

BIOGEOGRAPHIC SHIFTS IN A TRANSGRESSIVE SUCCESSION: THE CAMBRIAN (FURONGIAN, JIANGSHANIAN; LATEST STEPTOEAN– EARLIEST SUNWAPTAN) AGNOSTOID ARTHROPODS *KORMAGNOSTELLA* ROMANENKO AND *BICIRAGNOSTUS* ERGALIEV IN NORTH AMERICA

STEPHEN R. WESTROP¹ AND JONATHAN M. ADRAIN²

¹Oklahoma Museum of Natural History, and School of Geology and Geophysics, University of Oklahoma, Norman, OK 73072, USA; and ²Department of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City, IA 52242, USA

ABSTRACT—The first records of the upper Cambrian agnostoid genera *Kormagnostella*, E. Romanenko, *in* Romanenko and Romanenko, 1967, and *Biciragnostus* F. Ergaliev, *in* Eraliev and Ergaliev, 2001, in Laurentian North America are from a narrow stratigraphic interval in the Steptoean—Sunwaptan boundary interval (Furongian, Jiangshanian) of Nevada and Utah. In Nevada, both genera occur in a condensed bioclastic lag below a major flooding surface, and *Kormagnostella* also appears in a transgressive interval in Utah. Immigration of these genera is associated with sea level rise, and also with faunal turnover. *Biciragnostus* is confined to the latest *Elvinia* Zone, immediately below the onset of a trilobite and agnostoid extinction event at the base of the *Irvingella major* Zone (basal Sunwaptan). *Kormagnostella* is present in the latest *Elvinia* Zone, and has its highest occurrence in the *I. major* Zone. Stratigraphic data from the Karatau-Naryn Terrane, Kazakhstan indicate that both genera disappear near the local extinction of *Irvingella*, suggesting that faunal turnover in that region may have been broadly correlative with the more profound extinction in Laurentia. New species are *Kormagnostella advena*, *K. insolita* and *Biciragnostus viator*.

INTRODUCTION

OR MUCH of the Cambrian, the new, global stadial nomenclature (Babcock and Peng, 2007) relies upon international biostratigraphic correlation using agnostoid arthropods. Agnostoids are common in outer shelf to slope lithofacies but are less common in inner shelf setting (Robison, 1976; Lenz et al., 1993), making correlation more difficult. The youngest Cambrian Furongian Series will be divided into three stages, although the uppermost has yet to be defined. The middle, Jiangshanian Stage was recently ratified by the IUGS International Commission on Stratigraphy (Peng et al., 2011, 2012) and is defined by the first appearance of the agnostoid Agnostotes orientalis Kobayashi 1935, as interpreted by Peng and Babcock (2005). In Laurentian North America, species of Agnostotes Öpik, 1963, have been recorded from sites in northern (Pratt, 1992) and western (Chatterton and Ludvigsen, 1998) Canada, where they occur in an outer shelf to continental slope setting. Recognition of the base of the Jiangshanian farther into the interior of the shelf is more problematic. Here we report on the abrupt appearance of two rare agnostoids in the late Cambrian successions of Nevada and Utah, Kormagnostella E. Romanenko (in Romanenko and Romanenko, 1967) and Biciragnostus F. Ergaliev (in Ergaliev and Ergaliev, 2001). They occur in an interval of sea level rise, and also in association with the trilobite extinction interval (base of the Irvingella major Zone) at the base of the Sunwaptan Stage of Laurentian North America. These genera provide important links for international correlation, as both are present in the lower Jiangshanian of the Peri-Gondwanan Karatau-Naryn Terrane, southern Kazakhastan. They also indicate that faunal turnover in the Karatau-Naryn Terrane may have been broadly coeval with the extinction interval in Laurentia. We also illustrate two pygidia of Agnostotes that co-occur with Biciragnostus in Nevada, and which confirm the correlation with the Jiangshanian.

STRATIGRAPHIC SETTING, AGE, AND CORRELATION

Localities and stratigraphy.-Two of the sample localities (Barton Canyon, Fig. 1.2; Orr Ridge, Fig. 1.3) and the stratigraphy of the study interval have been described briefly by Westrop and Adrain (2007, p. 988, figs. 1, 2) and this need not be repeated here. The third locality, Steptoe Ranch in the North Egan Range, White Pine County, Nevada (Fig. 1.1), like Barton Canyon, about 47 km to the north, exposes a succession through the Barton Canyon Limestone into the overlying Catlin Member of the Windfall Formation (Westrop and Adrain, 2007, fig. 2). At both localities, the Barton Canyon Limestone comprises about 11 m of bioturbated lime mudstone and wackestone with cm-thick layers of bioclastic packstone. These carbonates are mostly light gray in color, but include dark gray beds in the upper few meters. The agnostoids described in this paper occur in a condensed bioclastic lag at the very top of the Barton Canyon Limestone, immediately below a major flooding surface that is marked by the appearance of dark colored cherty lime mudstone, wackestone and calcisiltite of the Catlin Member. The bioclastic lags are similar at both localities. They are about 10-20 cm in thickness and can be divided into three (Steptoe Ranch) or four (Barton Canyon) discrete, cm-thick bioclastic layers that are separated by conspicuous hardgrounds; each layer was sampled separately. In both cases, the basal layer yields a pre-extinction, latest Steptoean (Elvinia Zone) fauna that includes Biciragnostus and rare Agnostotes and Kormagnostella. The overlying layers comprise the basal Sunwaptan Irvingella major Zone, and are dominated by sclerites of I. major.

Almost all of the sclerites of *Kormagnostella* were collected from the *Irvingella major* Zone in the Sneakover Member of the Orr Formation Orr Ridge, northern House Range, Utah. The succession is expanded relative to Nevada, and the *I. major* Zone increases in thickness to almost a meter (85 cm). The Sneakover Member is strongly cyclical (see also Osleger and Read, 1991, fig. 5; Evans et al. 2003, p. 29), and equivalents of the Barton Canyon Limestone in the lower part of the member are marked by



FIGURE 1—Locations of sample localities (in part modified from Westrop and Adrain, 2007). 1, Steptoe Ranch (section STR), North Egan Range, White Pine County, Nevada (NV); 2, north side of Barton Canyon (section CHC-1), Cherry Creek Range, White Pine County, Nevada; 3, Orr Ridge (section ORR), northern House Range, Millard County, Utah (UT).

cycles that include lithologically similar, mostly light gray, bioturbated wackestone with cm-thick packstone layers. In the Steptoean-Sunwaptan boundary interval, color changes from light to dark gray, and packstone horizons become less common in units of lime mudstone-wackestone, suggesting deepening (see also Evans et al., 2003, fig. 7). Thus, the overall context of the succession is transgressive, although facies shifts at the base of the Sunwaptan are less dramatic than at down-ramp sites in Nevada. This interpretation is consistent with previous studies of the sequence stratigraphy of the Steptoean succession (Evans et al., 2003, fig. 8), which viewed Corset Spring Shale (lower Elvinia Zone) as recording a lowstand (likely a shale-rich interval at the base of the unit that we can identify widely in western Utah and eastern Nevada), and the Barton Canyon-lower Catlin and Sneakover as transgressive. Osleger (1995, fig. 10) published a similar interpretation, with most of the Corset Spring Shale and the Sneakeover representing a transgressive systems tract.

An association between flooding surfaces, transgression and immigration is not unexpected (Holland, 2000), and the abrupt appearance of *Biciragnostus* and *Kormagnostella* is part of a broader pattern in the Steptoean–Sunwaptan boundary interval. Other unequivocal immigrants recorded in our collections include the trilobites *Comanchia* Frederickson, *in* Wilson and Frederickson, 1950, and *Aciculolenus* Palmer, 1965b. Lower in the transgressive systems tract (upper Corset Spring Shale), the appearances of two genera with Gondwanan affinities, *Oligometopus* Resser, 1936 (Westrop et al., 2008) and *Xenocheilos* Wilson, 1949 (Westrop and Adrain, 2009), also record immigration, although *Oligometopus* is known from older (*Dunderbergia* Zone) strata in shelf margin environments of Alaska and Newfoundland. Moreover, this pattern may extend beyond trilobites. Freeman et al. (2011) reported immigration of lingulate brachiopods into Laurentia from the Kazakh terranes and Gondwana at Cambrian trilobite extinctions, including the basal Sunwaptan event.

