Historical insights on nearly 130 years of research on Paleozoic radiolarians

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ABSTRACT
This paper summarizes and highlights the history of descriptive genus-level taxonomy on Paleozoic radiolarians grouped in five major phases: 1) initial discoveries in the 1890s; 2) ignored during the first half of the 1900s; 3) renewed interest during the 1950s to 1970s; 4) the "fast" years of the late 1970s to 1990s; and 5) the early 21st century quest for the oldest and significant progress in the late Permian. In the 1890s, radiolarians were identified with certainty by Hinde in Ordovician radiolar-

ian cherts. Following Hinde's great discovery, and after a 50-year dormant period, Deflandre revived the study of Paleozoic radiolarians through his groundbreaking study of *Albaillella* from Carboniferous phosphatic nodules, combined with his genius for understanding evolutionary implications. Additional important work was conducted in this third phase by Foreman, particularly with respect to the description of the radiolarian internal structures based on material extracted from Devonian carbonate nodules. The late 1970s saw an expansion in studies that made extensive use of the SEM for the description of Paleozoic radiolarians, many of which had been extracted from chert using HF methods. The potential of radiolarians to unveil the structure and geodynamic evolution of Paleozoic orogenic belts stimulated taxonomic interest during the 1980s and 1990s, a prerequisite for the elaboration of radiolarian biostratigraphic schemes, which was successfully achieved for the upper Paleozoic. The fifth phase follows the discovery of well-preserved Middle Cambrian radiolarians from Australia at the end of the 20th century and subsequent description by Won of beautifully preserved Cambrian and Ordovician fauna from western Newfoundland. Research on early Paleozoic radiolarians was the main driver for the increase of the number of new genera for the last two decades.

KEY WORDS
History of science,
Paleozoic,
radiolarians,
taxonomic analysis.

RÉSUMÉ

Regard historique sur presque 130 ans de recherches sur les radiolaires paléozoïques.

Ce travail synthétise l'histoire des études taxonomiques des radiolaires paléozoïques que l'on peut répartir en cinq phases majeures : 1) découvertes initiales durant les années 1890 ; 2) ignorés durant la première moitié du 20ème siècle ; 3) renouveau d'intérêt pendant les années 1950 à 1970 ; 4) les années glorieuses de la période 1970 à 1990 ; et 5) le début du 21ème siècle avec ses travaux sur les formes les plus anciennes, accompagnés de progrès importants pour le Permien supérieur. Pendant les années 1890, les premiers radiolaires ont été déterminés avec certitude par Hinde ; ils provenaient de radiolarites ordoviciennes. Suite à la grande découverte de Hinde, et après une période dormante de plus de 50 ans, Deflandre a réveillé l'intérêt de l'étude des radiolaires paléozoïques par son étude révolutionnaire du genre *Albaillella*, issu de nodules phosphatés du Carbonifère; son talent lui a aussi permis d'en déduire les implications évolutives. Un travail, également important, a été mené lors de cette troisième phase par Foreman, plus particulièrement avec la description des structures internes des radiolaires sur la base d'assemblages extraits de nodules carbonatés du Dévonien. La fin des années 1970 a enregistré un accroissement du nombre d'études grâce à l'utilisation généralisée du microscope électronique à balayage (MEB) pour décrire des radiolaires paléozoïques dont un grand nombre a été extrait de jaspes en utilisant l'acide fluorhydrique. Le potentiel des radiolaires pour dévoiler la structure et l'évolution géodynamique des ceintures orogéniques a stimulé l'intérêt pour la taxonomie durant les années 1980 et 1990, condition indispensable pour l'élaboration des échelles biostratigraphiques basées sur les radiolaires ; cela fut fait avec succès pour le Paléozoïque supérieur. La cinquième phase a commencé après la découverte de radiolaires bien préservés du Cambrien moyen d'Australie à la fin du 20e siècle et la description par Won, ultérieurement, de magnifiques faunes à radiolaires d'âge Cambrien supérieur à Ordovicien inférieur provenant de l'ouest de Terre Neuve. Les recherches sur les radiolaires du Paléozoïque inférieur furent donc le moteur principal de la description de nouveaux genres durant ces deux dernières décennies.

