Paleozoic radiolarian biostratigraphy

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ABSTRACT
The current knowledge of Paleozoic radiolarian ranges, proposed zonations, and faunal assemblages that have been used in biostratigraphy over the past few decades is compiled herein. More than 90 assemblages can currently be readily recognized and many of these, although regional in their construction, have elements that can be correlated throughout a widespread paleogeographic area. A number of the existing zonations utilize robust, relatively common, and easily recognized morphotypes that may be easily identified when they are moderately or even poorly preserved. These schemes are readily applied to deciphering stratigraphic complexities in complex orogenic belts. Other assemblages and zones summarized herein have been developed from well preserved materials, such as that from concretions, and their applicability to dating chert sequences remains relatively untested. Uneven geographic coverage is apparent, where some time periods are largely represented by only a few well known regional radiolarian rich units. There is also uneven temporal coverage, where certain time periods have few data. Undoubtedly, the Permian schemes are the most robust, relying heavily on data acquired from Asia, and to a lesser extent North America. The present work provides an opportunity to address critical gaps and opportunities for future work in radiolarian biostratigraphy, and to provide information on the ranges of biostratigraphically useful genera and species employed in the Paleozoic which can be used for both correlation and understanding the evolution of this important group.

KEY WORDS
Paleozoic,
radiolarians,
zonation,
evolution,
biostratigraphy.

RÉSUMÉ

Biostratigraphie des radiolaires du Paléozoïque.

Les connaissances actuelles sur les répartitions stratigraphiques des radiolaires paléozoïques sont ici compilées, ainsi que les biozonations proposées et les assemblages fauniques utilisés en biostratigraphie au cours des dernières décennies. Plus de 90 assemblages peuvent actuellement être facilement reconnus et beaucoup d'entre eux, bien que régionaux dans leur construction, ont des éléments qui peuvent être corrélés à travers une région paléogéographique très répandue. Un certain nombre de zonations existantes utilisent des morphotypes robustes, relativement fréquents, et facilement reconnus, qui peuvent être aisément identifiés quand ils sont modérément ou même mal préservés. Ces schémas biostratigraphiques sont facilement appliqués afin de déchiffrer la complexité stratigraphique des ceintures orogéniques complexes. D'autres assemblages et des zones résumées ici ont été développés à partir de matériaux bien préservés, comme celui issu de concrétions, et leur applicabilité à la datation de séries radiolaritiques reste pratiquement non testée. La couverture géographique inégale est apparente, où certains intervalles temporels sont largement représentés par seulement quelques unités régionales bien connues, riches en radiolaires. Il y a aussi un recouvrement temporel inégal, pour certaines périodes pour lesquelles il y a peu de données. Les schémas biostratigraphiques du Permien sont sans aucun doute les plus robustes, et ils se basent essentiellement sur des données acquises en Asie, et dans une moindre mesure, en Amérique du Nord. Le présent travail offre l'occasion d'aborder des lacunes importantes et, dans le futur, d'entreprendre de nouveaux travaux biostratigraphiques sur les radiolaires. Il permettra également de fournir des informations sur les répartitions stratigraphiques des genres et espèces utiles au Paléozoïque, lesquels peuvent être déployés aussi bien pour des corrélations, mais également pour comprendre l'évolution de ce groupe important.

MOTS CLÉS
Paléozoïque,
radiolaires,
zonation,
évolution,
biostratigraphie.

INTRODUCTION

It is important to recognize that many of the end-users of radiolarian taxonomy are concerned with their application in biostratigraphy. Historically, Paleozoic radiolarian research has been closely tied to its near immediate application to dating basinal siliceous strata otherwise devoid of biostratigraphically useful information (see Danelian *et al.* 2017, this volume). In fact, many of the early biostratigraphic schemes (e.g. Holdsworth & Jones 1980; Ishiga *et al.* 1982) arose from fieldwork aimed at resolving the tectonic history of complex orogenic belts. Although radiolarian biostratigraphy, as a specialty field, has been an active area of research for over 50 years, there remain many gaps in our current knowledge base and many taxa remain undescribed. Improvement to the zonal schemes is an on-going task and much work remains to be done.

The past three decades have witnessed on-going refinement of detailed Mesozoic radiolarian biozonations (e.g. Blome 1984; Carter *et al.* 1988; 2010; Baumgartner *et al.* 1995; Gorican *et al.* 2006). These zonations have been applied to investigations in orogenic zones worldwide (e.g. Aitchison & Murchey 1992) and have been pivotal in resolving regional tectonic histories. Radiolarian research has wide-reaching effects as it provides the stratigraphic constraints necessary to understand the development of Panthalassa, Tethyan, and other tectonic collages. Likewise, the publication of a Late Paleozoic radiolarian zonation by Holdsworth & Jones (1980) has led to similar advances in the understanding of older rocks in areas such as Japan, China, SE Asia and other Paleotethyan suture zones. This work was followed by Noble & Aitchison (2000) who contributed an Early Paleozoic radiolarian biozonation applicable to yet older orogenic zones. Almost two additional decades have now passed and in light of work published elsewhere in this volume, which reviews the taxonomy of Paleozoic radiolarian genera, it is appropriate to consider a revision of Paleozoic radiolarian zonation.

Radiolarians have been reported from shallow and deep marine depositional sequences throughout the Paleozoic. The common factor amongst the strata in which they occur is slow to negligible rates of clastic sedimentation. The preservation of radiolarians tends to be best amongst marine sediments from outer shelf settings, and in several cases faunas from these shelfal settings are exceptionally well-preserved, particularly those found in nodules or concretions. Paleozoic radiolarians may also be accompanied by other biostratigraphically useful, fossil groups, such as conodonts, foraminifers, or graptolites, that importantly allow for calibration of established assemblages and zonations. The preservation is typically poor in lithologies such as ribbon-bedded radiolarian chert from deeper water settings, sequences are structurally more complex and disrupted, and co-occurrence of other biostratigraphically useful fossils groups less common. For these reasons, the calibration and application of zonations derived from chert sequences can be difficult. Meaningful comparison with the diversity and abundance of radiolarians in coeval assemblages from shallow water settings remains a challenge. Nonetheless, the widespread occurrence of radiolarian-bearing lithologies in Paleozoic orogenic belts indicates their potential for a biostratigraphically constrained improvement in understanding their tectonic evolution similar to that experienced in younger tectonic collages.

Problems arise, particularly in Lower Paleozoic strata, mainly due to the difficulty in examining details of internal structures, many of which are obscured by diagenesis and/or poor preservation. To some extent these issues are being addressed by new technology such as micro-CT imaging that has the potential to revolutionize this field in much the same way as did development of the scanning electron microscope. For any biostratigraphic zonation to be useful to the wider geological community the taxa upon which it is based need to be readily identifiable. It is no different with radiolarians although taxonomic assignment can be problematic as much of the higher-level taxonomy (i.e., ordinal and family level) is based on internal details that are often not revealed or preserved in typical states of preservation. This difficulty is particularly true for many of the spherical forms that dominate the Cambrian through Devonian periods. As such, the focus has been on external morphologies readily observed in matrix free specimens. Early pioneers in radiolarian taxonomy and biostratigraphy, like Nazarov (1988 and many other papers), who worked throughout the Paleozoic time scale, recognized several key morphotypes that dominate early Paleozoic faunas, and noted their stratigraphic distribution. Regardless of whether these morphotypes represented monophyletic groups at the family or subfamily level, or polyphyletic groupings, these morphotypes have proven to have distinct stratigraphic value irrespective of whether or not phylogenetic lineages are well understood. De Wever *et al.* (2001: fig. 199) illustrate how broad evolutionary trends can be ascertained at the level of families and for certain key genera. Maletz (2011) provides a more up-to-date view of these trends from the Cambrian and Ordovician. From the Late Devonian onwards, rapid evolution amongst distinctive non-spherical forms, particularly the albaillellids has proved useful in developing a robust understanding and widely applicable biostratigraphy. However, correlation of different zonations independently developed from investigations of different pelagic cherts where radiolarians are accompanied by few other fossils, except conodonts remains difficult. Given the revision of the Paleozoic radiolarian taxonomy presented in this volume (Caridroit *et al.* 2017; Noble *et al.* 2017) it is timely to also consider the current state of Paleozoic radiolarian biostratigraphy. This not only reveals intervals where a robust zonation exists it also serves to indicate where additional investigation is required.

FIRST APPEARANCE

The nature of the first radiolarians and when they might first have appeared in the geological record remains the subject of active research. Numerous early reports of putative radiolarians have been discounted either because the fossils in question are not radiolarians, are *nomina dubia* or because the fossiliferous strata have been stratigraphically reassigned. Work in progress suggests radiolarians first appeared in the earliest Cambrian (Terreneuvian) (Suzuki & Oba 2015). The presence of spherical forms (Braun & Chen 2003; Braun *et al.* 2005, 2007; Cao *et al.* 2014) in some of the reported faunas from South China has raised questions about possible contamination and this work is not without controversy (Maletz 2011, 2017). However, a number of morphological characters of spherical siliceous forms observed on both thin sections and in residues (i.e., recrystallized hollow shells with residual spines) from black cherts in South China favor of the possible existence of polycystine radiolarians since the late Terreneuvian (Atdabanian-early Botoman of the Russian stratigraphic scale, Zhang *et al.* 2013). Intense investigation of similar-aged small shelly fossil-bearing strata from several widely-separated localities has led to the recovery of similar faunas from at least four locations (Prof Q.L. Feng, CUGS Wuhan pers. comm.). More verifiable results are needed before any definitive statement can be made.

CAMBRIAN

The oldest presently documented and undisputed radiolarian faunas are from the upper part of the Lower Cambrian (Botoman) of Russia (Obut & Iwata 2000; Pouille *et al.* 2011). Although the two faunas are only moderately preserved they contain forms attributable to the Archaeospicularia with the echidninid *Altaiesphaera* present in the material described by Obut & Iwata (2000) and the archaeospicularid *Archaeoentactinia*? present in the material described by Pouille *et al.* (2011).

The oldest well-preserved material is from the Middle Cambrian of the Georgina Basin in Australia (Won & Below 1999). This fauna is dominated by spicular forms such as *Echidnina runnegari*. How and whether this fauna can be readily compared with those extracted from the pelagic cherts typical of tectonic collages in orogenic zones remains a subject of active research.

Building on earlier studies such as those of Nazarov & Ormiston (1993) and Noble & Aitchison (2000), Maletz (2011) suggested that on the basis of knowledge at that time the Cambrian radiolarian succession can be subdivided into two intervals. They are a lower archeoentactiniid and palaeospiculid-dominated interval that is succeeded by an echidninid and aspiculid-dominated upper interval in which archeoentactiniids are no longer present.

The best preserved Upper Cambrian radiolarian faunas are those described from the Cow Head Group in western Newfoundland (Won & Iams 2002; Won *et al.* 2005). From these well described sections Pouille *et al.* (2014a) discriminated two radiolarian assemblages from the Upper Cambrian (Fig. 1). The *Subechidnina* assemblage of Franconian age is characterized by *Subechidnina florae* and overwhelmingly dominated by members of the family Echidninidae especially *Echidnina irregularis*. It is succeeded by the *Ramuspiculum* assemblage of Trempealeauan age (Pouille *et al.* 2014a) that is characterized by the presence of *Echidnina curvata*, *Parechidnina variospina*, *Protoentactinia primigena* and the first occurrence of species belonging to the genera *Grosmorneus* and *Ramuspiculum*. This fauna is dominated by the Archeoentactiniidae and Echidninidae.

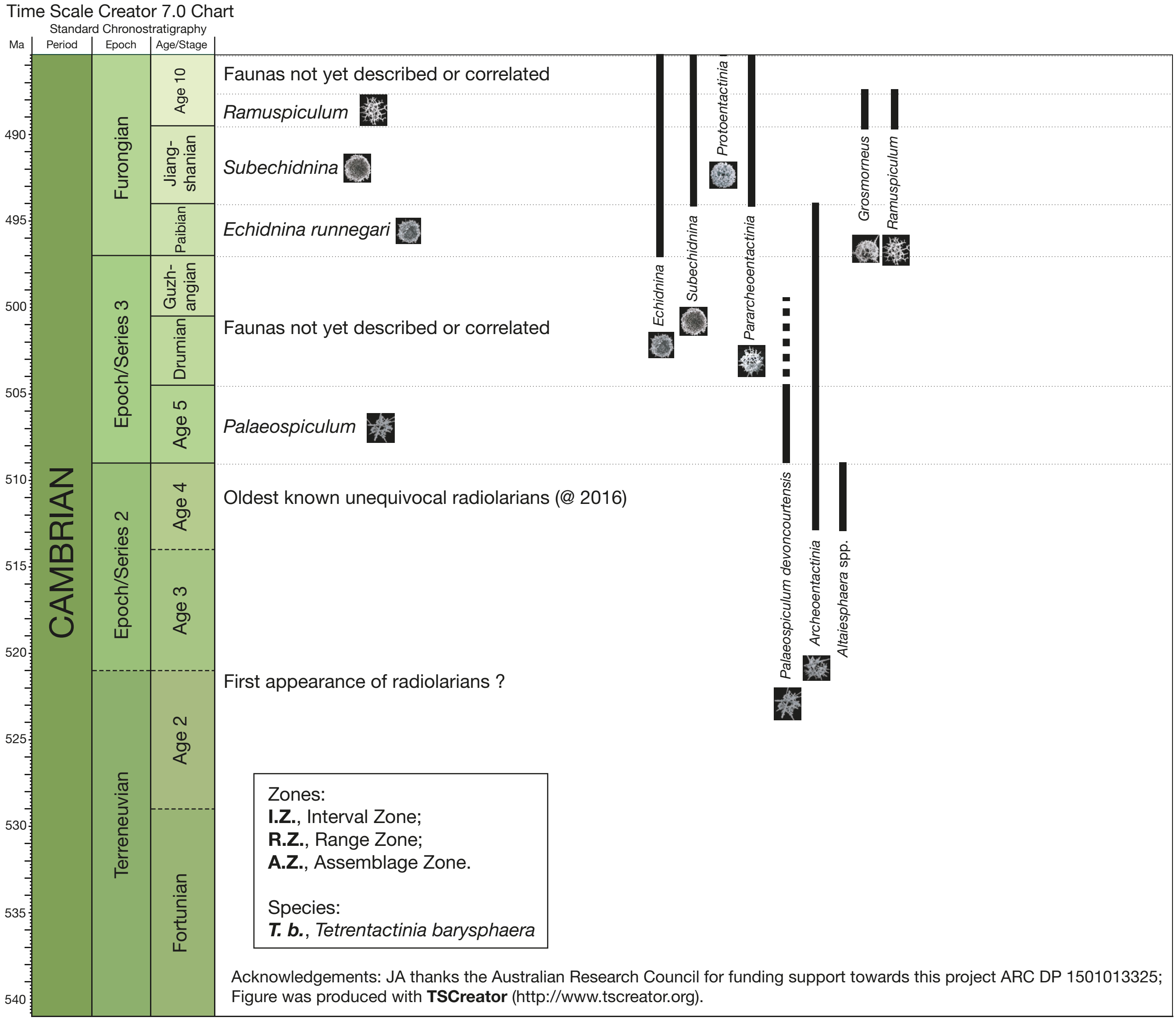

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FIG. 1. — Four assemblages presently recognized from the Cambrian in stratigraphic order are the: *Palaeospiculum*, *Echidnina runnegari*, *Subechidnina* and *Ramuspiculum* assemblages.