Geographic and stratigraphic distribution of Biciragnostus and Komagnostella.-Biciragnostus is known from only one other region, the Malyi Karatau Range in southern Kazakhstan, where it occurs in the Zumbay Formation (Ivshinagnostus ivshini-Irvingella "major" Zone; see Ergaliev and Ergaliev, 2008). The Malyi Karatau region is part of the Karatau-Naryn Terrane, and the upper Cambrian succession may have developed on an isolated seamout (Popov et al., 2009). Biciragnostus enters the succession at the Kyrshabakty section about 50 m above the first appearance of Agnostotes, and overlaps in range with species of Irvingella Ulrich and Resser, in Walcott, 1924; its highest appearance apparently coincides with the youngest occurrence of Irvingella (Ergaliev and Ergaliev, 2008; Ergaliev et al. 2009, figs. 4, 7). This places Biciragnostus firmly within the global Jiangshanian Stage and, in terms of the regional nomenclature of Laurentian North America, the upper Steptoean Stage (Elvinia Zone) (Fig. 2).



FIGURE 2—Correlation of zonations for the Steptoean–Sunwaptan boundary interval in Laurentia (Nevada and Utah; Westrop and Adrain, 2007) and the Sackian of the Karatau-Naryn Terrane (Kazakhastan; Ergaliev and Ergaliev, 2008; Ergaliev et al., 2009), showing relative stratigraphic ranges of the agnostoid arthropods *Biciragnostus* and *Kormagnostella*, and the trilobite *Irvingella*. The zonations are aligned using the first and last appearances of *Irvingella*. Note that *Biciragnostus* and *Kormagnostella* appear later in Laurentia, at a level that may correlate closely with the base of the Sunwaptan regional stage. Using the highest occurrence of *Irvingella* may correlate near the base of the *Irvingella major* Zone of Laurentia, and the last orcurrence of *Kormagnostella* may correlate near the base of this zone. In Laurentia, the lower and upper boundaries of the *I. major* Zone record pulses of trilobite extinction at a "biomere" event (Westrop and Cuggy, 1999).

Kormagnostella has also been recorded from the Kyrshabakty section in the Karatau-Naryn Terrane, where it is represented by several species (Ergaliev and Ergaliev, 2008). The genus extends from the *Lejopyge laevigata* Zone to the *Ivshinagnostus ivshini-Irvingella major* Zone (Ergaliev et al., 2009, fig. 3), and its highest occurrence is about 20 m below the last appearances of *Biciragnostus* and *Irvingella*. This range spans the Guzhangian, Paibian and lower Jiangshanian global stages, and the upper Marjuman and most of the Steptoean stages of the Laurentian nomenclature. The highest occurrence in Karatau-Naryn Terrane is probably older than in Nevada, which is lowest Sunwaptan.

In Hunan, China (South China Terrane; Cocks and Torsvik, 2002; Fortey and Cocks, 2003), Kormagnostella was recorded under the name Kormagnostus minutus (Schrank, 1975) by Peng and Robison (2000), although we are doubtful about the identification (see Systematic Paleontology, below). The genus occurs in Guzhangian strata (Proagnostus bulbus-Linguagnostus reconditus zones; Peng and Robison, 2000, figs. 3, 4). A related species, also identified as Kormagnostus minutus, is present in upper Guzhangnian strata of the Ogon'or Formation in the Khos-Nelge River section, Siberia (Siberian craton; Cocks and Torsvik, 2007), with a questionable occurrence possibly extending the range into the basal Jiangshanian (Lazarenko et al., 2008, fig. 19). The type material of Kormagnostella minuta is from Liaoning, China (North China Terrane; Cocks and Torsvik, 2002; Fortey and Cocks, 2003), and is probably from basal Paibian strata (Peng and Robison, 2000, p. 35).

The type species of *Kormagnostella*, *K. glabrata* E. Romanenko (in Romanenko and Romanenko, 1967) is from the Western Altai Terrane unit, Altai-Sayan area, southern Siberia, which is peripheral to the Siberian craton (Cocks and Torsvik, 2007). From its association with *Clavagnostus cuneatus* E. Romanenko, *in* Romanenko and Romanenko, 1967 (regarded as a synonym of *C. spinosus* [Resser, 1938] by Peng and Robison, 2000), this species is Guzhangian in age. The record of *Kormagnostella* from northern Queensland, Australia, (tropical "east" Gondwana; Cocks and Torsvik, 2002; Fortey and Cocks, 2003), is from the late Idamean *Stigmatoa diloma* Zone, with the highest occurrence some 20 m below the first appearance of *Irvingella tropica* Öpik, 1963 (Shergold, 1982, fig. 7). This correlates into the late Paibian Stage and, in terms of the Laurentian nomenclature, probably with a level high in the Steptoean *Dunderbergia* Zone.

Compared to the occurrences in other Cambrian continents, the stratigraphic ranges of *Biciragnostus* and, particularly, *Kormagnostella* in Laurentia are abbreviated and clearly record immigration during an interval of sea level rise and faunal turnover. They provide further evidence for shifts in biogeographic and environmental distribution during Cambrian trilobite and agnostoid extinction events (e.g., Ludvigsen and Westrop, 1983; Westrop and Ludvigsen, 1987).

Correlation of faunal turnover at the base of the Sunwaptan Stage in Laurentian North America.—The basal Sunwaptan Irvingella major Zone marks the onset of a trilobite and agnostoid extinction event (base of the "Ptychaspid Biomere"; Westrop and Cuggy, 1999, fig. 1), which can be correlated readily across Laurentian North America. However, there is less certainty regarding correlation of this extinction beyond Laurentia, and it is far from clear whether it is expressed elsewhere. The presence of *Biciragnostus* and *Kormagnostella* in Nevada and Utah provides an important link with the succession in Karatau-Naryn Terrane, Kazakhastan (Fig. 2), and allows a comparison of faunal turnover in two distinct Cambrian continents.

The biostratigraphic data suggest that the disappearance of *Kormagnostella* and *Biciragnostus* in the Karatau-Naryn Terrane falls in the Steptoean–Suwaptan boundary interval of Laurentia. The level of local extinction of *Biciragnostus* and *Irvingella* in Kazakhstan may correlate into the earliest Sunwaptan. This provides the first evidence for broadly coeval faunal turnover in the Karatau-Naryn Terrane and Laurentia. In Laurentia, the basal Sunwaptan extinction is a complex event characterized by



FIGURE 3—Kormagnostella advena, Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah; all ×25 and all from collection ORR 60.3– 60.4. *1–*3, cephalon, OU 12893, dorsal, anterior and lateral views; 4–6, cephalon, OU 12894 (holotype), lateral, anterior and dorsal vews; 7–9, cephalon, OU 12895, dorsal, lateral and anterior views; *10*, cephalon, OU 12896, dorsal view; *11*, pygidium, OU 12897, dorsal view; *12–14*, cephalon, OU 12898, lateral, dorsal and anterior views; *15*, pygidium, OU 12899, dorsal view; *16–18*, pygidium, OU 12900, dorsal, lateral and posterior views; *19*, pygidium, OU 12901, dorsal view; *20*, pygidium, OU 12902, dorsal view; *21, 22*, pygidium, OU 12903, posterior and dorsal views.

diversity decline, immigration and termination of clades (Westrop and Cuggy, 1999; Westrop et al., 2010). However, range charts for the Kyrshabakty section (Ergaliev et al., 2009, fig. 7) suggest a different pattern of change in this interval in the Karatau-Naryn Terrane of Kazakhstan. Although some trilobite genera, including Irvingella and Stigmatoa Öpik, 1963 disappear at or near the top of the Ivshinagnostus ivshini-Irvingella major Zone, much of the turnover involves replacement of species within genera (e.g., Proceratopyge Wallerius, 1895), or loss of genera that reappear higher in the section (e.g., Maladioidella Endo, 1937; Onchonotellus Lermontova, 1951). As far as can be determined from range charts, there is only a modest decline in species diversity. The reasons for the apparent differences in the impact of the basal Sunwaptan event in Karatau-Naryn Terrane are unclear. The upper Cambrian succession at Kyrshabakty accumulated in deep water (possibly on a seamount; Popov et al., 2009) and includes numerous debris flows and turbidites (Ergaliev et al., 2008). Greater faunal continuity in deeper water, off-shelf settings has been a persistent theme in interpretations of "biomere" extinctions for almost half a century (e.g., Palmer, 1965a), and the Karatau-Naryn Terrane may provide some support for this widely held view.