MOTS CLÉS
Histoire des sciences,
Paléozoïque,
radiolaires,
analyse taxonomique.

INTRODUCTION

Many studies have provided insights to the historical development of research on radiolarians (e.g. De Wever 1982; Ichikawa 1982; Zhamoida 1981; Nagai 1995; Wang 2001; De Wever *et al.* 2001; O'Dogherty *et al.* 2009) and they have recognized several distinct periods discussed below. The remarkable early taxonomic work of Haeckel (1887) provided a simple taxonomic framework. However, this study was largely based on external characteristics and geometry rather than biological concepts. The artificial character of this classification had the unintended consequence of misleading the scientific community into concluding that there was a high level of evolutionary conservatism in this important plankton group. The development of the Deep Sea Drilling Project (DSDP) during the 1960s and 1970s provided adequately complete material to establish that there was a great degree of evolutionary change that could be observed in the radiolarian fossil record. Most importantly, from the very onset of DSDP (Riedel 1967a; Riedel & Hays 1969; Riedel & Sanfilippo 1974) radiolarians provided critical evidence in support of the sea-floor spreading hypothesis that played a crucial role in establishment of the theory of plate tectonics. The impetus provided by DSDP drove new radiolarian studies and the taxonomic focus shifted progressively towards closer examination of most internal elements and structures of the test, finally breaking free of the constraints imposed by Haeckel's scheme. During the 1970s, the extensive use of the Scanning Electron Microscope (SEM) and the development of the hydrofluoric acid method for the extraction of radiolarians from cherts provided an abundance of matrix free material and the means to study their fine structure. The establishment of increasingly elaborate biostratigraphic schemes stimulated the interest of the scientific community for taxonomic studies. At the same time realization that radiolarians could be extracted from deep sea cherts, and that they held the key to unlocking the stratigraphy of subduction complexes, associated with the newly recognized convergent plate margins gave rise to the radiolarian revolution (Irwin *et al.* 1977; Ishigaki & Yao 1982). This was pioneered by researchers such as Pessagno in North America (Pessagno 1976, 1977a, b), Nakaseko and Yao in Japan (e.g. Nakaseko & Nishimura 1979; Yao *et al.* 1980) and De Wever (1982) and Baumgartner (1984) in Europe. Aware of the work on late Paleozoic radiolarians that was being carried out by Brian Holdsworth from Keele University, Davey Jones of USGS saw the potential for application of Paleozoic radiolarian biostratigraphy amongst the accretionary terranes of the western US and Alaska (Holdsworth & Jones 1980).

As we will see in the text below, the same overall picture also holds true for the historical trajectory of studies on Paleozoic radiolarians, as this may be perceived through an analysis of the number of new genera defined yearly (see also the inventory of Paleozoic species, Aitchison *et al.* 2017b). Our revision of the status of Paleozoic genera (see Caridroit *et al.* 2017; Noble *et al.* 2017) takes into account a total of 344 radiolarian genera, for which only 208 (60.5%) are considered as valid (see Table 1 and Fig. 1). 82 of them (23.8%) are regarded as junior synonyms, 35 as *nomina dubia* (10.2%), 2 as *nomina nuda* (0.6%), 7 genera (2%) are homonyms, most of the previously homonym names being already replaced, and 10 of them are "not Radiolaria" (2.9%).

