

Conodonts from the mid-Carboniferous boundary GSSP at Arrow Canyon, Nevada, USA

H. Richard Lane^{1†}, Qi Yuping^{2*}, Wang Zhihao³,
Tamara I. Nemyrovska⁴, Barry C. Richards⁵ and Hu Keyi^{6*}

¹National Science Foundation, 4201 Wilson Blvd., Arlington, Virginia 22230, USA

²Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Rd., 210008 Nanjing, PR China

*corresponding author email: ypq@nigpas.ac.cn

³Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Rd., 210008 Nanjing, PR China
email: zhwang@nigpas.ac.cn

⁴Institute of Geological Sciences, National Academy of Sciences of Ukraine, O. Gonchar Str. 55-b, 01601 Kiev, Ukraine
email: tamaranemyrovska@gmail.com

⁵Geological Survey of Canada, 3303 33rd St. N. W., Calgary, Alberta T2L-2A7, Canada
email: barry.richards@canada.ca

⁶Centre for Research and Education on Biological Evolution and Environment, Nanjing University, 163 Xianlin Avenue, 210023 Nanjing, PR China
*corresponding author email: kyhu@nju.edu.cn

ABSTRACT: The Global Stratotype Section and Point of the mid-Carboniferous boundary was selected in the Arrow Canyon section within the lower Bird Spring Formation at the first evolutionary appearance of the conodont *Declinognathodus noduliferus* (Ellison and Graves) *sensu lato*. The studied boundary beds, spanning a 38.8-m interval from the Upper Mississippian into the Lower Pennsylvanian, occur in bryozoan-brachiopod-crinoidal grainstones/packstones with conodonts and foraminifers. The conodonts of the studied interval belong to the shallow-water *Adetognathus*-*Rhachistognathus* biofacies. The *Adetognathus* and *Rhachistognathus* species/subspecies *A. lautus* (= *A. gigantus*), *A. spathus*, *R. minutus minutus*, *R. muricatus*, *R. primus*, *R. prolixus*, *R. websteri* and transitional forms dominate the succession. *Gnathodus girtyi simplex*, *G. lanei* n. sp., *G. defectus* and transitional forms between them are abundant. The elements of the boundary-marker *D. noduliferus* s. l. and transitional forms between *G. girtyi simplex* and *D. inaequalis* are less common. The occurrences of *Idiognathoides* spp. are very rare. *Neognathodus* spp. only occur in the upper part of the studied interval. The mid-Carboniferous boundary stratotype has been studied by many workers but its conodonts have been rarely described systematically. The detailed updated descriptions of the most stratigraphically important taxa are given in this paper. The evolution of *Gnathodus*, *Adetognathus* and *Rhachistognathus* species within the mid-Carboniferous interval is discussed. Four lineages are summarized: 1) *C. unicornis*, *A. unicornis*, *A. lautus* and *A. spathus*; 2) *G. girtyi girtyi*, *G. g. simplex* and *D. inaequalis*; 3) *G. lanei* and *G. defectus*; and 4) *R. prolixus*, *R. muricatus* and *R. websteri*/*R. primus*/*R. minutus*.

Keywords: Carboniferous, Conodonts, mid-Carboniferous GSSP, Arrow Canyon, Nevada.

INTRODUCTION

The Arrow Canyon section, located near Las Vegas, Clark County, Nevada, southwestern United States (text-fig. 1), was selected as the stratotype for the MCB (mid-Carboniferous boundary) by the International Subcommission on Carboniferous Stratigraphy in 1995 after more than 10 years of extensive work by the International Mid-Carboniferous Boundary Working Group. The Arrow Canyon section, the Upper Mississippian through Pennsylvanian succession, comprising the Battleship Wash, Indian Springs and overlying lower Bird Spring formations, is exceptionally well exposed at Arrow Canyon (text-fig. 2A). The MCB GSSP (Global Stratotype Section and Point) is located at 82.90 m (between measured intervals A55 and A56) above the base of the Indian Springs Formation within the lower Bird Spring Formation at the first evolutionary appearance of the conodont *Declinognathodus noduliferus*

(Ellison and Graves 1941) *sensu lato* (Lane et al. 1999; text-fig. 2B). *Declinognathodus noduliferus* s. l. consists of two groups of species – one group contains species with nodose P₁ elements and another group – the species with ridged P₁ elements (Hu et al. 2018). The former group is cosmopolitan and occurs abundantly in most marine deposits, thus facilitating reliable correlations between deep- and shallow-water settings and carbonate and clastic facies.

The Arrow Canyon section was deposited in the Bird Spring Basin, which developed on the North American plate in response to the Ouachita/Marathon Orogeny along with the Ancestral Rocky Mountains and several other major block-fault uplifts and basins. The Ouachita/Marathon Orogeny resulted from the collision of Gondwana with Euramerica to form the continent Pangea (Ross 1991; Richards et al. 2002). Deposition

within the Bird Spring Basin occurred in a tropical to subtropical pericratonic seaway extending from southern California northward into western Canada (Richards et al. 1993).

The studied interval is within the lower part of the Bird Spring Formation (Upper Mississippian–Lower Pennsylvanian) (text-figs. 2A, 3), which is a heterogeneous succession of shallow-water carbonates and subordinate siliciclastics of neritic to terrestrial lithofacies. These constitute several high-order transgressive-regressive sequences that were produced mainly by eustatic fluctuations driven by ongoing glaciation in Gondwana (Langenheim 1993; Richards et al. 2002; Barnett and Wright 2008; Bishop et al. 2009). The MCB horizon (GSSP) occurs within Unit G of Richards et al. (2002), a 1.61-m thick limestone, composed of pelmatozoan ossicles, brachiopods, bryozoans and scattered foraminifers and ostracods in its upper part, that displays a fourth-order transgressive-regressive sequence.

The lithology, sedimentology, sequence stratigraphy and biostratigraphy of the Arrow Canyon section have been studied by numerous researchers (e.g., Langenheim et al. 1962; Lane 1967; Webster 1969; Brenckle 1973; Baesemann and Lane 1985; Lane et al. 1985, 1999; Brenckle et al. 1997a, b; Richards et al. 2002; Ellwood et al. 2007; Barnett and Wright 2008; Bishop et al. 2009). However, the upper Serpukhovian to lower Bashkirian conodonts from the MCB interval were only partly systematically described by few authors (Webster 1969; Baesemann and Lane 1985). Considering the significance of the Arrow Canyon as the MCB GSSP, the stratigraphically important conodonts within the interval of the section from samples 42 to 107 of Brenckle et al. (1997a, b) are described and illustrated in this paper.

The phylogenetic relationships among shallow-water conodonts from the North American MCB beds have been discussed by a number of researchers (e.g., Dunn 1970a; Lane and Straka 1974; Baesemann and Lane 1985; Grayson et al. 1990). The diverse conodont faunas, containing numerous transitional forms, recovered from the MCB beds at Arrow Canyon provide an opportunity to test the previously proposed lineages. Because the section is dominated by shallow-water conodont taxa, the evolutionary lineages of *Gnathodus*, *Adetognathus* and *Rhachistognathus* species are emphasized.

This work was initiated by Dr. H. Richard Lane, who studied, measured and sampled the Arrow Canyon section over many years, prepared a modified version of previously published distribution chart, established the conodont zonation and published many papers on the Arrow Canyon sequences together with his colleagues (see references). He brought the majority of his samples (part of the previously published and newly collected samples) to the Nanjing Institute of Geology and Palaeontology (Nanjing, China) to start joint work on illustrating and describing the most important Arrow Canyon species. He and Dr. Wang Zhihao finished the scanning microscope pictures before 2015. Unfortunately, Dr. H. Richard Lane passed away before all pertinent materials could be assembled. Specimens of some species listed in a previously published distribution chart (Lane et al. 1999, table 1) could not be found, although some US colleagues have tried to locate them (see table 1). For this reason, we have not studied specimens of *Neognathodus symmetricus* (Lane 1967), *Neolochriea hisaharui* Mizuno 1997, *Rhachistognathus minutus havlenai* Baesemann and Lane

1985, *Idiognathoides sinuatus* Harris and Hollinsworth 1933, *Id. corrugatus* (Harris and Hollinsworth 1933), *Id. sulcatus* (Higgins and Bouckaert, 1968), some *Declinognathodus* species and a majority of *G. girtyi simplex*–*D. inaequalis* transitional specimens of Brenckle et al. (1997a, b, Pl. 1, figs. 2–4) in our examined slides, although they are shown in the distribution chart (see table 1 for more information). Specimens, previously identified as discrete elements of *Ozarkodina*, *Hibbardella* and others, were named as ramiforms in this paper. Nevertheless, we updated the distribution chart (text-fig. 4) in this study by correcting identifications of some species, including the number of conodonts received from newly collected samples, and establishing one new species, *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp. (table 1).

MATERIAL and METHODS

A total of 65 carbonate samples, 4 to 5 kg each, were collected from the studied interval and then dissolved with standard procedures using formic or buffered acetic acid solutions of Jeppsson and Anehus (1995) by H. Richard Lane and his colleagues. More than 2000 P₁ and more than 150 P₂ and ramiform elements were recovered (table 1). The most numerous associations of conodonts were registered in the boundary beds, probably because the weight of the samples was bigger up to 10 to 15 kg.

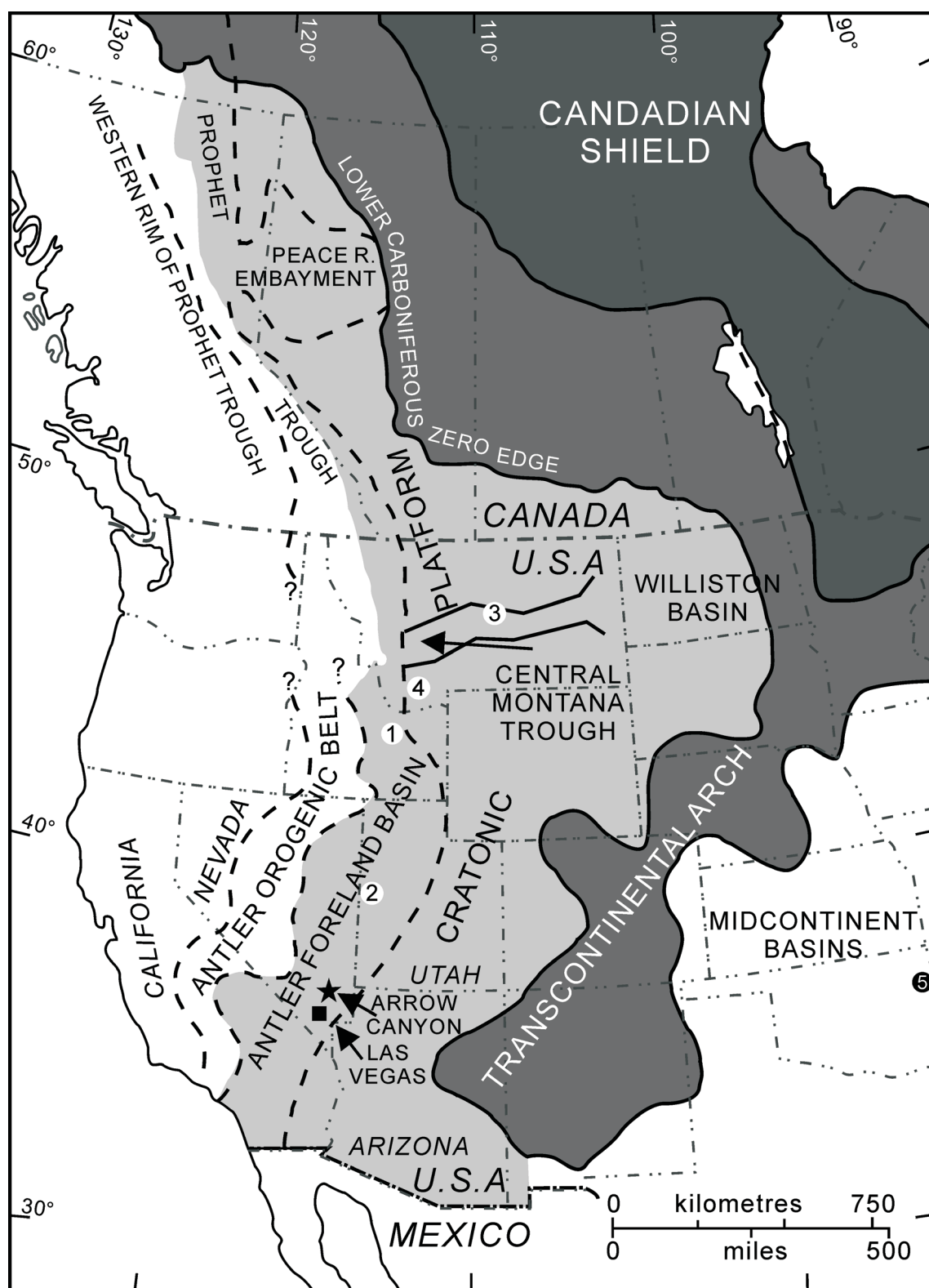
Most of the studied conodont elements were pictured by SEM (scanning electron microscope) at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. All specimens are deposited at the University of Iowa Paleontology Repository, Iowa City; catalogue numbers prefixed by SUI.

CONODONT BIOSTRATIGRAPHY

The studied interval at Arrow Canyon section contains most important conodont genera known in other coeval deposits of North America, i.e., *Adetognathus* Lane 1967, *Rhachistognathus* Dunn 1966, *Gnathodus* Pander 1856 and *Declinognathodus* Dunn 1966. The most abundant elements are the species of *Adetognathus* and *Rhachistognathus*, which are common throughout the whole sequence.

Adetognathus unicornis (Rexroad and Burton 1961) was found only in the Indian Springs Formation and lowermost beds of the Bird Spring Formation up to sample 51 (Brenckle et al. 1997a, b; Lane et al. 1999). The first occurrence of *A. lautus* (Gunnell 1933) [= *Adetognathus gigantus* (Gunnell 1933)] was registered below the MCB in the upper Serpukhovian sample 43. Both dextral and sinistral forms of *A. lautus* are abundant not only in the uppermost Mississippian but in the Lower Pennsylvanian beds as well. *Adetognathus spathus* (Dunn 1966) appears a short distance above the MCB in sample 63. It is common in the Pennsylvanian part and is more abundant than *A. lautus* in some samples (e.g., samples 91 and 95 in table 1). Ramiform elements occur throughout the section, but the most robust ramiforms (pl. 1, figs. 14, 15; pl. 2, figs. 6–13) were found together with large *A. lautus* and *A. spathus* P₁ elements in samples 93 and 94 (pl. 1, figs. 1–10). They probably belong to *Adetognathus*, as there are no other P₁ elements in these samples except for few juvenile *Rhachistognathus*.

Rhachistognathus species are as common as those of *Adetognathus* throughout the studied interval. Most abundant are *R. muricatus* (Dunn 1965) in the Upper Mississippian part of the section and *R. primus* (Dunn 1965) in the Lower Pennsylvanian.



TEXT-FIGURE 1

Map showing location of Arrow Canyon, Clark County, Nevada and principal Late Mississippian paleogeographic elements (modified from Richards et al. 1994). Other similar mid-Carboniferous conodont fauna were found in North America: 1. east Central Idaho (Skipton et al. 1985; Abplanalp et al. 2009); 2. Granite Mountain, Utah (Morrow and Webster 1992); 3. central Montana (Davis and Webster 1985); 4. Southwest Montana (Abplanalp et al. 2009); 5. Northeastern Oklahoma (Lane and Straka 1974).

TABLE 1

Numerical conodont chart for the 38.8-meter study interval that includes the mid-Carboniferous boundary GSSP at Arrow Canyon. Samples are shown along the second row of spreadsheet and equate to those shown on Text-Figures 4. Some of the individual sample measurements within the section are available in Brenckle et al. (1997a, b, Appendix 2). Light-gray showing data newly included in this study; dark-gray showing data were not available for this study but have been published previously; the other samples have all been reinvestigated.

[illegible]

nian. Specimens of *R. prolixus* Baesemann and Lane 1985 and *R. websteri* Baesemann and Lane 1985 are relatively scarce in the uppermost Mississippian part of the section, but above the MCB they become rather common to dominant along with *R. minutus minutus* (Higgins and Bouckaert 1968), which is characteristic for the beds higher in the succession (samples 80–99).

Gnathodus is represented by several taxa such as *G. girtyi simplex* Dunn 1965, *G. defectus* Dunn 1966, *G. lanei* and transitional forms between *G. girtyi simplex* and *Declinognathodus inaequalis*. These elements are common throughout the Mississippian part of the lower Bird Spring Formation of the studied section and extend above the MCB up to sample 76. The highest occurrence of the *Gnathodus bilineatus* group is at sample 37 (Lane et al. 1999, table 3), which is below the stratigraphic interval considered in this paper.

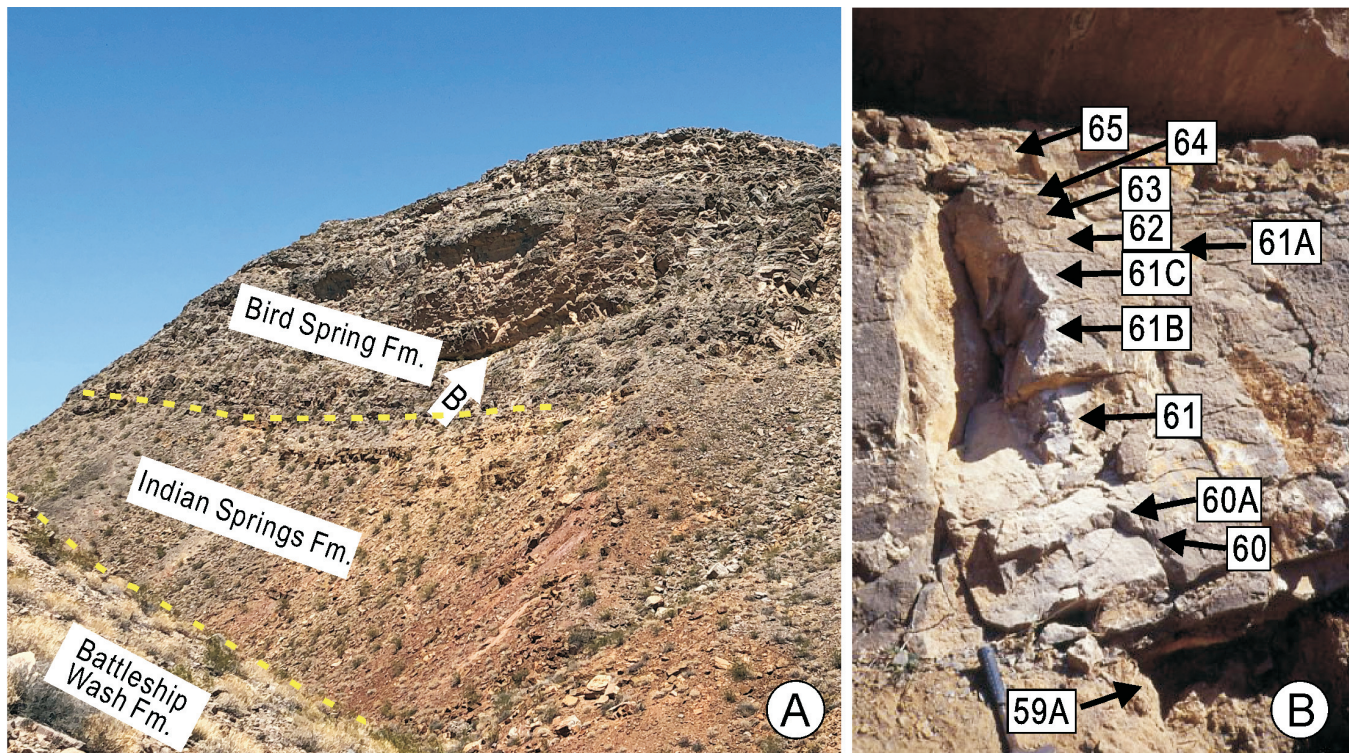
Previously, *Declinognathodus noduliferus* s. l. as used for the boundary-defining taxon at Arrow Canyon was identified as *D. inaequalis* (Higgins 1975), *D. noduliferus* and *D. japonicus* (Brenckle et al. 1997a, b; Lane et al. 1999). Those three species were subsequently included in the nodose *Declinognathodus* group (Hu et al. 2018). In this study, we recognized both nodose and ridged *Declinognathodus* group. The published data for Arrow Canyon demonstrates that the first *D. noduliferus* s. l. (= *D. inaequalis*) occurs in sample 61B (Brenckle et al. 1997a, b; Lane et al. 1999); however, we recovered a juvenile specimen of *D. inaequalis* (pl.3, fig. 8) and a broken specimen of *D. cf. D. noduliferus* (pl. 3, fig. 9) from sample 61, which underlies sample 61B. The discrepancy in first appearances could be caused by the 5-cm overlap of sample 61 (82.70–82.95 m above the base of the Indian Springs Formation) and 61B (82.90–83.05 m above the base of the Indian Springs Formation) (Brenckle et al. 1997a, b, Appendix II). Two other species, *D. noduliferus* and *D. japonicus* (Igo and Koike 1964), were first found in sample 62. The next occurrences of *D. noduliferus* are small single specimens recovered in samples 69 and 71, but the overlying beds up to sample 83 are barren of this taxon. Beds between sample 86 and sample 107 yield a number of *D. noduliferus*, *D. japonicus* and few *D. tuberculosus* Hu, Qi and Nemyrovska 2018. In sample 107, numerous specimens of *D. noduliferus* and *D. japonicus* of nodose group and few *D. tuberculosus* of ridged group were recovered.