SYSTEMATIC PALEONTOLOGY

Illustrated material is housed at the Oklahoma Museum of Natural History (OU). Sample localities are indicated by the abbreviations: CHC, Barton Canyon; ORR, Orr Ridge; STR, Steptoe Ranch. In order to maximize depth of field, digital images were rendered from stacks of images focused at 200 micron intervals using Helicon Focus 4.0 for the Macintosh http://www.heliconsoft.com>.

Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimetre using the Measure Tool of Adobe PhotoshopTM.

Family Ammagnostidae Öpik, 1967

Remarks.—Öpik (1967) assigned *Ammagnostus* Öpik, 1967 (=*Agnostoglossa* Öpik, 1967; see Robison, 1988), and *Kormagnostus* Resser, 1938, to a new agnostoid subfamily, Ammagnostinae (later elevated to family level by Peng and Robison, 2000, which is arbitrarily followed here); Shergold and Laurie (in Whittington et al., 1997) added *Proagnostus* Butts, 1926, *Hadragnostus* Öpik, 1967, *Formosagnostus* Ergaliev, 1980, *Tentagnostus* Sun, 1989, and, questionably, *Kormagnostella*. Diagnoses compiled by both Shergold and Laurie (in Whittington et al., 1997, p. 344) and Peng and Robison (2000, p. 23) are descriptive in nature and potential synapomorphies are far from obvious. It is possible, however, that the very long, parallel-sided to gently expanded pygidial axis will unite this group of genera.

Genus KORMAGNOSTELLA E. Romanenko *in* Romanenko and Romanenko, 1967

Type species.—Kormagnostella glabrata E. Romanenko, *in* Romanenko and Romanenko, 1967, from Cambrian strata of Gorny Altai, West Altai Terrane unit, Altai-Sayan region, southern Siberia (by original designation).

Diagnosis.—Anteroglabella effaced entirely, so that glabella terminates at F3 transglabellar furrow. Pygidial acrolobe almost completely effaced with at most vestigial axial furrows expressed near anterior margin. Pygidial border furrows narrow, well-incised grooves. Pygidial border broad and convex, and lacks posterolateral spines throughout holaspid ontogeny.

Remarks.—All recent authors (Shergold, 1982; Shergold and

Laurie, in Whittington et al., 1997; Peng and Robison, 2000; Ergaliev and Ergaliev, 2008) have treated Litagnostoides Schrank, 1975, as a junior synonym of Kormagnostella, but have disagreed on the relationship between the latter and Kormagnostus Resser. Peng and Robison (2000) argued that Kormagnostus and Kormagnostella are synonyms, a position that was followed by Jell (in Jell and Adrain, 2003) but was rejected more recently by Ergaliev and Ergaliev (2008). Following study of types and associated, previously unillustrated sclerites of the type species of Kormagnostus, K. simplex Resser, from Tennessee, as well as the holotype of K. seclusus (Walcott, 1884), we concur with Ergaliev and Ergaliev and treat Kormagnostella as a distinct taxon. We will deal with Kormagnostus elsewhere, although we do note that our study of the respective types leads us to reject synonymy of K. simplex and K. seclusus, as advocated by Robison (1988); Shergold and Laurie (in Whittington et al., 1997, p. 347) also regarded K. simplex and K. seclusus as distinct species.

Peng and Robison (2000, p. 32) noted that the original diagnosis of Kormagnostella by Romanenko and Romanenko (1967) emphasized loss of pygidial marginal spines as a diagnostic character. As spine loss can occur in individual species within typically spinose genera, they argued that Kormagnostella should be suppressed. In effect, because spine loss is open to homoplasy, they implied that this character state is disqualified as a source of character support for monophyly of any agnostoid clade. However, a blanket dismissal of a character state in this way is unjustified, and utility should be evaluated on a case-by-case basis. Homoplastic character states may act as a synapomorphies for clades (indeed, the retention index is a measure of this property in quantitative phylogenetic analysis), and spine loss may in fact help support monophyly of Kormagnostella. As recognized by Shergold (1982) and Ergaliev and Ergaliev (2008), there are additional characters that contribute to the diagnosis of Kormagnostella. Effacement of the pygidium is extreme, with no more than a vestige of the axial furrows expressed anteriorly on even the smallest holaspid (e.g., Fig. 3.20; Fig. 4.9, 4.10). This contrasts with the condition in Kormagnostus, where the axis and axial furrows are expressed fully in smaller holaspids (e.g., Robison, 1988, figs. 11.9, 11.10a, 11.10b, 14) and recognizable over the anterior half of the pygidium in larger individuals (e.g., Robison, 1988, fig. 11.15). Although the acrolobe is almost entirely effaced, the border furrow of Kormagnostella is narrow but firmly impressed (deliquiate of Shergold, 1975, p. 41), and the border itself is broad and convex (Figs. 3.11, 3.15-3.20, 4.9, 4.10, 4.12, 4.13, 4.15-4.19, 5.1-5.4). Both states separate Kormagnostella from Kormagnostus. Spine loss covaries with these other pygidial characters, and we interpret this state as an additional synapomorphy.

Although effacement contributes to the diagnosis of *Kormagnostella*, it obscures broader phylogenetic relationships. Cephalic morphology is similar in *Kormagnostella* and *Kormagnostus*, with loss of the anteroglabella as a potential synapomorphy uniting them (compare Fig. 4.1–4.8 with Robison, 1988, fig. 11.6–11.7). It is, however, less clear as to whether *Kormagnostus* is monophyletic. Characters cited by Öpik (1967, p, 138) to differentiate *Kormagnostus* from *Ammagnostus* (wide cephalic border; loss of anteroglabella) are also present in *Kormagnostella*. Moreover, pygidial anatomy of *Kormagnostus* (e.g., Westrop et. al, 1996, fig. 13.9, 13.10) is similar to that of *Ammagnostus* (e.g., Peng and Robison, 2000, fig. 22.14–22.18) and it is conceivable that the former will prove to be paraphyletic. However, further investigation of the status of *Kormagnostus* will require a broad



FIGURE 4—Kormagnostella insolita, Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah; all ×25 and all from collection ORR 60.3– 60.4. *I*–3, cephalon, OU 12904 (holotype), dorsal, anterior and lateral views; 4–6, cephalon, OU 12905, anterior, lateral and dorsal views; 7, cephalon, OU 12906, dorsal view; 8, cephalon, OU 12907, dorsal view; 9, 10, pygidium, OU 12908, posterior and dorsal views; 11, cephalon, OU 12909, dorsal view; 12, 13, pygidium, OU 12910, dorsal and posterior views; 14, cephalon, OU 12911, dorsal view; 15, 16, pygidium, OU 12912, posterior and dorsal views; 17–19, pygidium, OU 12913, lateral, dorsal and posterior views.



FIGURE 5—1–4, *Kormagnostella advena*?, Barton Canyon Limestone Member, Windfall Formation, north side of Barton Canyon, Cherry Creek Range, Nevada; all ×25 and all from collection CHC-1–0 (basal layer): *1–3*, pygidium, OU 12914, dorsal, posterior and lateral views; *4*, pygidium, OU 12915, dorsal view; *5*, *6*, *Agnostotes* cf. *A. clavatus* (Lu, *in* Wang, 1964), Barton Canyon Limestone Member, Windfall Formation, Steptoe Ranch, North Egan Range, Nevada; all ×20 and all from collection STR 10.9–11.1 (basal layer): *5*, pygidium, OU 12916, dorsal view; *6*, pygidium, OU 12917, dorsal view.

phylogenetic analysis and it will be dealt with elsewhere. In contrast, monophyly of *Kormagnostella* seems secure.