ORDOVICIAN

Several biostratigraphically significant assemblages can be recognized through the Ordovician (Nazarov 1988; Nazarov & Ormiston 1993; Noble & Aitchison 2000) (Fig. 2). Pouille *et al.* (2014a) reported a *Protoentactinia kozuriana* assemblage from lowermost Tremadocian strata at the base of the Ordovician that is characterized by the nominative species and dominated by the Echidninidae and Protoentactinidae. Maletz (2011) recognized several assemblages including, in ascending order: *Paracheoentactinia*, *Protoproventocitum*, *Beothuka terranova*, *Antygopora bella*, *Proventocitum procerulum*, *Haplentactinia juncta-Inanigutta unica*, *Protoceratoikiscum* spp. assemblages and the pylomate large concentric sphaerellarian zone 1. These assemblages do not form a continuous zonation and he indicated at the time of his writing in 2010 that radiolarians remained undescribed from some intervals (e.g. lower Floian). Amongst these and between the *Protoproventocitum* and *Beothuka terranova* assemblages of Maletz (2011) upper Tremadocian to lower Floian radiolarians have now been described from Kazakhstan (Danelian *et al.* 2011). The reported material contains a distinctive form *Inanigutta* ? *kyrgyza*. Tentative assignment of this taxon to the genus *Inanigutta* reflects the poorly preserved nature of the type material in which details of internal skeletal structure could not be resolved. Nonetheless, given its distinctive external morphology this form may yet prove to be a useful biostratigraphic marker.

Considerable disagreement exists over correlation of the so-called *Beothuka terranova* assemblage of Maletz (2007, 2011). Won & Iams (2015) regard the Maletz (2007) identification of the nominative taxon reported from the

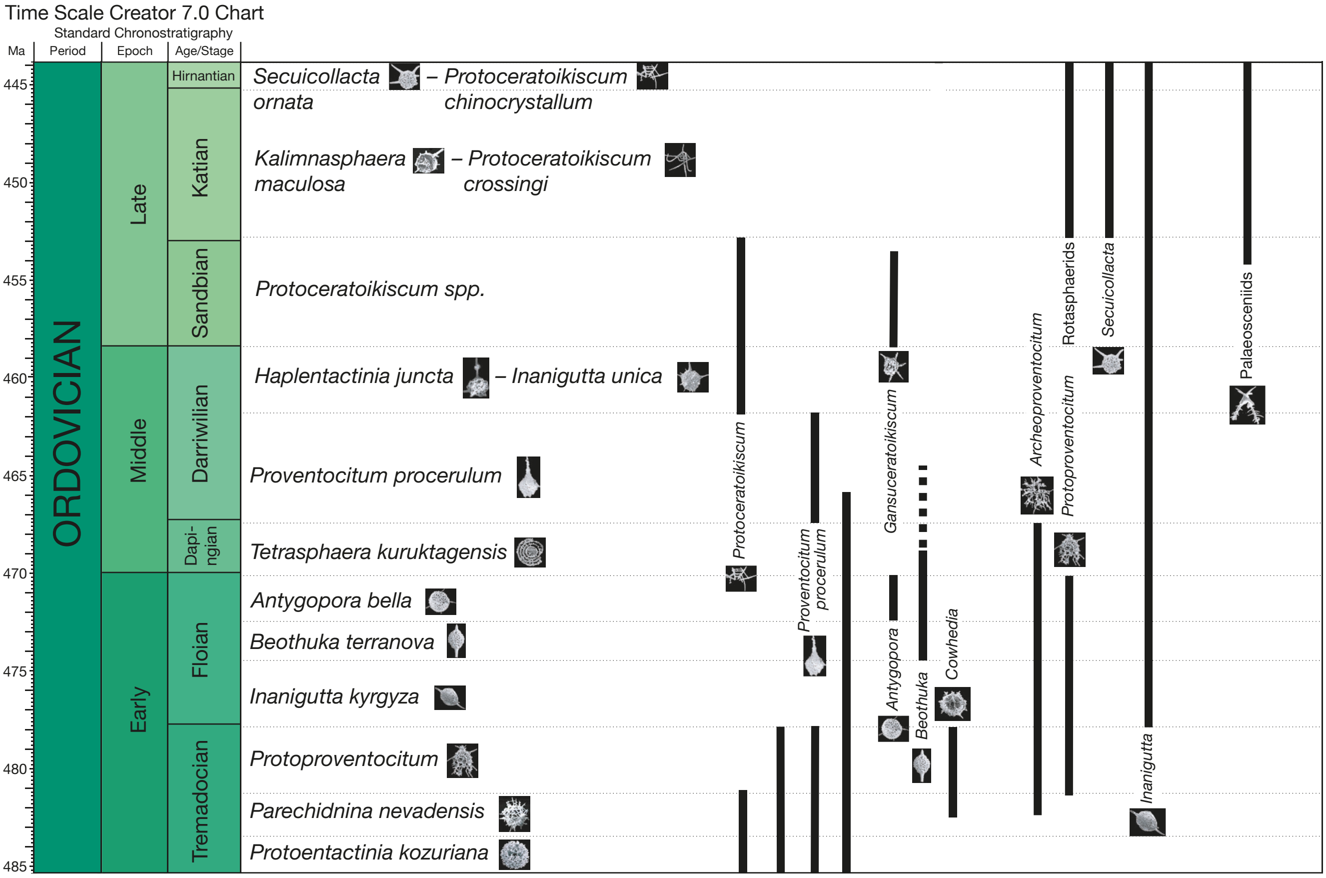

FIG. 2. — Twelve assemblages presently recognized from the Ordovician in stratigraphic order are the: *Protoentactinia kozuriana*, *Protoentactinia nevadaensis*, *Protoproventocitum*, *Inanigutta kyrgyza*, *Beothuka terranova*, *Antygopora bella*, *Tetrasphaera kuruktagensis*, *Proventocitum procerulum*, *H. juncta-I. unica*, *Protoceratoikiscum* spp., *Kalimnasphaera maculosa-Protoceratoikiscum crossingi*, *Secuicollacta ornata-Protoceratoikiscum chinocrystallum* assemblages.

Isograptus victoriae lunatus Zone in Unit 70 of the St Paul's Inlet section of the Cow Head Group in western Newfoundland as incorrect. Furthermore, they also consider the corresponding reassignment of the red chert of the Little Port Complex sample from which this taxon was originally described to the uppermost Floian by Maletz (2007) to be erroneous. Won & Iams (2015) suggest that the Little Port Complex radiolarian fauna is coeval with their (Won & Iams 2013) early Arenigian (middle Floian) radiolarian assemblage. Moreover, they comment that the assertion by Maletz & Bruton (2007) that the Little Port Complex type material has been recrystallized and/or pyritized and thickened is incorrect. However, as first describer of *Beothuka terranova* the senior author of this paper is in agreement and can confirm that no pyritized material was present in the original sample.

In the upper Dapingian interval between the *Antygopora bella* and *Proventocitum procerulum* assemblages of Maletz (2011) rather poorly preserved radiolarians have been described by Wang *et al.* (2008) from the Tarim Basin in Xinjiang Province of western China. Material in a considerably better state of preservation from the Table Point Formation in western Newfoundland is currently being investigated and described (Kachovich *et al.* 2016).

The distinctive *Haplentactinia armillata-Proventocitum procerulum* assemblage reported by Nazarov (1988) and then Noble & Aitchison (2000) is typically associated with pelagic cherts for which age constraint is commonly poor. Aitchison (1998) reported this assemblage from red cherts in the Ballantrae ophiolite in Scotland. The age of these cherts has recently been radiometrically constrained to between 466-474 Ma using zircons from tuffs interbedded with the chert (Fujisaki *et al.* 2015) confirming more precise biostratigraphically-based correlations to the lower Darriwilian (mid-Middle Ordovician) from occurrences in shallow marine successions in Spitsbergen and Newfoundland (Maletz & Bruton 2008).

The upper part of the Middle Ordovician to which the *Haplentactinia juncta-Inanigutta unica* assemblage was assigned by Nazarov & Popov (1980) and Danelian & Popov (2003) sees an increase in radiolarian biodiversity. The significance of the appearance of several new genera of the Inaniguttidae at this time is such that Noble & Aitchison (2000) recognized the Long-spined inaniguttid Zone 1. The interval is marked by the first appearance of an important and very distinctive spider's web-shaped taxon *Protoceratoikiscum* in deep water facies from NSW Australia (Goto *et al.* 1992), Nevada USA (Renz 1990a), western China (Li 1995; Buckman & Aitchison 2001), Scotland UK (Danelian & Floyd 2001) and SW Siberia

Russia (Obut & Semenova 2011). Numerous radiolarian taxa have been reported from the Middle and Upper Ordovician of Kazakhstan (Nazarov 1988; Nazarov & Ormiston 1993; Nazarov *et al.* 1975; 1977; Nazarov & Popov 1980; Danelian & Popov 2003; Pouille *et al.* 2013; 2014b).

The most notable first appearance of higher level radiolarian forms in the Upper Ordovician is that of the Secuicollactidae. Based on their appearance, Noble & Aitchison (2000) recognized their Rotasphaerid superzone, which extends to the end of the Silurian. Palaeoscenidiids also appear and become abundant and even locally dominate shallow marine faunas (Renz 1990a, b). Well preserved faunas of Sandbian and Katian ages are described from the Pingliang Formation in Gansu Province of western China (Wang 1993; Wang *et al.* 2010) and the Malongulli Formation of eastern Australia (Webby & Blom 1986; Noble & Webby 2009) respectively. The first true ceratoikiscids appear with the arrival of *Gansuceratoikiscum* in the Sandbian (Wang *et al.* 2010). Many faunas in the uppermost Ordovician are characterized by the large concentric spongy form *Haplotaeniatum*, species of which are commonly pylomate. *Secuicollacta* is also common (Noble *et al.* 1997; Noble & Aitchison 2000). The *Haplentactinia baltica-Inanibigutta aculeata* assemblage was recognized in this interval by Nazarov (1988) and also occurs in the Vinini Formation in Nevada, western North America (Noble 2000). The Late Ordovician also see the arrival of the distinctive genus *Protoceratoikiscum* with two assemblages *Kalimnasphaera maculosa-Protoceratoikiscum crossingi* and *Secuicollacta ornata-Protoceratoikiscum chinocrystallum* recognized in the Katian and Hirnantian respectively of NSW, eastern Australia (Goto *et al.* 1992; Noble & Webby 2009).

SILURIAN

Silurian biostratigraphic zones were proposed in Japan (Furutani 1990), Urals (Nazarov & Ormiston 1993), West Texas (Noble 1994), and several assemblages are assigned to intervals of short durations in the Silurian (e.g. MacDonald 2006). The biostratigraphic scheme of Furutani (1990) has been widely correlated to schemes of other regions because of the presence of the same taxa. Ages assigned to various stratigraphic levels within his scheme, however, were drastically recalibrated based on recent field studies (Kurihara & Sashida 2000; Kurihara 2003, 2004, 2007; Nuramkhaan *et al.* 2013a, b).

Early attempts at subdividing the Lower Silurian recognize basic elements present in the assemblages, including a preponderance of haplotaeniatid-dominated assemblages in the Llandovery and a shift to inaniguttid-dominated assemblages beginning sometime in the Wenlock. Initially, knowledge of these assemblages was based on limited sampling, and imprecise age control. Nazarov (1988) recognized two zones in the Silurian that encompassed this shift; the *Haplotaeniatum tegimentum* assemblage and the *Fusalfanus* (*Inanigutta*) *tarangulica-Secuicollacta cassa* assemblage from the Sakmarsky suite in the southern Urals (note that *I. tarangulica* was transferred to the genus *Fusalfanus* by Tetard *et al.* [2015]). Noble & Aitchison (2000) provided some refinements, noting three broad zones that spanned the Llandovery and Wenlock strata, their pylomate- large concentric sphaerellarian zone 2 (PL2), and long spined inaniguttid zones 2 and 3 (LS2 and LS3). Noble & Aitchison (2000) further documented the presence of the biostratigraphically useful *Orbiculopylorum* in PL2, and *Labyrinthosphaera* in the Llandovery assemblages, and the FA of *Ceratoikiscum* and *F. tarangulica* in Wenlock assemblages (i.e., base of LS3), separated by an interval zone, LS2.

The most comprehensive work on the Lower Silurian comes from the Cape Phillips Formation of Arctic Canada, where MacDonald (2006) synthesizes his Llandovery and lower Wenlock data and recognizes four local biozones that are well constrained through graptolite stratigraphy (Fig. 3). The basal Silurian (Rhuddanian) is characterized by a *Haplotaeniatum* assemblage, overlain by the *Orbiculopylorum* assemblage in the Aeronian. The FA of *Orbiculopylorum* is a useful marker, as this form occurs in both limestone and chert-derived assemblages, which have been reported from Nevada and Germany (Noble *et al.* 1998) Britanny, France (Tetard *et al.* 2014a, b), Sweden (Umeda & Suzuki 2005), and Alaska (Won *et al.* 2002). The LA of *Orbiculopylorum* occurs in the middle of the Telychian in the Arctic succession, and may also be of biostratigraphic utility.

The upper Telychian is represented by the *Plussatispila* assemblage described from Arctic Canada by MacDonald (2006). This interval correlated with the lower part of the Long-spined inaniguttid biozone 2 of Noble & Aitchison (2000) and is also known from Alaska (Won *et al.* 2002) and Sweden (Noble & Maletz 2000) where *Haplotaeniatum cathenatum*, is the dominant species along with the genera *Secuicollacta* and *Diparvapila*.