The first elements of *Idiognathoides*, *Id. sinuatus* Harris and Hollingsworth 1933, *Id. corrugatus* (Harris and Hollingsworth 1933) and *Id. sulcatus* Higgins and Bouckaert 1968, were previously documented in sample 89 (Brenckle et al. 1997a, Appendix II; Lane et al. 1999, table 3). In this study, poorly preserved specimens of *Id.* aff. *Id. convexus* (pl. 3, fig. 4) were found in sample 61 together with the first *D.* cf. *D. noduliferus*. In general, *Idiognathoides* species are very rare and are represented mostly by juveniles or small broken specimens.

The conodont zonation of the Arrow Canyon section was first established by Baesemann and Lane (1985). The *Rhachistognathus muricatus* Zone comprises the Upper Mississippian part of the section (samples 42–61). It is subdivided into Lower and Upper *R. muricatus* zones. The Lower *R. muricatus* Zone, identified only in sample 42 in this study, is characterized by *R. muricatus*, *Adetognathus unicornis*, *Gnathodus girtyi simplex* and *G. defectus*. The Upper *R. muricatus* Zone (samples 43–61), defined by the FAD (First Appearance Datum) of *Adetognathus lautus* (= *A. gigantus*) (Baesemann and Lane 1985; Lane et al. 1999), contains a conodont assemblage similar to that of the Lower *R. muricatus* Zone with the addition of *Gnathodus lanei* and transitional forms from *G. girtyi simplex* to *Declinognathodus inaequalis*.

The *Declinognathodus noduliferus*-*Rhachistognathus primus* Zone comprises the lowermost Pennsylvanian part of the section (samples 61b–79). Its lower boundary is defined by the FAD of *D. noduliferus* s. l. (*D. inaequalis*). The upper boundary coincides with the FAD of *R. minutus*. Included species are *R. primus*, *R. muricatus*, *R. prolixus*, *R. websteri*, *Adetognathus laevis*, *A. spathus* and rare *Idiognathoides* aff. *Id. convexus* and *Declinognathodus* elements.

The second Pennsylvanian zone *Idiognathoides sinuatus-Rhachistognathus minutus* Zone was previously marked by the co-occurrence of *Id. sinuatus* and *R. minutus* in sample 89 (Lane et al. 1999). In this study, the entry of *R. minutus* was recorded below and *Id. sinuatus/Id. corrugatus* were not found, thus the base of the zone was shifted down to sample 80. As a result, the *Id. sinuatus-R. minutus* Zone is revised and named as *R. minutus* Zone (samples 80–89). The lower and upper boundaries of the *R. minutus* Zone are defined by the FADs of *R. minutus* (sample 80) and *Neognathodus symmetricus*, respectively (Baesemann and Lane 1985). Other taxa found in this



TEXT-FIGURE 2

A. Picture showing lithological units exposed at Arrow Canyon section, white arrow indicating the position of the MCB GSSP horizon within the lower Bird Spring Formation; B. Close-up view of boundary bed and sample locations. The mid-Carboniferous boundary lies within the middle of the bed at sample 61B. The thickness between samples 60 and 65 is 1.5 m (after Brenckle et al. 1997b, fig. 5).

zone are nodose *Declinognathodus* species, *R. muricatus*, *R. primus*, *R. websteri*, *R. prolixus*, *Adetognathus lautus*, *A. spathus* and scarce *Id. aff. Id. convexus*.

Only the lower part of the *Neognathodus symmetricus* Zone is included in this study by the first occurrence of *N. symmetricus* (sample 90 according to Lane et al. 1999). Other conodonts in this part of the sequence include nodose *Declinognathodus* species, *Adetognathus lautus*, *A. spathus* and rare *Idiognathoides* aff. *Id. convexus* and *D. tuberculosus*. *Rhachistognathus prolixus* and *R. websteri* are also common.

REMARKS ON CONODONT BIOFACIES.

Abundant *Adetognathus* and *Rhachistognathus* and scarce *Declinognathodus*/*Idiognathoides* demonstrate that Arrow Canyon MCB fauna belongs to *Adetognathus*-*Rhachistognathus* biofacies that characterizes the offshore, barrier-shoal and nearshore lagoon environments contrasting to the normal marine, offshore environments of the *Declinognathodus*/*Idiognathoides* fauna (Davis and Webster 1985; Morrow and Webster 1991). The shallow-water conodont fauna of the Arrow Canyon section is very similar to that found in other North American *Adetognathus*-*Rhachistognathus* biofacies. Similar conodont sequences have been reported from Idaho (Skipp et al. 1985), Arctic Alaska (Krumhardt et al. 1996; Harris et al. 1997; Baesemann et al. 1998), Granite Mountain (Morrow and Webster 1992), central Montana (Davis and Webster 1985), western US (Dunn 1966, 1970a), central US (Lane and Straka 1974), east-central Idaho and northern Rocky Mountains of

southwestern Montana (Abplanalp et al. 2009) and northwest Mexico (Navas-Parejo et al. 2017) (see text-fig. 1 for part of their locations). The aforementioned biofacies has not been reported from Eurasia but correlation is possible by the occurrences of cosmopolitan conodonts such as nodose *Declinognathodus*, *Adetognathus lautus* and *Rhachistognathus minutus*.

PHYLOGENETIC REMARKS

Based on conodont data of the Arrow Canyon section and previously published North American shallow-water sections, the evolution of *Adetognathus*, *Gnathodus*, and *Rhachistognathus* species within MCB intervals are discussed as follows (text-fig. 5).

Adetognathus

When Lane (1967, p. 930) established the genus *Adetognathus*, he integrated the Chesterian (Upper Mississippian) conodont data published by Rexroad (1958) and Rexroad and Burton (1961) and concluded that the first *Adetognathus* species, *A. unicornis*, evolved from *Cavusgnathus unicornis* Youngquist and Miller 1949. Brown et al. (1990, fig. 5) outlined two main morphological stages from *C. unicornis* to *C. monocerus* (= *A. unicornis*). The Arrow Canyon material shows that the early stage may be represented by a transitional specimen (pl. 3, fig. 22), which displays a medially offset free blade; and the late stage displaying intraspecific variation of *A. unicornis*, may be demonstrated by those specimens (pl. 3, figs. 18, 23), which have rostrally positioned junction of free blade and platform.

Both stages are recorded below the studied interval in sample 35.

Adetognathus lautus follows *A. unicornis* and includes two form-species, the sinistral P₁ element of *A. lautus* and the P₁ element of dextral *A. gigantus* (Lane and Straka 1974). Due to the non-symmetrical paired nature of *A. lautus*, it was likely evolved from a similarly paired ancestor. Dunn (1970a, text-fig. 10) believed that *A. unicornis* gave rise to *A. lautus*, while Lane and Straka (1974) suggested that *A. unicornis* could have given rise to *A. lautus* via *A. spathus*. Later, Lane et al. (1985, fig. 3) illustrated the transformation from *A. unicornis* to *A. lautus* but only shown sinistral transitional element. Brown and Rexroad (in Brown et al. 1990) reassigned *A. unicornis* to *C. monocerus* and indicated that *A. lautus*, due to its fixed blade in the dextral element, is closer to *Cavusgnathus unicornis* than *A. unicornis*. Weibel and Norby (1992) illustrated a conodont fauna dominated by *A. unicornis* and *A. lautus* from the Grove Church Shale (uppermost Mississippian) and Wayside Member of the Caseyville Formation (lowermost Pennsylvanian) in southern Illinois and discussed the morphological differences between these two particular species. However, none of the aforementioned researchers could provide direct evidence to prove that *A. lautus* evolved from *A. unicornis*.

The last *Adetognathus* species recorded in the studied interval is *A. spathus*, which has a typical dorsal free blade (row of nodes). Dunn (1970a) suggested that *A. unicornis* was a direct, common ancestor of *A. lautus* and *A. spathus*. Lane and Straka (1974) considered that *A. unicornis* possibly gave rise to *A. lautus* through *A. spathus*. Rexroad and Merrill (1985) suggested that *A. spathus* could be a recurrent ecophenotype of *A. lautus*. Our analysis of the *Adetognathus* fauna proposes different conclusion based on FADs of *A. lautus* and *A. spathus* and the transitional forms in the Arrow Canyon section. *Adetognathus lautus* appears in the uppermost Mississippian and defines the lower boundary of the Upper *Rhachistognathus muricatus* Zone, while *A. spathus* was first recorded in the lowermost Pennsylvanian within the *D. noduliferus*-*R. primus* Zone (see Table 1 and text-fig. 4). The probable transitional form (pl. 1, figs. 1, 2) between *A. lautus* and *A. spathus* was recovered in sample 62 slightly below the first occurrence of *A. spathus*. Its dorsal free blade ornamented by small nodes is less developed than that of typical *A. spathus*. The occurrence of transitional forms within the Arrow Canyon stratigraphic sequence lead us to conclude that *A. lautus* gave rise to *A. spathus* in middle of the Carboniferous. (text-fig. 5A).

Gnathodus

In the studied interval we are dealing with only one group of species – the latest Mississippian species of the *Gnathodus girtyi* group. The *G. girtyi* group consists of a number of species and subspecies, which have been reported from Eurasia and North America by many researchers (e.g., Rhodes et al. 1969; Higgins and Bouckaert 1968; Higgins 1975; Dunn 1970a; Kozitskaya et al. 1978; Meischner and Nemyrovskaya 1999; Nemyrovskaya 2005; Pazukhin et al. 2010; Qi et al. 2014). Most species of the *G. girtyi* group are Mississippian in age and do not cross the MCB except of *G. girtyi simplex*, *G. defectus* and *G. lanei*. The latter two species are currently known only from North America.

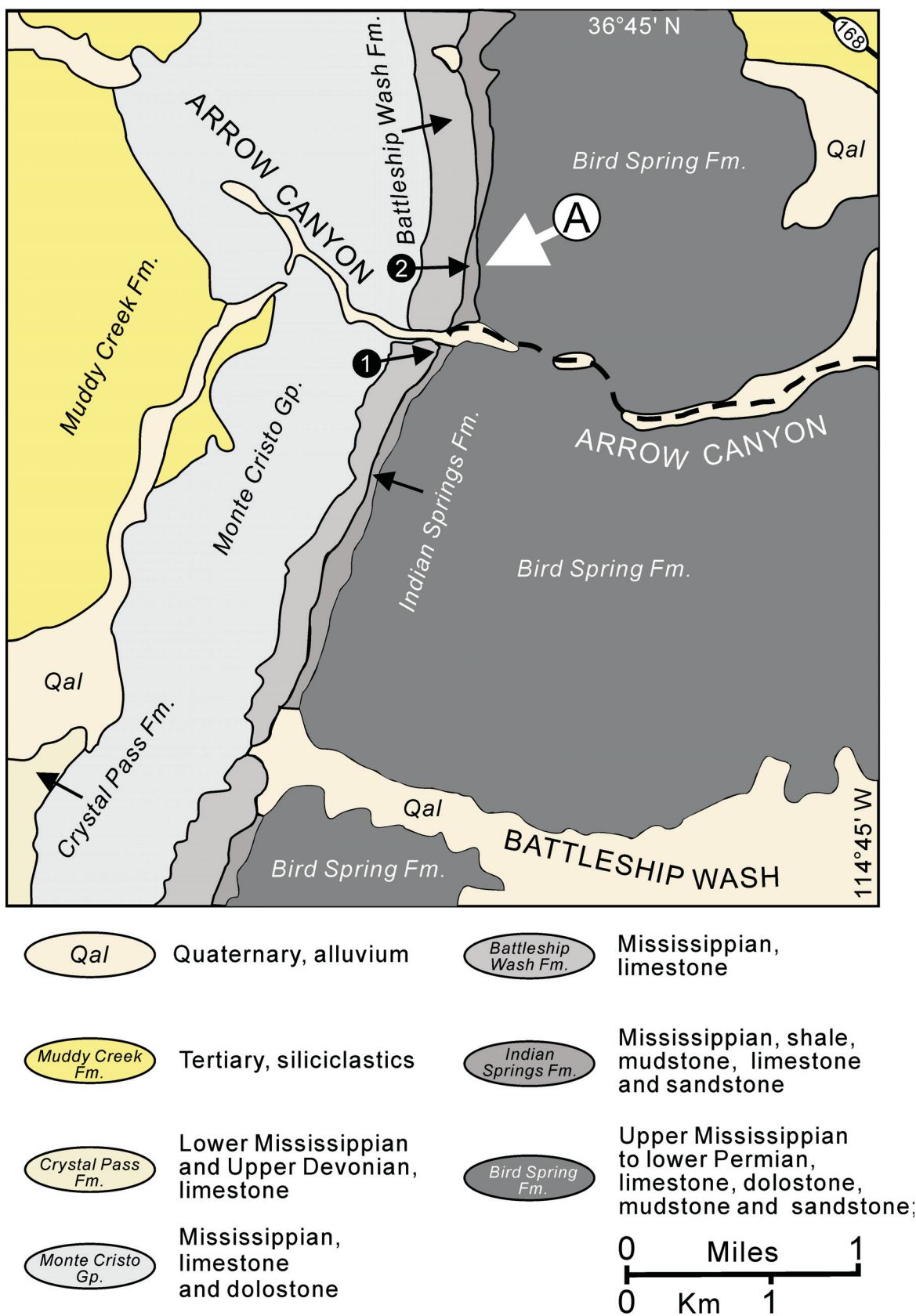
Dunn (1970a) introduced a lineage consisting of *Gnathodus girtyi girtyi*, *G. g. simplex* and *G. defectus*. The transformation

from *G. g. girtyi* to *G. g. simplex* happened during the late Viséan–early Serpukhovian time (e.g., Nemyrovskaya 2005; Qi et al. 2014), and thus was not recorded in the studied interval of the Arrow Canyon section. *Gnathodus g. simplex* probably gave rise to *G. defectus* by shortening the caudal parapet and reducing the number of rostral nodes. Length of parapet/parapets and number of rostral nodes (if rostral parapet reduced) were regarded as criterion in subspeciation of *G. girtyi* group (Higgins 1975). Brenckle et al. (1997a, b, pl. 1, figs. 11–13) illustrated from the Arrow Canyon section a morphotype called “*G. g. simplex*–*G. defectus* transitional specimens”, which is typified by a single rostral node. In this paper, this morphotype is introduced as a new species because it displays distinct features and links the evolutionary sequence of *G. g. simplex* and *G. defectus*, and thus can be recognized as of species rank. As a result, Dunn’s lineage is revised as *G. g. girtyi*–*G. g. simplex*–*G. lanei*–*G. defectus*. *Gnathodus lanei* and *G. defectus* clearly represent new evolutionary stages of *G. girtyi* group although their biostratigraphical value is not so important so far. Additionally, comparing with another morphotype of *G. defectus* (Dunn 1966, pl. 158, figs. 1, 5; Dunn 1970a, pl. 62, fig. 15), which has a carina fused with caudal nodes dorsally, *G. defectus* in this study have shorter caudal parapet that does not fuse with carina dorsally. It is probably because parapet-shortening and nodes-reducing progresses did not always happen simultaneously and thus produced slightly variable morphotypes in both *G. lanei* (compare pl. 4, figs. 6 and 9) and *G. defectus* (compare pl. 4, figs. 15 and 19). Due to that the FADs of *G. lanei* and *G. defectus* cannot be precisely located in the Arrow Canyon by this study, we suggest that *G. lanei* could be derived from *G. g. simplex* within the Lower *Rhachistognathus muricatus* Zone, and then gave rise to *G. defectus* slightly later (text-fig. 5B).

There are two opinions on the derivation of *Declinognathodus noduliferus s. l.* The first one is *Gnathodus girtyi simplex*–*D. noduliferus s. l.* (Lane et al. 1985; Krumhardt et al. 1996), which can be traced only in North America; and another alternative lineage *G. postbilineatus*–*D. noduliferus s. l.* The latter lineage was proposed when the species of ridged *Declinognathodus* was recovered (e.g., Nigmatdjanov and Nemyrovskaya 1992; Sanz-López et al. 2006; Nemyrovskaya 2011; Sanz-López and Blanco-Ferrera 2013; Fallon and Murray 2015). This lineage was also established by Grayson et al. (1990) by tracing both P₁ and P₂ elements belonging to *G. bilineatus* group and *Declinognathodus*. The study of deep-water MCB conodonts of South China (Hu et al. 2018) also suggests that ridged and nodose *Declinognathodus* groups were probably derived from *G. postbilineatus* and *G. girtyi simplex*, respectively. Thus, now we retain the lineage *G. girtyi simplex*–*D. noduliferus s. l.* (*D. inaequalis*) in the Arrow Canyon.

RHACHISTOGNATHUS

Baesemann and Lane (1985) have elaborated the evolution of *Rhachistognathus* species based on material from twelve sections including Arrow Canyon (text-fig. 5C). Their ideas have been partly confirmed by Krumhardt et al. (1996) based on conodonts from the Wahoo Limestone, northeast Brooks Range, Alaska. We have examined some newly collected samples from Arrow Canyon (see table 1) and agree with the point of view of Baesemann and Lane (1985) in this specific regard.



TEXT-FIGURE 3

Geological map showing location of GSSP in the mid-Carboniferous boundary section at Arrow Canyon [after Cassity and Langenheim (1966) and Richard et al. (2002)]. 1. Base of measured section; 2. upper continuation of mid-Carboniferous boundary section; A. mid-Carboniferous GSSP.

SUMMARY

Although the stratotype of the mid-Carboniferous boundary was studied by many workers, the systematic descriptions of the conodonts from that section was just partly done. The complete systematic descriptions of all the conodonts of the studied interval of the Arrow Canyon section is given in this paper. One new species *Gnathodus lanei* was distinguished and described. We found the lowest occurrence of *Idiognathoides* in the Arrow Canyon section and updated the distribution chart and the zonation. Four lineages are summarized as follows: 1) *C. unicornis*, *A. unicornis*, *A. lautus* and *A. spathus*; 2) *G. girtyi*, *G. g. simplex* and nodose *D. noduliferus* s. l.; 3) *G. lanei* and *G. defectus*; and 4) *R. proluxus*, *R. muricatus* and *R. websteri*/*R. primus*/*R. minutus*.