KORMAGNOSTELLA ADVENA new species Figures 3, ?5.1–5.4

Diagnosis.—Kormagnostella with relatively narrow cephalon, length equal to width (99%; 96–104); lateral margins weakly curved and anterior margin nearly transverse medially. Pygidium strongly effaced, with axial furrows obsolete (e.g., Fig. 3.15, 3.16) or expressed as mere vestiges (e.g., Fig. 3.22); posterior pygidial margin weakly rounded. Pygidial length 86%(80–90) of width at axial node.

Description.-Strongly arched cephalon subsemielliptical in outline, with gently curved lateral margins, anterior margin nearly transverse in front of glabella; relatively narrow, length equal to width (99%; 96-104). Glabella with anteroglabella effaced, although subtle, barely perceptible inflation may be present in front of F3 (e.g., Fig. 3.2, 3.3); axial and transglabellar F3 furrows firmly impressed. Posteroglabella convex, elevated well above adjacent regions of acrolobe, length equal to 46% (45-47) of cephalic length, and relatively narrow, width equal to 75% (67-81) of length, and occupying 34% (31-36) of cephalic width; tapers gently forward. Basal lobes conspicuous, subtriangular in outline, length equal to 26% (24-30) of posteroglabellar length, and separated from inflated, medial portion of posteroglabella by well defined basal furrows. In some larger specimens (e.g., Fig. 3.1, 3.6), short (tr.), shallow F1 and F2 furrows present; M2 lobe expanded gently outward. Small axial node on M2. Acrolobe unconstricted (Fig. 3.13) to slightly constricted (Fig. 3.1); occupies 86% (85-89) of cephalic length. Borders convex and widest anteriorly, narrowing posteriorly; border furrows firmly impressed, deliquiate. External surface smooth.

Pygidium slightly subquadrate in outline with gently rounded posterior margin, length 86% (80–90; higher values in larger specimens) of width and gently rounded posteriorly; strongly arched in posterior and lateral views. Acrolobe effaced, with vestigial axial furrows expressed anteriorly on some specimens, and weakly constricted (e.g., Fig. 3.22); occupies 80% (76–84) of pygidial length; acrolobe length 87% (84–91; higher values in larger specimens) of acrolobe width. Conspicuous median node located near mid-length of acrolobe, distance from anterior margin of acrolobe to posterior tip of node equal to 49% (41–55; higher values in smaller specimens with relatively shorter acrolobes; e.g., Fig. 3.11, 3.20) of acrolobe length. Border furrows strongly incised, deliquiate; borders gently convex, broad posteriorly, but tapering anteriorly; posterolateral spines absent. External surface smooth, but acrolobe roughened with coarse granules on internal molds; some specimens with small terminal node.

Etymology.—From advena (Latin), immigrant.

Holotype.—A cephalon (OU 12894; pl. 2, figs. 4–6) from the Sneakover Member of the Orr Formation at Orr Ridge (collection ORR 60.3–60.4).

Material and occurrence.—Six cephala and seven pygidia from the Sneakover Member (collection ORR 60.3–60.4), *Irvingella major* Zone. Two pygidia from the top of the Barton Canyon Limestone (collection CHC-1-0, basal layer), uppermost *Elvinia* Zone and one pygidium from the same stratigraphic level at Steptoe Ranch (STR 10.9–11.1, basal layer) may also belong to *K. advena.*

Remarks.--Cephala of Kormagnostella from Orr Ridge fall into two groups differentiated by relative width. Those assigned here to K. advena n. sp. are relatively narrow, with length equal to width (99%; 96-104), whereas those of K. insolita n. sp. are wider, so that length is equal to about 90% of width (89%; 86-92); lateral margins of the latter are more strongly rounded (e.g., compare Figs. 3.6 and 4.7). Associated pygidia also seem to fall into two groups of different relative widths, and this is the basis for sclerite associations. However the number of pygidia is small and our pygidial assignments are tentative. All of the sclerites of K. advena from Orr Ridge are from the Irvingella major Zone. Two pygidia (Fig. 5.1–5.4) from the top of the underlying *Elvinia* Zone at Barton Canyon are relatively narrow and their length/ width proportions (86%, 92%) are comparable to similarly sized specimens from Orr Ridge. They likely represent the same species, although in the absence of associated cephala, assignment is tentative.

The type species of *Kormagnostella*, *K. glabrata* E. Romanenko *in* Romanenko and Romanenko (1967, pl. 1, figs. 22, 23; see also Shergold and Laurie, *in* Whittington et al., 1997, fig. 220.6), is known only from three figured specimens, a cephalon, a pygidium, and an incomplete articulated cephalon and thorax. As far as can be determined from published photographs, this species is similar to both *K. advena* and *K. insolita* in grade of effacement. Like *K. advena*, the cephalon appears to have been relatively narrow, but the only known pygidium has an axial node that is located closer to the anterior margin than in both *K. advena* and *K. insolita*, and the borders are relatively narrow.

Kormagnostella inventa Shergold (1982, pl. 6, figs. 12-17), from the Pomegranate Limestone of western Queensland, Australia, has a relatively narrow cephalon that resembles K. advena, although the well rounded anterior margin (e.g., Shergold, 1982, figs, 12-14) contrasts with a margin that is nearly transverse medially in the latter (e.g., Fig. 3.1, 3.6, 3.13). Pygidia of K. inventa are relatively wider than those of K. advena, and are less effaced, retaining weak axial furrows that extend back to the level of the axial node. Ergaliev and Ergaliev (2008, pl. 36, figs. 25, 26; pl. 40, figs. 22–28) assigned sclerites from the Kumabay Formation of the Karatau-Naryn Terrane, Kazakhstan, to K. inventa. Like Shergold's (1982) types, the figured cephala are relatively narrow and well rounded anteriorly, although at least one (Ergaliev and Ergaliev, 2008, pl. 36, fig. 25) may be somewhat deformed. The pygidia are illustrated by small photographs and are generally poorly lit. All appear to be relatively narrower than Shergold's material and more strongly effaced, and they are most likely misidentified.

Kormagnostella minuta (Schranck, 1975, pl. 1, figs. 4–10) from the "Paishan Formation" (=Changshan Formation; Zhang and Jell, 1987; Sun, 1989), Liaoning, North China Terrane, is characterized by a strongly effaced pygidium that is similar to those of the species described here. The most obvious difference in pygidia of *L. minuta* is that the posterior margin is well rounded in all figured specimens. In contrast, posterior margins of pygidia of both *K. advena* and *K. insolita* are gently rounded and may be nearly transverse medially in some specimens (e.g., Fig. 4.16). Cephala of *K. minuta* are relatively broad with lateral margins that are strongly curved anteriorly. In these respects, they are close to cephala of *K. insolita*, differing only in having somewhat more constricted acrolobes.

Following a broad reinterpretation of the species by Peng and Robison (2000, p. 33), K. minuta has been recognized widely (e.g., Lazarenko et al., 2008; Ergaliev and Ergaliev, 2008). Unfortunately, their decision to assign sclerites from the Huaquiao Formation of Hunan, South China Terrane (Peng and Robison, 2000, fig. 24), to this species is undermined by the limited material illustrated to support the original description of K. minuta. Most pygidia illustrated by Peng and Robison (2000, fig. 24.6-24.10, 24.14, 24.15, 24.18, 24.19) have elongate, semielliptical acrolobes that are bluntly pointed posteriorly. However, the smallest figured pygidium (Peng and Robison, 2000, fig. 24.11) has a relatively shorter, subcircular acrolobe that is well rounded posteriorly. If conspecific with the other pygidia, it implies a sharp ontogenetic change in acrolobe outline between pygidial lengths (sag.) of about 1.3 mm and 1.5 mm (compare figs. 24.11 and 24.6). The data are limited, but a similar shift in outline cannot be demonstrated in the type lot of K. minuta. All figured pygidia possess subcircular acrolobes, albeit across a size range of only 1 mm to 1.6 mm (sag.). Accordingly, we consider identification of K. minuta from the Huaqiao Formation to be premature, and it cannot be justified given the current state of knowledge of this species. If, as we think likely, Peng and Robison's material represents a distinct species, then K. taoyuanensis (Peng, 1987, pl. 4, figs. 5–9) is an available name; we are uncertain about the status of K. latilimbata (Qian and Zhou, 1984), although Peng and Robison (2000) treated it as a senior synonym of K. taoyuanensis.