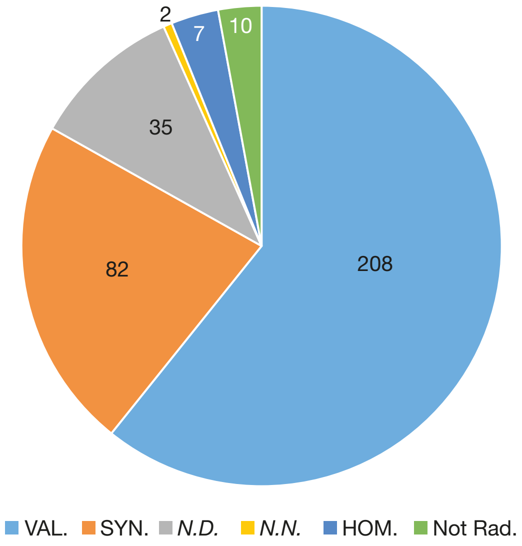

FIG. 1. — Pie chart showing the percentage distribution of 344 Paleozoic genera based on their current taxonomic status: **VAL.**, valid, 208 genera, 60.5%; **SYN.**, junior synonyms, 82 genera, 23.8%; ***N.D.***, *nomina dubia*, 35 genera, 10.2%; ***N.N.***, *nomina nuda*, 2 genera, 0.6%; **HOM.**, homonyms, 7 genera, 2%; **Not Rad.**, not radiolaria, 10 genera, 2.9%.

THE GREAT DISCOVERIES OF THE 1890s

The first Paleozoic radiolarian genera were defined by Hinde (1890) on the basis of material from the Southern Uplands (Scotland, United Kingdom). The presence of radiolarians in these Ordovician cherts was previously announced by Prof. Nicholson of Aberdeen (Nicholson 1889). However, the specimens that he had shown were not convincing for the scientific community. A year later, Hinde (1890) introduced six new genera based on observations made from thin sections of cherts that were collected by Peach during the geological mapping of Scotland. This was a groundbreaking study as it established for the first time that radiolarians existed since the early Paleozoic. Nearly 100 years afterwards, Danelian & Clarkson (1998), Danelian (1999) and Danelian & Floyd (2001) succeeded in extracting matrix-free specimens from cherts of the Southern Uplands and attempted to link them to the forms described initially by Hinde.

Hinde (1899a, b) also published two important works on Devonian radiolarians from the Tamworth Belt in northeastern New South Wales, Australia and Cornwall in England. These radiolarians were all described from thin sections. The New South Wales material was collected by T. W. Edgeworth David (David 1897) and remained in the collections of the University of Sydney for many years. The original thin section blocks were processed to extract matrix-free specimens, which together with the original thin sections are housed in the Museum of Natural History, London, approximately 100 years later (Aitchison & Stratford 1997).

Hinde's genus *Trilonche* is an important and abundant component of mid and late Paleozoic assemblages. Regrettably, due in part to the limitations of working with material in thin-section, most of the other genera introduced by Hinde (1890, 1899a, b) are now considered as *nomina dubia* and two of them as junior synonyms of *Trilonche* (see Aitchison & Stratford 1997; Caridroit *et al.* 2017; Noble *et al.* 2017).

IGNORED FOR OVER 50 YEARS DURING THE FIRST HALF OF THE 20TH CENTURY

As can be seen in Figure 2, with the exception of a single genus (*Carposphaeridium*) defined by Chapman in 1923, few taxonomic advances were made on Paleozoic radiolarian studies during the first half of the 20th century. The lack of interest amongst the scientific community was possibly compounded by misunderstanding introduced by the uncritical application of the Haeckelian taxonomy, inspired essentially by the study of living forms, to the group's fossil representatives. This was amplified by the "juristic" application by Campbell (1954) of "Copenhagen's Rules of 1953", the basis of the first International Code of Zoological Nomenclature (Hemming 1957). A critical commentary of this problem is presented by Deflandre (1960).

TABLE 1. — Yearly number of new valid/invalid Paleozoic genera introduced since 1890. Abbreviations: **SYN.**, junior synonyms; ***N.D.***, *nomina dubia*; ***N.N.***, *nomina nuda*; **HOM.**, homonyms.