The stratigraphically uppermost assemblage recognized from Arctic Canada by MacDonald (2006) is the *Ceratoikiscum* assemblage the base of which is marked by the first appearance of the nominative genus in the Sheinwoodian *Monograptus instrenuus-Cyrtograptus kolobus* graptolite Zone (MacDonald 2006). The FA of *Ceratoikiscum* is an important biostratigraphic datum, as this genus is easily recognized, global in its distribution and is found in both deep chert facies, and in shallower limestone assemblages. Jones & Noble (2006) reported data from the upper Sheinwoodian *Cyrtograptus perneri-Monograptus opimus* zone, the next graptolite zone above the top of MacDonald's sections, and provide useful range information on three biostratigraphically useful taxonomic groups, which caused them to revise the definition and move the position of the Noble and Aitchison's Long spined inaniguttid zone 2/3 boundary upward to the base of the Homerian. First, Jones & Noble (2006) show that LA of *Haplotaeniatum* extends well above the top of the Llandovery in the Arctic sections, and persists through the Sheinwoodian to the base of the Wenlock, albeit in low numbers. Second, the FA of *F. tarangulica* group taxa occurs above the Sheinwoodian, at the base of the Wenlock (lower Homerian) in the *lundgreni-testis* biozone, higher up than had been indicated by Noble & Aitchison (2000). Well-preserved material including *Inanihella sapena* and *Secuicollacta hexatinia* is present

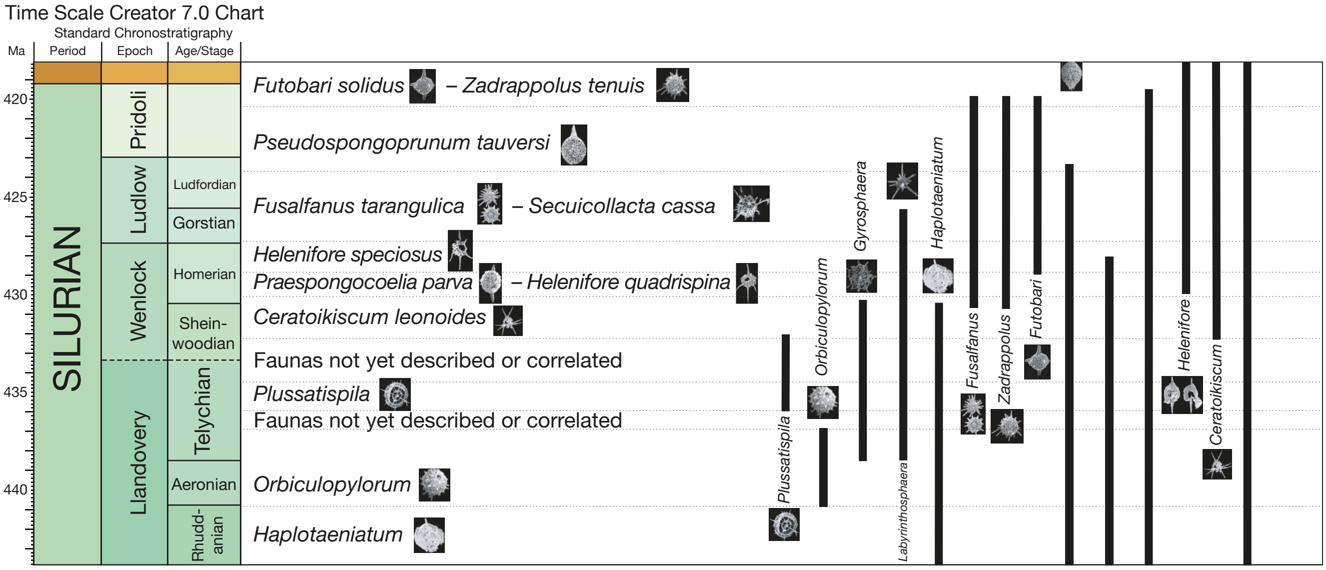

Fig. 3. — Nine assemblages presently recognized from the Silurian in stratigraphic order are the: *Haplotaeniatum*, *Orbiculopylorum*, *Plussatispila*, *Ceratoikiscum leonoides*, *Praespongocoelia parva-Helenifore quadrispinosa*, *Helenifore speciosus*, *Fusalfanus tarangulica-Secuicollacta cassa*, *Pseudospongoprunum tauversi*, *Futobari solidus-Zadrappolus tenuis* assemblages.

in the Sheinwoodian-Homerian boundary interval of the Herefordshire Konservat lagerstatten locality (Siveter *et al.* 2007). Finally, two other groups, *Labyrinthosphaera* and *Gyrosphaera*, of early Silurian Haplotaeniatid genera also persist through the Sheinwoodian.

Very well-preserved Wenlockian faunas have also been documented from the Homerian of Arctic Canada but to date, only the Palaeoscenidae, Entactiniidae (Goodbody 1986) and Ceratoikiscidae are well described (Noble & Lenz 2007; Renz 1988). Noble *et al.* (2012) provides biostratigraphic information regarding composition of both early and late Homerian assemblages. The lowest Homerian graptolite zone (*lundgreni-testis* zone) contains a diverse assemblage containing five species of ceratoikiscids, eight species of palaeoscenidiids, and a diverse array of inaniguttids that include the FA of the *Fusalfanus tarangulica* group, and the FA. of *Zadrappolus*. Secuicollactines, and rare haplotaeniatids (i.e., *Labyrinthosphaera*) are also present in the *lundgreni-testis* zone, and the distinct bipolar spine-bearing radiolarian *Praespongocoelia parva*, makes its appearance near the top of the biozone. *P. parva* is a zonal taxon recognized in Silurian chert assemblages in Japan (Furutani 1990) and west Texas (Noble 1994). Late Homerian radiolarians from the Arctic sections are more sporadic in their occurrence, but have been recovered from two of the three late Homerian graptolite zones, the *Pristiograptus dubius-Gothograptus nassa* and the *Colonograptus praedeubeli-C. deubeli* zones. These assemblages are lower in diversity than the lower Homerian (Noble *et al.* 2012). In the *P. dubius-G. nassa* zone, five species range through from the lower Homerian, and in the *C. praedeubeli-C. deubeli* zone, there is the FA of several new taxa, including *Futobari*. The important and easily recognizable ceratoikiscid genus *Helenifore* makes its first appearance in the Homerian (Noble & Lenz 2007) with *H. quadrispina* appearing in the upper part of the lower Homerian and *H. speciosus* appearing in the upper Homerian.

Zonation of the Upper Silurian (Ludlovian and Pridolian) is more problematic because of the scarcity of other biostratigraphically diagnostic forms in known sections such as those from chert sequences in Texas (Noble 1994) and Japan (Furutani 1990; Wakamatsu *et al.* 1990; Aitchison *et al.* 1991). The cherts from Japan, particularly in the Fukuji area of the Hida Marginal Belt (Furutani 1990) and Kurosegawa Tectonic Zone (Wakamatsu *et al.* 1990) yielded a sequence of radiolarian assemblages based on robust inaniguttids, secuicollactines, and bipolar spherical forms. Radiometric age-dating of zircons from tuffs amongst the radiolarian-bearing strata allows for calibration of the zonation in Japan (Aitchison *et al.* 1996; Nuramkhaan *et al.* 2013a, b).

The Upper Silurian Caballos Novaculite of West Texas, USA contains abundant and moderately well-preserved radiolarian assemblages from radiolarian chert. Noble (1994) defined local biozones, and although independent age controls are scarce, strong faunal similarities exist between Japan, America and Russia, and formed the basis for some of the Silurian zones proposed by Noble & Aitchison (2000). For example, they designated the uppermost Silurian interval between the last appearances of rotasphaerids and inaniguttids as a Post Rotasphaerid zone in which inaniguttids such as *Zadrappolus* and *Oriundogutta* are common.

Some of the better preserved and well dated material is reported from limestone beds and concretions in basinal sequences of the southern Urals and Arctic Canada. The classic *Fusalfanus tarangulica-Secuicollacta cassa* assemblage described by Nazarov (Nazarov 1988; Nazarov & Ormiston 1993) was originally assigned a broad age encompassing the Wenlock and Ludlow. New collections from the Tarangul locality of Nazarov (1988) and an additional locality in the Varnenskian zone of the Southern Urals add further documentation of the assemblage, and are dated by middle Ludlovian conodonts of the *Ancoradella ploekensis* zone recovered from the section in the Varnenskian zone sample (Amon *et al.* 1995). This assemblage is dominated by the nominal taxa of the assemblage, but also contains numerous palaeoscenidiids, *Ceratoikiscum*, *Helenifore*, and *Labyrinthosphaera*. Tetard *et al.* (2015), reported on Arctic material from the Gorstian (basal Ludlow), which has many similarities to the *F. tarangulica-S. cassa* assemblage in the Urals which Amon *et al.* (1995) reported. One difference between the Ural and Arctic material from the Ludlow is that *Secuicollacta* is very rare in many of the Gorstian Arctic samples examined. Other differences include the occurrence of several Wenlockian genera, including rare occurrences of *Franklinia* and *Zadrappolus*, and *Futobari*. Tetard *et al.* (2015) also reported the occurrence of *Fusalfanus osobudaniensis*, which occurs in both the Japan and west Texas sequences, but presumably in Wenlock age material. Additional work is needed to fully explore the range of *Fusalfanus*, and determine correlations between assemblages in the chert sequences to those of the better-preserved Arctic and Ural material recovered from limestones.

DEVONIAN

Numerous investigations have been made of Upper Silurian to Middle Devonian sections in Japan within the Hida-Gaien Belt of central Japan (Furutani 1990), the Kurosegawa terrane in SW Japan (Wakamatsu *et al.* 1990; Umeda 1997, 1998a) and the South Kitakami Belt in NE Japan (Suzuki *et al.* 1996; Umeda 1996). However, few other fossils (e.g. corals) are preserved (Kato *et al.* 1980; Hada *et al.* 2001; Williams *et al.* 2014) and correlation to the geological timescale requires validation in the manner of Kurihara (2004). Precise correlation is poorly controlled as little is known about stratigraphic relationships amongst studied sections at the time of radiolarian investigations and the correspondence between numerical age and stages has changed considerably at various times when revisions to the geologic timescale have been proposed (see Gradstein *et al.* 2012: 21).

Amongst the known Devonian sections a variety of assemblages have been described. Differences in preservation of radiolarians between sections have resulted in description of a variety of assemblages that although sharing some common taxa are not entirely identical. A paucity of other age diagnostic fossils prevents precise age correlation. None-theless the general biostratigraphic successions are similar and the relative levels of assemblages are known. Radiolarians in these Japanese localities typically occur in tuffaceous cherts or siliceous mudstones that were deposited in an island arc setting. The maximum depositional age of 427.2 ± 7.6 Ma for the uppermost tuff bed (Aitchison *et al.* 1996) in the Gomi Formation of Umeda (1998b) at Yokokurayama provides a Late Silurian Homerian/Gorstian (= Wenlock/Ludlow) boundary age in the GTS2012 time scale (Gradstein *et al.* 2012) constraint for radiolarian assemblages from that section. Given that radiometrically-dated zircons from tuffs in the Joryu or Nakahata Formation (unit G4) at Konomori yielded an age of 408.9 ± 7.6 Ma this numerical age correlates with the late Pragian (middle Early Devonian) in the GTS2012 timescale. As Umeda (1998b) and Kurihara (2004) already noted, the implication is that all radiolarian assemblages from Joryu and Nakahata formations (unit G4) at Konomori are of Devonian age.

The relative ages of uppermost Lower to Upper Devonian sections in eastern Australia from which radiolarian faunas have been described (Aitchison & Flood 1990; Hinde 1899) are also somewhat loosely constrained. As in Japan although a succession of radiolarian assemblages can be recognized within volcaniclastic strata and recognized between different sections (Aitchison *et al.* 1999; Stratford & Aitchison 1997) few other fossils are available for use in correlation. Correlation has been partially resolved by investigations of conodont faunas in limestone beds but many of these are allochthonous and only provide maximum age constraints (Mawson *et al.* 1997).

The Middle Devonian to earliest Carboniferous interval sees a global flourishing of radiolarians. Numerous occurrences of radiolarian-bearing rocks occur in which faunas are diverse and radiolarians are well-preserved. In relatively shallow marine (shelfal) settings radiolarian occurrences include those within the oil-bearing Domanik-style lithologies of Russia (Afanasieva & Mikhailova 2001; Afanasieva & Amon 2011, 2012), the Ohio, Woodford and other shale formations in central areas of the USA (Foreman 1963; Cheng 1986; Schwartzapfel & Holdsworth 1996) and the Canning Basin in the north of Western Australia (Nazarov *et al.* 1982; Nazarov & Ormiston 1983b; Aitchison 1993; Won 1997a, b). Middle Devonian to lowermost Carboniferous radiolarians are also commonly found in shallow shelf sediments of the Indochina Terrane (Thassanapak *et al.* 2012) and in the suture zones between the Laurasia and Gondwana in South China (Feng & Ye 1996), between Gondwana and the Cathaysian block (Spiller 2002), between the Cathaysian and Yangtze blocks, between the Tarim and Junggar blocks in Tianshan (Liu 2001; Liu & Hao 2006) and along the Bentong-Raub suture zone in Malaysia (Jasin & Harun 2011).

The Middle Devonian to earliest Carboniferous is characterized by faunas dominated by entactinids with strongly developed three-bladed spines. Although typically only a minor component of faunal assemblages, together with the entactinids, readily identifiable ceratoikiscids have allowed the development of a biozonation. Other forms that make significant albeit short-term appearances around the end of the Devonian and into the earliest Carboniferous include the popofskyellids as well as pylomate forms such as the archocyrtids.

