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PART V, SECOND REVISION, CHAPTER 7: BIOSTRATIGRAPHY

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BIOSTRATIGRAPHY AND THE FOSSIL RECORD OF THE HEMICHORDATA

It is now accepted that the Hemichordata are likely to have originated during the late Precambrian to early Cambrian (Fig. 1), given that the fossil record indicates a presence of pterobranchs as early as the Fortunian (basal Cambrian), with the possible rhabdopleurid *Sokoloviina costata* (Kirjanov, 1968) discovered in the Ukraine (Maletz, 2019). However, early Cambrian records of Pterobranchia are rare, and it isn't until the upper Cambrian (Series 2, Stage 4) and the Miaolingian (Wuliuan) (Fig. 1) that a better fossil record became available, following the discovery of the first Enteropneusta fossils in the Burgess Shale in Canada (Caron, Conway Morris, & Cameron, 2013).

The fossil record of the Enteropneusta is limited to very few specimens and few localities in the Palaeozoic to Mesozoic. The described fossil taxa have been incorporated into the taxonomic scheme and, in part, are referred to extant groups (Cameron, 2018). The early genera *Oesia* Walcott, 1911 and *Spartobranchus* Caron, Conway Morris, & Cameron, 2013 are included in a stem group.

The Cambrian record of the Pterobranchia is of interest largely for taxonomy and evolutionary studies, but the planktic Graptolithina represent one of the most important fossil groups of the Paleozoic for biostratigraphical dating of rock sequences. Their origin close to the base of the Ordovician System (Cooper, Nowlan, & Williams, 2001; Wang & others, 2019) can be regarded as one of the major evolutionary events in the history of life on planet Earth and marks the onset of the evolution of planktic macro-organisms. The extinction of the planktic graptoloids during the early Devonian was a slow process. The reason for this remains unexplored but may be related to the emergence of plankton feeders in the world's oceans (Maletz, 2017). This chapter focuses on the interval of biostratigraphical use of the Graptolithina and does not discuss the sparse younger fossil record of the Hemichordata.

GRAPTOLITE BIOSTRATIGRAPHY

As early as 1850, Hall estimated that graptolites, although at that time poorly known, were valuable for identifying certain geological periods. Thus, Hall's 1850 study might be regarded as the starting point of graptolite biostratigraphy, even though at the time few graptolite species had been described, and a precise biostratigraphical use was not yet possible. In the same year, Barrande (1850) indicated the practical biostratigraphic use of the Silurian graptolite faunas in the Barrandean region. Nicholson (1868) provided the first chart showing the distribution in time (biostratigraphic distribution, in modern terms) of graptolite faunas in Britain. It was, however, the impact of Lapworth's (1878) influential study on the Moffat Series that established graptolites as a prime fossil group for biostratigraphy

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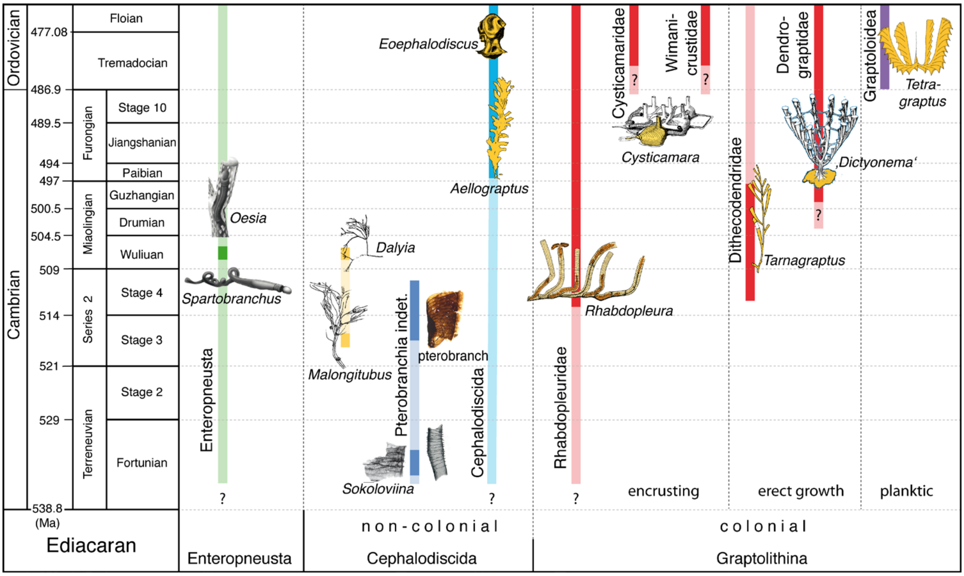

FIG. 1. The Cambrian fossil record of the Enteropneusta and Pterobranchia (Hemichordata) (adapted from Maletz, 2019, fig. 3).

and relative dating of rock sequences of the Paleozoic (FORTEY, 1993).

Inevitably, mistakes are made in science, and it has occurred in the interpretation of graptolite biostratigraphy. One of the most glaring examples may be the record of supposed Ordovician graptolites on a small island in the South Orkney Island complex of Antarctica (DALZIEL, 1979). Fossil material from the island, now called Graptolite Island, was initially identified as Ordovician graptolites by GERTRUDE ELLES and published by PIRIE (1905), leading to considerable problems for the interpretation of the geology of the region. The fossils were later identified as possible Carboniferous plant material (STRACHAN in ADIE, 1957, p. 22), but the name of the island still exists and is present today on Google Earth. The geological map of the South Orkney Islands shows a Carboniferous to Triassic age of the Greywacke Shale Formation, but paleontological data are poor, and the dating is based on Triassic radiolarians from the Weddell Islands to the northwest (FLOWERDEW, RILEY, & HASELWIMMER, 2011). This example shows how important precise identification of fossil material is.

Currently used graptolite biozones are often quite different from those first developed during the late 19th and early 20th centuries. Scientists most commonly use the concept of the First Appearance Datum (FAD) to define the base of a fossil biozone, which in general is a local level and may not represent the worldwide first appearance of a taxon. This is especially noticable in the definitions of chronostratigraphic units based on graptolites. There are now 13 out of 16 stage boundary levels from the base of the Ordovician System to the base of the Devonian System that are defined by the level of the FAD of a particular graptolite species in a certain section (OGG, OGG, & GRADSTEIN, 2016). Absolute dates for the following charts (Fig. 2–7) are generally taken from GRADSTEIN and others, 2020, which represents the latest available information. Dates have changed considerably over the years as a result of new information. Details are available from the website of the International Commission on Stratigraphy (https://stratigraphy.org), The website also includes uncertainty intervals of radiometric dates.

