. The carina is composed of four to eight nodular, subtly elongated denticles with pustulose microornamentation along the oral surface. The ventral-most and dorsal-most denticles of the carina are often small, laterally depressed, discrete nodes and are more hemispherical, closely resembling those of *S. 'merrilli'. The broadly flared basal cup is smooth in oral view and may be ventrally flared, tapering to the dorsal termination of the carina. Two morphotypes of *S. binodosus*, “Type A” and “Type B,” are recognized in the assemblage from the upper part of the Riepe Spring Limestone. The carinal denticles of “Type A” display subtle transverse elongation and may have a faint, weakly-developed dorsoventral ridge, resembling forms exemplified by the holotype specimen of Chernykh (2005) and those illustrated by Dehari (2016, unpublished thesis). The denticles of “Type B” specimens are more bulbous and distinctly bilobate. *Sweetognathus binodosus* is classified as a Type III sweetognathid.

Occurrence.—5.3 m, 26.8 m, 51.7 m, and 59.3 m above the base of the section; level - lower part of the Sakmarian to the Artinskian Stage.

Remarks.—The “Type A” morphotypic variant of *S. binodosus* is best represented by the holotype specimen of Chernykh (2005), specimens illustrated by Dehari (2016, unpublished thesis), and by two of the North Spruce Mountain Ridge specimens collected from 51.7 m above the base of the section (Pl. 2, Figs. 1, 2) in association with *S. anceps*. “Type B” specimens have carinal denticles that are slightly more laterally depressed than those of “Type A” forms (Pl. 2, Fig. 3). Two “Type B” specimens were collected from 5.3 m above the base of the measured section.

*Sweetognathus duplex* n. sp.

Pl. 1, Figs. 7–13

Holotype.—Pl. 1, Fig. 10, SUI 145779.

Type locality and horizon.—Upper part of the Riepe Spring Limestone, Spruce Mountain Ridge, Elko County, Nevada; beds 2 and 9.

Etymology.—Duplex (Lat.) - double; two-faced. The name *S. duplex* n. sp. is derived from the juxtaposition of two distinct carinal morphologies along a single dorsal process.

Diagnosis.—A species of *Sweetognathus* with both a well-developed median sulcus and discrete bulbous nodes, one following the other (dorsoventrally), along the carina.

Description.—The free blade of the P element of *Sweetognathus duplex* n. sp. is slightly arcuate in oral view, approximately one-third of the overall length, and bears five to six laterally compressed denticles becoming more strongly fused dorsally. A sharp, continuous transition from the fused denticles of the blade to the v-shaped, ventral portion of a median sulcus occupies the junction of the free blade and the dorsal process. The sulcus is narrow and dorsoventrally oriented, much like the sulci observed in members of *Neostreptognathodus*. Both the lateral parapets and the trough of the sulcus are ornamented with secondary pustules. The parapets of the sulcus in transitional forms may exhibit an undulating profile, with indentations in correspondence to remnants of ancestral denticles. The sulcus extends to the midpoint of the carina and is abruptly supplanted by nodose denticles resembling those of the “Type B” morphotype of *S. binodosus*. Three to four sets of bifurcated nodes comprise the dorsal half of the carina, uniformly decreasing and tapering in width dorsally. The maximum width of the nodose denticles is scarcely wider than the maximum width of the preceding sulcus. A single small node occupies the dorsal termination of the carina. The basal cup is ventrally flared and tapers tightly to the dorsal terminus. *Sweetognathus duplex* n. sp. is classified herein as a Type V sweetognathid.

Occurrence.—5.3 and 26.8 m above the base of the section; type level - Sakmarian Stage.

Remarks.—The ventral sulcus of *Sweetognathus duplex* n. sp. most closely resembles that of *Neostreptognathodus pnevi* Kozur & Movshovitsch in Movshovitsch et al., 1979. However, the sulcus of *N. pnevi* is narrower, steeper, and not as intensely pustulose. The junction of the free blade and dorsal process is often discontinuous or asymmetrical in *N. pnevi* as well.

*Sweetognathus expansus* (Perlmutter, 1975)

Pl. 1, Figs. 1–3

*Ozarkadina expansa* Perlmutter, 1975, pp. 98, 99, pl. 3, figs. 1–27.

*Sweetognathus adenticulus* Ritter, 1986, p. 165, pl. 4, figs. 9, 18, 19, 21.
Sweetognathus expansus von Bitter & Merrill, 1990, p. 107, pl. 3, figs. A–O; Ritter, 1995, pp. 1148, 1149, fig. 10.7; Mei et al., 2002, p. 84, fig. 10.27; Chernykh, 2005, pl. 20, figs. 1, 9, 10; Boardman et al., 2009, p. 140, pl. 17, fig. 7; pl. 20, fig. 13; pl. 24, figs. 5, 6; pl. 25, figs. 16–19; pl. 26, figs. 1–12, 14–18; pl. 27, figs. 9, 13, 14; pl. 29, figs. 1–11; Wardlaw et al., 2015, p. 376, pl. 1, fig. 1.


Diplognathodus expansus Chernykh, 2006, pp. 66–68, pl. 2, fig. 28.

**Diagnosis.**—A comparatively small species of Sweetognathus in which the P1 element is characterized by a short free blade and a pustulose, adenticulate to subtly nodose carina.

**Description.**—The P1 element has a short free blade consisting of three to five fused denticles subequal in height. The junction of the free blade and carina occurs just beyond the ventral margin of the broadly expanded platform and is marked by a transition from short, fused free blade denticles to a pustulose carina. The dorsal process occupies two-thirds to four-fifths of the length. A straight, dorsoventral furrow bisects the aboral side of the basal cavity. Two morphotypes of S. expansus are recognized: an adenticulate form and a subtly denticulate form. Boardman et al. (2009) proposed that the two morphotypes likely demonstrate ecophenotypic variability, whereas others have considered the nodular forms transitional morphotypes (Chernykh et al., 2013). The nodose form generally has partially fused to undulating, low pustulose denticles either along the entire oral surface of the carina or the dorsal one-third. The carina gradually decreases in height dorsally in both morphotypes. Sweetognathus expansus is classified as a Type I sweetognathid.

**Occurrence.**—4 m, 5.3 m, 15.3 m, and 26.8 m above the base of the section; level - upper part of the Asselian to the lower part of the Sakmarian Stage.

Sweetognathus ‘merrilli’ Kozur, 1975

Pl. 1, Figs. 4–6


Sweetognathus inornatus Ritter, 1986, p. 163, pl. 3, figs. 13, 15; 165, pl. 4, fig. 13; Holterhoff et al., 2013, p. 116, fig. 4.10.


**Diagnosis.**—A species of Sweetognathus having a P1 element characterized by a nodose carina bearing a single row of low, hemispherical denticles with pustulose microornamentation.

**Description.**—The free blade of Sweetognathus ‘merrilli’ is of short to moderate length, with three to six partially to strongly fused, laterally compressed denticles increasing in height ventrally. The blade attaches to the dorsal process in a median position. The low, dorsal-most denticles of the free blade transition smoothly into the knot-like denticles of the carina, and the junction is occupied by the first small, pustulose node. The dorsal process is composed of four to eight discrete, nodose denticles reaching a maximum diameter between one-half and two-thirds length (dorsally) along the carina. Carinal denticles of S. ‘merrilli’ typically reach a maximum diameter of one-fifth to one-seventh the length of the carina itself. Beyond the broadest denticles, the dorsal-most nodes decrease slightly in diameter, but the carina very rarely displays a papillary termination like those observed in more derived forms of Sweetognathus. In some cases, the carina may exhibit a dorsal curvature or minor torsion. The basal cavity is wide and spans approximately two-thirds the length of the P1 element. Sweetognathus ‘merrilli’ is classified as a Type II sweetognathid.

**Occurrence.**—4 m, 5.3 m, 26.8 m, and 36.2 m above the base of the section; level - upper part of the Asselian to the lower part of the Artinskian Stage.

**Remarks.**—Discrepancies regarding Sweetognathus merrilli and S. aff. merrilli (herein referred to as S. ‘merrilli’) arose from the discovery of Bolivian forms of the genus that were isotopically dated as middle Asselian in age, but strongly resembled Sakmarian forms known from the Urals (Chernykh, 2005, 2006; Henderson et al., 2009). The older S. merrilli is also known from the North American Midcontinent (Boardman et al., 2009) and bears highly irregular pustulose nodes, whereas the younger S. ‘merrilli’ has more orderly, hemispherical carinal nodes (Chernykh et al., 2013; Henderson, personal communication, 2016). Both the regular nature of the denticles of the dorsal process and the co-occurrence with S. binodosus serve as the rationale for the taxonomic assignment of the forms illustrated from North Spruce Mountain Ridge.

Sweetognathus cf. obliquidentatus (Chernykh in Chuvashov et al., 1990)

Pl. 3, Figs. 7, 8

**Diagnosis.**—A species of Sweetognathus in which the P1 element bears a partially developed dorsoventral sulcus and sinuous, pustulose transverse ridges along the carina.

**Description.**—Only one partial specimen of Sweetognathus cf. obliquidentatus was recovered from the Riepe Spring Limestone of North Spruce Mountain Ridge. A complete
discussion of the specimen is not possible because it lacks the free blade and the ventral portion of the dorsal process. The median and dorsal portions of the carina display a narrow sulcus and thin, raised transverse denticles, respectively. The sulcus is bordered by low transverse ridges that fully connect to close the sulcus. The ridges are irregular and are composed of single rows of pustules. Spacing between the ridges is widest beyond the midpoint of the carina (dorsally). Both the carina and the basal cup taper to a papillary dorsal termination of the platform. *Sweetognathus* cf. *obliquidentatus* has characteristics of both Types III and IV, but does not meet the criteria of Type V.

**Occurrence.**—82.8 m above the base of the section; level - upper part of the Sakmarian to the Artinskian Stage.

*Sweetognathus sulcatus* Ritter, 1986

*Pl. 2, Fig. 5

*Sweetognathus sulcatus* Ritter, 1986, p. 165, pl. 4, fgs. 8, 12.

**Diagnosis.**—A species of *Sweetognathus* with a median platform sulcus that is laterally bounded by partially to fully nodose irregular parapets on either side.

**Description.**—The nature of the free blade of *Sweetognathus sulcatus* (as described by Ritter, 1986) is not known from the available specimens imaged. The carina is dominated by a dorsoventral sulcus that runs nearly the full length of the oral surface of the dorsal process. Nodose ridges on each side of the sulcus outline the lateral margins of the carina, tapering to close the sulcus both ventrally and dorsally. Pustulose microornamentation is present along the entire carina. The dorsal termination of the carina displays a large, u-shaped denticle that wraps around the end of the sulcus. The oral surface of the basal cup is broadly flared and unornamented. *Sweetognathus sulcatus* is classified as a Type IV sweetognathid.

**Occurrence.**—26.8 m above the base of the section; level - middle to upper part of the Sakmarian Stage.

**Remarks.**—It may be inferred from the specimens shown by Ritter (1986) that the free blade attaches to the dorsal process in a median position. Ritter (1986) noted that the free blade spans approximately one-fifth of the overall length, but there was no accompanying image. The supplemental specimen of *Sweetognathus sulcatus* illustrated alongside the holotype by Ritter (1986) is similar to *N. labialis* (Chernykh, 2012), known from Kungurian age strata of the southern Ural Mountains near Mechetlino (Chernykh, 2012). A single specimen recovered from North Spruce Mountain Ridge has an auxiliary carinal denticle beyond the initial U-shaped dorsal termination. The smaller, dorsal-most denticle maintains a shape similar to the immediately preceding denticle.

*Sweetognathus wardlawi* n. sp.

*Pl. 2, Figs. 4–8

**Holotype.**—Pl. 2, Fig. 6, SUI 145787.

**Type locality and horizon.**—Upper part of the Riepe Spring Limestone, Spruce Mountain Ridge, Elko County, Nevada; bed 2.

**Etymology.**—For Dr. Bruce Wardlaw (deceased, 1947–2016).

**Diagnosis.**—A species of *Sweetognathus* that has a P₁ element displaying large, partially fused, hemispherical to hemi-oblate pustulose denticles that transition from concave to convex nodes along the oral surface near the midpoint of the carina.

**Description.**—The P₁ element bears four to six laterally depressed, fused denticles decreasing in size dorsally. The lower, dorsal denticles are more strongly fused. The dorsal process is composed of a nodose carina with six to seven inflated, hemispherical to hemi-oblate denticles, the oral profiles of which invert between the midpoint and two-thirds length of the carina. The three to five ventral-most denticles are strongly fused and exhibit a concave, dish-like interior with pustulose microornamentation. The concave denticles may be partially connected by a shallow sulcus. Beyond the transitional point, the two to four dorsal denticles are discrete to partially fused, hemi-oblate nodes that decrease in size dorsally. The longitudinal trough does not extend beyond the transitional point of the carina. The cup of the P₁ element is caudoventrally flared with a steeply tapered dorsal region, whereas the rostral margin has a shallower, symmetrically flared base. *Sweetognathus wardlawi* n. sp. is classified herein as a Type V sweetognathid.

**Occurrence.**—5.3 m above the base of the section; type level - Sakmarian Stage.

**Remarks.**—*Sweetognathus wardlawi* n. sp. most closely resembles *S. binodosus*, its inferred evolutionary predecessor, but differs with the presence of depressed dimples in the center of the strongly fused ventral denticles of the carina. Unlike *S. duplex* n. sp., the depressed portion of the carina in *S. wardlawi* n. sp. is not fully and uniformly connected by a median sulcus.
Sweetognathus ‘whitei’ (Rhodes, 1963)

Pl. 3, Figs. 9–12

Sweetognathus whitei (Rhodes). Igo, 1981, p. 72, pl. 7, figs. 2, 4, 5, 6; Orchard, 1984, p. 211, pl. 23.1, figs. 3–5; Henderson & McGugan, 1986, p. 229, figs. 7.4–7.7; Ritter, 1986, p. 63, pl. 3, figs. 17, 20, 21; Wang et al., 1987, p. 1052, figs. 6.17, 6.18; Riglos Suárez et al., 1987, p. 329, pl. 19.2, figs. 9–11, 13; p. 331, pl. 19.3, figs. 12, 14, 15; Mei et al., 2002, p. 72, fig. 10.25; Chernykh, 2005, p. 211, pl. 24, figs. 6, 7, 11; Wardlaw et al., 2015, p. 379, pl. 1, figs. 11–14, 16, 17.


Sweetognathus aff. whitei (Rhodes). Chernykh, 2005, p. 211, pl. 24, fig. 8; Chernykh, 2006, p. 103, pl. 15, figs. 1, 8; Henderson, 2014, p. 15, figs. 2.5–2.7.

**Diagnosis.**—A species of Sweetognathus bearing a P₁ element characterized by a nodose carina with well-developed dumbbell to lightly subcrescentic denticles. The carina has a thin, raised dorsoventral ridge typically accented with a single row of pustules.

**Description.**—The P₁ elements of Sweetognathus ‘whitei’ have a free blade of moderate length with as many as seven partially fused, laterally compressed denticles. The dorsal process is flat to lightly arcuate in lateral view with the largest carinal denticles often located at the highest point. When compared with other members of the genus, the carinal surface of S. ‘whitei’ appears laterally expanded in oral view. The carina is ornamented with seven to nine transverse dumbbell or bow tie-shaped denticles, where the median region of the node is thinner than the marginal extent. The oral surface dips steeply between carinal denticles, forming narrow lateral grooves between the transverse nodes. The dorsoventral ridge serves as the only ornamentation of the depressed lateral grooves. The dorsal-most denticles of the carina abruptly narrow to a papillary termination, occasionally accompanied by a single node. Sweetognathus ‘whitei’ is classified as a Type III sweetognathid.

**Occurrence.**—82.8 m, 114.5 m, 132.4 m, 161.5 m, 173.9 m, and 177.3 m above the base of the section; level - Artinskian Stage.

**Remarks.**—Topotype specimens of Sweetognathus whitei from the uppermost part of the Tensleep Sandstone of Wyoming have yielded isotopic values that fit those of late Asselian time (Chuvaishov et al., 2013). For this reason, the form that serves as the index for the base of the Artinskian Stage has been designated S. ‘whitei’, or S. aff. whitei. The motivation supporting the distinction has been discussed by Dr. Charles Henderson (pers. comm. 2017) and in Permophiles (Henderson, 2014) and the two forms are readily distinguished from one another. The dumbbell-shaped denticles of the Asselian age S. whitei are somewhat irregular and the margins of the denticles gently taper to the lower platform, whereas the margins of the much more regular denticles of S. ‘whitei’ (S. aff. whitei) drop steeply toward the platform (Henderson, 2014).

**BIOSTRATIGRAPHY**

Conodont yields throughout the Cisuralian part of the Ripe Spring Limestone at North Spruce Mountain Ridge are low, with 20 of 40 samples bearing few taxonomically identifiable P₁ elements (Table 1). Productive limestone beds yielded an average of fewer than six P₁ elements per five kg of digested sample material. The paucity of conodont elements, high volume of terrigenous clastic material within nearly all of the limestone present, and the thin intervals of fusulinid wackestone and packstone indicate the presence of a significant dilution factor related to high sedimentation rates associated with regional tectonism and the close proximity of the Ferguson trough to the fluctuating coastline.

Six genera of conodonts were recovered from the Sakmarian-Artinskian measured section, including Sweetognathus, Hindeodus, Sweetina, Mesogondolella, Pseudohindeodus, and Neostreptognathodus. Several rounded fragments of Streptognathodus P₁ elements were collected at 5.3 m and 20 m above the base of the section, but the extreme degree of abrasion to which the elements have been subjected suggests that the grains have undergone significant reworking and these are excluded from the faunal distribution. The lowest Cisuralian conodont specimens recovered from the section include S. expansus (Perlmutter, 1975) and S. ‘merrilli’ Kozur, 1975. The suite of conodonts recovered from the second lowest conodont-producing Permian-age limestone bed at 5.3 m above the base of the section is composed primarily of sweetognathids (e.g., Sweetognathus and Neostreptognathodus) and includes S. expansus, S. ‘merrilli’, S. binodatus Chernykh, 2005, S. wardlawi n. sp., and S. duplex n. sp. A GSSP proposal by the Subcommission on Permian Stratigraphy has tentatively assigned S. binodatus the status of co-index species for the base of the Sakmarian Stage alongside Mesogondolella monstra Chernykh, 2005, the primary biostratigraphic signal (voting in progress) (Chernykh et al., 2016). The S. binodatus Zone (partial range lineage biozone) spans from the base of the Sakmarian to the first occurrence of S. aniceps in the late Sakmarian (Henderson, 2016).

Sweetognathus duplex n. sp. has been recovered from two levels within the measured section, at 5.3 m and 26.8 m, allotting the new species a narrow range within the Sakmarian S. binodatus Zone. Although there is a co-occurrence of S. duplex n. sp. and S. wardlawi n. sp. at 5.3 m above the base...
of the section, this bed has proven to be the only point of the section to yield S. wardlawi n. sp. A single specimen of S. sulcatus Ritter, 1986 was also recovered from 26.8 m above the base of the section. Sweetognathus sulcatus has been previously reported from Sakmarian deposits of the Cerro Alto Formation in the Franklin Mountains of west Texas (Ritter, 1986) and the Kurort Formation of the Dal’ny Tulkas section in Russia (Davydov et al., 2005). Fusulinid associations within the S. binodosus Zone of the Riepe Spring Limestone include Schwagerina neolata Thompson, 1954, Schwagerina wellsensis Thompson, 1954, and Eoparafusulina linearis (Dunbar and Skinner, 1937) (Text-fig. 4). Sweetognathus anceps Chernykh, 2005, the evolutionary predecessor of S. ‘whitei’, occurs along with S. binodosus at 51.7 m, denoting the base of the S. anceps Zone (late Sakmarian; partial range lineage zone) (Henderson, 2016). Beyond the first occurrence of S. anceps, the dip-slope and thick accumulations of talus make the recovery of adequate sample material more difficult, but a partial, immature specimen of S. anceps was also recovered from 59.3 m above the base of the section.

The approximate base of the Artinskian Stage, denoted by the first occurrence of Sweetognathus ‘whitei’, is estimated to be 82.8 m above the base of the section, 31.1 m above the lowest recovered specimens of S. anceps (Text-fig. 4). The lowest specimens of S. ‘whitei’ occur in association with highly irregular and poorly preserved specimens of S. cf. obliquidentatus (Chernykh in Chuvashov et al., 1990), which has been previously reported from Sakmarian and Artinskian age strata of the Urals (Chuvashov & Chernykh, 1998; Chuvashov et al., 2013) and, most recently, Carlin Canyon, Nevada (Dehari, 2016, unpublished thesis). Pseudohindeodus stevensi (Clark & Carr, 1982), S. behnkeni (Kozur, 1975), and a large, transitional form of S. ‘whitei’ (to S. behnkeni) were collected at 177.3 m along with the continued occurrence of S. ‘whitei’ within the Artinskian age uppermost part of the Riepe Spring Limestone.

### CISURALIAN CONODONT FAUNA

**Type V Sweetognathids: A Novel Carinal Configuration**

P₁ elements of Sweetognathus are known for their high degree of intraspecific morphological plasticity and are characterized by dense pustulose microornamentation along the oral surface of the dorsal process (Behnken, 1975; Wang et al., 1987; Vuolo et al., 2014; Henderson, 2016). Sweetognathid P₁ elements display either adenticulate (Type I), discretely nodose
Text-fig. 4. Detailed lithologic column of the Cisuralian portion of the upper part of the Riepe Spring Limestone at North Spruce Mountain Ridge with accompanying conodont (circles) and fusulinid (ovals) distributions. Sample numbers are provided for the conodont material collected. The chronostratigraphic scale includes international standards and the corresponding North American stage.
(Type II), transversely ridged (Type III), or dorsoventrally troughed (Type IV) carinal morphologies (Ritter, 1986; Wang et al., 1987). Type I remained the singular carinal configuration of the family until the differentiation of the carina in S. merrilli (Type II) occurred during the middle part of the Asselian (Chernyk et al., 2013). The discretely denticulate sweetognathid forms of the Asselian (S. merrilli and S. ‘merrilli’) provided opportunities for further carinal modification during the early part of the Sakmarian when S. binodosus arose from S. ‘merrilli’ and introduced the Type III morphological group (Chuvashov et al., 2013). The Type III carinal configuration was initially produced by the lateral development of hemispherical nodes and gradually became more pronounced into the Artinskian Stage. Type IV sweetognathids include the members of Neostreptognathodus and a few earlier, sulcus-bearing forms of Sweetognathus, such as S. sulcatus, S. obliquidentatus, and S. clarki (Kozur in Kozur & Mostler, 1976) (Ritter, 1986; Wang et al., 1987). In addition to these previously described sweetognathid classifications, a new group, herein regarded as Type V, has been demonstrated by the recently discovered forms S. wardlawi n. sp. and S. duplex n. sp. recovered from the upper part of the Riepe Spring Limestone. Sweetognathids exhibiting a Type V configuration have a carina resembling a composite of the Type III and Type IV groups, in which the ventral half of the carina is predominantly centrally concave along the oral surface, but the dorsal portion is composed of subtly elongated, nodose (convex) denticles, much like those of S. binodosus (Read & Nestell, 2017). The half-and-half arrangement observed in the Type V group is most similar to the transition near the midpoint of the carina in some specimens of N. pnevi Kozur & Movshovitch in Movshovitsch et al., 1979) (those designated N. lectulus Chernyk, 2012), in which the parapets are adenticulate (or nearly so) along the ventral portion of the carina and strongly transversely ridged dorsally, and N. sp. 4 Chernyk, 2005. Neither S. wardlawi n. sp. nor S. duplex n. sp. have been reported from any nearby, approximately coeval marine deposits.

The strongly fused, vaguely molariform, ventral carinal denticles of Sweetognathus wardlawi n. sp. have dish-like fossae, herein regarded as “dimples,” which are connected by a very faint, shallow median groove that partially interrupts the outer rim of the denticles. The concave nature of the denticles is not a product of surface damage or occlusal microwear over time, as close inspection has revealed that the surface texture on the interior of the dimples remains highly pustulose (see Pl. 2, Fig. 8). Type V dimples may represent a lineal feature that preceded the somewhat irregular and nodular sulci observed in specimens of S. sulcatus. The faint groove bisecting the ventral denticles of S. wardlawi n. sp. and a pronounced rim separating the dorsal-most denticles of S. sulcatus (Pl. 2, Fig. 5) demonstrate potential transitional features between the two species. Samples collected just beneath the limestone bed that produced the only specimens of S. wardlawi n. sp. failed to provide any identifiable conodont elements, and the truncation of Cisuralian strata by the underlying disconformity renders the study of any potential lower range of the species impossible at this locality.