All the results of this study contribute to our knowledge about the distribution and evolution of the Carboniferous conodonts and provide the opportunity of regional and international correlation.

SYSTEMATIC PALEONTOLOGY

Phylum CHORDATA Bateson 1886

Subphylum VERTEBRATA Cuvier 1812

Class CONODONTA Pander 1856

Order OZARKODINIDA Dzik 1976

Family CAVUSGNATHIDAE Austin and Rhodes 1981

Adetognathus Lane 1967

Type species: *Cavusgnathus lautus* Gunnell 1933, Pennsylvanian of North America.

Diagnosis: “A genus having the platform dissected by a deep median longitudinal trough. The blade may be attached to either margin. The fixed blade, if present, is shorter than the long free blade. No carina is developed (Lane 1967, p. 930).”

Remarks: “*Adetognathus* differs from *Cavusgnathus* by complete absence or weak development of a fixed blade and in symmetry characteristics. All known representatives of *Cavusgnathus* have a fixed blade equal to, or longer than, the free blade and display Class IV symmetry. Lateral profile of the oral (upper) margin of the free blade also serves to distinguish these genera. *Cavusgnathus* possesses a short free blade, and its apex is in the posterior half; whereas, excepting an abnormally large posteriormost denticle, the longer free blade of *Adetognathus* has its highest point in the anterior (ventral) half (Lane and Straka 1974).”

Adetognathus lautus (Gunnell 1933)

Plate 1, figures 8–10

Cavusgnathus lautus GUNNELL 1933, p. 286, pl. 31, figs. 67–68, pl. 33, fig. 9. – ELLISON 1941, pl. 21, figs. 47–48. – MERRILL and KING 1971, p. 655, pl. 75, figs. 23–29. – Von Bitter 1972, p. 61, pl. 4, figs. 3a–3h, pl. 5, figs. 1a–1h. – WHITESIDE and GRAYSON 1989, pl. 1, figs. 17, 31 (non cet.).

Cavusgnathus gigantis GUNNELL 1933, p. 286, pl. 33, figs. 7, 8.

Adetognathus lauta (Gunnell). – LANE 1967, p. 1933, pl. 121, figs. 1–3, 7, 10, 11, 14, 15, 17 (non figs. 4, 5, 18 = *A. spathus*).

Adetognathus lautus (Gunnell). – DUNN 1970a, p. 327, pl. 61, figs. 1, 4. – LANE and STRAKA 1974, p. 64, Figs. 36.17, 36.21, 36.22, 36.25–36.31, 38.1–38.4, 38.6–38.8, 38.10–15, 38.20, 39.1–39.3, 39.7–39.14 (cum. syn.). – PERLMUTTER 1975, p. 101, pl. 3, figs. 34–39, 42–45. – BENDER 1980, p. 8, pl. 4, figs. 26–33. – GOREVA 1984, pl. 1, figs. 8–13. – GRAYSON 1984, pl. 2, fig. 6, pl. 3, figs. 8–9, 26–27. – NEMIROVSKAYA and ALEKSEEV 1995, pl. 2, fig. 6. – KRUMHARDT, HARRIS and WATTS 1996, p. 32, pl. 1, figs. 13–15,

21–24 (cum. syn.). – BRECKLE et al. 1997a, pl. 1, figs. 16–18. – BRECKLE et al. 1997b, pl. 1, figs. 16–18. – NEMYROVSKA 1999, p. 51, pl. 1, fig. 10 (cum. syn.). – NASCIMENTO et al. 2009, fig. 4D. – ABPLANALP et al. 2009, Figs. 7.34–7.37. – NAVAS-PAREJO et al. 2017, p. 387, pl. 1, fig. 6.

Adetognathus lautus (Gunnell) morphotype A. – WEIBEL and NORBY 1992, text–fig. 5, pl. 2, figs. 1–34.

Adetognathus gigantis (Gunnell). – NEMYROVSKA 1999, p. 51, pl. 1, fig. 10 (cum. syn.).

Diagnosis: Free blade joins the platform in rostral lateral position and gradually transforms into the rostral parapet in the sinistral form; in the dextral form it joins the platform in the rostral parapet and creates the short fixed blade with the largest denticle on its dorsal end.

Description: Both sinistral and dextral P₁ elements are elongated and consist of two almost equal long ridged parapets with a deep trough between them. The free blade is relatively short, the greater height is in its ventral, or middle, part. In the dextral P₁ element the free blade joins the platform and transforms into the short fixed blade with the largest denticle on its dorsal end (*Adetognathus gigantis*) (pl. 1, figs. 9, 10). In this case, the caudal parapet is longer than the rostral one in dextral element. Sinistral P₁ elements are characterized by gradual transformation of free blade into the rostral parapet with the absence of fixed blade (pl. 1 fig. 8). The parapets are ornamented by the regularly spaced transverse parallel ridges. The median groove is wide and deep. The basal cavity is rather shallow, asymmetrical.

Remarks: Lane and Straka (1974) assigned *Adetognathus lautus* and *A. gigantis* to one symmetrically paired species *A. lautus* because the two single-sided form species share similar abundance in samples and stratigraphic ranges. Both form species are described here under the name *A. lautus* because it was designated type species of *Adetognathus* (Lane 1967).

Adetognathus lautus is similar to *A. spathus* in its groove, parapets and largest denticle in dextral elements. *Adetognathus lautus* (both dextral and sinistral elements) can be distinguished from *A. spathus* by absence of the short “dorsal blade” behind the medial groove and by having a shorter free blade. There are some forms that could be transitional between *A. lautus* and *A. spathus* (pl. 1 figs. 1, 2). *Adetognathus lautus* differs from *A. unicornis* by a longer fixed blade gradually transforming into the parapet and by a wider and deeper medial groove. In upper view, *A. unicornis* has two parapets with equal width, whereas *A. lautus* has a wider caudal parapet.

Range: Pennsylvanian and lower Permian of Eastern Europe and Urals; uppermost Mississippian through lower Permian of North America.

Occurrence: Samples 43–100; Upper *Rhachistognathus muricatus* Zone to *Neognathodus symmetricus* Zone and above in the Arrow Canyon section.

Material: 182 sinistral elements and 154 dextral elements.

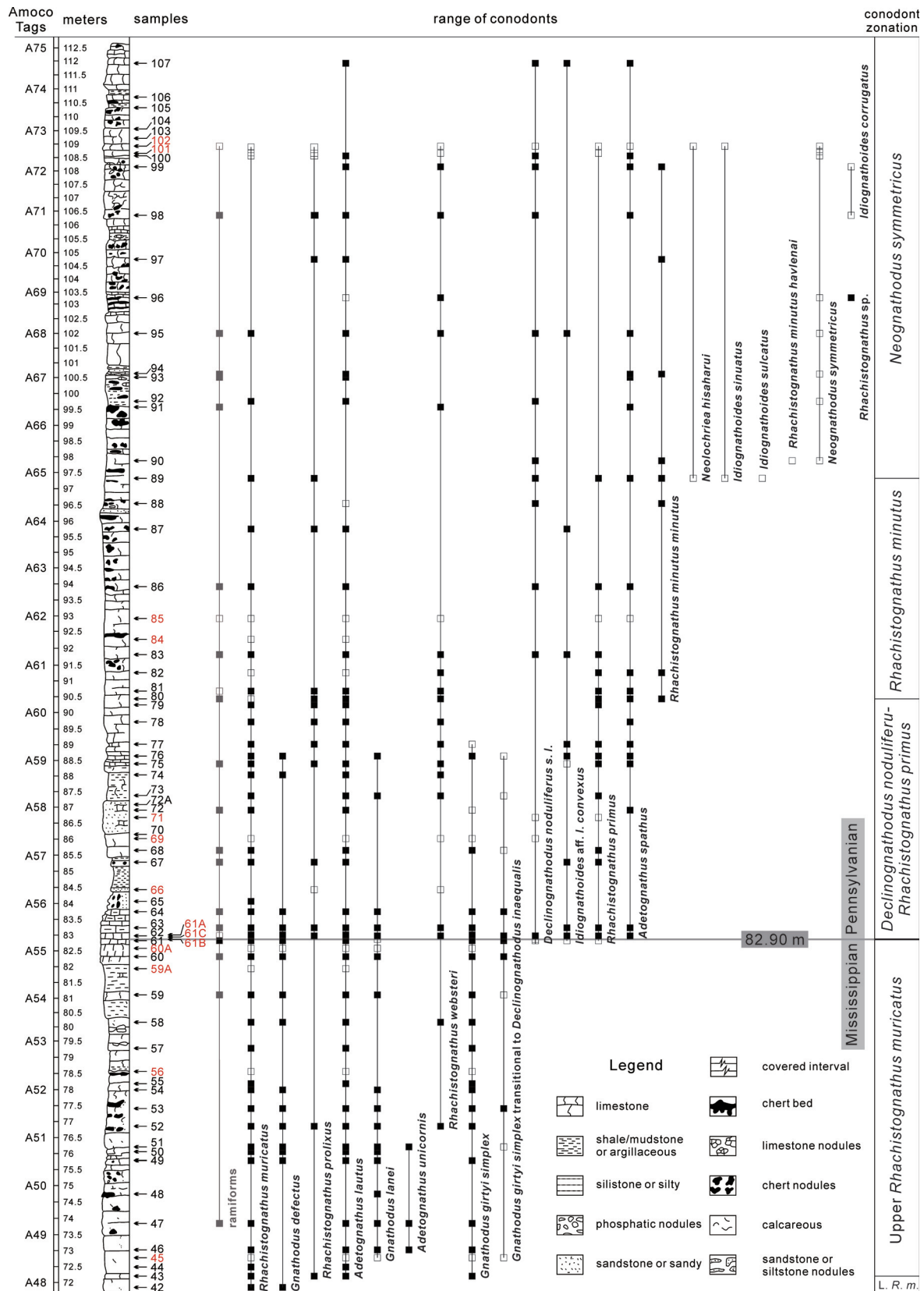
Adetognathus spathus (Dunn 1966)

Plate 1, figures 3–7

Cavusgnathus spatha DUNN 1966, p. 1297, pl. 157, figs. 3, 7, 8.

Adetognathus lauta (Gunnell). – LANE 1967, p. 933, Pl. 121, figs. 4, 5, 18 (non figs. 1–3, 7, 10, 11, 14, 15, 17 = *A. lautus*).

Adetognathus spathus (Dunn). – WEBSTER 1969, p. 28–29, pl. 4, figs. 1, 4, 5. – DUNN 1970a, p. 327, pl. 61, figs. 11–13. – LANE and



TEXT-FIGURE 4

Conodont range through studied interval of the Arrow Canyon section. Ramiform occurrences are marked in gray on the left side of the range chart; red numbers showing unavailable samples in this study; hollow square showing previously published conodont data (Brenckle et al. 1997a, b; Lane et al. 1999) which are unavailable in this study and cf. elements (see Table 1 for more information). L. R. m. = Lower *Rhachistognathus muricatus*.

STRAKA 1974, p. 65–66, Figs. 38.5, 38.9, 38.16–38.19, 40.4–40.6. – KRUMHARDT, HARRIS and WATTS 1996, p. 33, pl. 1, figs. 16–20, 25, 26 (cum. syn.). – NAVAS-PAREJO et al. 2017, p. 388, pl. 1, fig. 7.

Diagnosis: Elongate P_1 elements, both dextral and sinistral, with two parapets, short ventral denticulated fixed blade transforming into a rostral parapet and a dorsal free blade ornamented by prominent discrete denticles.

Description: Free blade joins the platform in rostral position and continues dorsally as a rostral parapet. The highest denticle of the blade is near the junction of blade and platform and located on the ventral part of the rostral parapet, which in majority of specimens is convex. The caudal parapet is mostly straight, but in some specimens, it may also be convex. Both parapets are covered by regularly spaced, parallel transverse ridges. The parapets merge near the dorsal end of the element. A short dorsal free blade ornamented by several discrete prominent denticles can reach one quarter of the platform length. It extends either from parapet (pl. 1, figs. 3, 4) or has a medial position (pl. 1, figs. 5–7).

Remarks: *Adetognathus spathus* differs from *A. lautus* and *A. unicornis* by having a dorsal free blade. The dorsal free blade of *A. spathus* resembles the dorsal nodes of some *Rhachistognathus* species (e. g., *R. muricatus*), but differs from the latter by a much narrower platform part beneath it.

Range: Lower Pennsylvanian (Morrowan–lower Atokan) of North America (including Mexico).

Occurrence: Samples 63–107; *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 174 specimens.

Adetognathus unicornis (Rexroad and Burton 1961)

Plate 3, figures 18, 19, 23, 24

Streptognathodus unicornis REXROAD and BURTON 1961, p. 1157, pl. 138, figs. 1–9. – DUNN 1965, p. 1149, pl. 140, figs. 5–6, 13–14. – WEBSTER 1969, p. 49, pl. 4, fig. 13.

Adetognathus unicornis (Rexroad and Burton). – LANE 1967, p. 930, pl. 119, figs. 16–21. – DUNN 1970a, p. 327, pl. 61, figs. 20–22. – NEMIROVSKAYA, in KOZITSKAYA et al. 1978, p. 17, pl. 15, figs. 1–2 (cum. syn.). – NEMIROVSKAYA 1983, pl. 1, fig. 20. – GRAYSON 1990, pl. 2, figs. 25–26. – WEIBEL and NORBY 1992, text-figure 4, pl. 1, figs. 1–16. – NEMYROVSKA 1999, p. 52, pl. 1, fig. 11 (cum. syn.). – ABPLANALP et al. 2009, Figs. 7.24–8.28. – NEMYROVSKA 2017, pl. 1, figs. 9–1.

Cavusgnathus tyththus BROWN and REXROAD in BROWN et al. 1990, p. 81, pl. 1, figs. 1, 4–6, 8, 10–12, 14 (non fig. 18 = ?*C. unicornis*). – KRUMHARDT, HARRIS and WATTS 1996, p. 34, pl. 1, figs. 7–10 (non figs. 11–12 = ?*C. unicornis*).

Cavusgnathus monocerus BROWN and REXROAD in BROWN et al. 1990, p. 82.

Diagnosis: Elongate narrow P_1 element lacking fixed blade, having two almost equal ridged parapets and a deep groove between them. Free blade joins the platform in a median position, or offset close to rostral position, and bears one large denticle on its dorsal end.

Description: Both sinistral and dextral P_1 elements are narrow and elongated. Two almost equal parapets are ornamented by regularly spaced transverse ridges. A deep and rather wide groove separates the parapets. The free blade is short, it joins the platform in its median position or in a submedian rostral po-

sition. The largest prominent denticle is on the dorsal end of the free blade.

Remarks: The original description of *Adetognathus unicornis* (Rexroad and Burton 1961, p. 1157) indicated that “the blade is median (except in some forms believed to be transitional with *Cavusgnathus*).” Lane and Straka (1974) noted that “the position of the free blade and platform junction is marginal, although in oral view, the junction commonly appears to be central or subcentral due to the presence of the broadened abnormally large denticle at the posterior end of the free blade.”

Brown and Rexroad (in Brown et al. 1990) established a new species *Cavusgnathus tyththus* representing the intermediate form between *C. unicornis* and *C. monocerus* (= *A. unicornis*). We consider that *C. tyththus* is possible a junior subjective synonym of *A. unicornis* because of the absence of a fixed blade and other features in the former species, except morphotype á (Brown et al. 1990, pl. 1, figs. 4, 8, 14, 18) that remains as *Cavusgnathus* due to its fixed blade. In addition, “*A. tyththus*” was identified in the lowest Pennsylvanian samples in the Arrow Canyon section (Lane et al. 1999, table 1). However, we failed to find such forms in the samples we examined.

Due to the poor preservation of *A. unicornis* specimens within the studied interval, only older specimens from samples 21 and 35 have been illustrated. In our specimens of *A. unicornis*, the junction of the free blade and platform can show subtle variations from median to rostral placement. We regard such variation as intraspecific. A sinistral example from sample 21 (pl. 3, fig. 24) probably is a “*C. tyththus*” morphotype due to its rostral-positioned junction with the platform. “*Cavusgnathus tyththus*” was previously known only from right-handed (dextral) elements, which was the reason that Brown et al. (1990) and Krumhardt, Harris and Watts (1996) excluded the “*C. tyththus*” morphotype from *Adetognathus*.

Adetognathus unicornis differs from the other *Adetognathus* species by having its free blade not attached to the parapet.

Range: Upper Mississippian (Chesterian) of North America, upper Serpukhovian of Eastern Europe (Donets Basin, Moscow Syncline).

Occurrence: Samples 8–51; *Adetognathus unicornis* Zone to lower part of the Upper *Rhachistognathus muricatus* Zone of the Arrow Canyon section.

Material: 10 specimens.

Family GNATHODONTIDAE Sweet 1988

Declinognathodus Dunn 1966

Type species: *Cavusgnathus nodulifera* Ellison and Graves 1941; Lower Pennsylvanian (Morrowan) of North America.

Diagnosis: *Declinognathodus* contains two large groups of species. One group is characterized by nodose decoration of the main structures of the platform, another group bears the platform covered by transverse ridges.

Nodose group: Sinistral and dextral P_1 elements with an elongate and narrow platform consisting of two unequal parapets, separated by trough. Parapets are decorated by nodes. Free blade joins the platform in medial position and extends dorsally

as a carina. Carina commonly declines rostrally, merges with the parapet and continues as one structure (carina-parapet) to the dorsal end. Or carina declines to the rostral parapet, and touching it continues to the dorsal end parallel to the parapet. Ventral part of the rostral parapet is reduced to one or series of nodes. The number of nodes and length of this ventral part of the parapet before fusion it with carina is the main feature to differentiate the important species of nodose *Declinognathodus* such as *D. inaequalis*, *D. noduliferus* and *D. japonicus*. The youngest *Declinognathodus* – *D. marginodosus* and *D. donetzianus* have very short ventral part of the rostral parapet (big node, nodes or bar) isolated from the fused carina and rostral parapet. Caudal and rostral parapets are separated by a groove or connected by transverse ridges after fusion with carina.

Ridged Group: Symmetrically paired P_1 elements with an elongate and narrow platform covered by transverse ridges. A median groove or a notch commonly occur and cut the transverse ridges. Free blade joins the platform in medial position and extends dorsally as a carina. Carina declines to rostral side of the platform and commonly merges with it. Node or a series of nodes present on the ventral-rostral side of the platform, except in *D. praenoduliferus*.

Remarks: “*Declinognathodus* differs from *Idiognathoides* by median junction of the blade with the platform and presence of ventral-rostral nodes in most species. *Declinognathodus* can be distinguished from *Gnathodus* and *Neognathodus* by its commonly rostrally declined carina which merges with the rostral parapet and the presence of ventral-rostral nodes/node in most species (Hu, Nemyrovska and Qi 2018)”.

Declinognathodus noduliferus (Ellison and Graves 1941) *sensu lato*

Plate 3, figures 8–17, 20, 21

Cavusgnathodus nodulifera ELLISON and GRAVES 1941, p. 45, pl. 3, fig. 4 (only).

Streptognathodus parallelus CLARKE 1960, p. 29, pl. 5, figs. 6–8, 14–15.

Declinognathodus nevadensis DUNN 1966, p. 1300, pl. 158, figs. 4, 8.

Gnathodus nodulifera (Ellison and Graves). – KOIKE 1967, pl. 3, figs. 9–12. – HIGGINS and BOUCKAERT 1968, p. 33–35, pl. 2, figs. 6, 12.