Stratford & Aitchison (1997) (refined in: Aitchison *et al.* 1999) recognized a succession of assemblages through the Middle and Upper Devonian of eastern Australia (Fig. 4). Because of the scarcity of conodonts or other taxa in deep-water island arc-related tuffaceous siliceous mudstone, calibration of these assemblages remains difficult but possible (Mawson *et al.* 1997). Importantly, the radiolarian assemblages

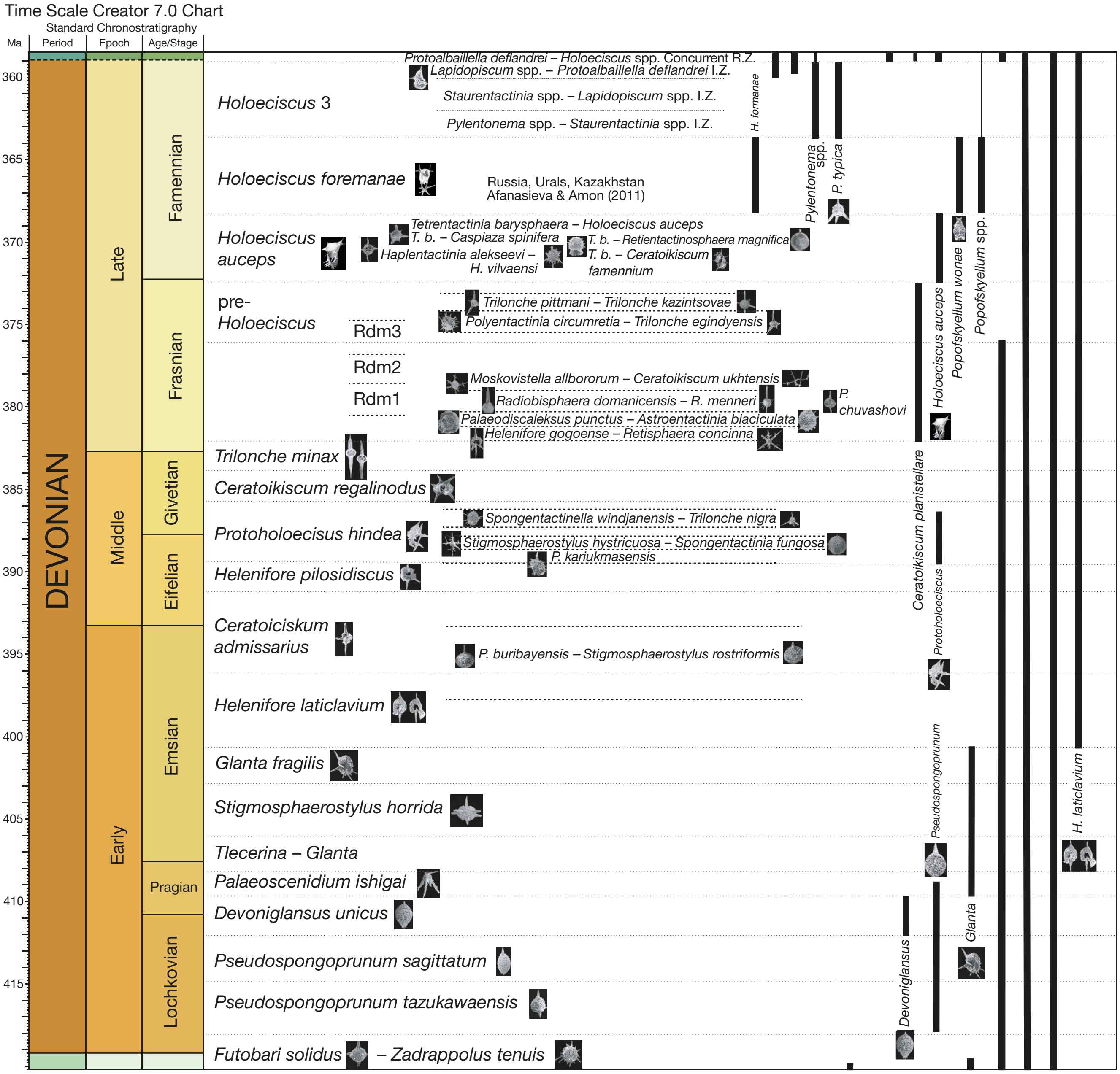

FIG. 4. — Seventeen assemblages presently recognized from the Devonian in stratigraphic order are the: *Pseudospongoprunum tazukawaensis*, *Pseudospongoprunum sagittatum*, *Devoniglansus unicus*, *Palaeoscenidium ishigai*, *Tlecerina-Glanta*, *Stigmosphaerostylus horrida*, *Glanta fragilis*, *Helenifore laticlavium*, *Ceratoikiscum admissarius*, *Helenifore pilosidiscus*, *Protoholoecisus hindea*, *Ceratoikiscum regalinodus*, *Trilonche minax*, *pre-Holoeciscus*, *Holoeciscus auceps*, *Holoeciscus foremanae*, *Holoeciscus* 3 assemblages. Numerous other local assemblages are described by Afanasieva & Amon (2011) and Schwartzapfel & Holdsworth (1996).

occur in the same succession that can be correlated across numerous geographically separated localities. Aitchison & Stratford (1997) also re-examined thin sections from which G. J. Hinde (1899) described the famous Tamworth, eastern Australia fauna and were able to process the blocks from which those thin sections were cut, which remained at the University of Sydney in the collections of T. W. Edgeworth David. This work resulted in important revision of the taxonomic status of several key spherical forms. More attention was paid to this issue by Won (1997a, b) in her investigations of the West Australian Gogo Formation in which the preservation of internal detail of radiolarian microfossils is significantly better.

Numerous assemblages are described from Russia where radiolarians are common fossils within bituminous shale of the Domanik facies. Faunas are dominated by spherical forms and there appear to be significant differences between individual sub-basins. Afanasieva & Amon (2011) describe many of these assemblages and use conodonts and ammonoids for correlation. The *Primaritripus buribayensis-Stigmosphaerostylus* (*Entactinia* in the original paper) *rostriformis* assemblage correlates to the upper Emsian *patulous* conodont zone. (We note here the difficulties with assemblages that bear the name *Primaritripus* given its *nomen dubium* status). From the Upper Eifelian their *Primaritripus kariukmasensis* assemblage co-occurs with conodonts characteristic of the *australis-kockelianus* conodont zones. *Stigmosphaerostylus* (*Apophisisphaera* in the original paper) *hystricuosa-Spongentactinia fungosa* assemblage corresponds to the range of the *Tortodus kockelianus* conodont zone. The *Spongentactinella windjanensis-Bientactinosphaera nigra* assemblage is reported from the lower Givetian. The lower Frasnian in western Australia contains the *Helenifore gogoense-Retisphaera concinna* assemblage. Elsewhere, the *Palaeodiscaleksus punctus-Astroentactinia biaciculata* assemblage occurs in the lower Frasnian of the northern Timan-Pechora Basin. The *Primaritripus chuvashovi* assemblage is known from the middle Frasnian of the southern Urals. The mid-Frasnian also sees the *Radiobisphaera domanicensis-Radiobisphaera menneri* assemblage in the Domanik Formation of the southern Urals and Volga-Ural Basin and the *Moskovistella allbororum-Ceratoikiscum ukhtensis* assemblage in correlatives of the same formation in the Timan-Pechora Basin and Rudny Altai with three sub-asemblages (Rdm 1-3) that are also detailed by Afanasieva & Amon (2011). They report two further assemblages from the upper Frasnian: the *Polyentactinia circumretia-Trilonche* (*Bientactinosphaera*) *egindyensis* assemblage, which occurs in the middle and upper Frasnian of the Southern Urals, Northern Mugodzhary, and Rudny Altai and the *Trilonche* (*Bientactinosphaera*) *pittmani-Trilonche* (*Russirad*) *kazintsovae* assemblage from the Upper Frasnian of the Timan-Pechora Basin. Early Famennian radiolarians include those of the *Tetrentactinia barysphaera-Ceratoikiscum famennium* assemblage from the Pripyat Depression, Evtropiny Noski of the Malaya Pechora allochthon of the western slope of the northern Urals, Southern Urals, and northern Mugodzhary; the *Tetrentactinia barysphaera-Retientactinosphaera magnifica* assemblage from the northeastern part of the Timan-Pechora Basin the *Tetrentactinia barysphaera-Caspiaza spinifera* assemblage from the Lemvin Zone of the Polar Urals the *Haplentactinia alekseevi-Haplentactinia vilvaensis* assemblage from the western slope of the Middle Urals and the *Tetrentactinia barysphaera-Holoeciscus auceps* assemblage from the northern slope of the Caspian Depression. *Tetrentactinia barysphaera* is a common element in most of these assemblages.

EARLY CARBONIFEROUS: RISE OF THE ALBAILLELLARIANS

Five families are discriminated within the Order Albaillellaria (De Wever *et al.* 2001). Of these, the families Albaillellidae and Follicucullidae are used to establish the Carboniferous and Permian biozones. Members of the Albaillellidae such as *Protoalbaillella* evolved in the Late Devonian and diversified in the Carboniferous. Many faunas have been described from Europe, North America, Australia, SE Asia and China. Initial descriptions of key taxa are contained in the numerous works of Deflandre who introduced *Albaillella* (Deflandre 1952; 1963a, b; 1964; 1973a, b; Caulet 2013). On the other side of the English Channel, Holdsworth (1966, 1969a, b, 1971) also described well preserved material. The importance of radiolarians towards the resolution of stratigraphy in complex orogenic collages containing Late Paleozoic chert sequences was quickly recognized by Davey Jones of USGS, who worked together with Brian Holdsworth (Holdsworth *et al.* 1978; Jones *et al.* 1978) to produce the first radiolarian biozonation for the Late Devonian through the end Paleozoic (Holdsworth & Jones 1980). The overall succession of taxa recognized by Holdsworth has largely been validated by subsequent studies in continental North America (Cheng 1986, Schwartzapfel & Holdsworth 1996) and is broadly followed herein. Many distinctive taxa that can be identified amongst the albaillellids on the basis of external morphological characteristics appear in the early Carboniferous and these taxa are used as the basis of the biostratigraphic zonation outlined in Figure 5. Important radiolarians include the albaillellids, which flourished until their ultimate demise at the Permian/Triassic boundary. In the early Carboniferous (the Mississippian of North America) the pylomate archocyrtids are important and common in faunas from France (Gourmelon 1987), Turkey (Holdsworth 1973; Noble *et al.* 2008), USA (Cheng 1986; Schwartzapfel & Holdsworth 1996) and eastern Australia (Aitchison 1988; Aitchison & Flood 1990) as are to a lesser extent the popofskyellids. Nonetheless, the zonation is a work in progress and later researchers are encouraged to use the most recent information from studies of the taxa that they use for correlation.

Numerous local lower Carboniferous radiolarian biostratigraphies have been proposed in various places such as Pyrénées in France (Gourmelon 1987), the Rheno-Hercynian Zone in Germany (Won 1983; Braun 1990; Braun & Schmidt-Effing 1993; Won & Seo 2010), Pre-Caspian Basin and southern Urals (Afanasieva *et al.* 2002), Oklahoma and Arkansas (Cheng 1986; Schwartzapfel & Holdsworth 1996), Nevada (Murchey 1990), Sibumasu block (Wonganan *et al.* 2007), and South China block (Wang & Kuang 1993; Wu *et al.* 1994). Many of these biostratigraphies were established as assemblage zones for which ages are well controlled by correlation with conodont zones. The age reliability and the number of localities differ significantly between the lower and upper Carboniferous. There are important facies controls on the assemblages present and difference between assemblages from different water depths and paleolatitudes. Early Carboniferous radiolarians commonly occur in both shallow and deep water sediments in the continental shelf, and with notable exceptions in eastern Australia (Aitchison 1988) and SE Asia (Spiller 1996) they appear to be less common in pelagic sediments. Thus, we will attempt to explain faunal differences in a manner that seeks to clarify the reliability and the age control.

TOURNAISIAN

The base of the Tournaisian is currently positioned by the first appearance of the conodont *Siphonodella sulcata* within the evolutionary lineage from *Siphonodella praesulcata* to *S. sulcata* (Paproth *et al.* 1991), although the GSSP position needs to be re-located in the stratotype or a new stratotype

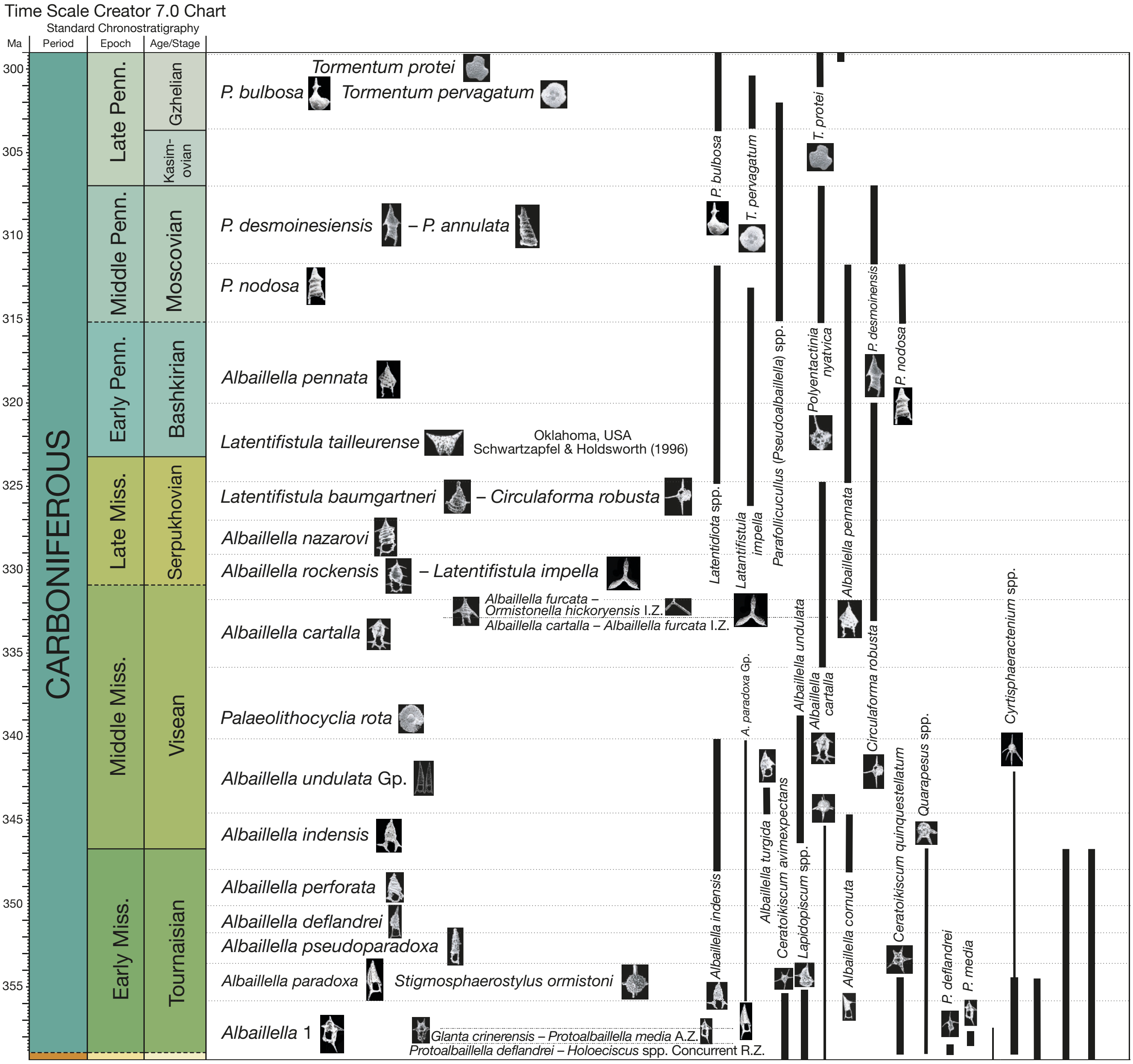

FIG. 5. — Twenty assemblages presently recognized from the Carboniferous in stratigraphic order are the: *Albaillella* 1, *Albaillella paradoxa* –*Stigmosphaerostylus ormistoni*, *Albaillella pseudoparadoxa*, *Albaillella deflandrei*, *Albaillella perforata*, *Albaillella indensis*, *Albaillella undulata* Gp., *Palaeolithocyclia rota*, *Albaillella cartalla*, *A. rockensis*-*Latentifistula impella*, *Albaillella nazarovi*, *Latentifistula baumgartneri*-*Circulaforma robusta*, *Latentifistula tailleurense*, *Albaillella pennata*, *P. nodosa*, *P. desmoinesiensis*-*P. annulata*, *P. bulbosa*, *Tormentum pervagatum*, *Tormentum protei*, and *Latentifistula crux* assemblages.