A cephalon and pygidium identified as *K. minuta* by Lazarenko et al. (2008, pl. 14, figs. 4, 8) from the Ogon'or Formation of the northeastern Siberian craton resembles material from the Huaquiao Formation, but more information is needed for critical evaluation. It is, however, doubtful that they are conspecific with

Schrank's types. In particular, the pygidium is elongate with a long acrolobe that is unlike the more equant, rounded acrolobes that characterize pygidia of *K. minuta*.

Sclerites from the Zhumabay Formation, Karatau-Naryn Terrane, Kazakhstan, attributed to K. minuta by Ergaliev and Ergaliev (2008), are so poorly illustrated as to be essentially uninterpretable. One pygidium (Ergaliev and Ergaliev, 2008, pl. 20, fig. 10) is proportionately wider than any specimen illustrated by Schrank; other figured pygidia cannot be evaluated because they are incorrectly oriented (Ergaliev and Ergaliev, 2008, pl. 20, fig. 8) or are poorly lit and obscured by shadows (Ergaliev and Ergaliev, 2008, pl. 23, fig. 23). Figured cephala (Ergaliev and Ergaliev, 2008, pl. 26, figs. 21-23) represent Kormagnostella, but little more can be said. Kormagnostella longa (Ergaliev, 1980, pl. 4, fig. 20) was named for a single figured pygidium that resembles some specimens of K. advena (e.g., Fig. 3.15). Additional material assigned to this species by Ergaliev and Ergaliev (2008, pl. 20, figs. 1–4; pl. 23, figs. 19–21; pl. 26, figs. 19, 20; pl. 27, fig. 14) include cephala with well rounded anterior margins and relatively long, narrow, strongly effaced pygidia. These cephala are similar to those of K. advena, differing in possessing well rounded anterior margins (e.g., Ergaliev and Ergaliev, 2008, pl. 20, figs. 1-4), but the pygidia clearly differ in outline (compare Ergaliev and Ergaliev, 2008, pl. 23, figs. 19-21 with Fig. 3.11, 3.15, 3.16, 3.19, 3.20, 3.22), although specimens from Kazakhstan encompass a larger size range than those from Nevada and Utah. Finally K. carinata Ergaliev and Ergaliev (2008, pl. 32, figs. 31, 32) is illustrated by one cephalon and a single pygidium, and is thus difficult to evaluate. The cephalon appears to be relatively narrow and is most similar to K. advena. However, the strongly effaced pygidium differs from those of both K. advena and K. insolita in having an axial node that is located close to the anterior margin. In this respect, K. carinata resembles K. glabrata Romanenko.

KORMAGNOSTELLA INSOLITA new species Figure 4

Diagnosis.—Kormagnostella with relatively wide cephalon, length equal to about 90 % of width (89%; 86–92); lateral margins well rounded anteriorly. Pygidial length less than 80% (78%; 77–79) of width.

Description.—See remarks below.

Etymology.—From insolitus (Latin), unaccustomed, unusual.

Holotype.—A cephalon (OU 12904; Pl. 3, figs. 1–3) from the Sneakover Member of the Orr Formation at Orr Ridge (collection ORR 60.3–60.4).

Material and occurrence.—Eight cephala and three pygidia from the Sneakover Member (collection ORR 60.2–60.3), *Irvingella major* Zone.

Remarks.—Kormagnostella insolita n. sp. is sufficiently similar to *K. advena* that a comparison between these species will be presented instead of a full description. *Kormagnostella insolita* is relatively wider than *K. advena*, and this is expressed most clearly in the cephala. Cephalic length of the former species is about 90% (89%; 86–92) of width, whereas length equals width (99%; 96–104) in *K. advena*. The lateral cephalic margins of *K. insolita* are more strongly curved than those of *K. advena*, and the posteroglabella of the former tends to be relatively wider (compare Fig. 4.1, 4.6 and 4.7 with Fig. 3.1, 3.6 and 3.7). As would be predicted from cephalic differences, pygidia from collection ORR 60.2–60.3 also fall into two groups that differ in relative width. Pygidia tentatively assigned to *K. advena* have lengths that are less 80% of width, whereas that value averages 86% in pygidia attributed to *K. insolita*.



FIGURE 6—Biciragnostus viator n. sp., Barton Canyon Limestone Member, Windfall Formation, north side of Barton Canyon, Cherry Creek Range, Nevada; all ×20 and all from collection CHC-1-0 (basal layer). *1–3*, cephalon, OU 12918, dorsal, lateral and anterior views; *4–6*, cephalon, OU 12919, dorsal, lateral and

Family Agnostidae M'Coy, 1849

Genus BICIRAGNOSTUS F. Ergaliev in Ergaliev and Ergaliev, 2001

Type species.—Biciragnostus biformis F. Ergaliev *in* Ergaliev and Ergaliev, 2001, from the Zhumabay Formation, Malyi Karatau Range, Karatau-Naryn Terrane, southern Kazakhstan (by original designation).

Diagnosis.—Cephalon scrobiculate. Anteriorly tapered glabella with deep F1 and F2 furrows defining large, subequal M1 and M2 lobes. Pygidium with tripartite M1 and M2, with continuous, barshaped median lobe raised well above lateral lobes and inflated into prominent tubercle posteriorly. Pygidial posteroaxis expands backwards and with well-defined intranotular axis.

Remarks.—In their original description of the genus, Ergaliev and Ergaliev (2001) consistently used the name, *Biciragnostus*, but used an alternate spelling, *Biceragnostus*, without comment (i.e., without indication of intent) in a later work (Ergaliev and Ergaliev, 2008, p. 50). The derivation of the name is indicated (Ergaliev and Ergaliev, 2001, p. 178) as from the Latin words *bi* (double) and *circa* (circle). We therefore follow the original spelling from the 2001 paper and interpret the spelling in the 2008 paper as an "incorrect subsequent spelling" as defined by Article 33 of the ICZN, rather than an emendation.

The original description of *Biciragnostus* was accompanied by photographs of only three specimens of the type species (Ergaliev and Ergaliev, 2001, figs. 5–7; the same images are reproduced in Ergaliev and Ergaliev, 2008, pl. 40, figs. 8–10), one of which is an internal mold; range charts for the Kyrshabakty section (Ergaliev and Ergaliev, 2008, table 4) indicates that the genus occurs in four collections through about 30 m of section and is represented by about 15 sclerites (Ergaliev and Ergaliev, 2008, p. 50). The images are very small and of poor quality, so that the anatomy of the sclerites is difficult to interpret. They are, however, sufficient to be confident that the Kazakh material is congeneric with our specimens, with the latter providing the basis for the diagnosis presented above.

Cephalic character states shared between B. biformis and B. viator n. sp. include well developed scrobiculation (e.g., Figs. 6.1-6.3, 7.1-7.3) and deeply incised F1 and F2 furrows that define large M1 and M2 lobes (e.g., Fig. 6.1-6.10); on B. viator, both M1 and M2 are isolated from the central part of the glabella by finely etched grooves, but quality of both preservation and published images of the only figured cephalon of B. biformis (Ergaliev and Ergaliev, 2008, pl. 40, fig. 8) does not reveal whether the lobes are isolated in a similar way. Pygidial characters include tripartite M1 and M2, and a posteroaxis that is expanded posteriorly and which contains a well-defined intranotular axis (e.g., Fig. 8); again, image quality (Ergaliev and Ergaliev, 2008, pl. 40, figs. 9, 10) prevents us from determining whether B. biformis possesses the strongly convex borders evident in B. viator (e.g., Fig. 8.1-8.3). These pygidial features recall Lotagnostus Whitehouse, 1936 (e.g., see Westrop et al., 2011, fig. 2), as recognized by Ergaliev and Ergaliev (2001), who also made comparisons with the poorly known L.? mystacinus Tjernvik, 1953 (see Ahlberg and Ahlgren, 2000, fig. 1A-1D). Species of Lotagnostus lack the expansion of the pygidial posteroaxis evident in Biciragnostus. F2 glabellar furrows may be conspicuous on cephala of Lotagnostus, but F1 is weak or absent, so that the expression of M1 and M2 lobes is entirely different (e.g., Rushton, 2009, fig. 2E, 2F); both M1 and M2 are much larger in *Biciragnostus*.