Sweetognathus duplex n. sp. may represent the next phyletic step in the “depressed” or sulcus-bearing lineage of Sweetognathus. The denticles along the dorsal half of the carina in specimens of S. duplex n. sp. resemble those of S. binodosus (see Pl. 1, Figs. 9, 12), but the latter species shows no sign of sulcus development. The oldest recovered specimen of S. duplex n. sp., which was acquired from the same bed as all specimens of S. wardlawi n. sp., retains marginal relict denticles along the sulcus. The sulcus feature of S. duplex n. sp., like the dimples of S. wardlawi n. sp., maintains pustules within the central depression that extend upward to the lateral margins of the carina. Sweetognathus duplex n. sp. does not bear resemblance to either S. obliquidentatus or S. clarki and was not recovered higher than the S. binodosus Zone within the section. Therefore, the species does not seem to have extended the sulcus-bearing lineage of Sweetognathus beyond the end of the Sakmarian Stage.

Déjà Vu: Sweetognathus and Neostreptognathodus

Instances of morphological innovation resulting in near homeomorphism between members of Sweetognathus (Type IV) and Neostreptognathodus have been previously reported from Cisuralian conodont faunas in China, Iran, Russia, and the western United States (Ritter, 1986; Wang et al., 1987; Mei et al., 2002; Davydov et al., 2005). The Type V sweetognathids described herein represent a similar expression of this sulcus-based platform morphology. In each instance, members of Sweetognathus developed depressions, or a partial to complete sulcus along the carina, a trait that was later reproduced with greater degrees of success and proliferated by various species of Neostreptognathodus (e.g., N. razhencevi Kozur in Kozur & Mostler, 1976 and N. pnevi) during the late Artinskian and Kungurian (late Cisuralian).

Similarly, repetitive manifestations of platform depressions in ozarkodinid P. elements through late Paleozoic time are well-known from troughed and untroughed members of the Idiognathodontidae. During the Middle and Late Pennsylvanian, troughed platforms evolved, disappeared, and subsequently reappeared several times throughout the complex and interwoven lineages of the genera Idiognathodus, Streptognathodus, and Swadelina (Lambert et al., 2003; Roscoe & Barrick, 2009, 2013; Hoganamp et al., this volume). The successive development of a dorsal trough in Swadelina and Streptognathodus has been attributed to neoteny.
(paedomorphosis) in species of *Idiognathodus*, which lack a
trough in adult forms (Sweet, 1988; Lambert *et al.*, 2003).
However, in Cisuralian Type IV and Type V representatives
of *Sweetognathus*, the unique forms appear to have evolved
particularly rapidly from a stock that bore no ancestral sulci.
Furthermore, juvenile specimens of most sweetognathids are
often difficult to distinguish at the species level, and
typically display a Type I or Type II configuration with no
early signs of carinal differentiation, and, therefore, sulcus
development through paedomorphism may be ruled out.
Perhaps the timing of this early Cisuralian experimentation,
which coincides with the departure of troughed and/or
nodular Carboniferous holdovers, such as *Adetognathus*
and *Streptognathodus*, left morphospace vacancies that were
quickly filled by *Sweetognathus*, the next available, innovative
shallow-water taxon.

$P_1$ elements bearing a striking resemblance to
*Neostreptognathodus* *pequopensis* Behnken, 1975 were
recovered from 5.7 m above the lowest occurrence of
*Sweetognathus*, and continue to occur intermittently over the
next 55.8 m. The occurrence of these forms, herein regarded
as *Neostreptognathodus* aff. *pequopensis*, within the Sakmarian
stratigraphic interval of the upper part of the Riepe Spring
Limestone at a level significantly below the first occurrence of
*S. 'whitei'* (Rhodes, 1963) is noteworthy and seemingly
anomalous. *Neostreptognathodus* *pequopensis* is regarded as the
progenitor of the genus and a cosmopolitan species denoting
the latest part of the Artinskian (early part of the North
American Leonardian) (Behnken, 1975). If *N*. aff. *pequopensis*
is indeed *N. pequopensis*, these specimens would represent the
earliest known occurrence of the species, predating the base of
the recognized *N. pequopensis* Zone (partial range lineage
biozone) by five to seven million years (Henderson, 2016).
Although *N*. aff. *pequopensis* was one of the most commonly
recovered forms within the lower portion of the section (along with
*S. expansus*, *S. 'merrilli',* and *S. binodosus*), there is no
observed co-occurrence with *S. 'whitei'* at any level within
the North Spruce Mountain Ridge section. Presently no data
support a more sustained temporal range and a definitive
claim of earliest occurrence. The high degree of diachronity
between these forms, potential for homeomorphy among
conodonts, and lack of continuous recovery has prompted the
tentative assignment herein of the older specimens to *N*. aff.
*pequopensis*. Interestingly, the original early Leonardian age
type specimens described by Behnken (1975) were collected
from the Peqoup Formation in the Peqoup Mountains, mere
miles to the northeast of the North Spruce Mountain Ridge
locality. The lower and upper parts of the Peqoup Formation
comprise the entire eastern half of North Spruce Mountain
Ridge at the given locality, but this interval is separated from the
Riepe Spring Limestone by a thick sequence of the
predominantly unfossiliferous Rib Hill Formation (Text-fig.
1). Of all other closely related conodont studies from the
Peqoup Range, Nevada (Wardlaw *et al.*, 1998; Henderson
*et al.*, 2012), Carlin Canyon, Nevada (Dehari, 2016,
unpublished thesis), Ferguson Mountain, Nevada (Clark,
1974; Behnken, 1975), and Moorman Ranch, Nevada (Clark,
1974; Behnken, 1975; Ritter, 1986), none have demonstrated
a Sakmarian age occurrence of any form so closely resembling
*N. pequopensis* (or *N*. aff. *pequopensis*). The specimens of
*Sweetognathus obliquidentatus* illustrated by Chernykh (2005,
2006) from the southern Ural Mountains bear a general
resemblance, but the denticles are more transversely elongated.
Further sampling of coeval regional strata is necessary before a
detailed discussion of potential phylogenetic implications for
*Sweetognathus* and *Neostreptognathodus* is issued.

**CONCLUSIONS**

The Cisuralian part of the Riepe Spring Limestone at North
Spruce Mountain Ridge, Elko County, Nevada, preserves a
sparse and distinctive Sakmarian to Artinskian conodont
fauna that is dominated by species of the ozarkodinid genus
*Sweetognathus*. The measured section, which was included in
the upper part of Section 1 from Hope (1972), records 180
m of nearshore and open shelf deposition along the northern
Ferguson trough in the post-Antler foreland. Two new, rare
Sakmarian age forms of the genus *Sweetognathus*, *S. duplex*
n. sp. and *S. wardlawi* n. sp., were recovered from the upper
part of the Riepe Spring Limestone in association with the *S.
binodosus* Zone (partial range lineage biozone; lower to middle
Sakmarian). Each of the new species demonstrates a partially
depressed and nodose carinal morphology, categorized herein
as the Type V sweetognathid configuration. The Type V carinal
configuration resembles an amalgamation of the *Type II* and
Type *IV* sweetognathid groups described by Ritter (1986).
In addition to the newly described species of *Sweetognathus*,
peculiar forms representing an apparent early occurrence of the
genus *Neostreptognathodus* were recovered from multiple
levels within a 55.8 m thick (9.7 m to 65.5 m) Sakmarian
age interval of the measured section. The anomalous forms,
herein regarded as *N*. aff. *pequopensis*, may call into question
some aspects of the accepted phylogeny of *Sweetognathus* and
*Neostreptognathodus*, but more regional sampling must be done
before these relationships are well understood. Beyond the last
occurrence of *N*. aff. *pequopensis* at 65.5 m, an estimated base
of the Artinskian stage has been identified in association with the
first occurrence of *S. 'whitei'* at 82.8 m above the base of the
section.

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Chuvashov, B. I., G. V. Dyuspina, G. A. Mizens, & V. V. Chernykh. 1990. Basic Sections of Carboniferous and Lower Permian of the western slope of the Urals, Ural Branch Academy Science of Russia, Sverdlovsk; 369 pp. (in Russian)


All illustrated specimens were collected from the upper part of the Riepe Spring Limestone, North Spruce Mountain Ridge, Elko County, Nevada, U.S.A. SUI 145772–145803. Scale bar at lower left corresponds with Figs. 8 and 9. Scale bar at lower right corresponds with Figs. 11 and 12.

### Plate I

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>1.</td>
<td>SUI 145772, 5.3 m above the base of the section (sample no. 3). Oral view of broken P₁ element.</td>
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<tr>
<td>2.</td>
<td>SUI 145773, 5.3 m above the base of the section (sample no. 3). Oral view of P₁ element.</td>
</tr>
<tr>
<td>3.</td>
<td>SUI 145774, 5.3 m above the base of the section (sample no. 3). Oral view of P₁ element.</td>
</tr>
<tr>
<td>4-6.</td>
<td><em>Sweetognathus 'merrilli'</em> Kozur, 1975.</td>
</tr>
<tr>
<td>4.</td>
<td>SUI 145775, 5.3 m above the base of the section (sample no. 3). Oral view of broken P₁ element.</td>
</tr>
<tr>
<td>5.</td>
<td>SUI 145776, 5.3 m above the base of the section (sample no. 3). Slightly oblique oral view of broken P₁ element.</td>
</tr>
<tr>
<td>6.</td>
<td>SUI 145777, 34 m above the base of the section (sample no. 16). Oral view of P₁ element.</td>
</tr>
<tr>
<td>7-13.</td>
<td><em>Sweetognathus duplex</em> n. sp.</td>
</tr>
<tr>
<td>7.</td>
<td>Paratype, SUI 145778, 26.8 m above the base of the section (sample no. 13). Oral view of broken P₁ element.</td>
</tr>
<tr>
<td>8.</td>
<td>Paratype, SUI 145778, 26.8 m above the base of the section (sample no. 13). Detail of ventral median sulcus.</td>
</tr>
<tr>
<td>9.</td>
<td>Paratype, SUI 145778, 26.8 m above the base of the section (sample no. 13). Detail of dorsal denticles.</td>
</tr>
<tr>
<td>10.</td>
<td>Holotype, SUI 145779, 26.8 m above the base of the section (sample no. 13). Oral view of P₁ element.</td>
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<td>11.</td>
<td>Holotype, SUI 145779, 26.8 m above the base of the section (sample no. 13). Detail of ventral median sulcus.</td>
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<td>Holotype, SUI 145779, 26.8 m above the base of the section (sample no. 13). Detail of dorsal denticles.</td>
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<td>Paratype, SUI 145780, 5.3 m above the base of the section (sample no. 3). Oral view of broken P₁ element.</td>
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<td><em>Sweetognathus binodosus</em> Chernykh, 2005. SUI 145781, 5.3 m above the base of the section (sample no. 3). Oral view of broken P₁ element.</td>
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Read and Nestell: Riepe Spring Limestone, NE Nevada
All illustrated specimens were collected from the upper part of the Riepe Spring Limestone, North Spruce Mountain Ridge, Elko County, Nevada, U.S.A.

Figure | Page
--- | ---
1–3. *Sweetognathus binodosus* Chernykh, 2005. 1. SUI 145782, 51.7 m above the base of the section (sample no. 25). Oral view of P\(_1\) element. 2. SUI 145783, 51.7 m above the base of the section (sample no. 25). Oral view of broken P\(_1\) element. 3. SUI 145784, 5.3 m above the base of the section (sample no. 3). Oral view of broken P\(_1\) element.

4, 6–8. *Sweetognathus wardlawi* n. sp. 4. Paratype, SUI 145785, 5.3 m above the base of the section (sample no. 3). Slightly oblique oral view of P\(_1\) element. 6. Paratype, SUI 145787, 5.3 m above the base of the section (sample no. 3). Oral view of broken P\(_1\) element. 7. Holotype, SUI 145788, 5.3 m above the base of the section (sample no. 3). Oral view of P\(_1\) element. 8. Holotype, SUI 145788, 5.3 m above the base of the section (sample no. 3). Detail of a carinal denticle illustrating the pustules along the interior of a “dimple” amidst heavy recrystallization.

5. *Sweetognathus sulcatus* Ritter, 1986. SUI 145786, 26.8 m above the base of the section (sample no. 13). Oral view of broken P\(_1\) element. 9–11. *Neostreptognathodus* aff. *pequopensis* Behnken, 1975. 9. SUI 145789, 65.5 m above the base of the section (sample no. 29). Oral view of P\(_1\) element. Immature specimen. 10. SUI 145790, 9.7 m above the base of the section (sample no. 5). Oral view of P\(_1\) element. 11. SUI 145791, 30.8 m above the base of the section (sample no. 15). Detail of carinal denticles of broken P\(_1\) element.
All illustrated specimens were collected from the upper part of the Riepe Spring Limestone, North Spruce Mountain Ridge, Elko County, Nevada, U.S.A.

1. SUI 145792, 30.8 m above the base of the section (sample no. 15). Oral view of $P_1$ element. 
2. SUI 145793, 34 m above the base of the section (sample no. 16). Oblique oral view of $P_1$ element. 
3. SUI 145794, 30.8 m above the base of the section (sample no. 15). Oral view of $P_1$ element.

4. SUI 145795, 51.7 m above the base of the section (sample no. 25). Oral view of broken $P_1$ element.
5. SUI 145796, 59.3 m above the base of the section (sample no. 26). Oral view of broken $P_1$ element. Immature specimen.

6. *Pseudohindeodus stevensi* (Clark & Carr, 1982). SUI 145797, 177.3 m above the base of the section (sample no. 40). Oral view of $P_1$ element. ................................................................. 93

7. SUI 145798, 82.8 m above the base of the section (sample no. 31). Oral view of broken $P_1$ element.
8. SUI 145798, 82.8 m above the base of the section (sample no. 31). Detail of dorsal denticles.

9. SUI 145799, 114.5 m above the base of the section (sample no. 34). Oblique view of broken $P_1$ element.
10. SUI 145800, 132.4 m above the base of the section (sample no. 35). Oral view of broken $P_1$ element.
11. SUI 145801, 173.9 m above the base of the section (sample no. 39). Oral view of $P_1$ element.
12. SUI 145802, 177.3 m above the base of the section (sample no. 40). Oral view of broken $P_1$ element. Transitional specimen to *S. behnkeni*.

13. *Sweetognathus behnkeni* Kozur, 1975; 13. SUI 145803, 177.3 m above the base of the section (sample no. 40). Oral view of broken $P_1$ element. ................................................................. 94
THE MULTIELEMENT APPARATUSES OF GUADALUPIAN TO LOPINGIAN (MIDDLE-UPPER PERMIAN) SWEETOGNATHIDS FROM NORTH AMERICA, AND THEIR SIGNIFICANCE FOR THE PHYLOGENY OF LATE PALEOZOIC CONODONTS

MARTYN L. GOLDSING
Geological Survey of Canada, 1500-605 Robson Street, Vancouver, BC, Canada, V6B 5J3

ABSTRACT
Monospecific collections of the conodonts Iranognathus Kozur et al., 1975 and Pustulognathus n. gen. have been recovered from the Permian of the Cache Creek terrane in central and northern British Columbia, Canada. These collections have allowed the reconstruction of the multielement apparatuses of three species belonging to these genera, I. moschovitschi Kozur & Pjatakova, 1975, P. monticola n. sp. and P. vigilans n. sp. Both genera share a similar apparatus composed of carminiscaphate P_1 elements, angulate P_1 elements, digyrate M elements, an alate S_0 element, and bipennate S_1 and S_3 elements. The presence of S_1 and S_3 elements in the apparatus is inferred by comparison with reconstructions of other Permian conodonts, such as Sweetognathus and Hindeodus. These new reconstructions allow a tentative phylogeny to be proposed for the families Sweetognathidae and Anchignathodontidae based on apparatus architecture.

INTRODUCTION
The phylogenetic relationships between genera of the Sweetognathidae during the Guadalupian and Lopingian are complex, with particular uncertainty surrounding the generic assignment of species with pustulose carinas and unornamented basal cups. Such species include Ozarkodina expansa Perlmutter, 1975, Diplagnostodus moschovitschi Kozur & Pjatakova, 1975, Diplagnostodus lanceolatus Igo, 1981, Diplagnostodus par lanceolatus Wang & Dong, 1991, Wardlawella jinensis Wang et al., 2004, and Wardlawella n. sp. A Orchard et al., 2001. Various authors have subsequently assigned these species to Diplagnostodus Kozur & Merrill, 1975, Sweetognathus Clark, 1972, Iranognathus Kozur et al., 1975, or Wardlawella Kozur, 1995 (e.g., Wang et al., 1987; Kozur, 1995; Mei et al., 2002). Each of these assignments is problematic. Diplagnostodus does not have pustules on its carina (Wang et al., 1987) and therefore should be excluded from the Sweetognathidae. Iranognathus was originally defined for specimens bearing ornamentation on their basal cups (Kozur, 1975), and it is not clear whether forms with unornamented cups should be assigned to this genus. The validity of Wardlawella as a genus has been questioned, with most authors choosing to refer its constituent species to Sweetognathus (e.g., Mei et al., 2002; Wardlaw et al., 2015a). Most species of Sweetognathus possess a wide, nodular carina (Mei et al., 2002), whereas the majority of species named above possess a narrow, fused ridge.

These taxonomic issues are largely due to differing interpretations of the significance of ornamentation on the upper surface of the basal cup of the P_1 element. Therefore, it has not been possible to resolve these issues by examination of the P_1 elements alone; instead, the present paper considers the composition of the multielement apparatus, and the morphology of the elements that comprise it. This has allowed the defining characteristics of genera to be determined, and has provided the basis for recognition of a new genus, herein named Pustulognathus. This in turn has allowed the suprageneric relationships within the Sweetognathidae to be elucidated and a new phylogeny for the family to be proposed.

MATERIAL AND METHODS
The recovery of monospecific collections of Iranognathus and Pustulognathus from samples collected during regional mapping expeditions in British Columbia, Canada, has allowed the reconstruction of the multielement apparatuses for these genera (Table 1). One such sample (GSC curation number V-003598), collected from the Horsefeed Formation in the Atlin region of northwestern British Columbia (UTM Zone 8 593605 6585239; Text-fig. 1), contains elements herein assigned to I. moschovitschi. A second sample (GSC curation number C-303806), collected from the Copley Limestone succession in the Nechako region of central British Columbia (UTM Zone 10 367755 6087832; Text-fig. 1), contains numerous elements of P. monticola n. sp., the P_1 elements of which were previously figured by Orchard et al. (2001) as Wardlawella n. sp. A. Additional samples containing P_1 and ramiform elements of I. moschovitschi, P. monticola, and P. vigilans n. sp. were collected from the Atlin, Nechako, and Ashcroft regions of British Columbia (Text-fig. 1). All of these samples come from thick limestone accumulations, referred to as the Copley Limestone (Nechako region), the Horsefeed Formation (Atlin region), and the Marble Canyon Formation (Ashcroft region). These limestones are located within the Cache Creek terrane, an oceanic terrane consisting...
Table 1. Number of elements of *Iranognathus* and *Pustulognathus* identified in samples from the Atlin (northern), Nechako (central), and Ashcroft (southern) regions of the Cache Creek terrane, British Columbia.

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mostly of imbricated carbonate, chert, basalt, gabbro, and ultramafic rocks, interpreted to have formed as a forearc accretionary complex during the accretion of the Stikine and Quesnel island arc terranes (Mihalynuk, 1999).

All samples were processed at the conodont processing facility of the Geological Survey of Canada in Vancouver, using standard techniques as outlined in Stone (1987) and Jeppsson et al. (1999). A total of 418 elements of *Iranognathus*, and 57 elements of *Pustulognathus*, were recovered from 27 samples (Table 1). Illustrated specimens are housed at the National Type Collection of Invertebrate and Plant Fossils at the Geological Survey of Canada in Ottawa.

**SYSTEMATIC PALEONTOLOGY**

The collections from British Columbia enable the recognition of six different element types in the apparatuses of both *Iranognathus* and *Pustulognathus* (Text-figs. 2 and 3). Based on comparison with the reconstructions of *Sweetognathus* and *Pseudohindeodus* Gullo & Kozur, 1992 by Wardlaw et al. (2015a), it is considered likely that the apparatuses of *Iranognathus* and *Pustulognathus* were octomembrate, with unidentified $S_2$ and $S_3$ elements resembling the $S_1$ and $S_4$ elements, respectively. Differentiation of $S_1$ elements from $S_2$, and $S_3$ from $S_4$, has also been shown to be difficult in other related genera such as *Hindeodus*, where an octomembrate apparatus is indicated by natural assemblages (Agematsu...
et al., 2014, 2017), despite the similarity of the ramiform elements. The assignment of elements to anatomical position in *Iranognathus* and *Pustulognathus* follows the reconstruction of *Sweetognathus* by Ritter & Baesemann (1991), which was based on natural assemblages. Element notation follows Purnell et al. (2000).

Class **CONODONTA** Pander, 1856
Order **OZARKODINIDA** Dzik, 1976
Family **SWEETOGNATHIDAE** Ritter, 1986
Genus **IRANOGNATHUS** Kozur, Mostler & Rahimi-Yazd, 1975

**Text-fig. 2**

*Multielement apparatus of Iranognathus Kozur, Mostler & Rahimi-Yazd, 1975. 1–11, Iranognathus movschovitschi (Kozur & Pjatakova, 1975 in Kozur, 1975). 1, M element, GSC type no. 131607; 2, P<sub>4</sub> element, GSC type no. 131608; 3–5, P<sub>3</sub> element, GSC type no. 131609; 6, S<sub>1</sub> element, GSC type no. 131610; 7, S<sub>2</sub> element, GSC type no. 131611; 8, S<sub>3</sub> element, GSC type no. 131612; all from sample V-003598, Horsefeed Formation, Atlin region of British Columbia. 9–11, P<sub>1</sub> element with close-up of pustules on carina, GSC type no. 119917, from sample C-303781, Copley limestone succession, Nechako region of British Columbia.*

**Type species.**—*Iranognathus unicostatus* Kozur, Mostler & Rahimi-Yazd, 1975.

**Diagnosis.**—Genus with a carminiscaphate P<sub>4</sub> element bearing a series of small pustules arranged in a row on the tops of the fused denticles of the carina; the blade is long, consisting of at least five denticles; the basal cup may or may not bear ornamentation on its upper surface. The M element is digyrate and possesses a short, denticulate anterior process, a longer, curved posterior process, and lacks an anticusp.

**Description.**—Six different elements have been recognized and assigned to this genus. The P<sub>4</sub> element is carminiscaphate, with a narrow, fused carina. The tips of the denticles remain free along most of the length of carina, and their upper surface bears a single row of small pustules. The carina passes uninterrupted into the anterior free blade, which is long and of relatively uniform height. The posterior of the carina is lower and continues to the end of the element. The basal cup is wide and sub-circular in outline, and its upper surface may bear ridges or nodes, or it may be unornamented. The P<sub>3</sub> element is angulate, with a long anterior process bearing numerous high denticles, and a shorter posterior process bearing fewer, lower denticles. The M element is breviform digyrate, with a short denticulate inner lateral process, and a long, curved, outer lateral process. An anticusp is not present. The S<sub>1</sub> element is alate, with two denticulate anterolateral processes that diverge at the cusp. The S<sub>2</sub> element is bipennate, with a long, straight posterior process bearing posteriorly inclined denticles, and a shorter anterior process that bends slightly downwards. The S<sub>3</sub> element is also bipennate, with a large cusp and a long denticulate posterior process. The shorter anterior process in curved downwards and inwards. Elements referable to the S<sub>1</sub>, S<sub>2</sub>, and S<sub>3</sub> positions have not been recognized; however, they are inferred to be present, and to be similar in number and morphology to the S<sub>1</sub>, S<sub>2</sub>, and S<sub>3</sub> elements, respectively.

**Occurrence.**—Lopingian of Iran (Kozur et al., 1975), South China and Pakistan (Wang et al., 1987; Mei et al., 2002), Azerbaijan (Kozur, 1975), and the Cache Creek terrane, British Columbia (Beyers & Orchard, 1991; Orchard et al., 2001).

**Remarks.**—The genus *Iranognathus* was originally defined for specimens bearing ridges or nodes on the upper surface of the basal cup (Kozur et al., 1975). The emended diagnosis of Mei et al. (1998) is followed here, and specimens with smooth basal cups are retained in *Iranognathus*. In North America, only the smooth forms are recognized, whereas in the Tethyan region both ornamented and un-ornamented specimens are
abundant. It is possible that the smooth forms represent a separate genus, and that true, ornamented *Iranognathus* is restricted to the Tethys.

**Iranognathus movschovitschi** (Kozur & Pjatakova, 1975 in Kozur, 1975)

Diagnosis.—Species of *Iranognathus* with a P1 element bearing no ornamentation on the upper surface of the basal cup.

Material.—413 elements.

Occurrence.—Wuchiapingian of the Copley Limestone, Horsefeed and Marble Canyon formations, Cache Creek terrane, British Columbia (Beyers & Orchard, 1991; Orchard et al., 2001; Golding et al., 2016); Lopingian of the Shangsi and Heshan formations, South China (Wang et al., 1987; Mei et al., 2002); Wuchiapingian of Azerbaijan (Kozur, 1975).

Remarks.—*Iranognathus movschovitschi* can be differentiated from all other species of *Iranognathus* by the lack of ornamentation on the upper surface of the cup. This feature is shared by *I. movschovitschi* and *I. nudus* Wang et al., 1987, which herein is considered a junior synonym of *I. movschovitschi*. In lateral view, the carina is similar in shape to that of *Pustulognathus vigilans* n. sp., which can be differentiated from *I. movschovitschi* by the denser accumulation of pustules on its carina.