section should be designed for lithologic and reworked issues at the stratotype (Kaiser 2009). Radiolarians occur across the Devonian-Carboniferous (Famennian-Tournaisian) boundary in Thailand (Saesaengseerung *et al.* 2007a; Wonganan *et al.* 2007), but no applicable zones have been proposed. A radiolarian zone correlative to some of the Tournaisian conodont *S. sulcata*, *S. dublicata* and *S. sandbergi* zones is "the Entactiniidae gen. et sp. indet. Zone" in Pre-Caspian Basin (Afanasieva & Amon 2009). The preservation of the specimens from the Entactiniidae gen. et sp. indet. Zone shown in Afanasieva (2000: pl. 130, figs 24-28) are so poor as to be unusable for any correlative radiolarian zone. We note that entactinarians (*Trilonche palimbola*, *Stigmosphaerostylus variospina*, *Astroentactinia stellata*, *Astroentactinia multispinosa*) and Archocyrtiidae (*Archocyrtium*, *Cyrtisphaeractenium*, *Pylentonema*) occur across the Devonian-Carboniferous (D-C) boundary in Thailand (Saesaengseerung *et al.* 2007a; Wonganan *et al.* 2007). In terms of zonation we retain the *Albaillella* 1 zone of Holdsworth cited in Cheng (1986), the base of which is marked by the FA of *Cyrtisphaeractenium* and the top by the FA of *Albaillella*. The next conodont zone above the *Siphonodella sandbergi* Zone is the lower *Siphonodella crenulata* Zone. The radiolarian zones correlative to this conodont zone are the *Stigmosphaerostylus ormistoni* Zone (*Entactinia* in the original paper) (Afanasieva & Kononova 2009) and *Albaillella paradoxa* Zone (Won & Seo 2010). The *Stigmosphaerostylus ormistoni* Zone includes *Belowea tenuistesta*, *Trilonche altasuleata*, *T. linquidombarfructa*, *Stigmosphaerostylus inaequoporosa*, *S. ormistoni*, *S. rostriformis*, *S. vulgaris*, and *Palacantholithus stellatus*. Like many faunas across the D-C boundary, this assemblage does not include *Albaillella*. The oldest known *Albaillella* is the *Albaillella paradoxa* group whose first occurrence is correlated to the Lower *Siphonodella crenulata* conodont Zone, dated as middle Tournaisian. The *A. paradoxa* group includes *A. paradoxa*, *A. pseudoparadoxa*, *A. brauni*, *A. tuboforma*, *A. crenulata*, and *A. gracilifroma* according to Won & Seo (2010), and thus *A. paradoxa* group has a longer range from the middle Tournaisian to middle Visean than the *A. paradoxa* in the sense of Won & Seo (2010) in the middle Tournaisian (Won 1991; Park & Won 2012). The *A. paradoxa* Zone of Braun & Schmidt-Effing (1993) corresponds to the *A. paradoxa* and lower part of the *A. pseudoparadoxa* zones of Won & Seo (2010). Radiolarians of the *A. paradoxa* group, are commonly found in France and Germany (Won & Seo 2010) and to a lesser extent in North America (Harwood & Murchey 1990), eastern Australia (Aitchison 1988; Aitchison & Flood 1990), south China (Zhang & Feng 2002; Wang *et al.* 2012), Turkey (Noble *et al.* 2008) and SE Asia (Spiller 1996; Jasin & Harun 2001; Wonganan *et al.* 2007).

An evolutionary descendant of *A. paradoxa* sensu stricto, *A. pseudoparadoxa* has been recorded from South China, Thailand, Germany, and Oklahoma (Schwartzapfel & Holdsworth 1996; Wonganan *et al.* 2007; Won & Seo 2010; Wang *et al.* 2012). The appearance of *A. pseudoparadoxa* may be related to diversification of *Albaillella* or the development of radiolarian-bearing strata in the late Tournaisian. The upper Tournaisian is divided into the upper *A. pseudoparadoxa*, *A. deflandrei*, *A. perforata*, and the lower *A. indensis-Palaeolithocyclia rota* zones by Won & Seo (2010), or alternatively the upper *A. paradoxa* group, *A. deflandrei* Zone, and the lower to middle *A. indensis* zones by Braun & Schmidt-Effing (1993). Both zonations were established in Germany, but similar biozones to those of Braun & Schmidt-Effing (1993) are also recognized in South China (Wang *et al.* 2012) and Thailand (Wonganan *et al.* 2007).

VISEAN

The base of the Visean is defined by the first appearance of the fusulinid *Eoparastaffella simplex* in the lineage *Eoparastaffella ovalis-Eoparastaffella simplex* (Devuyst *et al.* 2003). Radiolarian biostratigraphy is indirectly correlated to fusulinid zones via conodont zones. The Tournaisian-Visean boundary (TVB) is placed below the base of the conodont *Pseudognathodus homopunctatus* Zone (*Gnathodus* in the original paper). The direct correlation between conodonts and radiolarians is confirmed in that the TVB is placed within the *Albaillella indensis* group Assemblage (Wonganan *et al.* 2007). Although the *A. indensis* group is also grouped with *A. indensis*, *A. perforata perforata* and *Albaillella perforata brauni* (synonym of *A. indensis brauni*) (Won 1991; Won & Seo 2010), Wonganan *et al.* (2007) placed the *A. perforata* group Assemblage below the *A. indensis* group Assemblage. Wonganan *et al.* (2007) divided the lower-middle Visean radiolarian biostratigraphy into the *A. indensis* group Assemblage and *Palaeolithocyclia rota* Sub-assemblage of the *Albaillella cartalla-Albaillella furcata furcata* Assemblage, and subsequently *Palaeolithocyclia rota* (Won) appeared in the lower-middle Visean. Earlier work in Europe and North America recognized the significance of the *Albaillella undulata* Group at stratigraphic levels between these early Visean assemblages (Holdsworth & Jones 1980; Cheng 1986). *Palaeolithocyclia* is known as the oldest flat radiolarian with a concentric internal structure

The Visean witnesses the first appearance of the Order Latentifistularia, which were formerly referred to as "stauraxon radiolarians" and continue through to the earliest Triassic. This interval is also characterized by the diversification of Latentifistulid precursors such as *Tetragregnon* and *Staurentactinia*, which first appeared as early as the Famennian (Schwartzapfel & Holdsworth 1996; Afanasieva 2000), as well as many genera (*Tetratormentum*, *Latentifisula*, and its junior synonyms *Ouaka*, *Trilacertus*, and *Wonia* [itself a replacement name for the junior homonym *Scharfenbergia*] that diversified in the Visean. Such forms are common in Russia, USA, Germany France and East Asia (Ormiston & Lane 1976; Nazarov & Ormiston 1983a, 1985a, 1986; De Wever & Caridroit 1984; Sashida & Tonishi 1986; Yao *et al.* 1993; Feng *et al.* 2006). In addition, approximately 30 out of 100 described *Albaillella* species appeared in the Visean.

SERPUKHOVIAN

The formal stage name for the uppermost lower Carboniferous (= upper Mississippian) is designated as the Serpukhovian. This can be correlated to the upper Chesterian in North America (Davydov *et al.* 2012: 605) and lower Namurian in Western Europe (Heckel & Clayton 2006). The base of the Serpukhovian is tentatively placed at the first appearance of the conodont species *Lochriea ziegleri*, and the Visean-Serpukhovian transition coincides with a major glaciation event in Gondwana (Davydov *et al.* 2012). Limited Serpukhovian radiolarian localities are known from Oklahoma (Cheng 1986; Schwartzapfel & Holdsworth 1996), Germany (Braun & Schmidt-Effing 1993), the Precaspian Basin (Afanasieva & Amon 2009), and South China (Wang & Yang 2011). The lowermost Serpukhovian is correlated to the uppermost part of the Visean radiolarian zones such as the *Albaillella rockensis* Zone in Germany (Braun & Schmidt-Effing 1993), *Latentifistula impella-L. turgida* Abundance Zone in South China (Wang & Yang 2011), and *Albaillella furcata rockensis-Latentifistula impella* group Assemblage in Thailand (Wonganan *et al.* 2007). Like the Visean faunas the early Serpukhovian radiolarians include common species in these regions, but most parts of the Serpukhovian are characterized by endemism between different regions (Oklahoma and Pre-Caspian). In Oklahoma, Schwartzapfel & Holdsworth (1996) proposed the *Latentifistula* (*Trilacertus*) *baumgartneri-Circulaforma robusta* Zone, which is characterized by *Albaillella nazarovi* and other *Albaillella* species. In the Precaspian Basin, three zones (*Caspiaza* spp.-*Astroentactinia paronae*, *Caspiaza calva*-*C. aculeata*, and *Caspiaza* spp.-*Bientactinosphaera acnigma* zones) were proposed (Afanasieva & Amon 2009). The genus *Caspiaza* is considered to have evolved from *Pylentonema* by reduction of spines and the development of robust skirts (Afanasieva 1986, 1993), but this evolutionary trait is not yet confirmed. Diverse *Albaillella*-species such as *A. cartalla*, *A. cylindrica* group, *A. spinosa* group and *A. lanceolata* group of Schwartzapfel & Holdsworth (1996: 52-86) became extinct by the Serpukhovian. The Serpukhovian-Bashkirian (lower-upper Carboniferous) boundary may be an important biotic event for radiolarians as pointed by Afanasieva & Amon (2006), but this assumption in fact could be an artifact of very poor fossil records amongst both Serpukhovian and Bashkirian radiolarians (Suzuki 2016: 25).

UPPER CARBONIFEROUS

In contrast to the rich occurrences of early Carboniferous radiolarians, reports of Late Carboniferous (Pennsylvanian) radiolarians are patchy from Japan (Ishiga 1982), the South Urals (Isakova & Nazarov 1986; Nazarov 1988; Nazarov & Ormiston 1993), and mid-continental North America (Holdsworth & Murchey 1988; Nestell *et al.* 2012). The upper Carboniferous to the lower Permian are predominantly dated using the biozones established in Japan (Ishiga 1986, 1990), but it is noted that little age controls was available for use as tie points in this interval. In the Late Carboniferous provincialism progressed in variable marine biota including ammonoids and conodonts, and subsequently high resolution correlation even amongst the same biota becomes difficult (Davydov *et al.* 2012). Possibly in relationship to this progressive marine biota provincialism, upper Carboniferous radiolarian faunal compositions differ between Japan, the South Urals and mid-continental North America.

Bashkirian

The base of the Bashkirian is defined by the first appearance of the conodont *Declinognathodus noduliferus* sensu stricto (Lane *et al.* 1999). The Bashkirian is correlated with the Morrowan and the lower Atokan in North America and the Namurian and the lowermost Westphalian in Western Europe (Heckel & Clayton 2006). The "Namurian" radiolarian fauna including *Albaillella pennata*, *Ceratoikiscum tricancellatum* and *Popofskyellum undulatum* was reported from goniatite limestone bands in Staffordshire and Derbyshire (Holdsworth 1966, 1969a), but correlation of this fauna might now be extended to the Visean on the basis of the total range of *A. pennata* (e.g. Wonganan *et al.* 2007). The *Pseudoalbaillella nodosa* (note: *Parafollicucullus* should replace *Pseudoalbaillella* following synonymies detailed in this volume) Assemblage of Ishiga (1982, 1986, 1990) was initially correlated with the "upper Atokan", which is now correlated with the Moscovian because of the co-occurring lower to middle Moscovian conodont *Gondolella clarki* (Nestell *et al.* 2012). The *Latentifisula* (*Scharfenbergia*) *tailleurense* Assemblage provides a reliable basal Bashkirian zone as this species occurs with the age-diagnostic conodont *Declinognathodus noduliferus* (Holdsworth & Murchey 1988).

Moscovian

This stage is important because provincialism amongst conodont faunas is so much more significant such that correlation between even the Donets and Moscow basins (Schmitz & Davydov 2012) is not possible. The base of the Moscovian is tentatively determined by the first appearance of the conodonts *Idiognathoides postsulcatus*, *Declinognathodus donetzianus* or *Diplognathodus ellesmerensis* (Nemyrovska *et al.* 1999; Wang *et al.* 2011a; Alekseev & Task Group 2013). The stratigraphic positions of these bioevents are significantly different such that the same conodont fauna is assignable to both the upper Bashkirian and lower Moscovian depending on which opinions are applied. The Moscovian is correlated with the upper Atokan and Desmoinesian in North America and the middle to upper Westphalian in Western Europe (Heckel & Clayton 2006). Limited reliable occurrences of Moscovian radiolarians are known as the *Pseudoalbaillella nodosa* Zone of Ishiga (1982, 1986, 1990) in Japan, and the *P. nodosa* and *P. desmoinesiensis*-*P. annulata* zones of Nestell *et al.* (2012) in mid-continental North America. Another Moscovian *Polyentactinia nyatvica* Assemblage dated using ammonoids is reported from the Prikolyma region in eastern Russia (Nazarov & Ormiston 1993: 30). The *P. nyatvica* Assemblage is marked by an absence of any albaillellarians possibly representing some sort of facies control.

