Ordovician biostratigraphy: index fossils, biozones and correlation



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Abstract: Two remarkable events in the history of life on the Earth occur during the Ordovician Period (486.9–443.1 Ma). The first is an exceptionally rapid and sustained radiation of marine life known as the 'Great Ordovician Biodiversification Event' (GOBE), and the second is a catastrophic Late Ordovician mass extinction (LOME). Understanding the duration, rate and magnitude of these events requires an increasingly precise global correlation framework. In this chapter we review the major subdivisions of the Ordovician System, their Global Stratotype Section and Points, and the chronostratigraphic levels that define their bases. We also present a detailed set of correlation charts that illustrate the relationships between most of the regional graptolite, conodont and chitinozoan successions across the world.

Supplementary material: Undivided versions of Figures 1, 2 and 3 are available at https://doi.org/10.6084/ m9.figshare.c.6246574

Introduction

Two remarkable events in the history of life on the Earth occur during the Ordovician Period (486.9-443.1 Ma). The first is an exceptionally rapid and sustained radiation of marine life known as the 'Great Ordovician Biodiversification Event' (GOBE), and the second is a catastrophic Late Ordovician mass extinction (LOME). Each of these evolutionary events fundamentally changed the Ordovician marine ecosystem (e.g. see Sheehan 2001; Webby et al. 2004b; Harper 2006; Cooper et al. 2014; Servais and Harper 2018 and the references therein). Understanding their duration, rate and magnitude requires well-established biostratigraphic zonations that facilitate precise global correlations. Integrating and age dating multi-clade fossil zonal schemes, particularly those from different biofacies, is an important and ongoing task for palaeontologists. Fortunately, the Ordovician has been studied intensely and several groups of marine fossils (primarily graptolites, conodonts and chitinozoans) have the evolutionary (short species durations) and ecological (widespread distribution) characteristics necessary for detailed biostratigraphic zonation and precise correlation. In this chapter we review the major subdivisions of the Ordovician System, their Global Stratotype Section and Points, and the chronostratigraphic levels that define their bases. We also present a detailed set of correlation charts that illustrate the relationships between most of the regional graptolite, conodont and chitinozoan successions across the world.

The base of the Ordovician Period is defined at the level of the first appearance of the conodont *Iapetognathus fluctivagus* at the Green Point Newfoundland section. Its top, the base of the Silurian Period, is set as the level of the first appearance of the graptolite *Akidograptus ascensus* at Dob's Linn, Scotland.

Graptolites and conodonts, the two groups used to recognize the levels that define the beginning and end of the Ordovician Period, are also the fossils most often employed for the correlation of Ordovician strata. The stratigraphic ranges of these two groups have been thoroughly studied, and are considered to provide the most precise and reliable data for building widely applicable biostratigraphic zonations. However, recent work has demonstrated the importance and utility of a third group, chitinozoans (Achab 1989; Paris 1990, 1996; Nõlvak and

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Grahn 1993; Paris *et al.* 2004; Grahn and Nõlvak 2007). Graptolite successions are most often described from dark shale sections, particularly those of the outer continental shelf, slope and oceanic settings; conodonts are most commonly extracted from carbonate sections of the shelf and platform, and chitinozoans are found in almost all fine-grained sediments, both shales and limestones.

In some instances, limestone successions have yielded biostratigraphically important graptolites; and conodonts and chitinozoans have been identified from shale surfaces. These uncommon but critically important occurrences have facilitated zonal ties between otherwise disparate biofacies (e.g. Bergström 1986; Goldman et al. 2007a, b; Vandenbroucke et al. 2013). When precisely integrated, these fossil zonations facilitate precise biostratigraphic correlations that can be utilized with confidence across a wide range of facies and latitudes (Bergström 1986; Cooper 1999). Other fossil groups that are useful for regional and inter-regional correlation include trilobites, brachiopods, radiolarians, acritarchs, and, in Upper Ordovician carbonate facies, corals and stromatoporoids (Webby et al. 2004a, b; Pouille et al. 2014; Servais et al. 2017).

Evolution and ecology of key index fossil clades

Graptolites

The Graptolithina comprise the colonial members of the Class Pterobranchia (Phylum Hemichordata). and include both benthic and planktic groups. Recent phylogenetic analyses have suggested that the Graptolithina is not an extinct clade, and that the extant genus Rhabdopleura is a 'living' benthic graptolite (Mitchell et al. 2013). Planktic graptolites (Order Graptoloidea) are known only from the fossil record, and are the taxa used for Ordovician biozonation and correlation. The evolutionary origin of planktic graptoloids (from here on referred to as graptolites) is not well understood but is considered to lie among members of the Middle-Upper Cambrian Dendrograptidae (Maletz 2019). The first graptoloid species to appear in the earliest Ordovician is Rhabdinopora proparabola (Maletz et al. in press), and it provides a useful marker for the lowermost Ordovician in clastic facies that do not yield conodonts.

Graptolites were a major component of the Ordovician macroplankton and represent the first substantial fossil record of zooplankton. They lived at various depths in the ocean waters (Chen 1990; Cooper *et al.* 1991, 2012, 2017; Chen *et al.* 2001), were particularly abundant along continental margins in upwelling zones (Fortey and Cocks 1986; Finney and Berry 1997) and are found in a wide range of sedimentary facies, although most are abundant in distal shelf/slope deposits.

Many graptolite species spread rapidly after origination, are widespread globally and have relatively short stratigraphic durations, lasting for 2 myr or less. It is estimated (Foote *et al.* 2019) that the published graptoloid record captures up to 75% of the original species richness and, on average, 85% of the original durations for species known from more than one collection. These attributes combine to make graptolites extremely valuable fossils for subdividing and correlating Ordovician and Silurian strata (Skevington 1963; Cooper and Lindholm 1990; Webby *et al.* 2004*a*; Cooper and Sadler 2012; Loydell 2012; Maletz 2021).

Conodonts

Conodonts represent an extinct microfossil group whose phylogenetic relationships remain controversial. The main reason for this is the fact that complete specimens (including soft tissue) are exceedingly rare in the fossil record and the few found have been the subject of different interpretations. Although common in rocks of Cambrian– Triassic age, as a rule they occur only as parts of the phosphatic-feeding apparatus and complete assemblages of such apparatuses are quite uncommon. Most species are known only from isolated denticles from the feeding apparatus. These isolated denticles are referred to as conodont elements.

Most conodont elements have a size of less than 1 mm but specimens up to a size of several millimetres are known. The size of the conodont animal appears to have had a considerable range from a few centmetres up to perhaps 0.5 m. The global distribution of many taxa in a variety of marine environments suggests that they were active swimmers, although it has been suggested that at least some taxa were parasitic. Most authors interpret conodonts as primitive vertebrates (e.g. Aldridge et al. 1993, 2013; Donoghue et al. 2000, 2008) but others suggest that they belong to an isolated group of marine fossils. Their widespread occurrence in rocks deposited in a wide variety of environments indicates that they were an important and very common part of the marine faunas.

Because of the phosphatic composition of the conodont elements, they can be isolated from calcareous marine rocks by acid treatment or by the boiling of soft shales in water. Conodont elements also occur on bedding surfaces of hard graptolite shales from which they are not easily isolated. Extensive work on conodonts extracted from limestone samples has resulted in the establishment of detailed conodont zonations of Ordovician successions in several regions of the world (e.g. Bergström 1971), which has made these microfossils very valuable for both

short- and long-distance correlations. Together with graptolites, they are currently the biostratigraphically most globally useful Ordovician index fossils.

Chitinozoans

Chitinozoans are an extinct group of organic-walled microfossils that are abundant in Lower-Middle Paleozoic strata. They have bottle-shaped, radially symmetrical organic-walled tests with an opening sealed with an apertural plug (either operculum or prosome). Their taxonomic affinity is unknown but multiple hypotheses have been proposed to explain their biological origin, including classification as protists (e.g. Eisenack 1931, 1932; Collinson and Schwalb 1955; Obut 1973; Reid and John 1981; Cashman 1990, 1991), fungi (Locquin 1981) and a new but hitherto unknown group (Bockelie 1981). The most prevailing hypothesis for the last four decades is that chitinozoans are the eggs or egg capsules of cryptic metazoans (e.g. Kozlowski 1963; Grahn 1980; Paris 1981; Jaglin and Paris 1992; Paris and Nõlvak 1999; Grahn and Paris 2011). However, recent work carried out by Liang et al. (2019, 2020) on the magnitude of size variations in chitinozoan populations, and on exceptionally preserved specimens fossilized during reproduction, has questioned the egg hypothesis. Liang et al. (2020) proposed that chitinozoans most plausibly represent a new, isolated group of protists.