Numerous biostratigraphic range charts have been published over the years, many of them providing local biozones, but general overviews are rare. Elles and Wood (1914) tabulated the biostratigraphic ranges of all graptolites known at the time from Britain in 36 graptolite zones, preceded only by the succession of Lapworth (1880), which counted 20 zones. This initially local (British) Elles and Wood biozonation became a worldwide standard and was used unchanged for more than 60 years until Rickards (1976) and later Zalasiewicz and others (2009) revised the British standard biozonation and counted 60 biozones and subzones leading up to the middle Ludlow. Younger graptolite zones were not recognized in Britain. Bulman (1955, fig. 5) provided a chart in *Treatise,* Part V showing the stratigraphic distribution of the main groups of graptolites and later added graptolite biozonal schemes for Britain and Australia as a guideline to the graptolite biostratigraphy in the second edition of *Treatise,* Part V (Bulman, 1970). Unified international biostratigraphies are difficult to construct due to the biogeographic differentiation of many faunas (e.g., Goldman & others, 2013), but a generalized graptolite zonal sequence for the Silurian was proposed by Jaeger (1991) and Koren' and others (1995, 1996). A standard graptolite biozonation may also be used for the Lower Devonian, as the faunas of this time interval are fairly monotonous (Jaeger, 1978, 1988; Lenz, 2013).

A number system was introduced in Germany by Eisel (1899), based on the succession of Lapworth (1880, table 11–12), but slightly different index species were employed (Eisel, 1903). This scheme was still used by Münch (1952) in his overview on Silurian graptolites of Germany, but Jaeger (1991) used and adjusted the succession of Elles and Wood (1914) for the German Silurian and indicated a number of intervals not covered in their scheme. Maletz (2001) suggested abandoning the number system in Germany, following Rickards (1995, p. 133) and advocated using only index species for the biozonation.

The graptolite biozonation presented here is largely based on the excellent compilation of Loydell (2012), including additional references in his figure captions. New information needing to be incorporated is reflected herein.

ORDOVICIAN

According to Goldman, Sadler, and Leslie (2020), the Ordovician System (Lapworth, 1879) is approximately 43.78 Ma long (486.85–443.07 Ma), including three series, the Lower Ordovician (15.59 Ma), the Middle Ordovician (13.08 Ma), and the Upper Ordovician (15.11 Ma), of which the middle one is somewhat shorter. The three series include seven stages, highly uneven in length. The Darriwilian Stage (458.18–469.42 Ma) is the longest stage at approximately 11.24 Ma, and the Hirnantian (443.07–445.21 Ma) is the shortest at only about 2.14 Ma, including two graptolite zones (note, the precise radiometric ages may differ considerably based on the source used). Gradstein and others (2012, 2020) is used for all units discussed here, but numbers may change in the future (compare with Cooper & Sadler; 2012; Ogg, Ogg, & Gradstein, 2016).

The (informal) Ordovician stage slices of Bergström and others (2009) are not correlated herein. They were introduced as defined chronostratigraphical units, based on biostratigraphical data and explained to have "potential for precise correlations in both carbonate and shale facies" (Bergström & others, 2009, p. 97). They were used to correlate the $\delta^{13}C_{org}$ curve to the chronostratigraphy. These stage slices should not be confused with the time slices in Webby and others (2004), a term created to provide a precise key to correlate biostratigraphic intervals based on various fossil groups. The individual intervals were estimated to be between 1.6 and 2.5 Ma long.

THE LOWER ORDOVICIAN

The Lower Ordovician includes the Tremadocian and Floian stages (Fig. 2). The base of the Ordovician System and the Tremadocian Stage is defined at the level of the FAD of the conodont *Iapetognathus fluctivagus* Nicoll & others, 1999 (Cooper, Nowlan, & Williams, 2001; Terfelt, Bagnoli, & Stouge, 2012; Wang & others, 2019, 2020). The occurrence of *Rhabdinopora* Eichwald, 1855 is often more easily recognized in dark shale in basal Ordovician strata (Henningsmoen, 1973; Bassett & Dean, 1982; Norford, 1982, 1988), although the FAD of *Rhabdinopora* occurs at a level slightly higher than the Global Stratotype Section and Point (GSSP) level. The biozones in the Australasian succession are named by index species, but their widely known and commonly used zonal notations are not shown here (Fig. 2–4). See VandenBerg and Cooper (1992) and Percival, Quinn, and Glen (2011) for details and full biozonal names.

The base of the Floian Stage is defined at the level of the FAD of *Paratetragraptus approximatus* (Nicholson, 1873) in the Diabasbrottet section, Västergötland, Sweden (Bergström, Löfgren, & Maletz, 2004; Bergström & others, 2006). This level is equivalent to the level of the FAD of the common Scandinavian graptolite *Tetragraptus phyllograptoides* Strandmark, 1902. The name *Tetragraptus phyllograptoides* Biozone is usually used to identify the interval in Scandinavia (Baltica) and South America (Egenhoff, Maletz, & Erdtmann, 2004; Toro & others, 2015).

Maletz, Egenhoff, and Alonso (2010) and Maletz and Ahlberg (2018) published the latest biozonation for the Tremadocian to early Darriwilian of Baltica, representing one of the most complete successions known (Fig. 2). Maletz, Egenhoff, and Alonso (2010), following Maletz and Egenhoff (2001), identified a local *Kiaerograptus stoermeri* Biozone beneath the *Kiaerograptus supremus* Biozone of Lindholm (1991), which is not indicated in the chart (Fig. 2), because it has been identified in only a single section. Zalasiewicz and others (2009) discussed the graptolite biostratigraphy of Britain and listed the known faunas of the Lower Ordovician. Maletz and Ahlberg (2011, fig. 8) provided a correlation of the British succession to the Scandinavian succession, showing that the British graptolite succession is fairly incomplete, and some intervals are not documented by fossil faunas (Fig. 2). Zhang and others (2019) provided the latest overview on the Ordovician graptolite biostratigraphy of China as a combination of the North China platform and the Yangtze Region. The North China succession starts with the *Rhabdinopora proparabola* interval (Fig. 2) but is not known with certainty from other regions of China (Wang & others, 2019).

The basal Ordovician (early Tremadocian) and the Floian intervals of the North American succession are best known from western Newfoundland (Williams & Stevens, 1988; Cooper, Nowlan, & Williams, 2001), but the late Tremadocian to early Floian succession of Yukon Territory, Canada (Jackson & Lenz, 2003, 2006) is a more detailed succession of *Paradelograptus* Erdtmann, Maletz, & Gutiérrez Marco, 1987 species used to subdivide the latest Tremadocian strata. Williams and Stevens (1991) recognized only the *Aorograptus victoriae* Biozone in the late Tremadocian of western Newfoundland, which is probably correlatable with the *Kiaerograptus kiaeri* interval of Baltica (Maletz, 1999).