Genus *PUSTULOGNATHUS* n. gen. Golding & Orchard

Text-fig. 3

Type species.—*Pustulognathus monticola* n. sp.

Other species.—*Pustulognathus vigilans* n. sp.; *Iranognathus* n. sp. A Mei et al. 2002.

Etymology.—In reference to the distinctive pustulose nature of the upper surface of the carina.

Diagnosis.—Genus with a carminiscaphate P1 element which bears numerous small pustules on the upper surface of its fused carina; the blade is short, commonly consisting of two to three denticles; and the top of the basal cup lacks ornamentation. The M element is digyrate and possesses a short, denticulate anterior process; a longer, straight posterior process; and lacks an anticusp.

Description.—Six different elements have been recognised and assigned to this genus. The P1 element is carminiscaphate, with a carina that is fused into a low ridge. The upper surface of the carina is covered in numerous small pustules, with no clear pattern to their arrangement. The carina is separated from the anterior free blade by a distinct notch. The blade itself is short, commonly consisting of only two or three denticles, which increase in height to the anterior of the blade. The end of the carina may terminate abruptly before the posterior of the cup, or continue to the end of element as a series of low denticles. The cup is wide and sub-circular in basal outline, and its upper surface lacks ornamentation. The P1 element is angulate, bearing numerous denticles on a long anterior process and a shorter posterior process. The denticles are similar in height on both processes. The M element is breviform digyrate, with two straight, downward curved denticulate processes. The inner lateral process is bipennate, with a long, straight posterior process that is curved slightly downwards (but not laterally), and bears small denticles which are inclined to the posterior. The S3 element is also bipennate, with a long, straight posterior process and a long anterior process that is curved slightly downwards (but not laterally), and bears small denticles which are inclined to the posterior. The S4 element is bipennate, with a long, straight posterior process and a shorter anterior process that is curved slightly downwards and inwards. Both processes bear numerous upright denticles. Elements referable to the S4 and S4 positions have not been recognized; however, they are inferred to be present, and to be similar in number and morphology to the S4 and S4 elements, respectively.

Occurrence.—Guadalupian to Lopingian of the Cache Creek terrane in British Columbia, Canada (Orchard et al., 2001; this study); potentially the Guadalupian of South China (Mei et al., 2002).
Remarks.—In the present material, the densely pustulose, fused carina of this genus is often partly obscured by recrystallization; nevertheless, this feature serves to separate *Pustulognathus* from *Diplognathodus*, which lacks pustules on its carina. *Iranognathus* differs from *Pustulognathus* in possessing a single, narrow row of small pustules on top of its denticles. The carina of *Sweetognathus* is pustulose like that of *Pustulognathus*; however, it is commonly expanded into broad, differentiated nodes. Additionally, the M element of *Sweetognathus* lacks an anterior process, and possesses an anticusp, in contrast with that of *Pustulognathus*. The specimens illustrated by Mei et al. (2002) from South China as *Iranognathus* n. sp. A are tentatively included in *Pustulognathus*; they differ from the B.C. examples in their longer blades. *Pustulognathus* was first recognized during examination of the type material with Dr. M. J. Orchard, who therefore shares authorship of the genus and type species.

**Pustulognathus monticola** n. sp. Golding & Orchard

Text-fig. 3.13–3.21

*Wardlawella* n. sp. A, Orchard et al., 2001: pl. 1, figs. 14, 15.

Holotype.—GSC Type No. 119916 (Text-fig. 3.13–3.16), from the Wordian (Guadalupian) of the Copley Limestone, GSC Cur. No. C-303806, Mt. Copley, British Columbia.

Material.—51 elements.

Etymology.—From the Latin for mountaineer, in reference to the type locality near Mt. Copley.

Diagnosis.—Species of *Pustulognathus* with a P₁ element bearing a fused carina that terminates abruptly before the posterior end of the basal cup.
**Description.**—The carminiscaphate P<sub>1</sub> element is short, with a low, fused carina in the posterior half of the element separated from the anterior blade by a small notch. The fused carina bears small pustules on its upper surface, and terminates abruptly prior to the posterior end of the element. The blade consists of two to three denticles which are largely unfused. The basal cup is large and sub-circular in outline, and bears no ornamentation. Ramiform elements are as described for the genus.

**Occurrence.**—Wordian to Wuchiapingian of the Copley Limestone, Cache Creek terrane, British Columbia.

**Remarks.**—*Pustulognathus monticola* is differentiated from *P. vigilans* by the more abrupt termination of the posterior carina. This feature is shared with *Sweetognathus expansus* (Behnken), which differs from *P. monticola* by possessing a more nodular carina, and in its multielement apparatus (see below).

**Pustulognathus vigilans** n. sp. Golding

Text-fig. 3.1–3.12

**Holotype.**—GSC type no. 131613 (Text-fig. 3.1–3.4), from the Wordian (Guadalupian) of the Horsefeed Formation, GSC Cur. No. V-003665, Sentinel Mountain, British Columbia.

**Material.**—6 elements.

**Etymology.**—From the Latin for watchful, in reference to the location of the type locality on top of Sentinel Mountain.

**Diagnosis.**—Species of *Pustulognathus* with a P<sub>1</sub> element bearing a carina that is fused in the middle, and passes into low denticles, which continue to the posterior end of the basal cup.

**Description.**—The carminiscaphate P<sub>1</sub> element is relatively long and bears a carina which is fused most strongly in the middle of the element, and is separated from the anterior blade by a small notch. The blade consists of two to four unfused denticles which increase in size towards the anterior. The fused portion of the carina bears small pustules on its upper surface. Towards the posterior, the last two or three denticles of the carina become more weakly fused, and decrease in size until the posterior end of the element. The basal cup is unornamented, and is relatively wide and long, forming an elongate, sub-elliptical basal cavity. Ramiform elements are as described for the genus.

**DISCUSSION**

**Comparisons with Other Genera**

The multielement apparatuses of *Iranognathus* and *Pustulognathus* allow them to be distinguished from other genera with similar P<sub>1</sub> elements (Table 2). Contemporary Permain genera that have had their multielement apparatuses reconstructed include *Sweetognathus, Neostreptognathodus* Clark, 1972, *Meiognathus, Pseudohindeodus*, and *Hindeodus* *Sweetognathus*: Five species of *Sweetognathus* have had their multielement apparatuses reconstructed: *S. expansus* (Perlmutter, 1975), *S. windi* Ritter, 1986, *S. cf. inornatus* Ritter, 1986, *S. guizhouensis* Bando et al., 1982, and *S. whitei* (Rhodes, 1963) (Perlmutter, 1975; Ritter, 1986; Ritter & Baesemann, 1991; Shen et al., 2013; Wardlaw et al., 2015a). Based on these reconstructions, the apparatus of *Sweetognathus* is very similar to those of *Iranognathus* and *Pustulognathus* (Table 2). In particular, the P<sub>1</sub>, S<sub>0</sub>, S<sub>1</sub>, and S<sub>2</sub> elements of these genera are morphologically very close. However, the M elements of *Iranognathus* and *Pustulognathus* lack the distinct anticusp of *Sweetognathus* (e.g., Shen et al., 2013, pl. 4, fig. 5; Wardlaw et al., 2015a, pl. 1, figs. 9, 10), and have a denser denticulation on their short inner lateral process.

**Neostreptognathodus**: An incomplete reconstruction of the apparatus of *N. stahlbordersis* Szaniawski, 1979 has been presented by Szaniawski & Malkowski (1979), and general reconstructions for the genus were proposed by Sweet (1988) and Wardlaw (1995). Although the P<sub>1</sub> element of *Neostreptognathodus* differs markedly from those of *Iranognathus* and *Pustulognathus*, it is included here as it appears to share the distinctive S<sub>1</sub> element of these genera (A<sub>1</sub> element of Szaniawski & Malkowski, 1979, fig. 7; S<sub>2</sub> element of Wardlaw, 1995, fig. 3B).

**Meiognathus**: An incomplete reconstruction of *M. pustulus* Shen et al., 2013 was illustrated by Shen et al. (2013). This reconstruction is lacking an S<sub>0</sub> element. Otherwise, the apparatus is very similar to that of *Sweetognathus*, although the posterior process of the P<sub>1</sub> element is much shorter and more similar to the P<sub>1</sub> element of *Pustulognathus* (Shen et al., 2013, pl. 2, fig. 12). The apparatus differs from those of *Iranognathus* and *Pustulognathus* primarily in the morphology of the M element, which possesses an anticusp (Shen et al., 2013, pl. 2, figs. 18, 19).
Table 2. Comparison between the multielement apparatus of representative species of Pustulognathus, Iranognathus, Sweetognathus, Neostreptognathodus, Meiognathus, Pseudohindeodus, and Hindeodus. Elements have been assigned anatomical positions on the basis of comparison with reconstructions from natural assemblages of Sweetognathus (Ritter & Basemann, 1991) and Hindeodus (Agematsu et al., 2014). Element notation has been standardized following Purnell et al. (2000).

<table>
<thead>
<tr>
<th>Genus</th>
<th>Pustulognathus</th>
<th>Iranognathus</th>
<th>Sweetognathus</th>
<th>Neostreptognathodus</th>
<th>Meiognathus</th>
<th>Pseudohindeodus</th>
<th>Hindeodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author</td>
<td>This Study</td>
<td>This Study</td>
<td>Wardlaw et al. (2015a)</td>
<td>Wardlaw (1995)</td>
<td>Shao et al. (2013)</td>
<td>Wardlaw et al. (2015a)</td>
<td>Hindeodus latidensia</td>
</tr>
<tr>
<td>Species</td>
<td>Pustulognathus monticola</td>
<td>Iranognathus movschovitschi</td>
<td>Sweetognathus whitei</td>
<td>Neostreptognathodus sp.</td>
<td>Meiognathus pustulus</td>
<td>Pseudohindeodus aegeri</td>
<td>Hindeodus latidensia</td>
</tr>
<tr>
<td>Age</td>
<td>Guadalupian</td>
<td>Lopingian</td>
<td>Cisuralian</td>
<td>Guadalupian</td>
<td>Cisuralian</td>
<td>Lopingian</td>
<td>Lopingian</td>
</tr>
<tr>
<td>M</td>
<td>Digrate: breviform, asymmetrical, straight processes, lacking anterolateral divergent processes</td>
<td>Dolobrate: anticusp present, which may bear denticles</td>
<td>Dolobrate: anticusp present, short posterior process</td>
<td>Dolobrate: anticusp present, long posterior process</td>
<td>Dolobrate: anticusp present, long posterior process</td>
<td>Dolobrate: anticusp present, long posterior process</td>
<td>Dolobrate: anticusp present, long posterior process</td>
</tr>
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<td>S2</td>
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<td>Not recognized</td>
<td>Not recognized</td>
<td>Not recognized</td>
<td>Not recognized</td>
<td>Not recognized</td>
</tr>
</tbody>
</table>

Notes: Angulate: long anterior process, short posterior process; Digrate: breviform, asymmetrical, straight processes, lacking anterolateral divergent processes; Dolobrate: anticusp present, which may bear denticles; Bipennate: anterior processes long, curves slightly downwards, bears inclined or upright denticles; Not recognized: element not recognized or illustrated.
Pseudohindeodus: The only species of Pseudohindeodus to have their multielement apparatuses reconstructed are *P. stevensi* (Clark & Carr, 1982) and *P. ramovsi* Gullo & Kozur, 1992 (Clark & Carr, 1982; Wardlaw, 2000; Wardlaw et al., 2015a). *Pseudohindeodus stevensi* was assigned to Diplognathodus by Clark & Carr (1982) and Wardlaw et al. (2015a); however, its P element differs from that of *Diplognathodus* by the presence of a pustulose carina and a distinctive flange encircling the basal cup. The S₀ and S₁ elements of *Pseudohindeodus* are similar to those of *Iranognathus* and *Pustulognathus* but the P₂ element of *Pseudohindeodus* has a much shorter posterior process (Wardlaw, 2000, pl. 3-1, fig. 16; Wardlaw et al. 2015a, pl. 2, fig. 5), and its M element also possesses an anticusp that is absent in *Iranognathus* and *Pustulognathus* (Wardlaw, 2000, pl. 3-1, fig. 17; Wardlaw et al. 2015a, pl. 2, fig. 6).

*Hindeodus*: The Lopingian species *H. typicalis* (Sweet, 1970), *H. julvensis* (Sweet, 1973), and *H. latidentatus* Kozur et al., 1975 all have had their apparatuses reconstructed (Sweet, 1970; Nestell & Wardlaw, 1987; Metcalfe, 2012; Wardlaw et al., 2015b). The S₀ element of *Hindeodus* is very distinctive in lacking a posterior process, and possessing two broad, anterolateral processes that form a large angle between them (e.g., Nestell & Wardlaw, 1987, pl. 4, figs. 14, 15). The P₂ element also differs from those of *Iranognathus* and *Pustulognathus* in possessing a much longer posterior process with posteriorly inclined denticles (e.g., Wardlaw et al., 2015b, pl. 6, fig. 8), and the M element once again bears an anticusp (Wardlaw et al. 2015b, pl. 7, figs. 9, 10).

Kozur (1995) erected the genus *Wardlawella* to encompass carminiscaphate P₁ elements with pustulose carinas and smooth basal cups from the Permian. The type species of *Wardlawella* was designated by Kozur (1995) as *W. expansa* (Perlmutter, 1975); however, the M element of this species illustrated by Perlmutter (1975) appears to be similar to that of *Sweetognathus*. It is therefore likely that the type species of *Wardlawella* should be referred to *Sweetognathus*, as suggested by previous authors (e.g., von Bitter & Merrill, 1990; Ritter, 1995; Mei et al., 2002; Chernykh, 2005, 2006, 2012; Boardman et al., 2009; Shen et al., 2013; Wardlaw et al., 2015a), and that *Wardlawella* is a nomen nudum.

The P₁ elements of *Diplognathodus*, *Homeoiranognathus* Ritter, 1987, *Rabeignathus* Kozur, 1978, *Xiazhognathus* Ding & Wan, 1990, *Parasweetognathus* Reimers, 1992 and *Protosweetognathus* Reimers, 1992 are morphologically similar to those of the other genera discussed here; however, none of these genera have had their multielement apparatuses reconstructed. Previous reconstructions of *Diplognathodus* (Clark & Carr, 1982; von Bitter & Merrill, 1985; Sweet, 1988; Wardlaw et al., 2015a) have been based on elements of *D. expansa*, herein assigned to *Sweetognathus*, and *D. stevensi*, herein assigned to *Pseudohindeodus*. The apparatus of true *Diplognathodus* therefore remains unknown. Mei et al. (2002) considered the majority of these genera (except for *Diplognathodus*) to be synonyms of *Sweetognathus*; however, without multielement apparatus reconstructions for these genera, it is not possible to determine whether they are valid or not, and if they are, what their relationships with the other genera discussed in this paper would be.
Phylogeny of the Sweetognathidae and Anchignathodontidae

Based on the multielement apparatus reconstructions discussed above, it is possible to draw tentative conclusions on the phylogenetic relationships between these taxa (Text-fig. 4). Following Sweet (1988), Iranognathus, Sweetognathus, Pseudohindeodus, and Neostreptognathodus are assigned to the family Sweetognathidae, together with Pustulognathus, whereas Hindeodus is assigned to the Anchignathodontidae. These two families are united herein by their shared possession of carminiscaphe P\textsubscript{1} elements and angulate P\textsubscript{2} elements. They are distinguished from each other by the morphology of the S\textsubscript{0} element and the presence or absence of pustulose ornament on the carina of the P\textsubscript{1} element. The S\textsubscript{0} element of Meioognathus has not been described; however, the presence of pustules on the carina of the P\textsubscript{1} element suggests a relationship with the Sweetognathidae. Within the Sweetognathidae, it is proposed that Pustulognathus and Iranognathus form a distinct group due to the similar morphology of their M element. The apparatus of Sweetognathus contains a P\textsubscript{1} element that is very similar to those of Pustulognathus and Iranognathus, and so it is suggested as the sister genus to this group. Neostreptognathodus is considered to be more closely related to this group than Pseudohindeodus or Meioognathus due to the long posterior process of the M element. The relative positions of Meioognathus and Pseudohindeodus within the family remain uncertain.

This phylogeny is consistent with the model of evolution elucidated by Mei et al. (2002), with initial divergence of the Sweetognathidae from the Anchignathodontidae occurring at the appearance of Sweetognathus in the Asselian. Subsequent to this, Neostreptognathodus and Pustulognathus diverged from Sweetognathus in the Artinskian and Wordian respectively, and Iranognathus evolved from Pustulognathus in the Wuchiapingian.

Sweet (1988) also included the genera Diplognathodus, Homeoiranognathus, Rabeignathus, and Isaricella within the Sweetognathidae, but as mentioned previously, it is not possible to determine their relationship with other genera in this family whilst their apparatuses remain unknown. Recent cladistic analyses based solely on P\textsubscript{1} elements (Jiang et al., 2011) suggest that Isaricella is more closely related to Hindeodus, and may be more appropriately placed in the Anchignathodontidae. Further work on these genera is required to define their multielement apparatuses and to clarify their phylogenetic position.

ACKNOWLEDGMENTS

Thanks are due to A. Zagorevski and M. J. Orchard for collecting samples from the Atlin and Nechako regions respectively; these samples were processed by H. Taylor and P. Krauss. M. J. Orchard also provided comments on an earlier draft of this paper. Two anonymous reviewers, and the editors C. M. Henderson and D. J. Over, provided further helpful comments. Funding for this study was provided by the GEM 2 Cordillera Project of the Geological Survey of Canada.

LITERATURE CITED


CONTRASTING APPARATUS RECONSTRUCTIONS OF THE MIDDLE PERMIAN CONODONT
PSEUDOHINDEODUS RAMOVSII

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ABSTRACT
The conodont species Pseudohindeodus ramovsi Gullo and Kozur was first described in 1992 from Wordian strata in western Sicily. In West Texas, the genus has been reported but is rare. It appears to range from the late Roadian to late Capitanian (Guadalupian, Permian) of the Delaware Basin area, and is reported from the Artinskian to Capitanian in other areas such as Nevada, Iran, Tajikistan, and south China. Other than a few specimens from Guadalupian strata of west Texas, the apparatus elements of any species of Pseudohindeodus, other than the P1 element, have rarely been illustrated. Contrasting models of the elemental structure of Pseudohindeodus ramovsi are proposed based on new materials containing a varied assemblage of elements recovered from an outcrop of the Hegler Limestone (Guadalupian) in the Patterson Hills, Guadalupe Mountains area, West Texas. The first model is a 15 member apparatus with ozarkodinid-style architecture with two M elements, nine S elements (an unpaired S outcrop of the Hegler Limestone (Guadalupian) in the Patterson Hills, Guadalupe Mountains area, West Texas. The first model is a 15 member apparatus with ozarkodinid-style architecture with two M elements, nine S elements (an unpaired S, and symmetrically paired S1, S2, S3, and S4), and paired P1 elements and paired P2 elements. The paired P1 elements are clearly bipennate and not of “Ozarkodina” type. This model is similar to the reconstruction proposed by Agematsu et al. (2014) for the species Hindeodus parvus and Hindeodus typicalis from the late Permian and early Triassic in the Mino Terrane in central Japan. The element in the P1 position of their model is what appears to be a somewhat modified S element that could also be considered to be of “ozarkodinid” type. A second model has slightly modified ozarkodinid-style architecture composed of a 13 member apparatus, but lacking the two distinctive paired ozarkodinid P2 elements. The general arrangement of this Pseudohindeodus ramovsi apparatus is similar in structure to the 13 element apparatus recently proposed by Zhang et al. (2017) for the species Hindeodus parvus from the Early Triassic of the Shangsi section in Sichuan, China. A third possible model with a rearrangement of the S elements is also noted.

INTRODUCTION
Gullo & Kozur (1992) described Pseudohindeodus ramovsi from Wordian strata in Sicily. A few species of the genus have since been described from the upper part of the Lower Permian (Kungurian) and Middle Permian strata from several parts of the world, for example, P. augustus from Japan (Shen et al., 2012). In West Texas, forms referable to this particular species were possibly first reported in an unpublished thesis by Sturm (1975), who illustrated three specimens of Anchignathodus typicalis Sweet from the Hegler and Pinery Limestone members of the Bell Canyon Formation (Middle Permian) of the Guadalupe Mountains area. From the pictures it is difficult to tell if these specimens are Hindeodus or Pseudohindeodus. From the same general area, Croft (1978)—in an unpublished thesis—illustrated several possible apparatus ramiform elements (pl. 6, figs. 1, 13, and 16). The illustrated specimens from Croft were stated to have come from the Lamar Limestone (late Capitanian) in the Guadalupe Mountains. Also from the Guadalupe Mountains area, Lambert et al. (2010) illustrated two specimens of P. ramovsi and noted their occurrence in the uppermost Lamar Limestone Member and lower part of the Reef Trail Member. Pseudohindeodus ramovsi was also reported from the late Wordian to late Capitanian (Guadalupian, Middle Permian) of the Delaware Basin area by Wardlaw (2000), who illustrated P1 elements with several possible apparatus elements. Recently, thesis work by students of Lambert in an area of the Patterson Hills a short distance to the north of our PI section (Wardlaw and Nestell, 2015) has resulted in reports of the several occurrences of P. ramovsi in strata ranging from the South Wells Member (Wordian) of the upper part of the Cherry Canyon Formation to the Rader Member (Capitanian) of the middle part of the Bell Canyon Formation (Christie et al., 2012; Lambert et al., 2014). This species has also been reported from the late Kungurian to Capitanian in other areas such as the Tabas area in central Iran and the Kubergandy section of the southeastern Pamirs,
Tajikistan (Vuolo, 2014), and south China (Sun et al., 2008; Sun et al., 2010; Sun et al., 2017).

The conodont material that is the subject of this study was obtained during the course of bed by bed sampling of a complete sequence of basinal Hegler and Pinery strata in the Patterson Hills area just to the west of the Guadalupe Mountains. The Hegler Limestone Member of the Bell Canyon Formation in the PI section in the southern Patterson Hills is exposed along US Highway Route 62/180, with the base of the section at 31.78640° - 104.87542° about 3 km south of the southernmost boundary of Guadalupe Mountains National Park (Text-fig. 1). At this locality, the Hegler Limestone Member is 4.48 m thick with a 22 cm bentonite at its base and two limestone dominated successions interbedded with medium-bedded fine sandstone (Text-fig. 2). *Caenodontus serrulatus* occurs at two intervals in the basal part of the limestone succession with abundant *Pseudohindeodus* to the exclusion of all other conodonts (Text-fig. 3). The species *P. ramovsi* is abundant in two samples, PI-7A and PI-7G, from the Hegler Limestone Member, and occurs with common *Caenodontus serrulatus*, whose apparatus was described by Nestell & Wardlaw (2015). *Pseudohindeodus ramovsi* is scarce throughout much of the overlying Pinery part of the section (Text-fig. 4), and overlaps with its successor, *P. brevis* (Wardlaw & Nestell, 2015). *Jinogondolella* dominated faunas do not occur until the uppermost part of the Hegler Limestone Member, in samples PI-7H and above (Text-fig. 4).

Behnken (1975) reported abundant *Hindeodus typicalis* from the Guadalupe Mountains area, forms subsequently placed in *P. brevis* (Wardlaw & Nestell, 2015). Specimens of *P. ramovsi* have also been recovered from two samples from our K section in the Apache Mountains (Nestell & Wardlaw, 2010) taken above the first appearance of *Jinogondolella posterrata* and probably in post-Pinery age equivalent strata in that section. The range of *P. ramovsi* in the West Texas area appears to be Wordian-Capitanian. Some of the types of elements in apparatus constructions presented herein, especially the ramiform ones, were present in material illustrated by Behnken (1975) and Wardlaw (2000), but are not as well preserved as our specimens.

**APPARATUS RECONSTRUCTIONS**

The first proposed apparatus construction of *Pseudohindeodus ramovsi* has an ozarkodinid construction similar to that of *Idiognathodus* proposed by Purnell & Donoghue (1997) based on bedding plane assemblages of that genus from the Pennsylvanian of Illinois. This 15 element reconstruction of the *P. ramovsi* apparatus (Pl. 1, Fig. 2)—with two M elements, nine S elements (an unpaired S₀, and symmetrically paired S₁, S₂, S₃, and S₄), and paired P₀ and P₂ elements—was only one considered before Wardlaw passed away in March of 2016 because careful processing and searching of many samples failed to produce any clearly ozarkodinid type P₂ elements (angulate elements with a well-developed cusp). Thus, to follow the model of Agematsu et al. (2014), a distinctive bipennate S type element was chosen as the P₂ element. The element in the P₂ position of their model is what appears to be a somewhat modified S element that also could be considered of “ozarkodinid” type. The element (Pl. 1, Fig. 2) chosen for the P₂ position was slightly different from all of the bipennate S elements chosen and was one of the few found of its type that was essentially unbroken. Thus, the reconstruction is very similar in the arrangement of elements to the apparatus reconstruction proposal by Agematsu et al. (2014) for *Hindeodus parvus* (Pl. 1, Fig. 1) and *H. typicalis*, based on bedding plane assemblages (Pl. 1, Fig. 2). The proposed 15 element arrangement of the apparatus of *P. ramovsi* is certainly subject to alternate interpretations, especially with respect to the placement of the M and S elements and the ozarkodinid-style arrangement with P₂ paired elements. The
by fortunate preservation that many complete specimens were found in the strata of the PL section of West Texas that permit the newly proposed reconstructions.