Along with graptolites and conodonts, chitinozoans have been studied intensely and utilized in high-Ordovician–Silurian biostratigraphy resolution (Achab 1989: Paris 1990, 1996: Nõlvak and Grahn 1993; Paris et al. 2004; Grahn and Nõlvak 2007). They are generally considered to be planktic or epiplanktic (Paris 1996; Paris and Verniers 2005) and have been recovered in almost all types of sediments, from shallow-water deposits to outer-shelf and slope sediments (although there are no firm occurrences recorded from abyssal deposits). These widespread occurrences indicate that chitinozoans were not strongly controlled by environmental factors, and thus could be used as an efficient tool in biostratigraphy. Chitinozoans were thought to have their greatest overall abundance on the shelf, which then diminishes towards both shallower and deeper water (Paris and Verniers 2005), but case studies are limited and more comprehensive data are required to better demonstrate this issue. Chitinozoans are commonly isolated from carbonates by acid dissolution but important work on extracting specimens from black shale (e.g. see Achab 1980; Paris 1981; Vandenbroucke et al. 2005, 2013; Achab and Maletz 2022) has improved correlation across biofacies and added important data to some longstanding stratigraphic problems in Ordovician stratigraphy.

Subdivision of the Ordovician System

Many fossil faunas exhibited strong biogeographical differentiation during the Lower Paleozoic, particularly in the Ordovician. Historically, because of the strong faunal provincialism and facies differentiation that existed throughout most of the Ordovician, no regional suite of stages or series proved entirely satisfactory for global application. Therefore, the Ordovician Subcommission determined that a set of globally applicable set of chronostratigraphic (and chronological) units defined by fossilbased levels that had the potential for precise widespread correlation needed to be developed (Webby 1995, 1998).

The International Commission on Stratigraphy (ICS) recognized a three-fold subdivision of the Ordovician System (Webby 1995): the Lower, Middle and Upper Ordovician Series. Seven chrono-stratigraphic levels were established as primary correlation levels for seven international stages. These stage boundaries are based on the first appearance of key graptolite or conodont species, have been formally voted on, and are defined by a Global Boundary Stratigraphic Section and Point (GSSP). From the oldest to youngest, they are Tremadocian, Floian, Dapingian, Darriwilian, Sandbian, Katian and Hirnantian (Figs 1a–e, 2a–e & 3a–e).

A short review of how the stage boundary levels are recognized is provided below. Photographs of the key index taxa whose first appearance marks the level of the GSSPs for the Floian (*Paratetragraptus approximatus*), Sandbian (*Nemagraptus gracilis*) and Hirnantian (*Metabolograptus extraordinarius*) stages are shown in Figures 4, 5 and 6, respectively. These graptolite species were not illustrated in the 2020 revision of the geological timescale (Goldman *et al.* 2020).

The Tremadocian Stage

The GSSP for the base of the Tremadocian Stage, the Lower Ordovician Series and the Cambrian–Ordovician boundary is in the Green Point section of western Newfoundland. The boundary is defined as the level of the first appearance of the conodont species *Iapetognathus fluctivagus* in Bed 23, in the lower Broom Point Member of the Green Point Formation, 4.8 m below the first appearance level of the planktic graptolite *Rhabdinopora preparabola* in Bed 25 (cf. Cooper *et al.* 2001). The relatively close similarity of the oldest occurrence of these widespread key taxa also made it possible to recognize the Cambrian– Ordovician boundary level in successions lacking conodonts.

However, it is appropriate to note that there is currently some controversy regarding the taxonomy and appearance level of *I. fluctivagus* at the GSSP.

	Ordovician Biozones								
				Gra	otolite Zor	nes			
AGE (Ma)	S	Stage	E	Baltica	Britain	South China	Australasia		
470	dle	Deningian	Arienig	raptus dumosus	lsograptus gibberulus	Exigraptus clavus	Oncograptus upsilon		
471	Mid	Dapingian	Isog	rogr. scrimaienseei iraptus rigidus	Isograptus victoriae	Expansograptus hirundo	Isograptus vict. maximus Isograptus vict. victoriae		
	-	4/1.20	sn	l. spjeldnaesi		Azygograptus suecicus Baltograptus deflexus	Isograptus vict. lunatus		
472			ohyllograpt ngatus	Baltograptus minutus	Expansograptus simulans	Didymograptellus eobifidus	Didymograptellus		
473		an	Pseudop elo	Baltograptus jacksoni		Tshallograptus	kremastus		
474		Floia	Baltogi Cyi	raptus vacillans matograptus rotobalticus	Baltograptus varicosus	Acrograptus filiformis	Tshallograptus fruticosus		
475			Para	atetragraptus	Tetragraptus phyllograptoides	Paratetragraptus approximatus	Paratetragraptus approximatus		
476		477.08	ap	proximatus					
478	ver	ocian	H	unnegraptus copiosus	Sagenograptus	Hunnegraptus copiosus	Sagenograptus		
480	Lo		Sa	genograptus murrayi	murrayi	Sagenograptus murrayi	murrayi		
=		jac	K. suprer	nus / stoermeri / kiaeri	[?]	Aorograptus victoriae	Aorogr. victoriae - Paradelogr. antiquus		
482		Trem	Adelo	graptus tenellus	Adelograptus tenellus	Adelograptus tenellus	Psigraptus		
483			Rhabdinopora	dinopora anglica	Rhabdinopora	Rhabdinopora anglica	[?]		
=			Anisogi	raptus matanensis	napellitormis	Anisograptus matanensis	Anisogr. & Rhab. scitulum		
485			Rhabd	inopora parabola		Rhabdinopora parabola	[?]		
486			RI pi	habdinopora raeparabola	[?]	[?]	[?]		
407		486.85							
487	C	ambrian							

(a)

Fig. 1. (a)–(e) Lower Ordovician timescale, stages, and graptolite, conodont and chitinozoan zonal schemes. The leftmost column is the chronometrical timescale from Goldman *et al.* (2020, in Gradstein *et al.* 2020). Zonations and correlations for graptolites are modified from the following (and references therein): Vandenberg and Cooper (1992), Zalasiewicz *et al.* (2009), Cooper and Sadler (2012), Loydell (2012), Maletz and Ahlberg (2018), Hererra Sánchez *et al.* (2019), Goldman *et al.* (2020) and Maletz (2021); for conodonts they are modified from Bergström and Wang (1995), Zhen and Percival (2003), Zhen *et al.* (2015, 2017), Zhen (2021), Albanesi and Ortega (2016), Z. H. Wang *et al.* (2019), Goldman *et al.* (2012). ¹The South Gondwana graptolite zonation for the Lower Ordovician is adapted from Gutiérrez-Marco and Martin (2016).

According to Terfelt *et al.* (2012), the *Iapetognathus* specimens in Bed 23 belong rather to *I. praeengensis*, and this latter species also occurs below Bed

23 in the Green Point succession. Other authors, however, do not agree with this interpretation (Miller *et al.* 2014).

(b)

	Ordovician Biozones									
			Grap	tolite Zone	S					
AGE (Ma)	S	Stage	North America	Argentina Precordillera	NW Argentina	South Gondwana ¹				
470	Middle	Dapingian	Oncograptus Isograptus vict. maximus Isograptus vict. victoriae	Oncograptus Isograptus vict. maximus	[?]					
		471.26	Isograptus vict. lunatus		Azygograptus lapworthi	Azygograptus Interval				
472			Didymograptellus bifidus	[?]	Didymograptellus bifidus	Baltograptus minutus				
		an	Tshallograptus f <u>ru</u> ti <u>cosu</u> s		Baltograptus cf. B. deflexus	?Baltograptus jacksoni				
474		Floi	Tetragraptus akzharensis		Tetragraptus akzharensis	[?] Cymatograptus protobalticus				
475		477 08	Paratetragraptus approximatus	T. fruticosus/ P. approximatus	Tetragraptus phyllograptoides	Tetragraptus phyllograptoides				
477	ver		Paradelograptus	Sagenograptus	Hunnegraptus copiosus	— — — — — — — — Hunnegraptus copiosus				
480	Lo	cian		murrayi	Sagenograptus murrayi	Sagenograptus murrayi				
		ор	Paradelograptus antiquus [?]		Aorograptus victoriae	Aorograptus victoriae				
482 -		na	Adelograptus tenellus or		Bryograptus kjerulfi	[?]				
		er	tenenus yr.		Adelograptus	Adelograptus tenellus				
483		Ц	Rhabdinopora anglica		Rhabdinopora anglica	Rhabdinopora anglica				
			Anisograptus matanensis	[?]	Anisograptus matanensis	Anisograptus matanensis				
485			Rhabdinopora parabola		Rhabdinopora parabola	(0)				
486			Rhabdinopora praeparabola			[/]				
		486.85								
48/	C	ambrian								

Ordovician biozonation

Fig. 1. Continued.

Miller *et al.* (2014) refuted many of Terfelt *et al.*'s (2012) stratigraphic and taxonomic interpretations, including the level at which the various species of *Iapetognathus* appear (see Stouge *et al.* 2017). In order to acknowledge the ongoing research and discussion related to this important boundary level, and to facilitate its precise international correlation, the Ordovician Subcommission approved two Auxiliary Stratotype Sections and Points (ASSPs) for the base of the Ordovician System. These are the Lawson Cove Section, Ibex area, Utah, USA (Miller *et al.* 2016) and the Xiaoyangqiao section at Dayangcha, North China (Wang *et al.* 2021).