Lower Ordovician successions are widely distributed in South America and have been described in some detail from Bolivia and Argentina (Maletz & Egenhoff, 2003; Egenhoff, Maletz, & Erdtmann, 2004; Toro & others, 2015). They have been correlated with the Scandinavian successions by Maletz and Ahlberg (2011). Albanesi and Ortega (2016) discussed the Ordovician successions of Argentina and provided the latest information on the graptolite biostratig-

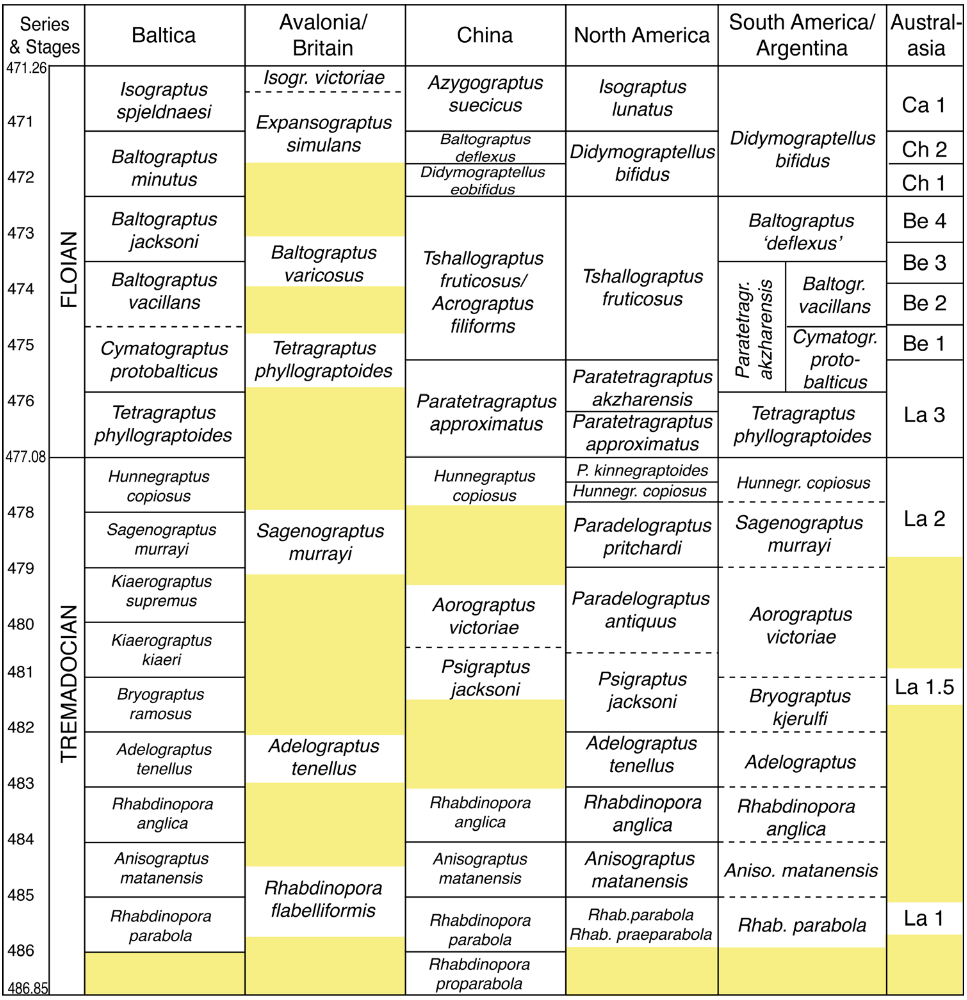

FIG. 2. Correlation of Lower Ordovician graptolite biozones. Yellow intervals indicate possible gaps (not recognized faunal intervals) in the successions.

raphy (Fig. 2–4), showing distinct differences between the Argentinian Precordillera and the Gondwanan part of South America. In the eastern Cordillera of Argentina, a differentiation of the *Tetragraptus akzharensis* Biozone into two subzones, *Cymatograptus protobalticus* and *Baltograptus vacillans* biozones, may even be possible (VENTO & TORO, 2011; VENTO, TORO, & MALETZ, 2012).

The Australasian succession appears to be quite incomplete, at least in the Lower Ordovician (Fig. 2). VANDENBERG and COOPER (1992) provided index species for the biostratigraphic intervals, and PERCIVAL, QUINN, and GLEN (2011) updated the succession in New South Wales. MALETZ and AHLBERG (2011) discussed the correlation of the Australasian succession and noted this incompleteness of the Tremadocian, in which only a few graptolitic horizons were recognized, leading to a number of biostratigraphic gaps (Fig. 2). VANDENBERG (2017) revised the early Floian succession, but new data on the Middle and Upper Ordovician are not available.

THE MIDDLE ORDOVICIAN

The Middle Ordovician includes the Dapingian and Darriwilian stages (Fig. 3). The base of the Dapingian is set at the stratigraphical level of the FAD of the conodont *Baltoniodus triangularis* (Lindström, 1955) in the Huanghuachang section of China (Wang & others, 2009). This level is within the local *Azygograptus suecicus* graptolite Biozone, but the graptolite record is poor in the type section. Wang and others (2013) described the graptolite fauna of the GSSP section and provided a detailed international correlation of the graptolite faunas. The base of the Dapingian is approximately correlatable with the base of the *Isograptus victoriae* Biozone in other regions (Maletz, 2011). The Dapingian is characterized by a succession of isograptid species (*Isograptus, Oncograptus, Cardiograptus*) as important index taxa (Cooper, 1973; VandenBerg & Cooper, 1992; Maletz, 2011). Recently, Herrera-Sánchez, Toro, & LoValvo (2019) and Toro and others (2020) discussed the correlation of the Floian and Dapingian succession of Argentina and correlated the regional *Azygograptus lapworthi* Biozone with the early Dapingian (Fig. 3), followed by the *Isograptus victoriae* Biozone of the Central Andean Basin of Argentina and Bolivia.

The base of the Darriwilian is defined at the level of the FAD of *Levisograptus austrodentatus* (Harris & Keble, 1932) in the Huangnitang section, Zhejiang Province, China, and two subzones are differentiated (Mitchell & others, 1997). Maletz and Ahlberg (2020) and Maletz, Ahlberg, and Lundberg (2020) discussed the international correlation of the Darriwilian in some detail. The authors also included the complex succession of Bohemo-Iberia (Gutiérrez-Marco & others, 2017), in which the chronostratigraphical differentiation includes the regional Arenigian, Oretanian, and Dobrotivian Stages (not shown in Fig. 3). In the past, the correlation of the Darriwilian had been difficult due to the presence of latitudinally restricted taxa, especially the pendent didymograptids (see Goldman & other, 2013), but Maletz (1997a) and Maletz and others (2011) used pandemic faunal elements to introduce a biostratigraphical succession of the late Darriwilian (the Llanvirn of the British regional chronostratigraphy) as an international standard. Maletz (1997b) revised the Darriwilian succession of Quebec, Canada, and differentiated the *Levisograptus austrodentatus* and *Levisograptus dentatus* biozones into two subzones each (Fig. 3). Maletz, Ahlberg, and Lundberg (2020) discussed the Darriwilian interval of South America, showing a fairly complete succession from the *Levisograptus austrodentatus* Biozone to the *Pterograptus elegans* Biozone. This succession was pieced together from numerous localities. The *Pseudamplexograptus distichus* Biozone from the Puna region of Argentina (Brussa, Toro, & Vaccari, 2008) was not used in their compilation. Kaufmann (2019) described the Darriwilian to basal Katian succession of the Sierra de Villicum in the Argentinian Precordillera.

THE UPPER ORDOVICIAN

The Upper Ordovician is differentiated into three stages, the Sandbian, Katian, and Hirnatian (Fig. 4), each stage being defined at the level of the FAD of a graptolite species.