Kasimovian

The Kasimovian roughly corresponds to the Missourian in North America and the major part of Stephanian in Western Europe. The base of the Kasimovian is the subject of discussion relating to the first appearances of various conodonts: *Idiognathodus sagittalis*, *I. turbatus*, and *I. heckeli* (Ueno & Task Group 2014). Differences are critical in that the first appearances of *I. turbatus*, and *I. heckeli* are placed approximately one substage higher than the traditional base of the Kasimovian. Radiolarians considered to be Kasimovian have been reported as the *Haplodiacanthus*-*Albaillella* Assemblage from the Cis-Ural (Afanasieva *et al.* 2002) and the *Pseudoalbaillella bulbosa* Assemblage from Japan (Ishiga 1982). According to Afanasieva *et al.* (2002), the *Haplodiacanthus*-*Albaillella* Assemblage was found in "Bed 4" in which the fusulinid "*Triticites arcticus* Zone" co-occurs. We note that this fusulinid Assemblage from this horizon was not associated with *Schellwienia arctica* (Chuvashov & Chernykh 2002: 32), although *T. arcticus* is now regarded as *S. arctica* and this species is used as a Kasimovian marker (see the synonym list in Blazejowski *et al.* 2006). However, this Bed 4 is a critical horizon because Chernykh *et al.* (2006) pinned the interval of Bed 4 as the Kasimovian-

Gzhelian boundary and it is a potential candidate for the base of the Gzhelian. The exact occurrence horizon of the *Haplodiacanthus-Albaillella* Assemblage is uncertain because later publication has not indicated this occurrence in the Usolka section (e.g. Chernykh *et al.* 2006). Therefore, this radiolarian assemblage should be regarded as "an assemblage that occurs around the Gzhelian-Kasimovian boundary" rather than "a Kasimovian assemblage."

The *Pseudoalbaillella bulbosa* Assemblage is dated by the occurrence of *Streptognathodus elongatus* and the absence of *Idiognathoides sinuatus* and *Neognathodus roundyi*. The first occurrence of *P. bulbosa* (Ishiga 1982: table 1, sample 91) is placed significantly higher than that of "*S. elongatus*" (sample 58). Since "*Streptognathodus elongatus*" has been subdivided into *S. bellus*, *S. elongatus*, *S. postelongatus*, *S. constrictus*, *S. longissimus*, and *S. postconstrictus* (Boardman *et al.* 2009: fig. 48), correlation of *P. bulbosa* needs revision, following the modern taxonomic scheme applied to conodonts. Given that the "*S. elongatus*" of Ishiga (1982) includes all these current species, the first occurrence of *P. bulbosa* has to be regarded as Gzhelian or younger because the first occurrence of the oldest "*S. elongatus*", *S. bellus* is placed in the upper Gzhelian. In conclusion, little is known about typical Kasimovian radiolarian faunas.

GZHELIAN

The base of the Gzhelian is tentatively determined by the first occurrence of the conodont *Idiognathodus simulator* sensu stricto in its potential lineage *Idiognathodus eudoraensis-I. simulator* (Ueno & Task Group 2014). The Gzhelian is correlated with the Virgilian except in its lowest part as well as with the upper Stephanian and Autunian in Western Europe (Ueno & Task Group 2014). Gzhelian radiolarian faunas are reported from China (Zhang *et al.* 2002), Japan (Ishiga 1982), Mexico (Caridroit *et al.* 2002), and the South Urals (Nazarov & Ormiston 1985b; Isakova & Nazarov 1986). The biozones established in the South Urals are well dated using co-occurring conodonts and fusulinaceans in the same sections (Isakova & Nazarov 1986).

The *Tormentum pervagatum* Assemblage is correlated to the middle Gzhelian (the Pavlovoposadian in the Boreal Province) based on the correlative fusulinid *Jigulites jigulensis* Assemblage (Davydov *et al.* 2010) and the conodont *Streptognathodus ruzhencevi* Assemblage (Sobolev & Nakrem 1996). The *Tormentum protei* Assemblage is correlated with the upper part of the middle Gzhelian by reference to the fusulinid *Daixina sokensis* Assemblage and the conodont *Streptognathodus elegantulus-Streptognathodus elongatus* Assemblage. The *D. sokensis* Assemblage of Isakova & Nazarov (1986) is associated with *Daixina enormis*, *D. sokensis*, and *Pseudoschwagerina robusta* (*Schwagerina* in the original paper) such that the *T. protei* radiolarian assemblage covers the interval from the lower Noginskian to Melekhovian regional stages in the Boreal Province. As explained in the Permian section in this paper, the basal part of the *Latentifistula crux* Assemblage is placed in the uppermost Gzhelian and lowermost Asselian.

The Gzhelian assemblage from San Salvador Patlanoya, Mexico is also well dated by the conodont *Streptognathodus bellus*, an early Gzhelian marker, although this assemblage is not formally named due to poor species composition regardless of its excellent preservation (Caridroit *et al.* 2002). As mentioned previously, a known Gzhelian radiolarian fauna is the *Pseudoalbaillella bulbosa* Assemblage of Ishiga (1982, 1986, 1990). This age is also supported by the co-occurrence of the Gzhelian *Streptognathodus* fauna in the Pope succession, British Columbia (Orchard *et al.* 2001). The top of this assemblage appears to be placed above the Carboniferous-Permian boundary (Gzhelian-Asselian boundary) based on correlation using ΣREE chemostratigraphy in the Bacheng section, South China (Zhang *et al.* 2002). Provincialism amongst conodont and fusulinid faunas is highly enhanced by the middle Gzhelian (Schmitz & Davydov 2012), suggesting probable provincialism in radiolarian faunas. Gzhelian radiolarian assemblages contain rare taxa in common, but the cause of differences is not easily interpreted because their assignable age, paleogeographic position, and depositional settings differ to various degrees. However, the *P. bulbosa* Assemblage with the representative species appears to have been widely distributed in the eastern Peri-Tethys and the low latitudinal Panthalassa Ocean (Wang *et al.* 1998; Metcalfe *et al.* 1999; Orchard *et al.* 2001; Shimakawa & Yao 2006; Saesaengseerung *et al.* 2007b; Xie *et al.* 2011; Nestell & Blome 2015), showing a widely common paleo-province in these oceans.

PERMIAN

Albaillellids continued to diversify until the end of the Permian and provide the key taxa in biozonations (Fig. 6). The uppermost Paleozoic (upper Carboniferous to Permian) has a well-developed radiolarian biostratigraphy initially recognized in accretionary terranes in Japan and now also studied in China (Ishiga 1986; Kuwahara 1997; Yao & Kuwahara 2004; Shimakawa & Yao 2006; Wang & Yang 2007; Zhang *et al.* 2014) and elsewhere in SE Asia (Jasin 1994; Jasin *et al.* 1995) are fairly well constrained for some intervals by the conodont zonal scheme (e.g. Ma *et al.* 2016). The zonation is also applicable to both North (Murchey 1990; Blome & Reed 1992; Nestell & Nestell 2010) and South America (Ling *et al.* 1985) as well as Russia (Nazarov & Ormiston 1985b). In light of additional observations from the Urals and Thailand Caridroit in De Wever *et al.* (2001) suggested further modifications to the zonation and these are incorporated herein.

Before the Permian radiolarian biozones are explained the historical evolution of terminology applied to subdivision into Series merits discussion. Harland *et al.* (1989) a widely applied geologic timescale at the time, subdivided the Permian into two series, namely the Rotliegendes and Zechstein (relevant to Lower and Upper series), whereas the International Commission on Stratigraphy ratified three series, namely the Cisuralian, Guadalupian and Lopingian (relevant to Lower, Middle and Upper series) to the Permian

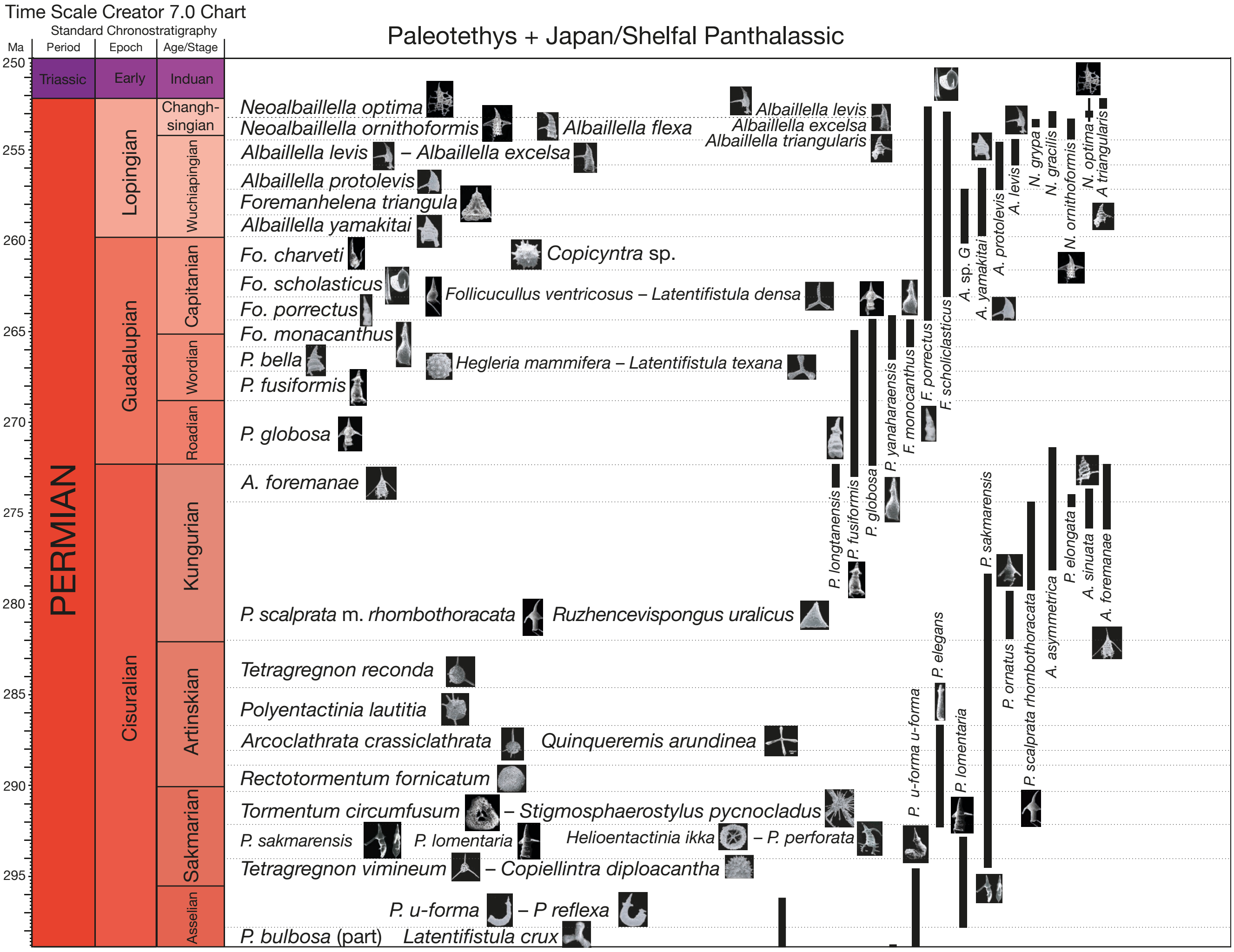

Fig. 6. — Thirty-four assemblages presently recognized from the Permian in stratigraphic order are the: *Latentifistula crux*, *P. u-forma-P. reflexa*, *Tetragregnon vimineum-Copiellintra diploacantha*, *P. lomentaria-P. sakmarensis*, *Helioentactinia ikka-P. perforata*, *Tormentum circumfusum-Stigmosphaerostylus pycnocladus*, *Rectotormentum fornicatum*, *Arcoclathrata crassiclathrata-Quinqueremis arundinea*, *Polyentactinia lautitia*, *Tetragregnon reconda*, *P. scalprata* m. *rhombothoracata*, *Ruzhencevispongus uralicus*, *A. foremanae*, *P. globosa*, *P. fusiformis*, *P. bella*, *Hegleria mammifera-Latentifistula texana*, *Fo. monacanthus*, *Fo. porrectus*, *Fo. ventricosus-Latentifistula densa*, *Fo. scholasticus*, *Fo. charveti*, *Copicyntra*, *Albaillella yamakitai*, *Foremanhelena triangula*, *Albaillella protolevis*, *Albaillella levis-Albaillella excelsa*, *Neoalbaillella ornithoformis*, and *Neoalbaillella optima* assemblages with the *Albaillella triangularis*, *Albaillella flexa*, *Albaillella excelsa* and *Albaillella levis* recognized in east Asia amongst the latter two zones.

(Henderson *et al.* 2012). Thus, the lower Permian and upper Permian do not always mean the same ages in different timescales. To avoid such confusion, we use Cisuralian, Guadalupian and Lopingian.

The accuracy of age assignments for radiolarian assemblages is variable. Radiolarian ages for the Cisuralian to the upper Guadalupian are well controlled in the South Urals using both conodonts and fusulinids. The southern Ural sections also have the advantage of GSSP candidates. Amongst contemporaneous radiolarian assemblages in the east Peri-Tethys and the low-latitudinal Panthalassa Ocean, there are many reasons why the age assignments in existing publications need to be updated. The time interval from the upper Kungurian of the Cisuralian to the end-Permian has now been well dated with conodonts, particularly with contributions from sections in China. In consideration of these differences in reliability we carefully reviewed and evaluated the age control for each radiolarian assemblage.

CARBONIFEROUS-PERMIAN BOUNDARY (GZHELIAN-ASSELIAN BOUNDARY)

The start of the Permian is defined by the first occurrence of the conodont *Streptognathodus isolatus* in the Aiadalarash Creek section as GSSP (Davydov *et al.* 1998). This ratified Carboniferous-Permian (C-P) boundary is slightly lower than traditional fusulinacean and ammonoid boundaries. The C-P boundary lies within the *Pseudoalbaillella bulbosa* Assemblage in China and the *Latentifistula crux* Assemblage in the South Urals (Nazarov & Ormiston 1985b; Isakova & Nazarov 1986). Isakova & Nazarov (1986) depicted the *L. crux* Assemblage as correlating with the conodont *Streptognathodus wabaunsensis* Assemblage. Subsequently, a morphotype of "*Streptognathodus wabaunsensis*" included in *S. isolatus* by Chernykh *et al.* (1997) and it is now correlated with the uppermost Gzhelian (e.g. Chernykh *et al.* 2012). As it is now the key species defining the base of the Asselian, the *Latentifistula crux* Assemblage clearly crosses the C-P boundary.