Other useful but less known index fossils found in the Green Point succession are radiolarians, which occur in the upper part of Beds 23, 25 and 26, and represent the *Protoentictinia kuzuriana* (**c**)

	Ordovician Biozones									
			Chitinozo	an Zones	Conodo	nt Zones				
AGE (Ma)	S	Stage	Baltica	North Gondwana	Baltica	N. America Midcontinent				
470	e			Belonechitina	M. parva	Histiodella altifrons				
=	lbb	Dapingian		henryi	Paroisto. originalis Baltoniodus navis	Microzarkodina				
471 -	Σ	471.26		ornensis	Baltoniodus triangularis	Tripodus laevis				
472				Eremochitina brevis	Oepikodus evae	Reutterodus andinus				
473		Floian	Euconochilina primitiva	Eremochilina baculata	Prioniodus elegans	Oepikodus communis				
476		477.08		Euconochitina symmetrica						
478	-ower		Lagenoci conifun	Lagenochitina conifundus	Paroistodus proteus	Acodus deltatus / Oneotodus costatus				
480	_	docian	Lagenochitina destombesi							
482		ema			Paltodus deltifer	Macerodus dianae Scolopodus subrex				
483		Tre		Lagenochitina destombesi		Rossodus manitouensis				
484			[?]		Cordylodus angulatus	Cordylodus angulatus				
486		486.85			lapetognathus fluctivagus	lapetognathus fluctivagus				
487	С	ambrian								
	_									

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Fig. 1. Continued.

Assemblage (Won *et al.* 2005; Pouille *et al.* 2014). The radiolarians may be useful for correlation of the boundary in slope facies sections.

Trilobites and other shelly fossils are not common in the systemic boundary interval at the GSSP. However, trilobite species belonging to *Symphysurina* have been found in Bed 25 just below the first appearance datum (FAD) of *R. praeparabola* (Stouge *et al.* 2017). These fossils provide a straightforward correlation into the western Laurentian platform sections, which also contain the trilobite *Jujuyapsis borealis*, species of *Symphysurina* (Loch and Taylor 2012) and *I. fluctivagus*.

The upper and lower boundaries of the Tremadocian Stage correlate well with those of the British Tremadoc Series (Rushton 1982). The name was approved by the ICS in 1999 (Cooper and Sadler 2012). (d)

(**)											
		C	<u>Prdovici</u>	an Bioz	ones						
			Conodont Zones								
AGE (MA)	5	Stage	N. China	S. China (platform)	S. China _(slope)	Kazakhstan					
470	dle	D	[?]	M. parva Paroisto. originalis	Paroistodus originalis	Periodon					
471	Mid	471.26		Baltoniodus navis Balton. triangularis	[?]	ct. P. hankensis					
472			ganada	Oepikodus evae	Oepikodus evae	Oepikodus evae					
473 -		_	Paraserratognathus	Oepikodus communis							
474 -		oiar	Paraserratognathus paltodiformis								
475		Ξ	Serratognathus extensus	Prioniodus honghuayuanensis	Prioniodus elegans	Prioniodus elegans					
476		477.08	Serratognathus bilobatus	Serratognathus diversus	Serratognathus bilobatus	Prioniodus oepiki					
478	wer		Scalpellodus ersus	Triangulodus bilīdus	Triangulodus bifidus	Acadus					
480	Lo	ocian	Colaptoconus quadraplicatus	Triangulodus proteus / Colaptoconus quadraplicatus	Paroistodus proteus	longibasis					
482		Jad			Paltodus deltifer						
483		ren	Rossodus manitouensis	Rossodus manitouensis	Chosonodina	Rossodus manitouensis					
484			Chosonodina herfurthi	Ozatikatus	herfurthi						
485			Cordylodus angulatus	angulatus	Cordylodus angulatus	angulatus					
486		486.85	Cordylodus lindstromi / lapetognathus fluctivagus	Monocostodus sevierensis	lapetognathus fluctivagus	Cordylodus lindstromi					
487	С	ambrian									

Ordovician biozonation

Fig. 1. Continued.

The Floian Stage

In the current classification of the Ordovician System, the second stage above its base is the Floian Stage. This unit received its name from the Village of Flo, which is located about 5 km SE of the Floian GSSP, which is at Diabasbrottet. This GSSP is located about 80 km NNW of the city of Göteborg and 12 km SE of the town of Vänersborg in the province of Västergötland in southwestern Sweden. The Diabasbrottet Quarry, long inactive, is located on the northwestern slope of Mount Hunneberg (Maletz *et al.* 1996; Bergström *et al.* 2004, 2019).

At the Diabasbrottet GSSP, the succession consists of the Tøyen Shale, which is a black shale with some, generally thin, beds of dense fossiliferous limestone. The black shale contains numerous graptolites and the limestone beds have yielded taxonomically diverse conodonts. At its GSSP, the base of the Floian Stage, now marked by a 'golden spike', is (e)



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placed at the level of the first appearance of the globally distributed graptolite *Paratetragraptus approximatus* (Fig. 4). This biostratigraphic level can be widely recognized throughout low- to middlepalaeolatitude regions where it commonly includes the FAD of *Tetragraptus phyllograptoides*, which also debuts in the GSSP horizon at Diabasbrottet. *Tetragraptus phyllograptoides* is well known from high-latitude localities (e.g. the Central Andean Basin: see Herrera Sánchez *et al.* 2019) and, hence, a precise correlation of the boundary level can be traced through graptolite successions around the world.

In terms of conodont biostratigraphy, this level is a little above the base of the *Oelandodus elongatus– Acodus deltatus* Subzone of the *Paroistodus proteus* Zone of the Baltoscandian (mid-palaeolatitude) succession (Löfgren 1993; Maletz *et al.* 1996; Bergström *et al.* 2004). In the North American Midcontinent (low-latitude) succession, this level is close to the base of the *A. deltatus–Oneotodus costatus* Zone; and in North China and the Canning Basin (a)

	Ordovician Biozones											
	Graptolite Zones											
AGE (Ma)	ę	Stage		Baltica	Britain	South China	Australasia					
457	Upper	Sandbian 458.18	Nen	nagraptus gracilis	Nemagraptus gracilis	Nemagraptus gracilis	Nemagraptus gracilis					
459			Jian	gxigraptus vagus	Hustedograptus teretiusculus	Jiangxigraptus vagus	cograptus ensis					
460			Psei g	ıdamplexo- graptus listichus	Didymograptus murchisoni	Didymograptus murchisoni	Archiclima riddeli					
462 1 463 1 464 1	ddle	arriwilian	Pte e	rograptus Ilegans		Pterograptus elegans	limacograptus ecoratus					
465	Mi	Δ	Nicho fa	lsonograptus sciculatus	Didymograptus artus	Nicholsonograptus fasciculatus	Archic d					
467				Holmograptus lentus	Acrograptus	Levisograptus						
469		469.42	Eogl cu	yptograptus mbrensis	Aulograptus cucullus	Levisoor austrodentatus	Levisoar austrodentatus					
470		Dapingian	Arienigi Pseudi Maeand	raptus dumosus/ so. manubriatus rogr. schmalenseei	lsograptus gibberulus	Exigraptus clavus	Cardiograptus morsus Oncograptus upsilon Isograptus vict. maximus					
471 -		471.26	Isog	raptus rigidus	Isograptus victoriae victoriae	P. caduceus imitatus	Isograptus vict. victoriae					
472	Lower	Floian	P. elongatus	Isograptus spjeldnaesi Baltograptus minutus	Expansograptus simulans	Azygograptus suecicus Baltograptus deflexus Didymograptellus eobifidus	Isograptus v. iunatus Isograptus primulus					

Ordovician biozonation

Fig. 2. (a)–(e) Middle Ordovician timescale, stages, and graptolite, conodont and chitinozoan zonal schemes. The leftmost column is the chronometrical timescale from Goldman *et al.* (2020, in Gradstein *et al.* 2020). Zonations and correlations for graptolites are modified from the following (and references therein): Vandenberg and Cooper (1992), Zalasiewicz *et al.* (2009), Cooper and Sadler (2012), Loydell (2012), Maletz and Ahlberg (2018), Goldman *et al.* (2020) and Maletz (2021); for conodonts they are modified from Bergström and Wang (1995), Zhen and Percival (2003), Zhen and Nicoll (2009), Albanesi and Ortega (2016), Z. H. Wang *et al.* (2019), Zhang *et al.* (2019), Goldman *et al.* (2020) and Zhen *et al.* (2020, *b*), Zhen (2021); and for chitrinozoans from Goldman *et al.* (2020). ¹The South Gondwana graptolite zonation for the Middle Ordovician is adapted from Gutiérrez-Marco *et al.* (2017).

in Australia, this level is near the base of the Serratognathus bilobatus Zone (Zhen et al. 2017; Z.H. Wang et al. 2019). In Baltoscandia, this level is also within the Megistaspis (Paramegistaspis) planilimbata Trilobite Zone. In 2002, the ICS ratified the GSSP for the Floian Stage and the stage was named in 2005. This biostratigraphic level was also adopted for the base of the revised British Arenig Series (Fortey *et al.* 1995).