Declinognathodus noduliferus (Ellison and Graves). – DUNN 1970a, pl. 62, figs. 1, 2. – AISENVERG et al. 1979, pl. 6, figs. 17, 18. – PARK 1983, pl. 5, figs. 1–3. – SAVAGE and BARKELEY 1985, Fig. 9, figs. 1–8. – NEMYROVSKAYA and ALEKSEEV 1995, pl. 1, figs. 2–4, 7. – MIZUNO 1997, Figs. 12, 6–8. – BRECKLE et al. 1997a, b, pl. 1, figs. 2–4. – NEMYROVSKA 1999, pl. 2, figs. 3, 6, 10. – KULAGINA et al. 2000, pl. 2, figs. 8, 10. – WANG and QI 2003a, pl. 2, fig. 3. – WANG and QI 2003b, pl. 1, fig. 18. – WANG et al. 2004, pl. 2, fig. 10. – SANZ-LÓPEZ et al. 2006, pl. 1, figs. 3, 4. – BONCHEVA et al. 2007, pl. 1, figs. 2, 3, 5, 8, 10, 11. – ATAKUL-ÖZDEMİR et al. 2012, pl. 1, figs. 8–11 (only). – HU et al. 2017, Figs. 4O, 4P, 4Q. – HU, QI and NEMYROVSKA 2018, p. 18, Figs. 6G–6L (cum. syn.).

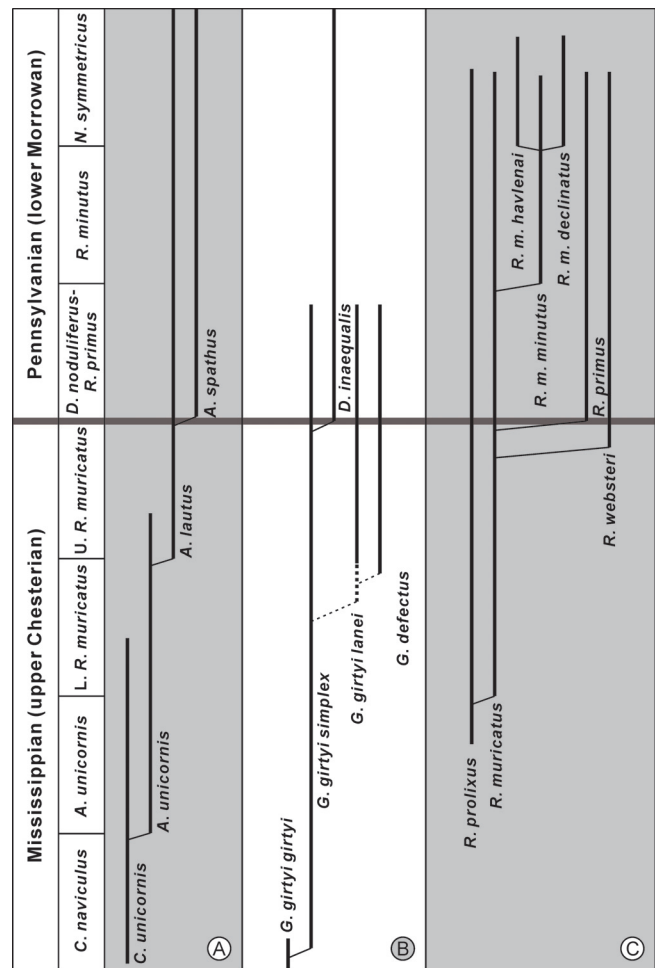
Gnathodus noduliferus (Ellison and Graves). – LANE et al. 1971, pl. 1, fig. 32.

Idiognathodus noduliferus (Ellison and Graves). – LANE and STRAKA 1974, figs. 35, 4–35, 6, 35.10–35.12 (only); figs. 41.15–41.17.

Idiognathoides noduliferus noduliferus (Ellison and Graves). – HIGGINS 1975, p. 54, pl. 14, figs. 15, 16. – METCALFE 1980, pl. 38, figs. 16, 18.

Idiognathoides noduliferus inaequalis HIGGINS 1975, p. 53, pl. 12, figs. 1–7, 12, pl. 14, figs. 11–13, pl. 15, figs. 10, 14. – METCALFE 1980, pl. 38, figs. 10, 11, 12, 15.

Declinognathodus noduliferus noduliferus (Ellison and Graves). – GRAYSON et al. 1985, pl. 1, figs. 9, 15. – RUI, WANG and ZHANG 1987, pl. 1, figs. 5, 11. – WANG and HIGGINS 1989, pl. 2, figs. 5, 9. – KRUMHARDT, HARRIS and WATTS 1996, p. 36, pl. 3, figs. 10–14



TEXT-FIGURE 5

Phylogenetic hypothesis of the shallow-water mid-Carboniferous (late Chesterian-early Morrowan) conodonts. A. = *Adetognathus*, C. = *Cavusgnathus*, G. = *Gnathodus*, D. = *Declinognathodus*, N. = *Neognathodus*, R. = *Rhachistognathus*. The heavier gray line showing mid-Carboniferous boundary.

(only). – WANG and QI 2002, pl. 1, fig. 14. – SANZ-LÓPEZ and BLANCO-FERRERA 2012, Figs. 4.20–21.

Declinognathodus noduliferus inaequalis (Higgins). – GRAYSON et al. 1985, pl. 1, figs. 1, 5, 10. – HIGGINS 1985, pl. 6.2, fig. 11, 12, 14, pl. 6.3, figs. 1, 4. – WANG, RUI and ZHANG 1987, pl. 3, figs. 1, 2, pl. 6, fig. 10. – SKOMPSKI 1996, p. 196, pl. 8, figs. 14, 15. – NEMYROVSKA 1999, pl. 1, figs. 7, 9, 12. – WANG and QI 2003b, pl. 1, figs. 9, 19. – FALLON and MURRAY 2015, Figs. 7b, c.

Declinognathodus inaequalis (Higgins). – RILEY et al. 1987, pl. 3, figs. 28–46. – VARKER 1994, pl. 4, figs. 1. – MIZUNO 1997, p. 248, Fig. 12. 1–12, 5. – KULAGINA et al. 2000, pl. 2, figs. 4–6, 14. – SANZ-LÓPEZ et al. 2006, pl. 1, figs. 1, 2. – ATAKUL-ÖZDEMİR et al. 2012, pl. 1, fig. 3–7. – SANZ-LÓPEZ and BLANCO-FERRERA 2013, Figs. 5G–5O. SANZ-LÓPEZ et al. 2013, Fig. 4K. – HU et al. 2017, Figs. 4M, 4N. – HU, QI and NEMYROVSKA 2018, p. 11, Figs. 6A–6C (cum. syn.).

Declinognathodus lateralis (Higgins and Bouckaert). – WANG and QI 2003b, pl. 1, fig. 3 (only). – HU, QI and NEMYROVSKA 2018, p. 11, Figs. 8A–8D (cum. syn.).

“*Declinognathodus*” *noduliferus* (Ellison and Graves). – GRAYSON, MERRILL and LAMBERT 1990, pl. 1, figs. 21, 22.

Declinognathodus japonicus (Igo and Koike). – HU, QI and NEMYROVSKA 2018, p. 15, Figs. 6M–6P (cum. syn.).

Declinognathodus tuberculosus HU, QI and NEMYROVSKA 2018, p. 20, Figs. 5N, 5O, 8M, 9A–9S (cum. syn.).

Declinognathodus noduliferus s. l. NAVAS-PAREJO et al. 2017, p. 390, pl. 1, figs. 3, 4.

Diagnosis: see diagnosis of *Declinognathodus* genus.

Description: Both sinistral and dextral P_1 elements have a lanceolate, elongate shape. The dorsal end is pointed, or less commonly sub-rounded. Blade is the same length with the platform or slightly longer. It joins the platform in its median position and continues as a rostrally declined short carina that merges with the rostral parapet. The ventral part of rostral parapet is reduced to one to six nodes, which is separated from carina by a narrow sulcus and may be semi-fused. The rostral parapet is parallel with the caudal one and of equal height or slightly elevated. They are both ornamented with regularly spaced nodes or ridges and separated by a groove, which is as long as the platform. The groove is deep ventrally and gets shallower or is even absent dorsally. Sometimes the groove displays as a notch in the dorsoventral direction. In this case, the rostral parapet is commonly elevated. Laterally the platform is flat. The basal cavity is deep, moderately wide and almost symmetrical.

Remarks: The nodose *Declinognathodus noduliferus s. l.* group includes *D. noduliferus*, *D. inaequalis* and *D. japonicus*. These species differ from each other mainly by the length of carina and number of nodes on the ventral part of reduced rostral parapet. For instance, *D. noduliferus* (pl. 3, figs. 14, 15) differs from *D. inaequalis* (pl. 3, figs. 10–12) by a shorter carina and fewer nodes on the rostral side of the platform, and differs from *D. japonicus* (pl. 3, fig. 13) by a longer carina and more nodes on rostral side of the platform. *Declinognathodus noduliferus* is similar to the late Bashkirian and early Moscovian species *D. marginodosus* but the latter has more loosely spaced nodes on the parapets and an isolated node or longitudinal ridge on ventral-rostral side of the platform.

The ridged *Declinognathodus noduliferus s. l.* group consists of *D. lateralis*, *D. praenoduliferus* Nigmatdganov and Nemirovskaya 1992, *D. berneseae* Sanz-López et al. 2006, *D. pseudolateralis* Nemyrovska 1999, *D. tuberculosus* and *D. intermedius* Hu et al. 2018. Except for *D. lateralis*, most of the ridged *D. noduliferus* group species were recovered from deep-water sections, e.g., Central (Middle) Asia (Nigmatdganov and Nemirovskaya 1992), Cantabrian Mountains, Spain (Sanz-López et al. 2006; Nemyrovska et al. 2011), South China (Hu et al. 2017; Hu et al. 2018) and South Urals, Russia (Kulagina et al. 2014; Nikolaeva et al. 2017). In the shallow-water Arrow Canyon section, some specimens were assigned as *D. tuberculosus* by their ridged parapets and elevated rostral parapet (pl. 3, figs. 17, 20, 21) but they may represent a younger morphotype of *D. tuberculosus*. In central Iran, a similar fauna including *Rhachistognathus* and ridged *Declinognathodus* species was also recorded (Bahrami et al. 2014).

The nodose *Declinognathodus noduliferus* group can be easily distinguished from ridged *Declinognathodus* forms by nodose parapets with equal height and a groove extending to the dorsal end of the platform.

Range: Morrowan of North America (USA, Canada and Mexico) and Bashkirian of Eurasia (South China, North China,

Eastern Europe, South Urals, Central Asia, Western Europe, Spain).

Occurrence: Samples 61–107 and upwards; *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone through the *Neognathodus symmetricus* Zone and upwards in the Arrow Canyon section.

Material: More than 268 specimens (more than 200 specimens in sample 107).

Gnathodus Pander 1856

Type species: *Polygnathus bilineatus* Roundy 1926, by subsequent designation (Lane and Ziegler 1984), Mississippian of North America.

Diagnosis: P_1 element with a long blade, which joins the platform in median position and extends to the dorsal end as nodose carina. One or two ridged or nodose parapets vary in length. Rostral expansion of the platform is smooth, or weakly to strongly ornamented with nodes. Basal cavity is deep, wide and asymmetrical.

Remarks: *Gnathodus* of the Mississippian-Pennsylvanian boundary interval differs from *Declinognathodus* by lack of declination of the carina to the rostral parapet. *Gnathodus* differs from *Idiognathoides* by median junction of free blade to the platform.

Gnathodus defectus Dunn 1966

Plate 4, figures 13–15, 17, 19

Gnathodus defectus DUNN 1966, p. 1300, pl. 158, figs. 1, 5. – WEBSTER 1969, p. 32, pl. 5, fig. 16. – DUNN 1970a, text-fig. 4. – DUNN 1970b, p. 331, pl. 62, figs. 15, 16, text-fig. 9C. – TYNAN 1980, pl. 1, fig. 20. – MORROW and WEBSTER 1991, pl. 3, figs. 6, 7. – MORROW and WEBSTER 1992, pl. 1, fig. 2. – DUMOULIN and HARRIS 1993, Fig. 8B. – KRUMHARDT, HARRIS and WATTS 1996, p. 40, pl. 2, figs. 23, 24, 31–33; pl. 4, fig. 26 (cum. syn.). – BRECKLE et al., 1997a, b, pl. 1, fig. 20.

Diagnosis: P_1 element with nodose carina, one very short, ridged caudal parapet. Rostral side of the platform is unornamented, smooth.

Description: P_1 element of subtriangular shape has a high nodose carina and one short caudal parapet. The nodes of the carina are loosely spaced in the dorsal half of the element. Dorsal end of carina is prominent, smooth and beak-like in shape. Caudal parapet is developed mostly in the ventral part of the platform and is commonly flared caudally. It consists of several transverse ridges and occupies one-third to one-half of the platform length. A shallow groove separates the short parapet from the carina. The rostral side of the element is smooth, unornamented.

Remarks: Although the original description of *G. defectus* (Dunn 1966, p. 1300) indicated “nodes of carina on posterior half of platform fused with laterally located nodes, forming short, prominent transverse ridges,” the dorsal part of the holotype of *G. defectus* (Dunn 1966, pl. 158, fig. 1) appears not to be prominent ridge-like. Only one other specimen (Dunn 1966, pl. 158, fig. 5) fits his description well. In our examined samples, the specimens of *G. defectus* are closer to Dunn (1970a, pl. 62, fig. 16). The caudal parapets of *G. defectus* illustrated by Dunn (1966, pl. 158, fig. 5) and Dunn (1970a, pl. 62,

fig. 15) are more nodose and fused with the carina dorsally, but the short parapet of our specimens is caudally flared and consists of transverse ridges. The specimen assigned to *G. defectus* illustrated by Webster (1969, pl. 5, fig. 16) is similar to Dunn's holotype of *G. defectus* except for the presence of a large node on the rostral side of the platform in Webster's specimen. The specimens illustrated by Morrow and Webster (1991; 1992) and Krumhardt et al. (1996) are very similar to ours.

Gnathodus defectus differs from *G. girtyi simplex* by having a shorter caudal parapet and by absence of the reduced rostral parapet, which consists of several nodes in *G. girtyi simplex*. The smooth, unornamented rostral side of the platform distinguishes *G. defectus* from *G. lanei*.

Range: Uppermost Mississippian (Chesterian)–lowermost Pennsylvanian (lower Morrowan) of North America.

Occurrence: Samples 42–76; Lower *Rhachistognathus muricatus* Zone to *Declinognathodus noduliferus*–*R. primus* Zone of the Arrow Canyon section.

Material: 215 specimens.

***Gnathodus girtyi simplex* Dunn 1965**
Plate 4, figures 1, 2, 18

Gnathodus girtyi simplex DUNN 1965, p. 1148, pl. 140, figs. 2, 3, 12. – DUNN 1970a, text-fig. 4. – DUNN 1970b, p. 331, pl. 62, fig. 17, text-fig. 9B. – TYNAN 1980, p. 1303, pl. 1, figs. 5–7. – LANE et al. 1985, figs. 7A, 7B. – MORROW and WEBSTER 1992, pl. 1, fig. 4. – DUMOULIN and HARRIS 1993, Fig. 8C. – KRUMHARDT, HARRIS and WATTS 1996, p. 41, pl. 2, figs. 25–27. – BRECKLE et al. 1997a, b, pl. 1, fig. 1.

Gnathodus girtyi rhodesi Higgins. – WARDLAW 1985, pl. 1, fig. 11.

Diagnosis: P₁ element of subtriangular shape with nodose carina, which extends to the dorsal end of the element, and two unequal parapets. The caudal parapet is prominent and consists of generally irregular transverse nodes or ridges; rostral parapet is reduced to one to four nodes, sometimes even more, and having ventral margin offset dorsally from that of the caudal parapet.

Description: P₁ element is characterized by nodose carina and two unequal parapets. Carina is ornamented by irregularly spaced nodes. They are more tightly spaced in its ventral half but very loosely spaced in its dorsal half. Carina can be slightly declined rostrally before its nodes merge with the caudal parapet in the dorsal third of the element. The caudal parapet is well developed, ornamented by short transverse ridges and extends to the dorsal end (pl. 4, fig. 1). Only the ventral half or two thirds of the caudal parapet are well developed in some specimens. In its dorsal third the transverse ridges may be replaced by loosely spaced nodes, which are much lower in height than the ventral part of the parapet. The rostral parapet is reduced to one or two nodes, sometimes more, which are always offset dorsally from the ventral margin of the platform. The nodes are commonly located on the low thin longitudinal step-like structure that goes dorsally parallel to carina and resembles the remnant of the rostral parapet (pl. 4, fig. 2). The basal cavity is large and deep, it is the widest beneath the ventral part of the platform.

Remarks: Nodes of the rostral parapet in *Gnathodus girtyi simplex* vary from one to four (pl. 4, figs 1 and 17 respectively) in

number and in their distance from the ventral margin of the element.

Gnathodus girtyi simplex differs from all other subspecies of *G. girtyi* by having a much reduced rostral parapet consisting of several discrete nodes located offset dorsally from the ventral margin of the element. The well-developed caudal parapet helps to distinguish *G. girtyi simplex* from *G. defectus* and *G. lanei*. The dorsally offset rostral parapet (nodes) differentiate *G. girtyi simplex* from similar nodose *Declinognathodus* species.

The specimens illustrated by Nemyrovska (2005, pl. 7, figs. 16–20) from the Triollo section, Palencia, Cantabrian Mountains, northern Spain, are very similar to *Gnathodus girtyi simplex*. Although they were identified as transitional forms between *G. girtyi* and *G. girtyi simplex*, more specimens are needed for a positive assignment. The specimens from England identified by Higgins (1975) as *G. girtyi simplex* do not have the characteristic features of *G. girtyi simplex*—a reduced rostral parapet to one or several nodes located offset of the ventral margin of the platform. *Gnathodus girtyi simplex* and transitional forms between *G. girtyi girtyi* and *G. girtyi simplex* have been recorded from the Viséan–Serpukhovian boundary interval in South China (Wang et al. 2014; Qi et al. 2014). However, only one specimen of *G. girtyi simplex* has been found in the lowermost Pennsylvanian in South China (Hu, Qi and Nemyrovska 2018, Fig. 3A).

Range: Upper Mississippian–lowermost Pennsylvanian (Morrowan) of North America and lowermost Pennsylvanian of South China.

Occurrence: Samples 5–77; *Adetognathus unicornis* Zone to *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone of the Arrow Canyon section (Lane et al. 1999; this study).

Material: 190 specimens.

***Gnathodus girtyi simplex* Dunn 1965 transitional to *Declinognathodus inaequalis* (Higgins and Bouckaert 1968)**
Plate 4, figures 10–12

Gnathodus girtyi simplex transitional to *Declinognathodus noduliferus*, LANE et al. 1985, fig. 7C. – BRECKLE et al. 1997a, b, pl. 1, figs. 5–7.

Remarks: The specimens display intermediate features between *Gnathodus girtyi simplex* and *Declinognathodus inaequalis*. The caudal parapet of our specimens is similar to that found in both of these taxa, but is closer to that of *D. inaequalis* because it is less caudally flared than the prominent caudal parapet of *G. girtyi simplex*. The rostral parapet consists mostly of one node, which is shifted ventrally. It is less offset from the ventral margin of the element than that of *G. girtyi simplex*. These features make it morphologically closer to *D. inaequalis*.

Occurrence: Samples 45–76, Upper *Rhachistognathus muricatus* Zone to *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone (uppermost Chesterian–lowermost Morrowan) of the Arrow Canyon section.

Material: 83 specimens.

***Gnathodus lanei* Nemyrovska, Qi and Hu n. sp.**
Plate 4, figures 4, 5, 7–9, 16a–16

Gnathodus defectus Dunn. – WEBSTER 1969, p. 32, pl. 5, fig. 16.

Gnathodus girtyi simplex–*G. defectus* transitional specimen. – BRECKLE et al. 1997a, b, pl. 1, figs. 11–13.