The base of the Sandbian Stage is taken at the level of the FAD of the distinctive *Nemagraptus gracilis* (Hall, 1847) in the Fågelsång section, Scania, Sweden (Bergström & others, 2000), a species that is known to have a worldwide distribution (Brussa & others, 2007). The precise level of the FAD of this species in southern Scandinavia has recently been questioned (Maletz & Ahlberg, 2020). Chitinozoan records may also indicate problems with the GSSP section at Fågelsång (Vandenbroucke, 2004; Hennissen & others, 2010). A detailed correlation of the Sandbian graptolite succession, including the *Nemagraptus gracilis* Biozone and the overlying *Climacograptus bicornis* Biozone, is difficult to make (Williams & others, 2004).

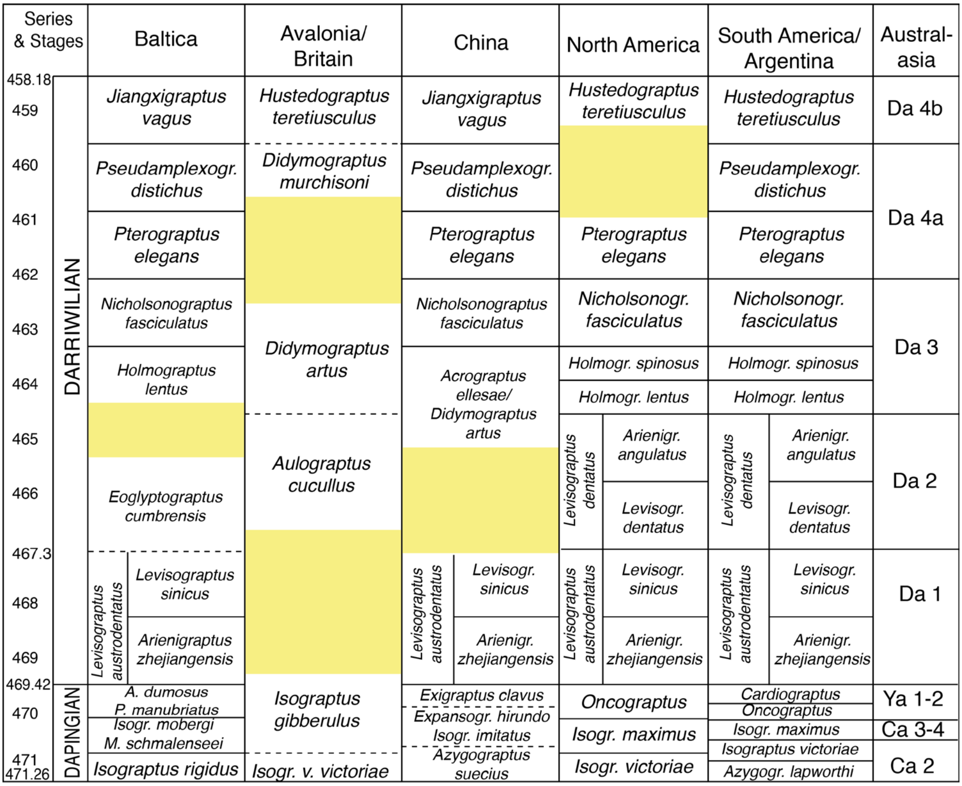

FIG. 3. Correlation of Middle Ordovician graptolite biozones. Yellow intervals indicate possible gaps.

The base of the Katian is defined at the level of the FAD of *Diplacanthograptus caudatus* (LAPWORTH, 1876) in the Black Knob Ridge section, Oklahoma, USA (GOLDMAN & others, 2007) and is followed by a rapid succession of first appearances of other graptolite species useful for a wider correlation of the level. Katian graptolite faunas are widely distributed, but the correlation is invariably difficult due to the presence of endemic faunal elements. A separate biozonation was established in the Appalachian Basin of eastern North America (RUEDEMANN, 1912, 1925; RIVA, 1974; GOLDMAN, MITCHELL, & JOY, 1999; ACHAB & others, 2011) and is shown here (Fig. 4). It includes a number of endemic faunal elements of the genera *Geniculograptus* MITCHELL, 1987 and *Paraorthograptus* MU & others, 1974 that are found only in this basin (GOLDMAN & others, 2013). They represent the best example of a restriction of Upper Ordovician graptolite faunas to a certain biogeographic area.

The Katian includes a *Geniculograptus pygmaeus* Biozone in China (CHEN & others, 1995; ZHANG & others, 2019), but the taxon is not discussed or illustrated in MU and others (2002). Thus, since *Geniculograptus* is considered to be an endemic taxon of eastern North America, its presence in China may be questioned (GOLDMAN & others, 2013). *Alulagraptus uncinatus* (KEBLE & HARRIS, 1934) is used in Australia to determine the Australasian Bolindian 1 (Bo 1), the *Alulagraptus uncinatus* Biozone, in the middle Katian. The species was recently found in the *Anticostia macgregorae* beds in East Qilianshan, northwestern China (CHEN & others, 2019), a region in which a highly local biostratigraphy was described for the Katian interval (not shown in Fig. 4). It is

Series & Stages (Ma)	Stage	Baltica	Avalonia/ Britain		China	North America		South America Argentina	Austral-asia
443.07–444	HIRNANT.	*Metabolograptus persculptus*	*Metabolograptus persculptus*		*Metabolograptus persculptus*	*Metabolograptus persculptus*		*Metabolograptus persculptus*	Bo 5
445.21	HIRNANT.	graptolite faunas unknown	*Metabolograptus extraordinarius*		*Metabolograptus extraordinarius*	*Metabolograptus extraordinarius*		*Metabolograptus extraordinarius*	Bo 4
446	KATIAN	graptolite faunas unknown	*Dicellograptus anceps*		*Diceratograptus mirus*; *Paraorthograptus pacificus*	*Diceratograptus mirus*; *Paraorthograptus pacificus*		possible gap	Bo 3
447	KATIAN	graptolite faunas unknown	*Dicellograptus anceps*		*Dicellograptus complexus*	*Dicellogr. ornatus*	*Paraorthogr. prominens*	*Dicellograptus ornatus*	Bo 2
448–449	KATIAN	*Dicellograptus complanatus*	*Dicellograptus complanatus*		*Dicellograptus complanatus*	*Dicellograptus complanatus*	*Dicellograptus complanatus*	*Dicellograptus complanatus*	Bo 1
450	KATIAN	*Pleurograptus linearis*	*Pleurograptus linearis*		*Dicellogr. elegans* / *O. quadrimucronat.*	*Styracograptus tubuliferus*	*Paraorthogr. manitoulinensis*	*Styracograptus tubuliferus*	Ea 4
451	KATIAN	*Pleurograptus linearis*	*Pleurograptus linearis*		*Geniculograptus pygmaeus* ?	*Styracograptus tubuliferus*	*Geniculogr. pygmaeus*	*Styracograptus tubuliferus*	Ea 3
452	KATIAN	*Dicranograptus clingani*	*Dicranogr. clingani*	*Dicellogr. morrisi*	*Diplacanthogr. spiniferus*	*Diplacanthogr. spiniferus*	*Diplacanthogr. spiniferus*	*Diplacanthograptus caudatus*	Ea 2
452.75	KATIAN	*Dicranograptus clingani*	*Dicranogr. clingani*	*Diplacanthogr. caudatus*	*Diplacanthograptus caudatus*	*Diplacanthogr. caudatus*	*O. ruedemanni*; *C. americanus*	*Diplacanthograptus caudatus*	Ea 1
453–456	SANDBIAN	*Mesograptus foliaceus*	*Mesograptus foliaceus*		*Climacograptus bicornis*	*Climacograptus bicornis*	*Diplogr. foliaceus*	*Climacograptus bicornis*	Gi 2
457–458.18	SANDBIAN	*Nemagraptus gracilis*	*Nemagraptus gracilis*		*Nemagraptus gracilis*	*Nemagraptus gracilis*		*Nemagraptus gracilis*	Gi 1

FIG. 4. Correlation of Upper Ordovician graptolite biozones. Local biozonation of Appalachian Basin (*blue*).

also common in the Bolindian 1 of Idaho, USA (CARTER, 1972; MITCHELL & others, 2003). A *Diceratograptus mirus* Subzone of the *Paraorthograptus pacificus* Biozone may be differentiated locally on the Yangtze Platform of China and in Nevada, USA (CHEN & others, 2006a; ŠTORCH & others, 2011).