The Dapingian Stage

The GSSP for the base of the Dapingian Stage and the base of the Middle Ordovician Series is the (b)

	Ordovician Biozones										
	Graptolite Zones										
AGE (Ma)	3	Stage	North Argentina America Precordillera		NW Argentina	South Gondwana ¹					
457	Late	Sandbian 458.18	Nemagraptus gracilis	Nemagraptus gracilis	[?]	Orthograptus bekkeri					
459			Hustedograptus teretiusculus	Hustedograptus teretiusculus	Hustedograptus teretiusculus	Hustedograptus teretiusculus					
460			[?]	[?]		Pseudamplex. distichus					
462 463 464	iddle Darriwilian	Pterograptus elegans	Pterograptus elegans	[?]	Didymograp murchisor Pterograptus elegans						
465	Mi	Δ		Nicholsonograptus fasciculatus	[?]		Didymograptus artus /				
467						Holmograptus spinosus Holmograptus lentus	Holmograptus spinosus Holmograptus lentus		Didymograptus spinulosus		
468		469.42	Levisograptus dentatus	Levisograptus dentatus	Levisograptus dentatus	Corymbograptus retroflexus					
470		Dapingian	Levisogr. austrodentatus Oncograptus	Levisogr. austrodentatus Cardiograptus Oncograptus	[Levisogr. austrodentatus]	[?]					
471		471.26	Isograptus vict. maximus Isograptus vict. victoriae Isograptus vict. lunatus	Isograptus vict. maximus	Azygograptus lapworthi	Expansograptus hirundo					
472	Lower	Floian	Didymograptellus bifidus	[?]	Didymograptellus bifidus	[?]					

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Fig. 2. Continued.

stratigraphic level of the FAD of the conodont *Baltoniodus triangularis*, which is 10.57 m above the base of the Dawan Formation at the base of Bed SHOD-16 in the Huanghuachang section, 22 km NE of Yichang city, Hubei Province, South China (Wang *et al.* 2009). The FAD of the conodont *Microzarkodina flabellum* occurs 0.2 m above this horizon. The conodont succession across the Lower–Middle Ordovician boundary records important speciation events in the *Baltoniodus, Gothodus, Microzarkodina* and *Periodon* lineages. The appearance of these new taxa, which dispersed rapidly,

enables the correlation of the GSSP into conodont successions where *B. triangularis* is uncommon.

Based on the graptolite succession from the Huanghuachang section, X.F. Wang *et al.* (2009) and C.H. Wang *et al.* (2013) placed the base of the Dapingian Stage close to the boundary between the lower and upper *Azygograptus suecicus* Zone (as defined by the first appearance of *Azygograptus ellesi*). X.F. Wang *et al.* (2009) correlated the GSSP level with the North Gondwana *Belonechitina henryi* Chitinozoan Zone and noted that it also falls within the *Ampullulae–Barakella felix* acritarch assemblage zone.



Fig. 2. Continued.

Correlation of the conodont-defined Dapingian Stage GSSP into graptolite-bearing sections devoid of conodonts is facilitated by the co-occurrence of graptolites and conodonts in the Huanghuachang section itself (X.F. Wang *et al.* 2009; C.H. Wang *et al.* 2013), as well as in the Cow Head Group of western Newfoundland (Williams and Stevens 1988; Stouge 2012) and the Trail Creek region of Idaho, western USA (Goldman *et al.* 2007b). There are, however, some differences in the recent literature regarding the correlation of the base of the Dapingian Stage with graptolite-bearing successions. X.F. Wang *et al.* (2009) and C.H. Wang *et al.* (2013) correlated the GSSP level with the

base of the *Isograptus victoriae victoriae* Zone (Ca2 in the Australasian zonation) but recent work by Zhen *et al.* (2020*b*) suggests that the base of the Dapingian Stage could correlate with a slightly younger level that is closer to the base of the *Isograptus victoriae maximus* Zone (Ca3). Herrera Sánchez *et al.* (2019) and Toro *et al.* (2020) correlated the basal Dapingian with the *Azygograptus lapworthi* Biozone of the Central Andean Basin, which was then succeeded by a slightly younger first appearance of *I. victoriae.*

These small differences notwithstanding, the base of the Dapingian Stage and the Middle Ordovician can be recognized and globally correlated with

	Ordovician Biozones										
		Conodont Zones									
AGE (Ma)		Stage	N. China	S. China (platform)	S. China (slope)	Kazakhstan					
457	per	Sandbian	Plectodina aculeata	Baltoniodus variabilis							
458	ŋ	458.18	Pygodus anserinus	Yangtzeplacognatus jianyeensis / Pygodus anserinus	Pygodus anserinus	Pygodus anserinus					
460			Pygodus serra	Pygodus serra	Pygodus serra	Pygodus serra					
462 463 464 464 465	Middle	Darriwilian	Eoplacognathus suecicus / Histiodella kristinae	Eoplacognathus suecicus	Histiodella kristinae						
466					Tangshanodus tangshanensis /	Eoplacognathus pseudoplanus / D. tablepointensis	Histiodella holodentata	Periodon aculeatus			
467			Histiodella holodentata	Yangtze- placognathus crassus	Yangtze- placognathus crassus						
469 470 471		469.42 Dapingian	[?]	Lenodus variabilis L. antivariabilis Microzarkodina parva Paroisto. originalis Baltoniodus navis Bolton. triongul.	Paroistodus originalis [?]	Paroistodus horridus Periodon cf. P. hankensis					
472	Lower	Floian	Jumudontus ganada	Balton, triangularis Oepikodus evae	Oepikodus evae						

(**d**)

Fig. 2. Continued.

reasonable precision in both the relatively shallowwater carbonate facies and the deeper-water graptolite facies. The Dapingian Stage was ratified by the ICS in 2007.

The Darriwilian Stage

The global Darriwilian Stage retains its original concept from the Australasian succession (see Vandenberg and Cooper 1992) spanning the interval from the first appearance of the graptolite *Levisograptus austrodentatus* to the first appearance of *Nemagraptus gracilis*. Unfortunately, no continuous section in Victoria, Australia crossed the lower boundary of the regional stage (Vandenberg and Cooper 1992) and an appropriate section for the global stage needed to be found elsewhere. The GSSP for the base of the Darriwilian Stage is set at the level of the first appearance of *Levisograptus austrodentatus* at the base of Bed AEP 184, 22 m below the top of the Ningkuo Formation at the Huangnitang section, near Changshan, Zhejiang Province, SE China (Mitchell *et al.* 1997). At the Huangnitang section, the FAD of *L. austrodentatus* occurs within a wellstudied succession of graptolite first appearances (including *Levisograptus sinodentatus, Arienigraptus zhejiangensis, Undulograptus formosus* and *Undulograptus primus*) that occur in a similar



Fig. 2. Continued.

order in many regions around the world. Hence, the level stage boundary can be identified even without the presence of the key taxon. The base of the Darriwilian Stage correlates with the *Aulograptus cucullus* Graptolite Zone in high-latitude successions (Britain).

Limestone interbeds in the Ningkuo Formation at Huangnitang yield diagnostic conodonts (Mitchell *et al.* 1997). Samples from below the GSSP level (beginning with sample AEP 167) contain conodonts that correlate with the *Paroistodus originalis* Zone, and samples from Bed AEP 250, approximately 13 m above the GSSP, contain *Yangtzeplacognathus crassus*. By interpolation, the stage base is close to the base of the *Lenodus* antivariabilis Conodont Zone, which is defined by the appearance of *L. antivariabilis* and *Baltoniodus norrlandicus* in the Baltoscandian succession. The GSSP correlates with a level slightly above the FAD of the zonal index *Histiodella sinuosa* in the North American (midcontinent) conodont succession (Chen and Bergström 1995). In the Argentine Precordillera and Laurentia, species of the evolving conodont genus *Histiodella* provide a biostratigraphically useful set of biozones that span the lower and middle Darriwilian. From oldest to youngest, these are the *Histiodella sinuosa*, *Histiodella holodentata*, *Histiodella kristinae* and *Histiodella bellburnensis* zones (Stouge 2012; Serra *et al.* 2019) (Fig. 2c, e).