**SYSTEMATIC PALEONTOLOGY**

Phylum **CHORDATA** Bateson, 1886
Subphylum **VERTEBRATA** Cuvier, 1812
Class **CONODONTA** Pander, 1856
Subclass **EUCONODONTA** Janvier, 1996
Order **CONODONTOPHORIDA** Eichenberg, 1930
Family **SWEETOGNATHIDAE** Ritter, 1986
Genus **PSEUDOHINDEODUS** Gullo & Kozur, 1992

*Pseudohindeodus ramovsi* Gullo & Kozur, 1992

Plates 3–6

Diagnosis.—Carminate $P_1$ elements (paired) completely denticate with a medium-sized anterior blade and an ovate triangular basal cavity ending in a narrow groove; denticles compressed near the blade and the bases expanded distally from the blade, 10–18 in number, 3 or 4 posteriormost less compressed and distally decreasing in size; in upper view, surface spade shaped with a distinct nonsymmetrical fringing crimp or flange. In one reconstruction model presented (Pl. 1, Fig. 2), the $P_2$ element is bipennate; in the other (Pl. 2, Fig. 2) there is no $P_2$ element.

Description.—$P_1$ element (Pls. 3, 4): carminate; anterior “blade” or cusp formed by one (or sometimes two fused) high and posterio-anteriorly wide, but laterally thin, denticles. Denticles generally 10–15 in number, are pointed, fused at their base and sometimes display a discontinuous vertically striated microtexture. First few denticles from the cusp fused and compressed, sometimes thinner, of near equal height, with parallel sides (Pl. 3, fig. 16), then posteriorly have a wider base and a more triangular pyramidal shape; toward the distal end, denticle bases become wider, and then last few are narrower. Posteriormost three or four denticles are much less compressed and fused, become free posteriorly, and sharply decrease in size distally. The posteriormost denticle is small and located just above fringing crimp. Distinct fringing crimp forms an asymmetrical platform extending nearly around the element; in larger specimens may be missing on the anteriormost part of the cusp, or may form a slight notch.
Table 4. Ranges of important conodont species in the Bell Canyon Formation of the PI section (b = bentonite; pl = platy). See Wardlaw & Nestell (2015) for more detail. Modified from Wardlaw & Nestell (2015); one time use granted and reproduced with permission from Micropaleontology Press.

<table>
<thead>
<tr>
<th>C C Fm.</th>
<th>Bell Canyon Formation</th>
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</thead>
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<tr>
<td>Hegler Mb.</td>
<td>undivided</td>
</tr>
</tbody>
</table>

- 

- Caenodontoidea serrulatus
- Pseudohindeodus ramovsi
- Pseudohindeodus brevis
- Jinogondolella nankingensis nankingensis
- transitional morphotype
- Jinogondolella nankingensis behnkeni
- Jinogondolella aserrata
- Jinogondolella palmata
- Hindeodus wordensis
- Sweetina triticum
- Hindeodus capitansensis
- Jinogondolella errata
- transitional morphotype
- Jinogondolella postserrata
in lateral profile at the anterior end. Lower surface consists of extremely flared and wide basal cavity which is deep and widest near the midline, and narrows to deep groove beneath the cusp (Pl. 4, Figs. 25, 31).

M element (Pl. 5, Figs. 20, 21): dolabrately shaped; cusp wide, medium sized and distinct from denticles; small cup-shaped basal cavity; inner lateral process extends as an anticusp with a one or two very short denticles adjacent to the cusp. Long downward outer lateral process curves inward and has 14–16 nonfused denticles slightly recurved and uniformly diminishing in size distally.

S₁ element (Pl. 5, Figs. 1–5; Pl. 6, Figs. 1–4): alate; with a well-developed distinct cusp, erect, two lateral processes symmetrically turned downward bearing closely spaced medium-sized denticles of varying lengths. Medium-sized distinctly arched posterior process bears closely spaced but distinct medium-sized denticles with varied basal width; they become thicker, longer, and widen posteriorly from cusp (Pl. 5, Fig. 1).

S₂ element (Pl. 5, Figs. 6–11; Pl. 6, Figs. 5, 6): bipennate; anterior process short, slightly downturned and weakly curved, perpendicular to the long posterior process to slightly backwards bending; bears sharply pointed denticles that are curved and diminish in size to the end. Posterior process long, bears slightly curved pointed reclined denticles, curved at tip, of varying lengths and project at a low angle from process. This distinctive element lacks prominent denticle at or near intersection of the processes that could be construed as a main cusp.

S₃ element (Pl. 5, Figs. 15–18; Pl. 6, Figs. 8–12): bipennate; anterior process short, weakly developed, and slightly curved from the posterior process; bent slightly downwards and laterally, bearing denticles of subequal size; long posterior process sometimes slightly curved and upturned distally and with denticle arrangement similar to S₁ element, but denticles are more erect at steeper angle. This element also lacks a prominent denticle at or near intersection of processes that could be construed as a main cusp.

S₄ element (Pl. 5, Figs. 19, 29–33; Pl. 6, Figs. 18–21): bipennate; cusp well developed, thick at the base, erect to reclined at a slight angle. Short anterior process strongly curved downward from posterior process; contains 5–7 prominent denticles of varying sizes, some over half as long as cusp; long well-developed posterior process with 18–20 denticles of varying lengths, and reclined at increasing angles from vertical distally, becoming smaller at end of the process that tapers to a tip. This element is very similar to the S₁ element, but is consistently smaller in length.

Possible P₁ element (Pl. 6, Fig. 8): bipennate; anterior process very short, very weakly developed and slightly curved from the posterior process; bent slightly downwards and laterally, bearing small denticles of subequal size; long posterior process with base continuously first sharply and then slightly curved and with denticle arrangement similar to S₂ element, but denticles more erect at steeper angle. A few denticles significantly more elongate than others. This element lacks prominent denticle at or near intersection of processes that could be construed as a main cusp.

Remarks.—The number of conodont elements of *Pseudohindeodus* recovered in samples from the PI section varies greatly from sample to sample. The best sample was PI 7G (sampled twice) that had abundant ramiform elements. In most samples, P₁ elements are somewhat common, S₂, S₃, and S₄ elements relatively scarce, and M and S₀ elements are rare. Only seven S₁ elements were recovered in total. Complete specimens of the element illustrated in the P₁ position are scarce. The M, S₀, and S₁ elements of *Pseudohindeodus* are very similar in structure (but much smaller) to the same type of elements of *Idiognathodus*, a typical ozarkodinid conodont (Nestell et al., 2016). It should be clearly noted that no typical “ozarkodinid” P₁ type elements were found in our samples. All illustrated specimens are in Nestell’s conodont collection and mounted on SEM stubs with maps of the scan numbered specimens that will be deposited along with the illustrated specimens of *Caenodontus, Jinogondolella*, and other forms from the papers of Wardlaw and Nestell (2015) and Nestell and Wardlaw (2015) under the number NMMNH P-55918 in the New Mexico Museum of Natural History in Albuquerque.

Distribution.—*Pseudohindeodus ramovsi* is present in the Hegler and Pinery Limestone Members of the Bell Canyon Formation (Guadalupian, Middle Permian). Sturm (1975) reported forms similar to it from the Hegler and Pinery Limestone Members of the Bell Canyon Formation of the Guadalupe Mountains area. Croft (1978) illustrated two specimens referred to *Hindeodus* that are clearly *Pseudohindeodus* along with several possible apparatus ramiform elements. Wardlaw (2000, pl. 3–1, figs. 5–9, S elements; 10–15, 19–24, P₁ elements) described several specimens of the apparatus from the Road Canyon, Word, and Altuda formations in the Glass Mountains of west Texas. Herein, this species is reported from
the Hegler Limestone Member as exposed in the Patterson Hills just to the west of the Guadalupe Mountains. In west Texas, the species appears to be restricted to a narrow stratigraphic interval of the Roadian-Capitanian (Middle Permian) in the Guadalupe, Apache, and Glass mountains areas. However, elsewhere, it appears to range from the late Kungurian to the middle part of the Capitanian (Henderson, 2016; Vuolo, 2014; Sun et al., 2017).

CONCLUSIONS
Based on the excellently preserved materials recovered from limestone of the Hegler Member of the Bell Canyon Formation (Guadalupian, Middle Permian) in the Guadalupe Mountains area of west Texas, two clearly possible apparatus reconstructions, one containing 15 elements (following a typical ozarkodinid arrangement with paired P₂ elements) and the other containing 13 elements (following a modified ozarkodinid arrangement without paired P₂ elements), are presented for the conodont species Pseudohindeodus ramonii. The reconstructions are very similar in arrangement to two contrasting models recently proposed for the species Hindeodus parvus based on bedding plane assemblages present in Permian/Triassic boundary strata in China and Japan. A third possible reconstruction that has an increased number of S position elements is also noted.

ACKNOWLEDGMENTS
We thank Jeffrey Over, John Repetski, James Barrick, Michael Orchard, Yadong Sun, Tea Kolar-Jurkovášek, and Charles Henderson for their thoughtful reviews and/or useful comments. We also thank Galina Nestell for her review and for doing the careful SEM photography of the various conodont elements. Jenny Rashall aided with illustrations. Plates 3–6 and the lower part of plate 1 presented herein were constructed by Wardlaw before his untimely death in March of 2016.

LITERATURE CITED


PLATES
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>The apparatus construction of <em>Hindeodus parvus</em> from Agematsu <em>et al.</em> (2014, fig. 6) is shown for comparison with the proposed reconstruction of <em>Pseudohindeodus ramovsi</em> (reproduced with permission from John Wiley &amp; Sons Ltd. on behalf of The Palaeontological Association).</td>
<td>128</td>
</tr>
<tr>
<td>2.</td>
<td>Proposed apparatus reconstruction for the species <em>Pseudohindeodus ramovsi</em> with P₂ elements. All elements illustrated can be found on the plates of this paper.</td>
<td>128</td>
</tr>
</tbody>
</table>
Nestell and Wardlaw: Contrasting Apparatus Reconstructions of *P. ramovsi*
1

Hindeodus parvus

2

Pseudohindeodus ramovsi
The apparatus construction of *Hindeodus parvus* is shown for comparison with the proposed reconstruction of *Pseudohindeodus ramovsi* and is slightly modified from Zhang et al. (2017) figure 10 (reproduced with permission from John Wiley & Sons Ltd. on behalf of The Palaeontological Association). Note the similarity of the \( S_2 \) element to the \( P_2 \) element of Agematsu et al. (2014).

Proposed apparatus reconstruction for the species *Pseudohindeodus ramovsi* without \( P_2 \) elements. All elements illustrated can be found on the plates of this paper. In a third reconstruction, the paired \( P_2 \) elements of the first model would be considered as distinct from the illustrated \( S_2 \) elements and would be placed between the left and right paired \( S_2 \) and \( S_2 \) elements, thus making a total of 11 elements in the S and M positions.
PLATE 3

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–28.</td>
<td>( P_1 ) elements of <em>Pseudohindeodus ramosi</em> shown at approximately 120x magnification.</td>
</tr>
<tr>
<td>1, 2.</td>
<td>Upper view (scan 135559) and oblique lateral view (scan 114021), sample PI-25.</td>
</tr>
<tr>
<td>3, 4.</td>
<td>Upper view (scan 141943) and oblique lateral view (scan 115528), sample PI-24.</td>
</tr>
<tr>
<td>5, 10.</td>
<td>Upper view (scan 144918) and oblique lateral view (scan 120509), sample PI-23B top.</td>
</tr>
<tr>
<td>6, 7.</td>
<td>Oblique lateral view (scan 110301) and upper view (scan 161147), sample PI-16.</td>
</tr>
<tr>
<td>8, 9.</td>
<td>Upper view (scan 145825) and oblique lateral view (scan 113538), sample PI-23A base.</td>
</tr>
<tr>
<td>11, 12.</td>
<td>Upper view (scan 153812) and oblique lateral view (scan 111352), sample PI-1.</td>
</tr>
<tr>
<td>13, 14.</td>
<td>Upper view (scan 153541) and oblique lateral view (scan 111601), sample PI-1.</td>
</tr>
<tr>
<td>15, 16.</td>
<td>Upper view (scan 165735) and oblique lateral view (scan 104616), sample PI-10A.</td>
</tr>
<tr>
<td>17, 18.</td>
<td>Upper view (scan 161800) and oblique lateral view (scan 105446), sample PI-10B.</td>
</tr>
<tr>
<td>19, 20.</td>
<td>Upper view (scan 131416) and oblique lateral view (scan 132739), sample PI-10.</td>
</tr>
<tr>
<td>21, 22.</td>
<td>Upper view (scan 164935) and oblique lateral view (scan 134350), sample PI-9a.</td>
</tr>
<tr>
<td>23, 28.</td>
<td>Upper view (scan 152504) and oblique lateral view (scan 112431), sample PI-10C.</td>
</tr>
<tr>
<td>24, 25.</td>
<td>Oblique lateral view (scan 103722) and upper view (scan 171238), sample PI-10A.</td>
</tr>
<tr>
<td>26, 27.</td>
<td>Upper view (scan 152742) and oblique lateral view (scan 112622), sample PI-10C.</td>
</tr>
</tbody>
</table>
### Plate 4

1–31. Elements of *Pseudohindeodus ramovsi* shown at approximately 120x magnification.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–3</td>
<td>Oblique lateral view (scan 140018), sample PI-7.</td>
</tr>
<tr>
<td>4, 5</td>
<td>Upper view (scan 131329) and oblique lateral view (scan 170151), sample PI-7G.</td>
</tr>
<tr>
<td>6, 7</td>
<td>Upper view (scan 131527) and oblique lateral view (scan 170408), sample PI-7G.</td>
</tr>
<tr>
<td>8, 9</td>
<td>Upper view (scan 131720) and oblique lateral view (scan 170712), sample PI-7G.</td>
</tr>
<tr>
<td>10, 11</td>
<td>Upper view (scan 132904) and oblique lateral view (scan 172439), sample PI-7G.</td>
</tr>
<tr>
<td>12, 13</td>
<td>Upper view (scan 133706) and oblique lateral view (scan 173246), sample PI-7G.</td>
</tr>
<tr>
<td>14, 15</td>
<td>Upper view (scan 161409) and oblique lateral view (scan 142750), sample PI-7E.</td>
</tr>
<tr>
<td>16, 17</td>
<td>Upper view (scan 161727) and oblique lateral view (scan 143140), sample PI-7D.</td>
</tr>
<tr>
<td>18, 19</td>
<td>Upper view (scan 162356) and oblique lateral view (scan 143431), sample PI-7C.</td>
</tr>
<tr>
<td>20, 21</td>
<td>Upper view (scan 154747) and oblique lateral view (scan 153224), sample PI-7B.</td>
</tr>
<tr>
<td>22, 23</td>
<td>Upper view (scan 154507) and oblique lateral view (scan 153035), sample PI-7B.</td>
</tr>
<tr>
<td>24</td>
<td>Upper view (scan 150400), sample PI-7A.</td>
</tr>
<tr>
<td>25</td>
<td>Basal view (scan 013638), sample PI-7G.</td>
</tr>
<tr>
<td>26, 27</td>
<td>Upper view (scan 162603) and oblique lateral view (scan 143611), sample PI-7C.</td>
</tr>
<tr>
<td>28, 29</td>
<td>Oblique lateral (scan 145019) and upper view (scan 150143), sample PI-7A.</td>
</tr>
<tr>
<td>30</td>
<td>Upper view (scan 133249), sample PI-7G.</td>
</tr>
<tr>
<td>31</td>
<td>Basal view (scan 013301), sample PI-7G.</td>
</tr>
</tbody>
</table>
All specimens are S and M elements of *Pseudohindeodus ramovsi* shown at approximately 120x magnification.

1. Lateral view, $S_0$ element (scan 155353), sample PI-7B.
2. Oblique posterior view, $S_0$ element (scan 142224), sample PI-7G.
3. Posterior view, $S_0$ element (scan 142636), sample PI-7G.
4. Lateral view, $S_0$ element (scan 142427), sample PI-7G.
5. Lateral view, $S_0$ element (scan 170022), sample PI-7E.
6. Inner view, $S_1$ element (scan 140545), sample PI-7G.
7. Inner view, $S_1$ element (scan 141639), sample PI-7G.
8. Inner view, $S_1$ element (scan 141119), sample PI-7G.
9. Upper view, $S_1$ element (scan 140937), sample PI-7G.
10. Inner view, $S_1$ element (scan 141306), sample PI-7G.
11. Inner view, $S_1$ element (scan 141451), sample PI-7G.
12. Lateral view, M element (scan 135521), sample PI-7G.
13. Lateral view, M element (scan 135326), sample PI-7G.
14. Lateral view, M element (scan 135714), sample PI-7G.
15. Inner view, $S_1$ element (scan 144711), sample PI-7G.
16. Inner view, $S_1$ element (scan 155611), sample PI-7B.
17. Inner view, $S_1$ element (scan 145215), sample PI-7G.
18. Inner view, $S_1$ element (scan 144852), sample PI-7G.
19. Inner view, $S_1$ element (scan 160236), sample PI-7B.
20. Lateral view, M element (scan 135001), sample PI-7G.
21. Lateral view, M element (scan 135142), sample PI-7G.
22. Inner view, $S_1$ element (scan 145416), sample PI-7G.
23. Inner view, $S_1$ element (scan 143616), sample PI-7G.
24. Inner view, $S_1$ element (scan 150141), sample PI-7G.
25. Inner view, $S_1$ element (scan 144523), sample PI-7G.
26. Inner view, $S_1$ element (scan 150518), sample PI-7G.
27. Lateral view, $S_0$ element (scan 151200), sample PI-10C.
28. Oblique posterior view, M element (scan 134822), sample PI-7G.
29. Inner view, $S_1$ element (scan 142944), sample PI-7G.
30. Inner view, $S_1$ element (scan 143215), sample PI-7G.
31. Inner view, $S_1$ element (scan 144337), sample PI-7G.
32. Inner view, $S_1$ element (scan 145750), sample PI-7G.
33. Inner view, $S_1$ element (scan 145935), sample PI-7G.
34. Inner view, $S_1$ element (scan 143939), sample PI-7G.
35. Inner view, $S_1$ element (scan 150331), sample PI-7G.
36. Inner view, $S_1$ element (scan 145603), sample PI-7G.
37. Inner view, $S_1$ element (scan 145037), sample PI-7G.
Nestell and Wardlaw: Contrasting Apparatus Reconstructions of *P. ramovsi*
Plate 6

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–21. All specimens are S and M elements of <em>Pseudohindeodus ramovsi</em> shown at approximately 120x magnification.</td>
<td>129</td>
</tr>
<tr>
<td>1. Lateral view, $S_0$ element (scan 162826), sample PI-10B.</td>
<td></td>
</tr>
<tr>
<td>2. Lateral view, $S_0$ element (scan 154441), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>3. Lateral view, $S_1$ element (scan 154627), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>4. Lateral view, $S_1$ element (scan 154923), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>5. Oblique upper view, $S_1$ element (scan 163337), sample PI-10B.</td>
<td></td>
</tr>
<tr>
<td>6. Oblique lateral view, $S_1$ element (scan 164330), sample PI-10A.</td>
<td></td>
</tr>
<tr>
<td>7. Lateral view, M element (scan 134222), sample PI-25.</td>
<td></td>
</tr>
<tr>
<td>8. Inner view, $P_2$ element (scan 155500), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>9. Inner view, $S_2$ element (scan 165340), sample PI-10A.</td>
<td></td>
</tr>
<tr>
<td>10. Inner view, $S_2$ element (scan 134410), sample PI-25.</td>
<td></td>
</tr>
<tr>
<td>11. Inner view, $S_2$ element (scan 162511), sample PI-10B.</td>
<td></td>
</tr>
<tr>
<td>12. Inner view, $S_2$ element (scan 162649), sample PI-10B.</td>
<td></td>
</tr>
<tr>
<td>13. Inner view, $S_2$ element (scan 164142), sample PI-10A.</td>
<td></td>
</tr>
<tr>
<td>15. Inner view, $S_3$ element (scan 155640), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>16. Inner view, $S_3$ element (scan 165200), sample PI-10A.</td>
<td></td>
</tr>
<tr>
<td>17. Inner view, $S_3$ element (scan 134600), sample PI-25.</td>
<td></td>
</tr>
<tr>
<td>18. Inner view, $S_3$ element (scan 155820), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>19. Inner view, $S_3$ element (scan 160015), sample PI-1.</td>
<td></td>
</tr>
<tr>
<td>20. Inner view, $S_3$ element (scan 151727), sample PI-10C.</td>
<td></td>
</tr>
<tr>
<td>21. Inner view, $S_3$ element (scan 164843), sample PI-10A.</td>
<td></td>
</tr>
</tbody>
</table>
NEW CLUSTERS OF PSEUDOFURNISHIUS MURCIANUS FROM THE MIDDLE TRIASSIC OF SLOVENIA (DINARIDES)

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ABSTRACT

This work reports recovery of an abundant monospecific conodont association with clusters of Pseudofurnishiarius murcianus found after the reassessment of the classical locality of Prikrnica (Slovenia, Middle Triassic). Conodont clusters are an important source of information for apparatus reconstruction, but they are very rare from the Triassic record of the world. Based on lithofacies study, the strata were deposited in a low energy, relatively deep, pelagic environment. Pelagic sedimentation was interrupted by gravity flow deposits (carbonate turbidites) with resedimented, mainly skeletal detritus from the shallow to the deep part of the carbonate platform located in the western part of the Tethys. Thus, the environmental conditions could have favored a good preservation potential (burial or concentration by gravity flows) or slow decay rates increasing the chance of cluster preservation. Ladinian strata of the Prikrnica section show a great potential for the finding of new complete clusters that together with the application of novel tomographic techniques would allow the reconstruction of the P. murcianus apparatus.

INTRODUCTION

Conodonts are an extinct group of jawless vertebrate with a series of mineralized oral elements arranged in a complex apparatus (Briggs et al., 1983). The conodont elements that form this apparatus normally become disarticulated after the death and decay of the animal, so the vast majority of the conodont fossil record is composed of their isolated elements usually found after the acid dissolution of carbonate rocks. However, under special preservation circumstances, the conodont apparatus can be (partially or totally) preserved as clusters or assemblages. This exceptional preservation is of great significance, allowing us to understand the general structure and composition of the conodont apparatus of several taxa (see Donoghue et al., 2008 and references therein), thereby differentiating species or even genera (Orchard, 2005).

Fused clusters are rare structures composed of two or more elements diagenetically fused that provide information about the structure and disposition of elements in the conodont apparatus, representing, in some cases, the real topological arrangement (Goudemand et al., 2011). Nevertheless, they are fragile and very difficult to manipulate, and if more than two elements are involved, the external elements and/or the matrix can mask the morphology of the different elements, making it more complicated to analyze them. Thus, until now, the study of clusters have only partially helped in the debate of conodont apparatus reconstruction, basically confirming the hypothesis of a multielemental apparatus, associating pectiniform and ramiform elements that had previously been

considered as separate species. However, the introduction of novel techniques, such as high resolution computed tomography, has opened new opportunities in paleobiologic studies, not only for apparatus reconstructions (Goudemand et al., 2011, 2012; Suttner et al., 2017; Agematsu et al., 2017; Zhang et al., 2017), but also to unravel the function and development of these skeletal elements (Jones et al., 2012a, b; Murdock et al., 2013a, b; 2014; Martínez-Pérez et al., 2014a, b; 2016; Maizza & Martínez-Pérez, 2015, 2016; Suttner et al., 2017).

As conodont clusters represent very rare structures, any new findings could provide valuable information to understand the composition and architecture of the conodont apparatus. In this sense, this work reports a new abundant record of *Pseudofurnishius murcianus* clusters found after the reassessment of the classical locality of Priknica (Slovenia, Middle Triassic) (Krivic & Stojanović, 1978). In order to understand the origin of this special conodont record, a full stratigraphic and sedimentologic background for the cluster-bearing strata is provided.

Therefore, the aim of this work is to document the discovery of abundant conodont clusters from the Ladinian Priknica section in Slovenia. The paper emphasizes the sedimentologic context of the clusters, paleogeography, age, and correlation of the form-species. A complete description and discussion of the apparatus is beyond the scope of this paper, but will be the focus of future work.

**Triassic Conodont Clusters**

Triassic conodont clusters provide valuable information for the architecture of the apparatus of Gondolelloidea as the best represented conodont superfamily prior the decline of the entire group (Clark, 1983; Giordano et al., 2010; Kolar-Jurkovšek, 2011; Martínez-Pérez et al., 2014a, c, 2015).