The base of the Hirnantian is defined in the Wangjiawan North section, near Wangjiawan Village, Hubei Province, China, at the level of the FAD of *Metabolograptus extraordinarius* (SOBOLEVSKAYA, 1974) (CHEN & others, 2005, 2006a). The whole Hirnantian is less than 80 cm thick in the type section. It includes the *Metabolograptus extraordinarius* Biozone, overlain by the *Metabolograptus persculptus* Biozone. A thin limestone with the Hirnantian brachiopod fauna (the Kuanyinchiao bed) separates the graptolite biozones. CHEN and others (2006b) discussed the worldwide correlation of the Hirnantian Stage in some detail.

The British Upper Ordovician succession of ZALASIEWICZ and others (2009) combined elements of the biozonations used in Baltica and Scotland. A detailed biostratigraphic zonation for the Upper Ordovician of South America does not presently exist because few faunas have been described from this interval. ALBANESI and ORTEGA (2016) indicated a possible gap between the *Dicellograptus ornatus* Biozone (Katian) and the *Metabolograptus extraordinarius* Biozone (Hirnantian).

SILURIAN

After the introduction of the Silurian System by Murchison (1839), numerous changes were made before the modern concept emerged and series and stages were established. Davies and others (2011) provided the latest overview on its development in Britain, along with information to understand the individual chronostratigraphic intervals. According to Melchin, Sadler, and Cramer (2020), the Silurian System is approximately 24.07 Ma long (443.07–419.0 Ma) and is quite unevenly differentiated into four series, the Llandovery (10.14 Ma), Wenlock (6.19 Ma), Ludlow (4.01 Ma), and Pridoli (3.73 Ma). Interestingly, the GSSPs were initially defined biostratigraphically with reference to standard graptolite zones, although the index taxa for these zones are not found in some of the GSSP localities (Melchin, Sadler, & Cramer, 2012, p. 526). Some of the stages are currently under revision and details may change accordingly (see Melchin, Sadler, & Cramer, 2020). The main information on the Silurian graptolite biostratigraphy (Fig. 5–7) is based on Loydell (2012) with revisions as indicated herein.

THE LLANDOVERY SERIES

The Llandovery Series (Fig. 5) is differentiated into three stages: the Rhuddanian, Aeronian, and Telychian (Bassett, 1985; Holland, 1985; Melchin, Cooper, & Sadler, 2004). The base of the Rhuddanian is defined at Dob's Linn, Scotland at 1.6 m above the base of the Birkhill Shale at the level of the FAD of *Akidograptus ascensus* (Cocks, 1985). Originally, the base of the Rhuddanian was defined at the level of the FAD of *Parakidograptus acuminatus* (Nicholson, 1867) in the same section, but due to a revison of the graptolite fauna, the definition was revised (Melchin & Williams, 2000; Rong & others, 2008).

The base of the Aeronian has been defined at a level "just below the level of occurrence of *Monograptus austerus sequens,* which indicates the *Demirastrites triangulatus* Zone" (Melchin, Sadler, & Cramer, 2012, p. 526). Štorch (2015) and Štorch and Melchin (2019) discussed the graptolites from the Rhuddanian-Aeronian boundary interval of the Czech Republic. The authors redescribed the zonal index for the base of the Aeronian, *Demirastrites triangulatus* (Harkness, 1851), and the anagenetic changes in the *Demirastrites triangulatus* lineage. The GSSP level has recently been re-investigated at Rheidol Gorge, Wales, since the original location was insufficient for further correlations (see Melchin & others, 2018). The gap in the late Aeronian of the Yangtze Platform of China indicated by Loydell (2012) can be closed, at least in part, by the record of *Stimulograptus sedgwickii* (Portlock, 1843) (Maletz & others, 2021). Maletz and others (2019) recognized a considerably extended *Lituigraptus convolutus* Biozone in the Yichang region, Hubei Province, China, and subdivided it into the *Metaclimacograptus sculptus* and *Paramonoclimacis sidjachenkoi* subzones based on the common occurrence of the index species.

The base of the Telychian is defined between the LAD of the brachiopod *Eocoelia curtisi* Ziegler, 1966 and the FAD of *Eocoelia intermedia* (Hall, 1860), a level correlated to the base of the *Spirograptus turriculatus* Biozone by Holland (1985). According to a revision of the genus *Spirograptus* Gürich, 1908, this level now equals the base of the *Spirograptus guerichi* Biozone (Loydell, Štorch, & Melchin, 1993; Melchin, Sadler, & Cramer, 2012). The detailed biostratigraphy of the *Spirograptus guerichi* and *Spirograptus turriculatus* biozones (seven subzones) in Wales (Loydell, 1992) has not been used outside this region and is not discussed herein. Melchin and others (2017) revised the Llandovery succession of Arctic Canada and subdivided the *Campograptus curtus* Biozone into two subzones, a lower *Demirastrites triangulatus/Demirastrites pectinatus* Subzone and a *Rastrites orbitus* Subzone.

THE WENLOCK SERIES

The base of the Wenlock Series and the Sheinwoodian Stage (Fig. 6) is defined in the