	Ordovician Biozones									
			G	rap	tolite Z	ones				
AGE (Ma)		Stage	Baltica		Britain	South China	Australasia			
443	443.07	Silurian								
444		L Barran Gara	Metabolograptus persculptus	Meta pe	abolograptus ersculptus	Metabolograptus persculptus	Metabolograptus persculptus			
445		445.21	[?]	Meta exti	abolograptus raordinarius	Metabolograptus extraordinarius	Metabolograptus extraordinarius			
446 447 448			[3]	Dic	ellograptus anceps	Paraorthograptus pacificus	Paraorthograptus pacificus			
449 -		Katian				Dicellogr. complexus	pre-P. pacificus			
=	Б.		Dicellogr. complanatus	Dicellogr. complanatus		Dicellogr. complanatus	Alulagraptus uncinatus			
450	d		Pleurograptus linearis	Pleurograptus linearis		Orthograptus quadrimucronatus	Diceilograptus gravis Dicranograptus kirki			
451	J			aptus ni	Dicellograptus morrisi	Diplacanthograptus spiniferus	Diplacanthograptus spiniferus			
452		452.75	Dicranograptus clingani	Dicranogr clinga	Diplacantho- graptus caudatus	Diplacanthograptus caudatus	Diplacanthograptus caudatus			
453		Sandbian	Mesograptus foliaceus	Mesograptus foliaceus	Climacograptus bicornis	Climacograptus bicornis	Orthograptus calcaratus			
457		458.18	Nemagraptus gracilis	Ne	magraptus gracilis	Nemagraptus gracilis	Nemagraptus gracilis			
459	Mid	Darriwilian	Jiangxigraptus vagus	Hus ter	tedograptus retiusculus	Jiangxigraptus vagus	Archiclimacograptus riddellensis			

(a)

Fig. 3. (a)–(e) Upper Ordovician timescale, stages, and graptolite, conodont and chitinozoan zonal schemes. The leftmost column is the chronometrical timescale from Goldman *et al.* (2020, in Gradstein *et al.* 2020). Zonations and correlations for graptolites are modified from the following (and references therein): Vandenberg and Cooper (1992), Goldman *et al.* (2007*a*, 2020), Zalasiewicz *et al.* (2009), Cooper and Sadler (2012), Loydell (2012), Maletz and Ahlberg (2018), and Maletz (2021); for conodonts they are modified from Bergström and Wang (1995), Zhen and Percival (2003, 2017), Albanesi and Ortega (2016), Z. H. Wang *et al.* (2019), Zhang *et al.* (2019) and Goldman *et al.* (2020); and for chitinozoans from Paris *et al.* (2004), Nölvak *et al.* (2006) and Goldman *et al.* (2020). ¹The South Gondwana graptolite zonation for the Upper Ordovician is adapted from Gutiérrez-Marco *et al.* (2017).

At the West Bay Centre Quarry, Newfoundland, Canada, a well-dated K-bentonite bed (464.57 \pm 0.95 Ma) occurs within the *Holmograptus spinosus* graptolite Zone (Maletz *et al.* 2011; Sell *et al.* 2011). Limestone samples collected around the K-bentonite bed yield *Histiodella* cf. *holodentata* followed by *Histiodella kristinae* higher in the section (upper Table Cove Formation). These data

	Ordovician Biozones									
	Graptolite Zones									
AGE (Ma)	S	Stage	North America	Argentina Precordillera	NW Argentina	South Gondwana ¹				
443	443.	₀₇ Silurian								
			Metabolograptus persculptus	Metabolograptus persculptus		Metabolograptus persculptus				
444		Hirnantian 445.21	Metabolograptus extraordinarius	Metabolograptus extraordinarius		Normalograptus charis				
446			Paraorthograptus pacificus	[?]		[?]				
448	er	Katian	Dicellograptus ornatus Dicellogr. complanatus S Amplexograptus manitoulinensis	Dicellograptus ornatus Dicellogr. complanatus Styracograptus tubuliferus		Archi- climacograptus vulgatus				
451	Upp		ぶ 割 pygmaeus Diplacanthograptus spiniferus Diplacanthograptus Diplacanthograptus	[?]	Archi- climacograptus trubinensis					
453		452.75	Climacograptus bicornis	Climacograptus bicornis		[?]				
456		Sandbian	Nemagraptus gracilis	Nemagraptus gracilis		Orthograptus bekkeri				
459	Mid	Darriwilian	Hustedograptus teretiusculus	Hustedograptus teretiusculus	Hustedograptus teretiusculus	Hustedograptus teretiusculus				

(**b**)

Fig. 3. Continued.

provide an important age-dated tie point for Middle Darriwilian graptolite and conodont biostratigraphy (Klebold *et al.* 2019).

Zhen et al. (2020b) reported graptolites and conodonts from the Abercrombie Formation of southern New South Wales. The fauna included the graptolites *Isograptus divergens* and *Levisograptus austrodentatus*, along with conodonts identified as *Periodon flabellum* and *Paroistodus* sp. They noted that the specimens of *Periodon flabellum* represented an advanced morphotype of the species, a morphotype that also occurs in the Cow Head Group of Newfoundland (*Periodon* sp. aff. *P. flabellum* of Stouge 2012). This new report confirms that the range of *P. flabellum* extends into the basal Darriwilian, and facilitates the international correlation of the base of the Darriwilian Stage.

The boundary between the Dapingian and Darriwilian stages marks the decline of the dichograptid and isograptid graptolite clades, and the radiation



(**c**)

Fig. 3. Continued.

of the diplograptids and glossograptids. The rapid evolution and dispersal of the Diplograptacea along with the appearance of several distinctive pseudisograptid and glossograptid species is a globally recognized faunal transition (Mitchell *et al.* 1997; Sadler *et al.* 2011). The appearance and rapid diversification of diplograptids in the lower Darriwilian leads to a high point in Ordovician graptolite species richness. This diversity peak is followed by a decline and then short recovery in the *Archiclimacograptus decoratus* Zone (Da3 of the Australasian succession). The short-lived Da3 diversity rise is due to a brief, final radiation of dichograptids and glossograptids, including didymograptids, sigmagraptids, sinograptids, isograptids and glossograptids (Cooper *et al.* 2004, 2014; Sadler *et al.* 2011). The disappearance of nearly all these taxa (some glossograptids and didymograptids persist into the Sandbian) records a significant extinction event at the end of Da3, an event that precedes the radiation of a distinctive and abundant group of Late Ordovician graptolites, the Dicranograptacea.



Fig. 3. Continued.

The Darriwilian Stage was approved by the ICS in 1997. The level and location of the GSSP in the Huangnitang section are widely accepted and uncontroversial.

The Sandbian Stage

The lowermost stage of the Upper Ordovician Series, the Sandbian Stage, has its GSSP in an outcrop named E14 along the Sularp Brook in the Fågelsång Nature Preserve in the village of Södra Sandby, about 8 km east of the city of Lund in the province of Scania in southern Sweden. The biostratigraphic level of the base of the Sandbian is the first appearance level of the widespread graptolite *Nemagraptus gracilis* (Fig. 5), which is 1.4 m below the lithologically distinctive Fågelsång Phosphorite, a marker bed in the Almelund Shale known from several localities in Scania (Bergström *et al.* 2000). This biostratigraphic level is coeval with the base of the Caradoc Series in the British succession (Fortey *et al.* 1995), the base of the Chinese Neichanian Stage (Zhang *et al.* 2019) and the base of the Australian Gisbornian Stage (Vandenberg and Cooper 1992). (e)

	Ordovician Biozones									
				Cond	odont Zone	es				
AGE (Ma)	S	Stage	/ Pr	Argentina ecordillera	NW Argentina	Australia (platform)	E. Australia (slope-basinal)			
443 -	443.0	₇ Silurian								
4443	Upper	Hirnantian 445.21 Katian	derensis	morphognathus ordovicicus morphognathus superbus Baitoniodus alobatus	No formal conodont zones	[?] Aphelognathus grandis Taoqupognathus tumidus/ Protopanderodus insculptus Taoqupognathus blandus Taoqupognathus philipi Phragmodus undatus/ Tasmanognathus careyi	[?] Periodon grandis			
455 1 1 1 456 1 1 1 1 1 1 1 1 1		Sandbian	Amorphognathus t	Baltoniodus gerdae Baltoniodus variabilis		Belodina compressa				
458	Mid	^{458.18} Darriwilian	Py	rgodus anserinus		Pygodus anserinus	H erriodom a culeatus anserinus			

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Fig. 3. Continued.

In terms of conodont biostratigraphy, this level is at about the middle of the *Pygodus anserinus Zone* and near the base of the *Amorphognathus inaequalis* Subzone. Relative to the Baltic chitinozoan zonation, this level correlates with the base of the *Eisenaichitina rhenana* Subzone of the *Laufeldochitina stentor* Zone.

The stage is named after the village of Södra Sandby, the location of the GSSP. The type section was approved by the IGS in 2002 and the stage designation in 2005 (Nõlvak *et al.* 2006). The greater

part of the Sandbian Stage corresponds to the *Amorphognathus tvaerensis* Conodont Zone. Based on the evolution of the *Baltoniodus* lineage, three subzones are recognized in this conodont zone, namely the *B. variabilis*, *B. gerdae* and *B. alobatus* subzones (Bergström 1971). These subzones have been recognized in many parts of the world and they provide useful long-distance correlations (e.g. Nõlvak and Goldman 2007; Goldman *et al.* 2015; Albanesi and Ortega 2016; Chen *et al.* 2017).



Fig. 4. Photograph of the graptolite *Paratetragraptus approximatus*, index fossil for the base of the Floian Stage. The figured specimen is from Diabasbrottet, Hunnberg. Specimen Cn 1545 Naturhistoriska riksmuseet (Swedish Museum of Natural History), Stockholm, Holm Collection. The photograph was kindly provided by Jörg Maletz. Top-left of scale bar in mm.