BICIRAGNOSTUS VIATOR new species Figures 6–8

Diagnosis.—Biciragnostus with tapering glabella that terminates at narrow (tr.) anteroglabella whose width equals about half (49%; 46–53) of glabellar width at M2. M1 and M2 isolated from medial, more convex part of glabella by finely etched furrows, and depressed very slightly below adjacent region of acrolobe. Median preglabellar furrow well defined and terminates at, or very close to, border furrow. F2 pygidial furrows curved backward and inward. Acrolobe gently inflated near pygidial axis before sloping steeply downward to conspicuous, convex borders.

Description.--Cephalon convex, semielliptical in outline, with length about 10% greater than width at F3 furrow (109%; 102-115, with lowest values in small sclerites; e.g., Fig. 7.7, 7.12); acrolobe broad, occupying about 90% of cephalic length (92%; 89-95) and width (90%; 87-96). Well incised preglabellar median furrow terminates, at or close to, border furrow; weak deltoid depression may be present (e.g., Fig. 6.1). Axial furrows narrow but firmly impressed grooves. Glabella occupies 67% (64–73) of cephalic length and 41% (37–43) of cephalic width; tapers forward, with abrupt narrowing at anteroglabella, so that anteroglabella width is half (49%; 46-53) of glabellar width at midpoint of M1. Medial portion of glabella strongly convex posteriorly, raised well above adjacent basal and M1 glabellar lobes, but convexity declines anteriorly, becoming similar to M2 lobes. Basal lobes subtriangular in outline, length equal to 17% (15-22) of glabellar length; basal furrow finely etched groove. F1 furrow well incised, transverse near axial furrow, but deflected forward adaxially; F2 also well-defined, narrow (exsag.) at axial furrow but expands adaxially; F3 transglabellar furrow shallow, nearly transverse medially but deflected forward near axial furrow. M1 and M2 weakly convex, very slightly depressed below adjacent parts of acrolobe, of similar maximum length (exsag.), equal to 24% (23-26) and 27% (25-29) of glabellar length, respectively; isolated on adaxial side by faint furrows that run from F1 to F2, and from F2 to F3. Anteroglabella weakly convex, subpentagonal in outline, with pointed (e.g., Figs. 6.4, 7.1) to bluntly rounded (e.g., Fig. 7.17) anterior terminus; occupies 26% (22-29) of glabellar length. Border furrows deep, deliquiate. Borders narrow, convex, widest anteriorly but tapering backward, particularly behind level of F2. Anterior half of acrolobe strongly scrobiculate but posterior half nearly smooth.

Pygidium convex, semielliptical in outline, length slightly less (96%, 87–105) than width. Axial furrows narrow but firmly impressed grooves. Pygidial axis strongly convex, standing well above adjacent parts of acrolobe, and occupies 73% (70–78) of pygidial length. Axis bulb-shaped with expanded posteroaxis, minimum width at M2 equal to 84% (74–92) of maximum posteroaxis width. F1 furrows nearly transverse, isolated by continuous, elevated median bar that extends across central region of M1 and M2 and which expands posteriorly into axial node; adaxial termination of furrows pit-like (e.g., Fig. 8.1, 8.13). Lateral lobe of M1 subquadrate in outline, equal to about one-fifth (19%; 15–22) of axis length. Transaxial F2 furrows curve backward and inward; M2 lobe expands adaxially and pentagonal

anterior views; 7, cephalon, OU 12920, dorsal view; 8–10, cephalon, OU 12921, lateral, anterior and dorsal views; 11–13, pygidium, OU 12922 (holotype), dorsal, lateral and posterior views; 14–16, pygidium, OU 12923, lateral, dorsal and posterior views; 17–19, pygidium, OU 12924, dorsal, posterior and lateral views; 20, 21, pygidium, OU 12925, dorsal and posterior views; 22, 23, pygidium, OU 12926, dorsal and posterior views; 24, pygidium, OU 12927, dorsal view; 25, pygidium, OU 12928, dorsal view; 26, pygidium, OU 12929, dorsal view; 27, pygidium, OU 12930, dorsal view.



FIGURE 7—Biciragnostus viator n. sp., Barton Canyon Limestone Member, Windfall Formation, Steptoe Ranch, North Egan Range, Nevada; all cephala ×20 and from STR 10.9–11.1 (basal layer). *1–3*, OU 12931, dorsal, lateral and anterior views; *4–6*, OU 12932, lateral, dorsal and anterior views; *7*, OU 12933, dorsal view; *8–10*, OU 12934, anterior, dorsal and lateral views; *11*, OU 12935, dorsal view; *12*, OU 12936, dorsal view; *13*, OU 12937, dorsal view; *14–16*, OU 12938, dorsal, anterior and lateral views; *17*, OU 12939, dorsal view.

in outline; accounts for 20% (17–23) of axis length. Posteroaxis suboval in outline, occupies half (50%; 40–55) of pygidial width. Notular furrows shallow but notulae well defined; inflated intranotular axis occupies about one-third of posteroaxis width. Border furrows narrow, deliquiate. Borders are convex rims, widest between posterolateral spines but tapering anteriorly. Posterolateral spines conspicuous, triangular, located behind tip of axis. External surface and internal mold is smooth.

Etymology.-From viator (Latin), traveler.

Holotype.—A pygidium (OU 12922; Fig. 6.11–6.13) from the top of the Barton Canyon Limestone at Barton Canyon, White Pine County, Nevada, collection CHC-1-0 (basal layer).

Material and occurrence.—The top of the Barton Canyon Limestone at Barton Canyon (collection CHC-1-0, basal layer; six cephala and eight pygidia); and Steptoe Ranch (collection STR

10.9–11.1, basal layer; eleven cephala and ten pygidia); uppermost *Elvinia* Zone.

Remarks.—Although the quality of published images of *Biciragnostus biformis* hinders comparisons with *B. viator*, several characters seem to separate these species. Both the cephalon and pygidium of *B. biformis* (Ergaliev and Ergaliev, 2008, pl. 40, figs. 8–10, respectively) appear to have inflated acrolobes near the glabella and axis. Inflation appears to be particularly pronounced on the cephalon, with the glabella seemingly depressed, and the acrolobe rising from the axial furrows to form low ridges that circumscribes the glabella. Inflation of the cephalic (e.g., Fig. 6.3, 6.6, 6.8, 6.15) and pygidial (e.g., Fig. 8.3, 8.12) acrolobe is weak in *B. viator*. In addition, the preglabellar median furrow appears to be expressed only between the glabella and the low inflated ridge in *B. biformis* but is



FIGURE 8—Biciragnostus viator n. sp., Barton Canyon Limestone Member, Windfall Formation, Steptoe Ranch, North Egan Range, Nevada; all pygidia ×20 and from STR 10.9–11.1 (basal layer). *1–3*, OU 12940, dorsal, lateral and posterior views; *4–6*, OU 12941, dorsal, posterior and lateral views; *7*, OU 12942, dorsal view; *8*, OU 12943, dorsal view; *9*, OU 12944, dorsal view; *10*, OU 12945, dorsal view; *11*; degree 1 meraspis, OU 12946, dorsal view; *12*, *13*, OU 12947, posterior and dorsal views.

complete, or nearly so, in *B. viator*. The most obvious difference between the pygidia is in the course of F2, which appears to be nearly transverse in *B. biformis* but is curved backward and inward in *B. viator*. Also, the posteroaxis is proportionately shorter in *B. viator*, occupying 50% (47–54) of axis length, versus about 65% in *B. biformis*.

Genus Agnostotes Öpik, 1963

Type species.—Agnostotes inconstans Öpik, 1963 from the Pomegranate Limestone, Pomegranate Creek area, western Queensland (by original designation).

Agnostotes cf. A. clavata (Lu *in* Wang, 1964) Figure 5.5, 5.6

- 1992 cf. *Agnostotes clavata* Lu *in* Wang; PRATT, p. 39, pl. 4, figs. 29–34 (see for synonymy).
- 1992 cf. Agnostotes (Pseudoglyptagnostus) clavata Lu in Wang; PENG, p. 25, fig. 10H–10S.