Diagnosis: P₁ element of subtriangular shape with high, nodose carina, one short prominent ridged parapet at the ventral part of the caudal side of the platform and one node at its rostral side. Dorsal end of carina is beak-like in shape.

Description: P₁ elements with elongated subtriangular platform. Prominent carina consists of fused nodes and extends much longer dorsally than the parapet. Its ventral part is smooth; its dorsal end is prominent, smooth, beak-like in shape. A short well-developed parapet is located in the ventral half of the platform, it consists of transverse ridges and usually does not reach the height of the carina. The rostral side of the platform bears a node opposite to the middle part of the caudal parapet. Commonly, the rostral node is small. The caudal and rostral slopes of the platform are steep and high but the highest one is the carina. Laterally the element is flat and declines sharply to the dorsal end.

The basal cavity is large and deep; it is the widest beneath the ventral part of the platform.

Remarks: The new species was formally identified as transitional between *Gnathodus girtyi simplex* and *G. defectus* (Breckle et al. 1997a, b, pl. 1, figs. 11–13). The *Gnathodus girtyi simplex*–*G. defectus* transition form listed in the previously published range chart of Lane et al. (1999, table 3) was revised and identified as *G. lanei* in this paper. *Gnathodus lanei*

is very similar in morphology to *G. defectus*, especially in its prominent smooth beak-like dorsal end (pl. 4, figs. 4b, 7b, 16c), but differs from the latter by having a node at the rostral side of the platform. *Gnathodus lanei* differs from *G. girtyi simplex* by its shape and much shorter length of the parapet and by having only one node at the rostral side of the platform. The beak-like, dorsal end of *G. girtyi simplex* is not as prominent as in *G. defectus* and *G. lanei*. Such a prominent smooth and high dorsal end is also the characteristic feature of conodonts of the genus *Ferganaegnathodus* Nemirovskaya and Nigmatdjanov 1993 (Nemirovskaya and Nigmatdjanov 1993, p. 214–215, pl. 1, figs. 1–3, 6).

Holotype: dextral P₁ element, sample 54, SUI 147446, Plate 4, figs. 16a, 16b and 16c. Upper *Rhachistognathus muricatus* Zone, Bird Spring Formation, uppermost Mississippian, Arrow Canyon, Nevada.

Etymology: The species is named for Dr. H. Richard Lane, the outstanding Carboniferous conodont worker.

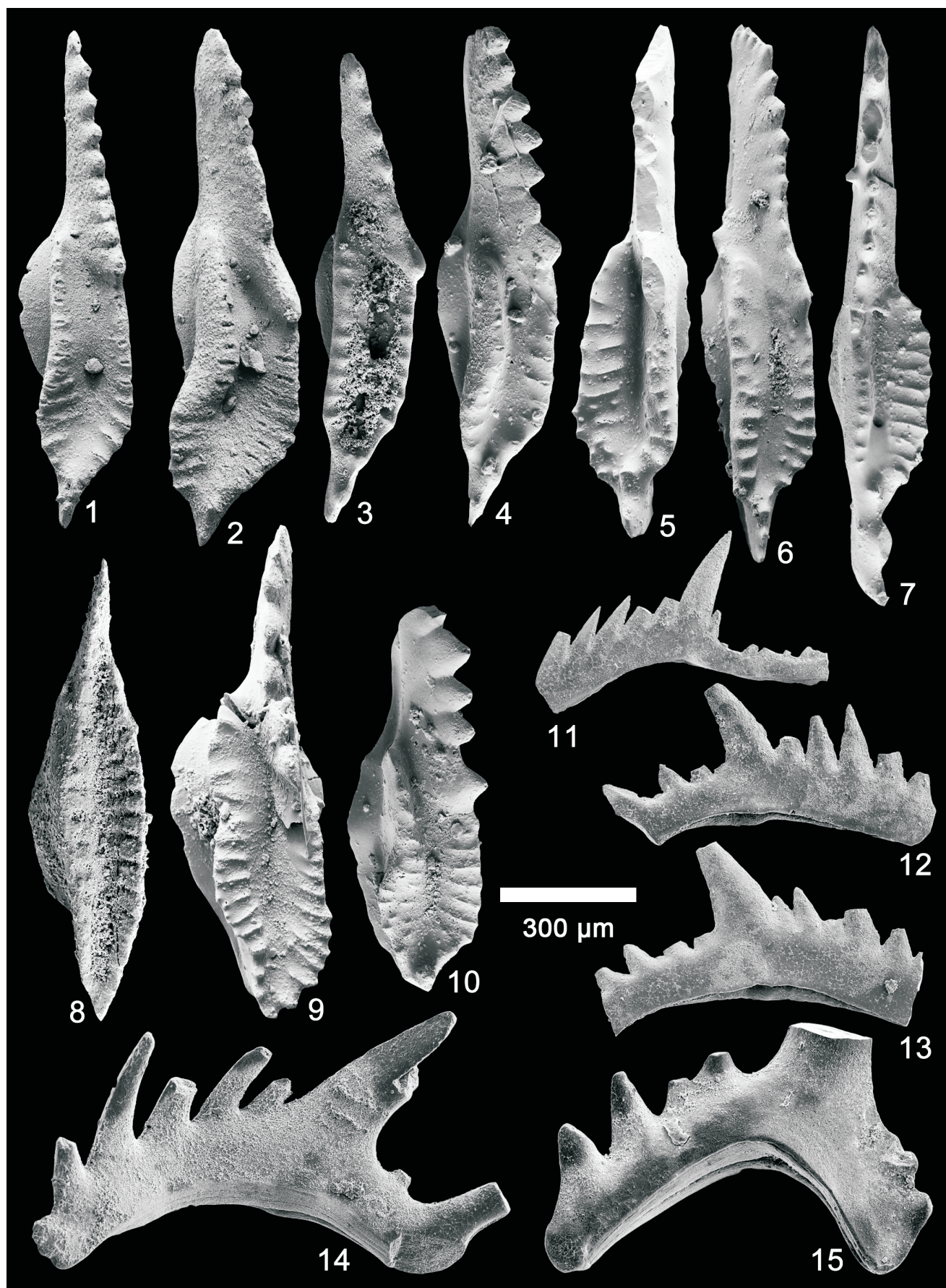
Occurrence: Samples 45–76; Upper *Rhachistognathus muricatus* Zone to *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone (Uppermost Chesterian–lowermost Morrowan) of the Arrow Canyon section.

Material: 117 specimens.

PLATE 1

Figures 1–10 are upper views of P₁ elements; figures 11–13 are lateral views of P₂ elements; and figures 14, 15 are lateral views of S elements. Scale bar = 300 µm.

- 1 *Adetognathus lautus* (Gunnell 1933)–*Adetognathus spathus* (Dunn 1966) transitional form, dextral element, SUI 147380, sample 62.
- 2 *Adetognathus lautus* (Gunnell 1933)–*Adetognathus spathus* (Dunn 1966) transitional form, dextral element, SUI 147381, sample 62.
- 3 *Adetognathus spathus* (Dunn 1966), dextral element, SUI 147382, sample 72.
- 4 *Adetognathus spathus* (Dunn 1966), dextral element, SUI 147383, sample 63.
- 5 *Adetognathus spathus* (Dunn 1966), dextral element, SUI 147384, sample 63.
- 6 *Adetognathus spathus* (Dunn 1966), dextral element, SUI 147385, sample 72.
- 7 *Adetognathus spathus* (Dunn 1966), sinistral element, SUI 147386, sample 63.
- 8 *Adetognathus lautus* (Gunnell 1933), sinistral element, SUI 147387, sample 100.
- 9 *Adetognathus lautus* (Gunnell 1933), dextral element, SUI 147388, sample 53.
- 10 *Adetognathus lautus* (Gunnell 1933), dextral element, SUI 147389, sample 63.
- 11 P₂ element of *Gnathodus girtyi simplex* Dunn 1965, SUI 147390, sample 64.
- 12 P₂ element of *Gnathodus girtyi simplex* Dunn 1965, SUI 147391, sample 64.
- 13 P₂ element of *Gnathodus girtyi simplex* Dunn 1965, SUI 147392, sample 64.
- 14 S element of *Adetognathus* sp., SUI 147393, sample 94.
- 15 S element of *Adetognathus* sp., SUI 147394, sample 93.



Family IDIOGNATHODONTIDAE Harris and Hollingsworth 1933

Idiognathoides Harris and Hollingsworth 1933

Type species: *Idiognathoides sinuata* Harris and Hollingsworth 1933, Lower Pennsylvanian (Morrowan) of North America.

Diagnosis: Narrow elongated platform with lateral junction of long free blade, which continues onto the platform to the dorsal end as a high rostral parapet. Median groove of different length and depth, if present, can separate the rostral and caudal parapets. Parapets are decorated by nodes or ridges, which in turns can be continuous or dissected. In lateral view the elements can be straight or arched. The basal cavity is large and deep.

Remarks: see remarks of genera *Declinognathodus* and *Gnathodus*.

Idiognathoides aff. *convexus* (Ellison and Graves 1941)

Plate 3, figs 1–7

Diagnosis: Asymmetrically paired P₁ elements are narrow, lanceolate in shape, with lateral junction of free blade to the platform. The platform is covered by convex transverse ridges. Short groove/sulcus occurs in the ventral part of the platform; it separates there two parapets. The platform is straight to moderately convex orally and laterally.

Description: Asymmetrically paired elements are narrow.

Dextral elements: The greater part of the platform is covered by regularly spaced transverse ridges. Relatively short groove (sulcus) occurs at the ventral end of the platform; its length and depth can vary; it can be wider and longer with growth. The convexity of the ridges, which directed toward the dorsal end, is also variable from straight to moderately convex orally and laterally.

Sinistral elements: Platform is also covered by transverse ridges, they can be only partly covered in juveniles in their dorsal part. The groove between the parapets is much longer in the sinistral elements. The parapets are of different height; the rostral one is higher like in *Idiognathoides sinuatus*.

Remarks: The dextral elements of *Idiognathoides* aff. *Id. convexus* are close to *Id. corrugatus* (dextral elements of *Id. sinuatus*) by the transverse-ridged decoration of the platform. But the convexity of the transverse ridges and constantly narrow platform distinguishes *Id. aff. Id. convexus* from *Id. corrugatus*, which has mostly flat or slightly concave platform in its middle part. Both dextral and sinistral elements of *Id. aff. Id. convexus* remind *Id. asiaticus* Nigmadganov and Nemirovskaya 1992 but the convexity of ridges differentiates these species.

Our specimens show the closest similarity to the illustrated conodonts of *Idiognathoides convexus* of Ellison and Graves (1941, p. 9, pl. 3, fig. 10), Webster (1969, Arrow Canyon, p. 37, pl. 5, figs. 17, 18), Dunn (1970, p.334, pl. 63, fig. 20), Lane et al. (1971, pl. 1, fig. 18) and *Polygnathodella* cf. *convexa* of Koike (1967, p. 308, pl. 3, fig. 1, 2) and sinistral element of *Id. pacificus* of Savage and Barkeley (1985, p. 1467, pl. 9, figs. 9, 19) but poor preservation, small number of specimens mostly presented by juveniles prevent us to identify this species with confidence. Webster (1969) shown the range of *Id. convexus* from the basal through the middle Morrowan, while the other workers found *Id. convexus* higher in Morrowan.

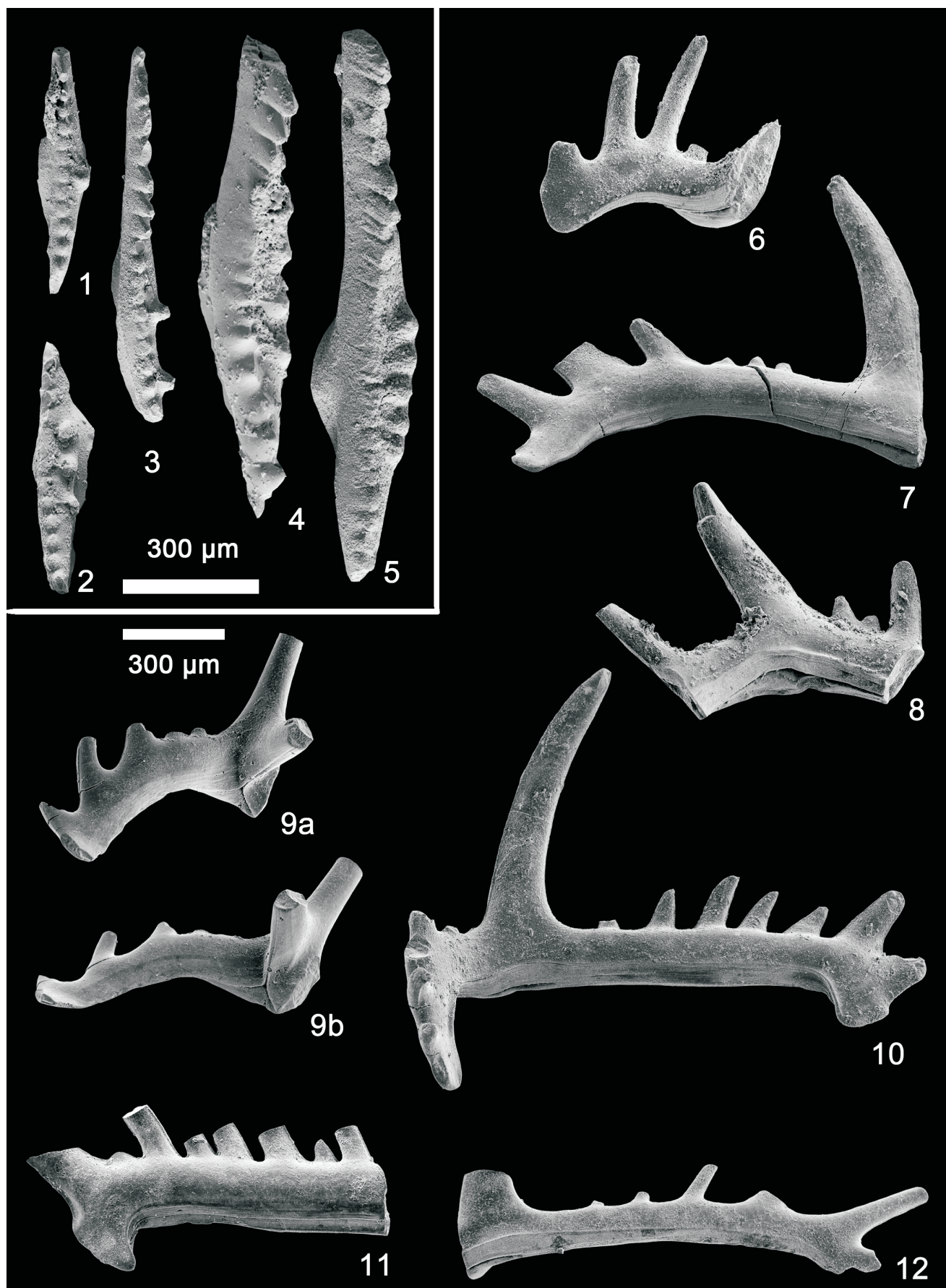
Occurrence: Samples 61–107 and upwards; *Declinognathodus noduliferus*-*Rhachistognathus primus* Zone through the *Neognathodus symmetricus* Zone and upwards in the Arrow Canyon section.

Material: 17 specimens

PLATE 2

Figures 1–5 are upper views of P₁ elements; figures 6–12 are lateral views of S elements.
Scale bar = 300 µm; note that the different magnification scales between figures 1–5 and figures 6–12.

- | | |
|---|--|
| 1 <i>Rhachistognathus prolixus</i> Baesemann and Lane 1985, sinistral element, SUI 147395, sample 81. | 7 ?S ₄ element of <i>Adetognathus</i> sp., <i>Hindeodella</i> sp., SUI 147401, sample 94. |
| 2 <i>Rhachistognathus prolixus</i> Baesemann and Lane 1985, sinistral element, SUI 147396, sample 81. | 8 S ₂ (?) element of <i>Adetognathus</i> sp., <i>Kladognathus</i> sp., SUI 147402, sample 94. |
| 3 <i>Rhachistognathus prolixus</i> Baesemann and Lane 1985, sinistral element, SUI 147397, sample 81. | 9a-b Broken S element of <i>Adetognathus</i> sp., <i>Hibardella ortha</i> Rexroad 1958, SUI 147403, sample 94. |
| 4 <i>Rhachistognathus prolixus</i> Baesemann and Lane 1985, sinistral element, SUI 147398, sample 62. | 10 ?S ₄ element of <i>Adetognathus</i> sp., <i>Hindeodella</i> sp., SUI 147404, sample 94. |
| 5 <i>Rhachistognathus prolixus</i> Baesemann and Lane 1985, sinistral element, SUI 147399, sample 63. | 11 S element of <i>Adetognathus</i> sp., SUI 147405, sample 93. |
| 6 S element of <i>Adetognathus</i> sp., SUI 147400, sample 94. | 12 S ₄ element of <i>Adetognathus</i> sp., SUI 147406, sample 94. |



Family SPATHOGNATHODONTIDAE Hass 1959

Rhachistognathus Dunn 1966

Type species: *Rhachistognathus prima* Dunn 1966

Diagnosis: P₁ element is characterized by the rostral junction of blade and platform in both sinistral and dextral elements, a deep trough, two nodose or ridged parapets and a series of nodes on the dorsal part of the platform (dorsal carina). Basal cavity is relatively large (in comparison with spathognathodids) and shallow (in comparison with gnathodontids), subsymmetrical. It extends beyond the ventral and dorsal margins of the platform.

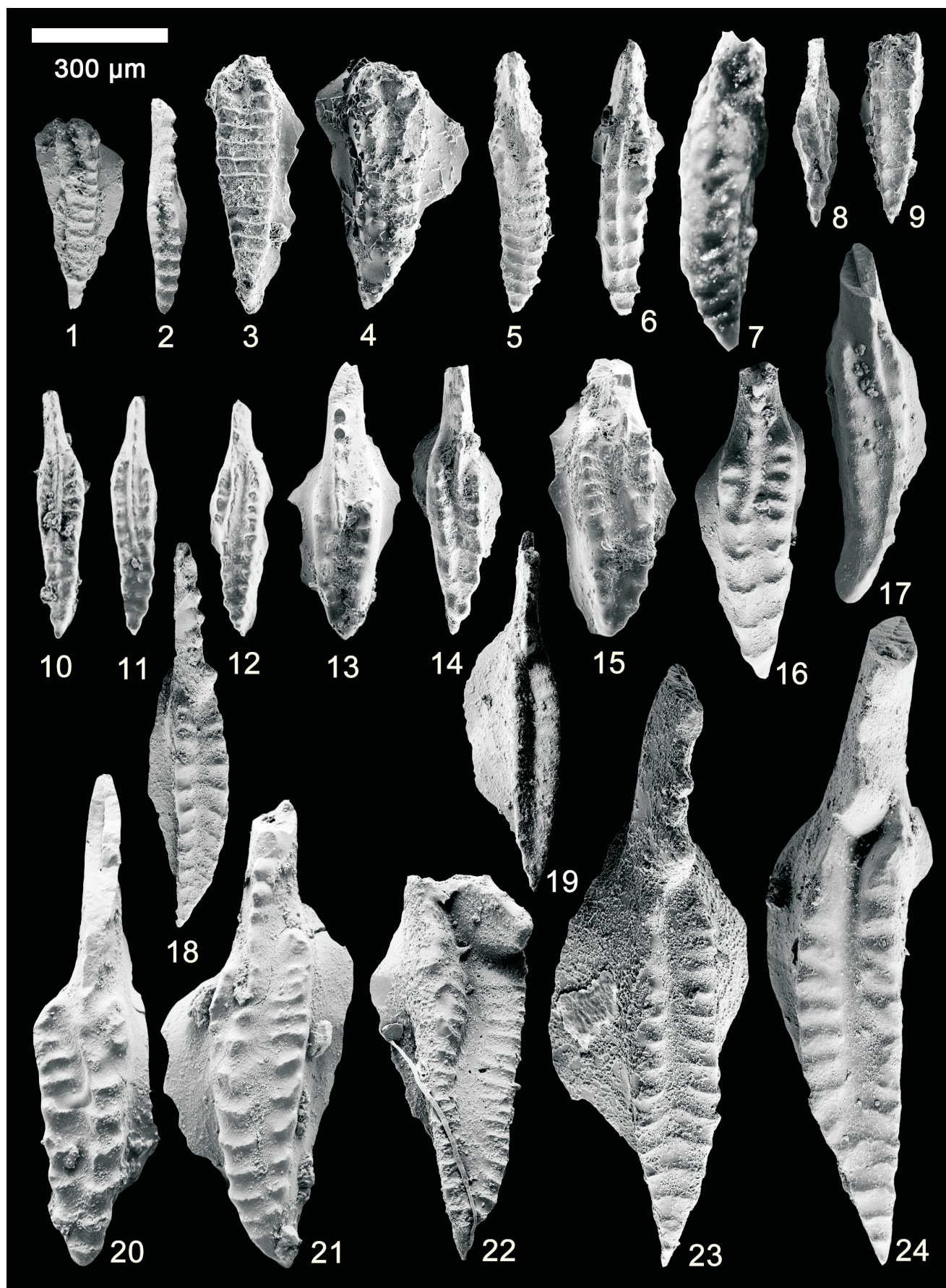
Remarks: Dunn (1966, p.1301) described the conodont genus *Rhachistognathus* with *R. primus* as type-species of this genus.