It should be noted that based on the graphic correlation of North American and Welsh sections with the Koängen drill core in Scania, Bettley et al. (2001) suggested that the FAD of Nemagraptus gracilis is younger in the GSSP than at other sites and that there is a gap in the succession at the Fågelsång Phosphorite. However, this latter level is well above the FAD of N. gracilis and, hence, does not affect the definition of the stage base at the GSSP. Vandenbroucke (2004) noted that two chitinozoan zones (Angochitina curvata and Armoricochitina granulifera) are missing at the level of the Fågelsång Phosphorite but whether this is due to a stratigraphic gap or if the time represented by these zones is contained within the apparently slowly deposited phosphorite bed remains unknown. Further work using



Fig. 5. Photograph of the graptolite *Nemagraptus gracilis*, index fossil for the base of the Sandbian Stage and Upper Ordovician Series. The figured specimen was collected from the Mount Merino Shale (Normanskill) near Albany, NY. Specimen AMNH 36766, the American Museum of Natural History, New York City. Originally figured by Hall (1859, p. 512, fig. 6). Scale bar at bottom in mm.



Fig. 6. Photographs of the graptolite *Metabolograptus extraordinarius*, index fossil for the base of the Hirnantian Stage. The figured specimens are from the Honghuayuan section, Tongzi, China: (a) specimen NIGP133403, also figured in Chen *et al.* (2005, pl. 1, fig. 1); and (b) specimen NIGP133400, also figured in Chen *et al.* (2005, pl. 1, fig. 2). Both specimens X4.5. The photographs were kindly provided by Chen Xu and Chen Qing.

quantitative correlation and multiple fossil groups is needed to resolve these issues.

The Katian Stage

The base of Katian Stage is one of the most tightly constrained levels in the Ordovician timescale (Goldman *et al.* 2020). The GSSP for the base of the Katian Stage is set at the level of the first appearance of the morphologically distinctive and globally distributed graptolite *Diplacanthograptus caudatus* at a quarried exposure along Black Knob Ridge, about 5 km NE of Atoka in southeastern Oklahoma, USA (Goldman *et al.* 2007*a*). The level is 4.0 m above the base of the Bigfork Chert.

The FAD of *Diplacanthograptus caudatus* is very close to the first appearances of several other widespread graptolite species, including *Diplacanthograptus lanceolatus*, *Corynoides americanus*, *Orthograptus pageanus*, *Orthograptus quadrimucronatus*, *Dicranograptus hians* and *Neurograptus margaritatus*. The base of the Katian Stage is also close to the first appearance of the zonal index graptolite *Dicranograptus clingani*, a species common in middle- to high-palaeolatitude locations.

At Black Knob Ridge, two K-bentonites occur in the upper Womble Shale (*Climacograptus bicornis* Zone) at 5.5 and 6.6 m below the Katian GSSP level. These beds were dated by Sell *et al.* (2013) and yielded ages of $453.98 \pm 0.33/0.38/0.62$ and $453.16 \pm 0.24/0.31/0.57$ Ma, respectively. In the Mohawk River Valley of New York State, USA, MacDonald *et al.* (2017) calculated exceptionally precise dates for two K-bentonites that occur low in the *Diplacanthograptus caudatus* Zone. These Kbentonites yielded dates of 452.63 ± 0.06 and 451.71 ± 0.13 Ma, respectively. By interpolation, the base of the Katian Stage is estimated to be 452.75 ± 0.7 Ma in age (Goldman *et al.* 2020).

With respect to conodont biostratigraphy, the base of the Katian Stage occurs in the upper part of the North Atlantic conodont zone of *A. tvaerensis*, just below the base of the *Plectodina tenuis* Zone and in the middle–upper part of the chitinozoan *Spinachitina cervicornis* Zone (approximately coincident with the base of the *Angochitina multiplex* Subzone).

The base of the Katian Stage is also constrained by other important marker horizons. The Millbrig and Kinnekulle K-bentonite complexes in eastern North America and Scandinavia, respectively, lie just below the GSSP level, as does the beginning of the positive δ^{13} C Guttenberg isotopic carbon excursion (GICE).

Graptolite biodiversity fluctuates sharply during the Katian (Cooper *et al.* 2014). In the lowermost part of the Katian, perhaps in response to global climate perturbations (Goldman and Wu 2010; Pohl *et al.* 2016), graptolite faunas exhibit a distinct decline in both morphological and taxonomic diversity (Goldman and Wu 2010). This post-Sandbian decline is followed by a brief diversity rebound, and then another decline in the middle Katian. The upper part of the Katian Stage contains a species diversity peak, driven by a diversification of the dicranograptid–climacograptid–orthograptid (DCO) graptolite fauna (Chen *et al.* 2005).

The end of the Katian Stage (and beginning of the overlying Hirnantian Stage) is marked by the most severe decline in graptolite diversity within the entire Ordovician, during which the DCO fauna, along with a wide range of other fossil groups, became extinct (Melchin and Mitchell 1991; Chen *et al.* 2005; Finney *et al.* 2007). Global conodont diversity is low in the early Katian, rises in the middle Katian but stays well below their peak Middle Ordovician levels (Sweet 1988).

The name 'Katian' is taken from Katy Lake (now drained) near the southern end of Black Knob Ridge (Bergström *et al.* 2006). The ICS ratified the GSSP and the stage name in 2005.

The Hirnantian Stage

The GSSP for the uppermost stage of the Ordovician, the Hirnantian Stage, is placed at the stratigraphic level of the first appearance of the graptolite *Metabolograptus extraordinarius* (Fig. 6) at the Wangjiawan North section, 0.39 m below the base of the Kuanyinchiao Bed, 42 km north of Yichang city, western Hubei, China (Chen *et al.* 2006). The stage is named after the Hirnant Limestone at Bala in Wales and closely matches the classical Hirnantian, the uppermost subdivision of the Ashgill Regional Series of Britain.

The Hirnantian Stage records a remarkable interval in Earth history. It spans an interval of major climatic and eustatic changes, and one or more strong positive carbon isotope excursions, which are events associated with the end-Ordovician glaciation (Brenchley et al. 2003; Melchin et al. 2013). The first of the Phanerozoic's five great extinction events, the Late Ordovician mass extinction (LOME), ostensibly driven by global climate change and associated sea-level fluctuations, produced a dramatic decline in the diversity of the Earth's marine biota, including graptolites (e.g. Harper et al. 2014; Crampton et al. 2018). The LOME is most severe in the M. extraordinarius and Metabolograptus persculptus graptolite zones, although some diversity decline began in the latest Katian.

A distinctive shelly fossil association, the *Hir-nantia–Dalmanitina* fauna (commonly referred to as the '*Hirnantia* fauna'), is globally distributed in strata of latest Ordovician (generally Hirnantian) age (Rong and Harper 1988). There is some

published disagreement regarding the correlation of the graptolite-defined Hirnantian GSSP into carbonate facies sections, particularly its correlation with the Baltic chitinozoan zonation (cf. Holmden *et al.* 2013; Bergström *et al.* 2014). However, recent work from Baltoscandia and Anticosti Island place the boundary in the *Belonechitina gamachiana* Chitinozoan Zone (Melchin 2008; Mauviel and Desrochers 2016; Amberg *et al.* 2017).

The stratigraphic level of first appearance of the graptolite *Akidograptus ascensus* in the Dob's Linn section of southern Scotland defines the base of the Silurian System and the top of the Hirnantian Stage (Melchin *et al.* 2012, 2020).

Ordovician biozones

Regional zonations and their correlation with Ordovician chronostratigraphic units and ages are shown in Figures 1a–e (Lower Ordovician zones), 2a–e (Middle Ordovician zones) and 3a–e (Upper Ordovician zones).

Graptolite zones

Graptolite faunas exhibited strong biogeographical differentiation during the Ordovician, a fact reflected in the abundance of regional zonations. Skevington (1973, 1974) recognized two major graptolite faunal provinces: the mid- to high-palaeolatitude 'Atlantic Province' and the low-palaeolatitude 'Pacific Province': but these have been shown to be overly general and simplistic, particularly because the controls on faunal provincialism are numerous and complex (see Goldman et al. 2013 and references therein for a comprehensive review of graptolite biogeography). Nevertheless, graptolite zonations, which have been erected from multiple regions around the world (Loydell 2012; Maletz 2021), tend to fall into lowand high-latitude groups. In low-latitude environs ('Pacific Province', 30° N-30° S), the Australasian zonal scheme spans almost the entire Ordovician and is one of the most finely subdivided and useful regional frameworks (Figs 1a, 2a & 3a) (Harris and Thomas 1938; Thomas 1960; Vandenberg and Cooper 1992). It comprises 30 zones, two of which are split into subzones, with an average duration of 1.5 myr each. The Australasian graptolite succession is, however, incomplete in the Tremadocian (Maletz and Ahlberg 2011; Maletz 2021).

The Australasian zonation is widely applicable in most Pacific Province graptolite successions but faunal endemism in some regions and intervals required the construction and use of local zonations, which may better fit the local succession and provide a finer resolution for correlation (e.g. the endemic lower-middle Katian zonation from the Appalachian Basin of eastern North America).