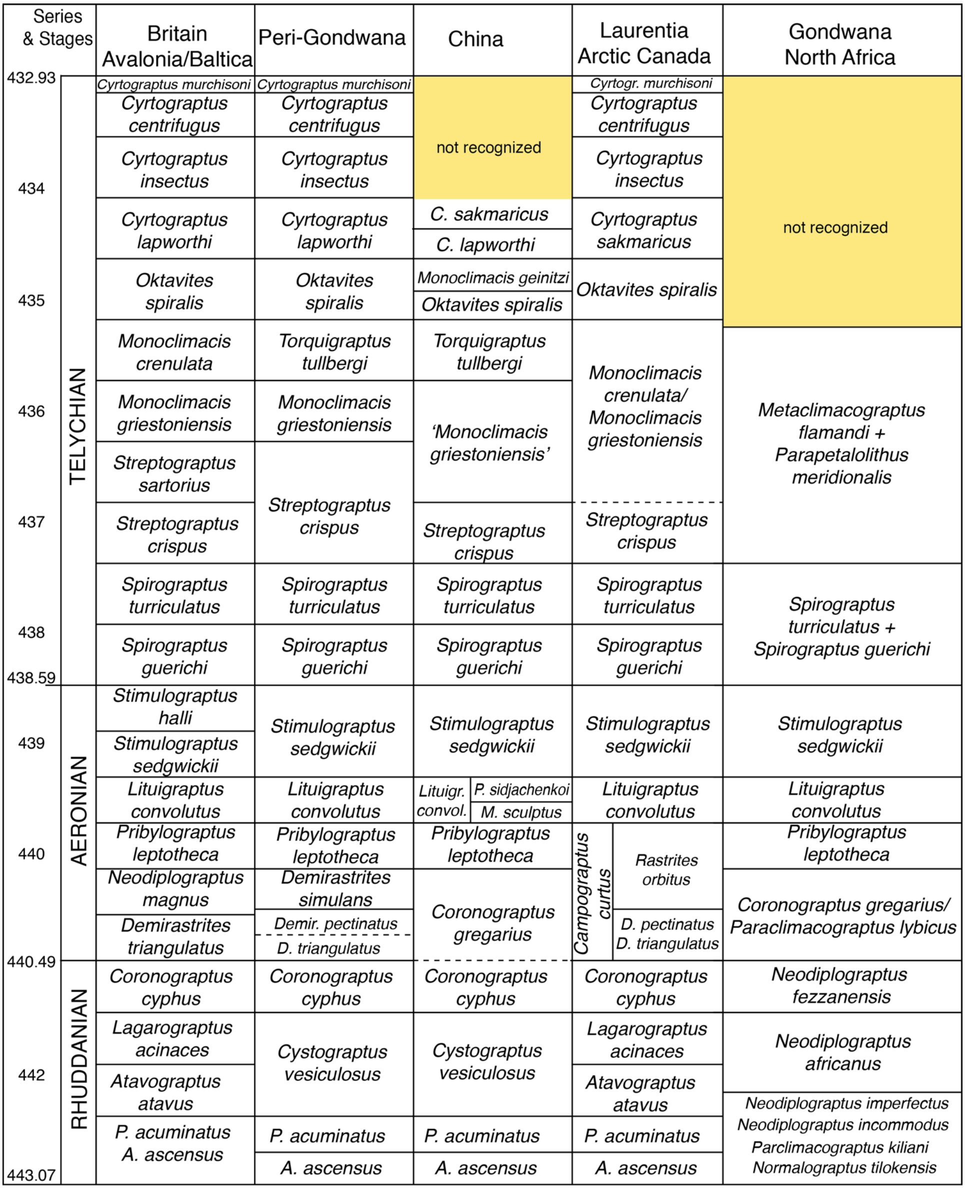

FIG. 5. Correlation of Llandovery (Rhuddanian to Telychian) graptolite biozones.

Hughley Brook section, Shropshire, UK, at the base of bed G of the Buildwas Formation (BASSETT & others, 1975; HOLLAND, 1980; MARTINSSON, BASSETT, & HOLLAND, 1981). This level was supposed to correlate with the base of the *Cyrtograptus centrifugus* Biozone, but no graptolites were found in the section and the inference was based on other localities. MULLINS and ALDRIDGE (2004) indicated that the GSSP level correlates with a level in the upper *Cyrtograptus centrifugus* Biozone or the lower *Cyrtograptus murchisoni* Biozone. MELCHIN, SADLER, and CRAMER (2012) considered the GSSP level to be in the lower part of the *Cyrtograptus murchisoni* Biozone. The Sheinwoodian is largely zoned by species of the genus *Cyrtograptus* CARRUTHERS in MURCHISON, 1867, which are the most conspicuous faunal elements. LOYDELL and LARGE (2019) revised the British biozonation of the Sheinwoodian slightly and eliminated the *Cyrtograptus perneri/Cyrtograptus ramosus* Biozone (see LOYDELL, 2012, fig. 5) in the uppermost Sheinwoodian. LENZ and others (2012) revised the succession of Arctic Canada. ZALASIEWICZ and others (2009) listed *Cyrtograptus perneri* BOUČEK, 1933 from the British *Cyrtograptus lundgreni* Biozone of basal Homerian age and questionably from the *Cyrtograptus rigidus* Biozone of the latest Sheinwoodian age.

The base of the Homerian is defined at the level of the FAD of *Cyrtograptus lundgreni* TULLBERG, 1883 at Sheinton Brook, Homer, UK (HOLLAND, 1980; MARTINSSON, BASSETT, & HOLLAND, 1981). The Homerian time interval includes one of the largest extinction events in graptoloid history, the *Lundgreni* Extinction Event (KOREN', 1987; JAEGER, 1991) during which most graptoloid taxa disappeared at the top of the *Cyrtograptus lundgreni* Biozone (e.g., JAEGER, 1991). PORĚBSKA, KOZŁOWSKA-DAWIDZIUK, and MASIAK (2004) discussed three separate events from the local biostratigraphic scheme of the Bartoszyce section of Poland (Fig. 6; Poland), partly supported by an investigation by MANDA and others (2019) from the Czech Republic. Both suggested additional graptolite biozone intervals above the *Cyrtograptus lundgreni* Biozone and below the *Pristiograptus parvus* interval. However, these biozone intervals are not recognized worldwide.

BARCA and JAEGER (1989) refined the Wenlock graptolite biostratigraphy supported by the detailed work of KOREN' (1992, 1994) from Central Asia. The Wenlock is poorly represented in China, and very few graptolites have been described from this region. CHEN (1984) provided information on the Silurian graptolite biozonation, including the Wenlock succession of southern Shaanxi, China, as the most complete succession of this interval, listing a number of biozones defined by *Cyrtograptus* species. LENZ, CHEN, and NI (1996) discussed Wenlock to Pridoli graptolites from Guangxi, China, and recognized a few levels with late Homerian (late Wenlock) and Gorstian to early Ludfordian (Ludlow) graptolites. They also reported a single taxon from the Pridoli, *Monograptus* cf. *rectiformis* PŘIBYL, 1981. NI (1997) described a fauna of late Homerian graptolites from western Yunnan, China, indicating the presence of the *Colonograptus praedeubeli/Colonograptus deubeli* Biozone.

THE LUDLOW SERIES

The Ludlow Series and Gorstian Stage (Fig. 6) have their stratotype at Pitch Coppice, Shropshire, England, at the base of the Lower Elton Formation, based on the level of the FAD of *Neodiversograptus nilssoni* (BARRANDE, 1850) (HOLLAND, 1980; HOLLAND & BASSETT, 1989). However, the fossil record of the GSSP section is extremely poor and unreliable; only two poorly preserved specimens identified as *Neodiversograptus nilssoni* and *Saetograptus varians* (WOOD, 1900) have been found (WHITE, 1981). ŠTORCH and others (2016) discussed the graptolite fauna of the Wenlock-Ludlow boundary interval of the Czech Republic. These authors stated that *Saetograptus varians* first appeared in the biostratigraphically higher *Lobograptus progenitor* Biozone. Biostratigraphically important successions can be found in Arctic Canada (LENZ & KOZŁOWSKA-DAWIDZIUK, 2004), Kyrgyzstan (KOREN' & SUJARKOVA, 2004) and the East European Platform (URBANEK & TELLER, 1997).)