Year	**VALID**	**INVALID**	**Total**	**SYN.**	***N.D.***	***N.N.***	**HOM.**	**Not Radiolaria**
1890	–	6	6	–	6	–	–	–
1891	–	–	–	–	–	–	–	–
1892	1	–	1	–	–	–	–	–
1893	–	–	–	–	–	–	–	–
1894	–	–	–	–	–	–	–	–
1895	–	–	–	–	–	–	–	–
1896	–	–	–	–	–	–	–	–
1897	–	–	–	–	–	–	–	–
1898	–	–	–	–	–	–	–	–
1899	1	4	5	2	2	–	–	–
1900	–	–	–	–	–	–	–	–
1901	–	–	–	–	–	–	–	–
1902	–	–	–	–	–	–	–	–
1903	–	–	–	–	–	–	–	–
1904	–	–	–	–	–	–	–	–
1905	–	–	–	–	–	–	–	–
1906	–	–	–	–	–	–	–	–
1907	–	–	–	–	–	–	–	–
1908	–	–	–	–	–	–	–	–
1909	–	–	–	–	–	–	–	–
1910	–	–	–	–	–	–	–	–
1911	–	–	–	–	–	–	–	–
1912	–	–	–	–	–	–	–	–
1913	–	–	–	–	–	–	–	–
1914	–	–	–	–	–	–	–	–
1915	–	–	–	–	–	–	–	–
1916	–	–	–	–	–	–	–	–
1917	–	–	–	–	–	–	–	–
1918	–	–	–	–	–	–	–	–
1919	–	–	–	–	–	–	–	–
1920	–	–	–	–	–	–	–	–
1921	–	–	–	–	–	–	–	–
1922	–	–	–	–	–	–	–	–
1923	–	1	1	–	1	–	–	–
1924	–	–	–	–	–	–	–	–
1925	–	–	–	–	–	–	–	–
1926	–	–	–	–	–	–	–	–
1927	–	–	–	–	–	–	–	–
1928	–	–	–	–	–	–	–	–
1929	–	–	–	–	–	–	–	–
1930	–	–	–	–	–	–	–	–
1931	–	–	–	–	–	–	–	–
1932	–	–	–	–	–	–	–	–
1933	–	–	–	–	–	–	–	–
1934	–	–	–	–	–	–	–	–
1935	–	–	–	–	–	–	–	–
1936	–	–	–	–	–	–	–	–
1937	–	–	–	–	–	–	–	–
1938	–	–	–	–	–	–	–	–
1939	–	–	–	–	–	–	–	–
1940	–	–	–	–	–	–	–	–
1941	–	–	–	–	–	–	–	–
1942	–	–	–	–	–	–	–	–
1943	–	–	–	–	–	–	–	–
1944	–	–	–	–	–	–	–	–
1945	–	–	–	–	–	–	–	–
1946	–	–	–	–	–	–	–	–
1947	–	–	–	–	–	–	–	–
1948	–	–	–	–	–	–	–	–
1949	–	–	–	–	–	–	–	–
1950	–	–	–	–	–	–	–	–
1951	–	–	–	–	–	–	–	–
1952	1	–	1	–	–	–	–	–
1953	2	–	2	–	–	–	–	–
1954	–	–	–	–	–	–	–	–
1955	–	–	–	–	–	–	–	–
1956	–	–	–	–	–	–	–	–
1957	–	–	–	–	–	–	–	–
1958	1	–	1	–	–	–	–	–
1959	–	–	–	–	–	–	–	–
1960	–	2	2	–	–	2	–	–
1961	–	–	–	–	–	–	–	–
1962	–	–	–	–	–	–	–	–
1963	8	1	9	1	–	–	–	–
1964	1	–	1	–	–	–	–	–
1965	–	–	–	–	–	–	–	–
1966	–	3	3	–	3	–	–	–
1967	–	–	–	–	–	–	–	–
1968	–	–	–	–	–	–	–	–
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–	–
1972	7	1	8	1	–	–	–	–
1973	6	5	11	1	3	–	–	1
1974	–	1	1	–	1	–	–	–
1975	2	5	7	4	1	–	–	–
1976	3	2	5	1	–	–	–	1
1977	–	2	2	–	–	–	–	2
1978	1	–	1	–	–	–	–	–
1979	1	1	2	–	1	–	–	–
1980	4	2	6	2	–	–	–	–
1981	6	4	10	4	–	–	–	–
1982	–	–	–	–	–	–	–	–
1983	8	7	15	5	1	–	1	–
1984	8	4	12	3	–	–	1	–
1985	10	2	12	2	–	–	–	–
1986	13	10	23	10	–	–	–	–
1987	1	4	5	–	–	–	–	4
1988	5	2	7	2	–	–	–	–
1989	6	13	19	13	–	–	–	–
1990	9	6	15	5	1	–	–	–
1991	1	2	3	1	1	–	–	–
1992	2	1	3	–	1	–	–	–
1993	3	7	10	3	3	–	–	1
1994	8	3	11	3	–	–	–	–
1995	3	4	7	1	3	–	–	–
1996	5	1	6	1	–	–	–	–
1997	10	5	15	3	1	–	1	–
1998	4	4	8	3	–	–	1	–
1999	7	2	9	2	–	–	–	–
2000	10	9	19	5	2	–	2	–
2001	–	1	1	1	–	–	–	–
2002	5	2	7	2	–	–	–	–
2003	1	–	1	–	–	–	–	–
2004	2	–	2	–	–	–	–	–
2005	2	–	2	–	–	–	–	–
2006	7	1	8	–	–	–	1	–
2007	11	1	12	1	–	–	–	–
2008	1	5	6	–	4	–	–	1
2009	5	–	5	–	–	–	–	–
2010	3	–	3	–	–	–	–	–
2011	2	–	2	–	–	–	–	–
2012	1	–	1	–	–	–	–	–
2013	–	–	–	–	–	–	–	–
2014	1	–	1	–	–	–	–	–
2015	7	–	7	–	–	–	–	–
2016	2	–	2	–	–	–	–	–