Later Dunn (1970, p.338) included this species together with two the other species (*Cavusgnathus muricatus* and *C. transitorius*) to the generic concept of *Rhachistognathus*. The similarity of this genus to other “double-rowed” spathognathodids prevented to accept *Rhachistognathus* as a valid form-genus. Conodont workers assigned the distinguished species to different genera. Webster (1969, p. 32) assigned all the species of Dunn to *Gnathodus muricatus*, which he considered them to derive probably from *G. girtyi simplex*, whereas Lane et al. (1971, p. 398) and Thompson (1972, p. 39) assigned them to the form-genus *Spathognathodus*. Higgins and Bouckaert (1968, p. 40) and Higgins (1975, p. 50) described the species of *Idiognathoides* (*Id. minuta*) that later was assigned to *Rhachistognathus* (Higgins 1985). *Rachistognathus minutus* resembles the species of *Idiognathoides* by having two parapets

PLATE 3

All illustrations are upper views of P₁ elements. Scale bar = 300 µm.

- 1 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), dextral element, SUI 147407, sample 76.
- 2 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), dextral element, SUI 147408, sample 63.
- 3 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), dextral element, SUI 147409, sample 67.
- 4 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), dextral element, SUI 147410, sample 61.
- 5 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), dextral element, SUI 147411, sample 107.
- 6 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), sinistral element, SUI 147412, sample 77.
- 7 *Idiognathoides* aff. *Id. convexus* (Ellison and Graves 1941), sinistral element, SUI 147413, sample 107.
- 8 *Declinognathodus inaequalis* (Higgins 1975), juvenile dextral element, SUI 147414, sample 61.
- 9 *Declinognathodus* cf. *D. noduliferus* (Ellison and Graves 1941), sinistral element, SUI 147415, sample 61.
- 10 *Declinognathodus inaequalis* (Higgins 1975), sinistral element, SUI 147416, sample 61B (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 2).
- 11 *Declinognathodus inaequalis* (Higgins 1975), dextral element, SUI 147417, sample 62 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 3).
- 12 *Declinognathodus inaequalis* (Higgins 1975), sinistral element, SUI 147418, sample 62 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 4).
- 13 *Declinognathodus japonicus* (Igo and Koike 1964), sinistral element, SUI 147419, sample 107.
- 14 *Declinognathodus noduliferus* (Ellison and Graves 1941), dextral element, SUI 147420, sample 95.
- 15 *Declinognathodus noduliferus* (Ellison and Graves 1941), dextral element, SUI 147421, sample 107.
- 16 *Declinognathodus noduliferus* (Ellison and Graves 1941), sinistral element, SUI 147422, sample 86.
- 17 *Declinognathodus tuberculosus* Hu, Qi and Nemyrovska 2018, dextral element, SUI 147423, sample 86.
- 18 *Adetognathus unicornis* (Rexroad and Burton 1961), dextral element, SUI 147424, sample 35.
- 19 *Adetognathus unicornis* (Rexroad and Burton 1961), dextral element, SUI 147425, sample 35.
- 20 *Declinognathodus tuberculosus* Hu, Qi and Nemyrovska 2018, dextral element, SUI 147426, sample 86.
- 21 *Declinognathodus* aff. *D. tuberculosus* Hu, Qi and Nemyrovska 2018, sinistral element, SUI 147427, sample 86.
- 22 *Cavusgnathus unicornis* Youngquist and Miller 1949–*Adetognathus unicornis* (Rexroad and Burton 1961) transitional element, dextral element, SUI 147428, sample 35.
- 23 *Adetognathus unicornis* (Rexroad and Burton 1961), dextral element, SUI 147429, sample 35.
- 24 *Adetognathus unicornis* (Rexroad and Burton 1961), sinistral element, SUI 147430, sample 21.



and trough between them in the upper view and relatively large basal cavity in lower view.

Rhachistognathus minutus minutus (Higgins and Bouckaert 1968)

Plate 5, figures 13–15

Idiognathoides minuta HIGGINS and BOUCHAERT 1968, p. 40, pl. 6, figs. 7–12.

Streptognathodus lanceolatus WEBSTER 1969, p. 47–48, pl. 6, figs. 14–15.

Rhachistognathus minutus minutus (Higgins and Bouckaert). – BAESEMANN and LANE, p. 102, pl. 2, figs. 7, 10, 11; pl. 3, figs. 1–12. – NEMIROVSKAYA and ALEKSEEV 1995, pl. 1, fig. 1. – KRUMHARDT, HARRIS and WATTS 1996, p. 48, pl. 4, figs. 13–15 (cum. syn.). – BONCHEVA et al. 2007, p. 343, pl. 1, figs. 1, 7; pl. 2, fig. 4. – ATAKUL-ÖZDEMİR, ALTINER and ÖZKAN-ALTINER 2012, pl. 1, figs. 17–19. – BAHRAMI et al. 2014, p. 198, Figs. 7.9–7.13. – HU, QI and NEMYROVSKA 2018, p. 26, Figs 5K–M (cum. syn.).

Idiognathoides minutus Higgins and Bouckaert. – HIGGINS 1975, p. 50–51, pl. 13, figs. 1–5 (non figs. 6–10, figs. 6–8 = *R. minutus havlenai*, figs. 9–10 = *R. minutus declinatus*, non pl. 15, figs. 12, 13 = *R. minutus havlenai*).

Rhachistognathus minutus (Higgins and Bouckaert). – FALLON and MURRAY 2015, Fig. 7f.

Rhachistognathus sp. JI et al. 2007, pl. 1, fig. 3.

Diagnosis: Sinistral P₁ element of a lanceolate shape, with a short platform and a long free blade attached to the platform in a rostral or submedian position, two parallel parapets consisting of nodes, a deep, relatively wide median trough and a dorsal row of 1–3 nodes. The basal cavity is relatively large and asymmetrical.

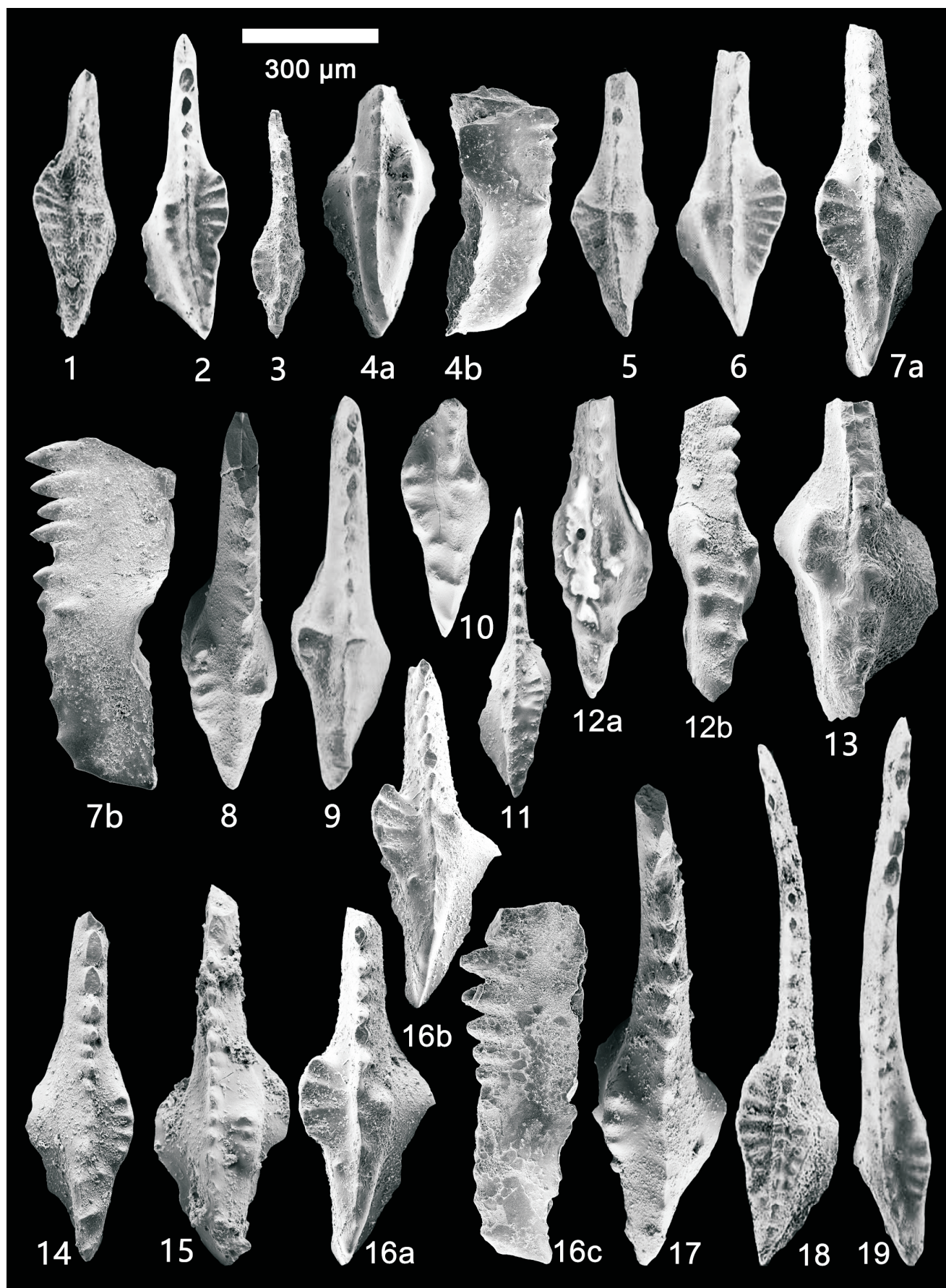
Remarks: Baesemann and Lane (1985) recognized three subspecies of *Rhachistognathus minutus*, i.e., *R. minutus minutus*, *R. minutus havlenai* and *R. minutus declinatus*, based on the position of the junction of free blade and platform and the degree of curvature of the ventral part of the rostral platform margin. *Rhachistognathus minutus minutus* is distinguished from the similar *R. muricatus* by the more tightly spaced and more uniform size and shape of the nodes on the parapets. *Rhachistognathus minutus minutus* differs from *R. primus* and *R. websteri* by having less nodes on the dorsal end of the platform and more uniform length of parapets.

PLATE 4

All illustrations are upper views of P₁ elements except for lateral views of 4b, 7b and 16c and upper-lateral view of 16b.

Scale bar = 300 µm.

- 1 *Gnathodus girtyi simplex* Dunn 1965, dextral element, SUI 147431, sample 61B (re-illustration of Brenckle et al. 1997 a, b, pl. 1, fig. 10).
- 2 *Gnathodus girtyi simplex* Dunn 1965, sinistral element, SUI 147432, sample 61B.
- 3 *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., dextral element, SUI 147433, sample 49.
- 4a, 4b *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., sinistral element, SUI 147434, sample 46.
- 5 *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., dextral element, SUI 147435, sample 64 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 12).
- 6 *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., sinistral element, SUI 147436, sample 61B (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 11).
- 7a, 7b *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., holotype, dextral element, SUI 147437, sample 54.
- 8 *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., dextral element, SUI 147438, sample 53.
- 9 *Gnathodus lanei* Nemyrovska, Qi and Hu n. sp., dextral element, SUI 147439, sample 61 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 13).
- 10 *Gnathodus girtyi simplex* Dunn 1965–*Declinognathodus inaequalis* (Higgins 1975) transitional form, dextral element, SUI 147440, sample 53.
- 11 *Gnathodus girtyi simplex* Dunn 1965–*Declinognathodus inaequalis* (Higgins 1975) transitional element, dextral element, SUI 147441, sample 62.
- 12a, b *Gnathodus girtyi simplex* Dunn 1965–*Declinognathodus inaequalis* (Higgins 1975) transitional element, dextral element, SUI 147442, sample 53.
- 13 *Gnathodus defectus* Dunn 1966, dextral element, SUI 147443, sample 59.
- 14 *Gnathodus defectus* Dunn 1966, sinistral element, SUI 147444, sample 54.
- 15 *Gnathodus defectus* Dunn 1966, sinistral element, SUI 147445, sample 52.
- 16a–c *Gnathodus lanei* Qi, Nemyrovska and Hu n. sp., dextral element, SUI 147446, sample 54.
- 17 *Gnathodus defectus* Dunn 1966, dextral element, SUI 147447, sample 54.
- 18 *Gnathodus girtyi simplex* Dunn 1965, dextral element, SUI 147448, sample 45 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 1).
- 19 *Gnathodus defectus* Dunn 1966, sinistral element, SUI 147449, sample 62 (re-illustration of Brenckle et al. 1997a, b, pl. 1, fig. 20).



Range: Lowermost Pennsylvanian of Eurasia and North America.

Occurrence: Samples 80–99, *Rhachistognathus minutus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 33 specimens.

***Rhachistognathus muricatus* (Dunn 1965)**

Plate 5, figures 4–9

Cavusgnathus muricata DUNN 1965, p. 1147, pl. 140, figs. 1, 4.

Rhachistognathus muricatus (Dunn). – KRUMHARDT, HARRIS and WATTS 1996, p. 48, pl. 4, figs. 27–30 (cum. syn.). – BRECKLE et al. 1997a, b, pl. 1, figs. 14, 15. – BONCHEVA et al. 2007, p. 343, pl. 2, figs. 8, 10, 12. – ATAKUL-ÖZDEMİR, ALTINER and ÖZKAN-ALTINER 2012, pl. 1, fig. 20. – BAHRAMI et al. 2014, p. 198, pl. 1, figs. 7.5–7.8.

Rhachistognathus proluxus (Baesemann and Lane). – NAVAS-PAREJO et al. 2017, p. 394, pl. 2, fig. 7.

Diagnosis: Sinistral P₁ element of a lanceolate shape, with a short platform and a long free blade attached to the platform in a rostral position, two parallel parapets decorated by coarse nodes or transverse ridges, a median trough and a dorsal row of 2–4 nodes.

Remarks: The morphology of *Rhachistognathus muricatus* specimens is rather variable in our collection. The original description and illustration of the species (Dunn 1965) shows that *R. muricatus* is typified by a narrow platform and nodose parapet. Baesemann and Lane (1985), however, indicated that the decoration of the *R. muricatus* parapets vary from nodes to

ridges, which are commonly irregular in size and shape. By this criterion, we illustrate some specimens with subtle differences. In addition, Lane and Straka (1974) indicated that both sinistral and dextral forms of *R. muricatus* are present. However, we have found only sinistral elements in examined samples. *Rhachistognathus muricatus* can be distinguished from its potential descendant *R. minutus minutus* by more irregular size and shape of nodes/ridges on the parapets. It differs from *R. websteri* and *R. primus* by possession of two, almost equal parapets and only few nodes at the dorsal platform (in comparison to the development of dorsal carina in *R. websteri*).

Range: Uppermost Mississippian–Lower Pennsylvanian of North America, Iran and Turkey.

Occurrence: Samples 21–102; Lower *Rhachistognathus muricatus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 483 specimens.

***Rhachistognathus primus* Dunn 1966**

Plate 5, figures 10–12

Rhachistognathus prima DUNN 1966, p. 1301, pl. 157, figs. 1, 2.

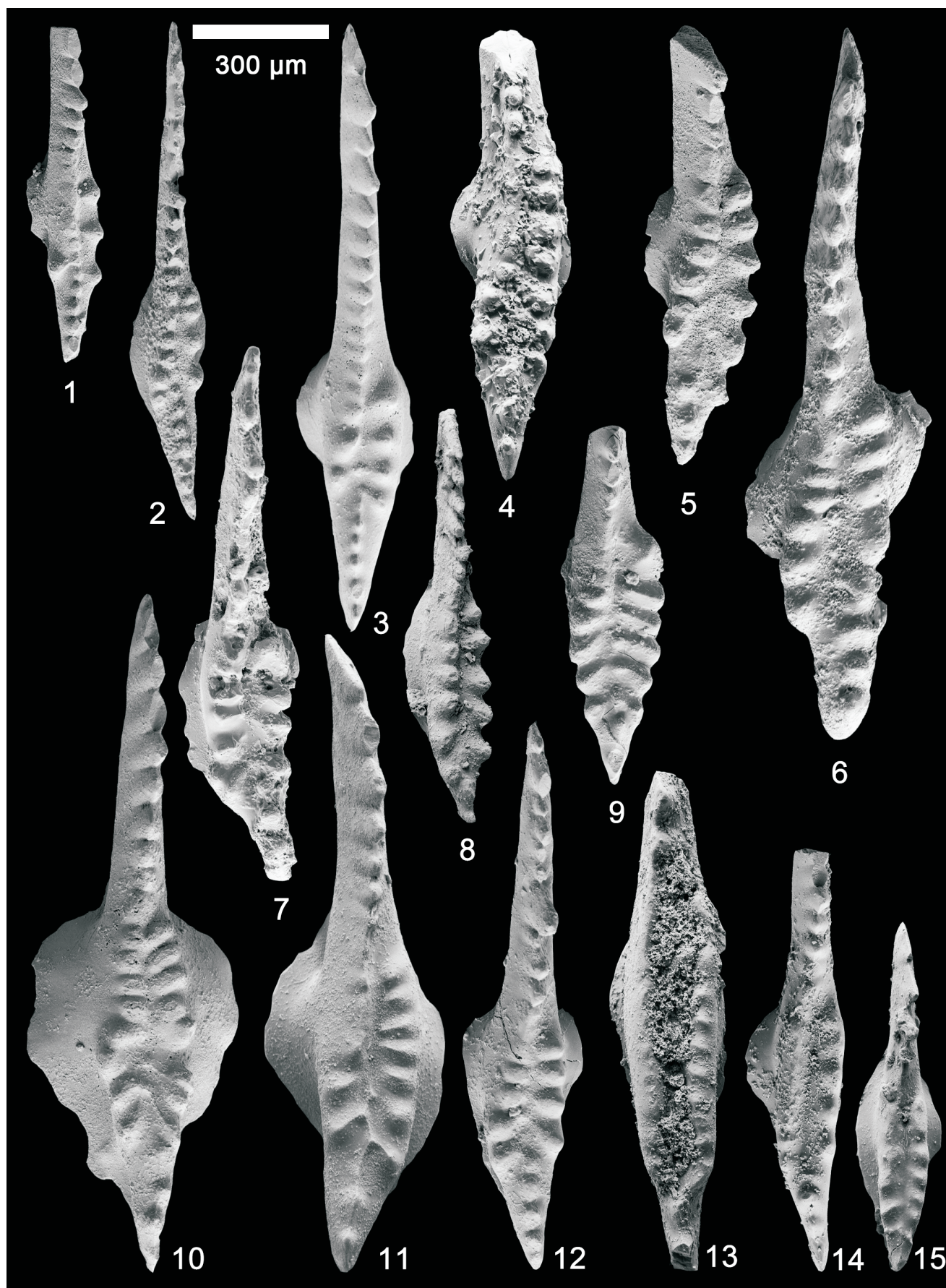
Rhachistognathus primus Dunn. – BAESEMANN and LANE 1985, p. 114, pl. 4, figs. 6, 7, 9–11 (cum. syn.). – BRECKLE et al. 1997a, b, pl. 1, fig. 8.