Many of the late Wenlock (*Cyrtograptus lundgreni* Biozone) to Ludlow (*Saetograptus leintwardinensis* Biozone) graptolites are known from chemically isolated specimens collected from glacial boulders of northern Germany and Poland (e.g., URBANEK, 1958; RADZEVIČIUS & others, 2010; MALETZ & SCHÖNING, 2017). This material has its origin in the Silurian foreland basin succession of the Colonus Trough of Scania, southern Sweden (BEIER, MALETZ, & BÖHNKE, 2000; ERIKSSON, 2012), which is poorly exposed.

Ma	Series	Stages	Baltica/ E. European Platform		Peri-Gondwana (Europe)	Britain	Laurentia Arctic Canada
422.73 / 423	LUDLOW	LUDFORDIAN	*Uncinatograptus spineus*		*Formosograptus formosus*	No later zones recorded in Britain	*Formosograptus formosus*
			Uncinatogr. protospineus				
			Uncinatograptus acer				
			Ps. latilobus/S. balticus		*Ps. latilobus/S. balticus*		*Bohemograptus tenuis + Bohemograptus praecornutus*
424			*Neocucullogr. kozlowskii*		*Neocucull. kozlowskii*		
			Neocucull. inexpectatus		*Neocucull. inexpectatus*	*Bohemograptus*	
			Neolobogr. auriculatus		*Bohemograptus tenuis*		
			Bohemograptus cornutus				
			Bohemogr. praecornutus			*Saetograptus leintwardinensis*	
			C. aversus/S. leintwardinensis		*Saetogr. linearis*		*'M.' ceratus-S. linearis*
425.01		GORSTIAN	*Cucullogr. hemiaversus*		*Lobograptus scanicus/ Saetograptus chimaera*	*Saetograptus incipiens*	*Lobograptus scanicus*
			Lobograptus invertus				
426			*Lobogr. parascanicus*			*Lobograptus scanicus*	
			Lobograptus progenitor		*Lobograptus progenitor*	*Neodiversograptus nilssoni*	*Lobograptus progenitor*
			Neodiversogr. nilssoni		*Neodiversogr. nilssoni*		
426.74 / 427	WENLOCK	HOMERIAN	*Colonograptus ludensis*		*Colonograptus ludensis*	*Colonograptus ludensis*	*Colonograptus ludensis*
428			*Colonograptus deubeli + Colonogr. praedeubeli*		*Colonograptus deubeli+ Colonogr. praedeubeli*	*Gothograptus nassa*	*Colonograptus deubeli+ Colonograptus praedeubeli*
429			*Gothograptus nassa*		*Gothograptus nassa*		*Pristiograptus dubius+ Gothograptus nassa*
			Pristiograptus dubius	Poland	*Pristiograptus parvus*		
			M. flemingii/P. dubius				
430			*Testograptus testis*				
			Cyrtograptus lundgreni		*Cyrtograptus lundgreni*	*Cyrtograptus lundgreni*	*Cyrtograptus lundgreni*
430.62 / 431		SHEINWOODIAN	*Cyrtograptus perneri*		*Cyrtograptus perneri/ Cyrtograptus ramosus*	*Cyrtograptus rigidus*	*Cyrtograptus perneri*
			Cyrtograptus rigidus		*Cyrtograptus rigidus+ Monogr. belophorus*		*Monograptus opimus*
432			*Pristiograptus dubius*		*Pristiograptus dubius*	*Pristiograptus dubius*	*Monoclimacis flumendosae*
			Monogr. riccartonensis		*Monograptus riccartonensis*	*Monograptus riccartonensis*	*Monograptus instrenuus Cyrtograptus colobus*
433			*Monograptus firmus*		*Cyrtograptus murchisoni*	*Monograptus firmus*	*Cyrtograptus murchisoni*
432.93			*Cyrtograptus murchisoni*			*Cyrtograptus murchisoni*	

FIG. 6. Correlation of Wenlock-Ludlow (Silurian) graptolite biozones.

These graptolites have been investigated mainly in drill core material from Poland (e.g., Urbanek, 1963, 1966, 1970).

THE PRIDOLI SERIES

Kříž and others (1986) discussed and defined the Přídolí (now Pridoli) Series (Fig. 7) in great detail, based on the GSSP section in the Prague Basin. The level of the FAD of *Skalograptus parultimus* (Jaeger, 1975) defines the base of the Pridoli. Their work also provided a detailed graptolite biostratigraphy of the whole interval. Teller (1997a, 1997b) and Urbanek (1997) provided the latest overview on the Pridoli graptolite biostratigraphy and taxonomy of the East European Platform. Ni, Lenz, and Chen (1998) discussed the record of Pridoli graptolites in China and recognized only a single biozone, based on collections from northern Xinjiang, northwest China. The fauna is similar to that described by Koren' (1983, 1989) from Kazakhstan and Koren' and Sujarkova (1997) from southern Tian Shan, Kyrgyzstan. Lenz and Kozłowska-Dawidziuk (2004) introduced the *Uncinatograptus birchensis* Biozone in the Arctic Islands, Canada, and suggested it to be largely of basal Devonian age. They suggested a possible latest Silurian age for the base of the interval, but Lenz (2013) included it entirely in the Pridoli.

DEVONIAN

It is well established that planktic graptolites range biostratigraphically into the Lower Devonian (Fig. 7), but the exact level of their disappearance is still in discussion. The base of the Devonian System is defined at the level of the FAD of *Uncinatograptus uniformis* (Přibyl, 1940) in the Klonk section, Czech Republic (Chlupáč & Kukal, 1977; Chlupáč & Vasek, 2003). The absolute ages of the Devonian graptolite zone FADs are based on Becker, Gradstein, and Hammer (2012) and indicates a much longer duration of Early Devonian graptolite biozones in comparison with the Silurian time intervals (Fig. 7). The base of the Pragian Stage (Lower Devonian) is based on the level of the FAD of the conodont *Eognathodus sulcatus sulcatus* Philip, 1965 in the Velká Chuchle Quarry, Czech Republic. This level is considered to be above the *Uncinatograptus hercynicus* graptolite zone (Chlupáč & Oliver, 1989). The base of the Emsian is defined at the level of the FAD of the conodont *Polygnathus kitabicus* Yolkin & others, 1994 in Uzbekistan (Yolkin & others, 1997), but a discussion for revision has begun (Carls, Slavík, & Valenzuela-Ríos, 2008). Jaeger (1978) suggested an early Emsian age for the youngest monograptids and later supported this view in his discussion of the correlation with the conodont record (Jaeger, 1988). Jaeger (1970, 1978, 1988) described the Devonian graptolite biostratigraphy in some detail using all data available to him at the time. Jaeger (1970) suggested *Uncinatograptus pacificus* Jaeger in Churkin, Jaeger, and Eberlein, 1970 as the youngest Devonian monograptid and established the *Uncinatograptus pacificus* Biozone as the latest graptolite zone, but it is now known that the interval can be correlated with the *Uncinatograptus yukonensis* Biozone (Lenz, 2013).