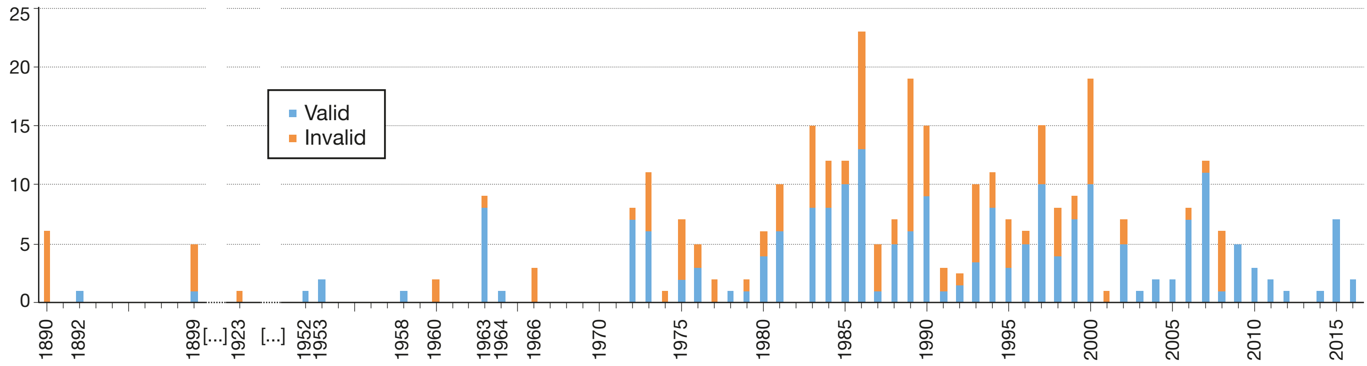

FIG. 2. — Number of new Paleozoic genera introduced yearly since 1890.

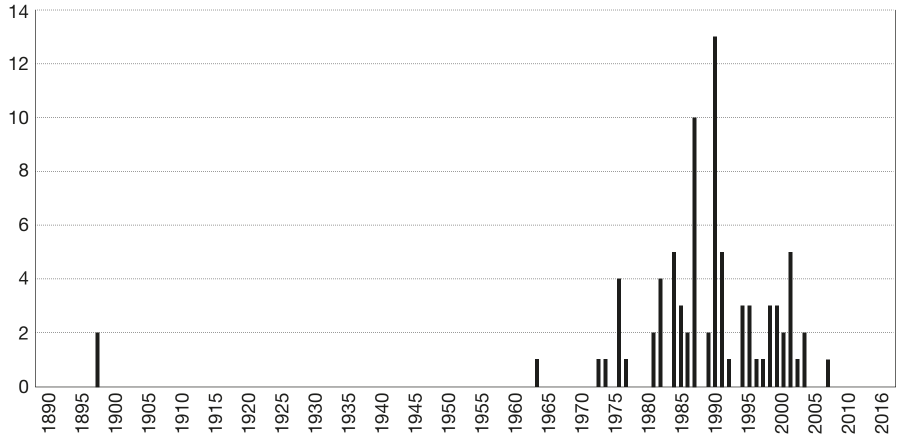

FIG. 3. — Number of synonymised new Paleozoic genera introduced yearly.