The classic zonal scheme for middle-high palaeolatitudes (Atlantic Province) is that of England and Wales (Zalasiewicz et al. 2009) (Figs 1a, 2a & 3a) where some 17 zones span the Tremadoc-Ashgill (Tremadocian-Hirnantian global stages), averaging 2.3 myr each. The focus on defining global series and stages for the Ordovician has had an interesting but unfortunate effect on our understanding of highpalaeolatitude biostratigraphy and biodiversity. In an attempt to define globally recognizable biozones, graptolite workers concentrated on finding cosmopolitan species that would be useful in inter-regional correlations. Endemic taxa were sometimes misidentified, ignored or shoehorned into better-known tropical species (e.g. see Goldman et al. 2013; Kraft et al. 2015).

Recent work on the taxonomy and biostratigraphy of central European graptolite faunas (Kraft et al. 2015; Gutiérrez-Marco et al. 2017), however, has helped to refine a peri-Gondwanan graptolite zonation. Similarly, new detailed work by Toro et al. (2015), Toro and Maletz (2018), Herrera Sánchez et al. (2019) and Toro and Herrera Sánchez (2019), to cite just a few, has greatly improved the global correlations of Tremadocian-mid-Dapingian strata in the Central Andean Basin. Although many species were cosmopolitan and correlation between low- and high-palaeolatitude regions is fairly well constrained throughout most of the period, understanding high-palaeolatitude biodiversity and correlating regional zonal schemes with global series and stages remains a work in progress (Gutiérrez-Marco and Martin 2016; Gutiérrez-Marco et al. 2017; Herrera Sánchez and Toro 2022). For a short summary of the history of graptolite biostratigraphy, the reader is directed to Maletz (2021).

Conodont zones

Ordovician conodont faunas are distributed in two major biogeographical realms: a Shallow-Sea Realm (SSR) and an Open-Sea Realm (OSR) (Zhen and Percival 2003). Sweet and Bergström (1976, p. 123; 1984, p. 70) described a 'warm-water North American Midcontinent Province' that ranged about 30 degrees N and S of the Equator, and a 'coolwater North Atlantic Province' that extended polewards from 30 to 40 degrees latitudes. Zhen and Percival (2003) recognized that the North American midcontinent region of Sweet and Bergström (1976) was one of up to seven provinces in what they defined as the SSR, and what Sweet and Bergström (1976, 1984) described as the North Atlantic Province encompasses both the OSR and the Temperate and Cold Domains of the SSR. Carbonate facies and associated rocks from these two realms

contain diverse and rich faunas that can be finely zoned into 26 zones, some of which are further divided into subzones (Figs 1b, 2b & 3b). It is important to note that the zones of the North American midcontinent region (Laurentian Province of Zhen and Percival 2003) were initially based on traditional biostratigraphic zonal practices (Sweet and Bergström 1976 and references therein). Sweet (1984, 1995) used graphic correlation to construct and formally name midcontinent conodont chronozones, using many of the same taxon names that were used for the biostratigraphic zones. Sweet (1988) provided a useful range charts for many taxa in his conodont chronozonation but refers to them as conodont-defined biozones, and they are generally based on the first appearance of the biozone namebearing taxon. This changing of definitions between graphic correlation-defined chonozones to biozones, together with the apparent control of many Laurentian conodont species ranges by local habitat conditions related to water depth, has led to conflicting or misleading correlations. The Cold Domain of Zhen and Percival (2003) is best known from the Baltic region in which 17 zones and several subzones are recognized. Zonations derived from faunas in North and South China (Zhang et al. 2019; Z.H. Wang et al. 2019), the Argentine Precordillera and NW Argentina (Albanesi and Ortega 2016), Australia (Zhen and Nicoll 2009; Zhen et al. 2015, 2020a; Zhen and Percival 2017), and Kazakhstan (Tolmacheva et al. 2021) have added substantially to our understanding of conodont provincialism and biostratigraphy. These regional zonations are correlated with the GTS 2020 Carbonate Facies biozones of Goldman et al. (2020) in Figures 1, 2 and 3 but additional work to establish precise zonal ties is required.

Chitinozoan zones

Chitinozoans are widely occurring marine microfossils that have proved to be very useful index fossils in the Middle and Upper Ordovician. They are less diverse in the Lower Ordovician (Paris et al. 2004). Chitinozoans are currently best known from northern Gondwana (e.g. Paris 1990) where 25 zones have been recognized in the Ordovician. A significant amount of work has also been conducted in the Ordovician of Baltoscandia where 18 zones and 10 subzones have been distinguished (e.g. Nõlvak et al. 2006). Less work has been carried out on this group in North America where chitinozoans currently remain unstudied in large regions. Exceptions to this include the Middle and Upper Ordovician faunas of Anticosti Island in eastern Canada (e.g. Achab 1989). The diverse chitinozoan faunas of the Upper Ordovician of the North America Midcontinent have been the subject of some study (e.g. Jenkins

1969; Liang *et al.* 2019, 2020) but those of the Lower Ordovician of that vast region remain virtually unknown. In recent years, the Ordovician chitinozoans of the Yangtze Platform in China have been investigated by several workers (e.g. Chen *et al.* 2009; Liang and Tang 2016; Liang *et al.* 2018; W.H. Wang *et al.* 2019). The successions of Baltoscandic and Gondwana chitinozoan zones are illustrated in Figures 1c, 2c and 3c.

Integration of graptolite, conodont and chitinozoan zones

On a global scale, Ordovician rocks show a striking latitudinal differentiation in biofacies. This probably reflects the influence of climatic belts and depositional depth. For instance, the low-latitude tropical faunas of the North American Midcontinent have very little in common with coeval faunas of Baltoscandia, which inhabited more high-latitude, temperate environments. There is also a striking difference between the shallow-water and deep-water faunas in these regions. These differences in biofacies cause longrange biostratigraphic correlation problems that may be difficult, or impossible, to solve using a single fossil group. One way to clarify the relations between different biofacies is to use co-occurences of fossils that tend to occur in different biofacies. such as stratigraphic intervals in which biostratigraphically important conodonts co-occur with graptolites. Conodonts may be preserved on shale surfaces in graptolite shales, as is the case at the Sandbian GSSP in southern Sweden (Bergström et al. 2000; Bergström 2007) and at the Katian GSSP at Black Knob Ridge, Oklahoma, USA (Goldman et al. 2007a). Unfortunately, such cooccurrences are not very common.

More common are conodonts that occur in carbonate-rich intervals in graptolite shales. Examples of such important occurrences include the Darriwilian–Sandbian Athens Shale of Alabama (Finney 1977), the Cow Head Group of western Newfound-land (Cooper *et al.* 2001; Stouge 2012), the Dawangou Section in the Tarim region of northwestern China (Chen *et al.* 2006, 2017), the Viola Group of Oklahoma (Finney 1986), Darriwilian–Sandbian limestones in Sweden (Jaanusson 1960) and the Kandava drill core of Latvia (Goldman *et al.* 2015).

In an attempt to clarify the relations between conodont and graptolite donations globally, Bergström (1986) reviewed the literature and found 78 direct ties between the fossil zonations. In a later study, Bergström *et al.* (in Chen *et al.* 2017) presented 27 additional tie points, reaching a total of 105 graptolite–conodont zonal ties.

Chitinozoans are commonly present in both shales and limestones within graptolite shale

successions. In such cases it is possible to isolate chitinozoans from the shales using strong acids that can dissolve clastics (e.g. Vandenbroucke 2004, 2008*a*, *b*; Goldman *et al.* 2007*a*, *b*; Leslie *et al.* 2008; Vandenbroucke *et al.* 2013).

In a few regions of the world, there is a series of juxtaposed biofacies/lithofacies belts that range from shallow to deep water. Perhaps the best known such region is Baltoscandia, where Jaanusson (1976, 1995) recognized a series of such belts. He referred to these as confacies belts. These confacies belts - the Scanian (slope; black shale), Central Baltoscandian (outer shelf; argillaceous limestones) and North Estonian (carbonate platform) belts - record an offshore to onshore transition along the eastern to southeastern margin of the East European Craton. In terms of water depth, the shallowest is the North Estonian confacies belt, which represents a shallowwater carbonate platform. Somewhat deeper depositional environments are represented by the central Baltoscandian confacies belt, which represents the outer shelf and is characterized by more or less argillaceous limestones. The deepest-water deposits are found in the Scanian confacies belt where dark shales dominate. The densely sampled outcrops and drill cores across this region, which commonly exhibit interfingering lithofacies at the confacies belt transitional areas, have facilitated detailed zonal ties between graptolites, conodonts and chitinozoans (e.g. Goldman et al. 2015). Comprehensive searches for fossil occurrences outside their common biofacies association, detailed sampling of regions that have onshore-offshore transects and the use of quantitative stratigraphic methods to interleave datasets have further advanced the integration of graptolite, conodont and chitinozoan zones (Goldman et al. 2020).