ASSELIAN

The Asselian is correlated with the lowermost Wolfcampian in North America and the Zisongian Stage of the Chuanshanian Series in China (Henderson *et al.* 2012). The Asselian radiolarian zones are known as the *Latentifistula crux* and *Pseudoalbaillella anfracta* assemblages (*Haplodiacanthus anfractus* in the original paper) in the South Urals and as the *Pseudoalbaillella bulbosa-P. u-forma* s.s. (*Pseudoalbaillella u-forma* morphotype I in Ishiga *et al.* 1984) and *P. reflexa* (= *Pseudoalbaillella u-forma* morphotype II in Ishiga *et al.* 1984) assemblages in Japan (Metcalfe 2000). The ages of these radiolarian zones are, however, poorly controlled by other fossils and some contradictions in species compositions exist amongst various papers. Saesaengseerung *et al.* (2009) dated the same sample with *P. bulbosa*, *P. u-forma* s.s., and *P. reflexa* using a co-occurring conodont *Streptognathodus constrictus* Chernykh & Reshetkova (note: this is not the same form that was described using this species name by Wardlaw *et al.* in Boardman *et al.* 2009) from a quarry section in Thailand, indicating assignment to the middle Asselian (Chernykh 2006). Ishiga *et al.* (1984) placed the *P. u-forma* s.s. Assemblage and the overlying *P. reflexa* Assemblage in the Cisuralian, but these two assemblages are from different blocks, which are separated by a significant fault. If we refer to several conodont studies (Chernykh 2006; Boardman *et al.* 2009), the lower block with *P. u-forma* s.s. contains apparent Carboniferous-type *Streptognathodus* and typical *Gondolella* (*sensu stricto*), whereas the upper block with *P. reflexa* Assemblage should be middle Asselian (following Saesaengseerung *et al.* 2009). The age assigned to the *P. anfracta* Assemblage and the taxonomy of this species are to a certain extent problematic. According to Amon (1999), it is likely that the *P. anfracta* Assemblage can be dated using conodonts and ammonoids, but it is uncertain without the original data. *P. anfracta* was assigned to the Artinskian using the fusulinid *Pseudofusulina concavutas-P. pedissequa* Assemblage (Chuvashov *et al.* 1999) and was considered to have appeared in the Artinskian (Nazarov & Ormiston 1985b). As to the taxonomy, Cordey (1998) synonymized *P. anfracta* with *Pseudoalbaillella lomentaria* of Sakmarian-early Artinskian age. No verifiable data can conclusively be used to give an Asselian assignment to *P. anfracta*. Therefore, it is concluded that: 1) the Saesaengseerung *et al.* (2009) sample should belong to the *P. reflexa* Assemblage because among the three species *P. bulbosa*, *P. u-forma*, and *P. reflexa* the species *P. reflexa* is the youngest first appearance; 2) the type section of *P. bulbosa* was apparently dated as Carboniferous; 3) the *L. crux* Assemblage correlates with the lowermost Asselian; 4) the *P. u-forma* sensu stricto Assemblage in the type section is possibly Carboniferous; and (5) the *P. reflexa* and *P. anfracta* Assemblages cannot necessarily be assigned the same age.

The top of the *Pseudoalbaillella bulbosa* Assemblage probably lies within the lowermost Asselian. Ling *et al.* (1985) dated this assemblage using the fusulinid *Schwagerina* aff. *S. munaniensis*, *Chalaroschwagerina tarltonensis*, and *Triticites tarltonensis*. However, this fusulinid fauna does not directly indicate the age of the *P. bulbosa* Assemblage. The fusulinids were obtained from the upper detrital calcareous beds, which overlie the radiolarian-bearing red chert. The detrital beds with fusulinids accumulated *in situ* over the older chert with older fusulinids potentially being reworked into the depositional sites of younger chert, or contemporary deposits. As these fusulinids are endemic to Chile (Douglass & Nestell 1976; Chisaka & Corvalan Diaz 1979) and Peru (Roberts 1953) their age is presumed by the co-occurrence of *Chalaroschwagerina* and *Triticites* to be indicative of the Sakmarian on the basis of Loeblich & Tappan (1987). The Sakmarian assignment to the *P. bulbosa* Assemblage contradicts other well-dated radiolarian assemblages that suggest the top of the *P. bulbosa* Assemblage can be correlated within the Asselian.

SAKMARIAN

The GSSP candidates for the base of the Sakmarian are the first occurrence of the conodont *Sweetognathus merilli* in the Kondurovsky section, in the South Urals (Chuvashov *et al.* 2002) or that of the conodont *Mesogondolella uralensis* in the Usolka, in the South Urals (Schmitz & Davydov 2012). The Sakmarian is correlated with the lower Wolfcampian in North America, and the Longlinian Stage of the Chuanshanian Series in China. The radiolarian zones correlative to the Sakmarian are the *Pseudoalbaillella lomentaria* Assemblage in East Asia (Metcalfe 2000; Jasin & Harun 2001) and four zones in the Southern Urals (Amon & Chuvashov 2002). The Sakmarian in the South Urals is divided into the *Tetragregnon vimineum-Copiellintra diploacantha*, *Helioentactinia ikka-Pseudoalbaillella perforata* (*Haplodiacanthus perforatus* in the original paper), and *Tormentum circumfusum-Stigmosphaerostylus pycnocladus* (*Entactinia pycnoclada* in the original paper), *Rectotormentum fornicatum* Assemblages in chronological order (Amon & Chuvashov 2002; Kozur 1981; Nazarov & Ormiston 1985b; Nazarov 1988; Isakova 1998; Afanasieva 1999). The lower three radiolarian zones are well controlled using associated conodont, fusulinid, and ammonoid fossils in the sections where the type localities of these radiolarians were designated. For example, the type locality of the *T. vimineum-C. diploacantha* Assemblage is designated as the lower Sakmarian interval in the Kondurovsky section where the candidate GSSP was proposed. The *Rectotormentum fornicatum* Assemblage is correlated with the uppermost Sakmarian by Amon & Chuvashov (2002), but should be reassigned to the middle Artinskian because the middle Artiskian fusulinid *Pseudofusulina juresanensis* (see Henderson *et al.* 2012) occurs below the horizon containing this radiolarian assemblage (Afanasieva & Zamilatskaya 1993).

Radiolarian assemblages in the South Urals contain some *Pseudoalbaillella* and *Albaillella* species. *Pseudoalbaillella anfracta* ranged until the early middle Sakmarian, *P. perforata*, *P. sakmarensis* and *P. nazarovi* ranged from the early middle to early late Sakmarian and *Albaillella permica* existed from the early middle to late Sakmarian. Similarly, *Pseudoalbaillella simplex* occurs in the Cis-Urals in Sakmarian beds well-dated by ammonoids and conodonts (Kozur & Mostler 1989).

In contrast to the well-dated assemblages in the South Urals, those in East Asia are rarely able to be dated using other fossils. The *Pseudoalbaillella lomentaria* Assemblage was reported from the eastern Peri-Tethys and the low latitudinal Panthalassa pelagic sediments. If one follows Cordey's (1998: 34) synonymy of *Holdsworthella permica* and *Haplodiacanthus anfractus* with *Pseudoalbaillella lomentaria*, this assemblage can be assigned to the Sakmarian. Even if these species are separated as independent species, *P. lomentaria* is commonly associated with *P. sakmarensis* in Japan (Kuwahara 1992), South China (Shimakawa & Yao 2006), and Malaysia (Spiller 1996). This interpretation suggests that the *P. lomentaria* Assemblage is likely to be Sakmarian. Kozur & Mostler (1989) suggested the range of *P. lomentaria* from the late Artinskian to the early Kungurian, but they did not present any examinable data. However, several papers applied a very wide concept of *P. lomentaria* (e.g. Wang *et al.* 2012) and this may lead to biostratigraphic inconsitency.

ARTINSKIAN

As the term "Artinskian" has been used to represent different intervals (Ritter 1986), the concept relating to "Artinskian" needed to be checked in each case where it is applied. The base of the Artinskian is tentatively defined by the first occurrence of the conodont *Sweetognathus whitei* (Rhodes) *sensu* Chernykh within the chronomorphocline of *S. binodosus*, *S. anceps* to *S. whitei* (Henderson *et al.* 2012). The Artinskian is correlated with the upper Wolfcampian to the lowermost Leonardian in North America, the lower Chihsian Stage of the Luodianian Series in China and Yakhtashian in the Pamirs. The Sakmarian-Artinskian transition roughly coincides with the end of the Glaciation III (Grossman *et al.* 2008), and the early Permian Crisis in conodont faunas with the disappearance of the Carboniferous holdovers such as *Streptognathodus* (Clark 1972; Ritter 1986) and the rebuilding of climate-sensitive conodont provinces worldwide (Mei *et al.* 2002)

In the South Urals, three assemblage zones, namely *Arcoclathrata crassiclathrata-Quinqueremis arundinea* (*Entactinosphaera crassiclathrata* in the original paper by Nazarov & Ormiston 1985b was assigned to a new genus established by Afanasieva & Amon 2016), *Tetracircinata reconda*, and *Polyentactinia lautitia* Assemblages (Nazarov & Ormiston 1985b; Amon & Chuvashov 2002) have been defined. According to Amon (1999), the *A. crassiclathrata-Q. arundinea* Assemblage can be correlated using the middle Artinskian fusulinid *Pseudofusulina*? *concavutas* (or *Concavutella concavutas* in Filimonova *et al.* 2015), the *T. reconda* Assemblage by the latest Artinskian conodont *Neostreptognathodus pequopensis*, and the *P. lautitia* Assemblage by the late Artinskian fusulinid *Parafusulina solidissima* which is correlated with the upper part of the conodont *S. clarki* zone from the middle Artinskian. This correlation indicates that the last two assemblages occur in the reverse order with the *P. lautitia* Assemblage being older than the *T. reconda* Assemblage. Unfortunately, these assemblages yield no Albaillellaria correlative to radiolarian assemblages from the east Peri-Tethys and the low latitudinal Panthalassa Ocean making correlation with any zonations based on Albaillellaria difficult.

Age control for radiolarian zones from the eastern Peri-Tethys and the low latitude Panthalassa Ocean need to be carefully examined. For instance, correlation of *Pseudoalbaillella scalprata*, *P. scalprata* m. *rhombothoracata*, and their relevant assemblages has been proposed as late Sakmarian (Yao *et al.* 2004; Jasin & Harun 2011), the Artinskian (Wang *et al.* 1994; Spiller 1996), "lower middle Permian" in Sikhote-Alin (Rudenko & Panasenko 1997), late Artinskian to the early Kungurian (Metcalfe 2000), and Kungurian (Kozur & Mostler 1989; Xian & Zhang 1998). Ishiga (1986, 1990) figured *P. scalprata scalprata*, *P. scalprata* m. *rhombothoracata*, and *Albaillella asymmetrica* appearing in this order. The *P. scalprata* m. *rhombothoracata* Assemblage was dated on the basis of co-occurrence with "*Sweetognathus whitei*" (Ishiga & Imoto 1980). Subsequently, *S. whitei* and similar morphotypes have been subdivided into several species (e.g. Chernykh 2006) and the species concept of *S. whitei* by Chernykh is applied to determine the base of the Artinskian (Henderson *et al.* 2012). Following Chernykh (2006) the specimen of *S. whitei* illustrated in Ishiga & Imoto (1980) is likely to be concordant with the Kungurian *Sweetognathus modulatus* rather than his *S. whitei*. Murchey & Jones (1992) correlated the assemblage with *P. scalprata scalprata*, *P. scalprata postscalprata* and *P. elongata* using the conodont *Mesogondolella intermedia* a species that ranged from the latest Artinskian to the early Kungurian. Murchey & Jones (1992) obtained a conodont *Mesogondolella idahoensis* from their sample with *P. scalprata*, *P. longicornis* and *Albaillella asymmetrica*. Although the range of *M. idahoensis* has serious problems in relation to differences in taxonomic concepts amongst specialists (e.g. Kozur & Wardlaw 2010) since Mei & Henderson (2002) established a new subspecies *M. idahoensis lamberti*, the taxonomic concept applied for the specimen in Murchey & Jones (1992) is presumably similar to the concept in 1980s and 1990s. This *M. idahoensis* indicates the Kungurian and the lowermost Wordian (Henderson *et al.* 2012; Wardlaw & Nestell 2015). In consideration of updated information on conodonts, the *Pseudoalbaillella scalprata*, *P. scalprata* m. *rhombothoracata*, and their relevant assemblages are correlative to the Kungurian or upper but not lower Artinskian.

KUNGURIAN

The base of the Kungurian is tentatively determined by the first occurrence of the conodont *Neostreptognathodus pnevi* within the chronomorphocline of *Neostreptognathodus pequopensis* to *N. pnevi* (Chernykh 2012; Henderson *et al.* 2012). The Kungurian is correlative to the regional Kungurian and Ufimian in the Russian Platform, middle to upper Leonardian in North America, upper Luodinian and partial Xiangboan stages of the Chihsian Series in China and Bolorian through Kubergandian to lower Murgabian in the Pamirs (Henderson *et al.* 2012). The problems and various proposals regarding the Kungurian are summarized in Wang *et al.* (2011b).

In the South Urals, a single zone namely the *Ruzhencevispongus uralicus* Assemblage has been reported (Amon & Chuvashov 2002). This assemblage was first defined by the Artinskian fauna by Nazarov & Ormiston (1986), but was later correlated with the conodont *Neostreptognathodus pnevi* Zone (Chuvashov *et al.* 1999). Nothing is known about the species composition of the *R. uralicus* Assemblage (Nazarov & Ormiston 1986), and *R. uralicus* is easily misidentified (Nestell & Nestell 2010: 56). Consequently, correlation using this assemblage is difficult.