1950s TO MID 1970s: THE TIME OF RENEWED INTEREST

In 1952, Deflandre introduced a carefully defined new genus *Albaillella*, which he immediately recognized as a distinct Carboniferous form unknown from post-Paleozoic sediments and understood the importance of its evolutionary implications. The history behind this discovery is well-described by Caulet (2013). Mr. Albaille, a winemaker from the Montagne Noire area of southern France, whose hobby was Natural History, sent some nodules to the Muséum national d'Histoire naturelle in Paris in order to learn more about their composition. Deflandre, who had been appointed at the Museum since 1930, examined these nodules. The siliceous microfossils that he found in them prompted him in 1940 to pay a visit to Mr Albaille to obtain a better material. In 1946 he mentioned the discovery of these "unknown" creatures in a short communication of the *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences (Paris)*. It was not until 1952 that he formally described the type species of *Albaillella*.

During the period between 1952 and 1973, Deflandre defined 23 new genera as a single author (Deflandre 1952, 1953, 1958, 1960, 1963, 1964, 1972, 1973a, b, c, d) and three others with Ters (Deflandre & Ters 1966). The majority of them are still considered to be valid and a good number of them are amongst the most important clades of late Paleozoic radiolarians (e.g. *Albaillella*, *Ceratoikiscum*, *Palaeoscenidium*, *Lapidopiscum*, *Pylentonema* and *Popofskyellum*).

Other important contributions to radiolarian genera were made during this period by Brian Holdsworth and Helen Foreman. Although not introducing new genera, important studies by Holdsworth (1966, 1969a, b) on age-correlative strata in England confirmed the widespread occurrence and potential of late Paleozoic radiolarians. In 1959, Helen Foreman reported on the potential of Upper Devonian carbonate nodules from the Ohio Shale to yield a well-preserved radiolarian fauna, from which she later defined eight new genera (Foreman 1963). She paid particular attention to their most internal structures, keeping thus a distance from Haeckelian philosophy of taxonomic classification and adhering to Deflandre's approach.

Around the time of Foreman's work significant contributions at a suprageneric taxonomic level were made. More particularly, the higher-level classification of some radiolarian families by Riedel (1967b) and Petrushevskaya (1971) had a significant contribution to undoing the constraints set by Haeckel and saw the introduction of two important Paleozoic families, the Entactiniidae and Palaeoscenidiidae.

Meanwhile, Boris Nazarov was making significant contributions to radiolarian studies in the USSR, working on materials from throughout the Paleozoic time scale. Initially, his work in Kazakhstan was made on materials from thin section

(Nazarov 1975a, b), but later work discussed below, especially in partnership with Alan Ormiston, lead to re-analysis of matrix-free material.

LATE 1970s TO 1990s: THE "FAST" YEARS

The discovery and description in the early 1970s of the dilute hydrofluoric acid (HF) method to extract radiolarians from cherts (Dumitrica 1970; Pessagno & Newport 1972) opened up the potential for radiolarians to be developed as a valuable biostratigraphic tool for radiolarian chert sequences that commonly occur in complex orogenic zones. During the 1970s, Scanning Electron Microscopes (SEM) became progressively available in geological/paleontological laboratories. Consequently, the common use of the SEM during the late 1970s and early 1980s has had a profound impact on the taxonomic study of Paleozoic radiolarians, in the same way as it has had for the Mesozoic ones. Thus, following the widespread use of the HF method to extract radiolarians from cherts and the routine use of the SEM for the description of their minute structural details, the main driver to conduct taxonomic research on Paleozoic radiolarians was the development of their biostratigraphic potential (see Aitchison *et al.* 2017a). In Japan, HF methods were independently introduced for conodont research (Hayashi 1968) and since 1967 Yao had managed to extract radiolarians with the use of HF from "Paleozoic" cherts (see Ishigaki & Yao 1982: 97), although they all turned out to be Mesozoic in age. Thus, the first occurrence report of Paleozoic radiolarians from Japan with an SEM image was delayed until Takemura (1980) in which an illustration of a future "*Neoalbaillella*" was included.