Material and occurrence.—Two incomplete pygidia from the top of the Barton Canyon Limestone, Steptoe Ranch (collection STR 10.9–11.1, basal layer), uppermost *Elvinia* Zone.

Remarks.—The holotype of *Agnostotes orientalis* (Kobayashi, 1935) consists of a fragmentary pygidium and associated incomplete internal mold (e.g., see Peng and Babcock, 2005, fig. 1.1, 1.2) that are essentially uninterpretable. Choi et al. (2004, fig. 10) attempted to revise *A. orientalis* using badly flattened material but, given the poor quality of the holotype, we consider use of this name to be ill-advised and prefer to treat it as a nomen

dubium that is best restricted to the type. Two incomplete pygidia from Nevada are similar to sclerites of *Agnostotes clavata* (Lu, *in* Wang, 1964) illustrated from northern Canada by Pratt (1992) and by Peng (1992) from South China. More material is needed for a firm identification.

ACKNOWLEDGMENTS

We gratefully acknowledge support from National Science Foundation grants EAR 9973065 and EAR 0308685. R. Burkhalter assisted in both field and lab work. Reviewers A. Rushton and N. Heim contributed a number of helpful comments on an earlier draft of the manuscript.

REFERENCES

- AHLBERG, P. AND J. AHLGREN. 2000. Lotagnostus? mystacinus, a rare agnostid from the upper Cambrian of Sweden. Acta Palaeontologica Polonica, 45: 91–96.
- BABCOCK, L. E. AND S.-C. PENG. 2007. Cambrian chronostratigraphy: Current state and future plans. Palaeogeography, Palaeoclimatology, Palaeoecology, 254:62–66.
- BUTTS, C. 1926. The Paleozoic rocks, p. 41–230. In G. I. Adams, C. Butts, L.W. Stephenson, and W. Cooke. Geology of Alabama. Geological Survey of Alabama, Special Report 14.
- CHATTERTON, B.D.E. AND R. LUDVIGSEN. 1998. Upper Steptoean (upper Cambrian) trilobites from the McKay Group of southeastern British Columbia, Canada. Paleontological Society Memoir, 49:1–43.
- CHOI, D.K., J. G. LEE, AND B. C. SHEEN. 2004. Upper Cambrian agnostoid trilobites from the Machari Formation, Yongwol, Korea. Geobios, 37:159–189.
- Cocks, L. R. M. AND T. H. TORSVIK. 2002. Earth geography from 500 to 400 million years ago: A faunal and paleomagnetic review. Journal of the Geological Society of London, 159:631–644.

- COCKS, L. R. M. AND T. H. TORSVIK. 2007. Siberia, the wandering terrane, and its changing geography through the Paleozoic. Earth-Science Reviews, 82: 29–74.
- ENDO, R. 1937. Addenda to parts 1 and 2. Manchurian Science Museum Bulletin, 1:302–369; 435–461.
- ERGALIEV, G. K. 1980. Middle and upper Cambrian trilobites of the Lesser Karatau Range. Academy of Sciences, Kazhakstan SSR. Kazakhstan SSR Publishing House, Alma Ata, 201 p. (In Russian)
- ERGALIEV, G. K. AND F. G. ERGALIEV. 2001. Asaky Geological State Reserve world heritage trilobite faunas of the middle and upper Cambrian of central Asia. Geology of Kazakhstan 2001(3–4):173–188. (In Russian) ERGALIEV, G. K. AND F. ERGALIEV. 2008. Middle and upper Cambrian
- ERGALIEV, G. K. AND F. ERGALIEV. 2008. Middle and upper Cambrian Agnostida of the Askai National Geological Reserve, south Kazakhstan (Kyrshabakty River, Malyi Karatau Range). P. I. Almaty: Gylym. 376 p. (In Russian)
- ERGALIEV, G. K., V. G. ZHEMCHUZHNIKOV, L. E. POPOV, M. G. BASSET, O. I. NIKITINA, S. V. DUBININA, F. G. ERGALIEV, AND E. M. FAZYLOV. 2009. Field excursion guide for the 14th international field conference of the Cambrian Stage subdivision working group, Malyi Karatau range, southern Kazakhstan. K. I. Satpaev Institute of Geological Sciences, Alma Ata, 70 p.
- EVANS, K. R., J. F. MILLER, AND B. F. DATILLO. 2003. Sequence stratigraphy of the Sauk Sequence: 40th anniversary field trip in western Utah, p. 17–35. *In* T. W. Swanson (ed.), Western Cordillera and adjacent areas. Geological Society of America Field Guide 4.
- FORTEY, R. A. AND L. R. M. COCKS. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. Earth-Science Reviews, 61:245–307.
- FREEMAN, R. L., J. F. MILLER, L. E. HOLMER, AND M. STRENG. 2011. Lingulate brachiopod extinction and global migration coinciding with three Laurentian trilobite extinction events during the late Cambrian-earliest Ordovician. Geological Society of America Abstracts with Programs, 43(5): 543
- HOLLAND, S. M. 2000. The quality of the fossil record: A sequence stratigraphic perspective, p. 148–168. *In* D. H. Erwin and S. L. Wing (eds.), Deep Time: Paleobiology's Perspective. The Paleontological Society, Lawrence, Kansas.
- JELL, P. A. AND J. M. ADRAIN. 2003. Available generic names for trilobites. Memoirs of the Queensland Museum, 48(2):331–553.
- KOBAYASHI, T. 1935. The Cambro–Ordovician formations and faunas of South Chosen, Palaeontology, Part 3, Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. Journal of the Faculty of Science, Imperial University of Tokyo, Section II, 4:49–344
- LAZARENKO N. P., I. YA. GOGIN, T. V. PEGEL, S. S. ŠUKHOV, G. P. ABAIMOVA, L. I. EGOROVA, A. B. FEDOROV, E. G. RAEVSKAYA, AND G. T. USHATINSKAYA. 2008. Excursion 1b. Cambrian stratigraphy of the northeastern Siberian Platform and potential stratotypes of lower boundaries of proposed upper Cambrian Chekurovkian and Nelegerian stages in the Ogon'or Formation section at Khos-Nelege River: The boundaries are defined by the FAD of *Agnostotes orientalis* and *Lotagnostus americanus*, p. 61–139. *In* A. Yu. Rozanov and A. I. Varlamov (eds.), The Cambrian System of the Siberian Platform. Part 2: North-east of the Siberian Platform. Moscow—Novosibirsk PIN RAS.
- LENZ, A. C., J. JIN, A. D. MCCRACKEN, J. UTTING, AND S. R. WESTROP. 1993. Paleoscene 15. Paleozoic biostratigraphy. Geoscience Canada, 20:41–73.
- LERMONTOVA, E. V. 1951. Upper Cambrian trilobites and brachiopods from Bosche-Kul. VESGEI, Moscow, 49 p. (In Russian)
- LUDVIGSEN, R. AND S. R. WESTROP, 1983. Trilobite biofacies of the Cambrian– Ordovician boundary interval in northern North America. Alcheringa, 7: 301–319.
- M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of some new forms in the University collection at Cambridge. Annals and Magazine of Natural History (Series 2), 4:161–179, 330–335, 392–414.
- Öрік, A. A., 1963. Early upper Cambrian fossils from Queensland. Bureau of Mineral Resources, Geology and Geophysics Bulletin, 74, 133 p.
- Öрік, A.A. 1967. The Mindyallan fauna of north-western Queensland. Bureau of Mineral Resources, Geology and Geophysics Bulletin, 74, 404 p.
- OSLEGER, D. 1995. Depositional sequences on upper Cambrian carbonate platforms: Variable sedimentologic responses to allogenic forcing, p. 247– 276. In B. U. Haq (ed.), Sequence Stratigraphy and Depositional Response to Eustatic, Tectonic and Climatic Forcing. Klewer Academic Publishers, Amsterdam.
- OSLEGER, D. AND J. F. READ. 1991. Relation of eustasy to stacking patterns of meter-scale cycles, late Cambrian, U.S.A. Journal of Sedimentary Petrology, 61:1225–1252.
- PALMER, A. R. 1965a. The biomere—a new kind of biostratigraphic unit. Journal of Paleontology, 39:149–153.
- PALMER, A. R. 1965b. Trilobites of the late Cambrian Pterocephaliid Biomere in the Great Basin, United States. United States Geological Survey Professional Paper 493, 105 p.