Diagnosis: Sinistral P₁ elements have a lanceolate shape. Long free blade attaches a narrow platform in rostral position. Carina and caudal parapet are decorated by coarse nodes or short transverse ridges. A narrow median trough between them occupies a

PLATE 5

All illustrations are upper views of P₁ elements. Scale bar = 300 µm.

- 1 *Rhachistognathus websteri* Baesemann and Lane 1985, sinistral element, SUI 147450, sample 81.
- 2 *Rhachistognathus websteri* Baesemann and Lane 1985, sinistral element, SUI 147451, sample 63.
- 3 *Rhachistognathus websteri* Baesemann and Lane 1985, sinistral element, SUI 147452, sample 58.
- 4 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147453, sample 60.
- 5 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147454, sample 62.
- 6 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147455, sample 63.
- 7 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147456, sample 52.
- 8 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147457, sample 63.
- 9 *Rhachistognathus muricatus* (Dunn 1965), sinistral element, SUI 147458, sample 63.
- 10 *Rhachistognathus primus* Dunn 1966, sinistral element, SUI 147459, sample 62.
- 11 *Rhachistognathus muricatus* (Dunn 1965) – *Rhachistognathus primus* Dunn 1966 transition, dextral element, SUI 147460, sample 58.
- 12 *Rhachistognathus primus* Dunn 1966, dextral element, SUI 147461, sample 63.
- 13 *Rhachistognathus minutus minutus* (Higgins and Bouckaert 1968), sinistral element, SUI 147462, sample 82.
- 14 *Rhachistognathus minutus minutus* (Higgins and Bouckaert 1968), sinistral element, SUI 147463, sample 87.
- 15 *Rhachistognathus minutus minutus* (Higgins and Bouckaert 1968), sinistral element, SUI 147464, sample 99.



half of the ventral platform. A row of 2–5 nodes occur in the dorsal end of the platform.

Remarks: Although Baesemann and Lane (1985) added “absence of a trough” to Dunn’s (1966) original description of *Rhachistognathus primus*, but their illustrations show splits or very narrow troughs on the ventral part of the platform. The carinal nodes of *R. primus* are gradually offset rostrally unlike the approximately median-positioned carina of *R. websteri*. In addition, the nodes on the dorsal part of the platform in *R. primus* are fewer in number than that in *R. websteri*. *Rhachistognathus primus* can be distinguished from *R. muricatus* by a narrower and shorter troughs (splits) and more nodes on the dorsal part of the platform.

Range: Lowermost Pennsylvanian (Morrowan) of North America.

Occurrence: Sample 61–102; *Declinognathodus noduliferus*–*Rhachistognathus primus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 54 specimens.

Rhachistognathus prolixus Baesemann and Lane 1985
Plate 2, figures 1–5

Rhachistognathus prolixus BAESEMANN and LANE 1985, p. 115, pl. 2, fig. 12; pl. 5, fig. 3–7 (cum. syn.). – RUI, WANG and ZHANG 1987, pl. 1, fig. 3. – WANG and HIGGINS 1989, p. 286, pl. 1, figs. 4, 5. – WANG and QI 2003a, pl. 2, fig. 2 (only). – HU, QI and NEMYROVSKA 2018, p. 27, Figs. 5A–5C (cum. syn.).
Rhachistognathus sp. B TYNAN 1980, p. 1305, pl. 1, figs. 28–36.

Diagnosis: Sinistral P₁ element of a lanceolate shape. A long free blade joins a narrow platform in rostral position and extends as a carina-like rostral parapet, which in turn passes into a row of nodes to the dorsal end of the platform. A caudal parapet consists of 1–5 irregularly spaced nodes. A narrow groove occurs between the two parapets.

Remarks: *Rhachistognathus prolixus* can be easily distinguished from other *Rhachistognathus* species by its linear arrangement of blade, carina and dorsal nodes, which form a carina-like parapet on the platform (Baesemann and Lane, 1985). The variable number and location of nodes on the caudal parapet also help to distinguish *R. prolixus* from other rhachistognathids. Baesemann and Lane (1985) and the other conodont workers found only sinistral elements of *R. prolixus*. The dextral forms (Wang and Qi 2003a, pl. 2, fig. 1; Hu et al. 2018, Figs. 5D, 5E) reported from the Naqing section, South China may prove the paired elements of *R. prolixus*.

Range: Uppermost Mississippian (Chesterian)–Lowermost Pennsylvanian (Morrowan) of North America; lower Bashkirian of South China.

Occurrence: Samples 43–102; Upper *Rhachistognathus muricatus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 71 specimens.

Rhachistognathus websteri Baesemann and Lane 1985
Plate 5, figures 1–3

Rhachistognathus websteri BAESEMANN and LANE 1985, p. 117, pl. 5, figs. 1, 2, 8–12 (cum. syn.). – KRUMHARDT, HARRIS and

WATTS 1996, p. 49, pl. 4, figs. 17–21. (cum. syn.). – BRENCKLE et al. 1997a, b, pl. 1, fig. 9.

Diagnosis: Sinistral P₁ element of a lanceolate shape. A long free blade attached to the platform in rostral position extends to the middle of the platform as a carina-like parapet. A caudal parapet consists of 3–4 irregularly spaced nodes on the ventral half of the platform. 1–2 rostral nodes are offset along the carina dorsally; a row of 6–7 small nodes occurs on the dorsal half of the platform as a dorsal carina. A narrow groove occurs between the carina-like rostral parapet and caudal parapet.

Remarks: The carina-like rostral parapet of *Rhachistognathus websteri* can be connected to the dorsal nodes (dorsal carina) in some specimens (pl. 5, fig. 1) and forms a linear arrangement as in *R. prolixus*. *Rhachistognathus websteri* can be distinguished from all the other *Rhachistognathus* species by a node or nodes distinctly offset rostrally on the dorsal end of the carina-like rostral parapet. This species is close to *R. primus* but can be distinguished from the latter by having more dorsal nodes and a less rostrally declined carina.

Range: Uppermost Mississippian (Chesterian)–lower Pennsylvanian (Morrowan) of North America.

Occurrence: Samples 52–102; Upper *Rhachistognathus muricatus* Zone to *Neognathodus symmetricus* Zone of the Arrow Canyon section.

Material: 83 specimens.

ACKNOWLEDGMENTS

We are very grateful to Paul Brenckle (Westport, MA, U.S.A.) for proofreading the draft manuscript, coordinating the Arrow Canyon sampling numbers and providing the picture of text-fig. 2B. We thank John Murray (Galway, Ireland) and Javier Sanz-López (Oviedo, Spain) for the thorough review of the manuscript. Special gratitude is offered to Sherry Lane (Washington, DC, U.S.A.), Dr. H. Richard Lane’s widow, and Dr. John Repetski (Reston, VA, U.S.A.) for kindly looking for the key conodont slides of the Arrow Canyon section and sending indispensable documents for this paper from Dr. Lane’s computer. Thanks also to Tiffany Adrain (Iowa City, IA, U.S.A.) for arranging the repository numbers. This work was supported by the National Natural Science Foundation of China (Grant nos. 41630101, 41802010) and State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) (Grant no. 173110).

REFERENCES

- ABPLANALP, J. M., ISAACSON, P. E., BATT, L. S. and POPE, M. C., 2009. Conodont biostratigraphy of Chesterian strata (Late Mississippian–Early Pennsylvanian), east-central Idaho and southwestern Montana. *The Mountain Geologist*, 46: 89–104.
- AISENVERG, D. E., BRAZHNKOVA, N. E., VASSILJUK, N. P., VDOVENKO, M. V., GORAK S. V., DUNAIEVA, N. N., ZERNETSKAYA, V. I., POLETAIEV, V. I., POTIEVSKAYA, P. D., ROTAI A. P. and SERGEEVA, M. T., 1979. The Carboniferous sequence of the Donets Basin: a standard section for the Carboniferous System. In: Wagner, R. H., Higgins, A. C. and Meyen, S. V., Eds., *The Carboniferous of the U.S.S.R.*, 197–224. Leeds: The Yorkshire Geological Society, Occasional Publication 4.
- ATAKUL-ÖZDEMİR, A., ALTUBER, D. and ÖZKAN-ALTINER, S., 2012. Conodont distribution across the mid-Carboniferous boundary

- in the central Taurides, Turkey. *Rivista Italiana di Paleontologia e Stratigrafia*, 118: 213–222.
- AUSTIN, R. I. and RHODES, F. H. T. 1981. Family Cavusgnathidae. In: Robinson, R. A., Ed., *Treatise on Invertebrate Paleontology, Part W., Supplement 2, Conodonta*, 158–160, Lawrence, KS: Geological Society of America and the University of Kansas.
- BAESEMANN, J. F., BRECKLE, P. L., and GRUZLOVIC, P. D., 1998. Composite standard correlation of the Mississippian-Pennsylvanian (Carboniferous) Lisburne Group from Prudhoe Bay to the eastern Arctic National Wildlife Refuge, North Slope, Alaska. In: Clough, J. G., and Larson, F., eds., *Short notes on Alaska geology 1997*, 23–36. Fairbanks: Alaska Department of Natural Resources, Division of Geological and Geophysical Surveys. Professional Report 118.
- BAESEMANN, J. F. and LANE, H. R., 1985. Taxonomy and evolution of the genus *Rhachistognathus* Dunn (Conodonta; Late Mississippian to Early Middle Pennsylvanian). In: Lane, H. R. and Ziegler, W., Eds., *Toward a boundary in the middle of the Carboniferous: stratigraphy and paleontology*, 93–136. Frankfurt: Courier Forschungsinstitut Senckenberg, 74.
- BAHRAMI, A., BONCHEVA, I., KÖNIGSHOF, P., YAZDI, M. and KHAN-ABADI, E. A., 2014. Conodonts of the Mississippian/Pennsylvanian boundary interval in Central Iran. *Journal of Asian Earth Sciences*, 92: 187–200.
- BARNETT, A. J. and WRIGHT, V. P. 2008. A sedimentological and cyclostratigraphic evaluation of the completeness of the Mississippian-Pennsylvanian (Mid-Carboniferous) Global Stratotype Section and Point, Arrow Canyon, Nevada, USA. *Journal of the Geological Society of London*, 165: 859–873.
- BATESON, W., 1886. The ancestry of the chordate. *Quarterly Journal of Microscopical Science*, 26: 535–571.
- BENDER, K. P., 1980. *Lower and Middle Pennsylvanian conodonts from the Canadian Arctic Archipelago*. Ottawa: Geological Survey of Canada, Paper 79–15, 24 pp.
- BISHOP, J., MONTAÑEZ, I. P., GULBRANSON, E. L. and BRECKLE, P. L. 2009. The onset of mid-Carboniferous glacio-eustasy: Sedimentologic and diagenetic constraints, Arrow Canyon, Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 276: 217–243.
- BONCHEVA, I., BAHRAMI, A., YAZDI, M. and TORABI, H., 2007. Carboniferous conodont biostratigraphy and late Paleozoic depositional evolution in South Central Iran (Asadabad section–SE Isfahan). *Rivista Italiana di Paleontologia e Stratigrafia*, 113: 329–356.
- BRECKLE, P. L., 1973. Smaller Mississippian and Lower Pennsylvanian calcareous foraminifers from Nevada. *Cushman Foundation for Foraminiferal Research, Special Publication*, 11: 1–82.
- BRECKLE, P. L., BAESEMANN, J. F., LANE, H. R., WEST, R. R., WEBSTER, G. D., LANGENHEIM, R. L., BRAND, U., and RICHARD, B. C., 1997a. Arrow Canyon, the Mid-Carboniferous Boundary Stratotype. In: Breckle, P. L. and Page, W. R., Eds., *Paleoforams '97 Guidebook: Post-Conference Field Trip to the Arrow Canyon Range, Southern Nevada U. S. A.*, Cushman Foundation Foraminiferal Research Supplement to Special Publication 36: 13–32.
- , 1997b. Arrow Canyon, the Mid-Carboniferous Boundary Stratotype. *Proceedings of the XIII International Congress on the Carboniferous and Permian, Krakow 1995*, Part 3: 149–164.
- BROWN, L. M., REXROAD, C. B., BEARD, J. and WILLIAMS, D., 1990. Phylogenetic and zonal implications of *Cavusgnathus tythus* n. sp. (Conodonta) from the Kinkaid Limestone (Upper Mississippian) of western Kentucky, U.S.A. *Geologica et Palaeontologica*, 24: 77–87.
- CASSITY, P. E. and LANGENHEIM, R. L. Jr., 1966. Pennsylvanian and Permian fusulinids of the Bird Spring Group from Arrow Canyon, Clark County, Nevada. *Journal of Paleontology*, 40: 931–968.
- CLARKE, W. J., 1960. Scottish Carboniferous conodonts. *Transactions of the Edinburgh Geological Society*, 18: 1–31.
- CUVIER, G., 1812. *Rescherches sur les ossements fossils, où l'on rétablit les caractères de plusieurs animaux dont les revolutions du globe ont détruit les espèces*. Paris: Chez 1st Edition, de Terville Librairie.
- DAVIS, L. E. and WEBSTER, G. D., 1985. Late Mississippian to Early Pennsylvanian conodont biofacies in central Montana. *Lethaia*, 18: 67–72.
- DUMOULIN, J. A. and HARRIS, A. G., 1993. Lithofacies and conodonts of Carboniferous strata in the Ivotuk Hills, western Brooks Range, Alaska. In: Dusel-Bacon, C. and Till, A. B., Eds., *Geologic Studies in Alaska by the U.S. Geological Survey, 1992*, 31–47. Washington: U.S. Geological Survey Bulletin, 2068.
- DUNN, D. L., 1965. Late Mississippian Conodonts from the Bird Spring Formation in Nevada. *Journal of Paleontology*, 39: 1145–1150.
- , 1966. New Pennsylvanian platform conodonts from Southwestern United States. *Journal of Paleontology*, 40: 1294–1303.
- , 1970a. Middle Carboniferous conodonts from western United States and phylogeny of the platform group. *Journal of Paleontology*, 44: 312–342.
- , 1970b. conodont zonation near Mississippian-Pennsylvanian boundary in Western United-States. *Geological Society of America Bulletin*, 81: 2959–2974.
- DZIK, J., 1976. Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica*, 21: 395–455.
- ELLISON, S. P., 1941. Revision of the Pennsylvanian conodonts. *Journal of Paleontology*, 15: 107–143.
- ELLISON, S. P. and GRAVES, R. W., 1941. *Lower Pennsylvanian (Dimple Limestone) conodonts of the Marathon region, Texas*. Rolla: University of Missouri School of Mines and Metallurgy, Technical Series Bulletin 14 (3), 21 pp.
- ELLWOOD, B. B., TOMKIN, J. H., RICHARDS, B. C., BENOIST, S. and LAMBERT, L. L., 2007. MSEC data sets record glacially driven cyclicity: Examples from the Arrow Canyon Mississippian-Pennsylvanian GSSP and associated sections. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255: 377–390.
- FALLON, P. and MURRAY, J., 2015. Conodont biostratigraphy of the mid-Carboniferous boundary in Western Ireland. *Geological Magazine*, 152: 1025–1042.
- GOREVA, N. V., 1984. Conodonts of the Moscovian Stage of the Moscow Syncline. In: Menner, V. V., Ed., *Paleontological characteristics of the stratotype and supporting sections of the Carboniferous of the Moscow Syncline (conodonts, cephalopods)*, 44–122. Moscow: Moscow State University. [in Russian].
- GRAYSON, R. C., JR., 1984. Morrowan and Atokan (Pennsylvanian) conodonts from the eastern margin of the Arbuckle Mountains, southern Oklahoma. In: Sutherland, P. K. and Manger, W. L., Eds.,