Although Triassic conodonts are really abundant, just a few clusters have been reported in the literature. The first Triassic conodont clusters were figured by Ramović (1977, 1978) and Krivic & Stojanović (1978). They reported clusters of *Pseudofurnishius murcianus* van den Boogaard, 1966 from Ladinian strata of Slovenia. Later, some interesting findings of conodont clusters have been documented in Italy, such as a cluster of *Metapolypynathus mungoensis* (Diebel, 1956) from the Middle Triassic (Ladinian) at the Trento area (NE Italy) (Mietto, 1982) and a Late Triassic *Miskella Kozur & Mock*, 1974 cluster from Calabria in southern Italy (Mastandrea et al., 1999). More recently, a Lower Triassic (Smithian) cluster from South Primorye in the Russian Far East has been described as well (Bondarenko et al., 2013). This list is completed with the clusters recorded in China. Huang et al. (2010) reported clusters from the Middle Triassic of Yunnan Province, China (Huang et al., 2010; Goudemand et al. (2011, 2012) described the Early Triassic *Neospathodus* and *Novispathodus* clusters from Guangxi Province and more recently Zhang et al. (2017) studied *Hindeodus* clusters from Sichuan Province. It is important to highlight that other conodont assemblages have been recorded as bedding planes (no clusters) highlighting the Middle Triassic *Neogondolella* natural assemblage from the Monte San Giorgio of Switzerland published by Rieber (1980). The multielement was reconstructed by Orchard & Rieber (1999) and Goudemand et al. (2011), which has been adopted as the architectural template for all apparatuses of the superfamily Gondolelloidea (Orchard & Rieber, 1999; von Bitter & Merrill, 1998). Finally, other bedding plane assemblages from the Lower Triassic of Japan have been recently described, allowing the reconstruction of the multielement apparatus of the earliest Triassic conodont *Hindeodus parvus* (Agematsu et al., 2015, 2017).

**Geological Setting**

The territory of present-day Slovenia is located at the junction of the Dinarides, Southern Alps, Eastern Alps, and the Pannonian Basin (Text-fig. 1). All geotectonic units belong to the Adriatic lithosphere plate, the southern edge of which was initially connected to the African plate, but later, from the Mesozoic times onwards, it existed as an independent plate.

Paleogeographically, during the Permain and Early Triassic there was a unified and very extensive carbonate platform, part of which in Slovenia is called the Slovenian Carbonate Platform (Buser, 1989). This began to break apart during the Anisian and Ladinian as a result of extensional tectonics at the edge of Eurasia, where the Meliata Ocean began to open. The Slovenian Basin divided the Slovenian Carbonate Platform from the Julian Carbonate Platform to the north, and the Adriatic-Dinaric Carbonate Platform to the south (Buser et al., 2008).

Triassic limestones with *Pseudofurnishius* were deposited at the southern edge of the Slovenian Basin during sedimentation of the Pseudogaital beds. The Priknica locality is situated in the transitional region between the External and Internal Dinarides. The complex tectonic structure of the region makes it difficult to limit this unit and to define precisely (Text-fig. 1). Generally, this region encompasses almost the entire Sava Folds area east of Ljubljana. In the Sava Folds, the Mesozoic rocks form one, or more, large thrust units, which can be correlated only with the Dinaridic thrusts of southwestern Slovenia, indicating that the Sava Folds thrusts belong to the Dinaridic provenance (Placer, 2008).

The conodont fauna with *P. murcianus* clusters was recovered from the carbonate strata of the Priknica section, which is located north-west of the village of Moravče in Central Slovenia (Text-fig. 1). The Priknica section is represented by a ~ 40 m thick homogeneous carbonate rock succession.
that rests in tectonic contact with Middle Triassic dolomite (Text-fig. 2). The lowermost part of the section, a 3 m thick interval, consists of microbial-like dolostone, but the majority of the section consists of black platy-bedded limestone. The section was originally measured and sampled for conodonts by Krivic and Stojanović (1978), who reported a conodont fauna containing clusters of the species *P. murcianus* associated with elements of *Hindeodella (Metaprioniodus) suetica* (Tatge, 1956) and *Enantiognathus ziegleri* (Diebel, 1956). The strata with conodonts range from the late Ladinian to the early Carnian (Krivic & Stojanović, 1978), marking the *P. murcianus* zone (Kolar-Jurkovšek, 1991).

**MATERIAL AND METHODS**

The Prikrnica section was measured and sampled for conodonts and microfacies studies during field work carried out in 2013–2015. Middle Triassic carbonate strata are exposed along the forest path where the lower part of the section begins with coordinates 46° 9’ 2.08”N, 14° 43’ 12.29”E, and the upper part ends with coordinates 46° 2’ 20.17”N, 14° 5’ 47.94”E. The position of the 38 rock samples collected in the first set is shown in Text-fig. 2. Samples with a minimum weight of 4 kg were processed for conodont study using standard laboratory techniques with acetic acid digestion (ca. 7-10%). In addition, the most prolific levels for conodont clusters (samples PR 8 and PR 9) were additionally subdivided and sampled in detail (marked with letters A to D). The laboratory preparation was mostly carried out at the Geological Survey of Slovenia (GeoZS) and partly at the University of Valencia. All micropaleontological materials are stored, inventoried, and abbreviated GeoZS under the repository numbers 5456–5493 and 5554–5563. The elements selected to show the diversity and abundance of clusters were photographed with a Hitachi S-4800 scanning electron microscope (SEM) hosted at the University of Valencia.

Petrographic thin sections from each of the 38 conodont samples marked in Text-fig. 3 were prepared for microfacies analyzes at University of Zagreb. All thin sections were stained by Alizaren Red S and K-ferricyanide.

**SEDIMENTOLOGY**

The Prikrnica section consists dominantly of medium-thick bedded grey limestone with subordinate occurrences of dolostone beds (Text-fig. 2). Four lithotypes were differentiated: i) mudstone; ii) laminated mudstone/wackestone, iii) wackestone/flintstone (limestone/dolostone) with bivalves and, iv) intraclastic packstone. Carbonate mud-rich lithotypes (mudstone and laminated mudstone/wackestone) predominates in the section.

**Microfacies Description**

Lime mudstone consists of homogenous lime mud with rare occurrences of small bioclasts containing radiolarians and ostracods. Sometimes dark thread-like microbial (?) forms are present, giving this rock-type a laminated appearance (Text-fig. 3A). At the beginning of the section, layers of dolomitized laminated mudstone occur in which thread-like forms remain fairly well preserved.

In laminated mudstone/wackestone, mud- and fossil-rich laminae alternate (Text-fig. 3B). Fossil-rich laminae consist mainly of ostracods and rarely planktic foraminifera or small bivalve fragments. In the micritic lamina, rare radiolarians and holothurians are present.

Wackestone/floatstone with bivalves appears interlayered
Text-fig. 2. Geological column of the studied strata of the Prikrnica section in Slovenia.
with dominantly mud-rich lithology. Coarse-grained unsorted bivalve fragments (often > 2 mm) occur in micritic matrix. This lithotype can be thoroughly dolomitized. Polymodal microcrystalline texture is observed. Primary prismatic bivalve structure is replaced with dolomite crystals (Text-fig. 3C).

Intraclastic packstone comprises intraclasts, peloids, and bioclasts (<2 mm) in micritic matrix (Text-fig. 3D). Bioclasts are represented mainly by ostracods, less often foraminifers, and fragments of echinoderms, bivalves, and gastropods.

Partial silicification occurs in mud rich lithotypes.

Depositional Environment of the Prikrnica Section

The depositional environment of the Prikrnica limestone and dolostone is interpreted in the context of regional geologic development in the Western Tethys. During the Middle Triassic, the Slovenian Carbonate Platform disintegrated, forming uplifted blocks with shallow marine deposition of carbonates, while in the subsided area (basin) sediments were characteristic of pelagic open marine deposition (Buser, 1989; Buser et al., 2007; Bitner, 2010). The global sea-level rise occurred in the Middle Triassic, documented in the whole Western Tethys,
caused drowning of the existing carbonate platforms (Gallet et al., 1998; Kovács et al., 2010, 2011; Lein et al., 2012; Sudar et al., 2013). Pelagic environments were reported in the Western Tethys by Keim & Neri (2005), Sudar & Kovács (2006), Schefer et al. (2010) and Missoni et al. (2012). Slump structures, found in the sedimentary rocks of the same age in the vicinity of the investigated Prikrnica section (see Text-fig. 4) indicate possible redeposition of shallow water carbonate sediment into deeper marine areas, including a variety of redeposition processes such as slides, slumps, or submarine gravity flows. Redeposition that started as slumping might have been triggered by slope failures and then developed as turbidite gravity flows. A transition of sediments from uplifted blocks with shallow marine carbonate sedimentation to a deeper environment is apparent in the Prikrnica section. Allochthonous shallow-marine platform material composed of sand- and gravel-sized particles (skeletal fragments of shallow-water biota, intraclasts, and peloids) derived from platform margin carbonates were redeposited to a deep-water pelagic environment. Submergence of the platform might have even increased contribution of platform-margin material to the slope, leading to a higher input of shallow water detritus. Presence of radiolarians and rare pelagic holothurians in sediments of the Prikrnica section implies a deposition in a relatively deep, open pelagic environment. Abundance of lime mud indicates slow sedimentation in a low energy environment, possibly by settling from suspension. Presence of ostracods, foraminifers (pelagic forms), and rare holothurians represent in situ bioclastic particles typical of pelagic communities. Interlayers of wackestone/floatstone with bivalves indicate a connection with the shallow water periplatform carbonate and apparent redeposition of shallow-water material. Fragments of shallow water biota (bivalves, echinoderms, and gastropods), as well as intraclasts and peloids, are interpreted as primarily accumulated periplatform debris at the platform break that were also possibly redeposited as periplatform turbidites to a deep part of the basin, where they are intercalated with pelagic deposits of lime-mud dominated varieties (mudstone and laminated mudstone/wackestone types). In the outcrop there was no evidence of deposition as carbonate turbidites, but microfacies characteristics—such as occurrences of non-graded, poorly sorted skeletal packstones consisting of shell accumulations (bivalves or brachiopods)—indicate gravity flow deposition (Flügel, 2004). In an overall calm suspension dominated pelagic sedimentation, gravity flow deposits suggest sudden depositional events, possibly causing quick burial and therefore concentration of fossil fragments preventing them from further redeposition and destruction. Fossils can also be concentrated in turbidity-like gravity flows by entraining fossil detritus from a slope surface during transport. Deposition occurred at the toe of the slope or at the foot of a steep platform.

Thread-like forms (found in mudstones) are interpreted as microbial in origin and are not uncommon, even in the deep marine, slope conditions. Nevertheless, the presence of microbial deposits could have favored low decay rates of fossils, increasing the potential of preservation of the clusters (Wilby et al., 1996; O’Brien et al., 2008; Iniesto et al., 2016, among others).

The dolomitization is interpreted as late diagenetic secondary processes. Silicification can be related also to the secondary processes or possibly to the influence of the Si-enriched deep basin ocean water.

CONODONTS OF THE PRIKRNICA SECTION

The recovered conodont fauna in the entire section show a color alteration index (CAI) around 5 sensu Epstein et al. (1977), and is characterized by abundant representation of clusters and isolated elements belonging to Pseudofurnishius murcianus. This species is present in 32 out of a total 47 samples processed (Table 1) The only exception is sample PR 5, where a single P1 element of Budurovignathus (= Sephardiella sensu Plasencia et al., 2007) was also obtained. The almost monospecific assemblage of P. murcianus could represent stressful and/or specialized environmental conditions that were unfavourable for other conodont taxa (Kolar-Jurkovšek & Jurkovšek, 2010). Even though biotic (e.g., predation, scavenging, or bioturbation) and abiotic factors (e.g., current activity) can affect the conodont fossil record (Purnell & Donoghue, 2005; von Bitter & Purnell, 2005), we think that the monospecific assemblage of P. murcianus represents a real biological association. This assumption is supported by several data. The recovery of well-preserved conodonts showing all the typical morphologic types (Text-fig. 5),
Together with the preservation of the clusters themselves, indicate that the elements didn’t suffer any kind of transport or dynamic selection, nor were they the result of predation or scavenging. In addition, similar monospecific assemblages of *P. murcianus* have been recorded in several localities of the western Tethys and in shallow water conditions, more exposed to eustatic events and salinity changes (Plasencia, 2009; Plasencia & Márquez-Aliaga, 2011; Plasencia et al., 2007, 2015), suggesting that our assemblage is not affected by strong taphonomic biases, and hence represent a normal taphocoenosis.

On the other hand, the existence of a monofaunal assemblage together with sedimentologic data could indicate a quick burial by gravity flow deposits or concentration of fossil fragments in turbidity currents by entraining them during transport along slope.

In total, approximately 3500 *P. murcianus* elements have been recovered (see Table 1), including an exceptional collection of more than 300 clusters. From the 32 samples that yielded conodonts, just three lacked clusters, an unusual richness for this kind of conodont record worldwide. In addition to this cluster abundance, a rich collection of isolated elements have also been recorded from the same levels, showing all the different element types that represent the general structure of the gondolelloid apparatus (Orchard, 2005; Goudemand et al., 2012) (see Text-fig. 5).

The majority of clusters are represented by a small number of fused elements (between 2 and 4), although a few clusters show a great number of elements (Pl. 1, Figs. 7–9, 12, 25–26). In these cases, to study its apparatus architecture and reconstruct it accurately, the application of tomographic tools is required. It is important to highlight that the richness of abundant isolated elements and the completeness of the clusters—showing a significant number of elements and apparently their relative position within the apparatus—prevents the reconstruction of the conodont apparatus and architecture of *P. murcianus*.

Together with the conodont fauna of the Prikbnica section, frequent remains of fish teeth and scales (*Acodina, Nurrella*), ostracods, and rare holothurians—predominantly representatives of *Theelia*—are also present. The latter is the most common holothurian genus in the pelagic Middle and Late Triassic strata of Slovenia (Kolar-Jurkovšek, 1991; Jamnik & Ramovš, 1993).

**Age of Pseudofurnishius murcianus**

In central Slovenia a belt of pelagic Ladinian-Carnian strata crops out and is marked by the presence of *P. murcianus*. This fauna was studied by Ramovš (1985) and, due to its co-occurrence with the Langobardian bivalve marker *Posidonia wagensis* Wissmann, 1841 in some locations of Slovenia, he considered these strata to be stratigraphically restricted to the late Ladinian, whereas a recovered palynoflora is characteristic for the late Langobardian and earliest Carnian (Premru, pers. comm.).

Occurrence of *P. murcianus* in the Ladinian is indisputable as determined from numerous sections in the western Tethys (Plasencia, 2009; Plasencia & Márquez-Aliaga, 2011; Plasencia et al., 2015). According to Benjamini & Chepstow-
Text-fig. 5. Isolated elements assigned to Pseudofurnishius murcianus van den Boogaard showing the different morphologies of the typical gondolellid conodont apparatus according to Orchard (2005). 1–3, S₀ element type, sample PR5, GeoZS 5460, scale bar = 100 μm; 4, 5, M element type, sample PR8A, GeoZS 5555, scale bar = 100 μm; 6, 7, P₁ element type, sample PR9D, GeoZS 5562, scale bar = 200 μm; 8, S₁ element type, sample PR15, GeoZS 5470, scale bar = 300 μm; 9, P₂ element type, sample PR24, GeoZS 5479, scale bar = 100 μm; 10, S₃d element type, sample PR22, GeoZS 5477, scale bar = 300 μm; 11, S₂ element, sample PR15, GeoZS 5470, scale bar = 200 μm.
Lusty (1986), the species is characteristic of the Ladinian, but possibly it extends down to the late Anisian, whereas the entire stratigraphic range of *P. murcianus* is late Ladinian—early Carnian according to Kovács & Kozur (1980). There are a few more reports on the recovery of *P. murcianus* from Cordevolian strata (van den Boogaard & Simon, 1973; Kozur, 1980, 1993; Kozur et al., 1974; Nicora, 1981).

**Paleobiogeographic distribution of *Pseudofurnishius***

During most of the Triassic a greater part of Europe was covered by the Tethys Ocean and only during the Middle Triassic were conodont provinces formed; at first German and Balkanid conodont provinces, but later in Ladinian-Cordevolian time also a Sephardic conodont province (Kozur, 1980; Budurov et al., 1983; Sudar, 1986). The latter province was first introduced by Kozur & Mostler (1971) as West Mediterranean-African-North American province and later other terms appeared (West Mediterranean province sensu Kozur & Mostler, 1972; West Mediterranean-Arabic province sensu Kozur, 1980). The Sephardic province designates partly endemic faunal communities characterized by conodont genera *Pseudofurnishius* and *Budurovignathus* of the circum-mediterranean area (Hirsch, 1972). According to Kozur (1993), *P. murcianus* is a typical element only present in the western Tethys and its marginal seas, and therefore, it is an important paleobiogeographic marker. However, some findings of *P. murcianus* in Asia confirm its paleobiogeographic extension outside the Sephardic province.

*Pseudofurnishius murcianus* has been documented to have an extensive distribution in the Spanish Middle Triassic that is interpreted as epeiric carbonate platforms of the western part of the Sephardic province (Márquez-Aliaga et al., 2000). During the late Ladinian this species occurs monospecifically and is confined to the shallow or slightly hypersaline intervals of the Sephardic province, whereas the worldwide presence of *Budurovignathus* indicates a more open environment (Hirsch et al., 1987; Budurov et al., 1985; Márquez-Aliaga et al., 2000). This species has been known to occur in the Dinarides of Croatia (Jelaska et al., 2003) and Bosnia and Herzegovina (Kolar-Jurkovšek et al., 2015), as well as in Italy (Sicily: Catalano et al., 1990; Gullo & Kozur, 1991; Southern Alps: Mastandrea et al., 1998; Balini et al., 2000; Jadoul et al., 2002), Romania (Kozur, 1980), Hungary (Kozur, 1993), Albania (L. Krystyn, pers. comm., 2016), Turkey (Nicora, 1981), Jordan (Bandel & Waksmundzki, 1985), Tunisia (Rakus, 1981), Egypt, and Israel (Huddle, 1970; Hirsch, 1972; van den Boogaard & Simon, 1973; Eicher & Mosher, 1974; Benjamini & Chepstow-Lusty, 1986). However, some findings of *P. murcianus* in Asia confirm its paleobiogeographic extension outside the Sephardic province: South Western China (Shouren et al., 2001) and Malaysia (Nogami, 1968; Hirsch et al., 2007; Ishida & Hirsch, 2011) (see Text-fig. 6).

**CONCLUSIONS**

The abundant conodont fauna of the Prikrnica section, represented by the monospecific association of *P. murcianus*, with more than 3500 conodont elements recovered (including more than 300 clusters), provides evidence of exceptionally good preservation due to sudden burial by gravity flow deposits (carbonate turbidites) or accumulation of fossil fragments by entraining surface slope debris during resedimentation processes that transport material from a shallow carbonate platform to a pelagic environment. The exception is a single *Budurovignathus* specimen obtained in sample PR 5. This fauna suggests a Ladinian age.

The stratigraphic and sedimentologic study of the Prikrnica section in Slovenia allowed us to interpret its depositional history. Accordingly, the studied strata were deposited in a low energy environment in a relatively deep, pelagic environment at the toe of the slope or at the foot of a carbonate platform in the Western Tethys. Those environment conditions, together with the high sedimentation rates, and probably the presence of microbial mats on the sea floor, which were identified in several parts of the section, could have favored low decay rates, increasing the chance of cluster preservation (Wilby et al., 1996; O’Brien et al., 2008; Iniesto et al., 2016, among others). Hence, the Prikrnica section shows a great potential for the finding of new complete clusters that, together with the application of state-of-the-art tomographic techniques, would allow us in the future to reconstruct the *P. murcianus* apparatus.

**ACKNOWLEDGMENTS**

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LITERATURE CITED


PLATE
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–26.</td>
<td><em>Pseudofurnishius murcianus</em> van den Boogaard clusters from Prikrnica section.</td>
</tr>
<tr>
<td>1, 2.</td>
<td>Cluster showing remains of M, and S₁-₄ elements, sample PR4, GeoZS 5459; scale bar = 200 µm.</td>
</tr>
<tr>
<td>3.</td>
<td>P₁ cluster, sample PR5, GeoZS 5460; scale bar = 100 µm.</td>
</tr>
<tr>
<td>4.</td>
<td>P₁ cluster, sample PR8B GeoZS 5556; scale bar = 200 µm.</td>
</tr>
<tr>
<td>5.</td>
<td>P₁ cluster, sample PR9B GeoZS 5560; scale bar = 200 µm.</td>
</tr>
<tr>
<td>6.</td>
<td>P₁ cluster, sample PR11 GeoZS 5466; scale bar = 100 µm.</td>
</tr>
<tr>
<td>7.</td>
<td>Cluster showing remains of S₁ to S₄ element, sample PR8 GeoZS 5463; scale bar = 300 µm.</td>
</tr>
<tr>
<td>8, 9.</td>
<td>Cluster showing S₁-₄ elements and other indeterminate S elements fragments, sample PR10 GeoZS 5465; 8) scale bar = 400 µm; 9) scale bar = 300 µm.</td>
</tr>
<tr>
<td>10, 11.</td>
<td>Cluster showing fragments of S₁-₄ elements, sample PR14 GeoZS 5469; scale bar = 200 µm.</td>
</tr>
<tr>
<td>12.</td>
<td>Cluster showing fragments of S₁-₄ elements, sample PR15 GeoZS 5470; scale bar = 200 µm.</td>
</tr>
<tr>
<td>13.</td>
<td>Cluster showing fragments of indeterminate S element, sample PR6 GeoZS 5461; scale bar = 100 µm.</td>
</tr>
<tr>
<td>14.</td>
<td>Cluster showing fragments of several S elements, sample PR16 GeoZS 5471; scale bar = 200 µm.</td>
</tr>
<tr>
<td>15.</td>
<td>P₁ cluster, together with other indeterminate S element fragments, sample PR17 GeoZS 5472; scale bar = 100 µm.</td>
</tr>
<tr>
<td>16.</td>
<td>Cluster showing fragments of S₁-₄ elements, sample PR20 GeoZS 5475; scale bar = 100 µm.</td>
</tr>
<tr>
<td>17, 18.</td>
<td>Cluster showing several fragments of S element, probably S₂-₄, samples PR11 GeoZS 5466; scale bar = 200 µm.</td>
</tr>
<tr>
<td>19.</td>
<td>Cluster with fragments of S₂-₄ elements, sample PR22 GeoZS 5477; scale bar = 300 µm.</td>
</tr>
<tr>
<td>20.</td>
<td>P₁ cluster, sample PR22 GeoZS 5477; scale bar = 100 µm.</td>
</tr>
<tr>
<td>21, 22.</td>
<td>Cluster showing fragments of S₃-₄ elements. Sample PR24 GeoZS 5479; scale bar = 100 µm.</td>
</tr>
<tr>
<td>23.</td>
<td>Cluster showing fragments S₃-₄ elements, sample PR21 GeoZS 5476; scale bar = 200 µm.</td>
</tr>
<tr>
<td>24.</td>
<td>Cluster showing fragments of S₁-₃ elements, sample PR9C GeoZS 5561; scale bar = 200 µm.</td>
</tr>
<tr>
<td>25, 26.</td>
<td>Cluster apparently showing fragments of a complete dextral series of S₁-₄ and remains of the sinistral one, samples PR19 GeoZS 5474; scale bar = 100 µm.</td>
</tr>
</tbody>
</table>
Kolar-Jurkovšek et al.: New Clusters of *Pseudofurnishius murcianus*
THE LOWER-MIDDLE NORIAN (UPPER TRIASSIC) BOUNDARY: NEW CONODONT TAXA AND
A REFINED BIOZONATION

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ABSTRACT
Markedly different conodont faunas occur on either side of the known Lower–Middle Norian boundary (LMNB) identified in the Pardonet Formation of northeast British Columbia (Canada). A faunal gap separates ammonoids of the Lower Norian Magnus and those of the Middle Norian Rutherfordi zones, and conodonts of, respectively, the Ancyrogondolella triangularis and Orchardella multidentata zones. A new conodont zone, with Ancyrogondolella transformis n. sp. as the nominal index, is bracketed by the boundary ammonoid zones in four sections in the Western Canada Sedimentary Basin: Pink Mountain, Carbon Creek east, McLay Spur, and Brown Hill. Seven new species are described: Ancyrogondolella inegalis, A. diakowi, A. equalis, A. transformis, A. praespiculata, Mockina spinosa, and Orchardella n. sp. A. Most of these taxa appear first in the A. transformis Zone and five are confined to it. Species of the transformis Zone are shown to fill a stratigraphic and morphological (phyletic) gap between Ancyrogondolella and successor species assigned to Epigondolella and Orchardella, whereas Mockina arises earlier from Ancyrogondolella close to the top of the preceding triangularis Zone. These changes occur over a remarkably thin stratigraphic interval (<1 m) and reveal a rapid morphological radiation and faunal turnover. The name Ancyrogondolella replaces Epigondolella for species characterized by a bifid keel, and criteria are presented for distinguishing the three successive genera with single keels. The new conodont zone is not presently known in direct association with ammonoids, but its base provides an easily recognizable datum for defining the LMNB.