As explained in the Artinskian part of this paper, *Pseudoalbaillella scalprata*, *P. scalprata* m. *rhombothoracata*, and their relevant assemblages are correlative to the Kungurian. This is also supported by the occurrence of the Kungurian fusulinid *Misellina* in the same sedimentary sequences of the Tusurukoba Formation, Kyushu, Japan, which contains *P. scalprata scalprata*, *P. scalprata scalprata*, *P. scalprata* m. *rhombothoracata*, *P. aidensis*, and *Albaillella asymmetrica* (Miyamoto *et al.* 1997).

Ishiga (1986, 1990) established the *Albaillella sinuata* and *Pseudoalbaillella longtanensis* Assemblages with sections in Japan. These two assemblages are roughly correlated with the *Albaillella foremanae* Zone in the Dachongling cherty section, South China, of Zhang *et al.* (2010). The *A. foremanae* Zone is finely correlated with the Kungurian part of the conodont *Jinogondolella nankingensis gracilis* Zone. Zhang *et al.* (2010) and Burrett *et al.* (2015) reported *P. scalprata* from the Roadian, but their specimens are undoubtedly different species. The last occurrences of *Pseudoalbaillella longicornis*, *Albaillella asymmetrica*, *A. xiaodongensis*, and *A. praeforemanae* are placed within the Kungurian.

GUADALUPIAN

Prior to ratification of the GSSP for the base of the Roadian at the first occurrence of the conodont *Jinogondolella nankingensis* in 2001 (Henderson *et al.* 2012), the range of the Guadalupian was different amongst authors (see Leven 2001). Guadalupian radiolarian zones using the Albaillellaria are well established with reliable age controls in China (Zhang *et al.* 2010, 2014).

ROADIAN

Recognition of the Roadian is very difficult because formal definition of the base and top of this stage uses "relatively rare conodonts" worldwide (Leven & Bogoslovskaya 2006) and taxonomic and diachronous issues relating to *Jinogondolella nankingensis* and *J. aserrata* (Burrett *et al.* 2015). Despite these issues, a single zone, the *Pseudoalbaillella globosa* Zone has been established (Zhang *et al.* 2010). The base of this zone is defined by the first occurrence of *Pseudoalbaillella globosa* and its top is defined by the first occurrence of *Pseudoalbaillella fusiformis*.

WORDIAN

The base of the Wordian is defined by the first occurrence of the conodont *Jinogondolella aserrata*. The Wordian is divided into three radiolarian zones (Zhang *et al.* 2010; Zhang *et al.* 2014). The lower one is the *Pseudoalbaillella fusiformis* Zone defined by the first occurrence of the index species, the *P. bella* Zone with the first occurrence of *P. bella*, and the *Follicucullus monacanthus* Zone whose base is defined by the first occurrence of *F. monacanthus* and the top by the first occurrence of *F. porrectus*. They were dated using co-ocurrence of the conodont *J. aserrata* to the lower part of the *J. postserrata* zones (Zhang *et al.* 2014).

CAPITANIAN

The base of the Capitanian is defined by the first occurrence of *Jinogondolella postserrata* within the morphocline from *J. nankingensis* through *J. aserrata* to *J. postserrata* in the upper part of the Pinery Limestone Member of the Bell Canyon Formation, West Texas (Henderson *et al.* 2012). Although there are no reports of radiolarians from the Pinery Limestone Member, the underlying Hegler Member yields the *Hegleria mammifera-Latentifistula texana* Assemblage and the overlying Lamar Limestone contains the *Follicucullus ventricosus-Latentifistula densa* Assemblage of Nazarov & Ormiston (1985a, b) (Nestell & Nestell 2010). The Reef Trail Member that succeeds the Lamar Limestone also yields rich radiolarian assemblages (Maldonado & Noble 2010). In South China, the Capitanian is subdivided into three radiolarian zones. The *Follicucullus porrectus*, *F. scholasticus*, and *F. charveti* Zones. They are defined by the first occurrences of *F. porrectus*, *F. scholasticus*, and *F. charveti*, respectively (Zhang *et al.* 2014). The range of *F. scholasticus* is significantly short in South China, in contrast to its long range in Japan (Nishikane *et al.* 2011) and West Texas (Maldonado & Noble 2010). The middle Capitanian experienced a strong cooling event referred to as the "Kanuma event", which is recorded as a high-positive carbonate carbon isotope excursion in association with the end-Guadalupian extinction of the large fusulinids such as the Verbeekininae, gigantic bivalves such as the Alatoconchidae, and rugose corals of the Waagenophyllidae (Isozaki *et al.* 2007). No significant extinction has been detected amongst radiolarian faunas in the Capitanian. Instead, many *Follicucullus*-species (morphological characters of which fit with the genus *Cariver*) abruptly diversified in the late Capitanian (Wang *et al.* 2012; Zhang *et al.* 2014).

LOPINGIAN "UPPER PERMIAN" ISSUE

This section of the paper starts with discussion of issues regarding the subdivision scheme of the upper Permian and previous papers that assigned the *Follicucullus japonicus*, *F. scholasticus* morphotype I, *F. charveti*, and relevant zones to the "Upper Permian" on the basis of the fusulinid *Lepidolina kumaensis* (Ishiga 1984; Ishiga & Miyamoto 1986). Such a correlation has been repeatedly cited for determination of the upper Permian in Japan (Ishiga 1986, 1990), China (Yu 1996), North America (Blome & Reed 1995). Since the base of the Wuchiapingian GSSP was ratified as the first occurrence of the conodont *Clarkina postbitteri postbitteri* in the Penglaitan Section, South China (Jin *et al.* 2006a), the range of *L. kumaensis* has been revised into the late Capitanian (Ota & Isozaki 2006; Kobayashi 2011; Kasuya *et al.* 2012; Ghazzay *et al.* 2015). This update has been followed by Wang *et al.* (1994), Metcalfe (2000), and Jasin & Harun (2011).

GUADALUPIAN-LOPINGIAN BOUNDARY
(CAPITANIAN-WUCHIAPINGIAN BOUNDARY)

Recognition of the Guadalupian-Lopingian (G-L) boundary by *Albaillella yamakitai* is an important topic (Nestell & Nestell 2010; Nishikane *et al.* 2011, 2014; Xia *et al.* 2005). Xia *et al.* (2005) revised the concept of *A. yamakitai* to include *Albaillella* sp. G of Kuwahara (1999), and designated the G-L boundary with this species. On the other hand, Nestell & Nestell (2010) and Maldonado & Noble (2010) rejected the boundary definition of Xia *et al.* (2005) although their species concept of *A. yamakitai* follows Xia *et al.* (2005)'s opinion. Nishikane *et al.* (2011, 2014) examined the type section of *A. yamakitai* investigating radiolarian, conodont and carbon isotope stratigraphies, and concluded that the first occurrence of *A. yamakitai sensu stricto* occurs directly belowthe G-L boundary in the upper Capitanian.

WUCHIAPINGIAN

Kuwahara (1999) placed the *Follicucullus charveti-Albaillella yamakitai* Zone between the first occurrences of *A. yamakitai* and *A. protolevis*. Kuwahara *et al.* (2005) examined the base of the Wuchiapingian GSSP section in China to find *Foremanhelena triangula*, *Latentifistula similicutis*, *Raciditor scalae*, *Ishigaum trifustis*, and *Triplanospongos* cf. *angustus*, and interpreted the lack of albaillellids to indicate shallow water conditions during sediment deposition. Wang *et al.* (2006) established six zones from composite sections in South China. Their relative age assignment is based on correlation of the successions of assemblages between sections in South China and comparison with radiolarian successions elsewhere globally. Based on revised correlation with the geologic timescale, the *Foremanhelena triangula*, *A. protolevis*, and *A. levis-A. excelsa* Zones are correlative with the Wuchiapingian (Xia *et al.* 2004), although these zones need re-examination given the near complete overlap of the nominal species ranges in the Gujo-hachiman section in the Mino Belt of Japan (Nishikane *et al.* 2011).

CHANGHSINGIAN

The base of the Changhsingian is defined by the conodont *Clarkina wangi* within the lineage from *C. longicuspidata* to *C. wangi* (Jin *et al.* 2006b). The taxonomy of *Clarkina* species is very complex due to 30 described species (e.g. Mei *et al.* 1994; Kozur 2004), but recently Yuan *et al.* (2014) integrated its taxonomy with morphological variations into only eight species (*Clarkina orientalis*, *C. longicuspidata*, *C. wangi*, *C. subcarinata*, *C. changxingensis*, *C. yini*, *C. meishanensis* and *C. zhejiangensis*). Yao *et al.* (2001) examined the conodont biostratigraphy in the Gujo-Hachiman section in Japan where the Lopingian radiolarian zones were established by Kuwahara *et al.* (1998). The first occurrence of *C. wangi* is placed at the horizon Gc-94 in their upper 'GD' section. This horizon is situated just above the first occurrences of *Neoalbaillella ornithoformis*, *N. grypa* and *N. gracilis* (Kuwahara *et al.* 1998; Yao *et al.* 2001). Thus, the base of *N. ornithoformis* Zone is just below the Wuchiapingian-Changhsingian boundary. Referred to this designation, the *N. ornithoformis* (except for the basal part) and *N. optima* zones are correlated with the Changhsingian. In the Changhsingian, Kuwahara *et al.* (1998) introduced the *Albaillella levis*, *A. flexa*, *A. excelsa* and *A. triangularis* Abundance zones, which are correlative to the upper *N. ornithoformis* Zone to the entire *N. optima* Zone.

Xia *et al.* (2004) proposed the *N. optima-Albaillella lauta*, *A. flexa-A. angusta*, *A. triangularis*, *A. yaoi*, *A. degradans*, and *A. simplex* subzones for the Changhsingian. The interval from the *N. optima-A. lauta* to the *A. yaoi* subzone is correlated with the *N. optima* Total Range Zone. The *A. degradans* and *A. simplex* Zones overlie the *N. optima* Zone. However, these two zones have never been recognized since their proposal. Takahashi *et al.* (2009) synonymized *A. degradans* and *A. simplex* with *A. triangularis* on the basis of preservation effects. Because no sections exist where identifiable radiolarians continuously occur across the Permian-Triassic boundary (PTB) (Feng & Algeo 2014), nothing is known about the exact fauna change across the boundary.

PERMIAN-TRIASSIC BOUNDARY: CRITICAL FAUNAL TURNOVER

Some studies argue that at the Permian-Triassic boundary (PTB) there is no evidence of any marked decline in radiolarian abundance or diversity (Yao 2009), whereas others establish an important drop in taxonomic richness, both at genus (Kiessling & Danelian 2011) and species level (Feng & Algeo 2014). Perhaps more remarkable is the major increase in biodiversity after the Permian-Triassic mass extinction event (De Wever *et al.* 2006) with radiolarians continuing to be an important group of organisms through Mesozoic then Cenozoic time.

It is appropriate to carefully consider the dating of radiolarian assemblages across PTB because "Permian radiolarians" are found in the Induan, whereas "Triassic genera" are recorded from the Changhsingian. The interval from the end-Permian to the earliest Triassic is an important faunal turnover from the Permian-type radiolarians to the Triassic-type radiolarians. High resolution biostratigraphic work as well as faunal analysis reveals the appearance of Triassic-type progenitors in the Changhsingian, the survival of the Permian-type radiolarians in the early Induan, and the demise of the Permian-type radiolarians in the early Olenekian (Kamata *et al.* 2007; Suzuki *et al.* 2007; Yamakita *et al.* 2007).

Radiolarians experienced mass extinction with double extinction steps at the end-Permian (Feng *et al.* 2007). In the Changhsingian, the Latentifistularia still evolved at the species level and radiolarians showed high species diversity. Triassic genera including *Paroertlispongus*, *Tetrapaurinella*, *Paurinella* and *Tamonella* also appeared as "progenitor taxa" (Feng *et al.* 2007; Maldonado & Noble 2010; Noble & Jin 2010). The first step was an extinction event at the species level and the next happened at the genus level. This extinction process is explained by different extinction steps in water of different depths. Just prior to the PTB, radiolarians living in deep-water such as the Albaillellaria were first decimated, then shallow-water radiolarians such as the Latentifistularia started to become extinct (Feng & Algeo 2014). Accumulation of radiolarian chert, which was continuously deposited since the Late Carboniferous in the low latitudinal Panthalassa Ocean was interrupted between the latest Changhsingian and the late Olenekian (Feng & Algeo 2014). By contrast, biogenic chert was continuously deposited in the Oruatemanu Formation at higher latitude in the southern Hemisphere (Suzuki *et al.* 2007; Yamakita *et al.* 2007). The Oruatemanu Formation records the replacement of the Paleozoic-type radiolarians by the Mesozoic-type ones between the conodont *Neospathodus dieneri* and *N. cristagallii* zones, corresponding to the middle late Induan (Hori *et al.* 2007). The lower Induan "Paleozoic-type" radiolarians include *Albaillella aotearoa*, *Hegleria*? *arrowrockensis*, *Trilonche*? *spoerlii* (*Entactinosphaera* in the original paper), *Oruatemanua triassica*, *O. primitiva*, *Hegleria mammilla*, *Triaenosphaera minuta*, and *Cauletella manica* (Takemura & Aono 2007). The discussion regarding "survivors" always involves considerations and caution regarding possible "reworking". No doubt arises with these assemblages because five of the eight species are limited to the lower Induan and together with one genus *Oruatemanua* evolved after the PTB. In turn, as *H. mammilla*, *T. minuta* and *C. manica* are common in the Changhsingian (Sashida & Tonishi 1985, 1988), their occurrences may indicate the lower Induan but not the true Permian. Similarly, Feng *et al.* (2007) documented that *Stigmosphaerostylus* (synonym of *Entactinia*), *Trilonche*, *Polyedroentactinia*, *Copicyntra*, *Hegleria* and *Uberinterna* are Lazarus taxa from the Permian.

CONCLUSIONS

Although further research will undoubtedly lead to refinement of the zonation discussed herein (see Appendix 1 for downloadable wall chart) we hope that this summary of the present state of knowledge on Paleozoic radiolarian biostratigraphy, and compilation of the stratigraphic ranges of selected genera and species (Figs 1-6) will prove useful to a wide range of geologists dealing with stratigraphic issues involving radiolarian-bearing rocks. The zonation appears to be broadly applicable to a wide range of marine lithologies including fine-grained shelfal limestones as well as deeper water cherts.

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APPENDIX

APPENDIX 1. — Downloadable Appendix: Wall chart showing Paleozoic zonation as it stands in July 2016. Calibration to Geological Time Scale of Ogg *et al.* (2016) made using TS Creator (https://engineering.purdue.edu/Stratigraphy/tscreator/).