- The Atokan Series (Pennsylvanian) and its boundaries—a symposium*, 41–61. Norman: Oklahoma Geological Survey, Bulletin 136.
- , 1990. Canyon Creek: A significant exposure of a predominantly mudrock succession recording essentially continuous deposition from the Late Devonian through the Middle Pennsylvanian. In: Ritter, S. M., Ed., *Early to Middle Paleozoic conodont biostratigraphy of the Arbuckle Mountains, southern Oklahoma*, 85–114. Norman: The University of Oklahoma, Oklahoma Geological Survey Guidebook 27.
- GRAYSON R. C., JR., MERRILL, G. K. and LAMBERT, L. L., 1990. Carboniferous gnathodontid conodont apparatuses: evidence of a dual origin for Pennsylvanian taxa. In: Ziegler, W., Ed., *1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V) Contributions IV: papers on conodonts and Ordovician to Triassic conodont stratigraphy*, 353–396. Frankfurt: Forschungsinstitut Senckenberg, Courier 118.
- GRAYSON, R. C., DAVIDSON, W. T., WESTERGAARD, E. H., ATCHLEY, S. C., HIGHTOWER, J. H., MONOGHAN, P. T. and POLLARD, C., 1985. Mississippian–“Pennsylvanian” (mid-Carboniferous) boundary conodonts from the Rhoda creek Formation. In: Lane, H. R. and Ziegler, W., Eds., *Toward a boundary in the middle of the Carboniferous: stratigraphy and paleontology*, 149–180. Frankfurt: Forschungsinstitut Senckenberg courier 74.
- GUNNELL, F. H., 1933. Conodont and fish remains from the Cherokee, Kansas City, and Wabaunsee groups of Missouri and Kansas. *Journal of Paleontology*, 7: 261–297.
- HARRIS, A. G., BRECKLE, P. L., BAESEMANN, J. F., KRUMHARDT, A. P. and GRUZLOVIC, P. D., 1997. Comparison of conodont and calcareous microfossil biostratigraphy and lithostratigraphy of the Lisburne Group (Carboniferous), Sadlerochit Mountains, northeast Brooks Range, Alaska. In: Dumoulin, J. A. and Gray, J. E., Eds., *Geologic Studies in Alaska by the U.S. Geological Survey, 1995*, 195–219. Washington: U.S. Geological Survey, Professional Paper 1574.
- HARRIS, R. W. and HOLLINGSWORTH, R. V., 1933. New Pennsylvanian conodonts from Oklahoma. *American Journal of Science, Series 5*, 25: 193–204.
- HASS, W. H., 1959. Conodonts from the Chappel limestone of Texas, U. S. *Geological Professional Paper*, 294-J: 365–399.
- HIGGINS, A. C., 1975. *Conodont zonation of the late Visean–early Westphalian strata of the south and central Pennines of northern England*. London: Bulletin of the Geological Survey of Great Britain, 53, 90 pp.
- , 1985. The Carboniferous System: Part 2. Conodonts of the Silesian Subsystem from Great Britain and Ireland. In: Higgins A. C. and Austin, R. L., Eds., *A Stratigraphical Index of Conodonts*. 211–227. Chichester: Ellis Horwood.
- HIGGINS, A. C. and BOUCKAERT, J., 1968. *Conodont stratigraphy and paleontology of the Namurian of Belgium*. Brussels: Service Géologique de Belgique, Mémoires pour servir à l’explication des cartes géologique et minières de la Belgique, 10, 64 pp.
- HIGGINS, A. C. and WAGNER-GENTIS, C. H. T., 1982. Conodonts, goniatites and the biostratigraphy of the earlier Carboniferous from the Cantabrian Mountains, Spain. *Palaeontology*, 25: 313–350.
- HU, K. Y., QI, Y. P. and NEMYROVSKA, T. I., 2018. Mid-Carboniferous conodonts and their evolution: new evidence from Guizhou, South China. *Journal of Systematic Palaeontology*. DOI:10.1080/14772019.2018.1440255.
- HU, K. Y., QI, Y. P., WANG, Q. L., NEMYROVSKA, T. I. and CHEN, J. T., 2017. Early Pennsylvanian conodonts from the Luokun section of Luodian, Guizhou, South China. *Palaeoworld*, 26: 64–82.
- IGO, H., and KOIKE, T., 1964. Carboniferous conodonts from the Omi Limestone, Niigata Prefecture, central Japan (Studies of Asian conodonts, part I). *Transactions and Proceedings of the Palaeontological Society of Japan (New Series)*, 53: 179–193.
- Ji, Z. S., YAO, J. X., WU, G. C., LIU, G. Z., JIANG, Z. T. and FU, Y. H., 2007. The Late Carboniferous conodont *Neognathodus* fauna in Xainza, Tibet, China and its significance. *Geological Bulletin of China*, 26 (1): 42–53 [in Chinese].
- KOIKE, T., 1967. A Carboniferous succession of conodont faunas from the Atetsu Limestone in southwestern Japan (Studies of Asiatic conodonts, Part IV). *Science Reports of the Tokyo Kyoiku Daigaku, Section C., Geology, Mineralogy and Geography*, 9: 279–318.
- KOZITSKAYA, R. I., KOSSENKO, Z. A., LIPNYAGOV, O. M. and NEMYROVSKAYA, T. I., 1978. *Carboniferous conodonts of the Donets Basin*. Kiev: Izdatel Naukova Dumka, 136 p. [in Russian].
- KRUMHARDT, A. P., HARRIS, A. G. and WATTS, K. F., 1996. Lithostratigraphy, microlithofacies, and conodont biostratigraphy and biofacies of the Wahoo Limestone (Carboniferous), eastern Sadlerochit Mountains, Northeast Brooks Range, Alaska. *U.S. Geological Survey Professional Paper*, 1568: 1–69.
- KULAGINA, E. I., PAZUKHIN, V. N., NIKOLAEVA, S. V. and KOCHETOVA, N. N., 2000. Biozonation of the Syuran horizon of the Bashkirian Stage in the South Urals as indicated by ammonoids, conodonts, foraminifers, and ostracodes. *Stratigraphy and Geological Correlation*, 8: 137–156.
- KULAGINA, E. I., NIKOLAEVA, S. V., PAZUKHIN, V. N. and KOCHETOVA, N. N., 2014. Biostratigraphy and lithostratigraphy of the mid-Carboniferous boundary beds in the Muradymovo section (South Urals, Russia). *Geological Magazine*, 151 (02): 269–298.
- LANE, H. R., 1967. Uppermost Mississippian and lower Pennsylvanian conodonts from the type Morrowan region, Arkansas. *Journal of Paleontology*, 41: 920–942.
- LANE, H. R., BOUCKAERT, J., BRECKLE, P., EINOR, O. L., HAVLENA, V., HIGGINS, A. C., YANG J.-Z., MANGER, W. L., NASSICHUK, W., NEMIROVSKAYA, T., OWENS, B., RAMSBOTTOM, W. H. C., REITLINGER, E. A. and WEYANT, M., 1985. Proposal for an international Mid-Carboniferous boundary. *Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, Compte Rendu*, 4: 323–339.
- LANE, H. R., BRECKLE, P. L., BAESEMANN, J. F. and RICHARDS, B. C., 1999. The IUGS boundary in the middle of the Carboniferous: Arrow Canyon, Nevada, USA. *Episodes*, 22: 272–283.
- LANE, H. R., MERRILL, G. K., STRAKA, J. J. and WEBSTER, G. D., 1971. North American Pennsylvanian conodont biostratigraphy. In: Sweet, W.C. and Bergstrom, S. I., Eds., *Symposium on conodont biostratigraphy*, 395–414. Boulder: Geological Society of America. Memoir 127.
- LANE, H. R. and STRAKA, J. J., 1974. *Late Mississippian and Early Pennsylvanian conodonts, Arkansas and Oklahoma*. Boulder: Geological Society of America. Special Paper 152, 144 p.
- LANGENHEIM, R. L. Jr., 1993. Is the cyclicity in late Mississippian and Pennsylvanian carbonates of southwestern United States a result of Gondwana glaciation? In: Archangelsky, S., Ed., *Douzième Congrès International de la Stratigraphie et Géologie du*

- Carbonifère et Permien, Buenos Aires 1991, Comptes Rendus*, 1: 305–312.
- LANGENHEIM, R. L., Jr., CARSS, B. W., KENNERLY, J. B., MCCUTCHEON, V. A. and WAINES, R. H., 1962. Paleozoic section in Arrow Canyon Range, Clark County, Nevada. *AAPG Bulletin*, 46: 592–609.
- MEISCHNER, D. and NEMYROVSKA T. I., 1998. Origin of *Gnathodus bilineatus* (Roundy, 1926) related to goniatite zonation in Rheinisches Schiefergebirge, Germany. *Bollettino della Società Paleontologica Italiana*, 37(2-3): 427–442.
- MERRILL, G. K. and KING, C. W., 1971. Platform conodonts from the lowest Pennsylvanian rocks of northwestern Illinois. *Journal of Paleontology*, 45: 645–664.
- METCALFE, I., 1980. Upper Carboniferous conodont faunas of the Panching limestone, Pahang, West Malaysia. *Palaeontology*, 23: 297–314.
- MIZUNO, Y., 1997. Conodont faunas across the Mid-Carboniferous boundary in the Hina Limestone, Southwest Japan. *Paleontological Research*, 1: 237–259.
- MORROW, J. R. and WESTER, G. D., 1991. Carbonate microfacies and related conodont biofacies, Mississippian-Pennsylvanian boundary strata, Granite Mountain, west-central Utah. *Brigham Young University Geology Studies*, 37: 99–124.
- , 1992. New stratigraphic, petrographic, and Biostratigraphic Data on the proposed Mississippian – Pennsylvanian Boundary Stratotype, Granite Mountain, West-Central Utah. In: Sutherland, P. K. and Manger, W. L., Eds., *Recent advances in Middle Carboniferous biostratigraphy*, 55–67. Norman: Oklahoma Geological Survey. Circular 94.
- NASCIMENTO, S., SMANIOTTO, L. P., SOUZA, P. A., LEMOS, V. B. and SCOMAZZON, A. K., 2009. Biochronostratigraphy (conodonts and palynology) from a selected strata of the Itaituba Formation (Pennsylvanian of the Amazonas Basin) at Itaituba, Pará State, Brazil. *Pesquisas em Geociências*, 36: 37–47.
- NAVAS-PAREJO, P., PALAFOX, J. J., VILLANUEVA, R., BUITRÓN-SÁNCHEZ, B. E. and VALENCIA-MORENO, M., 2017. Mid-Carboniferous shallow-water conodonts from northwest Mexico. *Micropaleontology*, 63: 383–402.
- NEMIROVSKAYA, T. I., 1983. Serpukhovian and early Bashkirian conodonts of the Dnieper-Donets Depression. *Izvestiya Akademii Nauk SSSR, Seriya geologicheskaya*, 11: 59–68. [in Russian].
- NEMIROVSKAYA, T. I. and ALEKSEEV, A. S., 1995. The Bashkirian conodonts of the Askyn section, Bashkirian Mountains, Russia. *Bulletin de la Société Belge de Géologie*, 103: 109–133.
- NEMIROVSKAYA, T. I. and NIGMADGANOV, I. M., 1993. Some new conodonts of the Mid-Carboniferous deposits of Middle Asia. *Jahrbuch der Geologischen Bundesanstalt*, 136 (1): 213–221.
- , 1994. The Mid-Carboniferous conodont event. In: Königshof, P. and Werner, R., Eds., *Willi Ziegler-Festschrift I*, 319–333. Frankfurt: Courier Forschungsinstitut Senckenberg, 168.
- NEMYROVSKA, T. I., 1999. Bashkirian conodonts of the Donets Basin, Ukraine. *Scripta Geologica*, 119: 1–115.
- , 2005. Late Viséan/early Serpukhovian conodont succession from the Triollo section, Palencia (Cantabrian Mountains, Spain). *Scripta Geologica* 129: 14–89.
- NIGMADGANOV, I. M. and NEMIROVSKAYA, T. I., 1992. Mid-Carboniferous boundary conodonts from the Gissar Ridge, South Tienshan, Middle Asia. In: Ziegler, W., Ed., *Papers on Paleozoic Conodonts from Eurasia and North Africa*, 253–275. Frankfurt: Courier Forschungsinstitut Senckenberg, 154.
- NIKOLAEVA, S. V., KULAGINA, E. I., GOROZHANINA, E. N., ALEKSEEV, A. S. and KONOVALOVA, V. A., 2017. Conodonts, ammonoids, foraminifers, and depositional setting of the Serpukhovian and Bashkirian stages in the Kugarchi Section in the South Urals, Russia. In: Barrick, J. E. and Brenckle, P. L., Eds., *Papers in celebration of H. Richard Lane, Stratigraphy*, 14 (1–4): 319–347.
- PANDER, C. H., 1856. *Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements*. St. Petersburg: Akademie Wissenschaften, 91 pp.
- PARK, S., 1983. *Zonenfolge, Phylogenie und Taxonomie Karbonischer Conodonten zwischen Tournai und Westfal (Westeuropa)*. Dissertation Philipps-Universität Marburg. 87 pp.
- PAZUKHIN, V. N., KULAGINA, E. I., NIKOLAEVA, S. V., KOCHETOVA, N. N. and KONOVALOVA, V. A., 2010. The Serpukhovian Stage in the Verkhnaya Kardailovka section, South Urals. *Stratigraphy and Geological Correlation*, 18(3): 269–289.
- PERLMUTTER, B., 1975. Conodonts from the uppermost Wabauensee Group (Pennsylvanian) and Admire and Council Grove Groups (Permian) in Kansas. *Geologica et Palaeontologica*, 9: 95–115.
- QI, Y. P., NEMYROVSKA, T. I., WANG, X. D., CHEN, J. T., WANG, Z. H., LANE, H. R., RICHARD, B. C., HU, K. Y. and WANG, Q. L., 2014. Late Viséan–early Serpukhovian conodont succession at the Naqing (Nashui) section in Guizhou, South China. *Geological Magazine*, 151(2): 254–268.
- REXROAD, C. B., 1958. Conodonts from the Glen Dean Formation (Chester) of the Illinois Basin. *Illinois State Geological Survey Report of Investigations*, 209: 1–27.
- REXROAD, C. B. and BURTON, R. C., 1961. Conodonts from the Kinkaid Formation (Chester) in Illinois. *Journal of Paleontology*, 35(6): 1143–1158.
- REXROAD, C. B. and MERRILL, G. K., 1985. Conodont biostratigraphy and paleoecology of Middle Carboniferous rocks in southern Illinois. In: Lane, H. R. and Ziegler, W. Eds., *Toward a boundary in the middle of the Carboniferous: stratigraphy and paleontology*, 35–64. Frankfurt: Courier Forschungsinstitut Senckenberg, 74.
- RHODES, F. H. T., AUSTIN, R. L. and DRUCE, E. C., 1969. *British Avonian (Carboniferous) conodont faunas, and their value in local and intercontinental correlation*. London: Bulletin of the British Museum (Natural History), Geology. Supplement 5, 313 pp.
- RICHARDS, B. C., BAMBER, E. W., HIGGINS, A. C., and UTTING, J., 1993. 4E. Carboniferous. In: Stott, D. F., and Aitken, J. D., Eds., *Sedimentary cover of the craton in Canada*, 202–271. Ottawa: Geological Survey of Canada. Geology of Canada no. 5 (also in Geological Society of America. The Geology of North America v. D-1).
- RICHARD, B. C., BARCLAY, J. E., BRYAN, D., HARTLING, A., HENDERSON, C. M. and HINDS, R. C., 1994. Chapter 14–Carboniferous strata of the Western Canada Sedimentary Basin. In: Mossop, G. D. and Shetson, I., Eds., *Geological atlas of the Western Canada Sedimentary Basin*, 221–250. Calgary: Canadian Society of Petroleum Geologists and Alberta Research Council.
- RICHARDS, B. C., LANE, H. R. and BRECKLE, P. L., 2002. The IUGS Mid-Carboniferous (Mississippian-Pennsylvanian) Global

- Boundary Stratotype Section and Point at Arrow Canyon, Nevada, USA. In: Hills, L. V., Henderson, C. M. and Bamber, E. W., Eds., *Carboniferous and Permian of the World: XIV ICCP Proceedings*, 802–831. Calgary: Canadian Society of Petroleum Geologists Memoir 19.
- RILEY, N. J., VARKER, J., OWENS, B., HIGGINS, A. C. and RAMSBOTTOM, W. H. C., 1987. Stonehead Beck, Cowling, North Yorkshire, England: A British proposal for the Mid-Carboniferous Boundary stratotype. In: Brenckle, P. L. and Lane, H. R., Eds., *Selected Studies in Carboniferous Paleontology and Biostratigraphy*, 159–177. Frankfurt: Courier Forschungsinstitut Senckenberg 98.
- ROSS, C. A., 1991. Pennsylvanian paleogeography of the western United States. In: Cooper, J. D. and Stevens, C. H., Eds., *Paleozoic paleogeography of the Western United States II*, 137–148. Los Angeles: Pacific section, Society of Economic Paleontologists and Mineralogists Book 67.
- ROUNDY, P. V., 1926. Part II: The micro-fauna. U.S. *Geological Survey Professional Paper*, 146: 5–23.
- RUI, L., WANG, Z. H. and ZHANG, L. X., 1987. Luosuan—a new chronostratigraphic unit at the base of the Upper Carboniferous, with reference to the Mid-Carboniferous boundary in South China. In: Wang, C. Y., Ed., *Carboniferous boundaries in China*, 107–121. Beijing: Science Press.
- SANZ-LÓPEZ, J. and BLANCO-FERRERA, S., 2012. Lower Bashkirian conodonts from the Iraty Formation in the Alduides-Quinto Real Massif (Pyrenees, Spain). *Geobios*, 45: 397–411.
- , 2013. Early evolution of *Declinognathodus* close to the Mid-Carboniferous Boundary interval in the Barcaliente type section (Spain). *Palaeontology*, 5: 927–946.
- SANZ-LÓPEZ, J., BLANCO-FERRERA, S., SÁNCHEZ DE POSADA, L. C. and GARCÍA-LÓPEZ, S., 2006. The mid-Carboniferous boundary in northern Spain: difficulties for correlation of the global stratotype section and point. *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 3–22.
- SAVAGE, N. M. and BARKELEY, S. J., 1985. Early to Middle Pennsylvanian conodonts from the Klawak Formation and the Ladrone Limestone, southeastern Alaska. *Journal of Paleontology*, 59: 1451–1475.
- SKIPP, B. A., BAESEMANN, J. F. and BRECKLE, P. L., 1985. A reference area for the Mississippian-Pennsylvanian (mid-Carboniferous) boundary in east-central Idaho, U.S.A. *Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid, 1983, Compte Rendu* 4: 403–428.
- SKOMPSKI, S., 1996. Stratigraphic position and facies significance of the limestone bands in the subsurface Carboniferous succession of the Lublin Upland. *Acta Geologica Polonica*, 46: 171–268.
- SWEET, W. C., 1988. *The Conodonts: morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum*. London: Oxford University Press, Oxford Monographs on Geology and Geophysics 10, 212 pp.
- TYNAN, M. C., 1980. Conodont Biostratigraphy of the Mississippian Chainman Formation, Western Millard County, Utah. *Journal of Paleontology*, 54: 1282–1309.
- VARKER, W. J., 1994. Multielement conodont faunas from the proposed Mid-Carboniferous boundary stratotype locality at Stonehead Beck, Cowling, North Yorkshire, England. *Annales de la Société Géologique de Belgique*, 116: 301–321.
- VON BITTER, P. H., 1972. *Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of eastern Kansas*. Lawrence, KS: The University of Kansas. Paleontological Contributions 59, 105 pp.
- WANG, Q. L., QI, Y. P., HU, K. Y., SHENG, Q. Y. and LIN W., 2014. Conodont biostratigraphy of the Viséan-Serpukhovian boundary interval in the Luokun section, Ludian, Guizhou, South China. *Journal of Stratigraphy*, 38: 277–289. [in Chinese].
- WANG, Z. H. and HIGGINS, A. C., 1989. Conodont zonation of the Namurian–Lower Permian strata in South Guizhou, China. *Palaeontologia Cathayana*, 4: 261–325.
- WANG, Z. H. and QI, Y. P., 2002. Restudy of Upper Carboniferous Luosuan and Huashibanian conodont sequence in Ludian of Guizhou. *Acta Micropalaeontologica Sinica*, 19 (2): 134–143.
- , 2003a. Upper Carboniferous (Pennsylvanian) conodonts from South Guizhou of China. *Rivista Italiana di Paleontologia e Stratigrafia*, 109: 379–397.
- , 2003b. Review of Carboniferous–Permian conodont biostratigraphy in North China. *Acta Micropalaeontologica Sinica*, 20 (3): 225–243. [in Chinese].
- WANG, Z. H., RUI, L. and ZHANG, L. X., 1987. Conodont and fusulinid sequence of the Upper Carboniferous–Lower Permian of Nashui, Ludian, South Guizhou. *Journal of Stratigraphy*, 11: 155–159. [in Chinese].
- WANG, Z. H., QI, Y. P., WANG, X. D. and WANG, Y. J., 2004. Restudy of the Upper Carboniferous (Pennsylvanian) strata from Nashui of Ludian, Guizhou. *Acta Micropalaeontologica Sinica*, 21: 111–129. [in Chinese].
- WARDLAW, B. R., 1985. Latest Mississippian-earliest Pennsylvanian (Namurian) conodont biostratigraphy of the Northern Rocky Mountains, USA. *Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid, 1983, Compte Rendu* 4: 391–401.
- WEBSTER, G. D., 1969. *Chester through Derry conodonts and stratigraphy of northern Clark and southern Lincoln counties, Nevada*. Berkeley and Los Angeles: University of California Press. University of California Publication in Geological Sciences 79, 121 pp.
- WEIBEL, C. P. and NORBY, R. D., 1992. Paleopedology and Conodont Biostratigraphy of the Mississippian-Pennsylvanian Boundary Interval, Type Grove Church Shale Area, Southern Illinois. In: Sutherland, P. K. and Manger, W. L., Eds., *Recent advances in Middle Carboniferous biostratigraphy*, 39–53. Norman: Oklahoma Geological Survey. Circular 94.
- WHITESIDE, J. R. and GRAYSON, R. C., 1989. Carboniferous conodont faunas, northern Ouachita Mountains, Oklahoma. In: Suneson, N. H., Campbell, J. A. and Tilford, M. J., Eds., *Geology and resources of the Frontal belt of the western Ouachita Mountains, Oklahoma. Guidebook for Field Trip No. 2, September 27–28, 1989, American Association of Petroleum Geologists, Mid-Continent Section Meeting*, 149–167. Oklahoma City: Oklahoma Geological Survey Special Publication 90–1.
- YOUNGQUIST, W. and MILLER, A. K., 1943. Conodonts from the Late Mississippian Pella beds of south-central Iowa. *Journal of Paleontology*, 23: 617–622.