During the 1970s and 80s, Nazarov in the USSR and Ormiston in the USA played an important role in Paleozoic radiolarian taxonomy, by describing biostratigraphically useful assemblages from the Ordovician through the Permian. Importantly, they established that some of these assemblages were geographically widespread. Nazarov (1973, 1974, 1975b, 1977) and Nazarov & Popov (1976, 1980) introduced fifteen new genera based on type material coming from Kazakhstan and other parts of the former Soviet Union. His monograph on all the valid Paleozoic genera (Nazarov 1988) remains an important reference with this work providing SEM images of many of his genera. He carefully drew the internal structure of many of them, although they are often difficult to observe in his assigned type species. Only three out of the 15 new genera mentioned above are here considered as valid (see Caridroit *et al.* 2017; Noble *et al.* 2017); four are treated as *nomina dubia*, four others as junior synonyms and finally four are now considered to be parts of sponges (*Azyrtalia*, *Konyrium*, *Anakrusa* and *Auliela*; see Won *et al.* 2007). Following the study of Ormiston & Lane (1976), Nazarov & Ormiston worked together in the 1980s (Nazarov & Ormiston 1983a, b, 1985, 1986, 1987), and finally in the posthumous paper (Nazarov & Ormiston 1993), which reviewed many of his career contributions in a biostratigraphic context, and added new genera. Nazarov did not treat middle to upper Permian radiolarians. In practice, Permian radiolarian studies were made possible after the definition of several middle Permian genera such as *Follicucullus* and *Pseudoalbaillella* (Ormiston & Babcock 1979; Holdsworth & Jones 1980), and the middle-late Permian *Neoalbaillella*, which was described from cherts of the Jurassic accretionary complex of Japan (Takemura & Nakaseko 1981).

The 1980s saw an upsurge of new genera introduced owing largely to the wide use of the HF acid method for extracting radiolarians from cherts and the routine use of the SEM for description of their minute structural details. Thus, most descriptive taxonomy papers were made in the context of improving the biostratigraphic resolution of radiolarians (e.g. Ishiga *et al.* 1982a, b; Cheng 1986, De Wever & Caridroit 1984). More particularly, based on upper Permian material from the Kamigori belt of SW Japan, De Wever & Caridroit (1984) defined six new Latentifistularian genera. In the same year Nazarov & Ormiston (1984) defined six other genera, including the important spumellarians *Inanigutta* and *Inanihella* and the archaeospicularian genus *Secuicollacta*.

An all-time high is recorded in 1986 (Fig. 2) when 23 new genera were formally defined in the literature. However, nearly half of them (10) are now considered as junior synonyms (see Figure 3 and Caridroit *et al.* 2017; Noble *et al.* 2017). Most of the new genera introduced in 1986 come from the upper Paleozoic sequences of Oklahoma, such as the 12 genera defined by Cheng (1986) from Upper Devonian to Carboniferous material, although six of them are now regarded as junior synonyms. Three additional new genera were defined ten years later based on material from the same rock succession (Schwartzapfel & Holdsworth 1996). The study published by Kozur & Mostler (1989) also represents a substantial contribution towards Lower Permian radiolarian taxonomy; however, out of the nineteen new genera defined by these authors, thirteen are now considered as junior synonyms (see Figure 3 and De Wever *et al.* 2001; Caridroit *et al.* 2017; Noble *et al.* 2017). In the words of Dumitrica & Aita (2017) Kozur and Mostler were "great splitters, producing thus a large number of synonyms".

Work lower in the timescale, particularly on Ordovician through Middle Devonian assemblages, was underway in the 1980s and 1990s. Unique palaeosceniid genera with a cortical shell (*Pactarentactinia* and *Tlecerina*) were defined based on material from the Lower Devonian Nakahata Formation of the Kurosegawa terrane (Japan; Furutani 1983). Seven new upper Silurian and Lower Devonian genera were further defined from the Yoshiki and Hitoegane Formations of the Hida-gaien Belt (Furutani 1990) and four others from the Yokokurayama Group (Wakamatsu *et al.* 1990). With the exception of *Nazaromistonella* all these genera are still regarded as valid. In addition to occurrences in Japan, they have been found also in North America and Europe.