INTRODUCTION
The Norian, the medial stage of the Upper Triassic, has the distinction of being the longest stage of the Phanerozoic, although absolute ages are scarce and researchers have generally relied on cyclostratigraphic calculations in non-marine successions combined with magnetostatigraphic correlations to the marine realm to arrive at numeric dates for stages. Most recently, the base of the Norian has been regarded as 227 Ma (Kent et al., 2016), and its top as ~205.7 Ma (Maron et al., 2017), depending on eventual definition (Li et al., 2017). Within the Norian, a zircon age of ~224 Ma has been reported around the Lower-Middle Norian boundary (LMNB) by Diakow et al. (2012). As a consequence of its ~20 My duration, the substages of the Norian will likely become more important in Triassic chronostratigraphy. The Lower-Middle Norian boundary (LMNB) is of particular interest because it represents a big change in the composition of both ammonoid and conodont faunas, as is particularly apparent in western Canada, which was situated at the western edge of Pangea during the Late Triassic. Elsewhere, in the former Tethys, the boundary is less clear because the record of mid-Norian strata is sparse, disturbed, and incomplete, even in the condensed Hallstatt facies (Krystyn, 2008; Karádi, 2017; Rigo et al., 2018). It was from the latter facies that the basal Middle Norian ammonoid zone of Cyrtopleurites bicornatus was first established in the nineteenth century by Mojisivosics at Sommeraukogel, Austria. This zone was originally based on mixed fissure-fill deposits (Tozer, 1984, pp. 127, 128) in which ammonoids indicative of the North American Fuvatites magnus, Drepanites rutherfordi, and Mesohimavatites columbianus zones (hereafter abbreviated) were found. This led Tozer (1967) to erroneously include the Magnus Zone in the Middle Norian, although later the correct ammonoid succession was worked out in the Peace River valley of northeast British Columbia and thoroughly described by Tozer (1994), who built on the pioneering work of Frank McLearn (1953, 1960). This is the same area in which the present study is based (Text-fig. 1).

The standard ammonoid biochronology in North America as defined by Tozer (1967, 1994) places the Lower-Middle Norian boundary between the Magnus and Rutherfordi zones (Text-fig. 2). Until 1980, all the work on the Norian ammonoids in this region was achieved through collecting in partial outcrops of the Pardonet Formation in the foothills of the Rocky Mountains, but with the construction of the W. A. C. Bennett Dam, new outcrop around the perimeter of an enlarged Williston Lake displayed continuous sections covering the entire formation. Starting in 1980, Brown Hill, the most important site for McLearn and the main reference sections for both Lower and Middle Norian substages, was visited by Tozer and the author and large collections of ammonoids representative of much of the Norian were made. At the same time, matrix from those collections and from intervening carbonate beds was sampled for conodonts:

BIOSTRATIGRAPHY OF THE L-M NORIAN BOUNDARY

In North America, the Norian Stage of the Upper Triassic has been subdivided into six ammonoid zones, and a total of 13 subzones (Tozer, 1994). Conodont faunas from the Pardonet Formation were intercalibrated with these zones by Orchard (1983, 1991c; Text-fig. 2). For ammonoids, the Lower Norian *Juvavites magnus* Zone is succeeded by the Middle Norian *Drepanites rutherfordi* Zone at several localities in the region (Text-fig. 1), and the boundary between them has been designated the Lower-Middle Norian Boundary (Tozer, 1984). In all cases, the strata containing Magnus Zone ammonoids yield conodont faunas dominated by *Anacyrogonodolella triangularis* Budurov, 1972, while the Rutherfordi Zone matrix contains common *Orchardella multidentata* (Mosher, 1970) (Orchard, 1983, fig. 8; note both species were formerly assigned to *Epigondolella* – see taxonomy). The conodont morphological change across the LMNB is pronounced, as expressed by the modern assignment of the boundary species to separate genera. The abruptness of this conodont faunal change encouraged the author to undertake a detailed examination of strata bounded by the LMNB ammonoid zones in order to better understand the faunal succession.

In Europe and Tethys as a whole, Lower-Middle Norian ammonoid successions are rare and often condensed and incomplete in Hallstatt facies and sedimentary breccia (Krystyn, 2008; Karádi, 2017; Rigo et al., 2018). The LMNB corresponds to the boundary between the Lucian and Alauian substages, that is the boundary between Lower Norian *Juvavites magnus* Zone and the Middle Norian *Cyrtopleurites bicrenatus* Zone, with corresponding conodont faunas characterized by, respectively, an association of *Anacyrogonodolella triangularis* and *Norigondolella hallstattensis* (Mosher, 1968) and, in the Middle Norian, by *Mockina medionorica* (Kozur & Weems, 2007, fig. 8). The latter species, which remains poorly known (Karádi, 2017), has been correlated with *Orchardella multidentata*, although both species may be endemic in their respective regions. *Norigondolella hallstattensis* also appears to be largely a Tethyan species (Orchard, 1991b, p. 15).

High latitude faunas often lack epigondolellins and consist of *Norigondolella* alone. This is the case in Kotel’nyi Island, Siberia, where Konstantinov et al. (2003) reported exclusive *Norigondolella* faunas, with Lower Norian *N. navicula* (Huckriede, 1958) succeeded by *N. steinbergensis* (Mosher, 1968) in the Middle and Upper Norian, although this succession has not been well documented. The discovery of *Cyrtopleurites* in Siberia demonstrates proximity to the LMNB, although no conodonts were recovered from that interval or immediately below it. This distribution was emphasized by Klets (2008), who stated that *Norigondolella* alone inhabited the high latitude basins, including the Shublik...
Formation in Alaska. This is supported by geochemical data that suggests that *Norigondolella* was stenothermal, preferring cooler, deeper waters (Trotter et al., 2015). In the Pardonet Formation, *Norigondolella* occurs abundantly at certain times, including in the basal Norian Kerri Zone, the Middle Norian Columbianus II Zone, and the Upper Norian Cordilleranus Zone; it is uncommon across the LMNB.

**BOUNDARY SUCCESSIONS**

The localities (Text-fig. 1) that have provided a detailed record of the LMNB conodont succession are described below.

**Pink Mountain**

This locality, the most inboard (northeastern) of the present sections in the Western Canada Sedimentary Basin, was sampled during the Trutch NatMap project (1998–2000).

Initially, samples were taken at 2–3 m intervals throughout the entire ~50 m of Pardonet Formation to establish a broad age range and broadly delineate, if possible, the conodont zones established earlier on Williston Lake (Orchard, 1983, 1991c). The *triangularis* Zone was identified at several horizons including one associated with a poorly preserved *Juvavites* ammonoid fauna of probable Magnus Zone age (Text-fig. 3A, B, sample 98/B21). No additional ammonoids were found in the 10 m of overlying Pardonet Formation. The next reconnaissance sample (sample 98/B22) contained a diverse conodont fauna typical of the *Orchardella multidentata* Zone. The LMNB was thereby constrained within ~2.5 m of intervening strata. Subsequently, ~5 m of strata above the *Juvavites* ammonoid level was re-sampled in more detail, which yielded 11 individual conodont collections (samples 00/B1-B11). This succession (Text-fig. 4) serves as a relatively

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**Table: Stages, Substages, Zones, Subzones**

<table>
<thead>
<tr>
<th>STAGE</th>
<th>SUBSTAGE</th>
<th>AMMONOID ZONES &amp; SUBZONES</th>
<th>CONODONT ZONES &amp; FAUNAS</th>
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<tr>
<td>RHAE</td>
<td>U</td>
<td><em>Gnomohalorites cordilleranus</em></td>
<td><em>bidentata</em></td>
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<tr>
<td>ALA</td>
<td>M</td>
<td><em>Mesohimavatites columbianus</em></td>
<td><em>serrulata</em></td>
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<td></td>
<td></td>
<td><em>Drepanites rutherfordi</em></td>
<td><em>posterata</em></td>
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<td></td>
<td></td>
<td><em>Juvavites magnus</em></td>
<td><em>longata</em></td>
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<td></td>
<td></td>
<td><em>Malayites dawsoni</em></td>
<td><em>spiculata</em></td>
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<tr>
<td></td>
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<td><em>Stikinoceras kerri</em></td>
<td><em>multidentata</em></td>
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<td><em>E. tozeri</em></td>
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<td><em>primitia</em></td>
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*Text-fig. 2. Ammonoid and conodont biochronology for the Norian of western Canada. The question mark between Lower (Lacian) and Middle (Alaunian) Norian zones marks an apparent faunal break that is filled here by the transformis Zone. Dashed horizontal lines in the right column delineate new informal subzonal boundaries. The suggested placement of the LMNB is the base of the transformis Zone.*
complete template for comparing collections from much thinner and perhaps less complete LMNB sections.

**Carbon Creek East**

A shoreline section on the south side of Williston Lake a short distance to the east of Carbon Creek exposes about 160 m of (ascending) Charlie Lake, Baldonnel, and Pardonet formations. The upper ~50 m consists of the Pardonet Formation, which has yielded a succession of Norian conodont faunas that are as young as the Middle Norian *Mockina postera* Zone (Orchard, 1991c, fig. 3). The upper 10 m of section at the western end of the outcrop has been most intensively sampled. Beds full of oyster shells, like those seen in profusion lower in the Pink Mt. section, provide a datum a few meters below beds containing ammonoid faunas indicative of the LMNB. About 7–8 m below the top of section, large ichthyosaurian bones are associated with *Juvavites magnus* ammonoids at the base of the bed sampled as 93/U3 (Text-fig. 3C). At the top of that bed the succession gives way to ~1 m of more recessive, thin-bedded calcareous argillites and siltstones with *Halobia* shells followed by a thick carbonate bed (Sample 93/U4) bearing Rutherfordi Zone ammonoids. The strata intervening between the ammonoid levels were subsequently sampled bed-by-bed (Figure 3C, samples 07/A through 07/L).

**McLay Spur–Childerhose Cove**

To the north of Carbon Creek, on the north shore of Williston Lake, the section between McLay Spur and Childerhose Cove extends from the Baldonnel Formation to Middle Norian strata of the Pardonet Formation. The upper ~50 m consists of the Pardonet Formation, which has yielded a succession of Norian conodont faunas that are as young as the Middle Norian *Mockina postera* Zone (Orchard, 1991c, fig. 3). The upper 10 m of section at the western end of the outcrop has been most intensively sampled. Beds full of oyster shells, like those seen in profusion lower in the Pink Mt. section, provide a datum a few meters below beds containing ammonoid faunas indicative of the LMNB. About 7–8 m below the top of section, large ichthyosaurian bones are associated with *Juvavites magnus* ammonoids at the base of the bed sampled as 93/U3 (Text-fig. 3C). At the top of that bed the succession gives way to ~1 m of more recessive, thin-bedded calcareous argillites and siltstones with *Halobia* shells followed by a thick carbonate bed (Sample 93/U4) bearing Rutherfordi Zone ammonoids. The strata intervening between the ammonoid levels were subsequently sampled bed-by-bed (Figure 3C, samples 07/A through 07/L).

**Brown Hill**

This locality, the most westerly (outboard) of the four, lies on the north shore of Williston Lake and is the approximate site of McLearn’s early work, and the first section visited after the flooding of the Peace River Valley. It is also the type locality for several ammonoid zones defined by Tozer (1994). The upper part of the Brown Hill section extends from base of the Carnian Baldonnel Formation through the Upper Norian *Monotis* beds of the Pardonet Formation. About 50 m of Pardonet Formation were exposed in 1980, when the top of the exposed beds were assigned to the *elongata* Zone (Orchard, 1991c, fig. 3). Overlying strata newly exposed in 1999 included *Eomonotis* and *Monotis*. Original collections were made of the Magnus Zone Subzone II fauna (sample 80/24), a possible Rutherfordi Zone fauna (sample 80/20) separated by ~2.25 m of halobiid bearing argillite, and then several additional Rutherfordi Zone collections (sample 80/15A) extending for ~7 m and including *Cyrtopleurites bicrenatus* near its upper range (sample BH10; Tozer, 1994). Resampling of the section in 1999 included ammonoids of Magnus Zone Subzone I (sample 99/2) 1 m below Magnus Zone Subzone II (99/3), and a small limestone concretion 0.6 m above the latter (sample 99/4).

**SYSTEMATIC PALEONTOLOGY**

All illustrated material is deposited in the National Type Collections of the Geological Survey of Canada and bear 6-digit type numbers prefixed with “GSC”. Curation catalogue numbers for the conodont collections from which they come are given in the Appendix.
Class CONODONTA Eichenberg, 1930
Order OZARKODINIDA Dzik, 1976
Superfamily GONDOLELLOIDEA Lindstrom, 1970
Family GONDOLELLIDEA Lindstrom, 1970
Subfamily EPIGONDOLELLINAE Orchard, 2005

Remarks.—Members of this subfamily have a history of changing nomenclature and taxonomic scope. They include Ancyrogondolella, Epigondolella, Mockina, and Orchardella. Amongst these, Epigondolella has been the most widely used and all Norian species were assigned to the genus by Orchard (1983, 1991c). Later, Orchard (2005) used Cypridodella rather than Epigondolella for one Middle Norian species based on the proposed association of its type species, C. confoexa, in the multielement apparatus of E. bidentata Mosher, 1968 (in sample Sb-F from Steinbergkogel, Austria, Mosher, 1968, p. 945), and the page priority of the former genus (Mosher, 1968). However, notwithstanding the fact that E. bidentata has subsequently been assigned to Mockina (Kozur, 1990a, b), and that E. multidentata (Cypridodella multidentata sensu Orchard, 2005) has been denoted the type species of Orchardella (Kozur, 2003), the correct nomenclature rests on multielement considerations that are not central to the present biostratigraphy analysis. Hence, I am setting aside the use of Cypridodella whilst the relationships of the pectiniform P₁ elements are resolved.

The type species of Epigondolella was designated Polygnathus abneptis Huckriede, 1958, a broad concept that was used initially to include all ornate Upper Carnian and Norian species. Orchard (1991c, p. 307; also see Karádi, 2017) described the uncertainty surrounding the identity of the holotype, which came from a fissure-fill in Hallstatt Limestone at Sommeraukogel, Austria. Although the holotype came from a sample identified as representing the Middle Norian Cyrtopleurites bicrenatus Zone, its precise stratigraphic origin is in doubt (see Introduction). Seeing no objective criteria for separating Lower and Middle Norian species of "Epigondolella abneptis"-like forms, all Norian taxa were retained in Epigondolella by Orchard (1991c), who regarded Ancyrogondolella Budurov—introduced for the species triangularis—as a junior synonym.

The classification proposed by Budurov & Sudar (1990) brought together the species multidentata, postera, and bidentata under Epigondolella, and the species triangularis as the sole representative of Ancyrogondolella. In so doing they narrowed the scope of Epigondolella to those species with a simple (non-bifid) basal field (or keel in the broad sense used here), contrasting with the bifurcated keel of Ancyrogondolella. However, at the same time Budurov & Sudar (1990) regarded abneptis as a species of Metapolygnathus, and therefore selected
a new type species for their revised concept of *Epigondolella*. They chose *Tardogondolella abneptis* postera Kozur & Mostler, 1971, an action that coincided with Kozur (1990b) selecting the same type species for his new genus, *Mockina*. Since “*E. abneptis*” is no longer regarded as an example of the largely late Carnian *Metapolygnathus* (see Orchard, 2014), the species still serves as type for *Epigondolella*. Revised concepts of both *Mockina* and *Epigondolella* are adopted for some largely Middle Norian single-keeled species in this paper.

The uncertainty about the identity and stratigraphic origin of the holotype of the type species of *Epigondolella* has resulted in varying usage of generic names. *Ancyrogondolella* was adopted for Lower Norian species by some (e.g., Budurov & Sudar, 1990; Hirsch, 1994), but others continued using *Epigondolella* (e.g., Kozur, 2003, Mazza et al., 2012), as did Orchard (2014), who regarded the Lower Norian *Epigondolella quadrata* Orchard, 1991c and its associates as the first examples of the genus. In this paper I assign the latter species to *Ancyrogondolella*, whilst restricting the use of *Epigondolella sensu stricto* to single lobed Norian species.

Meanwhile, use of *Mockina* Kozur became widely accepted for Middle and Upper Norian species although several of the new species described by Orchard (1991c) did not fit the diagnosis of that genus. Hence, *Orchardella* was introduced by Kozur (2003), with *Epigondolella multidentata* Mosher as type species. *Orchardella* has not been widely used, largely because *O. multidentata* is probably a North American endemic. In this work, I retain *Orchardella* and show it developed along a separate line from *Epigondolella* and *Mockina* near the base of the Middle Norian.

Kozur (2003) and Moix et al. (2007) have characterized true *Epigondolella abneptis* as a Middle Norian species with large blade denticles and have illustrated examples. Due to damage of the holotype, stabilization of the specific identity of *E. abneptis* may require a neotype to be selected from amongst the Middle Norian Tethyan faunas. In this work, I regard the more ornate *E. tozeri* Orchard, 1991c and *E. spiculata* Orchard, 1991c as additional examples of true *Epigondolella*, characterized by spinose platform elements that lack a strong posterior carina, and generally having a simple basal field/keel that is pointed, truncated, or sinuous with a remnant secondary keel, but not including elements with two secondary keels extending from the pit.

*Ancyrogondolella* Budurov, 1972


Remarks.—This genus includes most of the Lower Norian species that were previously assigned to *Epigondolella* by Orchard (1991c) and Orchard (2014), plus several newly introduced here that share the essential feature of a bifid basal field or keel. This bifurcation generally arises close to the subcentral or anteriorly shifted pit, with the secondary keels being widely divergent in older representatives and much less so in younger species. The carina may also bifurcate close to the cusp, or far to its posterior in several younger species introduced here. The genus is regarded as ancestral to *Epigondolella*, *Mockina*, and *Orchardella* (Text-Fig. 5), all of which differ in their lack of a secondary keel. This progressive loss is observed in species assigned to *Ancyrogondolella* *praespiculata* n. sp. (Pl. 3, figs. 1–6), and some *A. transitia* n. sp. (Pl. 2, figs. 8–10) in which the outer secondary keel is markedly reduced in length: these taxa are transitional to, respectively, *Epigondolella* and *Orchardella* (Text-fig. 5, transition zone). Different species of *Mockina* (?) appear to arise through the retention of juvenile morphology (neoteny) of *Ancyrogondolella* (Text-fig. 5i, ii), and by complete reduction of the secondary keel and lobe, as in *Mockina* *transitia* (Orchard, 1991c) (Text-fig. 5.4).

*Ancyrogondolella diakowi* n. sp.

Plate 2, Figs. 1–7, 14, 15

Derivation of name.—Named for Larry Diakow (British Columbia Geological Survey), whose collection of a sample yielded this species and precipitated the study.

Holotype.—GSC 131626, Plate 2, Figs. 1–3.

Type stratum, locality.—Sample 00/B2, Pardonet Formation, Pink Mt., British Columbia.

Description.—The P₁ platform element is relatively long with an anterior half that has subparallel margins and a posterior half that is laterally expanded with acute posterolateral corners that mark the broadest part of the element. The anterior margins bear 3–4 high and upright, sharp to transverse ridge-like denticles; to the posterior, the margins bear smaller denticles, and others on the platform are aligned as one or two secondary carinae. The posterior margin often has a medial indentation. The blade is about 1/3 element length and its denticle tips define a convex crest that descends onto the platform as a row of low, discrete nodes that reduce in size to the sub-central cusp; 2–3 larger carinal nodes occur posterior of the cusp and end about the center of the expanded posterior platform. The lower side bears a small pit located a little anterior of platform midlength; it lies within a broad keel that bifurcates posterior of the pit, beyond which long secondary keels extend close to the postero-lateral corners of the platform.
Text-fig. 5. Suggested phylogeny of conodonts across the Lower-Middle Norian boundary and partition of genera. The origin of most of the following specimens are given in the plate descriptions, others are shown in parentheses. i, ii, Juvenile Ancyrogondolella (i, see Orchard, 1983, fig. 15f; ii, from sample 81/243C, McClay Spur). 1, 2, Ancyrogondolella triangularis. 3, A. aff. A. triangularis. 4, Mockina? transitia. 5, M.? spinosa. 6–8, M. ex gr. M. matthewi. 9, M. postera (see Orchard, 1983, fig. 15R). 10, Ancyrogondolella uniformis. 11, A. equalis. 12, A. diakowi. 13–15, A. transformis. 16, Orchardella? n. sp. A. 17, Orchardella multidentata. 18, A. inequalis. 19, A.? praespiculata. 20, Epigondolella tozeri. 21, E. spiculata. Specimens bounded by dashed lines are in the morphological transition zone from Ancyrogondolella with a bifid keel to other genera with a single keel; arrows indicate evolutionary trajectories. See text for details.
Comparisons.—Compared with Ancyrogondolella triangularis, this new species has a longer carina that does not stop at a large central cusp, but continues for ~3 nodes beyond a small cusp. The expanded anterior platform of this species is also relatively long with 3–4 rather than 2–3 marginal nodes, and its postero-lateral expansion is not as pronounced. The secondary carinae and posterior nodes are less strongly differentiated in A. diakowi. The posterior platform expansion is lacking in A. equalis n. sp.

Ancyrogondolella equalis n. sp.
Plate 1, figs. 15–19

Derivation of name.—Refers to the constant width of the rectangular platform.

Holotype.—GSC 131624, Plate 1, Figs. 15-17.

Type stratum, locality.—Sample 00/B2, Pardonet Formation, Pink Mt., British Columbia.

Diagnosis.—The P₁ platform elements have a symmetrical rectangular platform with a length: breadth ratio of 2:1, and sharp denticles on all margins that are highest and upright near the anterior and decline in height to the posterior. Each postero-lateral corner has a sharp, obliquely orientated denticle, and others occur on the posterior margin. The blade denticles form a high convex crest, while the cusp is the anteriormost and smallest of four carinal nodes. Secondary carina may occur in large specimens. The pit lies beneath the anterior platform within a wide keel that is clearly bifurcated into two secondary keels posterior of the pit.

Comparisons.—The older Ancyrogondolella uniformis (Orchard, 1991c) has a shorter and broader platform, with a more central pit and broader keel. The present species lacks the postero-lateral platform expansion of A. diakowi, whereas the otherwise similar and younger Epigondolella tozeri has a non-bifid keel.

Ancyrogondolella inequalis n. sp.
Plate 3, Figs. 7–15, 19–24

Derivation of name.—Refers to the unequal development of the posterior inner and outer platform and secondary keels.

Holotype.—GSC 131637, Plate 3, figs. 10-12.

Type stratum, locality.—Sample 00/B3, Pardonet Formation, Pink Mt., British Columbia.

Diagnosis.—The P₁ platform elements have an asymmetric subrectangular platform with a breadth to length ratio of ~1:2.0–2.5 and a variably indented posterior margin with unequally developed postero-lateral corners. The upper surface bears sharp denticles on all margins, the 2–3 anterior of which are the largest; isolated nodes may occur on the posterior platform and may align as a secondary carina on the inner and/or outer side. On the lower surface, the keel bifurcates a short distance posterior of the pit and secondary keels of unequal length are directed toward the postero-lateral corners.

Comparisons.—These elements are quite variable in terms of posterior morphology and length to breadth ratio. Some (Pl. 3, figs. 19–21) bear a strong resemblance to Ancyrogondolella diakowi, but differ in having asymmetric development of both the postero-lateral platform and secondary keels. Others (Pl. 3, figs. 7–9) resemble Epigondolella spiculata in platform outline, but unlike the latter they retain a clearly bifid keel. In upper view, the asymmetric platform of Mockina transformis (Text-fig. 5.4) has a more pronounced posterior ‘tongue’ with more upright or ridge-like denticles; significantly, it also has a non-bifid keel.

Remarks.—This species is the least common Ancyrogondolella species in the transformis Zone, but it illustrates transition to Middle Norian Epigondolella (Text-fig. 5). Two variants of the species are recognized, each of which can also be visualized as leading to A.? praespiculata through the modification of the posterior platform and reduction of the outer secondary keel.

Morphotype A (Pl. 3, figs. 19–24): the posteriormost platform extends beyond that of the extended outer margin. See also Ancyrogondolella aff. A. triangularis.

Morphotype B (Pl. 3, figs. 7–15): two equally extended nodes on the posterior margin define an indented posterior margin; one node may be aligned with the carina, as in the holotype.

Ancyrogondolella transformis n. sp.
Plate 2, Figs. 8–13, 19–26

Derivation of name.—Latin, transformare, to change shape. Refers to the transformational morphology of this ancestor of Orchardella.

Holotype.—GSC 131633, Plate 2, Figs. 21–23.
Type stratum, locality.—Sample 00/B2, Pardonet Formation, Pink Mt., British Columbia.

*Description.*—The $P_1$ element has a long, narrow platform with parallel lateral margins for much of its length and often with a posteriormost part that is expanded laterally. The anterior one-third of the platform has 2–4 marginal upright denticles, and the postero-lateral corners of the platform often have an obliquely directed denticle, and sometimes a single node occurs in the center of the posterior margin. The lateral margins of the central platform may be unornamented or bear small, irregularly developed nodes. The blade is about 1/3 element length and its denticles define a convex crest that descends onto the platform as a row of low discrete nodes of which the cusp is the smallest. Posterior of the cusp, 4–5 carinal nodes increase in size and may be more elevated close to the posterior margin, in front of which a narrow platform brim occurs: the carina is not continuous to the platform tip. On the underside, a weakly to strongly bifid keel occurs, with secondary keels equal, or markedly unequal.