Koren' (1974, 1975, 1978) discussed the early Devonian graptolite faunas of central Asia. Lenz (2013) provided the most recent overview on the early Devonian graptolite faunas of the Arctic Islands, Canada, which has a fairly high number of these faunas interpreted as cosmopolitan. Porębska (1984) described the early Devonian graptolites from the Bardo Mountains and established a very detailed biostratigraphy for the region. The author discussed a 30 cm thick linograptid interregnum (Porębska, 1984) at the top of the Pridoli *Skalograptus transgrediens* Biozone that Lenz (2013) correlated with the *Uncinatograptus birchensis* Biozone of Arctic Canada.

Lenz (1988) recognized *Uncinatograptus yukonensis* (Jackson & Lenz, 1963) as the youngest Devonian monograptid in the Yukon region of Canada. Lenz (2013)

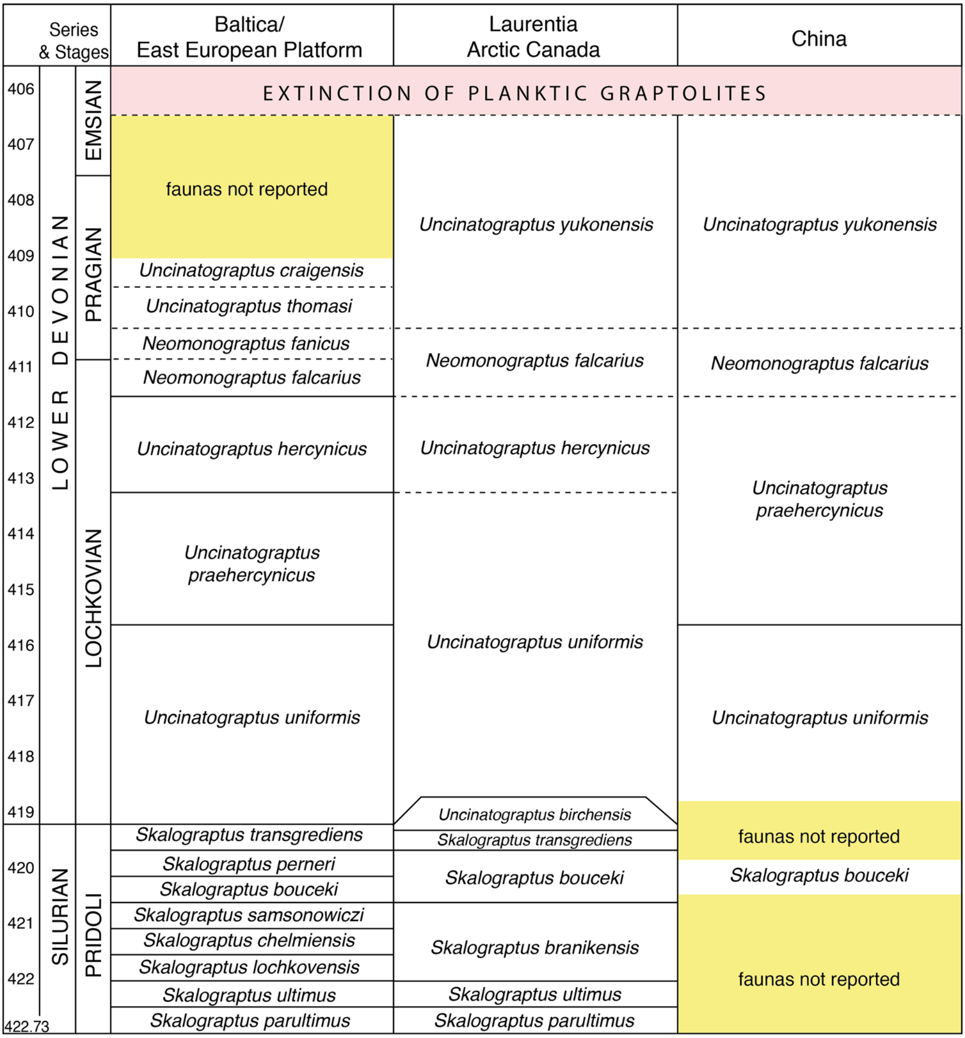

FIG. 7. Correlation of Pridoli (Silurian) and early Devonian graptolite biozones.

rejected the *Uncinatograptus pacificus* Biozone of JAEGER (1970) due to new records in Arctic Canada and considered the *Uncinatograptus yukonensis* Biozone as the youngest Devonian graptolite biozone (Fig. 7). CHEN and others (2015) revised the Devonian graptolite faunas of China (Fig. 7) and differentiated four biozones, stating that the succession has only moderate diversity and that certain intervals are not recognizable by their index species. However, this general succession compares well with the worldwide standard.

THE DURATION OF GRAPTOLITE BIOZONES

The duration of graptolite biozones has always been considered quite variable, and the duration of Silurian intervals was regarded as shorter than the Ordovican or Devonian intervals (RICKARDS, 1976; HUGHES, 1995; ZALASIEWICZ & others, 2009). The advent of radiometric dating finally provided better information on the precise duration of biostratigraphic intervals, but there are few reliable radiometric dates from the early Palaeozoic. Loydell (2012) used the timescale of Ogg, Ogg, and Gradstein (2008) to estimate the duration of graptolite zones. General estimates for the early and middle Ordovician based on Gradstein and others (2020) indicate a duration of ~1 Ma of a graptolite zone and for the late Ordovician a duration of ~1.5 Ma. The estimates are between 400,000 and 600,000 years for the Silurian and about 2 Ma for the Lochkovian. The estimation for the Pragian, the youngest interval for a graptolite biozone, is ~1.5 Ma. Only a few intervals may be zoned more precisely, as the differentiation of the *Spirograptus guerichi* and *Spirograptus turriculatus* biozones demonstrates. Loydell (1992, fig. 7) indicated a combined seven subzones for this interval, which lasted ~1 Ma.

Because graptolites are most common in dark and black shales, in which other fossils are rare or lacking, a precise correlation of the graptolite biostratigraphy with the succession of other fossil groups is often difficult. More information on other groups exists in biostratigraphic literature and especially in the discussion of chronostratigraphy (see Gradstein & others, 2012; Ogg, Ogg, & Gradstein, 2016). Biostratigraphic relevant acritarchs and chitinozoans are most commonly associated with graptolites; but because they are microfossils, different methods have to be used for their extraction from the sediments. Graptolites are associated in limestones with numerous other fossils, including conodonts, radiolarians, ostracods, and other small organisms, and these cases can be used for direct biostratigraphic integration (e.g., Bergström, 1986; Noble & Maletz, 2000).

Graphic correlation and quantitative biostratigraphy is very useful—and in some cases, absolutely key—to determining biostratigraphic successions and gaining insight into the correlation of various fossil groups as well as to integrating sedimentological data and event horizons with paleontological data (Sadler, 2004, 2012; Sadler, Cooper, & Melchin, 2009, 2011; Sadler, Cooper & Crampton, 2014; Goldman, Nõlvak, & Maletz 2015). Efforts to produce a more precise chronostratigraphic time scale for the Palaeozoic have been undertaken by integration of various means. (Cramer & others, 2010).

Automated stratigraphic correlation (see Sadler, 2004, 2012) integrates biostratigraphic and chemostratigraphic data with radiometric dates, producing a single composite of stratigraphic data. This method has increasingly been used to develop the Ordovician and Silurian time scales. It has also enabled analysis of the changing global graptolite biodiversity and its relationship with environmental change

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