The late 1980s and 90s saw also the introduction of the genus *Protoceratoikiscum*, defined based on material extracted from Ordovician cherts of the Lachlan Fold Belt (eastern Australia; Goto *et al.* 1992), the Late Ordovician genus *Kalimnasphaera* (Webby & Blom 1986) and the Early Ordovician genus *Beothuka* from Newfoundland (Aitchison *et al.* 1998). The lower Paleozoic family Proventocitidae was established by Aitchison (1998) based on material reported from Scotland, Spitsbergen and Russia (the original spelling Proventocitiidae, which applied an incorrectly formed suffix was corrected to Proventocitidae in De Wever *et al.* 2001).

In North America, eleven new Silurian genera were introduced based on material extracted from carbonate nodules of the Canadian Archipelago (Goodbody 1986; Mac Donald 1998, 1999, 2006; Jones & Noble 2006) and six others by Noble (1994) from the Marathon uplift in west Texas. Working at the same time on similar Devonian-aged rocks but on different continents, Aitchison (1993) and Feng & Liu (1993) introduced *Paraholoeciscus* and *Eoalbaillella*, respectively and synonyms thereof. In detailed studies of exceptionally well preserved material from the Upper Devonian Gogo Formation of Western Australia Won (1997a, b) introduced a total of 20 new genera. By the mid 1980s, the SEM was routinely used in micropaleontological studies in China and gave the opportunity to define new genera based on material from Permian (Sheng & Wang 1985; Feng & Liu 1993; Wang 1995), as well as Ordovician and Silurian strata (Li 1994, 1995). However, the quality of images provided was sometimes unsatisfactory and made evaluation of their taxonomic validity difficult (e.g. *Longtanella*).

THE EARLY 21ST CENTURY QUEST FOR THE OLDEST AND SIGNIFICANT PROGRESS IN THE LATE PERMIAN

The description by Won & Below (1999) of well-preserved Middle Cambrian radiolarians from Australia, in which they defined six new genera, created the perception of a wide breadth of distinct structural features of primitive radiolarians and help us discard controversial material from China (Maletz 2017). Subsequent description by Won & Iams (2002) of upper Cambrian radiolarians from western Newfoundland was equally paramount, as the pelagic limestones of the Cow Head Group have become a key for understanding the radiolarian evolution and faunal changes throughout the Late Cambrian-Early Ordovician interval (Won *et al.* 2005, 2007; Pouille *et al.* 2014). Generally speaking, interest in the early Paleozoic diversity and evolution of radiolarians was the main driver for the increase of the number of new radiolarian genera for the last two decades. Amongst the 68 valid genera defined since 1999, thirty six of them concern Cambrian and Ordovician radiolarians (Aitchison *et al.* 1998; Won & Below 1999; Obut & Iwata 2000; Won & Iams 2002, 2011, 2015; Danelian & Popov 2003; Maletz & Bruton 2005, 2007; Won *et al.* 2005, 2007).

This century has also seen continuing work on Devonian radiolarians with Afansieva and colleagues describing various genera that mostly come from the well-preserved faunas recovered from the Domanik-facies in Russia (e.g. Afanasieva 2000).

Interest in improving our understanding of the radiolarian biotic response during the Permian-Triassic mass extinction event has stimulated high quality taxonomic research on late Permian radiolarians. Until the turn of the 20th century, Permian radiolarian genera were often defined based on faunas that were generally of medium to poor preservation. More recently, extremely well-preserved radiolarians have been described and illustrated from the uppermost Permian Dalong Formation in South China (Feng *et al.* 2004, 2006a, b, 2007a, b), with special attention being paid to adequate documentation and illustration of their internal structure. Thus, the genus level taxonomy of Latentifistularian radiolarians was revised based on observations on well-preserved specimens (Feng *et al.* 2007b). This century is expected to allow the development of a classification system that better reflects natural phylogenetic relationships.

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