*Comparisons.*—The posterior platform expansion is similar to that seen in other species of *Ancyrogondolella* but is much less pronounced, and the posterior platform ornament is much reduced. The narrower, less-ornamented platform signals an affinity with *Orchardella multidentata* but that species has a conspicuously high posterior carina and a single, rather than bifid, keel. *Orchardella?* n. sp. A is apparently transitional between the two species in lacking the high carina but having a single keel (Text-fig. 5).

*Remarks.*—The species embraces variation in keel bifurcation, posterior platform ornament, and platform symmetry. Nevertheless, it appears as a morphological and a stratigraphic link between *Ancyrogondolella* and *Orchardella* with the latter genus derived through further narrowing of the posterior platform, strengthening of the posterior carina, and reduction to a single lobed keel. Variation in the latter is illustrated by specimens that show a progressive loss of the secondary keel (Pl. 2, Figs. 21 > 12 > 10), and eventually the complete loss in *Orchardella?* n. sp. A (Pl. 2, Fig. 16).

A single specimen from the Buda Hills, Hungary, assigned to *Mockina* aff. *M. matthewi* (Orchard, 1991c) (Karádi, 2017, pl. 2, fig. 3) differs from the *Mockina* species in having a bifid keel similar to that of *Ancyrogondolella transformis*. In common with Canadian elements within the transition zone (Text-fig. 5), this specimen could be the forebear of single-keeled species, and both its stratigraphic position and faunal associates support an age broadly contemporaneous with the transformis Zone.

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**Ancyrogondolella triangularis** Budurov, 1972
Plate 1, figs. 4–12

*Epigondolella abneptis* (Huckriede, 1958). *Sweet et al.*, 1971, pl. 1, fig. 27; Cañiero & De Capoa Bonardi, 1981, p. 58, fig. 9 (only).


*Epigondolella abneptis spatulatus* (Hayashi, 1968). *Sudar*, 1981, pl. VIII, fig. 1 (only); *Mao & Tian*, 1987, pl. II, fig. 1 (only).

*Epigondolella triangularis* (Budurov). *Koike*, 1981, pl. 2, fig. 39; *Orchard*, 1991a, pl. 4, fig. 12; *Karádi*, 2017, pl. 1, figs. 4, 8.

*Epigondolella triangularis triangularis* (Budurov). *Orchard*, 1991c: p. 315, pl. 3, figs. 7–9; *Orchard*, 2006, pl. 8, figs. 4, 5.

*Description.*—The $P_1$ element of this *Ancyrogondolella* species is relatively short and broad with a platform strongly expanded laterally or postero-laterally in its posterior half into a sub-triangular outline. One postero-lateral lobe may be longer than the other. The margins are strongly denticulated throughout with upright nodes and denticles that often extend as ridges onto the platform. The often large, but variable cusp and underlying pit lie close to the center of the platform and secondary posterior carinae commonly diverge from that point. Secondary keels extend close to each postero-lateral corner.

*Remarks.*—This species was broadly interpreted by *Orchard* (1983) and more narrowly by *Orchard* (1991c). Many of the specimens assigned to this species in the literature lack the distinctive secondary carina that characterize both the type material of Budurov (1972) and the mature specimens illustrated here from Carbon Creek east. A typical specimen, also from the Magnus Zone of Canada, was illustrated by *Sweet et al.* (1971). It may be useful in the future to restrict the species to such specimens.

**Ancyrogondolella aff. A. triangularis** Budurov, 1972
Plate 1, Figs. 13, 14.

*Epigondolella transitia* *Orchard*, 1991c. *Orchard*, 2006, pl. 8, fig. 8.

*Remarks.*—These elements differ from *Ancyrogondolella triangularis* in the strongly asymmetrical development of the posterior platform whereby the inner posterior lobe is directed posteriorly and the inner platform margin is relatively straight. The inner secondary carina is more developed. This asymmetry mirrors that seen in *A. inequalis* Morphotype A, but that species is less robust, has fewer nodes, and has obliquely
orientated posterior nodes that give the elements a more irregular outline. In common with the latter, Ancyrogondolella aff. *A. triangularis* has a bifid keel in which respect it differs from its probable descendant Mockina* transitia* (see below). The element from the Yukon Territory figured in upper view only by Orchard (2006) has a bifid keel and is therefore not an example of *M.? transitia*.

**Ancyrogondolella uniformis** (Orchard, 1991c)

Plate 1, fig. 1–3.


*Epigondolella triangularis uniformis* Orchard, 1991c: p. 315, pl. 3, figs. 1–3; Orchard, 2006, pl. 8, fig. 6.

*Epigondolella triangularis* (Budurov, 1972). Orchard, 2005, fig. 3.

*Epigondolella uniformis* Orchard. Karádi et al., 2013, pl. 3, fig. 9–10.

Remarks.—The *P₁* element of this species differs from *Ancyrogondolella triangularis* in its relatively unexpanded posterior platform and consequent subrectangular outline. The slightly rounded postero-lateral corners of the holotype figured by Orchard (1991c) are regarded as intraspecific variation. The conservative morphology expressed by *A. uniformis* may be typical of early growth stages of contemporaneous *Ancyrogondolella* species. Both the platform and carina of *A. equalis* are longer than in *A. uniformis*.

**Ancyrogondolella praespiculata** n. sp.

Plate 3, figs. 1–6

Mockina spiculata (Orchard, 1991c); Karádi, 2017, pl. 2, figs. 7 (only).

Derivation of name.—Alluding to the similarity and earlier stratigraphic appearance compared with *Epigondolella spiculata* Orchard, 1991c.

Holotype.—GSC 131635, Plate 3, figs. 4–6.

Type stratum, locality.—Sample 00/B5, Pardonet Formation, Pink Mt., British Columbia.

Diagnosis.—The *P₁* elements have a relatively broad, plano-convex platform outline, several high anterior denticles, generally smaller posterior marginal denticles, and a discontinuous carina aligned with a node on the posterior margin. On the lower surface, the pit occupies a mediad to anterior position within a broad basal keel that tapers and terminates beneath the posterior carina. A short, weakly developed secondary keel projects toward the convex outer margin from a position posterior of the pit, which produces a forked posterior margin to the keel.

Comparisons.—The *P₁* elements have a similar, asymmetrical platform shape to *Epigondolella spiculata* but they are broader, more ornate posteriorly, and retain a short secondary keel that is lost in typical *E. spiculata* (Pl. 4, Figs. 11, 14), although the holotype (re-illustrated on Pl. 3, Fig. 16) shows the remnant of that feature. *Ancyrogondolella inequalis* differs from *A.? praespiculata* by having two well-developed secondary keels.

Remarks.—This species appears to be a further step in the transformation of bifid *Ancyrogondolella inequalis* to the single lobed keel of *Epigondolella spiculata* (Text-fig. 5. 18 > 19 > 21). The species is included in the genus with question because it has much less developed secondary keels than is typical of the genus. Karádi (2017) illustrated a very similar specimen from the Buda Hills, Hungary. The range of *A.? praespiculata* is uncertain (Text-fig. 4). It is not common in the present collections, but is found within the upper *transitus* and *multidentata* zones. It may range higher but the *spiculata* Zone collections require further study.

**Epigondolella** Mosher, 1968

Type species.—Polygnathus abneptis Huckriede, 1958.

Description.—The *P₁* platforms are commonly asymmetric (-plano-convex) and less commonly symmetric (-subrectangular) in outline with a length to breadth ratio of ~2:1. The small anterior cusp is followed posteriorly by larger carinal denticles that form a discontinuous carina that may be aligned with or fused to a posterior marginal denticle. The anterior platform margins bear 2–4 high, sharp and vertical denticles, and the posterior platform margins are variably ornamented with sharp, obliquely orientated denticles. The small cusp lies in the anterior carina and carinal nodes increase in size to the posterior, and similarly rise progressively anteriorly and pass into the blade denticles that form a convex crest with the anteriormost 2–3 denticles being lower. The lower side bears a small pit beneath the anterior half of the platform and a wide keel that may be a single pointed lobe, posteriorly squared-off, or obliquely truncated.

Comparisons.—Some *Ancyrogondolella* species may have similar platform shapes, but they differ from *Epigondolella* in possessing a keel that bifurcates close to the pit. In *Epigondolella*, a bulge may occur on the posterior outer margin of the keel that is regarded as a vestige of the former secondary keel. In contrast with *Epigondolella*, *Orchardella* has a high and fused posterior carina and a comparatively long
and narrow platform. *Mockina* has a relatively broad, lobate platform often with rounded margins and a stronger axial carina.

**Remarks.**—The use of *Epigondolella* as a genus has a variable history. It originally embraced all ornate Upper Carnian and Norian species (see also Moix et al., 2007). Many Carnian representatives are now assigned to *Carnepigondolella*, although several Tethyan species of that age have been recently assigned to the *Epigondolella* (e.g., Mazza et al., 2012). The oldest Norian representative described by Mosher (1970) was *Epigondolella primitia*, which Orchard (1991a, c) later reassigned to *Metapolygnathus*, and most recently to *Primatella* (Orchard, 2013). The oldest species of *Epigondolella* recognized in North America by Orchard (2014) was *E. quadrata* and several associates that appear in the Lower Norian: those taxa are here assigned to *Ancyrogondolella*.

*Epigondolella abneptis* Huckriede, 1958


*Epigondolella abneptis* (Huckriede). Moix et al., 2007: p. 291, pl. 1, figs. 1, 2.

**Remarks.**—As discussed above, both *Epigondolella abneptis* and the genus for which it serves as type species, have been variously interpreted and Huckriede’s holotype no longer serves to fully characterize the species (Karádi, 2017). Moix et al. (2007) illustrated Turkish elements from comparable stratigraphic levels to the holotype, which is from the upper Alaunian. They noted that the unornamented posterior platform and the large denticles of the free blade were diagnostic features shared by the Austrian holotype, although these features are regarded as diagnostic for the species rather than the genus. Moix et al. (2007) provided no description of lower surface characteristics that might serve to distinguish *E. abneptis* from its Lower Norian homeomorph *Ancyrogondolella quadrata*, but it is here proposed that a non-bifid keel is diagnostic of *Epigondolella sensu stricto*.

*Epigondolella spiculata* Orchard, 1991c

Plate 4, figs. 11–16

*Epigondolella multidentata* Mosher, 1970; Mao & Tian, 1987, pl. 1, figs. 16, 20 (only).

*Epigondolella n.* sp. C. Orchard. Orchard, 1991a, pl. 4, figs. 18, 20.

*Epigondolella spiculata* Orchard, 1991c: pp. 312, 313, pl. 3, figs. 10, 14, 15.


*Epigondolella tozeri* Orchard, 1991c

Plate 4, figs. 10, 17–22.

*Epigondolella tozeri* Orchard, 1991c: p. 313, pl. 5, figs. 6–8 (only).

Non *E. tozeri* Orchard. Ji et al., 2003, pl. 1, figs. 12–16.
**Diagnosis (revised).—**Long, subrectangular P₁ platform elements of *Epigondolella* in which the posterior platform is broadly truncated and has sharp denticles located on each postero-lateral corner and another on the posterior margin commonly aligned with the carina. Additional denticles may be present on the lateral margins posterior of the large anterior denticles. The small anterior cusp is followed by 2–4 relatively discrete and larger carinal nodes. The anterior pit is located within a keel that is posteriorly pointed or truncated.

**Comparisons.**—These elements most closely resemble *Ancyrogondolella equalis* in platform shape, but differ from that species in lacking a bifid keel. *Epigondolella spiculata* is similar but has a strongly asymmetric platform. *Mockina* spinosa n. sp. has a pointed, more ornate platform and stronger carina.

**Remarks.**—Orchard (1991c) established this species for strongly ornate elements that were both pointed or truncated, as in the large holotype from the Columbianus Zone in the Middle Norian of Pardonet Hill. In those collections, assigned to the conodont *elongata* Zone, elements regarded as small growth stages of this species have pointed platforms rather than truncated elements like the holotype (Pl. 4, Fig.10). In the present collections there are relatively small truncated elements and relatively large pointed elements, all of which have strong nodes on all margins. The pointed elements are here separated as *Mockina* spinosa.

**Mockina** Kozur, 1990b


**Type species.**—*Tardogondolella abneptis posteria* Kozur & Mostler, 1971, from the Middle Norian of Sommeraukogel, Austria.

**Description.**—*Mockina* species are characterized by relatively broad, biconvex to lobate platform outlines. They commonly bear 1–3 anterior denticles on each anterior margin, and typically have an unornamented posterior platform and a broadly to narrowly rounded posterior margin. The small anterior cusp is the smallest of the carinal nodes that enlarge to the posterior where they may be fused in front of a variably wide, usually narrow platform brim. The small anterior pit sits in a keel that is posteriorly pointed, lobate, or truncated.

**Remarks.** The original diagnosis provided by Kozur focussed on the type species *Mockina posteria* (Kozur & Mostler, 1971) and small derivatives like *M. zappi* (Kozur, 1973), but this was prior to the introduction of *M. matthewi* (Orchard, 1991c), which is here regarded as ancestral to the former species. New, posteriorly ornate species introduced here are referred with question to the genus.

The first representatives of *Mockina* appear close to the LMNB and many are referred to *M. ex gr. M. matthewi* in order to express the observed variation in these early representatives. Early growth stages of these *Mockina* may have fewer anterior nodes (1–2) on each anterior margin and thus mimic both younger species of the genus and early growth stages of *Ancyrogondolella* (Text-fig. 5i, ii): they are thought to have developed through retention of this juvenile morphology. An alternate trajectory is illustrated by mature specimens showing progressive loss of the secondary keel that leads from *A. aff. A. triangularis* to *M.? transitia* (Orchard, 1991c), and then to *M.? spinosa* (Text-fig. 5. 3 > 4 > 5). Whereas the linguiform *M.? transitia* retains one posterior lobe and carina, *M.? spinosa* has a straight axis and a more developed posterior carina than in many *Mockina*; both differ from other species of *Mockina* in their strong posterior margin ornament.

*Mockina* differs from *Ancyrogondolella* in lacking a bifid keel. Compared with other genera with a single keel, platform shapes in *Epigondolella* species are subquadrate or asymmetric rather than rounded or lobate, and they often have a poorly defined posterior carina. *Orchardella* differs in its relatively long and narrow platform and prominent posterior carina.

**Mockina ex gr. M. matthewi** (Orchard, 1991c)
Plate 3, Figs. 17, 18, 25–33.
or occasionally wide posterior platform brim is developed, or the posterior margin may have a small node aligned with
the carina. In profile, the lower edge of the blade is straight and then steps up to the basal pit. The pit lies beneath the
anterior platform a little in front of its midlength. A broad, flat single keel surrounds the pit and occupies \( \frac{1}{3} \) to \( \frac{2}{3} \) of the
lower surface, tapering progressively under the blade, and terminating beneath the posterior platform with a rounded
to straight outline.

Remarks.—A few elements have a slightly sinuous, plano-
convex posterior outline similar to that seen in the typical
elements of the probable successor species *Mockina postera*. The
latter is smaller and is characterised by a single anterior
denticle on the outer side and two on the inner side (compare
Plate 3, fig. 32 and Orchard, 1991c, pl. 4, fig. 16). Variation
in *M. ex gr. M. matthewi* is also seen in size and extent of
carinal nodes, and presence of small posterior nodes. The
species differs from *Mockina? spinosa* in lacking the strong
marginal ornament on the posterior platform and longer
carina. Specimens from Hungary (Karádi, 2017) have a
 carina that is both lower and shorter, with a broad posterior
platform brim, as in one specimen from Canada (Pl. 3, Fig.
17). In this regard, they appear similar to the poorly known
*M. medionorica* (see Karádi, 2017).

The holotype of this present species comes from a
Rutherford Zone of Childerhose Cove/McClay Spur (sample
82/307C). Examples have also been found in the Yukon
Territory (Orchard, 2006), and Hirsch & Ishida (2002)
figured a similar specimen from the accreted Izanami
Plateau preserved in southwest Japan. These Japanese
collections from the chert-pelagic limestone successions represent an
outcrops of the Izanami Plateau
preserved in southwest Japan. These Japanese
collections from the chert-pelagic limestone successions represent an
intermediate paleogeographic affinity compared with North
American and Tethyan faunas. The same applies to the area
from which Katvala & Stanley (2008) reported a specimen from the Middle Norian of Gil Harbor, southern Keku Islets
of SE Alaska, part of the allochthonous Insular Terrane.

A specimen of *Mockina aff. M. matthewi* from the Buda
Hills, Hungary illustrated by Karádi (2017) is excluded from
this group as it has a bifid keel (see *Ancyrogyndolella
transformis*).

**Mockina? spinosa** n. sp.
Plate 4, Figs. 1–9

*Epigondolella abnegiti* (Huckriede, 1958); Mosher, 1970, pl.
110, figs. 14, 18.

*Epigondolella postera* (Kozur & Mostler, 1971); Wang & Wang,
1990, pl. 1, fig. 10; pl. 2, fig. 7 (only).

*Epigondolella tozeri* Orchard, 1991c: p. 313, pl. 5, figs. 1–3
(only).

**Mockina? transitia** (Orchard, 1991c)


*Epigondolella transitia* Orchard; Karádi, 2017, pl. 1, figs. 1, 7.
Remarks.—This species, first described from the upper Magnus Zone at the Childerhose Cove-McClay Spur locality of this report (sample 81/243C), is characterized by a laterally deflected posterior platform and carina, and a non-bifid keel in which the position of the reduced secondary keel is represented by a bump on its outer edge. As noted by Orchard (1991c), the asymmetric species is morphologically transitional between the broad, bi-lobed Ancyrgondolella triangularis with bifid keel and the narrower Middle Norian forms with a straight carinal axis and unidivided keel, as in Mockina spinosa. Each of these species has relatively upright denticles on the straight margins of the posterior platform, which contrasts with the irregular outlines of similar asymmetric platforms with obliquely directed marginal nodes characteristic of Epigondolella and their foreruns A. inaequalis and A.? praepecticulata.

Two specimens from the Buda Hills in Hungary assigned to this species (Karádi, 2017) differ from the holotype in having a much broader, less extended posterior platform lobe, as well as a suggestion of keel bifurcation. A third Hungarian specimen from the Côvár Borehole (Karádi et al., 2013, pl. 3, fig. 11) may be an example of this species but it is illustrated only in upper view.

Orchardella Kozur, 2003

Orchardella Kozur, 2003: p. 70.

Type species.—Epigondolella multidentata Mosher, 1970, from the Middle Norian Rutherfordi Zone near Crying Girl Prairie Creek, northeast British Columbia.

Description.—P1 elements of Orchardella have a long narrow platform that generally tapers, sometimes sinuously, to a point. Ornate anterior margins typically consist of 3–5 denticles on each side, and posterior margins are unornamented or may bear small isolated nodes. The anterior cusp is small and is followed posteriorly by 5–6 increasingly higher, fused carinal denticles that produce a characteristic prominent posterior carina that extends to or beyond the platform. An anterior pit lies within a single keel that is narrowly rounded posteriorly.

Remarks.—The long and tapered platform of the type species of Orchardella, O. multidentata, with its high posterior carina contrasts with the broad, more rounded platform of typical Mockina with carina nodes that generally stop in front of the platform margin. Orchardella has a much narrower platform, lacks common posterior denticles, and has a much stronger carina than Epigondolella.

Kozur (2003) regarded some North American ‘Epigondolella’ species introduced by Orchard (1991c) as intermediate between Orchardella and Mockina, but he assigned E. elongata Orchard, 1991c, E. mosheri (Kozur & Mostler, 1971), and E. tozeri to Orchardella. In this paper, I assign the holotype of E. tozeri to Epigondolella, but its paratypes to Mockina spinosa (q.v.), whereas the phylogeny of the younger species is under review. Kozur (2003) also compared an Upper Carnian species to Orchardella, but these have now been named as Acuminatella Orchard, 2013 (see also Orchard, 2014). The anterior denticles of these homeomorphs differ, with those of Orchardella being far higher.

Orchardella multidentata is thought to be a North American endemic and most illustrations of specimens identified as the species outside North America are judged to be either erroneous, or at least ambiguous. However, the species O. elongata may occur outside North America, and certainly the Rhaetian O. mosheri does.

Orchardella multidentata (Mosher, 1970)
Plate 4, Figs. 23–31.

Non Epigondolella multidentata Mosher. Budurov, 1977: pp. 44, 45, pl. II, figs. 1, 2; Tian, 1982, Pl. 4, figs. 10a–c; Mao & Tian, 1987, pl. 1, figs. 16–20; Buryi, 1996, pl. 1, figs. 17, 18.
\( ? \)Epigondolella multidentata Mosher. Wang & Dong, 1985, pl. 1, figs. 9, 16 (only).
Epigondolella multidentata Mosher. Orchard, 1991c: p. 310, pl. 4, figs. 1–3, 7; Orchard, 2006, pl. 8, figs. 14, 15.
Cypridodella multidentata (Mosher). Orchard, 2005, fig. 4.

Diagnosis.—See Orchard, 1991c.

Remarks.—Although Mosher (1973) did not mention it, Orchard (1991c) emphasized the high posterior carina as distinctive for this species, which is very evident in the holotype. Mosher (1970, pl. 110, fig. 26) illustrated one specimen that had a lower carina, although it is still well developed. Some elevation of the posterior carinal nodes is seen in contemporaneous Mockina species although it is not as conspicuous and nor does it generally reach the posterior platform margin. There are at least two (often 3–5), pointed anterior nodes on each margin in Orchardella multidentata compared with a single denticle on one margin of O. elongata. Smaller elements of the present species may resemble O. elongata in this regard and rare large specimens appear transitional (Pl. 4, figs. 29–31).
Orchardella multidentata may be endemic to North America (see Orchard, 1991a, p. 180). Outside British Columbia and Yukon Territory (Orchard, 2006), Meek (1984) illustrated one specimen from western Nevada but it is not typical. The same is true of the specimens illustrated from Haida Gwaii in allochthonous Wrangellia (Orchard, 1991a), and as Epigondolella cf. multidentata by Krystyn (1973, taf. 1, figs. 7) from Sommeraukogel, Austria. One or two specimens illustrated by Wang & Dong (1985) from western Yunnan, China may be examples of this species, but those from Tibet (Tian, 1982; Mao & Tian, 1987) are not. Other records lack convincing documentation. For example, in their review of Triassic stratigraphy in Japan, Nakazawa et al. (1994) showed a range for O. multidentata and a zone of that name, and Hirsch and Ishida (2002) included O. multidentata in a list of conodonts typical of the Middle Norian Tethyan association based on a report from the Kamura section in Kyushu, Japan (but see Zhang et al., 2017). One specimen illustrated from the Mino-Tamba Belt of southwest Japan by Isozaki & Matsuda (1982) does have a high posterior carina, but it is only shown in one view. Similarly, in a broader review of Triassic conodont distribution, Klets (2008, table 7) showed E. multidentata as occurring in Primor’e region of Russia, SW USA, and Japan. However, none of these records are yet confirmed.

**Orchardella?** n. sp. A Plate 2, figs. 16–18.

**Remarks.**—The long narrow P₁ element has overall dimensions typical of both Ancyrogondolella transformis with its bifid keel, and Orchardella with its single keel. It has a similar arrangement of 2–3 prominent anterior denticles, 5 posterior carinal nodes, a small anterior cusp, and anterior pit. It differs from O. multidentata in having a shorter and lower carina that does not reach the posterior platform margin. The squared off posterior margin and laterally extended posterolateral corners resemble A. transformis elements, from which derivation through loss of a secondary keel is envisaged.

**CONODONT SUCCESSION ACROSS THE LOWER–MIDDLE NORIAN BOUNDARY**

The conodont succession across the LMNB at Pink Mountain comprises six faunas in close succession through ~5 m of Pardonet Formation (Text-figs. 4, 6). These span the interval from the upper part of the triangularis Zone, through the multidentata Zone, and into the lower part of the spiculata Zone of Orchard (1991c). A new transformis Zone now intervenes above the triangularis Zone, and tentative subdivision of the lower three zones is presented based on the composite record of the four sections, correlations between which are shown in Text-fig. 6.

**Ancyrogondolella triangularis Zone**

Near identical faunas indicative of the triangularis Zone were recovered from Pink Mountain (Text-fig. 6, samples 98/20, 21), Carbon Creek east (samples 93/U1, U2), McLay Spur (samples 81/243C, 82/1, 01/1), and Brown Hill (samples 99/2, 3). They are composed of abundant examples of the name giver accompanied by Ancyrogondolella aff. A. triangularis and A. uniformis, a population illustrated by Orchard (1983, fig. 6). Rare specimens of Mockina? spinosa and M.? transitia appear at the top of Magnus Subzone II at McLay Spur, and represent the first appearance of adult Mockina-like forms with reduced non-bifid keels, a link to descendants (Orchard, 1983, pp. 182, 191). Unlike the adult rectangular or triangular platform elements of A. triangularis and its associates, early growth stages in this fauna (e.g., Orchard, 1983, fig. 6U, T; 1991c, pl. 3, figs. 4–6) have a single keel, bear fewer nodes, and have a longer carina that reaches to, or close to, the pointed to rounded posterior platform margin. These early neotenic features are retained in the Mockina descendants.