- PENG, S.-C. 1987. Early late Cambrian stratigraphy and trilobite faunas of Taoyuan and Cili, Hunan, p. 53–134. *In* Nanjing Institute of Geology and Palaeontology, Academica Sinica, Collection of Postgraduate Theses, Volume 1. Jiangsu Science and Technology Publishing House, Nanjing. (In Chinese)
- PENG, S.-C. AND R. A. ROBISON. 2000. Agnostoid biostratigraphy across the middle-upper Cambrian boundary in Hunan, China. Paleontological Society Memoir 53, 104 p.
- PENG, S.-C. AND L. E. BABCOCK. 2005. Two Cambrian agnostoid trilobites, Agnostotes orientalis (Kobayashi, 1935) and Lotagnostus americanus (Billings, 1860): Key species for defining global stages of the Cambrian System. Geosciences Journal, 9:107–115.
- PENG. S.-C., L. E. BABCOCK, J. ZUO, X. ZHU, H. LIN, X. YANG, Y. QI, G. BAGNOLI, AND L. WANG. 2012. Global standard stratotype-section and point (GSSP) for the base of the Jiangshanian Stage (Cambrian: Furongian), Duibian, Jiangshan, Zhejiang, southeast China. Episodes, 35:462–477.
- PENG. S.-C., X. ZHU, J. ZUO, H. LIN, Y. CHEN, AND L. WANG. 2011. Recently ratified and proposed Cambrian global standard stratotype-section and points. Acta Geologica Sinica, 85:296–308.
- POPOV, L. E., M. G. BASSETT, V. G. ZHEMCHUZHNIKOV, L. E. HOLMER, AND I. A. KLISHEVICH. 2009. Gondwanan faunal signatures from early Palaeozoic terranes of Kazakhstan and Central Asia: Evidence and tectonic implications, p. 23–64. In M. G. Bassett (ed.), Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography. Geological Society, London, Special Publications, 325.
- PRATT, B. R. 1992. Trilobites of the Marjuman and Steptoean stages (upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. Palaeontographica Canadiana, 9, 179 p.
- QIAN, Y. AND Z. ZHOU. 1984. Middle and early upper Cambrian trilobites from Kunshan, Jiangsu, with reference to their distribution in the lower Yangtze region. Acta Palaeontologica Sinica, 23:170–184. (In Chinese)
- RESSER, C. E. 1936. Second contribution to the nomenclature of Cambrian trilobites. Smithsonian Miscellaneous Collections, 95(4):1–29.
- RESSER, C. E. 1938. Cambrian System (restricted) of the southern Applachians. Geological Society of America Special Paper, 15, 140 p.
- ROBISON, R. A. 1976. Middle Cambrian biostratigraphy of the Great Basin. Brigham Young University Geological Studies, 23:93–109.
- ROBISON, R. A. 1988. Trilobites of the Holm Dal Formation (late middle Cambrian), central Greenland. Meddelelser om Grønland, Geoscience, 20: 23–103.
- ROMANENKO, E. V. AND M. F. ROMANENKO. 1967. Some aspects of the Cambrian paleogeography and trilobites of Gorny Altay. Regional Geographical Society of the USSR, 1967(8):62–96. (In Russian)
- RUSHTON, A. W. A. 2009. Revision of the Furongian agnostoid *Lotagnostus trisectus* (Salter). Memoirs of the Association of Australasian Palaeontologists, 37:273–279.
- SCHRANK, E. 1975. Kambrische Trilobiten der China-Kollektion v. Richthofen. Teil 2, Die Fauna mit Kaolishania? quadriceps von Saimaki. Zeitschrifte für geologische Wissenschaften, 3:591–619.
- SHERGOLD, J. H. 1975. Late Cambrian and Early Ordovician trilobites from the Burke River Structural Belt, western Queensland, Australia. Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin, 153, 251 p.
- SHERGOLD, J. H. 1982. Idamean (late Cambrian) trilobites, Burke River Structural Belt, western Queensland. Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin, 187, 69 p.
- SUN, X-W. 1989. Cambrian agnostids from the North China Platform. Palaeontologia Cathayana, 4:53–129.
- TJERNVIK, T. 1953. Notes on two new trilobites from the upper Cambrian of Sweden. Geologiska Foreningens i Stockholm Forhandlingar, 75:72–76.
- WALCOTT, C. D. 1884. The paleontology of the Eureka District, Nevada. United States Geological Survey Monograph 8:1–298.
- WALCOTT, C. D. 1924. Cambrian geology and paleontology V, no. 2, Cambrian and lower Ozarkian trilobites. Smithsonian Miscellaneous Collections, 75(2):53–60.
- WALLERIUS, L. D. 1895. Undersökningar öfver zonen med Agnostus laevigatus i Vastergötland. Lund, 72 p.
- WANG, Y. (ed.). 1964. Handbook of Index Fossils of China, Hunan Region. Geology Press, Beijing, 173 p. (In Chinese)
- WESTROP, S. R. AND J. M. ADRAIN. 2007. Bartonaspis new genus, a trilobite species complex from the base of the upper Cambrian Sunwaptan Stage in North America. Canadian Journal of Earth Sciences, 44:987–1003.
- WESTROP, S. R. AND J. M. ADRAIN. 2009. The late Cambrian (Furongian; Steptoean) trilobite genus *Xenocheilos* Wilson, 1949: systematics and biostratigraphic significance. Memoirs of the Association of Australasian Palaeontologists, 37:351–368.
- WESTROP, S. R. AND M. B. CUGGY. 1999. Comparative paleoecology of Cambrian trilobite extinctions. Journal of Paleontology, 72:337–354.
- WESTROP, S. R. AND R. LUDVIGSEN. 1987. Biogeographic control of trilobite mass extinction at an upper Cambrian "biomere" boundary. Paleobiology, 13:84–99.

817

- WESTROP, S. R., E. LANDING, AND J. M. ADRAIN. 2011. The Cambrian (Sunwaptan, Furongian) agnostoid arthropod *Lotagnostus* Whitehouse, 1936, in Laurentian and Avalonian North America: Systematics and biostratigraphic significance. Bulletin of Geoscience, 86:569–594.
- WESTROP, S. R., R. LUDVIGSEN, AND C. H. KINDLE. 1996. Marjuman (Cambrian) trilobites of the Cow Head Group, western Newfoundland. Journal of Paleontology, 70:804–829.
- WESTROP, S. R., R. A. WASKIEWICZ POOLE, AND J. M. ADRAIN. 2010. Systematics of *Dokimocephalus* and related trilobites from the late Cambrian (Steptoean; Millardian and Furongian Series) of Laurentian North America. Journal of Systematic Palaeontology, 8:545–606.
- WESTROP, S. R., J. D. EOFF, T.-W. NG, A. A. DENGLER, AND J. M. ADRAIN. 2008. Classification of the late Cambrian (Steptoean) trilobite genera *Cheilocephalus* Berkey, 1898 and *Oligometopus* Resser, 1936 from Laurentia. Canadian Journal of Earth Sciences, 45:725–744.
- WHITEHOUSE, F. W. 1936. The Cambrian faunas of northeastern Australia, Part 1, stratigraphic outline; Part 2, Trilobita (Miomera). Memoirs of the Queensland Museum, 11:59–112.
- WHITTINGTON, H. B., B. D. E CHATTERTON, S. E. SPEYER, R. A. FORTEY, R. M OWENS, ET AL. 1997. Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita Revised. Geological Society of America, Boulder, CO and University of Kansas, Lawrence, KS, 530 p.
- WILSON, J. L. 1949. The trilobite fauna of the *Elvinia* Zone in the basal Wilberns Formation of Texas. Journal of Paleontology 23:25–44.
- WILSON, J. L. AND E. A. FREDERICKSON. 1950. The *Irvingella major* ("*Ptychopleurites*") faunizone of the upper Cambrian. American Journal of Science, 248:891–902.
- ZHANG, W. AND P. A. JELL. 1987. Cambrian trilobites of North China. Science Press, Beijing, 332 p.
- ACCEPTED 15 MARCH 2013