Outcrops that provide perhaps the most valuable data for precise global correlations and timescale construction contain stratigraphic range data from two or more clades, as well as radioisotope dated K-bentonite beds. Examples of these localities include the mid-Darriwilian West Bay Centre Quarry in Newfoundland (graptolite and conodont biostratigraphy with a dated K-bentonite: see Maletz *et al.* 2011; Sell *et al.* 2013; Klebold *et al.* 2019) and the Black Knob Ridge section in Oklahoma, USA (Katian GSSP, graptolite and conodont biostratigraphy with a dated K-bentonite: see Goldman *et al.* 2007*a, b*; Sell *et al.* 2013).

Chemostratigraphy, and especially that based on δ^{13} C, has become of major importance in Ordovician stratigraphy over the last two–three decades. This technique has been of great significance in resolving many stratigraphic relationships that were problematic for conventional biostratigraphy. Chemostratigraphy must, however, be closely integrated with biostratigraphy in order to achieve its greatest utility.

Such detailed integration is an ongoing process. Bergström *et al.* (2009) provided a general summary of the relationship between the major Ordovician isotopic excursions and important chronostratigraphic subdivisions.

In a recent global summary paper, Bergström et al. (2020) reviewed the relationships between 15 major δ^{13} C excursions and Ordovician graptolite and conodont zones. Although focused on North America, Baltoscandia and Argentina, each of the major carbon isotope excursions are discussed in terms of their presence in both local and global biostratigraphic frameworks, particularly graptolite and conodont zonations. Hence, Bergström et al. (2020) describes the biostratigraphic position and duration of four major δ^{13} C excursions in the Lower Ordovician, two in the Middle Ordovician and nine in the Upper Ordovician. A full discussion of the importance of Ordovician chemostratigraphy is well beyond the scope of this chapter but, in addition to the summaries cited above, the subject is extensively dealt with elsewhere in this Special Publication.

Quantitative biostratigraphy

The construction of useful biozonations and precise correlation frameworks commonly require the evaluation of large numbers of taxon ranges from multiple stratigraphic sections. In addition, the data may be mined from the published work of many different authors. Hence, these large datasets can have inherent biases such as sampling inconsistencies, range truncations, missing taxa and taxonomic misidentifications. Quantitative biostratigraphic techniques were developed to help manage large datasets, and to more effectively recognize and overcome human and palaeontological biases (Shaw 1964; Miller 1977; Edwards 1995; Kemple et al. 1995; Sadler and Cooper 2003; Sadler 2020 among many others). A short review of the graphic correlation and quantitative biostratigraphic technique used in the construction of the 2020 Ordovician timescale (CONOP9) is provided below.

Stratigraphic correlation requires three separate tasks: (1) establishing a temporal sequence of events; (2) determining the relative interval length between those events; and (3) locating the horizons that match in age with each event in every section (Kemple *et al.* 1995). Unfortunately, due to uneven sampling, partial preservation of taxon ranges and missing taxa, the sequence of events (primarily taxon FADs and last appearance datums (LADs)) is often inconsistent between stratigraphic sections (Sadler *et al.* 2009). Traditional graphic correlation (Shaw 1964) solves this problem by plotting the levels of stratigraphic data that two sections have in common on an X-Y biplot. The line of correlation

(LOC) between these two sections represents a proposed solution, which is typically constrained not to allow range contractions in either section, and to require a monotonic relationship between time and rock thickness in each section (Miller 1977; Edwards 1995). The best solution to the correlation problem is the one where the LOC requires the minimum net range extension necessary to make all local ranges match a single sequence and spacing of events. This is called 'economy of fit' (Shaw 1964), and, as well as defining a best solution, it can be used to examine levels of 'misfit' and define a penalty function that can rank alternate solutions (Kemple *et al.* 1995).

Unlike graphic correlation, which adds data to a composite one section at a time, constrained optimization (CONOP9: Sadler and Cooper 2003) is multidimensional – it works with observations from 'n' numbers of sections simultaneously. CONOP9 proposes sequences of FADs and LADs, rejects impossible solutions (enforcing a constraint), and then searches for the best possible solution (optimization) by searching through many possible solutions using a numerical method called simulated annealing (Kemple *et al.* 1995). The best correlation solutions are those that require the minimum net adjustment of observed ranges in local sections.

Thus, a penalty function based on the sum of range extension for all taxa in all sections can be calculated and used to rank the various possible solutions. Computer software (Sadler 2003) is used to generate large numbers of possible solutions and search for the one with the minimum possible penalty. In sum, CONOP9 eliminates impossible correlation solutions, those that contain last before first appearance datums for any individual species; minimizes unobserved taxon co-existences; and chooses the 'best' among the possible solutions – the one that has the minimum net adjustment of observed ranges in local sections and smallest number of unobserved taxon co-existences.

As with all quantitative correlation techniques, composite taxon ranges and correlation models generated in CONOP9 must be carefully examined for inaccuracies, and conflicts with expert observation and opinion should be thoroughly evaluated. Seemingly out of place taxon range ends or unusual species coexistences can have several possible explanations. The most common problem with CONOP9 taxon range charts is taxonomic misidentification. If a species occurrence is misidentified in any input section, its stratigraphic range in the composite could be greatly extended. In traditional biostratigraphy, these outliers can be ignored but CONOP9 accepts the erroneous occurrence as valid. Species ranges that are extended from misidentification can also create unobserved co-existences, which complicates the task of constructing

a workable zonation from the composite range chart. Conversely, CONOP9 makes the recognition of taxa that are out of place in time and space easy to find, and an investigation into possible misidentifications can be carried out. Taxon range ends and section tops or bottoms can also float or sink well beyond any reasonable age assignment for other reasons. Generally, this occurs when there is no constraint on a range or section end. For example, the last collection in a section may contain a single taxon LAD that is artificially truncated at the section top. With no other constraint, CONOP may let the section top float upwards to the actual LAD of that taxon (as it occurs in another section). Finally, of course, unusual taxon ranges may really reflect a better range estimation than can be determined with traditional biostratigraphy.

The current Ordovician and Silurian timescales (Goldman *et al.* 2020; Melchin *et al.* 2020) employ constrained optimization (CONOP9: Sadler 2003; Sadler *et al.* 2009) to construct a composite graptolite range chart (837 stratigraphic sections, 2651 species, and 5302 FADs and LADs) into which radioisotope dates are interpolated.

The stratigraphic ranges of taxa in a composite range chart that is compiled from hundreds of global sections are generally different from those ranges observed at any local section. In addition, the various algorithms used to sequence and space the taxon range ends can themselves produce different taxon ranges and range relationships. Hence, picking biozones and stage boundaries in a CONOP9 composite section requires careful consideration and can be accomplished in a variety of ways (Sadler *et al.* 2011; Goldman *et al.* 2020; Sadler 2020).

First, the GSSP level itself, which is entered into the CONOP database as a single occurrence in the stratotype section, can be picked as the stage base. However, as a single section, single event, the GSSP level is not necessarily well constrained in the composite sequence. This means that the CONOP9 algorithm may move the single event to different positions without incurring substantial additional penalty. Second, biozone and stage bases may be located based on the first appearance in the composite sequence of the taxon that defines the GSSP level. This is not always the same level in the composite section as the GSSP level. In addition, in CONOP the placement of all the local first appearances of a zonal index taxon as projected into the composite can be displayed. This provides a means to find outliers (Sadler 2020).

Finally, many biostratigraphic studies with published range charts include their authors' best estimates of the position of stage boundaries. Sometimes the boundary position is inferred from the taxon ranges of species other than graptolites, conodonts or chitinozoans. These local stage

boundary approximations were included in the CONOP9 compositing process as very conservative minimum–maximum uncertainty intervals (Gold-man *et al.* 2020; Sadler 2020). Hence, one could choose the midpoint, for example, of one of these uncertainty intervals.

In most cases, the GSSP level and the FAD of the species that defines it are very close to one another and within the minimum–maximum uncertainty interval in the CONOP9 composite range chart used for the Ordovician timescale in GTS 2020. However, it is important to note that the enormous benefit of quantitative biostratigraphy in examining and removing biases in the empirical data also generates uncertainties that must be taken into consideration by experts (Sadler *et al.* 2011; Sadler 2020).

On regional scales, Goldman *et al.* (2012, 2013) used CONOP methodology to construct a fully integrated multiclade range chart (graptolites, conodonts, chitinozoans and ostracods) from Middle and Upper Ordovician strata in outcrops and drill cores that spanned all three confacies belts in Baltoscandia. Bryan *et al.* (2018) and Serra *et al.* (2019) also used quantitative correlation to integrate conodont and graptolite biostratigraphy in the Argentine Precordillera, and Herrera Sánchez and Toro (2022) used CONOP9 to establish a correlation model for the Lower and Middle Ordovician of the Central Andean Basin.

Quantitative biostratigraphy is a powerful tool for resolving taxon range inconsistencies between sections and for choosing between multiple possible correlation models. Quantitative methods, which may examine many thousands of reasonable event sequences, can also provide various options to estimate confidence intervals on boundary placements (Sadler 2020). Finally, we have also found that utilizing these methods forces us to examine our datasets critically, which helps uncover and correct many errors in the original literature data, in operator input and in the processing of the data.

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