The Ancyrogondolella triangularis conodont fauna—recognized to occur with ammonoids of the Malayites dawsoni Zone through the top of the succeeding Juuvaites magnus Zone by Orchard (1983, 1991c; Text-fig. 2)—is known from many localities in British Columbia. This zone was formerly identified on the basis of a variety of posteriorly ornate elements that differed in other respects, and subdivision of the interval is possible. In this work, the scope of the zone is revised to correspond to the range of Ancyrogondolella triangularis sensu stricto, which is within the Magnus Zone. The additional occurrence of Mockina? spinosa and M.? transitia identify an uppermost part of the zone (Text-fig. 4).

According to both Katvala & Stanley (2008, tbl. 3) and Karádi (2017), Ancyrogondolella triangularis ranges into the Middle Norian where it co-occurs with Epigondolella spiculata. However, the specimens of the latter species illustrated by the first authors do not show the lower surface and cannot be confirmed, and nor can this association be verified based on the illustrated specimens from Hungary (Karádi, 2017; see also E. spiculata). Ancyrogondolella triangularis s. s. does not occur in Middle Norian strata of the Pardonet Formation.

**Ancyrogondolella transformis Zone**

The triangularis Zone fauna is succeeded by the Ancyrogondolella transformis fauna at each of the four localities (Text-fig. 6), but it is best illustrated at Pink Mountain (samples 00/B2, B3) and Brown Hill (sample 99/4). The faunal contrast between zones is less abrupt than that known previously, but is still marked and if a stratigraphic gap exists it would be at this level. Compared with the Ancyrogondolella elements of the triangularis Zone, those from the transformis Zone (maximum 1 m thick) at Pink Mt. are generally longer, narrower, and
include more asymmetric platform elements, as exemplified by *A. diakowi*, *A. equalis*, *A. transformis*, and rare *A. inequalis*. In addition, single keeled *Mockina* ex gr. *M. matthewi*, *M.? spinosa*, and *Orchardella* n. sp. A occur. Small growth stages are common and similar to those seen in the underlying *triangularis* Zone, but are also longer and may have more elevated posterior carina nodes. At Brown Hill, the zone is represented by a single collection but it could extend up through the overlying silty argillites. It is notable that no adult *Mockina* (?) specimens occur in the single collection (Text-fig. 6, sample 99/4). At Pink Mt., the succeeding collection from the top of the ‘basal’ limestone bed at Pink Mt. (sample 00/B4) differs from the previous in containing far fewer *Ancyrogondolella* species and being instead dominated by *Mockina? spinosa* and diverse small elements collectively assigned to *M. ex gr. M. matthewi*. The *Mockina* growth series require further study to determine their relationship with younger species like *M. carinata* (Orchard, 1991c) and *M. poster*. Additional taxa in

the Pink Mt. sample (sample 00/B4) are rare specimens of *A.? praeagulata* and a single *Norigondolella* sp. At Carbon Creek east, a sample taken from a ~5 cm. bed (Text-figs. 3C, 6, sample 07/A) immediately above the *A. triangularis* Zone also contains the association of *A. diakowi*, *A. transformis*, and *A. equalis*, but two-thirds of the fauna consists of *Mockina? spinosa*, a few mature *M. ex gr. M. matthewi*, and many small *Mockina* growth stages like those at Pink Mt. As at Pink Mt., rare specimens of *A.? praecipulata* occur at Carbon Creek east, which correlates well with the upper horizon (sample 01/B4) of the fauna at Pink Mt. The same is thought to apply to the collection (sample 82/2) from McClay Spur, where *Ancyrogondolella equalis* is rare and *Norigondolella* occurs. At both Carbon Creek east and McClay Spur, the *transformis* Zone is remarkably thin (5–20 cm) and may be incomplete.

Hence, the *transformis* Zone is introduced as the combined range zone of the several new species of *Ancyrogondolella*, the disappearance of which coincides with the appearance of *Orchardella multidentata*. This interval of faunal turnover
also shows an inverse relationship of *Ancyrogondolella* and *Mockina* (?) species with the latter genus becoming dominant in stratigraphically younger strata at Pink Mt. On this basis, the *transformis* Zone is provisionally subdivided (Text-fig. 4) by reference to the dominant taxa: *Ancyrogondolella* in the lower part (Pink Mt., samples 00/B2, 3; Brown Hill, sample 99/4) and *Mockina* (?) with rare *A.? praepubicata* in the upper part (Pink Mt., sample 00/B4; Carbon Creek east, sample 07/A; McClay Spur, sample 82/2).

*Ancyrogondolella diakowi* and *A. equalis* share homologous characters with and are assumed derivatives of *A. triangularis* and *A. uniformis*. Similarly, *A. inequalis* resembles *A. aff. A. triangularis*. These successive faunas have this characteristic triad of rectangular, triangular, and asymmetric morphology. The appearance of *Mockina* (?) species just prior to this zone is an innovation and involves retention of the ancestral juvenile morphology into maturity, as in *M. ex gr. M. matthewi*, and the loss of one posterior lobe and the bifid keel in adults to produce *M.? spinosa* via *M.? transita*. In both collections, the posterior carina is strengthened and the keels are reduced, but whereas *M.? spinosa* retains strong marginal nodes like those of *A. triangularis*, *M. ex gr. M. matthewi* has a broader unornamented posterior platform (Text-fig. 5).

An additional cline represented in the *transformis* Zone is represented by the transitional nature of the name giver between *Ancyrogondolella diakowi* and *Orchardella* (?). This morphogenesis involves a narrowing of the posterior platform, growth of a stronger carina, and suppression of the bifid keel, which is manifest first by unequal development of the secondary keels and then by loss of one in *Orchardella? n. sp. A* (Text-fig. 5.13–5.15).

A final cline involves the development of *Ancyrogondolella? praepubicata* from *A. inequalis*, which has a similar asymmetric platform, through suppression of the secondary keel (Text-fig. 5.18, 5.19). These elements are transitional to the single keeled *Epigondolella spiculata*. Hence, *A. transformis, A.? praepubicata, and Orchardella? n. sp. A*, as well as the slightly older *Mockina? transita*, are each representative of a morphological transition zone ( bracketed by dashed lines in Text-fig. 5) between *Ancyrogondolella* and the three successive genera that characterize Middle Norian strata of the Pardonet Formation.

**Orchardella multidentata Zone**

At Pink Mountain, the more recessive bed (sample 00/B5) immediately above the *transformis* Zone produced fauna showing further innovation with the appearance of common *Orchardella multidentata* in addition to large *Mockina* ex gr. *M. matthewi* and *M.? spinosa*, and a few *Ancyrogondolella? praepubicata*. As in older collections, some earlier growth stages mimic younger taxa (e.g. *O. elongata*) in having fewer anterior denticles than is typical. In general, the ~2 m of Pardonet Formation strata at Pink Mt. embracing samples 00/B5 through 00/B11 are characterized by common *O. multidentata* with far fewer *Mockina* and some *Norigondolella*. The first elements assigned to *Epigondolella tozeri* and *E. spiculata* appear in sample B6 (Pl. 4), but they are very rare and are not seen again until sample B10 and B11, where they become abundant. In spite of these early appearances, the collections (00/B5 through 00/B11) are all assigned to the *multidentata* Zone, defined as an acme zone lying between the first appearance of *O. multidentata* and its replacement by more common *Epigondolella* spp. Subdivision of this zone may be possible based on the common appearance of *E. tozeri* in the upper part of the *multidentata* Zone in each section.

At Carbon Creek east, successive bed by bed sampling over the ~1 m of flaggy, calcareous argillites and siltstones (Text-fig. 6, samples 07/B through H) overlying the *transformis* Zone (sample 07/A) produced fauna dominated by typical *Orchardella multidentata*. Many of these collections contain small conodont elements suggesting an unfavourable environment, but nevertheless they all display the high posterior carina typical of the species. *Mockina* ex gr. *M. matthewi* is much less common initially, but becomes more common higher, whereas *M.? spinosa* is rare in this part of the section.

At McClay Spur, several meters of strata (Text-fig. 6, samples 82/3 through 82/7; 01/2 through 01/7) contain an association of *Orchardella multidentata, Mockina* ex gr. *M. matthewi*, and *M.? spinosa* in differing proportions. Uncommon *Ancyrogondolella? praepubicata* and some *Norigondolella steinbergensis* also occur within this interval. At Brown Hill, a thick *multidentata* Zone includes samples 80/20 through 80/10, and 99/5 and 99/6.

**Epigondolella tozeri Fauna**

As noted by Orchard (1991c, p. 304), *Epigondolella tozeri* becomes more common in the higher parts of the *multidentata* Zone in Williston Lake collections. The same is true at Pink Mt. where strongly ornate *E. tozeri* occur in sample 00/B10 and then becomes dominant in sample 00/B11. At Carbon Creek east, fauna from the base of a thick limestone (sample 07/J) that contains a Rutherfordi Zone ammonoid fauna consists of large individuals of *Orchardella multidentata* with *Mockina* ex gr. *M. matthewi* and *M.? spinosa* accompanied by rare *E. tozeri*, whereas a sample from the top of the limestone (sample 93/U4) is almost exclusively *O. multidentata* with some *M.? spinosa*. Higher samples (samples 93/U5, U6) contain large *O. multidentata*, *M. ex gr. M. matthewi, M.? spinosa*, uncommon *E. tozeri*, and rare *Norigondolella*, and then *E. tozeri* becomes far more common in samples 93/U8 through U10. At McIay Spur, the upper part of the *multidentata* Zone (samples 82/5
through 82/7) also carries increasing numbers of *E. tozeri*. This species is therefore regarded as an indicator of the upper part of the multidentata Zone, although its formal delineation as a separate zone is premature.

*Epigondolella tozeri*, as more narrowly defined herein, is regarded as a true representative of the genus that arose from *Ancyrogondolella* via *A. transformis*. Some elements of the latter have a similar rectangular matrix with extended postero-lateral corners. Whereas the platform of *E. spiculata* emphasized asymmetry, that of *E. tozeri* was relatively symmetrical. The transition was complete through loss of the secondary keel (compare Text-fig. 5.15 and 5.20).

**Epigondolella spiculata Zone**

At Pink Mt. samples from higher beds (e.g. samples 99/K30, 98/B24) are dominated by strongly ornate *Epigondolella tozeri*, typical *E. spiculata*, and *Mockina? spinosa*. The same fauna occurs at Carbon Creek east (sample 83/119A), and Brown Hill (sample 99/7). At McLay Spur, *E. spiculata* dominates the higher collections (samples 01/9, 82/8).

**SUMMARY**

This study has demonstrated the existence and transitional nature of a new conodont fauna described from around the Lower-Middle Norian boundary (LMNB) in the Pardonet Formation of western Canada. The *Ancyrogondolella transformis* Zone (new) is both a stratigraphic and a morphologic intermediary between the conodont faunas known previously from the *Ancyrogondolella triangularis*-bearing Lower Norian Magnus Zone and the *Orchardella multidentata*-bearing Middle Norian Rutherfordi Zone, between which the LMNB has hitherto been defined. The zone is remarkably thin (5–100 cm), but it documents a rapid faunal change in which the phyletic trends appear relatively clear and the faunal record more complete than known previously.

In addition to *Orchardella*, the genera *Epigondolella* and *Mockina* also appear about the LMNB concurrent with the demise of *Ancyrogondolella*. This work includes the description of seven new species that occur in the *transformis* Zone and, in most cases, are confined to it. The genus *Ancyrogondolella*, characterized by a bifid keel, is here used for some species formerly assigned to *Epigondolella*. Loss of the secondary keel led first to *Mockina?*, then to *Orchardella*, and finally to *Epigondolella sensu stricto*, all of which are recognized as separate lineages arising from *Ancyrogondolella* within or just before the *transformis* Zone. The base of this zone is easily recognized and favoured as a datum for future definition of the LMNB.

**ACKNOWLEDGMENTS**

On-going support from the Geological Survey of Canada through many seasons of fieldwork starting in 1980 is acknowledged, as is the collaboration of the late Tim Tozer and, more recently, J-P. Zonneveld as a logistical lead on Williston Lake. The Pink Mt. sampling was undertaken in conjunction with Marij Johns. Peter Krauss and Hillary Taylor are thanked for laboratory and technical support. Michel Mazza and Charles Henderson provided useful reviews, although the author takes full responsibility for the taxonomy presented here.

**LITERATURE CITED**


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### APPENDIX

The following lists the Geological Survey of Canada curation numbers for the collections from which specimens are illustrated:

- Brown Hill sample 99/4 = GSC Cur. No. 304356
- Carbon Creek east sample 01/2 = GSC Cur. No. C-3056910
- Carbon Creek east sample 01/4 = GSC Cur. No. C-3056913
- Pink Mt. sample 00/B2 = GSC Cur. No. C-305275
- Pink Mt. sample 00/B3 = GSC Cur. No. C-305276
- Pink Mt. sample 00/B5 = GSC Cur. No. C-305278
- Pink Mt. sample 00/B6 = GSC Cur. No. C-305279
PLATES
Plate I

Figure Page


4–12. *Ancyrogondolella triangularis* Budurov, 1972; all from Carbon Creek east (01/2). Note variable posterior symmetry and cusp size. 173
4–6. GSC 131620.
7–9. GSC 131621.
10–12. GSC 131622.


15–19. *Ancyrogondolella equalis* n. sp. 172
15–17. Holotype GSC 131624, from Pink Mt. (00/B2).
18, 19. GSC 131625, from Brown Hill (99/4).

Scale bar = 200 microns.
PLATE 2

Figure Page

1–7, 14, 15. *Ancyrogondolella diakowi* n. sp. .................................................. 170
  1–3. Holotype GSC 131626, from Pink Mt. (00/B2).
  4–6. GSC 131627, from Pink Mt. (00/B2).
  7, 14, 15. GSC 131628, from Pink Mt. (00/B3).

8–13, 19–26. *Ancyrogondolella transformis* n. sp. ........................................... 172
  8–10. GSC 131629, from Pink Mt. (00/B2), shows strongly reduced bifurcation.
  19, 20. GSC 131632, from Pink Mt. (00/B3).
  21–23. Holotype GSC 131633, from Pink Mt. (00/B2).
  24–26, GSC 131634, from Brown Hill (99/4), shows keel asymmetry and more tapered platform.

16–18. *Orchardella*? n. sp. A. GSC 131631, from Pink Mt. (00/B3). Note strong similarity to *A. transformis*. . . 179

Scale bar = 200 microns.
### Plate 3

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–6. <strong>Ancyrogondolella praespiculata</strong> n. sp.</td>
<td>174</td>
</tr>
<tr>
<td>1–3. GSC 131655, from Pink Mt. (00/B5).</td>
<td></td>
</tr>
<tr>
<td>4–6. Holotype GSC 131635, from Pink Mt. (00/B5).</td>
<td></td>
</tr>
<tr>
<td>7–15. <strong>Ancyrogondolella inequalis</strong> n. sp., Morphotype B.</td>
<td>172</td>
</tr>
<tr>
<td>10–12. Holotype GSC 131637, from Pink Mt. (00/B3).</td>
<td></td>
</tr>
<tr>
<td>13–15. GSC 131638, from Pink Mt. (00/B2).</td>
<td></td>
</tr>
<tr>
<td>19–24. <strong>Ancyrogondolella inequalis</strong> n. sp., Morphotype A.</td>
<td>172</td>
</tr>
<tr>
<td>19–21. GSC 131639, from Pink Mt. (00/B3).</td>
<td></td>
</tr>
<tr>
<td>16. <strong>Epigondolella spiculata</strong> Orchard, 1991c. Lower view of Holotype GSC 95274, from GSC O-98877.</td>
<td>175</td>
</tr>
<tr>
<td>17, 18, 25–33. <strong>Mockina ex gr. M. matthewi</strong> (Orchard 1991c).</td>
<td>176</td>
</tr>
<tr>
<td>17, 18. GSC 131641, from Pink Mt. (00/B3), specimen with exceptionally short carina.</td>
<td></td>
</tr>
<tr>
<td>25–27. GSC 131642, from Carbon Creek east (01/4).</td>
<td></td>
</tr>
<tr>
<td>28–30. GSC 131643, from Pink Mt. (00/B6).</td>
<td></td>
</tr>
<tr>
<td>31–33. GSC 131644, from Pink Mt. (00/B6), specimen has sinuous lobate shape of <em>M. posterata</em>.</td>
<td></td>
</tr>
</tbody>
</table>

Scale bar = 200 microns.
### Plate 4

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–9.</td>
<td>177</td>
</tr>
<tr>
<td><em>Mockina? spinosa</em> n. sp.</td>
<td></td>
</tr>
<tr>
<td>1–3.</td>
<td>GSC 131645, from Pink Mt. (00/B4).</td>
</tr>
<tr>
<td>4–6.</td>
<td>GSC 131646, from Pink Mt. (00/B6).</td>
</tr>
<tr>
<td>7–9.</td>
<td>Holotype GSC 131647, from Carbon Creek east (01/4).</td>
</tr>
<tr>
<td>10, 17–22.</td>
<td>175</td>
</tr>
<tr>
<td><em>Epigondolella tozeri</em> Orchard, 1991c.</td>
<td></td>
</tr>
<tr>
<td>10.</td>
<td>Lower view of Holotype GSC 95287, from GSC cur. no. O-98518, Pardonet Hill;</td>
</tr>
<tr>
<td>17–19.</td>
<td>GSC 131648, from Pink Mt. (00/B6).</td>
</tr>
<tr>
<td>20–22.</td>
<td>GSC 131649, from Pink Mt. (00/B6).</td>
</tr>
<tr>
<td>11–16.</td>
<td>175</td>
</tr>
<tr>
<td><em>Epigondolella spiculata</em> Orchard, 1991c.</td>
<td></td>
</tr>
<tr>
<td>11–13.</td>
<td>GSC 131650, from Pink Mt. (00/B6); specimen with relatively high carina.</td>
</tr>
<tr>
<td>14–16.</td>
<td>GSC 131651, from Pink Mt. (00/B6).</td>
</tr>
<tr>
<td>23–31.</td>
<td>178</td>
</tr>
<tr>
<td><em>Orchardella multidentata</em> (Mosher, 1970).</td>
<td></td>
</tr>
<tr>
<td>23–25.</td>
<td>GSC 131652, from Carbon Creek east (01/4).</td>
</tr>
<tr>
<td>26–28.</td>
<td>GSC 131653, from Pink Mt. (00/B6).</td>
</tr>
<tr>
<td>29–31.</td>
<td>GSC 131654, specimen transitional to <em>O. elongata</em>, from Pink Mt. (00/B6).</td>
</tr>
</tbody>
</table>

Scale bar = 200 microns.
INDEX

Adetognathus  102
Alaska  8–11, 76, 166, 167, 175, 177, 183
Alate  115, 118, 119, 122, 131
Alba Formation  71–78
Altura Formation  131
Ammonellipes  77
Ammonellipes Fauna  77
Ammonellipes keyseri  78
Ammonellipes–Mesocaricus Assemblage  72, 77
ammonoid(s)  15, 72, 73, 74, 77, 78, 81, 158, 165–168, 179, 180, 181, 183, 184
Anchignathodontidae  115, 124
Anchignathodus typicalis  127
Ancyrogondolella  165, 169–182
Ancyrogondolella aff. An. triangularis  171, 173, 174, 186
Ancyrogondolella diakowi  170, 171, 172, 181, 189
Ancyrogondolella equalis  171, 172, 176, 180, 181, 186
Ancyrogondolella inequalis  165, 171, 172, 174, 190
Ancyrogondolella quadrata  165, 171–173
Ancyrogondolella transformis  175, 177, 179, 182, 189
Ancyrogondolella triangularis  165, 166, 171–175, 178, 179, 182, 186
Ancyrogondolella uniformis  171, 172, 174, 178, 186
Ancyrogondolella psocipulata  170, 174, 175, 181, 190
angulate  115, 118, 119, 122–124, 128
anterior process  118–120, 122, 123, 131
Antler orogenic belt  89, 90, 102
Apache Mountains  30, 31, 33, 128, 132
Artinskian  89–99, 101, 102, 127
Ashcroft  115, 116
Aspe-Brousset Formation  75
Artin  115–118, 120, 124
Atrasado Formation  36, 37, 48–51, 57, 60, 63, 64, 67, 68
Avon Gorge section  76, 86
Baleas Formation  72, 73, 77–79
Baylor University  25
Beberino section  75, 86
Belgium  72, 76, 77, 79
Bell Canyon Formation  31, 127–132
bentonite  128, 130
Beyrichoceras  78
bipennate  115, 118, 119, 122, 127–129, 131
Bird Spring Platform  89–91
Black Bear Ridge  166
Black Rock Limestone  74, 75
Bristol-Mendips region, England  74
British Columbia  32, 76, 115
Brooklyn College  7
Brooks Range  9
Brown Hill  165, 166, 168, 179–182, 184, 186, 189, 190
Butte Basin  90
Cache Creek Terrane  115–119, 121
Caenodonites serrulatus  128, 130
Cabahagnathus sweeti  17
Camperona section  72–74, 77
Camplongo section  72, 74, 77
Canalón Member  72, 73, 74, 77, 79
canonical variance analysis (CVA)  39–47, 53
Cantabrian Mountains, Spain  71, 72, 78
Capitanian  32, 127, 128, 130, 132
Carbon Creek east  165, 166, 168, 173, 177, 179–182, 184, 186, 190, 193
Carlin Canyon, Nevada  90, 91, 99, 102
Carlsbad Caverns  32
carminate  129
Carnic Alps  76, 77
Case Western Reserve University  9, 29
Cavusgnathus  24, 79
Cerros de Amado  37, 48–51, 57, 60, 63, 64, 67, 68
Chairman Formation, Nevada and Utah  76
Cherry Canyon Formation  30, 127
Chief Panderer  13, 15, 20, 21, 23, 24
China  29–32, 71, 76–78, 101, 118–120, 127, 150, 157, 179
China University of Geosciences Beijing  31
chirality  38–41, 43, 45, 53, 93
Chonetipustula–Plicochonetes Zone  74
College of Charleston  24
columbianus  165, 167, 176, 180
codonotid clusters  129, 149–151, 154, 155, 157, 162
codonotid color alteration index  8, 29, 154
cusp  93, 118, 119, 122, 128, 129, 131, 170, 172–174, 176–179, 186
Cystotheres Fauna  74
cyclolems  24, 25, 36, 90
Cyrtopleurites bicrenatus  165, 166, 168, 177, 178, 180–182
Cyathaxonia Fauna  74
Donets Basin  71, 79
denticle  73, 96, 101, 118, 123, 129, 177
dimples  93, 97, 99, 101
Dinarides  149, 150, 157
Diplognathodus  25, 93, 96, 115, 119, 120, 123, 124
dolabrate  131
Dollognathus latus  71, 79
Donets Basin  71, 79
Drypanites rutherfordi  165, 166, 168, 177, 178, 180–182
Dry Mountain Trough  90, 91
Duke University  9
Duraiphiacoceras hispanicum  78
eigen analysis  39
Elko County, Nevada  89, 90, 95, 97, 99, 102, 108, 111, 112
elongata Zone  168, 176, 178
Ely Basin  90
Ely Shelf  90
Enewetak Atoll  29, 32
Eoparafusulina linearis  99
Eoparastaffella simplex Zone  79
Epigoniodellea  165, 166, 169, 170, 172, 174–176, 178, 182
Epigoniodellea spiculata  171–176, 179, 181, 182, 190, 193
Epigoniodellea tozeri  171, 172, 175, 177, 181, 182, 193
Ermita Formation  73
Eudora Shale Member  35, 38, 48–51, 57, 63, 64, 67
Eurites corpulentum  78
Eurites brownii  77
Ferguson Mountain, Nevada  102
Ferguson Trough  89–91, 98, 102
Franklin Mountains, Texas  99
Fremont Formation  13, 14
glacioeustasy  90
triangularis Zone 165, 167, 179, 180
Triassic 8, 9, 13, 15, 16, 29, 37, 127, 132, 149–151, 153, 155, 157, 165, 166, 179
United States Geological Survey 7, 29
University of British Columbia 32
University of Calgary 31
University of California – Riverside 29
University of Houston Downtown 24, 25
University of Iowa 13, 14, 19, 20, 25, 31, 46, 60, 63, 64, 67, 68, 92
University of Missouri 19, 23
University of Texas-Arlington 24, 31, 89, 127
University of Texas-Austin 23, 24
Ural Mountains 97, 102
Vegamián Formation 73, 74
Venta de Getino section 72, 74, 77
Villabellaco section 72–74, 76–78, 86
Virgilian 35, 36, 54
Virginia 8, 76
Viséan 29, 71, 72, 74, 76–79
Walsorian Limestone 74
Wardlaw, Bruce 8, 29–32
Wells, Nevada 89
Williston Lake 165–168, 181, 182
Winchelloceras marshallensis 78
Winchelloceras palentinus 78
Winterset, Iowa 38, 48–51, 63, 64, 67
wireframe models 38, 39, 41–47
Word Formation 131
Wordian 32, 120, 121, 124, 127–130
PREPARATION OF MANUSCRIPTS

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